LATE CARBONIFEROUS AND EARLY PERMIAN

BRACHIOPODA AND MOLLUSCA

FROM THE LOWER JUNGLE CREEK AND UPPER ETTRAIN

FORMATIONS

OF THE YUKON TERRITORY, CANADA

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Abstract.

Brachiopods and molluscs are described from Carboniferous and Permian boundary beds in the Ettrain and Jungle Creek Formations exposed in the Ogilvie Mountains of the Yukon Territory, Canada. For brachiopods, 155 taxa are described, belonging to 89 named genera, with other members traceable to tribal,subfamily or family groups. There are 95 named and compared species, of which 46 are new, and two further species are proposed from elsewhere. Bivalves are scarce, belonging to twenty one taxa, only one in a named species, together with gastropod fragments of five species. Indeterminate ammonoid fragments, rare corals and Bryozoa are set aside. Newly named brachiopod genera, not all from the Yukon Territory and some of them named in an Appendix, are *Dutroproductus*, type species *D. dutroi* new species, *Nassichukia*, type species *N. nodosa* n. sp. (Productidina), *Yukonalosia*, type species *Y. arctica* n. sp. (Strophalosiidina), *Rugivestigia*, type species *R. commarginalis* n. sp., *Pumilusia*, type species *Linoproductus pumilus* Sutherland & Harlow, 1973, *Poletaevia,* type species *Liraria stepanowensis* Carter & Poletaev, 1998 (Linoproductidina), *Yanzaria,* type species *Camarophoria dowhatensis* (Diener, 1915), *Latisulcus*, type species *Hustedia hessensis* King, 1931, *Stataria*, type species *Hustedia stataria* Cooper & Grant, 1976b (Rhynchonellida), *Mirandifera*, type species *Martinia miranda* Cooper & Grant, 1976a, *Ettrainia*, type species *Ettrainia costellata* n. sp., *Forticosta*, type species *Forticosta transversa* n. sp., *Eridmatina*, type species *Eridmatus marathonensis* Cooper & Grant, 1976a, and *Heella*, type species *Attenuatella mengi* He et al. 2007 (Spiriferida). A new bivalve genus *Meekopecten* is proposed for an acanthopectenin, based on *Acanthopecten meeki* Newell, 1938. Two new minor family groups are proposed, Rugivestigiinai in Tribe Retimarginiferini Shi & Waterhouse, and new tribe Megousiini within Anidanthinae Waterhouse.

Canada appears to have been the source of new genera, supplying to Asia, especially Russia, genera modified from stock of mid-continental United States, and supplying to United States genera modified or passed on from Russia. A few genera suggest an early or first appearance of stock later prominent in faunas of Gondwana, notably amongst Linoproductidina.

International Period	Stage	Yukon Formation	Biozone	Member
LOWER PERMIAN	Artinskian	Tahkandit		
		Jungle	*Jakutoproductus verchoyanicus*	
	Sakmarian		*Ogilviecoelia inflata*	
			"Harkeria transversa"	Member F
	Asselian	Creek	*Ogilviecoelia shii*	Member E
			Rugivestigia commarginalis	Member D
			Kochiproductus imperiosus	Member C
			Ogilviecoelia initiatus	Member B
UPPER CARBONIFEROUS	Gzhelian		*Septospirifer tatondukensis*	Member A
	Kasimovian	Ettrain		
	Moscovian			
	Bashkirian	?Blackie	(Clarification needed)	
	Serpukhovian		*Quadralosia delicata*	
	Serpukhovian	Hart River	*Quadralosia delicata*	

Table 1. Summary of Carboniferous and Permian formations and biozones in the Ogilvie Mountains of Yukon Territory. There is uncertainty over the correlation of the lower Ettrain Formation, and rocks assigned to the Blackie Formation. In the northern Ogilvie Mountains, rocks assigned to the Blackie Formation have possible *Quadralosia*, known from Serpukhovian faunas, and Mamet in Bamber et al. (1989) reported Moscovian or younger foraminifera. Table not to scale.

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INTRODUCTION

This study describes macrofossils, chiefly brachiopods, with a few molluscs, from the northern Ogilvie Mountains, located approximately at 65º24'N, 140º44'W, just south of the Arctic Circle in the Yukon Territory of Canada. The fossils were collected mostly by the writer during summer seasons of 1969 through to 1972, following initial study by E. W. Bamber, working for the Geological Survey of Canada on "Operation Porcupine". This operation entailed the geological survey of approximately 207 000 km^2 of the Yukon Territory and Northwest Territories north of latitude 65º and west of longitude 132ºW, as published by Norris (1997; and see also Richards et al. 1997). The particular collections in this study come mostly from the Jungle Creek Formation of Bamber in Bamber & Waterhouse (1971) in the Ogilvie Mountains, and are found in a succession of five macro-fossil complexes in sedimentary units that span the Carboniferous and Permian boundary. A few occurrences of species are extended into the underlying Ettrain Formation of Bamber in Bamber & Waterhouse (1971). The brachiopods are strong in links with the faunas of northeast Russia, as may be expected from their northerly paleolatitudes, and also share links with the Urals of Russia and western North America, as well as some taxa shared with or allied to those of Texas and mid-continental United States. Of most interest is the entry into these Carboniferous faunas of genera that elsewhere are found only in Permian faunas, to strongly suggest that northwest Canada was a region generating a number of forms that became prominent in Permian time. A somewhat similar early entry of Permian palynomorphs was recorded by Barss in Bamber & Barss (1969, Bamber & Waterhouse 1971, p. 111). In addition, a very few taxa show unexpected affinities with faunas of the southern paleohemisphere. Also significant was the extreme scarcity of the prominent brachiopod group, the Terebratulida,and the sparseness of Bivalvia in the Canadian faunas.

STRATIGRAPHY

The Jungle Creek Formation, principal source of the fossils, was named and described by Bamber in Bamber & Waterhouse (1971) as a medium to dark brownish grey-weathering sequence of varied lithology, including skeletal partly conglomeratic limestone, micritic skeletal and spicular limestone, calcareous shale, siliceous mudstone and siltstone. As Bamber noted, it forms a relatively recessive interval above the light grey-weathering and cliff-forming Ettrain Formation below, and below the Tahkandit Formation, composed of sandy and skeletal limestone, sandstone and conglomerate (Mertie 1930). The type section of the Jungle Creek Formation is exposed along the banks of the Tatonduk River (Bamber & Waterhouse 1971, Fig. 7), and the area collected for this study lies in the Ogilvie Mountains approximately 40km to the north, in the headwaters of the Jungle and Ettrain Creeks, close to the Alaska border. It is this area that provides the type section for the underlying Ettrain Formation, and two critical sections were measured and analyzed by Bamber in Bamber & Waterhouse (1971, Fig. 2, 3, 7; Bamber 1972), called 116F-9 for the type Ettrain (see Bamber & Waterhouse 1971, Fig. 6), continuing into Jungle Creek and Tahkandit Formations, and 116F-16 for a sequence to the south. These two sections, together with more extensive and intensive study by the writer, strongly suggest that the type Jungle Creek Formation exposed along the Tatonduk River, as in section 116C-2 (Bamber & Waterhouse 1971, Fig. 7), is not as complete as in the headwaters of Jungle and Ettrain Creeks. Indeed three of the five biozones described in this report appear to be missing. Waterhouse & Waddington (1982) therefore suggested that the nomenclature could be improved and the stratigraphy clarified by naming a new formation, which would apply to beds best exposed in the headwaters of the Jungle and Ettrain

Creeks, between the Ettrain Formation and a more restricted Jungle Creek Formation, revised as starting at the *Yakovlevia transversa* Zone and what is here called Member F in this study. The beds are composed of yellow weathering limestone, green siltstone,black shale and quartz conglomerate and grits. These beds are incompletely represented at the Tatonduk River type section by only thin shaly beds marked “Dos”and Eta in Bamber &

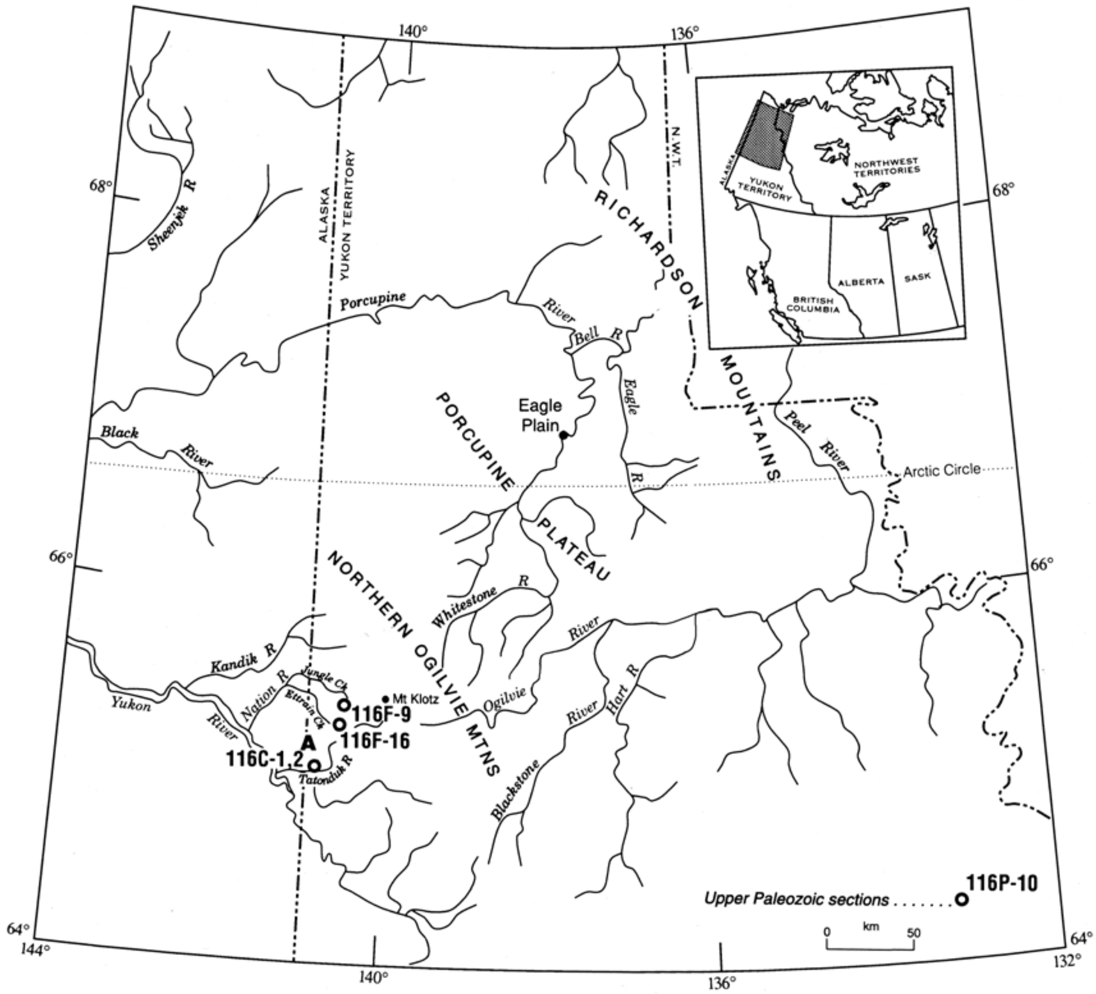

Fig. 1. Index map showing Ogilvie Mountains, Tatonduk River and Ettrain Creek in the Yukon Territory, northwest Canada, with three important measured sections of Bamber & Waterhouse (1971). Altered from Shi & Waterhouse (1996, Fig. 1).

Waterhouse (1971, Fig. 7). The new formation would have included the more carbonate-rich beds of the Ogilvie Mountains and the *Septospirifer tatondukensis* to *Ogilviecoealia shii* Zones with intervening zones as recognized in this study. But the proposal is set aside, at least for the meantime, because Norris (1982, 1997) retained the beds in the Jungle Creek Formation. Instead, it is proposed to recognize five informal members, lettered from A to E, in the lower half of the Jungle Creek Formation, with only A and B represented in the lower outcrops of the Jungle Creek Formation along the Tatonduk River, and followed by faunas of Member F.

Ettrain Formation

The Ettrain Formation is a light grey-weathering sequence of micritic and skeletal limestone that forms cliff-forming outcrops (Fig. 385, p. 494), below the Jungle Creek Formation and above the underlying dark relatively recessive Hart River Formation of Early Carboniferous age and Blackie Formation of Pugh (1983) as interpreted by Bamber et al. (1989), under poor age control. The Ettrain Formation was mapped in the region under discussion as undivided Ettrain and unit a, equivalent to upper Ettrain, by Shi & Waterhouse (1996, Fig. 4, pp. 10, 11). Its fossils were briefly surveyed in Bamber & Waterhouse (1971), and brachiopods later monographed in an unpublished thesis by Nazer (1977). Waterhouse & Waddington (1982) monographed some spiriferellid brachiopod species, and several productid and spiriferid species and genera have been described in Waterhouse (2013, 2016). A number of Ettrain species not examined by Nazer are also shared with the overlying Jungle Creek Formation, and some of these are recorded and illustrated in the present study. Nazer (1977) judged the Ettrain faunas to be of Kasimovian age, in the Pennsylvanian (Upper Carboniferous) Subsystem, but the oldest and youngest Ettrain faunas were not studied.

Jungle Creek Formation

The Jungle Creek Formation (Fig. 386-389, pp. 494-496) was named by Bamber in Bamber & Waterhouse (1971) and is moderately complex, and diversified in its members, including cyclothems of conglomerate, finer clastic sediment, culminating in limestone, and units of limestone, dolomite, and fine siltstone and shale, especially in the area under study. Lithologies are more uniform in the type section provided by the Tatonduk River. After preliminary overview of the faunas in Bamber & Waterhouse (1971) and study of Spiriferelloidea by Waterhouse & Waddington (1982), Shi & Waterhouse (1996) described rock and faunas from the upper Jungle Creek Formation, recognizing assemblage zones named *Yakovlevia transversa, Ogilviecoelia inflata* and *Jakutoproductus verchoyanicus*, and dated as Sakmarian and Lower Artinskian (Aktastinian) in age. In this study, the *Yakovlevia transversa* Zone is placed in inverted commas because of uncertainties about the generic position of Jungle Creek material assigned to *Muirwoodia transversa* Cooper (see pp. 238-240). It is treated as belonging to and typifying Member F. The underlying rocks of the Jungle Creek Formation are divided into five lithologically based members, from A to E, and their faunas described. The fauna of each member is distinctive, and clearly depended not only on age and succession, but on the nature of the substrate.

Member A

Standard section: Ridge 42 in Shi & Waterhouse (1996, Fig. 4), above Ettrain Formation, closing at shales below Member B.

Description: Member A (Fig. 386, p. 494) lies immediately above the Ettrain Formation, as mapped by E. W. Bamber. It largely corresponds with unit b of Shi & Waterhouse (1996, Fig. 4), and is approximately 230m thick at section 116F-9. There are a number of cyclothems, commencing with coarse clastics followed by shale, and capped by limestone, with increasing quartz conglomerate to the north at section 116F-9. Conglomerate pebbles are chiefly of chert and quartz, with subangular to well rounded pebbles up to 4cm diameter, which include rare ammonoids now quartz-filled. The pebbles are often flattened along the bedding plane to suggest beach deposits, whereas at other and more numerous sites, there are subangular breccias to conglomerate with pebbles rounded like those

Fig. 2.Subangular breccia in granular limestone, lower Member A of Jungle Creek Formation, at ridge continuing from type section of Ettrain Formation in section 116F-16, x1.5.

Fig. 3. Silicified fossils preserved at JBW 450, Member A, Jungle Creek Formation, including specimens of *Orthotetes*(O)*, Rugaria* near (R), *Yukonalosia*(Y) and other genera, x1 approx.

shaped under riverine conditions. Limestone is varied and mostly skeletal micritic ,but maybe silty, siliceous or weakly dolomitic. The limestone is usually light grey, and often dominated by fenestellid bryozoa with or without echinoderm fragments. Conglomerate is most common to the north, and to the south, limestones are more shelly, with brachiopods. Sandstone bands 1-5m thick in beds 5 to 20cm thick are generally light to medium grey in colour with fine grains of quartz and chert, weathering medium brown, and as a rule have scattered brachiopods, bryozoans and echinoderms,. Siltstone is grey, made up largely of clay-sized quartz and micrite, somewhat calcareous, may be shelly, and has disseminated organic matter, and is recessive, in bands 1-20m thick. Detailed petrography of measured sections is provided by Bamber (1972, pp. 33-40) for the Jungle Creek section F116F-9 (which includes type Ettrain), from unit 127 to unit 72 (Bamber 1972, p. 40). Beds of the upper Jungle Creek Formation are steeply dipping to overturned in this area. The lithologies for the Ettrain Creek East section 116F-16 start at unit 14 (Bamber 1972, p. 64) and continue to unit 67 (Bamber 1972, p. 58), if not slightly higher.

Fauna: The faunas are rich and varied, and are classed as the *Septospirifer tatondukensis* Zone. Unfortunately the diverse faunas of the limestone bands have been largely unstudied – because they are silicified and require dissolution in acid, a process beyond my available resources. Preservation is variable, some well preserved, and many broken and incomplete.

The age is determined as Gzhelian, Late Carboniferous.

Member B

Standard section: Ridge 42 grading into 34, mapped as part of the upper unit c in Shi & Waterhouse (1996, Fig. 4) and comprised ofsilty shale seven metres thick above Member A, and below the carbonates of Member C.

Fauna: These beds have yielded specimens of *Ogilviecoelia* and rare *Eridmatina petita* (Waterhouse & Waddington), and represent a distinct biozone, or at least a fossil community, scarcely developed elsewhere in the region. It is characterized by silty shale close slightly more sandy than that of Member E. The member appears to fall within unit 68 of Bamber (1972, p. 58).

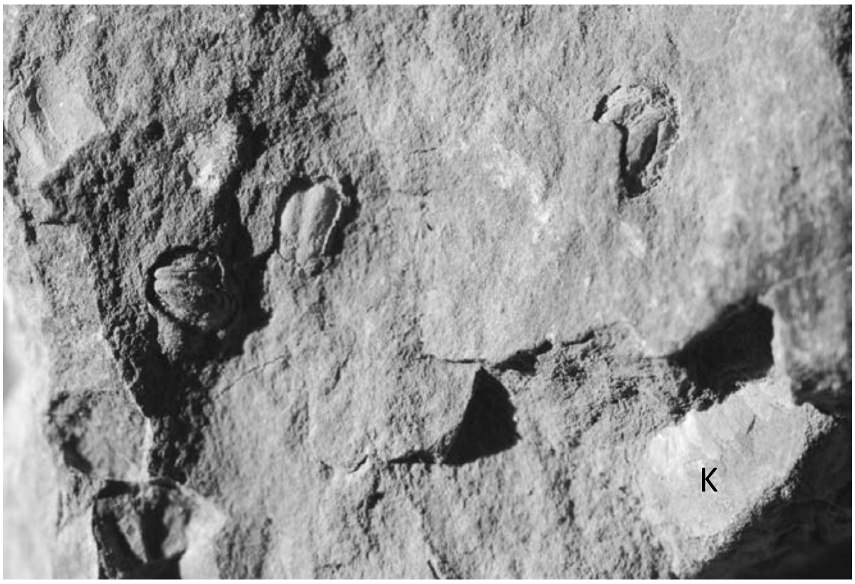

Fig. 4.A small slab from JBW 69 from Member B, showing scattered specimens of *Ogilviecoelia initiatus* n. sp., with a ventral valve of *Komiella* sp. (K) at lower right, x2.

The age is regarded as putatively early Asselian. The fauna is linked with younger Permian faunas through the presence of *Ogilviecoelia*, member of a genus found in overlying faunas but absent from Ettrain and Member A faunas of Carboniferous age. Possibly the fauna is found at the type section of the Jungle Creek Formation along the Tatonduk River at GSC locality 57044, figured as Eta in Bamber & Waterhouse (1971, Fig. 7). (See p.382).

Member C

Standard section: Ridge 42, grading into ridge 34, carbonates about twenty metres thick exposed above Member B and Member A, below the dolomitic sandstones of Member D.

Description: Member C is a thin unit, represented by the middle part of unit c in Shi & Waterhouse (1996, Fig. 4). It consists of coarsely granular and shelly limestone, lying above shale and sandstone. The limestone thins to a unit two to four metres thick to the south and north, where it resembles underlying carbonate bands, but has a distinctive species of the brachiopod *Kochiproductus*, and the restricted genus *Juresania* is found further north.

Fauna: The member provides a rich and unusual brachiopod assemblage of large individuals, discriminated as the *Kochiproductus imperiosus* Zone. The zone is confined to this area, and has not been recognized at the type section of the Jungle Creek Formation at Tatonduk River. Material is well preserved, and includes many large specimens, which are easily cracked out from the matrix. Overall the fauna is unusual compared with other fossil faunas of the region. From stratigraphic position, it is judged to be of Asselian (basal Permian) age.

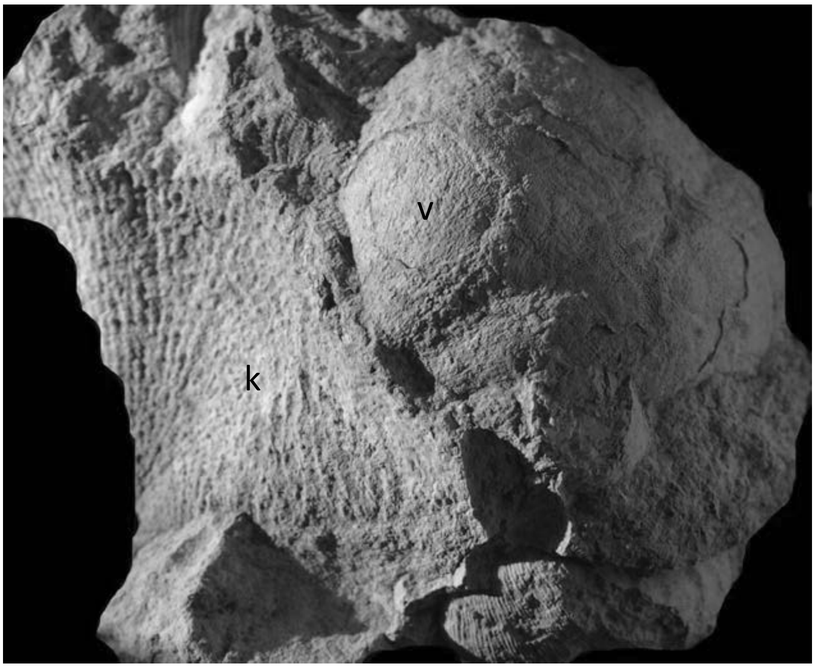

Fig. 5. Block from JBW 18, Member C, Jungle Creek Formation, x1, showing *Kochiproductus* (k) and *Villaconcha* (v), with fragments of other species.

Member D

Standard section: Ridge 42, immediately overlying Member C, and below Member E.

Description: Member D is a distinctive unit, dominated by dolomite and up to 300m thick. It thins markedly to the north, and many of the fossils come from the standard section, scattered over bedding planes, and difficult to extract. It was mapped as the upper part of unit c by Shi & Waterhouse (1996, Fig. 4). The beds involve those itemized as units 70 to 96 in section 116F-16 ofBamber (1972, pp. 56-58) and consist of sand-grain-sized dolomite and fine clasts, with sandstone, and occasional chert and shale.

To the north and south, limestones are more shelly, with brachiopods. Sandstone bands 1-5m thick in beds 5cm to 20cm thick are generally light to medium grey in colour with fine grains of quartz and chert, weathering medium brown, and as a rule have scattered brachiopods, bryozoans and echinoderms. Siltstone is grey, made up largely of clay-sized quartz and micrite, somewhat calcareous and may be shelly. It has disseminated organic matter, and is recessive, in bands 1-20m thick.

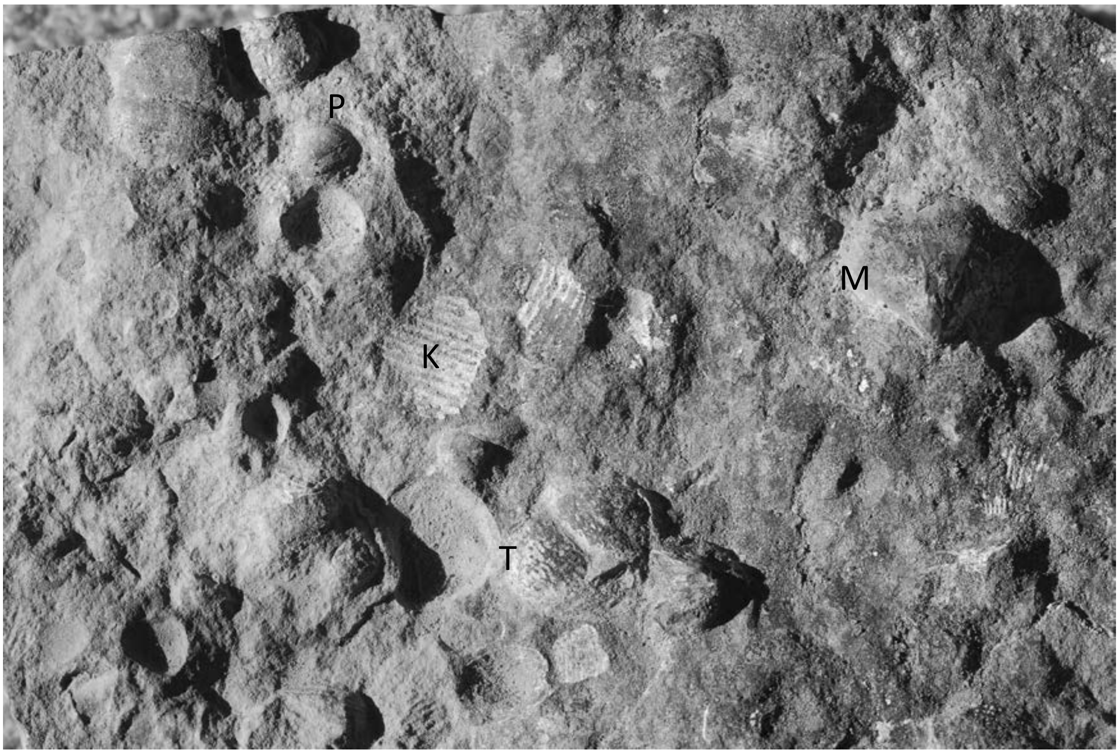

Fig. 6. Slab from Member D at JBW 72, x1, showing scattered specimens of *Tubersulculus* (T) and *Mirandifera* (M), a small phricodothyrid (P), and fragments of *Kutorginella* (K).

Member E

Standard section: Ridge 42, immediately overlying Member D, closing at sandstones of the "*Yakovlevia transversa*" Zone in Member F of the Jungle Creek Formation.

Description: Member E (Fig. 388-389, p. 496) is a very distinctive unit, recessive, and exposed between the sandstone-dominated scarp of the "*Yakovlevia transversa*" Zone, and the carbonate-dominated members A, C and D: it thus can be readily traced by binoculars and on aerial photographs. At the standard section the unit is close to 80m in thickness, characterized by shelly siltstone, with intervals of fine sandstone, which were measured as units 97-103 by Bamber (1972, p. 56), and mapped as unit d in Shi & Waterhouse (1996, Fig. 4). The unit is not known for certain and seems likely to be absent from the type section of the Jungle Creek Formation in the Tatonduk River.

Fauna: The fauna belongs to the *Ogilviecoelia shii* biozone. The fossils are crowded and are small as a rule, with detail well preserved on external and internal moulds, shell material being rarely preserved. Large specimens tend to be broken by close fracturing of the rock. The member underlies Member F with the "*Yakovlevia transversa*" Zone, which has been assigned to the lower Sakmarian Stage and Tastubian Substage of the Permian Period by Shi & Waterhouse (1996).

Fig. 7. Fossil block from Member E with specimens of *Ogilviecoelia shii* n. sp. from Member E, x3.

Member F and biozones for the upper Jungle Creek Formation

Standard section: Ridge 42, immediately above Member E, and corresponding with unit e in Shi & Waterhouse (1996, Fig. 4).

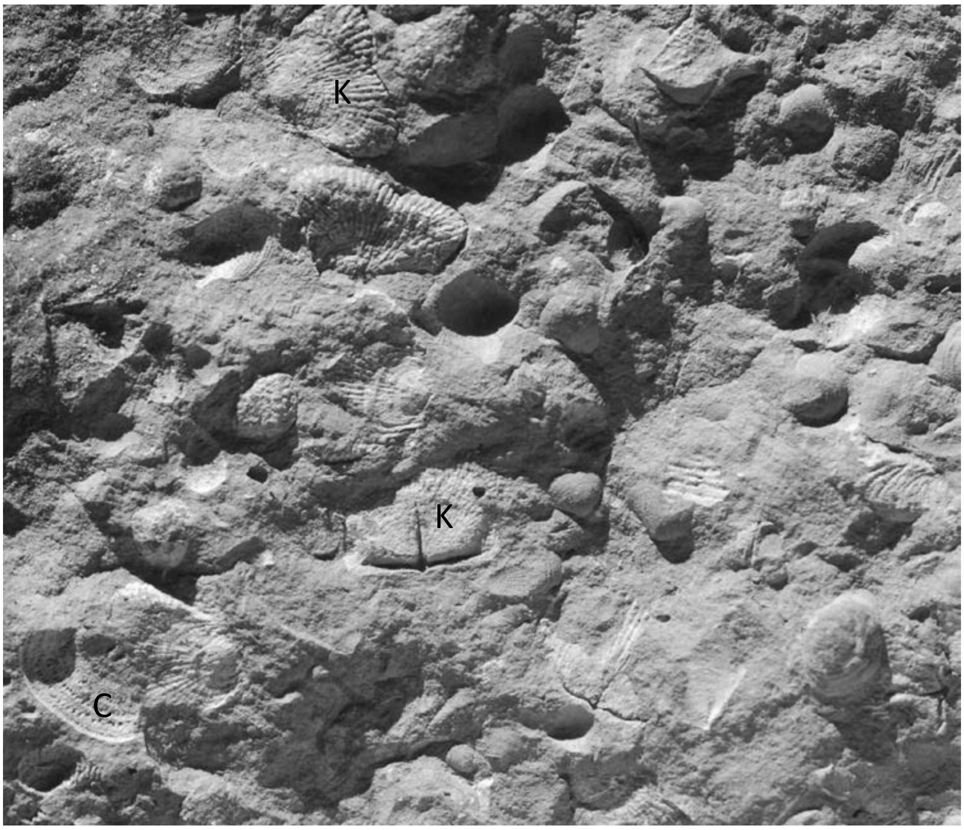

Fig. 8. A slab of fossiliferous rock from Member F, showing crowded shells that include *Kutorginella* (K) and *Calliprotonia* (C), x1, from JBW locality 672.

Description: This member (Fig. 388-389, p. 496) was the focus, together with overlying units, of the study on fossil content by Shi & Waterhouse (1996). The zone was named the *Yakovlevia transversa* Zone, as an acme zone, because the species was prominent in the zone but persisted higher in the column. Now the genus and species come under some question, because the spination does not appear to agree fully with that of *Muirwoodia transversa* as named and described by Cooper (1957), as discussed on p.238ff.There is no appropriate substitute species, and pending revision of the Shi-Waterhouse material, it may be simplest to refer to the zone as the "*Yakovlevia transversa*" Zone, remembering that the genus is certainly not *Yakovlevia*, and possibly not *transversa*, but likely to belong to *Harkeria*.

Impact of the current work on biozones for the upper Jungle Creek Formation

Study of the faunas from the lower Jungle Creek Formation has some impact on the ranges and relationships of fossil species from the upper Jungle Creek Formation, as enumerated in Shi & Waterhouse (1996). Many species thought to have been confined to the Ey or "*Yakovlevia transversus*" Zone have been found to range into older faunas, so that their value for indicating zonal affinity and restricted age has been diminished. Species now thought to be limited to that zone are few in number, involving so-called *Costispinifera paucispinosa* Shi & Waterhouse, now referred to *Tuberculatella, Antiquatonia cooperi* Shi (now *Rigrantia*), *Junglelomia junglensis* (Shi & Waterhouse) and *Dielasma brevicostatum* Cooper, not many for a fauna deemed to have some seventy brachiopod species. None of these particular species are very numerous, and so are not well suited to be nominated for delimiting a range-zone species. In many respects, the species identified as *Yakovlevia transversus* remains appropriate for categorizing the zone, preferably as an acme zone rather than range zone.

The overlying *Ogilviecoelia inflata* Zone is well delineated, by a species limited in range to that zone. But the name-giving species for the overlying zone, called *Jakutoproductus verchoyanicus*, may not be limited to that zone, because somewhat similar and apparently allied specimens occur below the "*Yakovlevia transversus"* Zone in Member E. Two species that appear to be limited to that zone are *Tityrophoria nelsoni* Waterhouse and *Timaniella convexa* Shi & Waterhouse. The zone was defined as an assemblage zone rather than range zone, and that remains valid, even though a few of its characteristic species, such as *Nahoniella plana* (Shi & Waterhouse), have been found in older faunas.

Distribution of the biozones for the lower Jungle Creek Formation

Three of the five members and their biozones in the lower Jungle Creek Formation are extremely limited in distribution, occupying a small region in the northern Ogilvie Mountains, much as implied by a paleogeographical reconstruction of facies in Bamber & Waterhouse (1971, Fig. 14). There are no clear correlates over the rest of the northern Yukon Territory and western Mackenzie District, nor in Canadian Arctic Archipelago or to the south in western Canada. Nor are equivalent faunas yet known in Alaska, but pervasive systematic study has not been attempted for this region. Even so, Member A is comparatively thick, and its faunas diverse and distinctive, largely corresponding with a so-called Dos fauna in Bamber & Waterhouse (1971), Waterhouse & Waddington (1982) and Shi & Waterhouse (1996), the letter o standing for *Orthotichia*, and s for *Septospirifer.* The faunas are now termed the *Septospirifer tatondukensis* Zone, and though found chiefly in the headwaters of Jungle and Ettrain Creeks, are thinly represented in the Tatonduk River (Bamber & Waterhouse 1971, Fig. 7). As well, Bamber & Waterhouse

(1971, Fig. 7) indicated a "Dos" fauna at section 116C-1 on the Peel River. One apparent error by the writer in that study should be corrected. Waterhouse in Bamber & Waterhouse (1971, Fig. 6) showed a diminished "Dos" fauna followed by an "Eta" fauna immediately above the Ettrain type section 116F-9. In fact, as shown by Waterhouse & Waddington (1982, Fig. 6), the "Dos" fauna, or *Septospirifer tatondukensis* Zone, is thick in this area, and continues well down along the ridge. The Ea shown along the section 116F-9 in Bamber & Waterhouse (1971, Fig. 6) is of uncertain correlation, because no material is at hand to pin down the age, but perhaps it could prove to be equivalent to the *Ogilviecoelia shii* Zone.

The rocks and faunas of Members B to E are extremely limited in distribution, and those of C to E are not known in the Tatonduk River. The *Ogilviecoelia initiatus* fauna that is found in dark grey shales of Member B at GSC 53999 and JBW localities 19, ?27, 69, 993 and 994 comes from a thin band, lithologically close to shales in the underlying member, and so treatable as lying at the top of Member A, but with fossils closer to those of the overlying members. Overlying limestone that makes up Member C is thickest at section 42 in Shi & Waterhouse (1996, Fig. 4) and thin elsewhere, the limestone becoming less granular and shelly away from the type section, and so resembles carbonates in Member A. They generally lack fossils, and given the failure to recognize Member B well away from ridges 34 and 42, and the paucity of fossils away from the standard Member C section, the beds cannot be readily distinguished from those of Member A. A possible faunal link through *Juresania* is found half-way up the ridge immediately to the north of section 116-F9, but verification of its age is desirable. Member D with the *Rugivestigia commarginalis* Zone is also thick at section 42, and thins in either direction away from this area. The member is made up of dolomitic sandstone, representing shallow-water deposits accumulated perhaps under hot dry conditions, exceptional for the region of western Canada during early Permian time. Elsewhere in the northern Yukon and western Mackenzie District of the Northern Territories, it is possible that no marine deposition occurred, or the deposits passed laterally into shallow water beds with fauna very like those of the overlying zone, a matter that can be tested through detailed petrographic study of sediments and paleontological analysis.

Marine deposition resumed in the area as Member E, a silty shale with numerous fossils in the area under study, and extending into the Peel River area. Approximate zonal equivalents are widely represented in the Rocky Mountains as the Kindle Formation (see Logan & McGugan 1968). The overlying "*Yakovlevia transversa*" Zone was also more widespread, and extended north into the Northern Richardson Mountains of the Yukon Territory.

Age of the members and their faunas

The general assumptions over the age of the faunas in previous work are sustained largely by this study, although there must be reservations, because no published conodont studies are available. The world stratotype sequences for Early Permian are based in Russia and Kazakhstan, to yield subdivisions based on conodonts, but there is virtually no information to clarify the relationship of conodonts to brachiopod faunas recorded in numerous detailed studies from the Urals and Kazakhstan, unlike the data published for northeast Russia (see Klets 2005, tables 1, 2). Mammoth studies on Early Permian brachiopods in west Texas by Cooper & Grant (1969-1976b) provide an impressive source of information, but the faunas are poorly if at all integrated with international studies, and the faunas have not been placed in biozones, making interpretation extremely difficult. Moreover there has been dispute over the ages of the faunas. Fusulines and ammonoids have been interpreted as indicating that the Lenox Hills

Formation is Sakmarian, whereas conodonts assessed by Wardlaw & Davydov (2000) were said to indicate an Asselian age. The conodonts still have not been integrated adequately with huge brachiopod studies. From that point of view, it is considered that the delineation of sequential biozones, as conducted for northeast Russia by Klets (2005) and Gondwana (eg. Shi et al. 2010, Waterhouse & Shi 2010, Waterhouse 2002A, 2008b, 2015a, b), would prove invaluable for wide-ranging correlation and interpretation of biofacies, age and paleoclimatology.

At present, Members B, C, D and E are allocated to the Asselian Stage, of basal Permian age, in what is now called Cisuralian Series, following Waterhouse (1983b), as endorsed by Jin (1996) and Jin et al. (1997). There are faunal links in support, and the zones underlie the "*Yakovlevia transversa*" Zone of the middle Jungle Creek Formation, which Shi & Waterhouse (1996) interpreted as Tastubian, or basal Sakmarian age. However a number of species also relate to especially Sakmarian species in Russia. Member A, in the basal Jungle Creek Formation, appears to be Gzhelian, or latest Carboniferous. There are numerous faunal ties with the Gzhelian and slightly older beds of northeast Russia and the Moscow Basin. A study of various brachiopods from the bulk of the underlying Ettrain Formation by Nazer (1977) favoured a Kasimovian age. Early Moscovian fusulines have been described by Ross (1967, p. 713) from the basal biozone in the Ettrain Formation, and further Moscovian Foraminifera have been listed from the lower part of the formation (Bamber & Waterhouse 1971, p. 138; Mamet & Ross 1971).

It has to be acknowledged that there are some discrepancies in the evidence for age from ammonoids and fusulines from overlying beds. Nassichuk et al. (1965) reported *Metalegoceras crenatum* from the "*Yakovlevia transversa***"** Zone in the North Richardson Mountains, and Shi & Waterhouse (1996) found *Tabantalites bifurcatus* Ruzencev, of upper Asselian-lower Sakmarian age, so that a Sakmarian age is to be favoured, though the evidence is not consistent. Ammonoids from the overlying *Ogilviecoelia inflata* Zone where outcropping in the Peel River, north of the Ogilvie Mountains, include *Properrinites, Prothalassoceras, Eoasianites, Medlicottia, Somoholites, Tabantalites* and *Uraloceras*, which suggested a lower Sakmarian age to Nassichuk (1971). But Asselian links are strong, and Nassichuk also pointed to Lenox Hills similarities, judged to be Asselian by Wardlaw & Davydov (2000). According to Klets (2005, table 1, p. 44), *Eoasianites* and *Somoholites* species characterize Kasimovian faunas of northeast Russia, but *Metalegoceras crenatum* was recorded with *Agathiceras* and *Neoshumardites* in a *Jakutoproductus rugosus* and *Alispiriferella gydanensis* assemblage, judged to be of upper Sakmarian age (Klets 2005, table 2, p. 60). From the younger *Jakutoproductus verchoyanicus* Zone in the upper Jungle Creek Formation in the Tatonduk River section, Ross (1967) identified the Lenox Hills fusuline *Eoparafusulina yukonensis* (Skinner & Wilde): this species also is found in the McLeod Limestone, and indicated an early Sakmarian age to Mamet & Ross (1971), which is much older than the age as assessed from ammonoids. Thus there have been arguments in favour of an early Sakmarian age for beds and faunas much younger than the *Ogilviecoelia shii* Zone of Member E, and it has to be retained as a possibility that the "*Yakovlevia transversa*" Zone is Asselian rather than Sakmarian. Ross (1967) reported *Schwagerina* sp. from high in the Tahkandit Formation, again of Lenox Hills affinities, but possibly reworked from Jungle Creek beds (Mamet & Ross 1971), and also *Schwagerina hyperborea* (Salter), regarded as equivalent to lower Leonardian of the Glass Mountains, and equivalent to lower Artinskian (Aktastinian) in world standard terms.

Shi & Waterhouse (1996) to a degree set aside the fusuline evidence provided in the studies by Ross. But uncertainty remains: perhaps the "*Yakovlevia transversa*" to *Jakutoproductus verchoyanicus* Zones are Asselian, or partly Asselian, rather than Sakmarian to lower Artinskian.

Previous brachiopod and molluscan studies

Virtually all of the species described in this report, more than 180 in number, are new to the region, except for some that are shared with younger Jungle Creek faunas, especially in the "*Yakovlevia transversa*" Zone. The only brachiopods described previously and specifically from the stratigraphic intervals of Members A through E are *Spiriferella yukonensis* Waterhouse & Waterhouse, 1982, *Eridmatina petita* (Waterhouse & Waddington, 1982), and *Septospirifer tatondukensis* Waterhouse, 1971a (from Member A), together with *Kutorginella yukonensis* Sarytcheva & Waterhouse,1972, and additional Productida and Spiriferida recorded in Waterhouse (2013, 2016). A few species have been figured in the preliminary report in Bamber & Waterhouse (1971), identified usually only to genus level, and not always accurately.

Preservation

Preservation varies, but most species are broken and incomplete, and a number are somewhat distorted, compressed longitudinally. It is therefore difficult to illustrate entire specimens, but incomplete specimens may display much or all of the original morphology on at least one side of the bilaterally symmetrical shells. Lithologies from Member A are diverse, ranging from conglomerate through sandstones and silty shales into limestones in which the shells are often silicified. But it has not been possible to dissolve the silicified carbonates and so obtain well preserved silicified shells, so that these remain unexamined, other than from surface material. Member B fossils are found in silty shale, and are few in number. Member C fossils come from granular carbonate, and may be slightly silicified. In Member D, the fossils are difficult to extract and are exposed over the surface of slabs of dolomite. By contrast, siltstones and mudstones are predominant in Member E, and detail is well preserved: the fossils are most found as natural moulds, but many have suffered breakage, because rocks of the member are closely fractured. Casts have been prepared by the use of rubber latex, and from a lab-putty based on polysiloxane, trade-marked coltène whaledent.

Photographs, all prepared by the writer, were taken on a Nikon camera, using direct sun-light of fossils coated with ammonium chloride. All photographed material is registered serially by number, and is housed at the Geological Survey of Canada, Ottawa, Canada.

FOSSIL LOCALITIES

Some fossil localities, with prefix GSC or C-, were made by staff of the Geological Survey of Canada, and details are kept at the Geological Survey of Canada at Calgary. They were further documented in Bamber & Waterhouse (1971), Waterhouse & Waddington (1982) and Shi & Waterhouse (1996). Most of the localities were collected by the writer, with some located on geological maps prepared by the writer in Waterhouse & Waddington (1982, Fig. 6) and Shi & Waterhouse (1996, Fig. 4). They have the prefix JBW, and original notes on a number of the measured sections with localities, and aerial photographs with position of the localities, have been offered to the Geological Survey of Canada at Calgary (3303 33rd St. NW, Calgary, Alberta). The material was collected during the summer of 1969, with Hugh Reid, summer of 1970 with assistance from Janet Waddington, Ian A. Nicholls and Ray Zimmerman, summer of 1971 with John Scott, and the 1972 summer with Alan E. Oldershaw and Peter von Bitter, as well as stays without assistance.

REPOSITORIES

BR, Brachiopod Register, Institute of Geological and Nuclear Sciences (GNS), Lower Hutt, New Zealand. **CNPM**, Geological Museum of the Central Scientific Naturalists Museum in Kiev, Ukraine. **GSC**, Geological Survey of Canada, Ottawa, Canada. **DP**, **DPO,** Departamento de Geologia, Oviedo University, Oviedo, Spain. **PIN**, Paleontological Institute, Russian Academy of Science, Moscow, Russia. **ROM**, Royal Ontario Museum, Toronto, Canada. **TsNIGRA**, Central Scientific Geological Exploration Museum (Tschernyschew Museum), also CNIGR Chernyshev Museum, St Petersburg, Russia. **UC**, The University, Calgary, Canada. **USNM**, United States National Museum, Washington D.C., United States. **YPM,** Yale University, Museum of Natural History, New Haven, Connecticut, United States.

ACKNOWLEDGEMENTS

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SYSTEMATIC DESCRIPTIONS

Morphological terms

In describing aspects of morphology, use is made of terms newly modified or recently proposed. These are as follows for BRACHIOPODA:

buttress plates: a pair of slender septa extending obliquely forward from the cardinal process in some Productida, especially Balkhasheconchinae and Rhamnariidae. Not to be applied to Productida in which the posterior dorsal septum has a median slit. See Waterhouse (2013, pp. 17, 18, Fig. 8, 9).

commarginal: a descriptor used to replace the commonly used term concentric. The preferred term is more accurate.

commargons: a term proposed for regular commarginal bands developed on various brachiopods such as *Echinoconchus* (Productida) and *Phricodothyris* (Spiriferida), usually with a step-like or cuesta profile, a flat tread and steep anterior margin, and usually bearing spinose ornament.

connector plate: the plate that spans the delthyrial gap of the ventral valve and lies between the junction of the dental plates and adminicula. (See Waterhouse 2016, pp. 8, 12). The plate has also been called a subdelthyrial plate in various studies.

myosepta: a pair of low ridges in the posterior ventral valve, dividing adductor from diductor impressions, found in *Cyrella* Archbold (Waterhouse & Chen 2007), or as low ridges that border the dorsal adductor scars in some Spiriferiformi.

propping plates: The propping plates in *Septacamera* and allied genera are ventral plates lying at an oblique angle to the spondylium and/or septalium, which they support. They have been termed buttress plates, and here it is suggested that buttress plates be reserved for plates placed in front of the cardinal process in the dorsal valve. The propping plates are of quite different function.

spine base: refers to the base of the spine in Productida where it emerges from the body of the shell. In a number of genera the shell surface behind the base is elongately raised, and this may also be termed a spine base. See Waterhouse (2013, p. 17, Fig. 10).

spine tunnel: The hollow core of the spine may be prolonged anteriorly and/or posteriorly from the base of the spine through the shell, and may leave an elongate tube internally through the inner surface of the shell. This is termed spine tunnel.

tabellae: (plural) – name for the plates supporting crural plates in the dorsal valve. Also inconsistently called dorsal adminicula in parts of the Treatise studies. See Waterhouse (1971b, 2016, pp. 10, 15-19). The *Revised Brachiopod Treatise* frequently confused tabellae with crural plates, and often adminicula with dental plates, (Waterhouse 2016, pp. 15-19).

BIVALVIA: See Waterhouse (2001, p. 115, text-fig. 9; 2008a, pp. 9, 10, text-fig. 2).

auricle: the anterior extension of the valve like a wing, above a byssal notch, and containing the ligament on the inner side, in pteriomorph bivalves.

ear: the slender anterior portion of shell above a byssal notch, without ligament on inner side.

lativincular ligament: a ligament with a very broad resilifer.

lineavincular ligament: ligament slender or broad, without resilifer.

wing: the slender and often differently ornamented portion of shell along the hinge posterior to the umbo in pteriomorph bivalves, usually bearing ligament on inner side.

Abbreviations

OD – by original designation. SD – by subsequent designation.

In the synonymy: use of square brackets […] enclose the conclusion that the attribution of species and author was incorrect.

PHYLUM BRACHIOPODA Dumeril

Classification

The classification of Brachiopoda has been subject to considerable revision since its appearance in the *Revised Brachiopod Treatise*, even though the treatment in that work marked a substantial advance on previous studies (see Williams, Carlson & Brunton 2000a, b). Parts of the classification may now be regarded as out-of-date and remote from the actual interrelationships and course of evolution within the phylum. We may still be a long way from achieving adequate understanding, but as an interim step, beyond the *Revised Brachiopod Treatise* though far from any finality, the interpretations are followed after Waterhouse (2013) for Productida, which take full account of the insightful revisions by S. S. Lazarev, and Waterhouse (2016) on Spiriferida, in which the severe criticisms of the *Revised Brachiopod Treatise* by Mena Schemm-Gregory are integrated. These works included studies on some of the brachiopods covered in the present report.

The International Subcommission for Zoological Nomenclature has published rules and recommendations for aspects of family group nomenclature, and not touched on nomenclature for categories of ordinal groupings. The *Treatise* series has partly filled this gap, with each series independently laying out formats for subdividing phyla or classes. For the forthcoming revised Treatise on Bivalvia, an elaborate arrangement for ordinal groups has been prepared, whereas the categories used in the published *Revised Brachiopod Treatise* are somewhat simpler, and to my mind, need to be expanded to better express interrelationships and differences dependent on paths of evolution. It is considered that the introduction of two categories into ordinal group nomenclature will help indicate interrelationships, namely infrasuborders, that group superfamilies into a category of less than subordinal ranking, and superorders, that group orders. These clusters were outlined in part by Waterhouse (2010), and the superordinal groups that incorporate most of the Rhynchonellata may be summarized as follows:

CLASS STROPHOMENATA WILLIAMS et al. 1996
Superorder Strophomeniformi Öpik, 1934
Order Triplesiida Moore, 1952
Order Strophomenida Öpik, 1934
Order Clitambonitida Öpik, 1934
Superorder Productiformi Waagen, 1883
Order Chonetida Muir-Wood, 1955
Order Productida Waagen, 1883

CLASS RHYNCHONELLATA WILLIAMS et al. 1996
Superorder Pentameriformi Schuchert & Cooper, 1931
Order Pentamerida Schuchert & Cooper, 1931
Order Orthida Schuchert & Cooper, 1932
Order Protorthida Williams & Harper, 2000
Superorder Rhynchonelliformi Kuhn, 1949
Order Rhynchonellida Kuhn, 1949
Superorder Atrypiformi Moore,1952
Order Atrypida Moore, 1952
Order Athyrida Boucot, Johnson & Staton, 1964
Order Retziida Boucot, Johnson & Staton, 1964
Superorder Spiriferiformi Waagen, 1883
Order Spiriferida Waagen, 1883
Order Spiriferinidina Ivanova, 1972
Superorder Terebratuliformi Waagen, 1883
Order Terebratulida Waagen, 1883

In this scheme, and throughout the present study, the author or authors of each ordinal group category are considered to be the first proposer of any rank within the particular ordinal group, following the procedure mandated for family group names. Furthermore, it is considered that the first author of a family group name cannot be transferred at the whim of a later study to an ordinal group name. These procedures result in the revision of a number of names adopted in the *Revised Brachiopod Treatise*, which was inconsistent in its application of principles of priority and authorship. (See p. 27 and p. 172).

Endings for Family-group and Ordinal-group names

In constructing various family group and ordinal group names, extraneous letters such as id have been added to the stem of the genus name, so as to try to adhere to rules of Latin usage as conventionalized by scholars long after the language became defunct except in religious and academic circles. That did conform with the Code of Zoological Nomenclature, but the procedure has been deemed unnecessary by the Code for family-group names proposed after 1999, provided that the name is based on the correct Greek or Latin suffix (ICZN 1999, p. 33, 29.4). This means that we may well end up with names that add extra letters, and other names that do not add extra letters, pre- and post- 1999. It was moreover ruled acceptable that names may be proposed without any input from Latin or Greek, so that the question of having the correctly Latinized genitive stem is less than rigid.

It is here suggested that we should aim at a uniform mode of family-group and ordinal-group names, based as far as may be acceptable, on the full generic name, and that eventually, generic names and group name endings should remain inviolable. Which means that group names should not receive additional prefixes, and generic stems no added suffixes. The simplest methodology would seem to be to add group and ordinal and other endings, such as idae and ida, after the last consonant or vowel, regardless of what the letter is. Then there would be no ambiguity: the genus name would be perfectly clear, and the change to indicate family group or ordinal group ranking would be clear. That I suggest should be the ultimate aim of zoological nomenclature, to have clarity and simplicity, and avoid any uncertainty or ambiguity. It would lead to a multiplication of vowels for some instances, awkward to pronounce, but it is easy to slur pronunciation: the written word remains intact. Admittedly simplification of nomenclatural endings may result in a certain uneasy feeling of dissonance for at least those accustomed to Latinate suffixes, and I am afraid that includes me. If the last vowel is s, preceeded by a vowel, it seems acceptable to remove the last consonant and vowel, which does add a layer of exceptionalism, and it is suggested as a compromise that that will mark a progression towards full adherence to simplicity and clarity. As a further concession to custom, it is proposed to remove the last vowel, at the end of the generic term. That does violence in some instances to the stem of the genus term, but will achieve uniformity, and make matters much easier for paleontologists without a Latinate training, which nowadays includes many of non-European descent, not to mention other paleontologists who simply cannot be bothered with what seem to be irrelevant procedures.

For some, even these exceptions will come to be treated as unacceptable compromises, and come to be rejected, though deletion remains more acceptable than addition. To my mind, the imperative is to have the generic name conform as closely as possible, or preferably exactly, with family group and ordinal group names. We should seek both to avoid any alienation between the generic name and the family and ordinal group names, and reject Latin-based or supposedly Latin-based emendations that are applied to some but not all such names.

The insertion of id between the stem of the genus name and the standard family group ending has seen many historical exceptions, and many authors rely on the *Revised Brachiopod Treatise* to provide the correct if convoluted rendition. *Athyris* is rendered Athyrididae (Alvarez & Rong 2002, p. 1497 – see p. 296), but simple addition of the family group ending to the full genus name as Athyrisidae offers a readily pronounceable word.

There are further distortions to group nomenclature which should be immediately set aside. A widely used example concerns family- and ordinal-group renditions related to genus *Pecten*. In conformity with usage in Latin, the name is changed to Pectinidae, but the change seems unnecessary for family-group understanding, and moreover complicates the rules for endings, because whereas idae is the accepted family ending, here the ending has become inidae, and so on through the full range of family- and ordinal group names. A further example is offered by *Pugnax*, a brachiopod recognized as name giver for Pugnaxidae by Rhzonsnitskaya (see p. 277). The name was later changed to Pugnacidae, because Latin has no letter x. I support the original family group name. Either our Russian colleague saw no reason to introduce rules of Latin procedure into terminology, or was unaware of supposedly correct procedures. Here is another example of interference with the accepted ending for family group names, this time, cidae, instead of idae. Rules for nomenclature should be as consistent as possible, and we do not need numerous grammatically contingent exceptions to handicap those from a non-Latinate background in their interpretation of zoological classification.

Subphylum Rhynchonelliformea Williams et al., 1996

Class Strophomenata Williams et al., 1996

[Strophomenata Williams et al. 1996, p. 1193].

Superorder STROPHOMENIFORMI Öpik, 1934

[Nom. transl. Waterhouse 2010, p. 8 ex Suborder Strophomenoidea Öpik, 1934, p. 75].

This includes Orders Strophomenida, Triplesiida Moore and Clitambonitida Öpik (Waterhouse (2010, pp. 8, 9).

Order TRIPLESIIDA Moore, 1952

[Order Triplesiida Moore, 1952]

Wright (2000, p. 681) placed Triplesiidina as a suborder within Orthotetida Waagen, 1884, but Waagen (1884) had only recognized Orthotetinae as a new subfamily, so that attribution of Orthotetidina or Orthotetida to Waagen is incorrect, and arguably patronising. Instead, Orthotetidina is attributed by courtesy to Cooper & Grant (1974, p. 256), even if not in conformity with the rules, for even I could formally propose the name. It is they who were first to recognise the ordinal ranking, but wrongly attributed the name to Waagen (1884). The name Orthotetidina Cooper & Grant postdated the proposal of Triplesiida Moore, 1952, p. 221. In the same way Billingsellidina is ascribed to Williams & Harper (2000a), rather than accept their promotion from a family proposed by Schuchert, 1893.

Suborder ORTHOTETIDINA Cooper & Grant, 1974

[Nom. transl. and auct. correct. Waterhouse 2010, p. 9 ex Orthotetida [not Waagen] Cooper & Grant, 1974, p. 256].

Diagnosis: Strophic semicircular to subrounded shells, ventrally subconical, pedicle reported only in earliest members, finely costellate, ventral interarea usually with perideltidium and pseudodeltidium, teeth may be supported by dental plates, cardinal process large and laminate, variably disposed socket ridges and plates, shell typically pseudopunctate, impunctate in older stock, and less commonly extropunctate.

Superfamily **ORTHOTETOIDEA** Waagen, 1884

[Nom. transl. Williams 1953, p. 9 ex Orthotetinae Waagen, 1884, p. 576].

Diagnosis: Shell normally pseudopunctate.

Family **ORTHOTETIDAE** Waagen, 1884

[Nom. transl. McEwan 1939, p. 619 ex Orthotetinae Waagen, 1884, p. 576].

Diagnosis: Finely costellate usually rectimarginate shells with symmetrical ventral umbo, interarea with well developed perideltidium and convex pseudodeltidium, dorsal interarea short, with small chilidium, dental ridges normally convergent on median ridge or septum, no dental plates. Socket plates recurved as a rule, discrete cardinal process lobes, septum variably developed.

Genus ***Orthotetes*** Fischer de Waldheim, 1829

Diagnosis: Small delthyrial chamber formed by dental ridges, socket ridges recurved, ventral muscle scars large and flabellate, dorsal septum low.

Type species: *Orthotetes radiata* Fischer de Waldheim, 1850, p. 491 from Moscovian of Russia.

Discussion: Williams & Brunton (2000) stressed that *Orthotetes* was rectimarginate, but it is considered desirable to allow a less restrictive circumscription for the genus. Some specimens of the present Canadian species are unisulcate, especially at early maturity, but only differ only in that regard from typical *Orthotetes.*

Orthotetes dorsosulcata n. sp.

Fig. 9, 10

Derivation: dorsum – back, sulcus – furrow, Lat.

Diagnosis: Small and wide specimens with anterior margin laterally extended and almost parallel to hinge, costellae fine. Dorsal valve with narrow and shallow sulcus as a rule.

Holotype: GSC 136682, here designated.

Material: Three ventral valves from JBW 615, single ventral valves from JBW 122, 126, 417, 606, 610 and 817, poorly preserved single ventral valves from JBW 86, 94, 417, and 677, two ventral valves and one dorsal valve from JBW 610 and 675. Single dorsal valves from JBW 431, 579, 597, 725 and 749, one specimen with valves conjoined and a dorsal valve from JBW 78. A dorsal valve and ventral valve from JBW 789.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimens moderately small, ventral valve gently convex and subpentagonal in shape with slightly extended and undeformed ventral umbo, not incurved, umbonal angle close to 80º; hinge wide with low interarea bearing convex pseudodeltidium in ventral valve and linear dorsal interarea with chilidium, cardinal extremities angular and varying in angle between 80º and 90º. No clearly formed sulcus, but may be slightly flattened medianly or weakly raised in broad fold. One ventral valve has a very narrow sulcus: it is deemed to be conspecific, but might prove to be a member of a second species likely to belong to the same genus. Dorsal valve gently convex and roundly subrectangular in shape. Maximum width for both valves lies a little in front of the hinge. Most dorsal valves bear a narrow median sulcus with angle of 20-25º, which becomes less emphasized anteriorly. Both valves are ornamented by fine costae, ten in 5mm anteriorly, in at least three orders, increasing by both bifurcation and intercalation, with lamellar growth increments prominent in interspaces. Fine pseudopunctae are visible, but not amenable to closer study, the shell being partly to completely silicified.

Ventral interior obscure but shows a median septum extending for a third of the valve length, and a low shorter ridge each side, bordering muscle scars which appear to be unusually narrow: the delthyrial chamber is very small. Cardinal process low and broad with four lobes, supported by very short widely divergent socket plates; very low dorsal median septum extends anteriorly for much of the valve length, coinciding with an external rib. Muscle impressions too faint to be discerned.

Resemblances: This species is much smaller than *Orthotetes canadensis* Shi & Waterhouse (1996, p. 48, pl. 2, fig. 1-10, pl. 3, fig. 1-9, 11) from the "*Yakovlevia transversa*" and *Ogilviecoelia inflata* Zones of the Jungle Creek

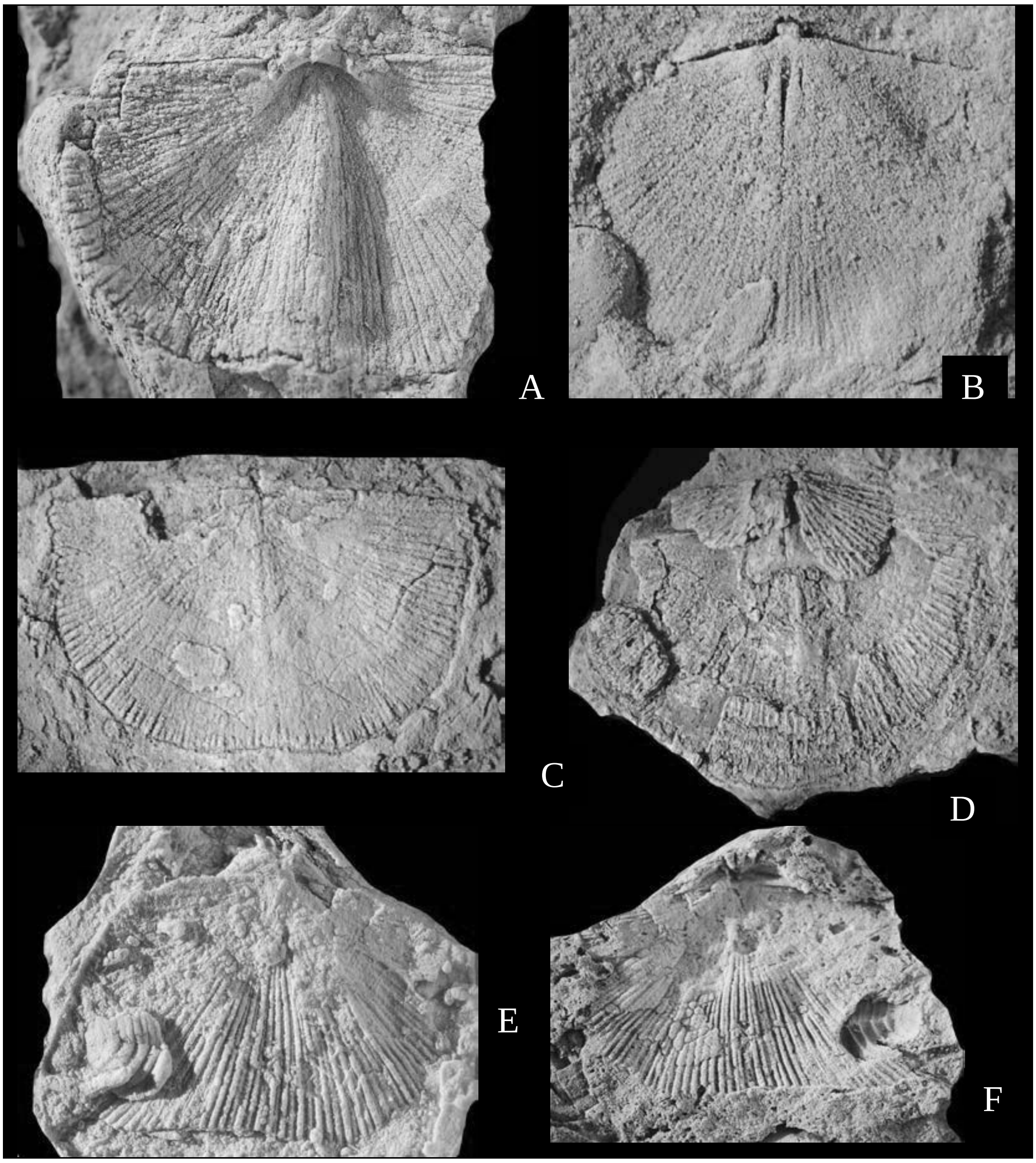


Fig. 9. *Orthotetes dorsosulcata* n. sp. A, dorsal valve interior, holotype GSC 136682 x2 from JBW 675. B, ventral internal mould GSC 136683 x2 from JBW 615. C, dorsal valve exterior GSC 136684 x2 from JBW 610. D, ventral valve exterior GSC 136685 x2 from JBW 789. E, F, dorsal exterior cast and external mould GSC 136686 x3 from JBW 817. Member A, Jungle Creek Formation.

Formation, and has a dorsal sulcus absent from the younger form. *Orthotetes sulcus* Branson (1930, p. 27, pl. 2, fig. 20, pl. 3, fig. 1-4) from the so-called *Pustula* Member of the Phosphoria Formation of Wyoming, United States, has a slender dorsal sulcus less defined than in the present form, and a ventral fold is moderately developed. The species is larger and more elongate than the Canadian species.

The Upper Carboniferous species *Orthotetes waageni* (Schellwien, 1892, p. 32, pl. 6, fig. 4-5, pl. 7, fig. 7-10) from the Auernig Austrian Alps, also described by Enderlie (1901, p. 78, pl. 6, fig. 7) and Metz (1936, pl. 5, fig. 3), is close overall, though no ventral valves have a well defined sulcus or fold, nor does the dorsal valve display a fold or sulcus. Sokolskaya (1968, p. 58, pl. 2, fig. 3-5, text-fig. 6) reported specimens from the Upper Carboniferous of Kazakhstan that are similar in costation and shape, and Manankov (1979, p. 47, pl. 2, fig. 1, 2) stated that the species ranged from Moscovian to Gzhelian in Russia. *Orthotetes radiata* Fischer de Waldheim, 1850, emend Sokolskaya, 1954, from the Vereian, Kashirian and Podolian subdivisions of the Moscovian Stage, and Gzhelian faunas of the Russian Platform and Urals and reported from Novaya Zemlya, is moderately close but shows a more extended and rounded anterior margin (Stepanov 1975, p. 156, pl. 62, fig. 8, 9; Manankov 1979, p. 45, pl. 1, fig. 9-11). Manankov (1979) included *O. regularis* Sarytcheva & Sokolskaya (1952, p. 52) and *Derbyia waageniformis* Licharew & Einor 1939, p. 19) in synonymy.

Czarniecki (1969) ascribed two suites of *Orthotetes* from the Treskelloden beds of Spitsbergen to Russian species, but they are more elongate, larger, and more inflated than the present species, and lack a dorsal sulcus.

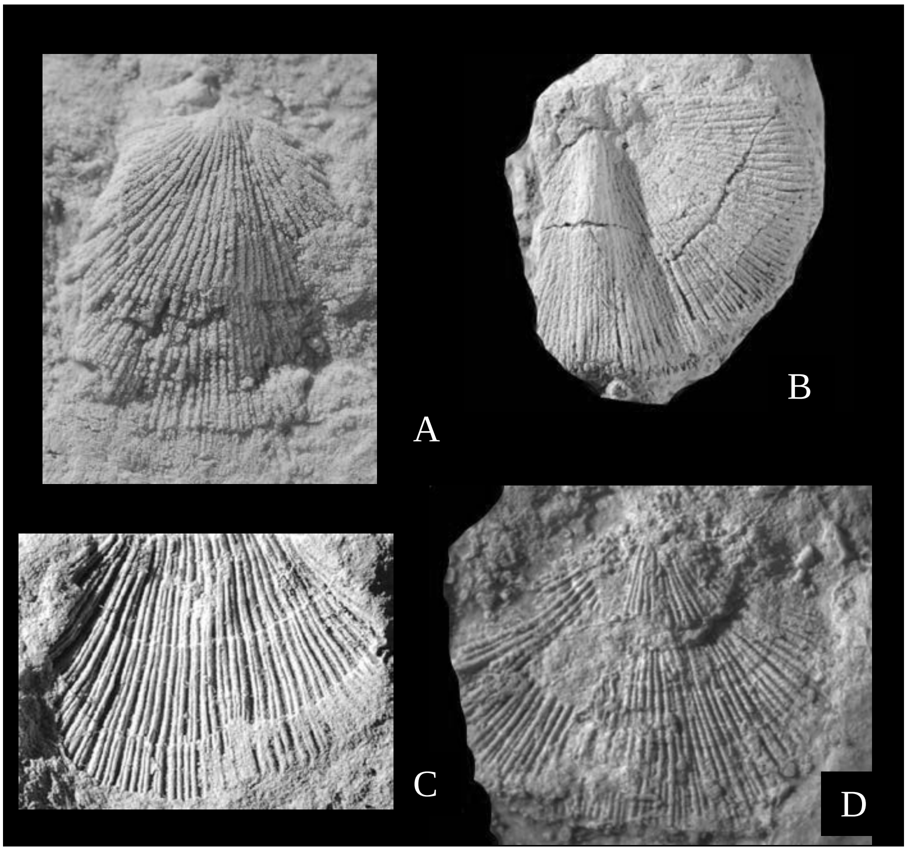


Fig. 10. *Orthotetes dorsosulcata* n. sp. A, dorsal external cast, GSC 136688 x2 from JBW 417. B, dorsal valve exterior, GSC 136687 x2 from JBW 597. C, external mould showing ventral valve ornament, GSC 136690 x2 from JBW 610. D, dorsal valve external cast, GSC 136691 x2 from JBW 675. Member A, Jungle Creek Formation.

Family **SCHUCHERTELLIDAE** Williams, 1953

[Nom. transl. Stehli 1954, p. 298 ex Schuchertellinae Williams, 1953, p. 9].

Diagnosis: Ventral valve may be deformed by attachment, ventral interarea low to very high, shell finely costellate, dental ridges and teeth, cardinal process lobes low to high, fused proximally, socket ridges divergent or recurved, brachiophores developed. Shell extropunctate.

Subfamily **SCHUCHERTELLINAE** Williams, 1953

[Schuchertellinae Williams, 1953, p. 9].

Diagnosis: Costellate with variable interarea, linear dorsal interarea, low cardinal process lobes, recurved socket ridges and diverging erismata.

Subfamily **STREPTORHYCHINAE** Stehli, 1954

[Streptorhynchinae Stehli, 1954, p. 299].

Diagnosis: Ventral interarea low to high with convex pseudodeltidium which is not folded into monticulus, perideltidium usually present, dorsal low interarea with chilidium, socket ridges and low median myophragm.

Discussion: The subfamily is readily distinguished from the otherwise closely related subfamily Tropidelasminae Waterhouse, 1983d, based on *Tropidelasma* Cooper & Grant, 1969. This latter genus like the subfamily is characterized by the presence of a monticulus – a conspicuous median ridge that longitudinally traverses the pseudodeltidium of the ventral valve (Waterhouse & Chen 2007, p. 33). No monticulus is developed in *Streptorhynchus* King, *Arctitreta* Whitfield, *Grumantia* Ustritsky, *Bothrostegium* Cooper & Grant, or *Chelononia* Cooper & Grant. On the other hand a monticulus is well developed in the distinctive genus *Erismatina* Waterhouse, 1983d from the Permian faunas of Thailand and Western Australia, a genus distinguished by its long erismata, as discussed by Waterhouse & Chen (2007, p. 34).

Genus ***Arctitreta*** Whitfield, 1908

Diagnosis: Subpentagonal shells ornamented by fine costellae, ventral interarea high with broad pseudodeltidium bordered by teeth ridges, dental ridges, cardinal process poorly known for type species.

Type species: *Arctitreta pearyi* Whitfield, 1908, p. 57 from Grant Land, Cape Sheridan, Canadian Arctic Archipelago, OD.

Discussion: Williams & Brunton (2000, p. 667) claimed that *Grumantia* Ustritsky, 1963 was a synonym of *Arctitreta* and figured its type species *Streptorhynchus kempei* Wiman as typifying *Arctitreta* rather than the true type species of *Arctitreta*, A*. pearyi*. Type *Grumantia* has a lower ventral interarea than *Arctitreta*, and lower dental ridges, differences that may not sgnify. The types of *pearyi* were refigured by Waterhouse & Chen (2007, text-fig. 3, 4) and it was noted that the genus appears to be close to *Streptorhynchus* King, and lacks a monticulus from the pseudodeltidium. It is not clear that a perideltidium is present in the type species, because of imperfect preservation.

Arctitreta? sp. A

Fig. 11A

Material: Incomplete ventral valves from JBW 8, 95, 417, 606, 615, 645, 802 and 817.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: A moderately well preserved ventral valve is 35mm wide, 32mm long and 9mm high. The largest fragment suggests a specimen close to 70mm wide. There is a broad shallow sulcus and differentiated costellae arising by intercalation, with eight ribs in 5mm, including four or five that are strong, and likely to be primary ribs. The posterior shell shows a myophragm ridge.

Resemblances: *Arctitreta peelensis* Shi & Waterhouse (1996, pl. 1, fig. 19-24, text-fig. 15) from the "*Yakovlevia transversa"* Zone of the Jungle Creek Formation is smaller and lacks a ventral sulcus.

***Arctitreta*? sp. B**

Two fragmentary specimens from JBW 18, Member C.

***Arctitreta* cf. *peelensis* Shi & Waterhouse, 1996**

Fig. 11B

cf. 1996 *Arctitreta peelensis* Shi & Waterhouse, p. 46, pl. 1, fig. 19-24, text-fig. 15.

Diagnosis: Medium-sized roundly subpentagonal shells, costellae fine, muscle field distinctive and impressed.

Holotype: GSC 96860 from GSC 53713, figured by Shi & Waterhouse (1996, pl. 1, fig. 23) from Jungle Creek Formation, Yukon Territory, OD.

Material: Single ventral valves from JBW 406 and 413.

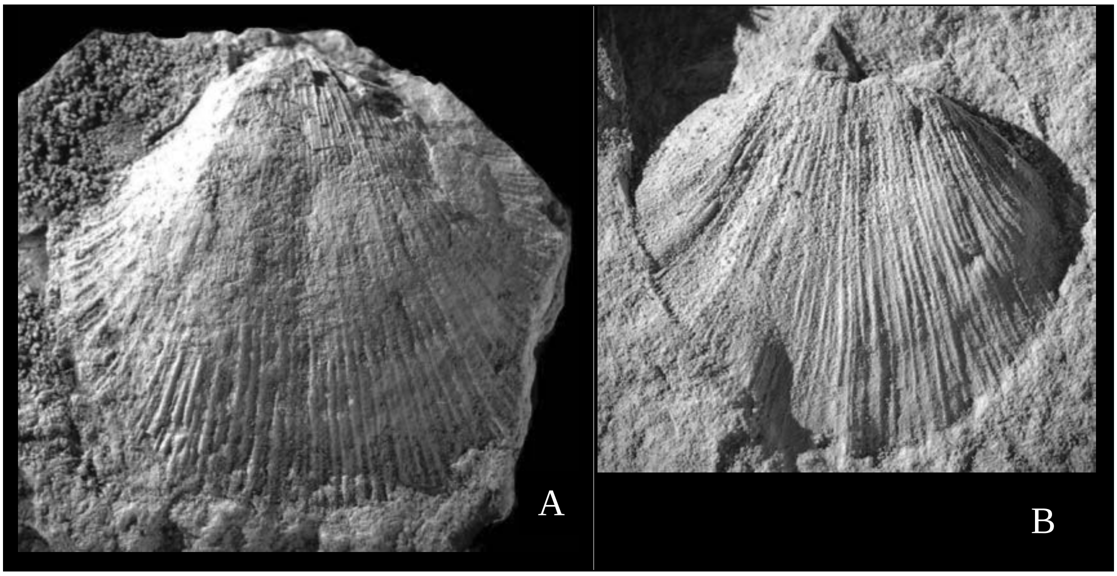


Fig. 11. A, *Arctitreta*? sp. A. ventral valve GSC 136692 x2 from JBW 615, Member A, Jungle Creek Formation. B, *Arctitreta* cf. *peelensis* Shi & Waterhouse, ventral valve GSC 136693 x2 from JBW 406, Member D, Jungle Creek Formation.

Stratigraphic and biostratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Description: Specimen from JBW 406 measures 35mm wide, 31mm long and approximately 3.5mm high, with subpentagonal ouline, broad umbo and comparatively short posterior walls. The shell shows irregularly placed lateral fold and channels, but no median fold or sulcus. Costellae number nine in 5mm anteriorly, and the anterior margin is crenulated by some fifteen fila in 5mm. Costellae are moderately differentiated, and increase by intercalation, with minor splitting. Short posterior septum, separating oval depressed muscle scars.

Resemblances: The overall shape suggests *Arctitreta peelensis* Shi & Waterhouse (1996, pl. 1, fig. 19-24) from the overlying "*Yakovlevia transversa"* Zone of the Jungle Creek Formation.

Genus ***Chelononia*** Cooper & Grant, 1974

Diagnosis: Elongately pyramidal shells with moderately strong costellae and wide hinge bearing high ventral interarea with convex pseudodeltidium, cardinal extremities alate with small differentiated ears. Cardinal process high with moderately long erismata. No monticulus.

Type species: *Chelononia neali* Cooper & Grant, 1974, p. 327, from Neal Ranch Formation (Asselian), west Texas, OD.

Discussion: Williams & Brunton (2000) did not provide any clear distinction between *Chelononia* and *Streptorhynchus*, and the elongate pyramidal shape described as typifying *Chelononia* is just as characteristic of *Streptorhynchus*. The socket ridges are a little longer in *Chelononia,* and the hinge is extended so that the two lateral extremities jut laterally to suggest two small ears. Cooper & Grant (1974, p. 327) also noted the significance of the auriculate hinge, which is not seen in *Streptorhynchus*.

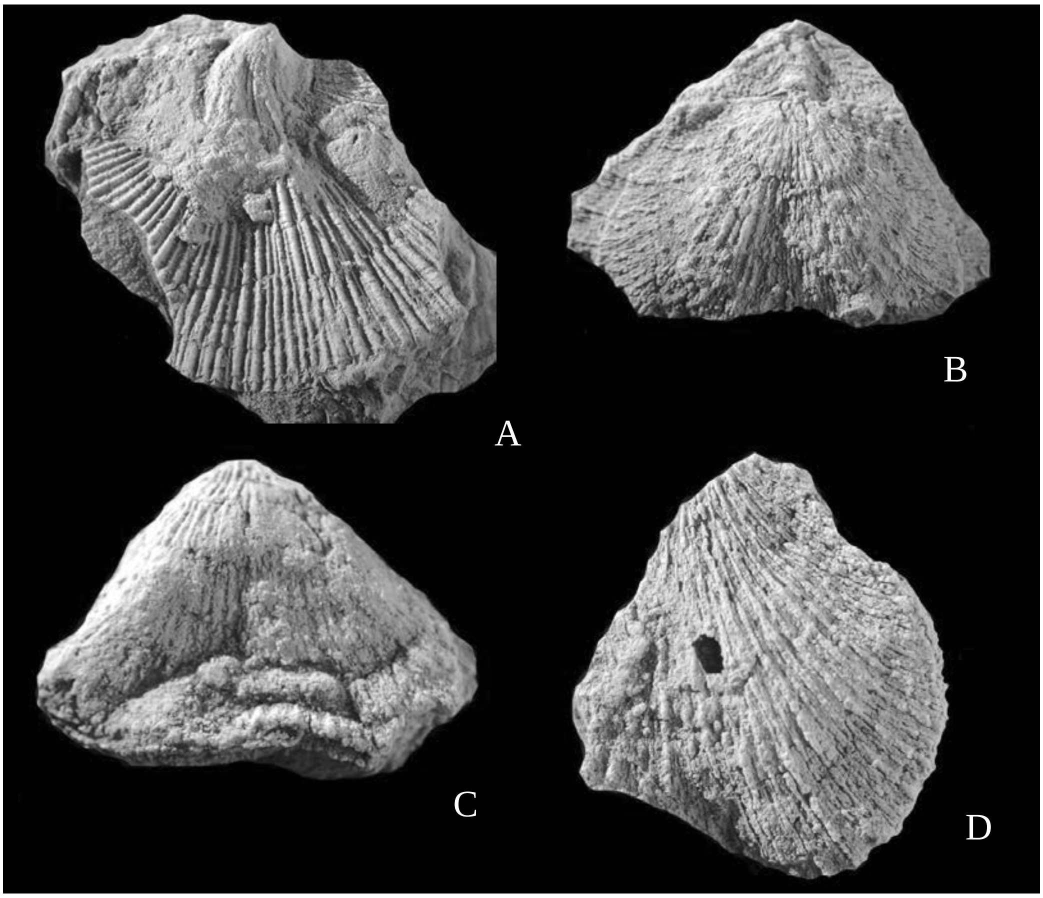


Fig. 12. *Chelononia minimauris* n. sp. A, ventral valve GSC 136694 from JBW 802 x3. B, C, dorsal and ventral aspects of holotype, GSC 136698 from JBW 802 x3. D, ventral fragment GSC 136695 from JBW 524 x3.5. Member A, Jungle Creek Formation.

Chelononia minimauris n. sp.

Fig. 12, 13

Derivation: minime – very little, auris – ear, Lat.

Diagnosis: Small shells with relatively strong costae, small ears, dorsal and ventral sulcus.

Holotype: GSC 136698, here designated.

Material: Five ventral valves, one dorsal valve and eight specimens with valves conjoined from JBW 802. Two ventral valves from JBW 524, dorsal valve from JBW 166 and ventral valve from JBW 627, possible two ventral valves from JBW 181.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation, *Septospirifer tatondukensis* Zone.

Description: Specimens are small and subtriangular. The ventral valve has an extended not incurved ventral umbo, which is pointed and not strongly deformed, with angle of 95°. The hinge extends for half the maximum width, which is placed near anterior third of shell length. The ventral interarea is high, planar, slightly incurved under beak, with arched pseudodeltidium bearing commarginal growth-lines that persist onto the interarea, lacking a monticulus. The interarea is heavily marked by growth-increments and does not clearly show if a perideltidium was present. Tiny ears present at the cardinal extremities. Shallow ventral sulcus, and anterior margin deflected. Dorsal valve has slightly larger ears, gently convex overall, with shallow sulcus commencing a little in front of hinge and widening at 20-25°, hinge with very low interarea, chilidium obscure. Both valves ornamented by costae, up to ten in 5mm, arising in three bands separated by growth stops, remaining differentiated, increasing by intercalation and also on the ventral valve by splitting into two ribs of equal or uneven strength, with the outer rib finer than the inner rib, as a rule. The ribs have rounded crests and steep sides, and are slightly more prominent on the dorsal valve.

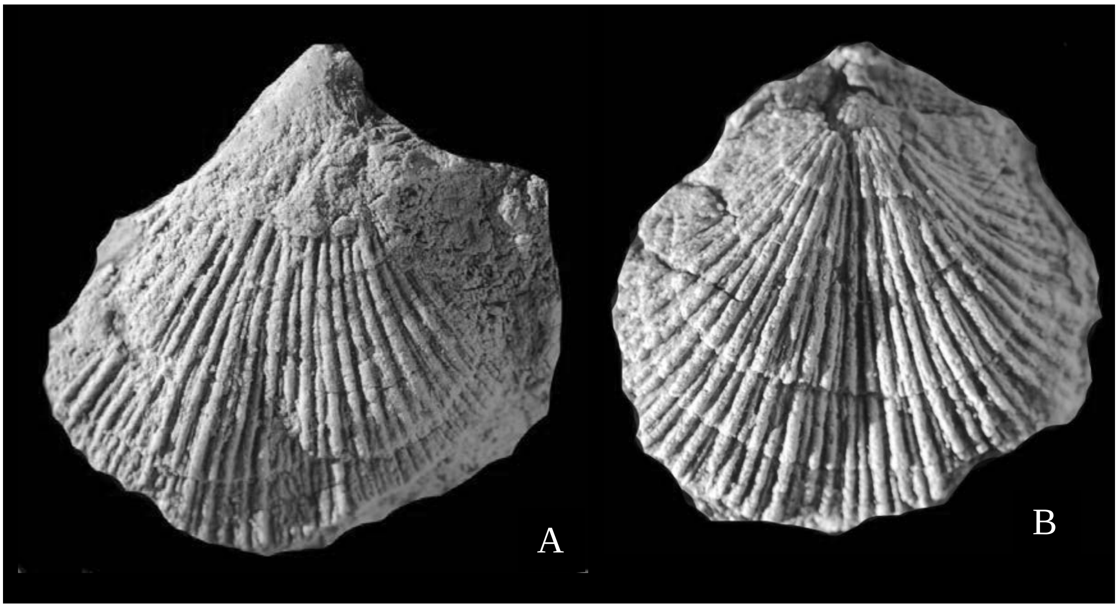


Fig. 13. *Chelononia minimauris* n. sp. A, ventral valve GSC 136696 from JBW 802, x3. B, dorsal aspect of GSC 136697 from JBW 802 x3. Member A, Jungle Creek Formation.

Resemblances: Externally these specimens are very close to *Chelononia* and share the distinctive ornament, shape and cardinal ears. The type species *C. neali* Cooper & Grant (1974, p. 327, pl. 126, fig. 1-47) from the Neal Ranch

Formation in Texas, of early Cisuralian age, is moderately close and has much the same ornament and a number of dorsal valves indicate a shallow sulcus, but the west Texan species tends to be a little more elongate than present material. *C. straminea* Cooper & Grant (1974, p. 329, pl. 95, fig. 1-22) from the Neal Ranch Formation is distinguished by its extended ventral umbonal region and has a narrow ventral sulcus, according to the text. The Canadian form is new, and is slightly older than other species so far described.

Superorder PRODUCTIFORMI Waagen, 1883

[Nom. transl. Waterhouse 2010, p. 9 ex Suborder Productacea Waagen, 1883, p. 447].

Discussion: This superorder contains the Orders Chonetida Muir-Wood and Productida Waagen, with an outstanding suborder Lyttoniidina Williams (Waterhouse 2010, pp. 9-11).

Order CHONETIDA Muir-Wood, 1955

[Nom. transl. Nalivkin 1979, p. 23 ex Chonetidina Muir-Wood, 1965a, p. 420, pro suborder Chonetoidea Muir-Wood, 1955, p. 68].

Superfamily **CHONETOIDEA** Bronn, 1862

[Nom. correct. Racheboeuf 2000, p. 368 pro Chonetacea Schrock & Twenhofel, 1953, p. 317, pro Chonetidae Bronn, 1862, p. 301].

Family **RUGOSOCHONETIDAE** Muir-Wood, 1962

Nom. transl. Cooper & Grant 1975, p. 1212 ex Rugosochonetinae Muir-Wood, 1962, p. 32].

Subfamily **RUGOSOCHONETINAE** Muir-Wood, 1962

[Rugosochonetinae Muir-Wood, 1962, p. 32].

Diagnosis: Shells finely ribbed, internal structures may include anderidia lying between and often projecting beyond the dorsal adductor scars.

Discussion: Capillomesolobini Pecar, 1986 is closely allied in shape, ornament, and internal morphology, but has a more profound ventral sulcus that bears a median fold.

Genus ***Chonetinella*** Ramsbottom, 1952

Diagnosis: Bilobate with deep median sulcus and high fold, shell surface capillate, long dorsal median septum.

Type species: *Chonetes flemingi* Norwood & Pratten, 1855b, p. 26 from Pennsylvanian of Texas, OD.

Chonetinella? sp.

Fig. 14

Material: Single ventral valves from JBW 561, 566 and 577 from Member E, Jungle Creek Formation.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Ventral valve from JBW 561 measures 10mm wide and 5.5mm long, with hinge at maximum width, cardinal extremities alate, with preserved spine directed postero-laterally on one side. The sulcus is deep with angle of 40º. The sulcus and lateral shell inside the large ears bear distinct capillae, four or five up to six in 1mm. A small specimen from JBW 577 appears to be congeneric.

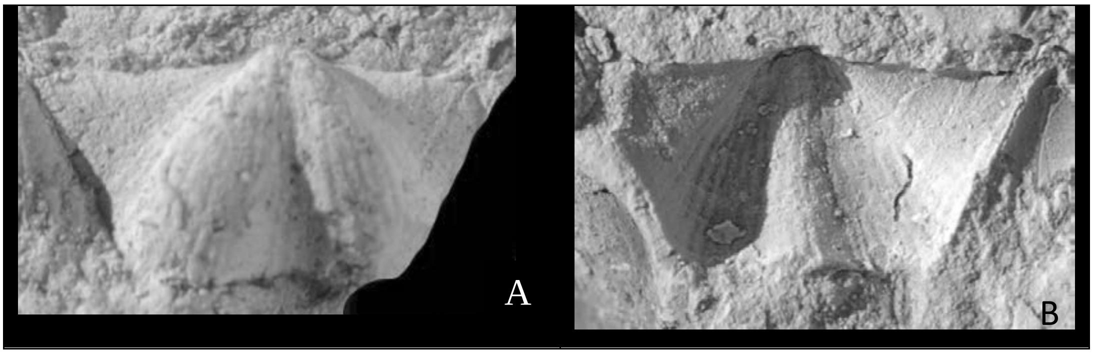


Fig. 14. *Chonetinella*? sp. A, B, external cast and mould of ventral valve GSC 136697 x7 from JBW 561. Member E, Jungle Creek Formation.

Resemblances: The specimens from Member E are similar to *Dyoros* (*Dyoros*) *pseudotrapezoidalis* (Miloradovich, 1949), reported by Shi & Waterhouse (1996) from the "*Yakovlevia transversa*" to *Jakutoproductus verchoyanicus* Zones of the Jungle Creek Formation, but appear to have definite ribs, whereas the younger specimens were considered to be smooth, and apparent ribbing was ascribed to wear of the surface, perhaps contentiously, given that the ventral plicae each side of the sulcus are as strong as those of *Chonetinella* rather than for *Dyoros*. The strength of these undulations strongly suggests identity with type *Chonetinella* rather than type *Dyoros*. *Chonetinella* was described from the younger Permian of the Glass Mountains in Texas (Cooper & Grant 1975), but a number of species ascribed to that genus by Cooper & Grant (1975) are deemed to belong to *Rugaria* Cooper & Grant by virtue of their bundled costae, and the few species that lack bundled costae have a sulcus much shallower than that of *Chonetinella* or the present species. The Early Permian species *C. biplicata* (King) from the Bone Spring and Skinner Ranch Formations is more rounded in outline with much less defined sulcus and less alate cardinal extremities, and *C. costellata* Cooper & Grant (1975, pl. 479, fig. 1-23) from the Neal Ranch Formation differs considerably in shape and sulcus, compared with present material.

Fig. 15. *Dyoros pseudotrapezoidalis* (Miloradovich), cast of dorsal interior GSC 137239 x9 from JBW 549, *Jakutoproductus verchoyanicus* Zone, upper Jungle Creek Formation.

Specimen GSC 137239 from JBW 549 in the *Jakutoproductus verchoyanicus* Zone is the internal mould of a dorsal valve (Fig. 15), with median septum extending for half the length of the shell. It belongs to the taxon identified as *Dyoros* (*Dyoros*) *pseudotrapezoidalis* in Shi & Waterhouse (1996). This particular specimen is moderately close to type *Chonetinella*, but has a shorter and weaker dorsal median septum than in the type species, and there are short possible anderidia figured in Shi & Waterhouse (1996, Fig. 18), whereas such are apparently lacking from type *Chonetinella*.

Subfamily **PLICOCHONETINAE** Sokolskaya, 1960

[Plicochonetinae Sokolskaya in Sarytcheva, Licharew & Sokolskaya, 1960, p. 232].

Diagnosis: Small strongly costellate to costate rugosochonetids, hinge spines oblique, high-angled.

Tribe **RUGARIINI** Waterhouse, 2004a

[Rugariini Waterhouse, 2004a, p. 60].

Diagnosis: Ventral sulcus and low dorsal fold.

Discussion: The tribe is discussed by Waterhouse (2004a, pp. 60-62).

Genus ***Rugaria*** Cooper & Grant, 1969

Diagnosis: Small elongate shells with roundly arched or very narrowly sulcate ventral valve, concave dorsal valve, spines few along hinge and oblique. Costae increase by bifurcation and may be bundled, and bear tiny spines on ventral valve. Ventral median septum, dorsal valve with low median septum and strong socket ridges, no apparent anderidia in the type species and several other species.

Type species: *Chonetes hessensis* King, 1931, p. 61 from the Hess Formation, Taylor Ranch Member (Sakmarian), Texas, OD.

Discussion: *Chonetinella* Ramsbottom is distinguished by its transverse outline, deeper sulcus and simple ribs without fascicles. Genus *Arctochonetes* Ifanova, 1968, type species *Chonetina postartiensis* Ustritsky, 1960b, p. 112 is similar in some respects, but has very fine and even costellae, without bundling, and dorsal accessory septa are very long. *Rugaria* Cooper & Grant, 1969 with its bundled costae is close to *Sulcirugaria* Waterhouse, 1983a, but this latter genus includes intercalated as well as branching ribs, and there are no tiny spines over the ventral ribs. It was initially described from Permian faunas of south Asia. The type species of both genera appear to lack anderidia, as named by Sadlick (1965). Anderidia are missing also from *Plicochonetes* (Racheboeuf 2000, Fig. 270.1c). *Prorugaria* Waterhouse, 1982c is of Upper Carboniferous age in Thailand, and has weakly bundled ribs and possible though feebly developed anderidia. Another related genus is *Nisalarinia* Waterhouse 2004a, p. 58, type species *Rugaria nisalensis* Waterhouse, 1978, p. 60 from the Late Permian of Nepal, which has fine costellae in bundles, and is characterized by the exceptionally long anderidia. *Tethyochonetes* Chen et al. 2000, p. 5 from the Late Permian of south China, similar in some respects to *Fusichonetes* Liao in Zhao et al., 1981, has short stout anderidia. Two subgenera assigned, very dubiously, to genus *Neochonetes* Muir-Wood, show considerable approach. *Neochonetes* (*Nongtaia*) Archbold, 1999 from early mid-Permian of Thailand is a tiny chonetid with bundled costellae, long ventral septum and relatively coarse anderidia. *Neochonetes* (*Zhongyingia*) Shen & Archbold, 2002 from the Late Permian of south China is somewhat similar, with short anderidia. Racheboeuf (2007, p. 2628) commented adversely on the supposed status of various subgenera referred to *Neochonetes* and his criticisms seem well justified. These particular taxa should be dissociated from *Neochonetes*, and are typified by their comparatively coarse and branching or bundled ribs. They differ from the present genus in being less inflated with fewer ribs and more hinge spines, and presence of distinct anderidia. On the other hand *Neochonetes* (*Huangichonetes*) Shen & Archbold (2002, p. 335) from the Late Permian of south China lacks anderidia, and appears to be close to *Rugaria*, but has mutiple bifurcating costae. The presence or absence of anderidia in *Fanichonetes* Xu & Grant, 1994 from the Late Permian of southeast China, is not known. The description mentions only a cardinal process, bifid cardinal process and alveolus, and indeed reports of aspects of its morphology had to be corrected by Racheboeuf (2000, p. 405). The illustration in Xu & Grant (1994, Fig. 16.20) purports to show a dorsal valve, but illustrates a ventral valve. *Waagenites* Paeckelmann, 1930 has strong costae, with few subsidiary ribs. It is not clear from Waagen's figures of various species whether or not anderidia are present. *Striochonetes* Waterhouse & Piyasin, 1970 is somewhat similar externally, but has long anderidia and lateral septa in the dorsal valve, whereas *Waterhousiella* Archbold, 1983a has no more than short high anteridia.

The varying presence or absence and strength in anderidia in these genera of somewhat similar external appearance, and rather similar branching ribs raises the question of interrelationships, and may be taken to indicate that there were two evolutionary streams, one with prominent anderidia, involving *Schistochonetes, Prorugaria?, Waterhousiella*, *Tethyochonetes, Nisalarinia, Nongtaia* and *Zhongyingia* on the one hand, and a second without anderidia, involving *Rugaria, Sulcirugaria,* and *Huangichonetes*. But there is need for hesitation. Species of *Rugaria*, including the type species *Chonetes hessensis* King, 1931, do not have prominent anderidia: indeed none were described or figured by Cooper & Grant (1969, p. 4; 1975, p. 1295) or Rachebouef (2000, p. 411, 413, Fig. 270a-d), but Racheboeuf (2007, p. 2636) regarded the presence or absence of such plates as within the morphological range of the genus *Rugaria*. The species described as *Chonetinella magna* Cooper & Grant (1975, pl. 479, fig. 24-45) has bundled ribs very like those of *Rugaria*, but has well developed anderidia. This on the one hand might imply a generic difference from *Rugaria*, but on the other hand could indicate that the presence of absence of anderidia is, in some instances, a matter of shell maturity or specific variation, just as stated by Racheboeuf. Many externally similar species described by Cooper & Grant (1975) do not show internal detail, so that it is not possible to definitely rule out generic distinction or variation on the presence or absence of anderidia for this particular group. Cooper & Grant (1975) referred the species *magna* to *Chonetinella* Ramsbottom, 1952, but type *Chonetinella* does not have bundled costae, unlike those of type and other *Rugaria*.

Whether there are further possible morphological aspects that would allow generic distinction may now be discussed. One outstanding feature of type *Rugaria, R. hessensis* (King), is the presence of tiny spines over the ventral valve, clearly visible in Cooper & Grant (1975, pl. 498, fig. 2), and also for *R*. *crassa* Cooper & Grant (1975, pl. 496, fig. 17), and found in a new species from Canada, as described below. Figures for *Chonetinella magna* Cooper & Grant (1975, pl. 479, fig. 24-45) do not clearly indicate the presence of ventral body spines, although they could be present as very slender disruptions to the ribs. A further distinction between the species *magna* and the species like type *Rugaria* on the basis of ribbing, ventral body spines and no prominent anderida is the evenly concave or very gently folded dorsal valve of *Rugaria hessensis*, compared with a high and narrow dorsal fold in *Chonetinella magna* and allied forms. But the difference in fold-sulcus between the various taxa is not great.

Early Carboniferous genera have bundled but finer ribs, with thin anderidia and short ventral myophragm, but no dorsal septum. These involve *Riosanetes* Martínez-Chacón & Winkler Prins (2000, p. 226) and *Aitegounetes* Chen & Shi (2003, p. 138), and are classed as Riosanetinae Martínez-Chacón & Winkler Prins, 2000.

Rugaria arcula n. sp.

Fig. 16 - 19

Derivation: arcula – small box, casket for jewels, Lat.

Diagnosis: As for genus, very small, weakly bundled costae and slender ventral sulcus.

Holotype: GSC 136702, here designated.

Material. Some twenty complete specimens from JBW 449 and 450; four specimens from JBW 169 and some ten specimens with valves conjoined from JBW 181, dorsal valve from JBW 187.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

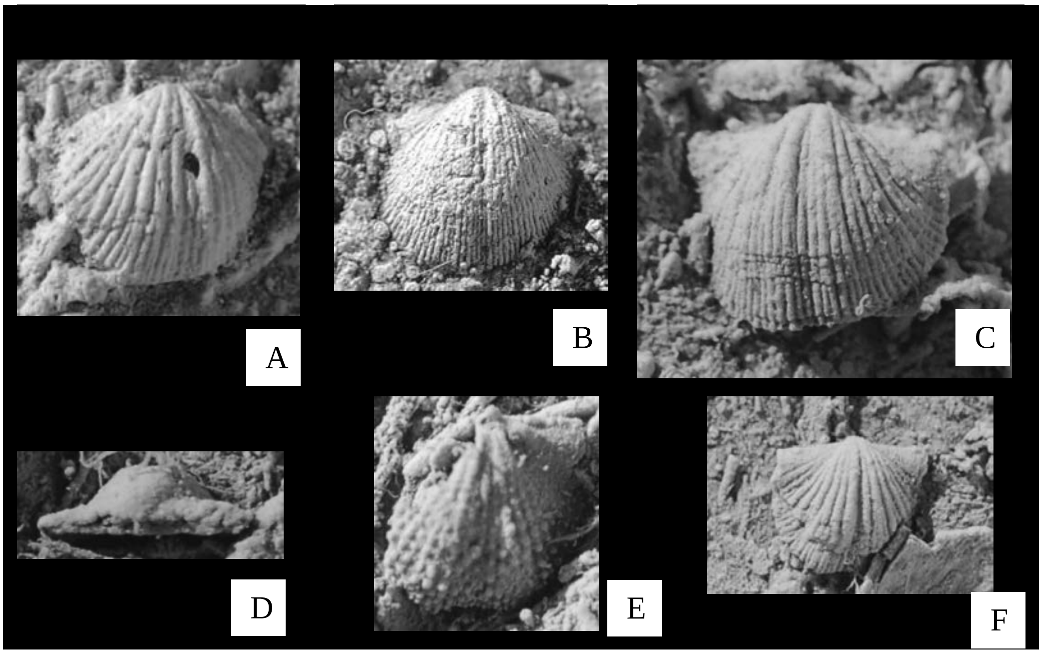


Fig. 16. *Rugaria arcula* n. sp. A, ventral valve GSC 136706. B, ventral valve GSC 136701. C, ventral valve holotype, GSC 136702. D, posterior aspect of specimen with valves conjoined, ventral valve on top, GSC 136703. E, dorsal interior, GSC 136704. F, ventral valve GS 136705. Specimens x6 from JBW 450. Member A, Jungle Creek Formation.

Description: Shells small, one specimen measuring 7mm wide, 5.8mm long and 3mm high, another measuring 6.5mm wide, 5mm long and 2mm high. Hinge at maximum width with alate cardinal extremities, moderately developed interareas, ventral interarea postero-dorsally inclined, almost in plane of commissure, dorsal interarea lower and at high angle to commissure. Ventral valve arched, with narrow median sulcus commencing at beak or just in front, and this may disappear anteriorly, or persist without further deepening and widening; narrow distinct but subdued dorsal fold on only some specimens. Ventral ornament of radial fascicles with some four pairs prominent posteriorly, strengthening forward and bifurcating into two or three finer ribs, may bifurcate anteriorly, four to five ribs in 1mm at anterior margin. Unbundled ribs lie over the lateral posterior shell. Tiny body spines arise from some ventral costae, and three to four spines emerge along hinge. Dorsal ribs also bifurcate, less bundled, no spines.

Ventral septum high and short, ending just in front of teeth. Dorsal interior with slender cardinal process, wide alveolus and two short strong ridges extending laterally within ears subparallel to hinge. Median septum indistinct, between two smooth adductor platforms, without clearly developed anderidia; shell floor bears well defined radial rows of pustules in one specimen, less aligned in another.

Resemblances: *Rugaria hessensis* (King, 1931), extensively figured by Cooper & Grant (1975), from the Taylor Ranch Member of the Hess Formation in west Texas, is slightly more transverse with less well defined sulcus, and *R. crassa* Cooper & Grant (1975) from the Decie Ranch Member of the Skinner Ranch Formation is also more transverse with poorly defined sulcus.

Fig. 17. *Rugaria arcula* n. sp. ventral valves GSC 137240-137242 (numbered from top to bottom) and partly concealed internal dorsal valve GSC 137243, from JBW 449 x8. Member A, Jungle Creek Formation.

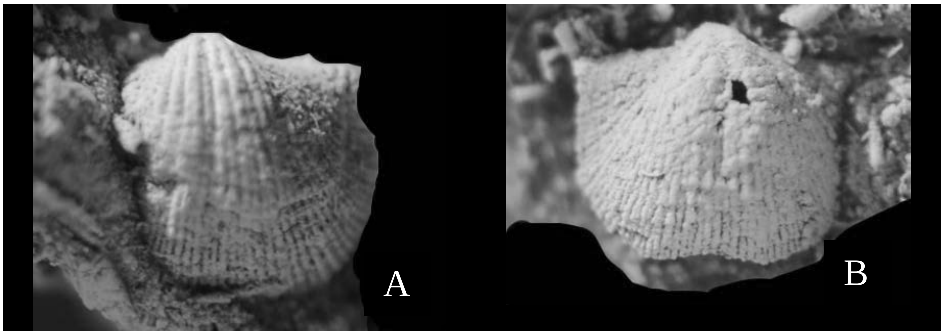


Fig. 18. *Rugaria arcula* n. sp. A, ventral valve GSC 137311 x6 from JBW 449. B, ventral valve 137310 x6 from JBW 450. Member A, Jungle Creek Formation.

There is considerable approach to specimens from the *Uddenites*-bearing shale of the Gaptank Formation which Cooper & Grant (1975, p. 1277, pl. 479, fig. 46-67) called *Chonetinella parva*. The generic similarity of *parva* to *Chonetinella* is dubious, because the shape is elongate and not strongly alate and the deep sulcus and high fold typical of *Chonetinella* are lacking, and its ribs are branching and fascicled, whereas those of type *Chonetinella* lack obvious fascicles (Ramsbottom 1952, p. 13), as in the type species *Chonetes flemingi* Norwood & Pratten (1855b, p. 26). The interior is not shown. The shell described as *Chonetinella biplicata* (King, 1931) by Cooper & Grant (1975, pl. 478, fig. 13-46) provides a good Permian example that externally is closer to the type species of the genus, although with a much narrow sulcus and fold than in type *Chonetinella*, and the species lacks fascicles and has high interadductoral ridges in pl. 478, fig. 33, equivalent to anderidia.

Fig. 19. *Rugaria arcula* n. sp., dorsal view of a somewhat obscure specimen GSC 137357 x8 from JBW 450, showing well formed dorsal ribs and absence of median fold. Member A, Jungle Creek Formation.

The species described as *Chonetinella magna* by Cooper & Grant (1975, p. 1276, pl. 479, fig. 24-45) from the Bone Spring Formation is larger, but otherwise close and shows a short dorsal median septum in front of an alveolus, and short anderidia, as recognized by Cooper & Grant (1975). They do not project beyond the adductor field. Somewhat similar species were described as *Chonetinella crassiparva* Cooper & Grant (1975, p. 1274, pl. 500, fig. 1-10) from the upper Neal Ranch Formation, with coarse and occasionally branching ribs, and narrow high dorsal fold, and *C. ciboloensis* Cooper & Grant (1975, p. 1272, pl. 500, fig. 41-49) from the Cibolo Formation, with less bundled ribs. Both these species have a better defined ventral sulcus. The interior of a dorsal valve was illustrated for *crassiparva* by Cooper & Grant (1975, pl. 500, fig. 10) to show a short septum and long socket (prosocket) ridges, and anderidia were recorded as small and protruding.

Genus ***Sulcirugaria*** Waterhouse, 1983a

Diagnosis: Transverse to subelongate with large ears and well formed ventral sulcus; costae strong and increasing by both intercalation and bifurcation, inner costae associated in fascicles. Row of ventral hinge spines and no body spines. Ventral interior with short septum, teeth and adductor scars, dorsal valve with low medium septum and no anderida or accessory septa.

Type species: *Sulcirugaria subquadrata* Waterhouse, 1983a, p. 112 from Pija Member, Senja Formation (Changhsingian), Nepal, OD.

Discussion: *Sulcirugaria* is very close to *Rugaria* Cooper & Grant (1969, 1975), a genus from the Permian of Texas, and distinguished by its very shallow and narrow ventral sulcus, body spines over the venter (see Cooper & Grant 1975, pl. 498, fig. 2), and mode of costal increase, those of *Rugaria* increasing only by bifurcation, those of *Sulcirugaria* increasing by bifurcation and intercalation. Both genera have similar fasciculate costae, and row of hinge spines, and anderidia if present are inconspicuous or probably absent, at least in the type species. The possible Canadian occurrence is represented by a single ventral valve with no hinge spines or interior preserved, so that it can only be tentatively identified from shape and costation. It approaches the Nepal occurrences in shape, but lacks any sign of tiny possible spines, because the specimen is only an internal mould.

Taxonomy: Racheboeuf (2000, p. 413) mistakenly cited *Sulcirugaria transversa* Waterhouse as type species of *Sulcirugaria*, but illustrated the correct type species *S*. *subquadrata* (Racheboeuf 2000, Fig. 270.4a-c), calling it *transversa.*

***Sulcirugaria*?** sp.

Fig. 20

Material: A ventral valve from JBW 694.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimen measures 20mm in width, 11mm long, and 2mm high, transverse, with subalate cardinal extremities at maximum width and large ears. The umbo is low and broad with angle of 110º, the interarea low, and the ventral sulcus commences on the beak and widens at an angle of 30º. Ornament consists of well formed ribs with rounded crests, associated in four fascicles each side of the sulcus, and in the fascicles some costae are intercalated and others branch. Further costae lie laterally and cover the ears, and two costae lie within the sulcus, close to the mid-line, and with median rib. The sulcus widens to incorporate much of the inner pair of plicae. Micro-ornament is not preserved, but the specimen shows traces of growth increments.

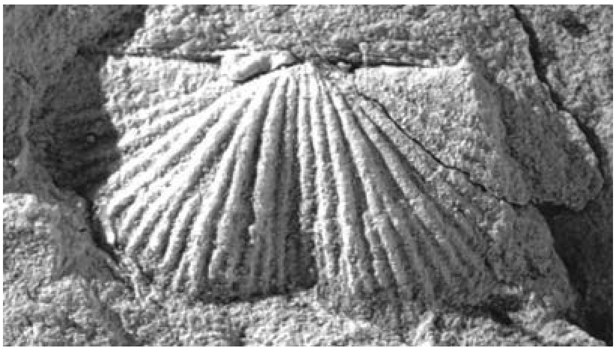


Fig. 20. *Sulcirugaria*? sp. ventral valve GSC 136706 x3 from JBW 694. Member A, Jungle Creek Formation.

Resemblances: The specimen is characterized by the number of costae that increase by both splitting and intercalation, and the well defined ears and well formed sulcus. In general ornament it is closest to *Sulcirugaria transversa* Waterhouse (1983a, p. 114, pl. 1, fig. 3-9; 2004a, p. 63, pl. 2, fig. 1, text-fig. 20) from the Pija Member of Changhsingian age in Nepal, but the sulcus is slightly narrower and deeper. A ribbed chonetid from the "*Yakovlevia transversa"* Zone was identified as *Rugaria*? by Shi & Waterhouse (1996, p. 54, pl. 4, fig. 7, 8), but differs slightly in shape from *Rugaria arcula* n. sp. and has stronger ribs. With its well-formed ventral sulcus and strongly branching as well as intercalated ribs, it approaches *Sulcirugaria* Waterhouse, and could well prove to belong to the same species as the present specimen. Lack of information about the interior hinders close assessment, and the nature of the ventral exterior is uncertain, so that the presence or absence of ventral spinules cannot be ascertained.

The otherwise somewhat comparable genus *Rugaria* Cooper & Grant, 1969) has well preserved body spines over the ventral valve, especially well illustrated in Cooper & Grant (1975, pl. 498, fig. 2) for *R. hessensis* (King), and also indicated for *R. crassa* Cooper & Grant (1975, pl. 496, fig. 17). No ribs arise by intercalation.

Subfamily **SVALBARDIINAE** Archbold, 1982

[Subfamily Svalbardiinae Archbold, 1982, p. 4].

Diagnosis: Small to medium-sized externally smooth rugosochonetids, with hinge spines orthomorph-oblique.

Genus ***Komiella*** Barchatova, 1970

Diagnosis: Widely rectangular in outline, hinge wide with tiny if any ears, gentle and comparatively narrow sulcus and fold, spines oblique, no observable brachial ridges.

Type species: *Chonetes omolonensis* Licharew, 1934 from Omolon Horizon (Guadalupian) of Kolyma-Omolon, north-east Russia, OD.

Discussion: The present species is assigned to *Komiella*, a genus discussed by Racheboeuf (2000) without any illustration of the types, although these were well figured by Licharew (1934). Shape and ornament agree with attributes of the type species, the anderidia are well developed, and the brachial ridges appear to be absent, as pointed out by Shi & Waterhouse (1996).

Present material is close in *Leurosina* Cooper & Grant, 1975 in many aspects, with its brachial ridges bearing numerous prominent pustules in the mature shell. The Canadian species is larger and older than any species so far ascribed to that genus, and has a narrower sulcus and fold. *Leurosina* is very close to *Lissochonetes* Dunbar & Condra, 1932, and was differentiated by Cooper & Grant (1975, p. 1260) through its less pointed cardinal extremities, thicker shells, more strongly developed internal septa, and the way the anterior shell is broadly deflected in a dorsal direction rather than being sulcate. The outline of *Lissochonetes* tends to be less subrectangular. Such differences are not strong, because the strength of the septa may depend on substrate, maturity of species and geographic differences. The shape, including cardinal extremities, of individuals vary, to the extent that some *Lissochonetes* (see Mudge & Yochelson 1962, pl. 13, fig. 20) are like *Leurosina*, and the anterior margin also varies somewhat. The material identified by Dunbar & Condra (1932, p. 175, pl. 20, fig. 46-52) from the Hughes Creek Shale of Nebraska as *Lissochonetes geinitzianus senilis* is very like *Leurosina* in appearance. Overall it may be argued that *Leurosina* is at best a subgenus of *Lissochonetes*, a suggestion to be tested through further assessment, and consideration of what exactly distinguishes the two taxa. Racheboeuf (2000) has drawn attention to the differing views over the validity of distinctions between *Komiella* and *Lissochonetes* Dunbar & Condra, 1932.

Sulcataria Cooper & Grant, 1969 has a smooth shell with deeply sulcate ventral valve and high fold, with flattened margins and brachial shield ridges.

Komiella bitteri n. sp.

Fig. 21 - 23

Derivation: Named for Peter von Bitter.

Diagnosis: Wide hinge and large ears.

Holotype: GSC 136710, here designated.

Material: Six ventral valves, six dorsal valves and fragments from JBW 451**,** one ventral valve each from JBW 644 and 646.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimens transverse, hinge wide, at maximum length or slightly narrower than shell near mid-length, cardinal extremities rarely obtuse, usually weakly alate, ventral umbo small. A shallow and very broad sulcus with angle of 25**-**35**º** commences anteriorly, with corresponding very low and broad dorsal fold in an otherwise concave dorsal valve. The surface is smooth apart from seven to eight low commarginal growth-steps, but slight wear brings out fine capillae, seven to eight in 1mm anteriorly. A row of spines emerges from the ventral interarea, estimated to number eight to ten each side of the umbo, the basal core of each spine sloping inwards towards the umbo through the interarea and outwards from the commissure.

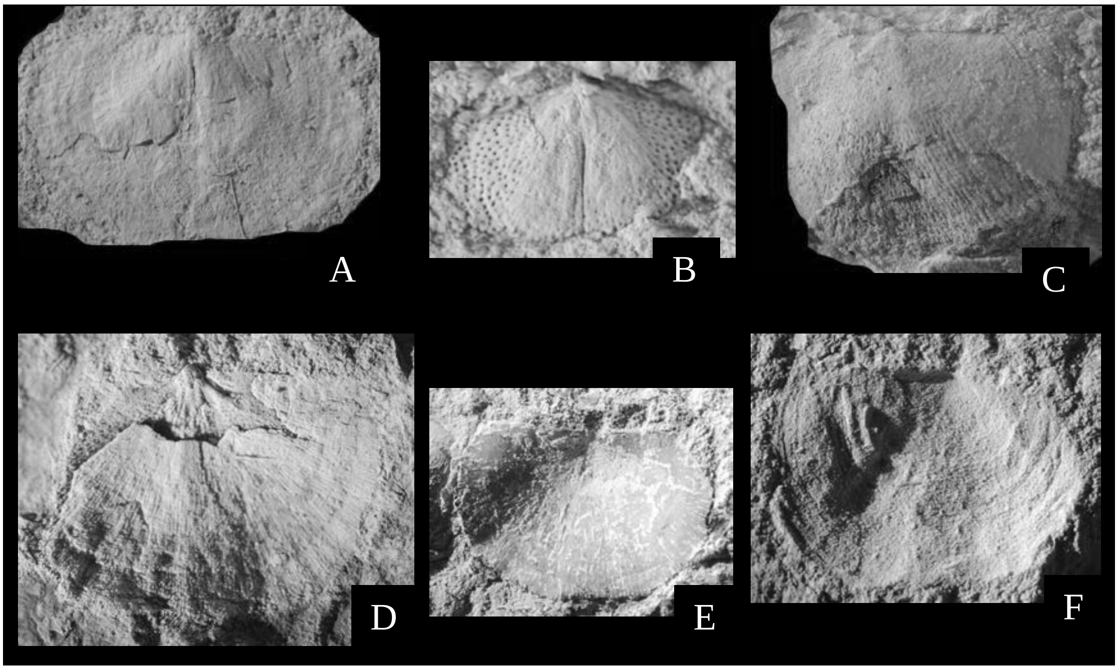


Fig. 21. *Komiella bitteri* n. sp. A, cast of ventral valve holotype, GSC 136710, x 2.5. B ventral internal mould, GSC 136712, x3. C, cast of ventral valve, GSC 136707, x2. D, dorsal valve, GSC 136708, x2.5. E, dorsal valve, GSC 136709, x3. F, cast of dorsal valve, GSC 136711, x2.5. From JBW 451, Member A, Jungle Creek Formation.

Two teeth are developed, one each side of a very long median septum, which is broad posteriorly, with gently convex crest, dividing small adductor scars and larger moderately impressed diductor scars. Vascular trunks are prominent in larger specimens, extending to mid-length. Much of the floor bears sturdy pustules of comparatively uniform size, not arranged in bands. In the dorsal valve, the cardinal process is broad and bilobed, and socket plates are short, posteriorly curved and high. The median septum extends well past mid-length, but is weakly defined in front. There are two short but high anderidia, but adductor ridges are not well defined, and brachial scars are not visible. The floor is marked by radially aligned pustules, two to three rows in 1mm anteriorly.

Resemblances: There is considerable approach in shape to *Komiella* Barchatova, 1970. The type species *Komiella omolonensis* (Licharew, 1934, p. 11, pl. 9, fig. 1-3, 5-7), with further synonymy provided in Shi & Waterhouse (1996,

p. 51), has a narrower ventral sulcus and no sign of a dorsal fold, and the ventral adductor ridges are better developed. The species is supposedly represented in the younger beds of the Jungle Creek Formation (Shi & Waterhouse 1996, pl. 3, fig. 12-23), but the Jungle Creek material is slightly more flattened across the venter, and therefore belongs to a different species. The ventral valve is more transverse, and pseudopunctae are more strongly developed (Shi & Waterhouse 1996, pl. 3, fig. 16). Internal and other features of their specimens appear consistent with *omolonensis*, so that the species is named *Komiella sarytchevae* n. sp., distinguished by its more arched venter, and named for T. G. Sarytcheva. The holotype is GSC 96891 from GSC loc. 53856 figured by Shi & Waterhouse (1996, pl. 3, fig. 21, 23), here selected partly because a number of topotype specimens are also available.

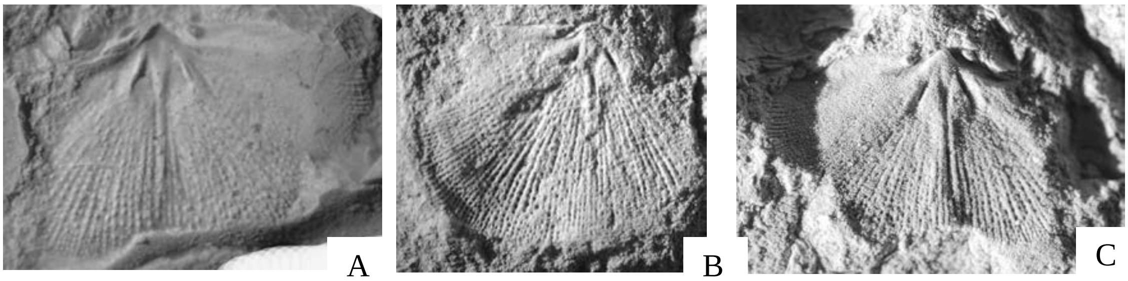


Fig. 22. *Komiella bitteri* n. sp. A, C, cast and internal mould of dorsal valve, GSC 136713, x3. B, mould of dorsal interior, GSC 136714, x3. From JBW 451, Member A, Jungle Creek Formation.

Leurosina Cooper & Grant, 1975, p. 1260 is close in shape and has a broad sulcus and low fold, and short but high anderidia. The genus appeared in the Bone Spring Formation and ranged as high as the Cherry Canyon Formation in Texas, United States. The cardinal extremities are not alate. Compared with Canadian species, none of the species from Texas are exactly the same in shape, and all are smaller. The dorsal papillae become larger in fully mature specimens of *Leurosina*, unlike the present material, and as in *Komiella*, brachial ridges are weakly and usually not defined. *Lissochonetes geinitzianus senilis* Dunbar & Condra (1932, p. 175, pl. 20, fig. 46-52) from the Hughes Creek Shale of Nebraska is somewhat smaller, with broader sulcus and fold, but otherwise close.

Fig. 23. *Komiella bitteri* n. sp., cast of internal dorsal valve, GSC 136716, x3. From JBW 451, Member A, Jungle Creek Formation. Although the specimen is at late maturity, brachial ridges do not appear to be developed, but brachial shields are represented by raised oval areas. There are no large endospines.

There is external similarity in shape and sulcus-fold and smooth shell to *Undulella* Cooper & Grant (1969) from upper Cisuralian and lower Guadalupian of west Texas, but the spines along the hinge in this genus are few and are orthomorph. *Dyoros* (*Lissosia*) Cooper & Grant, 1975, p. 1241 is closer in this regard, but the various species as described from the Cathedral Mountain and Road Canyon Formations and Willis Ranch Member (Kungurian, Roadian) are more transverse and subalate.

The dorsal valve from JBW 561, as described below, is close, but has a dorsal fold more anteriorly placed.

***Komiella*? sp. A**

Fig. 24

Material: Two ventral valves and a dorsal valve, poorly preserved, from JBW 69.

Stratigraphic and biostratigraphic level: Member B, Jungle Creek Formation. *Ogilviecoelia initiatus* Zone.

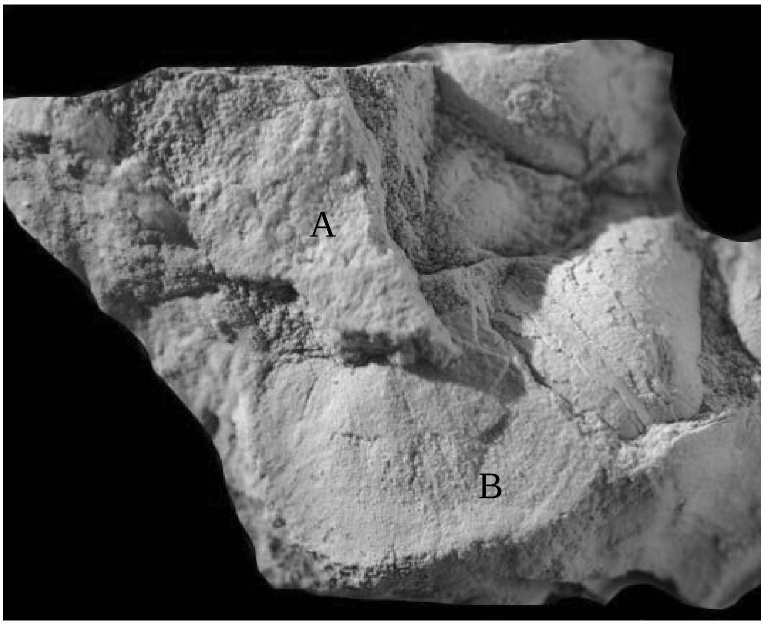


Fig. 24. *Komiella*? sp. A, showing A, dorsal internal mould, now disintegrated, and B, ventral exterior, GSC 137442 x6, from JBW 69. Member B, Jungle Creek Formation.

Description: The figured ventral valve is nearly 11mm wide and a little over 7mm long, gently convex, and 2mm high. The umbo with umbonal angle of approximately 100º protrudes a little beyond the hinge, which is wide, with obtuse cardinal extremities. Unfortunately the nature of the beak terminus and any interarea if present are not shown, and no hinge spines are visible. Whether a shallow sulcus or low fold is present is not clear, because the specimen is slightly deformed. Apart from deformation, the surface is smooth, without visible spines or definite micro-ornament, and internally only the anterior part of two vascular trunks is preserved. Another specimen could have been part of the interior of a dorsal valve, with two suboval moderately impressed adductor scars, and large pustules laterally. An obscure and discontinuous dorsal median septum was present, but no brachial shields were visible. This specimen later disintegrated, so that only the photographic record remains.

***Komiella* sp. B**

Fig. 25

Material: A dorsal valve from JBW 561.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

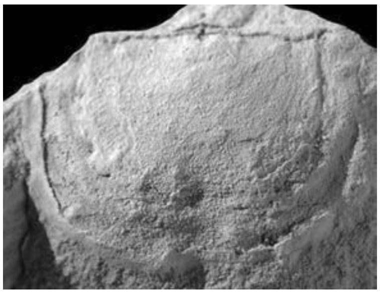


Fig. 25. *Komiella* sp. B, external mould of dorsal valve, GSC 136715, x3. From JBW 561, Member E, Jungle Creek Formation.

Description: The dorsal valve measures nearly 15mm in width and just over 10mm in length. The valve is comparatively smooth apart from fine dimples and pustules that appear to have resulted from weathering of the external surface. There is a low anterior and narrow fold.

Resemblances: The fold of this specimen is more anteriorly placed than in the species from Member A, described as *Komiella bitteri* n. sp. and this also appears to be true of *Komiella omolonensis* (Licharew) and *K. sarytchevae* n. sp. *Sulcataria latisulcata* Cooper & Grant (1975, pl. 478, fig. 57-68) from the Neal Ranch Formation is close but has a broader dorsal fold, whereas *S. rostrata* (Dunbar & Condra, 1932, p. 150, pl. 19, fig. 1-3, 5-7), also figured from the Graham Formation of United States by Cooper & Grant (1975, pl. 480, fig. 37-55), has a slightly narrower fold. The present specimen differs from *Sulcataria* in having a slightly narrower and more anteriorly placed dorsal fold, but the lack of the ventral valve and dorsal interior makes any identification no better than conjectural.

There is some similarity in shape to the specimen figured as *Chonetes variolatus* (d'Orbigny) from the Paren Horizon (Kasimovian) of northeast Russia by Zavodowsky (1970, p. 76, pl. 23, fig. 8a, b), but the Russian specimens are ribbed, and *variolatus* belongs to *Neochonetes* Muir-Wood.

Genus ***Lissosia*** Cooper & Grant, 1975

Diagnosis: Wide hinge and highly transverse shell.

Type species: *Dyoros* (*Lissosia*) *concavus* Cooper & Grant, 1975, p. 1241 from the Word Formation (Wordian) of Texas, OD.

Discussion: *Lissosia* was treated as a subgenus of *Dyoros* by Cooper & Grant (1975), justifiably because of its large ears. The sulcus and fold developed late in maturity in some of the constituent species, and large endospines typical of *Dyoros* developed only late in ontogeny. The shells approach *Lissochonetes* Dunbar & Condra, 1932, but shells are thicker and the ventral valve more highly arched. The type species of this latter genus, *Chonetes geinitzianus* Waagen, 1884, p. 621, from Upper Pennsylvanian of Nebraska, is transverse and weakly concavo-convex with smooth shell, very shallow sulcus and orthomorph oblique hinge spines. The ventral median septum is long.

Assignment of *Chonetes alatus* Stuckenberg to *Lissosia* is uncertain, because the interior of the species to which the Canadian specimen is assigned is not known. It is more transverse that any known *Lissochonetes* and does approach *Lissosia vagabundus* Cooper & Grant in shape, but lacks any clear sign of sulcus and fold. Its generic position and subfamily affinities remain to be consolidated.

Lissosia*? *alatus (Stuckenberg, 1898)

1898 *Chonetes alatus* Stuckenberg, p. 353, pl. 5, fig. 1a, b.
1902 *C. alatus* – Tschernyschew, pp. 230, 594, pl. 56, fig. 8.
1957 *Paeckelmanella* aff. *Chonetes alatus* – Cooper, p. 25, pl. 1C, fig. 8.
1971 "*Lissochonetes*" aff. *alatus* – Bamber & Waterhouse, pl. 12, fig. 3.

Diagnosis: Very transverse with no ventral sulcus.

Holotype: Sole specimen figured by Stuckenberg (1898), through monotypy, from Early Permian of Urals.

Material: A ventral valve GSC 26916 from GSC locality 56946, in section 116F-16, figured in Bamber & Waterhouse (1971, pl. 12, fig. 3), and a dorsal valve from JBW 559.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: The ventral valve is markedly transverse, with no sulcus and extremely alate cardinal extremities.

Resemblances: The species *alatus* is highly distinctive, and has been reported from the Early Permian of the Urals and central Oregon, as well as Member E of the Jungle Creek Formation. *Lissochonetes* is similar in its glabrous shell, but is shaped differently, with much less acute and extended cardinal extremities. It seems possible that a different and possibly new genus is involved, but more needs to be known about the interior.

Order PRODUCTIDA Waagen, 1883

[Nom. transl. Waterhouse 2010, p. 9 ex Suborder Productacea Waagen, 1883, p. 447. The order has been widely credited to Sarytcheva & Sokolskaya 1959, p. 182, but it is proposed that authorship of ordinal categories should follow the procedure set forward for families, with any change in rank not affecting the name of the original author throughout the range of proposed family or ordinal rankings (Waterhouse 2010).

Suborder PRODUCTIDINA Waagen, 1883

[Nom. correct. Muir-Wood 1965b, p. 448 pro Suborder Productacea Waagen, 1883, p. 447].

Diagnosis: Shells normally without interareas, teeth and sockets. As for Chonetidina and Strophalosiidina, ventral and dorsal valves differ but not hugely so, unlike those of Oldhaminiidina Williams, 1953.

Infrasuborder PRODUCTIMORPHI Waagen, 1883

[Nom. transl. Waterhouse 2010, pp. 10, 11 ex Order Productacea Waagen, 1883, p. 447].

Diagnosis: Shells varied in morphology, arose from various Productelloidea, often with ribs and/or commarginal growth steps or rugae over both valves, spines of general or moderately specialized nature; muscle impressions smooth, dendritic or striate.

Discussion: Superfamily Productelloidea is incorporated in the suborder but excluded from the infrasuborder, because it is fully strophalosiform in many attributes and was ancestral to Productimorphi (see Waterhouse 2013).

Superfamily **OVERTONIOIDEA** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 2013, p. 49 ex Overtoniinae Muir-Wood & Cooper, 1960, p. 183].

Diagnosis: Genera productiform in lack of teeth and sockets, interareas, umbonal attachment scar and often pseudodeltidium. Shells small, without differentiated spines or marginal ridges, spine bases may be prolonged posteriorly, ribbing subdued or absent, rugation strong to fine or absent, trail simple and not geniculate. Muscle impressions commonly smooth, cardinal process commonly bifid, even in members of Upper Permian age.

Family **OVERTONIIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 2002b, p. 11 ex Overtoniinae Muir-Wood & Cooper, 1960, p. 183].

Diagnosis: Commarginal ornament well developed on both valves, radial ornament subdued or lacking. Spines on both valves or only ventral valve, subuniform in size except for a few distinctive genera, and arranged in quincunx, with short or no extended bases. No interareas, teeth or buttress supports, adductor scars smooth as a rule and may become dendritic in later ontogeny, brachial shields tend to be productiform, low to moderately defined cardinal ridges, dorsal endospines fine and numerous.

Subfamily **OVERTONIINAE** Muir-Wood & Cooper, 1960

[Overtoniinae Muir-Wood & Cooper, 1960, p. 183].

Diagnosis: Moderately strong spines arranged in commarginal rows on both valves as a rule. Corpus cavity deep, prominent dorsal adductor scars, low to moderately well formed marginal ridges especially in dorsal valve, dorsal internal pustules small.

Discussion: There is a weak suggestion of lateral buttress plates in *Overtonia* and *Fimbrinia* (Muir-Wood & Cooper 1960, pl. 46, fig. 8, 20), and in *Fimbrininia transversa* (Shi & Waterhouse, 1996, pl. 4, fig. 19), but the appearance seems insignificant, and none are shown in the silicified material of *Fimbrinia* that was figured by Brunton (1966, pl. 9, fig. 7-9, pl. 10, fig. 2, 3). *Jakutella* Abramov, 1970 has elongate ventral spine bases in quincunx posteriorly and more or less in rows anteriorly, and fine dorsal spines interspersed with dimples. It is of Moscovian and Kasimovian (Upper Carboniferous age) in Yakutsk, northeast Russia. *Overtoniina* Grunt in Grunt & Dmitriev, 1973 is supposed to have broad costae over the trail according to Brunton et al. (2000, p. 464). But none have been figured (Grunt in Grunt & Dmitriev 1973, pl. 5, fig. 8, 9, fig. 19; Brunton et al. 2000, Fig. 308.1a-d), and Grunt (op. cit., pp. 94, 96) stated that "the trails of both ventral and dorsal valves are smooth, sometimes with weak ribs and fine growth lines, and fine spines" as verified by e-mail. Low broad pustules in commarginal rows over the ventral valve suggest that the genus is overtoniin.

Genus ***Fimbrininia*** Waterhouse, 2013

Diagnosis: Subelongate shells with sturdy spines emerging from the crests of commarginal rugae over ventral valve. Dorsal ornament of prominent dimples in quincunx, as well as numerous spines.

Type species: *Fimbrininia spinosa* Waterhouse, 2013, p. 52 from Jungle Creek Formation (Asselian), Yukon Territory, OD.

Discussion: This genus is very closely related in most aspects to *Fimbrinia* Cooper, 1972, based on *Overtonia plummeri* King, 1938 from the Gaptank Formation (his *Uddenites*-bearing Shale Member) and the Neal Ranch Formation of west Texas, United States. One of the chief difference lies in the ventral spines. These emerge from the crests of the commarginal rugae or close by in the present form, whereas the spine bases are stronger and longer, emerging from the interspaces or treads between the rugal crests in *Fimbrinia*, as illustrated by R. E. King (1931, pl. 20, fig. 1-3), R. H. King (1938, pl. 39, fig. 19-22), Muir-Wood & Cooper (1960, pl. 46, fig. 1-9), Cooper & Grant (1975, pl. 311, fig. 5-14) and Brunton et al. (2000, Fig. 283.2a-e). Texan forms such as *Fimbrinia* spp. from the Cibolo Formation and Lenox Hills Formation are typical *Fimbrinia*, as is possiby *F. ovata* Cooper & Grant, 1975 from the Bone Spring Formation. A species from the Ettrain Formation in Yukon Territory has spines of this character. There is a little variability in the spines, but the differences are reinforced by differences in the dorsal ornament, where dimples and pustules are much less conspicuous in type *Fimbrinia* (see Brunton et al. 2000, Fig. 283.2b, 2d for *Fimbrinia*, compared with Fig. 27E, 29A, B herein for *Fimbrininia*). Various Russian species are congeneric with the Canadian genus. Carter & Poletaev (1998, p. 123) have drawn attention to a possibly unusual ?*Fimbrinia borealis* Carter & Poletaev from Ellesmere Island, Canadian Arctic Archipelago. In this species, the ventral spines arise from the crest of the rugae, as in *Fimbrininia*. On the dorsal valve, commarginal rugae are strong, but spines characteristic of the genus are not developed (see p. 455), and the species is type of genus *Fimbrinusia* Waterhouse, 2013.

Fimbrininia sp.

The external mould of a dorsal valve from JBW 19, Member B, Jungle Creek Formation. The specimen is too incomplete to allow specific recognition. *Ogilviecoelia initiatus* Zone.

Fimbrininia spinosa Waterhouse, 2013

Fig. 27 - 29

2013 *Fimbrininia spinosa* Waterhouse, p. 52, Fig. 2.3.

Diagnosis: Comparatively transverse shells with some twelve spines along each of the commarginal rugae of the ventral valve.

Holotype: GSC 133266, Member E (Asselian), Jungle Creek Formation, Ogilvie Mountains, Yukon Territory, Canada, figured as Waterhouse (2013, Fig. 2.3A) OD, and herein, Fig. 27A, OD.

Material: For Member E, single ventral valves from JBW 99 and 561, five ventral valves from JBW 539 and 577, three ventral valves from JBW 580, twelve ventral valves and two specimens with valves conjoined from JBW 581. From Member D, a ventral valve each from JBW 17, 68 and 72, a dorsal valve from JBW 73, a dorsal and ventral valve from JBW 762, seven ventral valves and a dorsal valve from JBW 522, two ventral valves and three dorsal valves, as well as seven fragmentary ventral valves and seven dorsal valves, from JBW 549. One ventral valve from JBW 17 and obscure fragments from JBW 189, 444, 522 and 550 in the D band have rather coarse spine bases and not very high rugae: otherwise they are difficult to compare, being so incomplete.

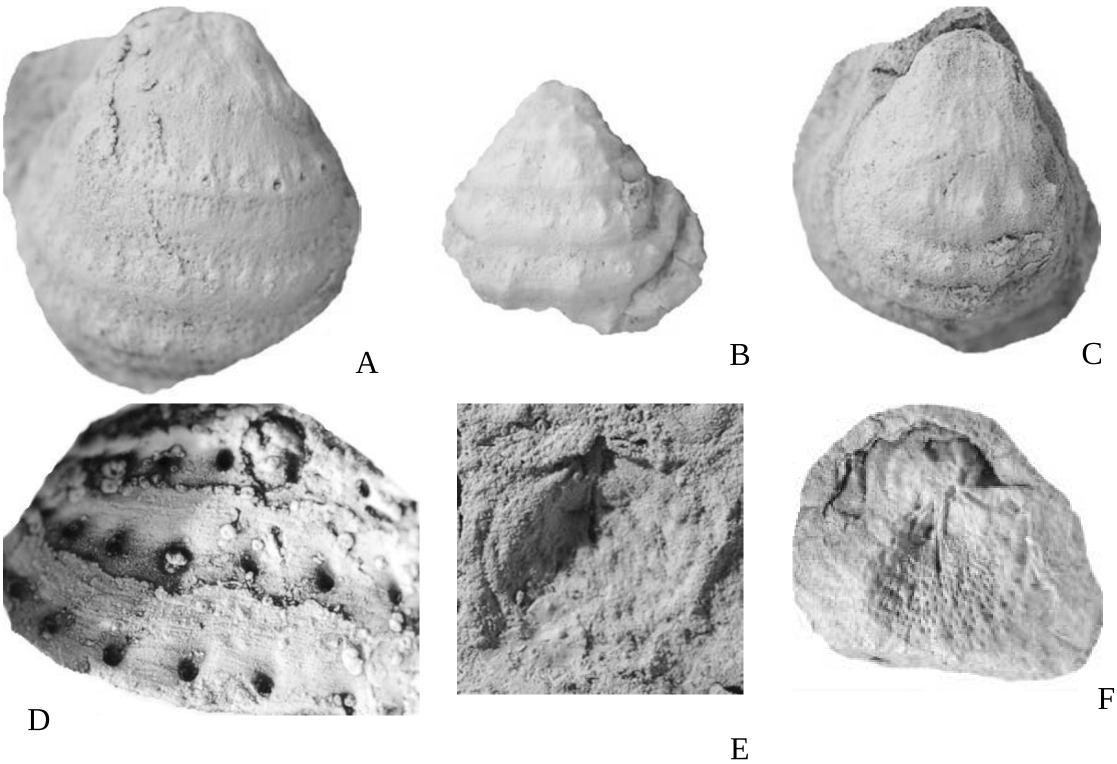
Stratigraphic and biostratigraphic levels: Members D and E, Jungle Creek Formation. *Rugivestigia commarginalis* Zone and *Ogilviecoelia shii* Zone.

Description: Shell large for genus, up to 17mm long, 19mm wide and 8mm high, with incurved prominent ventral umbo, steep posterior walls, large ears which are weakly alate with acute extremities, and maximum width sited towards anterior third of shell length. The dorsal valve is gently concave so that the visceral disc is thick, and the dorsal ears are gently concave with alate extremities. The trail is slender, curving smoothly from the disc. Ornament is strong, made up of more than twelve prominent commarginal rugae on the ventral valve, increasing in spacing and strength from the umbo, and becoming lower and more closely spaced over the anterior third of the shell length. Some twelve spines emerge from the crest of each rugation that crosses the shell, increasing in size towards the middle of the shell, with swollen bases over 1mm across that extend only slightly back from the crest of the ramp of each rugation. There are ten to twelve growth increments per mm over mid-length. Commarginal rugae are not so regular and high over the dorsal valve, and the shell surface is diversified by low regularly spaced radial mounds and pits, which are less persistent laterally over the anterior shell, as well as commarginal laminae, and numerous spines in at least twenty five commarginal rows. The dorsal spines are erect and up to 0.25mm in diameter, and arise in commarginal rows between large shallow pits. Spines form a well defined row in front of the dorsal ears along the junction with the visceral disc (not seen in *Fimbrinia*), and the ears lack spines.

The ventral adductor platform is small and only slightly longer than wide: on one specimen the scars are marked by irregular subdendritic growth lines. Diductor scars are small, anteriorly placed, and marked by faint longitudinal striae and lines parallel to the anterior margin. The posterior floor is smooth, and small pustules lie in front, in bands behind and in front of the spine rows. One shell has a low forked ridge across the umbo.

In the dorsal valve the medium septum extends for about half the length of the valve and the anterior adductor scars are large and tear-shaped, with faint markings parallel to the anterior margin. Posterior adductors are very small and are bordered each side by a low oblique ridge. A stronger ridge lies close to the hinge, and a broad platform lies in front of the cardinal process. Brachial scars are not visible. The posterior shell bears fine closely spaced pustules, and larger pustules lie in front of the septum around the anterior shell.

Resemblances: This species is closely allied to the slightly younger form described as *Fimbrinia transversa* Shi & Waterhouse (1996, p. 55, pl. 4, fig. 9-20), now referred to *Fimbrininia,* and coming from the "*Yakovlevia transversa"* to *Jakutoproductus verchoyanicus* Zones in the Jungle Creek Formation of the Ogilvie Mountains in northwest



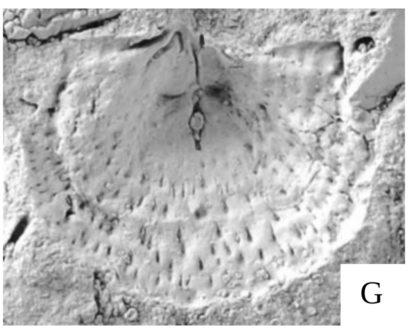


Fig. 27. *Fimbrininia spinosa* Waterhouse. A, holotype ventral valve GSC 133266 from JBW 581, x3. B, ventral aspect of internal mould, GSC 133265 from JBW 581, x3. C, ventral internal mould GSC 133308 from JBW 581, x3. D, external mould showing spines of ventral valve, GSC 133270 from JBW 581, x7. E, dorsal internal mould, GSC 133308 from JBW 549, x4. F, dorsal aspect of internal mould of specimen with valves conjoined, GSC 133272 from JBW 581, x3. G, dorsal internal mould of GSC 133269 from JBW 581, x5. Specimens from Member E, except E, from Member D. Jungle Creek Formation, Canada.

Canada. Differences are that the younger shells are slightly narrower, and have eight to ten spines as a rule along the commarginal rugae, fewer than in the present form. The dorsal valve as figured by Shi & Waterhouse (1996, pl. 4, fig. 12, 17) is smoother, with more subdued commarginal ornament other than a few prominent layers, and apparently fewer spines. According to the text there are only some four to five growth increments per mm, much fewer than in present material. Ventral spines emerge from the crests of the rugae in both species. A faint ridge in the position of the lateral buttress ridge was shown for *transversa* by Shi & Waterhouse (1996, pl. 4, fig. 19).

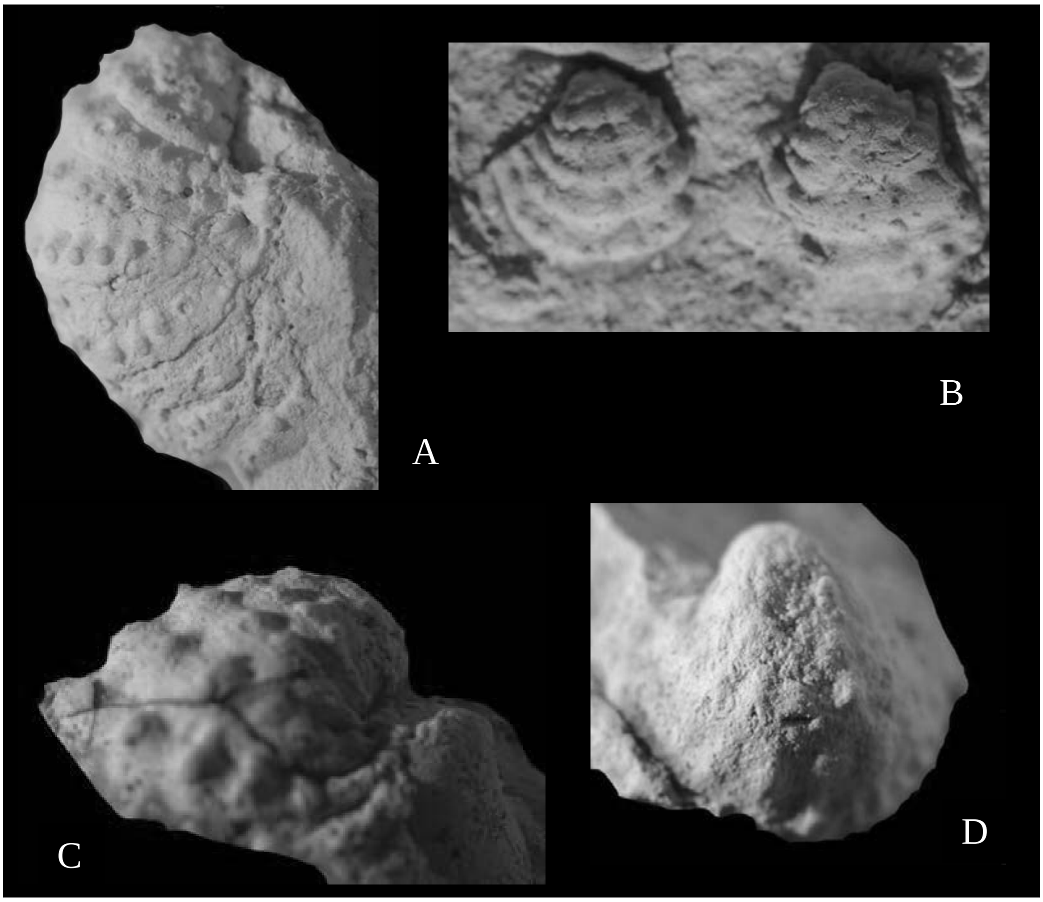


Fig. 28. *Fimbrininia spinosa* Waterhouse. A, lateral aspect of external cast of ventral valve, GSC 136717, JBW 561, x5. B, external casts of two ventral valves, GSC 136719 and 136720 from JBW 519, x 3. C, D, lateral and ventral aspects of external cast, GSC 136718, JBW 561, x5. Member E, Jungle Creek Formation.

Fimbrinia? gracilis Abramov & Grigorieva (1983, pl. 3, fig. 10-14) from the Upper Carboniferous of the southern Verchoyan Mountains, northeast Russia, dated as Moscovian by Klets (2005, p. 44), is close in the number of ventral spines along the rugae, but is more transverse with fewer rugae. *Overtonia gijigensis* Zavodowsky (1970, pl. 35, fig. 1-3) from the Sakmarian Irbichan Suite of the Kolyma-Omolon massif of northeast Russia is very transverse, with further specimens assigned to the species from the lower Kigiltass Suite of Verchoyan by Abramov & Grigorieva (1983, pl. 3, fig. 15-17). "*Fimbriaria" kolymaensis* Zavodowsky (1970, pl. 37, fig. 8-10) from the Sakmarian Yasachnin Suite of the same region is also moderately transverse. Details in figures for these two species are obscure, and none of the Russian forms shows much of the interior or dorsal valve. The occurrences of the genus in Russia indicate that the genus began there, and spread to Canada.

Productus cristatotuberculatus Kozlowski (1914, pl. 2, fig. 61, 62), also figured by Branisa (1965, pl. 66, fig. 34–35a), from the Asselian Copacabana Group of Bolivia, differs in having fewer commarginal rugae. The nature of the spine bases is not clear in figures but the text indicates that the spines are like those of *Fimbrinia.* Specimens from Kazakhstan that were ascribed to this species in Sarytcheva (1968, pl. 6, fig. 5-10) are small and subelongate, with few commarginal rugae, although the spines do commence over the posterior part of each rugation, whereas spines arise from the crests in Kigiltass specimens from west Verchoyan figured (wrongly) as *cristatotuberculatus* by Kashirtsev (1959b, pl. 15, fig. 6, 7), as do the spines in Turuzov specimens assigned to the species by Ustritsky & Chernyak (1963, pl. 4, fig. 11, 12), together with material figured by Einor (1946, pl. 4, fig. 8, pl. 5, fig. 7-9) from Taimyr, north Russia.

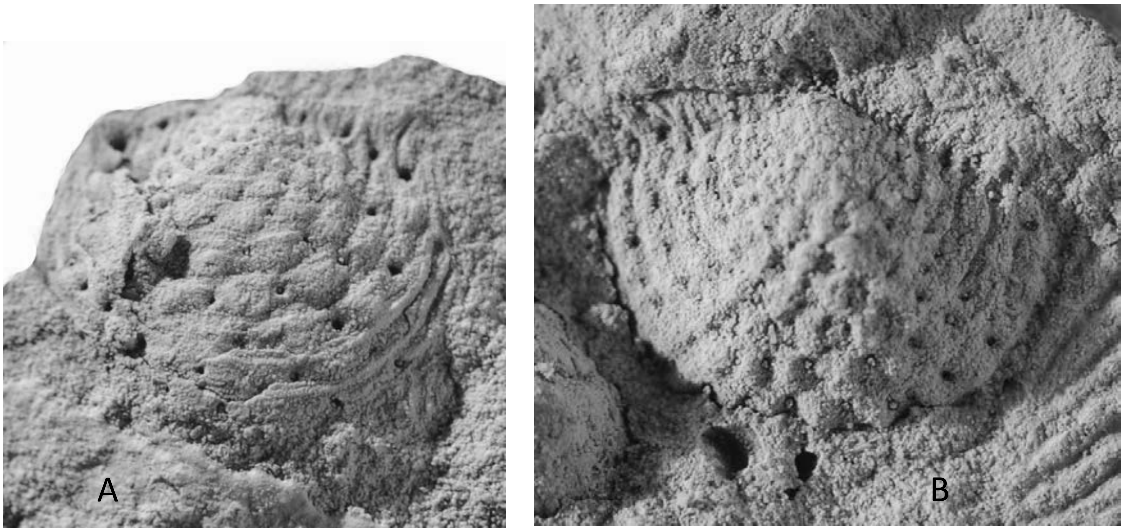


Fig. 29*. Fimbrininia spinosa* Waterhouse. A, external mould of dorsal valve GSC 133268 x5 from JBW 581, Member E. B, external mould of dorsal valve, GSC 136721 x4 from JBW 73, Member D. Jungle Creek Formation.

Tribe **LANIPUSTULINI** Waterhouse, 2013

[Lanipustulini Waterhouse 2013, p. 61].

Diagnosis: Shells externally and internally close to Levipustulini, but lacking lateral buttress plates.

Discussion: Members in this group of genera, involving *Lanipustula* Klets, *Impiacus* Lazarev & Suur'suren (syn. *Nudymia* Lazarev), *Jakutoproductus* Kashirtsev and *Verchojania* Abramov, were placed in Plicatiferinae, Family Overtoniidae, by Brunton et al. (2000, p. 452) but they have much more subdued commarginal ornament, without the well organized rugae seen in Overtoniidae. Internal detail is close to that of Tubersulculini Waterhouse (see p. 143), and spines are similar but have more prominent bases and are spaced further apart on the ventral valve, and a number of genera lack dorsal spines.

Genus ***Jakutoproductus*** Kashirtsev, 1959a

Diagnosis: Transverse with well differentiated ears, weakly convex ventral disc, dorsal disc almost flat, ventral spines well spaced, in quincunx, bases elongate over disc, shorter in front, no dorsal spines, weak commarginal rugae.

Cardinal process pit at posteror end of median dorsal septum, low lateral ridges in both valves, marginal ridge in dorsal valve.

Type species: *Marginifera verchoyanica* Fredericks, 1931, p. 211 from Russia, of mostly Asselian-Sakmarian age, although the type was sourced from Sakmarian – lower Artinskian beds, OD.

Discussion: The genus has been extensively analyzed by Shi (1994). Genus *Verchojania* Abramov, 1970, based on *Jakutoproductus cheraskowi* Kashirtsev, 1959a, p. 30 from Yakutsk (Bashkirian-Moscovian), north-east Asia, has been distinguished from *Jakutoproductus* by very weak or lack of commarginal rugae over the ventral disc, possession of relatively large tear-shaped dorsal adductor scars, and posteriorly thickened posterior dorsal septum, differences yet to be confirmed for all species allocated to the genus. According to Brunton et al. (2000, p. 453), *Verchojania* differs from *Jakutoproductus* in lacking dorsal spines, but the analyses by Shi (1994) and Ganelin (1991) claimed that both genera lacked dorsal spines. However there are nodes, or pustules, or spine bases indicated by Abramov (1970, pl. 7, fig. 5b) in one specimen of *verchoyanicus*, though no spines are clearly shown in illustrations of other dorsal valves (pl. 7, fig. 4, 7). Subsequently, it has been announced that *Verchoyania* displays dorsal spines near the start of the trail (Ganelin & Durante 2002, Ganelin & Biakov 2006). The genus has been found in Patagonia (Taboada 2008).

Jakutoproductus verchoyanicus (Fredericks, 1931)

Fig. 30 - 33

1931 *Marginifera verchoyanica* Fredericks, p. 211, pl. 1, fig. 3, 11-13.
1939 *Productus* (*Avonia*?) *verchoyanicus* – Licharew & Einor, p. 30, pl. 3, fig. 4-6.
1946 *P.* (*Avonia*?) *verchoyanicus* – Einor, p. 31, pl. 2, fig. 6, 7, pl. 4, fig. 9.
1946 *P.* (*Plicatifera*?) *verchoyanicus* – Stepanov, p. 201, pl. 2, fig. 2-9.
1959a *Jakutoproductus verchoyanicus* – Kashirtsev, p. 35, pl. 13, fig. 9, 10.
1960 *J. verchoyanicus* – Kashirtsev, p. 28, pl. 3, fig. 16.
1963 *J. verchoyanicus* – Ustritsky & Chernyak, p. 75, pl. 5, fig. 1-4, pl. 28, fig. 2, 3.
1967 *J. verchoyanicus* – Kotlyar & Popeko, p. 103, pl. 18, fig. 1-8.
1970 *J. verchoyanicus* – Solomina, p. 76, pl. 3, fig. 10, 11.
1970 *J. verchoyanicus* – Zavodowsky, p. 82, pl. 40, fig. 5-10, pl. 41, fig. 2-4.
1974 *J. verchoyanicus* – Abramov, p. 79, pl. 1, fig. 3, 4.
1981 *J. verchoyanicus* – Solomina, p. 61, pl. 5, fig. 1-3.
1988 *J. verchoyanicus* – Abramov & Grigorieva, p. 111, pl. 4, fig. 4, 7, 8, 13, 14, pl. 5, fig. 20.
1991 *J. verchoyanicus* – Ganelin, p. 51, pl. 3, fig. 10, 11.
2005 *J. verchoyanicus* – Klets, pl. 6, fig. 1-6.

Diagnosis: Moderately large, weakly transverse with moderately well defined simple commarginal rugae, geniculate trail and small subalate ears, sulcus narrow and moderately shallow.

Lectotype: TsNIGRA no. 2320/1, figured by Fredericks (1931, pl. 1, fig. 3) from Echi Suite (upper Sakmarian, Artinskian), north Verchoyan, SD Solomina (1981).

Material: Eight ventral valves from JBW 561, dorsal valve and specimen with valves conjoined and possible dorsal valve from JBW 581. Ventral valve from GSC 56920.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: One ventral valve from JBW 561 is moderately well preserved, 27mm wide, 15mm long, and 9mm high, with wide hinge, gentle median sulcus, numerous fine commarginal rugae, and long spine bases. Another is a fragment of a larger and probably late mature shell from JBW 561, more than 35mm wide, with large spine bases arranged in quincunx. Other specimens are small and probably immature, a ventral valve measuring 13mm wide, 10.5mm long and 2.5mm high. Ventral umbo small, broad and inconspicuous, hinge wide, at maximum width

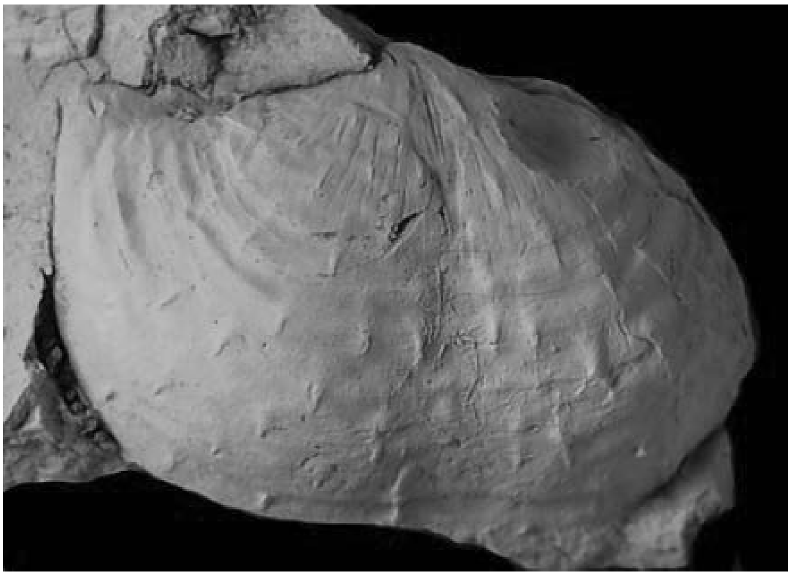


Fig. 30. *Jakutoproductus verchoyanicus* (Fredericks), ventral valve BR 3052 x4 from Member E (JBW 581), Jungle Creek Formation.

with tiny alate ears, and almost as wide near mid-length, umbonal walls low and ears not clearly separated, disc gently convex, the dorsal valve concave with moderately large concave ears and largely obtuse cardinal extremities. The specimen with valves conjoined from JBW 581 is 17mm wide and 12mm long. A shallow narrow sulcus arises near mid-length and persists to the anterior margin, but the corresponding part of the dorsal valve is not preserved. A row of well-spaced spines extends close to the ventral hinge, some relatively large for the species, up to 1mm in diameter in a specimen 19mm wide, and nearly 10mm long in the specimen with valves conjoined. Spines cover the ventral disc in front of a largely smooth posterior shell, well spaced at up to 3.5mm apart and in rows 2mm apart, but spacing and distribution vary on each specimen. As a rule, each spine lies in front of a short narrow base, though on one specimen the spines are erect. Four ventral valves have growth increments and faint irregular mounds, and on one specimen 20mm wide there are subdued commarginal rugae in front of the first formed part of the specimen 10mm wide. There are no spines on the dorsal valve of the conjoined specimen and a possible dorsal valve from JBW 581 has well developed pits postero-laterally but no spines. The dorsal valve shows very subdued growth rugae. Internally, the dorsal median septum extends for less than half the length of the valve, and a low hinge ridge and weakly raised adductor scars are present.

Resemblances: The small suite of Canadian specimens comes close to *Jakutoproductus verchoyanicus* (Fredericks) in size, shape, sulcus, commarginal rugae, and spacing and strength of spines. Amongst the synonymy provided, specimens that are particularly close have been figured by Abramov & Grigorieva (1988), Ganelin (1991) and Klets (2005), and these are assumed to represent the recent and hopefully stabilized interpretation of the species: the present material is moderately like that from the Cigsk Suite of south Verchoyan (Abramov & Grigorieva 1988, pl. 4, fig. 4, 7, 8, 13, 14, Klets 2005). But the actual original material figured by Fredericks (1931, pl. 1, fig. 11-13) shows finer more close-set rugae and less conspicuous spine bases, whereas the specimen figured in Abramov & Grigorieva (1988, pl. 4, fig. 13) is closer to present material. It thus appears that further clarification of the morphologic limits is required. The type material has been reported from the upper Sakmarian – .lower Artinskian

Echi Suite: other reported occurrences range into the Upper Carboniferous. Klets (2005, p. 60) showed the species as occurring in and indeed typifying the lower Sakmarian and Asselian faunas of northeast Russia.

Another species that is particularly close is *Jakutoproductus omolonensis* Zavodowsky (1970, p. 85, pl. 24, fig. 3-6) from the Paren Horizon of northeast Russia, agreeing in shape, size, sulcus and commarginal rugae, but with slightly less developed ventral spine bases. The Paren faunas are now regarded as Late Carboniferous Kasimovian (Klets 2005). *J. crassus* Kashirtsev (1959a, pl. 13, fig. 11, 12; Abramov 1970, pl. 7, fig. 11, pl. 8, fig. 5-7; Solomina 1981, p. 74, pl. 5, fig. 4, 5; Abramov & Grigorieva 1988, pl. 5, fig. 15-19, 22-26, pl. 6, fig. 1, 2) is larger and

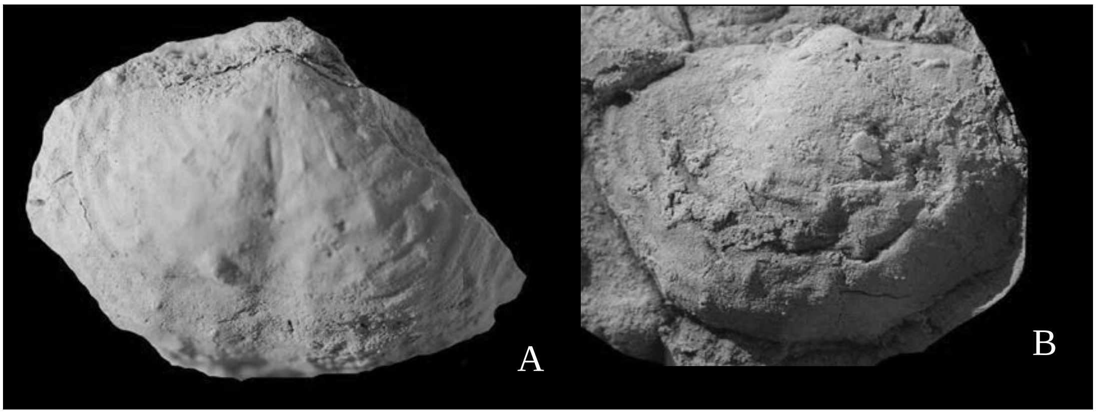
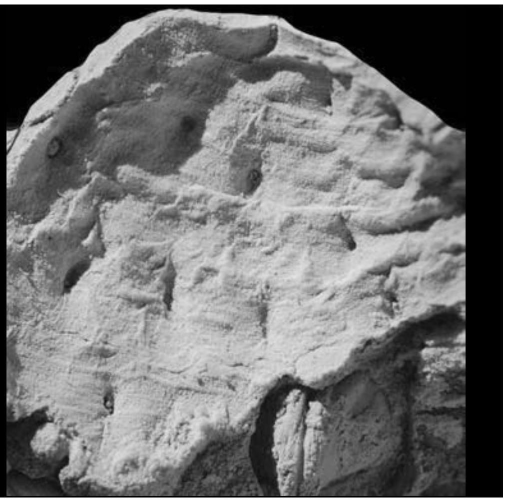


Fig. 31. *Jakutoproductus verchoyanicus* (Fredericks). A, ventral valve GSC 136722 x2.5 from JBW 581. B, ventral external cast, GSC 136724 x3, from JBW 561, showing hinge row of spines. Member E, Jungle Creek Formation.

more elongate, with similar to deeper ventral sulcus and less closely arranged ventral spines. It comes from the Echi Suite (Upper Sakmarian – Artinskian) of west Verchoyan, and Cigsk Suite of south Verchoyan. A number of the specimens figured as *crassus* by Abramov & Grigorieva (1988) have more emphasized commarginal rugae than in the Canadian material from the Ej zone (see Shi & Waterhouse 1996, p. 63), but some (pl. 5, fig. 15) are like the Canadian specimens, and most have a similar sulcus and ventral spines. *J. taimyrensis* Ustritsky, 1963, p. 76, pl. 6, fig. 2, 3 from the Turuzov Suite (Kasimovian-Gzhelian) of Taimyr Peninsula is close in spines and subdued wrinkles. Baikal specimens were reported by Kotlyar & Popeko (1967, pl. 16, fig. 8-12) from the Shazgaitu Suite, and further material described by Abramov & Grigorieva (1983, pl. 2, fig. 1-3) from Upper Carboniferous Tugasir Suite of north Verchoyan, but spines are more numerous and have elongate bases.

Fig. 32. *Jakutoproductus verchoyanicus* (Fredericks) A, ventral valve GSC 137160 x5 from JBW 581. B, dorsal internal mould, GSC 137162 x3, from JBW 561. Note two posterior ridges suggestive of buttress plates. C, cast of ventral valve GSC 137452 x 3 from JBW 561. Member E, Jungle Creek Formation.

Fig. 33. *Jakutoproductus verchoyanicus* (Fredericks). A, cast of ventral valve GSC 136723, x3. B, ventral external cast, GSC 136725 x2. From JBW 561, Member E, Jungle Creek Formation.



The material figured from the eponymous *Jakutoproductus verchoyanicus* Zone of the Jungle Creek Formation by Shi (1994, Fig. 4A-J) and Shi & Waterhouse (1996, pl. 5, fig. 10-23, text-fig. 19, 20) is close to present material, but specimens are more elongate, and more deeply sulcate, and commarginal rugae tend to be slightly lower than in the present suite of specimens. The suite is not particularly close to the original specimens figured by Fredericks (1931), having stronger and fewer commarginal rugae and less transverse outline. Although not exactly identical, as noted, Fredericks' species overall is closer in size and shape and ornament to the present material, and has been widely reported from Late Carboniferous and Early Permian faunas of north Asia. On the other hand, *J. tatjanae* Abramov & Grigorieva (1983, p. 67, pl. 1, fig. 19-26) from the lower Kigiltass Group of west Verchoyan has a shallow anterior sulcus and ventral spines are more closely spaced. *J. morosovi* Zavodowsky (1970, pl. 2, fig. 14) from the lower Permian Burgali Horizon is comparable in shape with inconspicuous spine bases and broad anterior sulcus: the dorsal valve was not figured. From the Paren level, *J. maslennikovi* Kotlyar, 1967**,** as also figured by Zavodowsky (1970, pl. 7, fig. 1, 2, pl. 25, fig. 8, 9, pl. 26, fig. 1-3), shows no sulcus in most ventral valves and the ventral valves are somewhat worn. Zavodowsky (1970) described a number of species, close in a general way to the present form, but as for other studies focused on the ventral valve, and for several taxa, figured only one ventral valve, so that the generic and specific position of his taxa is not always clear. Many species have been revised and described in Abramov & Grigorieva (1988), though no dorsal valves were figured. The critical aspects appear to centre on the presence of a distinct but narrow ventral sulcus and numerous very low commarginal rugae in the present material: the spines are crowded and with age become very large. These features place the present form in the *verchoyanicus* superspecies, which includes *crassus* Kashirtsev, *paranensis* Zavodowsky*, expositus* Ganelin and ?*tatjanae* Abramov & Grigorieva. A very large number of species have been named, as summarized by Shi (1994), but present specimens can only be provisionally identified, thanks to the low number of specimens.

The wide hinge, well spaced spines and anterior sulcus are features of the ventral valve in *Verchoyania*, of upper Carboniferous age in north Asia. The specimens of *Verchoyania* figured by Abramov (1974, pl. 1, fig. 3, 4) have strong wrinkles. *Jakutoproductus* (now *Verchoyania*) *cheraskovi* Kashirtsev, 1959a as recorded by Kotlyar & Popeko (1967, pl. 16, fig. 8-16, fig. 4-7) from Zabaikal is close in ornament, and of Late Carboniferous age, having subdued if any commarginal wrinkles, but is more inflated. The species was also figured in Sarytcheva (1968, pl. 6, fig. 1-4) from Kazakhstan from west Verchoyan. A large suite was figured by Abramov (1970, pl. 6, fig. 1-20): some specimens have inconspicuous wrinkles and others have low but defined wrinkles over the ventral valve. The specimens figured by Abramov (1970, pl. 7, fig. 1-10, pl. 8, fig. 1-4) from the Djuptagin Suite (Early Permian) seem closer, and the material figured by Abramov & Grigorieva (1983, pl. 1, fig. 18, 27-33) from Orulgania and west Verchoyan, involving the Middle and Upper Carboniferous Imtanjin Suite of south Verchoyan (Natalin Horizon) of northeast Russia, are certainly comparable in many respects.

Family **AVONIIDAE** Sarytcheva, 1960

[Avoniidae Sarytcheva, 1960, p. 226].

Diagnosis: Ornament dominated by spines, well spaced to close-set, especially on ventral valve, with bases swollen or prolonged, may be weakly aligned commarginally, low commarginal laminae and low or anterior ribs only as a rule. No teeth, sockets or interareas, adductor scars not dendritic, brachial ridges productiform.

Discussion: Avoniids appear to have evolved from productelloid shells, losing interareas, teeth and sockets, and reducing the size of the brachial shields. They retained a predominantly spinose ornament, the bases in some groups short and impersistent, in others becoming longer and more prominent, and developed ribs to varying degree. Although treated as a mere tribe by Brunton et al. (2000), the group is considered to incorporate those productiform tribes and subfamilies with commarginal lamination much less marked than in Overtoniidae Muir-Wood & Cooper. The prolonged spine bases over the ventral valve may suggest a source close to Helaspinae Waterhouse, but the low commarginal rugae of the earliest Avoniinae, coupled with the simple dorsal septum, indicates that the family evolved from Dotswoodiinae Waterhouse, 2013, close to Overtoniidae, and unlike that family, displaying reduction in the ornament of commarginal rugae with more emphasis on spines and elongate bases, and introduction of more linear ornament and alveolus.

Subfamily **SEMICOSTELLINAE** Nalivkin, 1979

[Semicostellinae Nalivkin, 1979, p. 67. Syn. Breileeniini Brunton in Brunton & Lazarev, 1997, p. 389].

Diagnosis: Commarginal rugae fine, subprominent, costae on long trails, often geniculate. The dorsal valves have discontinuous or anterior ribs and pits. Spines of moderate number on both valves in several genera, bases may be extended in ventral valve. Low to moderately developed hinge ridge and often marginal ridges may be present. No cardinal process pit or septal slit. Corpus cavity moderate to deep.

Discussion: This subfamily is very close to Avoniinae and some distinctions seem slight or inconsistent, so that some reservations about its usefulness may be necessary. Some genera in Avoniinae have a more transverse shape, and pits and ribs are more evident on the dorsal valve. Members of Avoniinae have a thick corpus cavity, costae developed over long trails, and strong tendency to develop internal marginal ridges. Members of Semiproductinae also have a deep corpus cavity, but internal marginal structures are limited to the posterior dorsal ridge, and a cardinal process pit is lacking. Ornament of Semiproductinae tends to differ from that of Avoniinae, in being less dominated by crowded ventral spines over disc and trail, though a number of members of Avoniinae do share ribbed trails.

Genus ***Tuberculatella*** Waterhouse, 1982c

Diagnosis: Small to medium-sized shells, ventral ornament of well spaced large often elongate tubercles each bearing a spine, dorsal spines arise from tubercles or between dimples, commarginal lamellae moderately developed, short irregular radial ridges anteriorly on ventral valve. Adductor scars smooth in both valves, without emphasized rims, floor of valve densely covered by sharp-pointed narrow pustules, in two orders over the dorsal valve.

Type species: *Tuberculatella bunnakia* Waterhouse n. sp., renamed here from *T. tuberculata* Waterhouse 1982c not *Productus tuberculata* Moeller, 1862. Originally the type species was called *tuberculata* Waterhouse, 1982c, p. 44 from Huai Bun Nak, northeast Thailand, of Late Carboniferous (likely to be Kasimovian to Gzhelian) age. As another and earlier named species of what is believed to be the same genus is also named *tuberculata* (*Productus tuberculatus* Moeller, 1862), the Thai species is therefore a junior homonym, and is here renamed *bunnakia,* based on the geographic source of the type material.

Discussion: This genus was omitted from the *Revised Brachiopod Treatise* by Brunton et al. (2000), and was eventually acknowledged by Brunton (2007, p. 2641), without citing the correct reference, which is Waterhouse 1982c, rather than the reference cited herein as Waterhouse, 1982a. No note of the genus was made by Lazarev in Brunton & Lazarev (1997). He clearly overlooked or misinterpreted the genus in proposing genus *Maemia* Lazarev, in Brunton & Lazarev, 1997 of Bashkirian – lower Moscovian age, based on small shells from Cape Chayka, Yugorsky Peninsula, in the Barents Sea at the northern extremity of the Ural Mountains (not Mongolia as in Brunton et al. 2000, p. 463), with spines and elongate tubercles over both valves, low radial ribs over anterior ventral valve, low commarginal lamellae or rugae, very weak marginal ridges and ear baffles, and comparatively thick body corpus. Although the genus shares a number of attributes with species of Tournaisian age assigned to *Avonia* by Sarytcheva in Sarytcheva et al. (1963, pl. 14), it was classed in Semicostellini Nalivkin by Brunton et al. (2000, p. 463). *Maemia* is particularly close to *Tuberculatella* Waterhouse, 1982c of Late Carboniferous (Moscovian) to Lower Permian (Asselian) age. This was named for small medium-sized shells, with ventral ornament of well spaced large more or less elongate tubercles each bearing a spine, dorsal spines arising from tubercles or between dimples, commarginal lamellae moderately developed, and short irregular radial ridges anteriorly on the ventral valve. In type *Tuberculatella*, the adductor scars are smooth in both valves, and the floor of the valve is densely covered by sharply pointed pustules, of two orders in the dorsal valve. There is a very weak marginal ridge, and short bifid cardinal process, and simple median dorsal septum, without obvious alveolus. *Maemia gelida* Carter & Poletaev (1998, p. 127) from an Atokan fauna on Ellesmere Island, Canada, is very like *Tuberculatella,* as far as described and illustrated, and shows no regular radial ribs on the ventral valve, but only irregular low and short radial riblets. *Maemia archboldi* Martínez-Chacón & Winkler Prins (2008, Fig. 2) from a Bashkirian fauna of north Spain has ventral spine bases slightly shorter than those of *Tuberculatella bunnakia*, the type species, and clearly belongs to *Tuberculatella*.

The type species of *Tuberculatella* has irregular long radial swellings anteriorly, and although they are less regular than in type *Maemia*, they suggest a position intermediate between type *Maemia* and *M. gelida*, indicating that there was an irregular cline of species that varied in the development of anterior costae, within one genus. In *Tuberculatella*, the dorsal spines arise from pustules between dimples, much it seems as in *Maemia*. In

Tuberculatella, the internal pustules are both dense and in two grades, fine and dense, better spaced and coarser. The arrangement is, so far, obscure for type *Maemia.* But the dorsal adductor scars in *Maemia* bear high rims, not seen in *Tuberculatella*, and this possibly provides a generic distinction. Unless the nature of the adductor scars can be determined as being like those of *Maemia*, material should be assigned to *Tuberculatella,* because this has priority, and is based on well-preserved material.

A question remains about the affinities of *Tuberculatella*. Brunton (2007) referred the genus to Lethamiini Waterhouse, and there is considerable approach, although spines are more spaced and ventral spine bases more swollen. Waterhouse (2002b, p. 9) referred the genus to Avoniini Sarytcheva, which seems a more likely position. Admittedly the nature of the internal pustulation is like that of *Lethamia*, but the invariant nature of this character is yet to be established.

Tuberculatella subtuberculata (Grabau, 1936)

Fig. 34A

1936 *Productus subtuberculatus* Grabau, p. 111, pl. 11, fig. 7-9.

Diagnosis: Large ventral spines, long posterior walls diverging well forward.

Holotype: Serial no. 4219, cat. no. 5288, figured by Grabau (1936, pl. 11, fig. 7a-c) from Maping Formation (Asselian) at Nantan, Kweichow, China, OD.

Material: Three ventral valves from JBW 624, and one from JBW 502.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: The specimen is subtriangular in shape, measuring 22mm wide, 17mm long and 10mm high, with long posterior walls, steep in cross-section, and only slightly diminished in convexity across the mid-line, with no sulcus. Spines are well spaced with slightly elongated bases.

Resemblances: The species *subtuberculata* Grabau (1936, pl. 11, fig. 7-9) from the Maping Limestone of China lacks a sulcus or anterior tube, and has coarse and well spaced spines. It is characterized by its subtriangular shape with long posterior walls. Grabau (1936) referred the specimens figured by Tschernyschew (1902, pp. 267, 615, pl. 47, fig. 3-5, pl. 52 fig. 7) to *subtuberculatus*, but these are more like *tuberculata*. He also compared his species to Trogkofel specimens of Austria figured by Schellwien (1900, p. 50, pl. 8, fig. 12, 13), specimens that are small with umbonal groove.

Tuberculatella aff. ***tuberculata*** (Moeller, 1862)

Fig. 34B

aff. 1862 *Productus tuberculatus* Moeller, pl. 10, fig. 3.
aff. 1875 *P. tuberculatus* – Stuckenberg, p. 91, pl. 4, fig. 6.
aff. 1902 *P. tuberculatus* – Tschernyschew, p. 615, pl. 47, fig. 3-5, pl. 52, fig. 7.
aff. 1938 *P. tuberculatus* – Kulikov, pl. 1, fig. 15.
aff. 1963 *Avonia tuberculata* – Ustritsky & Chernyak, p. 75, pl. 4, fig. 7, 8.

Diagnosis: Subequilateral shells with well spaced ventral spines and swollen bases, anterior spine bases tend to be elongate, many specimens faintly sulcate.

Holotype: Sole specimen figured by Moeller (1862), from Early Permian of Urals, Russia, holotype by monotypy.

Material: Eleven ventral valves from JBW 18, a few poorly preserved dorsal interiors.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

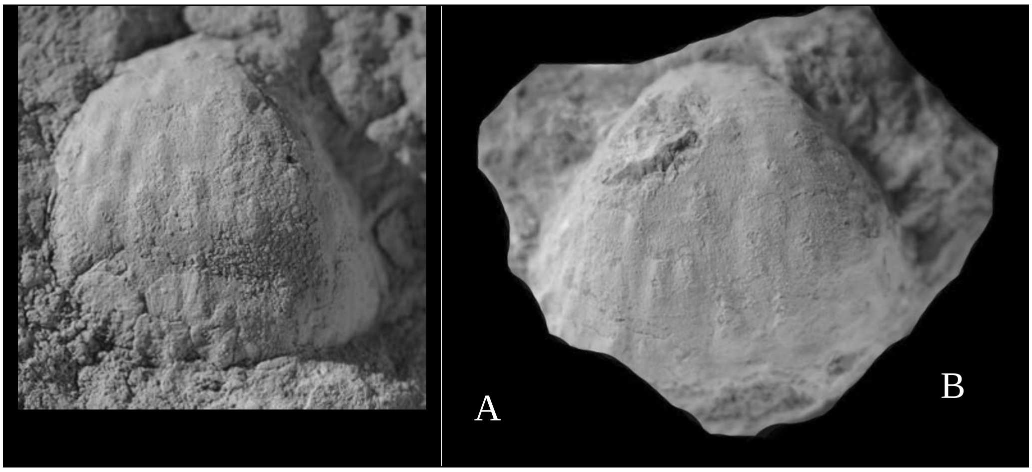


Fig. 34. A, *Tuberculatella subtuberculata* (Grabau), ventral valve GSC 136726 from JBW 624, Member A.
B, *Tuberculatella aff. tuberculata* (Moeller), ventral valve GSC 136727 x2 from JBW 18, Member C. Jungle Creek Formation.

Description: Specimens swollen with arched venter, one measuring 26mm wide, 18.5mm long and 14.5mm high, another 25mm wide, 21.5mm long and 11.5mm high, with incurved ventral umbo, angle of 90º, and steep posterior walls and obtuse cardinal extremities. A very shallow sulcus extends over the anterior half of the shell. Spines with swollen bases cover the shell, spaced 2.5 to 3mm apart, and short radial swellings extend over the anterior disc and trail, somewhat uneven and impersistent in height and width. One specimen has two well defined ribs over the mid-valve and trail.

Resemblances: In this species, the sulcus commences in front of the umbonal part of the shell, unlike the arrangement in the type species, *Tuberculatella bunnakia* (formerly *tuberculata* Waterhouse not Moeller), and the shells are less tumid and broader, and the sulcus where present is broader anteriorly. The spine bases are slightly more swollen than in the type species *T. bunnakia*, and the shell less laminate. The Urals specimen called *Avonia tuberculata* Moeller from the Kirov Suite (C2m) by Stepanov (1975, pl. 64, fig. 8) lacks a sulcus, and is more transverse. Permian specimens assigned to this species (Moeller 1862, pl. 10, fig. 3; Stuckenburg 1875, pl. 4, fig. 6; Tschernyschew 1902, pl. 47, fig. 3-5, pl. 2, fig. 7; Kulikov 1938, pl. 1, fig. 15) have a distinct and narrow sulcus, and spine bases are more rounded. However the suite of specimens figured from the Artinskian – Kungurian faunas of the Tarim Basin, China, by Chen & Shi (2006, p. 133, pl. 3, fig. 1-5) includes several specimens that lack a sulcus, and are otherwise close to but slightly broader than the present species. *Krotovia tuberculata* (Moeller) as described by Mironova (1967, pl. 1, fig. 14, 15) is more transverse and less inflated, one ventral valve being sulcate, the other not. It is of Late Carboniferous age in Russia. The Canadian specimens are particularly close to but larger than individuals figured by Ustritsky & Chernyak (1963, pl. 4, fig. 7, 8) as *Avonia tuberculata* from the Turuzov Suite of Taimyr Peninsula. The Taimyr specimens have a shallow sulcus and fewer anterior radial ridges.

The Late Carboniferous species *Tuberculatella karpinskina* (Yanishevsky, 1900), also figured by Ivanov (1935, pl. 1, fig. 3), Sokolskaya (1948, pl. 8, fig. 21), Sarytcheva & Sokolskaya (1952, pl. 14, fig. 97) and Semenova in Ifanova & Semenova (1972, pl. 1, fig. 16, 17) from the Urals and Yepenchin Suite of Verchoyan, northeast Russia, is close, with thin corpus cavity, widely spaced spines over the ventral umbo, and no elongate spine bases anteriorly.

Productus tanankouensis Ozaki (1931, p. 129, pl. 12, fig. 8, 9) from south Manchuria appears to be congeneric, and is distinguished by its large size.

Tuberculatella cf. ***boulei*** **(**Kozlowski, 1914)

Fig. 35, ?36

1914 *Productus boulei* Kozlowski, p. 47, pl. 3, fig. 8, 9, text-fig. 13.

Diagnosis: Small highly arched shells of subrounded outline and ventral spines evenly spaced with slightly elongated to moderately extended ribs.

Lectotype: Specimen figured by Kozlowski (1914, pl. 3, fig. 8a-d) from Copacabana Group (Asselian), Bolivia, here designated.

Material: Six ventral valves from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Dimensions in mm: ventral valve

Width	Length	Height
15	13	9.5
14.5	13.5	11.5
26	22	13

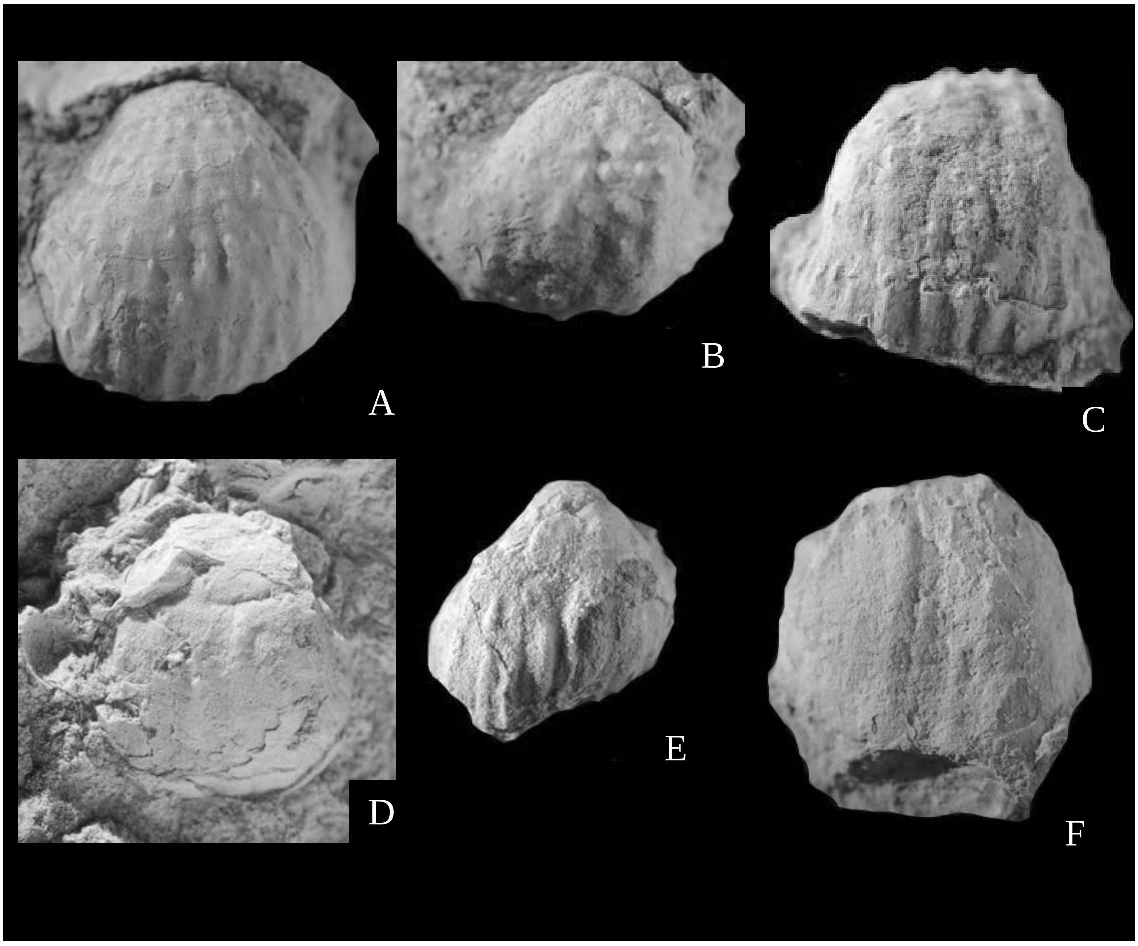


Fig. 35. *Tuberculatella* cf. *boulei* (Kozlowski). A, ventral valve GSC 136730. B, C, median and anterior aspects of ventral valve GSC 137280. D, ventral valve GSC 137281. E, median aspect of ventral valve GSC 137244. F, anterior ventral valve, GSC 137312. Specimens x3, from JBW 18, Member C. Jungle Creek Formation.

Description: Specimens small, subrounded in outline, ventral umbonal angle 65º, hinge wide with gently convex large ears, venter arched, no sulcus but trail long and medianly flattened, and the trail of one specimen has a sulcus. Spines over ears and somewhat irregularly over the disc and trail, bases tend to be weakly swollen over disc. Low broad impersistent costae commence near the start of the trail, four in 5mm, with more in one specimen (Fig. 36).

Resemblances: *Productus boulei* Kozlowski (1914, p. 47, pl. 3, fig. 8, 9, text-fig. 13) from the Early Permian Copacabana Group of Bolivia is very close in its ventral valve to that of the present form and has no sulcus. It seems likely that *Costispiniferina paucispinosa* Shi & Waterhouse, 1996, p. 74, pl. 6, fig. 29-39 from the "*Yakovlevia transversa"* Zone in the higher Jungle Creek beds belongs to *Tuberculatella*. The dorsal exterior is well displayed, and the anterior ventral valve has well defined anterior riblets, close to those of cf. *boulei*, and the shells are less elongate.

Fig. 36. *Tuberculatella* aff. *boulei* **(**Kozlowski), ventral valve GSC 137244 x3, showing exceptionally fine and numerous anterior ribs, from JBW 18. Member C, Jungle Creek Formation.

A specimen from the Kindle Formation of British Columbia in Canada that was figured as *Krotovia* cf. *oregonensis* [not Cooper] by Bamber & Waterhouse, 1971, pl. 12, fig. 15 shows some approach to *Tuberculatella*, given the density of spines and the slightly elongate spines, but the specimen is more transverse and has a shallow sulcus and very short spine bases, approaching those of *Tubersulculus* (see p. 144, and Fig. 112B, Fig. 113A). On the other hand, *K. oregonensis* Cooper, 1957, pl. 2C from the Coyotte Butte beds of Oregon is close to *Tuberculatella*, lacking a sulcus and displaying anterior ribs on the ventral valve.

Superfamily **HORRIDONIOIDEA** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 2002b, p. 16 ex Horridoniinae Muir-Wood & Cooper, 1960, p. 292].

Diagnosis: Ornament characteristic, with minor radial and commarginal ornament, spines few to moderately numerous and well spaced, may be specialized and very stout along the hinge of ventral, dorsal or both valves, may be aligned along ventral mid-line. Corpus cavity generally but not always thick. Trail well developed in younger forms and may be geniculate. Fine numerous pustules internally, no heavy marginal ridges.

Family **HORRIDONIIDAE** Muir-Wood & Cooper, 1960

[Horridoniinae Muir-Wood & Cooper 1960, p. 292, = Horridoniidae Sarytcheva, 1960, p. 234].

Diagnosis: Medium to large shells as a rule, with spines well spaced and erect, often on both valves and along hinge. Limited radial or commarginal ornament as a rule, no ventral median rib, minor internal thickening, may show dense pustulation over both valves. Cardinal process broad, may be squat, usually trilobed, but median lobe usually deeply cleft on dorsal side; no lateral buttress plates and no dorsal hinge ridge as a rule.

Subfamily **HORRIDONIINAE** Muir-Wood & Cooper, 1960

[Horridoniinae Muir-Wood & Cooper, 1960, p. 292].

Diagnosis: Spines in one or more rows near hinge of either or both valves, scattered few to numerous other spines. External surface may be pustular.

Genus ***Inflatusia*** Waterhouse, 2013

Diagnosis: Medium size, ventral valve highly swollen, dorsal valve gently concave over disc, well defined ventral sulcus and low dorsal fold, long trail. Row of spines close to hinge on each valve, other spines limited to ventral valve, as strong as those along the outer ventral hinge.

Type species: *Inflatusia ogilviensis* Waterhouse, 2013, p. 82 from Member A (Gzhelian), Jungle Creek Formation, Yukon Territory, Canada, OD.

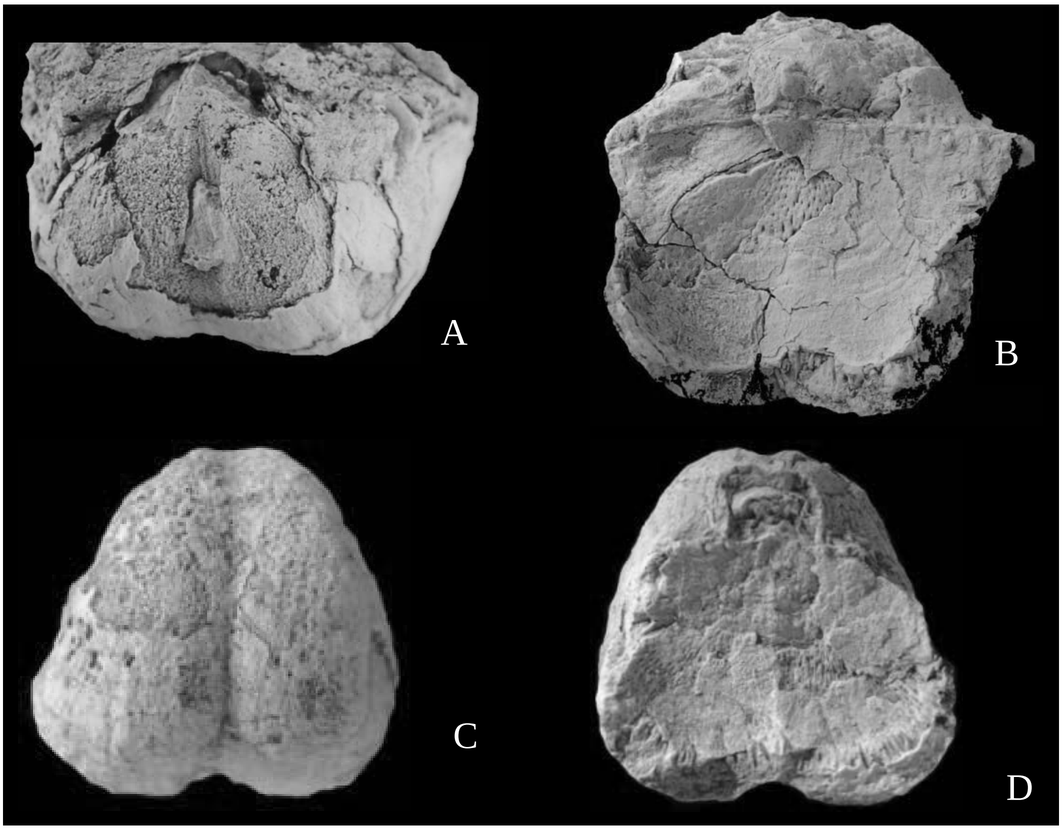


Fig. 37. *Inflatusia ogilviensis* Waterhouse. A, posterior view of ventral valve GSC 133289 from JBW 606. B, dorsal aspect of GSC 133281 from JBW 516. C, D, ventral and dorsal aspect of specimen with conjoined valves, GSC 133282 from JBW 606**.** Specimens x1.5, from Member A, Jungle Creek Formation.

Discussion: *Sangredonia* Waterhouse, 2013 from the Late Carboniferous of United States is distinguished from *Inflatusia* by its lower inflation, and presence of more ventral spines. Commarginal rugae, growth laminae, and growth stops are moderately defined on the two valves, and small pustules are developed over the shell surface. The genus *Horridonia* Sowerby is readily distinguished by the presence of more spine rows close to the hinge of each valve, and *Pleurohorridonia* Dunbar is somewhat similar, and largely of Late Permian age. *Calvadonia calva* (Sowerby) from the Late Permian of England is much closer to *Inflatusia*, though less inflated (see Waterhouse 2013, pp. 85, 86), and with fewer spines. Various taxa named from the Zechstein (Late Permian) of Germany by Eisel (1909) and Jordan (1966) are somewhat comparable, but have one or more very thick spines in front of the hinge row of dorsal spines, sited on the ears.

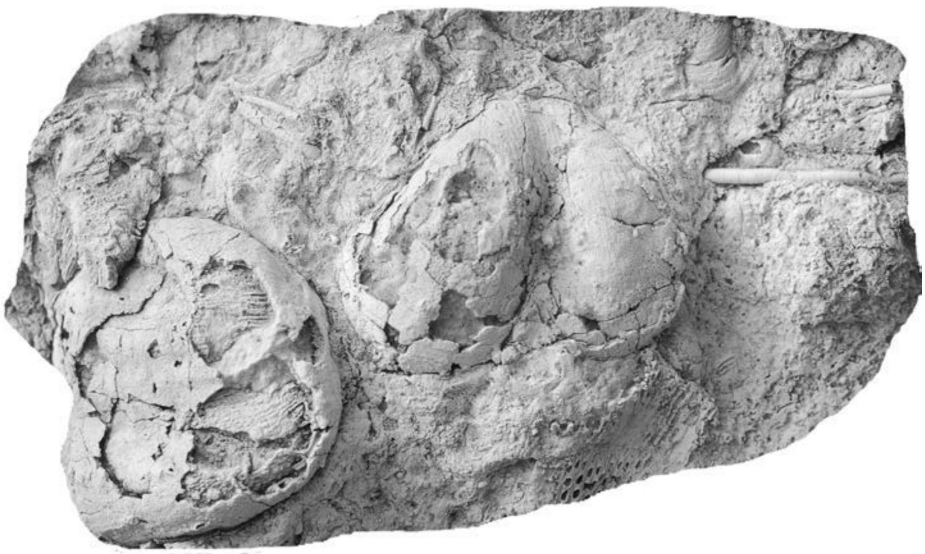


Fig. 38. *Inflatusia ogilviensis* Waterhouse. GSC 133361 in centre, showing faint ventral costae, and GSC 133362 to left, x1. From JBW 181, Member A, Jungle Creek Formation.

Inflatusia ogilviensis Waterhouse, 2013

Fig. 37 - 40

2013 *Inflatusia ogilviensis* Waterhouse, p. 83, Fig. 3.12-3.15, except Fig. 15E = *Sangredonia* (see p. 68).

Diagnosis: Ventral valve highly arched and body corpus thick, ventral hinge row of spines becoming thick and long laterally, spines just as stout on anterior trail, low radial costae anteriorly, and sulcus well formed. Dorsal valve smooth over disc, trail may be weakly costate, fold low.

Holotype: GSC 136036, figured in Waterhouse (2013, Fig. 3.15A, B) and herein as Fig. 40A, B, from Member A (Gzhelian), Jungle Creek Formation, Canada, OD.

Material: Single ventral valves from JBW 181, 186, 412, 606, 610, 615, 745, 748, 752?, 801?, 807, two ventral valves from JBW 119, one ventral valve and seven specimens with valves conjoined from JBW 170, a ventral and dorsal valve from JBW 666, and two of each from JBW 509 and 515, and single specimens with valves conjoined from JBW 108, 156, and 516. A ventral valve and specimen with valves conjoined comes from JBW 125. Two ventral valves from JBW 119.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Dimensions in mm: ventral valve

Specimen GSC	Width	Length	Height	
136036	19	14	7	holotype
136037	24	22	15	
133282	35	34	23	
133281	39	37	28	
133209	42	37	22	
136038	40	38	25	

Description: Mature shells highly inflated and of medium size, with only moderately wide hinge and subangular to abruptly rounded cardinal extremities, maximum width placed well forward near anterior quarter of length. The ventral umbo is strongly incurved, with angle of 90-110º. The sulcus is well defined, commencing just in front of the umbonal tip, with angle of 22-25º and narrow subangular floor, and the fold of the dorsal valve is less conspicuous than the sulcus on the ventral valve, with very narrow to broad gently rounded to subangular crest. Ventral ears are small and convex. Shell 1mm thick, and up to 1.6mm thick in a large specimen. Some ventral valves are smooth apart from spines, whereas a few have low broad-crested costae, eleven to eighteen each side of the sulcus, and on some shells costae are of even strength, and on others in two or three orders, whereas dorsal valves are smooth, or in some specimens faintly ribbed. Fine pustules are present in the sulcus of the holotype, but for the most part the surface seems too worn to preserve pustules. Fine pustules cover the surface of the dorsal valve, but whether they are true surface ornament seems questionable. Very low and irregular growth-lines are present on some dorsal

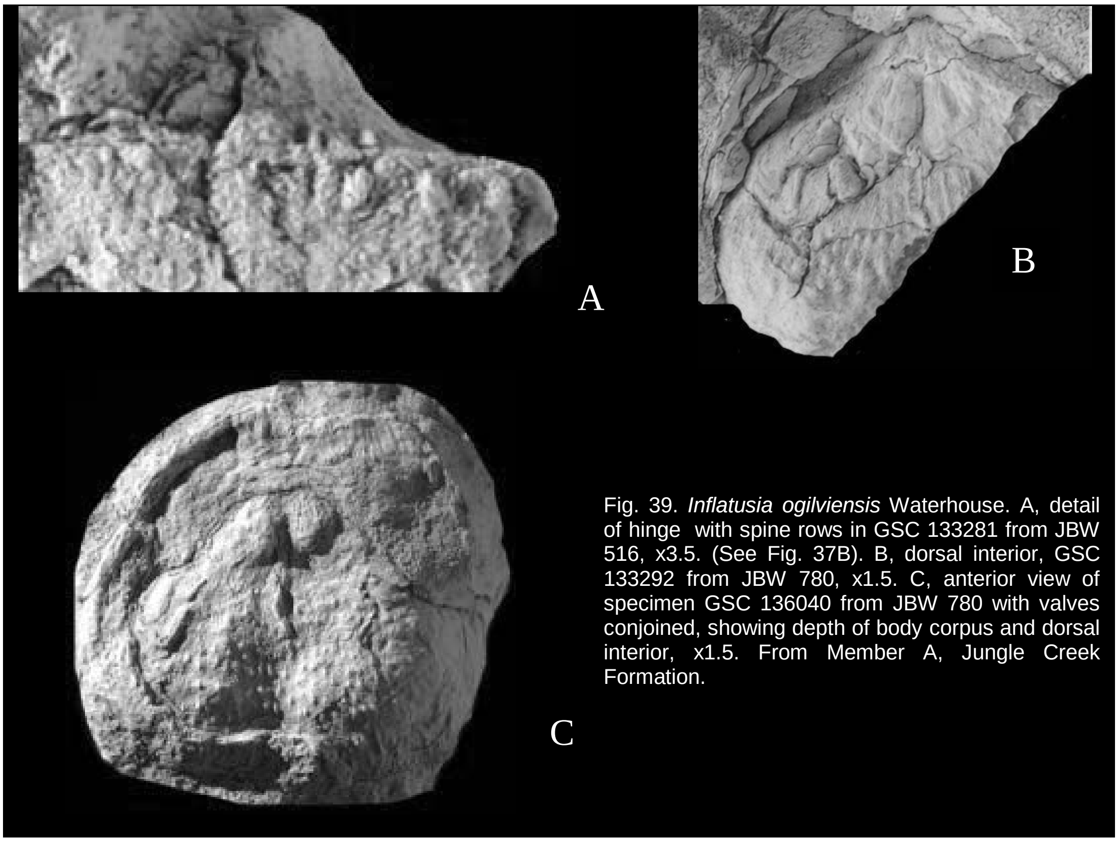


Fig. 39. *Inflatusia ogilviensis* Waterhouse. A, detail of hinge with spine rows in GSC 133281 from JBW 516, x3.5. (See Fig. 37B). B, dorsal interior, GSC 133292 from JBW 780, x1.5. C, anterior view of specimen GSC 136040 from JBW 780 with valves conjoined, showing depth of body corpus and dorsal interior, x1.5. From Member A, Jungle Creek Formation.

valves, but otherwise are not pronounced. Spines form a hinge row just front of the hinge on the ventral valve, numbering eight or nine each side of the umbo. They are less than 1mm in diameter until full maturity, when outer spines become up to 1.5mm in diameter and over 20mm long. Spines cover the ventral disc and trail, and are thick anteriorly, up to 2.5mm in diameter. The spines are most prominent along the high flanks each side of the sulcus, whereas spines are missing from the sulcus itself. On the small and immature holotype, 17mm wide, only two spines are developed along the hinge, and erect spines are developed on the flanks, 2 to 2.5mm apart anteriorly. Three well developed spines lie along the dorsal hinge, inclined postero-laterally, the outer spines measuring 0.6mm in diameter. No other dorsal spines are developed. A larger dorsal valve 26mm wide has nine spines each side of the umbo, and the outermost spine is just over 1mm wide.

The adductor field in a large mature ventral valve is over 15mm long and 3.5mm wide in a specimen nearly 40mm long, raised on a platform, with low median ridge and shallow groove each side. Diductor scars are large with longitudinal striae, commencing near the posterior third of the adductor platform and extending moderately far in front. Cardinal process obscure, base juts out slightly externally; low and slender median dorsal septum extending close to the anterior edge of visceral disc, dorsal adductor scars raised, and outer pair slightly lower and more slender. The brachial shields and ridges are visible, and heavy pustules are concentrated over the anterior disc, and only fine papillae lie over the trail. In a late mature specimen low ridges lie behind the anterior disc pustules. There is no lateral marginal ridge and no posterior marginal hinge ridge, but the papillae build up thickened shell anteriorly.

Resemblances: The genus so far is known only from the Yukon Territory of Canada, and comparisons with other genera were offered in Waterhouse (2013).

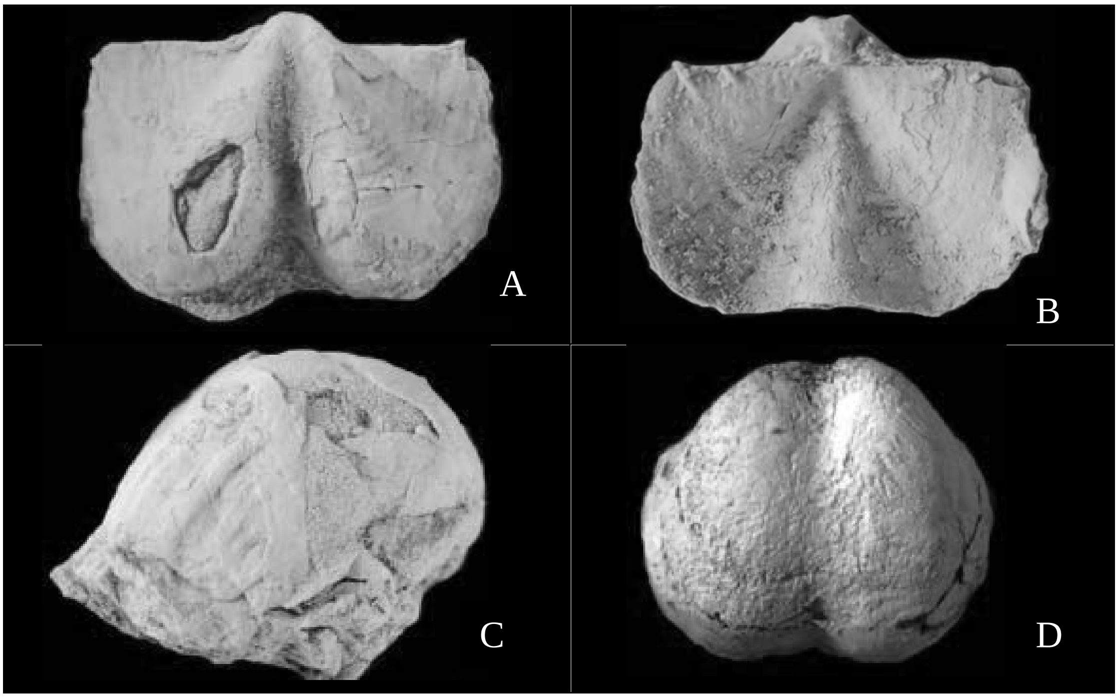


Fig. 40. *Inflatusia ogilviensis* Waterhouse. A, B, ventral and dorsal aspects of holotype, GSC 136036 from JBW 181, x3. C, lateral view of GSC 133289 (see also Fig. 37A), x1.5. D, anterior ventral view of small ventral valve GSC 136037 from JBW 606, x2. Member A, Jungle Creek Formation.

Genus ***Sangredonia*** Waterhouse, 2013

Diagnosis: Small, each valve with row of hinge spines, spines numerous over ventral valve, comparatively sparse over dorsal valve, no spines very robust.

Type species: *Horridonia*? *daltonensis* Sutherland & Harlow, 1973, p. 55 from Desmoinesian (mid-Pennsylvanian) of New Mexico, United States, OD.

Discussion: This genus has ventral ornament like that of *Bailliena* Nelson & Johnson, but the dorsal valve differs in having a row of hinge spines that are missing from both *Bailliena* and *Praehorridonia* Ustritsky in Ustritsky &

Chernyak, 1963. The row of hinge spines in each valve is like that of genera with Horridoniinae, but unlike most genera within that subfamily, including *Inflatusia* Waterhouse, there are no very stout spines.

Sangredonia alaminata n**.** sp.

Fig. 41, 42

2013 *Inflatusia ogilviensis* not Waterhouse, Fig. 3.15E (part, not p. 83, Fig. 3.12A-D, Fig. 3.13, Fig. 3.14A-C, Fig. 3.15A-D = *Inflatusia ogilviensis*).

Derivation: a – separation from; lamina – layer, slice, Lat.

Diagnosis: Row along hinge of each valve and dense over ventral valve, commarginal laminae poorly developed, dorsal valve only slightly concave.

Holotype: GSC 136038, here designated.

Material: Four ventral valves and two dorsal valves and fragments from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Description: The specimens are small and mostly immature with maximum width just in front of moderately large ears, and a gentle and narrow ventral sulcus. A small specimen measures 26mm wide, 16mm long and 7mm high, and another specimen is 28mm wide, 18.5mm long and 9mm high. The hinge is wide and bears a row of only moderately thick ventral spines, and the remainder of the ventral valve, including lateral flanks, bears numerous and moderately large spines in quincunx, forming rows over but not at the foot of the umbonal slopes, with low swollen bases, and discontinuous radial rugae over the trail. A sulcus is developed over the anterior disc and trail in some ventral valves, and a low fold is present on the dorsal valve. The dorsal valve shows a row of spines along the hinge, and a few anterior fine spines, but no pits.

Resemblances: In details of spination, this species is close to *Sangredonia daltonensis* from the Upper Carboniferous of New Mexico, but the dorsal valve is more planar, and both valves lack the commarginal laminae that characterize both valves of the type species of that genus, and lack the dorsal pits of the types.

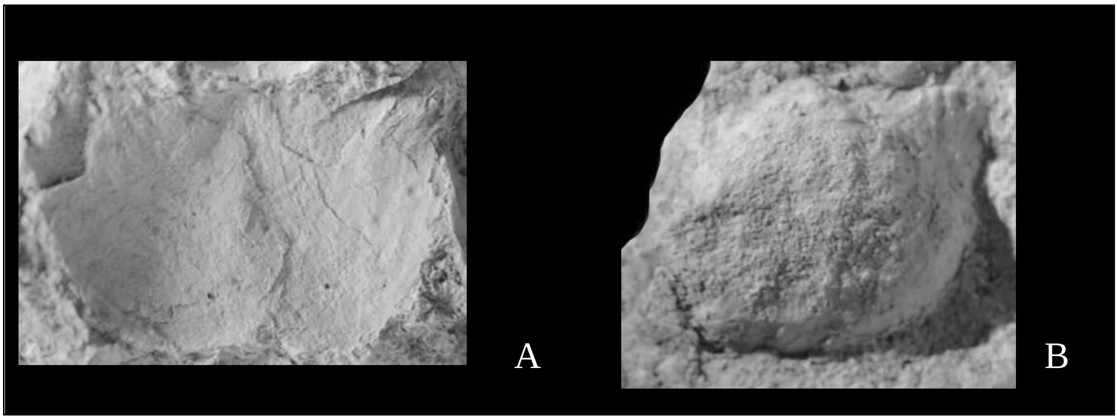


Fig. 41. *Sangredonia alaminata* n**.** sp. A, dorsal valve GSC 133283, x2. B, ventral valve GSC 137245 x2. From JBW 18, Member C, Jungle Creek Formation.

Bailliena yukonensis Nelson & Johnson (1968, pl. 90, fig. 1-11, pl. 91, fig. 13, 14, text-fig. 3a, b) is found in the Ettrain Formation of this region, older than this level. Spine bases are more closely spaced on the present form, and dorsal spines include a row along the hinge.

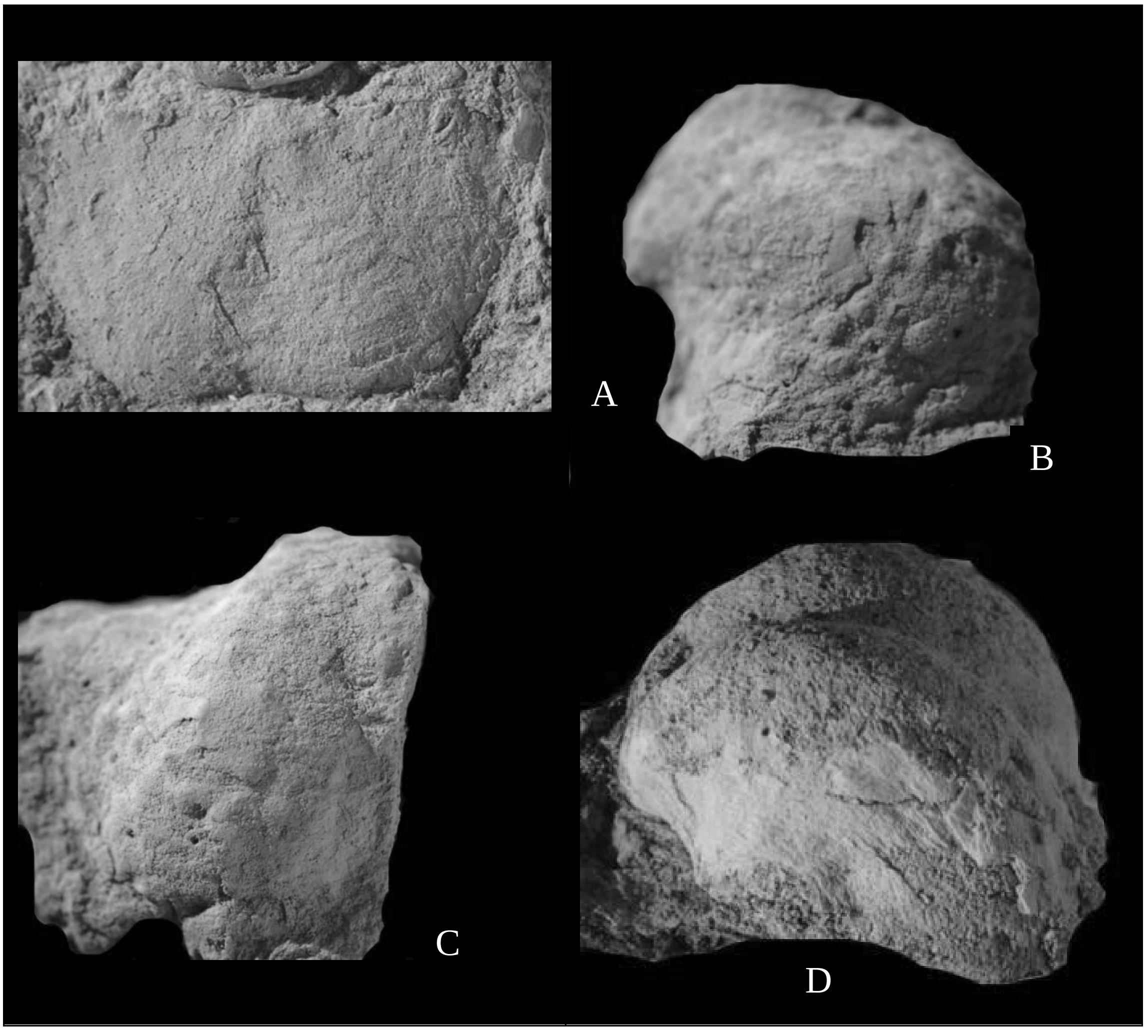


Fig. 42. *Sangredonia alaminata* n**.** sp. A, dorsal valve GSC 136729 x2.5. B, C, lateral and ventral aspects of ventral valve, GSC 136728, x2.5. D, tilted lateral view of ventral valve holotype, GSC 136038 x1.5. From JBW 18, Member C, Jungle Creek Formation.

Subfamily **BAILLIENINAE** Waterhouse, 2013

Diagnosis: Ventral spines moderately numerous over valve, dorsal valve bearing spines over anterior valve and trail, no dorsal hinge row of spines. Costae moderately well developed, on either ventral or dorsal valve, or both. Hinge and ear spines not strongly specialized on either valve. Lateral buttress plates may be present.

Discussion: The subfamily is characterized by the lack of dorsal hinge row of spines, presence of numerous thick but subequal spines and common presence of well developed costae. It involves the genera *Bailliena* Nelson & Johnson and *Praehorridonia* Ustritsky (spelled *Praechorridonia* by Lazarev 2011).

Genus ***Bailliena*** Nelson & Johnson, 1968

Diagnosis: Well inflated subequilateral shells, ventral valve covered by spines, including hinge row, dorsal valve with spines and pits over anterior disc and trail, no dorsal hinge row. Spines seldom very broad for the size of the shell, costae may be developed anteriorly. Lateral buttress plates.

Type species: *Bailliena yukonensis* Nelson & Johnson, 1968 from Ettrain equivalents (Kasimovian) at Peel River, Yukon Territory, Canada, OD.

Discussion: The presence of numerous spines on both valves, without a dorsal hinge row and often well ordered costae, provides a ready distinction from Horridoniinae Muir-Wood & Cooper and Sowerbininae Lazarev.

Bailliena aff. ***yukonensis*** Nelson & Johnson, 1968

Fig. 43

aff. 1961 *Pleurohorridonia scoresbyensis* Nelson, pl. 18, fig. 9, 10.
aff. Horridonid (sic) sp. Nelson, pl. 1, fig. 1a-e.
aff. 1968 *Bailliena yukonensis* Nelson & Johnson, p. 723, pl. 90, fig. 1-11, pl. 91, fig. 13, 14, text-fig. 3a, b.
aff. 1971a *Praehorridonia yukonensis* – Waterhouse, pl. 5, fig. 2, 3, pl. 7, fig. 4
aff. 2000 *B. yukonensis* – Brunton et al., p. 480, Fig. 323.2a-d.
aff. 2013 *B. yukonensis* – Waterhouse, p. 87, Fig. 3.17, Fig. 3.18.

Diagnosis: Large with low ribs over ventral valve, well formed ventral sulcus, low narrow dorsal fold.

Holotype: UC F1088 figured by Nelson & Johnson (1968, pl. 90, fig. 1-3) from Ettrain equivalents (Kasimovian), Peel River, Yukon Territory, Canada, OD.

Material: A specimen with valves conjoined from JBW 108.

Stratigraphic and biostratigraphic level: Ettrain Formation.

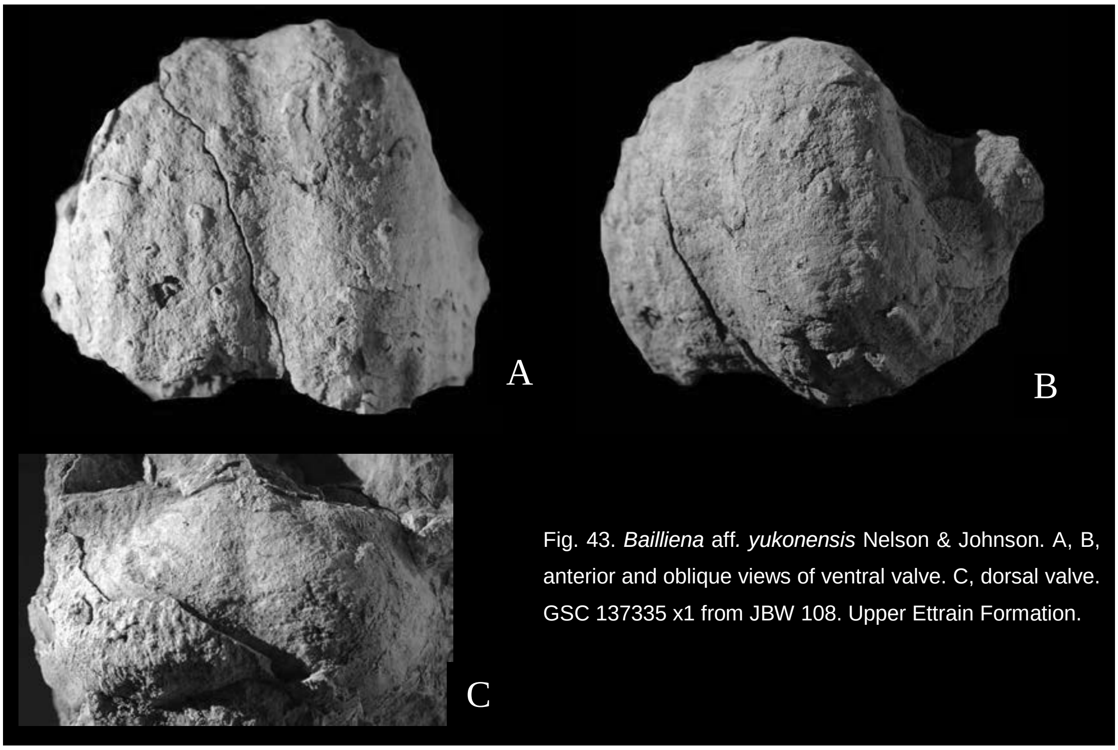


Fig. 43. *Bailliena* aff. *yukonensis* Nelson & Johnson. A, B, anterior and oblique views of ventral valve. C, dorsal valve. GSC 137335 x1 from JBW 108. Upper Ettrain Formation.

Description: The specimen is large, measuring 56mm in width, 45mm in length, and 47mm height, the visceral disc being nearly 25mm high anteriorly, and the trail is moderately long, extending 15mm beyond the abrupt curve from the disc. The ventral valve is highly convex with median sulcus and steep lateral flanks, and the ears extend to maximum width, with convex surface. The dorsal valve is concave with concave large ears and narrow anterior fold, and low anterior commarginal rugae. Broad erect spines are numerous over the ventral valve, and are semi-aligned in longitudinal rows, and some are connected by weak radial ribs. The ventral ears bear a few spines, with suggestions of a weak row along the hinge, and, exceptionally, one spine in front of the hinge is over 2.5mm in diameter. There are signs of a very few dorsal spines over the geniculation.

Resemblances: In size and shape and ventral spines, this specimen comes close to *Bailliena yukonensis* Nelson & Johnson, 1968, though ventral ribs are less developed in the present specimen and possibly slightly fewer in number, and there is no sign of lamellar shell, nor of pits regularly spaced over the dorsal valve. The types were said to lack dorsal hinge spines, as in the present specimen. There is a better formed ventral hinge row in the types. The overall shape, size and ornament point to a close relationship to *Bailliena yukonensis,* but more material might indicate that these differences are constant, and possibly of a different taxon. The present specimen came from near the top of the Ettrain Formation as defined in Bamber & Waterhouse (1971), whereas the types came from Ettrain equivalents exposed along the Peel River north of the Ogilvie Mountains.

Superfamily **PRODUCTOIDEA** Gray, 1840

[Nom. transl. Mailleux 1941, p. 7 ex Productidae Gray, 1840, p. 151].

Diagnosis: Spines few to numerous, halteroid and fine over ventral valve, may be clustered laterally, strong in some groups, may be numerous over dorsal valve. Radial ornament prominent, commarginal ornament varied but present and usually strong, shells small to large in size, simple to moderately elaborate and often geniculate trails. Corpus cavity shallow to deep, muscle adductor scars generally dendritic, marginal ridges moderate to high in Productidae and variably developed in other families.

Family **RETARIIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. Sarytcheva 1971, p. 35 ex Retariinae Muir-Wood & Cooper, 1960, p. 230].

Diagnosis: Medium to large shells with well formed reticulate ornament, spines form distinct row along ventral umbonal slopes.

Discussion: This family is large and varied, with well formed reticulate ornament, and lacks the diaphragm of Productidae, but is otherwise close.

Subfamily **RETARIINAE** Muir-Wood & Cooper, 1960

[Retariinae Muir-Wood & Cooper, 1960, p. 230].

Diagnosis: Medium-sized shells with large ears as a rule, dorsal spines commonly present. Dorsal median septum long, marginal ridge and ear baffles usually high in dorsal valve.

Tribe **RETARIINI** Muir-Wood & Cooper, 1960

[Nom. transl. Brunton, Lazarev & Grant 1995, p. 928 ex Retariinae Muir-Wood & Cooper, 1960, p. 230].

Diagnosis: Generally somewhat transverse shells with large ears and reticulate disc, may have strong spines at base of ventral umbonal flanks or over anterior shell, dorsal spines commonly present. External dorsal pits present in many genera. Dorsal adductor platform not high and cup-like.

Discussion: The two genera *Spyridiophora* Cooper & Stehli and *Alexenia* Ivanova in Ivanov, classed as Spyridiophorini Muir-Wood & Cooper by Brunton et al. (2000, p. 475), are very close to Retariinae, and may be retained as a tribe within Retariinae (Waterhouse 2013, p. 130). They share reticulate posterior shell, somewhat similar ventral spines and high ear baffles.

Genus ***Kutorginella*** Ivanova, 1951

Diagnosis: Ventral spines subuniform in strength, including well-formed row along umbonal slopes, dorsal spines erect, may be numerous. Trail may be nasute.

Type species: *Kutorginella mosquensis* Ivanova, 1951 from Kasimovian – Gzhelian of Moscow Basin, Russia, OD.

Discussion: The synonymy provided by Brunton et al. (2000, p. 472) needs to be modified. *Retaria* Muir-Wood & Cooper, 1960, p. 230), placed in synonymy of *Kutorginella*, may be distinguished by having a few halteroid ventral spines, much coarser than any spines in type *Kutorginella. Calliomarginatia* Jin, 1976, p. 181 is regarded as typified by the lack of dorsal spines, a feature shared with *Aspinosella* Waterhouse (1982c, p. 47). The type species of *Calliomarginata* is *C. himalayensis* Jin (Ching), 1976, p. 182, and this species has a row of hinge spines and row of spines over the ventral umbonal slopes. The type species of *Aspinosella, Kutorginella uddeni* Cooper & Grant, 1975, has more spines over the venter and umbonal slopes and few hinge spines. Both were synonymized with *Kutorginella* by Brunton et al. (2000, p. 472), but *Calliomarginatia* is now regarded as a close ally of *Kutorginella*, and *Aspinosella* as an ally of *Thamnosia*, both distinguished from sibling genera by the absence of dorsal spines. *Pitakpaivania* Waterhouse 2004a, p. 69 is closely allied to *Kutorginella* and *Retaria*, and is based on *K. aprica* Grant (1976, p. 143, pl. 38, fig. 1-18) from the early Middle Permian of south Thailand. It is distinguished by the weak development of hinge and umbonal slope rows of ventral spines, numerous spines over the venter and admixed coarse halteroid and very fine spines over the anterior ventral valve: dorsal spines are fine. In these respects the form differs from the array of species that belong to *Retaria* from the Permian of the Glass Mountains in Texas, which had been described as *Kutorginella* by Cooper & Grant (1975), and although they share large strut spines, the strut spines are differently placed from those of the American species, with the anterior pair lying further from the mid-line. The coarser ribs and better developed sulcus and fold of the United States species help circumscribe a closely similar set of species, distinguishable as the genus named *Retaria* Muir-Wood & Cooper, later questionably placed in synonymy with *Kutorginella*. Russian and Canadian species lack the large strut spines and have better developed umbonal slope and hinge spines as a rule, and moderately well formed sulcus and fold, and so form another subset, referable to *Kutorginella*. Another close ally is *Tubaria* Muir-Wood & Cooper, 1960, characterized by its extended and tubiform anterior margin. *Tesuquea* Sutherland & Harlow, 1973 has fine ribs and a prominent row of spines which may increase to two rows over the umbonal slopes, and lacks a groove in front of the dorsal ears, unlike members of Rigrantinai Lazarev (see p. 82). *Thamnosia* Cooper & Grant, 1969 has numerous spines on lateral slopes and ears, and spines are also numerous on the anterior shell.

Brunton et al. (2000, p. 475) synonymized the genus *Thuleproductus* Sarytcheva & Waterhouse, 1972 with *Thamnosia*. This genus is based on a very large species, much larger than any Texan species of *Thamnosia. Thuleproductus* has also been synonymized by Ustritsky with *Svalbardoproductus* Ustritsky, 1962**,** p. 82, based on a similarly large species *S. striatoauritus* Ustritsky from Spitsbergen. Brunton et al. (2000) suggested that *Svalbardoproductus* was to be distinguished by the lack of spine clusters from the ears and weak ribbing that faded anteriorly, but these facets are yet to be verified, and therefore, if *Thamnosia* is senior synonym for *Thuleproductus*, it is possible that *Svalbardoproductus* is senior synonym for *Thamnosia* (see pp. 79-80).

Other genera allocated to Tribe Retariini by Brunton et al. (2000) are further removed from *Retaria* and *Kutorginella. Keokukia* Carter, 1990 is not particularly close, but possibly represents a step between Productinae and

Retariinae, externally close to *Productus*, internally closer to *Retaria.* The well-described *Promarginifera* Shiells, 1966, another Early Carboniferous genus, stands apart, especially in terms of ornament. *Kelamelia* Zhang Zi-xin in Zhang et al. 1983 is poorly known, and seems moderately close to *Inflatia* Sarytcheva, and Inflatinae Sarytcheva, whilst *Marginoproductus* Tan Zhen-xiu, 1986 shows little similarity, and Brunton et al. (2000) suggested that the genus might be closer to Tolmachoffiinae.

Kutorginella yukonensis Sarytcheva & Waterhouse, 1972

Fig. 44 - 50

1971 *Kutorginella* n. sp. Bamber & Waterhouse, pl. 12, fig. 1, 2.
1971 *Kutorginella* sp. Bamber & Waterhouse, pl. 14, fig. 14, pl. 16, fig. 16.
?1971 *Kutorginella neoinflatus* (not Licharew) – Bamber & Waterhouse, pl. 12, fig. 4.
1972 *Kutorginella yukonensis* Sarytcheva & Waterhouse, p. 501, pl. 7, fig. 1, 2.
1972 *K. triangulata* Sarytcheva & Waterhouse, p. 505, pl. 7, fig. 3-8.
1996 *K. yukonensis* Shi & Waterhouse, p. 82, pl. 7, fig. 1-19.

Diagnosis: Moderately large usually transverse shells with well defined ventral sulcus and broad umbo, seven to nine costae in 10mm at mid-length. Ventral myophragm well developed.

Holotype: GSC 26353 from GSC 53722, Jungle Creek Formation (Sakmarian), figured by Sarytcheva & Waterhouse (1972, pl. 7, fig. 1), OD.

Material: From Member A, a ventral fragment from JBW 562, a ventral valve from JBW 82 and possibly from JBW 420, a specimen with valves conjoined from JBW 4, three ventral valves and two incomplete specimens with valves conjoined from JBW 71, and two ventral valves from JBW 77 and 591, twenty ventral valves and nine dorsal valves, poorly preserved, from JBW 75, two dorsal valves from JBW 122, seven ventral valves, and single dorsal valve from JBW 518 and 548, two ventral valves each from JBW 66, 136, 571 and 591, two ventral valves and a dorsal valve from JBW 95, dorsal valve from JBW 643 and two dorsal valves and specimen with valves conjoined from JBW 513. From Member E, single ventral valves from JBW 195, 557 and C-6167, three ventral valves from JBW 66, five ventral valves and specimen with valves conjoined from JBW 538, two ventral valves and a dorsal valve from JBW 577, twelve ventral valves and three dorsal valve from JBW 580, a ventral valve and specimen with valves conjoined from JBW 539, three dorsal valves and specimen with valves conjoined from JBW 561, three ventral valves, a dorsal valve and four specimens with valves conjoined from JBW 99, and thirty five ventral valves, twenty one dorsal valves and six specimens with valves conjoined from JBW 581. Two ventral valves and dorsal valve from GSC 56920 and 56946. From Member D, poorly preserved specimens are also close to the same species. Material includes three ventral valves and two dorsal valves from JBW 17, one dorsal and one ventral valve from JBW 65, a ventral and dorsal valve from JBW 72, five ventral valves and a dorsal valve from JBW 73, one dorsal valve, two ventral valves and specimen with both valves conjoined from JBW 137, a dorsal valve from JBW 564, two ventral valves from JBW 132, and four ventral valves and five dorsal valves from JBW 762.

Stratigraphic and biostratigraphic level: Members A, D and E, Jungle Creek Formation. *Septospirifer tatondukensis* Zone, *Rugivestigia commarginalis* Zone and *Ogilviecoelia shii* Zone.

Description: The specimens from Member A include broken fragments of internal and external moulds. One ventral valve from JBW 75 measures 30mm wide, 31mm long and 15mm high, another 17mm wide, 16.5mm long and 5.5mm high, but both are broken, and ears lost. A specimen from JBW 82 is 56mm wide, 28mm long and +12mm high. The disc is 14mm thick in an internal mould from JBW 99 that is 45mm wide. There is a gentle to moderately deep sulcus. The dorsal valve is flat over the disc, with a geniculate trail, but other specimens have a low anterior fold over the disc. Costae number four in 5mm. Slender spines form a single row on the inner umbonal slopes, and are few over the ventral disc in specimens from JBW 135. Fine pits lie over the floor of the ventral valve, and the dorsal median septum extends just past mid-length. Only a few spines lie over the dorsal valve, concentrated over the ears and start of the trail.

In specimens from Members D and E, the ventral valve is strongly convex and normally transverse, umbonal angle between 90º and 120º, umbonal slopes steep and high, ears set well below disc, but usually

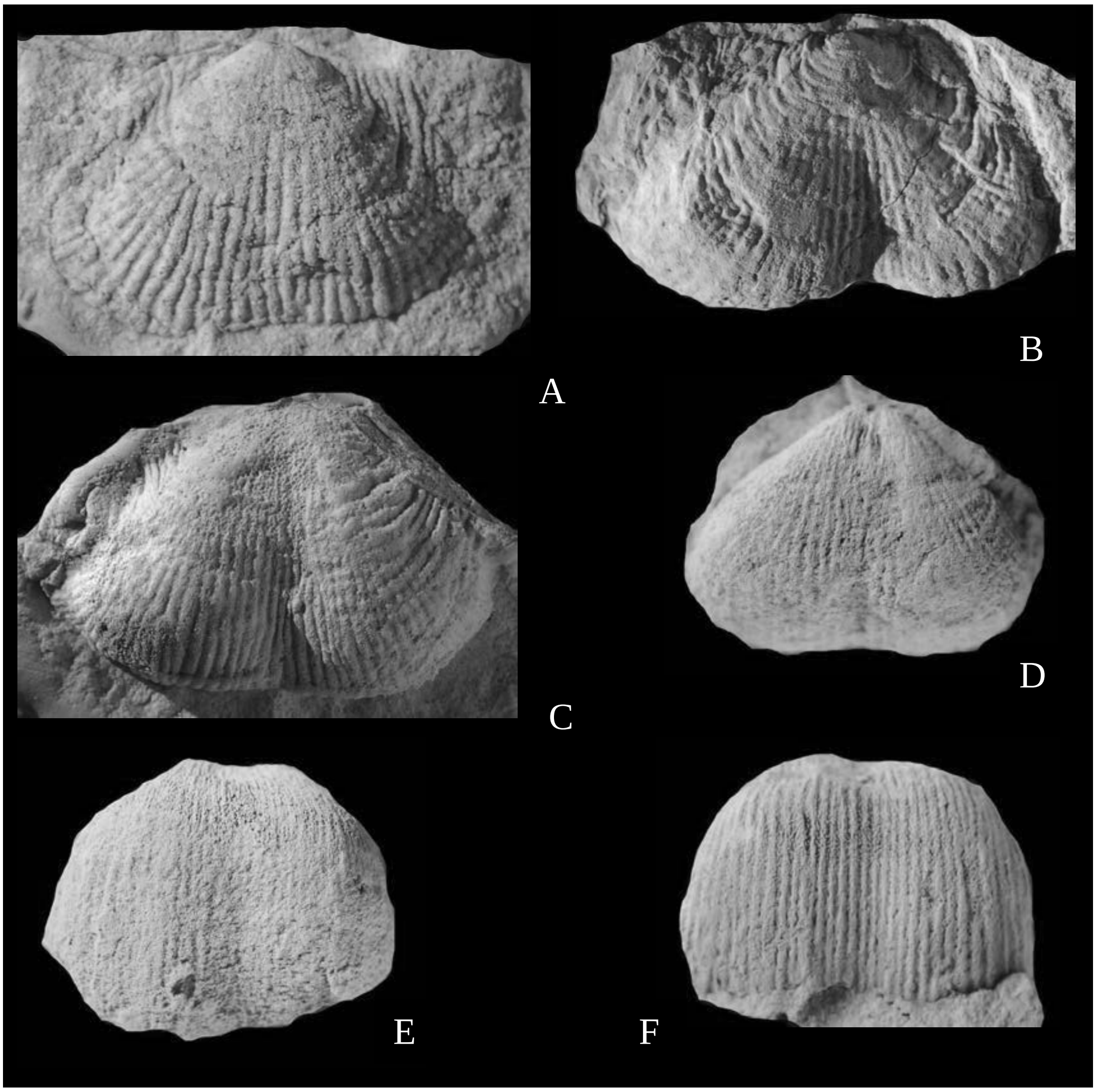


Fig. 44. *Kutorginella yukonensis* Sarytcheva & Waterhouse. A, cast of ventral valve, GSC 136735 from JBW 136, x1.5. B, ventral internal mould, GSC 137742 from JBW 518, x1.5. C, cast of ventral valve GSC 137732, x1, from JBW 82. D, ventral internal mould GSC 136733, x1.5 from JBW 71. E, anterior ventral aspect of internal mould GSC 136734, x1, from JBW 99 (Member E). F, anterior ventral aspect of internal mould, GSC 137735, x1.5, from JBW 71. All except Fig. 44E from Member E come from Member A, Jungle Creek Formation.

broken, sulcus commences in front of umbo, and widens at angle close to 30º, usually persists to anterior margin, but in some shells the sulcus is best defined at start of trail, which is as long as the disc. Hinge of the disc, excluding ears, extends for only half of the width of the shell. Dorsal disc comparatively flat and with very low swelling or fold commencing mid-disc, and increasing in definition to anterior margin, trail geniculate and more than half the length of the disc. Ribs commence at ventral umbo and strong over the disc except laterally and over the trail, some eight in 10mm at mid-length and six or seven in 10mm anteriorly, with well rounded crests and interspaces of comparable definition, the ridges branching anteriorly. Lateral shell is smoother, and low growth rugae lie over umbonal slopes. Dorsal valve ribs finer and at least some increase anteriorly by intercalation. Low growth rugae more prominent on the dorsal valve than on ventral valve. Stout and erect ventral spines form a row in front of the ears, and another row extends along the hinge. There is a scattering of spines over the disc, and erect spines almost 1mm in diameter form four to six rows in quincunx over the trail, all erect and emerging from the crests of the costae. Dorsal spines are erect and sturdy, and are restricted to a scattering rather than regular row or rows over the ears and just in front, with diameter of 0.6mm, and spines may develop in one or two rows on the trail, especially in front of the geniculation. A dorsal exterior from JBW 561 displays a number of ear spines and trail spines, and the disc is ornamented by both ribs and commarginal fine rugae.

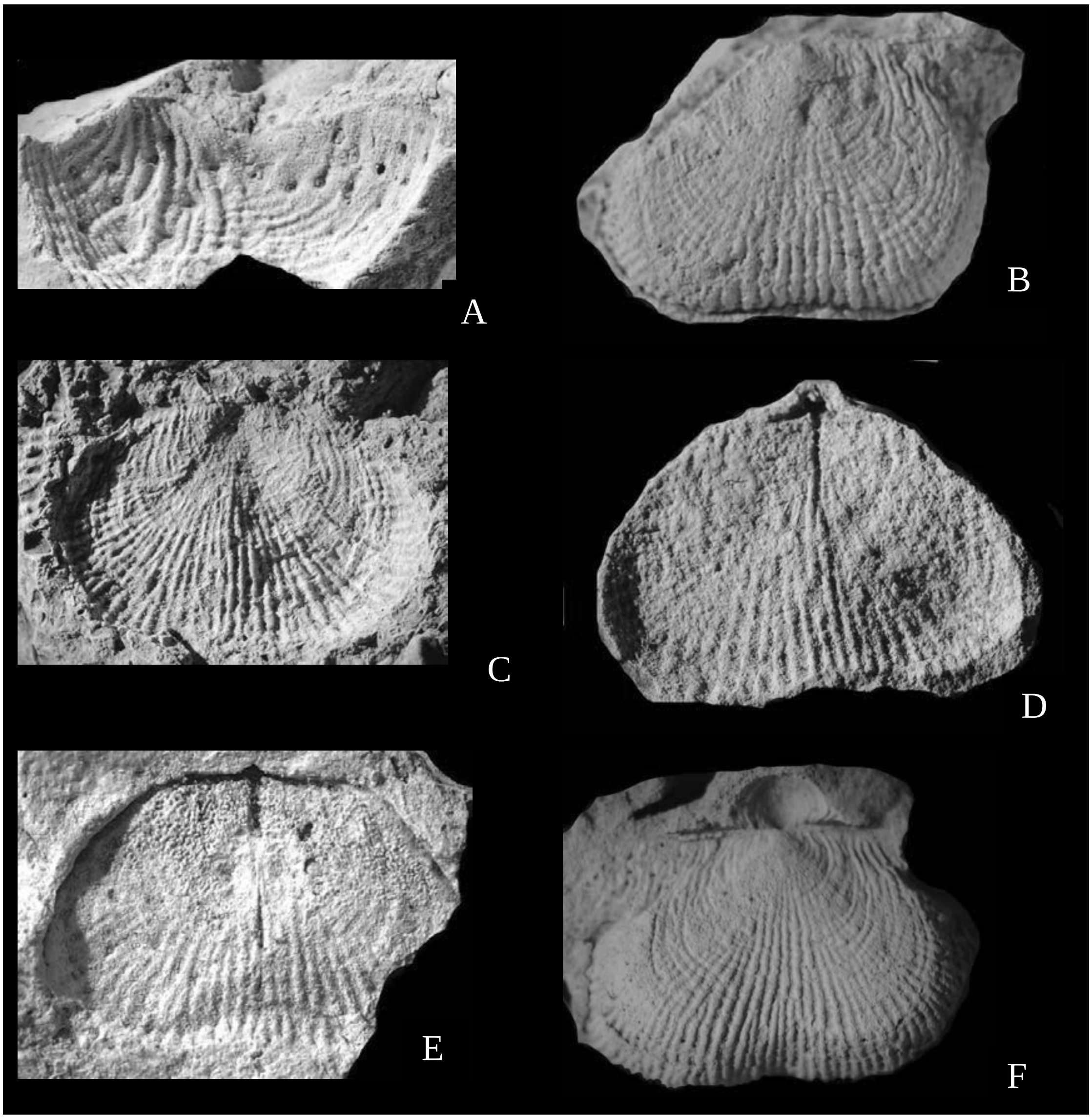


Fig. 45. *Kutorginella yukonensis* Sarytcheva & Waterhouse. A, part of external ventral mould showing row of spines along umbonal slopes, GSC 136736 x2 from JBW 65 (Member D). B, external mould of dorsal valve, GSC 136750 x2 from JBW 561 (Member E). From Member A, the following: C, dorsal exterior, GSC 136738 x1.5 from JBW 543. D, dorsal aspect of internal mould, GSC 136739 x2 from JBW 66. E, dorsal internal mould, GSC 136740 x2 from JBW 75. F, dorsal external mould, GSC 136737 x2 from JBW 71. Jungle Creek Formation.

Ventral adductor platform small, often divided by strong myophragm, diductor scars anteriorly placed and impressed, marked by longitudinal ridges. Remainder of floor marked by fine dense pustules, that in smaller shells are restricted to the posterior shell. Dorsal medium septum extends beyond mid-length, posteriorly broad with median groove; adductor scars narrow and not strongly delineated, may be weakly dendritic or smooth anteriorly; brachial ridges seldom visible, posterior floor covered by dense pustules. Marginal ridge high but slender, and extends from cardinal process along hinge and inside the ears to enclose the disc.

Resemblances: Although some Member A specimens have a more elongate outline, and flatter dorsal disc than type *Kutorginella yukonensis* Sarytcheva & Waterhouse from the younger Jungle Creek Formation, and in some ventral valves the sulcus is shallower than in type *yukonensis*, they show a degree of variation that encourages a merging of populations under one taxon.

There is considerable approach to *Kutorginella stepanovi* (Lapina, 1957), but specimens attributed to *Kutorginella*? *stepanovi* by Abramov & Grigorieva (1983, pl. 5, fig. 3-9, text-fig. 20) have a more elongate shape,

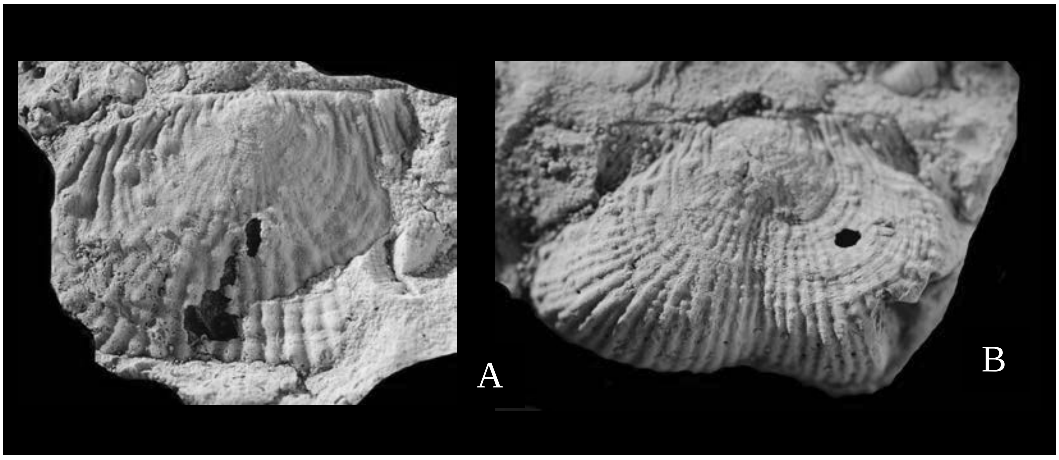


Fig. 46. *Kutorginella yukonensis* Sarytcheva & Waterhouse. A, external mould of dorsal valve GSC 137282 x2.5 from JBW 581. B, external mould of dorsal valve GSC 136746 x2 from JBW 581. Member E, Jungle Creek Formation.

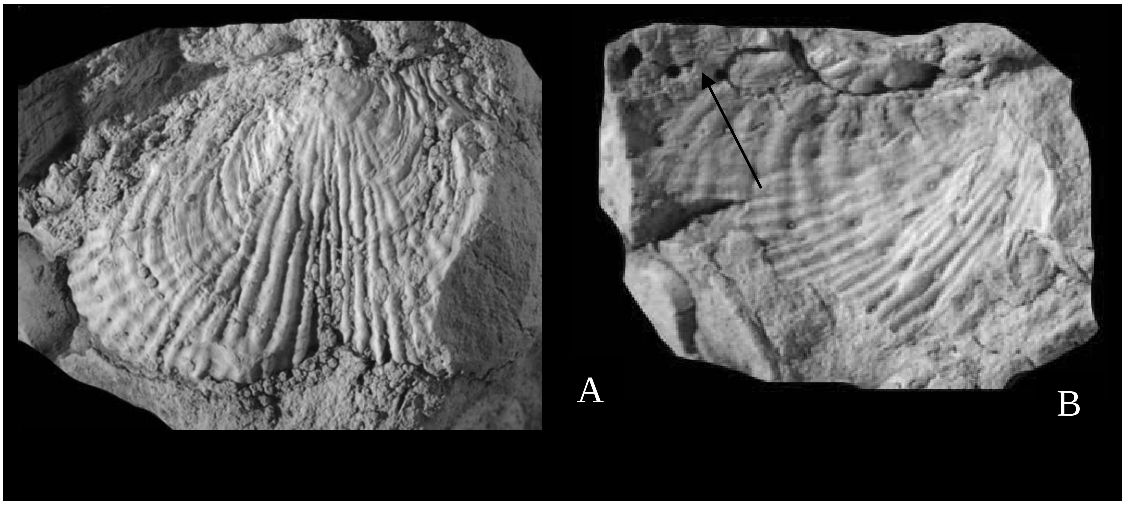


Fig. 47. *Kutorginella yukonensis* Sarytcheva & Waterhouse. A, dorsal external mould, GSC 136753. B, external cast of ventral valve GSC 136747, arrow pointing to umbonal slope row of spines. From JBW 581, x2. Member E, Jungle Creek Formation.

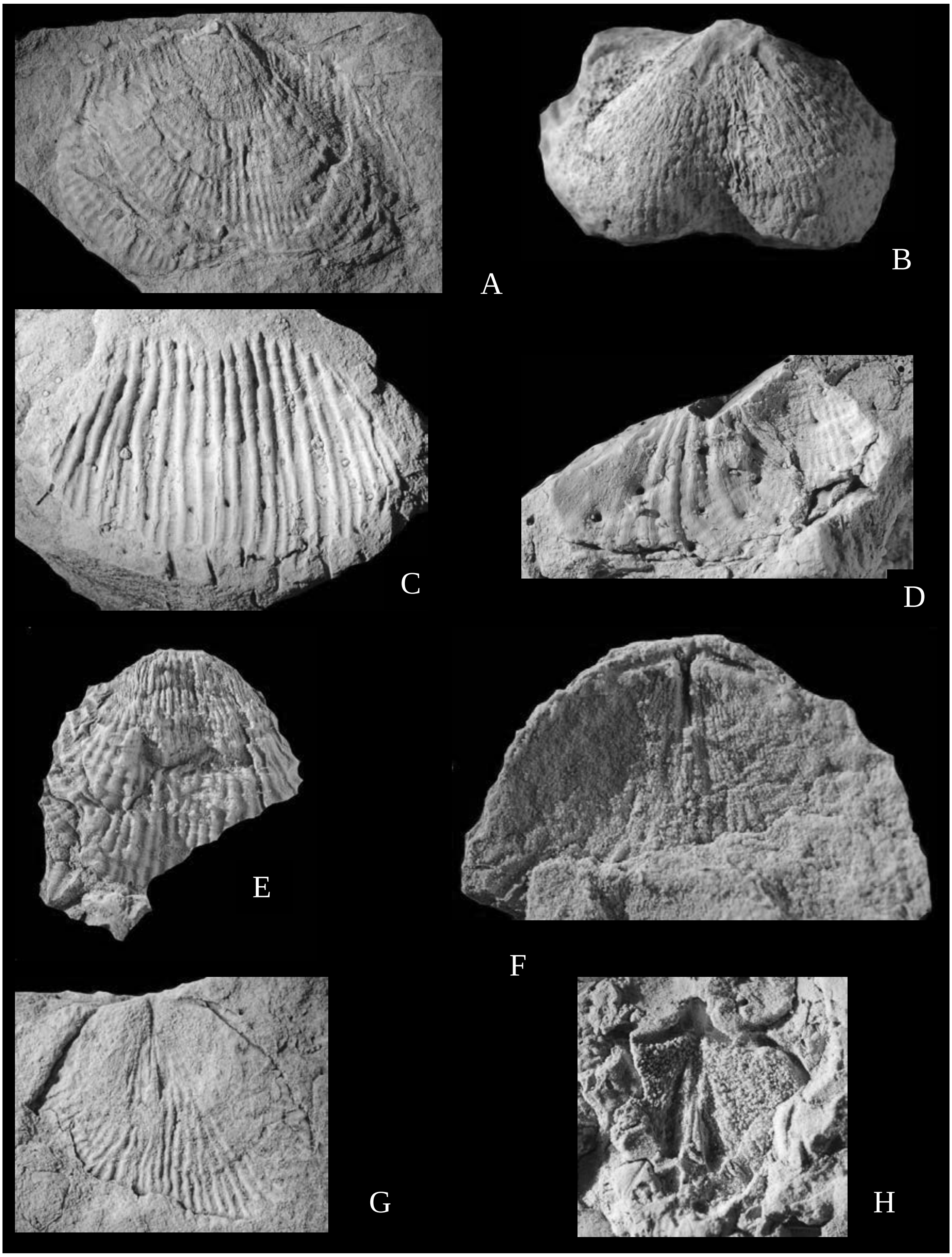


Fig. 48. *Kutorginella yukonensis* Sarytcheva & Waterhouse. A, ventral valve GSC 136741 x2 from JBW 77. B, ventral aspect of internal mould GSC 136742 x1.5, from JBW 66 (Member A). From Member E, the following: C, external mould of anterior ventral valve, GSC 136749 x2 from JBW 581. D, fragment of ventral external mould showing umbonal row of spines, GSC 136794 x2, from JBW 580. E, F, ventral and dorsal aspects of internal mould, GSC 136745 x2, x4, from JBW 581. G, dorsal internal mould GSC 136747 x2 from JBW 581. H, internal mould GSC 137247 x2 from JBW 581. Jungle Creek Formation.

and finer costae. Spine detail is not entirely clear, and specimens have a shallower sulcus than in the Canadian material (cf. Stepanov 1975, pl. 77, fig. 3, 4). The Russian form comes from the Kigiltass, Davnin, Mishkin and Etiken

Suites of Middle Late Carboniferous age in Verchoyan, and chiefly from the lower Late Carboniferous (Kirov level) of the Urals. *K. mosquensis* Ivanova, as figured by Lazarev (1990, pl. 19, fig. 1-11) from Kasimovian faunas of the Moscow Basin, has slightly finer ribs and transverse shape.

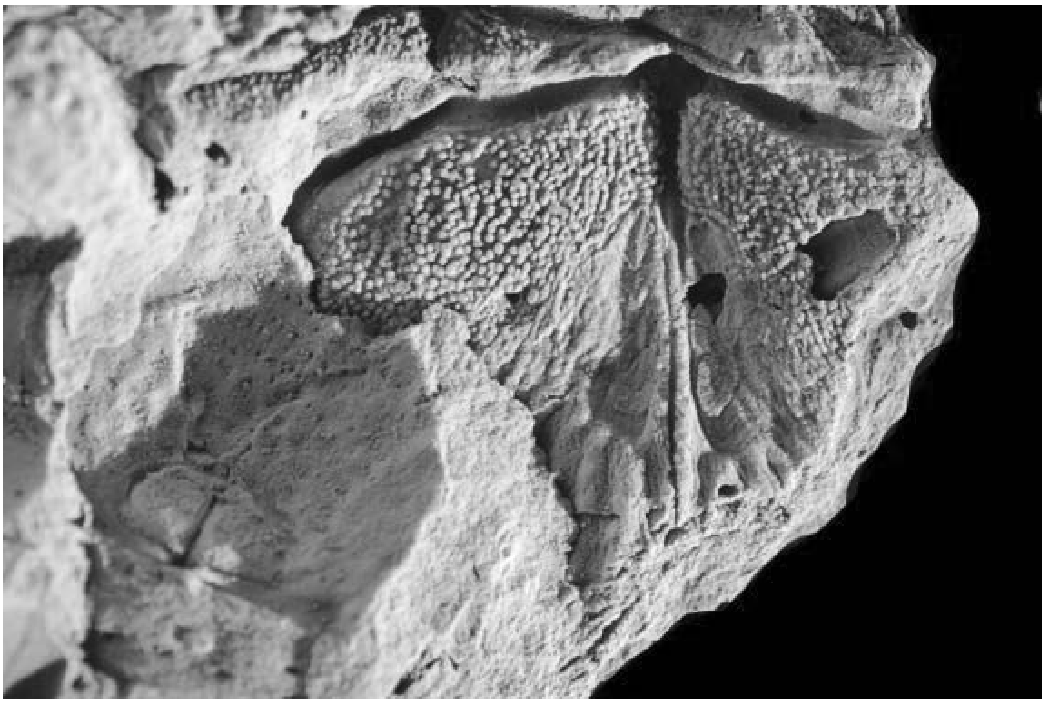


Fig. 49. *Kutorginella yukonensis* Sarytcheva & Waterhouse, internal mould, of dorsal mould GSC 137246 from JBW 581, x7, with dorsal internal mould of the strophalosioid species *Echinalosia minuta* n. sp. GSC 136887 to lower left (see p. 179). Member E, Jungle Creek Formation.

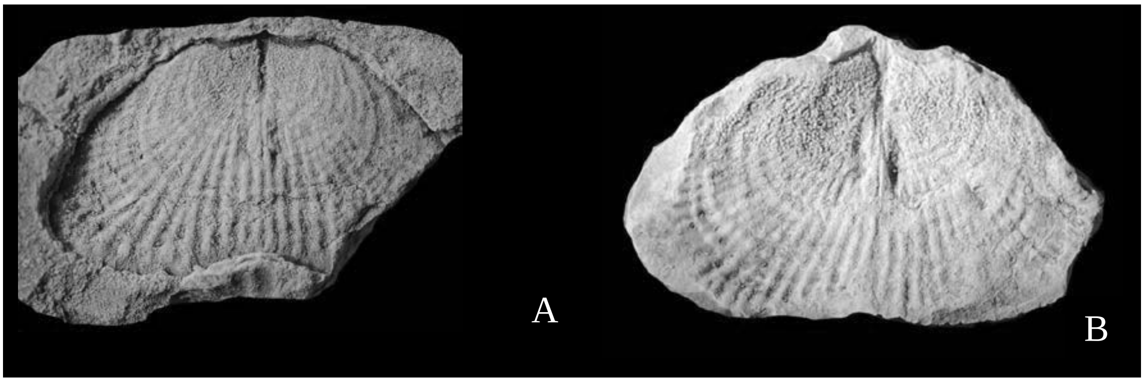


Fig. 50. *Kutorginella yukonensis* Sarytcheva & Waterhouse. A, internal mould, of dorsal mould GSC 136751. B, dorsal internal mould GSC 136752. From JBW 581, x2. Member E, Jungle Creek Formation.

***Kutorginella*? sp.**

Fig. 51

A specimen with valves conjoined from JBW 18, Member C, Jungle Creek Formation. The generic position is not confirmed, because spine detail is not revealed. *Kochiproductus imperiosus* Zone.

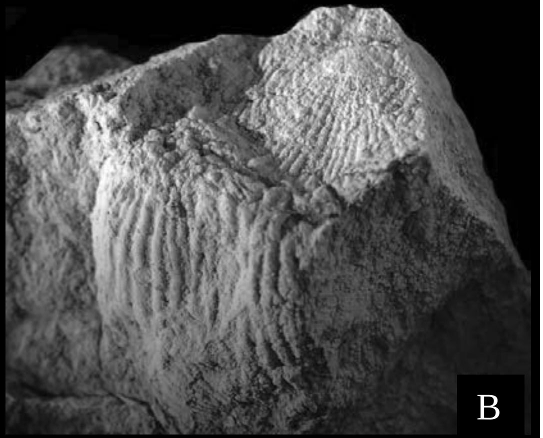


Fig. 51. *Kutorginella?* sp., ventral oblique aspect of specimen with valves conjoined, showing anterior ventral trail and dorsal disc, both from external aspect, GSC 137284 x2 from JBW 18. Member C, Jungle Creek Formation.

Genus ***Thamnosia*** Cooper & Grant, 1969

Diagnosis: Of medium size with maximum width at hinge, sulcate, trail long, ventral spines numerous over ears, lateral slopes and anterior trail, dorsal spines thin and erect.

Type species: *Thamnosia anterospinosa* Cooper & Grant, 1969, p. 10 from Cathedral Mountain Formation (Kungurian) of west Texas, OD.

Discussion: *Svalbardoproductus* Ustritsky (1962, p. 82) from the Kungurian of Spitsbergen looks like *Thamnosia*, but is much larger. Ustritsky (1979, pp. 127, 128) claimed that *Thuleproductus* Sarytcheva & Waterhouse is a synonym of *Svalbardoproductus* Ustritsky (1962). I am greatly obliged to Dr Tatiana Grunt for translating his published opinion, and for providing translations of his earlier work on the subject. Ustritsky claimed that his material of *S. striatoauritus* (*stratoauritus* according to Brunton et al 2000) from the basal horizon of the Cape Starotsin Formation on Svalbard had been passed on to the Paleontological Institute in Moscow, and that it had been redescribed as *Tuleproductus* (sic) *subarcticus* Sarytcheva (1977a – see pp. 78, 79, pl. 9, fig. 1-3, text-fig. 48). It was further considered that the Spitsbergen outcrops yield a succession of species, *subarcticus* = *striatoauritus*, followed by *arcticus* Whitfield, followed in the Selander Formation by *crassauritus* Sarytcheva & Waterhouse, all three belonging to the one genus.

But certainty is still lacking, although it may well prove that Ustritsky is right. Here are the difficulties. In the first place, the species *subarcticus* was based on material from River Kozhim, Petchora Basin, not Spitsbergen, and even in the Sarytcheva account, the exterior of the dorsal valve is not illustrated. It is very difficult to reconcile the original description of *Svalbardoproductus* by Ustritsky (1962) with the description of *Thuleproductus* Sarytcheva & Waterhouse, 1972. Ustritsky (1962) emphasized the lack of concentric (=commarginal) ornament from the ventral ears of *Svalbardoproductus striatoauritus*, but it might prove somewhat variable, because commarginal ornament is visible on at least the inner ears in the type of *subarcticus* Sarytcheva (1977a, pl. 9, fig. 1a, 1b). Ustritsky (1962) stated that spines were absent from the ears in *striatoauritus*, and Brunton et al. (2000, p. 475) repeated this observation, stating that *Svalbardoproductus* was "lacking spine clusters from ears" and noting that ribs were indistinct anteriorly. These observations were not qualified in any way by Ustritsky (1979), to imply they did not need changing. Yet these aspects of the description of *Svalbardoproductus* are completely different from the ornament in

Thuleproductus crassauritus, which has numerous spines over the ventral ears, and firm ribs persisting to the anterior margin. Finally, Ustritsky (1962) rated his genus as being closest to *Peniculauris* Muir-Wood & Cooper (1960), apart from the lack of ear spines. It is doubful whether any expert would confuse *Thuleproductus* with *Peniculauris,* a buxtoniid rather than retariid. Somehow, were Ustritsky (1979) correct, *Svalbardoproductus* Ustritsky, 1962 has morphed over the years into *Thuleproductus* Sarytcheva & Waterhouse, 1972. The name *Thuleproductus* goes, but the description stays. The name *Svalbardoproductus* stays, but the description goes. That is by no means impossible, for paleontological descriptions are not infallible. Yet Ustritsky (1979) did not adjust his description.

In summary, it may well prove necessary to synonymize *Thuleproductus* with *Svalbardoproductus*. But first, there have to be corrections to the original description of *Svalbardoproductus*, and acceptance that ear spines are numerous, not absent as asserted by Ustritsky, and that ribs do not necessarily disappear or become very faint at the anterior margin. And that there is little similarity to *Peniculauris*. And of equal importance, the nature of the dorsal exterior needs to be determined, to clarify the nature of the spines. The ignorance concerning dorsal spinosity for *subarcticus* is bad enough, but the ignorance concerning a proposed genus, *Svalbardoproductus*, is crippling. Why? Because various genera in Retariinae have been recognized partly on the basis of dorsal spinosity. *Svalbardoproductus* might be senior synonym for *Thuleproductus*. But it equally might be senior synonym for *Thamnosia* Cooper & Grant, 1969, which differs from *Thuleproductus* in having fewer dorsal spines, especially over the ears. Until clarification, we can only guess at the limits of *Svalbardoproductus*, because *Kutorginella, Thamnosia* and *Thuleproductus* all potentially occur in Arctic faunas.

A dorsal valve figured as *Svalbardoproductus* sp. from Timan, Russia, by Lazarev (1990, pl. 19, fig. 10) is small with well formed marginal ridge and numerous pustules over the inner ventral ears, suggestive of spines, but the dorsal exterior and most of the ventral valve are not shown, leaving the identity insecure.

Brunton et al. (2000, p. 475) synonymized the genus *Thuleproductus* Sarytcheva & Waterhouse, 1972, p. 67 with *Thamnosia* Cooper & Grant, 1969, p. 10. This appears to be a mistake. The type species of *Thamnosia, T. anterospinosa,* has been examined and compared at the Smithsonian Institution, Washington, D. C., and is large with numerous spines over the ventral ears and umbonal flanks, and near the anterior margin. Dorsal spines are not very numerous. *Thuleproductus* is based on a very large species, much larger than any Texan species of *Thamnosia,* and has much larger ears than in the type species *Thamnosia anterospinosa*, and notably far more numerous spines over the dorsal ears. Spines are much less numerous over the ventral flanks and ears than in *anterospinosa*, but are numerous over the dorsal valve anteriorly. Internally the dorsal marginal ridge is high posteriorly and laterally, but stops short of the anterior margin, whereas the ridge persists around the anterior in a number of well preserved *Thamnosia*. Of other species from the Permian of Texas that belong to *Thamnosia, T. phragmophora* Cooper & Grant (1975) has moderately large ears, and largish anterior lateral ventral spines (Cooper & Grant 1975, pl. 346, fig. 19) but the dorsal ear spines are not fully clear. *T. parvispinosa* (Stehli) certainly has moderately large ears and numerous ventral spines, so many that lateral rows are not clearly observable, and as in *T. anterospinosa*, dorsal spines are not nearly as numerous as in *Thuleproductus*. Although smaller, *T. silicica* Cooper & Grant, 1975, p. 1036, pl. 351, fig. 1-18 from the Hess Formation of the Glass Mountains Texas, is closer to *Thuleproductus crassauritus* in some respects, in that spines are numerous over the dorsal valve, including, it appears, the ears, and also numerous over the anterior dorsal valve and over the ventral valve, including fine numerous spines over the lateral slopes. It may be identified as *Thuleproductus silicica* (Cooper & Grant), ancestral to younger *Thuleproductus* and to *Thamnosia* through loss of numerous ear spines. Or is it *Svalbardoproductus*? Of course, if *Thamnosia* is senior synonym of *Thuleproductus*, as proposed by Brunton et al. (2000), and if *Svalbardoproductus* is senior synonym of *Thuleproductus*, as analyzed by Ustritsky (1979), then *Svalbardoproductus* must be senior synonym of *Thamnosia* as well. I suspect that *Thamnosia* will prove valid, and *Svalbardoproductus* could be senior synonym of *Thuleproductus*. But that is only a suspicion: evidence is needed, and relies on the supposition that Ustritsky (1962) had completely misrepresented the genus he was proposing as new.

Thamnosia? cf. ***spinosa*** Shi & Waterhouse, 1996

Fig. 52

cf. 1996 *Thamnosia spinosa* Shi & Waterhouse, p. 84, pl. 7, fig. 20-22, pl. 8, fig. 1-8.

Diagnosis: Medium to large shells with long trail and ventral spines in two to four rows over posterior lateral slopes, numerous over middle and anterior trail.

Holotype: GSC 96968 from "*Yakovlevia transversa*" Zone (Sakmarian), figured by Shi & Waterhouse (1996, pl. 8, fig. 6, 8) from Jungle Creek Formation, Yukon Territory, OD.

Material: Three small and incomplete ventral valves from JBW 135, anterior trail of ventral valve and part of external dorsal mould from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

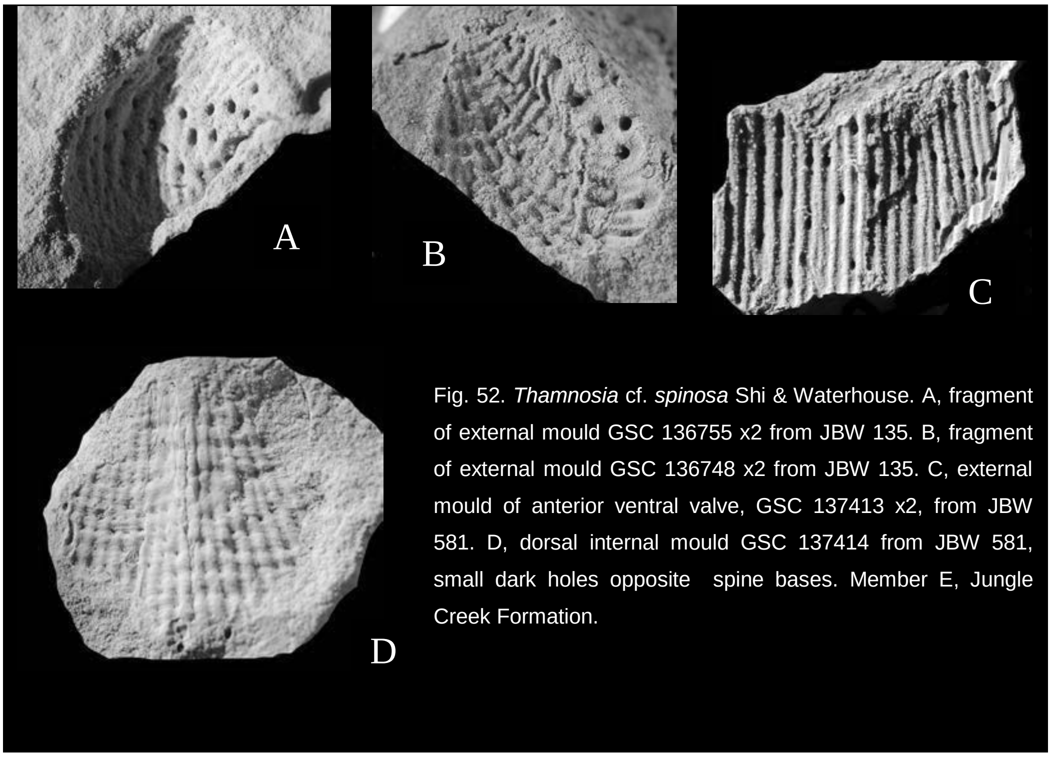


Fig. 52. *Thamnosia* cf. *spinosa* Shi & Waterhouse. A, fragment of external mould GSC 136755 x2 from JBW 135. B, fragment of external mould GSC 136748 x2 from JBW 135. C, external mould of anterior ventral valve, GSC 137413 x2, from JBW 581. D, dorsal internal mould GSC 137414 from JBW 581, small dark holes opposite spine bases. Member E, Jungle Creek Formation.

Description & Resemblances: The specimens display an umbonal row of erect spines passing laterally into two to four rows over the umbonal flanks, and spines are moderately numerous over the adjoining venter, and crowded over the trail. Ribs on the ventral trail number three in 5mm, compared with four in 5mm on the dorsal disc. There is a shallow sulcus, opposed by a low fold on the dorsal valve. The dorsal valve has a long slender medium septum, and numerous spines arise over the disc, at the intersections of low rugae with the well defined costae. These specimens are smaller than *Thamnosia spinosa* Shi & Waterhouse (1996) from the overlying "*Yakovlevia transversa*" Zone, with a probable width close to 25mm, and ribs on the ventral trail of the types number seven to nine in 10mm. Doubt remains over the generic identity of *spinosa*, because of the lack of preserved ears in type material.

Tribe **RIGRANTIINI** Lazarev, 2000b

[Rigrantiini Lazarev, 2000b, p. 28].

Diagnosis: Spines well developed in single rows along hinge and single row arising from low ridge, rarely double row at the base of ventral umbonal flanks; reticulate ornament over entire disc. Dorsal dimples in some genera.

Subtribe **RIGRANTIINAI** Lazarev, 2000b

[Nom. transl. Waterhouse (2013, p. 122) ex Rigrantiini Lazarev, 2000b, p. 28].

Diagnosis: Medium size, dorsal ears bordered anteriorly by groove, and dorsal dimples distinct.

Discussion: The subtribe ranges from Middle Carboniferous (Moscovian) to Middle Permian (Wordian). Constituent genera, *Rigrantia* Lazarev, *Bicarteria* Lazarev and *Pseudantiquatonia* Zhan & Wu (see Waterhouse 2013), and possibly *Tesuquea* Sutherland & Harlow (see below) are believed to be distinguished by having a rib traversing the ventral slope each side of the umbo, and having a groove on the inner anterior side of the dorsal ears. In other respects, the genera come moderately close in ornament to Retariinae, in having reticulate ornament over at least part of the visceral disc, and in possessing a row of spines along the hinge, another row arising from the ridge each side of the umbo, and spines over the disc and trail. Elongate pits are moderately well developed over the dorsal valve. They certainly show little approach to *Yakovlevia*, even though classed with that genus as a tribe within Yakovleviinae by both Lazarev (2000b) and Brunton (2007). These authors overlooked the even closer approach of *Rigrantia* and allies, in terms of ornament and interior, to members of Spyridiophorini Muir-Wood & Cooper and Retariini Muir-Wood & Cooper, and the tribe is therefore transferred to Family Retariidae.

Another genus that merits closer enquiry is *Lazarevia* Carter & Poletaev, 1998, p. 125 from late Bashkirian or early Moscovian (Atokan) beds of Ellesmere Island, Canadian Arctic Archipelago. This genus was ascribed to Plicatiferinae Muir-Wood & Cooper, 1960, but whereas members of that subfamily have dominant commarginal rugae, the ornament of *Lazarevia* is reticulate, with well developed radial ribs. In addition there appears to be a groove dividing the dorsal ears from the dorsal disc, to strongly suggest a position within Rigrantiinai. Spine detail includes a hinge row of spines, and a row of erect spines described as "wrapping around ears to posterior lateral margins". The meaning to me is not fully clear: it might mean a row below the ventral umbonal slopes.

Genus ***Dutroproductus*** n. gen.

Name: For Thomas Dutro.

Diagnosis: Reticulate ornament on both valves, row of fine hinge spines and row of stronger spines on ridge along base of umbonal slopes, becoming a double row further from the umbo. Dorsal ears separated from disc in front by well-formed groove.

Type species: *Dutroproductus dutroi* n. gen., n. sp., from lower Jungle Creek Formation (Asselian), Yukon Territory, Canada, here designated.

Discussion: Other members of this subtribe have only a single row of spines over the lateral slopes and anterior slopes of the ventral valve. The genus in many respects approaches *Tesuquea* Sutherland & Harlow (1973, pl. 6, fig. 1-11, 17, 18) from the early Pennsylvanian of New Mexico, especially in having closely costellate ornament. *Tesuquea* appears to show a groove along the inner side of the dorsal ears (pl. 6, fig. 4b, 7). But it has a double row of spines along virtually all of the umbonal slopes, unlike the arrangement in the present form.

Dutroproductus dutroi n. sp.

Fig. 53 - 55

Derivation: Named for Thomas Dutro.

Diagnosis: Large shells with very long trail, fine ribs and numerous spines over the ventral lateral slopes and dorsal valve.

Holotype: GSC 136756, here designated.

Material: Three ventral valves, two dorsal valves and two specimens with valves conjoined from JBW 18. Dorsal valve from JBW 810. Member C. Possible ventral valve from JBW 132, Member D.

Stratigraphic and biostratigraphic levels: Member C and possibly Member D, Jungle Creek Formation. *Kochiproductus imperiosus* and possibly *Rugivestigia commarginalis* Zones.

Dimensions in mm: ventral valves, from JBW 18

	Width	Length	Height
Ventral valve	46	34	27
Dorsal valve	54	34	22

Description: Specimens moderately large with incurved broad ventral umbo and hinge at maximum width, large convex ears and high vaulted disc grading imperceptibly into long trail. A shallow sulcus extends for most of the length of the ventral valve, shallowing anteriorly. The dorsal disc is gently concave, curving abruptly into a long high trail at a high angle to the disc, large ears. The fold commences just before the start of the trail and is highest at the start of the trail. The ventral valve is closely costellate with some five ribs in 5mm over most of the valve, but ears are not costate. There is only a subdued ridge at the base of the umbonal slope, and spines form a double row, rather than the single row seen in allied genera. Many spines lie over the ears and anterior lateral slopes. Preservation is such that the presence of a hinge row cannot be completely endorsed, but there are indications of a row of rather slender spines. There are scattered spines over the disc and trail, rarely up to 1mm in diameter, and a single costa behind the spine may be replaced by two or three costae in front of the spine. The dorsal ears have a number of dimples, and they are separated from the disc in front by a groove across the anterior rim of each inner ear. A number of spines may be observed over the disc and trail but the arrangement and number is not clearly shown. Rugae are fine and crowded on the ventral as well as dorsal valve.

Resemblances: These specimens have fewer ventral spines than *Thamnosia* from the Glass Mountains of Texas, but have more numerous spines than in *Kutorginella*. *T. parvispinosa* (Stehli, 1954) as figured by Cooper & Grant (1975, pl. 346, fig. 1-6, pl. 347, fig. 1-13) from the Bone Spring Formation of west Texas has coarse costae and more ear spines but is close in shape. From the younger Jungle Creek Formation, *Thamnosia spinosa* Shi & Waterhouse (1996, p. 84, pl. 7, fig. 20-22, pl. 8, fig. 1-8) has coarser anterior costae and coarser anterior spines, and the

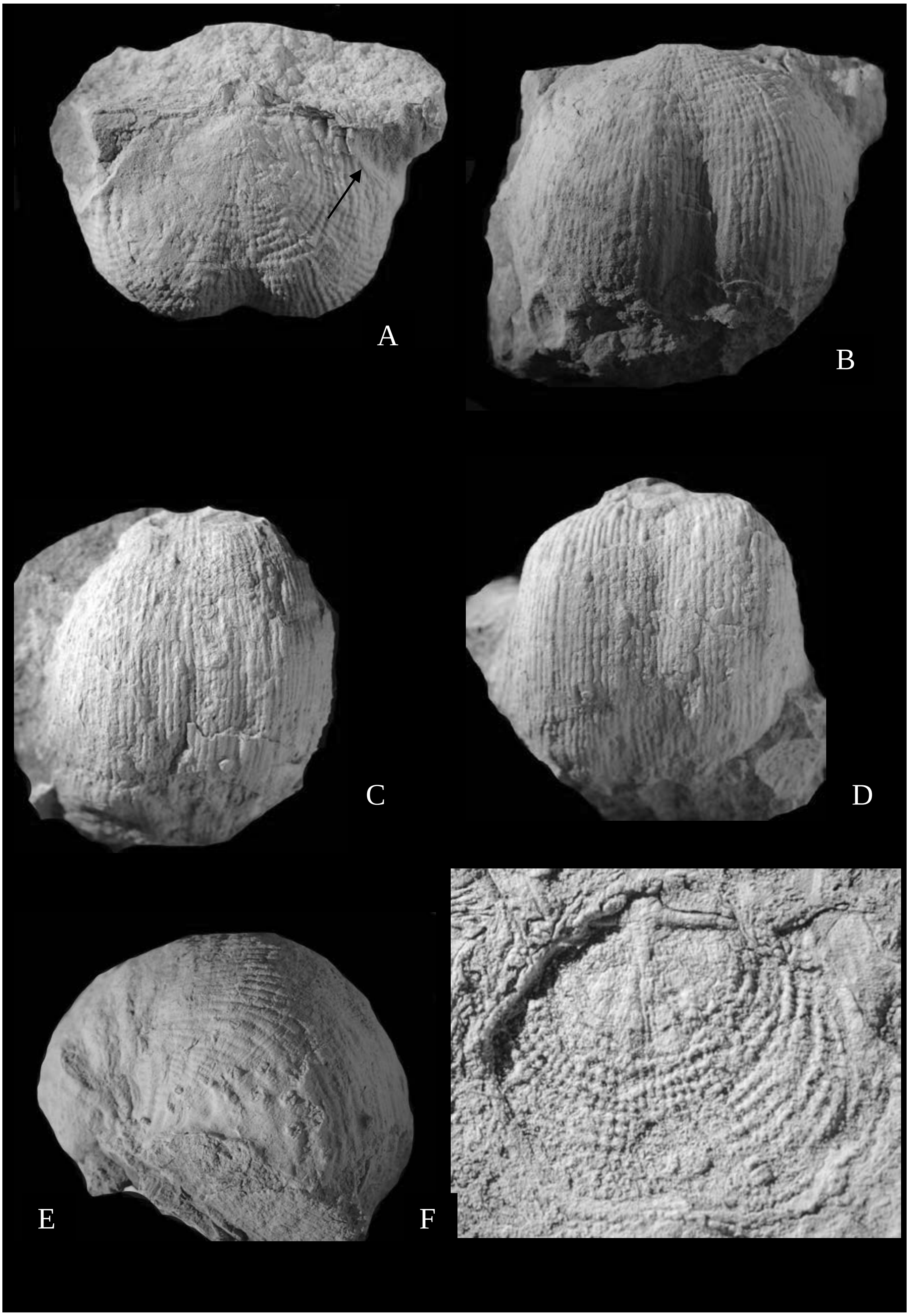


Fig. 53. *Dutroproductus dutroi* n. sp. A, B, posterior and anterior aspects of dorsal valve, holotype, GSC 136756 x1.5, with arrow pointing to a ridge that externally is a groove in front of the dorsal ear. See Fig. 55B. C, anterior aspect of ventral valve GSC 136757 x1.5. D, anterior aspect of ventral valve GSC 136758 x1.5. E, lateral view of ventral valve GSC 136759 x3, showing umbonal slope spines, a single row becoming a double row anteriorly. F, dorsal valve interior, GSC 133293 x2. Specimens from JBW 18, Member C, Jungle Creek Formation.

dorsal valve is more concave. The nature of the dorsal ears is obscure in this form, although one specimen (Shi & Waterhouse 1996, pl. 8, fig. 2) suggests the possibility of a dorsal groove in front of the ear. But ears are poorly preserved, and there appear to be numerous posterior lateral spines on the ventral valve, as in *Thamnosia*. *Thamnosia silicica* Cooper & Grant (1975, pl. 351, fig. 1-18) from the Hess Formation, Taylor Ranch Member, is smaller, with more spines, as in *Thuleproductus*, and is similar in ribbing and sulcation.

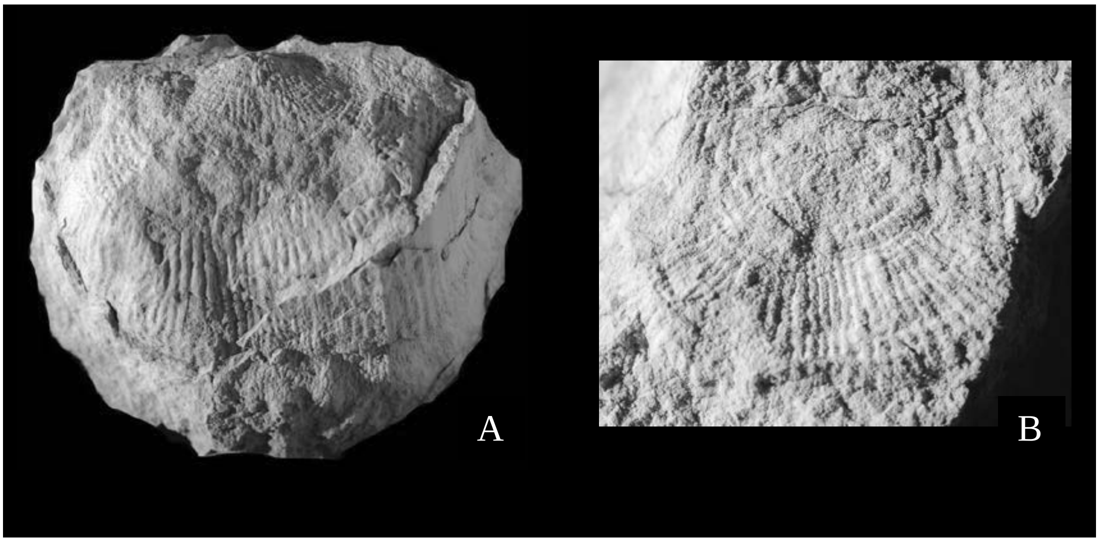


Fig. 54. *Dutroproductus dutroi* n. sp. A, anterior aspect of dorsal valve, GSC 137218 x1.5, showing dorsal disc with part of anterior ventral trail. Lateral posterior part broken so that ear grooves are largely lost. B, dorsal external mould GSC 136761 x2. Grooves (as ridges) present, but lighting unfavourable. Specimens from JBW 18, Member C, Jungle Creek Formation.

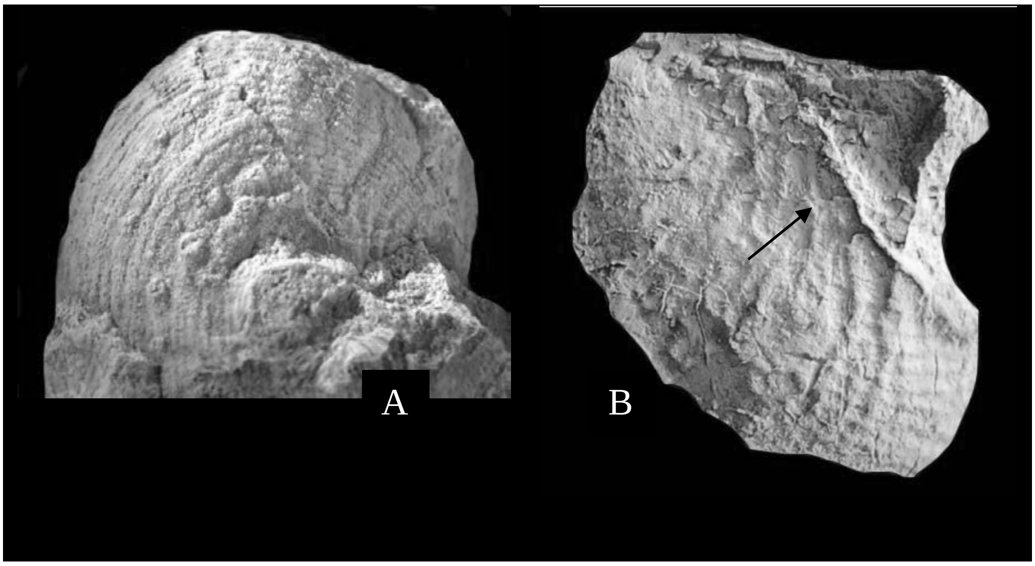


Fig. 55. *Dutroproductus dutroi* n. sp. A, lateral aspect of ventral valve GSC 136758 x1.5 (see Fig. 53D above), showing double row of umbonal slope spines. B, cast of part of dorsal valve GSC 136756 showing groove crossing inner ear as arrowed, holotype (see Fig. 53A, B). Specimens x2.3. From JBW 18, Member C, Jungle Creek Formation.

Subtribe **ANTIQUATONIINAI** Waterhouse, 2013

[Antiquatoniinai Waterhouse, 2013, p. 124].

Diagnosis: Ventral spines well developed in single rows along hinge and base of umbonal flanks, arising from low ridge; reticulate ornament over entire disc. No groove in front of dorsal ears. Dorsal dimples in some genera.

Discussion*:* *Antiquatonia* Miloradovich, 1945 is a Carboniferous genus known from many species, and displays reticulate ornament over the disc, scattered ventral spines, a row of spines along the ridge that is developed along the lower umbonal flanks of the ventral valve, just as in *Rigrantia*, and a row of spines close to the hinge. The dorsal valve, rarely figured or described, has a few dorsal spines according to Muir-Wood & Cooper (1960, p. 270), and appears to lack dorsal external pits. It differs from members of Rigrantiinai in lacking a groove in front of the dorsal ears. *Antiquatonia* was classed in Dictyoclostidae by Muir-Wood & Cooper (1960), and in Tribe Retariini by Brunton et al. (2000, p. 472). *Antiquatonia* is close in size and many aspects of ornament to Retariini, whilst noting that many Retariini have dorsal external pits, and often more dorsal spines. But no Retariini have a ventral external ridge, and the internal dorsal marginal ridge that is usually well developed in members of Retariini may be missing, although the posterior internal hinge ridge is well displayed each side of the cardinal process. Type *Rigrantia* lacks an internal marginal ridge and hinge ridges, but hinge ridges are developed in *Bicarteria*, and in some other species of *Rigrantia*. Given that the external ventral ridge along the umbonal slopes is a rare feature in Productidina, and given that many morphological features are shared by *Rigrantia, Bicarteria* and *Antiquatonia*, it is deemed feasible to consider that *Antiquatonia* evolved within Family Retariidae by developing an external ridge along the ventral umbonal slopes, and changed through time into *Bicarteria*, followed by *Rigrantia*. The genus *Antiquatonia* is classed in a separate subtribe, Antiquatoniinai Waterhouse, 2013, p. 124, together with two further Carboniferous genera, *Costacondria* Waterhouse and *Nazeriproductus* Waterhouse. These genera are distinguished from *Rigrantia* by lacking a groove in front of the inner anterior side of the dorsal ears, and share with members of Rigrantiinai a variably defined ridge bearing a row of spines at the base of the ventral umbonal slope.

Genus ***Nazeriproductus*** Waterhouse, 2013

Diagnosis: Ventral spines form distinct row along the hinge and another along umbonal slopes above variably developed ear ridge, scattered over remainder of ventral valve, visceral disc finely reticulate. Ridge in front of the ventral ears low, and no groove or incision placed in front of the inner dorsal ears. No dorsal spines.

Type species: *Nazeriproductus nazeri* Waterhouse, 2013, p. 126 from Ettrain Formation (Kasimovian) of Yukon Territory, Canada, OD.

Discussion: The genus is distinguished from *Antiquatonia* by its extended ears and presence of pits over the dorsal disc, features discussed in Waterhouse (2013, p. 125).

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Nazeriproductus lazarevi n. sp.

Fig. 56 - 59

Derivation: Named for S. S. Lazarev.

Diagnosis: Closely reticulate transverse shells with moderately large ears, hinge spines of moderate width, ears with very subdued ribs or largely smooth. Dorsal pits well developed but few and scattered.

Holotype: GSC 136059, here designated.

Material: Dorsal valve from JBW 85, two dorsal valves from JBW 84, one ventral valve from JBW 404, two ventral valves from JBW 125, two ventral valves from JBW 166, several specimens with both valves preserved from JBW 532, 571 and 802. Member A, Jungle Creek Formation. Two specimens with valves conjoined from JBW 123 and two ventral valves from JBW 671, Ettrain Formation.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Description: Specimens transverse with shallow ventral sulcus commencing a little in front of the umbo, hinge at maximum width with moderately developed convex ears; dorsal valve with weak median fold, gently concave disc and geniculate trail. Six or seven costae in 5mm crossed by fine commarginal rugae over the posterior disc, gradually strengthening anteriorly to become five to six in 5mm, commarginals not developed over trail, and ears largely smooth in mature specimens near the hinge. Finer ornament on dorsal valve, reticulate over the visceral disc, commarginal rugae tend to persist on to the ears, and no ribs cover the ears. Dorsal pits are well formed and subrounded, but are not numerous, and are scattered. In some specimens, a low ridge lies near the base of the ventral umbonal slope, near the inner side of the ears. Spines form a row along the hinge and another along the umbonal slopes of ventral valve, along the ridge at the inner anterior margin of each ear, up to 1mm in diameter, spines scattered and well spaced in comparatively regular quincunx over the disc and trail. Dorsal valve without spines. There is no deep groove bordering the inner anterior side of each ear.

Ventral adductors sited on elongate subrectangular platform, posterior highly dendritic. Diductor scars very large and deeply scored.

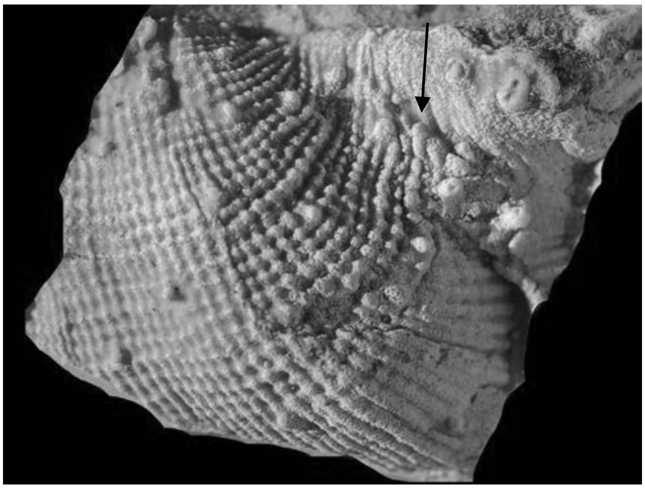
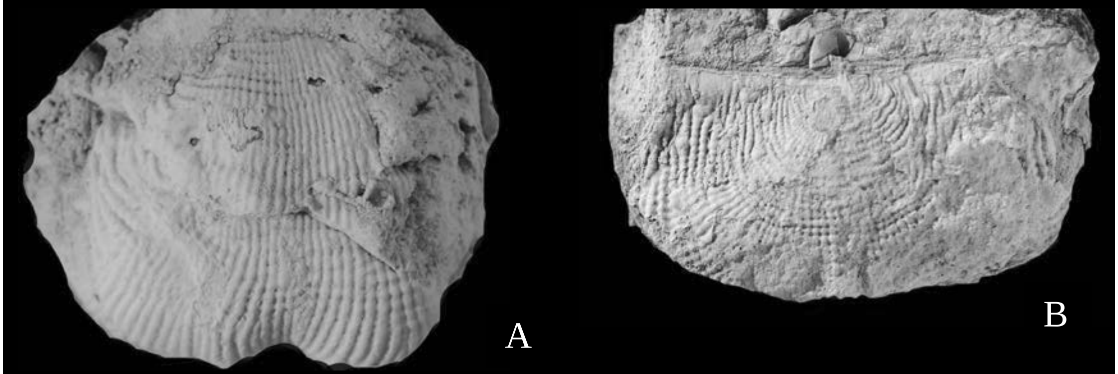


Fig. 56. *Nazeriproductus lazarevi* n. sp., cast of ventral exterior, holotype GSC 136059 x2 from JBW 123, with a very low ridge at the base of the umbonal slope, as arrowed. Ettrain Formation.

Resemblances: The size, shape and details of spine distribution and reticulate ornament all strongly suggest the genus *Nazeriproductus* from slightly older beds in the Ettrain Formation. The type species is much larger than present material with extended ears, and has an umbonal slope row of spines on a ridge slightly more prominent than in the present form, and has similar strongly reticulate but more finely costate ornament, dorsal dimples, and no groove in front of the dorsal ears. There are no dorsal spines and only a few pits in the present species.

Rigrantia planumbona (Stehli, 1954, pl. 20, fig. 1-5; Cooper & Grant 1975, pl. 390, fig. 8-22) from the Bone Spring Formation of Texas is a little larger than the Canadian species, with similar distribution of ventral spines and strongly reticulate ornament, but lateral spines along the hinge and umbonal slope rows are thicker. The ventral ears bear more ribbing, and there are dorsal ear grooves. *Antiquatonia* (now *Rigrantia*) *regularis* Cooper & Grant (1975, p. 1093, pl. 391, fig. 1-5) from the Lenox Hills Formation of Texas is more convex with shallow ventral sulcus and fewer spines over the disc: the lateral spines are not as strong as in *planumbona*. *Productus hessensis* King, 1931, pl. 11, fig. 6, also referred to *Antiquatonia* by Cooper & Grant (1975, p. 1090, pl. 391, fig. 6-17), from the basal Skinner Ranch Formation in Texas, is closer in shape, and more geniculate. Spines are not well preserved, but were described as "heavy" along the umbonal slope ridge. *A. costellata* Cooper & Grant (1975, p. 1090, pl. 453, fig. 30-33) from the Lenox Hills Formation of Texas is also larger with longer trail and stronger umbonal slope spines, and comparatively transverse, although ears are not very large. There are no figured dorsal valves.



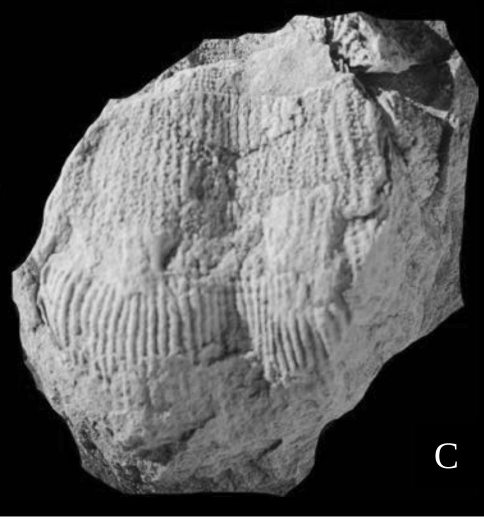


Fig. 57. *Nazeriproductus lazarevi* n. sp. A, damaged specimens with valves conjoined, GSC 136000 x1.5 from JBW 571. B, dorsal valve GSC 136061 x1.5 from JBW 84. Member A, Jungle Creek Formation. C, ventral aspect of mould of specimen with valves conjoined, GSC 136762 x1.5 from JBW 123. Ettrain Formation.

The species assigned to *Antiquatonia cooperi* Shi, 1990 from the Jungle Creek Formation by Shi & Waterhouse (1996, pl. 13, fig. 3-11) from the "*Yakovlevia transversa*" Zone of the Jungle Creek Formation has larger ears and coarser costae and transverse rugae. According to the text, a row of spines is developed along the hinge and another over the umbonal slopes, as in *Rigrantia*, but the ventral valve appears to be more convex and the ornament less markedly reticulate. The presence or absence of dorsal ear grooves is difficult to determine as far as the Canadian specimens are concerned, but may be present in pl. 13, fig. 7. The types were described from the Coyote Butte Formation of Oregon by Cooper (1957, p. 35, pl. 5C, fig. 18-22) as *Antiquatonia sulcata* Cooper [non *sulcata* Sowerby, 1822], and this species is more elongate than other forms ascribed to *Rigrantia*, but is close in long trail and convex ventral valve to *Rigrantia costellata* and *hessensis*, and the types have dorsal ear grooves.

Lazarev (2000b) regarded *Antiquatonia inflativentra* Cooper & Grant (1975, p. 1091, pl. 386, fig. 2-9) from the *Uddenites* shale of the Gaptank Formation and Neal Ranch Formation as being closer to *Bicarteria* Lazarev in its disc outline and ornamentation than to *Rigrantia*. Certainly the spine rows are less conspicuous, and the trail long and ventral valve more highly arched than is usual for *Rigrantia* or *Antiquatonia*. The reticulation is almost as marked as in type *Rigrantia* and in most specimens appears to cover virtually all of the visceral disc. The overall outline agrees moderately well with that illustrated for *Antiquatonia cooperi* Shi. This implies that *Bicarteria* extended from its putative age of Serpukhovian – Kasimovian (Upper Carboniferous) into Early Permian, and is characterized principally by elongate shape, long trail and less reticulate disc. The present Canadian species *lazarevi* matches the species ascribed to *Rigrantia* in terms of shape and reticulate ornament, even though its spines are not as strong laterally as in type *Rigrantia*, and an ear groove is not developed. In the original circumscription of *Rigrantia*, Lazarev (2000b) laid considerable stress on the relative strength and position of hinge and umbonal slope spines, as repeated by Brunton (2007), but the various specimens in the type and allied species do not always substantiate the analyses, though they must surely provide some guidance (Waterhouse 2013, p. 122).

Antiquatonia insculpta kasakhstanica Nasikanova in Sarytcheva (1968, p. 127, pl. 16, fig. 1-4) from the Keregetass Suite of west Kazakhstan, of Late Carboniferous age, is moderately close in shape, especially to *Bicarteria*, yet has a very well developed row of umbonal slope spines that are strong laterally. *A. bublitchenkoi* Sarytcheva in Sarytcheva (1968, p. 128, pl. 16, fig. 5-7) from the Kokpekten Complex of Kazakhstan has spines in hinge and umbonal slope rows that become very strong laterally. The costae are slightly coarser, the commarginals weaker, and trail long, although the shape is transverse. From the Carboniferous Makarov Horizon of Taimyr, *A. posthindi* Solomina (1970, pl. 7, fig. 3, 4; Lapina 1960, pl. 1, fig. 3, 4 as *A*. ex gr. *hindi* and Sarytcheva 1977a, pl. 10, fig. 5, 6, text-fig. 49, 50) is another species that comes close in reticulate ornament and shape apart from longer trail, though anterior ventral costae are slightly coarser in the Taimyr specimens. Spine detail is not certain.

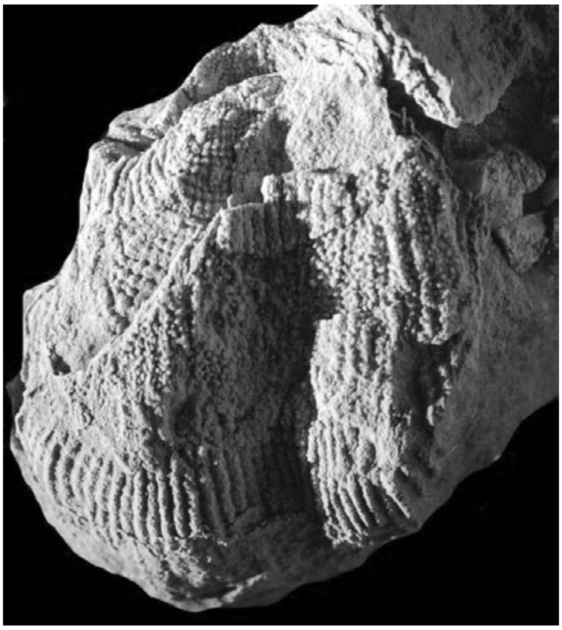


Fig. 58. *Nazeriproductus lazarevi* n. sp. ventral aspect of mould of specimen with valves conjoined, GSC 136762 x2 from JBW 123. A slightly different angle from Fig. 57C, showing that the posterior ear is not separated from the dorsal disc by any groove, unlike the arrangement in members of Rigrantiini. Ettrain Formation.

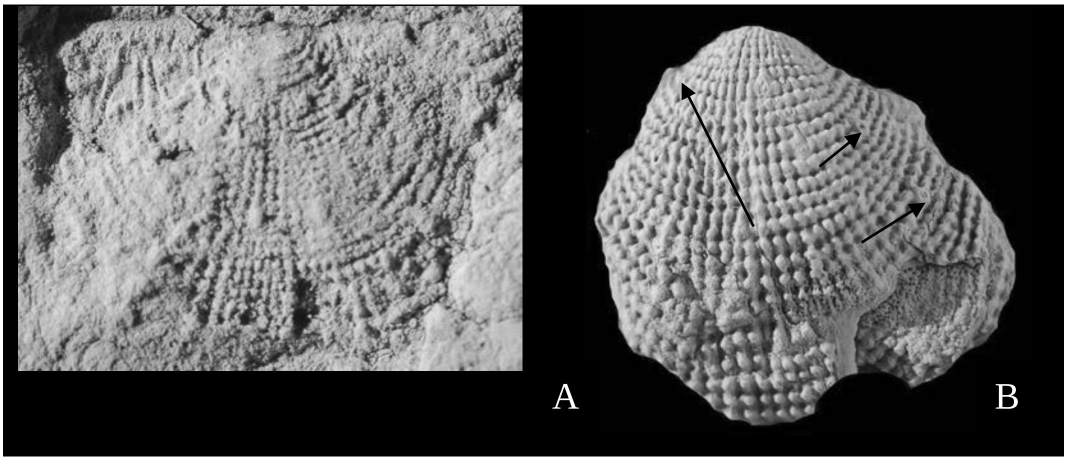


Fig. 59. *Nazeriproductus lazarevi* n. sp. A, dorsal disc GSC 136062 x2 from JBW 84. B, part of ventral exterior, GSC 136763 x3 from JBW 404. Short arrows point to spines, and on the other side, one spine lies at the start of a possible umbonal ridge, its position indicated by a long arrow. Member A, Jungle Creek Formation.

Subfamily **RETICULATIINAE** Lazarev, 2000a

[Nom. promoveo Waterhouse 2013, p. 130 ex Reticulatiini Lazarev, 2000a, p. 40. Syn. Latispiniferini Lazarev, 2000b, p. 26 and Callytharrellini Waterhouse, 2002b, p. 21].

Diagnosis: Mostly large shells with relatively small ears as a rule, strongly reticulate disc with spines sparse as a rule, usually in row along base of umbonal flanks, spines may be more numerous on ears, moderate to rare over venter and trail, may include a few strong anterior spines. No external ridge at base of umbonal slopes, nor groove along inner side of dorsal ears. Dorsal disc with no spines, dimples as a rule, matching positions of ventral spines. Moderate to low if any internal marginal ridge, internal posterior papillation possibly not developed.

Discussion: There are a modest number of ventral spines, variously disposed, but not numerous, and in some genera the ornament includes stout spines on the ears and anterior disc or trail. As a rule, dorsal dimples are also present. Compared with Retariinae, the size is generally larger, the shape less transverse, with less extended ears, and there is no high marginal ridge around the dorsal interior. Members of Family Dictyoclostidae are rather similar in general appearance (see Waterhouse 2013, pp. 154 - 174), but lack the row of spines along the base of the umbonal slopes, and reticulation is a little less sharply defined.

Genus ***Reticulatia*** Muir-Wood & Cooper, 1960

Diagnosis: Large with reticulate ornament, ginglymus, ventral spines in variable row along hinge and another along base of umbonal slopes, often more but not very numerous spines on outer ears and over disc and trail, no spines and variable and often small pits on dorsal valve, moderate internal hinge ridge and low dorsal marginal ridge. There is no ridge along the ventral umbonal slopes or groove along the anterior inner margin of the dorsal ears.

Type species: *Productus huecoensis* King, 1931, p. 68 from Hughes Creek Shale (Lower Permian), Nebraska, United States.

Discussion: Although Lazarev (2000a, p. 40) insisted that *Reticulatia* was restricted to Permian deposits, a species close to the genus is represented in Upper Carboniferous faunas of Canada, including Member A at the base of the Jungle Creek Formation. The species *americanus* (Dunbar & Condra, 1932) of Missourian or Kasimovian age in Nebraska was regarded as belonging to *Reticulatia* by Carter & Poletaev (1998, p. 128), and by Muir-Wood & Cooper (1960, p. 284), who synonymized the species with the type, *huecoensis* King, 1931.

Reticulatia oldershawi Waterhouse, 2013

Fig. 60, 61

2013 *Reticulatia oldershawi* Waterhouse, p. 132, Fig. 5.20, Fig. 5.21.

Diagnosis: Large and weakly transverse with moderately large ears and high trail. Ventral spines few and lie in row along hinge, another row along base of umbonal slopes, rare over venter and trail. Sulcus and fold moderately well formed anteriorly. Commarginal fine wrinkles form crenulate pattern, dorsal pits not clearly defined.

Holotype: GSC 136049 figured by Waterhouse (2013, Fig. 5.20C) and as Fig. 60C herein, from Member A, Jungle Creek Formation (Gzhelian), Yukon Territory, Canada, OD.

Material: Single ventral valves from JBW 92, 419, 516, 597, 615, 628, 636, 667, 675, 705, 731, 735, 802, two ventral valves from JBW ?523, 536, 596 and 656, three ventral valves from JBW 125 and 783, single dorsal valves from JBW 84, 119, ?141, 504, 649 and 668, ventral and dorsal valve from JBW 748, single specimens with valves conjoined from JBW 420, 591, 708 and 814, three ventral valves and specimen with valves conjoined from JBW 172, a ventral valve and specimen with valves conjoined from JBW 606, three ventral valves, one dorsal valve and three specimens with valves conjoined from JBW 173, possible ventral valve, dorsal valve and specimen with valves conjoined from JBW 119, specimen with valves conjoined from JBW 117, two ventral valves and one specimen with valves conjoined from JBW 787, large ventral valve and a dorsal valve from JBW 578. All from Member A, Jungle Creek Formation. Ventral valve from JBW 707 and one ventral valve and three specimens with valves conjoined from JBW 686. Ettrain Formation.

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Dimensions in mm: ventral valve

Specimen GSC	Width	Length	Height	
136049	75	50	28	holotype
136052	70	49	27	
136048	63	52	29	

Description: Shells large, weakly transverse as a rule and high with long trail. Ventral umbo weakly incurved, umbonal angle of 100-120°, umbonal walls steeply convex and of moderate height, ears large and convex, with obtuse cardinal extremities. A well formed ginglymus is developed along the hinge. Sulcus commences some 12-15mm in front of umbonal tip, and widens at angle of 27-30°, deepest over the trail, with concave floor. Dorsal valve gently concave over disc, with concave ears and median fold commencing close to hinge and persisting on to a trail which is subgeniculate and as long as the disc. A dorsal ginglymus is developed. Ventral spines are comparatively inconspicuous, forming an oblique row close to the hinge, plus an umbonal slope row of finer spines, and a few spines lie over outer ears, and are scattered rarely over the visceral disc and trail, where spines are rarely 1.8mm in diameter, and usually 0.8-0.9mm in diameter, compared with diameter of 1.5mm along the outer hinge. There are no dorsal spines. The predominant ornament comprises well formed costae crossed by commarginal rugae, with four to five radials in 5mm and three commarginals in 5mm at about 20mm from the umbo, and two to three radials and two commarginals in 5mm at 40mm from the umbo. Ribs are round-crested, and separated by interspaces just as wide, with concave floors; the commarginals form nodes or slightly crescentic ridges arching posteriorly over the costae. Ears are free of costae, but display commarginal ornament. The commarginals fade over the anterior anterior disc and are not developed over the trail, but the ribs continue with gradually increasing strength, and in some specimens the ribs become bundled, or are arranged over broad low plicae. A few ribs may converge at the start of the trail, and a very few costae may arise by intercalation near the anterior margin. Dorsal ornament of ribs and commarginals is similar to that of the ventral valve, with some variation shown in relative strength of the commarginals and radials. On some specimens the costae increase by intercalation near the anterior margin. Visceral disc of only moderate thickness, close to 10mm in large specimens, and no conspicuous pits lie over the disc of the dorsal valve.

Ventral adductor scars are placed on a high narrow platform, divided by a low myophragm, with posterior dendritic scars that flare postero-laterally, and narrow anterior scars bearing low linear ridges. Diductor scars are only moderately impressed and deeply grooved, and very wide, extending as far as the lateral umbonal slopes. The floor of the valve behind the scars is lightly marked by fine more or less commarginal lines, and the shell floor behind

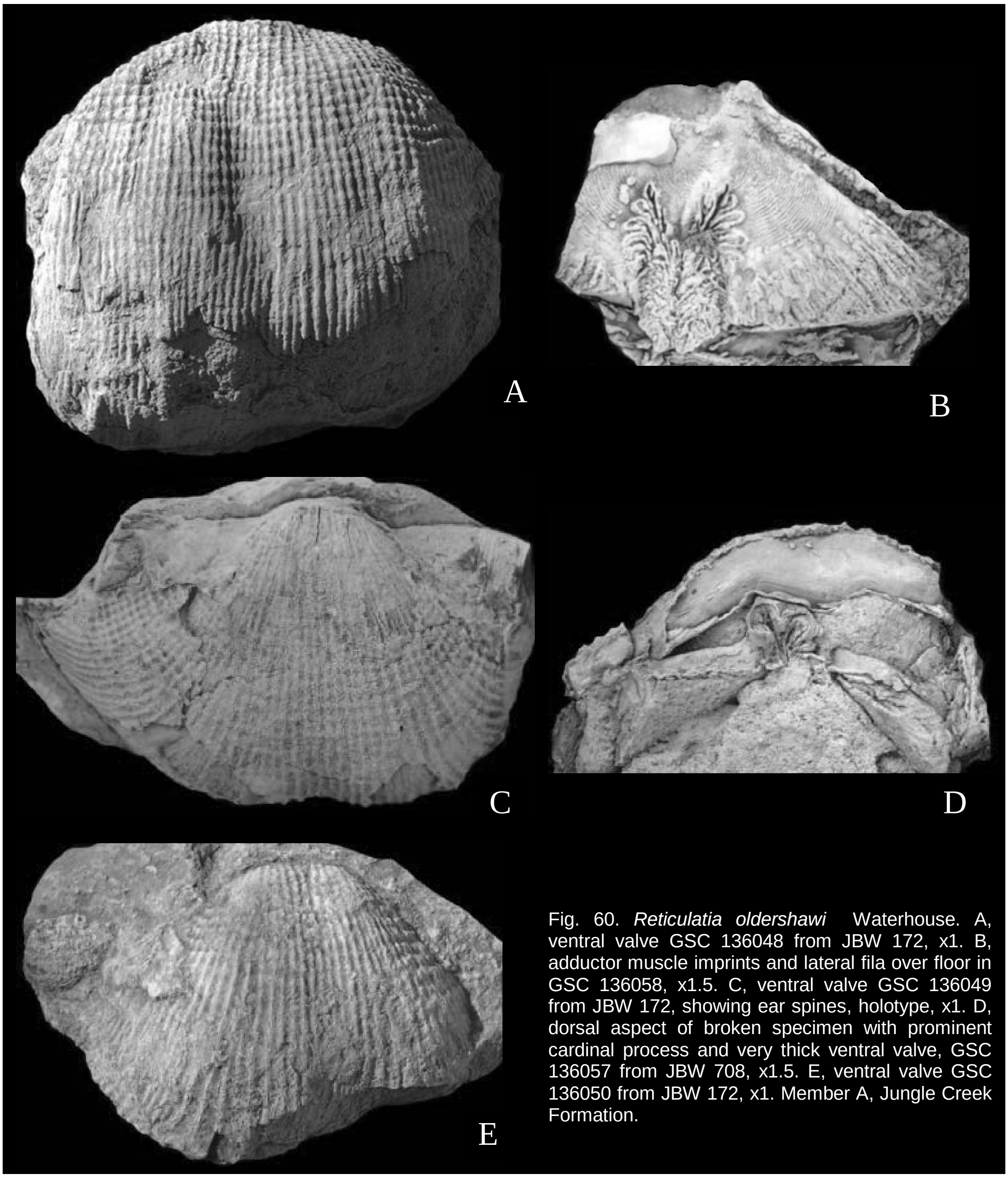


Fig. 60. *Reticulatia oldershawi* Waterhouse. A, ventral valve GSC 136048 from JBW 172, x1. B, adductor muscle imprints and lateral fila over floor in GSC 136058, x1.5. C, ventral valve GSC 136049 from JBW 172, showing ear spines, holotype, x1. D, dorsal aspect of broken specimen with prominent cardinal process and very thick ventral valve, GSC 136057 from JBW 708, x1.5. E, ventral valve GSC 136050 from JBW 172, x1. Member A, Jungle Creek Formation.

the adductor scars is marked by short and low irregular ridges, more or less commarginal, with fine pits, and no development of smooth surface. Shell some 8mm thick posteriorly, due to secondary thickening.

Cardinal process large and trilobed, with narrow median shaft bent ventrally, and high lateral lobes directed posteriorly and well separated from the median lobe. The process is supported by a short broad platform, joined laterally by a ridge along the hinge, and leading forward into a slender median septum that extends to anterior third or fourth of the visceral disc, but ends behind mid-length in one specimen from JBW 141. Posterior adductors are large with dendritic markings, and anterior adductors are more raised, and may be smooth or bear dendritic ridges. Brachial shields small, not clearly outlined, and placed well behind the anterior terminus of the septum. Posterior shell smooth, anterior shell with pustules, which become very large (JBW 141).

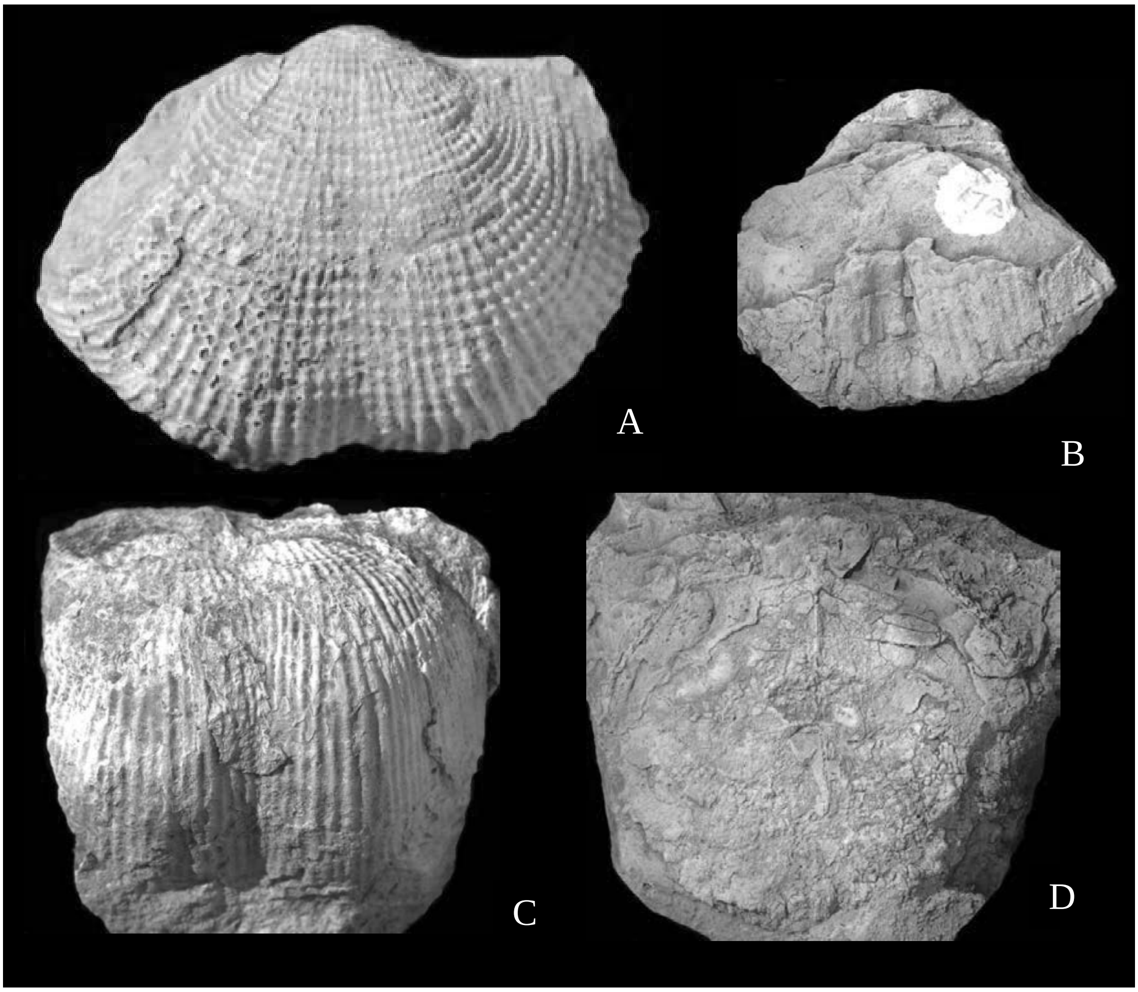


Fig. 61. *Reticulatia oldershawi* Waterhouse. A, ventral valve showing spines along hinge and umbonal slope, GSC 136052 from JBW 707, x1.3. Ettrain Formation. B, ventral valve, the trail recurved by distortion and showing broad anterior ribbed subplicae, as well as high ginglymus, GSC 136053 from JBW 172, x1.2. C, anterior dorsal valve showing high geniculate trail, GSC 136054 from JBW 417, x1. D, dorsal interior, nested within ventral valve, GSC 136056 from JBW 649, x0.8. Member A, Jungle Ceek Formaton.

Resemblances: This species is like type *Reticulatia* in its reticulate ornament and more or less in spine detail, except that ear spines are more numerous in one specimen figured by Muir-Wood & Cooper (1960, pl. 105, fig. 1), and in one specimen of *americana* (Dunbar & Condra) figured by Branson (1964, pl. 1, fig. 3), although spines are fewer in other figured specimens (Muir-Wood & Cooper 1960, pl. 105, fig. 4; Branson 1964, pl. 1, fig. 1). The present material does not show the fine external dorsal pits seen in at least some type *Reticulatia* (Muir-Wood & Cooper 1960, pl. 105, fig. 2), has a narrower median lobe in the cardinal process and lateral lobes inclined posteriorly rather than more laterally, and apparently lacks a marginal ridge. The ventral interior was not figured by Muir-Wood & Cooper (1960) or Brunton et al. (2000). In overall shape, the Canadian species has a longer trail and is more sulcate. The dorsal interior of the Canadian species is too imperfect to show if papillation was developed. Type *Latispinifera* Lazarev is similar and differs in many of the same aspects: the one clear difference lies in the lack of large and elongate dorsal pits from the Canadian form, and type *Reticulatia* has small if any dorsal pits. Type *Latispinifera* as figured by Sarytcheva (1977a) may show more reticulation over the anterior disc and dorsal pitting, but details of its posterior spination are obscure, and whether or not an internal marginal ridge was developed is far from clear.

Upper Carboniferous specimens compared to *Reticulatia uralica* (Tschernyschew, 1902) by Sarytcheva (1977a, p. 99, pl. 13, fig. 2. 3) show very similar ornament and shallower sulcus. The Tschernyschew (1902) specimens from the Early Permian of the Urals, with extensive synonymy provided by Shi & Waterhouse (1996, p. 85), and with Kulikov (1974a, pl. 4, fig. 3) to be added, are close overall but smaller with slightly finer ornament and slightly less strong commarginal wrinkles. The species *uralica*, as represented by Tschernyschew (1902, pl. 33, fig. 1) from the Early Permian of Urals, with type specimen selected by Volgin (1960, p. 91), has large ears with more spines than in the Canadian species, but is close in reticulation and in its long trail and presence of ventral sulcus. Specimens from the "*Yakovlevia transversa*" to *Jakutoproductus verchoyanicus* Zones of the younger Jungle Creek Formation that were described as *Reticulatia uralica* (Tschernyschew) by Shi & Waterhouse (1996, pl. 11, fig. 11, pl. 12, fig. 1-11, pl. 13, fig. 1, 2, pl. 32, fig. 1) are also large with somewhat comparable radial and transverse ornament. They have smaller ears, a shallower ventral sulcus, and more ventral spines over the visceral disc and umbonal slopes, and larger spines along the hinge, as well as scattered dorsal pits. Overall the general appearance in size, shape and reticulate ornament is close. There is no dorsal marginal ridge, and a shorter dorsal septum.

Reticulatia americana Dunbar & Condra (1932, pl. 34, fig. 3-6), treated as a synonym of *R. huecoensis* not King of Muir-Wood & Cooper (1960, pl. 104, 105) by Cooper & Grant (1975, pl. 383, fig. 14-22), but opposed by Branson (1964), is slightly smaller and more equilateral in shape, and with finer costellae, especially on the dorsal valve. It is found widely in the United States in Nebraska, Kansas, Oklahoma, and Neal Ranch Formation of west Texas, in beds of Wolfcampian age. *R. robusta* Cooper & Grant (1975, p. 1088, pl. 386, fig. 1, pl. 392, fig. 1-6) is closer to the present species in the strength of the ribbing, but the shell is smaller and less sulcate, and anterior spines are coarser.

Reticulatia magna Sarytcheva (1977a, pl. 13, fig. 4, pl. 14, fig. 1, text-fig. 60) from the Moscovian Stage of Moscow Basin, Russia, is close in size and ornament to the present species: both sets of specimens show strong commarginal ornament, but many details for the Russian species remain poorly known. The species *ivanovi* (Lapina, 1957, pl. 13, fig. 1-4) from the Kashirian and Kirov levels of the Urals has finer ornament as figured in Stepanov (1975, pl. 77, fig. 5), but Upper Carboniferous specimens from the Arctic that were illustrated in Sarytcheva (1977a, p. 90, pl. 11, fig. 1-6, text-fig. 54, 55) are moderately close in ornament and shape, although smaller with shallower sulcus. Lapina's species was referred to *Latispinifera* by Lazarev (2000b), together, as a possibility, with *posthindi* Solomina. The species *ivanovi* has been reported extensively from Russian faunas of Bashkirian – Moscovian and slightly younger age, and was considered to include shells identified as *R. moelleri* by Winkler Prins (1968, pl. 7, fig.

fig. 7, 8) from Spain. The Spitsbergen species *Reticulatia holtedahli* Gobbett (1964, pl. 8, fig. 1-5, text-fig. 13) comes from the Passage Beds (Minkinfjellet Formation with part of Ebbadalen Formation – Moscovian – early Kasimovian), Lower Gypsiferous Series (Ebbadalen Formation without the Odellfjellet Member – approximately Bashkirian) and Ambigua beds (Kapp Kåre Formation – Bashkirian – Moscovian), to follow the adjustments in stratigraphic nomenclature set out in Dallman et al. (1999). The species is readily distinguished, with more rounded venter and less conspicuous ornament. *R. pamirica* Grunt in Grunt & Dmitriev (1973, pl. 6, fig. 1-4, pl. 7, fig. 1, text-fig. 20) from the Sakmarian to lower Artinskian Bazardarin Suite of the Pamirs has a more triangular outline with slightly deeper sulcus. *Antiquatonia bublitchenkoi* Sarytcheva in Sarytcheva (1968, p. 128, pl. 16, fig. 5-7) from the Kokpekten Complex of Kazakhstan has spines in hinge and umbonal slope rows that become very strong laterally, and the costae are slightly coarser, the commarginals weaker, and trail long, whilst the shape is transverse. The generic placement as *Antiquatonia* Miloradovich by Sarytcheva (1968) implies the present of ventral slope ridges, though no ridges are visible in illustrations.

***Reticulatia*? sp.**

Fig. 62

Material: One internal mould of a dorsal valve from JBW 72 and another from JBW 762.

Stratigraphic and biostratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Dimensions in mm: dorsal disc

Specimen GSC	Width	Length	Height
137451	46	32	5

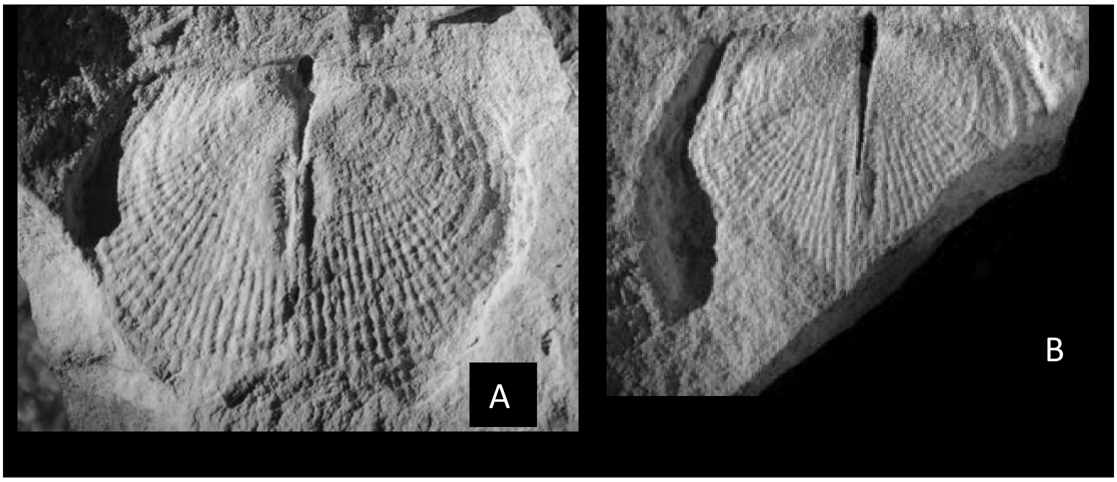


Fig. 62. *Reticulatia* sp. A, dorsal internal mould GSC 137451 from JBW 72. B, dorsal internal mould GSC 137452 from JBW 762. Specimens x1.5, Member D, Jungle Creek Formation.

Description: The specimens are large, ornamented by three or four ribs in 5mm, crossed by low commarginal growth rugae, two in 5mm. The disc is very gently concave, with anterior median depression, and surrounded by a very low marginal ridge, with part of the trail preserved, inclined at a steep angle from the disc. The median septum is well developed, thick but low, extending for well over half the length of the disc, with a pair of long narrow adductor scars marked by low irregular transverse ridges. The cardinal process is high and sturdy, projecting at an angle to the disc, and the posterior margin along the hinge is strengthened by a thick ridge. Sharply-pointed pits are developed in the dorsal internal moulds.

Resemblances: These specimens have a disc that is less concave than that of *Reticulatia oldershawi* Waterhouse, and the trail is more geniculate, whereas it curves abruptly but without angularity from the disc in *oldershawi*. In addition, commarginal rugae are low and less defined in the present specimens. The genus cannot be securely identified, given the absence of any ventral valve and dorsal exterior, but appears to belong to a species distinct from *Reticulatia oldershawi* Waterhouse.

Family **BUXTONIIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 1978, p. 20 ex Buxtoniinae Muir-Wood & Cooper, 1960, p. 255].

Diagnosis: Large shells with deep body corpus as a rule, ribs over both valves somewhat irregular, costae may swell in front of and behind especially ventral spines, no strut spines, dorsal spines and pits generally present and spines often numerous. Commarginal ornament moderate to subdued. Narrow elongate cardinal pit and generally long split in the posterior dorsal septum, dorsal valve may have closely spaced buttress plates. Adductor scars dendritic, dorsal endospines large and numerous across anterior shell, marginal ridges generally subdued but hinge ridge or lateral cincture developed in some genera.

Discussion: Members of the Upper Devonian to Lower Carboniferous Family Lomatiphoridae Roberts are deemed to have been ancestral, because genera such as *Lomatiphora* Roberts and *Spinocarinifera* Roberts have short diverging lateral buttress plates or median slit in the posterior dorsal median septum, and spines in *Spinocarinifera* are erect and arise from ribs, though without the basal swelling typical of Buxtoniidae. They lack dorsal spines and clusters of ventral ears, and so approach members of Marginatiinae Waterhouse, a group within Buxtoniidae. (See Waterhouse 2013, p. 110).

Subfamily **BUXTONIINAE** Muir-Wood & Cooper, 1960

[Buxtoniinae Muir-Wood & Cooper, 1960, p. 255].

Diagnosis: Spines on both valves as a rule.

Tribe **SPINIFRONSINI** Waterhouse, 1981

[Nom. transl. Waterhouse 2013, p. 140 ex Spinifronsinae Waterhouse, 1981, p. 82. Syn. Kochiproductini Lazarev, 1985, p. 67].

Diagnosis: Costae well defined to rarely erratic in course, crossed by low but defined commarginal ribs which leave low nodes or ridges over costae, from which spines may arise. Spines scattered over disc and trail of both valves, crowded over ventral ears, and wider, as wide as, or narrower than costae. Dorsal pits.

Discussion: Genera include *Spinifrons* Stehli, ?*Bellaclathratus* Winters, *Kochiproductus* Dunbar (= *Tschernyschewiella* Fredericks, 1924a not Toll, 1899), *Kochiproductus* (*Dunbarovia*) Waterhouse, *Peniculauris* Muir-Wood & Cooper, ?*Rugoclostus* Easton and *Squamaria* Muir-Wood & Cooper, with a new genus *Nassichukia*, described below.

Genus ***Kochiproductus*** Dunbar, 1955

Diagnosis: Large shells with large ears, prominent costae which do not anastomose anteriorly in *Kochiproductus* ss, dominated over disc by closely spaced elongate spine bases, costae crossed posteriorly by prominent commarginal rugae, spines numerous over both valves, semi-erect over ears and trail. Cardinal ridges long.

Type species: *Productus porrectus* Kutorga, 1844, p. 96 from Lower Cisuralian (Asselian, lower Sakmarian) of Urals, Russia, SD Muir-Wood & Cooper 1960, p. 260.

Discussion: Dunbar (1955, p. 107) regarded his name *Kochiproductus* as a replacement for *Tschernyschewiella* Fredericks, 1924a, p. 20, named for *Productus porrectus* Kutorga, 1844, not *Tschernyschewiella* Toll, 1899. But Dunbar proposed a new type species for his *Kochiproductus, K. plexicostatus*. Although Ustritsky (1960a, p. 8) accepted *plexicostatus* as type*,* Muir-Wood & Cooper (1960, p. 260) emphatically declared this procedure invalid, and because *Kochiproductus* was proposed as a substitute name, considered that the type species had to be retained as *Productus porrectus* Kutorga. This has been followed ever since in all available literature, including the *Revised Brachiopod Treatise*. Dunbar's species *flexicostatus* is not in fact completely identical with *porrectus*, and has been assigned to a subgenus *Dunbarovia* Waterhouse, 2013, as outlined on p. 459.

Kochiproductus saranaeanus (Fredericks, 1933)

Fig. 63 - 66

1902 *Productus longus* (not Meek) – Tschernyschew, p. 637, pl. 27, fig. 2, pl. 34, fig. 4, pl. 35, fig. 2.
1933 *Buxtonia saranaena* Fredericks, p. 37, pl. 5, fig. 1.
1939 *Productus* (*Buxtonia*) *saranaeana* – Licharew & Einor, p. 37, pl. 5, fig. 1.
1974a *B. saranaeana* – Kulikov, p. 93, pl. 2, fig. 7.
1986 *Kochiproductus saranaeanus* – Kalashnikov, pl. 118, fig. 5.
1996 *K. saranaeaenus* – Shi & Waterhouse, p. 81, pl. 11, fig. 7-10, 12.

Diagnosis: Large and transverse with strong branching ribs, ventral spines numerous.

Lectotype: TsNIGRA specimen figured by Tschernyschew (1902, pl. 34, fig. 4) from Cora Horizon of Urals, SD Shi & Waterhouse 1996, p. 81.

Material: From Member A, single dorsal and ventral valves from JBW 615, single dorsal valve from 679. Single dorsal valves from JBW 141 and 513, ventral and dorsal fragments and specimens with valves conjoined from JBW 4, 677, 679, 680 and 818, dorsal valve from JBW 423. Ventral valve from JBW 158 and specimen with valves conjoined from JBW 188. Three specimens with valves conjoined from JBW 533, Ettrain Formation.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Description: Ventral valve large with shallow sulcus, dorsal valve very gently concave with low anterior fold. Ventral ribs number five or six in 10mm, bearing numerous close-set erect spines, strong ornament, ribs numbering eight in 10mm on smaller specimens. The best preserved specimen is a transverse dorsal valve with large wide ears and low anterior dorsal fold commencing a little in front of the hinge. Over the dorsal disc, costae number five or six in 10mm and coarsen to four in 10mm over the geniculation of the trail, then become finer again. Costae especially on the ventral valve swell at intervals, thickening forward for a length of up to 5-6 mm, and give rise to spines, then reduce in size, yielding an elongately nodular ornament. Costae branch conspicuously on both valves. Specimens from JBW 513, 677, 679 and 680 have ribs slightly finer than those from JBW 533, 615 and 818, in which the ribs swell into prominent spine bases. Dorsal spines numerous and emerge from short bases up to 1-2mm long, usually from crests of rugae, separated by short elongate pits. Short subgeniculate trail. Posterior face of cardinal process bifid and divided by deep groove, median dorsal septum extending to mid-length. Several internal dorsal moulds show that the posterior septum of the dorsal valve is subdivided by a narrow median slit.

Resemblances: Specimens identified as *Kochiproductus saranaeanus* (Fredericks) by Shi & Waterhouse (1996, pl. 11, fig. 8-10, 12) from the younger Jungle Creek Formation in Yukon Territory, Canada, are close in size, though not as elongate, and have large ears. The sulcus is not as deep as in the present species, but the ribs are comparable at the anterior edge of the disc: much of the material is exfoliated and so difficult to compare further. As noted by Shi &

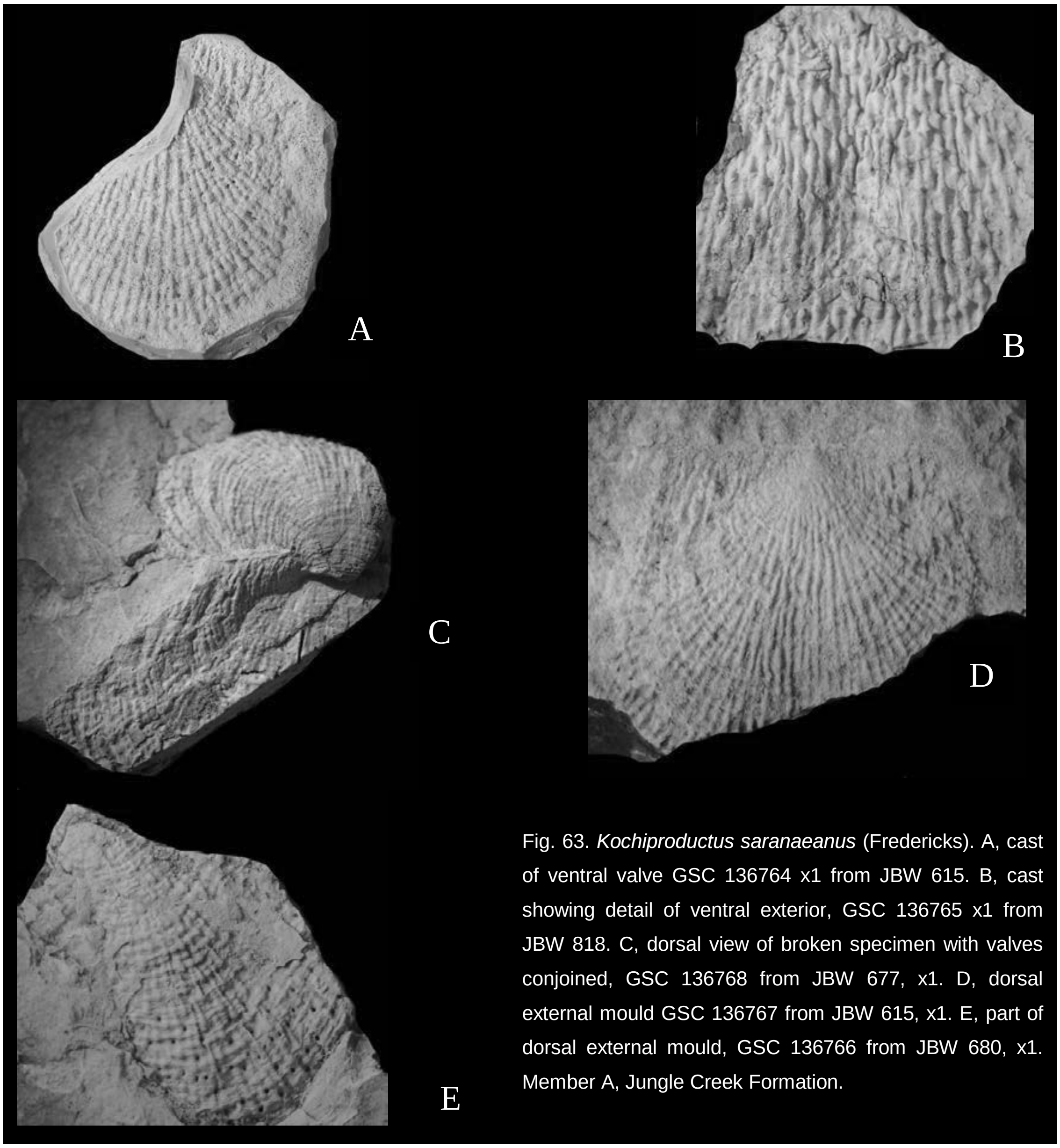


Fig. 63. *Kochiproductus saranaeanus* (Fredericks). A, cast of ventral valve GSC 136764 x1 from JBW 615. B, cast showing detail of ventral exterior, GSC 136765 x1 from JBW 818. C, dorsal view of broken specimen with valves conjoined, GSC 136768 from JBW 677, x1. D, dorsal external mould GSC 136767 from JBW 615, x1. E, part of dorsal external mould, GSC 136766 from JBW 680, x1. Member A, Jungle Creek Formation.

Waterhouse (1996), the anterior costae in type and Yukon *saranaeanus* become fine with frequent bifurcation, much as in the present material (see Fig. 63A, D, E). Type *saranaeanus* was figured from the Urals by Tschernyschew (1902, pl. 27, fig. 2, pl. 34, fig. 4, pl. 35, fig. 2) as *Productus longus* (not Meek) and shows large ears and coarse costae, less sulcate ventral valve and wide dorsal valve: the ears are similarly large. Further material was

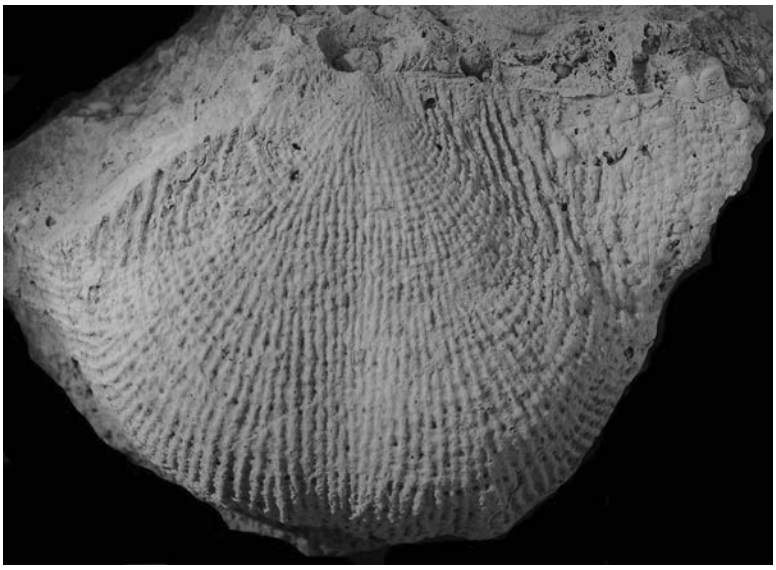


Fig. 64. *Kochiproductus saranaeanus* (Fredericks), dorsal external mould GSC 136769 from JBW 513, x 1. Member A, Jungle Creek Formation.

figured as *Buxtonia saranaeana* by Fredericks (1933, pl. 5, fig. 1) and Kulikov (1974a, pl. 2, fig. 7), and to *Kochiproductus* by Kalashnikov (1986, pl. 118, fig. 5, from Asselian to Artinskian faunas of the Urals and Timan. The species was also reported from Novaya Zemlya by Licharew & Einor (1939, p. 37, pl. 5, fig. 1). The Mongolian specimens figured as *saranaeana* by Li & Gu (1976) are large, but decorticated, with the cardinal extremities lost. A Kungurian specimen assigned to *saranaeanus* by Ifanova in Ifanova & Semenova (1972, pl. 4, fig. 1) is elongate. *Buxtonia peruvianus* not d'Orbigny of Fredericks (1915, p. 26, pl. 3, fig. 1) was included in synonymy by Solomina (1960, p. 43), together with references to the species by Licharew (1939, p. 86, pl. 17, fig. 12, pl. 18, fig. 1, 2; Licharew & Einor 1939, p. 37, pl. 5, fig. 1) from Taimyr, and compared to *P. theodossianus* Gerassimov (1953, p. 44, pl. 6, fig. 1, 2) and *P. georgianus* Gerassimov (1953, p. 52, pl. 6, fig. 1-3). (See below).

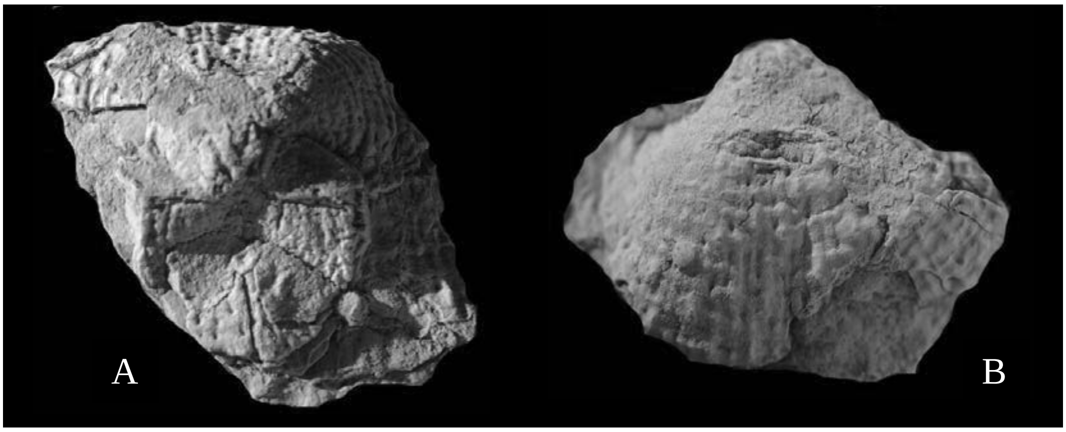


Fig. 65. *Kochiproductus saranaeanus* (Fredericks), posterior part of specimen with valves conjoined, dorsal and ventral views of GSC 136773 from JBW 188, x 2**.** Member A, Jungle Creek Formation.

The material is more transverse, and displays coarser ornament and larger ears than shown by *Kochiproductus imperiosus* from Member C. The interspaces between dorsal costae swell into short elongate pits, unlike the ornament of *Kochiproductus imperiosus*.

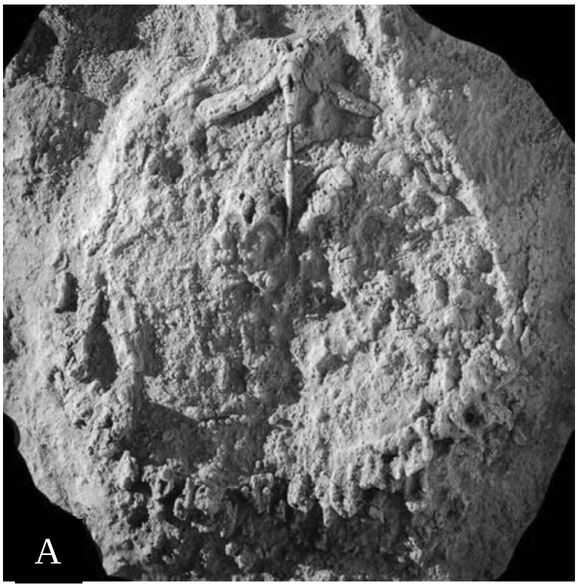


Fig**.** 66. *Kochiproductus saranaeanus* (Fredericks), dorsal interior, GSC 136781 from JBW 141, x1. B, dorsal internal mould, GSC 136770 from JBW 818, x1.5. Member A, Jungle Creek Formation.

Productus theodossianus Gerassimov (1953, p. 44, pl. 5, fig. 8, pl. 6, fig. 1, 2, pl. 20, fig. 5) from Early Permian of the Urals is transverse with similar fold and sulcus, but slightly finer ornament. Allowing for the poor quality of the figures, it looks to be moderately close to *saranaeanus* (Fredericks). *P. georgianus* Gerassimov (1953, p. 52, pl. 7, fig. 1a-c, 2, 3, pl. 20, fig. 6) is less complete and is difficult to assess. It was shown as ranging into younger faunas. Gerassimov's taxa have been referred to *porrectus* by several authors.

Kochiproductus sp**.**

Fig. 67

A fragment of the ventral valve comes from Member B in the Jungle Creek Formation. *Ogilviecoelia initiatus* Zone.

Fig. 67*. Kochiproductus* sp. external cast of ventral valve GSC 136771 from JBW 19, x4. Member B, Jungle Creek Formation.

Kochiproductus imperiosus Waterhouse, 2013

Fig. 68 - 77

2013 *Kochiproductus* (*Kochiproductus*) *imperiosus* Waterhouse, p. 142, Fig. 5.25- 5.31.

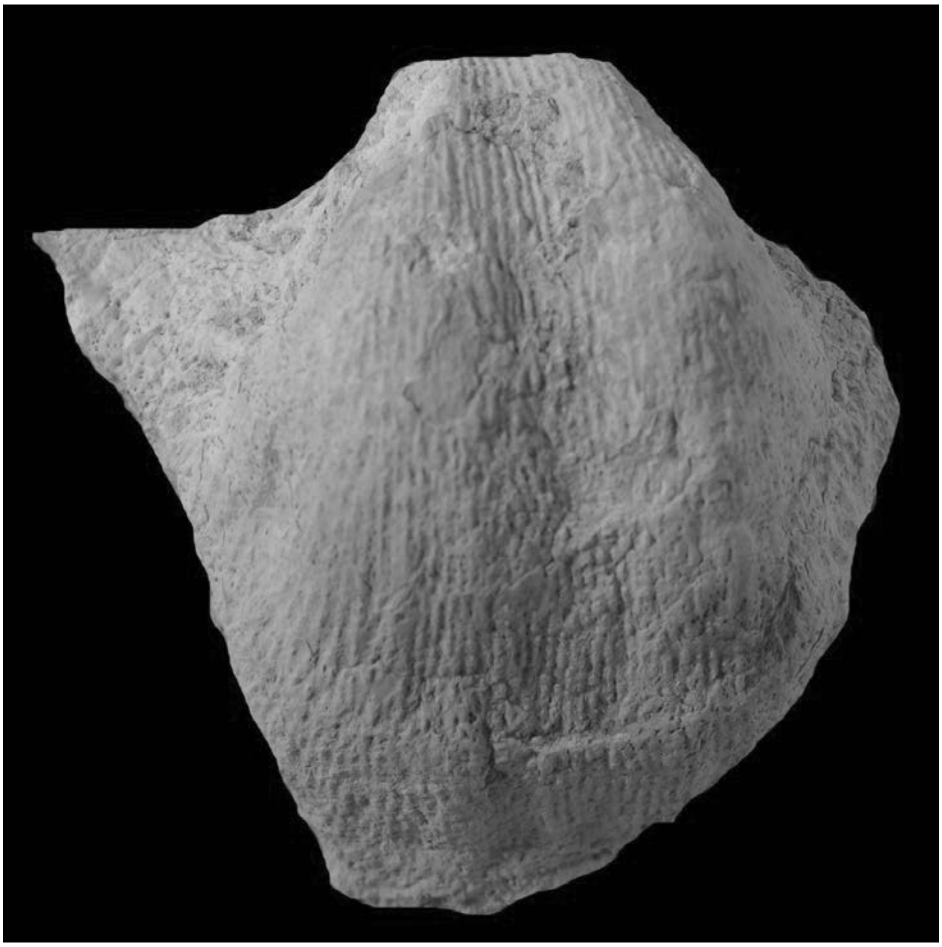


Fig. 68. *Kochiproductus imperiosus* Waterhouse, ventral valve of holotype GSC 133304, x1 from Member C, Jungle Creek Formation. The dorsal valve is present but buried in matrix.

Diagnosis: Large, elongate with moderately well formed ventral sulcus, moderate dorsal fold, wide ears and strong ornament. Commarginal rugae restricted to posterior shell and relatively weak.

Holotype: GSC 133304 figured in Waterhouse (2013, Fig. 5.25, Fig. 5.26 and Fig. 5.29), and herein as Fig. 68, 70 and 72 from Member C, Jungle Creek Formation, Canada, OD.

Material: Seven ventral valves, six dorsal valves from JBW 18, a ventral valve from JBW 403, dorsal valve from JBW 741 and 809 and specimen with valves conjoined and ventral valve from JBW 815.

Stratigraphic and biostratigraphic levels: Member C and possibly Member D, Jungle Creek Formation. *Kochiproductus imperiosus* Zone, possibly *Rugivestigia commarginalis* Zone.

Dimensions in mm: ventral valve

Specimen GSC	Width	Length	height	
133303	75	79	40	
Unregistered	81	76	43	
133304	106	91	58	holotype

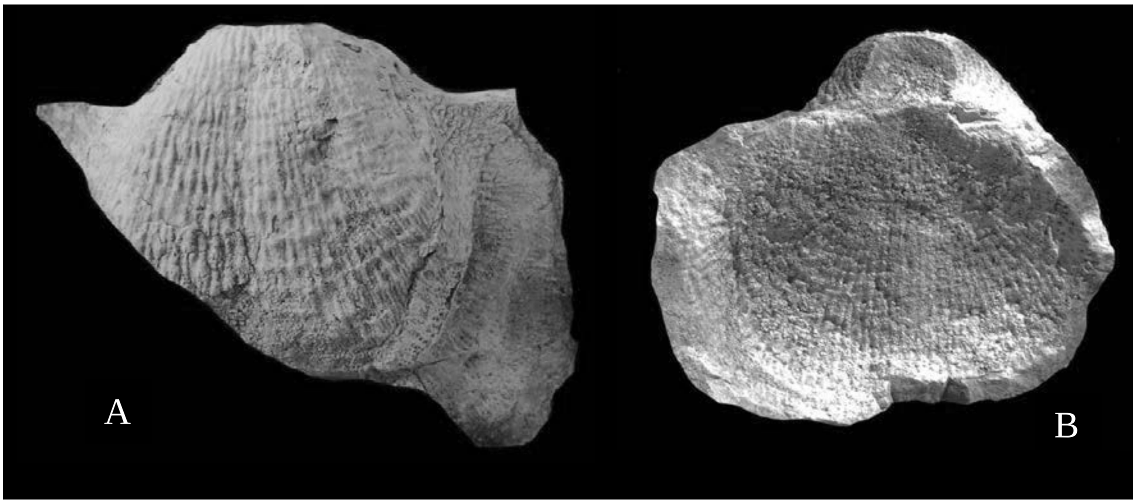


Fig. 69. *Kochiproductus imperiosus* Waterhouse. A, ventral valve, showing skirt (which is equivalent to a stolidium in *Stenoscisma*) GSC 133306. x0.8. B, dorsal valve GSC 133309, x0.9. Specimens from Member C, Jungle Creek Formation .

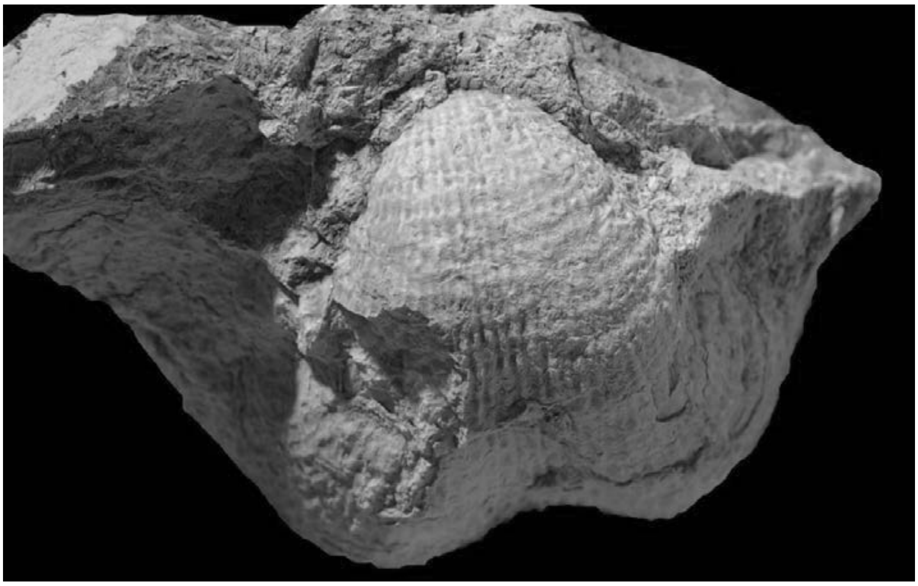


Fig.70. *Kochiproductus imperiosus* Waterhouse, slightly tilted because of light-blocking lump of matrix, posterior ventral aspect of ventral valve holotype GSC 133304 x1 from Member C, Jungle Creek Formation.

Description: Specimens very large, ventral valve highly convex, with broad incurved umbo, umbonal walls high and steeply convex, diverging at 60-70º, and large gently convex ears at maximum width though with obtuse extremities; sulcus well defined, commences some 10-15mm in front of umbonal tip and widens at angle of 30º. Dorsal valve almost flat across disc apart from subdued narrow fold which varies in strength on different specimens, large concave ears, and high geniculate trail almost as long as the disc. The body cavity is extremely thick. Ornament on ventral valve of low costae, some four in 10mm at 45mm from the beak, and five to six anteriorly, with five in 10mm on the anterior flanks, increasing mainly if not entirely by intercalation, with rounded crests and interspaces of similar width.

There are numerous fine erect spines with very slightly swollen and moderately prolonged bases, arising from the costal crests over the disc and umbonal flanks, and as shown by the specimen from JBW 815, a cluster of ear spines 0.5mm in diameter and 55mm long extends posteriorly. The shell is crossed by low rugae, 2mm apart posteriorly, increasing to 2.5mm anteriorly, and strengthening over the umbonal walls. The intersections of rugae and spinose ribs impart a particular and peculiar spinifronsin texture to the shell surface, termed “bumpy” by Stehli & Grant (1971). The dorsal ornament is similar, except that commarginal rugae are slightly more prominent and spines less common, largely restricted to the anterior disc and trail at maturity, with only a few slender erect spines over the dorsal ears of mature shells. Ribs do branch anteriorly.

In the ventral valve, the adductor scars are narrow and the diductor scars large and oval and moderately impressed, but are not well known. In the dorsal valve, the cardinal process is slender and bilobed, with a sturdy ridge extending in front along each side of the hinge, and the median septum continues as a narrow blade as far as the start of the trail.

Resemblances: Specimens ascribed to *Kochiproductus porrectus* (Kutorga, 1844, p. 26, pl. 10, fig. 3) from the “*Yakovlevia transversa”* to *Jakutoproductus verchoyanicus* Zones in the younger Jungle Creek Formation by Shi & Waterhouse (1996, pl. 10, fig. 5-12, pl. 11, fig. 1-6, Fig. 28) are smaller with finer ornament, compared with the present material, involving seven to eight ribs in 10mm, and have less inflated disc, lower trail, shallower sulcus and high dorsal fold. They are not as large or as coarsely costate, and have weaker wrinkles than the Russian species, but the lack of true external ornament makes them difficult to assess. The species *porrectus* as interpreted from material figured by Tschernyschew (1902, pl. 32, fig. 4, pl. 55, fig. 1, pl. 56, fig. 4; Sarytcheva in Sarytcheva & Sokolskaya 1952, pl. 36, fig. 4; 1960, Fig. 216, 217) is very close in shape, size and ornament to the present form, displaying some five or usually six costae and four commarginals in 10mm over mid-ventral valve, but the ventral sulcus is deeper especially over the disc anteriorly in the present form and costae are slightly coarser. The specimen figured by Tschernyschew (1902, pl. 62, fig. 2) has distinctly finer costae. Some features, such as the large ears of the Canadian material, or the fold over the dorsal trail, are not preserved in Tschernyschew’s material. Internal fragments were figured as aff. *porrectus* by Gerassimov (1953, pl. 7, fig. 4, pl. 8, fig. 1, 2), difficult to assess. A suite of specimens was figured by Solomina (1960, p. 41, pl. 5, fig. 5-10, pl. 6, fig. 1-3) from the Talatin Suite of Pai Hoi, of late Early Permian age. Solomina (1960, p. 41) included in synonymy *P.* (*Buxtonia*) *lesnikowae* Stepanov (1934, p. 24, pl. 2, fig. 8-10) and *P.* (*Buxtonia*) *freboldi* Stepanov (1937a, p. 122, pl. 2, fig. 2). Of other specimens referred to *porrectus* from Russian outcrops, those figured in Abramov (1970, pl. 13, fig. 1-5) from the Verchoyan Suite of Verchoyan, northeast Russia, are smaller with broad shallow sulcus and fine ornament, not closely allied to the Urals species, whereas the large Taimyr specimens figured by Ustritsky & Chernyak (1963, pl. 9, fig. 4, 5) from the Holodnin Suite (C_2^b according to the text), show considerable approach to the Canadian specimens in the depth of ventral sulcus and coarseness of costae: the dorsal fold seems low, much as in present material. A rather damaged specimen from the Urals that was illustrated by Kulikov (1974, pl. 2, fig. 6) does suggest the presence of large ears, and a Talatin Formation specimen figured by Kalashnikov (1990, pl. 1, fig. 10) as *porrectus* lacks strong transverse ornament and has prominent spine bases close to those of *Taeniothaerus* Whitehouse or *Glabrispinus*. The latter genus is based on *Kochiproductus elongatus* Cooper & Grant (1975, pl. 358, fig. 4-6) from the Skinner Ranch Formation of west Texas, and was named by Waterhouse (2013, p. 196). Unlike *Kochiproductus*, it lacks radial ribs.

The specimen reported by Tschernyschew & Stepanov (1916a, b, p. 41, pl. 5, pl. 8, fig. 5) as *porrectus* from Great Bear Cape, Ellesmere island, Arctic Canada), is less inflated with deeper sulcus. (Great Bear Cape was wrongly stated as being in Arctic Russia in the *Revised Brachiopod Treatise*.)

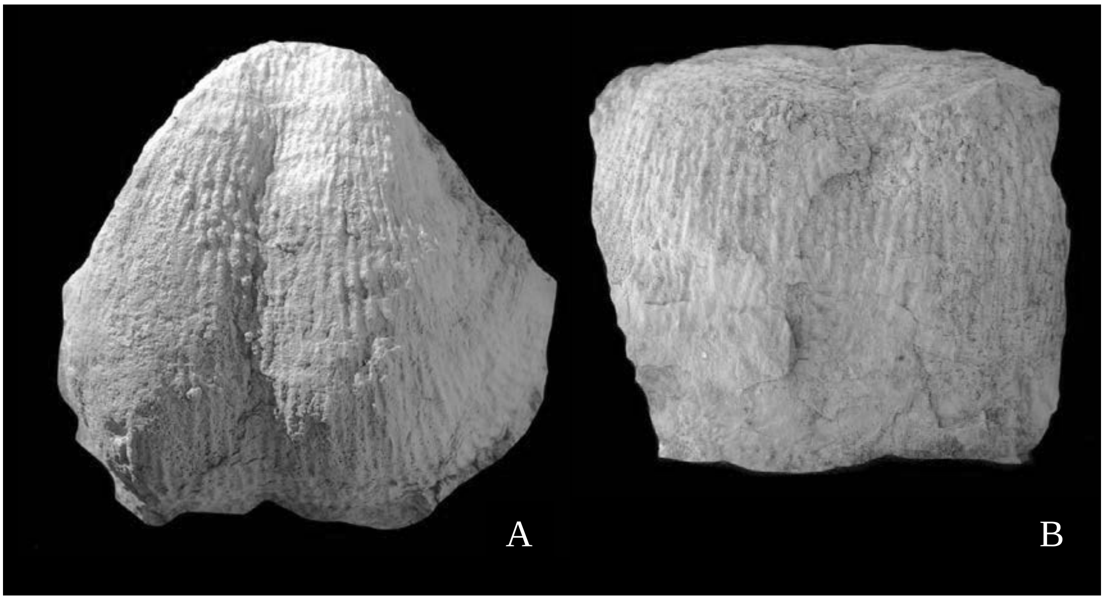


Fig. 71. *Kochiproductus imperiosus* Waterhouse. A, ventral valve GSC 133303, x0.8. B, trail of dorsal valve, decorticated, inner view, GSC 133319, x0.8. Specimens from Member C, Jungle Creek Formation.

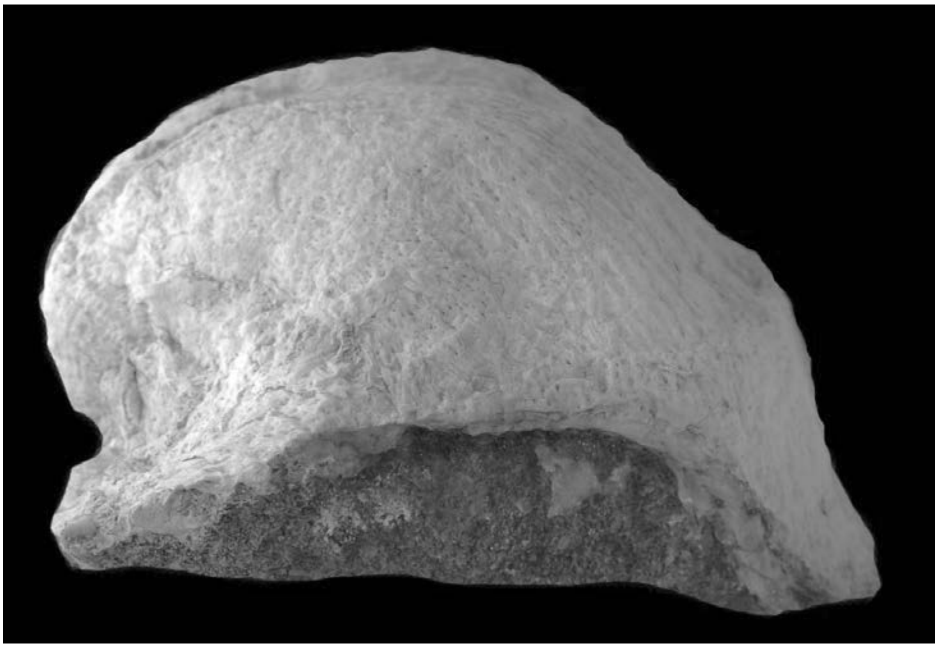


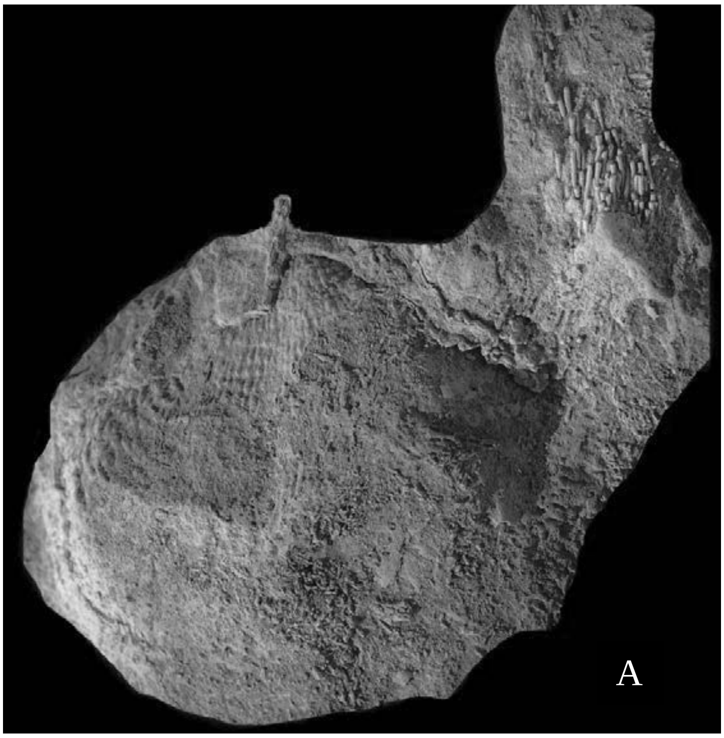
Fig. 72. *Kochiproductus imperiosus* Waterhouse, lateral view of ventral valve GSC 133304, holotype, x1. See Fig. 68 and Fig. 70. Specimen from Member C, Jungle Creek Formation.

Kochiproductus levinsonlessingi Zavodowsky (1970, pl. 5, fig. 1) from the Asselian Burgali Horizon of northeast Russia is wide with virtually no sulcus and finer ribs. *K. sultanaevi* Kulikov & Stepanov in Stepanov et al. (1975) of Middle Permian age from the Kanin Peninsula, Russia, is not well known with regards its anterior costae. Kalashnikov (1983, pl. 54, fig. 1-3) figured worn specimens with coarse ornament and shallow sulcus from the Talatin Suite of the Petchora Basin, northwest Russia.

Other species include *Productus peruvianus* d'Orbigny (1842, p. 52, pl. 4, fig. 4; Kozlowski 1914, p. 38, pl. 5, fig. 1-4, text-fig. 7) from the Copacabana Group of Bolivia. The specimens are smaller with more prominent spine bases. Muir-Wood & Cooper (1960, pl. 75, fig. 13-15, pl. 77, fig. 1-7) figure smaller specimens from the Hueco and Hess limestones of Texas, United States, with less sulcate ventral valve and finer nodose ribs. From west Texas, *Kochiproductus occidentalis* (King, 1931, pl. 17, fig. 20, 21; Cooper & Grant 1975, pl. 358, fig. 7-9) from the Neal Ranch Formation is moderately close in shape, but is too worn and damaged to allow adequate comparison. *K. quadratus* Cooper & Grant, 1975 from the Hueco Canyon Formation is large with finer and more nodose ribs, and *K. victorioensis* (King, 1931, pl. 19, fig. 1; Cooper & Grant, 1975, pl. 360, fig. 8-12) is similar in shape and other aspects but has finer ornament, shallower sulcus and transverse outline, more as in the genus *Gemmulicosta* Waterhouse (see p. 112 herein). It comes from the Victorio Peak Member of the Bone Spring Formation.

There is is some similarity to the material assigned to *Kochiproductus freboldi* (Stepanov) by Harker in Harker & Thorsteinsson (1960, p. 59, pl. 17, fig. 5, 6) from the Assistance Formation of Roadian age at Grinnell Peninsula, Devon Island, in the Canadian Arctic Archipelago. The Assistance specimens are comparably large with well formed ventral sulcus and low dorsal fold, wide weakly obtuse hinge, though without the comparatively large ears of better preserved specimens of *imperiosus* (see Fig. 74), and with broad somewhat incurved ventral umbo, and the typical kochiform "bumpy" ornament. Differences are that *K. imperiosus* is more swollen, the shell higher even near the hinge compared with the height in specimens from the Assistance Formation, and the trail in *K. imperiosus* is particularly high, but in the Assistance material, only the start of a semigeniculate trail is preserved, so that its full height in not known. The ribs on the latter specimens tend to be slightly finer, and the commarginal rugae are more emphasized on the lateral flanks of the ventral valve in the Assistance material. On the dorsal valve the rugae tend to be more prominent in *imperiosus*. The history of taxonomic assessment for the Assistance material is rather complicated. Harker in Harker & Thorsteinsson (1960) identified the specimens with *Kochiproductus freboldi* from Spitsbergen, together with further Arctic material described by Frebold (1931, 1942) and synonymized it with *K. plexicostatus* Dunbar, 1955 from the late Permian of Greenland. But the type of *freboldi* does not look much like *Kochiproductus*, given the lack of bumpy ornament"in the figure, and *plexicostatus* differs significantly. The question is further discussed in the Appendix starting on p. 455.

Kochiproductus plexicostatus Dunbar (1955, p. 109) comes from Late Permian (Changhsingian) of Greenland. Unlike anterior costae in older species referred to *Kochiproductus* (*Kochiproductus*), or the specimens from the Assistance Formation, the anterior costae show irregular swellings and branching, and may anastomise. None of the Greenland specimens display the split dorsal septum or short buttress plates of older species assigned to *Kochiproductus*, although this may be because no immature specimens have been described or figured. Dunbar's species, because of the difference in ornament, has been assigned to a separate subgenus, *Dunbarovia* Waterhouse, 2013, p. 147, as illustrated in the Appendix on p. 459**,** Fig. 382.



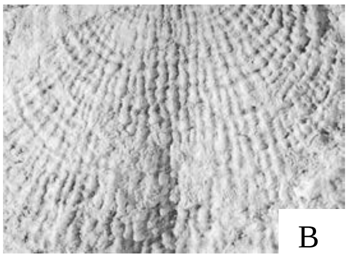


Fig. 73. *Kochiproductus imperiosus* Waterhouse. A, dorsal valve showing cardinal process and posterior lateral spines from ventral valve, GSC 133301, x0.8. B, dorsal valve, panel detail of external ornament on dorsal valve, preserved as mould, GSC 133307, x1. Specimens from Member C, Jungle Creek Formation.

Fig. 74. *Kochiproductus imperiosus* Waterhouse, dorsal valve external mould and posterior interior, GSC 133302, x1. Specimen from Member C, Jungle Creek Formation.

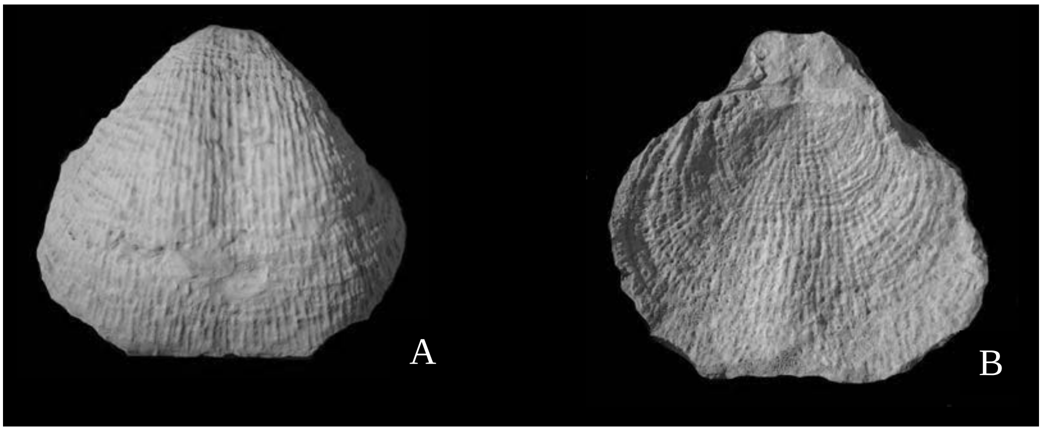


Fig. 75. *Kochiproductus imperiosus* Waterhouse, ventral and dorsal aspects of GSC 136772, x1. Specimen from JBW 18, Member C, Jungle Creek Formation.

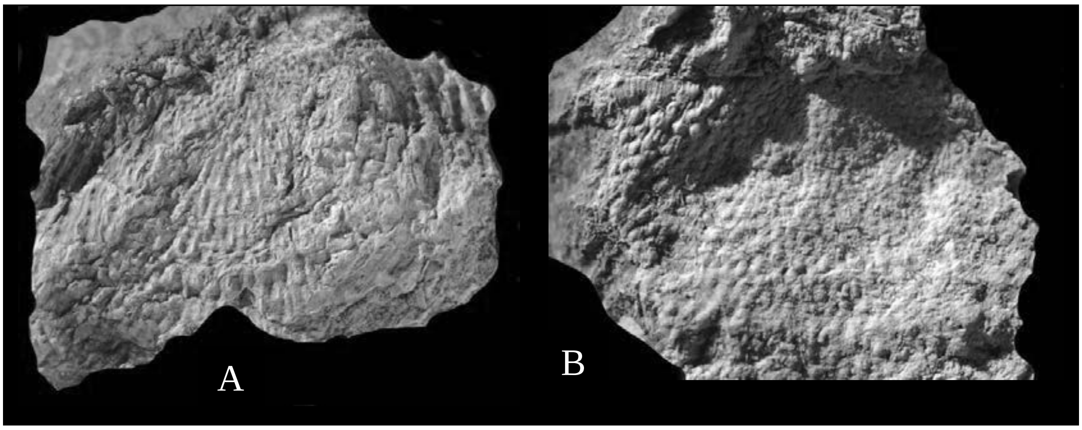
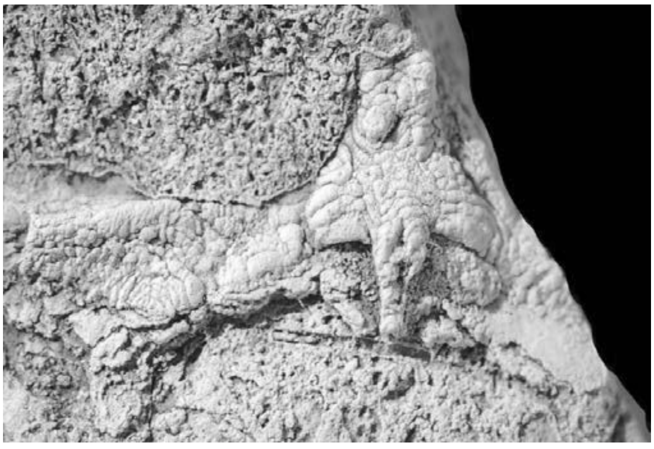


Fig. 76. *Kochiproductus imperiosus* Waterhouse, views of internal and external aspects of dorsal valve GSC 137284 x2 from JBW 18, Member C, Jungle Creek Formation.

Fig. 77. *Kochiproductus imperiosus* Waterhouse, silicified cardinalia in dorsal valve, x3, GSC 133305 x 4 from JBW 18. Member C, Jungle Creek Formaton.



Kochiproductus porrectus (Kutorga, 1844)

Fig. 78

1844 *Productus porrectus* Kutorga, p. 26, pl. 10, fig. 3.
1902 *Productus porrectus* – Tschernyschew, p. 634, pl. 32, fig. 4, pl. 55, fig. 1, pl. 56, fig. 4 (part, not pl. 62, fig. 2 = sp. indet.).
1953 *P*. aff. *porrectus* Gerassimov, p. 57, pl. 7, fig. 4.
1959b *Buxtonia* cf. *B. porrecta* – Kashirtsev, p. 38, pl. 15, fig. 1, 2.
1960 *Kochiproductus porrectus* – Muir-Wood & Cooper, pp. 260-261.
1970 *K. porrectus* – Solomina, p. 82, pl. 5, fig. 1.
1971 *K.* cf. *transversus* [non Cooper] – Bamber & Waterhouse, pl. 12, fig. 5.
1974 *K. porrectus* – Kulikov, pl. 2, fig. 6,
?1976 *K. porrectus* – Li & Gu, p. 253, pl. 253, pl. 168, fig. 2, 3, pl. 183, fig. 2-4.
1980 *K. porrectus* – Kalashnikov, p. 40, pl. 7, fig. 3, 4.

Diagnosis: Large shells with shallow but well formed sulcus, very low dorsal fold, well formed ribs numbering six in 10mm.

Holotype: Specimen figured by Kutorga (1844) from Sterlitamak, south Urals, kept at Tschernyschew Museum, St Petersburg.

Material: An internal mould with both valves conjoined from JBW 581, small fragments, a ventral and separate dorsal valve from JBW 580 and dorsal valves from JBW 560 and 581. Ventral valve from GSC 55135.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Specimen from JBW 581 is 59mm wide, 50mm long and 18mm thick, with edges, ears and trail lost. There is a well defined ventral sulcus that shallows near the anterior margin and low dorsal fold limited to the anterior disc. The ornament is that typical of *Kochiproductus*, with the ventral valve covered by undulose irregular ridges bearing slender erect spines, little disrupted by the low commarginal rugae. The rugae are more conspicuous on the dorsal valve and slightly disrupt the spinose ribs, which number six in 10mm over the anterior disc. The dorsal median septum extends to mid-length, and divides large adductor scars which are anteriorly striate. Specimen GSC 26918 from GSC locality 55135 is large with slightly coarser ornament, and similar sulcus and shape (Bamber & Waterhouse 1971, pl. 12, fig. 5). In a small and immature specimen, the adductor impressions are covered by fine irregular ribs and grooves that merge anteriorly.

Resemblances: The ribs of these specimens are slightly coarser than those of *Kochiproductus porrectus* described by Shi & Waterhouse (1996, p. 79, pl. 10, fig. 5-12, pl. 11, fig. 1-6, Fig. 28) from the younger Jungle Creek Formation, and those of the Oregon specimen figured as *Kochiproductus* cf. *K. porrectus* by Cooper (1957, p. 47, pl. 4B, fig. 7), and the ventral spine bases are more swollen and prominent, approaching those of *Kochiproductus imperiosus* from Member C. In addition, the younger Jungle Creek specimens have well marked commarginal rugae crossing the ventral valve, but these are not seen on present material. The present specimens are particularly close to type *Kochiproductus porrectus* in ornament and sulcus-fold, as summarized in the synonymy. The rib strength and spacing, and development of sulcus and fold are similar, whilst making allowance for the likelihood that the Canadian specimens are not fully grown.

There is also considerable approach to *Kochiproductus transversus* Cooper (1957, p. 46, pl. 4A, fig. 1-6) from the Coyotte Butte Formation of Central Oregon. Shells like this species were also figured as *Kochiproductus* n. sp. by Yole (1963, pl. 1, fig. 4, 5) and as *K*. cf. *transversus* in Bamber & Waterhouse, 1971, pl. 12, fig. 5, though this specimen does not appear to be fully identical. The species *transversus* is slightly smaller than present material, but was judged to be fully mature by Cooper (1957). It has seven to eight ribs in 10mm.

The identification of various specimens as *Kochiproductus porrectus*, or compared with *porrectus*, appears to have been based mostly on generic similarity of the "bumpy" ornament. Examples include Grabau (1931, p. 295, pl. 1, fig. 10), and Ustritsky et al. (1963, p. 9, pl. 1, fig. 4, 5) from west Gansu, China. Mansuy (1913, pl. 3, fig. 10) figured a supposed specimen from the Early Permian of Kham-Kheut, Laos, that shows only the posterior part of a dorsal valve. *K. egragius* Li & Gu (1976, p. 254, pl. 182, fig. 3, 4) from the Early Permian of Mongolia is very incomplete, with somewhat decorticated surface, and the outer hinge apparently lost. It appears to be more transverse than the present species. So called *porrectus* of Grabau (1936, pl. 6, fig. 1) from the Maping Limestone of China may be related but is an exfoliated fragment, difficult to identity.

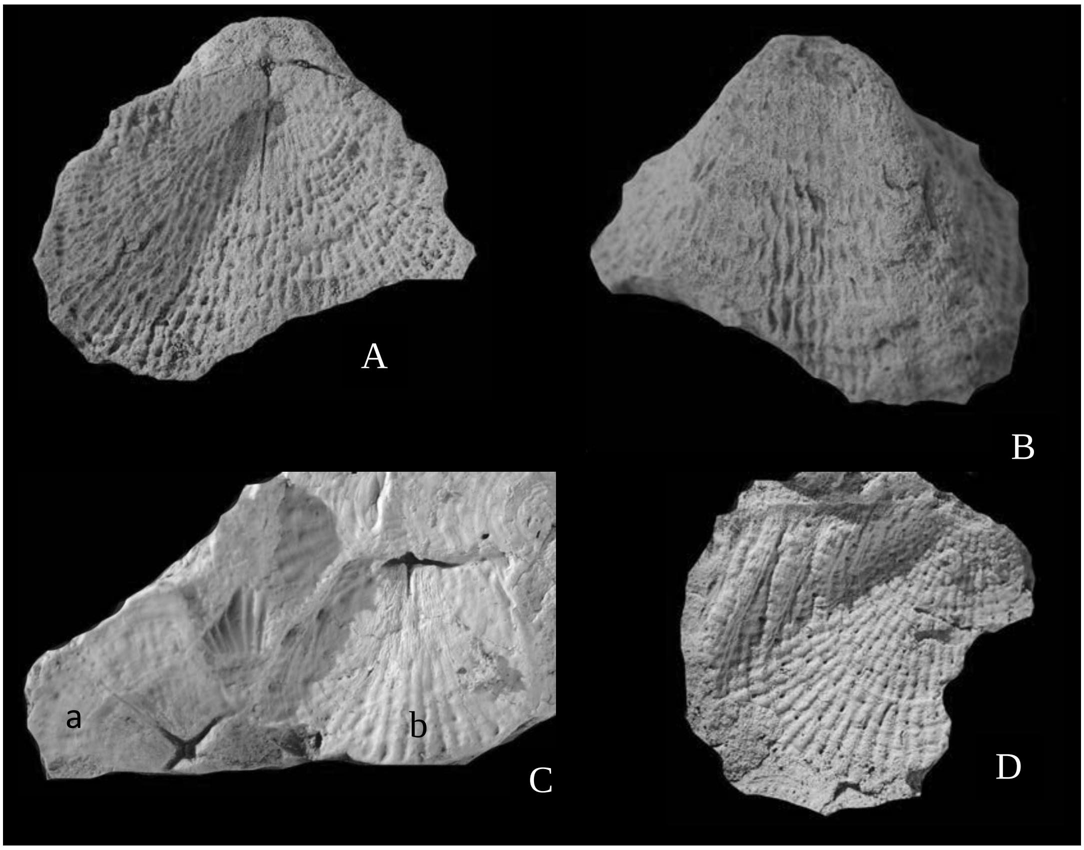


Fig. 78. *Kochiproductus porrectus* (Kutorga). A, B, dorsal and ventral aspects of internal mould, GSC 136774 from GSC 581 x1. C. part of internal moulds of dorsal valves GSC 136775 (b) and GSC 137346 (a) x2 from JBW 581. D, dorsal immature internal mould, GSC 136776 from JBW 580 x2. Member E, Jungle Creek Formation.

Gobbett (1964, pl. 7, fig. 1-3) described broken specimens from the Spirifer Limestone or Vøringen Member of Spitsbergen that are only moderately close, having more nodose ribs, but it is difficult to compare the material fully. Gobbett (1964, p. 80) included some material originally described as *Productus payeri* Toula (1874, pl. 4, fig. 1, 3) in possible synonymy with *porrectus*, as well as *Productus* (*Buxtonia*) *freboldi* Stepanov (1937a, p. 122, 176, pl. 2, fig. 4, part) and a shell figured by Harker in Harker & Thorsteinsson (1960, pl. 17, fig. 5, 6) from the Assistance Formation of Canada, material that is discussed further in the Appendix **(**p. 456). Gobbett (1964) reported that the other Toula specimens, labelled as *payeri* at the Natural History Museum in Vienna, Austria, resembled *Waagenoconcha irginae* (Stuckenberg) and *Horridonia timanicus* (Stuckenberg). Dunbar (1955, p. 85) had ascribed all Toula material to *Waagenoconcha payeri* (Toula), but only that of Toula (1874, pl. 4, fig. 2) seems likely to belong to Waagenoconchidae. A lectotype for *payeri* is cited on p. 456 and illustrated in Fig. 381, p. 458.

Genus ***Nassichukia*** n. gen.

Derivation: Named for W. W. Nassichuk.

Diagnosis: Medium-size, subgeniculate, ventral valve sulcate, two or three spine rows along hinge, posterior shell smooth apart from low tubercles and low rugae, middle and anterior shell with broad low ribs, spines arising from low tubercles along ribs on both valves.

Type species: *Nassichukia nodosa* n. gen., n. sp., from basal Jungle Creek Formation (Gzhelian), Ogilvie Mountains, Canada, here designated.

Discussion: This genus is close to *Kochiproductus* and allied genera, with prominent commarginal undulations, and costae that swell episodically, and give rise to narrow erect spines. It has spines on both valves, and two or three hinge rows of ventral spines. Unlike *Kochiproductus*, the posterior ventral and dorsal valve is comparatively smooth apart from commarginal rugae and scattered spines. The genus is small for members of the tribe.

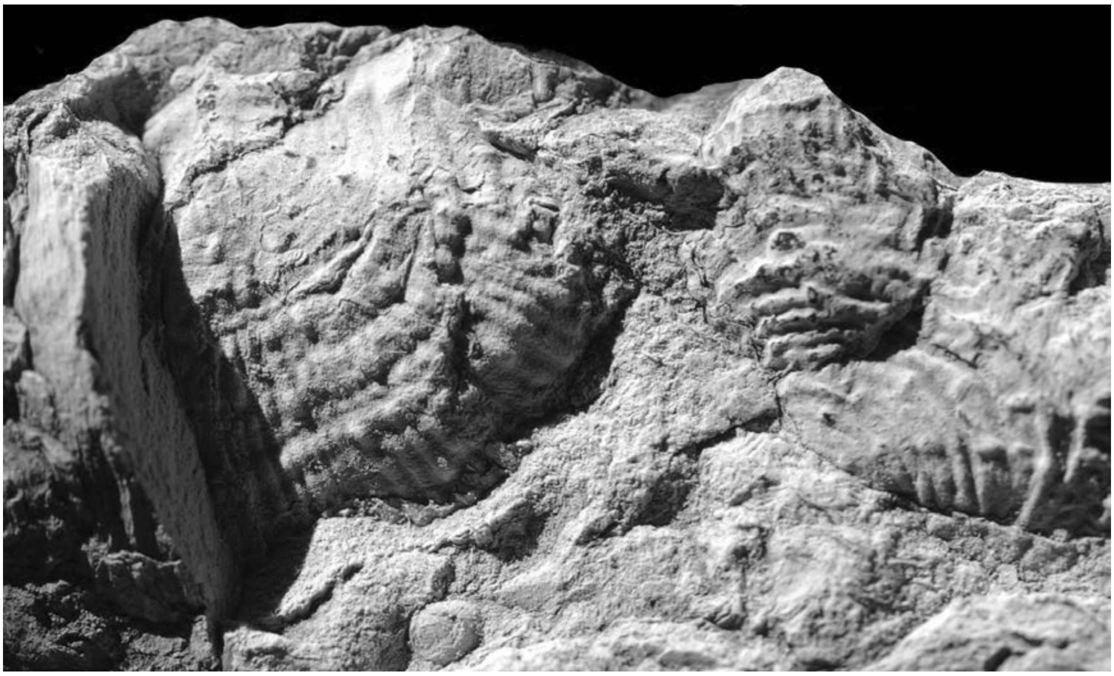


Fig. 79. *Nassichukia nodosa* n. gen., n. sp., enlarged view of GSC 137254 (to left) and GSC 137251 x3 from JBW 451, Member A, Jungle Creek Formation.

Nassichukia nodosa n. sp.

Fig. 79, 80

Name: nodosus – full of knots, Lat.

Diagnosis: As for genus, with only one species known.

Holotype: GSC 137249, here designated.

Material: Two specimen with valves conjoined, two ventral valves and three dorsal valves, with other fragments, from JBW 451.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

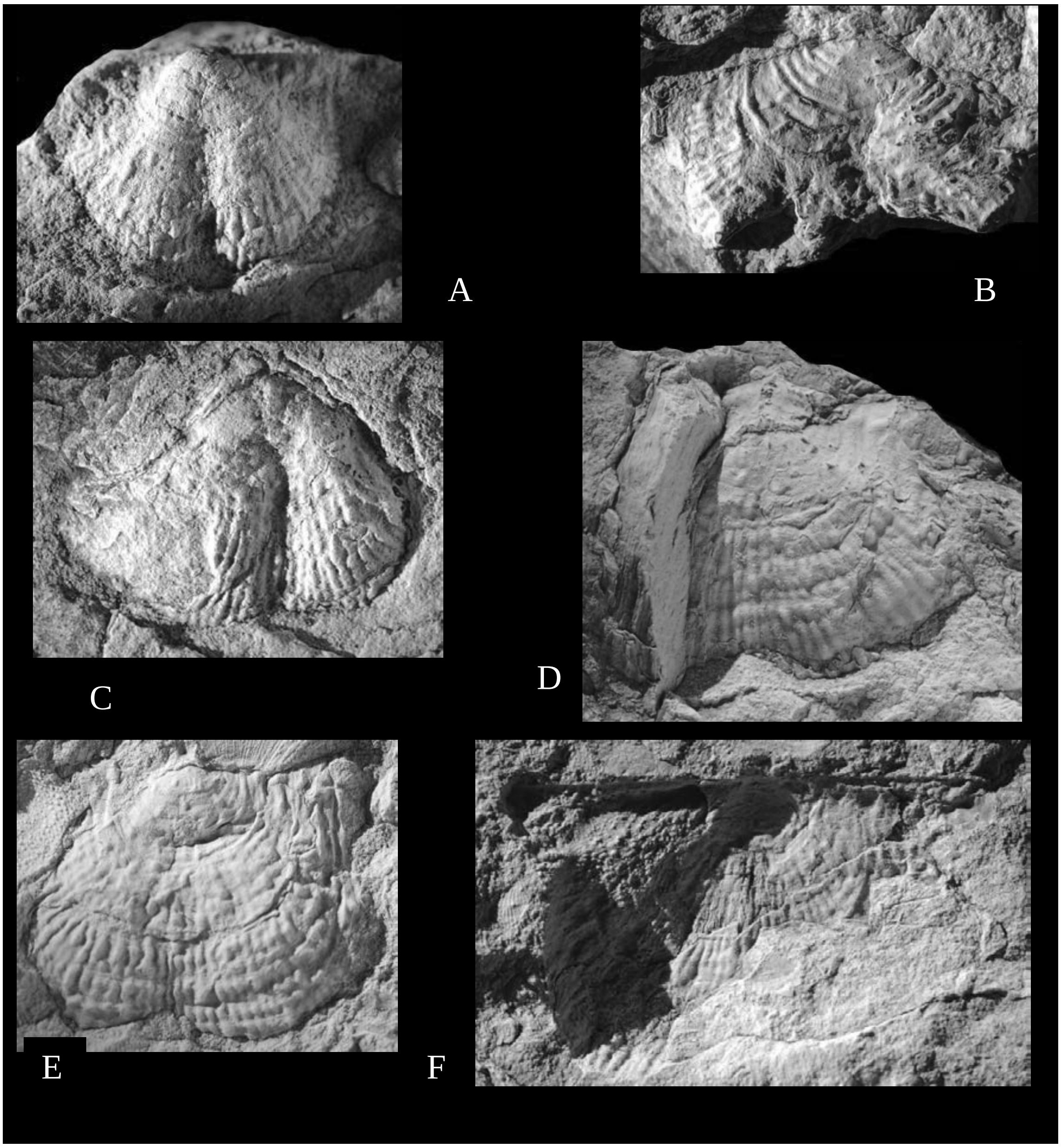


Fig. 80. *Nassichukia nodosa* n. gen., n. sp. A, ventral valve GSC 137249, holotype. B, ventral valve GSC 137251 (see Fig. 79). C, worn ventral valve GSC 137250. D, specimen GSC 137254 with much of ventral valve (to left) concealed, showing disc thickness and exposing much of dorsal valve, to right, with cardinal process and hinge ridges. See Fig. 79. E, dorsal valve GSC 137253 showing worn exterior from inner view with cardinal process. F, dorsal valve GSC 137252. Specimens x2, from JBW 451, Member A, Jungle Creek Formation.

Description: The holotype is 22mm wide, 19mm or so long and 8mm high, and a dorsal valve is 38mm wide.

Maximum width lies at the hinge, and ventral ears are large and gently convex, and the dorsal ears gently concave.

The ventral umbo broadens at an angle close to 110º, and is not incurved, and the posterior walls are convex and steep but not high. The ventral valve is moderately convex, and the dorsal valve concave, forming a visceral disc 7mm thick in a shell 32mm wide. A well formed but not very deep sulcus develops in front of the beak, with an angle of 20º, opposed in the dorsal valve by a low fold with rounded crest. Both valves are crossed by commarginal rugae that may be irregular in strength, but are not high and fade anteriorly, and costae commence six or seven mm in front of the beak in front of posterior shell that is smooth apart from spines and lateral rugae, to cover both valves, numbering five to six in 5mm, and missing from the ears. Spines are developed in both valves, and form two or three rows along the hinge over the ventral ears, opposed by dimples in the dorsal ears. Over the ventral valve, spines are scattered and arise each from a small swelling, between the commarginal rugae near the umbo, and anteriorly at the crest of costae. Spine bases are less conspicuous on the dorsal valve, though also arising from costal crests, and there are a number of small well formed pits along the interspaces. The trail is semigeniculate and low.

Ventral adductor scars are narrow and small, and diductor impressions suboval with radial grooves. A low dorsal marginal ridge lies close to the hinge and the cardinal process is low and deeply embayed on its inner face, with four low lobes, the median two well spaced or close together in different specimens. The median septum extends over the posterior third of the shell length, and lacks a median cleft.

Resemblances: This genus is distinctive externally, with its prominent rugae and nodes posteriorly, and nodose ribs in front, and no species or genus appears comparable.

Genus ***Gemmulicosta*** Waterhouse, 1971a

Diagnosis: Medium to large in size, ventral ribs persistent, spines arise from low swellings that gradually emerge from ribs crests, dorsal ornament of erect spines, ribs and commarginal fine rugae. Numerous spines over ventral and dorsal ears.

Type species: *Gemmulicosta gemma* Waterhouse, 1971a, p. 210 from Ettrain Formation (Kasimovian), Yukon Territory, Canada, OD.

Discussion: Brunton et al. (2000, p. 496) synonymized *Gemmulicosta* with *Buxtonioides* Mendes, 1959, p. 43, based on type species *Productus amazonicus* Katzer, 1903, p. 264, pl. 7, fig. 1a-f, from Pennsylvanian beds of the Amazon valley in Brazil. For this genus, the original figures as in Mendes (1959, pl. 3, fig. 1, 2, pl. 2, fig. 1, text-fig. 10, 11, 13, 14) and reproductions in Brunton et al. (2000, Fig. 339a-c) indicate that the ventral spines are virtually erect and arise without significant swelling from rib crests that are only moderately disturbed, so that radial ornament is more dominant than in *Kochiproductus* or *Gemmulicosta.* This appears to be confirmed by the figures provided of more or less topotype *Buxtonioides* from Brazil by Chen et al. (2004, Fig. 4J). Interestingly, their Fig. 4I shows that only the umbonal region has posteriorly prolonged spine-bases. By comparison, the ventral spines in mature *Gemmulicosta* arise from swellings, posteriorly prolonged well behind each spine, though only a little wider and higher than the rib. That is judged to be generically significant. In the ornament of mature *Buxtonioides* the ribs are comparatively fine and branch less than is usual in *Kochiproductus*, and commarginal rugae and spine swellings are less conspicuous than in *Gemmulicosta*. *Gemmulicosta* has ornament moderately close to that of *Kochiproductus* over the disc, and closer to that of ornament over the trail, but its ornament is decidedly less “bumpy”, to use a term applied by Stehli & Grant (1971).

Gemmulicosta undulata n. sp.

Fig. 81

Derivation: unda – wave, billow, Lat.

Diagnosis: Comparatively small, distinguished by fine costae from which spines emerge with slightly swollen and short spine bases, valves crossed by well defined commarginal rugae.

Holotype: GSC 136780, here designated.

Material: Single ventral valves from JBW 101, 189, 190, 192, 195, 617?, 675, 677 and 801, two ventral valves from JBW 3, single specimen with valves conjoined from JBW 198.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimens comparatively small and not strongly inflated, ventral valve with broad umbo of 100º and low umbonal walls, ears not well preserved laterally, but inner ears well formed near umbonal slopes, sulcus shallow and fades anteriorly. Ventral ornament of fine costae, five in 5mm, crossed over disc by two to three commarginal rugae in 5mm. Spines numerous over ventral valve, emerge from bases only slightly wider than costae and extending for up to 3mm. Dorsal ornament of ribs and somewhat irregular interspaces, numerous fine spines**.** Internal detail obscure, dorsal median septum extends to almost mid-length; adductor scars faintly impressed.

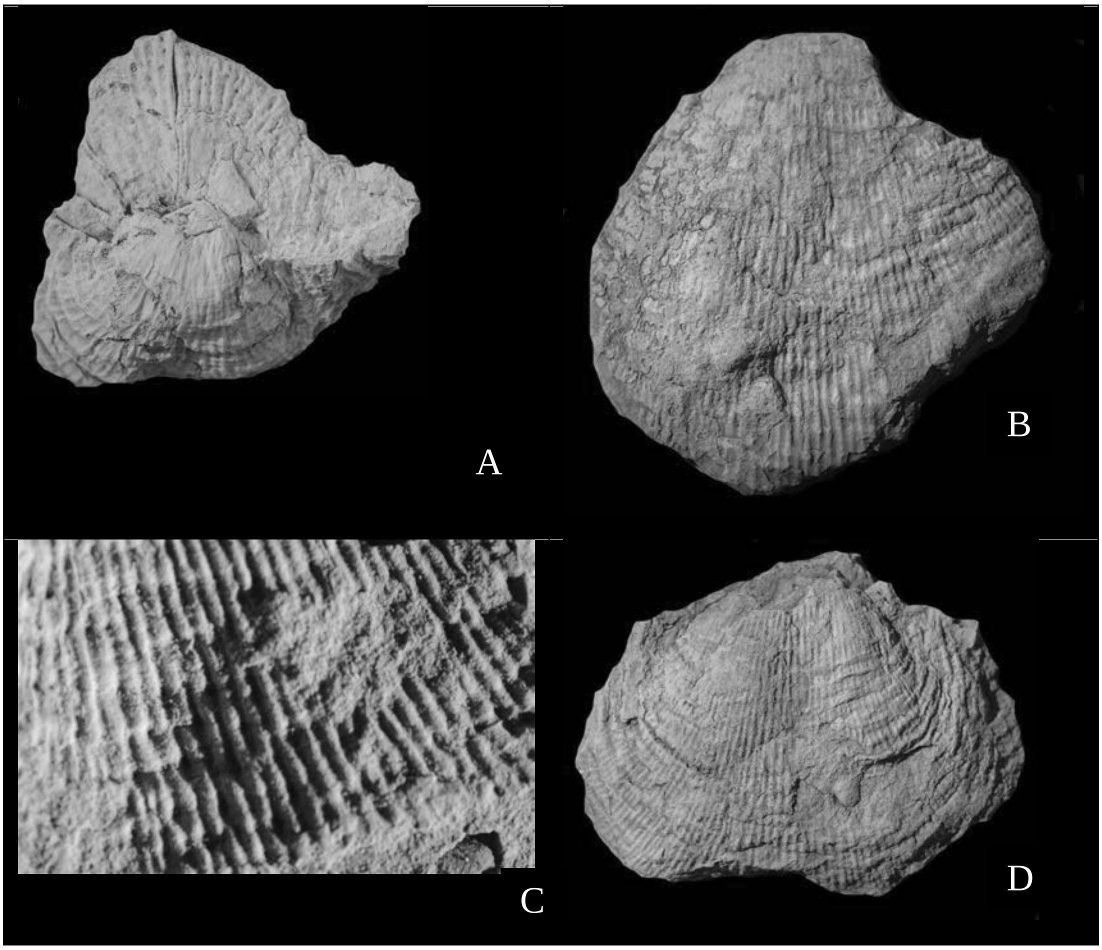


Fig. 81. *Gemmulicosta undulata* n. sp. A, crushed specimen with valves conjoined, dorsal valve on top, GSC 136777 x1.5 from JBW 198. B, broken ventral valve GSC 136778 x1.5 from JBW 195. C, detail of external mould of ventral valve GSC 136779 x2 from JBW 3. D, ventral valve holotype GSC 136780 x1 from JBW 3. Member A, Jungle Creek Formation.

Resemblances: *Gemmulicosta gemma* Waterhouse, 1971a from the Ettrain Formation of the Ogilvie Mountains in the Yukon Territory of Canada is a much larger species with coarser ribbing and prominent spine bases, and much less conspicuous commarginal ornament.

Buxtonia gjeliensis Ivanov (1935, p. 31, pl. 1, fig. 11, pl. 4, fig. 9, 11, 12), also figured by Sarytcheva & Sokolskaya (1952, p. 102, Fig. 17) and Mironova (1967, pl. 2, fig. 1) from the Late Carboniferous (Gzhelian) of the Moscow Basin and Urals in Russia is a broader shell with wide shallow sulcus. Lazarev (1990, pl. 23, fig. 4-7) referred this species to *Gemmulicosta*, and figured dorsal valves. *Gemmulicosta* sp. of Lazarev (1990, pl. 23, fig. 1-3) from the Kasimovian of the Moscow Basin has slightly coarser but more spaced ribbing. He referred *Kochiproductus coronus* Shiells and *K. magnus* Shiells (1968) of Visean age to the genus, but these species are judged to belong to *Coronatonia* Waterhouse, 2013, p. 149, within Subfamily Tolmachoffinae Sarytcheva. *Buxtonia victorioensis* King, 1931, p. 80, pl. 19, fig. 1) from the Bone Spring Formation, Victoria Peak Member, in west Texas is close in its ornament and approaches *Gemmulicosta* in many respects. It is more inflated with weaker commarginal rugae, and shows predominant persistent but fine ribs, with slight swellings below the spines, stronger than in the present species. The species was referred to *Kochiproductus* by Cooper & Grant (1975, p. 1052, pl. 360, fig. 8-12).

The ornament of this new species is much finer than in *Kochiproductus* from the region and is further distinguished by the distinct commarginal rugae across the venter. *Kochiproductus levisonlessingi* Zavodowsky (1970, pl. 5, fig. 1a, b) from the Burgali Horizon of Early Permian age from northeast Russia has fine but lower ribs and less conspicuous spines and low commarginal ornament, and although its generic position is uncertain, with no figures for dorsal valves, it closely approaches *Gemmulicosta* in many respects.

Family **DICTYOCLOSTIDAE** Stehli, 1954

[Nom. transl. Waterhouse 1978, p. 20 ex Dictyoclostinae Stehli, 1954, p. 316].

Diagnosis: Large shells with generally wide hinge and well-formed ears, may have ginglymus, ornament of costae over both valves, as a rule reticulated by commarginal growth rugae over disc, spines limited to ventral valve as a rule, may be large and halteroid, no umbonal slope row of spines. Internal posterior hinge ridge generally well formed, marginal ridges low, may be broad, trails long and simple as a rule, or may be multiple.

Discussion: The family appears to have evolved during the Early Carboniferous from a buxtoniid, such as *Coronatonia* Waterhouse, 2013, because this genus has persistent and moderately reticulate ribs, no or few dorsal pits and non-cleft dorsal septum (see Waterhouse 2013, p. 149). Reticulation is less well developed than in Retariidae, and a row of spines along the base of the ventral umbonal slopes is not developed. This constitutes a readily determinable difference from Retariidae, including genera within Reticulatiinae, which otherwise are somewhat similar in size and reticulation, athough the reticulation is slightly better defined in members of Reticulatiinae.

One matter to be pursued in questions over classification for Dictyoclostidae centres on the significance or otherwise of posterior central papillation or Lazarev's “shagreen texture” (the term was preempted a long time previously by Waagen for a style of external micro-ornament, as sustained in other studies). A number of dictyoclostid-like genera, as judged on the basis of reticulate or subreticulate ornament, were discriminated from Dictyoclostidae and assigned by Lazarev (2000a, b, etc.) to Yakovleviinae, which he later came to regard as a subfamily of Productidae rather than tribe in Plicatiferinae as in Brunton et al. (2000). Both these placements marked considerable reassessment of earlier positions. The move to Plicatiferinae by Lazarev was based, it was said, on meronomic analysis, deemed to be a major revelatory advance on previous procedures. Within a few years, that meronomic analysis was overturned, again by meronomic analysis. The re-assessment was based on the absence of Lazarev's "shagreen" texture from the posterior dorsal and ventral valves in some genera. By contrast, *Dictyoclostus* itself has posterior central papillation. Throughout this study, it is deemed that caution is required over the significance of posterior central papillation, because well preserved New Zealand material shows that it changes during ontogeny and with substrate (Waterhouse 2013, pp. 18-22).

Subfamily SPINARELLINAE Waterhouse, 2002b

[Nom. transl. Waterhouse 2013, p. 21 ex Spinarellini Waterhouse, 2002b, p. 21].

Diagnosis: Medium-sized transverse shells with large ears and subdued reticulate ornament. Dorsal valve tends to be gently concave to almost flat, and curves often abruptly into a trail. Row of spines inclined forward laterally from the ventral hinge, and scattered other ventral spines, no umbonal slope row of spines and no dorsal spines or external dorsal pits. Hinge ridge well developed, marginal ridges low or not developed, long dorsal median septum, anterior dorsal pustules moderately numerous. Cardinal process trifid and short. (See Waterhouse 2013, p. 165).

Tribe **CHAOIELLINI** Lazarev, 2011

[Tribe Chaoiellini Lazarev, 2011, p. 28].

Diagnosis: Weakly transverse shells with subdued radial ribs and weak commarginal rugae, row of spines close to ventral hinge, not becoming strong laterally, and spines as strong over trail. Corpus cavity varies from low to high in different genera.

Discussion: Genera include *Chaoiella* Fredericks, *Altaiproductus* Lazarev and *Tityrophoria* Waterhouse (syn. *Alpavlia* Lazarev). *Chaoiella* Fredericks was included in Dictyoclostinae by Brunton et al. (2000, p. 489), but Lazarev (2011) pointed out that costation took a different form, and was weaker, together with commarginal ornament. He included with a query the genus *Rugoclostus* Easton, 1962, not a well known genus, and placed for some reason that must remain totally obscure in Horridoniini by Brunton et al. (2000, p. 480). *Rugoclostus* does not show a strongly developed row of spines close to the ventral hinge, and, with relatively small ears and moderately strong commarginal rugae over the disc, may at best be a highly deviant member of Chaoiellini. The genus was placed as a shrivelled member of Retariiinae by Waterhouse (2013). *Praehorridonia* Ustritsky was also included in Chaoiellini by Lazarev (2011), but is regarded as Horridoniidae, given its usually subelongate outline, and apparent lack of posterior internal hinge ridge (Ustritsky & Chernyak 1963, pl. 18, fig. 7, pl. 21, fig. 5). Members of Chaoiellini are comparatively close to Spinarellini, which have more prominent posterior spines especially strong on the ears, and on some forms stronger ribs on the trail. The body corpus is more slender, and diductor scars are placed at almost the same distance from the hinge as the adductor scars, a point emphasized by Lazarev (2011), though similar dispositions of ventral muscle scars are observable in many Productoidea, including *Retaria, Kutorginella, Thuleproductus, Antiquatonia* etc. Papillae are distinctly finer and more numerous at the start of the trail in these genera than in members of Chaoiellini. The gently concave dorsal disc, and longitudinal profile of many genera classed as

Productoidea are close to features of *Chaoiella* and allies. Shallow and scattered pits may be present over the dorsal exterior in *Chaoiella*, but are not strongly developed, and there is no well developed row of spines along the umbonal slopes.

Genus ***Tityrophoria*** Waterhouse, 1971a

Diagnosis: Shells with spines largely limited to row close to ventral hinge, spines may be large along outer hinge, genus further distinguished by presence of fine radial costellae, especially over ventral valve.

Type species: *Tityrophoria nelsoni* Waterhouse, 1971a, p. 214 from upper Jungle Creek Formation (lower Artinskian), Yukon Territory, Canada, OD.

Discussion: The spines in this genus are limited to the ventral hinge, with a few over the anterior ventral valve, as shown in the original description and figures (Waterhouse 1971a, pl. 25, fig. 12, 13), reinforced by a diagram in Shi & Waterhouse (1996, Fig. 30A). Ribbing is fine and consistent over both valves (Waterhouse 1971a, pl. 25, fig. 12, 13, 14; Shi & Waterhouse 1996, pl. 15, fig. 1, 3). Internal pustulation and dorsal interior are shown in Waterhouse (1971a, pl. 25, fig. 10, 11, 15) and Shi & Waterhouse added information of the posterior hinge ridge and ventral musculature. Brunton et al. (2000, p. 483) claimed that dorsal spines were rare or absent in *Tityrophoria*, but no specimen is known to have dorsal spines. The type species is found in Sakmarian and lower Artinskian deposits of the Jungle Creek Formation. In a Late Carboniferous species from Canada, the hinge row of spines is stronger, and the surface is similarly marked by fine ribbing, especially prominent on the ventral valve; anterior plicae also appear. In its fine costellae, *Tityrophoria* shows some approach to *Nudauris* Stehli and allies of the Spinarellini Waterhouse, which have ventral spines, including an umbonal slope row, and spines that are not excessively robust, and ears are large, and the corpus slender.

Lazarev (2011) evaluated *Tityrophoria* as a member of Chaoiellini. He noted that *Tityrophoria* has five spines each side of the umbo compared with three in *Chaoiella* (in fact the number varies up to eight or more in *Tityrophoria*), and noted that the posterior row was more steeply inclined forward from the hinge in *Chaoiella*. He indicated that anterior trail spines were possibly thicker than the last spines on the ears in *Chaoiella*, and this observation is applicable for *Tityrophoria*. Commarginal ornament is more marked in *Chaoiella*, but is present, although slightly variable and often subfusc in *Tityrophoria*. One particular aspect that requires attention lies in the apparent variation displayed by the disposition of the ventral muscle scars. Shi & Waterhouse (1996, pl. 15, fig. 2, Fig. 30C) illustrated narrow long adductor scars with rounded diductor scars well in front of most of the adductors. But another specimen shows an adductor platform that extends almost as far forward as the anterior diductor scars (Shi & Waterhouse 1996, pl. 15, fig. 5). Similar variation is displayed in material described below as *Tityrophoria zimmermani* Waterhouse.

Tityrophoria zimmermani Waterhouse, 2013

Fig. 82 - 86

2013 *Tityrophoria zimmermanni* Waterhouse, p. 168, Fig. 5.46 - Fig. 5.50, Fig. 5.52.

Diagnosis: Moderately large with thick visceral disc, spines form a row along the ventral hinge, scattered and few over the remainder of the ventral valve. Ribs low and even, six in 5mm anteriorly.

Holotype: GSC 133300, figured in Waterhouse (2013, Fig. 5.52A, B) and herein as Fig. 84A, B from Member A, Jungle Creek Formation, OD.

Material: Single ventral valves from JBW 181, 186, 412, 610, 615, 745, 748, 752?, 801?, 807, two ventral valves from JBW 119, one ventral valve and seven specimens with valves conjoined from JBW 170, a ventral and dorsal valve from JBW 666, two ventral valves and two dorsal valves each from JBW 509 and 515, and single specimens with valves conjoined from JBW 108 and 156. Eight specimens with valves conjoined from JBW 606, a ventral valve and specimen with valves conjoined comes from JBW 125 and two ventral valves from JBW 119. From Member A. Single specimen with valves conjoined from JBW 516, Ettrain Formation.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Dimensions in mm: ventral valve

Specimen GSC	Width	Length	Height	
133300	47	34	19	holotype
133291	46	35	19	
136041	52	36	17	
133248	54	35	23	
136047	55	32	23	

Description: Moderately large transverse shells with thick visceral disc. Ventral umbo incurved, umbonal angle close to 90^{o}, steep but not extremely high umbonal walls and large gently convex ears with obtuse cardinal extremities,

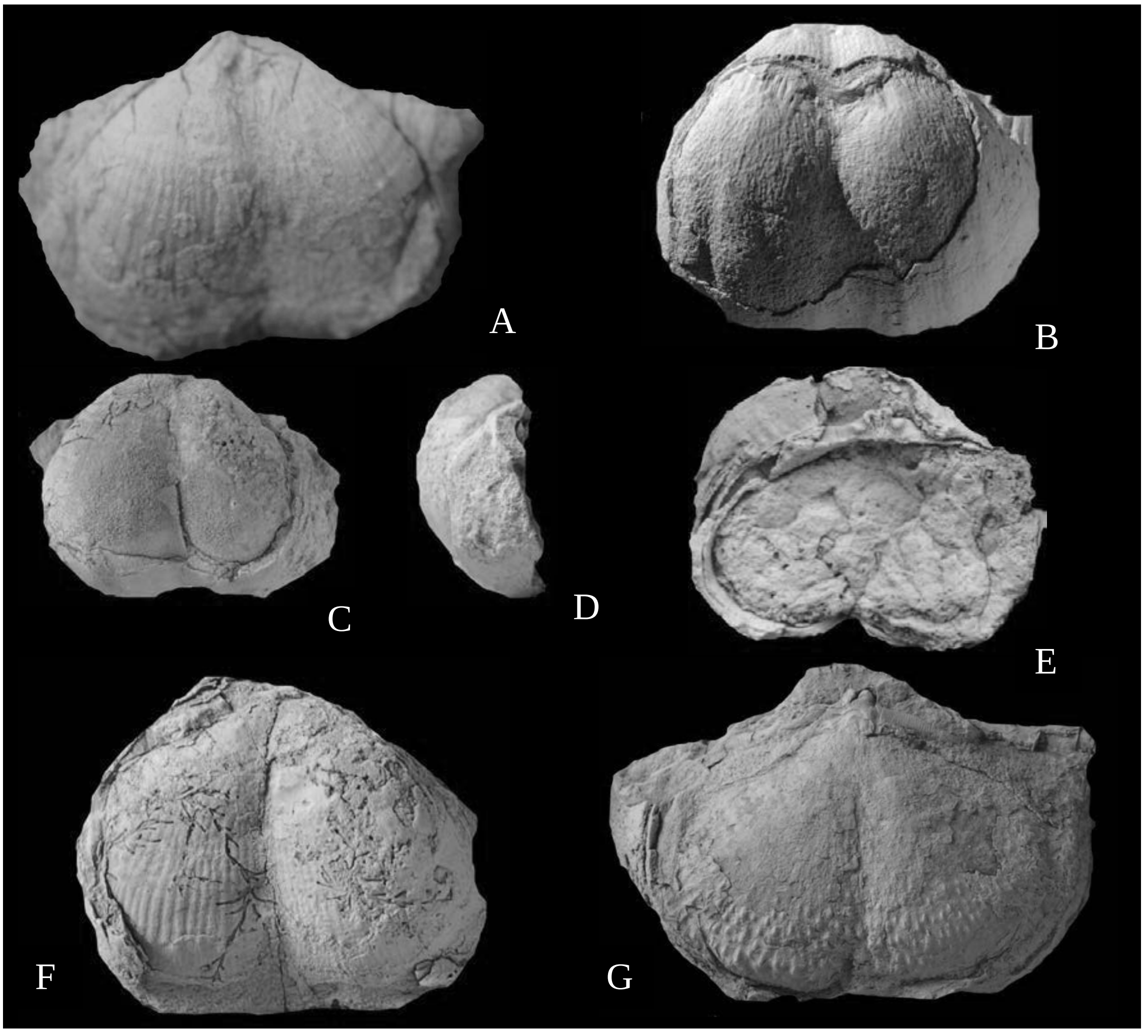
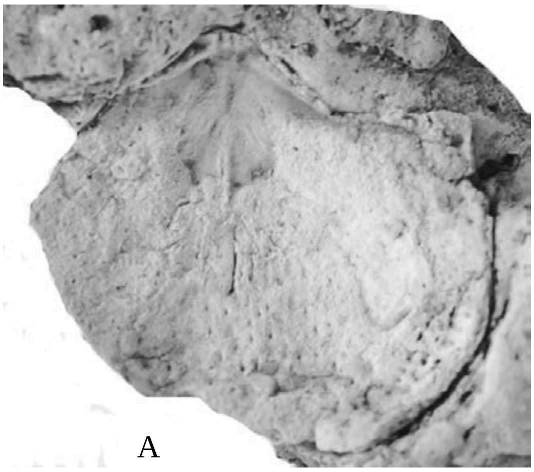


Fig. 82. *Tityrophoria zimmermani* Waterhouse. A, ventral valve, largely internal mould, GSC 133291 from JBW 127, x1.3. B, ventral valve GSC 136041 from JBW 606, x1.5. C, D, ventral and lateral aspects of GSC 136042 from JBW 84, x1. E, dorsal aspect of specimen with valves conjoined, GSC 133290 from JBW 127, x1. F, dorsal interior of GSC 133287 from JBW 127, x1.5. G, decorticated dorsal valve with surrounding ventral valve, GSC 136041 from JBW 606, x1.8. See Fig. 84E. From Member A, Jungle Creek Formation.



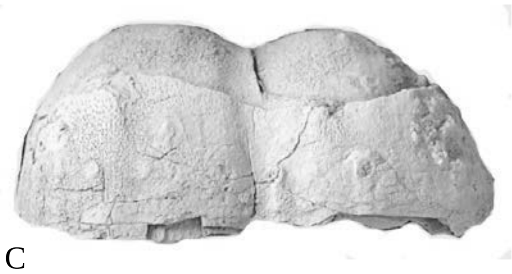
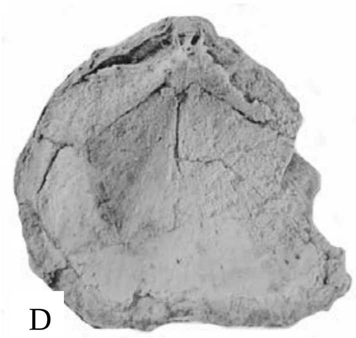
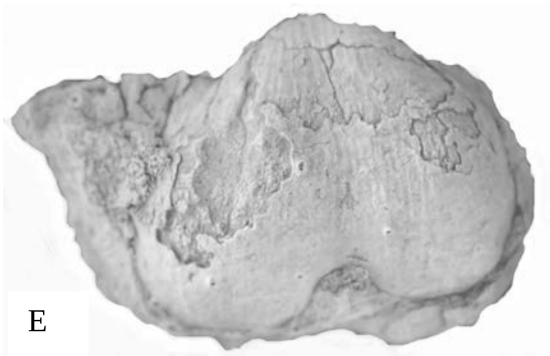


Fig. 83. *Tityrophoria zimmermani* Waterhouse. A, dorsal aspect of internal mould, specimen with valves conjoined, GSC 136043 from JBW 606, x2. B, internal view of dorsal valve, with covering ventral valve broken back, showing height of visceral disc, GSC 133288 from JBW 127, x1.5. C, anterior view of GSC 136042 from JBW 84, x1.5. (See Fig. 82C, D). D, dorsal internal mould GSC 136046 from JBW 606, x2. E, ventral valve GSC 136047 from JBW 127, x1.5. From Member A, Jungle Creek Formation.





placed at maximum width, but broken short in many specimens. The shell is also wide near the anterior third of the shell length. A well formed ventral sulcus commences a little in front of the umbo and widens at 20º, with subangular or less commonly trench-like median trough, and gently convex lateral walls. The dorsal valve is gently concave over the disc, with large concave ears, and is subgeniculate, curving steeply into a moderately long trail that as preserved is usually half the length of the visceral disc, but in well preserved more complete specimens is as long as the disc. The fold commences mid-disc or in front over the trail, and remains low and scarcely visible in some specimens. Ventral spines form a row that passes obliquely forward over the ears from the hinge, with individual outer spines more than 1.8mm in diameter. A few fine or strong spines up to 1.8 mm in diameter lie over the ventral disc and trail, but there are also finer spines less than 1mm thick anteriorly. A few radial rugae are developed anteriorly on some specimens, as well as weakly differentiated commarginal bands. The dorsal valve has no spines. Ribs are low

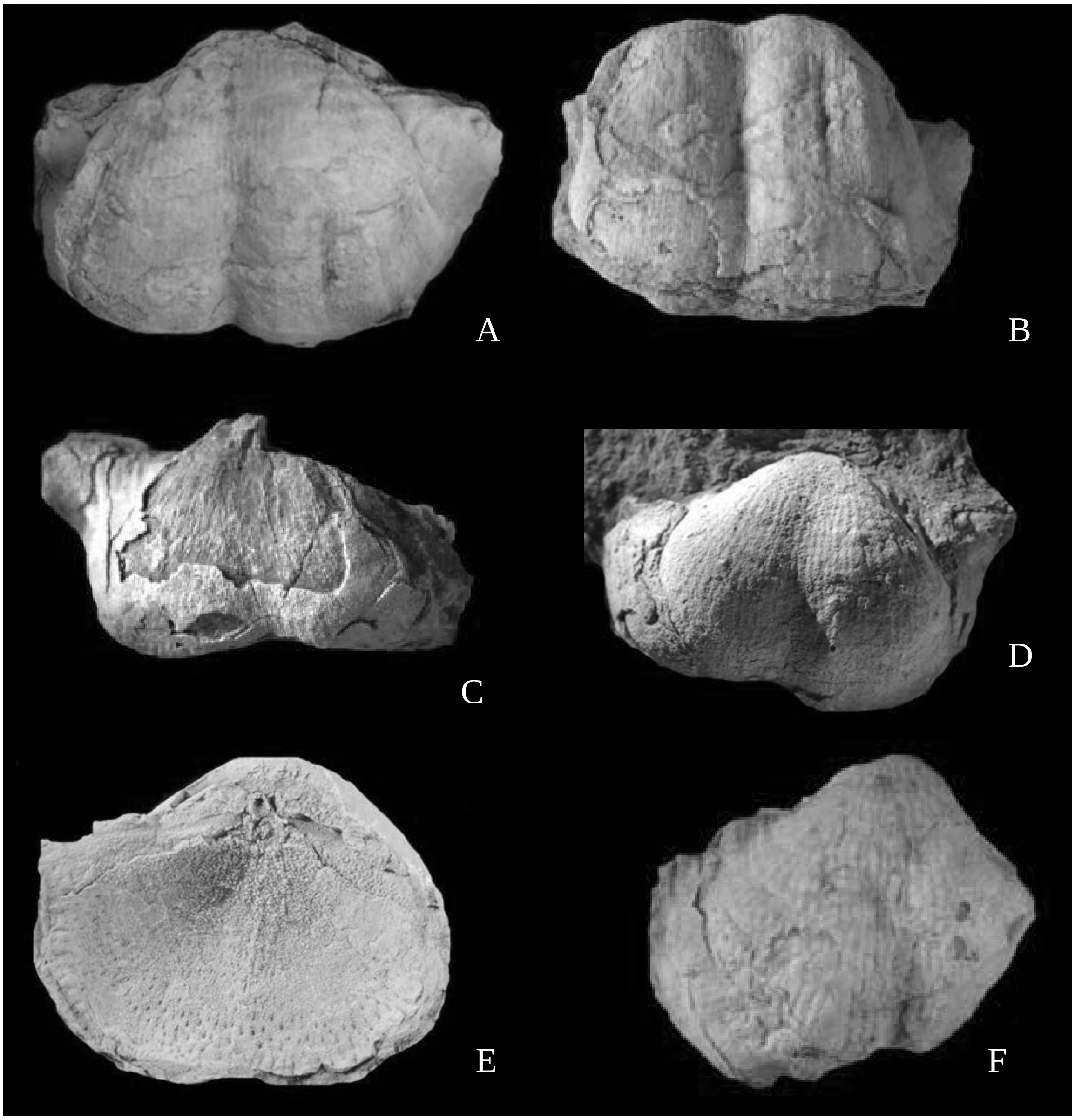


Fig. 84. *Tityrophoria zimmermani* Waterhouse. A, B, posterior ventral and anterior ventral aspects of ventral valve GSC 133300 from JBW 127, holotype, x1.5**.** C, posterior ventral aspect of ventral valve GSC 136039 from JBW 127, showing muscle imprints, x1.7. D, ventral aspect of GSC 133299. from JBW 606, x1.5. E, dorsal aspect of specimen with valves conjoined, GSC 136041 from JBW 606, x1.5. (See Fig. 82G). F, ventral aspect of GSC 136043 from JBW 606, x2 (see Fig. 83A). From Member A, Jungle Creek Formation.

and even, numbering six in 5mm anteriorly on the ventral valve, commencing within 2-3mm of the umbonal tip, and five in 5mm on the dorsal valve: the ribs become subdued on large specimens towards the anterior margin. No ribs on ears, which are smooth in some specimens or bear low commarginal wrinkles in others, and ribs often missing from umbonal flanks. Pustulation is not clear, because the shell has been silicified and the surface possibly worn, so that although pustules appear, they may not reflect the true nature of the original exterior.

The ventral adductor platform is high and elongate, and diductor scars strongly grooved. In one specimen the diductor scars commence in front of the adductors, but in another the two pair lie side by side. Papillae over the floor of the valve are fine and even. The cardinal process lies in the plane of the commissure and has a deep cleft on the ventral side, with two broad lateral lobes, and two deep dorsal clefts: there is no zygidium. The median lobe from a dorsal aspect is convex, and shows a slit nearer the base in one specimen, but the slit is missing from another shell. The median septum is sturdy posteriorly and extends for three quarters of the disc length in a fully mature specimen, for less than half the length of the disc in an immature specimen, and for nearly two thirds of the length in a specimen at early maturity. Dorsal adductor scars are large, not highly raised, somewhat tear-shaped, and largely smooth at immaturity into early maturity, and become highly raised in maturity, with somewhat dendritic outer posterior division and irregular but semi-smooth inner anterior portion. Brachial shields are well defined at maturity, and a stout posterior ridge extends along the hinge, but in a less mature specimen the brachial shields lie further from the median septum. Only low fine papillae lie over most of the floor at early maturity, with a band of stouter pustules between the anterior end of the dorsal septum and the start of the trail. Papillae are large and slightly elongate at maturity in the anterior band, numbering four or five irregular rows, and the trail bears finer pustules. The ventral shell is 2mm thick under the sulcal margins, and may be thinner anteriorly; the dorsal shell is as thick, though thin over the ears.

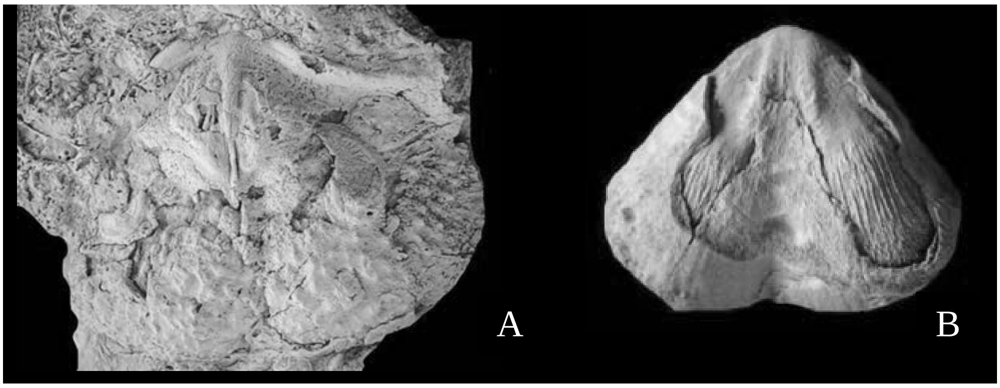
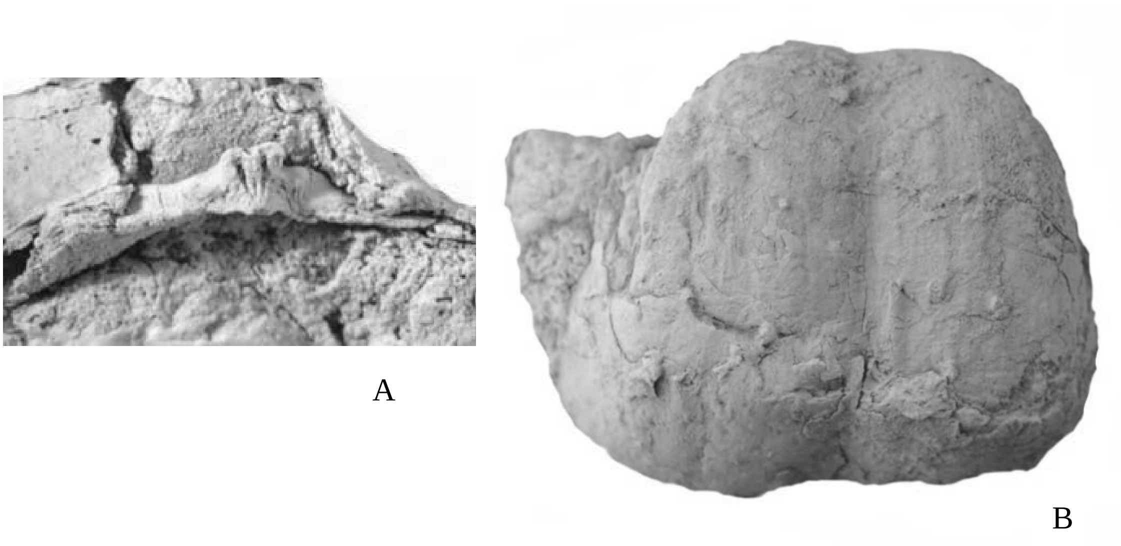


Fig.85. *Tityrophoria zimmermani* Waterhouse. A, dorsal interior, GSC 136044 from JBW 179, x1.5. B, internal mould of ventral valve GSC 136045 from JBW 606, x2. From Member A, Jungle Creek Formation.

Resemblances: This species is characterized by wide shell and ears of moderate size (usually incomplete because they are broken laterally), well formed ribs and by having a single row of spines along the ventral hinge, with the disc marked by costellae, reinforced anteriorly by coarse subplicae in some specimens. *Tityrophoria nelsoni* Waterhouse in Bamber & Waterhouse (1971, pl. 25, fig. 1-11; Shi & Waterhouse 1996, p. 91, pl. 14, fig. 22-26, pl. 15, fig. 1-8, text-fig. 30; Brunton et al. 2000, Fig. 323.3a-c) from higher members in the Jungle Creek Formation of northern Canada is smaller with narrower ribs and finer hinge spines and better defined ventral sulcus.

Horridonia geniculata Gobbett (1964, p. 97, pl. 10, fig. 5-7) has a row of ventral hinge spines and has fine radial threads and anterior rugations. Only two ventral valves were available, and no dorsal valves known. The species comes from the Cora Limestone of Bear Island. The radials of Gobbett's species are slightly finer than in the Canadian species. Unfortunately many details remain unknown, but provisionally the species is regarded as belonging to *Tityrophoria*.

The species described as *Alpavlia gzheliensis* Lazarev (2011, pl. 4, fig. 1-13) from Gzhelian of the Moscow Basin in Russia is moderately close, but has wider ears, with ventral costae commencing a little further from the beak, and ventral hinge row of spines that slopes slightly more forward laterally from the hinge. The median septum is consistently long and brachial shields lie well away from the mid-line. There are various additional differences, arguably specific rather than generic, and the validity of the genus therefore remains under a cloud, pending closer examination.



A

B

Fig. 86. *Tityrophoria zimmermani* Waterhouse. A, external aspect of cardinal process, GSC 133290 from JBW 127, x3. (See Fig. 82E). B, ventral valve GSC 133298 from JBW 179, x1.5. Member A, Jungle Creek Formation.

Superfamily **ECHINOCONCHOIDEA** Stehli, 1954

[Nom. transl. Lazarev 1990, p. 109 ex Echinoconchidae Stehli, 1954, p. 326].

Family **ECHINOCONCHIDAE** Stehli, 1954

[Echinoconchidae Stehli, 1954, p. 326].

Diagnosis: Planoconvex to concavoconvex profile, short dorsal trail, spines slender and erect to recumbent, in commarginal bands. Corpus cavity generally deep.

Subfamily **ECHINOCONCHINAE** Stehli, 1954

[Nom. transl. Muir-Wood & Cooper, 1960, p. 243, ex Echinoconchidae Stehli, 1954, p. 326].

Diagnosis: Spines erect, differentiated in size as a rule, no buttress plates or cardinal pit.

Tribe **ECHINOCONCHINI** Stehli, 1954

[Nom. transl. Brunton et al. 1995, p. 929 ex Echinoconchidae Stehli, 1954, p. 326. Syn. Calliprotoniinae Lazarev, 1985, p. 71].

Diagnosis: Medium to large shells, smooth posteriorly, spines arranged along narrow commarginal rows or commarginal bands called commargons, and often differentiated in size, thicker in a few spine rows posteriorly and thin in rows anteriorly over each commargon, often subprostrate.

Discussion: Subfamily Calliprotoniinae Lazarev, 1985, sole member *Calliprotonia*, was distinguished only by its smaller size, higher marginal ridges, and slight differences in ornament involving more lamellose commarginal bands: it is synonymized with Echinoconchini. *Laminatia* Muir-Wood & Cooper is included on the basis of its similar ornament with two series of spines on each valve, whereas only one series is developed in *Praelaminatia* Waterhouse, 2013.

Genus ***Calliprotonia*** Muir-Wood & Cooper, 1960

Diagnosis: Small to median in size, spines of two sizes over commarginal bands on each valve, tend to be uniform posteriorly and anteriorly on shell, marginal ridge high.

Type species: *Calliprotonia renfrarum* Muir-Wood & Cooper, 1960, p. 247 from the Finis Shale (Upper Pennsylvanian), Texas, United States, OD.

Discussion: The genus ranged from Lower Carboniferous (upper Visean) to Lower Permian (Artinskian), with Upper Devonian (Famennian) forebears. The spinose ornament is more complex on the Canadian species *mclareni* than in the type species, and varies also in another Canadian species (Shi & Waterhouse (1996). There is only one indeterminate species present in the rich Permian brachiopod faunas of west Texas, in the Neal Ranch Formation.

Calliprotonia kerrae n. sp.

Fig. 87- 90

Derivation: Named for Faye W. Kerr.

Diagnosis: Dorsal disc gently concave and curves gradually into trail. Spines tend to be slightly more numerous than in the other Canadian species in the lower Jungle Creek Formation, called *sulcata* and *umbonalis*, often up to five rows of coarse spines as a rule, compared with three rows in a number but far from all of the commargons in *umbonalis* and *mclareni* over the posterior part of each commarginal band.

Holotype: GSC 136787, here designated.

Material: Single dorsal valves from JBW 71, 78, 95, 108, 518, 548, 627 and 646, single ventral valves from JBW 82, 170, 193, 221, 500, 531, 534, 536, 562, 610, and 731, ventral valve and specimen with valves conjoined from JBW 787, one specimen with both valves, one ventral valve and a dorsal valve from JBW 531, ventral valve and three dorsal valves from JBW 615. Two specimens with valves conjoined and ventral valve from JBW 593 and one ventral and dorsal valve from JBW 166.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimens subelongate or equidimensional to transverse, umbo with angle of 80-90º, weakly incurved, umbonal walls steeply convex in profile, hinge moderately wide and cardinal extremities well rounded, maximum width of shell near mid-length. Middle of ventral valve gently convex, dorsal valve gently concave over disc and curving gradually into short trail which extends for a third to quarter of length of shell: exceptionally has low broad anterior fold. Ventral valve covered by at least eleven and probably thirteen commarginal narrow rugae or growth steps ending ventrally in short steep section laterally and steeply convex without a step medianly; dorsal rugae of similar number, but tend to form narrow convex-crested ridges separated by concave intervals. Each ventral band over disc has three up to rarely six rows of erect spines, followed anteriorly by one to two rows and rarely three up to five rows of finer spines, and anteriorly the spines as far as they are preserved are 4mm long. Dorsal spines similar, with two to four rows of coarser spines over the posterior part of each band and finer spines in two or three rows in front. The spines have been found preserved for a length of 3mm long, but could have been broken short: they form a fine and dense mesh.

Internally, a well preserved dorsal valve has a slender trifid cardinal process supported by a firm median septum extending just past mid-length. The posterior adductors are rhomboid and postero-laterally emplaced, and anterior dorsal adductors are elongate and triangular in outline with one or two growth rugae near their anterior margin. Brachial shields are small, and a ridge lies inside the hinge. Fine pustules lie over the posterior floor, and laterally directed ridges are present laterally. Between the anterior brachial shields there are bands of coarse and fine pustules with low radial ridges usually passing into them, perhaps related to spine bases, and in front are three bands of increasingly coarse pustules separated by very tiny circular rings, appearing to be related to the commarginal bands and external spinose ornament.

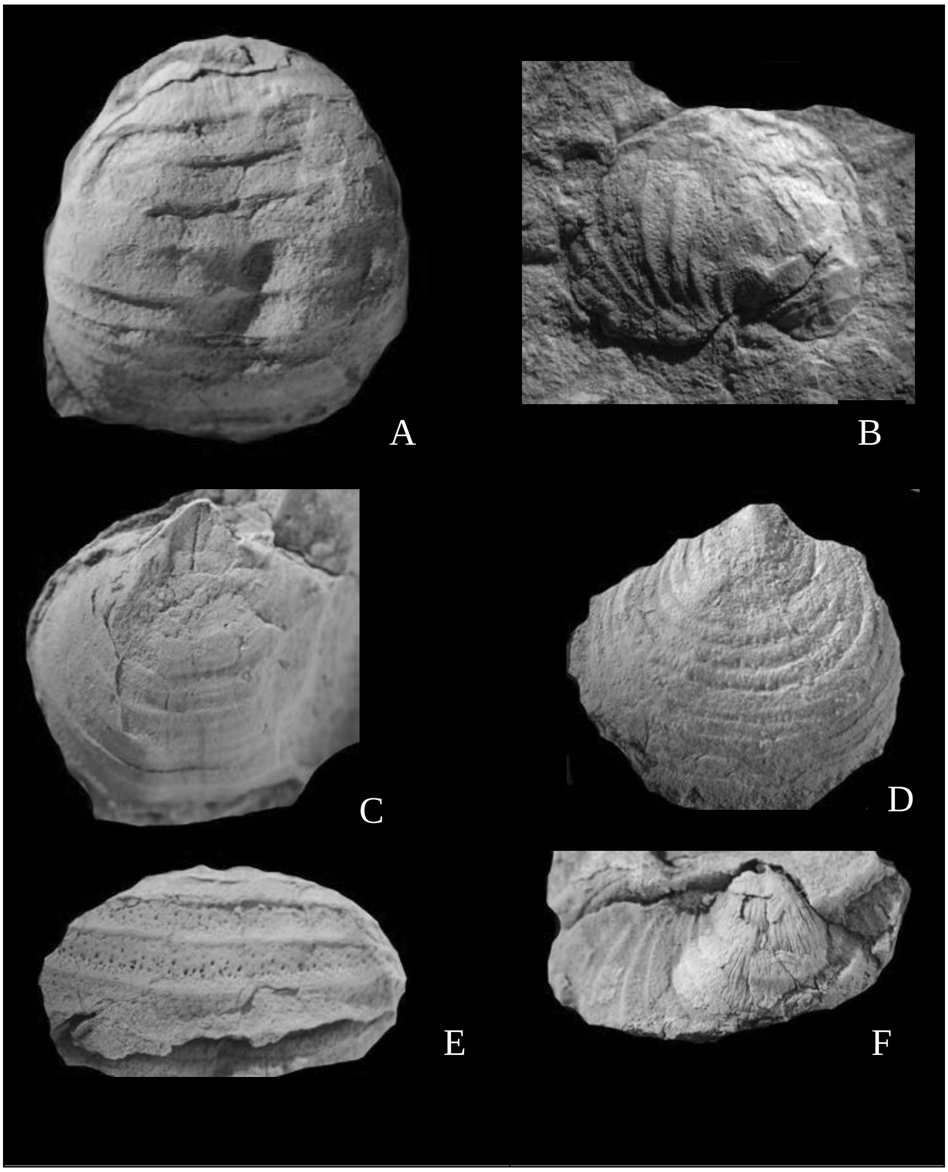


Fig. 87. *Calliprotonia kerrae* n. sp. A, anterior aspect of ventral valve GSC 136783 from JBW 615, x 2. B, oblique aspect of ventral valve GSC 136791 from JBW 82, x2. C, internal mould of ventral valve GSC 136785 from JBW 166, x3. D, worn ventral valve GSC 136786 from JBW 531, x2. E, F, anterior and posterior aspects of a bent ventral valve GSC 136784 from JBW 593, x2. Member A, Jungle Creek Formation**.**

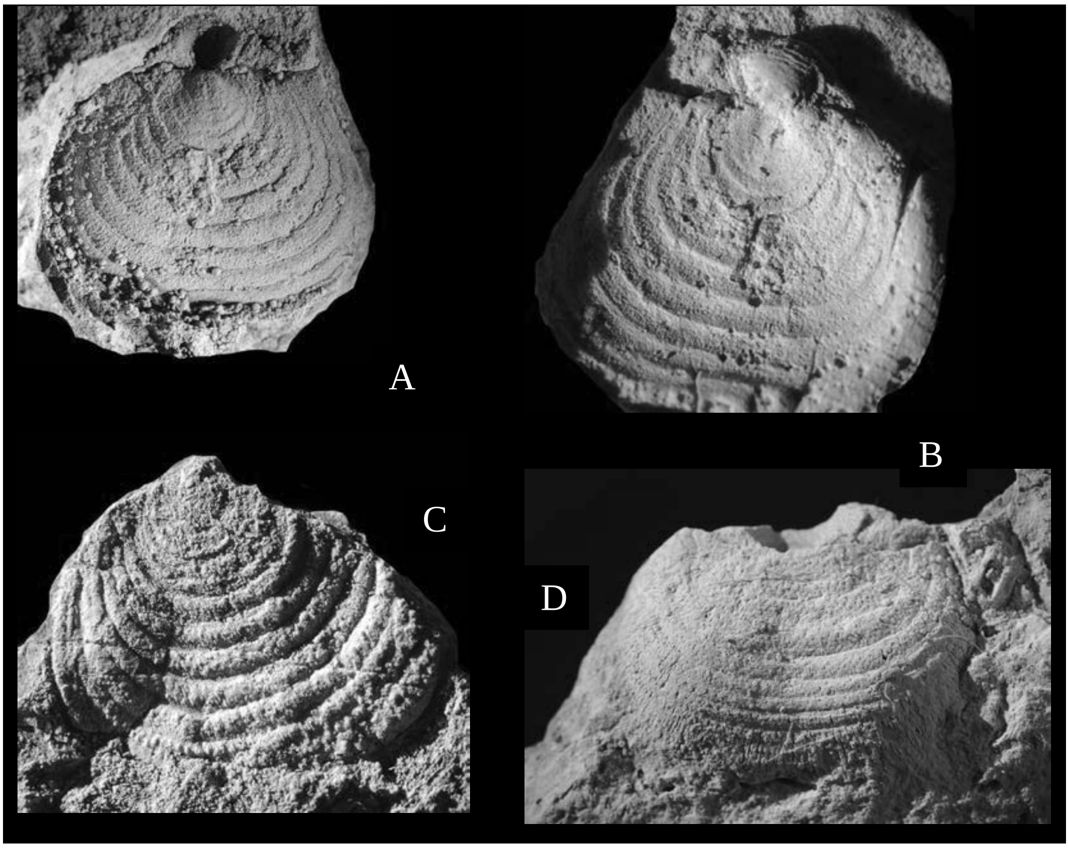


Fig. 88. *Calliprotonia kerrae* n. sp. A, B, dorsal aspect of external mould and cast, holotype GSC 136787 from JBW 530, x2, x3. C, ventral valve GSC 136793 from JBW 610, x3. D, dorsal external mould GSC 137336 from JBW 627, x2. Member A, Jungle Creek Formation.

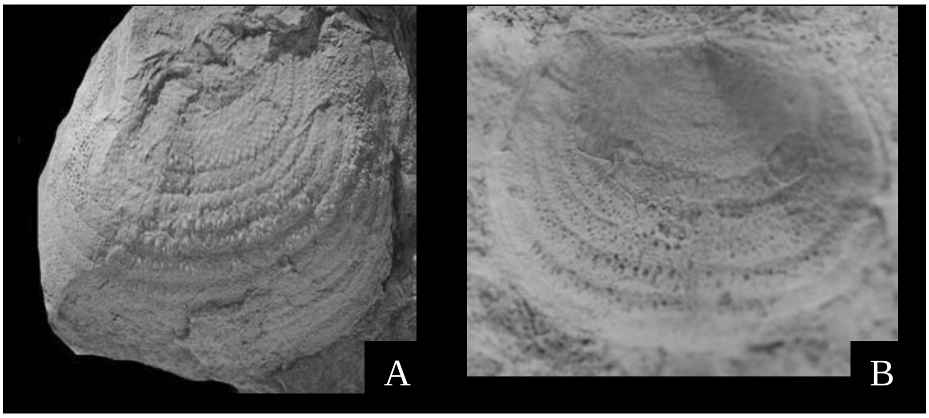


Fig. 89. *Calliprotonia kerrae* n. sp. A, external mould of dorsal valve, GSC 136789 from JBW 518, x2. B, dorsal external mould GSC 136790 from JBW 615, x2. Member A, Jungle Creek Formation.

Resemblances: The ventral valve of this form is close to that of *Calliprotonia mclareni* Waterhouse, 2013 (and see below), apart from tending to have more predominantly coarse spines over the posterior band on each commargon, more emphasized commargons and more concave dorsal valve. Some ventral valves are more sulcate, but others have a rounded venter, and in overall shape, allowing for intraspecific variation, the two suites come very close. The dorsal valve of the present form is more concave over the disc, and the disc curves more gradually into the trail whereas the dorsal valve in *mclareni* tends to be flatter, and curves with more geniculation into the trail.

Calliprotonia sterlitamakensis (Stepanov, 1934, p. 26), also figured by Solomina (1960, pl. 8, fig. 1, 2) and Mironova (1967, pl. 1, fig. 12) from the Sakmarian Bryozoa Limestone of the northern Urals is transverse and small with close-set bands. *C*. cf. *sterlitamakensis* Stepanov, 1937b as figured by Lazarev (1990, pl. 30, fig. 1-6) from Moscovian and Kasimovian faunas of the Moscow Basin, Russia, is somewhat similar in many respects, as weakly transverse shells with broad bands bearing two or three rows of coarse spines posteriorly on the ventral valve, and showing rows of fine spinules anteriorly in the dorsal valve. A Gzhelian specimen (Lazarev 1990, pl. 30, fig. 7) has up to four rows of coarse spines over each band, with two or three rows of finer spines in front, even closer to the present form, which shows four or five rows of finer spines. Another Gzhelian specimen shows three or four rows of coarse spines and no finer spines. Two Lower Permian specimens (Lazarev 1990, pl. 30, fig. 9, 10) are also moderately close, with less well preserved detail of the ventral exterior.

Echinoconchus ekatchanensis Abramov (1970, pl., 10, fig. 2-7) from mid-upper Carboniferous Ekachan Suite of Sette Davan is somewhat similar in size and shape, but detail of micro-ornament is obscure.

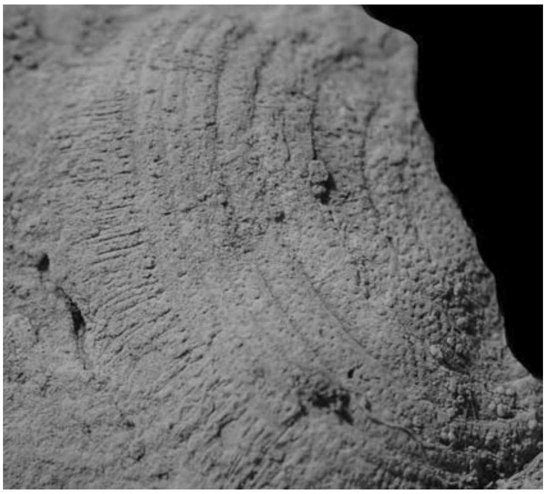


Fig. 90. *Calliprotonia kerrae* n. sp., external mould of dorsal valve, GSC 137336 from JBW 627, x5, showing length of delicate spines anteriorly. Member A, Jungle Creek Formation.

Calliprotonia sp.

Fig. 91

An external mould of part of a ventral valve from JBW 19. Member B, Jungle Creek Formation. Several rows of coarse spines, with no apparent fine spines, become fewer and smaller laterally. *Ogilviecoelia initiatus* Zone.

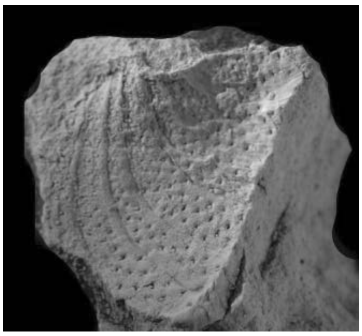


Fig. 91. *Calliprotonia* sp., part of external mould of ventral valve GSC 137255 x4, from JBW 19, Member B, Jungle Creek Formation.

Calliprotonia umbonalis n. sp.

Fig. 92 - 94

Derivation: umbo – knob, rounded swelling, Lat.

Diagnosis: Small shells, ventral umbo elongate, narrowly diverging posterior walls, dorsal disc moderately concave and corpus cavity comparatively thick, stout spines over each growth step in usually three rows – rarely five – and two up to five rows of finer spines anteriorly for some commargons.

Holotype: GSC 136796, here designated.

Material: Thirteen ventral valves and six dorsal valves from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Description: Specimens small, varying in shape from subequidimensional to slender, and well inflated. Ventral umbo extended beyond hinge, incurved, with umbonal angle of 65º, and relatively high umbonal walls curving out laterally.

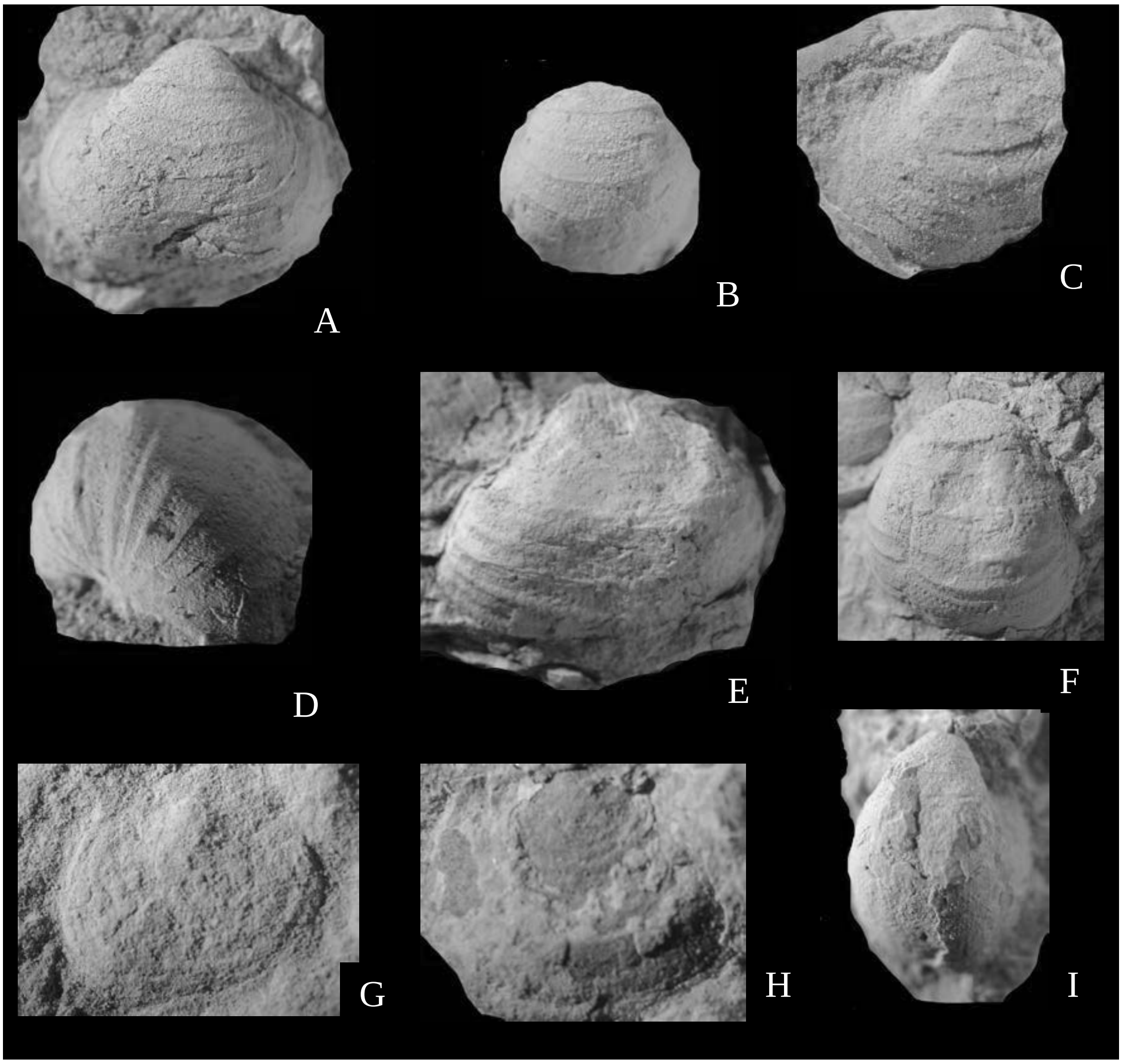


Fig. 92. *Calliprotonia umbonalis* n. sp. A, ventral valve holotype GSC 136796 x2. B, ventral aspect of specimen with valves conjoined GSC 136797 x2. C, external cast of ventral valve GSC 136798 x2**.** D**,** lateral aspect of ventral valve GSC 136799 x3. E, worn ventral valve showing posterior muscle impressions, GSC 136800 x2. F, ventral valve GSC 136801 x2. G, dorsal external mould GSC 136802 x3. H, dorsal external mould, GSC 136804 x3. I, ventral valve GSC 136805 x2. Specimens from JBW 18, Member C, Jungle Creek Formation.

Fig. 93. *Calliprotonia umbonalis* n. sp. A, anterior aspect of ventral cast, GSC 136803 x2. B, interior of worn dorsal valve GSC 137285 x3. C, external mould of worn dorsal valve GSC 137286. From JBW 18, Member C, Jungle Creek Formation.

Hinge slightly narrower than maximum width which is placed in front of mid-length; ears small, gently convex, cardinal angle angular at 110º in some specimens but 75º in others. Venter may show slight diminution in convexity medianly, or even gentle concavity for part of the length, but no well formed and persistent sulcus is developed, except over the trail in a few specimens. Dorsal valve gently concave, helping to enclose a comparatively thick visceral disc, measuring 7mm thick in a shell 14.5mm wide, and curving abruptly into short trail. Ventral valve crossed by comparatively thick commarginal ridges separated by concave bands, numbering eleven to thirteen, without the count being complete. Spinules comparatively thick and in three up to five rows, with some commargons bearing one or two up to five rows of finer erect spines. No radial ornament. The dorsal valve also has commarginal ribs and bands, commencing in front of a posterior smooth concave posterior shell 3mm wide, and covering the trail as well in two or three rows.

Fig. 94. *Calliprotonia umbonalis* n. sp., micro-ornament on anterior ventral valve GSC 136806, x 4. From JBW 18, Member C, Jungle Creek Formation.

Little of the internal detail remains. Ventral adductor scars are subrectangular with light longitudinal striae, and lightly impressed suboval diductor scars lie each side and extend anteriorly, also with light longitudinal striae. A dorsal valve shows a row of prominent pustules developed over the front of each commarginal band near the start of the trail. The cardinal process is slender and erect, with two terminal lobes, and joined by a marginal ridge that encircles the visceral disc.

Resemblances: Compared with *Calliprotonia kerrae*, individuals of the present species are more inflated with higher posterior walls, and often more elongate outline. Specimens are smaller and more elongate than *Calliprotonia mclareni* Waterhouse from the *Ogilviecoelia shii* Zone, and have posteriorly prolonged ventral umbo and long steep posterior umbonal walls. In addition the dorsal visceral disc is more concave, approaching that of specimens from the *Septospirifer tatondukensis* Zone, but the ornament of both valves is like that of *C. mclareni* in having mostly three rows of spines over each posterior band, although the number of rows of finer spines over the anterior part of each commargon is generally fewer.

Calliprotonia mclareni Waterhouse, 2013

Fig. 95 - 99

2013 *Calliprotonia mclareni* Waterhouse, p. 178, Fig. 6.3, 6.4.

Diagnosis: Ventral valve with shallow or no anterior sulcus and low anterior dorsal fold. Three to five rows of coarse spines as a rule and two or three up to five rows of fine spines over each commarginal band.

Holotype: GSC 133333 figured by Waterhouse (2013, Fig. 6.3A, Fig. 6.4A), and Fig. 95A and 96A herein, from Member E, Jungle Creek Formation, OD.

Material: Single ventral valves from JBW 44, 76, 80, 539, 561 and 567, and two from JBW 563 and 580; eleven ventral valves, three dorsal valves and a specimen with valves conjoined from JBW 581 in Member E. From Member D, single dorsal valves from JBW 535, 564 and 762; two dorsal valves from JBW 44, specimen with valves conjoined from JBW 83 and ventral valve from JBW 413. Obscure fragments from JBW 711.

Stratigraphic and biostratigraphic levels: Members D and E, Jungle Creek Formation. *Rugivestigia commarginalis* Zone and *Ogilviecoelia shii* Zone.

Description: Shells small, subquadrate in outline with broad ventral umbo and small ears with obtuse cardinal extremities. Ventral valve holotype GSC 133333 measures 28mm in width, 22mm in length, and 14mm in height. The venter is gently rounded with no sulcus, or very weakly sulcate. The dorsal valve is comparatively flat, with weakly differentiated ears, and gently concave disc which becomes broadly and gently convex anteriorly, and the lateral and anterior shell curves steeply at right angles, to form a subgeniculate trail. The ventral valve is crossed by a series of commarginal bands separated by growth-stops, and posteriorly each of these bears crowded fine erect spines in three to five rows, and over most of the shell there are some three up to six rows of erect spines, six to seven in 5mm, arranged in rows and fairly regularly in quincunx, and slightly inclined forward with traces of faint posterior bases and becoming slightly coarser anteriorly over each commargon; the anterior part of each commargon, about 1mm across, bears a further three up to six rows of much finer spines, often in quincunx, or in short commarginal rows of five to twenty spines. Anteriorly the spine pattern may be less regular, and part of the shell in some specimens has single rows of coarse spines, or fewer rows of coarser spines and none or only few fine spines. Rarely fine spine bases are interspersed with the coarser spines. On the dorsal valve the posterior nepionic shell is convex with evenly spaced fine erect spines, and the commarginal bands bear fairly uniform spines close in size to the coarser series on the ventral valve, and anterior commargons bear three to five rows of finer spines posteriorly and three to five rows of finer spines anteriorly. The anterior bands are usually ornamented only by growth lines, and are narrow, less than 1mm across. Very fine spines appear anteriorly on one or two bands, and the outermost band carries no spines in one specimen, though this is a rare occurrence.

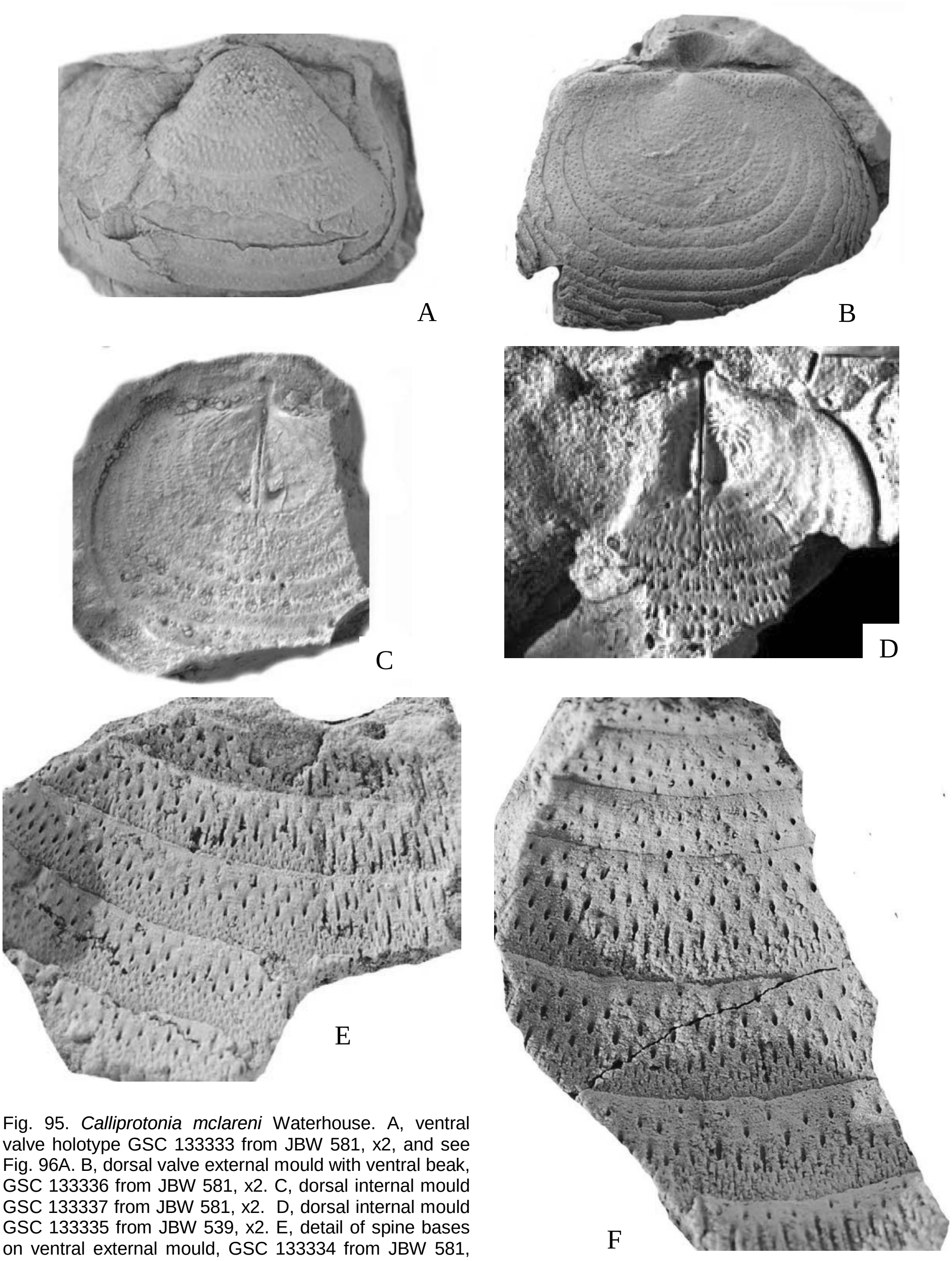


Fig. 95. *Calliprotonia mclareni* Waterhouse. A, ventral valve holotype GSC 133333 from JBW 581, x2, and see Fig. 96A. B, dorsal valve external mould with ventral beak, GSC 133336 from JBW 581, x2. C, dorsal internal mould GSC 133337 from JBW 581, x2. D, dorsal internal mould GSC 133335 from JBW 539, x2. E, detail of spine bases on ventral external mould, GSC 133334 from JBW 581, x3.5. F, detail of spine bases on ventral external mould, GSC 133338 from JBW 581, x5. Member E, Jungle Creek Formation.

The ventral interior is poorly known, with small and weakly delineated muscle scars, and floor pitted by pustules that reflect the external bands and spines. The dorsal valve has a low shafted cardinal process and medium septum extending just past half length of the shell in one specimen but much longer in another. Posterior adductors are dendritic and small, and anterior tear-shaped adductors are marked by low growth lines parallel to the anterior margin. In a more mature specimen, the posterior adductors are very narrow and comparatively smooth and the anterior adductors weakly dendritic. The posterior floor is closely pustulose and pitted and the posterior marginal ridge high. Brachial impressions are faint, forming slender shields inclined obliquely forward. A marginal ridge extends along the hinge and around the lateral margins. The floor is marked by pustules related to the spine bases, as well as linear striae that may be reflecting spines adpressed against the shell, and the posterior lateral shell carries well spaced pustules, and single rows of fine pustules followed by a row of coarse pustules anteriorly, possibly underlying external commargons.

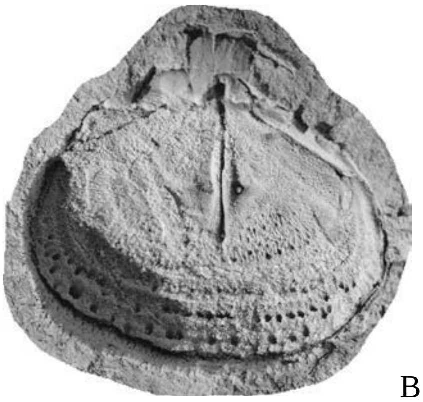


Fig. 96. *Calliprotonia mclareni* Waterhouse. A, anterior ventral valve GSC 133333, holotype. (See Fig. 95A). B, dorsal view of internal mould of specimen with valves conjoined, GSC 133339 from JBW 787. Specimens x2, from Member E, Jungle Creek Formation.

Resemblances: This species is moderately like the material from younger Jungle Creek beds especially in the "*Yakovlevia transversa"* Zone that was identified as *Calliprotonia inexpectans* (Cooper, 1957), and overall, interiors are similar. Although the dorsal septum was shown to be unusually long for the species, one specimen possesses a septum of only moderate length (Shi & Waterhouse 1996, pl. 8, fig. 26). The dorsal marginal ridge is present but low, unlike that of type *Calliprotonia.* The ventral spines possibly differ, in so far as the finer spine rows were shown to occupy a steep anterior slope in front of each band (Shi & Waterhouse 1996, Fig. 27B), whereas in the present material they occupy the anterior only moderately sloping part of each band behind the growth step, just as figured by Shi & Waterhouse (1996, pl. 8, fig. 23). The fine spines were described for Yukon *inexpectans* as occurring in only one or two rows, compared with three up to five rows in present material.

The relationship to the Oregon material originally described as *Echinoconchus inexpectans* Cooper (1957, p. 48, pl. 8c, fig. 13-26) is far from certain. Overall shape and interior are much the same, but neither figures nor text provided in Cooper (1957) clearly indicate the presence of rows of finer spines along the anterior part of the ventral bands, but suggest that commargons have relatively thick spines anteriorly: however figures are not good enough or clear enough to allow full understanding, and the matter is not clarified by the text. The overall similarity of shape and age compatibility suggest the species is congeneric with the Yukon material, but doubtfully conspecific, and the morphology for the types of *inexpectans* requires clarification.

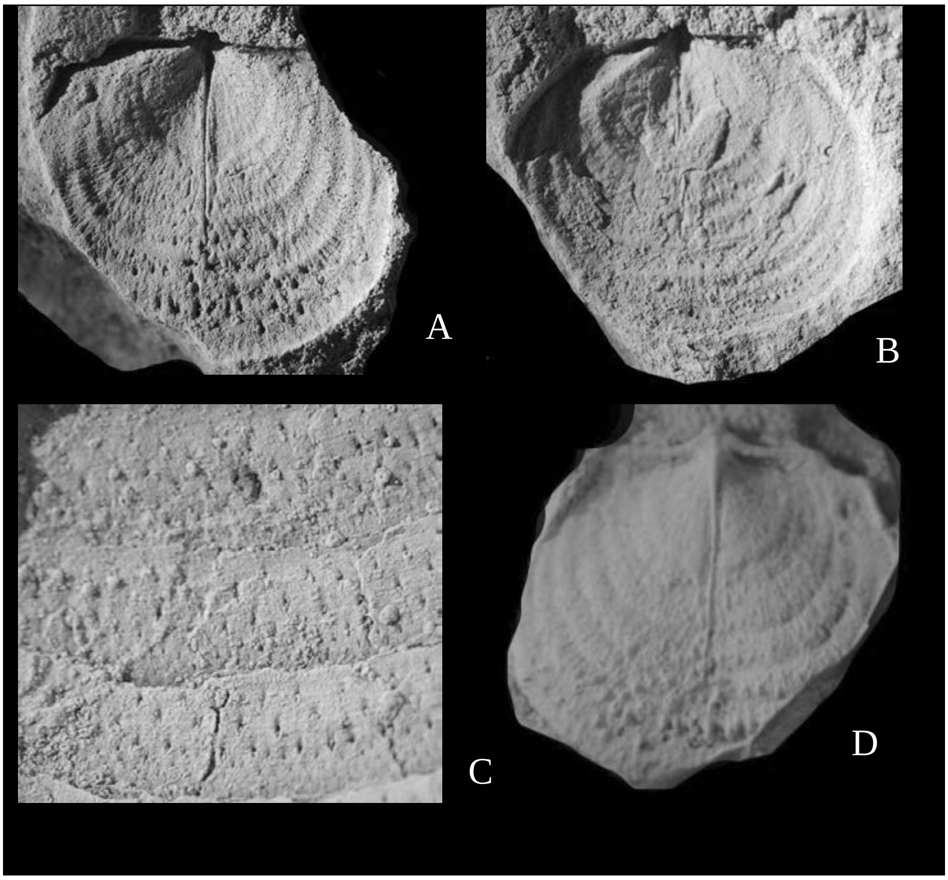


Fig. 97. *Calliprotonia mclareni* Waterhouse. A, D, internal mould and cast of dorsal valve, GSC 136807 from C-6167, x2.5. B, dorsal internal mould GSC 136808 from JBW 65, x2.5. C, micro-ornament on anterior ventral valve, GSC 136809, from JBW 581, x6. Member E, Jungle Creek Formation.

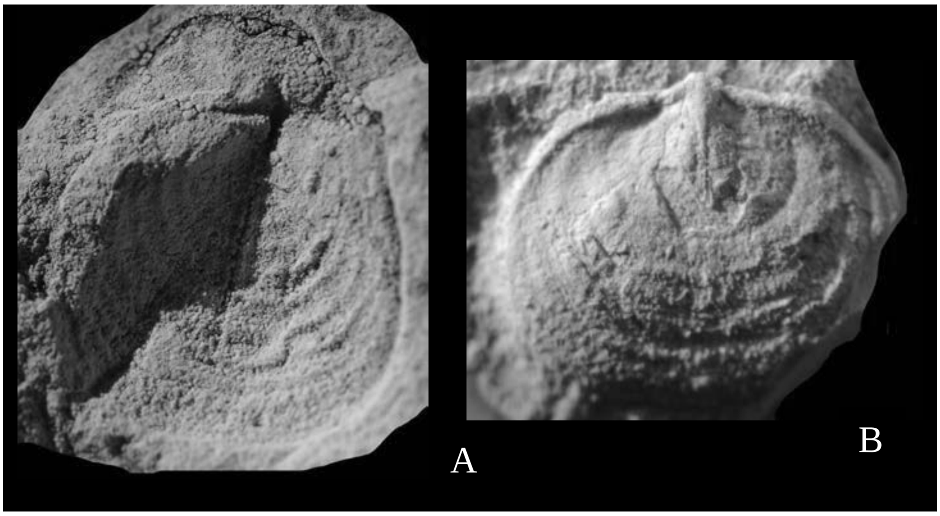


Fig. 98. *Calliprotonia mclareni* Waterhouse, dorsal aspect of internal mould JBW 137262 with valves conjoined, from JBW 83, x2. Member D. B, cast of internal dorsal valve GSC 136808 from JBW 65, x2. Member E, Jungle Creek Formation.

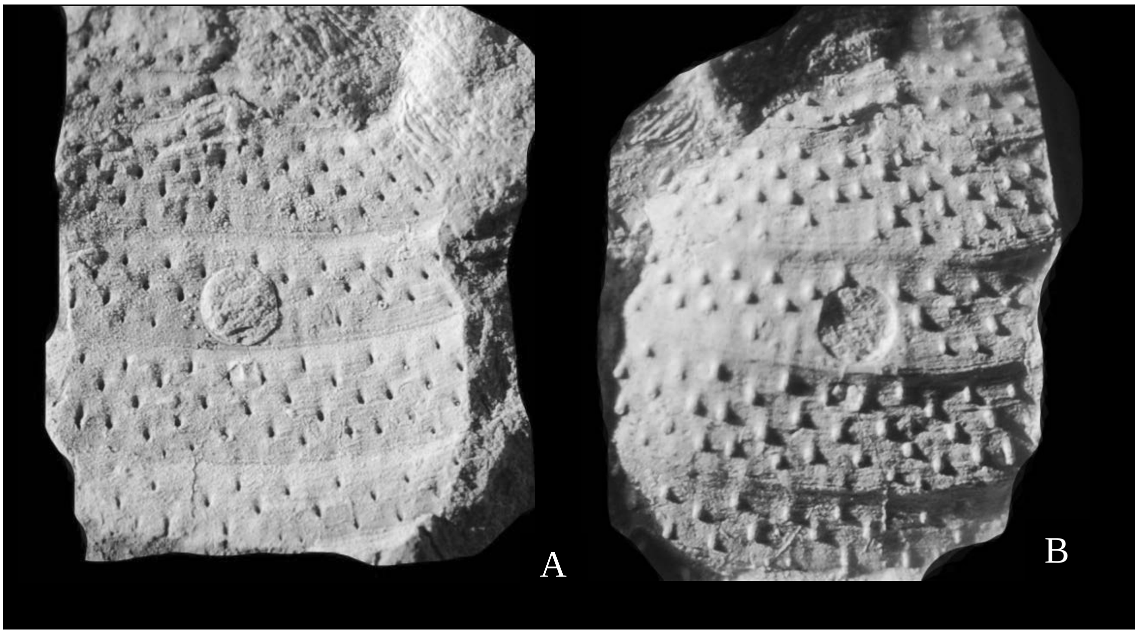


Fig. 99. *Calliprotonia mclareni* Waterhouse, micro-ornament on anterior ventral valve, external mould and cast for GSC 137256 from JBW 580, x6. Member E, Jungle Creek Formation.

Genus ***Echinaria*** Muir-Wood & Cooper, 1960

Diagnosis: Large semicircular to oval shells with commarginal bands over entire shell, bearing spines often but not in all species of two different diameters, in rows over each commargon.

Type species: *Productus semipunctatus* Shepard, 1838, p. 153 from Virgilian (Gzhelian) of Texas, OD.

Discussion: This genus comes very close to *Echinoconchus* Weller, 1914, described from Early Carboniferous world-wide. Muir-Wood & Cooper (1960, p. 249) distinguished *Echinaria* by its more tapering visceral disc, more incurved umbo and narrower hinge, but such aspects seem to be based largely on comparison between type species. They more critically pointed out that the bands bearing spines commenced over the umbo in *Echinaria*, whereas in *Echinoconchus* the posterior shell usually lacks commarginal bands and the spines are more quincunxially arranged. That aspect cannot be resolved for present material, and the identification of the present specimens with *Echinaria* is based on age and on the large size of the individual shells.

Echinaria circularis n. sp.

Fig. 100 - 103

Derivation: circulus – circle, Lat.

Diagnosis: Large shells with subcircular outline and low ventral umbo, shallow median sulcus, numerous commarginal bands. Spines predominantly of one diameter, apart from restricted parts of some anterior commargons with finer spines.

Holotype: GSC 136810, here designated.

Material: Seven ventral valves and additional fragments from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Description: Three large ventral valves, one sitting inside the other (GSC 136810, 136811), with the outer specimen 117mm wide, 118mm long and 49mm high, and margins are incomplete. The lateral and anterior outline is rounded, with incurved umbo of angle at 80º, rounded umbonal slopes, and hinge at maximum width, near posterior quarter of shell length, with obtuse cardinal extremities as far as preserved, and poorly differentiated ears. There is possibly a low ginglymus. The sulcus commences within 20mm of the umbonal tip, and is narrow with evenly concave floor, and fades over the anterior shell, where the margin is slightly produced. The entire valve is crossed by low round-crested rugae, numbering sixty on the holotype, in front of an umbonal portion 15mm long: interspaces are of similar width. Spacing of the rugae is slightly irregular, and increases forward to the anterior third before becoming slightly more closely spaced, and a few rugae are very narrow. Spine ornament is largely lost – worn from the exteriors exposed, and on parts of the shell, the outer surface appears to have been dissolved and recalcified. But one external mould strongly suggests that some three or rarely four rows of fine subequal spines or spinules, seven to eight in 5mm, emerge from the anterior face of each rugation, measured at 40mm from the beak. On another specimen the entire rugation bears five up to eight rows of spines (Fig. 102B, 103), in which two or three rows of anterior spines on each commargon are slightly finer. A juvenile specimen has spines of only one diameter. The spines are subequal in size, without the strong difference shown in type *Echinaria*, and are quincunxially arranged.

Adductor scars and slightly raised and smooth in a small specimen only half the size of the large shells.

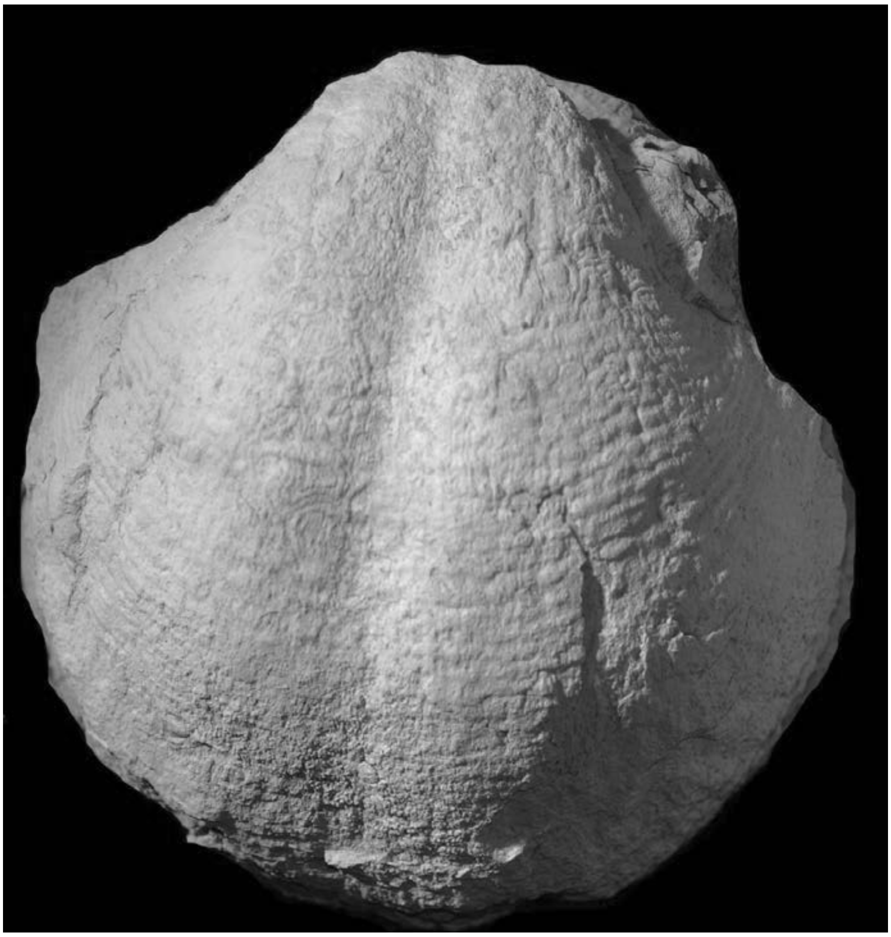


Fig. 100. *Echinaria circularis* n. sp., holotype, ventral valve GSC 136810 from JBW 18, x1. Member C, Jungle Creek Formation.

Resemblances: These specimens are so distinctive in size, shape and macro-ornament that they are easily recognizable. They differ strongly from the type species of *Echinaria*, in having most of the spines in only one coarser series, at least as far as preserved. The type species *Productus semipunctatus* Shepard, 1838, p. 153, fig. 9, also figured by Dunbar & Condra (1932, pl. 24, fig. 6, pl. 25, fig. 1-3) and Muir-Wood & Cooper (1960, pl. 85, fig. 1-5, pl. 86, fig. 1-9) from Missourian rocks of Kansas is more elongate with shallower ventral sulcus. Somewhat similar but fragmentary material of Missourian age in New Mexico was reported by Sutherland & Harlow (1973, pl. 9, fig. 8).

Fig. 101. *Echinaria circularis* n. sp., lateral view of holotype, ventral valve GSC 136810 with part of GSC 136811 below, from JBW 18, x1. Member C, Jungle Creek Formation.

Echinoconchus moorei Dunbar & Condra (1932, p. 209, pl. 24, fig. 1-5) from the Iowa Point Shale at the top of the Virgilian Shawnee Group of Kansas is much smaller and elongate with indistinct sulcus. Sutherland & Harlow (1967, pl. 134, fig. 6-8) compared specimens from the Late Pennsylvanian of New Mexico to the same species. *E. semipunctatus knighti* Dunbar & Condra (1932, p. 208, pl. 26, fig. 1-3; Gehrig 1958, pl. 2, fig. 10-12, 20, 23; Sturgeon & Hoare 1968, pl. 14, fig. 6-9) from Desmoinesian faunas of central United States, including Missouri and adjacent states, and also Ohio, is smaller and narrower, with weakly defined but somewhat similar ventral sulcus. Sutherland & Harlow (1973, pl. 9, fig. 4-7) compared New Mexican specimens of Desmoinesian age to the species, noting a slightly narrower umbo and more pointed beak. Coarse spines lie in one to three rows, with one or two rows of finer spines in front (pl. 9, fig. 6). *Echinaria* sp. A of Sutherland & Harlow (1973, p. 46, pl. 10, fig. 12, 13) from Morrowan and Atokan faunas of New Mexico is shaped very like the present material, but is smaller.

Muir-Wood & Cooper (1960, p. 248) reported occurrences of the genus in Asia and South Manchuria. *Echinaria bereensis* Kotlyar in Kotlyar & Popeko (1967, p. 112, pl. 21, fig. 1-4) from the Shazagaituisk Suite of east Baikal is small with distinct sulcus: detail of the ventral ornament is obscure in the figures. A fragment recorded from the Atokan Hare Fiord Formation of Ellesmere Island in the Canadian Arctic by Carter & Poletaev (1998, p. 133, Fig. 7.1) as *Echinaria*? sp. is smaller than the present species with less rounded outline or evenly arched venter. A large dorsal valve with gentle median fold from the Carboniferous of Amdrups Land, Greenland, might prove to be conspecific, having similar large size and well rounded outline. It was identified as *Productus punctatus* Martin by Grönwall (1917, p. 585, pl. 29, fig. 5).

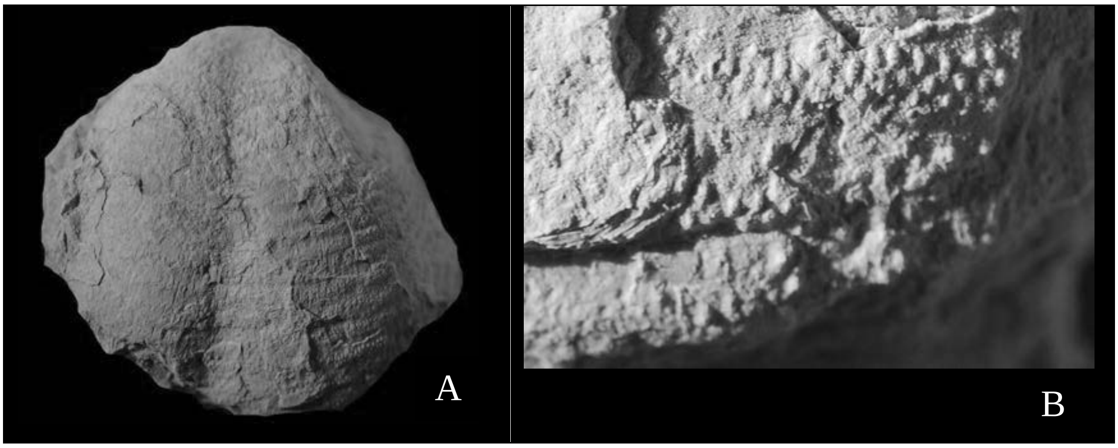


Fig. 102. *Echinaria circularis* n. sp. A, ventral valve GSC 136812, x1. B, detail of micro-ornament on ventral valve, GSC 136812, x5. From JBW 18. Member C, Jungle Creek Formation.

Fig. 103. *Echinaria circularis* n. sp. Micro-ornament on the flank of the holotype, GSC 136810 x4. From JBW 18. Member C, Jungle Creek Formation.

Echinaria (?) *densiformis* Aisenberg (1983, p. 78, pl. 41, fig. 1-6) from Serpukhovian of the Donbass is smaller and obscure over some details. Winkler Prins (1968, p. 90) noted some approach to *Pustula defensus* (Thomas, 1914, pl. 17, fig. 20-23), a moderately well rounded species of Lower Carboniferous age in Great Britain. Thomas (1914, p. 311) reported only one row of coarse spines posteriorly on each band for *defensus*, and smaller spines in front. In shape the specimens compared to *Echinaria defensa* from Spain by Winkler Prins (1968) approach the type material in being elongate, and having well developed ventral sulcus. They were judged to be of lower Bashkirian age. From the Late Carboniferous of Fergana, Kyrgystan, the specimen figured as *Echinoconchus komischani* by Volgin (1960, p. 59, pl. 5, fig. 1a, b) is almost as large as the Canadian species, though a little less inflated with shallower sulcus, and has an almost comparable but slightly broader subcircular outline, with less prominent ventral umbo, and more closely spaced commarginal rugae. Volgin stated that the name had been proposed as a nomen nudum by Licharew (1946), without specifying the reference.

According to Brunton et al. (2000, p. 511), the genus ranges from Gzhelian into Early Permian, but a number of older occurrences have been reported in the literature.

Fig. 104. *Echinaria* sp. showing ventral muscle impressions. GSC 137337 x1.2 from JBW 134, upper Ettrain Formation.

Subfamily **JURESANIINAE** Muir-Wood & Cooper, 1960

[Juresaniinae Muir-Wood & Cooper, 1960, p. 266].

Diagnosis: Commarginal bands generally confined to anterior half or so of shell, spines may be differentiated by size anteriorly, not separated by growth stops, cardinal process with elongate pit, or two ridges passing forward in parallel, one each side of the dorsal median septum, buttress plates may be present in Carboniferous juveniles. Dorsal spines are more homogeneous and not in bands as distinctive as those of Echinoconchinae.

Tribe **JURESANIINI** Muir-Wood & Cooper, 1960

[Nom. transl. Brunton et al. 1995, p. 929 ex Juresaniinae Muir-Wood & Cooper, 1960, p. 266].

Diagnosis: Quincunxial elongate pustules and spine bases posteriorly, commarginal bands as a rule limited to anterior of both valves, poorly differentiated.

Discussion: *Septiconcha* Termier et al. (1974, p. 125, pl. 23, fig. 4-6) from the lower Murghabian of Afghanistan is possibly a member of Juresaniini, but is difficult to circumscribe. The dorsal ornament appears to be not known. The question of relationship between Juresanini and Septasteginae Waterhouse is discussed in Waterhouse 2013, p.

266. Bathymyoniini Lazarev (nom. transl. Waterhouse 2002b, p. 24 ex Bathymyoninae Lazarev 1990, p. 117) has *Juresania*-like ornament posteriorly and subechinoconchiform ornament anteriorly. The group was incorporated in Juresaniini by Brunton et al. (2000, p. 513), but was recognized as a distinct tribe by Waterhouse (2013, p. 182).

Genus ***Juresania*** Fredericks, 1927

Diagnosis: Small medium in size with subquadrate outline and hinge at maximum width, weakly geniculate and weakly sulcate, thick spines with elongate bases posteriorly, median and anterior bands with thinner spines as well. Small buttress plates may be developed close to median dorsal septum.

Type species: *Productus juresanensis* Tschernyschew, 1902, p. 276 from Schwagerina-Kalk (lower Cisuralian), Russia, OD.

Discussion: The buttress plates of *Juresania* are very close-set, and normally converge anteriorly into a single septum: they are not like the widely divergent buttress plates of *Rhamnaria* Muir-Wood & Cooper, *Septasteges* Waterhouse & Piyasin, and various other genera.

Densepustula Lazarev, 1982, p. 66 was discriminated for *Juresania*-like shells that, according to Brunton et al. (2000, p. 514), lack commarginal bands anteriorly. The type species is *Flexaria* (?) *russiensis* Semenova, 1972 from the Moscovian Stage. Certainly the banding is more emphasized in *J. juresanensis*, but the type species *russiensis* does show rows of coarse spines followed by erratic rows of smaller spines, so that the difference is not great, nor consistent. *Parajuresania* Lazarev, 1982, p. 70 was erected for *Productus nebraskensis* Owen, 1852 in the Iowa Point Shale (Virgilian) of Kansas, because it showed a small cicatrix, and differentiated spines were said to appear only anteriorly, and buttress plates were subparallel at a juvenile phase, as endorsed by Brunton et al. (2000, p. 514). From inspection of figures, the finer of the two sets or orders of spines appear moderately early in *nebrascensis*. No available figures have been published that establish that fine spines appear over the actual ventral umbo of *Juresania juresanensis*. Spine bases are small and rounded in *nebraskensis,* whereas figures in Lazarev (1982, pl. 8, fig. 9, 10) indicate only coarse spines posteriorly in *J. juresanensis*, and the first-formed ventral spine bases are elongate in Canadian material. Martínez-Chacón & Winkler-Prins (1985, p. 439) disputed the validity of the differences, and synonymized *Parajuresania* with *Juresania*, but there is a difference in first-developed spination, whatever the generic significance.

Buntoxia Lazarev, 1986b, p. 94 is also very close to *Juresania*, and has an almost flat dorsal valve.

Juresania juresanensis (Tschernyschew, 1902)

Fig. 105 - 111

1902 *Productus juresanensis* Tschernyschew, pp. 276, 620, pl. 29, fig. 1, 2, pl. 47, fig. 1, 2, pl. 53, fig. 4.
1924 *P*. cf. *nebrascensis* [not Owen] – Holtedahl, p. 17, pl. 20, fig. 4-5.
1932 *P.* (*Juresania*) *juresanensis* – Frebold, p. 24, pl. 1, fig. 6, 7.
1935 *P. juresanensis typicus* Miloradovich, pp. 79, 140, text-fig. 29, pl. 5, fig. 25, 26.
1935 *Buxtonia juresanensis* – Ivanov, p. 28, pl. 4, fig. 1-4.
1952 *B. juresanensis* – Sarytcheva & Sokolskaya, p. 97, pl. 17, fig. 117.
1960 *J. juresanensis* – Muir-Wood & Cooper, p. 266, pl. 79, fig. 5-7.
1964 *J. juresanensis* – Gobbett, p. 82, pl. 4, fig. 34-37.
1966 *B. juresanensis* – Czarniecki, pl. 1.
1969 *B. juresanensis* – Czarniecki, p. 282, pl. 7, fig. 1-10, pl. 8, fig. 1-5, pl. 9, fig. 1-5.
1982 *J. juresanensis* – Lazarev, p. 70, pl. 8, fig. 8-11, text-fig. 2.
1990 *J. juresanensis* – Lazarev, pl. 33, fig. 8-11.
2000 *J. juresanensis* – Brunton et al., p. 513, Fig. 352a-e.

Diagnosis: Subelongate to subquadrate small-medium shells as a rule with broad shallow sulcus or gently rounded venter, spines bases elongate and sturdy, and finer bases in bands especially towards anterior over ventral valve.

Lectotype: Specimen figured by Tschernyschew (1902, pl. 47, fig. 2) from Schwagerina-Kalk (lower Cisuralian) at Juresan River, Urals., SD Gobbett, 1964, p. 82.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

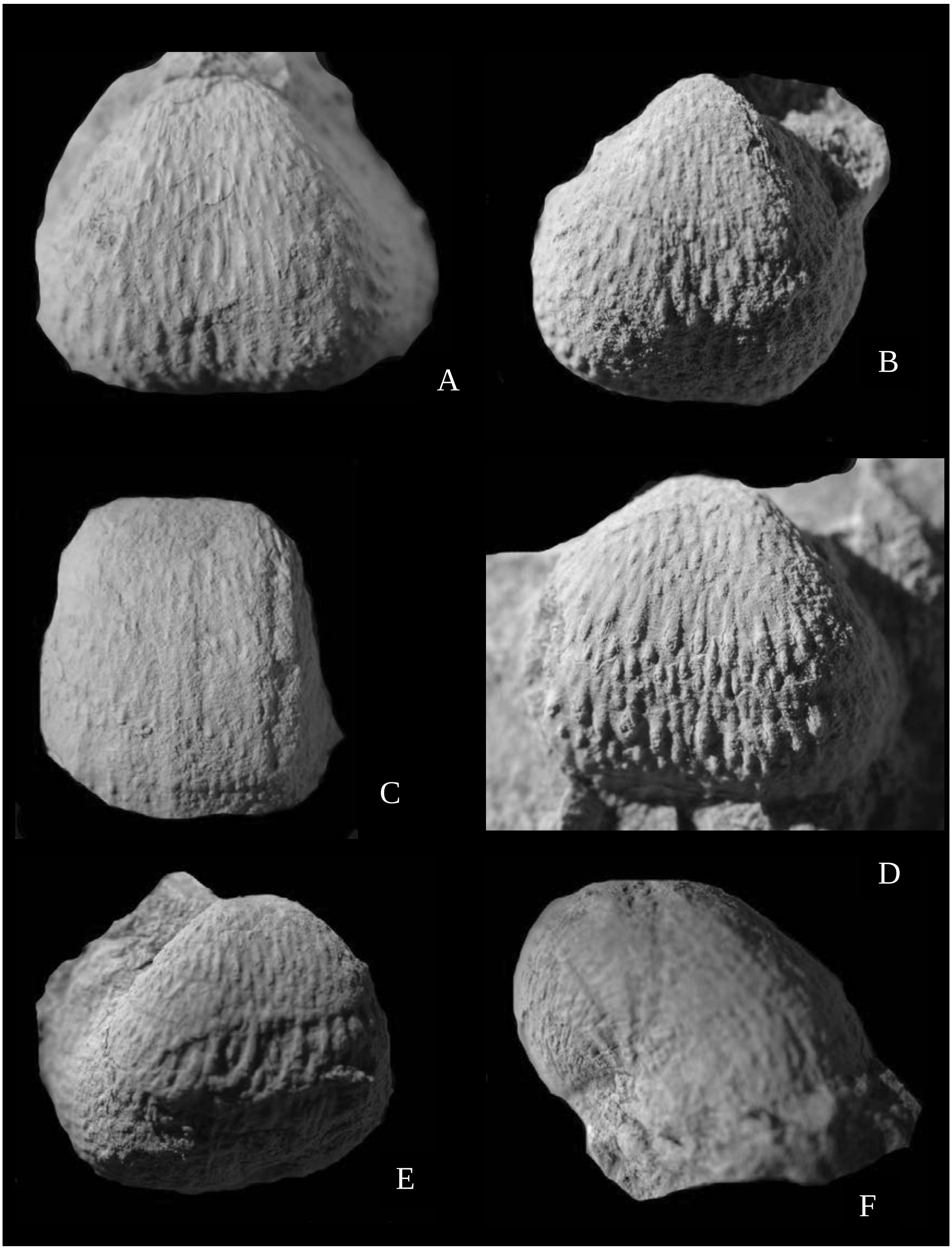


Fig. 105. *Juresania juresanensis* (Tschernyschew). A, ventral valve GSC 136814 x3. B, ventral valve GSC 136816 x3. C, anterior view of decorticated ventral valve, GSC 136815 x2. D, ventral valve GSC 136817 x3. E, F, ventral and lateral aspects of ventral valve GSC 136818 x3. From JBW 18, Member C, Jungle Creek Formation.

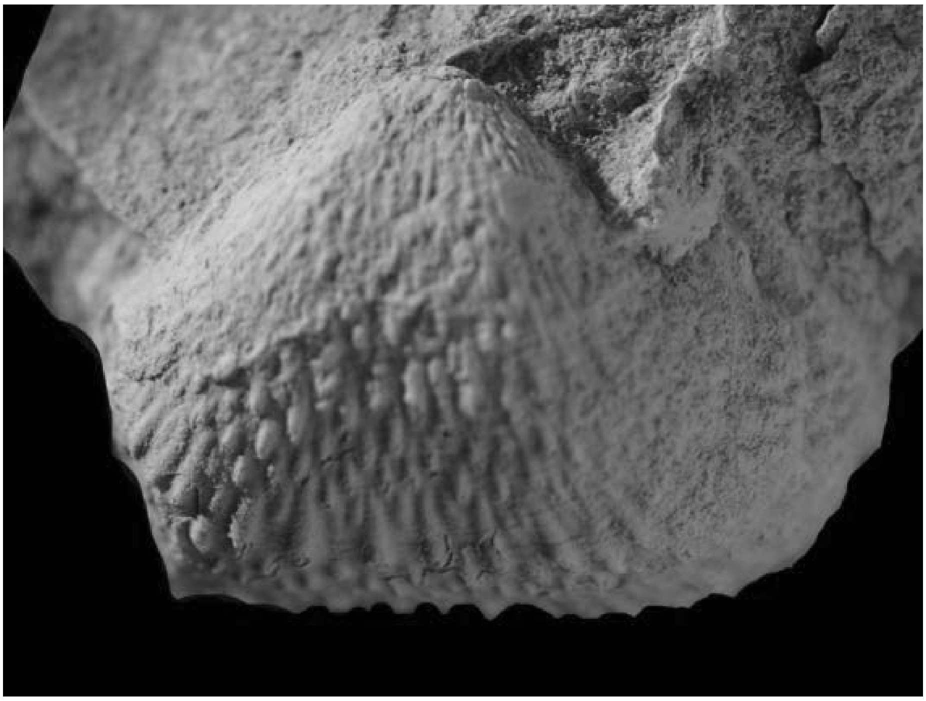


Fig. 106. *Juresania juresanensis* (Tschernyschew), umbonal part of ventral valve GSC 136819, x5. JBW 18, Member C, Jungle Creek Formation.

Description: Specimens small and elongate, incurved ventral umbo with angle of 80-90º, steep high posterior walls and flatly convex to gently sulcate wide venter. The hinge is slightly narrower than maximum width placed well forward near anterior margin, and ears are small and inconspicuous. The dorsal valve is almost flat over the disc apart from a small convex nepionic portion close to 2mm wide, low anterior broad very subdued fold, and small concave ears, and short subgeniculate trail at high angle to disc. Ventral ornament over much of the valve consists of short elongate spine bases in quincunx, with a spine nearly 4mm long emerging from the anterior end. The

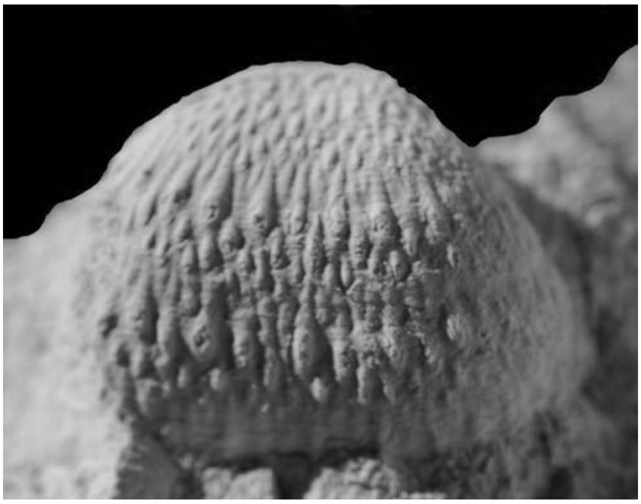


Fig. 107. *Juresania juresanensis* (Tschernyschew), ventral valve GSC 136819 x4, showing differentiated spine bases over mid-length. JBW 18, Member C, Jungle Creek Formation.

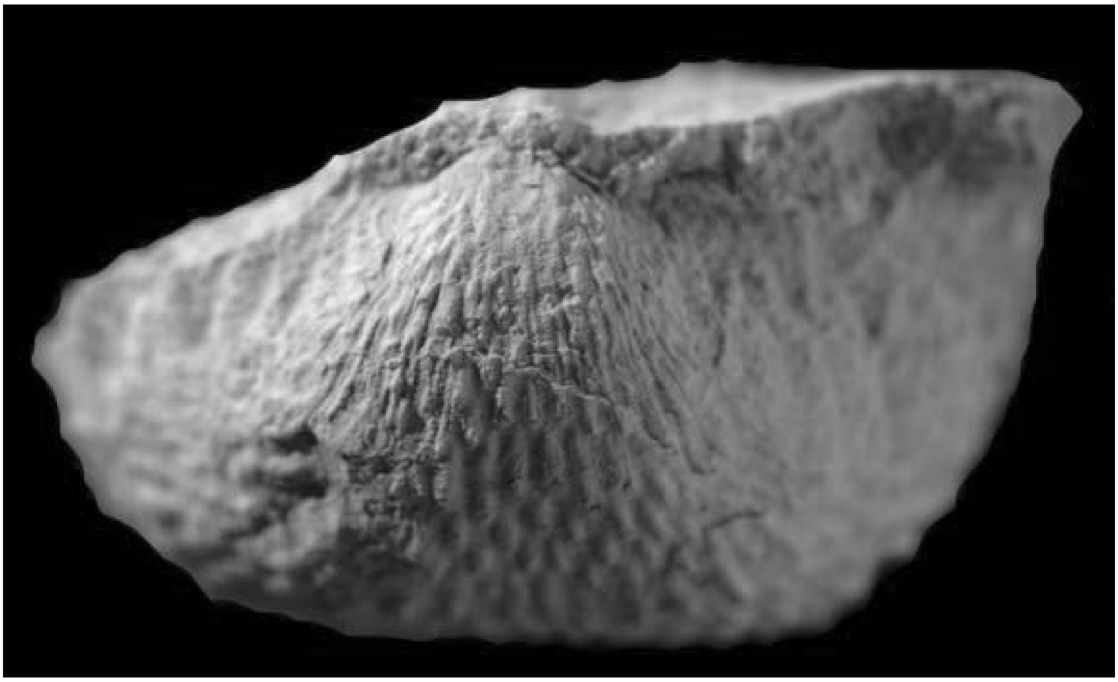


Fig. 108. *Juresania juresanensis* (Tschernyschew, 1902), umbonal area of ventral valve GSC 136814 x5. JBW 18, Member C, Jungle Creek Formation. See Fig. 105A.

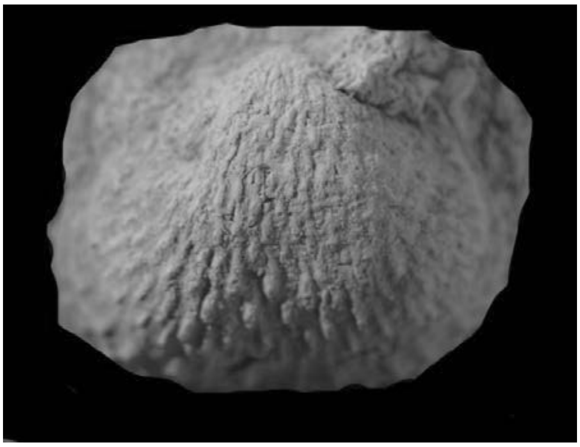


Fig. 109. *Juresania juresanensis* (Tschernyschew), posterior aspect of ventral valve GSC 137248 x5, showing long spine bases over umbonal shell. JBW 18, Member C, Jungle Creek Formation.

spine bases vary from 0.3mm to over 1mm in width and 1.5 to 4mm in length. Anteriorly, spine bases are less well developed, but many have bases just as elongate as posteriorly. However one specimen has two anterior commarginal bands each bearing three rows of irregularly spaced spines, six to eight along 5mm. Dorsal spines are scattered over the disc and trail, with a number on the ears between large dimples, and the anterior disc and trail are marked by subelongate to round pits and pustules. Low transverse rugae lie over the posterior umbonal slopes of the ventral valve, and on a few specimens weak commarginal divisions cross the posterior shell each with two rows of spine bases. Very subdued wrinkles cross the dorsal valve.

Adductor scars are small, and diductor scars scarcely discernible. Little of the dorsal interior is displayed: a septum extends past mid-length, adductor scars are small, subrounded and smooth and much of the floor bears small well-spaced pustules. A well preserved specimen shows a wide antron in front of the cardinal process.

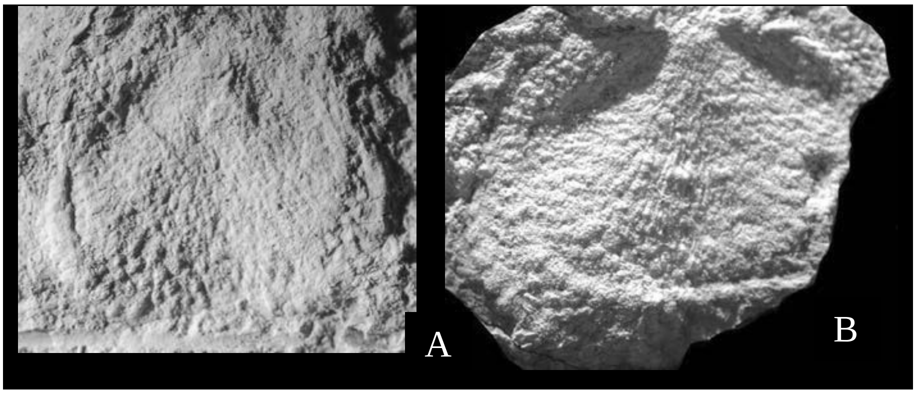
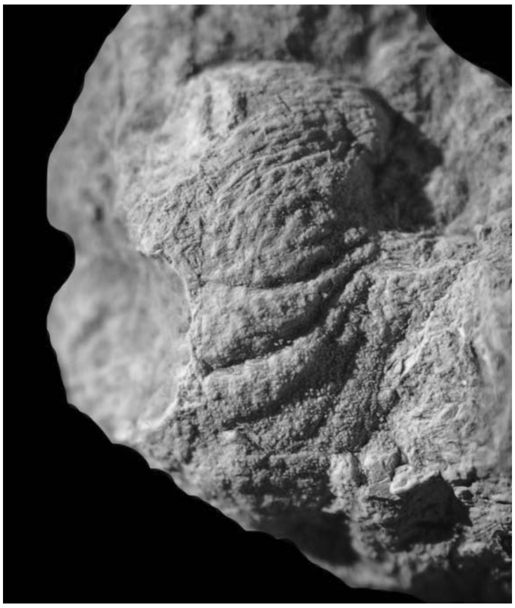


Fig. 110. *Juresania juresanensis* (Tschernyschew). A, dorsal valve GSC 136821 x3. B, dorsal valve, GSC 136822 x2.5. From JBW 18, Member C, Jungle Creek Formation.

Fig. 111. *Juresania juresanensis* (Tschernyschew), tilted lateral aspect of ventral valve, GSC 137293 x4. JBW 18, Member C, Jungle Creek Formation.



Resemblances: *Productus juresanensis* Tschernyschew (1902, p. 620, pl. 19, fig. 1, 2, pl. 47, fig. 1, 2, pl. 53, fig. 4; Muir-Wood & Cooper 1960, pl. 79, fig. 5-7) comes from the Schwagerina Limestone of the Urals, the types having been found at Juresan River in Timan. Lazarev (1990, pl. 33, fig. 8-11) added figures from the Asselian of the Urals. The Russian specimens are slightly larger, and very slightly more transverse, whereas the Canadian specimens tend to be slightly narrower and more polliciform, although a few Canadian specimens are as broad as the Timan types. Both suites have similar ventral sulcus, incurved ventral umbo, and similar ventral ornament. Specimens assigned to

Buxtonia juresanensis by Ivanov (1935, p. 28, pl. 4, fig. 1-4) have more elongate spine bases posteriorly, which may be a matter of spines pressed against the shell, a question difficult to decide from illustrations, and the figure of *juresanensis* provided by Licharew & Einor (1939, pl. 4, fig. 5) from Novaya Zemlya only shows a dorsal valve, insufficient to identify to species level. Czarniecki (1969, p. 282) recorded a large suite of specimens as this species from the Treskelloden beds of Spitsbergen, assigning the species to *Buxtonia:* a number of the specimens are polliciform, and Gobbett (1964) figured specimens from the Upper Wordiekammen Limestone of Spitsbergen, slightly smaller than the Canadian specimens and with diverging posterior walls. Czarniecki (1969) referred *Buxtonia* sp. of Gobbett (1964, pl. 7, fig. 10, 11) from the Tårnkanten Limestone of Spitsbergen to *juresanensis*, but these particular specimens are very broad. Holtedahl (1924) reported the species from Novaya Zemlya, and Frebold (1932) from central-east Greenland. *Buxtonia juresanensis* was described from the Taiyuan Series of China by Chao (1927a, p. 81, pl. 8, fig. 4-8), and Grabau (1936, p. 140, pl. 13, fig. 5, 6) illustrated the species from the Maping Limestone of China, but they are broad specimens, with sulcus and emphasized commarginal bands. The specimen assigned to the species by Yang et al. (1977, p. 357, pl. 141, fig. 7) is close in shape but has more swollen spine bases anteriorly, and a specimen figured by Wang et al. (1987, pl. 46, fig. 1) from Henan Province, China, is less elongate. *Buxtonia juresanensis* of Mironova (1967, pl. 1, fig. 18) from the Zelim beds of Bashkiria does not appear close, and Early Permian specimens from northeast Thailand that were identified with the species by Yanagida (1967, pl. 15, fig. 1-7) are broader with more marked sulcus. Rotai (1951, p. 40, pl. 3, fig. 4) referred to *juresanensis* Ivanov not Tschernyschew, meaning Ivanov, 1935 for material from the Martiyarnov Suite of the Donetz Basin. Gauri (1965, p. 82, pl. 15, fig. 1-4) recorded specimens from Late Carboniferous of Austria that have more pronounced commarginal rugae and slender spine bases.

The figure in Löweneck (1932, pl. 4, fig. 9) of a specimen from the Tien Shan Mountains shows a large specimen with well spaced and elongate spine bases, but the number of well defined commarginal bands suggests a possible echinoconchid. Winkler Prins (1968, pl. 5, fig. 3-8) assigned material to the species from the Lower Moscovian of Spain, but ornament differs, with denser spines and higher spine bases. *J. subpunctata* (Nikitin 1890, pl. 1, fig. 5, 6) of Kasimovian and Gzhelian age in the Moscow Basin, and reported from Spain by Winkler Prins (1968, pl. 5, fig. 9 a, b) is more transverse and ornament differs. *Productus* (*Juresania*) *juresanensis* of Renz in Visser & Visser-Hooft (1940, pl. 4, fig. 3) from the Early Permian of the Karakorum has sturdy crowded spines over the posterior shell, and the anterior is not figured. Early Permian specimens from Cambodia (Mansuy 1913, pl. 2, fig. 13a-h) are sulcate and show elongate spine bases posteriorly, although it is not clear from figures that the typical anterior bands are present, perhaps because the specimens are immature, Mansuy (1913, p. 35) did state that commarginal bands were present on some specimens.

Juresania rituensis Sun (1983, p. 125, pl. 15, fig. 1, 2) from the Rutog Duomo region of Tibet appears to be very close to *J. juresanensis* in shape and size, whereas *J. kueichowensis* (Chao), also figured by Yang et al. (1977, p. 357, pl. 141, fig. 7a, b), is broader with shallow sulcus. Specimens identified as *Buxtonia juresanensis* in Ustritsky (1960a, p. 31, pl. 5, fig. 6, 7) from the western Kunmon Mountains of China are shaped like this species, but detail of ornament is not clear. *Juresania hispida* Chronic, 1949, p. 89, 1953, p. 84, pl. 14, fig. 10 from the Copacabana Group of south central Peru has fine and numerous spines with fine bases.

Productus nebrascensis (Owen, 1852, pl. 5, fig. 3 = *asperus* McChesney, 1860) from the Pennsylvanian

Kansas City Group of Nebraska, also figured by Muir-Wood & Cooper (1960, pl. 79, fig. 9-16, pl. 80, fig. 1-14) from beds of Permian age in Kansas, is broader with slightly more elongate ventral spine bases over much of the shell, apart from the ventral umbonal region which has small rounded spine bases. Sutherland & Harlow (1967, p. 1074, pl. 134, fig. 9-11, text-fig. 6) added specimens from the Late Pennsylvanian Jemez Spring Shale Member of Late Pennsylvanian age in New Mexico, and included *J. rectangularia* King (1938, p. 271, pl. 39, fig. 9-12) from the Canyon-Brad Formation of west Texas in synonymy. This species *nebrascensis* was made type of *Parajuresania* Lazarev, 1982, and although its validity has fallen under question, it does appear to have ventral umbonal spines finer than those typical of *Juresania* (see p. 137).

Subfamily **TUBERSULCULINAE** Waterhouse, 1971a

[Tubersulculinae Waterhouse, 1971a, p. 205]

Diagnosis: Spines uniformly fine and arranged in quincunx over the ventral valve, with short to subelongate bases, dorsal spines erect and numerous or absent, radial ornament weakly developed or absent, trail short. Corpus slender. Dorsal marginal ridges subdued to moderately developed, dorsal median septum usually entire, endospines large and crowded in front of dorsal septum, brachial ridges productiform.

Discussion: Brunton et al. (2000, p. 434) synonymized this subfamily with Costispiniferini Muir-Wood & Cooper, 1960, but that suggestion is highly contentious. *Costispinifera* is distinguished by the presence of strong and persistent ribs, cardinal process with zygidium and heavy marginal ridges indicative of a relationship to Marginiferidae (Waterhouse 2001, 2002b, p. 10), whereas *Tubersulcus* and allies are allied to echinoconchids through ornament and internal morphology, including cardinal process and nature of the marginal ridges.

Tribe **TUBERSULCULINI** Waterhouse, 1971a

[Nom. transl. Waterhouse 2013, p. 188 ex Tubersulculinae Waterhouse, 1971a, p. 205. Syn. Krotoviini Brunton et al. 1995, p. 926].

Diagnosis: Ventral spines subuniform and evenly arranged and usually closely spaced over ventral valve in quincunx or commarginal rows, dorsal spines fine, crowded.

Discussion: Genera involve *Tubersulculus* Waterhouse, *Archboldina* Waterhouse, *Echinauriella* Lazarev, *Krotovia* Fredericks, and perhaps *Scoloconcha* Gordon. As pointed out by Waterhouse (2001), the genus *Tubersulculus* lacks specialized and varied ventral spines, and lacks any heavy marginal ridge around the anterior dorsal disc. The genus has a high cardinal process with zygidium, and large few anterior dorsal pustules. These and other attributes indicate that *Tubersulculus* does not belong to Costispiniferini, counter to Brunton et al. (1995, 2000). *Tubersulculus* is very close to *Krotovia,* and Late Carboniferous species of *Tubersulculus* from Canada suggests a gradual but step-wise divergence from species to species upwards through time, whilst *Krotovia* also persisted. *Scoloconcha* Gordon, 1966 of middle Visean age is small with smooth ventral valve and erect fine spines. It has a high dorsal posterior lateral ridge, just as in *Tubersulculus* (see Shi & Waterhouse 1996, pl. 4, fig. 27), to reinforce the external similarities in the nature of spines and distribution. *Echinauriella* has a smooth ventral ear sector, fewer dorsal spines, and high inner dorsal oblique ridges, and lacks an anterior thick marginal ridge. Lethamini Waterhouse constitutes a companion tribe.

Genus ***Tubersulculus*** Waterhouse, 1971a

Diagnosis: Deeply concavo-convex with ventral sulcus and dorsal fold producing or incipiently producing tubiform trail, regular ribbing absent but ventral valve may display faint longitudinal ridging, low commarginal lamellae, spines numerous over both valves in quincunx and in commarginal rows, ventral spines with weakly swollen weakly elongate bases, lateral ridges cross ears internally, dorsal endospines strong and numerous.

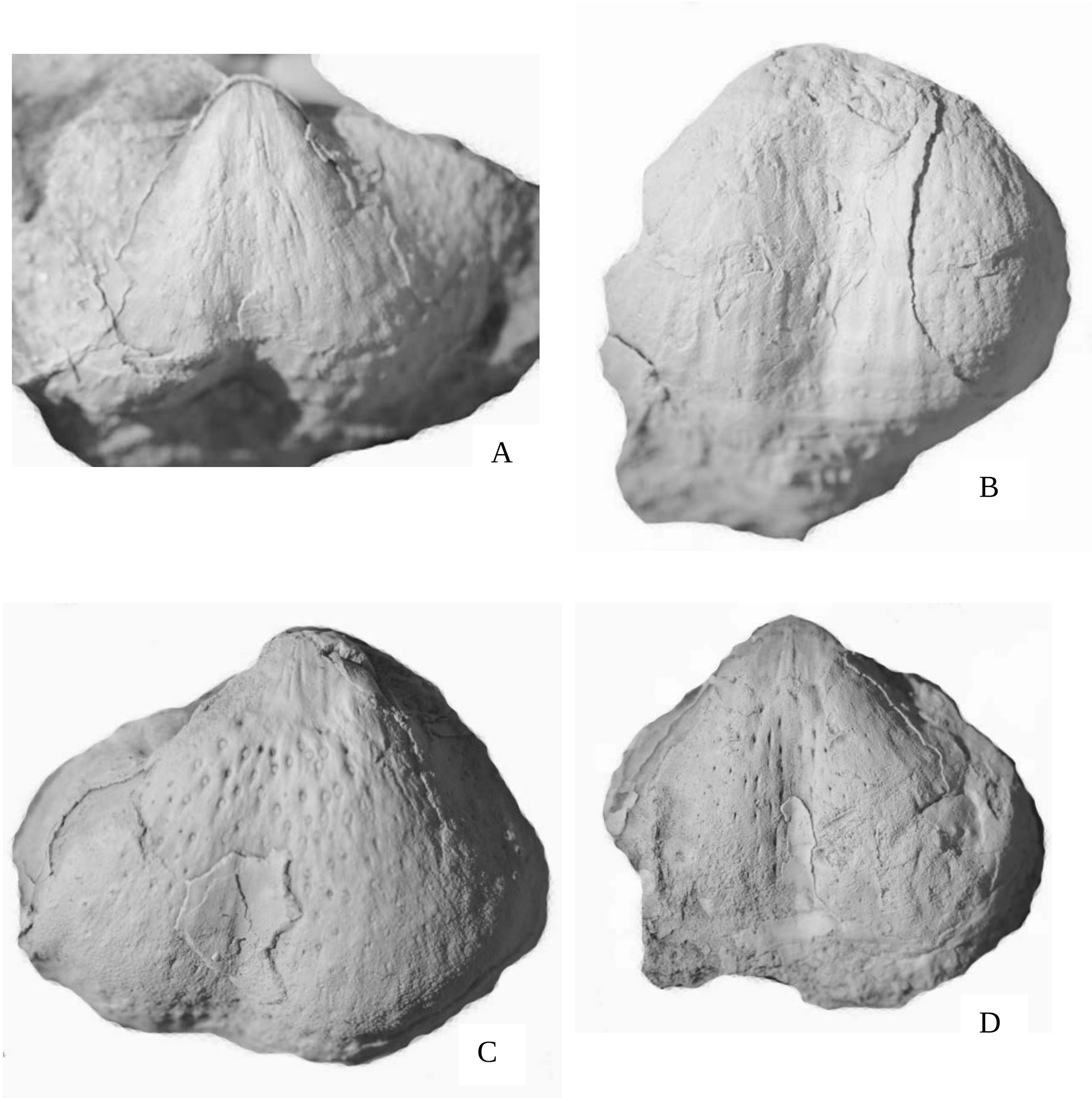


Fig. 112. *Tubersulculus ovalis* n. sp. A, decorticated ventral valve, GSC 136823 from JBW 593. B, anterior view of decorticated ventral valve GSC 136829 from JBW 694. C, decorticated ventral valve GSC 136824 from JBW 593. D, ventral internal mould, GSC 136825 from JBW 593. Specimens x3. Member A, Jungle Creek Formation.

Type species: *Tubersulculus maximus* Waterhouse, 1971a, p. 209 from the Jungle Creek Formation (Tastubian), Ogilvie Mountains, Yukon Territory, Canada, OD.

Discussion: Notably, the genus is lacking from paleotropical Permian faunas of the Pamirs (Grunt & Dmitriev 1973) or Texas (Cooper & Grant 1975), as well as from Gondwana, but its precursor and contemporaneous genus *Krotovia* Fredericks is well represented in paleotropical faunas of Lower Carboniferous age.

Tubersulculus ovalis n. sp.

Fig. 112 - 115

Derivation: ovum – egg, Lat.

Diagnosis: Shells transverse, ventral sulcus shallow, small or no tubiform trail.

Holotype: GSC 137287, here designated.

Material: Fifteen specimens from JBW 452, four ventral valves from JBW 518, single ventral valves from JBW 66, 75, 173, 448, 549, 562, 614 and 615. Six ventral valves, dorsal valve and specimen with valves conjoined from JBW 694; specimen with valves conjoined and three ventral valves from JBW 593 and dorsal valve from JBW 95. One possible specimen from JBW 533 and a ventral and dorsal valve from JBW 530**,** Ettrain Formation.

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Description: Specimens of small to moderate size, a ventral valve measuring 24mm wide, 22mm long and 10mm high. The ventral umbo measures 75º to 80º, is slightly incurved, and extended a little beyond the hinge, and the hinge is moderately wide, with angular slightly alate cardinal extremities; ears poorly distinguished from the umbonal

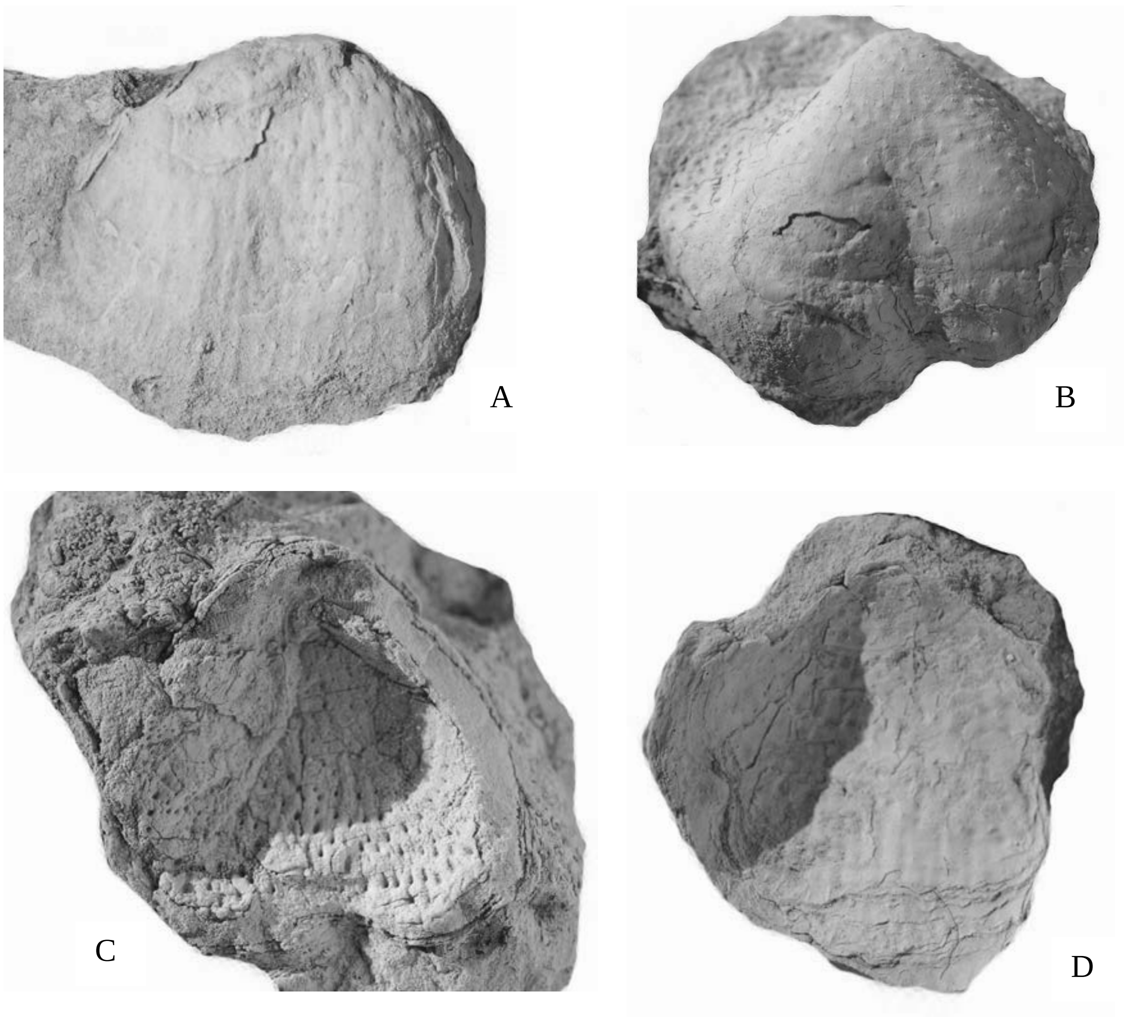


Fig. 113. *Tubersulculus ovalis* n. sp. A, decorticated ventral valve GSC 136828 from JBW 593. B, ventral valve holotype, GSC 137287 from JBW 593. C, dorsal aspect of damaged internal mould, GSC 137323 from JBW 694. D, dorsal view of decorticated specimen with valves conjoined, GSC 136827 from JBW 694. Specimens x3, from Member A, Jungle Creek Formation.

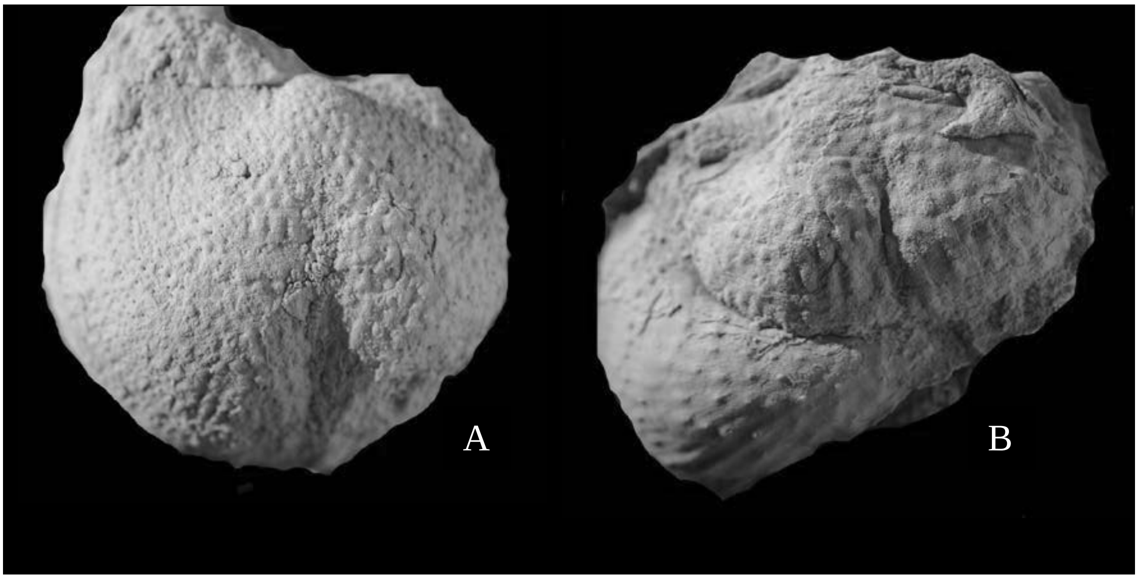


Fig. 114. *Tubersulculus ovalis* n. sp. A, dorsal external mould, GSC 137259 from JBW 66. B, ventral valves GSC 137352 and 137353 from JBW 549. Specimens x3 from Member A, Jungle Creek Formation.

slopes, which are steeply convex and moderately high. Maximum width lies near mid-length, and a deep sulcus commences 5-7mm in front of the umbonal tip and widens at an angle close to 20º. The anterior margin is only slightly produced, and a tubiform trail present in only a few specimens. The dorsal valve is concave, with ears, and curves steeply into the trail. Ventral ornament consists of well spaced fine erect spines, five to six in 5mm medianly, in rows and roughly in quincunx: spines are fine and spaced slightly closer at less than 1mm apart over the umbonal region, and may be finer over the anterior trail. Spine bases may be slightly swollen and subelongate. There are faint low commarginal rugae starting at the umbonal region, and such cover the shell, and may be more prominent at the anterior trail or start of the trail, roughly 1mm apart. Similar rugae are found on the dorsal valve, especially the trail, with spines emerging from rather than between pustules, and also from shell with only fine growth increments. Fine radial ribs appear anteriorly on some ventral valves. The trail margin is laminate, and the visceral disc is 3.5mm thick in the largest specimen 28mm wide, and 2.5mm thick in another specimen 24mm wide.

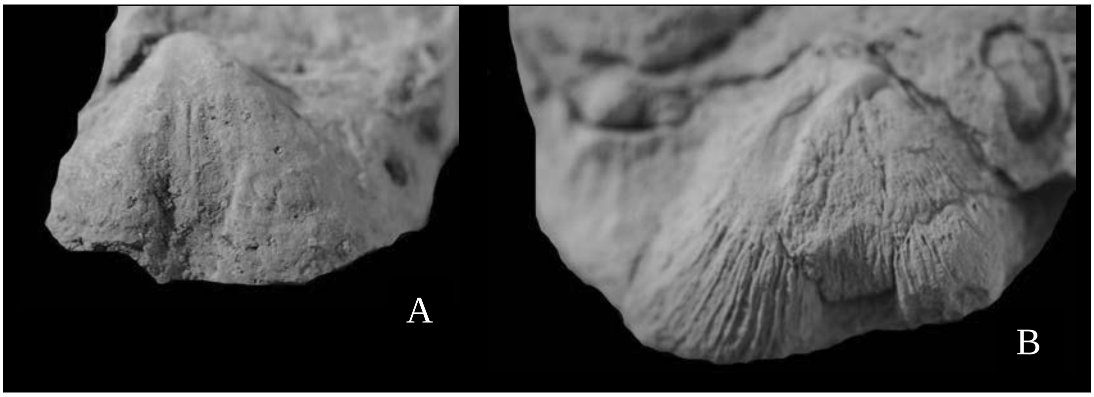


Fig. 115. *Tubersulculus ovalis* n. sp. A, posterior part of internal mould of ventral valve GSC 136830 x3 from JBW 75. B, posterior part of internal mould of ventral valve GSC 136831 x3 from JBW 173. Member A, Jungle Creek Formation.

The ventral adductor platform is small and posteriorly placed, smooth and divided by low myophragm or groove, with shallow subrounded diductor impressions placed well forward. In front, the disc bears large pustules, and the anterior disc and trail floor has fine pits. In the dorsal valve the median septum extends for three quarters of the visceral disc, and large pustules lie over the anterior floor. There is a low marginal ridge (GSC 136826).

Resemblances: The shells have a sulcus that is slightly broader and shallower, with corresponding dorsal fold, compared with *Tubersulculus reidi* Waterhouse, 2013 from the *Ogilviecoelia shii* fauna, and only rare specimens show a short anterior tubiform extension. There appears to have been an episodic change in morphology through the stratigraphic record from present specimens with shallow broad sulcus and rare tubiform trail, to more elongate specimens with slightly deeper and narrower sulcus and incipient tubiform trial (*T. reidi*), to shells with deeper sulcus and tubiform trail as in *T. maximus* in Canada and *T. pseudoaculeatus* (Krotow) in Russia.

Tubersulcus reidi Waterhouse, 2013

Fig. 116 - 121

2013 *Tubersulculus reidi* Waterhouse, p. 188, Fig. 6.12, Fig. 6.13.

Diagnosis: Weakly transverse with wide hinge and gentle ventral sulcus over median length, ventral spines fine and closely spaced, may be coarse near start of trail and very fine in bands over trail, dorsal spines fine and especially numerous over ears and trail. Myophragm well developed.

Holotype: GSC 133278 figured in Waterhouse (2013, Fig. 6.12A) and Fig. 116A herein, from Member E, Jungle Creek Formation, OD.

Material: For Member E, single ventral valves from JBW 99, 551, 577, 578 and 791, ventral valve and dorsal valve from JBW 539, ten ventral valves, three dorsal valves and three specimens with valves conjoined from JBW 561, four ventral valves and a dorsal valve from JBW 580, and eighteen ventral valves, eight dorsal valves and two specimens with valves conjoined from JBW 581. Poorly preserved specimens from JBW 563 include four ventral valves and three dorsal valves. From Member D, JBW 72 has two ventral valves and a dorsal valve. Three ventral valves come from JBW 413, four ventral valves and five dorsal valves from JBW 762, and single ventral valves come from JBW 132, 162 and 782, and two ventral valves from JBW 44.

Stratigraphic and biostratigraphic levels: Members D and E, Jungle Creek Formation. *Rugivestigia commarginalis* Zone, *Ogilviecoelia shii* Zone.

Dimensions in mm: ventral valve

Specimen GSC	Width	Length	Height
133278	28	22	8
133277	30	22	12
133276	32	27	11.5

Description: Shells transverse, ventral valve gently convex with sulcus having an angle of 30º, commencing 6-7mm in front of umbonal tip, narrowing and shallowing anteriorly over trail and may persist to anterior margin, which is extended. Dorsal fold conforms with ventral sulcus, becoming low and narrow anteriorly over trail. Ventral umbo broad with angle of 100º, slightly extended beyond hinge, which is wide, with obtuse cardinal extremities as a rule, although a few specimens have tiny alate acute extremities. Very low interareas are developed along the hinge in each valve, marked by growth striae parallel to the hinge, but it is not certain that a ginglymus is developed on all specimens. The postero-lateral shell is weakly convex for the ventral valve, and concave in the corresponding part of the dorsal valve. Ornament is spinose. Ventral spines are arranged in close-set commarginal rows, seven in 5mm at 5mm from the umbo, five in 5mm at 12mm from the umbo, with rows 1 to 1.7mm apart. In some specimens rows are 3mm apart with some seven spines in 5mm; in rare specimens spines are in rows 2.5mm apart and coarse, at only four in 5mm. In front over the anterior shell and involving the trail, spine development varies, but as a rule spines are fine with seven to ten in 5mm along rows 1mm to 3mm apart. Low and short radial ridges appear, often in front of the spines, and dimples may develop, especially laterally. There are eight to ten growth laminae per mm at mid-length, and coarser subfusc commarginal rugae present, numbering more than fifty. The dorsal valve is more dimpled than the ventral valve, and dorsal spines are finer and more close-set over the postero-lateral ears, and spines at the posterior cardinal extremities are slightly larger and spaced further apart. As over the ventral valve, spines form a few well developed commarginal rows at the start of the trail, with ten to twelve in 5mm, and are fine and variably spaced over the trail.

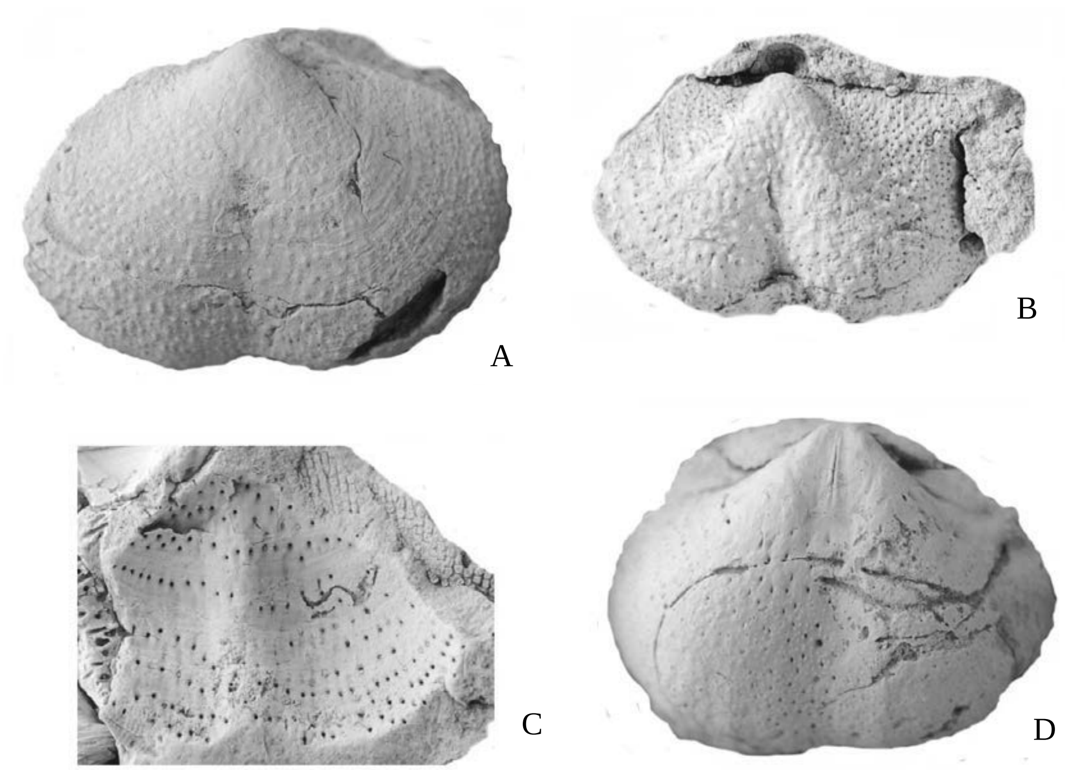


Fig. 116. *Tubersulculus reidi* Waterhouse. A, ventral valve holotype GSC 133278 from JBW 561. B, dorsal aspect of external mould showing dorsal exterior and ventral beak, GSC 133279 from JBW 581. C, external mould of ventral anterior, GSC 133340 from JBW 580. D, internal mould of ventral valve GSC 133277 from JBW 561. Specimens x 2 from Member E, Jungle Creek Formation.

Ventral adductors are large and smooth, apart from weak growth rugae parallel to the rounded anterior, and elongately oval in shape, and divided by a narrow but comparatively well defined myophragm, with a narrow groove each side. The diductor scars are very faintly impressed and are suboval and small, and anteriorly placed, overlapping only the anterior part of the adductor scars. A short ridge crosses the floor of the valve at the anterior margin of the ears, and the floor of the valve bears sharp pustules and small pits, coarse near the muscle scars and finer in front. In the dorsal valve, a medium septum extends to mid-length, broad posteriorly and narrow between the adductors and in front. The posterior adductors are small, subrectangular and smooth, and the anterior adductors large, suboval, elongate, marked in one specimen by growth-lines parallel to the rounded anterior margin. In a well preserved small specimen, a short well defined ridge lies postero-laterally to the adductors, and a higher ridge extends along the hinge. The cardinal process is not preserved, and the brachial ridges are not clearly visible, but one large mature specimen shows a single fine ridge extending forward from just behind the end of the median septum, representing the inner arm of the brachial shield, comparable in outline with that figured in Shi & Waterhouse (1996, pl. 4, fig. 25, 27). Large pustules are developed over the floor of the valve, and a narrow marginal ridge is well developed, even in small specimens.

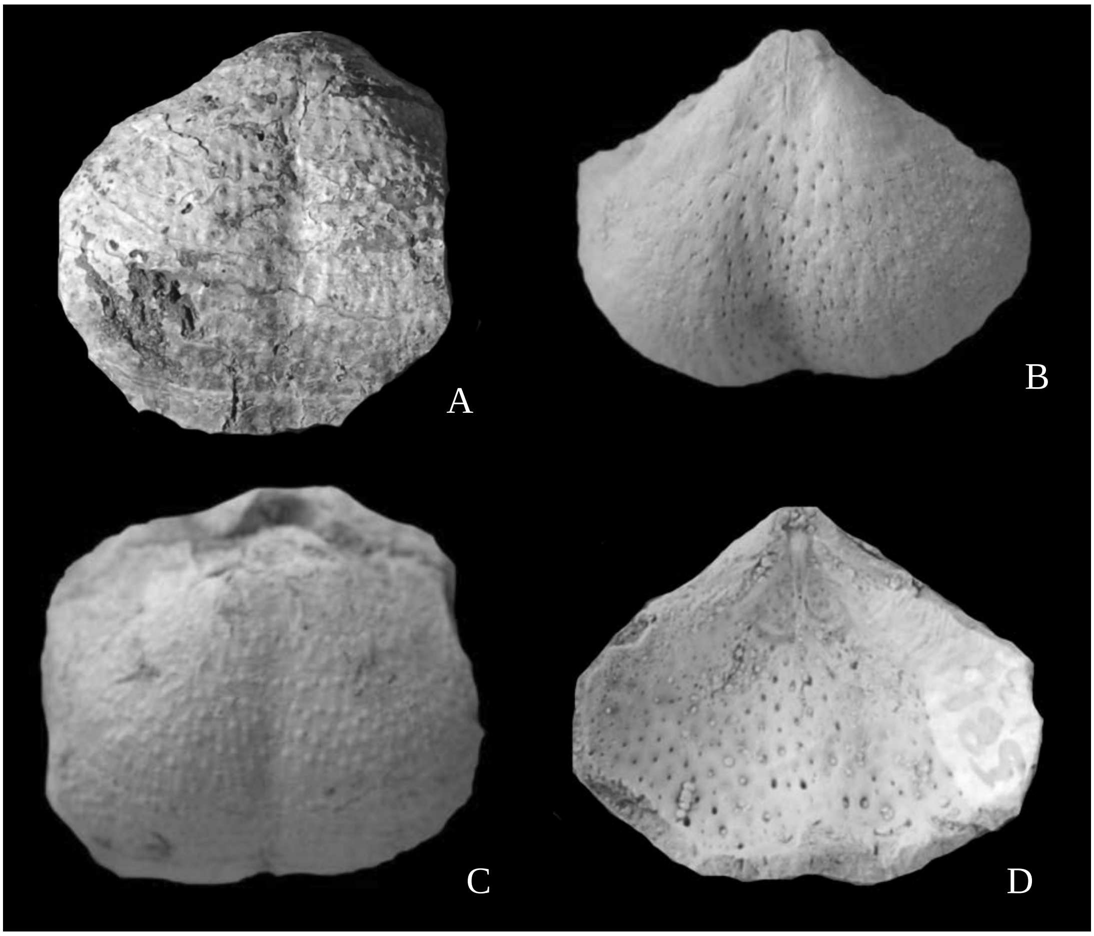


Fig. 117. *Tubersulcus reidi* Waterhouse. A, ventral valve GSC 133276, from JBW 581 x2. B, D, ventral and dorsal aspects of internal mould GSC 133275 from JBW 581 x2.5. C, dorsal view of specimen with valves conjoined, GSC 133280 from JBW 561 x2. A thin calcite coating covers much of the surface, but spine bases are visible over the trail. Member E, Jungle Creek Formation.

Resemblances: This species is very close to the type species of the genus, *Tubersulculus maximus* from the "*Yakovlevia transversa"* to *Jakutoproductus verchoyanicus* Zones of the upper Jungle Creek Formation, Yukon Territory, Canada, as described by Waterhouse (1971a, pl. 23, fig. 1-11) and Shi & Waterhouse (1996, pl. 4, fig. 24-29, pl. 5, fig. 1-9), but most specimens of *reidi* are more transverse, and have a shallower broader ventral sulcus, and the sulcus persists to the anterior margin, whereas it is replaced by an anterior fold in *T. maximus*. Ventral spines are less varied in spacing on *maximus*: the spacing is similar at five to six in 5mm at 5mm from the umbo, but spines become more close-set in front, often six or seven in 5mm, with some well spaced rows, and finer and denser over the anterior shell and trail, at eight or nine in 5mm. Dorsal spines are more close-set posteriorly, and dense over the trail. Internally the myophragm is better developed in the ventral valve of the present form. The species *maximus*

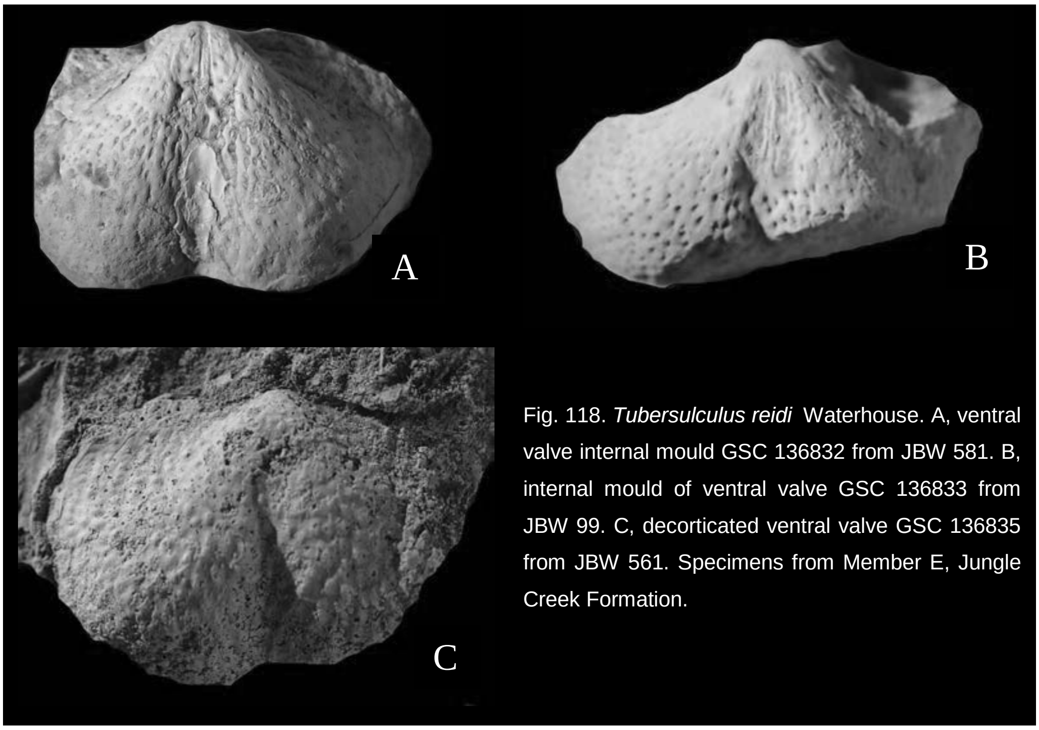


Fig. 118. *Tubersulculus reidi* Waterhouse. A, ventral valve internal mould GSC 136832 from JBW 581. B, internal mould of ventral valve GSC 136833 from JBW 99. C, decorticated ventral valve GSC 136835 from JBW 561. Specimens from Member E, Jungle Creek Formation.

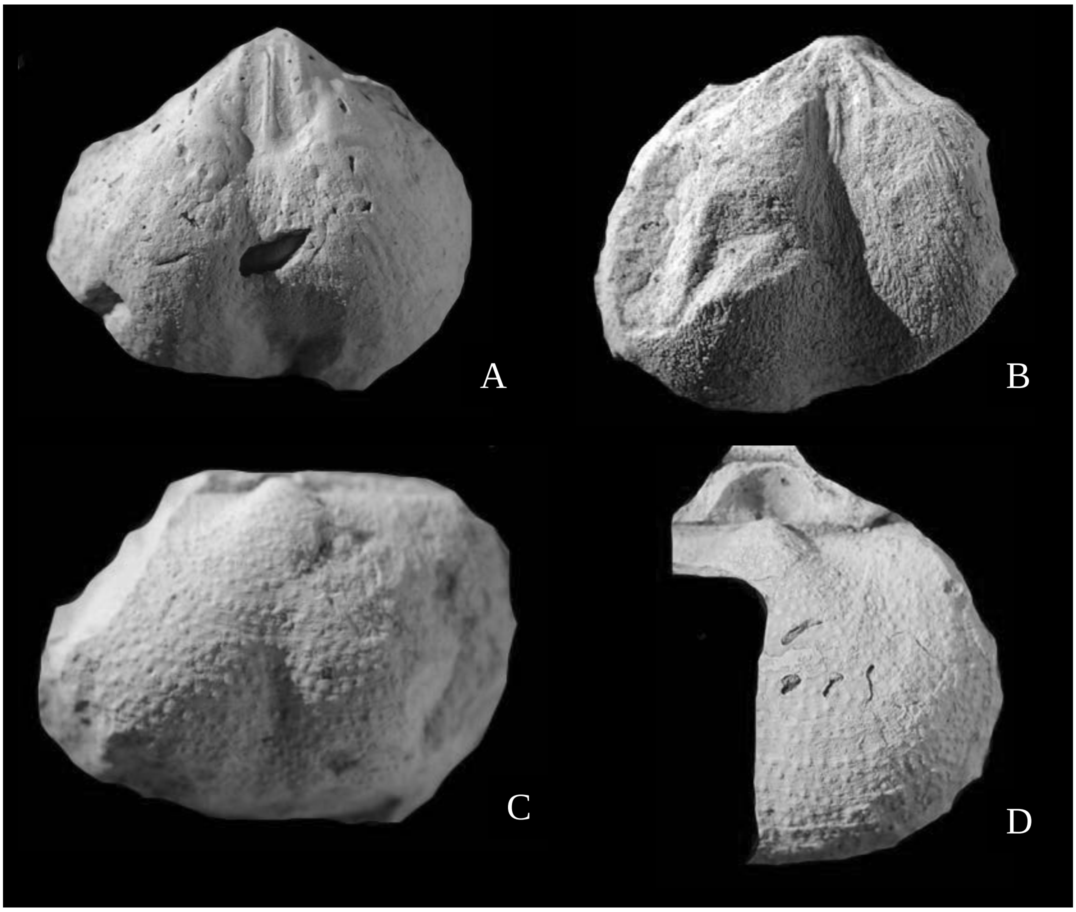


Fig. 119. *Tubersulculus reidi* Waterhouse. A, ventral valve internal mould GSC 136837 from JBW 561. B, internal mould of ventral valve GSC 136838 from JBW 561**.** C, dorsal external mould GSC 137271 from JBW 561. D, dorsal external mould with attached ventral umbonal external mould, GSC 137288 from JBW 561. Specimens x2 from Member E, Jungle Creek Formation.

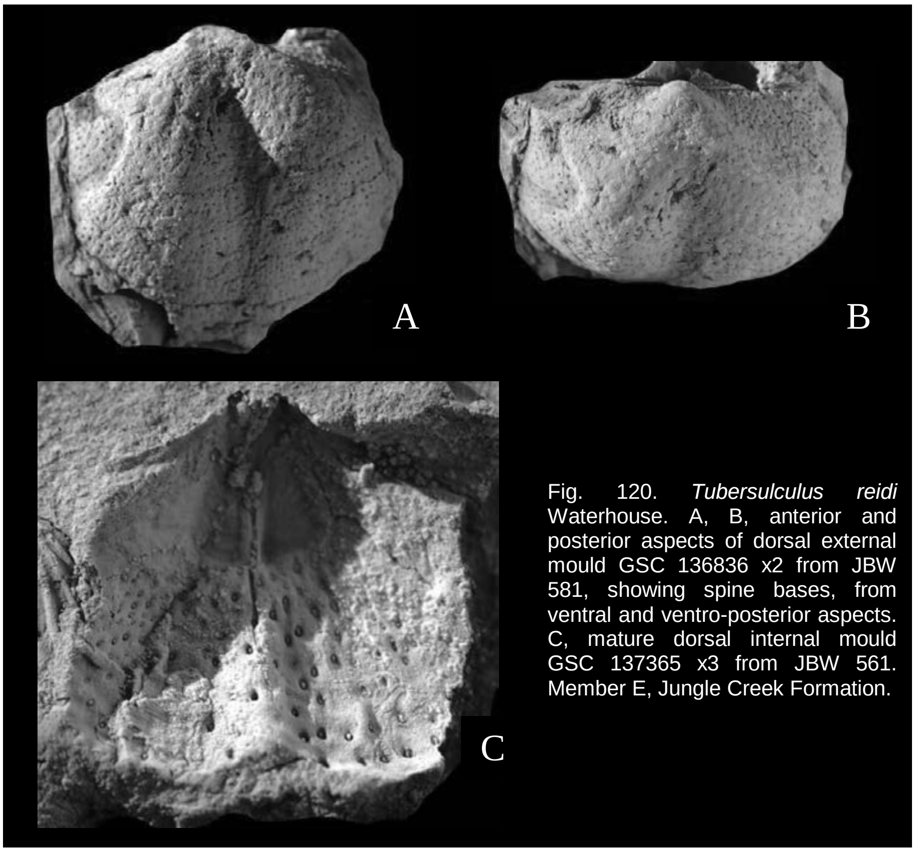


Fig. 120. *Tubersulculus reidi* Waterhouse. A, B, anterior and posterior aspects of dorsal external mould GSC 136836 x2 from JBW 581, showing spine bases, from ventral and ventro-posterior aspects. C, mature dorsal internal mould GSC 137365 x3 from JBW 561. Member E, Jungle Creek Formation.

Fig. 121. *Tubersulculus reidi* Waterhouse, GSC 137315, internal mould of posterior dorsal valve, with an internal mould of *Echinalosia minuta* n. sp. GSC 137316 to right, x5 from JBW 581, Member E, Jungle Creek Formation.

is slightly younger than *reidi*, being Sakmarian-Artinskian, whereas *reidi* is found in underlying beds and is considered to be upper Asselian in age.

Russian specimens figured as *Productus pseudoaculeatus* Krotow by Tschernyschew (1902, p. 615, pl. 30, fig. 7, pl. 53, fig. 10-12) suggest a sulcus like that of the present species, similar to the ventral valve figured as *pseudoaculeatus* by Kalashnikov (1983, p. 209, pl. 47, fig. 9) from the late Early Permian Talatin Suite of the Petchora Basin. The original specimen figured by Krotow (1888, pl. 1, fig. 8) and further specimens (Stepanov 1934, pl. 3, fig. 1-8) have a more tubiform trail, and are closer to *Tubersulculus maximus* than the present species, and are of Sakmarian age. Figures identified as *pseudoaculeatus* in Gerassimov (1953, pl. 10, fig. 4-8, 10, 18, aff. 13) are poorly reproduced, but suggest a ventral sulcus and tubiform trail, though they are small. *Productus tundrae* Fredericks (1926, p. 87, pl. 3, fig. 7-9) from Sakmarian beds in Kejim-Terovey River, north Urals, has a tubiform trail and more emphasized commarginal rugae.

Avonia oregonensis Cooper (1957, p. 31, pl. 2C, fig. 13-24) from the Coyote Butte Formation of central Oregon shows some similarities, although distinguished by the lack of a sulcus from most ventral valves, and its well developed spine-bases anteriorly suggest *Tuberculatella*. (See p. 63).

Genus ***Krotovia*** Fredericks, 1927 (1928)

Diagnosis: Small thin-disced species, numerous spines arranged in quincunx, with slightly swollen not elongate bases, intervening dimples prominent on dorsal valve, weakly developed marginal ridges and quadrifid cardinal process.

Type species: *Productus spinulosus* Sowerby, 1814, p. 155 from Lower Carboniferous (Asbian) of Fermanagh, Ireland, OD.

Discussion: This genus is very close to *Tubersulculus* Waterhouse, but tends to have no faint radial rugae, rounded rather than often slightly elongate spine bases, no or only very subdued sulcus and fold, and never displays a tubiform trail. The strong similarities in internal features and rather similar spines suggest that *Tubersulculus* evolved from *Krotovia* in the Late Carboniferous, and the progression of species in the Canadian succession strongly supports this thesis. Brunton et al. (1995) referred *Krotovia* to a separate tribe Krotoviini, a tribe difficult to justify as discussed by Waterhouse (2002b, 2013). Brunton et al. (1995) referred *Tubersulculus* to the marginiferid tribe Costispiniferini Muir-Wood & Cooper, 1960 (Waterhouse 2002b, p. 15), but *Tubersulculus* is not marginiferid.

Krotovia norfordi n. sp.

Fig. 122 - 124

cf. 1928: *Krotovia pustulata* [not Keyserling] – Chao, p. 52, pl. 5, fig. 18-20.
cf. 1967 *K. pustulata* [not Keyserling] – Mironova, p. 14, pl. 1, fig. 16, 17.
cf. 1968 *K. pustulata* [not Keyserling] – Sarytcheva, p. 79, pl. 5, fig. 9.
cf. 1980 *K. pustulata* [not Keyserling] – Li Li, Gu Feng, Su Yangzheng, p. 351, pl. 167, fig. 12.

Derivation: Named for Brian Norford.

Diagnosis: Comparatively large and transverse with comparatively close-set spines arising from low tubercles over ventral valve, similar on dorsal valve, with intervening dimples prominent.

Holotype: GSC 136840, here designated.

Material: From Member A, a ventral valve from JBW 75, specimen with valves conjoined and dorsal valve from JBW 122, two ventral valves from JBW 143, one ventral valve each from JBW 181 and 197, two dorsal valves from JBW 677, one ventral valve and a dorsal valve from JBW 593, dorsal valve from JBW 592, two fragmentary ventral valves from JBW 792. Exceptional ventral valve from JBW 448. A dorsal valve from JBW 601 is similar. Two ventral valves, two dorsal valves and one specimen with valves conjoined from JBW 182, Member D.

Stratigraphic and biostratigraphic levels: Members A and D, Jungle Creek Formation. *Septospirifer tatondukensis* Zone, *Rugivestigia commarginalis* Zone.

Description: Specimens transverse, a ventral valve from JBW 593 measuring 27mm wide, 19mm long and 5mm high, ventral umbo broad with angle of 100º, not strongly incurved, and posterior walls low, hinge wide, and maximum width near mid-length, cardinal extremities obtuse. Development of ventral sulcus variable, may be absent or limited to anterior shell, and varying slightly in depth and length. Disc slightly raised above poorly defined ears, and dorsal valve gently concave. Ventral ornament of pustules aligned in commarginal rows, four to six in 5mm along rows, five rows in 5mm anteriorly, giving rise to fine spines; and dorsal spines arise between crowded pits, six in 5mm along rows five or six in 5mm, and on some specimens the pits lie along the interspace between two low commarginal rugae which support the spines.

Visceral disc very thin. Bifid cardinal process, dorsal median septum extends to mid-length, and adductor scars are slightly raised but not well defined. The floor is covered by well spaced pustules separated by numerous very fine dimples.

Resemblances: The comparatively large size and transversely oval shape of this species are also features of *Productus pustulatus* Keyserling, 1853, first described from the Schwagerina Limestone of the Urals. Material was illustrated by Tschernyschew (1902, pl. 30, fig. 1, 2, pl. 53, fig. 5, 6); Gerassimov (1953, pl. 10, fig. 1) from Krasnoufim; Ustritsky (1963, pl. 4, fig. 3-5) from Holodnin Suite, Taimyr; Cooper (1957, pl. 8A, fig. 1-5) and Muir-Wood & Cooper, 1960, p. 386, pl. 50, fig. 6-9) from central Oregon, and from the “*Yakovlevia transversa*” and *Jakutoproductus verchoyanicus* Zones of the Jungle Creek Formation (Shi & Waterhouse, 1996, p. 57, pl. 4, fig. 21-23; Bamber & Waterhouse, 1971, pl. 15, fig. 21, pl. 16, fig. 2). Additional material has been described from Early Permian of Russia by Grünewaldt (1860, pl. 3, fig. 3), Stepanov (1948, p. 28, pl. 5, fig. 6) and Sarytcheva & Sokolskaya (1952, p. 93, pl. 14). The spines in the Canadian specimens of *norfordi* are distinctly finer and more closely spaced, numbering four to five in 5mm along rows, the number usually four in 5mm towards the middle anterior margin, and so close to specimens listed in the synonymy. By comparison, the spines on ventral valves described and figured by Tschernyschew (1902) and Cooper (1957) from Early Permian faunas number some three in 5mm, along rows that number three in 5mm. Mironova (1967, pl. 1, fig. 16, 17) recorded material from the Late (C3) Carboniferous Zilim Suite in the Urals of Bashkiria with spines close in density to those of the present suite, and allied material was described by Sarytcheva (1968, p. 79, pl. 5, fig. 9), from the Keregetass Suite of PreBalkhash. From China, specimens figured by Chao (1928) and Li, Gu & Su (1980) have moderately comparable fine spines.

As noted above, *Krotovia pustulata* was recorded from the “*Yakovlevia transversa*” and *Jakutoproductus verchoyanicus* Zones of the Jungle Creek Formation (Shi & Waterhouse 1996). The spines are a little coarser in those specimens, three to four in 5mm, but the sample was small. The taxon *pustulata* stands as a highly distinctive large and transverse form that varies a little in density of spines. It ranges through Russia, North America and China (Li et al. 1980). A single valve figured by Grabau (1936, pl. 14, fig. 4a-c) has some four spines in 5mm, but has acute cardinal extremities, unlike the obtuse extremities typical of *pustula* and the present species. Specimens ascribed to

Avonia pustulata of Einor (1946, p. 32, pl. 5, fig. 3-6) and Ustritsky & Chernyak (1963, p. 74, pl. 4, fig. 5, 6) from the Holodnin Suite (Zavodowsky 1960) look closer to *K. wallaciana* (Derby), being less transverse with fewer spines. Specimens from the Paren Suite (Kasimovian) of northeast Russia figured as *pustulata* by Zavodowsky (1970, pl. 26, fig. 10, 11) are transverse with comparatively strong commarginal lamellae, and a specimen from the Burgali fauna (Zavodowsky 1970, pl. 12, fig. 4) is similar with well spaced spines and pits.

A Mongolian specimen figured by Li Li & Gu Feng (1976, pl. 140, fig. 12) is too obscure to identify from the figure, and specimens from west Taimyr (Einor 1946, pl. 5, fig. 3-6) appear to have elongate spine bases. In recording the species from the basal Permian of Laos, Mansuy (1913, pl. 2, fig. 8) also compared a specimen to the species, but first hand examination seems advisable, although the specimen looks close. The various reports indicate specimens that are close to each other in shape, size and ornament, and close inspection of the specimens

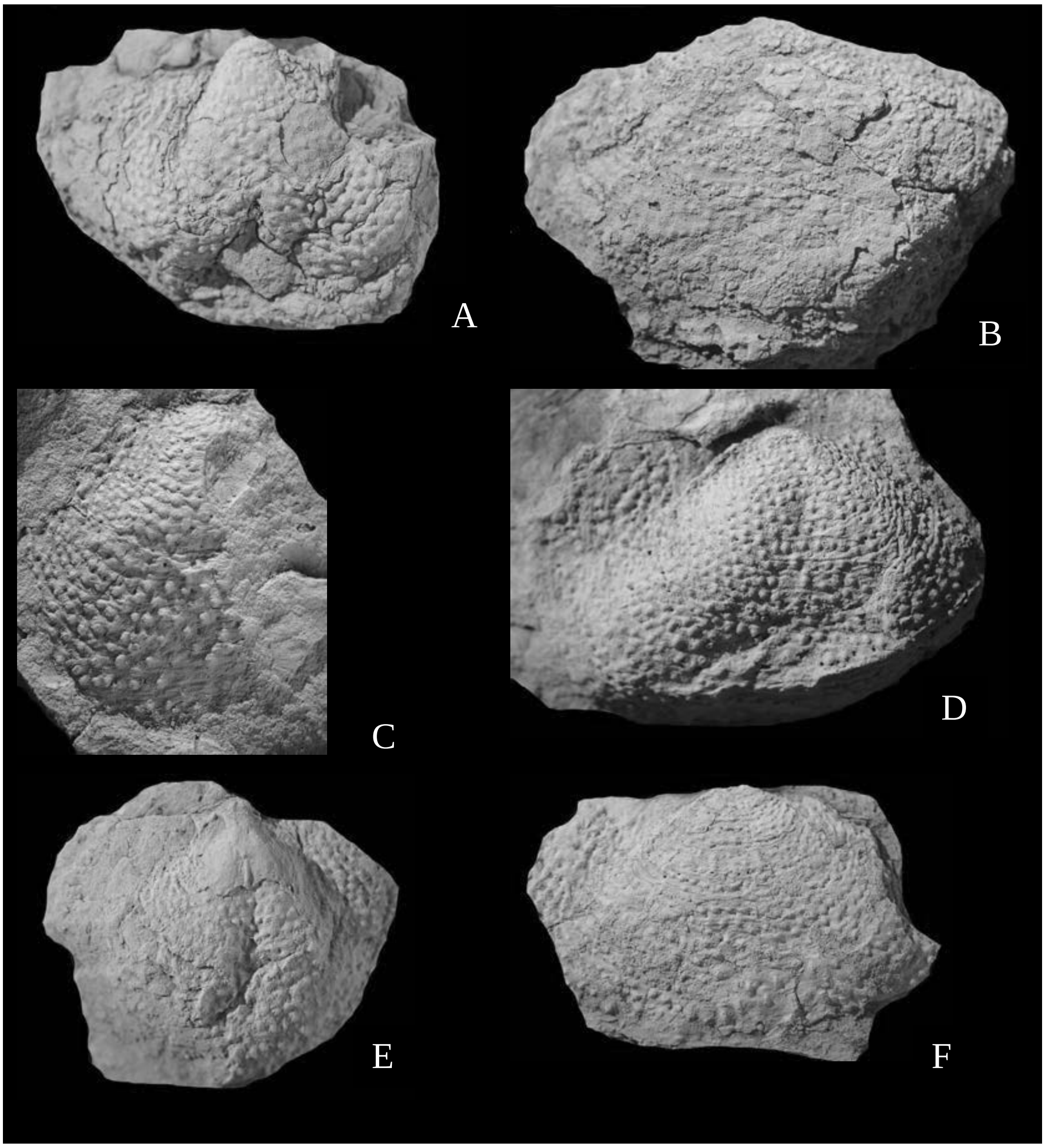


Fig. 122. *Krotovia norfordi* n. sp. A, ventral valve GSC 136839 x2 from JBW 593. B, ventral valve holotype, GSC 136840 x1.5 from JBW 122. C, external mould of dorsal valve GSC 136841 x2 from JBW 677. D, ventral valve GSC 136842 x2 from JBW 593. E, ventral valve GSC 136844 x2 from JBW 197. F, external mould of dorsal valve GSC 136843 x2 from JBW 593. Member A, Jungle Creek Formation.

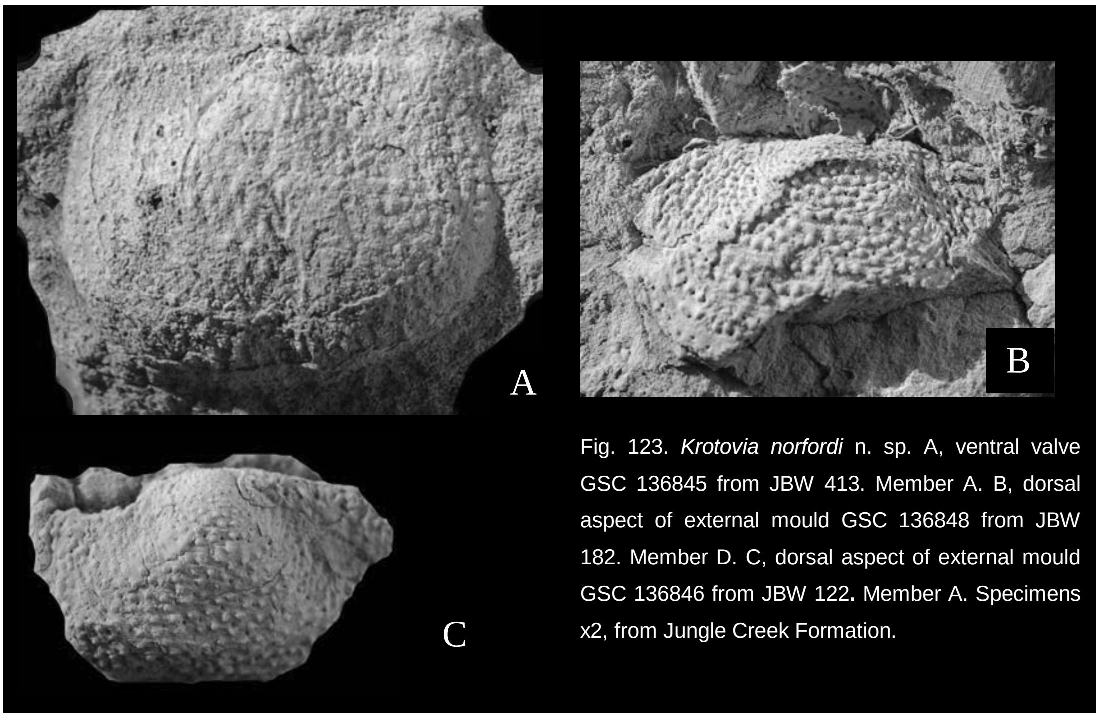


Fig. 123. *Krotovia norfordi* n. sp. A, ventral valve GSC 136845 from JBW 413. Member A. B, dorsal aspect of external mould GSC 136848 from JBW 182. Member D. C, dorsal aspect of external mould GSC 136846 from JBW 122**.** Member A. Specimens x2, from Jungle Creek Formation.

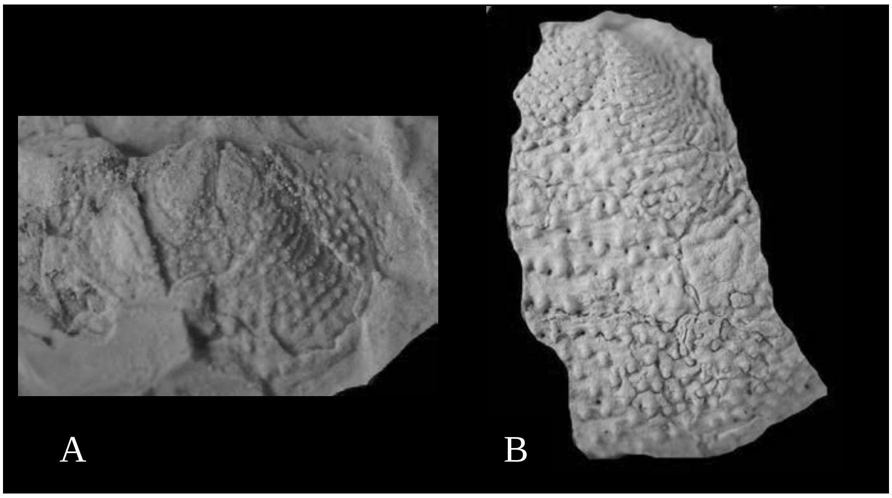


Fig. 124. *Krotovia norfordi* n. sp. A, cast of ventral valve GSC 137257 from JBW 182. B, dorsal aspect of external mould showing spine bases as round black holes, between pits (shown as rises in the mould), GSC 137259 from JBW 592. Specimens x2 from Member A, Jungle Creek Formation.

is required to determine whether several species are involved, or whether there was one widespread species.

Productus (*Avonia*?) *multituberculatus* Janischewsky (1918, p. 54, pl. 8, fig. 25-30, 33, 34) from the Early Carboniferous of Russia is also close in shape with denser and finer spines, as also figured by Gladchenko (1955) and Volgin & Kushnar (1975).

Krotovia wallaciana (Derby, 1874)

Fig. 125 - 127

1874 *Productus wallacianus* Derby, p. 78, pl. 3, fig. 46-48, pl. 6, fig. 5.
1902 *P. wallacei* (sic) – Tschernyschew, p. 270, pl. 30, fig. 8, pl. 60, fig. 19-23.
1903 *P. wallacianus* – Katzer, pl. 6, fig. 1.
1911 *P*. cf. *wallacei* (sic) – Holtedahl, p. 31, pl. 5, fig. 14.
?1917 *P. wallacianus* – Grönwall, p. 583, pl. 29, fig. 1, 2 (part).
1934 *P*. (*Krotovia*) *wallacianus* – Stepanov, p. 31, pl. 3, fig. 8-11.
1938 *P.* (*Avonia*) *wallacei* (sic) – Kulikov, p. 157, pl. 2, fig. 5, 6.
1938 *Strophalosia cornelliana* (not Derby) – Duarte, p. 27, pl. 5, fig. 6, 7.
1959 *Krotovia wallaceiana* (sic) – Mendes, p. 73, pl. 4, fig. 1a-d, text-fig. 29.
1960 *K. wallacianus* – Muir-Wood & Cooper, p. 188, pl. 50, fig. 10, 11.
1964 *K*. cf. *wallacei* (Tschernyschew) [sic] – Gobbett, p. 60.
1969 *K*. *wallaciana* – Czarniecki, p. 275, pl. 5, fig. 1-4.

Diagnosis: Small subrounded shells with moderately prominent umbo and fine to median spines.

Type: The repository of Derby's collection is not certain. Hypotypes were figured by Muir-Wood & Cooper (1960) and are kept at the Smithsonian Institution, Washington DC.

Material: From Member A, single ventral valves from JBW 166, 170, 199, 607, 609, 801, 781?, 792 and 899, five ventral valves and four dorsal valves from JBW 108, a specimen with valves conjoined from JBW 184, possible dorsal valve from JBW 184, and ventral valve from JBW 899. Worn and poorly preserved ventral valves from JBW 59, 73 and 444 and four ventral valves from JBW 535 of Member D. Two possible ventral valves from JBW 707 and silicified material from JBW 999 in upper Ettrain Formation.

Stratigraphic and biostratigraphic levels: Member A and possibly Member D, Jungle Creek Formation. *Septospirifer tatondukensis* Zone and possibly *Rugivestigia commarginalis* Zone. Ettrain Formation.

Description: Ventral valve from JBW 899 highly arched, 20mm wide, 17mm long and 8mm high, and the specimen from JBW 792 is 19mm wide, 18mm long and 8mm high. A silicified specimen is 16mm wide, 14.5mm long, and 5.2mm high. Umbo broad, moderately incurved, angle 95º, posterior walls steeply convex but low, curve out slightly to sides, hinge moderately wide, cardinal extremities obtuse, maximum width at mid-length. No sulcus, but convexity slightly reduced medianly. Ornamentation of small spinose pustules, three in 5mm posteriorly and five in 5mm anteriorly, along rows, about four in 5mm medianly over ventral valve, spines tend to be finer and more closely spaced near anterior margin, low lamellar growth stops. The dorsal valve is concave and shows evenly spaced dimples in quincunx, but dimples are less prominent than in the transverse species *Krotovia pustulata* and *K. norfordi*, and spines occur usually in commarginal rows, and in some specimens between the dimples, and in other specimens along rows between rows of dimples, with which they alternate. Spines number six to seven over mid-valve in 5mm. Small pointed pustules lie over much of the ventral interior in specimen from JBW 792. The internal mould from JBW 196 shows elongate smooth subrectangular adductor scars separated by low myophragm for full

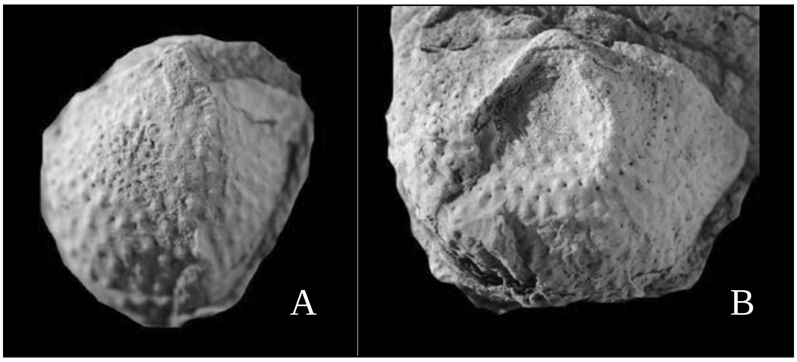


Fig. 125. *Krotovia wallaciana* (Derby). A, dorsal valve external mould GSC 136849. B, dorsal external mould GSC 136850. Specimens x3 from JBW 108. Member A, Jungle Creek Formation.

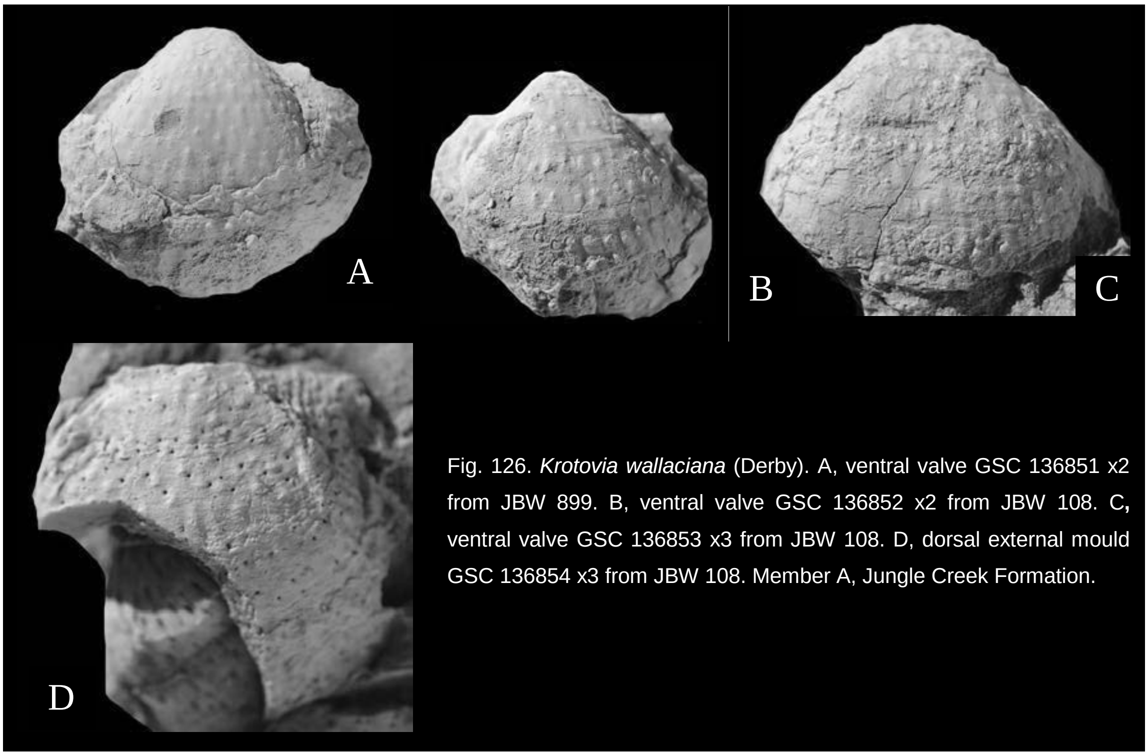


Fig. 126. *Krotovia wallaciana* (Derby). A, ventral valve GSC 136851 x2 from JBW 899. B, ventral valve GSC 136852 x2 from JBW 108. C, ventral valve GSC 136853 x3 from JBW 108. D, dorsal external mould GSC 136854 x3 from JBW 108. Member A, Jungle Creek Formation.

length, and shallow rounded diductor impressions with weak grooves parallel to the anterior margin. Fine pustules are found over much of the floor, with a few narrow ridges medianly, and signs of spines opening into the interior.

Ventral valves from JBW 59 and 444 of Member D are somewhat similar in shape, but ornament is not well preserved.

Resemblances: Treskelloden specimens figured as *Krotovia wallaciana* (Derby) by Czarniecki (1969, p. 275, pl. 3, fig. 1-4) are close in shape and ventral spines. The original material (Derby 1874, pl. 3, fig. 46, 47, 48, pl. 6, fig. 5) from Itaituba, Brazil, with further contributions from Katzer (1903), Duarte (1938) and Mendes (1959), is similar but slightly more rounded and transverse than the Canadian material, and specimens from the same area that were figured by Muir-Wood & Cooper (1960, pl. 50, fig. 10, 11) are close but more transverse with broader umbo and widely diverging umbonal walls, and larger spine bases. On the other hand, Schwagerina-Kalk specimens figured by Tschernyschew (1902, pl. 30, fig. 8, pl. 60, fig. 19-23) are like the present form. Gerassimov (1953, pl. 10, fig. 14, 15) also compared specimens to *wallacei* = *wallaciana,* but unfortunately the figures are very poorly reproduced.

Fig. 127. *Krotovia wallaciana* (Derby), dorsal valve exposed below part of ventral valve, GSC 136731 x3 from JBW 184. Member A. Jungle Creek Formation.

Gobbett (1964, p. 60) reported the species from the Scheteligfjellt Beds and Passage Beds (Minkinfjellet Formation with part of Ebbadalen Formation – Moscovian, early Kasimovian) of Svalbard, and from the Ambigua Limestone (Kapp Käre Formation of Bashkirian. – Moscovian age) of Bjørnøya. Gobbett ascribed the species to Tschernyschew, not Derby. The shape and other aspects suggest derivation from *Krotovia spinulosa* (Sowerby) as reviewed by Brunton (1966, p. 224), of Early Carboniferous age, and widely reported from Europe and Russia, but the posterior walls are longer and spines slightly fewer and coarser in the present species. A ventral valve figured from the "Upper Uralian" of the Karakorum Mountains by Renz in Visser & Visser-Hooft (1940, pl. 4, fig. 11a, b) is close in shape and size, but spines are spaced further apart.

There is some similarity in shape to *Krotovia licharewi* (Frebold, 1942, pl. 3, fig. 7-9), also described by Gobbett (1964, pl. 3, fig. 1-10) from the middle Brachiopod Chert (upper Cape Starosin Formation) of Svalbard, but spines are finer on this species.

Many specimens from Russia that are close in size, shape and ornament have been referred to *Krotovia pseudoaculeata* (not Krotow 1888, pl. 1, fig. 18). Examples are provided by Solomina (1960, pl. 1, fig. 1-3), Sarytcheva (1968, pl. 5, fig. 10-13, fig. 21-23) and Kulikov (1974, pl. 2, fig. 3) from Late Carboniferous of Russia, and reports range widely through the Early Permian, including the Kokpecten Suite of Kazakhstan. Type *pseudoaculeata* is regarded as a member of *Tubersulculus* (see p. 152).

Krotovia sp. A

Fig. 128A, B

Material: Three ventral valves from JBW 449, single dorsal valves from JBW 122 and 677. Single ventral valves from JBW 170 and 196.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimens are elongate and convex with incurved ventral umbo, long posterior umbonal walls diverging at 80^o and well spaced but slender erect spines, numbering five in 5mm over mid-valve and seven to nine in 5mm anteriorly. Ventral adductor scars are large and smooth with dividing myophragm. They are moderately close to *Krotovia* sp. B (see below), but have more extended umbonal walls and much coarer spines. One specimen is 11.5mm wide 9.5mm long and 5.3mm high.

Resemblances: There is some approach to *Krotovia tareiaensis* Ustritsky (1963, p. 75, pl. 4, fig. 4a, b) in shape, but ornament is poorly shown on the Russian species. It comes from the Late Carboniferous (Bashkirian) Makarov Suite of Taimyr, north Russia.

Krotovia sp. B

Fig. 128C, D, 129

Material: Two ventral valves from JBW 780, Member A, and one ventral valve and specimen with valves conjoined from JBW 80, Member D.

Stratigraphic and biostratigraphic levels: Members A and D, Jungle Creek Formation. *Septospirifer tatondukensis* and *Rugivestigia commarginalis* Zones.

Description: Specimens are elongate and convex with incurved ventral umbo, long posterior umbonal walls diverging at 60-70^o and persisting well forward and crowded slender erect spines, numbering three to usually five in 1mm.

They are moderately close to *Krotovia* sp. C but have more extended umbonal walls. GSC 136856 is 9.5mm long and wide.

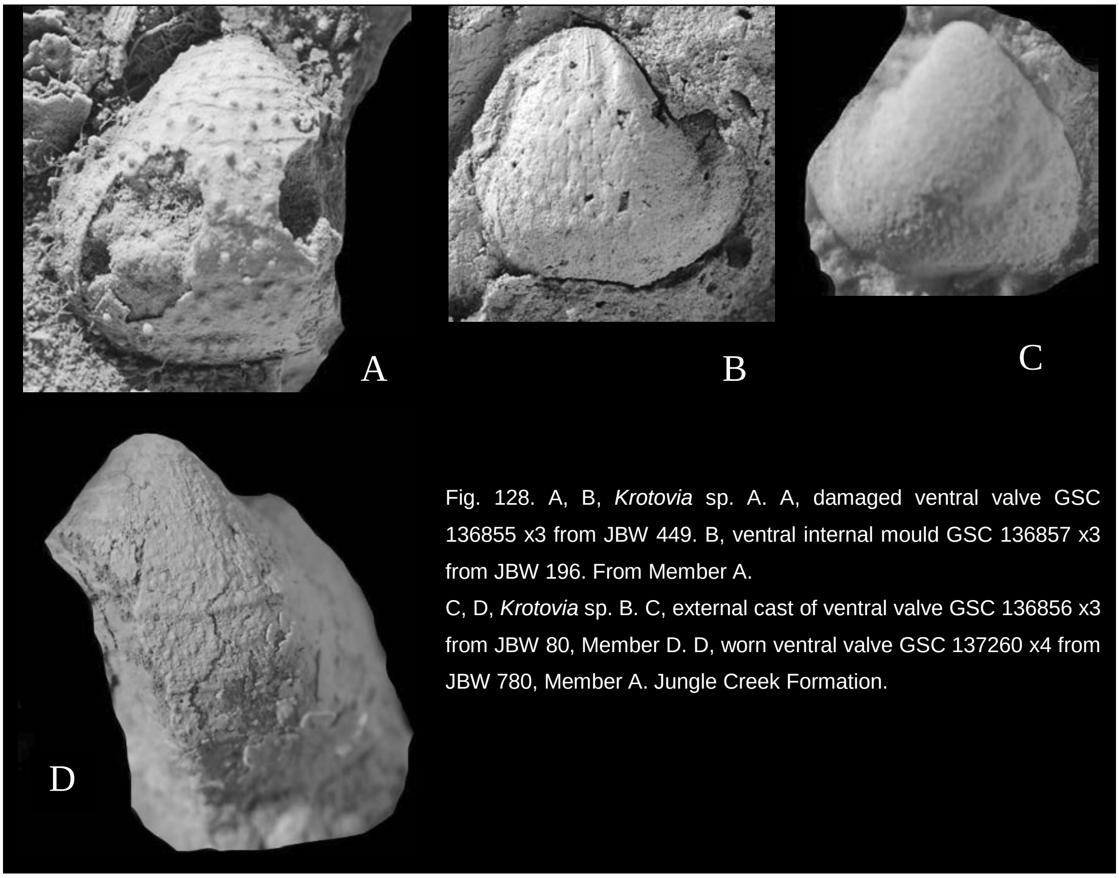


Fig. 128. A, B, *Krotovia* sp. A. A, damaged ventral valve GSC 136855 x3 from JBW 449. B, ventral internal mould GSC 136857 x3 from JBW 196. From Member A.
C, D, *Krotovia* sp. B. C, external cast of ventral valve GSC 136856 x3 from JBW 80, Member D. D, worn ventral valve GSC 137260 x4 from JBW 780, Member A. Jungle Creek Formation.

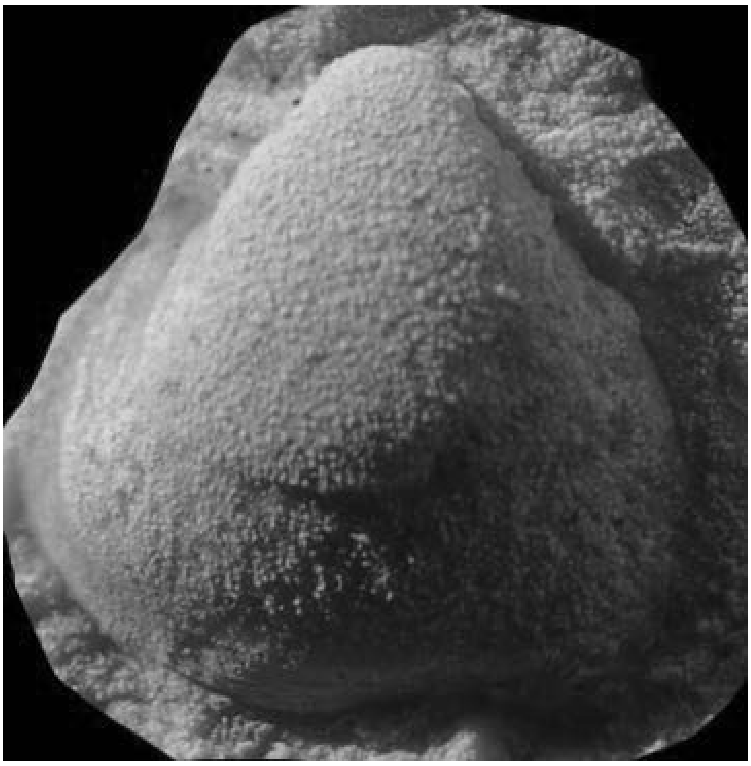


Fig. 129. *Krotovia* sp. B. external cast of ventral valve GSC 136856 x7 from JBW 80, enlarged to show tiny spines over entire shell. Member D, Jungle Creek Formation.

Krotovia cf. ***parva*** Cooper, 1957

Fig. 130

cf. 1957 *Krotovia parva* Cooper, p. 33, pl. 2B, fig. 5-12.

Diagnosis: Small transverse shells without sulcus or fold, spines crowded and arising from small pustules.

Holotype: USNM 125355a figured by Cooper (1957, pl. 2B, Fig. 5-7) from Coyote Butte Formation (Asselian? – Sakmarian), United States.

Material: A ventral valve from JBW 448.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: The specimen measures 26mm in width, 21mm in length and 9mm in height. It lacks a sulcus and has dense spines numbering two in 1.5mm and becoming finer anteriorly at three to four in 1mm. Cardinal extremities are abruptly acute at approximately 80°.

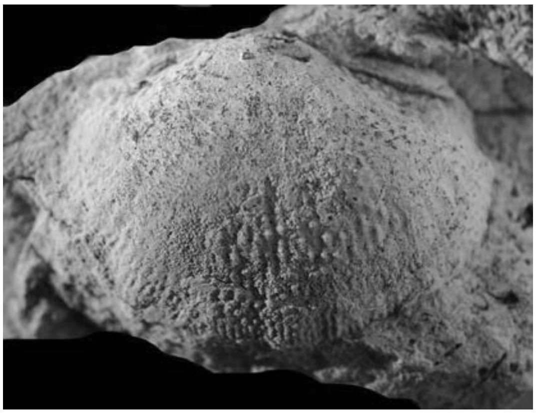


Fig. 130. *Krotovia* cf. *parva* Cooper, ventral valve, GSC 136847 x3 from JBW 448. Member A, Jungle Creek Formation.

Resemblances: This specimen is close in several respects to the suite of species described as *Krotovia parva* by Cooper (1957). The Oregon species is barely half the size, and has much finer denser spines than over much of the present shell, but the anterior spines on the Canadian specimen are similarly fine. The Oregon specimens are especially Sakmarian, perhaps Asselian, whereas the present specimen is rated as Gzhelian.

Krotovia sp. C

Fig. 131

Material: Seven ventral valves valves from JBW 535.

Stratigraphic and biostratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Diagnosis: Small weakly transverse shells with numerous spines which may have slightly swollen bases over the ventral valve.

Description: Shells small and weakly transverse, with umbonal angle 85-95°, and obtuse cardinal extremities, the umbonal walls rising above comparatively large ears, and a weak occasionally erratic sulcus lying over mid-valve, commencing in front of the sulcus and not reaching the trail. Ventral spines fine, numbering four to five in 5mm along a row close to the anterior margin, bases often slightly swollen and may be anteriorly prolonged. Ventral muscle field well defined, lacrimate, with narrow median groove bordered by narrow ridge each side. A marginal ridge lies around the anterior shell, moderately high across the ears.

Resemblances: The specimens are distinguished by their subequilateral shape and by their spines which are coarser than those of most other Jungle Creek species, and which tend to have slightly swollen bases.

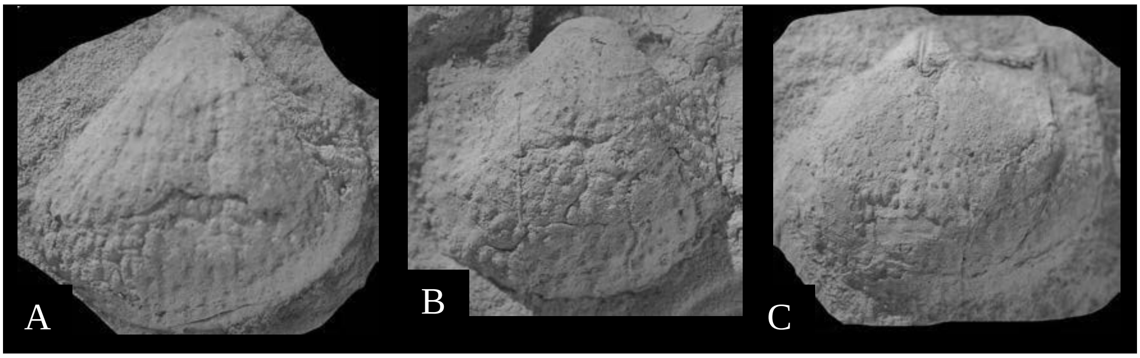


Fig. 131. *Krotovia* sp. C. A, cast of external ventral valve GSC 136858. B, cast of external ventral valve GSC 136859. C, cast of worn external ventral valve showing adductor scars, GSC 136860. Specimens x2, from JBW 535, Member D, Jungle Creek Formation.

Krotovia **sp. D**

Fig. 132

Material: Three specimens, two from JBW 580, two possible dorsal valves and one ventral valve from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: The ventral valve from JBW 580 is an external mould, 7mm wide and 7.5mm long, with fine spines numbering six in 5mm near the anterior margin, and no sulcus. A ventral valve from JBW 581 is an internal mould, 13.5mm wide, 12.5mm long and 6mm high, rounded in outline with arched venter and no sulcus. The adductor scars are small, smooth and posteriorly placed, and the diductors small and faintly impressed. The floor of the valve is marked by pits.

Resemblances: These specimens are narrow or subequidimensional with rounded outline, unlike the large and transverse specimens named as *Krotovia norfordi* n. sp. from Member A and rarely Member D in the lower Jungle Creek Formation, or the coarsely spinose specimens ascribed by Shi & Waterhouse (1996) to *Krotovia pustulata* (Keyserling) from the "*Yakovlevia transversa*" and *Jakutoproductus verchoyanicus* Zones in the overlying faunas of the Jungle Creek Formation. They are close in shape to *Krotovia wallaciana* (Derby) as described from the *Septospirifer tatondukensis* Zone, but have finer spines. In many respects the material comes close to *Krotovia* sp. A from Member A at the base of the Jungle Creek Formation, but has shorter posterior walls and less prominent ventral umbo. Some aspects of shape, inflation, and fine spines suggest an approach to *Krotovia* aff. *K. barenzi* (Miloradovich, 1935, pl. 5, fig. 12) as figured from the Early Permian of Oregon by Cooper (1957, p. 32, pl. 10C, fig. 12-17), but the Oregon specimens are less triangular in shape and have a more arched venter. The shape also approaches that of *Productus curvirostris* Schellwien (1892, pl. 3, fig. 12-14) from the Carnian Alps, but this species has comparatively few spines.

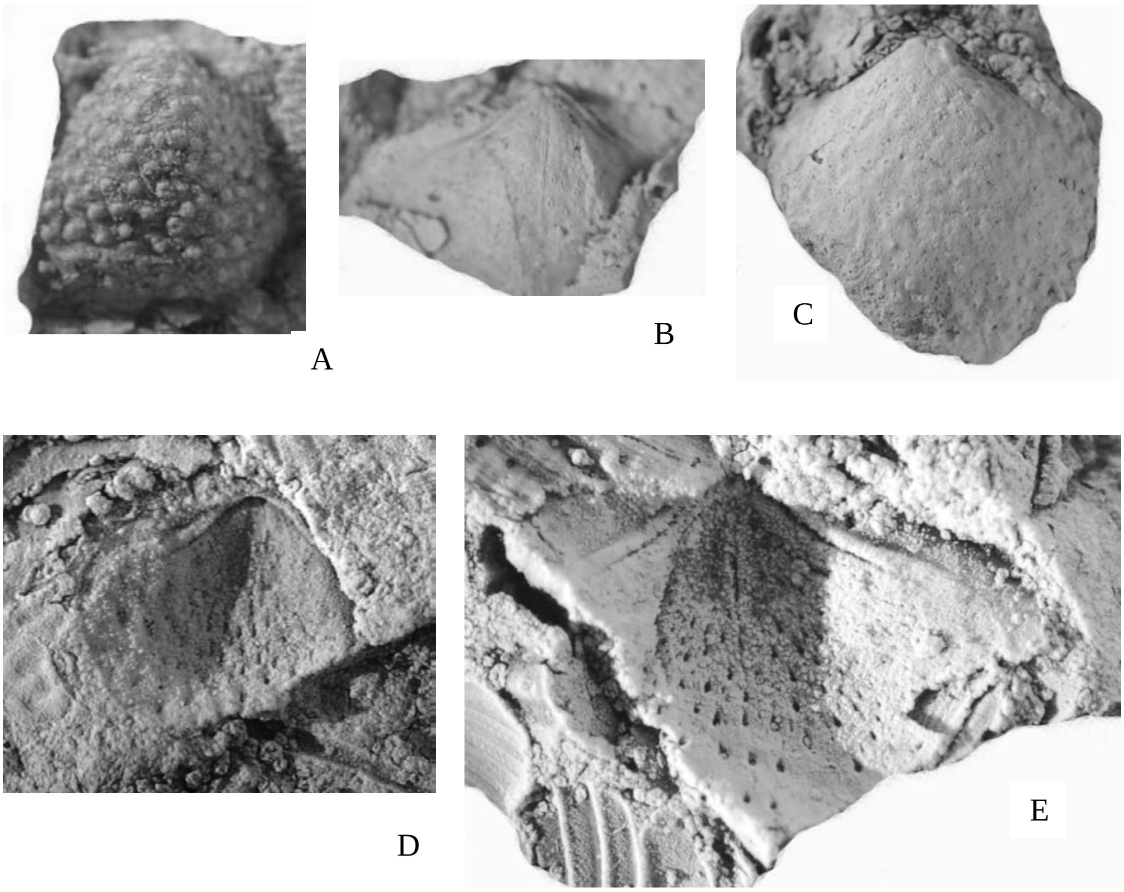


Fig. 132. *Krotovia* sp. D. A, cast of external ventral valve, GSC 136861 x4 from JBW 581. B, E, cast and mould of internal dorsal valve, GSC 137368 x3, x5. C, external mould of dorsal valve, GSC 136862 x3. D, internal mould of dorsal valve GSC 136788 x4. Specimens from JBW 581. Member E, Jungle Creek Formation.

Family **WAAGENOCONCHIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 1978, p. 21 ex Waagenoconchinae Muir-Wood & Cooper, 1960, p. 252].

Diagnosis: Spines may vary in size, but are subuniform over different parts of the shell, associated in broad bands, rather than numerous repeated patterns of commargons. Spines dense and uniform on dorsal valve. Cardinal process with high shaft.

Discussion: The family group was downgraded to a tribe by Brunton et al. (2000), but its ornament differs considerably from Echinoconchidae in lacking commargons with differentiated spines. Furthermore the source may have been different, stemming from *Praewaagenoconcha* of Caucasiproductinae through Sentosiinae, whereas Echinoconchidae may have arisen from *Praelaminatia* and *Laminatia*, and although the two groups seem likely to have shared a common ancestry within Sentosiidae (Waterhouse 2013), Waagenoconchidae is closer to Sentosiidae in morphology.

Subfamily **WAAGENOCONCHINAE** Muir-Wood & Cooper, 1960

[Waagenoconchinae Muir-Wood & Cooper, 1960, p. 252].

Diagnosis: Spines fine, suberect to erect, may vary in size but crowded and subuniform over different parts of the shell and not associated in repeated patterns over commarginal bands, ie. commargons. Cardinal process without buttress supports.

Discussion: The sister subfamily is Pustulinae Waterhouse, 1981.

Tribe **WAAGENOCONCHINI** Muir-Wood & Cooper, 1960

[Nom. transl. Brunton, Lazarev & Grant 1995, p. 929 ex Waagenoconchinae Muir-Wood & Cooper, 1960, p. 252].

Diagnosis: Spines fine, suberect to erect, may vary in size but crowded and subuniform over different parts of the shell. Dorsal disc subplanar, curving into short trail.

Discussion: The sister tribe is Wimanoconchini Waterhouse, 2013 (see p. 167).

Genus ***Waagenoconcha*** Chao, 1927a

Diagnosis: Umbonal region of ventral valve bearing slender spines with elongate bases, spines more erect and in bands larger than commargons anteriorly, mostly of uniform diameter. Dorsal spines erect.

Type species: *Productus humboldti* d'Orbigny, 1842, p. 54 from Copacabana Group, Early Permian of Bolivia, OD.

Discussion: *Contraspina* Waterhouse, 2002b, p. 46, type species *Productus purdoni* Davidson, 1862, p. 31 has fine close-set spines with short bases over the umbonal region of the ventral valve and the spine bases become more elongate anteriorly, then change to being very small. *Fostericoncha* Waterhouse, 2002b, p. 48, type species *Waagenoconcha gigantea* Waterhouse, 1983a has wide ears, strong dorsal fold and ventral sulcus, and coarse spines postero-laterally. *W*. (*Gruntoconcha*) Angiolini 1995, p. 106 was proposed for *W*. (*G*.) *macrotuberculata* Angiolini, and is characterized by comparatively stout ventral spines. It should be considered a full genus. Brunton et al. (2000, p. 517) followed Angiolini (1995) in classing *Productus abichi* Waagen, 1884 in *W.* (*Gruntoconcha*), but this species has spines like those of *Waagenoconcha* according to Noetling (1903). Brunton et al. (2000) also referred to *W.* (*Waagenochocha*), a lapsus calamni. *Glabrispinus* Waterhouse, 2013, p. 196 is based on *Kochiproductus elongatus* Cooper & Grant, 1975, p. 1049 from the Skinner Ranch and Bone Spring Formations of Texas, a large elongate shell with well spaced short spine bases replaced anteriorly by fine spines on the ventral valve, and dorsal valve with fine erect spines.

Waagenoconcha sp.

Fig. 133

Diagnosis: Subquadrate to subpentagonal transverse shells with shallow anterior sulcus, low wide dorsal anterior fold, low geniculate trail. Ventral spines with slightly elongate bases over entire disc, dorsal spines with shorter bases, rounded over trail. Median dorsal septum long.

Material: Single dorsal valves from JBW 81 and 804, and specimen with valves conjoined from JBW 802 (Member A). Possibly allied dorsal valve from JBW 538 (Member E).

Stratigraphic and biostratigraphic levels: Members A and E?, Jungle Creek Formation. *Septospirifer tatondukensis* Zone and possibly *Ogilviecoelia shii* Zone.

Description: The material is transverse with wide ventral umbo, angle of 110º, shallow ventral sulcus, low and anterior wide dorsal fold. Ventral spines over the disc have elongate bases, usually 2mm long, up to 3mm long anterior wide dorsal fold. Ventral spines over the disc have elongate bases, usually 2mm long, rarely up to 3mm long; dorsal spines with less elongate bases over the disc and rounded over the trail. Median dorsal septum about two thirds of the length of the valve, brachial ridges are not visible.

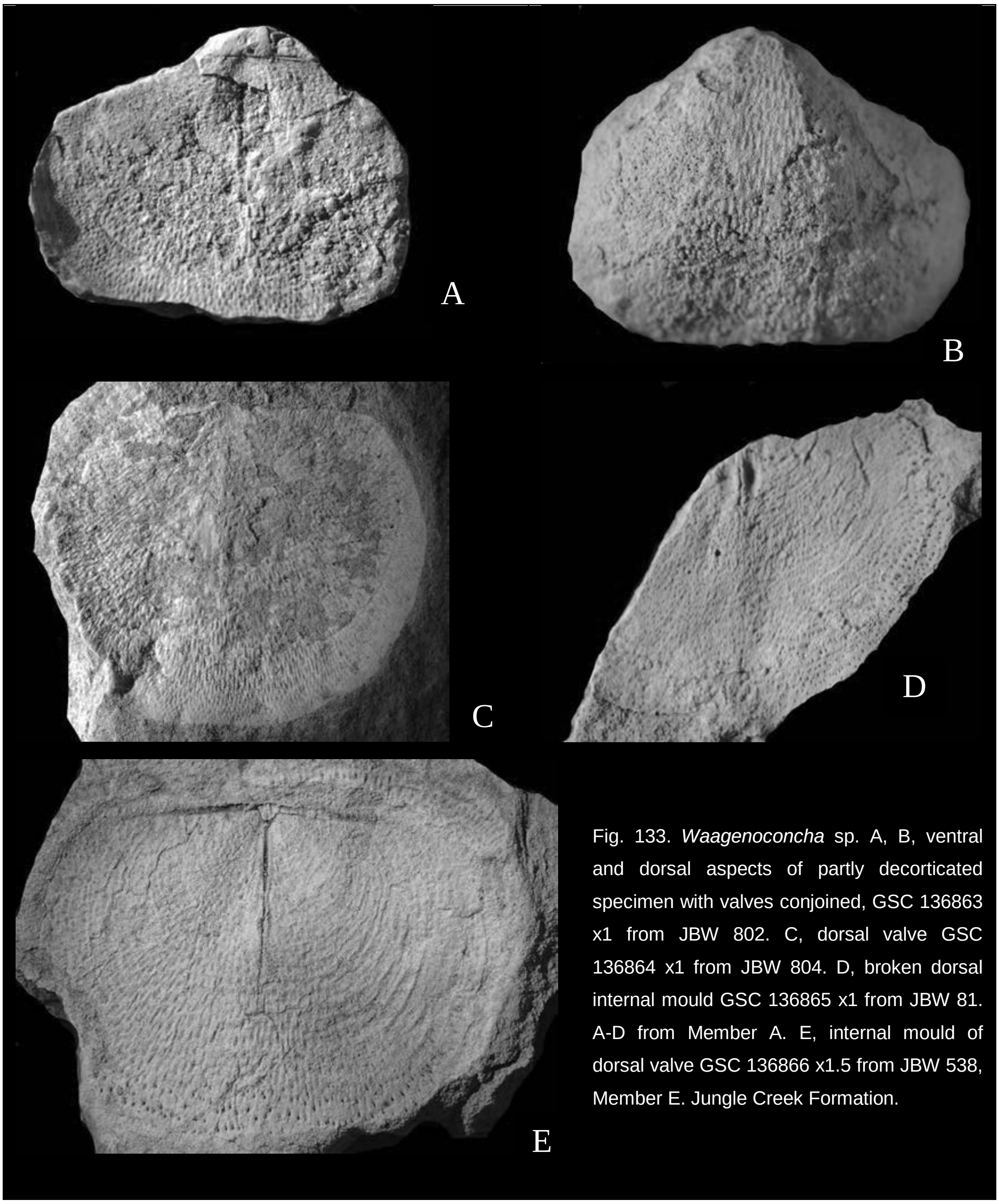


Fig. 133. *Waagenoconcha* sp. A, B, ventral and dorsal aspects of partly decorticated specimen with valves conjoined, GSC 136863 x1 from JBW 802. C, dorsal valve GSC 136864 x1 from JBW 804. D, broken dorsal internal mould GSC 136865 x1 from JBW 81. A-D from Member A. E, internal mould of dorsal valve GSC 136866 x1.5 from JBW 538, Member E. Jungle Creek Formation.

Resemblances: *Waagenoconcha permocarbonica* Ustritsky, 1963, p. 79, pl. 7, fig. 6, pl. 8, fig. 1-3 from the mid-Carboniferous Makarov Horizon of western Taimyr is distinguished by its better defined dorsal fold, and the spine bases over the anterior ventral disc are less elongate. *W. irginae* (Stuckenberg) is very close to the present form, but has a narrower anterior dorsal fold, and may prove to belong to *Balkhasheconcha* (see p. 183).

Waagenoconcha irginaeformis Stepanov, 1937b

Fig. 134, 135

1898 *Productus grunewaldti* [not Krotow] – Stuckenberg, p. 220, pl. 4, fig. 17.
1902 *P. irginae* [not Stuckenberg] – Tschernyschew, pp. 273, 619, pl. 52, fig. 2-4, text-fig. 67, 68 (part, not pl. 52, fig. 1, pl. 30, fig. 3, 4).
1936 *P. irginae* [not Stuckenberg] – Stepanov, p. 120, pl. 3, fig. 3.
1937a *P*. (*Waagenoconcha*) *irginaeformis* Stepanov, pp. 124, 178 (part, not pl. 6, fig. 4, 5).
1939 *P*. (*Pustula*) *irginaeformis* – Licharew, p. 84, pl. 21, fig. 5.
1939 *P*. (*Waagenoconcha*) *irginaeformis* – Licharew & Einor, p. 35, 205, pl. 4, fig. 2-4.
1957 *Waagenoconcha parvispinosa* Cooper, p. 47, pl. 4C, fig. 8-12.
1960 *W. irginae* [not Stuckenberg] – Muir-Wood & Cooper, pl. 89, fig. 15, 16.
1964 *W. irginae* [not Stuckenberg] – Gobbett, p. 76, pl. 5, fig. 7 [part?, not pl. 6, fig. 1-5).
1964 *Waagenoconcha* sp. Gobbett, p. 78, pl. 5, fig. 6.
?1971 *Waagenoconcha* sp. Bamber & Waterhouse, pl. 12, fig. 7.
1996 *W. parvispinosa* – Shi & Waterhouse, p. 77, pl. 9, fig. 1-3.

Diagnosis: Transverse, comparatively flat dorsal disc with median low fold and geniculate trail, shallow ventral sulcus. Spines fine and crowded with very slightly prolonged posterior bases.

Syntypes: Syntypes were indicated by Stepanov (1937a) as those figured by Tschernyschew (1902, pl. 52, fig. 1-4), from lower Cisuralian of Urals, Russia.

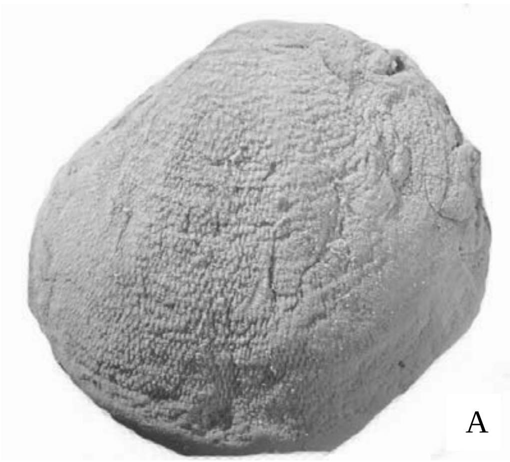
Material: A dorsal valve from JBW 581, and dorsal valve from GSC 56946 (Member E). Specimen with valves conjoined and two ventral valves from JBW 100, and single ventral valves from JBW 83 and 535 (Member D).

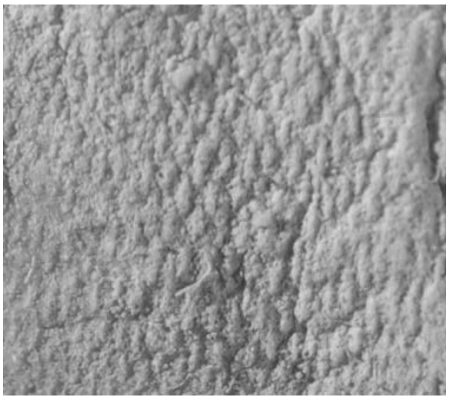
Stratigraphic and biostratigraphic levels: Members D and E, Jungle Creek Formation. *Rugivestigia commarginalis* Zone, *Ogilviecoelia shii* Zone.

Description: The ventral valve has a shallow sulcus and crowded spines bearing short prolonged bases. A dorsal valve from JBW 581 measures 31mm wide, 21.5mm long and 7mm high, with very wide hinge, weakly alate cardinal extremities, flat disc, bearing very low anterior fold, and short geniculate trail. The surface of the shell is densely pustulose and pitted, pits round or weakly elongate in outline, with numerous erect spines: ornament is somewhat finer over the trail. The dorsal valve figured in Bamber & Waterhouse (1971) from GSC 56946 is more transverse.

Resemblances: The shape and size, ornament and trail display the features of the material described from the "*Yakovlevia transversa"* Zone of the Jungle Creek Formation as *Waagenoconcha parvispinosa* Cooper. This species in turn looks to be indistinguishable from the material described by Tschernyschew (1902, pl. 52, fig. 2-4) from the Lower Permian of the Urals. The dorsal fold in one is slightly more elevated, but otherwise is close. The synonymy proferred for these specimens is selective and tentative, to indicate similar-looking species from Late Carboniferous to Early Permian in age. Provisionally the interpretation by Stepanov (1937b) that the material named by Stuckenberg (1898, pl. 2, fig. 16) as *Productus irginae*, together with *Productus grunewaldti* (Stuckenberg, 1898, p. 220, pl. 4, fig. 17) were not the same, and needed to be distinguished together with specimens figured by Tschernyschew (1902, pl. 30, fig. 3, 4, pl. 52, fig. 1). That of Tschernyschew (1902, pl. 30, fig. 3) certainly shows a deeper sulcus, and the dorsal valve in pl. 30, fig. 4 has buttress plates as in *Balkhasheconcha* (see p. 183). Solomina (1960, p. 31) accepted the distinction, whereas it was denied by Gobbett (1964). Adding to the complexity, a number of articles have referred younger Cisuralian and Middle Permian specimens to synonymy, and these certainly look close. But they are provisionally excluded, it being preferred to have detailed comparison before incorporating them in the same taxon. The Spitsbergen material assigned by Stepanov (1937a, pl. 6, fig. 4, 5) to *irginaeformis* is younger. In addition, at least some of the Kazakhstan specimens described by Sarytcheva in Saytcheva (1968) belong to *Balkhasheconcha*, not *Waagenoconcha*. As noted, the Early Permian species from

Oregon, *Waagenoconcha parvispinosa* Cooper, 1957, is tentatively regarded as belonging to the same species, but no internal detail has been provided. Indeed the only certain *Waagenoconcha* within this group is the dorsal valve figured in Shi & Waterhouse (1996, pl. 9, fig. 1). It will be clear that uncertainties remain, but at present, the species is interpreted as being of Late Carboniferous and Early Permian age, and ranging through the Urals into the Arctic of northern Russia and Canada, and extending into Oregon of the United States.





C

Fig. 134. *Waagenoconcha irginaeformis* Stepanov. A, C, cast of shell and micro-ornament detail of ventral exterior, GSC 136867 from JBW 535, x1.5, x5. Member D. B, dorsal external mould GSC 136868 from JBW 581, x1.5. Member E. Jungle Creek Formation.

B

Fig. 135. *Waagenoconcha irginaeformis* Stepanov, external mould of ventral valve GSC 137261 from JBW 83, x1, and detail of micro-ornament, x5. Member D, Jungle Creek Formation.

The dorsal valve from Member E looks very like the dorsal valve from Heibergs Land that was assigned by Tschernyschew & Stepanov (1916a, p. 35, pl. 6, fig. 3) to *Productus irginae* Stuckenberg (1898, p. 20, pl. 2, fig. 16). The specimens figured as *irginae* by Tschernyschew (1902, p. 618, pl. 52, fig. 2-4), and recast as *irginaeformis*, are similar, with low geniculate trail, dense spines on both valves and well defined ventral sulcus and low dorsal fold. Spitsbergen specimens figured from the Spirifer Limestone (now Vøringen Member) by Gobbett (1964, pl. 5, fig. 7, pl. 6, fig. 1-5) are particular close with fine spines and flat dorsal valve but are small with better developed sulcus and low fold. Gobbett (1964, p. 76) provided a detailed but flawed synonymy for this species and its occurrences throughout the Arctic, and his specimen of pl. 6, fig. 5 might prove to have buttress plates, as in Tschernyschew (1902, pl. 30, fig. 4).

Tribe **WIMANOCONCHINI** Waterhouse, 2013

Diagnosis: Usually large, with dorsal valve that is almost flat, varying to gently concave, without externally distinct trail or geniculation, or with only extremely short trail.

Discussion: Genera placed in Waagenoconchini have a dorsal valve that is flat over the disc, and a geniculate to subgeniculate distinct dorsal trail. By contrast, the dorsal valves in genera of Wimanoconchini have a flat or gently concave visceral disc and very short if any trail. *Wimanoconcha* Waterhouse, based on *Ruthenia wimani* Fredericks, 1934 from Middle Permian of Spitsbergen, has a thickened dorsal valve with no external trail. Ventral spines are posteriorly fine with slender elongate bases, and anteriorly the bases are short and broad. *Wimanoconcha* is distinguished by its flat dorsal valve that is thickened into a wedge, and is found in Arctic Permian faunas (Kalashnikov 1986, Grunt 2006a), and reported from Western Australia by Archbold (1993). Brunton et al. (2000, p. 517) synonymized this form with *Waagenoconcha* (which they mis-spelled *Waagenochocha*), by misrepresenting the analysis presented by Archbold (1993). They claimed that Archbold has synonymized the two. In truth and in complete contradiction of their assertions, Archbold (1993) had recognized a number of species in *Wimanoconcha,* which he treated as a subgenus of *Waagenoconcha.* He included *Waagenoconcha imperfecta* Prendergast, 1935 (syn. *W. vagrans* Prendergast, 1943) from the Late Permian of Western Australia, and reported from Late Permian of New Zealand (Waterhouse 1982a) and possibly south Kitakami Mountains of Japan (Tazawa 1974a). Although Archbold (1993) considered that he found criteria different from Waterhouse for distinguished the taxon, he allowed that the dorsal valve did become thickened. He stressed radial crenulations on large ventral valves but that is a feature not rare in large Waagenoconchinae, and the crenulations are not developed in various species now allocated to *Wimanoconcha.* Later Archbold (2002) further endorsed his recognition of *Wimanoconcha* as a full genus, in distinction to the misrepresentations of *Wimanoconcha* in the *Revised Brachiopod Treatise*, and in agreement with Russian assessments of the validity of the genus.

Genus ***Villaconcha*** Waterhouse, 2013

Diagnosis: Large shells with fine and subuniform spines on both valves, dorsal valve almost flat externally apart from low median fold matching shallow ventral sulcus, dorsal trail short.

Type species: *Waagenoconcha magnifica* Cooper & Grant (1975, p. 1044) from mid-Permian of Texas, OD.

Discussion: *Villaconcha* Waterhouse, 2004b, p. 13, type species *Waagenoconcha magnifica* Cooper & Grant (1975, p. 1044) from the Willis Ranch, China Tank and Appel Ranch Members (Word, early Capitanian, or Middle Permian) of Texas, United States, has uniformly fine spines over the ventral valve, with no elongate bases, and no bands of spines with different diameters. The shape is distinctive with wide hinge, and the dorsal valve almost flat, with short trail. *W. prophetica* Cooper & Grant from the Graham Formation (Gzhelian Stage) has slightly elongate spine bases. Unlike *Wimanoconcha*, the dorsal valve of these species is not thickened into a wedge. *Patellamia* Waterhouse is close, but has a gently concave and unthickened dorsal valve that is not flat and lacks an anterior short trail. It appears in that respect to be close to *Quenstedtenia* Waterhouse 2004b, p. 12, type species *Q. rugosa* Waterhouse from the Basleo beds (Wuchiapingian ie. Upper Permian) of Timor. This genus has close-set rugae and growth steps, and elongate spine bases over most of the ventral valve, with erect spines restricted to the posterior shell.

Evidently Wimanoconchini arose from fine-spined waagenoconchids, quite possibly from the species at present under description, given its high paleolatitudinal position, for it appears to be one of the oldest known of a suite of species and genera with comparatively flat dorsal valves, and as a rule, fine spines with short bases.

Villaconcha planiconcha n. sp.

Fig. 136 - 139

Derivation: planus – flat; concha – shell, bivalve, Lat.

Diagnosis: Large gently convex ventral valve with shallow sulcus, dorsal valve almost flat with short geniculate trail, little secondary thickening, ornament of fine dense subuniform spines.

Holotype: GSC 136869, here designated.

Material: Thirteen ventral valves and nine dorsal valves from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Description: Ventral valve large and gently convex, umbo incurved, angle of 80-110º, umbonal walls gently convex, ears poorly differentiated in relatively inflated and elongate specimens, more distinct in transverse shells, but remaining convex, cardinal extremities obtuse. A narrow and shallow sulcus with evenly concave floor extends to the anterior margin, with angle close to 15º. Dorsal valve very gently concave over disc, with very low fold medianly, and curving abruptly into very short trail at 35-60º to disc. Ventral valve covered by dense fine spines with elongate bases, up to fifteen in 5mm posteriorly, six to eight in 5mm anteriorly, bases 1-1.5mm long: lying in semirecumbent rows along commarginal bands with the spines emerging at the end of each row, at least over the lateral shell. Spine-bases up to 2mm long over much of some shells, and spines are erect anteriorly without prolonged bases. Tthe outer surface has been worn to reveal dense and closely spaced pseudopunctae, seemingly more crowded than the spine-bases. The dorsal valve surface is worn, and the shell shows pits over the posterior shell and elongate ridges anteriorly and over the trail. The ventral valve is crossed by well spaced growth-steps, numbering eight or nine on one specimen, and growth steps are preserved around the outer disc on the dorsal valve.

Ventral adductor scars long and diductor scars faintly impressed: neither set well exposed. The ventral shell is thin. Cardinal process elongate and narrow, projecting in the plane of the shell. Dorsal median septum extends two thirds of length of the disc between large slightly raised oval adductor scars; which do not show clear subdivision into posterior and anterior or lateral elements. No antron or buttress plates; brachial impressions weak and cardinal process not exposed. Dorsal hinge thickened, to form low ginglymus, and the shell is slightly thickened overall, but not nearly as much as in *Wimanoconcha*.

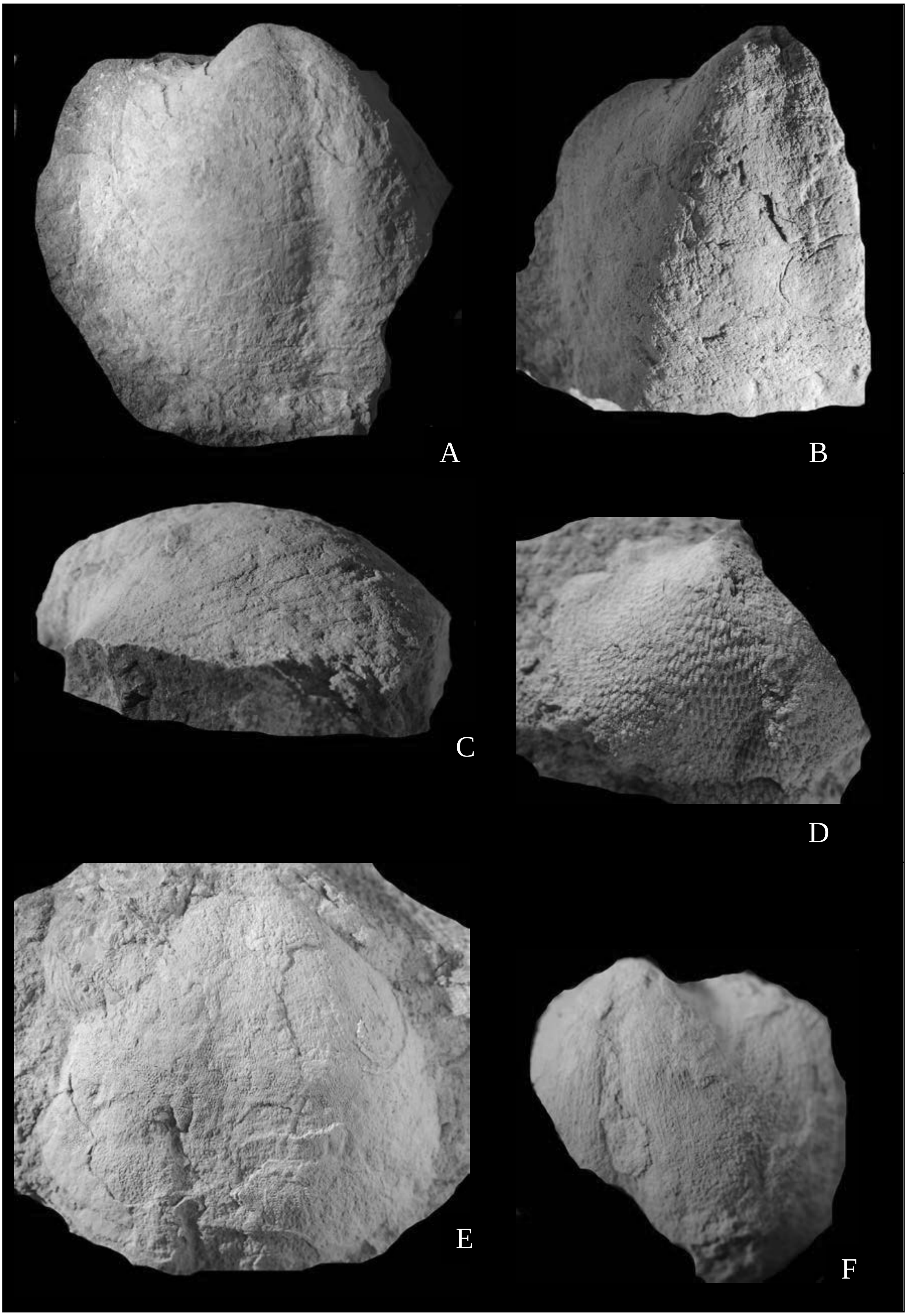


Fig. 136. *Villaconcha planiconcha* n. sp. A, ventral valve GSC 136869 x1. B, C, ventral and lateral aspects of holotype, ventral valve GSC 136871 x1. D, small ventral valve GSC 137347 x2. E, ventral valve GSC 136872 x1. F, ventral valve GSC 136870 x1. JBW 18, Member C, Jungle Creek Formation.

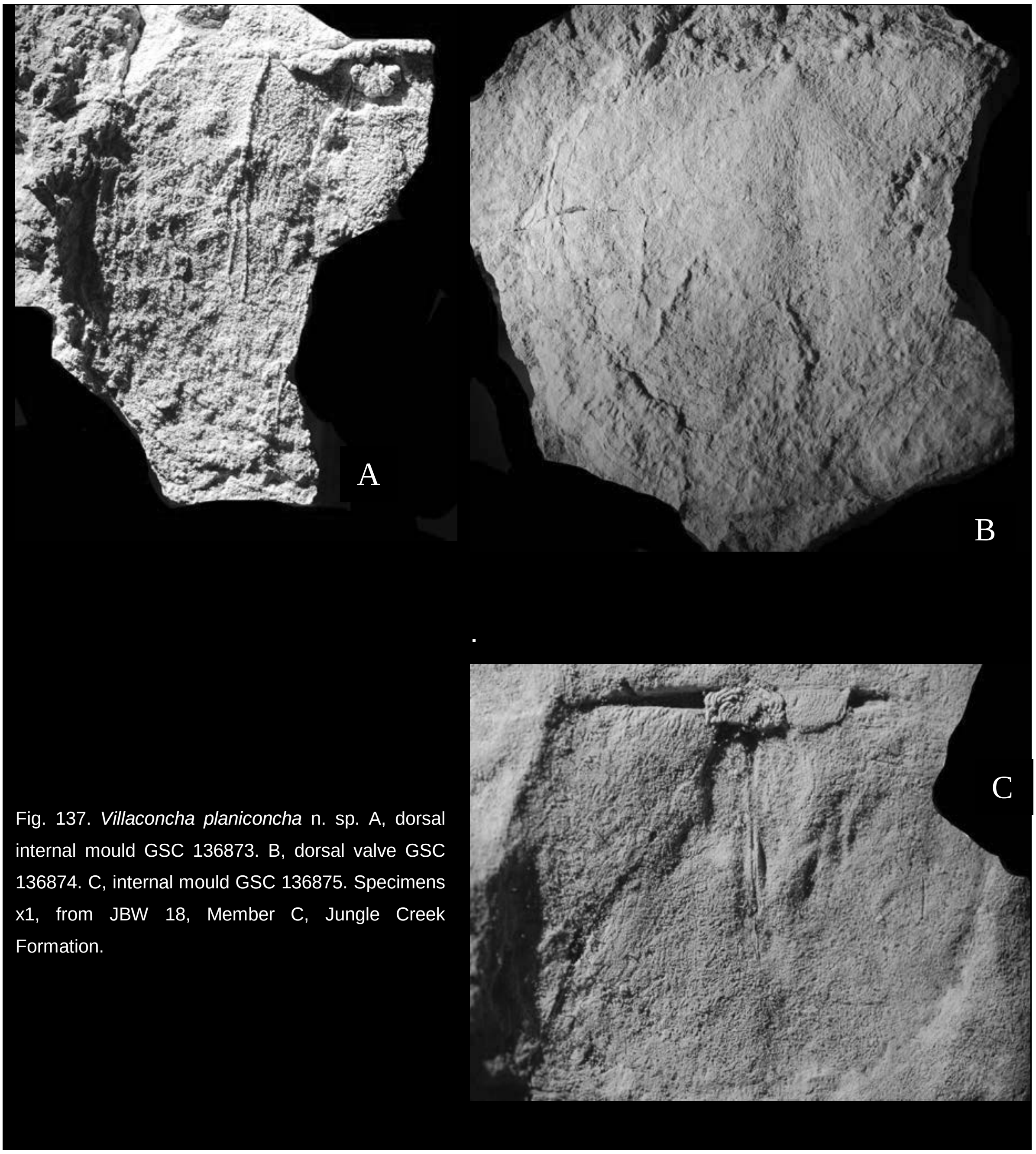


Fig. 137. *Villaconcha planiconcha* n. sp. A, dorsal internal mould GSC 136873. B, dorsal valve GSC 136874. C, internal mould GSC 136875. Specimens x1, from JBW 18, Member C, Jungle Creek Formation.

Resemblances: The species is distinguished by its large size and flat but not wedge-shaped dorsal valve. The ventral valve is highly convex with very shallow median sulcus and ventral spines with short elongate bases, largely in quincunx, succeeded anteriorly by fine erect spines without posteriorly prolonged bases. The dorsal valve is comparatively flat with very short trail, and very fine dorsal spines without elongate bases: the valve is only sightly thickened. Both valves have short growth bands around the anterior shell. No buttress plates are developed. The species is very close to *Wimanoconcha* in its ornament and large flat dorsal valve, but differs in that the dorsal valve is not wedge-shaped or thickening anteriorly, and does have a very short dorsal trail.

From the Word Formation of Texas, *Villaconcha magnifica* (Cooper & Grant 1975, pl. 354, fig. 1-15, pl. 355, fig. 18-24, pl. 356, fig. 7-16) is close in many respects but with more transverse with extended ears. Its spine bases may be slightly elongate, but are usually erect. *V. platys* (Cooper & Grant, 1975, pl. 355, fig. 1-11) from the Road Canyon Fomation is much smaller, but otherwise close in shape, with slightly narrower and deeper anterior dorsal fold, and *V. prophetica* (Cooper & Grant, 1975, pl. 352, fig. 20-23, pl. 355, fig. 12-17) from the Jacksboro Member of the Graham Formation, of Texas is closer to the present species in age, but is small with wider ventral sulcus.

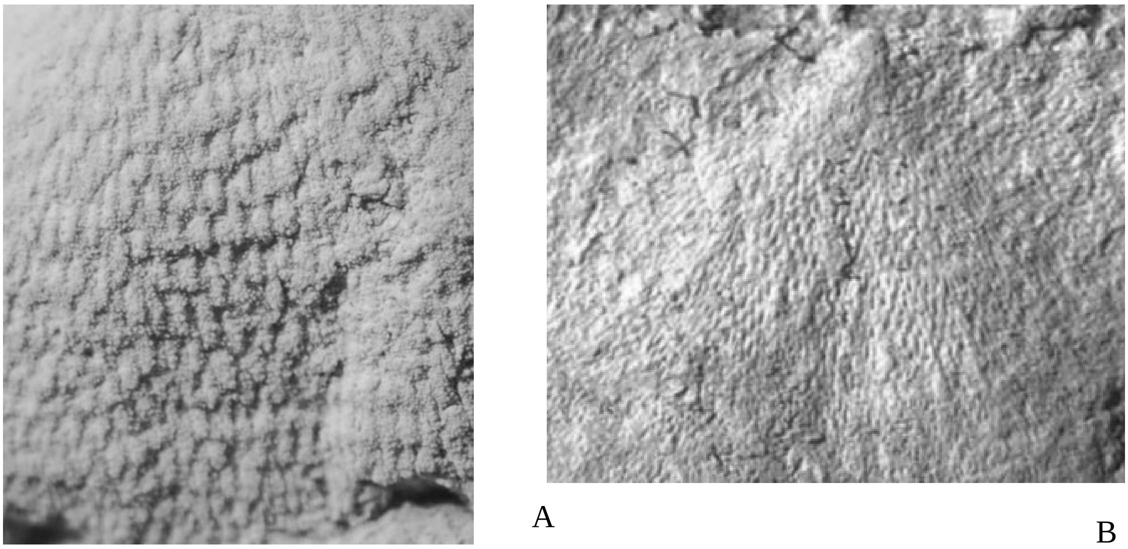


Fig. 138. *Villaconcha planiconcha* n. sp. A, micro-ornament on ventral valve, GSC 137347 x5. B, micro-ornament on dorsal valve GSC 136874 x3.5. JBW 18, Member C, Jungle Creek Formation.

Aspects of especially the ventral ornament approach those of *Balkhasheconcha* Lazarev, 1985, but species of this have a less inflated ventral valve with spines in which the core appears to turn forward in the shell, unlike spines in the present material. *Balkhasheconcha* also has distinct buttress plates, not developed in present material. Therefore in view of its flat disc and short trail, and geographic location, the present form is interpreted as a waagenoconchiform ally that could have developed into *Wimanoconcha*.

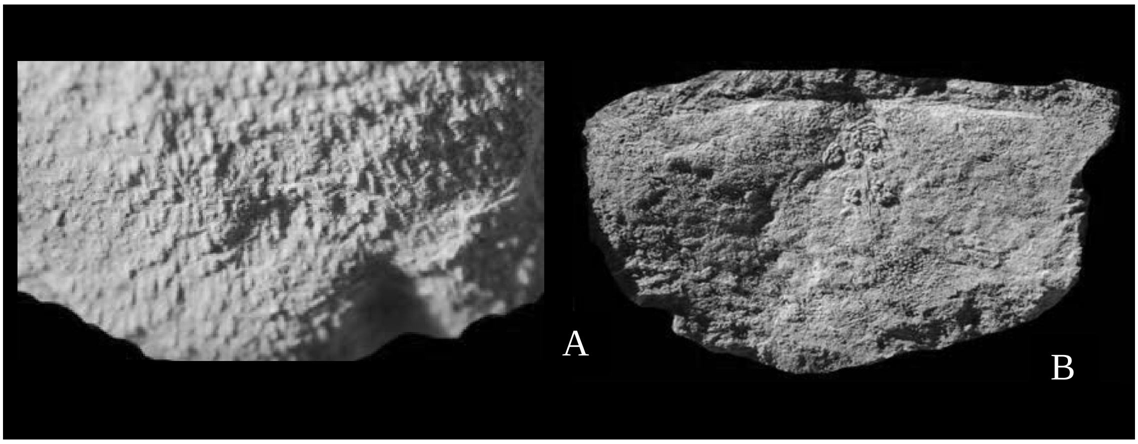


Fig. 139. *Villaconcha planiconcha* n. sp. A, micro-ornament on anterior ventral valve, GSC 137290 x4. B, interior of dorsal valve GSC 137289 x2. JBW 18, Member C, Jungle Creek Formation.

Suborder STROPHALOSIIDINA Waterhouse, 1975

Taxonomy: The taxonomy of this suborder has been discussed by Waterhouse (2001, 2013). Brunton et al. (1995) erroneously ascribed the suborder to Waagen (1883), although Waagen had not even proposed a family group unit for the genus *Strophalosia*: instead he had included it in Chonetinae. Without explicitly correcting the statement, after I had pointed out the misattribution by e-mail, Brunton et al. (2000, p. 565) shifted ground and ascribed the suborder to Schuchert (1913, p. 389), claiming that that step was made by Brunton et al. 1995. Not so. Moreover Schuchert (1913) had never proposed an ordinal grouping for *Strophalosia* – he had regarded it as a subfamily. Separately, a chapter by Brunton, Lazarev & Grant (2000, p. 351) acknowledged that Cooper & Grant (1975) had "retained the Productidina with four superfamilies (Strophalosiacea, Aulostegacea, Richthofeniacea, and Productacea)"... whereas Waterhouse (1978) had recognized.... "Strophalosiidina (divided into Strophalosiacea, Richthofeniacea, and Aulostegacea.....)". The three subdivisions of Strophalosiidina used by Waterhouse (1975, 1978) are the same as those recognized by Brunton et al. (2000, p. 365). Yet this later text (in small print) claimed that it preferred to follow Lazarev. Lazarev (1987, p. 48) in fact had excluded Richthofenioidea from the suborder. Indeed Lazarev (1987, p. 48; 1990, p. 77) included Lyttoniacea [Oldhaminidina or Lyttoniidina], which is excluded from Strophalosiidina by Brunton et al. (2000), as in Waterhouse (1978). In Strophalosiidina "sensu Lazarev 1989", explicitly asserted by Brunton et al. (2000, p. 365 in small print) as containing the understanding of Strophalosiidina in the *Revised Brachiopod Treatise*, the article by Lazarev referred only to what is regarded as Strophalosioidea. Thus the original understandings of the *Strophalosia* group in Schuchert (1913) and Lazarev (1987, 1989, 1990) were far removed from Strophalosiidina as understood by both Brunton et al. (2000) and by Waterhouse (1975, 1978). Brunton et al. (2000, p. 595) misrepresented the prior proposals by Waterhouse, ascribed the suborder to Schuchert long after the suborder had already been proposed by a different author, stated that Lazarev had given the "correct" version, and claimed that the Lazarev version had been followed by Brunton et al. (2000). None of these claims withstand examination. Lazarev (2003, p. 492) later complained about the first section on Strophalosiidina (ie. Brunton, Lazarev & Grant 2000), which he evidently regarded as less than acceptable, and wrote that he took no part in it. That means C. H. C. Brunton wrote the entire section (for by that time, Grant had died). The historical summary in which Lazarev says he took no part (Brunton, Lazarev & Grant, 2000) was far more accurate than the second account (eg. Brunton et al. 2000). So who wrote the second part? According to Lazarev, it was R. E. Grant, which seems unlikely, and may not accord fully with the statement by Brunton (p. 362) that Permian Productida being written up by Grant had to be redistributed between Brunton and Lazarev after Grant's death. That confusion prevailed is possibly implied by the title to the section in the *Revised Brachiopod Treatise* by Brunton et al. (2000, p. 424). The section is headed "Productidina". Yet it includes not only Productidina (p. 424), but Strophalosiidina (p. 565) as well, signifying perhaps a change of mind during publication, or oversight, or hasty and late adjustment.

Diagnosis: Genera either exhibiting well formed hinge apparatus with cardinal areas, teeth and sockets, and ventral cicatrix, pseudodeltidium usually present, or evolved from such genera. Ornament of spines which may be halteroid or rhizoid but no strut spines, spines as a rule arranged in quincunx, but may involve ventral cardinal spines, adductor scars usually only slightly or not dendritic, cardinal process distinctive. Simple to semi-elaborate brachiophore feeding apparatus of various constructs, generally occupying large part of dorsal floor in ancestral superfamily, morphing into a productiform or sublyttoniid construct in later superfamilies.

Superfamily **STROPHALOSIOIDEA** Schuchert, 1913

[Nom. correct. Brunton et al. 1995, p. 931 pro Strophalosiacea Muir-Wood & Cooper, 1960, p. 71, nom. transl. ex Strophalosiinae Schuchert, 1913, p. 391].

Diagnosis: Well formed cardinal areas, teeth and sockets, ventral cicatrix, spines halteroid or rhizoid but no strut spines, spines as a rule arranged in quincunx, but may involve ventral cardinal spines, adductor scars usually only slightly or not dendritic, cardinal process distinctive. Brachiophore apparatus generally occupying large part of dorsal floor.

Family **STROPHALOSIIDAE** Schuchert, 1913

[Nom. transl. Stehli 1954, p. 328 ex Strophalosiinae Schuchert, 1913, p. 391].

Subfamily **STROPHALOSIINAE** Schuchert, 1913

[Strophalosiinae Schuchert, 1913, p. 391].

Diagnosis: No dorsal spines.

Tribe **HETERALOSIINI** Muir-Wood & Cooper, 1960

[nom. transl. Waterhouse 2010, p. 45 ex Heteralosiinae Muir-Wood & Cooper, 1960, p. 80].

Diagnosis: Spines of two orders on ventral valve, no dorsal spines.

Discussion: Like Strophalosiini, the dorsal valve lacks spines. *Strophalosia* has sturdy comparatively uniform spines over the ventral valve, whereas the spines on the ventral valve of *Heteralosia* belong to two orders. The relationships have been discussed by Waterhouse (2010, pp. 45-48). A number of species from the Permian of west Texas were referred to *Heteralosia* by Cooper & Grant (1975), but their *Heteralosia hystricula* (Girty) is exceptional in its very large umbonal cicatrix and surrounding circlet of spines, and is now placed in genus *Cicatricia* Waterhouse, 2010, p. 46, together with *H. vidriensis* Cooper & Grant, 1975. *H. paucispinosa* Cooper & Grant, 1975 has a large cicatrix and crinkled dorsal valve, as the type species of *Crenalosia* Waterhouse 2010, p. 47, together with *H. magnispina* Cooper & Grant, 1975 and *H. tenuispina* Cooper & Grant, 1975.

Genus ***Heteralosia*** King, 1938

Diagnosis: Small subcircular concavo-convex shells with varied cicatrix development, dorsal valve sublamellate without crinkles, ventral spines of two orders, without rhizoid spines and not crowded on ears.

Type species: *Heteralosia slocomi* King, 1938, p. 278 from the Graham Formation (Gzhelian) of Texas, OD.

Heteralosia scotti n. sp.

Fig. 140, 141

Derivation: Named for John Scott.

Diagnosis: Moderately large for genus, with ventral spines that markedly increase in diameter to anterior margin, few prostrate slender spines. Dorsal valve largely planar, without strong lamellae, spines or dimples.

Holotype: GSC 137334, here designated.

Material: Three specimens with valves conjoined, three ventral valves and four dorsal valves from JBW 521.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Dimensions in mm:

GSC	valve	Width	Length	Height
137334	ventral	25	22	12
137335	dorsal	29	22	6.5

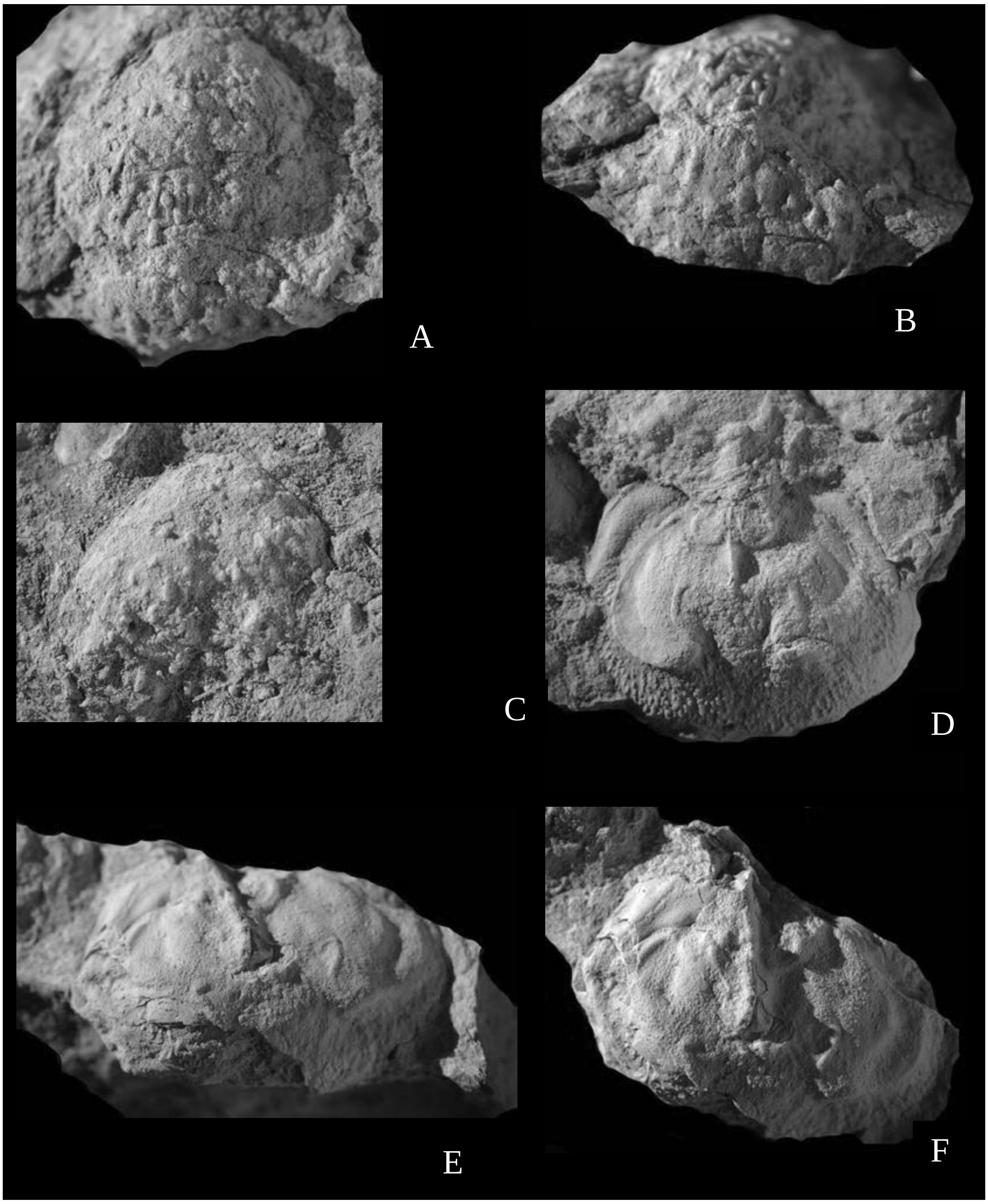


Fig. 140. *Heteralosia scotti* n. sp. A, B, ventral and anterior views of ventral valve GSC 137334, holotype, showing marked increase in diameter of anterior spines. C, ventral valve GSC 137336. D, dorsal interior GSC 137337. E, F, tilted anterior and inner aspects of dorsal interior, GSC 137338. Specimens x2, from JBW 521, Member A, Jungle Creek Formation.

Description: Shells of moderate size, ventral valve gently convex with no sulcus, steeper lateral flanks and only slightly incurved umbo with angle of close to 90º, no conspicuous cicatrix, dorsal valve concave with short semigeniculate trail. Hinge wide, measuring 17mm in the dorsal valve with width of 22mm, but the interareas are not exposed. Ventral spines fine and semiprostrate over the umbonal region, four in 5mm at 6mm from beak, spines less than 0.3mm wide posteriorly, increasing gradually in diameter to become 0.7mm in diameter in front, rare prostrate slender spines and scattered thick erect spines. Most spines tend to be semi-prostrate and aligned along irregular commarginal rows. Dorsal valve surface comparatively smooth and without spines (GSC 137335).

Dorsal interior well displayed, which seems to reflect the fine muddy matrix which has softened and been removed naturally under weathering. Cardinal process with high thick shaft in plane of the disc, terminated by four swollen lobes, but lateral supporting ridges are poorly developed, if not entirely absent. Median septum extends over the disc for more than half of length of valve in one specimen and about half the length in another, moderately thick and without terminal pillar. Adductor scars raised and subrounded, with posterior adductors obscure. Brachial shields well defined, following the normal course as illustrated in Fig. 140D. Low marginal ridge surrounds the disc. Fine low papillae developed over the surface, best developed over the trail, with a cluster of finer papillae in front of the adductor scars, and others in front of and between the anterior brachial shields. Fine papillae are well spaced within the brachial shields.

Fig. 141. *Heteralosia scotti* n. sp., dorsal interior of immature specimen, GSC 137339. Specimen x2, from JBW 521, Member A, Jungle Creek Formation.

Resemblances: *Heteralosia slocomi* King, 1931, type species of the genus from the Wayland Shale, Graham Formation of Texas, is very close in shape but is somewhat smaller: its ventral spines are varied, and slightly more closely spaced and do not display the same progression in size, but as in the present form, tend to be aligned in slightly irregular and impersistent commarginal rows, and prostrate spines are few but even so, many of them not more slender than other spines. The hinge is wide as in the present form (King, 1938; Muir-Wood & Cooper 1960, pl. 3, fig. 6-13). *Strophalosia spondyliformis* Hall & Clarke, 1893 not White & St John is regarded as belonging to the same species. *H. mexicana* Cooper (1953, pl. 7, fig. 1-3) from the upper Monos Formation of Sonora, Mexico, is close in shape and size, with denser spines and gently concave dorsal valve. From the Upper Pennsylvanian of Brazil, *Strophalosia cornelliana* Derby (1874, pl. 3, fig. 28-38) has denser spines over the ventral valve. *Heteralosia lanensis* Klets (2005, pl. 5, fig. 7-13) from Upper Carboniferous of the Lan Basin in northeast Russia has much finer and less conspicuous ventral spines.

Cicatricia hystricula (Girty, 1908, pl. 30, fig. 14, 14a) from the Word Formation (Willis Ranch Member), also figured by Muir-Wood & Cooper (1960, pl. 4, fig. 1-12) and Cooper & Grant (1975, pl. 193, fig. 45, 46, pl. 194, fig. 16-31, pl. 195, fig. 1-43), has thick and thin prostrate ventral spines without the strong anterior increase in diameter, and the cardinal process is similarly massive, and has small lateral supporting septa. It is particularly characterized by its very large ventral cicatrix (Waterhouse 2010, p. 46).

The species *fortispinosa* Hinchey & Ray, 1935 from the Mississippian Warsaw Formation of Missouri was placed in *Heteralosia* by Muir-Wood & Cooper (1960), but strong lateral ridges support the base of the cardinal process and a high number of prostrate spines lie over the ventral valve. It is assigned to a distinct genus, *Fortispinalosia* Waterhouse, 2013, p. 215.

Family **DASYALOSIIDAE** Brunton, 1966

[Nom. promoveo Waterhouse 2013, p. 225 ex Dasyalosiinae Brunton, 1966, p. 192].

Diagnosis: Both valves spinose as a rule, ribs and commarginal lamellae subdued as a rule.

Subfamily **DASYALOSIINAE** Brunton, 1966

[Dasyalosiinae Brunton, 1966, p. 192].

Diagnosis: Spines of at least two orders on both dorsal and ventral valves. Dorsal disc usually of low concavity, may develop short to long trail at high angle.

Discussion: Genera include *Dasyalosia* Muir-Wood & Cooper, *Acanthalosia* Waterhouse, *Maxwellosia* Waterhouse and *Yukonalosia* n. gen., and they range from Late Carboniferous (Gzhelian) to Upper Permian (Wuchiapingian).

Genus ***Yukonalosia*** n. gen.

Name: Yukon – Canadian territory, alos – disc, Greek.

Diagnosis: Small shells, ventral valve with well differentiated thick suberect spines interspersed with finer prostrate spines. Dorsal valve spines of two series, thick erect spines and much thinner erect spines, scattered over valve and not numerous, dorsal valve not thickened.

Type species: *Yukonalosia arctica* n. gen., n. sp. from basal Jungle Creek Formation (Gzhelian), Yukon Territory, Canada, here designated.

Resemblances: The present Canadian genus *Yukonalosia* differs from shells typical of the three dasyalosiin genera listed above, insofar as dorsal spines do not blanket the dorsal valve, but are scattered, and not numerous. Moreover the present species is considerably older than species known hitherto, being Gzhelian, greater than the Sakmarian age ascribed to the first appearance of *Acanthalosia* and *Maxwellosia*. It appears that the genus is new, and is the first known dasyalosiin, assuming that all these genera belonged to one lineage. Unlike the other genera, especially *Acanthalosia* and *Maxwellosia*, the dorsal valve is not particularly thick or wedge-shaped.

Yukonalosia arctica n. sp.

Fig. 142, 143

Derivation: Arctos – Great Bear (constellation visible from near North Pole), Lat.

Holotype: GSC 136875, here designated.

Diagnosis: Small subcircular shells with short hinge, ventral spines vary in diameter from coarse suberect to fine prostrate, and rare scattered erect dorsal spines of two different diameters.

Material: Some eight ventral valves and four dorsal valves with several spats from JBW 450, two specimens with valves conjoined, two ventral valves and other fragments from JBW 449, ventral valve from JBW 198 and dorsal valve from JBW 136.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimens small, concavo-convex, a ventral valve measuring 10mm wide, 9mm long and 3mm high, with broad little incurved umbo of angle 100º, no umbonal cicatrix, wide hinge slightly less than maximum width which lies near mid-length, small concave ears with acute cardinal angle of 80º, and bordered by low but steep umbonal slopes. There is no sulcus. The dorsal valve is concave and not wedge-shaped. Cardinal interarea high, concave, but largely in plane of commissure in mature specimens, marked by horizontal striae, with pseudodeltidium in ventral valve, dorsal interarea low and at high angle to commissure, with notothyrium. Spines are crowded, with thick semi-recumbent to semi-erect spines up to 1mm in diameter, not regularly distributed, and finer erect or prostrate spines: spines are numerous over the ears in one or two rows or scattered. Some spine bases are swollen, without being posteriorly prolonged, and there are irregular rugae, sometimes between spines. Dorsal valve with rare scattered thick and thin erect spines, one set less than 0.1mm in diameter and the other 0.3-0.4mm in diameter.

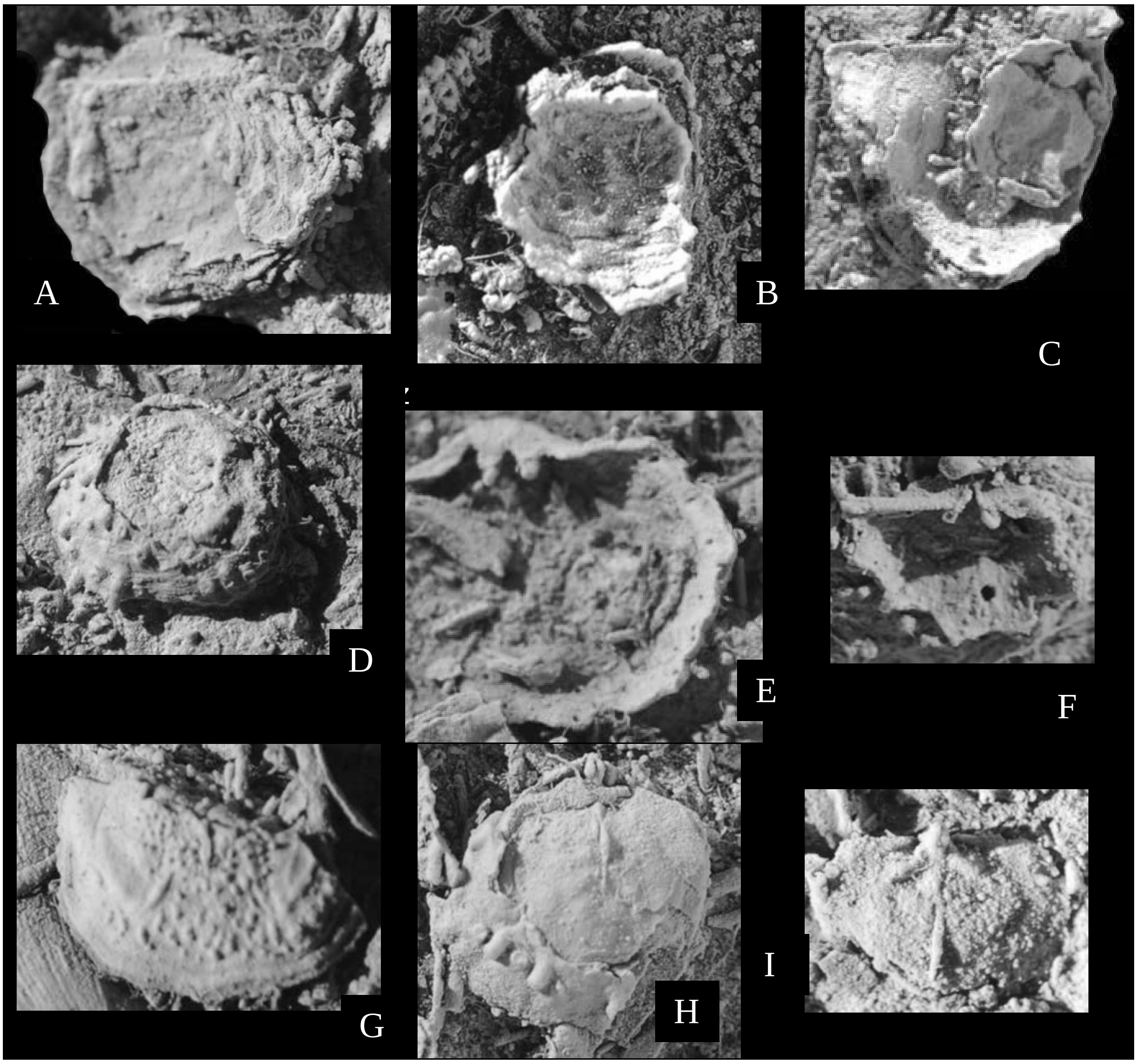


Fig. 142. *Yukonalosia arctica* n. gen., n. sp. A, dorsal aspect of specimen with valves conjoined, GSC 136875, holotype. B, dorsal exterior, GSC 136876. C, dorsal aspect of specimen with valves conjoined, GSC 136877 from JBW 449. D, ventral aspect of specimen with valves conjoined, GSC 136878. E, ventral valve showing hinge and teeth, GSC 136879. F, ventral valve showing interarea and teeth, GSC 136880. G, anterior part of interior dorsal valve, GSC 136881. H, dorsal valve interior and part of ventral exterior, GSC 136882. I, dorsal valve interior, GSC 137263 x5. From JBW 450, except Fig. 142C from JBW 449. Specimens x4 except Fig. 142I, x5. Member A, Jungle Creek Formation.

Ventral teeth large and triangular, ventral adductor platform small with planar surface, diductor impressions oval, extending well in front of adductors, with no strong striae; floor may open into spines. Cardinal process slender with tiny adpressed lateral lobes, supported by two short curved lateral ridges, small smooth adductor scars, posterior elements raised posteriorly, anterior adductors rounded, impressed. In mature specimens, the median septum extends just past mid-length. Mature specimen shows large brachial shields and strong pustules between and in front of the shields onto the first part of the trail, and a cincture passes around the middle of the trail.

Several small spats up to 3mm wide are attached to other shells by ventral spines.

Resemblances: This species is outstanding, because the dorsal spines are of two different diameters, but are comparatively few and irregularly dispersed.

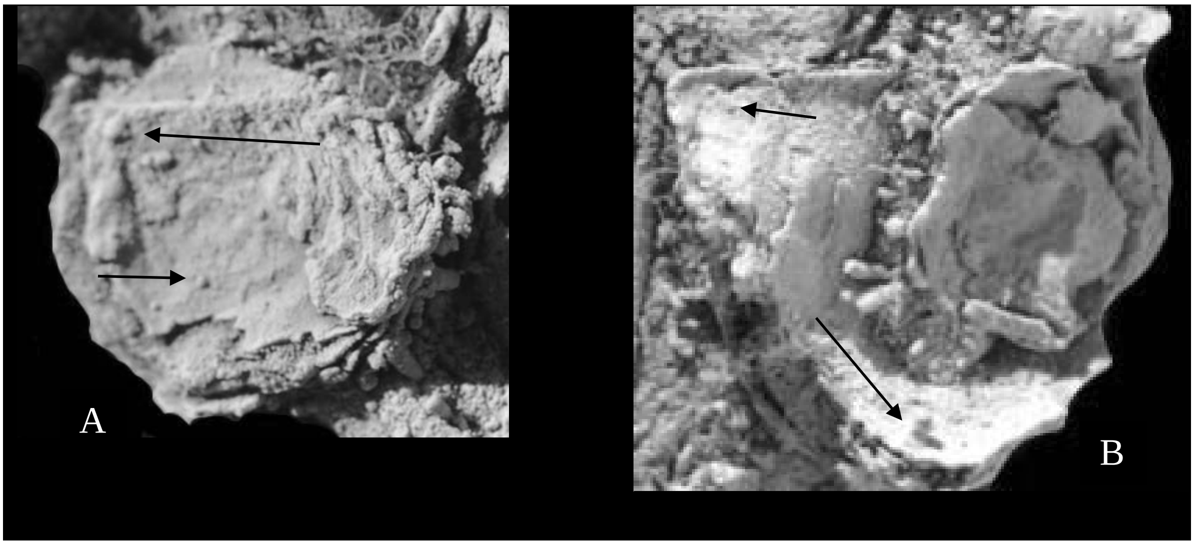


Fig. 143. *Yukonalosia arctica* n. gen., n. sp., enlarged views. A, dorsal aspect of specimen with valves conjoined, GSC 136875 x6, holotype, showing thick (long arrow) and thin spines (short arrow). From JBW 450. B, dorsal aspect of specimen with valves conjoined, GSC 136877 x6, showing thick (long arrow) and thin spines (short arrow). From JBW 449. Member A, Jungle Creek Formation.

Subfamily **ECHINALOSIINAE** Waterhouse, 2001

[Echinalosiinae Waterhouse, 2001, p. 57].

Diagnosis: Shells distinguished from other members of the family by possessing erect spines of one series over dorsal valve, spines of two series as a rule on ventral valve. Commarginal lamellae developed to varying but never marked degree, radial fila variably developed, generally weak or absent. Cardinal process usually trifid.

Tribe **ECHINALOSIINI** Waterhouse, 2001

[Nom. transl. Waterhouse 2013, p. 229 pro Echinalosiinae Waterhouse, 2001, p. 57].

Diagnosis: Ventral valve with two series of spines as a rule. Dorsal valve thin, with trail and erect slender spines.

Genus ***Echinalosia*** Waterhouse, 1967b

Diagnosis: Small to medium in size with ventral cicatrix and non-thickened dorsal valve; ventral spines in two orders, regularly spaced as a rule over the valve; dorsal spines fine and erect.

Type species: *Strophalosia maxwelli* Waterhouse, 1964 from Letham Burn Formation (Roadian) of southern New Zealand, OD.

Echinalosia minuta n. sp.

Fig. 49, 121, 144 - 146

Derivation: minutus – small, Lat.

Diagnosis: Small with umbo lacking an umbonal cicatrix as a rule, hinge short, ventral spines with a robust semi-inclined series and numerous finer erect spines, gently concave dorsal valve bearing a few fine and erect spines.

Holotype: GSC 136886, here designated.

Material: Three ventral valves from JBW 195, six ventral valves from JBW 561, three ventral valves from JBW 580, and eleven ventral valves, eight dorsal valves and two specimens with valves conjoined from JBW 581. Possibly allied ventral valves from JBW 73 at Member D.

Stratigraphic and biostratigraphic levels: Member E, and possibly Member D, Jungle Creek Formation. *Ogilviecoelia shii* Zone and possibly *Rugivestigia commarginalis* Zone.

Description: Shells small and rounded in outline with moderately wide hinge and small distinct obtusely alate ears, maximum width usually at or just in front of mid-length. Ventral interarea well developed, inclined at steep angle to commissure in small specimens, curved slightly posteriorly, but largely in plane of commissure in more mature material, with inconspicuous pseudodeltidium. Umbo broad and with broad irregular cicatrix on some specimens. Dorsal valve moderately concave with convex nepionic portion and low interarea at high angle to commissure and small notothyrium, short subgeniculate trail. Many ventral spines erect, some becoming subprostrate, up to 0.6mm in diameter, coarse for size of shell, crowded and exceptionally only 1-2mm apart, but slightly variable, arranged in erratic commarginal rows, may be thick laterally, interspersed with few to a number of fine prostrate or erect spines; ears where developed have few or no spines. Anteriorly the coarse spines may alternate in rows with erect spines. Dorsal valve with fine erect spines thinly scattered over disc, concentrated near lateral margin in one specimen, some irregular radial rugae. Broad dimples are prominent on the specimen from JBW 195, as well as fine erect spines. Shell also crossed by growth increments, some fifteen per mm anteriorly, and irregular rugae and laminae. Surface also ornamented by fine growth increments and large well spaced dimples, with some tubercles, and may display fine radial capillae, counted at six or seven per mm anteriorly; nepionic area convex and comparatively large.

Ventral valve with small teeth and low subquadrate posteriorly placed adductor platform, valve floor smooth apart from sharp pustules: anteriorly the spines may open into the interior. Diductor scars feebly impressed.

In the dorsal valve, the cardinal process extends in plane of commissure, supported by weak ridges along the hinge and short lateral socket ridges in front of dental sockets and behind adductor platform, dorsal adductor scars large and oval, and in one specimen marked by close-set pits, posterior adductors not clearly discriminated. In another specimen from JBW 581, the posterior elements are large, impressed and bear fine sharply pointed tubercles. Medium dorsal septum extends past mid-length, and brachial impressions are large. There are no clearly defined adductor impressions, and only a short septum in a convex dorsal valve spat 4.5mm wide. Fine pustules over floor, smooth posteriorly, pustules larger and better spaced and regular over anterior disc, behind short trail.

Resemblances: It is difficult to find any species that compares with the present one. East Australia and New Zealand species are all larger with larger spines and as a rule more concave dorsal valve.

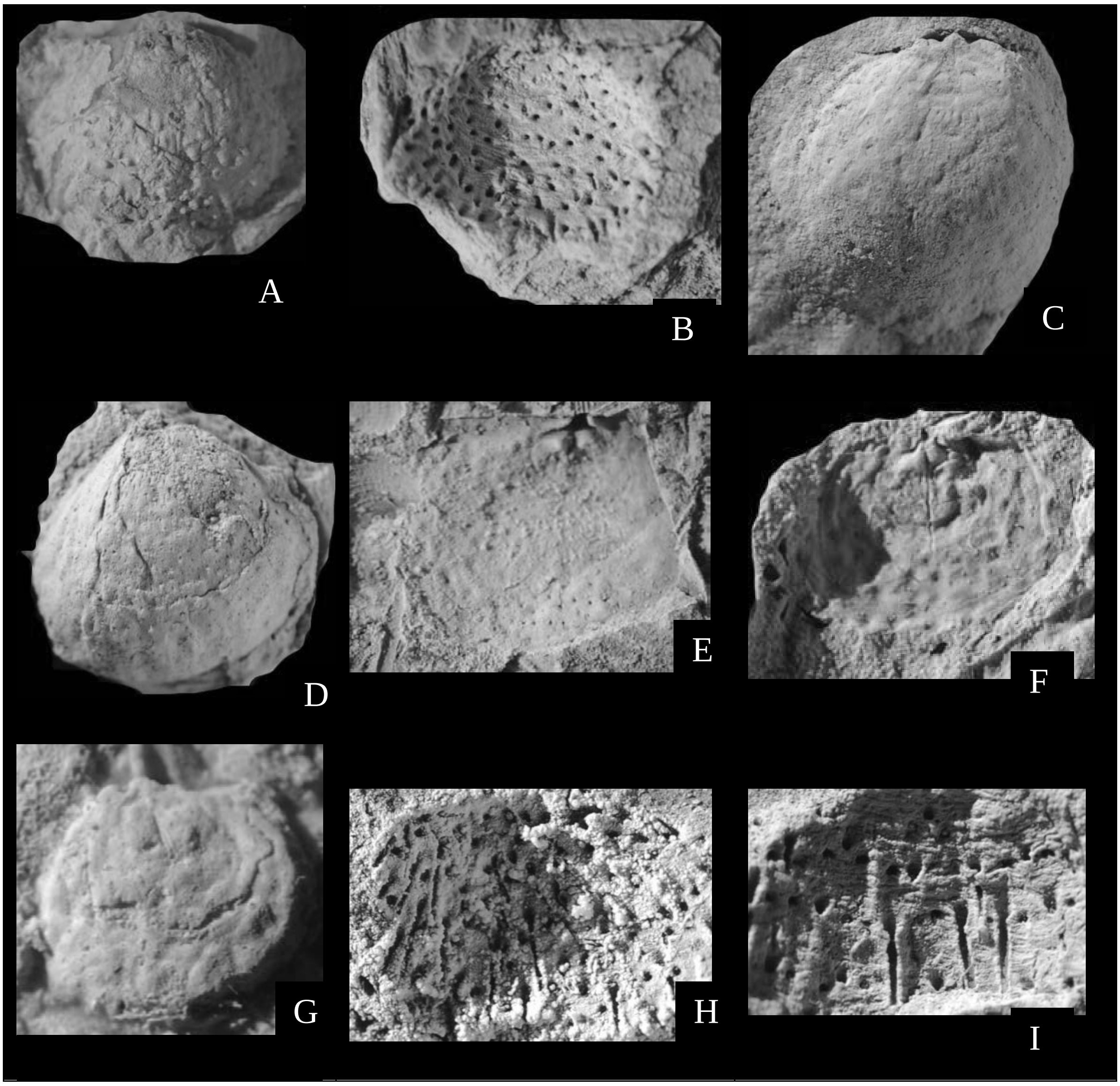


Fig. 144. *Echinalosia minuta* n. sp. A, cast of ventral valve GSC 137332 x3 from JBW 581. B, ventral external mould showing spination, GSC 136885 x3 from JBW 581. C, ventral internal mould GSC 136886 holotype x3 from JBW 195. D, ventral valve internal mould GSC 136888 x3 from JBW 581. E, dorsal valve internal mould GSC 136889 x4 from JBW 581. F, G, internal mould and cast of dorsal valve, GSC 136890 x4 from JBW 581. H, detail of spines on external mould of ventral valve, GSC 137273 x4 from JBW 581. I, detail of spines on anterior external mould of ventral valve, GSC 137291 x4 from JBW 580. Member E, Jungle Creek Formation.

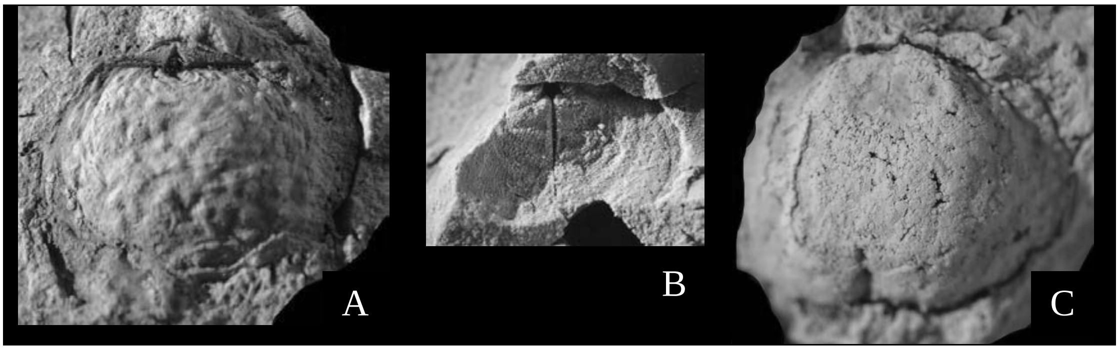


Fig. 145. *Echinalosia minuta* n. sp. A, dorsal aspect of external mould, GSC 136884. B, internal mould of dorsal valve, GSC 136890. C, internal mould of ventral valve, GSC 137272. Specimens x4, from JBW 581, Member E, Jungle Creek Formation.

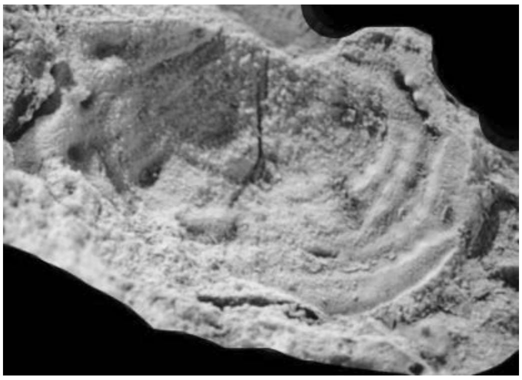


Fig. 146. *Echinalosia minuta* n. sp., dorsal internal mould, broken posteriorly, GSC 137415 x8 from JBW 581. Member E, Jungle Creek Formation.

Superfamily **SCACCHINELLOIDEA** Licharew, 1928a, b

[Nom. transl. Rozanov 2003, p. 112 ex Scacchinellinae Licharew, 1928b, p. 265].

Diagnosis: Well developed lateral buttress plates. Spines subprostrate, suberect or usually erect and with short posteriorly prolonged bases, dorsal valve usually spinose. Interareas present as a rule, no teeth or sockets. Widely bilobed cardinal process and median ventral septum prominent in two families.

Discussion: The superfamily is named from *Scacchinella* Gemmellaro, 1891, which has an extraordinary morphology, in which the ventral valve became very deep, to lift the aperture high above the substrate, and developed a median septum. *Scacchinella* and allies were derived ultimately from Araksalosiidae Lazarev, an outstanding strophalosiiform group typified by fine even ventral disc spines, often with elongate bases over disc and trail, and well developed lateral buttress plates, though without a median septum (Waterhouse 2013).

Appraisal of the ornament for *Scacchinella* shows that both valves are spinose, those of the dorsal valve fine and erect, those of the ventral valve fine and including halteroid spines which helped to anchor the ventral valve. The spines tend to be fine and closely spaced, with prolonged bases externally, and are moderately like those of aulostegoids, and also especially close to those echinoconchoids which have erect spines, such as Waagenoconchinae Muir-Wood & Cooper and Pustulinae Waterhouse. Members of Tschernyschewiidae Muir-Wood & Cooper are instructive in this regard. *Tschernyschewia* Stoyanow is regarded as an ally of *Scacchinella* because it also has a high ventral median septum. Several genera are known, each distinguished by the nature of its spines. *Tschernyschewia* itself looks externally close to *Waagenoconcha* Chao. A double row of rhizoid spines lies along the ventral hinge in *Trigonoproductus* Waterhouse and the ventral disc bears low ribs with numerous somewhat swollen short spine bases, whereas a network of rather coarse ventral spines and dorsal dimples characterizes the genus *Sierradiabloa* Waterhouse. These genera thus show a range of ornament styles close to those found in some echinoconchoids and to lesser extent, aulostegoids.

Family **RHAMNARIIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. hic ex Rhamnariinae Muir-Wood & Cooper, 1960, p. 119].

Diagnosis: Variable spine development on both valves, with or without elongate spine bases, cicatrix may be prominent, interarea absent to moderately high, cardinal process supported by long buttress plates, and no high ventral septum.

Discussion: Rhamnariids are regarded as allies of *Scacchinella*, through the presence of well developed lateral buttress plates (Waterhouse 2013, pp. 246, 248). Judged from the fossil record, Rhamnariinae evolved from subfamily Balkhasheconchinae, changing the spinose ornament to a degree and restoring the ventral interarea and short trail. Rhamnariinae gave rise to a more specialized group Septasteginae Waterhouse, characterized by increased height of the lateral buttress plates which supported the dorsal adductors, and further distinguished by the increased height of the marginal ridge which is present but low in various genera within Rhamnariinae.

Subfamily **BALKHASHECONCHINAE** Waterhouse, 2002b

[Nom. transl. et correct. Waterhouse 2013, p. 256 ex Balkasheconchini Waterhouse, 2002b, p. 25].

Diagnosis: Waagenoconchiform shells with lateral buttress supports in the dorsal valve, extending each side of dorsal adductors. No interareas, no cicatrix, trail very short. Spines over both valves subprostrate or erect especially around margins, largely uniform in bands. Cardinal process with tall median pillar or shaft.

Discussion: Genera include *Balkhasheconcha* Lazarev, *Buxtoniella* Abramov & Grigorieva, *Campbelliconcha* Waterhouse and *Ramaliconcha* Waterhouse. Lazarev (1985) and Brunton et al. (2000, p. 518) placed constituent genera of this subfamily within Tribe Waagenoconchini, but the genera were discriminated as distinctive by Waterhouse (2002b). The external ornament is moderately characteristic, dominated as a rule by spines which are mostly subprostrate with elongate bases, arranged in quincunx over the ventral and dorsal valves, and showing in the ventral valve evidence of having recurved spine cores, in which the spine emerged gradually through the shell outwards and forwards into the spine, and then continued forward forward into the shell from the base of the spine. The interior is also distinctive, with well formed lateral buttress plates. Such plates are absent from any genus within Echinoconchidae, Waagenoconchidae, and Sentosiidae. Araksalosiinae Lazarev, 1989 has disc and trail spines over the ventral valve like those of Balkhasheconchinae, and internally displays lateral buttress plates. Araksalosiinae clearly differs from *Balkhasheconcha* and allies in having interareas, teeth and sockets, and a row of strong ventral hinge spines in several genera. Araksalosiin genera are of Upper Devonian (Famennian) to Lower Carboniferous (lower Tournaisian) age, whereas the earliest known balkhasheconch genera are of Visean age. The closest of known Araksalosiinae likely to have provided a progenital source is *Hamlingella* Reed, 1943 of upper Devonian age. This species has moderately strong hinge spines, fine spines on both valves and similar dorsal interior with dendritic posterior dorsal adductors and long lateral buttress plates.

The predominantly spinose ornament and the presence of lateral buttress plates in the dorsal valve of Balkhasheconchinae are aspects shared with members of Rhamnariinae Muir-Wood & Cooper, 1960, and agree in displaying mostly elongate spine bases with southerly members of Rhamnariinae, such as *Saeptasteges, Colemanosteges*, and *Geniculatusia*, which have longer lateral buttress plates. Members of Rhamnariinae display attributes of Aulostegoidea, and have moderately high interareas, and a cicatrix on some specimens, and a distinctive cardinal process. Members of Balkhasheconchinae do not show the same aulostegoid attributes, lacking interareas and cicatrix, and having a non-aulostegoid cardinal process, and in shape approaching the build of Waagenoconchidae. Rhamnariinae is younger than early Balkhasheconchinae, and has reverted through regaining interareas and cicatrix to features typical of Strophalosiidina. Theorists may discount such possibilities, claiming that reversion is impossible, and progression always linear in one direction, but the fossil record yields examples in a number of phyla and classes.

Genus ***Balkhasheconcha*** Lazarev, 1985

Diagnosis: Fine erect or subprostrate spines over both valves, fine (rarely coarse) and erect anteriorly on ventral valve, and apparently with recurved bases. Short lateral buttress plates.

Type species: *Waagenoconcha balkhashensis* Nasikanova in Sarytcheva 1968, p. 106 from Keregetass Formation (Bashkirian?), Kazakhstan.

Discussion: *Buxtoniella* Abramov & Grigorieva (1986, p. 94) of middle Visean age in Verchoyan, northeast Russia, is said to lack the anterior band of thinner spines on the ventral valve, although a number of fine spines are present. *Campbelliconcha* Waterhouse from middle Visean of east Australia has fine spines posteriorly, and very fine spines anteriorly: none have notably elongate bases.

Balkhasheconcha cf. ***piassinaensis*** (Einor, 1939)

Fig. 147

1939 *Productus* (*Waagenoconcha*) *gangeticus piassinaensis* Einor, p. 42, pl. 7, fig. 2.
1963 *Waagenoconcha piassinaensis* – Ustritsky & Chernyak, p. 78, pl. 7, fig. 1.

Diagnosis: Large shells with moderately well defined sulcus, elongate ventral spine bases.

Holotype: Specimen figured by Einor (1939) by monotypy from Makarov Suite (Bashkirian) of central Taimyr.

Material: Two specimens with valves conjoined from JBW 748, single specimen with valves conjoined from JBW 188 and ventral valve from JBW 66.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

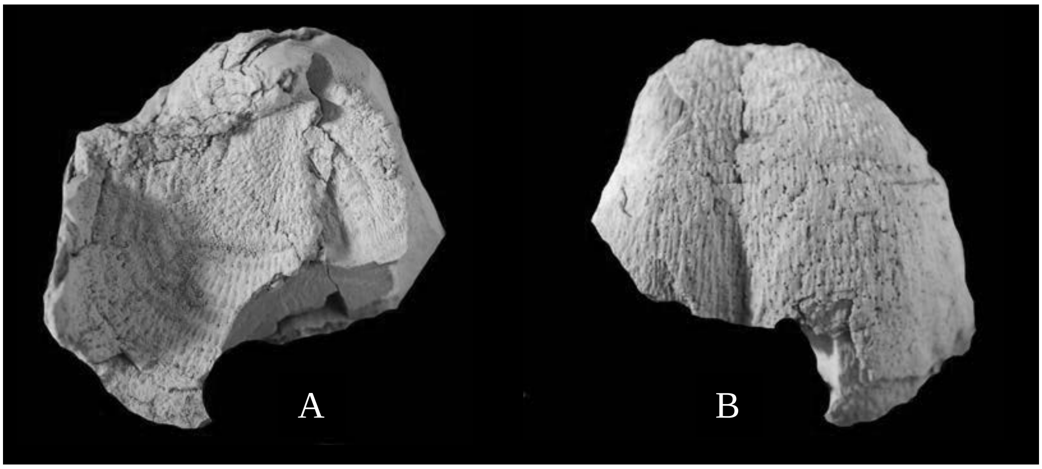


Fig. 147. *Balkhasheconcha* cf. *piassinaensis* (Einor). A, B, dorsal and ventral aspects of GSC 136891 x1 from JBW 748. Member A, Jungle Creek Formation.

Description: Specimens moderately large, one measuring 58mm wide, 48mm long and 19mm high, with transversely oval outline, broad ventral umbo with angle of 100°, and wide hinge with low ginglymus and obtuse cardinal extremities. The ventral valve is moderately convex, and the dorsal valve very gently concave, almost flat disc and moderately extended trail at high angle. The sulcus commences some 10mm in front of the beak, and widens at an angle of 30°, with shallow evenly concave floor, and the fold commences near mid-length and is low and broad anteriorly. Ventral spines are dense and closely packed, with slender bases 3mm long, some five occurring in 5mm across the shell, and appearing to be erect around the anterior margin. Dorsal spines poorly preserved, appear to have elongate bases, becoming more erect anteriorly. Commarginal rugae are fine and low in one specimen, and more prominent rugae are developed over the anterior ventral valve, but not over the dorsal valve or trail of the other specimen. Little of the interior is visible. The larger specimen shows part of a large and deep diductor impression, and a buttress plate in the dorsal valve on the side that is exposed. In the other specimen, the median dorsal septum extends well past mid-length. The visceral disc is comparatively thick.

Resemblances: The Canadian specimens are smaller than those from northeast Russia, but agree overall in shape and in proportionately smaller and denser spine ornament. The figured specimen shows on one side the development of a buttress plate, indicating that it belongs to *Balkhasheconcha*, but the generic affinities of the Russian material is not firmly established, and depends on its apparent relationship to the Canadian material.

Balkhasheconcha sp.

Fig. 148

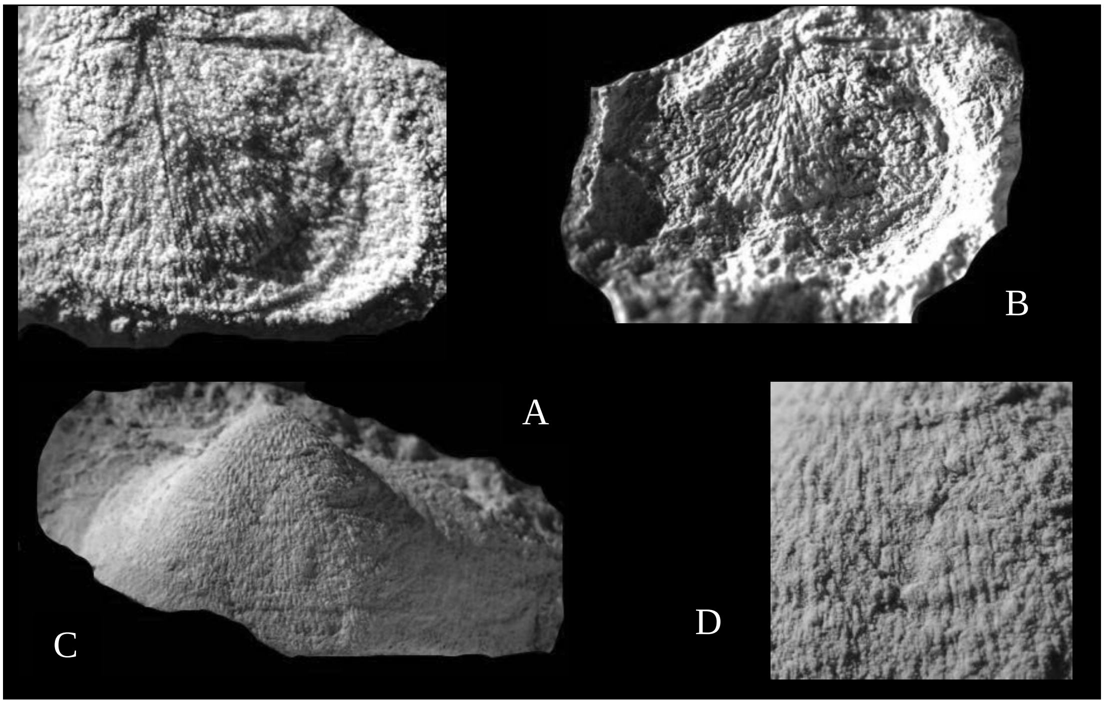


Fig. 148. *Balkhasheconcha* sp. A, mould of internal dorsal valve, showing buttress plates, GSC 136883 x4. B, mould of internal dorsal valve, showing buttress plates, GSC 137292 x3. C, lateral aspect of ventral valve, GSC 137293 x2. D, micro-ornament in median part of the ventral valve GSC 137293 x5, showing long grooves dissolved from hollow spine core tunnels passing forward from the spine base within the shell. From JBW 18. Member C, Jungle Creek Formation.

Material: A fragment and ventral valve, and three internal moulds of dorsal valves from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Description: The material is close to that described as *Villaconcha planiconcha* n. sp., but the dorsal valves show a low median fold not seen in dorsal valves ascribed to *planiconcha*, and there is a distinct short trail at high angle to the disc, suggesting that the specimens, although small, are approaching maturity. Dorsal spines are erect. Unlike *planiconcha* the dorsal buttress plates are clearly developed, and the cores of the ventral spines appear to bend and pass forward from the base of each spine through the body of the shell.

Balkhasheconcha bamberi Waterhouse, 2013

Fig. 149 - 153

cf. 1968 *Waagenoconcha* cf. *abichi* [not Waagen] – Logan & McGugan, p. 1133, pl. 141, fig. 7-10.
2013 *Balkasheconcha* (sic) *bamberi* Waterhouse, p. 257, Fig. 8.12 – Fig. 8.14.

Diagnosis: Medium-sized shells characterized by well formed ventral sulcus and commarginal rugae over ventral valve.

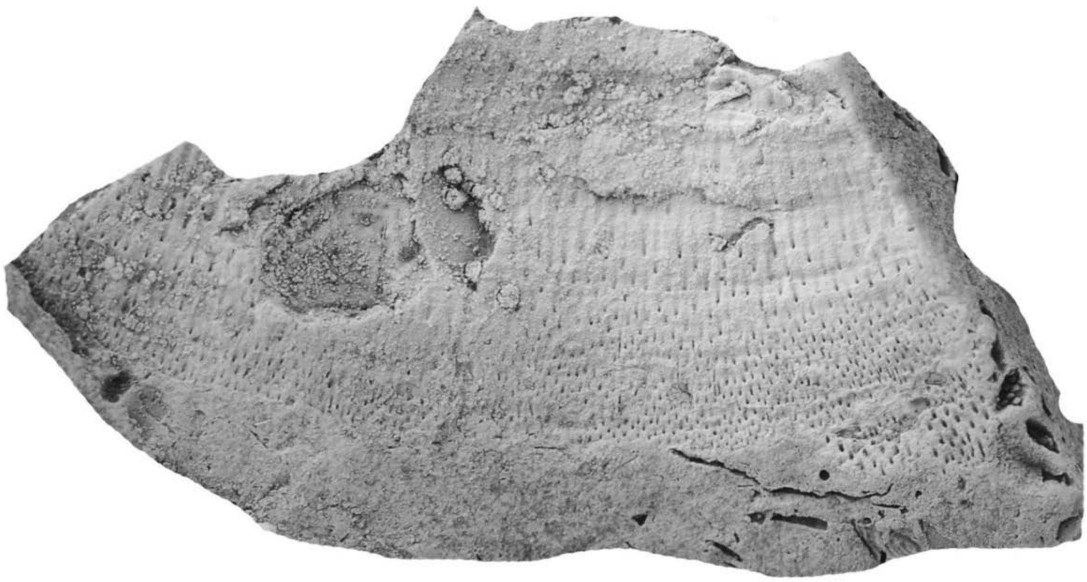


Fig.149. *Balkhasheconcha bamberi* Waterhouse. External mould showing elongate spine bases giving way to erect spines anteriorly, GSC 133347 from JBW 581, x6. Note the outer band of coarse erect spines developed in front of the band of fine erect spines, exceptional for *Balkhasheconcha*, but not in my opinion mandating generic distinction. Even so, *Buxtoniella* Abramov & Grigorieva (1986, p. 94) was discriminated on the basis that it lacked an anterior band of finer spines. On that basis, this specimen should be referred to *Buxtoniella*, but I have doubts. From Member E, Jungle Creek Formation.

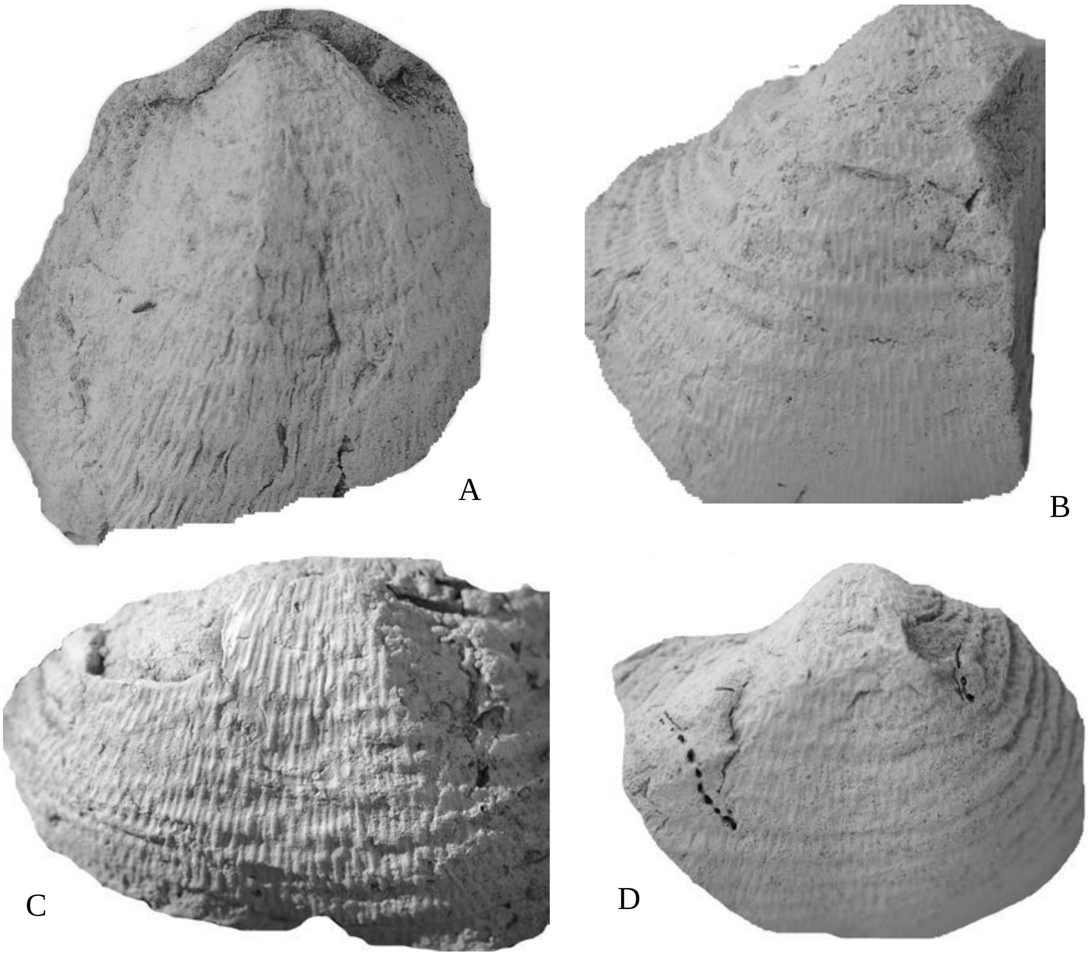
Holotype: GSC 133343 figured by Waterhouse (2013, Fig. 8.14A), and herein as Fig. 151A, from Member E, Jungle Creek Formation, Yukon Territory, OD.

Material: One ventral valve from JBW 96**,** two ventral valves from JBW 561, four ventral valves from JBW 580, eight ventral valves and three dorsal valves from JBW 538, seven ventral valves and a specimen with valves conjoined from JBW 581. Also C-6167.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Dimensions in mm: (ventral valves incomplete and preserved as internal moulds)

Specimen GSC	Width	Length	Height	
133344	53	35	20	
133343	42	37	10	holotype
133346	34	34?	14	



E

Fig. 150. *Balkhasheconcha bamberi* Waterhouse. A, ventral internal mould, GSC 133346 from JBW 135, x2. B, ventral aspect of internal mould with valves conjoined, GSC 133344 from C-6167, x1.8. C, ventral valve GSC 133349 from JBW 580, x2. D, ventral valve GSC 133348 from JBW 135, x2. E, external mould of ventral valve GSC 133350 from JBW 538, x2. Member E, Jungle Creek Formation.

Description: Plano-convex shells, ventral umbo incurved, with angle of 60-70º, umbonal walls steeply to gently convex in profile and persist well forward, hinge wide and cardinal extremities obtuse, ears not clearly distinguished, but slightly upturned laterally. A sulcus commences a little in front of the umbonal tip and widens at 25-30º, with gently concave floor. Dorsal valve almost flat, with very low fold broadening from posterior third of shell length, leaving a shallow depression each side. There is no geniculate trail. Entire ventral valve ornamented by spines, 0.5mm in diameter posteriorly, arranged in quincunx and emerging from short raised spine bases 2mm long posteriorly and 7mm long anteriorly and little more than 1mm apart: there are some irregularities and some erect spines without extended bases. In some specimens the bases are aligned in semicontinuous ridges, and in one specimen the lateral shell has only erect spines. Anteriorly there is a band of slender, crowded and erect spines, about three per mm, and in one ventral valve, as figured, there is a peripheral band of stouter spines, unlike the ornament of other known species (see Fig. 149). Bases are recurved forward on one well preserved fragment (Fig. 152A). The valve is crossed by firm commarginal rugae, faint posteriorly, and strongest over mid-length. The dorsal valve is densely ornamented by erect spines with short elongate bases 1.5mm long, separated by elongate pits, crossed by fine growth increments numbering nine per mm anteriorly, and fine close-set growth rugae, overall imparting a rough texture to the surface. The commarginal rugae are not as prominent as those of the ventral valve.

The shell is thin and the ventral valve reflects the external ornament, to the extent that muscle scars are obscure, with only faint signs of adductor scars. In the dorsal valve the cardinal process is slender, and the median septum extends beyond mid-length. A broad low smooth platform lies in front of the cardinal process, and a low slender lateral buttress plate extends obliquely forward each side of the posterior adductor scars, which are faintly impressed with irregular ridges, behind slender elongate smooth anterior adductor impressions. Brachial ridges are not visible. The floor is marked by crowded sharp pustules and dimples, and a strong ridge lies along the hinge.

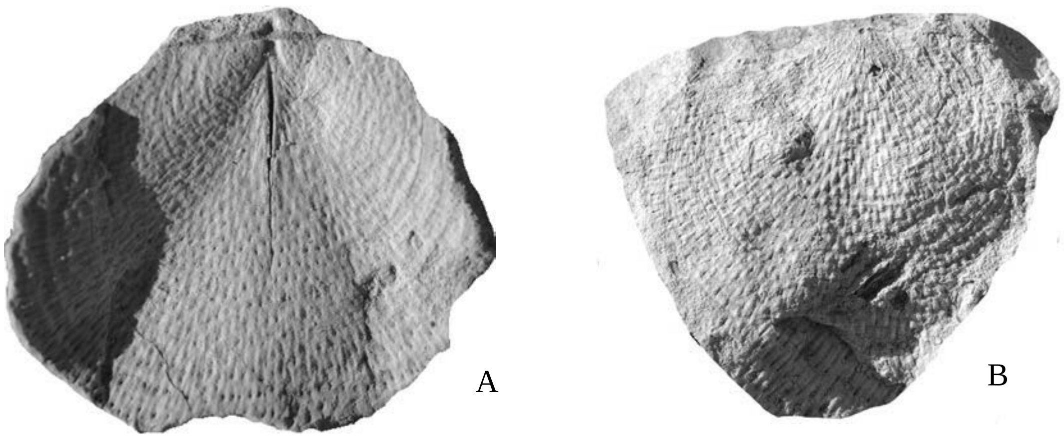


Fig. 151. *Balkhasheconcha bamberi* Waterhouse. A, internal mould of specimen with both valves conjoined, holotype, at early maturity, dorsal aspect, GSC 133343 from JBW 581, x1.5. B, dorsal external mould GSC 133342 from JBW 538, x2. Member E, Jungle Creek Formation.

Resemblances: This species is distinguished by its moderately well-formed ventral sulcus and strong commarginal rugae, and detail of its spine pattern. Specimens from the Mt Greene beds of northeast British Columbia are similar (Logan & McGugan 1968). The present species is exceptional for the genus insofar as the anterior spines form a double band, a posterior band of very fine erect spines, as in other species of *Balkhasheconcha*, bordered by an outer band of coarser erect spines on at least one specimen. (See Fig. 149). A species from the younger Jungle Creek Formation was described as *Waagenoconcha permocarbonica* Ustritsky by Shi & Waterhouse (1996, p. 77, pl. 9, fig. 4-15, pl. 10, fig. 1-4) from the "*Yakovlevia transversa", Ogilviecoelia inflata* and *Jakutoproductus verchoyanicus* Zones, might belong to *Balkhasheconcha.* (See Shi & Waterhouse 1996, pl. 9, fig. 7, 8). Compared with *B. bamberi*, they are of larger size, and have shallow ventral sulcus, less prominent commarginal ornament and less elongate spine bases and dimples on the dorsal valve. Ustritsky's species *permocarbonica* (Ustritsky & Chernyak, 1963, pl. 7, fig. 6, pl. 8, fig. 1-3) and his so-called *wimani* [not Fredericks] (pl. 6, fig. 6, pl. 7, fig. 1) differ in much the same way, although the dorsal valve does show more elongate spine bases. The types come from the Upper Carboniferous Makarov Horizon (Bashkirian) of western Taimyr, north Russia.

The type species of the genus, *Balkhasheconcha balkhashensis* (Nasikanova) in Sarytcheva (1968, p. 106, pl. 9, fig. 1-4; Ganelin 1984, pl. 12, fig. 1-3) from the Upper Carboniferous Keregetass Suite of north pre-Balkhash and Makarsk Suite of the Kolyma Basin, northeast Russia, is larger with shallower sulcus and less conspicuous growth steps. The original types are moderately close, but ventral spine bases are shorter. The species was also figured by Lazarev (1990, pl. 34, fig. 1-3). *B. gigantea* (Ganelin, 1984, pl. 18, fig. 4, 5, pl. 19, fig. 1-4, pl. 20, fig. 1-7, pl. 21, fig. 1-5; Lazarev, 1990, pl. 35, fig. 1-4) from the same level, in the Hayran Suite, is even larger, but otherwise close to the type species: both show spines like those of the present form. Various specimens referred to *Waagenoconcha irginaeformis* Stepanov are somewhat similar to the present species, including those described by

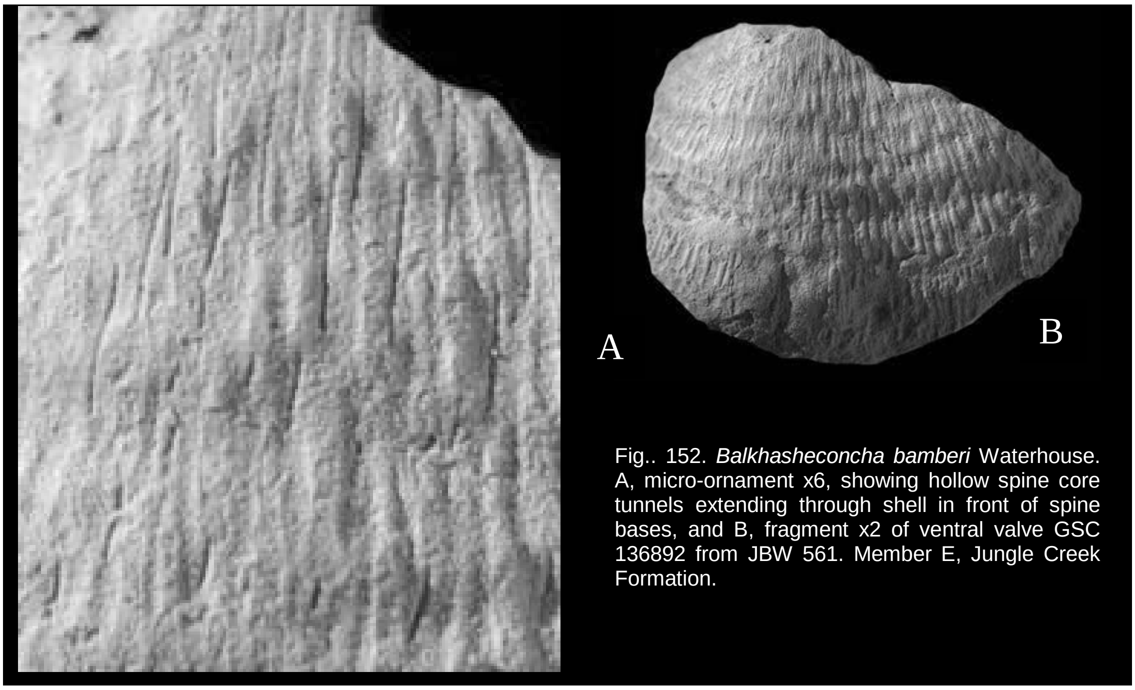


Fig.. 152. *Balkhasheconcha bamberi* Waterhouse. A, micro-ornament x6, showing hollow spine core tunnels extending through shell in front of spine bases, and B, fragment x2 of ventral valve GSC 136892 from JBW 561. Member E, Jungle Creek Formation.

Abramov & Grigorieva (1983, pl. 3, fig. 26-29; 1988, pl. 6, fig. 9) from the younger Early Permian Echi Suite of west Verchoyan, northeast Russia, whereas Gobbett (1964, p. 76) referred the species to synonymy of *irginae* Stuckenberg. Sarytcheva in Sarytcheva (1968, pl. 10, fig. 1-8) in figuring Kazakhstan material included both a dorsal interior apparently without lateral buttress plates (Fig. 46) and shells with lateral buttress plates (Fig. 47) as belonging to *irginaeformis.* Judged from the figure, the dorsal plates in the latter form diverge very narrowly, but clarity is required over the width and nature of the muscle scars, although they do seem to be laterally bordered by the plates. The specimens assigned to *irginaeformis* (not the syntyes) by Stepanov (1937b, p. 124, pl. 6, fig. 4, 5) – see also Licharew (1939, p. 84, pl. 21, fig. 5) – appear to belong to Waagenoconchidae. Kulikov (1974, pl. 3, fig. 5) illustrated a specimen from the west Urals: he kept *irginae* separate. Specimens assigned to *W. irginae* (Stuckenberg) by Ifanova & Semenova (1972, pl. 3, fig. 14-16) from upper Artinskian and Kungurian beds of Petchora are moderately close. But whether or not they belong to *Balkhasheconcha* is not clear from available figures, or from the descriptions. The specimens lack the conspicuous commarginal rugae of the present form. *Waagenoconcha asiatica* Zavodowsky (1970, p. 89, pl. 3, fig. 1, 2) from the Burgali Suite (Asselian) of northeast Russia has elongate spine bases but differs in size and shape from the Canadian species.

Fig.. 153. *Balkhasheconcha bamberi* Waterhouse, posterior view of internal mould with valves conjoined, GSC 137294 x2 from JBW 581. Member E, Jungle Creek Formation.

Genus ***Ramaliconcha*** Waterhouse, 2013

Diagnosis: Of medium size, both valves ornamented by raised, elongate and crowded spine-bases, spines erect only over posterior lateral ventral valve; low trail. Lateral buttress plates may be short, narrowly diverging in type species.

Type species: *Ramaliconcha bitteri* Waterhouse 2013, p. 261 from Member A (Gzhelian), Jungle Creek Formation (Gzhelian), Ogilvie Mountains, Yukon Territory, Canada, OD.

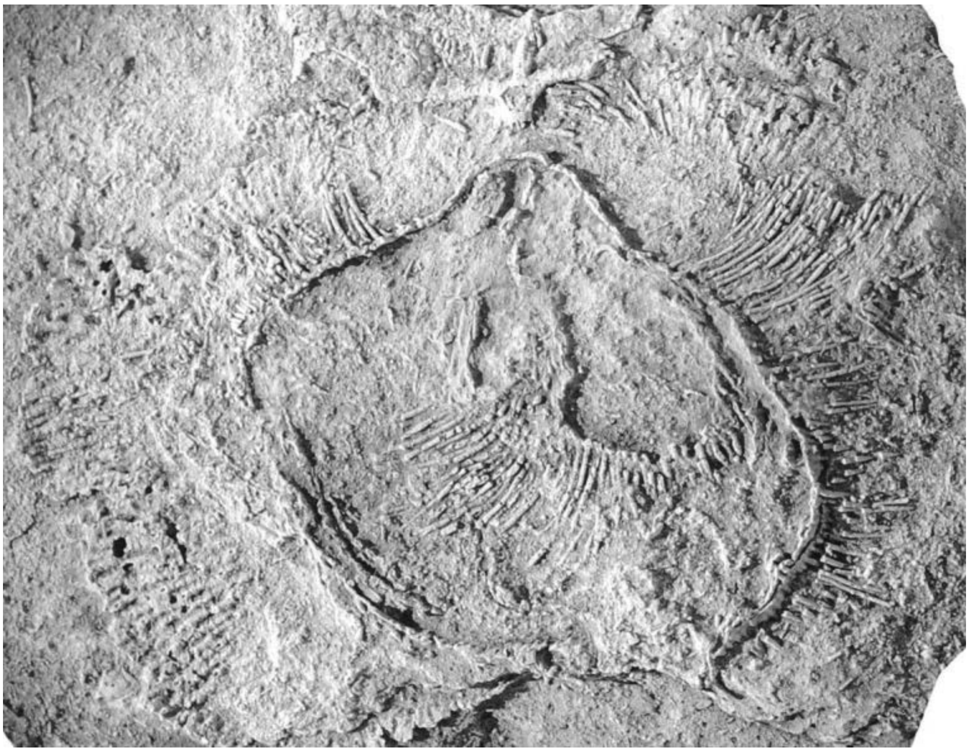


Fig. 154. *Ramaliconcha bitteri* Waterhouse. GSC 133360 from JBW 517, x2, showing several valves and arrays of ventral spines. Member A, Jungle Creek Formation.

Discussion: *Buxtoniella* Abramov & Grigorieva (1986, p. 94) of middle Visean age in Verchoyan, northeast Asia, is said to lack the anterior band of thinner spines on the ventral valve, although a number of fine spines are present, scattered over the venter and anteriorly. The spine bases are lower, shorter and less conspicuous than in *Ramaliconcha*. *Balkhasheconcha* also has more subdued spine-bases and anterior spines are erect. *Campbelliconcha* Waterhouse, 2013 from middle Visean of east Australia has fine spines posteriorly, and very fine spines anteriorly: none have very elongate bases. The dorsal valve is slightly thickened.

Ramaliconcha bitteri Waterhouse, 2013

Fig. 154-158, aff. Fig. 159

2013 *Ramaliconcha bitteri* Waterhouse, p. 261, Fig. 8.16 - Fig. 8.20.

Diagnosis: Small shells with ventral sulcus and semigeniculate short trail, spine bases coarse and elongate over both valves, with erect spine bases restricted to the posterior lateral shell.

Holotype: GSC 133352 figured as Waterhouse (2013, Fig. 8.17A) and herein as Fig. 155A, from Member A, Jungle Creek Formation, Canada, OD.

Material: Single ventral valves from JBW 75, 188, 515, 610 and 748, ventral valve and fragments from JBW 517, a dorsal valve from JBW 615 and 725, three ventral valves from JBW 597. More than ten ventral valves and two dorsal valves from JBW 412 and numerous ventral and dorsal valves from JBW 40. About twenty dorsal and ventral valves from JBW 426. Six ventral and six dorsal valves from JBW 175, a specimen with valves conjoined from JBW 802, and two ventral valves and specimen with valves conjoined from JBW 803. Member A, Jungle Creek Formation. Two ventral and two dorsal valves from JBW 529, Ettrain Formation, are allied.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Aff. Ettrain Formation.

Dimensions in mm:

Specimen GSC	Width	Length	Height	
133357	30	22	9.5	holotype
136060	28	28	7	
133360	42	35	10?	
133359	29	23	9	

Description: Moderate to large in size, a specimen from JBW 802 measuring 58mm wide, 39mm long and 17mm high, without the trail preserved. The ventral umbo is broad with angle of 110º, and not strongly incurved, and the maximum width is placed towards the anterior third of the shell length, with obtuse cardinal extremities and low umbonal walls. A median sulcus commences 10-15mm in front of the umbonal tip and widens at 20-25º, and ventral ears are not well defined. The dorsal valve is very gently concave with low median swelling over the anterior disc and trail, ears are weakly defined, and the disc curves steeply into the very short trail. Ventral ornament consists of crowded elongate spine bases, widening forward, up to 3.5mm long anteriorly, numbering five in 5mm, and these are shorter anteriorly over the first formed part of the trail, and short over the ears. Dorsal ornament is similar: in both valves the bases are comparatively high and crowded.

Details of the ventral interior are masked by ornament from the exterior. Dorsal valve with low cardinal process supported by two high cardinal ridges, median septum extending to the posterior third and in some shells to the anterior third of the length. The dorsal adductors form two elongate weakly raised platforms, bordered by low and narrowly diverging lateral buttress plates, which commence in front of the ventral face of the cardinal process and are short in many specimens, longer in a few.

Resemblances: The ventral valve is more convex and the visceral disc thicker than in *Balkhasheconcha bamberi*

Waterhouse and the ornament coarser, and the dorsal valve moderately concave. Externally the species is externally close to material described as *Waagenoconcha skinderi* Sarytcheva in Sarytcheva (1968, p. 111, pl. 9, fig. 7-12), sharing similar ventral spines and spine bases that are prolonged and swollen. The species *skinderi* comes from the Kokpekten Suite of west Kazakhstan. Klets (2005, p. 40) recorded the species as *Waagenoconcha skinderi* from the Kasimovian Stage, and tabulated the Kokpekten Complex as Serpukhovian and Visean (Klets 2005, Fig. 36). The lateral spines are finer in the Russian species and the sulcus shallower, and growth steps more defined, compared with the Canadian form. No dorsal valves were figured, so that the generic position is not necessarily the same as the Canadian form, and the assignment to *Waagenoconcha* by Klets (2005), if correct, indicates that it is not congeneric. Another larger possible ally with slightly thinner ventral spines was named as *Waagenoconcha infima* Ganelin (1984), of early Carboniferous age in the Hayarmsk Suite of northeast Russia.

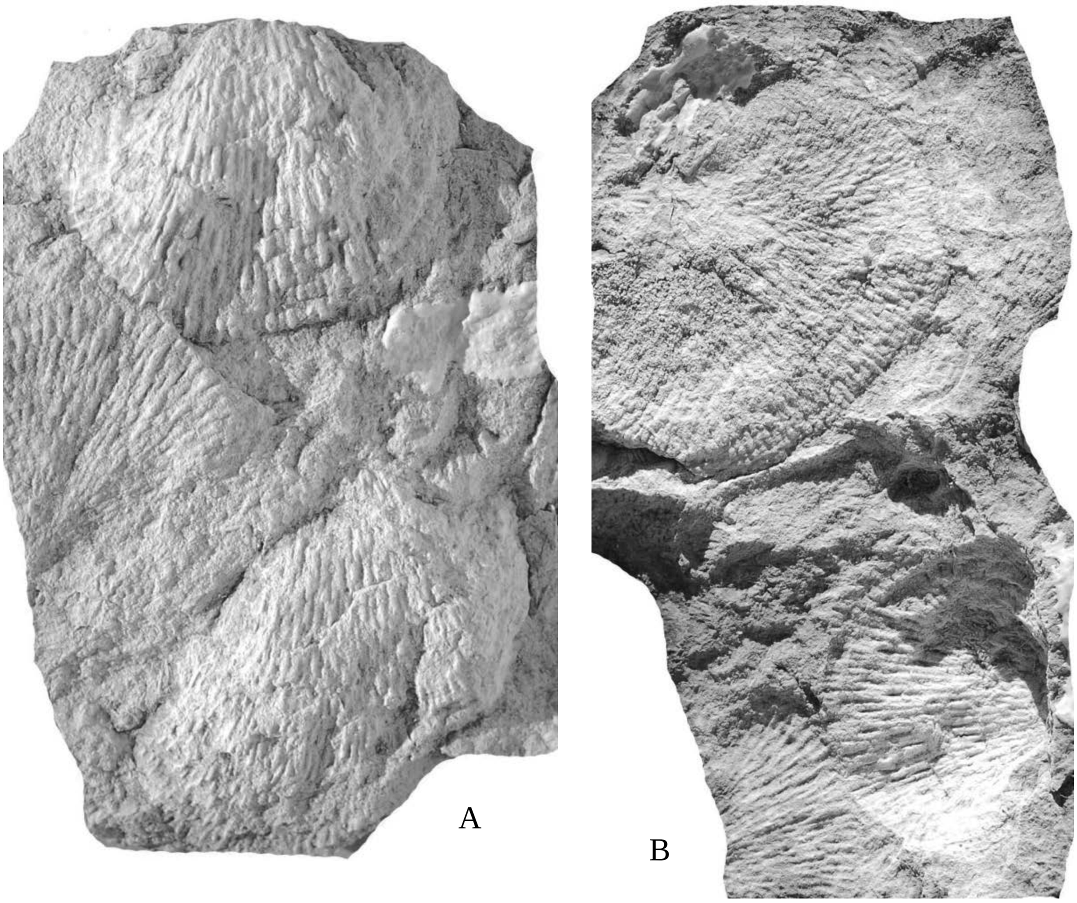


Fig. 155. *Ramaliconcha bitteri* Waterhouse. A, ventral valves holotype GSC 133352 (above) and GSC 136069, with part of dorsal valve, x2. B, dorsal valve interior GSC 133358 (above) and external mould of ventral valve GSC 133359 (below), x1.5. From JBW 40. Member A, Jungle Creek Formation.

Waagenoconcha irginaeformis in Sarytcheva (1968, pl. 10, fig. 1-8, fig. 44, 45, ?46, 47) from Kazakhstan has rather similar lateral buttress plates in Fig. 47, and though none were shown in Fig. 46, perhaps they were worn from the specimen, or more likely the figure illustrates a different taxon. The ventral spines are much finer than in the present species, but figures of the internal dorsal valve (pl. 10, fig. 4b, 5-8) show coarse internal ridges like those of *Ramaliconcha bitteri*.

Fig. 156. *Ramaliconcha bitteri* Waterhouse. Slab of mostly dorsal valves, from JBW 40. Member A, Jungle Creek Formation, x1.4.

A

B

Fig. 157. *Ramaliconcha bitteri* Waterhouse, dorsal valves showing lateral buttress plates. A, internal mould GSC 133356. B, internal mould GSC 133355 from JBW 529. Specimens x2.5, from JBW 40, Member A, Jungle Creek Formation.

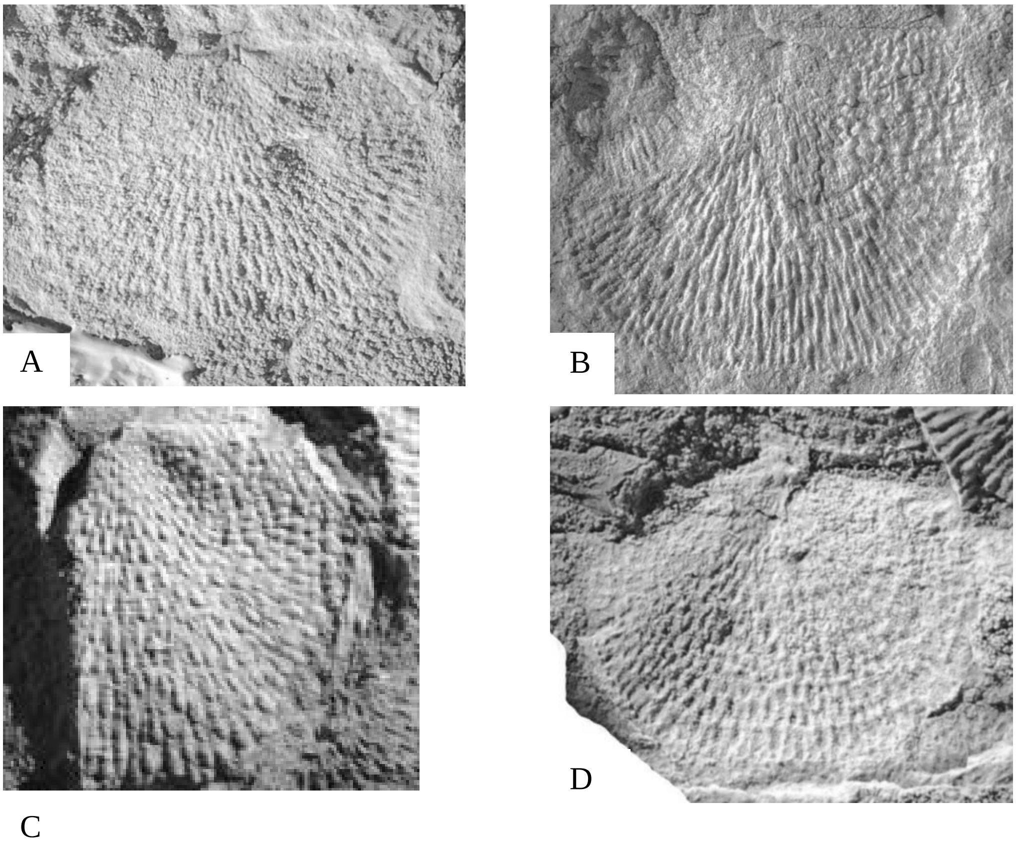


Fig. 158. *Ramaliconcha bitteri* Waterhouse, dorsal valves. A, interior of GSC 133354, x1.7. B, exterior of GSC 133357, x1.7. C, part of dorsal exterior, GSC 136071, x2. D, dorsal interior of GSC 133351, x2.2. From JBW 40, Member A, Jungle Creek Formation.

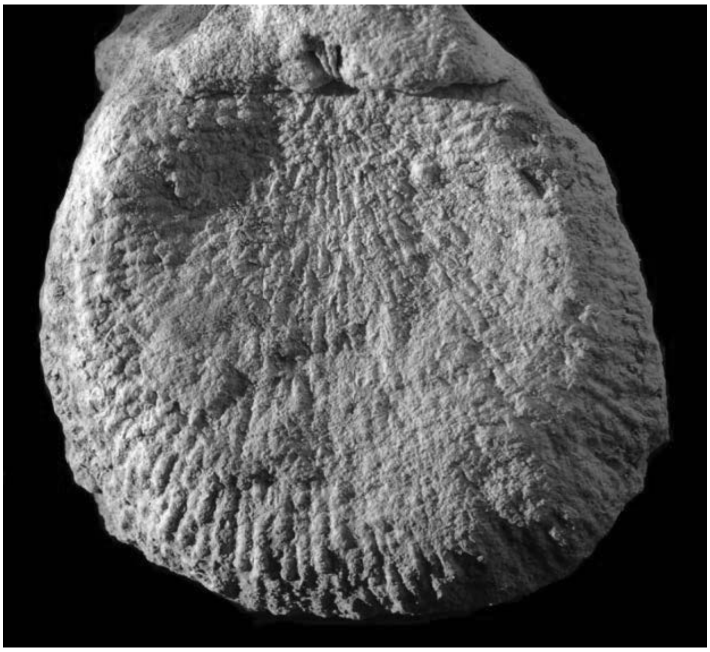


Fig. 159. *Ramaliconcha* aff. *bitteri* Waterhouse, external mould of dorsal valve GSC 136893 x2 from JBW 529, Ettrain Formation. The coarseness of the ornament implies a related species, in the same genus.

Superfamily **AULOSTEGOIDEA** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse, 1975, p. 6 ex Aulostegidae Muir-Wood & Cooper, 1960, p. 94].

Diagnosis: Shells generally but not always attached by spines, often rhizoid, or attached by direct cementation, ventral interarea generally present, dorsal interarea small or often absent, no chilidium. Trails may be simple, geniculate, or elaborate. Shallow to deep body corpus, brachial ridges enclose small productiform shields, each side of anterior adductor scars. Cardinal process bilobate in early genera, high in later genera and may have anterior supporting shafts but no lateral buttress plates.

Discussion: For many years, *Aulosteges* and allies have been associated with strophalosiids, principally on the bases of deformed ventral umbo and common presence of interarea, with insistence that strophalosiids and allies were primarily distinguished by being cemented at the ventral umbo. Researchers in Australia and New Zealand have not been satisfied with that interpretation (Coleman 1957), as elaborated by Briggs (1998), and that view was accepted by Archbold (2001). Waterhouse (1983b, p. 192) remarked on the productiform outline of the brachial ridges .

The Briggs' study provides the best rationale published to date, and the nature of the brachial shields remains the most convincing of morphological ties. But the analysis of evolution and source of the aulostegoids in Waterhouse (2013) shows a more complicated relationship. It appears that the aulostegoids evolved independently of other productiform superfamilies, directly from Strophalosioidea, and not through any intermediate productelloid source. The aulostegoids like other superfamilies lost various attributes typical of Strophalosioidea, such as teeth and sockets and large brachial shields, but evolved into subproductiform shells, not from Productelloidea, but from Strophalosioidea. So the prevalent view of origins and relationships as suggested in Muir-Wood & Cooper (1960) and elaborated by Waterhouse (1975, 1978) is regarded as correct. Furthermore, Aulostegoidea gave rise to a new superfamily, Richthofenioidea.

Family **AULOSTEGIDAE** Muir-Wood & Cooper, 1960

[Aulostegidae Muir-Wood & Cooper, 1960, p. 94].

Diagnosis: Spines on both valves, varied, erect and/or prostrate, often differing in diameter, no regular ribs. Interarea may be well developed on especially ventral valve. Shells often large, planoconvex as a rule, with dorsal valve planar or gently convex over visceral disc, trail simple.

Subfamily **AULOSTEGINAE** Muir-Wood & Cooper, 1960

Diagnosis: Spines not rhizoid. Cardinal process large, bifid to quadrifid, often at angle to commissure, may be supported by high anterior supporting shafts, adductor scars dendritic, marginal ridge generally low except in some groups.

Tribe **TAENIOTHAERINI** Waterhouse 2002b

[Nom. transl. Waterhouse 2013, p. 277 ex Taeniothaerinae Waterhouse, 2002b, p. 27].

Diagnosis: Large shells with erect and/or prostrate spines on both valves, not rhizoid, spine bases usually elongate, and patterns variable. Large lateral shafts as part of the cardinal process in dorsal valve.

Discussion: This tribe was centred in the southern palaeohemisphere during Permian time, and includes the genera

Taeniothaerus Whitehouse, *Taeniothaerus* (*Lakismatia*) Waterhouse, *Carilya* Archbold (syn. *Miniliconcha* Waterhouse) and *Lipanteris* Briggs, with *Reedoconcha* Kotlyar a synonym of *Taeniothaerus*. The genera lack rhizoid spines, unlike Aulosteginae, and shells are consistently large with strong and well spaced often slightly elongate spine bases on the ventral valve. It seems unlikely that these shells were closely attached other than through halteroid spines, and their stability may have depended substantially on their large size and thick corpus, as well as ear spines. The ventral umbo acted more as a resting platform than cemented attachment area. They have a large erect cardinal process supported anteriorly by a large shaft on each side, protruding in front of the hinge.

Taeniothaerin? gen. & sp. indet.

Fig. 160

Material: A fragment showing the posterior part of a dorsal valve from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Hinge wide, close to maximum width, with comparatively high and incurved ventral interarea. Cardinal process as preserved shows two diverging shafts, without buttress plates, behind a median septum, that divides two subelongate deeply impressed adductor scars, which are lightly marked by erratic ridges and grooves. The floor each side is thickened and deeply pitted.

Resemblances: Without any exterior for the dorsal valve, and with only the interarea preserved for the ventral valve, this fragment is difficult to identify, but the wide hinge, high ventral interarea, and high cardinal process supported anteriorly by two diverging shafts points to Aulostegidae. This is the only sign of the family in the lower Jungle Creek Formation, and no member of the group has been recorded from the upper Jungle Creek Formation in Shi & Waterhouse (1996). Aulostegids are abundant in the prolific Middle Permian faunas of Texas, but these as a rule have a slightly different anterior cardinal process, whereas that of the present specimen looks to be closer to that of Taeniothaerini, a group known extensively from the Lower Permian in the southern paleolatitudes of Gondwana (Waterhouse 2013, p. 277), and represented in northeast Russia, for example by *Taeniothaerus rusticus* Grunt in Grunt & Dmitriev (1973). *Aulosteges* itself has cardinal shafts (Kulikov 1974b, pl. 1, fig. 7, 9-11) but is of Middle Permian age.

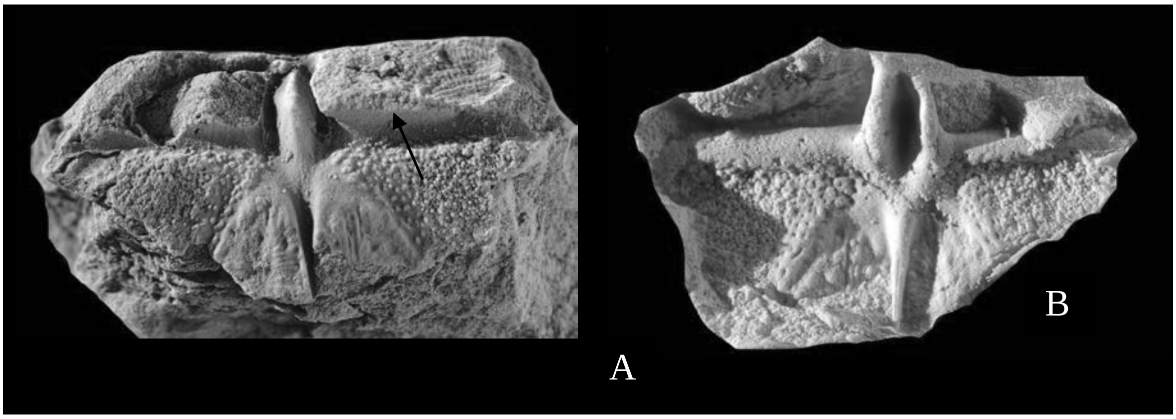


Fig. 160. Taeniothaerin? gen. & sp. indet. A, B, mould and cast of posterior fragment of dorsal valve, GSC 136894 x3 from JBW 581, Member E, Jungle Creek Formation. The arrow points to the curved ventral interarea.

Suborder Linoproductidina Waterhouse 2013

[Linoproductidina Waterhouse, 2013, p. 307].

Discussion: This group incorporates three superfamilies Paucispiniferoidea Muir-Wood & Cooper, Linoproductoidea Stehli and Proboscidelloidea Muir-Wood & Cooper, symplesiomorphic superfamilies that arose from the strophalosiiform Family Devonoproductidae. They share predominantly radial ornament but differ in details of spination and interior. Origins appear, from the fossil record, to have stemmed from a costellate chonetid, at least generically different from the smooth anopliid ancestors of Productidina and Strophalosiidina.

Superfamily **PAUCISPINIFEROIDEA** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 2013, p. 310 ex Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319].

Diagnosis: Characterized by ventral strut spines in a number of genera. Shells small to medium in size, radial ornament usually prominent, no dorsal spines as a rule, interior may be close to that of marginiferoids in usually displaying prominent marginal ridges. Dorsal trails simple or mutiple.

Family **PAUCISPINIFERIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 2013, p. 310 ex Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319].

Diagnosis: Genera with low number of strut spines on ventral valve, usually symmetrically disposed. No dorsal spines.

Discussion: The distinctive ventral ribbing and dorsal commarginals in early members strongly suggest derivation from Devonoproductinae, a Devonian strophalosiiform family (Waterhouse 2013, p. 307). Strong deviation must have been involved, with the loss of teeth, sockets, interareas, and change to the size and outline of the brachiophores. Devonoproductinae Muir-Wood & Cooper has ventral ribs and erect spines, and dorsal laminae. Internally, members of the subfamily display smooth adductor scars, strophalosiiform brachial ridges, teeth and sockets and interareas, and low marginal ridges in each valve, high across the ventral ears. It appears that two groups, Productininae and Anidanthinae were each sourced from Devonoproductinae, because they shared many features, especially the lamellate dorsal valve. Both lost teeth, sockets, interareas and large brachial shields, and both retained the large comparatively smooth ventral adductor platform. One group developed strut spines to evolve into Productininae, followed by other subfamilies and tribes within Paucispiniferidae, with varied and often specialized spines and often high marginal ridges. The other group developed into Anidanthidae, much closer to the original stock, and retaining low marginal ridges and non-specialized usually only ventral spines.

Subfamily **PAUCISPINIFERINAE** Muir-Wood & Cooper, 1960

[Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319].

Diagnosis: Shells with generally six or more large strut spines on ventral valve. Dorsal trail simple or mutiple.

Tribe **PAUCISPINIFERINI** Muir-Wood & Cooper, 1960

[Nom. transl. Brunton et al. 1995, p. 927 ex Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319].

Diagnosis: Transverse shells with varied radial and commarginal ornament and three pair of large strut spines on ventral valve, large ears, transverse outline. Dorsal trail simple.

Genus ***Paucispinifera*** Muir-Wood & Cooper, 1960

Diagnosis: Of medium size to small, usually transverse, with light radial ribs, six prominent strut spines and row of spines along ventral hinge and another row along the ventral umbonal slopes, fine other ventral spines, dorsal marginal ridge well developed.

Type species: *Paucispinifera auriculata* Muir-Wood & Cooper, 1960, p. 319 from Word Formation (Wordian), Texas, OD.

Discussion: This genus is well represented in the Late Carboniferous of Canada, but the Canadian species at first glance do not resemble type *Paucispinifera* from the Glass Mountains of Texas, being smaller, and often less transverse. Yet the basic ornament, including row of hinge spines and row of umbonal slope spines, and large strut spines and low ribs on the ventral valve, is the same. Therefore, although various species superficially resemble *Anemonaria* Cooper & Grant, 1969, they are referred to *Paucispininifera*. Even though the description of the spine ornament in Muir-Wood & Cooper (1960) made no mention of a hinge row of spines, spines are clearly developed along the hinge in figures of the type species by Cooper & Grant (1975, pl. 420, fig. 1, 3, 6, 7, 8, 17; pl. 422, fig. 19, 20), with other examples, and rather few spines along the hinge in Muir-Wood & Cooper (1960, pl. 122, fig. 3, 4). Other species from the Glass Mountains of Texas are less clear over the presence of hinge spines. That may be taken to imply variation in the genus, or the presence of another genus, assuming that poor preservation has not been involved. Some mid-Permian species assigned to *Paucispinifera* by Cooper & Grant (1975) definitely lack a hinge row of spines, and in other respects come very close to *Paucispinifera*. They were interpreted as a special development from *Paucispinifera*, and discriminated as *Glabauriella* Waterhouse, 2013, p. 315. Members of *Glabauriella* are more inflated with stronger ribs compared with *Anemonaria*, and have internal features close to those of type *Paucispinifera,* including prominent dorsal marginal ridge and anterior tubercles.

Genus *Anemonaria* Cooper & Grant, 1969, type species *Marginifera sublaevis* King, 1931 from the Cathedral Mountain Formation (Kungurian) of west Texas, involves ovally subrectangular shells bearing extended ears and distinct sulcus as a rule and shells are moderately to weakly concavo-convex, with ribs subdued or absent. As in *Paucispinifera,* spines are restricted to the ventral valve, and include six strut spines and a row along the base of the umbonal slopes, but there is no hinge row of spines. The cardinal process has a zygidium. Only the type species is found in west Texas, from the Cathedral Mountain Formation (Kungurian) of west Texas. The Middle Permian species *Anemonaria pseudohorrida* (Wiman) is widespread in Arctic faunas, as reviewed by Angiolini & Long (2008, p. 79), with *A. pinegaensis* (Licharew) from faunas of Kungurian age in Kanin Peninsula, and the genus is represented in Mongolia as *A. sulankherensis* Manakov. The genus made an earlier appearance in northern Canada, with *A. auriculata* Shi & Waterhouse of Sakmarian-Artinskian age. *Anemonaria* is very close to *Kozlowskia* Fredericks, and is distinguished through its smoother shell and lower more restricted marginal ridges, not, it may be admitted, very strong discriminants.

Genus *Kozlowskia* Fredericks, 1933, type species *Productus capaci* d'Orbigny, 1842, p. 50, was named for small transverse shells with maximum width at hinge, light radial ribs crossed by very low commarginals, and fading anteriorly. There are spines in a row along or close to the hinge, but no umbonal slope row of spines. This genus is characterized by its shape, with weak or no sulcus and fold, low ribs and spines which appear to include several strut spines. There are substantial similarities to the genus *Caruthia* Lazarev & Carter, 2000, type species *Caruthia borealis* Lazarev & Carter, 2000, p. 13 from the Ladrones Limestone (Atokan), Prince of Wales Island, southeast Alaska. The type species of *Caruthia* differs from *Kozlowskia* in being more rounded in outline with lower umbonal walls, and slightly more ventral spines, and apparently lacking subdued commarginal ornament over the venter, but is close in some respects, except for the presence of an umbonal slope row, and allegedly, no hinge row. Lazarev & Carter (2000) evaluated the genus *Caruthia* as a member of Productinini, which they equated with Chonetellini, and provided a suggested interpretation of the evolution of the tribes. The genus as a member of Productinini was accepted by Brunton (2007, p. 2639) but he refused to merge Chonetellini with Productinini. *Caruthia* does share some attributes with Productinini, especially in general shape and subdued ribbing, but the high marginal ridges in both valves (Lazarev & Carter 2000, Fig. 1Q, 1AA, 1CC, 1DD), and the apparent presence of large anterior strut spines (see Lazarev & Carter 2000, Fig. 1.Q, R) would appear to be consistent with a position with Paucispiniferinae. Strut spines do occur in Productini, but members are not reliably known above Visean (Lower Carboniferous), as analysed in Brunton et al. (2000, p. 426) and Waterhouse (2013, p. 319), and genera within the tribe lack dorsal marginal ridges. Indeed, as described by Lazarev & Carter, *Caruthia* is very close to *Anemonaria* Cooper & Grant, but is older at mid-Carboniferous. The type species is moderately large and transverse with wide hinge, but the numerous species illustrated for various species of *Liosotella* and *Paucispinifera* and other marginiferid genera illustrated by Cooper & Grant (1975) show that attributes of width, auriculation and length vary considerably within a genus. The validity of the genus remains contentious, for the material has not been examined at first hand for the present study, and elucidation of the posterior ventral spines would be helpful.

Retimarginifera Waterhouse, 1970 has rows of spines along the hinge and umbonal slopes (see Grant 1976) but is distinguished by its coarse costae. *Liosotella* Cooper, 1957 has weak developed spines along the hinge and umbonal slopes, but strut spines are less developed.

Paucispinifera carboniferica n. sp.

Fig. 161 - 166

Derivation: Named for Carboniferous Period.

Diagnosis: Small transverse shells with well defined ventral sulcus and narrow anterior dorsal fold, low costae, three pairs of ventral strut spines, row along umbonal slope, few well spaced spines along ventral hinge, scattered additional and usually thin spines over disc.

Holotype: GSC 137296, here designated.

Material: Single ventral valves from JBW 62, 78, 87, 170, 171, 172, 173, 177, 179, 180, 187, 198, 445, 536, 593, 628, 672, and 930, twenty ventral valves, one dorsal valve and six specimens with valves conjoined from JBW 84, two ventral valves from JBW 122, 136, 182, 667 and 778, ventral valve and specimen with valves conjoined from JBW 104, two ventral valves from JBW 136, seven ventral valves from JBW 433, three ventral valves from JBW 528, four ventral valves from JBW 668, three ventral valves from JBW 706, four ventral valves and four specimens with valves conjoined from JBW 742, three ventral valves from JBW 780. Two specimens with valves conjoined and fragments from JBW 420. Six ventral valves and three specimens with valves conjoined from JBW 802. Some ventral valves are possibly both valves conjoined. Specimens recorded as ventral valves may include the concealed dorsal valve. Member A, Jungle Creek Formation.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Shells small and transverse, ventral valve arched with incurved umbo measuring 90-100°, umbonal walls convex in profile, ears moderately large and gently convex with acute cardinal extremities; sulcus commences 2-4mm in front of umbo, and widens at angle of almost 30°, with gently concave floor. Dorsal valve concave and curving gradually into moderately high slender trail, nepionic shell slightly more concave than rest of valve. Anterior shell may be produced into trail. Ornament of six strut spines, on outer ears, lateral slopes and anterior sides of sulcus, each just over 1mm in diameter. A row of well spaced sturdy erect spines lies along the outer umbonal slopes.

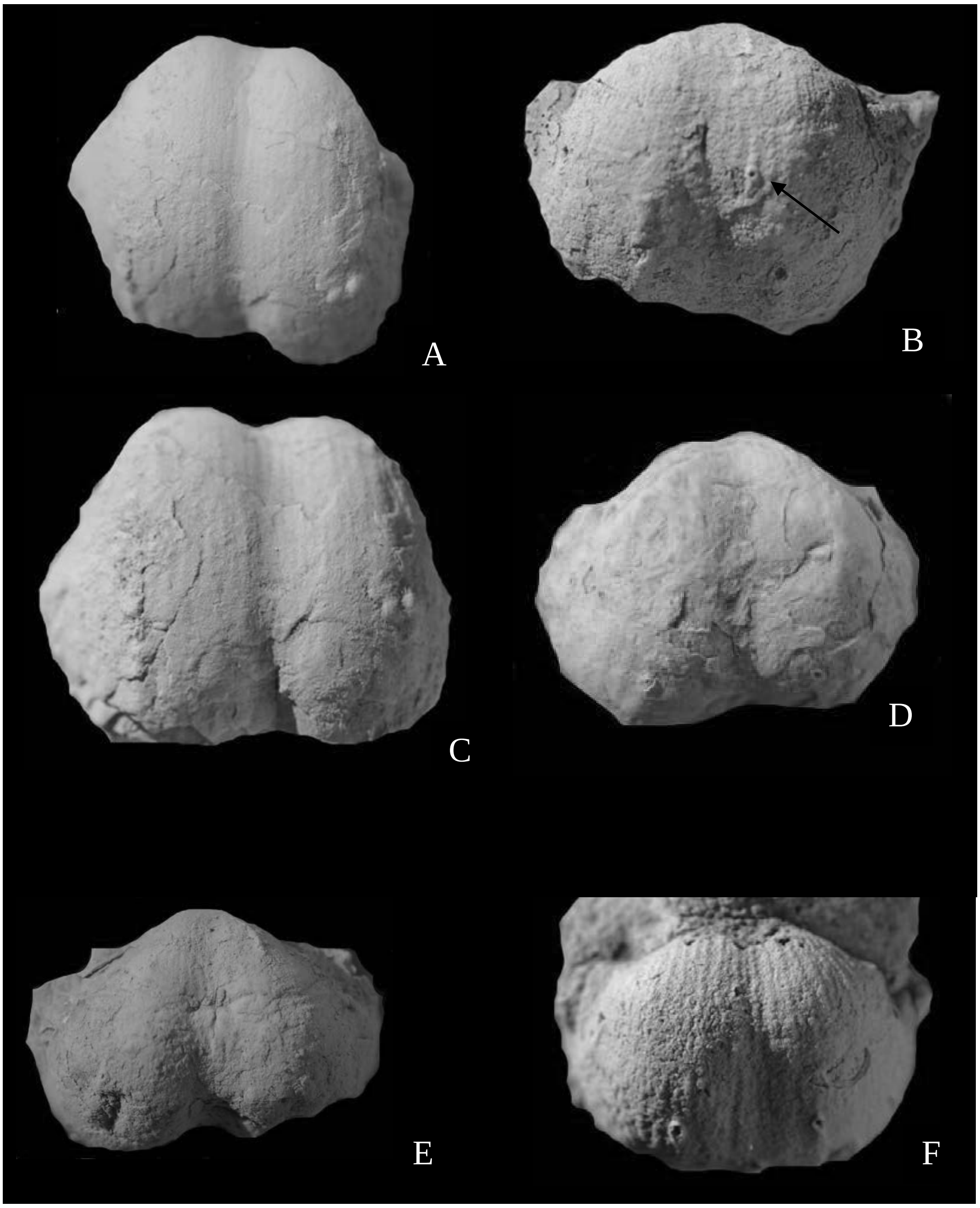


Fig. 161. *Paucispinifera carboniferica* n. sp. A, ventral valve GSC 136895 x2.5 from JBW 84. B, ventral valve GSC 137296 holotype x3 from JBW 84, with arrowed strut spine. C, ventral valve GSC 136896 x2.5, from JBW 84. D. ventral valve GSC 137295 x2.5 from JBW 84. E, ventral valve GSC 136897 x3 from JBW 87. F, ventral view of GSC 137338 x2.5 from JBW 802 with lateral and anterior strut spines. Member A, Jungle Creek Formation.

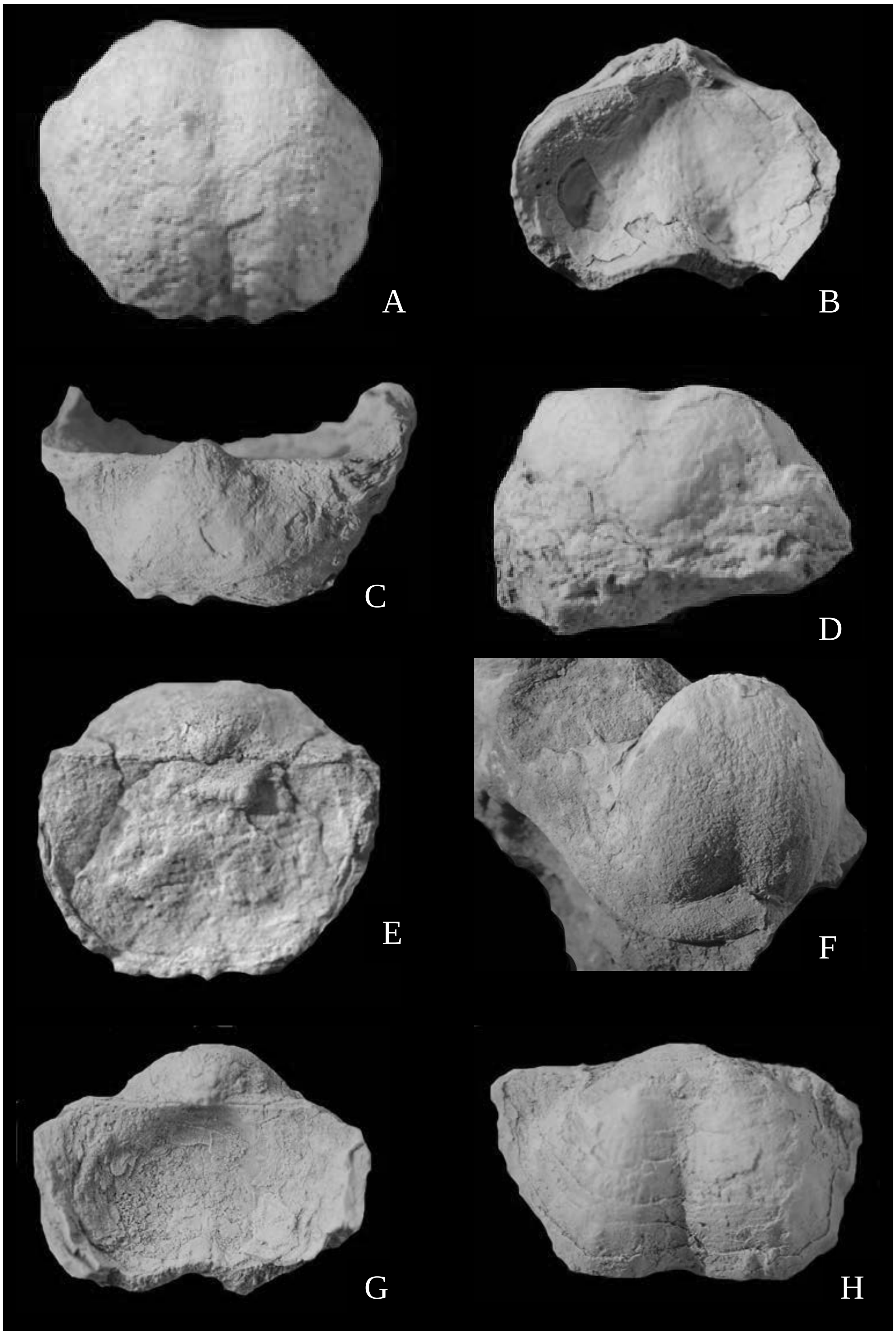


Fig. 162. *Paucispinifera carboniferica* n. sp. A, D, E, ventral, posterior and dorsal views of specimen GSC 136899 x3 from JBW 742. B, dorsal aspect of specimen with valves conjoined, GSC 136900 x2.5 from JBW 742. C, G, posterior and dorsal views of specimen with valves conjoined, GSC 136898 x3 from JBW 742. F, ventral valve GSC 136913 x2.5 from JBW 170. H, external mould of dorsal valve, GSC 136901 x3 from JBW 802. Member A, Jungle Creek Formation.

few other scattered body spines, and one or two on the hinge or outer ears, and row of sturdy usually well spaced spines along the outer umbonal slopes, but because of varying preservation, only some of the specimens show the row of well-spaced fine spines along the hinge. Low radial ribs are present over the anterior two thirds of the shell, four or five in 5mm anteriorly, though these are faint in most specimens, because the outer shell is decorticated. Commarginal rugae are faint and rare on most specimens. The dorsal valve is comparatively smooth, with no spines and faint if any ribs.

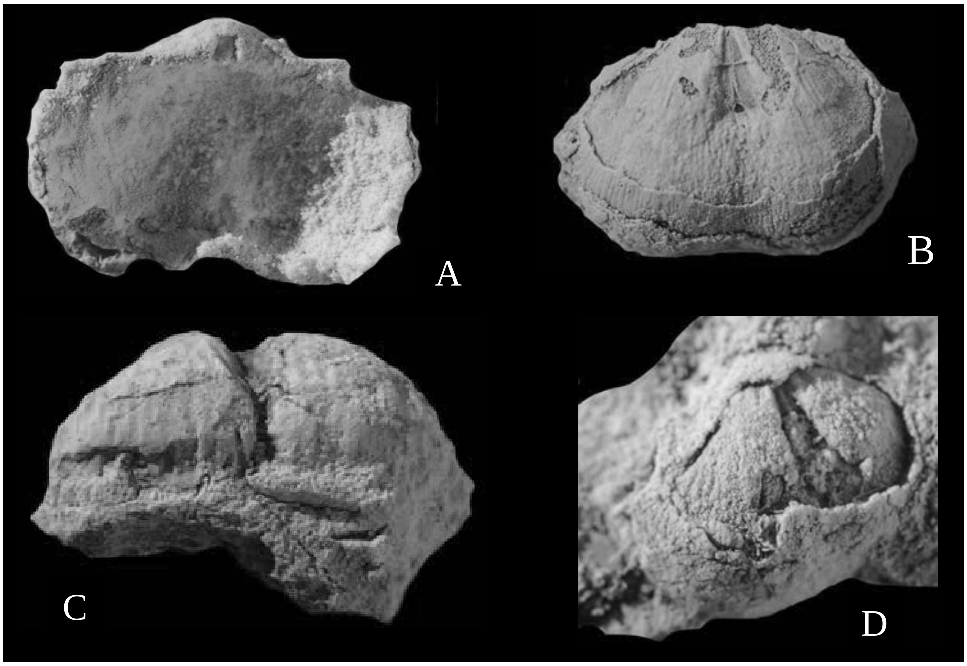


Fig. 163. *Paucispinifera carboniferica* n. sp. A, dorsal aspect of specimen with valves conjoined, GSC 136897 x3 from JBW 104. See Fig. 161E. B, ventral internal mould GSC 136902 x3 from JBW 742. C, anterior aspect of ventral internal mould GSC 136903 x2.5, showing thick marginal ridge, from JBW 136. D, ventral valve GSC 136904 from JBW 445, x3. Member A, Jungle Creek Formation.

Ventral adductors not strongly raised until late in maturity. They form two smooth oval scars divided by a shallow median groove which may be divided by a slender myophragm and become high at late maturity and marked by two or three radial ribs and striae. Large diductor impressions lie to each side, marked by well spaced radial grooves. Strong marginal ridge crosses posterior lateral slopes and encircles the anterior disc; floor lightly pitted. Cardinal process broad and trilobed, supported by sturdy median septum that extends beyond mid-length. Dorsal adductor scars somewhat obscure, posterior and anterior inner pairs, subrounded and apparently smooth. Brachial scars small and close to anterior septum. High ridge along hinge, and marginal ridge encircles the visceral disc.

Fig. 164. *Paucispinifera carboniferica* n. sp., lateral aspect of GSC 137339 x3, showing umbonal slope row of spines. From JBW 84. Member A, Jungle Creek Formation.

Resemblances: This species is distinguished by the depth of the sulcus, which is slightly greater than normal for the genus. In other respects, such as transverse outline, costae and spine detail, and internal marginal ridge, it is typical of *Paucispinifera*. A large number of species of *Paucispinifera* were lavishly illustrated from the Permian of Texas by Cooper & Grant (1975), and tend to be more transverse and ornamented by more prominent costae. They are thus readily distinguished from the Canadian species, although displaying a similar distribution of spines.

Compared with *Anemonaria auriculata* Shi & Waterhouse (1996, pl. 6, fig. 10-28, text-fig. 22-24) from the "*Yakovlevia transversa*" to *Jakutoproductus verchoyanicus* Zones of the Jungle Creek Formation, the present species is close to slightly larger in size, with less incurved ventral umbo, sulcus slightly shallower over the umbonal region

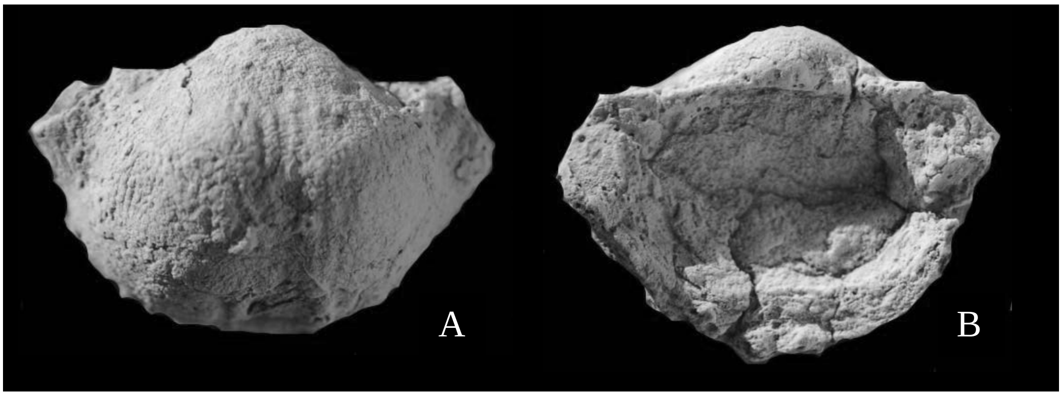


Fig. 165. *Paucispinifera carboniferica* n. sp. A, B, ventral and dorsal aspects of GSC 137339 x3. From JBW 802. Member A, Jungle Creek Formation.

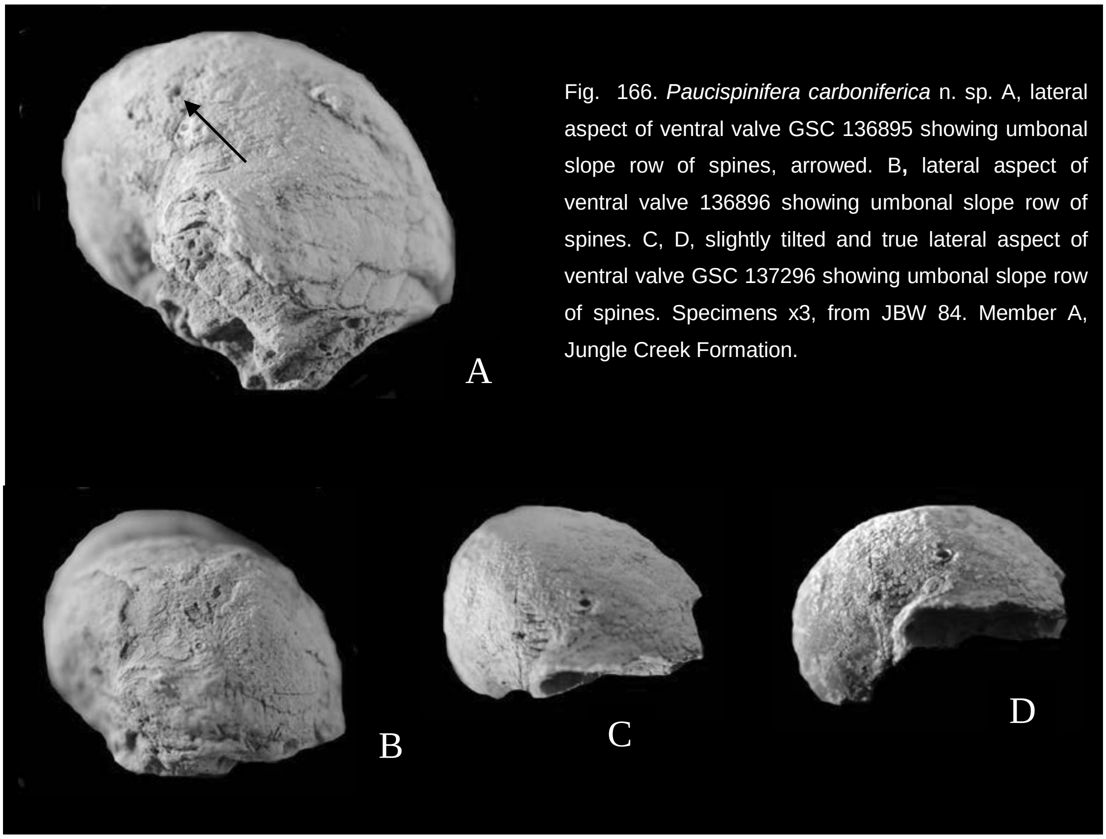


Fig. 166. *Paucispinifera carboniferica* n. sp. A, lateral aspect of ventral valve GSC 136895 showing umbonal slope row of spines, arrowed. B, lateral aspect of ventral valve 136896 showing umbonal slope row of spines. C, D, slightly tilted and true lateral aspect of ventral valve GSC 137296 showing umbonal slope row of spines. Specimens x3, from JBW 84. Member A, Jungle Creek Formation.

and not as deep anteriorly, and ribs are present anteriorly. There is no hinge row of ventral spines in *Anemonaria auriculata*. The Mongolian species *A. sulankherensis* Manankov, 1998 from the early Middle Permian of Outer Mongolia has a shallow but broad sulcus (see Afanasieva 2003, pl. 45, fig. 19, 20), but spine detail is obscure.

Kozlowskia splendens (Norwood & Pratten, 1855a) from Pennsylvanian beds in Texas and New Mexico is particularly close in most details apart from slightly shallower sulcus and fewer differently disposed ventral spines. It has been well figured by Muir-Wood & Cooper (1960, pl. 63, fig. 1-11).

Paucispinifera abramovi n. sp.

Fig. 167 - 173

1971 *Kozlowskia* sp. Bamber & Waterhouse, pl. 11, fig. 1.

Derivation: Named for B. S. Abramov.

Diagnosis: Characterized by virtual lack of ventral sulcus, ventral costae moderately well developed anteriorly, commarginals very faint or missing. Strut spines in three and rarely up to to five pairs on ventral valve.

Holotype: GSC 136906, here designated.

Material: From Member A, single ventral valves from JBW 92, 445, 789 and 802, two ventral valves from JBW 84 and 170, five ventral valves from JBW 182, one ventral valve and three specimens with valves conjoined from JBW 433, three ventral valves and five specimens with valves conjoined from JBW 198, four specimens with valves conjoined from JBW 423, and specimen with valves conjoined and ventral valve from JBW 627. Specimens counted as ventral valves may include specimens with both valves, the dorsal valve being concealed. Jungle Creek Formation. Dorsal valve from JBW 707 and single ventral valve from GSC locality 53991, upper Ettrain Formation.

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Description: Shells transverse, ventral umbo broad with angle of 100º, and low convex posterior umbonal walls diverging at 100-110º, hinge wide with moderately well formed convex and subauriculate ears, maximum width may lie at hinge or at anterior third of shell length, venter convex, sulcus absent from most specimens, and if present commencing near posterior third to half length and very shallow and narrow. Dorsal valve concave with distinct concave ears and none show any fold, but some dorsal valves show slight recession at anterior margin. Low costae arise on a number of ventral valves, often near mid-length or anteriorly, and low broad costae are developed on the anterior dorsal valve. Two to four coarser radial rugae may be present over the anterior trail. Prominent ventral strut spines are developed, a pair on the posterior slopes, and an anterior pair on the flanks of the mid-line or gentle sulcus: rarely not developed or at least not visible, and one or two pair additionally in some shells. Posterior-lateral strut spine on each ventral ear. Other erect spines are scattered over the disc and trail. Hinge spines lie in a row, but one specimen shows several hinge spines in more than one row, and some other specimens have a few additional ear spines. A row of sturdy spines is developed along the lower umbonal slopes, though not always clear due to poor preservation. Low growth wrinkles are present on some ventral valves, on the anterior disc or anterior trail. Such are more prominent on the dorsal valve. Some six or seven growth increments are present in 1mm over mid-length of the ventral valve.

Ventral adductors small, lie on a narrow platform, posteriorly placed. Two large gently impressed diductor scars scored by low longitudinal grooves. Marginal ridge appears to have been low. Fine pustules over posterior floor. Dorsal median septum extends well forward. Marginal ridge much larger than in ventral valve, lying outside that of ventral valve, extends in front of hinge and especially thick in three or four layers anteriorly.

Resemblances: This species co-existed with *Paucispinifera carboniferica* n. sp. and differs by its sulcus being much shallower or complete absent over the posterior shell. Possibly there are more ventral spines. The presence of some specimens that are intermediate in terms of sulcal development does suggest that the two could be regarded as subspecies, or as members of highly variable populations. Several specimens appear to lack the hinge row of ventral spines, and so approach the mid-Permian genus *Glabauriella* Waterhouse, 2013, p. 315, based on *Paucispinifera quadrata* Cooper & Grant, 1975 from Texas, which is characterized by ventral umbonal slope row of spines and large strut spines, with no hinge row of spines. But there are a large number of Canadian specimens, and most display the hinge row of spines, or at least some of those spines, and preservation is such that spines are deemed likely to have been lost, or obscured by imperfect preservation. One Texan species of *Paucispinifera* that may have only a short and shallow ventral sulcus is *P. suspecta* Cooper & Grant, 1975 from the Pinery Member of the Bell Canyon Formation, but this species is elongate with well developed costae.

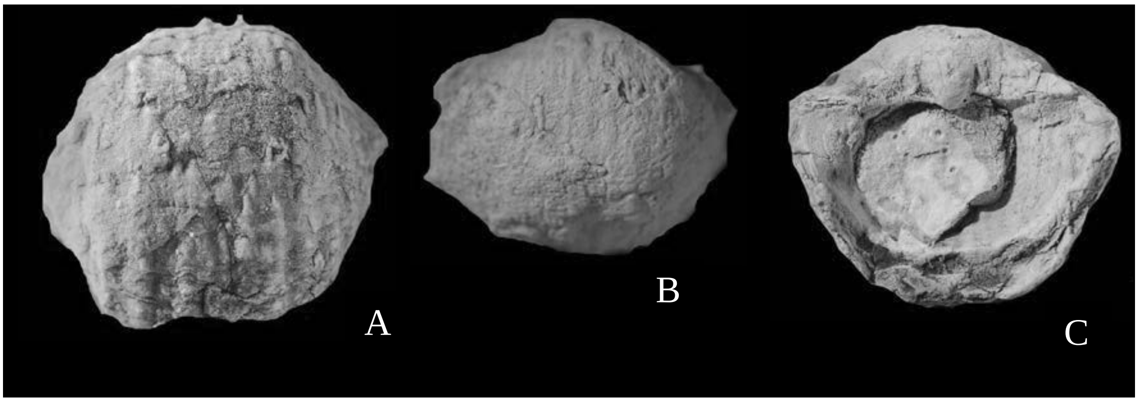


Fig. 167. *Paucispinifera abramovi* n. sp. A, C, ventral and dorsal aspect of holotype with valves conjoined, GSC 136906 x2.5 from JBW 433. B, ventral valve GSC 136908 x2 from JBW 170. Member A, Jungle Creek Formation.

Caruthia borealis Lazarev & Carter, 2000 from the Atokan Ladrones Limestone of Alaska is very close in general appearance, being slightly more elongate, with larger ears, slightly stronger ribs and fewer body and trail spines. There is no row of hinge spines according to Lazarev & Carter (2000), although occasional hinge spines are visible as in their Fig. 1K, which suggests that the hinge row may in fact have been present on well preserved material.

Whether this species *abramovi* involves the upper Ettrain specimen identified as *Kozlowskia* sp. in Bamber & Waterhouse (1971, pl. 11, fig. 1) is not certain, because the specimen was not described, and is not available for the present study. The specimen was deemed to mark a characteristic species of the upper Ettrain Formation, recognized as the Ck zone, and it is likely, in view of various occurrences of *Paucispinifera* in the upper Ettrain beds, collected for the present study, that the generic identity of the specimen needs to be changed.

The species in having a well developed umbonal slope row of spines is distinct from *Kozlowkia* Fredericks, but does at least superficially resemble various species assigned to that genus. A number of species of *Kozlowskia* were summarized by Lazarev in Ivanova & Afanasieva (1984, pl. 1, 2) and Lazarev (1990) from Late Paleozoic faunas of Russia. *Kozlowskia* sp. (Lazarev 1990, pl. 21, fig. 20, 21) from the Rusavkin Horizon of Gzhelian age is close in many respects, though with few ventral spines, whereas *Kozlowskia* sp. of Lazarev (1990, pl. 21, fig. 24-29) from Moscovian beds has stronger anterior ribbing. The Gzhelian species *K. borealis* (Ivanov, 1935, pl. 14, fig. 1-3, 5, 6; Lazarev in Ivanova & Afanasieva 1984, pl. 2, fig. 9-7, Sokolskaya 1952, pl. 45, fig. 238; Lazarev 1990, pl. 21, fig. 9-17) is close in outline, and shows much the same variation in outline, sulcation and ribbing, but has slightly larger ears and fewer spines. Other slightly older species are more strongly ribbed and some are more transverse. The distribution of spines distinguishes the two genera.

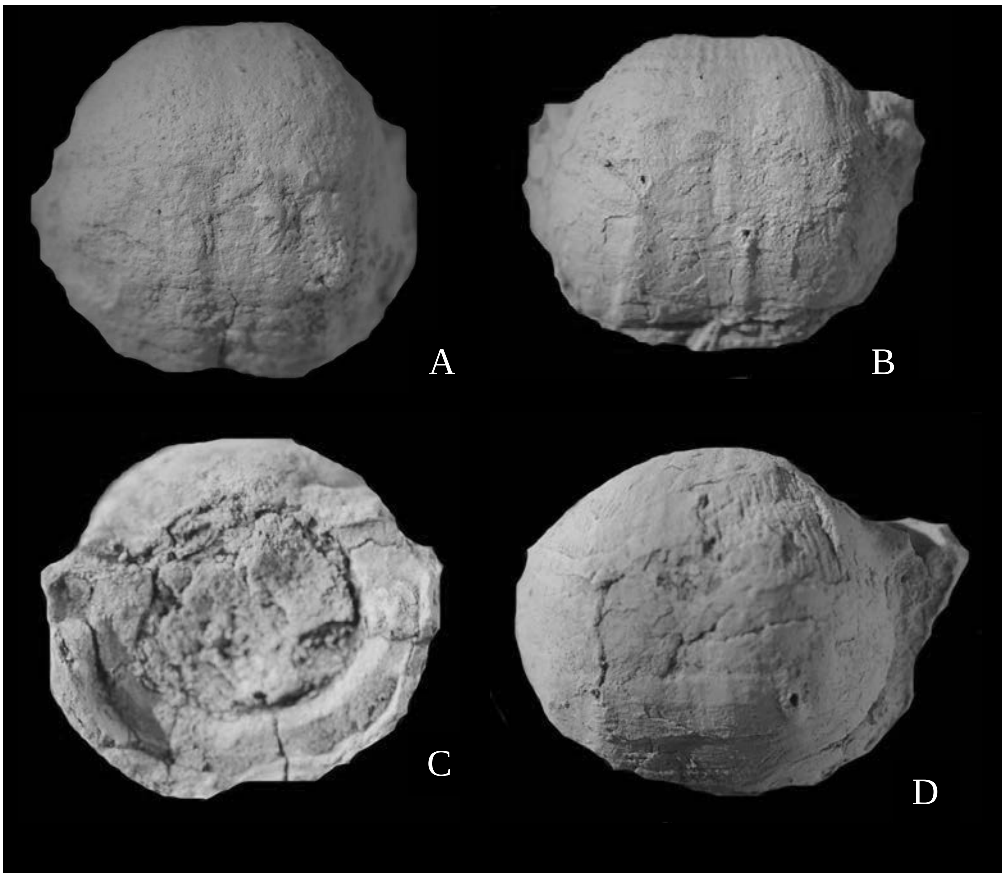


Fig. 168*. Paucispinifera abramovi* n. sp. A, B, C, ventral and more anterior aspect of specimen with valves conjoined, and dorsal aspect of GSC 136907 x3 from JBW 433. D, ventral valve GSC 136909 x3 from JBW 170. Member A, Jungle Creek Formation.

Some of the narrower specimens of *Paucispinifera abramovi* approach *Kozlowskia alata* Cooper & Grant (1975, pl. 312, fig. 1-20, pl. 453, fig. 34) from the Skinner Ranch Formation of west Texas, but this species has larger ears and conspicuous mutiple trails. *K. subsphaeroidalis* Cooper & Grant (1975, pl. 314, fig. 1-20) from the same formation is closer to the broader specimens, and has slightly larger ears and is more costate.

Fig. 169*. Paucispinifera abramovi* n. sp., lateral tilted aspect of ventral valve GSC 137365 x3 from JBW 170, showing spine bases of umbonal slope row. Member A, Jungle Creek Formation.

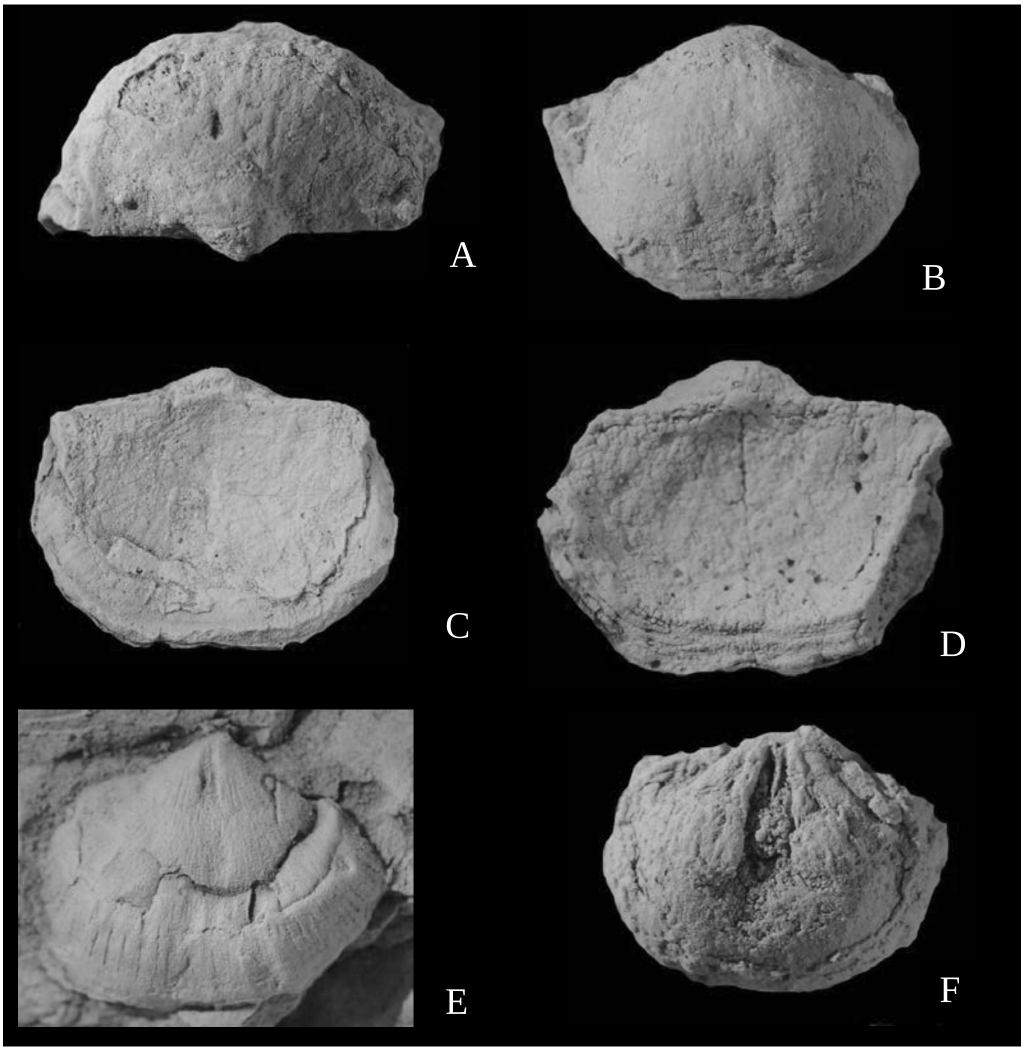


Fig. 170. *Paucispinifera abramovi* n. sp. A, posterior view of ventral valve GSC 136908 x3 from JBW 170 (see Fig. 167B, and 173A, B). B, posterior ventral aspect of GSC 136055 from JBW 170, x3. C, dorsal aspect of specimen with valves conjoined, GSC 137298 x3 from JBW 433. D, dorsal aspect of specimen with valves conjoined, GSC 137297 x3 from JBW 433. E, internal ventral valve GSC 136911 x3 from JBW 445. F, ventral internal mould GSC 136912 x3 from JBW 802. Member A, Jungle Creek Formation.

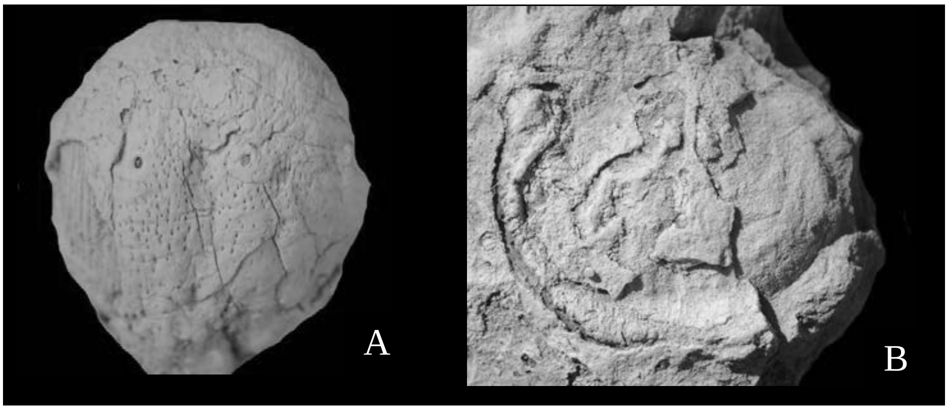


Fig. 171. *Paucispinifera abramovi* n. sp. A, ventral valve GSC 137299 x3 from JBW 433, Member A, Jungle Creek Formation. B, dorsal internal mould, GSC 139975 x3 from JBW 707, Ettrain Formation.

Fig. 172. *Paucispinifera abramovi* n. sp. ventral valve GSC 137453 x3 from JBW 433, showing anterior spines. The specimen is exceptional, having a disc like that of *abramovi,* and a narrowly sulcate trail. Member A, Jungle Creek Formation.

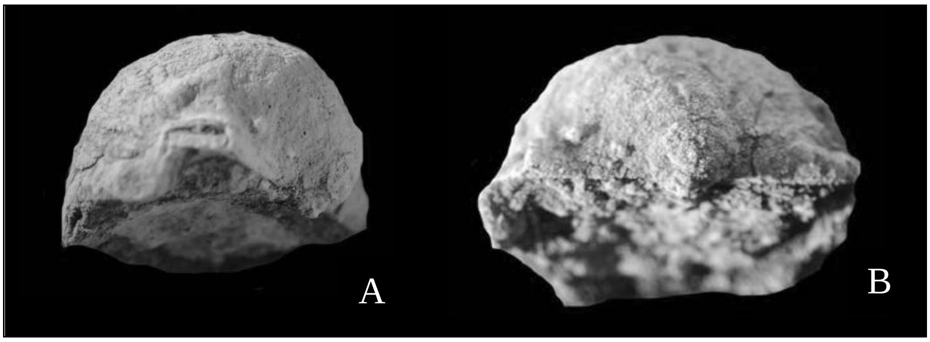


Fig. 173. *Paucispinifera abramovi* n. sp. A, B, lateral tilted aspect and posterior view of ventral valve GSC 136908 x3 from JBW 170. Member A, Jungle Creek Formation.

Paucispinifera sulcata n. sp.

Fig. 174 - 176

Derivation: sulcus – a furrow, Lat.

Diagnosis: Highly arched with deep ventral sulcus.

Holotype: Specimen GSC 136915, here designated.

Material: Nine ventral valves, two dorsal valves and specimen with valves conjoined from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Description: Shells small, umbo small and not strongly incurved, umbonal angle 85-105º, hinge wide at maximum width, ears well separated from umbonal slopes with cardinal angle of 80º, shells also wide near the anterior margin; sulcus commences a little in front of the umbo and from the umbonal tip measures 25º: it becomes deep anteriorly. The dorsal valve is moderately concave, helping to enclose a disc of only moderate thickness, and the fold commences close to mid-length. The surface of both valves is smooth, with low radial ribs weakly suggested beside the sulcus on one or two specimens. There is a prominent pair of spines on the side of the sulcus anteriorly, and a row of spines lies along the outer umbonal slopes, and another row lies along the hinge. There are apparently two extra spines antero-laterally**.** No dorsal spines are developed. Low radial ribs lie over the trail of a few ventral valves.

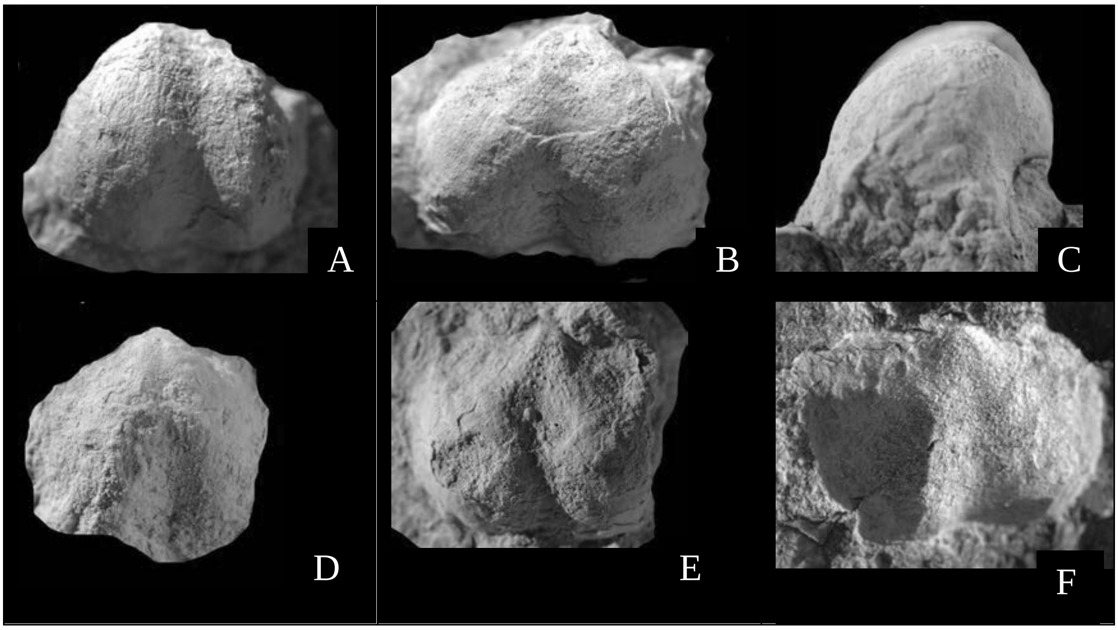


Fig. 174. *Paucispinifera sulcata* n. sp. A, ventral valve GSC 136914 x2. B, C, ventral and lateral aspects of ventral valve GSC 136915 x2, holotype. D, ventral valve GSC 136916 x2. E, worn ventral valve GSC 136917 x2. F, dorsal valve, GSC 137268, with pits opposite ventral spine row. From JBW 18, Member C, Jungle Creek Formation.

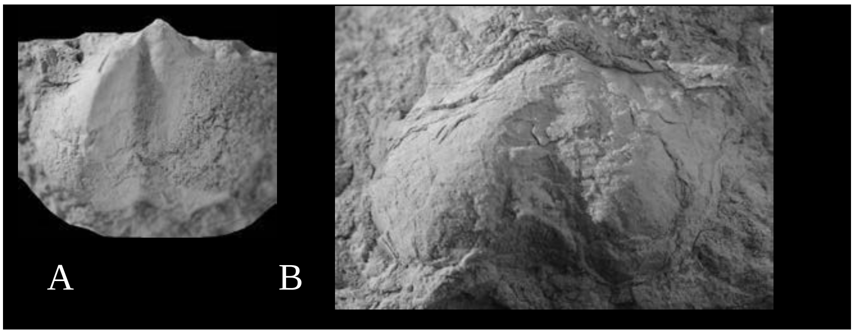


Fig. 175. *Paucispinifera sulcata* n. sp. A, ventral valve GSC 137354. B, decorticated dorsal valve with posterior ventral valve, GSC 137366 x3 from JBW 18, Member C, Jungle Creek Formation.

Subrectangular to trapezoidal adductor scars are smooth, and diductor scars are small and anteriorly placed. Little of the dorsal interior is preserved, other than comparatively large brachial shields.

Resemblances: The specimens come close in shape to *Anemonaria auriculata* Shi & Waterhouse (1996, pl. 6, fig. 10-28, text-fig. 22-24) from the "*Yakovlevia transversa*" to *Jakutoproductus verchoyanicus* Zones of the Jungle Creek Formation but have slightly shallower ventral sulcus, dorsal fold slightly higher in one specimen, low in another, and less conspicuous ears, and they definitely have a ventral hinge row of spines. Although the specimens are somewhat decorticated, enough of the spine detail is visible on different specimens to enable generic placement, and the shape is highly distinctive.

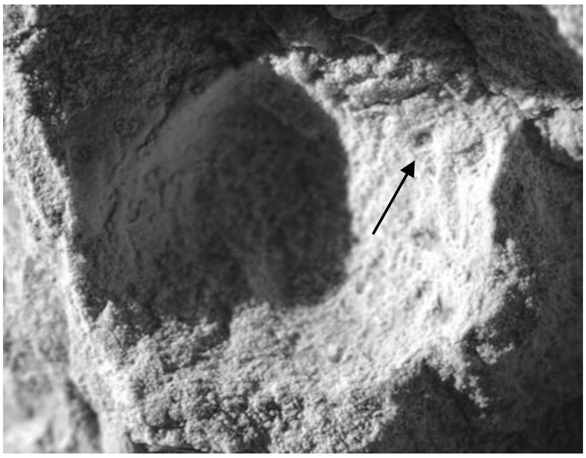


Fig. 176. *Paucispinifera sulcata* n. sp. external mould of ventral valve GSC 137419 x 3, impressed in matrix, showing bases of umbonal slope row of spines as arrowed. From JBW 18, Member C, Jungle Creek Formation.

Genus ***Anemonaria*** Cooper & Grant, 1969

Diagnosis: Spines in row along base of ventral umbonal slopes, a few strut and other ventral spines, no ventral hinge row of spines, costellae absent or faint, sulcus variably developed. Dorsal marginal ridge low, tubercles subdued.

Type species: *Marginifera sublaevis* King, 1931 from Cathedral Mountain Formation (Kungurian), Texas, United States, OD.

Discussion: This genus is very close to *Glabauriella* Waterhouse and possibly *Caruthia* Lazarev & Carter, with much less developed internal marginal ridges, and rather smooth external shell.

Anemonaria sp.

Fig. 177

Material, Description: The broken external mould of a specimen with valves conjoined comes from JBW 19. It has a wide hinge at maximum width, with alate cardinal extremities. There is no row of fine spines along the ventral hinge, but no further detail of ventral spines is revealed, and there are no dorsal spines and only faint very fine ribbing, and large ears. There is no deep ventral sulcus or high dorsal fold, at least over the posterior shell.

Stratigraphic and biostratigraphic level: Member B, Jungle Creek Formation. *Ogilviecoelia initiatus* Zone.

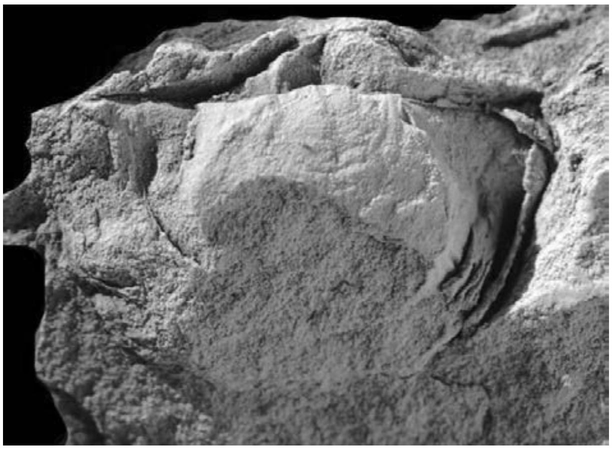


Fig. 177. *Anemonaria* sp., dorsal external mould with part of ventral mould, GSC 136918 x4 from JBW 19. Member B, Jungle Creek Formation.

Anemonaria auriculata Shi & Waterhouse, 1996

Fig. 178

1996 *Anemonaria auriculata* Shi & Waterhouse, p. 68, pl. 6, fig. 10-28, text-fig. 22-24.

Diagnosis: Small with alate cardinal extremities, deep sulcus, well formed fold anteriorly.

Holotype: GSC 96932 from *Jakutoproductus verchoyanicus* Zone (lower Artinskian), Jungle Creek Formation, figured by Shi & Waterhouse (1996, pl. 6, fig. 17-19, 23), OD.

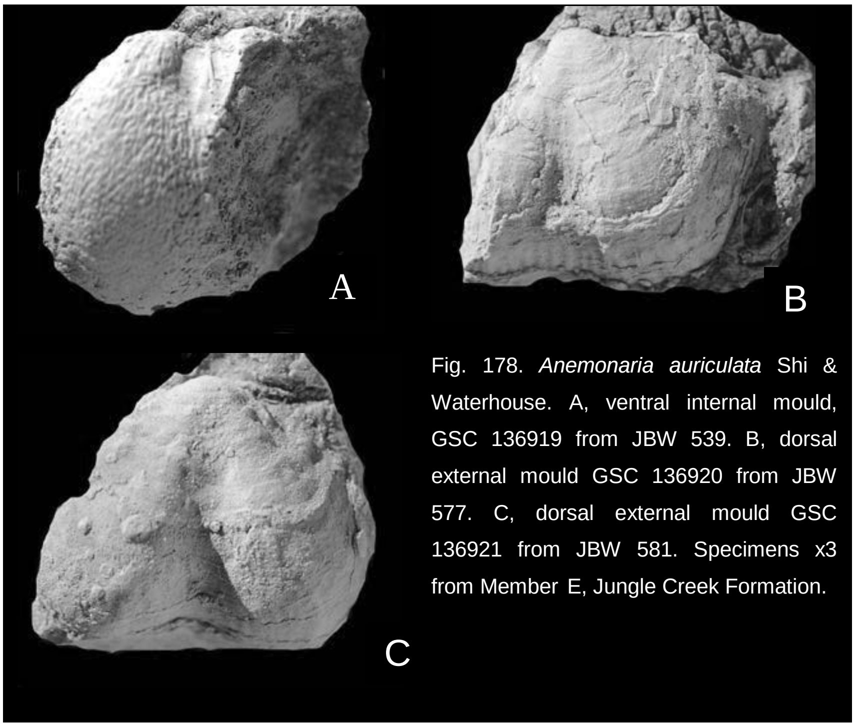


Fig. 178. *Anemonaria auriculata* Shi & Waterhouse. A, ventral internal mould, GSC 136919 from JBW 539. B, dorsal external mould GSC 136920 from JBW 577. C, dorsal external mould GSC 136921 from JBW 581. Specimens x3 from Member E, Jungle Creek Formation.

Material: A specimen with valves conjoined and a dorsal valve from JBW 581, a ventral valve from JBW 539, four ventral valves and two specimens with valves conjoined from JBW 577.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: The material shows a deep sulcus, high fold and low discontinuous radial costae. Spines are obscure but, judged from a row of dimples on the dorsal valve, include an umbonal slope row, and there is no clearly defined hinge row. Faint ribs are developed on the ventral valve of the types, and not visible on the dorsal valve, unlike the anterior dorsal valve of one of the present specimens from the *shii* Zone.

Resemblances: These specimens strongly approach *Anemonaria auriculata* Shi & Waterhouse, 1996 from the younger Jungle Creek Formation in their distinctive shape which features a deep sulcus and so extend the stratigraphic range downwards.

Tribe **RETIMARGINIFERINI** Shi & Waterhouse, 1996

[Nom. transl. hic ex Retimarginiferinae Shi & Waterhouse, 1996, p. 70].

Diagnosis: Visceral disc reticulate, may have hinge and umbonal slope rows of spines, strut spines symmetrically disposed as a rule, trail simple or mutiple.

Discussion: This tribe is very close to Paucispiniferini, but commarginal rugae are more strongly developed. *Retimarginifera* Waterhouse is treated as senior synonym of *Uraloproductus* Ustritsky, as discussed by Waterhouse (2013, p. 456). Immature specimens of *Rugivestis* are close in appearance to immature *Retimarginifera*, apart from being not as broad, and for example, supposed *Uraloproductus* sp. A of Shi & Waterhouse (1996, p. 71, pl. 6, fig. 40-42, text-fig. 25A) appears to be immature *Rugivestis*. What distinguishes *Rugivestis* from *Retimarginifera* is the nasute nature of the mature ventral valve, a feature not shown by mature *Retimarginifera* or *Caricula* Grant. *Spinoparyphella* Liang 1990, p. 11 was tabulated with type species in a stratigraphic column, but does not appear to have been described. *Rugivestis* was placed as Paramarginiferini by Brunton et al. (2000), and Brunton (2007) evaluated *Tethysiella* Kotlyar et al., 2004 as falling close to *Rugivestis,* although there are no conspicuous rugae over the ventral valve of *Tethysiella*, and even those of the dorsal valve are less defined. Ventral spines appear to be fine and few, scattered in a band across the middle of the ventral valve. *Kurtomarginifera* Xu, type species *K. spinata* Xu (1987, p. 225, pl. 12, fig. 1, 2, 9) from the Upper Permian (lower Changhsingian) of South China has reticulate posterior, ventral sulcus, geniculate dorsal valve, halteroid spines near the posterior margin, and row of spines along the umbonal slopes, and large anterior strut spines (Xu 1987, pl. 12, fig. 9). The genus was placed as a synonym of *Transennatia* by Brunton et al. (2000, p. 447), but the arrangement and nature of spines rule this out. (See Waterhouse 2013, p, 317).

The distribution of the tribes is suggestive. Lower Carboniferous members were largely paleotropical in a broad sense, and Paucispiniferini and Probolioniini remained so and extended into northerly paleotemperate regions. But Retimarginiferini developed as well a strong presence in south paleotemperate latitudes.

Subtribe **RUGIVESTIGIINAI** new subtribe

Name genus: *Rugivestigia* new genus from lower Jungle Creek Formation (Asselian) of Canada, here designated.

Diagnosis: Small elongate shells with strong radial costae, strong commarginal rugae over dorsal disc and in some genera varying in strength over the ventral disc, trail long, becoming nasute. Spines limited to ventral valve, may include six symmetrically disposed possible strut spines: and spines well spaced in rows along umbonal slopes and hinge, with other scattered spines especially on the lateral slopes bordering the sulcus.

Discussion: *Rugivestis* Muir-Wood & Cooper, 1960 was classed as Paramarginiferini Lazarev, 1986 by Brunton et al. (2000, p. 431), and there are certainly considerable similarities, including the presence of strut spines, marginal ridges and nasutation. On the other hand the ornament of costae and rugae is particularly close to that of members of the Retimarginiferinae, which also have strut spines and marginal ridges, and the shape although elongate is also close, with ventral valve being less swollen and less circular in outline, compared with Bibatiolinae Waterhouse, 2002b, a subfamily which involves several related allies that are not completely identical. *Paramarginifera* itself is deemed to be yakovleviid, as discussed by Waterhouse (2013, p. 352).

Genus ***Rugivestigia*** n. gen.

Derivation: alteration to genus name *Rugivestis.*

Diagnosis: Small elongate shells with firm radial ribs, commarginal rugae strong over both valves, anteriorly nasute. Well spaced spines in rows along umbonal slopes, and possibly a median row, few anterior and ear spines, including a stout pair. Internal marginal ridge in each valve.

Type species: *Rugivestigia commarginalis* n. gen., n. sp. from Member D (Asselian), Jungle Creek Formation of Canada, here designated.

Discussion: Species assigned to this genus and to *Rugivestis* are characterized by subelongate shape with sturdy costae and strong posterior rugae, and by nasute anterior. Both valves have a low internal marginal ridge. Spine details vary. Muir-Wood & Cooper (1960) reported "probably six spines, symmetrically placed", with no further detail, in the type species of *Rugivestis*, though this is is not clearly confirmed in figures of the type species. Not that that is essential – the description should not be ignored. No posterior spines were mentioned in the text, implying that none were present. In the present form, the best preserved specimens have two well developed rows of spines on each side of the sulcus, one row along the borders of the sulcus, and another row laterally. A strong spine lies near each cardinal extremity, and two or three additional spines are developed near the anterior margin within or beyond the sulcus. The ventral ears may bear a scattering of fine erect spines, and one or two slender spines may lie within the sulcus. The pattern is distinguished from that of *Rugivestis*, chiefly by the two rows each side of the sulcus.

Rugivestis arctica Shi & Waterhouse (1996, Fig. 26; Waterhouse 2013, Fig. 15.7B) was considered to have six symmetrically disposed strut spines, close to the arrangement in type *Rugivestis,* as well as a few spines near the ventral umbo.

Rugivestigia commarginalis n. sp.

Fig. 179A, 180, 181

Derivation: co – together; margin – border, Lat.

Diagnosis: Characterized by having very faint radial ornament anteriorly.

Holotype: GSC 136294, here designated.

Material: Six ventral valves and two dorsal valves from JBW 603, five ventral valves from JBW 74 and three ventral valves from JBW 100, five ventral valves and dorsal fragments from JBW 711.

Stratigraphic and biostratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Description: Specimens small, ventral valve measuring 21mm wide 15mm long, with broad little incurved ventral umbo of 100°, and hinge at maximum width with large ears and cardinal angle of 75°. The valve is subpentagonal in outline, with a shallow sulcus of 20° that anteriorly is replaced by nasutation. The dorsal valve is gently concave with low anterior fold over the disc but the trail is not preserved. Ornament consists of seven or eight up to twelve prominent and strong commarginal rugae over the disc, and possibly further fine rugae over the umbonal part, 3mm long, which is now obscure. The rugae vary in strength over the ears: they may be faint, or limited to the inner ear, or

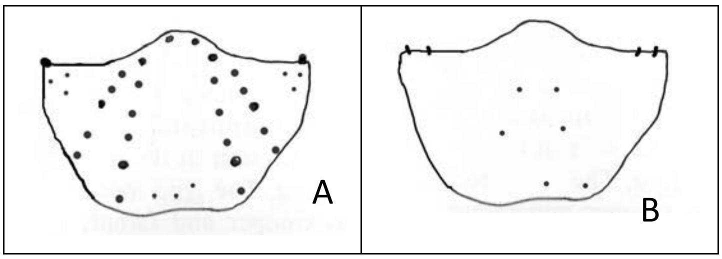


Fig. 179. Spine pattern for ventral valve on A, *Rugivestigia commarginalis* n. gen., n. sp., from Member D. B, spine distribution for *Tethysiella impudens* n. sp. From top of Member C, Jungle Creek Formation.

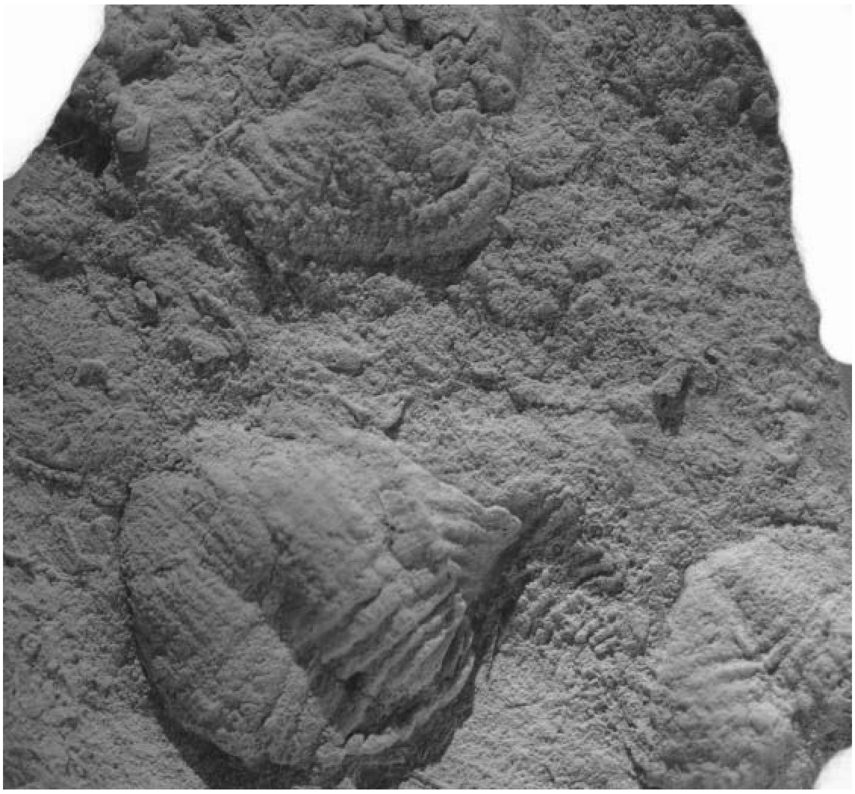


Fig. 180. *Rugivestigia commarginalis* n. sp., cast of block showing ventral valves, including GSC 136928 (lower left) and 136929 (lower right), x3, from JBW 74. Member D, Jungle Creek Formation.

be strong, and in one specimen the lateral rugae meet the interspaces between the rugae over the main disc. The trail is free of rugae. Radial ornament is relatively subdued, up to six ribs in 5mm, and becomes fine and closely spaced over the trail. Dorsal ornament is similar and faint. Spines are restricted to the ventral valve, with spines distributed as in Fig. 179A, mostly as well spaced spines along two rows each side of the sulcus. Some specimens show signs of a hinge row, and in GSC 137264 there is a median row of spines, but this row is not observed in other specimens. A few fine spines are scattered over the disc, ears and trail, and two sturdy strut spines lie on the anterior disc, each side of the sulcus in front of the inner row, and one at each cardinal extremity. If there were a posterior pair of strut spines on the disc, they can no longer be seen.

The anterior disc of the ventral valve is densely pitted, and bends abruptly into a cincture and nasute swelling. The dorsal interior has a low cardinal process supported by a short broad median septum, small tear-shaped adductors, and large pustules over the anterior disc. Another specimen suggests the presence of two high narrow hinge ridges curving laterally from the cardinal process.

Resemblances: *Rugivestis carinatus* (Muir-Wood & Cooper) displays a different pattern of ventral spines, and the anterior nasutation is arched into a tight fold, from a ventral aspect. *Rugivestis pristina* Carter & Poletaev (1998) from Atokan of Ellesmere Island in the Canadian Arctic Archipelago has one or two pairs of spines posteriorly on the ventral disc, and one or two others anteriorly, indicative of *Rugivestis*. Lazarev & Carter (2000) were not able to provide much detail on the distribution of ventral spines over *R. girtyi* Lazarev & Carter from the Ladrones Limestone of Alaska, of lower to perhaps mid-Pennsylvanian age, but ornament was said to be faint over the visceral disc, and there is virtually no ventral sulcus. *Proboscidella*? *kutorgae* Tschernyschew (1902, p. 643, pl. 59, fig. 1-3) from the Schwagerina-Kalk of the Urals is more finely ornamented by firmly reticulate commarginal and radial ribs over the disc, and the nasute carination less developed. The cincture lies behind a very long trail, with well developed costae. Details of spine distribution are not known.

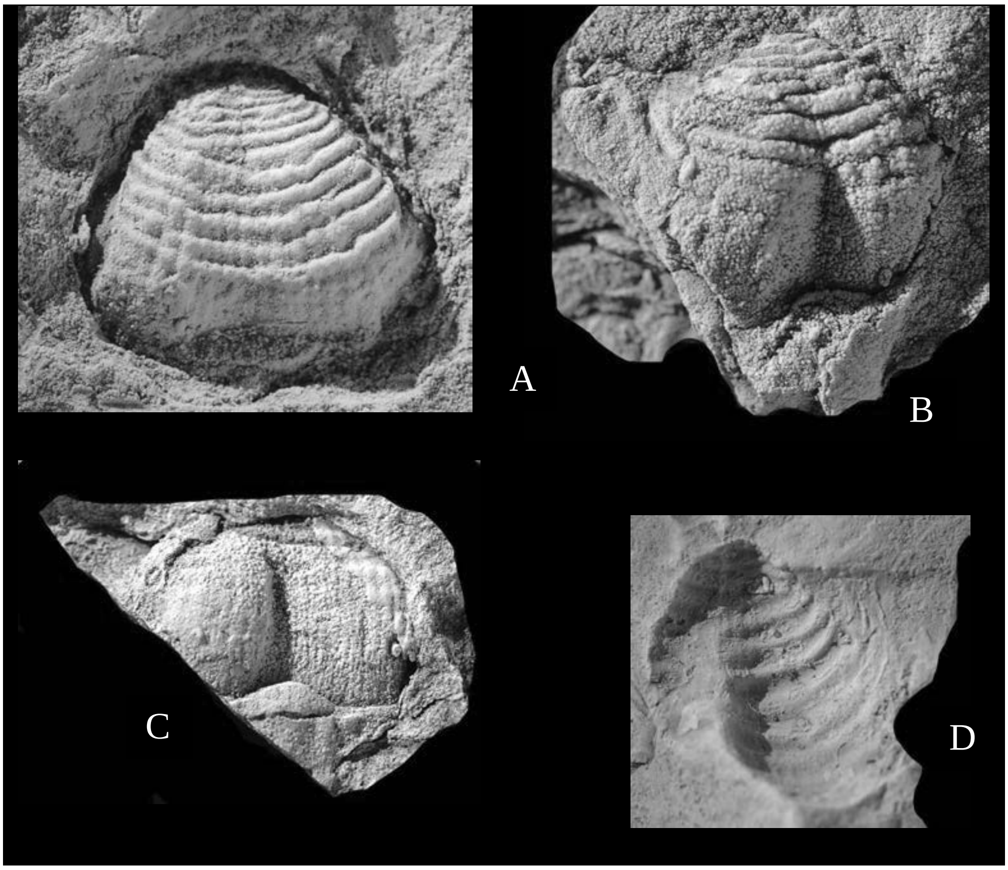


Fig. 181. *Rugivestigia commarginalis* n. gen., n. sp. A, ventral valve GSC 136923 from JBW 100. B, holotype ventral valve GSC 136924 from JBW 74. C, anterior ventral valve with anterior nasute blister and the basal cores of anterior strut spines, GSC 136925 from JBW 74. D, ventral external mould of ventral valve, GSC 136926 from JBW 74. Specimens x3, from Member D, Jungle Creek Formation.

Genus ***Tethysiella*** Kotlyar, Zakharov & Polubotko, 2004

Diagnosis: Small transverse shells with prominent ventral ears and strong costae, weak posterior commarginal rugae laterally, ventral spines few and scattered. Anteriorly nasute, may have cincture.

Type species: *Productus* (*Productus*) *urushtenensis* Licharew, 1937, p. 36 from Urushten Formation (Changhsingian), north Caucasus, Russia, OD.

Discussion: Brunton (2007, p. 2639) claimed that ventral spines, deemed to be absent by Kotlyar et al. (2004), were present on the ventral valve. However Brunton misquoted Kotlyar et al. because those authors did not deny the presence of spines, simply that spines were absent from most of the valve (Kotlyar et al. 2004, p. 521). The present species is close in the predominance of radial ribs and nasute shell and spines, but does not show any posterior commarginal rugae. That leaves open the full alliances of the Canadian species, which is substantially older than the type species, but is not that well preserved, hindering full analysis.

Tethysiella impudens n. sp.

Fig. 179B, 182 - 185

Derivation: impudens – shameless, Lat.

Diagnosis: Small shells with comparatively strong costae, and only moderately developed spines.

Holotype: GSC 137420, here designated.

Material: Some ten specimens with valves conjoined and additional fragments from JBW 862.

Stratigraphic and biostratigraphic level: Fossil band at top of Member C, Jungle Creek Formation. Between *Kochiproductus imperiosus* and *Rugivestigia commarginalis* Zones.

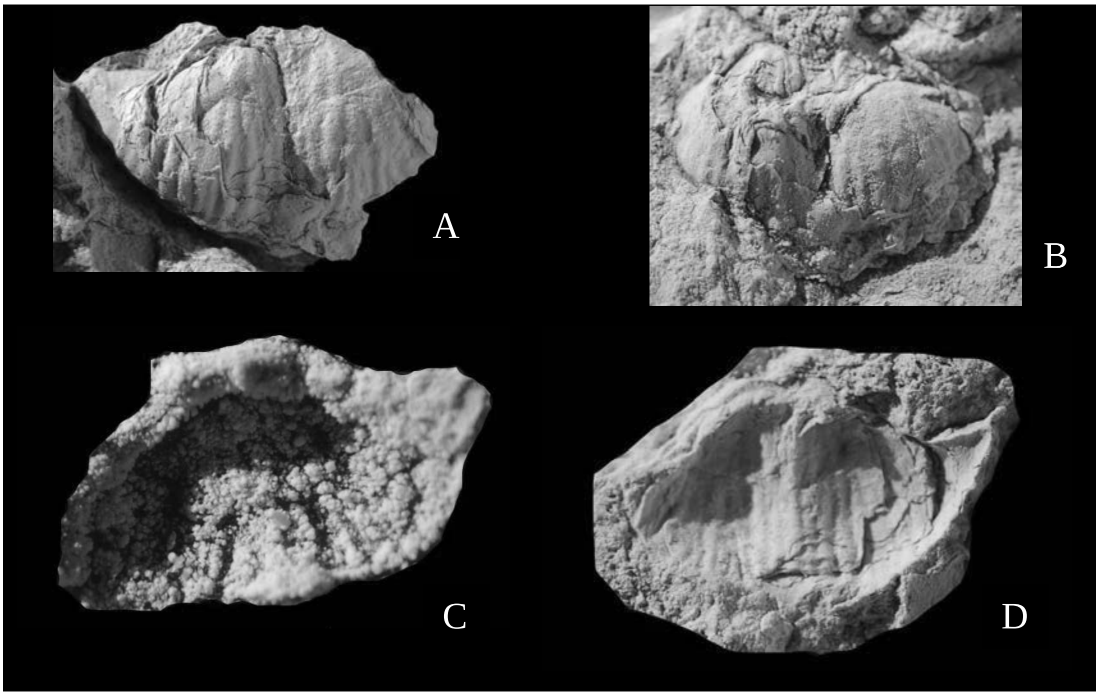


Fig. 182. *Tethysiella impudens* n. sp. A, view of ventral valve, GSC 137420, holotype. B, ventral valve showing nasute anterior, GSC 137421. C, dorsal aspect of GSC 137422. D, exterior of part of ventral valve, GSC 137423. Specimens from JBW 862 in the band between *Kochiproductus imperiosus* and *Rugivestigia commarginalis* Zones, x4. Upper Member C, Jungle Creek Formation.

Description: Specimens are small, one measuring 12mm wide, 7mm long and 4.5mm high, another 13mm wide and 7.8mm long, another 13mm wide, 9mm long and nearly 4mm high, though these dimensions are only approximate because of damage to the specimens. The ventral umbo is broad with an angle close to 110º, the umbonal walls low, and ears comparatively large and gently convex. The sulcus is well defined with angle of close to 25º. The dorsal valve is concave with well defined median fold commencing a little in front of the hinge, and the anterior commissure is slightly produced, with indications of a weakly geniculate ventral trail, and cincture and nasutation typical of the subtribe, but for most specimens, only the disc is preserved. Both valves are ornamented by strong costae, four over

Fig. 183. *Tethysiella impudens* n. sp. A, view of worn ventral valve, GSC 137424. B, ventral valve, GSC 137425. C, ventral valve, GSC 137426, showing nasute anterior. Specimens from JBW 862 in the band between *Kochiproductus imperiosus* and *Rugivestigia commarginalis* Zones, x4. Upper Member C, Jungle Creek Formation.

the fold and four laterally to each side on the dorsal valve, and six within the sulcus and four or five pair laterally on the ventral valve. They bifurcate rarely. No firm commarginal rugae are visible, and no costae lie over the ears. Spines are limited to the ventral valve, preserved in patches over different specimens, to indicate well developed erect spines in a pair, one each side of the posterior sulcus, another pair further from the mid-line in front, and one or two spines near the anterior margin. Two spine bases are visible along the outer hinge of some specimens. These are illustrated in Fig. 179B, but it is not clear that all specimens show exactly the same pattern. The spines are sturdy, but not particularly broad, and so cannot be definitely regarded as strut spines for some specimens.

The ventral adductor platform is well formed, and a thick high marginal ridge is developed around the dorsal valve.

Resemblances: This species is distinguished from *Tethysiella urushtenensis* (Licharew) by its deeper sulcus, coarser ribs and stronger although small anterior nasute bulge.

Fig. 184. *Tethysiella impudens* n. sp. , views of broken ventral valves, GSC 137430 and 137421 from JBW 862 between *Kochiproductus imperiosus* and *Rugivestigia commarginalis* Zones, x2. Upper Member C, Jungle Creek Formation.

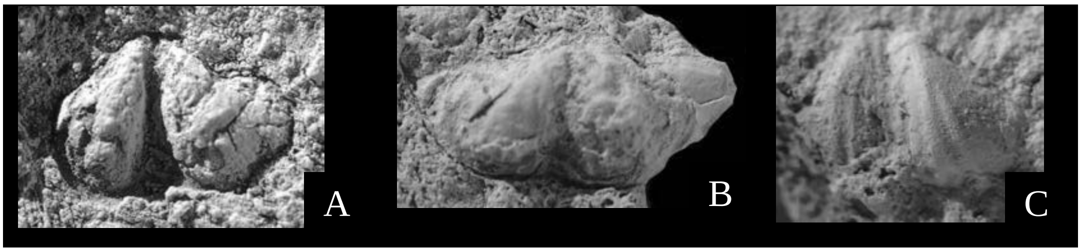


Fig. 185. *Tethysiella impudens* n. sp. A, view of ventral valve, GSC 137427. B, ventral valve, GSC 137428. C, part of ventral valve, GSC 137429. Specimens from JBW 862, found between *Kochiproductus imperiosus* and *Rugivestigia commarginalis* Zones, x4. Upper Member C, Jungle Creek Formation.

Family **ANIDANTHIDAE** Waterhouse, 1968a

[Nom. transl. Sarytcheva 1977a, p. 53 ex Subfamily Anidanthinae Waterhouse, 1968a, p. 1172].

Diagnosis: Costellate, with ventral row of hinge spines, erect ventral body spines, no strut spines, dorsal spines rarely present. Adductor scars comparatively smooth, brachial shields productiform but comparatively large for productiform families.

Discussion: Anidanthidae evolved from Family Devonoproductidae, Subfamily Devonoproductinae Muir-Wood & Cooper, 1960, which has ornament close to that of Anidanthinae, but is strophalosiiform, with teeth, sockets, interareas and large brachial shields. One intriguing aspect is that this same subfamily Devonoproductinae appears to have also given rise to Productininae, which in turn evolved into Paucispiniferinae. Years before, the approach of *Anidanthus* to such genera was noted by Waterhouse (1967a), and earlier, Muir-Wood & Cooper (1960) had considered that *Paucispinifera* and *Anidanthus* to be related in so far as both were treated as Linoproductidae. Those prospective relationships were not elucidated in the *Revised Brachiopod Treatise*.

Subfamily **ANIDANTHINAE** Waterhouse, 1968a

[Subfamily Anidanthinae Waterhouse, 1968a, p. 1172].

Diagnosis: Well defined costellae, hinge spines moderately developed, visceral disc and trail spines inconspicuous as a rule, no dorsal spines, apart from rare exception. Dorsal valve lamellate to varying degree.

Discussion: Brunton et al. (2000, p. 531) recognized *Protanidanthus* Liao, 1979 and *Zia* Sutherland & Harlow, 1973 as members of Anidanthinae, but *Zia* shows little similarity to the subfamily, belonging to Reticulatiinae (Waterhouse 2013, p. 130), and *Protanidanthus* Liao lacks dorsal lamellae and so is deemed to belong to Lirariinae (Waterhouse 2013, p. 332): it is probably a junior synonym of *Fusiproductus* Waterhouse, 1975 from east Asia. As well, *Protoanidanthus* Waterhouse, 1986b was overlooked by Brunton et al. (2000), but appears to be a valid genus and is widespread in high paleolatitudes of both hemispheres (Briggs 1998), although the genus appears to have been most diverse and most prolific in the southern paleohemisphere during Permian time, centred in eastern Australia. *Pseudomarginifera* Stepanov, 1934 was synonymized with *Anidanthus* by Brunton et al. 2000 but is a distinct genus, characterized by large ventral ears and nasute anterior, as outlined shortly **(**p. 221**).** *Nothokuvelousia* Waterhouse, 1986b, based on material from the Rose's Pride Formation of the southeast Bowen Basin, Queensland, Australia, is now considered to be the same as *Anidanthus,* and the type species *aurifera* is synonymized with *springsurensis*. It was synonymized with *Kuvelousia* Waterhouse, 1968a by Brunton et al. (2000), but differs in the nature of its dorsal extended ears, which are differently oriented, and smooth, not ribbed. The dorsal ears on *Anidanthus* are very large, not small as portrayed by Muir-Wood & Cooper (1960) or Brunton et al. (2000), nor variable as claimed by Brunton (2007) in asserting that *Protoanidanthus* had no validity, and it should be realized that assessments by these authors were made without recourse to field study or even perusal of extensive collections at Australian institutions: they relied on small collections of misidentified and non-topotypic material kept in northern museums, as if type material and descriptions, especially from the southern hemisphere, were not important. The genus *Megousia* Muir-Wood & Cooper, 1960 has dorsal ears which typically curve and twist forward at maturity, whereas those of *Anidanthus* extend laterally. As well, *Megousia* has a non-thickened strongly geniculate dorsal trail, and denticulate ventral hinge. *Kuvelousia* Waterhouse, 1968a is close to *Megousia*, and differs in having a massively thickened dorsal valve with laterally extended large untwisted dorsal ears, and high ventral marginal ridge, similar in some respects to *Anidanthus*, but the shape is more inflated, the ears turn forward, and often the hinge is denticulate. *Akatchania* Klets in Abramov & Grigorieva 1988, p. 135 of northeast Russia has low dorsal lamellae and ventral spines only near the hinge. The ventral adductor scars are smooth and elongate. *Mongousia* Manankov, 2008, based on *Anidanthus spineus* Manakov, 1992 from the Wordian of Mongolia is exceptional in having numerous dorsal spines. As noted by Waterhouse (2013, p. 332), its large twisted dorsal ears are like those of *Megousia* Muir-Wood & Cooper, 1960.

Tribe **ANIDANTHINI** Waterhouse, 1968a

[Nom. transl. hic pro Anidanthinae Waterhouse, 1968a, p. 112].

Diagnosis: Ears where large laterally extended.

Discussion: Genera involve *Anidanthus* Whitehouse (syn. *Nothokuvelousia* Waterhouse), *Pseudomarginifera* Stepanov, *Anidanthia* Waterhouse and *Protoanidanthus* Waterhouse. The synonymy for *Anidanthus* in Brunton et al. 2000, p. 531 was peculiar, because according to them, *Anidanthus* was named in 1950 by Hill, yet was treated as senior synonym to *Pseudomarginifera* named in 1934. The genus *Anidanthus* was named by Whitehouse (1928), not Hill (1950), as discussed by Waterhouse & Chen (2007, p. 16). Whitehouse (1928) did not cite a formally named species as type, making it a *genus caelebs*, but indicated to a species subsequently named by Booker (1932, p. 67) as *Linoproductus springsurensis*. Melville (1984) stated that Hill was therefore first to use the generic name in conformity with the ICZN Article 50. 1, but ignored the discussion by Waterhouse (1966, pp. 16, 20) which pointed out that genera proposed before 1931 were deemed acceptable despite failure to designate a described type species (see ICZN 1999, p. 67, article 67.2.2).

Genus ***Pseudomarginifera*** Stepanov, 1934

Diagnosis: Medium-sized weakly elongate to transverse shells with usual anidanthin dorsal ornament and low to firm ventral rugae as a rule, extended ventral as well as dorsal ears, stretching out laterally in line with the hinge, ventral spines, anterior may be nasute, dorsal trail sharply geniculate.

Type species: *Productus ussuricus* Fredericks, 1924a, p. 8 from Middle Permian of Primoyre, Russia, OD.

Discussion: Hill (1950) and Brunton et al. (2000, p. 531) considered that *Pseudomarginifera* was probably the same as *Anidanthus,* whereas Muir-Wood & Cooper (1960) kept the two separate. *Pseudomarginifera* is distinguished primarily by the long ventral ears, and at least occasional nasute ventral interior. A further exceptional aspect lies in the presence of distinct low rugae over the ventral valve. The full size of the dorsal ears is not known, having been broken short from the figured specimens, but seem likely to have opposed the ventral ears, which are extended laterally, without twisting or forward curvature. As well, it seems highly probable that the dorsal valve is not wedge-shaped, and is clear that the trail was sharply geniculate. The type species of *Pseudomarginifera*, *Productus ussuricus* Fredericks, 1924a, p. 8, pl. 2, fig. 17', 17" from Ussuriland, east Russia, involves a ventral valve without large ears, but possibly broken, and a dorsal valve with moderately large ears, not as extended as those of *Anidanthus*, but possibly incomplete. It appears that the dorsal valve was not thickened anteriorly into a wedge. Specimens identified with *ussuricus* from South Primoyre were examined and figured by Kotlyar in Sarytcheva (1977a, p. 56, pl. 5, fig. 1-5, Fig. 34). Her specimens come closest to *Protoanidanthus* Waterhouse, but have somewhat larger ventral ears than in this genus, and even so the ears may have broken short, as for the dorsal valve. The anterior shell is strongly nasute, whereas nasutation is rare in the species so far ascribed to *Protoanidanthus* from east Australia (Briggs 1998; Waterhouse 2015a, b). The anterior dorsal valve could have been geniculate, and a few low commarginal rugae cover the ventral valve.

Productus (*Linoproductus*) *boikowi* Stepanov (1946, p. 198, pl. 1, fig. 13-16) as revised by Kotlyar in Sarytcheva (1977a, p. 57, pl. 5, fig. 4-13) is a more transverse shell, also with ventral rugae and geniculate trail, although none of the figured shells show nasutation. The dorsal ears are comparatively large and extended laterally along a wide hinge without a forward bend, and the ventral ears in pl. 5, fig. 16 are extraordinarily wide, extending laterally along the hinge with no forward deviation. If they represent *Pseudomarginifera*, then they point to a striking difference from other members in Anidanthinae. Other specimens were figured by Solomina (1970, p. 90, pl. 6, fig. 8) and Zavodowsky in Zavodowsky & Stepanov (1970, p. 111, pl. 41, fig. 5 [not 1]. Klets (2005, pl. 9, fig. 1-6) also figured the species *boikowi* as *Anidanthus* and his high quality illustrations suggest that the dorsal valve was geniculate but not thickened (eg. Klets 2005, pl. 9, fig. 1b), and indicate that the dorsal ears were large and not laterally twisted or extended forwards, as far as they are preserved (Klets 2005, pl. 9, fig. 4, 8). There are low ventral rugae. but no definite anterior nasutation, apart from a strong suggestion in the figure in Klets (2005, pl. 9, fig. 6). The various specimens come from the Cisuralian of Verchoyan.

Genus ***Protoanidanthus*** Waterhouse, 1986b

Diagnosis: Small for subfamily, with comparatively large ventral ears and dorsal ears, but dorsal ears not as extended as in various other anidanthin genera. Ventral spines few to numerous, with hinge row, no dorsal spines, dorsal valve not thickened. Adductor scars smooth as a rule, marginal ridge may be well developed.

Type species: *Protoanidanthus compactus* Waterhouse, 1986b, p. 61 from Dresden Formation (Sakmarian), southeast Bowen Basin, Queensland, OD.

Discussion: Brunton et al. (2000) made no mention of the genus *Protoanidanthus*, and later Brunton (2007, p. 2652) asserted that the genus was a synonym of *Anidanthus*. But he gave no adequate reason for setting aside the detailed studies of the group by Briggs (1998), Shi & Waterhouse (1996) and Waterhouse (1986a, 2001, 2013), and ignoring type material. Those authors found that extensive collections from high latitudes in both hemispheres consistently showed populations of specimens close to each other in details of shape, ornament and musculature that have extended dorsal ears and wedge-shaped dorsal valve, as in *Anidanthus*. Other populations of specimens differ from *Anidanthus* species and show consistent attributes of shape, size, ornament and musculature, much less extended dorsal ears and concave unthickened dorsal valves, as in *Protoanidanthus*, the attributes persisting through ontogenetic development and various substrates. In east Australia, the genus is common in early Permian deposits of possible Asselian and especially Sakmarian age.

Protoanidanthus sp.

Fig. 186

Diagnosis: Shells small with few and broad ribs.

Material: Single ventral valves from JBW 92, 504, 526, 615, 628, 780 and two ventral valves from JBW 173 and 814.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone,

Description: Specimens small, an internal ventral mould measuring 18mm wide, 10.5mm long and 7mm high. Ventral umbo broad, not strongly incurved, angle 95-105º, posterior umbonal walls steeply convex and of moderate height, ears very gently convex, distinct, and at maximum width of valve, with subangular extremities, large for the genus. The median valve is less convex than the flanks, and the anterior shell curves steeply from the visceral disc. Ornament of sturdy costae, ten in 5mm anteriorly. The visceral disc on the ventral valve is crossed by low commarginal rugae, becoming stronger on the inner ears. Ventral costae increase rarely, by branching and apparently by intercalation, may be irregular over mid-anterior trail. Ventral spines thin and emerge without disturbance from the costal crests, not numerous: hinge row of a few thicker spines.

Ventral adductor platform slightly raised, diductor scars lightly impressed, with weak longitudinal grooves. Rest of floor bear pits and pustules over the disc, which are finer over the ears and trail.

Resemblances: The simple although moderately large ventral ears are found also in *Anidanthus gijigensis* Zavodowsky (1970, p. 112, pl. 62, fig. 1-4, 12) from the Omolon Horizon of late Middle Permian age. But this taxon has a wedge-like dorsal valve, and although none of the figured specimens show large dorsal ears, it seems possible that the species belongs to *Anidanthus* or *Kuvelousia*. Kungurian material from west Russia assigned to *Megousia kulikii* (Fredericks) by Ifanova & Semenova (1972, pl. 5, fig. 1-14) include well preserved dorsal valves with long ears, and although closer inspection is needed, the specimens appear likely to belong to *Kuvelousia*. Ventral spines are fewer than in the specimens described from overlying members of the lower Jungle Creek Formation.

Fig. 186. *Protoanidanthus* sp., ventral internal mould GSC 136936 x3 from JBW 814, Member A, Jungle Creek Formation.

Protoanidanthus nichollsi n. sp.

Fig. 187 - 190

Derivation: Named for Ian A. Nicholls.

Diagnosis: Small, elongate, and highly inflated shells with low ventral ribs, numbering close to fourteen in 5mm anteriorly.

Holotype: GSC 136947, here designated.

Material: From Member E, single ventral valve and specimen with valves conjoined from JBW 561 and single ventral valve from JBW 577 and four specimens with valves conjoined, eighteen ventral valves, two dorsal valves and further fragments from JBW 581. Single ventral valve and dorsal valve from JBW 538, a ventral valve and specimen with valves conjoined from JBW 195. A ventral valve from JBW 73, Member D.

Stratigraphic and biostratigraphic level: Members D and E, Jungle Creek Formation. *Rugivestigia commarginalis* and *Ogilviecoelia shii* Zones.

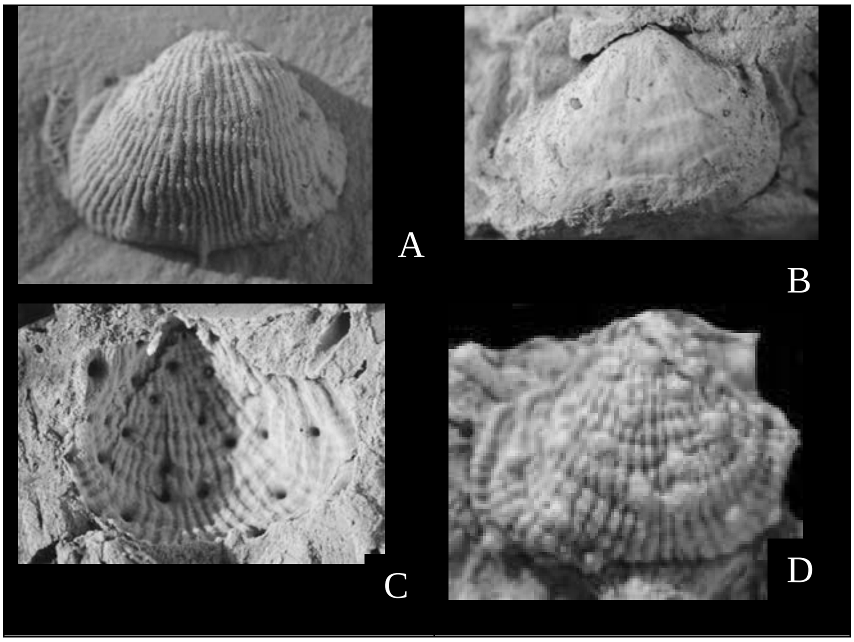


Fig. 187. *Protoanidanthus nichollsi* n. sp. A, cast of ventral valve GSC 136940 x3 from JBW 561. B, internal mould of ventral valve GSC 136942 x3 from JBW 195. C, D, external mould and cast of ventral valve GSC 136941 x4 from JBW 581. Member E, Jungle Creek Formation.

Description: Shells small, elongate and inflated, a specimen from JBW 581 measuring 12.5mm wide, 13mm long and 9mm high, with incurved umbo, high posterior walls convex in profile and diverging at 90°. Other shells also small and transverse, a ventral valve measuring 17mm in width, 11.4mm long and 6.5mm high, with hinge at maximum width as a rule, but shell becoming wide at the antero-lateral margins in mature specimens. Medianly there is a slight diminution in convexity, but no sulcus, and the anterior margin may be arched ventrally. Ears are comparatively large and gently convex, sited at the maximum width of the shell, and with roundly acute cardinal extremities. The venter is medianly convex and anteriorly may pass into a tubiform trail, with median arching of the commissure in several specimens. The dorsal nepionic shell is convex for a width of about 1.5mm, and the remainder of the dorsal valve is gently concave over the disc, with ears no larger than those of the ventral valve, and the subgeniculate trail mirrors the ventral trail with median sulcus. The ventral valve bears fine ribs, twelve to fifteen, usually fourteen, in 5mm anteriorly, crossed by low growth rugae which are pronounced in some of the specimens, spaced about three in 5mm on the trail, and the trail displays one or two incisions,. Mode of costal increase, especially on the lateral trail, is by intercalation. In some ventral valves the commarginal rugae are well developed, and give rise to spines along the crests of the rugae. Ventral ears are smooth. The dorsal valve bears similar ribs, some sixteen in 5mm over the anterior disc, increasing rapidly in strength to ten to twelve in 5mm over the trail, crossed by sharply raised or step-like rugae, that become sublamellar at the start of the trail. The ventral hinge bears a row of erect spines, which become relatively large on the ears and up to 0.7mm in diameter. Erect spines close to 0.4mm in diameter lie over the remainder of the shell, and may form a band of two rows near the start of the trail, and an erratic row of spines lies over the outer umbonal slopes next to the ears. They arise from costal crests, which continue anteriorly, in some cases joined by up to two further costae. There are no dorsal spines, although the external moulds of some specimens do suggest spines, preserved as slender hollow tubes. As the surrounding matrix also shows such hollows, it is believed they are caused by spicules of calcite in the rock matrix, which in some cases have rested against the shell to give the impression of leached-out spinules.

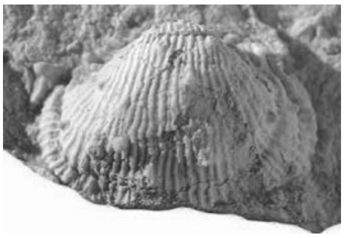


Fig. 188. *Protoanidanthus nichollsi* n. sp. cast of ventral valve GSC 136939 x2 from JBW 581. Member E, Jungle Creek Formation.

The visceral cavity is 3mm thick in small specimen with disc 8mm long. The adductor scars are small subtriangular posteriorly placed impressions, without markings. Diductor scars small; posterior floor bears small pustules. Weak spine tunnels are suggested over the posterior disc in some specimens. Cardinal process broad with alveolus on anterior face, median septum extends to mid-length, may have median slit, brachial impressions laterally placed and small; adductor scars faintly impressed. A lateral ridge crosses the ears obliquely and the start of the trail is marked by low close-set growth ridges.

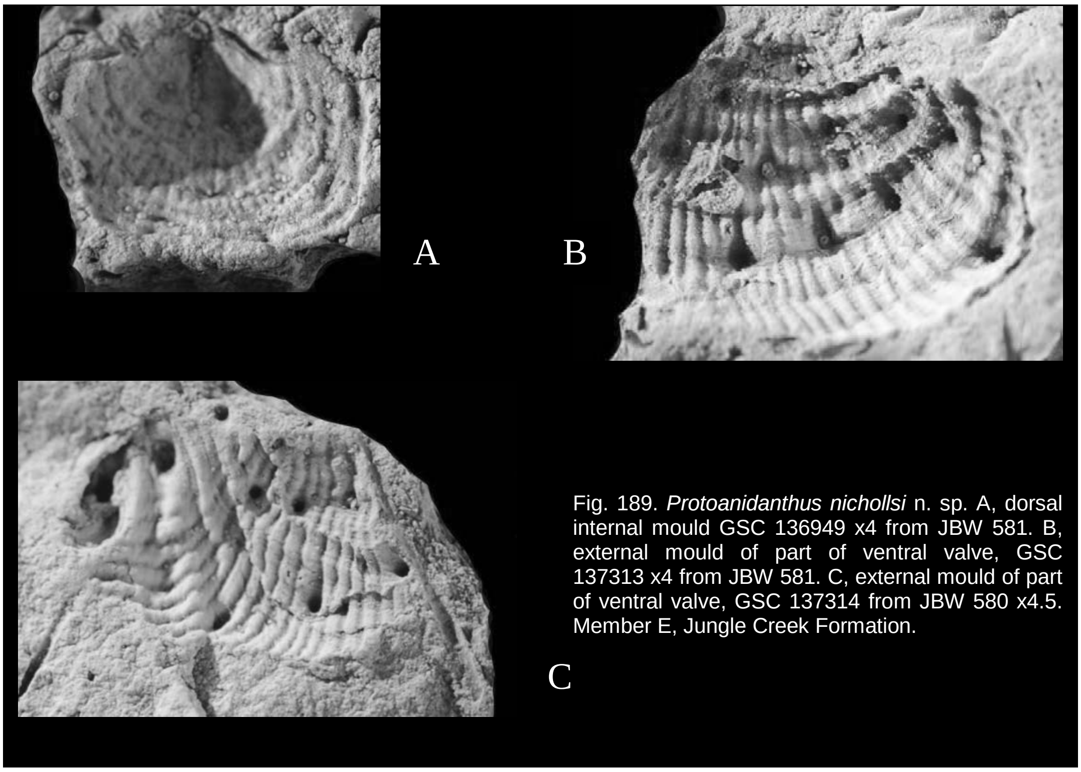


Fig. 189. *Protoanidanthus nichollsi* n. sp. A, dorsal internal mould GSC 136949 x4 from JBW 581. B, external mould of part of ventral valve, GSC 137313 x4 from JBW 581. C, external mould of part of ventral valve, GSC 137314 from JBW 580 x4.5. Member E, Jungle Creek Formation.

Resemblances: This species is narrow and has fine ribbing, and moderately but not excessively large dorsal ears and small ventral ears. Some Russian species ascribed to *Anidanthus* and *Megousia* from northeast Russia by Klets (2005, pl. 9, 10) belong to *Protoanidanthus*, but none are as elongate or as inflated as the present species. One of the few species to show any approach is *Anidanthus rugosus* (Licharew), as described by Ustritsky & Chernyak (1963, p. 88, pl. 11, fig. 7-10) from the Baikursk Suite (Middle Permian) of Taimyr, this species being moderately high and narrow, but not to the same extent as the present species. Kulikov (1974, pl. 3, fig. 5) identified as

Anidanthus aagardi (Toula) an inflated and narrow ventral valve from the Artinskian of the Urals and Russian Platform, but the specimen is not as compressed or highly arched as the Canadian species. *Protoanidanthus umbonatus* Shi & Waterhouse (1996, p. 101, pl. 18, fig. 1- 16) is small with coarse ribs numbering six or seven ribs in 5mm, and no nasutation.

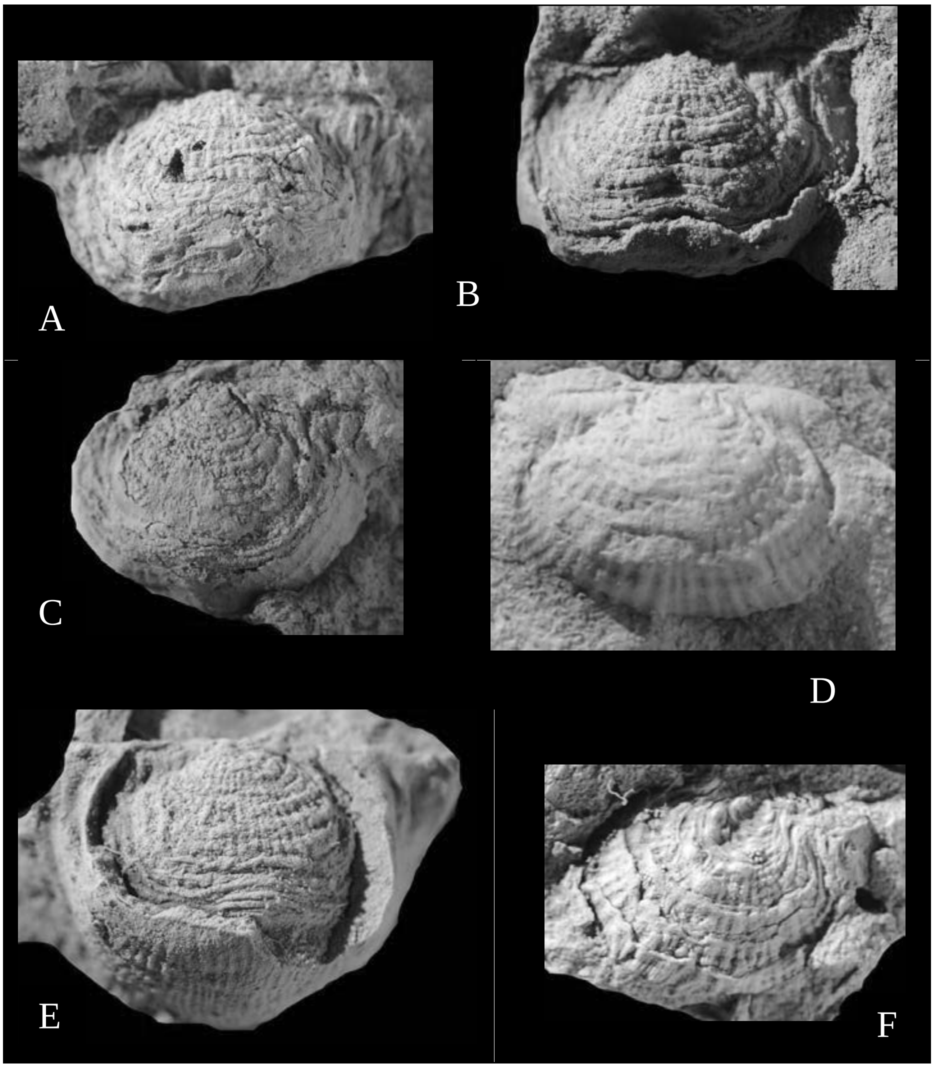


Fig. 190. *Protoanidanthus nichollsi* n. sp. A, external mould of dorsal valve GSC 136945 x3 from JBW 581. B, external mould, dorsal valve GSC 136944 x4 from JBW 538. C, external mould of dorsal valve, holotype GSC 136947 x3 from JBW 581, showing exceptional nasute anterior. D, external mould of dorsal valve GSC 136946 x4 from JBW 581. E, specimen with valves conjoined, ventral valve broken to reveal dorsal valve, GSC 136948 x3 from JBW 561. F, external mould of dorsal valve GSC 136943 x6 from JBW 581. Member E, Jungle Creek Formation.

From the Treskelloden beds of Spitsbergen, ventral valves figured as *Cancrinella singletoni* Gobbett by Czarniecki (1969, pl. 6, fig. 1-3) are narrow and high, with fine wrinkles confined to the lateral flanks. *Cancrinella singletoni* Gobbett (1964, p. 102, pl. 12, fig. 1-7) is much more like *Terrakea* Booker, and is larger and broader. No data on the dorsal valve of the Treskelloden material was provided by Czarniecki (1969). Specimens figured as *singletoni* by Sarytcheva (1977a, pl. 19, fig. 16?, 17) look close to the Gobbett material.

"*Anidanthus*" *inflatus* Li & Gu (1976, p. 260, pl. 162, fig. 9) from the Permian of Mongolia is elongate with strong ribs: the dorsal valve and posterior ventral valve are not figured, and the generic position uncertain.

Protoanidanthus umbonatus Shi & Waterhouse, 1996

Fig. 191

1996 *Protoanidanthus umbonatus* Shi & Waterhouse, p. 101, pl. 18, fig. 1-16.

Diagnosis: Small shells with exceptionally strong ribs.

Holotype: GSC 97128 from "*Yakovevia transversus*" Zone (Sakmarian), Jungle Creek Formation, Yukon Territory, figured by Shi & Waterhouse (1996, pl. 18, fig. 6), OD.

Material: Several broken ventral valves from JBW 580 and single ventral valve from JBW 549. A ventral valve and dorsal valve from JBW 432 from Member D are possibly allied.

Stratigraphic and biostratigraphic level: Members D and E, Jungle Creek Formation. *Rugivestigia commarginalia* Zone, *Ogilviecoelia shii* Zone.

Description: The fragments show large ventral ears, no ventral sulcus and very coarse costae, numbering six to seven in 5mm anteriorly, and lack of sulcus or fold. The dorsal valve is gently concave with large concave ears extending laterally on each side beyond the anterior trail: it is a little thickened anteriorly by up to three trail layers developing in front of the visceral disc, but is concave rather than almost flat, and does not form a wedge. A dorsal valve measures 14mm wide, 8.5mm long and 3mm high; another measures 26mm wide and 13mm long, not including the ears. Both valves are ornamented by sturdy costae, four to six in 5mm anteriorly. Within 5mm, they number six to seven in 5mm on dorsal valve from JBW 432. Dorsal valve without spines, crossed by commarginal rugae, numbering ten to twelve over the disc, with none over the trail. Costae and commarginal rugae are present on the ears of a small dorsal valve, but the ears of a larger dorsal valve are smooth.

Dorsal septum extends to mid-length. Pustules within the brachial shield are very small and crowded. A high marginal ridge crossed the ears and is low around the remainder of the valve.

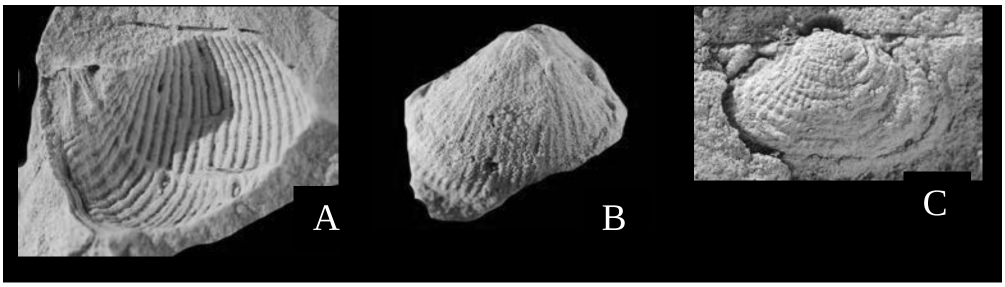


Fig. 191. *Protoanidanthus umbonatus* Shi & Waterhouse. A, external mould of ventral valve GSC 136931 x2 from JBW 581, Member E. B, ventral internal mould, GSC 136937 x2 from JBW 432. C, dorsal valve GSC 136930 x2 from JBW 432. B and C from Member D. Jungle Creek Formation.

Resemblances: Material is not well preserved, but the coarseness of the costae is exceptional for the genus and suggests a likely identification with *Protoanidanthus umbonatus* Shi & Waterhouse. Commarginal rugae are inconspicuous and no specimens show a nasute anterior, unlike rare specimens of *P. nichollsi*, or some shells of *Pseudomarginifera*, which are considered to be further distinguished by the extended ventral ears.

Tribe **MEGOUSIINI** new tribe

Name genus: *Megousia* Muir-Wood & Cooper, 1960, p. 309.

Diagnosis: Ears where large project laterally and then curve forward.

Discussion: Genera include *Megousia* Muir-Wood & Cooper, *Kuvelousia* Waterhouse, *Mongousia* Manankov and probably *Akatchania* Klets. Members are restricted to the northern paleohemisphere, and apparently evolved from *Pseudomarginifera* or more likely *Protoanidanthus,* in view of the short ventral ears*.*

Genus ***Kuvelousia*** Waterhouse, 1968a

Diagnosis: Hinge row and scattered ventral spines, dorsal ears very large, and projecting forward untwisted, dorsal valve wedge-shaped with short trail and strong laminae, hinge often strongly crenulate.

Type species: *Kuvelousia sphiva* Waterhouse, 1968a, p. 1175 from Degerbols Formation (Wordian), Canadian Arctic, OD.

Kuvelousia? sp. A

Fig. 192

Material: A dorsal valve from JBW 439. Ventral valve from JBW 605.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: The dorsal valve is gently concave with apparently large concave ears extending laterally on each side beyond the anterior trail: it is thickened anteriorly by trails developing in front of the visceral disc, but is concave rather than almost flat. A ventral valve which has lost the ears has fine ribs numbering twelve to fourteen in 5mm anteriorly, and a highly arched venter.

Discussion: The anteriorly thickened dorsal valve and forward projecting large ears suggest *Kuvelousia* Waterhouse, and the ears are not twisted, unlike those of *Megousia*.

Fig. 192. *Kuvelousia*? sp. A, exterior of worn dorsal valve showing large ear on right side, GSC 136931 x2 from JBW 439. Member A, Jungle Creek Formation.

Kuvelousia? sp. B

Fig. 193

Description: A ventral valve from JBW 18 is inflated, measuring 22mm wide, 18mm long and 11mm high, with broad incurved umbo and shallow anterior sulcus. Costellae are fine, eighteen to twenty in 5mm, and a number converge and fuse anteriorly. Low rugae cross the shell at the start of the trail, but the presence of spines is uncertain, although they could have been comparatively numerous. Possible identification with *Kuvelousia* is suggested by the bulky and inflated nature of the ventral valve, which is typical of *Kuvelousia*. But this is far from certain.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

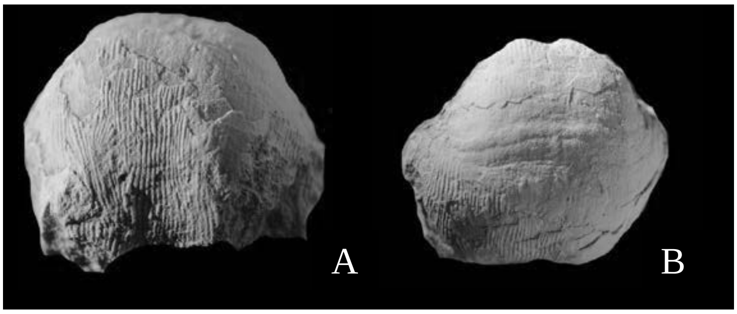


Fig. 193. *Kuvelousia*? sp. indet. B. A, B, anterior and ventral view of largely decorticated ventral valve GSC 136932 x2 from JBW 18. Member C, Jungle Creek Formation.

Subfamily **LIRARIINAE** Waterhouse, 2013

[Larariinae Waterhouse, 2013, p. 332].

Diagnosis: Both valves costellate, spines inconspicuous, limited to ventral valve, forming row along or close to hinge, spines may be scattered and erect over ventral valve. Dorsal valve not lamellate, no spines. Ventral adductors smooth or deeply scored by longtudinal grooves.

Discussion: *Liraria* Cooper & Grant, 1975 from Bone Spring Formation (Artinskian) of Texas has fine ribs over both valves, a row of ventral hinge spines, and small erect spines over the ventral disc. Unlike *Anidanthus* and allies, the dorsal valve lacks commarginal laminae. No member of the subfamily displays very large dorsal ears, or wedge-like dorsal valve. In *Liraria*, the cardinal process is low with median shaft deeply divided in two, with a zygidium. Ventral adductor scars for *Liraria* were described as small and located within a pit, and dorsal adductor scars are not strongly impressed, and neither smooth nor clearly dendritic. Cooper & Grant (1975, p. 1157, pl. 434, fig. 28, 30) drew attention to the presence of two dorsal ridges, one each side of the median septum, between the adductor scars. They erred in stating (1975, p. 1156) that spines lay only on the dorsal valve: in fact they lie only over the ventral valve. *Cimmeriella* Archbold in Archbold & Hogeboom, 2000, p. 101, based on *Productus foordi* Etheridge, 1903, and best illustrated in Archbold (1983), is characterized by strong ribs. It has rather smooth ventral and dorsal adductor scars, and although two lateral ridges are not clearly developed in the dorsal valve, the medium septum shows two fine longitudinal slits between the adductors (Archbold 1983, Fig. 5S, T), and the adductors appear to be bordered laterally by a ridge to each side. The ventral adductors in an allied species *C. flexuosa* (Waterhouse) are somewhat longer. *Protanidanthus* Liao, 1979, although referred to Anidanthinae by Brunton et al. (2000, p. 533), is said to lack dorsal laminae by Brunton et al. (2000), and may be placed in Larariinae, and it is probably a junior synonym of *Fusiproductus* Waterhouse, 1975. *Calandisa* Waterhouse & Campbell in Waterhouse (2013, p. 263) has a hinge row of spines and several sturdy additional spines over the ventral ears, and is found in a Sakmarian fauna of New Zealand. *Chianella* Waterhouse, 1975 from China (=possibly *Achunoproductus* Ustritsky, and not *Haydenella* Reed despite Shen et al. 2017) is yet another ally. The oldest known member of thesubfamily so far known is *Poletaevia* n.

gen. **(**see p**.** 459), based on *Liraria paucispina* Carter & Poletaev, 1998, p. 133 from late Bashkirian or early Moscovian from Ellesmere Island, Canadian Arctic Archipelago. It is distinguished by the ventral spines, which are few along the hinge, and may include one or two pair on the ventral ears, not as strong as in *Calandisa*.

Genus ***Cimmeriella*** Archbold & Hogeboom, 2000

Diagnosis: Small globose shells with strong ribs on both valves, undifferentiated as a rule, small ears, few spines limited to ventral valve and in row along hinge.

Type species: *Productus foordi* Etheridge, 1903, p. 19 from Callytharra Formation (Sakmarian), Western Australia, OD.

Discussion: This genus is very close to *Globiella* Muir-Wood & Cooper, 1960, and yet may be judged congeneric. It has ribs that are stronger than in that genus. It ranged chiefly through high to moderate latitudes in both hemispheres, and especially characterized Early Permian faunas of Gondwana, whereas *Globiella* is found especially in Middle Permian of Russia. Present material shows that the genus ranged into the Upper Carboniferous of Canada, and a number of species described under different names in Russia also appear to belong to the genus.

Cimmeriella orientalis (Abramov & Grigorieva, 1983)

Fig. 194

1983 *Linoproductus orientalis* Abramov & Grigorieva, p. 87, pl. 7, fig. 9-21.

Diagnosis: Transversely suboval medium-sized shells with firm ribs.

Holotype: PIN no. 3908/917 from Natalin Horizon (Bashkirian) of northeast Russia, figured by Abramov & Grigorieva (1983, pl. 9, fig. 9), OD.

Material: From Member A, single ventral valves from JBW 60, 75, 107, 190 and 591; three ventral valves each from JBW 173 and 528, eight ventral valves from JBW 802, ten ventral valves from JBW 562, and twenty ventral valves and one specimen with valves conjoined from JBW 615. From Member D, single ventral valves from JBW 17 and JBW 527.Three ventral valves from JBW 528, Ettrain Formation.

Stratigraphic and biostratigraphic levels: Members A and D, Jungle Creek Formation. *Septospirifer tatondukensis Zone, Rugivestigia commarginalis* Zone. Ettrain Formation.

Description: Specimens transversely suboval in outline with short hinge and maximum width placed near mid-length, a specimen from JBW 615 in Member A measuring 30mm wide, 21.5mm long and 11mm high, umbo broad with angle of 100-110^{o}, cardinal extremities obtuse, shell convex with curvature slightly eased over mid-valve, ears moderately large and convex. Costae number usually number seven to eight in 5mm anteriorly, rarely only five in 5mm in specimens from JBW 107 and 173. Row of spines lie along the hinge, with obscure indications of a second row on the ears in one specimen. Dorsal valve with ribs and a few low rugae, no spines.

Adductor scars ovoid, almost smooth, posteriorly placed and impressed in heavy posterior thickening, diductor impressions deep and transversely oval, placed in front of adductor scars and scored by longitudinal grooves. Shell floor marked by elongate grooves. A transversely elongate depression lies each side of the adductors.

Specimens from Member D are transversely subrounded in outline, a specimen from JBW 17 measuring 31mm wide, 25mm long and 11.5mm high. From the Ettrain Formation, a ventral valve at JBW 528 measures 32mm, 23?mm long and 6mm high. Obtuse cardinal extremities, hinge close to half the shell width, maximum width near mid-length, and ornament of radial costae, six to seven up to eight in 5mm, with narrow crests and wider concave interspaces, ribs increase by intercalation. No spines are visible over the venter, and hinge spines, if any, are obscured by poor preservation. The specimens from Member A and Ettrain Formation are close to those from Member D, apart from the development of finer costae on material from JBW 615 of Member A.

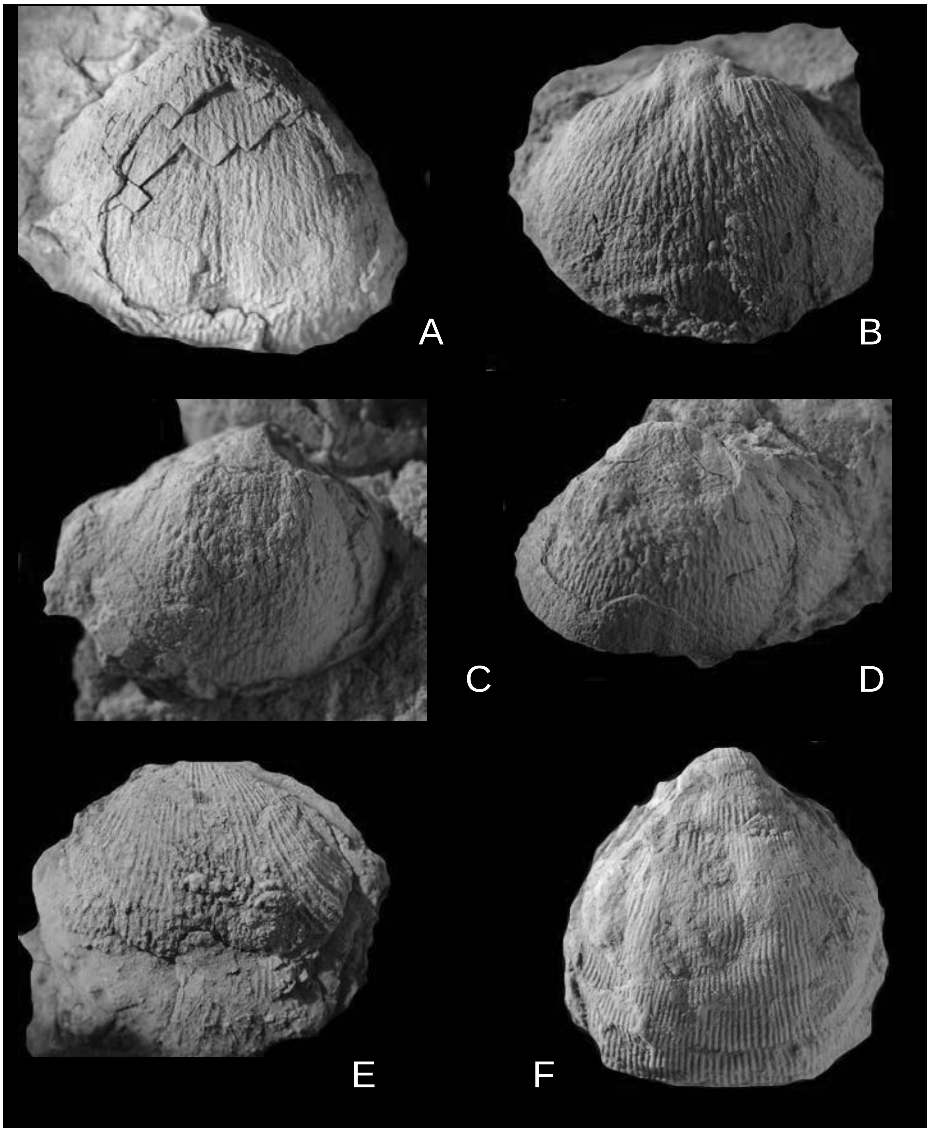


Fig. 194. *Cimmerella orientalis* Abramov & Grigorieva: ventral valves. A, GSC 136950 from JBW 190. B-D, internal moulds from JBW 615. B, GSC 136951. C, GSC 136952. D, GSC 136953. E, ventral exterior GSC 136954 from JBW 107. F, ventral exterior GSC 136955 from JBW 592. Specimens x1.5, from Member A, Jungle Creek Formation.

Resemblances: *Linoproductus orientalis* Abramov & Grigorieva (1983, p. 87, pl. 7, fig. 9-21) is close in shape with six to eight ribs in 5mm, slightly coarser on the whole, and some specimens have a narrow umbo with extended posterior walls and large ears as in a few of the Canadian specimens. The Russian specimens come from the Lower Pennsylvanian Natalin Suite (Bashkirian) of northeast Russia. *Linoproductus velgurensis* Lapina (1957, pl. 5, fig. 1-3), also figured by Volgin (1965, pl. 1, fig. 7, 8), and coming from Bashkirian beds of south Fergana, is moderately inflated and elongate, with fine ribs and postero-lateral wrinkles. *Globiella* (now *Cimmeriella*) *costellata* Shi & Waterhouse (1996, p. 98, pl. 15, fig. 9-24, text-fig. 32) from the “*Yakovlevia transversa*” to *Jakutoproductus* *verchoyanicus* Zones of the younger Jungle Creek Formation is more transverse, with costae numbering eight in 5mm at mid-length, ranging from seven to nine, and low commarginal rugae, not seen in present material. *Linoproductus popowi* (Zavodowsky, 1968, p. 93, pl. 34, fig. 3a-d; 1970, p. 97, pl. 6, fig. 1) from the Burgali Formation (Asselian), Kolyma Basin, northeast Russia, has fine ribs, approaching those of type *Globiella*, and is more inflated. *Linoproductus kulikovi* Zavodowsky (1970, pl. 4, fig. 4-6) from the same level is more elongate, and also has fine ribs. A few other species were described from the region by Zavodowsky (1970), but only *popowi* is close to the Canadian material. Abramov & Grigorieva (1983, pl. 7, fig. 6) reported ex gr. *popowi* from the upper Carboniferous Mishkin Suite of Verchoyan: the specimen is more elongate with finer ribs. *Productus simensis* Tschernyshev (1902, pl. 55, fig. 2-5) from the Schwagerina-Kalk at Tastuba in the Urals is more elongate with *Globiella*-like costellae. Zavodowsky (1970, pl. 5, fig. 4) reported the same species from the Burgali fauna, and given that his figured specimen is small, it may prove to be an immature specimen conspecific with *popowi.*

Cimmeriella mucronata Shen, Shi & Zhu (2000, p. 272, pl. 2, fig. 10-15) from the Early Permian Dingjiazhai Formation of the Baoshan Block in west China has coarse costae but is decidedly more transverse.

Type *Liraria* Cooper & Grant, 1975, based on species of late Early Permian age in west Texas, has more numerous spines along the ventral hinge, which lies at maximum width of the shell, whereas the width of the hinge varies somewhat in species of *Globiella* and *Cimmeriella*, and is never as wide, nor are the shells as transverse. Thin body spines are scattered over the ventral valve.

From the lowermost Hare Fiord Formation of Ellesmere Island in the Canadian Archiipelago, *Liraria paucispina* Carter & Poletaev, 1998, p. 133, is close in some respects, but the spines along the hinge are few in number, numbering only two pair as a rule, with one or two additional and fine spines on the ears. The species is now referred to a new genus *Poletaevia* (see p. 459). The genus *Globiella* is relatively close, differing mostly in the fine nature of the ribs, twelve or so in 5mm. Muir-Wood & Cooper (1960, p. 304) stated that spines were arranged in a row along the hinge and on the ears in type *Globiella*, and rare elsewhere. They did not provide any figure to show the distribution.

There is some approach to specimens figured from the Hare Fiord Formation (Bashkirian) of Axel Heiberg and Melville Islands of the Canadian Arctic Archipelago by Carter (1975, pl. 1, fig. 8-20, 23-32) as *Ovatia* cf. *minor* (Snider, 1915), but ventral valves are more inflated and ribs slightly finer in this material. The Early Carboniferous genus *Ovatia* is more vaulted with larger spines than in *Cimmeriella*, and the entire Hare Fiord fauna was dated as Visean, whereas it is clearly Late Carboniferous, of likely Atokan age, as shown by Nassichuk (1969). The age was corrected by Carter & Poletaev (1998).

Family **YAKOVLEVIIDAE** Waterhouse, 1975

[Nom. transl. Waterhouse 1978, p. 20 ex Yakovleviinae Waterhouse, 1975, p. 11. See Shi 1995, p. 54].

Diagnosis: Wide hinge and geniculate trail, fine radial ornament and weak if any commarginal ornament, may display strut spines. Marginal ridges low to well formed, corpus thickness varies from thin to thick.

The affinities of *Yakovlevia* Fredericks, 1925

The genus *Yakovlevia* Fredericks, name giver of Yakovleviinae Waterhouse, 1975, has been assigned over a few years to various family groups, ranging from chonetid, paucispiniferid, linoproductid, productellin, plicatiferin, to productid. Fredericks (1925, p. 7) treated it as a subgenus of *Chonetes*, on the basis of its wide hinge, row of hinge spines, and fine costellae. Stepanov (1937a, p. 112) transferred the taxon to a subgenus of *Productus*, and Muir-Wood & Cooper (1960, p. 323) allocated the genus to Paucispiniferinae Muir-Wood & Cooper, 1960, then regarded as a subfamily within Linoproductidae. Kotlyar (1961) synonymized *Muirwoodia* Licharew, 1947 with *Yakovlevia*. Yakovleviinae Waterhouse was considered by Waterhouse (1975) to be readily distinguished from Paucispiniferinae, which displays more numerous strong spines, a zygidium and cardinal process and dorsal marginal ridge, and the subfamily was deemed to be linoproductoid, because of the fine costellae, and distinguished by transverse shape with wide hinge, and the presence on at least the allied genus *Muirwoodia* of a few thick strut spines, otherwise unknown in linoproductids. This position was endorsed in a detailed study of the genus by Shi (1995), and Lazarev (1990) followed Waterhouse (1978) in elevating the subfamily to a full family. Further appraisal by Lazarev in Brunton & Lazarev (1997) transferred the genus and allies to Tribe Yakovleviini of Subfamily Productellinae. Brunton et al. (2000, pp. 464ff) shifted Yakovleviini to being a tribe in Subfamily Plicatiferinae, along with numerous other tribes and families in Family Productellidae, and were followed without offering any critical analysis by Tazawa (2001) and Angiolini & Long (2008). Although that position had been elaborated at length by Lazarev (1996) on the basis of what was strongly advocated as a very superior technique called “meronomic analysis”, his conclusions did not last any longer than Fredericks’ initial claim that *Yakovlevia* was chonetid. In a further shift, the group was restored to subfamily status by Lazarus (2000a, 2000b, 2000c), and retained as belonging to Productellidae, as again endorsed by Brunton (2007, p. 2648). Three additional dictyoclostiform tribes were recognized within Yakovleviinae, namely Latispiniferini Lazarev, Reticulatiini Lazarev, and Rigrantiini Lazarev. All genera assigned to these three tribes tend to show large size and strong reticulation of radial and commarginal ornament over the visceral disc, morphological features missing from *Yakovlevia* and *Muirwoodia*. In addition, *Muirwoodia* has massive strut spines, which are never developed in members of Latispiniferini, Reticulatiini, and Rigrantiini, nor Dictyoclostidae. Despite such differences, Lazarev argued for a strong approach to a number of dictyoclostiform genera, based on the presence of a posterior central smooth shell, or what may be termed a Lazarevian patch, due to lack of posterior central papillation or what he called “shagreen” texture over the internal surfaces of the valves, especially in the ventral umbonal region (Lazarev 2000b, p. 25). This interpretation appears less than conclusive, because such a pattern is also found in some specimens of other groups and genera (such as *Umboanctus* Waterhouse in Buxtoniidae) and although it must be allowed that *Yakovlevia* and allies constitute an unusual group, their relationship to dictyoclostid-like genera appears remote. Observations on shagreen pattern are summarized and discussed by Waterhouse (2013, pp. 18-22). The Lazarev application of the term has to be set aside, because the same word had already been used in a different sense by Waagen and other authors. Lazarev (2011) again reassessed the position, now asserting a preference for placement in Productidae, and noting the less than usual profile with its comparatively gently convex ventral valve and anterior disc thickening, and trail at high angle to the disc. His frequent changes in understanding of the *Yakovlevia* affinities reflect the complexity of productidin evolution, and to my mind showed a praiseworthy willingness to grapple with those complexities, rather than accept whatever was current in classification proposals – including his own. That offers a refreshing contrast to some students of paleontology, who defend their previous work at any cost, and other students who copy without question whatever they deem to be in vogue.

Of obscure derivation and relationships, *Yakovlevia* is transverse with flat disc, and its fine radial ornament and sharply geniculate trail suggest Linoproductoidea. Yet there are differences from Linoproductoidea, or at least, other families assigned to that superfamily. The hinge is unusually wide with acute cardinal extremities and muscle scars differ (Tazawa 2001). In the allied genus *Muirwoodia* Licharew, there are four very prominent strut spines, as well as few other body spines and poorly developed row of spines along the ventral hinge. A ginglymus may be developed, and internally the ventral muscle platform is broad and raised, the body cavity moderate to thick, and pustules dense, large and numerous anteriorly. Apart from the strut spines, aspects of the shell, including flat disc, geniculate trail, fine ribs, ginglymus, raised adductor platform, wide low cardinal process, long dorsal septum, and rather elongate brachial shields, suggest aspects of Monticuliferidae Muir-Wood & Cooper. The strut spines and arguably the fine ribs recall Paucispiniferoidea, but the marginal and ear baffle ridge development is low and the trail comparatively simple, in contrast to multiple trails common in Paucispiniferidae and Anidanthidae.

Lazarev (1996) considered that *Yakovlevia* and *Muirwoodia* were related to *Inflatia* Muir-Wood & Cooper, 1960, a Lower Carboniferous (upper Visean) genus of somewhat different appearance, with sulcus, reticulate ornament, prominent hinge row of ventral spines but no strut spines, and weak development of marginal ridging. Given the presence of thicker costae in *Inflatia*, reticulate disc, the different spine ornament, and the different nature of the adductor scars which are broad and strongly dendritic in the ventral valve (Gordon at al. 1993), and different anterior pustulation, it is suggested that *Inflatia* is indeed dictyoclostid, and not closely related to *Yakovlevia* and allies. Possibly *Inflatia* has posterior central internal papillation, considered to be missing from *Yakovlevia*. In 2011, Lazarev dropped any reference to *Inflatia* as being part of the yakovlevinin scenario.

It was claimed by Lazarev (1996) that the Carboniferous genus *Sajakella* Nasikanova in Sarytcheva (1968, p. 141), of upper Visean to Bashkirian age, provided the link between *Yakovlevia* and *Inflatia*. Even though the relevance of *Inflatia* is deemed unlikely, *Sajakella* is close to *Yakovlevia* and *Muirwoodia* in the presence of fine radial ornament and overall shape. Two anterior strut spines are developed in *S.* (?) *martianovi* (Nasikanova), as shown in Sarytcheva (1968, pl. 19, fig. 7b), and though such are less apparent in some specimens belonging to the type species, strut spines were clearly figured for the type species by Klets (2005). The three species assigned to *Sajakella* in Sarytcheva (1968) have wide hinge, moderately high trail, rather gently convex ventral disc, and moderately well defined although low commarginal rugae over the visceral disc. There are slender non-dendritic adductors, although the anterior adductors are broader and narrow and posterior adductors are slender and dendritic in the ventral valve of *S. dzhinsetuensis* Lazarev (1992), as figured in Rozanov (2003, pl. 44, fig. 4). *Sajakella* does have coarser ribs than in *Yakovlevia*, and shows commarginal rugae, which are absent or weak in *Muirwoodia* or *Yakovlevia*. According to Lazarev (2011), so-called *Marginatia monachovae* (Litvinovich et al. 1969 – see p. 218, pl. 31, fig. 4-6) from the Early Visean Ishim Horizon of Kazakhstan belongs to a new genus similar in appearance to *Sajakella*, with reticulate disc, rare large spines on the trail, and no dorsal spines, representing the earliest yakovleviid. This is close in age to the putative ancestral subfamily Bibatiolinae (Waterhouse 2013, p. 321).

Were the *Yakovlevia* group to be regarded as non-linoproductoid, it could be considered as an ally of Paucispiniferidae, just as first evaluated by Muir-Wood & Cooper (1960), through sharing comparable ornament and spine detail, and somewhat similar build and profile. There are some further indications: the dorsal pustules are large and limited to one or two rows in yakovleviid genera, notably *Muirwoodia* (*Grandaurea*) Waterhouse, 2013, much as in *Paucispinifera* itself, and the dorsal adductors may be separated by suggestions of slender anderidia, again as indicated in some *Paucispinifera* (see Muir-Wood & Cooper 1960, pl. 122, fig. 7, 9). The inner adductors of *Paucispinifera* tend to be smooth until later ontogeny, just as in *Muirwoodia* (*Grandaurea*), which has been well figured as *Muirwoodia* by Muir-Wood & Cooper (1960) and in allied shells misidentified as*Yakovlevia* by Cooper & Grant (1975). Large and dendritic outer adductors are similarly disposed in both paucispiniferid and yakovleviid genera. The cardinal processes differ to some extent in each suite, but from an internal aspect may be somewhat similar in the way the two lateral lobes slope inwards with thickened lips along the posterior inner margins, parallel to the hinge, though more exaggerated in several *Paucispinifera* (cf. Cooper & Grant 1975, pl. 423, fig. 23, pl. 424, fig. 33 for *Paucispinifera* with Cooper & Grant, 1975, pl. 471, fig. 22 for "*Yakovlevia*"). No adequate figures for the ventral muscle scars are provided for *Paucispinifera* by Cooper & Grant (1975), because of reliance on silicified material, and the valve is deeply convex, hindering photography. But the much greater convexity would probably have led to a different shape anyway, in comparison with the gentle disc convexity of *Yakovlevia* and allies. In dictyoclostiform genera, which offer the alliance preferred by Lazarev (2000a) and Brunton (2007), the internal and anterior pustules of the dorsal valve are much more numerous and less prominent, and cardinal process taller and with different lobes, often quadrifid. The posterior adductors are relatively larger and more posteriorly placed, without the ridges found in paucispiniferids or yakovleviids. These differences are reinforced by the differences in shape, ribs and spines. Figures in Cooper & Grant (1975) suggest that posterior central internal papillation is missing from mature dorsal valves they called *Yakovlevia*, and since renamed *Muirwoodia* (*Grandaurea*) Waterhouse, 2013, p. 343, whereas papillation appears to be present in some but not all *Paucispinifera*.

There are further differences between Paucispiniferidae and Yakovleviidae. The yakovleviid shape is more transverse and trail shorter in some species and genera, matters that may be ascribed to familial constraints, but other species, including *Muirwoodia pseudoartiensis*, have long but simple trails. A substantial difference lies in the development of marginal ridges. Marginal ridges are high in the ventral valves and in virtually all dorsal valves of Paucispiniferidae, whereas ridges are not clearly developed in *Muirwoodia* or *Yakovlevia*. In the very well preserved material from the Permian of the Glass Mountains, Texas, United States, there is a very low marginal ridge in each valve (see Cooper & Grant 1975, pl. 472, fig. 27, 32). It may therefore be proposed that *Yakovlevia* and allies are a special group which virtually lost its marginal ridges, except for *Paramuirwoodia* Zhang in Zhang et al., 1983, *Paramarginifera* Fredericks, 1916, and *Archboldina* Angiolini & Long, 2008. This interpretation is favoured by details of ribs and spines, and the shape is unusual but is reflected to some extent by a few other genera, notably *Paucispinifera* itself. The differences from other families are so great that a separate family appears to be warranted. The purported ties with *Inflatia* Muir-Wood & Cooper, 1960 are rejected: this is regarded as a dictyoclostid – together with *Tenaspinus* Brunton & Mundy, 1994, despite their inclusion in Yakovleviini by Brunton et al. (2000, pp. 466, 467). *Sajakella* is regarded as a likely yakovleviid, together with *Muirwoodia*, and the Lazarev report of affinities with *Marginatia monachovae* (Litvinovich et al.) remains to be consolidated.

At present, members of Yakovleviidae are found almost exclusively in the northern paleohemisphere. The one example of what may appear to be a southerly occurrence is in the Huentelauquén Formation of Coquimbo Province of Chile, where Minato & Tazawa (1977, p. 101, pl. 5-1, fig. 15, 16) recorded *Muirwoodia* sp. However the identification is difficult to confirm from the figures, and anyway, it would seem likely that the fauna came from a low paleolatitude, and has been moved relatively southwards.

Subfamily **MUIRWOODIINAE** Waterhouse, 2013

[Muirwoodiinae Waterhouse, 2013, p. 243].

Diagnosis: Strut spines well developed, usually two up to six. Ventral marginal ridge not conspicuous.

Discussion: *Muirwoodia* is the most common of all yakovleviid genera, and the subfamily is readily distinguished from Yakovleviinae by the presence of strut spines, and from Paramarginiferinae through the lack of strong marginal ridges.

Discussion: The conclusion by Kotlyar (1961) that *Muirwoodia* Licharew, 1947 was junior synonym of *Yakovlevia* Fredericks, 1925 was accepted by Cooper & Grant (1975, p. 1178) and Brunton et al. (2000, p. 465). But such was opposed by Kalashnikov (1980), Abramov & Grigorieva (1983, p. 92), Lazarev (1990) and Klets (2005), and the difference in spination confirms the distinction, *Yakovlevia* lacking the large long erect strut spines found in *Muirwoodia* and allies.

Genus ***Harkeria*** Waterhouse, 2013

Diagnosis: Six strut spines on ventral valve, two at cardinal extremities and two spines on each flank in front of geniculation. Hinge row of fine spines. Corpus moderately thick.

Type species: *Harkeria studiosus* Waterhouse from Assistance Formation (Roadian), Devon Island, Canada, OD.

Discussion: This genus is characterized by having six strut spines. Unlike *Duartea*, *Harkeria* lacks a row of spines along the umbonal flanks and commarginal rugae are not conspicuous. The genus is represented by a number of species in Neimongol (Inner Mongolia), as described by Li & Gu (1976), Liu & Waterhouse (1985) and others. The genus is close in appearance to *Muirwoodia* Licharew, 1947, but this genus has two strut spines at the cardinal extremities and only one pair anteriorly, as shown by Shi (1995) and Klets (2005).

Harkeria elongata n. sp.

Fig. 195 - 198

Derivation: longus – long, extended, Lat.

Diagnosis: Medium-small with wide hinge, moderately fine costae, pointed cardinal extremities, lateral walls diverging weakly, sulcus commencing in front of beak, high trail. Costellae moderately fine, spines form somewhat irregular row along hinge, scattered other ventral spines, two pair of anterior strut spines on flanks of sulcus and another pair at cardinal extremities.

Holotype: GSC 136957, here designated.

Material: From Member A, single ventral valves from JBW 77, 182, 192, 404, 432, 524, 562, 630, 656, 706, 728, 742, 780 and 789, two ventral valves from JBW 513, two ventral valves and two specimens with valves conjoined from JBW 125, two ventral valves from JBW 187, three ventral valves from JBW 739, ventral valve and specimen with valves conjoined from JBW 34, ten ventral valves and twelve specimens with valves conjoined from JBW 802, one specimen with valves conjoined from JBW 189, 433, 524, 536 and 606 and two from JBW 171, 628 and 739, and two dorsal valves from JBW 524. Single ventral valve from JBW 528, Ettrain Formation**.**

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Description: Specimens small, often preserved with both valves conjoined, ventral umbo protruding slightly beyond hinge, not incurved, broad at angle close to 110º, hinge at maximum width with slightly produced convex and narrow ventral ears, umbonal slopes very low. Visceral disc broad and gently convex, sulcus commencing near anterior third

Fig. 195. *Harkeria elongata* n. sp. dorsal view of specimen with valves conjoined showing long anterior strut spine and the lower part of another strut spine to the left from ventral valve. GSC 136956 x2 from JBW 189. Member A, Jungle Creek Formation.

of disc, and continuing over trail, which lies at 75-80º from plane of disc and is slightly longer than the disc. There is no ginglymus in some specimens but other specimens bear a low ventral and very low dorsal ginglymus. Dorsal valve concave and geniculate, with concave ears. Spines in inconspicuous row close to ventral hinge, rare over disc and trail, with often prominent pair postero-laterally, and two pair on flanks of sulcus, one pair near start of trail and other pair more anteriorly placed, one spine extending for 23mm in shell 26mm wide. Valve covered by costae, seven to eight in 5mm near start of trail, posterior ears smooth, but anterior ears bear fine costae. Spines do not appear to disturb the costae, which do not clearly increase by intercalation or branching. Dorsal valve has strong costae and no spines. Low irregularly spaced growth steps cross the venter of only some specimens, and there are no regular commarginal rugae. The ventral shell over the anterior disc and first part of the trail is up to 2mm thick, compared with the dorsal valve which is close to 1mm thick, and the disc in a specimen over 34mm wide is 5.5mm thick.

There is a narrow and elongate ventral adductor platform with longitudinal striae, and large longitudinally striate diductor impressions placed laterally, not extending in front of the adductors. In the dorsal valve, the median septum extends well forward, and large suboval adductor impressions lie well apart and close to the hinge. Part of a deeply impressed brachial shield is visible of one side of a worn internal mould.

Resemblances: This species is close in its disc to *Harkeria studiosus* Waterhouse, 2013 from the Assistance Formation (Roadian) of Arctic Canada, but the trail is much longer, and the anterior strut spines are arranged a little differently.

Muirwoodia pseudoartiensis (Stuckenberg, 1905, p. 73, pl. 9, fig. 3; Sarytcheva & Sokolskaya 1952, p. 159, pl. 145), also figured by Lazarev (1990, pl. 39, fig. 4-11) from Late Carboniferous of the Urals and Kasimovian and ?Gzhelian beds of the Moscow Basin, is very close in size, shape and ornament. The ribs are slightly coarser in some specimens, but not in others, measuring for example some seven in 5mm in the original figures, compared with five or six in 5mm in the material figured by Stepanov (1948, p. 34, pl. 6, fig. 6, 7), and a large spine lies on the

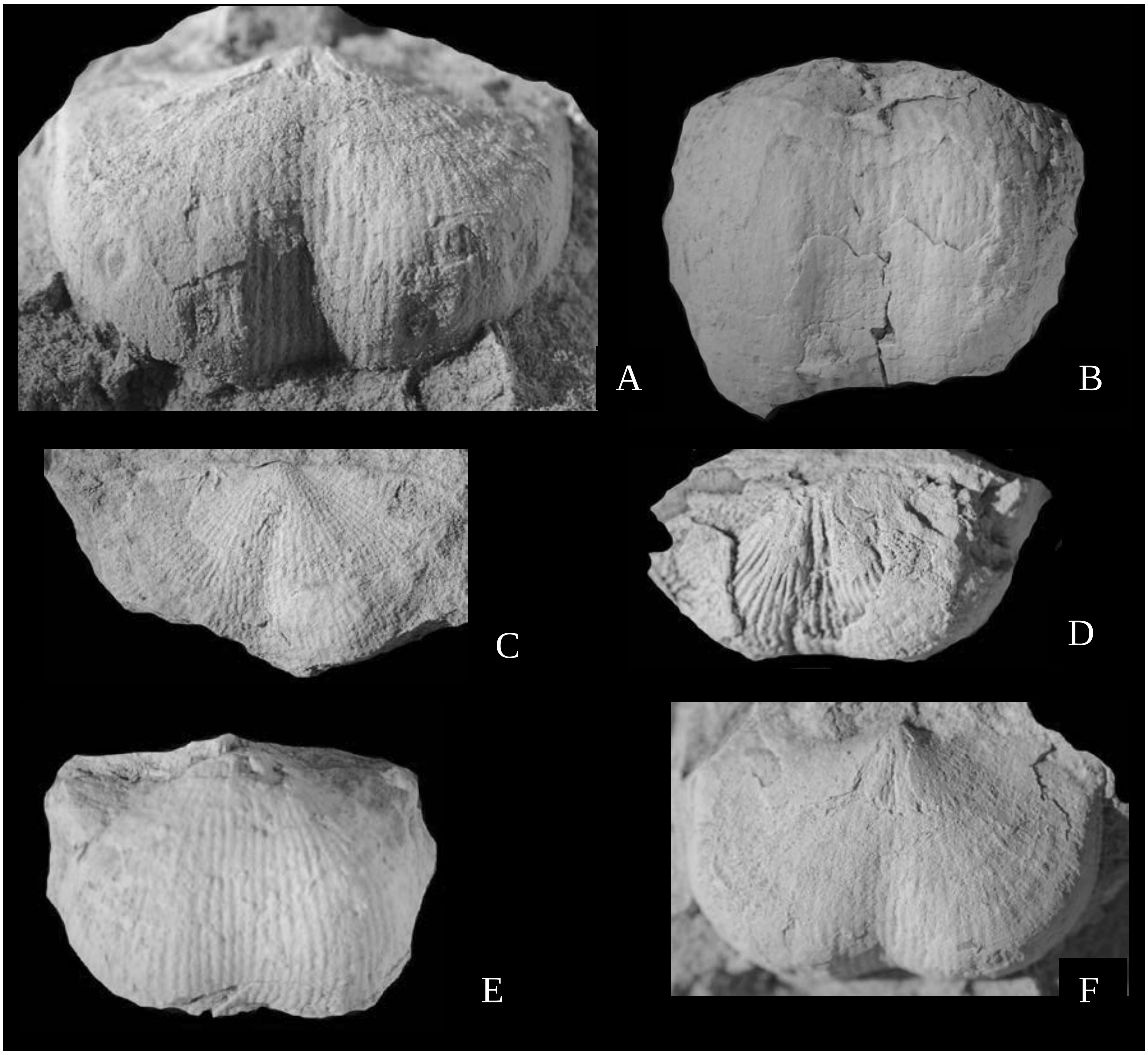


Fig. 196. *Harkeria elongata* n. sp. A, F, anterior and ventral aspects of ventral valve, holotype GSC 136957 x4, x3, from JBW 739. B, anterior view, ventral valve GSC 136959 x2 from JBW 802. C, ventral valve GSC 136958 x2 from JBW 432. D, posterior aspect of decorticated ventral valve showing muscle scars, GSC 136965 x1.5 from JBW 187. E, anterior aspect of ventral valve GSC 136960 x2 from JBW 789. Member A, Jungle Creek Formation.

ventral flanks anteriorly: other spines are not clearly shown, and the full number and disposition of strut spines and any variation in number are aspects that remain uncertain. Further material has been described by Semichatova (1934, p. 8, pl. 1, fig. 8, pl. 3, fig. 12), Ivanov (1935, p. 75, pl. 7, fig. 9), Sarytcheva & Sokolskaya (1952, p. 159, pl. 145) and Mironova (1967, p. 24, pl. 2, fig. 14), as well as material recorded as *Duartea* aff. *pseudoartiensis* by Lazarev (1996, Fig. 1, pl. 3, fig. 7-11).

The present species differs from specimens identified in Shi & Waterhouse (1996) as *Yakovlevia transversa* from the younger Jungle Creek Formation in its longer visceral disc, shallower sulcus commencing further from the umbo, higher trail and less reticulate ventral disc. Ventral costae tend to fan out forwards from the crest of the umbonal flanks in those Jungle Creek specimens assigned to *transversa,* and only some specimens in the Shi &

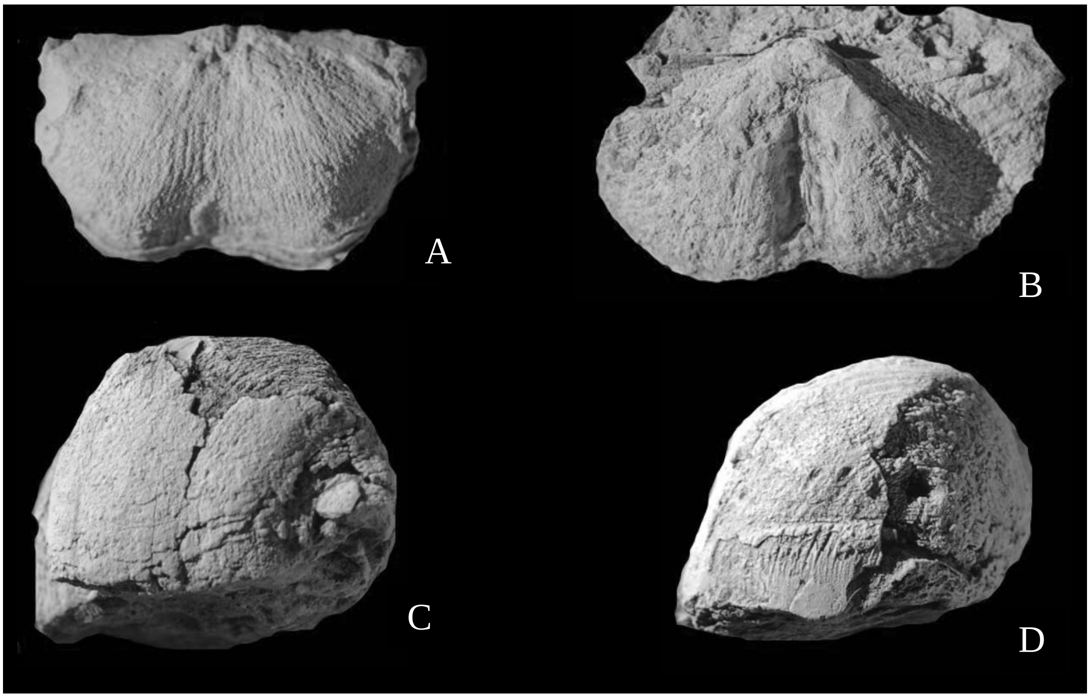


Fig. 197. *Harkeria elongata* n. sp. A, C, posterior and lateral aspects of ventral valve GSC 136963 x1.5, x2, from JBW 802. B, ventral internal mould showing muscle field, GSC 136962 x1.5 from JBW 630. D, lateral aspect of GSC 136964 x2 from JBW 562. Member A, Jungle Creek Formation.

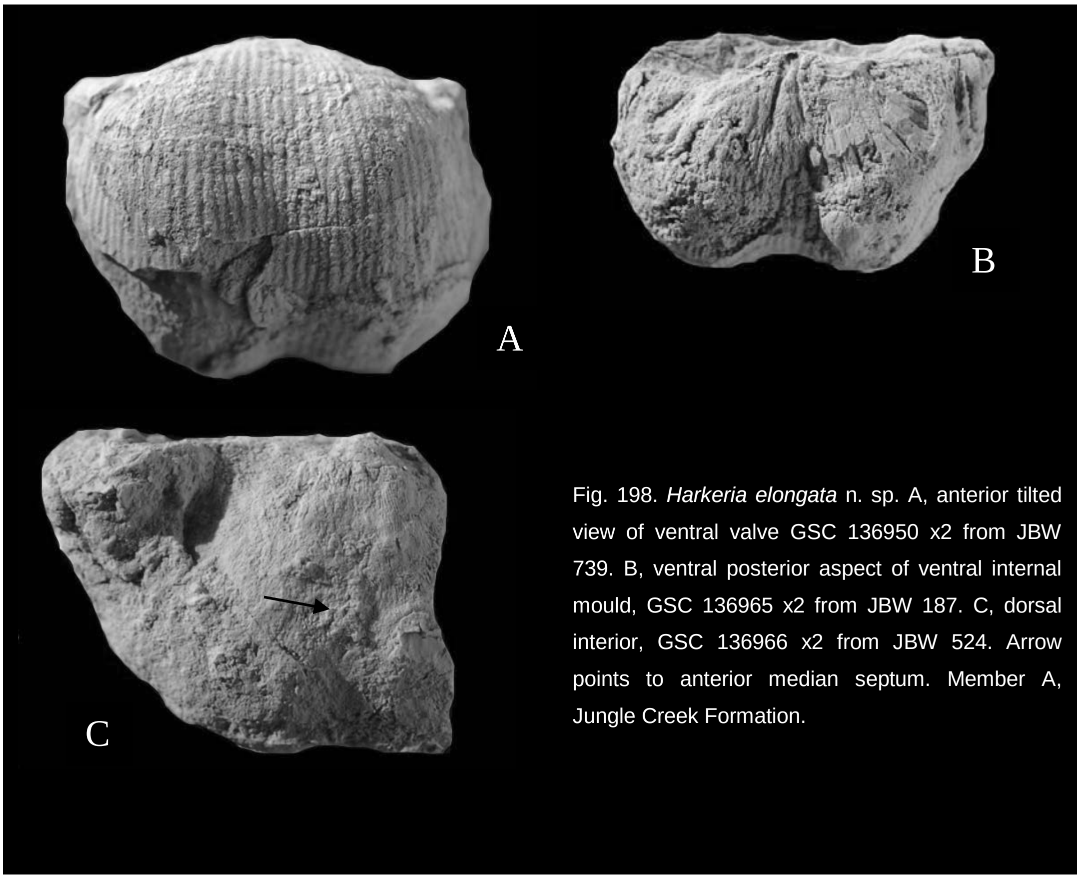


Fig. 198. *Harkeria elongata* n. sp. A, anterior tilted view of ventral valve GSC 136950 x2 from JBW 739. B, ventral posterior aspect of ventral internal mould, GSC 136965 x2 from JBW 187. C, dorsal interior, GSC 136966 x2 from JBW 524. Arrow points to anterior median septum. Member A, Jungle Creek Formation.

Waterhouse account share the presence of two pair of anterior strut spines. These specimens are discussed below, on pp. 239-240**.** Specimens from units below the Shi-Waterhouse material and above the present species have a slightly shorter trail.

Muirwoodia mammata (Keyserling) from Artinskian beds of the Petchora Basin has anteriorly diverging flanks and comparatively short trail (Tschernyschew 1902, pp. 295, 631, pl. 35, fig. 4a,b, 6; Stepanov 1937b, p. 177, pl. 2, fig. 5-7; Muir-Wood & Cooper 1960, pl. 120, fig. 9-11; Zavodowsky 1970, pl. 62, fig. 13 [from the Omolon Horizon]; Ivanova & Semenova 1972, pl. 7, fig. 4, 5 and Brunton et al. 2000, Fig. 310a, b). Klets (2005, pl. 11, fig. 1-7) added specimens of *mammata* from the Upper Carboniferous lower Akachan beds of Verchoyan, with slightly narrow ventral sulcus than the Canadian specimens, and tabulated the species as being of Kasimovian age. Material from the Brachiopod Limestone of Spitsbergen that was figured by Gobbett (1964, pl. 13, fig. 23-26) displays a longer trail, as does *M. duplex* (Wiman 1914, pl. 14, fig. 3-7; Gobbett 1964, pl. 14, fig. 5, 6), and recorded according to Gobbett as *Productus weyprechti* (not Toula) by Tschernyschew & Stepanov (1916a, b, pl. 7, fig. 5, 6) from Great Bear Cape on Ellesmere Island. Gobbett noted some approach of his *mammatus* to the specimens figured as *Muirwoodia mammatus* by Harker in Harker & Thorsteinsson (1960, pl. 16, fig. 1-5) from the Assistance Formation (Roadian) of Devon Island, which is now the type species of *Harkeria*. Gobbett's specimens at least superficially recall *Productus geniculatus* Girty, 1910 from the Park City Formation of Idaho, but both sets of material require closer examination.

Shells assigned to *Muirwoodia multistriata* (Meek 1861, 1876, pl. 1, fig. 8; 1877, pl. 8, fig. 3 – 3c) and cf. Muir-Wood & Cooper (1960, pl. 120, fig. 1-8) are larger and less inflated with prominent spines at the posterior lateral extremities and one on each anterior sulcal flank. The same species *multistriata* has also been figured by Girty (1920, pl. 56, fig. 7, 7a) and Cooper & Grant (1975, p. 1186, pl. 469, fig. 12-14): it is reliably found in the Phosphoria Formation of Wyoming, Nevada and Utah, and reported from the Word Formation of west Texas. Other species from North America, as described by Cooper & Grant (1975) are mostly from the Guadalupian Series and show little resemblance to either of the Canadian species in the Jungle Creek Formation or Ettrain Formation and its equivalents.

Harkeria sulcoprofundus n. sp.

Fig. 199, 200

1971 *Yakovlevia* sp. Bamber & Waterhouse, pl. 14, fig. 2-5, pl. 15, fig. 1, pl. 16, fig. 7.

Derivation: sulcus – furrow; profundus – deep, Lat.

Diagnosis: Medium-sized transverse shells with flattened central disc, sulcus and fold well developed, five to seven ribs in 5mm on central ventral valve.

Holotype: GSC 136967, here designated.

Material: Single ventral valves from JBW 66, 561 and 577, three ventral valves from JBW 539, two from JBW 580, a specimen with valves conjoined from JBW 538 and eleven ventral valves, and a dorsal valve from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Shells of average size for the genus, a ventral valve measuring 30mm in width, 16mm in length and 6mm in height, with low umbo extending slightly beyond the hinge, and umbonal angle of 100º. The hinge is at maximum width, with large alate ears that are gently concave before curving into the commissure, and a very low

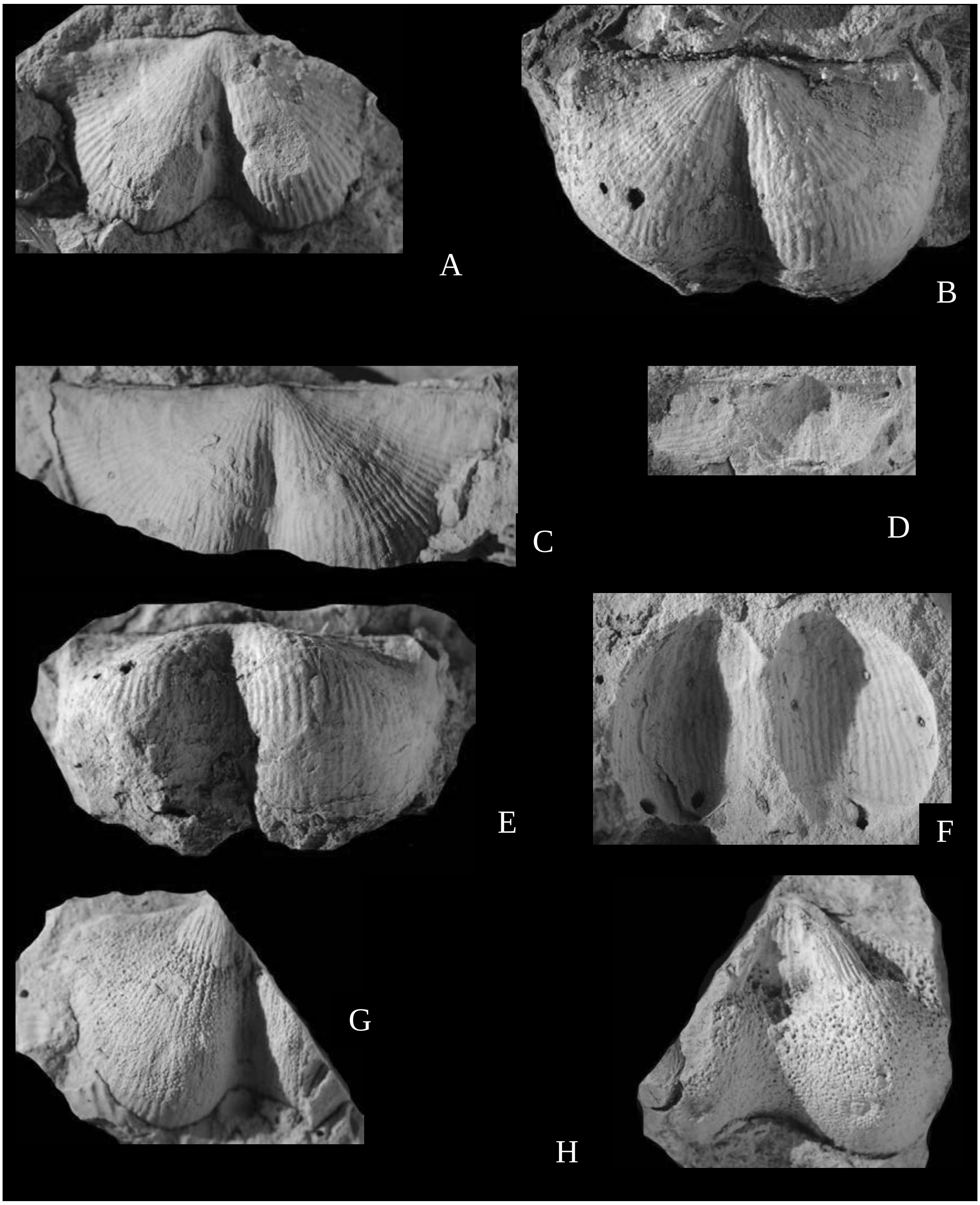


Fig. 200. *Harkeria sulcoprofundus* n. sp. A, ventral valve GSC 136967, holotype, from JBW 581. B, E, ventral and anterior aspects of ventral valve GSC 136970 from JBW 581. C, ventral valve GSC 136969 from JBW 581. D, posterior external mould of ventral valve GSC 136968 from JBW 580. F, external mould of anterior ventral valve, showing position of strut spines, GSC 136972 from JBW 581. G, part of internal ventral mould, GSC 137179 from JBW 577. H, internal mould of ventral valve GSC 136971 from JBW 539. Specimens x2, except F x 3, from Member E, Jungle Creek Formation.

ginglymus is developed. The valve is divided by a deep narrow sulcus widening at angle of some 20°, and the disc each side is gently convex and subplanar, before curving abruptly into a trail. The visceral cavity is narrow so that the dorsal valve reflects the ventral profile, with geniculate trail. Both valves are ornamented by firm ribs, numbering five or six in 5mm medianly near the anterior margin, and seven to eight in 5mm near the posterior lateral margin in front of the ears. The ribs are regular and in some specimens branching is evident: ribs cover the ears. Commarginal growth lines are inconspicuous. A row of sturdy spines reaching 1.3mm in diameter is developed along the ventral hinge and a few erect slender spines lie over the disc. Two pairs of strut spines lie on the anterior slopes near the start of the trail, and a strut spine lies at each cardinal extremity of mature specimens. Some exceptional specimens have one or two other spines, some thick and irregularly disposed. The dorsal valve lacks spines.

The ventral adductors are narrow, the diductors deeply impressed and scored by longitudinal ridges and grooves, and the posterior floor marked by dense pits and pustules: the hinge and strut spines open into the interior. In the dorsal valve, a broad low platform lies in front of the broad and squat cardinal process, and is traversed by a low median septum. Little of the septum and muscle scars is preserved, but the typical brachial shield that is smooth inside and bordered posteriorly by a low ridge is well developed, and partly surrounded by dense pustules in at least four rows over most of the floor of the valve in front of a broad hinge ridge. The anterior shell under the trail is smoother, apart from rows of strong pustules.

Resemblances: In shape and most aspects of ornament these specimens are close to material described by Cooper, (1957, p. 39, pl. 5A, fig. 1-13) as *Muirwoodia transversa* from the Coyotte Butte Formation of central Oregon, and reported from southeast British Columbia by Nelson & Nelson (1985). The present specimens have a hinge row of spines and anterior pair of strut spines each side of the sulcus, just as in type *transversa* (Cooper 1957, p. 40, pl. 5, fig. 2), and commarginal rugae are particularly well developed, like the Oregon material, but the ventral sulcus is much deeper, and ribs finer in present material, with eight rather than five or six in 5mm in *transversa*.

The position of the allied material from the younger Jungle Creek Formation requires clarification. Whereas the distribution of strut spines appears to be comparatively consistent in substantial populations of yakovleviids, such as for the present species and for younger species from Arctic Canada, just as for the Glass Mountains species examined by Cooper & Grant (1975), the arrangement is less regular in material described from the younger Jungle Creek Formation by Shi & Waterhouse (1996, p. 107). They recorded a pair at the cardinal extremities, one or rarely two pair bounding the sulcus, and sometimes a strut spine in the sulcus, as well as a row of finer spines along the hinge line, and rare over the trail and visceral disc. Such variation is not established for the Oregon types described as *Muirwoodia transversa* Cooper, but the Oregon material is represented by much less material, with limited data on spination and on internal detail. Identification with that species is therefore subject to uncertainty, and it is noticeable that a number of the Canadian specimens show a deeper wider sulcus (as in specimens from the *Ogilviecoelia shii* Zone), and that commarginal rugae are better developed on both valves than in Oregon or *Ogilviecoelia shii* Zone specimens. Of course it could well be that such differences reflect intraspecific variation, but it does impose a degree of caution in identifying the Shi-Waterhouse specimens with *transversa*. The generic position also becomes a matter of concern. The spination of type *transversa* is clear for a few specimens, and allows provisional assignment to *Harkeria*. But the spination of the Canadian material indicates some departure from typical *Harkeria*. At present, given various uncertainties, this is interpreted as potentially indicating aberrant forms of *Harkeria* and uncertain specific affinities, pending closer and more extensive study.

The present Canadian specimens differ from a number of species in having the hinge row of spines gradually increase laterally in strength to the outer strut spine, whereas in well preserved exemplars of species ascribed to *Yakovlevia* from Texas in particular, the outermost hinge spine is much stronger than other hinge spines, as shown for "*Muirwoodia*" cf. *multistriata* (Meek) by Muir-Wood & Cooper (1960, pl. 120, fig. 1-8). The Texan species are now distinguished as a subgenus *Muirwoodia* (*Grandaurea*) Waterhouse, 2013, characterized by its large ears, and usually only two pair of strut spines. The hinge spines are not well preserved for the material described by Shi & Waterhouse (1996), nor entirely clear for material from Oregon.

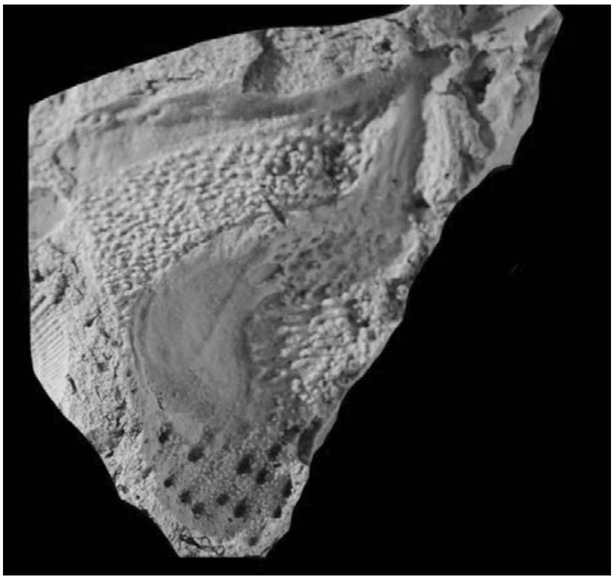


Fig. 200. *Harkeria sulcoprofundus* n. sp.. A, internal mould of dorsal valve GSC 137360 x4, From JBW 581. Member E, Jungle Creek Formation.

Specimens identified as *Muirwoodia* sp. cf. *greenlandica* Dunbar by Logan & McGugan (1968, pl. 143, fig. 1-3) from the Telford Formation, southeast British Columbia, are more elongate.

The species shows considerable resemblance to the Early Permian species from the Urals, *Productus mammatiformis* Fredericks (1926**,** pl. 3, fig. 2-6), also figured by Mironova (1964, fig. 14) and Kulikov (1974, pl. 3, fig. 6). This species was listed as *Yakovlevia* by Klets (2005).

Superfamily **LINOPRODUCTOIDEA** Stehli, 1954

[Nom. transl. Waterhouse, 1978, p. 20 ex Linoproductinae Stehli, 1954, p. 319. Syn. Striatoidea Nalivkin, 1979].

Diagnosis: Small to large shells usually with trail, often geniculate; ornament of well developed ribbing as a rule on both valves, spines varied and often numerous, never forming strut spines, spines rarely present on dorsal valve. Muscle scars normally dendritic to some degree, or striate, cardinal process bilobed or trilobed, papillation may be distinctive in different groups.

Family **LINOPRODUCTIDAE** Stehli, 1954

[Nom. transl. Muir-Wood & Cooper 1960, p. 296 ex Linoproductinae Stehli, 1954, p. 319].

Diagnosis: Shells oval in outline, transverse or elongate, usually symmetrical and free-living, umbo prominent, ears developed, venter arched. Ventral spines only, shell often large, body cavity deep or shallow, both valves with fine close-set radial ornament, commarginal ornament inconspicuous. Cardinal process large, outer lobes not fused dorsally.

Discussion: Treatment of Linoproductinae has to be very different from that offered in the *Revised Brachiopod Treatise* by Brunton et al (2000, pp. 527-530). Those authors provided a generalized diagnosis, as consisting of "linoproductids without marginal structures or dorsal spines", yet *Linoproductus* itself has a narrow marginal ridge, as illustrated by Brunton et al. (2000, Fig. 365.1f), and *Marginovatia* Gordon & Henry (1990), incorporated in the subfamily by Brunton et al., is diagnosed in part by a high dorsal marginal ridge (Brunton et al. 2000, Fig. 365.3f). Many linoproductoids, not just Linoproductinae, lack dorsal spines. Eight genera were placed in the subfamily by Brunton et al. (2000), and of these, only one, *Linoproductus* itself, remains in the subfamily. The improved understanding rests substantially on more careful study of the family by one of the Treatise authors, S. S. Lazarev, which swept away the claims of the *Revised Brachiopod Treatise*, rendering it thoroughly out of date.

The probable source of Linoproductidae is provided by *Eoproductella* Rzhonsnitzkaya, in Subfamily Eoproductellinae Lazarev, 1987, p. 49, of Devonoproductidae. This genus is ribbed on both valves and displays spines only on the ventral valve. It is strophalosiiform, with interareas, teeth and sockets, and is of Early and Middle Devonian (Pragian – upper Givetian) age. To judge from the fossil record, Eoproductellinae evolved into Ovatiidae, Subfamily Ovatiinae, represented by a few genera of Late Devonian and Early Carboniferous age, characterized by swollen ventral valve, a number of spines along the ventral hinge, and scattered few erect body spines. This developed into Linoproductidae, characterized by larger size, stronger spines and different cardinal process. Another subfamily descendent from Eoproductellinae, Gilmoriinae of Late Devonian and Early Carboniferous age, characterized by wider shells with more extended hinge, evolved into Schrenkiellidae, with wide hinge and fewer spines, and possibly into the very large Gigantoproductidae (See Waterhouse 2013).

Linoproductid gen. & sp. indet. A

Fig. 201

Material: Two ventral valves from JBW 615, one from JBW 75, and JBW 451.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimens are not large for the family, one from JBW 615 measuring 43mm wide, 31.5mm long and 11mm high. The umbo is pointed, the hinge moderately wide, and ventral valves moderately convex, without any sulcus. Both valves are ornamented by fine even costellae, six in 5mm which increase by intercalation, with a single row of spines along the hinge and rare erect body spines. Moderately strong rugae are developed laterally in the specimen from JBW 451. As far as they are preserved, the specimens agree with *Linoproductus.*

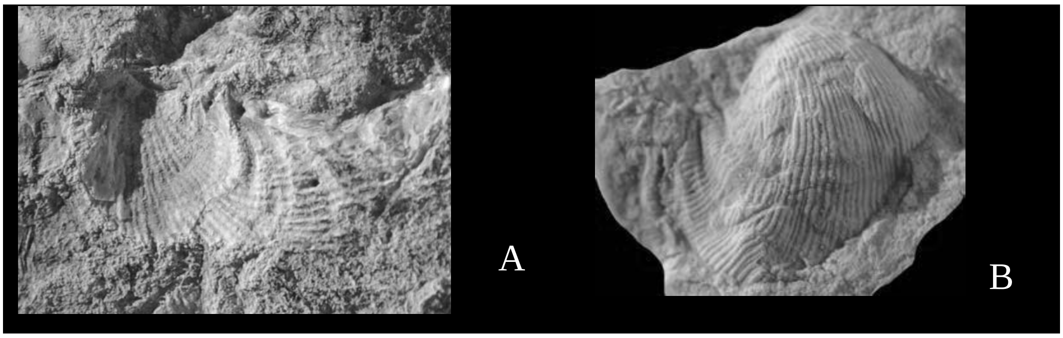


Fig. 201. Linoproductid sp. A, B, cast and external mould of part of ventral valve, GSC 137318 x2. From JBW 451. Member A, Jungle Creek Formation.

Linoproductid gen. & sp. indet. B

Fig. 202, 203

Material: A fragment of a ventral valve from JBW 85 (Member D), and another from JBW 533, upper Ettrain Formation.

Stratigraphic and biostratigraphic levels: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone. Ettrain Formation.

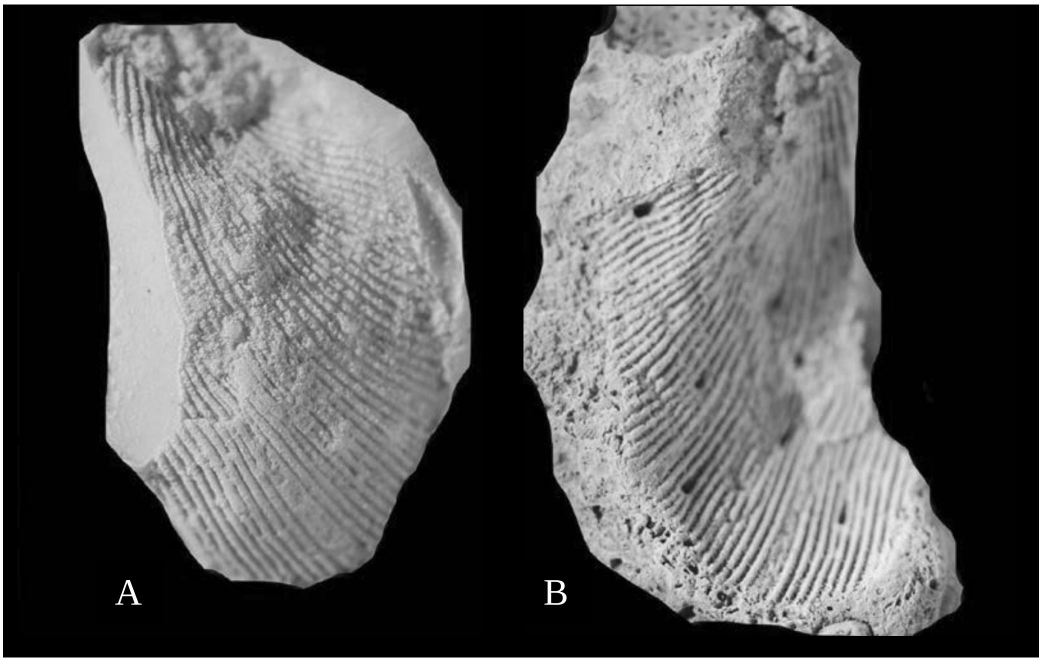


Fig. 202. Linoproductid gen. & sp. indet. B. A, B, external cast and mould of part of a ventral valve, GSC 136793 x2 from JBW 85. Member D, Jungle Creek Formation.

Description: The fragments are distinguished by the well developed erect spines emerging from the ribs. The presence of these spines recalls the ornament in shells ascribed by Shi & Waterhouse (1996) to *Linoproductus*

Fig. 203. Linoproductid gen. & sp. indet. B, external mould of part of a ventral valve, GSC 136793 x3 from JBW 533. Ettrain Formation.

dorotheevi (Fredericks) from the "*Yakovlevia transversa*" and *Jakutoproductus verchoyanicus* Zones in the younger Jungle Creek Formation. These specimens display one row of spines along the hinge, and so seem likely to have belonged to *Linoproductus* Chao, 1927a, but the hinge is not preserved in the present fragments.

Linoproductid gen. & sp. indet. C

Fig. 204

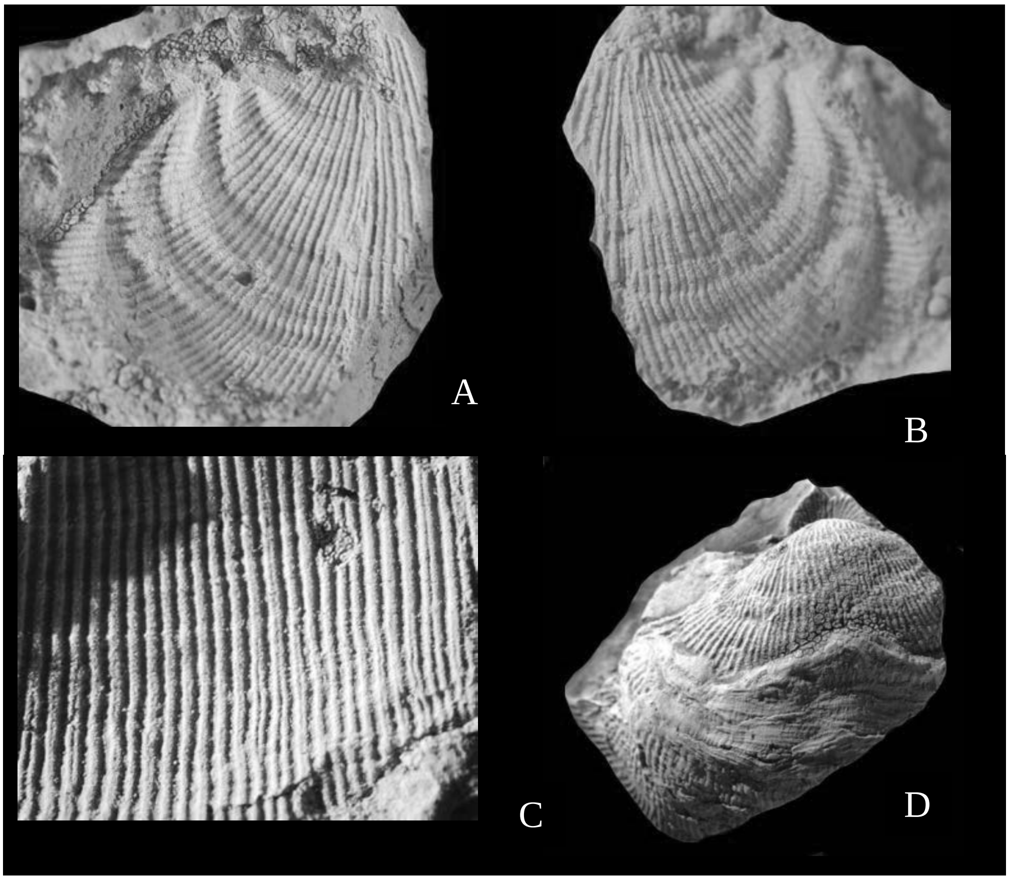


Fig. 204. Linoproductid gen. & sp. indet. C. A, B, external mould and cast of part of a ventral valve, GSC 136794 x3. C, detail of ornament on ventral external mould, GSC 136795 x5. D, specimen with valves conjoined, showing exterior of dorsal valve, overlapped anteriorly by trail of ventral valve, GSC 136796 x2. From JBW 561, Member E, Jungle Creek Formation.

Material: Two fragments of ventral valves and a specimen with valves conjoined from JBW 561.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Only fragments are available, to indicate elongate specimens of which the largest is about 40mm long and wide and 24mm high, though these dimensions are approximate and incomplete. Costae number about fifteen in 10mm at 15mm and 35mm from the umbo on the dorsal valve and counts are similar for the ventral valve: the costae appear to increase by intercalation on the ventral valve and branching on the dorsal valve. The interspaces may bear a median riblet which does not progress forward into a full rib (Fig. 204C). A very few erect spines are present over the ventral disc, but hinge spines are not preserved, and there are no dorsal spines. Commarginal rugae are well developed laterally on the ventral valve.

Resemblances: The present specimens are shaped like *Lineacrassus inflatus* Waterhouse from the underlying Member C with the *Kochiproductus imperiosus* Zone, but are smaller and have much finer costellae, fifteen in 10mm compared with ten in 10mm for *inflatus.* On the other hand, so-called *Linoproductus dorotheevi* from the overlying "*Yakovlevia transversa*" and *Jakutoproductus verchoyanicus* Zones of Jungle Creek Formation as described by Shi & Waterhouse (1996, p. 93, pl. 15, fig. 25-28, pl. 16, fig. 1-9, 11, text-fig. 31) has costae reported as numbering twenty two in 10 mm at 10mm from the umbo and fifteen in 10mm at mid-length.

Subfamily LINISPININAE Lazarev, 2006

[Linispininae Lazarev, 2006, p. 523].

Diagnosis: Ears of ventral valve bear two to three or more rows of spines or sometimes clusters of spines in poorly to clearly discernible rows.

Genus ***Lineacrassus*** Waterhouse, 2013

Diagnosis: Large swollen shells with well developed costellae: spines of modest thickness in row along hinge, row of thin spines between or in front of these spines near the umbo, become as strong laterally, outer ears with additional spines. Body spines arise from single costae, usually slender but include rare much thicker spines. Cardinal process largely in plane of posterior dorsal valve, median septum short.

Type species: *Lineacrassus inflatus* Waterhouse from Member C (Asselian), Jungle Creek Formation, Yukon Territory, Canada, OD.

Discussion: This genus is large and inflated, close to *Linoproductus* Chao, 1927a, but with few moderately thick spines over the ventral disc and trail, that intersect two up to often four costae. The ventral ears of *Linoproductus* lack any extra spines, unlike the ventral ears of *Lineacrassus*, and the type species is less elongate. Internally, the cardinal process of *Linoproductus* is bent ventrally and a well developed alveolus is developed, whereas the ventral face of the cardinal process in *Lineacrassus* leans only a little dorsally from the plane of the dorsal interior, and a median notch is shallow. The dorsal median septum is shorter in *Lineacrassus* than in *Linoproductus*, and does not extend as far forward as the inner terminus of each brachial shield. Both *Linoproductoides* Lazarev, 2006 and *Sublinoproductus* Lazarev, 2008 which belong to Linoproductini have more strong spines over the ventral disc and trail, close in thickness to strongest spines along the hinge, whereas such spines are rare in *Lineacrassus*, although present. *Linoproductoides* has usually two rows of hinge spines, and the median lobe of the cardinal process is little higher than the lateral lobes, and a deep alveolus is developed. The type species is of Moscovian age in Russia. *Sublinoproductus* from the Late Carboniferous and Early Permian of Russia has two cardinal rows of spines, the outer lobes of the cardinal process rather than the whole process inclined ventrally, and long median septum extending beyond the distal end of the brachial shields. *Liniunus* Waterhouse has a single row of spines along the hinge, thick and thin spines over the visceral disc, and the cardinal process is bent ventrally, and the median septum long.

Linispinus Lazarev, name-giver to the tribe Linispininae Lazarev, has a number of ventral hinge spines in two, three or more rows, and body spines are close in diameter to those of the outer hinge – there are no finer body spines, unlike the arrangement in *Lineacrassus*. The cardinal process is moderately close to that of *Lineacrassus*, and buttress mounds are poorly developed or absent as a rule. There are many small points of difference between *Liniunus* and *Lineacrassus*. *Linispinella* Lazarev, 2006 from Bashkirian faunas of the southern Urals is placed in the same tribe, and has many fine spines, 0.6mm in diameter over the ears, and larger body spines, up to 1mm in diameter. *Lineaproductus* Waterhouse, 2013 has more rows of finer spines arranged along the ventral hinge, and body spines are similarly fine, without the additional coarser spines displayed by *Lineacrassus*.

Levisapicus Tong (1990, p. 66, pl. 11, fig. 1a-e, Fig. 10), type species *giganteus* Tong from Yanbian, Sichuan, China, considered to be very Late Carboniferous, is close in many respects, although with more concave dorsal valve and stronger postero-lateral wrinkles, and more splitting of ribs into what Tong called '"sheaves". Ribbing was said to be missing posteriorly, a ventral interarea or ginglymus is well developed, and a dorsal hinge ridge is not developed, all constituting differences from *Lineacrassus*. The cardinal process is more massive, and ear spines are more numerous, crowded and finer, and ears are finely rugose.

Lineacrassus inflatus Waterhouse 2013

Fig. 205, 206

2013 *Linaecrassus inflatus* Waterhouse, p. 367, Fig. 16.9, Fig. 16.10.

Diagnosis: Large, a little variable in shape, typically with incurved ventral umbo and swollen venter, rarely somewhat less convex medianly, costellae fine, spines few, many inconspicuous, some thick.

Holotype: GSC 133323, figured in Waterhouse (2013, Fig. 16.10A, C, F, G) and Fig. 206A, C, F, G herein, from Member C (Asselian), Jungle Creek Formation, Yukon Territory, OD.

Material: Sixteen ventral valves, one dorsal valve and four specimens with valves conjoined from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Dimensions in mm:

Specimen GSC	Width	Length	Height	
133323	71.5	102	48	holotype
133325	72	66+	39	
133324	73	90est.	41	

Description: Shells large and elongate, ventral valve swollen with broad umbo, umbonal angle 100º, convex umbonal walls, and hinge either at maximum width or almost at maximum width; large gently convex ears, weakly set off from the umbonal walls, and bearing alate cardinal extremities with angle of 70º. The disc is high and vaulted, convex in most shells or with gentler convexity medianly and the trail extended, one specimen measuring 97mm long, 70mm wide and 58mm high. There is no sulcus or fold, but anteriorly the margin may be recessed, and in other shells extended as a swollen tongue. The dorsal valve is gently concave with large concave ears, and the disc very thick, with a small gently convex nepionic portion, and anterior shell curving gently into an extended trail. Both valves are covered by fine ribs, twelve in 10mm posteriorly and ten in 10mm anteriorly, but the number varies slightly: crests are rounded and interspaces of similar width. Over the anterior trail the ribs may become erratic in course. Costal increase appears to be by intercalation on the ventral valve and by branching on the dorsal valve. A row of closely spaced spines about 0.5mm up to 1mm in diameter as a rule emerge postero-laterally from the ventral hinge, and the slightly swollen bases may measure 1.5 even up to 2.5mm across, without the spines themselves becoming very sturdy at the cardinal extremity. A second row of spines is visible in several specimens, only half the diameter or less, and gradually diverging, at 2mm from the hinge row at a distance of 25mm or more from the beak, where the

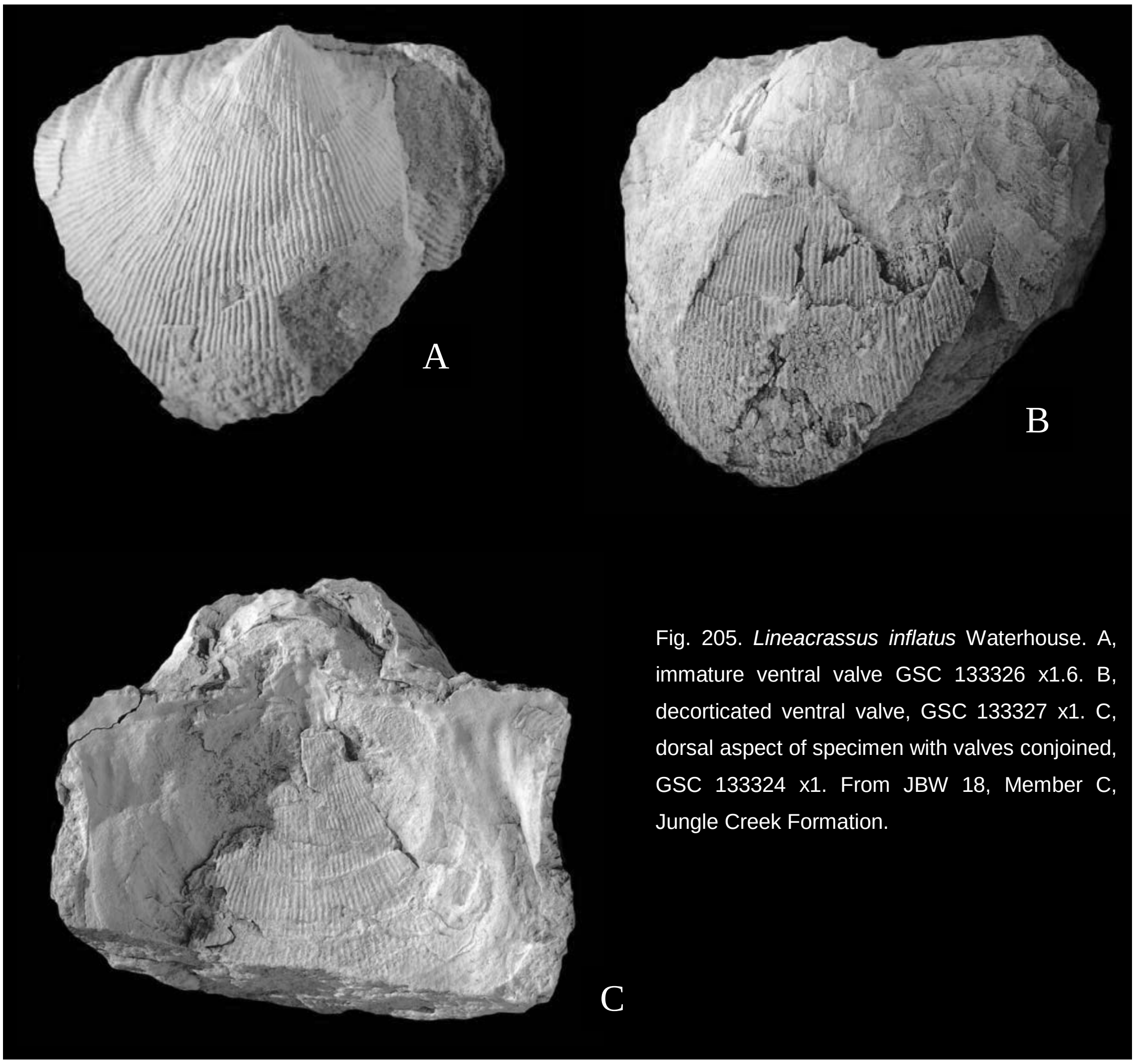


Fig. 205. *Lineacrassus inflatus* Waterhouse. A, immature ventral valve GSC 133326 x1.6. B, decorticated ventral valve, GSC 133327 x1. C, dorsal aspect of specimen with valves conjoined, GSC 133324 x1. From JBW 18, Member C, Jungle Creek Formation.

spines become as thick or thicker than those of the hinge row. Two further and shorter rows lie on the anterior ear, the third row becoming sturdy, up to 1.5mm wide, and the fourth row nearest the umbonal slope comparable in thickness as far as can be seen. Other spines over the visceral disc and trail are rare, slender and erect, emerging from the crests of costellae without perturbation over the disc, and less than 1mm across. Spines up to 1.5mm wide lie on the trail of some specimens, where they lie athwart three ribs, which resume unaltered in front. The dorsal valve has no spines. Rugae may be limited to the ventral ears or faintly suggested on the trail of the ventral valve: other specimens have few or no rugae. Rugae tend to be somewhat stronger over the dorsal disc of at least some specimens.

Ventral adductor scars large and dendritic, diductor scars large and bearing longitudinal grooves. In the dorsal valve, the cardinal process is broad and trilobate, the ventral face lying in the plane of the posterior dorsal valve, with shallow median groove on the ventral face of the shaft and shallow posterior notch. It is supported by hinge ridges curving each side from the base, placed behind a very low and broad platform, without raised buttress mounds. Median septum may be slender or broad posteriorly, extending for almost half of the length of the disc.

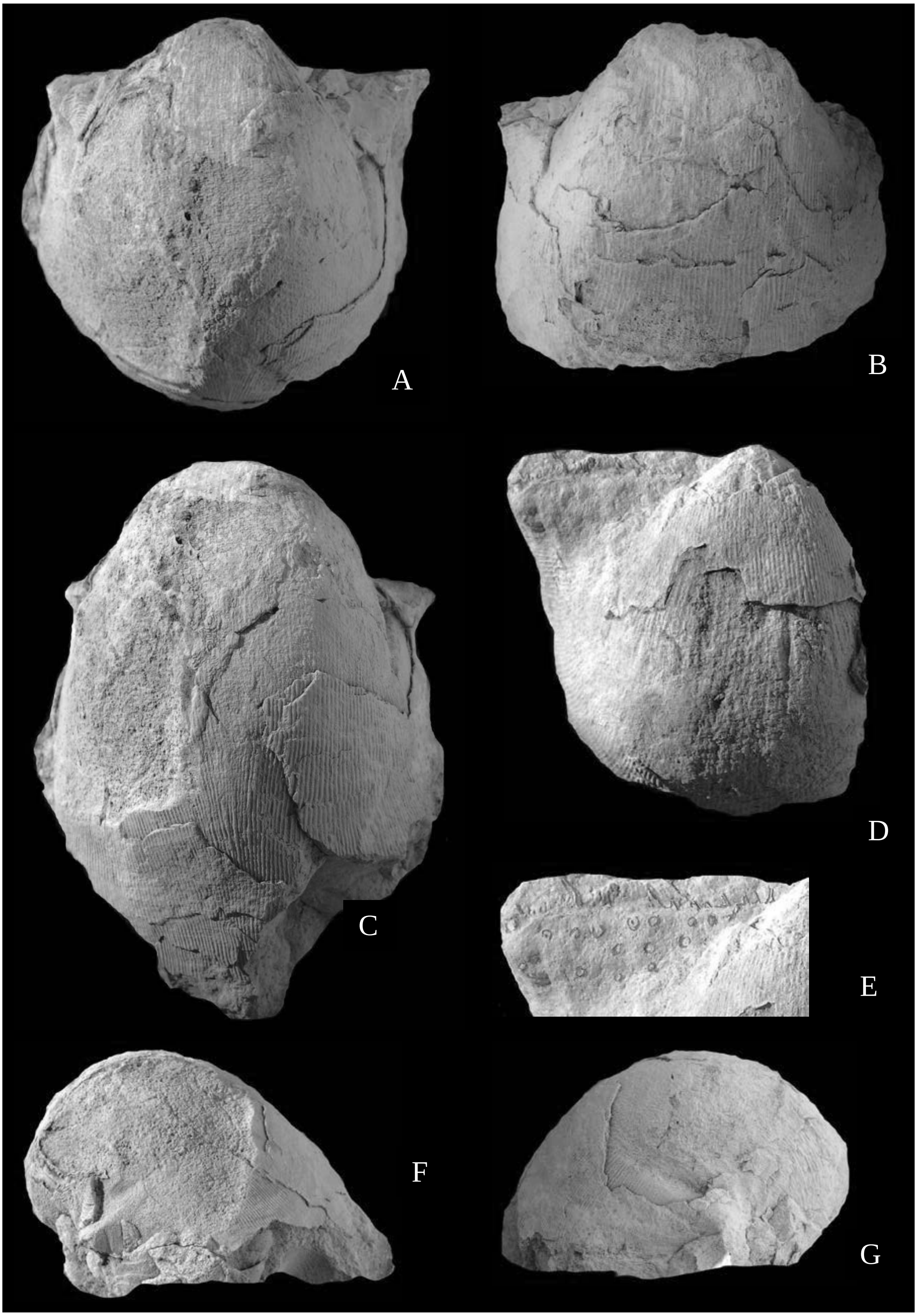


Fig. 206. *Lineacrassus inflatus* Waterhouse. A, C, F, G, ventral valve holotype, GSC 133323, ventral posterior, x0.8, ventral view, x0.7, and two lateral views, x0.6. B, ventral view of GSC 133324, x0.9. (See Fig. 205C). D, E, ventral valve and retouched ear detail of spine position, GSC 133325, x1, x1.5. From JBW 18, Member C, Jungle Creek Formation.

Adductor scars large and dendritic, but subdivision not clear. Only part of the brachial loops is visible, and the inner termini lie in front of the end of the median septum. The posterior floor is smooth, and the shell is thin, only 1mm thick.

Resemblances: This species is characterized by its large size, with highly vaulted ventral valve and large spinose ears. The Canadian material is especially close in shape and size to the cited lectotype of the Russian species commonly called *Linoproductus dorotheevi* Fredericks, but differs over the number and distribution of ear spines, as far as can be ascertained. A number of the original suite of specimens figured by Tschernyschew (1902) include broader specimens with more gently convex median venter, and one specimen has a shallow ventral sulcus. The costellae appear to number ten to fifteen in 10mm anteriorly on the ventral valve of Tschernyschew's material, a degree of variation which renders it difficult to circumscribe the Tschernyschew species, but the number of costae is usually close to twelve in 10mm, slighter finer than in the present suite. Material figured by Gobbett (1964, pl. 10, fig. 8, 9, pl. 11, fig. 1-5) from the Upper Wordiekammen Limestone of Bunsow Land, Spitsbergen, indicates moderately thick spines in the hinge spine row, and what seem to be comparable spines over the disc, but no additional spines over the ventral ears, at least in pl. 11, fig. 2. The material described as *Linoproductus dorotheevi* (Fredericks) from the "*Yakovlevia transversa*" and *Jakutoproductus verchoyanicus* Zones of the overlying Jungle Creek Formation in the Ogilvie Mountains in the Yukon Territory of Canada by Shi & Waterhouse (1996, pl. 15, fig. 25-28, pl. 16, fig. 1-9, 11; text-fig. 31) includes smaller specimens, none of which display the fully arched median venter, and the sole specimen figured by Cooper (1957, pl. 6D, fig. 27-29) as *L.* cf. *lutkewischi* (Stepanov) from Coyote Butte Formation of Oregon has a broad gently convex venter, and slightly stronger ribbing. By contrast, the material from Spitsbergen (Wiman 1914, Gobbett 1964, Czarniecki 1969) resembles the lectotype of *dorotheevi.* Canadian specimens tend to be flatter medianly over the ventral valve, and have more conspicuous coarse disc spines, although some very fine spines are also visible (Shi & Waterhouse 1996, pl. 16, fig. 1, 3), and no additional spines lie on the ventral ears. Some caution is required concerning aspects of the material. Shi & Waterhouse (1996) recorded ventral hinge spines as reaching 0.5mm in diameter, but figured none, and did not make it clear how far from the umbo such fine spines were sited. They also stated that coarser spines were developed over the ventral valve, but such are shown in only one badly damaged, and therefore challengeable specimen (pl. 15, fig. 25). Their identification with *dorotheevi* must be deemed open to question, but when they published the description, little detail was available to them over Russian *Linoproductus*, because Lazarev had not commenced his revision of Russian linoproductoids, and they had to rely largely on similarities of shape. Major clarification of the ornament on *dorotheevi* was provided by Lazarev (2008) from material and a previously unavailable manuscript of B. K. Licharew, to show two thick spines 1.3mm to 1.5mm in diameter along the hinge, and spines as thick on the trail. Whether the spines were arranged along the hinge in one or two rows was not made clear, and Lazarev did not proceed to clarify its generic position.

Linoproductus semisulcatus Cooper & Grant (1975, p. 1148, pl. 431, fig. 7-12) from the Neal Ranch and Lenox Hills Formations of Early Permian age in west Texas is possibly allied to *Lineacrassus*. This species has a staggered double row of ventral hinge spines, and scattered rare moderately strong and also thinner spines over the disc and trail, and the dorsal trial is long. Cooper & Grant (1975) described a tuft of fine spines on the posterior margin and ears, and a sulcus that is confined to the median part of the ventral valve. The United States species is smaller and slightly less arched than the Canadian form, with stronger posterior lateral wrinkles.

Family **SCHRENKIELLIDAE** Lazarev, 1990

[Nom. transl. Lazarev 2000a ex Schrenkiellinae Lazarev, 1990, p. 122].

Taxonomy: The family group unit was proposed as a nomen nudum with no diagnosis, discussion or indication of name genus by Lazarev (1986a, p. 30) in an unpublished summary of a doctoral thesis. Brunton et al. (2000, p. 562) mistakenly indicated the date of the taxon as Lazarev, 1986a. That is incorrect, and the name was eventually published by Lazarev (1990, p. 122), as changed without formal correction by Brunton (2007, p. 2660).

Diagnosis: Medium-sized to large transverse and costate shells with long hinge, inconspicuous ventral umbo, medianly flattened ventral disc, spines in row near hinge margin, with or without further spines. Body corpus slender, outer cardinal process lobes not fused. Development usually symmetrical.

Subfamily **SCHRENKIELLINAE** Lazarev, 1990

[Schrenkiellinae Lazarev, 1990, p. 122].

Diagnosis: Large shells with trail continuing in plane of disc and virtually imperceptible externally.

Discussion: Schrenkiellinae are characteristically medium to large shells with shallow corpus cavity and wide hinge bearing usually a single row of moderately thick spines, and no or rare other erect spines, restricted to the ventral valve. The group is limited to comparatively few genera, that probably evolved from a genus such as *Gilmoria* Waterhouse, 2013. Upper Carboniferous members such as *Praeschrenkiella*, *Meniscuria* and *Plicatomedium* have a few body spines, lost by Permian time for the genera *Schrenkiella* and *Striatospica*. In *Xanthoserella devargasi* (Sutherland & Harlow, 1973, pl. 12, fig. 11), the median septum begins well in front of the cardinal process, without buttress platform or mounds. The trail, indicated by a fold, continues in the curved plane of the disc. (See also p. 254). Exceptionally, dorsal valves are preserved for *Praeschrenkiella*, and for *Chhidrusia* Waterhouse, 2013 from the Indian subcontinent.

Lazarev (2004) claimed that Linoproductidae were characterized by two rows of spines along the ventral hinge, and Schrenkiellidae by having one row of spines along the hinge, but this is not clearly established. The type species *Linoproductus cora* (d'Orbigny) from the Copacabanba Group of Bolivia appears to display a single row of spines (Kozlowski 1914, pl. 6, fig. 2; Chronic 1953, pl. 7, fig. 7-9; Muir-Wood & Cooper 1960, pl. 111, fig. 3, 6; Branisa 1965; Ahfeld & Branisa 1960; Samtleben 1971, pl. 7, fig. 3 and Brunton et al. 2000, Fig. 365.1b). Not all figures are clear, and some could be interpreted as displaying two uneven rows. But that would not establish that two rows are typical, but rather that there was some variation, so that the one or two row presence was variable within even *Linoproductus*, and could not be used as a discriminant. It is noteworthy that other allied linoproductid genera have one row (eg. *Haereospina* Waterhouse 2004b, based on *L. undatus* Cooper & Grant, 1975). Some genera associated with *Schrenkiella* by Lazarev in Brunton et al. 2000) have more lateral spines along the hinge, as in *Striatospica* Waterhouse, so that the number of hinge rows does not provide an infallible basis for family distinction. This genus was identified as *Edriosteges* Muir-Wood & Cooper in Shen et al. (2017), even though *Edriosteges* has a large posterior ventral burst of spines and high interaea, not seen in figures of *Striatospica*, so that the claim requires justification. *Permundaria* Nakamura, Kato & Choi, 1970 appears to have no hinge spines. To Waterhouse (2004a), *Linoproductus* and *Schrenkiella* were deemed to be related at superfamily level, by sharing the same style of costate ornament, lack of dorsal spines, presence of dendritic muscle scars, and concentration of spines along the hinge.

Schrenkiella is much closer to *Linoproductus* than to Anidanthinae, Grandaurispininae and Siphonosiinae, which were classed as subfamilies of Linoproductidae by Brunton et al. (2000).

Sone & Leman (2005) claimed that Waterhouse (2001, p. 28) had transferred Schrenkiellinae to Linoproductidae on the basis that it had a conspicuous row of ventral hinge spines, but this is a gross simplification, with the further implication that Waterhouse was unaware that other linoproductoids had a row of ventral hinge spines. The implication is incorrect, and Waterhouse (2001, 2002b etc.) clearly stated that *Schrenkiella* and allies shared not only a hinge row of ventral spines, but particular form of radial costation, and dendritic muscle scars with *Linoproductus* and allies. Lazarev (1990) and Brunton et al. (2000) rightly stressed the width of hinge and thinness of visceral disc as some of the prime parameters for the distinction of *Schrenkiella* and allies. Brunton et al. (2000) placed *Schrenkiella* and allies in Monticuliferidae, but the ornament differs considerably from that typical of Monticuliferidae, and is much closer to that of Linoproductidae, as noted by Sone & Leman (2005).

Taxonomy: Brunton et al. (2000, p. 562) synonymized with a query the genus *Indigia* Barchatova, 1973, p. 100, type species *I. ilibeica* Barchatova, which appears acceptable. They also synonymized the genus *Achunoproductus* Ustritsky, 1971, p. 21 with a query, but this proposal seems unlikely. Neither Brunton et al. (2000) or Ustritsky (1971) had provided the date of publication or reference for the nominated type species, given as *Linoproductus achunoproductus* Stepanov, and the reference is *Productus* (*Linoproductus*) *achunoproductus* Stepanov, 1948, p. 23, from the Upper Carboniferous of Bashkiria in northern Russia. Klets (2005) also listed the genus. The species as described and figured by Stepanov (1948, p. 5, fig. 2a-c, 3, 4) was based on small transversely oval ventral valves with strong ribs, and looks like a member of Lirariinae Waterhouse, 2013 (see p. 226). The proposed genus of Ustritsky was not supported by any diagnosis, and therefore has at present no validity.

Genus ***Schrenkiella*** Barchatova, 1973

Diagnosis: Large transverse finely costate shells with median ventral fold over anterior half of shell as a rule, spines limited to row along ventral hinge.

Type species: *Productus schrenki* Stuckenburg, 1875, p. 88 from Timan (Sakmarian), Urals, Russia, OD.

Discussion: The name *Schrenkiella* was proposed by Barchatova (1970, p. 67) in a footnote with reference to *Productus schrenki* Stuckenberg (1875, pl. 2, fig. 1A). A diagnosis was later provided by Barchatova (1973, p. 98).

According to Brunton et al. (2000), *Schrenkiella* is found only in Sakmarian deposits of Russia and questionably Australia. The possible Australian occurrence was recorded as *Linoproductus* sp. by Archbold (1983, Fig. 1A, B) from the Lyons Group in Western Australia shows some approach to the genus, but no hinge row of ventral spines has been described, so the occurrence is yet to be established. The Lyons Formation has been judged to be of Asselian age by Waterhouse (2015a). In Canada the genus appears to have had a longer range than in Russia, from Asselian to lower Artinskian.

Schrenkiella triangulata Barchatova, 1973

Fig. 207, 208

1973 *Schrenkiella triangulata* Barchatova, p. 99, pl. 29, fig. 2.
2000 *S. triangulata* – Brunton et al. p. 562, Fig. 396e.

Diagnosis: Large little inflated shells with subtriangular shape and anterior sharply defined ventral fold.

Holotype: TsNIGRA No. 1/10 315, St Petersburg, Russia, figured by Barchatova (1973, pl. 29, fig. 2) from Sakmarian of Urals, OD.

Material: Two ventral valves and a dorsal valve from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Dimensions in mm: ventral valve

Specimen GSC	Width	Length	Height
136797	92	81	44

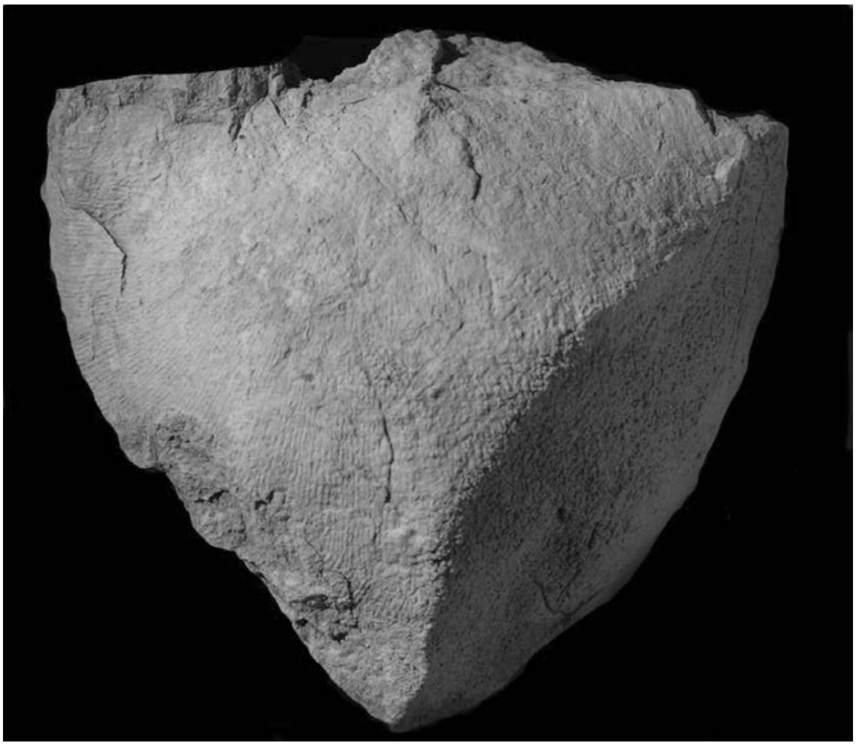


Fig. 207. *Schrenkiella triangulata* Barchatova, ventral valve GSC 136797 from JBW 18, x1. Member C, Jungle Creek Formation.

Description: The ventral valve is large with wide hinge, umbonal region slightly raised, with umbonal angle of 85º, and shell elevated into narrow fold anteriorly. The trail passes smoothly on from the disc, and is not geniculate. No spines are visible in the available material, and the entire shell is covered by fine costellae, seven to eight in 5mm. The dorsal valve has low anterior rugae, a large cardinal process and slender median septum.

Resemblances: The ventral valve is larger than type *Schrenkiella schrenki* (Stuckenberg, 1875) of Sakmarian age in the Urals, but is close in shape, and the anterior median fold is found in *S. triangulata* Barchatova, 1973, of similar age.

Plicatomedium oklahomae (Dunbar & Condra 1932, p. 251, pl. 44, fig. 1, 2; Waterhouse 2004b, p. 29) from the Stanton Formation in Oklahoma has a strong medium fold in the anterior ventral valve, but the overall valve is more convex and the umbo swollen. As well as the prominent row of hinge spines, there are rare body spines over the ventral valve. There is no trail, unlike *Chhidrusia* Waterhouse which has a high and geniculate trail.

Taxonomic note: Brunton et al. (2000, p. 562) placed the author of this species in brackets, but I am not sure if the species had been named before 1973.

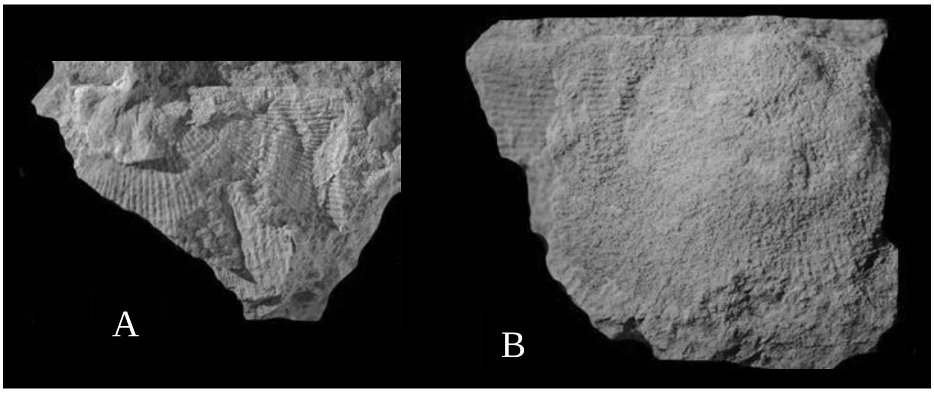


Fig. 208. *Schrenkiella triangulata* Barchatova. A, part of dorsal valve GSC 136799. B, ventral valve GSC 136798. Specimens x2 from JBW 18. Member C, Jungle Creek Formation.

Schrenkiella schrenki (Stuckenberg, 1875)

Fig. 209

1875 *Productus schrenki* Stuckenberg, p. 88, pl. 2, fig. 1.
1964 *Linoproductus* (?) *schrenki* – Barchatova, pl. 2, fig. 8.
1970 *Schrenkiella schrenki* – Barchatova, p. 67.
1971 *Linoproductus shrenki* (sic) – Bamber & Waterhouse, pl. 12, fig. 6.
1971 *L.* cf. *shrenki* (sic) – Bamber & Waterhouse, pl. 14, fig. 6.
1973 *Schrenkiella schrenki* - Barchatova, p. 97.
1996 *Schrenkiella* sp. Shi & Waterhouse, p. 95, pl. 16, fig. 10, 12.
2000 *S. schrenki* – Brunton et al. p. 562, Fig. 396.1a, b.
2013 *Praeschrenkiella waddingtonae* [not Waterhouse] – Waterhouse, Fig. 16.20E (part, not Fig. 16.20A-D, F = *P. waddingtonae*).

Diagnosis: Transverse with wide ears and dorsal valve of shallow concavity, anterior ventral valve with low fold and corresponding dorsal sulcus which may be extended anteriorly.

Holotype: Specimen figured by Stuckenberg (1875, pl. 2, fig. 1A) from Sakmarian of north Timan, Russia, SD Barchatova (1973).

Material: A dorsal valve from GSC 56946, Member E, and another from JBW 88, Member F, Jungle Creek Formation.

Stratigraphic and biostratigraphic levels: Members E and F, Jungle Creek Formation. *Ogilviecoelia shii* and "*Yakovlevia transversa*" Zones.

Discussion: This species was reported by Bamber & Waterhouse 1971, pl. 12, fig. 6 from GSC locality 56946 at section 116F-16 in Member E, but no further specimens at this stratigraphic level have been found. Costae number six, seven or eight in 5mm. Specimens from the "*Yakovlevia transversa*" Zone in the Ogilvie Mountains were figured by Shi & Waterhouse (1996). These are of Sakmarian age, and further material was reported from the *Jakutoproductus verchoyanicus* Zone, judged to be of lower Artinskian age. Shi & Waterhouse (1996) had only the figure of the *schrenki* specimen figured by Tschernyschew (1902, pl. 27, fig. 1a, b) for comparison, and reported that the Yukon material from the "*Yakovlevia transversa*" Zone were finer than those of the Tschernyschew specimen. But the exemplar figured in the *Revised Brachiopod Treatise* by Brunton et al. (2000) shows costae as fine as those of the Yukon specimens, up to eight in 5mm, with five to six in 5 mm common, so that the specific limits of *schrenki* are reassessed. In Russia the species appears to be limited to faunas of Sakmarian age. The reports of some *schrenki* were discounted by Shi & Waterhouse (1996, p. 95), that by Ustritsky & Chernyak (1963, pl. 12, fig. 4-7) having a more transverse and convex ventral valve and deeply concave dorsal valve. One of the Sakmarian dorsal valves figured by Shi & Waterhouse (1996, pl. 16, fig. 10) is exceptional, in that a low median fold is present in the dorsal sulcus. A characteristic feature of many of the Yukon shells, as well as the specimen figured by Tschernyschew (1902), lies in the present of a low anterior fold over the anterior ventral valve, and corresponding anterior dorsal sulcus, but this is less apparent in the specimen figured as typical by the *Revised Brachiopod Treatise*. Provisionally this is assumed to be a variant within the species *schrenki,* but further study of a larger assemblage of type and other specimens of *schrenki* would be desirable.

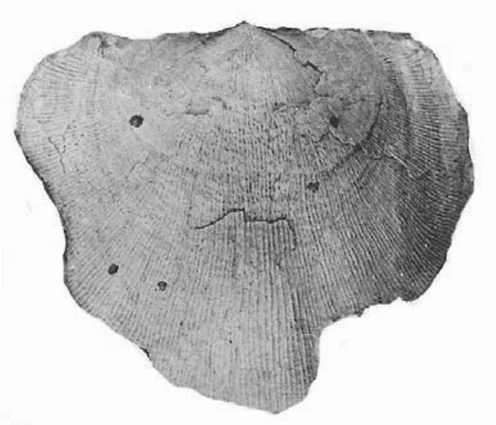


Fig. 209. *Schrenkiella schrenki* (Stuckenberg), GSC 26919 x1.2 from GSC 56946, Member E, Jungle Creek Formation.

It has been found that one of the dorsal valves figured as *Praeschrenkiella waddingtonae* by Waterhouse (2013, Fig. 16.20E) comes from the "*Yakovlevia transversa*" Zone at JBW 88, and it seems likely that this belongs to *Schrenkiella schrenki*, although only the posterior part of the specimen is preserved. Its spinosity is not known, being a dorsal valve, but the location indicates likely *schrenki.*

Genus ***Praeschrenkiella*** Waterhouse, 2013

Diagnosis: Large transverse shells with ventral spines in row along hinge and in a few anterior rows.

Type species: *Praeschrenkiella waddingtonae* Waterhouse 2013, p. 381 from Member A (Gzhelian), Jungle Creek Formation, Yukon Territory, Canada, OD.

Discussion: *Schrenkiella* has only a row of hinge spines (Brunton et al. 2000, p. 562). *Indigia* Barchatova, 1973, p. 100 was referred to synonymy of *Schrenkiella* by Brunton et al. (2000), as was ?*Achunoproductus* Ustritsky, 1971, p. 21, wrongly as analysed on p. 250. All three taxa are of Sakmarian age, from the northern Urals. Of other genera referred to the subfamily by Brunton et al. (2000), *Striatospica* Waterhouse, 1975, p. 11 is moderately (but not unreservably) close to *Schrenkiella* as a small capillate form with hinge spines only, from the upper Capitanian of China. Further members of Schrenkiellidae are to be included from the Pennsylvanian of United States, including *Plicatomedium* Waterhouse, 2004b, p. 29, based on *Linoproductus oklahomae* Dunbar & Condra, with well developed ventral hinge row and high anterior ventral fold, distinguished from *Schrenkiella* by its more vaulted ventral valve, and triangular shape with hinge at maximum width and lateral margins converging anteriorly to the narrow median fold, approaching that of *S. triangulata* (Barchatova, 1973) from Timan, of Sakmarian age, and from Member C in the Yukon Territory, of Asselian age. Commarginal rugae are few and strong, and there are rare body spines over the ventral valve in *Plicatomedium*.

Meniscuria Waterhouse, 2004b, p. 31, type *Linoproductus meniscus* Dunbar & Condra, 1932, p. 255, pl. 30, fig. 4, 5 of Pennsylvanian age from Texas, is a large little inflated transverse form with gentle if any sulcus and fold, slender visceral disc, non-geniculate trail, and spines in a double row along the hinge and scattered over the ventral valve: all spines are slender and without prominent bases. The genus is close in its arched yet thin disc to *Elalia* Lazarev, 2004, which was proposed earlier in the same year for a Bashkirian – Gzhelian genus in the Moscow Basin of Russia, but has larger ears, less conspicuous commarginal rugae, and more transverse less vaulted shape.

The type species of *Xanthoserella* Waterhouse, 2004b, p. 30, *Linoproductus devargasi* Sutherland & Harlow, 1973, from the Morrowan (Pennsylvanian) of United States, has a row of hinge spines and no body spines, and there is no ventral anterior fold, but low commarginal rugae are present. The visceral disc is thin and markedly elongate. A Visean New South Wales species described as *Fluctaria campbelli* Roberts, 1964 (see Waterhouse 2013, Fig. 16.19A) is very close to type *Xanthoserella*, apart from better developed rugae and subvertically or even inwardly directed rather than laterally directed hinge spines, as evaluated by Waterhouse (2010, p. 29, fig. 7).

Praeschrenkiella waddingtonae Waterhouse, 2013

Fig. 210 - 214

2013 *Praeschrenkiella waddingtonae* Waterhouse, p. 381, Fig. 16.20 (part, not Fig. 20E = *Schrenkiella schrenki*).

Diagnosis: Large shells with low inflation, obtuse cardinal extremities not extended into ears, narrow anterior fold on ventral valve, costae fine.

Holotype: GSC 136098 figured by Waterhouse (2013, Fig. 16.20A) and Fig. 210A herein, from Member A, Jungle Creek Formation, OD.

Material: From Member A, one ventral valve from JBW 101, ventral fragment and specimen with valves conjoined from JBW 578, two ventral valves and two dorsal valves from JBW 615 , two ventral valves from JBW 642, single dorsal valves from JBW 511, 725 and 764. One ventral valve GSC 26919 from GSC 56946. Dorsal valve and ventral valve from JBW 516, upper Ettrain Formation.

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Dimensions in mm:

Specimen GSC	Width	Length	Height	
133328	66	54	13	
133331	65	45	13	
136098	43	27	4	holotype

Description: Specimens large, weakly transverse, wide hinge without extended extremities, cardinal angle obtuse, maximum width placed a little in front near posterior third of shell width. Ventral umbo subdued, broad with angle of 120°, little incurved, low ginglymus developed, ears weakly differentiated, especially in specimens not fully mature, and gently convex, disc gently convex without sulcus, and a narrow fold arises over the trail which extends for the anterior third of the shell length. Dorsal valve gently concave with poorly differentiated but slightly dorsad ears, and a very low anterior fold arises behind mid-length: shallow anterior sulcus corresponds with the ventral fold. Ventral

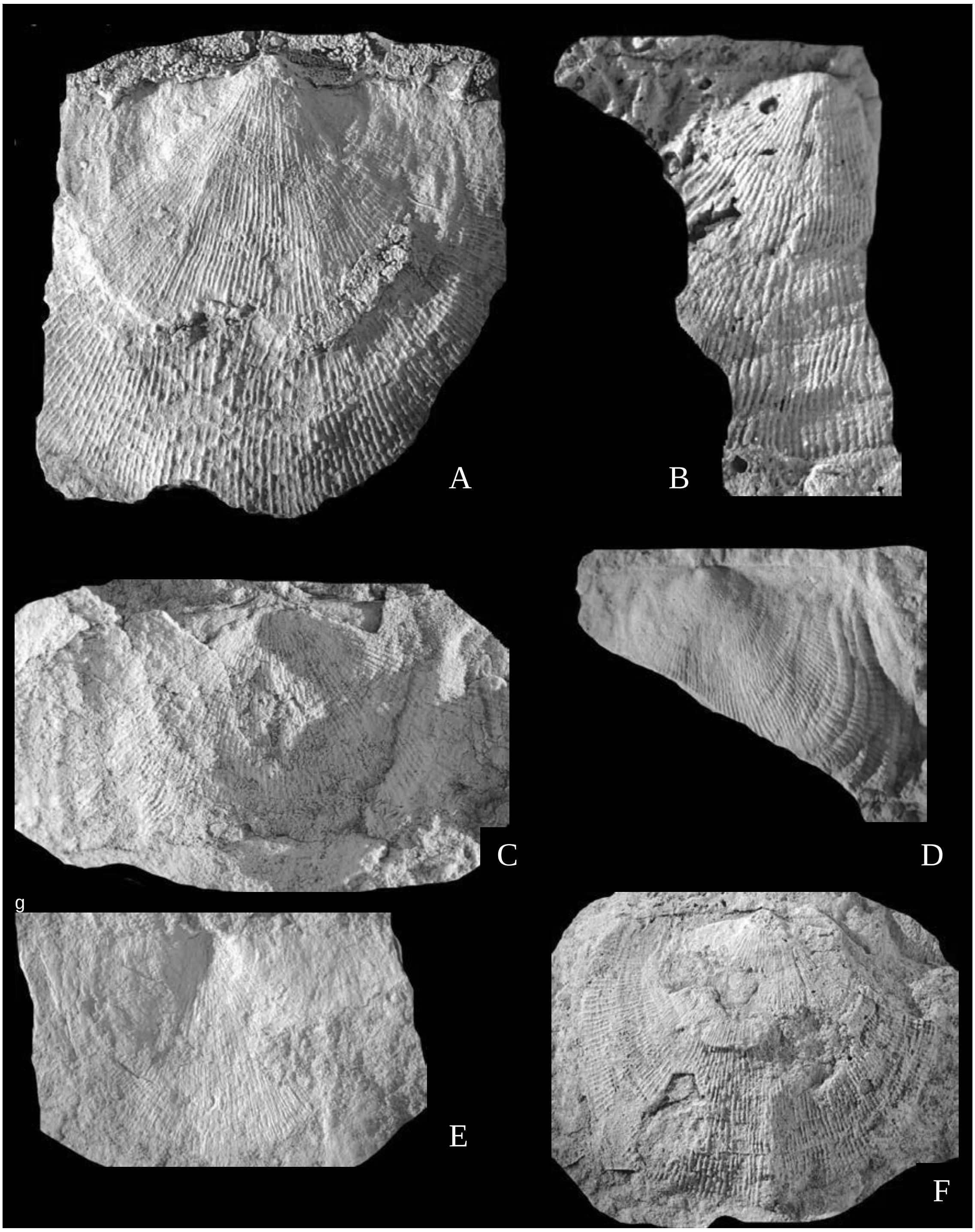


Fig. 210. *Praeschrenkiella waddingtonae* Waterhouse. A, ventral internal mould GSC 136098 from JBW 615, holotype, showing hinge spines projecting posteriorly in plane of disc, x1.5. Many spines lie around the anterior margin. B, internal mould of ventral valve GSC 133329 from JBW 642 x1.8. C, dorsal valve GSC 133330 from JBW 725 x1. This is concave and has been backlit from right. D, dorsal external mould from JBW 516 x1. Ettrain Formation. E, exterior of dorsal valve GSC 133331 from JBW 615 x1.5. F, ventral valve GSC 133328 from JBW 615 x0.9, showing narrow ears. A-C, E, F from Member A, Jungle Creek Formation, and D from Ettrain Formation..

valve ornamented by costellae, seven to eight in 5mm at mid-valve and four to five in 5mm at lateral anterior margin, increase by intercalation, ribs with rounded crests. Dorsal costellae similar, numbering six in 5mm near anterior margin, arise by intercalation and bear rounded crests. Fine growth increments number up to ten in 1mm, coarse often alternating with fine, and two to four minor growth steps. Very fine growth laminae are developed at least over the middle and anterior shell. Spines in a row along the ventral hinge, only 2mm apart along much of the length, but spaced further apart laterally, erect, and 1mm in diameter. Short ventral spines in six to ten irregular rows anteriorly, arising in commarginal rows in some specimens and more spaced in others**.** They have slightly swollen bases and the hollow spine core is very slim. Internal detail not revealed, apart from a low median septum extending from near the hinge of the dorsal valve.

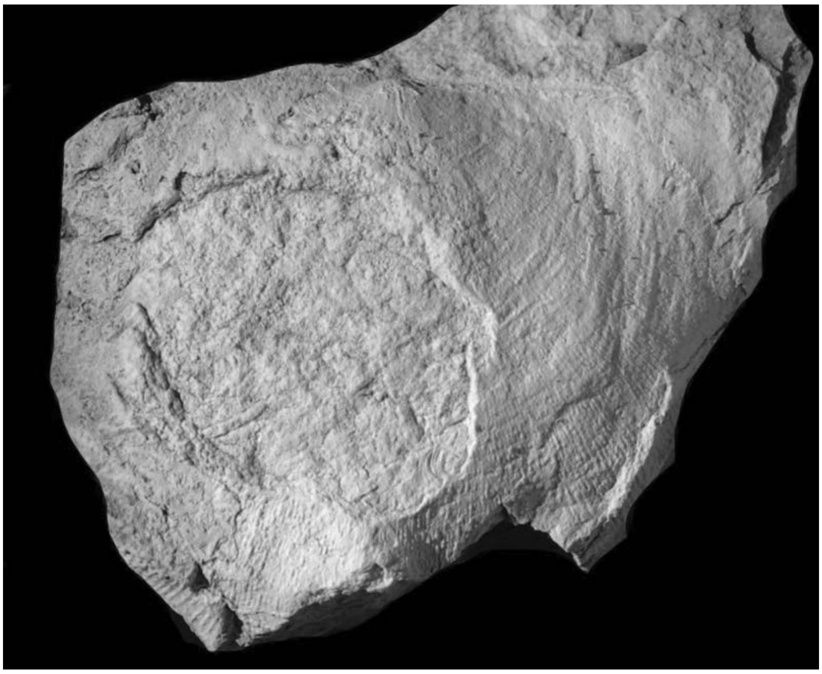


Fig. 211. *Praeschrenkiella waddingtonae* Waterhouse, ventral valve GSC 137266 x2 from JBW 615. Member A, Jungle Creek Formation.

Resemblances: The genus is distinguished by the short spines in rows along anterior growth lamellae. In the type species of *Schrenkiella* Barchatova, 1973, p. 97, *Productus schrenki* Stuckenberg (1875, p. 88), also figured by Tschernyschew (1902, pp. 290, 628, pl. 27, fig. 1), Brunton et al. (2000, Fig. 396. 1a, b) and Lazarev (2004), from the Indiga River of Sakmarian age in the Urals, the ventral valve is more arched than the Canadian form and

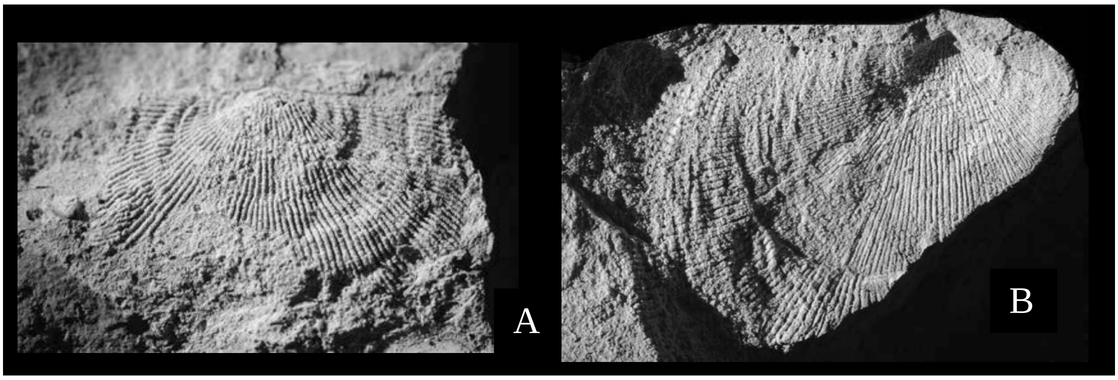


Fig. 212. *Praeschrenkiella waddingtonae* Waterhouse. A, dorsal valve GSC 137251 x2 from JBW 764. B, ventral valve GSC 137431 x1.5 from JBW 615, showing many anterior spines and larger hinge row of spines as dark round holes in the external mould, formed from dissolved spines, as in Fig. 214. Member A, Jungle Creek Formation.

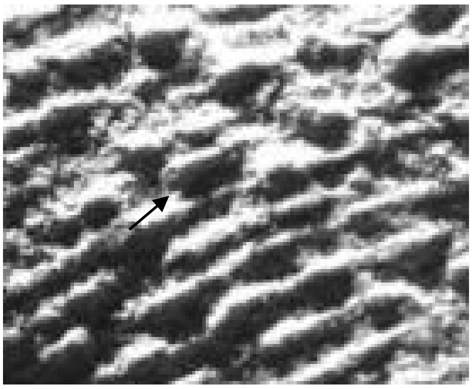


Fig. 213. *Praeschrenkiella waddingtonae* Waterhouse, ventral valve holotype GSC 136098 x4 from JBW 615**,** with spine base arrowed. Member A, Jungle Creek Formation.

Fig. 214. *Praeschrenkiella waddingtonae* Waterhouse, ventral valve external mould GSC 137431 x3 from JBW 615**,** with some of the spine bases arrowed. See Fig. 212B. Member A, Jungle Creek Formation.

has a broader and lower anterior ventral fold, a row of fine ventral spines, and projecting cardinal extremities. Allied specimens, probably of a separate species, were figured as this form from the Turuzov Suite of Taimyr Peninsula by Ustritsky & Chernyak (1963, p. 82, pl. 12, fig. 4-7), with broader anterior fold and less extended cardinal extremities. *S. timanica* Barchatova (1973, pl. 29, fig. 1), also figured by Brunton et al. (2000, Fig. 396.1c, d), is also more inflated, and *S. triangulata* (Barchatova 1973; Brunton et al. 2000, Fig. 396.1e) has subangular cardinal extremities at maximum width, and anterior narrow median ventral fold. *S. umboplanata* Barchatova (1973, pl. 30, fig. 2) has a broad anterior ventral fold and well rounded postero-lateral extremities. These Russian species are of Sakmarian age. The suggestion in Waterhouse (2004a) that *Linoproductus periovalis* Waterhouse, 1983b, p. 221 from the Khisor Sandstone Member (or White Sand of Waagen 1891) might belong to *Schrenkiella* remains conjectural, because no spines are preserved.

Praeschrenkiella costata Waterhouse, 2013

Fig. 215, 216

2013 *Praeschrenkiella costata* Waterhouse, p. 383, Fig. 16.21.

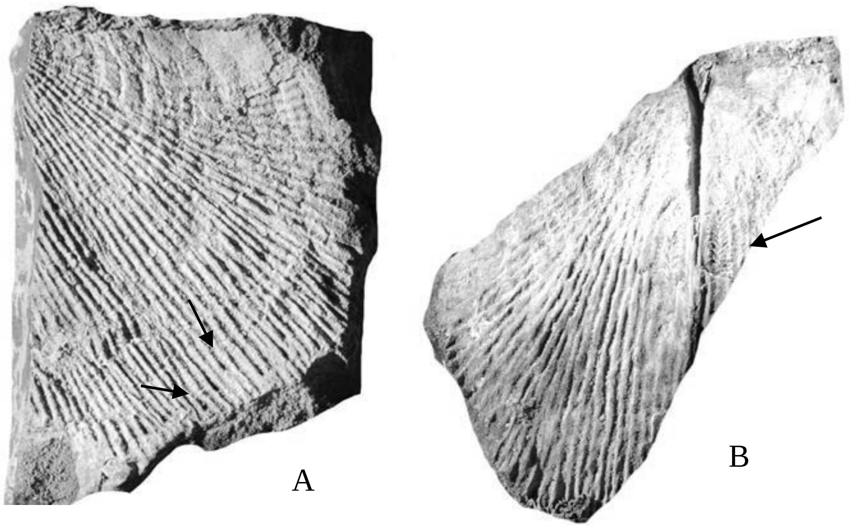


Fig. 215. *Praeschrenkiella costata* Waterhouse. A, external mould of ventral valve GSC 133312, holotype, x1. Arrows point to some of the spine base. B, internal mould of dorsal valve GSC 133315. Member A, Jungle Creek Formation, x1. Arrow points to adductor scars.

Derivation: costa – rib, Lat.

Diagnosis: Ribs comparatively coarse.

Holotype: GSC 133312, from Member A (Gzhelian), Jungle Creek Formation, Yukon Territory, Canada, figured in Waterhouse (2013, Fig. 16.21) and herein, Fig. 215A, 216, OD.

Fig. 216. *Praeschrenkiella costata* Waterhouse, external mould of ventral valve GSC 133312, holotype. Arrows point to some of the spine bases, some with spine core infilled by matrix. Member A, Jungle Creek Formation, x4.

Material: A few fragmentary but otherwise well preserved specimens from JBW 578 of Jungle Creek Formation, Yukon Territory, Canada.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Shells moderately large. The ventral fragment was originally between 80 and 100mm wide, at least 60mm long and 8mm high: it is very gently convex, with no well formed fold or sulcus. Cardinal extremities obtuse, short anterior ventral sulcus fading anteriorly, ribs coarse, three to four in 5mm anteriorly, ventral ribs increase by intercalation, crossed by fine growth laminae, six to eight in 1mm anteriorly. Dorsal valve concave, with narrow anterior sulcus and low swelling each side. Row of fine ventral hinge spines, and distinct broader short anterior ventral spines in a few irregular rows. The columnar cardinal process is supported by a long median septum extending well beyond mid-length of the fragment, broad posteriorly, and continued anteriorly as very low fine ridge, which divides two elongate adductor scars scored by fine feathery dendritic markings. The posterior floor is slightly thickened and bears dimples and short erratic grooves. There is no heavy hinge ridge or clear development of brachidia.

Resemblances: The species is characterized by the coarse costae, fine hinge spines in a row, and scattered sturdy anterior spines, less numerous than in *Praeschrenkiella waddingtonae*.

Family **STRIATIFERIDAE** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 2013, p. 384 ex Striatiferinae Muir-Wood & Cooper, 1960, p. 328].

Diagnosis: Elongate and often asymmetric shells, not free living, narrow hinge, spines may be on dorsal valve, cardinal process with single myophore lobe.

Discussion: This minor but highly distinctive family group was placed in Monticuliferidae by Brunton et al. (2000), and shifted to Linoproductidae (Linoproductoidea) on account of the nature of the spines by Waterhouse (2002b). Brunton et al. (2000, p. 560) regarded Proboscidellini Muir-Wood & Cooper as a sister tribe, but proboscidellin spines are quite different, having elongate posterior bases which recurve and extend forward through tunnels within the shell. Members of Striatiferinae adopted a nesting habit, crowded in clusters, or resting propped against other shells, whereas in the allied subfamily Compressoproductinae, *Compressoproductus* was more solitary in habit according to Cooper & Grant (1975), though individuals often rested against shells of varying shape. The origins are difficult to judge, but the open coiling and expansion of the shell in Gilmoriinae Waterhouse suggests a source more likely than Ovatiinae Lazarev.

Subfamily **COMPRESSOPRODUCTINAE** Jin & Hu, 1978

[Compressoproductinae Jin & Hu, 1978, p. 115].

Diagnosis: Characterized by fine radial ornament, few and erect ventral spines found especially near hinge, low body corpus. Shells often with well defined commarginal rugae, may become asymmetric from nestling in host.

Discussion: The subfamily is close to Striatiferidae, not Monticuliferidae as in Brunton et al. (2000, p. 546). The high and often narrow ventral valve and fine radial ornament are reminiscent of *Striatifera* Chao, of Carboniferous age, with narrow short spine bases. *Substriatifera* Kotlyar, 1964, p. 123, was based on *Productus mytiloides* *vladivostokensis* Fredericks, 1925, p. 17, pl. 2, fig. 80, 81 and is difficult to decipher. It was synonymized with *Compressoproductus* by Brunton et al. (2000), and there is no obvious difference between the two genera, judged from figures. Possible *Compressoproductus* is found in Gzhelian deposits of the Ogilvie Mountains in northwest Canada: otherwise the genus and associated forms are Permian in age.

Genus ***Compressoproductus*** Sarytcheva, 1960

Diagnosis: Medium-sized shells with radial ribs and closely spaced commarginal rugae, ventral ears large and often inclined in plane of lateral walls, bearing few to usually many spines, and fine erect spines may form nodes over the ribs. Ventral adductor scars scalloped. Cardinal process unifid.

Type species: *Compressoproductus morahpressus* Waterhouse & Piyasin, 1970, p. 133, replacement name for *Productus compressus* Waagen, 1884, p. 710 not Say, 1823. In Case 3352 Dr M. Sone asked the International Code for Zoological Nomenclature to suppress the proposed name *morahpressus* on the grounds that workers had ignored, or were ignorant of, the change (eg. Brunton et al. 2000, p. 546). The ICZN opinion 2201 concluded that "An application for the proposed conservation of *Productus compressus* Waagen, 1884 is not approved". Of course *Productus compressus* Waagen not Say is the type species of *Compressoproductus*, and it would be reasonable to cite this, and indeed the matter was never in doubt. But the omission of "not Say" or even Waagen by various authors is in error, and the failure to cite the correctly named taxon does not reflect well on the understanding of the genus and its taxonomy. Nor should careless taxonomy be defended by suspension of the rules. Perhaps it is time to set aside permanently the prospect of any endorsement of such an egregious procedure. If an author knows the correct name, he should use it, and correct any error, not seek to protect the error. The problem lies in the present Code for Zoological Nomenclature, which undercuts the science of taxonomy by being open to sanctify carelessness or error, and being willing to endorse the claim that "customary usage" is of merit. Science should always strive to reflect reality, and reject error, no matter how well enshrined and for how long it has persisted in human usage.

Discussion: One outstanding attribute of at least some *Compressoproductus* lies in the scalloped diductor muscle field, with thickened shell and strong pustules just in front. Some of the species described by Cooper & Grant (1975) show such a ventral interior, including *C. curtus* Cooper & Grant (1975, pl. 460, fig. 16, 21, 32, 33) and *C. flabellatus* Cooper & Grant (1975, pl. 461, fig. 48, 50, 66), both species coming from the Cathedral Mountain Formation in the Glass Mountains, west Texas, United States. As stressed by Brunton (2007), the body cavity is slender, not thick as mistakenly asserted by Waterhouse (2002b).

***Compressoproductus*?** sp.

Fig. 217

Diagnosis: Broadly triangular in shape with strong regular commarginal rugae.

Material: A ventral valve with fragments from JBW 615.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Ventral valve triangular and elongate in outline, measuring 26mm wide, 24mm long, and 6mm high. The ventral umbo is broad and not incurved, and posterior umbonal walls are high and steep posteriorly, and extend well forward, diverging at 70-75º, and curve outwards with slightly concave outline, but are gently convex in profile. The hinge is not exposed. There is no sulcus or fold, but the convexity is reduced over mid-valve. Surface covered by fine even costellae, numbering six to eight in 5mm over much of the valve, with round low crests and interspaces of comparable or slightly greater width: increase on the ventral valve is by branching. Fine spines arise from the crests of costellae, variously from the crest or anterior slope of rugae as a rule: they are rare posteriorly and more numerous anteriorly. Valve crossed by a few commarginal rugae, of varying strength.

Internal detail is not visible and detail of the hinge is obscure.

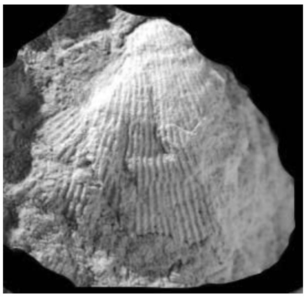


Fig. 217. *Compressoproductus*? sp., ventral valve GSC 136700 x2 from JBW 615. Member A, Jungle Creek Formation.

Resemblances: This occurrence is significantly older than most previous reports of *Compressoproductus*, Brunton et al. (2000, p. 546) having given an age range of “Upper Permian – Kazanian-upper Tatarian)”, meaning in modern terms, Wordian (ie. Middle Permian) to late Changhsingian (Upper Permian). Whether the wrinkles of the Jungle Creek ventral valve pass posteriorly into smooth shell with spines is not shown, and the shells are less inflated than type species of *Compressoproductus* or *Sarytchevinella* Waterhouse, 1983d and are more rugose than *Fallaxoproductus* Li, Gu & Li, 1982.

Compressoproductus morahpressus Waterhouse & Piyasin, 1970, nom. nov. for *C. compressus* (Waagen 1884), is less elongate with umbonal walls diverging at a greater angle, but is similar in ornament of ribs and wrinkles. Some material assigned to the species, such as that described from the Kitakami Mountains of Japan by Tazawa et al. (2000, pl. 1, fig. 2a, b), are narrower with elongate ventral umbo, but commarginal wrinkles are less in evidence. *C*. *prinadai* (Fredericks, 1916) is close in shape but has fewer wrinkles, and *C. vladivostokensis* (Fredericks) is a wider more broadly triangular shell, with more but subdued wrinkles. Both species come from the upper Barabash Horizon of south Primoyre, dated as Ufimian to lower Kazanian (ie. Roadian or lower Wordian) by Licharew & Kotlyar (1978). *C. mongolicus* (Diener 1897, pl. 4, fig. 8-10; 1899, pl. 6, fig. 1-8) from the *Lamnimargus himalayensis* Zone of the Himalaya, of Wuchiapingian age, is moderately close in outline and has close-set wrinkles, and very fine ribs. The same species has also been recorded by Chao (1927a, pl. 9, fig. 5, 6) and Huang (1932, pl. 3, fig. 21) from south China, and by Grunt & Dmitriev (1973, pl. 8, fig. 4, 5) from the Pamirs, and by Licharew (1937, pl. 8, fig. 1-3) from the Nikitin Uralpin levels of the north Caucasus. *C. compressus corniformis* (Chao in Grabau, 1931, p. 291, pl. 29, fig. 6-9) from Mongolia is close in size and has well developed commarginal rugae, and the shape is elongate and variable from specimen to specimen, presumably reflecting the nature of the host.

Grönwall (1917, p. 580, pl. 28, fig. 15-18) recorded a specimen of *Compressoproductus* from what was considered to be Carboniferous from Greenland, but it is small and broader than the present species.

From the Middle Permian Lengwu Formation of Zhejiang, China, *Compressoproductus fengshuijiangensis* Liang (1990, p. 210, pl. 34, fig. 6-8) is larger, but similar in being covered by commarginal rugae and is very elongate, with a more attenuated ventral umbo.

Genus ***Sarytchevinella*** Waterhouse, 1983d

Diagnosis: Convex ventral valve with wide hinge and swollen umbonal region, steep and normal umbonal walls without numerous spines and wide hinge, low commarginal rugae which may be irregular.

Type species: *Productus djulfensis* Stoyanow, 1915, p. 94 from Lopingian of Armenia, OD.

Sarytchevinella praecursor n. sp.

Fig. 218

Derivation: praecursor – forerunner, Lat.

Diagnosis: Massive incurved ventral umbo, low irregular commarginal rugae.

Holotype: GSC 137317, here designated.

Material: Seven ventral valves from JBW 451.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

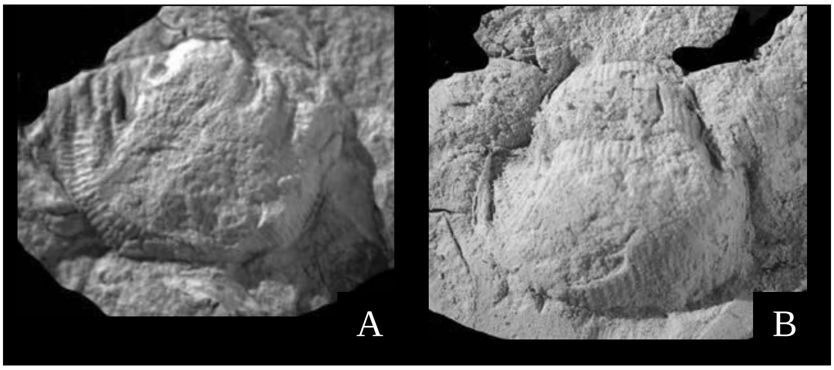


Fig. 218. *Sarytchevinella praecursor* n. sp. A, internal mould of ventral valve GSC 136703, x2. B, external cast of ventral valve GSC 137317 holotype x3. From JBW 451. Member A, Jungle Creek Formation.

Description: Specimens small and incomplete, one measuring 16.5mm wide and 13 mm long and nearly 5mm high. Ventral umbo blunt and hinge wide, shells of irregular shape and may be widest at hinge or well in front, no sulcus. Rugae irregular and strongest towards hinge, costellae number about ten in 5mm at anterior margin. Spines in row along hinge, and rare and slender over visceral disc, with rows near the anterior margin in GSC 136703, without prolonged bases.

Resemblances: This material seems likely to belong to Compessoproductinae, given the overall shape and finely ribbed ornament with slender ventral body spines that lack prolonged bases. The shells lack the high posterior walls with numerous spines typical of *Compressoproductus*, and differ in shape from *Fallaxoproductus* Li, Gu & Li (1982), with its extended ventral umbo and long umbonal walls, and lack of commarginal rugae. *Sarytchevinella djulfensis* (Stoyanow) has similar spines and ribs, with more regular rugae, and *S. tenuissima* Waterhouse (1983d) from northern Thailand is less inflated with weaker rugae. *S. chaoi* Waterhouse (1983d, p. 128) from China is more elongate and less inflated with lower ventral umbo and lower inflation (Chao 1927a, pl. 11, fig. 5, 6). These species are of Lopingian age, very much younger than the present species, which admittedly is based on limited material, but appears to point to a significant early entry of the genus in faunas from high temperate latitudes, compatible with the early entry of possible *Compressoproductus* and other Linoproductidina in the Canadian faunas.

Superfamily **PROBOSCIDELLOIDEA** Muir-Wood & Cooper, 1960

[Nom. transl. Waterhouse 2013, p. 404 ex Proboscidellinae Muir-Wood & Cooper, 1960, p. 325].

Diagnosis: Both valves costate unless ribbing secondarily lost; ventral spines over disc with elongate bases.

Discussion: During the Late Carboniferous and Permian Periods, linoproductiform brachiopods flourished as major groups, one centred on linoproductoids, the other represented by auriculispinids and paucispinauriids. But this was not recognized by Muir-Wood & Cooper (1960), because they focused on Early Carboniferous faunas of United States and Europe, and Permian of United States and northern Europe, those regions at that time having supplied most of the initial descriptions of genera. All of these areas were of paleotropical affinities during Late Paleozoic time, which encouraged a plethora of evolution with development of some peculiar deviations from the norm. Auriculispinidae and Paucispinauriidae, which had been recognized first in high rather than low paleolatitudes, were initially lumped with linoproductids by Muir-Wood & Cooper (1960). A few close relatives were discriminated as highly exceptional groups, such as Proboscidellinae, named for peculiar brachiopods with ventral valve which developed into a long tube. So when superfamily groupings were recognized, proboscidellids assumed naming rights, even though they were highly exceptional and far from typical.

In Linoproductoidea, the ventral disc spines are erect as a rule without posteriorly or anteriorly prolonged bases. In Proboscidelloidea spine-bases are prolonged posteriorly over the outer surface, and, in at least Permian and Late Carboniferous members of the group, the spine bases recurve to be prolonged forwards within the shell from the spine base (see Waterhouse 2013, Fig. 11, p. 18), forming spine tunnels in the shell in front of the emergent spine, as if keeping contact with the mantle edge (Waterhouse 2004b, 2010). Possibly this explains the considerable degree of variability in the ribbing on the ventral valve, in contrast to the consistent pattern of ribs for members of Superfamily Linoproductoidea. Because ventral disc spines followed a tortuous course into and through the shell, they could never have developed a substantial diameter, in contrast to spines which passed directly from the interior to exterior through the shell. In addition, commarginal rugae are widely present, and much more organized than in Linoproductoidea. The fossil record indicates that the two superfamilies arose each from within a different subfamily of Family Devonoproductidae, Superfamily Proboscidelloidea from Subfamily Plicoproductinae, and Superfamily Linoproductoidea from Subfamily Eoproductellinae. Plicoproductinae Waterhouse, 2004b, p. 42 is based on *Plicoproductus* Ljaschenko and *Striatoproductella* Krylova, of Early and Middle Devonian (Eifelian – middle Givetian) age. In these genera, spines are limited to the ventral valve, with posteriorly prolonged bases, and both valves bear ribs. The genera are strophalosiiform, with low interareas, small teeth and sockets (Waterhouse 2013, p. 308).

Members of Proboscidelloidea are comparatively rare in Devonian and Early Carboniferous faunas world-wide. They seem to have been scarce in China, where, as an example, Chen & Shi (2003, pl. 9, fig. 18, 19) were able to record only two specimens from Visean – Serpukhovian faunas of the Tarim Basin, northwest China. Allies are also very rare in the Devonian and Early Carboniferous of Gondwana, and a number of studies on Australian Carboniferous faunas have found very few proboscidelloids. But the family flourished during Permian time in Gondwana at high paleolatitudes, especially in the southern paleohemisphere, involving mostly Australia and New Zealand, as well as throughout the paleotropics.

Family **PAUCISPINAURIIDAE** Waterhouse, 1986a

[Nom. transl. Waterhouse 2013, p. 416 ex Paucispinauriinae Waterhouse, 1986a, p. 2. Syn. Grandaurispininae Lazarev, 1990, p. 130].

Taxonomy: Paucispinauriinae was proposed and published by Waterhouse (1986a, June, p. 2) at the same time as Grandaurispininae Lazarev (1986a, June, p. 32) was listed, but not discussed, in a non-publication. Brunton et al. (2000, p. 533) claimed that Paucispinauriinae had not been proposed until September, 1986 (Waterhouse 1986b, p. 37), and did not acknowledge that the Lazarev proposal was in a list, with no diagnosis or explanation. Lazarev (1986a) did not provide a description or definition that stated in words characters which purported to differentiate the taxon as stipulated by the International Commission for Zoological Nomenclature (1999, article 13.1, p. 17). Waterhouse (1986a) did provide a brief explanation, and indicated both the name genus and allied genera. The proposal was reinforced shortly afterwards in Waterhouse (1986b). Not until 1990 did Lazarev (1990, p. 130) provide validation, and the validity of Grandaurispinidae dates from 1990. Prior mentions, even though promoted by Brunton et al. (2000), carry no standing, according to the rules of zoological nomenclature. This was accepted without acknowledging any correction by Brunton (2007, p. 2652).

Diagnosis: Shells small to medium in size, ventral spines generally with elongate bases in regular quincunx over disc, crowded or rare over ears and in row or rows along hinge, dorsal spines usually present, crowded, erect, sometimes differentiated and unusually large for Productida. Radial ribs and weak to strong commarginal rugae. Body corpus usually moderately thick and trail extended, often geniculate. Cardinal process trilobed, dorsal medium septum single or with shallow slit near the adductors, forming double ridge in some genera, but less commonly than in many Auriculispinidae.

Family relationships: Paucispinauriidae differs from Linoproductidae in having less well defined radial ribs that may be spaced further apart, and in ventral disc spines having prolonged bases. Various paucispinauriid genera have a thick body cavity as in Linoproductidae, but this is regarded as of lesser importance, because ontogenetic studies show that species and genera which are thin-disced at maturity could become thick-disced at a gerontic stage of development. A number of paucispinaurian genera carry thin and even thick spines also on the ventral ears, and also on dorsal ears and trail, where the spine bases are not recurved, and several otherwise similar genera differ only in the presence or absence of dorsal spines.

The oldest member appears to be Magniplicatininae which is represented by at least one genus *Globicorrugata* Waterhouse in Visean faunas, and by genera of Engellini Waterhouse, 2013. It may be noteworthy that *Proboscidella* Muir-Wood & Cooper of comparable age and with bifid rather than trifid cardinal process, may display somewhat paucispinauriiform dendritic adductor scars, not to mention a very long trail.

Because members of this group are often typified by strong commarginal rugae, they superficially resemble members of Fluctuariinae Nalivkin, but spines and cardinal process differ (see Waterhouse 2013, p. 413ff).

Subfamily **MAGNIPLICATININAE** Waterhouse, 2001

[Nom. transl. Waterhouse 2013, p. 422 ex Magniplicatinini Waterhouse, 2001, p. 49].

Diagnosis: Commarginal rugae moderately to strongly developed, otherwise close to Paucispinauriinae in costation. Spines not differentiated to same extent. Interior much as in Paucispinauriinae.

Discussion: Compared with Auriculispinidae Waterhouse, 1986b, disc spine bases are generally more elongate and wrinkles are stronger. Ventral adductors are striate and especially dendritic throughout ontogeny (Shi & Waterhouse 1996, p. 96), at least in Permian members, and are not posteriorly impressed into the posterior wall, whereas ventral adductor scars are striate and subelongate rather than dendritic at early into full maturity in Auriculispinidae, and are impressed into the posterior wall. Brunton et al. (2000, pp. 533, 543) assigned *Cancrinella* Fredericks to Grandaurispininae (ie. Paucispinauriinae) and *Magniplicatina* Waterhouse to Auriculispininae, but the two genera are close in many respects, so that the difference in dorsal spinosity is not considered to mandate subfamilial distinction. *Magniplicatina* was considered to be widespread in the northern hemisphere, including Glass Mountains of Texas in United States. Such species were assigned to *Cancrinella* by Cooper & Grant (1975), until changed by Brunton et al. (2000, p. 544), but most species (except for *Cancrinella subquadrata* Cooper & Grant) lack dorsal spines and seem likely to belong to *Commarginalia* Waterhouse.

Tribe **MAGNIPLICATININI** Waterhouse, 2001

[Magniplicatinini Waterhouse, 2001, p. 49].

Diagnosis: Commarginal wrinkles regular and strongly developed. Body corpus thin to rarely moderately thick. Close to Paucispinauriinae in costation, ventral spines in one or more hinge rows. Dorsal spines present in at least one genus. Ventral adductors dendritic, cardinal process trilobed.

Subtribe **MAGNIPLICATININAI** Waterhouse, 2001

[Nom. transl. Waterhouse 2013, p. 423 ex Magniplicatinini Waterhouse, 2001, p. 49].

Diagnosis: Commarginal wrinkles equally developed on both valves.

Genus ***Commarginalia*** Waterhouse & Nazer, in Waterhouse, 2013

Diagnosis: Commarginal wrinkles strong on both valves over disc and trail, ventral spines in one to three rows along hinge, disc spines in quincunx. No dorsal spines.

Type species: *Commarginalia yukonensis* Nazer & Waterhouse, 2013, p. 426, from Ettrain Formation (Kasimovian), Yukon Territory, Canada, OD.

Discussion: This genus looks very like *Magniplicatina* Waterhouse, 1983a, but lacks dorsal spines. *Helenaeproductus* Lazarev in Pavlova et al. (1991, p. 117), type species *H. khubsugulensis* Lazarev, is a synonym of *Magniplicatina* according to Brunton et al. (2000, p. 543). An Early Carboniferous ally is *Globicorrugata* Waterhouse, 2013, with less dendritic adductor scars and fewer spines over the ears. *Cancrinella* Fredericks (Brunton et al. 2000, p. 533) also lacks dorsal spines, but has a non-plicate disc, and is placed in a separate subtribe, Cancrinellinai Waterhouse, 2013. *Platycancrinella* Waterhouse, 1983a is another member of this subtribe, lacking dorsal spines, with weak commarginal wrinkles, and ears bearing a cluster of numerous spines.

Commarginalia sp. A

Fig. 218

Material: A specimen with valves conjoined from JBW 593 and ventral valve from JBW 595. Three ventral valves and dorsal valve from JBW 66, one ventral valve from JBW 95 and 511.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

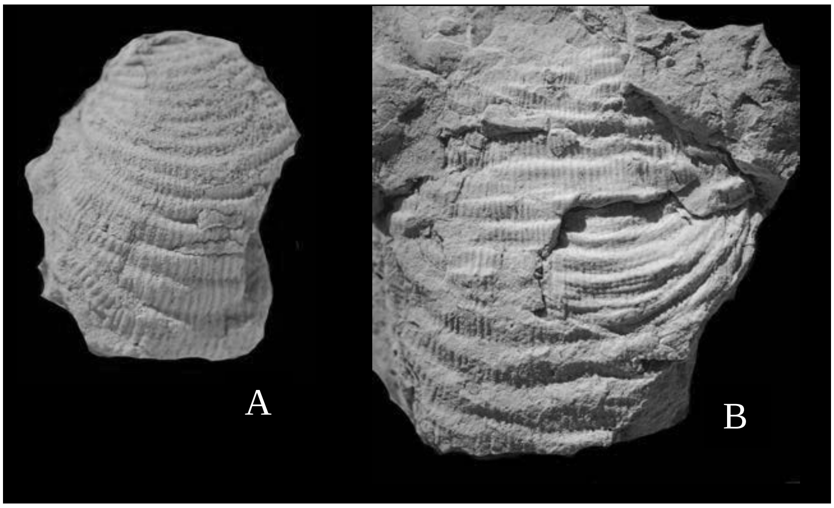


Fig. 218. *Commarginalia* sp. A. A, ventral valve GSC 136701 x2 from JBW 595. B, ventral aspect of specimen with valves conjoined GSC 136702 x2 from JBW 593. Member A, Jungle Creek Formation.

Description: Specimens triangular and elongate in outline, a ventral valve measuring 22mm wide, 24mm long and 6mm high. The ventral umbo is broad and not incurved. Posterior umbonal walls are low and steep posteriorly. They extend well forward, diverging at 70-75º, and curve outwards with slightly concave outline, but are gently convex in profile. The hinge is not exposed. There is no sulcus or fold, but the curvature is reduced over mid-valve. Both valves are covered by fine even costellae, numbering seven or eight in 5mm over much of the valve with round low crests and interspaces of comparable or slightly greater width: increase on the ventral valve is by branching. Fine spines are limited to the ventral valve, and arise from costellae, over the crest or anterior slope of rugae as a rule: they are rare posteriorly and more numerous anteriorly. Both valves are crossed by mostly regular commarginal rugae, three or four in 5mm and low posteriorly, four in 5mm towards mid-length, two in 5mm anteriorly, fairly symmetrical in profile, becoming slightly irregular anteriorly, whereas the dorsal wrinkles may develop smaller secondary wrinkles over the anterior face. The wrinkles match each other on the two valves, and ribs form nodes across the crests of the wrinkles.

Detail of the hinge is obscure., and internal detail not visible.

Commarginalia sp. B

Fig. 220

Material: Three ventral valves and a fragment from JBW 19.

Stratigraphic and biostratigraphic level: Member B, Jungle Creek Formation. *Ogilviecoelia initiatus* Zone.

Description: Ribs number ten to eleven in 5mm. Rugae are well developed, and somewhat irregular, especially on the dorsal valve. Body spines are numerous over the ventral valve with elongate bases up to 1.5mm long.

Resemblances: The few specimens are too distorted and incomplete to allow adequate comparison.

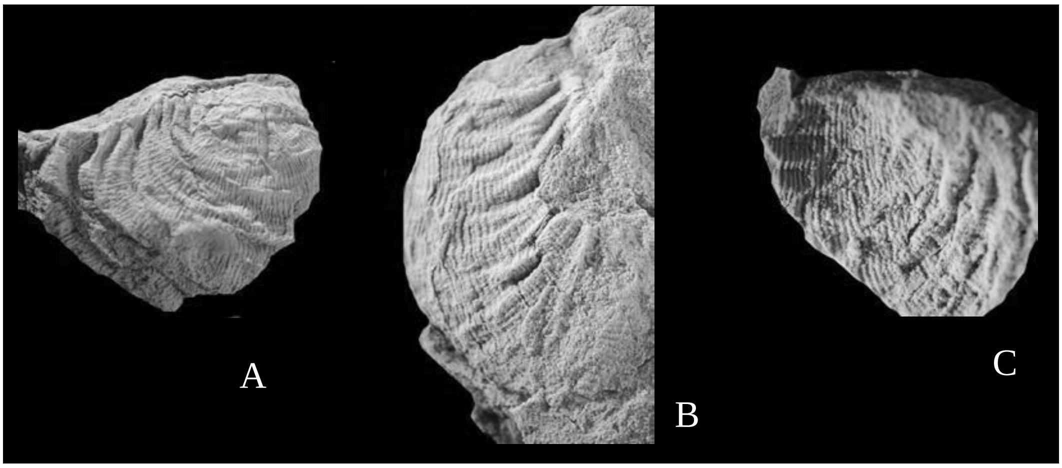


Fig. 220. *Commarginalia* sp. B. A, external mould of dorsal valve GSC 136705. B, lateral view of ventral valve, GSC 136704. C, part of external mould of ventral valve GSC 136706. Specimens x2, from JBW 19, Member B, Jungle Creek Formation.

Commarginalia norrisi n. sp.

Fig. 221 - 226

Derivation: Named for Don K. Norris.

Diagnosis: Small with ears of medium size, close-set moderately strong commarginal rugae, fine costellae and closely spaced ventral spines in quincunx.

Holotype: GSC 137010, here designated.

Material: From Member E, single ventral valves from JBW 538 and 577, two ventral valves from JBW 539, twenty ventral valves and four dorsal valves from JBW 561, nine ventral valves and four specimens with valves conjoined from JBW 581. From Member D, single ventral valves from JBW 76, 137 and 145.

Stratigraphic and biostratigraphic levels: Members D and E, Jungle Creek Formation. *Rugivestigia commarginalis* Zone, *Ogilviecoelia shii* Zone.

Description: A complete specimen measures 17mm wide, 20.5mm long and 15mm high, and one fragment is nearly 29mm wide. A specimen from JBW 581 is 19mm wide, 16mm? long (valves are displaced) and possibly 8.5mm high. Ventral valve highly convex with incurved umbo with angle of 100-120°, and steep to gentle umbonal walls, with small ears close to maximum width, which lies between mid-length and anterior third of shell length, long trail. The venter may be less convex medially, but there is no sulcus. The valve is crossed by at least sixteen irregular commarginal rugae, with rounded or angular crests up to 2.5mm high and 1.5mm apart, low over the posterior shell, and especially high over the anterior disc and trail. The surface is closely costellate, twelve to fourteen ribs in 5mm near mid-length, increasing by intercalation, but ears are smooth. Erect spines extend along the hinge with a few additional spines on the ears to total seven or eight, and spines are arranged in quincunx over

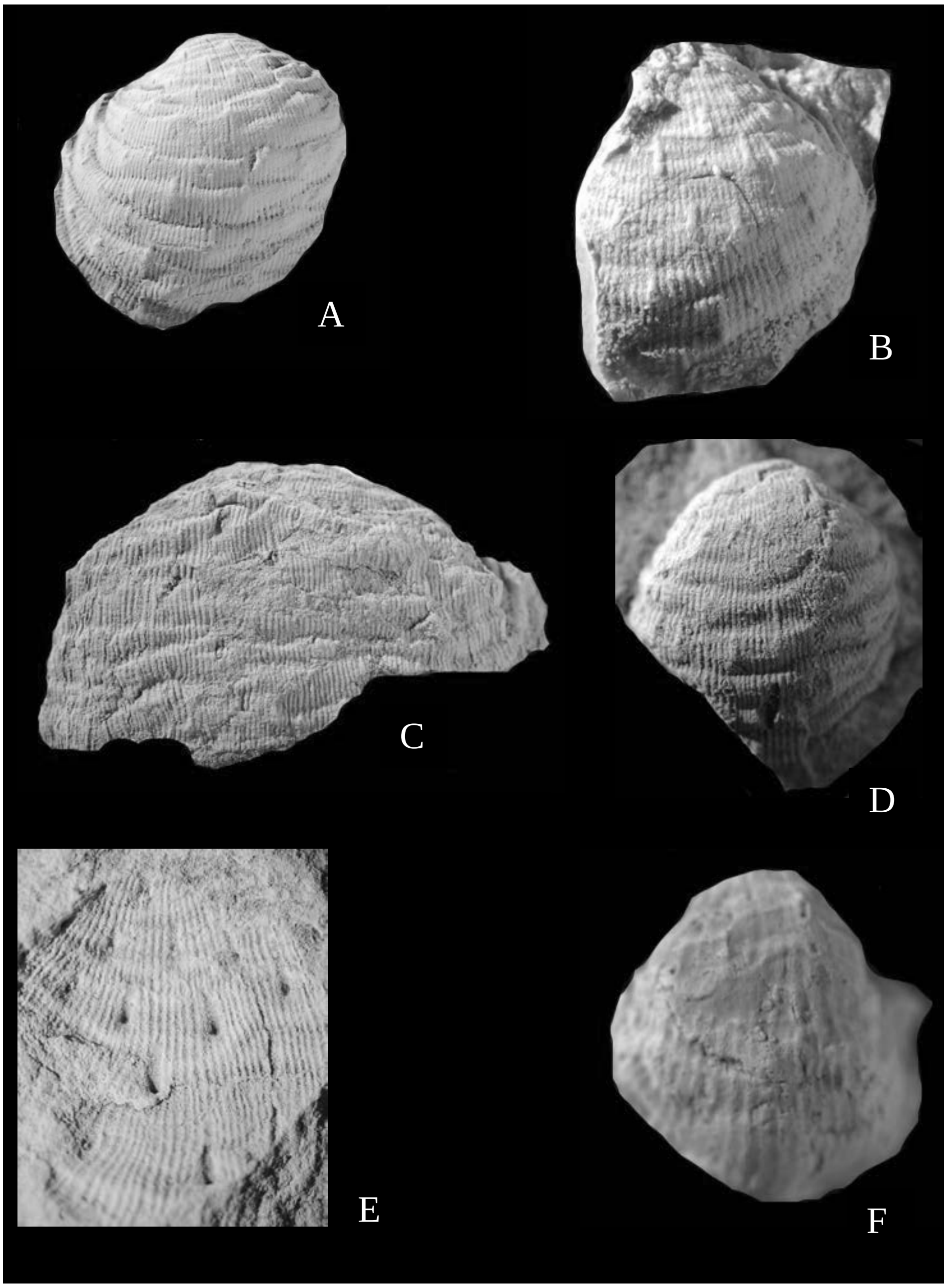
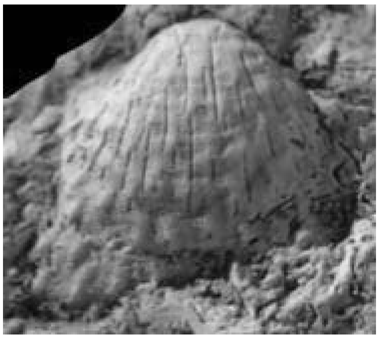


Fig. 221. *Commarginalia norrisi* n. sp. A, ventral internal mould, GSC 137007 x2 from JBW 561. B, external cast of ventral valve, holotype GSC 137010 x2 from JBW 561. C, anterior internal mould of ventral valve, GSC 137008 x2 from JBW 561. D, ventral internal mould, GSC 137012 x2 from JBW 581. E, part of ventral external mould, GSC 137009 x2 from JBW 561. F, narrow ventral internal mould, GSC 137013 x3 from JBW 581. Member E, Jungle Creek Formation.

the valve, generally with distinct elongate bases up to 1mm and seldom 2mm in length, and becoming usually twice as wide as the rib. The relationship to the ribs varies considerably: often two ribs merge into a spine base, or a single rib expands. In front of the spine; one, two or rarely four ribs may continue forward. The spines often emerge at the crest of a rugation, but in some shells emerge at the interspatial trough. Over the anterior trail, the spines are more erect with swollen rather than elongate bases, and fine erect close-set spines emerge from the crest along part of length of one or even two wrinkles. Coarse wrinkles are developed on a ventral valve from JBW 577.

Fig. 222. *Commarginalia norrisi* n. sp., ventral internal mould GSC 137358 showing spine tunnels extending forward from emergent spine. From JBW 581, x3, Member E, Jungle Creek Formation.



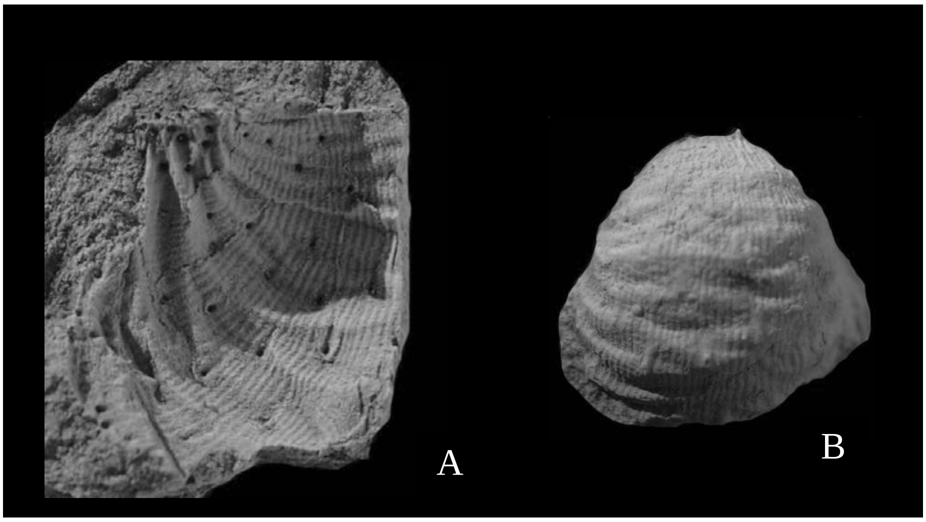


Fig. 223. *Commarginalia norrisi* n. sp. A, enlargement of GSC 137361 x4, showing a number of spines on ear, from JBW 581. Member E. B, ventral internal mould GSC 137011 x4 from JBW 581. Member D. Jungle Creek Formation.

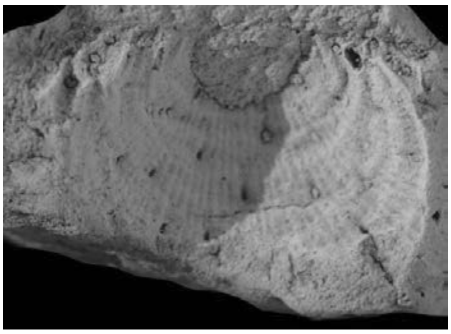


Fig. 224. *Commarginalia norrisi* n. sp., ventral external mould GSC 137454 x5 from JBW 561, showing unusually short bases of spines. Member E, Jungle Creek Formation.

Dorsal ornament is like that of the ventral valve, other than the lack of spines, and numerous round or elongate pits that are often in quincunx. The disc is some 5mm thick in a specimen over 18mm long.

Little of the ventral musculature is visible, but some long spine channels are present posteriorly.

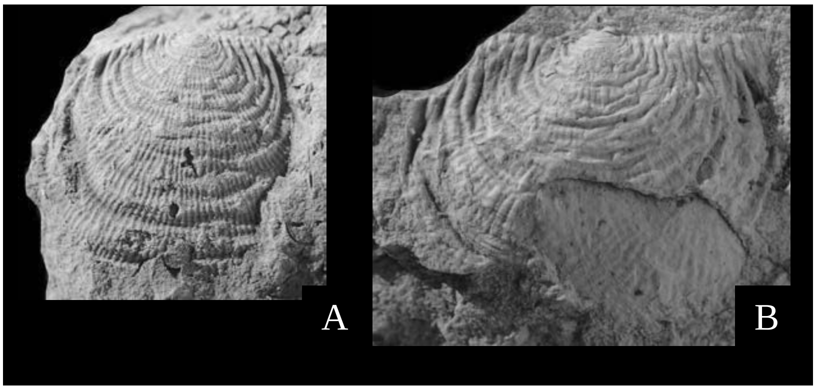


Fig. 225. *Commarginalia norrisi* n. sp. A, ventral internal mould, GSC 137020 x3 from JBW 581. B, internal mould of ventral valve, GSC 137021 x3 from JBW 561. Member E, Jungle Creek Formation.

Resemblances: Specimens of *Commarginalia* were identified as *Cancrinella* by Shi & Waterhouse (1996, p. 96, pl. 17, fig. 1-9) from the "*Yakovlevia transversa*" Zone of the Jungle Creek Formation. It was noted that dorsal spines were not developed. Commarginal wrinkles are well developed, so that the specimens are now reidentified as *Commarginalia*, subject to the proviso that hinge spines were not well preserved, and the number of spines in a cluster over the ears appears from figures to be slightly less than in older species. The specimens are similar in strength of costellae to present specimens, but have lower and fewer commarginal wrinkles and less conspicuous and regular spines. The specimens were ascribed to *Cancrinella cancriniformis* Tschernyschew (1889, pl. 7, fig. 32, 33, refigured in Tschernyschew 1902, p. 629, pl. 52, fig. 5, 6, and Sarytcheva 1977a, pl. 20, fig. 1) from the Asselian? Stage of the Kijas River, southern Urals. But in these regards, the Russian material is closer to the present suite rather than the younger specimens described by Shi & Waterhouse (1996). What is not clear is the generic position of the Russian species, because the presence of spines on the dorsal valve needs to be clarified from topotype material, or at least material from the same general level. In this case, the costellae, assuming they have been accurately portrayed and interpreted, are distinctly finer in the original material figured by Tschernyschew (1889, 1902). So-called *C. cancriniformis* (in Sarytcheva 1968, p. 152, pl. 22, fig. 4-6) from the Kokpekten Suite (considered to be of Bashkirian and even upper Visean age) in Kazakhstan is moderately close to present material, although ventral spine bases are more swollen, and dorsal spination not clear.

Cancrinella ogonerensis Zavodowsky (1960, p. 65, pl. 1, fig. 13, 14, 16; Abramov 1970, p. 86, pl. 5, fig. 10-12) from the Early Permian Omolon Suite and Late Carboniferous of Haraulakh in northeast Russia is moderately close but has less developed ears and broader ventral umbones and only moderate inflation: the presence of dorsal spines has not been ascertained. The same is largely true for *Cancrinella alazeica* Zavodowsky (1968; 1970, pl. 7, fig. 3-5, pl. 37, fig. 6, 7), also described in Sarytcheva (1977a, p. 136, pl. 20, fig. 3-7) and by Abramov & Grigorieva (1983, p. 90, pl. 9, fig. 15-24; aff. Abramov & Grigorieva 1988, pl. 11, fig. 13, 14) from the Burgali Suite (Asselian) etc. of Taimyr and levels of Verchoyan and Kolyma-Omolon Massif, of Middle and Upper Carboniferous age. Many species from northeast Russia were assigned to *Cancrinella* by Zavodowsky (1970), and *Cancrinella alazeica* Zavodowsky (1970, p. 100, pl. 7, fig. 3-5, pl. 37, fig. 6, 7) could prove to be congeneric with the present form, though its rugae are lower than those of the present species. The type material comes from the Burgali and Yarsachnin faunas of northeast Russia. The upper Carboniferous species *Cancrinella subtilis* Abramov & Grigorieva (1983, pl. 9, fig. 10-14; 1988, pl. 10, fig. 17, 18) from south Verchoyan has close-set wrinkles. The Upper Carboniferous species *Cancrinella ostrogensis* Kotlyar in Kotlyar & Popeko (1967, p. 126, pl. 28, fig. 5-10, pl. 29, fig. 1-4) from the Shazagaitu Suite of Zabaikal shows some similarities in shape and ribbing, but has fewer and lower wrinkles and fewer ventral spines.

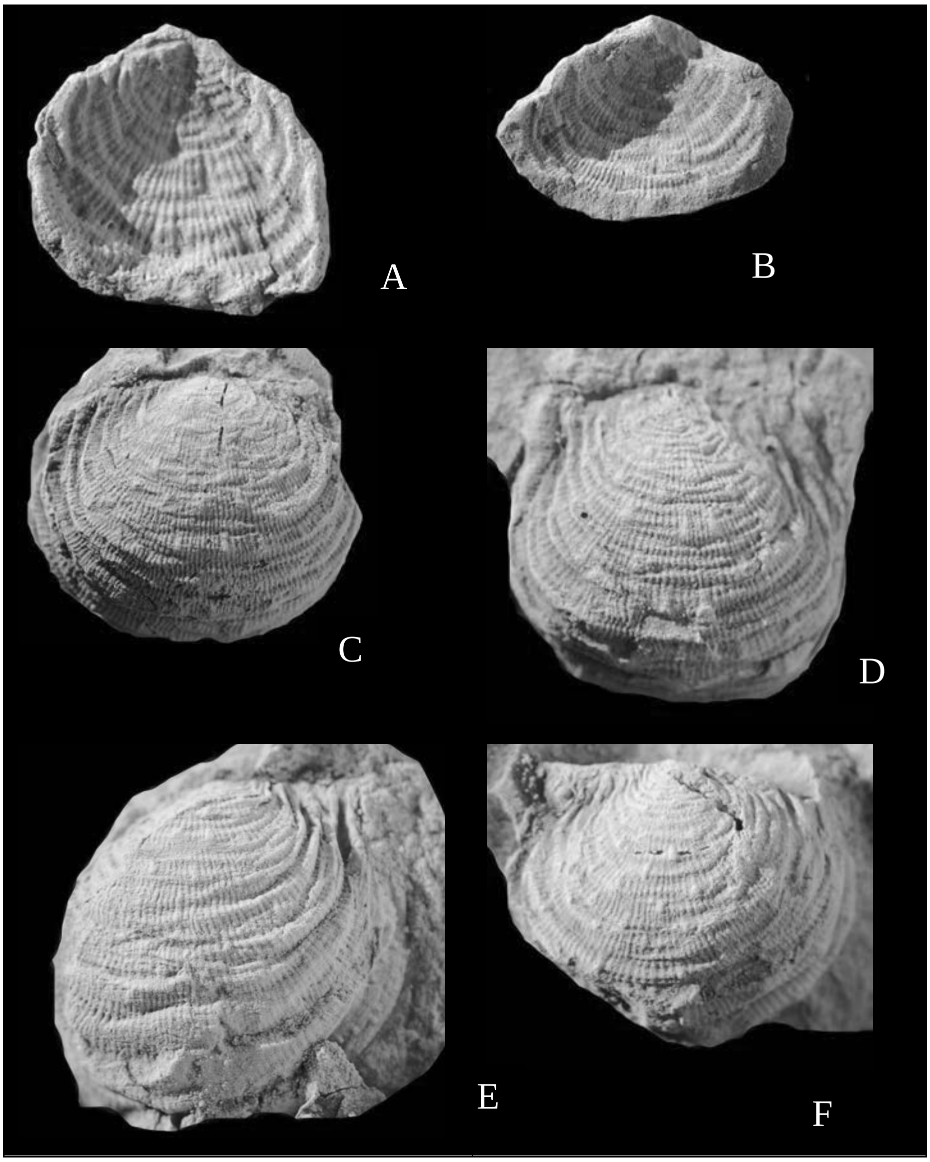


Fig. 226. *Commarginalia norrisi* n. sp. A, dorsal internal mould, GSC 137014 x3 from JBW 561. B, dorsal internal mould, GSC 137015 x2 from JBW 581. C, dorsal external mould, GSC 137016 x2 from JBW 561. D, external cast of dorsal valve, GSC 137017 x3 from JBW 561. E, dorsal external mould, GSC 137018 x3 from JBW 581. F, dorsal external mould, GSC 137019 x3 from JBW 561. Member E, Jungle Creek Formation.

From Spitsbergen, *Cancrinella* cf. *crassa* Gobbett of Czarniecki (1969, pl. 6, fig. 4-7) from the Treskelloden beds is moderately close in shape and inflation, with twelve to fifteen ribs in 5mm and fewer spines and wrinkles. The original types of Gobbett (1964, pl. 12, fig. 1-7) from the Upper Wordiekammen Limestone have spines with long bases, and together with *C. spitsbergiana* Gobbett (1964), look closer to *Cancrinella* Fredericks and *Terrakea* Booker, because commarginal rugae are scarcely developed. The presence of hinge and ear spines needs to be clarified, in order to ascertain the generic position. Australian and New Zealand species of *Magniplicatina* are larger than the present species, with coarser costellae and one to three distinctive and well formed rows of usually conspicuous spines along the hinge, and ventral body spines arranged in quincunx over the venter. Dorsal spines are often numerous.

Several species described as *Cancrinella* by Cooper & Grant (1975) from the Permian of west Texas lack dorsal spines, and so are now referred to *Commarginalia*. These include *C. distorta,* a large and elongate species from the Appel Ranch Member of the Word Formation, and *C. fragosa*, an elongate and highly arched species from the Skinner Ranch Formation. *C. sparsispinosa* Cooper & Grant (1975) from the Bone Spring Formation is closer in shape to the present form, but larger with thicker spines and more spines near the outer hinge. The spines over the ears vary a little in density for each of these species, and their pattern is somewhat obscured by their crowded nature, but they seem to be possibly clustered rather than in rows. Some species, such as *C. expansa* Cooper & Grant, were described with no dorsal valves available, so that their generic position remains obscure.

Subfamily **COOLKILELLINAE** Waterhouse, 2001

Diagnosis: Small compact shells with moderately thin to thick body cavity and steep high umbonal slopes, long ventral body spine bases, few or weak hinge spines, no dorsal spines, closely costellate, weak or scarcely any commarginal wrinkles. Dorsal valve geniculate, surface may be pitted.

Discussion: *Coolkilella* Archbold, *Kasetia* Waterhouse, *Liaozhuotingia* Waterhouse, *Magadania* Ganelin and *Nisalaria* Waterhouse belong to this subfamily. These genera are a small subset of subrectangular to subquadrate only weakly plicate or non-plicate shells close to members of Paucispinauriinae, but lack dorsal spines, and have weakly striate or weakly dendritic ventral adductors.

Coolkilellin? gen. & sp. indet.

Fig. 227

Material: One ventral valve and external ventral mould from JBW 3.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

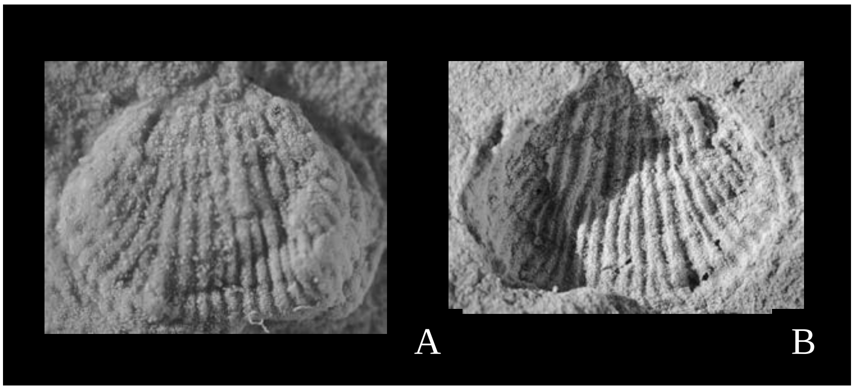


Fig. 227. Coolkilellin gen. & sp. indet. A, B, external cast and mould GSC 137022 x3 from JBW 3, Member A, Jungle Creek Formation.

Description: Specimen 16.2mm wide and 12.2mm long, and 4.4mm high, with maximum width near mid-length, and hinge almost as wide. Cardinal extremities abruptly obtuse, with small ill-defined ears. Umbo wide and incurved but obscure and shell broadly convex, without sulcus, but possibly slightly crushed. Ribs well defined, six in 5mm at mid-length, eight in 5mm anteriorly, the number increasing by intercalation, crossed by subdued subangular rugae. Spines few, with comparatively long spine bases, up to 3mm long and stronger than the costal crests.

Resemblances: Of the genera allocated to Coolkilellinae, this specimen appears to be closest to *Coolkilella* Archbold, 1993 in its subquadrate shape, strong costae, low rugae and strong ventral spine bases. *Coolkilella* is found in the Permian of Western Australia, and other genera are scattered in Permian deposits of China, Thailand, Russia and Himalaya. This occurrence marks the first appearance of the subfamily in deposits of Upper Carboniferous age.

Class Rhynchonellata Williams et al., 1996

[Rhynchonellata Williams et al. 1996].

Superorder PENTAMERIFORMI Schuchert & Cooper, 1931

[Nom. transl. Waterhouse 2010, pp. 7, 12 ex Pentamerida Schuchert & Cooper, nom. transl. Moore in Moore, Lalicker & Fischer, 1952, p. 220, ex suborder Pentameroidea Schuchert & Cooper, 1931, p. 247].

Discussion: This superorder includes Pentamerida Schuchert & Cooper, Orthida Schuchert & Cooper and Protorthida Williams & Harper (Waterhouse 2010, pp. 7, 12). In the *Revised Brachiopod Treatise*, these were separated, whereas Afanasieva & Dagys (1989) grouped the three as a Class Orthata.

Order ORTHIDA Schuchert & Cooper, 1932

[Nom. transl. et correct. Moore in Moore, Lalicker & Fischer, 1952, p. 220 ex suborder Orthoidea Schuchert & Cooper, 1932, p. 43].

Diagnosis: Strophic biconvex radially ornamented shells, teeth supported normally by dental plates, sockets supported by fulcral plates, divergent brachiophores, canal systems distinctive.

Superfamily **ENTELETOIDEA** Waagen, 1884

[Nom. transl. Alichova 1960, p. 193 ex Enteletinae Waagen, 1884, p. 548].

Diagnosis: Costellate ornament normally with aditicules, cardinalia normally with simple, rarely lobate crenulated myophore and shaft, brachiophores high, long and usually tusk-like.

Discussion: Aditicules, named for hollow ribs, are discussed and figured by Williams & Harper (2000) in their introduction to Orthida.

Family **SCHIZOPHORIIDAE** Schuchert & LeVene, 1929

[Nom. transl. Schuchert & Cooper, 1932, p. 139 ex Schizophoriinae Schuchert & LeVene, 1929, p. 15].

Diagnosis: Dorsi-biconvex, multicostellate, variably developed median ventral septum, dorsal interior with petaloid adductor field bordered postero-laterally by brachiophore plates.

Genus ***Orthotichia*** Hall & Clarke, 1892

Diagnosis: Fine costellae, strong dental plates and median ventral septum. Vascular media bitruncate in dorsal valve.

Type species: *Orthis*? *morganiana* Derby, 1874, p. 29 from the Upper Carboniferous Itaituba Formation, Brazil.

Discussion: Lazarev (1969, 1976b) stressed that the dorsal cardinalia in *Schizophoria* is quadritruncate, but Williams & Harper (2000) did not recognize the distinction.

Orthotichia morganiana (Derby, 1874)

Fig. 228 - 230

1874 *Orthis*? *morganiana* Derby, p. 29, pl. 3, fig. 1-7, 9, 11, 34, pl. 4, fig. 6, 14, 15.
1902 *Orthotichia morgani* (sic) – Tschernyschew, p. 594, pl. 26, fig. 8-10, pl. 48, fig. 1-3.
1911 *O. morganiana* – Holtedahl, p. 28, pl. 4, fig. 8, pl. 5, fig. 4-7.
1914 *O. morganiana* – Kozlowski, p. 62, pl. 3, fig. 11, 12.
1925 *O. morganiana* – Reed, p. 76, pl. 3, fig. 7.
1927b *O. morganiana* – Chao, p. 99, pl. 1, fig. 2, pl. 2, fig. 2a-c, 3a-d.
1934 *O. morganiana* – Grabau, p. 9, pl. 1, fig. 4.
1939 *O. morganiana* – Licharew in Gorsky, p. 80, pl. 16, fig. 2, 3.
1939 *O. morganiana* – Licharew & Einor, p. 13, pl. 1, fig. 3, 5.
1952 *O. morganiana* – Sarytcheva & Sokolskaya, pl. 15, fig. 11, 12.
1954 *O. morganiana* – Dresser, p. 24, pl. 1, fig. 8-11, 13.
1964 *O*. cf. *morganiana* – Gobbett, p. 48, pl. 1, fig. 8-10.
1969 *O. morganiana* – Lazarev, p. 211, pl. 10, fig. 6-12, Fig. 3a-f.
1971 *Orthotichia* sp. Bamber & Waterhouse, pl. 13, fig. 1.
1971 *O*. cf. *morgani* (sic) – Bamber & Waterhouse, pl. 11, fig. 3, 5, 12.
1976 *O. morganiana* – Li & Gu, p. 230, pl. 151, fig. 3.
1976b *O. morganiana* – Lazarev, p. 114, pl. 7, fig. 1-10, text-fig. 66, 67.
1985 *O. morganiana* – Dong & Li in Ding et al., p. 101, pl. 32, fig. 1-3.
1996 *O. morganiana* – Shi & Waterhouse, p. 44, pl. 1, fig. 2-18.

Diagnosis: Finely costellate, subrounded, ventral valve slightly longer but less inflated than dorsal valve, weakly sulcate anteriorly.

Lectotype: Specimen figured by Derby (1874, pl. 4, fig. 6) from Itaituba Group (Upper Carboniferous), Brazil, SD Shi & Waterhouse (1996, p. 44).

Material: From Member A, single ventral valves from JBW 66, 94, 141, 591, 651, 759, 787 and GSC localities 26904 and 57143, three ventral valves from JBW 802, ventral valve and dorsal valve from JBW 34 and 78, and two ventral valves and one possible dorsal valve from JBW 112 and 513, three ventral valves and one dorsal valve from JBW 562, and specimen with valves conjoined from JBW 4. Twelve specimens with valves conjoined from JBW 84, and single specimen with valves conjoined from JBW 754, some thirty small specimens with valves conjoined from JBW 41, two dorsal valves from JBW 644. Single ventral valve from JBW 503 (provisionally Member A). Specimen with valves conjoined from JBW 620, Ettrain Formation.

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Description: Specimens available in a wide range of sizes, biconvex with ventral umbo of 95-100º, slightly extended beyond hinge, and dorsal umbo slightly wider and not as extended, dorsal valve much less inflated, hinge short, close to a third of maximum width which lies towards anterior third of shell length. Ventral interarea high, concave, marked by striae, divided by an open delthyrium with angle of 25º, bordered by low ridges. Anteriorly a shallow sulcus is developed in a few specimens, not clear in most specimens, probably because they are not fully mature. Dorsal interarea low with broader open notothyrium. Costellae fine, numbering seventeen in 5mm on larger specimens at anterior margin, twenty one or twenty two in 5mm in some very large specimens. Shell crossed by a few growth steps, with steep anterior face crenulated by the costae. A dorsal valve from JBW 84 is 22mm wide, 18mm long and 8.5mm high, rounded in outline with short hinge, rounded cardinal extremities, no sulcus but a short ventrad arching of the anterior commissure, and low commarginal growth rugae. The dorsal valve is slightly shorter, but more swollen

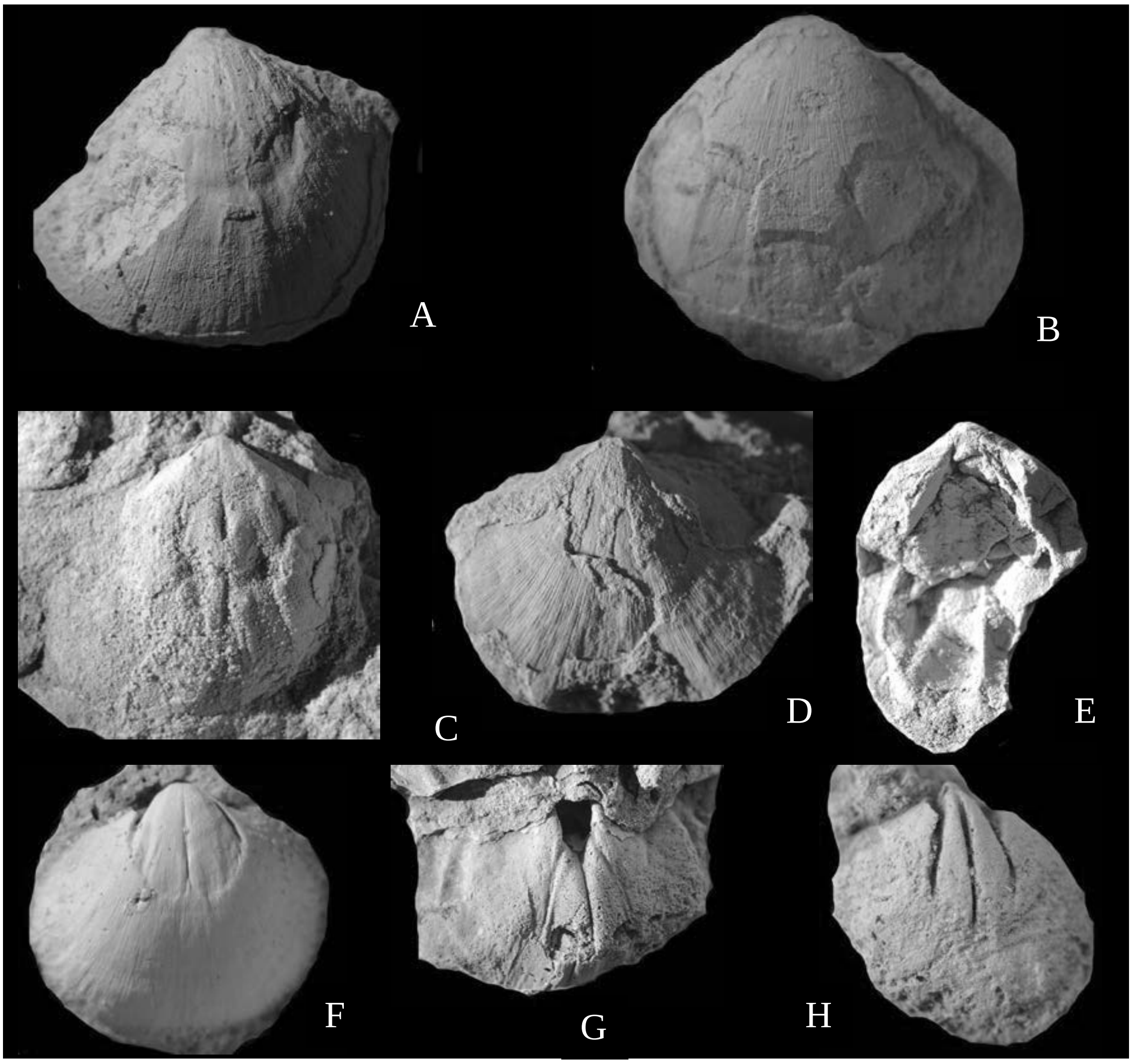


Fig. 228. *Orthotichia morganiana* (Derby). A, D, dorsal and ventral views of specimen with valves conjoined, GSC 137023 x2 from JBW 84. B, ventral valve GSC 137024 x2 from JBW 84. C, ventral internal mould, GSC 137026 x2 from JBW 562. E, broken ventral valve, internal aspect, GSC 137029 x2 from JBW 802. F, dorsal internal mould GSC 137027 x2 from JBW 94. G, internal mould of posterior dorsal valve GSC 137028 x2 from JBW 644. H, dorsal valve internal mould GSC 137025 x1.5 from JBW 562. Member A, Jungle Creek Formation.

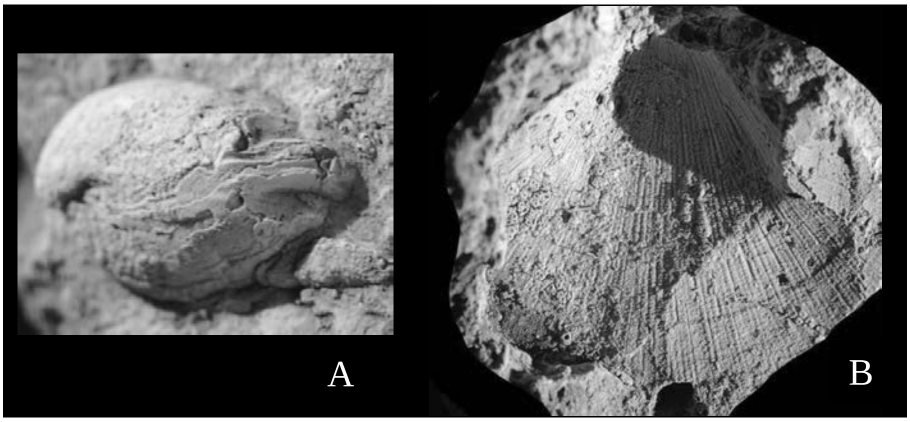


Fig. 229*.* *Orthotichia morganiana* (Derby). A, lateral aspect of specimen with valves conjoined, ventral valve on top, GSC 137030 x2 from JBW 620, Ettrain Formation. B, external mould showing ornament on dorsal valve, GSC 137031 x3 from JBW 78. Member A, Jungle Creek Formation.

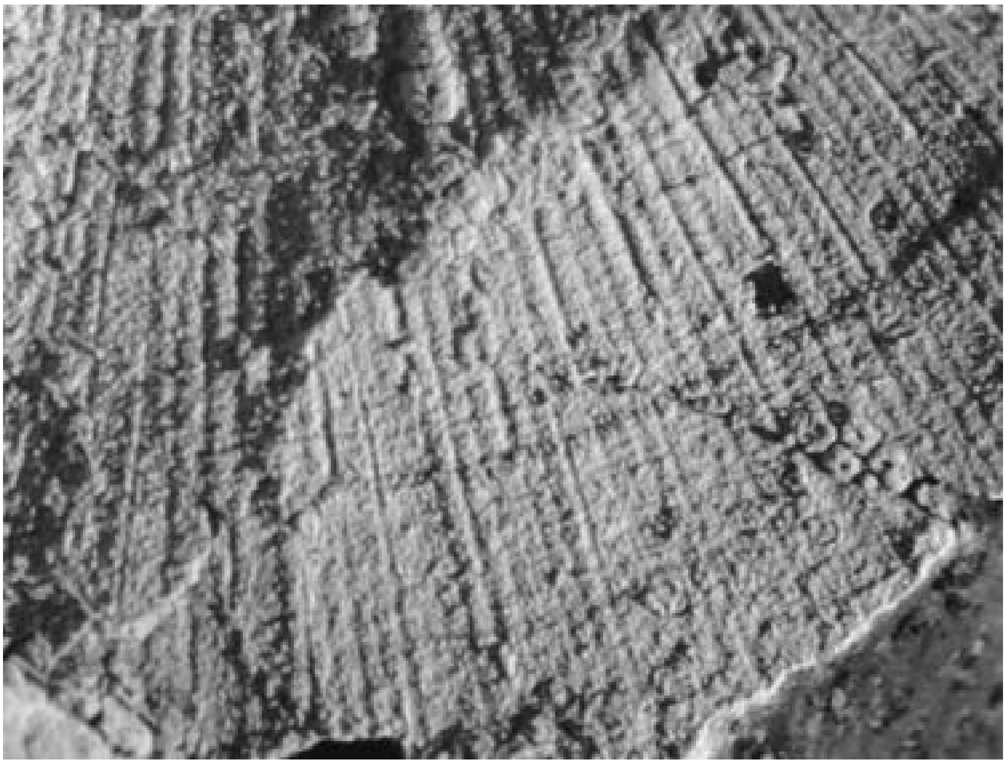


Fig. 230. *Orthotichia morganiana* (Derby), detail of ornament on dorsal valve, GSC 137031 x11 (see Fig. 229B), from JBW 78. Member A, Jungle Creek Formation.

than the ventral valve.

Dental plates extend beside the muscle field, with low median septum. Cardinal process with three separate lobes, lying behind short widely diverging plates and very low median ridge. Dental sockets slender, brachiophore bases large and well spaced, lying each side of muscle field, which extends for nearly one third to nearly half the length of the valve, myophragm well developed. The floor of the valve is marked by low radial striae medianly, with narrow portions each side smoother, and the radial striae are stronger anteriorly, suggestive of external costellae.

Resemblances: The species *Orthotichia morganiana* (Derby) has been widely reported from faunas of Late Carboniferous and Early Permian age, to the extent that such reports become hackneyed, and may be viewed as testifying to a lumping of attributes. But it has not been possible to reliably detect any consistent or significant difference between the Canadian exemplars and Brazilian types of the species, which are also of Late Carboniferous age. Further material was figured by Dresser (1954) from the Tapajos River in Brazil. A significant attribute is the presence of a shallow anterior sulcus in the ventral valve. Such an anterior sulcus is not clearly visible in the figures provided by Derby (1874), but was clearly described in his text.

Tschernyschew (1902) reported the species from Asselian deposits of the Urals, Semichatova (1975) recorded possible examples of the species from Late Carboniferous and Early Permian of Russia, and Lazarev (1969, 1976b) analyzed Late Carboniferous material from Russia, and provided comparisons between different species (Table 14, pp. 116, 117). From Spitsbergen**,** Gobbett (1964, p. 48, pl. 1, fig. 8-10) compared material to the species from the Passage Beds and Tårnkanten Beds, and Holtedahl (1911, p. 28, pl. 4, fig. 8, pl. 5, fig. 4-7) identified specimens from the Scheteligfjellet Beds. The material from the Chihsia Limestone (Feilaifang Limestone of Chekiang and Hsiaokiang Limestone) of Kiangsi, China, that was identified as *Orthotichia morganiana* by Chao (1927b, p. 99, pl. 1, fig. 11, pl. 2, fig. 2, 3) and Grabau (1934, p. 9, pl. 1, fig. 4) shows an anterior median sulcus, and *O. morganiana* of Kozlowski (1914, pl. 3, fig. 11, 12) from the basal Permian Copacabana Group of Bolivia appears to have a lateral plication, perhaps due to distortion, and otherwise very close. The Chao material included "var. *sinensis* Grabau." *O*. cf. *morganiana* of Renz in Visser & Visser-Hooft (1940) from the Karakorum is close but has stronger ribbing. *Orthotichia*? *mapingensis* Grabau (1936, p. 61, pl. 3, fig. 11-13) from the Maping Limestone of south China appears to be moderately like *morganiana*, but differs slightly in shape and costation.

Orthotichia dorsistrigis Carter & Poletaev (1998, p. 116, Fig. 2.3-2.7) from the Hare Fiord Formation (Atokan) of the Canadian Arctic Archipelago has a dorsal fold and ventral sulcus.

Superorder RHYNCHONELLIFORMI Kuhn, 1949

[Nom. transl. Waterhouse 2010, p. 12 ex Rhynchonellida Kuhn, 1949].

Discussion: This superorder incorporates the very large Order Rhynchonellida (Waterhouse 2010, p. 12). Schuchert (1913) first drew attention to the association, but used a name without the generic stem, a usage subsequently changed. The order is upscaled to match other superorders, but unlike others, except for Terebratuliformi, is not divided into several orders.

Order RHYNCHONELLIDA Kuhn, 1949

[Nom. correct. Moore in Moore, Lalicker & Fischer 1952, p. 221 pro Order Rhynchonellacea Kuhn, 1949, p. 104].

Diagnosis: Rostrate biconvex coarsely costate shells with dental plates, dorsal median septum commonly supporting septalium or hinge plates, crura well formed, supporting spirolophous lophophore in recent genera.

Suborder RHYNCHONELLIDINA Kuhn, 1949

[Nom.transl. hic ex Order Rhynchonellacea Kuhn, 1949, p. 104].

Diagnosis: Lacking a spondylium.

Discussion: Members of Stenoscismoidea and Rhynchotetroidea that have usually been included in Rhynchonellida are segregated as a distinct suborder. (See p. 283).

Superfamily **PUGNAXOIDEA** Rzhonsnitskaya, 1956

[Nom. correct. hic ex Pugnacoidea Savage 1996, p. 253 pro Pugnaxinae Rzhonsnitskaya, 1956, p. 125].

Schmidt, 1965b, p. 572 elevated the subfamily name to Pugnacidae, and Savage 1996, p. 253 ranked the group as Pugnacoidea. The groups were based on genus *Pugnax* Hall & Clarke (1893, p. 202), and as Latin has no letter x in its alphabet, a c was substituted for x. These changes are deemed unnecessary. Biological nomenclature should not be an exercise in Latin grammar and alphabet, nor modified to cope with limitations in the Latin alphabet.

Diagnosis: Rhynchonelliform, well defined sulcus and fold, strongly inflated anteriorly, long tongue, plicae or costae few, missing from posterior shell, foramen with conjunct deltidial plates as a rule. Dental plates absent or short, rarely long. Dorsal median septum short to absent, hinge plates divided as a rule, may merge with crural plates, septalium rare to absent, short where present, no cardinal process, crura commonly calciform or septiform.

Family **PUGNAXIDAE** Rzhonsnitskaya, 1956

[Nom. transl. hic ex Pugnaxinae Rzhonsnitskaya, 1956, p. 125].

Diagnosis: Umbones smooth, high fold and tongue, most attributes same as in superfamily.

Genus ***Rhynoleichus*** Abramov & Grigorieva, 1983

Diagnosis: Subpentagonal to transversely oval with wide sulcus and fold, flanks narrow, plicae few and weak over sulcus and fold and faint over flanks. Dental plates short, septalium short, hinge plates divided and median septum short and low.

Type species: *Rhynoleichus delenjaensis* Abramov & Grigorieva, 1983, p. 96 from the upper Sieder Suite (Upper Carboniferous) of Verchoyan Mountains, Russia, OD.

Discussion: This is a distinct genus, but was treated as a nomen dubium by Savage (2002d, p. 1375). He complained that only seven specimens were available, although that seems hardly relevant, because there is no specified number required to validate a taxon, and indeed Savage failed to note that other species had also been described in the same work by the same authors, and a number of species were described by Abramov & Grigorieva (1988), including additional material for the type species, followed by further analysis in Shi & Waterhouse (1996). The type species comes from the Upper Carboniferous Kigiltass Suite of Verchoyan, but Savage (2002c) claimed the type species had come from Taimyr, which is incorrect. Shi & Waterhouse (1996, p. 108) described a species from the Jungle Creek Formation which they assigned to Pugnacidae (= Pugnaxidae), as in Abramov & Grigorieva (eg. 1988). That assignment disagrees with the placement by Savage (2002c), who suggested that placement with Leiorhynchoidea seemed possible, although material was allegedly “too poor” to determine features – just which features were not enumerated. Shi & Waterhouse (1996) considered that the low and thin median dorsal septum ruled out an alliance with Leiorhynchoidea, because the dorsal septum in that group is high and strong.

Rhynoleichus? sp. or spp.

Fig. 231

Diagnosis: Small elongate shells with few anterior plicae.

Material: A dorsal valve with part of the posterior ventral valve and another dorsal valve from JBW 581, a ventral valve from JBW 561.

Fig. 231. *Rhynoleichus*? sp. or spp. A, dorsal aspect of cast of specimen with valves conjoined, GSC 137032 x4 from JBW 581. B, internal mould of ventral valve GSC 137034 x4 from JBW 561. Member E, Jungle Creek Formation**.**

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: The valves are oval in shape. Two lateral anterior plicae, the outer pair subdued, lie next to a narrow median fold in the dorsal valve from JBW 581. The ventral valve from JBW 561 has a prominent umbo and three fine plicae in the anterior sulcus, with two broader ribs each side on the lateral slopes. Such lateral plicae are not seen in the other specimen, possibly because it is less mature or of a different taxon.

Resemblances: Specimens of *Rhynoleichus dorsoconvexa* Shi & Waterhouse (1996, p. 108, pl. 20, fig. 1-13) from the "*Yakovlevia transversa*" and *Ogilviecoelia inflata* Zones of the Jungle Creek Formation are much larger than the present specimens, and at a comparable size are smooth and lack plicae. The anterior fold has three anterior plications, and two plicae lie in the sulcus. *R. delenjaensis* Abramov & Grigorieva is also larger, but does have comparably few plicae in the sulcus. Material from the Echi Suite of Verchoyan figured by Abramov & Grigorieva (1988, p. 141, pl. 15, fig. 8-14, 18, 20, text-fig. 45, 46) includes small specimens that come close – the particular material is younger than the types. *R. bulgakovae* Abramov & Grigorieva (1983, p. 98, pl. 12, fig. 1-4) is smaller and with few anterior plicae, so that there is some approach to the present material. This species comes from the Upper Carboniferous Davnin Horizon of south Verchoyan. There is some approach to *R. etschiensis* Abramov & Grigorieva (1988, p. 139, pl. 15, fig. 1-6, 16, text-fig. 44) but plicae may commence close to the umbones, and lateral plicae appear on two of the figured specimens (Abramov & Grigorieva 1988, p. 139, pl. 15, fig. 5, 16) as in the specimen from JBW 561. The Russian specimens are more transverse than the present material, and come from the upper Early Permian Echi Suite of west Verchoyan. A specimen figured as *Rhynoleichus* sp. by Abramov & Grigorieva (1988, pl. 15, fig. 17) is small with three fine ribs in the sulcus, as in a small specimen of *R. delenjaensis* Abramov & Grigorieva (1983, pl. 15, fig. 14) from the Echi Suite of Verchoyan.

Superfamily **RHYNCHOPOROIDEA** Muir-Wood, 1955

[Nom. transl. Erlanger 1993, p. 120 ex Rhynchoporidae Muir-Wood, 1955, p. 91].

Diagnosis: Shell endopunctate, costal interspaces may extend into marginal spines.

Family **RHYNCHOPORIDAE** Muir-Wood, 1955

[Rhynchoporidae Muir-Wood, 1955, p. 91].

Diagnosis: Endopunctae simple or merging. Sulcus and fold variably developed.

Subfamily **RHYNCHOPORINAE** Muir-Wood, 1955

[Nom. transl. Savage 2002a, p. 1232 ex Rhynchoporidae Muir-Wood, 1955, p. 91].

Diagnosis: Endopunctae simple. Sulcus and fold well developed. Costae simple, flattened and grooved anteriorly, prolonged around the periphery as sharp spines.

Genus ***Rhynchopora*** King, 1865

Diagnosis: As for subfamily.

Type species: *Terebratula geinitziana* Verneuil, 1845, p. 83 from north Dvina River Basin (Kazanian), Russia.

Discussion: *Rhynchopora* is the sole member of the subfamily Rhynchoporinae. It was a moderately long-ranging genus, and species that are based on shape and costation appear to have had considerable time ranges.

Rhynchopora grigorievae n. sp.

Fig. 232 - 234

Diagnosis: Large pentagonal shells with broad sulcus and anterior fold with six costae in sulcus, five costae over the fold, and six or seven costae on each flank.

Holotype: GSC 137267, here designated.

Material: From Member E, two dorsal valves from JBW 561, eight ventral valves and three specimens with valves conjoined from JBW 581, a ventral valve from JBW 577 and 580, and a ventral valve and three specimens with valves conjoined from JBW 195. Ventral valve GSC 26923 from GSC locality 56946. Ventral valve from JBW 74 and dorsal valve from JBW 137 (Member D), and ventral valve from JBW 18 (Member C).

Stratigraphic and biostratigraphic levels: Members C, D, E, Jungle Creek Formation. *Kochiproductus imperiosus*, *Rugivestigia commarginalis* and *Ogilviecoelia shii* Zones.

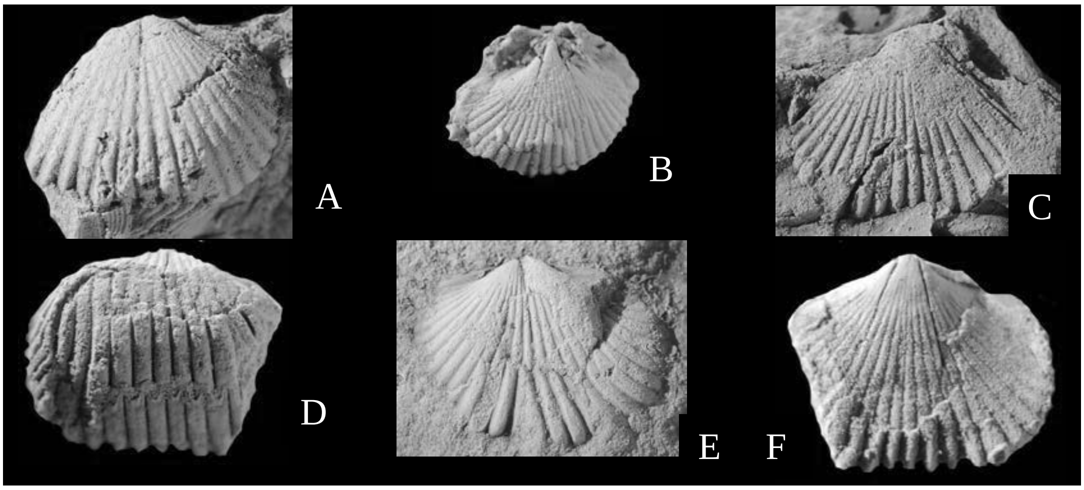


Fig. 232. *Rhynchopora grigorievae* n. sp. A, dorsal internal mould, GSC 137035 from JBW 137, Member D. B, ventral internal mould GSC 137039 from JBW 581. C, ventral valve GSC 137037 from JBW 561. D, F, anterior and ventral aspects of specimen with valves conjoined, GSC 137267 holotype from JBW 581. The height in D is exaggerated by longitudinal compression. E, dorsal internal mould GSC 137036 from JBW 561. Specimens x3, from Member E. Jungle Creek Formation.

Description: Shells subpentagonal in shape with posterior walls straight and diverging forward at close to 100º, umbo with small round foramen, palintrope concealed. Ventral sulcus commences near mid-length and occupies about half the width of the valve, with steep flanks and broad floor in front. Anteriorly the valve bends sharply, almost at right angles. Dorsal valve with shorter posterior walls and suboval outline, and although convex, is less inflated than the ventral valve. The fold is restricted in length to the anterior part of shell, and bends sharply in front to meet the sulcus. Ventral valves from JBW 195 ornamented by up to thirty to as low as twenty two costae with round crests and narrow grooved interspaces, being very fine over the umbo and broad with narrow interspaces over the trail, six costae in the sulcus. Dorsal costae are similar, meeting the ventral valve along the commissure with interspaces opposed to costae, and in one specimen from JBW 561, the crests of the dorsal costae carry a faint median groove for several mm, opposite each grooved ventral interspace of the ventral valve. Five costae cover the fold. Both valves are finely punctate, five to six punctae in 1mm.

The dental lamellae on the ventral valve extend for a fourth of the length in a small shell from JBW 581, and the dorsal median septum is approximately one fifth of the length of the valve.

Resemblances: The species is readily distinguished from the upper Jungle Creek Formation specimens that were identified by Shi & Waterhouse (1996, p. 112, pl. 20, fig. 28-34, pl. 21, fig. 1-3, Fig. 37, 38) with *Rhynchopora magna* Cooper, 1957. It consistently has fewer costae over the sulcus and fold, whereas the younger specimens have eight or more finer and high costae in the sulcus, allowing that there is room for uncertainty over the exact number of sulcal ribs, insofar as a costa may either be in the sulcus, or bordering its edge. But the difference between the two assemblages is marked. Cooper (1957) provided different figures again type *Rhynchopora magna* from Oregon, with seven costae in the sulcus and nine on the flanks. Yole (1963, pl. 2, fig. 19) illustrated a specimen as comparable to *R. magna* Cooper from the Early Permian of Vancouver Island, Canada, and the specimen may be related, but was figured without the anterior aspect. The Cooper material is close to *Rhynchopora nikitini* Tschernyschew as described in various Russian studies, from Early Permian of Darvas, and reported from Late Carboniferous and Early Permian of the Moscow Basin and Urals, and Burgali and Paren Formations of the Omolon Basin in northeast Russia. Specimens figured as *R. nikitini* Tschernyschew by Ustritsky & Chernyak (1963, p. 98, pl. 26, fig. 13-17) from the lower Baikur Suite of Taimyr Peninsula are close in number of sulcal costae but the costae are broad with rounded crests and the specimens less triangular in shape, unlike older material assigned to the species. The material considered to be ex gr. *nikitini* by Abramov (1970, pl. 17, fig. 7-10) from the Ekachan Suite of Upper Carboniferous age in Cette Darvan has slightly fewer and coarser sulcal costae.

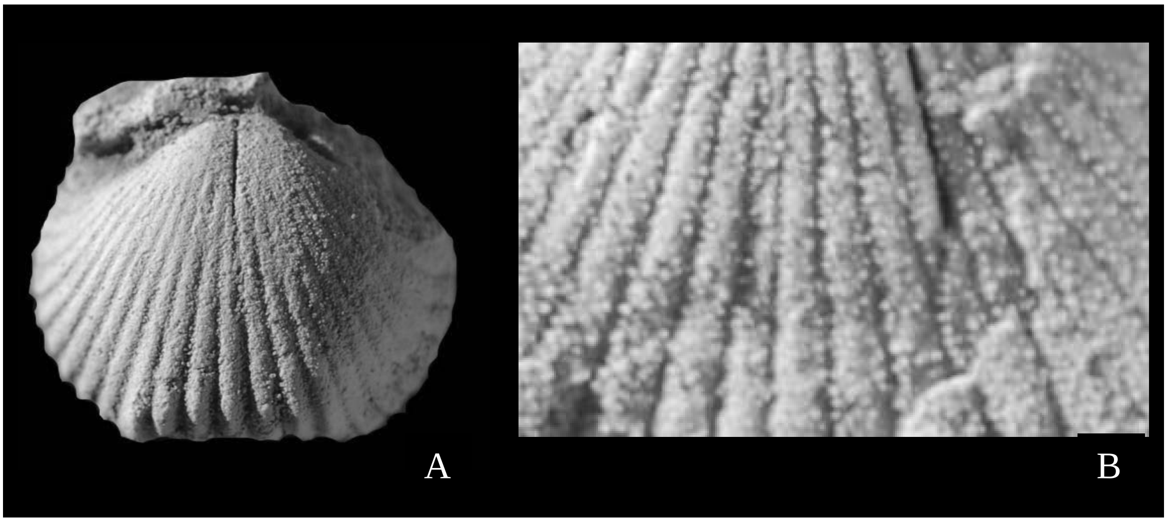


Fig. 233. *Rhynchopora grigorievae* n. sp. A, dorsal internal mould GSC 137038 x6 from JBW 561. B, punctation in GSC 137267, holotype, ventral valve from JBW 581. (See Fig. 232D, F), x 14. Member E. Jungle Creek Formation.

Type *Rhynchopora nikitini* Tschernyschew (1885, p. 245, pl. 18, fig. 24-36) and refigured in Gorsky (1939, p. 99, pl. 23, fig. 6) has numerous fine ribs, but the posterior shell is smooth and the shape moderately elongate. However specimens figured by Stepanov (1937b, pl. 7, fig. 6-11, pl. 12, fig. 1, 2) from the northern Urals in Kolwa Peninsula appear very close to the present species. The species was reported from the Namurian Valdeteja Formation of lower Bashkirian age in the Cantabrian Mountains of Spain by Martínez-Chacón (1979). *R. nikitini* of

Kozlowski (1914, pl. 9, fig. 67-70) from the Copacabana Group of Bolivia is close but has a gentler fold. The northern Urals material figured as *R. nikitini plana* by Stepanov (1937b, pl. 6, fig. 3, 4) is elongate with many fine ribs that split a little in front of the umbones. *R. nikitini* of Gobbett (1964, p. 129, pl. 16, fig. 18-21) from the Spirifer Limestone (now Vøringen Member) of Bunsow Land has fewer and stronger sulcal costae, and was referred by Czarniecki (1969, p. 296, pl. 11, fig. 12-15) to a new subspecies *R. arctica minima*, in describing material from the Treskelloden faunas of Spitsbergen.

Fig. 234. *Rhynchopora grigorievaae* n. sp., dorsal internal mould GSC 137455 x6 from JBW 561. Member E. Jungle Creek Formation.

Ifanova & Semenova (1972, p. 128) referred *Rhynchopora arctica* Licharew & Einor (1939, p. 64, pl. 13, fig. 6-10; Ustritsky, 1961, p. 50, pl. 3, fig. 3-7; Ustritsky & Chernyak 1963, p. 99, pl. 26, fig. 18-20 and Zavodowsky 1970, p. 130, pl. 29, fig. 8, pl. 32, fig. 11) to synonymy of *R. nikitini*, but the entire shell is costate, with some four ribs in the sulcus and four pair laterally, and a more elongate shell. Further material belonging to *arctica* was described by Abramov & Grigorieva (1983, p. 110, pl. 15, fig. 12-17, text-fig. 34) from the Upper Carboniferous Natalin and Davnin Suites of Verchoyan. The material from the Turuzov and Birrang Formations of Taimyr Peninsula as figured by Ustritsky & Chernyak (1963) has one or two fewer costae in the sulcus, and the costae are round-crested, and the overall shell shape subrounded. The Upper Artinskian and Kungurian specimens figured by Ifanova & Semenova (1972, pl. 9, fig. 4-6) are more triangular in shape but have mostly five costae in the sulcus.

Rhynchopora lobjaensis Tolmachev (1912, p. 130, pl. 4, fig. 6) from northeast Siberia has very fine costae in the sulcus, numbering about eight. The species was synonymized with *Camarotoechia sjedovi* Tolmachev (1912, pl. 5, fig. 12-14) and *C. kojewnikovi* Tolmachev (1912, pl. 5, fig. 8-12) and *C. weberi* Tolmachev (1912, p. 141, pl. 5, fig. 17-20) in Sarytcheva (1968, p. 162). These have somewhat stronger sulcal costae that are fewer in number, especially amongst the specimens assigned by Tolmachev (1912, pl. 5, fig. 8-10) to *kojewnikovi,* with only four or five costae in the moderately well defined sulcus, the inner ones bearing a distinctive anterior median groove. The species has also been reported from the northeast Russia by Licharew (1934, p. 40, pl. 9, fig. 12-24) and Kashirtsev (1959b, p. 52, pl. 33, fig. 4, 5) and by Ustritsky & Chernyak (1963, pl. 27, fig. 1-6) from the upper Baikur Horizon of Taimyr Peninsula, and in Sarytcheva (1968, pl. 23, fig. 17, 18, text-fig. 76-78) from the Kokpecten Suite of Kazakhstan, and by Abramov & Grigorieva (1988, p. 143, pl. 16, fig. 4, 6-9) from the younger Permian faunas of Kolyma-Omolon and Verchoyan.

Suborder STENOSCISMIDINA Waterhouse, 1981

[Nom. correct. hic ex Stenoscismatidina Waterhouse, 1981, p. 91].

Diagnosis: Relatively large shells. Ventral spondylium commonly on low duplex septum, strong dorsal septum and camarophorium or septalium developed, hinge plates usually undivided, crura raduliform.

Discussion: The principal feature distinguishing members of the suborder from members of Rhynchonellidina is the presence of a spondylium in the ventral valve, as also argued by Sapelnikov & Mizens (1989). The spondylium is a morphological feature shared with a number of Pentamerida. Two superfamilies are recognized, Stenoscismoidea and Rhynchotetroidea. Later members of Rhynchotetroidea came to lose the spondylium, and reverted in morphology so as to look like Rhynchonellidina.

Superfamily **STENOSCISMOIDEA** Oehlert, 1887

[Nom. correct. hic ex Stenoscismatoidea Carlson in Carlson & Grant, 2002, p. 1218 pro Stenoscimatacea Muir-Wood, 1955, p. 69, nom. correct. pro Stenoscismacea Schrock & Twenhofel, 1953, p. 317, nom. transl. et correct. ex Stenoschismatinae Oehlert, 1887, p. 1304].

Diagnosis: Spondylium not supported by lateral plates. Camarophorium and often intercamarophorial plate present in dorsal valve.

Discussion: The classification of the group is discussed by Carlson & Grant (2002) with some modifications by Waterhouse (2004a, pp. 75-90) and Carlson (2007). The letters *a* and *t* inserted between the genus name and family group ending are regarded as redundant.

Family **STENOSCISMIDAE** Oehlert, 1887

[Nom. correct. hic ex Stenoscismatidae Muir-Wood, 1955, p. 91, nom. transl. ex Stenoschismatinae Oehlert, 1887, p. 1304].

Diagnosis: Shell smooth or strongly costate, deltidial plates usually present, disjunct or conjoined, spondylium on low septum duplex.

Subfamily **STENOSCISMINAE** Oehlert, 1887

[Nom. correct. hic ex Stenoscismatinae Muir-Wood, 1955, p. 91, nom. correct. pro Stenoschismatinae Oehlert, 1887, p. 1304].

Diagnosis: Stolidium narrow to broad in various species, cardinal process robust, intercamarophorial plate thick.

Genus ***Stenoscisma*** Conrad, 1839

Diagnosis: Subtriangular medium-sized shells with variable development of costae, large ventral spondylium and small camarophorium bearing strong intercamarophorial ridge, covered by hinge plate, supported on high septum.

Type species: *Terebratula schlotthemii* von Buch, 1834, p. 59 from Zechstein (Wuchiapingian) of Germany, OD.

Stenoscisma winkleri Martínez-Chacón, 1977

Fig. 235, 236

1902 *Camarophoria mutabilis* (not Tschernyschew) – Tschernyschew, pl. 23, fig. 9, 10 (part only, see p. 287).
1977 *Stenoscisma winkleri* Martínez-Chacón, p. 218, pl. 29, fig. 13, 14, pl. 30, fig. 1-22, text-fig. 6, 7.

1978 *S. winkleri* – Martínez-Chacón, p. 256, pl. 28, fig. 14, pl. 29, fig. 1-23.

Diagnosis: Small shells with extended posterior walls, posterior half to two thirds of length smooth, anterior sulcus and fold bear three or five ribs in the sulcus, and lateral flanks may be marked by two or three additional short ribs in a few specimens, rarely longer.

Holotype: Specimen DPO 7005, figured by Martínez-Chacón (1977, 1978, pl. 29, fig. 1) from the Beleno Formation (Westphalian C – B, Kashirian) of Cantabrian Mountains, Spain, OD.

Material: Specimen with valves conjoined and ventral valve from JBW 122 and 433, three ventral valves and two specimens with valves conjoined and ventral valve from JBW 180, single ventral valves from JBW 95, 128 and 592, two ventral valves from JBW 182 and two specimens with valves conjoined from JBW 593.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimens small, a complete specimen measuring 15.5mm wide and long and 9mm high, with roundly subpentagonal outline. The ventral umbo is posteriorly produced and slightly incurved, with small open foramen and umbonal walls diverging at 70º, curving out slightly, and steeply convex in cross-section. Maximum width lies in front of mid-length, towards the anterior third of the shell length. The sulcus commences close to mid-length as a wide shallow trough, persisting to the anterior margin. The dorsal fold commences a little nearer the hinge, with a wide gently convex crest: maximum valve height is close to the hinge. Three costae commence at the start of the sulcus, and four at the start of the fold, and two or three costae lie each side anteriorly in some specimens, not in others. There are one to three subdued growth steps, and no sign of any stolidium.

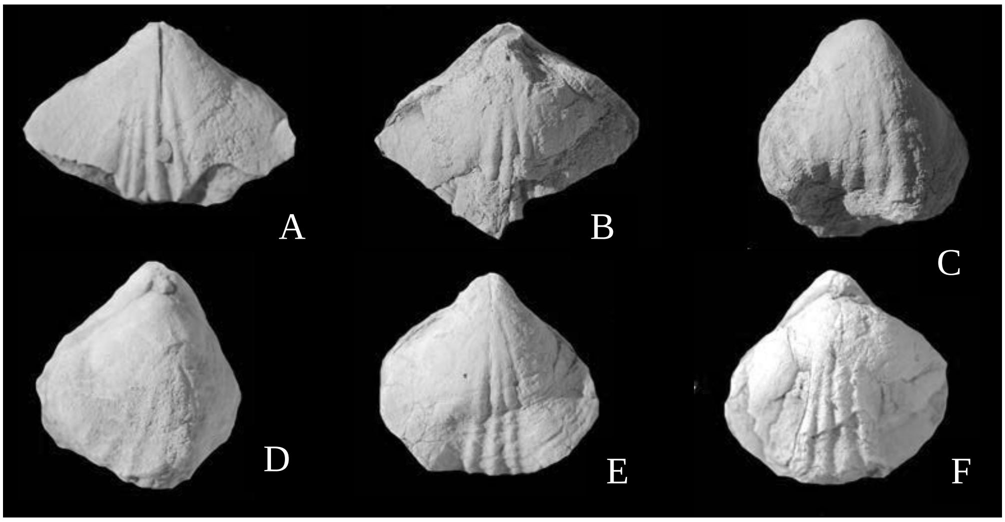


Fig. 235. *Stenoscisma winkleri* Martínez-Chacón. A, B, ventral and dorsal aspects of specimen with valves conjoined, GSC 137040 from JBW 180. C, D, ventral and dorsal aspects of specimen with valves conjoined, GSC 137041 from JBW 433. E, F, ventral and dorsal aspects of specimen with valves conjoined, GSC 137042 from JBW 180. Specimens x2, from Member A, Jungle Creek Formation.

The ventral septum extends for more than one third of the shell length, supporting a well developed spondylium. The dorsal septum is bicameral and supports a camarophorium with median ridge, and crural supports arise from the cruralium towards the outer margin. The presence of a cardinal process is not clear.

Resemblances: This form is assigned to *Stenoscisma* because of the presence of a median intercamarophorial ridge, although a stolidium, which was regarded by Grant (1965a) as characteristic of the genus, is not clearly developed, possibly due to preservation. The extensive review of the group by Grant (1965a) illustrates well the degree of variation and consistency in morphological detail of shape, size and ornament in related taxa, and assessment of the variation suggests that the present suite is characterized by shape, smooth posterior, and the number of costae over the anterior sulcus, fold and lateral flanks. *Stenoscisma schlottheimi* (von Buch) from the lower Zechstein (Wuchiapingian) of Germany is itself rather similar in overall attributes, slightly more rounded in shape, with costae restricted to the anterior sulcus and fold, and also present on the anterior lateral shell in some specimens, and preserving a stolidium.

The present specimens are identified with *Stenoscisma winkleri* Martínez-Chacón (1977, p. 218, pl. 29, fig. 13, 14, pl. 30, fig. 1-22, text-fig. 6, 7; 1979, p. 256, pl. 28, fig. 14, pl. 29, fig. 1-13) from the Beleno Formation of the Cantabrian Mountains in Spain. This is similar in shape and and size, and shows much the same variation in the distribution and number of ribs, except that the Spanish material includes some specimens with a single anterior rib, not found in the Canadian material. Specimens from the Alps that were described as *Camarophoria purdoni* (not Davidson) by Gortani (1906, p. 34, pl. 2, fig. 29, 30) look moderately close, although differing slightly in costation. *Camarophoria thevenii* Kozlowski (1914, pl. 9, fig. 71-76) from the Early Permian Copacabana Group of Bolivia is also somewhat similar, but costae are mostly limited to the sulcus and fold.

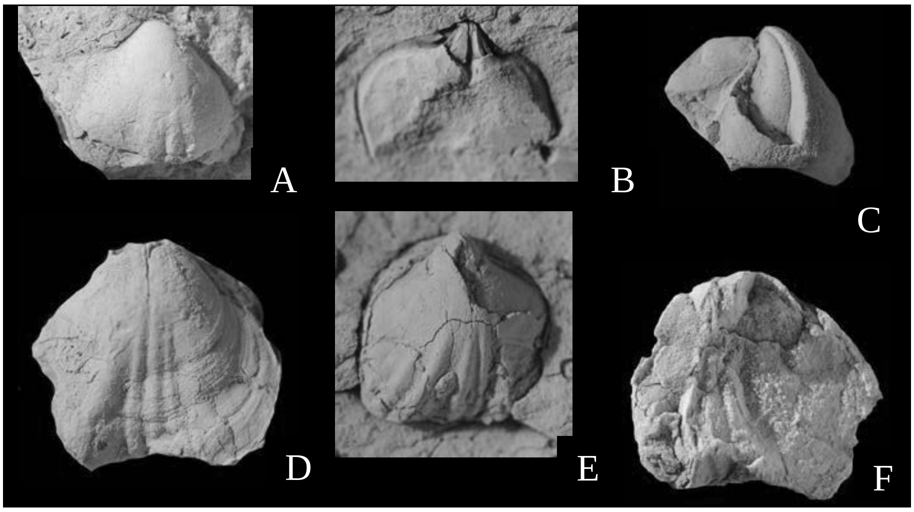


Fig. 236. *Stenoscisma winkleri* Martínez-Chacón. A, dorsal valve GSC 137043 from JBW 433. B, internal ventral mould GSC 137044 from JBW 182. C, broken ventral valve showing spondylium, GSC 137045 from JBW 180. D, F, ventral and dorsal aspects of specimen with valves conjoined, GSC 137046 from JBW 593. E, ventral aspect of specimen with valves conjoined, GSC 137047 from JBW 593. Specimens x2, from Member A, Jungle Creek Formation.

Stenoscisma biplicatum Stuckenberg is also moderately close, with more globose shell and fewer stronger plicae. A number of specimens figured as *Camarophoria biplicata* Stuckenberg from the Schwagerina-Kalk of the Urals by Tschernyschew (1902, p. 494, pl. 50, fig. 8-10) are very close in shape and size, and have two or three similar costae over the sulcus and fold, and usually two rather stronger ribs, like subplicae, on the lateral flanks. The Early Permian species *S. hueconianum* (Girty, 1929, fig. 14-21; Grant 1965a, p. 147, pl. 19, fig. 1, 1b) and a taxon regarded as synonymous, *S. deloi* King (1931, pl. 34, fig. 19; Stainbrook & Madera 1941, pl. 55, fig. 15-27) is closer in shape, as a small shell with somewhat similar, and relatively coarse costae commence nearer the umbones.

The present specimens come close to the younger Jungle Creek collections assigned by Shi & Waterhouse (1996, p. 114, pl. 21, fig. 4-14) to *Camarophoria mutabilis* Tschernyschew (1902, p. 491), agreeing in size, shape and somewhat variable costation, in which the umbonal and often more than half of the posterior shell is smooth, although some specimens are costate over much of the shell. But the Urals material figured by Tschernyschew (1902, pl. 22, fig. 18, pl. 45, fig. 1-18, pl. 46, fig. 14) is much more costate, and only the material figured in Tschernyschew (1902, pl. 23, fig. 9, 10) approaches the present Canadian specimens. The costate specimens include the lectotype of *mutabilis* that was designated by Shi & Waterhouse (1996, p. 114) as the specimen figured by Tschernyschew (1902, pl. 22, fig. 18). Specimens were referred to *mutabilis* by Stepanov (1937b, pl. 8, fig. 12), Mironova (1967, pl. 3, fig. 6) and Kalashnikov (1980, pl. 20, fig. 9-11). An Early Permian specimen figured by Mansuy (1913, pl. 9, fig. 14a-c) from Kham-Kheut, Laos, lacks lateral ribs. Amongst the various species of *Stenoscisma* figured by Tschernyschew (1902), the closest is arguably *C. netschajewi* (Tschernyschew, 1902, pl. 46, fig. 7-9) but this is more inflated and usually narrower. *Stenoscisma mutabilis oregonense* Cooper (1957, p. 50, pl. 9C, fig. 15-28) shows a closer approach to the present collections, with smooth posterior shell, and two long ribs within the sulcus. It is similar in age to that of the younger Jungle Creek collections, but differs in costation. *S. biplicatoideum* Cooper (1957, pl. 9E, fig. 34-46) from the same Oregon faunas approaches this species, with slightly different costation. The Spitsbergen material figured as *Camerophoria spitzbergiana* Stepanov (1937a, pp. 157, 182, pl. 9, fig. 11), which, according to Gobbett (1964, p. 125, pl. 16, fig. 4-9), includes *C. biplicata* (not Stuckenberg) of Frebold (1950, p. 67, pl. 16, fig. 3, 3a) from the Spirifer Limestone (now Vøringen Member of the Kapp Starotsin Formation), is rather similar to the Oregon form.

Camerisma murgabica Grunt in Grunt & Dmitriev (1973, pl. 8, fig. 11, 12) from the Kizidjilgin Suite of the Darvas Stage (upper Early Permian) in the Pamirs is somewhat similar externally, with few and coarse sulcal ribs.

Stenoscisma sp.

Fig. 237

Fig. 237. *Stenoscisma* sp., ventral internal mould, GSC 137048 x3 from JBW 562. Member A, Jungle Creek Formation.

Material, Description: An internal mould of a ventral valve from JBW 562 is covered by ribs and has no sulcus (Member A). Two somewhat allied ventral valves with strong ribs and faint sulcus come from JBW 85 (Member D).

Stratigraphic and biostratigraphic levels: Member A and cf. Member D, Jungle Creek Formation. *Septospirifer tatondukensis* Zone, possibly *Rugivestigia commarginalis* Zone.

Stenoscisma mutabilis (Tschernyschew, 1902)

Fig. 238

1902 *Camarophoria mutabilis* Tschernyschew, p. 491, pl. 22, fig. 18, pl. 45, fig. 1-18, pl. 46, fig. 14 (part, not pl. 23, fig. 9, 10 = *winkleri* Martínez-Chacón).
1934 *Camerophoria mutabilis* – Grabau, p. 16, pl. 1, fig. 1, 2.
1937a *Stenoscisma mutabilis* – Stepanov, p. 158, pl. 9, fig. 12.
1937b *Camarophoria mutabilis* – Stepanov, p. 5, pl. 6, fig. 9, 10.
1939 *C. mutabilis* – Gorsky, p. 97, pl. 23, fig. 3.
1967 *Stenoscisma mutabilis* – Mironova, p. 38, pl. 3, fig. 6.
1980 *S. mutabilis* – Kalashnikov, p. 71, pl. 20, fig. 9-11.
?1996 *S. mutabilis* – Shi & Waterhouse, p. 114, pl. 21, fig. 4-14.

Diagnosis: Subtriangular shells with long posterior walls, moderate size, both valves covered by costae.

Lectotype: Specimen figured by Tschernyschew (1902, pl. 22, fig. 18) from Schwagerina-Kalk, near Sim, Urals, SD Shi & Waterhouse (1996, p. 114).

Material: Two specimens with valves conjoined from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: One shell measures 19mm wide, 15mm long and nearly 12mm high. Specimen with extended umbo bearing small foramen, angle over 70º. . The posterior walls which are weakly concave in outline extend to the maximum width of the shell at anterior third of shell length. Sulcus commences close to beak, sulcal angle of 40º, with broad gently concave floor, fold broad with almost flat crest and steep flanks anteriorly. Two costae extend for the length of the sulcus, joined anteriorly by a pair that branches from the rib bordering the sulcus. Five costae pass along the crest of the fold, joined anteriorly by a rib branching from the bordering rib. Four costae lie on the lateral flanks of ventral and dorsal valves.

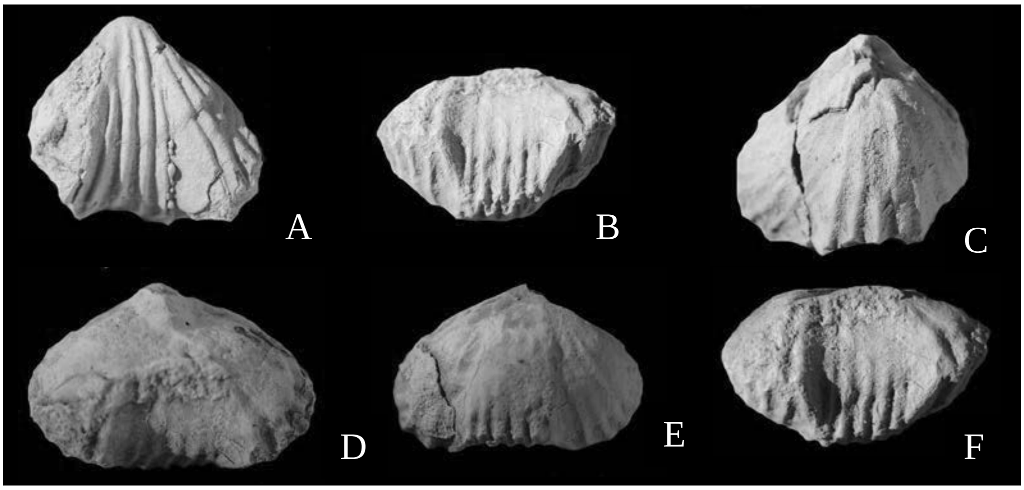


Fig. 238. *Stenoscisma mutabilis* (Tschernyschew). A, B, C, ventral, anterior and dorsal aspects of GSC 137049 from JBW 581. D, E, F, ventral dorsal and anterior aspects of GSC 137050 from JBW 581. Member E, Jungle Creek Formation.

Resemblances: These specimens are close in shape and ornament to *Stenoscisma mutabilis* Tschernyschew, first described from the Schwagerina-Kalk of the southern Urals in Russia, and later from Late Carboniferous faunas of Russia. As in this species, the ribs bordering the sulcus and fold of the Canadian material split into two and the inner ribs become involved anteriorly in the sulcus and fold. The Canadian specimens described by Shi & Waterhouse

(1996, p. 114, pl. 21, fig. 4-14) as *S. mutabilis* are close to the Russian form, but the umbones are smoother, and the sulcus shallower. Plicae bordering the sulcus do apparently divide, but not so clearly. Li & Gu (1976, p. 272, pl. 159, fig. 14-17; 1980, pl. 1, fig. 4, 5) ascribed specimens from the Late Carboniferous rocks of Jilin, northeast China, to the species, but they have smooth umbones and numerous peripheral costae. Specimens so identified by Frebold (1937, p. 43, pl. 11, fig. 2, 3, 4?, 5?) as *Camerophoria* sp. indet. 1 & 11, and compared to *mutabilis* by Gobbett (1964, p. 127, p. 127, pl. 16, fig. 12), and *Camerophoria purdoni* (not Davidson) of Holtedahl (1911, p. 18, pl. 2, fig. 7) have fewer plicae and come from younger beds in Spitsbergen. The Chinese material described by Grabau (1934, p. 16, pl. 2, fig. 1, 2?) is very close to the original types, and the figure in Grabau (1934, pl. 2, fig. 1) even shows the anterior splitting of the plication that borders the sulcus and fold.

There is little similarity to the Mongolian specimens ascribed to the species by Grabau (1931, p. 211, pl. 4, fig. 7, pl. 5, fig. 1, 2), because these have fewer and more robust plicae.

Subfamily **CYROLEXINAE** Carlson in Carlson & Grant, 2002

[Cyrolexinae Carlson in Carlson & Grant, 2002, p. 1227].

Diagnosis: Somewhat rounded in outline, costae absent or present over anterior half, with narrow stolidium rarely present, delthyrium constricted by dorsal umbo, spondylium sessile, intercamarophorial plate present as a rule, hinge plates do not cover the camarophorium.

Discussion: This subfamily was placed in Psilocamaridae by Carlson & Grant (2002, p. 1227), although the presence of an intercamarophorial ridge strongly suggests a closer relationship to Stenoscismatidae, whereas Psilocamaridae, or least the subfamily Psilocamarinae, was deemed to be typified by lack of an intercamarophorial plate (Waterhouse 2004a). On the other hand, the dorsal cardinalia differ from the arrangement in Stenoscismatinae in the poor development or absence of covering hinge plates. Therefore different possible avenues of classification arise, but provisionally, Cyrolexinae are deemed to be close to Stenoscisminae. In *Stenoscisma*, crural bases extend from the base of the ctenophoridium independently of the camarophorium, whereas in *Psilocamara*, the crural bases pass along the upper edge of the camarophorium (Waterhouse 1964). In one constituent member of Cyrolexinae, *Callaiapsida*, the bases are not in touch with the camarophorium for at least part of their length (see Fig. 239C, D).

Genus ***Callaiapsida*** Grant, 1971

Diagnosis: Large strongly ventribiconvex subtrigonal shells without costae, median groove along sulcal floor, beak elongate, camarophorium delicate with low intercamarophorial ridge.

Type species: *Camerisma* (*Callaiapsida*) *kekuensis* Grant, 1971, p. 323 from Halleck Formation (Artinskian?), Kuiu Island, Alaska, OD.

Discussion: Grant (1971, p. 323) erected *Callaiapsida* as a subgenus of *Camerisma* Grant, 1965a, characterized by large size and presence of deep peripheral grooves with flaps and flanges. Similar material was described from Bashkirian faunas of Spain by Martínez-Chacón (1977), though Lazarev (1976a) had argued that the grooves were due to irregular growth rhythyms, of no taxonomic value. Carlson & Grant (2002) treated the two taxa as full and separate genera, placing *Camerisma* in Stenoscismatinae, which seems justified from the internal dorsal cardinalia, and placing *Callaiapsida* in Cyrolexinae: in this genus the dorsal cardinalia were shown to have a low intercamarophorial ridge, not covered by hinge plates.

Callaiapsida divitiae n. sp.

Fig. 239, 240

Derivation: divitiae – riches, Lat.

Diagnosis: Large and transverse, with weak or no median groove ventrally, fold sharp-crested anteriorly.

Holotype: GSC 137051, here designated.

Material: Single ventral valves from JBW 82, 172, 182, 433, 628 and 678, two ventral valves from JBW 193 and 591, single specimens with valves conjoined from JBW 119, 173, 180, 198, 441, 513, 523, 606, 735 and 802, one ventral valve and two specimens with valves conjoined from JBW 190, one ventral valve and four specimens with valves conjoined from JBW 127, a specimen with valves conjoined and a ventral valve from JBW 196, three specimens with valves conjoined from JBW 630, four specimens with valves conjoined from JBW 536, single dorsal valves from JBW 112 and 615, one ventral valve and nine specimens with valves conjoined from JBW 606, two ventral valves and three specimens with valves conjoined from JBW 649, eleven ventral valves and one specimen with valves conjoined from JBW 672, and three ventral valves and three specimens with valves conjoined from JBW 801. Five ventral valves and two specimens with valves conjoined from JBW 122. Six specimens with valves conjoined from JBW 125. Two specimens with valves conjoined from JBW 620 in the Ettrain Formation appear to be identical.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Rare in upper Ettrain Formation.

Description: Shells large for suborder, rhomboidal in outline, ventral valve with incurved umbo, angle measuring 80-95º, long steeply convex umbonal walls extending well forward, with maximum width near anterior third of shell width. Sulcus commences within 12-20mm of the umbonal tip, widens rapidly and extends anteriorly as narrow triangular tongue. Delthyrium wide and open, plugged by dorsal umbo which is broad with angle of 120-135º, and is overlapped by ventral umbo. Fold commences some 20mm in front of hinge, and becomes higher and narrower, reaching the anterior commissure as a narrow high ridge. Both valves smooth, apart from low commarginal growth rugae and growth pauses, three in 5mm.

Ventral valve with teeth supported by large spondylium, resting on a low median septum extending for posterior third of shell length. The septum is formed from a median continuation of the two sides of the spondylium, which is marked by faint growth lines. Dorsal median septum of similar length, thick, of two parallel plates, supporting a small camarophorium (or septalium?) that bears a median ridge which is low or high in different specimens. The structure seems very narrow to have been the seat of muscle attachments (see Fig. 239C). The crura emerge from a short ventrally curved platform below the posterior end of the camarophorium, dorsal to a lamellate cardinal process and trend forward above and ventral to the lateral edges of the camarophorium. This is the same arrangement as in *Stenoscisma*, and differs from *Psilocamara* of Waterhouse (1964, p. 104). Both valves have pallial markings.

Resemblances: This species is represented by a larger suite of specimens than the Jungle Creek material described from the "*Yakovlevia transversa*" to *Jakutoproductus verchoyanicus* Zones of the Jungle Creek Formation by Shi & Waterhouse (1996, pl. 21, fig. 15-22, pl. 32, fig. 2-4, text-fig. 39). Those specimens were identified as *Camerisma* (*Callaiapsida*) *pentameroides* Tschernyschew, a species which lacks a ventral median groove and dorsal median crest, whereas a groove may be developed, albeit faintly, in present material, and the anterior fold is narrow-crested. The Russian types as figured by Tschernyschew (1902, pl. 22, fig. 1, pl. 23. fig. 1, 3, not 2) are much more elongate than present specimens. The type species of *Callaiapsida, C. kekuensis* Grant (1971, pl. 3, fig. 11-17, 22, text-fig. 10) from putative Artinskian of the Halleck Formation in Kuiu Island, Alaska, is smaller than the present form, and has a deeper median ventral groove and less narrowly crested anterior dorsal fold, but is close in shape, although the anterior-lateral margins are more fully rounded and less truncated in the present material. Considerable attention has been focused on the presence or absence of the median ventral groove, which is certainly real in Grant's species, but is slightly variable in the present suite. On the whole, a groove is absent from present Canadian material, but the shell often splits down the centre line under the septum, and may become slightly worn there. On the other hand, the

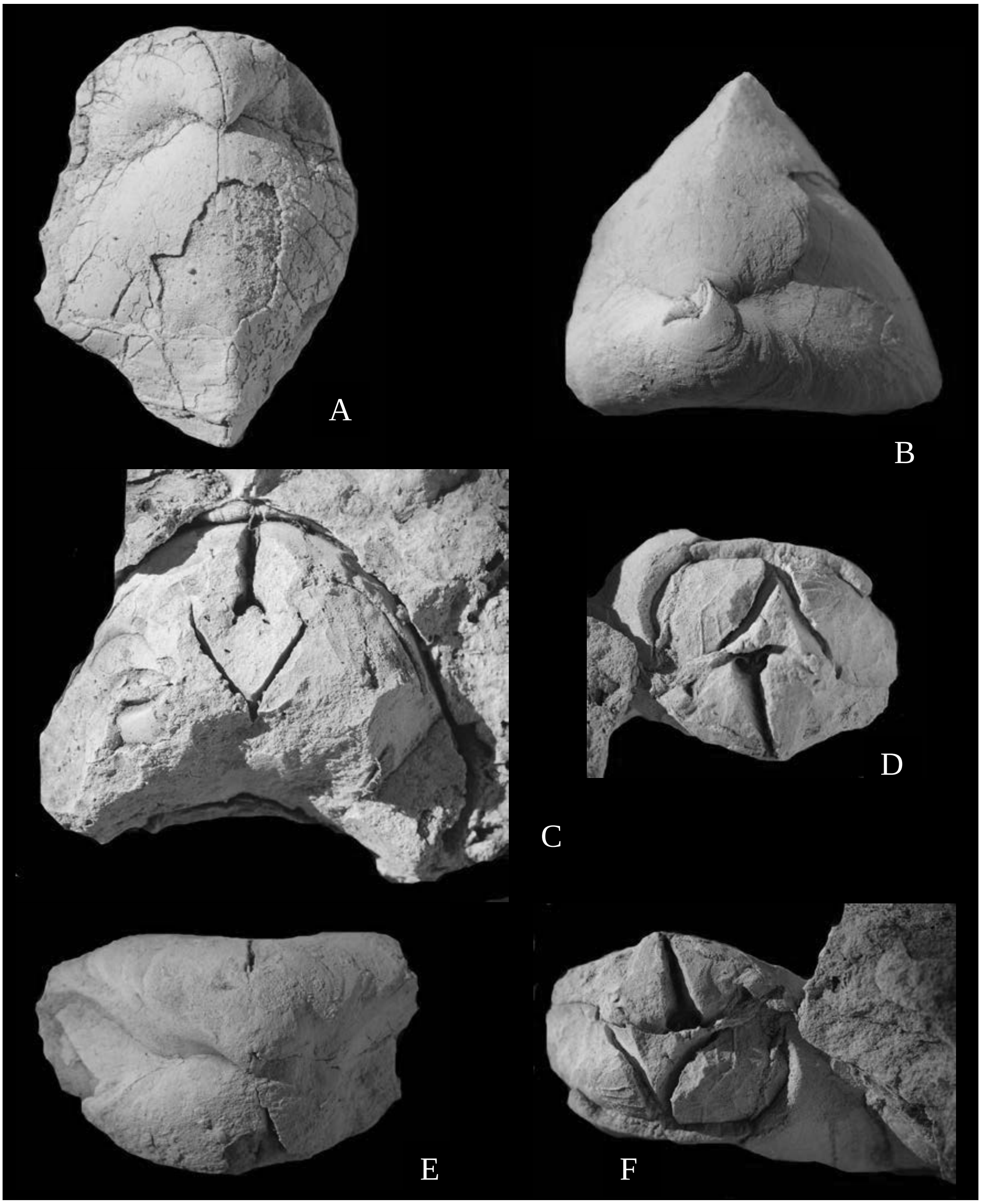


Fig. 239. *Callaiapsida divitiae* n. sp. A, dorsal view of specimen with valves conjoined, holotype GSC 137051 from JBW 127. B, posterior-dorsal view of specimen with valves conjoined, GSC 137052 from JBW 127. C, posterior view of posterior part of specimen with valves conjoined, showing spondylium (below) and camarophorium, GSC 137053 from JBW 441. D, posterior view of posterior part of specimen with valves conjoined, showing spondylium (above) and camarophorium, GSC 137054 from JBW 630. E, posterior aspect of GSC 137319 from JBW 672, ventral valve on top. F, posterior view of GSC 137054 from JBW 630, a different aspect from that of Fig. 239D, with dorsal valve on top. Specimens x1.5, from Member A, Jungle Creek Formation.

fold, deemed to be rounded in shells without a groove (see Shi & Waterhouse 1996, p. 118), is sharp-crested in this species.

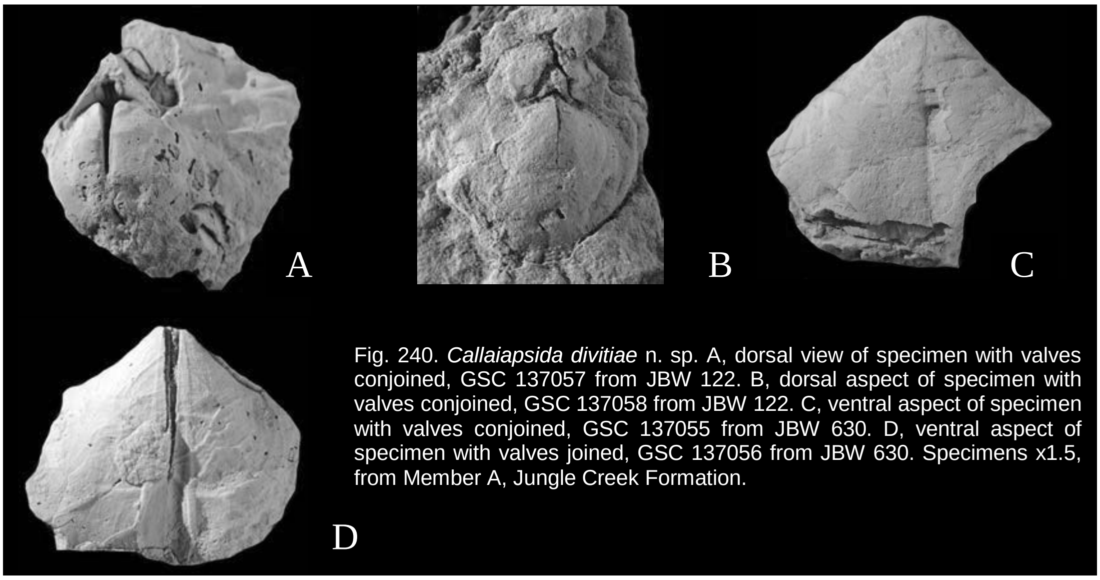


Fig. 240. *Callaiapsida divitiae* n. sp. A, dorsal view of specimen with valves conjoined, GSC 137057 from JBW 122. B, dorsal aspect of specimen with valves conjoined, GSC 137058 from JBW 122. C, ventral aspect of specimen with valves conjoined, GSC 137055 from JBW 630. D, ventral aspect of specimen with valves joined, GSC 137056 from JBW 630. Specimens x1.5, from Member A, Jungle Creek Formation.

From the Upper Carboniferous of Novaya Zemlya, *Calliapsida arctica* (Holtedahl, 1911, p. 19, pl. 2, fig. 5, 6), which was initially named as *pentameroides* [not Tschernyschew]; see also Holtedahl (1924, p. 34, pl. 21, fig. 1, 2) and Grant (1971, p. 327, pl. 3, fig. 1-10) and cf. *Camerophoria sella arctica* of Licharew & Einor (1939, pl. 208, fig. 14, fig. 5), has long sharp-crested dorsal fold, and a a more prominent median ventral groove in Grant's specimens. Gobbett (1964, pl. 16, fig. 13-16) figured small specimens as *Laevicamara arctica* with broad dorsal valve and little in the way of a ventral sulcus from the Passage beds and Wordiekammen Limestone and Cyathophyllum Limestone of Spitsbergen. The Upper Carboniferous species *Callaiapsida pyramidata* Lazarev (1975, p. 216) has ventral groove, sharp-crested fold and dorsal valve much more inflated than the ventral valve. The Spanish species described as *C. alcadei* Martínez-Chacón (1979, pl. 27, fig. 18-21, pl. 28, fig. 1-3) and *C. paucicostata* Martínez-Chacón (1979, pl. 28, fig. 4-8) have sulcal grooves and sharp-crested anterior fold: both are smaller than the present form, and are found in the Namurian Valdeteja Formation of the Cantabrian Mountains.

Superfamily **RHYNCHOTETROIDEA** Licharew, 1956

[Nom. correct. hic ex Rhynchotetradoidea Savage, 1996, p. 254, ex Rhynchotetratidae McLaren, 1965, p. 585, nom. alt. Rhynchotetraidae Licharew in Rhzonsnitskaya, 1956, p. 126]. Admittedly *tetra* rather than *tetr* is part of the stem word for the genus *Rhynchotetra*, and other than rules of customary usage and medieval and more recent rules of Latin grammar, the original Russian proposal could well and arguably should stand. The letter d rather than t as in Stenoscismatinae was inserted, perhaps to contrast with the t's.

Diagnosis: Weak sulcus and fold, distinct planareas, narrow plicae often with superimposed striae anteriorly, foramen with conjunct deltidial plates. Ventral spondylium sessile posteriorly, with lateral propping plates. Dorsal medium septum strong, with septalium [fide Savage et al. 2002, p. 1246] that lacks a cover plate, no cardinal process, crural bases usually triangular in section.

Discussion: This superfamily was discriminated by Savage (1996), and its position is adjusted by noting the close relationship to Stenoscismoidea (Stenoscismatoidea), primarily because a spondylium is well developed in Palaeozoic members. Savage (2002b, p. 1251 ff) incorporated further families of Mesozoic age with similar stout ribbing, namely ?Austrirhynchidae Ager, with dental plates, and Prionorhynchiidae Manceñido & Owen, and these younger members came to lose their spondylium. A new genus, described below as *Yanzaria*, has a spondylium that passes forward into sturdy dental plates, and so adding support for Savage's interpretation, especially as an Early Permian species close to *Yanzaria* has a very small sessile spondylium with long plates in front.

In the *Revised Brachiopod Treatise*, what is termed a camarophorium in the dorsal valve of Stenoscismoidea is matched by what has been called a septalium in Rhynchotetroidea. The difference is that a camarophorium is regarded as having been the seat of dorsal adductor muscle scars, and typically, is larger and may extend further forward than a septalium. Grant (1965a) termed the dorsal structure a camarophorium in his descriptions of North American species assigned to *Septacamer*a, and indeed Russian authorities such as Licharew (1960) and Stepanov (1937b) were in no doubt that a camarophorium was present in *Septacamera* (before a septalium had been proposed). But Grant (1971) demonstrated that dorsal muscle scars lay on the floor of the valve in specimens of *Septacamera* from Alaska, and changed the name of the dorsal structure to a septalium. *Septacamera* shows the same unusual spondylial buttress plates, here called propping plates, as developed in Tetracameridae, and the classification by Licharew (1960) and Grant (1971) is accepted, even though the genus was not mentioned by Savage (2002b) in the *Revised Brachiopod Treatise.*

Family **TETRACAMERIDAE** Licharew, 1956

[Nom. transl. Rzhonsnitskaya, 1958, p. 115 ex Tetracamerinae Licharew in Rzhonsnitskaya 1956, p. 126].

Diagnosis: Lateral propping plates in the ventral valve support the spondylium. Shell surface without radial striae.

Discussion: Savage (2002b, p. 1249) recognized three genera in this family, stated to be of Tournaisian age, and made no mention of *Septacamera* Licharew, which also has spondylium-supporting propping plates, and has been discussed in a number of articles. The genus is not listed in the Index for the *Revised Brachiopod Treatise*, and was not retrieved in the last volume of the *Revised Brachiopod Treatise*, which endeavoured to correct at least some of the previous omissions. In the first *Brachiopod Treatise*, Grant (1965b, p. 632) recognized *Septacamera* as a member of Torynechinae Grant, in Family Stenoscismatidae Oehlert, and Tetracameridae was placed in Paleozoic Rhynchonellacea by McLaren (1965, p. 588).

Note on the proposed term propping plates: The propping plates in *Septacamera* and allied genera have been been termed buttress plates, and here it is suggested that buttress plates be reserved for plates in the dorsal valve in Productida. The propping plates are of quite different function.

Genus ***Septacamera*** Stepanov, 1937b

Diagnosis: Subtrigonal moderately large shells with high gently convex or flat anterior shell, strong subplicae beginning at beaks and uniplicate commissure, open foramen, shallow sulcus. Spondylium sessile posteriorly, may be elevated and placed anteriorly on a septum and supported laterally by propping plates. Dorsal valve with anterior fold, large septalium supported by high septum, without propping plates.

Type species: *Camarophoria kutorgae* Tschernyschew, 1902, p. 90 from Sakmarian of Urals, Russia.

Discussion: Studies of this genus, with its morphology and with aspects of uncertainty, have been discussed by Grant (1965a, 1971). Although there has been some uncertainty over the presence of ventral propping plates in Russian material, Grant (1971) and Shi & Waterhouse (1996) have demonstrated their presence in North American forms, whilst Grant (1965a) has expressed the need to clarify the nature of type material from Russia. Grant believed that the genus was limited to Permian deposits, and occurrences in Spitsbergen seem likely to be Early Perman, Gobbett (1964, pl. 15, fig. 25, pl. 16, fig. 1-3) recording similar-looking forms in the Cyathophyllum and upper Wordiekammen limestones, although the interior of these forms is not known. Czarniecki (1969) in an article not mentioned by Grant (1971) reported three species of *Septacamera* from the Treskelloden beds of Spitsbergen, and stated that the genus was found in Upper Carboniferous as well as Lower Permian of the Urals, and Licharew (1960, p. 249) indicated possible Carboniferous occurrences in Timan and the Urals.

Septacamera sp.

Fig. 241

Material: A shell with valves conjoined from JBW 736. Fragments from JBW 66, including part of a dorsal valve and the umbonal part of a ventral valve, and part of a dorsal valve from JBW 95.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: The specimen from JBW 736 is 42mm wide, at least 39mm long and 21mm high with moderately well formed sulcus and low anterior fold. Subplicae are strong, with narrow crests, and those of the dorsal valve appear to be prolonged as short spikes at the anterior margin. There are four subplicae in the sulcus, a ridge bordering the sulcus, and three or four further subplicae laterally. The shell surface lacks striae. The crest of the fold has five subplicae, with at least five pair of plicae each side.

Two poorly preserved external moulds from JBW 66, including GSC 137061, belong to smaller specimens with somewhat similar ribbing. One shows a ventral spondylium, but specimens allocated provisionally to the taxon are few and poorly preserved.

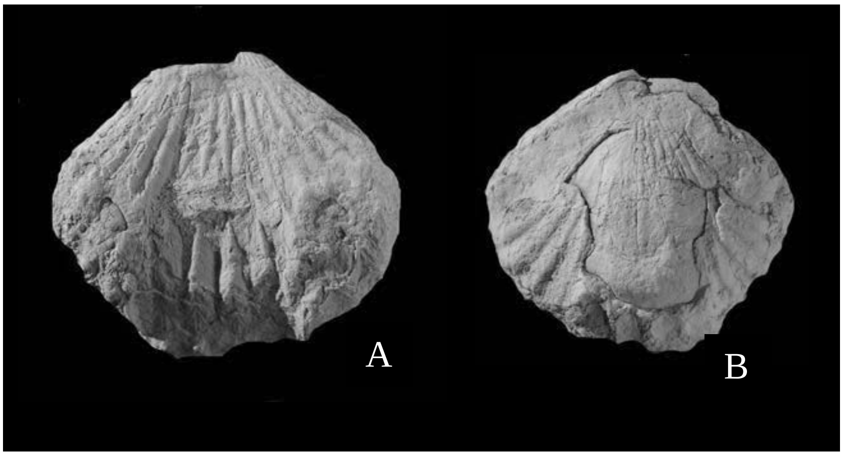


Fig. 241. *Septacamera* sp., ventral and dorsal aspects of GSC 137059 x1 from JBW 736. Member A, Jungle Creek Formation.

Septacamera triangulata Shi & Waterhouse, 1996

Fig. 242

1971 *Septacamera* cf. *plicata* [not Kutorga] – Waterhouse in Bamber & Waterhouse, pl. 16, fig. 9.
1996 *Septacamera triangulata* Shi & Waterhouse, p. 110, pl. 20, fig. 14-27, text-fig. 26.

Diagnosis: Broadly triangular in shape with maximum width placed well forward, costae strong with well rounded crests.

Holotype: GSC 97163 from *Jakutoproductus verchoyanicus* Zone (Aktastinian) and lower Tahkhandit Formation, Yukon Territory, figured by Shi & Waterhouse (1996, pl. 20, fig. 27), OD.

Fig. 242. *Septacamera triangulata* Shi & Waterhouse, cast of broken ventral valve GSC 137060 from JBW 135**,** x1.5. Member E, Jungle Creek Formation.

Material: The external mould of part of a ventral valve from JBW 135.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description, Resemblances: The specimen is 52mm wide and estimated to be close to 35mm long. Ribs are strong, and number nine in the sulcus between the ribs passing along the borders of the sulcus, with at least four ribs laterally. Crests of the ribs are subrounded, and the ribs as strong as those of *Septacamera triangulata*, with similar cross-profile, and the specimen is similarly transverse.

Genus **_Yanzaria_** n. gen.

Diagnosis: Strongly plicate shells distinguished by the nature of the ventral spondylium, which is sessile posteriorly and prolonged anteriorly as two subvertical plates continuing forward from the sides of the spondylium and attached to the floor of the valve. Short propping plates. Septalium narrow, without supporting plates.

Type species: *Camarophoria dowhatensis* Diener, 1915, p. 45 from Fenestella Shales (Visean, lower Serpukhovian) of Kashmir, India, here designated.

Discussion: In an Appendix (p. 460), the typology and description is provided for *Yanzaria*, based on *Camarophoria dowhatensis* Diener, 1915, p. 45, and distinguished by the nature of the spondylium, which is sessile posteriorly and continues forward as two long vertical plates.

Yanzania solitarius n. sp.

Fig. 243

Derivation: solitarius - alone, isolated, Lat.

Diagnosis: Three ribs in sulcus, four on fold, four pair laterally. Spondylium very short.

Holotype: GSC 137062, here designated.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Discussion: Only one specimen is available, but is named as signifying an unexpected occurrence in the Canadian Arctic Permian and related according to present knowledge to an Early Carboniferous genus known in northwest India, which then belonged to the southern paleohemisphere.

Description: Specimen small, 18mm wide and compressed to shorten the length and possibly exaggerate the width as well as height. Large ventral foramen, sulcus commences at mid-length, but anterior fold subdued. Ribs coarse with rounded crests and evenly concave interspaces, three ribs in sulcus and four on the matching fold, some four pairs of plicae laterally on both valves but faint laterally and arising anteriorly. The ribs in the sulcus are terminated anteriorly each in a shallow scoop (Fig. 243C).

Teeth supported by long diverging and subvertical plates, extending more than one third the length of valve, and forming a short sessile spondylium posteriorly, which is supported by a short propping plate on each side, extending antero-laterally. There is a low and short median ridge, and oval depressions each side, likely to signify adductor impressions. The dorsal cardinal process is small and multilaminated, sited between two slender dental sockets, and a high median septum extends medianly for more than half the length of the valve. There appears to be a tiny septalium, but its length and nature are largely uncertain.

Resemblances: *Yanzaria dowhatensis* (Diener 1915) from the Fenestella Shales of Kashmir, India, is larger with more numerous plicae and better formed spondylium and septalium. (See pp. 460-462, Fig. 383, 384).

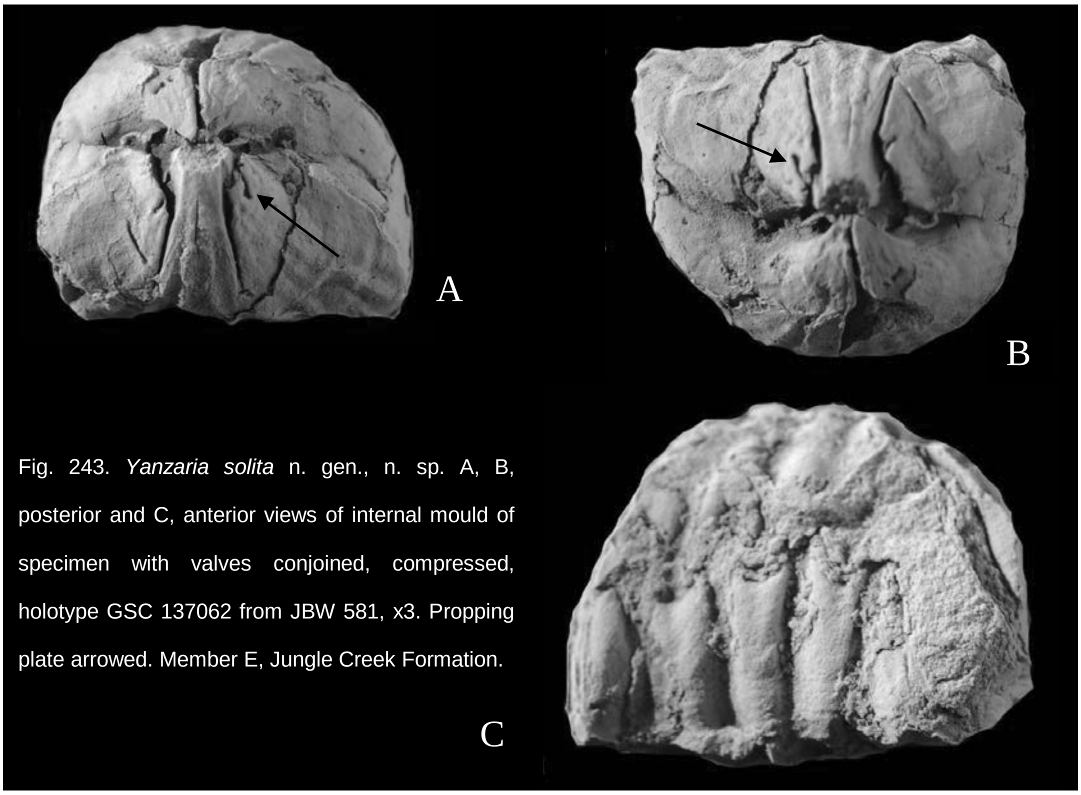


Fig. 243. *Yanzaria solita* n. gen., n. sp. A, B, posterior and C, anterior views of internal mould of specimen with valves conjoined, compressed, holotype GSC 137062 from JBW 581, x3. Propping plate arrowed. Member E, Jungle Creek Formation.

Superorder ATRYPIFORMI Moore, 1952

Discussion: This group is allied to Rhynchonelliformi, most obviously through possessing a functional pedicle, and often sharing prominent ribs, but differs in brachial apparatus, internal plates, and spinose ornament.

Order ATHYRIDA Boucot, Johnson & Staton, 1964

[Nom. emend hic ex Athyridida, nom. transl. Dagys, 1974, p. 152 ex suborder Athyridoidea Boucot, Johnson & Staton, 1964, p. 815].

Diagnosis: Biconvex with ventral meso- to permesothyrid foramen, open or closed delthyrium partly overlapped by dorsal beak, teeth and sockets, cardinal plate commonly present, conospiral brachidia joined by more or less elaborate jugum. Tertiary shell layer present or absent.

Suborder ATHYRIDINA Boucot, Johnson & Staton, 1964

[Nom. emend. hic ex Athyrididina Boucot, Johnson & Staton 1965, p. 654, pro Suborder Athyridoidea Boucot, Johnson & Staton, 1964, p. 815].

Diagnosis: Dental plates commonly present, outer hinge plates present, inner hinge plates usually form septalium or flat hinge that is perforated, laterally directed spiralia, jugal saddle variably developed or absent. Tertiary shell may be present.

Discussion: The modification of ordinal and family group names for *Athyris* and allies is different from that approved over recent years (Alvarez & Brunton 1993, who relied on Ride et al. 1985), and simply adds the agreed and accepted suffix to the truncated genus name, as proposed by Davidson (1881) and Williams (1956), avoiding the additional letters imposed by medieval and more recent rules of grammar for Latin-based terminology. However it may be better to retain the final letter of the generic name s and add the one form of agreed ending, as Athyrisidina.

Superfamily **ATHYROIDEA** Davidson, 1881

[Nom. emend. hic ex Athyridoidea Alvarez & Brunton 1993, p. 310 pro Athyridacea Boucot, Johnson & Staton 1965, p. 654, nom. emend. pro Athyracea Williams, 1956, p. 284, nom. transl. ex Athyridae Davidson, 1881, p. 4].

Diagnosis: Ornament of commarginal lamellae usually bearing flat spine-like outgrowths. Jugum commonly projecting anteriorly as jugal saddle and posteroventrally as thin jugal lamellae that bifurcates into accessory jugal lamellae which terminate behind the lateral branches of jugum or intercalate with spiral loops up to apex; rarely the accessory jugal lamellae extended posterodorsally from jugal saddle.

Family **ATHYRIDAE** Davidson, 1881

[Athyridae Davidson, 1881, p. 4].

Diagnosis: Pedicle supports commonly absent, cardinal plate subtriangular to subtrapezoidal, rarely absent, apically perforate, cardinal flanges poorly developed or absent but become serrate and moderately to well developed in Carboniferous and Permian forms.

Subfamily **CLEIOTHYRIDININAE** Alvarez, Rong & Boucot, 1998

[Cleiothyridininae Alvarez, Rong & Boucot, 1998].

Diagnosis: Short to long numerous spinose growth lamellae, short dental plates, striate flanks to the cardinal plate variably developed, low median septum variably developed, jugal saddle usually well developed with long accessory jugal lamellae terminating anterior to lateral branches. Tertiary shell layer may be present.

Discussion: The subfamily was revised by Waterhouse & Chen (2007) from Alvarez & Rong (2002), particularly with regard to the dorsal cardinalia and diagnoses of several genera.

Genus ***Cleiothyridina*** Buckman, 1906

Diagnosis: Somewhat rounded in outline, perforate cardinal plate well developed, and well developed dorsal median septum.

Type species: *Atrypa pectinifera* Sowerby, 1840 from Magnesian Limestone (Wuchiapingian), England, OD.

Discussion: This genus is close to *Cleiothyridellina* Waterhouse, 1978 from the Himalayan Late Permian, but that genus is swollen and subpentagonal in outline, and lacks the well formed dorsal septum typical of *Cleiothyridina*. A Yukon genus of mid-Carboniferous age is externally close to *Cleiothyridina*, but lacks the cardinal plate (Waterhouse & Chen 2007, p. 35, text-fig. 5) and is referred to *Deltachania* Waterhouse, 1971a. Various other genera such as *Carteridina* Alvarez, Rong & Boucot, *Crinisarina* Cooper & Dutro and *Pinegathyris* Grunt are virtually indistinguishable from *Cleiothyridina* at genus level, though the latter deserves the rank of a subgenus. *Rawdonia* Peou, treated as cleiothyridinin by Alvarez & Rong (2002), was deemed to be spirigerellid by Waterhouse & Chen (2007, p. 35).

Cleiothyridina gzhelensis Grunt, 1980

Fig. 244 - 246

1952 *Athyris* (*Cleiothyridina*) *pectinifera* [not Sowerby] – Sarytcheva & Sokolskaya, p. 237, pl. 70, fig. 408.
1957 *Cleiothyridina gerardi* [not Diener] – Cooper, p. 61, pl. 11E, fig. 28-31.
1968 *Athyris* (*Cleiothyridina*) *pectinifera* – Prokofiev, p. 102, pl. 1, fig. 8-11.
1970 *Cleiothyridina* sp. Zavodowsky, p. 178, pl. 15, fig. 6.
1980 *C. gzhelensis* Grunt, p. 82, pl. 9, fig. 1-6, text-fig. 39-41.

Diagnosis: Small and transversely oval in shape, without sulcus or fold, ventral umbo moderately projecting.

Holotype: PIN No. 544/1104 from Gzhel (Gzhelian), Moscow Basin, Russia, OD.

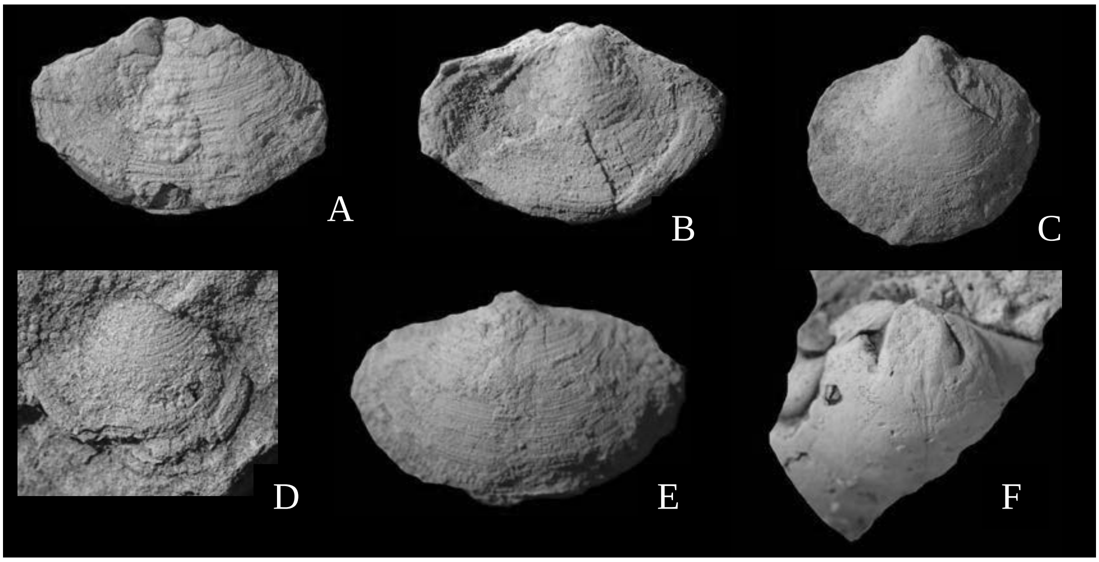


Fig. 244. *Cleiothyridina gzhelensis* Grunt. A, B, ventral and dorsal aspects of specimen with valves conjoined, GSC 137063 x2 from JBW 602. C, ventral aspect of specimen with valves conjoined, GSC 137064 x2 from JBW 84. D, ventral valve GSC 137065 x3 from JBW 43. E, ventral aspect of specimen with valves conjoined, GSC 137066 x2 from JBW 602. A-E from Member A. F, ventral internal mould GSC 137067 x3 from JBW 580, Member E. Jungle Creek Formation.

Material: From Member E, two specimens with valves conjoined from JBW 99, a specimen with valves conjoined from JBW 561, three ventral valves and a dorsal valve from JBW 580, eight ventral valves and three specimens with valves conjoined from JBW 581, and one ventral valve from JBW 616. From Member A, single ventral valves from JBW 43, 177, 182 and 563, five specimens with valves conjoined from JBW 602, two specimens from JBW 419 and specimen with valves conjoined from JBW 84. A ventral valve of uncertain affinities from Member D at JBW 44**.**

Stratigraphic and biostratigraphic levels: Members A, D? and E, Jungle Creek Formation. *Ogilviecoelia shii* Zone and *Septospirifer tatondukensis* Zone. Possibly *Rugivestigia commarginalis* Zone.

Description: Shells small and oval. As an example of specimens from the *Ogilviecoelia shii* Zone, a ventral valve measures 15.5mm wide, 16mm long and 3.5mm high, and a dorsal valve measures 13mm wide, 7mm long and 2.5mm high. The specimen from JBW 561 with valves conjoined is 21mm wide, 15.5mm high and approximately 8mm high. In a small conjoined specimen, the ventral valve is 3.8mm high and the dorsal valve 4.5mm high. The largest specimen from Member A measures 25mm wide, 15.5mm long and 10.5mm high. There is a well developed epithyrid pedicle foramen, a low ventral umbo with posterior walls diverging at 90º, and small dorsal umbo with posterior walls diverging at 120º. No sulcus or fold is developed. Both valves are covered by commarginal lamellae, each bearing a single row of close-set flattened spines, two up to three in 1mm anteriorly on the ventral valve, and at least 5mm long. Specimens from the *Septospirifer tatondukensis* Zone are transversely oval little inflated biconvex specimens. The ventral umbonal angle is 80º to 90º, slightly produced, with small foramen, and the hinge is moderately wide at 16mm in the measured ventral valve, with obtuse cardinal extremities, and no sulcus or fold. There are a number of prominent commarginal growth steps or laminae, with additional intervening finer growth increments numbering three in 1mm, bearing fine low-angle flat spines, on both valves.

Fig. 245. *Cleiothyridina gzhelensis* Grunt, showing external moulds with spines, GSC 137068 to the left and GSC 137069 x6 from JBW 581, Member E, Jungle Creek Formation.

In overall appearance the specimens from the *Septospirifer tatondukensis* Zone are very close to the material from the *Ogilviecoelia shii* Zone, agreeing in size and lack of sulcus or fold at a general level, although some are more elongate and others more transverse. The ventral umbo tends to be slightly more extended, and the growth lamellae are less ragged. In the specimens from Member E, short dental plates concave inwards lie each side of the pedicle, and a low ridge persists for half the valve length in one specimen, and for three quarters of the length in another, and the adductors form a small rhomboid area, marked by growth-lines parallel to the long lateral anterior margin. The teeth are received by two slender sockets in the dorsal valve, and a slender median septum extends for close to a third of the shell length. The cardinal plate is hidden, and muscle imprints are not clear, but low grooves radiate over the posterior shell.

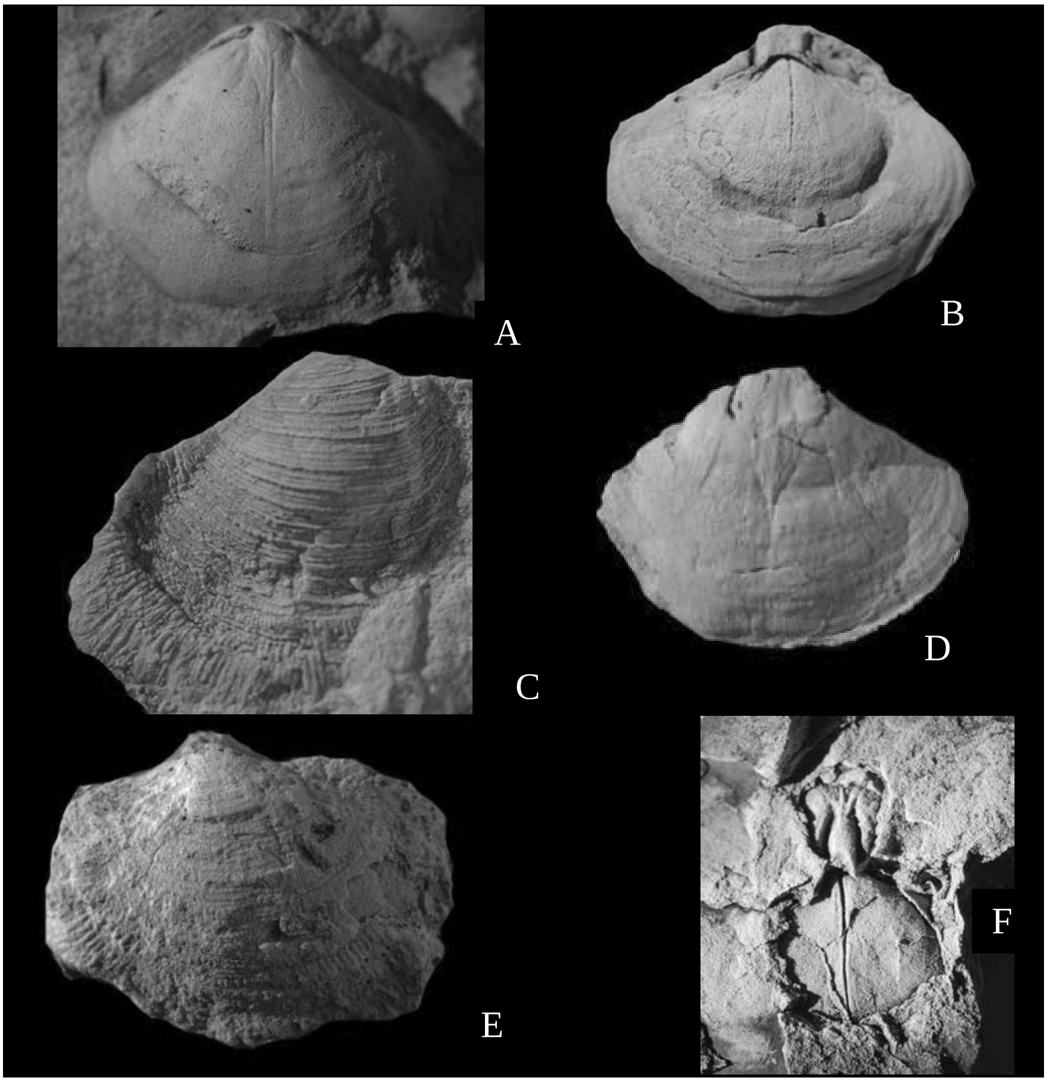


Fig. 246. *Cleiothyridina gzhelensis* Grunt. A, ventral internal mould GSC 137070 x2 from JBW 99. B, D, dorsal and ventral aspects of internal mould, GSC 137073 x3 from JBW 581. C, cast of ventral valve showing spines, GSC 137069 x3 from JBW 581. See Fig. 245. E, ventral view of specimen with valves conjoined, GSC 137074 x3 from JBW 602. F, posterior part of internal mould of specimen with valves conjoined and splayed apart, ventral valve on top, GSC 137302 x2 from JBW 197. Specimens of Fig. 246A-D from Member E and specimens of Fig. 246E and F from Member A. Jungle Creek Formation.

Resemblances: This material in its transversely oval outline with no sulcus or fold and close-set spinose lamellae, and ventral umbo that is small and protrudes somewhat beyond the hinge is very close to the well-illustrated suite of specimens assigned to *Cleiothyridina gzhelensis* Grunt from the Moscow Basin. The genus is not known from faunas of the upper Jungle Creek Formation, recorded in Shi & Waterhouse (1996). There is considerable approach to specimens allocated to *Cleiothyridina gerardi* Diener, 1899 by Cooper (1957, p. 61, pl. 11E, fig. 28-31) from the Coyote Butte Formation of Oregon. The Oregon species appears to be genuine *Cleiothyridina*, whereas Diener's species *gerardi* is the type species of *Himathyris* Waterhouse, 1986c, which differs considerably in shape and has a different interior, as shown by Waterhouse (1986c). Waterhouse & Chen (2007) and Shen et al. (2003) consequently discounted the analysis proferred in the *Revised Brachiopod Treatise* by Alvarez & Rong (2002). *Himathyris* has an unusual shape with extended hinge, lacks dental plates (cf. *Bajtugania* Grunt, 1980), and has dorsal hinge plate and posterior wall pierced by narrow tubule apparently from ventral foramen and extending to the dorsal floor. There is no dorsal septum.

Cleiothyridina sp. of Zavodowsky (1970, p. 178, pl. 15, fig. 6) is also similar to Grunt's species in shape and lack of sulcus or fold, and is slightly larger. It comes from the Early Permian Burgali Suite of northeast Russia. Specimens from the Visean Kuranakh Suite of Cette Davan that were assigned to *C. obmaxima* McChesney by Abramov (1970, p. 157, pl. 38, fig. 1-3) are moderately close. The types and further material described by Weller (1914, p. 475, pl. 79, fig. 1-11) are close in shape, but somewhat larger and bear a very shallow sulcus anteriorly, and low fold, whereas none of the present specimens shows such features.

Cleiothyridina orbicularis (McChesney, 1860) from the Pennsylvanian of United States (see Brew & Beus 1976, p. 901, pl. 1, fig. 21, 22 for summary) and also reported from the Itaituba Group of Brazil by Chen et. al. (2004, p. 462) is moderately close, but slightly more rounded in outline.

Subfamily **SPIRIGERELLINAE** Grunt, 1965

[Spirigerellinae Grunt, 1965, p. 237].

Diagnosis: Small biconvex shells, smooth apart from growth lines and lamellae, thin and short dental plates, cardinal plate and socket plates, well developed crural bases, jugum athyriform.

Genus ***Composita*** Brown, 1845

Diagnosis: Roundly subpentagonal shells with variably developed sulcus and fold, foramen large, epi- to permesothyrid, no deltidial plates.

Type species: *Spirifer ambiguus* Sowerby, 1822 from Derbyshire (Visean) of England.

Composita sp.

Fig. 247

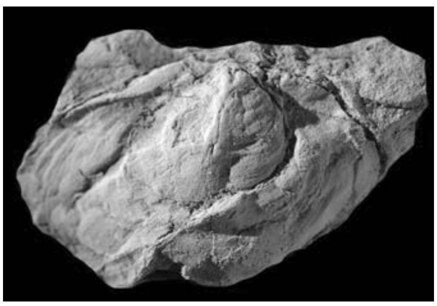


Fig. 247. *Composita* sp., dorsal view of GSC 137432 with valves conjoined, x2. From JBW 127, Member A, Jungle Creek Formation.

Material: A specimen with valves conjoined from JBW 127.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: The specimen is slightly distorted, transverse in shape, with deep narrow anterior ventral sulcus and smooth exterior. A dorsal median septum extends for half of the length of the valve.

Composita mutabilis Czarniecki, 1969

Fig. 248, 249

?1875 *Athyris ambigua* [not Sowerby] – Toula, p. 546, pl. 2, fig. 6 (part, not 4, 5).
1964 *Cleiothyridina* aff. *maynci* [not Dunbar] – Gobbett, p. 22, fig. 11-13.
1969 *Composita argentea mutabilis* Czarniecki, p. 313, pl. 14, fig. 1, 2, text-fig. 38.

Diagnosis: Small subpentagonal equilateral shells with prominent umbones, no sulcus or fold.

Holotype: Specimen no. A 1-8/1189, museum of Laboratory of Geology, Polish Academy of Sciences, Cracow, from Treskelloden beds (Gzhelian or Asselian) of Spitsbergen, figured by Czarniecki (1969, pl. 14, fig. 2), OD.

Material: Two specimens with valve conjoined and a ventral valve from JBW 16. One ventral valve from JBW 615. Member A, Jungle Creek Formation. Three likely specimens with valves conjoined from JBW 620, upper Ettrain Formation.

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

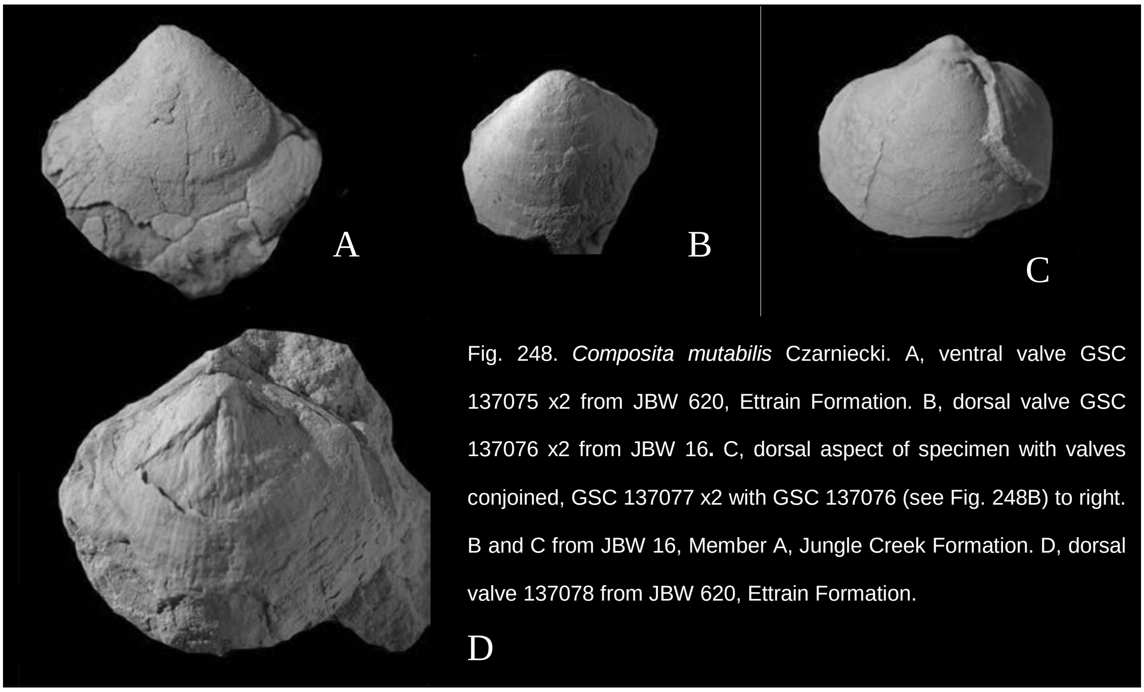


Fig. 248. *Composita mutabilis* Czarniecki. A, ventral valve GSC 137075 x2 from JBW 620, Ettrain Formation. B, dorsal valve GSC 137076 x2 from JBW 16**.** C, dorsal aspect of specimen with valves conjoined, GSC 137077 x2 with GSC 137076 (see Fig. 248B) to right. B and C from JBW 16, Member A, Jungle Creek Formation. D, dorsal valve 137078 from JBW 620, Ettrain Formation.

Description: Specimens small, roundly subpentagonal, dorsal valve slightly less inflated than ventral valve. Ventral umbo incurved, without foramen, and posterior walls are gently concave in outline, and diverge at 90° from the umbonal tip. Hinge of moderate length, weakly developed interareas, obtuse cardinal extremities, no ventral sulcus or dorsal fold other than slight dorsal swelling. Shells smooth, apart from worn prismatic structure over shell surface.

Resemblances: The specimens are very like those figured as *Composita argentea mutabilis* n. subsp. by Czarniecki (1969). The specimens figured by Toula (1875) as ?*Athyris ambigua* include one (fig. 6) that is close, but the other (fig. 5b) has a slender ventral sulcus, and another (fig. 4) is strongly sulcate. Material figured as *Cleiothyridina* aff. *maynci* Dunbar from the Wordiekammen Limestone of Bünsow land by Gobbett (1964) is also close, though it shows a unisulcate anterior commissure. *Composita bamberi* Shi & Waterhouse (1996) may be closely allied to the Spitsbergen form. *C. argentea* (Shepard, 1838, p. 152, Fig. 8; Dunbar & Condra 1932, p. 367, pl. 43, fig. 1-6; Gehrig 1958, p. 12, pl. 5, fig. 1-4) from Desmoinesian to Missourian faunas of United States is somewhat similar to present specimens, displaying slightly shorter posterior walls and more fully rounded anterior shell, and there is a shallow anterior ventral sulcus. Such a sulcus is lacking from *Composita ovata* Mather (1915, p. 202, pl. 14, fig. 6-6c; Dunbar & Condra 1932, p. 370, pl. 43, fig. 14-19; Pederson 1954, pl. 2, fig. 6-9). The species was synonymized by the latter author with *C. wasatchensis* Mather [not White] 1915, p. 200, pl. 14, fig. 7-10b. This species is very close in size and outline, and is most common in Morrowan rocks of Arkansas and Oklahoma, extending into younger Pennsylvanian faunas of Nebraska and Kansas. Ustritsky & Chernyak (1963, p. 120, pl. 45, fig. 9) recorded similar specimens from the Makarov Suite (Lower Pennsylvanian) of Taimyr Peninsula.

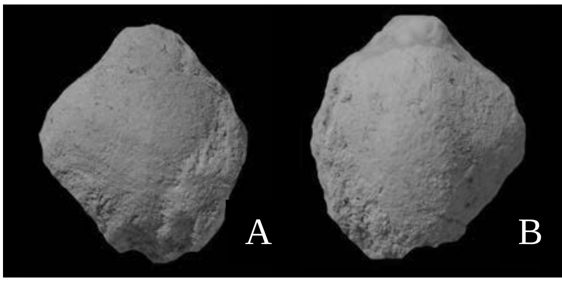


Fig. 249. *Composita mutabilis* Czarniecki. A, B, ventral and dorsal aspects of GSC 137456 x2 from JBW 16, Member A, Jungle Creek Formation.

Composita cf. ***bamberi*** Shi & Waterhouse, 1996

cf. 1996 *Composita bamberi* Shi & Waterhouse, p. 119, pl. 21, fig. 24-29.

Diagnosis: Suboval in shape with strongly convex dorsal valve, no distinct sulcus or fold, but anterior commissure uniplicate.

Holotype: GSC 97195 from GSC loc. 53703, figured by Shi & Waterhouse (1996, pl. 21, fig. 26-29), from Member F of upper Jungle Creek Formation (Sakmarian), Canada, OD.

Material: Single ventral valves from JBW 66? and 580, two ventral valves from JBW 99, two ventral valves and a dorsal valve from JBW 561, and seventeen ventral valves from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Ventral valves small, roundly subpentagonal in shape, a specimen measuring 15mm in width, 10mm long and 3mm high, with small protruding umbo, now largely destroyed, no sulcus or ribs, ornament of low somewhat irregular commarginal lamellae.

Resemblances: The specimens, preserved as incomplete fragments, are moderately close in shape to *Composita bamberi* Shi & Waterhouse (1996, p. 119, pl. 21, fig. 24-29) from the "*Yakovlevia transversa*" Zone of the Jungle Creek Formation. Compared with the specimens identified as *Composita mutabilis* from the *Septospirifer tatondukensis* Zone, the valves are less inflated, and the umbones less incurved. Specimens from both suites are small and lack sulcus and fold apart from unisulcate commissure in the types.

Order RETZIIDA Boucot, Johnson & Staton, 1964

[Nom. transl. Waterhouse, 1981, p. 93 ex Suborder Retzioidea Boucot, Johnson & Staton, 1964, p. 813].

Diagnosis: Strongly to moderately rostrate, astrophic to almost strophic shells with distinct ventral area, covered delthyrium, ribbed or plicate, rarely smooth, with or without spines. No dental plates except in *Retzia*, outer hinge plates well developed, moderate to high median dorsal septum as a rule, spirolophous brachidia, jugum spiny, posteriorly situated, no jugal saddle, jugal stem may be present, accessory jugal lamellae usually absent. Shell punctate, no tertiary layer of shell.

Discussion: Waterhouse (1981) considered that retziid shells constituted an order, rather than suborder within Athyridida (Athyrida), because there are critical differences in spire, shell structure (punctae, no tertiary layer), common lack of dental plates and certain details of the cardinal plate, which point to considerable morphological space between Retziida and Athyrida (Athyridida). Alvarez & Rong (2002, p. 1586) dismissed this arguement on the basis that it would increase (by one!) the number of paraphyletic groups. This argument may be persuasive for some, not for others, because there is no clear indication in brachiopodology that there should be x number of orders as opposed to x + 1 number of orders. The distinctive morphology of retziid shells suggests that it should be regarded as co-ranked with the very much more successful and diverse Athyridida and Atrypida, but in the end that depends on the exact path of development, as yet unknown, as well as weighting of the differences. The three are grouped as Superorder Atrypiformi, and are allied to Superorder Rhynchonelliformi.

Superfamily **RETZIOIDEA** Waagen, 1883

[Nom. correct. Harper 1993, p. 448 pro Retziacea Boucot, Johnson & Staton, 1964, p. 813, nom. transl. ex Retziinae Waagen, 1883, p. 486].

Diagnosis: Astrophic to almost strophic in younger taxa, strongly rostrate, dental plates usually absent, cardinal plate non-perforate, cardinal flanges may be well developed. Median septum may be well developed.

Family **RETZIIDAE** Waagen, 1883

[Nom. transl. Hall & Clarke 1894, p. 840, ex Retziinae Waagen, 1883, p. 486].

Diagnosis: Astrophic subequally biconvex shells, commonly without sulcus or fold, costae strong over sulcus, fold and flanks, foramen permesothyrid, pedicle collar developed. Arms of jugum commonly present but not developed into accessory jugal lamellae.

Subfamily **RETZIINAE** Waagen, 1883

[Retziinae Waagen, 1883, p. 486].

Diagnosis: Astrophic subequally biconvex and elongate shells with costae, no sulcus or fold as a rule, conjunct deltidial plates, permesothyrid foramen, with pedicle collar. Arms of jugum present but no accessory jugal lamellae.

Genus ***Eumetria*** Hall, 1863

Diagnosis: Foramen permesothyrid, no dental plates, pedicle collar poorly developed or absent, no dorsal median septum, outer hinge plates support median cardinal plate, lateral branches of jugum commence posteriorly, jugal arch projecting posteroventrally as long straight stem bifurcating into short arms.

Type species: *Retzia vera* Hall, 1858, p. 704 from Upper Carboniferous of Maryland, United States, SD Waagen 1883, p. 487.

Eumetria sp.

Fig. 250

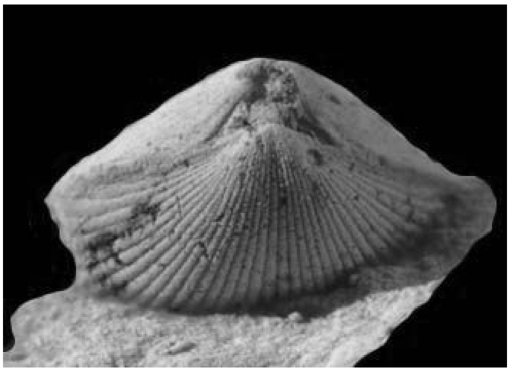
Material: The posterior half of an external mould from JBW 195, and dorsal external mould and mould of both valves (GSC 137221) from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: The specimen from JBW 195 is just under 10mm wide and 5mm high. The umbonal angle is 110º for the ventral valve, and little more for the dorsal valve, and the foramen is well developed, above a narrow interarea. Cardinal extremities are obtuse and the ventral valve is high posteriorly, and the dorsal valve highest anteriorly, giving a sinuous commissure. There is no ventral sulcus but a narrow and shallow sulcus extends medianly along the dorsal valve. Fine ribs number thirty six.

The specimens differ from the allied specimen GSC 137079 of JBW 74 (see below) in size and umbo and possibly umbonal structure, and have a dorsal sulcus, and more ribs.

Fig. 250. *Eumetria* sp. dorsal view of specimen with valves conjoined, GSC 137080 x6, from JBW 195, Member E, Jungle Creek Formation.



Retziid? gen. & sp. indet.

Fig. 251

Material: The posterior half of an external mould from JBW 74.

Stratigraphic and biostratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Description: The specimen is 14mm wide, more than 11mm long and 6.5 mm high, with broad umbo and walls diverging at 120º, slightly concave in outline and extending to well rounded cardinal extremities, with maximum width placed near mid-length. The delthyrial borders are apparently involved with some displacement of tissue, to form two structures that look like deltidial or dental plates, rather than pedicle collar. The dorsal umbo protrudes under the ventral beak, and measures approximately 110º. The hinge is astrophic, and both valves are gently convex and subevenly inflated, with no sulcus or fold. The dorsal valve is ornamented by approximately thirty low ribs, as figured, that become very low over the outermost shell, surface dimpled as if possibly punctate.

Resemblances: Uncertainty over the umbonal structure means that the generic position is not clear. Were dental plates to be present, the specimen would come close to *Retzia* King, 1850, but this genus is not known in deposits younger than Visean (Alvarez & Rong 2002, p. 1588). Perhaps the shell is related to Misoliinae Dagys (Alvarez &

Rong 2002, pp. 1550-1550), possibly including *Uncinella* Waagen, but this group is impunctate.

Fig. 251. Retziid? sp. dorsal view of specimen with valves conjoined, GSC 137079 x3, from JBW 74, Member D, Jungle Creek Formation. See p. 466.

Subfamily **HUSTEDIINAE** Grunt, 1986

[Hustediinae Grunt, 1986, p. 7].

Diagnosis: Small to medium size and usually strongly biconvex, ribs, sulcus and fold over anterior shell or narrow sulcus may extend from umbo of both valves, dorsal medium septum high and short, arms and accessory jugal lamellae absent.

Genus ***Hustedia*** Hall & Clarke, 1893

Diagnosis: Elongately oval, subequally biconvex, coarsely costate shells with submesothyrid to permesothyrid foramen, hinge almost strophic, blunt hinge teeth elongated along hinge, blade-like slightly divergent crura directed almost ventrally, short lingulate process extends forward from base of hinge plate, short median septum beneath hinge plate. Lateral branches of jugum originating posteriorly, projecting anteroventrally as spiny lamellae that join medianly and project posteroventrally in long sharp spiny stem.

Type species: *Terebratula mormoni* Marcou, 1858, p. 51 from Upper Carboniferous of Nebraska, United States, OD.

Hustedia trifida n. sp.

Fig. 252

Derivation: trifidus – split into three, Lat.

Diagnosis: Inner plicae pair each side of sulcus close together, median dorsal shell with median low rib and higher rib each side.

Holotype: GSC 137081, here designated.

Material: Three specimens from JBW 84 and one possible specimen with valves conjoined from JBW 78, seven ventral valves and specimen with valves conjoined from JBW 136, one ventral valve from JBW 802. Two dorsal valves from JBW 449 and three specimens with valves conjoined from JBW 450. Member A, Jungle Creek Formation.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: A specimen from JBW 84 is only 5.5mm long and 3mm wide, with triangular shape, foramen above a concave weakly delineated cardinal area, and six plicae or costae on the ventral valve, the inner two close together, and three pair on the dorsal valve with a median finer rib. A ventral valve from JBW 802 is 11mm wide with a narrow median sulcus bordered by narrow plicae, and three further ribs each side. A large dorsal valve has four pair of ribs and a median rib, and plicae are coarse with well rounded crests. The shell appears to be finely punctate.

Resemblances: From the Upper Carboniferous of Nebraska, the type species *Hustedia mormoni* (Marcou, 1858, p. 51, pl. 6, fig. 11, 11a), also figured by Girty (1915, p. 103, pl. 12, fig. 5, 6), Dunbar & Condra (1932, p. 356, pl. 42, fig.

9-11) and Sutherland & Harlow (1973, p. 63, p. 63, pl. 14, fig. 10-12), has some seven pairs of coarse plicae with well rounded crests. The species is unlikely to be older than Desmoinesian. The present species looks somewhat like material assigned to *Thedusia* Cooper & Grant, 1976b from the Cisuralian of west Texas, but its umbonal shell is far less extended. *Hustedia remota* (Eichwald) of Ustritsky & Chernyak (1963, p. 121, pl. 46, fig. 3, 4) from the Turuzov Suite of Taimyr displays some three or more pair of coarse plicae.

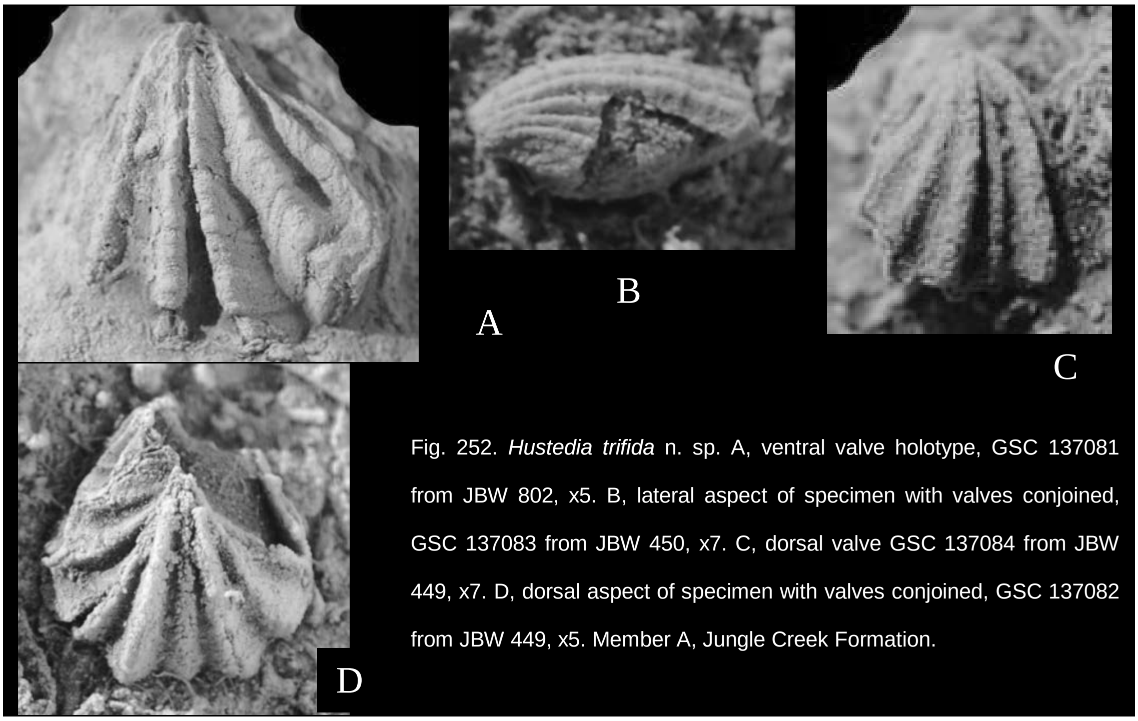


Fig. 252. *Hustedia trifida* n. sp. A, ventral valve holotype, GSC 137081 from JBW 802, x5. B, lateral aspect of specimen with valves conjoined, GSC 137083 from JBW 450, x7. C, dorsal valve GSC 137084 from JBW 449, x7. D, dorsal aspect of specimen with valves conjoined, GSC 137082 from JBW 449, x5. Member A, Jungle Creek Formation.

Hustedia quadrifidus n. sp.

Fig. 253 - 255

Name: quadrifidus – divided in four parts, Lat.

Diagnosis: Elongately triangular in shape with prominent ventral umbo and high cardinal area, plicae strong and few, usually four pairs on ventral valve, outer pair slender. Dental sockets crenulate.

Holotype: GSC 137087, here designated.

Material: Single ventral valves from JBW 561 and 577, a ventral valve and specimen with valves conjoined from JBW 580, and twelve ventral valves, four dorsal valves and three specimens with valves conjoined from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Shell trigonal in shape, with extended posterior walls concave in outline, that diverge at 55^{o} increasing to 70^{o}, small terminal foramen, and narrow high interarea traversed longitudinally by a convex median flat arch with groove each side. The ventral valve is ornamented by outward curving strong plicae in four pairs, all with narrowly rounded crests and deep concave-floored interspaces, and divided by a narrow well formed sulcal interspace with sulcal angle of 15^{o}. The dorsal valve is shorter with very low interarea, slender median fold, and similar strong ribs, the median rib bearing a groove along its crest anteriorly. Two additional pairs of fine plicae appear laterally in fully mature shells. The surface is very finely pitted by pores. Low teeth are present in the ventral valve, and the dental sockets are finely crenulate. Such crenulations were nowhere recorded or shown in fine illustrations of various *Hustedia* species recorded from west Texas by Cooper & Grant (1976b). A fine low median septum extends for half the shell length, commencing in front of the posterior wall, which lacks any visible cardinal process.

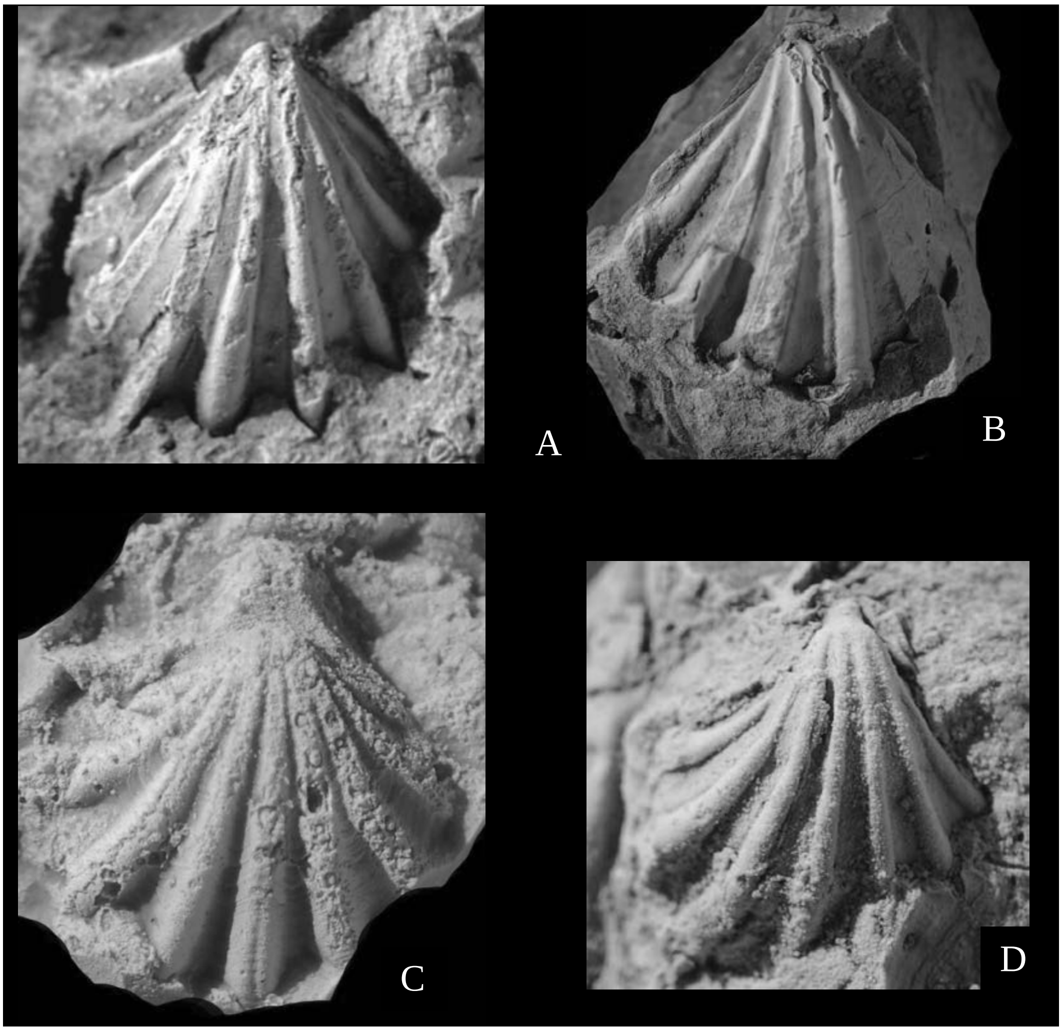


Fig. 253. *Hustedia quadrifidus* n. sp. A, ventral valve GSC 137085 x8. B, ventral valve GSC 137088 x5. C, dorsal view of external cast, holotype GSC 137087 x5. D, ventral valve GSC 137088 x5.x From JBW 581, Member E, Jungle Creek Formation.

Resemblances: A large number of species of *Hustedia* were described from Permian faunas of west Texas by Cooper & Grant (1976b), but most are broader forms with fewer plicae, and come mostly from faunas of Middle Permian age. *H. huecoensis* R. E. King (1931, p. 125, pl. 42, fig. 44-46, part not fig. 43 = *cepacea* Cooper & Grant) is close in general appearance but has usually twelve ribs. It comes from the Bone Spring and Skinner Ranch Formations and other levels in Texas. Further material was figured by Cooper & Grant (1976b, pl. 745, fig. 11-16) from the upper Gym Formation. *H. hessensis* King, 1931, also figured by Cooper & Grant (1976b, pl. 736, fig. 1-20) is moderately close in shape, but has only three pair of plicae. It comes from the Skinner Ranch Formation of the Glass Mountains in Texas. One species with four pair of plicae is *H. consuta* Cooper & Grant (1976b, pl. 734, fig. 1-20) from the Road Canyon Formation (Roadian), but this is less elongate with blunter beak. Four pairs of ventral plicae are also present in *H. culcitula* Cooper & Grant (1976b, pl. 734, fig. 41-76) from the Neal Ranch Formation, but the species is consistently broader with less attenuated umbo. *H. cuneata* Cooper & Grant (1976b, pl. 735, fig. 1-50) from the Road Canyon Formation is similar to the present species in shape but has five pair of plicae. Wordian forms include *H. pugilla pugilla* Cooper & Grant (1976b, pl. 739, fig. 1-34) with three pair of plicae, and slightly more attenuate *H. pugilla pluscula* Cooper & Grant (1976b, pl. 739, fig. 35-57) with four or five pair of plicae, and unusual varieties *H. pugilla habetata* and *H. pugilla nasiterna* of Cooper & Grant, 1976b, discussed further on p. 463. *H. trita* Cooper & Grant (1976b, pl. 272, fig. 20-70, divided into subspecies *trita* Cooper & Grant (1976b, pl. 742, fig. 47-71) and *H. trita leptyca* Cooper & Grant (1976b, pl. 742, fig. 20-46), both from the Neal Ranch Formation, have usually five pair of plicae and are more transverse.

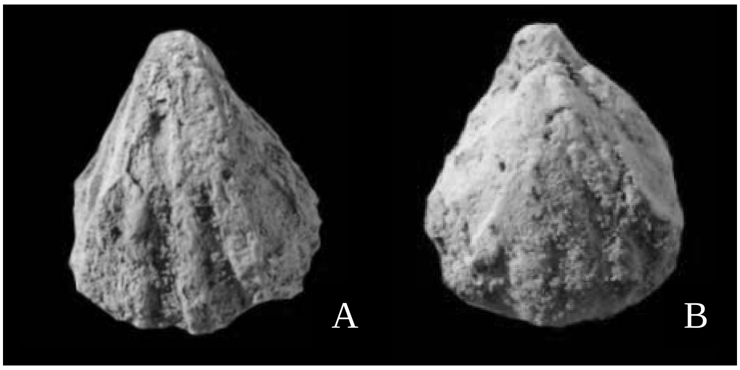


Fig. 254. *Hustedia quadrifidus* n. sp. A, B, ventral and dorsal aspects of internal mould of immature specimen, GSC 137089, x5. From JBW 581, Member E, Jungle Creek Formation.

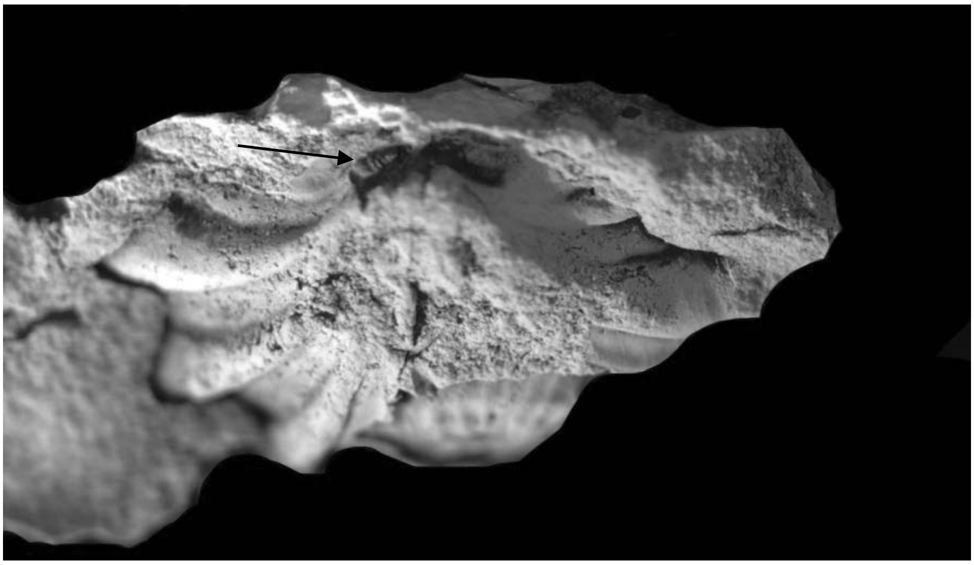


Fig. 255. *Hustedia quadrifidus* n. sp. posterior view of dorsal valve GSC 137303, x7, showing crenulate dental sockets, as arrowed. JBW 581, Member E, Jungle Creek Formation.

Hustedia remota Eichwald of Tschernyschew (1902, p. 107, pl. 47, fig. 8-11) from the Schwagerina-Kalk of the Urals is broader with four pair of plicae. It seems likely that this species includes the material reported from the

Coyote Butte Formation of central Oregon by Cooper (1957, pl. 12, fig. 42-44). Shi & Waterhouse (1996, p. 118, pl. 21, fig. 23) recorded *Hustedia* cf. *remota* (Eichwald) from the "*Yakovlevia transversa*" and *Jakutoproductus verchoyanicus* Zones in the Jungle Creek Formation, as a moderately transverse specimen with five pairs of sturdy ribs.

An incomplete specimen of possible *Hustedia* comes from JBW 762 in Member D, but is too poorly preserved to be allocated to any species.

Superorder SPIRIFERIFORMI Waagen, 1883

[Spiriferiformi Waterhouse, 2010, p. 12].

Spiriferiformi associates Orders Spiriferida and Spiriferinida, which share distinctive internal plates and have laterally directed spiralia in which primary lamellae are parallel and close to the sagital plane. No complete jugum is present.

Order SPIRIFERIDA Waagen, 1883

[Nom. correct. Moore, Lalicker & Fischer 1952, p. 221, pro Order Spiriferacea Kuhn, 1949, p. 104, nom. promoveo ex suborder Spiriferacea Waagen, 1883, p. 447].

Diagnosis: Shell impunctate. Median septum in ventral valve rare.

Suborder MARTINIIDINA Waterhouse, 2010

[Martiniidina Waterhouse, 2010, pp. 13, 63].

Diagnosis: Dental plates, adminicula and tabellae highly varied in presence and development. Shells biconvex, smooth or coarsely plicate, some broadly costate, with varied micro-ornament of commarginal and/or radial capillae, spinules, pustules, grooves or pits.

Discussion: A feature of the suborder is the variation in internal plates, which proceeded along a slender and acceptable range, consonant with external features of shape and micro-ornament, and no genus shows a spondylium, cruralium, or ventral or dorsal medium septum. In many family groups the delthyrium is open, and in smaller groups a connector plate may be developed, with a deltidium or deltidial plates present in one major family. Martiniidina is diverse, and is subdivided into two infrasuborders, united by the sharing of tabellae in at least some early members. That is proferred as the most conservative of available choices in classification, yet marks a radical departure from the first and second series of *Revised Brachiopod Treatise*. By contrast, Spiriferidina has moderately consistent internal plates, and Delthyridina shows a different style of external ornament and internal plates.

Infrasuborder MARTINIIMORPHI Waterhouse, 2010

[Nom. transl. Waterhouse 2016, p. 56 ex Martiniidina Waterhouse, 2010, pp. 13, 63].

Diagnosis: Genera smooth or plicate, seldom costate, micro-ornament varied, smooth, pitted, grooved, or minutely spinose. Interior with well developed dental plates and adminicula as a rule, but these may be absent from genera that are otherwise similar in shape and ornament. Dorsal valve with socket and crural plates, tabellae widely present, may be absent.

Discussion: To this infrasuborder are referred spiriferidan superfamilies and genera which display adminicula, dental plates and crural plates with tabellae, together with genera deemed to have secondarily lost plates. Overall shape is subrounded, plicae are more or less developed, and micro-ornament is varied, pitted, spinose, or grooved or smooth, with further variations, but without prominent commarginal lamellae, as pointed out by Carter & Gourvennec (2006b, p. 1747), apart from one exception, *Carteriopsis* Waterhouse (2016, p. 66).

The infrasuborder commenced in Silurian (upper Wenlock) time, and earliest genera displayed a shape and internal plates consonant with attributes of Cyrtioidea, specifically members of Eospiriferinae, such as *Endospirifer* Tachibana, *Hedeina* Boucot and *Myriospirifer* Havlíček of Silurian and early Devonian age. These genera differed in their micro-ornament. Unlike most members of Martiniimorphi, Cyrtioidea genera exhibit deltidial plates or delthyrial cover, although pleromal thickening and a connector plate are developed in some Permian stock, and extensions of the dental plates are seen in Heterariinae (Waterhouse 2016, p. 70). But overall, shape, internal plates and fossil record display a convincing source for the origin and development of the Elythynoidea, Gerkispiroidea and Ingelarelloidea that make up the infrasuborder Martiniimorphi.

Superfamily **INGELARELLOIDEA** Campbell, 1959a

[Nom. transl. Waterhouse 1998, p. 3 ex Ingelarellinae Campbell, 1959a, p. 333].

Diagnosis: Medium to large shells comparatively smooth apart from broad plicae, micro-ornament of shallow to deep pits and pustules or tiny spinules. Adminicula and tabellae present to varying degree.

Discussion: Earliest members existed in Russia, and by Permian time had become well established in Gondwana.

Family **INGELARELLIDAE** Campbell, 1959a

[Nom. transl. Archbold & Thomas 1986, p. 582 ex Ingelarellinae Campbell, 1959a, p. 333].

Diagnosis: Adminicula and tabellae well developed. Micro-ornament of shallow grooves in quincunx as a rule.

Discussion: Notospiriferidae Archbold & Thomas, 1986 is distinguished by having only short if any tabellae as a rule, and in being always plicate. Micro-ornament consists of pits, mesopunctae, spinules, or grooves.

Genus ***Martiniopsis*** Waagen, 1883

Diagnosis: Shell almost smooth, with no more than very shallow if any sulcus. Micro-ornament of elongate grooves, internal plates typical of the family.

Type species: *Martiniopsis inflata* Waagen, 1883, p. 524 from lower Chhiddu Formation (Wuchiapingian) of Salt Range, India, SD Etheridge in Jack & Etheridge (1892, p. 238).

Martiniopsis? sp. A

Fig. 256

Diagnosis: Moderately large, weakly transverse with narrow sulcus, commencing at umbo in some, commencing well in front of umbo in others, adminicula short.

Material: Single ventral valves from JBW 15, 75, 172, 412, 504, 591, 775, 789 and possibly 615, two ventral valves from JBW 518, three ventral valves from JBW 125, and specimen with valves conjoined from JBW 122. Two ventral valves from JBW 562.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

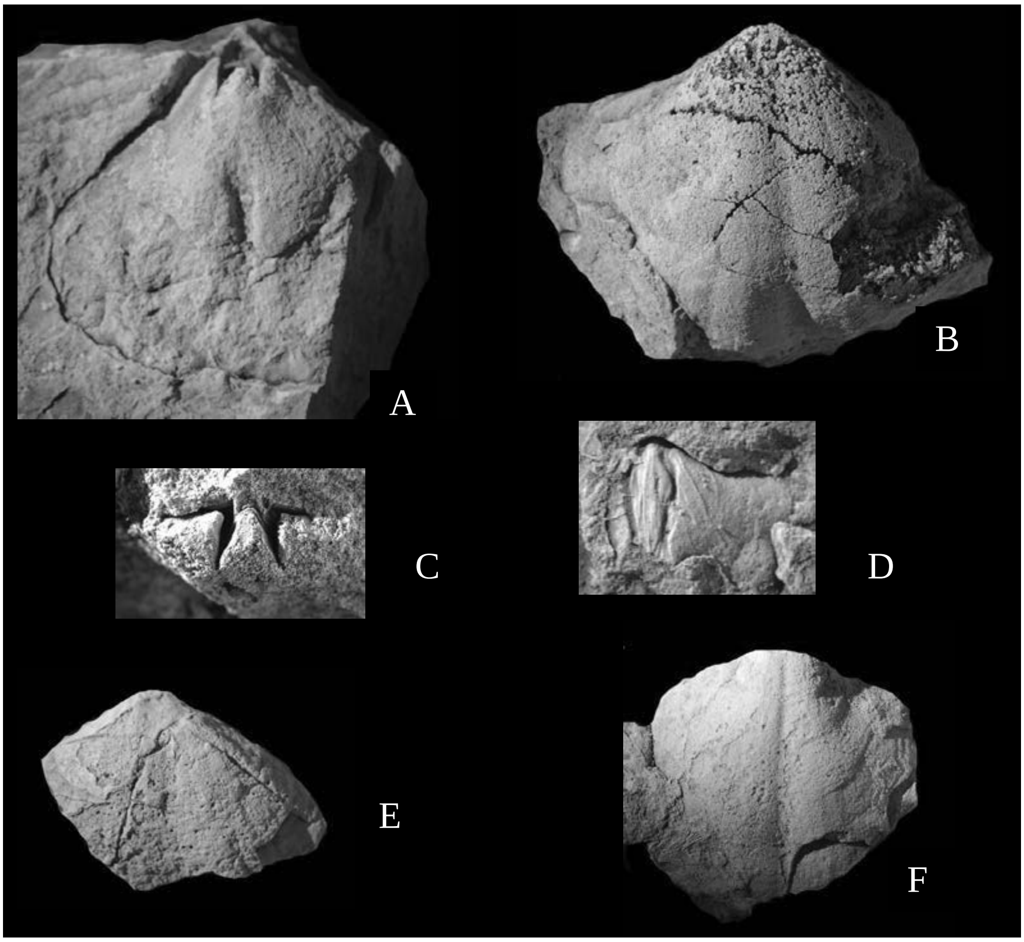


Fig. 256. *Martiniopsis*? sp. A. A, ventral internal mould, GSC 137090 x1.5, from JBW 504. B, silicified ventral valve GSC 137091 x1, from JBW 412. C, posterior ventral internal mould showing adminicula, GSC 137304 x2, from JBW 75. D, ventral internal mould GSC 137092 x1.5, from JBW 15. E, ventral valve GSC 137093 x1, from JBW 591. F, damaged ventral valve GSC 137095 x1, from JBW 172. Member A, Jungle Creek Formation.

Description: Specimens of moderate size, a ventral valve from JBW 504 measuring 57mm in width, 43mm in length and 15mm in height, ventral umbo prominent, angle of 90º with umbonal walls convex and of moderate height, curving outwards to convex cardinal extremities, interarea less than maximum width and weakly defined, with open delthyrium of 45º, maximum width near mid-length. Specimens from JBW 172, 789, 615, 518 and 189 have a narrow groove-like sulcus, commencing at the umbo, with a narrow angle of 17-20º , whereas the sulcus commences well in front of the umbo and is broad and shallow in specimens from JBW 775 and 591 (Fig. 256E), so that perhaps two species are involved, but there is not enough material to evaluate this possibility. There are no plicae. Micro-ornament poorly preserved, suggestive of subdued fine growth rugae anteriorly, and short radially aligned grooves. A better preserved exterior shows low growth rugae, very low with convex crests separated as a rule by grooves, more closely spaced around the margin. There are two major growth pauses, and the surface is covered very fine radial grooves and fila, ten to eleven in 1mm, possibly true ornament, possibly reflecting shell structure.

Teeth are supported by high scapular-shaped dental plates, resting on high subvertical adminicula, which extend for only a quarter of shell length. The lateral posterior shell is heavily thickened and marked by vascular grooves. Two ventral valves from JBW 562 show heavy posterior thickening and long adminicula and narrow sulcus.

No dorsal valve is preserved, leaving the identity conjectural.

Resemblances: This species is distinguished by shape, narrow long sulcus and short adminicula. Several species from the Early Permian of the Urals as described by Tschernyschew (1902) come close, but most are narrow and elongate, with virtually no sulcus, and the internal plates are not well known. *Martiniopsis lutugini* Tschernyschew (1902, pp. 174, 560, pl. 19, fig. 5, pl. 49, fig. 5) is the closest of Russian species so far described, with slender sulcus that commences in front of the umbo, and the shells are narrow. Zavodowsky (1970, p. 175, pl. 33, fig. 10) also figured a somewhat similar specimen from the Paren Suite of the Omolon Basin, northeast Russia, as *M*. ex gr. *orientalis* Tschernyschew. The original specimens are narrow shells with narrow sulcus commencing well in front of the umbo, and widening considerably at the anterior margin.

Martiniopsis orientalis Tschernyschew (1902, pp. 172, 556, pl. 19, fig. 7-12) from the Schwagerina-Kalk of the Urals is close in shape and has a narrow ventral sulcus that commences in front of the ventral umbo (Sokolskaya in Sarytcheva & Sokolskaya 1952, pl. 44, fig. 3). The length of the adminicula is not clear. The type species of *Martiniopsis, M. inflata* Waagen, 1883, p. 524 from the Chhidru Formation (Wuchiapingian) of the Salt Range, India, completely lacks any sulcal groove, but a Late Permian (upper Changhsingian) species from the Wairaki Breccia of New Zealand, *M. patella* Waterhouse, 1967a, 2002a, p. 98, has a shallow and narrow groove-like sulcus traversing the ventral valve. In this species the adminicula are long.

Eomartiniopsis? *susanae* Martínez-Chacón (1978, p. 24, pl. 2, fig. 13-18, text-fig. 3) has narrow sulcus and short adminicula, but lateral plicae are present. The species come from the Bashkirian San Emiliano Formation of the Cantabrian Mountains in Spain.

***Martiniopsis*? sp. B**

Fig. 257

Diagnosis: Adminicula short.

Material: Two ventral valves from JBW 100.

Stratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Description: Specimen 42mm wide, 37mm long and 13mm high, with narrow groove-like sulcus starting at the umbonal tip, and low narrow ribs anteriorly. Moderately short subparallel adminicula. The nature of the sulcus is close to that of specimens from JBW 172 and 789 from the *Septospirifer tatondukensis* Zone.

Fig.257. *Martiniopsis*? sp. B, internal mould of ventral valve GSC 137096 x4, from JBW 100, Member D, Jungle Creek Formation.

Genus ***Geothomasia*** Waterhouse, 1998

Diagnosis: Large shells with well formed sulcus, fold without median channel, lateral shell may have few strong plicae or none, fine surface grooves. Adminicula moderately long and well spaced, tabellae short, well spaced, may diverge widely.

Type species: *Tomiopsis teicherti* Archbold & Thomas, 1986, p. 593 from Wandagee Formation (Baigendzinian) of Western Australia, OD.

Discussion: The genus was prominent in the Permian of eastern and Western Australia, and first appeared in the Middle and Late Carboniferous of Verchoyan and Lake Baikal of east Russia (see Waterhouse 2015a, p. 171). In Canada, the species *Tomiopsis ovulum* Waterhouse, 1971b of early Permian age is a member of the genus.

Geothomasia? sp.

Fig. 258

Material: Part of a ventral valve from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: The fragment is 35mm wide, at least 31mm long and 14mm high, broad shallow sulcus with estimated angle close to 30^{o}, and bearing two low subplicae. There are subdued lateral plicae.

Discussion: So little of the valve is preserved that it is not possible to offer any confident identification. In general shape and size it is ingelarelliform, and approaches the genus *Geothomasia* which is represented by *G. ovulum* in the "*Yakovlevia transversa*" Zone and *Jakutoproductus verchoyanicus* Zone of the overlying Jungle Creek Formation (Shi & Waterhouse 1996, p. 144), as well as the Kindle Formation of British Columbia (Waterhouse 1971b). Reports of the genus in the Eta Zone in Bamber & Waterhouse 1971) referred to the Kindle Formation rather than Member E in the Ogilvie Mountains, and this specimen could prove to be related.

Fig. 258. *Geothomasia*? sp., internal mould of part of ventral valve, GSC 137433 x1 from JBW 581, Member E, Jungle Creek Formation.

Superfamily **MARTINIOIDEA** Waagen, 1883

[Nom. correct. Carter, Johnson & Gourvennec in Carter et al. 1994, p. 338, pro Martiniacea Ivanova, 1972, p. 41, nom. promoveo Martiniinae Waagen, 1883, p. 542].

Diagnosis: Suboval biconvex shells, smooth, sulcate and/or plicate, micro-ornament of fine pits, spinules, or commarginal or radial lirae. Dental plates may be reduced or absent, no adminicula; crural plates often reduced, never supported by tabellae (ie. "dorsal adminicula").

Discussion: Martinioidea embrace genera that lack adminicula and tabellae, and have moderately developed varying to virtually no dental plates or distinguishable crural plates. For Martiniinae, plates and septa were said to be absent from both valves (Carter in Carter & Gourvennec 2006b, p. 1747), but this statement is wrong, because dental plates, crural plates and socket plates are present in several genera. The family group that seems to be most closely related to Martiniidae is Brachythyridae Fredericks, which lack adminicula and tabellae, and may have reduced if any dental plates. Members have stronger ribs, and the similarity may be due to convergence, but in the favoured interpretation, reflected a modest degree of divergence from allied sources.

Family **MARTINIIDAE** Waagen, 1883

[Nom. promoveo Ivanova 1959, p. 56 ex Martiniinae Waagen, 1883, p. 542].

Diagnosis: As for superfamily. Dental plates present or absent, lateral slopes may be smooth or plicate. Delthyrium may be closed or partly closed by deltidial plates, or rarely, connector plate and pleromal ridges.

Subfamily **MARTINIINAE** Waagen, 1883

[Martiniinae Waagen, 1883, p. 542].

Diagnosis: Suboval biconvex shells with dental plates in some genera but no adminicula, crural plates small or large, no tabellae. Micro-ornament of pits in shagreen pattern, or commarginal growth lines common. Mantle canal system linear, ramniform or reticulate.

Genus ***Martinia*** M'Coy, 1844

Diagnosis: Medium to large, generally sulcate shells with no ornament other than fine pits, small ctenophoridium. Dental plates low or lacking. Mantle canals linear.

Type species: *Spirifer glaber* Sowerby, 1820 from Carboniferous Limestone (Visean), England.

Discussion: *Martinia* M'Coy 1844, type species *Spirifer glaber* J. Sowerby, 1820, is a large transverse shell of Lower Carboniferous age in the British Isles with weakly defined dorsal fold for the length of the valve, and numerous subparallel radial mantle canals on the surface of the inner shell (George 1931, Muir-Wood 1951, Waterhouse 1981, pl. 30. fig. 3, 6, 7, pl. 31, fig. 1). The interior of true *Martinia glaber* remains poorly known. Material identified with the species kept at the Natural History Museum, London, includes some forms bearing definite dental plates, and others without dental plates. No specimens have adminicula. Preparation or sectioning or non-destructive penetration of topotype material is required to clarify the nature of the interior.

Martinia cf. ***karawanica*** Volgin, 1959

Fig. 259, 260

cf. 1892 *Martinia* cf. *glabra* [not Martin] Schellwien, p. 41, pl. 6, fig. 14, 15.
cf. 1959 *Martinia karawanica* Volgin, p. 121, pl. 6, fig. 8-10.
cf. 1960 *M. karawanica* – Volgin, p. 138, pl. 18, fig. 2.

Diagnosis: Medium size, weakly transverse suboval shells with shallow and slender or no ventral sulcus.

Holotype: Specimen figured by Volgin (1959, pl. 6, fig. 8) from Dastarskii Horizon (Late Carboniferous), Kara-Chatir, Fergana, OD.

Material: From Member A, single ventral valves from JBW 16, 84, 166, 182, 504, 518, 584? and 585, and single specimen with valves conjoined from JBW 685. Single ventral valve from JBW 516, Ettrain Formation.

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Dimensions in mm: ventral valve

Specimen	Width	Length	Height	Locality
GSC 137100	40	35	16	JBW 504
GSC 137097	39	?27	17	JBW 585

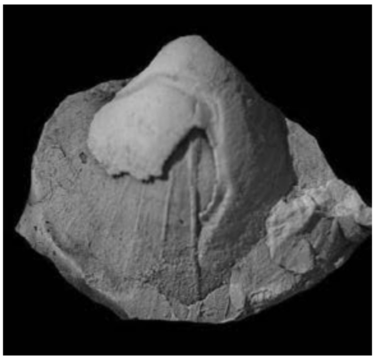


Fig. 259. *Martinia* cf. *karawanika* Volgin, ventral internal mould GSC 137101 x4, from JBW 182, Member A, Jungle Creek Formation. Lateral flanks have been lost.

Description: Ventral valve transverse with wide hinge, obtuse cardinal extremities, maximum width near mid-length, umbo slightly extended beyond hinge, umbonal angle of 80-90º, interarea poorly defined, delthyrium very narrow. No plicae or ribs. The dorsal valve of the specimen from JBW 84 has a very shallow anterior depression and low median dorsal swelling. Presence of teeth uncertain; no dental plates or adminicula. Muscle scars striate with vascular trunks radiating from the muscle field, adductor field depressed and compact with longitudinal ridges.

Resemblances: *Martinia karawanica* Volgin was described from the Late Carboniferous of Fergana, and was also identified from the Myachkovian-Kasimovian faunas of the Carnian Alps. It is similar in size, overall shape and

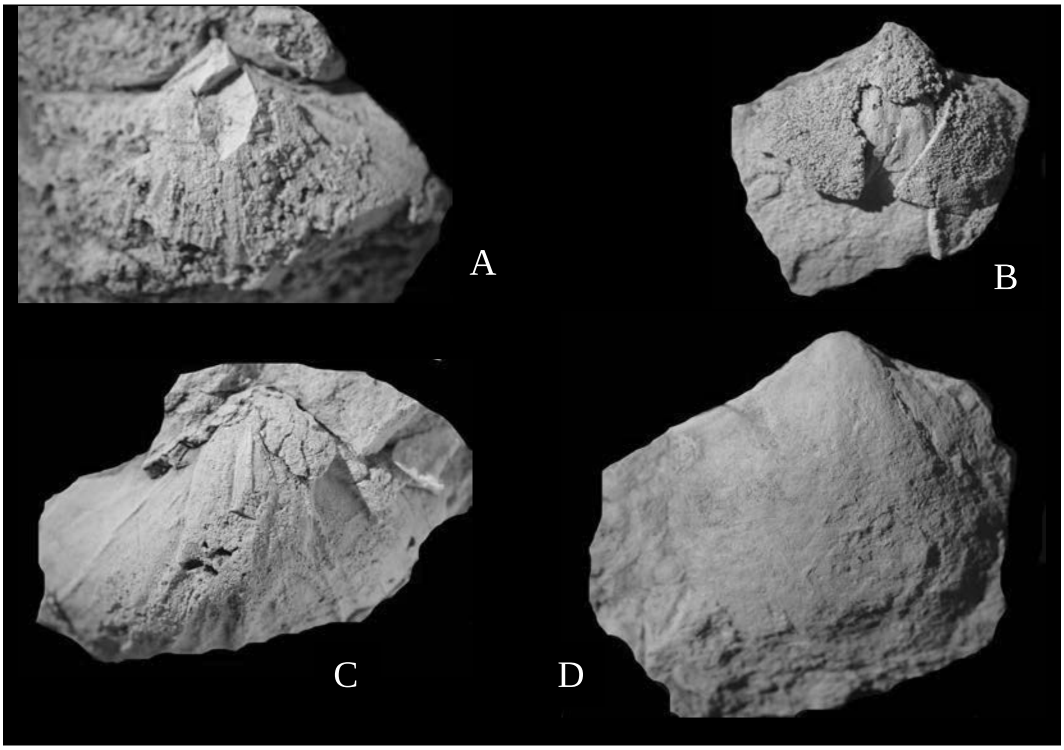


Fig. 260. *Martinia* cf. *karawanica* Volgin. A, ventral internal mould GSC 137097 x1.5, from JBW 585. B, ventral valve GSC 137098 x1.5, from JBW 518. C, ventral internal mould, GSC 137099 x1.5, from JBW 166. D, ventral valve GSC 137100 x1.5, from JBW 504. Member A, Jungle Creek Formation.

prominence of the ventral umbo to present material. Shells identified as *M.* cf. *karawanica* by Martínez-Chacón & Winkler Prins, 1985, p. 447, pl. 4, fig. 11, 12 from the Cantabrian Mountains of Spain appear to have long adminicula in the ventral valve, suggestive of Ingelarellidae.

Martinia sp. A of Gobbett (1964, p. 160, pl. 21, fig. 9, 10) from the Lower Gypsiferous Series of Bashkirian age in Spitsbergen is moderately close although slightly smaller. Gobbett commented that he could find no other described species of *Martinia* to compare with his material. *M*. *tschernyschewi* Grunt in Grunt & Dmitriev (1973, p. 144, pl. 11, fig. 6-9, text-fig. 44, 45) from the Asselian Kizildjilgin Horizon of the Pamirs in central Asia is close in shape and size, but displays a very short anterior ventral sulcus and fold, and more incurved ventral umbo. Grunt in Grunt & Dmitriev (1973, p. 144) referred *Martinia triquetra* not Gemmellaro, 1899 of Tschernyschew (1902, p. 178, pl. 16, fig. 1-6) from the Schwagerina-Kalk near Sim, Urals, to her species, and this has an even more marked ventral sulcus. *Tiramnia canadica* Shi & Waterhouse (1996, p. 149, pl. 29, fig. 5-19) from the "*Yakovlevia transversa*" to *Jakutoproductus verchoyanicus* Zones of the Jungle Creek Formation is slightly less transverse and has only a weakly defined sulcus in only some of the specimens, and low median swelling on the dorsal valve, so that the species is moderately close to *M. karawanika*, but is much less transverse.

***Martinia*? sp.**

Fig. 261

The internal mould of a ventral valve comes from JBW 85, of Member D, Jungle Creek Formation. The specimen is transverse like *Martinia*, rather than elongate like *Tiramnia* or *Mirandifera. Rugivestigia commarginalis* Zone.

Fig. 261. *Martinia*? sp., ventral internal mould GSC 137320 x2, from JBW 85. Member D, Jungle Creek Formation.

Genus ***Mirandifera*** n. gen.

Diagnosis: Narrow subrounded to subpentagonal shells with extended posterior walls, and comparatively well inflated dorsal valve, only slightly less swollen than ventral valve. Mantle canals weakly ramnifying to subreticulate. Micro-ornament of growth lines, prismatic surface in worn material, allied Canadian shell with shallow exopunctate.

Type species: *Martinia miranda* Cooper & Grant, 1976a, p. 2268 from Cathedral Mountain Formation (Kungurian), Texas, here designated.

Discussion: This new genus is discussed in the Appendix on p. 463. The dorsal valve is much more inflated than that of *Tiramnia* Grunt, and it appears there are no dental plates.

Mirandifera wolfcampensis (King, 1931)

Fig. 262

1931 *Martinia wolfcampensis* King, p. 121, pl. 40, fig. 9, 11-13 (part, not fig. 10).
1976a *M. wolfcampensis* – Cooper & Grant, p. 2274, pl. 645, fig. 15-19.

Diagnosis: Strongly incurved ventral valve, broad anterior sulcus with short tongue, convex ventral valve, less convex dorsal valve.

Holotype: YPM 12295, figured by King (1931) and Cooper & Grant (1976a), as in synonymy, from Gaptank Formation, OD.

Material: Two ventral valves and one dorsal valve from JBW 72, one ventral valve from JBW 73 and 762.

Stratigraphic and biostratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Description: Specimens small, the ventral valve with protruding umbo displaying an angle of 95-100º moderately long umbonal walls and well rounded lateral and anterior shell. Specimen GSC 137434 from JBW 72 measures 24mm wide, 21.5mm long and 8mm high. The dorsal valve from JBW 72 is slightly less inflated, with broad umbo of 130º and is raised medianly, GSC 137435 measuring 26mm wide (allowing for breakage), 22mm long and 7mm high. Details of interareas are not available. A ventral sulcus commences towards the anterior third of the shell length and develops low but steep sides and wide almost flat floor, which may be smooth or have very faint radial undulations that may also develop over the anterior lateral shell. Micro-ornament in GSC 137437 from JBW 72 is that of shagreen pattern of fine pits, typical of a number of Martiniinae. Low growth lines appear anteriorly, and one at mid-length of GSC 137436 shows that immature shells were more transverse, and that later growth extended the shell anteriorly.

The ventral muscle field is impressed in the pattern typical of Martininae, with a pronounced median groove, and there are no dental plates, but nothing is shown of mantle canals.

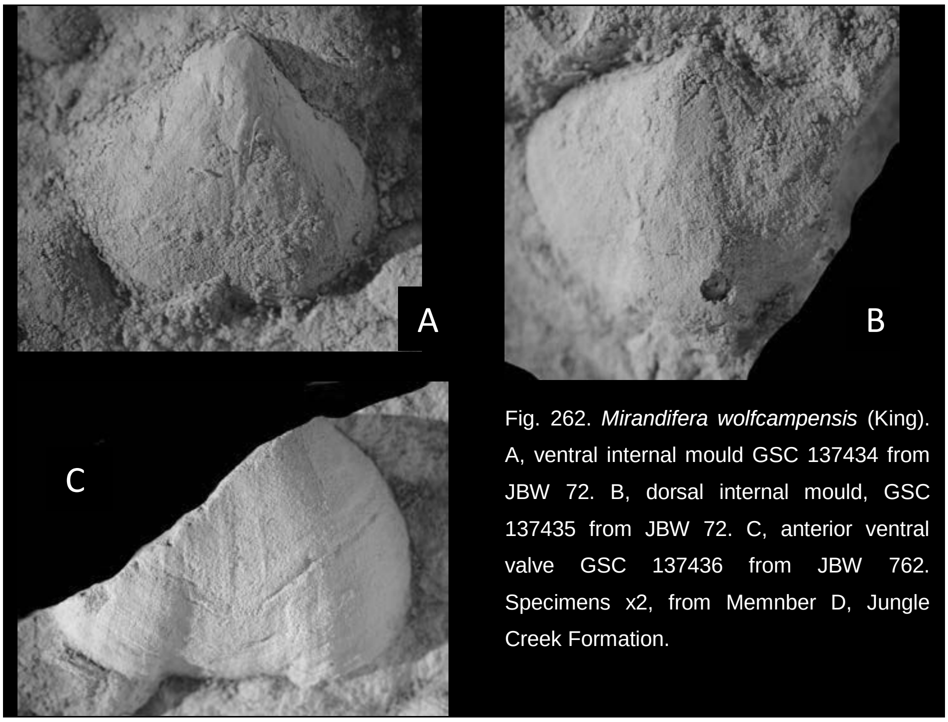


Fig. 262. *Mirandifera wolfcampensis* (King). A, ventral internal mould GSC 137434 from JBW 72. B, dorsal internal mould, GSC 137435 from JBW 72. C, anterior ventral valve GSC 137436 from JBW 762. Specimens x2, from Memnber D, Jungle Creek Formation.

Resemblances: The specimens are close in outline and size to younger specimens described as *Tiramnia canadica* Shi & Waterhouse*,* 1996, p. 149, pl. 29, fig. 5-19, reported as ranging from the "*Yakovlevia transversa*" to

Jakutoproductus verchoyanicus Zones of the younger Jungle Creek Formation. These shells have posterior walls that are straight or weakly concave in outline, and shallow sulcus limited to the anterior shell in some specimens, although others show a narrow median groove, not seen in any of the present specimens. The dorsal valve in *canadica* displays a distinct median arch much as in present material. The species *canadica* was referred to *Tiramnia* Grunt, 1977 by Shi & Waterhouse (1996), a genus characterized by weakly ramiform vascular impressions (Grunt & Grigorieva 1973, fig. 42), whereas those of *canadica* are illustrated as sublinear (see Shi & Waterhouse 1996, pl. 29, fig. 6, 10), approaching those of type *Martinia* (Waterhouse 1981, pl. 30, fig. 6, 7, pl. 31, fig. 1, 3). The difference from type *Martinia* is not great for either type *Tiramnia* or *canadica*, and clarification over other detail, involving micro-ornment and internal plates in the types would be desirable. Type *Martinia* is more transverse than *Tiramnia*, unlike *canadica,* and has a moderately high dorsal valve, relatively higher than that of *Tiramnia*. Dental plates are moderately well developed in type *Tiramnia*, but it was recorded that the teeth were not supported by prominent dental plates in *canadica*. Their development in type *Martinia* remains to be clarified (Waterhouse 2016).

Tiramnia semiglobosa (Tschernyschew 1902, pl. 17, fig. 6-10, 12, 13) from the Sakmarian faunas of the Urals in Russia is slightly more elongate and the dorsal valve is much less inflated than the ventral valve. *Tiramnia uralica* (Tschernyschew 1902, pl. 18, fig. 1-4) is of comparable age, with somewhat similar dorsal valve and highly convex ventral valve. The same is true of specimens assigned to this species by Grunt & Dmitriev (1973, pl. 11, fig. 2-5) from the Barzardin Suite of Sakmarian and lower Artinskian age in the Pamirs of central Asia. Shi & Waterhouse (1996) appeared to indicate that these species were similar to *canadica* in the low relative inflation of the dorsal valve, although this is not apparent from figures (see Shi & Waterhouse 1996, pl. 29, fig. 12, 18).

In the matter of relative dorsal/ventral inflation, the present specimens are closer to a number of martiniiform species from Texas, United States, which are referred to a distinct genus *Mirandifera*, based on *Martinia miranda* Cooper & Grant, 1976a, as explained on p. 463ff. *Martinia wolfcampensis* King from the *Uddenites*-bearing Shale Member of the Gaptank Formation is very close in this regard, and has somewhat similar shape and dorsal arch and sulcus, although the median fold is slightly better defined posteriorly. The holotype, refigured by Cooper & Grant (1976a), shows an anterior tongue for the sulcus comparable to that found in the Canadian specimens. Cooper & Grant also reported a possible specimen from the Neal Ranch Formation of Texas. *Martinia nealranchensis* Cooper & Grant (1976a, pl. 649, fig. 1-14) from the Neal Ranch Formation has a slightly more prominent dorsal fold and concave-floored anterior sulcus, and the shell overall is more transverse. *Martinia renfroae* Cooper & Grant (1976a, p. 2270, pl. 644, fig. 45-49) from the Jacksboro Member of the Graham Formation is also comparatively close, slightly more triangular in shape, with a low median fold in the anterior sulcus.

The present specimens are more rounded in outline than *Martinia* cf. *karawanica* from the *Septospirifer tatondukensis* Zone.

Family **BRACHYTHYRIDAE** Fredericks, 1924b

[Nom. correct. Waterhouse 2016, p. 99 pro Brachythyrididae Pitrat 1965, p. 706, transl. et correct. ex Brachithyrinae Fredericks, 1924b, p. 316].

Diagnosis: Oval usually inflated and biconvex shells with moderately narrow denticulate hinge, ornamented by narrow plicae, radial capillae widespread, but absent from some genera, micro-ornament rarely pustular. Delthyrium variably open or covered by subdelthyrial plate, deltidium or stegidial plates, no adminicula or tabellae. Mantle canal systems appear to be essentially close to those of Martinioidea.

Discussion: Brachythyridoidea was recognized as a superfamily by Carter in Carter et al. (1994), and was placed quite separately from Martinioidea, but still within the massive suborder Spiriferidina. An assessment of the mantle canal system challenges such a long favoured position, because the pattern in type *Brachythyris* is very close to that of type *Martinia*, exhibiting long straight radiating canals in the ventral valve. This is an unusual pattern, differing strongly from the reticulate network of choristitids and trigonotretids, and unlike the densely pitted field typical of spiriferids and the complex mantle canal pattern in ingelarellids. The pattern thus reinforces the information conveyed by the absence of adminicula and tabellae, and severe reduction as a rule in dental plates and crural plates, and shared type of ctenophoridium. Moreover, although Martiniidae was supposed to differ from Brachythyridae through lacking any form of delthyrial cover, the well preserved genus *Spinomartinia* Waterhouse has subdelthyrial plates, and *Beschevella* Poletaev has a delthyrial cover plate. On the other hand, denticles may be developed along the *Brachythyris* hinge. Denticles are widespread amonst younger members of Spiriferidina, as noted in the *Revised Brachiopod Treatise* but are also present in members of Spiriferinidina, such as *Rastelligera* Hector, and indeed the fact that spiriferiforms often have denticulate hinge implies a functional rather than genetic imperative for denticulations.

Brachythyrids are a tiny group, and two families were recognized by Carter (2006c), with another subfamily added in Waterhouse (2004a, p. 234). The family groups are united through the lack of adminicula and tabellae, but differ considerably from each other.

Subfamily **BRACHYTHYRINAE** Fredericks, 1924b

[Nom. correct. Waterhouse 2016, p. 101 pro Brachythyrididae Pitrat 1965, p. 706, nom. correct. pro Brachithyrinae Fredericks, 1924b, p. 316].

Diagnosis: Hinge short, cardinal extremities obtuse, interarea high, delthyrium partly closed by convex deltidial plate, ornament of low open plicae, simple or branching, sulcus and fold may be costate. Micro-ornament subdued, variable, commarginal or radial fila. Mantle canal system, at least in type *Brachythyris*, linear.

Genus ***Brachythyris*** M'Coy, 1844

Diagnosis: Shells small to medium large in size with narrow to moderate sulcus and fold. The sulcus may have faint costae on flanks, or be smooth, and critically, the dorsal fold is smooth. Lateral slopes bear broad plicae and narrow interspaces. Some species are faintly capillate.

Type species: *Spirifera ovalis* Phillips, 1836, p. 219 from Visean of England.

Discussion: According to Carter (2006c, p. 1821), *Brachythyris* is restricted to Devonian – Mississippian. But a few specimens from the basal Jungle Creek Formation – and certainly not as old as Mississippian – agree with *Brachythyris* in costate sulcus and smooth fold. They are only moderately well preserved and the interior is poorly known, but they seem to belong to M'Coy's genus. Perhaps the specimens have reverted to a brachythyrid morphology from *Meristorygma* stock, but species assigned to *Brachythyris* are also known of Pennsylvanian age in northeast Russia.

Brachythyris praeufensis Solomina, 1978

Fig. 263, 264

1971 *Brachythyris* sp. Bamber & Waterhouse, pl. 11, fig. 6, 8.
1978 *Brachythyris praeufensis* Solomina, p. 117, pl. 10, fig. 9, pl. 11, fig. 1.
1983 *B. praeufensis* – Abramov & Grigorieva, p. 133, pl. 29, fig. 4, 5, text-fig. 51.
2005 *B. praeufensis* – Klets, pl. 29, fig. 6-11.

Diagnosis: Large shells with two subplicae in sulcus, broadly convex smooth fold, five to nine pairs of lateral plicae.

Holotype: TsNIGRA no. 271-7/11540, Sider Suite (Late Carboniferous), north Orulgania, Russia, OD.

Material: Single ventral valves from JBW 84, 122, ?173, 417, 585, 648, 649, GSC 57143 and 57155, two ventral valves from JBW 518, dorsal valve from JBW 764, ventral and dorsal valve from JBW 611, and three specimens each with valves conjoined from JBW 197 and 628, and one from JBW 84. Specimen GSC 26907 from GSC 57155 and GSC 26908 from GSC 57143.

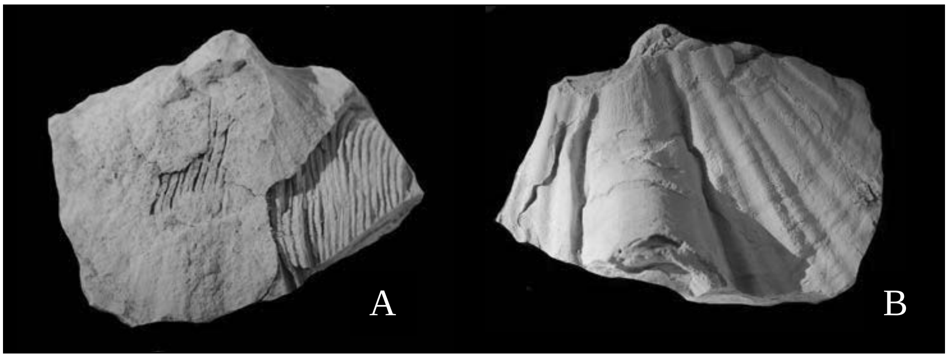


Fig. 263. *Brachythyris praeufensis* Solomina. A, B, ventral and dorsal aspects of specimen with valves conjoined, GSC 137101 x1, from JBW 197. Member A, Jungle Creek Formation.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Dimensions in mm:

Specimen	Width	Length	Height both valves	Height ventral valve	Locality
GSC 137102	59	50	29	17	JBW 628

Description: Shells elongate, ventral umbo slightly extended, weakly incurved, umbonal angle of 80-90º, posterior umbonal walls low and steeply convex, sweep out laterally to obtuse cardinal extremities, ventral interarea clearly delimited, marked by growth striae, concave under umbo, delthyrium wide with angle of 100º in specimen from JBW 628, closed by large convex plate bearing growth rugae, with angle of 70º under the umbo, and sides flaring laterally. Maximum width lies at mid-length. Ventral sulcus commences 10mm in front of umbo, shallow with broad floor, widens at angle of 20º, and anteriorly bears two broad costae, one each side, or only one on one side in a rare asymmetric specimen. Dorsal valve of similar inflation, with low broad convex fold, for which the flanks curve out anteriorly: on some specimens the fold crest remains entire, in others a median groove appears anteriorly. Ventral valve ornamented by five up to eight pairs of low round-crested plicae, separated by interspaces with slightly angular-floors. Dorsal valve with four pair of similar plicae and relatively wider interspaces: the outermost pair on each pair commences well forward. Micro-ornament consists of fine growth increments, up to fifteen in 1mm anteriorly. Fine radial fila appear on the worn surface, probably reflecting internal shell structure, with the suggestion of small subelongate dimples and perhaps pustules, due to wear of the shell surface.

No adminicula, but interior otherwise obscure. Dorsal valve has low median septum extending for a fifth of

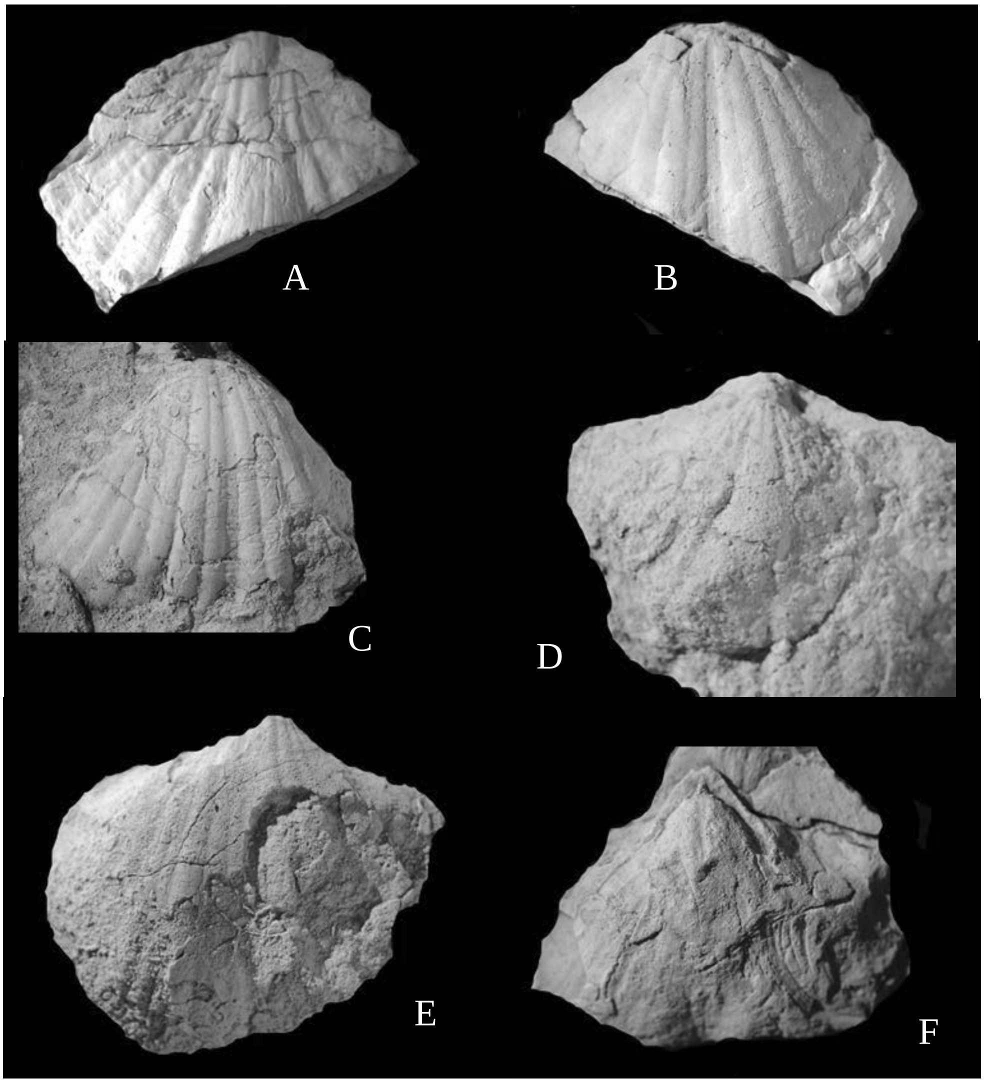


Fig. 264. *Brachythyris praeufensis* Solomina. A, B, dorsal and ventral aspects of specimen with valves conjoined, GSC 137102 x1, from JBW 197. C, ventral valve GSC 137103 x1, from JBW 417. D, E, dorsal and ventral aspects of specimen with valves conjoined, GSC 137104 x1, from JBW 628. F, ventral valve GSC 137105 x1.5, from JBW 122. Member A, Jungle Creek Formation.

the valve length, and lacks tabellae. The spire has fourteen coils in one specimen and well over twenty in another more mature specimen.

Resemblances: *Brachythyris praeufensis* Solomina, 1978 was originally described from the Cizder Suite of Orulgania, and further material described from the Late Carboniferous Surkechan Suite of south Verchoyan (Abramov & Grigorieva 1983; Klets 2005, pl. 29, fig. 6-11). The specimens from south Verchoyan described by Abramov & Grigorieva (1983) have two strong sulcal subplicae, much less evident in the specimens figured by Klets (2005). The Klets specimens have up to nine pairs of lateral plicae, slightly finer than in present material, but lateral pairs are fewer in the Abramov-Grigorieva figured material, closer to the Canadian specimens. Dark strips close to the mid-line in the Klets figures suggest possible internal plates resting on the floor of the valve, but this may be an effect due to the lighting.

Genus ***Meristorygma*** Carter, 1974

Diagnosis: Medium to large, moderately developed sulcus and fold, ribs clearly defined, sulcal ribs bifurcating from sulcal bounding ribs in type species, fold bearing well defined ribs, micro-ornament of growth increments, hinge not denticulate, ventral muscle field impressed, posterior shell thick.

Type species: *Meristorygma arctica* Carter, 1974, p. 689 from Atokan of Ellesmere Island, Canadian Arctic Archipelago, OD.

Discussion: Carter (2006c) stated that no micro-ornament was present, but the present Canadian material reveals the presence of fine commarginal growth filae.

Meristorygma sp. A

Fig. 265

?1971a *Brachythyris* sp. Waterhouse, pl. 11, fig. 6, 8.

Material: Single dorsal valves from JBW 82 and ventral valve from JBW 518.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

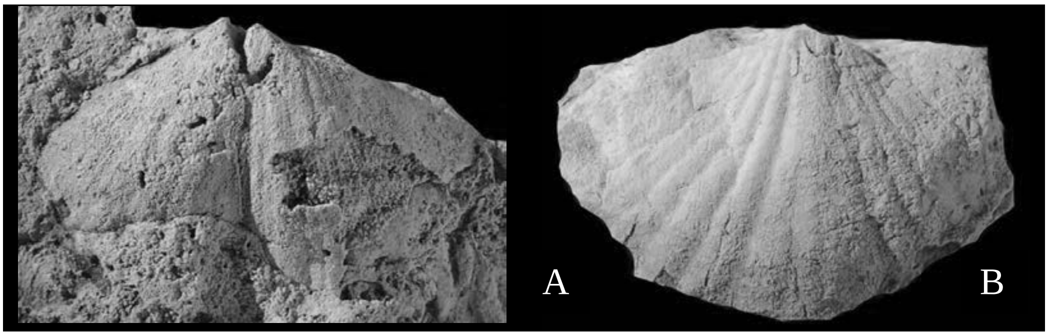


Fig. 265. *Meristoryga* sp. A, damaged ventral valve GSC 137094 x1.5, from JBW 518. B, dorsal valve GSC 137107 x1.5, from JBW 82. Member A, Jungle Creek Formation.

Description: Ventral valve with plicae and sulcal subplicae. Dorsal valve with low broad convex fold, bearing three broad costae anteriorly. Micro-ornament consists of fine growth increments, up to fifteen in 1mm anteriorly.

Resemblances: The type species of the genus, *Meristorygma arctica* Carter (1974, pl. 3, fig. 21-30, text-fig. 4; Carter & Poletaev 1998, p. 171, Fig. 27.11-27,14) from the Hare Fiord Formation (Atokan) of northwest Ellesmere Island, Canadian Arctic Archipelago, is smaller and slightly more elongate, with much better defined sulcal and fold ribs, though similar in many aspects. The same applies to the species *panduriformis* (Kutorga), figured also by Tschernyschew (1902, pp. 162, 549, pl. 7, fig. 1, pl. 8, fig. 2, pl. 13, fig. 3, 4) from the Schwagerina-Kalk of the Urals, and *Spirifer uralicus* Tschernyschew 1902, pp. 164, 549, pl. 38, fig. 9, pl. 49, fig. 4) from the same region. *Spirifer ufensis* Tschernyschew (1902, pp. 165, 551, pl. 13, fig. 5, pl. 15, fig. 1, pl. 38, fig. 6-8, pl. 39, fig. 1-3) is a little more transverse, but still elongate. Ventral valves identified with *Brachythyris* in Bamber & Waterhouse (1971, pl. 11, fig. 2, 6, 8) from the upper Ettrain Formation and *Orthotichia-Septospirifer* Zone of the Jungle Creek Formation in Yukon Territory might belong to *Brachythyris* or *Meristorygma*, but the ventral valve is more elongate than in the present species, and the dorsal valve is not figured, hindering further analysis.

***Meristorygma*? sp. or spp. B**

Fig. 267

Material: Two ventral valves from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Description: One specimen from JBW 18 measures approximately 57mm in width, 39mm long and 16mm high: the other is 50mm wide, 39mm long and 16mm high. Umbo extended beyond the hinge, with low steep umbonal walls curving out to obtuse cardinal extremities, maximum width near mid-length, interarea present but obscure, delthyrium obscure, sulcus narrow with angle of 15º, very shallow, occupied by two subplicae, seven pairs of low round-crested plicae laterally, interspaces narrow. The other specimen as here figured has finer plicae, numbering up to twelve pair, with narrow crests and wider interspaces, including several subplicae pairs in the sulcus.

Resemblances: The specimens are close in size and shape to those from the underlying faunas of the *Septospirifer tatondukensis* Zone, but have numerous and less well defined plicae that are especially subdued within the sulcus. They therefore can only doubtfully be assigned to Brachythyrinae, and each might belong to a different species.

Fig. 266. *Meristorygma*? sp. B, ventral valve GSC 137106 x1, from JBW 18, Member C, Jungle Creek Formation.

***Meristorygma*? sp. C**

Material: Dorsal fragment from JBW 100.

Stratigraphic and biostratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Description: The dorsal valve GSC 137142 from JBW 100 appears to have some ten pair of narrow plicae, the inner two pair subdivided, and the low fold bears a median groove and four narrow costae each side.

Resemblances: The specimen is close in size and shape to those from the underlying faunas of the *Septospirifer tatondukensis* Zone, but has more numerous and less well defined plicae that are especially subdued within the sulcus. It can only doubtfully be assigned to *Meristorygma*.

Infrasuborder CHORISTITIMORPHI Waterhouse, 2016

[Choristitimorphi Waterhouse, 2016, p. 112].

Diagnosis: Shells of characteristic shape, roundly suboval to slightly rectangular or subtriangular in outline, with broad incurved ventral umbones, weakly to moderately defined sulcus and fold, and usually well extended and well rounded antero-lateral margins. Broad or fine subequal strap-like ribs with flat crests and narrow interspaces cover entire shell as a rule, may be finer within sulcus and over fold. In many genera posterior broad flat-crested ribs splay anteriorly into a few finer costae. Micro-ornament usually of growth increments, may be capillate or pustulose. Delthyrium open or with deltidial or stegidial plates, dental plates usually well developed with supporting adminicula, rarely lost, tabellae long to short or absent; vascular canals may be reticulate, but rarely preserved. Hinge denticles in some younger genera.

Discussion: This infrasuborder is related to Martiniimorphi through the possession of tabellae in several genera, and is thereby distinguished from Spiriferidina. The group differs from Martiniimorphi through its distinctive shape and mode of costal development, as further discussed in Waterhouse (2016).

Superfamily **CHORISTITOIDEA** Waterhouse, 1968b

[Nom. transl. et correct. Waterhouse 2016, p. 125 ex Choristitidae transl. & correct. Ivanova 1972, p. 40 ex Choristitidinae Waterhouse, 1968b, p. 9].

Diagnosis: Shells may be weakly plicate, broadly costate or subcostate, micro-ornament weak, usually of low growth increments and often radial capillae. Dental plates and adminicula variably developed, tabellae may be present.

Discussion: Choristitoids are common in the higher latitudes of the northern hemisphere in faunas of Carboniferous and Permian age, but are missing from Permian faunas of United States, developed in low paleolatitudes, and from high southern paleolatitudes during Permian time in Gondwana, though present there in the earlier Carboniferous.

Family **CHORISTITIDAE** Waterhouse, 1968b

[Nom. transl. et correct. Ivanova 1972, p. 40 ex Choristitidinae Waterhouse, 1968b, p. 9].

Diagnosis: Shells transverse or elongate, ribbing fine with flattened crests, interspaces narrow as a rule, micro-ornament commonly capillate, denticulate hinge, adminicula usually long, may be short or absent, no tabellae, mantle canal system distinctive.

Discussion: Tabellae are not developed in this family. Carter (2006a, p. 1780) included Angiospiriferinae Legrand-Blain, 1985, but *Angiospirifer* of Visean to Bashkirian age has different ornament and different mantle canal system and delthyrial arrangement, as discussed by Waterhouse 2016, pp. 238ff. Waterhouse (2004a, p. 180) showed that the presence and nature of the mantle canal system, apical callosity, and subimbricated micro-sculpture in *Angiospirifer* indicated alliance with Trigonotretidae of Spiriferidina, rather than Choristitidae.

Subfamily **CHORISTITINAE** Waterhouse, 1968b

[Nom. correct. Ivanova 1972, p. 40 pro Choristitidinae Waterhouse, 1968b, p. 9].

Diagnosis: Hinge comparatively wide, adminicula subparallel.

Genus ***Ala*** Nalivkin, 1979

Diagnosis: Large transverse shells with well defined fold, multicostate, with numerous bifurcating costae over fold and broad sulcus.

Type species: *Ala tau* Nakivkin, 1979, p. 135 from Tournaisian of Ural Mountains, Russia, OD.

Ala alatiformis n**.** sp.

Fig. 267

1971 Choristitinid sp. Bamber & Waterhouse, pl. 11, fig. 10.

Derivation: ala – wing, formis – shaped like, Lat.

Diagnosis: Large transverse shells with comparatively simple ribbing.

Holotype: GSC 137108, here designated.

Material: A damaged specimen with valves conjoined from JBW 647 (Member D or E?) and ventral valve from JBW 722, Member A. Five ventral valves from GSC locality 57143 in Member A.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Equivalents of Member D or E, *Rugivestiga commarginalis* or *Ogilviecoelia shii* Zone.

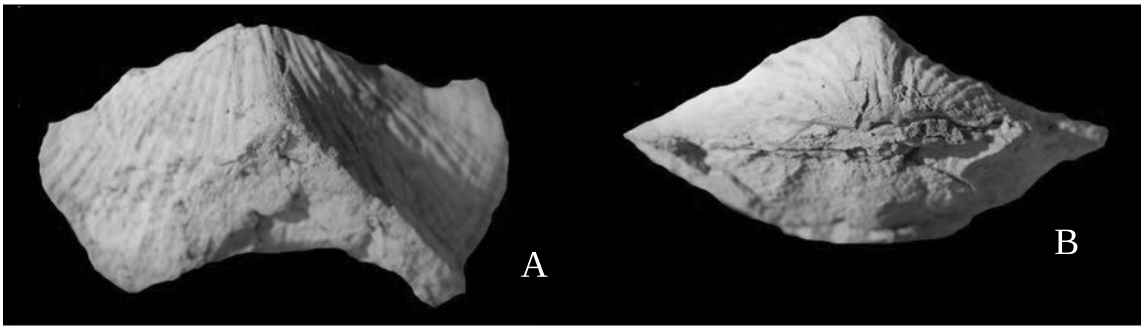


Fig. 267. *Ala alatiformis* sp. A, B, C, dorsal, posterior aspects (x0.6) and anterior ventral aspect (x1) of specimen with valves conjoined, GSC 137108 holotype, from JBW 647, Member E or D?, Jungle Creek Formation.

Description: The holotype from JBW 647 is large and transverse, some 103mm wide, with possible length no more than 60mm, and height of nearly 60mm. The hinge is wide with obtuse cardinal extremities, moderately well defined and raised dorsal fold, and very wide ventral sulcus anteriorly. Costae are broad with wide flat crests and narrow interspaces, and split without change in angle, in the manner typical of Choristitoidea. The ventral interarea is gently concave and wide with delthyrium widening at an angle of 50º, but most of the dental plates and all of the adminicula have been destroyed. There is a short dorsal median septum, and no tabellae. The ventral valve from JBW 722 has high adminicula and delthyrium of 60º. A somewhat similar large ventral valve was figured in Bamber & Waterhouse (1971) from GSC locality 57143 in the *Orthotichia-Septospirifer* Zone, now *Septospirifer tatondukensis* Zone, at section 116C-2.

Resemblances: The sulcus is wider with more costae than in *Ala tau* Nalivkin from the Early Carboniferous of the Urals, and the dorsal fold is less strongly costate. Fascicles are more prominent in the Russian species, with separate high costae present in twos and threes.

Family **PALAEOCHORISTITIDAE** Carter, 1994

[Palaeochoristitidae Carter in Carter et al., 1994, p. 334].

Diagnosis: Ribbing, micro-ornament with or without radial fila, may be pustulose. Ctenophoridium, adminicula and tabellae well developed. Delthyrial plate absent or rudimentary.

Discussion: Palaeochoristitidae is distinguished in part by the presence of tabellae. The definition is broadened from that of the *Revised Brachiopod Treatise*, which restricted the family group to genera without radial fila.

Subfamily **JUNGLELOMIINAE** Waterhouse, 2016

[Junglelomiinae Waterhouse, 2016, p. 133].

Diagnosis: Shells moderately large with broad hinge and wide-crested costae, capillate micro-ornament, and well formed sulcus and fold. Tabellae in the dorsal valve.

Discussion: The subfamily, named from *Junglelomia* Waterhouse 2016, p. 133 from basal Jungle Creek Formation (Gzhelian) of Yukon Territory, differs from members of Palaeochoristitinae through its well-developed sulcus and fold, broader ribs and capillate non-pustulose micro-ornament.

Genus ***Junglelomia*** Waterhouse, 2016

Diagnosis: Hinge wide, costae may show minor fasciculation, often flat-topped, fold and sulcus well formed and costate. Adminicula short to medium length, tabellae of medium length to long.

Type species: *Junglelomia ursus* Waterhouse, 2016, p. 133 from basal Jungle Creek Formation (Gzhelian), Yukon Territory, Canada, OD.

Discussion: This genus is of Pennsylvanian and Early Permian age, and is distinguished by the wide hinge and well formed sulcus and fold. One constituent species was initially described as belonging to *Domokhotia* Abramov & Grigorieva, 1983, but this genus does not have tabellae. It appears to have been reidentified as *Neomunella* Ozaki by Carter (2006a, p. 1780), probably because of its wide hinge, but this genus also lacks tabellae. *Parachoristites* Barchatova, 1968 from Pennsylvanian and Cisuralian faunas of Timan, Russia, has shorter tabellae, and is large in size. It is further distinguished by the hinge at maximum width, with alate cardinal extremities through early and early mature growth stages, whereas cardinal extremities are obtuse as a rule in early stages in *Junglelomia*.

Junglelomia ursus Waterhouse, 2016

Fig. 268 - 274

2016 *Junglelomia ursus* Waterhouse, p. 133, Fig. 144-148.

Diagnosis: Moderately large and transverse shells with broad plicae splitting into two or three costae, sulcus shallow and fold low, both costate.

Holotype: GSC 136654, figured in Waterhouse (2016, Fig. 147B) and Fig. 274B herein, from Member A (Gzhelian), Jungle Creek Formation, Canada, OD.

Material: From Member A, single ventral valves from JBW 84, 93, 172, 173, 187, 190, 412, 503, 536, 610, 647, 649, 667, 675, ?686, 800, 804, 811, 814, 1007, two ventral valves from JBW 533 and 742, single dorsal valve from JBW 562 and 787, single specimens with valves conjoined from JBW 125, 536, 647 and 735, one ventral valve, a dorsal valve and specimen with valves conjoined from JBW 82 and ventral and dorsal valve from JBW 591. Two ventral valves from JBW 615, five ventral valves from JBW 433, two specimens with valves conjoined and ventral valve from JBW 504, two ventral valves and specimen with valves conjoined from JBW 648. From Ettrain Formation, ventral valve from JBW 656, and two specimens with valves conjoined from JBW 671, as well as GSC locality 26930.

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Description: Specimens large and transverse, ventral umbo extended a little beyond hinge and incurved, with angle of 70-85º, ventral interarea of moderate height and curved postero-ventrally, with delthyrium covered only under the umbo by convex delthyrial plate, postero-ventrally inclined; dorsal interarea lower and postero-dorsally inclined, hinge slightly less than maximum width which is placed near mid-length, cardinal extremities overall obtuse, but may be slightly produced. Posterior walls convex in profile, steep posteriorly and becoming low in front. Sulcus commences at umbo and in most specimens has an angle between 15º and 25º, and in largest specimen flares out after shell reaches a width of 70mm, to protrude dorsally as an angular tongue. Dorsal valve much less inflated, close to a third of height of ventral valve, and in the largest specimen (Fig. 270A, 271C) the lateral extremities curve slightly outwards, with wide hinge. The fold is narrow and sharply defined with broad gently rounded crest, widening at an angle of 20º. Ventral ornament consists of some eight primary broad costae (or subplicae – the ribs are often coarser than costae, and finer than plicae) with broad gently convex crests and narrow interspaces, although near the umbo the crests are narrow and interspaces may be wider.

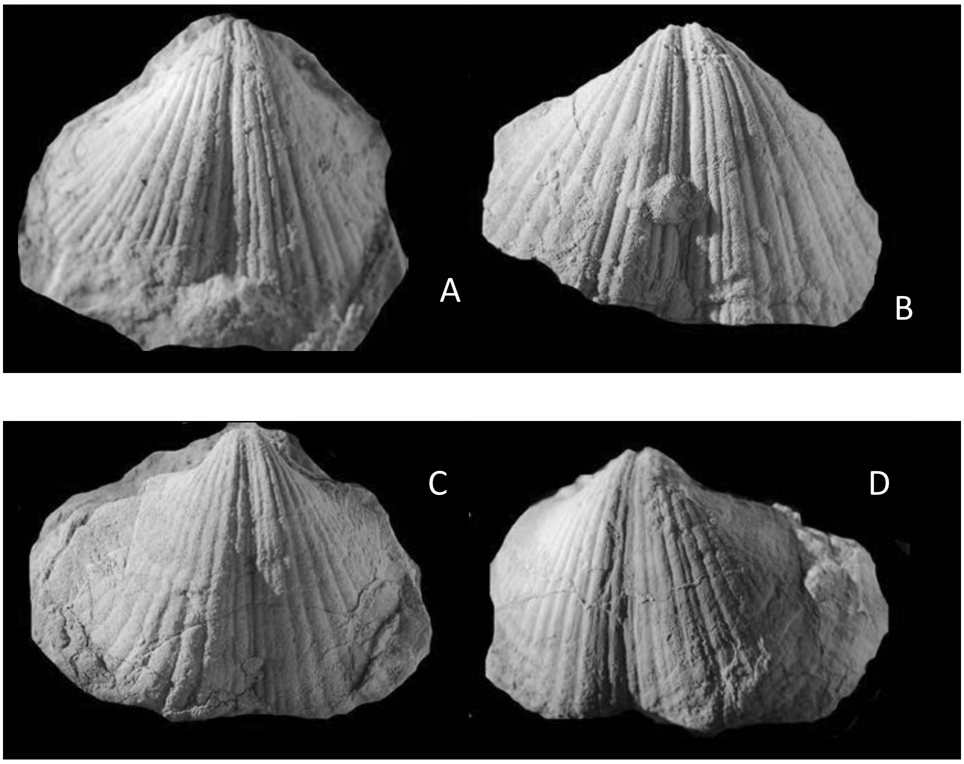


Fig. 268. *Junglelomia ursus* Waterhouse. A, ventral valve GSC 136649 from JBW 533. B, ventral valve GSC 136648 from JBW 172. C, ventral valve GSC 136647 from JBW 172. Member A, Jungle Creek Formation, x1 approx. D, ventral valve GSC 136650 x1 from JBW 656, Ettrain Formation.

A fine costa traverses the sulcus, and the inner primary ribs may subdivide into several finer costae. The lateral flanks are comparatively smooth over the immature shell, but may become costate in larger specimens. The primary ribs become fasciculate anteriorly, so that the ornament is more bundled in some shells than is usual for other species within the genus. Dorsal ornament is similar, and the fold is simple posteriorly and raised with defined lateral edges, and the crest becomes costate within 20mm. On the largest specimen, there are six additional ribs laterally, but the outermost shell near the cardinal extremities remains smooth. Micro-ornament is cancellate with radial and commarginal capillae. Some specimens suggest the presence of tiny pustules or pits, and these may reflect prismatic structure in the shell.

Delthyrium bordered by low ridge which passes into small tooth, supported by low inwardly concave dental plates, converging inwards, supported in turn by adminicula which diverge outwards to the floor of the valve, extending well in front of the teeth. Muscle field compact, placed in front of the adminicula, marked by broad longitudinal ridges and narrow grooves, with limited distinction between adductor scars and diductor impressions. Secondary thickening fills the umbonal shell cavity, almost burying the adminicula, and the valve floor carries pits in some specimens each side of the adminicula and vascular ribs in others. There is no umbonal callosity.

Dorsal socket plates enclose narrow sockets, each side of a broad laminate ctenophoridium, which is supported in front by a narrow median ridge that extends over the posterior fourth to third of shell length. Tabellae are well formed, and extend each side of the fold for up to a quarter of the length of the valve. Adductor impressions lie well forward, elongately subrectangular in outline, with light longitudinal striae. Shell floor with little thickening, showing the external ribbing, and bearing light small pustules. Spire with twenty five coils.

A large number of specimens are small and less transverse, but they cannot be distinguished from early growth stages of mature specimens, and are therefore regarded provisionally as juveniles. These specimens are smaller and narrower than mature *ursus*, but agree in essential detail of the exterior.

Resemblances: The closest of species so far described appears to be that described as *Domokhotia junglensis* Shi & Waterhouse, 1996, p. 140 from the upper Jungle Creek Formation (Sakmarian) of Yukon Territory, Canada, with its similarly wide hinge, broad costae and rather long tabellae. As a rule the species has broad costae, which in many

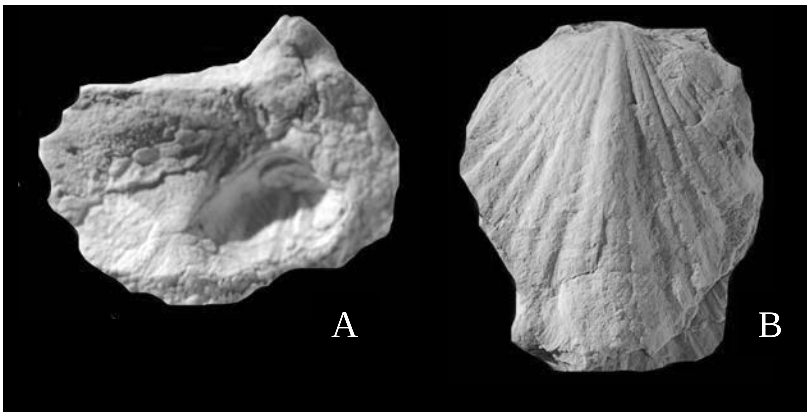


Fig. 269. *Junglelomia ursus* Waterhouse. A, fragment of ventral valve, GSC 136652, x1.5, showing muscle scars and somewhat broken and buried plates. B, dorsal valve, GSC 136653, x1.5. Specimens from JBW 503. Member A, Jungle Creek Formation.

individuals do not subdivide anteriorly, especially on the ventral valve, and the dorsal fold is better defined and higher. Tabellae are shorter in the present form, compared with the tabellae in *junglensis*. The present species also looks moderately close to shells described as *Larispirifer ettrainensis* Shi & Waterhouse (1996, p. 141, pl. 26, fig. 15-20, pl. 27, fig. 1-7, text-fig. 49) from the "*Yakovlevia transversa*" to *Jakutoproductus verchoyanicus* Zones of the younger Jungle Creek Formation. This species has a slightly deeper ventral sulcus with slightly less emphasized median groove, and the dorsal fold has more costae anteriorly, whereas the fold of the present form tends to become smooth. As far as is known, there are no tabellae in *ettrainensis*.

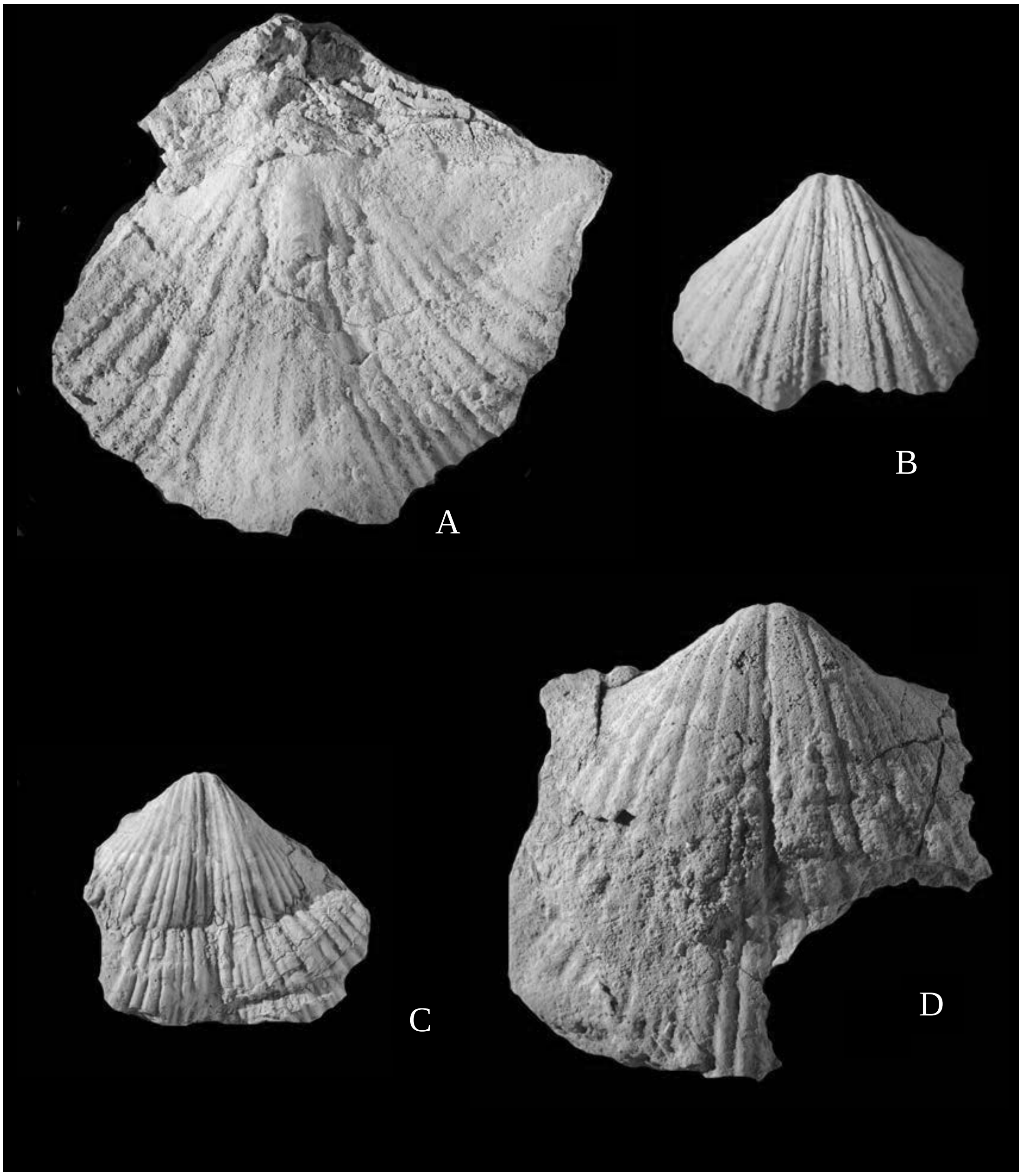


Fig. 270. *Junglelomia ursus* Waterhouse. A, dorsal view of squashed specimen with valves conjoined, GSC 137109 x1, from JBW 504. B, ventral valve GSC 137110 x1, from JBW 93. A, B, from Member A, Jungle Creek Formation. C, ventral valve GSC 137112 x1, from JBW 671, Ettrain Formation. D, ventral valve GSC 137111 x1 from JBW 504. Member A, Jungle Creek Formation.

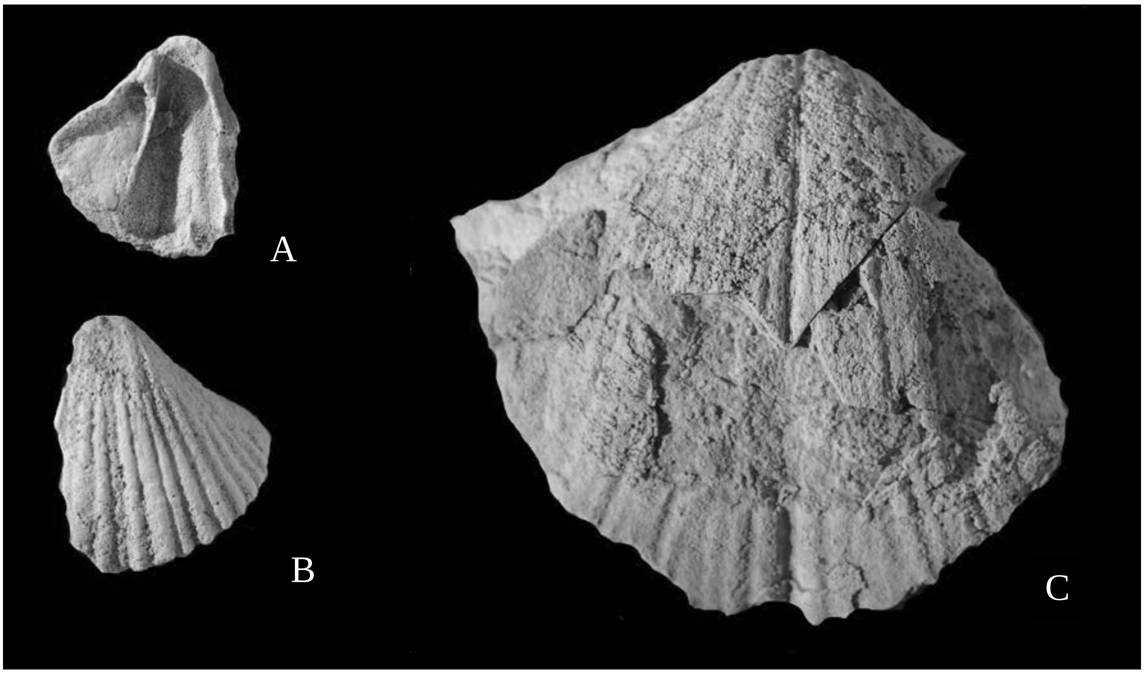


Fig. 271. *Junglelomia ursus* Waterhouse. A, B, internal and external aspects of small ventral valve, GSC 137113 x2, from JBW 671. Ettrain Formation. C, ventral view, squashed specimen with valves conjoined, GSC 137109 x1, from JBW 504. (See Fig. 270A). Member A, Jungle Creek Formation.

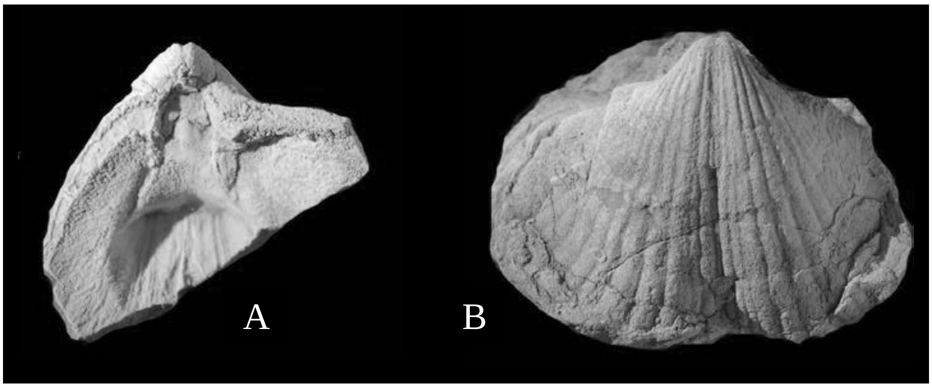


Fig. 273. *Junglelomia ursus* Waterhouse. A, interior of small ventral valve, GSC 137114 x1, from JBW 503. B, ventral valve GSC 137115 x1, from JBW 172. Member A, Jungle Creek Formation.

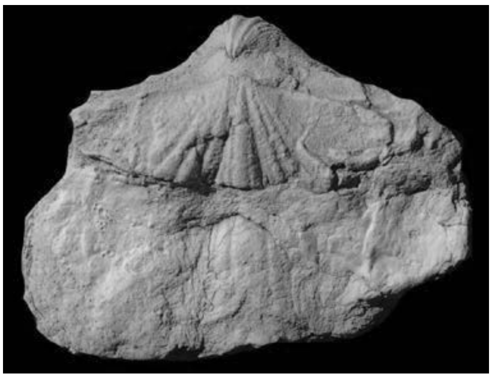


Fig. 273. *Junglelomia ursus* Waterhouse. A, dorsal aspect of specimen with valves conjoined, GSC 136648 x1, from JBW 172. Member A, Jungle Creek Formation. See Fig. 268B.

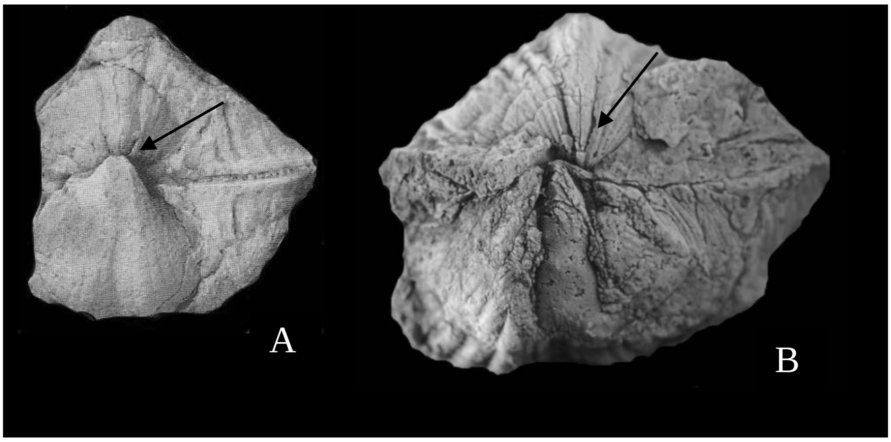


Fig. 274. *Junglelomia ursus* Waterhouse*,* Posterior view of specimens with both valves splayed open, dorsal valve on top, x1. A, GSC 26885 from GSC locality 26930, Ettrain Formation (from Bamber & Waterhouse 1971). B, GSC 136654, holotype, from JBW 640, Member A, Jungle Creek Formation. Arrows point to tabellae.

Junglelomia simplex n. sp.

Fig. 275, 276

Derivation: simplex – simple, plane, Lat.

Diagnosis: Small with ornament of broad simple ribs and narrow interspaces.

Holotype: GSC 136651, here designated.

Material: Single ventral valves from JBW 78, 172, 615, 640, 667, 800 and 804. Five specimens from JBW 172, and three from 804 (Member A). Allied specimen with valves conjoined from JBW 581 (Member E). Specimen with valves conjoined and ventral valve from JBW 620 and two ventral valves from JBW 686, Ettrain Formation.

Stratigraphic and biostratigraphic levels: Member A and aff. Member E, Jungle Creek Formation. *Septospirifer tatondukensis* Zone, aff. *Ogilviecoelia shii* Zone. Ettrain Formation.

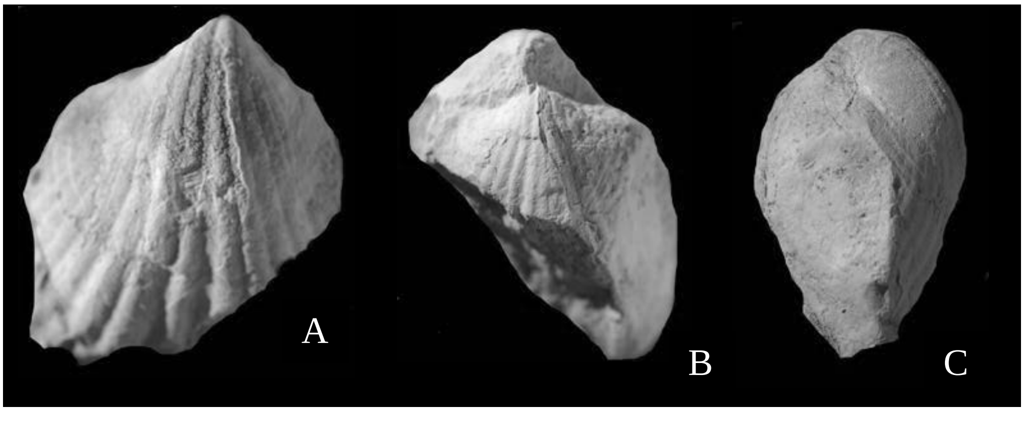


Fig.. 275. *Junglelomia simplex* n. sp.. A, B, C, ventral, dorsal and lateral views of GSC 136651, holotype from JBW 620, Ettrain Formation, x1.5.

Description: Subpentagonal shells with prominent ventral umbo bearing angle of 80 to 100º, posterior walls concave in outline, concave interarea, delthyrium obscure. The sulcal angle measures 25-30º. Specimen from Member A measures 37mm in width and length, but may well represent only the posterior portion of a much larger shell. Plicae are broad and ill-defined, occurring in three to five pairs with broad flat to gently convex crests and shallow narrow interspaces, and one or two very subdued ribs laterally. In one specimen, the plicae subdivide anteriorly. The sulcus is traversed by two low costae, of uneven strength. Four costae on dorsal fold.

Adminicula diverge forward narrowly, extend for about one fifth of shell length. Heavy posterior thickening and shell thickened in front. Tabellae slender in GSC 136651 and diverge at low angle along the lower slopes of the fold, extending for nearly one fourth of the length.

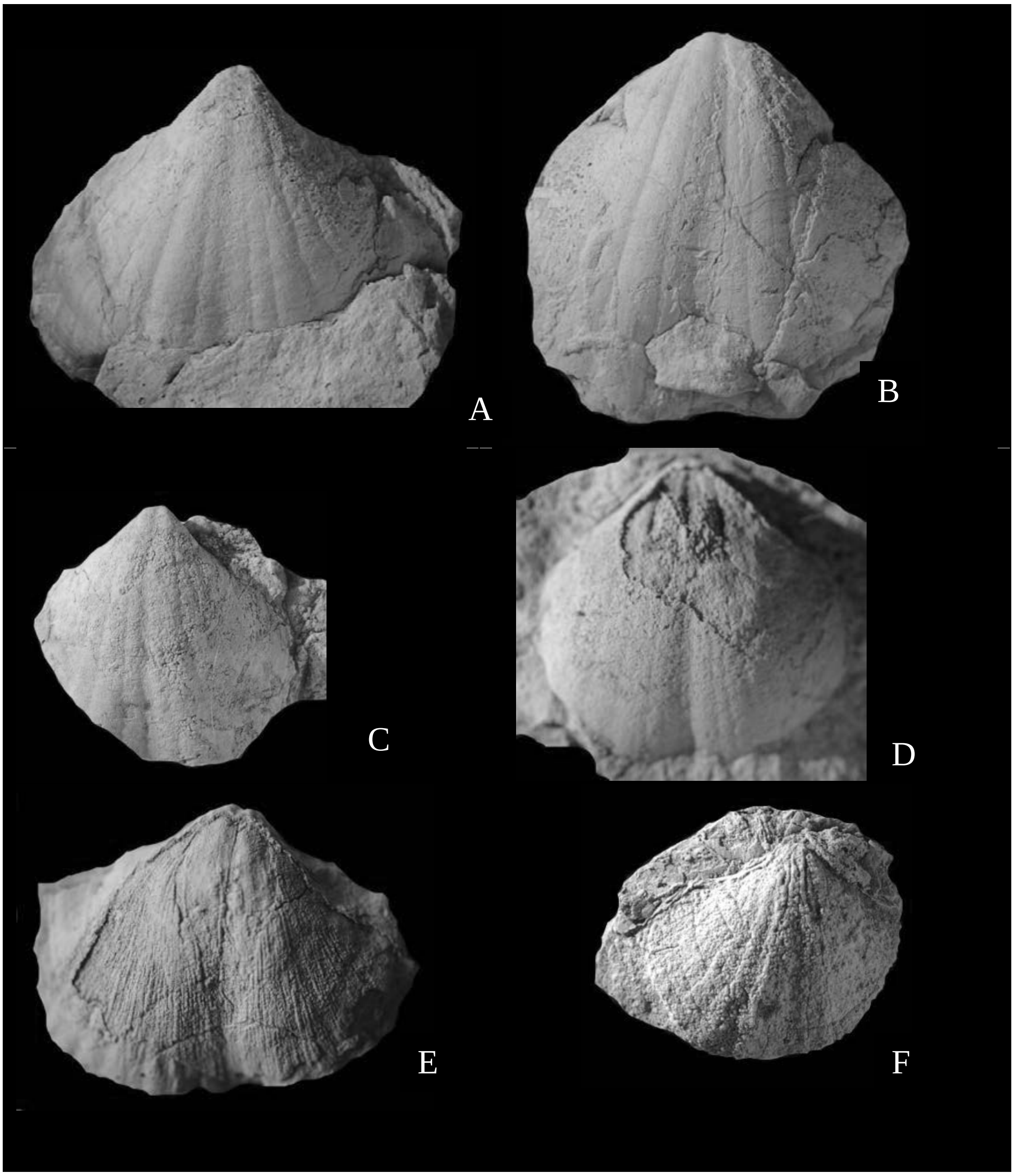


Fig. 276. *Junglelomia simplex* n. sp. A, ventral valve GSC 137116 from JBW 172, x2. B, ventral valve GSC 137119 from JBW 667. Member A, Jungle Creek Formation. C, ventral valve GSC 137118 from JBW 620. D, ventral valve GSC 137117 from JBW 686, E, ventral valve GSC 137120 from JBW 686. C-E from Ettrain Formation. F, ventral aspect of specimen with valves conjoined, GSC 137121 from JBW 581, Member E, Jungle Creek Formation. Specimens x 1.5, except Fig 276A, x2.

A specimen from JBW 581 is similar in shape, and has slightly better defined plicae that are narrower with wider interspaces, and better defined laterally. The sulcus is simple with angle of 20º and the fold bears four costae. Adminicula are like those of the older specimens, diverging forward at an angle of 17º, for less than a third the length of the shell. The dorsal valve has been crushed, but shows that tabellae are present, pointing to an identification with *Junglelomia*.

Resemblances: This species is distinguished by the few broad simple ribs without costae.

Genus ***Ettrainia*** n. gen.

Derivation: From Ettrain Creek, Yukon Territory.

Diagnosis: Small subpentagonal shells characterized by ornament of fine numerous ribs, shallow sulcus and low broad fold, tabellae one fifth of the length of shell.

Type species: *Ettrainia costellata* n. gen., n. sp. from basal Jungle Creek Formation, Ogilvie Mountains, Canada, here designated.

Discussion: This genus is distinguished by the numerous fine ribs, and the low poorly defined dorsal fold that merges anteriorly with the lateral flanks. The type species has costellae approaching those of *Gibbospirifer ettrainensis* Waterhouse (1971a, pl. 27, fig. 6-12), but is readily distinguished by its lower plicae that fade anteriorly, and the less groove-like sulcus, lower broader dorsal fold, less plicate dorsal valve, and presence of tabellae. Another species of *Gibbospirifer* was illustrated in Waterhouse (2016, p. 192, Fig. 235).

Ettrainia costellata n. sp.

Fig. 277 - 279

Derivation: costa - rib, Lat.

Diagnosis: Small subequilateral shells with low fold, weak posterior plication and very fine costellae.

Holotype: GSC 137125, here designated.

Material: Four ventral valves and two dorsal valves from JBW 18, dorsal valve from JBW 501.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Description: Specimens are weakly to moderately transverse, the largest but incomplete specimen measuring 51mm wide, 38mm + long, and 20mm high. The ventral umbo projects a little beyond the hinge, with an angle of 75º, and the hinge is wide, with obtuse cardinal extremities, and very high interarea bearing horizontal and vertical striae, disrupted by a delthyrium with angle of 50º, and bordered by low dental ridges. As far as can be seen, the delthyrium is open, without a connector plate. Maximum width of the shell lies a little in front of the hinge. The dorsal valve is less inflated, with low very broad umbo measuring 125º. A narrow and shallow sulcus extends from the ventral umbo with angle of 20-25º, and the dorsal fold is almost imperceptible posteriorly, and low and broad over the anterior half, scarcely differentiated from the lateral flanks. The valve is covered by very fine costellae, numbering five to six in 5mm at mid-length, and lying over three or four gentle undulations posteriorly. Micro-ornament is not preserved. The shell is thickened posteriorly, and very thin, less than 1mm over much of the shell.

The adminicula are spaced well apart and diverge, extending for less than a quarter of the shell length. The tabellae diverge weakly forwards and extend for a fifth of the length of the dorsal valve.

Resemblances: These specimens, incomplete as they are, mark a most distinctive choristitid, with fine ribs, poorly distinguished dorsal fold, and short tabellae. *Parachoristites* is a much larger form with broad strap-like ribs and narrow interspaces, better defined fold and short tabellae. *Junglelomia* has similar ornament and fold to that of *Parachoristites*, and longer tabellae.

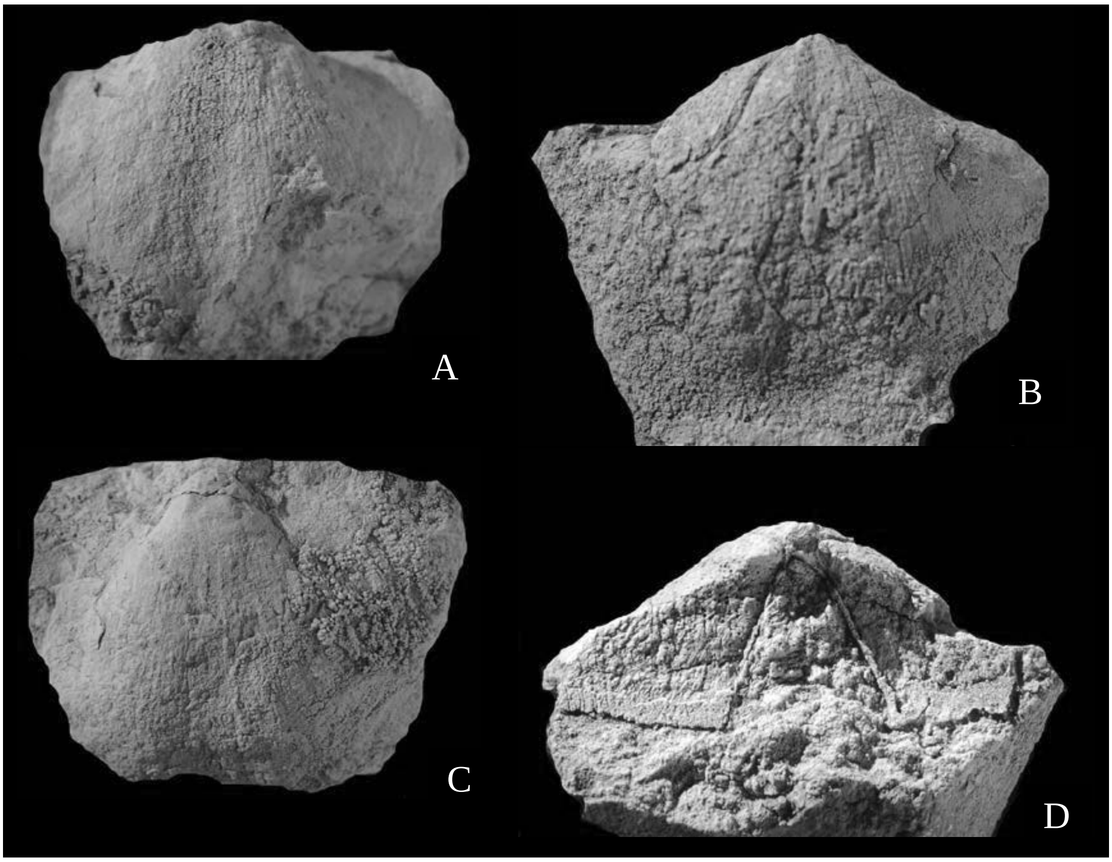


Fig. 277. *Ettrainia costellata* n. gen., n. sp. A, ventral valve GSC 137122 x1.5. B, D, ventral and posterior dorsal view of ventral valve GSC 137123 x1.5, showing adminicula in B. C, ventral valve GSC 137124 x1.5. From JBW 18, Member C, Jungle Creek Formation.

Fig. 278. *Ettrainia costellata* n. gen., n. sp. A, dorsal valve holotype, GSC 137125, x2, from JBW 501, showing tabellae. B, ventral valve showing adminicula, GSC 137127 x1.5, from JBW 18. Member C, Jungle Creek Formation.

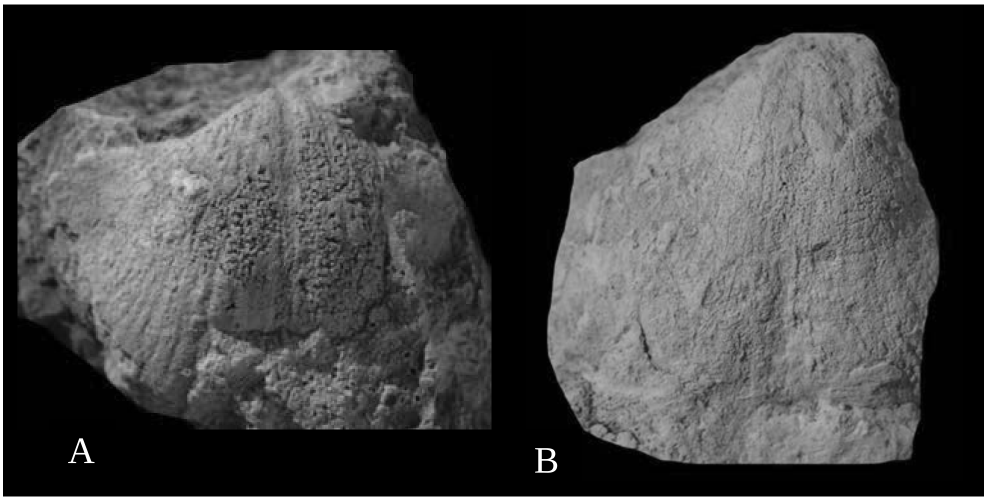


Fig. 279. *Ettrainia costellata* n. gen., n. sp. A, ventral valve GSC 137126 x2. B, ventral valve GSC 137457 x1.5, a worn specimen showing vestiges of the adminicula and low central myophragm. From JBW 18, Member C, Jungle Creek Formation.

Family **PURDONELLIDAE** Poletaev, 1986

[Nom. transl. hic ex Purdonellinae Poletaev, 1986, p. 65, nom. nov. pro Munellinae Fredericks, 1924b, p. 313, based on invalid homonym].

Diagnosis: Hinge short as a rule, subdelthyrial connector plate, fascicles may be present, surface capillate. Adminicula short to moderate in length.

Discussion: A connector plate is present below the delthyrium in members of this family, unlike the arrangement in other Choristitoidea, as far as is known.

Purdonellid? gen. & sp. indet*.*

Fig. 280, 281

Diagnosis: Moderately small with prominent ventral umbo, long posterior walls concave in outline, narrow groove-like sulcus and fine ribs.

Material: Fine ribbed single ventral valves from JBW 126, 518, 736 and 780, two ventral valves from JBW 127 and 189, two broader-ribbed ventral valves from JBW 125, two ventral valves with slightly finer ribs from JBW 93, 188, 190 and 433.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Ventral valve small, highly convex, with long incurved ventral umbo, angle 85-90°, steeply convex moderately high umbonal walls curving out to obtuse cardinal extremities, interarea high, concave, striate, with delthyrium closed by a convex plate subdivided by median cincture. A narrow channel-like sulcus commences at the beak and persists to the anterior margin, rising to gentle rolling borders each side, of which the crests diverge at angle of 18°. Umbonal shell tends to be smooth, possibly through wear, and remainder of shell covered by fine flat-crested ribs, six or seven in 5mm at 10mm from umbo and four in 5mm anteriorly, interspaces narrow: some specimens with slightly broader ribs that bifurcate, others with slender ribs that arise close to the umbo. Micro-

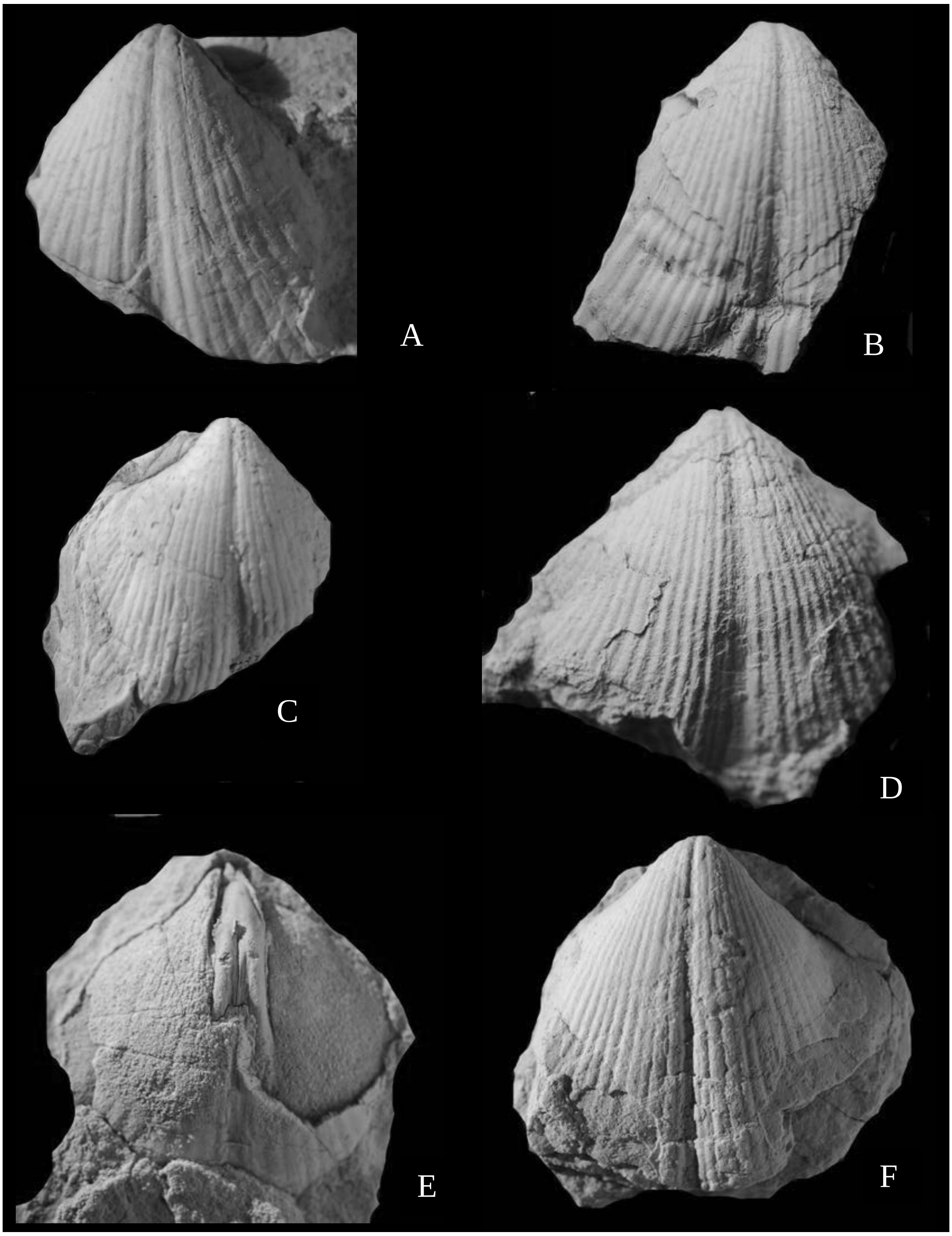


Fig. 280. Purdonellid gen. & sp. indet. A, ventral valve GSC 137127, from JBW 189. B, ventral valve 137128, from JBW 93. C, ventral valve GSC 137129, from JBW 433. D, ventral valve GSC 137130, from JBW 780. E, ventral valve showing internal plates, GSC 137269, from JBW 127. F, ventral valve GSC 137127. Specimens x2, from Member A, Jungle Creek Formation.

ornament is not well preserved but the surface is covered by small pits suggestive of prismatic structure for the outer shell.

Specimen GSC 137131 from JBW 518 is much larger than the other specimens although with similar ornament, sulcus and umbo. It has a wide hinge and obtuse cardinal extremities, apparently lost with anterior shell from the other examples. The specimen measures +55mm wide, +42mm length, and 17mm in height. By comparison, a specimen from JBW 780 is 31mm wide, 28mm long, and 11mm high, and is obviously incomplete.

Adminicula are high and extend for half the length of the valve. An outwardly convex connector plate is present in the specimen from JBW 736. Adductor scars elongate and narrow with slender radial grooves, and smooth diductors to each side. No dorsal valves are known.

Resembances: Given the lack of dorsal valve and incomplete knowledge of the ventral interior, the specimens are regarded as inadequate for specific identification.

The less complete ventral valves look very like *Purdonella nikitini* as figured by Tschernyschew (1902, pl. 10, fig. 1, 2), Stepanov (1937b, pl. 1, fig. 13, pl. 9, fig. 1-3) and Sarytcheva (1960, pl. 61, fig. 5, text-fig. 369), but the ribs are simple and rarely split. In *Purdonella nikitini*, plicae are weakly bundled in the type species due to splitting of the plicae into several costae. Admittedly this is not apparent in some other material referred to the species, such as the ventral valve figured by Tschernyschew & Stepanov (1916a, pl. 10, fig. 2) from Great Bear Cape of Ellesmere Island. *P. nikitiniformis jiyuanensis* Yan in Wang et al. (1987, p. 136. pl. 47, fig. 2a-d) from Henan, China, has finely split ribs, otherwise approaching the Canadian material. *P. edelchteini* Zavodowsky (1970, pl. 13, fig. 1-3, pl. 14, fig. 2) from the basal Permian Burgali Suite of the Kolyma Basin is close in its ornament but the ribs are slightly coarser and the shell larger.

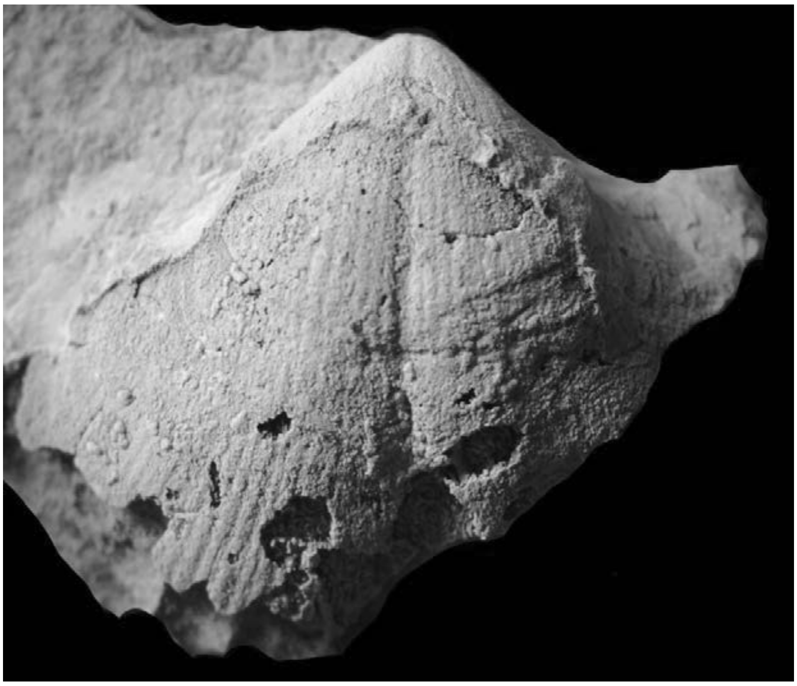


Fig. 281. Purdonellid gen. & sp. indet., more complete ventral valve GSC 137131 x2, from JBW 518. Other specimens have lost the thin shell of the anterior and lateral flanks. From JBW 188, Member A, Jungle Creek Formation.

Choristites miloradovitschi Einor in Licharew & Einor (1939, p. 121, pl. 20, fig. 1, pl. 21, fig. 1), initially described as *Spirifer* sp. by Miloradovich (1935, p. 98, pl. 6, fig. 34), and also figured from the Gzhelian Kigiltass Group of Verchoyan by Kashirtsev (1959b, p. 64, pl. 33, fig. 7, 8), is elongate with long posterior walls, grooved sulcus and fine costae. From the Late Carboniferous of Thailand, *Purdonella magna* Hamada (1964, p. 10, pl. 1, fig. 1a-d) is broader with coarser costae.

From the Late Carboniferous of northeast China (Manchuria), a ventral valve assigned to *Spirifer* (*Munella*) *nikitini* by Ozaki (1931, pl. 4, fig. 11) has ribs as fine as those of the present material, but other specimens have coarser ribs. Most are close in shape but have deeper wider ventral sulcus. *Spirifer* (*Munella*) *nikitini tschernyschewi* Ozaki (1931, p. 59, pl. 5, fig. 11a-c, pl. 6, fig. 2a-b) from the same region has shallow sulcus, and is moderately close but ribs are coarser. An extensive synonymy was summarized by Tazawa (2010, p. 22) in reporting the species from the Late Carboniferous of Fukuji, Japan, A Laos specimen at Kham-Kheut (Mansuy, 1913, pl. 6, fig. 4a-d) has a very shallow sulcus posteriorly, and is slightly broader in outline, but costae are obscure due to decortication.

Somewhat similar ventral valves were figured as *Purdonella* from the lower and upper *Purdonella* Zone in the Ettrain equivalents in the Tatonduk River section of the Yukon Territory by Bamber & Waterhouse (1971, pl. 10, fig. 2, 9).

Suborder SPIRIFERIDINA Waagen, 1883

This suborder groups Cyrtospiriferoidea, Paeckelmannelloidea, Spiriferoidea, Spiriferelloidea and Trigonotretoidea. They share plicate and often costate ornament with micro-ornament of radial and commarginal fila, and share denticulate hinge, and internal plates, involving as a rule dental and adminicula plates, connector plate as a rule (except Neospiriferidae and Trigonotretoidea), ctenophoridium, crural plates and spiralia, but no tabellae.

Superfamily **PAECKELMANNELLOIDEA** Ivanova, 1972

[Nom. correct. Waterhouse 2004a, p. 227**,** pro Paeckelmanelloidea Carter in Carter et al. 1994, p. 347, pro Paeckelmanellacea Ivanova, 1981, p. 22, nom. transl. ex Paeckelmanellidae Ivanova, 1972, p. 40].

Diagnosis: Moderately to strongly transverse with hinge at maximum width, plicate, may have a few costae, ventral interarea usually high, hinge line denticulate, micro-ornament comprised of a meshwork of radial and commarginal fila, short adminicula, ctenophoridium, no tabellae. Median ventral septum in one group.

Discussion: In essential detail one family is very close to Spiriferoidea, differing only in shape and in having simple usually non-costate plicae, but two allied families have exceptional internal morphologies (Waterhouse 2016).

Family **PTEROSPIRIFERIDAE** Waterhouse, 1975

[Nom. transl. Waterhouse 2016, p. 156 ex Pterospiriferinae Waterhouse 1975].

Diagnosis: Transverse and plicate, adminicula but no ventral median septum present.

Discussion: Paeckelmannellidae Ivanova has a ventral median septum, and Strophopleuridae Carter lacks median septum and adminicula (Waterhouse 2016).

Genus ***Spiriferinaella*** Fredericks, 1926

Diagnosis: Transverse and often alate shells with smooth sulcus and fold, or only weak sulcal rib, few simple plicae, fine growth lamellae.

Type species: *Spirifer artiensis* Stuckenberg, 1898, p. 266 from Upper Paleozoic of Russia, OD.

Spiriferinaella simplicata n. sp.

Fig. 282

Name: simplex – single, plain, Lat.

Diagnosis: Highly transverse with alate cardinal extremities, strong fold, sulcus defined by two unusually high lateral plicae, further plicae subdued and few.

Holotype: GSC 137133, here designated.

Material: Single ventral valve from JBW 606, and dorsal valve from JBW 520 and 615, Member A. A ventral valve from JBW 539 from Member E, Jungle Creek Formation. Single ventral valve from JBW 516, Ettrain Formation.

Stratigraphic and biostratigraphic levels: Members A and E, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. *Ogilviecoelia shii* Zone. Ettrain Formation.

Description: Specimens small and elongate, the larger specimen measuring 38mm wide, 13mm long and 5mm high; the other measuring 22mm wide and 6mm long. The hinge lies at maximum width, with tapered alate cardinal extremities, and the ventral umbo protrudes slightly beyond the hinge, with an umbonal angle of 90º. The sulcus commences at the umbonal tip, and is bordered by two sharply raised plicae that diverge at 30º in the larger specimen and at 20º in the smaller specimen, each side of an angularly concave floor. The lateral shell has one pair of plicae in the small specimen and two low growth stops, and the larger specimen shows four pair of low plicae. Delthyrium with concave cover plate, but secondary thickening may be masking any connector plate. The dorsal valve has a well defined round-crested fold with shallow and narrow median channel, and traces of plicae. The shell surface appears to be smooth and the shell is not punctate. Ventral interior with short high adminicula and no median septum. Dorsal interior poorly known, small socket plates, no medium septum, no tabellae.

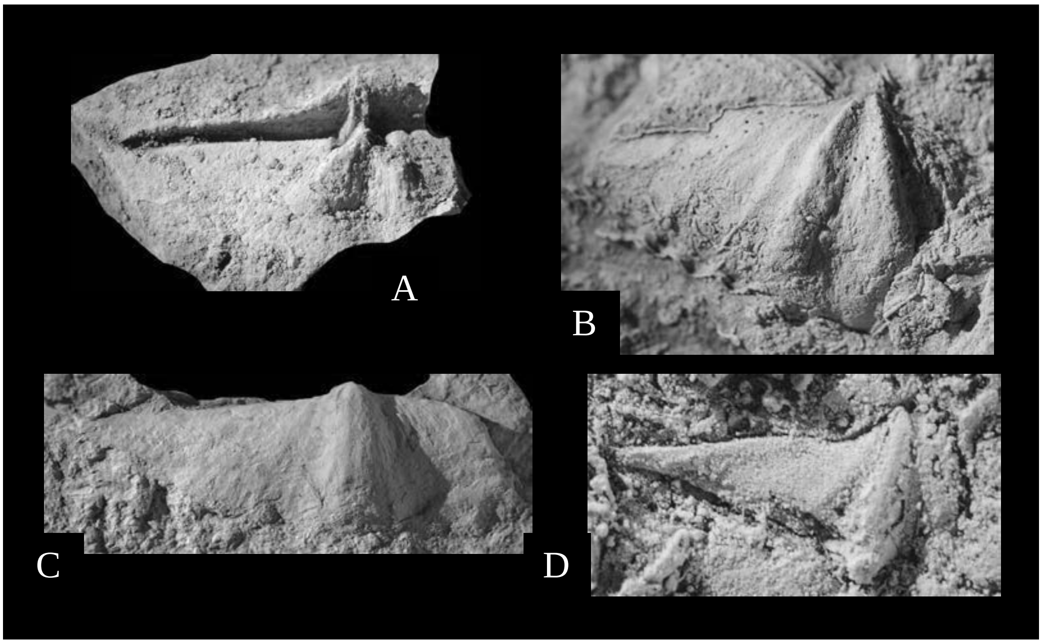


Fig. 282. *Spiriferinaella simplicata* n. sp. A, ventral internal mould GSC 137132 x1.5, from JBW 539, Member E, Jungle Creek Formation. B, ventral valve holotype GSC 137133 x2, from JBW 516, Ettrain Formation. C, dorsal valve GSC 137134 x1.5, from JBW 615. D, ventral valve GSC 137135 x3, from JBW 450. C and D both from Member A, Jungle Creek Formation.

Resemblances: The height of the ridges bordering the ventral sulcus appears close to that of the type species of *Spiriferinaella*, and the species is distinguished by the low number of plicae present on both valves.

Superfamily **SPIRIFEROIDEA** King, 1846

[Nom. correct. Carter 1994, p. 327 pro Spiriferacea Schuchert 1896, p. 333, nom. transl. ex Spiriferidae King, 1846, p. 28].

Diagnosis: Transverse with costae and/or plicae, hinge line denticulate as a rule, connector plate and delthyrial cover plate common. Dental plates well developed, adminicula short, crural plates present and no tabellae.

Discussion: Spiriferoidea is a characteristic Late Paleozoic superfamily, with many genera reaching a comparatively large size. Material from the lower Jungle Creek Formation is sparse.

Family **SPIRIFERIDAE** King, 1846

[Family Spiriferidae King, 1846, p. 28].

Diagnosis: Usually transverse, lateral slopes and fold-sulcus characteristically costate or costellate, ribs may be weakly associated in fascicles, micro-ornament of capillae and commarginal fila. Hinge denticulate, delthyrial cover moderately developed as a rule but weak or absent in Early Carboniferous members, better developed in younger members, mantle canal system impressions mostly displaying closely spaced pits between a network of canals, rarely reinforced by a few radiating canals.

Subfamily **SPIRIFERINAE** King, 1846

[Nom. transl. Waterhouse 1968b, p. 9 ex Spiriferidae King, 1846].

Diagnosis: Transverse, costae plain or in numerous fascicles. Delthyrial plate short to well developed, connector plate present.

Tribe **SPIRIFERINI** King, 1846

[Nom. transl. Waterhouse 2016, p. 167 ex Spiriferidae King, 1846, p. 28. Syn. Imbrexiinae Carter, 1992, p. 327].

Genus ***Fasciculatia*** Waterhouse, 2004

Diagnosis: Large transverse and subalate shells with seven or more pair of narrow fascicles on each valve, deep sulcus, high fold, faint radial capillae, commarginal lamellae subdued or absent, delthyrium open, possibly with posterior connector plate or small callosity, no ventral median septum.

Type species: *Fasciculatia greenlandicus* Waterhouse, 2004a, p. 95 from Foldvik Creek Group (Late Permian), Greenland, as figured by Dunbar (1955, pl. 23, fig. 1-7, pl. 24, fig. 1-5, pl. 28, fig. 1-6), OD.

Discussion: This genus is found in Permian faunas of the Arctic, and includes *Spirifer striatoparadoxus* Toula, 1873 and *Spirifer striatoplicata* Gobbett, 1964, as summarized by Angiolini & Long (2008, p. 93). These authors argued for a position in Neospiriferinae, but that is difficult to sustain, given the absence of a well-formed cover plate arching over the delthyrium from *Fasciculatia*, and possible presence of a small connector plate, as shown by Dunbar (1955, pl. 24, fig. 5). This was interpreted as an umbonal callosity by Waterhouse (2016), but is revaluated herein as a connector plate. Angiolini & Long (2008) argued that the close relationship to Neospiriferinae was supported by general similarity between *Fasciculatia* and *Kaninospirifer* Kulikov & Stepanov in Stepanov, Kulikov & Sultanaev, 1975, but *Kaninospirifer* has few plicae, which fade anteriorly, and has lower dental plates. Indeed the genus has been referred to a separate subfamily Kaninospiriferinae Kalashnikov, elevated to a family by Grunt (2006b), though the validity of this group remains open to clarification (see p. 351 and Fig. 297, p. 356). The present material is distinctly older than type *Fasciculatia* at Late Carboniferous, and identity is not fully secure because of uncertainty over the nature of the delthyrium and connector plate between the dental plates and adminicula.

In age and what is known of morphological attributes, the Canadian material is close to Late Carboniferous genera such as *Donispirifer* Poletaev. The type species of this genus, *D. toretzensis* Poletaev, 2000 from Moscovian of Ukraine, is medium-sized as a rule, and displays numerous well defined fascicles. It is much smaller than type *Fasciculatia*, and has relatively fewer and coarser costae, and is referred to a separate though closely related tribe Donispiriferini Waterhouse 2016, pp. 171 ff. (See Poletaev 2000, Gourvennec & Carter 2007, Fig. 1861, 1a-d, Waterhouse 2016, Fig. 198).

***Fasciculatia*? sp. indet.**

Fig. 283

Material: Single ventral valves from JBW 591 and 805.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: An anterior fragment of a large specimen from JBW 591 shows strong round-crested costae separated by concave interspaces of similar width, a broad sulcus incorporating two or three pairs of fascicles, and eight or more narrow fascicles to each side with further costae laterally. The original specimen was at least 85mm in width. A large ventral internal mould from JBW 805 is 88mm wide, 65mm long and 22mm high, with eight pairs of lateral fasciculations followed by costae on each lateral flank, and broad delthyrium with angle of over 90º, and moderately deep sulcus with angle of 30º. with seven narrow fascicles or broad costae. A delthyrial cover plate could be present, but is very obscure, and there is no visible connector plate, leaving the generic and family position insecure. The muscle field is moderately broad, and the adductor ridges not strongly defined and like the diductor scars are striated by fine grooves. The adjoining and thickened shell surface is marked by slender and intricate vascular markings.

Resemblances: This species is distinguished by its large size and strong costae, which form a number of narrow fascicles. The ornament and size are features typical of Spiriferini, including *Fasciculatia*. This genus is younger than other members of the tribe, which are mostly Early Carboniferous in age. But present material does not clearly show the presence of a connector plate, and indeed seems to suggest the possible presence of a delthyrial cover plate. Shells with delthyrial cover plate and without a connector plate are placed in Neospiriferinae, but all known members of this group have well developed and comparatively few plicae, rather than a number of slender fascicles. One of the few spiriferid species to display moderately strong costae is S*pirifer poststriatus* Nikitin var. *taimyrica* Einor, 1939, pl. 8, fig. 1-4 from the Lower Permian of Taimyr Peninsula, as figured also by Kashirtsev (1959b, p. 56, pl. 22, fig. 1), with narrow plicae or fascicles. Some members of Trigonotretidae have numerous narrow plicae or fascicles, with costae angular-crested and very much subsidiary to the plicae. *Trigonotreta* has a more openly reticulate mantle canal system and high umbonal callosity. (See Clarke 1979, pl. 1).

Morphology: Traces of fine anastomosing vascular patterns are unusual, and may be revealing a pattern obscured in less well preserved material.

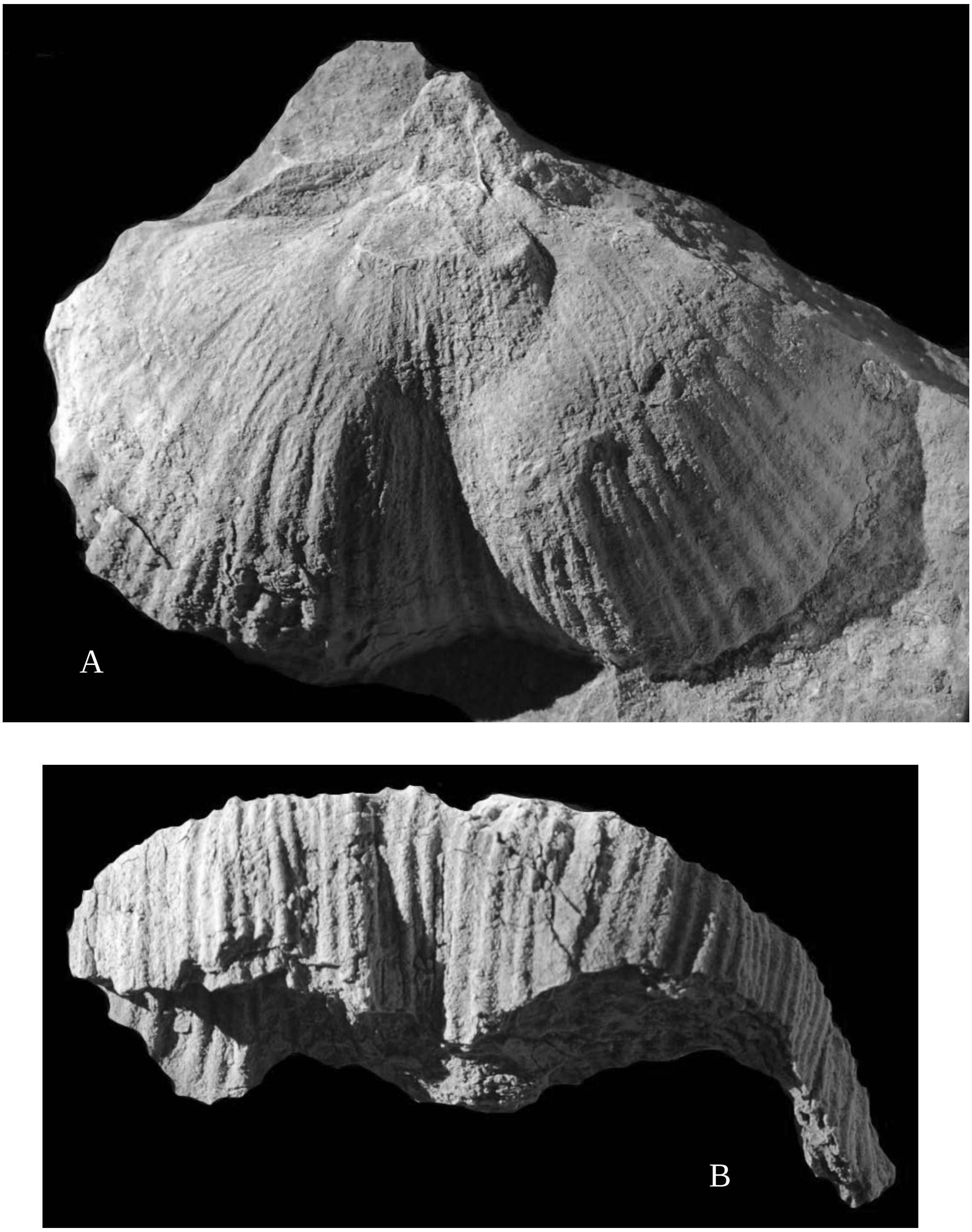


Fig. 283. *Fasciculatia?* sp. A**,** internal mould of ventral valve, GSC 137137 x1.5, from JBW 805. B, fragment of anterior mould, GSC 137136 x1.5, from JBW 591. Member A, Jungle Creek Formation.

Subfamily **SPIRIFERALARIINAE** Waterhouse, 2016

Diagnosis: Plicae well developed.

Discussion: Genera include *Spiriferalaria* Waterhouse, with widely alate cardinal extremities, *Gibbospirifer* Waterhouse, an elongate shell with narrow fading plicae, *Simplicisulcus* Waterhouse with strong costae, and inner plicae not normally entering the sulcus anteriorly, and *Tegulispirifer* Poletaev, with well formed plicae.

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Genus ***Tegulispirifer*** Poletaev, 2000

Diagnosis: Medium-sized to large transverse shells with extended hinge and well developed costate plicae, micro-ornament with strong commarginal laminae where well preserved, and fine radial capillae. Stegidial cover, small umbonal callosity and connector plate.

Type species: *Spirifer tegulatus* Trautschold, 1876, p. 354 from Moscovian (Middle Pennsylvanian) of Moscow Basin, Russia, OD.

Tegulispirifer*? *placitus n. sp.

Fig. 284, 285

Derivation: placitus – pleasing, Lat.

Diagnosis: Medium small and transverse with five or six pair of plicae, the inner pair entering the well defined sulcus anteriorly, well defined narrow fold, and numerous round-crested costae.

Holotype: GSC 137140, here designated.

Material: Specimen with valves conjoined, two ventral valves and dorsal valve from JBW 451, specimen with valves conjoined and fragments from JBW 122, single ventral valves from JBW 75, 417, 605, 772, 773 and 774.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Dimensions in mm: ventral valves from JBW 451

GSC	Width	Length	Height
137138	41	25	7
137140	59	36	
137139	+41	32	+6

Description: Specimens transverse, and those from JBW 451 slightly crushed. Ventral umbo extended a little beyond hinge, not strongly incurved, umbonal angle 100-110°, hinge wide with small acute cardinal extremities, maximum width placed near mid-length. Sulcus commences just in front of the beak, and steadily widens and deepens forward, with angle of 25-27°, bordered by inner pair of plicae, which gradually enter the sulcus anteriorly in the largest specimen. Some specimens show up to five or even six pair of plicae, but on most specimens only three pairs are well defined. Five pairs are defined on the dorsal valve, and the fold is narrow with rounded crest. Costae cover the exterior, including up to five on each inner plication, numbering three or four in 5mm anteriorly, increasing by intercalation and probably by bifurcation, with rounded crests. Up to twelve costae are present anteriorly in the sulcus of the largest specimen. Micro-ornament cannot be discerned, and growth-steps are present in two ventral valves from JBW 417 and 605, but not in others.

The delthyrium has an angle close to 50°. It is closed by an inwardly concave plate, that might be a connector plate, but detail is not clear. The specimen from JBW 122 has closely spaced moderately long adminicula diverging forward at a low angle.

Resemblances: Some aspects critical for generic placement are obscure in this material, so that identification is provisional, but is consistent with what is known about the material. The type species of *Tegulispirifer* from Moscovian – Kasimovian of the Moscow Basin, Russia, is moderately close in size, shape and ornament, other than micro-ornament, which has been worn off, but the dorsal fold is wider. From the Ettrain Formation, *T. ogilvieensis*

Waterhouse, 2016 is also close, but a little more alate, with wider ventral muscle field.

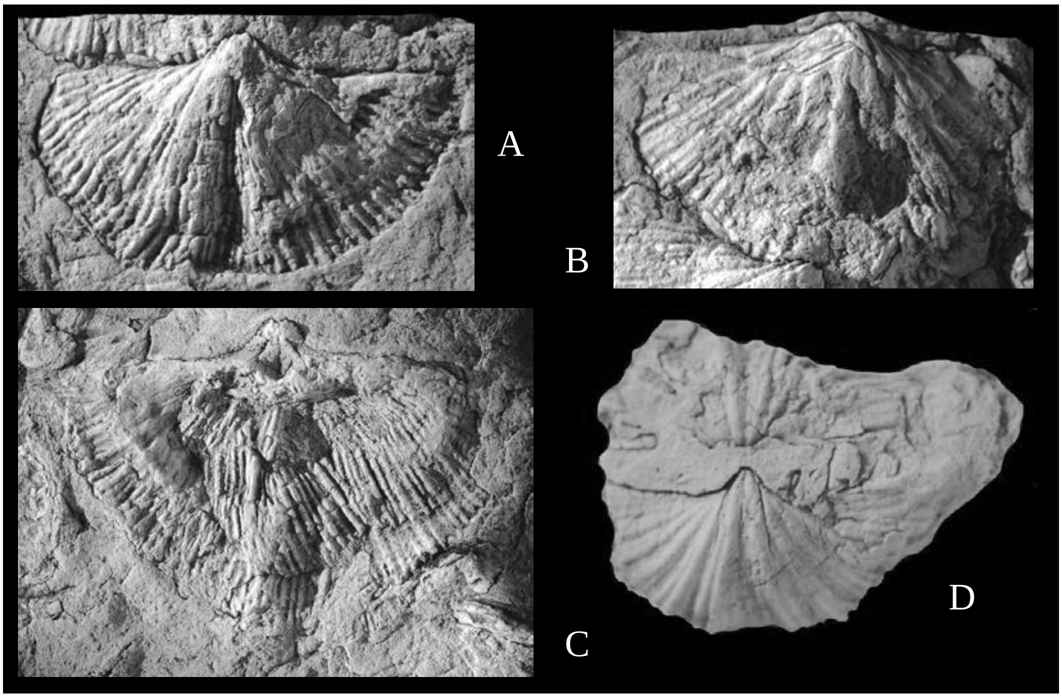


Fig. 284. *Tegulispirifer? placitus* n. sp. A, ventral valve GSC 137138 x1.5, from JBW 451. B, dorsal valve GSC 137139 x 1.5, from JBW 451. C, dorsal aspect of specimen with valves conjoined, holotype GSC 137140 x1, from JBW 451. D, posterior part of specimen with valves conjoined, GSC 137141 x2, from JBW 122. Member A, Jungle Creek Formation.

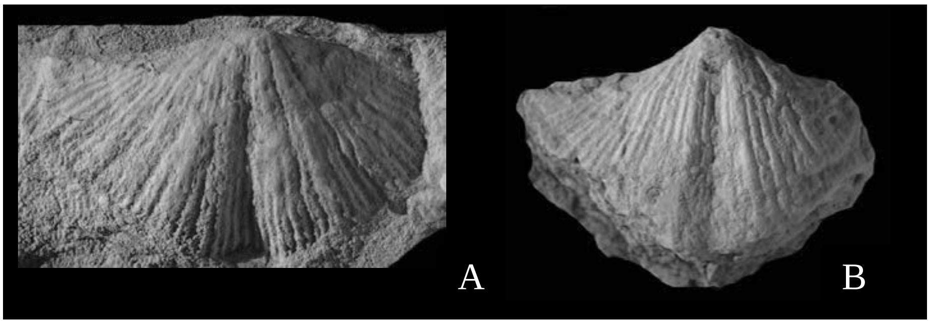


Fig. 285. *Tegulispirifer? placitus* n. sp. A, ventral valve GSC 137305 x1, from JBW 40. B, ventral valve GSC 137306 x1.5, from JBW 605. Member A, Jungle Creek Formation.

Family **NEOSPIRIFERIDAE** Waterhouse, 1968b

[Nom. transl. Waterhouse 2016, p. 197 pro Neospiriferinae Waterhouse, 1968b, p. 9].

Diagnosis: Ornament of well developed plicae and costae. Delthyrial cover plate, and no connector plate.

Discussion: Members of this family lack a connector plate, and so might have been allied to Trigonotretoidea, which also lacks a connector plate. But the stratigraphic evidence does not favour this view, because, as far as is known, plicate and costate neospiriferids are found in beds older than any costate trigonotretid, to suggest that neospiriferids might have arisen independently from spiriferoid stock, such as Spiriferalariinae Waterhouse, 2016, through loss of the connector plate. Unlike Trigonotretoidea, an umbonal callosity is not well developed.

Subfamily **NEOSPIRIFERINAE** Waterhouse, 1968b

[Neospiriferinae Waterhouse, 1968b, p. 9].

Diagnosis: Plicate and costate shells with sulcus that generally expands to incorporate innermost pair of plicae in many genera. Delthyrium as a rule covered by delthyrial cover plate. Dental plates, short adminicula, socket and crural plates, no connector plate or tabellae, no median septa. Mantle canal system possibly finely reticulate, but not well known.

Discussion: In shape and ornament, Neospiriferinae appears to have evolved from Spiriferidae, especially Spiriferalariinae or Fusispiriferinae (see Waterhouse 2016), with the development of stronger and restricted plicae rather than low numerous fascicles, the loss of a connector plate, and the development of a delthyrial cover plate. This plate did not arise from deltidial plates that developed each side of the delthyrium, because no neospiriferid even at immaturity is known to show any sign of deltidial plates. It seems likely that the cover plate was either a specialized form of stegidial plate, lacking any foramen, or a deltidium developed from inception as one plate.

Neospiriferin gen. & sp. indet. A

Fig. 286

Diagnosis: Large shells with coarse costae and three pair of dorsal plicae, well defined sulcus and fold, short hinge.

Material: Specimen with valves conjoined from JBW 702, juvenile specimen from JBW 611, ventral valve from JBW 75, ventral fragments from JBW 122.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Fig. 286. Neospiriferin gen. & sp. indet. A, posterior view of internal mould GSC 137143 x1, with ventral valve on top, from JBW 702. Member A, Jungle Creek Formation.

Description: The specimen with valves conjoined from JBW 702 measures more than 74mm in width, with moderately wide hinge and three pair of costate plicae on the dorsal valve, a ventral sulcus and dorsal fold, and strong costae numbering two to three in 5mm. The delthyrium with angle of 40º is not closed by a convex deltidial plate, which could have been lost. Dental plates are moderately high and diverge strongly from high and short adminicula, which diverge at 45º to enclose a ventral muscle field of moderate width. There is no connector plate. The ventral muscle field consists of two narrow adductor ridges and large diductor impressions, deeply impressed posteriorly, with no median septum. Ctenophoridium of medium size with less than twenty blades, and low median septum extends over the posterior third of the shell length. A tiny specimen from JBW 611 has sharply defined plicae in four pair.

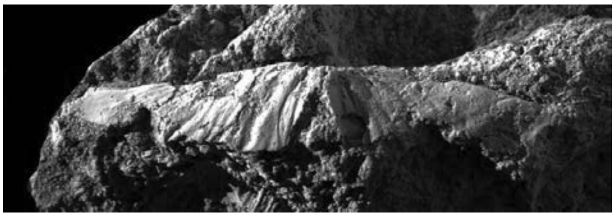
Resemblances: The strength of the costae and the well formed few pair of plicae on the dorsal valve are not replicated in other specimens from Member A. The nature of the delthyrial apparatus is not entirely clear, because any delthyrial plate has been lost, if ever present, but there is no connector plate. The hinge appears to have been comparatively narrow, which suggests possibly affinity with *Neospirifer* Fredericks (Carter et al. 1994, Poletaev 1997, Waterhouse 2016), as a species distinguished by its few and strong costae.

Neospiriferin? gen. & sp. indet. B

Fig. 287

A fragment from JBW 85, Member D, Jungle Creek Formation, *Rugivestigia commarginalis* Zone, of an internal mould of the posterior dorsal valve with wide hinge, showing several plicae, rounded fold, and moderately strong costae. The specimen is too incomplete to allow even the subfamily position to be determined. A small ventral valve is also present from this locality.

Fig. 287. Neospiriferin? gen. & sp. B, posterior part of dorsal internal mould GSC 137149 x1.5, from JBW 85, Member D, Jungle Creek Formation.



Genus ***Neospirifer*** Fredericks, 1924b

Diagnosis: Medium-sized transversely subrectangular shells with narrow triangular ventral interarea, well defined costae and strong lateral plicae.

Type species: *Spirifer fasciger* Keyserling, 1846, p. 231 from early Cisuralian of the Urals, Russia, OD.

Discussion: *Neospirifer* is small to medium in size with transversely rounded outline. It is close to *Betaneospirifer* Gatinaud, 1949, which is based on *Spirifera moosakhailensis* Davidson, 1862, p. 28 from the lower Wargal Formation (Wuchiapingian), Salt Range, Pakistan. *Neospirifer* as recognized by Carter et al. (1994), Carter (2006a) and Waterhouse (2004a, 2016) is distinguished by its smaller size and shorter hinge, which as far as known is not alate, by comparison with *Betaneospirifer.*

Fig. 288. *Neospirifer?* sp. A, part of dorsal internal mould GSC 137150 x2, from JBW 18, Member C, Jungle Creek Formation.

***Neospirifer*?** sp. A

Fig. 288

Material: A dorsal valve from JBW 18.

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Description: The specimen has fine costae and four well defined plicae pairs.

Neospirifer sp. B

Fig. 289

Material: A specimen with valves conjoined from JBW 581.

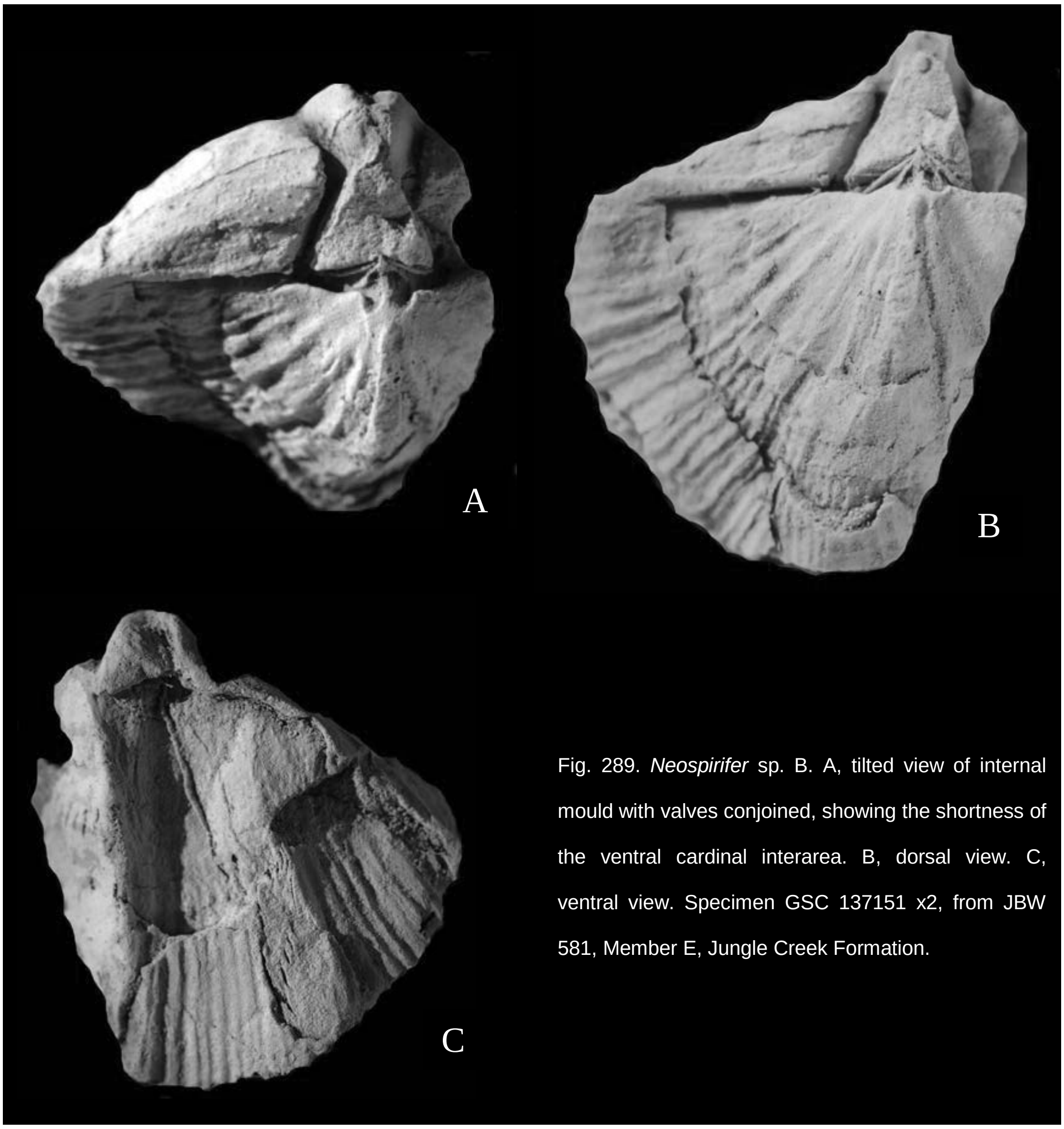


Fig. 289. *Neospirifer* sp. B. A, tilted view of internal mould with valves conjoined, showing the shortness of the ventral cardinal interarea. B, dorsal view. C, ventral view. Specimen GSC 137151 x2, from JBW 581, Member E, Jungle Creek Formation.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Specimen preserved as a damaged internal mould, 37mm wide and long and 18mm high. Ventral valve moderately inflated, interarea less than maximum width and moderately high, cardinal extremities obtuse, and umbonal walls high, convex in profile, and diverging forward at 80º. Delthyrial sides diverge at 40º, but damaged and without a cover plate, which may have been lost. Dorsal interarea at steep angle to commissure, disrupted by notothyrium with angle of 105º, bordered by slender deep groove each side. Ventral sulcus commences at umbo, with estimated angle of 28º, and concave floor. Dorsal fold distinct, with rounded crest and moderately broad in front with margins well defined and straight in outline. The outer margin of the fold bears a narrow fasciculation of two ribs, increasing to three ribs, and four to five narrow fascicles lie each side, with a few additional costae laterally: the fold bears more than twelve slender costae inside the bordering fascicle. Ventral ornament is more obscure, but the inner plication is prominent, and there are signs that a further three plicae developed laterally, with more than ten costae in the sulcus.

Short but high dental plates are supported by adminicula almost as high, diverging to the floor of the valve, and buried posteriorly in heavy secondary thickening, bordering ventral muscle field of moderate width. There is no connector plate. The ctenophoridium is large and laminate and recessed medianly, and small crural plates and very small socket plates are present. Other detail is not preserved, except for part of the spiralia, lying well forward and possibly displaced.

Resemblances: The type material of *Neospirifer fasciger* is not well known, but there are some clear resemblances in the short and comparatively high although narrow ventral interarea, and apparently obtuse cardinal extremities, and few well formed ventral plicae, poorly formed dorsal fascicles and moderately high narrow-crested dorsal fold (cf. Archbold & Thomas 1984a; Poletaev 1997). On the other hand the ventral muscle field, although badly preserved in the present specimen, is narrower than in the type material, and there appears to be at least one additional pair of dorsal fascicles.

Genus ***Forticosta*** n. gen.

Derivation: fortis – strong, costa – rib, Lat.

Diagnosis: Small transverse shells with moderate sulcus and low fold, costae relatively strong with a number of bifurcations. Very wide ventral muscle field.

Type species: *Forticosta transversa* n. sp. from basal Jungle Creek Formation (Gzhelian), Yukon Territory, Canada, here designated.

Discussion: This is a very distinct genus. A few genera are similarly transverse, but have weaker costae and narrower ventral muscle field, as in Fusispiriferinae Waterhouse, 2004a, a member of Spiriferidae. *Fusispirifer* Waterhouse 1966 is wider, but plicae are better developed, and *Cratispirifer* Archbold & Thomas, 1985 has strong costae, with higher ventral interarea, and more persistent fascicles. It appears to be the closest of other genera, and comes from the Early Permian of Western Australia. But members of Fusispiriferinae have a connector plate, not developed in *Forticosta*.

Forticosta transversa n. gen., n. sp.

Fig. 290, 291

Derivation: transversus – lying across, Lat.

Diagnosis: Coarsely costate with weak fascicles, transverse shells and wide muscle field.

Holotype: GSC 137147, here designated.

Material: Two ventral valves from JBW 66, ventral valve and dorsal valve from JBW 611, two ventral valves from JBW 77, single ventral valves from JBW 562 and 591, dorsal valve from JBW 84.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

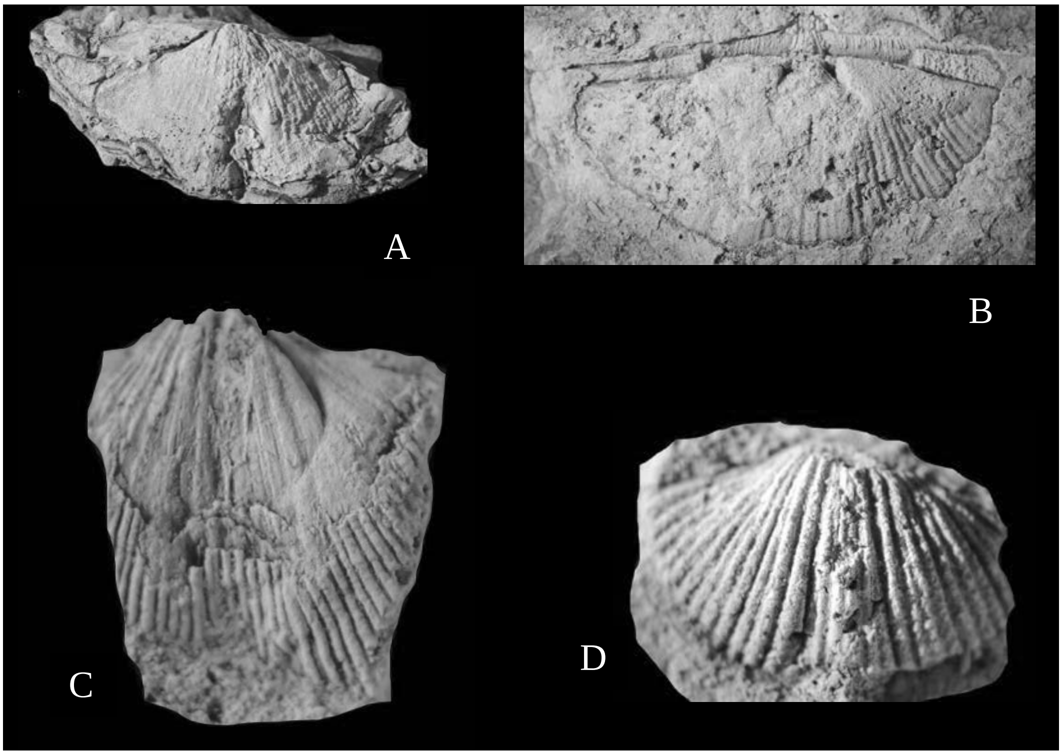


Fig. 290. *Forticosta transversa* n. gen., n. sp. A, ventral internal mould GSC 137144 x1, from JBW 591. B, ventral valve GSC 137145 x1 from JBW 119. C, partly decorticated ventral valve, exposing interior posteriorly, GSC 137146 x2, from JBW 611. D, dorsal valve GSC 137296, from JBW 611. Member A, Jungle Creek Formation.

Description: Shells transverse, hinge at maximum width with low ventral interarea curved under the umbo, horizontally striate and marked by strong vertical striae. The interarea is low in small shells but becomes high and planar with increase in size. Delthyrium closed by convex cover plate. Cardinal extremities obtuse in early growth stage, becoming submucronate, but poorly preserved. Ventral umbo broad, angle over 130º, weakly incurved, umbonal walls low, sulcus starts at umbo and widens with angle of 25º. Dorsal valve less inflated, interarea low and inclined at high angle to ventral interarea; notothyrial detail obscure. Fold narrow, raised with convex crest. Both valves ornamented by numerous strong costae with rounded crests and deep U-shaped interspaces, as few as three costae in 5mm anteriorly. A small specimen shows the immature shell, in which a number of costae branch into two at six to seven mm from the umbo, and a further costa arises in the interspace, to impart a triple replication, and very weakly developed fascicles. Other specimens suggest very low plicae, much less developed than in most members of Neospiriferidae. The sulcus and fold bear slightly finer costae, up to seven in the ventral valve and six on the dorsal valve. Micro-ornament is obscure, and possibly worn, to indicate the ends of small prisms, commarginal laminae not strong, and growth increments very fine, with only traces of radial fila.

Dental plates high and subparallel, and adminicula short, diverging widely at 80º in the small specimen from JBW 611 and at 70º in JBW 591. There is no connector plate. Adminicula extend for a quarter of the length of the valve, highly divergent, enclose muscle field with two adductor ridges and wider diductor scars. The ventral muscle field is extraordinarily wide, helping to distinguish the taxon. The mantle canal system is finely reticulate over the posterior shell, as if stretched longitudinally.

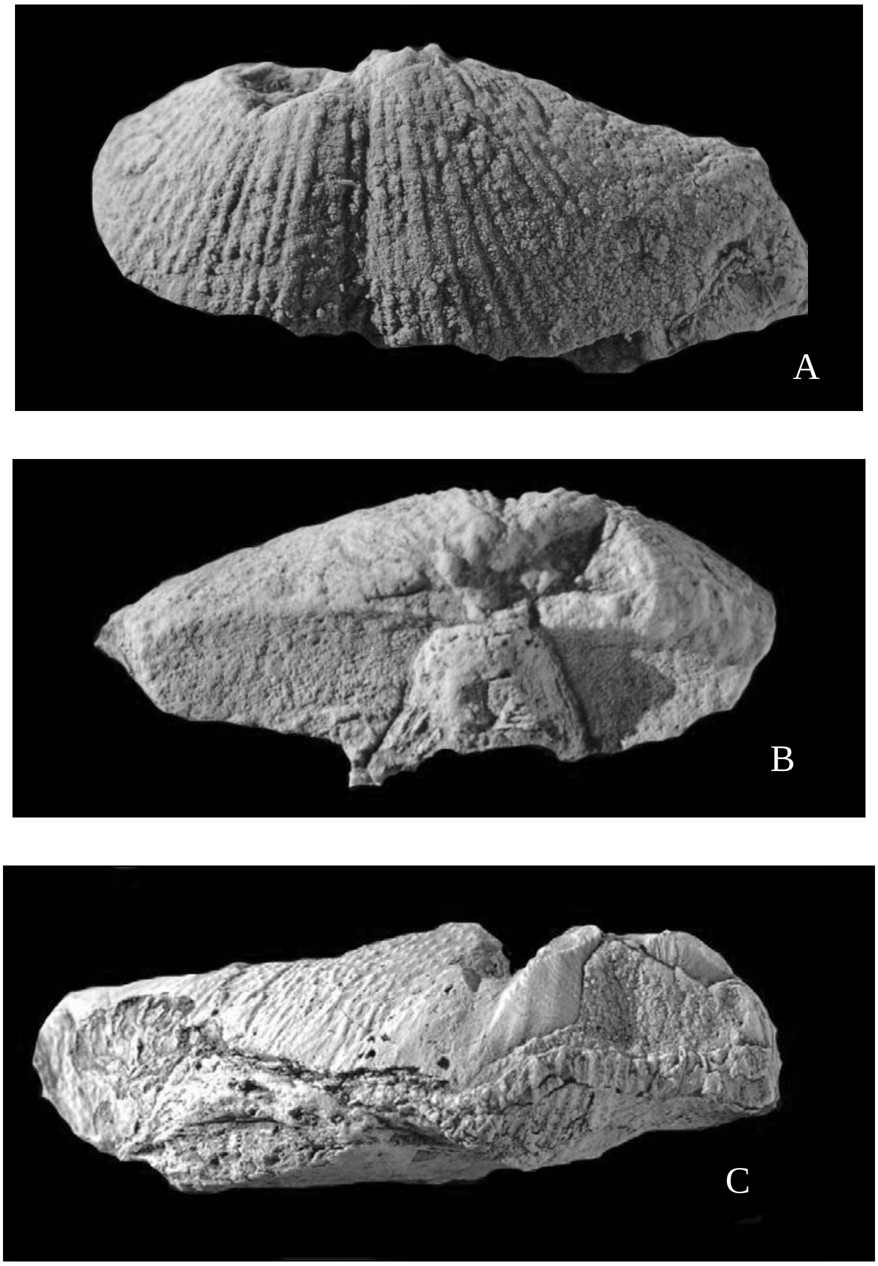


Fig. 291*.* *Forticosta transversa* n. gen., n. sp. A, B, ventral and posterior views of ventral valve GSC 137147 x2, holotype, showing well developed delthyrial cover plate in B, from JBW 66. C, internal ventral mould showing the unusually broad adductor scars and widely spaced adminicula, GSC 137148 x1.5, from JBW 66. Member A, Jungle Creek Formation.

Resemblances: This species is distinctive, not very transverse, with unusually wide ventral muscle field flanked by widely diverging short adminicula, high interarea and weakly developed plicae and sturdy costae. There are well formed high but narrow costae which occasionally bifurcate.

One Early Permian species that shows some approach is the Chinese form described from the Zhanjin Formation in the Duomo Rutog region of Xizang (Tibet) as *Neospirifer cameratiformis* Hu (1983, p. 111, pl. 14, fig. 7-12, text-fig. 7, 8). Ribs are strong with rounded crests, separated by deep interspaces. The species differs from the present form through the manner in which the costae branch much more than in the Canadian form, especially on the ventral valve. They bifurcate, and each branch bifurcates again for several inner fascicles. In the present species, costae branch as a rule near the umbo. The ventral muscle field in Hu's species does not appear appear be nearly as wide as in the present taxon.

Subfamily **SEPTOSPIRIFERINAE** Waterhouse, 2016

[Septospiriferinae Waterhouse 2016, p. 201].

Diagnosis: Typified by median septum in ventral valve. Ventral umbones extended, costae fine.

Discussion: *Gobbettifera* Waterhouse, 2004a, p. 100 from the Canadian Arctic Archipelago probably evolved from *Septospirifer*. It is more inflated and less transverse, and in the type species, the sulcus expands anteriorly to incorporate one or two pair of plicae in the sulcus and the innermost plicae pair fade anteriorly and are subsumed in the next pair of plicae, whereas the sulcus in *Septospirifer*, including specimens from the lower Jungle Creek Formation, tends to be bordered by the innermost pair of plicae, which remains persistent, although in some specimens the pair does become incorporated in the sulcus anteriorly. The median septum of *Gobbettifera* is higher but shorter than in *Septospirifer*, and has been illustrated in Waterhouse (2004a, text-fig. 25A, B) and Waterhouse & Chen (2007, text-fig. 11A, p. 49). *Septospirifer* has a somewhat pointed ventral umbo and narrow plicae, whereas the plicae in *Gobbettifera* are few, and the two inner plicae pairs merge to form a broad fold, much as in the type species of *Kaninospirifer*, so that externally the two genera look very similar to each other, with diffuse sulcal borders. Lee et al. (2016) considered that *Fasciculatia* was synonymous with *Gobbettifera*, but *Fasciculatia* has fascicles rather than plicae, as illustrated in Fig. 297, p. 356, and lacks the posterior septal development in the ventral valve, Gourvennec in Gourvennec & Carter (2007) on the contrary evaluated *Gobbettifera* as a synonym of *Septospirifer,* and it must be agreed that from what is known at present, the two are close to each other, and possibly will prove to be synonymous, if it be deemed that the differences in sulcus, plicae and particularly the length and the height of the ventral median septum are not generically significant.

Genus ***Septospirifer*** Waterhouse, 1971a

Diagnosis: Well developed median ridge in ventral valve. Plicae enter the sulcus anteriorly in some specimens.

Type species: *Septospirifer tatondukensis* Waterhouse, 1971a, p. 224 from Member A of Jungle Creek Formation (Gzhelian), Yukon Territory, OD.

Septospirifer tatondukensis Waterhouse, 1971a

Fig. 292 – 295

1971a *Septospirifer tatondukensis* Waterhouse in Bamber & Waterhouse, p. 224, pl. 27, fig. 1-5.
2006a *S. tatondukensis* – Carter, p. 1799, Fig. 1193, 2a-b.
2016 *S. tatondukensis* – Waterhouse, Fig. 248, p. 203.

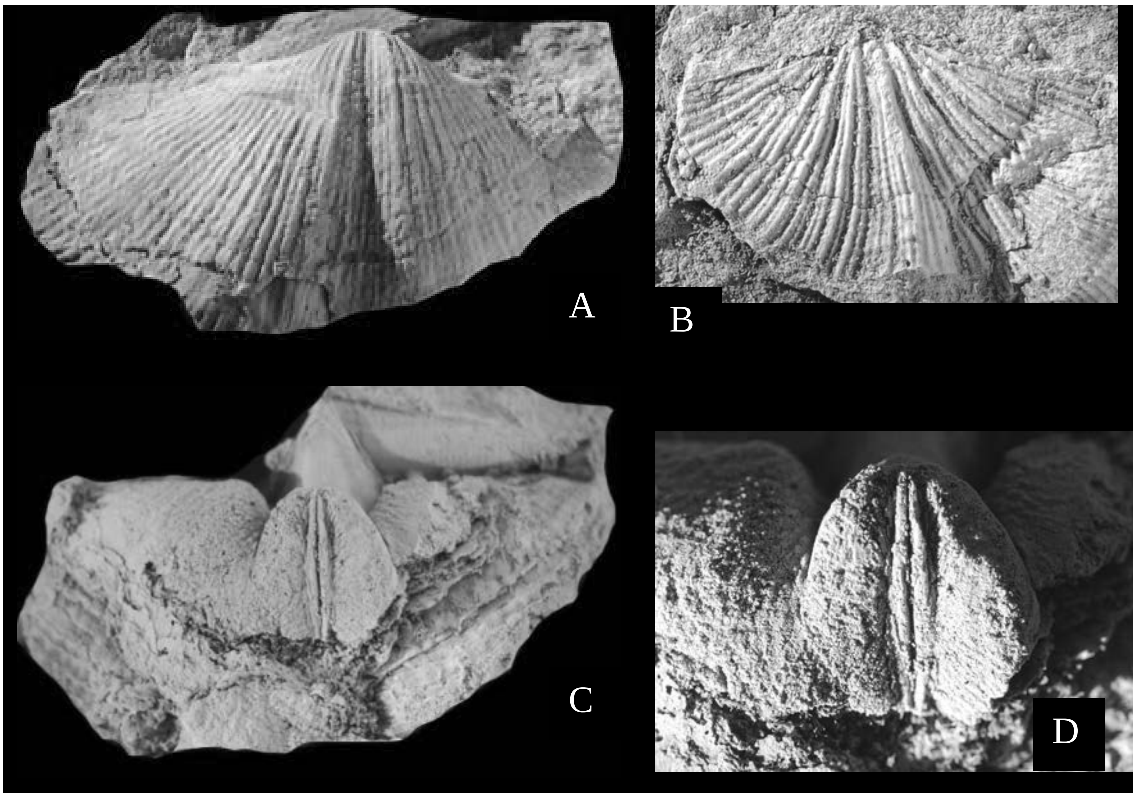


Fig. 292. *Septospirifer tatondukensis* Waterhouse. A, ventral valve GSC 136657 from JBW 531, x1. B, dorsal valve, GSC 136658 from JBW 644, x2. C, ventral internal mould, GSC 136659 from JBW 726, x1.3. D, detail of ventral muscle field of GSC 136659, x2 from JBW 126. Member A, Jungle Creek Formation.

Diagnosis: Medium size with sharp-crested plicae, fading anteriorly, well defined sulcus and fold, costae dividing anteriorly, interior characterized by low median ventral septum.

Holotype: GSC 26437 from GSC 57143, figured by Bamber & Waterhouse (1971, pl. 27, fig. 4, 5) and Carter (2006a, Fig. 1193, 2a, b).

Material: Single ventral valves from JBW 66, 112, 126, 180, 502, 515?, 531, 572, 588?, 591, 624, 650, 731, 764 and 780, two ventral valves from 562, three ventral valves from JBW 624, five ventral valves from JBW 134, one ventral valve and one dorsal valve from JBW 197 and 644, single dorsal valves from JBW 78, 172? and 187, two dorsal valves from JBW 112, one ventral valve, a dorsal valve and specimen with valves conjoined from JBW 122?, single specimens with valves conjoined from JBW 141, 164, 173, 677 and 826.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: The ventral umbo is narrow and prolonged over the interarea with narrow and sharply defined sulcus widening at angle of only 20º, bordered by innermost pair of plicae, which enter sulcus anteriorly in some specimens. The upper delthyrium is closed by a heavy build up of callus, with no connector plate. There are four to five pairs of plicae, well defined posteriorly, as narrow and high ridges persisting for some 10mm, before dividing into two or three costae, and costae divide into pairs after 17-19mm. Plicae vary in strength, persisting on one specimen for 25mm and only 20mm on another. Lateral to the plicae are several costae. The plicae fade anteriorly to become vague undulations, whereas the costae persist to the anterior margin. Micro-ornament consists of fine growth laminae, four to six in one mm, but radial fila are obscure. The dorsal fold is narrow and well defined with broadly rounded crest that becomes moderately low anteriorly. The sulcus protrudes in front as a rounded tongue. Small specimens are highly transverse with alate cardinal extremities, and the anterior and lateral shell expand after a width of 60mm.

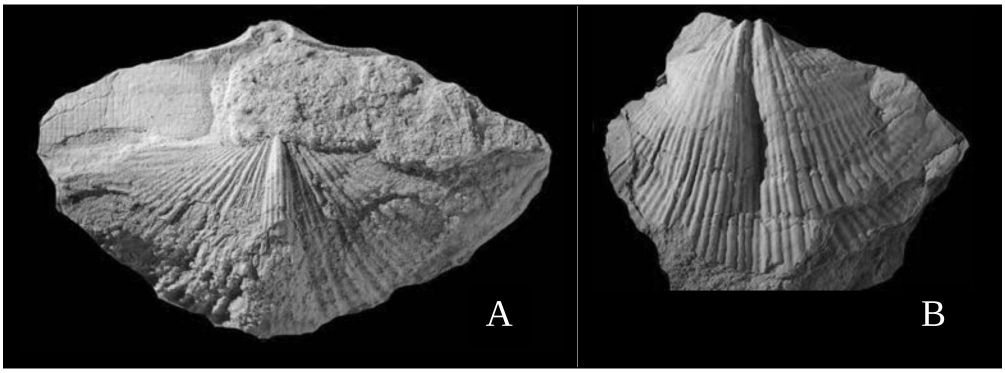


Fig. 293. *Septospirifer tatondukensis* Waterhouse. A, dorsal aspect of specimen with valves conjoined, GSC 137152 from JBW 173, x1. B, ventral valve, GSC 137153 x1 from JBW 650, x2. Member A, Jungle Creek Formation.

In the ventral valve the median septum is moderately well formed but low. High dental plates bear small teeth, and are supported by short high adminicula. Adductor scars are long and narrow, and diductor scars are broad and lightly impressed with growth markings parallel to the anterior margin. The specimen from JBW 624 is 62mm wide and close to 41mm long, with fine costae and very low plicae. A long but low median septum is indicated, extending for nearly half the length of the shell.

The dorsal median septum commences a little in front of the posterior wall and persists over the posterior third of the shell length. The ctenophoridium is broad with numerous vertical laminae, but dental sockets are very small in a specimen from JBW 75.

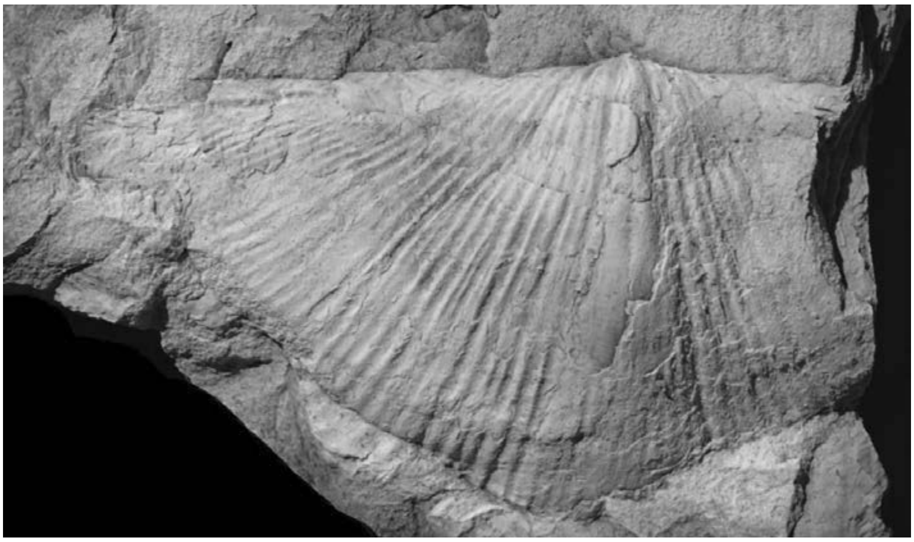


Fig. 294. *Septospirifer tatondukensis* Waterhouse, dorsal valve, GSC 137154 x1.5, from JBW 197, Member A, Jungle Creek Formation

Resemblances: *Gypospirifer romanovskyi* Poletaev (2000) from the Moscovian fauna of the Donets Basin is close in external appearance, but no ventral septum is reported, and plicae are less developed.

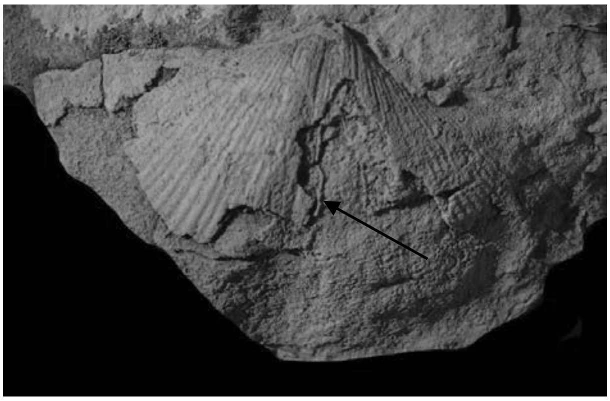


Fig. 295. *Septospirifer tatondukensis* Waterhouse, ventral valve, GSC 137155 x1, from JBW 624. The median septum as arrowed is long. Member A, Jungle Creek Formation.

The Schwagerina-Kalk specimens described from the Urals as *Spirifer cameratus* Morton from the Cora-Horizon by Tschernyschew (1902, pp. 138, 531, pl. 5, fig. 1-9, pl. 6, fig. 8, pl. 11, fig. 2-4) appear to belong to *Septospirifer*, possessing similar shape, sharply pointed ventral umbo, narrow well-defined ventral sulcus, weakly fasciculate costae, and well formed ventral septum (Tschernyschew 1902, pl. 6, fig. 8; pl. 11, fig. 2). They are here named as *Septospirifer bargasia*, with holotype figured by Tschernyschew (1902, pl. 11, fig. 2a-d), the name based on the source of the material from "Schlucht Bargasy". Compared with the Canadian species, they have slightly higher fold and wider sulcus anteriorly, more inflated ventral valve, and more alate cardinal extremities. The shape, ornament and ventral interior of Tschernyschew's material differ considerably from *Spirifer cameratus* Morton (1836, p. 150, pl. 2, fig. 3), also figured from Late Carboniferous faunas of United States by Beede (in Beede & Rogers 1898, p. 103, pl. 6, fig. 1-31), Girty (1915, pl. 11, fig. 4; 1927, pl. 27, fig. 24-27), Dunbar & Condra (1932, p. 334, pl. 39, fig. 4, 6-9), Dresser (1954, p. 57, pl. 5, fig. 11), Hoare & Burgess (1960, p. 714, pl. 91, fig. 9), Hoare (1961, p. 76, pl. 9, fig. 15-17, pl. 10, fig. 1, 2) and Sturgeon & Hoare (1968, p. 64, pl. 21, fig. 5-8). Plicae are low and rounded, the fold low and sulcus shallow, cardinal extremities bluntly angular, and shape subpentagonal. The taxon *cameratus* has often been reported from further afield, for example from Brazil, where Itaituba material identified as *Neospirifer cameratus* by Chen et al. (2004, p. 461, Fig. 9A, D) shows somewhat comparable costal splitting and fasciculation, close to that of *Septospirifer,* without necessarily being conspecific. The interior of the Brazilian specimens was not revealed, and the high degree of alation shows that the form was not close to *Neospirifer*. The specimens illustrated as *cameratus* [not Morton] by Ivanov & Ivanova (1937, p. 54, pl. 1, fig. 4-6, pl. 16, fig. 5, text-fig. 17) lack a median myophragm or septum from the ventral valve (pl. 1, fig. 5) and do not look like Tschernyschew's material.

Septospirifer hughi n. sp.

Fig. 296

1996 *Neospirifer* sp. Shi & Waterhouse, p. 137, pl. 26, fig. 3-9.

Derivation: Named for Hugh Reid.

Diagnosis: Shells with narrow ventral sulcus and high narrow fold, costae fine and branch near mid-length.

Holotype: GSC 97582, figured in Shi & Waterhouse (1996, pl. 26, fig. 3, 8) from "*Yakovlevia transversa*" Zone (Sakmarian), Jungle Creek Formation, in northern Ogilvie Mountains, Yukon Territory, Canada, here designated.

Material: Single specimen with valves conjoined from JBW 413, a ventral valve from JBW 527 and dorsal valve from JBW 530, fragment from JBW 535 and 85. Specimens incomplete.

Stratigraphic and biostratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Description: For specimens from Member D, ventral valve transverse with hinge at maximum width and subalate cardinal extremities. The interarea is moderately high and notably concave, curving through nearly 90º, and marked by horizontal and vertical striae. It bears a delthyrium with angle varying between 40º and 60º in different specimens, bordered by dental grooves: whether it was open is not shown. The dorsal interarea is low and also highly concave, with wide notothyrium, for which further detail is not clear. The ventral sulcus commences at the umbo, widens at 23º, is bordered throughout its length by innermost pair of plicae, and has a concave floor. The dorsal fold is also well defined with a narrowly rounded crest. There are three pairs of narrow plicae that fade after mid-length, and numerous fine costae laterally. Costae have round crests separated by slightly angular interspaces, and increase by branching. The sulcus is occupied by a median rib, with six ribs each side anteriorly in the specimen at JBW 527, and the dorsal fold bears a number of costae. Micro-ornament is poorly preserved, but indicates closely spaced growth laminae arching weakly hingewards over the costae, and pointing weakly forward in interspaces. There is some suggestion of tiny pustules, perhaps due to wear.

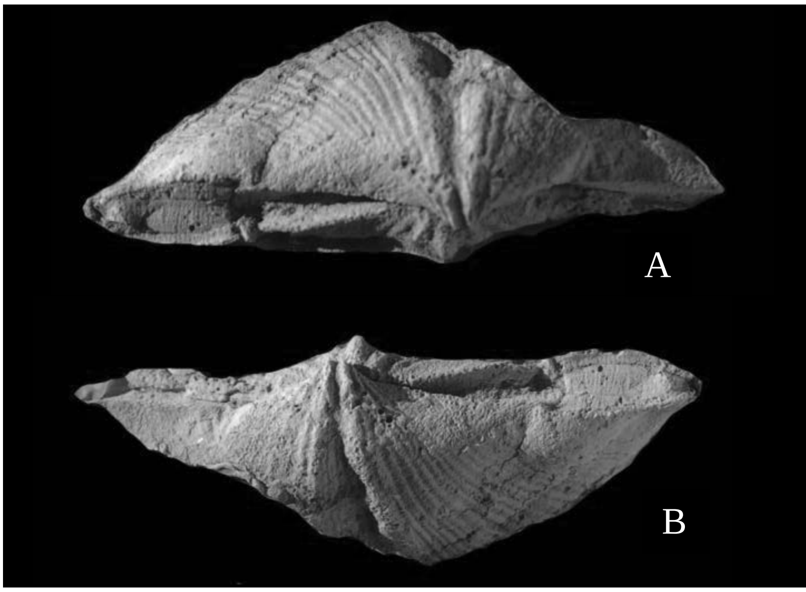


Fig. 296. *Septospirifer hughi* n. sp., latex cast of shell with valves conjoined, GSC 137156 x1.5, showing ventral valve above (in A) and below (in B). From JBW 413, Member D, Jungle Creek Formation.

Teeth supported by scapular-shaped high dental plates and moderately high adminicula, diverging slightly to the floor of the valve and diverging forward. Extending forward is a broad muscle field, with two narrow adductor ridges and wide diductor scars marked by striae radiating postero-laterally from the margin with the adductors. A slender but well formed median septum is exposed in the specimens from JBW 85 and 670 and the posterior floor is heavily thickened, and marked by shallow dimples.

Resemblances: The nature of the sulcus and plicae is strongly suggestive of *Septospirifer* from the underlying *Septospirifer tatondukensis* Zone, but complete specimens are slightly longer and more alate than *Septospirifer tatondukensis*. The specimens are identified with material from the "*Yakovlevia transversa*" Zone, figured as *Neospirifer* sp. by Shi & Waterhouse (1996, pl. 26, fig. 3-9). These specimens are close to *Septospirifer* *tatondukensis* Waterhouse in shape and are assigned to the same genus, given the close agreement in shape and ornament, even though no material is available to show the nature of the ventral interior. Like the material from Member D, the so-called *Neospirifer* has the median ventral sulcus well defined, and bordered by a pair of plicae that retains its height, and the sulcus may be slightly narrower by a few degrees at 22-25º than in *tatondukensis*, and the dorsal fold is slightly higher and narrower. The costae are also narrower in the new form, numbering five to six anteriorly in 5mm, compared with usually three in 5mm on *S. tatondukensis*. *Neospirifer neocameratus* Stepanov in Kalashnikov (1998, p. 47, pl. 11, fig. 7a, b) from the Cisuralian of the Urals is somewhat similar and may prove to

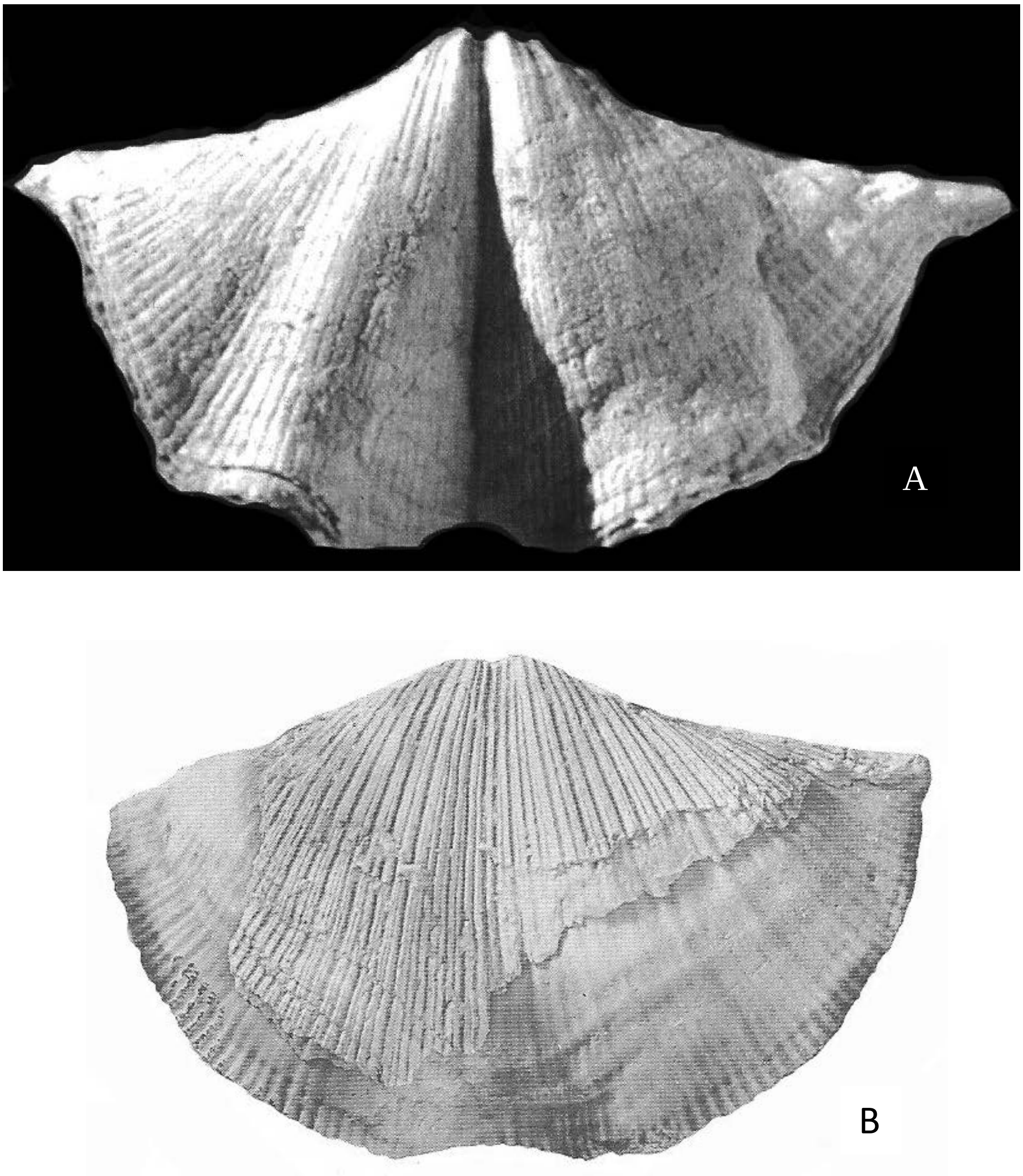


Fig. 297. A, *Gobbettifera angulata* Waterhouse, GSC 136656 from Assistance Formation, x1.4, showing well developed plicae. From Waterhouse (2016, Fig. 247). B, *Fasciculatia greenlandica* Waterhouse, ventral valve from "Productus Limestone" of Greenland, x 1.9. From Dunbar (1955, pl. 23, fig. 6). Cf. Fig. 283.

belong to *Septospirifer*, judged from external appearance. The species is distinguished from *S. hughi* n. sp. by its shallower and narrower ventral sulcus and broader lower ventral umbo. The proposed new species *S. bargasia* (see p. 354) has broader lower ventral umbo, much wider fold, and stronger costae.

Two species of *Septospirifer* have been identified from Mongolia. *S. sarcinatus* Li & Gu (1976, p. 287, pl. 149, fig. 12-17, pl. 150, fig. 1-3) is readily distinguished by its stronger and more round-crested plicae, and *S. extensus* Li & Gu (1976, p. 287, pl. 150, fig. 4-10) is closer to the two Canadian taxa, but smaller and less alate with more persistent dorsal plicae.

Superfamily **SPIRIFERELLOIDEA** Waterhouse, 1968b

[Nom. transl. Waterhouse 2016, p. 212 ex Spiriferellinae Waterhouse, 1968b, p. 9].

Diagnosis: Medium-small distinctively subpentagonal to subtriangular shape and subelongate with short hinge as a rule, plicate, sulcate, variably costate, with micro-ornament of commarginal and radial fila, often pustulose. Umbonal callosity or delthyrial cover plate and connector plate. Adminicula, dental plates, crural plates, no tabellae. Ventral valve often secondarily thickened.

Family **SPIRIFERELLIDAE** Waterhouse, 1968b

[Proposed de novo as full family by Termier et al., 1974, p. 136, independently of Spiriferellinae Waterhouse, 1968b, p. 10].

Diagnosis: Externally distinctive, with rounded plicae and narrow interspaces, may be smooth or costate, micro-ornament cancellate with pustules. Adminicula short, usually buried in secondary thickening, dental plates, ctenophoridium and crural plates. Posterior ventral valve heavily thickened as a rule.

Subfamily **SPIRIFERELLINAE** Waterhouse, 1968b

[Spiriferellinae Waterhouse, 1968b, p. 10. Syn. Hunzininae Angiolini, 2001, p. 332].

Diagnosis: Moderate to well developed dorsal fold, traversed by median groove. Shape weakly transverse to subelongate.

Genus ***Spiriferella*** Tschernyschew, 1902

Diagnosis: Elongate strongly plicate and variably costate, with cancellate and pustulose micro-ornament. Dorsal fold divided by narrow median groove.

Type species: *Spirifer saranae* de Verneuil, 1845, p. 169 from near Krasnoufimsk (Artinskian) in the Urals of Russia, OD.

Discussion: One of the characteristic features of *Spiriferella* lies in the nature of the dorsal fold. The crest is traversed by a shallow groove for its full length in all known species and individuals. Angiolini (1995) provided a different interpretation, and Angiolini & Long (2008) claimed that the fold crest may be rounded. But this is highly contentious. It appears to have been based on the acceptance by Angiolini (1995) that *Spiriferella saranae* (Verneuil) as figured by Tschernyschew (1902, pl. 12, fig. 4, pl. 40, fig. 7) had been correctly identified to genus and species. The specimen of Tschernyschew (1902, pl. 40, fig. 7) has a rounded fold, with no median groove. Inspection of the material by the writer in 1967 at the Tschernyschew Museum in Leningrad (now St Petersburg) suggested that the specimens did not belong to *saranae* (Verneuil), differing in shape and ornament, and moreover coming from a somewhat older level at the Sula River, whereas type *saranae* came from Artinskian beds, near Krasnoufimsk. The specimens were compared by the present author with more or less topotype collections of *saranae* from the Ufa River, and with the Artinskian specimens figured by Tschernyschew (1902, text-fig. 41-46, pp. 524, 525), and it is highly likely that the ventral and dorsal valves illustrated by Tschernyschew (1902, pl. 12, fig. 4, pl. 40, fig. 7) were not conspecific with *saranae*. They were therefore redescribed and named by Waterhouse & Waddington (1982, p. 19) as *Spiriferella barkhatovae* n. sp. and later the species was transferred to the genus *Arcullina* Waterhouse, 1986a (Waterhouse 2004a, p. 200). This genus is typified by its rounded fold-crest and plicae that as a rule are simple and paucicostate. *Arcullina* is based on *Spirifer polaris* Wiman, 1914, p. 39 from the Kungurian-Roadian of Spitsbergen. Kalashnikov (1998) and Grunt (2006b) have described several Russian members of the genus.

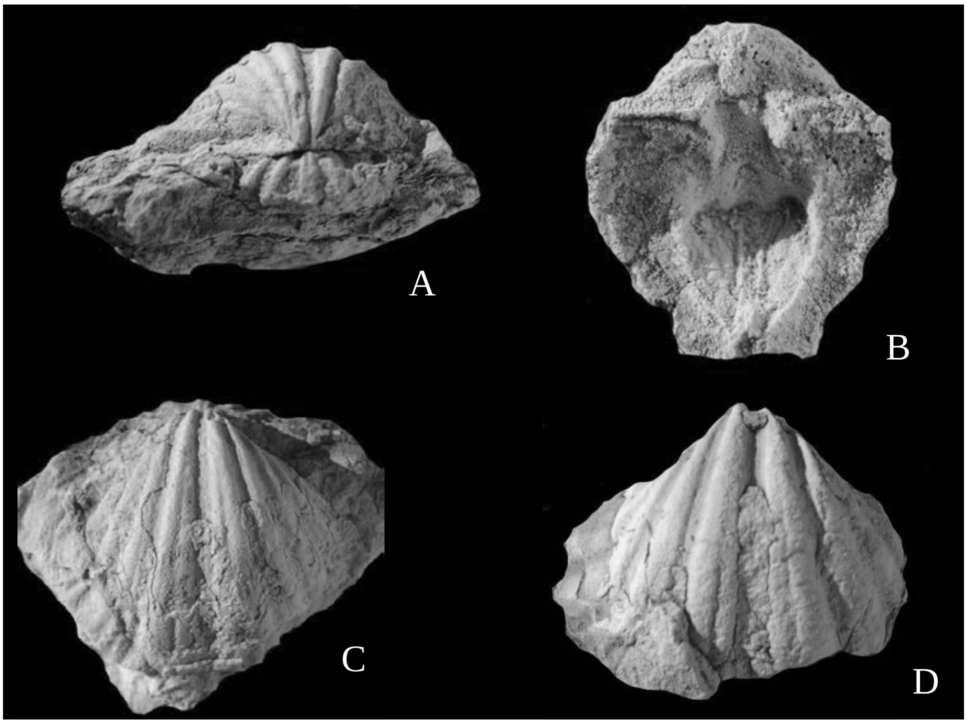


Fig. 298. *Spiriferella yukonensis* Waterhouse & Waddington. A, C, dorsal and ventral aspects of specimen with valves conjoined, GSC 137176 x1.5, from JBW 615, Member A. B, ventral valve 137157 x2, from JBW 57, Member D. D, ventral valve GSC 137175 x2, from JBW 852, Member A, Jungle Creek Formation.

Spiriferella yukonensis Waterhouse & Waddington, 1982

Fig. 298 - 300

1971 *Spiriferella* sp. Bamber & Waterhouse, p. 127, pl. 11, fig. 7.
1982 *Spiriferella yukonensis* Waterhouse & Waddington, p. 12, pl. 1, fig. 11-20, text-fig. 11c-f, 12.

Diagnosis: Moderately convex shells with small ventral umbo, plicae simple, rounded, three to five ventral pairs and four dorsal pairs, few or no costae as a rule, sulcus relatively deep and narrow with one to seven costae, crest of fold cleft for entire length, muscle platform slightly raised.

Holotype: ROM 28205 from basal Jungle Creek Formation of Gzhelian age, Ogilvie Mountains, Canada, figured by Waterhouse & Waddington (1982, pl. 1, fig. 11, 12), OD.

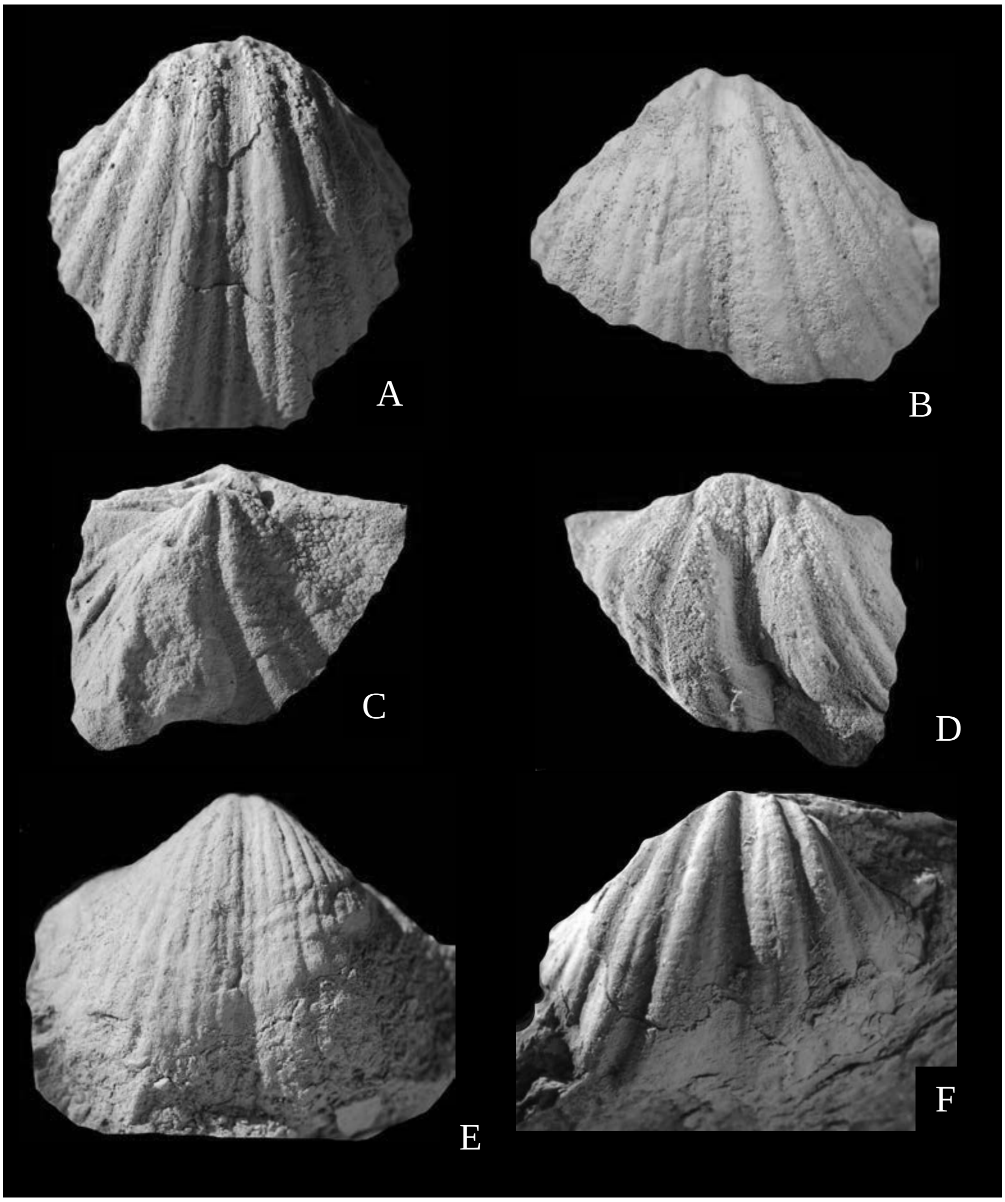


Fig. 299. *Spiriferella yukonensis* Waterhouse & Waddington. A, ventral valve GSC 137157 x2.5, from JBW 57. B, ventral valve GSC 137158 x2.5, from JBW 52. C, D, ventral and dorsal views of internal mould GSC 137159 x2, from JBW 136. E, ventral valve GSC 137163 x1.5, from JBW 516. F, ventral valve GSC 137161 x2, from JBW 197. A from Member D, B – F from Member A. Jungle Creek Formation.

Material: From Member A, single ventral valves from JBW 53, 77, 85, 135, 145, 180, 197, 198, 205, 220, 404, 433, 442, 515, 516, 597, 632, 725, 758, 792 and 852, and GSC loc. 57155, three ventral valves from JBW 628, twelve ventral valves and specimen with valves conjoined from JBW 615, and an internal mould of a specimen with valves conjoined from JBW 136. Single ventral valves from JBW 52 and 57 in Member D.

Stratigraphic and biostratigraphic levels: Members A and D, Jungle Creek Formation. *Septospirifer tatondukensis* Zone and *Rugivestigia commarginalis* Zone.

Discussion: This species was described and discussed in Waterhouse & Waddington (1982) from mostly Member A of the Jungle Creek Formation, where it is abundant, and a few specimens are found in Member D. The present overview illustrates a few mostly ventral valves from various localities.

Fig. 300. *Spiriferella yukonensis* Waterhouse & Waddington, dorsal aspect of specimen with valves conjoined, GSC 137176 from JBW 615, x8, showing slender groove along crest of dorsal fold (cross) opposing the ventral sulcus (star). See Fig. 298A, C. Member A, Jungle Creek Formation.

Genus ***Eridmatus*** Branson, 1966

Diagnosis: Distinctively shaped subpentagonal shells with wide hinge and wide anterior-lateral margins, deep angular sulcus and wide dorsal fold, hinge and anterior shell both close to maximum width. Small convex stegidium. Lateral plicae fine and sulcus and fold ornamented by numerous costae, pustules well spaced.

Type species: *Spirifer* (*Trigonotreta*) *texanus* Meek, 1871, p. 179 from Kansas (Desmoinesian), United States, OD.

Discussion: As illustrated by Carter (2006a, pp. 1805, 1806, Fig. 1199, 1a-d), the considerable width of the hinge, matched by extended anterior lateral margins, make up the principal differences from *Spiriferella*, and as well, the dorsal fold in the type species is comparatively broad at the anterior margin. The number of species – and specimens – referred to Spiriferellidae world-wide are so numerous that discernment of strands of species is possible, and although some supposed genera should be set aside after careful consideration, such as *Tintoriella* Angiolini, according to Shen et al. (2001), most proposals have withstood close scrutiny. The difficulty in the case of *Eridmatus* concerns the variation within the genus, and whether species have been correctly referred to the genus, other than the type species. Genus *Eridmatus* Branson, 1966, with type species *Spirifer* (*Trigonotreta*) *texanus* Meek, 1871, p. 179 from Desmoinesian beds in Kansas, United States, is a distinctively shaped subpentagonal shell with wide hinge and matching anterior lateral margins, deep angular sulcus and wide dorsal fold. Lateral plicae are fine and sulcus and fold ornamented by numerous costae. As stressed by Carter (2006a, pp. 1805, 1806, Fig. 1199, 1a-d), the width of the hinge offers a principal difference from *Spiriferella*, as suggested in Branson (1966, pl. 1, fig. 1a, b), and the wide hinge is apparent for some of the specimens in the type species, though some are not particularly outstanding in that particular regard. The comparably wide anterior offers a more striking discrimant.

Cooper & Grant (1976a) referred the species *Spiriferella editiareatus* (Einor in Licharew & Einor, 1939, pl. 26, fig. 1-4, pl. 25, fig. 8) to *Eridmatus*, but Kalashnikov (1998, p. 62, pl. 17, fig. 1-3, pl. 18, fig. 4) referred material so identified from the north of European Russia to *Arcullina*, together with other specimens.

Eridmatus parva (Cooper, 1957)

Fig. 301

1957 *Spiriferella parva* Cooper, p. 57, pl. 11A, fig.1-5.

Diagnosis: Elongate shells with anterior shell slightly wider than wide hinge, plicae in three or four pairs.

Holotype: USNM 125405, figured as above from Coyotte Butte Formation (Asselian?, Sakmarian), Oregon, OD.

Material: A specimen with valves conjoined and three ventral valves from JBW 4.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: The specimen with valves conjoined is 18mm wide, 25mm long and 16mm high, the ventral valve about twice as high as the dorsal valve. The hinge is moderately wide, and maximum width lies well forward near the anterior fourth of the length. The sulcus commences at the incurved beak, and forms a shallow groove-like channel occupied by a median rib, and the sulcus is bordered by a pair of plicae, of which the crests diverge at close to 30^{o}, and the angle broadens close to the anterior commissure, the crests curving out slightly. The corresponding dorsal fold also flares out anteriorly, but unfortunately the posterior part has been destroyed. There are four pairs of ventral plicae, the fourth and outer pair very low and not persisting far forward, and the interspaces are narrow. Five costae lie over the anterior part of the inner pair of plicae, in two pairs with a dividing rib, three costae on the next plication and two on the third pair. There are three pairs of dorsal plicae, only the inner pair bearing two costae anteriorly, and the interspaces are wider than those of the ventral valve.

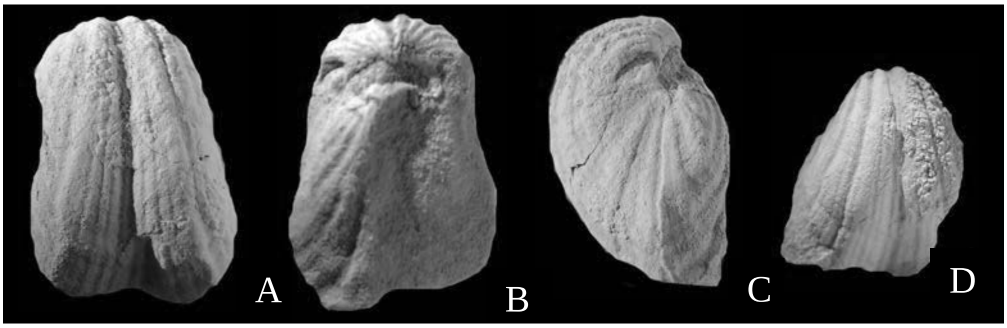


Fig. 301. *Eridmatus parva* (Cooper). A, B, C, ventral, dorsal and lateral aspects of GSC 137448, x1.5. D, ventral aspect of incomplete specimen GSC 137449, x1.5. From JBW 4, Member A, Jungle Creek Formation.

Resemblances: This material is identified with the highly distinctive species *parva*, based on a solitary specimen from the Coyote Butte Formation of Oregon. There are slght differences: the inner ventral plicae are straighter in outline in the type, the ventral umbo more incurved, and the dorsal valve is a little more inflated

The type species *Eridmatus texanus* (Meek, 1871) from the Desmoinesian of Kansas, United States, is larger with more and narrower plicae pairs, and, as well figured especially by Branson (1966) and Spenser (1967), has wide hinge and wide anterior shell, with fold flaring anteriorly. The sulcus is deeper than that of the Canadian species, but is equally wide. Dunbar & Condra (1932, pl. 38, fig. 6-10, 13) figured specimens from the Cisco Group in Texas and from Oklahoma that show a wide hinge, little if at all wider than the anterior shell, and moderately to not noticeably deep ventral sulcus, not as extreme in shape as those figured as typical by Carter (2006a). *Eridmatus petita* Waterhouse & Waddington, 1982 also has a wide hinge and more plicae pairs, though fewer than in *texanus,* and is assigned to a separate new genus, being close to *E. marathonensis* Cooper & Grant (1976a).

Eridmatus erjakhensis Kalashnikov (1998, p. 60, pl. 19, fig. 2, pl. 20, fig. 1-4, text-fig. 10) is somewhat intermediate in shape between the species *texanus* and *parva* (see especially Kalashnikov, 1998, pl. 19, fig. 2, pl. 20, fig. 1b). It comes from the younger Cisuralian Talatin Suite of Pai Hoi in north Russia. Another species assigned by Kalashnikov to *Eridmatus, Spiriferella talbeica* Ifanova (1972, pl. 13, fig. 3, 4; Kalashnikov 1990, pl. 20, fig. 7, 8) from the same beds is somewhat similar in shape.

Genus ***Eridmatina*** n. gen.

Diagnosis: Small to medium size, hinge wide and may be alate, anterior margins less produced than in *Eridmatus* Branson. Fold may flare anteriorly, and surface pustules comparatively few as in *Eridmatus*.

Type species: *Eridmatus marathonensis* Cooper & Grant, 1976a, p. 2220 from Gaptank Formation, *Uddenites*-bearing Shale Member (Gzhelian), United States, here designated.

Discussion: This genus is formally proposed and discussed on p. 464.

Eridmatina petita (Waterhouse & Waddington, 1982)

Fig. 302

1982 *Eridmatus petita* Waterhouse & Waddington, p. 29, pl. 2, fig. 1-6, Fig. 11g, h.

Diagnosis: Closely costate small to medium shells with strong plicae, well rounded outline, wide hinge and prominent ventral umbo.

Holotype: GSC 35502 from JBW 19, figured by Waterhouse & Waddington (1982, pl. 2, fig. 2, Fig. 11h) from Member B, Jungle Creek Formation (Asselian), Yukon Territory, OD.

Material: Two ventral valves from JBW 87 and JBW 195, four ventral valves from JBW 581, and a ventral valve and dorsal valve from JBW 99 from Member E may be added to the record of the species in Waterhouse & Waddington (1982). From Member D, poorly preserved specimens include some ten ventral valves from JBW 52, and ventral valve from JBW 565.

Stratigraphic and biostratigraphic level: Members D and E, Jungle Creek Formation. *Rugivestigia commarginalis* Zone and *Ogilviecoelia shii* Zone. Original types came from Member B.

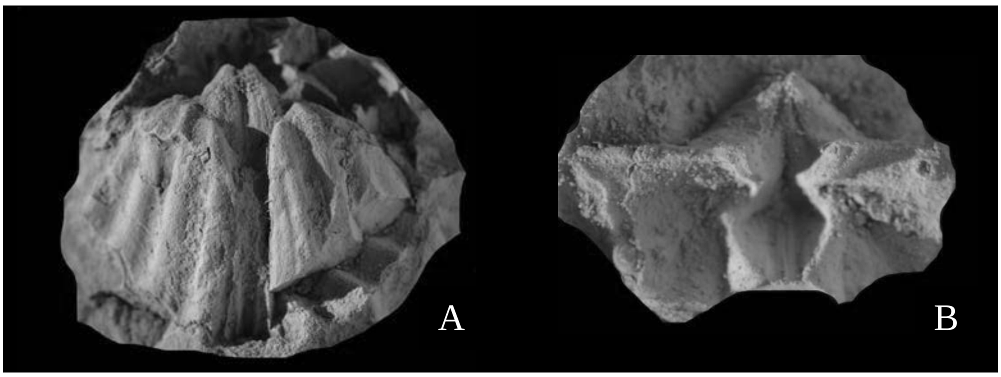


Fig. 302. *Eridmatina petita* (Waterhouse & Waddington). A, B, ventral internal mould and cast of ventral valve GSC 137164 x2, from JBW 195. Member E, Jungle Creek Formation.

Resemblances: The species *petita* is not that close to *Eridmatus texanus* Meek as figured by Spenser (1967), because the sulcus is not as deep and wide, and the shape somewhat different. It is much closer to *E. marathonensis* Cooper & Grant (1976a, pl. 626, fig. 10-20) from the Gaptank Formation of west Texas, especially the specimen of pl. 626, fig. 10-12, described as a juvenile. The hinge is wide as in *Eridmatus* and the dorsal fold (see Waterhouse & Waddington 1982, pl. 2, fig. 6) shows similar anterior flare.

The type specimens of *petita* comes from shales exposed at JBW 19, which lies just above JBW 4 with *Eridmatus parva* (Cooper) in the upper part of Member A of the Jungle Creek Formation, at sections 34 and 42 of Shi & Waterhouse (1996, Fig. 4).

Subfamily **ARCULLININAE** Waterhouse, 2016

[Arcullininae Waterhouse, 2016, p. 220].

Diagnosis: Dorsal fold with no median groove. Upper Pennsylvanian (Kasimovian) to Upper Permian (Changhsingian).

Genus ***Plicatospiriferella*** Waterhouse & Waddington, 1982

Diagnosis: Dorsal fold high with no median groove. Plicae moderately numerous, rounded broad crests.

Type species: *Plicatospiriferella canadensis* Waterhouse & Waddington, 1982, p. 34 from Ettrain equivalents (Kasimovian) of Yukon Territory, OD.

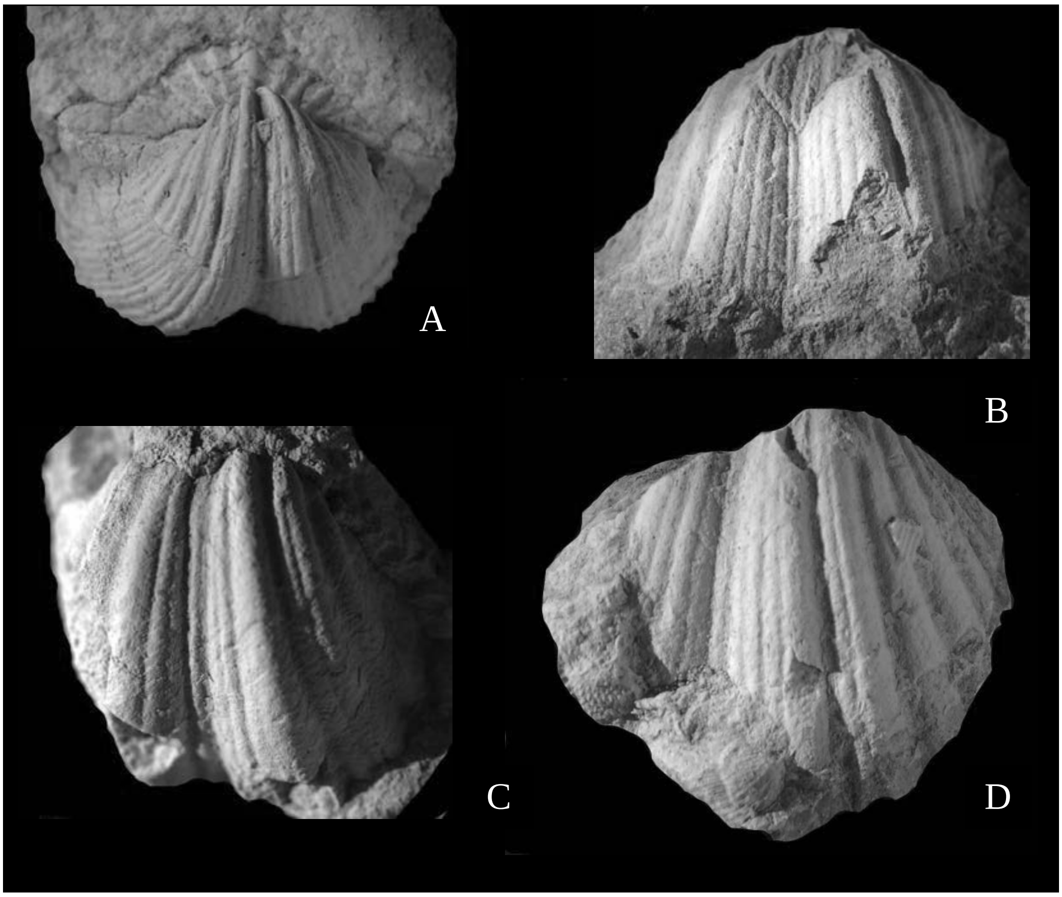


Fig. 303. *Plicatospiriferella undulata* n. sp. A, posterior view of specimen with valves conjoined, GSC 137165 x1.5, holotype. B, damaged ventral valve GSC 137166 x1.5. C, ventral valve GSC 137167 x2. D, broken ventral valve GSC 137160 x2. From JBW 18, Member C, Jungle Creek Formation.

Plicatospiriferella undulata n. sp.

Fig. 303 - 305

Diagnosis: Moderately large inflated shells with incurved umbo, bearing six or seven pair of rounded crested plicae, deep sulcus, low fold without median groove.

Holotype: GSC 137165, here designated

Material: Seven ventral valves and two dorsal valves from JBW 18, one ventral valve from JBW 91**.**

Stratigraphic and biostratigraphic level: Member C, Jungle Creek Formation. *Kochiproductus imperiosus* Zone.

Description: Largest specimen approximately 31mm wide, 32mm long, and 15mm high, another 36mm wide, 32mm long and 18mm high, whilst a smaller specimen is 24mm wide, 19mm long and 12mm high. Ventral valve swollen and highly arched, with umbonal angle of 70º and the umbo incurved, above a high interarea and arched delthyrium closed by a deltidium composed of two deltidial plates fused along the mid-line. Sulcus commences at umbonal tip and widens forward with an angle close to 20º, becoming deep and subangular in cross-section. There are seven pairs of plicae, rarely six, curving a little outwards and forwards, with broad crests and narrow interspaces. Anteriorly in the largest specimen the sulcus is occupied by four pairs of costae which split, and there is a median rib. A rib is present anteriorly on the plicae pair beyond the sulcal edge, and in some specimens the anterior parts of the inner plicae are costate, but in other specimens plicae are rounded with no costae. In the small measured specimen 24mm wide the sulcus is occupied by a pair of costae. Fine commarginal growth increments number five up to seven in 1mm, with fine small pustules, and on one fragment there are radial lirae as well, four or five in 1mm. The posterior shell is 6mm thick in a large specimen. The dorsal valve is much less inflated, with large ears, and the median fold is narrow and low with broadly rounded rounded crest. Only the posterior fold is preserved.

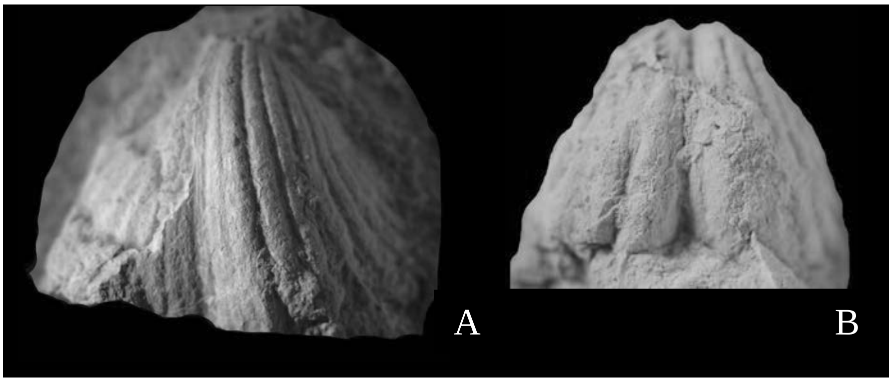


Fig. 304. *Plicatospiriferella undulata* n. sp.. A, ventral valve GSC 137168 x1.5. B, ventral valve GSC 137170 x2. From JBW 18, Member C, Jungle Creek Formation.

Resemblances: This species is comparatively large and inflated, with a high number of plicae that may become costate anteriorly, and a low fold without a median groove, at least as far as preserved. The simple plicae, and restriction of costae to the sulcus further suggests an approach to *Plicatospiriferella canadensis* Waterhouse & Waddington (1982, p. 34, pl. 1, fig. 7-10, text-fig. 11a, b) from Kasimovian beds equivalent to the Ettrain Formation.

The present specimens are larger as well as younger than *Plicatospiriferella canadensis*, which has five pairs of dorsal plicae and three lateral costae, and six pairs of ventral plicae. Costae are few and limited to the anterior shell. The median dorsal fold has a gently convex crest with no median groove. Several species from north-east Russia were ascribed to *Plicatospiriferella* by Klets (2005, pl. 16, 17) and agree in having more than the usual number of plicae, which have well rounded broad crests. Shells figured as *P. grata* by Klets (2005, pl. 15, fig. 1-3) from upper Carboniferous of northeast Russia have a similar fold and simple non-costate plicae, but others assigned to the same genus show a sulcate dorsal fold, including *P. akachanica* Klets and shells like the original types which were assigned by Klets (2005) to *P. ploskajae* (Zavodowsky). *P. costata* Klets (2005, pl. 17, fig. 1-14) is anteriorly costate. In these forms*, akachanica* and *ploskajae* and possibly in *costata*, the dorsal fold carries a distinct although shallow and narrow channel, especially over the anterior shell, whereas the fold in the type species *Plicatospiriferella canadense* Waterhouse & Waddington (1982) is flatly rounded.

The genus *Arcullina* Waterhouse, 1986a, type species *Spiriferina polaris* Wiman, 1914, p. 39 from Guadalupian faunas of Spitsbergen, also has a rounded crest to the dorsal fold, without a median groove. In this genus the plicae are more narrowly rounded, and are as a rule higher than those of *Plicatospiriferella.* One of the closest members of this genus in terms of overall size and shape, and the number of rounded-crested plicae was figured as *Spiriferella saranae* by Tschernyschew (1902, p. 522, pl. 12, fig. 4, pl. 40, fig. 7) from the Schwagerina-Kalk of the Urals in Russia.

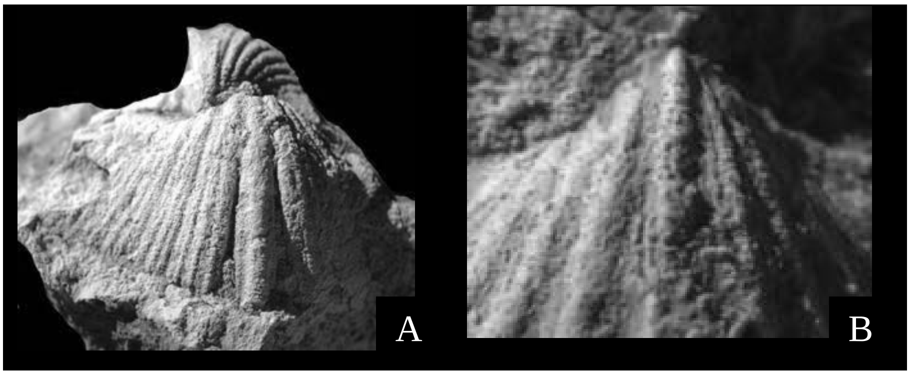


Fig. 305. *Plicatospiriferella undulata* n. sp. A, dorsal view of specimen with valves conjoined, GSC 136169 x2. B, posterior view of dorsal valve showing rounded dorsal fold which lacks a median groove (apart from a decorticated segment that shows the inner median ridge or myophragm), GSC 137171 x4. From JBW 18, Member C, Jungle Creek Formation.

Suborder DELTHYRIDINA Ivanova, 1972

[Delthyridina Ivanova, 1972, p. 41].

Diagnosis: Shells smooth or plicate, costae rare, sulcus and fold widespread, commargons or lamellae common, micro-ornament may be distinctively fimbriate, or with frilly laminae in some genera of one superfamily, but also involves closely related genera with capillate or cancellate micro-ornament, or finely spinose along commarginal rows in various groups, or with spines that are elaborate and double-barrelled as in members of another group. Delthyrium variously open, or covered in part or whole by deltidia, or connector plate. Internal plates varied.

Infrasuborder DELTHYRIMORPHI Ivanova, 1972

[Nom. transl. hic ex Delthyridina Ivanova, 1972, p. 41].

Diagnosis: Highly variable in many aspects of morphology, and typically biconvex and smooth or less commonly plicate, by contrast with more limited range of shape and ornament in Ambocoeliimorphi (see below). Micro-ornament highly variable, includes unusually elaborate spines in some lineages.

Superfamily **ELITOIDEA** Fredericks, 1924b

[Nom. transl. et correct. Waterhouse 2016, p. 326 ex subfamily Elythinae Fredericks, 1924b, p. 304].

Taxonomy: The name giver of the genus was proposed as *Elita* Fredericks, 1918, p. 87, although it has been mis-spelled as as Elythinae in many subsequent publications, starting with the proposal of the subfamily by Fredericks (1924b) as endorsed by Carter in Carter & Gourvennec (2006c, p. 1864). It is surely time to retrieve rather than consolidate the error, according to the principle of non-alienation between genus and family group names. Fredericks also proposed the subfamily Brachithyrinae, instead of Brachythyrinae, and this was speedly corrected, as noted previously on p. 319. It would seem that the letters y and i had understandably become confused, given the similarity – if not full identity – in sound, when the letter is used as a vowell.

Diagnosis: Shell smooth or plicate, fold and sulcus if present weakly developed, ornament of biramous spines.

Discussion: Double-barrelled spines are present in various genera that have been classed previously in Reticularioidea, which are reserved for genera with single-barrelled spines. Here the genera are allocated according to the nature of the spines, and the two strands, divided according to the development of single or double-barrelled spines, have been independent of each other since Pragian (Lower Devonian) times.

Family **TORYNIFERIDAE** Carter, 1994

[Nom. transl. Waterhouse 2016, p. 329 ex Toryniferinae Carter in Carter et al. 1994, p. 359].

Diagnosis: Connector plate well developed or absent. Internal plates varied.

Discussion: Spines are more elaborate than in Elitidae (Carter in Carter & Gourvennec 2006c, p. 1864).

Subfamily **SPIRELYTHINAE** Waterhouse, 2016

[Spirelythinae Waterhouse, 2016, p. 331]

Diagnosis: Distinguished from Toryniferinae by lack of dorsal cardinal plate and presence of ctenophoridium. Ornament of double-barrelled spines. Ventral valve with dental plates, adminicula, low well defined median ridge, connector plate and pleromal ridges as a rule. Dorsal valve with crural plates, low median ridge.

Discussion: This subfamily is based on *Spirelytha* Fredericks, 1924b, p. 304 from late Guadalupian of the Arctic, and is distinguished from Toryniferinae by the absence of a cardinal plate, with other differences.

Tribe **SPIRELYTHINI** Waterhouse, 2016

[Spirelythini Waterhouse 2016, p. 331].

Diagnosis: Distinguished from the other tribe within the subfamily, Kletsiini Waterhouse, 2016, p. 336, by lack of conjunct crural plates.

Discussion: Genera include *Spirelytha* Fredericks, *Stepanoviina* Zavodowsky and *Taimyrella* Einor. The type species of *Spirelytha* is comparatively obscure, having been based on *Spirifer scheii* Tschernyshew in Tschernyshew & Stepanov (1916a, b), not *Spirifer scheii* Meyer, 1913. The morphology was clarified by Archbold & Thomas (1984b, p. 313), in pointing out that silicified material from Axel Heiberg Island in the Canadian Arctic probably belonged to the genus and species. This had been described as *Spirelytha* for ventral valves, and as misidentified *Permophricodothyris* for dorsal valves by Stehli & Grant (1971). The ventral valves show median septum and moderately short adminicula with a posterior connector plate, and the dorsal valves show crural plates and very low if any median septum, with no tabellae. There are indications of a low pleromal ridge along the junction of the dental and adminicular plates, which potentially could have matured into a connector plate.

Genus ***Spirelytha*** Fredericks, 1924b

Diagnosis: Suboval shells with shallow ventral sulcus, low fold, lateral slopes smooth, micro-ornament of single row of double-barrelled spines along each commargon. Ventral valve with median septum, teeth and dental plates, short adminicula and connector plate, dorsal interior with very short or negligible median ridge, socket plates and no tabellae or cardinal plate.

Type species: *Spirelytha pavlovae* Archbold & Thomas, 1984b, p. 313 (nom. nov. pro *Spirifer scheii* Tshernyschew in Tschernyschew & Stepanov, 1916b, p. 45, non Meyer 1913) from Store Bjørnekap of Roadian age, Ellesmere Island, Arctic Canada (not the Russian Arctic as in the *Revised Brachiopod Treatise*).

Spirelytha biakovi n**.** sp.

Fig. 306 - 308

Name: For Alexander Biakov.

Diagnosis: Small subpentagonal shells with extended umbo and long posterior walls, no or only faint sulcus or fold. Micro-ornament of double-barrelled spines along commarginal rows.

Holotype: GSC 137321, here designated.

Material: From Member A, Jungle Creek Formation, single ventral valves from JBW 33, 193 and 444, three ventral valves from JBW 4, specimen with valves conjoined but displaced, and a ventral valve from JBW 673. Two ventral valves and dorsal valve from JBW 122. A specimen with valves conjoined and a ventral valve from JBW 622, and dorsal valve from JBW 404. Three ventral valves from JBW 4. From the Ettrain Formation, a specimen with valves conjoined and ventral valve from JBW 620.

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Fig. 306. *Spirelytha biakovi* n. sp., ventral valve GSC 137450 x2, from JBW 4, Member A, Jungle Creek Formation.

Description: Specimens small, transversely subrounded to subpentagonal in shape, extended ventral umbo weakly incurved with angle mostly close to 80º, up to 100º, and low steeply convex umbonal walls curving out to

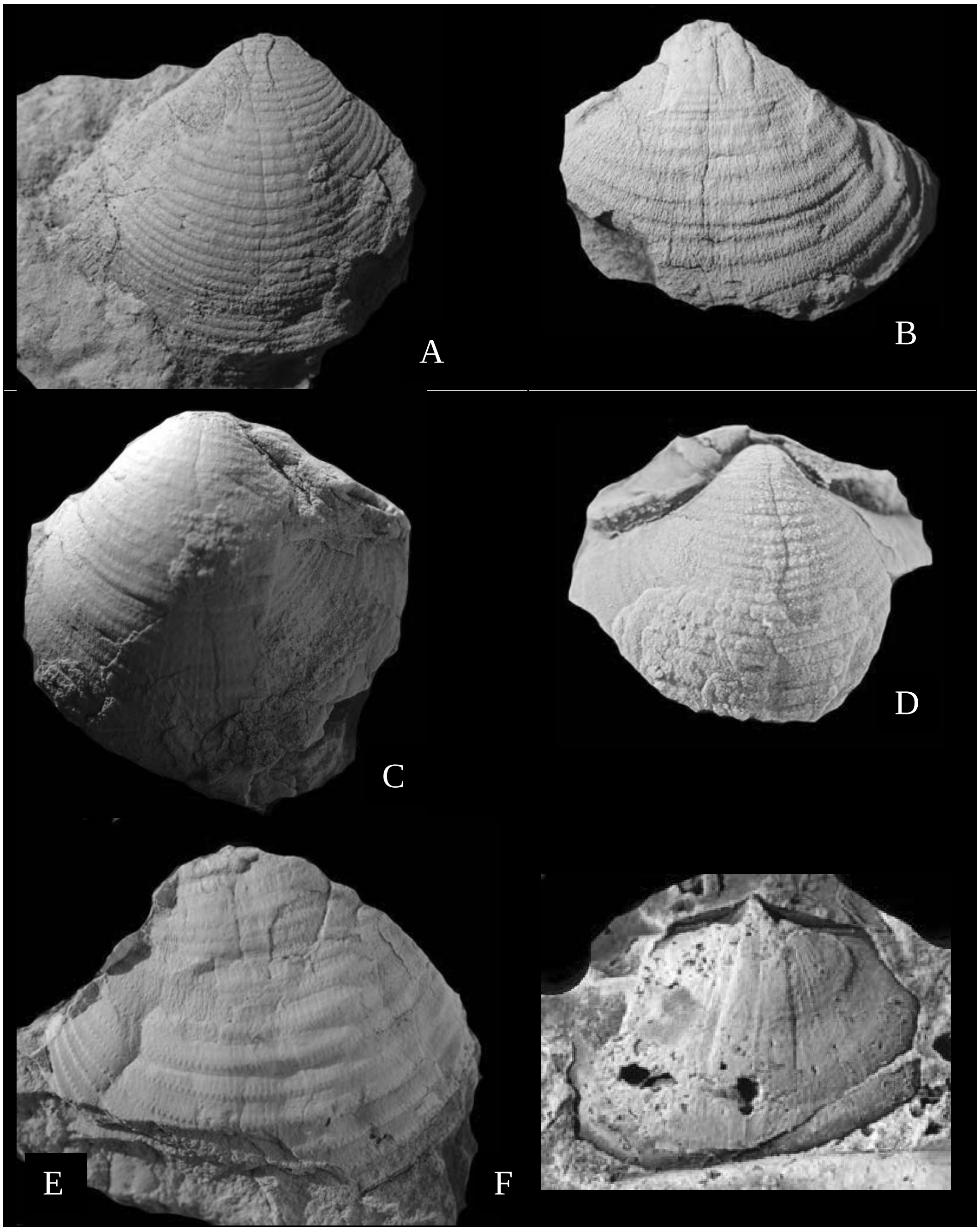


Fig. 307. *Spirelytha biakovi* n. sp. A, ventral valve GSC 137172 x2, from JBW 33. B, partly decorticated ventral valve GSC 137321 x2, holotype, from JBW 662. C, ventral valve GSC 137173 x2.5, from JBW 673. D, ventral valve GSC 136795 x4, from JBW 662. E, worn ventral valve GSC 136795 x2, from JBW 602. F, internal mould of dorsal valve GSC 137173 x5, from JBW 404. Member A, Jungle Creek Formation.

obtuse cardinal extremities, maximum width of shell placed in front of mid-length, faint anterior sulcus in some shells. Dorsal valve less convex with no fold. Hinge wide, ventral interarea moderately high, weakly defined with delthyrium of 60º but largely obscure, dorsal interarea planar, distinct, with broad notothyrium of angle close to 80º. Ornament on both valves of regular commarginal rugae bearing very fine spines, apparently arising in single row for each commargon, but often obscure because the spines lie prostrate over the surface to mask other spines in front.

Ventral interior with long median septum extending for approximately two thirds of shell length, and adminicula extending for a quarter of shell length. Dorsal valve with what may be a tiny cardinal process area, long median groove and no median septum, no tabellae. Long subrectangular adductor impressions.

Resemblances: The species is characterized by shape, the presence of a long ventral median septum, moderately well formed adminicula, absence of dorsal septum, and long dorsal adductors. *Spirelytha svartevargensis* Waterhouse (2016, p. 334) from Axel Heiberg Island of Canada is similar in the lack of a dorsal septum, but has broader umbo and different more transverse shape. The present species is closer to *S. fredericksi* Archbold & Thomas (1984b) from the Callytharra Formation (Sakmarian) of Western Australia, but this form has a more pronounced ventral sulcus and dorsal fold. Specimens ascribed to *Spirelytha fredericksi* Archbold & Thomas from the "*Yakovlevia transversa*" Zone in the younger Jungle Creek Formation by Shi & Waterhouse (1996, p. 145, pl. 28, fig. 13-21) have a long ventral septum, but the umbonal angle is consistently broader and shell more transverse, with other differences. A sulcus and low fold are developed on some specimens, and somewhat similar specimens were recorded from the Cisuralian of northeast Russia by Klets (2005, pl. 26, fig. 6-11). The Late Carboniferous species *S. stepanovi* (Zavodowsky 1970, pl. 36, fig. 5, 6; Pavlova 1977, p. 59, pl. 10, fig. 9; Abramov & Grigorieva 1983, pl. 29, fig. 15-17 and Klets 2005, pl. 29, fig. 1-5) from the Irbichan horizon of Kolyma-Omolon and Mishkinsk Suite of southern Verchoyan is more elongate. *S. kislakovi* Klets (1987, pl. 4, fig. 1-7; 2005, pl. 24, fig. 1-10, pl. 25, fig. 1-7) is more transverse, with broad ventral umbo and shorter adminicula, with other differences. The species is of Lower Permian age, and comes from southern Verchoyan.

Fig. 308. *Spirelytha biakovi* n. sp. external mould of GSC 137174 from JBW 193, x6. Member A, Jungle Creek Formation.

Family **PHRICODOTHYRIDAE** Caster, 1939

[Nom. transl. et correct. Waterhouse 2016, p. 339 pro Phricodothyridinae Carter in Carter et al. 1994, p. 359, pro Phricodothyriinae Caster, 1939, p. 145].

Diagnosis: Single- and predominantly double-barrelled spines generally in one or often two rows over each commargon. Dental plates reduced, no adminicula, no well developed ventral median septum. Deltidial plates and connector plate present or absent. No tabellae. Spiralia laterally or postero-laterally directed.

Discussion: Because of the absence of adminicula, this group is separated as a family from somewhat similar genera referred to Elitidae (Elythidae) in the *Revised Brachiopod Treatise.* The low ventral median septum tends to be less prominent in *Phricodothyris* and absent from other genera, and is absent from the other subfamilies, Anomaloriinae and Astegosiinae, and no genus displays tabellae. It seems likely that *Phricodothyris* as the oldest genus within the family inherited the median ventral septum along with Elitidae, and later family members soon lost the septum, or retained only a low median ridge. Several genera developed a connector plate.

Phricodothyrid? gen. & sp. indet. A

Fig. 309

Material: Ventral internal mould from JBW 189.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: The specimen has a well formed sulcus developing a short distance in front of the umbo. No trace is preserved of external ornament, apart from low anterior commarginal rugae, and there are no well-formed dental plates or adminicula. As shown in the figure, deep elongately oval adductor impressions are separated by a short moderately high myophragmal ridge that does not extend beyond the muscle field.

Fig. 309. Phricodothyrid? gen. & sp. indet. A internal ventral mould, GSC 137037 x5 from JBW 189. Member A, Jungle Creek Formation.

Phricodothyrid? gen. & sp. indet. B

Fig. 310

Material: A complete ventral valve, from JBW 437.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

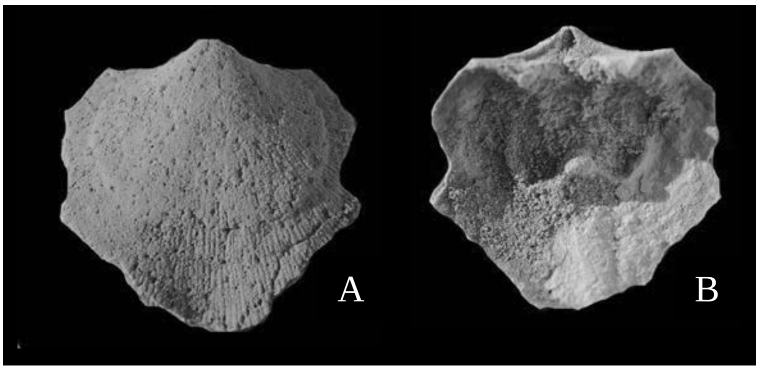


Fig. 310. Phricodothyrid gen. & sp. indet. B. A, B, external and internal aspects of ventral valve GSC 137175 x2, from JBW 437. Member A, Jungle Creek Formation.

Description: The specimen has a shallow and anteriorly placed sulcus, and has low dental projections with low if any dental plates and no adminicula. The delthyrium is now open. The external shell surface is covered by rows of fine double-barrelled spines flattened against the surface. As shown in Fig. 310B, two low ridges surround what appear to be diductor impressions, which is not the normal morphology in phricodothyrids.

Phricodothyrid gen. & sp. indet. C

Fig. 311

Material: Three ventral valves and two or more dorsal valves from JBW 762.

Stratigraphic and biostratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Description: Specimens are small and poorly preserved, with no external ornament preserved. The ventral valve has long posterior walls and ovally subpentagonal shape with no median septum and no adminicula. The dorsal valve is ovally transverse with no medium septum and no tabellae. There are some similarities to *Triramus canadensis* (see below), but the posterior internal mould of the dorsal valve is raised in a manner not seen in this species.

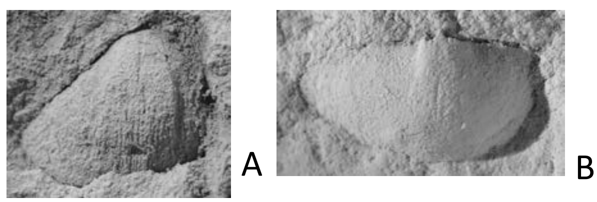


Fig. 311. Phricodothyrid gen. & sp. indet. C. A, incomplete internal mould of ventral valve GSC 137438 x2. B, internal mould of dorsal valve GSC 137439 x3. From JBW 762, Member D, Jungle Creek Formation.

Family **CONDRATHYRIDAE** Waterhouse, 2016

[Condrathyridae Waterhouse, 2016, p. 348].

Diagnosis: Ornament of spines, involving double-barrelled spines of one or two different diameters, and may have single-barrelled slender spines as well. Spiralia laterally or posteriorly directed. Dental plates reduced, separate deltidial plates may partly close delthyrium, connector plate short or as a rule absent; median ridges subdued or absent.

Discussion: Condrathyridae are a minor lineage delineating a sequence of genera with double-barrelled spines of two diameters, based on the genus *Condrathyris* Minato, 1953. One of the genera, *Khaophrikia* Waterhouse, is exceptional in that it displays strong and slender double-barrelled spines as in Condrathyridae, but approaches *Anomaloria* Cooper & Grant in some respects. The group as close to Phricodothyridae, with which it shares an interior lacking adminicula and tabellae, and distinguished by the more diverse spinose ornament.

Genus ***Triramus*** Waterhouse, 2016

Diagnosis: Oval smooth shells with shallow or imperceptible ventral sulcus and dorsal fold, ornamented over parts of the shell by one or more rows of thick double-barrelled spines, behind one or rarely more rows of evenly spaced single-barrelled spines over low commarginal growth lamellae or growth steps on each valve, as well as rows or scattered slender double-barrelled spines. Teeth supported by low dental ridges, median ventral ridge low or absent, no adminicula; dorsal socket and inner hinge plates, long low or no median dorsal ridge, no tabellae. Spiralia laterally directed.

Type species: *Triramus canadense* Waterhouse, 2016, p. 351 from Member E of Jungle Creek Formation (Asselian), Yukon Territory, Canada, OD.

Discussion: This genus is close to *Phricodothyris* George, 1932, but has more elaborate ornament, with rows of single-barrelled spines as well as double-barrelled spines of two diameters. Members of Phricodothyrinae tend to have single rows of biramous spines of subuniform diameter, but are similar in internal plates. Compared with *Phricodothyris* as described by Brunton (1984), and apart from the difference in spines, *Triramus* is distinguished by the presence of a dorsal septal ridge in many but far from all specimens, often a low ventral ridge, and open nature of the delthyrium, which is partly closed in *Phricodothyris* by flat deltidial plates. George (1932) emphasized the lack of a dorsal septum from the British type and associated material of *Phricodothyris*, and although it is true that Demanet (1938) reported a ventral septum in material from Belgium, such is less evident in the British material (Campbell 1955). The micro-ornament in *Phricodothyris*, as assessed by Pavlova (1969), displays only single rows of double-barrelled spines.

Condrathyris Minato has rows of slender and broader double-barrelled spines, and *Biramus* Waterhouse has broad double-barrelled spines and what appear to be single-barrelled spines in clusters along rows, both sets of spines bearing barbs. A specimen ascribed to *Phricodothyris insolita* George by Yanagida (1962, pl. 14, fig. 5b) shows a row of coarse double-barrelled spines and a row of finer double-barrelled spines, and a row of finer spines in front of the others along at least one commargon. The specimens came from the Carboniferous *Millerella* Zone in southwest Japan.

Triramus canadensis Waterhouse, 2016

Fig. 312 - 320

2016 *Triramus canadensis* Waterhouse, p. 351, Fig. 468-471.

Diagnosis: Small subrounded moderately inflated shells with both valves covered by commarginal growth laminae bearing rows of biramous spines in rows, occasionally preceeded by slender double-barrelled spines, followed anteriorly by a row – rarely more – of single-barrelled spines over parts of the shell.

Holotype: GSC 136662 from Jungle Creek Formation in Member E, of Asselian age, Yukon Territory, Canada, figured by Waterhouse (2016, Fig. 468C) and as Fig. 312C herein, OD.

Material: A ventral valve from JBW 66 and two from JBW 561, one ventral valve and three dorsal valves from JBW 99, two ventral valves and a dorsal valve from JBW 580 and eleven ventral valves and two dorsal valves from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Biconvex, ventral valve weakly transverse with pointed incurved umbo (angle 80-100º) and steep umbonal walls concave in outline; hinge close to half the width of the valve, open delthyrium widening at angle of 40-45º and no connector plate or high deltidial ridges; cardinal extremities obtuse, maximum width near or just behind mid-length and no sulcus or plicae. Dorsal valve transverse and convex with inconspicuous slightly protruding umbo and no fold. Both valves covered by low commarginal laminae, just over 1mm wide in ventral valves anteriorly, and bearing as a rule a row of biramous spines, at least 7.5mm long, and three to five in 1mm medianly, at mid-band, in front of shell marked by fine

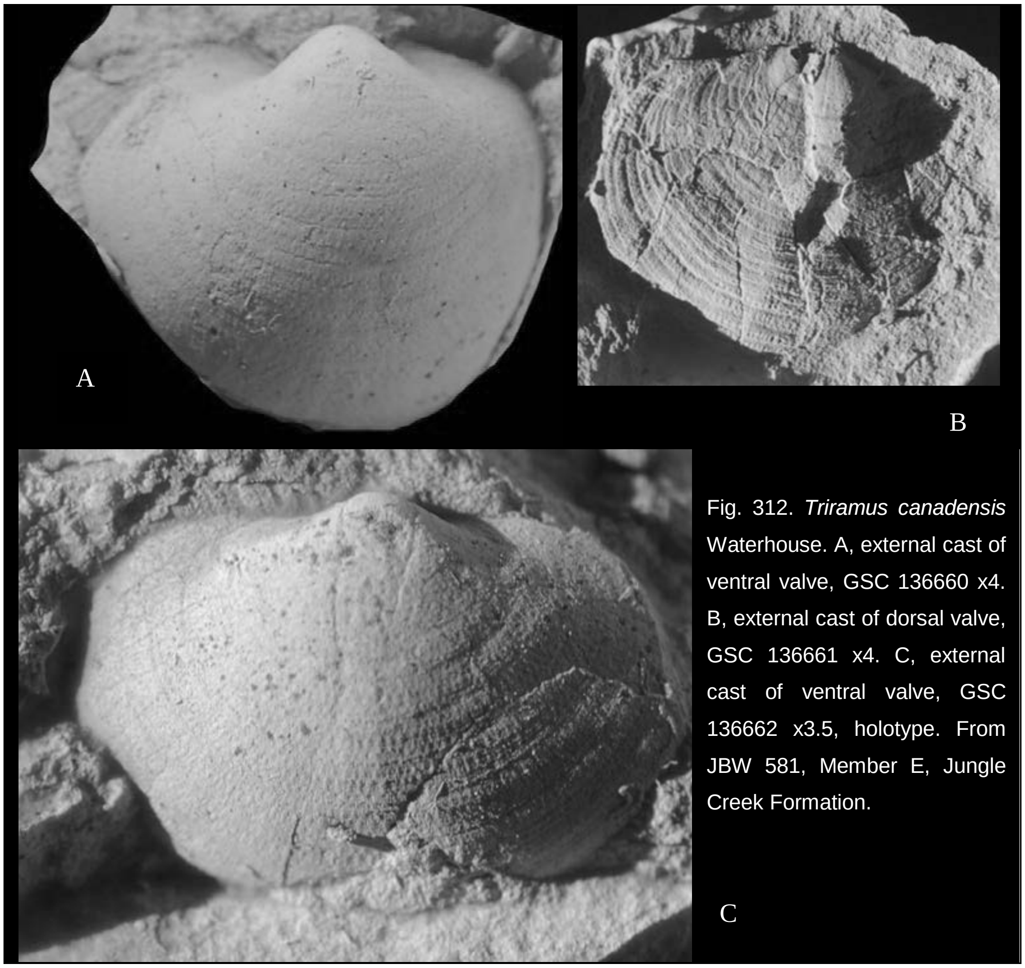


Fig. 312. *Triramus canadensis* Waterhouse. A, external cast of ventral valve, GSC 136660 x4. B, external cast of dorsal valve, GSC 136661 x4. C, external cast of ventral valve, GSC 136662 x3.5, holotype. From JBW 581, Member E, Jungle Creek Formation.

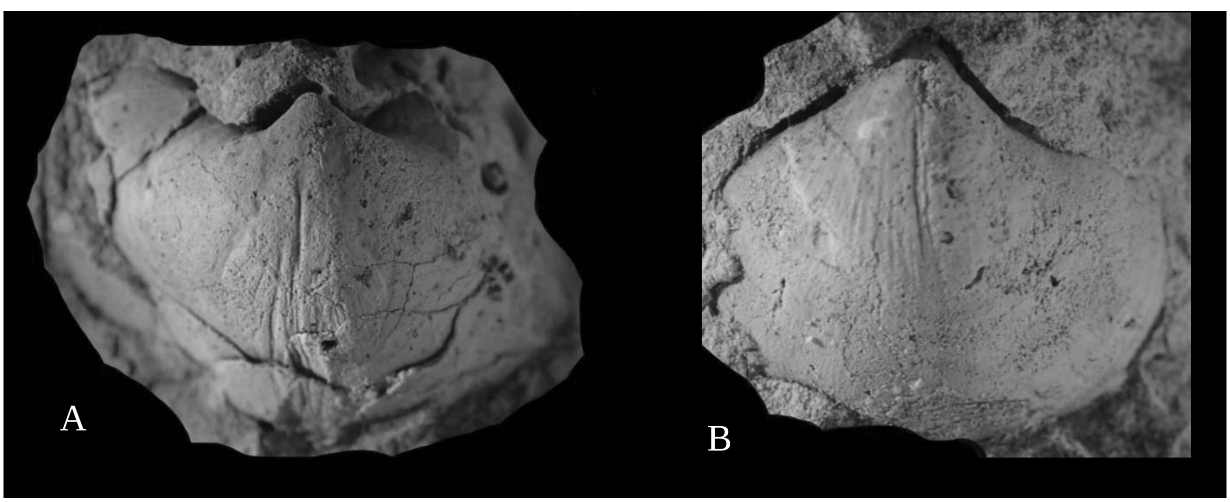


Fig. 313. *Triramus canadensis* Waterhouse. A, internal mould of ventral valve, GSC 136663 x4 from JBW 581. B, internal mould of dorsal valve, GSC 136664 x4, from JBW 66. Member E, Jungle Creek Formation.

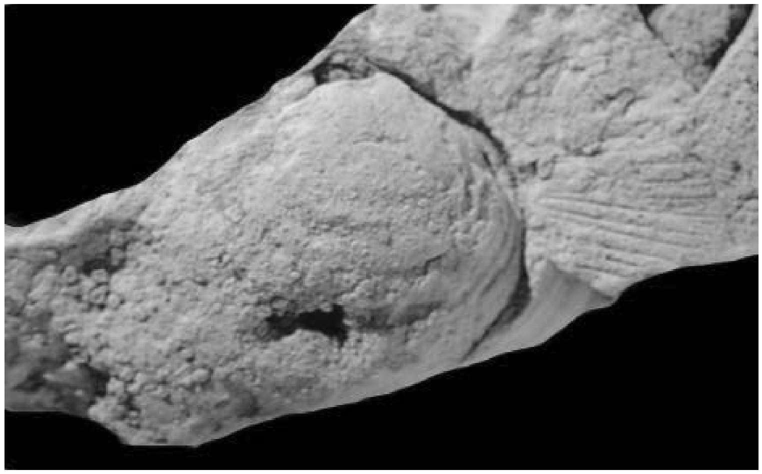


Fig. 314. *Triramus canadensis* Waterhouse, internal mould of ventral valve with spines directed away from the shell, GSC 137463 x4 from JBW 581. Faint incisions between the moulds of the spines possibly suggest the presence of small projecting hooks such as have been illustrated for phricodothyrids by George (1932), Pavlova (1969) and Samtleben (1971). See Waterhouse (2016, p. 341, Fig. 455). Member E, Jungle Creek Formation.

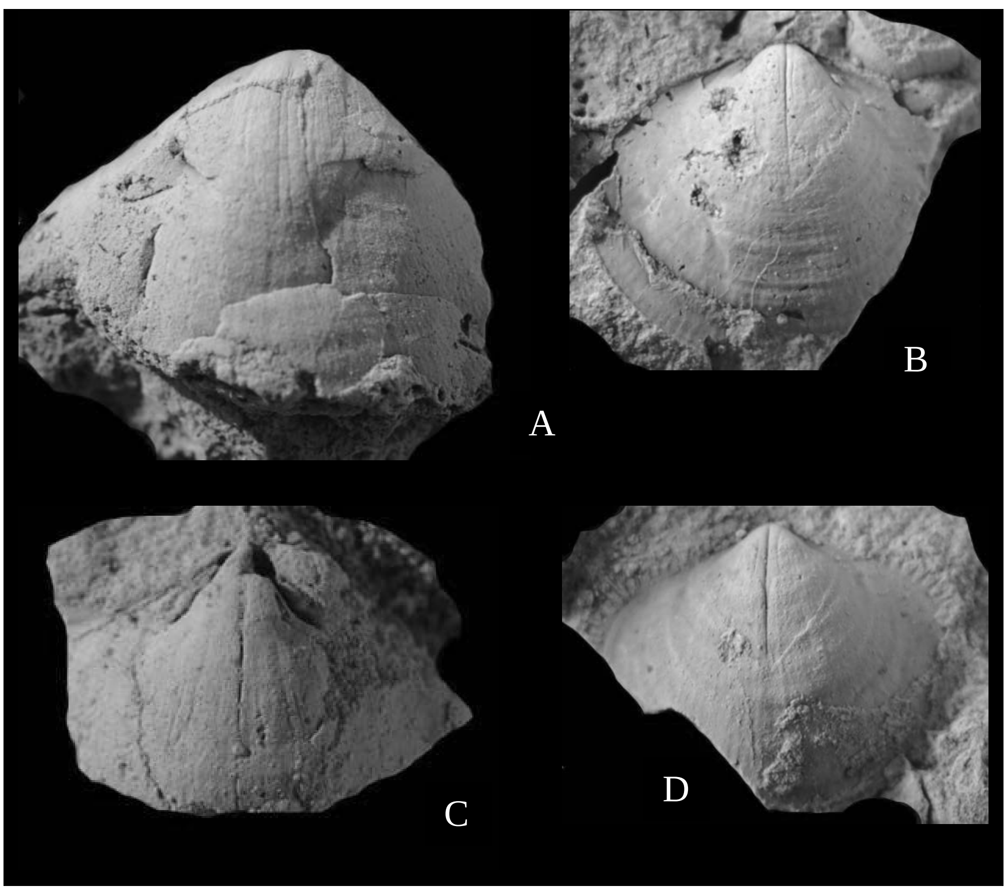


Fig. 315. *Triramus canadensis* Waterhouse. A, worn ventral valve GSC 137162 x3, with extremely low median ridge, from JBW 580. B, internal mould of ventral valve GSC 137179 x4, from JBW 577. C, internal mould of dorsal valve GSC 137180 x5, from JBW 99. D, ventral internal mould GSC 137181 x5, from JBW 581. Member E, Jungle Creek Formation.

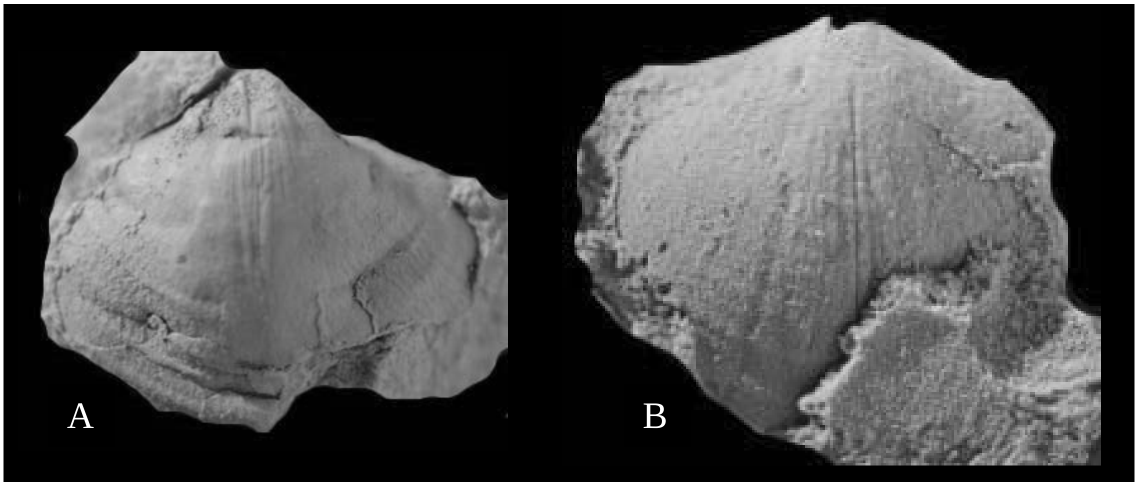


Fig. 316. *Triramus canadensis* Waterhouse. A, ventral internal mould GSC 137341 x6, from JBW 580. B, internal mould of ventral valve GSC 137342 x6, from JBW 581. Member E, Jungle Creek Formation.

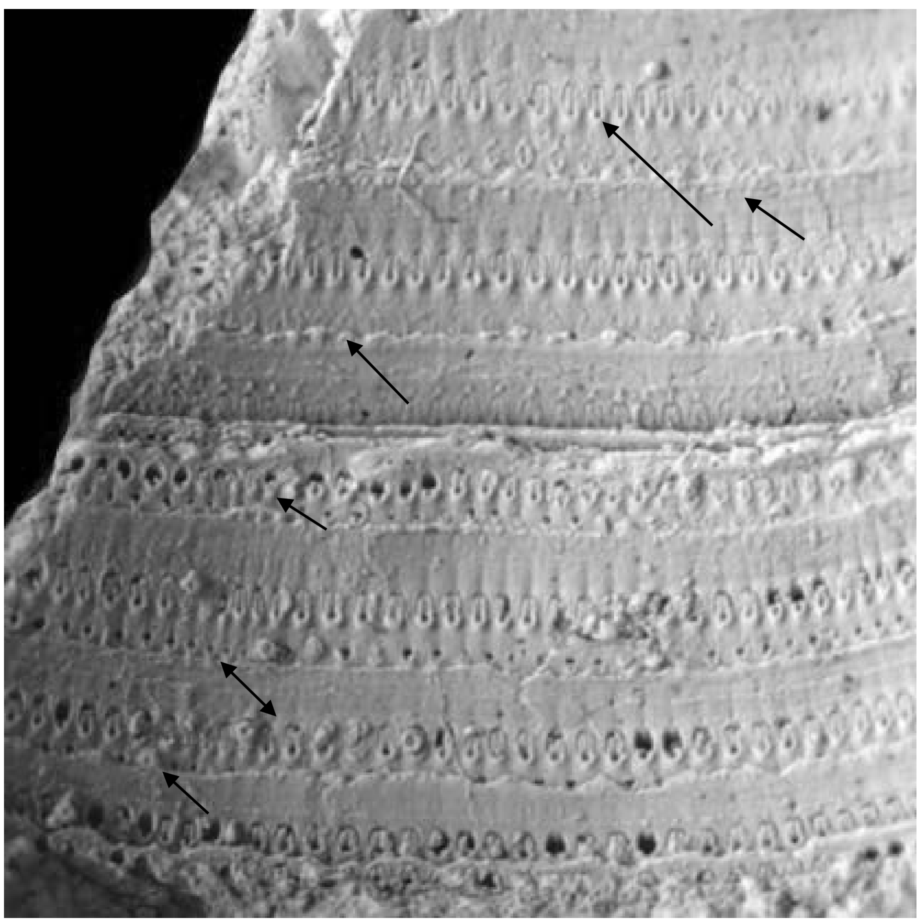


Fig. 317. *Triramus canadensis* Waterhouse*,* external mould showing ventral micro-ornament, GSC 136665 x20, JBW 581. Long arrow points to double-barrelled spines, small arrow to small double-barrelled spines, and single-barrelled spines, indicated by upper barb of double arrow. Member E, Jungle Creek Formation.

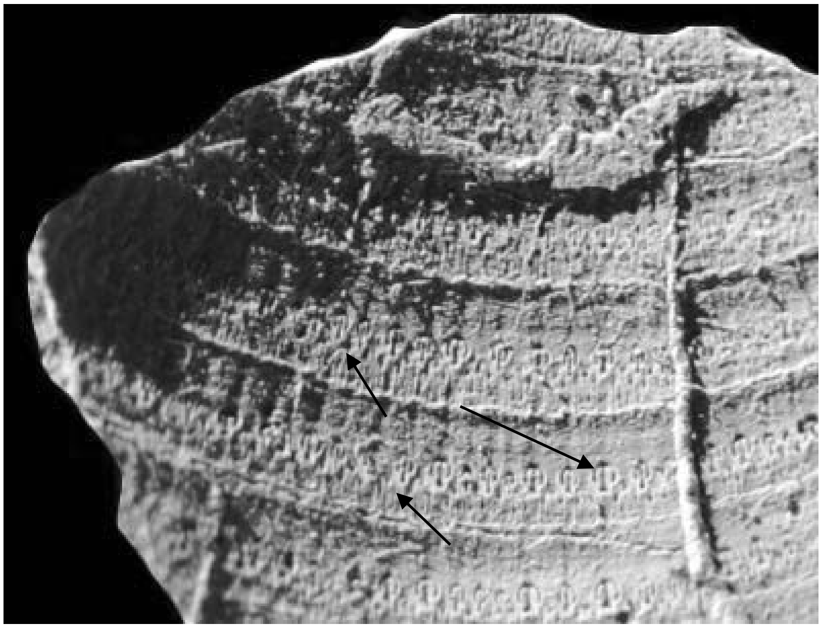


Fig. 318. *Triramus canadensis* Waterhouse, mould of micro-ornament on ventral valve GSC 137322 x7 from JBW 581, Member E, Jungle Creek Formation. Long arrow points to larger double-barrelled spine; shorter arrow to lesser double-barrelled spine. Single barrelled spines also present, some in multiple rows, others between larger spines.

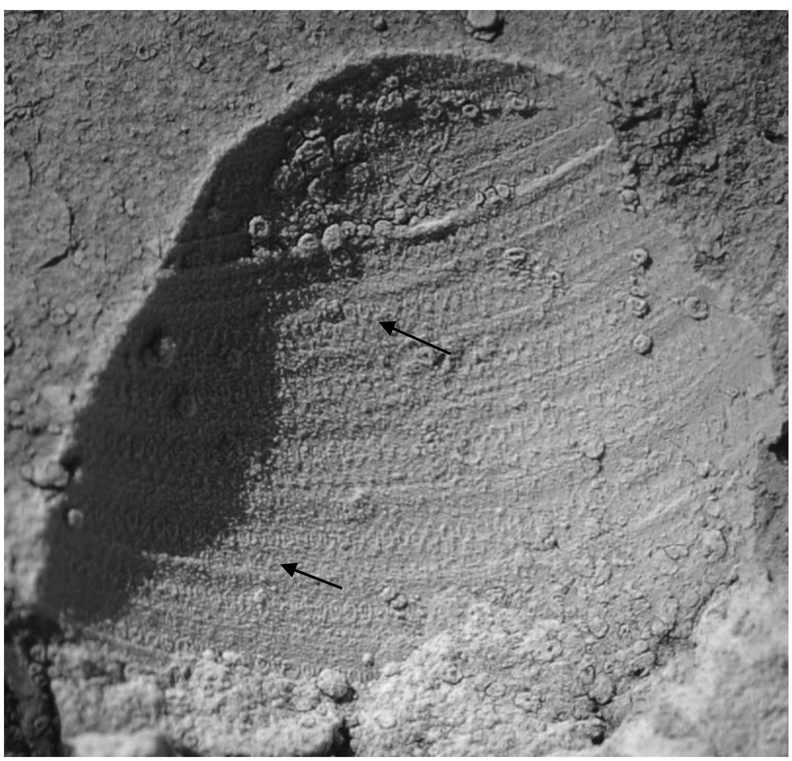


Fig. 319. *Triramus canadensis* Waterhouse, mould of micro-ornament on ventral valve GSC 136661 x5 from C-6167, Member E, Jungle Creek Formation. Short arrows point to lesser double-barrelled spines.

Fig. 320. *Triramus canadensis* Waterhouse, mould of micro-ornament on ventral valve GSC 137461 x6 from JBW 580, Member E, Jungle Creek Formation. The double-barrelled spines are all small and simple, to appear be like single-barrelled spines on the surface of the shell.

growth increments. Rarely, a row of short flutings lies over the posterior commargon behind each larger biramous spine. Laterally the biramous spines are replaced by uniramous spines in some specimens. In front of or sometimes behind the conspicuous spines is occasionally a few, or sometimes a row, often incomplete, of much more slender biramous spines. These are like the larger spines, and may represent only stunted developments of the larger biramous spines, or may belong to an entirely discrete series. Uniramous spines appear, rarely between the larger spines, more usually in a row or three in front of the larger spines, especially near the anterior margin, with no row of slender biramous spines. There is considerable variation, as illustrated in Fig. 317 to Fig. 320. Dorsal valves are more worn, and are of similar ornament, though not so well preserved.

Low dental flanges support the teeth, and there are no adminicula, and no fully developed median septum, but a low medium ridge is present in a number of the specimens. The adductors are very narrow and extend well forward: they may be bordered by a low ridge each side of a shallow concave trough, or form a slender ridge. Diductor scars also extend well forward and are scarcely impressed, but are marked by fine radial striae. The floor may be smooth or weakly marked by commarginal ridges reflecting the external laminae. The mature ventral valve carries light flexuous radiating vascular impressions.

The dorsal valve has small dental sockets, and a long but very low median ridge extending from the hinge to beyond mid-length in some specimens, whereas a median groove is present in other specimens. A pair of tear-shaped adductor impressions lies in front of the hinge, bearing light longitudinal striae, and faint radial mantle canals are developed over the floor of the valve. There is no fully developed cardinal plate, but crural flanges extend each side of the plates bounding the inner side of the sockets. Spiralia directed laterally.

Resemblances: From the Late Carboniferous Mishkin Suite and lower Akachan Suite of northeast Russia, including south Verchoyan, *Phricodothyris lenaensis* Abramov & Grigorieva (1983, p. 140, pl. 32, fig. 10-12, text-fig. 55) and Klets (2005, pl. 28, fig. 4-8), and judged to include *P. asiatica* of Solomina (1978, p. 120, pl. 11, fig. 10, 11) by Klets (2005, p. 152), is very close in shape but displays only one row of biramous spines along each growth step. Specimens identified as *Phricodothyris asiatica* (Chao, 1929) from the Talatin Suite figured by Kalashnikov (1983, pl. 49, fig. 1-3) show a row of coarse posterior spines and confused bands in front, possibly involving two rows of finer spines. Gobbett (1964, p. 132, pl. 17, fig. 1-3, text-fig. 19) recorded one to three rows of spines, of two sizes, so that his material, identified as *Neophricadothyris asiatica*, and coming from the Cora Limestone and Upper Wordiekammen Limestone of Spitsbergen, could prove to be allied to *Triramus canadensis*. Specimens are of similar shape and size, although figures are too small to allow satisfactory comparison. Specimens from northeast Russia, such as those figured as *Neophricadothyris asiatica* by Kashirtsev (1959b, pl. 36, fig. 1, 2) from the Kigiltass Suite of Verchoyan might be closely allied, but detail of the ornament is not available. However Stepanov (1937b, pl. 3, fig. 9) illustrated a specimen from the northern Urals with single rows of sturdy spines, and no finer spines. Ozaki (1931) reported the species from northeast China.

Infrasuborder AMBOCOELIIMORPHI Waterhouse, 2016

[Ambocoeliimorphi Waterhouse, 2016, p. 360].

Diagnosis: Small shells, may be biconvex but tending towards planoconvexity, ornament varied but most often spinose in commarginal rows. Internal plates highly varied, may involve adminicula and/or tabellae, and cruralium widely present, but many genera lack dental plates and adminicula. Most characteristic feature apart from size lies in the simple cardinal process, rather than ctenophoridium of most other than earliest Spiriferida. Radial ornament comparatively rare.

Discussion: The affinities of this group are open to controversy. They have over recent years been regarded as close to what is herein termed Martiniimorphi (Carter & Gourvennec 2006a, p. 1694). Many members have tabellae in common with that group, but the micro-ornament differs considerably, and ventral plates frequently lacking. Unfortunately the mantle canal system is poorly known. Delthyrimorphi are readily distinguished by the more ornate if equally dense micro-ornament for many genera, and this ornament is as a rule arranged over commarginal rows or over commargons as in some members of Ambocoeliimorphi. Yet Delthyrimorphi do include a number of genera that come close to ambocoeliids, such as members of the Obesariinae Gourvennec, discussed by Carter & Gourvennec (2006c, p. 1857ff), and members of Ladjiidae Waterhouse are internally close to members of Delthyrimorphi and have an ornament of fine closely spaced spines (Waterhouse 2016, pp. 374-380). In summary, a few groups come very close to either infrasuborder, and are distinguished principally by the tendency for adminicula and dental plates being better developed in Delthyrimorphi.

Superfamily **AMBOCOELIOIDEA** George, 1931

[Nom. promoveo Johnson & Carter in Carter et al. 1994, p. 336 ex Ambocoeliinae George, 1931, p. 42].

Diagnosis: Small plano-convex to biconvex shells lacking deep sulcus and high fold, often without costae or plicae, micro-ornament varied, usually dominated by fine spines or pustules in commarginal rows. The presence of a delthyrial cover plate or deltidium is variable, present in some genera, apparently absent from others, and as far as can be discerned, derived as a rule from deltidial plates, and some genera developed pleromal ridges and connector plate. Adminicula and dental plates absent from Ambocoeliidae, which has crural plates widely present, often supported by tabellae. A spondylium and/or cruralium are developed in some other groups. Cardinal process knob-like, tubercular or with few lamellae, brachia simple or spiriform.

Discussion: The supposition in the *Revised Brachiopod Treatise* that ambocoelioids were progenital stock for Martinioidea (which included Ingelarelloidea) was rejected in a comprehensive analysis of both stocks in Waterhouse (2016), and ambocoelioids are regarded as more or less a stand-alone group, which evolved from Cyrtimorphi at roughly the same time as Martinimorphi and Delthyrimorphi arose, during Silurian times. Members persisted into the Early Triassic, as summarized by Chen et al. (2005).

Family **AMBOCOELIIDAE** George, 1931

[Nom. promoveo Ivanova 1959, p. 56 ex Ambocoeliinae George, 1931, p. 42].

Diagnosis: Ventri-biconvex shells, smooth with varied micro-ornament, no adminicula or dental plates, cardinal plate present or absent, tabellae stubby or may be absent.

Subfamily **ATTENUOCURVINAE** Waterhouse, 2010

[Subfamily Attenuocurvinae Waterhouse, 2010, p. 64].

Diagnosis: No cardinal plate, tabellae small, spire complete or reduced to one coil. Micro-ornament varied, capillate, or pustulose.

Discussion: *Attenuocurvus* Waterhouse, *Attenuatella* Stehli and *Biconvexiella* Waterhouse, classed as Attenuacurviini, share a similar dorsal interior, and a simple spire with only one coil. They differ from each other to moderate degree in muscle impressions and shape. *Attenuatella* and *Biconvexiella* have a micro-ornament of scattered very coarse spines interspersed with numerous fine spines in commarginal rows, whereas *Attenuocurvus* has largely uniform fine spines in commarginal rows. An outstanding new genus *Heella* n. gen. (see p. 465) is internally like *Attenuocurvus* as far as known, but has commargons with fine spines varying in strength, somewhat like the micro-ornament of the productiform genus *Calliprotonia* Muir-Wood & Cooper (see p. 122), completely different from the arrangement in *Attenuatella* Stehli and the somewhat allied genera *Biconvexiella* Waterhouse and *Attenuocurvus* Waterhouse.

Tribe **OGILVIECOELIINI** Waterhouse, 2016

[Ogilviecoeliini Waterhouse, 2016, p. 367].

Diagnosis: Small non-plicate shells with micro-ornament varied, of capillae or spinules, spiralia complete as in crurithyrins, no dental plates , small delthyrial plate, no extensive cardinal plate, crural plates and thick short tabellae.

Discussion: *Ogilviecoelia* is close to members of Attenuocurvinae in several attributes. The ventral adductor field is longer and more raised than in crurithyrin genera, but is not as long nor as raised as in *Attenuocurvus*. The crura commence close to the floor of the valve on reduced crural plates, supported by tabellae, much as in *Attenuocurvus*. Internally, the cardinal process is sublaminate with two or rarely four high lobes or high swollen laminae rather than tuberculate. Most significantly, the spiralia are fully developed, with some six coils, whereas spiralia of *Attenuocurvus* and allies are truncated, with only one incomplete coil. See Waterhouse (1964, text-fig. 48A, B); Armstrong (1968) and Cooper & Grant (1976b, pl. 745, fig. 67).

Genus ***Ogilviecoelia*** Shi & Waterhouse, 1996

Diagnosis: Small almost planoconvex shells with attenuate ventral umbones, ornamented by fine elongate grooves, usually in quincunx and apparently in a peridermal layer, with external micro-ornament of miniscule spines and pits; dorsal valve may bear low ribs. Ventral adductors on low ridge, not large or strongly impressed; cardinal process sublaminate with very few elements, dorsal adductors in anterior and posterior pair, crural plates sessile. Four to six coils in each spire.

Type species: *Ogilviecoelia inflata* Shi & Waterhouse, 1996, p. 120 from upper Jungle Creek Formation (lower Artinskian), of Yukon Territory, Canada, OD.

Discussion: *Ogilviecoelia* resembles *Attenuatella* Stehli, *Biconvexiella* Waterhouse and *Attenuocurvus* Waterhouse in having attenuate ventral umbones and high ventral valve and low dorsal valve, and the ventral muscle scars are placed on a long ridge, not as long as in *Attenuocurvus* and like that of *Paracrurithyis* Liao. Ornament differs, because distinct spines are absent, and moderately well developed spiralia are present, unlike the long crura with flexed end found in *Attenuocurvus, Biconvexiella* and *Attenuatella* of Attenuocurvini.

Ogilviecoelia initiatus n. sp.

Fig. 321, 322

1971 *Attenuatella* cf. *omolensis* [not Zavodowsky] – Bamber & Waterhouse, pl. 12, fig. 8, 9.

Derivation: initiatus – beginning, Lat.

Diagnosis: Small, ventral valve incurved with moderately deep narrow ventral sulcus, dorsal valve variable, concave overall, with median posterior swelling as a rule. Micro-ornament of very fine pits and pustules, no radial ribs.

Holotype: GSC 137183, here designated.

Material: Several ventral valves and two specimens with valves conjoined from JBW 19. Over thirty ventral valves, some with possibly the dorsal valve attached but concealed in matrix, five specimens with valves conjoined and three separate dorsal valves from JBW 69. Specimen GSC 26922 with valves conjoined from GSC locality 57044.

Stratigraphic and biostratigraphic level: Member B, Jungle Creek Formation. *Ogilviecoelia initiatus* Zone.

Dimensions in mm: From JBW 19, ventral valve

Width	Length	Height
8	8	5
11.5	12	5.5

Description: Specimens small, ventral valve highly arched, incurved ventral umbo with angle of 50-65º, long steep posterior walls curving outwards to obtuse cardinal extremities and moderately well defined ventral sulcus, for which the angle widens at angle of 15º to rarely as much as 20º. The dorsal valve is very gently concave and almost flat, with narrow swollen nepionic portion, extending forward as a fading fold in most specimens, whereas in one specimen the dorsal valve is largely flat. Ventral interarea at right angle to commissure, but obscured by matrix. Dorsal interarea low, gently concave, with narrow notothyrial cavity of 10º, occupied by broad notothyrium. Micro-ornament is preserved only in patches, as being the same on both valves, of tiny dense pustules, four to six in 1mm, between shallow tiny dimples, anteriorly arrayed along commarginal growth-lines. There is no sign of radial capillae, but there are low crowded commarginal rugae anteriorly.

The ventral adductors lie on a weakly defined and longitudinally striate ridge each side of a low median ridge on the inner side of the ventral sulcus. The lateral shell is up to 1mm thick in a specimen only 3.3mm wide. In the dorsal

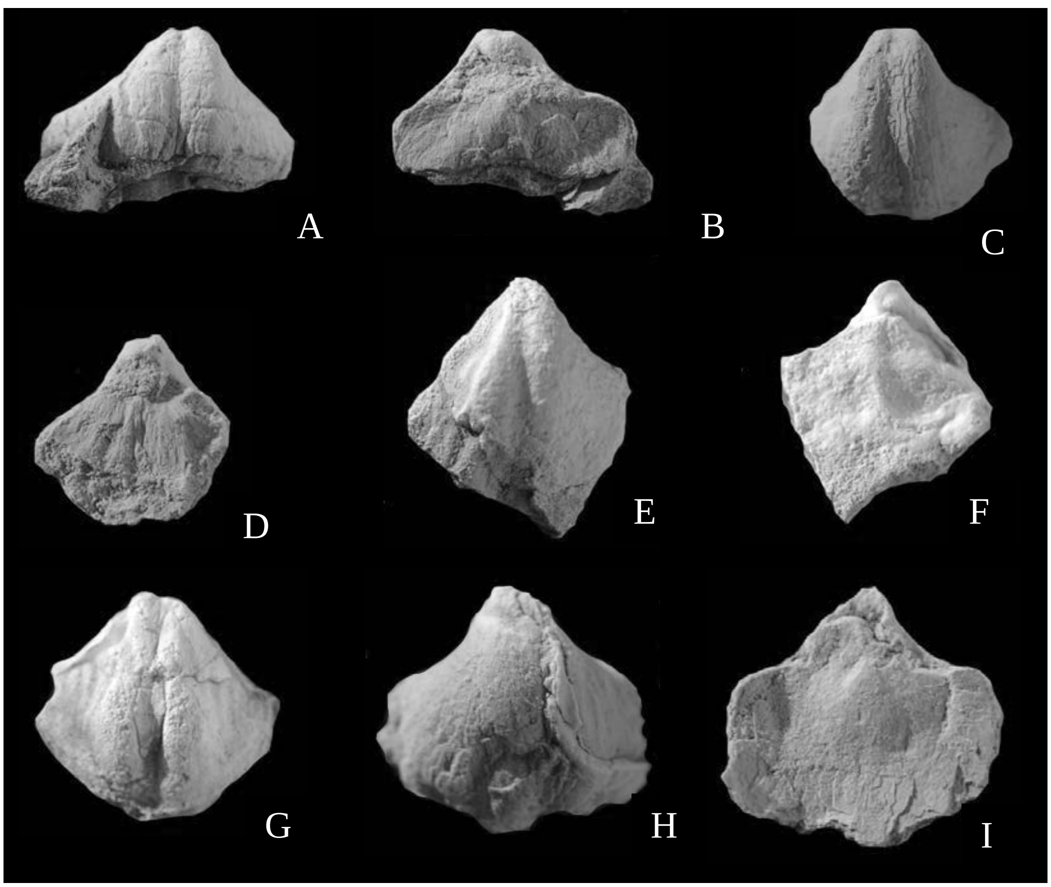


Fig. 321. *Ogilvecoelia initiatus* n. sp. A, B, ventral and dorsal aspects of GSC 137183 x4, holotype from JBW 19. C, D, ventral and dorsal aspects of GSC 137443 from JBW 69, x4. E, F, ventral and dorsal aspects of JBW 137444 from JBW 69 x4. G, ventral valve GSC 137445 from JBW 69, x4. H, I, ventral and dorsal views of GSC 137446 from JBW 69, x4. Member B, Jungle Creek Formation.

valve, the cardinal process is a long bulbous structure, with a shallow median cleft, and a long low septum extends in front for over half of the valve length, but muscle scars are not clearly defined. Sessile tabellae diverge from close to the hinge, supporting two widely diverging crural plates, and several specimens suggest that the spire contains five to six coils each side.

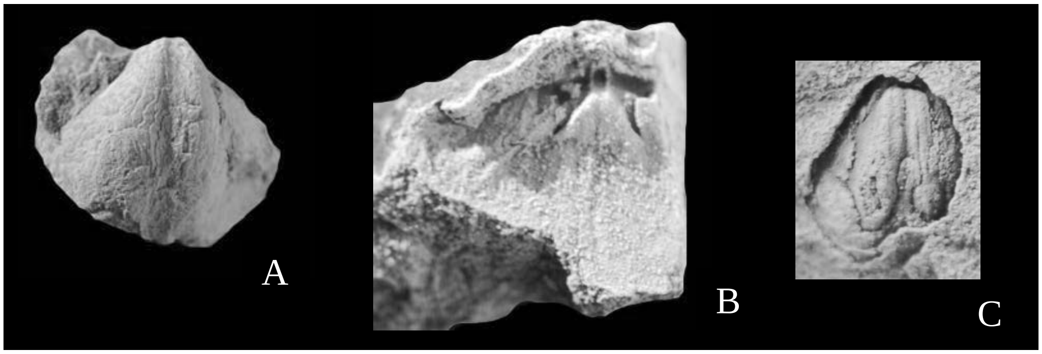


Fig. 322. *Ogilvecoelia initiatus* n. sp. A, ventral valve GSC 137183 x4, from JBW 69. B, dorsal internal mould GSC 137447 x6. C, internal mould of ventral valve GSC 137448 x6. Specimens from JBW 69, Member B, Jungle Creek Formation.

Resemblances: This species is comparatively close to *Ogilviecoelia inflata* Shi & Waterhouse (1996) from the upper Jungle Creek Formation in shape and size, with a characteristic dorsal valve that is slightly swollen medianly in front of the umbo and becomes concave anteriorly, and lacks radial ribs. The ventral muscle field is much the same, and dorsal adductor impressions are visible in *inflata* but are not preserved in the present species, which does show the tabellae that are obscure in *inflata*. It differs from *inflata* in having a more clearly defined ventral sulcus, although it is of comparable width in both species. The micro-ornament has been described as consisting of short grooves for *inflata*, whereas present material indicates the presence of very fine commarginally aligned low spustules and pits. But I have reservations over the reality of this difference, and Prof. Guang Shi agrees, considering it possible that true micro-ornament was not preserved on the types of *inflata*, which instead show a decorticated inner shell, as suggested by the poor development of growth lines on the figured specimen The micro-ornament in *initiatus* is identical with that of a species *Ogilviecoelia shii* n. sp., found between the other two species in Member E. *O. shii* has a gently convex dorsal valve, and both valves bear low fine radial ribs, and the ventral sulcus is less well defined.

The relationship to so-called *Attenuatella* cf. *omolonensis* figured in Bamber & Waterhouse, 1971

This species *Ogilviecoelia initiatus* n. sp. looks moderately like a specimen GSC 26922 figured as *Attenuatella* cf. *omolonensis* (not Zavodowsky) by Bamber & Waterhouse (1971, pl. 12, fig. 8, 9) from GSC locality 57044 at measured section 116C-2, shown in an aerial photograph as figured in Bamber & Waterhouse (1971, Fig. 7) as Eta, stratigraphically low in the type section of the Jungle Creek Formation, and above the “lower member of the Jungle Creek Formation”, which is probably equivalent to Member A in the present study. (See also Bamber 1972, p. 17). The dorsal valve is overall concave, with gently inflated nepionic portion, and although not exactly the same as specimens figured herein, is somewhat comparable. The ventral sulcus on the other hand is shallower, and the ventral beak more swollen and incurved. If the so-called *omolonensis* specimen were identical and coeval with *initiatus*, it would mean that the rocks were followed by paraconformity, with rocks and faunas equivalent to Members C, D, or E missing, because the overlying faunas match those of the "*Yakovlevia transversa*" Zone, according to Bamber & Waterhouse (1971).

Ogilviecoelia shii n. sp.

Fig. 323 - 330

2016 *Ogilviecoelia* n. sp. Waterhouse, Fig. 492, 493.

Derivation: Named for Guang R. Shi.

Diagnosis: Small shells with shallow ventral sulcus and many dorsal valves gently convex, may have a low median fold, fine radial ribs also present on both valves, micro-ornament of dense short grooves or pits and minute elevated pustules.

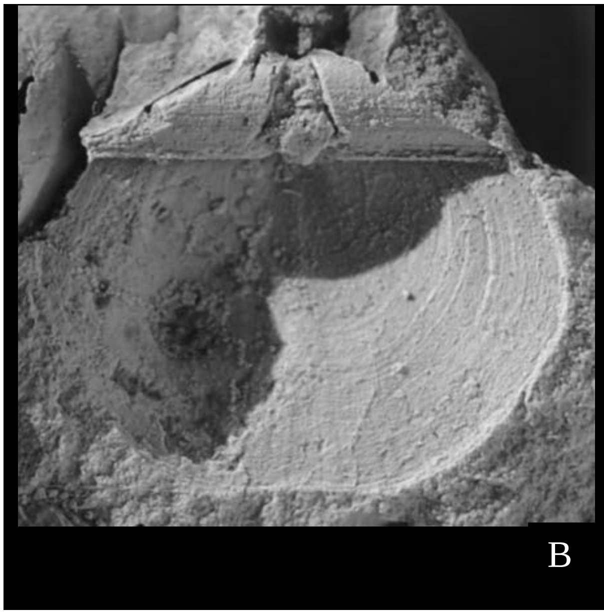
Holotype: GSC 137416, here designated.

Material: This species is abundant, preserved as ventral valves and specimens with valves conjoined. Single specimens, as ventral valves, are found at JBW 183, 538, 561, more than twenty five separate and conjoined valves from JBW 98 and twenty five specimens from JBW 99, five from JBW 195, twenty each from JBW 561 and JBW 580, twenty ventral valves, ten specimens with valves conjoined and six dorsal valves from JBW 581, ten specimens from JBW 587.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Specimens small, a typical ventral valve measuring 9.5mm wide, 8mm long and 3.5mm high; attenuated incurved ventral umbo measuring between 50º and 60º for the umbonal angle, with long steep posterior walls curving outwards to obtuse cardinal extremities, placed just behind mid-length, no distinct ears. The hinge is close to half of the shell width, with high curved interarea disrupted by a delthyrium of which the sides curve outward, with angle of 30º under the umbo, and the upper part is closed by a small plate consisting of comparatively flat flange each side of a narrow median ridge, that in mature specimens becomes large and bulbous. Delthyrial rims are not preserved. A slender median sulcus with concave floor arises at the umbonal tip of the ventral valve and passes to the anterior margin: within a few mm from the umbonal tip the sides become parallel, and anteriorly the sulcus shallows somewhat. The dorsal valve is gently convex or in rare examples flat, and may have a very subdued median fold, or the growth lines retract medianly. There is a low subplanar dorsal interarea at a high angle to the commissure, interrupted by a notothyrium, and the flanks formed by the dental socket plates jut out from the interarea. Ornament on a number of ventral valves consists of very fine short round or transversely extended pits, some ten in 1mm anteriorly, arranged in rows, sometimes in quincunx, and intervening tiny interspaces or pustules. Similar fine ornament is present on the dorsal valve, fine pits and pustules, eight to ten in 1mm, covering the valve in close-set rows, as well as closely spaced growth increments: the pits are very rarely elongate. Many of the dorsal valves and some of the ventral valves also carry some twelve fine thread-like ribs over the middle of the valve, and usually none laterally, though some valves bear ribs over the entire surface. Ribs have narrow crests and wide interspaces. The anterior laminae on some dorsal valves suggest the presence in the shell of very short hollow tubules; indeed there are a few narrow tubes of matrix through the shell of some specimens, and perhaps these are due to borings, unless they represent matrix fill of taleolae that have dissolved out of the shell (see Kozlowski 1929, Williams 1956, Campbell 1959a; Waterhouse 1964).

The ventral teeth are not supported by plates. The median sulcus is underlain by a long ridge of thickened



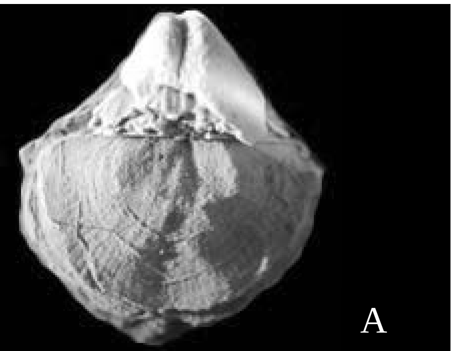


Fig. 323 *Ogilviecoelia* shii n. sp. A, incomplete specimen showing ventral beak shell and mould of dorsal valve, GSC 136666 x4. B, mould of ventral posterior and dorsal exterior, GSC 136667 x6. From JBW 580, Member E, Jungle Creek Formation.

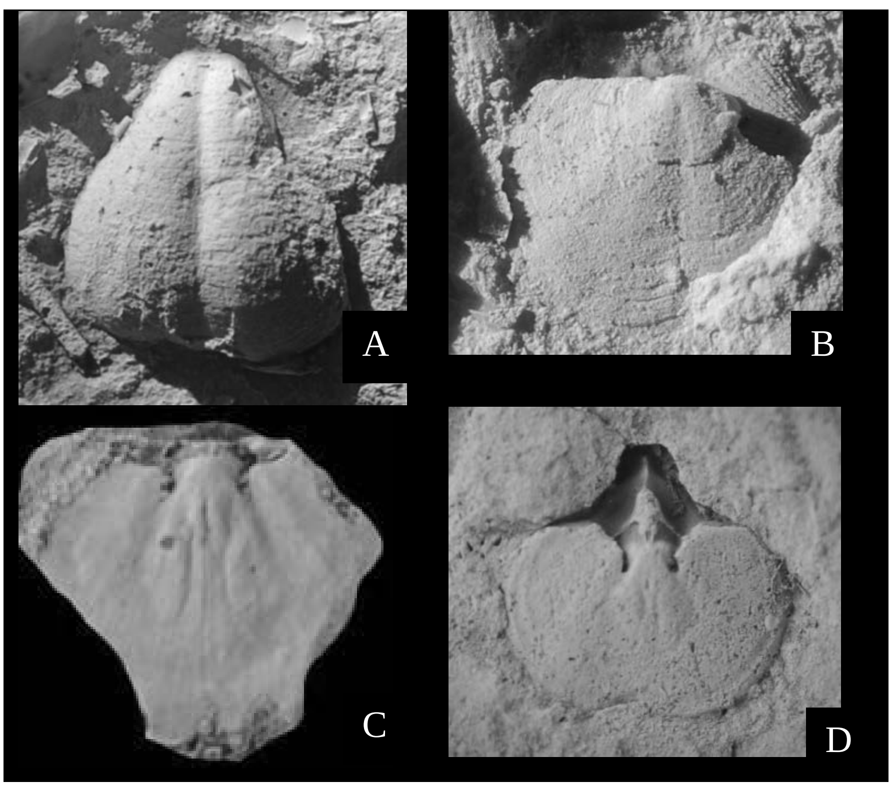


Fig. 324. *Ogilviecoelia* shii n. sp. A, ventral valve, external cast, GSC 136668 from JBW 580. B, external cast of dorsal valve, GSC 136669 from JBW 581. C. dorsal internal mould GSC 136670 from JBW 561, showing muscle scars. D, dorsal internal mould, GSC 136671 from JBW 561. Specimens x4. Member E, Jungle Creek Formation.

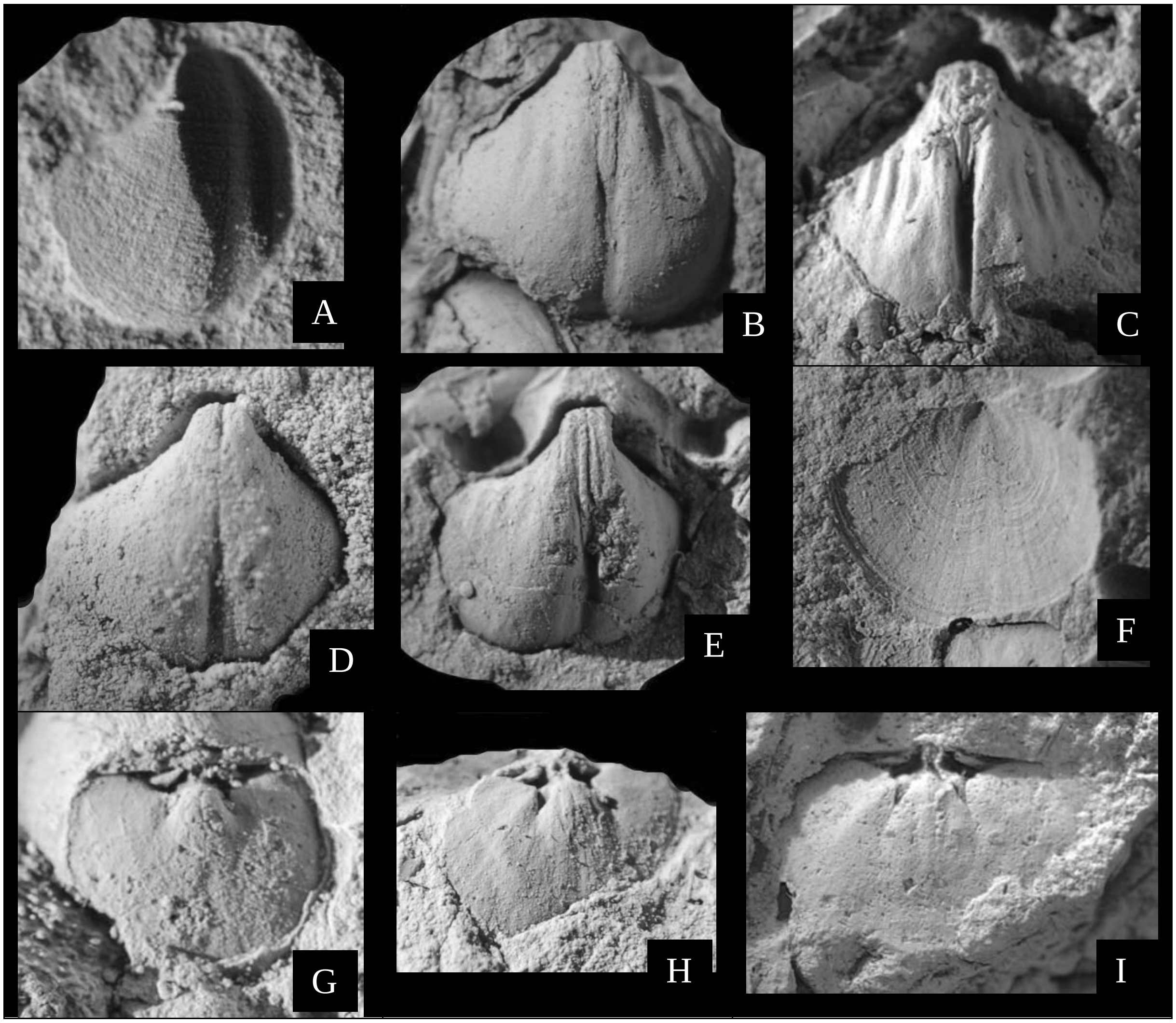


Fig. 325. *Ogilviecoelia shii* n. sp. A, ventral external mould showing ribs, GSC 137275 x6, from JBW 538. B, ventral internal mould, GSC 137276 x6, from JBW 580. C, ventral internal mould, GSC 137277 x4, from JBW 581. D, ventral internal mould GSC 137186 x4, from JBW 581. E, internal ventral mould GSC 137187 x4, from JBW 580. F, dorsal external mould, GSC 137279 x4, from JBW 66. G, dorsal internal mould, GSC 137280 x5, from JBW 581. H, dorsal internal mould GSC 137185 x4 from JBW 581. I, dorsal internal mould GSC 137308 x4, from JBW 581. Member E, Jungle Creek Formation.

shell, bearing adductors that extend in different specimens for less than a quarter to nearly half the length, sited on two ridges, or in a double groove separated by a low myophragm, or on a single ridge, and marked by fine radial striae. The length and detail varies considerably, with the muscle field as illustrated in Fig. 325B, C, E, broad close to the posterior margin and marked by several ridges and grooves, and constricted in front. The diductor impressions are represented by posteriorly placed shorter and broader scars marked by irregular longitudinal striae. The floor in mature specimens bears fine pits.

In the dorsal valve, the cardinal process is small and narrow with two or rarely four vertical lobes. The inner adductors are small, slender and elongate, and the lateral adductors are anteriorly placed and larger, both sets faintly marked by longitudinal grooves. There is a low myophragm but no median septum. The teeth are enclosed by socket plates which rest on short crural plates, supported by sturdy diverging tabellae, and the crura arise close to or at floor level, and support spiralia with some six coils.

Resemblances: This species is close in shape to *Ogilviecoelia inflata* Shi & Waterhouse (1996, p. 120, pl. 21, fig. 32-44, pl. 32, fig. 8-13) from the *Jakutoproductus verchoyanicus* Zone in the younger Jungle Creek Formation, but has a slightly shallower and less marked sulcus. There are other differences: the micro-ornament does not comprise elongate grooves, and both valves, especially the dorsal valve, carry low radial threads, and a low dorsal fold is present. But it must be allowed that the present description is based on better preserved material, so there may need to be some caution over the reality of some of these apparent differences, especially with regard to the micro-ornament.

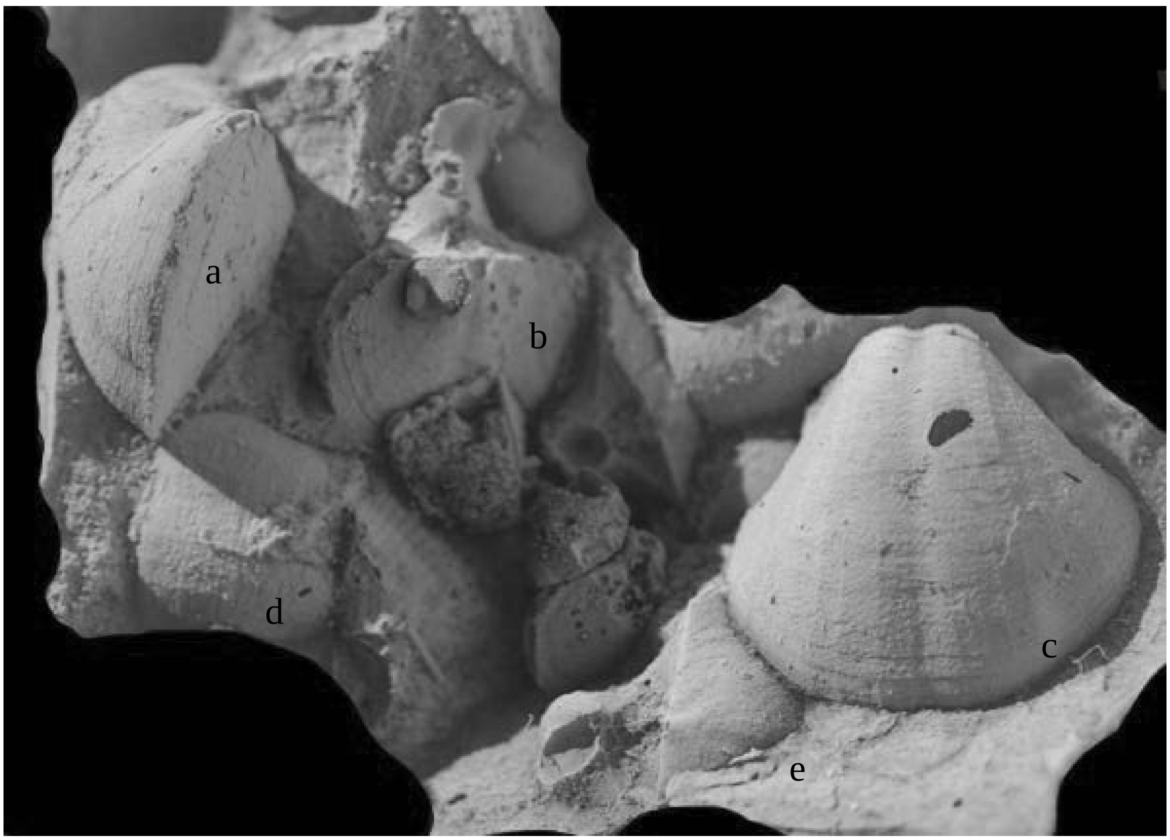
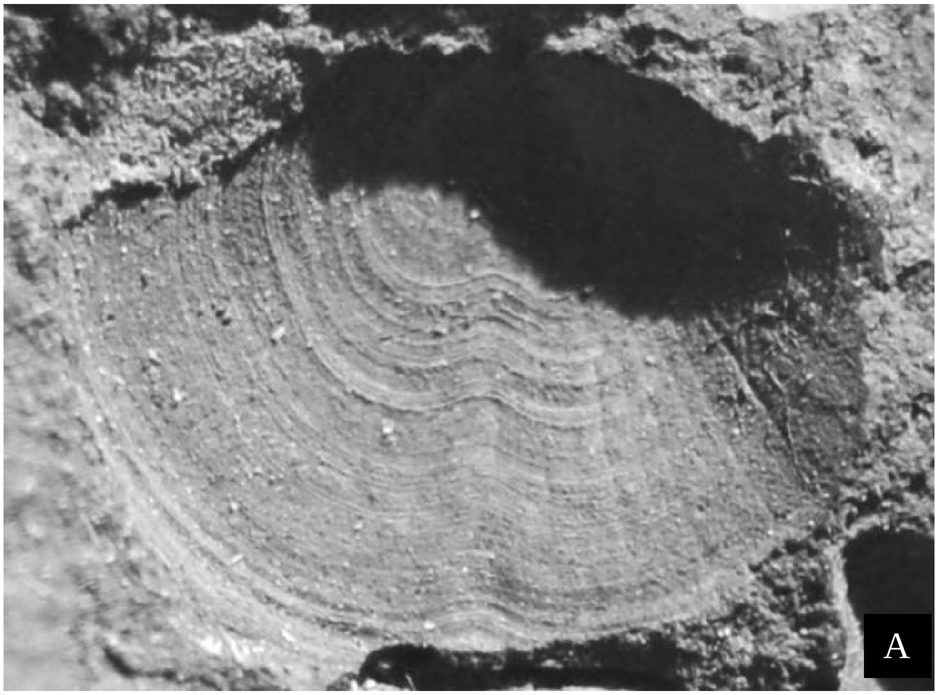


Fig. 326. *Ogilviecoelia* shii n. sp., latex cast of cluster of specimens including lateral view of specimen with valves conjoined at a, GSC 137362 and b, 137363. Specimen 137438 (c) shows ventral aspect of specimen with fine costae, also showing micro-ornament as on ventral valve GSC 137439 (d) and dorsal valve GSC 137440 (e). Specimens x8. Member E, Jungle Creek Formation.

It is possible that some of the occurrences of *Attenuatella* reported from other Arctic faunas, especially in Russia, will prove to belong to *Ogilviecoelia*. But mostly internal moulds have been figured, and micro-ornament not illustrated, so that the generic determination in the literature as *Attenuatella* may well be inaccurate. The specimens



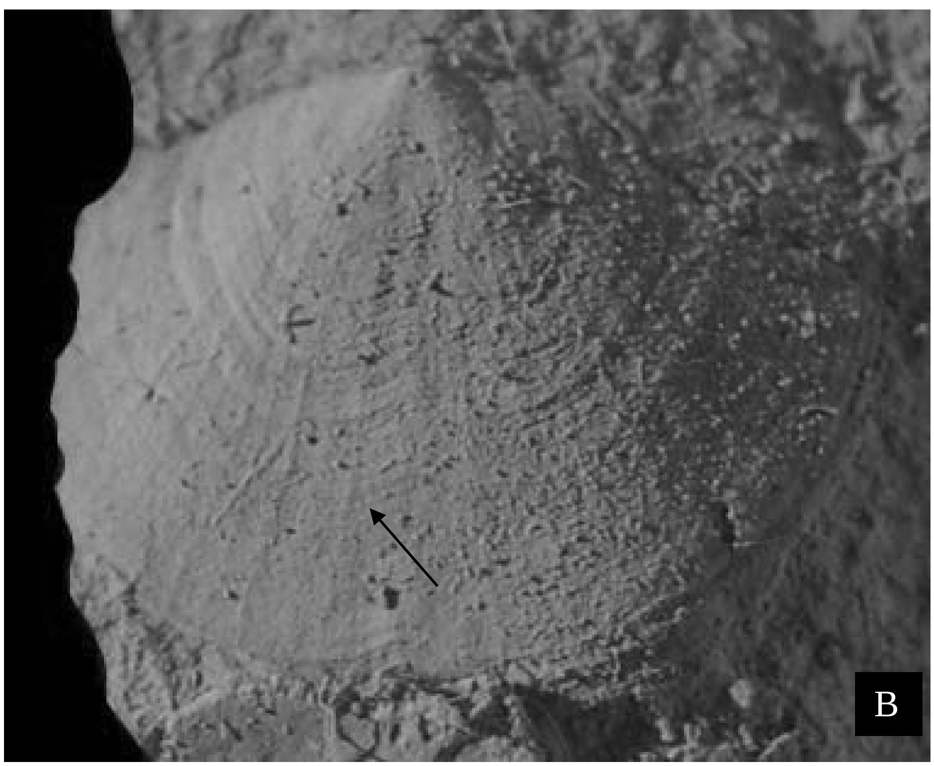


Fig. 327. *Ogilviecoelia shii* n. sp. A, B, dorsal internal mould and external cast, GSC 137184 x12, showing minute pits and pustules (arrowed) covering the surface, as well as radiating ribs. See Fig. 325F. From JBW 98, Member E, Jungle Creek Formation.

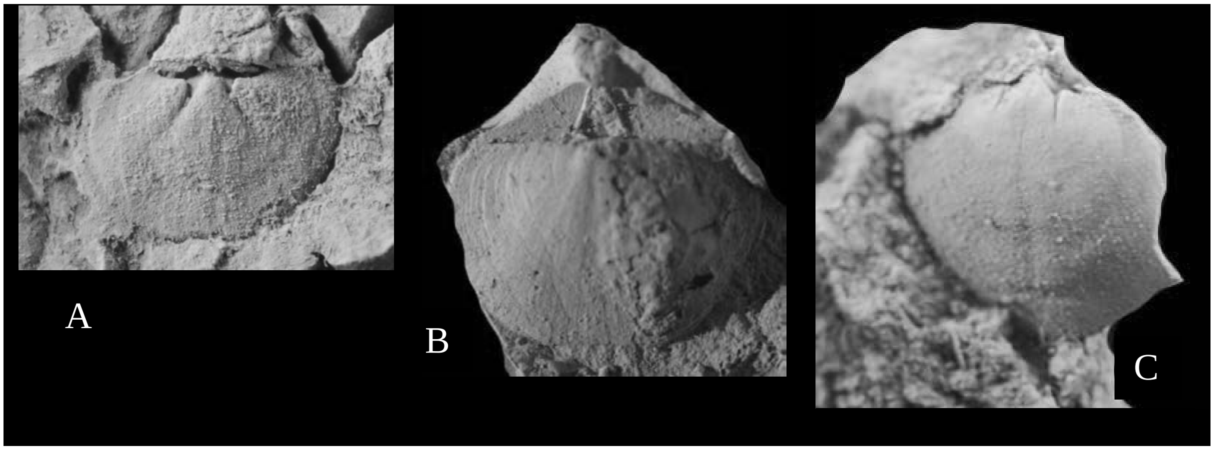


Fig. 328. *Ogilviecoelia shii* n. sp. A, dorsal internal mould, GSC 139976 x4, from JBW 98. B, 139977 x4, JBW 561. C, dorsal internal mould GSC 137184 x8. From JBW 580, Member E, Jungle Creek Formation.

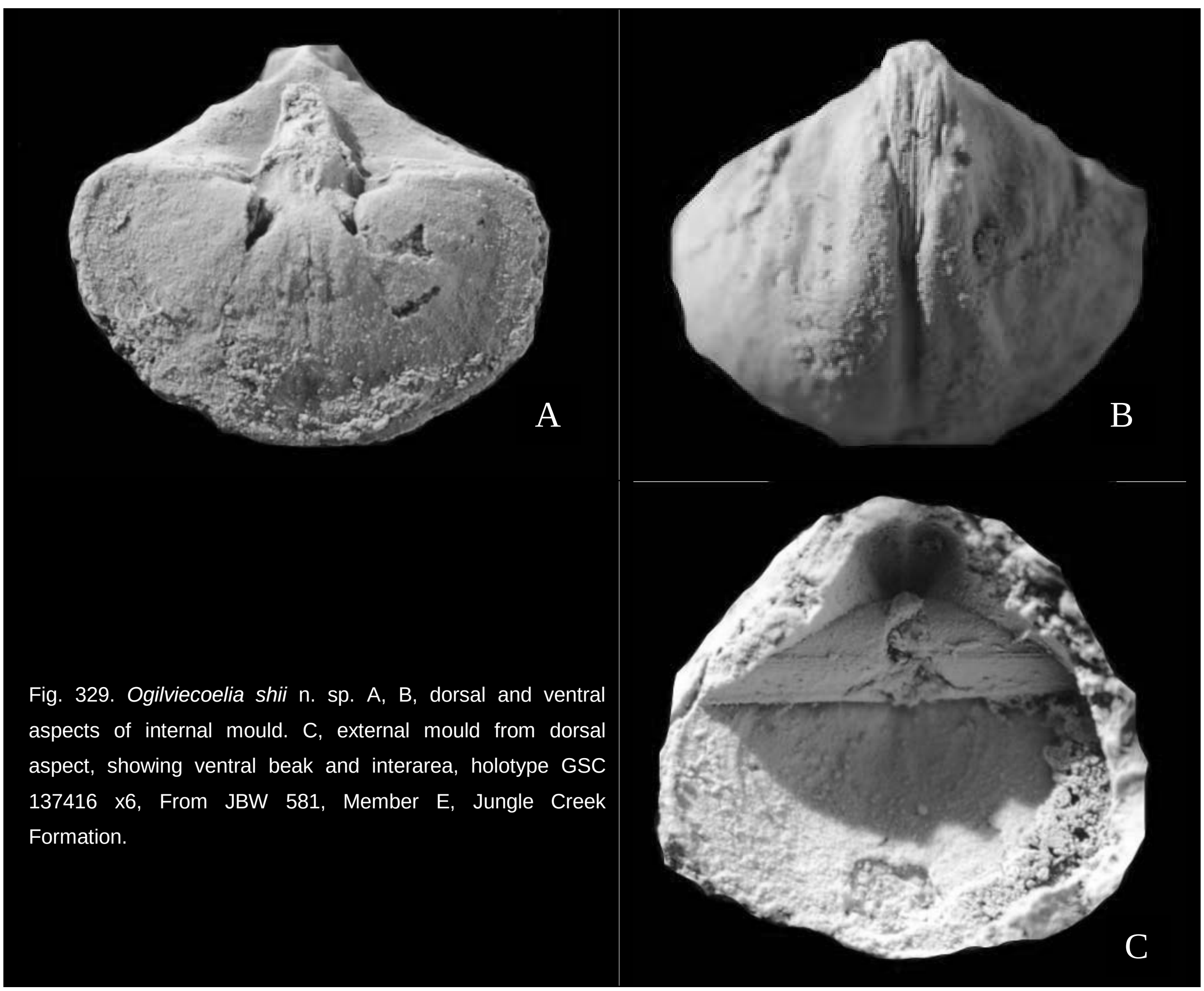


Fig. 329. *Ogilviecoelia shii* n. sp. A, B, dorsal and ventral aspects of internal mould. C, external mould from dorsal aspect, showing ventral beak and interarea, holotype GSC 137416 x6, From JBW 581, Member E, Jungle Creek Formation.

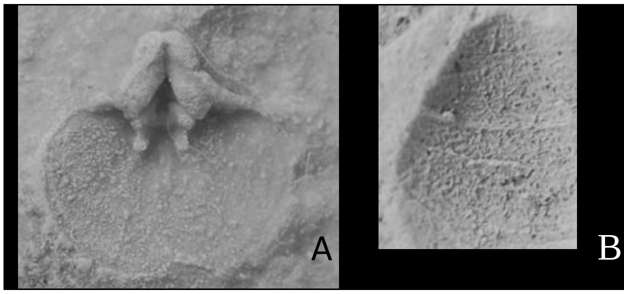


Fig. 330. *Ogilviecoelia shii* n. sp. A, cast of dorsal internal mould, GSC 136771 x4, from JBW 561. See Fig.324D. B, external mould of worn ventral exterior, GSC 137458 x6, from JBW 195. Member E, Jungle Creek Formation.

described from South Verchoyan as *Attenuatella omolonensis* Zavodowsky and as *A. majaensis* Klets from the upper Akachan Group of Lower Permian age and Upper Carboniferous Tilakhs Suite by Klets (2005, pl. 21, fig. 9-12) have ventral adductor impressions like those of *Orbicoelia*, and other features are compatible, with even suggestions of several coils to the spire (Klets 2005, pl. 21, fig. 9). *Attenuatella* has a much reduced spire.

Order SPIRIFERINIDA Ivanova, 1972

[Nom. transl. Carter & Johnson in Carter et al. 1994, p. 359, ex Spiriferinidina Ivanova, 1972, p. 41].

Diagnosis: Shells as a rule plicate with diverse often spinose micro-ornament, well developed cardinal areas, median ventral septum and punctate shell.

Discussion: The strophic shell and internal features apart from median ventral septum and only rare presence of tabellae are close as a rule to the morphology of Spiriferida. The shell is punctate as a rule, pierced by fine dense punctae, but in one group, Licharewioidea, it is here shown that the shell is densely taleolate, pierced by fine dense rods of calcite in place of punctae.

Suborder SPIRIFERINIDINA Ivanova, 1972

[Spiriferinidina Ivanova, 1972, p. 41].

Diagnosis: As above.

Discussion: In Cyrtinidina Carter & Johnson the lateral shell may be smooth, and the ventral interior has complex attachment structures, including a spondylium.

Superfamily **PENNOSPIRIFERINOIDEA** Dagys, 1972

[Nom. transl. Carter in Carter et al. 1994, p. 366 ex Pennospiriferininae Dagys, 1972, p. 36].

Diagnosis: Punctae well developed and usually dense, adminicula and median septum discrete, ventral interarea low to moderate in height, lateral shell coarsely plicate.

Family **SPIRIFERELLINIDAE** Ivanova, 1972

[Spiriferellinidae Ivanova, 1972, p. 41. Syn. Crenispiriferidae Cooper & Grant, 1976b, p. 2709].

Diagnosis: Micro-ornament usually with well spaced hollow spines.

Discussion: Reticulariinidae Waterhouse is distinguished by the coarseness of the punctae. Otherwise Spiriferellinidae Ivanova is similar: the differences suggested by Carter (2006d, pp. 1914, 1918) are of dubious value. Crenispiriferidae is similar in its family attributes to those of Spiriferellinidae, and *Crenispirifer* Stehli shows only moderate differences from *Spiriferellina* Fredericks, and shares similar spinose ornament, punctation and internal plates.

Genus ***Spiriferellina*** Fredericks, 1924b

Diagnosis: Small shells with few strong plicae, micro-ornament of fine well spaced spines.

Type species: *Terebratulites cristatus* von Schlottheim, 1816, p. 28, from Zechstein (Wuchiapingian) of Germany, OD.

Discussion: This genus is very close to *Crenispirifer* Stehli, and no difference between the two genera was provided by Carter (2000d, p. 1918). Although Cooper & Grant (1976b) indicated that *Crenispirifer* was larger, with their figures indicating slightly higher plicae and fold, the differences are not great. But present material is poorly preserved, discouraging any attempt for closer analysis, and will be referred provisionally to the first named and therefore senior of the two genera.

Spiriferellina sp. A

Fig. 331

Material: Single ventral valves from JBW 166 and 167, four ventral valves from JBW 518, specimen with valves conjoined from JBW 136 and dorsal valve from JBW 77. Two possible valves from JBW 802. Member A, Jungle Creek Formation.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimens have three pair of plicae and fine dense punctae, surface ornament obscure but pustules fine and numerous.

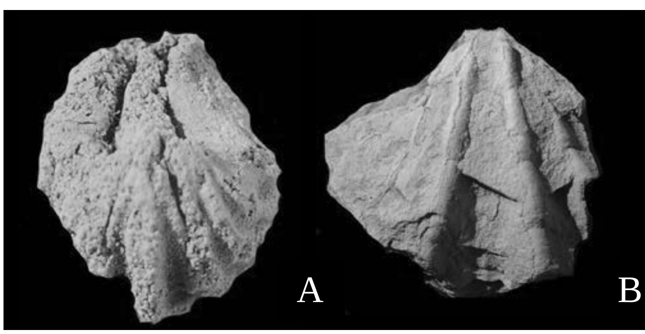


Fig. 331. *Spiriferellina* sp. A. A, dorsal view of internal mould, GSC 137189 x4, from JBW 136. B, ventral valve GSC 137190 x2, from JBW 166. Member A, Jungle Creek Formation.

Spiriferellina sp. B

Fig. 332, 333

Material: Four fragmentary ventral valves from JBW 581, a ventral and dorsal valve from JBW 99, specimen wih valves conjoined from JBW 135.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

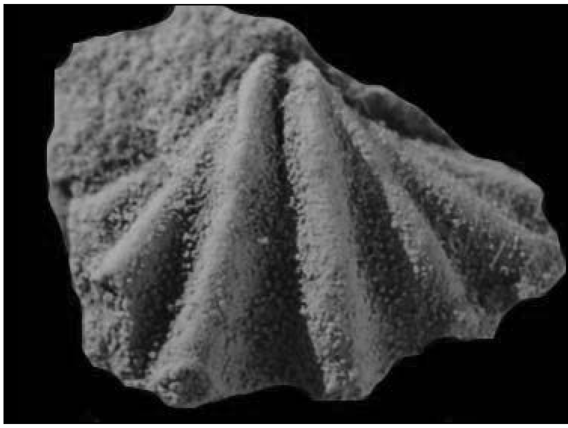


Fig. 332. *Spiriferellina* sp. B., internal mould GSC 137191 x6, from JBW 581. Member E, Jungle Creek Formation.

Fig. 333. *Spiriferellina* sp. B, dorsal internal mould, GSC 137072 x8, from JBW 99. Member E, Jungle Creek Formation.

Description: Specimens have three pair of strong subangular plicae and weak outer pair. The damaged surface suggests closely spaced spines and subdued laminae. The ventral valve is more than three times higher than the dorsal valve. A small and weathered specimen with valves conjoined from JBW 135 has similar ornament. The ventral valve is high with median septum, and very narrow delthyrium bordered by high dental plates, supported by lower adminicula. The dorsal valve has socket plates and short median septum extending over the posterior third of the shell length. Two low but distinct ridges extend from the base of the cardinal process forward across the innermost pair of plicae to enter the inner side of the bordering first pair of plicae. Similar ridges are visible in *Punctospirifer scabricosta* North as described by Campbell (1959b, pl. 58, fig. 7b), and appear to represent where arms of the spiralia have touched the floor of the valve.

Resemblances: The specimens are moderately close to shells from the younger Jungle Creek faunas described as *Spiriferellina*? sp. by Shi & Waterhouse (1996, p. 150, pl. 29, fig. 20-23), sharing three pair of ventral plicae on the ventral valve, and moderately well spaced spines, close to those in type *Spiriferellina*, as figured by Campbell (1959b, pl. 60, fig. 1) and Ivanova (1971, pl. 3, fig. 5). Plicae are broader with wider crests than in *Spiriferellina* sp. A.

Family **PARASPIRIFERINIDAE** Cooper & Grant, 1976b

[Paraspiriferinidae Cooper & Grant, 1976b, p. 2729].

Diagnosis: Micro-ornament regularly and finely lamellose with lamellae bearing fine hair-like spinules in some genera. Tabellae present in some genera.

Genus ***Zaissania*** Sokolskaya, 1968

Diagnosis: Transversely subtriangular with a number of strong plicae and angular interspaces, closely spaced laminae each bearing a fringe of minute spinules. Thick long tabellae.

Type species: *Zaissania zaissanica* Sokolskaya, 1968, p. 197 from Kazakhstan (Upper Carboniferous), OD.

Zaissania? sp.

Fig. 334

Material: Two fragmentary ventral valves from JBW 643 and fragment of anterior part of a specimen with valves conjoined from JBW 682. A ventral valve from JBW 802. Member A, Jungle Creek Formation.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimens show high angular plicae crossed by close-set subimbricate commarginal growth laminae, each fringed by tiny spines in a row, dense punctae.

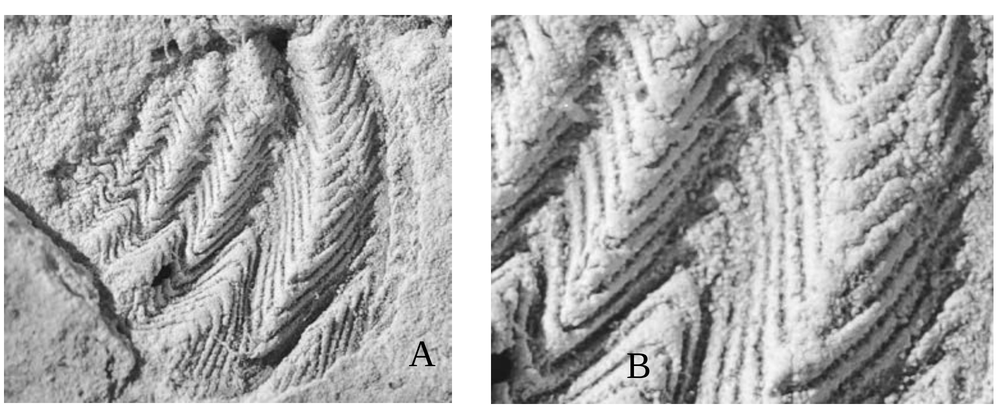


Fig. 334. *Zaissania* sp. A, B, anterior part of an external mould with valves conjoined, GSC 137192 from JBW 682, x4, x8, Member A, Jungle Creek Formation.

Suborder SYRINGOTHYRIDINA Grunt, 2006b

[Nom. correct. hic ex Suborder Syringothyrididina Grunt, 2006b, p. 158].

Diagnosis: Large transverse spiriferiform shells with numerous fine plicae as a rule, micro-ornament of short radial striae with fine pustules or spinules, ventral septum lacking as a rule, punctae either numerous or fine, may be lacking or rare.

Superfamily **LICHAREWIOIDEA** Slusareva, 1958

[Nom. transl. Grunt 2006b, p. 158 ex Licharewiinae Slusareva, 1958, p. 582].

Diagnosis: Large transverse spiriferiform shells, taleolate, with few or no punctae, numerous plicae and smooth sulcus and fold, may have fine pustules. Adminicula support dental plates, no ventral median septum, no tabellae.

Discussion: It is believed from examination of some Russian species and genera that the shell of Licharewioidea is densely taleolate, the taleolae replacing the pores of Syringothyrioidea. Specimens of *Licharewia stuckenbergi*

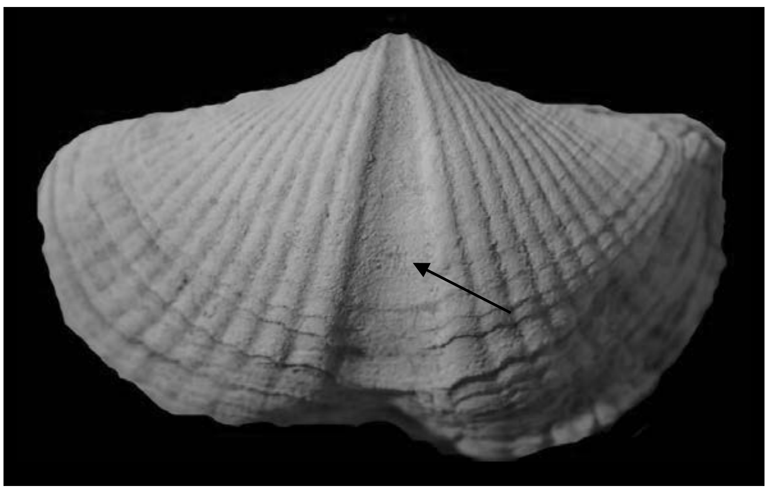


Fig. 335. *Licharewia stuckenbergi* (Netschajew) x2.2, showing ventral aspect, with tiny surface pustules, possibly taleolae as arrowed, from ?Volga River, Russia. GSC 137459, of Kazanian age.

Fig. 336. *Licharewia schrenki* (Keyserling), GSC 137417 from the Pinega River, Russia (topotype), showing ventral aspect x1.6, of Kazanian age.

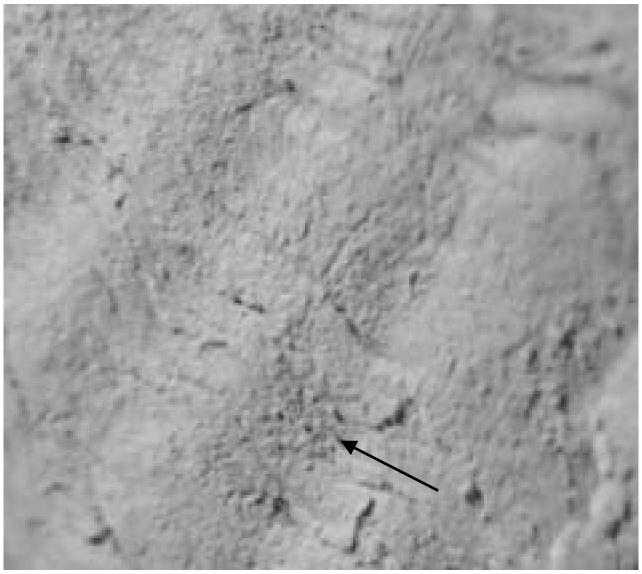


Fig. 337. *Licharewia schrenki* (Keyserling), GSC 137417 from the Kazanian at Pinega River, Russia (topotype), showing detail of slightly worn surface on another part of the shell, suggesting presence of taleolae, as arrowed, x 9.

Netschajew (type of the genus) and *L. schrenki* (Keyserling) from the Pinega River provided by M. V. Kulikov, Leningrad, and by T. G. Sarytcheva, Moscow, certainly show these dense taleolae, and so does the species *Spirifer keyserlingi* Netschajew from Kolos River, which is the type species of *Permospirifer*.

Fig. 338. *Licharewia schrenki* (Keyserling), GSC 137417 from the Kazanian at Pinega River, Russia (topotype), showing detail of slightly worn surface, suggesting presence of taleolae, x 6,

Family **LICHAREWIIDAE** Slusareva, 1958

[Nom. transl. Solomina 1988, p. 44 ex Licharewiinae Slusareva, 1958, p. 582].

Diagnosis: As for superfamily.

Discussion: Carter (2006d, p. 1906) treated Licharewiidae as a family with Syringothyridoidea, and Grunt (2006b, p. 158) placed the family as member of Licharewioidea, which is followed herein. Members of the impunctate Devonian family Spinocyrtiidae Ivanova, 1959 show considerable similarity in shape, size, ornament and internal plates, as if more closely related, and this potential relationship invites further enquiry.

Genus ***Tumarinia*** Grigorieva & Solomina, 1973

Diagnosis: Well developed delthyrial plate and long adminicula. Micro-ornament of pustules and grooves. Slightly rugose stegidium may be in contact with delthyrial plate. No calcite rod in umbonal cavity.

Type species: *Tumarinia orientalis* Grigorieva in Grigorieva & Solomina 1973, p. 36 from Omolon Horizon (Kazanian) of northeast Russia.

Discussion: The outer shell is pierced by numerous calcite cylinders, apparently equivalent to taleolae (Kozlowski 1929; Williams 1956). The genus appears to be very close to *Orulgania* Solomina & Chernyak, 1961, which has similar shape and ornament, and it appears, internal structure, apart from a prominent median calcite rod in the umbonal cavity. Carter (2006d, p. 1908) reported that the dorsal fold in *Orulgania* usually possessed a median furrow, and that is absent from type *Tumarinia*. But it will be noted that the median furrow may not be inevitably absent, because some Canadian specimens have a very faint and often discontinuous median furrow. That might qualify the shells as belonging to *Orulgania*, and they were so identified with that genus in Bamber & Waterhouse (1971), before the genus *Tumarinia* had been proposed. On the other hand, several ventral interiors show no sign of a median calcite rod in the ventral interior, and possibly the groove was caused or exaggerated by wear of shell above the dorsal median septum. The specimens are therefore treated as *Tumarinia*. Whilst it is possible that two species, one of *Tumarinia*, one of *Orulgania*, are present in present collections and have been mixed, it is preferred to allow that some variation may have occurred in the roundness of the dorsal fold profile, with further clarification dependent on the recovery of more and better material.

Tumarinia solominae n**.** sp.

Fig. 339 - 342

1971 Syringothyrinid Bamber & Waterhouse, pl. 10, fig. 5.

Derivation: Named for R. V. Solomina.

Diagnosis: Large and moderately transverse with simple sulcus and high fold, channelled posteriorly in some specimens, plicae moderately strong, some nine to eleven pairs well formed, with five to seven costae laterally.

Holotype: GSC 137196, here designated.

Material: Single ventral valves from JBW 166, 187, 199, 591, 600?, 745, 746 and 763, two ventral valves from JBW 187 and 609, five ventral valves from JBW 615, ventral and dorsal valve from JBW 196, single dorsal valves from JBW 192, 196, 404, 433, 519, 591, 677, and specimens with valves conjoined from JBW 92, 172, 593 and 674. A ventral valve GSC 26896 was recorded by Bamber & Waterhouse (1971) from GSC locality 57243.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Jungle Creek Formation. Ettrain Formation.

Dimensions in mm: specimens incomplete

Width	Length	Height	dorsal valve height
196	60	21	
61	35	18	
44	25	16	

Description: Ventral valve transverse with ventral umbo moderately extended posteriorly and angle varying between 70º to 100º; alate cardinal extremities, moderately high weakly concave interarea with delthyrium closed by concave connector plate, arched hingewards and extending forward each side, set below the rims of the delthyrium in large specimen from JBW 615, but shorter in a specimen from JBW 591, with concave anterior margin. Narrow well formed smoothly concave sulcus widening at 20-25º, and numerous plicae, nine to eleven pair usually clearly developed, with gently convex profile, and a number of finer ribs lie nearer the cardinal extremities. Dorsal valve transverse with alate cardinal extremities, low interarea mostly obscured, well developed fold with arched crest. Micro-ornament of small crescentic spines, in front of short shallow grooves, nine to ten in 1mm and tending to be aligned in commarginal rows: over parts of the shell only grooves are seen, and elsewhere small pustules are well developed.

Adminicula extend for approximately half the length of the length of the valve, diverging weakly forward, weakly converging from the floor of the valve to support high dental plates. A connector plate, as noted above, is well developed. A median septum extends for more than half the length of the valve. Dorsal valve with long low median ridge and no tabellae. Worn shell indicates circular and solid plugs of calcite penetrating the shell, apparently representing taleolae, at a high angle to the surface. They possibly relate to pustules over the internal floor surface.

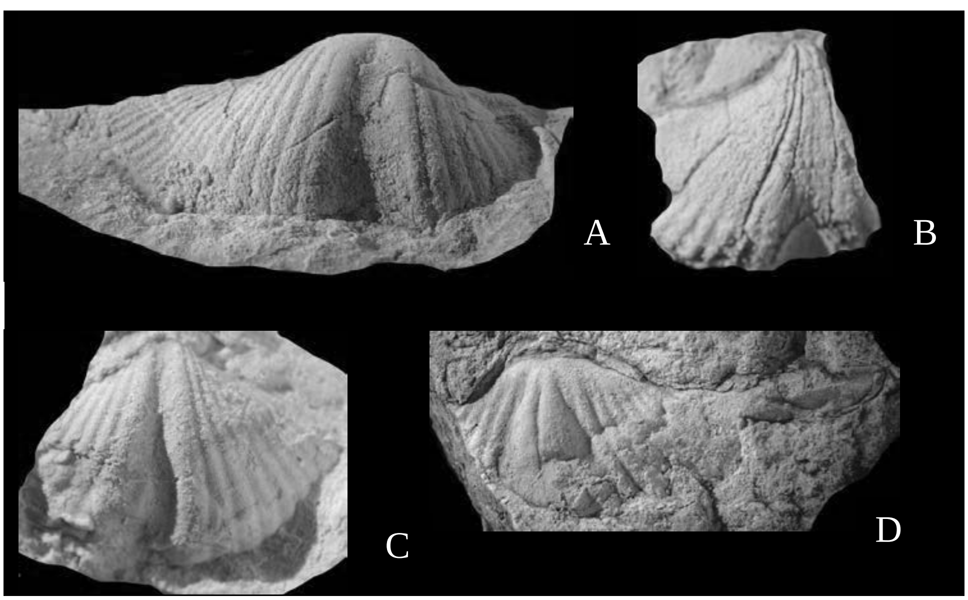


Fig. 339. *Tumarinia solominae* n. sp. A, external cast of ventral valve GSC 137196 x1.5, from JBW 609. B, ventral exterior worn to indicate position of adminicula, GSC 137198 x2, from JBW 433. C, external cast of ventral valve, GSC 137197 x2, from JBW 187. D, dorsal internal mould GSC 137199 x1.5, from JBW 196. Member A, Jungle Creek Formation.

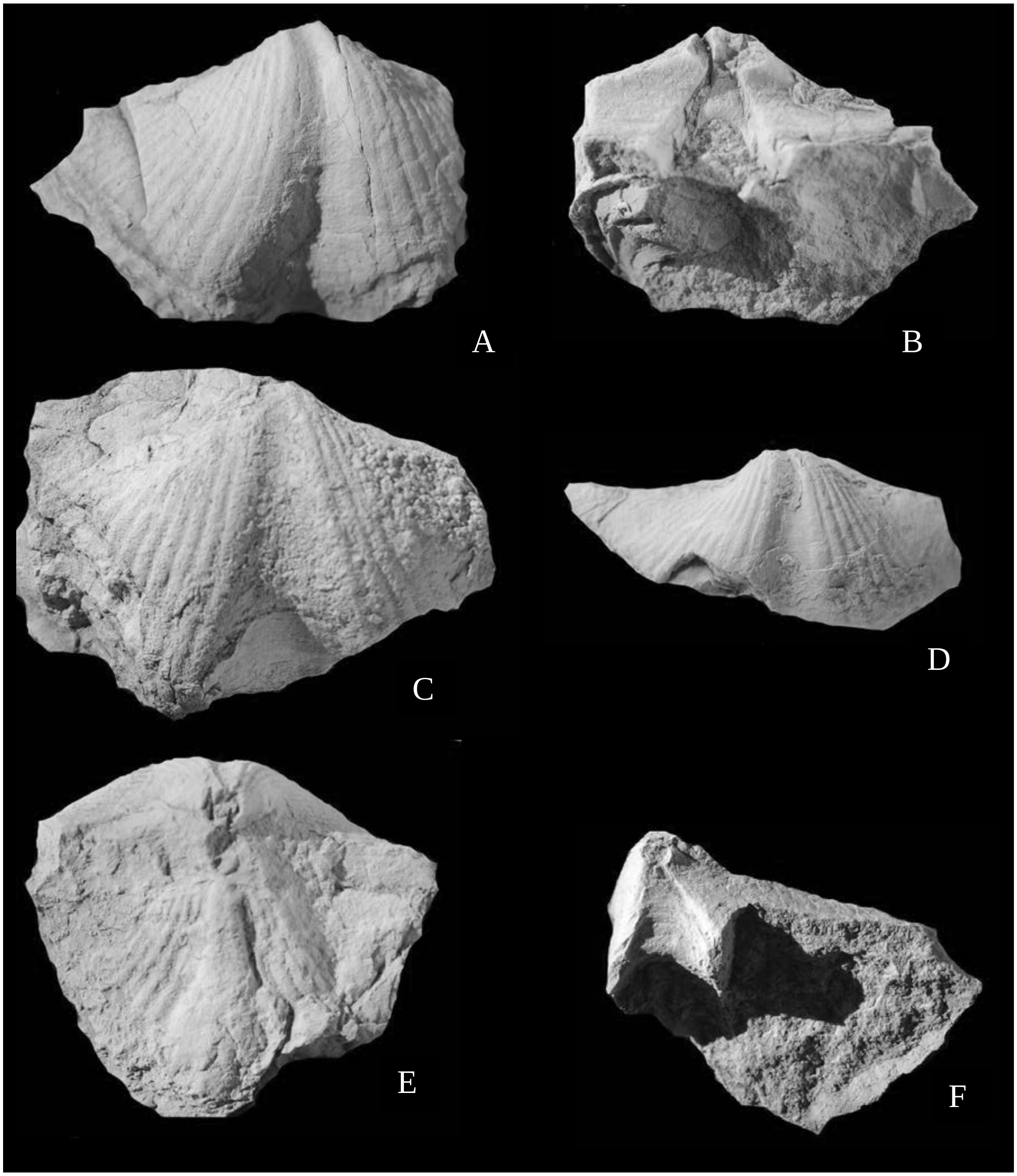


Fig. 340. *Tumarinia solominae* n. sp. A, B, ventral and posterior views of ventral valve GSC 137193 x2, from JBW 591. C, ventral exterior, GSC 137194 x1.5, from JBW 615. D, E, posterior ventral view and full dorsal view of specimen with valves conjoined, holotype GSC 137196 x1, from JBW 92. F, ventral valve GSC 137195 x2, showing interarea, delthyrium and connector plate from JBW 615. Member A, Jungle Creek Formation.

Resemblances: The species is more elongate and has fewer plicae than *Tumarinia yukonica* Shi & Waterhouse (1996, pl. 22, fig. 1-20, pl. 32, fig. 5, 6, text-fig. 43) from the "*Yakovlevia transversa*" to *Jakutoproductus verchoyanicus* Zones of the Jungle Creek Formation. The type species of *Tumarinia*, *T. orientalis* Solomina & Grigorieva in Grigorieva & Solomina

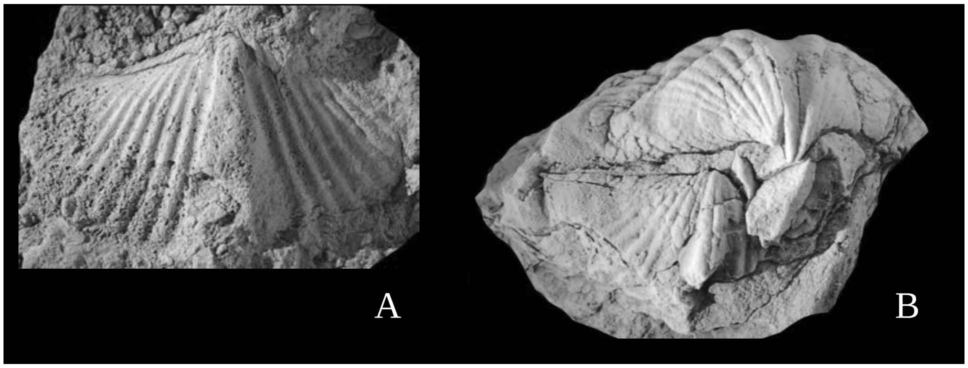


Fig. 341. *Tumarinia solominae* n. sp. A, dorsal internal mould GSC 137200 x1, from JBW 543. B, posterior view of specimen with valves conjoined, crushed, ventral valve on top, GSC 137201 x2, from JBW 593. Member A, Jungle Creek Formation.

(1973) is more elongate, with similar number of plicae. *Licharewia tumida* Zavodowsky (1970, p. 136, pl. 71, fig. 4), referred to *Tumarinia* by Solomina & Grigorieva (1973) and from the Middle Permian Omolon beds of Omolon Basin in northeast Russia, is more elongate with high ventral interarea, and *Licharewia ochotnikovi* Zavodowsky (1958, 1970, p. 137, pl. 84, fig. 1, 2), now assigned to *Tumarinia*, from the Gijigin Horizon of the Omolon Basin in northeast Russia is even more elongate. *T. kolymaensis* (Tolmachev, 1912; Abramov & Grigorieva 1988, pl. 18, fig. 1, 4, pl. 19, fig. 1, pl. 21,

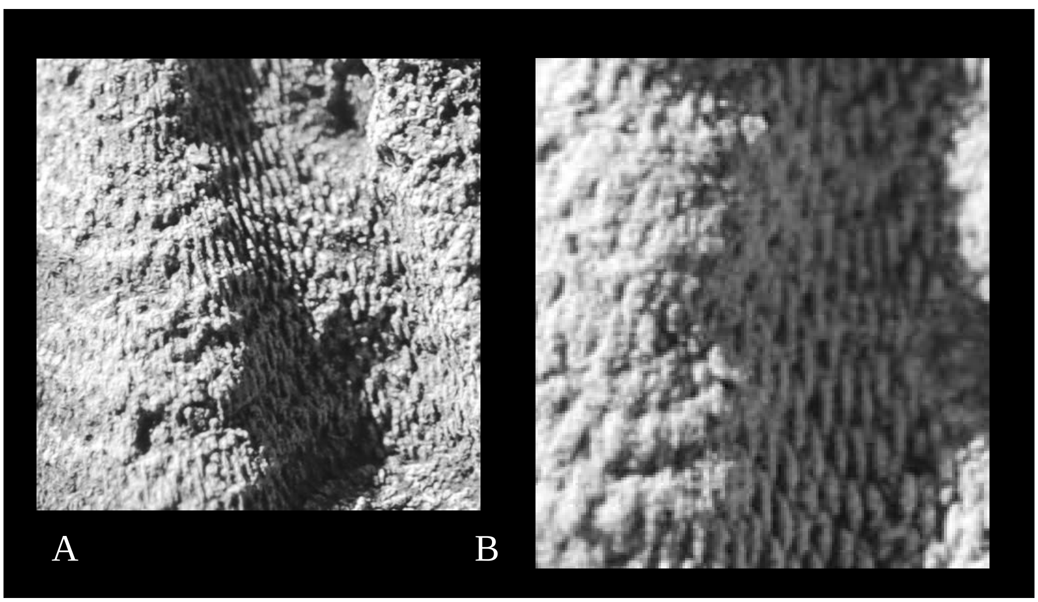


Fig. 342. *Tumarinia solominae* n. sp. A, B, detail of surface micro-ornament on ventral valve GSC 137270 x5 and x13, from JBW 615. Member A, Jungle Creek Formation.

fig. 6; Rozanov 2003, pl. 59, fig. 5, 6) is elongate with well developed ventral interarea and some nine to twelve plicae pairs in Kungurian specimens from Mongolia, Kolyma-Omolon and Verchoyan, whereas *T. narajensis* Solomina in

Grigorieva & Solomina 1973, pl. 6, fig. 5-8, a Middle Permian form from northeast Russia, including Tumarin Suite of west Verchoyan (see also Abramov & Grigorieva 1988, pl. 19, fig. 2-7, pl. 20, fig. 1, 2; Klets 2005, pl. 32, fig. 1, 2), is very transverse and may display alate cardinal extremities. *T. latiareata* (Netschajew 1900, p. 13, pl. 1, fig. 3, 4; Netschajew 1911, pl. 11, fig. 4, 9, 10) with synonymy summarized in Grunt (2006b, p. 163, pl. 16, fig. 3), is much more elongate with high ventral interarea.

The present species is close in many respects to the punctate genus *Syrella occidenta* Archbold, 1996, but has a more sharply defined ventral sulcus and lacks the well developed dorsal channel in the fold.

A specimen GSC 26896 figured in Bamber & Waterhouse (1971, pl. 10, fig. 5) strongly approaches the present species. It was identified as a syringothyrinid from Ettrain equivalents of Tatonduk River section at GSC locality 57243.

Tumarinia sp.or spp.

Material: A broken dorsal valve from JBW 577 (Member E), and a ventral valve from JBW 18, Member C.

Stratigraphic and biostratigraphic levels: Members C and E, Jungle Creek Formation. *Kochiproductus imperiosus* and *Ogilviecoelia shii* Zones. Jungle Creek Formation

Description, Resemblances: The dorsal valve is more elongate than *Tumarinia solominae* n. sp. and has fewer plicae. The ventral valve has sulcus, plicae and typical micro-ornament. The shell is taleolate. These specimens are too incomplete to allow adequate comparison.

Genus ***Yukonospirifer*** Shi & Waterhouse, 1996

Diagnosis: Transverse shells with numerous plicae, fold and sulcus costate.

Type species: *Yukonospirifer yukonensis* Shi & Waterhouse, 1996, p. 123 from the "*Yakovlevia transversa*" Zone (Sakmarian), Jungle Creek Formation, OD.

Discussion: *Verkhotomia* Sokolskaya, 1963 of Early Carboniferous age in Russia and North America is more elongate, with faint costae over the anterior sulcus, and smooth dorsal fold.

Yukonospirifer sp.

Fig. 343

Diagnosis: Large and transverse with numerous narrow plicae, six costae over anterior fold.

Material: Ventral valve from JBW 723, a single dorsal valve from JBW 591 and two from JBW 615.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: The specimens are transverse, the incomplete ventral valve from JBW 723 measuring 66mm wide and 25mm long, and the dorsal valve from JBW 615 measuring 46mm wide, 13.5mm long and 6.5mm high. Another dorsal valve from JBW 615 is at least 56mm wide, and probably 80mm wide, and 29mm long, and one from JBW 591 is 64mm wide. The cardinal extremities are subalate, and the ventral sulcus is narrow with angle of 20º, and the fold distinct. Some fifteen pairs of narrow plicae lie on the ventral valve, with minor splitting, more marked on the dorsal valve. A few costae lie posteriorly over the sulcus, and about fourteen in the anterior sulcus, and the fold has six costae. At least seven costae lie over the low fold of JBW 591, and there are at least ten pairs of plicae laterally. The shell is finely and densely taleolate.

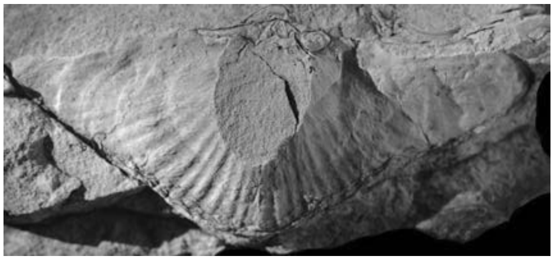


Fig. 343. *Yukonospirifer* sp., damaged dorsal internal mould, GSC 137202 x1, from JBW 591. Member A, Jungle Creek Formation.

Resemblances: This specimen is transverse and finely plicate with costae over the low dorsal fold, as in the type species from the "*Yakovlevia transversa*" Zone of the middle Jungle Creek Formation. But present material does not allow a full comparison. The inner shell on present material is taleolate, but not punctate. Shi & Waterhouse (1996, p. 123) had reported the shell as impunctate, and Carter in Gourvennec & Carter (2007, p. 2789) interpreted this as an indication that the genus belonged to Pterospiriferinae of Superfamily Paeckelmannelloidea, but the adminicula are long, as in many Syringothyridina (see Shi & Waterhouse 1996, pl. 23, fig. 11), and Carter was not aware of the likely presence of taleolae in the shell. The genus is therefore considered to be a member of Licharewioidea. A genus within Syringothyroidea, *Sulciplica* Waterhouse, has costate fold and sulcus, but the shell is punctate.

Genus ***Nahoniella*** Shi, 1998

Diagnosis: Transverse and biconvex, sulcus with well defined borders, prominent fold with round crest and sharply defined from lateral shell, numerous plicae, and micro-ornament of tubercles without grooves. Connector plate large, adminicula short, ovarian impressions poorly developed or absent.

Type species: *Yukonella plana* Shi & Waterhouse, 1996, p. 128 from *Jakutoproductus verchoyanicus* Zone (lower Artinskian), Jungle Creek Formation, Yukon, Canada, OD.

Discussion: Present specimens have dense taleolae in the shell, and it is deemed likely that the taleolae are also present in type material.

Nahoniella decorus n. sp.

Fig. 344, 345B

1971 ?*Orulgania* sp. Bamber & Waterhouse, pl. 11, fig. 9, 11.

Name: decorus – becoming, Lat.

Diagnosis: Large transverse moderately elongate shells with up to twenty plicae pairs, and dorsal median septum of moderate length.

Holotype: GSC 26910, here designated.

Material: A broken internal mould from JBW 674. Additional material, some figured, in Bamber & Waterhouse (1971).

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Fold sharply defined, crest rounded, lateral plicae numerous in at least fifteen pairs, varying to twenty pairs. Well defined median septum extends for almost half the length of the valve. Subrectangular impressions with fine radial lira over the median third suggest adductor scars. Shell densely taleolate.

Resemblances: The fold is higher than that of *Brachythyris*, and the lateral plicae are numerous and simple, rather than branching. The dorsal fold is wider and the dorsal septum slightly shorter than in *Nahoniella plana* (Shi & Waterhouse) from the younger Jungle Creek Formation. Two more complete specimens were figured in Bamber & Waterhouse (1971) from what is now Member A in the Jungle Creek Formation. They include the present holotype, and the shell is more elongate than *Nahoniella plana* (Shi & Waterhouse) – see below – with a dorsal septum not extending beyond mid-length, and slightly more lateral plicae.

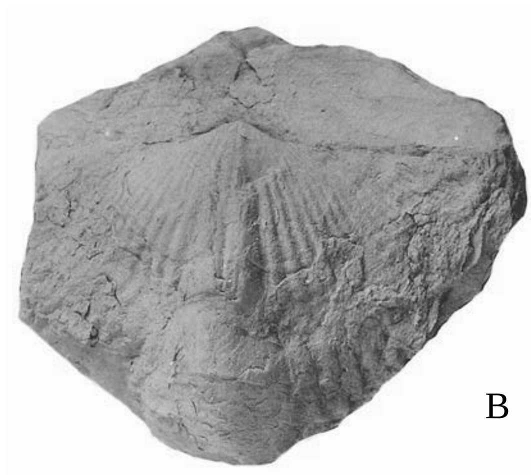


Fig. 344. *Nahoniella decorus* n. sp. A, dorsal valve GSC 26912. B, dorsal view of GSC 26910, holotype. Specimens x 1 from GSC 57143, Member A, Jungle Creek Formation. From Bamber & Waterhouse (1971).

***Nahoniella*? sp.**

A fragment of a dorsal valve with prominent dorsal fold and very narrow plicae may belong to the genus. It comes from JBW 69, from Member B in the *Ogilviecoelia initiatus* Zone.

***Nahoniella* cf. *plana* (Shi & Waterhouse, 1996)**

Fig. 345A

cf. 1996 *Yukonella plana* Shi & Waterhouse, p. 128, pl. 22, fig. 21-25, pl. 23, fig. 1-7, text-fig. 44, 45.
cf. 1998 *Nahoniella plana* – Shi, p. 935.

Diagnosis: Biconvex with well defined ventral sulcus and elevated narrow dorsal fold, numerous plicae, micro-ornament of tubercles without anterior grooves. Connector plate large, adminicula short.

Holotype: GSC 97217 from *Jakutoproductus verchoyanicus* Zone (lower Artinskian), Jungle Creek Formation, Nahoni Range, Yukon Territory, figured in Shi & Waterhouse (1996, pl. 23, fig. 2), OD.

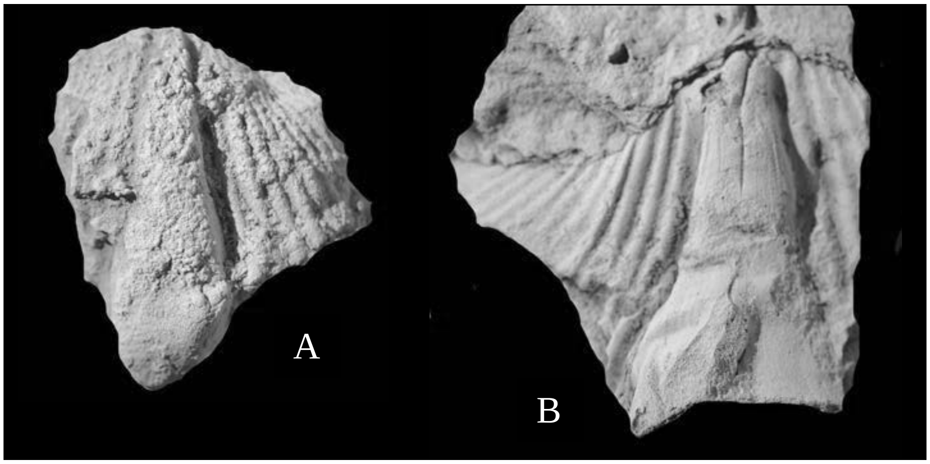


Fig. 345. A, *Nahoniella* cf. *plana* (Shi & Waterhouse, dorsal view of specimen with valves conjoined, GSC 137204 x2, from JBW 581, Member E. B, *Nahoniella decorus* n. sp. dorsal view of specimen with valves conjoined, GSC 137203 x2, from JBW 674, Member A. Jungle Creek Formation.

Material: A broken dorsal valve from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation, *Ogilviecoelia shii* Zone.

Description, Resemblances: The present specimen is incomplete, but looks close to *Nahoniella plana*, and has numerous fine pustules with no surface grooves. The shell is possibly but not definitely taleolate.

Superorder TEREBRATULIFORMI Waagen, 1883

This name is proposed as a companion for other superorders, and contains one highly diverse order.

Order TEREBRATULIDA Waagen, 1883

[Nom. correct. Moore 1952, p. 220 pro Order Terebratulacea Kuhn, 1949, p. 105, nom. transl. ex Suborder Terebratulacea Waagen, 1883, p. 447].

Members of the Order as a rule form an important constituent of Late Paleozoic marine invertebrate faunas all over the globe. But they are extremely rare in the Carboniferous and at least Early Permian of Canada, in strong contrast to the number of taxa in counterpart faunas of the southern paleohemisphere. Nazer (1977) found only one species, belonging to *Beecheria* Hall & Clarke, in the extensive faunas from the Ettrain Formation (Kasimovian), and just two species were described from the younger Jungle Creek Formation by Shi & Waterhouse (1996). A very few species were identified in the studies of faunas from Verchoyan in Abramov & Grigorieva (1983, 1986, 1988). For all the extensive search of Asselian and Gzhelian faunas in the present study, only three specimens have been found.

Suborder TERBRATULIDINA Waagen, 1883

[Nom. correct. Muir-Wood & Stehli 1965, p. 730, pro Suborder Terebratulacea Waagen, 1883, p. 447].

Gray (1848) was first to recognise terebratulids as belonging to a distinct order, which he called Ancyclobrachia, a name retained, with altered content, until Waagen (1883) introduced Terebratulida as an alternative.

Superfamily **CRYPTONELLOIDEA** Thomson, 1926

[Nom. transl. Stehli 1965, p. 762, ex Cryptonellinae Thomson, 1926, p. 529].

Family **CRYPTONELLIDAE** Thomson, 1926

[Nom. transl. Stehli 1965, p. 762, ex Cryptonellinae Thomson, 1926, p. 529].

Subfamily **CRYPTACANTHIINAE** Stehli, 1965

[Cryptacanthiinae Stehli 1965, p. 752].

Discussion: The diagnoses provided for Cryptonellinae and Cryptacanthiinae show some approach to the structure of the present genus, in so far as dental plates may be developed, and median dorsal septum missing, and the suggestion that a cardinal plate is not developed. But uncertainty over aspects of the dorsal morphology, including the all-important loop, makes any attempt at identification highly speculative. The broad shape of the Canadian specimen does conform with aspects of shape displayed by several North America genera assigned to the two subfamilies (Jin & Lee 2006, pp. 2024-2027), and is particularly close to that of *Cryptacanthia* White & St John, 1867.

Genus ***Cryptacanthia*** White & St John, 1867

Diagnosis: Small, biconvex to concavoconvex, unisulcate, ventral median septum usually absent or limited to posterior shell, hinge plate concave, perforate, loop with hood-like lamellae ascending lamellae and transverse band, descending lamellae becoming independent with advanced maturity, anterior extremities of loop spinose.

Type species: *Waldheimia? compacta* White & St John, 1867, p. 119, from Pennsylvanian of United States, OD.

Cryptocanthia? sp.

Fig. 346

Material: A specimen with valves conjoined from JBW 580.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Specimen 13mm wide and long, squashed flat. Ventral valve with moderately high and wide median swelling, rounded posteriorly, and only gently rounded in front, and short anterior sulcus. Dorsal valve with broad median sulcus commencing before mid-length, anterior margin unisulcate. Comparatively large foramen, apparently permesothyrid.

Dental lamellae well developed. Dorsal sockets very small, inner crural plates low and short, diverging, without cardinal plate. Crural bases not clear but possibly small and rounded at end of crural plates, crura and nature of loop not known. Pair of well defined elongately suboval muscle impressions lie each side of mid-line, and a short and low eccentric ridge lies behind, but no well formed median septum. Shell very finely and densely punctate.

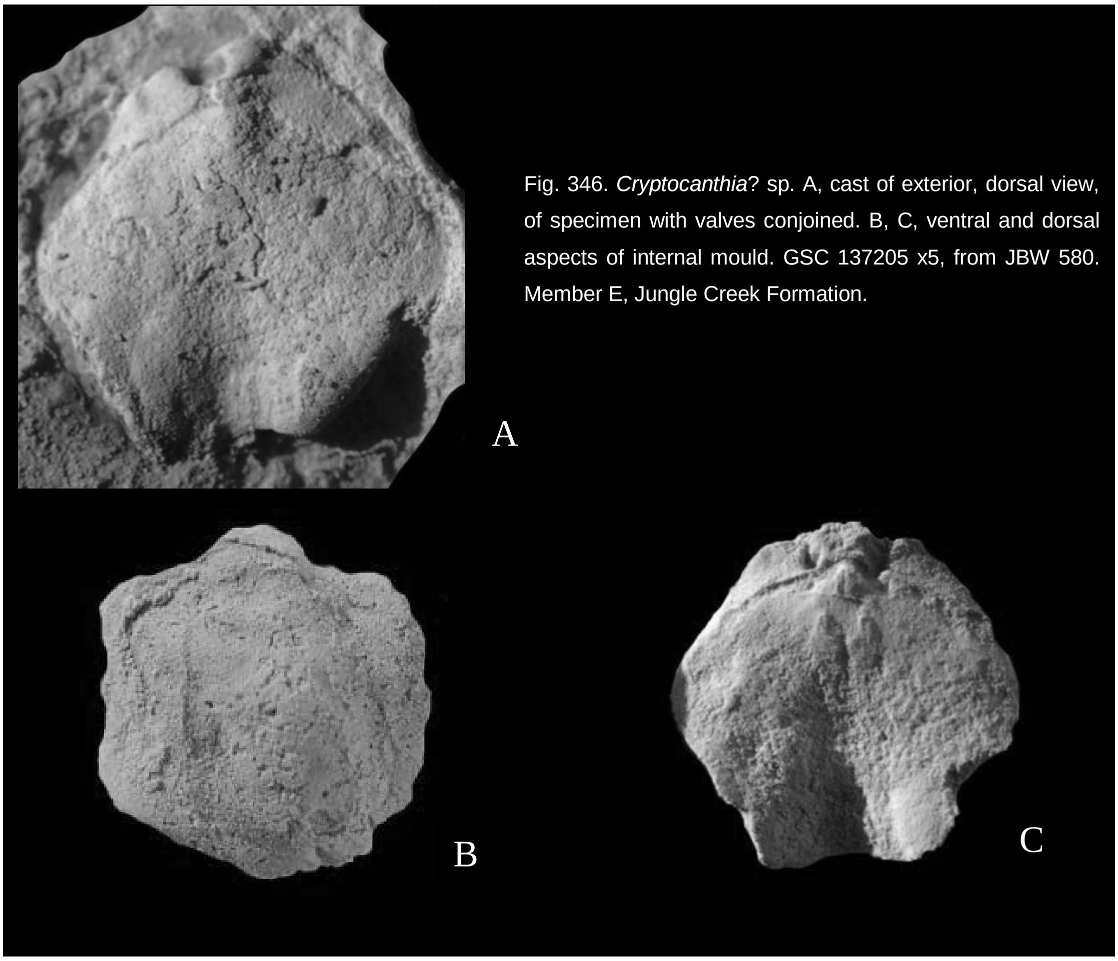


Fig. 346. *Cryptocanthia*? sp. A, cast of exterior, dorsal view, of specimen with valves conjoined. B, C, ventral and dorsal aspects of internal mould. GSC 137205 x5, from JBW 580. Member E, Jungle Creek Formation.

Resemblances: Material is too sparse to encourage specific comparisons. The genus is found in beds of middle Pennsylvanian to Early Permian age in North America, Asia and Europe.

Superfamily **DIELASMOIDEA** Schuchert, 1913

[Nom. correct. Waterhouse 2015a, p. 220 ex Dielasmatoidea Waterhouse 2001, p. 105, repeated as Dielasmatoidea Lee et al. 2005, p. 2029, pro Dielasmatacea Stehli, 1965, p. 754, nom. transl. ex Dielasmatinae Schuchert, 1913, p. 402].

Family **DIELASMIDAE** Schuchert, 1913

[Nom. correct. Waterhouse 2015a, p. 220 pro Dielasmatidae Schuchert & LeVene, 1929, p. 23 ex Dielasmatinae Schuchert, 1913, p. 402].

Diagnosis: Genera as a rule small in size, with variably flexed anterior commissure, foramen generally permesothyrid and labiate, collar well developed, dental plates developed as a rule but may be reduced, septalium well developed, may be sessile or supported on high septum, loop acuminate in juvenile form, deltiform at maturity, may develop anterior vertical blade medianly.

Subfamily **DIELASMINAE** Schuchert, 1913

[Nom. correct. hic ex Dielasmatinae Schuchert, 1913, p. 402]. See Waterhouse 2015a, p. 221.

Diagnosis: Dental plates well developed, septalium of inner and outer hinge plates, may be divided, sessile or raised on septum, loop deltiform.

Tribe **DIELASMINI** Schuchert, 1913

[Nom. correct. Waterhouse 2015a, p. 220 pro Dielasmatinae Schuchert, 1913, p. 402].

Discussion: Members of Fletcherithyrini Waterhouse, 2010a, p. 82 are distinguished from Dielasmini by having a much higher dorsal septum. The dorsal septum in Dielasmini is comparatively low. Fletcherithyrini were particular common in high paleolatitudes of the Permian Period, and it is they which survived into the Triassic Period (Waterhouse 2010b, p. 172; 2015a, p. 221; Waterhouse & Shi 2010, p. 26). The name Fletcherithyrisini may be a better alternative, whereas others would prefer Fletcherithyridini.

Genus ***Dielasma*** King, 1859

Diagnosis: Small elongately oval shells with permesothyrid foramen, dental plates, outer hinge plates join inner hinge plates that unite close to floor or meet floor separately, juvenile loop acuminate, adult loop developed by fission and resorption of echmidium (see Williams et al. 1997, pp. 376, 377) and insertion of transverse band.

Type species: *Terebratulites elongatus* von Schlottheim, 1816, p. 256 from Zechstein (Wuchiapingian) of Germany, OD.

Dielasma? sp A.

Fig. 347

Material: A specimen with valves conjoined from JBW 804.

Fig. 347. *Dielasma*? sp., ventral view of GSC 137206 x3, from JBW 804, Member A, Jungle Creek Formation.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimen small, elongately oval in shape, 13mm long and 5.5mm wide, and both valves 6.5mm high, with permesothyrid foramen, weak median diminution of curvature and uniplicate anterior margin. Dental plates short. The dorsal valve is less than half as high as the ventral valve and the shell is punctate.

***Dielasma*? sp. B**

Fig. 348

Material: A ventral valve from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: This specimen differs from *Dielasma* sp. A in having a larger foramen and a slender median groove. The dental plates are visible, each side of the foramen.

Fig. 348. *Dielasma*? sp., ventral valve GSC 137347 x3, from JBW 804, Member A, Jungle Creek Formation.

Phylum MOLLUSCA Linné

Class BIVALVIA Linné

Classification largely follows that summarized by Amler (1999), with some further updates and insertions of omitted families, and it may be pointed that J. G. Carter (1990) and Waller (1978, 1990, 1998) offer valuable insights. A study on Pteriomorphia by Waterhouse (2008a) is partly followed herein for some aspects of the terminology, analyses and explanations, and terms that have been recently introduced are explained in a section on morphology at the commencement of the systematic descriptions (p. 24). However the higher level classification is in a holding pattern, because of the current major review of classification being undertaken in preparation of the forthcoming *Revised Treatise* series on Bivalvia, and current ideas being circulated are set aside for considerations of intellectual property rights, apart from acknowledgement to Prof. J. G. Carter, who drew attention to the significant proposal of Heteroconchinae Beurlen, 1954. A preliminary overview of Bivalvia has been presented by Carter et al. (2011). Given that the Canadian Mollusca are so sparse, with a number of genera only represented by one or two often incomplete specimens, which may be far from mature, the taxonomic background and diagnoses are curtailed, and resemblances are seldom explored.

Subclass PROTOBRANCHIA Pelseneer, 1889

Superorder **NUCULANIFORMI** Carter, Campbell & Campbell, 2000

Order **NUCULANIDA** Carter, Campbell & Campbell, 2000

Superfamily **NUCULANOIDEA** H. Adams & A. Adams, 1858

Family **POLIDEVCIIDAE** Kumpera, Prantl & Růžička, 1960

This family has been reviewed by Gonzalez (2006, p. 132).

Genus ***Polidevcia*** **C**hernyshev, 1951

Polidevcia? sp.

Fig. 349

Material: An internal mould of a right and a left valve from JBW 580 and 581 respectively.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Umbones orthocresent, incurved, placed at anterior third of length, anterior shell with subrounded outline, posterior shell longer and tapering posteriorly. Exterior, to judge from fragments preserved of umbonal and ventral exterior, lightly marked by commarginal growth threads. Anterior hinge bears nine (JBW 581) or ten (JBW 580) strong and high vertical teeth. Posterior teeth slightly smaller and appear to slightly exceed the anterior number. Posterior and anterior adductor scars deeply impressed, and umbonal pedal scar clearly developed. The shell is thickened below the umbo and in front over the upper half, and a thick band is inclined obliquely across the posterior shell from below the pedal scar.

Resemblances: *Nuculana undosa* Muromseva (1984, pl. 1, fig. 35, 36, pl. 2, fig. 14) from the Djuptagin Suite of northeast Russia is somewhat similar in shape and ornament. But material is hardly sufficient to warrant any extensive search to find close comparisons, and as for virtually all the remainder of bivalve material from the lower Jungle Creek Formation, many more specimens need to be found and collected to allow the affinities to be assessed.

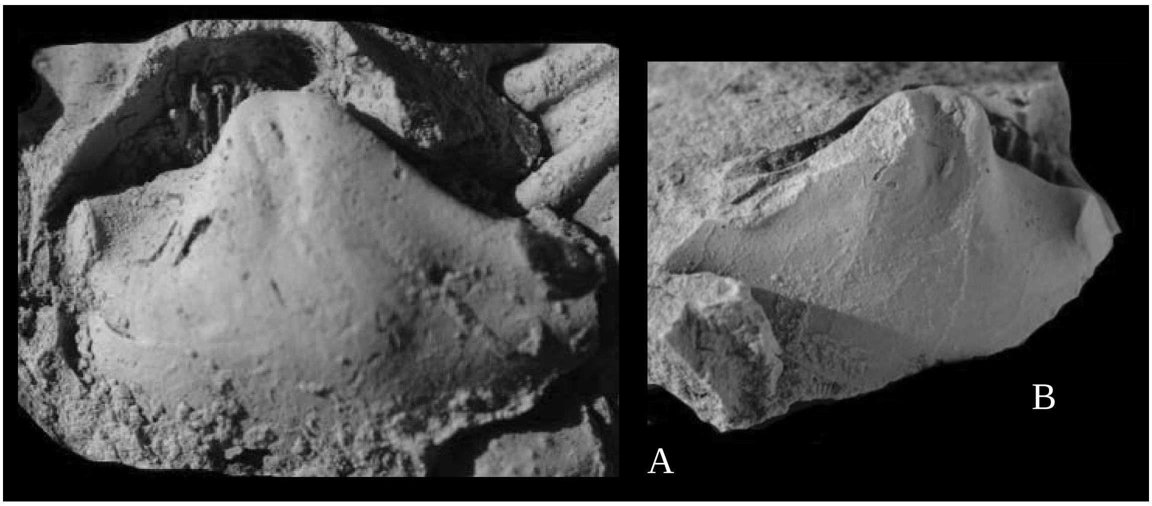


Fig. 349. *Polidevcia*? sp. A, internal mould of left valve, GSC 137207 x5 from JBW 581. B, internal mould of right valve, GSC 137208 x5, from JBW 580. Member E, Jungle Creek Formation.

Subclass AUTOBRANCHIA Grobben, 1894

Infraclass PTERIOMORPHIA Beurlen, 1944

Order ARCIDA Stoliczka, 1871

Superfamily **ARCOIDEA** Lamarck, 1814

Family **PARALLELODONTIDAE** Dall, 1898

Subfamily **PARALLELODONTINAE** Dall, 1898

Genus ***Parallelodon*** Meek & Worthen, 1866

Diagnosis: Shells elongate, ornament by radial ribs, area broad with chevron grooves.

Type species: *Macrodon rugosus* Buckmann, 1844, p. 99 from middle Jurassic of England, OD.

Parallelodon? sp. indet.

Fig. 350

Material: Three right valves and five left valves from JBW 581, one right valve from JBW 580.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

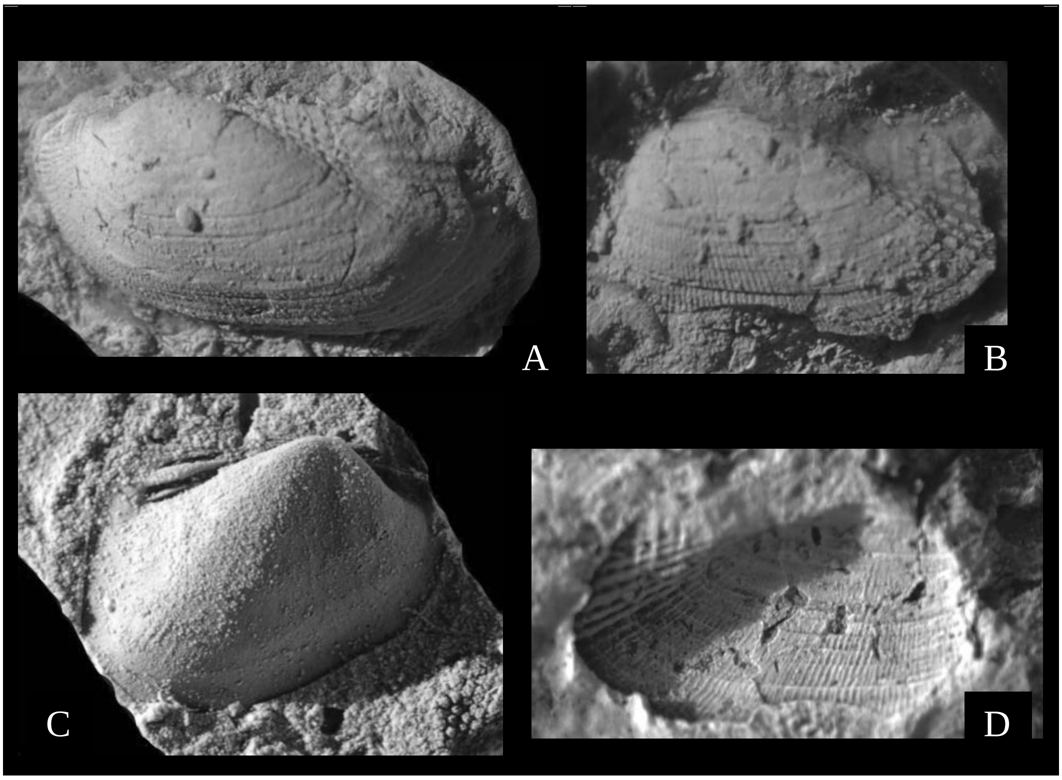


Fig. 350. *Parallelodon*? sp. A, external cast of left valve, GSC 137209 x6, from JBW 581. B, D, external cast and mould of left valve, GSC 137210 x6, from JBW 581. C, internal mould of right valve, GSC 137211 x6, from JBW 561. Member E, Jungle Creek Formation.

Description: Specimens small, equivalve, a left valve measuring 12.5mm long, 7mm high and 3.7mm high, with orthocrescent umbones weakly incurved at 3.5mm from anterior margin. High interarea marked by horizontal grooves, weak posterior shoulder with posterior upper shell weakly concave. Shell ornamented by fine radial threads, six to eight in 1mm, which become much stronger – one or two per mm – over the upper posterior concave shell; crossed by low growth lines and laminae, that form low nodes over the posterior dorsal costae.

A right valve has two slender anterior elongate teeth and sockets and three posterior teeth. This valve is shorter than the other specimens, and higher posteriorly with anterior lateral sulcus (see Fig. 350C).

Subcohort Ostreioni Férussac, 1822

Megaorder MYALINATA H. Paul, 1936

Order MYALINIDA H. Paul, 1936

Superfamily **AMBONYCHIOIDEA** Miller, 1877

Family **MYALINIDAE** Frech, 1891

Genus ***Pseudomyalina*** Dickins, 1956

Diagnosis: Right valve slightly less inflated than left valve, beaks terminal, low radial ribs over exterior, no umbonal deck.

Type species: *Pseudomyalina obliqua* Dickins, 1956, p. 26 from Coolkilya Formation (Roadian) of Western Australia, OD.

Pseudomyalina sp.

Fig. 351

Material: The external mould of a left valve from JBW 816. Possible shell fragments at JBW 433.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation, *Septospirifer tatondukensis* Zone.

Description: Specimen 30mm long and 28mm high, with terminal or subterminal beak, long posterior hinge bearing grooved ligament canal. Main body of shell bearing at least fourteen low radial ribs, posterior dorsal shell smooth.

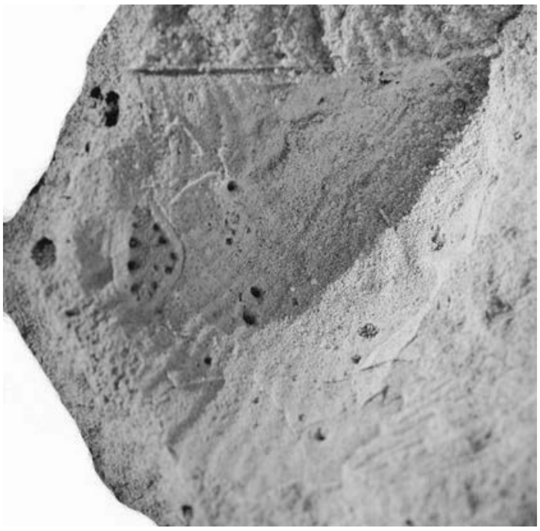


Fig. 351. *Pseudomyalina* sp., external mould GSC 137324 x2, from JBW 816. Member A, Jungle Creek Formation.

Fragments of prismatic shell come from JBW 433, and these could have belonged to *Pseudomyalina*, which has prismatic shell. In northeast Russia as in New Zealand and Queensland, prismatic shell fragments were commonly sourced from members of Atomodesmidae Waterhouse, and in Russia also from the myalinid *Kolymia* Licharew, but no members of these taxa have been found in the Jungle Creek Formation.

Resemblances: Unlike species of *Myalina* and various allied genera from United States (Newell 1942), this specimen bears radial ribs, which suggests a possible alliance with the Australian genus *Pseudomyalina* Dickins (see Waterhouse 2015a, p. 238). The ribs are slightly weaker than in Australian occurrences, and the posterior wing-like shell in these southern species are ribbed, whereas the corresponding shell of the Canadian specimen is marked only by growth increments.

Order PECTINIDA J. Gray, 1854

Hyporder AVICULOPECTENOIDEI Starobogatov, 1992

[Nom. emend hic ex infrasuborder Aviculopectinoidinei Starobogatov, 1992, p. 23].

Discussion: For a long time, the generic term *Pecten* when incorporated in family group and ordinal group terms has been emended to pectin. This goes against what is being proposed herein – that the spelling of generic terms should be altered as little as possible when adding the appropriate suffix. The only recommendation in favour of emending the generic name is that of customary usage, and there are far too many unscientifically based customs for this to be treated with deference in scientific studies.

The spelling is emended accordingly in this and subsequent renditions.

Superfamily **PTERINOPECTENOIDEA** Newell, 1938

Family **PTERINOPECTENIDAE** Newell, 1938

Subfamily **PTERINOPECTENINI** Newell, 1938

Genus ***Dunbarella*** Newell, 1938

Diagnosis: Large posterior wing on each valve, right valve anterior ear with small byssal notch. Costae intercalated on left valve and branching on right valve.

Type species: *Aviculopecten whitei* Meek, 1872, p. 195 from upper Pennsylvanian of Nebraska, OD.

Dunbarella sp.

Fig. 352

Material: Three right valves and four left valves from JBW 618, two valves from JBW 136.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation, *Septospirifer tatondukensis* Zone.

Description: The valves are identified from their symmetry, which indicates a large posterior wing grading gently from the body of the shell, with more inclined anterior umbonal slope, and both valves are almost similar in inflation. They are gently and evenly convex, and ornamented by fine ribs which increase by intercalation on the left valve, eight to ten in 5mm on both valves, crossed by faint growth laminae, and bearing small nodes at close intervals. Low commarginal rugae are also present. In the right valve, ribs are branching.

Resemblances*: Dunbarella* Newell, 1938 is close in shape, generally with coarser costae, and right valve costae increase by bifurcation, so that the Canadian material appears to belong to this genus, and is of somewhat comparable age. *Bifurcatia* Waterhouse, 2008a is close in shape and fine costae, but costae bifurcate on both valves.

It is of Lower Carboniferous age.

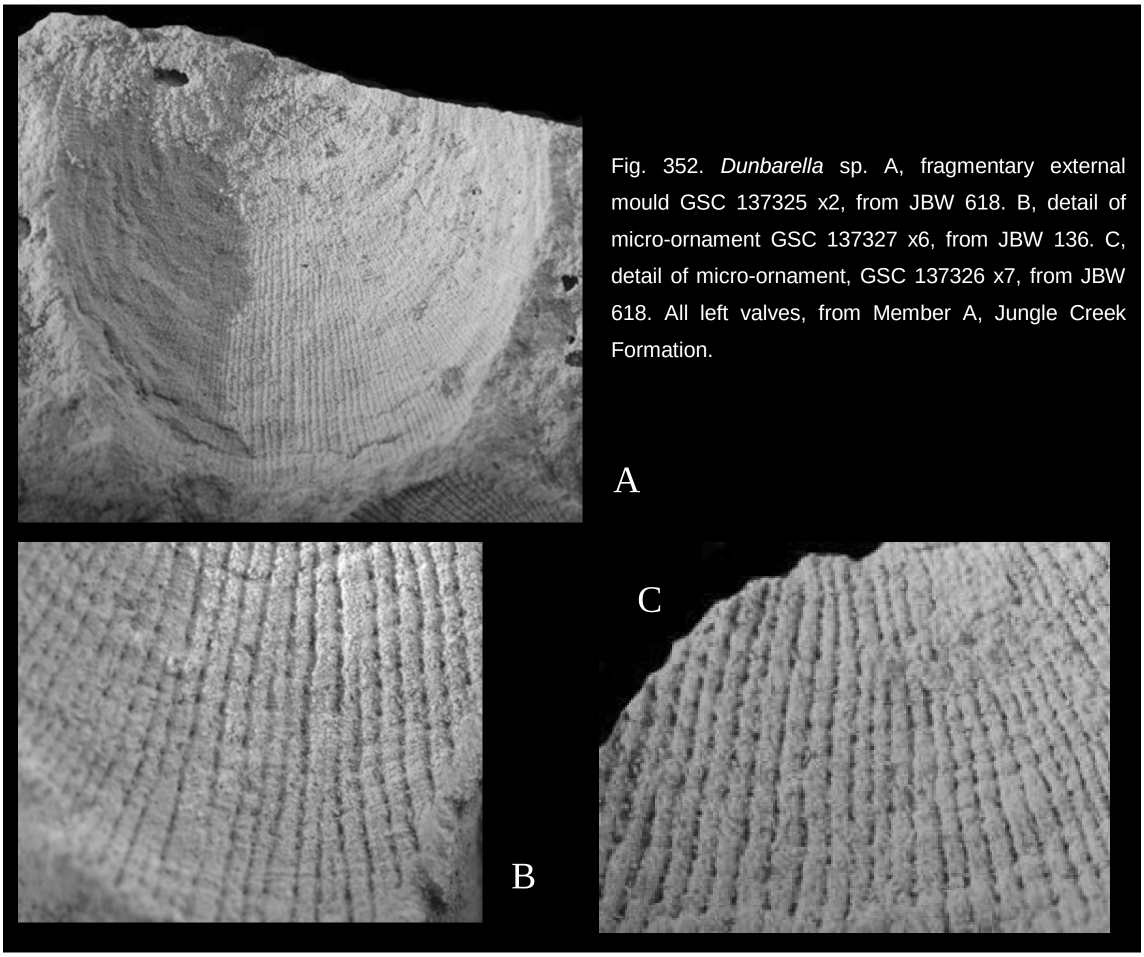


Fig. 352. *Dunbarella* sp. A, fragmentary external mould GSC 137325 x2, from JBW 618. B, detail of micro-ornament GSC 137327 x6, from JBW 136. C, detail of micro-ornament, GSC 137326 x7, from JBW 618. All left valves, from Member A, Jungle Creek Formation.

Subfamily **PTERINOPECTINELLINAE** Waterhouse, 2008a

[Pterinopectinellinae Waterhouse 2008a, p. 46. The spelling is retained as in the original].

Diagnosis: Shells biconvex, ornament of rib bundles or subplicae on both valves, tending to be nodose or usually spinose, hinge long.

Genus ***Pterinopectinella*** Newell, 1938

Diagnosis: Right valve with nodose bifurcate ribs, left valve with spinose subplicae and bundled ribs, hinge long.

Type species: *Pterinopectinella welleri* Newell, 1938, p. 41 from Missouri beds of Kansas, OD.

Pterinopectinella sp.

Fig. 353

Material: A right valve from JBW 593.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation, *Septospirifer tatondukensis* Zone.

Description: The valve is gently convex and measures 56mm long and at least 34mm high, but is possibly incomplete. There is a right auricle, and moderately long posterior wing bearing fine costae and low commarginal growth increments. The ornament consists of low broad ribs which bifurcate near the umbo into a prominent rib and finer rib on the posterior side. For some ribs, the bifurcation is not clear, and the subsidiary rib could have arisen through intercalation. There are nine or ten low and slightly irregular commarginal rugae, and nodes arise at the crest. These may have given rise to spines or tubercles, no longer preserved because of decortication.

Fig. 353. *Pterinopectinella* sp., right valve GSC 137328 x2, from JBW 593. Member A, Jungle Creek Formation.

Discussion: Several genera have been recognized within the subfamily (Waterhouse 2008a), and the decortication and lack of left valve for the present material makes identification uncertain. But from available information, the present specimen comes closest to *Pterinopectinella* in the right valve rib pattern and nodation.

Superfamily **CHAENOCARDIOIDEA** Miller, 1889

Diagnosis: Shell biconvex, equivalve to subequivalve with relatively small posterior wings in each valve as a rule. Right anterior auricle and byssal notch well developed. Ornament varies from coarse to fine, but no genus is known to be strongly plicate. Costae tend to increase by branching but implantation is also common, and growth lines often arch ventrally in interspaces and hingewards over costae. Ligament external and amphidetic, alivincular, lativincular or platyvincular (see p. 24), some genera with a few simple teeth.

Discussion: This is a superfamily of wide diversity, its members close to Aviculopectenidae in alivincular hinge and close to Deltopectenidae in having small posterior wings, but overall small and somewhat rounded in shape, with not very large anterior wing or auricle. The source of the group is yet to be clarified. Waterhouse (2008a) suggested that the superfamily might be a sister group with Aviculopectenoidea, being similarly subequivalved with ornament the same on each valve, and with usually alivincular hinge. The origins for Aviculopectenoidea lay within

Pseudaviculopecteninae Waterhouse, and the lack of plicae in most Chaenocardioidea suggest the likelihood of a separate pterinopecteniform source.

Family **STREBLOCHONDRIIDAE** Newell, 1938

Diagnosis: Shells biconvex, almost equivalve to inequivalve, upright to slightly procrescent, well defined umbonal slopes, posterior wings small, ornament variable. Short amphidetic alivincular ligament as a rule with small resilifer extended slightly forward. Teeth rarely developed.

Discussion: Members of the family are distinguished from members of Chaenocardiidae Miller by having a more symmetrically alivincular ligament.

Subfamily **STREBLOCHONDRIINAE** Newell, 1938

Diagnosis: Hinge alivincular, edentulous.

Streblochondriid gen. & sp. indet.

Fig. 354, 355

Material: Right and left valves from JBW 581, right valve from JBW 98 and 561, and external mould of larger specimen from JBW 195.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

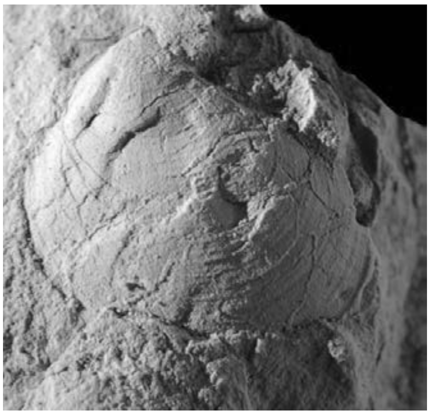


Fig. 354. Streblochondriid gen. & sp. indet. A, right valve GSC 137441 x4, from JBW 561, Member E, Jungle Creek Formation.

Description: Specimens small, one specimen measuring approximately 12mm long and high, and 3.5mm wide. Umbo placed behind mid-length, right anterior auricle small with byssal notch, growth lines parallel to the anterior margin, and four low ribs over the lower ear, short posterior wing. Left valve obscure with anterior and posterior wing. The external mould is over 30mm long, with gentle convexity. Commarginal threads are well developed, crossed by thin and low radial costae, five or six in 5mm near the anterior margin, apparently worn from part of the shell, which is marked by very fine radial threads that may be reflecting shell structure.

Resemblances: With no information on the internal hinge, this material cannot be identified to even genus level. The likely range of genera involves *Orbiculipecten* Gonzalez (1978) of Orbiculipecteninae Waterhouse, 2001, with lativincular hinge (see p. 24) and *Striochondria* Waterhouse, 1983c of Streblocondriinae, with well developed resilifer.

Streblocondria sp. of Shi & Waterhouse (1996, p. 154, pl. 30, fig. 21, 22) from the "*Yakovlevia transversa*" Zone in the Jungle Creek Formation is somewhat similar.

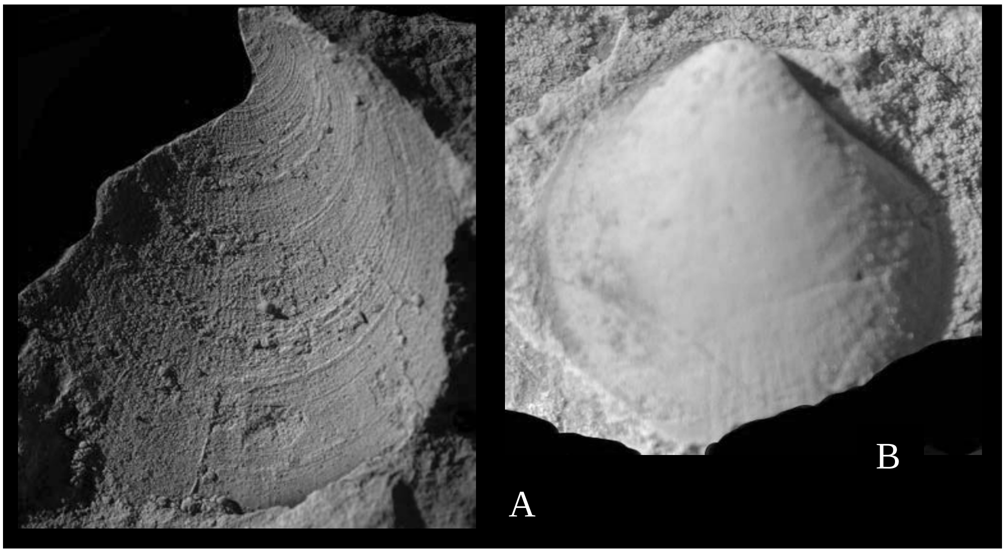


Fig. 355. Streblochondriid gen. & sp. indet. A, right valve GSC 137213 x2, from JBW 195, showing micro-ornament. B, decorticated right valve GSC 137212 x6, from JBW 98. Member E, Jungle Creek Formation.

Subfamily **SATURNELLINAE** Astafieva, 1994

Diagnosis: Strong commarginal rugae, radial ornament absent or very faint, strong radial ribs of right anterior auricle in some species.

Genus ***Montorbicula*** Waterhouse, 2008a

Diagnosis: Weakly procrescent to slightly retrocrescent, posterior wings not large, both valves ornamented by commarginal growth laminae, and low commarginal rugae or growth steps, right anterior auricle not costate. Ligament platyvincular.

Type species: *Streblopteria montgomeryi* Gonzalez, 2006, p. 140 from Early Permian faunas of Argentina, OD.

Discussion: *Montorbicula* Waterhouse, 2008a, p. 105 shows considerable approach to *Concentiolineatus* Waterhouse, 2008a, p. 100, which is based on *Streblopteria homevalensis* Waterhouse, 1986a, p. 5; 1987b from the Tiverton Formation (Sakmarian) of Queensland, a genus well established in Permian faunas of east Australia. It has been found since its proposal that the hinge of the type species lacks a resilifer (Waterhouse 2015a, p. 261), so that it resembles in many respects the genus *Montorbicula.* The types of both genera are like *Streblopteria* M'Coy, 1851a in lacking radial ornament over the body of the shell, but differ in lacking the very large posterior wings characteristic of that genus (see Waterhouse 2008a, p. 100). *Montorbicula* has commarginal rugae that are more prominent than seen in *Concentiolineatus*, and it lacks the radial ribs that are developed on the anterior auricle of *Concentiolineatus*, but these differences are not great.

The present material from Canada is close in a general way to the two taxa from high paleolatitudes of the southern paleohemisphere, but the nature of the ligament is not known. Nor is it well established that similar forms are absent or present in northerly or paleotropical faunas, there having been a dearth of studies on the entire bivalve component of a substantial Permian or Carboniferous fauna in the northern hemisphere for many decades, apart from a few notable exceptions such as Ciriacks (1963), Logan (1967), and Muromseva (1984).

***Montorbicula*? sp.**

Fig. 356

Material: A right valve from JBW 186.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: The specimen is 20.5mm long, 18mm high and 5mm wide, with broad low umbo of angle 110º, placed just front of mid-length, very small right anterior auricle, seemingly without costae as least as far as preserved, and high byssal notch. Shell ornamented by fine commarginal growth lirae, with growth steps close to the margin.

Resemblances: There is some similarity to Early Permian specimens assigned by Muromseva (1984, p. 69, pl. 34, fig. 1, 2, 5, 10, 24) to *Streblopteria englehardti* (Etheridge & Dun, 1906) from the Zihoshnin and Sokolov Suites of northeast Russia and Kungurian faunas of the Petchora Basin, a species with rather large right anterior auricle. The species *englehardti* is of mid-Permian age in east Australia and has fine radial ornament and costae over the right anterior auricle and resilifer, belonging to the genus *Striochondria* Waterhouse.

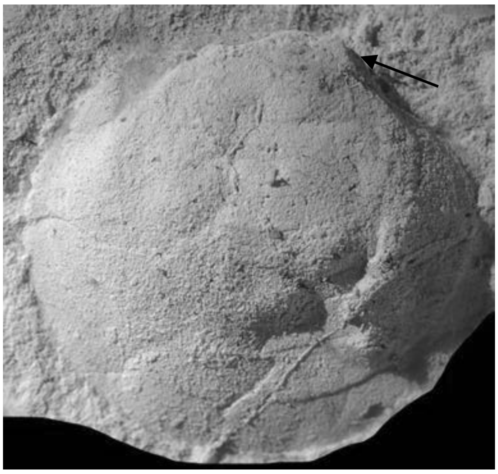


Fig. 356. *Montorbicula*? sp. cast of right valve exterior, GSC 137214 x4, from JBW 186. The anterior auricle, arrowed, is broken short and is highly convex. Member A, Jungle Creek Formation.

Superfamily **HETEROPECTENOIDEA** Beurlen, 1954

[Nom. emend. hic ex Heteropectinidae Beurlen, 1954].

Family **HETEROPECTENIDAE** Beurlen, 1954

[Nom. emend. hic ex Heteropectinidae Beurlen, 1954].

Diagnosis: Shells inequivalve, right valve comparatively flat, anterior and posterior wings large, umbonal slopes well defined, left valve ornament primarily costate and may be plicate, increase mostly by intercalation rather than branching on left valve. Right valve ribs usually increase by branching, less often by intercalation, costae bundled and often plicate. Growth-lines swing hingewards in interspaces. Hinge alivincular, no hinge teeth.

Subfamily **HETEROPECTENINAE** Beurlen, 1954

[Nom. emend. hic ex Heteropectinidae Beurlen, 1954

Diagnosis: Right valve with costae in clusters, increase by branching.

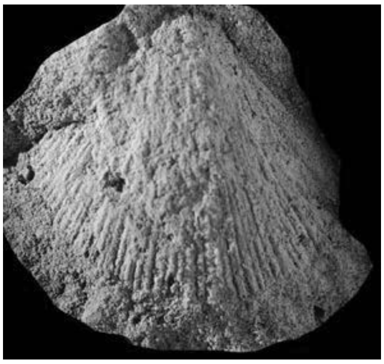
Heteropectenin gen. & sp. indet.

Fig. 357

Material: A left valve from JBW 607, with finely costate plicae.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Fig. 357. Heteropectenin gen. & sp. indet., left valve GSC 137355 x2 from JBW 607, Member A, Jungle Creek Formation.



Subfamily **ETHERIPECTENINAE** Waterhouse, 1982b

[Nom. emend hic ex Etheripectininae Waterhouse, 1982b, p. 15].

Diagnosis: Ornament of intercalate costae on left and right valve, branching exceptional, costae variably spinose. Right valve not plicate and costae not bundled.

Genus ***Etheripecten*** Waterhouse, 1963

Diagnosis: Left valve bears costae in several orders as a rule, arising by intercalation, primary costae generally remaining prominent. Right valve costae simpler and more uniform, may increase first by branching, but predominantly by intercalation, not associated in bundles. Growth lines arch dorsally in interspaces. Shell composition varies, apparently according to paleolatitude and temperature, and may be aragonitic or calcitic (Waterhouse 2015a, p. 270).

Type species: *Etheripecten striatura* Waterhouse, 1963, p. 195 from Kildonan Member (Changhsingian), New Zealand, OD.

Etheripecten sp. A

Fig. 358

Material: Single left valves from JBW 45 and 615, broken largely external moulds of single left valves from JBW 108 and 518, Member A, Jungle Creek Formation.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Best preserved specimen, a left valve from JBW 45, measures 25mm long and high, gently inflated, with ten primary ribs bearing rounded narrow crests and two further orders of ribbing, crossed by growth laminae which tend to arch hingewards across the interspaces. The anterior wing is damaged, and the posterior wing is flat and does not extend as far as the posterior shell margin. It bears a few costae crossed by growth lines which form nodes over the ribs. The specimen GSC 137330 from JBW 615 is larger, being 42mm long. The other specimens are small and broken. No right valve is preserved.

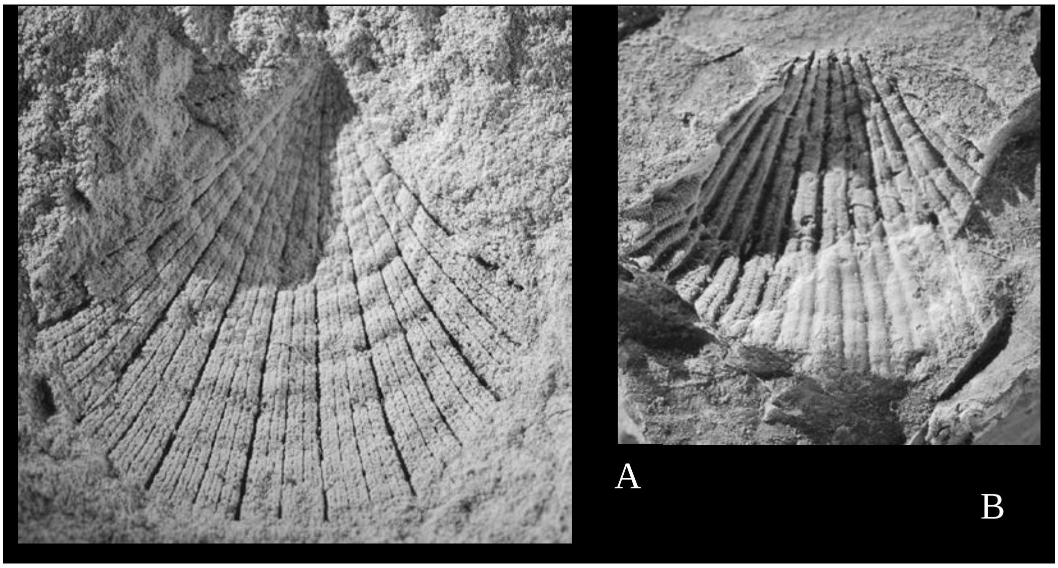


Fig. 358. *Etheripecten* sp. A. external mould of left valve GSC 137329 x3, from GSC 44. B, broken external mould of left valve GSC 137309 x3, from JBW 108. C, external mould of part of left valve GSC 137217 x3, from JBW 518. Member A, Jungle Creek Formation.

Etheripecten **sp. B**

Fig. 359

Material: Single left valve and possible right valve from JBW 19.

Stratigraphic and biostratigraphic level: Member B, Jungle Creek Formation. *Ogilviecoelia initiatus* Zone.

Description: The ventral valve is little inflated with three orders of intercalated costae, in which the primary order is prominent. The right valve has fine subeven ribs and low commarginal laminae.

Fig. 359. *Etheripecten* sp. B, fragment of left valve GSC 137215 x3, from JBW 19, Member B, Jungle Creek Formation.

Etheripecten sp. C

Fig. 360

Material: Single left valve from JBW 573.

Stratigraphic and biostratigraphic level: Member D, Jungle Creek Formation. *Rugivestigia commarginalis* Zone.

Description: This specimen is poorly preserved, and is little inflated, showing possibly three orders of intercalated costae. It measures 14.5mm long and 14mm high.

Fig. 360. *Etheripecten* sp. C, left valve GSC 137216 x3, from JBW 573. Member D, Jungle Creek Formation.

Etheripecten sp. D

Fig. 361 - 363

Material: Six left valves and fragments from JBW 561, five left valves and fragments with possible right valve from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Diagnosis: Small with well differentiated costae.

Description: Shells small, best preserved specimen from JBW 581 measuring 18mm wide, 19mm high, and 4mm high, with well defined anterior and posterior wings, shorter than maximum length. Ornament of fine costae in four orders, arising by intercalation, with narrow rounded crests, crossed by close-set growth laminae arching hingewards over interspaces; ribs closely spaced and becoming less differentiated with increase in size. Each wing on left valve has four primary ribs and short secondary ribs. A fragment of the lower part of the shell has closely spaced ribs and is comparatively flat, suggesting the possibility that it may be a right valve. Costae increase by intercalation ventrally, but the first formed part of the shell has been destroyed.

Resemblances: The specimens are more inflated with narrower umbo and more extended and curved posterior walls, compared with *Etheripecten* sp. A. They indicate a relatively distinctive species with well discriminated ribbing over the left valve.

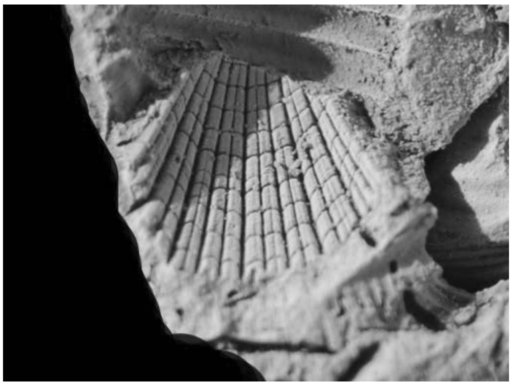
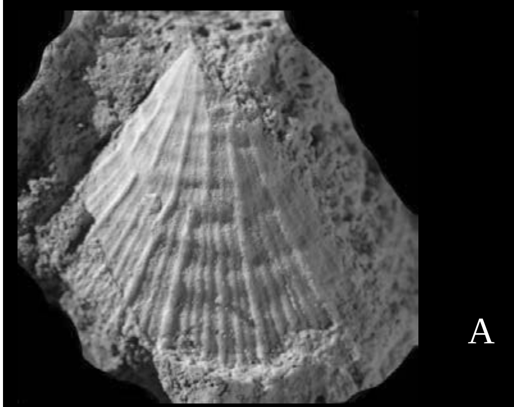


Fig. 361. *Etheripecten* sp. D, fragmentary external mould of left valve, GSC 137221 x6, from JBW 581. Member E, Jungle Creek Formation.



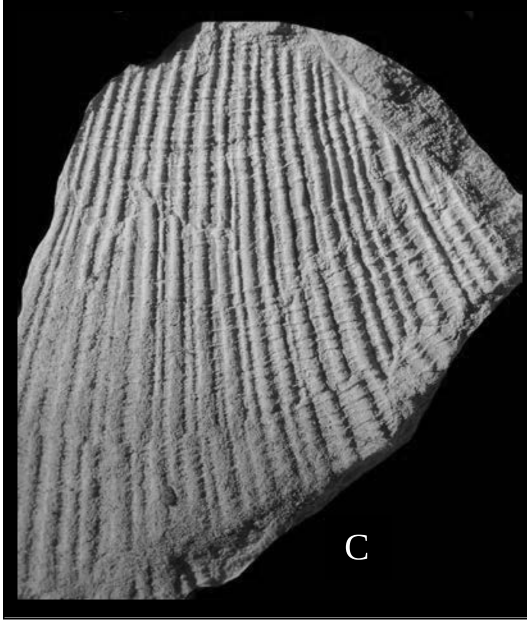


Fig. 362. *Etheripecten* sp. D. A, left valve internal mould, GSC 137218 x3, from JBW 581. B, fragment of external cast, GSC 137219 x3, from JBW 561. C, fragment of external cast of possible right valve, GSC 137220 x3, from JBW 581. Member E, Jungle Creek Formation.

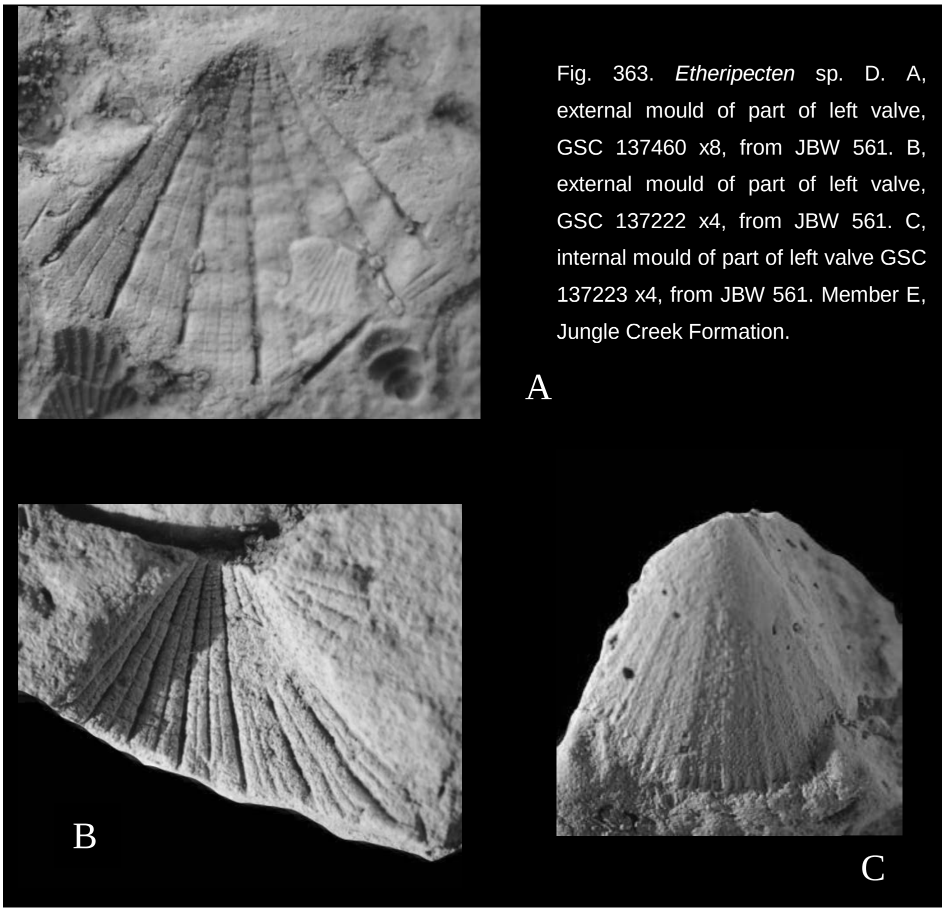


Fig. 363. *Etheripecten* sp. D. A, external mould of part of left valve, GSC 137460 x8, from JBW 561. B, external mould of part of left valve, GSC 137222 x4, from JBW 561. C, internal mould of part of left valve GSC 137223 x4, from JBW 561. Member E, Jungle Creek Formation.

Genus ***Primaspina*** Waterhouse, 2008a

Diagnosis: Left valve costae intercalated and spinose, right valve less inflated, costae intercalated. Hinge alivincular.

Type species: *Aviculopecten dawsonensis* Runnegar & Ferguson, 1969, p. 262 from Flat Top Formation (Wordian) of Bowen Basin, Queensland, OD.

Discussion: *Primaspina* Waterhouse, 2008a, p. 143 has spinose primary ribs on the left valve, and the right valve ribs are intercalated, with no clustering, so that the genus is deemed to belong to Etheripecteninae. There are several genera with left valve of somewhat similar appearance, and right valve with bundled and branching ribs that indicate an alliance to Heteropecteninae. These include *Vanvleetia* Waterhouse, 2001, p. 121 from United States, and *Nodulipecten* Waterhouse, 2008a, p. 149 from Western Australia, and *Neptunella* Astafieva (1997) from northeast Mongolia. *Neptunella* tends to have stronger primary ribs, sometimes split, on the left valve, with few spines, It is not very well known, and could prove to be a junior synonym of *Vorkutopecten* Guskov in Muromseva, 1984, which is based on two right valves with left valve not represented amongst the types. *Nodulipecten* has crowded left valve ribs with fewer spines, and *Vanvleetia* may have comparatively numerous spines, that where well preserved are large, tubular and opening ventrally. The right valve of each genus is distinctive.

The Canadian specimens cannot be identified with confidence, because there are no known right valves, making it difficult to ascertain the generic and subfamilial affinities. The left valves show primary ribs – more densely spinose than in type *Neptunella*, and approaching *Vanvleetia* Waterhouse, 2001, which is well represented in the

Permian of United States. But no left valve spines in present material are as large and tubular as those of *Vanvleetia*, so that the genus is provisionally assigned to *Primaspina*.

***Primaspina*? sp.**

Fig. 364

Material: Fragments of left valves from JBW 561 and JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: These fragments belong to specimens at least 35mm long, with fine closely spaced ribs in four orders, increasing by intercalation and crossed by fine growth laminae. The spines are comparatively solid, with only slight curvature, arching towards the hinge.

Resemblances: *Etheripecten* sp. A of Shi & Waterhouse (1996, p. 153, pl. 30, fig. 17, 18) has prominent spines at intervals on the primary costae of the left valve, and so is likely to be congeneric.

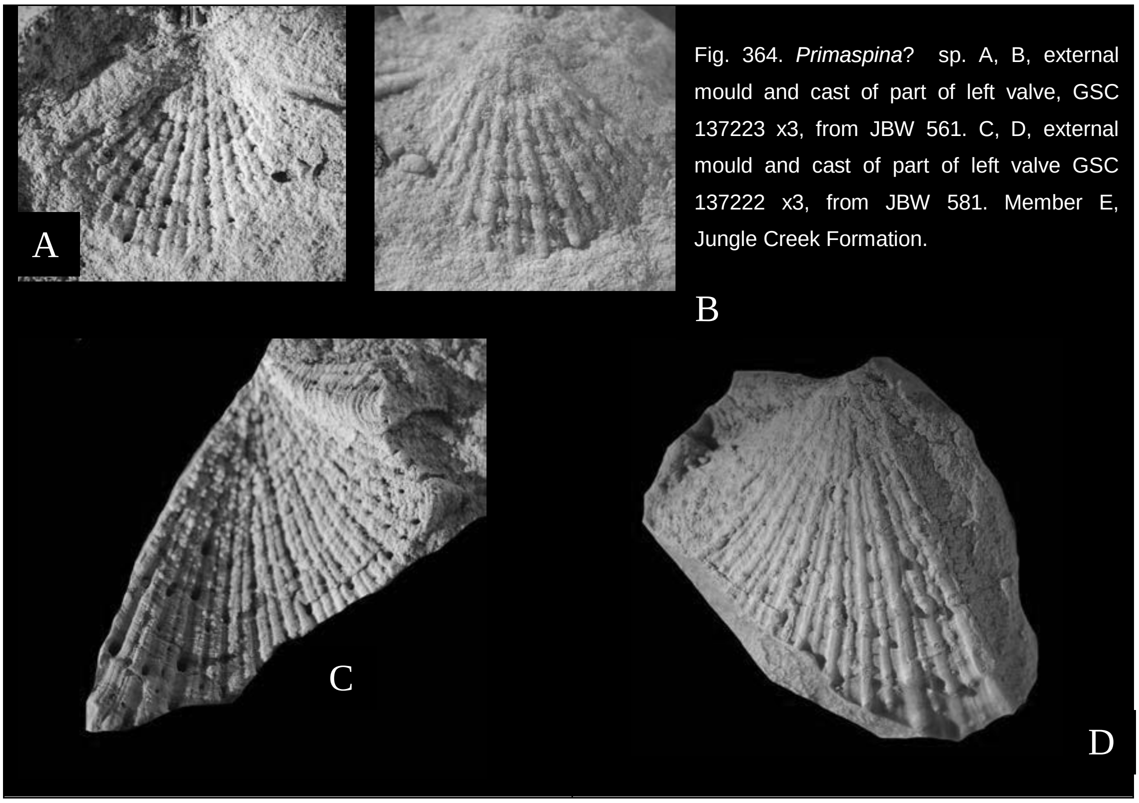


Fig. 364. *Primaspina*? sp. A, B, external mould and cast of part of left valve, GSC 137223 x3, from JBW 561. C, D, external mould and cast of part of left valve GSC 137222 x3, from JBW 581. Member E, Jungle Creek Formation.

Subfamily **GIRTYPECTENINAE** Waterhouse, 2008a

[Nom. emend. hic ex Girtypectininae Waterhouse, 2008a, p. 150].

Diagnosis: Ornament of strong well spaced primary costae which may be spinose, crossed by strong well spaced commarginal laminae, right valve with lower ribs and no prominent commarginals.

Genus ***Girtypecten*** Newell, 1938

Diagnosis: Strong radial ribs crossed by commarginal ribs of equal spacing, spinose or nodose at intersections.

Type species: *Aviculopecten sublaqueatus* Girty, 1908, p. 440 from Guadalupian of Texas, OD.

***Girtypecten*?** sp.

Fig. 365

Material: Single left valves from JBW 47 and 417, with possible right valve fragment from JBW 615.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

Description: Specimen from JBW 417 small and incomplete, at least 12mm long, showing the characteristic ornament of ribs but with hinge detail lost. External mould from JBW 47 more than 30mm long and 29mm high. Posterior wing moderately long, covered by raised commarginal laminae , concave posteriorly. Body of shell covered by slender high ribs, nine over much of shell, finer and fainter close to posterior margin, none over posterior wing. Shell crossed by slender high commarginal laminae, arching weakly hingewards in interspaces, forming low nodes but no spines where crossing the ribs. A few of the interspaces each bear a single very fine intercalated rib.

Discussion: The primary ribs are less robust than those of the type species *Girtypecten sublaqueatus* (Girty), and lack the prominent spines of this species.

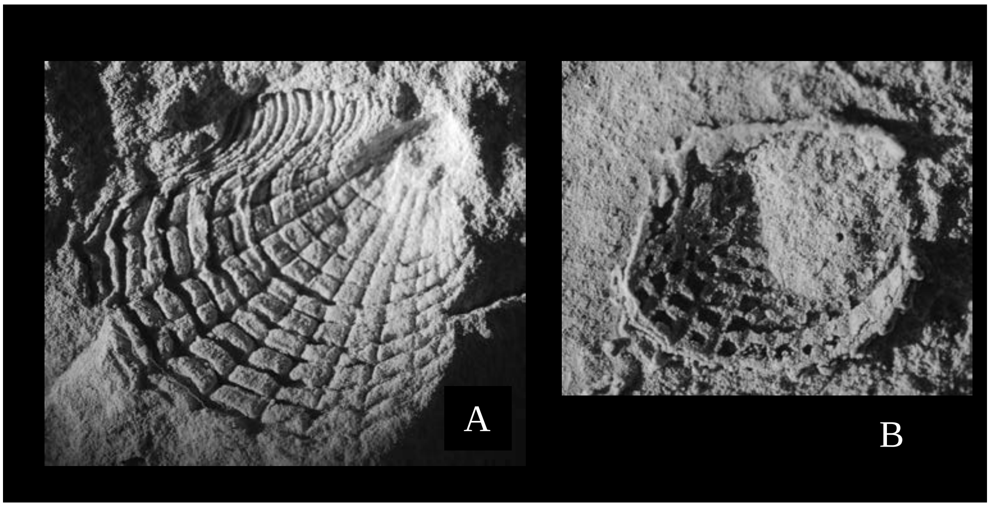


Fig. 365. *Girtypecten* sp. A, left valve external mould GSC 137331 x2, from JBW 47. B, left valve GSC 137224 x4, from JBW 417. Member A, Jungle Creek Formation.

Family **LIMIPECTENIDAE** Newell & Boyd, 1990

[Nom. emend. hic ex Limipectinidae Newell & Boyd, 1990, p. 4].

Discussion: This family, based on *Limipecten* Girty, 1904, was distinguished by Newell & Boyd (1990) through what was claimed to be a distinctive inner shell of nacre in two layers, separated by a cross-lamellar layer. Carter et al. (2011) expanded the content of the family, as followed herein, but the shell structure in the additional groups was not clarified. A further aspect in need of clarification is the relationship to Heteropectenidae Beurlen. *Limipecten* Girty, as illustrated by Newell (1937, pl. 9), is close in its subplicate left valve and right valve bundled ribs to *Heteropecten* Kegel & Costa, 1951, as figured in Waterhouse (2008a, text-fig. 84).

Subfamily **ACANTHOPECTENINAE** Newell & Boyd, 1995

[Nom. emend. hic ex Acanthopectinidae Newell & Boyd, 1995, p. 45].

Diagnosis: Left valve plicae moderate in number, sharp-crested. Growth laminae point strongly forward in left valve interspaces.

Discussion: Lamnipectininae Waterhouse, 2008a (to be emended to Lamnipecteninae), has numerous plicae and well developed commarginal laminae and may have numerous secondary costae. Right valves have simpler finer costae, variously differentiated, and well developed commarginal laminae and growth laminae do not point strongly in the interspaces. In Costatoplicatininae Waterhouse, 2008a, the left valve plicae are costate, and right valve has plicate or costate ornament. Further differences and various genera are discussed in Waterhouse (2008a, pp. 153-163). Carter et al. (2011) placed Acanthopectininae in Limipectinidae Newell & Boyd, and Costatoplicatinae and Lamnipectininae were reduced to tribes within Acanthopecteninae (Acanthopecteninae).

Genus ***Meekopecten*** n. gen.

Diagnosis: Left valve plicae moderate in number with narrow crests and subdued growth laminae pointing anteriorly in the interspaces. No median keel along the crests of the plicae. Right valve with slender ribs separated by wide concave interspaces.

Type species: *Acanthopecten meeki* Newell (1938, p. 73, pl. 12, fig. 1-5) from the Upper Carboniferous Stanton Formation of Kansas, United States, here designated.

Discussion: This new genus is described in the Appendix on p. 465. It is discriminated from genus *Acanthopecten* Girty, 1903 by the consistent absence of of a slender keel passing along the crest of each left valve plication.

Meekopecten sp.

Fig. 366

Material: Fragmentary left valves from JBW 420 (Member A) and JBW 103 (upper Ettrain Formation).

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

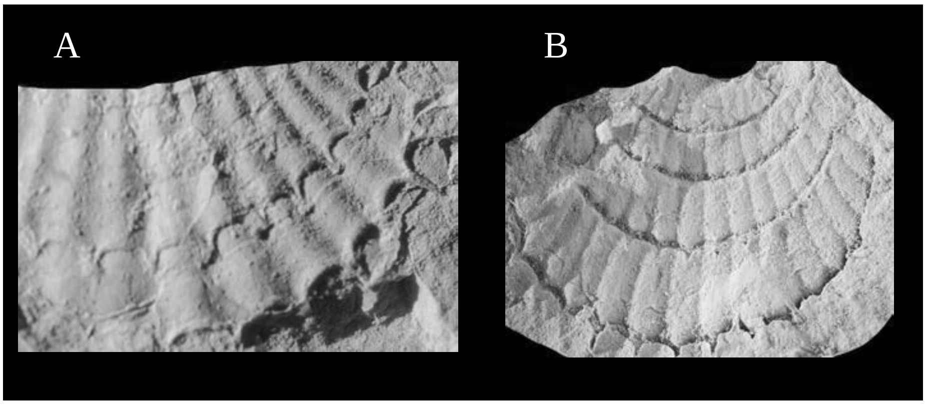


Fig. 366. *Meekopecten* sp. A, fragment of left valve GSC 137225 x3, cast from JBW 420, Member A, Jungle Creek Formation. B, external mould of left valve fragment GSC 137356 x3 from JBW 103, showing the interspaces projecting forward as spines along the anterior margin. From the Ettrain Formation.

Hyporder LIMOIDEI Moore in Moore, Lalicker & Fischer, 1952

Superfamily **LIMOIDEA** Rafinesque, 1815

Family **LIMIDAE** Rafinesque, 1815

Subfamily **ECHINORBINAE** Waterhouse, 2008a

Diagnosis: Ornament variable, smooth to papillate or ribbed. Hinge edentulous.

Discussion: This subfamily includes a number of Upper Paleozoic genera that are moderately close to Liminae in shape and ornament, but lack hinge teeth.

Genus ***Palaeolima*** Hind, 1903

Palaeolima? sp. A

Fig. 367, 368

Material: A small right valve from JBW 4, and two small left valves from JBW 533.

Stratigraphic and biostratigraphic levels: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone. Ettrain Formation.

Dimensions in mm:

GSC	Length	Height	Width
137447	33	26	8

Fig. 367. *Palaeolima*? sp. A. Two left valves GSC 137343 and 1373444 x2, from JBW 533. Ettrain Formation.

Fig. 368. *Palaeolima*? sp. A, right valve GSC 137447 x2, from JBW 4. Member A, Jungle Creek Formation.

Description: Right valve with extended anterior shell and long anterior umbonal slope; left valve somewhat similar. Wings short, with weak commarginal growth lines. Body of the shell covered by low broad bifurcated ribs with gently convex broad crests and narrow interspaces.

Resemblances: The symmetry of the shell and characteristic ribbing are features of a number of species assigned to *Palaeolima* Hind. *Lima krotowi* (Stuckenberg 1898, p. 204, pl. 1, fig. 29) and now assigned to *Palaeolima* (Lyutkevich & Lobanova 1960, pl. 19, fig. 4; Muromseva 1984, pl. 33, fig. 1) is moderately close in these respects, but the shell is higher. It comes from beds of Kazanian (ie. Wordian) age in European Russia.

Palaeolima? sp. B

Fig. 369

Material: A small left valve from JBW 581 has low round-crested ribs and weakly defined wings.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formtion. *Ogilviecoelia shii* Zone.

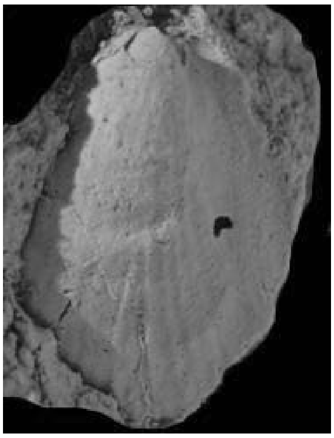


Fig. 369. *Palaeolima*? sp, B, left valve internal mould GSC 137226 x5, from JBW 581. Member E, Jungle Creek Formation.

Cohort Cardiomorphi Férussac, 1822

Subcohort Cardioni Férussac, 1822

Infrasubcohort Cardiidia Férussac, 1822

Family **SANGUINOLITIDAE** Miller 1877

Diagnosis: Elongate, lunule and escutcheon commonly present, long ligament, pallial line entire, hinge edentulous.

Genus ***Sanguinolites*** M'Coy, 1844

Diagnosis: Elongate, small anteriorly placed incurved umbones, lunule and escutcheon well developed, radial ribs may be present, and posterior umbonal ridge broadly rounded, shallow pallial sinus.

Type species: *Sanguinolites discors* M'Coy, 1844, p. 47 from Lower Carboniferous of Ireland, SD Stoliczka, 1871.

Sanguinolites sp.

Fig. 370

Material: A right valve from JBW 581 and left valve from C-6167.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Fig. 370. *Sanguinolites* sp, left valve GSC 137228 x8, from JBW 581, Member E, Jungle Creek Formation.

Description: Shell small, specimen from JBW 581 measuring 6mm in length, and less than 3mm high, with anteriorly placed orthocrescent umbo, extensive posterior depressed face, obtuse cardinal extremities and low commarginal rugae.

Megaorder CARDIATA Férussac, 1822

Order CARDIIDA Férussac, 1822

Superfamily **KALENTEROIDEA** Marwick, 1953

Family **KALENTERIDAE** Marwick, 1953

Diagnosis: Medium-sized trapezoidal to modioliform inequilateral shells, radial ribs may be present, tend to be obsolete or absent anteriorly, internal margin smooth, marginal ligament and long nymph. Cardinals partly obsolete, tuberculiform or elongate, 5b and laterals lacking in most shells, posterior lateral placed well back, that of left valve usually stronger, anterior and pedal scars, generally thickened anterior buttress, small anterior pedal scar prominent.

Discussion: Kalenteridae Marwick, 1953 has been discussed by Waterhouse (2010, pp. 96, 97; 2015a, pp. 301-302).

Genus ***Stutchburia*** Etheridge, 1900

Diagnosis: Elongate equivalve or subequivalve shells, umbones small and anteriorly placed, lunule and deep escutcheon present, commarginal ornament traversed by costae radiating from umbo in some species. Cardinals 2 and 3b obsolescent, P1 and P111 also obsolete and P11 well defined. Anterior adductor scar large, adjoining low myophore buttress posteriorly, posterior adductor scar large, less impressed.

Type species: *Orthonota*? *costata* Morris, 1845, p. 274 from Broughton Formation (Wordian), south Sydney Basin, New South Wales, OD.

Stutchburia ? sp. .

Fig. 371

Material: A left valve from JBW 561 and another from C-6167.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Specimen GSC 137232 from JBW 561 nearly 9mm long and 5mm high, anteriorly placed low umbones, low commarginal growth lines, with eight low fine ribs traversing the entire shell and single ribs intercalated posteriorly in three of the interspaces, fine commarginal growth lines. The other specimen GSC 137227 from C-6167 is 10mm long and 4.5mm high. Ribs traverse the posterior shell, differently placed from those of the other specimen. This difference in ribbing might well be pointing to specific differences.

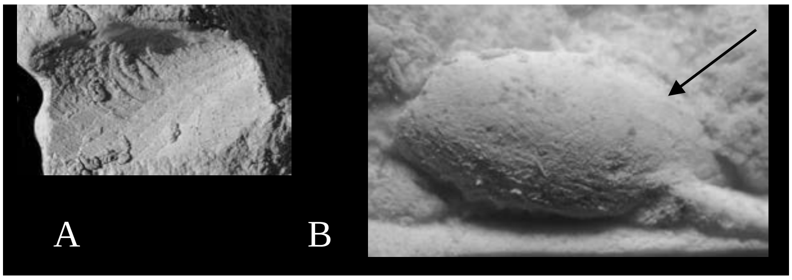


Fig. 371. *Stutchburia*? sp. A, external mould of left valve, GSC 137232 x5 from JBW 561, with fine ribs over the entire shell, more clearly shown in this figure over lower anterior shell. B, left valve cast showing fine posterior ribs as arrowed, GSC 137227 x5 from C-6167. Member E, Jungle Creek Formation.

Megaorder POROMYATA Ridewood, 1903

Order PHOLADOMYIDA Newell, 1965

Superfamily **PHOLADOMYOIDEA** King, 1844

Family **CHAENOMYIDAE** Waterhouse, 1966

Subfamily **VACUNELLINAE** Astafieva-Urbaiitis, 1973

Genus ***Exochorhynchus*** Meek & Hayden, 1864

Diagnosis: Equivalved with umbones anteriorly placed, and regular commarginal rugae.

Type species: *Allorisma? altirostrata* Meek & Hayden, 1858, p. 42 from Pennsylvanian of mid-United States, OD.

Exochorhynchus similis (Lyutkevich & Lobanova, 1960)

Fig. 372

1960 *Allorisma similis* Lyutkevich & Lobanova, p. 83, pl. 10, fig. 6-8.
1980 *Exochorhynchus similis* – Solomina & Astafieva-Urbaiitis, p. 31, pl. 3, fig. 1-3.
1984 *Vacunella similis* – Muromseva, p. 96, pl. 43, fig. 1, 2, 4, 6.
1996 *E. similis* – Shi & Waterhouse, p. 154, pl. 30, fig. 23-27, pl. 31, fig. 1-14, text-fig. 52.

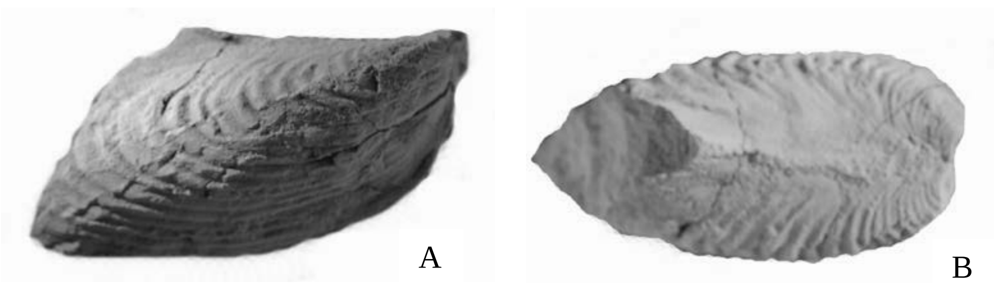


Fig. 372 *Exochorhynchus similis* (Lyutkevich & Lobanova, 1960). A, B, right valve and dorsal aspects of internal cast of specimen with valves conjoined, GSC 137229 x1.5, from JBW 561. C, right valve of specimen with valves conjoined, GSC 137230 x2, from JBW 581. Member E, Jungle Creek Formation.

Diagnosis: Large, moderately inflated with regular commarginal rugae, no sulcus, posterior gape slight.

Holotype: TsNIGRA no. 181/7443 figured as *Allorisma similis* by Lyutkevich & Lobanova (1960, pl. 10, fig. 8) from Taimyr Peninsula, north Russia, OD.

Material: Single specimens with valves conjoined from JBW 539, 561 and 616, three specimens with valves conjoined and part of right valve from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Shells equivalve with anteriorly placed slightly procrescent umbones, weak and rounded posterior umbonal ridge, regular commarginal rugae, fine commarginal growth lines, and small pustules. Internal detail not shown apart from opisthodetic ligament.

Resemblances: These specimens are identified with the specimens assigned to *Exochorhynchus similis* (Lyutkevich & Lobanova) as identified by Shi & Waterhouse (1996) from the "*Yakovlevia transversa*" and *Jakutoproductus verchoyanicus* Zones of the younger Jungle Creek Formation. The species *similis* was originally described from Taimyr outcrops of uncertain age, possibly Permian. Muromseva (1984) figured a number of specimens from the late Early Permian Talatin and Levorkut Suites of Petchora Basin in the northern Urals. She referred a range of specimens to the species, and here the synonymy is restricted to specimens with umbones anteriorly placed and projecting, but others are close, and probably belonged to one highly variable species.

Genus ***Palaeocosmomya*** Fletcher, 1946

Diagnosis: Medium-sized ovate or oblong shells with distinct escutcheon, posterior shell ornamented by two sets of converging ribs meeting to form V, anterior shell marked by stronger ribs only slightly oblique to growth lines.

Type species: *Palaeocosmomya teicherti* Fletcher, 1946, p. 401 from Wandagee Formation (upper Artinskian), Western Australia, OD.

Discussion: Dickins & Shah (1965) regarded the form as a subgenus of *Cosmomya* Holdhaus (1913) from the Late Permian of the Himalaya.

Palaeocosmomya? sp.

Fig. 373

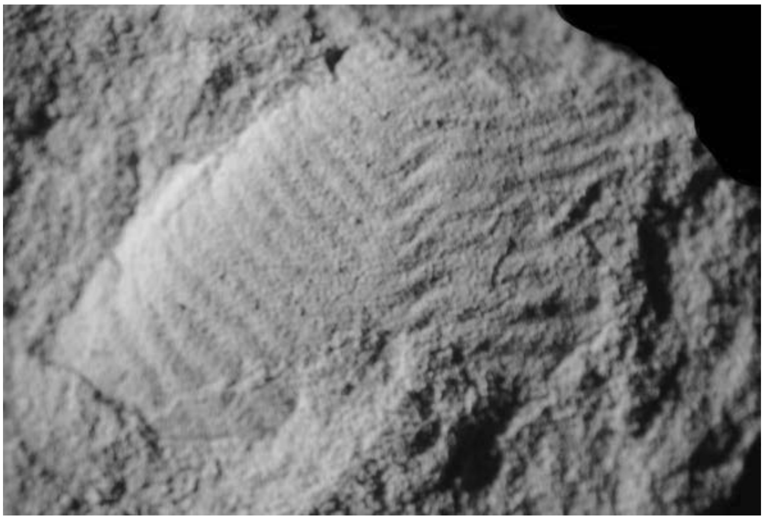


Fig. 373. *Palaeocosmomya*? sp., fragment of right valve GSC 137231 x4, from JBW 812, Member E, Jungle Creek Formation.

Material: A fragment from JBW 812.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: The fragment shows two sets of broad ribs converging to form a V, but the nature of the genus is otherwise obscure and the identification provisional.

Discussion: Here is yet another example of a genus hitherto known only from the southern paleohemisphere of Permian time being found in the Yukon Territory of northwest Canada. But whether the genus was in fact more widespread in temperate paleolatitudes of the northern hemisphere remains uncertain.

Class GASTROPODA Cuvier

Order BELLEROPHONIDA Ulrich & Scofield, 1897

[Nom. emend. hic ex Bellerophontida Ulrich & Scofield, 1897].

Superfamily **BELLEROPHONOIDEA** M'Coy, 1861

[Nom. correct. hic ex Bellerophontacea Wenz, 1938, nom. transl. ex Bellerophontidae M'Coy, 1851b].

Discussion: The family group name was proposed as Bellerophontidae, and used as such ever since. Yet the genus name was *Bellerophon* Montfort, though one would think from the family group name that the genus has been called *Bellerophont*. The t was added for reasons of euphony, which surely is in the eye (or ear) of the beholder.

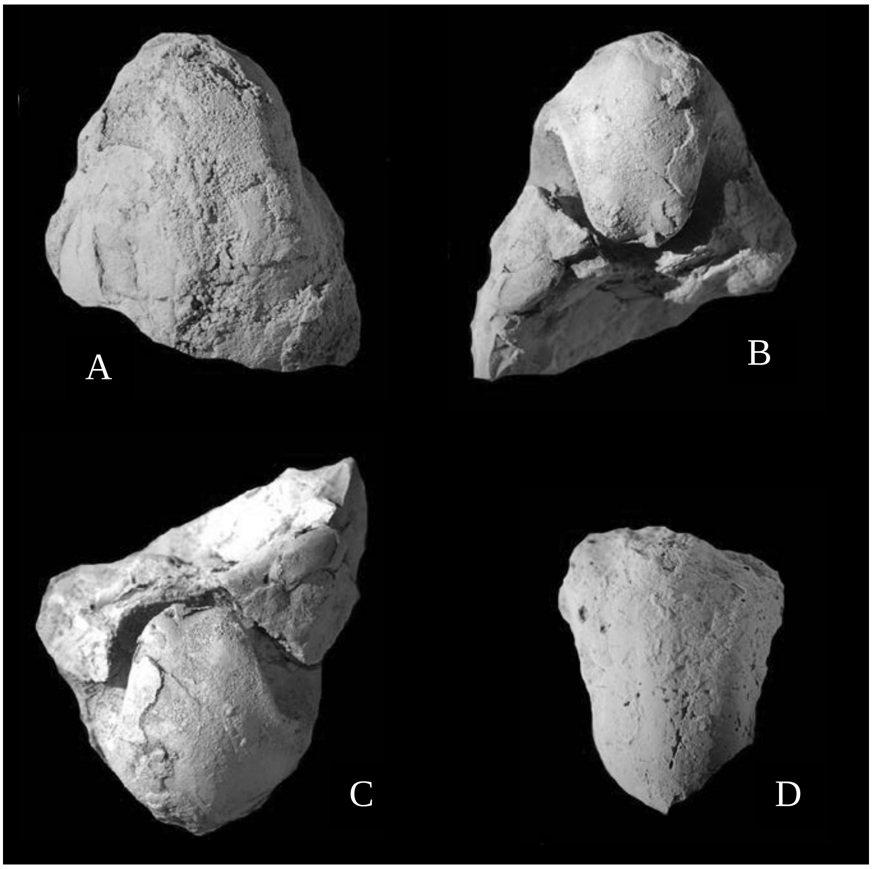


Fig. 374. *Warthia* sp. A, B, C, views of GSC 137233 x1.5 from JBW 581. D, outer whorl of GSC 137234 x1.5, showing shallow slit at aperture, from JBW 561. Member E, Jungle Creek Formation.

Family **EUPHEMITIDAE** Knight, 1956

Genus ***Warthia*** Waagen, 1880

Diagnosis: Involute symmetrically coiled smooth shells with apertural sinus but selenizone obscured by perinductural layer.

Type species: *Warthia brevisinuata* Waagen, 1880, p. 131 from Amb Formation? (late Cisuralian), Salt Range, Pakistan, SD Koninck (1882, p. 81).

Warthia sp.

Fig. 374

Material: Single specimens from JBW 561 and 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Specimen from JBW 581 42mm wide and 39mm long. The whorls are broad, twice as wide as high, and curvature on the outer whorl is tight. The shells are planospirally coiled, but have been rendered slightly asymmetric, judged to be by distortion and of non-biologic origin (cf. Peel 2002). A median ridge lies along the mid-line, and otherwise the shell surface is smooth, as seen on the inner side of the whorl, because the exterior surface is worn. There is a short notch in the aperture, as figured (Fig. 374D).

Suborder PLEUROTOMARIIDINA Cox & Knight, 1960

Superfamily **PLEUROTOMARIOIDEA** Swainson, 1840

Family **EOTOMARIIDAE** Wenz, 1938

Subfamily **EOTOMARIINAE** Wenz, 1938

Tribe **PTYCHOMPHALINI** Wenz, 1938

Genus ***Ptychomphalina*** Fischer, 1887

Diagnosis: Upper whorl surface somewhat flattened, selenizone placed near lower third of whorl, basal whorl gently convex, spiral ornament weak or absent, base anomphalous.

Type species: *Helix striata* Sowerby, 1817, p. 159 from Early Carboniferous of England.

Discussion: Dickins (1976) revised the type species of *Ptychomphalina* and defended its validity, compared with *Mourlonia* Sowerby. He dismissed the claim by Knight in Knight et al. (1960) and Batten (1967) that the genus was synonymous with *Mourlonia*. Nonetheless the two are very close, and although the Canadian specimen described here agrees in most attributes with *Ptychomphalina*, it has a slightly different selenizone closer in some respects to that said to be typical of *Mourlonia*. Hence their placement in different tribes seems questionable.

Ptychomphalina sp.

Fig. 375

Material: One specimen from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Specimen small, 13mm in diameter, with only part of body chamber and penultimate whorl preserved. Suture tight, bordered by slight shelf of adjoining whorl, upper whorl gently convex and becoming weakly concave just above selenizone, which is sited near lower third of whorl height, and projects slightly as a broad ridge with gently concave crest, bordered by bounding threads above and below. Lower whorl curves with gentle convexity over the base into an umbilical hollow, and the base appears to be anomphalous. Ornament consists of fine growth threads which curve abaperturally from suture to selenizone, without any sinus, cross the selenizone with weak forward concavity, and cross the base with faint forward convexity: they number four to six in 1mm.

Resemblances: The lack of spiral ornament, rather gently convex lower whorl, and apparent lack of an umbilicus suggest identity with *Ptychomphalina*. One difference that Dickins (1976) noted, the presence of a distinct groove below the selenizone in *Ptychomphalina*, and absent from *Mourlonia*, is not clearly discernible in the present specimen, although there is a very faint concavity – as is also present in *Mourlonia*, because the selenizone is raised above the remainder of the whorl.

Fig. 375. *Ptychomphalina* sp., cast of last whorl, abapertural view, GSC 137235 x4, from JBW 581. Member E, Jungle Creek Formation.

Genus ***Spiroscala*** Knight, 1945

Diagnosis: Trochiform with sharply conical spire, base nearly flat, narrowly phaneromphalous, ornament both spiral and mainly transverse as a rule.

Type species: *Spiroscala pagoda* Knight, 1945, p. 574 from Upper Pennsylvanian of Texas, OD.

Spiroscala sp.

Fig. 376

Diagnosis: No spiral ornament developed over the upper or outer whorl, radial ribs very fine.

Material: A specimen from JBW 736.

Stratigraphic and biostratigraphic level: Member A, Jungle Creek Formation. *Septospirifer tatondukensis* Zone.

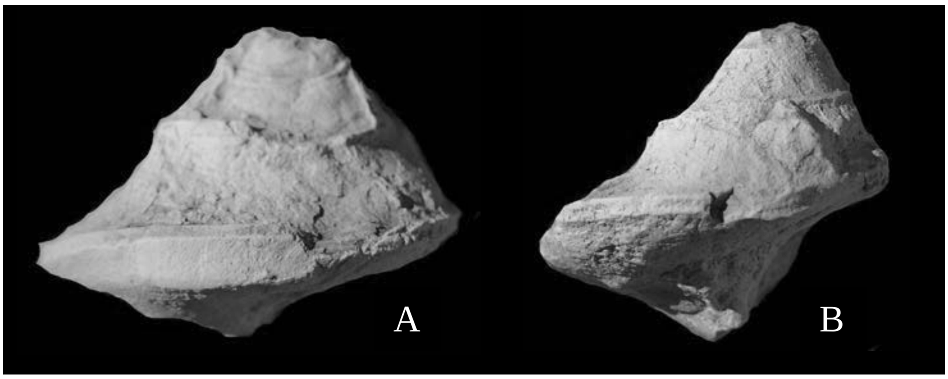


Fig. 376. *Spiroscala* sp. A, B, lateral views of specimen GSC 137236 x1.5, from JBW 736, Member A, Jungle Creek Formation.

Description: Specimen now 30mm high and 36mm across, but tip of spire lost and specimen deformed, so that only three whorls are preserved. Suture tight, without gutter, upper whorl concave, selenizone elevated with concave surface and placed near lower third of whorl, bordered by strong narrow keels. Lower whorl subvertical and low, curving abruptly on to a broad gently convexo-concave base. Much of the base is obscured by matrix, making it difficult to ascertain whether or not the base is phaneromphalous. Overlap of whorls in the spire extends to base of selenizone. Whorls ornamented by fine transverse radial threads, eight to ten per mm, sweeping with forward convexity across the upper whorl, and curving with forward (adapertural) convexity below the selenizone to the keel below the vertical outer shell, and then back across the base. No spiral ribs. The depth of the selenizone is not known.

Resemblances: *Spiroscala pulchra* Batten (1958, pl. 39, fig. 1, 2), from the Word Formation of west Texas, has no clearly developed spiral threads over the upper whorls, and the radial ornament is coarser than in the present form, but Batten (1958, p. 224) recorded fine spiral threads over the convex and basal parts of the whorl profile.

Tribe **EOTOMARIINI** Wenz, 1938

Genus ***Ananias*** Knight, 1945

Diagnosis: Gradate turbiniform, without funicle and with concave rather than convex selenizone, ornament elaborate.

Type species: *Phanerotrema*? *welleri* Newell, 1935, from Upper Pennsylvanian of Kansas, OD.

Discussion: *Ananias* has been treated as a subgenus of *Glabrocingulum* Thomas, 1940, but has a more turretted spire, and lacks a funicle at the base, though the consistency of differences has been disputed. It closely resembles *Worthenia* de Koninck, 1883, which is anomphalous or minutely phaneromphalous, and has a convex selenizone.

Ananias sp.

Fig. 377

Material: Fragments of single specimens from JBW 98, 195 and C-6167, four broken specimens from JBW 561 and six from JBW 581.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Largest specimens some 30mm high and 30mm in diameter with six whorls, tightly coiled and possibly narrowly phaneromphalous. Suture tight, encircled below by slight swelling at top of upper whorl which is concave, prominent selenizone at maximum width of shell and close to mid-height of the whorl, selenizone concave and bordered by prominent keels above and below. Outer face subvertical, gently concave and moderately high, rounding abruptly on to convex base, which is apparently anomphalous. Ornament elaborate. Spiral ornament over upper whorl numbers nine ribs, of uneven strength, the strongest rib lying along the crest of the swelling below the suture, and a second strong rib lying a little below at the top of the concave segment of the upper whorl. Two strong spiral ribs lie below the suture on the outer face of the penultimate and last whorl, one well below the selenizone, the other at the base of the outer whorl, where the base of the shell commences. A few finer costae are also present. The outer base is ornamented by three strong costae, and the remaining base is ornamented by fine costae. Radial growth-lines and low ribs of uneven strength pass almost straight across the upper whorl, with a very shallow sinus below mid-height, before curving more strongly back into the selenizone: they slightly disrupt or form low tubercles across the spiral ribs. Growth lines suggest that the slit was shallow, between five and seven mm deep. Growth-lines arch forward just below the selenizone, and then lie at right angles to the periphery, forming another shallow sinus at the junction with the base, and curve sinuously across the base. Costae are broad but very low, and form interference nodes where crossing the spiral ribs.

Fig. 377. *Ananias* sp. A, cast of lateral shell, GSC 137237 x2, from JBW 561. Member E, Jungle Creek Formation.

Order CAENOGASTROPODA Cox, 1959

Superfamily **SUBULITOIDEA** Lindstrom, 1884

Family **SUBULITIDAE** Lindstrom, 1884

Genus ***Procerithiopsis*** Mansuy, 1914a

Diagnosis: Small, minutely phaneromphalous, with strong collabral ribs, small siphonal notch and columellar folds.

Type species: *Procerithiopsis ambigua* Mansuy, 1914a, p. 51 from Early Permian of Asia, SD Cossmann, 1918.

Procerithiopsis sp.

Fig. 378

Material: A specimen from JBW 561.

Stratigraphic and biostratigraphic level: Member E, Jungle Creek Formation. *Ogilviecoelia shii* Zone.

Description: Small turretted specimen approximately 10mm long, top of spire lost, three whorls showing strong radial costae.

Discussion: Only a fragment of the specimen is preserved, and it agrees in shape and ornament with the figures presented for the genus by Mansuy (1914a, pl. 4, fig. 17).

Fig. 378. *Procerithiopsis* sp. lateral view of GSC 137238 from JBW 561, x3. Member E, Jungle Creek Formation.

OVERVIEW OF PALEONTOLOGICAL RESULTS

Table 2. LIST OF BRACHIOPOD OCCURRENCES

Member	A	B	C	D	E	Ettrain
Orthotetes dorsosulcatus n. sp.		x				
Arctitreta? sp. A	x					
Arctitreta? sp. B			x			
A. cf. *peelensis* Shi & Waterhouse				x		
Chelononia minimauris n. sp.	x					x
Chonetinella? sp.					x	
Rugaria arcula n. sp.	x					
Sulcirugaria? sp.	x					
Komiella bitteri n. sp.	x					
Komiella? sp. A		x				
Komiella sp. B					x	
Lissosia? *alatus* (Stuckenberg)					x	
Fimbrininia sp.		x				
Fimbrininia spinosa Waterhouse				x	x	
Jakutoproductus verchoyanicus (Fredericks)					x	
Tuberculatella subtuberculata (Grabau)	x					
T. aff. *tuberculata* (Moeller)			x			
T. cf. *boulei* (Kozlowski)			x			
Inflatusia ogilviensis Waterhouse	x					
Sangredonia alaminata n. sp.			x			
Bailliena aff. *yukonensis* Nelson & Johnson						x
Kutorginella yukonensis Sarytcheva & Waterhouse	x			**x**	x	
Kutorginella? sp.			x			
Thamnosia cf. *spinosa* Shi & Waterhouse					x	
Dutroproductus dutroi n. gen., n. sp.			x	?		
Nazeroproductus lazarevi n. sp.	x					x
Reticulatia oldershawi Waterhouse	x					x
Reticulatia? sp.				x		
Kochiproductus saranaeanus (Fredericks)	x					x
Kochiproductus sp.		x				
K. imperiosus Waterhouse			x			
K. porrectus (Kutorga)					x	
Nassichukia nodosa n. gen., n. sp.	x					
Gemmulicosta undulata n. sp.	x					
Tityrophoria zimmermanni Waterhouse	x					x

Member	A	B	C	D	E	Ettrain
Calliprotonia kerrae n. sp.	x					
Calliprotonia sp.		x				
C. umbonalis n. sp.			x			
C. mclareni Waterhouse				x	x	
Echinaria circularis n. sp.			x			
Juresania juresanensis (Tschernyschew)			x			
Tubersulculus ovalis n. sp.	x					x
T. reidi Waterhouse				x	x	
Krotovia norfordi n. sp.	x			?		
K. wallaciana (Derby)	x					x
Krotovia sp. A	x					
Krotovia sp. B	x			x		
K. cf. *parva* Cooper	x					
Krotovia sp. C				x		
Krotovia sp. D					x	
Waagenoconcha sp.	x				?	
Waagenoconcha irginaeformis (Stepanov)				x	x	
Villaconcha planiconcha n. sp.			x			
Heteralosia scotti n. sp.	x					
Yukonalosia arctica n. gen., n. sp.	x					
Echinalosia minuta n. sp.				?	x	
Balkhasheconcha cf. *piassinaensis* (Einor)	x					
Balkhasheconcha sp.			x			
B. bamberi Waterhouse				x		
Ramaliconcha bitteri Waterhouse	x					cf.
Taeniothaerin gen. & sp. indet.					x	
Paucispinifera carboniferica n. sp.	x					
P. abramovi n. sp.	x					x
P. sulcata n. sp.			x			
Anemonaria sp.		x				
Anemonaria auriculata Shi & Waterhouse					x	
Rugivestigia commarginalis n. gen, ,n. sp.				x		
Tethysiella impudens n. sp.			x			
Kuvelousia? sp. .A	x					
Kuvelousia? sp. B			x			
Protoanidanthus sp.	x					
Protoanidanthus nichollsi n. sp.				x	x	

	Member A	B	C	D	E	Ettrain
Protoanidanthus umbonatus Shi & Waterhouse				x	x	
Cimmeriella orientalis (Abramov & Grigorieva)	x			x		x
Harkeria elongata n. sp.	x					x
H. sulcoprofundus n. sp.					x	
linoproductid gen. & sp. indet. A	x					
linoproductid gen. & sp. indet. B	x			x		x
linoproductid gen. & sp. indet. C					x	
Lineacrassus inflatus Waterhouse			x			
Schrenkiella triangulata Barchatova			x			
S. schrenki (Stuckenberg)					x	
Praeschrenkiella waddingtonae Waterhouse	x					x
P. costata Waterhouse	x					
Compressoproductus? sp.	x					
Sarytchevinella precursor n. sp.	x					
Commarginalia sp. A	x					
Commarginalia sp. B		x				
Commarginalia norrisi n. sp.				x	x	
coolkilellin? gen. & sp. indet.	x					
Orthotichia morganiana (Derby)	x					x
Rhynoleichus? sp.					x	
Rhynchopora grigorieva n. sp.			x	x	x	
Stenocisma winkleri Martínez-Chacón	x					
Stenoscisma sp.	x			x		
S. mutabilis Tschernyschew					x	
Callaiapsida divitiae n. sp.	x					x
Septacamera sp.	x					
Septacamera triangulata Shi & Waterhouse					x	
Yanzaria solitarius n. gen., n. sp.					x	
Cleiothyridina gzhelensis Grunt	x			?	x	
Composita sp.	x					
Composita mutabilis Czarniecki	x					x
C. cf. *bamberi* Shi & Waterhouse					x	
Eumetria sp.				x		
retziid? gen. & sp. indet.					x	
Hustedia trifida n. sp.	x					
H. quadrifidus n. sp.					x	
Martiniopsis? sp. A	x					

Member	A	B	C	D	E	Ettrain
Martiniopsis sp. B				x		
Geothomasia? sp.					x	
Martinia cf. *karawanica* Volgin	x					x
Martinia ? sp.				x		
Mirandifera wolfcampensis (King)				x		
Brachythyris praeufensis Solomina	x					
Meristorygma sp. A	x					
Meristorygma? sp. or spp. B			x			
Meristorygma? sp. C				x		
Ala alatiformis n. sp.	x			? or	?	
Junglelomia ursus Waterhouse	x					x
J. simplex n. sp.	x				aff.	x
Ettrainia costellata n. gen., n. sp.			x			
purdonellid gen. & sp. indet.	x					
Spiriferinaella simplicata n. sp.	x				x	x
Fasciculatia? sp.	x					
Tegulispirifer placitus n. sp.	x					
neospiriferin gen. & sp. indet. A	x					
neospiriferin? gen. & sp. indet. B				x		
Neospirifer? sp. A			x			
Neospirifer sp. B					x	
Forticosta transversa n. gen., n. sp.	x					
Septospirifer tatondukensis Waterhouse	x					
S. hughi n. sp.				x		
Spiriferella yukonensis Waterhouse & Waddington	x			x		
Eridmatus parva (Cooper)	x					
Eridmatina petita (Waterhouse & Waddington)		x		x	x	
Plicatospiriferella undulata n. sp.			x			
Spirelytha biakovi n. sp.	x					x
phricodothyrid? gen. & sp. indet. A	x					
phricodothyrid? gen. & sp. indet. B	x					
phricodothyrid gen. & sp. indet. C				x		
Triramus canadensis Waterhouse					x	
Ogilviecoelia initiatus n. sp.		x				
O. shii n. sp.					x	
Spiriferellina sp. A	x					
Spiriferellina sp. B					x	

	Member A	B	C	D	E	Ettrain
Zaissania? sp.	x					
Tumarinia solominae n. sp.	x					
Tumarinia sp. or spp.			x		x	
Yukonospirifer sp.	x					
Nahoniella decorus n. sp.	x					
Nahoniella? sp.		x				
N. cf. *plana* (Shi & Waterhouse)					x	
Cryptacanthia? sp.					x	
Dielasma? sp. A	x					
Dielasma? sp. B					x	

SUMMARY OF FAUNAS

Fossils from the upper Ettrain Formation

This study does not systematically work through the faunas from the Ettrain Formation, which underlies the Jungle Creek Formation. But various Ettrain specimens are mentioned and illustrated in the text, showing that a number of species commenced at least in the Ettrain Formation and persisted into the Jungle Creek Formation. The specimens were collected by the writer, and were not examined by Nazer (1977) in his examination of principally GSC collections from all but the lower and upper Ettrain Formation.

BRACHIOPODA: *Chelononia minimauris* n. sp., *Bailliena aff. yukonensis* Nelson & Johnston, *Nazeroproductus lazarevi* n. sp., *Reticulatia oldershawi* Waterhouse, *Kochiproductus saranaeformis* (Fredericks), *Tityrophoria zimmermani* n. sp., *Tubersulculus transversus* n. sp., *Krotovia wallaciana* (Derby), *Ramaliconcha* aff. *bitteri* Waterhouse, *Paucispinifera abramovi* n. sp., *Cimmeriella orientalis* (Abramov & Grigorieva), *Harkeria elongata* n. sp., linoproductid gen. & sp. indet. B, *Praeschrenkiella waddingtonae* Waterhouse, *Orthotichia morganiana* (Derby), *Callaiapsida divitiae* n. sp., *Composita mutabilis* Czarniecki, *Junglelomia ursus* Waterhouse, *Spiriferinaella simplicata* n. sp., and *Spirelytha biakovi* n. sp., with BIVALVIA: Heteropectenin sp. & gen. indet., and *Meekopecten* sp.

Table 3. Brachiopods and molluscs figured in the text from the upper Ettrain Formation.

Bailliena aff. *yukonensis* is not found in the Jungle Creek Formation. *Echinaria* sp. is illustrated from the upper Ettrain Formation, but differs from the species from the Jungle Creek Formation, whereas purdonellid gen. & sp. indet. could well be shared, and *Tumarinia solominae* comes from low in the Ettrain Formation.

Most of these species are found in the uppermost beds of the Ettrain Formation in the type section and nearby, and are not found in topmost beds of the formation elsewhere. This is only an incomplete list, and many more species and genera have been enumerated by Nazer (1977) especially from the middle part of the formation.

Member A, *Septospirifer tatondukensis* Zone

Type section: Section 34, as shown in Shi & Waterhouse (1996, Fig. 4, p. 11), through unit c, above units a and b of Ettrain Formation, equivalent to Member A at the base of the Jungle Creek Formation, in the headwaters of Ettrain and Jungle Creeks.

Content: The zone, named after *Septospirifer tatondukensis* Waterhouse, is found in the carbonates and shales above the Ettrain Formation, and is dominated especially by *Tubersulculus transversus, Paucispinifera carboniferica, P. abramovi, Inflatusia ogilviensis*, *Tityrophoria zimmermani, Reticulatia oldershawi, Orthotichia morganiana, Callaiapsida divitiae, Brachythyris praeufensis, Junglelomia ursus* and *Spiriferella yukonensis* as well as the nominate species. Many species are limited to the zone, so far as studied, but a number commenced in older faunas, as tabulated for the Ettrain Formation, and some range into younger faunas. There was no abrupt incoming of an entirely different fauna in the basal Jungle Creek beds. The genera *Chelononia, Rugaria, Inflatusia, Nazeroproductus, Nassichukia, Gemmulicosta, Praeschrenkiella, Compressoproductus*?, *Sarytchevinella* and *Brachythyris* are not found in younger faunas immediately overlying Member A.

The faunas are found in thin bands of carbonate, mostly limestone with fossils silicified, but also with varying amounts of dolomite, as well as shaly bands. Because it has not been possible to leach and separate the silicified faunas, the present study understates the number of taxa to be found in Member A.

There are 75 brachiopod taxa in 63 genera, counting similar indeterminate subfamily or family group taxa as one, and 49 named brachiopod species. Counting Mollusca as well, there are 84 taxa in 73 genera. Overall the diversity is greater than that for the brachiopod assemblage of the overlying "*Yakovlevia transversa*" Zone, for which Shi & Waterhouse (1996) recorded 62 taxa in 58 genera, with 47 named species. Of species in the *Septospirifer tatondukensis* Zone, some twenty four (including Mollusca) extend into older faunas of the Ettrain Formation. Examination of the study by Nazer (1977) on Ettrain brachiopods suggests a further eighteen genera were closely related to brachiopods from Member A, in addition to those enumerated on p. 438, together with a further six likely alliances (including *Thamnosia* and *Tityrophoria*) at either generic or subfamilial level. Thus a total of 43 of the 63 genera are known to have had roots in the Ettrain Formation, and *Meristorygma* was first described from older faunas in the Canadian Arctic. A number of genera are related especially to forms from northern Russia, including *Tubersulculus, Protoanidanthus*, *Rhynoleichus,* and *Martiniopsis,* and choristitoid genera such as *Junglelomia* and licharewioid genera such as *Yukonospirifer* and *Nahoniella* may have arisen from Russian sources. *Ala* is apparently descended from an older Russia species. From United States, *Praeschrenkiella* has various allies in United States, *Nassichukia* evolved from *Kochiproductus* or ally, *Heteralosia* is found, and *Yukonalosia* may have arisen from allied stock. The sources of *Compressoproductus*?, *Sarytchevinella* and coolkilellin gen. & sp. indet*.* are obscure, and could be either Russia or United States, or indeed neither. Genera such as *Orthotetes, Cleiothyridina* and *Dielasma* are widespread, so their source cannot be ascertained, although *Cleiothyridina* is identified with a Russian species. For some taxa, such as phricodothyrin genera, little can be said, because they are too poorly known. *Sulcirugaria*, if accurate determined, is the only brachiopod genus that shows challengeable affinities with Gondwana.

BRACHIOPODA: *Orthotetes dorsosulcatus* n. sp*., Arctitreta*? sp. A, *Chelononia minimauris* n. sp., *Rugaria arcula* n. sp., *Sulcirugaria*? sp., *Komiella bitteri* n. sp., *Tubersulculatella subtuberculata* (Grabau), *Inflatusia ogilviensis* Waterhouse, *Kutorginella yukonensis* Sarytcheva & Waterhouse, *Nazeroproductus lazarevi* n. sp., *Reticulatia oldershawi* Waterhouse, *Kochiproductus saranaeanus* (Fredericks), *Nassichukia nodosa* n. gen., n. sp., *Gemmulicosta undulata* n. sp., *Tityrophoria zimmermanni* Waterhouse, *Calliprotonia kerrae* n. sp., *Tubersulculus ovalis* n. sp., *Krotovia norfordi* n. sp., *K. wallaciana* (Derby), *Krotovia* sp. A, *Krotovia* sp. B, *Krotovia* cf. *parva* Cooper, *Waagenoconcha* sp., *Heteralosia scotti* n. sp., *Yukonalosia arctica* n. gen., n. sp., *Balkhasheconcha* cf. *piassinaensis* (Einor), *Ramaliconcha bitteri* Waterhouse, *Paucispinifera carboniferica* n. sp., *P. abramovi* n. sp., *Kuvelousia*? sp., *Protoanidanthus* sp., *Cimmeriella orientalis* (Abramov & Grigorieva), *Harkeria elongata* n. sp., linoproductid gen. & sp. indet. A, linoproductid gen. & sp. indet. B, *Praeschrenkiella waddingtonae* Waterhouse, *P. costata* Waterhouse, *Compressoproductus*? sp., *Sarytchevinella praecursor* n. sp., *Commarginalia* sp*.* A, *Orthotichia morganiana* (Derby), *Stenocisma winkleri* Martínez-Chacón, *Stenoscisma* sp., *Callaiapsida divitiae* n. sp., *Septacamera* sp., *Cleiothyridina gzhelensis* Grunt, *Composita* sp., *Composita mutabilis* Czarniecki, *Hustedia trifida* n. sp., *Martinia* cf. *karawanica* Volgin, *Martiniopsis*? sp. A, *Brachythyris praeufensis* Solomina, *Meristorygma* sp. A, *Ala alatiformis* n. sp., *Junglelomia ursus* Waterhouse, *J. simplex* n. sp., purdonellid? gen. & sp. indet., *Spiriferinaella simplicata* n. sp., *Fasciculatia*? sp., *Tegulispirifer placitus* n. sp., neospiriferin gen. & sp. indet. A, *Forticosta transversa* n. gen., n. sp., *Septospirifer tatondukensis* Waterhouse, *Spiriferella yukonensis* Waterhouse & Waddington, *Eridmatus parva* (Cooper), phricodothyrid? gen. & sp. indet. A and B, *Spirelytha biakovi* n. sp., *Spiriferellina* sp. A, *Zaissania* sp., *Tumarinia solominae* n. sp., *Yukonospirifer* sp*., Nahoniella decorus* n. sp*.* and *Dielasma?* sp. A.
BIVALVIA: *Pseudomyalina* sp., streblochondriid sp., *Dunbarella* sp., *Pterinopectinella* sp., *Montorbicula*? sp., *Girtypecten* sp., *Meekopecten* sp. and *Palaeolima* sp. A. GASTROPOD: *Spiroscala* sp.

Table 4. List of brachiopods, bivalves and gastropods found in Member A.

Age:

Member A lies above the Ettrain Formation, which was dated as Kasimovian by Nazer (1977), and below further members in the lower Jungle Creek Formation, dated as Early Permian. The ages and affinities for constituent species within the member are discussed in Systematic Descriptions, and the following text summarizes some of the assessments over similarities and age.

Most species point to a Late Carboniferous age. *Orthotetes dorsosulcata* is close to *O. waageni* (Schellwien) from the Auernig Austrian Alps, and reported from Late Carboniferous of Kazakhstan and elsewhere (Sokolskaya 1968, Manankov 1979). *Rugaria arcula* n. sp. is closest to *R. parva* (Cooper & Grant) from the *Uddenites* Shale Member of the Graham Formation in Texas, of Upper Carboniferous age. The type species of *Tuberculatella* comes from Thailand beds of Upper Carboniferous age, but the genus is also found in Member C of the Jungle Creek Formation, and straddles Early Permian and Middle to Late Carboniferous faunas of Russia. *Kutorginella yukonensis* Sarytcheva & Waterhouse approaches *K. stepanovi* Lapina from lower Late Carboniferous Kirov level of the Urals and from Late Carboniferous levels in Verchoyan (Abramov & Grigorieva 1988), as well as *K. mosquensis* Ivanova from Kasimovian faunas of the Moscow Basin (Lazarev 1990), but the species ranges into Early Permian faunas in the overlying Jungle Creek Formation. *Reticulatia oldershawi* Waterhouse is close to several Late Carboniferous species in Russia. *Gemmulicosta undulata* n. sp. shows some approach to *G. gjeliensis* (Ivanova) from the Late Carboniferous (Gzhelian) of the Moscow Basin (Lazarev 1990). *Tubersulculus transversus* appears to be at the start of an evolutionary lineage that culminated in Early Permian species *T. maximus* and *T. pseudoaculeatus*. *Krotovia norfordi* n. sp. is very like *K. pustulata* (Keyserling) from mainly Early Permian and also Late Carboniferous of the Urals. *Krotovia* sp. A is closest to *K*. *tareiaensis* Ustritsky, 1963 from the Late Carboniferous (Bashkirian) Makarov Suite of Taimyr Peninsula. *K. wallaciana* (Derby) comes from Late Carboniferous of Brazil, and has been widely reported, including the Scheteligfjelt Beds, Passage Beds and Treskelloden beds of Svalbard and Ambigua Limestone of Bjørnøya (Gobbett 1964, Czarniecki 1969), but similar material comes from the Early Permian of the Urals (Tschernyschew 1902). *Echinaria circularis* is related to several species from the Pennsylvanian of central United States, and to *E. komischani* (Volgin 1960) from the Late Carboniferous of central Fergana. *Balkhasheconcha* is compared to *B. piassinaensis* (Einor) from the Makarov Suite of Taimyr Peninsula, and *Ramaliconcha bitteri* Waterhouse might prove to be close to the supposed *Waagenoconcha skinderi* (Sarytcheva, 1968) from the Kokpecten Suite of west Kazakhstan, of Early Carboniferous age. *Cimmeriella orientalis* (Abramov & Grigorieva, 1983) was first described from the early Pennsylvanian (Bashkirian) Natalin Horizon of Verchoyan. *Harkeria elongata* n. sp. looks a little like the species *postartiensis* Stuckenberg from the Late Carboniferous of the Urals and Kasimovian and ?Gzhelian of the Moscow Basin (Lazarev 1990), but the generic affinities of *postartiensis* have yet to be determined.

Orthotichia morganiana (Derby) was first described from Carboniferous deposits of Brazil, and has been widely reported from Late Carboniferous and Early Permian faunas. *Stenoscisma winkleri* Martínez-Chacón (1977) was initially described from the Westphalian B, C (Kashirian, Late Carboniferous) Beleno Formation of Spain, *Callaiapsida divitiae* n. sp. is close to *C. artica* (Holtedahl) from the Upper Carboniferous faunas of Novaya Zemlya, and from the Passage Beds, Wordiekammen Limestone and Cyathophyllum Limestone of Spitsbergen (Gobbett 1964) and *C. pyramidata* Lazarev from Late Carboniferous of Russia. *Cleiothyridina gzhelensis* Grunt was first recorded from the Gzhelian of the Moscow Basin, and ranges into younger beds in the Ogilvie Mountains, as well as being close to specimens from the Coyote Butte Formation of Oregon, and Early Permian Burgali Suite of northeast Russia. *Hustedia trifida* n. sp. approaches *H. mormoni* (Marcou) from the Late Carboniferous of several stations in the United States (Sutherland & Harlow 1973), and Taimyr specimens from the Turuzov Suite that were ascribed to *H*. *remota* (Eichwald) by Ustritsky & Chernyak (1963). *Martinia* is compared to *M*. *karawanica* Volgin described from the Late Carboniferous of Fergana and Carnian Alps and reported, seemingly unreliably, from the Cantabrian Mountains (Myachkovian – Kasimovian) of Spain (Martínez-Chacón & Winkler-Prins 1985), as discussed on p. 316. *Brachythyris* identified with *B. praeufensis* Solomina, 1978 from Late Carboniferous Cizder Suite of Orulgania and Surkechan Suite of Verchoyan (Klets 2005).

Permian affinities, often mixed with Carboniferous links, are weaker, but include indications from *Chelononia minimauris* n. sp., in a genus not previously known in Carboniferous faunas, and close to Neal Ranch (Asselian) species of west Texas (Cooper & Grant 1974). *Tuberculatella subtubercula* (Grabau) comes from the Maping Limestone of China, of basal Permian age. *Kochiproductus* is identified with *K*. *saranaeformis* (Fredericks) from Early Permian of various faunas in Russia. *Krotovia* cf. *parva* Cooper is allied to an Early Permian species from the Coyote Butte Formation of Oregon, United States. *Tityrophoria zimmermani* Waterhouse is closest to so-called *Horridonia geniculata* Gobbett (1964) from the Early Permian Cora Limestone of Bjørnøya. A few species, allied to *Compressoproductus, Sarytchevinella* and coolkilellin, more strongly indicate relationships with well established Permian genera, as if they constituted precursor stock, and *Kuvelousia* is also mostly Permian. *Composita mutabilis* Czarniecki was first described from the Treskelloden beds of Spitsbergen, but does occur in the Ettrain Formation as well. *Composita mutabilis* Czarniecki (1969) is shared with Treskelloden Formation of Spitsbergen, considered to be Permian by some authorities, but possibly Gzhelian in age. *Eridmatus* is identified with a distinctive species from the Coyote Butte Formation: this has been assigned varying ages from Early to Middle Permian, but evidence favours the greater age, and the fauna needs revision. However it seems possible that the species first appeared in Canada, and persisted in Oregon. *Tumarinia solominae* n. sp. compares with Permian species from northeast Russia.

Bivalves *Dunbarella* sp. and *Meekopecten* sp. favour a Late Carboniferous age, whereas *Pseudomyalina* suggests Early Permian.

Overall, there is a preponderance of affinities with Late Carboniferous faunas, with some holdovers from earlier Carboniferous, and some species and genera that became better established in Permian time, to the extent that several are supposedly limited to Permian according to the *Revised Brachiopod Treatise.* But those time ranges are deemed to be in need of reassessment. If the age of overlying beds is deemed to be basal Asselian, then the age of the present fauna is Gzhelian, as suggested in Bamber & Waterhouse (1971), and this would appear to be confirmed by the Kasimovian age assigned to the underlying faunas in the bulk of the Ettrain Formation by Nazer (1977), and Moscovian age assigned to fusulines in the lower Ettrain beds by Ross (1967) and to small foraminifera by Mamet in Bamber et al (1989).

Member B, *Ogilviecoelia initiatus* Zone

Type section: Ridge 42, Member B of Jungle Creek Formation in headwaters of Ettrain Creek, Ogilvie Mountains.

FAD: *Ogilviecoelia initiatus* n. sp. is the most common of rare fossils in this member.

BRACHIOPODA: *Komiella*? sp., *Fimbrininia* sp. A, *Kochiproductus* sp., *Calliprotonia* sp., *Anemonaria* sp., *Commarginalia* sp. B, *Eridmatina petita* (Waterhouse & Waddington), *Ogilviecoelia initiatus* n. sp. and *Nahoniella*? sp. indet. BIVALVIA: *Etheripecten* sp. B.

Table 5. List of brachiopods and mollusc from Member B.

Content: Exposures in the area under discussion are few, and include silty shales at JBW 69 in section 116F-9, above Member A, and JBW 19 to the north in section 42 of Shi & Waterhouse (1996, Fig. 4, p. 11). The fossils come from localities JBW 19, 27?, 69, 993, 994; and GSC 56920. In section 116C-2 on the Tatonduk River, GSC locality 57044, mapped in Bamber & Waterhouse (1971, Fig. 7) as representing fauna "Eta", has *Ogilviecoelia* that looks moderately close to *O. initiatus* n. sp., rather than *O. shii* n. sp. The beds in the Ogilvie Mountains underlie the distinctive limestone of Member C with the *Kochiproductus imperiosus* Zone in the same section. Member B has yielded fossil species that are not found in either the underlying or overlying biozone, involving *Anemonaria* Cooper & Grant, and the distinctive *Ogilviecoelia initiatus* n. sp. *Eridmatina petita* (Waterhouse & Waddington) is close to *Eridmatina marathonensis* (Cooper & Grant) from the *Uddenites*-bearing Shale Member of the Gaptank Formation in Texas, as well as specimens from the overlying Member E.

Significant entries include *Fimbrininia*, widespread in the Permian, *Anemonaria*, member of a genus first described from younger beds in United States, first entry of *Ogilviecoelia* as *initiatus* n. sp., and *Eridmatina*, descended apparently from a slightly older species in the United States. Whilst of interest, the sample is too small to allow adequate evaluation, and no species firmly indicates a restricted international age, which instead must be determined from stratigraphic position.

The fauna is clearly a meagre one, close to being a level to be signalled by what Waterhouse (2008b) termed a Black Flag level, as signalling a paraconformity. The fauna is found in a lithology differing from that of the overlying Member C, and so might represent simply a facies of Member C, whereas similar facies in the underlying Member A contain different faunas, and notably lack any confirmed attenuatellin brachiopods.

Member C, *Kochiproductus imperiosus* Zone

Type section: Ridge 42, Member C of Jungle Creek Formation in headwaters of Ettrain Creek, Ogilvie Mountains.

FAD: *Kochiproductus imperiosus* Waterhouse has been found at the base of Member C in JBW 18.

Arctitreta? sp. B, *Tuberculatella* aff. *tuberculata* (Moeller), *T*. cf. *boulei* (Kozlowski), *Sangredonia alaminata* n. sp., *Kutorginella*? sp., *Dutroproductus dutroi* n. gen., n. sp., *Kochiproductus imperiosus* Waterhouse, *Calliprotonia umbonalis* n. sp., *Echinaria circularis* n. sp., *Juresania juresanensis* Tschernyschew, *Villaconcha planiconcha* n. sp., *Balkhasheconcha* sp., *Paucispinifera sulcata* n. sp., *Kuvelousia*? sp. B, *Lineacrassus inflatus* Waterhouse, *Schrenkiella triangulata* Barchatova, *Rhynchopora grigorieva* n. sp. , *Meristorygma?* sp. B, *Ettrainia costellata* n. sp., *Neospirifer*? sp. A,, *Plicatospiriferella undulata* n. sp. and *Tumarinia* sp. Top layer *Tethysiella impudens* Waterhouse.

Table 6. List of brachiopods from Member C.

Content: This zone is found principally in bioclastic limestone. The zone is dominated by mostly large productids, involving species of *Dutroproductus*, *Villaconcha, Kochiproductus, Echinaria, Lineacrassus* and *Schrenkiella,* with numerous *Juresania*, and rather few spiriferids – such as *Ettrainia* and *Plicatospiriferella*. There are twenty two taxa in twenty one genera, with fifteen named species, and one additional species in the topmost layer. No other fauna throughout the Late Carboniferous and Permian of the Yukon Territory is comparable. A number of the genera are limited to the zone in the Jungle Creek and Ettrain sections, involving *Sangredonia, Dutroproductus*, *Villaconcha, Juresania*, *Lineacrassus* and *Ettrainia*, and at species level only *Rhynchopora grigorieva,* with possibly *Dutroproductus and Tumarinia,* are shared with underlying or overlying zones, whereas other well sampled zones above and below in the stratigraphic column have more numerous links. There are no bivalves or gastropods known in Member C.

In Member C, many genera persisted or reappeared from older faunas, involving *Arctitreta, Tuberculatella, Kutorginella, Kochiproductus, Calliprotonia, Echinaria* (in Ettrain faunas), *Balkhasheconcha, Paucispinifera, Rhynchopora* and *Meristorygma*. Stock likely to have affinities or sources amongst brachiopods of the United States are *Dutroproductus* and *Villaconcha* (found in the Graham Formation of Texas), and possibly *Schrenkiella* and *Lineacrassus* with links to older faunas in the neighborhood and in United States. *Sangredonia* is believed to be congeneric with an older species in New Mexico. *Juresania* marked a new entry, with links to American forms and conspecificity with a species in Spitsbergen and Russia. *Neospirifer*? sp. A shows Russian links, though widely reported from elsewhere, although it could have evolved locally in the first place, and later migrated.

The fauna overall is strong with remnant genera, saw input from southern and eastern United States that was more significant than in Member A, with a slender component of new genera, larger than that of Member A. There is a complete absence of bryozoa, molluscs and corals, and no suggestion of any input from Gondwana.

Age:

Amongst long-ranging genera, Member C testified to significant last appearances in the Yukon Territory of *Sangredonia* and *Echinaria,* and significant early appearance of *Villaconcha*. *Tuberculatella tuberculata* (Moeller) ranges from Gzhelian to Sakmarian in Russia, and is closest to material from the Turuzov Suite of Taimyr Peninsula, and also approaches the Late Carboniferous species *T. karpinskina* (Yanichev) from the Urals and Yepenchin Suite of Verchoyan (Semenova in Ifanova & Semenova 1972). Specimens are compared to *T.* cf. *boulei* (Kozlowski) from the Asselian Copacabana Group of Bolivia, whereas *Sangredonia alaminata* is related to and presumably descended from an Upper Carboniferous form from New Mexico. *Calliprotonia umbonalis* n. sp. is especially close to Gzhelian specimens figured as *C. sterlitamakensis* (Stepanov) by Lazarev (1990, pl. 30, fig. 7), *Echinaria circularis* compares to Late Carboniferous material from Amdrups Land, Greenland (Holtedahl 1917), and to a number of species from mid-Pennsylvanian age in the United States. *Villaconcha planiconcha* is only moderately close to *V. prophetica* Cooper & Grant, 1975 from the *Uddenites*-bearing Shale Member of the Graham Formation in Texas, United States, and *Schrenkiella* has been identified with *S. triangulata* Barchatova from the Sakmarian of Timan. It is judged to be older in Canada and so presumably later emigrated to Russia.

There are apparent similarities to the Treskelloden faunas of Spitsbergen, with *Juresania juresanensis* (Tschernyschew) shared with this fauna and with Early Permian (Asselian, Sakmarian) of the Urals, and the large linoproductinid *Lineacrassus* Waterhouse in some respects approaching shells from Spitsbergen that were identified by Czarniecki (1969) with *Linoproductus dorotheevi* (Fredericks), without being congeneric. Whilst this Treskelloden level has been judged to be partly Lower Artinskian by Dallmann et al. (1999, fig. 2.04) and entirely Artinskian by Cutbill & Challinor (1965), it was treated as Asselian and early Sakmarian by Federowski (1982) and Federowski et al. (2007, Fig. 9), and Czarniecki (1969) preferred an Early Asselian and Orenburgian age: Orenburgian is now a unit that has dropped out of favour, and is absorbed within the Gzhelian Stage.

Tethysiella impudens **layer**

A fossil locality at JBW 862 in section 42 has yielded a distinct species, described as *Tethysiella impudens* n. sp. The layer is of fine calcareous sediment, 1.5cm thick, less granular than that of the underying rocks of Member C, but without the dolomite typical of Member D. It may be regarded as belonging to either member, and is here provisionally placed at the top of Member C, representing the last phase of limestone depositon that made up the bulk of Member C, and has been counted as part of the *Kochiproductus imperiosus* Zone. The brachiopod species fails to indicate any precise age. It represents a meagre community between Members C and D.

Tethysiella was described from Changshingian deposits of the North Caucasus, of paleotropical affinities (Waterhouse & Bonham-Carter 1972, 1975), and so differs markedly in age and geographic constraints from the Canadian species. But spine distribution and rugation differ in the Canadian species, so that it may not be exactly the same genus, analysis being hampered by poor preservation of the Canadian form.

Member D, *Rugivestigia commarginalis* Zone

Type section: Ridge 42, Member D of Jungle Creek Formation in headwaters of Ettrain Creek, Ogilvie Mountains.
FAD: There is no widespread diagnostic species for this zone, which incorporates fossils that come mostly from a lithology largely restricted to Member D.

BRACHIOPODA: *Arctitreta* cf. *peelensis* Shi & Waterhouse (shared with Member F), *Fimbrininia spinosa* Waterhouse (shared with Member E), *Kutorginella yukonensis* Sarytcheva & Waterhouse (shared with older and younger levels), possible *Dutroproductus dutroi* n. gen., n. sp. (found mostly in Member C), *Reticulatia*? sp., C*alliprotonia mclareni* Waterhouse and *Tubersulculus reidi* Waterhouse (shared with Member E), *Krotovia norfordi* n. sp. and *Krotovia* sp. B (shared with Member A), *Krotovia* sp. C, *Waagenoconcha irginaeformis* (Stepanov) and ?*Echinalosia minuta* n. sp. (shared with Member E), *Rugivestigia commarginalis* n. sp., *Protoanidanthus umbonatus* Shi & Waterhouse and *P. nichollsi* n. sp. (shared with younger Jungle Creek faunas), *Cimmeriella orientalis* (Abramov & Grigorieva) (better represented in Member A), linoproductid gen. & sp. indet. B (shared with Member A and the Ettrain Formation), *Commarginalia norrisi* n. sp. (shared with Member E), together with *Rhynchopora grigorieva* n. sp. (also in Members C and E), *Stenoscisma* sp. (shared with Member A), *Cleiothyridina gzhelensis* Grunt (also in Member A and E), retziid? gen. & sp. indet., *Martiniopsis* sp. B, *Martinia*? sp., *Mirandifera wolfcampensis* (King), *Meristorygma*? sp. B, possibly *Ala alatiformis* n. sp. (or Member E, and shared with Member A), neospiriferin gen. & sp. indet. B, *Septospirifer hughi* n. sp. (shared with Member F), *Spiriferella yukonensis* Waterhouse & Waddington, shared with Member A, and *Eridmatina petita* (Waterhouse & Waddington), (shared with Member B and E), as well as phricodothyrid gen. & sp. indet. C. BIVALVIA: *Etheripecten* sp. C is the only known bivalve.

Table 7. List of brachiopods and a mollusc from Member D.

Content: The fauna is found in mostly dolomite beds, especially as scattered single valves over the exposed surface of bedding planes, and indeed shells were concentrated at that level. There are a few restricted species, including the nominate form. But there also generic links with older faunas of especially the *Septospirifer tatondukensis* Zone, including *Krotovia* and *Orthotichia,* and genera not known locally at younger levels, such as *Cimmeriella*, *Martinia, Martiniopsis* and *Meristorygma* (some conceivably reworked from older faunas) and totalling overall about twelve species of the thirty two brachiopod taxa found in the fauna, compared with fourteen taxa that range into younger faunas, including some that commenced in older faunas. Several significant species are shared with overlying zones, including the *Ogilviecoelia shii* and "*Yakovlevia transversa*" Zones, such as *Fimbrininia spinosa*, *Calliprotonia mclareni*, *Kutorginella yukonensis, Echinalosia minuta* and *Commarginalia norrisi*. There is little in common with the immediately underlying *Kochiproductus imperiosus* Zone, presumably in part at least because of facies differences, and indeed the numbers of specimens and limited range of genera and species suggest that conditions were not very favourable for brachiopods or other macro-invertebrates during the accumulation of the rocks that formed Member D. There is in summary a number of affinities and links with the underlying *Septospirifer tatondukensis* Zone, but some first entries that persisted into younger faunas.

One newly incoming form includes *Echinalosia,* a genus which is most abundant in the Permian faunas of Australasian segment*,* but the Canadian example is older. Another genus new to the sequence is *Rugivestigia*, apparently descended from *Rugivestis* Muir-Wood & Cooper, which is found widely in Permian faunas.

Age:

There are a number of shared species shared with other members, suggesting either persistence, or derivation through reworking. Given that the affinities within the sequence are somewhat mixed, and given that some species are shared with the overlying *Ogilviecoelia shii* Zone, it seems possible that the *Rugivestigia commarginalis* Zone is only slightly and perhaps not significantly older, with differences from the Member E fauna possibly to be attributed to or at least exaggerated by facies differences. There is the first entry of *Arctitreta* cf. *peelensis* Shi & Waterhouse, represented in younger Jungle Creek faunas. Material is close to *Krotovia norfordi* n. sp. from Member A, and *Krotovia* sp. A is close to material from the Makarov Suite of Bashkirian Late Carboniferous age in Taimyr Peninsula (Ustritsky 1963), (though possibly ranging up to Kasimovian according to early studies). *Fimbrininia spinosa* Waterhouse, shared with Member E, is allied to *F. gracilis* from the Upper Carboniferous of Verchoyan. *Waagenoconcha irginaeformis* Stepanov is of Late Carboniferous and Early Permian age in Russia, and appears to incorporate *W. parvispinosa* Cooper of the Coyote Butte Formation in Oregon. *Cimmeriella orientalis* Abramov & Grigorieva is identified with a species from the lower Pennsylvanian of northeast Russia. *Mirandifera wolfcampensis* (King) is identified with a species from the *Uddenites* Shale Member of the Gaptank Formation and possibly Neal Ranch Formation of Texas. To judge from these affinities, the fauna must be close to the Permian-Carboniferous boundary, with significant affinities, including first entries, slightly tilted towards the Asselian Stage.

Member E, *Ogilviecoelia shii* Zone

Type section: Section 42, Member E of Jungle Creek Formation, in headwaters of Ettrain Creek, Ogilvie Mountains.

FAD: *Ogilviecoelia shii* Waterhouse, found 1.4m above the start of the member.

Content: This zone is represented in recessive beds of the lower Jungle Creek Formation, immediately below the "*Yakovlevia transversa*" Zone. The fauna is diverse and well preserved, found often as external and internal moulds in mudstone and siltstone. Forty four brachiopod taxa are represented, in forty three genera, with possibly one additional genus *Ala*, depending on its source. There are thirty, or possibly thiry one named species. Mollusca are more numerous than in preceeding members, with ten bivalve taxa and four gastropod taxa. Affinities lie moderately with the overlying Jungle Creek Formation, including allied or identical taxa *Jakutoproductus verchoyanicus*, *Waagenoconcha irginaeformis, Kutorginella yukonensis, Thamnosia* cf. *spinosa, Kochiproductus porrectus, Anemonaria auriculata, Protoanidanthus umbonata, Schrenkiella schrenki, Septacamera triangulate, Composita* cf. *bamberi* and *Nahoniella plana* as well as bivalves including *Primaspina*? sp. and *Exochorhynchus simils* Lyutkevich & Lobanova) but there are some links with underlying faunas, involving *Calliprotonia mclareni* and *Echinalosia minuta* in the *Rugivestigia commarginalis* Zone, as well as *Rhynchopora grigorieva* shared with the *Rugivestigia commarginalis* and *Kochiproductus imperiosus* Zones.

BRACHIOPODA: *Chonetinella*? sp., *Komiella* sp., *Lissosia*? *alatus* (Stuckenberg), *Fimbrininia spinosa* Waterhouse, *Jakutoproductus verchoyanicus* (Fredericks), *Kutorginella yukonensis* Sarytcheva & Waterhouse, *Thamnosia* cf. *spinosa* Shi & Waterhouse, *Kochiproductus porrectus* (Kutorga), *Calliprotonia mclareni* Waterhouse, *Tubersulculus reidi* Waterhouse, *Krotovia* sp. D, *Waagenoconcha irginaeformis* (Stepanov), *Waagenoconcha* sp., *Echinalosia minuta* n. sp., *Balkhasheconcha bamberi* Waterhouse, taeniothaerin gen. & sp. indet., *Anemonaria auriculata* Shi & Waterhouse, *Protoanidanthus umbonatus* Shi & Waterhouse, *P. nichollsi* n. sp., *Harkeria sulcoprofundus* n. sp., linoproductinid gen. & sp. indet. C, *Schrenkiella schrenki* (Stuckenberg), *Commarginalia norrisi* n. sp., *Rhynoleichus*? sp., *Rhynchopora grigorievae* n. sp., *Stenoscisma mutabilis* Tschernyschew, *Septacamera triangulata* Shi & Waterhouse, *Yanzaria solitarius* n. gen., n. sp., *Cleiothyridina gzhelensis* Grunt, *Composita* cf. *bamberi* Shi & Waterhouse, *Eumetria* sp., *Hustedia quadrifidus* n. sp., *Geothomasia*? sp., *Ala alatiformis* n. sp. (or Member D), *Junglelomia* aff. *simplex* n. sp., *Spiriferinaella simplicata* n. sp., *Neospirifer* sp. B, *Eridmatina petita* (Waterhouse & Waddington), *Triramus canadensis* Waterhouse, *Ogilviecoelia shii* n. sp., *Spiriferellina* sp. B, *Nahoniella* cf. *plana* (Shi & Waterhouse), *Tumarinia* sp., *Cryptacanthia*? sp. and *Dielasma*? sp. B. BIVALVIA: *Polidevcia*? sp., *Parallelodon*? sp., streblochondriid gen. & sp. indet., *Etheripecten* sp. D, *Primaspina*? sp., *Palaeolima*? sp. A, *Stutchburia* sp., *Sanguinolites* sp., *Exochorhynchus similis* (Lyutkevich & Lobanova) and *Palaeocosmomya* ? sp. GASTROPODA: *Warthia* sp., *Ptychomphalina* sp., *Ananias* sp. and *Procerithiopsis* sp.

Table 8. List of brachiopods and molluscs from Member E.

Affinities of the fauna

This fauna marks a significant change in make-up of genera and species from underlying faunas, possibly because the underlying facies of the *Rugivestigia commarginalis* Zone was not favourable for benthos. Eleven of thirty three species are shared with younger faunas, and fourteen to sixteen with older faunas. Some ten genera are not found in older faunas, but only five genera are not found in younger faunas.

. A link to the western United States is provided by possible *Lissosia*, and *Triramus canadensis* has widespread ties, possibly with United States genera and species, certainly with Russian forms. *Chonetinella* and *Eumetria* have United States ties, and several taxa are strong in Russian affinities, including *Jakutoproductus,* taeniothaerin gen. & sp. indet., *Rhynoleichus*, *Neospirifer* and possibly *Ogilviecoelia.* Although the latter genus is not known elsewhere for certain, its subfamily affinities with Russia and Arctic are likely to be strong. *Cryptacanthia* is widespread, and well represented in faunas of the United States. Perhaps the most remarkable occurrence is indicated by *Yanzaria*, a genus otherwise found only in Carboniferous faunas of the Fenestella Shale in northwest India.

The bivalve component is comparatively strong, and many of the ties are strong with Gondwana faunas. But unfortunately the lack of full systematic coverage of faunas from the United States through recent times, with numerous genera never studied tells against the possibility of making any adequate assessment. Bivalves from the silicified faunas of Texas were made available to one renowned expert, but that resulted only in a selection of high-class but limited studies. *Pseudomyalina* and *Palaeocosmomya* mark two genera known from Gondwana, and whether they were more widespread is not known.

In summary, persisting genera are predominant, and apart from a few significant links with southern and eastern United States, ties lie with the faunas of western United States, through Oregon, and with Russia, together with the unexpected occurrence of a Gondwanan genus *Yanzaria*. The bivalve component appears to strengthen links with the southern paleohemisphere, but the bivalve component of United States Permian is too imperfectly known to fully assess the apparent absence of links with that part of the globe.

Age:

Species on the whole point to a Permian age, but there are significant ties with Late Carboniferous species. The five species *Lissosia*? *alatus, Kochiproductus porrectus, Schrenkiella schrenki*, *Composita* cf. *bamberi* and *Nahoniella* cf. *plana* reinforce a Permian age, and they are supported by the possible closeness of *Calliprotonia mclareni* Waterhouse to *C. inexpectans* Cooper from the Coyote Butte Formation of Oregon. A number of species are related to species of Russia that span the Permian and Late Carboniferous, such as *Jakutoproductus verchoyanicus* in Russia, also allied to *J. morosovi* Zavodowsky from the Burgali beds, and closest to specimens from the Cigsk Suite of south Verchoyan (Abramov & Grigorieva 1988). *Fimbrininia spinosa* n. sp. is close to the Sakmarian *F. gijigensis* (Zavodowsky, 1970) from the Irbichan Horizon of Kolyma-Omolon and material from the Kigiltass Suite and Abagin Horizon of Verchoyan (Abramov & Grigorieva 1983). *Kochiproductus porrectus* (Tschernyschew) is mainly Asselian-Sakmarian in the Urals and elsewhere. *Schrenkiella schrenki* (Stuckenberg) is found in the Sakmarian of Timan. *Waagenoconcha irginaeformis* Stepanov has been reported widely from Asselian-Sakmarian faunas of the Urals and northeast Russia (Klets 2005), and may include *W. parvispinosa* Cooper from Oregon in the United States. *Commarginalia norrisi*, which ranges into slightly older Canadian faunas, is allied to material from the Asselian Omolon and Burgali Formations, and the Haran beds of Russia, and *Stenoscisma mutabilis* Tschernyschew ranged from Late Carboniferous to Sakmarian. *Neospirifer* sp. approaches *N. fasciger* (Keyserling) from the early Cisuralian of Russia. *Septospirifer hughi* n. sp. finds a generic match in specimens identified from the Schwagerina-Kalk in the Urals, and is known in Member F.

Several species favour a Late Carboniferous age. *Rhynoleichus?* sp. is like *R. bulgakovae* Abramov & Grigorieva from the Upper Carboniferous Davin Suite of Verchoyan (although also recorded from the Echi Suite of upper Sakmarian Artinskian age), and *Cleiothyridina gzhelensis* Grunt was first identified from the Gzhelian of the Moscow Basin. Overall, the fauna seems most likely to be Asselian, because it is not difficult to accept that there should be surviving links with Gzhelian faunas as hold-overs. But given the precursor entry of forms into the Canadian sequence – just as seen for palynomorphs, a Gzhelian age cannot be completely dismissed from internal evidence, pending the discovery of well preserved fusulines, ammonoids or conodonts.

PALAEOGEOGRAPHIC AFFINITIES

For many years, assessments of palaeogeographic affinities for faunas have been based on analyses assisted by non-parametric statistically based snap-shots to compare overall assemblages, by lumping entire faunas. For living faunas, the time component is simple, whereas for fossil faunas in published studies, the time component has been too often artificially constrained, and stretched to long intervals, beyond the biological reality of communities and biozones, because stages, composed of such entities, are too long with too great a mixture of different affinities. (See also Waterhouse 2015a, p. 347). Here it is suggested that it would be possible to considerably expand the scope of paleogeographic and evolutionary studies, by segregating each different source of the faunas in each faunal biozone or even fossil community, thereby gaining information on the movements and evolution of faunal components. In the past, classification has been regarded as an entirely separate sphere of knowledge, yet increasingly refined classification uncovers a critical paleogeographic component in the origin of new taxa and their classification, because it emerges that genera, tribes and subfamilies have developed usually within a restricted region, or as offshoots from the main corpus in a different area. This accords with the importance of source areas for genera and subfamilies revealed in studies of Productida and Spiriferida in Waterhouse (2013, 2016). At least some modern studies of evolution amongst birds have found that geographic range is of prime significance. That understanding is returning the study of fossil faunas to their natural state of originating in a world governed by biota, and strongly influenced by past inheritance, geographic constraints and distributions, climate, and ever changing arrangements of geographic features.

These generalizations can be partly elucidated for the faunas under review from the Late Carboniferous and earliest Permian in the Yukon Territory of Canada. Even though paleogeographic affinities are complex, and cannot be fully assessed because many faunas world-wide of the same age remain to be described, or need to be closely and sympathetically revised, and further complicated by the genera that have more than one affiliation, and so need to be counted more than once, as in the following review, it is possible to show that affinities lie substantially with faunas from high northern paleolatitudes, including faunas from much of Russia, rather than with faunas from the southern and eastern United States. The following summary focuses principally on links to southern North America as against Europe and especially Arctic and Russian faunas, including Spitsbergen.

Especially Canada, Yukon, Oregon (western USA).

Arctitreta, Inflatusia, Bailliena, Nazeroproductus, Nassichukia, Gemmulicosta, Tityrophoria, Rugivestigia, Harkeria, Lineacrassus, Praeschrenkiella, Junglelomia, Ettrainia, Triramus, Ogilviecoelia, Yukonospirifer, Nahoniella. There is a modest but distinct component of genera as yet not found reliably other than in Canada and Arctic, as well as at least parts of the western seaboard of the United States. A number of these genera seem likely to be found also in Russia. The streptorhynchid *Arctitreta* may well occur more widely, but streptorhynchids remain poorly known, as is evident from the flaccid studies which failed to discriminate genera adequately in the *Revised Brachiopod Treatise* (Waterhouse & Chen 2007). Horridoniids *Inflatusia* and *Bailliena* are related to other genera with strong Arctic affinities. *Harkeria* is a member of Muirwoodiinae, which was especially prominent in Arctic and Russian faunas, and not entering Texas, United States, until the Middle Permian, although found in Early Permian of Oregon (as well Inner Mongolia). However it is suspected that a number of these genera will be found to have had wider links. *Junglelomia* and *Ettrainia* are choristitoid brachiopods of Canada, likely to be found in Russia. Choristitoids appear to be not known in Pennsylvanian or Permian of mid and eastern United States, or in Gondwana, but were widespread in the Permian of Russia and Arctic, including Canada and early Permian of Austria (Gauri 1965) and China. *Triramus* as a member of Delthyridina may well be found in Russia, for allies are widespread, and *Ogilviecoelia* is a member of Ambocoeliidae, with Russian – Arctic and even Australia – New Zealand allies, though probably beginning in the northern hemisphere. *Yukonospirifer* and *Nahoniella,* found as members of Licharewioidea only in Canada to date, approach genera found especially in northeast Russia, such as Kolyma-Omolon.

Russia including Urals, Arctic, Asia.

Komiella, Fimbrininia, Jakutoproductus, Tuberculatella, Kutorginella, Tubersulculus, Balkhasheconcha, Ramaliconcha, Pseudomarginifera, Kuvelousia, Commarginalia, Rhynoleichus, Callaiapsida, Septacamera, Meristorygma, Ala, Spiriferinaella, Fasciculatia, Tegulispirifer, Septospirifer, Arcullina, Plicatospiriferella, Zaissania, Tumarinia, with near or potential allies including *Nazeroproductus, Harkeria, Inflatusia, Bailliena, Junglelomia, Ettrainia, Yukonospirifer*, and *Nahoniella*. The overall impression of the Yukon faunas is that they have much in common with faunas of Late Carboniferous and Early Permian age in Russia, with links extending throughout the Arctic and into Oregon of western United States. The Urals have faunas more diverse than in Canada, with more fusulines and ammonoids, but close, and some Canadian forms, such as *Nazeroproductus,* are likely to have had Russian sources or allies through *Antiquatonia*, whereas *Juresania and Schrenkiella, al*though shared, are likely to have had an American source, to judge from fellow constituents of the tribes to which they belong (Waterhouse 2013). *Balkhasheconcha* and probably *Ramaliconcha* have had a long history in Russia and Kazakhstan. *Arcullina* and *Plicatospiriferella* of Kasimovian or greater age as early members of Spiriferellidae may well have commenced in Canada before extending into other parts of the Arctic. *Zaissania* in Canada is allied to older occurrences in Kazakhstan, but is also found in younger Permian of Nepal, and was wide-ranging in Asia.

Widespread, largely cosmopolitan, or at least shared between North America and Europe-Russia, and some but not all in east Australia-New Zealand.

Orthotetes, Chonetinella, Lissosia? alatus, Komiella, Reticulatia, Kochiproductus, Calliprotonia, Echinaria, Krotovia, Waagenoconcha, Rugivestis, Commarginalia, Orthotichia, Rhynchopora, Stenoscisma, Cleiothyridina, Composita, Hustedia, Martinia, Brachythyris, Spiriferellina, Dielasma, Cryptacanthia.

Few brachiopod genera were truly cosmopolitan, at least within restricted age-bands, but the preceeding named genera were widespread, and in particular shared between North America and Europe-Russia, as well as the Arctic. Several appear likely to have arisen from North American stock, because *Kochiproductus* and *Schrenkiella* for instance were members of subfamilies of predominantly North American distribution (Waterhouse 2013), and *Cryptacanthia* appears to have been of especially North American affinities. The origin of some genera, such as *Calliprotonia*, a prominent member of North American faunas, is highly involved, with Devonian sources and widely dispersed habitats (Waterhouse 2013) by Early Carboniferous times. Although a number of the preceeding genera are not found in east Australia and New Zealand, *Cleiothyridina, Composita, Stenoscisma* and *Spiriferellina* are present in warmer-water faunas of that area, especially Queensland and New Zealand.

Eastern and mid-United States, including Texas.

Chelononia, *Rugaria, Sangredonia, Dutroproductus, Kochiproductus, Juresania, Villaconcha, Heteralosia, Paucispinifera*, *Schrenkiella*, *Praeschrenkiella*, *Eridmatus, Eridmatina.*

Chelononia Cooper & Grant is a Permian genus named from Texan material, and a congeneric species "*Streptoryhynchus" variabilis* Thomas, 1958 is found in the upper Early Permian of Western Australia. The oldest species is of Late Carboniferous age in Canada. *Rugaria* and *Sangredonia* are based on species from United States, with *Rugaria* appearing early in Canada, and *Sangredonia* first in the United States. *Dutroproductus* was member of a tribe predominantly from the United States, and *Kochiproductus, Juresania, Schrenkiella* and *Praeschrenkiella* have North American forebears in the Pennsylvanian, although *Juresania* and *Schrenkiella* also displayed Russian links. *Heteralosia* is also principally from the United States, and *Paucispinifera* is principally United States, extending into the Arctic, but may be found to have commenced elsewhere. *Eridmatus* and *Eridmatina* have so far been recognized only from the United States, Canada and Russia.

Southern paleohemisphere Gondwana.

Sulcirugaria, taeniothaerin*, Echinalosia, Yukonalosia*?, *Yanzaria.*

The listing of these genera may reflect a degree of ignorance. Canadian *Sulcirugaria*, incompletely preserved, is known elsewhere in the Himalayas. and members of Taeniothaerini are found in Gondwanan faunas, with northerly occurrences few. *Echinalosia* is abundant in east Australia and New Zealand, and *Yukonalosia* is allied to a rare group Dasyalosiidae Brunton, most prominent in east Australia, though found in the Zechstein (Upper Permian) of Germany. So the distribution and time-ranges are remarkably dispersed, and might suggest polyphyletic sources. On the other hand, not enough is known of distributions to rule out a common relationship, and a possibly more likely alternative would posit that genera first evolved in moderately high northern paleolatitudes and moved later to southern high paleolatitudes, a possibility supported by the greater ages of some genera in Canadian faunas.

Gondwana, Arctic, including Russia, especially northeast Russia.

Protoanidanthus, Cimmeriella, coolkilellin, *Martiniopsis*?, *Spiriferella*, *Spirelytha*.

Protoanidanthus was named for early Permian genera of east Australia, but the genus is known in Carboniferous faunas of the Arctic, including northeast Russia and Canada. It evolved into a number of Permian genera, and stemmed from a Devonian group. *Cimmeriella* belonged to a related group, widely represented in United States and Russia, with allies in Asia and New Zealand. *Coolkilella* is member of another widely dispersed and allied Linoproductidina, including China (Chen & Shi 2006), so the three genera verge on being cosmopolitan, yet most strongly indicate northeast Russia and lower to moderate paleolatitudes of Gondwana. *Martiniopsis* is widely found in Russia and in southern hemisphere Permian in temperate rather than high paleolatitudes, though present in some highly diverse faunas of lower paleolatitudes, and *Spiriferella* is widely dispersed, and of uncertain origins. Widespread in many Permian faunas, especially in temperate latitudes, early occurrences include some in upper Pennsylvanian faunas of Canada and Russia.

Paleotropics.

Not many genera have links restricted according to present knowledge to the paleotropics, but *Tethysiella* and *Sarytchevinella* appear to constitute rare exceptions, having been found elsewhere only in the Caucasus of southern

Russia. But this number needs to be boosted by the number of ties with the Glass Mountains of Texas, including such forms as *Chelononia* and other genera.

SUMMARY OF FAUNA INHERITANCE

Summary through time

The next question concerns how such information should be represented. A simple procedure would be to graphically summarize the number of genera according to their paleogeographic affinities, and this would help systematize the kaleidoscope of affinities present in any fossil faunal assemblage. Waterhouse & Bonham-Carter (1972, 1975) refined this approach by offering a formula to summarize the total overall affinities. They contrived to add affinity scores, but it is also important not to conceal exceptions in the faunal attributes, which yield information on the complexity of fossil distributions. Further information may be provided by the analysis of paleolatitudinal constraints. Putatively an assignment of values keyed to paleolatitude and hemisphere should indicate whether faunas owed their nature to faunas previously resident in the region, or to immigration from comparable, higher, or lower paleolatitudes. In addition, it would be well to assess the prevailing climate for shallow-water benthos and allow for climatic shifts and their effect on biota. In the meantime, a simplestic summary is provided, in Fig. 379.

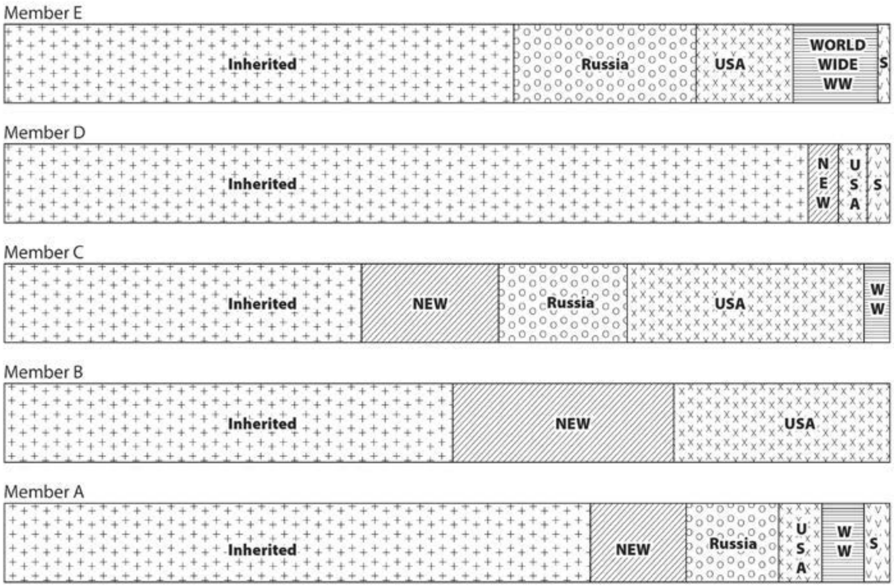


Fig. 379. The percentage of faunal components according to paleogeographic affinity for members in the lower Jungle Creek Formation. A very small component s displays southerly links, and a few with WW links elsewhere.

Member A

Faunas from Member A are highly diverse, with a preponderance of Russian and Arctic affinities, and a substantial but lesser number of components from the United States. The amount of inherited fauna is high. There is only one apparent component from the southern paleohemisphere, ie. Gondwana, in the form of *Yukonalosia*, but the origin of the genus is far from certain. Given age-ranges and distributions, this would appear to have originated not from the deep south of east Australia, but from a United States lineage, that later spread to Gondwana, although there may be an argument in favour of convergent evolution. Even though genera such as *Protoanidanthus* may imply Gondwanan links, this genus seems to have originated in the northern hemisphere.

To put percentage affinities on the brachiopod genera can only be at a generalized level, because world coverage is incomplete, and the source of genera new to the succession is therefore uncertain. The total inherited fauna approaches 60%, to judge from the presence in Member A of brachiopods congeneric with species from the underlying Ettrain Formation. New genera involve *Nassichukia, Inflatusia, Tubersulculus, Sarytchevinella, Forticosta* and *Nahoniella*. All may have first arisen from Canadian forms, amounting to almost 10%, although *Nahoniella* could have sourced from northeast Russian faunas*. Septospirifer* is another possible addition. The genera *Callaiapsida, Ala, Spiriferinaella, Tegulispirifer* and *Tumarinia* have Russian allies, but even given the possible addition of *Nahoniella*, the total would be at close to 10%, less than the percentage in some of the overlying faunas. Firm links with United States involve *Chelononia, Heteralosia* and probably *Praeschrenkiella* (given the presence of several related genera in the American mid-west), and *Nassichukia* should possibly be included, but the total is probably at the very most 6-10%. A few genera such as *Composita, Spiriferellina* and *Dielasma* were so widespread that their origins remain vague, and there can be little certainty about the sources for *Sulcirugaria* and *Yukonalosia*. They show links with genera from Gondwana, but seem likely to have originated from northern hemisphere sources.

Member B

Few species are preserved in Member B, though elements are more strongly affiliated to overlying Permian rather than underlying Carboniferous faunas. The species include *Komiella*, *Kochiproductus, Calliprotonia*, and *Commarginalia*, clearly inherited from local and earlier (Ettrain) faunas, as well as *Fimbrininia*: known in beds as old as Moscovian in northeast Russia. *Ogilviecoelia* and *Nahoniella* are new, though likely to have had links to Russia. *Anemonaria* and *Eridmatina* have possible links with the United States, although it could well be that *Anemonaria* will prove to have Arctic origins. Reducing these occurrences to percentages can only have low value, given ambiguities and uncertainties, and the low amount of data.

Member C

Brachiopods from Member C are moderately strong in affinities and links to contemporaneous faunas in the Arctic and Russia, with such well known forms as *Tuberculatella*, *Kochiproductus, Juresania, Tubersulculus,* and the distinctive genus *Plicatospiriferella,* shared especially with faunas of north Verchoyan. *Kochiproductus* appears related to Pennsylvanian members of Spinifronsinae in the United States. There is a substantial component with links to southern and eastern United States, involving *Dutroproductus, Villaconcha* and *Juresania*, and *Kochiproductus*, *Lineacrassus* and *Schrenkiella* seem likely to have origins from United States faunas. The component of what have been newly derived or locally inherited fauna is high, with *Arctitreta*, *Meristorygma* and *Ettrainia* having possibly arisen in Arctic Canada, including Yukon Territory, as well as *Rhynchopora grigorieva*. Some of these genera range more widely, but as they found in the Arctic, Russia or United States, those areas are regarded as offering their prime link. One species of *Tuberculatella* is compared with *T. boulei* (Kozlowski), originally described from Bolivia, then likely to have paleotropical. There are ambiguities, but it appears that relationships to southern United States were higher than usual, with a possible 25% of genera, and a reduction in Russia affinities ranging from 5% up to an unlikely 15%. Counting *Plicatospiriferella* as of Russian origin is feasible, but it seems likely that the genus originated in Canada. Forms with world or indeterminate affinities were few, and new forms, including with far northern Canada, possibly as high as 12%. That leaves an unusually low inherited component, perhaps as low as 40%.

In addition, there is the curious occurrence of *Tethysiella* immediately above the *Kochiproductus* *imperiosus* Zone, in upper Member C. This genus is elsewhere found in the North Caucasus, with paleotropical connotations, and so supports the contention that the member saw an influx of warm-water genera from the south.

Member D

Member D with its dolomite is regarded as having been unfavourable for fossil preservation and probably habitation. On the whole, links are shared with those of the overlying Member E, and a number of new species first appeared in this fauna, including *Fimbrininia spinosa, Waagenoconcha irginaeformis, Kochiproductus porrectus, Calliprotonia mclareni,* some possibly imported from the Arctic and Russia, but equally likely to have evolved locally. Ties with the southern and mid-United States involve *Mirandifera wolfcampensis* and *Eridmatina*, but this latter genus appeared first in older faunas of the Yukon. *Waagenoconcha irginaeformis* (Stepanov) may have been imported from Russia, but the genus was present in older faunas in the Yukon Territory. *Fimbrininia* also has ties with northeast Russia, but again the genus was present in older Canadan faunas. Apart from a few indefinite species and genera, of uncertain origin, the bulk of the species and genera appears to have been inherited from earlier faunas, making up about 90% of the total. A few species are newly evolved, including *Echinalosia minuta* and *Calliprotonia mclareni, Echinalosia* is a genus of obscure origin. It is best known from Sakmarian and younger faunas in east Australia and New Zealand, yet is present in Early Permian (Asselian) faunas of Canada, and there were potential forebears in United States.

Member E

Like Member A, Member E has rich faunas, and Arctic and Russian links are strong. A small component is exceptional, particularly *Yanzaria*, found elsewhere in Early Carboniferous faunas of Kashmir, India. Species and genera with wide-ranging affinities involve *Dielasma, Cleiothyridina* and *Composita*. All three genera are found in older faunas, but specific affinities for two indicate distant links. Ties with mid- and eastern United States are comparatively few, involving *Eumetria* sp., *Cryptacanthia* sp. and *Thamnosia*, as a distinct species *T*. cf. *spinosa*. Links with Russia, especially northeast Russia, are stronger, involving a few shared (or inherited) species such as *Lissosia alatus* (Stuckenberg), *Waagenoconcha irginaeformis*, *Cleiothyridina gzheliensis* Grunt (the latter two both persisting from Member D), and *Stenoscisma mutabilis* (Tschernyschew), and genera such as *Komiella, Jakutoproductus, Fimbrininia, Balkhasheconcha*, taeniothaerin, and *Neospirifer.* These are reinforced by a few species shared with Oregon in the western United States, with faunas close to those of the Arctic, and possibly locally evolved species and genera shared with the Yukon Territory, such as *Rhynchopora grigorieva* n. sp. The Arctic or Russian-Arctic component of newly introduced genera and species makes up barely 15% , the mid and southern United States component 7-10%, world-wide component 7-10%, the Gondwana element 2 to an unlikely 5% of the total number of brachiopod taxa in Member E, including an exceptional Gondwanan tie through *Yanzaria*. The remainder of the fauna is inherited from earlier Yukon-based faunas, involving identical and mainly newly evolved species, that make up half of the fauna in terms of number of taxa.

Significance of paleogeographic charts

In naming *Shuzhongia* from Xizang, Waterhouse (2013) pointed out that the fine spines pointed to affinities with northern faunas. Shen in Shen et al. (2017, p. 731) objected, claiming that Xizang Permian faunas were all peri-Gondwanan in their affinities. That is not correct. As shown here, although faunas have predominant affinities, faunas are complex and subtle, with unexpected ties, and should not be homogenized and generalized, let alone identified according to alleged paleogeographic affinities.

APPENDIX 1: ON GENERA AND SPECIES FROM BEYOND THE OGILVIE MOUNTAINS OF YUKON TERRITORY

PHYLUM BRACHIOPODA

Superfamily **OVERTONIOIDEA** Muir-Wood & Cooper, 1960

Family **OVERTONIIDAE** Muir-Wood & Cooper, 1960

Subfamily **OVERTONIINAE** Muir-Wood & Cooper, 1960

Genus ***Fimbrinusia*** Waterhouse, 2013

2013 *Fimbrinusia* Waterhouse, p. 54.

Diagnosis: Distinguished by lack of spines from dorsal valve.

Type species: ?*Fimbrinia borealis* Carter & Poletaev, 1998, p. 123 from Hare Fiord Formation (Bashkirian-Moscovian) of Ellesmere Island, Canada, OD.

Discussion: This genus is highly distinctive, and was discovered in distinctive beds informally named by Bonham-Carter (1966). The ventral valve is like that of *Fimbrininia* Waterhouse, 2013 in having prominent commarginal rugae, each bearing rotund spine bases along its crest, whereas the dorsal valve lacks the fine erect spines typical of *Fimbrininia* and *Fimbrinia* Cooper, 1972. The internal details are not known for *Fimbrinusia*, but the exterior is so close to *Fimbrininia* that it seems doubtful whether there are any unexpected attributes. One minor point: Carter & Poletaev stated that dimples were absent from the dorsal valve, but they are illustrated as being present in Carter & Poletaev (1998, Fig. 641-643).

Superfamily **PRODUCTOIDEA** Gray, 1840

Family **BUXTONIIDAE** Muir-Wood & Cooper, 1960

Subfamily **BUXTONIINAE** Muir-Wood & Cooper, 1960

Tribe **SPINIFRONSINI** Waterhouse, 1981

Genus ***Kochiproductus*** Dunbar, 1955

Kochiproductus freboldi? Stepanov, 1937a

Fig. 380

1916a, b *Productus porrectus* [not Kutorga] – Tschernyschew & Stepanov, p. 41, pl. 5, pl. 8, fig. 5.
?1937a *Productus* (*Buxtonia*) *freboldi* Stepanov, p. 122, pl. 2, fig. 4.
1960 *Kochiproductus freboldi* [not Stepanov] – Harker & Thorsteinsson, p. 59, pl. 17, fig. 5, 6.
cf. 1964 *K. porrectus* [not Kutorga] – Gobbett, p. 80, pl. 7, fig. 1-3.
1970 *K. freboldi* [not Stepanov] – Bamber & Copeland, pl. 14, fig. 16.
2008 *K.* cf. *K. plexicostatus* [not Dunbar] – Angiolini & Long, p. 91, Fig. 4G.

Diagnosis: Large little inflated shells with shallow sulcus and low fold, closely spaced ribs and prominent nodes each bearing a spine.

Holotype: Specimen figured by Stepanov (1937a, pl. 1, fig. 4) from Spitsbergen, by monotypy.

Description: This discussion centres on aspects of a species referred in recent years to *Kochiproductus freboldi* Stepanov, and its relationship to Canadian material recorded from the Assistance Formation (Roadian), Grinnell Peninsula, Devon Island, Canadian Arctic, by Harker & Thorsteinsson (1960). A specimen figured herein from the Assistance Formation measures 94mm wide (allowing for asymmetry due to breakage), 74mm long and 31mm high.

The umbo is incurved over the hinge-line, and is broad with angle of 90º, and umbonal walls moderately steep, diverging forward at close to 80º, and the hinge is wide, though slightly narrower than maximum width which lies close to mid-length. The umbonal extremities are obtuse, with no prominent ears, but it is possible that the latest growth phases have not been preserved, for there is virtually no trail, other than a short geniculation preserved on one side of the holotype. A well-formed sulcus traverses the ventral valve, commencing at the umbonal tip, with an angle of 30º. The ventral valve is only moderately inflated, whereas the dorsal valve is almost flat, apart from the median fold, which is very low posteriorly, and well formed in front with narrow gently rounded crest. Though little of the trail is preserved, it is likely from the juxtaposition of the two valves that it was not well extended. The ventral valve is ornamented by sturdy ribs, five in 10mm near mid-length, the ribs becoming slightly more numerous anteriorly, up to seven in 10mm, and dorsal ribs are slightly finer, with never less than six in 10mm. On both valves the ribs show occasional branching, as a sudden rather than gradual diversion, leading to marked forks. In the specimen figured by Harker & Thorsteinsson (1960), the ribs are slightly coarser, five in 10mm anteriorly on the dorsal valve, and six in 10mm on the ventral valve. Commarginal rugae are subdued, especially over mid-valve, and slightly stronger over the posterior-lateral slopes. On the dorsal valve the rugae are compressed with slender crests. The ventral ribs swell and pinch, usually but not always over the crests of the rugae, and laterally and over parts medianly the swellings are rounded rather than elongated. Each bears a slender spine, and posteriorly in front of the hinge such swellings are crowded and small. The dorsal pattern is more reticulate, without the "bumpy ornament", and fine pits are prominent. Internally, the figured specimen of Harker & Thorsteinsson shows that ventral muscle scars form a subcentral rounded area with slender adductor scars and broad diductor impressions with slender longitudinal ridges and grooves. In the dorsal valve the median septum is very long, extending almost for the length of the dorsal disc, and narrow adductor scars at the posterior third have weak diverse ridges.

Resemblances: The Assitance Formation material is distinguished by its large size, only moderately inflated disc, slender and apparently low trail and small ears, with well developed costal swellings, and long dorsal median septum. The ventral muscle field is difficult to match in other species, because it is so seldom displayed in material so far described. Gobbett (1964, pl. 7, fig. 1-3) described broken specimens as *Kochiproductus porrectus* (Kutorga) from the Spirifer Limestone or Vøringen Member of Spitsbergen that are only moderately close, having more nodose ribs, and these also display a long dorsal median septum. Gobbett (1964, p. 80) included some material originally described as *Productus payeri* Toula (1874, pl. 4, fig. 1, 3) in possible synonymy. According to Gobbett (1964, p. 76) the taxon *payeri* includes productids allied to *Kochiproductus, Waagenoconcha*, and *Horridonia*. Dunbar (1955, p. 85) had ascribed all Toula material to *Waagenoconcha payeri* (Toula), but this was judged incorrect. The best figured specimens were those of Toula (1874, pl. 1, fig. 1, 3), and these are extant at the Natural History Museum in Vienna (Gobbett 1964, p. 76). The specimen in Toula (1874, pl. 4, fig. 2) seems likely to belong to Waagenoconchidae according to Gobbett, though included by Toula (1874) and Dunbar (1955) within *payeri*. Gobbett (1964) reported that other Toula specimens, labelled as *payeri* at the Natural History Museum in Vienna, Austria, resembled *Waagenoconcha irginae* (Stuckenberg) and *Horridonia timanicus* (Stuckenberg). No type specimen for *payeri* has yet been cited, and this is here remedied: the specimen figured by Toula (1874, pl. 4, fig. 1a, b) is here nominated as lectotype (Fig. 381). It is a large internal mould, seeming to show little of the external ornament. But Gobbett was clearly satisfied that it belonged to *Kochiproductus*, and its lateral profile conforms well with a kochiproductiform

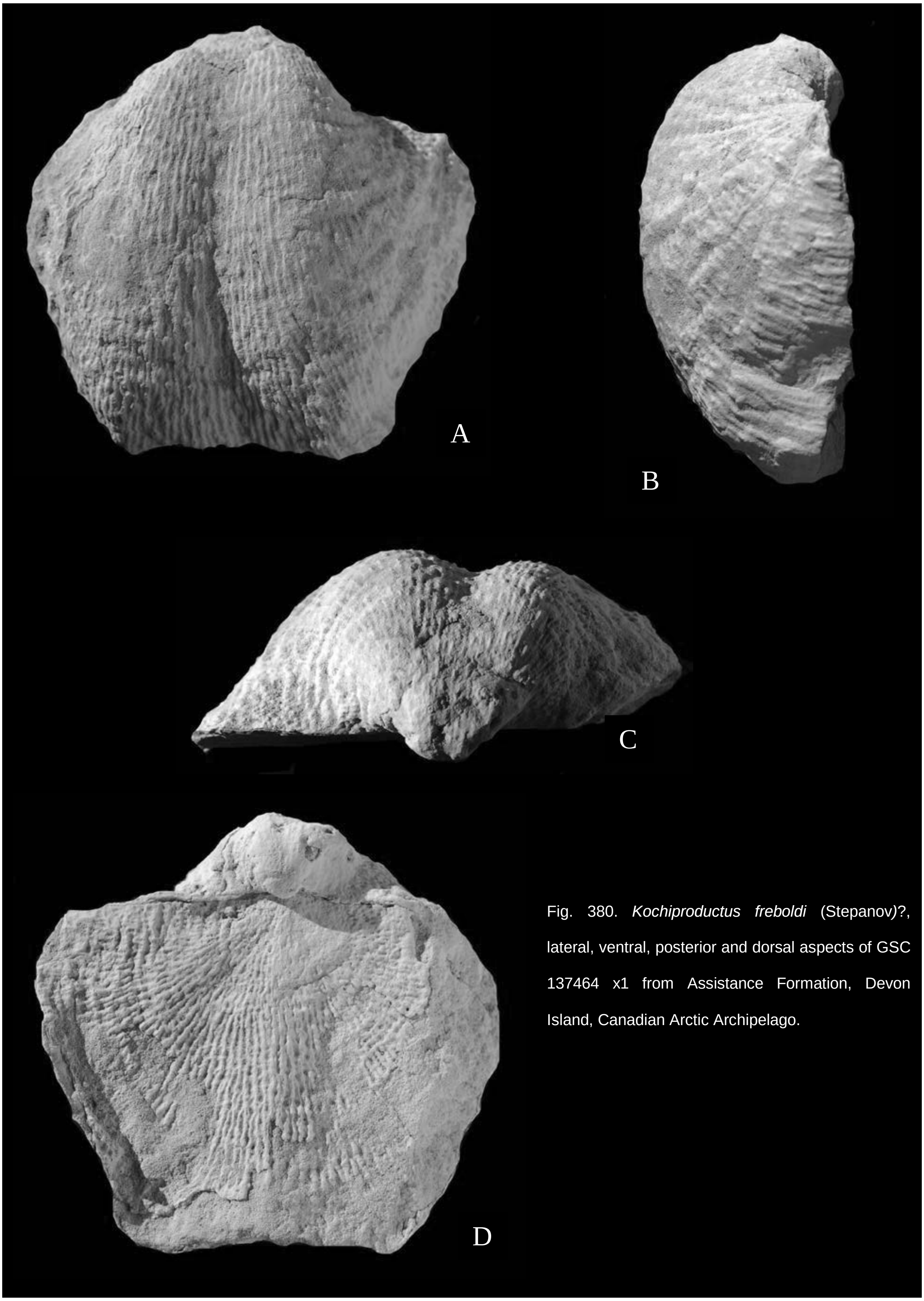


Fig. 380. *Kochiproductus freboldi* (Stepanov)?, lateral, ventral, posterior and dorsal aspects of GSC 137464 x1 from Assistance Formation, Devon Island, Canadian Arctic Archipelago.

outline, being close to that figured for example as *K. imperiosus* herein (see Fig. 72). The lateral ribs are as numerous as the lateral ribs (nine per 10mm) of the specimen from the Assistance Formation. The Toula species seems unlikely to be conspecific with the Assistance material, or with other specimens listed in the synonymy *gittinsi*, even though it comes from beds not much older than the Assistance Formation. Assuming that the figures are accurate, and that the specimen has not been deformed, it is very much more inflated, appears to have a slightly wider hinge, a more concave dorsal valve, and more elongate outline, the maximum width being rather less than the length. Moreover the ventral muscle field is smaller and much more posteriorly placed, compared with the position in *gittinsi*, as figured by Harker in Harker & Thorsteinsson (1960). Gobbett (1964, pl. 7, fig. 1-3) figured specimens from the Spirifer Limestone at Tempelfjorden as *Kochiproductus porrectus* [not Kutorga] that came from the same stratigraphic level as *payeri*, but these appear to be equidimensional, and have a largely flat dorsal valve, much as in the Assistance Formation material, and so are assigned to the same species.

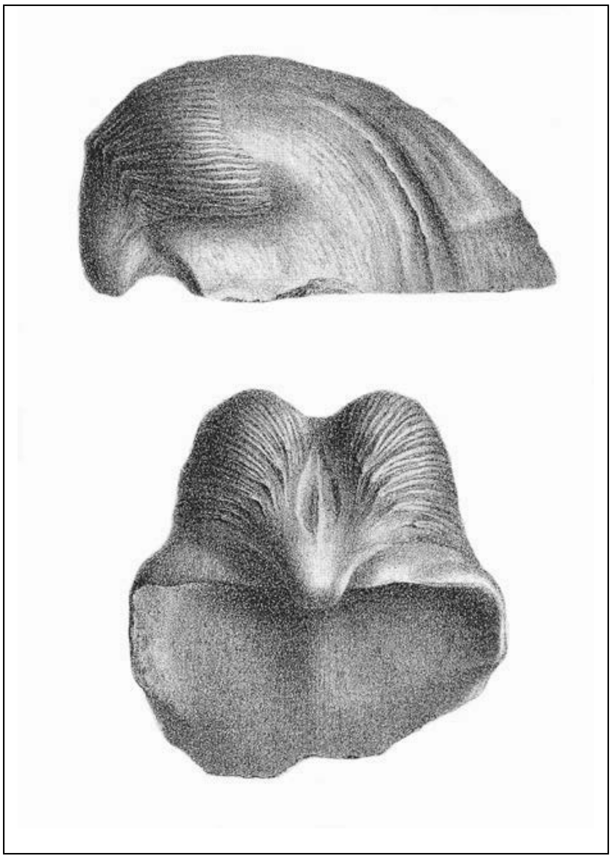


Fig. 381. *Kochiproductus payeri* (Toula), lectotype from Spirifer Limestone, Spitsbergen, as figured by Toula (1874, pl. 4, fig. 1a, 1b), x1.

Harker in Harker & Thorsteinsson (1960, pl. 17, fig. 5, 6) had allocated their Assistance Formation specimen to *Kochiproductus freboldi* (Stepanov, 1937a, pp. 122, 176, pl. 2, fig. 4) from Kapp Starotsin in Spitsbergen, together with material from east Greenland described by Frebold (1931, p. 20, pl. 1, fig. 1-3; 1942, p. 28, pl. 3, fig. 3) and Dunbar (1955, p. 109, pl. 17, fig. 1-6, pl. 18, fig. 1-6). The identification of *Productus* (*Buxtonia*) *freboldi* Stepanov with *Buxtonia* by Stepanov (1937a) and Frebold (1942) and with *Kochiproductus* by Harker is accepted tentatively, but with reservations. The figure of type *freboldi* fails to show much of the "bumpy" ornament typical of *Kochiproductus*, and the specimen shows intercalated and many branching ribs, some intercalated.

Similarly the Assistance material is not like that of *K. plexicostatus* Dunbar, which has strongly bumpy ornament and anteriorly anastomising ribs, used to discriminate a distinct subgenus *Dunbarovia* Waterhouse (2013, p. 147), as figured in Fig. 382. Gobbett (1964, p. 81) rejected the similarity of Harker's material and Stepanov's *freboldi* to *plexicostatus* Dunbar.

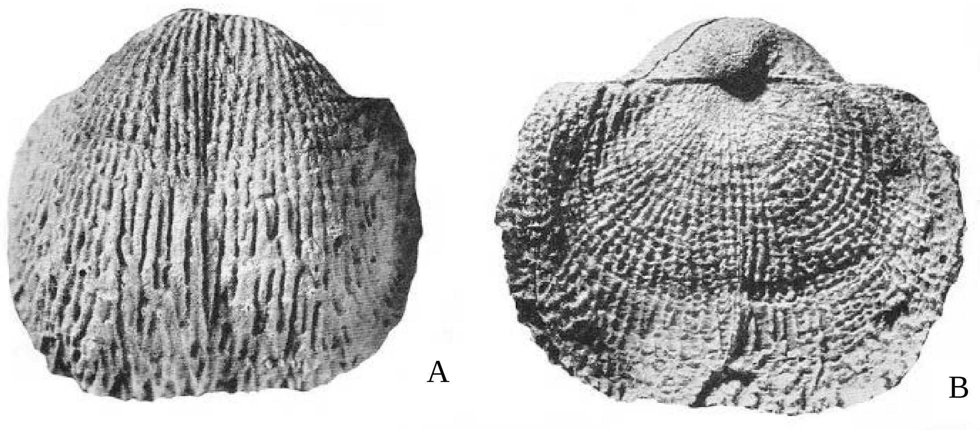


Fig. 382. *Kochiproductus* (*Dunbarovia*) *plexicostatus* Dunbar. Holotype as figured by Dunbar (1955, pl. 17, fig. 1, 2), x1. From Kap Stosch (Changhsingian), Greenland.

Gobbett (1964, p. 80) suggested that *Productus costatus* [not Sowerby] of Robert (1845, pl. 19, fig. D) might be conspecific with the material he described from the Spirifer Limestone of Spitsbergen.

Kochiproductus porrectus (Kutorga) as figured from the early Cisuralian of the Urals by Tschernyschew (1902, pl. 55, fig. 1, pl. 56, fig. 4) is close in shape and size to the present material, with more inflated disc, and more emphasized commarginal rugae. The dorsal median septum as figured by Tschernyschew (1902, pl. 32, fig. 4) is comparatively long, whereas the septum is much shorter in specimens identified with this species from the Jungle Creek Formation (see p. 108).

Superfamily **PAUCISPINIFEROIDEA** Muir-Wood & Cooper, 1960

Family **ANIDANTHIDAE** Waterhouse, 1968a

Subfamily **LIRARIINAE** Waterhouse, 2013

Genus ***Poletaevia*** n. gen.

Derivation: Named for V. I. Poletaev.

Diagnosis: Closely costate deeply concavo-convex shells, distinguished by paucity of spines along hinge row, up to two pair, may be one or two pair of spines over ventral ears.

Type species: *Liraria paucispina* Carter & Poletaev, 1998 p. 133 from lowermost Hare Fiord Formation (late Bashkirian or early Moscovian) of Ellesmere Island, Canadian Arctic Archipelago, here designated.

Discussion: Other genera assigned to Lirariinae have a full row of spines along the ventral hinge, including *Liraria* Cooper & Grant (see Cooper & Grant 1975, p. 1156), *Globiella* Muir-Wood & Cooper (see Muir-Wood & Cooper 1960, p. 304), *Cimmeriella* Archbold (see Archbold 1983, p. 250), and *Calandisa* Waterhouse & Campbell (see

Waterhouse & Campbell 2013, p. 334). These genera are all of Permian age, and all have a well formed hinge row of spines, without additional ear spines, except for *Calandisa*, which displays one to three very strong spines.

Superfamily **LINOPRODUCTOIDEA** Stehli, 1954

Family **OVATIIDAE** Lazarev, 1990

Subfamily **OVATIINAE** Lazarev, 1990

Genus ***Pumilusia*** n. gen.

Derivation: From specific name of type species, pumilus.

Diagnosis: Small arched shells with fine costellae and fine erect ventral body spines, a few erect prominent spines in two or three rows over ears. Cardinal process with deep median cleft.

Type species: *Linoproductus pumilus* Sutherland & Harlow, 1973, p. 59 from lower La Prasada Formation (late Morrowan or early Atokan), New Mexico, here designated.

Discussion: This genus is a member of Ovatiinae Lazarev, judged from size, shape and ornament, and is distinguished by the few strong and only moderately crowded spines over the ears, together with a number of body spines. *Diadematia* Waterhouse is readily distinguished by its median row of ventral spines, and *Marginovatia* Gordon & Henry has high internal median ridge, and fewer ventral hinge spines. *Arcatusia* Waterhouse has numerous ventral body spines and numerous ear spines arranged in rows, whereas *Igniculus* Waterhouse has few body spines and numerous ear spines not arranged in rows. These genera are all discussed in Waterhouse (2013, pp. 372-376). The genus that is closest to the present taxon is *Ovatia* Muir-Wood & Cooper, 1960. In this genus, ventral spines form one or two rows of numerous spines along the hinge, as well as a small group on the outer ears, and are scattered over the ventral valve and trail. Some species have body spines with an aureole. The cardinal process internally appears deeply cleft, with inconspicuous median lobe, and externally the lateral lobes unite on the external face. The new genus *Pumilusia* as figured in Sutherland & Harlow (1973, pl. 13, fig. 7-13) appears to have descended from *Ovatia*, which is slightly older, ranging from Upper Devonian to mainly Tournaisian-Visean, and perhaps Serpukhovian. The body spines are less numerous and finer in the new genus, and the ear spines are fewer, and the cardinal process somewhat similar, but the overall shape is slightly different, that of *Pumilusia* being more rounded and less elongate, with lower less narrowly and highly arched venter and trail.

Superfamily **RHYNCHOTETROIDEA** Licharew, 1956

Family **TETRACAMERIDAE** Licharew, 1956

Genus ***Yanzaria*** n. gen.

Fig. 383, 384

Derivation: From Yanzar, Kashmir, source of much of the material.

Diagnosis: Strongly plicate shells distinguished by the nature of the ventral spondylium, which is sessile posteriorly, and prolonged anteriorly as two subvertical plates continuing forward from the sides of the spondylium and attached to the floor of the valve. Low propping (supporting) plates. Septalium narrow, without propping plates.

Type species: *Camarophoria dowhatensis* Diener, 1915, p. 45 from Fenestella Shales (Visean, lower Serpukhovian) of Kashmir, India, here designated.

Discussion: Other members of the family have a large ventral spondylium that is sessile and supported by lateral propping (= buttress) plates, but unlike the present species and genus, the sides do not continue forward as stout vertical plates. (See Williams et al. 1997, p. 388). *Tetracamera* Weller, 1910 has vertical plates supporting the dorsal hinge plate, absent from the present genus, and *Rotaia* Rzhonsnitskaya, 1958 displays a complex arrangement, including inner hinge plates that partly cover the septalium. In *Rotaia*, according to Grant (1971, p. 315), the median dorsal septum does not bisect the septalium, and the ventral lateral plates do not extend as far forward as in *Septacamera*. *Yanishewskiella* Licharew, 1957, p. 139 has few coarse plicae and large spondylium supported by a low thick median septum and short propping plates. In *Yanzaria*, the lateral propping plates are short and posteriorly placed, near the hinge. In the dorsal valve of *Yanzaria*, there is a posterior cardinal plate, composed of outer hinge plates, and this is bisected by a narrow deep septalium, bearing traces of a fine median ridge or groove in some specimens, but with seamlessly concave median floor in other specimens. There are vague suggestions of a large oval impression each side of the median septum and spanning two plicae in front, but the impressions seem too large to have been muscle imprints. None of the specimens show the spikes at the anterior margin that are developed at the anterior margin in the plicae of both valves of *Septacamera*, and the plical crests are well rounded.

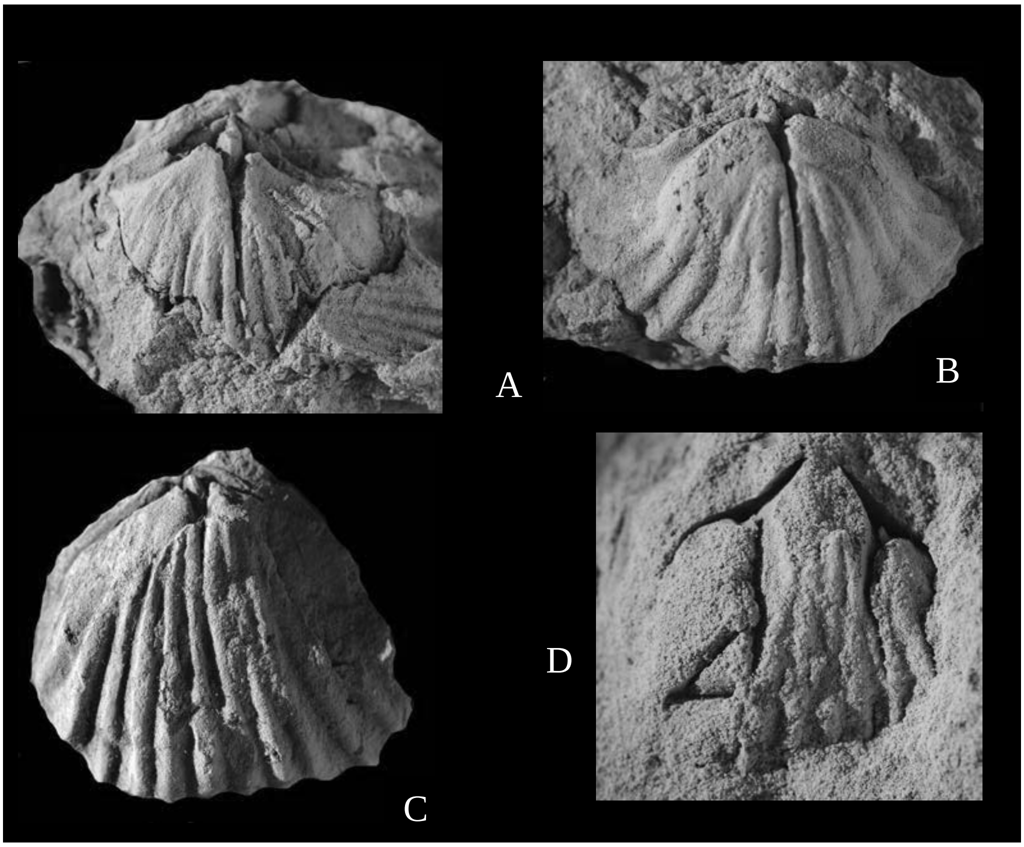


Fig. 383. *Yanzaria dowhatensis* (Diener). A, dorsal interal mould GSC 137348 x2. B, dorsal internal mould GSC 137349 x2. C, dorsal internal mould GSC 137350 x1.5. D, posterior part of ventral internal mould, GSC 137351 x2, showing spondylium and anterior plates. From Fenestella Shale, Kashmir.

Diener (1915, p. 45, pl. 5, fig. 1-4) described the type species of *Yanzaria* as *Camarophoria dowhatensis*, and this was adjusted to *Rotaia* by Waterhouse & Gupta (1977, p. 165, pl. 3, fig. 9-13; 1979, p. 130, pl. 10, fig. 10). It was suggested that *Camarophoria* n. sp. of Diener (1915, p. 46, pl. 5, fig. 6) and *C*. sp. ind. aff. *humbletonensis* [not Howse] of Diener (1915, p. 165, pl. 5, fig. 5) could prove to be conspecific. All the material came from the Fenestella Shales of Kashmir, which was evaluated as Visean-Serpukhovian in age. The species was accompanied by other species typical of the Fenestella Shales, and in Nepal the same fauna includes very large chonetids, typical of Serpukhovian faunas. In addition, Bion & Middlemiss (1928, pp. 20, 39ff) recorded the species from what supposed to have been lower Agglomeratic Slate of Asselian age in the Marbal Valley and Ruyil Valley of Kashmir. If correct, that would bring the known range of the genus in Kashmir more into harmony with the Canadian occurrence.

Fig. 384. *Yanzaria dowhatensis* (Diener), dorsal interal mould GSC 137348 x3. From Fenestella Shale, Kashmir.

Superfamily **RETZIOIDEA** Waagen, 1883

Family **RETZIIDAE** Waagen, 1883

Subfamily **HUSTEDIINAE** Grunt, 1986

Genus ***Stataria*** n. gen.

Derivation: statarius – standing fast, Lat.

Diagnosis: Numerous costae and elliptical outline, with no median ventral gutter or sulcus. Labiate foramen.

Type species: *Hustedia stataria* Cooper & Grant, 1976b, p. 2800 from Cathedral Mountain Formation (Kungurian), Texas, United States, here designated.

Discussion: This genus is very close to *Hustedia*, but has more numerous and less robust costae, eighteen to twenty or more as a rule (Cooper & Grant 1976b, pl. 741, fig. 41-59), compared with less than ten for most species assigned to *Hustedia*, and only a few more in exceptional species. The ventral sulcus in *Stataria* is replaced by a costal interspace no different from that between other costae, and a narrow median costa replaces the fold, close to the arrangement seen in typical *Hustedia*. The ribs are broader and flatter on the internal side of the shell, (as in *Eumetria*), and show no sign of inner striae like those seen in many *Hustedia*. Internally, the jugum is like that normal for *Hustedia*, without the strong supporting lamellae that typify *Eumetria* Hall, even though there is a degree of external similarity.

Uncinella Waagen looks similar externally, but has a labiate foramen unlike the mesothyrid, submesothyrid to permesothyrid foramen typical of *Stataria* and other Hustedinae. The type species of *Uncinella* has been clarified by Grant (1976, pp. 194, 195, pl. 52, fig. 35-38). The nature of the brachidia remains obscure for this genus, and placement in the athyrioid subfamily Misoliinae Dagys, 1996, Family Diplospirellidae Schuchert, 1894, by Alvarez &

Rong (2002), may be treated as yet to be fully confirmed. One unusual aspect of the present form is that punctae seem to be lacking, which is a feature of Misoliinae, but this was deemed to reflect an accident of preservation by Cooper & Grant (1976b). See also p. 466, The last word.

Genus ***Latisulcus*** n. gen.

Derivation: late – broad; sulcus – furrow, lat.

Diagnosis: Distinguished from *Hustedia* by presence of two depressed ribs medianly on ventral valve to suggest plicate sulcus.

Type species: *Hustedia hessensis* King, 1931, p. 125 from Bone Spring Formation (Sakmarian), Texas, here designated.

Discussion: The ventral valve in most species hitherto assigned to *Hustedia* displays two sturdy ribs, one each side of the mid-line, separated by an interspace, and grading laterally into slightly weaker and slightly lower ribs. But in *H. hessensis*, as well illustrated by King (1931, pl. 42, fig. 44-46 [not fig. 43]), the two median ribs are lower than the next pair, and so form what looks like a sulcus with two ribs, in contrast to the arrangement of a simple narrow median sulcus with no ribs that is normal for *Hustedia*. In the dorsal valve of *Latisulcus*, the median rib is at the same height as the lateral ribs, so as to give the appearance of a weak diminution of convexity or even shallow sulcus, whereas in *Hustedia*, the median rib varies between high or very low (as in *H. trifida* n. sp. on p. 305). Further material of *hessensis* has been figured by Cooper & Grant (1976b, p. 2784, pl. 732, fig. 86-90, pl. 736, fig. 1-36, pl. 745, fig. 1-10) from the Skinner Ranch Formation and Cibolo Formation as well as Bone Spring Formation.

A few other species ascribed to *Hustedia* are somewhat similar. *H. glomerosa* Cooper & Grant (1976b, pl. 735, fig. 87-108, pl. 736, fig. 61-69) from the Bone Spring Formation appears to be related. The same feature reappeared in two subspecies ascribed to *H. pugilla* by Cooper & Grant from the Appel Ranch and China Tank Members of the Word Formation of Texas, but in these the median dorsal rib is high. The taxa involve *H. pugilla hebetata* Cooper & Grant (1976b, pl. 738, fig. 24-34) and *H. pugilla nasiterna* Cooper & Grant (1976b, pl. 738, fig. 35-68). That opens up questions on their relationship to *H. pugilla pugilla*, and the possibility that the morphological change recurred in unrelated stock, or that interrelationships between forms assigned to *pugilla* have been misinterpreted.

Superfamily **MARTINIOIDEA** Waagen, 1883

Family **MARTINIIDAE** Waagen, 1883

Subfamily **MARTINIINAE** Waagen, 1883

Genus ***Mirandifera*** n. gen.

Derivation: Named for type species specifically called miranda, with -ifera appended as ending of Spirifer.

Diagnosis: Narrow subrounded to subpentagonal shells with extended posterior walls, and comparatively well inflated dorsal valve, only slightly less swollen than ventral valve. Mantle canals weakly ramnifying to subreticulate. Micro-ornament of growth lines, and prismatic surface in worn material; allied Canadian shell with shallow exopunctate.

Type species: *Martinia miranda* Cooper & Grant, 1976a, p. 2268 from Cathedral Mountain Formation (Kungurian), Texas, here designated.

Discussion: Several species described as *Martinia* by Cooper & Grant (1976a) from the Glass Mountains Permian of Texas are shaped like *Tiramnia* Grunt, 1977, but have more inflated dorsal valves. *Tiramnia* is based on *Martinia uralica* Tschernyschew, 1902, p. 183, from the early Cisuralian of Urals, Russia, and involves narrow subrounded to subpentagonal shells with extended posterior walls, and weakly ramnifying mantle canals. There do not appear to be any dental plates in the type species of *Mirandifera*, to judge from text and figures in Cooper & Grant (1975a), whereas *Tiramnia* does have dental plates, as described and illustrated by Grunt. Aspects of *Tiramnia* remain obscure, including micro-ornament, and knowledge of the full extent of variation in the pattern of mantle canals. The mantle canals of *Martinia* M'Coy consist as a rule of well spaced straight canals diverging forward. Those of *Tiramnia* commence closer together and fan out and forwards, but for the most part are not branching or convergent. The mantle canal patterns of various Texan specimens described by Cooper & Grant (1976a) are comparatively close to those of type *Tiramnia*, but in some specimens (see Cooper & Grant 1976a, pl. 645, fig. 22) the canal pattern is more complex. It is believed that this indicates a degree of natural variation, probably with increased maturity, to judge from the better known array of variation in related genera such as *Spinomartinia* in both New Zealand and Queensland (see Waterhouse 1968b, 1987a).

Certain species from the Permian of northern Canada and Texas are notably less transverse than type *Martinia* and close to *Tiramnia* in shape, but they differ in the much greater inflation of the dorsal valve, and have a more complex mantle canal system than in *Martinia*, and lack well developed dental plates. The difference in relative height of the two valves remains as a significant difference from Russian species described as *Tiramnia* by Grunt (1977). Interestingly, *Tiramnia walteri* Carter & Poletaev, 1998 has a dorsal valve of low inflation, whereas a co-extensive species. *T. grunti* Carter & Poletaev, 1998 has a moderately inflated dorsal valve and so approaches *Mirandifera*. Internal detail was not revealed. Both occur in the lower Hare Fiord Formation, of late Bashkirian or early Moscovian age on Ellesmere Island of Canada.

Superfamily **SPIRIFERELLOIDEA** Waterhouse, 1968

Family **SPIRIFERELLIDAE** Waterhouse, 1968

Subfamily **SPIRIFERELLINAE** Waterhouse, 1968

Genus ***Eridmatina*** n. gen.

Derivation: From allied genus name Eridmatus.

Diagnosis: Small to medium size, hinge wide and may be alate, anterior margins less produced than in *Eridmatus* Branson. Fold may flare anteriorly, and surface pustules comparatively few as in *Eridmatus*.

Type species: *Eridmatus marathonensis* Cooper & Grant, 1976a, p. 2220 from Gaptank Formation, *Uddenites*-bearing Shale Member (Gzhelian), United States, here designated.

Discussion: This genus is very close to *Eridmatus* Branson, 1966 from the mid-Pennsylvanian of United States, sharing the wide hinge, the flaring anterior fold and sulcus, shallow groove along the fold, and rather sparse surface pustules, but differs in shape, with much narrower anterior shell, whereas that of *Eridmatus* is often as wide as or wider than the hinge. Shells of *Eridmatus* have a much broader base to the subpentagonal outline, compared with those of *Eridmatina*.

Spiriferella ploskajae Zavodowsky, 1970, p. 165, pl. 33, fig. 6-9 from the Gzhelian Paren Horizon of northeast Russia shows some approach, but is more likely a member of *Spiriferella*.

Superfamily **AMBOCOELIOIDEA** George, 1931

Family **AMBOCOELIIDAE** George, 1931

Subfamily **ATTENUOCURVINAE** Waterhouse, 2016

Tribe **ATTENUOCURVINI** Waterhouse, 2016

Genus ***Heella*** n. gen.

Derivation: Named for He Weihong.

Diagnosis: Elongate ventral umbonal region, well developed ventral interarea, long adductor scars, dorsal valve weakly convex posteriorly and almost flat or weakly sulcate medianly. No ventral plates, trilobite cardinal process, crural plates and tabellae well developed, nature of spire not known. Distinguished primarily by development of commargons over both valves, bearing fine erect spines that vary somewhat in diameter, larger spines about as twice as wide as narrower spines, and each set aligned in growth rows.

Type species: *Attenuatella mengi* He, Shi, Feng & Peng, 2007, p. 276 from late Changhsingian of South China, here designated.

Discussion: This genus is readily distinguished from *Attenuatella* Stehli, 1954 in its micro-ornament of spines in bands bordered by lamellae and growth pauses that form commargons. In *Attenuatella* there are no commargons, and spines are mostly fine, with a number of much broader spines, as figured by Cooper & Grant (1976b, pl. 745, fig. 68). The spines in *mengi* are fine, and vary in diameter to some degree, so that the ornament looks somewhat like that of the productid genera *Calliprotonia* Muir-Wood & Cooper and *Echinaria* Muir-Wood & Cooper (see pp. 122, 132 herein). The new genus is close internally in its muscle scars and dorsal plates to *Attenuocurvus* Waterhouse, 2010, but this genus lacks commargons, and its spines are uniformly fine and aligned along growth lines, without commargons. (See Waterhouse 1964, pl. 20, fig. 1, 2, 5, 10, 11 for figures of the ornament in the type species). *Biconvexiella* Waterhouse, 1983c has ornament close to that of *Attenuatella* with mostly fine spines, and scattered much larger spines (see Armstrong 1968, pl. 142). The shape is different, involving a less inflated ventral valve and more convex dorsal valve, and different muscle impressions. The spire in all three of these genera is truncated (Waterhouse 1964, text-fig. 48A, B; Armstrong 1968; Cooper & Grant 1976b, pl. 745, fig. 67), but the nature of the spire has not been determined for *mengi*.

Superfamily **HETEROPECTENOIDEA** Beurlen, 1954

Family **LIMIPECTENIDAE** Newell & Boyd, 1990

Subfamily **ACANTHOPECTENINAE** Newell & Boyd, 1995

Genus ***Meekopecten*** n. gen.

Derivation: Named for F. B. Meek.

Diagnosis: Left valve plicae moderate in number with narrow crests and subdued growth laminae pointing anteriorly in the interspaces. No median keel along the crests of the plicae. Right valve with slender ribs separated by wide concave interspaces.

Type species: *Acanthopecten meeki* Newel (1938, p. 73, pl. 12, fig. 1-5) from the Upper Carboniferous Stanton

Formation of Kansas, United States, here designated.

Discussion: Genus *Acanthopecten* Girty, 1903, based on *Pecten carboniferus* Stevens, 1858 from Missourian of Illinois, United States, is typified by the presence of a slender keel passing along the crest of each left valve plication (see Newell 1938, pl. 12, fig. 8, 9), whereas a number of species from the United States, such as *meeki* Newell, *coloradensis* Newberry, *delawarensis* Girty, and *laqueatus* Girty, have comparable left valve plicae, but no median keel. These species are deemed to belong to *Meekopecten*.

APPENDIX 2: IMPLICATIONS FOR WORLD PERMIAN FAUNAS

Study of brachiopods from Carboniferous-Permian boundary beds in the Ogilvie Mountains points to the development of several lineages in the Late Carboniferous that in the Early Permian became prominent in the Gondwana faunas of Australia and New Zealand. These include the strophalosioid genera *Echinalosia* and members of Dasyalosiinae (*Pseudostrophalosia, Maxwellosia*), preceeded by *Echinalosia* and *Yukonalosia* in Canada. That is reinforced by the Carboniferous appearance of *Geothomasia* in earliest Permian of Canada, preceeded by late Carboniferous occurrences in northeast Siberia. A tribe Taeniothaerini that first appeared in the Sakmarian of Gondwana, and especially Australia, is found in basal Permian deposits of Canada. *Protoanidanthus* was the first member of Anidanthidae, appearing in Late Carboniferous of northeast Russia and Canada, evolved into Megousiini in the northern paleohemisphere, and penetrated east Australia in Early Permian time, where it diversified into several genera of Anidanthinae. A coolkilellin marked the first appearance of a subfamily later widely dispersed in Permian deposits, especially Western Australia, and the oldest member of Lirariinae is represented by *Poletaevia* in the late Bashkirian or early Moscovian Hare Fiord Formation of Ellesmere Island in the Canadian Arctic. Members of Compressproductinae also to appear to have first appeared in the Late Carboniferous of Canada, before more widespread Permian occurrences. *Compressoductus* is possibly present, as well as the earliest known species of *Sarytchevinella*. Northwest Canada therefore appears to been a fertile breeding ground for the development of new genera, especially amongst members of Linproductidina, with conditions highly favourable for Productida, and enhanced by the position between Russia with the Arctic on the one hand, and United States on the other, and apparently a number of the genera later penetrated and flourished in high southern paleolatitudes.

THE LAST WORD

The present study is based on material from numerous collections made over a small area, but there remain a number of taxa so imperfectly known that as author I would long to revisit and collect more material. There are only tantalizing glimpses of some of the more intriguing species, such as the specimens recorded as Coolkilellin sp. and *Sarychevinella praecursor*, not to mention *Tethysiella impudens*, and especially the fragment here tentatively assigned to Retziid? gen. & sp. indet. I still wonder about its possible relationship to Misoliinae Dagys, in view of the subrounded rather than subtriangular shape, and the apparent present of tiny pustules figured for *Uncinella* by Grant (1976, pl. 52, fig. 25), approaching those of the fragment from the Ogilvie Mountains. These taxa are mentioned because of their implications for evolution and distribution – of course there are many other taxa which need to be reinforced by further material.

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ILLUSTRATIONS OF LANDSCAPE AND STRATIGRAPHY

Fig. 385. The Ettrain Formation, viewed across the valley with glacial detritus shown in Shi & Waterhouse (1996, Fig. 4).

Fig. 386. Jungle Creek Formation north of a tributary of Ettrain Creek and west of the type Ettrain Formation, with overturning of beds. The layers have been picked out by hail from a heavy storm.

Fig. 387. Two views of Ettrain Formation thrust over Jungle Creek Formation, north of Fig. 385. The thrust is shown in the map by Waterhouse & Waddington (1982, Fig. 6).

Fig. 388. The southern area, exposing lower Jungle Creek Formation to left, with Member A, and saddle with Members B to Member E, followed by Member F in the hill to right. Member F extends from the crest to the base of the steep slope.

Fig. 389. Members E and D of Jungle Creek Formation, with Member F in background, occupying the face of the hill downslope to the hillock above E. Member A in foreground. Looking west across same features as in Fig. 388.

INDEX TO GENERA AND SPECIES mentioned in the text

Page numbers in bold refer to systematic descriptions for species

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