PERMIAN BRACHIOPODS

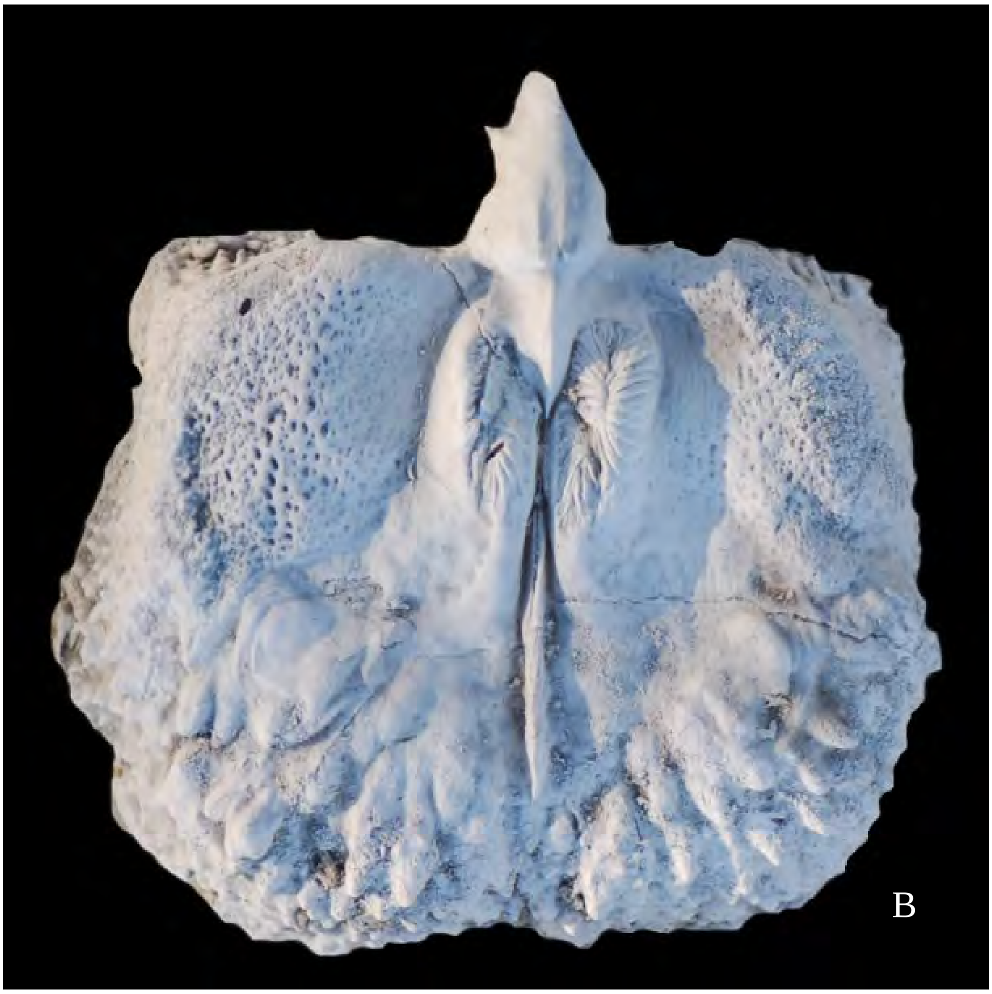
(UPPER ARTINSKIAN TO WORDIAN)

FROM THE CANADIAN ARCTIC

J.B Waterhouse

Earthwise 17

Wimanoconcha feildeni (Etheridge)



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Abstract

Brachiopods of late Cisuralian (Artinskian, Kungurian) and Guadalupian (Roadian, Wordian) and one of late Lopingian age are described for more than one hundred and forty species for faunas mostly from the extended Takhandit Formation and unnamed Permian beds of the Richardson Mountains in the Yukon Territory and Mackenzie district, and from the Great Bear Cape, Sabine Bay, Assistance, Trold Fiord, Van Hauen, Degerböls and lower Blind Fiord Formations of the Sverdrup Basin in the Canadian Arctic Archipelago, as well as a few from further afield, including Greenland, Spitsbergen, United States (Oregon), northeast Russia and Greece. The Canadian brachiopods are strong especially in links with faunas of Spitsbergen and northern Russia, display limited ties with faunas of Idaho, Wyoming and Texas, and include some genera that suggest affinities with those of Gondwana in east Australia and New Zealand, as well as a scattering of other ties. Forty five new species are described, and the nature of some early species named in the nineteenth century from the Canadian Arctic is clarified. Several new genera and subgenera are erected, *Fissulina delicatula* n. gen., n. sp. for an ally of *Streptorhynchus* from the Sabine Bay Formation of Axel Heiberg Island, *Gruntoconchinia payerinia* n. gen., n. sp. for a waagenoconchid from Greenland, *Liosella* n. gen., type species *Liosotella grandicosta* Dunbar, 1955 from Greenland, *Liosotellina* new subgenus of *Liosella* n. gen., with type species *Liosotellina multicostella* n. sp. from Trold Fiord Formation, Ellesmere Island, *Simplicitasia* n. gen. for *Spirifer osborni* Harker, 1960 from the Assistance Formation of Devon Island, *Undulatina* for *Spirifer keilhavii* (Toula, 1875b) from Bjørnøya, Spitsbergen, and *Sulcicostatina*, type species *S. claphami* n. sp. from Hydra, Greece. A new subtribe Anemonariainai (Anemonarinai) is proposed for *Anemonaria* Cooper & Grant, 1975 and allied genera, and Cartorhiuminae is proposed for Cartorhium Cooper & Grant, 1976a and allied genera. A new spiriferellinin tribe Arcullinaini (Arcullinini) is proposed for *Arcullina* Waterhouse, 1986a and allied genera.

Some of the Canadian species are Guadalupian survivors of genera previously thought to have been extinct by the end of the Cisuralian (Early Permian) Period.

Successive biozones are proposed for the late Cisuralian and early Guadalupian brachiopods in Arctic Canada.

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INTRODUCTION

This study covers the systematics of the brachiopods found in mostly Middle Permian rocks of Guadalupian age in the Yukon Territory and west Mackenzie district of mainland Canada, and in the Sverdrup Basin of the Canadian Arctic Archipelago, as well as a scattering of older species, and a few from other regions, including Greenland, Spitsbergen, north Russia, Oregon and Greece, where relevant to the Canadian succession. Almost all of the Canadian specimens have been collected by officers of the Geological Survey of Canada between 1950’s and 1960’s, partly under Operation Porcupine in the Yukon Territory (Norris 1997) and partly in separate expeditions to the northern Arctic islands. Attention is paid to much earlier collections made during explorations during the nineteenth century, and housed now in the National Museum of Eire, Dublin, and Natural History Museum of London, as well as an early twentieth century collection kept at the American Museum of Natural History, New York.

Arctic Permian faunas have long received attention from specialists, particularly European and Russian scientists, but those of Arctic Canada were collected in only two expeditions in the nineteenth century, as examined in Salter (1855), Haughton (1858) and Etheridge (1878). A few taxa were named in these studies, which, although they enjoyed seniority over later proposals, have largely been ignored. These are examined further. The Peary expedition to the North Pole collected brachiopods that were described by Whitfield (1908), and the Fram expedition made a substantial collection from Great Bear Cape on Ellesmere Island that was described in the first monograph to appear on Canadian Permian brachiopods, by Tschernyschew & Stepanov (1916). The first major contribution from the Geological Survey of Canada appeared with a monograph by Harker & Thorsteinsson (1960), which included extensive coverage of brachiopods from a rich fossil locality in the Assistance Formation on Devon Island. S. J. Nelson from the University of Calgary studied horridoniid and spiriferellid brachiopods of Middle Permian age from the Takhandit Formation in the Yukon Territory (eg. Nelson 1961), culminating in a study by Nelson & Johnson (1968). A collection from the Svartevarg Cliffs on Axel Heiberg Island was made and examined by Stehli & Grant (1971). At least two studies were prepared that have never been published. Alan Miller at the University of Toronto, under my supervision, studied Geological Survey collections from the Trold Fiord Formation, concluded in 1974. I have a copy of his thesis and quote from it with acknowledgement, because it was a fine work. The other was by Dr Liao Zhuoting, who was based at the Academy of Science, Nanjing. His major study on material collected by Charles Henderson, University of Calgary, Alberta, is yet to published, but Nakamura et al. (1992) in an article on brachiopods from the younger Permian of Spitsbergen were able to quote from a tabulation of species, which show refined biostratigraphic subdivisions, critical for the Trold Fiord Formation. My first study of the Middle Permian faunas appeared in 1967, and the publications are referenced where applicable throughout the text.

Regrettably the extensive Permian brachiopods of the adjoining State of Alaska have not received anything like even a modest amount of published systematic attention. Experts from the United States have in fact paid more attention to the faunas of Canada, including Whitfield (1908) and Stehli & Grant (1971), not to mention excellent studies by Carter (1975) and Carter & Poletaev (1998) on Carboniferous brachiopods from the Hare Fiord Formation of Axel Heiberg, Melville and Ellesmere Islands. Leaving aside the numerous outdated fossil lists which are no more than of limited value, a modest overview with figures and names was provided for the type Takhandit Formation in east Alaska by Brabb & Grant (1971), without detailed systematic study, and one truely systematic study on a few brachiopods has been provided by Grant (1971), which included Canadian material. That appears to be the sum total, which leaves a substantial void in our knowledge of Late Paleozoic brachiopods. The faunas may well be largely similar to those of the Yukon Territory, but faunal coverage of the Yukon has gaps, and many incompletely known fossils, and even at best, my coverage amounts to no more than a preliminary survey, which needs far more study in detail.

Fortunately, work on much of the remaining Permian faunas of the Arctic has been extensive, and often detailed, even though of course it can always be improved and refined. The faunas of east Greenland received attention from one of the great experts C. O. Dunbar (1955), in a monograph that was outstanding, partly for the excellent photography, partly for the attention paid to work in the Soviet Union, which was neglected by many contemporary workers, and indeed continues to be ignored even in some recent studies, whether from the Soviet Union or Russia. Knowledge of the faunas of Spitsbergen, under political control by Norway, has benefited by numerous specialist articles, Norwegian, Austro-Hungarian, Swedish, Polish, Russian, French, Belgium, British, Japanese, Korean and Australian. Early studies by F. N. Toula in the late nineteenth century were followed by a substantial monograph by Wiman (1914), and an even more extensive monograph by Gobbett (1964), which remains the single most outstanding overview. Even more recent articles fail to match the overall coverage in Gobbett (1964), with palpable short-comings in context and succession, and are no better than fragile in comparison, although extensive updating of Gobbett's memoir is clearly required. One critical aspect that needs to be kept in mind for future studies of the Spitsbergen Permian is that very large collections under tight stratigraphic control were made after the Gobbett study. One very detailed collection was made by Russian workers, as explained in Ustritsky (1979). The other was complied over several years by teams under the aegis of W. B. Harland and Peter Friend from Cambridge University, and is housed in the Colin Forbes Building at Maddingley Rise, Cambridge. Examination of these collections would almost certainly qualify and expand what is presently known. Dr Sangmin Lee has also made extensive collections, joined with collections by Japanese geologists, and the collections are currently now housed at Wollongong, Australia. Lee with colleagues has published specialized studies.

There is a very substantial literature on the Russian segment of the Arctic, extending from the Petchora Basin in north Russia, Novaya Zemlya, Kanin Peninsula, Taimyr Peninsula, Verchoyan and Kolyma-Omolon Basin. Publications commenced in Czarist Russia, proceeded apace under the Soviet Union, for instance by Abramov & Grigorieva (1983, 1988), and have continued as well illustrated monographs in Russian by Kalashnikov (1998), Grunt (2006a, b) and Klets (2005), with a major contribution that, whilst focused on bivalves, includes documentation on brachiopods by Biakov (2010).

The present study brings the Canadian segment up to the standards set for Greenland, Spitsbergen and Russia. Hopefully it will set the scene for much more detailed and extensive study, because much remains to be done.

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Help has been received in examining early collections made in the Canadian Archipelago and now kept at the National Museum of Eire, and in the Natural History Museum, London, with assistance from Sarah Long, Howard Brunton and Zoe Hughes,

and the American Museum of Natural History, with help from Bushra Hussaini. I also appreciate the help received from visits to institutions, including Australian Museum, Sydney; American Museum of Natural History, New York; The Natural History Museum, London; Institute of Geology, Chinese Academy of Geological Sciences, Beijing; Commonwealth Palaeontological Collections, Australian Geological Survey Organization, Canberra; Geological Survey of India, Kolkatta; Nanjing Institute of Geology & Palaeontology, Academia Sinica, Nanjing; Geological and Nuclear Sciences, Lower Hutt; Paleontological Institute, Moscow; Queensland Museum, Brisbane; Sedgwick Museum, Cambridge; Smithsonian Institution, United States National Museum, Washington D.C.; Tschernyschew Museum, St Petersburg; and National Museum of Victoria, Melbourne. This list is not exhaustive, but even so, some critical collections housed in Europe and Russia have not not seen.

OUTLINE OF STRATIGRAPHY

Takhandit Formation of Yukon Territory, Canada

The Takhandit Formation as mapped and described by Bamber in Bamber & Waterhouse (1971) and Norris (1997) is found in the headwaters of the Ogilvie and Tatonduk Rivers, where it forms prominent cliffs above the Jungle Creek Formation, and extends further north between the Ettrain and Jungle Creeks, and widely through the Yukon Territory. In the Ogilvie Mountains, the formation is made up of light to medium grey and brown-weathering fine grained spicular skeletal limestone and spicular chert, but more silt and sand of quartz and chert are found further north between Ettrain and Jungle Creeks. In the Tatonduk River, from sections 116C-1 and 116C-2 (Bamber 1972), Ross (1967) reported *Schwagerina* sp. from approximately 55ft to 120ft above the base, followed by the *Schwagerina jenkinsi* fusuline assemblage, which included *S. hyperborea* (Salter), some 180ft higher. Several brachiopod biozones were recognised in the Takhandit Formation by Waterhouse in Bamber & Waterhouse, starting with Zone Fa, now Fr, associated with *Schwagerina* sp., and Zone Fs, associated with the *S. jenkinsi* assemblage. These zones were considered to be Baigendzinian, upper Artinskian in age, correlative with the lower Leonardian of the Glass Mountains in Texas, and with the upper Belcher Channel Formation, now transferred to Great Bear Cape Formation, of the Canadian Arctic Archipelago (Harker & Thorsteinsson 1960, Beachamp & Henderson 1994). Overlying Takhandit zones were assigned to the Fps, Ft and Gc zones, and brachiopods from these zones and their correlations are discussed on pp. 388 ff. Few specimens have been available for the present study, and most have had to be interpreted from figures. Some available brachiopods come from the middle or Fps Zone, and from the topmost Gc zone, at Sheep Mountain and section 116F-9, near Jungle Creek (Bamber & Waterhouse, 1971, Fig. 6).

Brabb & Grant (1971) and Bamber & Waterhouse (1971) erred in correlating these beds and faunas with the type Takhandit Formation found some 30 miles to the west in Alaska, a unit proposed by Mertie (1930) and amended by Brabb & Grant (1971). Only the middle or Fps zone and uppermost Gc zone are found in the type Takhandit Formation. The underlying beds in Yukon Territory belong to two well defined biozones, and are distinctly older than the type Takhandit Formation, whereas the type Takhandit beds overlie Devonian. Given the recommendations in the International stratigraphic Code, and the limited value of the type Takhandit section in Alaska, and the evidence that the rocks containing the two lowermost zones are separated from overlying beds and zones by a faunal break lasting through much of the Kungurian stage, it may be prefered to propose a new name for the much more complete Yukon rocks, as displayed along the Tatonduk River and in the Ogilvie Mountains. On the other hand, it may be argued that the type section for the Takhandit Formation was not well selected, and that the name should be preserved, and applied with flexibility.

Northern Richardson Mountains, Yukon Territory, Mackenzie district

In the northern Richardson Mountains of the northern Yukon Territory, Permian rocks of comparable Guadalupian (Roadian, Wordian) age are represented by thick sandstone, shale, limestone and siltstone, yet to be formally assigned to stratigraphic units. Significant fossils are available. Brachiopods of the Fl and Gc zones (Bamber & Waterhouse, 1971, p. 87), come from the uppermost sandstone unit, over 2000ft thick. A number of the fossils have been silicified, and after extraction, are delicate, and prone to disintegration. The ammonoid *Neouddenites caurus* and brachiopods for the brachiopod zone originally designated Fn Zone have come from shale in the White Mountains to the west at sections 116P-1 and 116P-6 (Bamber & Waterhouse 1971, Fig. 2, Fig. 10).

Permian formations of the Sverdrup Basin, Canadian Arctic Archipelago

Rocks of the Sverdrup Basin have been closely studied (Fig. 1, 2) and superbly illustrated in various publications, lead by Benoit Beauchamp (eg. Beauchamp 1994, Beauchamp & Henderson 1994, Beauchamp et al. 2009), with close dating provided especially through conodont studies by Charles Henderson.

NEARSHORE DEPOSITS

YOUNGER EARLY PERMIAN:

Raanes Formation

The Raanes Formation, recognized in the early 1970's by W. W. Nassichuk and formally described by Beauchamp & Henderson (1994), consists of mainly recessive shale and a range of other lithologies, including limestone. It overlies Belcher Channel or other earlier Permian formations, and is overlain by the Great Bear Cape Formation, and partly by the Trappers Cove Formation, into which it may pass laterally.

Great Bear Cape Limestone

This formation is composed mostly of limestone that can be richly fossiliferous, and and includes fusulines. Faunas at Great Bear Cape on Ellesmere Island were classed as equivalent to what is now early Cisuralian by Tschernyschew & Stepanov (1916) and Dunbar (1955), and later the beds came to be matched lithologically with middle Permian Degerböls Limestone. But Beauchamp & Henderson (1994) showed that conodonts of upper Cisuralian age were present, and the beds are placed in a Great Bear Cape Formation, which is older than the Degerböls Formation, and judged in this report to partly match the rocks and faunas of the two basal zones in the Takhandit Formation of Yukon Territory.

Sabine Bay Formation

The Sabine Bay Formation consists of mainly non-marine sandstones and conglomerate, resting on the Great Bear Cape Formation and overlain by Assistance Formation (Tozer & Thorsteinsson 1964, Nassichuk 1965). A marine fauna was collected from outcrop exposed at Svartevarg cliffs of Axel Heiberg Island by Stehli & Grant (1971), and is considered herein to be of upper middle

Kungurian (Nevolin) age. This formation appears to be represented by a stratigraphic break, or by thin beds without faunas in the extended Takhandit Formation of Yukon Territory.

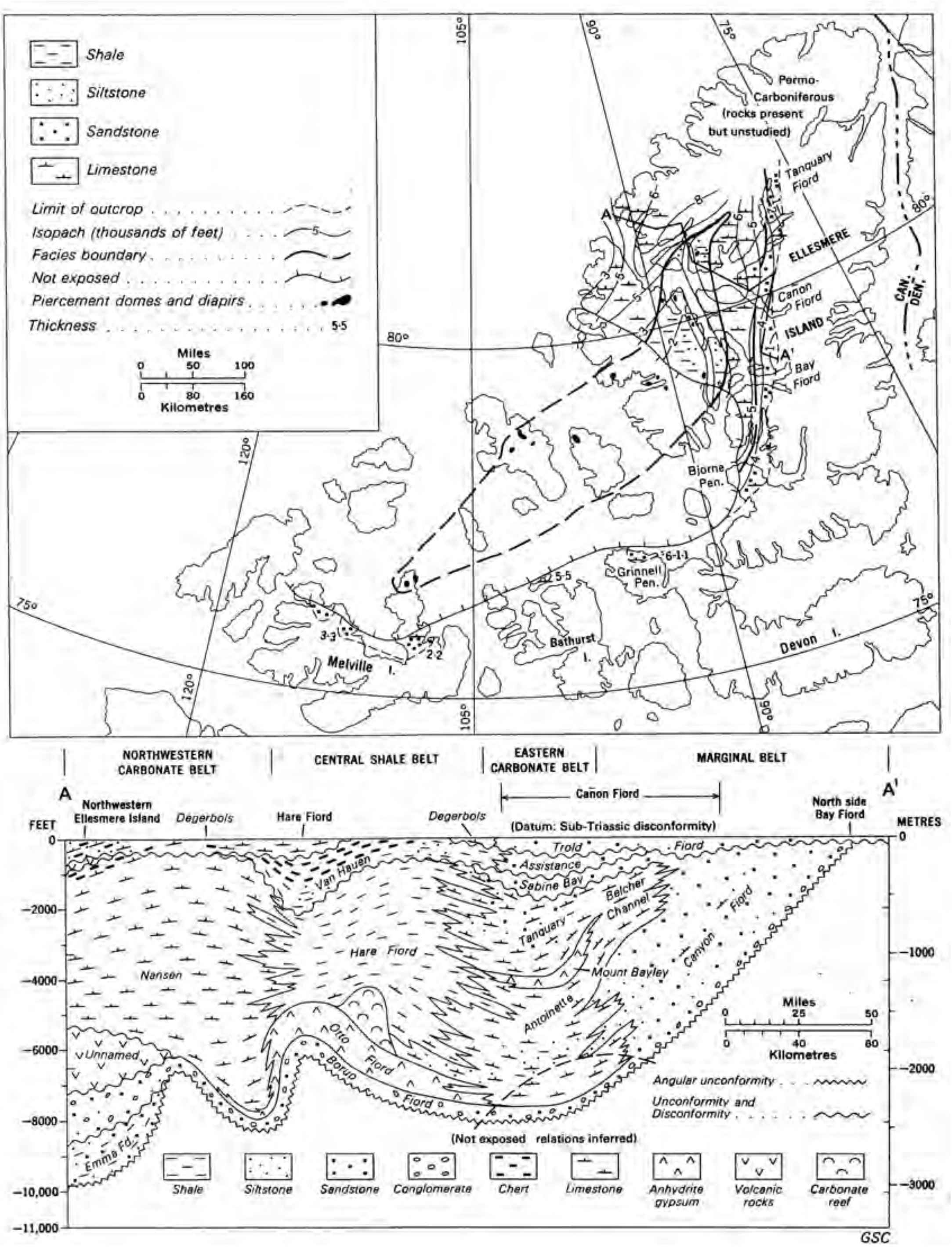

Fig. 1. The Sverdrup Basin of the Canadian Arctic, as constructed by Ray Thorsteinsson, first published in Douglas (1970, pl. x.8). See also Fig. 2, p. 14, showing an updated summary.

NEARSHORE, MIDDLE PERMIAN:

Assistance Formation

The Assistance Formation is composed mainly of grey or brown sandstone and siltstone, variably glauconitic, with numerous brachiopod fossils, and scattered ammonoids indicative of a Roadian (lower Middle Permian or Guadalupian) age. It is up to 1200ft thick, exposed along the south and eastern margins of the Sverdrup Basin, from northeast Melville Island to Greely Fiord on Ellesmere Island, and rests largely on the Sabine Bay Formation. A principal study of Assistance fossils was provided by Harker & Thorsteinsson (1960), and many more fossils are described from the formation in this report, to show that the Assistance fauna matches that of the third (middle) faunal biozone in the Takhandit Formation in the Yukon Territory, and basal beds of the type Takhandit in Alaska.

Trold Fiord Formation

The Trold Fiord Formation as proposed by Nassichuk & Christie (1969) overlies the Assistance Formation and is up to 1000ft thick, made up of glauconitic sandstone, with minor chert and limestone. The formation transgresses south and southeast, to overlie formations of earlier Permian age, and even lower Paleozoic age. Brachiopods are widespread, and many are very well preserved as complete silicified valves and conjoined specimens, especially in the lower beds. These point to a Wordian or middle Guadalupian age, as reinforced by the ammonoid *Neogeoceras* (Nassichuk et al. 1965). The faunas match those of the uppermost or fifth biozone in the Takhandit Formation of Yukon Territory.

OFFSHORE, MIDDLE PERMIAN:

Van Hauen Formation

The Van Hauen Formation is the basinal equivalent, at least in part, of the Assistance Formation, and composed of black siltstone and shale, up to almost 2500ft in thickness, and calcareous in parts. The upper part of some sections contains bedded black chert. Brachiopods largely confirm the early concept of it grading laterally into Roadian Assistance Formation (as at Bjorne Peninsula on Ellesmere Island) and further silicified brachiopods indicate a slightly younger age, correlative with faunas of the upper Roadian *Dyoros modestus* Zone and younger zones in the Yukon Territory.

Degerböls Formation

Cherty and fossiliferous limestone up to 1100ft thick makes up the Degerböls Formation, and is exposed in northern Axel Heiberg and Ellesmere Islands, above Van Hauen Formation as a rule, and judged to be largely equivalent to Trold Fiord Formation. In places the beds rest on Nansen Formation, truncating the Van Hauen beds.

LATE PERMIAN, NEARSHORE AND OFFSHORE:

Lindström, Black Stripe and Blind Fiord Formations

Late Permian conodonts have been found in formations recognized as Permian (Beauchamp et al. 2009), involving the Lindström Formation, of white spiculitic chert exposed on Ellesmere Island at the south margin of the Sverdrup Basin, dated as Wuchiapingian in age, and the Black Stripe Formation of dark to black spiculitic chert, and siliceous shale and siltstone, of Wuchiapingian and Changhsingian age, found in the centre of the basin. The Blind Fiord Formation lies above, with abundant pyrite in the basal beds, and the typical basal Triassic conodont *Hindeodus parvus* is found some tens of metres above the base of the formation. Below Early Triassic ammonoids, a brachiopod is found, presumably of Changhsingian age (Waterhouse 1972b).

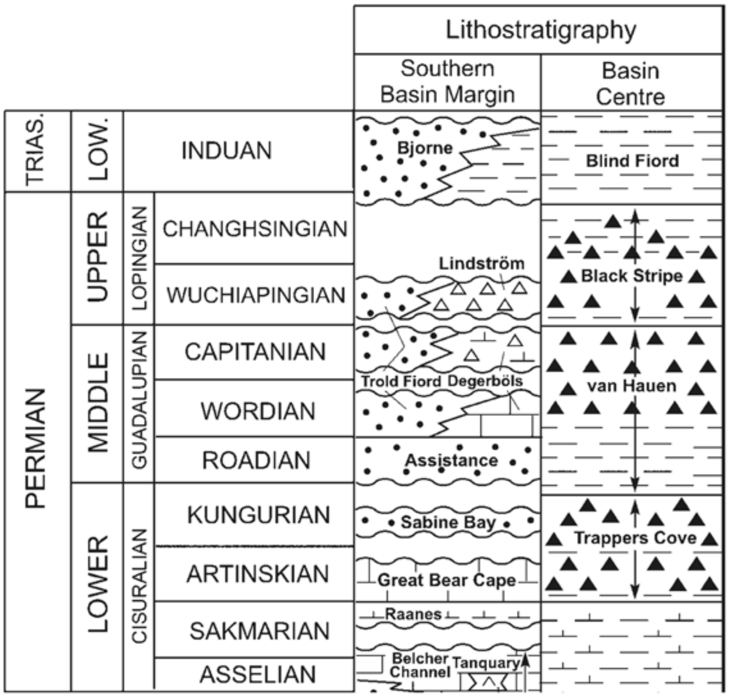

Fig. 2. The present classification and age of Permian sediments in the Sverdrup Basin, reproduced from Beauchamp et al. (2009, Fig. 3). Closed triangles signify black chert, open triangles white chert.

SYSTEMATIC STUDIES OF BRACHIOPODS

Background of the collections

The collections available for the present study were made in the 1960's and early 1970's, mostly by officers of the Geological Survey of Canada. They were passed on to the writer, and were taken later to Australia and then to New Zealand. Several problems arose. At Nelson, New Zealand, a conifer forest within city limits was consumed by fire, which then crossed a road and destroyed a shed containing many of the Canadian fossils and information on their source. Stratigraphy has been revised by later work in the Canadian Arctic Archipelago, as summarized by Beauchamp & Henderson (1994), with the formal recognition of additional formations, chiefly affecting the Belcher Channel Formation. That means that the name of the source formation has had to be revised, and for some of these collections, it has not been possible to verify source, as indicated throughout the text and in the summary of fossil localities, starting on p. 424**.** Their situation is akin to some of the older collections, especially those made in the 19th century, from stations no longer able to be pinpointed. And lastly, no one now at the Geological Survey of Canada has been able to supply details for the location and stratigraphy of a number of the fossil localities. For these localities, the nature of the lithology has been used to provisionally estimate the source formation, as recorded. At some time, perhaps, more reliable records will be found. In the meanwhile, there is still biological value in the description and figures, but the source constraints are much less than rigid. This is further exacerbated by the lack of information about the stratigraphic information ever provided for most of the collections, so that even where available, information is limited to the formation source. Therefore reservations are necessary about aspects of this study, particularly for the Canadian Arctic Archipelago, whereas collections from the Yukon Territory have been made with careful attention to stratigraphic sequence, as published by Bamber (1972).

The material has now been returned to Canada, and has been registered individually by number with the prefix GSC, and housed at the Geological Survey of Canada in Ottawa.

PRESERVATION OF FOSSILS

The preservation of the fossils examined in this report varies considerably. Some are outstandingly well preserved. Some silicified fossils show internal and in some cases external detail very well (see for example Fig. 79-81, pp. 109-111), and also exquisite internal moulds reveal in fine detail of minutae of muscle and other impressions (see Fig. 192, p. 225 and Fig. 301, p. 353). Other collections in which the fossils have been silicified involve fragile and delicate specimens that tend to crumble. In many specimens, the moderate calcareous component of the matrix ensures that preservation of internal detail is far from ideal.

CLASSIFICATION

The following descriptions are based partly on the *Revised Brachiopod Treatise*, updated in classification as referenced, and with higher category group names treated consistently and often simplified from their proposed modifications by removing extraneous letters such as at and id. These letters, added to only some of the names and overelaborate and ritualistic to the modern eye, were devised to conform with rules invented for medieval and modern (not classical) Latin, and although having played an important role in the past, now seem redundant and protected more by pedantry than utility. Nowadays, many paleontologists have to refer to the Treatise series to learn what sort of spellings are required, because the niceties of classification are a mystery to them. It is preferred to use a simplified and consistent addition of accepted endings to the unaltered name of the genus (Waterhouse, 2018a, pp. 26, 27). Admittedly such usage may seem unfamiliar, and even uneuphonious, so the versions approved by the Zoological Code of Nomenclature have been bracketted, cluttering the text, but hoping to show the simplicity, consistency and predictability of the proposals.

In the following account, OD means by original designation, and SD by subsequent designation.

BRACHIOPOD MORPHOLOGY

Structures associated with the delthyrium in spiriferiform brachiopods are important for classification. In many species and genera, a plate lies below the delthyrium in the ventral valve, and connects the junction between the pair of adminicula and dental plates. It has been variously called a delthyrial plate (Williams & Brunton 1997, p. 428; Carter 2006a), or better, a subdelthyrial plate. Waterhouse (2016, 2018a) in discussing the plate, suggested the term connector plate. The *Revised Brachiopod Treatise* is far from satisfactory over the terminology, offering varying terms in different sections of the text, and failing to offer a consistent presentation and explanation even for adminicula and dental plates. The plate is part of the dental supports, rather than part of the external delthyrial construct, so that the term delthyrial plate is far from appropriate. Subdelthyrial plate is better, but seems to have been deemed an inferior term in the *Revised Brachiopod Treatise*, and anyway, is not part of the delthyrium.

In addition, various spiriferiform genera have an arched plate across the delthyrium at the level or above the level of the adjoining interarea, and this was termed a cover plate by Waterhouse (2016). It may mimic a pseudodeltidium found in Strophomenata (Williams et al. 1997, Wright 1971), but the strophomenatan pseudodeltidium was largely invariant, whereas the delthyrial cover in Spiriferiformi was highly variable in size and formed by a single plate or junction of two deltidial plates, and associated with a delthyrial pedicle, which was not developed in Strophomenata. No study has shown that it was inherited unaltered from the pseudodeltidium of Strophomenata. It had a different history, and so may be termed a neodeltidium, as a feature especially amongst spiriferiform brachiopods.

REPOSITORIES

ANMH, American Museum of Natural History, New York, United States of America. **B**, **BD**, Natural History Museum, London, England. **BR**, Brachiopod Register, Institute of Geological and Nuclear Sciences (GNS), Lower Hutt, New Zealand. **CCGBH**, Changchun College of Geology, Jilin, China. **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. **NIGP**, Nanjing Institute of Geology & Palaeontology, Nanjing, China. **NMV**, National Museum of Victoria, Melbourne, Australia. **PIN**, Paleontological Institute, Russian Academy of Science, Moscow, Russia. **ROM**, Royal Ontario Museum, Toronto, Canada. **SME**, Sedgwick Museum, Cambridge, England. **TsNIGRA**, Central Scientific Geological Exploration Museum (Tschernyschew Museum), also **CNIGR** Chernyshev Museum, St Petersburg, Russia. **UA,** Department at the University of Alberta, Edmonton, Alberta, Canada. **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.

Phylum Brachiopoda Duméril, 1806

Subphylum Lingulaiformea (Linguliformea) Williams et al., 1996

Class Lingulaata (Lingulata) Gorjansky & Popov, 1985

Order LINGULAIDA (LINGULIDA) Waagen, 1885

Superfamily **DISCINAOIDEA** (**DISCINOIDEA)** Gray, 1840

Family **DISCINAIDAE** (**DISCINIDAE)** Gray, 1840

Genus ***Orbiculoidea*** d'Orbigny, 1847

Diagnosis: Strongly dorsibiconvex to convexo-planar, subcircular, ornamented by concentric growth rings, dorsal apex variably placed, ventral valve low with narrow pedicle track, closed anteriorly by a listrum, continued as internal tube to open in front of posterior margin.

Type species: *Orbicula forbesii* Davidson, 1848, p. 334 (1965 ICZN opinion 722) from Wenlock of England.

Orbiculoidea ornata n. sp.

Fig. 3, 4

1960 *Orbiculoidea* sp. Harker & Thorsteinsson, p. 49, pl. 15, fig. 10, 11.

Derivation: ornatus – adorned, Lat.

Diagnosis: Apex subcentral, fine slender ribs present over posterior face of dorsal valve and to varying degree over rest of shell.

Holotype: GSC 13513 from GSC loc. 26406, Assistance Formation of Devon Island, figured by Harker & Thorsteinsson (1960, pl. 15, fig. 10, 11), here designated.

Material: One specimen with valves conjoined, a ventral valve, and nine dorsal valves from GSC loc. 26406, Assistance Formation.

Description: The largest dorsal valve is 35mm in diameter and 14mm high, with subcentral apex, slightly flattened posterior and swollen anterior, ornamented by closely spaced concentric growth ridges, with fine variably continuous radial ribs posteriorly, ribs less dense and less consistently present over the rest of the shell. The only available ventral valve has been badly damaged, but a better preserved ventral valve has been described by Harker & Thorsteinsson (1960).

Resemblances: The specimens are larger than *Orbiculoidea* spp. A and B from the Carboniferous Hart River and Blackie Formations in the Yukon Territory of Canada (Waterhouse 2018b), and have more closely spaced growth lines with fine radials on the dorsal valves. *Orbiculoidea winsnesi* Gobbett (1964, pl. 1, fig. 4, 5) from the upper Brachiopod Chert of Spitsbergen has subcentral apex in each valve, but shows no sign of radial ribs. From the Magnesian Limestone of Wuchiapingian age in England, *Orbiculoidea* assigned to *speluncaria* Schlotheim, 1816 by King (1850, p. 85, pl. 6, fig. 28, 29) has no radials, and the apex is posteriorly placed. There are a number of differences from these and from Zechstein specimens assigned to the species. Figures in Dunbar (1955, pl. 32, fig. 4, 5) of *Orbiculoidea* sp. A from a "white block" in Triassic conglomerate near Kap Stosch of Greenland suggest radial ornament, but there is no mention of the ribs in the description (p. 62).

Note: Schlottheim rather that Schlotheim was claimed by Carlson & Grant 2002, p. 1220 to be the correct spelling of this author, but it was allowed that spelling varied, and his name has been more usually spelled Schlotheim.

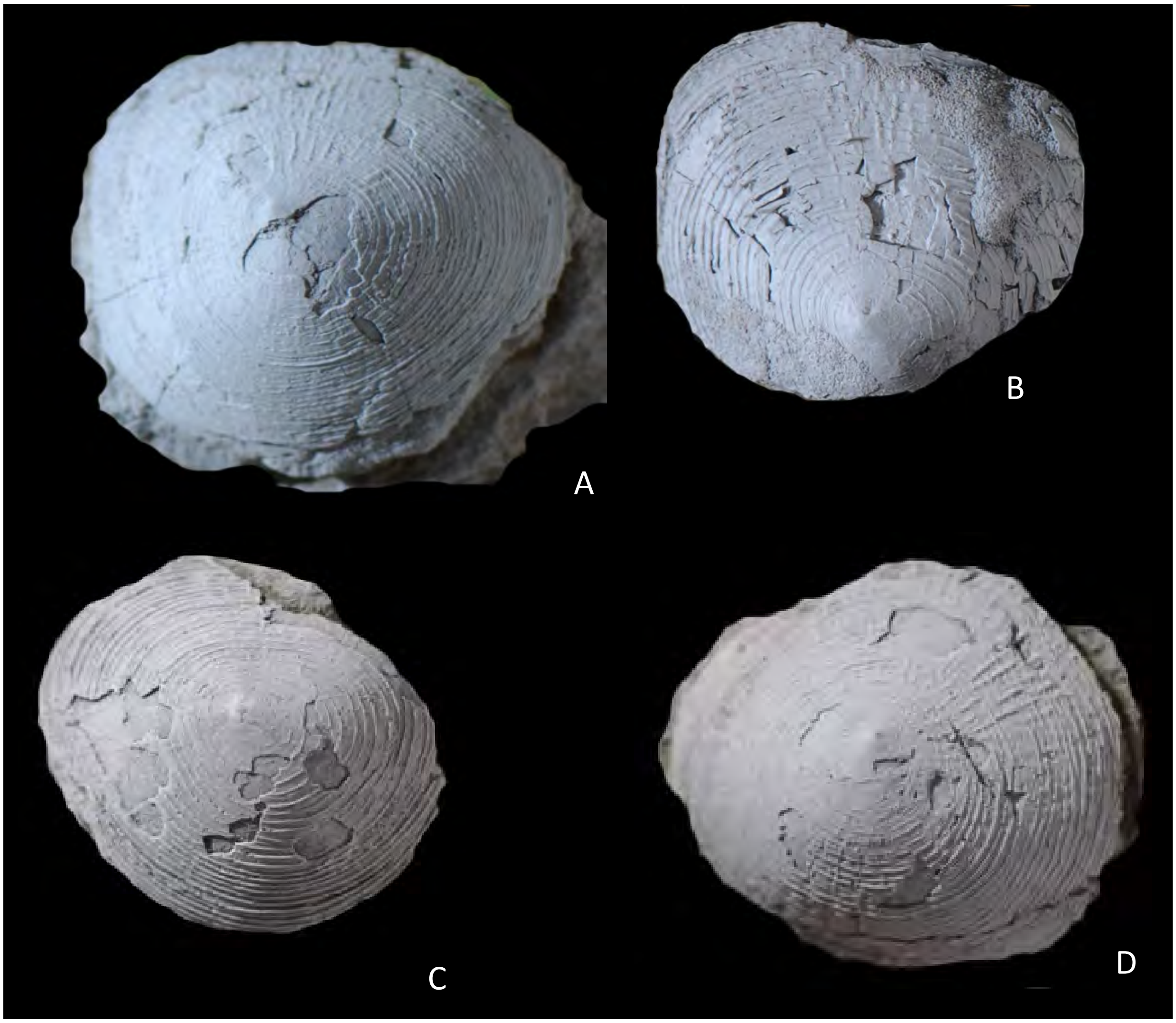

Fig. 3. *Orbiculoidea ornata* n. sp., dorsal valves. A, GSC 140674. B, GSC 140675. C, GSC 140676. D, GSC 160677. Specimens from GSC loc. 26406, Assistance Formation, Devon Island, x2.

Fig. 4. *Orbiculoidea ornata* n. sp., dorsal valve, GSC 140678, from GSC loc. 26406, Assistance Formation, Devon Island, x2. Note signs of anterior radial ribs on decorticated shell.

Subphylum Rhynchonellaiformea (Rhynchonelliformea) Williams et al., 1996

Class Strophomenaata (Strophomenata) Williams et al., 1996

Superorder STROPHOMENAIFORMI (STROPHOMENIFORMI) Öpik, 1934

Order TRIPLESIAIDA (TRIPLESIIDA) Moore, 1952

Suborder ORTHOTETESIDINA (ORTHOTETIDINA) Cooper & Grant, 1974

In the *Revised Brachiopod Treatise*, Williams & Brunton (2000) assigned orthotetids to full ordinal status as Order Orthotetida, ascribing the name to Waagen (1884), following Cooper & Grant (1974). But this ascription was fictitious, because Waagen had treated *Orthotetes* and allies as a family group, rather than an ordinal group. Therefore Waterhouse (2010; 2018a, p. 27; 2018b, p. 147) credited Orthotetidina to Cooper & Grant (1974), as they were the first to recognize ordinal standing for the group, even though they erroneously credited Waagen. This in turn meant that Triplesiidina Moore, 1952 needs to be recognized as the senior name for the ordinal grouping, as Order Triplesiaida (Triplesiida), with Orthotetesidina (Orthotetidina) relegated to being a suborder.

Williams & Brunton (2000) placed Orthotetida (now Triplesiida) as a group after Productida, and as a separate component of Class Strophomenata Williams et al. But it is preferred to continue to acknowledge the alliance between Strophomenida and Orthotetida (Triplesiida), as expressed in many articles, including Manankov (1979) and Williams & Brunton (1993), not withstanding differences in shell structure, by grouping the two in a superorder Strophomenaiformi Öpik, 1934, as in Waterhouse (2010, 2018a) even though such a category was not recognized in the *Revised Brachiopod Treatise.* This superorder is distinguished from Superorder Productusiformi by general lack of well-organized spinose ornament and different cardinal process and internal plates. Superorders are a most useful category for associating somewhat allied orders, and recognition helps upgrade the far too simplistic classification of the phylum Brachiopoda into a more realistic complexity approaching that recognized for the Class Bivalvia.

Superfamily **ORTHOTETESOIDEA** (**ORTHOTETOIDEA)** Waagen, 1884

Family **DERBYIAIDAE** (**DERBYIIDAE)** Stehi, 1954

Genus ***Derbyia*** Waagen, 1884

Diagnosis: Large, finely costellate, pseudodeltidium flat, monticulus usual, chilidium small and may have median groove, interarea may display perideltidium, dental ridges converge on well formed median ventral septum. Ventral muscle scars deeply impressed, ridge-like brachiophores arising from massive socket plates, subcircular dorsal adductor scars, may be divided by low myophragm.

Type species: *Derbyia regularis* Waagen (1884, p. 576) from Amb Formation (upper Cisuralian) of Salt Range, Pakistan, SD Hall & Clarke (1892, p. 262).

Derbyia semicircularis n. sp.

Fig. 5, 6

?1878 *Orthis*?, *Chonetes* or *Streptorhynchus* Etheridge, p. 635, pl. 29, fig. 4.
1914 *Derbyia* sp. Wiman, p. 59 (without reference to figure).
1914 *Derbyia grandis* [not Waagen] – Wiman, pl. 13, fig. 16 (without reference to textual description).
cf. 1916 *D. grandis* [not Waagen] – Tschernyschew & Stepanov, p. 67, pl. 10, fig. 1a, b.
1937b *D*. cf. *grandis* – Stepanov, p. 110, pl. 1, fig. 5.
1950 *D. grandis* Frebold – pl. 1, fig. 5, 5a.
1960 *D*. cf. *grandis* – Harker & Thorsteinsson, p. 52, pl. 16, fig. 9, 10.

1964 *D*. aff. *grandis* – Gobbett, p. 54, pl. 2, fig. 1, 2.
1971 *D*. cf. *grandis* – Bamber & Waterhouse, p. 172, pl. 18, fig. 1.
1992 *D. grandis* – Nakamura et al., p. 86, pl. 1, fig. 1.

Derivation: semi – half, circularis – circular, Lat.

Diagnosis: Large little inflated shells with low interareas and wide hinge. No perideltidium or monticulus.

Holotype: GSC 13521 from GSC loc. 26406, Assistance Formation (Roadian), Devon Island, figured by Harker & Thorsteinsson (1960, pl. 16, fig. 9, 10), here designated.

Additional material: Two specimens with valves conjoined from GSC loc. 26406, Assistance Formation, Devon Island. Four dorsal valves, of which two are very fragmentary, two fragmentary ventral valves, obscure ventral impression, and incomplete fragments of two specimens with valves conjoined from C-4034, Trold Fiord Formation, Ellesmere Island.

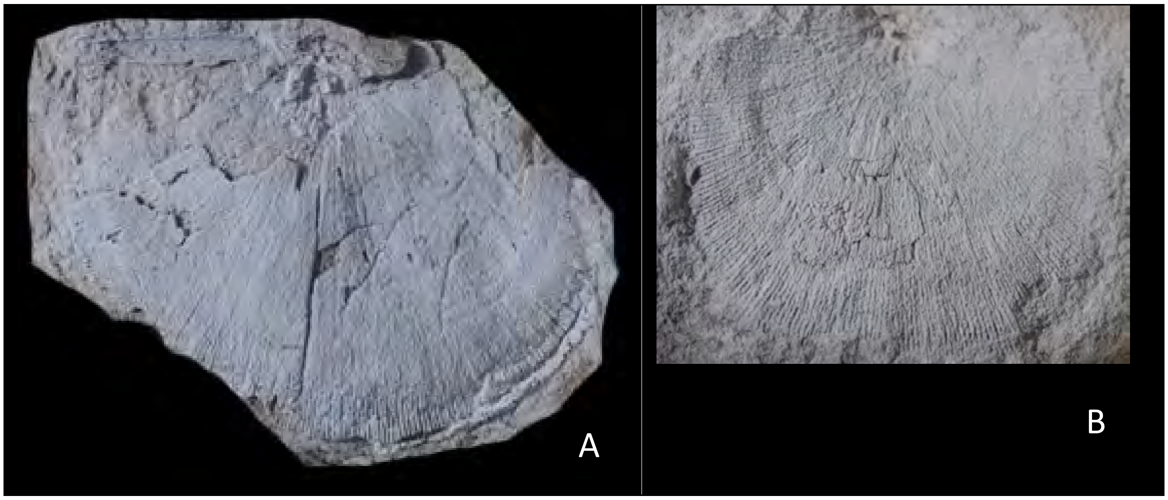

Fig. *5. Derbya semicircularis* n. sp. A, dorsal external valve GSC 140679, x1. B, dorsal external valve GSC 140680, x1. Specimens from C-4034, Trold Fiord Formation, Ellesmere Island.

Description: Presently available material from Canada is not well preserved, but the synonymy includes a range of previously described and well illustrated specimens from the Arctic, and the holotype is largely complete. The ventral valve is weakly convex, and the dorsal valve tends to be weakly concave, so that the disc is thin. In the holotype, the hinge is almost at maximum width, and the ventral interarea is well formed but low, and the pseudodeltidium convex without visible monticulus. Costellae are moderately strong for the genus, close to twelve in 10mm but varying up to eighteen in 10mm, tending to be in pairs, slightly differentiated, and increasing mostly by branching on the ventral valve, and just as dense on the dorsal valve. The ventral septum is slightly less than a third of the length of the valve.

Resemblances: Available specimens are poorly preserved, the costellae fine, and the outline semicircular, with the hinge at maximum width. The Tschernyschew-Stepanov specimen (1916, pl. 10, fig. 1) from Great Bear Cape is semicircular, and costellae number just over twelve in 10mm anteriorly, lying in pairs, as judged from the illustration. The specimen identified as *Orthis*?, *Chonetes* or *Streptorhynchus* by Etheridge (1878, p. 635, pl. 29, fig. 4) and kept at the Natural History Museum (BB 89157), possibly belongs to *Derbyia semicircularis* n. sp., given its shape and fine ribbing. A large subrectangular shell was figured from the Vøringen level of Spitsbergen by Nakamura et al. (1992). The Stepanov specimen from the Vøringen Member of Spitsbergen has more rounded borders, with slightly shorter hinge, and is shown to have fourteen or fifteen costellae in 10mm anteriorly. From much the same level, a specimen figured by Gobbett (1964) has perhaps sixteen costellae in 10mm anteriorly, though the exact number is difficult to determine, and the ribs tend to lie in pairs. The shape is like that of the Assistance material, and the pseudodeltidium lacks a monticulus. These specimens all differ from each other to some extent, notably in the spacing and strength of the ribs, but all are less inflated than *Derbyia grandis* Waagen (1884, pl. 51-53) from the Salt Range of Pakistan. This species has a much more convex ventral valve with narrower pseudodeltidium, as noted by Gobbett (1964). As well, the ventral interarea of the Salt Range species described by Waagen displays a perideltidium, not found in Arctic specimens. *Derbyia grandis* [not Waagen] of Tschernyschew (1902, pl. 24, fig. 1, 2, pl. 26, fig. 5) from the Schwagerina-Kalk of the Urals is certainly close to some individuals assigned to *semicircularis* in having a somewhat semicircular outline with costellae at the coarser end of the spectrum, but the ventral umbo is more extended and prominent. From the Barabashsk Suite of Primoyre, a figured specimen shows strong ribs and moderate sulcus (Licharew & Kotlar (1978, pl. 12, fig. 1), whereas fine ribs are developed in large transverse Pamir specimens of Sakmarian age recorded by Grunt & Dmitriev (1973, pl. 3, fig. 1-4)

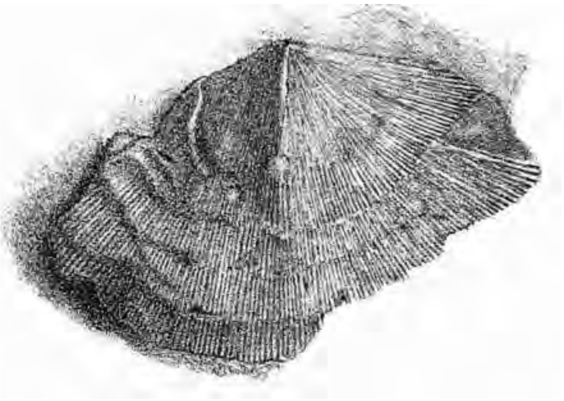

Fig. 6. Possible *Derbyia semicircularis* n. sp., figured as *Orthis*?, *Chonetes* or *Streptorhynchus* by Etheridge (1878, p. 635, pl. 29, fig. 4), BB 89157, presumably x1. From north Ellesmere Island, Trold Fiord Formation?.

Derbyia sp. A of Dunbar (1955, p. 66, pl. 2, fig. 16-20) from Cape Stosch, Greenland, is more elongate, with hinge of variable width, and like the present suite, without a visible monticulus or perideltidium. A large specimen figured by Stepanov et al. (1975, pl. 1, fig. 2) as *Derbyia*? sp. from Ufimian of Kanin Peninsula could be related, but is somewhat damaged and therefore difficult to interpret.

Numerous species of *Derbyia* have been described by Cooper & Grant (1974) from the Glass Mountains of Texas, but most if not all display a monticulus, and the ventral valve is more inflated, and often high. The overall implication of these observations is that *Derbyia* species from different geographic regions display minor differences in morphology, and Williams & Brunton (2000) pointed out that species from the Glass Mountains did display considerable variability in features that had been used by previous authors to discriminate genera. That may imply that Cooper & Grant were lumping different genera under one genus, or that too many genera had been recognized by other authors.

Family **SCHUCHERTELLAIDAE** (**SCHUCHERTELLIDAE)** Williams, 1953

Subfamily **STREPTORHYCHUSINAE** (**STREPTORHYCHINAE)** Stehli, 1954

Tribe **STREPTORHYCHUSINI** (**STREPTORHYCHINI)** Stehli, 1954

Discussion: Understanding the make-up of the subfamily Streptorhynchusinae is, it would appear, fraught with questions, because of uncertainty over the consistency of morphological features used to discriminate various genera. Even the long-known genus *Streptorhynchus* is affected in this way. Williams & Brunton (2000, p. 667) stated that a monticulus was present in the genus, but this is rarely true of many specimens that have been assigned to the type species in the literature. Amongst figures of *Terebratulites pelargonatus* von Schlotheim, 1816 from the Magnesian Limestone of England, those offered by King (1850, pl. 10, fig. 22-25) indicate a convex pseudodeltidium without a monticulus, but two (fig. 26, 27) are ambiguous. The larger illustrations provided by Davidson (1858a, pl. 2, fig. 37, 40) indicate a convex pseudodeltidium, without sign of a monticulus, unlike that figured for the type species by Williams & Brunton (2000, Fig. 481.4d). Further descriptions are provided in Schlotheim (1816, pl. 8, fig. 21-23), Geinitz (1848, pl. 5, fig. 11-15, 1861, pl. 16, fig. 26-33) and Mahlzahn (1937, pl. 3, fig. 23-25). Various species identified with *Streptorhynchus* from around the globe generally indicate a convex pseudodeltidium, examples including a number of well-illustrated species assigned to *Streptorhynchus* from the Glass Mountains of Texas by Cooper & Grant (1974). The presence of a monticulus in the figures provided by Thomas (1958, pl. 11, fig. 4, 16) is not certain. Other features used to characterize *Streptorhynchus* include the presence or absence of a perideltidium, stated by Williams & Brunton (2000) to be rarely absent, but in fact seldom present in faunas from paleotemperate and polar regions of the globe, to the extent that the presence or absence seems likely to have been variable, or of ecologic and paleolatitudinal import, and arguably of no or at least uncertain taxonomic implications. Within the ventral valve, as far as known, the dental constructs are limited to teeth and dental tracks or ridges, with no supporting plates (see Williams & Brunton 2000, Fig. 481.4f). In the dorsal valve, the crural plates may be well extended in front of the crural projections as erismata (see Williams & Brunton 2000, Fig. 481.4e). The cardinal process is variable, but its variations may be matched in most other genera recognized in the subfamily. *Lepsius* de Gregorio, 1930 and *Mammosum* de Gregorio, 1930 from the Wordian of Sicily were incorporated in synonymy of *Streptorhynchus* by Williams & Brunton (2000). The original published figures show little of various critical aspects, but the overall shape is moderately like that of *Streptorhynchus*, although it would be desirable to uncover the critical facets of pseudodeltidium and crural plates in these Sicilian taxa for confirmation of their generic position. Most of the streptorhynchid genera summarized in the *Revised Brachiopod Treatise* are assigned a Permian age, but there have been numerous reports of *Streptorhynchus* from Carboniferous faunas.

Arctitreta Whitfield, 1908 is moderately well known, and further described in this study. There is no perideltidium, a monticulus is widely developed, dental supports are found in at least early growth stages, and no specimens appear to show erismata because the crural supports are short, and end only a little in front of the socket plates, into which they appear to curve.

Four well described genera were discriminated by Cooper & Grant (1974), with numerous illustrations and several species assigned for each genus. *Chelononia* Cooper & Grant is the most distinctive genus, defined by the presence of auricules, though this was left unmentioned by Williams & Brunton (2000). The genus has a monticule (Cooper & Grant 1974, pl. 126, fig. 30, pl. 95, fig. 3), as clearly shown by Williams & Brunton (2000, Fig. 482, fig. 1e), but again omitted in the diagnosis offered by Williams & Brunton (2000), who offered a comparatively trivial diagnosis centred, imperfectly, on shape. *Bothrostegium* Cooper & Grant (1974) is also distinctive, with a channel instead of a monticule along the centre of the pseudodeltidium. It lacks dental supports, has moderately high interarea that is wide next to the umbo in a subrectangular rather than triangular outline, and conspicuous perideltidia, no dental supporting plates, and short if any erismata. The three species assigned to *Bothrostegium* are found in beds of Roadian age, wrongly stated to be of Lower Permian age by Williams & Brunton (2000), but in fact of Middle Permian age. *Tropidelasma* Cooper & Grant, 1969 has a well defined and unequivocal monticulus, much more sharply defined than in any *Streptorhynchus* or *Arctitreta,* in a triangular ventral interarea. There is no perideltidial interarea, and erismata are only spasmodically present, as in the type species and most other forms (see *T. curtum* Cooper & Grant 1974, pl. 58, fig. 11, 13), in contrast to *T. gregarium* (Girty) in Cooper & Grant (1974, pl. 61, fig. 22). *Erismatina* Waterhouse, 1983a was recognized for a species called *cooperi* Waterhouse from the Late Permian of Thailand. Although this genus was synonymized with *Tropidelasma* by Williams & Brunton (2000), and although it shares the same triangular interarea with high narrow monticule with *Tropidelasma*, it consistently has distinctive and long erismata extending outside of the muscle scars for their full length, unlike the thick, short and slightly recurved equivalent plates normal for *Tropidelasma*.

Kiangsiella Grabau in Chao, 1927a from China is readily distinguished by its radial plicae. Although various critical aspects are otherwise poorly known for type material, the genus has been reported widely, notably by Thomas (1958) from Western Australia, an occurrence omitted in Williams & Brunton (2000). Thomas showed that a monticule was present, but the nature of the crural plates remains obscure. It is assumed that there were no dental supports, an aspect in need of confirmation. Waterhouse (2018a) reported similarly plicate specimens in the Bashkirian (early Upper Carboniferous) of Canada, but various critical aspects are not preserved in that material. *Drapanorhynchus* Havliček, 1967 of Lower Carboniferous age was included tentatively in Streptorhynchinae by Williams & Brunton (2000), but was judged to display anomalous features and shows limited approach to other constituent genera of the subfamily. *Taimyropsis* Ustritsky, 1963 is based on one poorly preserved ventral valve, and is very difficult to interpret.

A southern paleohemisphere genus *Notostrophia* Waterhouse, 1973, 1982a from the Early Permian of New Zealand and also earlier Permian of Tasmania and possibly Western Australia (*Streptorhychus crassimurus* Thomas, 1958) is distinguished by its equidimensional to transverse shape, strong anterior costae especially over the dorsal valve and lack of erismata, but the nature of the pseudodeltidium is not preserved in type material examined so far. Williams & Brunton (2000, p. 670) aggressively criticized the description by Waterhouse (1982a) of pseudopunctae in the shell, and certainly it remains important to determine the nature of the shell structure, though one may wonder why only this genus was singled out for criticism, when descriptions of other genera also had reported pseudopunctae for the shell structure. Waterhouse had simply followed the then-current interpretation which failed to analyse different kinds of punctation and punctal infillings, and had accepted the flawed interpretation endorsed by Williams (1965, p. 409), Thomas (1958), Grant (1976), and Cooper & Grant (1974). The recognition of extropunctae as discriminated from pseudopunctae was only proposed somewhat later by Williams & Brunton (1993), applied to slender pillars of uparchings that penetrate the shell, as well illustrated in Williams (1997). Waterhouse (1982a, p. 28) had also reported minute pores through the shell (cf. Thomas 1958), but this was ignored. This difficulty over shell structure is reflected in other studies. Waterhouse & Piyasin (1970, p. 104) announced that the now silicified material of *Streptorhynchus* sp. was densely punctate, and this statement was contradicted by Grant (1976, p. 49), claiming “whereas it is pseudopunctate”. But silicification destroys calcite shell structure, and may convey unreliable data on the original shell. The shell, as preserved and as silicified, was objectively punctate. Whether the shell was pseudopunctate or extropunctate originally is beyond determination, because of the way that silicification destroys original shell structure, and can leave a silicified replacement bearing punctae, as an imperfect replication of the original shell structure.

There must be some reservation about the shell study by Williams (1997), apart from the devastating criticisms of its limitations by Afanasieva (2002), who showed that Williams had apparently ignored many pre-emptive and meticulous Russian studies. This lies in the discovery that the shells of at least some brachiopods otherwise close to well known genera, are in fact endopunctate, as well illustrated for two notospiriferid genera by Armstrong (1970, p. 293) and Waterhouse (1964, pl. 14, fig. 10, pl. 15, fig. 6, pl. 37, fig. 4, 6), with figures showing open punctae through the shell, as summarized by Waterhouse (1998). In other aspects of morphology, these genera are close to impunctate or taleolate members of the Notospiriferidae. Such a shell structure was never recognized by Williams (1997). Waterhouse called the punctae mesopunctae, because they are found in the principal and middle layer of shell, below the exolayer, and above the floor covering. Liang (1990, p. 370) claimed that a number of shells otherwise like Productida were punctate, and Mou & Liu (1989, pl. 2, fig. 8) have demonstrated undoubted perforations. But other authors have doubted the claim (Shen & Shi 1998), whereas Waterhouse (2013, p. 305), permitted some doubt as to whether the punctae were real, or whether critics were simply conforming with the prevalent interpretation of shell structure. Build-up of shell material is not free of environmental controls, and cold conditions must affect the chemical composition and possibly structure of shell material, which may have contributed to the presence of punctae in southern hemisphere Notospiriferidae from high paleolatitudes. Lowenstam (1954a, b) showed that calcite replaced aragonite at low temperatures, and Waterhouse (1982c, 2008) demonstrated that a number of bivalves from high temperate to polar paleolatitudes changed in shell composition from aragonite to calcite. For brachiopod shell studies, it may be a mistake to assume that shell structure is always identical for that particular brachiopod group. At least in some instances, brachiopod shell may differ in different parts of the globe, probably affected by temperature. Southern paleohemisphere shell structure in Permian shells remains only partially known, and was ignored by Williams (1997), despite various studies on east Australian material by J. D. Armstrong.

Summary of discriminants

The present account summarizes only some of the contentious aspects of the overall review of Streptorhynchinae by Williams & Brunton (2000). But overall, any omissions and misinterpretations can be excused because of understandable difficulties in diagnosing Permian genera, many of which have never been adequately defined, with further complexity caused by what appears to be an inherent high variability amongst some of the morphological features. This may be outlined with a summary of the principal features used for discrimination between streptorhynchin genera.

shape and ornament: *Chelononia*, *Bothrostegium*, *Tropidelasma*, *Erismatina*, and *Notostrophia* are all distinctive in shape and, in the case of *Notostrophia*, ornament is also distinctive.

monticule: The monticule is especially well developed as a high median ridge in *Tropidelasma* and *Erismata*, and is present as a much lower and broader ridge in a number of other genera. But it appears to be missing from many individuals of *Streptorhynchus* *pelargonatus*, although Williams & Brunton have figured a shell with a very low median ridge, interpreted as exemplifying the presence of a monticule in *Streptorhynchus,* but scarcely visible. So where does this leave the numerous species with convex pseudodeltidium and no sign of a monticule?

The nature of the pseudodeltidium has some relevance to the validity or otherwise of Tropidelasminae Waterhouse, 1983a, p. 117, based on *Tropidelasma* Cooper & Grant (1969). Given the uncertainty or at least apparent inconsistency over the presence of a monticule in *Streptorhynchus*, it may be better to reduce Tropidelasminae to tribal status, until the nature of the delthyrial cover can be resolved for *Streptorhynchus*. In the meantime, it may be noted that *Tropidelasma* and *Erismatina* are both characterized not only by consistently displaying a high monticulus with angular crest, but by possessing fulcral plates in the dental sockets.

pseudodeltidial channel: *Bothrostegium* and *Fissulina* have a pseudodeltidial channel that is well marked.

dental supports: in most genera, there are only tooth ridges. *Arctitreta, Grumantia* and *Fissulina* have dental plates extending to the floor of the valve, at least in early growth stages and into early maturity. These genera are obviously closely related. *Fissulina* is exceptional in having a pseudodeltidial channel.

erismata: mature *Streptorhynchus* displays erismata, as figured by Williams & Brunton (2000), and some genera appear to have no erismata, as in *Arctitreta*, *Fissulina*, *Grumantia,* and *Notostrophia. M*any shells develop erismata later in ontogeny, and there is the suggestion of some inconsistency in the presence/absence of erismata. In the well studied genus *Tropidelasma*, Cooper & Grant (1974) found that erismata were generally absent, except in a few specimens, and Waterhouse (1983) proposed that shells with exceptionally long erismata be assigned to a separate genus, *Erismatina*.

At present considerable weight is placed on the strong development or otherwise of some of these features. The strong development of pseudodeltidial channel or erismata or monticule is used to justify genera, provisionally at least, and ambiguous or variable signs of presence are attributed much less weight.

Streptorhynchusid gen. & sp. indet.

Fig. 7

Fig. 7. Streptorhynchusid sp., ventral fragment GSC 140681 x1, from C-4015, Trold Fiord Formation, Ellesmere Island.

Description: A single ventral valve from GSC loc. C-4015, Trold Fiord Formation, Ellesmere Island, is elongate with well defined and prominent primary ribs, bearing small spinose growth laminae at intervals. Secondary ribs are also differentiated.

Genus ***Arctitreta*** Whitfield, 1908

Diagnosis: Subpentagonal, subtriangular or subrounded shells ornamented by fine costellae, moderately differentiated, ventral interarea high, lacking perideltidium, bearing pseudodeltidium with low broad monticule and bordered by teeth ridges, vestigial or no dorsal interarea, ribs of comparable strength on both valves; thin dental supporting plates extending to floor of valve at least into early maturity, cardinal process poorly known for type species, crural supporting plates short, no erismata.

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

Discussion: *Grumantia* Ustritsky, 1963 was proposed for a species regarded as belonging to *Arctitreta* Whitfield by Brabb & Grant 1971, Cooper & Grant, 1974, Manankov 1979 and other authorities, but the genus is tentatively recognized as being apparently discriminated by its convex pseudodeltidium, without median groove or sign of monticulus. As in *Arctitreta*, thin dental supports are present, at least in smaller specimens.

Arctitreta was treated as of uncertain order, suborder and family by Williams (1965, pp. 862, 863) in the first edition of the *Brachiopod Treatise*. Later Williams & Brunton (2000) offered an incomplete diagnosis and figured non-type material for the type species. This was remedied by Waterhouse & Chen (2007, text-fig. 3A-F, 4A-D), who published figures of the type material, courtesy of Bushra Hussaini, American Museum of Natural History, New York.

Arctitreta pearyi Whitfield, 1908

Fig. 8A, B, 9 – 12

1908 *Arctitreta pearyi* Whitfield, p. 57, pl. 2, fig. 1-4.
1960 *Streptorhynchus kempei* [not Andersson] – Harker & Thorsteinsson, p. 50, pl. 15, fig. 1-6.
1970 *S. kempei* – Bamber & Copeland, p. 630, pl. 14, fig. 8a, b.
1982a *A. pearyi* – Waterhouse, p. 24.
2007 *A. pearyi* – Waterhouse & Chen, p. 29, text-fig. 3A-F, 4A-D.

Diagnosis: Moderately high interarea with monticulus over pseudodeltidium, umbonal angle usually close to 100º, posterior walls short and forming distinct angle with lateral walls. Ribs moderately differentiated, ventral muscle field becomes large with maturity.

Lectotype: AMNH F1 25034 figured by Whitfield (1908, pl. 2, fig. 1) and Waterhouse & Chen (2007, text-fig. 3A, D) from Cape Sheridan, designated by Waterhouse & Chen (2007, p. 30).

Material: Eighteen specimens with valves conjoined, two dorsal valves and eleven ventral valves from GSC loc. 26406, Devon Island, and one broken specimen with valves conjoined from GSC loc. 58968, Ellesmere Island, Assistance Formation. Fragments from GSC loc. 56922, mid-Takhandit Formation, Yukon Territory.

Dimensions in mm: entire specimens

Width	Length	Height
46	41	19
39	38.5	20
32	25.5	19

Description: Shells subequidimensional, with extended ventral umbo, slightly irregular, posterior walls extending to moderately wide hinge with angle varying between 90º and 110º, rarely as low as 80º, and tiny abruptly angled ears in some specimens. Ventral interarea high and triangular, in some shells ending abruptly at hinge, in others tapering because they were less mature, pseudodeltidium and lateral areas marked by grooves parallel to hinge, interareas also bearing fine longitudinal striae normal to the hinge: no specimen showing any sign of a perideltidium, although preservation is moderately good. The median delthyrial cover, if not worn, is occupied by a low convex ridge called a monticulus, with flat area each side that coincides with each dental flange,

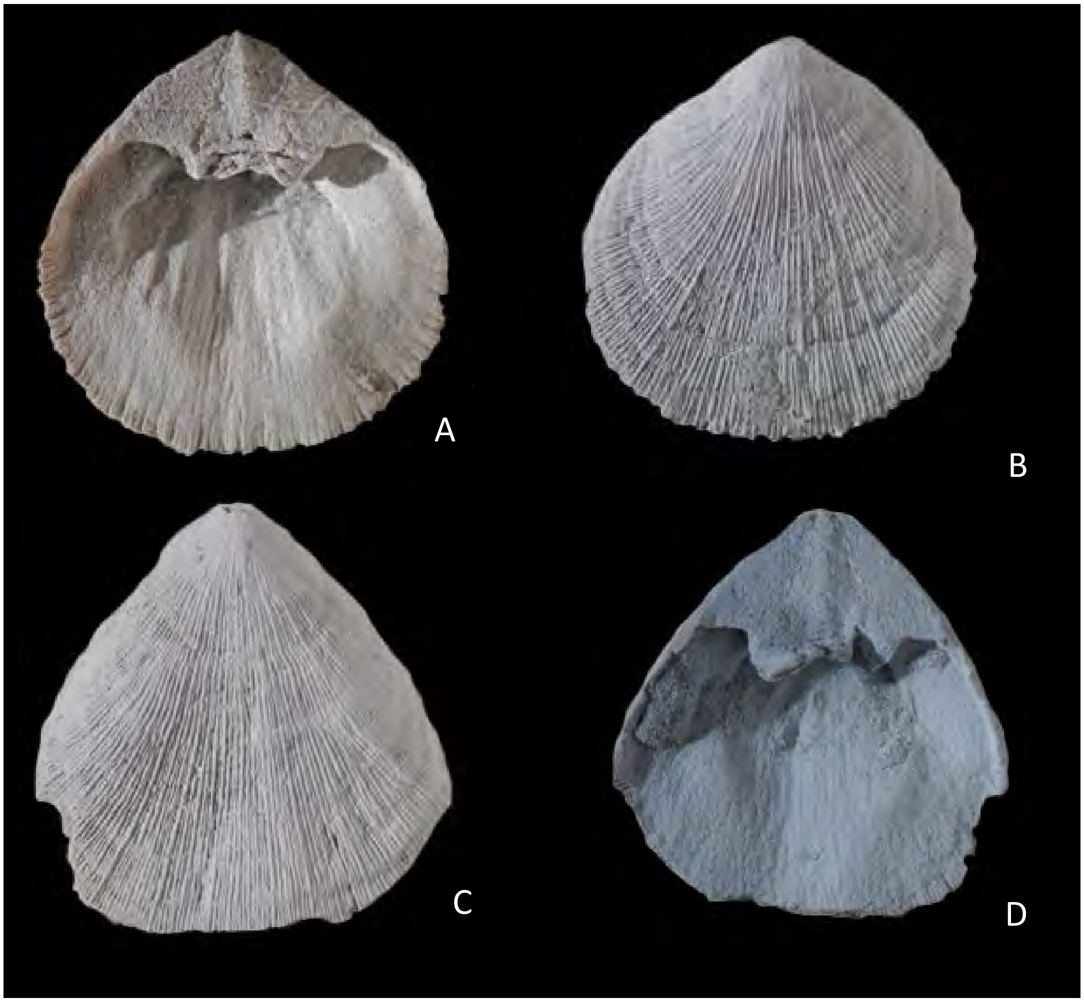

Fig. 8. *Arctitreta pearyi* Whitfield. A, B, internal and external aspects of ventral valve GSC 140682, x2. C, D, *Arctitreta triangularis* (Wiman) external and internal aspects of ventral valve GSC 140683, x2. From GSC loc. 26406, Assistance Formation, Devon Island.

Fig. 9. *Arctitreta pearyi* Whitfield, detail of ventral interarea and pseudodeltidium with gentle monticulus, GSC 140689 x2, from GSC loc. 26406, Assistance Formation, Devon Island. The monticulus is worn and poorly shown in some figured specimens.

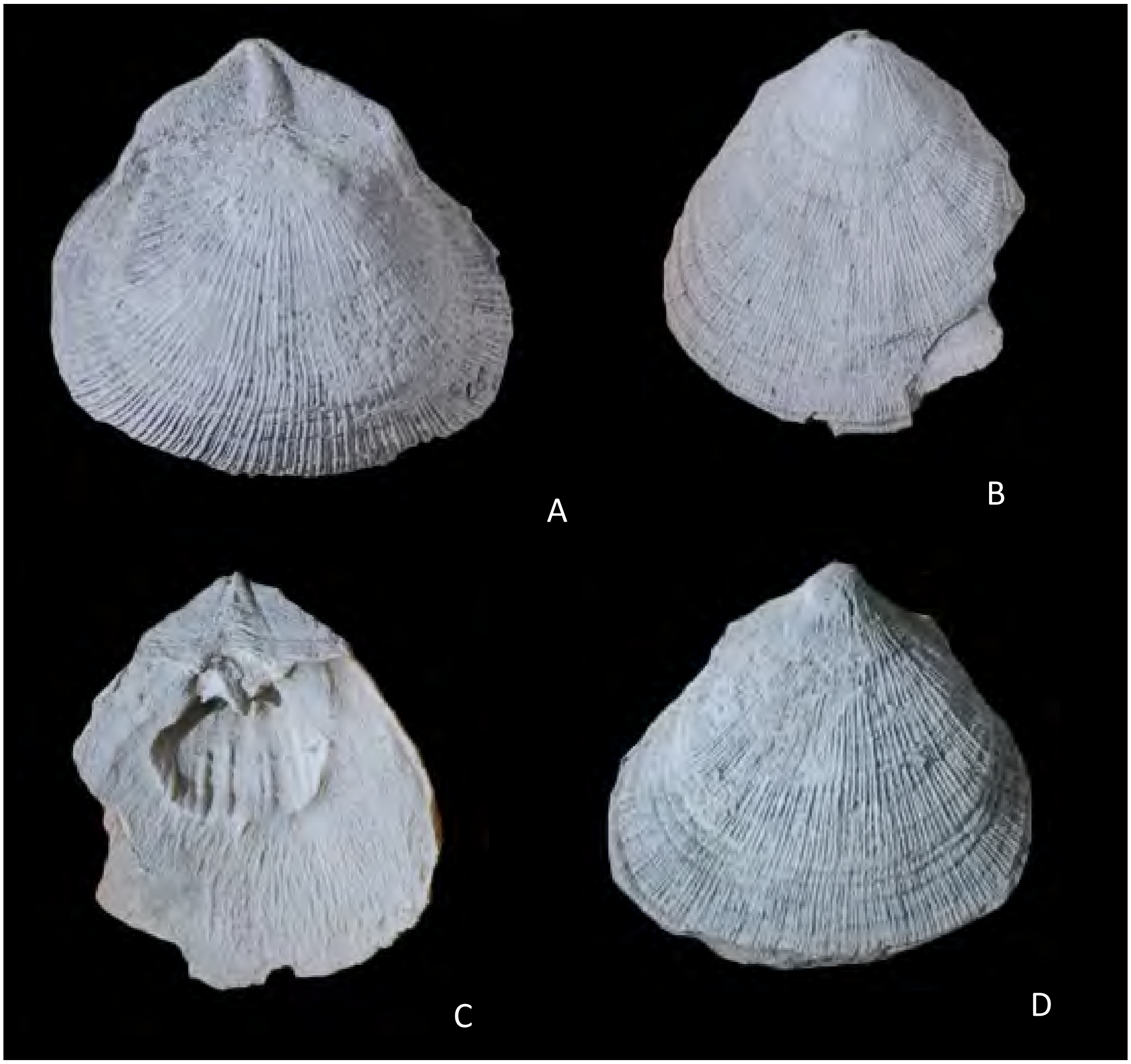

Fig. 10. *Arctitreta pearyi* Whitfield. A, D, dorsal and ventral aspects of specimen GSC 140686 with valves conjoined, x1.5. B, C, external and internal aspects of ventral valve GSC 140687, x1. From GSC loc. 26406, Assistance Formation, Devon Island.

the two teeth lying at the hinge in front of the outer edge of the flat area. The ventral valve is highest at the hinge, and is flatly convex, diminishing steadily in height to the commissure, and rarely with shallow median sulcus. The dorsal valve has a low interarea, steeply inclined back from the commissure, and is higher than the ventral valve, with maximum inflation just in front of the hinge, and maximum shell width lies close to mid-length. Both valves are ornamented by moderately differentiated costae in some four orders, numbering six to eight in 5mm mid-length, increasing by intercalation on both valves, with narrow crests and moderately wide interspaces, increasing to twelve in 5mm anteriorly on some specimens. There are signs of much finer ribbing, approaching thirty in 5mm.

Dental supports comparatively high but not extending to the floor of the valve in the available material. But posteriorly, shell fills the umbonal cavity, and it is possible that in early growth phases supporting plates extended to the floor of the valve, as observed in the type material housed at the American Museum of Natural History (Waterhouse 1982a; Waterhouse & Chen 2007). Muscle field wide, divided by high myophragm. Shell 1mm thick at anterior margin in comparatively transverse specimens, and up to 1.8mm thick in more elongate specimens.

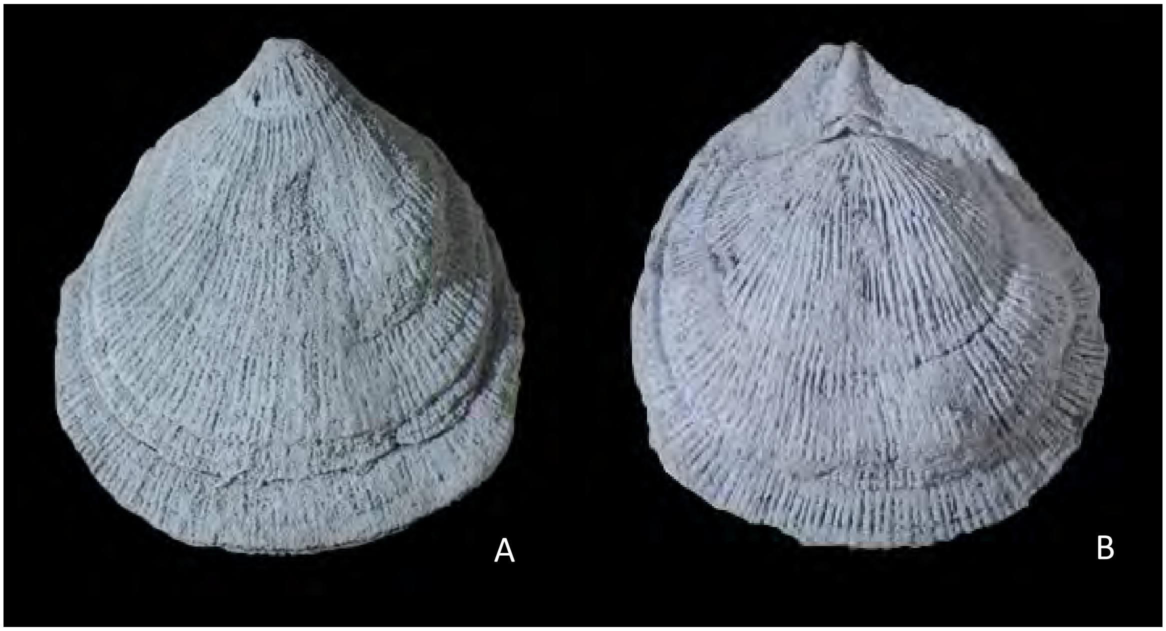

Fig. 11. *Arctitreta pearyi* Whitfield. A, B, ventral and dorsal aspects of specimen GSC 140688 with valves conjoined, x1.5. GSC loc. 26406, Assistance Formation, Devon Island. The specimen in B is slightly back-leaning and the pseudodeltidium has been abraded.

Resemblances: These shells are identified with *Arctitreta pearyi* Whitfield. They are intermediate in shape between the species *macrocardinalis* Toula, 1875b, reported from the Spiriferenkalk by Wiman (1914) and Vøringen Member of Spitsbergen by Nakamura et al. (1992), and shells found in Spitsbergen that were called *Streptorhynchus triangularis* Wiman (1914, p. 53, pl. 10, fig. 1-19, 28, 29). All three taxa as far as known share a monticulus and moderately differentiated ribbing. The species *macrocardinalis* has a generally subrounded shape, with wide ventral umbo often close to 130°, and well-rounded cardinal extremities, and little is known about internal plates. By contrast, *triangularis* is applied to narrow shells with an umbonal angle often close to 50°, and rarely exceeding 75°, at least a few degrees less than that of the narrower specimens here assigned to *pearyi*. The long posterior walls of *triangularis* pass smoothly into short lateral walls, and maximum width lies well forward. It could be argued that *pearyi* and *triangularis* belong to one variable suite (see Fig. 8), because present specimens do vary in umbonal angle and shell width. Within *triangularis*, the muscle field is just as wide, and because the shells are slightly narrower than *pearyi,* occupy more of the valve floor. The specimens referred to *triangularis* by Harker & Thorsteinsson (1960) and Gobbett (1964) are close to Wiman's types but approach *pearyi* in some diagnostic attributes.

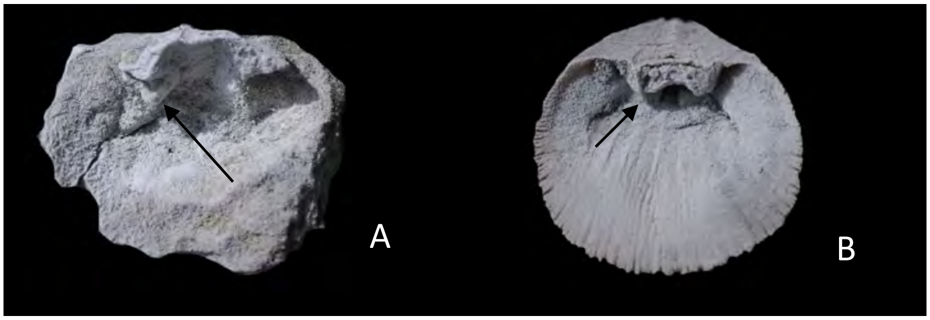

Fig. 12. *Arctitreta pearyi* Whitfield, internal aspects of mature specimens with arrow pointing to anterior dental support. A, GSC 141002 from GSC loc. 58968, Ellesmere Island. The dorsal cardinalia lie above. B, ventral valve GSC 141003 from GSC loc. 26406, Devon Island. Specimens x1.5 from Assistance Formation.

Arctitreta triangularis (Wiman, 1914)

Fig. 8C, D, 13

1914 *Streptorhynchus triangularis* Wiman, p. 55, pl. 10, fig. 1-19, 28, 29.
1937b *S. triangularis* – Stepanov, p. 109, pl. 1, fig. 3.
1960 *S. triangularis* – Harker & Thorsteinsson, p. 51, pl. 15, fig. 7-9.
1964 *S. triangularis* – Gobbett, p. 53, pl. 1, fig. 14, 15.
1979 *Arctitreta triangularis* – Manankov, p. 79, pl. 6, fig. 6.
?1990 *A. triangularis* – Kalashnikov et al., p. 146, pl. 4, fig. 5.

Diagnosis: Triangular shape and long narrowly diverging posterior walls, passing smoothly into short lateral walls.

Lectotype: Specimen figured by Wiman (1914, pl. 10, fig. 18, 19) from Spiriferenkalk, Spitsbergen, SD Gobbett (1964, p. 53).

Material: A ventral valve from GSC loc. 26406. and one from C-1872, Assistance Formation, Devon Island and three single ventral valves from C-4014, Trold Fiord Formation, Ellesmere Island.

Description: This species is very close to *Arctitreta pearyi*, and is distinguished by its narrower shell with narrower ventral umbo and very long diverging posterior walls. It could be regarded as no more than a variant of *pearyi.* A specimen from the Brachiopod Chert in Spitsbergen that was assigned to *triangularis* by Gobbett (1964, pl. 1, fig. 14, 15) has umbonal walls diverging at more than 75º, which approaches the narrower specimens assigned to *pearyi.* The angle for the lectotype as designated by Gobbett (1964) is 75º. But this leaves specimens with slightly greater angle in limbo, and perhaps the simplest way of subdividing the two taxa is to allow *triangularis* to have an umbonal angle of anything less than 80º, and long posterior walls, whereas *pearyi* has short posterior walls passing at an angle into extended lateral margins. The umbonal walls in shells assigned to *macrocardinalis* diverge by as much as 130º, to as little as just over 80º , and distinguished by a more rounded or oval outline, though specimens figured as this species by Grunt (2006a, pl. 4, fig. 1-3) from Kanin Peninsula are more quadrate in outline.

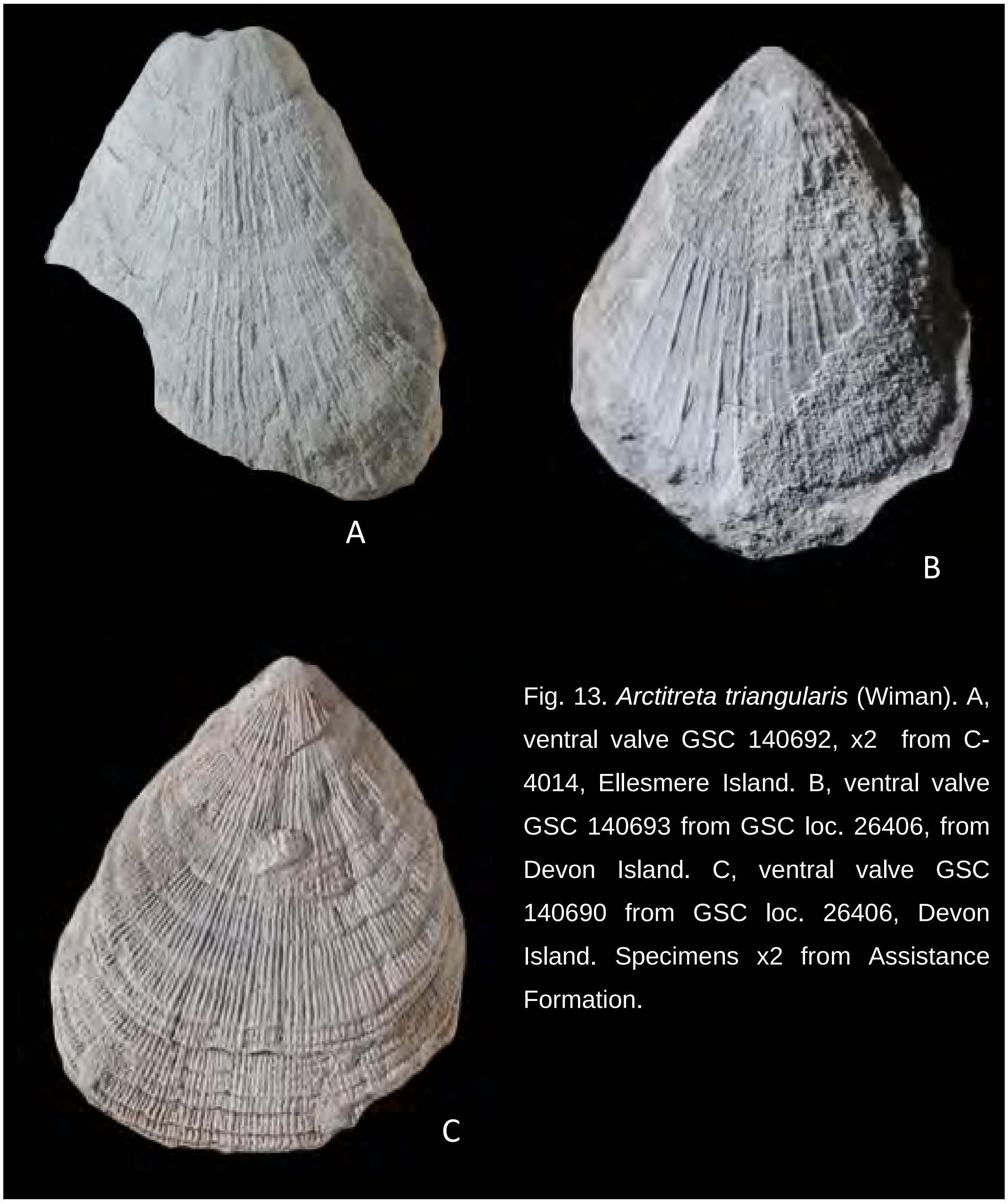

Fig. 13. *Arctitreta triangularis* (Wiman). A, ventral valve GSC 140692, x2 from C-4014, Ellesmere Island. B, ventral valve GSC 140693 from GSC loc. 26406, from Devon Island. C, ventral valve GSC 140690 from GSC loc. 26406, Devon Island. Specimens x2 from Assistance Formation.

Genus ***Grumantia*** Ustritsky, 1963

Diagnosis: Wide hinge, convex pseudodeltidium without monticulus, teeth supported by dental plates that reach the floor of the valve posteriorly, at least in small specimens, dorsal socket plates short and do not extend much beyond anterior edge of sockets.

Type species: *Streptorhynchus kempei* Andersson in Wiman, 1914, p. 58 from Spiriferenkalk, Spitsbergen, OD.

Discussion: The type species for *Grumantia* was cited as *Streptorhynchus kempei* Andersson in Wiman, 1914, as described below, and the genus later became widely synonymized with *Arctitreta* Whitfield, 1908 (Brabb & Grant 1971, Stehli & Grant 1971, Manakov 1979, Williams & Brunton 2000). On the other hand, Waterhouse (1982a, p. 24) noted that *Arctitreta* had moderately well-developed dental plates, and he and Clarke (1992) recognized *Grumantia*. Moreover *kempei* has a convex pseudodeltidium, like that of many species referred to *Streptorhynchus* rather than *Arctitreta* with its monticulus, although as a cautionary note, Williams & Brunton (2000) stated that a monticulus was present in *Streptorhynchus*, and provided a supporting illustration of a Zechstein specimen. Rudwick & Cowen (1968, pl. 33, fig. 9, text-fig. 3) pointed out that the socket support plates (ie. crural plates) were recurved towards the hinge in Sicilian material assigned to *Streptorhynchus*, and this was emphasized by Waterhouse (1982a). Although it may be conjectured that the length and outline of the plates is variable within genera, it appears that the plates in *Streptorhynchus* typically extend along the outer edge of the dorsal muscle field well in front of a socket ridge projection and the anterior end of the dental sockets, as supported by an illustration for *S. pelargonatum* provided by Williams & Brunton (2000, Fig. 481.4e). The corresponding plates of *kempei* are short like those of *Arctitreta*. Moreover, a juvenile specimen of *kempei* in present collections has been found has been found to have dental supports, just as in type *Arctitreta*. The species therefore closely approaches *Arctitreta* as regards internal morphology, to support the synonymizing of the two genera as assessed by various authorities, but possibly differs in the nature of the pseudodeltidium, which is convex, with no sign of a monticulus. Although Williams & Brunton (2000) stated that the nature of the pseudodeltidium varied, they provided no documentation, and in Canadian material, the nature of the pseudodeltidium is consistent in all known individuals of given species distinguished by other criteria, and the matter is therefore considered to be at the very least open for further exploration. In the meantime, it is considered that analysis is encouraged by provisionally accepting the proposed generic distinction, rather than concealment in what may well prove to be unjustified synonymy. But the matter is not settled, leaving *Grumantia* in a condition of precarious validity.

Waterhouse (1982a, p. 24) reported that the dental supports in type *Arctitreta* reached the floor of the valve, as quoted by Shen, Shi & Archbold (2003a), and that the supports in *kempei* and *triangularis* appeared to be slightly shorter, failing to reach the floor of the valve. That is possible, as is the possibility if not likelihood that the plates were variable in length according to maturity of the shell. The late Middle Permian species from Queensland, Australia, called *Streptorhynchus pelicanensis* Fletcher (1952, p. 8, pl. 1, fig. 1), and best figured by Etheridge Jnr (1892, pl. 12, fig. 1-6) and Dear (1971, pl. 1, fig. 1-8) was tentatively referred to *Grumantia* by Waterhouse (1982a), but this seems unlikely, given the lack of differentiated ribbing and lack of dental supports that reach the floor of the valve. The species has well developed socket plates, without extended erismata, unlike *Streptorhynchus*. *Grumantia costellata* Clarke (1990, p. 56, fig. 4A-M; 1992, p. 14, Fig.4A-K) from the basal Bundella Shale and other very early Permian localities in Tasmania has distinctly lower dental supports than in *Arctitreta-Grumantia*, and unlike *Streptorhynchus* has sturdy but thick crural plates like those of *Notostrophia* Waterhouse, 1973, 1982a from Early Permian of New Zealand. In the two described species assigned to this genus in New Zealand, the ribs are fine over the ventral valve and coarse over the dorsal valve, and similar ornament is developed in *Grumantia costellata* Clarke (see Clarke 1992, Fig. 4A, B, E), involving fine ventral ribs, and coarse dorsal ribs as figured in Clarke (1992, Fig. 4H). The species should be transferred to *Notostrophia*. There appears to be no monticulus (Clarke 1990, Fig. 4.6), but only as judged from an internal mould.

Grumantia kempei (Andersson, 1914)

Fig. 14 – 17

1914 *Streptorhynchus kempei* Andersson in Wiman, p. 58, pl. 10, fig. 22-27, pl. 11, fig. 1-10, pl. 12, fig. 1-8, pl. 13, fig. 11-13.
1931 *S. kempei* – Frebold, pp. 19, 41, pl. 6, fig. 1-3.

?1937b *S. kempei* – Stepanov, p. 109, pl. 1, fig. 2, 6.
1955 *S. kempei* – Dunbar, p. 63, pl. 1, fig. 1-13, pl. 32, fig. 9, 10.
1963 *Grumantia kempei* – Ustritsky, p. 70, pl. 2, fig. 1-3.
?1964 *S. kempei* – Gobbett, p. 52, pl. 2, fig. 3.
1971 *Arctitreta* cf. *A. kempei* – Brabb & Grant, p. 14, pl. 2, fig. 21, 22, 25.
1971 *Arctitreta* sp. Bamber & Waterhouse, pl. 22, fig. 1-4.
1979 *A. kempei* – Manankov, p. 76, pl. 6, fig. 1?, 2-4, pl. 13, text-fig. 31-33.
?2008 *Arctitreta* cf. *A. kempei* Angiolini & Long, p. 92, Fig. 4H.

Diagnosis: Moderately low inflation, broad ventral umbo and consistently wide hinge, convex pseudodeltidium, without a monticulus. Weakly differentiated ribs. Slender dental plates reaching floor of valve at least during early growth stages. Muscle field of moderate width in both valves, becoming very wide in fully mature shells. Perideltidium not developed.

Lectotype: Specimen figured as *Streptorhychus kempei* [Andersson in Wiman, 1914, pl. 10, fig. 24-27) from Spiriferenkalk, Bjørnøya, SD Gobbett (1964, p. 52).

Material: Two ventral valves from GSC loc. 36760, possible Degerböls Formation. Three ventral valves and specimen with valves conjoined from C-4015, and dorsal valve from GSC loc. 58951, both from Trold Fiord Formation, Ellesmere Island. A small silicified but obscure dorsal valve from GSC loc. 53846, *Dyoros modestus* Zone, unnamed sandstone unit, McDougall Pass, Richardson Mountains. A silicified ventral valve from GSC loc. 53872, *Cameronovia milleri* Zone, Scho Creek, unnamed sandstone, Richardson Mountains.

Dimensions in mm:

Width	Length	Height	Specimen
44	41.5	10.5	both valves
66	64+	20	GSC 36960 ventral valve
54	50+	13.5	GSC 36756 ventral valve C-4015
62	68	?9	vental valve

Description: Shells subequidimensional, with extended ventral umbo and angle measuring close to 110º up to 130º, slightly irregular, posterior walls extending to moderately wide hinge with cardinal angle varying between 90º and 110º, rarely as low as 80º, tiny abruptly angled ears in some specimens, maximum shell width placed towards the anterior third of shell length. Ventral interarea low and triangular, in some shells ending abruptly at hinge, convex pseudodeltidium bearing fine longitudinal striae, and each side marked by grooves parallel to hinge, no specimens showing any sign of a perideltidium. The ventral valve is highest at the hinge, and is flatly convex, diminishing steadily in height to the anterior and lateral commissure, and bearing shallow median sulcus. Ventral ribs are fine, with ten or eleven in 5mm near the anterior margin of the ventral valve, and differentiated into four orders, coarser ribs about three in 5mm though the number varies, with two common. Lower order finer ribs number fourteen in 5mm over both valves and lie over the primary and second-order ribs, and rarely very fine ribs numbering twenty five to thirty in 5mm are preserved on the outer layer of shell, though this has often been removed. The dorsal valve is more convex, with better formed narrow sulcus, and small less convex ears, with maximum inflation just in front of the hinge. Maximum shell width lies close to mid-length of the dorsal valve. No dorsal interarea is visible. Ribs on the dorsal valve are complex, in at least four orders, with narrow crests and moderately wide interspaces. Prominent ribs number usually eight in 5mm and numbering six to seven in 5mm near the anterior margin, and about 24 to 26 fine ribs lie in 5mm, though these are lost from parts of the shell. Some twenty five fine ribs are present in 5mm on the posterior dorsal valve GSC 36764 from GSC loc. 58951.

The Degerböls specimen GSC 36960 is close in shape, but has fine costellae that are slightly less differentiated, although the very fine ribs are present in patches. As suggested in Fig. 17, the apparent variability in ribbing may be caused by the loss of an outermost very thin layer with densely ribbed shell from some specimens.

Dental ridges comparatively high, but other internal aspects are not revealed in most specimens.

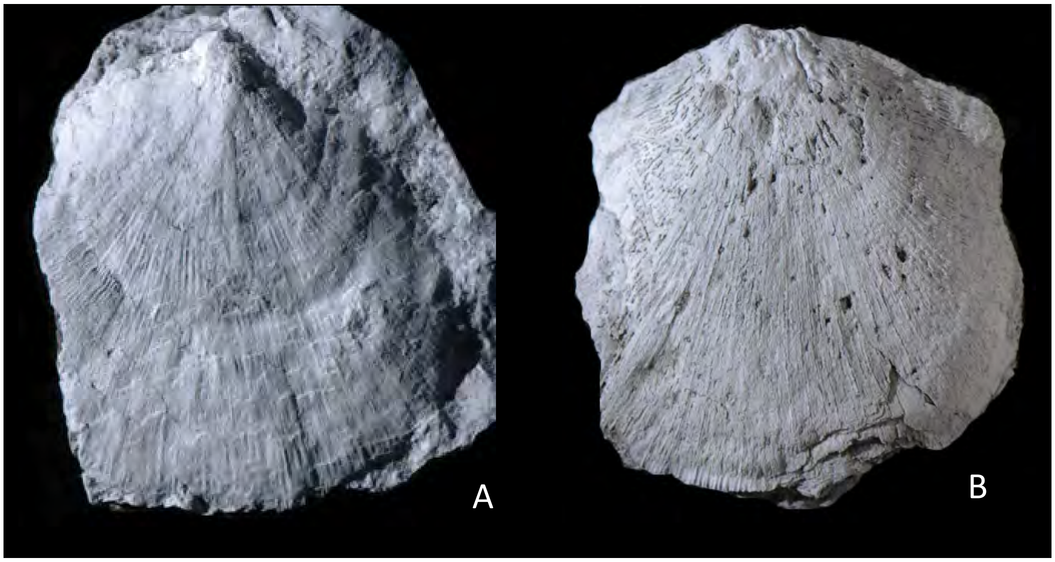

Fig. 14. *Grumantia kempei* (Andersson). A, worn ventral valve GSC 140694. B, worn ventral valve GSC 36756. From C-4015, Trold Fiord Formation, Ellesmere Island, x1.

The material figured from the Permian sandstone unit at section 116P-1 in the Yukon Territory, as described in Bamber & Waterhouse (1971, pl. 22, fig. 1-4) from GSC loc. 53850 and 53872 as detailed by Bamber (1972), is correlated with the *Cameronovia milleri* Zone at the top of the marine Permian in the Yukon Territory. The material is silicified, and figures show aspects of a ventral and dorsal valve, with exterior and interior intact. The small specimens are slightly transverse, and the ventral valve carries the suggestion of weakly differentiated ears, and the dorsal umbo projects slightly beyond the hinge. There is a low broad ventral interarea and no visible perideltidium, and rounded pseudodeltidium with no sign of a monticulus. Distinct dental plates are developed but do not reach the floor. The ventral valve has a moderately small but indistinct ventral muscle field. The dorsal muscle field is comparatively large, and divided by high myophragm. The shell appears to be densely extropunctate. A small ventral valve from GSC loc. 53846 in the Richardson Mountains shows slender dental supports that posteriorly rest on the floor of the valve, much like those of type *Arctitreta*.

Resemblances: These Canadian specimens are characterized by their wide hinge and low inflation, moderately differentiated ribbing, and convex pseudodeltidium. From shape and nature of the pseudodeltidium and dental plates, they are identified with *Grumantia kempei*, which is based on Spitsbergen material that is not completely well preserved, as analysed by Dunbar (1955), and involves occurrences from the Spiriferenkalk as in Wiman 1914, Gobbett 1964, and Angiolini & Long 2008 in the Spirifer

Limestone (Vöringen Member), whereas Stepanov (1937) recorded the species from younger beds, followed by other authors elsewhere in the arctic. The species is provisionally distinguished from *Arctitreta pearyi* Whitfield by its convex pseudodeltidium, absence of monticulus, broad hinge and different outline of lateral walls. The specimen described from the Vøringen Member as *Arctitreta* cf. *kempei* by Angiolini & Long (2008, Fig. 4H) from the ENS collection, made in central Spitsbergen, has wide hinge, low broad ventral umbo and weakly differentiated costae. Nothing is shown of the pseudodeltidium or interior. The synonymy includes material close in the presence of a wide hinge, but otherwise incompletely known, especially in the case of Stepanov (1937b), and moderately obscure material figured by Ustritsky (1963) and Gobbett (1964). The material reported from the Assistance Formation by Harker (1960) appears to be closer to *pearyi.* Material compared to *Arctitreta kempei* by Brabb & Grant (1971, p. 14, pl. 2, fig. 21, 22, 25) from the lower limestone of the Takhandit Formation in Alaska has a wide hinge, and subdued costation in the mature form, and is represented by a few specimens. The nature of the pseudodeltidium and dental supports, if any, were not indicated. Silicified material figured by Stehli & Grant (1971, p. 510, pl. 61, fig. 9-26) from Axel Heiberg Island appears to have a narrower hinge in several specimens (fig. 12-16) and one specimen shows a dental plate (fig. 15). The pseudodeltidium is traversed longitudinally by a shallow median groove, and the material is described below as a new species of a new genus *Fissulina*.

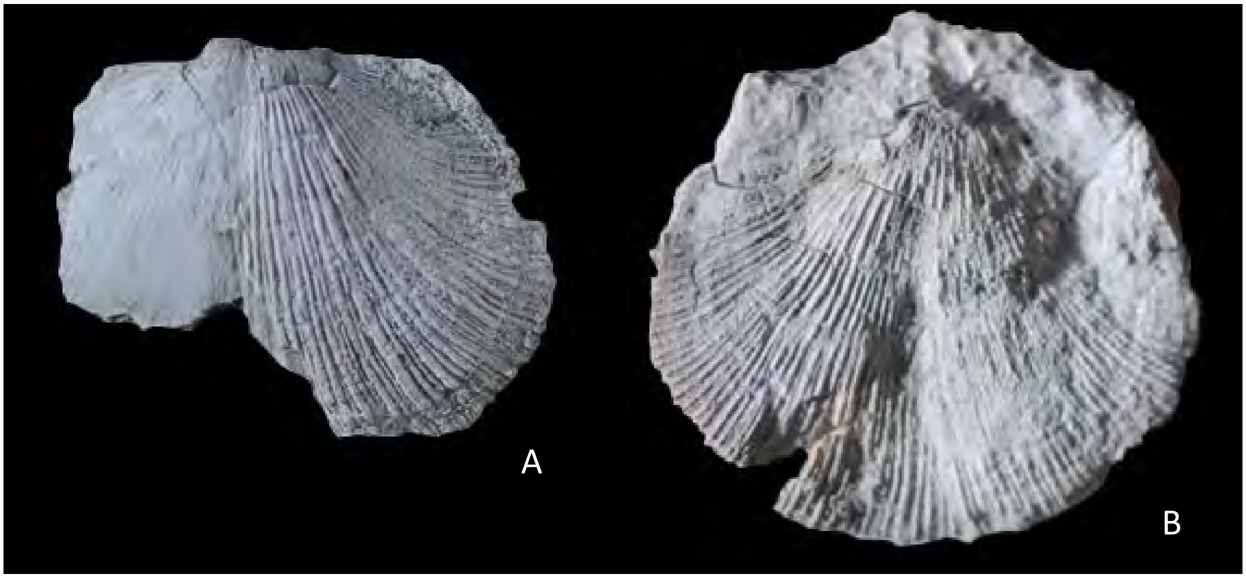

Fig. 15. *Grumantia kempei* (Andersson in Wiman). A, broken dorsal valve GSC 36764 x1.5 from GSC loc. 58951. B, dorsal aspect of specimen GSC 36754 x1.5 from C-4015. Trold Fiord Formation, Ellesmere Island.

An internal ventral valve was figured as *Arctitreta kempei* in Kalashnikov et al. (1990, pl. 4, fig. 4, pl. 9, fig. 9) from the Levorkut beds of the Petchora Basin, and is likely to belong to the present species, but is too incomplete to allow certainty. Of the

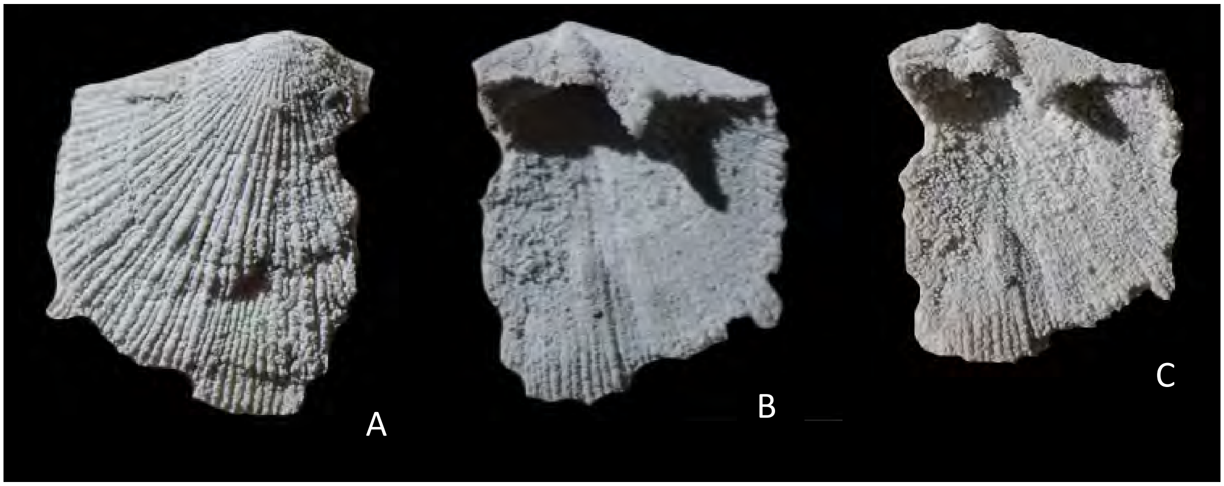

Fig. 16. *Grumantia kempei* (Andersson) in Wiman. A, B, C, external and internal aspects (with slightly different degrees of tilt for B and C) of broken ventral valve from GSC loc. 53872, Scho Creek, *Cameronovia milleri* Zone, unnamed limestone, Richardson Mountains, x3.

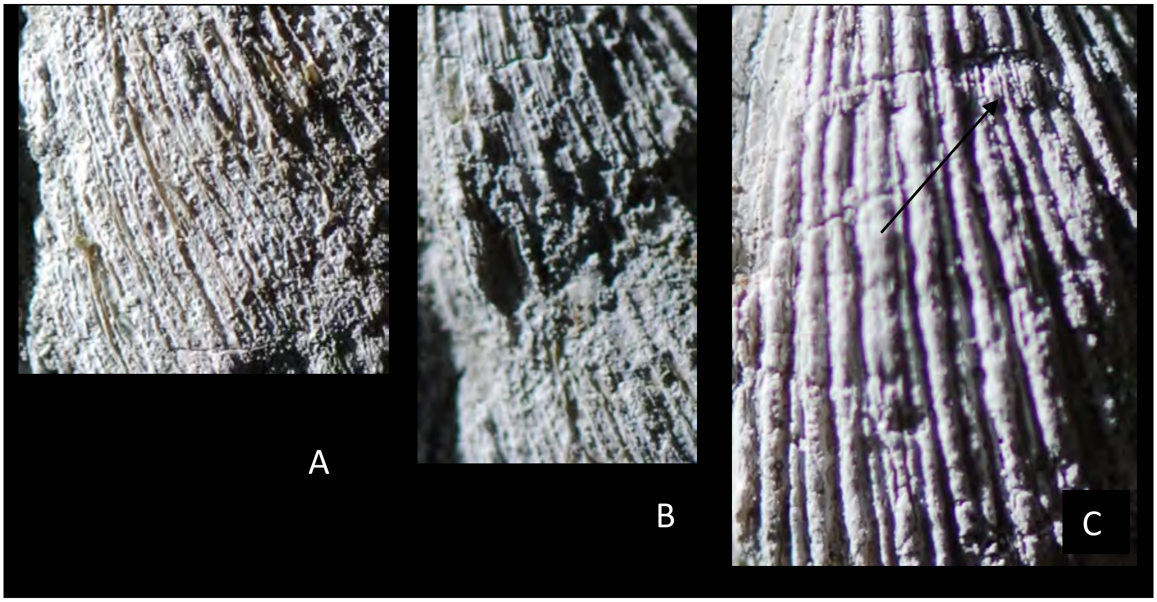

Fig. 17. *Grumantia kempei* (Andersson). A, B, dorsal ornament on different parts of GSC 36754 from C-4015, near umbo, x4. C, dorsal ornament part mid-length on GSC 37664 from GSC loc. 58951 x 6, with arrow pointing to fine ribs preserved over part of shell. Trold Fiord Formation.

Spitsbergen specimens figured by Manankov (1979), that of pl. 6, fig. 1 is not at all shaped like *kempei*, and none show the nature of the dental supports or the pseudodeltidium, and ornament is poorly shown. Manankov (1979) referred *Streptorhynchus liuricus* Ustritsky (1960, p. 103, pl. 3, fig. 3-9) to synonymy of *kempei.* Material figured by Ifanova (1972, p. 87, pl. 2, fig. 1-6) from upper Artinskian and Kungurian of mainland Russia appears to be allied, with dental supports and convex pseudodeltidium, and further material would be helpful in clarifying the morphological range of attributes. There may need to be similar reservations over the affinities of Pai Hoi material ascribed to *kempei* by Ustritsky (1960, p. 102, pl. 3, fig. 1, 2). The material ascribed to the species by Dunbar (1955, p. 63, pl. 1, fig. 1-13) has a consistently wide hinge, smaller ventral muscle in small specimens, and the interarea is less triangular in large specimens. Costae become more differentiated anteriorly (pl. 1, fig. 12, 13). Given the high variability in the original population as described in Wiman (1914), there must be hesitation about discriminating any population illustrated by only a few specimens. Ribs are slightly finer and slightly more differentiated than in some Canadian shells but close to those from C-4015. It seems possible that the Greenland specimens indicate a natural drift from the morphological range displayed by type *kempei*, possibly reflecting a different geographic position, or different age from that of the Canadian specimens.

According to Ustritsky (1979, table 1), *Grumantia kempei* is found in the middle and upper Selanderneset Suite, or Hotvinden Member of Spitsbergen.

. Material figured from Western Australia by Thomas (1958, pl. 13, fig. 1-6) as *Streptorhychus hoskingae* has a rounded pseudodeltidium and no erismata, and so may well belong to *Grumantia*.

***Grumantia*? sp.**

Fig. 18

Fig. 18. *Grumantia*? sp., GSC 140696, dorsal aspects of exterior, and internal mould after leaching. From JBW 631, Takhandit Formation, x1.25.

Description: A specimen with valves conjoined from JBW 613, Takhandit Formation of Yukon Territory, possibly belongs to *Grumantia*, because it has a broad and convex pseudodeltidium. But the hinge is shorter than in *Grumantia kempei* (Andersson), with high interarea, and no dental plates are preserved. The interior of the dorsal valve is seldom displayed in Canadian material, but this specimen, prepared by leaching in acid, shows a short high septum and short high crural plates, that help enclose ovally subtriangular muscle impressions. The ventral valve shows a very low posterior ridge, dividing two faintly raised oval areas opposing the dorsal muscle impressions.

Genus ***Fissulina*** n. gen.

Derivation: fissum – a cleft, Lat.

Diagnosis: Distinguished by groove along the midline of the convex pseudodeltidium. Ribs differentiated, teeth ridges with supporting plates reaching floor of the valve, at least in early growth stages.

Type species: *Fissulina delicatula* n. sp. from Sabine Bay Formation of Ellesmere Island, Canada, here designated.

Discussion: This genus is proposed for species distinguished by the nature of the pseudodeltidium, which lacks a monticulus and is not fully convex, but is traversed externally by a median groove, as is clearly shown in the original illustration provided by Stehli & Grant (1971, pl. 61, fig. 16). *Bothrostegium* Cooper & Grant (1974) from the Road Canyon Formation (Roadian) of Texas is similar in this respect, but is believed to lack dental supports, even in early ontogeny. A further likely species of *Fissulina* was described as *Streptorhynchus stoschensis* Dunbar (1955, pl. 2, fig. 1, 7, 9, 10, pl. 32, fig. 6) from the "white blocks" of Late Permian age in east Greenland, but the nature of dental supports in this species remains unknown. On the other hand, Thai specimens from the Roadian Rat Buri Limestone that were ascribed to species of *Streptorhynchus* (*khwaense* and *sulculatum*) by Grant (1976, pl. 7, fig. 24, pl. 8, fig. 29, 38, aff. 43, 47, 49) and *S. johnstonei* Thomas (1958, pl. 14, fig. 1-6) from Western Australia, are referable to *Bothostegium*, because the Thai specimens lack dental supports or erismata and show a channelled pseudodeltidium.

Fissulina delicatula n. gen., n. sp.

Fig. 19

1971 *Arctitreta kempei* (not Andersson in Wiman) – Stehli & Grant, p. 510, pl. 61, fig. 9-26.

Derivation: delicatus – alluring, Lat.

Diagnosis: Comparatively small for the subfamily, narrow hinge, moderately high ventral interarea with convex pseudodeltidium traversed by well defined median channel. Well developed dental plates extending to floor of the valve, crural plates short, without erismata.

Holotype: USNM 166262 figured in Stehli & Grant (1971, pl. 61, fig. 12-16) and herein as Fig. 19C from Svartevaeg cliffs, Sabine Bay Formation (Kungurian), Axel Heiberg Island, here designated.

Description: The material displays all critical features well, though valves are broken around the edges. The shape is elongate, with comparatively narrow hinge and moderately high interarea, with growth lineations parallel to the hinge, no visible perideltidium, and bearing a convex pseudodeltidium traversed by a median channel. The dorsal interarea is very low, or absent. No ventral sulcus or dorsal fold is developed, and ribs are fine, at six to seven in 5mm antero-laterally, not markedly differentiated. The teeth are stubby and the ridges supported by slender outwardly curved plates which extend to the floor of the ventral valve (Stehli & Grant 1971, pl. 61, fig. 15). The ventral muscle field is only moderately large, placed between the dental supporting plates, with longitudinal grooves and ridges, and the posterior lateral floor is thickened, with well defined and closely spaced pits. In the dorsal valve, the cardinal process is high with four terminal projections, which vary in different specimens. The cardinal process is supported by high crural plates with prominent crural points (also known as socket ridge projections). The crural plates extend a little beyond the dental sockets, and enclose a moderately wide muscle field. The floor each side is little thickened, and shows signs of the external ribbing.

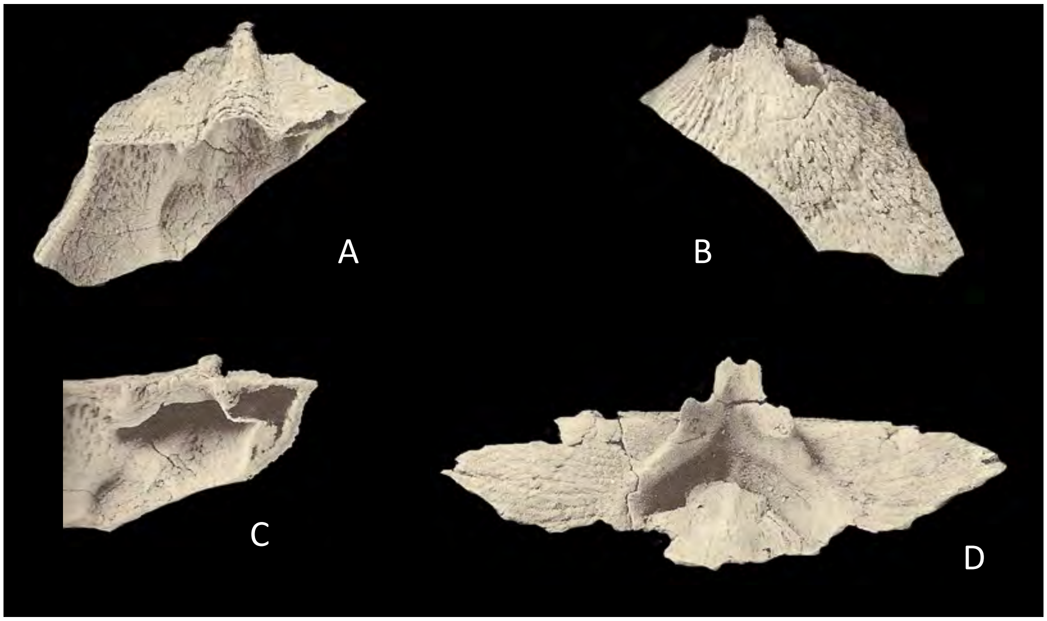

Fig. 19. *Fissulina delicatula* n. sp. A, B, dorsal and ventral aspects of ventral valve USNM 166261. The delthyrial channel is better defined than shown here. C, ventral interior 166262, holotype. D, dorsal interior, USNM 166265. Specimens from Sabine Bay Formation, Axel Heiberg Island, x2. (Stehli & Grant 1971).

Resemblances: Three species of *Bothrostegium* described by Cooper & Grant (1974) from the Road Canyon Formation of Texas have a similar channel along the middle of the pseudodeltidium. These have a broader hinge, higher ventral interarea, wider as a rule than in the present form, and usually stronger or more differentiated ribbing. In the ventral valve, there are no dental supporting plates that extend to the floor of the valve.

Streptorhynchus stoschensis Dunbar, 1955, p. 65 from “white blocks” of Permian limestone (?Lopingian) in Triassic conglomerate of Greenland seems likely to be congeneric with *Fissulina delicatula*, given its geographic proximity to Ellesmere Island, but the ventral interior is not known. Allied material was also figured by Frebold (1931, p. 11, pl. 1, fig. 5-11) as *S. pelargonatus*. Shells are small with wide subauriculate hinge and slightly more differentiated ornament, and the channel along the pseudodeltidium is clearly developed.

Material recorded from the Blackie Formation in the Yukon Territory by Waterhouse (2018b, p. 70, Fig. 52, 53) as Streptorhynchin gen. & sp. indet. has a ridge along the inner side of the pseudodeltidium, implying that an external channel was developed, but the outer shell is not preserved, and nothing is shown of internal plates. A similar channelled pseudodeltidium is preserved in *Bothrostegium* and *Fissulina*.

Superorder Productusiformi (Productiformi) Waagen, 1883

Order Chonetesida (Chonetida) Muir-Wood, 1955

Superfamily **CHONETESOIDEA** (**CHONETOIDEA**) Bronn, 1862

Family **RUGOSOCHONETESIDAE** (**RUGOSOCHONETIDAE)** Muir-Wood, 1962

Subfamily **RUGOSOCHONETESINAE** (**RUGOSOCHONETINAE)** Muir-Wood, 1962

Genus ***Neochonetes*** Muir-Wood, 1962

Diagnosis: Transverse moderately plano-convex shells with capillate ornament, feeble to distinct sulcus.

Type species: C*honetes dominus* King, 1938, p. 259 from Lower Pennsylvanian of Texas, OD.

Neochonetes culcita n. sp.

Fig. 20 – 22, 24B (part)

?1960 *Chonetes* (*Paeckelmannia*) *capitolinus* [not Toula] – Harker & Thorsteinsson, p. 53, pl. 16, fig. 11, 12.
?1971 *Chonetina*? cf. *C. superba* Gobbett – Brabb & Grant, p. 14, pl. 1, fig. 37.
1971 *Neochonetes* sp. Bamber & Waterhouse, p. 174, pl. 19, fig. 13-20.

Derivation: culcita – cushion, Lat.

Diagnosis: Transverse with alate cardinal extremities as a rule, fine capillae and shallow ventral sulcus.

Holotype: GSC 27019, from GSC loc. 53826, unnamed sandstone, shale and limestone of *Neochonetes culcita* Zone at north McDougall Pass, northern Richardson Mountains, figured in Bamber & Waterhouse (1971, pl. 19, fig. 16, 17), here designated.

Material: Four specimens with valves conjoined and four ventral valves from GSC loc. 26406, Assistance Formation, Devon Island, one ventral valve from C-4002, and four ventral valves and fragments from C-4016, Assistance Formation, Ellesmere Island. Two ventral valves from JBW 631, Takhandit Formation, Yukon Territory. Five silicified ventral valves and two silicified dorsal valves from GSC loc. 53826, *Neochonetes culcita* Zone, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory.

Dimensions in mm:

Width	Length	Height
32	22	7.5
34	22	7
30	21	6

Description: Shells transverse, broad ventral umbo with angle of 130-140° protruding a little beyond the posterior margin, maximum width at hinge or near mid-length, small ears with lateral margin inclined at 90° from posterior margin and curving outwards towards anterior. In some specimens the cardinal extremities appear obtuse, but this is probably due to breakage. The ventral interarea is wide and well formed, with pseudodeltidium that in one specimen is medianly grooved, possibly by damage, and the low dorsal interarea is now occupied medianly by the bilobed face of the cardinal process, protruding into the delthyrium. A ventral sulcus is variably developed, commencing at the umbo in one specimen and well defined for the length of the shell, widening a little anteriorly. In other specimens the sulcus is shallower and in one shell commences 9mm in front of the umbonal tip. The dorsal fold is broad and low, commencing a little in front of the hinge. Ornament consists of capillae, eighteen in 5mm at the anterior margin of the dorsal valve, and of much the same density over the ventral valve, which is commonly worn smooth, or worn to show minute pustules or pits of the internal shell. With wear, tiny pits appear along the interspaces, before the capillae are removed by further wear. A row of spines emerges from the posterior wall along the junction of the ventral interarea with the outer shell, and there are no definite body spines.

Specimens were recorded from GSC loc. 53826 in Bamber & Waterhouse (1971) as moderately well preserved specimens, showing ventral internal detail well. They came from a sandstone unit in the north McDougall Pass of the Richardson Mountains in northern Yukon Territory, at section 116P-9. A short septum is developed posteriorly, and the posterior shell between the teeth is slightly thickened. There are small slightly elongate oval or round adductor scars. Two vascular trunks (which are raised rather than impressed as according to the *Revised Brachiopod Treatise*) extend well forward, divided by a groove occupied by a low myophragm that extends beyond almost to the anterior margin. Radiating ridges and grooves are developed submedianly, and in front the anterior floor of the valve is covered by subevenly spaced pustules, which may be weakly aligned in radial rows.

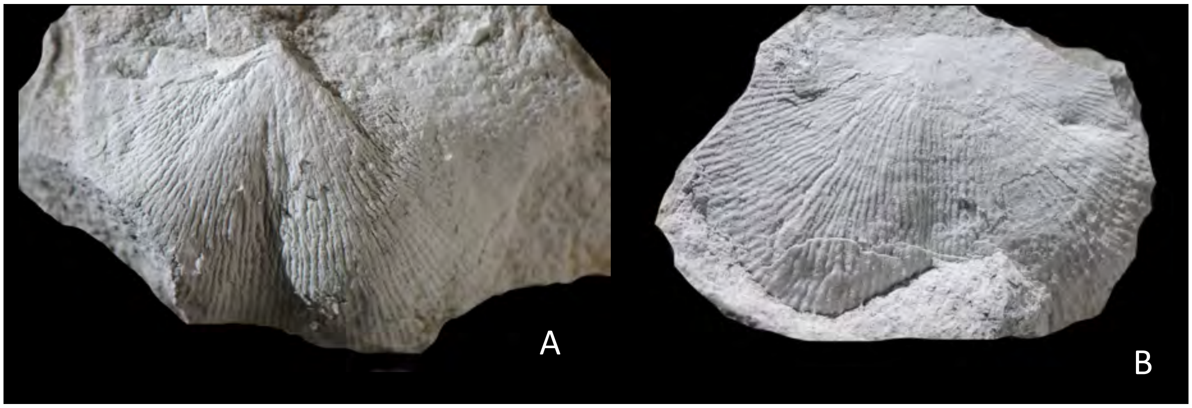

Fig. 20. *Neochonetes culcita* n. sp. A, B, ventral valves GSC 140703 and GSC 140704 from JBW 631, Takhandit Formation, x2.

The dorsal interior is exposed only in material from GSC loc. 53826, as figured in Bamber & Waterhouse (1971), to show the inner face of the cardinal process, a long median septum extending from in front of a large cardinal process pit to half or slightly more than half of the length of the valve, strong anderidia, small divided adductor scars, and high marginal ridge. Pustules lie over the anterior valve.

Resemblances: This species is characterized by its shape and slightly variable development of its sulcus. Bamber & Waterhouse (1971) figured silicified *Neochonetes* from the Permian sandstone unit of the Richardson Mountains in the north Yukon territory, which shows internal features of the dorsal valve well, and in two specimens the cardinal extremities are intact, but they may differ on opposite sides of the same individuals and have been worn for other specimens. The specimen recorded from the Assistance Formation by Harker & Thorsteinsson (1960, p. 53, pl. 16, fig. 11, 12) as *Chonetes* (*Paeckelmannia*)? *capitolinus* Toula might be conspecific, but has only a median flattening anteriorly rather than sulcus, and was evaluated by Harker as having had a smooth exterior originally, though it may well have been worn smooth. A shell identified as *Chonetina*? cf. *C. superba* Gobbett by Brabb & Grant (1971, p. 14, fig. pl. 1, fig. 37) is moderately close to the present form in outline, and has a weakly ribbed surface and

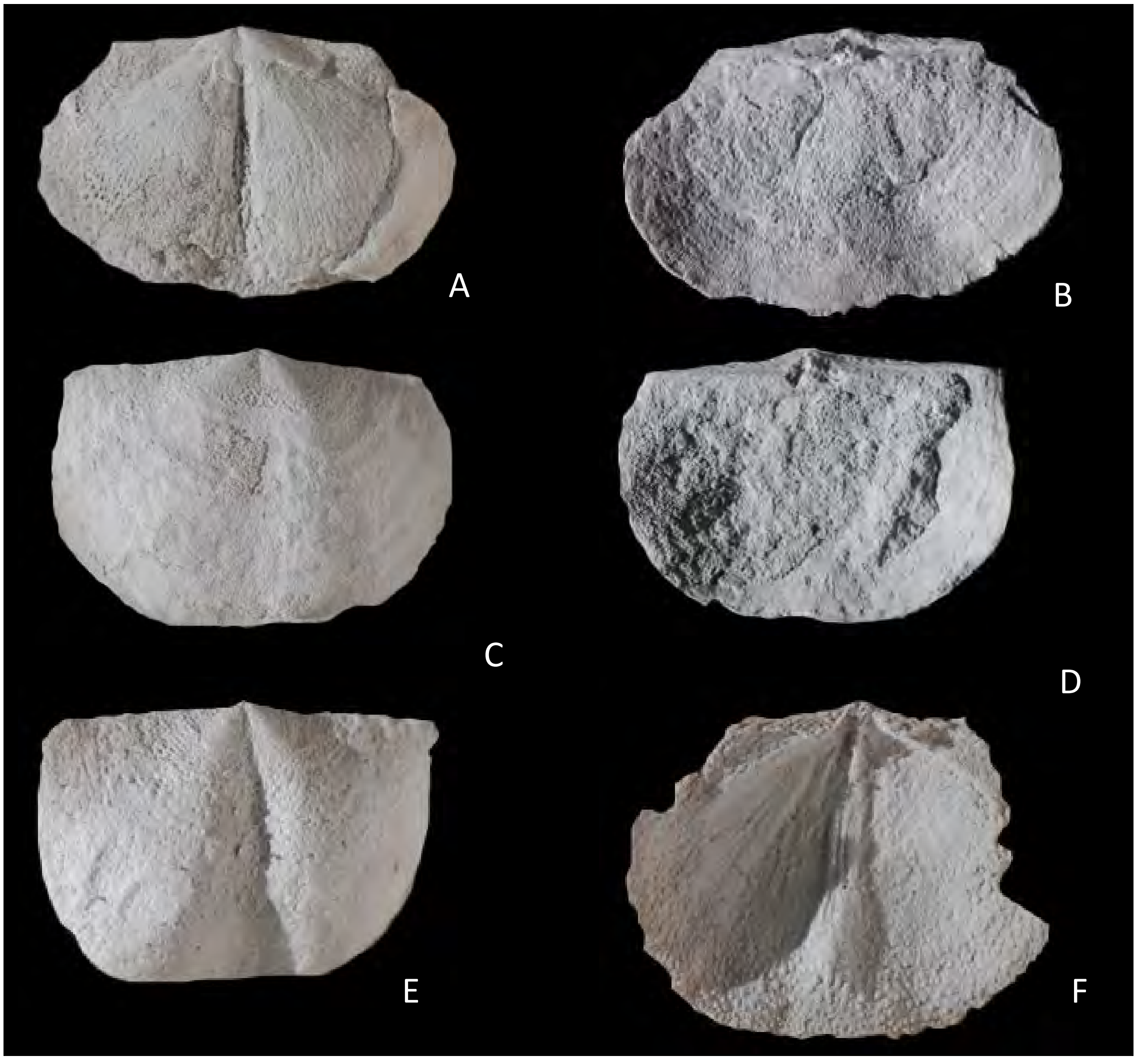

Fig. 21. *Neochonetes culcita* n. sp. A, B, ventral and dorsal aspects of specimen GSC 140697 with valves conjoined. Ribs are faintly visible in patches over the anterior left of the dorsal valve. C, D, ventral and dorsal aspects of specimen GSC 140698 with valves conjoined. E, ventral aspect of specimen with valves conjoined, GSC 140699. Specimens from GSC loc. 26406, Assistance Formation, Devon Island, x1.5. F, silicified internal ventral valve GSC 140700, x2, from GSC loc. 53826, McDougall Pass, Richardson Mountains.

shallow narrow sulcus. It was stated to be "fairly common" in the sandstone unit of the Takhandit Formation at the type section in Alaska, and more material would show the degree of variability and consolidate any approach to the present species. As noted by Brabb & Grant, the material is nothing like *Chonetina*, which is an anopliin with deep ventral sulcus and swollen lateral flanks. The original material compared with *superba* by Gobbett (1964, pl. 15, fig. 2-6) from the middle Brachiopod Chert shows no sign of radial ribs, and though moderately close in outline does not belong to *Chonetina*, having more diverging posterior walls and no raised median ventral valve and broad rather than narrow sulcus. Nor do any of the other Spitsbergen chonetoids described by Gobbett (1964) come close to the present specimens, all being described as smooth-shelled, except for some small capillate ventral valves from the earlier Permian Cora Limestone (Gobbett, 1964, p. 118, pl. 15, fig. 1). These are quite like the Canadian material, but much older, with small protruding ears and suggestions of a weak ventral sulcus. *Neochonetes dominus* (King) differs in shape with slightly smaller ears and more anterior shallow sulcus, and the diductor scars are rimmed posteriorly by a ridge, not seen in the present form.

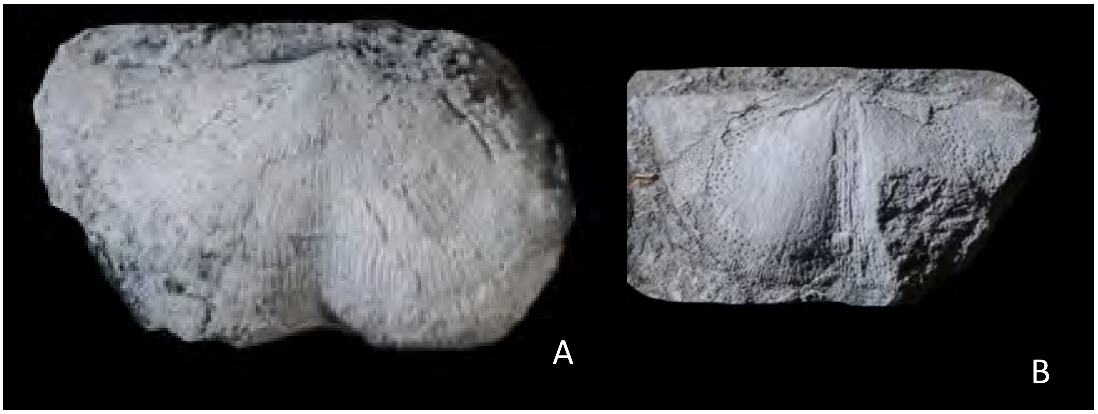

Fig. 22. *Neochonetes culcita* n. sp. A, ventral valve GSC 140701 from GSC loc. 26406, Assistance Formation, Devon Island, x2. B, ventral internal mould GSC 140702 from C-4002, Assistance Formation, Ellesmere Island, x1.5.

Only three species were ascribed to *Neochonetes* in the extensive overview of Russian Arctic material in Sarytcheva (1977a). *N. brama* (Fredericks) has a deep median ventral groove, and *N. dukhovae* (Sokolskaya) is very transverse. But specimens assigned to *N. acanthophorus* (Girty) from upper Carboniferous are closer, although they are distinguished by a more semicircular outline (Afanasieva in Sarytcheva 1977a, p. 38, pl. 3, g, i, h, 5, 6). *N. adzvensis* (Ifanova, 1972, p. 88, pl. 2, fig. 7-9; Kalashnikov et al. 1990, pl. 3, fig. 6) from the Talatin Suite and Kungurian Stage of Russia is more transverse and less elongate.

Some of the west Australian specimens ascribed to *Neochonetes* (*Sommeriella*) *pratti* (Davidson, 1859) from the Callytharra and other horizons of Sakmarian into lower Artinskian age by Archbold (1981a, Fig. 4-6) are close to the present form, whilst mostly having a slightly broader sulcus that in some individuals commences a little in front of the umbonal tip. Further species from the younger Permian, up to Wuchiapingian in age, are slightly more rounded in outline and may be slightly more elongate, but do come close. On the other hand, *N. beatusi* Waterhouse (1964a) from Wordian beds of New Zealand is more transverse, with very slight if any ventral sulcus. As in the Canadian species, the posterior cardinal process occupies most if not all of the notothyrium.

Further specimens of *Neochonetes*, not well enough preserved to be specifically identified, came from GSC loc. 53850, in the *Cameronovia milleri* Zone at McDougall Pass, as reported in Bamber & Waterhouse (1971, pl. 22, fig. 5-7).

Subfamily **SVALBARDIAINAE** (**SVALBARDIINAE**) Archbold, 1982

Genus ***Dyoros*** Stehli, 1954

Diagnosis: Wide-hinged smooth shells with ventral sulcus.

Type species: *Chonetes consanguineus* Girty, 1929, p. 409 from Bone Spring and Skinner Ranch Formations (mid-Cisuralian) of Texas, OD.

Dyoros gentilis n. sp.

Fig. 23, 24

Derivation: gentilis – gentle, sudued, Lat.

Diagnosis: Wide hinge with small acute ears and gentle sulcus.

Holotype: GSC 140708 from GSC loc. 26406, Assistance Formation (Roadian), Devon Island, figured as Fig. 23B, here designated.

Material: Twenty ventral valves and two dorsal valves are available from GSC loc. 26406, Assistance Formation, Devon Island.

Description: The ventral valve has a broad incurved umbo, hinge at maximum width and alate cardinal extremities, smooth shell, small spines largely in quincunx, moderately well-developed sulcus and spines in a row along the hinge. The lateral margins converge forward. A wide fold is developed on the dorsal valve.

Resemblances: These specimens are moderately close to *Dyoros spitzbergianus* (Toula 1875a, p. 149, pl. 1, fig. 10; 1875b, p. 231, pl. 5, fig. 4 and Gobbett (1964, p. 123, pl. 15, fig. 19-21) from the Kapp Starotsin Formation of Spitsbergen, but the sulcus is not as deep or well defined, and the holotype as refigured in Gobbett (1964, pl. 15, fig. 19) is more elongate, though said to have been distorted. In addition, the present specimens have a wider hinge, but overall the two species are very close, suggesting that they were related and geographically distinguished. Afanasieva in Sarytcheva (1977a, p. 21, pl. 1, fig. 19-21) figured as this

Fig. 23. *Dyoros gentilis* n. sp. A, ventral valve GSC 140985. B, ventral valve GSC 140708, holotype, on block 140705. From GSC 26406, Assistance Formation, Devon Island, x3.

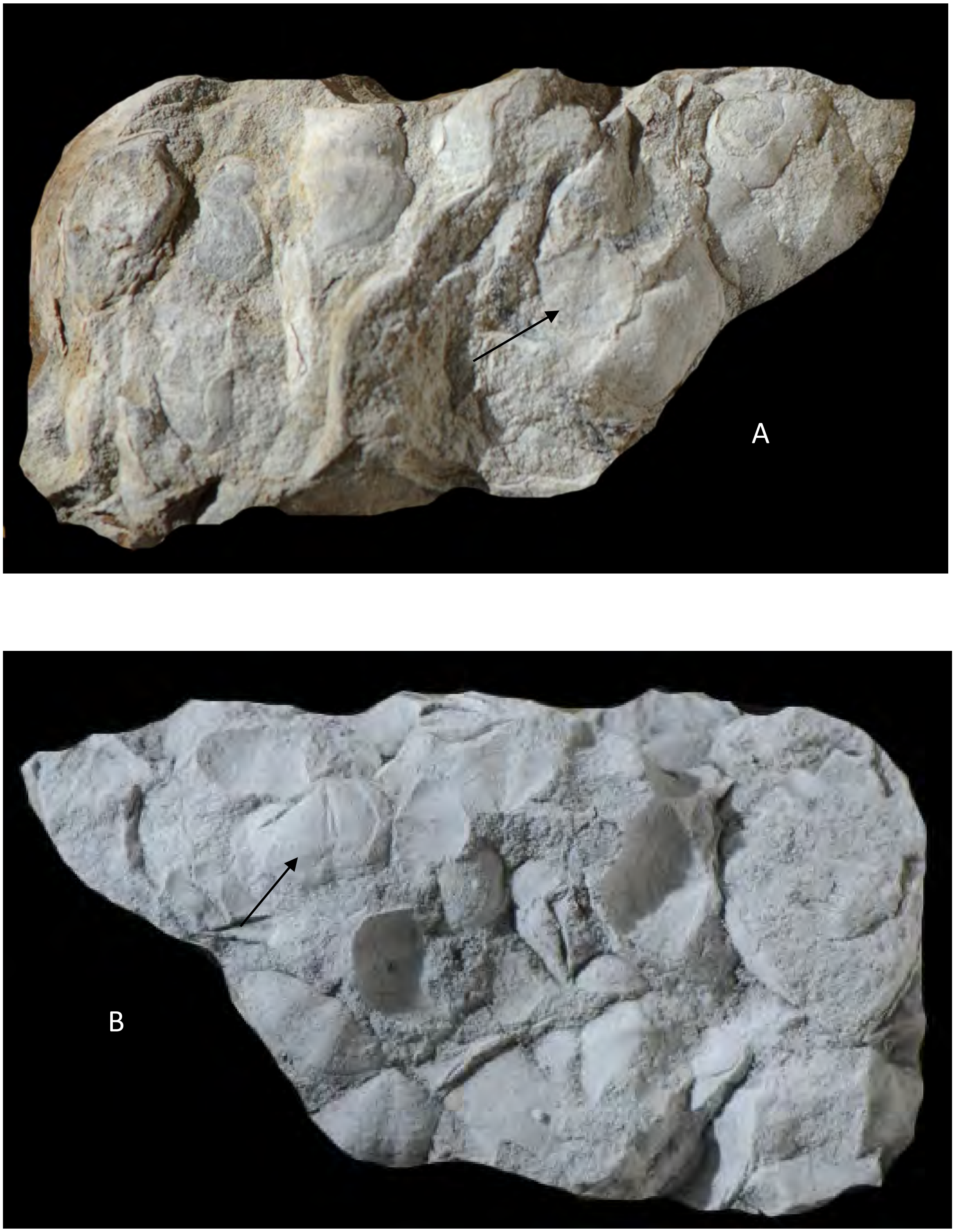

Fig. 24. *Dyoros gentilis* n. sp. A, block GSC 140705 showing crowded specimens, x1.5, from GSC loc. 26406. Worn dorsal internal mould GSC 140706 arrowed. B, the other side of the same block. The internal ventral valve GSC 140707 of *Neochonetes culcita* n. sp. amongst specimens of *Dyoros* is arrowed. Assistance Formation, Devon Island.

species material that is more elongate, and it appears unlikely to be conspecific, noting that the specimens came from a fauna of Moscovian age. The specimen identified with *Lissochonetes* cf. *spitzbergiana* (Toula) by Brabb & Grant (1971, p. 14, pl. 2, fig. 15-17) from the lower part of the limestone unit in the Takhandit Formation of Alaska is small and has a better-defined ventral sulcus and dorsal fold than in the present form. The hinge is short and the cardinal extremities well rounded.

Dyoros modestus n. sp.

Fig. 25

1971 *Lissochonetes* aff. *ostiolatus* [not Girty] – Bamber & Waterhouse, p. 178, pl. 21, fig. 4-7.

Derivation: moderate, discreet, Lat.

Diagnosis: Ears very small, ventral sulcus shallow and broad.

Holotype: GSC 27025 (Fig. 25A) from GSC loc. 53823, *Dyoros modestus* Zone, Permian sandstone unit in McDougall Pass, Richardson Mountains, Yukon Territory, here designated.

Fig. 25. *Dyoros modestus* n. sp. A, ventral valve GSC 27025, holotype. B, dorsal valve GSC 27027. C, dorsal interior, GSC 27026. Specimens from GSC loc. 53823, unnamed sandstone, north Richardson Mountains, x1. (Bamber & Waterhouse 1971).

Material: Some ten ventral and dorsal valves from GSC loc. 53823, silicified and etched from matrix.

Description: The holotype measures 37mm wide and nearly 23mm high, with wide hinge and weakly alate cardinal extremities. The sulcus commences in front of the beak and extends to the anterior margin with an angle of 50º, and is gently concave without median channel. The dorsal valve has a corresponding low fold, with angle close to 40º. The hinge lies at maximum width, but in both valves the ears are comparatively small for the genus. The shell surface is smooth, apart from low growth rugae especially on the ventral valve near the lateral margins. Spines form a row each side of the umbo along the ventral hinge, and possibly lie over the ventral disc, as suggested by scattered tubercles, but this is not certain.

The dorsal valve has a deep alveolus in front of the low cardinal process, and short high dental socket ridges, joined by two short moderately high anderidia. The median septum extends a little past mid-length and is highest over mid-valve, and the brachial ridges are strong and large in outline. Dense fine pustules are developed close to the lateral and anterior margins of mature specimens.

Resemblances: Similar specimens were observed by the writer in the Van Hauen Formation of the Sverdrup Basin, but none are available for the present study. *Dyoros spitzbergianus* (Toula, 1875a) has a deeper sulcus and wider hinge. *Dyoros gentilis* n. sp. from the slightly older Assistance Formation has a narrower ventral sulcus, and the ears are close or smaller than size, suggesting it could have been ancestral. These differences apply to most species so far ascribed to *Dyoros*, with an especially large spectrum of species described from the Glass Mountains of Texas by Cooper & Grant (1975). One somewhat similar species is *D. planiextensus* Cooper & Grant (1975, p. 1234, pl. 484, fig. 38-2, pl. 485, fig. 38-51) from a lens between the Willis Ranch and Appel Ranch Members of the Word Formation in the Glass Mountains of Texas, but this has larger more pointed ears and slightly deeper sulcus. Internal features are much the same as in the Canadian material, but the brachial ridges bear large pustules. Some specimens of *Dyoros tenuis* Cooper & Grant (1975, p. 1238, pl. 486, fig. 1-27) from the China Tank and Willis Ranch Members have small ears and a broad sulcus, and the anterior margin tends to be truncated, as suggested in some Yukon material. The Texas specimens are much smaller, and tend to have a longer dorsal septum, but in other respects, appear to be closest of species from the Glass Mountains. There is considerable approach to the shells described as *Chonetes ostiolatus* and “varieties” *impressus* and *minisculus* of Girty (1910, pp. 25-27, pl. 1, fig. 12-20) from the Phosphate beds of Park City Formation in Wyoming and Idaho. The shells are slightly smaller than those from the Yukon, and vary a little in the auriculation of the ears and cardinal extremities. They show the same broad shallow anterior sulcus, and appear to lack the low anterior dorsal fold found in the present form.

Dyoros grandis Afanasjeva, 1977, p. 15, pl. 1, fig. 15-18 from the lower Kapp Starotsin beds of west Spitsbergen, also figured by Grunt (2006a, pl. 2, fig. 1-4), has very slightly wider ventral sulcus and smaller ears, and may be rated as closely allied. A species called *D. lamellosa* from the Houtoumiao Formation in Inner Mongolia has ears more reduced than in the present form but is otherwise close in general proportions and sulcal development (Liu & Waterhouse 1985, p. 12, pl. 1, fig. 2-6, 9).

Order PRODUCTUSIDA (PRODUCTIDA) Waagen, 1883

Suborder PRODUCTUSIDINA (PRODUCTIDINA) Waagen, 1883

Superorder **OVERTONIAOIDEA** (**OVERTONIOIDEA)** Muir-Wood & Cooper, 1960

Family **OVERTONIAIDAE** (**OVERTONIIDAE)** Muir-Wood & Cooper, 1960

Subfamily **OVERTONIAINAE** (**OVERTONIINAE**) Muir-Wood & Cooper, 1960

Genus ***Fimbrininia*** Waterhouse, 2013

Diagnosis: Ventral spines aligned commarginally across the shell in single rows along rugae, spines with swollen bases not posteriorly prolonged, unlike those of *Fimbrinia* Cooper.

Type species: *Fimbrininia spinosa* Waterhouse, 2013 from Member D (Asselian) in lower middle Jungle Creek Formation, Yukon Territory.

Fimbrininia sp.

Fig. 26

Material: Three small ventral valves, two preserved as external moulds, from JBW 631, two ventral valves from GSC loc. 56922, mid-Takhandit Formation.

Description: The specimens are very small, and display low commarginal rugae each separated by a narrow groove across the entire valve. A row of spines is developed along the crest of each rugation, with evenly swollen bases, which are not prolonged posteriorly as in the allied genus *Fimbrinia* Cooper, 1972. That the specimens have been reworked from underlying sediment remains a possibility.

Fig. 26. *Fimbrininia* sp., a tiny ventral valve GSC 140709 from JBW 631, Takhandit Formation, x 3.

Superfamily **HORRIDONIAOIDEA** (**HORRIDONIOIDEA)** Muir-Wood & Cooper, 1960

Family **HORRIDONIAIDAE** (**HORRIDONIIDAE)** Muir-Wood & Cooper, 1960

Subfamily **HORRIDONIAINAE** (**HORRIDONIINAE**) Muir-Wood & Cooper, 1960

Genus ***Horridonia*** Chao, 1927b

Diagnosis: Large, three rows of spines close to ventral hinge and few scattered erect anterior spines; spines in two rows over dorsal ears, of subequal strength, short third row, few or no other dorsal spines. Low pustules may be present, as well as low costae and plicae.

Type species*: Productus horridus* Sowerby, 1823, p. 17 from Magnesian Limestone (Wuchiapingian), England, SD Schuchert & LeVene (1929, p. 68).

Discussion: *Horridonia* has spines close to the hinge in both valves. Shells ascribed to *Horridonia horrida* by Muir-Wood & Cooper (1960) and Brunton et al. (2000) are based mostly on Zechstein material, rather than type material from the Magnesian Limestone of England. *Horridonia horrida* (Sowerby), interpreted from the type specimen as figured by Sowerby (1823, pl. 319, fig. 1) [= Sowerby 1822 in Muir-Wood & Cooper 1960 and Brunton et al. 2000] and King (1850, pl. 11, fig. 2) and additional specimens from Derbyshire and Humbleton Hill, Durham, figured by King (1850, pl. 11, fig. 3, 6, 7), has two thick cardinal spines in an anterior dorsal ear row, and a better developed median row, and well developed dorsal hinge row, and displays a transverse fold across the dorsal ears, with variations figured by Gobbett (1961, pl. 3). Whereas the first ventral row in the Canadian species described below as *Horridonia grandis* consists of a few thin spines and does not extend far from the ventral umbo, the row in *Horridonia horrida* extends to the lateral margin, with lateral spines becoming large. The second row in the Canadian species commences well away from the ventral umbo and consists of three or four spines, developed only on the ears. The second row in *Horridonia horrida* commences close to the umbo on the umbonal slopes, and extends to the lateral margin. Nodes and rare spines suggest an incipient or sparsely developed third row on the Canadian species, and in *Horridonia horrida* the few spines of the third row are stronger. *Horridonia horrida* lacks plicae and costae, and the degree of papillation is not known. Spines are more numerous over the ventral disc, and low radial plicae may be developed (King 1850, pl. 11, fig. 3).

Pleurohorridonia scoresbyensis Dunbar (1955) from the Late Permian of Greenland is close, having two rows of posterior ventral spines, the posterior row close to the hinge being relatively complete, unlike the row in the Canadian species of *Horridonia*. No specimen shows signs of a third row, and spines in the anterior row on the dorsal ears are few (one or two, rarely three) and are much broader than spines along the posterior row, and pass towards the hinge into a row of pits. A low fold lies on the dorsal ears of type *Horridonia*, but there is no corresponding fold in type *Pleurohorridonia*. Spines over the ventral disc are possibly slightly more numerous in the type species of *Pleurohorridonia*, but not, it appears, to any significant degree. Pustules are present, and the decorticated anterior shell of *Pleurohorridonia* suggests the possible presence of costate plicae, although not so clearly as in the Canadian species called *Horridonia grandis*. In summary, the type species of *Pleurohorridonia* is distinguished from *Horridonia* by possessing one fewer row of spines near the hinge, a pair of thick dorsal spines on the anterior dorsal ear, and lack of fold on the dorsal ears. The dorsal valve in front of the hinge is smooth.

Horridonia grandis Waterhouse, 2013

Fig. 27, 28

2013 *Horridonia grandis* Waterhouse, p. 79, Fig. 3.9, 3.10.

Diagnosis: Large, with long ventral sulcus and convex ears, ventral posterior with a short row of small spines close to umbo and hinge, second row laterally over ears, short spines or mounds in front in third row on ears, a few scattered erect fine spines over disc and trail. Dorsal spines form two rows over ears, six or seven in posterior row, five in next row, and one or two spines or spinose nodes lie in front, forming a feeble third row; a few dorsal dimples. A low broad ridge crosses the dorsal ears. Shell plicate, bearing costae over anterior ventral disc and trail, dorsal trail.

Holotype: Specimen GSC 36835 figured by Waterhouse (2013, Fig. 3.9, Fig. 3.10) and herein as Fig. 27, 28, from C-13356, Trold Fiord Formation, Melville Island, Canada, OD.

Resemblances: The present form is moderately close to the specimen figured as *Productus horridus* Sowerby by King (1850, pl. 11, fig. 2), originally figured by Sowerby (1823, pl. cccxix, fig. 1) from Derbyshire, England. This specimen is kept at the Natural History Museum, London, and registered as B 60971. The dorsal ears show an outwardly inclined posterior row of at least five spines, and a poorly developed median row of spines or knobs, and two anterior spines, and the fold is placed between the hinge row and median spine row of the holotype. Two rows of spines are shown close to the hinge on the ventral valve, with outer spines stronger than on the dorsal valve. There appear to have been a number of other spines over the visceral disc of the ventral valve, to judge from King's figures. Differences from the Canadian species lie in the better development of an anterior (third) row of dorsal ear spines, more developed rows of ventral hinge spines, and the lack of costae or rarer presence of few and simple plicae, and more spines lie over the venter in some specimens. Other facets, such as the presence of ventral pustules, are obscure. Possibly the differences imply geographic separation: but it is preferred to interpret the difference as reflecting a slight difference in age, with *grandis* older than *horrida*, which has better developed posterior spine rows.

From the Zechstein of Germany*, Horridonia horridus bufoninus* Eisel (1909) has a row of fine ventral spines and fewer but larger spines in front, and the dorsal valve has a different anterior row of spines with no pits. There are more body spines. In some respects, *buffoninus* is similar to *hoppieanus* Eisel*.* The form *auritulus* Eisel appears to show one row of ventral spines at the base

Fig. 27. *Horridonia grandis* Waterhouse. A, B, holotype, ventral and dorsal aspects of GSC 36825, x1.5, from C-13356, Trold Fiord Formation, Melville Island, Canada. (Waterhouse 2013).

of the umbonal slope, and a row of dorsal hinge spines and a row of pits, but no outer ear spines. Jordan (1966, Fig. 1b) considered that *Producta calva* Sowerby (1829, pl. 560, fig. 2-4) was senior synonym of *auritulus*, *bufoninus* and some *initialis*, which seems doubtful because most Zechstein taxa have thick anterior dorsal ear spines and often numerous ventral spines over the disc.

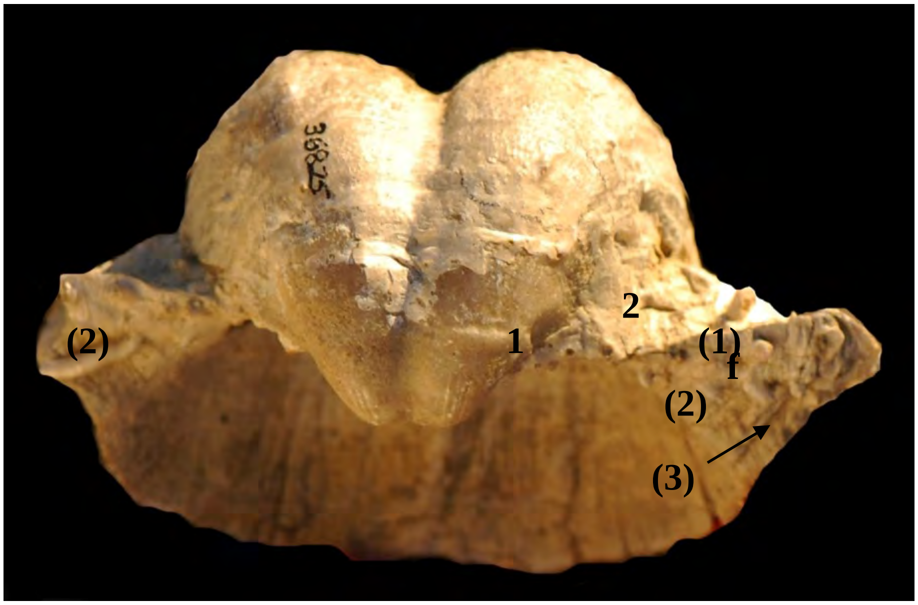

Fig. 28. *Horridonia grandis* Waterhouse, holotype GSC 36825 x 1.5, back-lit to show spine rows, numbered 1 and 2 along ventral hinge, and the mid-ear fold f along the dorsal ears. Numbers in brackets refer to first and second hinge rows and feeble third row on dorsal valve. From C-13356, Trold Fiord Formation, Melville Island. (Waterhouse 2013).

Genus ***Pleurohorridonia*** Dunbar, 1955

Diagnosis: Highly arched shells with well formed ventral sulcus, low dorsal fold, and radial costae as a rule, dorsal valve with large gently concave disc and long trail. Single row of spines along ventral and dorsal hinge, with one or two auricular spines on anterior lateral dorsal ears. Fine pustules appear at some stages of growth.

Type species: *Pleurohorridonia scoresbyensis* Dunbar, 1955, p. 90, from southern Scoresby Land and from blocks of Permian limestone in Triassic conglomerate, northeast Greenland, OD.

Discussion: No holotype was indicated by Dunbar (1955) for his type species. Hence a lectotype is selected as the specimen figured by Dunbar (1955, pl. 11, fig. 1-4). This was designated as a representative specimen by Dunbar (1955), and came from Scoresby Land.

Pleurohorridonia? sp.

Fig. 29

Material: A large specimen with valves conjoined from C-4016, Assistance Formation, Ellesmere Island.

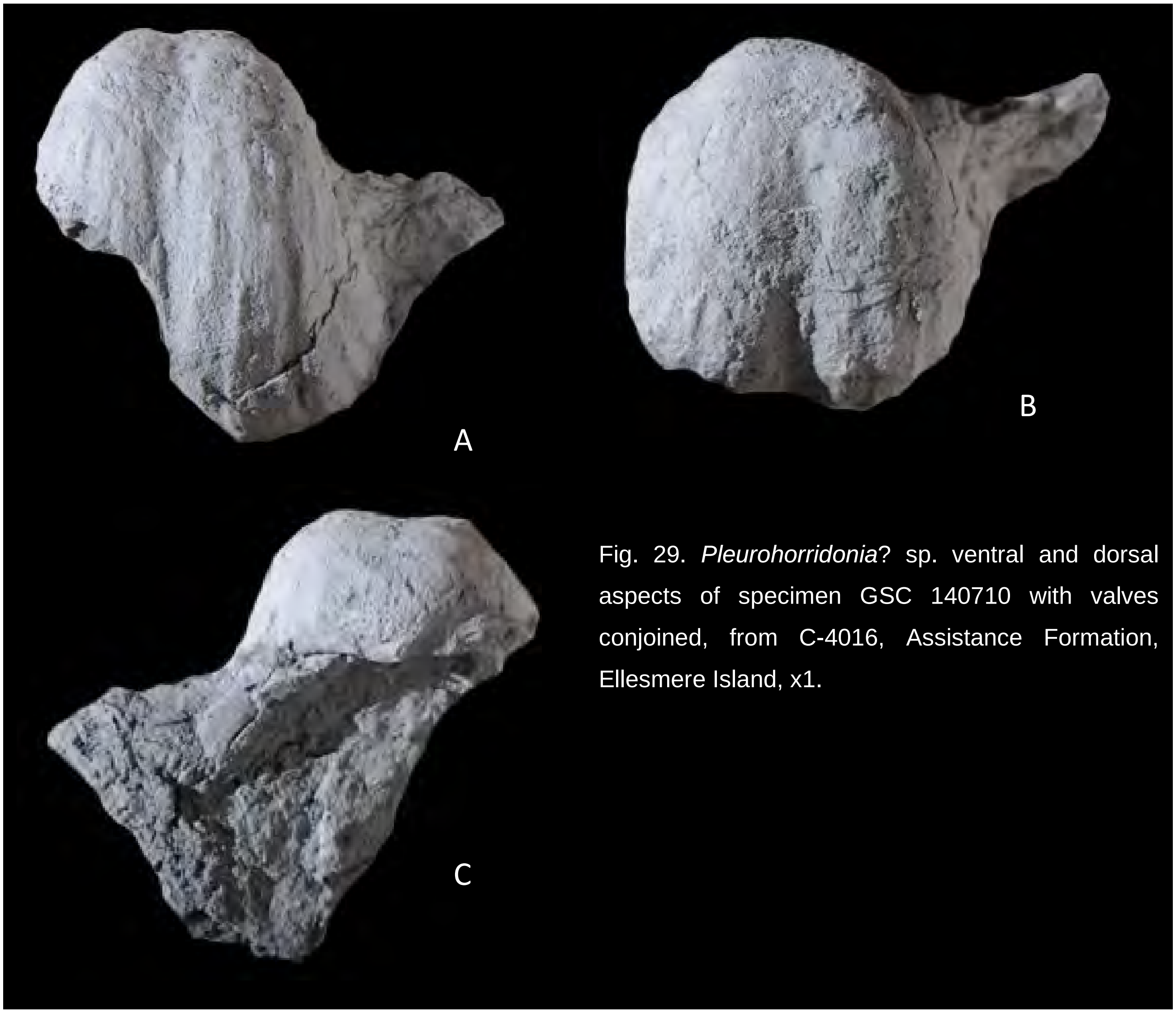

Fig. 29. *Pleurohorridonia*? sp. ventral and dorsal aspects of specimen GSC 140710 with valves conjoined, from C-4016, Assistance Formation, Ellesmere Island, x1.

Description: The complete specimen is is estimated to have been 88mm wide, 62mm long and 33mm high. It has incurved ventral umbo with sulcus commencing 12mm in front of the umbonal tip and persisting to the anterior margin. The most prominent aspect is the development of long radial rugae which extend over the anterior two thirds of the valve to the anterior margin, numbering five or six each side of the sulcus, and bearing a few finer costae anteriorly. Faint transverse rugae and growth steps are developed at the posterior third of the shell length, and there are traces of small pustules on the surface. Spine development is obscure, which hinders any secure generic determination, but the ventral body spines do not appear to be in radial rows. Scattered and slender spines are indicated by slight swellings over the rugae, and the hinge of each valve carries suggestions of a single row of slender spines, though these are not well preserved. Possible recumbent and erect large spines lie over the dorsal ear, indicating a row over mid-ear, which is not found in *Pleurohorridonia*, perhaps pointing to *Horridonia*, but this is far from certain. The poorly preserved dorsal disc, only partly exposed, does not display any further clear development of spines. Fine pustules are present over the shell surface. The dorsal valve is more concave than in *Pleurohorridonia platys* n. sp., closer to that of *P. scoresbyensis* Dunbar, 1955.

Pleurohorridonia platys n. sp.

Fig. 30 – 34

1971 *Horridonia* aff. *granulifera* [not Toula] – Bamber & Waterhouse, p. 178, pl. 21, fig. 8, 9.

Derivation: platys – flat.

Diagnosis: Moderately large shells, highly arched ventral valve, gently concave dorsal disc and long high semigeniculate trail. Hinge row of spines in each valve, one or questionably two dorsal auricular spines, and fine ventral spines over disc and trail. No conspicuous development of pustules or rugae.

Holotype: GSC 140711 as illustrated in Fig. 30A, B, from C-4004, Trold Fiord Formation, Ellesmere Island, here designated.

Material: Ten ventral valves and five dorsal valves from C-4004, and one obscure ventral valve and dorsal valve from C-4008, Trold Fiord Formation, Ellesmere Island. Three ventral valves from C-4095, Degerböls Formation, Ellesmere Island. A specimen from GSC loc. 53848, unnamed sandstone, *Dyoros modestus* Zone, Richardson Mountains.

Dimensions in mm:

Width	Length	Height	
47	35	23	holotype
40	27	18	

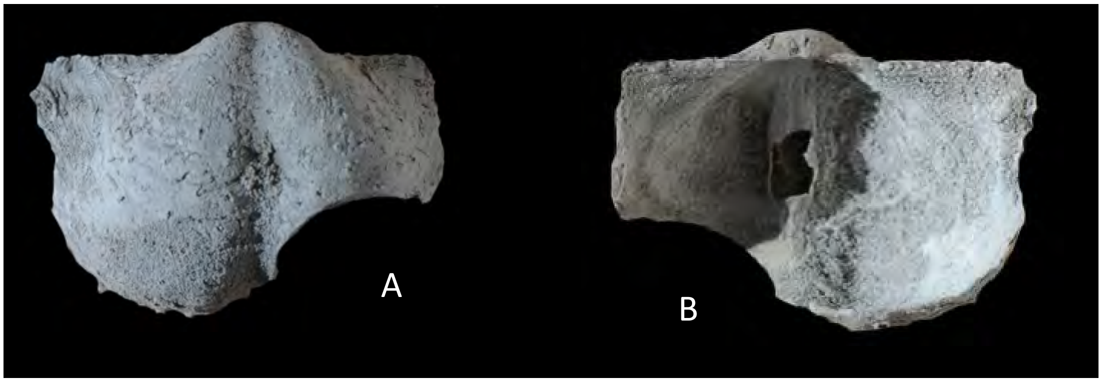

Fig. 30. *Pleurohorridonia platys* n. sp. A, B, ventral external and internal aspects of GSC 140711 holotype, ventral valve from C-4004, Trold Fiord Formation, Ellesmere Island, x1.

Description: The ventral valve is transverse with well defined but small convex ears, broad umbo with angle of 95° to 100°, and well-defined sulcus of 25°. The dorsal valve has a gently concave to almost flat disc, concave protruding ears, and high semigeniculate trail. A low narrow fold is developed medianly over much of the disc and trail, and the anterior margin is slightly recessed. A row of comparatively fine erect spines extends along the ventral hinge, and similar fine spines are developed near the anterior margin of the trail. Ear spines in front of the hinge appear variable, with scattered fine spines. Other fine spines suggested by low mounds lie over much of the ventral valve, well spaced and in rough quincunx, and definite spines are present anteriorly in another ventral valve, up to 1mm in diameter. Low commarginal rugae lie over the anterior shell of the holotype, and only one ventral valve shows irregular radial rugae. The dorsal valve has a row of fine erect spines along the hinge. The largest dorsal valve

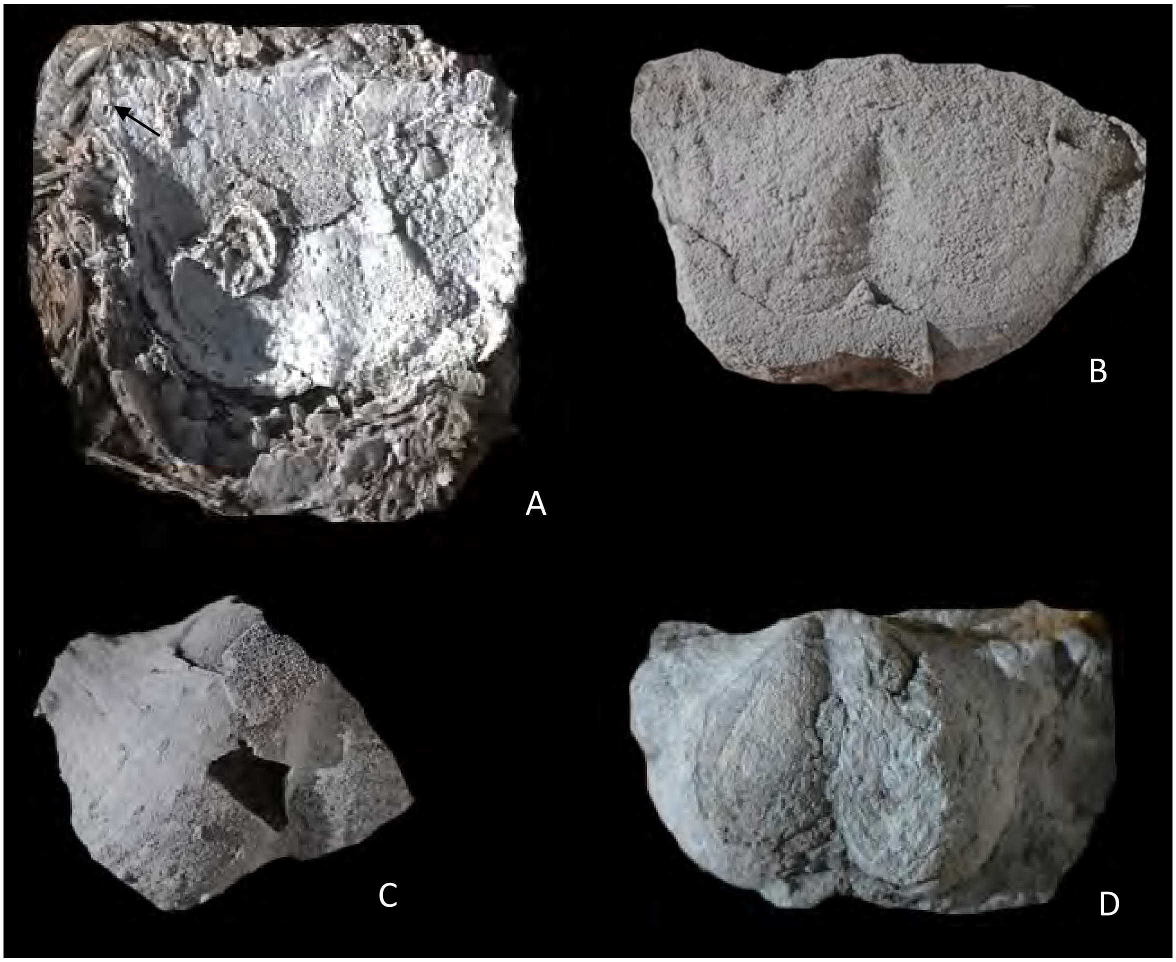

Fig. 31. *Pleurohorridonia platys* n. sp. A, dorsal aspect of specimen GSC 140712 with arrow pointing to cardinal spine in front of the hinge row. The ventral valve, largely obscured, lies in front, visible in section. B, dorsal valve exterior GSC 140713. C, incomplete ventral exterior, GSC 140714. D, damaged ventral exterior, GSC 140715. Specimens from C-4004, Trold Fiord Formation, Ellesmere Island, x1.5.

has one cardinal spine in front of the hinge row, and on a smaller dorsal valve a small spine lies in a similar position. There are a few fine spines over the trail. Parts of the shell indicate a micro-ornament of dense pustulation, but pustulation is not clearly developed.

The adductor scars lie on a raised elongate platform in front of a posterior hollow, and on each side very large diductor scars extend well in front of the adductors, and are scored by fine longitudinal ridges and grooves. There is no marginal ridge. The shell is up to 8mm thick, and postero-laterally is marked by elongate dimples and hollows. In the dorsal valve a poorly preserved cardinal process consists of two main tubercles, and there is no sign of a zygidium, but preservation is poor. A hinge ridge extends laterally each side of the shaft, and a median septum extends well forward almost as far as the front of the disc. Adductor scars are comparatively broad. The trail bears numerous slightly elongate pustules, and is semi-geniculate, though without a marginal ridge. Further detail is obscure, the floor markings not apparent, and dorsal muscle scars, cardinal process, hinge or marginal ridge and brachial shields being not known.

Two ventral valves from the *Dyoros modestus* Zone (formerly Fl zone) in unnamed sandstone at GSC loc. 53848, Richardson Mountains, were figured in Bamber & Waterhouse (1971).

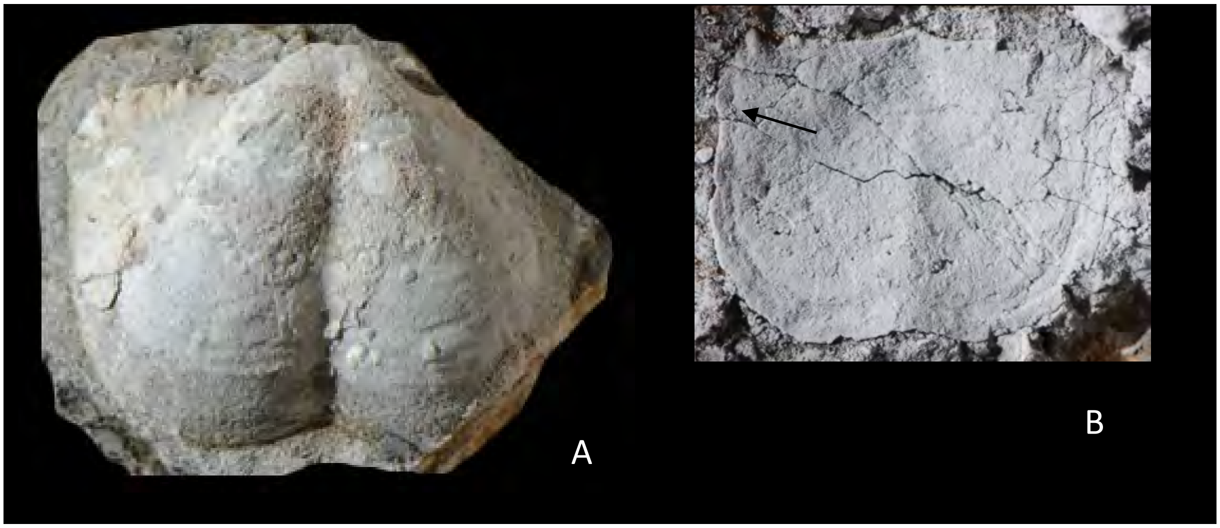

Fig. 32. *Pleurohorridonia platys* n. sp. A, ventral valve GSC 140716 from C-4095, Degerböls Formation, Ellesmere Island, x2. B, small dorsal valve GSC 140717, showing row of hinge spines, from C-4008, Trold Fiord Formation, Ellesmere Island, x2. The arrow points to an anterior cardinal spine.

Resemblances: The present species is close to type *Pleurohorridonia*, but not completely identical, with more spines present over the ears of both valves in the Greenland species, and more spines over the ventral disc in the Canadian species. The dorsal disc is flatter, and the ears are slightly smaller, and radial rugae found in only some specimens of the Canadian form, and external pustules are not conspicuous. Dunbar (1955) included in synonymy for type *Pleurohorridonia* various specimens described by Frebold

(1933), and Grönwall (1917), as well as shells figured as *Productus borealis* by Licharew & Einor (1939, pl. 10, fig. 6-11, pl. 11, fig. 1-5), which are elongate with radial rugae. He also drew attention to specimens figured as *Productus inflatus* [not McChesney] by Wiman (1914, pl. 14, fig. 2, pl. 15, fig. 3, 4) from Bear Island (Bjørnøya), and these look very close to *scorebyensis*, so far as they are preserved. The Djeltin material referred to *scoresbyensis* by Zavodowsky (1970, pl. 45, fig. 1) was allocated to *Karnellia pikvikensis* Lazarev by Lazarev (2005b, p. 47).

Fig. 33. *Pleurohorridonia platys* n. sp., ventral valve GSC 27029 from GSC loc. 53823, *Dyoros modestus* Zone, unnamed sandstone, Richardson Mountains, x1. (Bamber & Waterhouse 1971).

The Canadian material is close to specimens described by Ifanova (1972, pl. 8, fig. 1-7) from Petchora Basin, of Kungurian age. They have similar ventral spines (Ifanova 1972, pl. 8, fig. 1) and a row of dorsal hinge spines (pl. 8, fig. 7), and two anterior ear spines are developed on a larger dorsal valve (pl. 8, fig. 7). A narrow median dorsal fold is developed, and the ventral sulcus is well and even sharply defined. Although Ifanova (1972, p. 124) identified the specimens with *Horridonia granulifera* (Toula), the types of Toula's material shows ventral spines in well developed radial rows – three according to Dunbar (1955), two according to Logan (1966). The Russian material shows a row of ventral hinge spines, whereas type *granulifera* from Spitsbergen has no ventral hinge row of spines (see Toula 1875b, pl. 6, fig. 3a-c, reproduced by Gobbett 1961, pl. 5, fig. 13a-c). A related species is *Sowerbina notteiensis* Fredericks (1934, p. 16, pl. 2, fig. 5-8), ascribed to *Liosotella pseudohorrida* mut. *pinegensis* by Kalashnikov (1961, p. 46, pl. 1, fig. 5-8), before being classed as *Pleurohorridonia* by Grunt (2006a, p. 144, pl. 10, fig. 2, pl. 11, fig. 1-3) in recording Ufimian material from the Kanin Peninsula. The species is distinguished from the present form by its slightly deeper and wider ventral sulcus and fewer spines over the venter. Unlike *Pleurohorridonia* it has no ventral hinge row of spines.

Fig. 34. *Pleurohorridonia platys* n. sp., dorsal internal mould GSC 10718 from C-4004, Trold Fiord Formation, Ellesmere Island, x1.5.

Possible gerontic specimen of *platys*

Fig. 35, 36

Material: A ventral valve from GSC loc. 57687, Trold Fiord Formation.

Description: The specimen has thick shell and a single row of spines in a radial row each side of the well-developed sulcus, and weak signs of spine bases, possibly in quincunx, over the venter and trail, with anterior ribbing. The adductor scars are raised high on a broad ridge along the inner side of the sulcus, and the diductor scars are deeply impressed, with radial grooves.

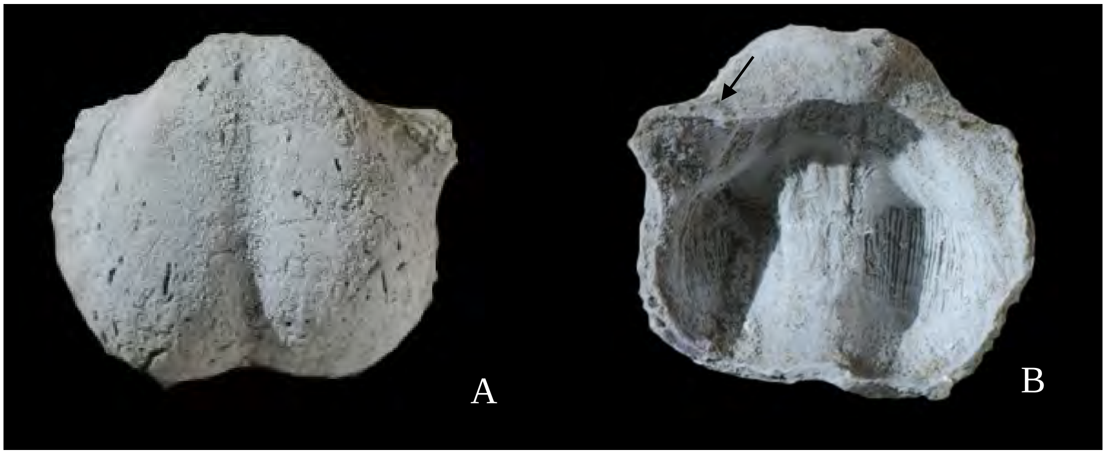

Fig. 35. Possible gerontic specimen of *Pleurohorridonia platys* n. sp., external and internal aspects of ventral valve GSC 36193 from GSC loc. 57687, Trold Fiord Formation, Ellesmere Island, x1. Arrow in Fig B points to cores of spines along the hinge.

Fig. 36. Possible gerontic specimen of *Pleurohorridonia platys* n. sp., anterior aspect of preceeding specimen (slightly tilted and so not showing ear that is preserved on right), with fine ribs. Ventral valve GSC 36193 from GSC 57687, Trold Fiord Formation, Ellesmere Island, x1.

Resemblances: The specimen differs from the specimens assigned to *Pleurohorridonia platys* in having very thick shell. The shape and sulcus and ears are much the same as those of less mature specimens assigned to *platys*, and there are signs that spines were much the same, although they are not well preserved. *Pleurohorridonia*? sp. as described above has coarser longitudinal rugae and larger ears and wider disc. The ventral valve is also highly thickened, with small ears, and spine cores lie in a row along the hinge, and over the disc in quincunx. In spite of the similarities, there is no certainty that the present specimen belonged to *platys*.

Subfamily **SOWERBINAINAE** (**SOWERBININAE)** Lazarev, 2005b

Diagnosis: No ventral spines in row along hinge, but present over disc; dorsal spines may be large along hinge or outer hinge and anterior ears. Dorsal valve may be wedge-shaped.

Discussion: The presence or absence of a zygidium was also stressed by Lazarev (2005b), but its presence or absence is not known for several critical species.

Tribe **SOWERBINAINI** (**SOWERBININI)** Lazarev, 2005b

Diagnosis: No ventral spines; dorsal spines large along hinge or outer hinge and anterior ears.

Discussion: *Productus timanicus* Stuckenberg (1875, p. 86) from Indiga River, Timan, Russia, is the type species of *Sowerbina*, with the specimen in Stuckenberg (1875, pl. 1, fig. 3a, b, c) later cited as lectotype for *Sowerbina.* Lazarev (2005a) declared that this specimen had been lost in 1974, and so nominated a dorsal valve figured by Stuckenberg (1875, pl. 1, fig. 2c, no. 24/43) as replacement.

Sowerbina has been synonymized with *Horridonia* by Muir-Wood & Cooper (1960), Stepanov (1961), Gobbett (1961, 1964, pp. 95-97), Logan (1966), Brunton et al. (2000) and Angiolini & Long (2008). By contrast, Dunbar (1955), Sarytcheva (1960, p. 235), Waterhouse (1971b, p. 214, 1982a, 2013, p. 90) and Shi & Waterhouse (1996) claimed that no ventral hinge row of spines was developed, and this was verified by Lazarev (2005a). Although this appears to be contradicted by a figure in Stuckenberg (1875), we argued that Stuckenberg's figure was based on a misinterpretation of the specimen, an observation ignored in other studies, yet based on inspection of the type specimens rather than inspection of figures. A drawing in Stuckenberg (1875) was regrettably assumed to be more accurate – especially as it had been endorsed by Muir-Wood & Cooper (1960) and Brunton et al. (2000). Against such a misinterpretation, Lazarev (2005a, b) showed that *Sowerbina* and allies have large spines confined to the dorsal hinge area, and allowed that *Sowerbina* has indeed no ventral hinge spines, just as claimed by Dunbar (1955) and others, although no acknowledgement of the earlier and preceeding correct observations was offered by Lazarev. On the basis of possessing dorsal hinge spines and no ventral hinge spines, *Sowerbina* was justifiably made the name bearer for a family group by Lazarev (2005a, b), treated in his study as a subtribe Sowerbinina in Horridoniini.

Genus ***Sowerbina*** Fredericks, 1928

Diagnosis: No spines along the ventral hinge, spines form a row along the dorsal hinge and occur in a second short row over anterior ears. Ventral spines arranged in quincunx, not in a few radial rows. Dorsal valve thickened, presence of zygidium variable.

Type species: *Productus timanicus* Stuckenberg, 1875, p. 86 from Early Permian of Urals, OD. Brunton et al., 2000 cited Stuckenberg (1905) as author, an error.

Discussion: The type species of *Sowerbina* lacks a ventral hinge row of spines, has ventral body spines in quincunx, and what has all too often been neglected in the past, a distinctive wedge-shaped dorsal valve, as figured for the type species, *Productus timanicus* Stuckenberg (1875, pl. 1, fig. 1, 2a, c, 4, 9) and reproduced by Gobbett (1961, pl. 5, fig. 9-12) from the Schwagerinen-Kalk in the Urals, and endorsed in Tschernyschew (1902, pl. 30, fig. 5, pl. 57, fig. 1, 2). According to the illustration in Stuckenberg (1875, pl. 1, fig. 9), the cardinal spine on the dorsal ear in front of the hinge row is no thicker than the outer hinge spines. In a specimen figured by Lazarev (2005b, pl. 3, fig. 1) it is marginally thicker. But in *Sowerbina kozhimensis* Lazarev (2005b, p. 48, pl. 3, fig. 3-6) of Artinskian age, the anterior cardinal spines are distinctly thicker, and there is even a rare appearance of a spine in a third row. (See also *S. timanica* Kalashnikov, 1983, pl. 53, fig. 2, 3 and *S. granulifera* [not Toula] of Kalashnikov et al. 1990, pl. 2, fig. 3).

?***Sowerbina*** sp.

Fig. 37

Material, Description: A querontic dorsal valve from the Trold Fiord Formation at GSC loc. 58951, Ellesmere Island, shows the wedge-shape typical of members of Sowerbininae, but spines are obscure, and the generic position therefore difficult to ascertain. The ears are exceptionally small for members of the subfamily, and no exact match can be found with other members described in the literature, apart from an approach to several dorsal valves figured by Wiman (1914) from the Spiriferenkalk of Spitsbergen which are similar in lacking ears from dorsal valves at late maturity. These include *Productus timanicus* Sowerby of Wiman (1914, pl. 18, fig. 4) from the Spiriferenkalk of Mt Misery, Bear Island. This specimen has small or no ears, approaching those of the present specimen. The dorsal valve is thicker and more wedge-shaped than in *Pleurohorridonia platys*. There is a long median septum, highly dendritic dorsal adductors, and brachial shields. The lack of spines from the present shell from Canada tells against any firm identification. Lazarev (2005b, Fig. 1) ascribed two of the figured specimens from Spitsbergen that show well preserved dorsal ear spines (Wiman 1914, pl. 17, fig. 21, pl. 18, fig. 2) to *Sowerbina* of the (Kapp) Starotsin Formation, which he regarded as being of Solikamian (upper Ufimian) age.

Fig. 37. ?*Sowerbina* sp., external and internal aspects of gerontic dorsal valve GSC 140719, from GSC loc. 58951, Trold Fiord Formation, Ellesmere Island, x1.

Sowerbina longi n. sp.

1961 *Horridonia timanica* [not Stuckenberg] – Gobbett, p. 46, pl. 4, fig. 1, 3 (part, not fig. 2, 4, pl. 5, fig. 1-4, 6).
1964 *H. timanica* [not Stuckenberg] – Gobbett, p. 94, pl. 10, fig. 1, 2, 4. (part, not fig. 3).
2008 *Bruntonia maynci* [not Dunbar] – Angiolini & Long, p. 84, Fig. 5A-G, 6A-C, F, G, 7A-C.

Derivation: Named for Sarah L. Long.

Diagnosis: Large transverse shells with extended ears, numerous spines along dorsal hinge and a few slender spines lie in a row across the anterior dorsal ears. Ventral spines scattered in quincunx, not in radial rows. Ventral sulcus with median gutter, narrow dorsal fold, fine surface pustules. No zygidium.

Holotype: BD48142 from Vøringen Member, Spitsbergen, figured by Angiolini & Long (2008, Fig. 5A-D), here designated.

Description: The species has been described as in the synonymy, and the source for the material was mapped in Angiolini & Long (2008, Fig. 1). Anterior dorsal ear spines are no stronger than those along the dorsal hinge: all are comparatively slender. The dorsal valve is thickened into a wedge. The presence of a zygidium was not clarified by Angiolini & Long (2008), but their Fig. 6G suggests there was none.

Resemblances*:* *Sowerbina timanicus* (Stuckenberg) of Asselian-Artinskian age in the Urals and best figured by Tschernyschew (1902, p. 638, pl. 30, fig. 5, pl. 57, fig. 1-6) has a well developed auricular spine on the anterior dorsal ear, and some of the body spines over the venter are long and strong. *S. kozhimensis* Lazarev (2005b, p. 48, pl. 3, fig. 3-6) of Kungurian age has coarse anterior dorsal ear spines. Lazarev (2005b) placed some emphasis on the relative thickness of auricular spines as compared with thickness of dorsal hinge row spines, but evaluation becomes a little precious in some instances, and for instance in specimens described as *Sowerbina kozhimensis* Lazarev (2005b, pl. 3, fig. 4a, 6), dorsal auricular spines seem to be much thicker than those of the dorsal hinge row, but received no generic discrimination from *Sowerbina timanicus*.

The synonymy has been restricted to a few references, but Angiolini & Long (2008) have provided more references, including some well-preserved specimens figured by Wiman (1914, pl. 17, fig. 19-21, pl. 18, fig. 1, 3-6, not fig. 2). The excluded specimen shows a number of spines along an anterior row on the dorsal ear and it was regarded as having a Solikamian age by Lazarev (2005b, Fig. 1). Another specimen was regarded as slightly older and matching a form from Pai Hoi (Lazarev 2005b, Fig. 1). The present specimens show many attributes of *Sowerbina*, including the distribution of ventral spines and the wedge-like nature of the dorsal valve. Angiolini & Long (2008) referred the Spitzbergen material to what they called *Bruntonia maynci* Dunbar, 1955 from east Greenland, but Dunbar's form shows many differences from their Spitsbergen material, and has ventral body spines in a few radial rows rather than in quincunx, in general pointing to a relationship with *Sowburia* Lazarev, as discussed shortly.

Genus ***Sowburia*** Lazarev, 2005b

Diagnosis: Few rows of spines arranged radially each side of the sulcus in the ventral valve, no row of ventral hinge spines. Radial costae on some species. Dorsal valve concave, with gently concave disc and moderately well-developed trail at steep angle. Row of prominent dorsal hinge spines and one or two large cardinal spines that may be comparable in thickness to those of the outer hinge row, or in some species, much thicker. Zygidium variable.

Type species: *Sowburia kaninensis* Lazarev, 2005b, p. 48 from upper Ufimian of Kanin Peninsula, Russia, OD.

Discussion: *Sowburia* Lazarev, 2005b is based on *S. kaninensis* Lazarev (2005b, p. 49, pl. 3, fig. 9-13), with further material figured as *Ruthenia granulifera* by Fredericks (1934, pl. 3, fig. 1-8, pl. 4, fig. 1-3, 5-8), *Sowerbina granulifera* of Kalashnikov (1983, pl. 2, fig. 1, 2; 1993, pl. 26, fig. 1-4) and *Horridonia* (*Sowerbina*) *granulifera* of Stepanov et al. (1975, pl. 1, fig. 21-23). Some figures even suggest the presence of some ventral ear spines on *Sowburia kaninensis* (see Lazarev 2005b, pl. 3, fig. 9). Presumably this indication is misleading, but it would have been useful to have the indication noted and explained. This apparent discrepancy between what is supposed to be the details of spination, and the strong suggestion of actual spines suggested by figures, is perplexing, and hardly reassuring with regards to the nature of proposed genera. The zygidium *in Sowburia* was described as variable by Lazarev (2005b). The genus is distinguished by its dorsal auricular spines, and by the dorsal valve which is not as strongly wedge-shaped as in *Sowerbina*. Indeed the dorsal valves appear to be deeply concave in some species. The arrangement of ventral disc spines in the type species is rather obscure, but seems to be arranged in radial rows. In establishing the genus for Ufimian or lower Kazanian species of Russia, with zygidium and more surface granules than in *Sowerbina*, and other minor features, Lazarev was able to point to an American species *Horridonia texana* King, 1931, that was congeneric, and occurred in the Roadian fauna of west Texas, of much the same age. Although Cooper & Grant (1975, p. 1101) stated there were no ventral spines, a very few are visible on the figures of the holotype in Cooper & Grant (1975, pl. 208, fig. 41, 42), as if remnant from one or two radial rows. *Burovia* Ustritsky, 1962 is of slightly younger age, with very thick dorsal ear spines, well formed zygidium and large pustules, and two or three radial rows of trail spines. Its ventral body spines are definitely in quincunx. Its character is masked in the *Revised Brachiopod Treatise*, because Brunton et al. (2000, Fig. 324b) mislabelled a dorsal valve as a ventral valve.

Bruntonia Angiolini & Long, 2008 was proposed for transverse shells with moderate ventral sulcus and dorsal fold, large ears, spines on dorsal valve in a row close to hinge and one to three spines as well over the anterior ears. Ventral spines lie in one to three or rarely more longitudinal rows extending from close to the ventral hinge, but there is no ventral hinge row of spines. The type species was designated as *Sowerbina maynci* Dunbar, 1955, p. 97 from Cape Stosch, Greenland. This species belongs to Sowerbininae, with a few well-developed ventral spines in a few radial rows, as best illustrated by Dunbar (1955). The cardinal process was considered to be distinguished by being erect by Angiolini & Long (2008), instead of sessile as in *Burovia* Ustritsky. Stress was also placed on the absence of a strong marginal ridge from *Bruntonia,* but that is normal for various Horridoniidae, such as *Sowerbina, Sowburia, Vigdalia* and *Karnellia* (Lazarev 2005a, b), with *Burovia* the exception. The presence or absence of a zygidium was not determined, but no zygidium is suggested in a figure of allied species *rudis* by Dunbar (1955, pl. 15, fig. 2).

The one known and arguably significant feature of type *Bruntonia* as opposed to type *Sowburia* concerns the thickness of the anterior cardinal spine on the dorsal ears. It is somewhat thicker than spines along the hinge in the species *maynci*, the type species of *Bruntonia*, and so this difference could be assessed as offering a potential difference between the two genera and possibly justify recognition of *Bruntonia*. Lazarez (2005b) did not grant generic weight to the difference, and some might argue that he was wrong, a matter for further consideration. The cardinal spines figured for Vøringen specimens from Spitsbergen by Angiolini & Long (2008) are not much if at all thicker that lateral hinge spines, helping to suggest their specific and generic identification was incorrect, and it is concluded that their specimens belong to *Sowerbina* Fredericks, as described earlier. Angiolini & Long (2008) described the anterior auricular spines as coarse, which seems more applicable as a description to the material described from Greenland by Dunbar (1955), rather than the Spitsbergen material. The shape is much the same as that displayed by Dunbar's species from east Greenland, but the Spitsbergen species differs in two critical ways. The ventral spines are fine, and scattered over the surface, as stated in the text and shown by Angiolini & Long (2008, Fig. 5A and 6B), whereas the ventral spines in type *maynci* are much larger and arranged in one to three radial rows. On the dorsal valve of the Spitsbergen specimens, the anterior cardinal spines are little thicker than those of the larger hinge row of spines. Dunbar (1955, Fig. 20) failed to provide a photograph of the dorsal valve for *maynci* but did give a text figure (Fig. 20) showing that the anterior cardinal spines, especially the inner one, were somewhat thicker that those of the hinge row.

Sowburia cf. ***rudis*** (Dunbar, 1955)

Fig. 38

cf. 1955 *Sowerbina rudis* Dunbar, p. 111, pl. 14, fig. 1-7, pl. 15, fig. 1-6, text-fig. 21.
2013 *Bruntonia* cf. *rudis* – Waterhouse, p. 91, Fig. 3.20.

Material: A specimen with valves conjoined and ventral valve from GSC loc. 57687, Trold Fiord Formation, Ellesmere Island.

Description: The conjoined specimen is well preserved and shows well developed sulcus, large convex ventral ears, and single radial row of large spines each side of the sulcus. The dorsal hinge row of spines is well developed. A single large auricular spine is preserved on the anterior dorsal ears, and a second spine might have been destroyed, or perhaps was not developed. The dorsal valve has a flat disc and thin trail at a steep angle.

Resemblances: The specimen with valves conjoined is close to *Sowerburia rudis* in details of shape, dorsal valve, ventral spines and dorsal spines, except for the possible lack or non-preservation of a second cardinal spine, and the one anterior spine that is preserved is only slightly thicker than the largest of the hinge spines. Radial costae are slightly more subdued than in the types, and the sulcus of the present specimen is a little wider than in type *rudis*. Dorsal spines in the Greenland species *rudis* vary somewhat. In the specimen as figured by Dunbar (1955, pl. 14, fig. 7), the spines measure 3.5mm along the hinge, and auricular spines measure 4.3mm to 4.5mm in diameter. That of Dunbar (1955, pl. 14, fig. 2) has a coarser auricular spine spine anteriorly, whereas that of pl. 14, fig. 5 has what appear to be large ventral ear spines in two rows and this with fig. 2 belongs to the holotype! The right-hand ear of the ventral valve in Dunbar (1955, pl. 13, fig. 1) seems to have prominent knobs close to the ventral hinge, on the ventral ear. For the dorsal valve in Dunbar (1955, pl. 14, fig. 7) the figure suggests three anterior auricular spines, the inner one especially thick. One row only of ventral body spines lies each side of the sulcus.

Dunbar (1955) suggested that *Ruthenia granulifera* var. *gibbosa* Fredericks (1934, pp. 19, 39, pl. 4, fig. 5, 6) from Kanin Peninsula might prove to be the same species, but judged the description “too poorly described to be recognisable” . He also referred to *Productus* (*Horridonia*) *borealis borealis* [not Haughton] in Stepanov (1936, p. 175, pl. 4, fig. 1a-c). There is reference to this species in Stepanov (1936, p. 116, pl. 2, fig. 1-3), as well as Stepanov, 1937b, p. 175, pl. 4, fig. 1a-c) from the Spirifer Limestone, as well as pl. 4, fig. 3, and a form intermediate between *borealis* and *granulifera*. Stepanov (1961, pl. 10, fig. 1, 2, also figured shells identified with *borealis*, for which pl. 10, fig. 2 provides clear coverage of the dorsal spines. But in none of the other figures are ventral spines very clearly shown, any more than in the original Haughton report. The spination therefore must become the focus of renewed attention in trying to interpret the nature of Haughton’s material, which surely is likely to claim priority, although over which later taxon is uncertain.

Fig. 38. *Sowburia* cf. *rudis* (Dunbar), ventral and dorsal aspects of GSC 36826 from GSC loc. 57687, Trold Fiord Formation, Ellesmere Island, x1.5. (Waterhouse 2013).

The species *rudis* was reported from the Vøringen Member as *Bruntonia rudis* by Angiolini & Long (2008, p. 89, Fig. 5J, 7D-I, 8I-L - not D-I as in text). The Spitsbergen specimens show a gently concave dorsal disc and low geniculate trail, and the dorsal valve may not be wedge-like. The specimen figured as *rudis* by Angiolini & Long (2008, Fig. 8I) shows moderately thick anterior auricular spines on the dorsal valve, to suggest a possible approach to *Karnellia* Lazarev, 2005b, but granules are well developed in the Angiolini-Long material, unlike the arrangement reported for *Karnellia* by Lazarev (2005b). *Karnellia* has ventral spines in quincunx and illustrations provided by Angiolini & Long (2008, Fig. 7D, H) suggest that the Vøringen material also has ventral spines in quincunx, although the pattern is not fully clear. Angiolini & Long commented that the species, meaning presumably their material, was close to *Horridonia bullocki* Nelson & Johnston, and this species appears to belong to *Karnellia*, and is possibly represented in the lower Takhandit Formation of Yukon Territory, of comparable age.

Tribe **KARNELLAINI** (**KARNELLINI**) Waterhouse, 2013

Diagnosis: No ventral hinge spines. Second dorsal ear row spines somewhat larger, tendency to no pustules.

Genus ***Karnellia*** Lazarev, 2005b

Diagnosis: Spines over the ventral valve sparse and distribution obscure but appear to be arranged in quincunx, no row of ventral hinge spines. Dorsal valve concave, with gently concave disc and low trail at steep angle. Row of prominent dorsal hinge spines and one or two moderately developed cardinal spines somewhat thicker than those of the outer hinge row. No zygidium.

Type species*: Karnellia pikvikensis* Lazarev, 2005b, p. 47, pl. 4, fig. 4-8 from Djeltin beds (Artinskian) of northeast Russia, OD.

Discussion: Lazarev (2005a, b) regarded his genus *Karnellia* as a member of Horridoniina and separate from subtribe Sowerbiina, but this remains open for further enquiry. The absence of spines from the ventral hinge strongly suggests that *Karnellia* and *Vigdalia* were more closely related to *Sowerbina* than to *Horridonia*. Lazarev (2005a) had stressed that the dorsal auricular spines were not as thick as those found in *Horridonia*. Waterhouse (2013, p. 92) noted that Lazarev had relied on figures provided in Muir-Wood & Cooper (1960) and Brunton et al. (2000) for interpreting *Horridonia*, but such specimens came from the Zechstein of Germany rather than the source of the types, in the Magnesian Limestone of Engand, and that the type dorsal auricular spines were not particularly wide in *Horridonia.*

The generic allegiances for the Canadian species *bullocki* Nelson & Johnson are far from certain. Some aspects such as zygidium are poorly known, and although the spines largely agree with those of type *Sowerbina*, the dorsal cardinal spines are poorly known but seem to be thicker than those along the hinge, and the dorsal valve does not appear to be fully wedge-shaped. *Sowerbina kozhimensis* Lazarev, p. 48, pl. 3, fig. 3-6 has dorsal cardinal spines thicker than those along the hinge, and could prove to be closely allied. It is of Kungurian age. The genus *Karnellia* Lazarev, 2005b, described from Artinskian of northeast Russia, appears to have no ventral hinge spines, and body and trail spines appear to lie in quincunx. The dorsal cardinal spines are few, and may be somewhat thicker than those of the dorsal hinge row. There is no zygidium. The dorsal valve is possibly not wedge-shaped. Combined with the uncertainty over the nature of the type species, and uncertainty over aspects of *bullocki*, its generic identification is strongly in need of verification.

Karnellia? ***bullocki*** (Nelson & Johnson, 1968)

Fig. 39

1961 Horridonid [sic] Nelson, pl. 2, fig. 2a-c.
1962 Horridonid [sic] Nelson, pl. 2, fig. 1a-e.
1968 *Horridonia bullocki* – Nelson & Johnson, p. 726, pl. 91, fig. 1-12, text-fig. 3c, d.
?1971 *Sowerbina* cf. *bullocki* – Bamber & Waterhouse, p. 168, pl. 17, fig. 10.

Diagnosis: Hinge spines along dorsal valve, large anterior auricular spine, ventral disc spines in quincunx, dorsal valve not thickened. No zygigium.

Holotype: Specimen UA 524, figured as *Horridonia bullocki* by Nelson & Johnson (1968, pl. 91, fig. 1-3) from Takhandit Formation, Yukon Territory, OD.

Discussion: Various aspects remain obscure for this species, but an assignment of the species to *Karnelia* is provisionally suggested. Ventral body spines are obscure, apparently few and in quincunx. The exact position with reference to the Bamber and Waterhouse subdivision of the Takhandit beds and faunas for the Nelson-Johnson material remains moot, but Bamber & Waterhouse (1971) compared material to *bullocki* from the lower Takhandit Formation at GSC loc. 57058 from zone Fs, which is the second lowest faunal assemblage. The drawings in Nelson (1962, pl. 2) might belong to this species, but were not included in the synonymy by Nelson & Johnson (1968). These authors referred to specimens identified as *Sowerbina maynci* [not Dunbar] in Nelson (1962, pl. 29, fig. 7-9), but the reference to Nelson 1962 is that provided in this study, with no plate 29.

Fig. 39. *Karnellia*? *bullocki* (Nelson & Johnson). A, B, C. ventral, dorsal and lateral aspects of holotype, UA 524 from Takhandit Formation, x2. (Nelson & Johnson 1968).

Discussion: Reports are accumulating on various Horridoniidae from Permian Arctic faunas, that need careful and wide-ranging study and integration, with more consideration of variation within species, and scrupulous evaluation of generic discriminants.

This identification for the Canadian material follows the description of *rudis* by Dunbar (1955, text-fig. 21). But the designated holotype, as figured by Dunbar (1955, pl. 14, fig. 4), seems to show large spines over the ventral ear on the right side. Were these indications merely an artifact, representing bulges of shell opposite the dorsal spines? They seem to have escaped notice by other studies. It would be desirable to have the specimen examined, and the apparent presence of ventral auricular spines dismissed, or the diagnosis reassessed. The situation is similar for a shell identified as *Sowerbina maynci* by Dunbar (1961, pl. 1, fig. 7). The figure appears to show a large auricular spine at the anterior lateral margin of the ventral valve ear on the left side, and even suggests an array of prominent spines emerging from the posterior margin of the same ear. That would not appear to be vindicated by Dunbar’s description of the species. It would have been useful to have had the illusion, if that what it is, explained. For many years, authorities have been confused by misleading preservation and figure of *Horridonia timanica* Stuckenberg, and only repeated examination of *timanica* by different experts managed finally to resolve the confusion, though still resisted in some quarters. It cannot be said that the Permian members of Horridonidae have been securely delineated, given the inadequate attention to many details of morphology, and the need to adequately accommodate the German studies by Jordan (1966) for instance on Zechstein material.

Superfamily **PRODUCTUSOIDEA (PRODUCTOIDEA)** Gray, 1840

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 Productusidae (Productidae) and variably developed in other families.

Family **RETARIAIDAE (RETARIIDAE)** Muir-Wood & Cooper, 1960

Diagnosis: Medium-sized 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 Productusidae, but is otherwise close to that family.

Subfamily **RETARIAINAE (RETARIINAE)** Muir-Wood & Cooper, 1960

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 **RETARIAINI (RETARIINI**) Muir-Wood & Cooper, 1960

Diagnosis: Somewhat transverse shells with reticulate disc and often large ears as a rule, 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, 1955 and *Alexenia* Ivanova in Ivanov, 1935, classed as Spyridiophorini Muir-Wood & Cooper by Brunton et al. (2000, p. 475), are very close to Retariainae, and may be retained as a tribe within Retariainae (Waterhouse 2013, p. 130). They share reticulate posterior shell, somewhat similar ventral spines and high ear baffles, and differ from Retariaini in the nature of the dorsal muscle scars.

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. Although the genus was synonymized with *Kutorginella* by Brunton et al. (2000), it is distinguished from *Kutorginella* by the lack of dorsal spines as shown by Waterhouse (2013). Shen (2017, p. 709) preferred to distinguish the genus from *Kutorginella* by its large size, lack of anterior tube, and less inclined lateral slopes, but these differences are likely to be of less than generic significance. The type specimens are only a little larger than many *Kutorginella*, and many species of *Kutorginella* lack an anterior tube. The statement that lateral slopes of the ventral valve are less inclined applies only to one specimen (Jin 1976, pl. 8, fig. 2). Four ventral valves that are better preserved as far as external features are concerned have widely diverging umbonal slopes (Jin 1976, pl. 8, fig. 4, 9, 17, 18), as in *Kutorginella*, as do two further internal ventral moulds (Jin 1976, pl. 8, fig. 13, 16). The difference from *Kutorginella* lies in the presence or absence of dorsal spines, not in the differences claimed by Shen. The type species of *Aspinosella, Kutorginella uddeni* Cooper & Grant (1975, pl. 343, fig. 1-17) from the Neal Ranch beds was also synonymized with *Kutorginella* by Brunton et al. (2000, p. 472), but is also validated by the absence of dorsal spines. The ventral valve has more spines over the venter and umbonal slopes, few hinge spines and no strut spines, to indicate alliance with *Thamnosia*, which differs in having 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 *Pitakpaivania* 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 it shares 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 to circumscribe a closely similar set of species, distinguishable as the genus named *Retaria* Muir-Wood & Cooper, later questionably placed in synonymy with *Kutorginella*. Allied material from Russia and Canada 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 Rigrantianai Lazarev, 2000 (see Waterhouse 2013, p. 113). *Thamnosia* Cooper & Grant, 1969 has numerous spines on lateral slopes and ears, and spines are also numerous on the anterior shell, and over the dorsal valve.

Kutorginella minuta n. sp.

Fig. 40

Diagnosis: Characterized by very small size.

Holotype: GSC 140720a from GSC loc. 26406, Assistance Formation (Roadian), Devon Island, illustrated herein as Fig. 40A-C, here designated.

Material: A ventral valve and dorsal valve, possibly disaggregated from the same specimen, from GSC loc. 26406, Assistance Formation, Devon Island.

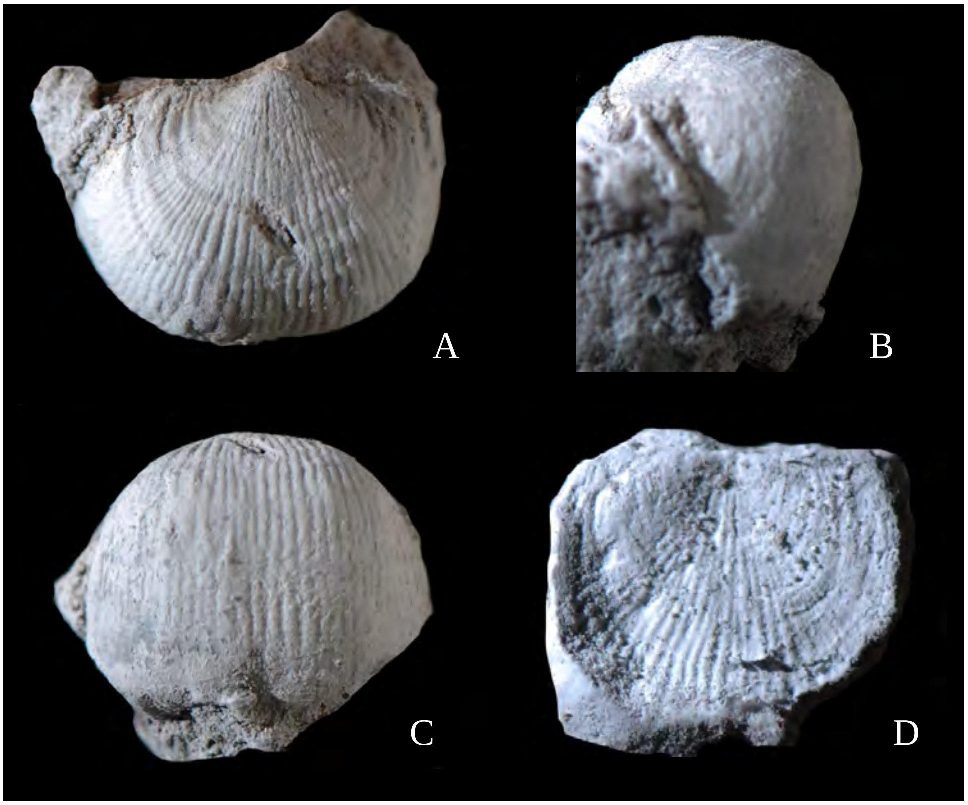

Fig. 40. *Kutorginella minuta* n. sp. A, B, C, posterior, anterior and lateral aspects of ventral valve GSC 140720a, holotype. D, dorsal valve GSC 140720b. From GSC loc. 26406, Assistance Formation, x3.

Dimensions in mm:

Width	Length	Height
15.3	12	9 ventral valve
13.5	11.2	3.5 dorsal valve

Description: Ventral valve small, with slightly protruding umbo and lateral walls diverging at 95º. There are small convex ears and an anterior median flattening mid-disc, which becomes a shallow sulcus extending over the anterior disc and trail as far as the anterior margin. There is no anterior tube, at least as far as preserved. The ears are small, but could have been broken laterally, although the shape is preserved, to judge from growth rugae which follow the curved lateral margin. The length of the trail is a little greater than the length of the visceral disc, and lies at a high angle to the disc. The dorsal disc is gently concave, with anterior very low fold, and small concave ears, and the dorsal trail is semigeniculate, and probably broken short. The ventral disc and trail are covered by fine but well-formed costae, numbering seven to eight in 5mm, and lacking from the ears. Similar costae lie over the dorsal valve, but one of the dorsal ears has two costae. Some eight or nine rugae cross the ventral valve, including the ears, but only two or three rugae lie over the trail, which also carries some well-developed commarginal growth increments. Commarginal rugae are slightly stronger over the dorsal disc and are narrow and sharply defined near the hinge. On the ventral valve, a row of slender spines lies along the hinge, and larger spines, each 0.3 to 0.35mm in diameter, form a row each side of the umbo along the lower umbonal slopes. Other fine erect spines up to 0.6mm in diameter are scattered over the remainder of the ventral valve, including a few over the anterior ears, and fine scattered erect spines lie over the dorsal disc. There are no strut spines.

Resemblances: This species is characterized by its very small size. In many respects it is moderately close to *Kutorginella yukonensis* Sarytcheva & Waterhouse, 1972; Shi & Waterhouse 1996; Waterhouse 2018a from the Jungle Creek Formation, of Gzhelian, Asselian, Sakmarian and early Artinskian age, apart from having much smaller ears, though these could have been broken short. But the overall size is much reduced, barely half that of the older species, and ribs, rugae and spines are all reduced in size, with seven or eight ribs in 5mm in *minuta*, compared with three or four in *yukonensis*. Nor is the difference due to the fact that the present form features only what might have been a nepionic or early mature version of *Kutorginella*. The density of the ornament, and small size of the disc and the relatively long trail all indicate maturity of the present material. Of considerable interest is the fact that *Kutorginella* is otherwise not known from beds of Kungurian or younger age: this present form is the first to be found in beds as young as Roadian (early Middle Permian). The implication appears to be that *Kutorginella* did survive, as a miniature or dwarf form. Minaturization is not unknown in the fossil record. Instances are found in the Late Permian of China, mistakenly claimed by Shen (2016) to have characterized all very late Permian faunas world-wide. This is emphatically untrue, because brachiopods of latest Permian age in Nepal and New Zealand are large and numerous (Waterhouse 1966, 1967c, 1978, 2013). Whereas minaturization in China has affected various species and genera, in this case, only the one taxon is reduced in size, and given the size of other fossils from the same formation, is likely to have been caused by inherited genetic factors rather than then prevailing unfavourable environmental parameters. Perhaps if other species developed into minature forms, they all perished. Minaturization may have been caused by a Bergman effect, responding to high temperatures during Baigendzinian time world-wide.

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

Diagnosis: Small to medium size with long trail, both valves spinose, characterized by numerous spines over umbonal slopes and trail. Dorsal ear spines few in number.

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

Discussion: Species described under the heading of *Thamnosia* in the Glass Mountains of Texas are all transverse, with long trails, and more than one row of spines along the lower umbonal slopes of the ventral valve. There is variation between species of the number of spines over the ventral and dorsal ears, and density of dorsal spines, and uncertainty remains over the generic implications of such differences. The possibility had emerged that *Thamnosia* would prove to be a junior synonym of *Svalbardoproductus* Ustritsky, 1962, with Ustritsky (1979) claiming that *Svalbardoproductus* was senior synonym to *Thuleproductus* Sarytcheva & Waterhouse, 1972, and Brunton et al. (2000) claiming that *Thamnosia* was senior synonym to *Thuleproductus*. But it is shown shortly that *Svalbardoproductus* differs from both genera.

Aspinosella Waterhouse, 1982b, p. 47, based on *Kutorginella uddeni* Cooper & Grant, 1975, p. 1029 from the Gaptank, Neal Ranch and Lenox Hills Formations of Texas, somewhat approaches *Thamnosia* in shape and its numerous ventral spines, but has one prominent row of spines along the umbonal slopes and a number of additional spines over the anterior ventral slopes (see Cooper & Grant 1975, pl. 343, fig. 6), and few spines along the hinge. Unlike *Kutorginella* or *Thamnosia*, *Aspinosella* lacks dorsal spines, whereas spines over its ventral ears are numerous and fine, matched by pits over the dorsal ears, according to the figures (Cooper & Grant 1975, pl. 343, fig. 1-17).

Thamnosia sangminlee n. sp.

Fig. 41 – 43

?1916 *Productus boliviensis* [not d'Orbigny] – Tschernyschew & Stepanov, p. 30.
?1916 *Productus inflatus* [not McChesney] – Tschernyschew & Stepanov, p. 30, pl. 5.

Derivation: Named for Sangmin Lee.

Diagnosis: Large transverse shells with broad ventral umbo, well defined ribs and commarginal rugae, sturdy spines in several rows along lateral slopes of ventral valve.

Holotype: GSC 140724 illustrated in Fig. 42 from GSC loc. 58977, Great Bear Cape Formation, Ellesmere Island, here designated.

Material: Two ventral valves and dorsal valve from GSC loc. 58977 and several specimens possibly from the same locality, involving five ventral valves, two dorsal valves and fragments. Great Bear Cape Formation, Ellesmere Island.

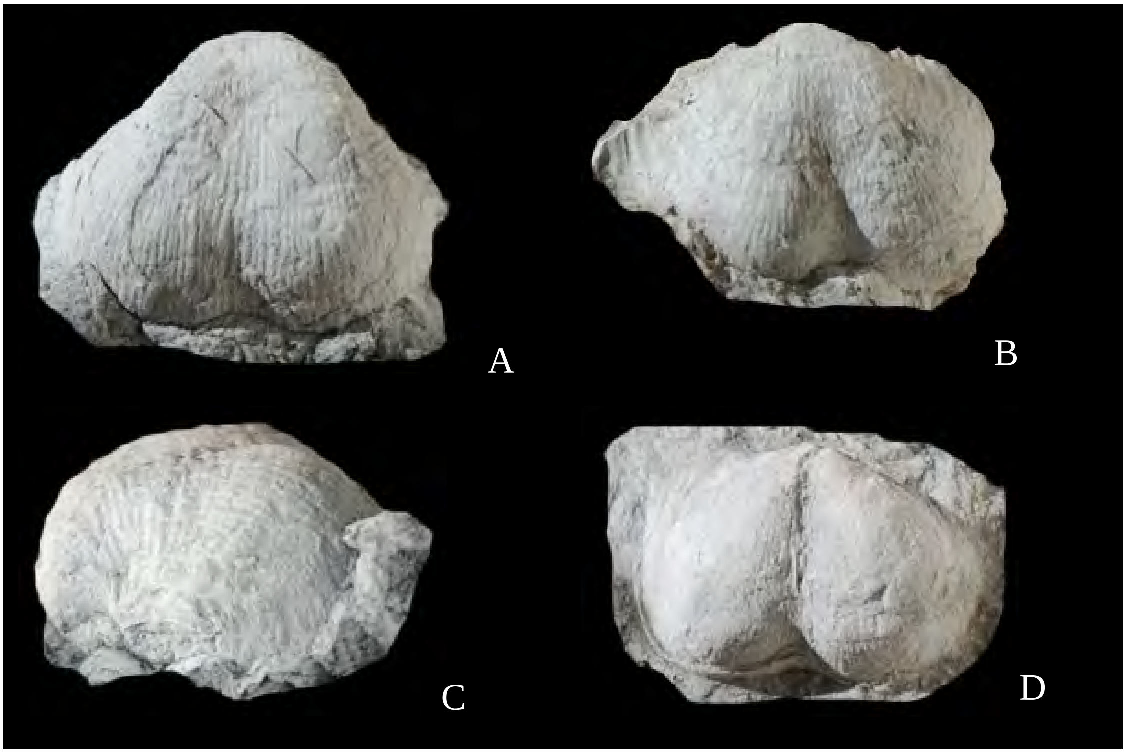

Fig. 41. *Thamnosia sangminlee* n. sp. A, C, ventral and lateral aspects of ventral valve GSC 140721. B, ventral valve GSC 140722. D, internal aspect of worn composite mould of dorsal valve GSC 140723. Specimens from uncertain locality, possibly GSC loc. 58977, Great Bear Cape Formation, Ellesmere Island, x1.

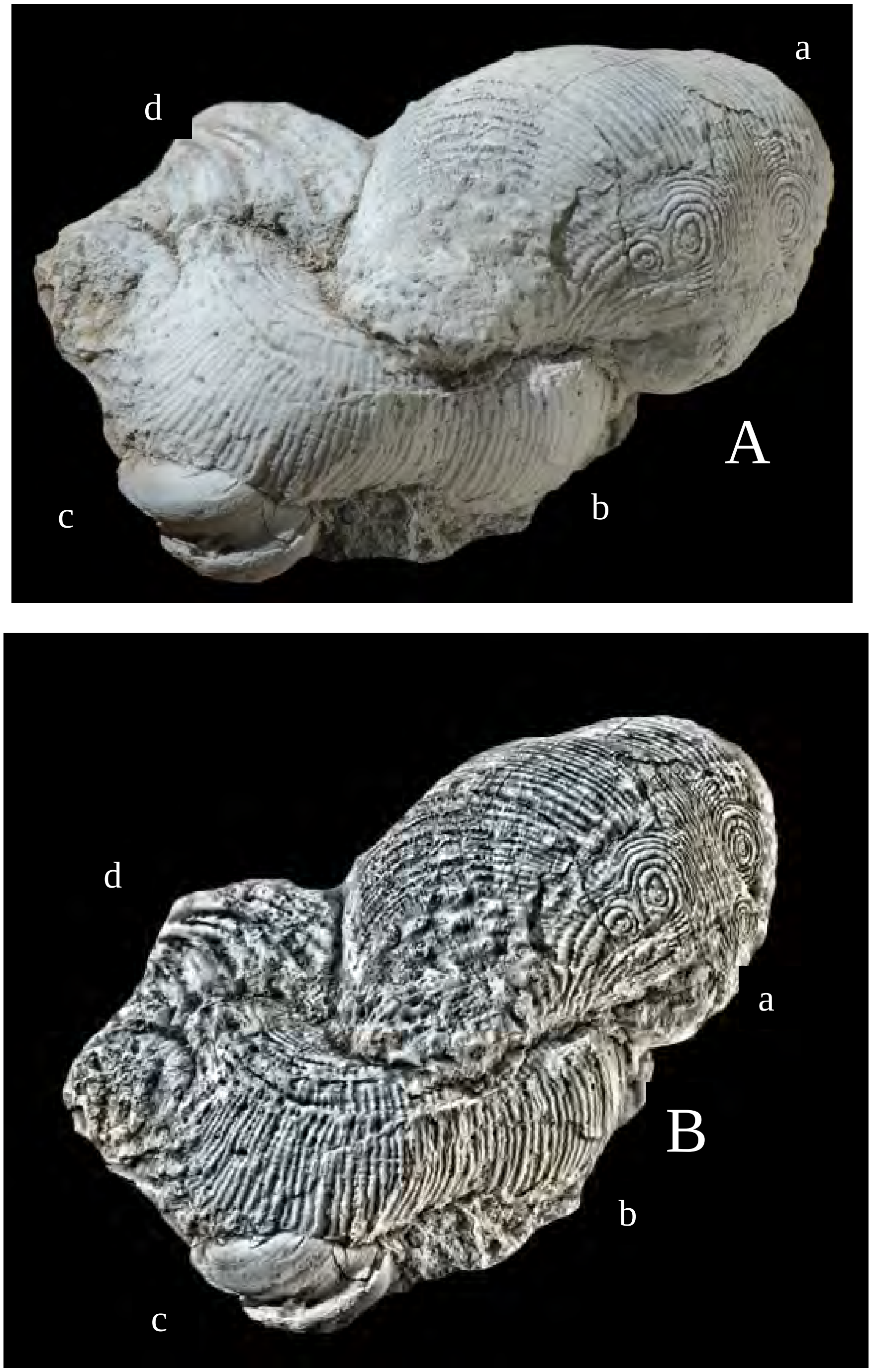

Fig. 43. *Thamnosia sangminlee* n. sp. A, B, small block under ordinary light and processed under slightly different orientation by local equalization, showing ventral valve GSC 140724 holotype (a), dorsal valve GSC 140725 (b), part of *Liosella* sp. (c) and dorsal valve GSC 140726 (d) of *Betaneospirifer striatoplicatus* (Gobbett). From GSC loc. 58977, Great Bear Cape Formation, Ellesmere Island, x1.

Dimensions in mm:

Width	Length	Height	Umbonal angle	Sulcal angle
70	45	27.5	95º	20º holotype

Fig. 43. *Thamnosia sangminlee* n. sp., ventral valve holotype GSC 140724 from GSC loc. 58977, Great Bear Cape Formation, Ellesmere island, x0.8. See Fig. 42A, B.

Description: The specimens are moderately large, and the ventral umbo is broad with angle close to 95º to 100º, not highly incurved, and moderately high umbonal walls extending towards maximum width which lies close to mid-length. Ears are moderately large, but cardinal extremities have been lost, although growth lines for earlier stages of development indicate they were obtuse. A gently concave sulcus extends from a little in front of the umbonal tip to the anterior margin with angle difficult to measure precisely because sulcal borders are vaguely defined, but close to 25º up to 35º. The dorsal disc is very gently concave with low median fold, and curves abruptly at a high angle into a short trail. Ribs cover both valves, four in 5mm anteriorly. Various specimens suggest a few spines close to the hinge near the umbo, with a scattering over the ventral ears, and there are at least three rows along the outer umbonal slopes inside the ears. Other scattered and slender largely erect spines lie over the disc, and three or four irregular commarginal rows lie around the anterior margin over the trail.

Fig. 44. *Thamnosia sangminlee* n. sp., small block showing specimens from GSC loc. 58977, Great Bear Cape Formation, Ellesmere Island, including GSC 140727 x1.

The dorsal valve has thin scattered spines over the disc, and somewhat thicker scattered spines over the trail. Dorsal ears are not preserved, and their spination detail not known.

Resemblances: Although some detail is not available, the specimens appear to belong to *Thamnosia* Cooper & Grant, and are similar in known detail of broad transverse shape, moderate inflation, similar costation and spine detail. They come especially close to *Thamnosia capitanensis* (Girty, 1908, p. 234, pl. 12, fig. 1-3b, pl. 20, fig. 8, 8a; King, 1931, p. 66, pl. 10, fig. 15; Cooper & Grant, 1975, p. 1033, pl. 345, fig. 1-17, pl. 349, fig. 6-19) from the Capitan Formation and Bell Canyon Formation of late Wordian and Capitanian age in Texas. These are large weakly transverse *Thamnosia*, distinguished from the present form by their more reticulate ornament and nasute anterior, and stronger sulcus and fold. On the other hand *T. phragmophora* Cooper & Grant (1975, p. 1035, pl. 316, fig. 52-56, pl. 346, fig. 7-19) and also figured as *arcticus* [not Whitfield] by King (1931, p. 66, pl. 10, fig. 16, 17), is closer in ribbing and commarginal rugae and definition of sulcus and fold, but differs in shape. It has numerous trail spines, and was found mostly in two members classed as part of the Word Formation, the China Tank (now Roadian in age) and Appel Ranch (now Wordian) of the Glass Mountains in Texas.

Nakamura et al. (1992, pl. 1, fig. 6) figured a specimen as *Chaoiella neoinflata* (Licharew) from the basal Vøringen Member in Spitsbergen. It is narrow and appears to show nothing of the spines, and commarginal rugae cannot be seen for sure over the disc. But overall shape and sulcus with ribbing suggest possible affinities, though *Chaoiella* remains possible. A possible member was recorded as *Productus boliviensis* d'Orbigny at Great Bear Cape by Tschernyschew & Stepanov (1916, p. 30), but was not figured. Other ventral valves were figured as *Productus inflatus* McChesney by Tschernyschew & Stepanov (1916, p. 30, pl. 5), and these show considerable similarity, but ears are lost and spine detail obscure, so that any comparison is insecure.

***Thamnosia*? aff. *sangminlee* n. sp.**

Fig. 45

Material: A specimen with valves conjoined from GSC loc. 26406 and and dorsal valve from C-4003, Assistance Formation, Ellesmere Island.

Description: Poorly preserved specimens from the Assistance Formation are close to *Thamnosia sangminlee* in the nature of their ribbing, but show little of the spines, so that generic and specific identification is not reliable. Ribs number four to five ribs in 5mm over the dorsal trail and some thirteen low rugae lie over the shell.

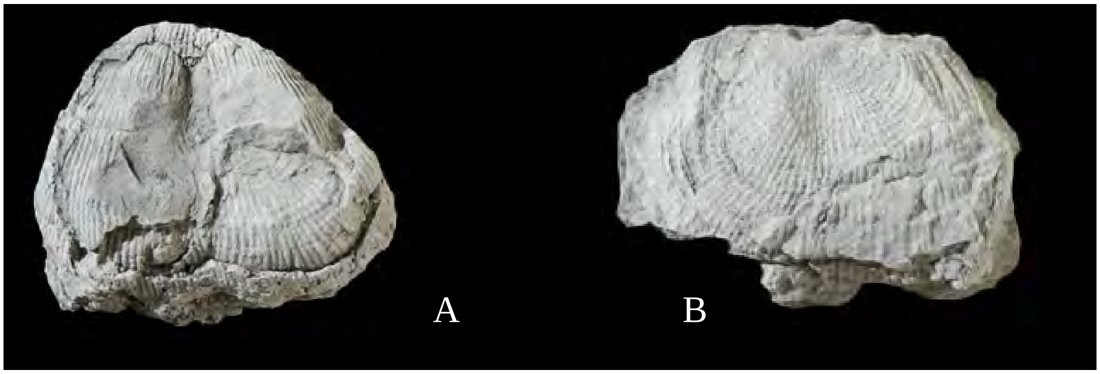

Fig. 45. *Thamnosia* aff. *sangminlee* n. sp. A, ventral valve squashed onto dorsal valve GSC 140728, from GSC loc. 26406. B, crushed dorsal valve GSC 140729 from C-4003. Assistance Formation, Ellesmere Island, x1.

***Thamnosia*? sp.**

Fig. 46 – 48

1971 *Thamnosia* sp. Bamber & Waterhouse, p. 176, pl. 20, fig. 1, 4.
1971 ?*Thamnosia* sp. Bamber & Waterhouse, p. 176, pl. 20, fig. 2.

Diagnosis: Small and subelongate with strong ribs, dorsal disc comparatively flat, trail exceptionally long, spines strong in several rows over the umbonal slopes of the ventral valve.

Material: Three ventral valves from C-4034, Trold Fiord Formation, Ellesmere Island, and two dorsal valves from C-3993, Degerböls Formation, Ellesmere Island. Unknown number of specimens from GSC loc. 53929 and possibly other localities in Takhandit Formation, zone 4.

Dimensions in mm:

Width	Length	Height
36	32	20 ventral valve, C-4034
36	27	21 dorsal valve, C-3993

Description: Specimens weakly transverse, with broad ventral umbo, not strongly incurved, and high umbonal slopes straight in outline and convex in profile, above large gently convex ventral ears. Maximum width lies in front of mid-length, and a well-formed sulcus with evenly concave floor arises in front of the umbo, and extends to the anterior commissure. The trail is longer than the disc. The dorsal disc is almost flat with large concave ears, and bends sharply into a high trail at right angles. Both valves are covered by firm costae, numbering four in 5mm over the anterior ventral valve, and apparently absent from the ears. In some specimens, the disc on both valves bears well developed commarginal rugae, but these are absent in some specimens or are found only over the geniculation and posterior disc in other specimens. Spines are fine and erect over the ventral disc, and numerous over the anterior trail. They are larger in three to four rows over the lower umbonal slopes, as well shown in the specimen figured by

Fig. 46. *Thamnosia*? sp. A, B, posterior ventral and oblique lateral aspects of ventral valve GSC 140730, from C-4034, Trold Fiord Formation, Ellesmere Island, x1.5. The long trail, visible in section, extends in B towards the lower right corner, as arrowed.

Bamber & Waterhouse (1971, pl. 20, fig. 1), but ears are too poorly preserved to show the presence of spines. Dorsal spines are rare and short. The dorsal valve also bears numerous short pits.

Resemblances: This suite of specimens is not that well preserved, and as ribs vary a little in spacing and strength on different specimens, there might be more than one species involved, and not necessarily belonging all to one genus. Specimens are characterized by weakly transverse outline, long trail, and scarcity of dorsal spines. There appears to be no other Arctic occurrence that is comparable, and there is little similarity to *Svalbardoproductus* Ustritsky or *Thuleproductus* Sarytcheva & Waterhouse, which are much larger and possibly have much more numerous ventral ear spines. *Thamnosia anterospinosa* Cooper & Grant (1969, pl. 5, fig. 26, 27; 1975, pl. 348, fig. 1-19, pl. 349, fig. 1-5) from the Cathedral Mountain Formation is more transverse with less defined sulcus and large ears. In this species, dorsal spines are numerous but fine. *T. capitanensis* (Girty, 1908, pl. 12, fig. 1-3b, pl. 20, fig. 8, 8a; King 1931, pl. 10, fig. 15; Cooper & Grant 1975, pl. 345, fig. 1-17, pl. 349, fig. 6-19) of the Glass Mountains comes from the Capitan Formation. (The lower Capitan Formation is Wordian, and the Rader Member and Pinery Member are both Capitanian in age). The species is also more transverse, with stronger reticulation, and a slightly deeper ventral sulcus, compared with the present form. From the Appel Ranch Member in the same region at the top of the Wordian Stage, *T. phragmophora* Cooper

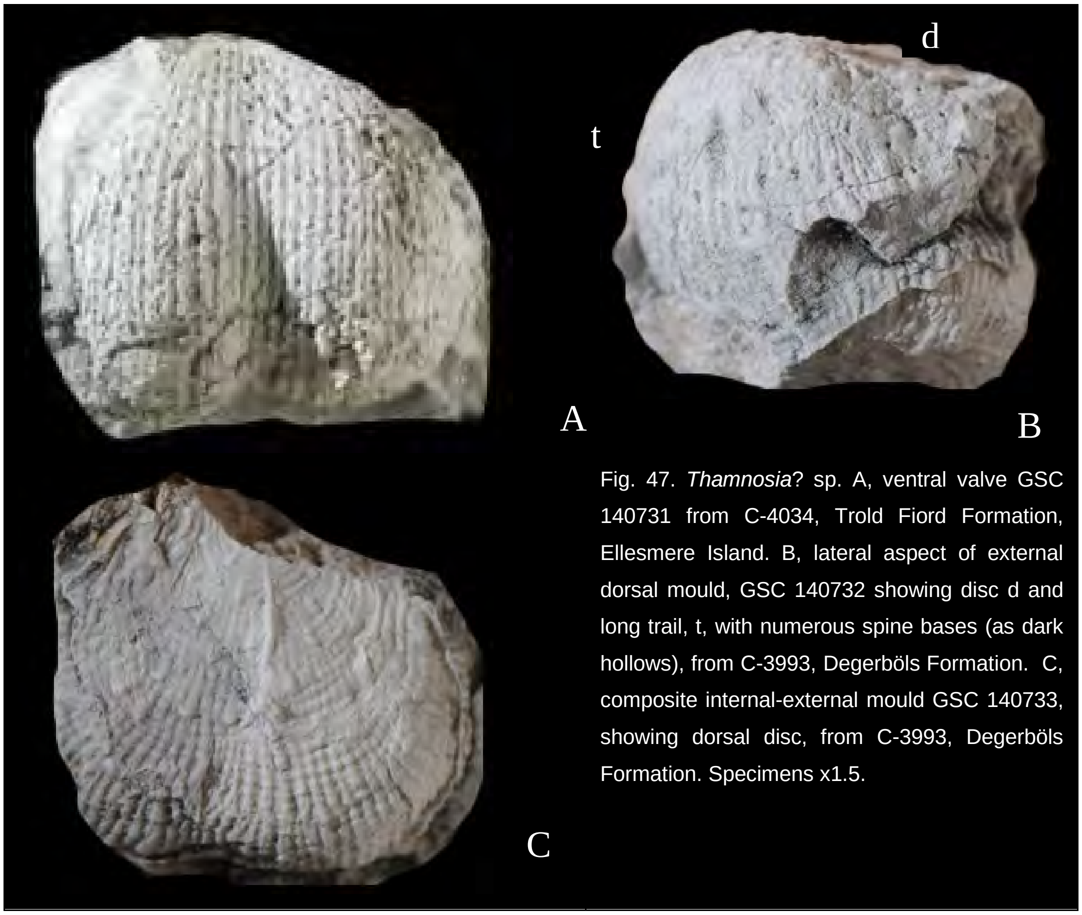

Fig. 47. *Thamnosia*? sp. A, ventral valve GSC 140731 from C-4034, Trold Fiord Formation, Ellesmere Island. B, lateral aspect of external dorsal mould, GSC 140732 showing disc d and long trail, t, with numerous spine bases (as dark hollows), from C-3993, Degerböls Formation. C, composite internal-external mould GSC 140733, showing dorsal disc, from C-3993, Degerböls Formation. Specimens x1.5.

& Grant has strong ribs, less reticulation, shallower sulcus, and lacks ventral ear spines, marking a distinctive form. *T. silicica* Cooper & Grant (1975, pl. 351, fig. 1-18) displays fine ribs and numerous fine spines over both valves, closet to *Thuleproductus*, but is shaped like *Thamnosia*. It comes from the Taylor Ranch Member of the Hess Formation in Texas.

Specimens including BB 81735 assigned to *Productus semireticulatus* (not Martin) by Etheridge (1878, p. 629) and kept at the Natural History Museum appear to belong to *Thamnosia,* but specific comparison is yet to be undertaken. The specimens from C-3993 were considered to come from the Degerböls Formation, but beds from Great Bear Cape Formation were in those times allocated to that formation. However, the C-3993 specimens are smaller and narrower than *Thamnosia sangminlee* n. sp. from the Great Bear Cape Formation.

Fig. 48. *Thamnosia*? sp., ventral valve showing well developed spine bases over the anterior umbonal slopes. GSC 26386 from GSC loc. 53929, *Dyoros modestus* Zone, Takhandit Formation, x1. (Bamber & Waterhouse 1971).

Genus ***Svalbardoproductus*** Ustritsky, 1962b

Diagnosis: Medium to large, enrolled ventral valve and concave dorsal valve with geniculate trail, very large ears, both valves costate, subdued posterior commarginal rugae. Both valves spinose, scattered, strong to numerous over ears of both valves, not numerous over umbonal flanks of ventral valve.

Type species: *Svalbardoproductus striatoauritus* Ustritsky, 1962b, p. 82 from lower Kapp Starotsin Formation (Kungurian), as shown in Fig. 50, OD.

Discussion: This genus has been substantially misdiagnosed in Brunton et al. (2000, p. 475) and with no figures provided. It was stressed that clusters of spines were missing from the ears, presumably on the basis of an assessment by Ustritsky (1962), but his figure shows that the large ventral ears carried a number of stout spines. What is noticeable about his figure of the ventral valve is that umbonal slope spines are not conspicuous, and this, together with the large ears on both valves, would distinguish the genus from both *Thamnosia* Cooper & Grant, 1969 and *Thuleproductus* Sarytcheva & Waterhouse, 1972. The assessment is only based on figures for *Svalbardoproductus*, but appears to point to significant differences that will allow the genus to be distinguished.

Svalbardoproductus subarcticus (Sarytcheva, 1977a)

Fig. 49

1914 *Productus boliviensis* [not d'Orbigny] – Wiman, p. 63, pl. 13, fig. 7-10.
1914 *P. inflatus* [not McChesney] – Wiman, p. 66, pl. 14, fig. 1, 2, pl. 15, fig. 3-5.
1917 *P. inflatus* [not McChesney] – Grønwall, p. 578, pl. 29, fig. 17-19.
1936 *P. arcticus* – Stepanov, p. 115, pl. 1, fig. 1-4.
1937b *P. arcticus* Stepanov, p. 113, pl. 1, fig. 9, 10.
1962 *Dictyoclostus neoinflatus* [not Licharew] – Dunbar, p. 7, pl. 1, fig. 8, 9.

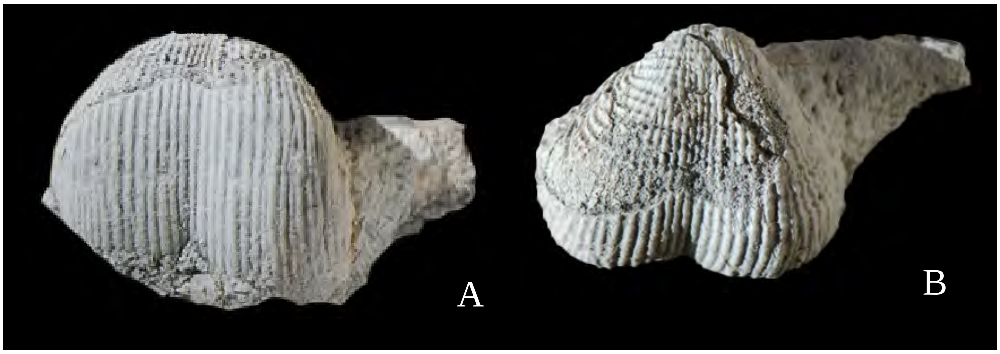

Fig. 49. *Svalbardoproductus subarcticus* (Sarytcheva), ventral valve GSC 140734 from GSC loc. 58977, Great Bear Cape Formation. A, B, anterior and posterior aspects of, x1. C, tilted lateral aspect showing spine bases over umbonal slope, x4.

1964 *Chaoiella*? sp. Gobbett, p. 91, pl. 9, fig. 1.
1964 *Costinifera* (sic) *arctica* – Gobbett, p. 91, pl. 9, fig. 2-6.
?1971 *Kutorginella* cf. *arctica* [not Whitfield] – Bamber & Waterhouse, p. 172, pl. 18, fig. 2.
1977a *Thuleproductus subarcticus* Sarytcheva, p. 78, pl. 9, fig. 1-4.
1998 *T. subarcticus* – Grunt et al., pl. 11, fig. 5.
?2008 *Thamnosia arcticus* [not Whitfield] – Angiolini & Long, p. 80, Fig. 3F-I, 4A-D.

Diagnosis: Shells with high narrow venter and large extended ears.

Holotype: Specimen figured by Sarytcheva (1977a, pl. 9, fig. 1a, b) from Talatin Formation (Kungurian), Petchora Basin, OD.

Material, Description: A small ventral valve from GSC loc. 58977, Great Bear Cape Formation, is much smaller than *Thuleproductus* *crassauritus* Sarytcheva & Waterhouse, 1972 as described below, and has more strongly developed commarginal rugae, and relatively large ventral ears. Spines over the ears are obscure near the hinge and moderately numerous anteriorly. It looks very like the specimen figured as *T*. *subarcticus* Sarytcheva (1977a, p. 78, pl. 9, fig. 1a, 1b) from the Talatin Suite of Kungurian age in the Petchora Basin of northwest Russia. Other specimens of this species were added by Sarytcheva (1977a) from the Urals and Kapp Starotsin beds of Spitsbergen,and a lengthy age assigned, although not all detail is clear. Gobbett (1964) declared that his Spitsbergen-Bjørnøya *arcticus (= subarcticus)* was found only in the Spiirfer Limestone, and the Wiman specimens suggest *subarcticus*.

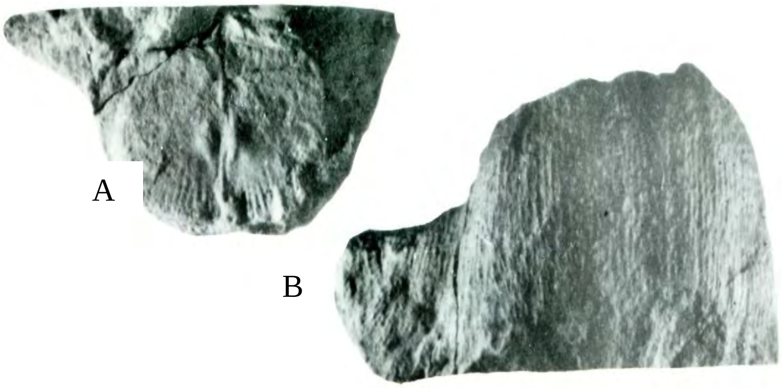

Fig. 50. *Svalbardoproductus striatoauritus* Ustritsky. Reproduction of two of the original figures of Ustritsky (1962, pl. 2, fig. 1, 2), provided by Tatjana Grunt, showing interior of dorsal valve (A) and anterior view of ventral valve (B), suggestive of numerous small anterior spines over the disc, and a few large ear spines over the inner ear, with no sign of one or more rows of spines along the umbonal slopes (in contrast arguably to species of *Thamnosia* and *Thuleproductus*. From Kapp Starotsin Formation of Spitsbergen.

Ustritsky (1979) listed specimens from low in what is the Vøringen Member, below and overlapping the species *arcticus.* He considered that *subarcticus* was junior synonym of *Svalbardoproductus striatoauritus* Ustritsky, as illustrated in Fig. 50. The specimen seems to have finer costae than in the types of *subarcticus* figured by Sarytcheva (1977a), and although this may transpire to be a variable feature, it is cautiously suggested that this may provide a specific difference, reinforcing the apparent differences in the coarser and few ear spines and finer scattered trail spines on the figured *striatoproductus*. It is yet to be confirmed that umbonal slope spines are rare over the ventral valve of *striatoproductus*, but no such spines are visible on the figured specimen, admittedly from an unfavourable aspect, and this requires further study.

Specimens that suggest large ventral ears now lost are included in the synonymy, from Amdrups Land, northeast Greenland, Vøringen Member of Spitsbergen, and lower Takhandit Formation, as referenced in the synonymy. No account of *subarcticus* has appeared in Nakamura et al. (1992). Specimens assigned by Wiman (1914, pl. 13, fig. 7-10) from the “Corakalk” of Bjørnøya show large ears, but seem to lack ear spines. (See his pl. 13, fig. 9).

Genus ***Thuleproductus*** Sarytcheva & Waterhouse, 1972

Diagnosis: Medium to large, enrolled ventral valve and concave dorsal valve with geniculate long trail, large ears, both valves costate, subdued posterior commarginal rugae. Both valves spinose, scattered, especially numerous over ears of both valves.

Type species: *Thuleproductus crassauritus* Sarytcheva & Waterhouse, 1972, p. 67 from Trold Fiord Formation (Wordian), OD.

Discussion: This genus has been synonymized with *Thamnosia* Cooper & Grant, 1969, p. 10 by Brunton et al. (2000), but Waterhouse (2013, 2018a) pointed out that *Thamnosia* has more ventral disc spines, and fewer spines over the ears of both valves. In addition, the species described from the Glass Mountains by Cooper & Grant (1975) are transverse, whereas *Thuleproductus* species are elongate, thanks to a long trail. Ustritsky (1979) claimed that his genus *Svalbardoproductus* Ustritsky 1962, was senior synonym for *Thuleproductus*, but *Svalbardoproductus* was recorded as having no ear spines, and showing other differences, Waterhouse (2013, 2018a) suggesting that if the two were synonymous, then *Svalbardoproductus* had been substantially misdiagnosed. *Svalbardoproductus* was based on large specimens like those of *Thuleproductus*, and Ustritsky's figure suggests that the original description of *Svalbardoproductus* erred, with a number of stout ear spines, and very few umbonal slope spines.

Thuleproductus arcticus (Whitfield, 1908)

Fig. 51, 52

1908 *Productus semireticulatus arcticus* Whitfield, p. 54, pl. 1, fig. 2, pl. 2, fig. 8-10.
?1960 *Dictyoclostus* cf. *neoinflatus* [not Licharew] – Harker & Thorsteinsson, p. 55, pl. 17, fig. 1-4.
1970 *Antiquatonia* cf. *neoinflatus* [not Licharew] – Bamber & Copeland, p. 630, pl. 14, fig. 3.
1971 *Thamnosia* cf. *T. arctica* – Brabb & Grant, p. 14, pl. 1, fig. 38, 39, 45.
1972 *Thuleproductus arcticus* – Sarytcheva & Waterhouse, p. 71, pl. 7, fig. 9, pl. 8, fig. 4, 5.
1977a *Thuleproductus arcticus* – Sarytcheva, p. 74, pl. 7, fig. 6-8, text-fig. 44, 45.
1998 *Thuleproductus arcticus* – Grunt et al., pl. 12, fig. 2, 3.
2013 *Thuleproductus arcticus* – Waterhouse, p. 118, Fig. 5.8.

Diagnosis: Subelongate shells with moderately extended ears and well defined narrow ventral sulcus, two or three rows of spines along umbonal flanks of ventral valve, numerous fine spines anteriorly and laterally, dorsal spines fine.

Lectotype: Specimen AMNH 31734 figured by Whitfield 1908, pl. 1, fig. 2, pl. 2, fig. 8, 9) and refigured in Waterhouse (2013, Fig. 5.8, p. 119) from Cape Sheridan, Ellesmere Island, Canada, designated by Gobbett (1964, p. 91). Stepanov (1936, pl. 1, fig. 3, 4) also refigured Whitfield originals.

Material: Four ventral valves, one specimen with valves conjoined and dorsal valve from GSC loc. 26406 and one ventral valve from C-4003, Devon Island. Single ventral valves from C-4019 and C-4025, one dorsal valve from C-4002, and two specimens with valves conjoined, a ventral valve and a dorsal valve from GSC loc. 58973. All from the Assistance Formation, Ellesmere Island.

Dimensions in mm: ears incomplete

Width	Length	Height	Umbonal angle	Sulcal angle	
47	61	38	105°	115°	
46	47+	28	115°	18°	GSC 36193

Description: Available specimens are incomplete and not well preserved, so that identification is provisional. The better preserved specimens are elongate, thanks to an extended trail, with narrow sulcus and persistent ribs. Spines are fine over the ventral disc and trail, and aligned in a row along the ventral umbonal slopes, and a hinge row lies each side of the ventral umbo. One elongate specimen shows a very few additional spines on the umbonal slopes. An ear is preserved on only one specimen, and it has signs of a number of poorly preserved spines. GSC 36193 shows a high long adductor platform divided by a low median ridge, and deeply impressed and longitudinally striate diductor impressions. The dorsal septum is long, increasing in strength anteriorly and dorsal muscle scars dendritic, and brachial shields well developed. A marginal ridge is firmly developed, especially postero-laterally.

Resemblances: These poorly preserved specimens are provisionally identified with Whitfield's taxon. *Productus semirecticulatus arcticus* on the basis of size and shape. Subsequently the species has been referred to three different genera, *Svalbardoproductus* by Ustritsky (1962, 1979), *Thamnosia* Cooper & Grant, 1969 by Brabb & Grant (1971), Brunton et al. (2000) and Angiolini & Long (2008) and *Thuleproductus* by Sarytcheva & Waterhouse (1972). Regrettably, Brunton et al. and Angiolini & Long ignored the

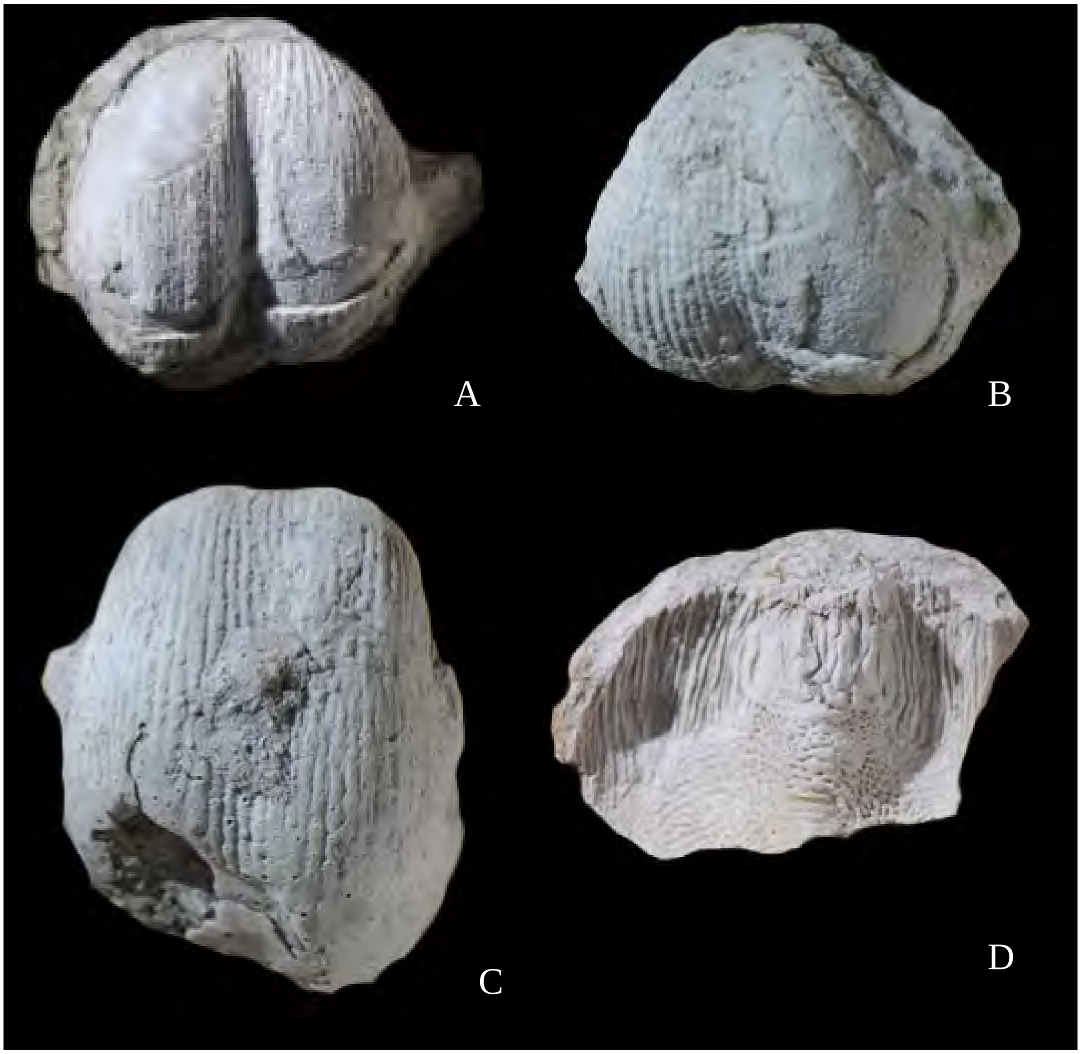

Fig. 51. *Thuleproductus arcticus* (Whitfield 1908). A, ventral valve GSC 140735 from C-4003. B, ventral valve GSC 140736 from C-3997. C, ventral valve GSC 140737 from C-4025. Specimens in A-C x1, from Ellesmere Island. D, internal fragment GSC 140738 from GSC loc. 26406, Devon Island, x1.5. All from Assistance Formation.

discussion by Ustritsky, so that their analysis was incomplete. That question was addressed by Waterhouse (2013, 2018a), and he concluded that *Svalbardoproductus* may well prove to have priority, provided that the Ustritsky description can be revised and adjusted, should that prove necessary. In the meantime, the diagnosis of *Svalbardoproductus* by Ustritsky (1962) and repeated without adjustment by Brunton et al. (2000) does not fit with that for *Thamnosia* or for *Thuleproductus,* but is incorrect as far as ventral ear spines are concerned, and failed to notice the comparative scarcity of ventral umbonal slope spines. First hand examination of type material of *Thamnosia* at the Smithsonian Institution in Washington D. C. showed that the type species, *T. anterospinosa* Cooper & Grant, like other *Thamnosia*, had a broader shape and less extended trail, and had far more numerous spines over the lateral flanks of the ventral valve than in *Thuleproductus crassauritus*, and far fewer spines over the dorsal ears. Angiolini & Long (2008) pronounced that the spines varied in various *Thamnosia*, but how did they know they were all congeneric? They provided no detailed analysis, and had not examined the Cooper-Grant types at first hand. Waterhouse (2013, 2018a) concluded that whilst uncertainty remained over *Svalbardoproductus*, it was possible to distinguish *Thuleproductus* from *Thamnosia* on the basis of the two type species.

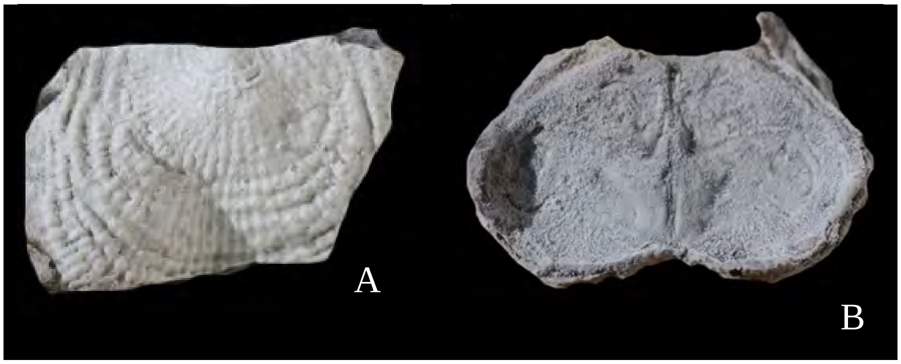

Fig. 52. *Thuleproductus arcticus* (Whitfield). A, dorsal external mould GSC 140739 x1.5, showing disc, from C-4002, Ellesmere Island. B, dorsal aspect of internal mould showing dorsal disc, GSC 141162 x1, from GSC loc. 26406, Devon Island. Both from Assistance Formation.

There are further uncertainties. The full description for *arcticus* is still incomplete. Nothing of the material so far described has determined the nature of the spines on the ears, apart from a dorsal valve figured by Angiolini & Long (2008, Fig. 4D), which shows the inner ear bearing a number of pits that may have opposed external spines. The ventral valves they figured, where moderately complete, have comparatively large ventral ears, approaching those of *striatoauritus* Sarytcheva and might prove conspecific. As well, a specimen figured as *Chaoiella*? by Gobbett (1964, pl. 9, fig. 1) shows many likely ventral ear spines, but its specific affinities are open to question. The stratigraphic range of the species *arcticus* is possibly restricted to the Assistance Formation of Arctic Canada and possibly Alaska, and additional reported material in Russia (Sarytcheva 1977a, p. 75), with possible material of uncertain provenance from Spitsbergen. Shells compared with *Thamnosia arctica* by Stehli & Grant (1971, pl. 62, fig. 1-14) and Angiolini-Long specimens from the Vøringen Member of Spitsbergen are rated as unlikely to be conspecific.

Thuleproductus crassauritus Sarytcheva & Waterhouse, 1972

Fig. 53 – 55

1875b *Productus semireticulatus* [not Martin] – Toula, p. 234, pl. 6, fig. 1a-d.
1972 *Thuleproductus crassauritus* Sarytcheva & Waterhouse, p. 67, pl. 8, fig. 1-3, text-fig. 1.
1977a *T. crassauritus* – Sarytcheva, p. 76, pl. 8, fig. 1-4, text-fig. 46, 47.
1998 *T. crassauritus* – Grunt et al., pl. 11, fig. 4.
1992 *T. crassauritus* – Nakamura et al., pp. 96, 98, pl. 3, fig. 1, 2, pl. 4, fig. 1.

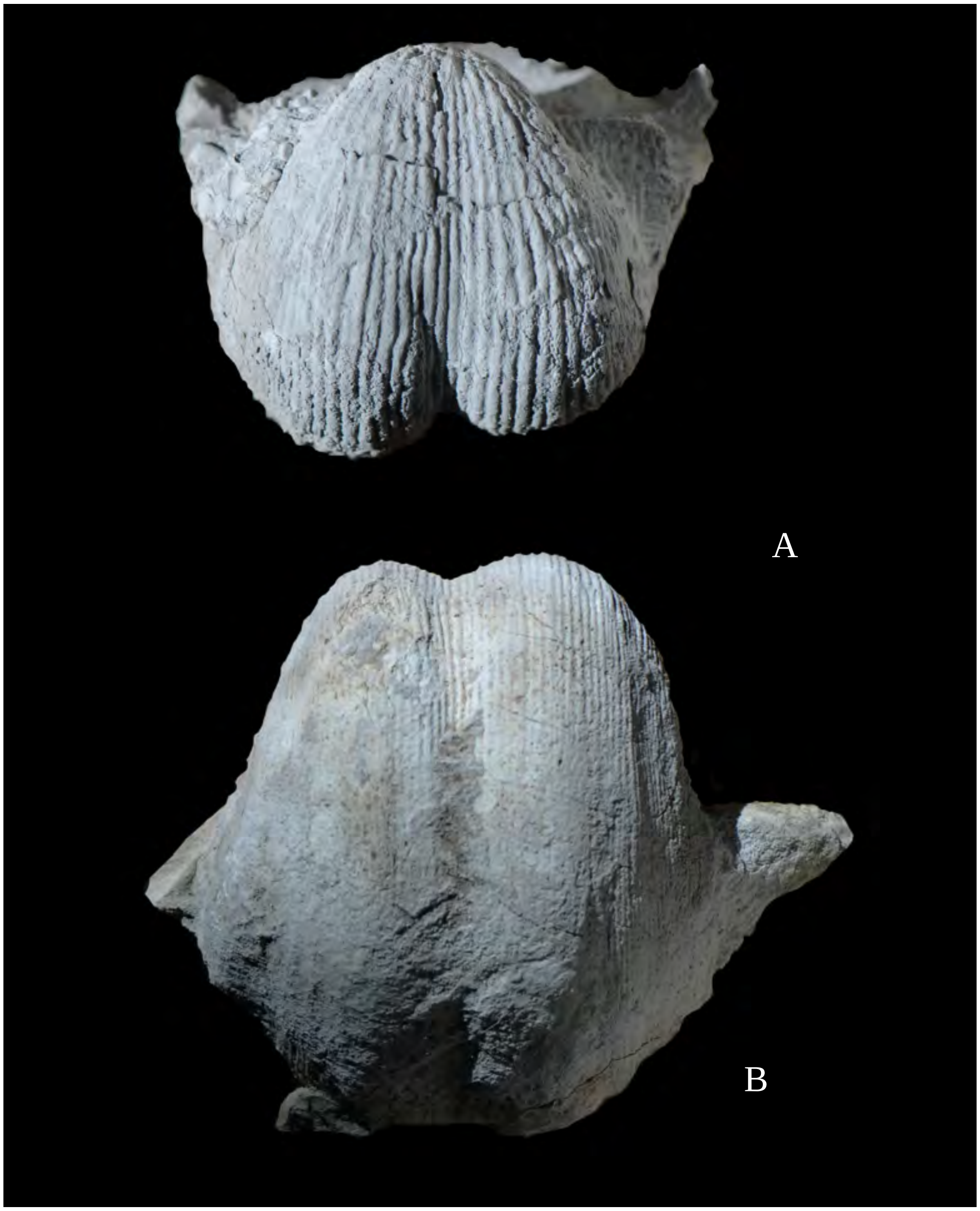

Fig. 53. *Thuleproductus crassauritus* Sarytcheva & Waterhouse. A, ventral posterior aspect for GSC 140740 (see also Fig. 55), from GSC loc. 57687, x0.9. B, ventral valve GSC 36779 from GSC loc. 57687, x0.9. Trold Fiord Formation, Ellesmere Island.

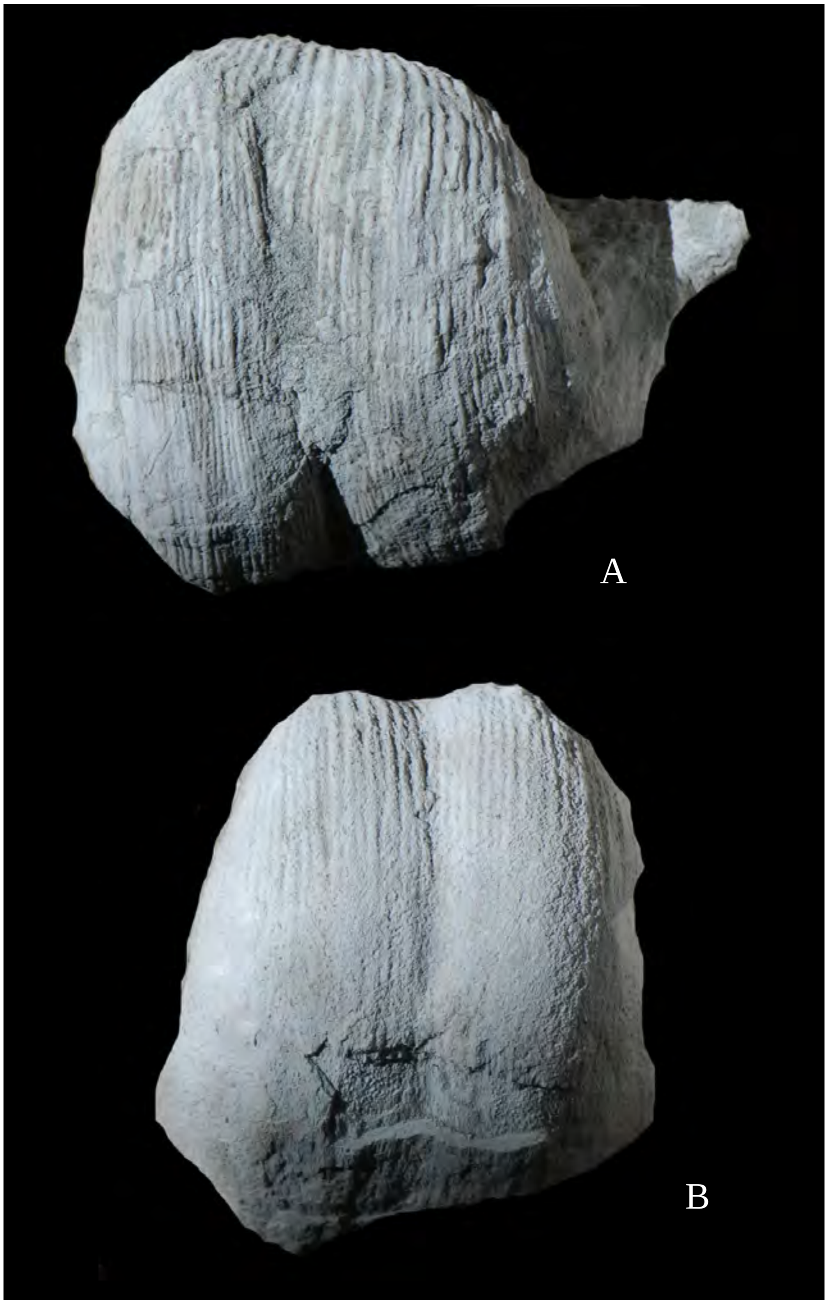

Fig. 54. *Thuleproductus crassauritus* Sarytcheva & Waterhouse. A, ventral valve GSC 36784 from GSC loc. 57689, Trold Fiord Formation, Ellesmere Island. B, ventral anterior view, GSC 36789 from C-4091, Degerböls Formation, Ellesmere Island. Specimens x1.

2013 *T. crassauritus* – Waterhouse, p. 117, Fig. 5.6, Fig. 5.7 (misnumbered 5.8).

Diagnosis: Very large with strong costae, becoming finer anteriorly, and numerous ear spines on both valves.

Holotype: GSC 26374 from GSC. loc. 70629, Trold Fiord Formation, Cameron Island, figured by Sarytcheva & Waterhouse (1972, pl. 8, fig. 1) and Waterhouse (2013, Fig. 5.6.D), OD.

Additional material: One ventral valve from GSC loc. 76029, Cameron Island. Five specimens with valves conjoined from GSC loc. 57687, one conjoined from GSC loc. 57689, one ventral valve from C-4034, plus GSC specimen 36715, locality not provided, Trold Fiord Formation. A ventral valve from C-4091, possible Degerböls Formation, Ellesmere Island.

Fig. 55. *Thuleproductus crassauritus* Sarytcheva & Waterhouse, lateral view of specimen GSC 140740, ventral valve from GSC loc. 58997, Trold Fiord Formation. Specimen x1. Note change in rib density, those of the trail being much finer than those over the disc.

Description: The species has been described in Sarytcheva & Waterhouse (1972), with more or less topotypic material further illustrated by Waterhouse (2013) and herein. One interesting aspect lies in the variation in density and strength of radial costation. In one topotype GSC 36784 from GSC loc. 57689, costae number four in 10mm over the disc, but become finer at up to fourteen in 10mm on the anterior disc and trail. In another, GSC 36776 from GSC loc. 57687, they number six in 10mm over mid-disc.

Taxonymy, Nomenclature: Further study needs to be directed towards the validity of the specific name for this form. It was named in 1972, but possibly another name has priority, proposed as *Productus semireticulatus* Martin var. *frigidus* Salter (1855, p. 388, pl. 36, fig. 13-15). The specimen, registered as BB 96960 or 40680 at the Natural History Museum, London, is a large and incomplete specimen with both valves present, but deformed, preserved in a matrix of light red, brown and green sandstone suggestive of Trold Fiord Formation, and coming from Depot Point, Ellesmere Island. It has worn, thick shell, pierced by slender borings, and carrying the suggestion of radial ribs on the ventral valve. No spines are preserved. Enquiries to the Natural History Museum have failed to elicit any response, so the matter still requires confirmation, reinforced by illustrations.

Family **BUXTONIAIDAE (BUXTONIIDAE)** Muir-Wood & Cooper, 1960

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 interior 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.

Subfamily **BUXTONIAINAE (BUXTONIINAE)** Muir-Wood & Cooper, 1960

Diagnosis: Spines on both valves as a rule.

Tribe **SPINIFRONSINI** Waterhouse, 1981b

Diagnosis: Costae well defined to rarely erratic in course, crossed by low but clearly 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 variously wider, as wide as, or narrower than costae. Dorsal pits.

Genus ***Kochiproductus*** Dunbar, 1955

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

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

Discussion: *Dunbarovia* Waterhouse, 2013, p. 147 is recognized as a closely related genus or subgenus, based on *Kochiproductus flexicostatus* with its highly distinctive with sharply defined commarginal rugae and crinkly branching costae anastomosing anteriorly over both valves. It has been reported from east Greenland and Spitsbergen. (See Fig. 59, p. 89).

Kochiproductus freboldi Stepanov, 1937b

Fig. 56 – 58, 60

?1916 *Productus porrectus* [not Tschernyschew?] – Tschernyschew & Stepanov, p. 41, pl. 5, pl. 8, fig. 5a-c.
1937b *Productus* (*Buxtonia*) *freboldi* Stepanov, p. 122, pl. 2, fig. 4.
1942 *P. freboldi* – Frebold, p. 28, pl. 3, fig. 3.
1960 *Kochiproductus freboldi* – 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* – Bamber & Copeland, pl. 14, fig. 16.
2008 *K.* cf. *K. plexicostatus* [not Dunbar] – Angiolini & Long, p. 91, Fig. 4G.
2018a *K. freboldi* – Waterhouse, p. 455, Fig. 380.

Diagnosis: Large little inflated shells with shallow sulcus and low fold, closely spaced ribs and prominent nodes, many bearing a spine.

Holotype: Specimen figured by Stepanov (1937b, pl. 2, fig. 4) from ”Productus beds”, Spitsbergen, by monotypy.

Material: Three specimens with valves conjoined from GSC loc. 26406, Assistance Formation, Devon Island, a specimen with valves conjoined and fragments from locality JBW 631, mid-Takhandit Formation, Yukon Territory, a ventral valve from C-3993 and several specimens from C-4095, Degerböls Formation, and a ventral valve from C-4034, Trold Fiord Formation, of Ellesmere Island.

Description: A specimen GSC 137464 figured from the Assistance Formation measures 94mm wide (allowing for breakage), 74mm long and 31mm high. The umbo is incurved over the hinge-line, and is broad with angle of 90°. Umbonal walls are moderately steep, diverging forward at close to 80°, 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. A well-formed sulcus traverses the ventral valve, commencing at the umbonal tip, with an angle of 30°. 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, or that the anterior trail was very slender. 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 usually no less than six in 10mm. On both valves the ribs show occasional branching, as a sudden rather than gradual diversion, leading to marked forks and divaricating ribs. In the specimen figured by Harker & Thorsteinsson (1960), the ribs are slightly coarser than in other specimens, 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 are 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 round rather than elongate. Each bears a slender spine, semi-erect to semi-recumbent over the disc, and posteriorly in front of the hinge such swellings are crowded and small. The dorsal pattern is more reticulate, without the “bumpy ornament” commented on by Stehli & Grant (1971), 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 bearing 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 material is distinguished by its large size, only moderately inflated disc, slender and apparently short trail and small ears, with well developed costal swellings, abruptly branching ribs, and long dorsal median septum. The ventral muscle field is difficult to match with that of 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. They 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. 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*, whereas Dunbar (1955, p. 85) had ascribed all Toula material to *Waagenoconcha payeri* (Toula), and Sarytcheva (1977a, p. 134) referred them to a separate species *Waagenoconcha* sp. A, later to be named *Wimanoconcha sarytchevae* by Grunt (2006a, p. 148). The best figured specimens were those of Toula (1874, pl. 1,

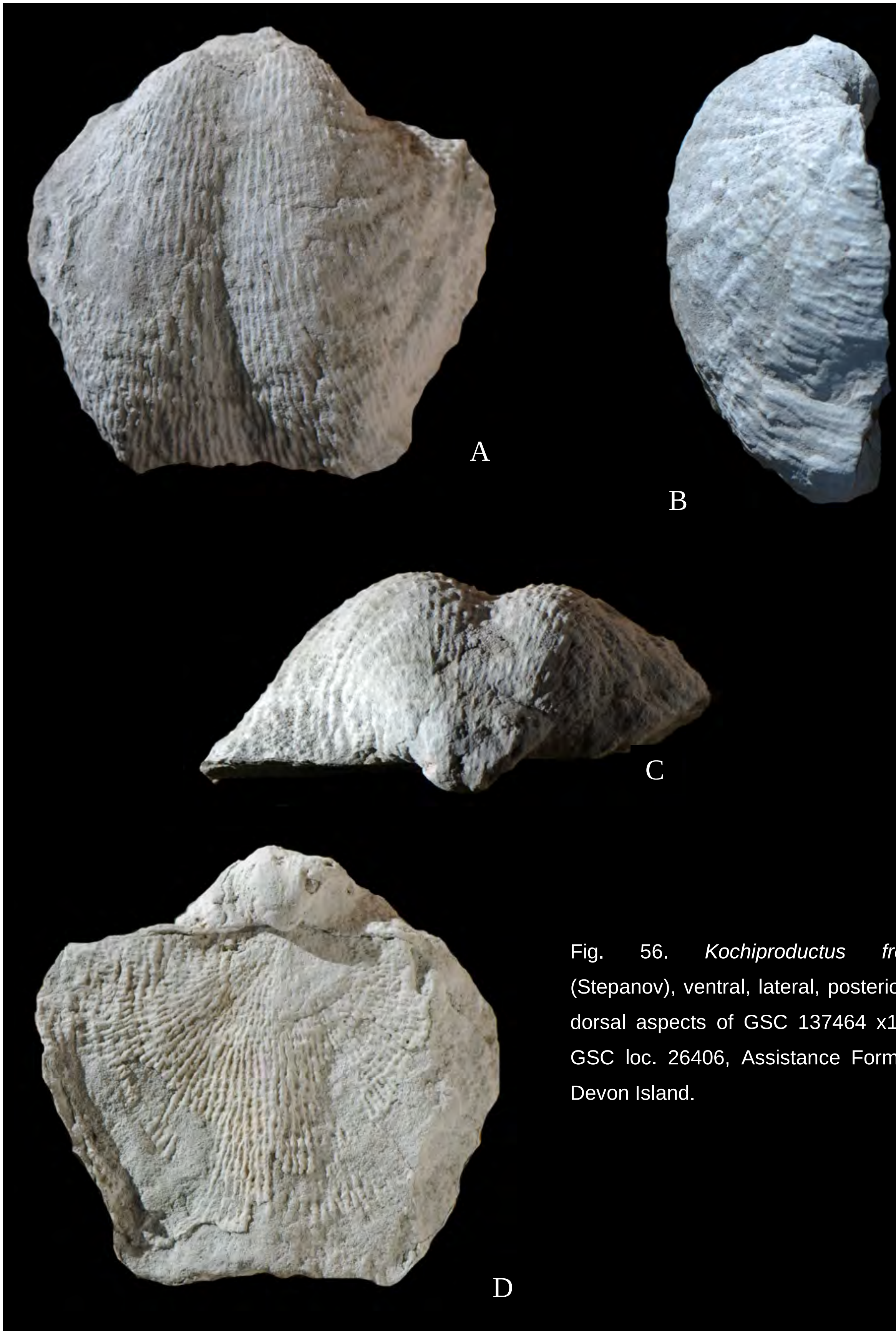

Fig. 56. *Kochiproductus freboldi* (Stepanov), ventral, lateral, posterior and dorsal aspects of GSC 137464 x1 from GSC loc. 26406, Assistance Formation, Devon Island.

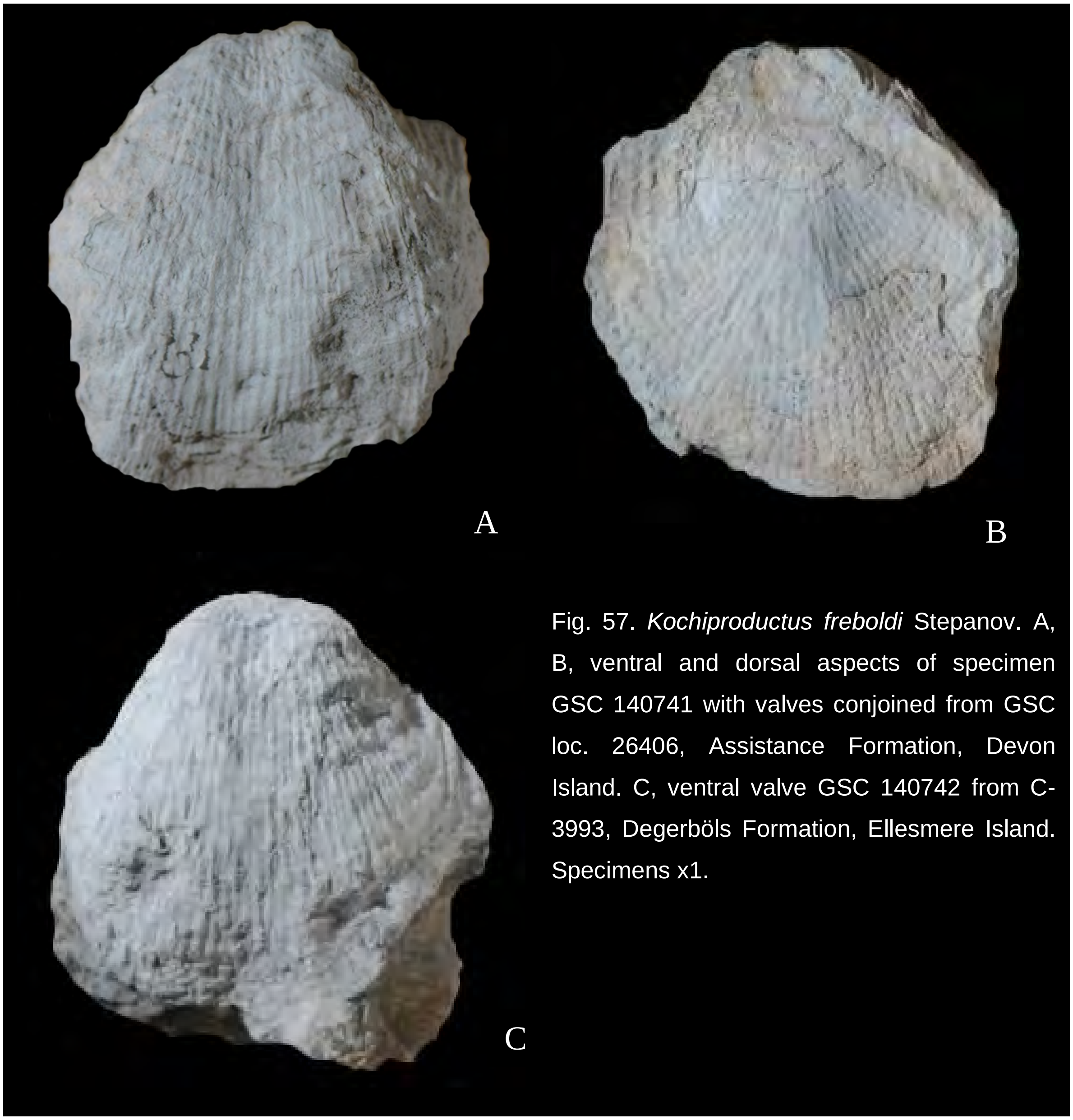

Fig. 57. *Kochiproductus freboldi* Stepanov. A, B, ventral and dorsal aspects of specimen GSC 140741 with valves conjoined from GSC loc. 26406, Assistance Formation, Devon Island. C, ventral valve GSC 140742 from C-3993, Degerböls Formation, Ellesmere Island. Specimens x1.

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, and was included by Toula (1874) and Dunbar (1955) with other specimens classed as *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). The lectotype for *payeri* was cited as the specimen figured by Toula (1874, pl. 4, fig. 1a, b) by Waterhouse (2018a, p. 456), and refigured by Waterhouse (2018a, 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 with that of *K. imperiosus* Waterhouse (2018a, Fig. 72). Compared with *freboldi*, the Toula specimen is relatively 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 figured by Harker in Harker & Thorsteinsson (1960).

Harker & Thorsteinsson (1960, pl. 17, fig. 5, 6) had allocated their Assistance Formation specimen to *Kochiproductus freboldi* (Stepanov, 1937b, 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 figure of type *freboldi* fails to show much of the "bumpy" ornament typical of *Kochiproductus*, but does not appear to be well

Fig. 58. *Kochiproductus freboldi* Stepanov, worn external mould of dorsal valve GSC 140743, from C-4095, ?Degerböls Formation. From Ellesmere Island, x1.

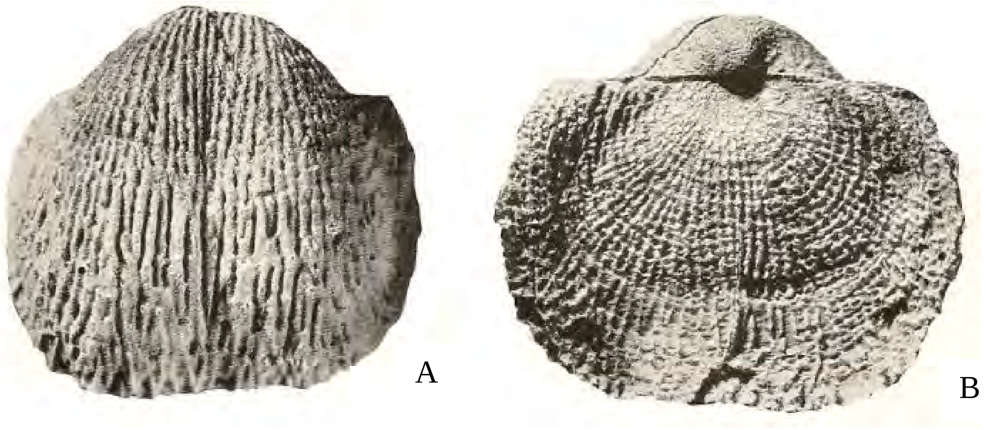

Fig. 59. *Kochiproductus* (*Dunbarovia*) *plexicostatus* Dunbar. Holotype as figured by Dunbar (1955, pl. 17, fig. 1, 2; 1961, pl. 1, fig. 12, 13), x1. From Kap Stosch, Greenland. This species has been reported from Spitsbergen as well as northeast Greenland, but has not yet been found in the Sverdrup Basin.

preserved, and the specimen shows intercalated and many branching ribs. At the same time, 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. 59. Gobbett (1964, p. 81) also rejected the similarity of Harker's material and Stepanov's *freboldi* to *plexicostatus* Dunbar. He further 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. A large ventral valve figured as *Productus porrectus* by Tschernyschew & Stepanov (1916, pl. 5, pl. 8, fig. 5a-c) from Great Bear Cape has fine ribs, seven to eight in 10mm and small spines, but no branching ribs are visible.

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 Waterhouse 2013, p. 108). As far as can be seen from figures, the costae do not branch as much as in *freboldi.*

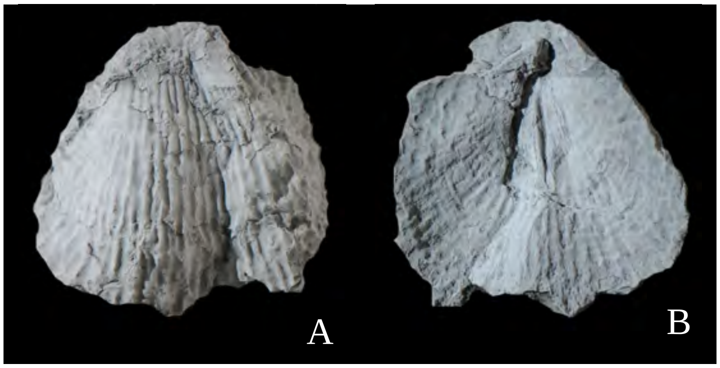

Fig. 60. *Kochiproductus freboldi* Stepanov, A, B, ventral and dorsal aspects of GSC 140744 from GSC loc. 26406, Assistance Formation Devon Island, x1.

Superfamily **ECHINOCONCHUSOIDEA (ECHINOCONCHOIDEA)** Stehli, 1954

Family **ECHINOCONCHUSIDAE (ECHINOCONCHIDAE)** Stehli, 1954

Subfamily **ECHINOCONCHUSINAE (ECHINOCONCHINAE)** Stehli, 1954

Tribe **ECHINOCONCHUSINI (ECHINOCONCHINI**) Stehli, 1954

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

Diagnosis: Large semicircular to oval shells with commarginal bands over entire shell, bearing spines of two different diameters, arranged in rows over each commargon. Commargons are especially well defined.

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 crucially 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. Moreover, *Echinaria* is distinguished even at first glance by its distinctive commargons over both valves, which are more numerous and better defined than those of *Calliprotonia* or *Echinoconchus* and other allied genera.

Echinaria tardus n. sp.

Fig. 61 – 64

Derivation: tardo – make slow, Lat.

Diagnosis: Small shells with broad dorsal valve and well defined numerous commargons. Spines largely uniform in diameter.

Holotype: Specimen GSC 140745 illustrated herein as Fig. 61A, B, 62A, B from C-4019, Assistance Formation, Ellesmere Island, here designated.

Material: Two specimens with valves conjoined and three dorsal valves from C-4019, Assistance Formation, Ellesmere Island. One dorsal valve from Assistance Formation, GSC loc. 26404, Devon Island. One dorsal valve from C-6167, locality detail not available, possibly Assistance Formation. One broken dorsal valve with part of ventral valve from C-3995, and a tiny ventral valve from C-4034, Trold Fiord Formation, Ellesmere Island. Two specimens from JBW 631, mid-Takhandit Formation.

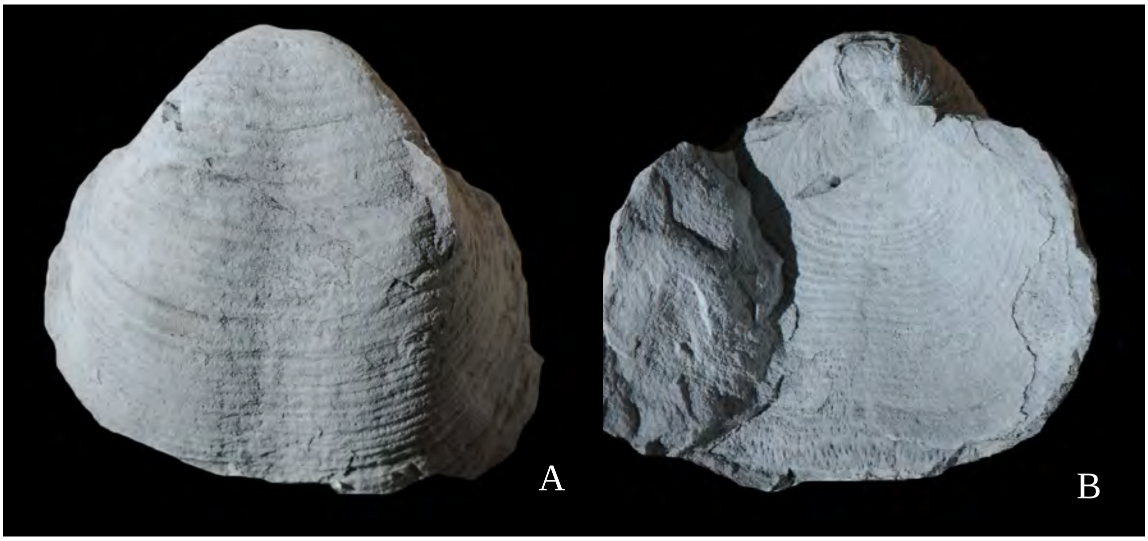

Fig. 61. *Echinaria tardus* n. sp. A, B, ventral and dorsal aspects of GSC 140745 holotype with valves conjoined, from C-4019, Assistance Formation, Ellesmere Island, x0.9.

Dimensions in mm: both valves, Assistance Formation

Width	Length	Height	Hinge width	Umbonal angle	Sulcal angle	Cardinal angle
36	40	23	27.5	65°	20°	85°
59	58	30	38	60°?		120° both valves
62	59	8.5 dorsal valve				

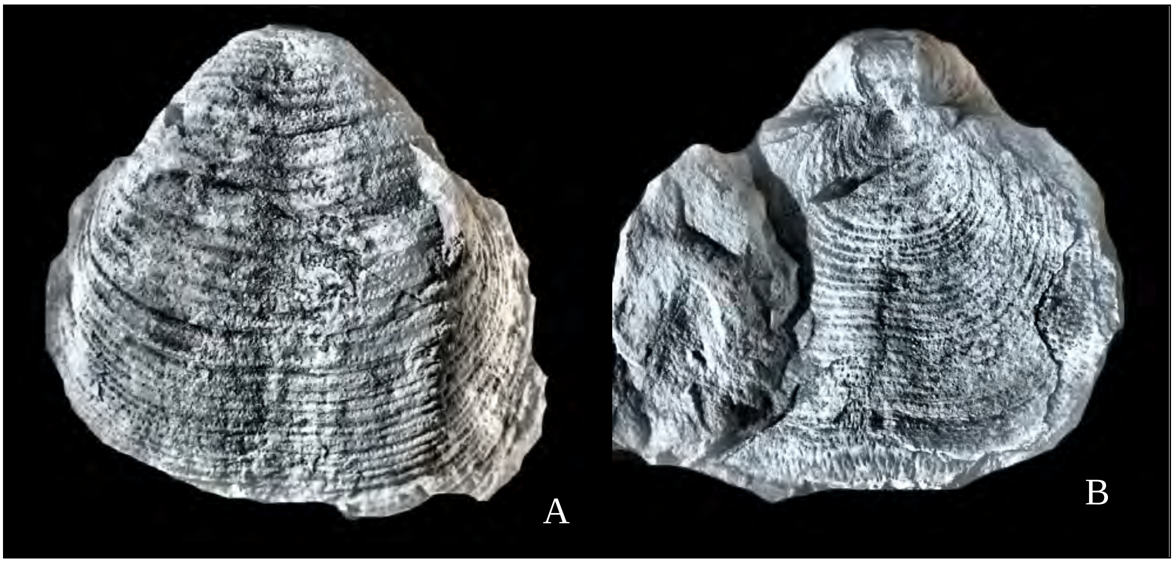

Fig. 62. *Echinaria tardus* n. sp. A, B, ventral and dorsal aspects of GSC 140745 holotype, specimen with valves conjoined, from C-4019, Assistance Formation, Ellesmere Island, x0.9. Reproduced by local equalization.

Description: Shells are small for the genus, and have extended and incurved ventral umbo, long umbonal walls, and moderately wide hinge with obtuse cardinal extremities and no ears. The sulcus commences an estimated 25mm in front of the beak tip and widens at 30º, with shallow concave floor, and shallows anteriorly. The dorsal valve is gently concave with a slightly more concave nepionic portion 5mm wide. A broad low fold commences near mid-length of

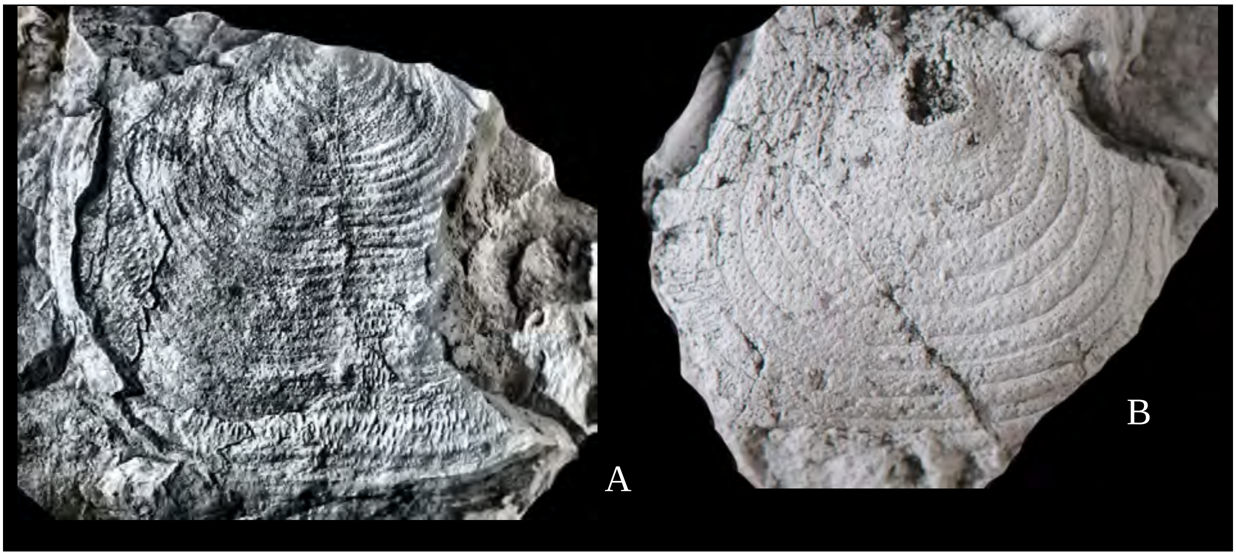

Fig. 63. *Echinaria tardus* n. sp. A, dorsal external mould GSC 140746 from C-4019, Assistance Formation, Ellesmere Island, x1, under local equalization. B, dorsal external mould GSC 140747 from C-6167, locality detail not available, possibly equivalent to Assistance Formation, x3.

the valve. Both valves are covered by numerous narrow and well defined commargons, each bearing two to three up to six rows of fine erect spines, most of which are subuniformly coarse. The commargons close to the ventral umbo are most strongly defined, convex and separated by sharply defined incisions or angular trenches, and they bear spines in two to five rows quite as coarse as those at the anterior margin: the commargons are distinguished by bearing signs of growth lines near their anterior margin. An external mould from GSC loc. 56922 shows elongate spinules over much of each commargon, and some commargons have finer spinules anteriorly (Fig. 64).

Internal detail is not exposed.

Resemblances: A scattering of species are just as small as the present form, and the species is named principally to mark the unusually late occurrence of the genus as well as its prevalent coarse spinules, with some especially anterior commargons bearing finer spinules anteriorly, Miller (1974) also figured a specimen, GSC 36798 from C-4049 from the Trold Fiord Formation that belongs to *Echinaria*, and is of comparable size. Brunton et al. (2000, p. 511) gave an age range of Gzhelian (latest Carboniferous) to Lower Permian (ie. Kungurian), but the genus commenced before in Visean time. Judged from present material, the genus ranged well into the Middle Permian Guadalupian Series, in the Roadian and Wordian Stages.

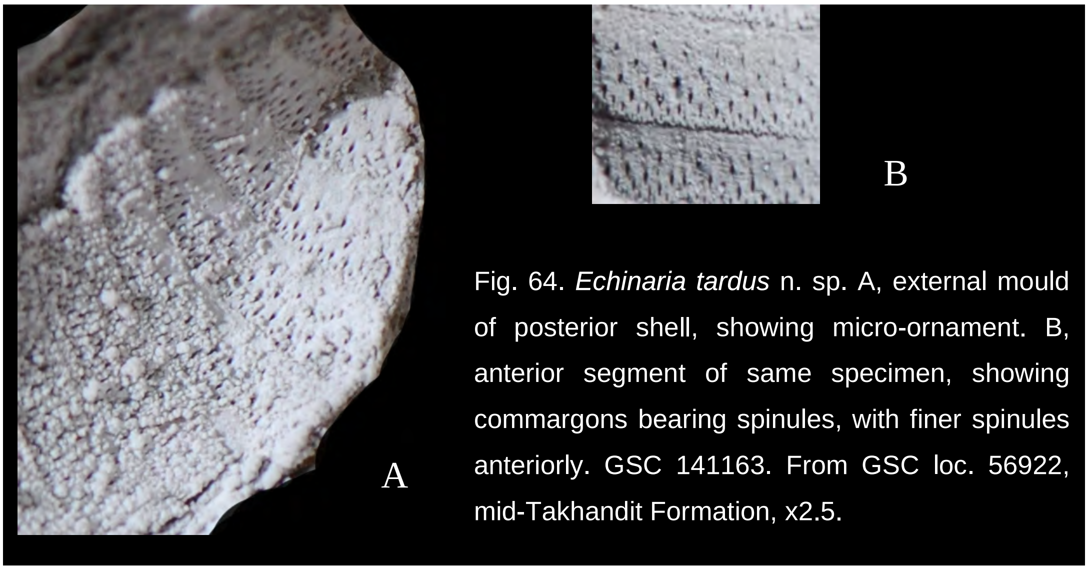

Fig. 64. *Echinaria tardus* n. sp. A, external mould of posterior shell, showing micro-ornament. B, anterior segment of same specimen, showing commargons bearing spinules, with finer spinules anteriorly. GSC 141163. From GSC loc. 56922, mid-Takhandit Formation, x2.5.

Subfamily **JURESANIAINAE** (**JURESANIINAE**) Muir-Wood & Cooper, 1960

Tribe **JURESANIAINI (JURESANIINI**) Muir-Wood & Cooper, 1960

Genus ***Ametoria*** Cooper & Grant, 1975

Diagnosis: Close to *Juresania* Fredericks, 1928, distinguished by lack of buttress plates and lack of anterior rugae.

Type species: *Ametoria residua* Cooper & Grant, 1975, p. 1055 from Road Canyon Formation of Texas, OD.

Ametoria nassichuki n. sp.

Fig. 65 – 68

Diagnosis: Small moderately well inflated shells with long steep posterior walls and maximum width placed well forward.

Holotype: Specimen GSC 140748 from C-4019, Assistance Formation (Roadian), Ellesmere Island, illustrated in Fig. 65A, B, here designated.

Material: Specimen with valves conjoined from C-4019 and single ventral valves from C-1872 and C-4065, Assistance Formation, Ellesmere Island, and ventral valve from GSC loc. 26406, Assistance Formation, Devon Island. Single ventral valves from C-23614, Degerböls Formation?, and from possibly C-4017, Trold Fiord Formation, Ellesmere Island.

Dimensions in mm:

Width	Length	Height
21	20	11.5 holotype
25	24	14 from C-23614

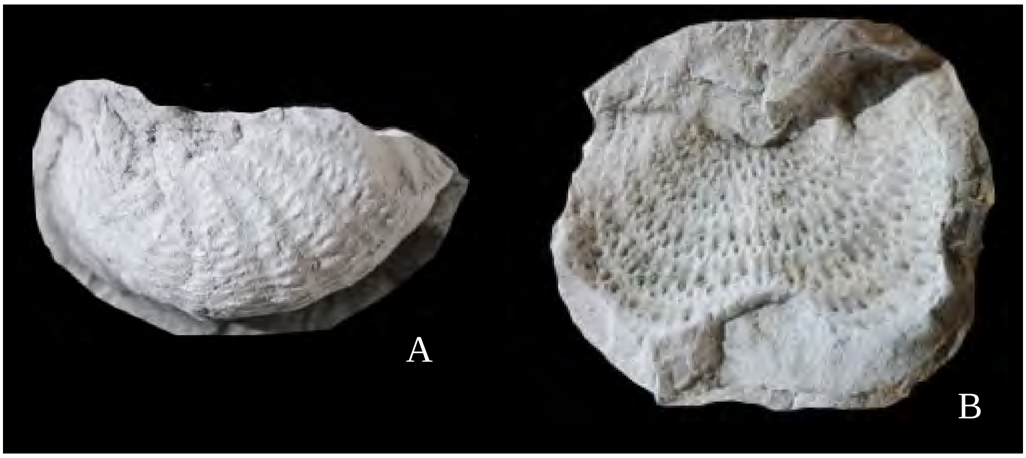

Fig. 65. *Ametoria nassichuki* n. sp. A, lateral view showing ventral valve with ornament, and B, dorsal view, showing dorsal valve overhung by ventral umbo, and showing the disc in section anteriorly. Holotype GSC 140748 from C-4019, Assistance Formation, Ellesmere Island, x2.5.

Description: The holotype has arched ventral valve and gently concave dorsal valve, and moderately thick visceral disc. The umbonal angle is close to 100º, and posterior walls are long and steep, extending well forward, with maximum width close to the anterior third of the length. The sulcus commences a little in front of the umbo, with angle varying between 30º and 40º, and deepens anteriorly in two specimens but shallows anteriorly in a third specimen. Ventral ears are small but well formed and gently convex. A low fold extends for the length of the dorsal valve and dorsal ears are gently concave. The ventral ornament consists of short and long spine bases typical of *Juresania* Fredericks and *Ametoria* Cooper & Grant, the mix of lengths being most evident over the anterior lateral slopes. The specimen with valves conjoined from C-4019, Assistance Formation of Ellesmere Island, shows convex commargons anteriorly over the lateral shell, and these strengthen over the lateral walls, as in the specimen from C-23614. The dorsal valve displays a dense array of rounded and subeleongate pits between raised elongate pustules.

Ametoria was differentiated by its lack of buttress plates. The interior of present material is not exposed, but shape and ornament are convincingly similar to features of *Ametoria*, and the time range appears to have extended from Roadian into Wordian.

Fig. 66. *Ametoria nassichuki* n. sp., anterior ventral valve GSC 140750 from ?C-4017, Trold Fiord Formation, x3. The collection number on this sample is obscure.

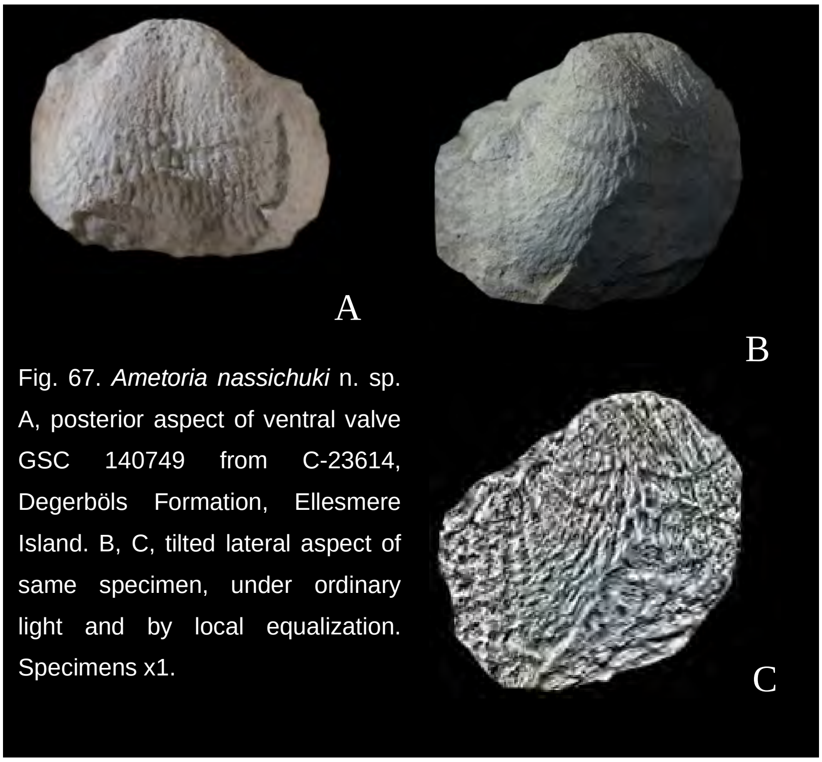

Fig. 67. *Ametoria nassichuki* n. sp. A, posterior aspect of ventral valve GSC 140749 from C-23614, Degerböls Formation, Ellesmere Island. B, C, tilted lateral aspect of same specimen, under ordinary light and by local equalization. Specimens x1.

Resemblances: The size, shape and ornament of these specimens are all consistent with the genus *Ametoria* Cooper & Grant (1975, pl. 256, fig. 1-14), known until now only as the type species in the Middle Permian (Roadian) of Texas. The type species is slightly larger than present material, with less conspicuous commargons laterally, and with maximum width placed near mid-length rather than anteriorly. Its sulcus is deeper anteriorly. A small ventral valve figured by Stepanov (1937b, pl. 2, fig. 3) from Cape Starotsin in Spitsbergen speculatively might be related, but the figure does not clearly display the ornament, apart from showing elongate spine bases.

Fig. 68. *Ametoria nassichuki* n. sp., anterior ventral valve GSC 140751 from C-1872, Assistance Formation, x1.

Subfamily **TUBERSULCULUSINAE** (**TUBERSULCULINAE**) Waterhouse, 1971b

Tribe **TUBERSULCULUSINI (TUBERSULCULINI**) Waterhouse, 1971b

Genus ***Tubersulculus*** Waterhouse, 1971b

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 subelongate bases, lateral ridges cross ears internally, dorsal endospines strong and numerous.

Type species: *Tubersulculus maximus* Waterhouse, 1971b, 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, and outlasted *Tubersulculus*.

Tubersulculus? sp.

Fig. 69

Material, Description: Two small ventral valves from C-4034, Trold Fiord Formation of Ellesmere Island, have a deep sulcus and display a shape typical of *Tubersulculus* Waterhouse, a genus that appeared in the Late Carboniferous of Canada and became moderately widespread in the northern paleohemisphere, lasting through Early Permian time until Kungurian. The present specimens are significantly younger. One has ventral spines that are unusually fine for the genus, and no swollen or slightly extended spine bases, but such are better developed anteriorly over the second and larger specimen. Both agree with typical *Tubersulculus* in the presence of a well-defined sulcus. The absence of the dorsal valve precludes further comparison with better known and older species, but on present evidence the occurrence of present specimens may be regarded as exceptional.

Fig. 69. *Tubersulculus*? sp. A, worn ventral valve GSC 140752. B, anterior ventral valve GSC 140753. From C-4034, Trold Fiord Formation, Ellesmere Island, x2.

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

Diagnosis: Small thin-disced species, numerous spines arranged in quincunx over both valves, with slightly swollen not elongate bases. 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), because Tubersulculinae has priority. Brunton et al. (1995) referred *Tubersulculus* to the marginiferid tribe Costispiniferini Muir-Wood & Cooper, 1960 (Waterhouse 2002, p. 15), but *Tubersulculus* is not marginiferid, and has no marginal ridge or other features typical of Marginiferidae.

Krotovia? sp. A

Fig. 70A

1972 *Krotovia* sp. Waterhouse, p. 491, Fig. 3b.

Material: A ventral valve from GSC loc. 58977, Great Bear Cape Formation, Ellesmere Island.

Fig. 70. A, *Krotovia*? sp. A, ventral valve from Great Bear Cape Limestone at GSC loc. 58977, x2. B, *Krotovia*? sp. B, ventral valve from GSC loc. 47849, Blind Fiord Formation, x2. (Waterhouse 1972b).

Description: An occurrence of possible *Krotovia* was recorded from the Great Bear Cape of Bjorne Peninsula by Waterhouse (1972b). The specimen is distinguished by its evenly spaced coarse spines, and has a gentle median anterior sulcus. No further material is available, but absence of the dorsal valve prevents full assessment.

Krotovia aff. ***licharewi*** (Frebold, 1942)

Fig. 71

aff. 1942 *Productus licharewi* Frebold, p. 38, pl. 3, fig. 7-9.
aff. 1955 *Krotovia nielseni* Dunbar, p. 84, pl. 8, fig. 1-6.
aff. 1964 *K. licharewi* – Gobbett, p. 59, pl. 3, fig. 1-10.

Diagnosis: Small shells with moderately long umbonal walls and prominent ventral umbo, spines fine at six to eight in 5mm.

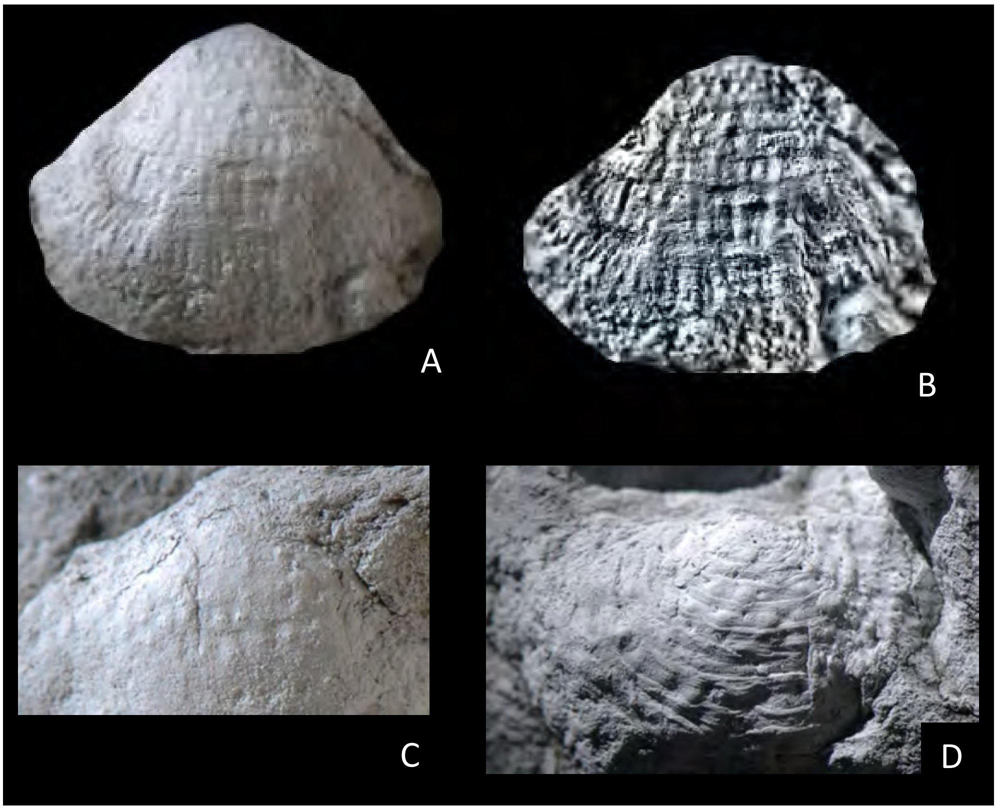

Fig. 71. A-C, *Krotovia* aff. *licharewi* (Frebold). A, ventral valve GSC 140754. B, same under local equalization. C, posterior aspect of the same specimen. From C-4065, formation uncertain, possibly Assistance, Ellesmere Island. D, *Guangia* sp., dorsal valve external mould GSC 140755, from JBW 631, middle Takhandit Formation. Fig. 71A, B, D x3, Fig. 71C x4.

Holotype: Specimen figured by Frebold (1942, pl. 3, fig. 7, kept at the Mineralogical Museum, Copenhagen. Holotype for *nielseni*, specimen figured by Dunbar (1955, pl. 8, fig. 1) from “Productus limestone” in northeast Greenland, OD.

Description: A specimen from C-4065, formation not known, but apparently Assistance Formation, Ellesmere Island, belongs to *Krotovia*. It is distinguished by its fine and numerous spines, six in 5mm posteriorly, eight in 5mm anteriorly, and well developed growth laminae and increments on the dorsal valve. The shell is slightly buckled and abraded. It is a little larger than the shells from northeast Greenland, and has umbonal walls slightly less concave in outline and broader umbo.

Resemblances: *Krotovia* is relatively common in the Jungle Creek Formation of Yukon Territory, of Early Permian age, but is rare in the Middle Permian of northern Canada. The present specimens are compared with *Krotovia licharewi* (Frebold) from Kap Stosch, central east Greenland. Specimens from the same area were later assigned a new name by Dunbar (1955), but were judged by Gobbett (1964) to be the same, in recording a suite of specimens from the middle Brachiopod Chert of Spitsbergen. The present specimens are few: the ventral valve is somewhat deformed, but appears close, whereas some of the ventral valves figured by Dunbar are more triangular in shape.

Krotovia tundra Fredericks (1926b, p. 87, pl. 3, fig. 7-9) as figured in Kalashnikov et al. (1990, pl. 1, fig. 3a, 3b, 4) from the Talatin Suite of the Petchora Basin in north Russia is close and has fine spines. It is weakly transverse and has a weak to narrow and defined median ventral sulcus over the median third of the length.

***Krotovia*? sp. B**

Fig. 70B

1972b *Krotovia* sp. Waterhouse, p. 491, Fig. 3b.

Material: A ventral valve from GSC loc. 47849, Blind Fiord Formation, Axel Heiberg Island.

Description: An intriguing occurrence of *Krotovia* was recorded from south of the Svartevaeg cliffs of Axel Heiberg Island by Waterhouse (1972b). The specimen is distinguished by its evenly spaced coarse spines, and has a gentle median anterior sulcus with long narrow median fold.

Discussion: This specimen appears to be of Changhsingian age. It is distinguished by the narrow fold traversing the ventral sulcus, and by the suggestion of commarginal rugae: it is far from being a typical member of the genus *Krotovia*, but more material is need to clarify more aspects of its morphology.

Genus ***Guangia*** Waterhouse, 2002b

Diagnosis: Characterized by regular development of dimples over dorsal valve.

Type species: *Krotovia inflata* Shen et al. 2000, p. 739 from Selong Group (Lopingian), south Tibet, OD.

Discussion: *Krotovia inflata* Shen et al. (2000) differs from typical *Krotovia* in the presence of numerous small pits over the dorsal valve, whereas the type species of *Krotovia*, *Productus spinulosus* Sowerby, 1814, p. 155, lacks such pits, as figured in a number of articles including Brunton (1984, pl. 12, fig. 4, 9, 14, 16, 17, pl. 13, fig. 2) and Brunton et al. (2000, Fig. 287.1b), just like various other species assigned to the genus. The proposal of *Guangia* was opposed by Brunton (2007, p. 2640), by ignoring the presence of pits, and focusing on the presence of spines in the dorsal valve, which are also present in *Krotovia*. He noted that Waterhouse had reported that dorsal spines were less numerous, and asserted that that was in comparison with *Krotovia*: however that assumption was mistaken, because the genus had been compared with *Stictozoster* Grant, 1976, p. 96, and distinguished from that genus by its less fine and numerous spines. Both taxa tend to have spines on both valves that are comparatively slender and numerous, and arranged in commarginal rows. Their family relations are discussed in Waterhouse (2002b). Shen (2017, p. 702) provided an account of *Guangia*, giving weight to the Brunton opinion, and again paying no attention to the presence of pits. However their presence are a concrete reality, highly persistent in a few species, and completely absent from most species assigned to *Krotovia*, including the type species.

Guangia pustulata (Keyserling, 1853)

Fig. 72

1853 *Productus pustulata* Keyserling, p. 247.
1902 *P. pustulata* – Tschernyschew, p. 617, pl. 30, fig. 1, 2, pl. 53, fig. 5, 6.
1928 *Krotovia pustulata* – Chao, p. 52, pl. 5, fig. 18-20.
?1957 *K. pustulata* – Cooper, p. 33, pl. 8A, fig. 1-5.
1960 *K. pustulata* – Muir-Wood & Cooper, p. 188, pl. 50, fig. 6-9.
1968 *K. pustulata* – Sarytcheva, p. 79, pl. 5, fig. 9.
1970 *K. pustulata* – Zavodowsky, p. 81, pl. 12, fig. 4, pl. 26, fig. 10, 11.
1971 *K. pustulata* – Bamber & Waterhouse, pl. 15, fig. 21, pl. 16, fig. 2.
1996 *K. pustulata* – Shi & Waterhouse, p. 57, pl. 4, fig. 21-23.

Diagnosis: Shells large for the genus, tending to transverse, both valves ornamented by closely spaced regularly arranged spines with slightly swollen bases.

Neotype: Specimen figured by Tschernyschew (1902, pl. 30, fig. 2) from Schwagerina-Kalk (Sakmarian), Ufa Plateau, Urals, kept at CNIGR Tschernyschew Museum, St Petersburg, SD Shi & Waterhouse, 1996, p. 57.

Material: An external mould of a ventral valve from C-4067, Great Bear Cape Formation, Ellesmere Island.

Description: The valve is broad with shallow anterior sulcus, and is ornamented by regularly and closely spaced spines with slightly swollen bases.

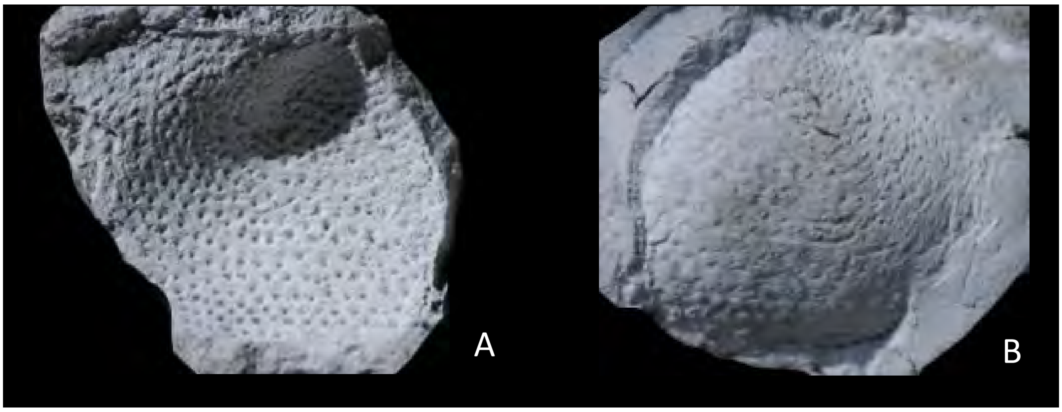

Fig. 72. *Guangia pustulata* (Keyserling). A, B, external mould and cast of ventral valve GSC 141007 from C-4067, Great Bear Cape Formation, Ellesmere Island, x2.

Resemblances: The overall shape and distribution, density and size of spines strongly recalls aspects of *Productus pustulata* Keyserling, for which specimens figured by Tschernyschew (1902) and other authors show the presence of dorsal pits as in *Guangia*. The species was originally described from the Schwagerina-Kalk in the Urals, and reported from the basal Permian Paren Horizon and Burgalin horizon of northeast Russia (Zavodowsky 1970), west

Kazakhstan (Sarytcheva 1968), and Early Permian of China (Chao 1928). A very weak sulcus is present in this Great Bear Cape specimen, as in specimens reported from the *Jakutoproductus verchoyanicus* Zone at the top of the Jungle Creek Formation by Bamber & Waterhouse (1971) and Shi & Waterhouse (1996). The present occurrence marks the youngest known occurrence of the species. Oregon shells recorded by Cooper (1957) are similar in shape, but seem to lack dorsal pits, placing a question against its generic position. Dorsal pits are also developed in *Krotovia norfordi* Waterhouse, 2018a, now *Guangia*, from Gzhelian and Asselian beds of the basal Jungle Creek Formation in Yukon Territory. This species is distinguished by its more closely spaced spines.

Guangia sp.

Fig. 71D

Single dorsal external moulds from GSC loc. 56922 and JBW 631, middle Takhandit Formation, have dorsal pits, four or five in 5mm. They are close in overall shape and ornament to the lower Jungle Creek specimens identified, perhaps contentiously, with *Productus wallacianus* Derby, 1874 in Waterhouse (2018a, p. 156).

Family **WAAGENOCONCHAIDAE (WAAGENOCONCHIDAE)** Muir-Wood & Cooper, 1960

Subfamily **WAAGENOCONCHAINAE (WAAGENOCONCHINAE**) Muir-Wood & Cooper, 1960

Tribe **WAAGENOCONCHAINI (WAAGENOCONCHINI**) Muir-Wood & Cooper, 1960

Genus ***Waagenoconcha*** Chao, 1927a

Diagnosis: Umbonal region of ventral valve bearing slender spines with elongate bases, spines often more erect and in large bands 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: The lectotype for *Productus humboldti* was nominated by Archbold (1993, p. 19) as the specimen figured by Tschernyschew (1904, p. 31, Fig. T1 and T1a), Tschernyschew having refigured the syntypic series of d'Orbigny (1842). The material is kept at the Museum d'Histoire Naturelle in Paris.

Waagenoconcha? sp.

Fig. 73 – 75

Material: Three ventral valves from C-4095, Degerböls Formation, Ellesmere Island.

Fig. 73. *Waagenoconcha*? sp. ventral valve GSC 140756 from C-4095, Degerböls Formation, Ellesmere Island, x1, reproduced by local equalization.

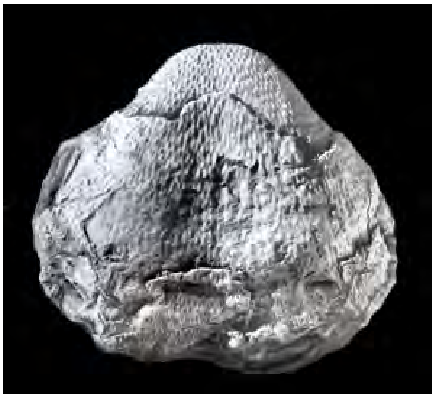

Fig. 74. *Waagenoconcha*? sp., ventral valve GSC 140758 from C-4095, Degerböls Formation, Ellesmere Island, x1.5.

Description: A ventral valve from the Degerböls Formation measures 44mm wide, 42mm long, and has been slightly squashed to a height of 12mm. The maximum width lies at mid-length but the hinge is almost as wide. A long and distinct sulcus extends from the beak to the anterior margin. Micro-ornament consists of dense elongate raised spine bases, just over 1mm long over much of the valve, and becoming 3.5mm long anteriorly, with six or seven in 5mm. A few growth steps lie near the anterior margin. There are no bands of erect spines.

Fig. 75. *Waagenoconcha*? sp. ventral valve GSC 140757 from C-4095, Degerböls Formation, Ellesmere Island, x1.5. Reproduced by local equalization.

Resemblances: The spine bases are moderately long and the sulcus and shape like those of many *Waagenoconcha*, but without the dorsal valve, it is difficult to be sure of specific and even generic affinities. The specimens are of much the same size and shape as an internal ventral mould figured as *Waagenoconcha arctica* n. sp. by Nakamura et al. (1992, pl. 1, fig. 9). But their article provided no diagnosis or description, and so the taxon would appear to be invalid. No true external ornament can be seen in the figure.

Genus ***Gruntoconchinia*** n. gen.

Derivation: Named for T. G. Grunt.

Diagnosis: Shells with thick visceral cavity, ventral spines vary from erect to moderately elongate posteriorly, becoming shorter and more crowded anteriorly, dorsal spines mostly erect. Trail distinct but of only moderate length, curving sharply from the dorsal disc.

Type species: *Gruntoconchinia payerinia* n. gen., n. sp. from Foldvik Creek Group of northeast Greenland, figured by Dunbar (1955, p. 85, pl. 9, fig. 1-8, pl. 10, fig. 1-8, text-fig. 16), here designated.

Discussion: The species described by Dunbar (1955) was referred to a new species *Wimanoconcha sarytchevae* by Grunt (2006a). However, the dorsal valve of the Greenland specimens is not wedge-shaped, but is gently concave, with geniculate trail (Dunbar 1955, p. 86). Moreover, the ventral spine bases have varied bases, some erect, some slightly elongate, as well figured by Dunbar (1955). Possibly allied more decorticated material from Spitsbergen was figured by Frebold (1937, p. 19, pl. 2, fig. 1, pl. 3, fig. 1-3, pl. 4, fig. 1-3), with so-called *purdoni* (Frebold 1931, pl. 3, fig. 1). The genus also approaches *Patellamia* Waterhouse, 2013 from the Sverdrup Basin, a genus which has uniformly short bases, and a very short trail, with more concave dorsal valve, and slender visceral disc, in contrast to the thick disc of the present genus.

Specimens from the Kapp Starotsin Formation (Brachiopod Chert) of Spitsbergen that were assigned to *Wimanoconcha sarytchevae* by Grunt (2006a) are regarded as a different species, characterized by less well developed anterior ventral sulcus (see next page).

Gruntoconchinia payerinia n. gen., n. sp.

1955 *Waagenoconcha payeri* (not Toula) – Dunbar, p. 85, pl. 9, fig. 1-8, pl. 10, fig. 1-8, text-fig. 16.
1961 *W. payeri* – Dunbar, pl. 1, fig. 11.

Derivation: Named for Julius von Payer.

Diagnosis: Medium to large shells with sulcus well developed anteriorly, moderately wide hinge, gently concave dorsal disc with broad fold and medium-length trail at steep angle to disc. Visceral disc comparatively thick. Ventral spines varied, often erect without elongate bases, elsewhere with short swollen bases.

Holotype: Specimen figured by Dunbar (1955, pl. 9, fig. 1, 3, 5) from "Productus limestone", northeast Greenland, here designated.

Description: Dunbar (1955) referred the Greenland material to *Waagenoconcha payeri* of Toula (1874) from what is now the Vøringen Member of the Kapp Starotsin Formation of Spitsbergen. Gobbett (1964, p. 76) re-examined the Toula types that were kept in Vienna, and declared that some were possibly internal moulds of *Kochiproductus*, not related to the Dunbar specimens assigned to *payeri*, and Waterhouse (2018b, p. 458, Fig. 381) refigured a newly nominated lectotype for Toula's species. Identification with *Kochiproductus* is not clear from the illustration, which indicates a thick visceral disc and wide hinge as in the present form, but arguably the posterior sulcus is deeper and the dorsal valve more concave in Toula's specimen. Only discovery of further type material, with internal and external moulds or shells can clarify the specific and even generic nature of the taxon, which in the meantime must remain in limbo, with weight attached to Gobbett's interpretation that the species belonged to *Kochiproductus*, because he had examined the original types. Ustritsky (1979, table 1) showed *payeri* as occurring in the upper part of his middle subdivision of the Kapp Starotsin Formation, considered by Hans Nakreem to match the Svenskeegga Member, and persisting through what Ustritsky called Selanderneset Suite.

Taking account of the Gobbett assessment, Sarytcheva (1984, p. 134, pl. 24, fig. 3, 4) assigned further Kapp Starotsin material to *Waagenoconcha* A, together with specimens figured by Gobbett (1964, p. 78, pl. 6, fig. 6-8), as well as Dunbar's specimens from Greenland. Grunt (2006a) referred all these specimens to one species, named *sarytchevae* after T. G. Sarytcheva, with holotype based on a ventral valve figured by Sarytcheva (1984, pl. 24, fig. 3), a debatable choice for holotype, because Sarytcheva had figured no dorsal valve, and the Gobbett material from what may be the same beds is similarly limited. No topotype dorsal valve has yet been figured, as far as I am aware. But whatever the nature of the dorsal valve, the ventral valve does show a ventral sulcus that is shallower anteriorly than in the Greenland material, signifying a different species. Grunt's species *sarytchevae* may provisionally be referred to *Gruntoconchinia*, subject to the nature of the dorsal valve when it comes to be described.

Should Gobbett's interpretation prove to be in error, and the Toula species in fact prove to be waageno-conchin, then it will possibly either belong to *Gruntoconchinia*, as a separate species, or if it cannot be discriminated, and if it is expanded by further topotype material, assume a fresh status of senior synonym to *payerinia*, and become type species for the genus.

Discussion: Julius von Payer was leader with Karl Weyprecht of the Austro-Hungarian polar expedition of 1872-1874. Toula was quick to name a species in his honour, but this has fallen under a cloud of uncertainty, as outlined above, so a further and well-preserved species is named after him.

Gruntoconchinia sp.

Fig. 76, 77

Material: Two specimens with valves conjoined from C-4019, Assistance Formation, Ellesmere Island

Dimensions in mm:

Width	Length	Height	Umbonal angle	Sulcal angle
36	36	24	80°	30°

Description: Shells small with highly convex ventral valve bearing a median sulcus that commences a little in front of the umbonal tip, and a dorsal valve with extensive gently concave disc and geniculate trail at right angles. Posterior ventral spine bases are about 1.5mm long, and become more erect anteriorly over the anterior half in the larger specimen, but remain elongate in the other specimen. Dorsal spines are erect and crowded.

Resemblances: The Canadian specimens are very like type *Gruntoconchinia payerinia* n. gen., n. sp. from Greenland in the wide hinge, well formed ventral sulcus and thick disc, with gently concave dorsal disc curving abruptly into a trail that is not very high but well formed, in keeping with its small size and possible immature state, not like the long trail recorded for larger specimens in Dunbar (1955). The ventral umbonal walls appear to be longer in the present form, and the ventral spine bases slightly shorter posteriorly.

Specimens from the Spirifer Limestone of Spitsbergen that were figured as *Waagenoconcha irginae* (Stuckenberg) by Gobbett (1964, p. 76, pl. 6, fig. 1-5, part, not pl. 5, fig. 7) are comparatively close in spine detail, but more subcircular in outline. Kungurian shells ascribed by Ifanova (1972, pl. 3, fig. 11-13) to *Waagenoconcha humboldti* (d'Orbigny) have somewhat similar ventral spines: identification with the basal Permian species from Bolivia is deemed unlikely, because these specimens are shaped differently, being more rounded in outline. They are close to the larger and less inflated species *Waagenoconcha irginaeformis* Stepanov, 1937a of Early Permian age, as reviewed by Waterhouse (2018a, p. 165), a species which is larger and less inflated, with only short ventral spine bases posteriorly.

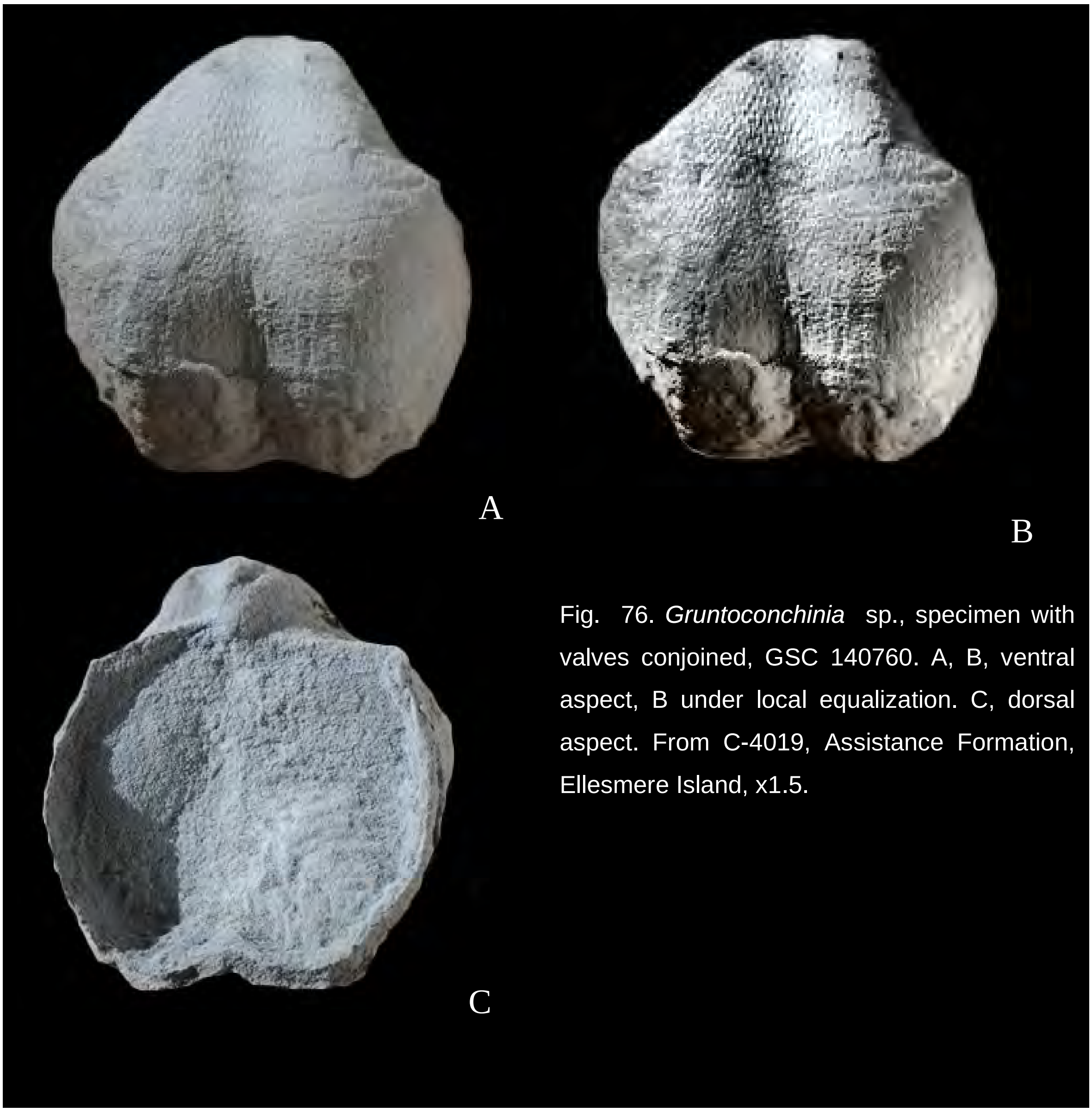

Fig. 76. *Gruntoconchinia* sp., specimen with valves conjoined, GSC 140760. A, B, ventral aspect, B under local equalization. C, dorsal aspect. From C-4019, Assistance Formation, Ellesmere Island, x1.5.

Productus payeri Toula, with lectotype figured by Toula (1874, pl. 4, fig. 1a, 1b) from the Kapp Starotsin beds of Spitsbergen, reproduced in Waterhouse (2018a, Fig. 381), is less elongate in outline and has a highly inflated disc. The sulcus is varies, a little deeper and the posterior wall is steeper. There is certainly a degree of similarity, and further topotype material is needed to verify or change the assessment by Gobbett (1964) that Toula's material belonged to *Kochiproductus*.

Fig. 77. *Gruntoconchinia* sp. A, B, specimen GSC 140760 with valves conjoined, lateral views, normal and local equalization, x1.5. From C-4019, Assistance Formation, Elllesmere Island.

Tribe **WIMANOCONCHAINI** (**WIMANOCONCHINI**) Waterhouse, 2013

Diagnosis: Usually large, with wedge-shaped dorsal valve that is almost flat, varying to gently concave, without externally distinct trail or with only very limited trail. Early Permian (Asselian) to Upper Permian (Wuchiapingian).

Discussion: Genera placed in Waagenoconchini have dorsal valves of low to moderate concavity that are almost flat over the disc, and display geniculate to subgeniculate distinct dorsal trails. By contrast, the dorsal valves in genera of Wimanoconchini have a flat or gently concave visceral disc and very short or no trail, or no perceptible trail: the dorsal trail as a rule cannot be distinguished from the disc externally. *Wimanoconcha* Waterhouse, based on *Ruthenia wimani* Fredericks, 1934 from the Permian of Spitsbergen, has a thickened dorsal valve with no external trail. Ventral spines are posteriorly fine with slender short 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 *Wimanoconcha* with *Waagenoconcha*, claiming to rely on a study by Archbold (1993). They completely misrepresented Archbold (1993, p. 20), who wrote “Based on the new material illustrated herein, the Western Australian species *Waagenoconcha imperfecta* Prendergast is assigned to *Wimanoconcha* on the basis of the morphology of mature specimens”. Archbold certainly did not synonymize the two genera, and the allegation by Brunton et al. (2000) was false.

Brunton et al. (2000, p. 516) also placed in synonymy with *Waagenoconcha* the genus *Biplatyconcha* Waterhouse, 1983a, p. 125 (nom. nov. for *Platyconcha* Waterhouse not Longstaff). This is surprizing, because *Biplatyconcha* is strophalosioid (Waterhouse 2013, p. 232). Their claim is rejected.

Villaconcha Waterhouse, 2004b, p. 13, type species *Waagenoconcha magnifica* Cooper & Grant (1975, p. 1044, pl. 354, fig. 1-15) from the Willis Ranch, China Tank and Appel Ranch Members (now Roadian and Wordian Stages of the 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. platys* Cooper & Grant from the Road Canyon Formation (lower Roadian Stage) is congeneric.

Patellamia Waterhouse, as described shortly, is close, but has a gently concave and unthickened dorsal valve. *Quenstedtenia* Waterhouse, 2004b, p. 12, type species *Q. rugosa* Waterhouse, 2004b from the Basleo beds of Timor, is like the latter genus in that the dorsal valve is not thickened into a wedge, and is gently concave, curving imperceptibly into a very short trail, much as in *Patellamia*. The genus has long ventral spine bases and marked commarginal rugae or growth-stops. Dorsal spine bases are also elongate. Fine specimens have been figured by Hamlet (1928, pl. 4, fig. 1a-c, pl. 5, fig. 1a-c) from Basleo-Wesleo in Timor, reinforced by additional material figured in Rothpletz (1892, pl. 10, fig. 20) and Archbold & Bird (1989, text-fig. 3C, D). *Waagenoconcha delectus* Waterhouse & Gupta (1979, pl. 2, fig. 11-16, pl. 3, fig 1-8) from the Wuchiapingian of the Himalayas is close but has a short trail.

Genus ***Wimanoconcha*** Waterhouse, 1983a

Diagnosis: Dorsal valve heavily thickened, without external trail. Spines on both valves with short or no posteriorly prolonged bases.

Type species: *Ruthenia wimani* Fredericks, 1934, originally described as *Productus purdoni* [not Davidson] by Wiman (1914) from Spiriferenkalk of Spitsbergen, OD.

Wimanoconcha wimani (Fredericks, 1934)

Fig. 78

1914 *Productus purdoni* [not Davidson] – Wiman, p. 68, pl. 14, fig. 8, 9, pl. 15, fig. 1, 2, pl. 16, fig. 1-4.
1934 *Ruthenia wimani* – Fredericks, p. 28.
1936 *P. wimani* – Stepanov, p. 120, pl. 4, fig. 1a-c.
1937b *P.* (*Waagenoconcha) wimani* – Stepanov, p. 126, pl. 6, fig. 1a-c.
1937 *P. payeri* [not Toula] – Frebold, p. 19, pl. 2, fig. 1, pl. 3, fig. 3 (part).
1964 *Waagenoconcha wimani* – Gobbett, p. 75, pl. 5, fig. 1, 2.
1983a *Wimanoconcha wimani* – Waterhouse, p. 125.

Diagnosis: Large and elongate shells.

Lectotype: Specimen figured by Wiman (1914, pl. 15, fig. 1, pl. 16, fig. 1, 2) from Spiriferenkalk, Spitsbergen, designated by Gobbett (1964, p. 75).

Material: Two dorsal valves from C-13356 and one dorsal valve from C-4015 in the Trold Fiord Formation of Ellesmere Island.

Description: This species was recognized in the Sverdrup Basin by Miller (1974), and his figures of one of the specimens are repeated herein. The species is highly distinctive, with thickened dorsal valve and with elongate overall shape, particularly for the ventral valve. Spines over both valves are erect or suberect, with only short bases.

Resemblances: The elongate shape is distinct from the more rounded outline (= *Balkhasheconcha*?) of Talatin, Vorkut and Kungurian specimens decribed as *Waagenoconcha wimani* by Ifanova (1972, p. 105, pl. 3, fig. 17, 18) and Solomina (1960, p. 32, pl. 2, fig. 5-7, pl. 3, fig. 1, 2).

The species named *feildeni* by Etheridge (1878) from his study on collections made in the Canadian Archipelago appears to belong to the same genus *Wimanoconcha* as the species *wimani* Fredericks. It was named before *wimani*, and so has clear priority over *wimani*, and may have come from approximatly correlative beds, but is believed to delineate a less elongate species, as outlined below.

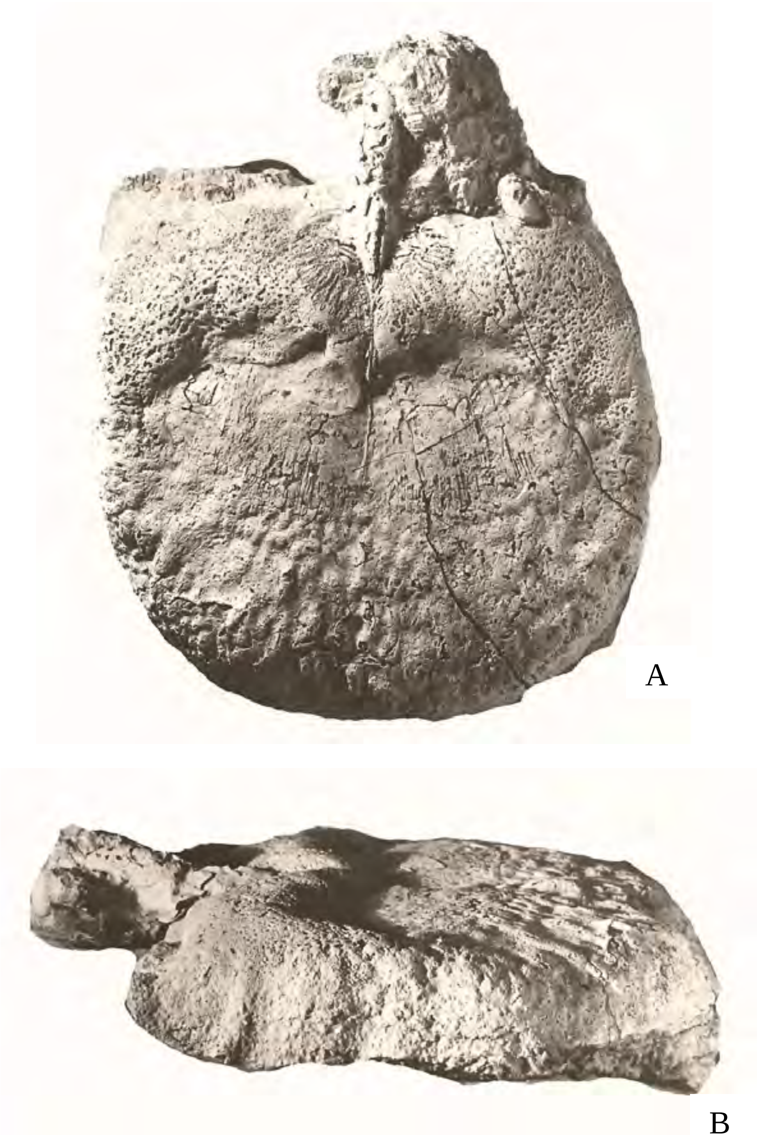

Fig. 78. *Wimanoconcha wimani* (Fredericks). A, B, dorsal internal and lateral aspects, GSC 36803 x0.6 from C-4015, Trold Formation Formation, Ellesmere Island. (Miller 1974).

Wimanoconcha feildeni (Etheridge, 1878)

Fig. 79 – 81, ?82, 83

1878 *Stropheodonta feildeni* Etheridge, p. 598, pl. 25, fig. 4.
?1960 *Waagenoconcha wimani* [not Fredericks] – Solomina, pl. 2, fig. 5-7, pl. 3, fig. 1, 2.
2013 *Wimanoconcha* sp. Waterhouse, p. 199, Fig. 6.18, 6.20, 6.21, 6.22.

Diagnosis: Dorsal valve transverse, strongly thickened, without dorsal external trail, cardinal process with strong median and two slender lateral lobes, strongly dendritic adductor scars, antero-laterally extended brachial shields, septum and large anterior pustules.

Holotype: Natural History Museum specimen figured by Etheridge (1878, pl. 25, fig. 4) and Fig. 83 herein, from beds possibly matching those of the Trold Fiord Formation, north Grinnell Land, Ellesmere Island, by monotypy.

Material: Three large silicified dorsal valves from C-13356, Trold Fiord Formation, Melville Island. A possible ventral valve from GSC loc. 47856, Degerböls Formation of Ellesmere island, but identity not certain.

Description: Some dorsal valves from the Trold Fiord Formation were used for illustrations in Waterhouse (2013). Internally, they are superbly preserved and silicified, for which the illustrations hardly require any elaboration of text. The dorsal valve is wedge-shaped, with crenulate hinge at maximum width, very small ears on some specimens, and thickened valve so that the trail is internal and very short, with large pustules. The exterior has been either worn or imperfectly silicified, and so shows little of the original ornament. The cardinal process is comprised of a broad high median shaft with two claw-like lateral lobes, and a massive anterior internal hump divided by a short and shallow median notch. The median septum extends well forward, almost to the anterior edge of the disc, and is moderately high between the strongly impressed adductor scars, which form a broad posterior lateral pair, and smaller anterior

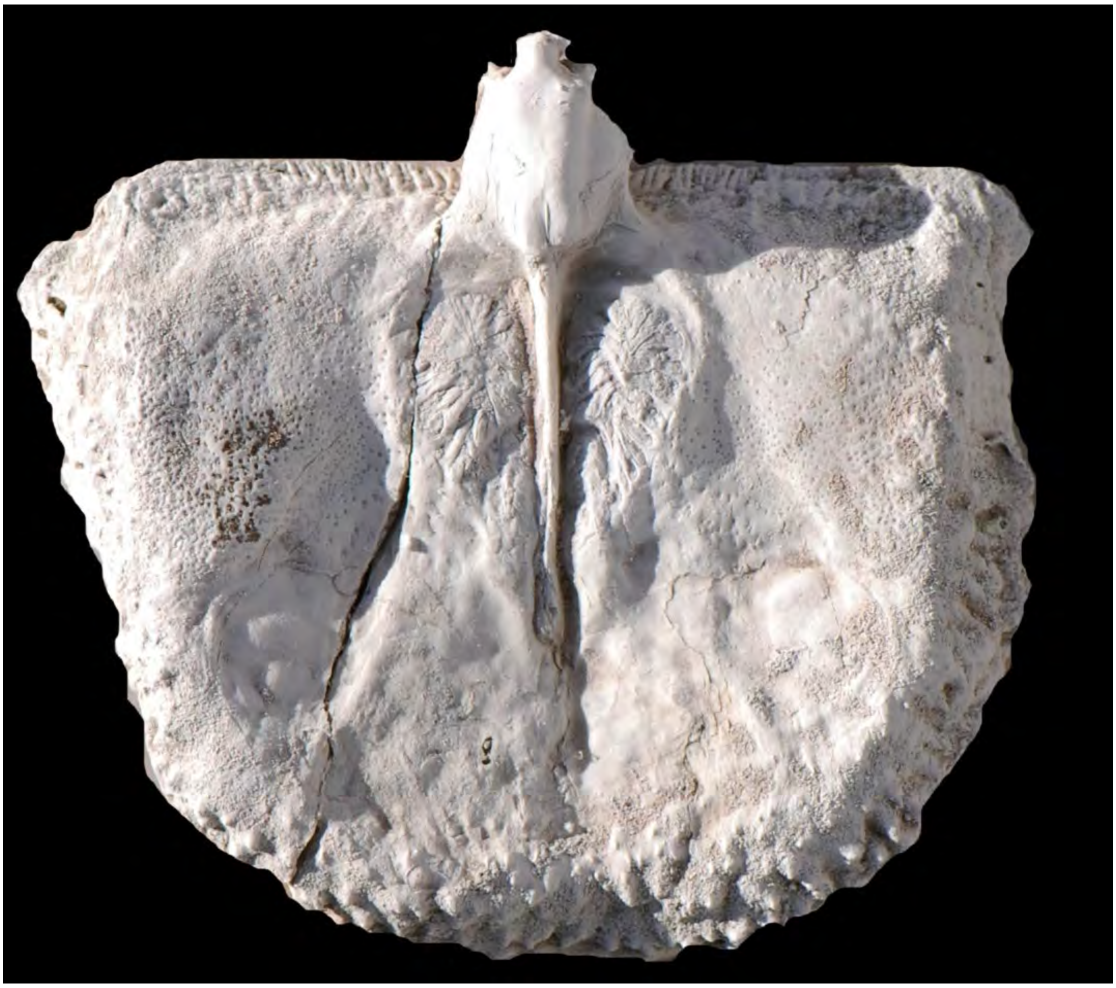

Fig. 79. *Wimanoconcha feildeni* (Etheridge, 1878), dorsal interior, GSC 36801 from C-13356, x1.7. Trold Fiord Formation, Melville Island, x1. See Fig. 80C. (Waterhouse 2013).

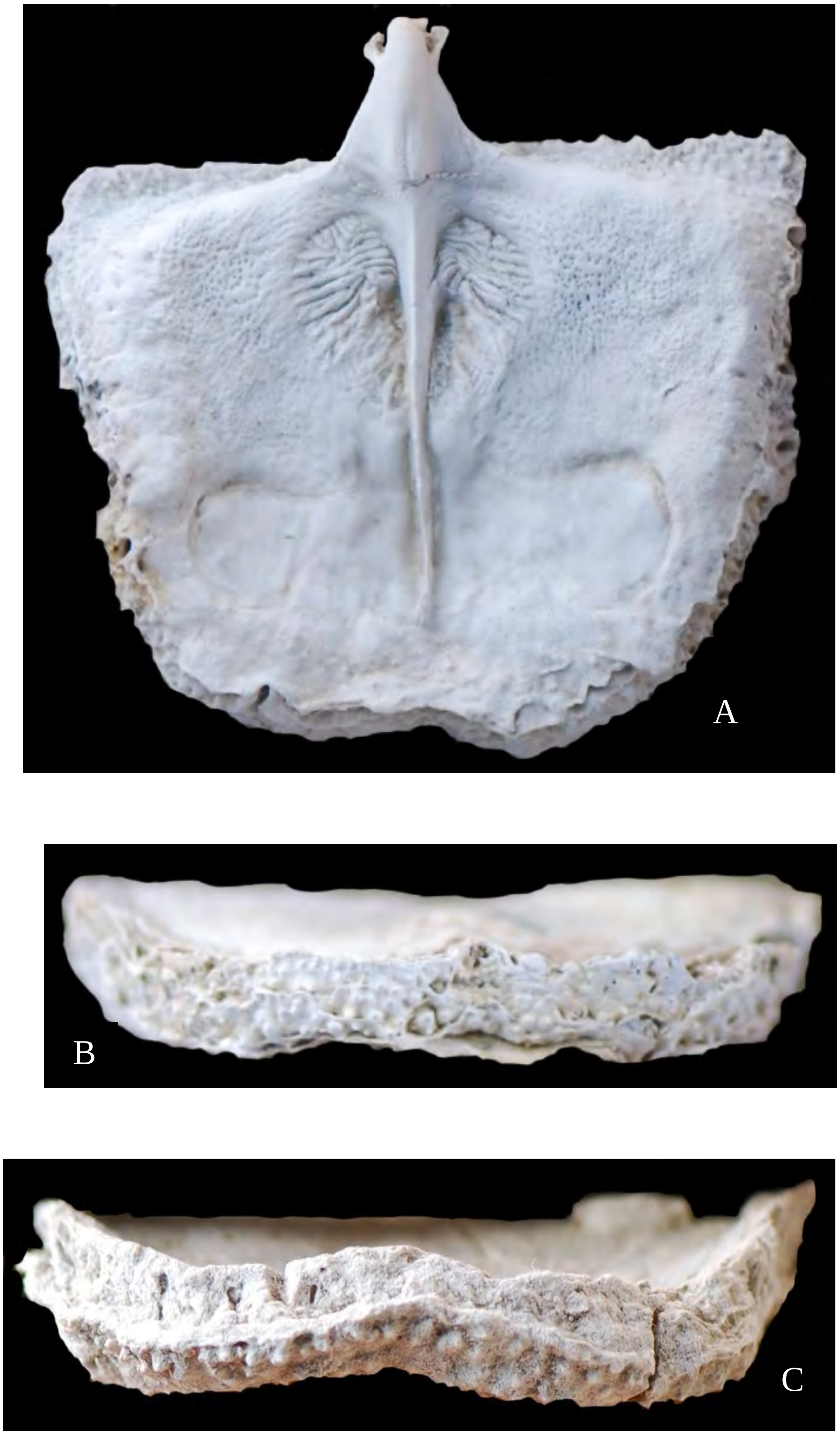

Fig. 80. *Wimanoconcha feildeni (*Etheridge, 1878). A, B, dorsal interior and anterior aspect of GSC 36800, inner side below, x2. C, anterior view of dorsal valve GSC 36801, showing anterior edge of dorsal valve**,** inner side below. (See also Fig. 79)**.** From C-13356, Trold Fiord Formation, Melville Island, x1.5. (Waterhouse 2013).

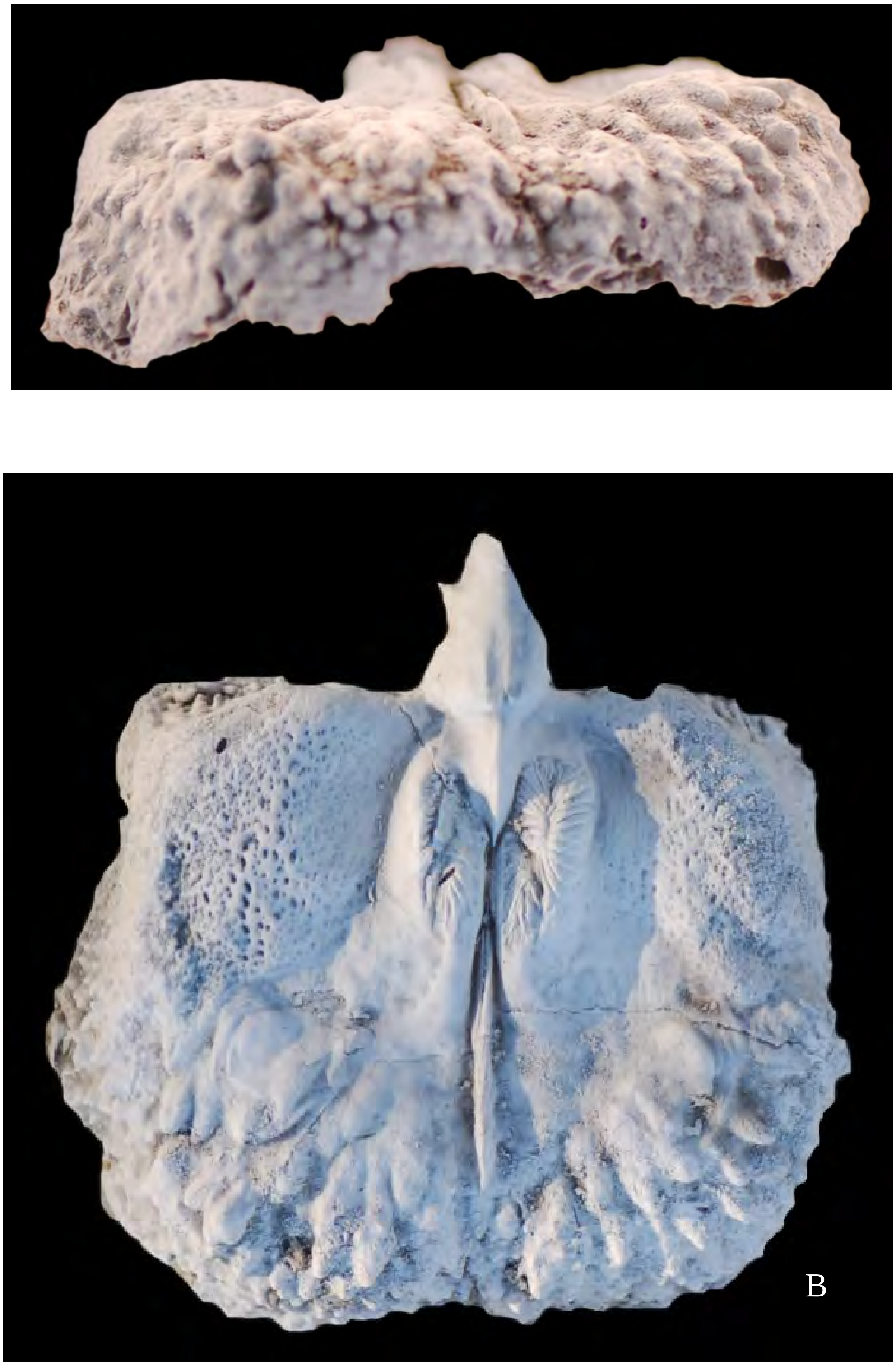

Fig. 81. *Wimanoconcha feildeni (*Etheridge, 1878). A, anterior edge (with inner side uppermost) and B, dorsal interior of GSC 133341 from C-13356, Trold Fiord Formation, Melville Island, x1.5. (Waterhouse 2013).

inner pair. In front the brachial loops extend laterally, enclosing smooth interior. The posterior thickened shell is profusely pitted, and the anterior shell smoother, with large pustules commencing near the geniculation and becoming larger over the inner anterior trail.

A ventral valve figured (as a different species) by Miller (1974) might belong to *Wimanoconcha feildeni*, and his illustration is reproduced here as Fig. 82. It is not as long as in *W. wimani*, is only moderately inflated, most inflated just front of the hinge, and has a shallow median sulcus, with faint signs of closely spaced and short spine bases. Unfortunately the specimen was figured only obliquely in side view, and there are similarities to the genus *Patellamia* and to its two known constituent species *P. confinis* and *P. sulcata*, as described shortly. Each of these species has a shallow ventral sulcus. Neither of these species has a thickened wedge-like dorsal valve comparable to that of *Wimanoconcha*, and the tentative assignment is all the more precarious because another ventral valve, shown in Fig. 85B, comes from the same locality, shows a deeper sulcus, and appears to belong to *Patellamia sulcata*.

Resemblances: A specimen collected by the Feilden expedition from the Sverdrup Basin in the 1870's and named *Stropheodonta feildeni* Etheridge (1878, p. 598, pl. 25, fig. 4) seems to belong to *Wimanoconcha*. It is found in shelly grey limestone, collected at Cape Hilgard, North Grinnell Land and is kept at the Museum of Natural History, London. The figure shows an almost flat dorsal exterior, measuring 95mm wide and 75mm long, of much the size and shape as features of the present dorsal valves (Fig. 83).

A possible candidate for synonymy was figured, but not described *as Waagenoconcha arctica* n. sp. by Nakamura et al. (1992, pl. 1, fig. 9) from Spitsbergen, as a large roundly subquadrate form with moderately large ears and rounded cardinal extremities, and moderately developed sulcus. This specimen is apparently decorticated, and without ornament and without the dorsal valve, is inadequate as a type specimen, and is a nomen nudum, without supporting description or diagnosis.

Fig. 82. ?*Wimanoconcha feildeni (*Etheridge, 1878), ventral valve GSC 36801 from GSC loc. 47856, x1. This specimen may prove to belong to *Patellamia sulcata* (see p. 117): it is known to me only from a photograph. Degerböls Formation, Ellesmere Island, x1. (Miller 1974).

From the somewhat equidimensional to weakly transverse outline of the dorsal valve, this species somewhat resembles *Wimanoconcha sarytchevae* Grunt, 2006a, p. 148, named to include *Waagenoconcha payeri* [not Toula] of Dunbar (1955, p. 85, pl. 9, fig. 1-5, pl. 10, fig. 4) from Late Permian of Greenland. But Dunbar's description indicated the presence of a long ventral trail, and stated that the dorsal valve is flat and curves upward into the trail. This does not read like the situation in *Wimanoconcha*, and the generic placement is further considered on p. 103.

Wimanoconcha wimani (Fredericks, 1934), based on material figured by Wiman (1914) from the Spiriferen-kalk of Spitsbergen, with lectotype illustrated by Wiman (1914, pl. 15, fig. 1) as designated by Gobbett (1964, p. 75), has a much more elongate ventral and dorsal valve. External detail is not well preserved on either valve, but the figure of Wiman (1914, pl. 15, fig. 2, pl. 16, fig. 3) suggests erect spines without elongate bases, at least over the ventral umbo. This is confirmed for the entire valve in the study by Sarytcheva (1984, pl. 22, fig. 1a, 2, 5) and other figures. The ornament is close to that of *Campbelliconcha* Waterhouse, 2013, p. 260 of Visean age in New South Wales, but *Campbelliconcha* has dorsal buttress plates as in Balkhasheconchinae, and lacks a thickened wedge-shaped dorsal valve.

The dorsal valve of *Waagenoconcha angustata* Sarytcheva (1984, p. 133, pl. 12, fig. 6, pl. 18, fig. 8, pl. 21, fig. 6, pl. 23, fig. 2-5, pl. 24, fig. 1, 2) is close in outline to that of the present specimens, and tends to have a median dorsal fold as in present specimens. It is judged to be of late Early Permian age, including specimens of Kungurian age. But data on its true affinities are ambivalent. One dorsal interior from Spitsbergen (Sarytcheva 1984, pl. 24, fig. 1) has buttress plates, indicating links to *Balkhasheconcha* (see p. 120), whereas another dorsal interior (Sarytcheva 1984, pl. 23, fig. 4), indicates no buttress plates. So it would appear that the species needs re-examination and confirmation of its generic position, because figures suggest that two genera were involved, but most figured specimens belong to *Balkhasheconcha*. Sarytcheva (1984) included in synonymy further specimens that had been figured in Ifanova (1972, pl. 3, fig. 17, 18), but these do not clearly indicate the presence or absence of buttress plates. Specimens figured as *Waagenoconcha wimani* (not Fredericks) by Sarytcheva (1968, pl. 11, fig. 1-8, text-fig. 48) show buttress plates, especially in Sarytcheva (1968, pl. 11, fig. 5, 8).

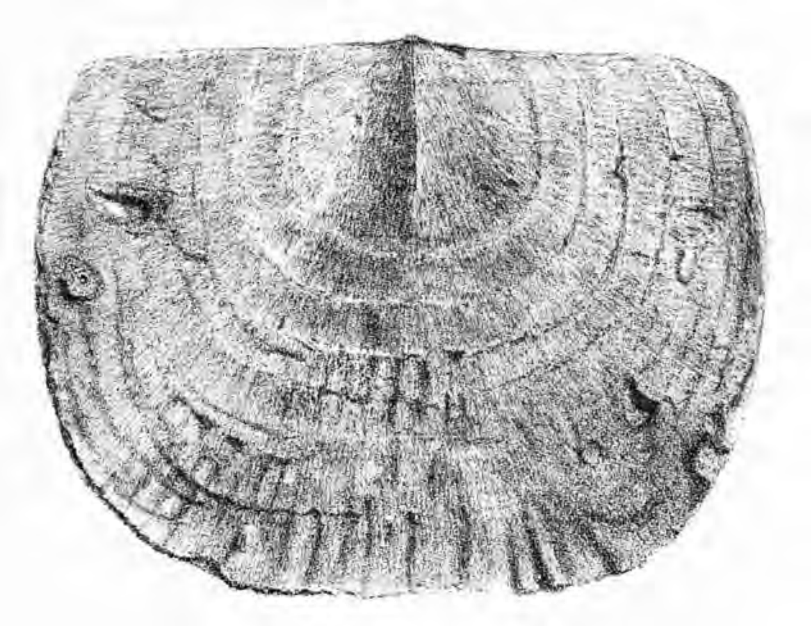

Fig. 83. *Wimanoconcha feildiana* (Etheridge), dorsal exterior of holotype (by monotypy), from north Ellesmere Island, Trold Fiord Formation, refigured from Etheridge (1878), presumably x1.

Specimens figured as *Waagenoconcha wimani* by Solomina (1960, pl. 2, fig. 5-7, pl. 3, fig. 1, 2) from the upper Talatin Formation of Petchora Basin have ventral spines which appear to be fine with no elongated bases, and were included in synonymy of *angustata* by Sarytcheva (1968). Ridges lie outside the dorsal adductor scars (Solomina 1960, pl. 2, fig. 5, pl. 3, fig. 2), but they are curved, not like the straight ridges typical of *Balkhasheconcha*, and appear to be ridges bordering the muscle scars rather than buttress plates.

Genus ***Patellamia*** Waterhouse, 2013

Type species: *Patellamia confinis* Waterhouse, 2013, p. 201 from Trold Fiord Formation, Melville Island, Canada, here designated.

Diagnosis: Medium to large, narrow body corpus and gently convex ventral valve, gently concave dorsal valve without flat disc or geniculate trail, spines over both valves fine and suberect, with only short bases.

Discussion: The genera *Waagenoconcha* Chao, *Waagenoconcha* (*Gruntoconcha*) Angiolini, *Fostericoncha* Waterhouse and *Contraspina* Waterhouse all have a somewhat similar shape in which the ventral valve is moderately arched, and the dorsal valve gently concave over the visceral disc, and curving more or less abruptly into a moderately long trail at high angle. The differences between genera are revealed by different spine patterns, that are particularly consistent for the most widespread of these genera, namely *Waagenoconcha* Chao. *Villaconcha* Waterhouse and *Wimanoconcha* Waterhouse, differ in having a dorsal valve that is largely flat or gently concave externally, with no trail, or only a very reduced or internal trail, and in *Wimanoconcha* the valve is considerably thickened. The present species is like *Villaconcha* and *Wimanoconcha* in that there is virtually no visible dorsal trail, the trail curving forward imperceptibly from the disc margin, but the dorsal valve is more concave, and the ventral valve is of low convexity. Spines are fine on both valves, with very short elongate bases, especially posteriorly, and many anterior spines are erect. A second species is also recognized, also in the Permian of the Canadian Arctic, with very large size, and presence of distinct ears, sulcus and fold.

Quendstedtia is somewhat similar, with elongate ventral and elongate dorsal spine bases, and conspicuous commarginal growth stops over both valves.

Patellamia confinis Waterhouse, 2013

Fig. 84A – C, E, 85A

2013 *Patellamia confinis* Waterhouse, p. 202, Fig. 6.23A, Fig. 6.24A-C, E.

Diagnosis: Large shells with slender corpus, gently convex ventral valve, shallowly concave dorsal valve without externally distinct trail, spines very fine on both valves, with short elongate bases posteriorly, erect anteriorly.

Holotype: GSC 36818 figured in Waterhouse (2013, Fig. 6.23A, Fig. 6.24B) and herein as Fig. 84B, 85A from C-13356, Trold Fiord Formation (Wordian), Melville Island, OD.

Material: Two complete specimens and ventral valve from C-13356, Trold Fiord Formation, Melville Island. Two specimens from C-4025, Assistance Formation, Ellesmere Island, ventral and dorsal valve from C-4026, single ventral valves from C-4005 and C-4006, Trold Fiord Formation. A possible specimen comes from GSC loc. 58951, cited as Assistance Formation in Waterhouse (2013, p. 479), although the matrix looks like Trold Fiord Formation, Ellesmere Island, and may require reassessment.

Dimensions in mm: ventral valve

GSC	Width	Length	Height
36824	89	76	18
36818	85	78	17.5
36817	90	70	27

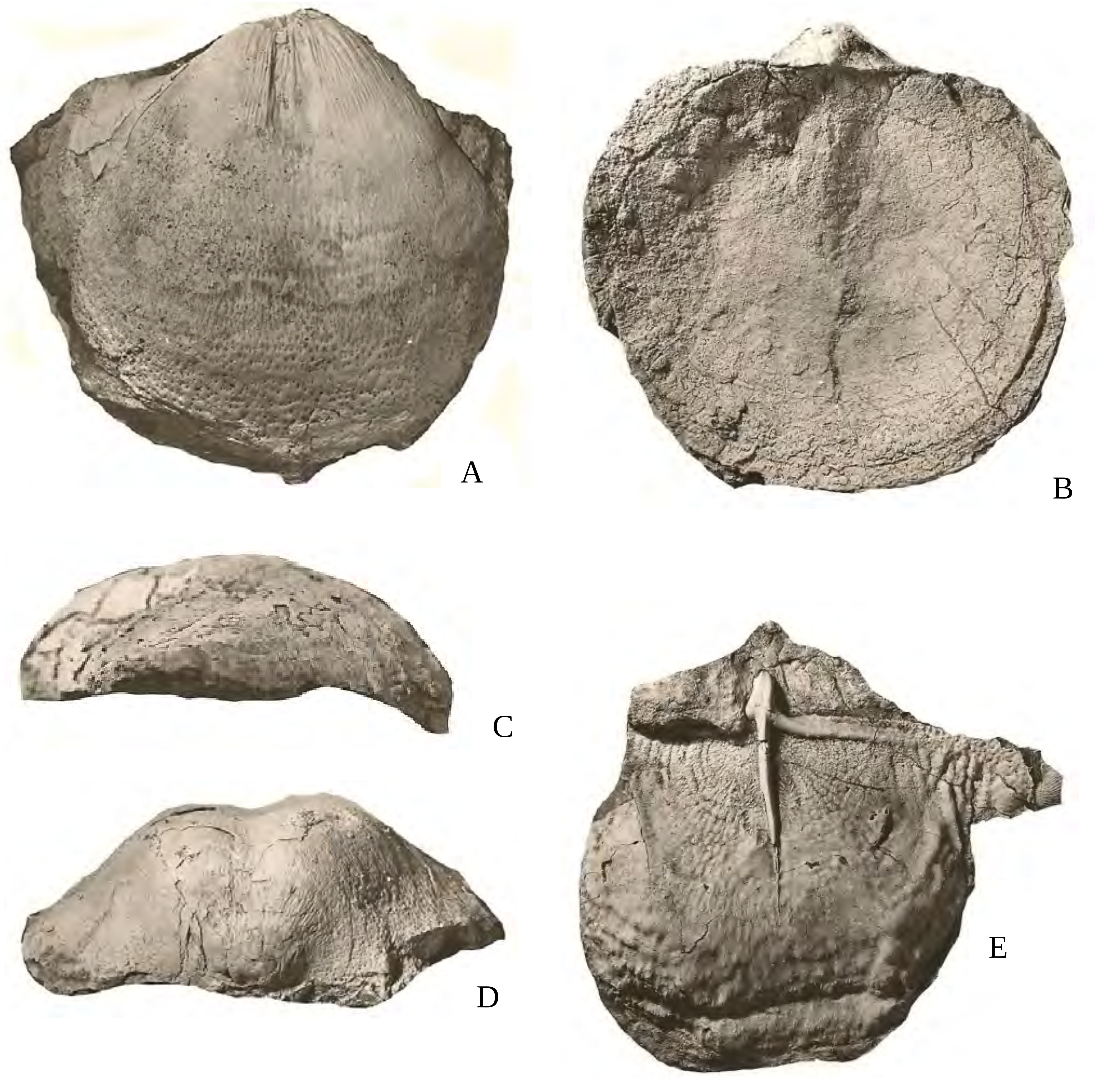

Fig. 84. A-C, E, *Patellamia confinis* Waterhouse. A, internal mould of ventral valve GSC 36809 from C-4006, Trold Fiord Formation, Ellesmere Island, x0.9. B, dorsal aspect of specimen with valves conjoined, holotype GSC 36818 from C-13356, Trold Fiord Formation, Melville Island, x0.8. C, lateral aspect of GSC 36824 from same locality, x0.8. Trold Fiord Formation. E, interior of dorsal valve, GSC 36819 from GSC loc. 58951, x 0.8. Trold Fiord Formation, Ellesmere Island. D, *P. sulcata* Waterhouse, posterior aspect of GSC 36823 from GSC loc. 47856, x0.8, ?Degerböls Formation, Ellesmere Island. (Waterhouse 2013).

Description: Shells gently concavo-convex, with trail not externally distinguished from visceral disc. The ventral umbo protrudes slightly beyond the hinge, with angle of 90-100º and is incurved, hinge moderately wide, well rounded cardinal extremities and no differentiated ears. The dorsal valve lacks differentiated ears, and is gently concave, curving imperceptibly into a trail, with no geniculation or subgeniculation. Ventral spines over the umbo and in front have short elongate bases up to 1mm long, numbering some ten in 5mm along a growth line, and many are erect, some fifteen in 10mm anteriorly, counted some 60mm in front of the umbo. Posterior dorsal spine bases are 1mm to 1.5mm long, over 2mm long in front of mid-length, and shorter close to the anterior margin. Both valves, especially the dorsal valve, have low ragged growth lamellae, becoming growth steps posteriorly, and as close as five in 5mm over parts of the shell. There are also subdued radial ventral plicae anteriorly, which are not evenly distributed.

The ventral adductor platform is impressed onto the dorsal exterior in GSC 36818, and forms a narrow long platform extending over the posterior third. In the dorsal valve, the cardinal shaft lies behind a median septum extending as far as mid-disc, and a posterior hinge ridge is well developed.

Fig. 85. *Patellamia confinis* Waterhouse. A, ventral aspect of holotype GSC 36818 from C-13356, x0.8. From Trold Fiord Formation (Capitanian), Melville Island. B, *P. sulcata* Waterhouse, ventral aspect of GSC 36823 from GSC loc. 47856, x0.9, with slightly crushed venter, Degerböls Formation, Ellesmere Island. (Waterhouse 2013).

Resemblances: There appear to be no described species that resemble this form, which as far as is known is limited to the Permian deposits of Arctic Canada.

The west Texas species *Waagenoconcha* (now *Villaconcha*) *platys* Cooper & Grant, 1975 from the Road Canyon Formation (Roadian) is somewhat similar in its low height, but its dorsal valve is almost flat, with upturned periphery, not gently concave. The hinge is wide and spines uniformly fine. The figure of the dorsal interior (Cooper & Grant 1975, pl. 355, fig. 11) suggests the possibility of a lateral buttress plate on one side, but this is not confirmed in the text, and is apparently an artifact, due to shell damage.

Patellamia sulcata Waterhouse, 2013

Fig. 84D, 85B, 86 – 89

2013 *Patellamia sulcata* Waterhouse, p. 203, Fig. 6. 23B, Fig. 6.24D, Fig. 6.25 – 6.27.

Diagnosis: Large shells with narrow ventral sulcus and dorsal fold.

Holotype: GSC 36811 from C-4095, Degerböls Formation, figured in Waterhouse (2013, Fig. 6.27B) and herein as Fig. 87B, OD.

Material: A ventral valve and dorsal valve from C-4095, Ellesmere Island, and three ventral valves and specimen with valves conjoined from GSC loc. 47856, Melville Island, both collections from Degeböls Formation. Ventral and dorsal valve from C-4026, Trold Fiord Formation, Ellesmere Island.

Dimensions in mm: ventral valve, GSC 36811

GSC	Width	Length	Height
36811	140	120	36
dorsal valve GSC 36813			
36813	124	112.5	8

Description: Specimens very large, ventral umbo broad, with umbonal angle of 100º, hinge wide with small convex ears, disc broadly convex, shallow sulcus commencing at umbo and with angle slightly less than 20º, no external distinction for trail. On the broken dorsal valve GSC 36810 from C-4026, plicae cover the anterior half to third of the valve (Fig. 88), possibly coinciding with the extent of the trail. Spine bases short, fine and crowded over both valves.

Fig. 86. *Patellamia sulcata* Waterhouse, ventral aspect of GSC 36809, x1, from C-4026, Trold Fiord Formation, Ellesmere Island. (Waterhouse 2013).

Adductor platform in GSC 36811 long and narrow, diductor scars large and striate, band of coarse pustules around anterior margin. The adductor platform is very long in the specimen from C-4026, extending for more than the posterior third of the shell length, and diductor scars do not extend as far forward. Behind them, each side of the

Fig. 87. *Patellamia sulcata* Waterhouse. A, worn interior of dorsal valve, GSC 36813, x0.75. B, ventral valve, GSC 36811, holotype, x0.65. From C-4095, Degeböls Formation, Ellesmere Island. (Waterhouse 2013).

posterior adductors, lie small lateral scars. Papillae cover much of the valve, and a low ridge lies under the umbonal slopes. Dorsal valve with no clearly differentiated ears, narrow fold commencing close to hinge, moderately conspicuous commarginal laminae, no visible trail. Medium septum short, moderately strong pustules laterally, becoming coarse in front.

Fig. 88. *Patellamia sulcata* Waterhouse, incomplete dorsal exterior, GSC 36810, x1. from C-4026, Trold Fiord Formation, Ellesmere Island. (Waterhouse 2013).

A ventral valve from the Degerböls Formation has only traces of fine, short and dense spine bases, but these are very poorly preserved. It is 62mm wide and 21mm high, with a shallow and narrow sulcus commencing at the posterior third of the shell length. The adductor platform is raised and posteriorly placed, and the two adductor scars medianly concave, and separated by a low broad myophragm. The subrounded diductor scars are weakly impressed and overlap the anterior half of the adductor platform.

Resemblances: This species clearly belongs to *Patellamia*, and is distinguished from the type species *P. confinis* by its larger size, more transverse outline, presence of small ventral ears, and presence of shallow sulcus and low dorsal fold that is broad anteriorly.

Fig. 89. *Patellamia sulcata* Waterhouse, ventral valve GSC 140759 from GSC 47856, Degerböls Formation, Ellesmere Island, x1.

Superfamily **SCACCHINELLAOIDEA (SCACCHINELLOIDEA**) Licharew, 1928a, b

Family **RHAMNARIAIDAE (RHAMNARIIDAE**) Muir-Wood & Cooper, 1960

Subfamily **BALKHASHECONCHAINAE (BALKHASHECONCHINAE**) Waterhouse, 2002b

Diagnosis: Waagenoconchiform shells with lateral buttress supports in the dorsal valve, extending each side of dorsal adductors. No interareas, no cicatrix, trail short. Spines over both valves subprostrate or erect especially around margins, largely uniform in bands. Cardinal process with tall median shaft.

Genus ***Balkhasheconcha*** Lazarev, 1985

Diagnosis: Fine erect or subprostrate spines over both valves, fine and erect anteriorly on ventral valve, and apparently with recurved anteriorly directed bases, leaving spine tunnels (Waterhouse 2018a, Fig. 152, p. 188). Short lateral buttress ridges.

Type species: *Waagenoconcha balkhashensis* Nasikanova in Sarytcheva 1968, p. 106 from Keregetass Formation (Bashkirian?), Kazakhstan, OD.

Discussion: *Buxtoniella* Abramov & Grigorieva, 1986 from a Visean fauna of Verchoyan has been distinguished from *Balkhasheconcha* by the absence of an anterior band of fine spines (Brunton et al. 2000, p. 518), but arguably some other difference needs to be found to justify the genus, because anterior spination over the anterior shell may vary in different species assigned to *Balkhasheconcha*. For instance a Canadian species of Asselian age has an anterior band of coarse spines (Waterhouse 2018a, p. 187), and the present species is somewhat variable, but without a clearly defined peripheral band of fine erect spines. Perhaps this is reflecting only variations in the degree of maturity.

Balkhasheconcha thorsteinssoni n. sp.

Fig. 90 – 94

?1873 *Productus humboldti* [not d'Orbigny] – Toula, p. 282, pl. 2, fig. 3a-c.
cf. 1931 *Productus humboldti* [not d'Orbigny] – Frebold, p. 39, pl. 3, fig. 8a, b.
1937b *P.* (*Waagenoconcha*) *humboldti* – Stepanov, p. 123, pl. 6, fig. 3.
1950 *P*. (*Waagenoconcha*?) *irginae* var. *irginaeformis* [not Stepanov] – Frebold, p. 45, pl. 2, fig. 5, 5a, 7, 7a.
1952 *W. humboldti* – Sarytcheva & Sokolskaya, p 98, pl. 15, fig. 103.
1955 *Waagenoconcha* sp. Dunbar, p. 88, pl. 8, fig. 7-16.
1960 *W. payeri* [not Toula] – Harker & Thorsteinsson, p. 61, pl. 18, fig. 9-11.
1960 *W. humboldti* – Solomina, p. 28, pl. 1, fig. 4-6.
aff. ?1964 *W. irginae* [not Stuckenberg?] – Gobbett, p. 76, pl. 5, fig. 7, pl. 6, fig. 1-5.
1972 *W. humboldti* – Ifanova, p. 102, pl. 3, fig. 11-13.

Derivation: Named for R. Thorsteinsson.

Diagnosis: Small to medium in size, wide hinge, weakly to moderately defined sulcus, dorsal disc gently convex with low fold, and short subgeniculate trail. Ventral spines with moderately long bases, dorsal spines with slightly less elongate bases. No anterior band of fine spines.

Holotype: Specimen GSC 140761 as shown in Fig. 90A, B from GSC loc. 58968, Assistance Formation (Roadian), Ellesmere Island, here designated.

Material: Nine ventral valves, one dorsal valve and three specimens with valves conjoined from GSC loc. 26406, Devon Island, one specimen with valves conjoined from GSC loc. 58968 and two specimens with valves conjoined from C-4081, Ellesmere Island, all Assistance Formation. One dorsal valve from C-4008, a small ventral valve from C-3996 and a ventral valve from C-4021, Trold Fiord Formation, Ellesmere Island. A specimen with valves conjoined from JBW 631, Takhandit Formation.

Dimensions in mm: both valves, internal moulds

Width	Length	Height	
25	21.5	7.5	Assistance Ftm
41	37	14.5	Trold Fiord Ftm
46	35	15	Trold Fiord Ftm
45.5	40	18.5	holotype
45	37	17	

Description: Specimens weakly transverse with broad low ventral umbo weakly incurved and extending over the hinge, displaying an angle of 85-95° as a rule. The hinge is wide, the cardinal angles obtuse, and maximum width lies close to mid-length. A shallow sulcus commences as a rule between the posterior third and mid-length, and exceptionally, closer to the ventral tip of the umbo. As measured from the umbo, the sulcus widens at 20° as far as the anterior margin, and an inner median segment within the sulcus may be slightly more depressed and better defined. No ears are differentiated on most specimens in the present suite, but a well-preserved specimen has tiny

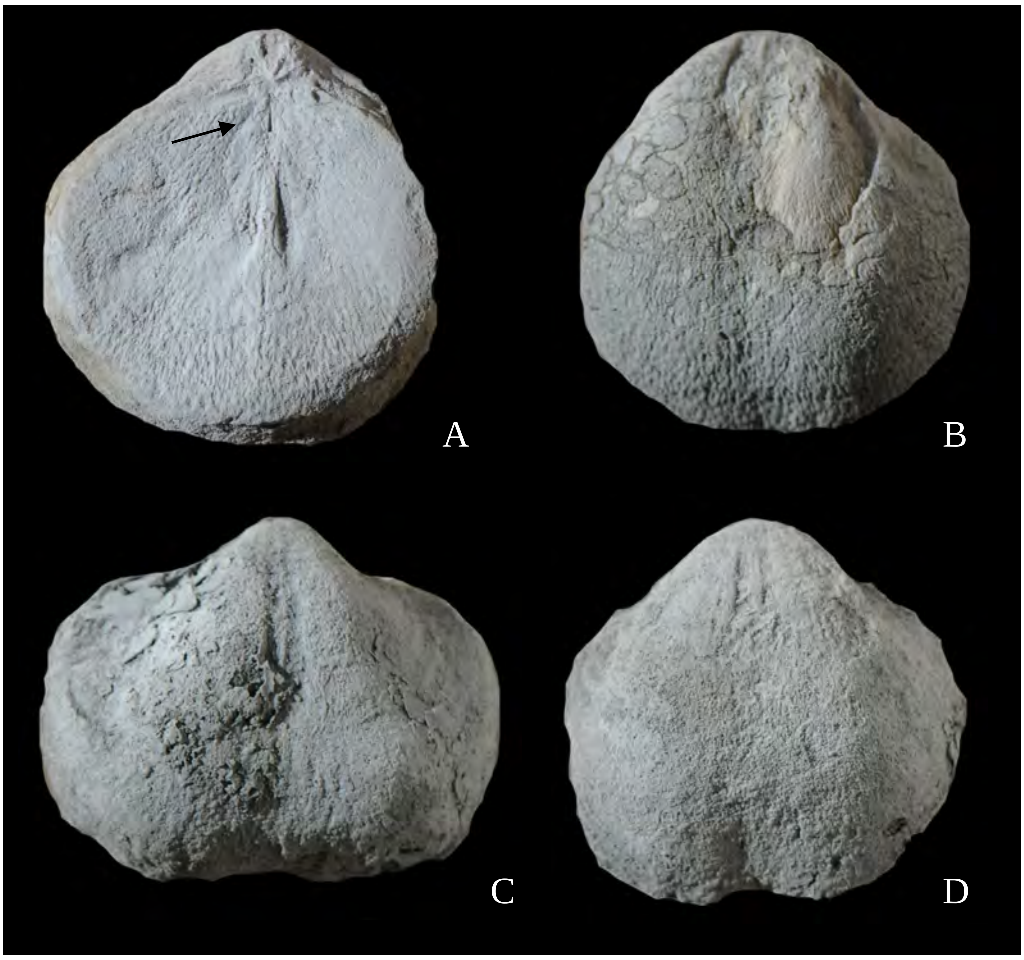

Fig. 90. *Balkhasheconcha thorsteinssoni* n. sp. A, B, dorsal and ventral aspects of GSC 140761 holotype, internal mould of both valves, from GSC loc. 58968, Assistance Formation, Ellesmere Island. Buttress plate arrowed. C, ventral aspect of internal mould GSC 140762 from same locality. D, ventral aspect of internal mould GSC 140763, same locality. Specimens x1.25.

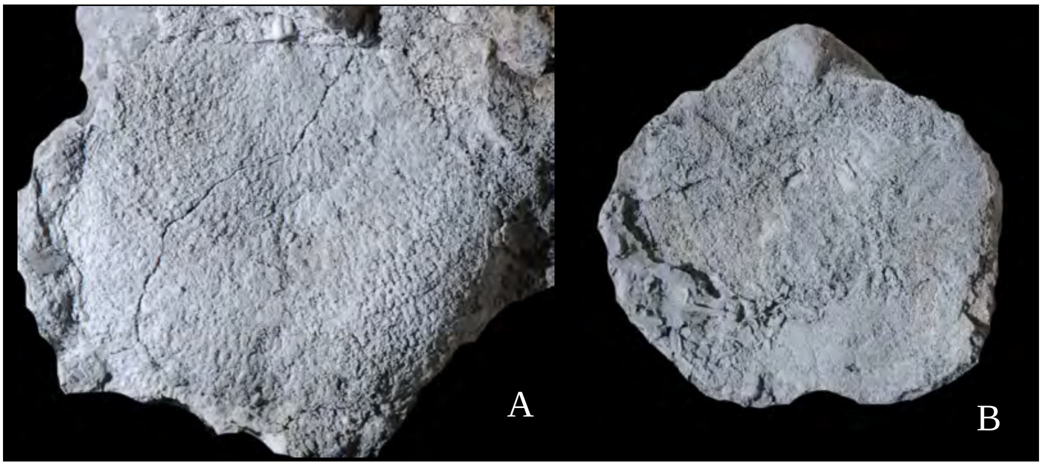

Fig. 91. *Balkhasheconcha thorsteinssoni* n. sp. A, dorsal external mould GSC 140764 from C-4008, Trold Fiord Formation, Ellesmere Island. B, dorsal aspect of internal mould GSC 140763 from GSC loc. 58968, Assistance Formation, Ellesmere Island. See Fig. 90D. Specimens x1.

ears with bluntly acute cardinal extremities (Fig. 93), though the extremities differ in angle from each other, reflecting either distortion or natural variation. The dorsal valve is very gently concave, depressed extensively near the hinge each side of a smooth more concave nepionic portion, and bearing a very low fold that commences near the posterior third of the valve and remains low as far as the anterior margin, crossing a low semigeniculate trail. Ornament on the ventral valve consists mostly of elongate spine bases, up to 3mm long, with six to eight in 5mm anteriorly. Around the anterior margin of larger specimens, the spine bases become crowded and fine, supporting very fine spines. Whether the spines recurve through the shell has not been determined, but a small ventral valve from C-3996 suggests spine tunnels (cf. Waterhouse 2018a, p. 88, Fig. 152). The dorsal valve is covered as a rule by short crowded and elongated spines which emerge from the anterior end of the spine bases.

Ventral adductor platform long and narrow, subdivided by median groove; diductor impressions to each side weakly impressed, most of valve floor covered by fine dimples. In the dorsal valve, buttress plates moderately defined, diverging, not long, but poorly preserved. Low median septum extends over at least the posterior third of the valve, dividing low suboval adductor scars, each with a posterior lateral small subdivision that widens laterally.

Resemblances: The very low concavity of the dorsal disc, and short subgeniculate trail of this species differs from the more concave dorsal valve found in species of *Balkhasheconcha* of the Jungle Creek Formation in the Yukon Territory, and from the various Russian species discussed in that report. One exception is provided by *Balkhasheconcha* sp. from Member C of the Jungle Creek Formation, in which shells are small, with better defined dorsal fold (Waterhouse 2018a). The dorsal valve figured by Tschernyschew (1902, pl. 30, fig. 4) as *Productus irginae* Stuckenberg is a member of *Balkhasheconcha*, showing buttress plates, and having an almost flat dorsal valve. Various specimens discussed in Russian literature come close in overall shape and ornament, and the dorsal

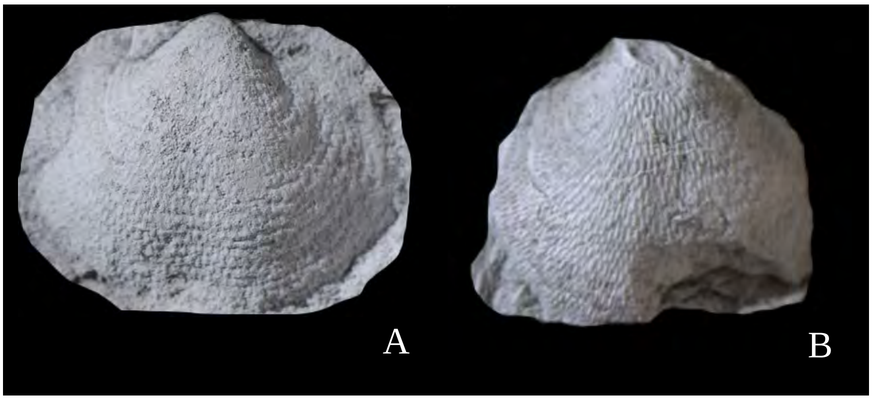

Fig. 92. *Balkhasheconcha thorsteinssoni* n. sp. A, juvenile ventral valve GSC 140765 from GSC loc. 26406, Assistance Formation, Devon Island, x2. B, juvenile ventral valve GSC 140766 from C-3996, Trold Fiord Formation, Ellesmere Island, x2.

valve described as *Waagenoconcha humboldti* in Ifanova (1972, pl. 3, fig. 12) shows dorsal buttress plates. Critically, the material assigned to *Productus silveanus* Stuckenberg (1898, p. 261, pl. 4, fig. 18) does not show internal features, and although there is a degree of external similarity to the present form, to the extent that Ifanova (1972, p. 102) synonymized the form with *humboldti*, the generic allegiance needs to be determined. The uncertainty about the

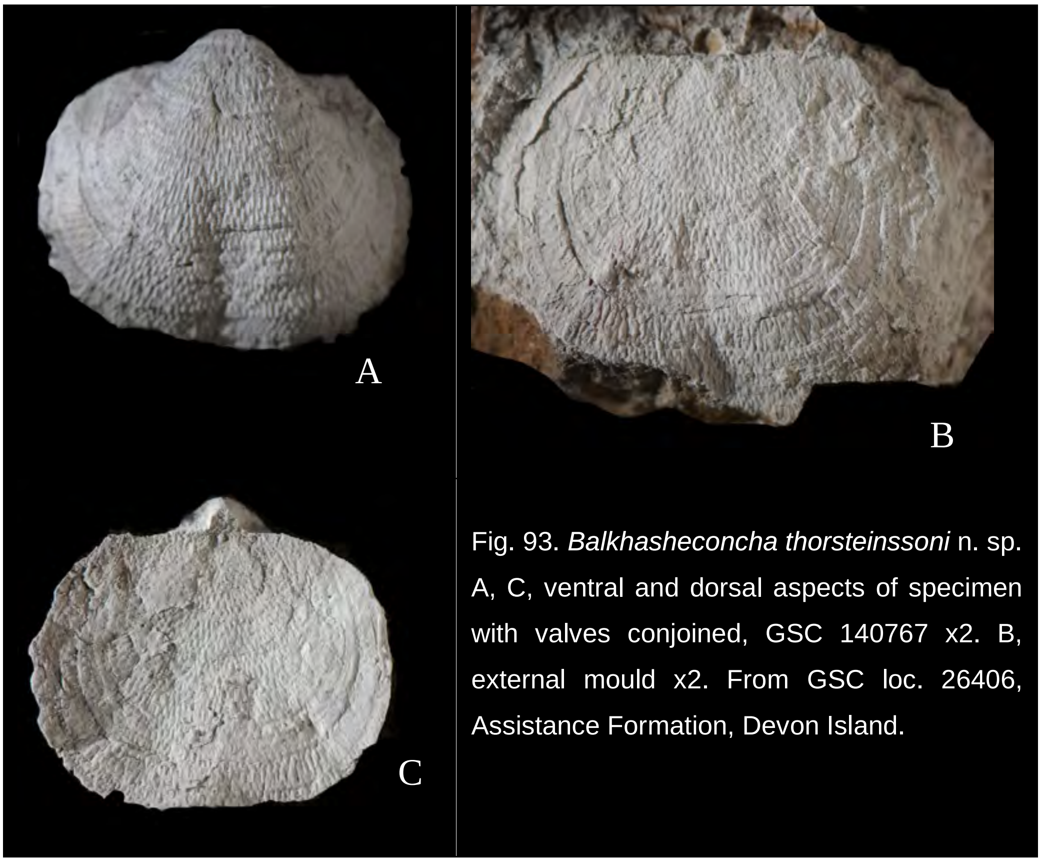

Fig. 93. *Balkhasheconcha thorsteinssoni* n. sp. A, C, ventral and dorsal aspects of specimen with valves conjoined, GSC 140767 x2. B, external mould x2. From GSC loc. 26406, Assistance Formation, Devon Island.

nature of the dorsal interior, and as a consequence the generic positions create a dilemma, as to whether the Russian and Arctic material should be assigned, speculatively, to *Balkhasheconcha* or not, and it has been opted to recognise a distinct taxon, definitely within *Balkhasheconcha*, but in some instances the specific assignment remains precarious. Most of the specimens assigned to *irginae* and *irginaeformis* in the literature come very close to this Canadian taxon in having gently concave dorsal disc and subgeniculate low trail, but fail to show the interior, so that the generic affinities remain uncertain. However, specimens ascribed to *Waagenoconcha irginae* by Gobbett (1964, pl. 5, fig. 7 – Cora Limestone, Bjørnøya, pl. 6, fig. 1-5 – Spirifer Limestone, Spitsbergen) include the worn interior of a dorsal valve that suggests the possible presence of buttress plates, now reduced by wear (Gobbett 1964, pl. 6, fig. 5). Ventral spines appear to have shorter bases compared with those of the present species. Externally similar specimens, also with shorter ventral spine bases, were also figured as *irginae* by Tschernyschew & Stepanov (1916, pl. 6, fig. 2-4) from Great Bear Cape, Ellesmere Island. No buttress plates are visible on the somewhat damaged dorsal interior. One ventral valve described as *Waagenoconcha* sp. by Dunbar shows well developed spine tunnels (Dunbar 1955, pl. 8, fig. 15), which is a feature of *Balkhasheconcha* (see Waterhouse 2018b, p. 188, Fig. 152A) and his other specimens are close to those the present suite, with possible buttress plates suggested in Dunbar 1955, pl. 8, fig. 8. Dunbar drew attention to other comparable specimens from Spitsbergen and east Greenland. The dorsal aspect of a specimen from east Greenland (Frebold 1931, pl. 3, fig. 8a) shows buttress plates, indicating Balkhasheconchinae.

The specimens described as *Waagenoconcha* cf. *abichi* by Logan & McGugan (1968, p. 1133, pl. 141, fig. 7-10) from the Ishbel Group in British Columbia and Alberta belong to *Balkhasheconcha*. They are close to the present species, but are more rounded in outline and without a sulcus.

The species *angustata* Sarytcheva, 1984 tends to be more elongate, and has no sulcus, or only a very slight sulcus, and the fold is narrow or absent.

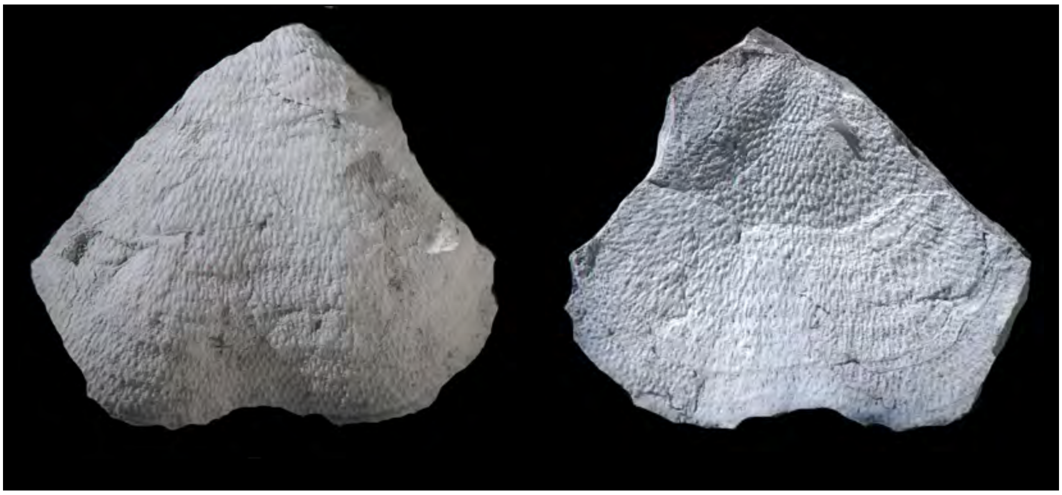

Fig. 94. *Balkhasheconcha thorsteinssoni* n. sp. A, B, ventral and dorsal aspects of specimen GSC 140768 with valves conjoined, showing micro-ornament well. Specimen from JBW 631, Takhandit Formation, x2.

Suborder Strophalosiaidina (Strophalosiidina) Waterhouse, 1975

Superfamily **STROPHALOSIAOIDEA** (**STROPHALOSIOIDEA)** Schuchert, 1913

Family **DASYALOSIAIDAE** (**DASYALOSIIDAE)** Brunton, 1966

Subfamily **ECHINALOSIAINAE** (**ECHINALOSIINAE**) Waterhouse, 2001

Diagnosis: Genera distinguished by having spines of one series on dorsal valve. Ventral valve usually has spines of one or two series, generally one erect and the other recumbent. Fine commarginal lamellae developed on dorsal valve, radial capillae generally faint or usually absent. Ventral attachment scar, teeth and sockets, interareas, dorsal median septum and muscle scars as in the family.

Tribe **ECHINALOSIAINI** (**ECHINALOSIINI**) Waterhouse, 2001

Diagnosis: Ventral spines of two series. Dorsal valve not thickened anteriorly.

Genus ***Echinalosia*** Waterhouse, 1967a

Diagnosis: Spines of two series interspersed over ventral valve, simple, normally not sinuous or arranged in special rows or aggregated to form lateral brush, usually present but may be few or missing over ventral ears; spine cores over middle valve may extend well forward from spine base. Dorsal spines fine and erect. Capillae present or absent, commarginal ornament subdued or absent.

Type species: *Strophalosia maxwelli* Waterhouse, 1964, p. 32, Letham Burn Formation (Roadian), New Zealand, OD.

Discussion: A Late Carboniferous example of this genus is found in the Yukon Territory, and the present species may have been derived from that species, or migrated de novo.

Echinalosia pondosus n. sp.

Fig. 95, 96

1969 *Echinalosia* sp. Waterhouse, p. 29, pl. 10, fig. 2, 4, 7-13.

Derivation: pondo – weight, Lat.

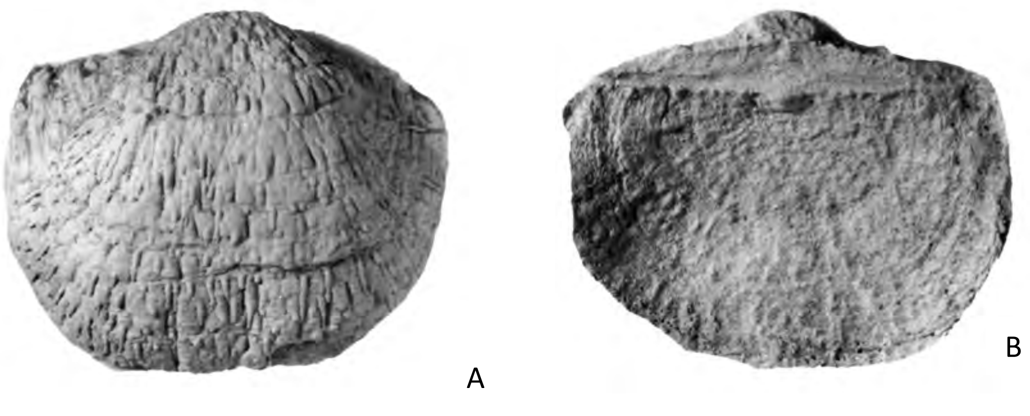

Fig. 95. *Echinalosia pondosus* n. sp. A, B, ventral and dorsal aspects of GSC 37666 from GSC loc. 35316, Trold Fiord Formation, Melville Island, x1.5. From Miller (1974).

Diagnosis: Medium-sized shells with highly convex ventral valve highest near hinge, thick disc, wide hinge. Spines of two series crowded over ventral valve, scattered and thin in one series over dorsal valve, interspersed with dimples and mounds and low commarginal lamellae; both valves with radial fila.

Holotype: GSC 23803, from GSC loc. 35316, Trold Fiord Formation, Melville Island, figured by Waterhouse (1969, pl. 10, fig. 2, 4, 7, 11) and in Fig. 96D, E herein, here designated.

Material: Four specimens were examined in 1969, with another added by Miller (1974) from GSC loc. 35316 in talus derived from Trold Fiord Formation, Sabine Peninsula, Melville Island.

Description, Resemblances: The species has been described, measured and illustrated by Waterhouse (1969). It was remarked then how exceptional the species appeared to be, and over subsequent years, despite various publications by authors over the world, no species has been found to resemble the present form. Its exceptional features are summarized in the diagnosis. The shape and longitudinal profile are particularly characteristic, the shell looking hunched because of the steep and unusually high ventral posterior walls. In addition, the spines are very dense over the ventral valve.

Strophalosia (*Wyndhamia*?) *gijigensis* Zavodowsky (1960, p. 340, pl. 82, fig. 13; 1970, p. 124, pl. 91, fig. 1; Sarytcheva 1977a, p. 51, pl. 4, fig. 9-15, text-fig. 29) comes from the Hivach suite of the Kolyma-Omolon region of northeast Russia. Apart from having slightly finer spines, the present species is very close, but has a more prominent ventral sulcus and wider hinge. *Strophalosia chivatschensis* Zavodowsky (1960, p. 68, pl. fig. 3-4; 1970, pl. 124, pl. 91, fig. 2, 3; Kashirtsev 1959, p. 49, pl. 20, fig. 5, 6) from the same level has been synonymized with the same species *gijigensis*, but has much smaller ventral adductor scars.

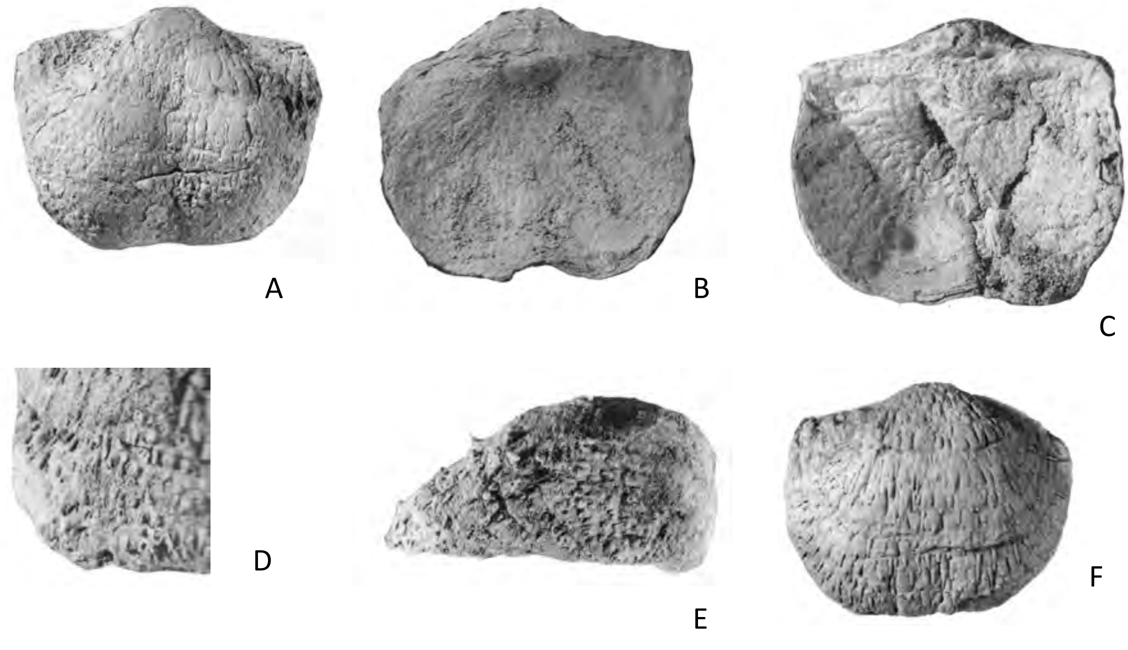

Fig. 96. *Echinalosia pondosus* n. sp. A, ventral view of GSC 23806, x0.8. B, dorsal view of GSC 23804, x1. C, dorsal view of GSC 23805, x1. D, ventral anterior spines on GSC 23803, holotype, x2. E, lateral view of same specimen, x1. F, ventral aspect of GSC 37666. From GSC loc. 35316, Trold Fiord Formation, Melville Island, x1. (Waterhouse 1969, Miller 1974).

Tribe **WYNDHAMIAINI** (**WYNDHAMIINI**) Waterhouse, 2010a

Diagnosis: Ventral body spines mostly coarse, semirecumbent, prostrate spines thin and often rare. Dorsal valve thickened and wedge-like with fine spines of one series.

Discussion: This group associates *Wyndhamia* and *Pseudostrophalosia.* The two genera are especially typical of the cold waters of the Permian Period in eastern Australia and New Zealand (Waterhouse 1964, 2001), so the presence of *Wyndhamia* in Arctic Canada is geographically and climatically significant. The genera are close to members of Tribe Arcticalosiini (see below) but have some fine ventral prostrate spines, which are missing from *Arcticalosia* Waterhouse, *Orthothrix* Geinitz and *Marginalosia* Waterhouse: these genera have only one order of spine on each valve. That contrasts with the ventral spines of Wyndhamiini, which may be varied in diameter, and include very sturdy spines either over the ventral disc or postero-laterally.

Genus ***Wyndhamia*** Booker, 1929

Diagnosis: Large suboval shells, the ventral valve moderately to well inflated with small cicatrix and numerous erect ventral spines, and as a rule, few prostrate slender spines. Dorsal valve with numerous fine spines. Internal features thickened, especially over the anterior disc, and dorsal valve heavily thickened into a wedge.

Type species: *Wyndhamia dalwoodensis* Booker, 1929, subjective synonym of *Branxtonia typica* Booker, 1929, OD.

Discussion: Until clarified by Briggs (1998), species of *Pseudostrophalosia* Clarke, 1970 were mistakenly assigned to *Wyndhamia* Booker, 1929, a genus which lacks the cluster of ventral ear-spines found in *Pseudostrophalosia,* and tends to have fewer fine prostrate spines over the ventral valve, as elaborated in Waterhouse (2001, p. 70). *Pseudostrophalosia* appears to be senior synonym of *Notolosia* Archbold, 1986, type species *N. dickinsi* Archbold, 1986 from the Hardman Member of the Canning Basin, Western Australia, with similar burst of ventral ear spines and wedge-shaped dorsal valve (Waterhouse 2013, p. 230). *Notolosia* was proposed as a subgenus of *Echinalosia*, and was treated as a full genus by Brunton et al. (2000, p. 574). This appears to be in error.

Wyndhamia sphenarctica Waterhouse, 1969

Fig. 97, 98

1969 *Wyndhamia sphenarctica* Waterhouse, p. 31, pl. 7, fig. 1-4, 6, 8, 10, 11, 13, pl. 8, fig. 1-15, text-fig. 1.

Diagnosis: Large with anterior ventral sulcus, spines dense and in distinctive pattern, with spine row and more prostrate spines than in species of *Wyndhamia* from east Australia or New Zealand.

Holotype: GSC 23817 figured by Waterhouse (1969, pl. 8, fig. 1, 3, 10, 14) and Fig. 97B herein, from Trold Fiord Formation (Wordian), Cameron Island, OD.

Material: Seven ventral valves and seven dorsal valves from GSC 76029, unit B, now Trold Fiord Formation, Cameron Island. Miller (1974) added single dorsal valves from GSC loc. 58951 and C-4015, both in the Trold Fiord Formation of Ellesmere Island.

Description, Resemblances: The species was described and illustrated in Waterhouse (1969). The species is outstanding, and arguably merits at least subgeneric distinction from *Wyndhamia* of east Australia and New Zealand, because it possesses a well-defined hinge row of ventral spines, and numerous prostrate ventral spines.

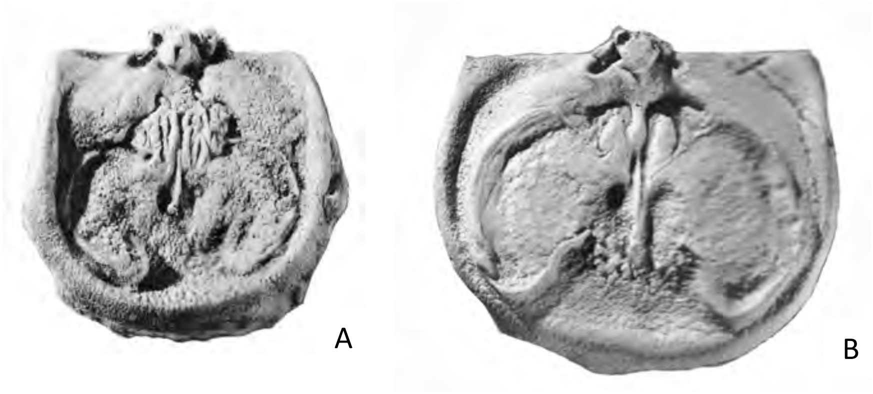

Fig. 97. *Wyndhamia sphenarctica* Waterhouse. A, dorsal interior GSC 23831. B, dorsal interior GSC 23817, holotype. From GSC loc. 76029, Trold Fiord Formation, Cameron Island, x1. (Waterhouse 1969).

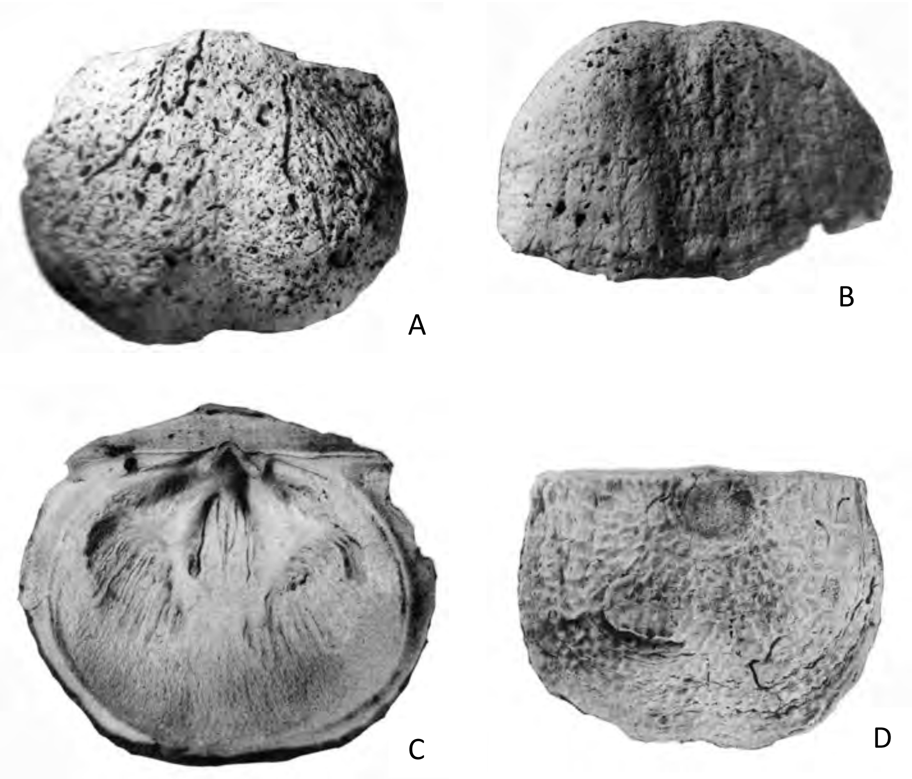

Fig. 98. *Wyndhamia sphenarctica* Waterhouse. A, ventral aspect GSC 23809. B, anterior aspect of ventral valve GSC 23810. C, internal aspect of ventral valve GSC 23807. D, dorsal exterior GSC 23833 with small ventral valve spat attached. From GSC loc. 76029, Trold Fiord Formation, Cameron Island, x1. (Waterhouse 1969).

Tribe **ARCTICALOSIAINI (ARCTICALOSIINI**) Waterhouse, 2001

Genus ***Arcticalosia*** Waterhouse, 1986a

Diagnosis: Ventral and dorsal spines uniform and of one order, closely spaced, numerous over ears. Dorsal valve wedge-shaped.

Type species: *Wyndhamia unispinosa* Waterhouse, 1969, p. 34 from Melville Island, Arctic Canada, OD.

Arcticalosia unispinosa (Waterhouse, 1969)

Fig. 99, 100

1967b *Wyndhamia* sp. Waterhouse, p. 48, fig. 2A.
1969 *Wyndhamia unispinosa* Waterhouse, p. 34, pl. 9, fig. 1-13, pl. 10, fig. 1, 3, 5, 6, text-fig. 2.
1986a *Arcticalosia unispinosa* – Waterhouse, p. 2.
2013 *A. unispinosa* – Waterhouse, Fig. 7.24.

Diagnosis: Large, ornamented by closely spaced sturdy erect spines in commarginal rows over ventral valve, larger over ears, also dense over dorsal valve.

Holotype: GSC 23818 figured in Waterhouse (1969, pl. 9, fig. 1, 3) and herein as Fig. 100A, B from GSC loc. 35317, talus from Trold Fiord Formation at Sabine Peninsula, Melville Island, OD.

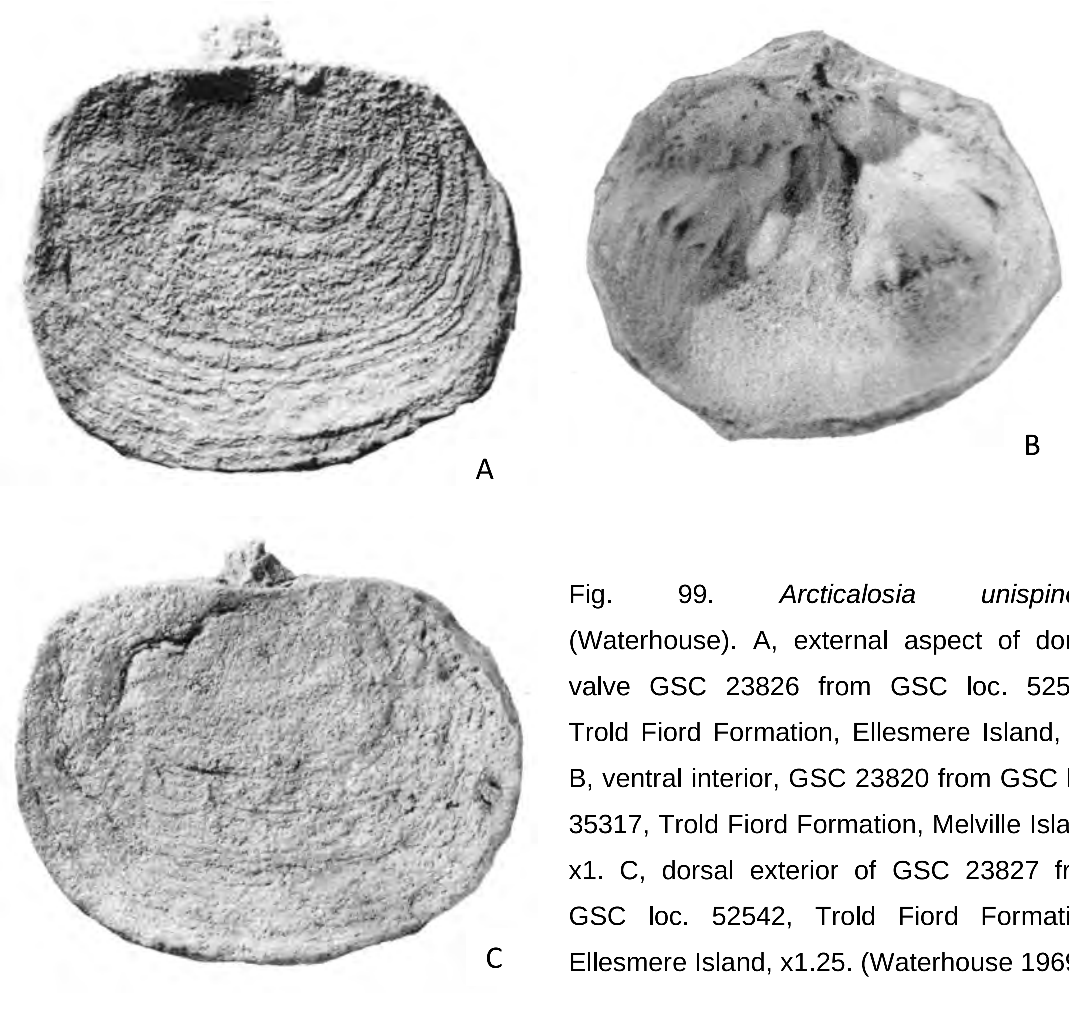

Fig. 99. *Arcticalosia unispinosa* (Waterhouse). A, external aspect of dorsal valve GSC 23826 from GSC loc. 52542, Trold Fiord Formation, Ellesmere Island, x1. B, ventral interior, GSC 23820 from GSC loc. 35317, Trold Fiord Formation, Melville Island, x1. C, dorsal exterior of GSC 23827 from GSC loc. 52542, Trold Fiord Formation, Ellesmere Island, x1.25. (Waterhouse 1969).

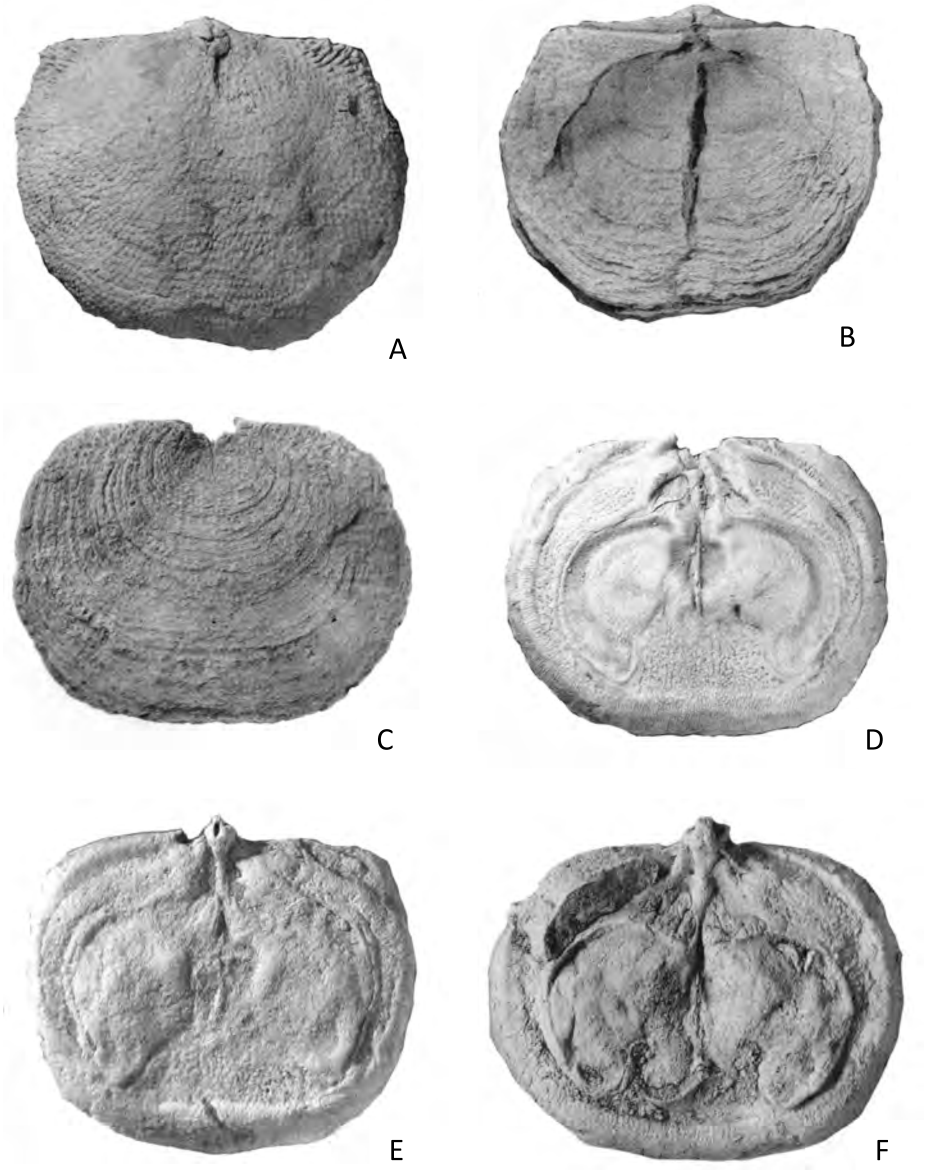

Fig. 100. *Arcticalosia unispinosa* (Waterhouse). A, B, ventral and dorsal aspects of holotype, GSC 23818 from GSC loc. 35317, Trold Fiord Formation, Melville Island. C, D, exterior and internal aspects of dorsal valve GSC 23823 from same locality. E, dorsal interior of GSC 23821 from same locality. F, dorsal interior, GSC 23827 from GSC loc. 52542, Trold Fiord Formation, Ellesmere Island. Specimens x1. (Waterhouse 1969).

Material: Specimens from GSC 35317, 52542 and 37161, Trold Fiord Formation, Melville Island, as in Waterhouse (1969, pp. 34, 35).

Description, Resemblances: The species has been described and illustrated in Waterhouse (1969). *Strophalosia*? *bajkurica* Ustritsky (1963, p. 96, pl. 14, fig. 2, pl. 25, fig. 2; Sarytcheva 1977a, p. 49, pl. 4, fig. 3-8) from the upper Baikur Suite of Taimyr Peninsula and Omolon Suite of the Kolyma-Omolon Massif is a smaller shell with subdued ventral sulcus, and appears to have similar uniform but possibly slightly coarser spines. Whether the dorsal valve is wedge-shaped is not clear. *Orthothrix* Geinitz from the Zechstein (Wuchiapingian) of northern Europe, including England, has very fine spines, and is distinguished by narrow hinge and prominent commarginal rugae.

Subfamily **CRASPEDALOSIAINAE (CRASPEDALOSIINAE**) Waterhouse, 2002b

Diagnosis: Ventral valve with rhizoid spines, dorsal spines absent or rare, dorsal valve lamellate with radial capillae present, faint, or absent. Hinge not denticulate.

Discussion: Two genera are known, *Craspedalosia* and *Melvillosia*, and the subfamily ranges from Middle Permian (Wordian) to Upper Permian (Wuchiapingian) in age. For these genera, Brunton (2007, p. 2667) claimed that Waterhouse (1969, 2001) had overlooked the significance of radial capillae, and did not consider the presence of dorsal spines on *Melvillosia* as significant, yet the diagnosis for *Melvillosia* in Waterhouse (2001, p. 56) reads “Close to *Craspedalosia*, distinguished by the presence of rare dorsal spines”, and radial capillae were diagnosed as an essential characteristic of *Craspedalosia* and *Melvillosia* (Waterhouse 2001, 2002b). There are numerous examples of this kind of mis-statement or ambiguity throughout the texts provided by Brunton et al. (2000) and Brunton (2007), underlining the need for caution in quoting or accepting such erratic statements, and the need for careful checking of the original literature, not to mention critical evaluation of figures. Brunton (2007) proceeded to suggest that the presence of dorsal spines in *Melvillosia* might suggest an approach to *Orthothrix* Geinitz, 1847. *Orthothrix* is readily distinguished from *Melvillosia* by having numerous fine rhizoid and non-rhizoid spines over both valves, and lacks capillae, as well illustrated by Muir-Wood & Cooper (1960, pl. 7, fig. 7-16) and Brunton et al. (2000, Fig. 406.3a-d), to suggest a position in Arcticalosiini. *Melvillosia* is not close to *Orthothrix*, and is certainly close to *Craspedalosia*.

Genus ***Melvillosia*** Waterhouse, 2001

Diagnosis: Ventral valve variably spinose, dorsal valve characterized by commarginal lamellae bearing radial fila, and rare dorsal spines.

Type species: *Melvillosia canadense* Waterhouse, 2001, p. 56 from Trold Fiord Formation of Wordian age, Melville Island, OD.

Melvillosia canadense Waterhouse, 2001

Fig. 101, 102

1969 *Craspedalosia pulchella* [not Dunbar] – Waterhouse, p. 38, pl. 7, fig. 5, 7, 9, 12, pl. 10, fig. 14.
2001 *Melvillosia canadense* Waterhouse, p. 56.
2013 *Melvillosia* Waterhouse, p. 245.

Diagnosis: Flat dorsal valve, distinguished by presence of spines, both valves ornamented by radial capillae, dorsal lamellae.

Holotype: GSC 23828 figured in Waterhouse (1969, pl. 7, fig. 5, 7) and herein as Fig. 101A, D, from GSC loc. 35320 in Trold Fiord Formation, Melville Island, OD.

Additional material. An internal mould with valve conjoined from GSC 35320.

Description: The species was described in Waterhouse (1969) and compared with other forms in Waterhouse (1969, p. 39) and Waterhouse (2001, p. 56).

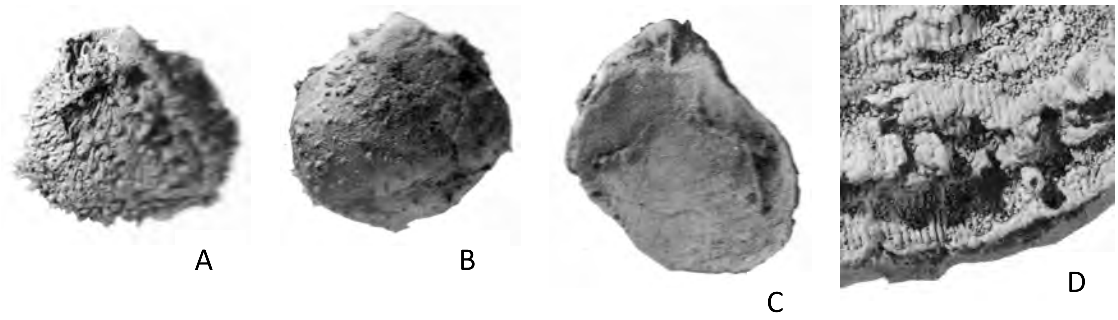

Fig. 101. *Melvillosia canadense* Waterhouse. A, ventral valve of holotype, GSC 23828, x1. B, C, posterior ventral and dorsal aspects of GSC 23829, x1. D, detail of dorsal valve on holotype, GSC 23828, x4, showing prominent spine. From GSC 35320, Trold Fiord Formation, Melville Island. (Waterhouse 1969).

Resemblances: *Strophalosia lamellosa linearis* Reed (1944, pl. 6, fig. 1, 2) especially pl. 6, fig. 1, registered as GSI F 16880 at the Geological Survey of India in Kolkata, has comparable recumbent and some erect ventral spines, and an unfigured specimen in the collections at the Geological Survey of Kolkata shows numerous protuberances suggestive of dorsal spine bases, to indicate the likely occurrence of *Melvillosia* in the Salt Range of Pakistan. The specimens come from the lower Chhidru Formation, and possibly from topmost Wargal Formation, of Wuchiapingian age (Waterhouse 2010).

Fig. 102. *Melvillosia canadense* Waterhouse, dorsal view of GSC 140769, x4, from GSC loc. 35320, Trold Fiord Formation, Melville Island.

Suborder Linoproductusidina (Linoproductidina) Waterhouse, 2013

Superfamily **PAUCISPINIFERAOIDEA (PAUCISPINIFEROIDEA)** Muir-Wood & Cooper, 1960

Family **PAUCISPINIFERAIDAE** (**PAUCISPINIFERIDAE)** Muir-Wood & Cooper, 1960

Subfamily **PAUCISPINIFERAINAE** (**PAUCISPINIFERINAE)** Muir-Wood & Cooper, 1960

Tribe **PAUCISPINIFERAINI** (**PAUCISPINIFERINI)** Muir-Wood & Cooper, 1960

Subtribe **PAUCISPINIFERAINAI** (**PAUCISPINIFERINAI)** Muir-Wood & Cooper, 1960

Discussion: The genera *Paucispinifera* Muir-Wood & Cooper, *Eomarginifera* Muir-Wood and *Eomarginia* Waterhouse, as discussed in Waterhouse (2013, pp. 312-315) are now grouped in subtribe Paucispiniferinai Muir-Wood & Cooper. They are distinguished from a newly recognized Anemonariinai, based on allied genera that lack a well developed row of ventral hinge spines, in contrast to the arrangement in Paucispiniferinai.

Subtribe **ANEMONARIAINAI (ANEMONARIINAI)** new subtribe

Name genus: *Anemonaria* Cooper & Grant, 1969 from Roadian of Glass Mountains, Texas, here designated.

Diagnosis: Shells close to *Paucispinifera* and allies, but lacking a well-formed row of ventral hinge spines.

Genera: *Anemonaria* Cooper & Grant, *Caruthia* Lazarev & Carter*,* *Glabauriella* Waterhouse, *Liosotella* Dunbar, *Liosella* n. gen., *Liosotellina* n. subgen.

Discussion: The proposed recognition of a subset of genera within Paucispiniferaini (Paucispiniferini) Muir-Wood & Cooper makes a distinction between the above-named genera, and the genera listed as belonging to the subtribe Paucispiniferainai (= Paucispiniferinai) Muir-Wood & Cooper.

Genus ***Anemonaria*** Cooper & Grant, 1969

Diagnosis: Spines in row along base of ventral umbonal slopes, a few strut and other ventral spines, no well-formed ventral hinge row of spines, costellae absent or faint, sulcus variably developed. Dorsal marginal ridge may be thick across inner ears, otherwise low, tubercles subdued.

Type species: *Marginifera sublaevis* King, 1931 from Cathedral Mountain Formation (Kungurian), Texas, United States, OD.

Discussion: *Anemonaria* is close to *Liosotella* Cooper, 1953 in some respects, the most obvious difference centering on the coarse costae that cover the anterior disc and trail of *Liosotella*. In addition, *Liosotella* lacks any ventral ear spines (Cooper 1953, Muir-Wood & Cooper 1960, Dunbar 1955), whereas *Anemonaria* may have a few spines along the hinge, though they are not numerous or in a well formed row. Both genera have a row of umbonal slope spines. Muir-Wood & Cooper (1960, p. 228) reported dorsal spines in *Liosotella*, whereas dorsal spines are missing from *Anemonaria.*

Anemonaria pseudohorrida (Wiman 1914)

Fig. 103

1875 *Productus horridus* [not Sowerby] – Toula, p. 232, pl. 4, fig. 2a-d.
1914 *P. pseudohorridus* Wiman, p. 74, pl. 17, fig. 1-11.
1917 *P. pseudohorridus* – Grönwall, p. 586, pl. 29, fig. 6-10.
1936 *Sowerbina pseudohorrida* – Fredericks, p. 98, pl. 1, fig. 18-21.
1937 *P.* (*Horridonia*) *pseudohorridus* – Frebold, p. 23, pl. 10, fig. 3, 4.

1937 *Marginifera involuta* [not Tschernyschew] – Frebold, p. 40, pl. 10, fig. 1, 2.
1937b *P*. (*Horridonia*) *pseudohorridus* – Stepanov, p. 120, 176, pl. 5, fig. 5-7.
1937b *P*. (*Marginifera*) *sublaevis* – Stepanov, pp. 137, 179, pl. 2, fig. 1, 2, pl. 5, fig. 8-10.
1939 *P*. (*Horridonia*) *pseudohorridus*? – Licharew & Einor, pp. 54, 206, pl. 10, fig. 4, 5.
1960 *Liosotella pseudohorrida* – Solomina, p. 38, pl. 5, fig. 1-4.
1963 *L. pseudohorrida* – Ustritsky & Chernyak, p. 93, pl. 18, fig. 6.
1964 *L. pseudohorrida* – Gobbett, p. 62, pl. 3, fig. 27-34.
1970 *Horridonia pseudohorrida* – Barchatova, p. 133, pl. 3, fig. 3.
1971 *Anemonaria* cf. *pseudohorrida* – Bamber & Waterhouse, p. 172, pl. 18, fig. 3, 4.
1971 *Anemonaria* sp. Bamber & Waterhouse, p. 178, pl. 21, fig. 3.
1971 *Liosotella pseudohorrida* – Brabb & Grant, p. 15, pl. 1, fig. 1-5, 18-20.
1977a *A. pseudohorrida* – Sarytcheva, p. 120, pl. 17, fig. 4, 5, pl. 18, fig. 1-4, text-fig. 71, 72.
1990 *A. pseudohorrida* – Kalashnikov et al., p. 145, pl. 1, fig. 5, 6.
1992 *A. pseudohorrida* – Nakamura et al., p. 78.
1996 *A. pseudohorrida* – Shi & Waterhouse, p. 70.
1998 *A. pseudohorrida* – Grunt et al., pl. 10, fig. 10, 11.
2008 *A. pseudohorrida* – Angiolini & Long, p. 79, Fig. 10G.
2013 *A. pseudohorrida* – Waterhouse, pp. 314, 315.

Diagnosis: Medium to small shells with deep ventral sulcus, faint radial ribs, slightly varied spine ornament.

Lectotype: Specimen figured by Wiman (1914, pl. 17, fig. 8-10) and Sarytcheva (1977a, pl. 18, fig. 1g) from the Spiriferenkalk (mid-Brachiopod Chert), Spitsbergen, SD Gobbett (1964, p. 62).

Material: Specimens preserved as exposed ventral valves. The dorsal valve is possibly present but concealed. One specimen from GSC loc. 36770, apparently from the Assistance Formation, but with no locality data available, one ventral valve from C-4002 and C-4024, two ventral valves from C-4019, and one ventral valve and one specimen with valves conjoined from C-4081, Assistance Formation, Ellesmere Island. One ventral valve from C-4004, which is rated as Trold Fiord but its matrix looks like Assistance, and one ventral valve each from C-4014 and C-4034, all from Trold Fiord Formation, Ellesmere Island. More than twenty poorly preserved specimens from GSC loc. 53931, mid-Takhandit Formation, Yukon Territory (Bamber 1972, p. 9). Material reported from GSC loc. 57259 in the lower Takhandit Formation in Bamber & Waterhouse (1971) is not available for the present study.

Dimensions in mm: ventral valves

Width	Length	Height	C-locality
27	25	17	4019
30	23	+12	4019 ears complete
23	16	11	4002
23	21	12	C4024

Description: This species has a characteristic shape, having a transverse and highly convex ventral valve with incurved ventral umbo showing an angle usually within the range of 85º to 95º, and deep sulcus commencing at or near the umbonal tip, the sulcal angle measuring close to 20º. On most specimens the shell is comparatively smooth. The ventral spine pattern is dominated by a row of spines along the base of the umbonal slopes, numbering up to eight, and a stout cardinal spine lies on each outer ear, but in many specimens spines are not preserved, and the shells assigned, tentatively, by shape and smooth shell, which at best suffice only to indicate a possible rather than confident identification. Other spines appear inconsistently over the trail, as documented in Waterhouse (2013), where they may be quite numerous, arising from the crests of low costellae where present, without disturbance to ribs and without elongate bases. A pair of sturdy spines lies near the umbo on the ears of at least some shells, and one or two additional spines lie over the umbonal region, and others on the sulcus in the trail, but distribution tends to vary on each specimen, though this may in part reflect a certain amount of decortication and imperfect preservation.

The ventral adductor scars are raised and somewhat tear-shaped, and the diductors are oval and weakly impressed, marked by longitudinal striae, and lying in some specimens beside the adductors and in other specimens in front. A low marginal ridge lies near the start of the trail. The dorsal interior shown in Bamber & Waterhouse (1971, pl. 21, fig. 3), and identified as *Anemonaria* sp. from a Permian sandstone unit in the *Neochonetes* zone (now *Neochonetes culcita* Zone) of the northern Yukon Territory. The septum is strong and extends a little past mid-length in this specimen, and reaches the start of the trail in the dorsal valve from GSC loc. 53931. Dorsal adductors are raised with a narrow posterior-lateral subdivision, and brachial ridges are well defined. Across the anterior disc just behind the start of the trail lies a row of sturdy pustules, much stronger than the fine pustules covering much of the rest of the dorsal floor. There is only a low if any marginal ridge.

Resemblances: Brabb & Grant (1971) referred the species *pseudohorrida* to *Liosotella*, whereas Waterhouse in Bamber & Waterhouse had illustrated specimens as *Anemonaria* cf. *pseudohorrida*. The Bamber-Waterhouse specimens come from the lower Takhandit Formation. Following that report, Sarytcheva (1977a) confirmed the placement of *pseudohorrida* in *Anemonaria*, providing excellent text figures and a number of photographs of material from Spitsbergen. Fine low ribs are visible in specimens figured in Sarytcheva (1977a, pl. 17, fig. 4b, 5b) from the Kapp Starotsin Formation of Spitsbergen. Specimens assigned in Sarytcheva (1977a, pl. 18, fig. 5-14) from Kungurian and Kazanian beds of Russia have an umbonal slope row of spines in the ventral valve, like the Spitsbergen specimens assigned to *Liosotella pseudohorrida* by Gobbett (1964, p. 62, pl. 3, fig. 27-34) from the lower and middle Brachiopod Chert of Spitsbergen.

Fig. 103. *Anemonaria pseudohorrida* (Toula), dorsal aspect of internal mould GSC 27022 from GSC loc. 53826, *Neochonetes culcita* Zone, north Richardson Mountains. (Bamber & Waterhouse 1971).

Anemonaria robusta n. sp.

Fig. 104 – 110

1908 *Productus wabashensis* [not Norwood & Pratten] – Whitfield, p. 65, pl. 2, fig.6.
1908 *P. verneuilianus* [not de Koninck] – Whitfield, p. 55, pl. 2, fig. 7, 8.

Derivation: robustus – firm, strong, Lat.

Diagnosis: Shell smooth apart from suggestions of fine anterior dorsal ribs, deeply sulcate, shell thick especially for the marginal ridge across the dorsal ears.

Holotype: Specimen GSC 140800 illustrated as Fig. 109A, B from C-4019, Assistance Formation (Roadian), Ellesmere Island, here designated.

Material: Six ventral valves and two specimens with valves conjoined with fragments from C-4019, one ventral valve from C-4024, and three ventral valves from C-4081, Assistance Formation, Ellesmere Island. Two ventral valves from C-4014, and single ventral valves from C-4034 and C-4017, all from Trold Fiord Formation, Ellesmere Island. A specimen with valves conjoined and six ventral valves, some fragmentary, from GSC loc. 53486, unnamed sandstone unit, *Dyoros modestus* Zone, McDougall Pass, Richardson Mountains, Yukon Territory.

Fig. 104. *Anemonaria robusta* n. sp. A, ventral valve, GSC 140795 from C-4019, Assistance Formation, Ellesmere Island. B, broken ventral valve GSC 140796 from C-4017, Troll Fiord Formation, Ellesmere Island, x2.

Dimensions in mm:

Width	Length	Height	
31.5	24	15.5	C-4019
15.5	12	6.3	conjoined specimen, GSC loc. 53486

Description: Specimens characterized by lack of ribs, other than occasional anterior and irregular radial rugae, with faint suggestions of broad low ribs on some shells. Hinge at maximum width, moderately large convex ears with alate cardinal extremities, umbonal angle of 95° to 100°, moderately high convex umbonal slopes, and deep sulcus with angle close to 20°. Spines are poorly preserved as a rule, apart from a massive spine arising as the outermost

Fig. 105. *Anemonaria robusta* n. sp. A, posterior ventral valve GSC 140797 from ?C-4081, with large lateral spine arising from anterior umbonal slope row. B, ventral valve GSC 140798, from C-4019. See also leached ventral valve, Fig. 108. Assistance Formation, Ellesmere Island, x2.

spine of the umbonal slope row in one specimen (Fig. 105A), but various specimens have a well defined umbonal slope row, and there are suggestions of a pair of anterior large spines near the sulcus, and in some specimens, suggestions of a second pair in front. The best-preserved specimens show either a complete absence of hinge spines, or only a few hinge spines, not consistently in a well-formed row. The posterior dorsal valve is smooth without spines or ribs, and gently concave, with large gently concave ears and a low median fold. Low fine radial ribs, up to seven in 5mm, may occur anteriorly.

The ventral adductor platform is high, short and wide, divided by a broad low round-crested ridge, and weakly subdivided into small posterior and larger anterior elements by a low narrow ridge in one specimen. The scars are largely smooth, apart from fine longitudinal ridges, of which one is prominent near the middle of the anterior set of scars. To each side, the diductor impressions are subrounded, transverse, and scored by low longitudinal ridges, deeper posteriorly. The posterior floor behind the muscle field is smooth, and in front the shell floor has crowded fine short elongated pits. A massive ridge lies across each inner ear, and the shell is up to 4mm thick.

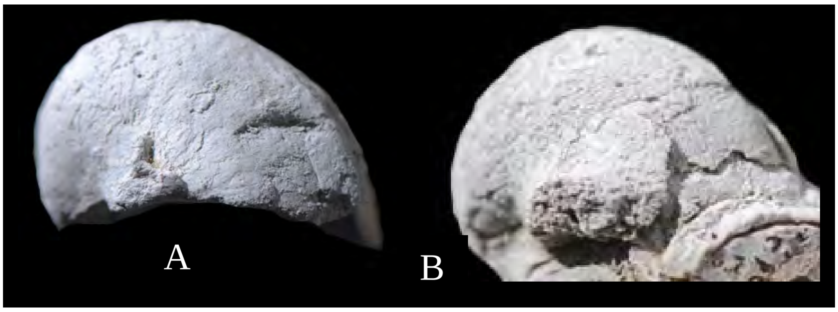

Fig. 106. *Anemonaria robusta* n. sp., lateral aspect of ventral valves. A, GSC 140795, x2. See Fig. 104A. B, holotype GSC 140800 before leaching, x3. Specimens from C-4019, Assistance Formation, Ellesmere Island.

In the dorsal valve, the cardinal process is broad and squat with wide median lobe and fine lateral lobes. A fine and low median septum extends forward in front of a low broad platform in front of the cardinal process, and is highest anteriorly. The adductor scars are raised, smooth and elongately oval, broadening anteriorly. Well spaced large pustules lie in front, but are incompletely preserved, and brachial shields lie laterally, exposing a smooth central area. There is only a very short and low hinge ridge each side of the cardinal process, and a low but well-defined marginal ridge extends past the ears to at least in front of mid-length.

Resemblances: This species is distinguished by its deep ventral sulcus and smooth posterior surface, without ribs in many specimens and only low ribs anteriorly in others, and very thick shell. Specimens figured by Whitfield (1908, pl. 2, fig. 5-7) for two species of *Productus* as in the synonymy from Cape Sheridan may be conspecific. Wiman's *pseudohorrida* is more elongate, with faints ribs as a rule and deepr anterior sulcus. They are shown with deep sulcus, and no sign of spines, though of course they could have been decorticated. The present specimens resemble individuals from the Ufimian and Kazanian faunas of Kanin Peninsula, Russia, figured by Stepanov et.

Fig. 107. *Anemonaria robusta* n. sp. A, B, ventral and lateral aspects of ventral valve GSC 140801 from C-4081. Specimen x2, from Assistance Formation, Ellesmere Island.

Fig. 108. *Anemonaria robusta* n. sp., ventral internal mould GSC 140798 x2.5 from C-4019, Assistance Formation, Ellesmere Island.

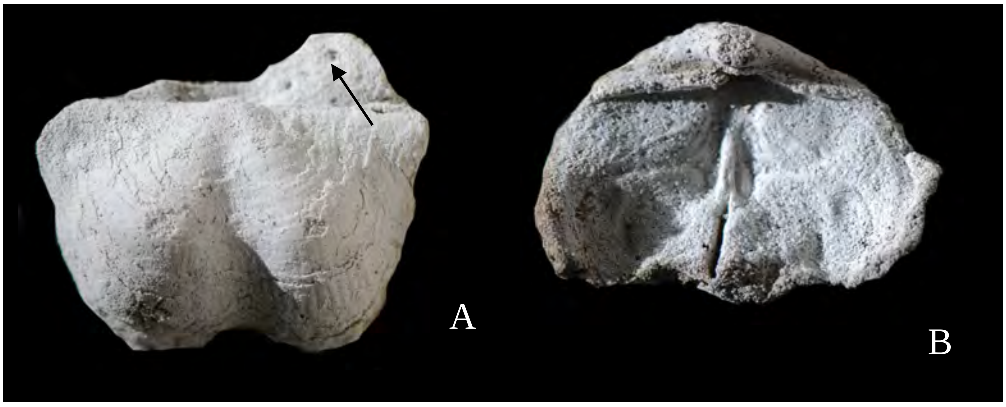

Fig. 109. *Anemonaria robusta* n. sp. Holotype, with valves conjoined, GSC 140800 from C-4019, Assistance Formation, Ellesmere Island. A, dorsal external mould with part of ventral valve, showing umbonal slope row of spine bases, as arrowed. Note faint anterior costae. B, dorsal aspect of internal mould. Specimens x2.

al. (1975, pl. 1, fig. 13-20) and assigned to *Paucispinifera notteiensis* (Fredericks), but not like the neotype cited by Grunt (2006a). *A. sulankherensis* Manankov (1998, p. 400, pl. 8, fig. 6-9) from the Tsaganui Horizon (Ufimian) of southeast Mongolia is small with wide shallow sulcus, and fine ribs limited to the trail of some specimens.

Anemonaria auriculata Shi & Waterhouse (1996, pl. 6, fig. 10-26, text-fig. 22-24) from the *Jakutoproductus verchoyanicus* Zone, also recorded from the *Ogilviecoelia shii* Zone by Waterhouse (2018a, Fig. 178) in the Jungle Creek Formation of Yukon Territory, has faint costae and much more emphasized sulcus and fold. The species is of Asselian and Aktastinian age.

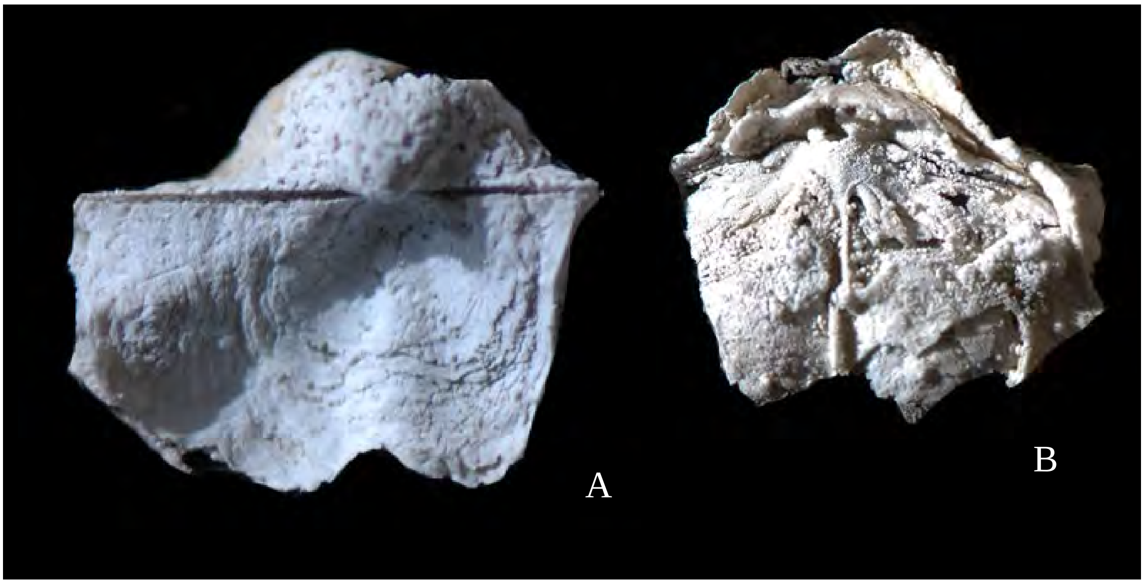

Fig. 110. *Anemonaria robusta* n. sp. A, B, dorsal exterior aspect and dorsal internal aspects of conjoined specimen GSC 140799, from C-4019. Specimen x4, from Assistance Formation, Ellesmere Island.

Anemonaria sp.

Fig. 111

Material: At least half a dozen ventral valves and on conjoined specimen from GSC 53486, in unnamed sandstone at McDougall Pass in the Richardson Mountains.

Description: Shells small, with hinge at maximum width, moderately large convex ears with alate cardinal extremities, which do not extend far laterally, umbonal angle of 95° to 100°, moderately high convex umbonal slopes, and shallow sulcus with angle close to 20°, commencing near mid-length, and in two specimens, containing a short median elevation. A few spines lie close to the hinge, and a few stronger spines pass along the umbonal slopes, well above the base. A few large spines lie along the crest of the ventral valve each side of the sulcus, and other slender erect spines are found especially over the outer slopes. There are subfusc signs of low ribs, twelve in 5mm over each valve, though overall the shell is almost smooth, with shallow sulcus.

Ventral adductor scars are slightly elongate and raised, and diductor scars to each side oval and impressed. A low ridge crosses inside each ear. But detail for the dorsal interior is not known.

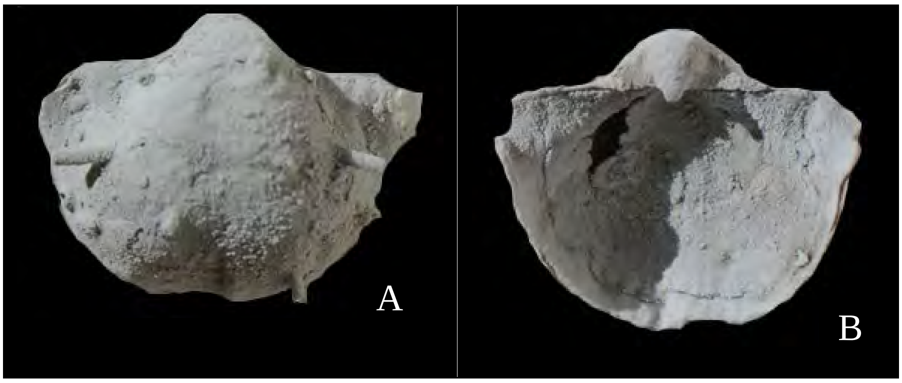

Fig. 111. *Anemonaria* sp., ventral and dorsal aspects of conjoined specimen from GSC 140802 from GSC loc. 53846, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory, x3.

Genus ***Liosella*** n. gen.

Derivation: Variation on *Liosotella* Cooper, 1953.

Diagnosis: Of small to medium size, with broad shallow to moderately well defined sulcus, light to strong radial ribs, prominent strut spines and row of spines along the ventral umbonal slopes, other scattered fine ventral spines, no dorsal spines. Low dorsal marginal ridge as a rule.

Type species: *Liosotella grandicosta* Dunbar, 1955, p. 78 from the Wegner Halvo and Schuchert Dal Formations (Wuchiapingian) of central east Greenland, here designated.

Discussion: This genus is prominent in Roadian and Wordian faunas of the Glass Mountains in Texas, and in Greenland. A number of specimens from the Canadian Arctic are referred to *Liosella*, because they have radial ribs, and no dorsal spines. In the ventral valve, strut spines are present, together with a few if any spines along the hinge and a row of spines along or near the base of the umbonal slopes.

Muir-Wood & Cooper (1960, p. 228, pl. 69, fig. 9) in their overview of Productida noted the presence of rare dorsal spines in type *Liosotella*, and these were clearly illustrated for the several species described by Cooper (1953) from Mexico, although no clear description of them seems to have been provided in the text. Glass Mountains species from Texas as described extensively by Cooper & Grant (1975) were not reported as displaying any dorsal spines, and although some figures in the Glass Mountains material seem ambivalent, as they might be displaying small flaws in the preservation rather than spines, it seems clear that at least for most specimens, no dorsal spines were present, signifying that the material was not congeneric with the Mexican genus. Dunbar (1955) in describing several species from central east Greenland did not observe any dorsal spines. This then clearly offers a difference from the type material of *Liosotella* from Mexico, and the difference is recognized with the proposal of a separate genus. Other instances are known, including occurrences in the Permian of Spitsbergen and Canada.

Liosella spitzbergiana (Toula, 1874)

Fig. 112 – 115

1874 *Productus spitzbergianus* Toula, p. 144, pl. 1, fig. 8a-d.
1931 *Marginifera typica septentrionalis* Frebold, p. 25, pl. 3, fig. 2.
1955 *Liosotella spitzbergiana* – Dunbar, p. 75, pl. 5, fig. 1-4, 7-13.

Diagnosis: Moderately strong ribs, shell weakly elongate as a rule, but posterior aspect transverse.

Lectotype: Sole specimen figured by Toula (1874, pl. 1, fig. 8a-c) from Kapp Starotsin Formation, Spitsbergen, here designated.

Material: Possible ventral valve each from C-4028 and C-4036, Assistance Formation, Ellesmere Island, and single ventral valve from C-4016, nine ventral valves from C-4019, and four ventral valves from C-4002, all from the Assistance Formation of Ellesmere Island. One ventral valve from C-4022 of uncertain source, possibly Degerböls Formation. Eleven ventral valves from C-4017, and one ventral valve from C-3995 and C-4014, from Trold Fiord Formation, and three ventral valves from C-3993, possibly from Degerböls Formation, all from Ellesmere Island.

Dimensions in mm:

Width	Length	Height	Umbonal angle	Sulcal angle
24	23	14.5	95^{o}	20^{o}
31	20	11.5	-	

Description: Shell transverse, ventral valve highly convex with wide incurved ventral umbo measuring 120^{o}, and wide hinge with large convex ears and acute cardinal extremities. The sulcus is deep with angle of 30^{o}. Ribs are strong, five to seven in 5mm, absent from the ears, and may involve some irregular branching. The ribs on the larger ventral valves become slightly finer and more closely spaced anteriorly over the ventral trail, at seven to eight in 5mm, and in some specimens radial rugae appear. Spines are patchily preserved, and include a row of spines close to the base of the umbonal slopes. There are indefinite signs of one or two weak hinge spines, which might represent the incomplete remnants of a full hinge row, or as deemed here, just occasional exceptions. Several specimens have a prominent spine on each outer ear, with signs of two or three finer spines. Body spines are scattered over the shell, with possible signs of an anterior strut spine each side of the sulcus anteriorly. None of the dorsal valves show any spines.

The adductor scars are small, oval and raised, with strong narrow radial ridges and grooves, and the diductor scars are impressed, oval and marked by radial grooves and ridges posteriorly, and smooth anteriorly: they

Fig. 112. *Liosella spitzbergiana* (Toula). A, anterior view of ventral valve, GSC 140780. B, dorsal valve interior, GSC 140781. From C-4019, Assistance Formation, Ellesmere Island, x2.

extend well in front of the adductors. The floor of the valve is otherwise smooth posteriorly and in front marked by dense pits. A low hinge ridge passes laterally into a broad marginal ridge lying across the inner margin of each ear.

Resemblances: Endeavours to identify these specimens are seriously handicapped by the uncertain nature of spine detail in various species described from the Arctic. *Liosella spitzbergiana* (Toula) as figured by Toula (1874, p. 144, pl. 1, fig. 8a-d) from Spitsbergen and Dunbar (1955, p. 75, pl. 5, fig. 1-4, 7-13) as well as *Marginifera typica* var. s*eptentrionalis* [not Tschernyschew] Frebold (1931, p. 25, pl. 3, fig. 2) from Greenland, are close in general shape

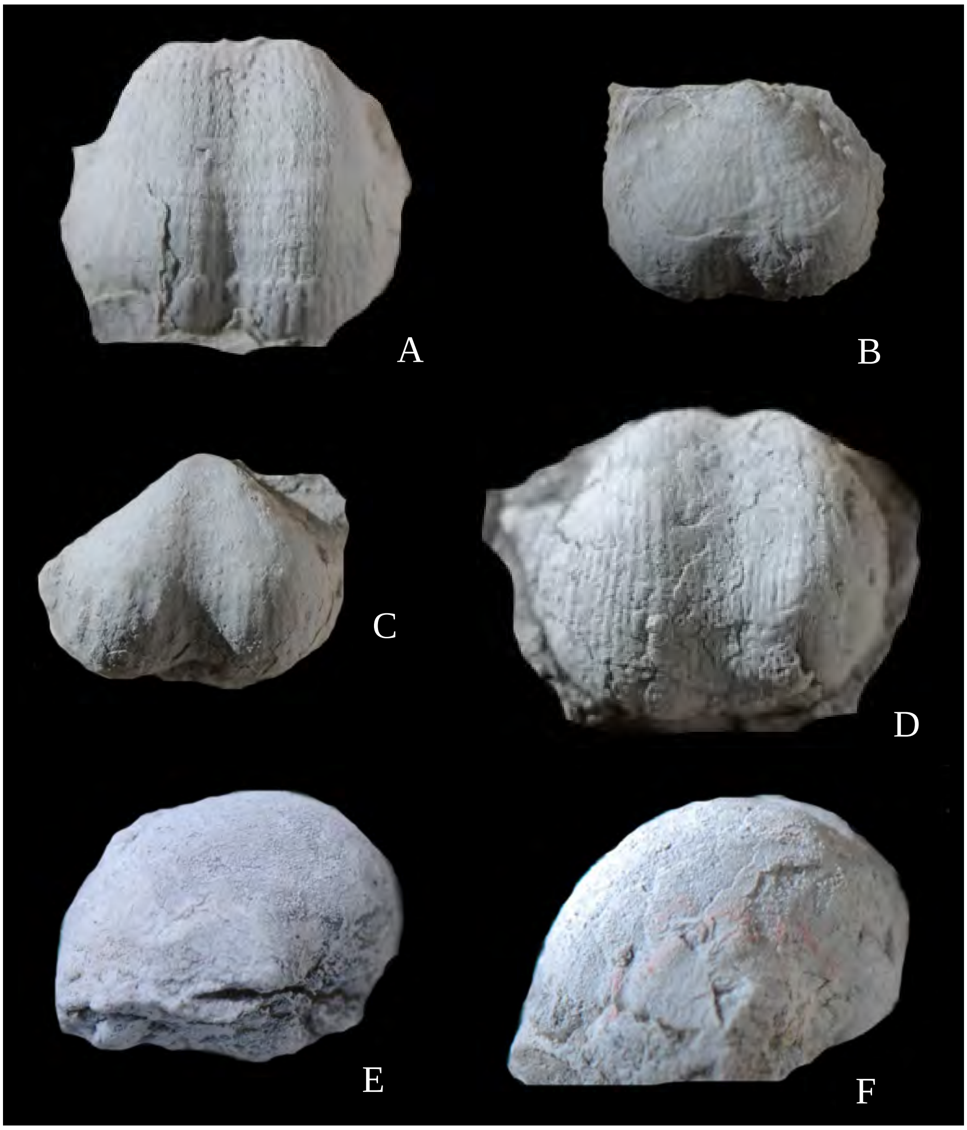

Fig. 113. *Liosella spitzbergiana* (Toula). A, ventral valve GSC 140784 from C-3993, Degerböls Formation. B, ventral valve GSC 140785 with exceptionally flat disc and well preserved bases of umbonal slope row of spines, from C-4022, possibly Degerböls Formation. C, ventral valve GSC 140786 from C-3993, possible Degerböls Formation. D, ventral valve GSC 140787 from C-4028, Assistance Formation. E, F, lateral aspects of decorticated ventral valves GSC 141000 and GSC 141001 x2 from C-3995, Assistance Formation. Specimens from Ellesmere Island, x2.

and ribbing. Some shells assigned by Dunbar to *spitzbergiana* have prominent ears and the strength of ribs appears to vary from like those of *spitzbergiana* to somewhat fainter. The present specimens have a sulcus no different from that of specimens previously assigned to *spitzbergiana*. A row of spines lies along the base of the umbonal slopes, but there is no well formed row of hinge spines, and few obvious strut spines, and no dorsal spines.

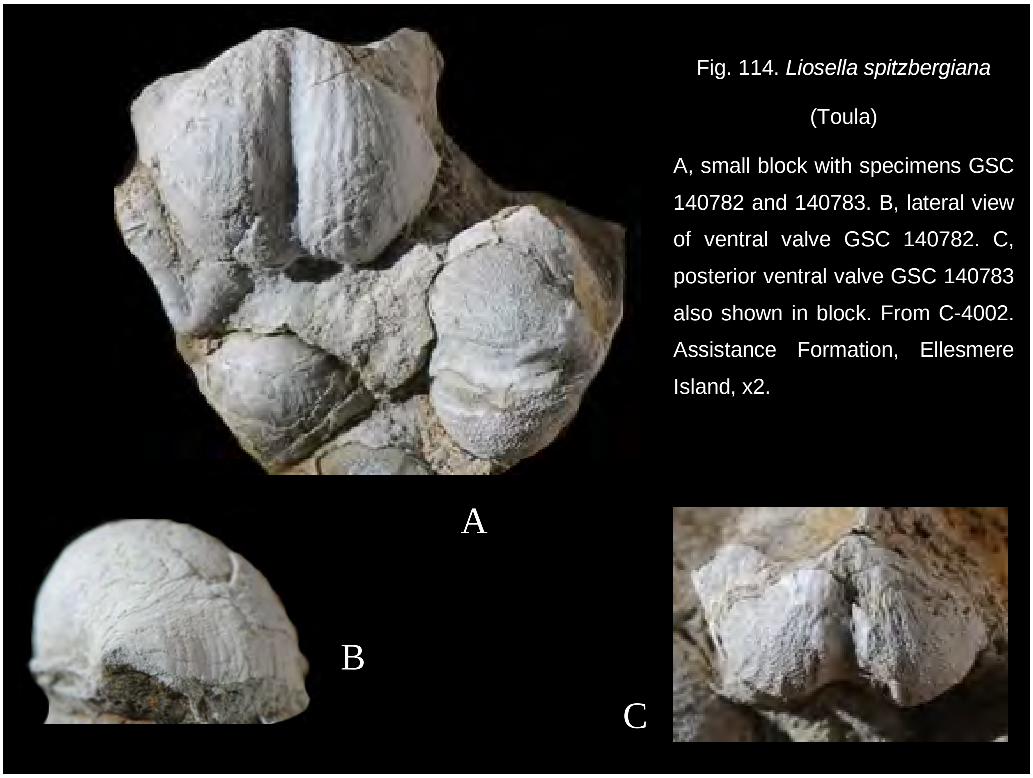

Fig. 114. *Liosella spitzbergiana* (Toula)

A, small block with specimens GSC 140782 and 140783. B, lateral view of ventral valve GSC 140782. C, posterior ventral valve GSC 140783 also shown in block. From C-4002. Assistance Formation, Ellesmere Island, x2.

Productus pseudohorrida Wiman (1914) includes many specimens that are less transverse, with faint signs of ribs that are of similar spacing to those of the present suite. Some of the Kungurian and Kazanian specimens assigned to *Anemonaria pinegensis* (Licharew) in Sarytcheva (1977a, pl. 18, fig. 5-14, text-fig. 73, 74) suggest the presence of a cardinal strut spine (see Sarytcheva 1977a, pl. 18, fig. 2b, 5b, 6b), but ribs are less prominent than in the present form. The present assemblage is close to a number of species described by Cooper & Grant (1975) from the Willis Ranch to Bell Canyon faunas of the Glass Mountains in Texas, apart from possessing slightly less extended less acute ears and weaker spines, but close overall in shape and costation.

Fig. 115. *Liosella spitzbergianus* (Toula), ventral anterior aspect GSC 140789 x1.5 from C-4014, Trold Fiord Formation, Ellesmere Island.

Liosella vadosisinuata (Dunbar, 1955)

Fig. 116

1955 *Liosotella vadosisinuata* Dunbar, p. 77, pl. 5, fig. 14-22.

Diagnosis: Highly transverse with acute cardinal extremities and fine ribs.

Holotype: Specimen figured by Dunbar (1955, pl. 5, fig. 14-16) from Cretaceous boulder, central east Greenland, OD.

Description, Resemblances: A few specimens, such as GSC 140788 figured in Fig. 115A, B from C-4014, Trold Fiord Formation, Ellesmere Island, are unusually transverse with prominent ears, and fine ribs.

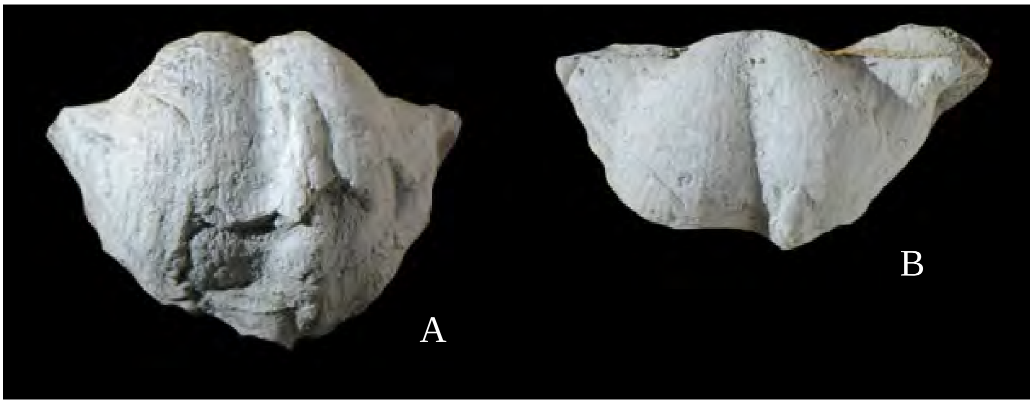

Fig. 116. *Liosella vadosisinuata* (Dunbar). A, B, ventral anterior and posterior aspects of ventral valve GSC 140788 x1.5 from C-4014, Trold Fiord Formation. Ellesmere Island.

Liosella delicatula **(**Dunbar, 1955)

Fig. 117 – 119

1955 *Liosotella delicatula* Dunbar, p. 77, pl. 5, fig. 23-31.

Diagnosis: Fine ribs and subelongate shell.

Fig*.* 117*. Liosella delicatula* (Dunbar). A, ventral anterior aspect and B, oblique lateral aspect of ventral valve GSC 140790 from C-4017, Trold Fiord Formation, Ellesmere Island, x2.

Fig. 118. *Liosella delicatula (D*unbar). A, anterior aspect of GSC 140791 showing ribs, with posterior aspect of decorticated ventral valve GSC 140792 above, from C-4017, Trold Fiord Formation, Ellesmere Island, the upper specimen showing spine bases in umbonal row, as arrowed, x3. B, posterior aspect of small ventral valve GSC 140793, x3, from C-4036, ?Assistance Formation, Ellesmere Island.

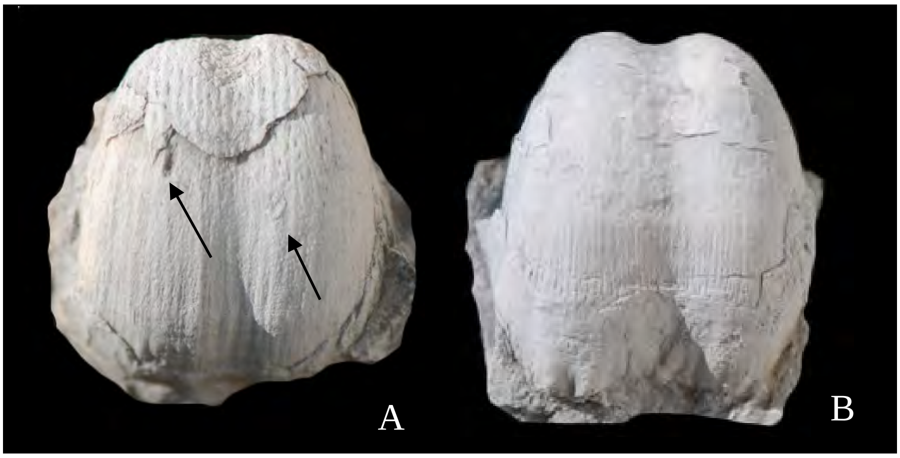

Fig. 119. *Liosella delicatula* (Dunbar). A, B, median and anterior aspects of ventral valve GSC 140794 with two strut spines arrowed from C-4017, Trold Fiord Formation, Ellesmere Island, x2, x4.

Holotype: Specimen figured by Dunbar (1955, pl. 5, fig. 23, 24) from northeast Greenland, OD.

Material: Two ventral valves from C-4036, possible Assistance Formation: five ventral valves and fragments from C-4017 and two ventral valves from C-4037, Trold Fiord Formation, Ellesmere Island.

Description: These specimens are subequilateral with deep sulcus, convex ears jutting out laterally, deep sulcus, and fine ribs, numbering eight to ten in 5mm. There are signs of umbonal slope spines and possibly a few spines along the hinge, and fine spines are moderately numerous over the valve, but cardinal spines are not preserved, except for a suggestion on one specimen from C-4037.

Dimensions in mm: C-4017

Width	Length	Height
18.5	16.5	10
22.5	19	14

Resemblances: These specimens are identified with *Liosotella delicatula* Dunbar, although they are larger than the types from Greenland. But they agree in overall proportions and sulcal definition and in what is known regarding the spines and the ribs.

Marginifera typica septentrionalis (not Tschernyschew, 1902) as figured by Tschernyschew & Stepanov (1916, pl. 7, fig. 1) from the Great Bear Cape Formation at Ellesmere Island is moderately similar, but inadequately known.

Subgenus ***Liosotellina*** n. subgen.

Derivation: Alteration from the genus name *Liosotella* Cooper.

Diagnosis: Small subelongate to weakly transverse shells with ventral spines over disc, row at base of umbonal slopes, rare or absent from hinge, some prominent ventral spines. No high marginal ridges. Distinguished by lack of distinct ventral sulcus. Given the geographic context, it is likely that no dorsal spines are present.

Type species: *Liosotellina multicostata* n. sp. from Trold Fiord Formation, Ellesmere Island, here designated.

Discussion: This species is distinguished from *Liosotella* and *Liosella* by the arched venter, without a sulcus. It otherwise is very close, as far as preserved, and has strut spines much as in these genera. There is no definite evidence on the nature of dorsal spination, but it is deemed likely that no spines were present.

Liosotellina multicostella n. sp.

Fig. 120 – 127

Derivation: multi – many, costella, narrow rib, Lat.

Diagnosis: Small shells with highly convex ventral valve, no sulcus, and wide ears with acute cardinal extremities. Ribs cover the ventral valve, and ventral spines lie in a row along the base of each umbonal slope, rare or absent from hinge and scattered over disc and trail. Strut spines vary in position. Commarginal rugae subdued over ventral valve, not strengthening close to hinge.

Holotype: Specimen GSC 140771 from C-4004, possibly Trold Fiord Formation of Ellesmere Island, Fig. 120C, D, here designated.

Material: Eleven ventral valves from C-4004, ?Trold Fiord or possibly Assistance Formation, Ellesmere Island.

Dimensions in mm: ventral valve, with ears intact

Width	Length	Height
29	18	12
15	10.5	8

Description: Specimens small and most are close in size to the smaller of the two measured specimens. They are transverse, highly arched, with incurved inconspicuous broad ventral umbo. The umbonal walls diverge at 115°, and the hinge is wide and at maximum width, with well formed convex ears, and obtuse cardinal extremities. There is no ventral sulcus, but convexity is reduced medianly in several specimens. The ventral valve apart from the ears is covered by costae, six to seven in 5mm anteriorly on the largest specimen, more posteriorly, and increase mostly by intercalation, but there are irregularities and rarely two costae fuse into one. Several central costae are prominent anteriorly in some ventral valves. In some specimens the trail is radially rugose, including a median rugation that looks like a narrow nasutation. The posterior disc is crossed by low closely spaced commarginal rugae, which

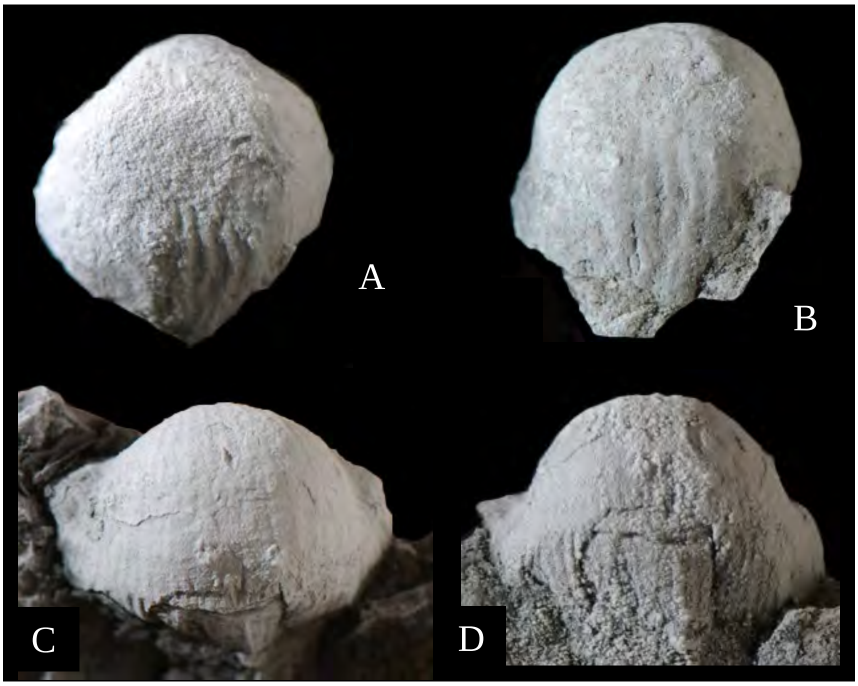

Fig. 120. *Liosotellina multicostella* n. sp., ventral valves A, B, GSC 140770; C, D, GSC 140771, holotype. From C-4004, Trold Fiord Formation, x3.

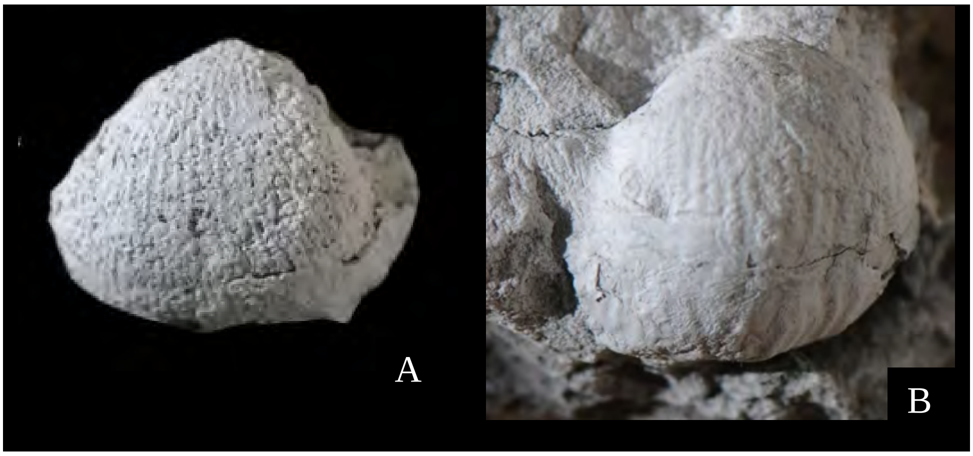

Fig. 121. *Liosotellina multicostella* n. sp. A, GSC 140776. B, 140774. Ventral valves from C-4004, ?Trold Fiord Formation, x3.

strengthen laterally to cover much of the ventral ears, except near the hinge. They are not conspicuous just in front of the hinge. Anteriorly and over the trial the rugae become more subdued. A very few and scattered spines may appear along the hinge, not forming a regular row, and umbonal slope formed by large spines lying in a well spaced row along the base of the ventral umbonal slopes inside the ears. Small spines similar to the hinge spines emerge from costal crests over the disc and trail, without being strong, and not particularly numerous, although in one individual they lie in a clump over the umbonal slope in front of the ear. Others show three or four finer spines in an anterior row. In some cases there is a degree of asymmetry. Thick and erect spines, here called strut spines, occur in varying patterns over each specimen. Typically, a pair emerges from close to the depression between umbonal slope and ear, and one or usually two pairs lie on the anterior flanks. Some individuals have a median posterior prominent spine, others have two pairs placed well forward each side of the shell.

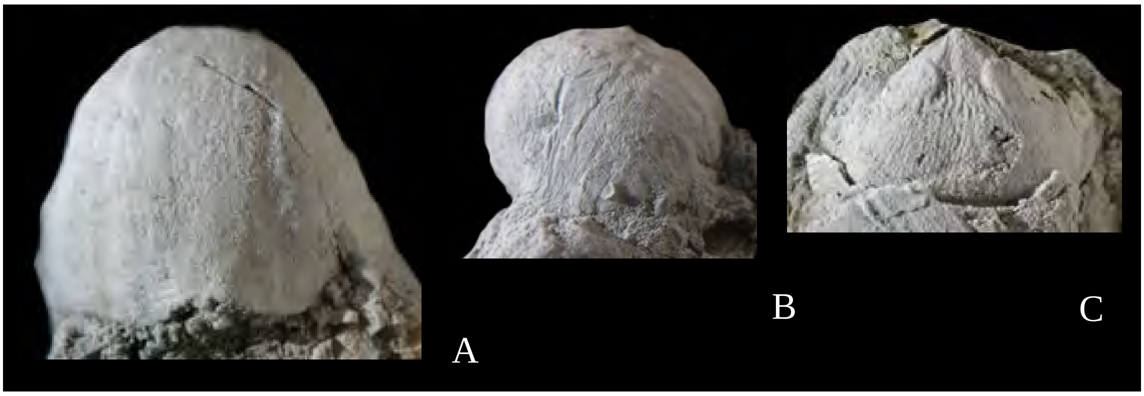

Fig. 122. *Liosotellina multicostella* n. sp., ventral valves from C-4004, ?Trold Fiord Formation. A, anterior aspect of GSC 140772, x3. B, lateral aspect of GSC 140774, x2. C, ventral internal mould, GSC 140774, x2.

The ventral adductor scars (Fig. 122C) are each comparatively smooth and tear-shaped, lying on a narrow platform, which is divided by a slender and low myophragm. Diductor impressions are shallow and oval and lie a little in front to each side. Both sets of scars bear erratic short ridges, rather than the deep longitudinal grooves

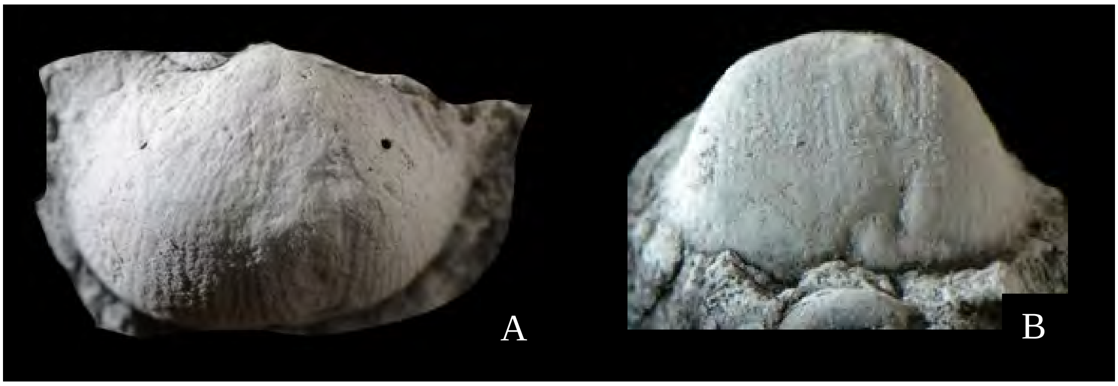

Fig. 123. *Liosotellina multicostella* n. sp. A, ventral valve GSC 140775 from C-4004, Trold Fiord Formation, x2, posterior and anterior ventral aspects.

typical of the arrangement in many species. The posterior floor is smooth and most of the floor bears short aligned radiating pits and short grooves, but there is no trace of a marginal ridge.

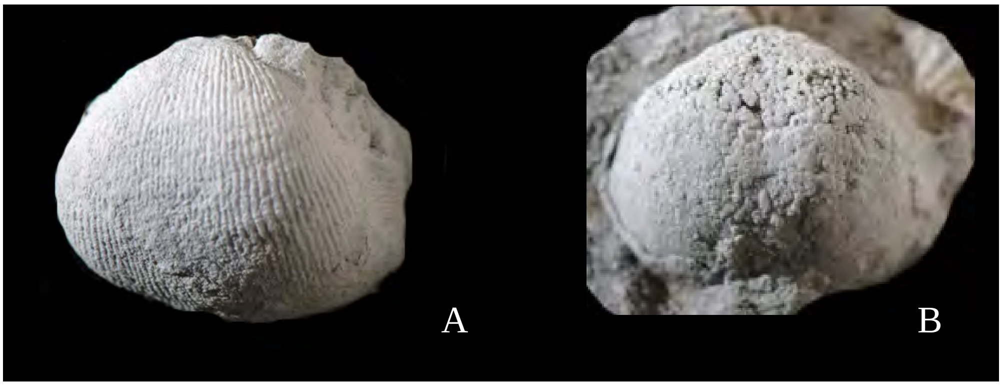

Fig. 124. *Liosotellina multicostella* n. sp. Ventral valves from C-4004, Trold Fiord Formation. A, GSC 140777 x3. B, GSC 140778, worn specimen x2.

Resemblances: This species is distinguished by the lack of a distinct sulcus, most individuals being rounded even across the mid-line. In shape and lack of sulcus, the specimens are moderately like *Liosotella hemisphaerica* Dunbar (1955, p. 74, pl. 4, fig. 1-21) from northeast Greenland, but ribbing is fainter posteriorly and slightly broader in front in the Greenland specimens. These Dunbar specimens have no sign of ventral hinge spines apart from rare examples (Dunbar 1955, pl. 4, fig. 4), but display a row of spines along the ventral umbonal slopes, as well as scattered ventral disc spines, and a few scattered sturdy spines, not clearly akin to the strut spines of the present species. Dunbar's species may prove to be allied to *Haydenella* Reed, as discussed below.

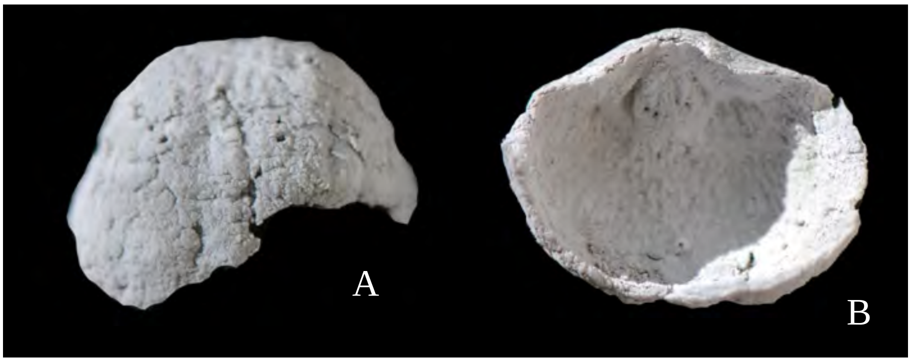

Fig. 125. *Liosotellina multicostella* n. sp. A, B, ventral and internal aspects of ventral valve GSC 140779 from C-4004, Trold Fiord Formation, x3.

In the swollen venter, the specimens approach the genus *Kozlowskia* Fredericks, 1933. This genus has a hinge row of ventral spines, but no row along the base of the ventral umbonal slopes, which does not accord with the spine detail for the present form. None of the numerous species described as *Paucispinifera* from the Glass

Mountains in Texas by Cooper & Grant (1975) come close in shape or in lack of sulcus, apart from a scattering of rare individuals, such as a few specimens classed in *Paucispinifera quadrata* Cooper & Grant. Individuals amongst different species do show some irregularity in the distribution of strut spines.

In various respects, the present species is marginiferid in shape and lack of sulcus. Spines may be strong over the venter, and there is ribbing, as revealed in Waterhouse (2013, pp. 93-101) to be found in some marginiferid genera world-wide. But unlike members of that family, there is no sign of marginal ridges, and the strut spines are strongly developed in the Canadian form.

Tribe **RETIMARGINIFERINI** Shi & Waterhouse, 1996

Genus ***Retimarginifera*** Waterhouse, 1970b

Diagnosis: Transverse with hinge at maximum width, ornament reticulate, ribs over shell, and commarginal rugae regular and strong over disc, six strut spines, involving pair on ears and two pairs over venter. Marginal ridge around posterior and lateral margins.

Type species: *Retimarginifera perforata* Waterhouse from Byro Group (upper Artinskian) of Western Australia, OD.

Discussion: Brunton et al. (2000, p. 447) allocated an age range of Artinskian-Kungurian to the genus, but material is known from at least Sakmarian to Roadian (Waterhouse 2013, p. 316). The genus, originally named for a species from Western Australia, has been reported from a high diversity fauna in the Khao Phrik limestone (Roadian) of Thailand by Grant (1976) and is represented widely in the Early Permian faunas of Arctic Russia and Canada.

Retimarginifera? sp.

Fig. 126

Description: A ventral valve from JBW 631, Takhandit Formation of Yukon Territory is 30mm wide, with hinge at maximum width, 15.5mm long and 11mm high. Ornament is reticulate, with well defined radial costae over the disc and trail, and firm commarginal rugae over the disc, and fine erect spines lie over the disc and along the hinge. But there are no clearly developed strut spines, so that the identification requires consolidation.

Fig. 126. *Retimarginifera*? sp., ventral valve UQF 140803 from JBW 631, Takhandit Formation, x2.

Resemblances: This specimen is moderately like the ventral valve figured as *Uraloproductus* sp. by Shi & Waterhouse (1996, p. 72, pl. 6, fig. 43, text-fig. 25B) from the Eog Zone of Late Sakmarian age in the Jungle Creek Formation in the Yukon Territory, a species with strut spines. *Uraloproductus* Ustritsky, 1971, considered to be a synonym of *Retimarginifera* by Waterhouse (2013, p. 456), was reported from what is now the *Dyoros modestus*

Zone of the Richardson Mountains by Bamber & Waterhouse (1971, pl. 21, fig. 13). All of these specimens are incompletely preserved, and too few in number to allow adequate comparison between the scattered and rare individuals that are available.

On the genus ***Haydenella***, Reed, 1944

Diagnosis: Small gently inflated shells with closely spaced and often fine radial ribbing, commarginal rugae fine, may be strong near ventral hinge, spines reported as occurring along hinge, form prominent row at base of ventral slopes, may develop strong outermost spine, presence of dorsal spines uncertain, though reported in type species.

Type species: *Productus kiangsiensis* Kayser, 1883, p. 185 from Lopingian of China, OD.

Discussion: No member of this genus has yet been found in Canada, but it is discussed here because of its reported occurrences in Greenland and Spitsbergen, and closeness in some of its attributes to *Liosotella, Liosella* and *Liosotellina*. The genus has been discussed by Muir-Wood & Cooper (1960) and other authors, with a summary of previous illustrations gathered by Shen (2017, p. 691, pl. P17, fig. 6-14), which show a gently convex ventral valve with light and closely spaced radial ribs, no sulcus, and commarginal rugae emphasized near the hinge. In some respects, the specimens approach *Liosotellina*, but have finer ribs, stronger commarginal rugae near the hinge, and crtically lack strut spines from the ventral disc and trail. The row of spines at the base of the umbonal slopes is well developed. Shen (2017) made two important observations. He recorded a row of ventral hinge spines, and stated that dorsal spines were developed. Such are suggested in a figure of a Salt Range specimen ascribed to the type species by Muir-Wood & Cooper (1960, pl. 65, fig. 13), which also shows the umbonal slope row. The Salt Range is no satisfactory substitute for China, even though Shen (2017, caption to pl. P 17) called this the holotype. He more acceptably also indicated a Kayser specimen as lectotype, for the same taxon. For another Salt Range species, *Productus tumida,* Waagen (1884, p. 703) recorded “not a trace” of dorsal spines. Hinge spines are seldom visible on any of the figured specimens, but I observed rare ventral hinge spines in *Productus vihiana* Diener (1915, pl. 8, fig. 12a, GSI 11151), on the types kept at the Geological Survey of India, Kolkata. A number of specimens have been identified with *Haydenella kiangsiensis* by various Chinese authorities, but none are very well preserved or illuminating. On the other hand, a well preserved specimen was illustrated from the Wuchiapingian fauna of Hydra, Greece, by Shen & Clapham (2009, p. 721, pl. 1, fig. 28, pl. 2, fig. 1), with no mention of ventral hinge spines, and a recorded absence of dorsal spines. Of interest in this specimen is the large spine at the outer end of the umbonal slope row, shown in the figure, and recalling the spine seen in *Anemonaria robusta* n. sp. (see Fig. 105A, p. 136).

In a study of brachiopods from the Pamirs, Grunt in Grunt & Dmitriev (1973, p. 111, pl. 8, fig. 6) recorded *Haydenella tumida*, and added a new species *H. dutkevichi* (1973, p. 110, pl. 8, fig. 7, 8, text-fig. 24), both of Djulfian (=Wuchiapingian) age. Grant (1976, p. 159) described a species of *Haydenella* from Thailand with a ventral row of hinge spines and umbonal slope row. He denied the presence of any dorsal spines, and declared that the cardinal process indicated linoproductide affinities, pointing also to material identified as *H. salinaria* Reed from the Amb Formation of lower Guadalupian age in the Salt Range, much older than the type species. Various forms were reported for Armenia in Ruzencev & Sarytcheva (1965) and several occurrences were recorded from South Primoyre by Licharew & Kotlyar (1978), including *H. dutkevichi* with *Parafusulina stricta* in the Chandalaz Suite (pl. 12, fig. 16-18), *H. tumida* (pl. 20, fig. 2, 3). *H. gefoensis* (Licharew) (pl. 20, fig. 4-6), and *H. khasorensis* Reed (pl. 20, fig. 7, 8) from the same suite with *Metadoliolina lepida,* in faunas deemed to be of Capitanian age.

The understanding of *Haydenella* gains significance for the Arctic Permian faunas through the identification of a Spitsbergen species described as *Productus wilczeki* Toula, which had been identified as *Haydenella* by Nakamura et al. (1992), and has been regarded as latest Permian by Shen (2016). Some clarification is provided in by Gobbett (1964). Gobbett considered that Toula had incorporated two species in his taxon called *wilczeki*, and judged that the ventral valve figured by Toula (1875a, p. 141, pl. 1, fig. 6a, b, d) belonged to *Liosotella*? *robertiana* (Koninck, 1850, p. 637, fig. 4), described from Bellsund, Spitsbergen, and reinforced by further but uncertain material from Hornsund, reported in Gobbett (1964, p. 67). The generic position was regarded as open to question by Gobbett. This author regarded the dorsal valve of *Productus wilczeki* Toula (1875a, p. 141, pl. 1, fig. 6c) as belonging to a different genus, distinguished by its more complex ribbing, and pointed to a further dorsal valve from Spitsbergen, described by Frebold (1937, p. 37, pl. 10, fig. 6, 6a). According to Gobbett (1964), a ventral valve identified by Frebold appeared to have similar ornament, and displayed a long spine emerging from the base of the umbonal slope, which reads somewhat like a spine described for *Haydenella* at Hydra, Greece, by Shen & Clapham (2009), and like that figured for *Anemonaria robusta* as in Fig. 105A herein. Gobbett (1964, pp. 66, 67) treated the species as belonging possibly to Marginiferidae, but could not assign a genus. The suggestion by Nakamura et al. (1992) that the species belongs to *Haydenella* Reed, 1944 certainly appears feasible, although some detail for *wilczeki* remains obscure.

Shen (2017, pp. 691, 692) synonymized a number of genera with *Haydenella*, including *Chianella* Waterhouse, ?*Planihaydenella* Chang*, Longyania* Zhu, and *Pseudohaydenella* Liang. But the types were not refigured (preferably by new illustrations) in Shen (2017) and it is by no means clear that the various type specimens show the same pattern of radial ribs, or hinge spines, or umbonal slope row of spines, with or without a large lateral spine, or dorsal spines. Those features need first to be ascertained and illustrated to justify Shen's synonymy.

For *Chianella*, as shown by Chen & Shi (2006, pl. 14, fig. 1-24) and Waterhouse (2013, Fig. 15.13, p. 322), there are obvious differences, in the way the ventral ribs branch, and in the presence of several rows of spines over the lower ventral umbonal slopes. No dorsal spines are present. *Haydenella* has finer and less branching ribs, and has only one row of spines along the ventral umbonal slopes, constituting a significant difference, like that between *Kutorginella* and *Thamnosia*. *Haydenella* allegedly has dorsal spines, unlike *Chianella*. As Chen & Shi (2006) noted, internal morphology remains to be clarified, and they noted possible similarities between *Chianella* and both *Longyania* and *Pseudohaydenella*. The species *wilczeki* from Spitsbergen thus needs to be far better known than at present, and indeed its branching strong ribs suggest a possible relationship to *Chianella* rather than *Haydenella*. In our present state of knowledge, it would seem possible that several genera are involved, with and without hinge spines, without or without dorsal spines, with or without a major lateral spine. These questions require close scrutiny of the type material of the taxa concerned, with adequate illustrations of the critical morphologies, rather than the reproductions of earlier figures, quarantined by unwarranted and totally anti-scientific claims of copyright!

The family position is certainly of interest. The genus was placed as a member of Chonetellinae Licharew, 1960 in the *Revised Brachiopod Treatise*. Many aspects of the spine distribution are close to those of Paucispiniferinae Muir-Wood & Cooper, 1960, and such a position finds support from the observation by Grant (1976) that the cardinal process was linoproductid (as in Paucispiniferinae). On the other hand there are no strut spines – except for a prominent spine at the outer end of the umbonal slope row.

Family **ANIDANTHUSIDAE** (**ANIDANTHIDAE**) Waterhouse, 1968a

Subfamily **ANIDANTHUSINAE** (**ANIDANTHINAE**) Waterhouse, 1968a

Diagnosis: Well defined costellae, hinge spines moderately developed, visceral disc and trail spines inconspicuous as a rule, no dorsal spines, apart from one exceptional genus *Mongolousia* Manankov, 2008. Dorsal valve lamellate to varying degree.

Tribe **MEGOUSIAINI (MEGOUSIINI**) Waterhouse, 2018a

Diagnosis: Ears large, project laterally and may then curve and twist forward, usually bifid. May be secondarily lost.

Discussion: Genera include *Megousia* Muir-Wood & Cooper, *leptosa* Waterhouse, referred in error to *Kuvelousia* and *Mongousia* Manankov. Members are restricted to the northern paleohemisphere.

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

Diagnosis: Costellate shells with large dorsal ears extending forward, and may be twisted. Dorsal valve concave.

Type species: *Megousia auriculata* Muir-Wood & Cooper, 1960 , p. 309 from Word Formation, United States, OD.

Megousia tortus n. sp.

Fig. 127 – 131

1971 *Kuvelousia* sp. Bamber & Waterhouse, p. 178, pl. 21, fig. 10-12.

Derivation: tortus – twist, Lat.

Diagnosis: Medium size, subelongate, swollen ventral valve with slender anterior sulcus, moderately fine ribs.

Holotype: GSC 27030 as figured by Bamber & Waterhouse (1971, pl. 21, fig. 10) and here as Fig. 131, from GSC loc. 53823, unnamed Permian sandstone unit, *Dyoros modestus* Zone, McDougall Pass, north Yukon Territory, here designated.

Material: Five ventral valves and two dorsal valves from GSC loc. 53823. Five ventral valves and nine dorsal valves from GSC loc. 53846 and five mature and one juvenile ventral valve and three dorsal valves from GSC loc. 53848, unnamed sandstone, *Dyoros modestus* Zone, McDougall Pass, Richardson Mountains, Yukon Territory.

Description: Ventral umbo only slightly extended over hinge, incurved, with umbonal angle of 90^{o} to 95^{o}, hinge at maximum width and ears slightly extended with bifid outer part (Fig. 128C). Very shallow sulcus anteriorly. Six to eight costellae occur in 5mm anteriorly. Increase as a rule by intercalation, though in some instances the new costella starts at a tiny growth step. Row of ten to twelve spines emerge from hinge, outer two or three spines may be relatively strong. In one specimen the spines emerge from the inner side of the hinge. The hinge itself is minutely crenulate. Ventral valves from C-3995 represent the species at an early growth stage. Dorsal ears are ornamented by costellae parallel to the anterior margin of ears, forming an abrupt transition with the disc costellae that are more strongly defined and raised, and radiate forwards at a higher angle over the disc. The dorsal costellae increase by branching. They are crossed posteriorly by a few very subdued lamellae, and at the anterior margin lamellae overlap

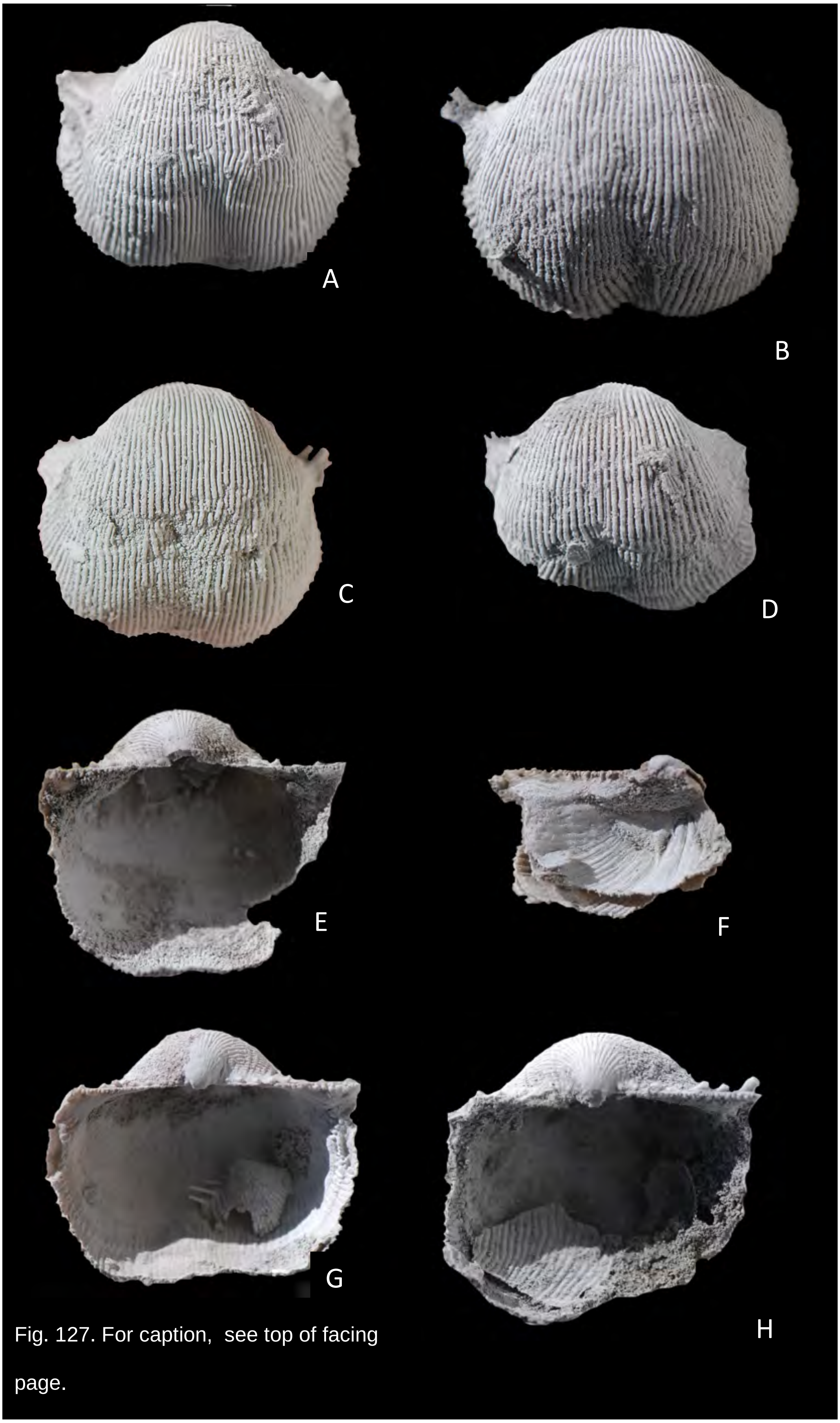

Fig. 127. For caption, see top of facing page.

Fig. 127. *Megousia tortus* n. sp. A, G, external and internal aspects of ventral valve GSC 140805. B, H, external and internal aspects of ventral valve GSC 140806. C, ventral valve GSC 140804. D, ventral valve GSC 140808. E, ventral interior GSC 140809. F, fragment GSC 141010 showing ventral interior. Specimens x2 from GSC loc. 53846**,** unnamed sandstone, McDougall Pass, Richardson Mountains, Yukon Territory.

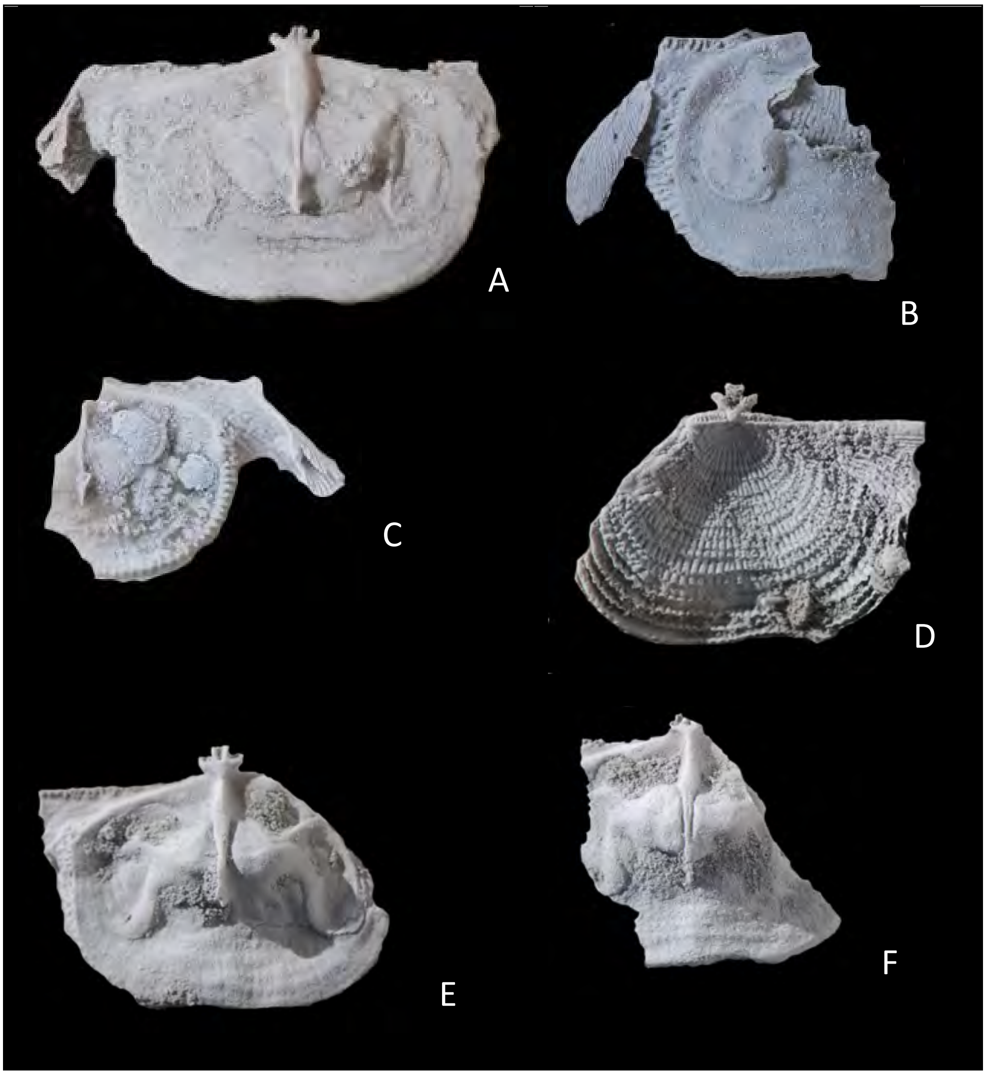

Fig. 128. *Megousia tortus* n. sp., dorsal internal moulds. A, dorsal internal mould, GSC 140811. B, dorsal internal mould, GSC 140812. C, dorsal internal mould, GSC 140813. Specimens x2, and show twisted dorsal ear. D, E, external and internal aspects, GSC 140814, x2. F, dorsal interior GSC 140815. From GSC loc. 53848, unnamed sandstone, McDougall Pass, Richardson Mountains, Yukon Territory, x2.

Fig. 129. *Megousia tortus* n. sp., internal aspect of ventral valve GSC 140804 x4, from GSC loc. 53846**,** unnamed sandstone, McDougall Pass, Richardson Mountains, Yukon Territory. See Fig. 127C.

and form a slightly thickened margin, without constituting a solid wedge. The hinge in small specimens is smooth, and in larger specimens, approaching maturity, becomes diversified by well spaced and low crenulations.

Details of the ventral interior are obscure. The adductor scars are raised on a low elongate platform divided by a groove, and diductor scars are large, oval and weakly impressed. In small specimens judged to be immature and at early maturity, the costellae are visible in the interior, showing that the shell was thin in early growth stages.

In the most mature dorsal valve from GSC loc. 53848, the cardinal process is low with four lobes, and the median septum continues forward as a thick ridge, narrowing between the adductors, and extending to a little beyond mid-length. The adductor scars are raised in two pairs, side by side, broad and smooth, and there is a broad low hinge ridge and a broad ridge around the anterior margin. In another specimen, the inner adductors are slender and elongate, with a subrounded lateral and larger pair placed well forward. The outer pair is more posteriorly placed in another specimen. The inner shell is smooth in all mature specimens, whereas in a small specimen 12mm wide, the interior is dominated by costellae from the exterior. Compared with that of the mature specimens, the cardinal process is more bilobed and narrow, the median septum broad and high behind small slightly raised smooth adductor scars, with slender septum extending forward, and no hinge ridge or marginal ridge. The hinge ridge and marginal ridge appear in shells over 20mm wide. In the best preserved specimen, the brachial shields lie each side, small, rimmed by a ridge that appears to arise from the median septum, extends laterally behind the adductor scars, and sweeps around in the usual arc and leads as a low ridge back to the anterior end of the median septum. In front are

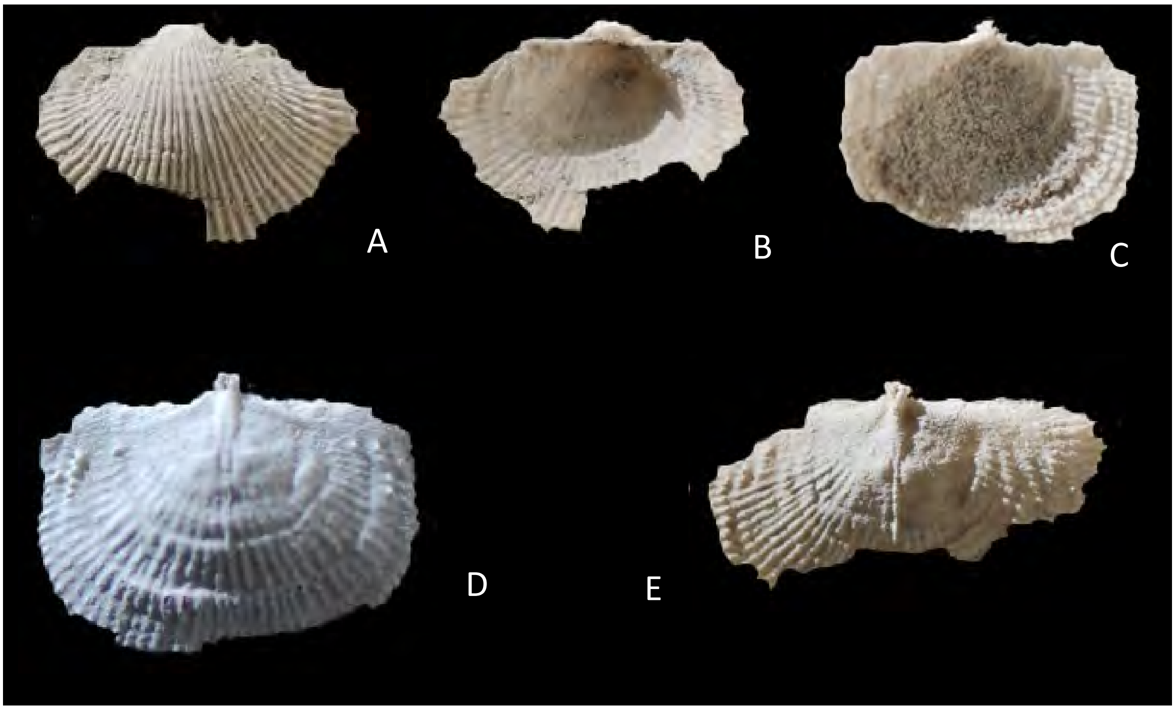

Fig. 130. *Megousia tortus* n. sp., immature valves. A, B, ventral exterior and interior of ventral valve GSC 140816, x4. C, D, external and internal aspects of dorsal valve, GSC 140817 x3, x4. E, dorsal internal mould, GSC 140818, x4. From GSC loc. 53848, unnamed sandstone, McDougall Pass, Richardson Mountains, Yukon Territory, x2.

elongate short ridges and tubercles. The hinge ridge is well developed in mature specimens and continues into the marginal ridge, with the shell ending abruptly at the low lightly thickened anterior face. All the mature specimens have well developed lamellae around the anterior margin.

Resemblances: This species is distinguished from *Kuvelousia sphiva* Waterhouse, as described below, by its twisted dorsal ears, overall thinner shell, especially in the dorsal valve, and much less crenulate hinge. Species of *Megousia*, described in abundance from the Glass Mountains of Texas by Cooper & Grant (1975), include species with twisted ears, though not in all specimens, and an only slightly thickened dorsal valve with anterior lamellae as in the present species, thin shell and finely rather than coarsely crenulate hinge. Most of the species have a disc that is more transverse than the present species. Individuals of *M. umbonata* Cooper & Grant (1975, p. 1199, pl. 447, fig. 40-43) from the Cathedral Mountain Formation of Kungurian age and rather more transverse specimens, including some from the Road Canyon Formation (pl. 452, fig. 6-18) of Roadian age are close in shape, with lamellate dorsal anterior, but the ears would appear to have been broken short so that their full extent and nature are not known. Costellae number eleven to thirteen in 5mm. Some specimens of *M. definita* Cooper & Grant (1975, p. 1194, pl. 449, fig. 1-46) from the Willis Ranch Member of the Word Formation are close, and have twisted ears and ten to twelve costellae anteriorly in 5mm. Many of the specimens are transverse, unlike any individual of the present suite. *M.*

auriculata Muir-Wood & Cooper, 1960, as figured by Cooper & Grant (1975, pl. 450, 451, 452, fig. 19-28) from the Road Canyon Formation shows a number of specimens without a forward twist to the ears, and the species is much more transverse. Some individuals of the same species figured in Cooper & Grant (1975, pl. 452, fig. 19-25) from the same Road Canyon Formation do show twisted ears, to indicate that the authors regarded this feature as variable. Perhaps it will prove that there is one group with untwisted ears, one with variable ears, and one group with twisted ears. That remains an open question, and the closest in shape and twisted ears are *M. umbonata* and *M. definita*, leaving aside the more transverse individuals assigned to *umbonata*.

Several species were recorded from the Arctic Permian in Sarytcheva (1977a), and none show twisted ears, and most are more transverse than the Canadian species. *Megousia kolymaensis* (Licharew) of Sarytcheva (1977a, pl. 6, fig. 4, 5) from the Kolyma-Omolon massif is shaped somewhat like the present species, but no ears are preserved. The species assigned to *Productus kulikii* Fredericks, 1915 from Pai Hoi and reported from Taimyr and Spitsbergen has coarse ribs and is more transverse, with well formed row of ventral hinge spines. The thickened dorsal valve, as figured in Sarytcheva (1977a, Fig. 35), suggests that the species should be referred to *Kuvelousia*. Unfortunately, the nature of the dorsal ears is not clear.

Of anidanthids described by Gobbett (1964), only *Megousia harlandi* Gobbett, 1964, p. 111, pl. 13, fig. 16-22) from the Spirifer Limestone or Vøringen Member in Spitsbergen comes close in shape, but no ears are preserved, and the dorsal fold is low. This then remains a potential senior synonym, but better-preserved material must be uncovered and described, with figures illustrating the nature of the dorsal ears. The species has a similar longitudinal profile and anterior sulcus. The dorsal valve shows fewer commarginal laminae, and there are more spines over the region of the ventral umbo. Ifanova (1972, p. 114, pl. 5, fig. 1-14) regarded *harlandi* as a synonym of *Productus kulikii* Fredericks, 1915, pl. 4, fig 8-12, from Pai Hoi, Timan, and Petchora Basin, and considered to occur in the Taimyr Peninsula. The species was treated as of Upper Artinskian and Kungurian age, and is somewhat elongate with forward-pointing large dorsal ears and low dorsal fold.

The material recorded in Bamber & Waterhouse (1971), mentioned in the synonymy, came from what was called the *Lissochonetes* zone, now *Dyoros modestus* Zone, at GSC loc. 53823 in the Permian sandstone unit of the Richardson Mountains, and from GSC loc. 53834 in talus at section 116P-11 of the same area.

Fig. 131. *Megousia tortus* n. sp., internal aspect of dorsal valve, GSC 27030 holotype from GSC loc. 53848, *Dyoros modestus* Zone, North Richardson Mountains, x1. (Bamber & Waterhouse 1971).

Tribe Anidanthusini (Anidanthini) Waterhouse, 1968a

Genus ***Kuvelousia*** Waterhouse, 1968a

Diagnosis: Hinge row and scattered ventral spines, dorsal ears very large, and projecting forward, never twisted, dorsal valve wedge-shaped with short trail and strong laminae, hinge strongly denticulate.

Type species: *Kuvelousia sphiva* Waterhouse, 1968a, p. 1175 from Trold Fiord Formation (Wordian), Canadian Arctic, OD.

Kuvelousia sphiva Waterhouse, 1968a

Fig. 132 – 136

1968a *Kuvelousia sphiva* Waterhouse, p. 1115, pl. 154, fig. 11, 14-20, pl. 155, fig. 1-21, text-fig. 1, 3.
1971b *K. sphiva* – Waterhouse, p. 180, pl. 22, fig. 9.
1971 *K. sphiva* – Brabb & Grant, p. 15, pl. 2, fig. 1-4, 11, 25.
2000 *K. sphiva* – Brunton et al. p. 532, Fig. 369.1a-f.
2013 *K. sphiva* – Waterhouse, p. 326, Fig. 15.17.

Diagnosis: Large for genus, with deep ventral sulcus, no dorsal fold, strong ribs. Hinge denticulate, wedge-shaped dorsal valve.

Holotype: GSC 22910, figured in Waterhouse (1968a, pl. 154, fig. 11, 15, 17, pl. 155, fig. 12) and Brunton et al. (2000, Fig. 369.1a-c) from GSC 76029, Formation B, now Trold Fiord Formation, above the Assistance Formation at Cape Fortune, Cameron Island.

Additional material: One ventral valve from GSC loc. 76029, Cameron Island Three ventral valves from C-4005 and nine ventral valves from C-3997, probably Trold Fiord Formation, Ellesmere Island. Eight ventral valves from C-3395, and one specimen with valves conjoined from C-3996, one ventral valve from C-4020, four ventral valves from C-4034, Ellesmere Island, all from Trold Fiord Formation. Two ventral valves from C-3993, Degerböls Formation. One doubtful specimen from C-4019, Assistance Formation, Ellesmere Island.

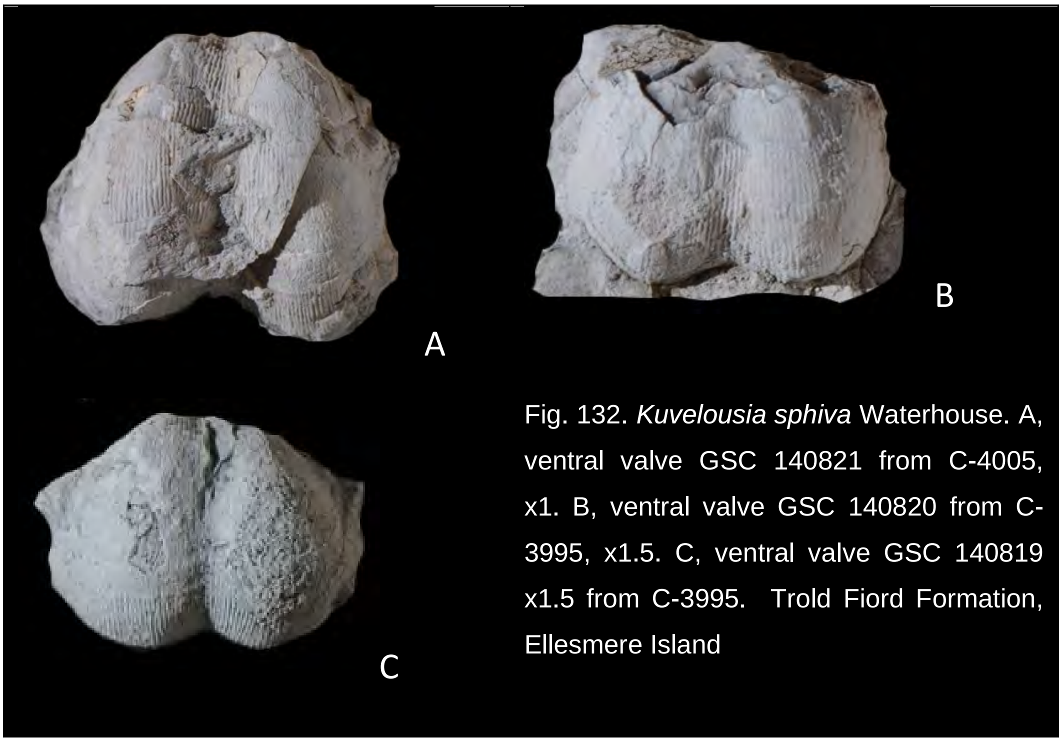

Fig. 132. *Kuvelousia sphiva* Waterhouse. A, ventral valve GSC 140821 from C-4005, x1. B, ventral valve GSC 140820 from C-3995, x1.5. C, ventral valve GSC 140819 x1.5 from C-3995. Trold Fiord Formation, Ellesmere Island

Description: The species is described in Waterhouse (1968a). The specimens from C-4005 and from C-3995 are large like those of the type material, whereas many of the specimens from other localities are much smaller. Dorsal valves are rare, and most are flatly concave without any sign of a median fold, but with shallow median sulcus. Only one (Fig. 133) shows a moderately well-preserved part of the dorsal ear, which extends far beyond the visceral disc, and bends at a low angle forward from the hinge after a brief interval.

Resemblances: This species is close to the Spitsbergen material described as *Productus weyprechti* Toula (1874, pl. 5, fig. 2, 3), with lectotype selected as fig. 2 by Gobbett (1964, p. 108) and amplified as *Megousia weyprechti* by Gobbett (1964, p. 107, pl. 12, fig. 27-29, pl. 13, fig. 1-6) from the Brachiopod Chert and Spirifer Limestone, and further by Sarytcheva (1977a, p. 63, pl. 6, fig. 1-3, Fig. 27-29), with additional references provided. I hesitate to synonymize *weyprechti* with *sphiva*, given the lack of opportunity to compare the two suites adequately, including the all-important nature of the dorsal ears and the nature of denticulation developed along the hinge, largely unknown for *weyprechti.* One possibly critical difference lies in the dorsal valve, which shows a definite median fold becoming broad anteriorly in *weyprechti.* There is no fold or only a very faint fold in the Canadian species. The Brachiopod Chert material assigned to *weyprechti* has a deep ventral sulcus slightly less developed near the umbonal tip, as figured by Gobbett (1964) and Sarytcheva (1977a) in providing more reliable figures than in other studies. In Brabb & Grant (1971, p. 15), it was stated that *weyprechti* was smaller, wider and more strongly costate, with a more variable sulcus, deep in some specimens, shallower in others. A specimen from the Assistance Formation appears to have a shallower sulcus posteriorly than in Trold Fiord or Degerböls specimens, so may not be *sphiva*. On the other hand, another ventral valve from possible Trold Fiord Formation at C-3997 on Ellesmere Island has a distinctly

Fig. 133. *Kuvelousia sphiva* Waterhouse, dorsal valve GSC 140823, exterior showing large ear, from C-3995, Trold Fiord Formation, Ellesmere Island, x2.

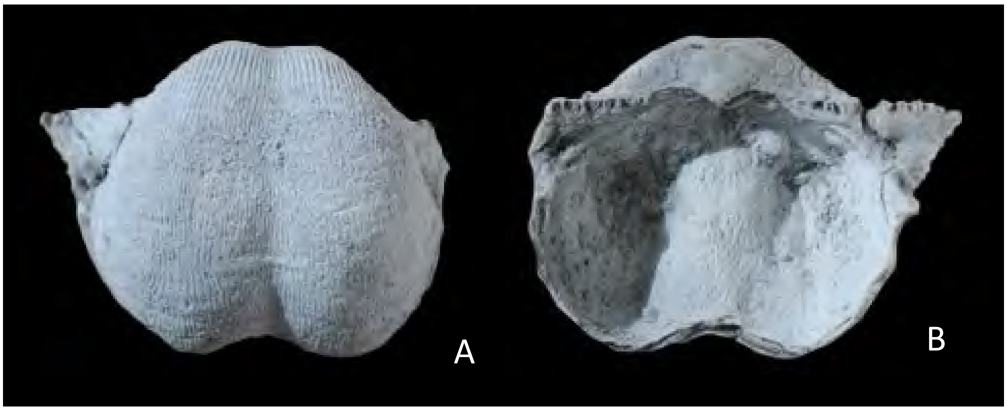

Fig. 134. *Kuvelousia sphiva* Waterhouse, external and internal aspects of ventral valve GSC 140825, from GSC loc. 76029, Trold Fiord Formation, Cameron Island, x1.5.

narrow and deep ventral sulcus (see Fig. 135). Type *sphiva* have some eight ribs in 5mm on the ventral valve, and Gobbett's specimens of *weyprechti* suggest eight to ten ribs in 5mm, like some specimens from the present suite. Gobbett (1964, p. 109) had described most of his material from the Brachiopod Chert, especially lower Brachiopod Chert, with occurrences in the lower Spirifer Limestone. Supposed *Kuvelousia weyprechti* of Angiolini & Long (2008, p. 91, Fig. 2K, L) from the Vøringen Member of Spitsbergen has more laminate dorsal valve without any median fold. *Productus svalbardensis* Frebold (1937, p. 5, fig. 1-5) was synonymized with *weyprechti* by Gobbett (1964), and has had no ears or dorsal valve described.

Fig. 135. *Kuvelousia sphiva* Waterhouse, internal ventral mould GSC 140822 from C-3997, possible Trold Fiord Formation, Ellesmere Island, x2. Note the deep sulcus.

Productus kulikii Fredericks, 1915, p. 30, pl. 4, fig. 8-12, is probably a related and slightly older species, with less prominent ventral sulcus and more elongate shell. Gobbett (1964, pl 13, fig. 13, fig. 7-15) suggested specimens from the Spirifer Limestone of Spitsbergen might belong to the species, and this was accepted by Ifanova (1972, p. 114, pl. 5, fig. 1-14). As noted on p. 158, Ifanova (1972) included *Megousia harlandi* Gobbett, 1964, pl. 13, fig. 16-22 from the same beds in synonymy, and also included in synonymy *P.* (*Productus*) *kolymaensis* Licharew, 1934b, p. 17, pl. 6, fig. 10, 12-116) and *Linoproductus auritus* Solomina (1957, p. 76, pl. 3, fig. 2, 3, 7).

Fig. 136. *Kuvelousia sphiva* Waterhouse, ventral valve GSC 140824, from C-4019. Assistance Formation, Ellesmere Island, x2.

Fig. 137. “*Kuvelousia*” *leptosa* (Waterhouse), now regarded as a megousiid, distinguished by its wedge-shaped dorsal valve, dorsal aspect of external mould, USNM 151591j, holotype, from Cornucopia Quadrangle, Oregon, x3. (Waterhouse 1968a).

Kuvelousia sphiva is readily distinguished from the Oregon species described as *K. leptosa* Waterhouse, 1968a, p. 1181 from the Early Permian of Oregon, United States, figured in Waterhouse (1968a, pl. 156, fig. 4, 9, 11, 12, 14, 15) and herein as Fig. 137. Denticles are developed along the hinge, finer than in type *Kuvelousia*, but unlike this and other genera, ventral spines are absent from the disc and trail, and unlike *Kuvelousia* and *Anidanthus*, the dorsal valve is not thickened into a wedge, and has a low broad fold with narrow crest. A moderately short trail is well developed. Further differences from type *Kuvelousia* were adduced by Waterhouse (1968a, p. 1182), but these appear of limited value, reflecting ecologic conditions. The dorsal valve has bifid ears. The upper ears project only moderately along the line of the hinge, and are matched by the ears of the ventral valve. The anterior ears are much larger and extend obliquely forward at a moderate angle, neither as laterally extended as in *Anidanthus* Whitehouse, 1928, nor as forward projecting as in many *Megousia* Muir-Wood & Cooper, 1960. Some specimens of *Megousia auriculata*, as figured by Cooper & Grant (1975, pl. 450, fig. 39 and pl. 451, fig. 49) also display bifid dorsal ears, and the Oregon species may be better transferred to *Megousia,* or better, a related genus.

Kuvelousia perpusillus n. sp.

Fig. 138 – 141

Derivation: perpusillus – small, Lat.

Diagnosis: Small transverse shells with very shallow sulcus and widely splayed dorsal ears. No commarginal growth stops or rugae on the dorsal valve, valve not thickened nor concave, no fold, and exceptional in lacking any extended trail.

Holotype: Specimen GSC 140827 from C-4022, Fig. 138B, from uncertain formation, possibly Degerböls Formation.

Material: Forty nine ventral valves, seven dorsal valves and two specimens with valves conjoined from C-4022, uncertain, possibly Degerböls Formation, Ellesmere Island. A small specimen with valves conjoined from GSC loc. 52755, Takhandit Formation, Sheep Mountain, Yukon Territory. A dorsal valve comes from C-4002, Assistance Formation, Ellesmere Island, together with two ventral valves that have a sulcus that is shallower than in Trold Fiord or Degerböls specimens of *Kuvelousia sphiva*.

Fig. 138. *Kuvelousia perpusillus* n. sp. A, ventral internal mould GSC 140826. B, ventral valve GSC 140827, holotype, shell preserved externally and showing hinge spines. Specimens from C-4022, Degerböls Formation?, Ellesmere Island, x2.

Description: These specimens are comparatively small and transverse, and the ventral sulcus is shallow posteriorly and ventral ears small. Dorsal valves are transverse, with no median fold or sulcus, and very large ears extending laterally with slight forward inclination. Ventral costae number twelve or so in 5mm posteriorly, and nine in 5mm near the anterior margin, and increase by intercalation. Dorsal costae may be as few as seven in 5mm at the anterior margin. The anterior ventral valve bears low commarginal rugae, and the dorsal valve has low erratic commarginal rugae or growth steps, and ends abruptly with a short geniculate trail and medianly retracted anterior margin. The

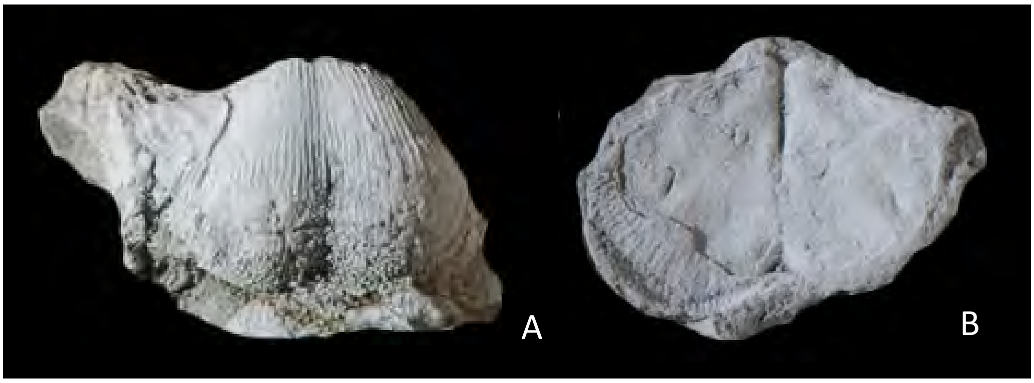

Fig. 139. *Kuvelousia perpusillus* n. sp. A, ventral valve GSC 140828 from C-4022, ?Degerböls Formation, Ellesmere Island, x2. B. Worn dorsal interior GSC 140827 from GSC loc. 52755, Takhandit Formation, Sheep Mountain, Yukon Territory, x2.

valve is not thickened. A row of spines lies along the ventral hinge and anterior small spines arise from the crest of some ribs, none conspicuous. Both valves are crossed by very fine radial growth increments.

Internally the ventral adductors are small and tear-shaped, and largely smooth, with gently impressed diductor scar to each side. The dorsal median septum is sturdy and extends past midlength, without reaching the anterior margin. Moderately small brachial shields lie laterally.

Fig. 140. *Kuvelousia perpusillus* n. sp. A, ventral valve GSC 140830. B, ventral valve GSC 140831 and dorsal valve GSC 140832. Specimens from C-4022, ?Degerböls Formation, Ellesmere Island, x2.

Resemblances: This species is unusual, and its generic position open to question. It has large dorsal ears moderately close to those of *Anidanthus, Anidanthia* and *Kuvelousia*, but the dorsal valve is without thickening, and so is closer to *Anidanthia* – or *Megousia*, though on the other hand both of these genera have a much more concave and lamellate dorsal valve. It is readily distinguished from *Kuvelousia sphiva* by its unthickened dorsal valve and virtually non-crenulate hinge, and has shallow ventral sulcus posteriorly, and dorsal exterior with low commarginal rugae or growth steps and shorter dorsal septum. It differs from *weyprechti* Toula in the lack of a dorsal fold, with other differences. There are some similarities to shells assigned to *Megousia kulikii*? by Gobbett (1964, pl. 13, fig. 7-15) from the Brachiopod Chert of Spitsbergen, and to *M. harlandi* Gobbett (1964, pl. 13, fig. 16-22) from the Spirifer

Fig. 141. *Kuvelousia perpusillus* n. sp., dorsal internal mould GSC 140833, showing large ear to right, from C-4022, ?Degerböls Formation, Ellesmere Island, x2.

Limestone, but these shells are more elongate with shallower posterior sulcus, and low dorsal median fold. Ifanova (1972, pl. 5) assigned these forms to *M. kulikii* Fredericks (1915), in recording material mostly from the upper Artinskian and Kungurian of the Petchora Basin and Pai Hoi.

Specimens from western Verchoyan that were figured as *Anidanthus boikovi* Stepanov by Abramov & Grigorieva (1988, p. 130, pl. 8, fig. 1-12) have typical anidanthid commarginal laminae and growth stops over the dorsal valve, and the dorsal median septum is short. This species has been widely reported from upper Cisuralian beds in Russia,

Subfamily **LIRARIAINAE** (**LIRARIINAE**) Waterhouse, 2013

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 and without spines. Ventral adductors smooth or deeply scored by longitudinal grooves.

Discussion: *Liraria* Cooper & Grant, 1975 from the 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, much like those of *Anidanthus*. 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, and a zygidium. Ventral adductor scars for *Liraria* were described by Cooper & Grant (1975) as small and located within a pit, and it was noted that 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, as indicated by the rest of their text.

Globiella Muir-Wood & Cooper, 1960 based on Kazanian material from Russia is a close ally, as a swollen shell with very fine ribs and slender spines, recorded below from Canadian outcrops. *Cimmeriella* Archbold in Archbold & Hogeboom, 2000, p. 101, type species *Productus foordi* Etheridge, 1903, as 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, and may be placed in Lirariinae. It was deemed to be a junior synonym of *Fusiproductus* Waterhouse, 1975, by Shen (2017, p. 720), but *Fusiproductus* has dorsal laminae (Diener 1915, pl. 6, fig. 19; Waterhouse 1966, 4, fig. 1). *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. The oldest known member of the subfamily so far known is *Poletaevia* Waterhouse (2013, p**.** 459), named for *Liraria paucispina* Carter & Poletaev, 1998, p. 133 from the late Bashkirian or early Moscovian Hare Fiord Formation of 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 ***Liraria*** Cooper & Grant, 1975

Diagnosis: Shells transverse, row of spines along hinge or just in front, few over venter, no dorsal spines. Rugae limited to dorsal valve and few in number.

Type species: *Liraria lirata* Cooper & Grant, 1975, p. 1156 from Bone Spring Formation (mid-Cisuralian), Texas, OD.

Discussion: As well as the occurrences in United States and Canada, ventral valves ascribed by Licharew & Kotlyar (1978, pl. 14, fig. 11, 12) to *Asperlinus asperulus* (Waagen) from the upper Barabash horizon of west Primoyre look as though they belonged to *Liraria*.

Liraria borealis n. sp.

Fig. 142

Derivation: borealis – north, Lat.

Diagnosis: Transverse with narrow ventral umbo and large convex ears. Costae moderately well differentiated.

Holotype: Specimen GSC 140834 from C-4034, Trold Fiord Formation, figured in Fig. 142A, B, C, here designated.

Material: Some fifteen small ventral valves and a larger ventral valve from C-4034, Trold Fiord Formation, Ellesmere Island.

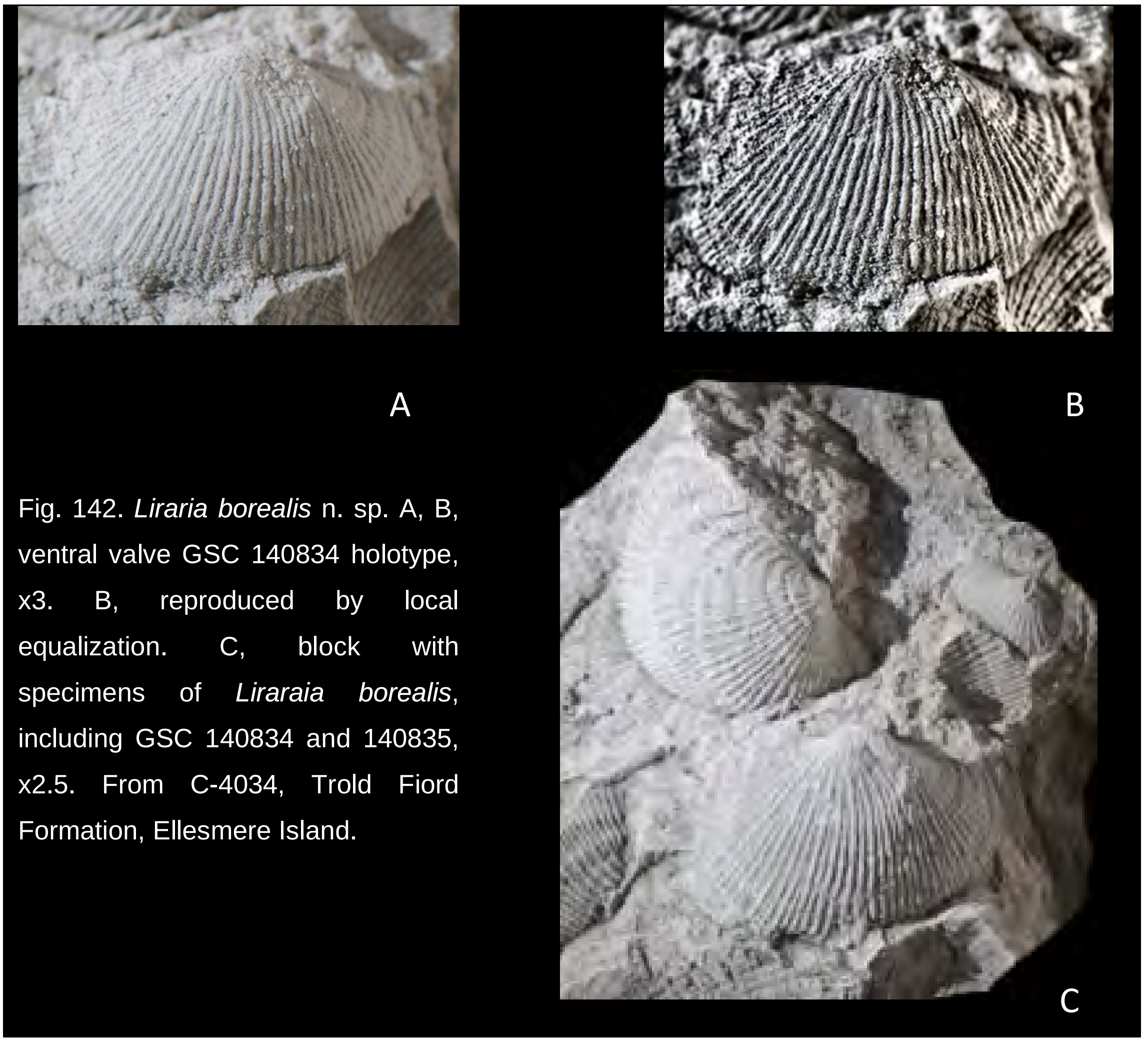

Fig. 142. *Liraria borealis* n. sp. A, B, ventral valve GSC 140834 holotype, x3. B, reproduced by local equalization. C, block with specimens of *Liraraia borealis*, including GSC 140834 and 140835, x2.5. From C-4034, Trold Fiord Formation, Ellesmere Island.

Description: The specimens are transverse, a moderately complete specimen measuring 15.5mm wide and 9.5mm long, and 5mm high. The ventral umbo protrudes only slightly over the hinge and is little incurved. The hinge is wide, and cardinal extremities abruptly obtuse, with angle of 110º, but gently obtuse in earlier growth phases. Ears are large but poorly distinguished from the venter, and are gently convex. Low rugae are developed anteriorly on some specimens. The distinctive ribs are differentiated into three orders, increasing by intercalation. The ribs count at fourteen in 5mm posteriorly, and vary from as few as six to seven to twelve in 5mm anteriorly. Fine spines arise from the crests of costellae, some arising just in front of a low growth step or lamellation. No spines are visible along the hinge in the small specimens. But a fragment of a much larger specimen that was at least 36mm wide and 22mm long with stronger ribs shows that spines developed in a row close to the outer hinge, as well as being scattered and well spaced over the posterior disc and umbonal slopes. A few spines display slightly elongated bases.

Resemblances: Compared with *Liraria lirata* Cooper & Grant (1975, pl. 434, fig. 9-30), the present specimens are close in shape, but have narrow ventral umbo and more differentiated costellae. Hinge spines lie along the outer hinge, as also suggested for *L. lirata* (cf. Cooper & Grant, 1975, pl. 434, fig. 9, 15). The Canadian specimens are younger than the type species, and no other species in the genus has yet been reliably reported. Partly for this reason, and even though the dorsal valve is not known, the species is named, and the ventral valve is distinctive. The ventral valves from the upper Barabash Suite of Primoyre that were ascribed to *Asperlinus asperulus* [not Waagen] in Licharew & Kotlyar (1978) are moderately close, but have more fine rugae near the hinge.

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

Diagnosis: Hemispherical to slightly elongate shells of medium size, highly convex ventral valve, ears small, umbo small and incurved, hinge wide. Both valves densely costellate, spines limited to ventral valve, in row along hinge and rare over remainder of ventral valve, either fine or slightly wider than the ribs. Dorsal valve weakly rugose, but without overlapping lamellae.

Type species: *Productus hemisphaerium* Kutorga, 1844, p. 99 from Kazanian (Wordian) of Orenburg, Russia, OD.

Globiella hemisphaerium (Kutorga, 1844)

Fig. 143, 144A, C

1844 *Productus hemisphaerium* Kutorga, p. 96, pl. 10, fig. 2.
1894 *P. hemisphaerium* – Netschajew, p. 145 (with additional synonymy).
1911 *P. hemisphaerium* – Netschajew, p. 140, pl. 1, fig. 1-4, 6, 8, 9, pl. 2, fig. 1-4, pl. 4, fig. 3.
1960 *Globiella hemisphaerium* – Muir-Wood & Cooper, p. 304, pl. 115, fig. 1-10.
1962 *Stepanoviella hemisphaerium* – Grigorieva, p. 42, pl. 9, fig. 1, pl. 13, fig. 6-9.
1965 *G. hemisphaerium* – Muir-Wood, p. 501, Fig. 574.1.
1970a *S. hemisphaerium* – Waterhouse, pl. 14, fig. 9-14.
1977a: *G. hemisphaerium* – Grigorieva *in* Sarytcheva, p. 164, pl. 27, fig. 9.
2000 *G. hemisphaerium* – Brunton et al. p. 539, Fig. 377a-g.

Diagnosis: Ventral valve subelongate and highly inflated, massive incurved umbo, arched venter, very fine ribs and low commarginal rugae, especially well developed over the dorsal valve, fine ventral spines.

Holotype (by monotypy): Sole specimen figured by Kutorga (1844) from Kazanian of Russia.

Material: Six ventral valves and two dorsal valves with part of ventral valve attached from C-12. No detail for this locality has been supplied, but the matrix suggests possible Trold Fiord Formation. Two ventral valves from C-3995, Trold Fiord Formation, Ellesmere Island.

Description: Shells from C-12 are small and incomplete, with the umbo and hinge poorly exposed. The ventral umbo is massive and strongly incurved, and the posterior walls diverge in most specimens at 60º to 70º, and at 80º in one specimen. A small ventral valve is 21mm long, 24mm long and 13mm high. There is no sulcus, and specimens are comparatively high for their small size. Ornament is composed of weakly differentiated fine ribs, some fifteen in 5mm, and regular very low commarginal rugae, which strengthen laterally and around the anterior margin of larger specimens, and are more pronounced over the trail of the ventral valve, and strong over the entire dorsal valve. Spines are scattered over the venter and trail, and are fine without noticeably prolonged bases, and there is no sign of spine tunnels.

The specimens from C-3995 have ribs as fine as those on the specimens from C-12, but the specimens are preserved as internal moulds, and the specimens show regular commarginal rugae and the fine ribs are slightly differentiated. Spines are slightly stronger than those from C-12.

Resemblances: The Canadian specimens agree in shape and ornament with *Globiella hemisphaerium* (Kutorga), especially well figured by Netschajew (1911), with supporting figures provided by Grigorieva (1962). Good figures were also provided by Muir-Wood & Cooper (1960), but they did not show how elongate the specimens are, and this was remedied in Brunton et al. (2000). The species is close to other species recognized by Netschajew (1894, 1911), as tabulated in Muir-Wood & Cooper (1960), but are more elongate with swollen ventral valve.

These specimens are smaller and narrower than *Magniplicatina* sp. (see p. 208), and the rugae are more regular. *Cancrinella* sp. undet. of Brabb & Grant (1971, p. 14, pl. 1, fig. 31, 32) from the sandstone unit of the type Takhandit Formation in Alaska is transverse rather than elongate, and so unlikely to be related, but little is known of the Alaskan material. The other specimen identified as *Cancrinella* sp. undet. in Brabb & Grant (1971, pl. 2, fig. 18, 19) is reassigned to *Cameronovia*. The material differs from the Canadian specimens assigned to *Cancrinella arctica*

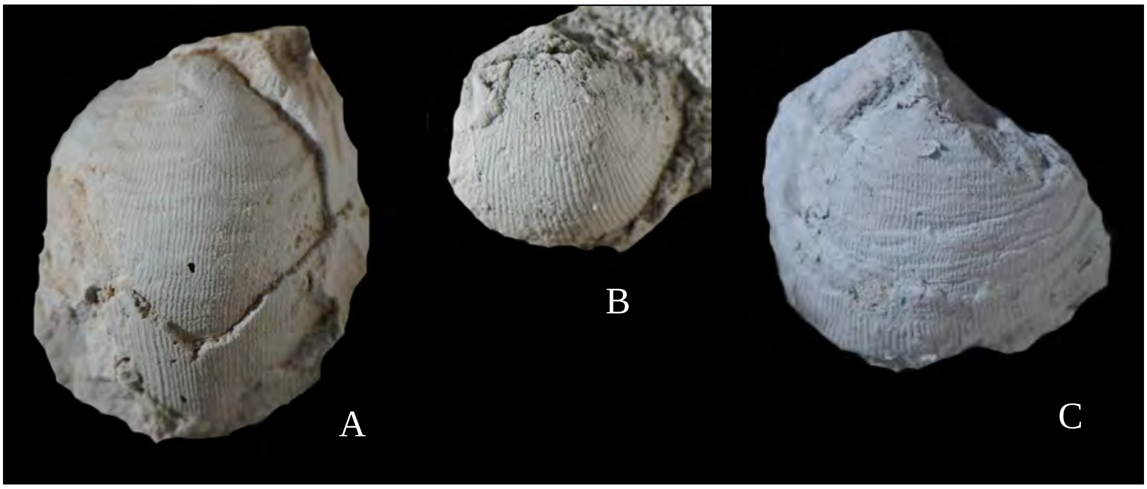

Fig. 143. *Globiella hemisphaerium* (Kutorga). A, dorsal external mould GSC 140836 with part of ventral valve x2. B, ventral valve GSC 140837, x3. C, dorsal external mould GSC 140838 with part of ventral internal mould x2. From C-12. Possibly Trold Fiord Formation, Ellesmere Island.

(Waterhouse) by having less prominent ventral spine bases and more convex venter. (See p. 210).

There is some similarity to the material from the Great Bear Cape Formation, Ellesmere Island, described as *Productus frami* Tschernyschew & Stepanov (1916, p. 34, pl. 7, fig. 4, pl. 12, fig. 4). These shells have long posterior walls, swollen venter, fine ribs, small spines without swollen bases, and subdued commarginal rugae. A lectotype is here nominated as the specimen figured as *Productus frami* Tschernyschew & Stepanov (1916, pl. 7, fig. 4a, b, c, d). In the type material no dorsal valve is preserved, and no figure shows the nature of the ventral hinge or ear spines. The species *frami* appears to come closest to *Striapustula* Ganelin & Lazarev (1999), and this is supported by Tschernyschew & Stepanov (1916), who noted an approach to *Productus konincki*, properly called *koninckianus* de Verneuil, a species now assigned to *Striapustula*. Other somewhat similar specimens were figured as *Cancrinella singletoni* [not Gobbett] by Czarniecki (1969, p. 287, pl. 6, fig. 1-3) from the Early Permian Treskelloden beds of Spitsbergen. The ventral valves are highly arched, narrow and elongate, with fine ribs and laterally developed rugae. The ventral valve displays fine spines, not so apparent on the Great Bear Cape material, and the dorsal valve was not recorded. The species *singletoni* has more prominent spines and is broader than the Czarniecki specimens.

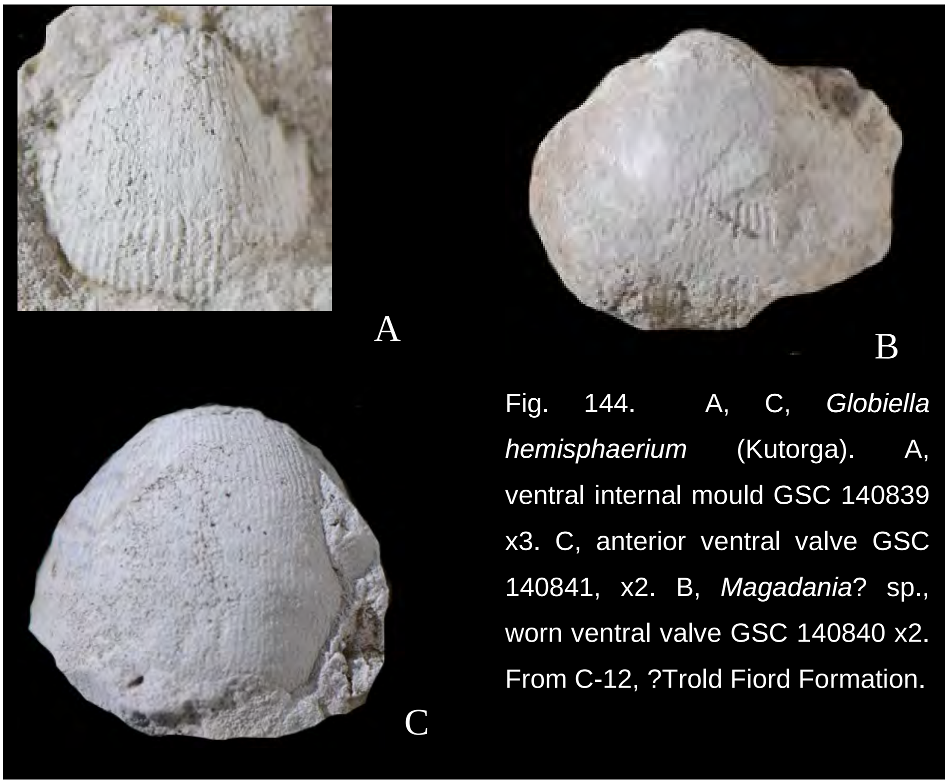

Fig. 144. A, C, *Globiella hemisphaerium* (Kutorga). A, ventral internal mould GSC 140839 x3. C, anterior ventral valve GSC 140841, x2. B, *Magadania*? sp., worn ventral valve GSC 140840 x2. From C-12, ?Trold Fiord Formation.

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, including a row along hinge.

Type species: *Productus foordi* Etheridge, 1903, p. 19 from Callytharra Formation (Sakmarian), Western Australia, OD.

Cimmeriella sp.

Fig. 145A, B

Material: A single ventral valve is known from C-4016, Assistance Formation, Ellesmere Island. Five ventral valves and fragments from JBW 631, Takhandit Formation.

Description: The Assistance specimen is 24mm wide, 22mm long and 12mm high, and has moderately prominent umbo with angle close to 100º, obtuse cardinal extremities and rounded anterior outline. Ribs are well defined, and five lie in 5mm anteriorly. A well preserved ventral valve from JBW 631 is 19.3mm wide, 16.3mm long and 11mm high. Curvature is reduced medianly. There are rare and erect sturdy body spines, well spaced spines along the ventral hinge, and at least three anterior ear spines. Ribs are firm, increasing by intercalation, numbering seven in 5mm. The ventral adductors lie on a small platform, posteriorly placed.

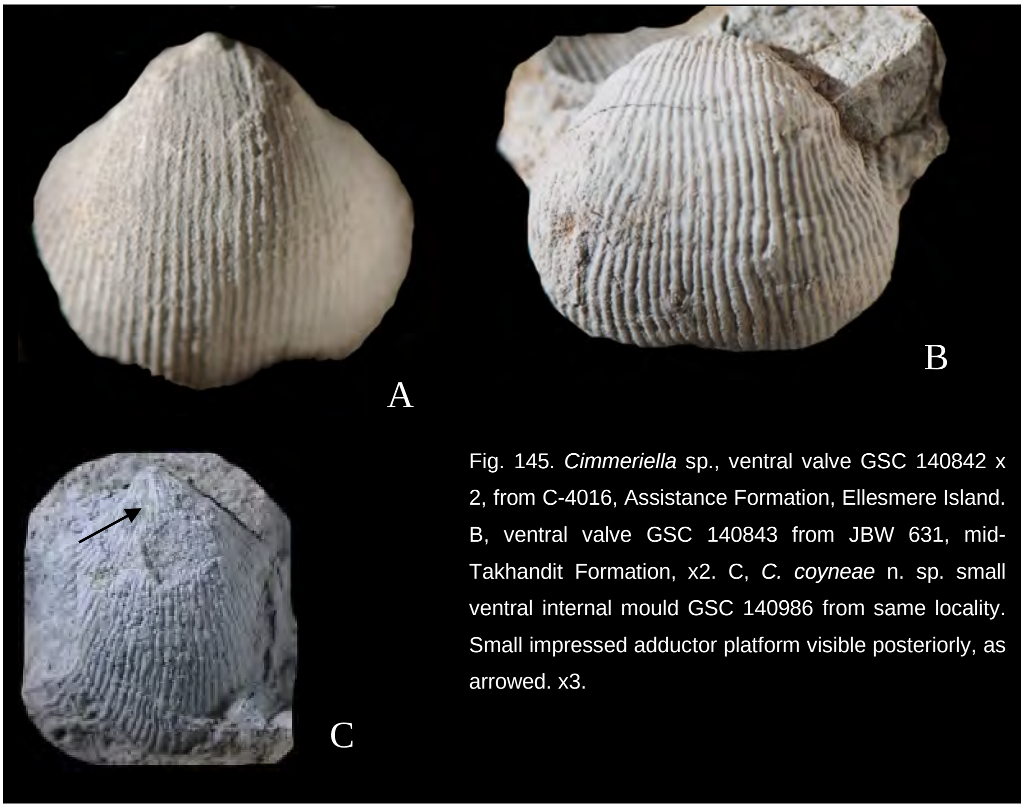

Fig. 145. *Cimmeriella* sp., ventral valve GSC 140842 x 2, from C-4016, Assistance Formation, Ellesmere Island. B, ventral valve GSC 140843 from JBW 631, mid-Takhandit Formation, x2. C, *C. coyneae* n. sp. small ventral internal mould GSC 140986 from same locality. Small impressed adductor platform visible posteriorly, as arrowed. x3.

Resemblances: *Cimmeriella* is widely known in beds of Cisuralian age, and is represented by species in the Jungle Creek Formation of Yukon Territory. *Cimmeriella costellata* (Shi & Waterhouse, 1996, p. 98, pl. 15, fig. 9-24, Fig. 32) from the upper Jungle Creek Formation in the Yukon Territory, of Aktastinian or lower Artinskian age, is more transverse, with costellae as fine as eight in 5mm over mid-length, and low commarginal rugae. *C. orientalis* (Abramov & Grigorieva, 1983), recognized in the members A (at the base) and D of the Jungle Creek Formation in Waterhouse (2018a, p. 227, Fig. 194), usually has seven or eight ribs in 5mm, with some specimens having as few as five in 5mm, and the shape is moderately similar. This species was originally described from northeast Russia, in beds as old as Bashkirian, and in the Yukon Territory allied specimens are found in the upper Ettrain Formation, of Kasimovian age. The specimens from the Ettrain Formation are more nearly circular in outline than those of the present Takhandit specimens, and the ventral valve is more gently convex. *Productus lutkewitschi* Stepanov, 1936, p. 121, pl. 1, fig. 5 from the Kapp Starotsin Formation of Spitsbergen is less convex than present material and has stronger lateral rugae, approaching *Lineabispina* (p. 187). There are closer similarities to Early Permian *simensis* Tschernyschew (1902, pl. 55, fig. 2-5) from the Urals, and to species from Western Australia.

Cimmeriella coyneae n. sp.

Fig. 145C, 146, 147

1971 Linoproductinid – Bamber & Waterhouse, p. 176, pl. 20, fig. 3.

Derivation: Named for Michelle Coyne.

Diagnosis: Transverse shells with subdued commarginal rugae posteriorly, and strong rugae anteriorly, ribs strong and crowded. Muscle scars small.

Holotype: Specimen GSC 140844 figured herein as Fig. 146A, C and Fig. 147A-G, from JBW 631, middle Takhandit Formation, Yukon Territory, here designated.

Material: Two ventral valves and a specimen with valves conjoined from JBW 631, mid-Takhandit Formation.

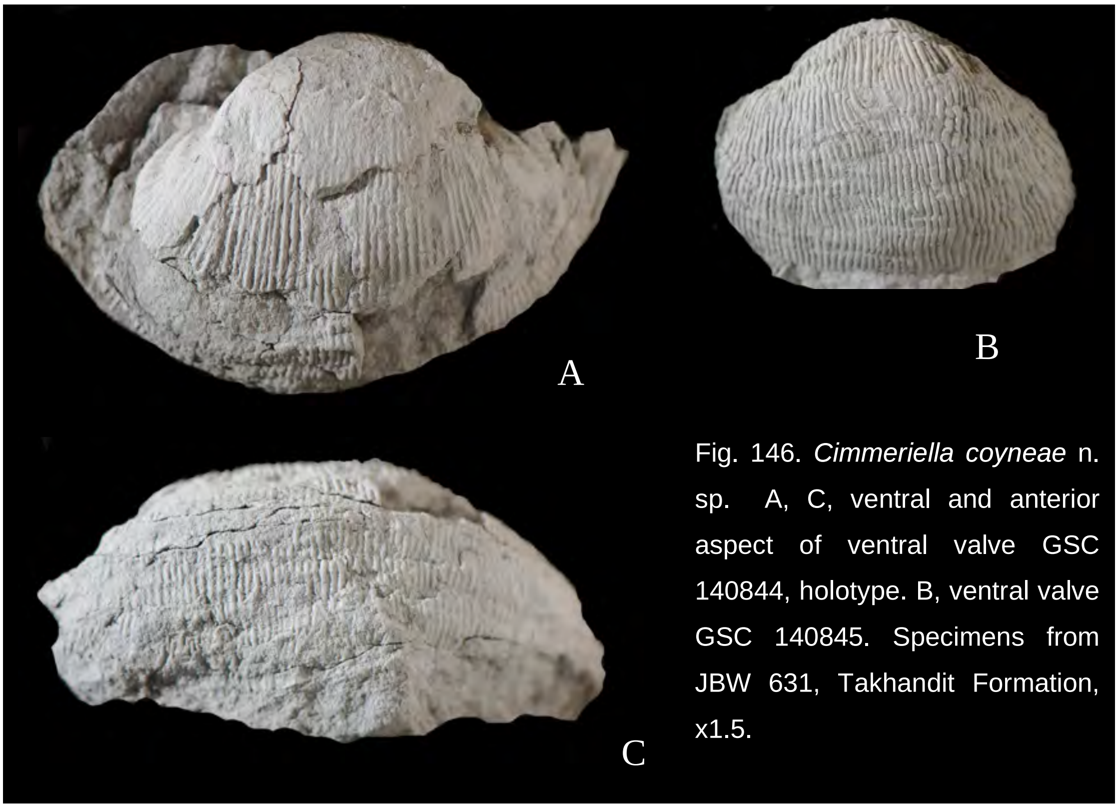

Fig. 146. *Cimmeriella coyneae* n. sp. A, C, ventral and anterior aspect of ventral valve GSC 140844, holotype. B, ventral valve GSC 140845. Specimens from JBW 631, Takhandit Formation, x1.5.

Description: One ventral valve measures 30mm wide, 21mm long and 13mm high. The holotype is wider, at nearly 45mm, and the anterior shell is bent under the disc. The hinge is wide, with small ears and maximum width placed well forward, and ornament is dominated by firm radial ribs, numbering about seven in 5mm over much of the shell, increasing by intercalation on the larger specimen, with some irregularity in patches. Dorsal costae increase by branching. The ribs are crossed posteriorly on the dorsal valve by low growth increments and subdued rugae and over the anterior half by stronger slightly irregular commarginal rugae. Anterior commarginal rugae are developed much more than is normal for this genus. Spines are rare, lying in a row along the ventral hinge, with a very few scattered erect spines arising from the crest of some costae. There are no dorsal spines.

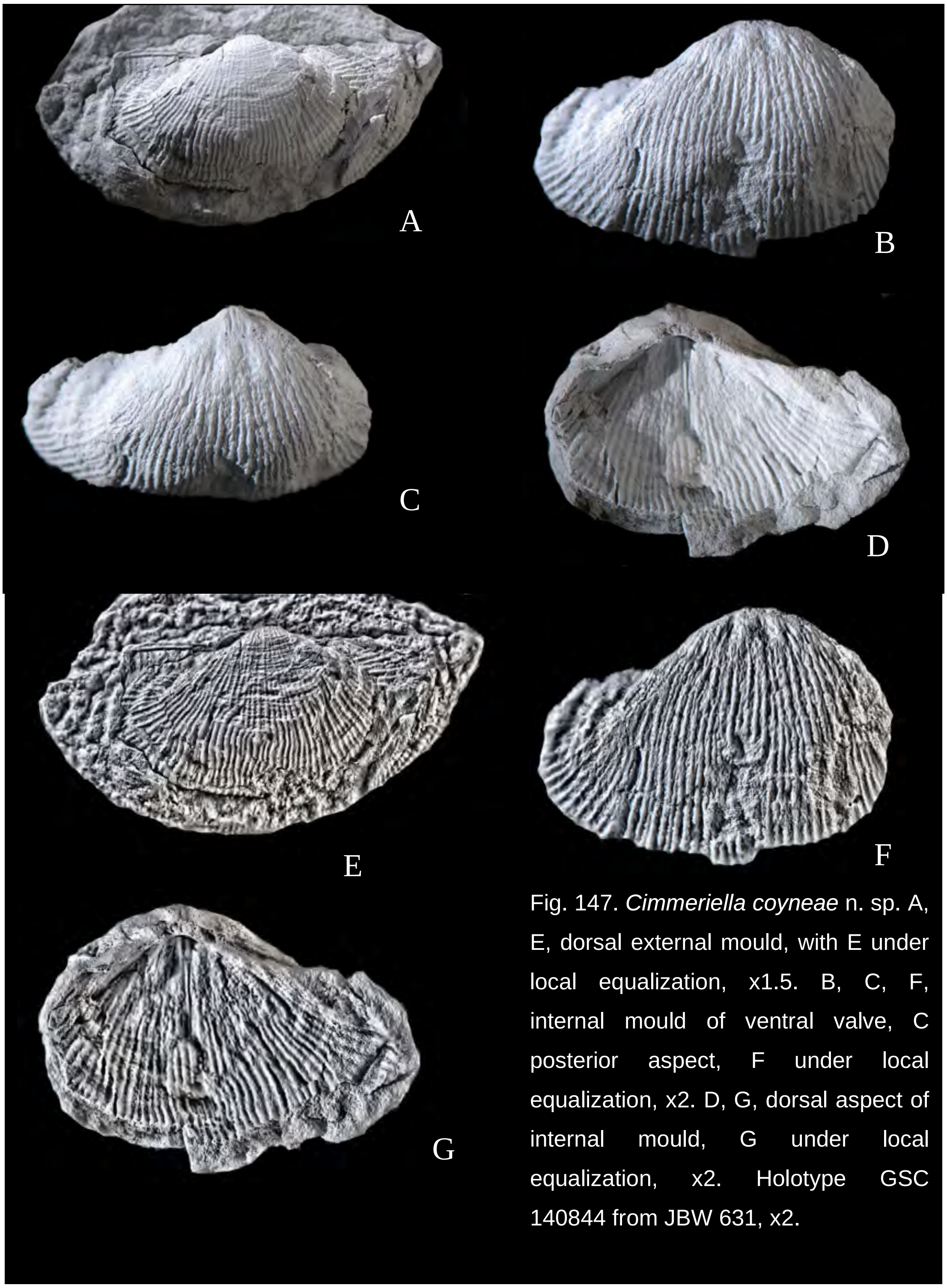

Fig. 147. *Cimmeriella coyneae* n. sp. A, E, dorsal external mould, with E under local equalization, x1.5. B, C, F, internal mould of ventral valve, C posterior aspect, F under local equalization, x2. D, G, dorsal aspect of internal mould, G under local equalization, x2. Holotype GSC 140844 from JBW 631, x2.

The ventral muscle scars are posteriorly placed and small, comprising subrectangular adductor scars, lightly impressed and marked by some fine longitudinal striae, with diductor scars each side. A low median ridge divides the adductor scars. The worn posterior shell of the smaller specimen suggests a slightly raised narrow adductor platform divided by a median groove, but as show in Fig. 147C, the impressed scar, covered like the rest of the shell by ribs from the exterior, is scarcely visible.

In the dorsal valve, a double median ridge lies posteriorly, and leads to a median septum extending over the middle third of the valve. Two small oval smooth adductor impressions lie at the anterior end of the double ridges, and a larger comparatively smooth area lies each side of the double ridge. Fine dense pustules lie over the posterior lateral walls. Brachial shields are possibly represented by smooth posterior lateral areas.

Resemblances: This species is more transverse than other species allocated to *Cimmeriella*, and anterior commarginal rugae are stronger than is normal for species assigned to this genus. A specimen figured in Bamber & Waterhouse (1971, pl. 20, fig. 3) from GSC loc. 52929, *Dyoros modestus* Zone, in the Takhandit Formation of the Yukon Territory is moderately close. Most species of *Cimmeriella*, including the type, are more elongate and globose, but show the same basic pattern of hinge spines and strong costae, and posteriorly placed muscle scars. As regards shape and costation, the closest species appears to be that described as *Globiella costellata* Shi & Waterhouse (1996, p. 98, pl. 15, fig. 9-24, text-fig. 32), a species that was reallocated to *Cimmeriella* by Waterhouse (2018a). The species has seven to nine costellae in 5mm over mid-length, a few commarginal rugae, and scattered rare spines over the ventral disc. Ventral muscle scars are posteriorly placed, but larger than those of the present form. The species is found in the same Canadian region, within the Sakmarian "*Yakovlevia*" zone of the upper middle Jungle Creek Formation in the Yukon Territory, and appears to be a likely ancestor for the present form.

***Cimmeriella*? sp.**

Fig. 148

A small block from C-4034, Trold Fiord Formation, Ellesmere Island, preserves a number of small ventral valves, with strong radial costae, and moderately developed posterior rugae. They are not as transverse as *Cimmeriella coyneae* n. sp., and are not adequately known, with no preserved dorsal valve, and with posterior margin, ears, spine detail and muscle impressions not preserved, so that the generic position is not fully established.

Fig. 148. *Cimmeriella?* sp., block with small ventral valves GSC 140979 x 1.5, from C-4034, Trold Fiord Formation, Ellesmere Island.

Family **YAKOVLEVIAIDAE (YAKOVLEVIIDAE**) Waterhouse, 1975

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.

Subfamily **MUIRWOODIAINAE** (**MUIRWOODIINAE**) Waterhouse, 2013

Diagnosis: Strut spines well developed, usually two up to six. Ventral marginal ridge not conspicuous.

Discussion: *Muirwoodia* Licharew, 1947 is the most common of all yakovleviid genera, and although synonymized with *Yakovlevia* Fredericks, 1925 by Brunton et al. (2000, p. 465) in the *Revised Brachiopod Treatise*, *Muirwoodia* and other members of the subfamily Muirwoodiinae are readily distinguished from Yakovleviinae Waterhouse, 1975 by the presence of strut spines. A third constituent subfamily, as assessed by Waterhouse (2013) is the group distinguished as Paramarginiferinae Lazarev, 1990, which has unusually well developed marginal ridges.

Genus ***Dzhiremulia*** Waterhouse, 2013

Diagnosis: Moderately large, strut spines limited to a pair at cardinal extremities, small spines along hinge margin and in one or two rows along posterior trail. Corpus moderately thick.

Type species: *Dzhiremulia conlustratus* Waterhouse, 2013 from Assistance and Trold Fiord Formations (Roadian, Wordian) of Arctic Canada, OD.

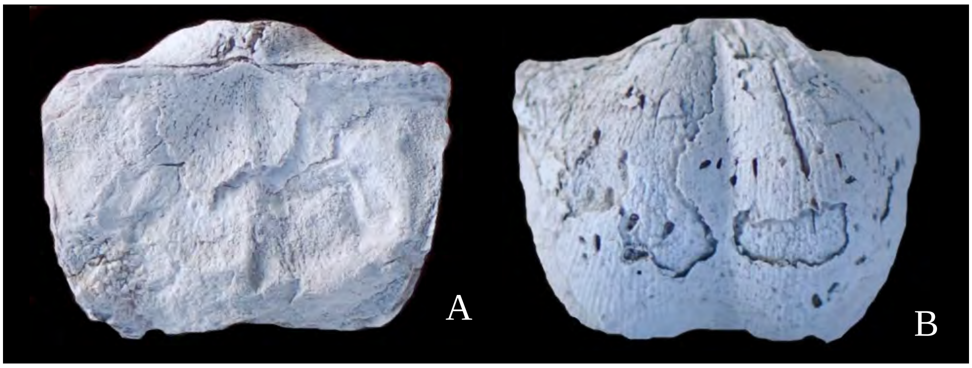

Fig. 149. *Dzhiremulia conlustratus* Waterhouse, dorsal and ventral aspects of GSC 36549, x1.5 from C-4016, Assistance Formation, Ellesmere Island.

Discussion: The genus *Dzhiremulia* is distinguished by the distribution of spines, with strut spines limited to one solitary pair, placed at the cardinal extremities of the ventral valve. The type species is found in Arctic Canada, and the name taken from a species name applied to a conspecific form described from Outer Mongolia. *Muirwoodia* (*Muirwoodia*) Licharew and *M.* (*Grandaurea*) Waterhouse have two pairs of strut spines, and *Duartea* Mendes and *Harkeria* Waterhouse have three pairs.

Dzhiremulia conlustratus Waterhouse, 2013

Fig. 149 - 154

2013 *Dzhiremulia conlustratus* Waterhouse, p. 347, Fig. 15.33 – Fig. 15.37.

Diagnosis: Large shells with prominent strut spine at each cardinal extremity of the ventral valve.

Holotype: GSC 136070 figured as Waterhouse, 2013, Fig. 15.34A, Fig. 35A, B and herein as Fig. 150A, 151A, D from C-4019, Assistance Formation, Ellesmere Island, Canada, OD.

Fig. 150. *Dzhiremulia conlustras* Waterhouse. A, ventral valve, posterior aspect, GSC 136070, from C-4019, holotype, x1. B, ventral view, GSC 136073 from C-4025, x1.3. C, ventral posterior view of GSC 136072 from C-4016, x1. D, dorsal view of GSC 52417 from C-4019, x1. Assistance Formation, Ellesmere Island. (Waterhouse 2013).

Original material: Original material involved a ventral valve from C-4003, four specimens with valves conjoined and several dorsal valves from C-4019, two specimens with valves conjoined from C-4016, a specimen with valves conjoined from C-4025, and three specimens with valves conjoined and four ventral valves (possibly with dorsal valves masked) from C-4028, Assistance Formation, Ellesmere Island. Two ventral valves from C-4008 and two ventral valves from C-3996 came from the Trold Fiord Formation, Ellesmere Island.

Additional material: One ventral valve and one specimen with valves conjoined from C-4002, three ventral valves and one specimen with valves conjoined from C-4028, and one ventral valve from C-4036, Assistance Formation, Ellesmere Island. A specimen with valves conjoined from C-4074, Van Hauen Formation, Ellesmere Island. One ventral valve and two specimens with valves conjoined from C-4014 and one specimen with valves conjoined, from

C-4015, and a specimen with valves conjoined from GSC loc. 58951, all from Trold Fiord Formation, Ellesmere Island. Two or possibly three ventral valves from C-3993, Degerböls Formation, Ellesmere Island.

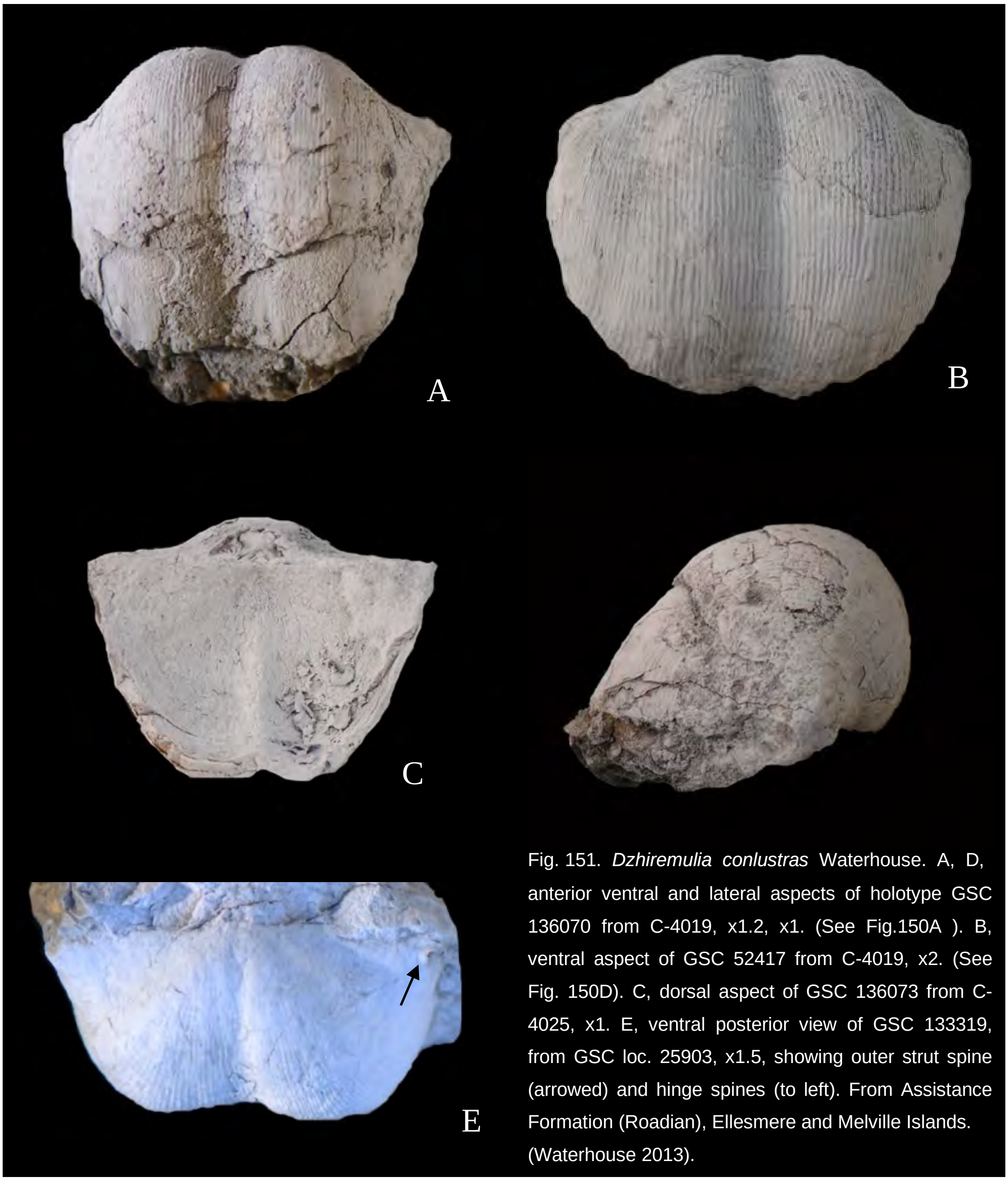

Fig. 151. *Dzhiremulia conlustras* Waterhouse. A, D, anterior ventral and lateral aspects of holotype GSC 136070 from C-4019, x1.2, x1. (See Fig.150A). B, ventral aspect of GSC 52417 from C-4019, x2. (See Fig. 150D). C, dorsal aspect of GSC 136073 from C-4025, x1. E, ventral posterior view of GSC 133319, from GSC loc. 25903, x1.5, showing outer strut spine (arrowed) and hinge spines (to left). From Assistance Formation (Roadian), Ellesmere and Melville Islands. (Waterhouse 2013).

Dimensions in mm:

GSC specimens	Width	Length	Height
133311 (C-4019)	46	28	24
133320 (C-4019)	40	35	20
136070 (C-4019)	52	43	27
136072 (C-4016)	52.5	32.5	26
136073 (C-4025)	49.5	37	22

Description: Specimens moderately large, the largest specimen being 56mm wide. The ventral umbo is low and extends only slightly beyond the hinge and umbonal walls are low and diverge at 130°. Umbonal slopes as a rule are

Fig. 152. *Dzhiremulia conlustras* Waterhouse. A, ventral valve GSC 36857 from C-4014. B, ventral valve GSC 136840 from GSC loc. 58951. Trold Fiord Formation, Ellesmere Island. Specimens x1.25. (Waterhouse 2013).

gently convex in section and grade gently into convex ears, and the median sulcus widens at 45º from the umbo, but the sulcus is constricted anteriorly, reducing the sulcal angle to 30º. Rarely the floor is channelled, but usually it is subangular to abruptly concave: in one specimen the sulcus disappears anteriorly. The maximum width of the shell lies at the hinge, and the ears protrude only slightly. Ginglymus low, with the median gap occupied by external face of cardinal process. For the dorsal valve, the fold commences a little in front of the hinge, and there is no nepionic area, and ears are poorly discriminated and weakly concave. Compared with the ventral valve, the dorsal disc is only weakly concave, so that the body corpus is comparatively thick. The trail is subgeniculate and well extended, and often curves so much as to lie parallel to the first formed part of the ventral disc, having grown in the opposite direction, although this may have been affected by gentle post-burial distortion. The fold and sulcus continue over the trail. Both valves are ornamented by costellae, numbering about 16 in 10mm over mid-valve, and weakly converging

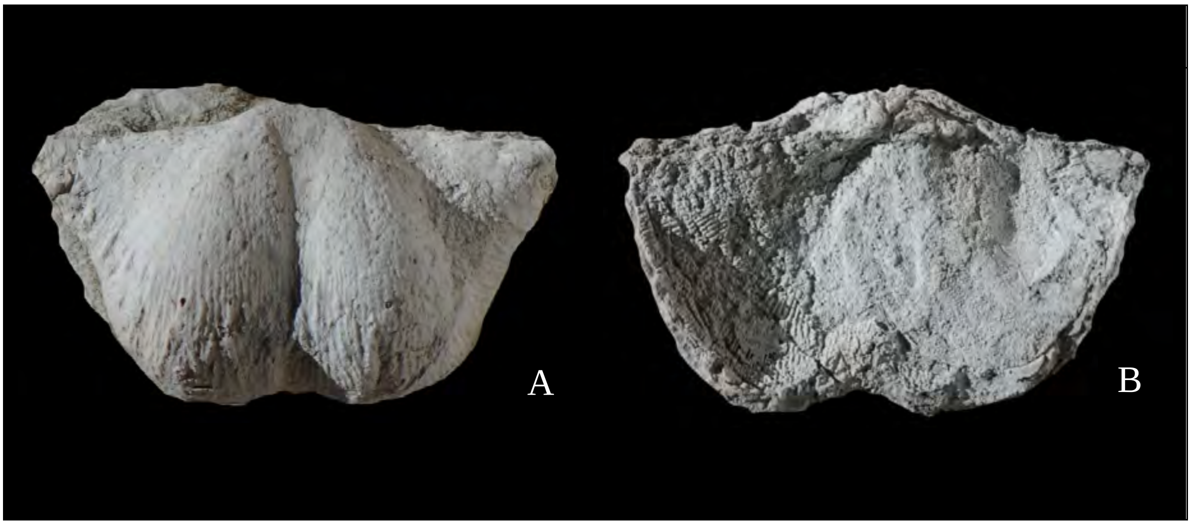

Fig. 153. *Dzhiremulia conlustras* Waterhouse. A B, dorsal and ventral aspects of specimen GSC 140846 with conjoined valves from C-4028, Assistance Formation, Ellesmere Island, x1.25.

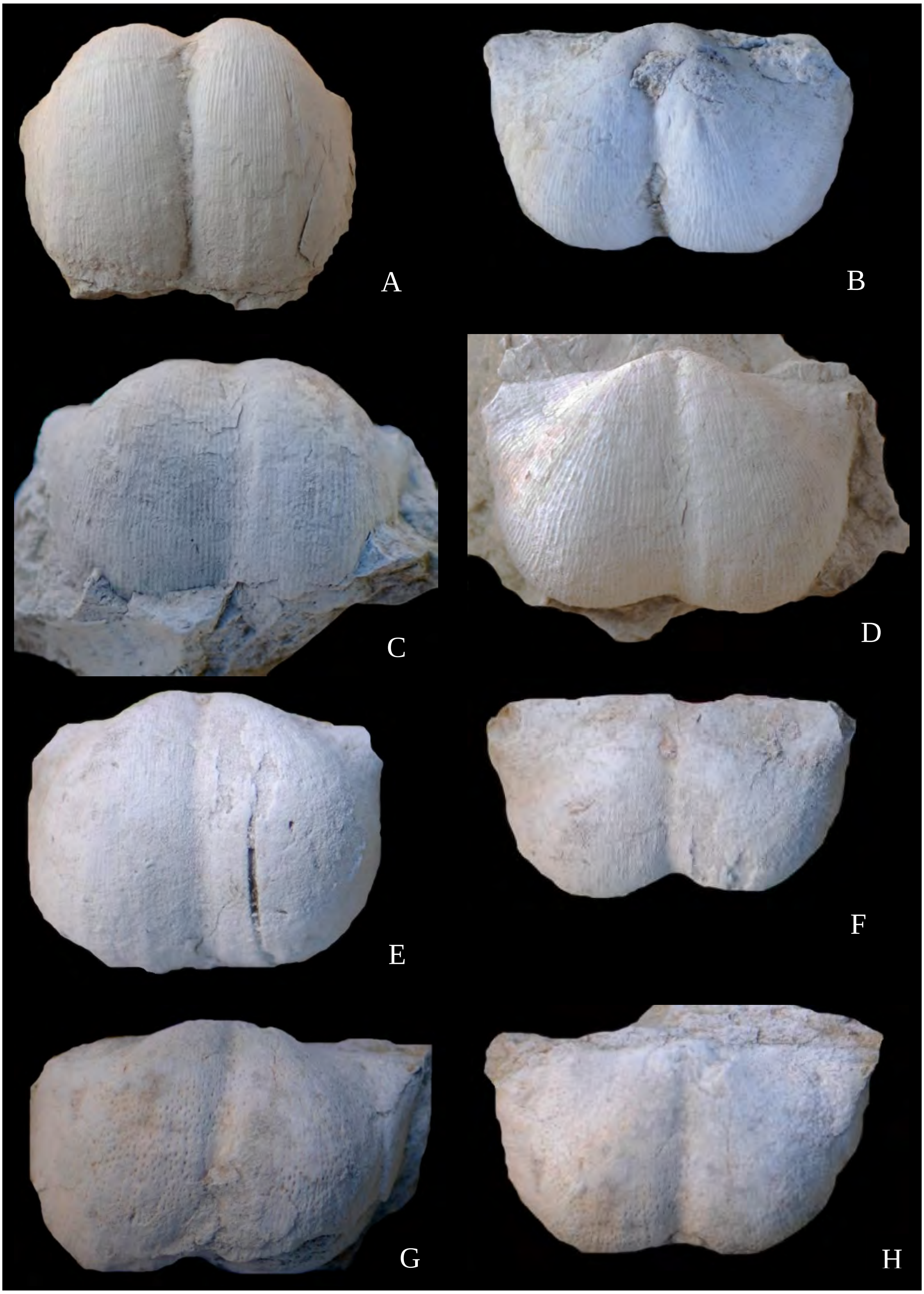

Fig. 154. For caption see top of next page.

Fig. 154. *Dzhiremulia conlustratus* Waterhouse. A, B, ventral and anterior views of GSC 133320 from C-4019, Ellesmere Island. C, D, anterior and posterior ventral valve GSC 133319 from GSC loc. 25903, Melville Island. (See Fig. 151E). E, F, anterior and posterior ventral aspects of worn GSC 136068 from C-4019. G, H, anterior and posterior ventral aspects of worn GSC 133311. Specimens from Assistance Formation, x1.5. (Waterhouse 2013).

into a trough-like anterior sulcus, or lying parallel in other specimens. Some specimens show erratic and impersistent traces of rugae or growth-steps, not well marked. A strut spine lies close to each posterolateral extremity of the ventral valve, extending postero-laterally, and up to 1.5mm in diameter. A row of fine hinge spines preserved in a number of specimens, more than nine in number each side of umbo, subevenly spaced, and up to 0.3mm in diameter. Other fine and erect spines lie over the ventral disc and trail, especially towards the anterior third of trail, where a short row of three to five spines may be discerned each side of the sulcus on some specimens, and less than 0.6mm in diameter (GSC 136074).

Ventral adductors sited on a very narrow and elongate platform, with shallow diductor impressions each side. GSC 36819 from locality C-4016 has a very long median dorsal septum extending well towards the anterior edge of the disc, and in the other specimen from the same locality the posterior septum is slender, and the muscle scars scarcely discernible. The brachial shields enclose a very small smooth area and large papillae cover the median floor.

Resemblances. A specimen illustrated as cf. *Muirwoodia duplex* by Nakamura et al. (1992, p. 88, pl. 2, fig. 11, 12) from unit f at Kapp Wijk in Spitsbergen is moderately like the present species, but the nature of the spines is not certain. The specimens described as *Productus duplex* from the same location by Wiman (1914, p. 65, pl. 14, fig. 3-7) are of comparable shape, and the species may prove to be closely allied, apart from deeper sulcus, but the spine distribution needs to be ascertained. It comes from the Brachiopod Chert of Spitsbergen, and according to Gobbett (1964, p. 113) has strong anterior spines, possibly equivalent to strut spines, and apparently without any match in present specimens, so that it is apparently not congeneric.

Yakovlevia dzhiremulensis Manankov, 1998, p. 490, pl. 8, fig. 15-17 is allied, with similar spines. It comes from Outer Mongolia in the *Alispiriferella lita–Fasciculatia adpressum* Zone, considered to be of Kazanian (Wordian) age, and a few specimens come from the overlying *Echinauris jisuensis* Zone, considered to be of “lower Tatarian,” ie. late Guadalupian age. The species is large with more pointed cardinal extremities and flanks converging more anteriorly, and sulcus deeper posteriorly in most specimens, compared with the Canadian form.

Waterhouse (2013, p. 347) recorded two ventral valves and a specimen with valves conjoined from GSC loc. 58977, Great Bear Cape Formation, Ellesmere Island. These specimens, no longer available for comparison, suggest that the genus, if not the species, was present in the formation, of greater age than the present species.

Genus ***Harkeria*** Waterhouse, 2013

Diagnosis: Six strut spines on ventral valve, two at cardinal extremities and two pairs on flanks in front of geniculation. Hinge row of fine spines. Corpus moderately thick.

Type species: *Harkeria studiosa* Waterhouse, 2013, Assistance Formation (Roadian), Devon Island, Canada, OD.

Discussion: Like *Duartea* Mendes, 1959 and unlike most other members of Muirwoodiinae, this genus is characterized by having six strut spines. Unlike *Duartea*, the new genus lacks a row of spines along the base of the umbonal flanks and commarginal rugae are not conspicuous. So far, the genus seems to have been comparatively rare in the Canadian Arctic Archipelago, but it is represented by a number of species in Neimongol (Inner Mongolia), as described by Lee & Gu (1976), Liu & Waterhouse (1985) and others. The genus is close in appearance to *Muirwoodia* Licharew, 1947, but this genus has a strut spine at each cardinal extremity and only one pair anteriorly, as shown by Shi (1995), Shi & Waterhouse (1996, fig. 34A) and Klets (2005).

In *Muirwoodia greenlandica* Dunbar (1955, pl. 16, fig. 1, 3, 9) there appears to be two anterior strut spines on several of the ventral valves, and suggestions in other figures of a cardinal strong spine, though the text recognized only one anterior sturdy spine. The specimens appear to be more arched than *Harkeria studiosus*.

Harkeria studiosa Waterhouse, 2013

Fig. 155 – 158

1960 *Muirwoodia mammata* [not Keyserling] – Harker, p. 58, pl. 16, fig. 1-5.
cf. 1961 *Muirwoodia greenlandica* [not Dunbar?] – Nelson, pl. 4, fig. 2a, b.
1971 *Yakovlevia* sp. Bamber & Waterhouse, p. 176, pl. 20, fig. 6.
2013 *Harkeria studiosus* Waterhouse, p. 350, Fig. 15.38, Fig. 15.39.

Diagnosis: Relatively small and transverse with shallow anterior ventral sulcus, fine ribs and six prominent strut spines.

Holotype: GSC 13531 from Assistance Formation (Roadian), Devon Island, Canada, figured by Harker in Harker & Thorsteinsson (1960, pl. 15, fig. 1-3), here designated.

Fig. 155. *Harkeria studiosa* Waterhouse, ventral valve GSC 133313, x1.5, from C-3996, Trold Fiord Formation, Ellesmere Island. Arrow points to base of an anterior strut spine.
(Waterhouse 2013).

Material: A small collection of specimens with valves conjoined from GSC loc. 26406, Assistance Formation, Devon Island, as well a few similar specimens from silty shale, at an unknown locality in northern Canada, possibly Van Hauen Formation. Rare in Trold Fiord Formation at C-3996, Ellesmere Island. Two dorsal valves from JBW 631, mid Takhandit Formation, and a specimen from GSC loc. 53929, zone 5 of Takhandit Formation, Yukon Territory, are likely to belong to the species.

Description: Specimens small, with the disc comparative flat and trail longer than disc and extending at high angle, the holotype measuring 27mm wide and 18mm long, the ventral umbo broad with angle of 150°, hinge at maximum width and acute cardinal extremities, and very low ventral ginglymus. The ventral sulcus is broad with angle of 40°, commencing close to the umbo and widening to the anterior commissure, with slightly angular or gently concave floor, and the dorsal fold commences a little in front of the hinge. The trail curves evenly on from the disc. Both valves covered by costellae, fourteen in 10mm on the anterior slope. Spines are limited to the ventral valve. Six strut spines are developed, a pair at the cardinal extremities, and two pairs on the flanks, in front of the start of the trail. Five or six finer spines lie along the hinge each side of the umbo, but no spines are developed over the umbonal slopes.

Four specimens with valves conjoined are allocated to this species from an uncertain Canadian Arctic locality (possibly in the Van Hauen Formation?), of mid-Permian age, judged from the associated fauna, and are used to demonstrate features of the interior. The largest measures 28mm wide and 17.5mm long, with 13-16 costellae in 10mm anteriorly. The sulcus is usually narrower than in the types, measuring 30° in three of the specimens and 40° in the other. Fig. 156D suggests an extra strut spine in the middle of one specimen. Ventral adductor scars are elongate and smooth in one specimen, and shorter in another: the scars of this specimen have slight oblique markings laterally at the anterior end. The adductors in both specimens are divided by a low narrow myophragm. Diductor scars are well rounded and moderately impressed. The posterior floor is slightly thickened and bears numerous papillae, and the four anterior strut spines are well marked internally. The dorsal interior is distinctive in the Van Hauen specimens, but the cardinal process is not preserved. The adductor scars lie in a single oval to tear-shaped pair, comparatively smooth and outlined by a bordering groove. The floor of the valve between the scars and to each side is smooth, and a slender median septum commences near the anterior part of the scars, and extends well forward, to a single row of large papillae. In one specimen the papillae are accompanied by two further somewhat irregular rows of papillae. Brachial shields are well outlined, and are small and project forward, to enclose comparatively smooth areas. The remainder of the floor bears sublinear pits and papillae. The posterior valve floor in front of the cardinal process is almost smooth, lacking the coarse pustules developed to each side, but showing extremely fine and scattered pits. The dorsal internal mould of a specimen from the Takhandit Formation is similar overall, but has a double row of prominent pustules.

Resemblances: *Yakovlevia* sp. of Bamber & Waterhouse (1971, pl. 20, fig. 6) is regarded as conspecific with *studiosus*, having the pair of anterior strut spines on each side of the sulcus. It came from GSC loc. 53929 in the Ft or *Thamnosia* Zone of the Takhandit Formation at Tatonduk River, now referred to the *Dyoros modestus* Zone. The type specimens of *Harkeria studiosa* were compared with *Muirwoodia mammata* (Keyserling, 1846) by Harker in Harker & Thorsteinsson (1960), but although there is some similarity in shape, the presence of six rather than four strut spines marks a ready distinction. This differentiates the species from various other species mentioned by Harker. Material figured by Nelson (1961, pl. 4, fig. 2a, b) from the Takhandit Formation might well belong to the present species. It was identified as *Muirwoodia greenlandica*. The Greenland specimens described as *Muirwoodia greenlandicus* by Dunbar (1955, p. 103, pl. 16, fig. 1-18, 1961) could be close, but need first-hand inspection. There is some suggestion of two prominent anterior spines on each flank and a spine at each cardinal extremity. The specimens tend to have more disc spines and more prominent ears. Nakamura et al. (1992, pl. 4, fig. 6) reported this species from the lower Hotvinden Member in Spitsbergen. Dunbar (1955, p. 105) noted that various specimens record-

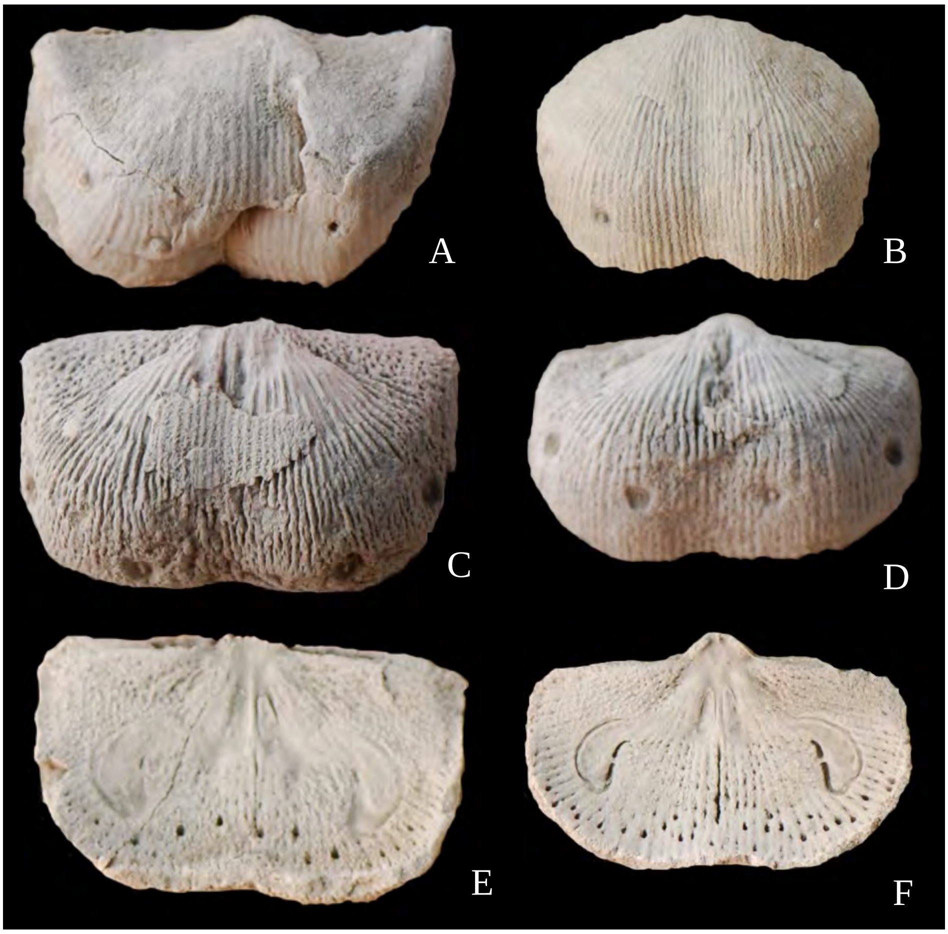

Fig. 156. *Harkeria studiosus* Waterhouse, x2. A, ventral aspect of GSC 133314 from GSC loc. 26406, Assistance Formation, Devon Island. B, ventral valve GSC 133318. C, E, ventral and dorsal aspects of mostly internal mould of specimen with valves conjoined, GSC 133321. D, F, ventral and dorsal aspects of specimen with valves conjoined, GSC 133322. Note exceptional centrally placed strut spine in D. B – F from Van Hauen Formation?, locality uncertain. (Waterhouse 2013).

ed as *Productus weyprechti* by Toula (1874, 1875b), Tschernyschew & Stepanov (1916) and Frebold (1931), and as *P*. (*Thomasina*) *weyprechti* by Stepanov (1936, 1937b) were likely to belong to his *Muirwoodia greenlandicus*, and they certainly do not belong to Toula's species.

A ventral valve from C-4067 in the Nansen Formation of the Canadian Arctic Archipelago, likely to be of Early Permian age, displays a number of strut spines, and has a comparatively flat disc and stronger commarginal rugae compared with the present species.

Specimens identified as *Muirwoodia mammata* [not Keyserling] by Gobbett (1964, p. 112, pl. 13, fig. 23-26) from the Brachiopod Chert of Spitsbergen are close, having two pair of anterior strut spines, but these are placed closer together than in the Canadian form. The ventral valve assigned by Ifanova (1972, p. 120, pl. 7, fig. 3) to *Yakovlevia artiensis* Tschernyschew (1889, pl. 7, fig. 29-31; Solomina 1960, pl. 1, fig. 19-21) appears to have two pairs of anterior strut spines. The species *artiensis* is of early Cisuralian age in the Urals and Petchora Basin of

Russia. *Muirwoodia timanica* Kalashnikov (1993, p. 63, pl. 17, fig. 8; Molin et al. 1983, pl. 1, fig. 7, Grunt 2006a, p. 150, pl. 8, fig. 8, 9) has two pairs of anterior strut spines, and a wider hinge, and is very close, but appears to have a shorter trail. It comes from beds of Kazanian age in the pre-Timan region.

Fig. 157. *Harkeria studiosa* Waterhouse, x2. A, B, lateral aspect and oblique anterior aspect of GSC 140847, showing disc (d) and long trail (t), with two prominent strut spines in B. From GSC loc. 26406, Assistance Formation (Roadian), Devon Island. Arrows point to the anterior strut spine.

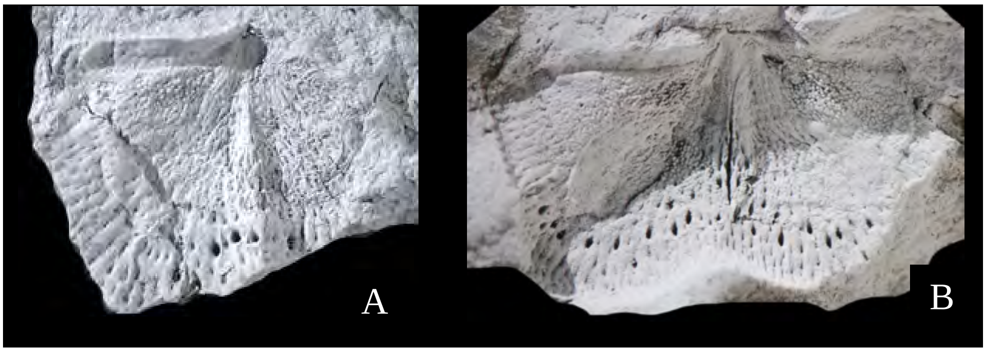

Fig. 158. *Harkeria studiosa* Waterhouse. A, dorsal internal mould, GSC 140987, x2, B, dorsal interior GSC 140848, x2. From JBW 631, Takhandit Formation.

A number of species with six strut spines have been described from the Permian of Neimongol or Inner Mongolia. One of the closest species was misidentified as *Muirwoodia mammata* by Liu & Waterhouse (1985, p. 17, pl. 4, fig. 4-6) from the Houtoumiao Formation in the *Dyoros lamellosa* – *Stenoscisma ovalia* assemblage, of Kungurian to Kazanian age. The specimens are similar in shape and ornament, but have more protruding cardinal extremities, shallow sulcus and coarser ribs, numbering eight to ten in 10mm. The species described as *Yakovlevia borealis* Liu & Waterhouse (1985, p. 19, pl. 3, fig. 4-6) from the lower Zhesi Formation of likely Middle Permian age in

Neimongol is much larger, but shows the same distribution of six strut spines and row of spines close to the hinge. *Y. convexa* Liu & Waterhouse (1985, p. 20, pl. 3, fig. 7, pl. 4, fig. 1-3 from the Zhesi Formation is large and convex with finer costellae and shallower more anterior sulcus, but the text and figures are not clear over the number of strut spines. A large number of Yakovleviidae have been described from Neimongol in studies by Lee & Gu (1976), Lee & Gu in Lee et al. (1980) and Zhan & Lee (1977), and although the spine detail is often obscure, masking the generic affinities, it is clear that six strut-spined species are more common in the Permian of Inner Mongolia than in other regions.

Superfamily **LINOPRODUCTUSOIDEA** (**LINOPRODUCTOIDEA**) Stehli, 1954

Family **SCHRENKIELLAIDAE (SCHRENKIELLIDAE**) Lazarev, 1990

Subfamily **SCHRENKIELLAINAE (SCHRENKIELLINAE**) Lazarev, 1990

Discussion: Schrenkiellinae are characteristically medium to large shells with shallow corpus cavity and wide hinge bearing usually a single row of moderately thick ventral spines. The group is limited to comparatively few genera, that probably evolved from a genus such as *Gilmoria* Waterhouse, 2013, p. 277 from the Early Carboniferous of United States. Upper Carboniferous members such as *Praeschrenkiella*, *Meniscuria* and *Plicatomedium* have a few body spines, lost by Permian time for the genera *Schrenkiella* and *Striatospica*. That is assuming that *Striatospica* is linoproductiform, as rated by Lazarev in Brunton et al. (2000, p. 563). Shen (2017, p. 734) reidentified the type material with *Edriosteges* Muir-Wood & Cooper, 1960, despite what appears to be obvious differences from *Edriosteges* in the apparent limitation of spines to a single row along the hinge, the presence of radial ribs, and no report of edriostegid interareas for the figures and descriptions of type *Striatospica*. The figure of type *Striatospica* by Chao (1927b, pl. 13, fig. 10) indicates that no ventral interarea was developed, and his pl. 13, fig. 10 shows that spines were limited to a single erratic row just in front of the ventral hinge. Type *Edriosteges* has numerous ventral spines, no radial ribs, and high interareas (see Muir-Wood & Cooper 1960, pl. 17). No additional figures of *Striatospica* were provided to establish the accuracy of Shen's observations, and these are awaited with interest. If *Striatospica* proves to be edriostegid, which would certainly be a most interesting development, it would seem likely to belong to a genus distinguishable from *Edriosteges*, but not related to *Schrenkiella*.

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 which 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 identification is yet to be established. The Lyons Formation has been judged to be of Asselian age by Waterhouse (2015a), rather than Sakmarian in Brunton et al. (2000). They had overlooked the documentation of Sakmarian *Schrenkiella* in Canada, provided by Bamber & Waterhouse (1971) and Shi & Waterhouse (1996). Indeed Brabb & Grant (1971, p. 15, pl. 1, fig. 40, 41) compared specimens with *Linoproductus schrenki* from the sandstone unit of the Takhandit Formation in Alaska, but their specimens are not close to *Schrenkiella*, resembling rather a genus found in the Canadian Arctic, called *Lineabispina* (see p. 187 herein).

In Canada, *Schrenkiella* appears to have had a longer range than in Russia, commencing in deposits of Asselian age, and with the present species as described below, extending well into Middle Permian. In South Primoye, a ventral valve figured as *Linoproductus triangularis* Licharew from the *Skinnerella* Zone of the upper Barabash Suite looks very like *Schrenkiella* (Licharew & Kotlyar 1978, pl. 13, fig. 2, 3). A young schrenkiellin ally, of Wuchiapingian age, is represented by *Chhidrusia* Waterhouse, based on *Productus* (*Linoproductus*) *simensis abrupta* Reed, 1944, p. 57 from the Kufri Member of the Chhidru Formation in the Salt Range (Waterhouse 2013, p. 385). This genus is distinguished from other schrenkiellin genera and species by its small size and unusually high trail.

Schrenkiella truncata n. sp.

Fig. 159

Derivation: truncus – dismember, Lat.

Diagnosis: Medium size, some shells with shallow anterior ventral fold and low dorsal fold, others evenly rounded, hinge moderately short for the genus. Low rugae over both valves, especially the dorsal valve.

Holotype: Specimen GSC 140849 from C-4077, figured as Fig. 159A, probable Assistance Formation, Ellesmere Island, here designated.

Material: Five ventral valves, one dorsal valve and one specimen with valves conjoined with fragments from C-4077 and one ventral valve and one dorsal valve and fragments from C-4028, both in the Assistance Formation, Ellesmere Island. One dorsal valve from C-4064, without locality data, but lithologically like Assistance Formation.

Dimensions in mm:

Width	Length	Height
31	26	6 growth line, holotype, ventral valve
30	23	6.5 growth-line, ventral valve
49	36	8 dorsal valve
41	36	9 dorsal valve, estimated

Description: The specimens are little inflated and of medium size for the genus. The ventral valve is weakly convex, with umbonal angle close to 90º, and low persistent umbonal walls. Ears are large and cardinal extremities weakly acute, measuring 80º. The dorsal valve is gently concave with inconspicuous umbo and large ears, and has a small convex nepionic portion in one specimen. A shallow anterior sulcus is developed anteriorly on two ventral valves, but none is present on a larger but broken specimen. A low fold is present anteriorly on all available dorsal valves. Costellae are fine, as a rule some six to eight in 5mm, and cover both valves, including the ears. Low rugae are present over the anterior half of the ventral valve, and over much of the dorsal valve. Spines are limited to a row along the ventral hinge, arising from small mounds, and not very strong. The visceral disc is less than 2mm thick in a shell more than 40mm wide. Muscle scars are not visible.

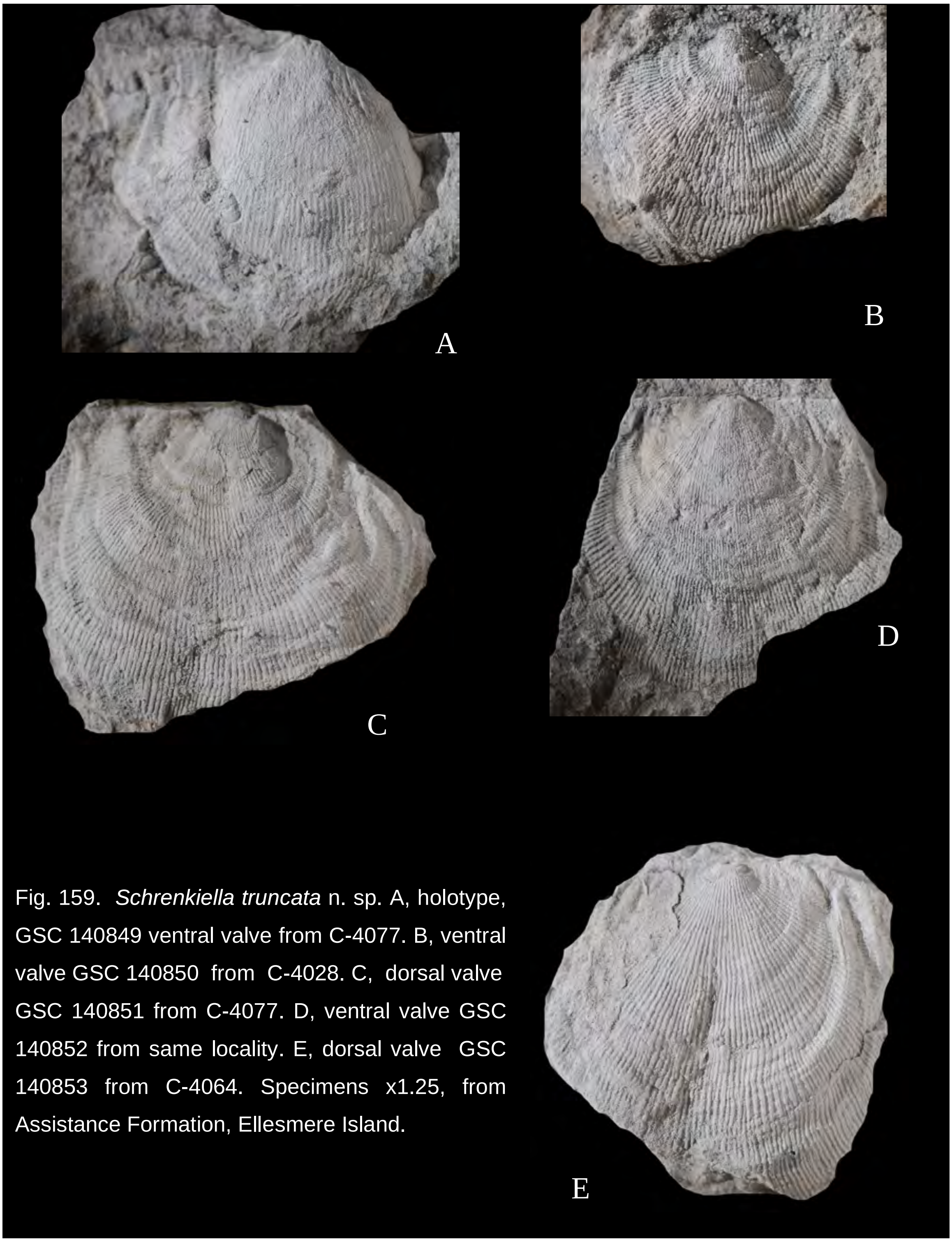

Fig. 159. *Schrenkiella truncata* n. sp. A, holotype, GSC 140849 ventral valve from C-4077. B, ventral valve GSC 140850 from C-4028. C, dorsal valve GSC 140851 from C-4077. D, ventral valve GSC 140852 from same locality. E, dorsal valve GSC 140853 from C-4064. Specimens x1.25, from Assistance Formation, Ellesmere Island.

Resemblances: The type species of *Schrenkiella, Productus schrenki* Stuckenberg, 1875, p. 88 as described from the Sakmarian of Russia, and also reported in Canada (Waterhouse 2018a, p. 252, Fig. 209 with synonymy), is moderately similar, with more commarginal rugae over the ventral valve, and tendency to develop a ventral fold. Other species, such as *S. triangulata* Barchatova, 1973, also of Sakmarian age in Russia and found in Asselian deposits of Canada, are readily distinguished by its more triangular shape and high anterior ventral fold.

Family **GIGANTOPRODUCTUSIDAE** (**GIGANTOPRODUCTIDAE**) Muir-Wood & Cooper, 1960

Subfamily **WARDLAWRIAINAE** (**WARDLAWRIINAE**) Waterhouse, 2004b

Diagnosis: Medium-sized to moderately large costellate shells with well formed row of ventral hinge spines, some to all ventral disc and trail spines having posteriorly prolonged bases, no dorsal spines, low commarginal rugae.

Discussion: Only two genera, *Wardlawria* Waterhouse and *Lineabispina* Waterhouse, are recognized in this subfamily. *Wardlawria* is based on *Productus missouriensis* Sayre, 1930 from the Dekalb Limestone of Missouri, United States (Dunbar & Condra 1932, p. 252, pl. 28, fig. 1-5, pl. 29, fig. 6, 7; Muir-Wood & Cooper 1960, pl. 114, fig. 13-16; Waterhouse 2004b, text-fig. 4C). In size this genus approaches *Linoproductus*, but has very different spines over the ventral disc and trail: the spines are numerous over the disc and slender with elongate bases, unlike the large and rounded spines that emerge directly from the disc in Linoproductinae. Members of the tribe are closer in shape to some Gigantoproductinae, being large, broad and with shallow disc, and the ventral spines with posteriorly prolonged bases resemble those of the much more transverse genus *Semiplanus* Sarytcheva, 1952 of upper Visean age. This genus is older than *Wardlawria*, and it is deemed possible that Wardlawriinae began as Upper Carboniferous survivors of gigantoproductid stock, which persisted as *Lineabispina* into the Middle Permian Period.

. The shell of *Lineabispina* is remarkably thin, allowing the course of the spine core to be analysed, and shows that the core of each spine with an elongate base does not pass forward from the spine base and leave a tunnel. Nor has any inner layer of shell been lost, as may be the case for Paucispiniferidae from the United States (see Waterhouse 2013, p. 418), because muscle scars are well preserved. By contrast, each spine with an elongate base in Proboscidelloidea has a core than persists forward from the spine base to leave a tunnel in the internal mould. Given these observations, coupled with the large size and the linoproductid nature of the ribbing, as opposed to the coarser and less regular ribbing typical of Proboscidelloidea Muir-Wood & Cooper, it is concluded that *Lineabispina* and its ancestral genus *Wardlawria* arose from Linoproductoidea, not Proboscidelloidea. The elongate spines are found over the ventral trail as well as disc, whereas in Proboscidelloidea, elongate spine bases occur over the ventral disc, and trail spines tend to be erect without prolonged bases.

Genus ***Lineabispina*** Waterhouse, 2013

Diagnosis: Medium large in size, ventral spines form row along hinge, scattered erect slender spines, and scattered or clustered larger spines with elongate bases over especially anterior disc and trail.

Type species: *Lineabispina ellesmerensis* Waterhouse from Assistance Formation (Roadian), Canadian Arctic, OD.

Discussion: The genus differs from *Wardlawria* in the presence of erect ventral spines over disc and trail without elongate bases, as well as spines with elongate bases: these are often larger than the erect spines.

Lineabispina ellesmerensis Waterhouse, 2013

Fig. 160 - 169

1937b *Productus* (*Linoproductus*) cf. *cora* [not d'Orbigny] – Stepanov, p. 130, pl. 2, fig. 10.
1971 *Linoproductus* (cf. *Stepanoviella*?) Bamber & Waterhouse, p. 174, pl. 19, fig. 3, 4.
1971 *Linoproductus* Bamber & Waterhouse, p. 174, pl. 19, fig. 6.
1971 *Linoproductus* cf. *L. schrenki* [not Stuckenberg] – Brabb & Grant, p. 15, pl. 1, fig. 40, 41.
2013 *Lineabispina ellesmerensis* Waterhouse, p. 396, Fig. 16.34 – Fig.16.40.

Diagnosis: Medium size, some shells with shallow anterior ventral fold and low dorsal fold, others evenly rounded, hinge moderately short for the genus. Low rugae over both valves, especially the dorsal valve.

Holotype: Specimen GSC 136083 from GSC 26406, figured as Fig. 16.34A, B, Fig. 16.40A and herein as Fig. 160A, B, 164A, from Assistance Formation, Devon Island, OD.

Original material: Fifteen ventral valve and three dorsal valves from GSC loc. 26406, Assistance Formation, Devon Island. Additional material: Five ventral valves, one dorsal valve and one specimen with valves conjoined with fragments from C-4077 and one ventral valve and one dorsal valve and fragments from C-4028, both in the Assistance Formation, Ellesmere Island. One dorsal valve from C-4064, of uncertain source, ? Assistance Formation.

Dimensions in mm:

GSC specimen	Width	Length	Height
136078	42	44	21
136080	57	63	24
136081	47	47	20
136085	54	53	22

Fig. 160*. Lineabispina ellesmerensis* Waterhouse. A, B, ventral posterior and ventral aspects of ventral valve holotype GSC 136083, x1.4. The apparent spines to the right of the umbo in A are ribs from another shell fragment. From GSC loc. 26406, Assistance Formation, Devon Island. (Waterhouse 2013).

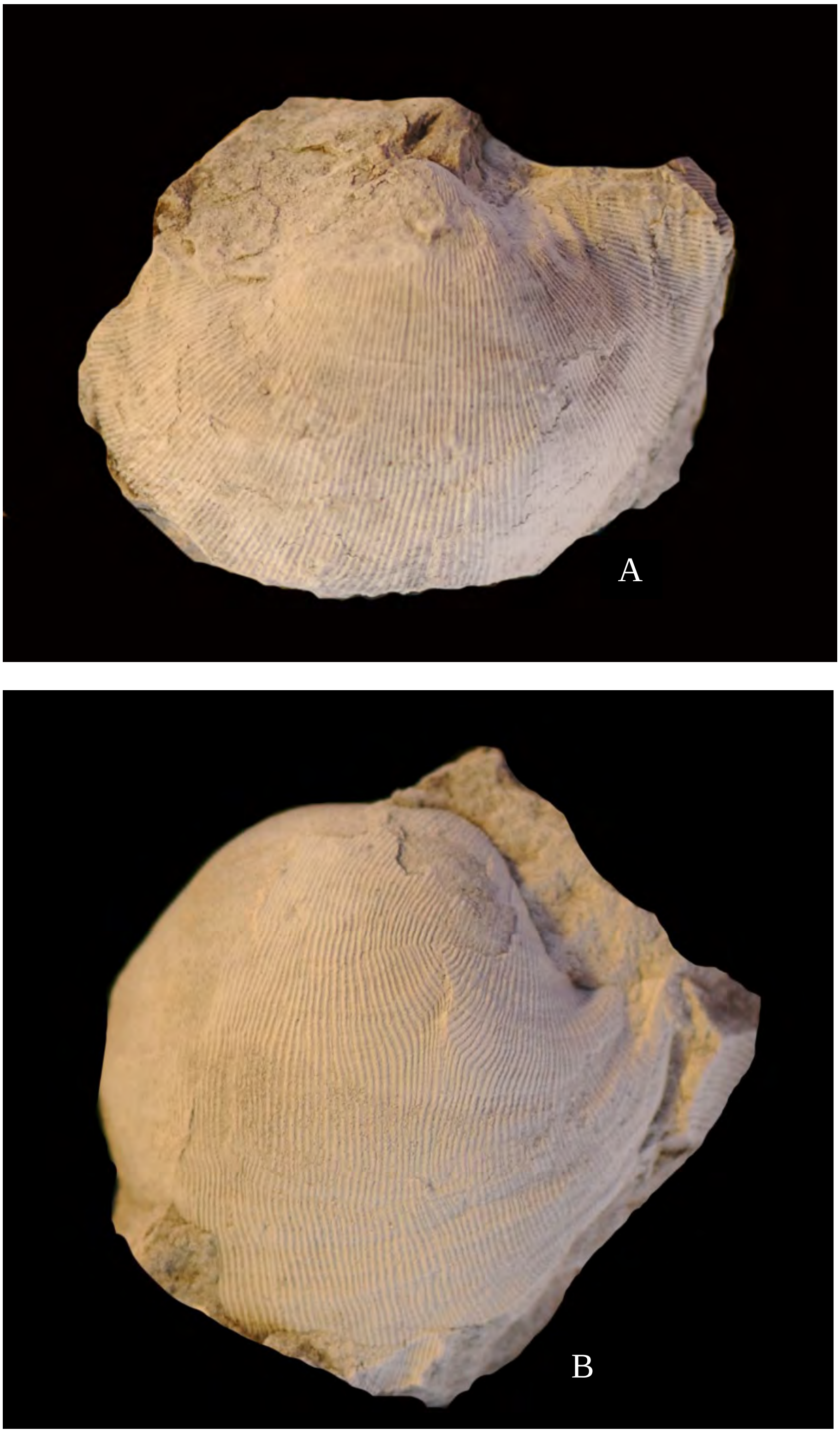

Fig. 161. *Lineabispina ellesmerensis* Waterhouse. A, ventral valve GSC 136077, x1.7. B, anterior view of ventral valve GSC 136085, x1.5, with few spines. From GSC loc. 26406, Assistance Formation, Devon Island. (Waterhouse 2013).

Fig. 162. *Lineabispina ellesmerensis* Waterhouse, ventral posterior aspects of worn ventral valve GSC 136080, x1. From GSC loc. 26406, Assistance Formation, Devon Island. (Waterhouse 2013).

Fig. 163. *Lineabispina ellesmerensis* Waterhouse, ventral posterior aspects of ventral valve GSC 136081, x1.5. From GSC loc. 26406, Assistance Formation, Devon Island. (Waterhouse 2013).

Description: Shells usually transverse, ventral umbo broad, as a rule 100º to 120º, and gently sloping and persistent umbonal slopes, ears may be large and convex and at maximum width, but poorly discriminated, the cardinal angle in some well rounded, in others bluntly angular at 75º-80º. No sulcus, but some shells are flattened medianly, and a few specimens are more elongate with broad only gently convex venter and steep umbonal flanks. Dorsal valve gently concave, with large ears, and no fold and no differentiated nepionic area. A possible skirt is displayed by some specimens. The visceral disc of a specimen more than 70mm wide is only six mm thick, but is 9mm thick in an exceptionally elongate specimen GSC 136082 which is at least 46mm long and 42mm wide. Ribbing is uniformly fine, six to seven in 5mm over much the ventral valve, rarely five in 5mm, and may form slightly irregular patterns. Ribbing covers the ears of both valves and is slightly finer over the dorsal valve. Crests are narrow and interspaces U-shaped

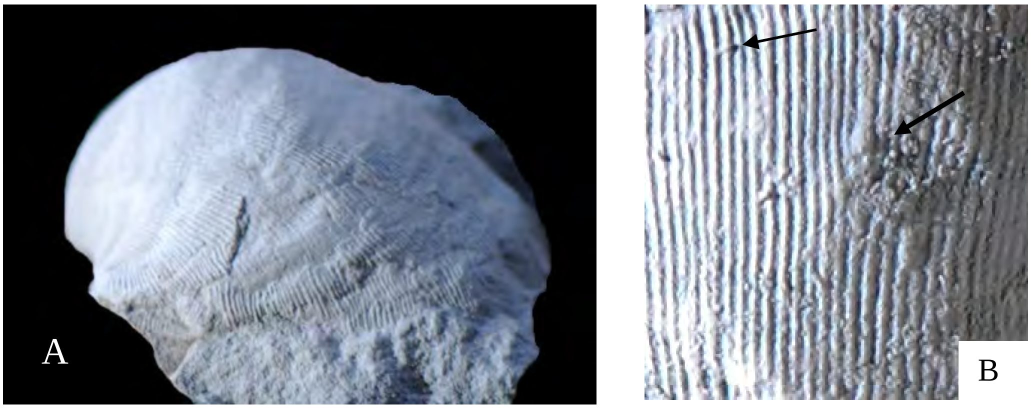

Fig. 164. *Lineabispina ellesmerensis* Waterhouse. A, lateral aspect of ventral valve holotype, GSC 136083, x1.5. B, detail showing coarse spines with elongate bases (thick arrow) and fine erect spines (fine arrow) on GSC 136078, x3. From GSC loc. 26406, Assistance Formation, Devon Island. (Waterhouse 2013).

Fig. 165. *Lineabispina ellesmerensis* Waterhouse, narrow ventral valve GSC 136078, x1. From GSC loc. 26406, Assistance Formation (Roadian), Devon Island. (Waterhouse 2013).

and ribs arise by intercalation. Low rugae lie over the inner ears and over the outer umbonal slopes on some specimens, with very subdued rugae over the entire shells in a few specimens. Growth increments number between five and seven per mm. Spines lie in a row close to the hinge, inner spines fine, outer spines becoming more prominent at 0.6mm diameter, and reaching 0.7mm diameter at 20mm from the umbo, and 1.3mm diameter at 25mm from the umbo in another specimen, but the diameter of outermost spines is not secure. Most spines over the disc and trail arise from the crest of a single rib, and measure less than 0.5mm in diameter, but on a number though not all specimens, larger spines are developed especially on the anterior disc and trail, the largest 1.3mm in diameter, disrupting the costae, with five costae converging forwards into the spine, four passing forward from the base and then the inner pair merging into one. These spines have elongate bases often 3 or 4 mm long, some up to 7.5mm long. A small nasute projection may be developed.

The ventral adductors are strongly dendritic, divided by a low myophragm, and impressed into very thin shell no more than 1mm thick. The diductors are very large, with radial grooves and ridges. Little of the dorsal interior is known. The dorsal median septum extends for two thirds of the length of the disc (GSC 136082), and the cardinal process lies largely in the plane of the visceral disc. In one very large but deformed specimen, small adductor scars are raised, and there is no sign of lateral buttress plates.

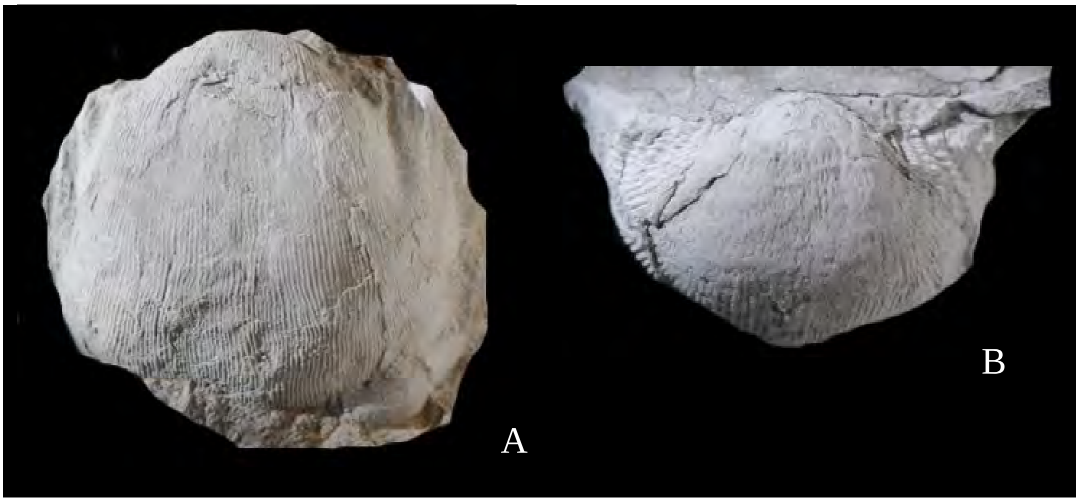

Fig. 166. *Lineabispina ellesmerensis* Waterhouse. A, ventral valve GSC 140855 from C-4072, Van Hauen Formation, Ellesmere Island, x1. B, small ventral valve GSC 140856 from C-4016, x1.5, Assistance Formation, Ellesmere Island.

Fig. 167. *Lineabispina ellesmerensis* Waterhouse, ventral valve GSC 140854, x1. From GSC loc. 26406, Assistance Formation, Devon Island.

Resemblances: Unlike *Wardlawria missouriensis* (Sayre), the spines with elongate bases are not regularly arranged over the disc, and there are a number of additional spines with small bases. In general shape and ornament the two are close, but *missouriensis* has more commarginal rugae visible on the dorsal valve. The present species is moderately close to *Liniunus kaseti* (Grant, 1976, p. 154; Waterhouse 2013, p. 357, Fig. 16.2), but has finer hinge spines. In other respects, the detail of body and trail spines comes close, but *Liniunus kaseti* has no elongate ventral spine bases.

Linoproductus cf. *L. schrenki* of Brabb & Grant (1971, pl. 1, fig. 40, 41) is apparently related. It was figured as a large subequidimensional ventral valve from the top of a sandstone unit in the Takhandit Formation in Alaska. Some specimens were recorded from the Fps, now *Neochonetes culcita* Zone, in the Takhandit Formation in Yukon Territory by Bamber & Waterhouse (1971), as listed in the synonymy. They are of similar shape and ornament, but are smaller than the type specimens or Alaskan specimen. They do show some approach to *Stepanoviella* Zavodowsky, 1960, but this genus has dorsal spines, and is found in very late Permian faunas of northeast Russia. *Productus* (*Linoproductus*) cf. *cora* (not d'Orbigny) of Stepanov (1937b, pl.. 2, fig. 10) differs from the present species in apparently having a medianly flat venter. The specimen came the western shore of the so-called Productus beds of Green Harbour in Spitsbergen. A specimen figured as *Productus* conf. *prattenianus* [not Norwood] by Toula (1874, pl. 1, fig. 5) from the Kapp Starotsin Formation of Spitsbergen shows some similariites, and would repay closer inspection.

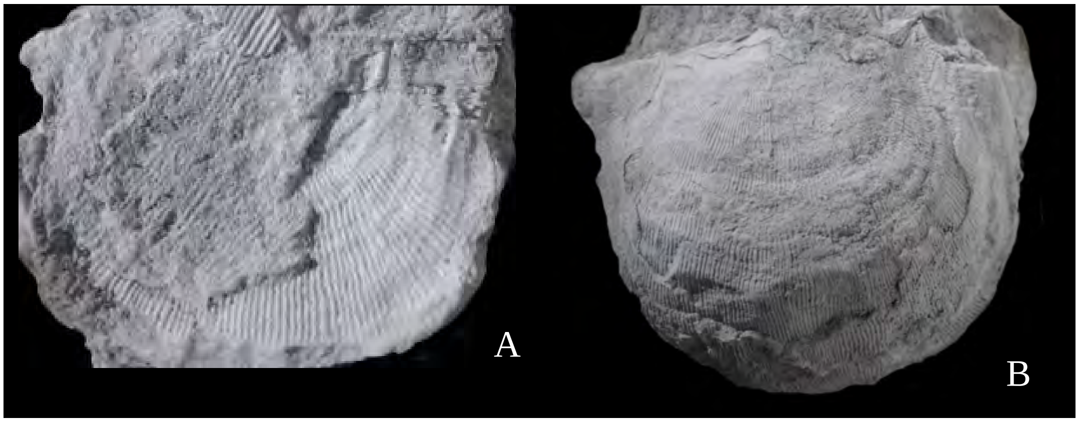

Fig. 168. *Lineabispina ellesmerensis* Waterhouse. A, dorsal valve GSC 140857, x1.5. B, dorsal external mould, GSC 140980, x0.8. Specimens from GSC loc. 26406, Assistance Formation, Devon Island.

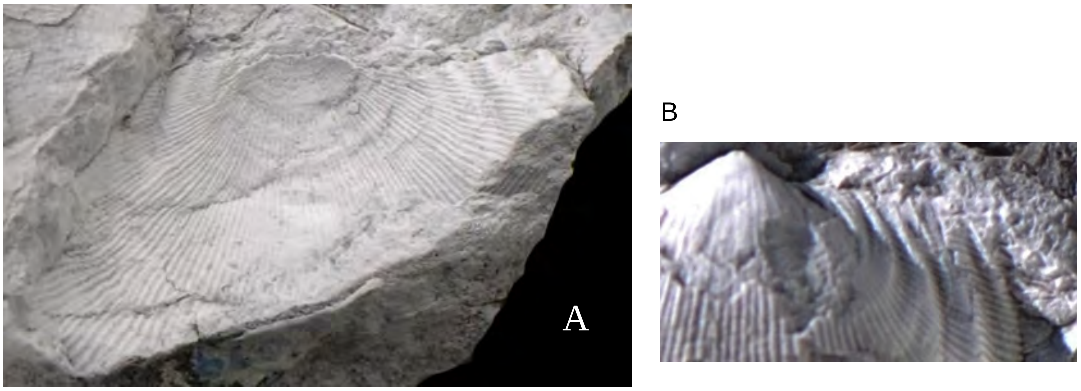

Fig. 169. *Lineabispina ellesmerensis* Waterhouse. A, dorsal valve GSC 136079, x2. B, detail showing ventral hinge spine bases, GSC 136084, x2. From GSC loc. 26406, Assistance Formation, Devon Island. (Waterhouse 2013).

There is some similarity to a shell named *Productus lutkewitschi* Stepanov (1936, p. 121, pl. 1, fig. 5a-c) from Spitsbergen. This has fine ribs and lateral rugae, but it appears to be less convex and broader than the present species. Possibly the species will prove to be congeneric, as a separate species, and this needs confirmation from further material.

Superfamily **PROBOSCIDELLAOIDEA** (**PROBOSCIDELLOIDEA)** Muir-Wood & Cooper, 1960

Family **AURICULISPINAIDAE** (**AURICULISPINIDAE**) Waterhouse, 1986b

Diagnosis: Both valves ornamented by slightly irregular ribs, ventral spines arranged along hinge in one to four rows, and lie in quincunx over the visceral disc, with slender to thick elongate bases: spines further prolonged anteriorly within the shell. Spines erect over ventral trail, and if present, erect and undifferentiated over dorsal valve, usually absent. Shell also crossed by very subdued to moderately well formed commarginal rugae. Ventral interior characterized by rectangular and striate adductor scars, often impressed into the posterior wall; dorsal valve may have low hinge ridge and low to broad median septum, often doubled posteriorly, without conspicuous marginal ridge. Visceral disc normally slender.

Discussion: Costellae are not as linear as in Linoproductidae, and the shells are smaller and often more transverse and less coiled. Proboscidellinae and Undariinae are similar, except for their much more extended ventral valve. The elongate spine bases in Auriculispinidae recall those of the larger shells *Wardlawria* and *Lineabispina*, but the core of the spine bends forward into the shell from the spine base (Waterhouse 2013, Fig. 10, p. 18), unlike the ventral spines in Wardlawriinae. The cardinal process has a high median shaft, and is not bilobed from a ventral view.

The family is close to Paucispinauriidae Waterhouse, which is distinguished by its dendritic adductor scars in both valves, and tendency to have thicker visceral disc and dorsal spines. The assignment of genera to Auriculispininae by Brunton et al. (2000, p. 537) in the *Revised Brachiopod Treatise* seems disorganized and inconsistent, and the stress in their diagnosis of the subfamily on the absence of sockets is completely unwarranted, an observation that should leave students baffled as to the relevance, because dental sockets and teeth are absent as well from other groups within Linoproductoidea and Proboscidelloidea. Moreover the statement that Auriculispinini was characterized by a cluster of hinge or ear spines is not true of several Permian members in Auriculispinini, and is true of several genera classed in paucispinauriid groups.

Subfamily **AURICULISPINAINAE (AURICULISPININAE**) Waterhouse, 1986b

Genus ***Magadania*** Ganelin in Grigorieva et al., 1977

Diagnosis: Elongate strongly concavo-convex with corpus cavity thick as a rule, very fine ribs, numerous ventral spines in quincunx with elongate bases, no dorsal spines. Ventral valve with elongate longitudinally striate adductor scars, and with spine tunnels. Dorsal septum dvided posteriorly.

Type species: *Cancrinella*? *bajkurica* Ustritsky in Ustritsky & Chernyak, 1963, p. 153 from upper Baikur Suite of Taimyr Peninsula, OD.

Discussion: The present species is based on only a few ventral valves, and the lack of a dorsal valve prevents a full diagnosis, but it is named because the shape is highly distinctive. Although the genus *Magadania* was referred to Coolkilinae by Waterhouse (2013, p. 437), the paucity of ventral ear spines and the nature of the ventral adductors suggest that a position within Auriculispinidae would be more appropriate. For the Canadian species, the dorsal valve is not preserved, hindering any assessment of corpus thickness, or dorsal ornament.

Magadania attenuata n. sp.

Fig. 170 – 174A

1963 *Stepanoviella curvata* [not Tolmachev] – Ustritsky in Ustritsky & Chernyak, p. 87, pl. 16, fig. 3a-g.

Derivation: attenuo – make thin, extend, slender, Lat.

Diagnosis: Umbonal angle close to 95º, extended ventral umbonal slopes, ventral valve swollen, external ornament close to that of *Globiella*, spine tunnels posteriorly over internal shell.

Holotype: GSC 140860 from C-3995, Trold Fiord Formation, Ellesmere Island, figured as Fig. 170A, C, 171, 173, here designated.

Material: Three ventral valves from C-3995 and a ventral valve from C-4034, Trold Fiord Formation, Ellesmere Island.

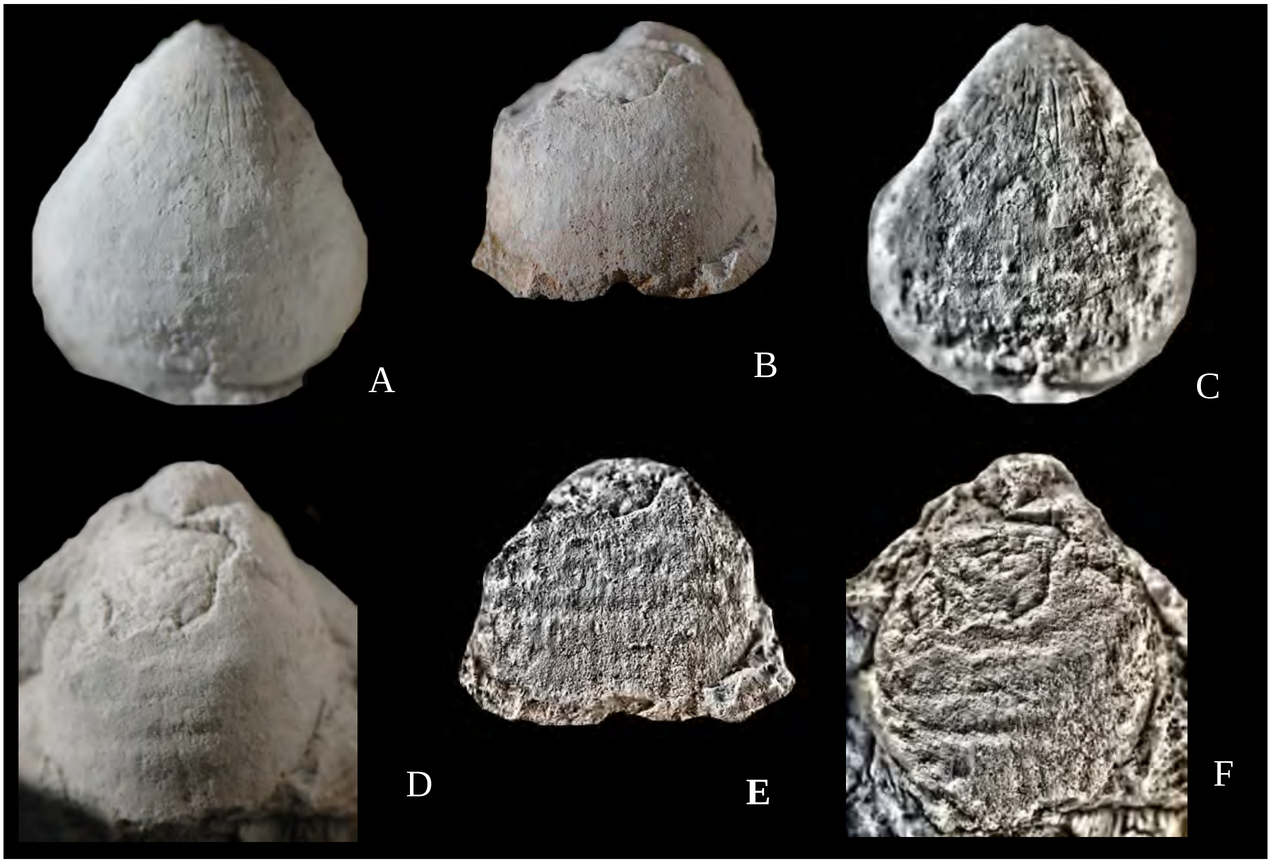

Fig. 170. *Magadania attenuata* n. sp. A, C, ventral valve GSC 140860 holotype. B, E, anterior aspect of GSC 140859. D, F, ventral aspect of specimen GSC 140858. Specimens from C-3995, Trold Fiord Formation, Ellesmere Island. Processed under ordinary light and by local equalization, x2.

Dimensions in mm: ventral valve

Width	Length	Height	
25	23	10	holotype
18	18	11	

Description: Shell distinctive in shape, umbo prominent with angle of 95º, and long steep umbonal walls extending well forward to mid-length, at maximum width of shell. In front the lateral walls pass smoothly with a circular outline into the anterior. There is no sulcus. The hinge is moderately wide, but less than the maximum width of the shell, and ears are reduced in size, displaying abruptly obtuse cardinal extremities with an angle of 130º. Posteriorly, internal capillae are fine, at an estimated twenty in 5mm, and anteriorly the capillae are only slightly coarser, and are shown with difficulty over parts of the illustrations, possibly because of slight abrasion to specimens. Spines are comparatively numerous and lie in quincunx over the entire valve, some five in 5mm posteriorly, three or four in 5mm anteriorly, but spacing is not completely regular, and some are more closely spaced. Posteriorly, the spines are up to 0.1 to 0.2mm in diameter, and anteriorly are up to 0.6mm in diameter, along commarginal rows numbering three in 5mm over mid-valve. Posteriorly many spines have slightly elongated slender bases about 1mm long, and towards the anterior margin the bases become shorter and broader, and a number of spines are erect. Low commarginal rugae are present anteriorly.

Fig. 171. *Magadania attenuata* n. sp., holotype GSC 140860, ventral valve from C-3995, Trold Fiord Formation, Ellesmere Island, lateral aspect, x2. The umbo lies to the right. See Fig. 170A, C.

Internally, the most striking feature is the presence posteriorly of slender spine tunnels (see Fig. 170A, 173), up to 6mm long, and these become shorter and less conspicuous anteriorly. There are only faint signs of muscle scars, which appear to have included lightly impressed narrow adductors with fine erratic linear striations.

Resemblances: *Magadania bajkurica* (Ustritsky in Ustritsky & Chernyak, 1963, p. 65; Ganelin 1977, p. 153, pl. 24, fig. 15-18) from the upper Baikur Suite of Taimyr Peninsula, displays a moderately swollen ventral valve and high posterior walls, not as long as those of the present species, and with broader sulcus. *Cancrinella grigorievae* Zavodowsky (1970, p. 109, pl. 67, fig. 11a, b) from the Omolon horizon was regarded as conspecific by Ganelin (1977). *M. modotoensis* Kotlyar in Grigorieva et al. (1977, p. 154, pl. 25, fig. 1-4) from the Ulidzin Suite of northwest Mongolia is even broader in outline and so may be readily distinguished. In the two Russian species, the ventral valve is more arched with steeper posterior walls, whereas the present posterior walls are lower and more extended. The shell from the lower Baikur Suite that was ascribed to *Stepanoviella curvata* by Ustritsky in Ustritsky & Chernyak, 1963 and synonymized with *M. bajkurica* by Ganelin (1977, p. 153), has elongate posterior walls just as in the present material, and it is therefore regarded as conspecific with the Canadian species. The specimen has extended lateral margins and so is considerably higher than the Canadian specimens, and clearly more mature.

Spine tunnels are well developed, unlike the ventral interior of *Globiella*.

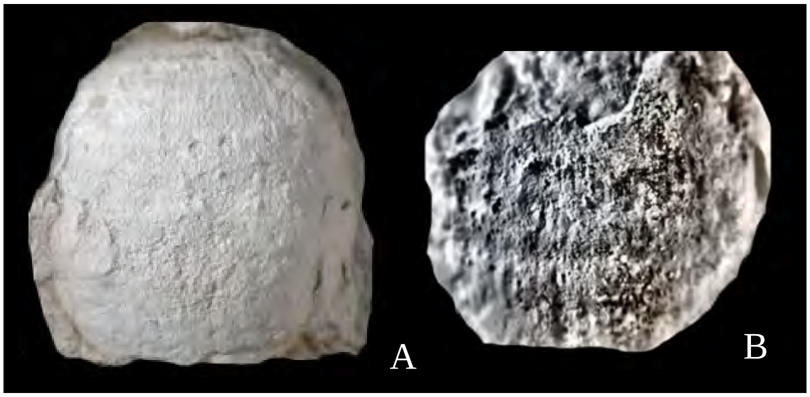

Fig. 172. *Magadania attenuata* n. sp. A, B, anterior aspect of GSC 140858, from C-3995, Trold Fiord Formation, Ellesmere Island, under ordinary light and processed by local equalization, x2. Ventral ribs and scattered fine spines are faintly visible.

Fig. 173. *Magadania attenuata* n. sp, part of holotype GSC 140860, ventral valve from C-3995, Trold Fiord Formation, Ellesmere Island, processed by local equalization, x5. Fine ribs as arrowed are visible towards the top of the figure, on the inner side of the shell between the spine tunnels.

***Magadania*? sp.**

Fig. 144C, 174

Description: Two obscure ventral valves from C-4034, Trold Fiord Formation, Ellesmere Island and C-12, possible Degerböls Formation, are shaped like *Magadania*, but have stronger ribs at eight in 5mm. The C-12 specimen has a row of hinge spines and several erect spines over the inner ears. Body are spines are rare, without conspicuously elongate bases. Identity is uncertain.

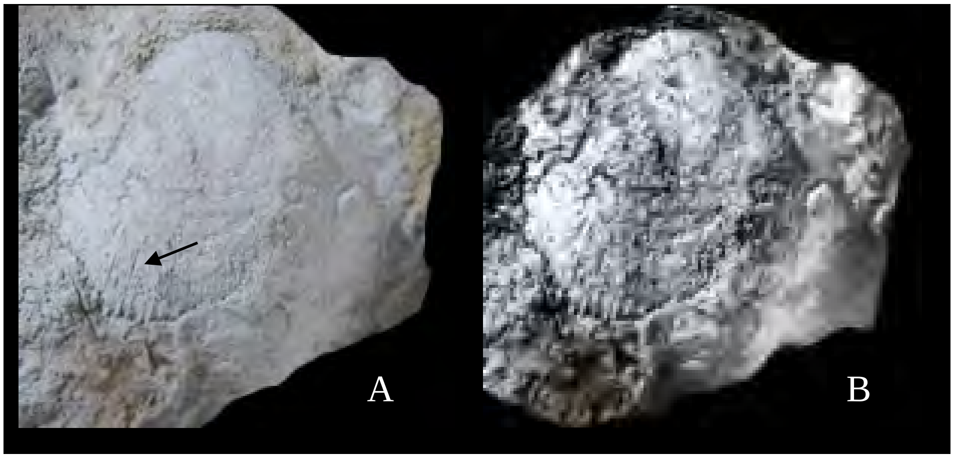

Fig. 174. *Magadania*? sp., ventral valve GSC 141006 from C-4034, Trold Fiord Formation, Ellesmere Island, under ordinary light (A) and processed by local equalization (B), x5, showing the external ribs.

Subfamily **FILICONCHAINAE** (**FILICONCHINAE**) Waterhouse, 2001

Genus ***Cameronovia*** Waterhouse, 2013

Diagnosis: Small slender gently concavo-convex disc, geniculate trail. Capillae well developed on both valves. Spines in three or more rows along ventral hinge, may have swollen or prolonged bases over the disc, dorsal spines well developed, erect over disc, crowded on trail, and may be semi-recumbent.

Type species: *Cameronovia milleri* Waterhouse, 2013, p. 451 from Assistance Formation (Roadian), Cameron Island, Canada, OD.

Discussion: This genus is like *Filiconcha* Dear, 1969 in having dorsal spines, thereby differing from the other related Arctic genera such as *Spitzbergenia* Kotlyar in Sarytcheva (1977a) and *Kolymaella* Ganelin & Lazarev, 2000, and, as far as known, the mystery species *Cancrinella snjatkovi* Zavodowsky, as discussed in Waterhouse (2013).

The spines are fewer over the ventral disc compared with those of *Filiconcha* Dear, 1966 which is found in the Middle and Late Permian of Queensland and New Zealand, and spines in *Cameronovia* are moderately numerous over the trail. On the ventral valve, one hinge row appears to be developed in *Filiconcha hillae* Dear, whereas three rows lie along the hinge, especially over the outer ears, in *Cameronovia*, and continue around the posterior outer margins. Internally the ventral adductor platform is more pronounced in *Filiconcha*, perhaps because of greater individual maturity. The dorsal interior is much the same in both genera, with the dorsal median septum a little longer in the Canadian genus.

Cameronovia milleri Waterhouse, 2013

Fig. 175

1971 *Cancrinelloides* aff. *loveni* [not Wiman] – Waterhouse in Bamber & Waterhouse, pl. 22, fig. 8, 10.
1971 *Cancrinella* sp. undet. Brabb & Grant, p. 14, pl. 2, fig. 18, 19 (part, not pl. 1, fig. 31, 32 = *Magniplicatina* or ally).
2013 *Cameronovia milleri* Waterhouse, p. 451, Fig.17.51.

Diagnosis: Small, comparatively flat disc, geniculate trail, ventral spines in rows close to hinge and prominent postero-laterally, elongate bases over disc and erect over trail. Dorsal spines occasionally with swollen or prolonged bases over disc, crowded and erect over trail.

Holotype: GSC 36839 figured in Waterhouse (2013, Fig. 17.51B-E) and herein as Fig. 175B-E, from GSC loc. 76029, Trold Fiord Formation (Wordian), Cameron Island, OD.

Original material: Single ventral valve from GSC loc. 35316, Trold Fiord Formation, Melville Island, and two specimens with valves conjoined from GSC loc. 76029, Trold Fiord Formation, Cameron Island. Two ventral valves from C-1886, Trold Fiord Formation, Ellesmere Island. Two ventral valves and fragments from GSC loc. 53821, Fish Creek, Permian sandstone unit, Yukon Territory.

Dimensions in mm:

GSC	Width	Length ventral	Length dorsal	Height	
36839	27.3	26.0	22.0	13.6	(GSC 76029, holotype)
36837	32.3	+32.5		9	(GSC 35316)
36838	+22.9	+23.9		13.6	(GSC 67255)

Description: Shell small, transverse, with umbo of 80º to 85º protruding only slightly beyond the broad hinge, cardinal angle close to 100º, subangular, with small slightly upturned or convex ears, poorly differentiated from broad umbonal slopes. Visceral disc gently rounded, with short anterior sulcus in some specimens, curving abruptly into short trail, the sulcus persisting to anterior margin, but weakly defined. Dorsal disc shallowly concave, especially over posterior third of length, tiny ears weakly reflected ventrally, and short geniculate trail. Both valves covered by capillae, measuring three per mm over anterior median ventral disc, increase by branching and by intercalation, especially in front of spines over ventral valve; increase mostly by intercalation over dorsal valve; ribs absent over posterior trail on holotype but appear over anterior ventral trail and over dorsal trail. A row of erect spines lies close to the ventral hinge, fine near the umbo, stronger laterally over the ears. Two or three further rows of spines appear along the hinge beyond the umbonal slopes, with an anterior row of rare slightly inclined spines, and these rows extend laterally, becoming moderately strong, and curving further around the lateral margin, where spines become finer. Body spines with elongate bases up to 4mm long cover the disc, in subregular quincunx, with shorter bases laterally, and bases only 2mm long near the start of the trail. Often two or three fine ribs extend forward from the spine base. Erect spines in some twelve commarginal rows cover the trail, crowded and not completely regular in distribution. A few fine erect spines lie over the tiny dorsal ears, and are well separated over the disc, and crowded in some six or so erratic commarginal rows over the dorsal trail. Some anterior disc and posterior trail spines semi-recumbent.

The ventral adductor platform is elongate and striate, impressed anteriorly into the shell, and diductor scars are striate and large. Spine bases leave short tunnels over the posterior trail in two specimens. Cardinal process incompletely preserved, bearing deep median groove from ventral aspect, broad elongate mound in front with median slit, joined anteriorly by two lateral septa extending almost to mid-length, very short median septum in front. To each side are dendritic posterior adductor scars, partly enclosing small less marked anterior adductor scars. There are faint traces of comparatively large brachial shields, and behind the posterior adductors lie suggestions of a low ridge, and low long hinge ridge. Fine pustules cover much of the floor and larger endospines lie in three or four rows over the anterior disc.

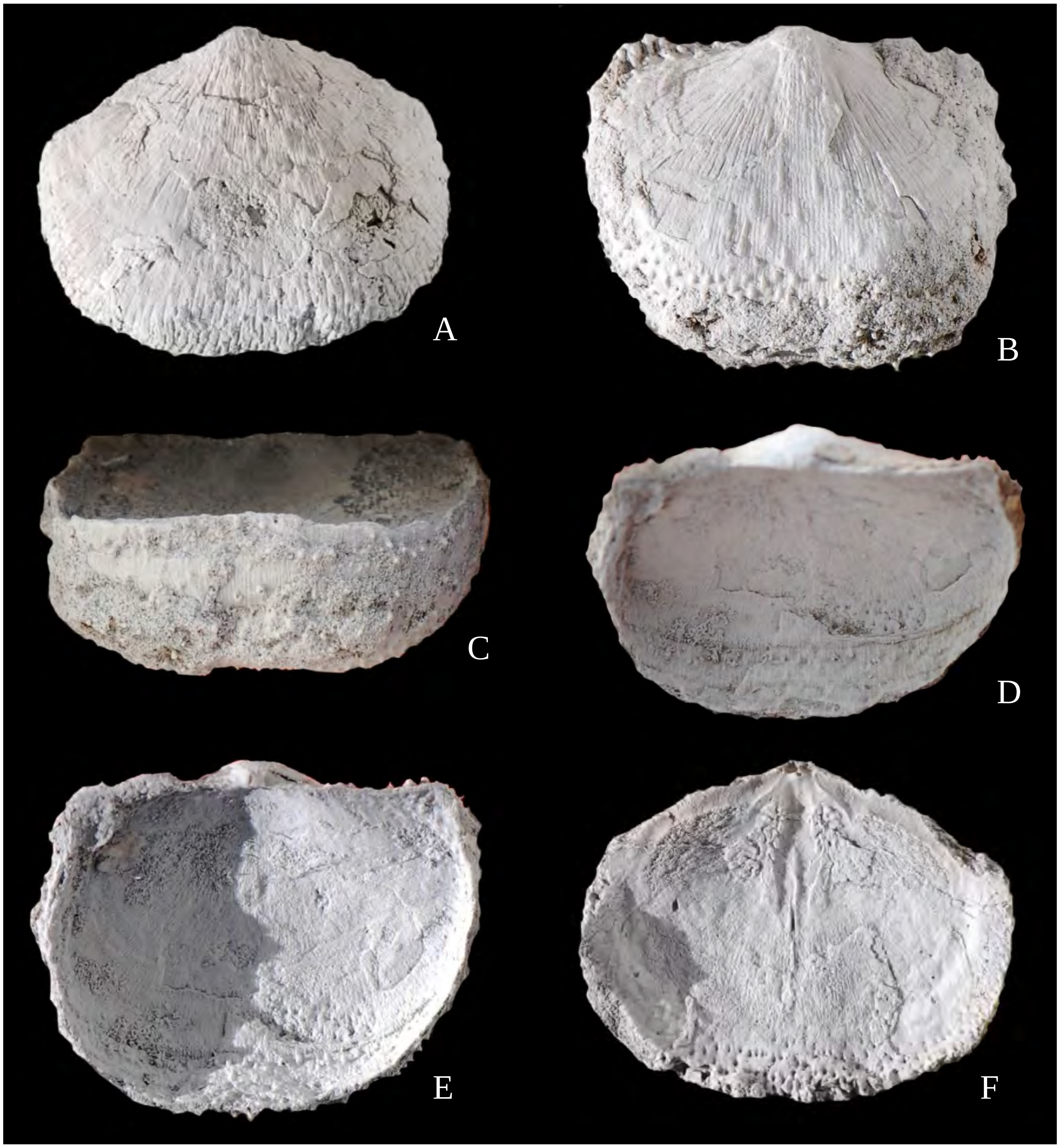

Fig. 175. *Cameronovia milleri* Waterhouse. A, F, ventral (x1.6) and dorsal (x1.7) views of GSC 36837, from GSC loc. 35316, Melville Island. The dorsal view shows the internal mould. B - E, ventral and dorsal views of holotype GSC 36839, from GSC loc. 76029, Cameron Island, x2.2, the dorsal views at various degrees of tilt. Trold Fiord Formation. (Waterhouse 2013).

Resemblances: The species is distinguished from *Filiconcha hillae* Dear, 1966 from the Flat Top Formation (Capitanian) of the south Bowen Basin in Queensland, Australia, by the flatter disc, less concave dorsal valve, more geniculate trail, and by more rows of spines along the ventral hinge and posterior lateral margins, shorter ventral disc spine bases, few dorsal disc spines, and more numerous spines over the ventral and dorsal trail (see Dear 1966, pl. 22, fig. 1-22; Waterhouse 1986b, pl. 11, fig. 10-18). There are various internal differences as well, including a longer dorsal septum in the Queensland species. *Filiconcha auricula* Waterhouse (1976a, Fig. 4.3-14) from the *Plekonella multicostata* and especially the *Spinomartinia spinosa* Zones (Changhsingian) of New Zealand has lower capillae and very short bases for ventral disc spines, as well as larger ears, and scarcely perceptible dorsal median septum. Most allied species from the Arctic Permian have been ascribed to *Spitzbergenia* Kotlyar, and are characterized in part by the absence of dorsal spines. No figures for this genus show hinge spines very well, and the trail appears worn, and dorsal exteriors seldom well preserved. The best-preserved species is *S. gracilis* Kotlyar (in Sarytcheva 1977a, pl. 25, fig. 10, 26, fig. 1-5, Fig. 88), described as coming from the Selander Suite of Spitsbergen, with moderately flat disc, less elongate ventral spine bases, and stronger lateral oblique dorsal hinge ridges. Trail and ear spines are poorly preserved.

Cancrinella sp. undet. of Brabb & Grant (1971, pl. 2, fig. 18, 19) from a few feet above the base of the limestone unit in the type Takhandit Formation of Alaska appears to belong to *Cameronovia milleri*, whereas the specimen of Brabb & Grant (1971, pl. 1, fig. 31, 32) is more like *Magniplicatina*.

Productus loveni Wiman (1914, p. 72, pl. 17, fig. 12-18) from the Spiriferenkalk of Mt Loven, Spitsbergen, looks somewhat like *Cameronovia*, and the faunal list provided by Ustritsky (1979) showed *loveni* as occurring in what he called the Selanderneset Suite, equivalent to the Hotvinden division. Wiman (1914) mentioned an ornament of fine ribs, and the shape, ventral disc spines, and dorsal interior with broad low cardinal process, divided median septum, lateral ridges diverging from in front of the umbo are all attributes suggesting *Cameronovia*. That may well place the specific name *milleri* in jeopardy, but it would be well to first of all establish the nature of the spines along the ventral hinge, and the presence or absence of dorsal spines, and to clarify the stratigraphic position. Grönwall (1917, p. 584, pl. 17, fig. 12, 17) recorded a specimen in a boulder at Holms Land, east Greenland, and Gobbett (1964, p. 116, pl. 14, fig. 7-9) also recorded rather poorly preserved specimens from the Brachiopod Chert of Spitsbergen, assigning the species to *Monticulifera* Muir-Wood & Cooper, 1960 with a query. No allied material described from Spitsbergen adequately shows the nature of spination close to the hinge or over the ventral valve.

Genus ***Kolymaella*** Ganelin & Lazarev, 2000

Diagnosis: Medium-small shells with gently convex ventral valve and gently concave dorsal valve, ornament of fine ribs, and ventral spines, forming a hinge row, disc spines with elongate bases, trail spines more erect, spines rare over ventral ears. Dorsal valve with two parallel posterior septa, no median septum.

Type species: *Cancrinella ogonerensis* Zavodowsky, 1960, p. 65 from Omolon Suite (lower Kazanian), Omolon Basin, OD.

Kolymaella sp.

Fig. 176

Material: The composite internal mould of a specimen with valves conjoined from JBW 631, Takhandit Formation, Yukon Territory.

Description: The Canadian specimen is small with vestiges of the ventral exterior preserved on the ventral valve. There are fine radial ribs, giving rise to spines with elongate bases over much of the disc, and anteriorly spines are erect. A row of erect spines lies along the hinge, but there are no other ear spines. The ventral valve appears to form a median arch, with a corresponding dorsal sulcus. The dorsal valve shows fine radial ribs and low radial rugae, strongest near the hinge, with no sign of dorsal spines. Internally, two short ridges diverge widely in front of the cardinal process, and two slender septa lie in front each side of the mid-line. There is no median septum.

Resemblances: This is the first report of an apparent occurrence of the distinctive genus *Kolymaella* Ganelin & Lazarev from beyond northeast Russia, and it is a pity that the Canadian specimen is not very well preserved. But it does show the diagnostic spine detail, a hinge row of ventral spines, spines over disc with long bases, fine ribs, and two short posterior dorsal septa with no median septum. The original material for *Kolymaella* was figured by Zavodowsky (1960, 1970, pl. 55, fig. 2, 3?, pl. 64, fig. 4-6), and a few spines are seen over the anterior ears in the specimen of Zavodowsky (1970, pl. 64, fig. 4c), but not in fig. 5, or in Brunton (2007, Fig. 1765.4b). The profile of the Canadian specimen, with its ventral fold and dorsal sulcus, is exceptional.

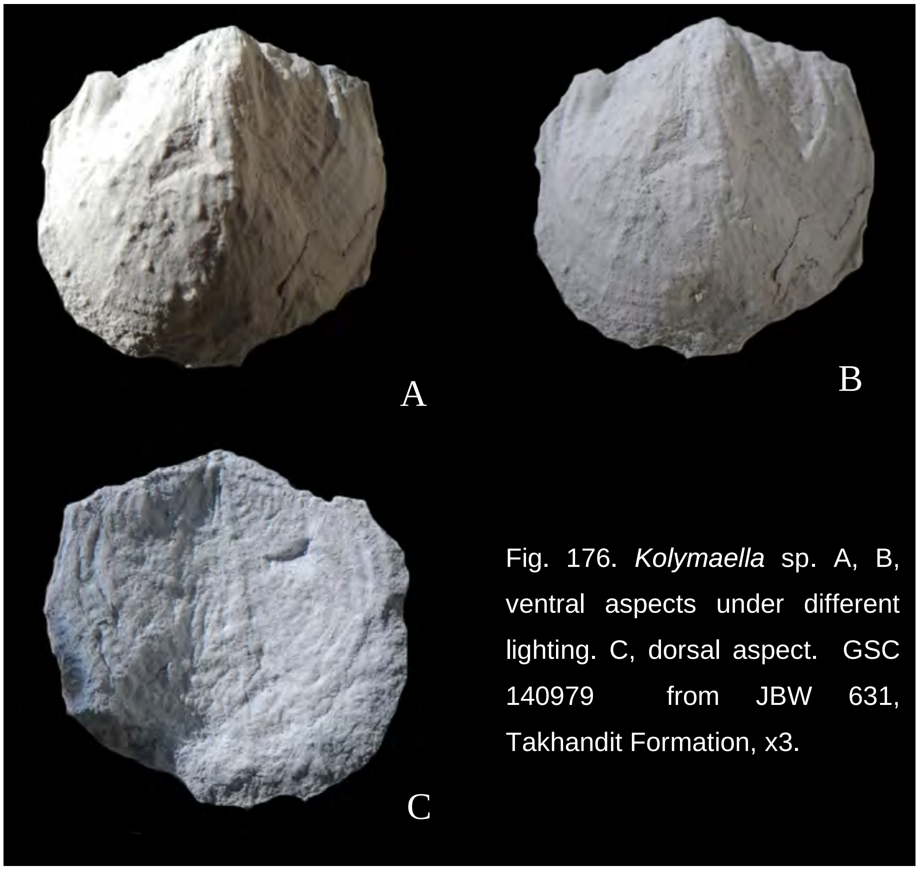

Fig. 176. *Kolymaella* sp. A, B, ventral aspects under different lighting. C, dorsal aspect. GSC 140979 from JBW 631, Takhandit Formation, x3.

Family **PAUCISPINAURIAIDAE** (**PAUCISPINAURIIDAE)** Waterhouse, 1986a

Subfamily **PAUCISPINAURIAINAE** (**PAUCISPINAURIINAE)** Waterhouse, 1986a

Discussion: Brunton et al. (2000) synonymized Paucispinaurinae with Grandaurispininae Lazarev, 1986c. Both names had appeared in June, 1986, but the Waterhouse proposal was in a publication, and the Lazarev name in a thesis document, and therefore without validity. Furthermore, the name Grandaurispininae was only provided as a list, with no diagnosis, which renders the name ineligible (ICZN 1999, article 13.1, p. 17). Not until 1990 did Lazarev provide a diagnosis. Later, Brunton (2007, p. 2652) wthout explanation assigned validity to Paucispinaurinae. Even so, he quoted the wrong reference, provided herein as Waterhouse 1986b. The correct reference is Waterhouse 1986a.

Subfamily **MAGNIPLICATINAINAE (MAGNIPLICATININAE)** Waterhouse, 2001

Tribe **MAGNIPLICATINAINI (MAGNIPLICATININI)** Waterhouse, 2001

Subtribe **MAGNIPLICATINAINAI** (**MAGNIPLICATININAI**) Waterhouse, 2001

Diagnosis: Commarginal wrinkles equally developed on both valves.

Genus ***Magniplicatina*** Waterhouse, 1983a

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: *Cancrinella magniplica* Campbell, 1953 from Ingelara Formation (Wordian), Queensland, Australia, OD.

Discussion: *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) has dorsal spines, and a non-plicate disc, so is placed in a separate subtribe, Cancrinellainai (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. *Platycancrinella* was synonymized with *Cancrinella* by Brunton et al. (2000), but unlike *Cancrinella* lacks dorsal spines. It does have well formed dorsal pits, whereas figures for the dorsal valve of type *Cancrinella* are obscure (Sarytcheva 1977a, pl. 19, fig. 4b). A genus that comes close to type *Cancrinella* is *Rugania* Waterhouse, 2013, based on *Cancrinella subquadrata* Cooper & Grant, 1975 from the Willis Ranch and Appel Ranch Members of the Glass Mountains, of Guadalupian age. This genus has dorsal spines akin to those of *Cancrinella*, but rugae lie over the disc of both valves, and spines occur along the ventral hinge in well ordered rows, rather than in a dense burst over the ventral ears, as shown in a revision of the type species of *Cancrinella* in Sarytcheva (1977a, pl. 19, fig. 1-9). *Commarginalia* Waterhouse & Nazer in Waterhouse, 2013, based on *C. yukonensis* Nazer & Waterhouse in Waterhouse, 2013 from the Upper Carboniferous Ettrain Formation of Yukon Territory, has dense ventral ear spines like those of *Cancrinella*, but lacks dorsal spines. Commarginal rugae cover both valves. It differs from *Magniplicatina* through its lack of well ordered rows of hinge spines. Older allied genera are also known (Waterhouse 2013).

Magniplicatina shii n. sp.

1996 *Cancrinella singletoni* [not Gobbett] – Shi & Waterhouse, p. 97, pl. 17, fig. 10-20.

Derivation: Named for G. R. Shi.

Diagnosis: Subequilateral shells with well developed ears and moderate to low rugae over disc and trail of both valves. A single row of spines lies along the ventral hinge, and ventral body spines are in quincunx with elongate bases.

Holotype: GSC 97080 from Jungle Creek Formation (Sakmarian), figured by Shi & Waterhouse (1996, pl. 17, fig. 12, 14, 15, 18), here designated.

Discussion: This species is described in Shi & Waterhouse (1996). Although referred to *Cancrinella singletoni* Gobbett (1964, p.

102, pl. 12, fig. 1-7) from the upper Wordiekammen Limestone of Spitsbergen, it differs in having less bulky posterior walls, and in having rugae that cross the disc and trail of both valves, and in having a single row of ventral hinge spines. Gobbett's species is now referred to *Striapustula* Ganelin & Lazarev, 1999, characterized in part by its largely non-rugose ventral disc, and by numerous erect spines along the ventral hinge, as discussed shortly. The Jungle Creek species belongs to *Magniplicatina*, and unlike *Cancrinella*, lacks spines from the dorsal valve. It is readily distinguished from the younger species described from the Yukon and Arctic Archipelago through its subequilateral shape, low though pervasive rugae, and by having spines in only a single row along the ventral hinge. The Skinner Ranch specimens described as *C. fragosa* from the Glass Mountains of Texas by Cooper & Grant (1975, p. 1152, pl. 428, fig. 12-18) are close in shape but have stronger rugae and numerous ear spines. *Magniplicatina parva* (Cooper & Grant 1975, p. 1153) from the Neal Ranch and Skinner Ranch Formations is also close in shape, with low rugae and prominent ventral ear spines.

Magniplicatina janischewskiana (Stepanov, 1934)

Fig. 177, 178

1934 *Productus* (*Linoproductus*) *janischewskianus* Stepanov, p. 39, pl. 3, fig. 23.
1937a *P.* (*Linoproductus*) *janischewskianus* – Stepanov, p. 134, pl. 3, fig. 7.
?1960 *Cancrinella janischewskiana* – Solomina, p. 54, pl. 9, fig. 1.
1970 *C. janischewskiana* – Solomina, p. 87, pl. 5, fig. 13, 14.
1972 *C. janischewskiana* – Ifanova, p. 112, pl. 6, fig. 1-3.
1977 *C. janischewskiana* – Sarytcheva, p. 135, pl. 20, fig. 2.
?1990 *C. janischewskiana* – Kalashnikov et al., pl. 7, fig. 7.
1992 *C. janischewskiana* – Nakamura et al., pl. 9, fig. 2.

Diagnosis: Large shells with wide hinge, fine ribs and closely spaced moderately strong rugae, becoming stronger towards hinge.

Holotype: Specimen figured by Stepanov (1934, pl. 3, fig. 23) and Saytcheva (1977a, pl. 20, fig. 2), of Kungurian age, OD.

Material: One ventral valve from GSC loc. 26406, Devon Island, and a small ventral valve from C-4016, Ellesmere Island, both Assistance Formation. An allied ventral valve from GSC loc. 53931, mid-Takhandit Formation, *Neochonetes culcita* Zone, Yukon Territory.

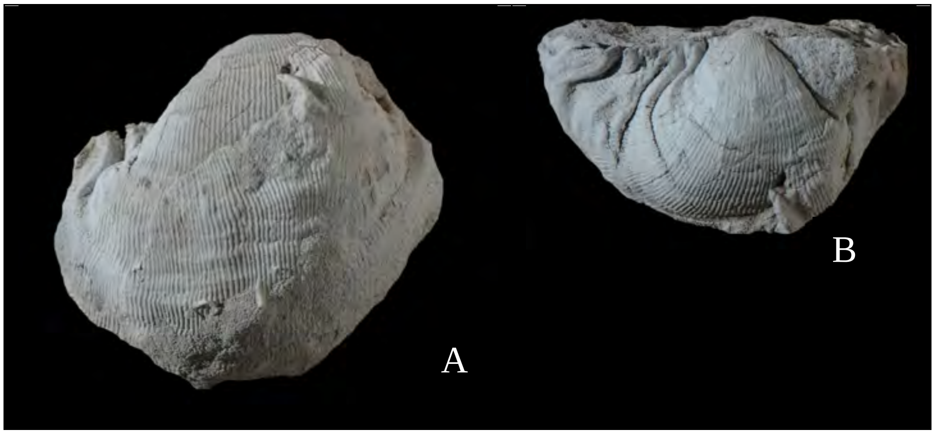

Fig. 177. *Magniplicatina janischewskiana* (Stepanov). A, B, ventral and posterior ventral aspects of specimen GSC 140861 from GSC loc. 26406, Assistance Formation, Devon Island, x1.

Description: The conjoined specimen from GSC loc. 26406 is distorted and now measures 42mm wide, 37mm long and 21mm high, with incurved ventral umbo and posterior walls diverging at 90º, steeply convex and high, and curving out laterally to weakly alate cardinal extremities along a hinge almost as wide as maximum width, which is placed a little in front of mid-length. The ventral valve is ornamented by costellae, numbering eleven in 5mm at mid-length, increasing by intercalation, and crossed by some fifteen low commarginal rugae, varying in strength and symmetry, and extending on to the ears, which lack costellae. Spines lie in two rows along the hinge close to the umbo, and a further row may appear laterally, but the ears are partly destroyed and the full number of spines is now lost. Spines are well spaced in a somewhat quincunxial pattern, often with slightly elongate bases, and each arising from a single rib, or more rarely stemming from two costae, with three ribs passing forward from the spine over the central anterior shell. A small ventral valve from C-4016 has a row of hinge spines, and signs of two further rows of very few spines occur over the anterior ears (Fig. 181). Little of the dorsal valve is exposed, being masked by tough matrix. It shows commarginal rugae and costellae, but the presence or absence of dorsal spines is uncertain.

Fig. 178. *Magniplicatina janischewskiana* (Stepanov), ventral valve GSC 140892 from C-4016, Assistance Formation, x6.

Resemblances: In size and shape GSC 140861 recalls *Productus* (*Linoproductus*) *janischewskianus* Stepanov (1934). The species has been reported widely through Russia, including northeast Verchoyan, mostly from beds of upper Cisuralian age, such as the Kungurian Talatin Formation of Petchora Basin. A ventral valve figured as *Cancrinella janischewskiana* in Kalashnikov et al. (1990, pl. 7, fig. 7) from the Adzvin Suite of the Petchora Basin is close in shape and costation and rugation but has more numerous spines, like the specimen figured by Solomina (1960). The dorsal external mould ascribed to *Linoproductus janischewskianus* Stepanov by Nakamura et al. (1992, pl. 2, fig. 13) from the Svenskeegga (alt. Svenskeega) Member of Spitsbergen is magniplicatin and apparently without dorsal spines, suggesting *Magniplicatina*. As a dorsal valve, it is difficult to compare the shape with that of the present material.

Magniplicatina phosphatica (Girty, 1910)

Fig. 179, 180?

1910 *Productus phosphaticus* Girty, p. 29, pl. 2, fig. 7-9.
1930 *P. phosphaticus* – Branson, p. 30, pl. 7, fig. 8, 9.
1971 *Cancrinella* aff. *phosphatica* (Girty) – Bamber & Waterhouse, p. 174, pl. 19, fig. 1.

Diagnosis: Fine radial ribs and numerous crowded commarginal rugae. Ventral body spines in quincunx with elongated bases.

Lectotype: Specimen figured by Girty (1910, pl. 2, fig. 8, a) from Montpelier, Idaho, here designated. This specimen was noted by Girty (1910) as characteristic.

Material: A ventral valve and external mould of three small ventral valves from JBW 631, Takhandit Formation.

Description: The larger specimen is 23mm wide and more than 29mm long (with the umbo lost) and 12mm high. The shell is elongate, with small ears, bearing a row of spines along the hinge and one anterior ear spine. Costellae cover the valve, commonly about nine in 5mm, but missing from the ears, and the valve is covered by closely spaced slightly irregular radial rugae. Small spines are scattered over the valve, with slightly swollen and elongate bases. The three small external moulds showing the same density of ribs and prominent rugae, and nature of ear spines are more transverse, perhaps because they are immature and would have become elongate with maturity, though this is not certain. Body spines have broad, elongate and raised bases.

The dorsal valve reported in Bamber & Waterhouse (1971) shows that there were no dorsal spines.

Fig. 179. *Magniplicatina phosphatica* (Girty), ventral valve GSC 140862 from JBW 631, Takhandit Formation, x2.

Resemblances: This form is distinguished from the other *Magniplicatina* described in this report by the elongate shape and closely spaced rugae. The new species *shii* is moderately close in its well developed rugae, but is much less elongate. A broad dorsal valve with similar closely spaced rugae was figured in Bamber & Waterhouse (1971, pl. 19, fig. 1) from GSC loc. 52707 in unnamed sandstone of the north Richardson Mountains, assigned to the mid-Takhandit Fps, now *Neochonetes culcita* Zone. It was regarded as close to *Productus phosphaticus* Girty, 1910 from the Phosphate beds of Montpelier, Idaho. The species was also discussed by Branson (1930, p. 30, pl. 7, fig. 8, 9) in recording the species from Wyoming. The description of the species by Girty (1910) is not clear over whether spines were developed over the dorsal valve, and his one figured dorsal valve suggests that spines, if any, were very few, but this requires confirmation. Should dorsal spines be present, then his species will belong to *Rugania* Waterhouse, 2013. No dorsal spines are developed in the Canadian specimens.

Cancrinella distorta Cooper & Grant (1975, pl. 428, fig. 1-11, 41-43; also King 1931, p. 77, pl. 17, fig. 6, 7; Muir-Wood &

Cooper pl. 133, fig. 1, 2 – as *C. phosphatica* [not Girty]) from the Appel Ranch Member of the Glass Mountains in Texas is moderately close in having an elongate shell, and in lacking dorsal spines, belongs to *Magniplicatina*. The ears are more prominent than in the present species, the plicae stronger, and the ventral umbo broader, with spreading flanks and more scattered ventral spines.

Fig. 180. *Magniplicatina phosphatica* (Girty)?, external moulds of immature ventral specimens GSC 140863-140865, x 4, slab from JBW 631, Takhandit Formation.

The appearance comes moderately close in some respects to that of a species named *Costatumulus tazawai* Shen et al. (2000, p. 743, Fig. 12.1-8, 11-14) from the Late Permian Selong Group of south Xizang (Tibet). Rugae are close to those of the present species, but costae are slightly finer, at five in 2mm. Another specimen (Shen et al. 2000, Fig. 12.9, 10) is similar in appearance. The generic position for *tazawai* is clearly closer to Magniplicatini rather than to Auriculispininae, including *Costatumulus* Waterhouse, 1986b, which has fewer and much less regular if any commarginal rugae. *Costatumulus* is further characterized by displaying a well formed subrectangular, radially striate and deeply impressed ventral muscle platform, unlike the dentritic ventral adductor platform of *Magniplicatina* and the species *tazawai*. Brunton (2007, p. 2656, Fig. 1765) endorsed the position with *Costatumulus*, consistent with his misunderstanding of Auriculispinidae in Brunton et al. (2000), but the differences between the genera, involving costation, rugation and internal musculature, are considerable. The generic position of the species *tazawai* has been further compromised, because the outstandingly large ventral ears had been cropped out of the figure presented in Shen et al. (2000, Fig. 12.7), as revealed by first-hand inspection of the types at the National Museum of Victoria, in Melbourne. A fresh and more accurate illustration was provided by Waterhouse (2013, Fig. 17.25, p. 429), and the species referred to a new and distinctive genus, *Auritusinia* Waterhouse, within Magniplicatininai. Brunton (2007) not only discounted the differences briefly summarized above, but discounted ear size as well, although such a difference had been acknowledged in Brunton et al. (2000) as significant for other genera, such as *Protoanidanthus*.

***Magniplicatina*? sp.**

Fig. 181

1971 *Cancrinella* sp. undet. Brabb & Grant, p. 14, pl. 1, fig. 31, 32.

Material: A ventral valve from C-4017, Trold Fiord Formation.

Description: The specimen is broad with wide hinge, but may have been squashed. Commarginal rugae are fine, and spine bases are short but moderately swollen. Radial ribs are fine, some ten in 5mm over mid-length. The ears are comparatively large.

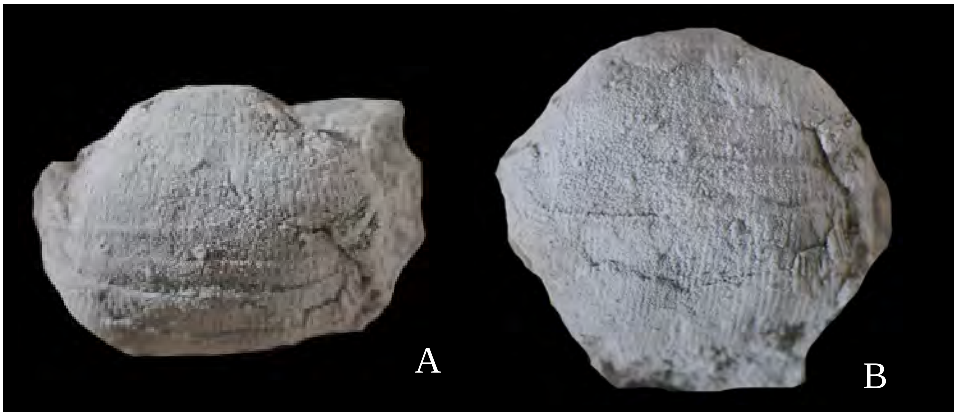

Fig. 181. *Magniplicatina*? sp. A, B, posterior and anterior ventral aspects of ventral valve GSC 140866, x2, from C-4017, Trold Fiord Formation, Ellesmere Island.

Resemblances: *Cancrinella* sp. undet. of Brabb & Grant (1971, p. 14, pl. 1, fig. 31, 32) from the sandstone unit 66ft above the base of the Takhandit Formation, Alaska, appears to be allied, having a transverse outline and closely spaced rugae that are low over the median disc and higher laterally. The other specimen assigned to *Cancrinella* sp. undet. by Brabb & Grant (1971, pl. 2, fig. 18, 19) is reidentified as *Cameronovia milleri* (see p. 198).

Subtribe **CANCRINELLAINAI** (**CANCRINELLINAI**) Waterhouse, 2013

Diagnosis: Close to Magniplicatini, distinguished by lack of prominent rugae from the ventral valve.

Discussion: Genera include *Cancrinella* Fredericks, *Striapustula* Ganelin & Lazarev, *Platycancrinella* Waterhouse and *Calytrixia* Waterhouse.

Genus ***Cancrinella*** Fredericks 1928

Diagnosis: Small compact shells with moderately thin body cavity, large ears with varying number of spines, short to prolonged ventral spine bases with recurved bases and spine tunnels over the disc, numerous dorsal spines, pits common (Saytcheva 1977a, pl. 17, fig. 4b). Commarginal rugae limited to dorsal valve. Double septum posteriorly in dorsal valve.

Type species: *Productus cancrini* de Verneuil, 1845, p. 245 from Kazanian of Russia, OD.

Discussion: Many species previously referred to *Cancrinella* differ from the type species in lacking dorsal spines, and differ further in having well developed commarginal rugae over the ventral disc and trail. These are now referred mostly to *Magniplicatina* Waterhouse. It appears that true *Cancrinella* is limited possibly to Arctic Permian faunas, although as usual there needs to be caution, given the inattention to dorsal ornament in many reports.

In overall appearance and morphology, *Cancrinella* comes close to *Striapustula* Ganelin & Lazarev, 1999, and like that genus has a double posterior dorsal septum, similar cardinal process, and well developed muscle scars and ventral spines. This genus has been recognized for several Arctic species that had often been lumped as *Cancrinella* by authors, although some features are not entirely clear. Ganelin & Lazarev (1999) did not illustrate the nature of the muscle scars, and the nature of the ventral ear spines is poorly shown by specimens ascribed by various authors to what is now called *Striapustula*. Ganelin & Lazarev, 1999 reported that spine bases formed two or three rows in a cluster (without specifying exactly where - see English version, Ganelin & Lazarev 1999, p. 247) but presumably over the ventral ears, and specified as extending on to the shell sides, though whether that means the umbonal slopes or lateral margins remains obscure, and in need of clarification. For *S. magna* Ganelin & Lazarev, the spine bases form a cluster of rare thin “tubercles that become larger on the sides”, and for *S. pectiniformis* Ganelin & Lazarev, there are numerous “tubercules” (= spine bases) in a two to three row band, extending “on to the lateral bases” (meaning umbonal slopes?). The descriptions, with measurements, are not reinforced by adequate illustrations.

There is a species from Asselian faunas of Western Australia that comes close in many aspects to *Striapustula*. It was described and named *Terrakea capillata* Waterhouse in Foster & Waterhouse (1988, p. 156, Fig. 8d-h), and revised by Archbold (1995, p. 106, Fig. 6A-L) with the demonstration that there were no dorsal spines. Waterhouse (2010) made the genus type of a new form *Calytrixia*. *Calytrixia* is close in many respects to *Striapustula* in its ventral ornament of ribs and spines, and lack of dorsal spines. The lateral ventral spines form a band over the ears and lateral margins, without crossing onto the umbonal slopes, and the spines are dense and erect, and vary in diameter from thick to thin, more diversified than in *Striapustula* or *Cancrinella*. Over the ventral disc, bases may be elongate, and especially the dorsal valve may be crossed by subdued commarginal rugae. Over the dorsal disc, there are no conspicuous dorsal dimples or pits. Within the dorsal valve, the median septum commences immediately in front of the cardinal process, without a double septum, and a low ridge diverges laterally at an angle from near the base of the septum. The arrangement differs in these minor ways from *Striapustula*, which was a younger genus.

Platycancrinella Waterhouse, 1983a from the Late Permian of the Himalaya in Nepal is larger than other genera in the tribe, and has crowded ventral ear spines over large ears and short ventral spine bases. *Platycancrinella* was synonymized with *Cancrinella* by Brunton et al. (2000), even though those authors had allowed that the *Cancrinella* dorsal valve has spines, whereas *Platycancrinella* lacks dorsal spines. It does have well formed dorsal pits, whereas type *Cancrinella* appears to lack dorsal pits, though figures are obscure (Sarytcheva 1977a, pl. 19, fig. 2b, 4b) and so perhaps should be regarded with caution. In many facets of its morphology, *Platycancrinella* shares the same attributes as those of *Striapustula*, but shells referred to *Striapustula* are narrow and swollen, whereas the type species of *Platycancrinella* is transverse. As *Platycancrinella* has clear priority, the relationship may need to be reviewed, but certainly the shape differs. Or is that a reflection of different geographic setting and/or younger age? Internally its ventral adductors are striate, which offers a potential point of difference, and the dorsal median septum is broad between the adductors, with only a median groove, rather than being clearly split in two. (See Waterhouse 1983a, 2013, Fig. 17.27).

As explained below, Yancey (1978) regarded Costellariinae Muir-Wood & Cooper, 1960 as Linoproductidae, equivalent to Linoproductoidea (or Proboscidelloidea in updated terminology). As understood by Yancey, this would assume naming rights over Paucispinauriidae Waterhouse, 1986a. *Costellaria* Muir-Wood & Cooper had proved to be a junior homonym for *Costellaria* Swainson, 1840, and was renamed *Costellarina* by Cooper & Muir-Wood, 1967, so Yancey (1978, p. 287) renamed the subfamily Costellarininae Muir-Wood & Cooper, and provided a fresh diagnosis. But the possibility that *Costellarina* is linoproductoid or even more tolerantly linoproductiform, cannot be sustained. Muir-Wood & Cooper preferred an aulostegid relationship, and Brunton et al. (2000, p. 599) classed *Costellarina* as a member of Aulostegidae, and treated Costellarinae as a synonym of Institellinae Muir-Wood & Cooper, 1960. Brunton et al. made no mention of the emendation proposed by Yancey (1978).

Cancrinella arctica (Waterhouse, 1971c)

Fig. 182 – 184

1971c *Terrakea arctica* Waterhouse, p. 354, pl. 1, fig. 1-15, pl. 2, fig. 1-14, 17, text-fig. 4.
1971c *Terrakea* sp. Waterhouse, Fig. 15.
1971 *T. arctica* - Bamber & Waterhouse, p. 180, pl. 22, fig. 11-13.
1978 *Costellarina arctica* – Yancey, p. 291.

Diagnosis: Small highly arched shells with fine costellae over both valves, ventral disc spines numerous and fine, either erect or with slightly prolonged bases and a spine tunnel pierces the shell in front of each spine, ear spines clustered and somewhat thicker. Dorsal valve with elongate pits in quincunx, and fine erect spines. No interarea and no ventral cicatrix, dorsal valve with double septum posteriorly, and median septum in front.

Holotype: GSC 24475, figured in Waterhouse (1971, pl. 2, fig. 1-3) and herein as Fig. 182G, I, from GSC loc. 53850, unnamed Permian sandstone (*Cameronovia milleri* Zone) of Richardson Mountains, north Yukon Territory, OD.

Material: Specimens came from what is now the *Dyoros modestus* Zone at GSC loc. 53848 and 53850, and slightly younger beds at GSC localities 53822, 53823 and 53834, in the *Cameronovia milleri* Zone of unnamed sandstones in the Richardson Mountains. Further specimens came from the Assistance Formation at Melville Island, at C462, C-463, C-464 and C-1872 and Trold Fiord Formation at C-465. An additional ventral valve comes from GSC loc. 26406, Assistance Formation, Devon Island.

Description: The species is described in Waterhouse (1971c). Dorsal spines were described and a dorsal valve has been borrowed from the Geological Survey of Canada to confirm their presence. Most of the spines are limited to the posterior lateral part of the valve, and whilst some are of uncertain length, others are definitely short and little better than tubercles. A very few erect spines lie over the posterior disc, and a few emerge from the trail. They emerge independently of the regularly arranged elongate dimples in quincunx, often beside or near a dimple, and emerge along the crests of two or three rugae over the posterior lateral margins. A row of slender erect spines extends along the dorsal hinge, and other spines lie over the posterior lateral shell and anterior trail, with scattered disc spines.

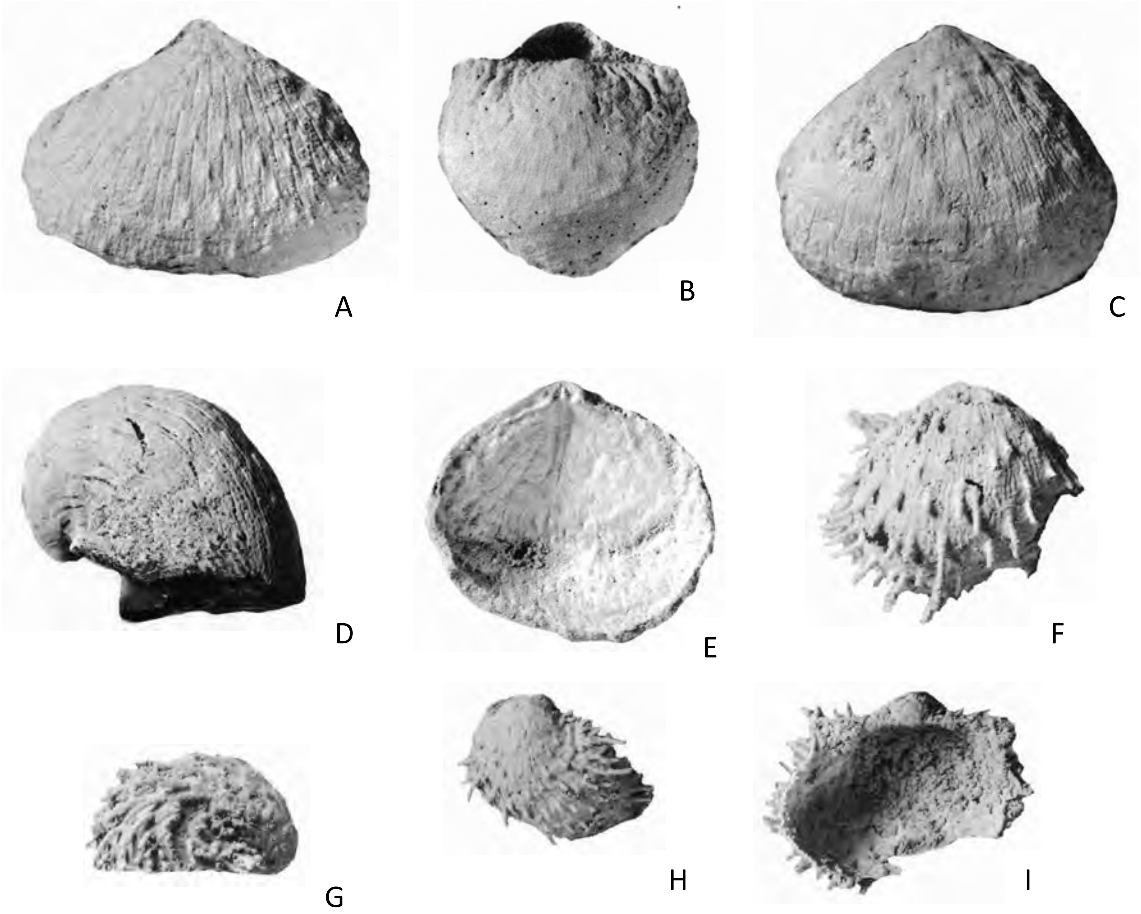

Fig. 182. *Cancrinella arctica* (Waterhouse). A, ventral internal mould GSC 22490 from C-463. B, dorsal aspect, external mould, GSC 24488 from C-462. Some of the spines have been enhanced by adding black dots. C, ventral internal mould GSC 24493 from C-464. D, lateral aspect of ventral internal mould, GSC 24492 from C-463. E, dorsal aspect of internal mould, GSC 24487 from C-462. Specimens x2 from Assistance Formation, Melville Island. F, ventral valve GSC 24476. G, I, lateral and internal view of ventral valve, holotype GSC 24475. H, tilted lateral view of ventral valve GSC 24479. Specimens F – I from GSC loc. 53850 and 53853 (fig. H), unnamed sandstone unit, McDougall Pass, Richardson Mountains, x2. (Waterhouse 1971c).

Resemblances: As figured in Sarytcheva (1977a, pl. 19, fig. 1-9), *Cancrinella cancrini* (Verneuil) is close in general shape, with less regularly arranged ventral spines, and broad posterior septum with two poorly defined divisions. Another Kazanian species, *C. missunae* (Mirchink) has very fine ribs.

The species approaches *Striapustula magna* Ganelin & Lazarev, 1999 in shape and size. In this species, ventral ear pustules were recorded as rare, becoming larger on the sides and reaching up to 1mm in diameter. The species comes from the Djigdalin Horizon, and *Megousia kulikii* regional Zone, which overlaps the range of *arctica*, but has no dorsal spines.

Cancrinella singletoni Gobbett (1964, p. 102, pl. 12, fig. 1-7) from the upper Wordiekammen Limestone of Spitsbergen is now placed in *Striapustula* by Ganelin & Lazarev (1999). This species has fine ribs and long ventral spine bases, and lacks dorsal spines. Unfortunately, the nature of ear spines has not been clearly described for *singletoni*. The shells are more elongate than *arctica*, but close in what is known of ornament. *Cancrinella spitsbergiana* Gobbett (1964, p. 104, pl. 12, fig. 8-12) from the Spirifer Limestone is also externally close to *Cancrinella arctica*, in respect of the ventral disc and trail, with long ventral spine bases and long ventral spine tunnels, but again, with no data on the ventral ear spines. The species was also reported by Grigorieva et al. in Sarytcheva (1977a, p. 132, fig. 13-15) and by Ganelin & Lazarev (1999, p. 251, pl. 7, fig. 26-31). Ganelin & Lazarev (1999) regarded the species as likely to be of Solikamian (ie. lower Ufimian) age, with occurrences in the upper Djigdalin beds of northeast Russia and in the Levorkut Formation of the Petchora Basin. Material so identified by Licharew & Kotlyar (1978, pl. 12, fig. 19-21) from the *Parafusulina stricta* Zone in South Primoyre differs specifically in its stout lateral ventral spines.

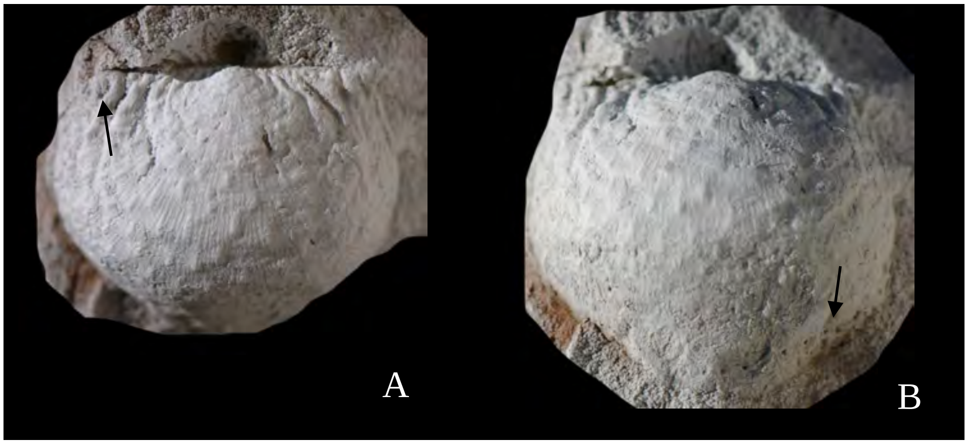

Fig. 183. *Cancrinella arctica* (Waterhouse), dorsal aspect, external mould, GSC 24488, C-462, Assistance Formation, Melville Island, x3. A, disc view, with spine position indicated by dot (not retouched). B, anterior view showing weak dorsal nasutation. Some spine positions indicated by arrows.

Two species from northeast Greenland belong to *Striapustula*. *Productus bolchovitiensis* Mirchink (1938, pp. 322, 340, pl. 2, fig. 10-12), also discussed by Frebold (1931, 1937) and extensively figured by Dunbar (1955, p. 71, pl. 3, fig. 9-20) as *Cancrin-*

ella, has many ventral ear spines, according to the text in Dunbar (1955), and no dorsal spines. The ventral valve is swollen and elongate, and dorsal pits are, if present, small. *Productus cancrini germanicus* Frebold (1933, p. 50, pl. 6, fig. 1-4, 11A, B) and possibly including ?*Productus* sp. of Mirchink (1938, p. 340, pl. 2, fig. 3-5) were referred to *Cancrinella* by Dunbar (1955, p. 72, pl. 3, fig. 21-29) but lack dorsal spines, unlike *Cancrinella*. The species is swollen, but distinctly less elongate than *bolchovitiensis*, and has prominent broad and moderately long spine bases over the ventral disc, and a very long median septum (Dunbar 1955, pl. 3, fig. 24).

Several potential allies are known from the Middle Permian of the Glass Mountains of Texas. These belong to Paucispinauriinae, having numerous dorsal spines. *Grandaurispina* Muir-Wood & Cooper, 1960 is diagnosed by the very large size of ear spines in the type species, whilst a few forms described by Cooper & Grant (1975) are indistinguishable from type *Terrakea,* as also noted by Briggs (1998, p. 163). *Appelinaria* Waterhouse, 2013, p. 418 from the Appel Ranch Member of Capitanian age has thick dorsal spines postero-laterally, and *Bellaspinosina* Waterhouse 2013, p. 419 from this level and underlying Willis Ranch Member (Wordian) has numerous fine spines over both valves.

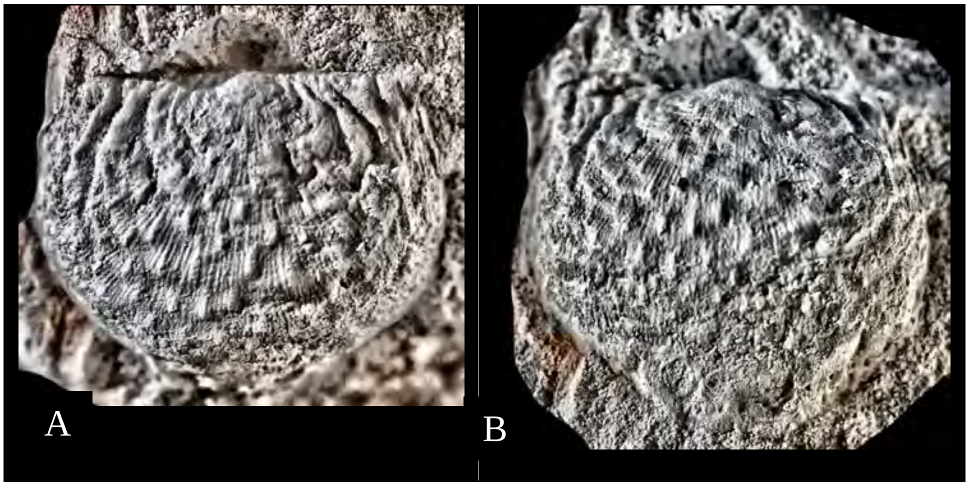

Fig. 184. *Cancrinella arctica* (Waterhouse), dorsal aspect, external mould, GSC 24488 from GSC loc. C-462, Assistance Formation, Melville Island. Under local equalization, x3. A, showing disc and part of trail. B, tilted view to show more of anterior, with nasutation.

Yancey (1978, p. 291) regarded the species *arctica* as a member of *Costellarina* Cooper & Muir-Wood, 1967, considering that the dorsal spines were absent, and discovering that the ventral disc spines of *Costellarina* continue forward from the spine base, just as in *Terrakea* (and allies). He regarded *Costellarina* as a member of Linoproductidae, as *T. arctica* used to be classed in those earlier days of cruder classification, and he excluded the hypotypes from the Assistance Formation, presumably because they were said to display dorsal spines, though there is otherwise close agreement between the various specimens described in Waterhouse (1971c), and the apparent lack of spines is deemed to be due to poor preservation and poor exposure.

The cardinal process and other aspects differ from features in *Costellarina*, which has a broad cardinal process like that of aulostegids and productellids. No specimens assigned to *arctica* show a large umbonal cicatrix, and none show a ventral interarea. Yet these features are strikingly developed in the type species of *Costellarina*, and in species described by Yancey (1978), which have a wide and slender cardinal process. Yancey was wrong: *Costellarina* is aulostegid, and *arctica*, whatever its generic affinities, is paucispinauriid.

A number of Russian Arctic species have definite dorsal spines, and were assigned to *Terrakea* in Sarytcheva (1977a). Two distinctive genera were recognized by Waterhouse (2001) as *Spargospinosa*, based on *Terrakea belokhini* Ganelin, and *Pinegeria*, based on *Terrakea*? *pinegensis* Grigorieva. Neither are congeneric with the present form, distinguished by different detail of spines and shape. *Terrakea* aff. *arctica* Waterhouse was recorded from the Ufimian of Kanin Peninsula, Russia, by Stepanov et al. (1975, pl. 1, fig. 9-11), but ventral spines on the Kanin specimen are more numerous and the spine bases appear to be shorter. A paucispinauriid genus is present in the Sakmarian fauna of the Jungle Creek Formation of Yukon Territory, described as *Terrakea*? sp. by Shi & Waterhouse (1996, p. 100, pl. 17, fig. 21, 22, 24; Shi & Grunt 2000, pl. 1, fig. F, I). It differs from the present form in its broad outline, comparatively flat dorsal disc, and well-developed dorsal spines.

Class Rhynchonellaata (Rhynchonellata) Williams et al., 1996

Superorder PENTAMERUSIFORMI (PENTAMERIFORMI) Schuchert & Cooper, 1931

Order ORTHISIDA (ORTHIDA) Schuchert & Cooper, 1932

Superfamily **ENTELETESOIDEA** (**ENTELETOIDEA**) Waagen, 1884

Family **RHIPIDOMELLAIDAE** (**RHIPIDOMELLIDAE)** Schuchert, 1913

Subfamily **RHIPIDOMELLAINAE** (**RHIPIDOMELLINAE**) Schuchert, 1913

Genus ***Rhipidomella*** Oehlert, 1890

Diagnosis: Dorsibiconvex, fine costellae, strong dental plates and median ventral septum.

Type species: *Terebratula michelini* Léveillé, 1835, p. 39 from Visean of Belgium.

Rhipidomella transfigona n. sp.

Fig. 185, 186

Derivation: transfigo – transix, pierce, Lat.

Diagnosis: Small, moderately developed hinge and delthyrium, no sulcus or fold, two to three fine ribs in one millimetre.

Holotype: GSC 140869 figured as Fig. 185C, D from GSC 53846, north Richardson Mountains, here designated.

Material. Eight specimens with valves conjoined, thirty seven ventral valves and two dorsal valves, silicified, from GSC loc. 53846, unnamed sandstone in Richardson Mountains.

Description: A small complete ventral valve measures 9mm in width, 9.8mm long and 3.5mm high. A dorsal valve is 7.5mm wide and long and 2.5mm high. In the specimens with valves conjoined the ventral valve is slightly higher than the dorsal valve, with maximum height over the hinge. The walls of the ventral umbo diverge at 90º to 95º approximately, and curve slightly into a greater angle, before rounding into obtuse cardinal extremities, and the remainder of the ventral valve is of gentle convexity, with rounded margins and a very shallow and narrow median groove or sulcus. The dorsal valve is rather similar, slightly less inflated, with broader umbo measuring 110º in angle, and with a shallow sulcus for most of the length in a few shells. Both valves are ornamented by fine ribs, two to three in 1mm anteriorly. The ribs are visible as crenulations around the periphery of both valves. As a rule, three or four growth steps are developed anteriorly in larger specimens. Slender punctae open to the exterior over parts of the shell, especially ventral valve, and are arranged in quincunx, opening in interspaces and over ribs, and also visible over the interior of some specimens.

There is a wide delthyrium, triangular, with angle close to 70º, bordered by dental plates that terminate each in a short stubby tooth. The posterior wall becomes thickened, with a ridge continuing forward from the teeth. Adductor impressions lie each in an oval slightly elongate depression with fine longitudinal markings, and continue forward as a low groove. On either side are faint oval diductor impressions extending as far forward as the anterior median ridge.

The dorsal valve displays dental sockets and low socket plates, which are possibly broken or incompletely silicified. In between lies a blunt knob-like cardinal process, bearing a median groove in one of the two specimens. The base in front is smooth, but a coarse ridge arises anteriorly, between two large oval depressions, and in one specimen there are posterior and two anterior rounded depressions, divided by a broad ridge with gently rounded crest.

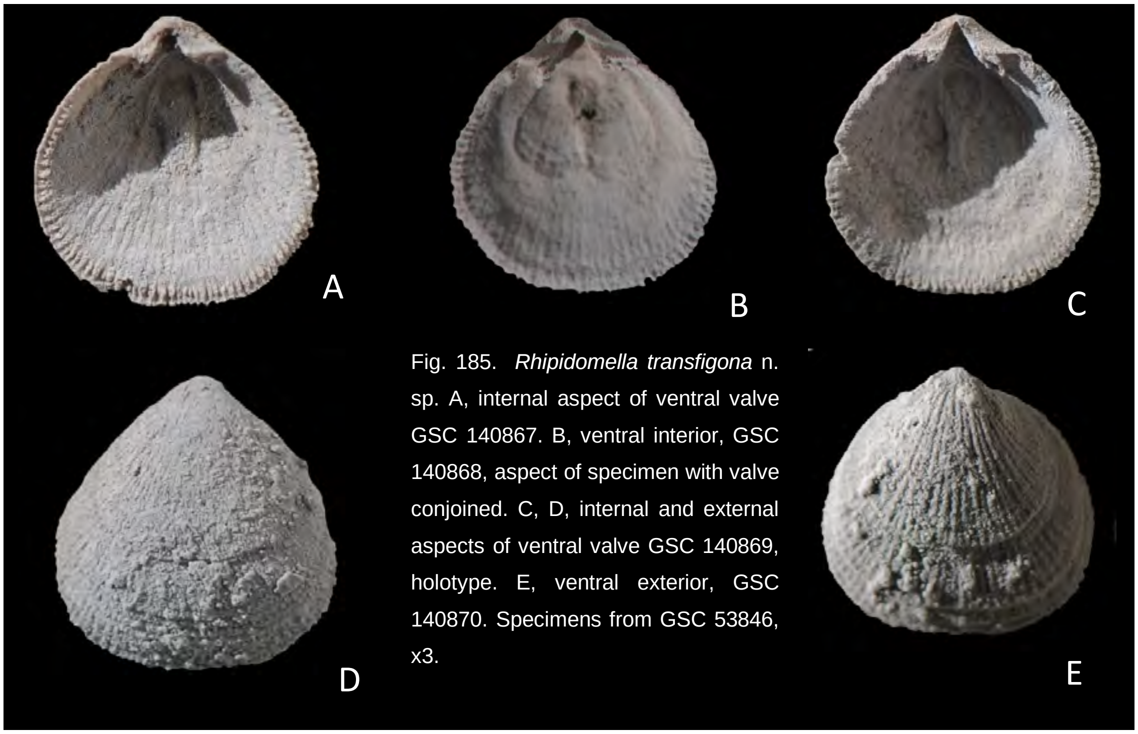

Fig. 185. *Rhipidomella transfigona* n. sp. A, internal aspect of ventral valve GSC 140867. B, ventral interior, GSC 140868, aspect of specimen with valve conjoined. C, D, internal and external aspects of ventral valve GSC 140869, holotype. E, ventral exterior, GSC 140870. Specimens from GSC 53846, x3.

Resemblances: *Rhipidomella* is rarely found in deposits of Permian age, and this form is the only representative known for the Middle Permian in Canada. Even in the Glass Mountains Permian of Texas, only three species are known. *R. hispidula* Cooper & Grant (1976b, p. 2612, pl. 664, fig. 39-90, pl. 667, fig. 44-65) from the Bone Spring and the Wedin Member of Cathedral Mountain Formation is readily distinguished by its wide delthyrium and reduced or even obsolete ventral interareas. The ventral umbo tends to be more pointed, and ribs are slightly finer, at three in 1mm. The abundantly illustrated *R. hessensis* King (1931, pl. 1, fig. 2a-d, 3a, b, 4; Stehli 1954, p. 291, pl. 17, fig. 1-6; Cooper & Grant (1976b, p. 2610) is a somewhat broader shell with sulcus suggested in many specimens, and broad ventral umbo. The species ranges through the Skinner Ranch, Hess, Hueco, Bone Spring and Cibolo Formations of the Glass Mountains and Sierra Diablo Range. A more restricted species confined to the early Permian Neal Ranch and Lenox Hills Formations was described as *R. miscella* Cooper & Grant (1976b, p. 2613, fig. 1-38), close to *R. hessensis*, and distinguished by a different pattern of open tubules scattered over the external surface of the ventral valve, whereas those in *hessensis* are concentrated in two lateral strips. These tubules open externally in all three species from Texas. Their opening externally does not reflect wear of the shell, or imperfect silicification, because the ribbing that is restricted to the outer shell is well developed, and the tubules or punctae open over and between the ribs, although it might be deemed that the ribs were formed by an extremely thin exolayer. Normal *Rhipidomella*, typified by the type species *Terebratula michelini* Léveillé, shows no external punctae, but well developed and crowded pores pierce the main layer of shell. Clearly more study is needed on the nature of the tubules in the Glass Mountains specimens. In the present species from the north Yukon Territory, fine open pores are visible externally in some specimens (see Fig. 186F), much finer than in the Texan specimens, and well and evenly spaced.

Rhipidomella cordialis Grant (1976, p. 37, pl. 2, fig. 31-41, pl. 3, fig. 1-53) from the Roadian Khao Phrik Limestone of Thailand has scattered fine pores. It is distinguished from the present species by its short hinge and relatively wide delthyrium, as well as its somewhat subpentagonal shape.

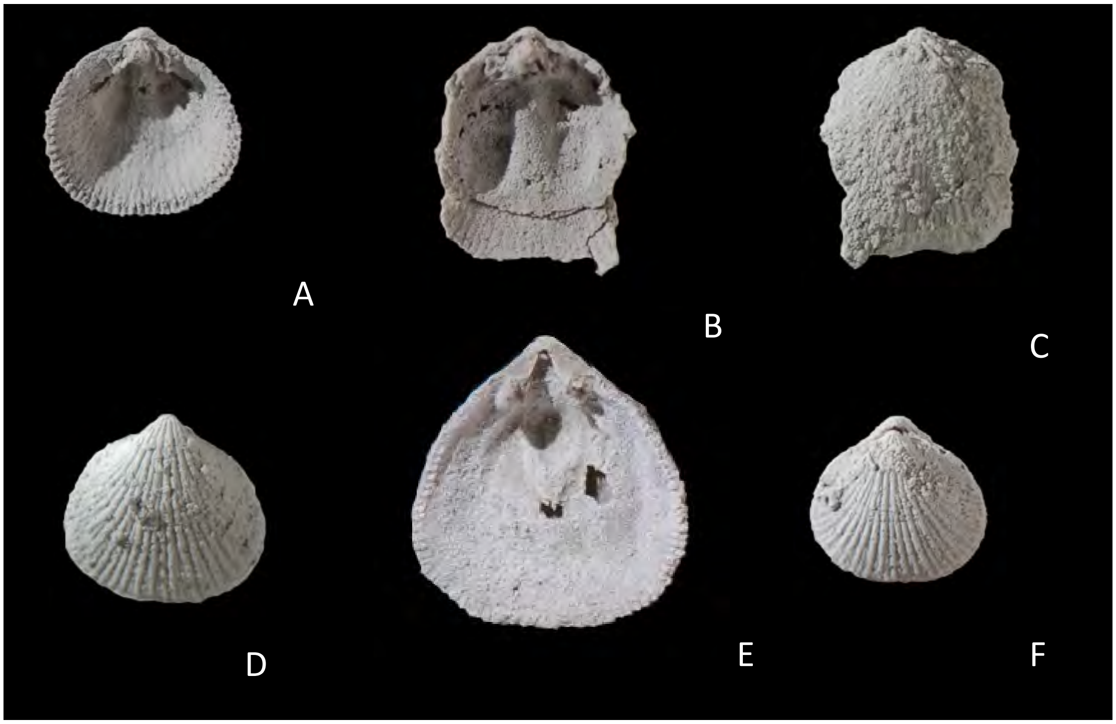

Fig. 186. *Rhipidomella transfigona* n. sp. A, dorsal interior GSC 140871. B, C, dorsal interior and external aspects of GSC 140872. D, F, ventral and dorsal aspects of specimen GSC 140873 with valve conjoined. E, interior of ventral valve, GSC 140874. Specimens from GSC loc. 53846, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory, x3.

Five species of *Rhipidomella* were described from Arctic Russia by Lazarev (1977), but they are all of Carboniferous age. Indeed the genus is widely developed and moderately common in faunas of Carboniferous age world wide, and occurrences relevant to Yukon material are reviewed in Waterhouse (2018b, pp. 157-161). *R. borealis* Waterhouse (2018b, p. 155, Fig. 116, 117) was described from the Wahoo Formation of the Lisburne Group in the northern Yukon Territory, with small Foraminifera judged to be of likely late Bashkirian to mid-Moscovian age. The species *borealis* has wider ventral hinge and wider delthyrium. Open tubules, their visibility enhanced through a degree of surface weathering, are regularly spaced and in quincunx.

Order RHYNCHONELLAIDA (RHYNCHONELLIDA) Kuhn, 1949

Discussion: The remarkable diversity of taxa within Order Rhychonellida suggest that much more than one order was involved in their make-up and interrelationships, and invites at least superordinal distinction from Pentameriformi. But such analysis must be deferred, at least for the present.

Suborder RHYNCHONELLAIDINA (RHYNCHONELLIDINA) Kuhn, 1949

Superfamily **RHYNCHOPORAOIDEA** (**RHYNCHOPOROIDEA)** Muir-Wood, 1955

Family **RHYNCHOPORAIDAE** (**RHYNCHOPORIDAE)** Muir-Wood, 1955

Subfamily **RHYNCHOPORAINAE** (**RHYNCHOPORINAE)** Muir-Wood, 1955

Genus ***Rhynchopora*** King, 1865

Diagnosis: Endopunctae simple. Sulcus and fold well developed. Costae simple, flattened and grooved anteriorly, prolonged as a rule around the periphery as sharp spines. In the dorsal valve, the septalium has a foramen overlain by a cover plate.

Type species: *Terebratula geinitziana* Verneuil, 1845, p. 83 from north Dvina River Basin (Kazanian), Russia.

Rhynchopora taylori Girty, 1910

Fig. 187 – 189

1910 *Rhynchopora taylori* Girty, p. 34, pl. 3, fig. 8, a-c.
1930 *R. taylori* – Branson, p. 34, pl. 2, fig. 17-19, pl. 3, fig. 5-9.
?1953 *R. taylori* – Cooper, p. 47, pl. 15A, fig. 1-21.
cf. 1963 *R. lobjaensis* [not Tolmachev] – Ustritsky & Chernyak, p. 99, pl. 27, fig. 1-6.
cf. 1970 *R. lobjaensis* – Zavodowsky, p. 130, pl. 55, fig. 5, 6, pl. 67, fig. 7-10.

Diagnosis :For Canadian material, small suboval usually weakly transverse shells with wide flat-floored anterior sulcus and broad anterior fold, costae cover the shell, usually four up to six over fold, four or five in sulcus as a rule, crests may be slightly narrowed. No specimens known to have steep anterior face, perhaps reflecting degree of maturity.

Holotype: Sole specimen figured by Girty, 1910, p. 34, pl. 3, fig. 8, a-c from Phosphate beds of Park City Formation, Idaho, by monotypy.

Material: Twelve specimens with valves conjoined from GSC loc. 53931, basal Takhandit Formation, Tatonduk River, and a ventral valve from GSC loc. 53847, unnamed sandstone, *Dyoros modestus* Zone, section 116P-11, McDougall Pass, Richardson Mountains (Bamber 1972, p. 143). A dorsal valve from C-4003, Assistance Formation and a ventral valve from C-4007, ventral valve from C-4039, probably the same formation, both from Ellesmere Island. A ventral valve from C-4020, Trold Fiord Formation, Ellesmere Island.

Description: Specimens from GSC loc. 53931 have four or rarely five sulcal costae, and the costae over especially the dorsal valve have narrow tented crests. Shells tend to be transverse, with rounded cardinal extremities and shallow sulcus commencing near mid-length, and low broad anterior fold. Possibly no specimens are mature, and only one specimen shows slit anterior costae. The shell is densely punctate. Efforts to clarify the internal structure of the dorsal valve have been frustrated by the calcareous matrix, and in other instances, the granular nature of the infilling sediment.

Resemblances: *Rhynchopora taylori* Girty (1910, pl. 3, fig. 8, 8a-c) from the Park City Formation of Idaho is a taxon close in shape to present specimens, with comparable number of ribs. The umbo is broader and the posterior walls diverge more than in the Canadian specimens. There are five costae in the sulcus. Further material was described by Branson (1930, p. 34, pl. 2, fig. 17-19, pl. 3, fig. 5-9) from the Phosphoria beds of the Park City Formation in Idaho and Wyoming, figuring a larger transverse specimen with steep anterior face to suggest that other specimens were less mature, with costae like those of the Canadian specimens.

Cross-sections show a cover plate. Cooper (1953, p. 43, pl. 15, fig. 1-21) reported the species from the mid-Permian faunas of the Monos Formation in Western Sonora, Mexico, but most of his figured specimens have more costae over the sulcus and fold. *R. palumbula* Cooper & Grant (1976b, p. 2661) from the Word Formation, including Appel Ranch Member, in the Glass Mountains of Texas is moderately close to *R. taylori*, but is more angular in shape and often has one or two more sulcal costae.

Fig. 187. *Rhynchopora taylori* Girty. A, D, dorsal and ventral views of specimen GSC 140875 with valves conjoined, x1, x3. B, dorsal view of specimen GSC 140876 with valves conjoined, x1, x3. C, dorsal view of specimen GSC 140877 with valves conjoined, x1, x3. Specimens from GSC loc. 53931, Takhandit Formation, Yukon Territory.

The Canadian specimens come close externally to a form from the Russian Arctic, *Rhynchopora lobjaensis* Tolmachev (1912, p. 130, pl. 4, fig. 6; Licharew 1934b, p. 40, pl. 9, fig. 12-24), and further described from the Baikur Suite by Ustritsky & Chernyak (1963, p. 99, pl. 27, fig. 1-6), and Omolon and underlying Djigdalin beds by Zavodowsky (1968). The specimens conform only to a degree in shape, sulcus, fold and costation with aspects in the present specimens, and appear to agree in the state of maturity. The Canadian specimens have fewer costae in the sulcus and over the fold than in Tolmachev's specimens, but are closer in those respects to the large suite of specimens figured from the Baikur Suite of Novaya Zemlya, as described by Ustritsky &

Chernyak (1963) and specimens from the Djigdalin and Omolon levels described by Zavodowsky (1970). These shells tend to be broad with widely diverging posterior walls, like the shape for some of the Canadian specimens.

Fig. 188. *Rhynchopora taylori* Girty. A, ventral view of specimen GSC 140876 with valves conjoined. See Fig. 187B. B, ventral view of specimen GSC 140877 with valves conjoined. See Fig. 187C. Specimens from GSC loc. 53931, Takhandit Formation, Yukon Territory, x4.

In rounded shape, the present specimens are indeed quite close to the type species of the genus, *Rhynchopora geinitzianus* (de Verneuil, 1845) from the lower Kazanian of Russia, but have stronger costae posteriorly, and a more sharply raised fold anteriorly, compared with the holotype. Material figured by Erlanger (1981) shows more elongate shells and finer posterior costae, whereas Zechstein specimens that were described by Mahlzahn (1937, p. 45, pl. 3, fig. 11-13) have a smooth ventral umbo and seven to eight costae in the sulcus. The shape is transversely rounded. Ufimian specimens from Kanin Peninsula, Russia, were figured as *Rhynchopora geinitziana* (Verneuil) by Stepanov et al. (1975, pl. 2, fig. 10-14). The interior of *Rhynchopora geinitzianus*, type species for the genus, was examined by Licharew (1960, pl. 52, fig. 15v), as summarized in the generic diagnosis.

Costae on the Canadian specimens are fewer and stronger than those of the numerous species of *Rhynchopora* that were described by Cooper & Grant (1976b) from approximately correlative beds of Texas.

Shells from the Spirifer Limestone of Spitsbergen that were referred to *Rhynchopora nikitini* Tschernyschew (1889, p. 369, pl. 6, fig. 20) by Gobbett (1964, p. 129, pl. 16, fig. 18-21, text-fig. 18) have a comparable number of sulcal costae, numbering four or five, and the costae are somewhat tented with narrow crests. Gobbett (1964, p. 129) included specimens described by Toula (1874, 1875a, 1875b) and Wiman (1914, pl. 1, fig. 13-20) and more transverse specimens figured by Stepanov (1937b, pl. 9, fig. 13) in synonymy. Most of the present specimens appear to be more transverse than the Spitsbergen specimens, and identification is discouraged by the lack of internal detail, and uncertainty about the degree of maturity of the Canadian specimens. Gobbett emphasized the sharply truncate nature of the anterior shell in his interpretation of the species, and such is not shown by the Canadian specimens, possibly because they are not at full maturity. The species *nikitini* has been widely reported (eg. Kashirtsev

(1959, pl. 33, fig. 1-4, from the Kigiltass Suite of Verchoyan), and discrimnation requires fuller knowledge of the morphology. Specimens figured as *nikitini* by Ifanova (1972, pl. 9, fig. 4-6) from upper Artinskian beds of the Petchora Basin are also close to the Canadian specimens, though more transverse with wider ventral umbo. They have a similar number of sulcal costae. Stehli & Grant (1971, p. 513, pl. 66, fig. 1-11) reported specimens as *Rhynchopora nikitini* Tschernyschew from the Svartevarg cliffs of Axel Heiberg Island that could well be related to the present suite, agreeing in outline, but having a high anterior face. The interior is moderately well preserved (Stehli & Grant 1971, pl. 66, fig. 6, 10), and reveals an apically perforated hinge plate, but no recorded or visible cover plate. The material is like *nikitini* in some respects, but has a less well-defined ventral sulcus and less steep anterior face, although full comparison is not possible, and the relationship between *nikitini* and *taylori* in need of further study.

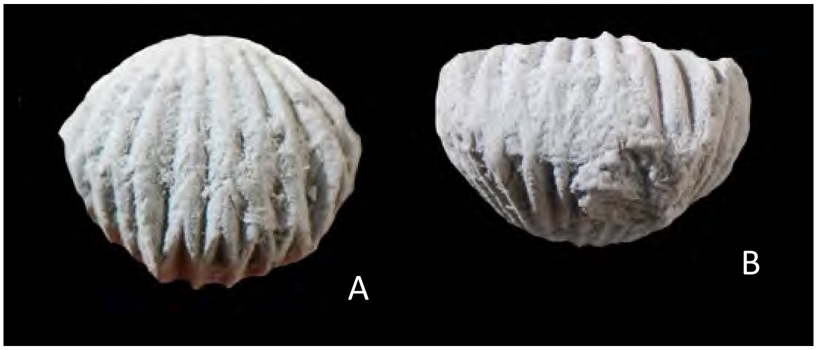

Fig. 189. *Rhynchopora taylori* Girty. A, anterior view of specimen GSC 140876 with valves conjoined. See Fig. 187B, 188A. Note the anterior costal notches, not seen in other specimens. B, anterior view of specimen GSC 140877 with valves conjoined. See Fig. 187C. Ventral valve on top for both figures. Specimens from GSC loc. 53931, Takhandit Formation, Yukon Territory, x3.

Another species assigned to *Rhynchopora* and of somewhat similar external appearance is *Rhynchopora kochi* Dunbar (1955, p. 114, pl. 19, fig. 7-23; 1961, pl. 2, fig. 1) from central east Greenland, although it is more transversely oval, and has finer ribs posteriorly, and more pointed ventral umbo. Anterior costal notches are present. Dunbar (1955, pl. 19, fig. 15) reported well developed dental plates, and a wide septum-supported hinge plate with a small foramen. The hinge plate, it was stated, was supported by a pair of crural lamellae that converge immediately in front of the perforation to form a median septum and enclose a very small triangular crural cavity.

Such occurrences suggest that the species *taylori*, like that of many reported *nikitini, lobjaensis* and *geinitzianus*, ranges throughout the Middle Permian. But the similarities noted in this account are based only on external similarities, and cannot be deemed conclusive, given the lack of information about the interiors of so much material. What is brought out is the similarity in general shape and costation amongst a widespread range of specimens, now in need of closer analysis and investigation of internal structures.

Suborder STENOSCISMA**I**DINA (STENOSCISMAT**I**DINA) Waterhouse, 1981b

Superfamily **STENOSCISMAOIDEA** (**STENOSCISMATOIDEA)** Oehlert, 1887

Family **STENOSCISMAIDAE** (**STENOSCISMATIDAE)** Oehlert, 1887

Subfamily **STENOSCISMAINAE (STENOSCISMATINAE)** Oehlert, 1887

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 median septum.

Type species: *Terebratula schlotheimii* (= *schlotthemi*) von Buch, 1834, p. 59 from Zechstein (Wuchiapingian) of Germany, OD.

Discussion: I leave out the superfluous "at" suffix from the ordinal and family name: it adds nothing of value, and misleads as to the name of the genus, which is *Stenoscisma*, not *Stenoscismata*. The subtleties of medieval Latin as interpreted in more recent times seem irrelevant to taxonomic nomenclature.

Stenoscisma opitula (Grant, 1971)

Fig. 190 – 193

1960 *Stenoscisma plicatum* [not Kutorga] – Harker & Thorsteinsson, p. 62, pl. 18, fig. 1-4.
1964 *Camerophoria* sp. aff. *spitzbergiana* [not Stepanov] – Gobbett, p. 126, pl. 16, fig. 10, 11.
1970 "*Stenoscisma*" *plicatum* [not Kutorga] – Bamber & Copeland, p. 630, pl. 14, fig. 10.
1971 *Septacamera opitula* Grant, p. 321, pl. 2, fig. 17, 18, ?19 -?21.

Diagnosis: Medium size, both valves covered by fine costae, apart from smooth umbonal portion of each valve on many specimens, four or five ribs in sulcus and four to five ribs each side. Anterior sulcus and fold.

Holotype: GSC 13737 figured by Harker & Thorsteinsson (1960, pl. 18, fig. 2-4) from Assistance Formation, Devon Island, OD.

Material: Six specimens with valves conjoined from GSC loc. 26406, Assistance Formation, Devon Island, and three specimens with valves conjoined from C-4003, two specimens with valves conjoined from C-4019 and C-4025, and one conjoined specimen from C-4081, Assistance Formation, Ellesmere Island. Two specimens with valves conjoined each from C-4004, C-4014 and C-4034, Trold Fiord Formation at Ellesmere Island, and a Yukon specimen with valves conjoined from the Takhandit Formation at JBW 631.

Dimensions in mm:

Width	Length	Height	Umbonal angle
25	22	18	90°
36	25	14	95°
24	22	12.5	100°
30	28	15	?85°
31	27	19	-

Description: Shells of medium size, subtriangular in outline with prominent ventral umbo that is incurved, bearing a terminal foramen of varying diameter, and incurved over delthyrium and beak of dorsal valve. The maximum width lies well forward near anterior quarter of shell length. A ventral sulcus commences at varying distances from the umbo, generally near mid-length, with angle close to or slightly exceeding 30° as measured from the umbonal tip, and comparatively flat floor. The fold commences nearer the anterior margin, and has a flat crest. Both valves are covered by fine costae with rounded crests and interspaces, except for the umbonal portion on both valves, where ribs become very faint or absent. Four and rarely up to six ribs lie in the sulcus and six to each side, the outer two very fine and low. Rarely a costa commences outside the sulcus and becomes incorporated anteriorly. Six to rarely eight costae lie over the fold, and five to seven laterally, the outer ones very fine.

A well developed spondylium is developed in the ventral valve, marked by low oblique growth ridges parallel to the oblique anterior margins, and there is a shallow and narrow median channel, and faint radial lira. The spondylium is supported by a median

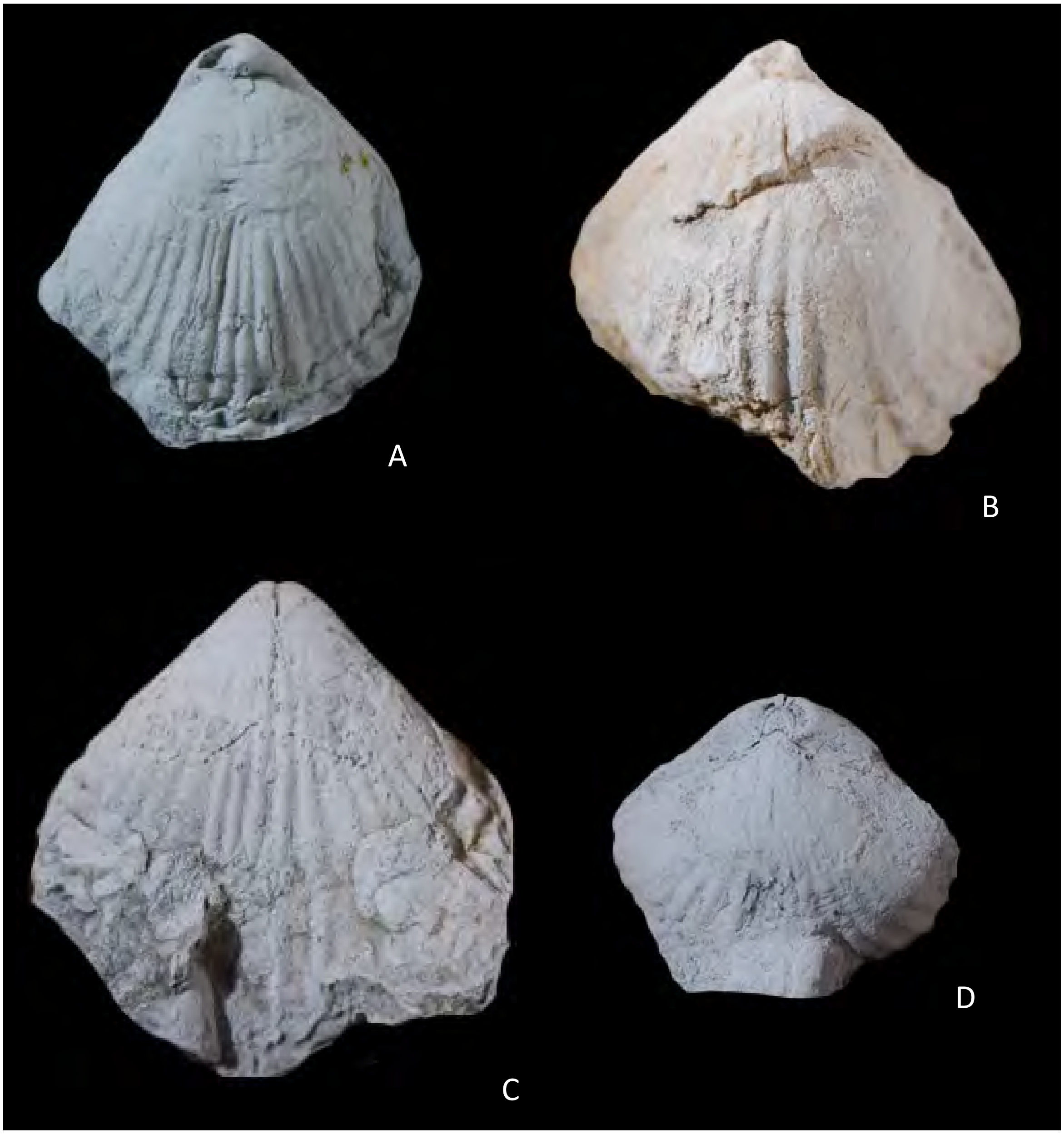

Fig. 190. *Stenoscisma opitula* (Grant). A, dorsal view of specimen GSC 140878 with valves conjoined, from C-4003. B, dorsal aspect of specimen GSC 140879 with valves conjoined, from C-4003. C, ventral valve GSC 140880 from C-4024. D, dorsal view of specimen GSC 140881 with valves conjoined from C-4081. Specimens from Assistance Formation, Ellesmere Island, x2.

septum that extends almost as far as mid-length. Branching vascular canals radiate over the valve postero-laterally, laterally and anteriorly from under the front of the spondylium.

The dorsal umbo fills much of the delthyrium, and immediately in front of the dorsal beak is a small area marked by radiating ridges and grooves, probably representing the site for muscle attachment from the ventral adductors. A complex platform lies between the dental sockets. In the middle is a strong and broad median ridge, partly enclosed by a deep groove each side and

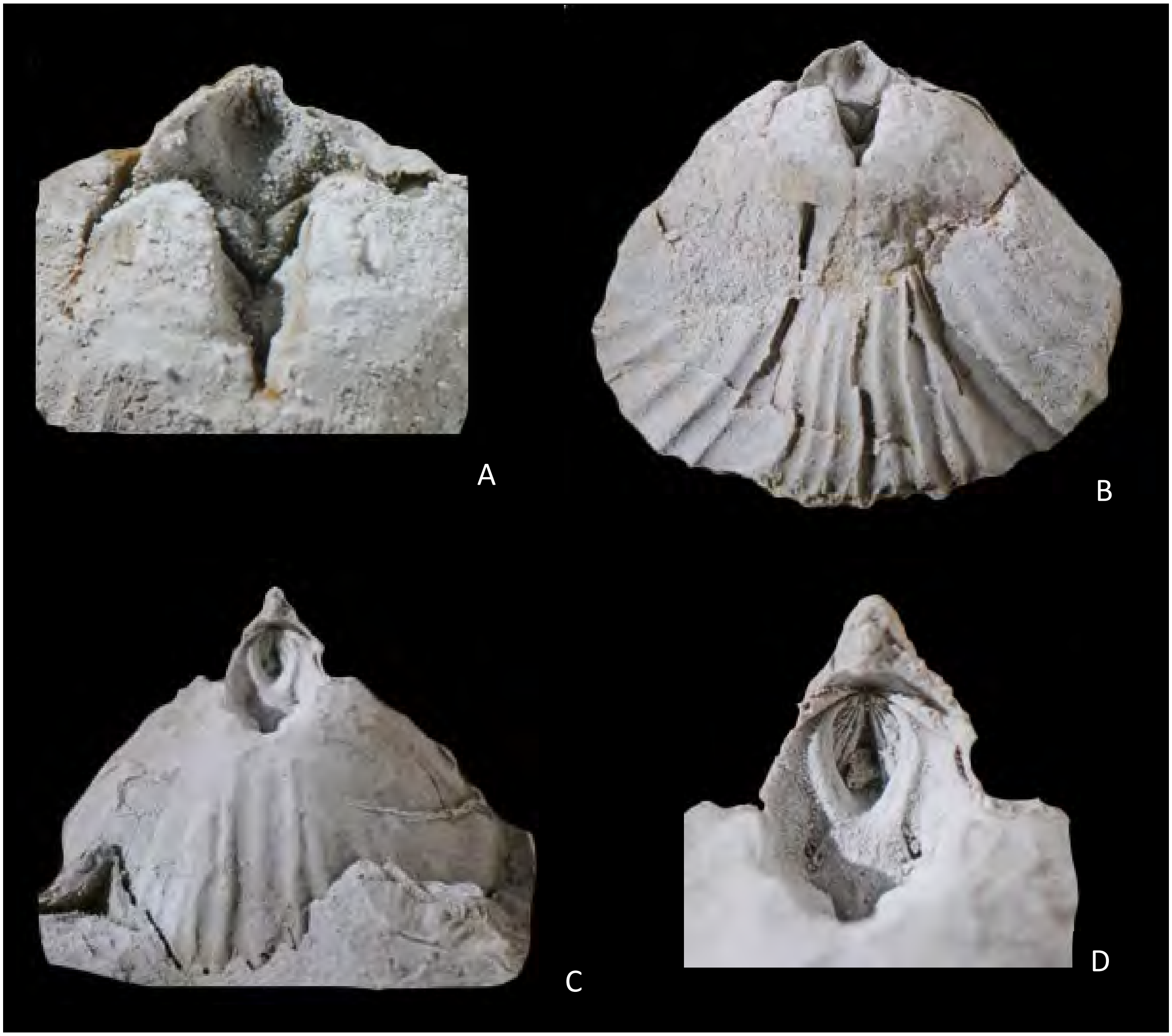

Fig. 191. *Stenoscisma opitula* (Grant). A, B, detail of cardinalia x4 and general dorsal view x2 of internal mould GSC 140882 with valves conjoined, from GSC loc. 26406, Assistance Formation, Devon Island. C, D, dorsal view x 2 and posterior detail of cardinalia x4 for internal mould GSC 140883 with valves conjoined, from C-4003, Assistance Formation, Ellesmere Island.

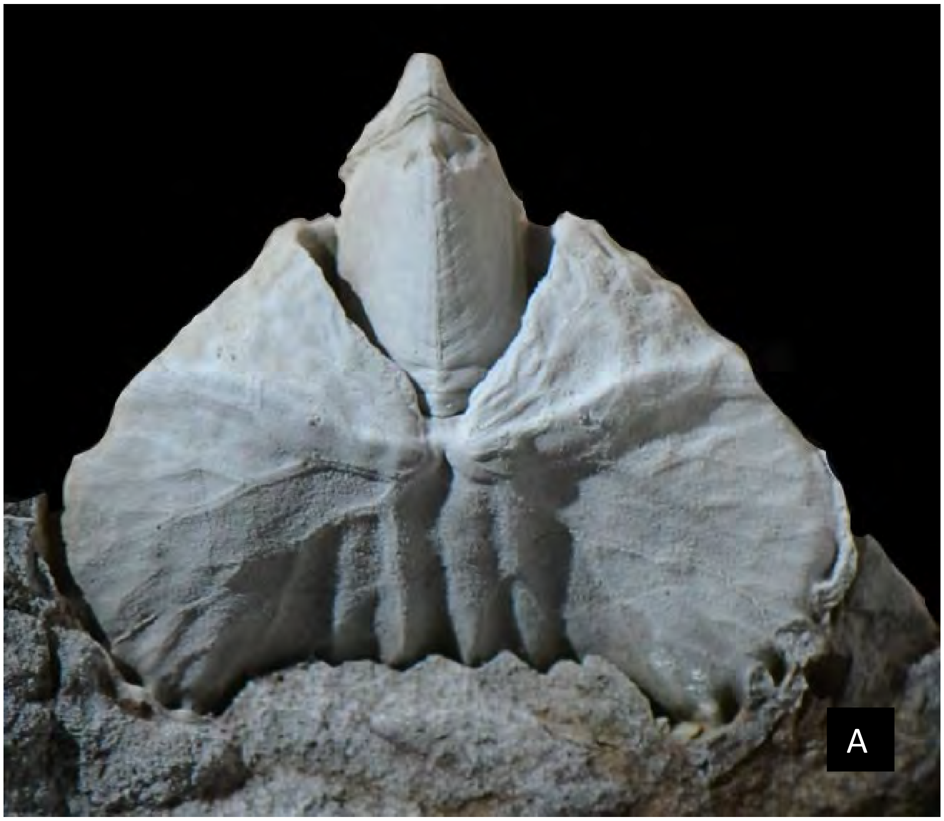

Fig. 192. *Stenoscisma opitula* (Grant). A, ventral view of internal mould GSC 140883 with valves conjoined and showing an elaborate spondylium, from C-4003, Ellesmere Island, x3. (See Fig. 191C, D). B, ventral aspect of internal mould GSC 140882 with valves conjoined, x2, from GSC loc. 26406, Devon Island. See Fig. 191A, B. From Assistance Formation.

the two grooves converge anteriorly to form a median broader shallower groove, which widens a little anteriorly. In front a small septalium continues forward from the platform, with a narrowing of the median groove. A swollen mass of shell lies below, with a median ridge. Faintly impressed vascular channels radiate from the floor of the valve in front of this structure. A large but less mature specimen is overall similar, having a larger cardinal process with strong vertical blades and lower median portion, and the enclosing grooves are shallower. In front lies a short small shelf, projecting forward, and not shown in the other specimen, like a tiny cover plate of the sort found in typical *Rhynchopora*. It is supported by a very short septum. The crura commence at the edge of this plate, and in front a well formed camarophorium extends forward, supported by a septum duplex, with a bulge of secondary shell each side. In the other more mature specimen, the septum has been largely buried by secondary shell, but is visible in smaller and therefore less mature specimens. The dorsal structures are moderately like those figured for *Stenoscisma renode* Cooper & Grant (1976a, pl. 575, fig. 4), except the crura commence just in front of the converging posterior grooves.

Resemblances: The species was described by Harker & Thorsteinsson (1960) and revised and elaborated by Grant (1971), partly on the basis of further topotype material collected by F. G. Stehli. Grant (1971, p. 322) ascribed the species to *Tetracamera*, but no specimen from the Assistance Formation has been found to contain the propping plates which support the spondylium and form an essential part of the diagnosis for this genus. Furthermore, Grant's description contains no reference to propping plates. Grant noted a close resemblance to material collected from the Pybus Formation at Kuiu Island of southeast Alaska, as figured in Grant (1971, pl. 2, fig. 19-21), though the figured specimen for the Pybus specimen has more and narrower costae and propping plates support the spondylium, unlike the interior of the present species, so that it is clearly not congeneric. He noted some evidence that pointed to a Sakmarian age for the Pybus Formation, but indicated that its correlation required further analysis. No further material has been described, as far as is known.

Fig. 193. *Stenoscisma opitula* (Grant), posterior view of specimen GSC 140884 with valves conjoined from C-4081, ventral valve on top. Specimen from Assistance Formation, Ellesmere Island, x2.

These specimens appear to be identical with material recorded as *Camerophoria* aff. *spitzbergiana* Stepanov by Gobbett (1964, pl. 16, fig. 10, 11) from the middle Brachiopod Chert. But otherwise no comparable material appears to have been recorded from approximately correlative beds in the Arctic. *Camerophoria spitzbergiana* Stepanov, 1937b, pl. 9, fig. 11 is triangular in shape with few costae, nothing like the present material. There is some approach to *Stenoscisma exutum* Cooper & Grant (1976a, pl. 560) from the Cathedral Mountain Formation, of Kungurian age in Texas, though this species has slightly more numerous costae, the similarity lying in the way the shells of both taxa are covered by subequal costae, not as fine as in some other Texan species. *S. problematicum* Cooper & Grant (1976a, pl. 570) from the Skinner Ranch Formation is also moderately close, but has more costae

Stenoscisma renode Cooper & Grant (1976a, pl. 574) from the Word Formation between the Willis Ranch and Appel Ranch Members, of early Capitanian or late Wordian age, is smaller with slightly stronger costae and ribbed umbonal shell, but costal numbers are much the same as those of the Canadian specimens. A further plate of figures (Cooper & Grant (1976a, pl. 575) illustrated internal features. It is considered that specimens close to this species are to be found in the same Assistance Formation, and are described below as *S*. aff. *renode*. Shells ascribed to *S. venustum* (Girty) possibly from the Delaware Formation, and lavishly illustrated *S. triqetrum* Cooper & Grant (1976a, pl. 578-582) from the Cathedral Mountain and Road Canyon formations also show some approach, without being quite so close. In short, similarities lie closest to *S. renode*, without identity being exact.

The species described as *Camarophorium kochi* Dunbar (1955) from the Foldvik Creek Group and derived boulders in central east Greenland has a comparatively smooth umbo, and the species is more triangular in shape.

Stenoscisma aff. ***renode*** Cooper & Grant, 1976a

Fig. 194

aff. 1976a *Stenoscisma renode* Cooper & Grant, p. 2107, pl. 573, fig. 1-18, pl. 574, fig. 1-22, pl. 575, fig. 1-19.

Diagnosis: Subtriangular, low fold and uniplicate commissure, four to seven costae, usually five, over fold, and some weaker costae laterally, costae arise a little in front of beak, broad stolidium as a rule.

Holotype: USNM 1553310i figured by Cooper & Grant (1976a, pl. 574, fig. 9-15) from lens between Willis Ranch and Appel Ranch Members, Texas, OD.

Material: Three conjoined specimens from C-4003, Assistance Formation, Ellesmere Island.

Description: Medium small subtriangular shells with three sulcal ribs and two or usually four ribs over the fold, with two to four ribs on each lateral flank, posterior shell smooth. Ventral valve slightly longer than dorsal valve, with small terminal foramen.

The ventral spondylium is visible on one specimen.

Resemblances: These specimens are smaller and more triangular in shape than *Stenoscisma opitula* (Grant) with fewer ribs and slightly larger area of smooth posterior shell, especially for the dorsal valve, and although they are moderately close to *opitula*, they are regarded a belonging to a separate although possibly related taxon.

The specimens are close in size, shape and costation to *Stenoscisma renode* Cooper & Grant from the Glass Mountains of Texas, though they appear to lack the prominent stolidium of that species, possibly reflecting preservation, the United States material having been derived through leaching in acid. The presence or absence of a stolidium is of uncertain significance in the classification of *Stenoscisma* and allies. The species is found in the Word Formation, younger than the occurrence in Canada. *S. spitzbergiana* (Stepanov (1937b, pl. 9, fig. 11; aff. Gobbett 1964, pl. 16, fig. 4-9, text-fig. 17) from the Spirifer Limestone of Spitsbergen is more triangular in shape with strong ribs. Brabb & Grant (1971, pl. 2, fig. 29-33) figured more transverse specimens as this species from the sandstone unit of the type Takhandit section in Alaska.

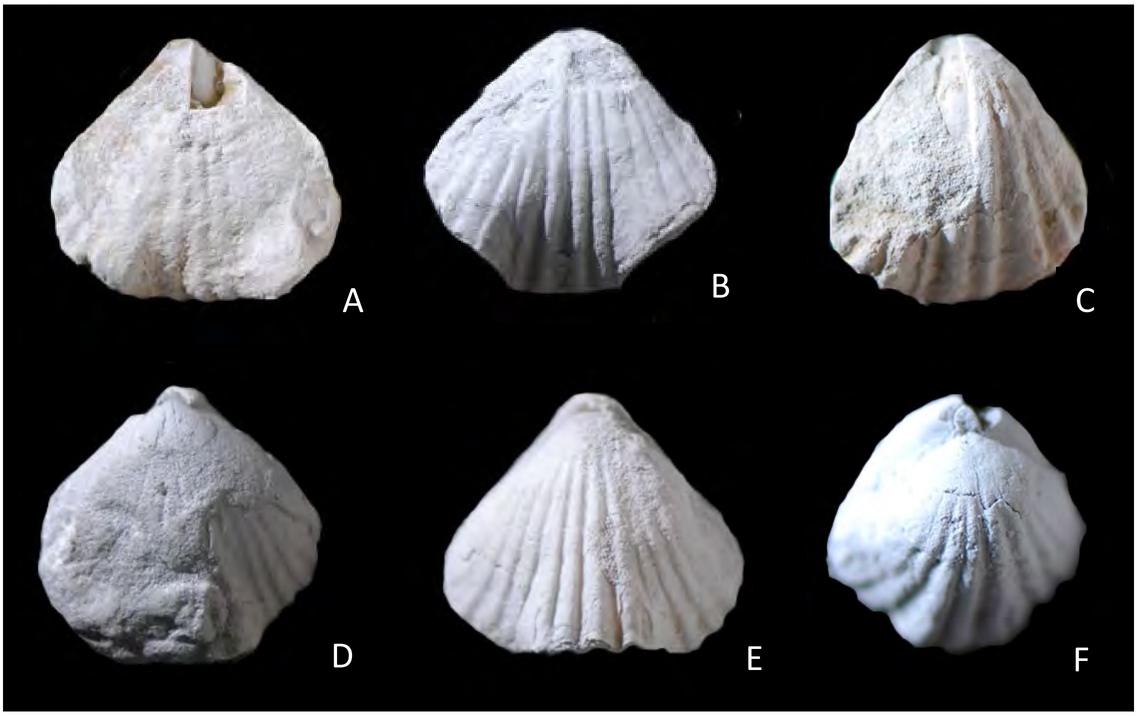

Fig. 194. *Stenoscisma* aff. *renode* Cooper & Grant. A, D, ventral and dorsal aspects of conjoined specimen, GSC 140885, x1.8. B, D, ventral and dorsal aspects of GSC 140886, x2. C, F, ventral and dorsal aspects of conjoined specimen GSC 140887, x2. Specimens from C-4003, Assistance Formation, Ellesmere Island.

Family **PSILOCAMARAIDAE** (**PSILOCAMARIDAE)** Grant, 1965a

Diagnosis: Costae absent as a rule, rarely present in sulcus or fold or more extensively, deltidial plates absent as a rule, spondylium elevated on low septum duplex, hinge plates narrow.

Subfamily **CYROLEXISINAE (CYROLEXINAE)** Carlson in Carlson & Grant, 2002

[Cyrolexinae Carlson in Carlson & Grant, 2002, p. 1227].

Diagnosis: Somewhat rounded in outline, costae absent or present only over anterior half, with narrow stolidium rarely developed, delthyrial opening 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), even though it displayed an intercamarophorial ridge, whereas Psilocamaridae, or least the subfamily Psilocamarinae, was deemed to be typified by lack of an intercamarophorial ridge or 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. 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 1964a). In one constituent member of

Cyrolexinae, *Callaiapsida*, the bases are not in touch with the camarophorium for at least part of their length (see Waterhouse 2018a, Fig. 239C, D, p. 290). Therefore, different possible avenues of classification arise, but provisionally, Cyrolexinae are deemed to be close to Psilocamarinae.

Genus ***Cyrolexis*** Grant, 1965a

Diagnosis: Small to medium in size, subequally biconvex, weakly costate around anterior margin; camarophorium curved ventrally, touching underside of hinge plates, intercamarophorial plate present as a rule, rarely weak or absent.

Type species: *Cyrolexis haquei* Grant, 1965 from Amb Formation (lower Guadalupian or uppermost Cisuralian), Salt Range, Pakistan, OD.

Cyrolexis? sp.

Fig. 195

Fig. 195. *Cyrolexis*? sp., A, B, ventral, dorsal and lateral aspects of specimen GSC 140888 with valves conjoined, x4, from GSC loc. 53846, unnamed sandstone in *Dyoros modestus* Zone, McDougall Pass, Richardson Mountains, Yukon Territory. Pustules indicated by arrow.

Material, Description: A specimen with valves conjoined from GSC loc. 53846, unnamed sandstone in the *Dyoros modestus* Zone at McDougall Pass, Richardson Mountains, Yukon Territory, agrees closely with the genus *Cyrolexis* Grant, 1965, but appears to be minutely pustuled along the growth lines. It is 12mm wide, 14.5mm long and 11mm high, characterized by smooth posterior, and some nine costae restricted to the anterior shell, with three costae anteriorly over a very low fold. The ventral umbo has an angle of 55º, and a tiny terminal foramen, overhanging a narrow delthyrium with angle close to 70º; dorsal umbo very broad. A ventral valve also comes from C-3997, Trold Fiord Formation, Ellesmere Island, and shows growth lines without any pustules.

Resemblances: The narrow shape and anterior costae approach features of *Cyrolexis* Grant, but further exploration of the morphology is required to confirm this position. Indeed, in some respects the Canadian specimens also resemble small *Stenoscisma oblisum* Cooper & Grant (1976a, pl. 567) from the Capitan Formation of Texas, although more mature specimens in this species develop more extended anterior lateral flanks, and costae become stronger over the anterior shell.

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.

Callaiapsida ustritskii n. sp.

Fig. 196, 197

1963 *Levicamera pentameroides* [not Tschernyschew] – Ustritsky in Ustritsky & Chernyak, p. 100, pl. 27, fig. 14, pl. 28, fig. 1.

Derivation: Named for V. I. Ustritsky.

Diagnosis: Both valves moderately inflated, ventral groove may commence near or at umbo, narrow high anterior dorsal fold.

Holotype: Specimen GSC 140890 figured herein as Fig. 196B, C, from C-4066, Assistance Formation, Ellesmere Island, here designated.

Material: A specimen with valves conjoined from GSC loc. 26406, Assistance Formation, Devon Island. Five specimens with valves conjoined from C-4066, Assistance Formation, Ellesmere Island.

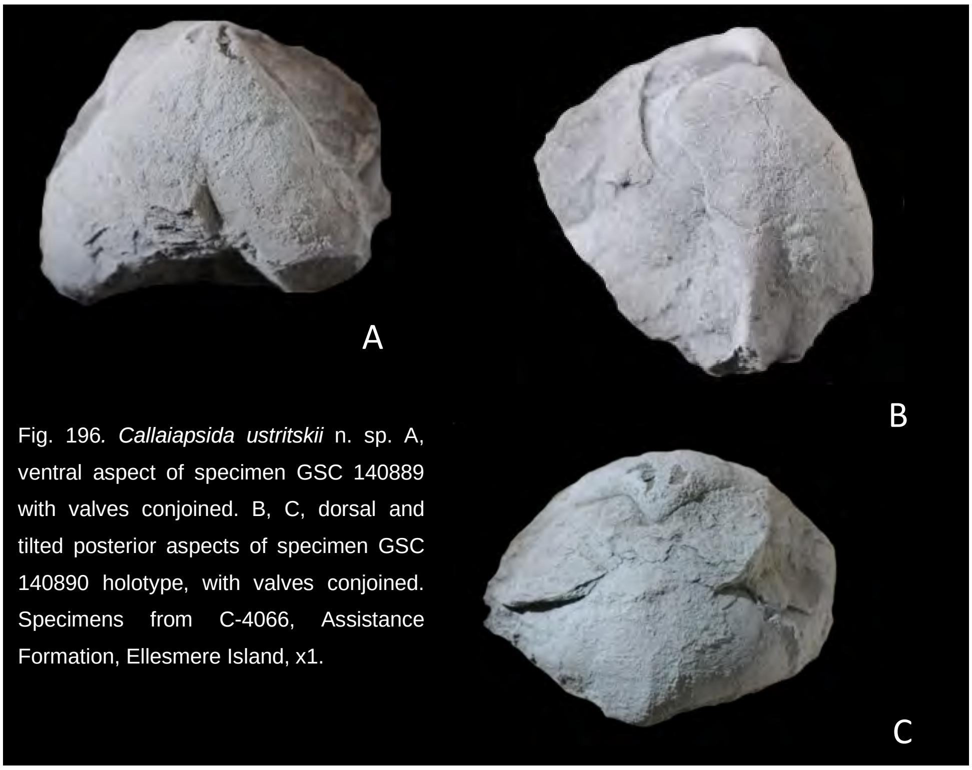

Fig. 196. *Callaiapsida ustritskii* n. sp. A, ventral aspect of specimen GSC 140889 with valves conjoined. B, C, dorsal and tilted posterior aspects of specimen GSC 140890 holotype, with valves conjoined. Specimens from C-4066, Assistance Formation, Ellesmere Island, x1.

Description: The specimen from GSC loc. 26406 is of triangular shape, strongly biconvex, with median groove commencing almost at the umbonal tip and persisting as far as the anterior half of the shell. Specimens from C-4066 have a narrow and shallow ventral groove commencing at the umbonal tip, and anteriorly, one shows a narrow high dorsal fold, whereas another shows a slightly broader fold. The ventral posterior walls are extended, and the dorsal valve is more ovally pentagonal in outline. Delthyrium broad and open, the sides diverging at 110º.

The spondylium extends for more than half of the length of the valve, and is sessile, with its flanks high and diverging narrowly.

Fig. 197*.* *Callaiapsida ustritskii* n. sp., ventral aspect of specimen GSC 140891 leached in HCl, to show spondylium, from C-4066, Assistance Formation, Ellesmere Island. Specimen x2.

Resemblances: One of the specimens described as *Levicamera pentameroides* (not Tschernyschew) in Ustritsky & Chernyak (1963) from Taimyr Peninsula is distinguished by the long median groove in the posterior ventral valve, and therefore resembles the present specimens, but the groove in the second Taimyr specimen has been obscured by breakage over mid-length. Both specimens show a low anterior dorsal fold, and outline similar to that of the Canadian specimens. The Taimyr species came from the lower Baikur Horizon, rated as lower to middle Guadalupian by Waterhouse (1976b), and shown as Kazanian in age by Klets (2005, p. 74). The species *pentameroides* Tschernyschew (1902, pl. 22, fig. 1-4, pl. 23, fig. 1-4) from the Schwagerinen-Kalk of the Urals is more elongate and lacks a median ventral groove. Specimens with a slightly shorter groove commencing further from the umbo and much less oval dorsal valve were assigned to *Callaiapsida arctica* (Holtedahl) by Grant (1971, pl. 3, fig. 1-10, 18-21, text-fig. 7, 9) from Alaska in rocks of uncertain age, possibly correlative with the Halleck Formation. The specimens are further characterized by a sharp-crested dorsal fold. Unlike the Alaskan material, the original material of *arctica* lacks a groove, as figured and described by and named in Holtedahl (1924, p. 34, pl. 21, fig. 1, 2). It came from Lower Permian rocks of Novaya Zemlya, as confirmed by Licharew & Einor (1939, pp. 69, 208, pl. 14, fig. 5a, b). The specimens have been judged to be close to shells described by Holtedahl (1911, p. 19, pl. 2, fig. 5, 6) as *Camerophoria pentameroides* [not Tschernyschew], considered to be identical with specimens recorded by Gobbett (1964, p. 128, pl. 16, fig. 13-16) from the Cyathophyllum Limestone of Spitsbergen. These lack a groove, and do not clearly show a peaked dorsal fold, perhaps because the specimens are too small.

Callaiapsida kekuensis Grant (1971, pl. 3, fig. 11-17, 22, text-fig. 10) has a shorter groove and more anterior sharpening of its dorsal fold, and especially low ventral valve. This species comes from the Halleck Formation of Alaska, thought to be of Leonardian age, though probably in need of tighter age control.

There is no sign in any of these species of the anterior lateral subplicae described by Martinez-Chaçon (1977) for the Upper Carboniferous *Callaiapsida alcaldei* from Spain. Other authors have considered that the genus lacked plicae.

Callaiapsida sp.

Fig. 198

Material: A ventral valve from C-4034, Trold Fiord Formation, Ellesmere Island.

Dimensions in mm:

Width	Length	Height
45	38	18+

Fig. 198. *Callaiapsida* sp. ventral valve GSC 140892 from C-4034, Trold Fiord Formation, Ellesmere Island, x1.5.

Description: This specimen has a median groove that passes into the sulcus which commences 7mm in front of the umbonal tip, and becomes a broader groove near mid-length of the shell, persisting as far as the shell is exposed. The shell is 45mm wide, 38mm high and possibly 18mm high, though height is obscure.

Resemblances: What little is known of this species would conform with *Callaiapsida kekuensis* Grant, 1971 from the Halleck Formation of Alaska, the ventral valve being comparatively flat in both forms, but the lack of a dorsal valve renders any determination highly speculative, and the present specimen is apparently younger.

Order ATHYRISIDA (ATHYRIDIDA) Boucot, Johnson & Staton, 1964

There are numerous and significant diffferences from pentarusiform and rhynchonellaiform brachiopods, not least in the nature of the spiralia, so the group is discriminated, primarily through its spiralia. Admittedly the group is small, but has an exceptional morphology.

Suborder ATHYRISIDINA (ATHYRIDIDINA) Boucot, Johnson & Staton, 1964

Superfamily **ATHYRISOIDEA** (**ATHYRIDOIDEA)** Davidson, 1881

Family **ATHYRISIDAE** (**ATHYRIDIDAE**) Davidson, 1881

For ordinal and family classification of the genus *Athyris*, it is proposed that the agreed and standard endings are simply added to the genus name. That preserved the genus name, without alteration. Otherwise the names become Athyridida, and Athyridoidea. But the name of the genus is *Athyris*, not *Athyrid.*

Subfamily **CLEIOTHYRIDINAINAE** (**CLEIOTHYRIDININAE**) Alvarez, Rong & Boucot, 1998

Genus ***Cleiothyridina*** Buckman, 1906

Diagnosis: Roundly subpentagonal with foramen and ornament of flat close-set solid spines arrayed along commarginal laminae. Ventral valve with pedicle collar and short dental plates. Dorsal valve with dental sockets, adjoining outer hinge plates, inner hinge plates forming a concave trough, bearing a foramen. Low median septum, not supporting the trough. Jugum as in *Athyris*, with long accessory jugal lamellae.

Tyep species: *Atrypa pectinifera* Sowerby, 1840, p. 14 from Magnesian Limestone (Guadalupian), England, ICZN Opinion 1041, p. 210 (1976).

Cleiothyridina maynci Dunbar, 1955

Fig. 199, 200, 208A

1931 *Athyris planosulcata* [not Phillips] – Frebold, p. 19, pl. 6, fig. 7, 8.
1955 *Cleiothyridina maynci* Dunbar, p. 125, pl. 22, fig. 1-8.

Diagnosis: Small subpentagonal shells, moderately inflated, arched venter, dorsal valve may be flattened medianly close to anterior commissure.

Holotype: Specimen figured by Dunbar (1955, pl. 22, fig. 1-4) from Foldvik Creek Group, central east Greenland, OD.

Material: A specimen with valves conjoined from C-13356, Trold Fiord Formation, Melville Island.

Description: The specimen is small with roundly subpentagonal outline, well-formed ventral foramen, maximum width near mid-length, very shallow anterior sulcus and low anterior fold. Long solid closely spaced flattened spines are arrayed in commarginal rows, each row emerging from a lamination.

The matrix was dissolved and the valves separated to show the interior. Low teeth are supported by short and slender dental plates placed close to the lateral walls. In the dorsal valve, the sockets are slender and deep, and widen anteriorly. To each side lie broad concave crural plates, also called outer hinge plates, which are lightly marked by growth increments, and bear crura at the anterior inner edge. The plates do not project over the dental sockets. The inner hinge plates form a trough with convex anterior margin, bearing a foramen at its posterior end, and this very slightly impinges on the tip of the dorsal beak. A low myophragm or septum extends well forward, and the dorsal floor bears light radial striations posteriorly, but muscle scars cannot be clearly discerned.

Resemblances: This specimen is identified with *Cleiothyridina maynci* Dunbar from central east Greenland. Gobbett (1964, p. 164, pl. 22, fig. 11-13) recorded similar-looking material from the upper Wordiekammen Limestone of Spitsbergen, referring the form to aff. *maynci.*

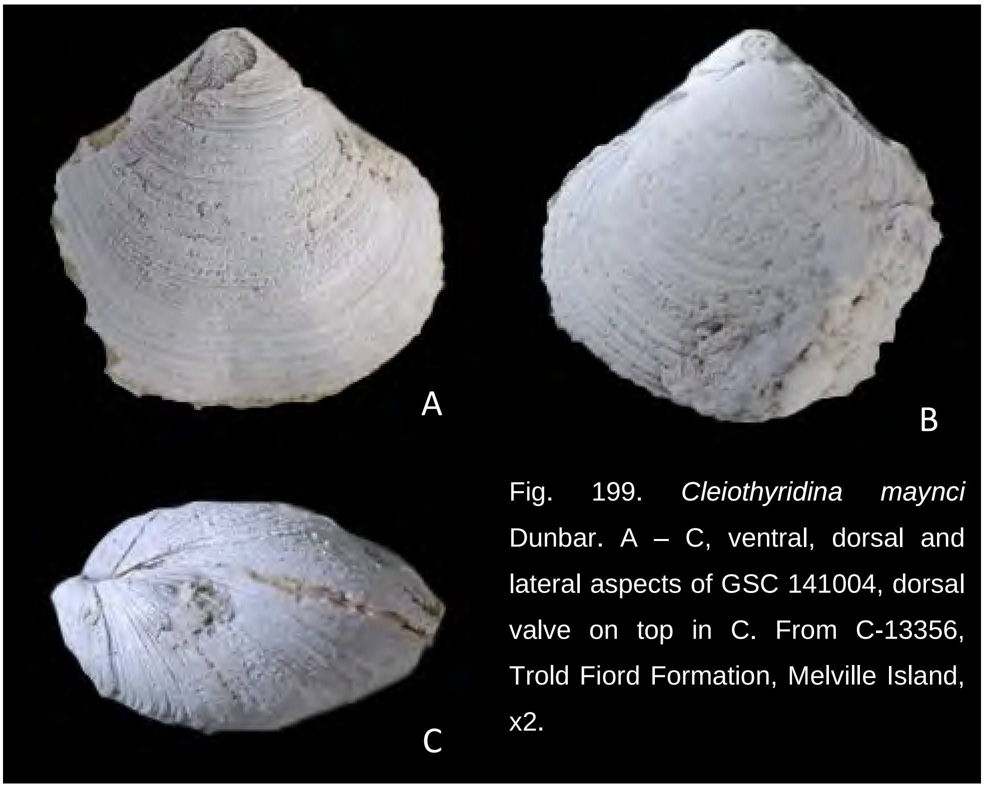

Fig. 199. *Cleiothyridina maynci* Dunbar. A – C, ventral, dorsal and lateral aspects of GSC 141004, dorsal valve on top in C. From C-13356, Trold Fiord Formation, Melville Island, x2.

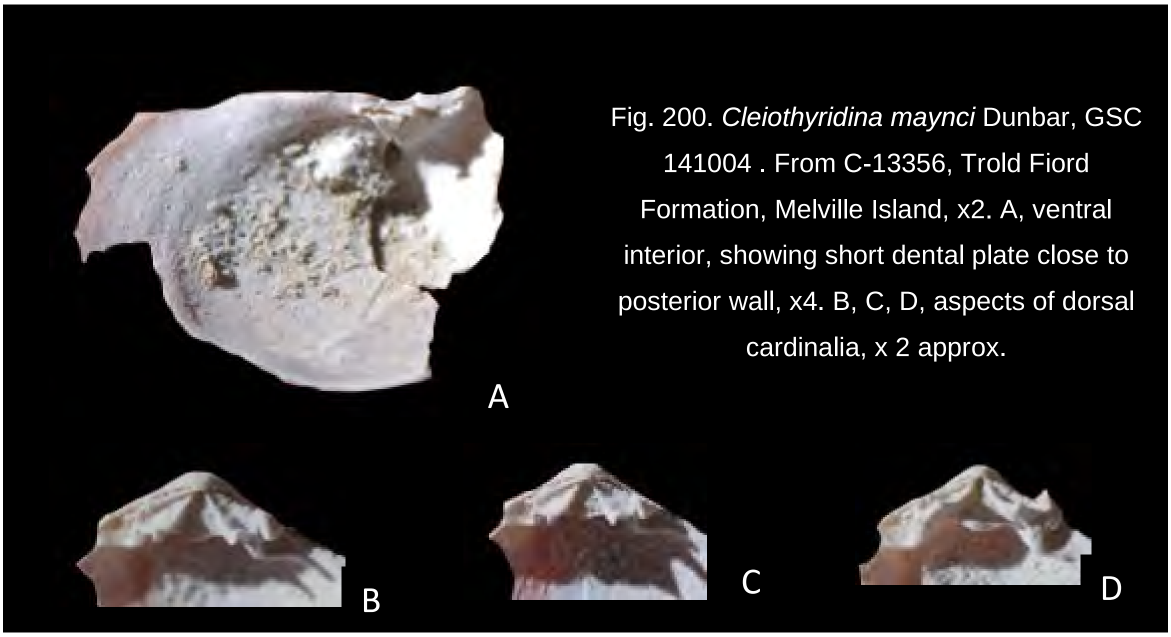

Fig. 200. *Cleiothyridina maynci* Dunbar, GSC 141004 . From C-13356, Trold Fiord Formation, Melville Island, x2. A, ventral interior, showing short dental plate close to posterior wall, x4. B, C, D, aspects of dorsal cardinalia, x 2 approx.

Genus ***Svalbardathyris*** Grunt, 2006b

Diagnosis: Shells large and little inflated, with ovally rounded outline. Ornament of flattened spines fringing the growth lamellae, small foramen. Short dental plates largely buried in shell, cardinal plate possibly not pierced by foramen.

Type species: *Athyris* (*Cleiothyridina*) *kotlukovi* Stepanov, 1936, pp. 124, 128, pl. 5, fig. 5, 6 from Brachiopod Chert of Spitsbergen, OD.

Discussion: Tatjana Grunt kindly supplied me with her version of the type species, and it would appear that the proposed genus is distinguished solely by its distinctive oval and little inflated shape. None of her material was conducive to conclusive clarification of the internal structures. A critical question centres on the presence and position of the foramen in the dorsal valve. The best figures of *kotlukovi* have been provided by Grunt (1977), and they fail to show any foramen in the dorsal cardinal plate, not that they show clearly a plate without foramen. Her Text-fig. 39 and pl. 15, fig. 4 suggests the possibility of a foramen through the dorsal umbo, but only as a possibility. Present material from the Assistance Formation and Trold Fiord Formation externally identical with *kotlukovi* does not show an internal foramen piercing the dorsal cardinal plate, nor sited at the tip of the dorsal umbo, but preservation is not perfect. Were the internal foramen absent, as seems to be the case, this certainly distinguishes at least the Canadian specimens from *Cleiothyridina*, and other allied genera, including *Himathyris* Waterhouse, 1986, which was originally described from the Himalayas, and is found in the Canadian Arctic. Furthermore the body cavity in the posterior dorsal valve is not extended posteriorly as a narrow passage way, as in *Himathyris.* The problem is that the Canadian specimens are not type *Svalbardathyris*, and therefore cannot be securely used as demonstrating the internal features of the genus. So the interpretation offered herein is provisional, and awaits further analysis of the Svalbard material of *kotlukovi*.

Svalbardathyris kotlukovi **(**Stepanov, 1936)

Fig. 201, 202, 208B

1914 *Athyris* sp. Wiman, p. 31, pl. 2, fig. 14.
1936 *Athyris* (*Cleiothyridina*) *kotlukovi* Stepanov, pp. 124, 128, pl. 5, fig. 5, 6.
1937b *A.* (*Cleiothyridina*) *kotlukovi* – Stepanov, pp. 137, 182, pl. 9, fig. 6, 7.
1960 *C*. cf. *subexpansa* [not Waagen] – Harker & Thorsteinsson, p. 73, pl. 24, fig. 1, 2.
1964 *C. kotlukovi* – Gobbett, p. 163, pl. 22, fig. 3, 4.
1977 *C. kotlukovi* – Grunt, p. 88, pl. 15, fig. 1-4, text-fig. 37-39.
1992 *C. kotlukovi* – Nakamura et al., p. 90, pl. 3, fig. 3, 5, pl. 4, fig. 3.
2006b *Svalbardathyris kotlukovi* – Grunt, p. 170.

Diagnosis: Slightly elongate to weakly transverse well rounded shells of large size but not greatly inflated, low ventral umbo little extended beyond hinge.

Lectotype: Specimen figured by Stepanov (1936, pl. 5, fig. 6; 1937a, pl. 9, fig. 7) from Brachiopod Chert of Spitsbergen, designated by Gobbett (1964, p. 163). Grunt (1977, p. 88) sought to designate the specimen figured by Stepanov (1937b, pl. 9, fig. 6) as lectotype, but her proposal lacked priority.

Material: Eight specimens with valve conjoined and a ventral valve from GSC loc. 26406, Assistance Formation, Devon Island, and a ventral valve each from C-4002 and C-4081, Assistance Formation, Ellesmere Island. A ventral valve from C-3993, Degerböls Formation. A ventral valve from C-3995, a specimen with valves conjoined from C-4005, and two ventral valves and one specimen with valves conjoined from GSC loc. 57687, Trold Fiord Formation, Ellesmere Island.

Dimensions in mm: valves conjoined

Width	Length	Height	Umbonal angle	Locality
50	44	27	60°	GSC 26406
46	40.5	19.5	95°	GSC 26406
44	40	20	100°	GSC 26406
55	44	22	100°	GSC 26406
40	34	18		C-4081

Description: The specimens are comparatively large for the genus, weakly transverse, and only moderately inflated for their large size. The ventral umbo varies in its umbonal angle, and is little extended beyond the hinge, and the dorsal

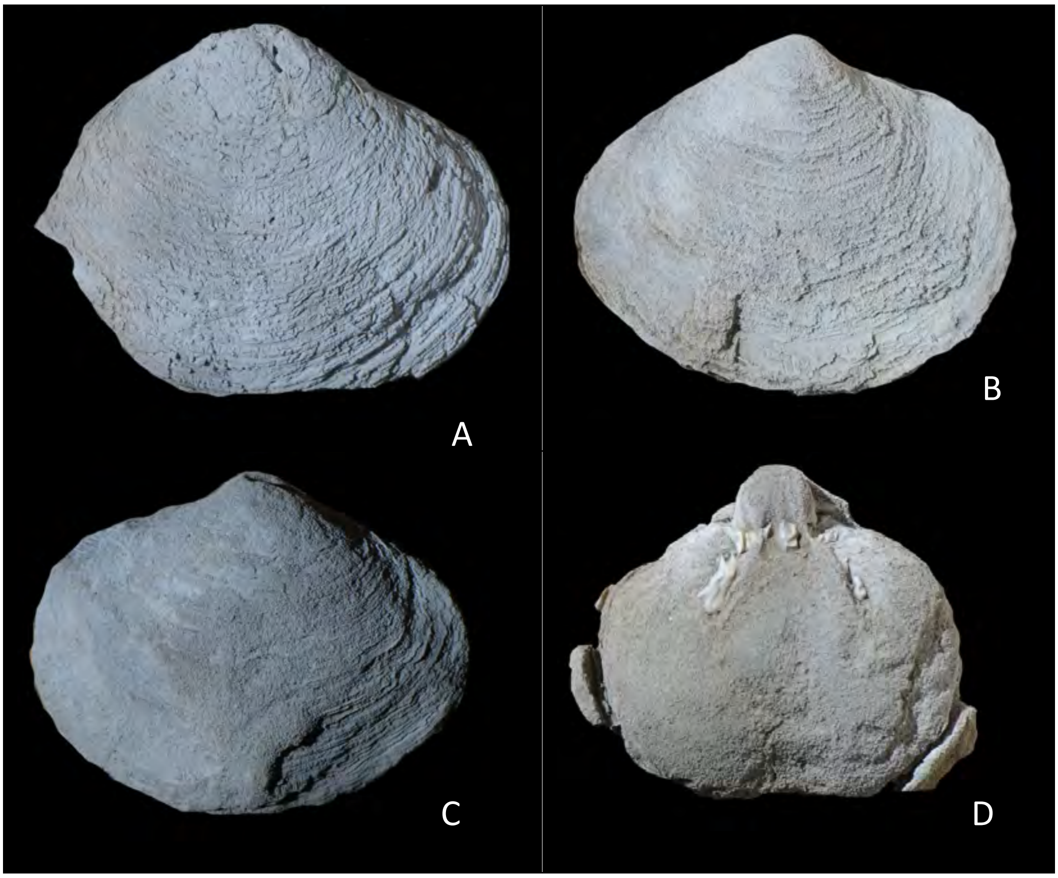

Fig. 201. *Svalbardathyris kotlukovi* **(**Stepanov). A, ventral valve GSC 35898. B, C, ventral and dorsal aspects of specimen GSC 140894 with valves conjoined. D, ventral view of internal mould GSC 140895. From GSC loc. 26406, Assistance Formation, Devon Island, x1.

umbo is broad and low, filling a wide delthyrium. The outline of the shell is well rounded, with maximum width varying in position between the posterior third of the shell length and mid-length. A very shallow sulcus develops anteriorly over the ventral valve in only some specimens, with slight alteration to the anterior commissure, and the dorsal valve is evenly convex as a rule. The ornament on both valves apparently consists of the normal cleiothyridin ornament of commarginal ragged lamellae and low rugae, fringed by flattened spines, but is poorly preserved. Such ornament is confirmed for better preserved material described by Miller (1974).

The pedicle collar is well developed and a tubular portion extends in front, with low median ridge. The ventral muscle field is impressed posteriorly, with narrow adductor ridges and broad diductor scars, and a low median ridge extends for a short distance over mid-length in front of the adductors. Teeth are small, and short dental plates are placed close to the lateral walls.

In the dorsal valve, the dental sockets are narrow, enclosed by low socket plates, and the cardinal plate is comparatively short and deeply and broadly concave, with concave anterior margin, extending laterally along the dental

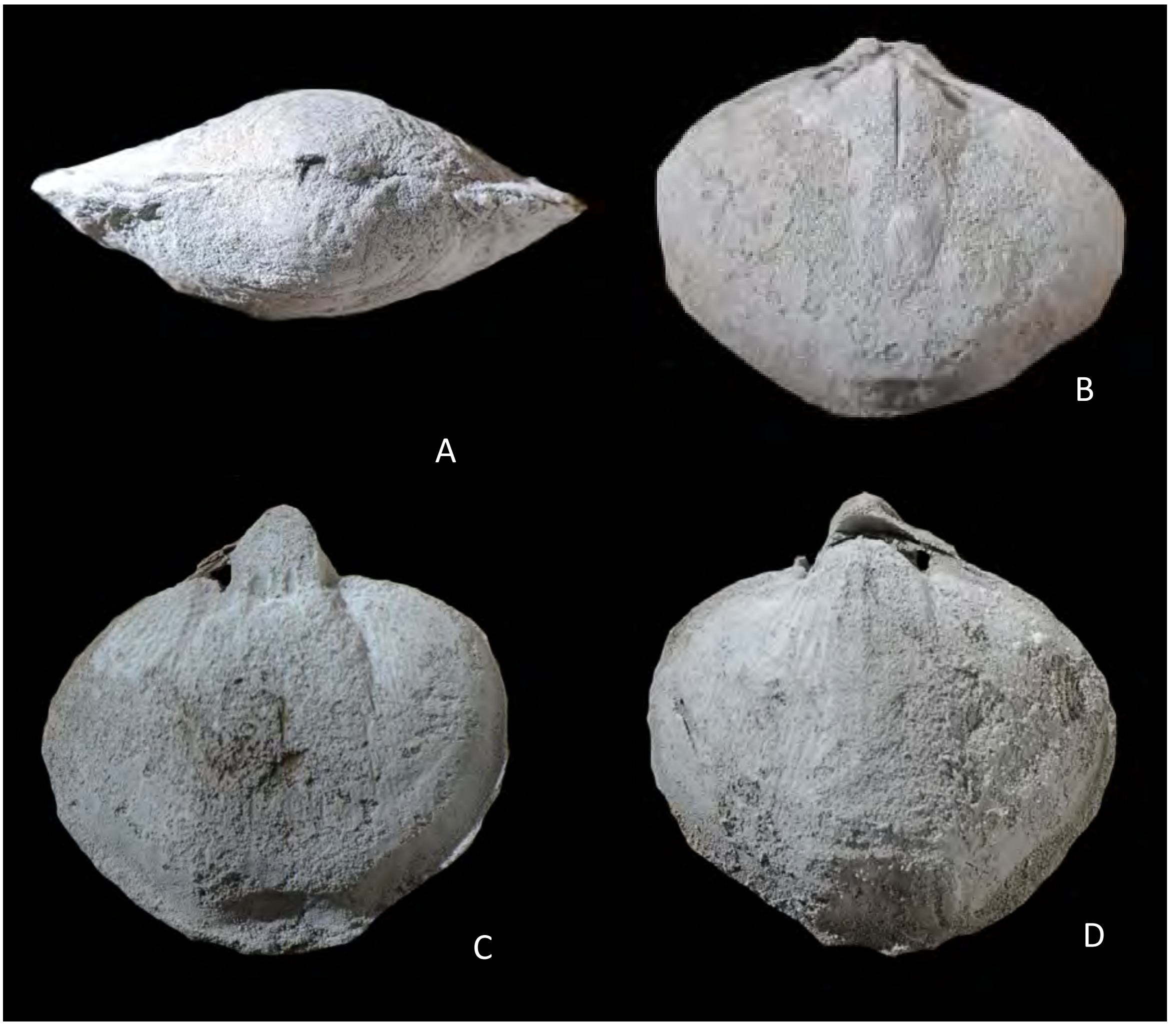

Fig. 202. *Svalbardathyris kotlukovi* **(**Stepanov). A, posterior view of specimen GSC 140894 with valves conjoined, ventral valve on top. B, dorsal aspect for internal mould of specimen GSC 140896 with valves conjoined. C, D, ventral and dorsal aspects for internal mould of specimen GSC 140897 with valves conjoined. The leached internal moulds are poorly preserved, because of too much calcium carbonate in the matrix. From GSC loc. 26406, Assistance Formation, Devon Island, x1.5.

sockets. There is no central foramen, but this cannot be unreservedly confirmed for all material: because preservation is not ideal for several specimens, the matrix being somewhat calcareous. The outer hinge plates are well formed. In front lie long weakly impressed subquadrate muscle impressions, divided by a well-defined median ridge extending over the posterior third of the shell length. The posterior shell on both valves is thinner over the centrally placed muscle scars and median septum. The remainder of the floor is covered by closely spaced elongate dimples in the mature shell. The posterior space under the cardinal plate is filled with secondary shell.

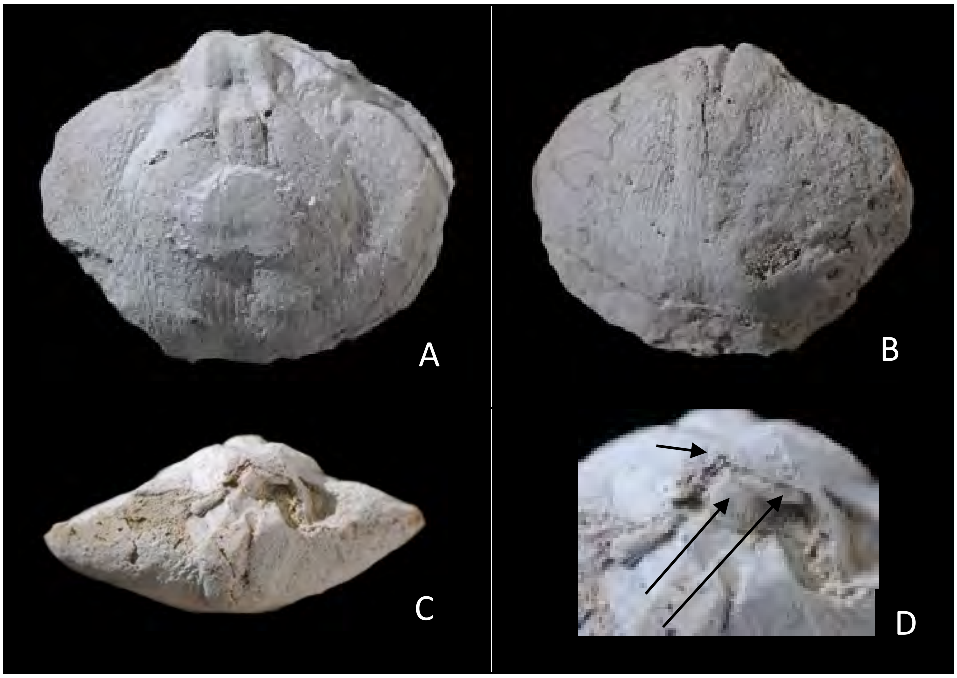

Fig. 203. *Svalbardathyris kotlukovi* (Stepanov). A-C, ventral, dorsal and posterior aspects of internal mould, ventral valve on top, x 2. D, closer view of cardinalia, x4, ventral valve on top. GSC 140993 from GSC loc. 26406, Assistance Formation, Devon Island. Very long arrow points to outer hinge plate, the long arrow points to trough formed by inner hinge plates (cardinal plate), and short arrow points to dorsal umbonal tip.

Resemblances: This species is characterized by its large size, shape and low inflation. In Spitsbergen, the type and additional material is found only in the Kapp Starotsin Formation and specified in Grunt & Blomeier (2013) as lower Hotvinden Member. In Canada externally similar specimens entered the geologic succession in the Assistance Formation, and persisted, rarely, into faunas of the Trold Fiord Formation. In the Petchora Basin, specimens that are moderately close appeared as early as the Talatin Suite, and persisted into the Levorkut Suite, though the figured specimen is more elongate than usual (Kalashnikov et al. 1990, pl. 3, fig. 4).

Genus ***Himathyris*** Waterhouse, 1986c

Diagnosis: Large shells, dorsibiconvex, with slender flattened spines. Ventral interior with laterally placed short dental plates, large muscle field. Dorsal interior with socket plates that may be finely crenulate, heavily thickened along inner flanks, thickened cardinal plate bearing a very narrow trough, and with terminal foramen at tip of the dorsal beak, and broad outer hinge plates which spread only slightly across the dental sockets and may be anteriorly extended. A slender open passage extends forward from the ventral delthyrium through the foramen in the dorsal beak into the dorsal valve interior. Low median posterior ridge and low median septum.

Type species: *Athyris gerardi* Diener, 1899, p. 56 from Gungri Formation (Wuchiapingian) of Spiti, OD.

Discussion: Reservations were expressed about the validity of *Himathyris* by Alvarez & Rong (2002) in their assessment of cleiothyridin genera in the *Revised Brachiopod Treatise,* but as pointed out by Waterhouse & Chen (2007, p. 40), *Himathyris* is a most distinctive genus, large, dorsibiconvex, with very large ventral muscle field, and Shen, Shi & Archbold (2003a, p. 89) were able to recognize the genus from the Qubuerga Formation of Xizang (Tibet), even on the basis of external size and shape. The figures in the original Waterhouse proposal of the genus suffered from poor reproduction, so a number of improved figures were issued by Waterhouse & Chen (2007, pl. 10, fig. 1-10, text-fig. 7, 8). The characteristic features of the genus include large size, large ventral muscle field, very small dental plates, and in the dorsal valve, cardinal plate and greatly thickened dental sockets, to leave a slender gap or passage from the ventral delthyrium through the posterior foramen in the dorsal umbonal beak forward into the body of the dorsal valve. The passage is narrow, whereas the umbonal cavity in *Cleiothyridina* and *Svalbardathyris* (in Canadian shells) is much broader, though often filled with secondary shell to leave no passageway. Unlike the cardinalia for *Cleiothyridina* illustrated by Alvarez & Rong (2002, text-fig. 1007.1, 1023f, g), all from Texas rather than from the type species of England, the outer hinge plates do not spread far across the dental sockets.

The Canadian material is like type *Himathyris* in having a narrow posterior umbonal passage-way and thick inner socket plates. It differs in having strongly crenulate dental sockets. The inner hinge plates form a shallow trough, less well developed than in type *Cleiothyridina* (see King 1850, Davidson 1861). A second apparent crural base is visible on one side of one specimen from Canada (see Fig. 207D), but the full nature of the brachial apparatus in this material is yet to be clarified.

Himathyris arctica n. sp.

Fig. 204 – 207, 208C

Derivation: arctos – costellation near North pole, Lat.

Diagnosis: Large, oval in outline without deep anterior sulcus.

Holotype: GSC 140989 from C-4005, Trold Fiord Formation, Ellesmere Island, illustrated in Fig. 204, here designated.

Material: A large specimen with only the posterior part of the dorsal valve, broken posterior part of the ventral valve, and a conjoined specimen from C-4005. One specimen with valves conjoined from uncertain locality, possibly C-4005. Trold Fiord Formation, Ellesmere Island.

Dimensions in mm: ventral valve, internal mould

Width	Length	Height	
68	+47	18	holotype, ventral valve
58	45	31.5	both valves

Description: Holotype large and suboval, the ventral umbo protruding posteriorly with angle of nearly 100°, but broken at the tip, posterior walls diverging at greater angle to well rounded lateral margins. Posteriorly there is a narrow median groove, and over the anterior fourth of the shell, a broad and very shallow sulcus. Any evidence of a ventral umbonal foramen has been largely destroyed. A broad delthyrium is present, with angle of 100°, occupied by the dorsal beak. The holotype suggests that the posterior dorsal valve is higher than the posterior ventral valve, 18mm high compared with 13mm high. The ventral valve is traversed by a number of low broad ribs, two in 5mm posteriorly, which split

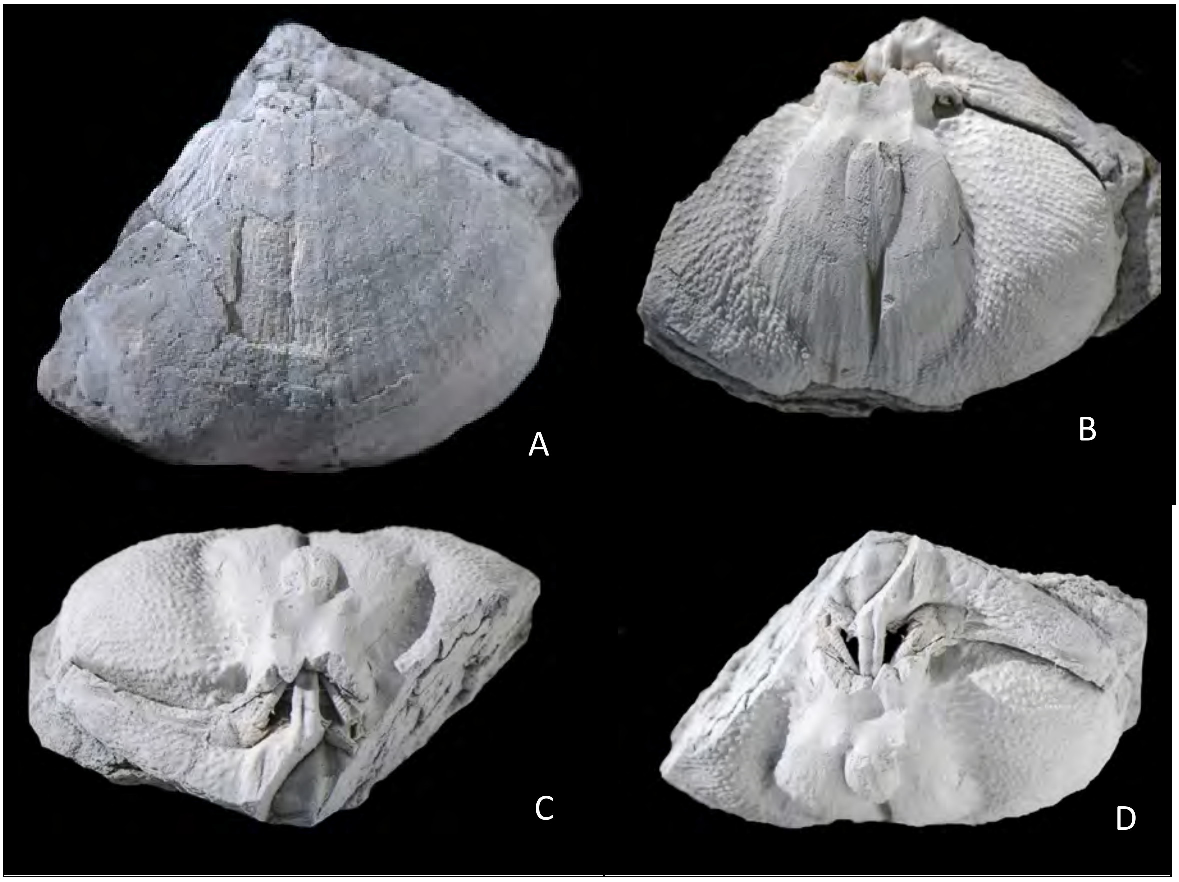

Fig. 204. *Himathyris arctica* n. sp. A, exterior of ventral valve, with part of dorsal valve above. B, ventral aspect of internal mould, leached in HCl from A. C, D, posterior aspects of same internal mould, with dorsal valve below (C) and on top (D). GSC 140989, holotype, from C-4005, Trold Fiord Formation, Ellesmere Island.

anteriorly, rather like the subfusc ribbing illustrated for *Cleiothyridina* by Alvarez & Rong (2002, Fig. 1023b). Such ribs may be seen in decorticated members of Cleiothyridinae and are not shown on the true exterior. In the present specimen, external ornament and micro-ornament are not preserved. A second specimen, GSC 140988 (Fig. 205), has widely diverging posterior walls at 125°, a broad foramen, and a short anterior widely concave sulcus. The dorsal valve is slightly higher than the ventral valve, and the anterior part of the dorsal valve is broadly arched, without forming a clearly defined fold. Both valves are crossed by low commarginal rugae, three in 10mm. The ventral valve is also crossed by faint and radial subdued ribs, much finer than those of the holotype, eight in 10mm. No true micro-ornament is preserved.

The small conjoined specimen is slender and rounded in outline, with very low anterior fold on the dorsal valve. The specimen shows no sign of external ornament. The ventral foramen is large and broad.

Internal detail in the holotype is well preserved. There are very short and obscure laterally placed dental

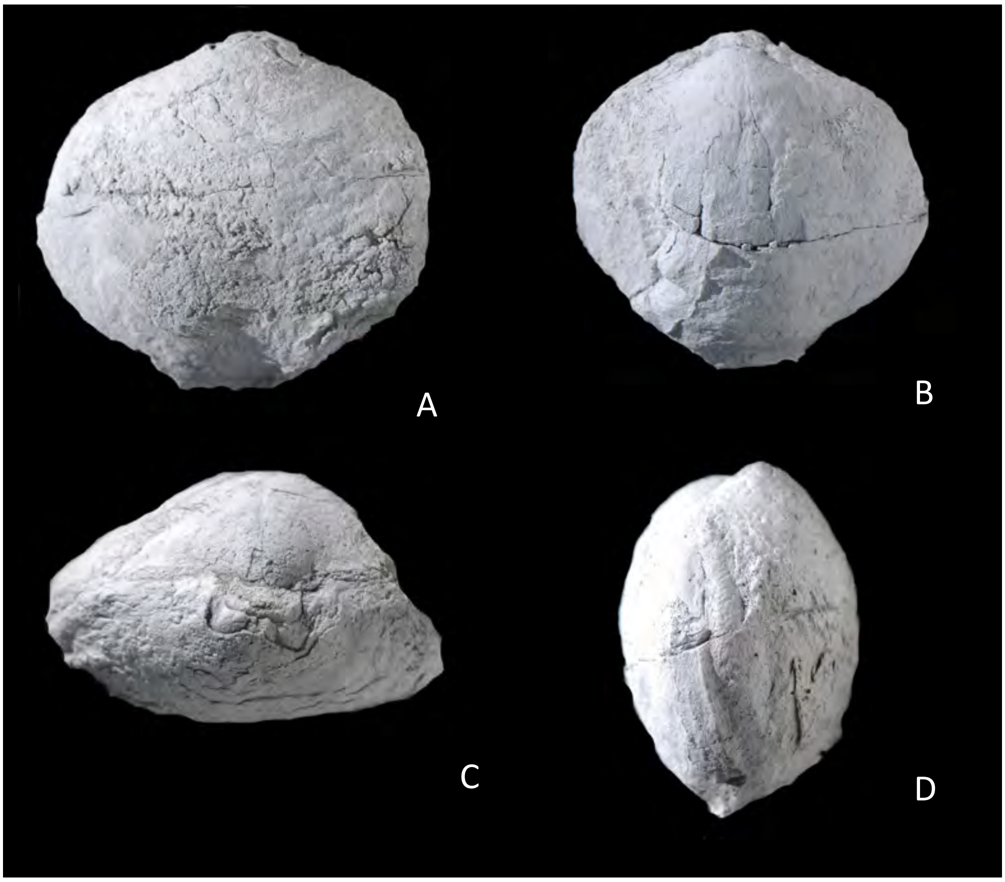

Fig. 205. *Himathyris arctica* n. sp. A, exterior of ventral valve, with part of dorsal valve above. B, dorsal aspect of specimen. C, posterior aspect, dorsal valve on top. D, lateral aspect, dorsal valve to left. GSC 140988, x1, from Trold Fiord Formation, Ellesmere Island.

plates, and the teeth are only small protuberances. The ventral muscle field is large, with posteriorly placed comparatively broad and short adductor scars, divided by a low ridge bearing a low median ridge posteriorly and shallow median groove anteriorly. Low ridges lie over each scar, parallel to the lateral margin. The adductor scars extend into a narrow ridge anteriorly. The diductor scars extend just as far posteriorly as the adductors, and are large, enclosing the adductors and extending well forward, with low radial ridges strongest anteriorly. To each side, the floor of the valve is heavily thickened and covered with dense dimples, passing laterally into low closely spaced ridges and grooves radiating laterally and curving gently forward. The posterior floor behind the muscle field is smooth.

Shallow and broad dental sockets occupy the posterior dorsal valve, passing forward each side of the ventral delthyrium. They bear fine growth increments. A broad almost flat cardinal plate spans the gap between the dental sockets, formed largely by the outer hinge plates, which pass smoothly into the inner hinge plates, and these carry

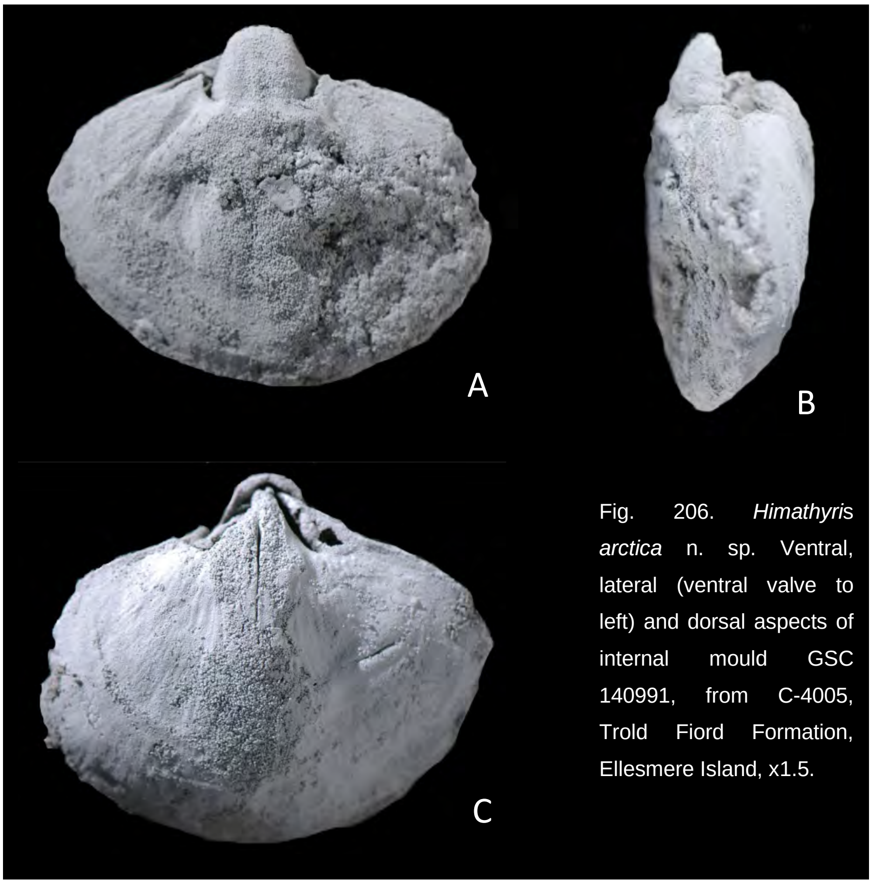

Fig. 206. *Himathyris arctica* n. sp. Ventral, lateral (ventral valve to left) and dorsal aspects of internal mould GSC 140991, from C-4005, Trold Fiord Formation, Ellesmere Island, x1.5.

a narrow median trough. The plates are separated by ridges formed by the crural bases. A terminal foramen lies at the apex of the trough, coinciding with the tip of the dorsal umbo. The most distinctive feature of the dorsal mould is the presence of a long narrow passage between very thick subvertical inner socket plates, which extends from the foramen dorsal to the cardinal plate, and between the thickened dental socket plates. This passage opens into the top of the ventral delthyrium. The passage-way is now occupied by a tube of matrix, which bears a low median ridge that was developed on the floor of the valve, and an impressed oval possible muscle scar lies each side posteriorly (under the letter p in Fig. 207B). Fine growth increments lie over the surface of the tubule, parallel to the longitudinal axis, and a slender tubular pore, now filled by matrix, passes through the shell between the passage-way and the inner side of the dental sockets. The lateral floor of the valve has dense dimples and radiating shallow grooves.

Internal detail is comparatively clear for the small conjoined specimen GSC 140991 (Fig. 206, 207). There is a well defined pedicle collar. A low median ridge extends along the posterior part of the specimen in front of the foramen. Muscle scars are only slightly impressed. The dorsal valve preserves a slender passage-way leading forward from the dorsal umbo, with narrow median ridge, and dorsal to the cardinal plate (Fig. 207B). The flanks of the tubule show very fine growth increments, along the radial or longitudinal axis. Two fine pores, the thicker one in front, now represented by fine tubules of matrix, pass parallel to the commissure through the shell on each side from the central space to the

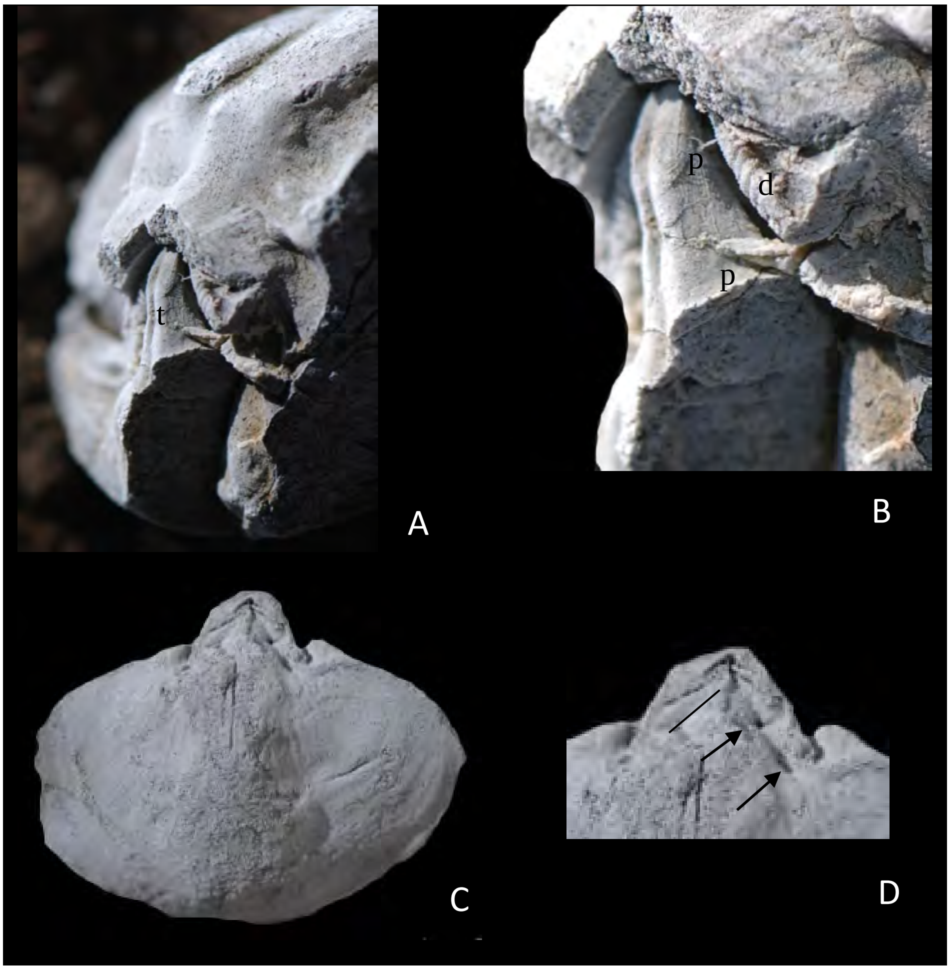

Fig. 207. *Himathyri*s *arctica* n. sp. A, B, detail of the matrix tubule (t), representing a passage way from the tip of the dorsal umbo between the ventral delthyrium and interior of the dorsal valve. Note the crenulate base of the dental sockets (d), and the two slender tubes of matrix (p), representing the pores that passed through the shell from the median passage-way into the inner side of the dental sockets. As well, fine growth increments are visible in Fig. 207B, with suggestions of a possible muscle scar at the upper p. C, D, dorsal valve with the matrix tubule removed to show the mould of the cardinal plate, with foramen at the umbonal tip. In D there is a narrow median trough (pointed to by a line). The crenulate base of the dental socket lies to each side, and the dorsal median septum is present in front. The crura emerge from in front of the cardinal plate, apparently from two sites, arrowed. Internal mould GSC 140991, from C-4005, Trold Fiord Formation, Ellesmere Island, x1.5 and x3.

inner side of the dental sockets. These are illustrated in Fig. 207A, B. The dental sockets are well developed, and are finely crenulate, lying slightly dorsal to the cardinal plate, and only slightly overlapped by the cardinal plate. The tubule of matrix which indicated the passage-way was removed to reveal a broad concave cardinal plate between the inner sides of the dental sockets, with a foramen developed at the umbonal tip. A short well-developed median septum lies in front over the floor of the valve, but muscle scars are indistinct. Possible crural bases arise at two locations, one in front of the other towards the anterior edge of the cardinal plate, just within the anterior end of the median trough.

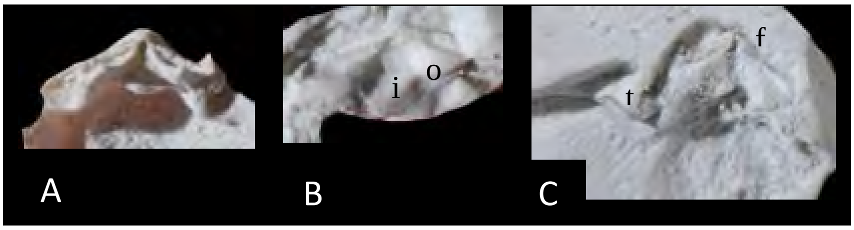

Fig. 208. Comparison of cardinalia. A, *Cleiothyridina maynci* Dunbar, GSC 140993. B, *Svalbardathyris kotlukovi* (Stepanov) GSC 141004, and with no foramen. C, *Himathyris artica* n. sp. GSC 140991 with shallow median trough in middle of inner hinge plates and outer hinge plate expanding anteriorly. Foramen (f), inner hinge plates (i), outer hinge plate (o), tooth (t).

Resemblances: The arrangement of internal detail, featuring the slender passage along the dorsal posterior floor between the greatly thickened inner flanks of the dorsal sockets is the same as that of the Himalayan genus *Himathyris*, of Wuchiapingian age. Regrettably, there is poor information for the present species on micro-ornament, but the interior is so distinctive and it marks such a significant match with faunas from the southern paleoworld of the Permian Period, that it is named specifically. The Arctic species is readily distinguished by its oval shape, compared with the much more pentagonal shape of Diener’s species. The narrow dorsal passage and position of the dorsal internal foramen mark strong differences from *Cleiothyridina* and allied genera.

The relationship to *Svalbardathyris* is more obscure, because the interior for the type material is poorly known, but shape differs considerably.

Subfamily **SPIRIGERELLAINAE (SPIRIGERELLINAE**) Grunt, 1965

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 ***Spirigerella*** Waagen, 1883

Diagnosis: Biconvex shells with uniplicate or parasulcate anterior margin, short incurved ventral umbo, nearly flat palintrope, dental plates if present buried in secondary shell, deltidial plate present. Cardinal plate, reduced outer hinge plates.

Type species: *Spirigerella derbyi* Waagen, 1883 from the upper Kalabagh Member and lower Chhidru Formation (Wuchiapingian) of the Salt Range, Pakistan, OD.

Discussion: This genus is very close to *Composita* Brown. Grabau (1932, p. 92) considered that the main internal difference lay in the nature of the cardinal process of *Spirigerella* being more massive than in *Composita*. Certainly Davidson (1858-1863, pl. 17, fig. 12) illustrated a very modest cardinal process for the type species of *Composita, C. ambigua* Sowerby. But for many species assigned to *Composita* from the Permian of United States, Cooper & Grant (1976a) illustrated much more prominent cardinalia, as endorsed by Alvarez & Brunton (1996) and Alvarez & Rong (2004, Fig. 1007.3a-c), with further study by Alvarez & Brunton (2008). The structure is more expansive terminally than that displayed by the present Canadian species assigned to *Spirigerella.*

Other criteria point to affinities of the Canadian material with *Spirigerella*. It is widely agreed that a foramen is better developed in *Composita*, and that that of *Spirigerella* may be small or often absent. The hinge is straighter in *Spirigerella* with a developed false interarea (Reed 1944). Grant (1976, pp. 204, 205, pl. 65, fig. 35-49) provided further useful comparisons and contrasts between the two genera, mentioning shape and shell thickness. The delthyrium of *Composita* is open, that of *Spirigerella* partially or wholly blocked by deltidial plates, Grant (1976) writing of two deltidial plates, which fuse in later maturity. The dental plates are stronger in *Composita*, and are short and thin in *Spirigerella*, and often merged with secondary shell along the walls. The crura extend from the median part of the hinge plate in *Composita* and from the sides in *Spirigerella*. Present material has been prepared to reveal internal moulds, as opposed to silicified material of Grant (1976), and serial sections in Grunt (1968). In Canadian material, there is a distinct triangular plate lying across the delthyrium (Fig. 210), and traversed by a median groove, which point to fusion of two plates, just as described by Grant (1976). The assessments by Grant (1976) were based on more or less topotype *Spirigerella*, but not directly on type *Composita*, and overlooked the study of type *S. derbyi* by Grunt (1968). She provided serial sections and supported the argument by Miloradovich (1937) and Makridin (1964) that the pedicle was responsible for the deltidium, which was a form of pedicle collar.

Present material is judged to belong to *Spirigerella* because dental plates are obscure, and because a fused plate lies under the delthyrium, and because cardinal flanges are described as serrated as recorded by Alvarez & Rong (2002, p. 1536). It was stated that the foramen is small or slit-like or missing from *Spirigerella*, but in present material of *S. inflata*, the foramen is well formed in young (ie. small) specimens of one species and has disappeared in larger specimens. It is less prominent in another Canadian species, described as *S. plana* (see below). The presence of the deltidial plate distinguishes the specimens not only from *Composita*, but also *Posicomta* Grunt, 1986 and *Gruntea* Shi & Shen, 1999, which are extremely close to *Composita*.

This appears to be the first report of possible *Spirigerella* from Permian Arctic faunas, as an extension of its geographic distribution, but agrees in occupying a northern paleolatitudinal counterpart for occurrences in the Salt Range, Himalayas and Western Australia.

Spirigerella inflata n. sp.

Fig. 209 – 213, 215A-C

Derivation: inflatus – swelled up, swollen, Lat.

Diagnosis: Elongate and well inflated shells with shallow anterior sulcus prolonged as an anterior tongue, uniplicate anterior margin, and strong commarginal growth steps.

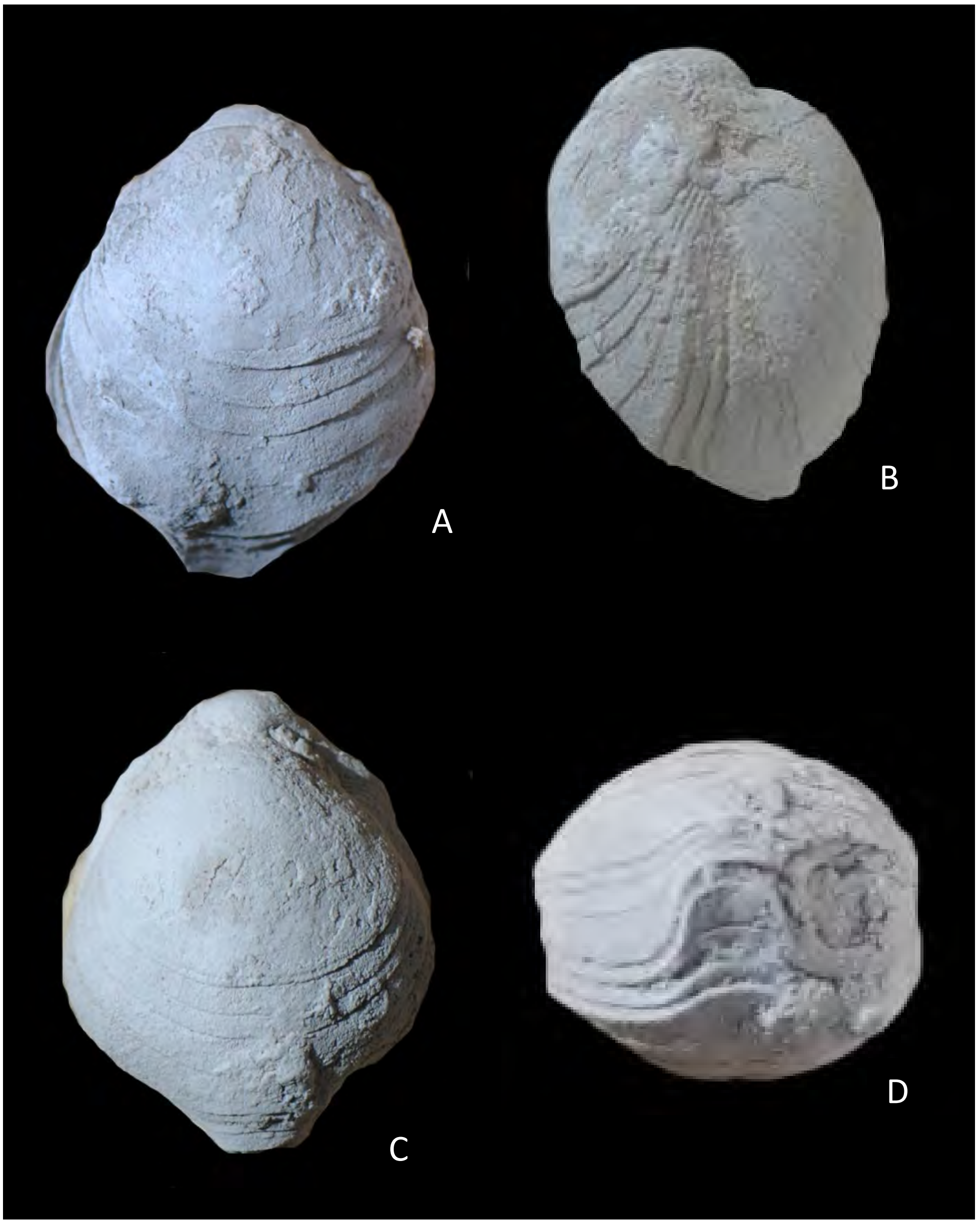

Fig. 209. *Spirigerella inflata* n. sp. A-D, GSC 140898 holotype, ventral, lateral, dorsal and anterior aspects of specimen. Dorsal valve on top in D. From GSC loc. 58973, Assistance Formation, Ellesmere Island, x2.

Holotype: GSC 140898 from GSC loc. 58973, Assistance Formation, Ellesmere Island, Fig. 209A-D, 212B, here designated.

Material: Three single ventral valves, and seven specimens with valves conjoined from GSC loc. 58973, and ventral valve from C-4025, Assistance Formation, Ellesmere Island.

Dimensions in mm: both valves

Width	Length	Height
30	37	27
26.5	37	24

25	31	22
39.5	21	20

Description: Shells elongate and smooth without ornament, ventral umbo little extended, small pedicle, umbonal walls diverging at 90° to 100°, valve swollen, with shallow anterior sulcus developing over the anterior third to half of valve, and extending as a short broad tongue anteriorly, to form a uniplicate margin. The dorsal valve is convex, most inflated anteriorly compared with maximum inflation near the hinge in the ventral valve, low anterior broadly rounded fold, and recessed anterior margin. Growth steps are well developed anteriorly, varying in number from five to eight.

Low dental ridges lie each side of the delthyrium, which is closed by a deltidium of two plates fused along the midline. Low dental plates are largely buried in secondary shell. Broad adductor scars are flanked laterally by diductor scars on narrow ridges. Low radial ridges score the floor of the mature ventral valve. Another specimen shows a deltidium with angle of 50°, bearing a narrow median groove. The pedicle collar lies each side of the plate and intersects the posterior shell.

Dental sockets are coarsely crenulate, each side of the two massive shafts of the cardinal process, which are separated dorsally by a broad groove fading upwards and terminating in a moderately large and rounded flat area. In front a median septum extends for more than half the length of the shell, and long narrow muscle impressions extend each side almost to mid-length. Low elongate pits radiate antero-laterally from the muscle scars.

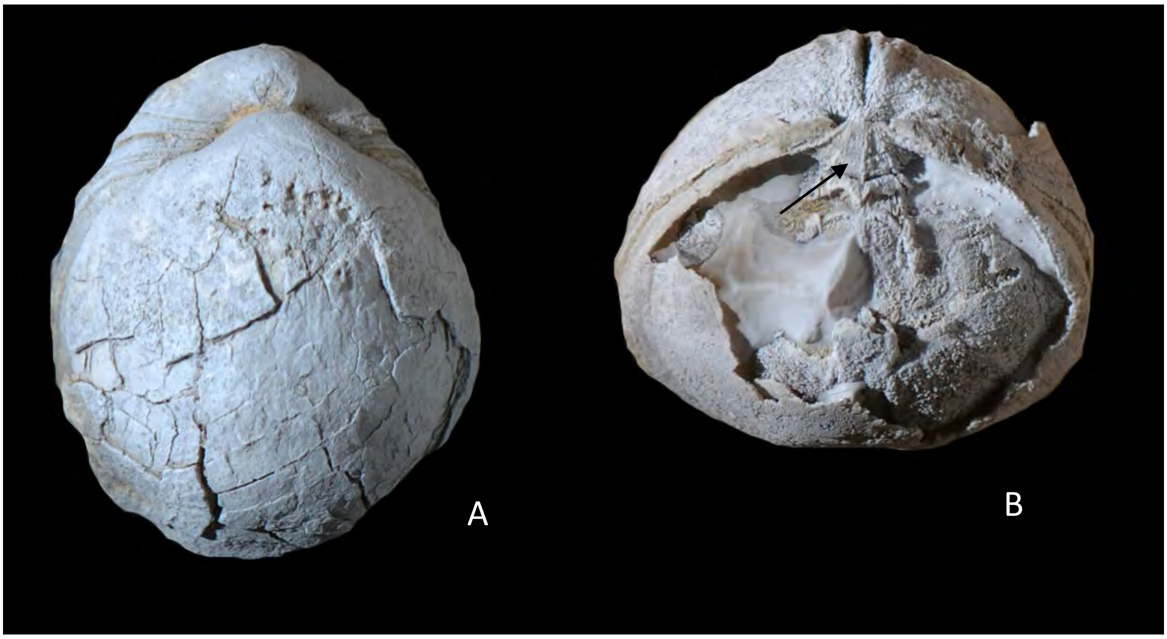

Fig. 210. *Spirigerella inflata* n. sp. A, dorsal aspect of specimen GSC 140899. B, posterior ventral aspect of same specimen, leached in acid to show deltidium, as arrowed. Dorsal valve on top. From GSC loc. 58973, Assistance Formation, Ellesmere Island, x2.

Resemblances: No comparable specimens have been observed from correlative faunas in northern Canada, but Gobbett (1964) reported three forms as *Composita* from somewhat older faunas in Spitsbergen, and all are more transverse than present material. Many species of *Spirigerella* have been described from the Wuchiapingian faunas of the Salt Range in Pakistan, and the present species conforms with species allocated to the *S. derbyi* group as recognized by Waagen (1883) and Grant (1976). *Spirigerella fusiformis* Waagen (1883, p. 467, pl. 38, fig. 5, 6) from the Chhidru Limestone of the Salt Range, Pakistan, is moderately close in inflation and lateral aspect, but has a more restricted and well-defined anterior fold and sulcus. *S. praelonga* Waagen (1883, p. 457, pl. 37, fig. 10) from the Cephalopod Bed also shows some similarities, but has wider hinge and different anterior fold. *S. grandis elongata* Reed (1944, pl. 43, fig. 4, 5) from the lower Chhidru Formation and possibly upper Wargal Formation (Kalabagh Member) is similarly inflated, with somewhat similar anterior sulcus and fold, but is much more elongate.

Fig. 211. *Spirigerella inflata* n. sp., lateral aspect of specimen. From GSC loc. 58973, Assistance Formation, Ellesmere Island, x2. This specimen has since been leached and partly destroyed.

Many species were described as *Composita* from the Permian faunas of the Glass Mountains, Texas, by Cooper & Grant (1976a), and a number share the elongate shape, small foramen, growth steps and style of anterior margin with the present form, whilst other taxa have a deeper or wider sulcus, and are slightly more transverse. *C. crassa* Cooper & Grant (1976a, pl. 655, fig. 1-39) from the Road Canyon Formation is moderately close, slightly more transverse with more tapered dorsal umbonal region, and *C. stalagmium* Cooper & Grant (1976a, pl. 662, fig. 1-65) from the same formation is close overall, though tending to have a low anterior dorsal fold and wider anterior sulcus. Specimens assigned to *C. discina* Cooper & Grant (1976a, pl. 656, fig. 1-20) are close to the present form in their widely diverging dorsal umbonal walls but are smaller with low dorsal fold, and they come from the Skinner Ranch Formation. *C. pitula* Cooper & Grant, 1976a, pl. 657, fig. 1-39) also has a comparable posterior dorsal valve and is highly inflated, distinguished by its smaller size and very low anterior fold in some specimens. There is also some approach to *C. pyriformis* Cooper & Grant (1976a, pl. 660, fig. 1-25) from the Pinery Member of the Bell Canyon Formation (Capitanian), though the anterior fold and sulcus are broader. *Composita mexicana* (Hall, 1857; Girty 1908), and further studied by Yancey (1978, p. 298) in describing material from the Pequop Formation in the Arcturus Group of Nevada and Utah has a rather similar sulcus and fold, but is much less elongate. These species all lack any form of delthyrial cover, and differ in foramen, hinge, and cardinal process.

There have been no report as far as I am aware of the genus from Greenland, Spitsbergen or northeast Russia, or even the extensive faunas of northern Russia.

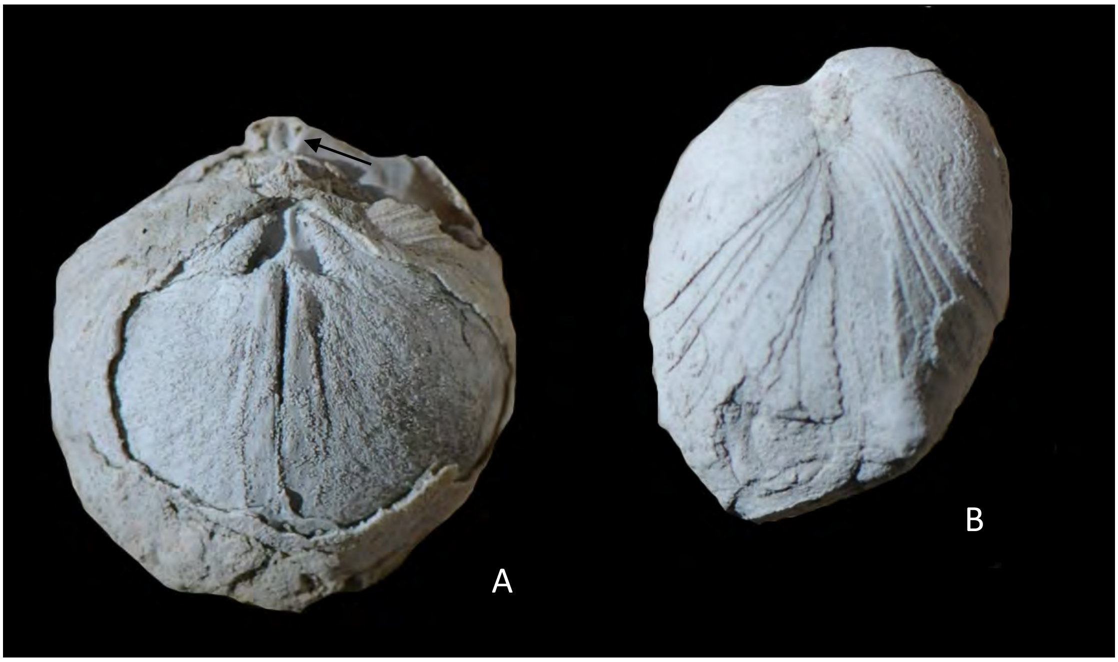

Fig. 212. *Spirigerella inflata* n. sp. A, dorsal aspect of specimen GSC 140899 with valves conjoined, leached in acid. Arrow points to delthyrium. B, lateral aspect of holotype GSC 140898. Specimens from GSC loc. 58973, Assistance Formation, Ellesmere Island, x2.

Fig. 213. *Spirigerella inflata* n. sp., anterior aspect of specimen with valves conjoined, GSC 140981, x2. Ventral valve on top. From GSC loc. 58973, Assistance Formation, Ellesmere Island.

Spirigerella plana n. sp.

Fig. 214, 215D-G

Derivation: plane – plane, simple, Lat.

Diagnosis: Small shells widest anteriorly with broad anterior sulcus and dorsal valve swollen anteriorly. Little inflated ventral valve, higher dorsal valve. Small foramen, disappearing in large specimens.

Holotype: GSC 140901 from GSC loc. 58973, Assistance Formation (Roadian), Ellesmere Island, illustrated in Fig. 214A -C, here designated.

Material: Four conjoined specimens and two fragmentary shells from GSC loc. 58973, Assistance Formation, Ellesmere Island.

Dimensions in mm:

Width	Length	Height
19	18	11.5
24	23	13.5
33	32	21

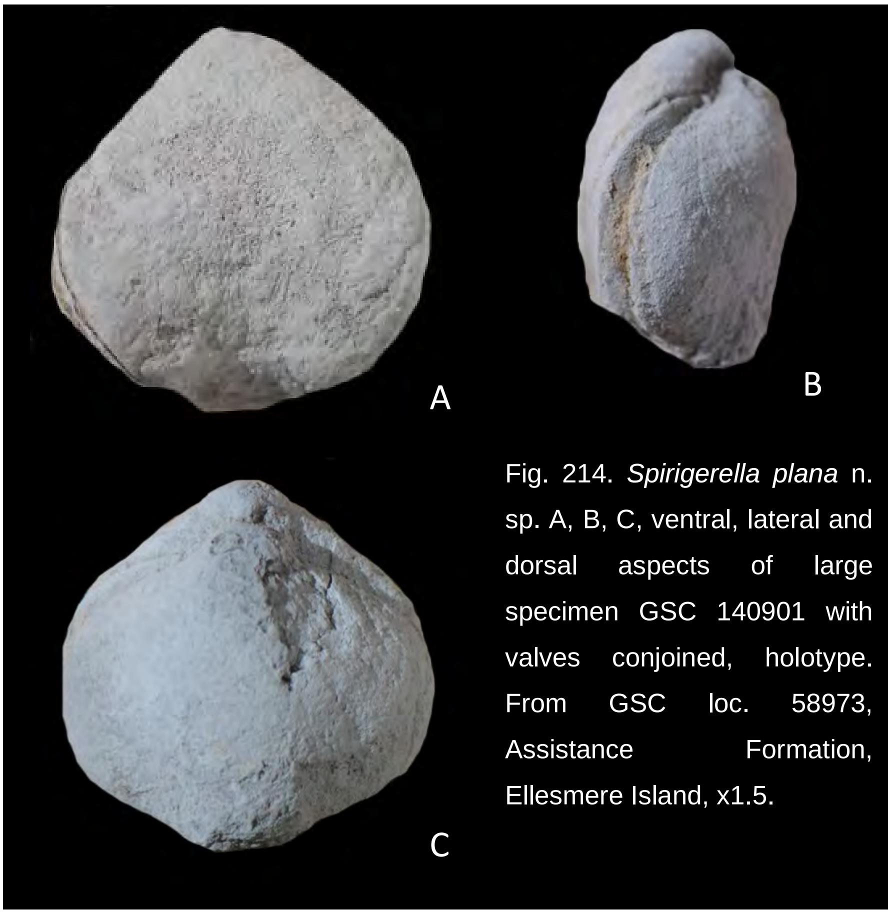

Fig. 214. *Spirigerella plana* n. sp. A, B, C, ventral, lateral and dorsal aspects of large specimen GSC 140901 with valves conjoined, holotype. From GSC loc. 58973, Assistance Formation, Ellesmere Island, x1.5.

Description: Shells are subequidimensional with ventral umbonal angle close to 100°, long posterior walls, and well defined palintrope. The ventral valve is broad and little inflated. A small foramen is developed, except in the largest specimen, which has no foramen. A broad sulcus with wide gently concave floor commences near mid-length, and extends dorsally in a short tongue. The dorsal valve has a broad low umbo with angle close to 110°, and widens and develops a low median fold anteriorly. The shell surface is smooth, apart from well defined small growth steps, and a hint of subdued low rugae on the largest specimen.

Attempts to determine internal features were frustrated by the calcareous nature of the matrix.

Resemblances: Compared with *Spirigerella inflata* n. sp., this species is closer in shape to some of the species of *Spirigerella* originally described from the Salt Range, Pakistan, given its shape, reduced foramen and wide anterior flattening, but no Salt Range species is identical. *S. obovata* Reed (1944, p. 280, pl. 40, fig. 6-9, pl. 43, fig. 1, 2) from the lower Chhidru Formation and possibly Kalabagh Member of the Wargal Formation of the Salt Range in Pakistan, of Wuchiapingian age, is somewhat similar, a little more inflated with slightly better defined fold, and slightly lower ventral umbo. *S. obovata selliformis* Reed (1944, p. 281, pl. 40, fig. 10, pl. 41, fig. 9) from either the Wargal or Chhidru Formation is close, with lower broader ventral umbo and deeper sulcus.

Fig. 215. A, B, C, *Spirigerella inflata* n. sp., ventral, dorsal, and lateral aspects of specimen GSC 140904 with valves conjoined. D, E, F, G, *S. plana* n. sp., lateral, ventral, dorsal and anterior aspects of specimen with valves conjoined, GSC 140902. Specimens x2 from GSC loc. 58973, Assistance Formation, Ellesmere Island.

Order RETZIAIDA (RETZIIDA) Boucot, Johnson & Staton, 1964

Subfamily **HUSTEDIAINAE** (**HUSTEDIINAE)** Grunt, 1986

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 troelseni Dunbar, 1955

Fig. 216

1955 *Hustedia troelseni* Dunbar, p. 160, pl. 32, fig. 12-15, ?16, ?17.
1955 *Hustedia* sp. Dunbar, p. 160, pl. 32, fig. 11.

Diagnosis: Small shells, three pairs of plicae in each valve, moderately developed ventral sulcus, and well developed dorsal median sulcus bearing low median rib.

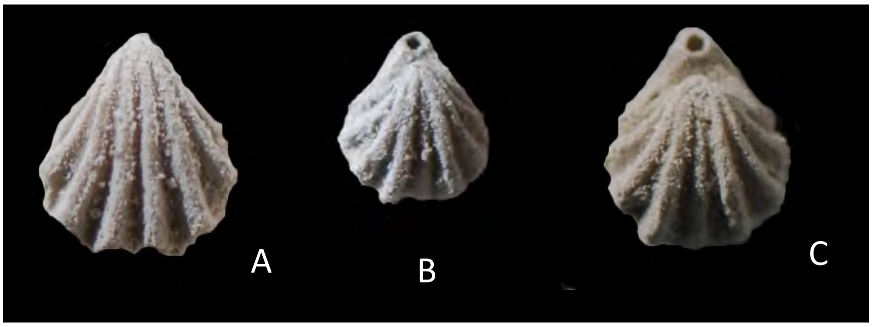

Fig. 216. *Hustedia troelseni* Dunbar. A, C, ventral and dorsal aspects of specimen GSC 140906 with valves conjoined. B, dorsal valve of specimen GSC 140907 with valves conjoined. From GSC loc. 53846, unnamed sandstone unit (*Dyoros modestus* Zone), McDougall Pass, Richardson Mountains, Yukon Territory, x6.

Holotype: Specimen from Foldvik Creek Group, Kap Stosch, central east Greenland, figured by Dunbar (1955, pl. 32, fig. 12, 13), OD.

Material: Three specimens with valves conjoined from GSC loc. 53846, unnamed sandstone unit, *Dyoros modestus* Zone, McDougall Pass, Richardson Mountains, Yukon Territory.

Description: The specimens are tiny, one measuring 4mm wide, 4.5mm long and 3.3mm high, with ventral umbonal angle of 80°, and three pairs of ventral plicae, either two or three pairs of dorsal plicae, and low median dorsal plication.

Resemblances: These specimens are identified with *Hustedia troelseni* Dunbar from northeast Greenland. The holotype of the species is not exactly the same, but displays a similar number and disposition of plicae on each valve, the difference lying in the slightly wider shell and slightly broader ribs in the holotype. One paratype (Dunbar 1955, pl. 32, fig. 14, 15) is broader with wide plicae, and another specimen (pl. 32, fig. 16, 17) has one fewer pair of ribs on each valve, with exceptionally narrow ventral sulcus, and may be a variant, or member of a different taxon. Another specimen described and figured as *Hustedia* sp. by Dunbar (1955, p. 160, pl. 32, fig. 11, not fig. 12 despite the text) is rather similar but was said to have four rather than three pairs of ribs. It came from the same beds in Greenland, and is very close to the Canadian specimens, and the fourth and outermost plication is very fine, so that the additional rib could well lie within the limits of specific variation.

Ustritsky (1979) stated that *Hustedia troelseni* occurred in the upper part of his so-called Starotsin Suite, to be matched probably with the Svenskeegga Member. It was not shown in his table, and not figured.

The Neal Ranch species of early Permian age, *Hustedia crepax* Cooper & Grant (1976b, pl. 734, fig. 31-40), has a low median dorsal rib, but one fewer pair of plicae, and *H. demissa* Cooper & Grant (1976b, pl. 735, fig. 69-86) has a slightly lower median dorsal rib, and more pairs of plicae. It comes from the Bell Canyon Formation of upper Guadalupian age. *H. hapla* Cooper & Grant (1976b, pl. 736, fig. 46-60) from the same formation is somewhat similar. *H. samiata* Cooper & Grant (1976b, pl. 740, fig. 28-38) from the Hegler Member of the Bell Canyon Formation is perhaps the closest of species described from the Permian of the Glass Mountains in Texas. It is larger, slightly broader and less elongate and some specimens have shorter posterior walls. Species assigned to *Thedusia* Cooper & Grant commonly have a low median dorsal rib, but are more elongated, with attenuated ventral beak.

The present material is moderately like a Gzhelian (Late Carboniferous) species from the basal Jungle Creek Formation in the Yukon Territory, called *Hustedia trifida* Waterhouse (2018a, p. 305, Fig. 252A-D), but the two central ribs of the ventral valve are spaced closer together in that species.

Hustedia sp.

1975 *Hustedia* sp. Stehli & Grant, p. 514, pl. 64, fig. 31-35.

Description: *Hustedia* was reported from Svartevarg cliffs of Axel Heiberg Island by Stehli & Grant (1971, p. 514, pl. 64, fig. 31-35), and the ventral valve looks similar to *troelseni*. But it differs in having a fine rib along each interspace, unlike any of the species described by Cooper & Grant (1976b) or Dunbar (1955). The dorsal valve of the Axel Heiberg material displays a strong median rib, not like the fine median rib of *Hustedia troelseni* Dunbar.

Superorder SPIRIFERIFORMI Waagen, 1883

Order SPIRIFERIDA Waagen, 1883

Suborder MARTINIAIDINA (MARTINIIDINA) Waterhouse, 2010a

Infrasuborder MARTINIAIMORPHI (MARTINIIMORPHI) Waterhouse, 2010a

Diagnosis: Genera smooth or plicate, seldom costate, micro-ornament varied, smooth, pitted, grooved, or minutely spinose. Interior with well developed dental plates and adminicula, may be secondarily absent. 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 those plates. Overall shape is subrounded, plicae are more or less developed, and micro-ornament is varied, pitted, spinose, grooved or smooth, with further variations, but as a rule without prominent commarginal lamellae, and rarely if at all costate.

The group is moderately well known so far as the Permian constituents are concerned, and contributes information on the variability that may be achieved within a brachiopod group. They stemmed from Cyrtioidea Fredericks, which differed in their small size, thin shell, and simple plication with capillae or spinules. Yet unlike Cyrtioidea, few of the known martiniiform genera exhibit deltidial plates or delthyrial cover. The infrasuborder commenced in Silurian (upper Wenlock) time, as members of Eospiriferinae, such as *Endospirifer* Tachibana, *Hedeina* Boucot and *Myriospirifer* Havlíček of Silurian and early Devonian age. These genera differed from members of Martiniaimorphi in their micro-ornament, but overall shape, internal plates and fossil record display a convincing source for the origin and development of the Elythynoidea, Gerkispiroidea and Ingelarelloidea.

Superfamily **INGELARELLAOIDEA (INGELARELLOIDEA)** Campbell, 1959a

Diagnosis: Smooth to sulcate and often plicate, micro-ornament varied, grooves or spinules being common, shell taleolate and exopunctate, adminicula well developed, tabellae well developed to rarely absent.

Discussion: Members of Ingelarelloidea were classed within Martinioidea by Carter & Gourvennec (2006a), but differ in having adminicula and usually tabellae. Both Martinioidea and Ingelarelloidea are large and diverse and comparatively long-lived groups, and each fully warrants recognition as a discrete and distinctive superfamily.

Family I**NGELARELLAIDAE** (**INGELARELLIDAE**) Campbell, 1959a

Diagnosis: Micro-ornament of grooves in quincunx, adminicula well formed, tabellae short to long, rarely absent.

Discussion: The family apparently developed from Rorespiriferidae Waterhouse, 1998 (see Waterhouse 2018b, pp. 166, 167), an allied but older family characterized by distinctive micro-ornament.

Subfamily **INGELARELLAINAE** (**INGELARELLINAE**) Campbell, 1959a

Tribe **INGELARELLAINI** (**INGELARELLINI**) Campbell, 1959a

Diagnosis: Shells smooth or plicate, may be sulcate, smooth or with two subplicae, rarely a median rib. Tabellae and adminicula long.

Discussion: The development of the internal plates appears to have allowed successful colonization, distribution and diversification as widely and successfully as any other member of Martiniaidina (Martiniidina): by Permian time the group made up a modest component of boreal faunas and flourished with significant biomass over Gondwana. The presence of long tabellae is exceptional for Spiriferida, and the fact that they developed so well, marking a return to morphologies in mid-Paleozoic genera such as *Eospirifer* and allies, shows that a morphological feature can be revived. The concentration of genera in high southerly latitudes probably explains why most workers, who study as a rule paleotropical fossil faunas especially each side of the Atlantic, have ignored or misunderstood the significance of the plates and the implications for mid-Paleozoic brachiopod morphology. Just as striking is the great gap in application of terms for internal morphology between workers on Late Paleozoic and Middle to Lower Paleozoic brachiopods. The latter group are decades behind their understanding of internal brachiopod morphology involving what are called dental plates as distinct from adminicula, especially for Spiriferida.

Genus ***Oviformia*** Waterhouse, 2015b

Diagnosis: Plicate shells, ventral sulcus characteristic with anterior median fold, dorsal fold with channel, micro-ornament of short grooves in quincunx. Adminicula and tabellae short to moderate in length and spacing.

Type species: *Spirifera* (*Brachythyris*) *oviformis* M'Coy, 1847, p. 234 from the Muree Formation (Wordian) at Barraba, Hunter Valley, New South Wales, Australia, OD.

Discussion: This genus is very close to *Ingelarella*, but unlike that genus, has a fold in the ventral sulcus. The oldest known species, *Oviformia sweeti* Waterhouse, 2015b from Asselian beds at Gympie, is older than known *Ingelarella*, which first appeared in east Australia in Sakmarian faunas of the Tiverton Formation of the north Bowen Basin (Waterhouse 2015a, p. 153), and became common as *Ingelarella plica* Campbell in the uppermost Tiverton Formation, of Aktastinian (lower Artinskian) age.

Oviformia is based on *Spirifera* (*Brachythyris*) *oviformis* M'Coy (1847, pl. 13, fig. 5, 6) from the Muree Formation (Wordian) and Fenestella Shales (Kungurian) of the Sydney Basin in New South Wales, and also reported from the Belford Formation of the Sydney Basin, as summarized by McClung (1978, p. 42, pl. 14, fig. 14-16, pl. 15, fig. 1-6). A counterpart has been recognized in Arctic Canada. The genus has a very limited distribution, as far as is known, being found only in Permian marine faunas of eastern Australia, and in the Canadian Arctic.

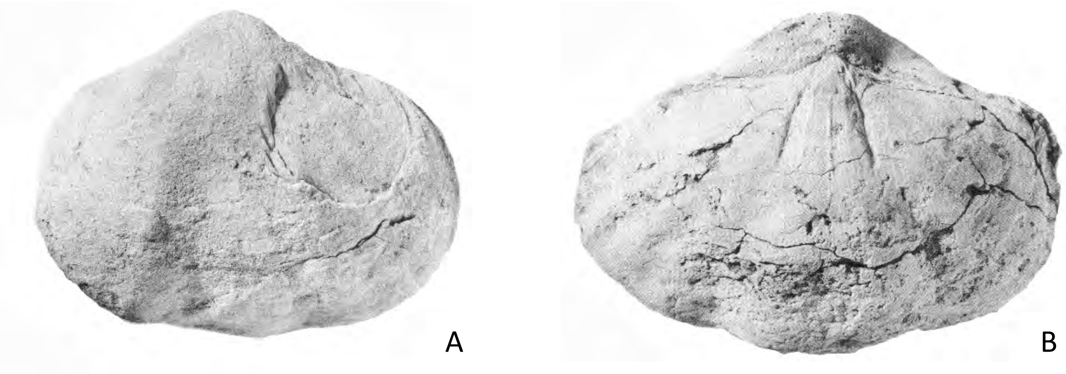

Fig. 217. *Oviformia bamberi* (Waterhouse), ventral and dorsal aspects of holotype, GSC 24832, x1, from C-1872, Assistance Formation, Melville Island. (Waterhouse 1971a).

Oviformia bamberi (Waterhouse, 1998)

Fig. 217, 218

1971a *Tomiopsis magna* [not Campbell] – Waterhouse, p. 77, pl. 17, fig. 1, 2, 4, 5, 9, 10.
1998 *T*. (*Ambikella*?) *bamberi* Waterhouse, p. 10.
2015b *Oviformia bamberi* – Waterhouse, p. 171.

Diagnosis: Transverse, unusually long tabellae.

Holotype: GSC 24832 figured by Waterhouse (1971, pl. 17, fig. 1, 2, 4, 10) and herein as Fig. 217A, B, from C-1872, Assistance Formation, Melville Island, OD.

Additonal material: A small dorsal valve comes from C-4017, Trold Fiord Formation, Ellesmere Island.

Discussion: This species is rare in Arctic Canada, and no comparable material appears to have been found elsewhere in the Arctic. The species was briefly mentioned by Clarke (1987) in dismissing its surface as having been abraded, but he had not examined the Canadian material, and in fact surface grooves are clearly preserved in patches.

Fig. 218. *Oviformia bamberi* Waterhouse, dorsal valve GSC 140915 x2, from C-4017, Assistance Formation, Ellesmere Island.

Superfamily **MARTINIAOIDEA** (**MARTINIOIDEA)**Waagen, 1883

Diagnosis: Shells without adminicula or tabellae.

Family **MARTINIAIDAE** (**MARTINIIDAE)** Waagen, 1883

Subfamily **MARTINIAINAE** (**MARTINIINAE**) Waagen, 1883

Genus ***Martinia*** M'Coy, 1844

Diagnosis: Medium to large generally sulcate shells with no ornament other than fine pits, small ctenophoridium and radiating vascular impressions. Dental plates low or lacking.

Type species: *Spirifer glaber* Sowerby, 1820 from Carboniferous Limestone (Visean), England, OD.

Discussion: 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 of topotype material is required to clarify the nature of the interior, and in the meantime, assignation of species to *Martinia* is highly provisional.

Martinia stehlii n. sp.

Fig. 219

1964 *Martinia*? sp. B Gobbett, p. 160, pl. 21, fig. 11, 12.
1971 *Martinia* sp. Brabb & Grant, p. 17, pl. 1, fig. 27-30.
1971 *Martinia* sp. Stehli & Grant, p. 518, pl. 63, fig. 1, 2, 7, 13, 21, 22.

Derivation: Named for F. G. Stehli.

Diagnosis: Small subrounded shells without sulcus or fold, ventral umbo not prominent and hinge short. Dental plates very low.

Holotype: USNM 166285 from Sabine Bay Formation (Kungurian), Axel Heiberg Island, figured by Stehli & Grant (1971, pl. 63, fig. 1, 2, 7) and herein as Fig. 219A, C, here designated.

Material: Only a few specimens were available to Stehli & Grant (1971), but the genus is so rare in Middle and late Early Permian faunas of the Sverdrup Basin, and indeed Yukon Territory and Arctic at large that it is named.

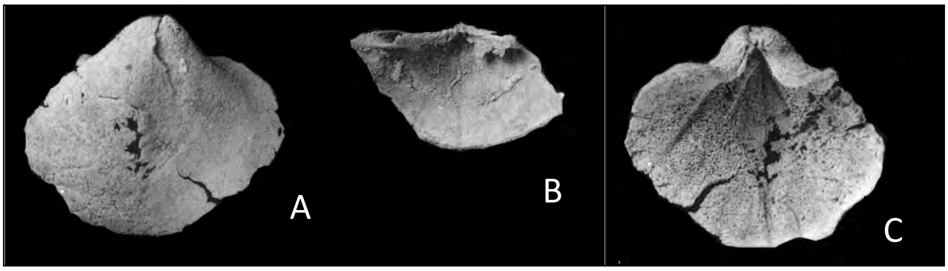

Fig. 219. *Martinia stehlii* n. sp. A, C, external and internal aspects of ventral valve holotype, USNM 166285 x2. B, internal aspect of dorsal valve, USNM 166286, x2. From Sabine Bay Formation, Axel Heiberg Island. (Stehli & Grant 1971).

Description: The ventral umbo has an angle close to 95°, and the umbonal walls are concave, sweeping out to well rounded cardinal extremities, and the shell is rounded and equilateral in outline with maximum width just in front of mid-length. The hinge is narrow and just over half the width of the valve, and there is no sulcus, apart from the suggestion of a short narrow median groove over the anterior ventral shell, which does not reach the anterior commissure. There are faint suggestions of subdued radial costae on a paratype (Stehli & Grant 1971, pl. 63, fig. 22), but these were discounted by those authors as a likely artifact due to imperfect silicification. The dorsal valve is transverse with low very wide umbo and no fold.

The ventral interior is characterized by low dental flanges, with no supporting plates and no adminicula. A median groove is faintly indicated with suggestions of fine radial grooves related to the vascular pattern. Dorsal socket plates are well developed and widely diverging.

Resemblances: Gobbett (1964, p. 160, pl. 21, fig. 11, 12) described one specimen as *Martinia*? sp. B, as well as indeterminate fragments, from Spitsbergen, in the Brachiopod Chert according to the text, and from the Spirifer Limestone according to the caption to pl. 21, fig. 11, 12. The specimen could well prove to have been close to the present form, given that it has a moderately wide hinge and no ventral sulcus, and is comparable in size. A lateral view shows that the dorsal valve was much less inflated than the ventral valve, as is normal for various martiniid genera, except *Mirandifera* Waterhouse (1918a, p. 463). Brabb & Grant (1971, p. 17, pl. 1, fig. 27-30) figured rather similar shells from the lower unit of the type Takhandit Formation in Alaska, commenting on its featureless morphology, and describing the valves as "empty".

This species is readily distinguished from *Martinia greenlandica* Dunbar (1955, p. 152, pl. 30, fig. 1-8) from the Martiniakalk of northeast Greenland. This species has well defined sulcus and fold, and is more pentagonal in outline, with a few well defined posterior vascular grooves. No mention of dental plates was made, nor of micro-ornament. The Greenland species is like various species described from the Permian in the Glass Mountains of Texas by Cooper & Grant (1976a). The closest of the Cooper-Grant species to the present form is *Martinia exigua* Cooper & Grant (1976a, p. 2266, pl. 644, fig. 24-44) from the Neal Ranch Formation of Asselian age, and this has shallow sulcus, low broad median dorsal swelling, and distinct although low dental plates. *Tiramnia canadica* Shi & Waterhouse (1996, pl. 29, fig. 5-19) from the upper Jungle Creek Formation of Yukon Territory has only a shallow ventral median groove, and no dental plates are developed. Especially small specimens approach the present form in outline, but an anterior sulcus is present.

***Martinia*? sp. A**

Fig. 220

Material: A ventral valve from GSC loc. 58973 and two from C-4024, both from Assistance Formation, Ellesmere Island, and a possibly related external mould from C-4004, Trold Fiord Formation, Ellesmere Island. Dorsal fragment from GSC loc. 53846, unnamed sandstone unit, *Dyoros modestus* Zone, McDougall Pass, Richardson Mountains, Yukon Territory.

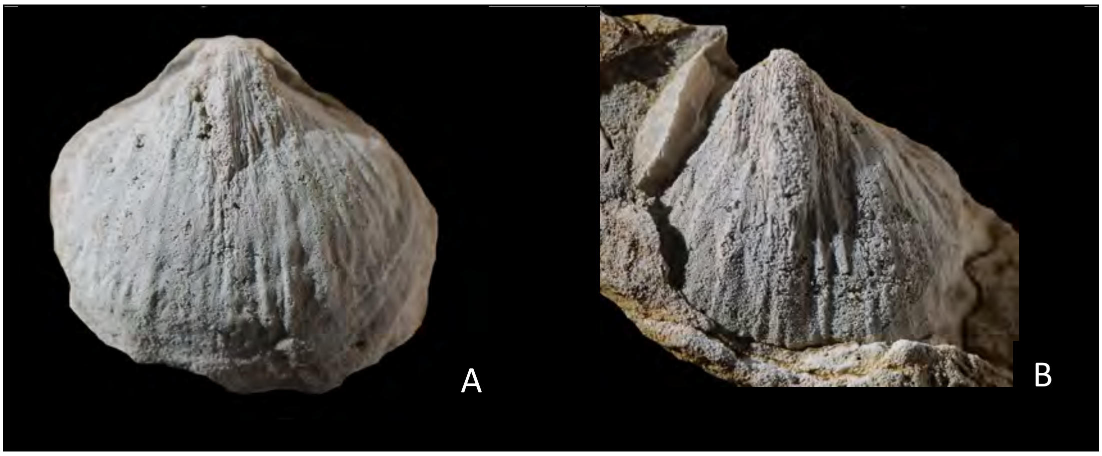

Fig. 220. *Martinia*? sp. A. A, leached ventral internal mould GSC 140908 from GSC loc. 58973. B, leached internal mould GSC 140909 from C-4024. Specimens from Assistance Formation, Ellesmere Island, x1.5.

Description: The ventral valve was externally smooth with micro-ornament of very small densely arranged pits, usually round, some slightly elongate, and without a sulcus and with moderately high concave interarea and open delthyrium. Etching in acid revealed an impressed elongate and large martiniiform posterior muscle field and radiating well defined grooves, mostly subparallel, with a few displaying bifurcation. Dental plates are very low, and there are no adminicula. The dorsal fragment shows no internal detail, nor micro-ornament.

Resemblances: These specimens are close in several respects to *Martinia stehlii* n. sp. from the underlying Sabine Bay Formation, but are much larger with thicker shell and more emphasized vascular channels, and more rounded outline. *Martinia greenlandica* Dunbar (1955, 1961) from northeast Greenland has a broad anterior sulcus and low dorsal fold.

***Martinia*? sp. B**

Fig. 221

Material: Four ventral valves from JBW 631, Takhandit Formation.

Dimensions in mm: specimens from JBW 631

Width	Length	Height
16	16.5	6.5
24.5	22.5	10.5
28.5	27	15

Description: The ventral valves from the Takhandit Formation are subequilateral to subpentagonal in shape with incurved ventral umbo of 95°, moderately broad hinge and well-rounded cardinal extremities. A very shallow sulcus is developed anteriorly, but otherwise the surface is smooth apart from faint suggestions of low commarginal rugae. Micro-ornament is unreliably preserved for the Takhandit specimens, suggestive of small pustules, conceivably formed by prismatic shell structure, but possibly original, given the suggestion of low growth increments, which would have been removed by very slight weathering.

The interior is distinctive, with no dental plates, and a narrow elongate adductor platform, close to the umbonal tip and long narrow median groove in front. There is only a suggestion of non-rbanching mantle canals.

Resemblances: These specimens are distinguished from *Martinia*? sp. A of the Assistance Formation by its shallow anterior sulcus, small adductor platform, and weak mantle canals, in contrast to the strong mantle canals, large adductor impressions and more globose shell of *Martinia*? sp. A. *Martinia stehlii* n. sp. from the Sabine Bay Formation is close in shape, but lacks any sign of a sulcus and has a larger ventral muscle field.

***Martinia*? sp. C**

Fig. 222

cf. 1971 *Martinia* sp. Bamber & Waterhouse, p. 176, pl. 20, fig. 8.

Material: A previously figured ventral valve from GSC 53929, Takhandit Formation. A ventral valve from C-1872, Assistance Formation, Ellesmere Island. A ventral valve from C-4072, Van Hauen Formation, Ellesmere Island.

Description, Resemblances: The specimen from the Van Hauen Formation is 28mm wide, 29mm long and 16mm high, with extended ventral umbo and wide hinge and cardinal angle measuring 100°. A broad shallow sulcus commences in front of mid-length. The small and narrow adductor platform lies well in front of the umbo, with shallow longitudinal striae. The surface of the shell is not reliably preserved, the numerous closely spaced pits possibly reflecting prismatic shell structure, although faint commarginal growth rugae are visible anteriorly, to suggest that the surface has not been worn. In shape and size and wide hinge the specimens are moderately close to

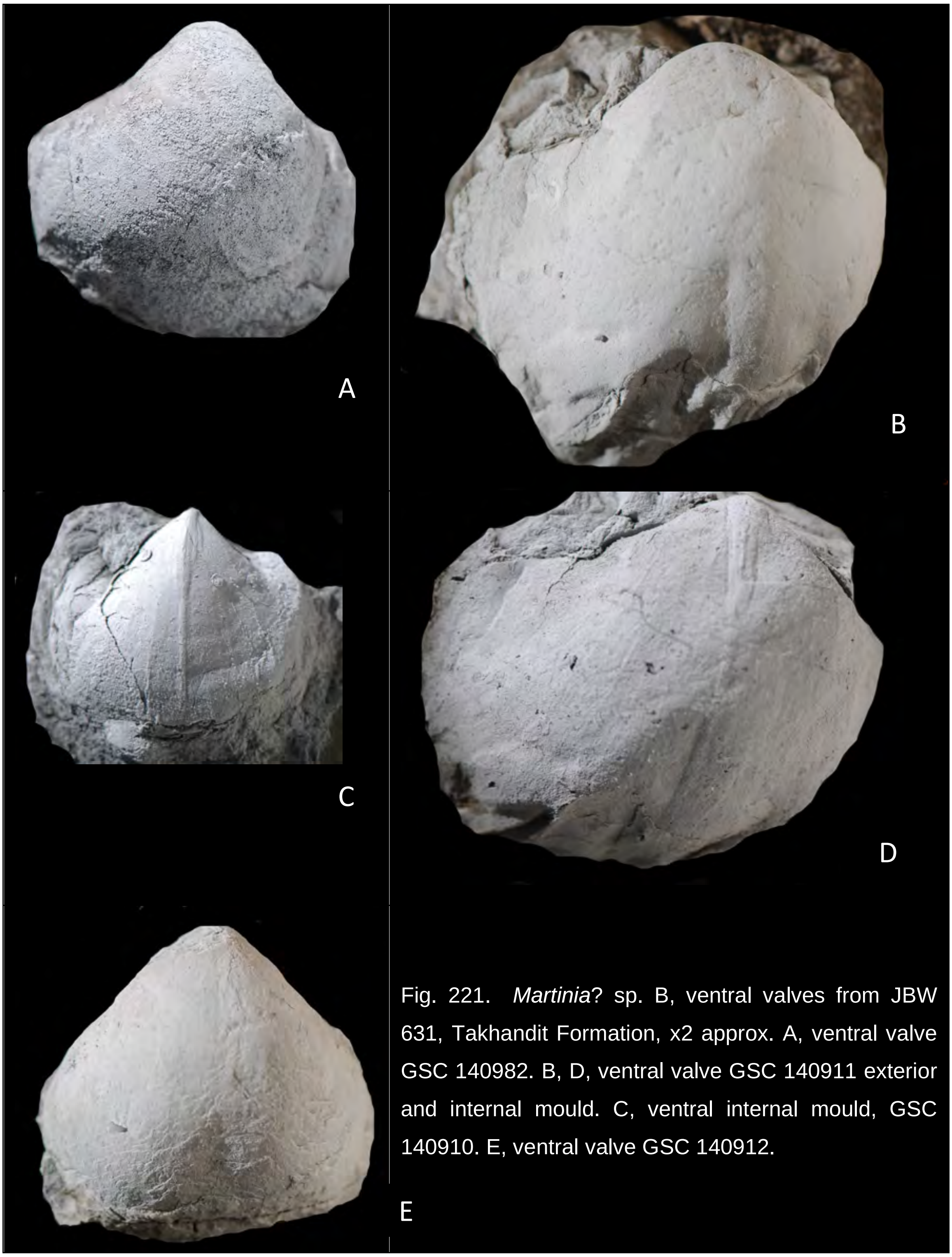

Fig. 221. *Martinia*? sp. B, ventral valves from JBW 631, Takhandit Formation, x2 approx. A, ventral valve GSC 140982. B, D, ventral valve GSC 140911 exterior and internal mould. C, ventral internal mould, GSC 140910. E, ventral valve GSC 140912.

Martinia greenlandica Dunbar (1955, p. 152, pl. 30, fig. 1-8) from northeast Greenland. This species has a more incurved ventral umbo, and the sulcus is a little more prominent, with a median groove commencing close to the umbo in some specimens. Dunbar's species is possibly a member of *Tiramnia* Grunt, though the mantle canal system shown in Dunbar (1955, pl. 30, fig. 8) is like that of *Martinia*.

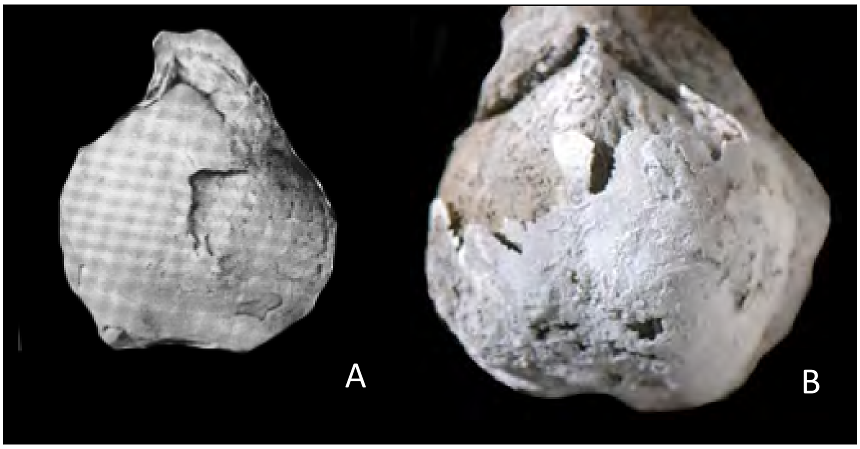

Fig. 222. *Martinia*? sp. C. A, ventral valve GSC 27041 from GSC loc. 53929, *Dyoros modestus* Zone, x2, from Takhandit Formation. (Bamber & Waterhouse 1971). B, ventral valve GSC 140913, posterior shell lost, x1.5, from C-1872, Assistance Formation, Ellesmere Island.

Superfamily **CHORISTITESOIDEA** (**CHORISTITOIDEA**) Waterhouse, 1968b

Family **CHORISTITESIDAE** (**CHORISTITIDAE**) Waterhouse, 1968b

Choristites? sp.

Fig. 223

1916 *Spirifer nikitini* [not Tschernyschew] – Tschernyschew & Stepanov, p. 48, pl. 10, fig. 2.

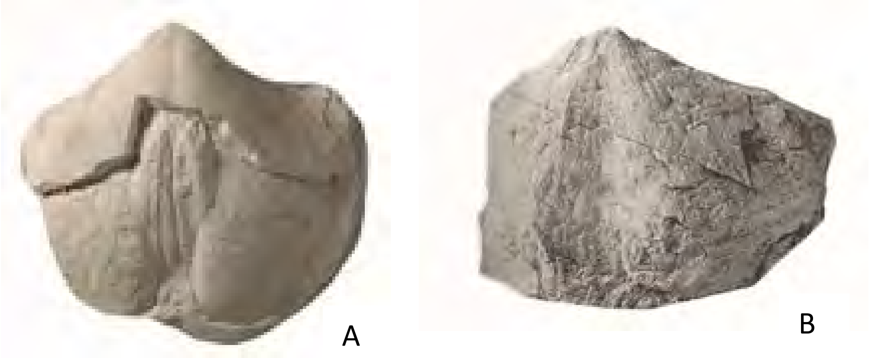

Fig. 223. *Choristites*? sp., ventral valve GSC 36950 from GSC loc. 57720, Great Bear Cape Formation, Ellesmere Island, x2. (Miller 1974). B, *Yukonospirifer* sp. ventral valve GSC 27005 from GSC loc. 53940, Takhandit Formation, x1. (Bamber & Waterhouse 1971). See p. 266.

Description: A ventral valve from GSC loc. 57720, Great Bear Cape Formation, Ellesmere Island, was recorded by Miller (1974), and his figure is reproduced herein. It is of value in showing the nature of the adminicula, which are well developed but not of great length, and are spaced quite far apart for Choristitidae. The specimen is probably conspecific with the specimen referred to *Spirifer nikitini* Tscherrnyschew, 1902 by Tschernyschew & Stepanov (1916) from the Great Bear Cape Formation. This is a ventral valve of somewhat similar shape and with moderately broad ribs. The species *nikitini* Tschernyschew, 1902 is somewhat similar, especially the specimen figured in Tschernyschew (1902, pl. 13, fig. 2), but with only two specimens (so far) and no dorsal valve as yet from the Great Bear Cape Formation, it is difficult to be sure of the specific affinities. The species *nikitini*, a well-preserved form from the Sakmarian Schwagerinen-Kalk of the Urals, is type species of *Purdonella* Reed, 1944.

"*Choristites*" *soederberghi* Dunbar, 1955

Fig. 224

1955 *Choristites söderberghi* Dunbar, p. 138, pl. 31, fig. 4-11.
1961 *C. söderberghi* – Dunbar, pl. 2, fig. 13.

Diagnosis: Overall shape close to *Choristites* and allies, but costae unusually fine, sulcus narrow and medianly slit-like, internal morphology not known.

Holotype: Specimen figured by Dunbar (1955, pl. 31, fig. 4; 1961, pl. 2, fig. 13) from the east slope of Canning Land, central east Greenland, OD.

Material: A damaged dorsal valve from C 4095, Degerböls Formation, Ellesmere Island.

Description: The shell before breakage was originally some 64mm wide, 33mm long, and 15mm high. It has a wide hinge, measuring at least 44mm, small dorsal umbo and the outline in front is well rounded. A narrow interarea is developed. The fold is narrow and only slightly raised, dominated by a median rib. A pair of ribs branch from the median rib a little in front of the umbo, followed by a second pair towards the anterior margin. Some six or possibly seven fascicles lie to each side, made up of two branching ribs, with at least three ribs laterally, that could be branching but are obscure. The ribs are crossed by fine growth laminae, three per mm, that are more or less straight, without visibly arching forward or back over ribs and interspaces.

Resemblances: This specimen is provisionally identified with the material described as *Choristites söderberghi* Dunbar, 1995, because its shape in front of the hinge is comparable: the fold is narrow in keeping with the narrow sulcus of the types, and the ribs are fine and bifurcate. No dorsal valve was recorded in the original description, hindering identification. The ribs are much finer than is normal for *Choristites*, and the shape, especially the holotype of *soederberghi,* is moderately close to that of *Simplicitasia*, as described on p. **290**, which unlike other figured specimens has coarse ribs approaching those of *Simplicitasia*. *Simplicitasia* is neospiriferin in internal morphology, and has coarser ribs comparable with those of most individuals of *soederberghi*, and slightly different sulcus, although it is narrow and slit-like in one figured specimen. Because clarification of internal structures is needed to ascertain a generic association, there must be reservations about the generic placement of *soederberghi*, and the geographic proximity to *Simplicitasia* might well be indicating a more likely identification, But such a possibility needs to be explored through unraveling the internal structures in *soederberghi*.

Nakamura et al. (1992, p. 94, pl. 5, fig. 8) recorded as *Choristites søderberghi* an internal ventral mould from the Middle Upper Hotvinden Member at Trygghamna, Spitsbergen, with ribs that appear coarser than those of type *soederberghi*, other than for the holotype of Dunbar (1955, pl. 31, fig. 4). In shape and strength of ribs the specimen comes moderately close to features of *Simplicitasia osborni* (Harker).

As noted by Dunbar (1955), *Spirifer* (*Choristites*) *anikeevi* Einor (1939, p. 80, pl. 12, fig. 7, pl. 13, fig. 1-

Fig. 224. "*Choristites" soederberghi* (Dunbar), dorsal valve GSC 140914, from C-4095, Degerböls Formation, Ellesmere Island, x1.5.

4, ,pl.14, fig. 4) from Taimyr Peninsula has numerous slender ribs in narrow fascicles, but the sulcus is broader with concave floor and the fold wider. Some of the middle Carboniferous (Moscovian) choristitids described by Fredericks (1928) have fine costae and ill-defined ventral sulcus. The present dorsal valve is moderately close to dorsal valves figured by Gemmellaro (1899, pl. 36, fig. 1-6) figured from the Sosio faunas of Sicily, but the ventral valves of the Sicily form have a deeper and more sharply defined ventral sulcus than in Dunbar's material. Gemmellaro (1899, p. 160) had named his species *Spirifer siculus*, and had noted a degree of similarity to *Spirifer wynnei* Waagen (1884, p. 527, pl. 44, fig. 6, 7) from the Kalabagh Member of the Wargal Formation in the Salt Range of Pakistan. Reed (1944, pp. 216, 218) discriminated between the two specimens figured by Waagen, assigning that of Waagen (1884, pl. 44, fig. 7) to his genus *Purdonella*, based on *Spirifer nikitini* Tschernyschew,1902, and pointing out that the specimen lacked the central rib along the fold whichn his view characterized *wynnei.* In the present specimen a central rib is joined by two lateral ribs close to the dorsal umbo, but the anterior fold has been destroyed. Whatever the nature of *soederberghi*, it does not closely resemble the shape characteristic of *Purdonella*. Reed (1944) referred the type specimen of *wynnei* to *Choristitella* Ivanov & Ivanova, 1937, from the Pennsylvanian of Russia, a genus similar in some respects, but with broader ribs.

Gemmellaro (1899) in discussing his species *siculus* also noted a degree of similarity to *Spirifer frischi* Schellwien (1892, pl. 5, fig. 4-8) from the Early Permian of the Carnian Alps of Austria. This has fine ribs, low fold and weakly defined but definite sulcus. The hinge is wide and long, imparting a different shape from the Arctic species. For this species, Schellwien (1892, pl. 5, fig. 8) figured long adminicula, indicative of a choristitid. *Choristites aliforme* Gobbett (1964, pl. 20, fig. 1-3) has fine ribs and a gutter-like sulcus as in some of the Dunbar specimens, but the hinge lies at maximum width and cardinal extremities are alate. It is much older than the Greenland species, coming from the mid-Carboniferous Ambigua Limestone of Bjørnøya, and including, according to Gobbett, materal described by Grönwall (1917) and Frebold (1950) from Greenland.

In conclusion, it appears necessary to consolidate the nature of the dorsal valve for *soederberghi,* and to determine the nature of the internal plates before generic and subfamily placement can be assured. And of course hopefully clarify the affinities of such species as *siculus* Gemmellaro. The species also somewhat approaches a number of forms placed in the Theodossioidea Ivanova, 1959, classed as early Choristitimorphi Waterhouse, and of Devonian age, as reviewed in Waterhouse (2016, pp. 119-124).

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Members of this suborder did not possess tabellae, or secondarily lose them. Subdelthyrial connector plate widespread, except in Trigonotretoidea and Neospiriferidae, shells plicate and often costate, dental plates and adminicula and crural plates normal. See Waterhouse (2016, p. 139).

Superfamily **PAECKELMANNELLAOIDEA (PAECKELMANNELLOIDEA)** Ivanova, 1972

Family **PAECKELMANNELLAIDAE (PAECKELMANNELLIDAE)** Ivanova, 1972

Subfamily **PAECKELMANNELLAINAE (PAECKELMANNELLINAE) I**vanova, 1972

Diagnosis: Transverse and plicate, adminicula and strong ventral median septum present.

Discussion: Paeckelmannellidae has a median ventral septum, whereas Pterospiriferidae Waterhouse, 1975 lacks a ventral median septum, and Strophopleuridae Carter, 1974 lacks median septum and adminicula, as interpreted by Poletaev (2001) and reviewed in Waterhouse (2016), to suggest a position within Martinioidea.

Genus ***Paeckelmannella*** Licharew, 1934a

Diagnosis: Transverse and often alate shells with sulcus bearing sulcal rib, few simple plicae, fine growth lamellae.

Type species: *Spirifer dieneri* Tschernyschew, 1902, p. 535 from Lower Permian of Russia, OD.

Discussion: It should be noted that the correct spelling of *Paeckelmannella,* which was named in honour of W. Paeckelmann, has two rather than one letter "n'', as pointed out by various authors, including Gourvennec in Gourvennec & Carter 2006, p. 2786), following Waterhouse (2004a, p. 227).

Paeckelmannella calignea Stehli & Grant, 1971

Fig. 225

1914 *Spiriferina expansa* [not Tschernyschew] – Wiman, p. 34, pl. 2, fig. 15-24.
1971 *Paeckelmanella* [sic] *calignea* Stehli & Grant, p. 515, pl. 65, fig. 1-9, 12-17, 21-24, 29-31, 36.
1992 *Paeckelmanella* [sic] sp. Nakamura et al., p. 88, pl. 2, fig. 1-7.

Diagnosis: Small acutely alate shells with subdued ribs and strong sulcal rib.

Holotype: GSC specimen 26169 figured from Sabine Bay Formation, Axel Heiberg Island, by Stehli & Grant (1971, pl. 65, fig. 23, 24, 29-31) and herein as Fig. 225C, OD.

Description, Resemblances: The material is well preserved and has been described and compared by Stehli & Grant (1971). They drew attention to the similarity of the Canadian material to Spitsbergen specimens figured by Wiman (1914, pl. 2, fig. 15-24), specimens which include some that are more transverse. *Paeckelmanella* [sic] of Nakamura et al. (1992) from the Svenskeega Member and lower Hotvinden Member in Spitsbergen has prominent alate cardinal extremities and prominent sulcal rib, but the dorsal fold is lower and broader. It certainly appears that

Paeckelmannella with somewhat similar attributes ranged through Sabine Bay and middle Kapp Starotsin faunas. There is some similarity to *P. wimani* (Stepanov) as interpreted by Ifanova (1972, p. 131, pl. 9, fig. 8, 9) in recording material from the upper Artinskian faunas of Pai Hoi, Russia. A ventral valve shows an anterior median fold in the sulcus (fig. 9), but the internal mould does not clearly show a median septum. The original material (Tschernyschew 1902, pl. 12, fig. 11; Stepanov 1937b, pl. 8, fig. 13) suggests a narrow median sulcal fold and ventral median septum, and so seems very close to *calignea*.

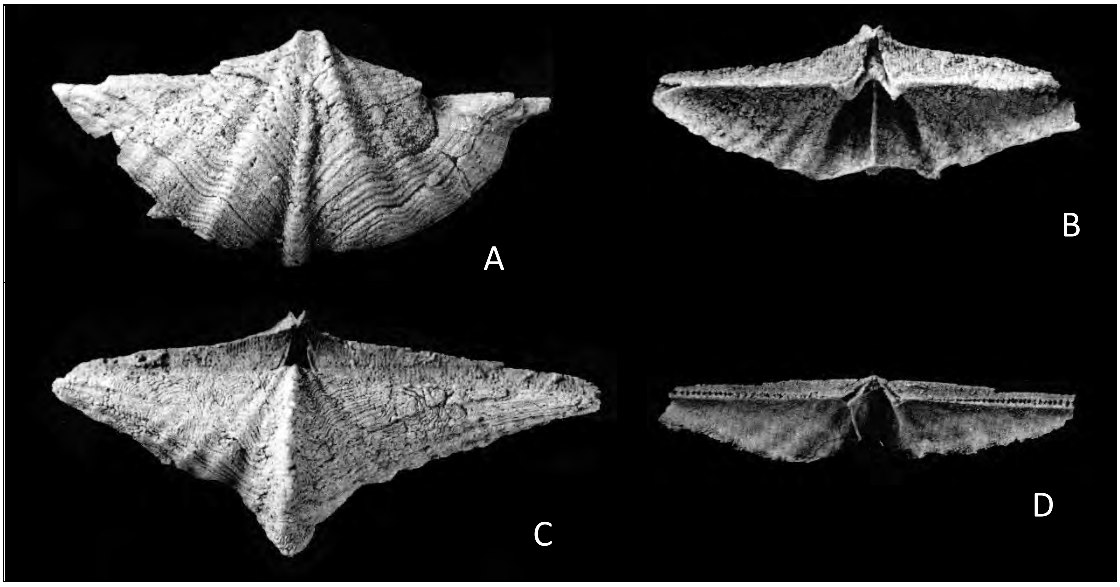

Fig. 225. *Paeckelmannella calignea* Stehli & Grant. A, ventral valve USNM 166314. B, ventral interior, USNM 166313. C, dorsal view of specimen with valves conjoined, GSC 26169 holotype. D, dorsal interior, USNM 166315. Specimens x2, from Sabine Bay Formation, Axel Heiberg Island. (Stehli & Grant, 1971).

?Subfamily **PTEROSPIRIFERINAE** Waterhouse, 1975

Genus ***Yukonospirifer*** Shi & Waterhouse, 1996

Diagnosis: Transverse subtrigonal shells with weakly defined sulcus and fold and low ventral umbo, high ventral interarea, external shell surface covered by fine bifurcating subfasciculate ribs. Well developed subdelthyrial connector plate, high adminicula, no median septum. Shell impunctate.

Type species: *Yukonospirifer yukonensis* Shi & Waterhouse from upper Jungle Creek Formation (Aktastinian), Jungle Creek Formation, Canada, OD.

Discussion: This genus was hesitantly classed as Syringothyrididae by Shi & Waterhouse (1996), but the shell is not known to be punctate, nor even taleolate. Carter in Gourvennec & Carter (2006, p. 2789) shifted the genus from Syringothyridae to Pterospiriferinae within Paeckelmanelloidea (sic = Paeckelmannellaoidea), given the lack of punctae and presence of a high interarea. On the other hand, the ribs are slender and conspicuously bifurcate, reminiscent of the style of ribbing in Spiriferidae, so that the family position requires consolidation.

Yukonospirifer sp.

Fig. 223B (p. 261)

1971 *Pseudosyrinx* sp. Bamber & Waterhouse, pl. 17, fig. 12.

Material: A ventral valve from GSC loc. 53940, second of five zones in the Takhandit Formation. Unknown amount of additional material.

Description: The ventral valve from the Takhandit Formation is highly transverse with acute cardinal extremities and costae, numbering at least an estimated twenty each side of the sulcus. The sulcus, with an angle slightly less than 30°, bears at least eight costae that are of much the same strength as the lateral plicae, and there appears to be a median pair of costae as well. The costae bifurcate anteriorly, and form weak fascicles. There is the suggestion of moderately long and widely diverging adminicula.

Resemblances: Hopefully more material will become available from this fossil locality, to enable the species to be more fully described. The sulcus and ornament are close to those of *Yukonospirifer yukonensis* Shi & Waterhouse, but fascicles are more prominent and the shape less transverse. There is some similarity to so-called *Tumarinia* cf. *T. wimani* [not Gobbett] of Angiolini & Long (2008, p. 97, Fig. 8D, E) from the Vøringen Member of Spitsbergen, but these specimens differ, having slightly stronger costae of which few appear to bifurcate. The shape of the Angiolini-Long specimen is triangular, and has a high interarea, as in *Yukonospirifer*.

A number of taxa are described from Novaya Zemyla by Licharew & Einor (1939) that look rather similar in costation and shape. One species identified as *Spirifer petrenki* Einor in Licharew & Einor (1939, pp. 81, 209, pl. 15, fig. 6a-e) from Early Permian of Novaya Zemlya is a large much more transverse shell with costae bifurcating both close to the umbo and well in front. The interarea is lower, so that its appearance is closer to that of Spiriferidae.

Superfamily **SPIRIFEROIDEA** King, 1846

Discussion: Spiriferoidea are of only modest diversity in the Middle Permian faunas of Arctic Canada, but generic and familial affinities remain unresolved for several species. The problem is that internal morphology has not been uncovered for several Arctic species, largely from Greenland and Spitsbergen, leaving a cloud of uncertainty. For one species and genus, *Fasciculatia* Waterhouse, the nominated type species *F. greenlandicus* is based largely on shells exposing little of the interior, although the nature of the ornament with its splitting costae and numerous fascicles, strongly suggests Spiriferidae, and this appears to be confirmed by a subdelthyrial connector plate figured for one ventral valve (Dunbar 1955, pl. 24, fig. 5). For another, *Gobbettifera* Waterhouse, the external ornament is composed of fine costae over sharply crested plicae that fade anteriorly. The ventral interior carries no subdelthyrial connector plate but does display a well formed median septum, at least in a number of specimens. The species *striatoplicatus* Gobbett was based on a ventral valve which shows the interior, and clearly lacks a connector plate so that its affinities lie with Neospiriferidae. The same is true of *Kaninospirifer* Kalashnikov. But the long-recognized *striatoparadoxus* Toula has never had adequate types or secure and strictly proven stratigraphic topotypes, and material assigned to the species show a range of internal features, as discussed shortly. Another species *groenwalli* Dunbar is based on a single external shell, with no topotypes, and no internal detail displayed. It remains, by any strict standard, a mystery as far as specific, generic and even family links are concerned, and other specimens are identified through shape and occurrences in correlative faunas. So there must be a measure of uncertainty about generic assignments for some taxa, which cannot be resolved until genuine topotypes are uncovered, and carefully examined with regard to internal as well as external morphology. Until that can be achieved, if ever, identifications with such taxa become highly insecure.

Family **SPIRIFERIDAE** King, 1846

Diagnosis: Fascicles well developed, plicae variably developed, connector plate in ventral valve, minor umbonal callus, without forming a prominent umbonal callosity.

Subfamily **SPIRIFERINAE** King, 1846

Genus ***Fasciculatia*** Waterhouse, 2004a

Diagnosis: Large transverse and subalate shells with unevenly and variably developed low broad plicae in three to six pairs, coupled with narrow mini-fascicles made up of bifurcate costae on each valve, deep sulcus, high fold, faint radial capillae, commarginal lamellae subdued or absent. Neodeltidium or fused stegidial plates rarely preserved, delthyrium largely open, underlain by a subdelthyrial connector plate, which may be thickened into a plug (see Fig. 234)., no ventral median septum.

Type species: *Fasciculatia greenlandica* Waterhouse, 2004a, p. 95 from Foldvik Creek Group (Upper Permian), central east Greenland, as figured by Dunbar (1955, pl. 23, fig. 1-7, pl. 24, fig. 1-5, pl. 28, fig. 1-6) and Waterhouse (2004a, Text-fig. 23 – see Fig. 235 herein), OD.

Discussion: This genus is found in Permian faunas of the Arctic. Angiolini & Long (2008, p. 93) argued for a position in Neospiriferinae, but that is difficult to sustain, given the absence from *Fasciculatia* of a well-formed cover plate or neodeltidium arching over the delthyrium, and the likely presence of a subdelthyrial connector plate, reinforced by underlying callus, here termed a connector plug. This is suggested in a figure provided for the type species by Dunbar (1955, pl. 24, fig. 5), interpreted as an umbonal callosity by Waterhouse (2016), but revaluated herein as a connector plate. Furthermore, the same construct is well developed in Canadian specimens assigned to *Fasciculatia striatoparadoxa*, as discussed and figured below, with further examination and figures in Waterhouse (in press, Fig. 30-32). Amongst ventral valves figured in Wiman (1914) and now assigned to *F. striatoparadoxa,* one shows a short cover or stegidial plate (Wiman 1914, pl. 5, fig. 16), and others have a small subdelthyrial connector plate bearing a narrow umbonal callosity (Wiman 1914, pl. 7, fig. 10, 11). Most of Wiman's relevant figures of ventral interiors, assigned by him to various species, suggest what looks like a subdelthyrial connector plate or connector plug (Wiman 1914, pl. 5, fig. 14, 16, 17; pl. 6, fig. 7), with no umbonal callosity ridge. If a connector plate or structure modified from a connector plate by umbonal callus is present, then affinities lie within Spiriferidae, and such species are further distinguished in part by the display of fascicles that were well developed in Spiriferinae.

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. Indeed, Gourvennec in Gourvennec & Carter (2006, p. 2781) suggested that *Fasciculatia* was a synonym of *Kaninospirifer* Kulikov & Stepanov. On the other hand, the name *Fasciculatia* was defended by Lee et al. (2016, p. 112), although the reason, that *Kaninospirifer* has a largely transverse outline, especially for the type species, in contrast to a generally pentagonal outline for *Fasciculatia*, would not seem highly convincing. The sulcus is more variable in the latter genus, and the fold is narrow with sharp crest, in contrast to a usually rounded fold in *Kaninospirifer,* as observed by Lee et al. The dental plates are strongly developed in *Fasciculatia*, along with adminicula, in partial contrast to the arrangement in *Kaninospirifer*, which was supposed to have deep dental "flanges" – ie. dental plates and low adminicula. Not that actual morphology supports their claim.

Best evidence for the claim that dental plates may be low in *Kaninospirifer* is provided by cross-sections for the type species by Kalashnikov (1998), which show adminicula of medium height and low dental plates. Other figures show the two sets of plates being moderately well developed (Kalashnikov in Molin et al. 1983), as reproduced in Waterhouse (2016, Fig. 252, 253, p. 205). One specimen of *K. stepanovi* Grunt (2006b, pl. 14, fig. 5b) has rather low dental plates. Lee et al. (2016, Fig. 3) relied on material from China that was identified with type *Kaninospirifer* to evaluate the relative heights of dental plates as high versus adminicula as low. China is not Russia. The Chinese material cannot validly replace let alone contradict topotype or other Russian studies, which clearly show well developed adminicula for *Kaninospirifer kaninensis*. (See Fig. 257, p. 302). There is no suggestion of any subdelthyrial plate in *Kaninospirifer*, unlike the arrangement in *Fasciculatia*.

Fasciculatia*? *groenwalli (Dunbar)

1916 *Spirifer marcoui* [not Waagen] – Tschernyschew & Stepanov, p. 47, pl. 9, fig. 4.
1962 *Neospirifer grønwalli* Dunbar, p. 9, pl. 2, fig. 6-8.
1964 *Spirifer striato-paradoxus* [not Toula] – Gobbett, p. 134, pl. 18, fig. 2.
2016 *Fasciculatia groenwalli* – Lee et al., p. 129, Fig. 6, 13G-I.

Diagnosis: Moderately large shells with tented plicae fading anteriorly, and fine ribs, eight to ten in 10mm anteriorly, fold with broad base and narrow crest.

Holotype: Specimen figured by Dunbar (1962, pl. 2, fig. 6-8) from Amdrup level G, now Mallemuk Mountain Group (late Artinskian, or ealy Kungurian), northeast Greenland OD.

Description, Resemblances: Specimens listed in the limited synonymy are characterized by sharply defined plicae that fade anteriorly and by fine ribbing. None are known internally, which renders assessments provisional. Lee et al. (2016) noted the similarity of a shell figured as *S. marcoui* [not Waagen] by Tschernyschew & Stepanov (1916, p. 47, pl. 9, fig. 4) from Great Bear Cape to *Fasciculatia striatoparadoxa*, but the figure suggests somewhat finer ribs, counted at for nine to eleven in 10mm, contrasting with five to rarely seven in shells assigned to *striatoparadoxa* and *greenlandica*. Compared with these two species, the Great Bear Cape shell is of different shape and has lower plicae. Gobbett (1964, p. 134, pl. 18, fig. 2) recorded a specimen from the Spirifer Limestone of Spitzbergen that shows limited similarity, and has fine ribs, numbering eight to nine in 10mm. He stated that the taxon, as represented in his figure, was abundant in the Spirifer Limestone (Gobbett 1964, p. 135), which raises the prospect of being able to clarify the nature of the specimens, though it has to be remembered that such specimens are not topotypes.

Fasciculatia striatoparadoxa (Toula, 1873)

Fig. 226 – 231, 247B, 248A

1873 *Spirifer striato-paradoxus* Toula, p. 271, pl. 1, fig. 2a-c.
1875b *Spirifer striato-paradoxus* – Toula, p. 254, pl. 8, fig. 1.
1875b *Spirifer striatus* var. *princeps* Toula, p. 254, pl. 8, fig. 2.
1914 *S. ravana* [not Diener] – Wiman, p. 43, part, pl. 5, fig. 17-19, pl. 6, fig. 1, 2.
1914 *S. marcoui* [not Waagen] – Wiman, p. 44, pl. 6, fig. 3-7, pl. 7, fig. 9-11.
2016 *Fasciculatia striatoparadoxa* – Lee et al., p. 123, Fig. 3D-F, 6, 7, 8, 9, ?10.
2018a *Kaninospirifer* sp. Waterhouse, p. 356, Fig. 297.

Diagnosis: Transverse, large, plicae fading anteriorly and anterior lateral margins extended in mature shells. Dorsal fold with narrow crest. Ornament of fine numerous ribs, often paired on each valve, generally with five to seven narrow plicae but dominated by broad low inner plicae pairs, rather variable in development.

Neotype: Specimen figured by Toula (1875b, pl. 8, fig. 1) and Dunbar (1955, pl. 28, fig. 1) from Spitsbergen, SD Gobbett (1964, p. 134). Probably Kapp Starotsin Formation, level not known.

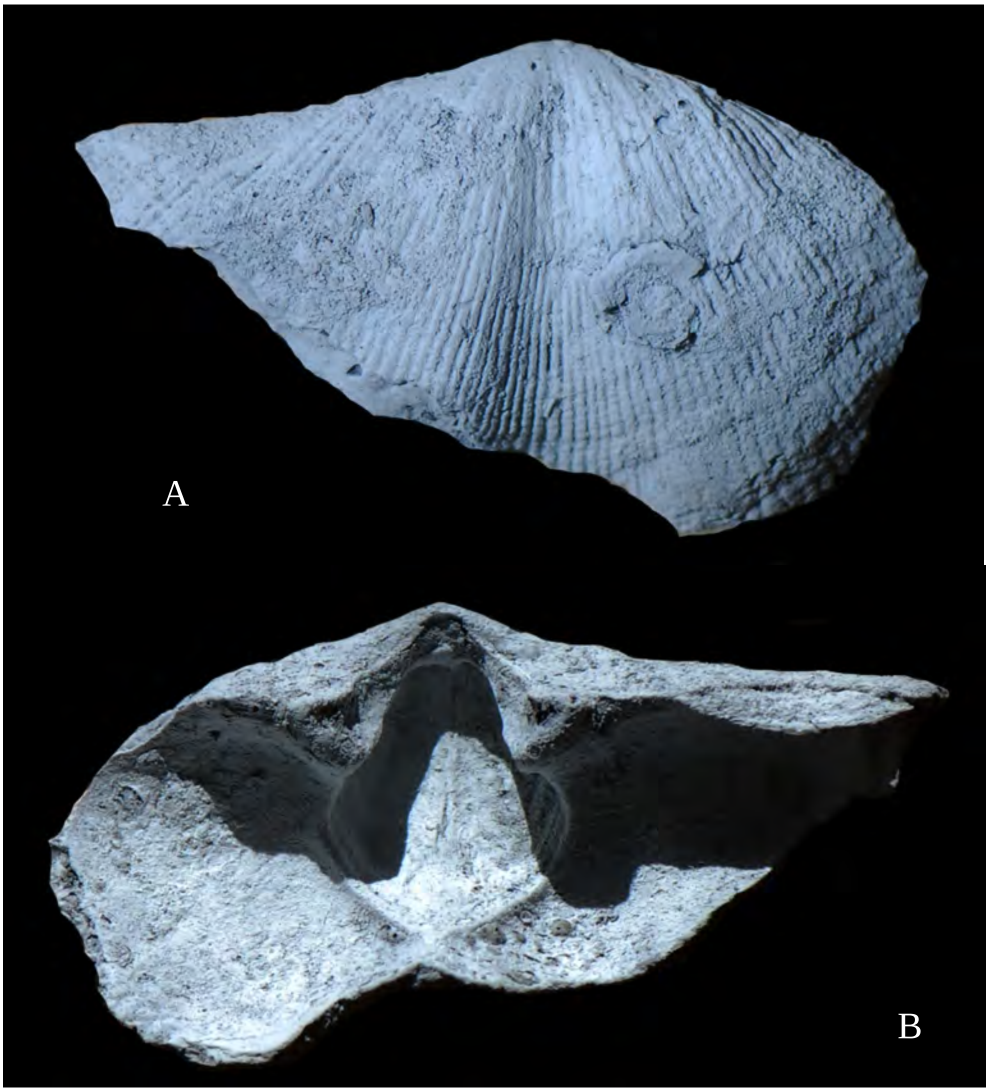

Fig. 226. *Fasciculatia striatoparadoxa* (Toula). A, ventral valve GSC 137345 from C-13356, external and internal views, showing in B a slender median groove dividing the adductor scars, rather than a ventral median septum typical of *Gobbettifera*, x1.5. There is an umbonal build up of callus, under a connector plate. Trold Fiord Formation, Melville Island. (Waterhouse 2018a).

Material: One ventral valve from C-3996, thirteen ventral valves, one dorsal valve and two conjoined specimens from C-4015, two ventral valves from C-4017, two ventral valves from GSC. loc. 58951, two specimens from C-4006 and a ventral valve from C-4021, all from the Trold Fiord Formation of Ellesmere Island, and two ventral valves from C-11356 from the same formation on Melville Island, together with one dorsal valve and a ventral valve from C-4074, Van Hauen Formation, Ellesmere Island. Tiny specimens, too small to be assured of generic position, involve a ventral valve, dorsal fragment and specimen with valves conjoined from GSC loc. 53846, unnamed sandstone unit in the *Dyoros modestus* Zone at McDougall Pass, Richardson Mountains, Yukon Territory.

Dimensions in mm: ventral valve

Width	Length	Height
81	?41	22
88	54	26
68	39	14
99	59	39
Width	Length	Height dorsal valve
67	35	16
88	43	28

Description: Shell large and transverse with maximum width at hinge in immature specimens, followed by extension of the anterior-lateral margins and shift of maximum width to a little in front of the hinge with increased maturity. The ventral umbo has an umbonal angle as high as 120º to 130º, incurved and with posterior walls extending beyond the hinge, and the dorsal umbo measures up to 140º. The hinge is wide, and alate during early growth stages, but ears become small and weakly alate with angle of 70º or 80º at larger sizes. The ventral interarea is high and strongly concave under the beak and becomes gently concave towards the hinge, marked by horizontal and vertical striae, with wide open delthyrium nearing 60º in angle, bordered by low dental tracks, without neodeltidium or stegidial plates. The dorsal interarea is low, and the notothyrium obscure. The ventral sulcus is distinctly concave with usually groove-like median channel and the flanks rise gradually each side, with crests diverging at close to 40º. The dorsal fold is sharply raised with angle of 15º, and narrowly rounded crest. The anterior margin is retracted. Plicae are few and narrow, with three well defined pairs and two or rarely three to four further lateral and very low pairs of weakly defined fascicles formed by splitting of the costae. The innermost plicae pair is moderately high and borders the sulcus posteriorly, with two costae appearing by bifurcation close to the umbonal tip, and each costa branching at least once further forward. Costae branch more frequently on the inner side into the sulcus, with about ten costae in the sulcus near the anterior margin, each side of a median costa traversing the middle of the sulcus. The second and third pairs of plicae are lower, with five or seven costae anteriorly in moderately large specimens, and the second pair of plicae comes to border the sulcus anteriorly, with the first pair incorporated in a progressively widening anterior sulcus. In a number of specimens, the first and second pair of plicae become indiscernible towards the anterior margin. Gradually, the inner three pairs of plicae merge to become replaced by a large broad plication in a number of specimens, followed laterally by a concave interspace and vaguely defined adjoining plication and rarely further plication, formed by the prolongation of the outer plicae from nearer the beak. On the dorsal valve, there are two or less commonly three pairs of weak inner plicae, and laterally, costae dominate the ornament. It must be emphasized that there is a degree of variation. The overall impression is that of very low and round-crested plicae over most of shell in front of posteriorly tented plicae, fading anteriorly, and numerous fascicles formed in the ventral valve, and plicae fade anteriorly. Detail of micro-ornament is masked by indifferent preservation.

Internal detail is known for several specimens. A ventral valve judged to be at early maturity has low teeth supported by short and only moderately high dental plates, resting at an angle on somewhat higher adminicula. No

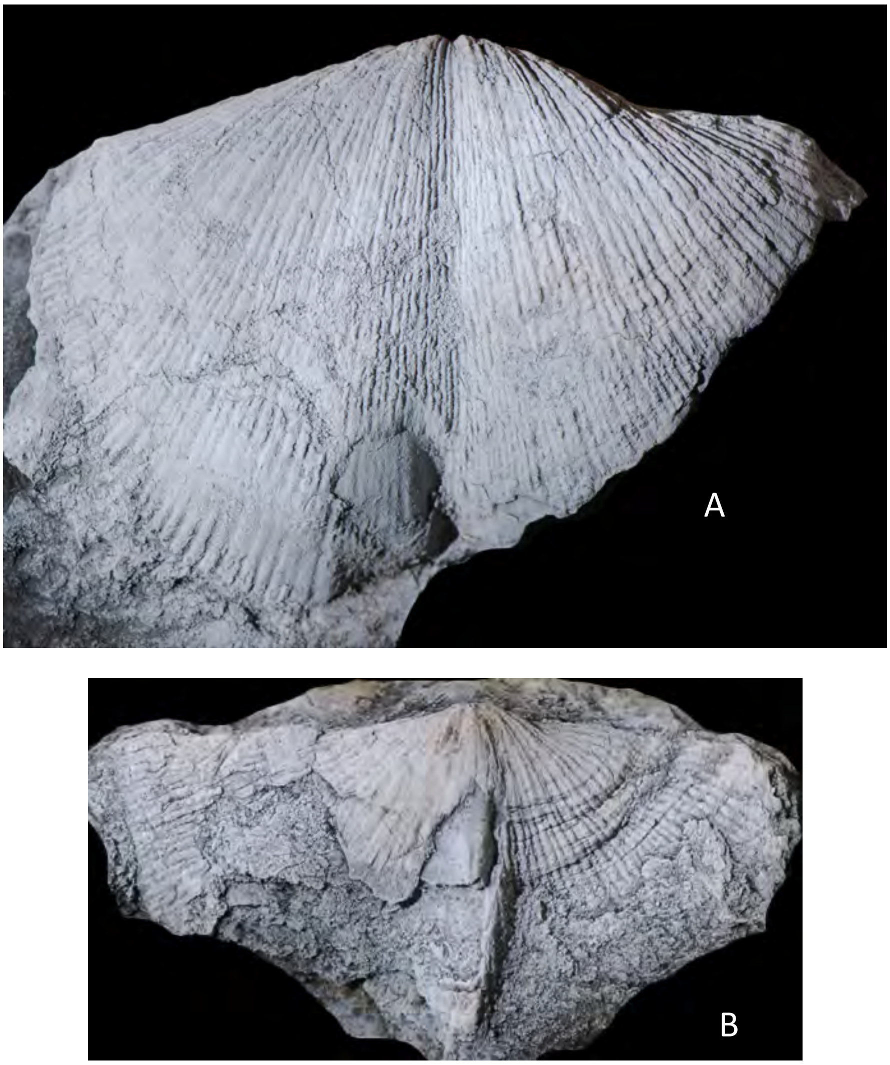

Fig. 227. *Fasciculatia striatoparadoxa* (Toula). A, ventral valve GSC 140915. B, dorsal valve GSC 140916, showing the narrow high fold typical of this species. From C-4015, Trold Fiord Formation, Ellesmere Island. Specimens x1.

specimen shows any trace of a delthyrial cover plate or stegidial plates. The adductor platform is low with fine longitudinal striae, separated by a low ridge from slightly broader diductor impressions to each side, and the posterior floor is heavily thickened and marked by dense pits in no discernible pattern. The best-preserved specimen is a conjoined specimen that has been leached in dilute HCl. Dental plates and adminicula are of equal height, and are joined across the posterior delthyrium by a flat platform (from a dorsal perspective), underlain by umbonal thickening (Fig. 231). It is similar in position to a subdelthyrial connector plate, which has been reinforced by thickening, and may be called a subdelthyrial or connector plug. Several other specimens also show the connector plug; none show a different arrangement. There is nothing like the high callosity typical of Trigonotretoidea. The muscle field is subelongate in large specimens, and broader in small specimens. Moderate posterior thickening covered by pustules, may bury much of the adminicula, and dental plates are relatively high. A pattern of branching mantle canals has developed In one specimen recorded by Miller (1974, pl 18, fig. 4), as reproduced in Fig. 231C.

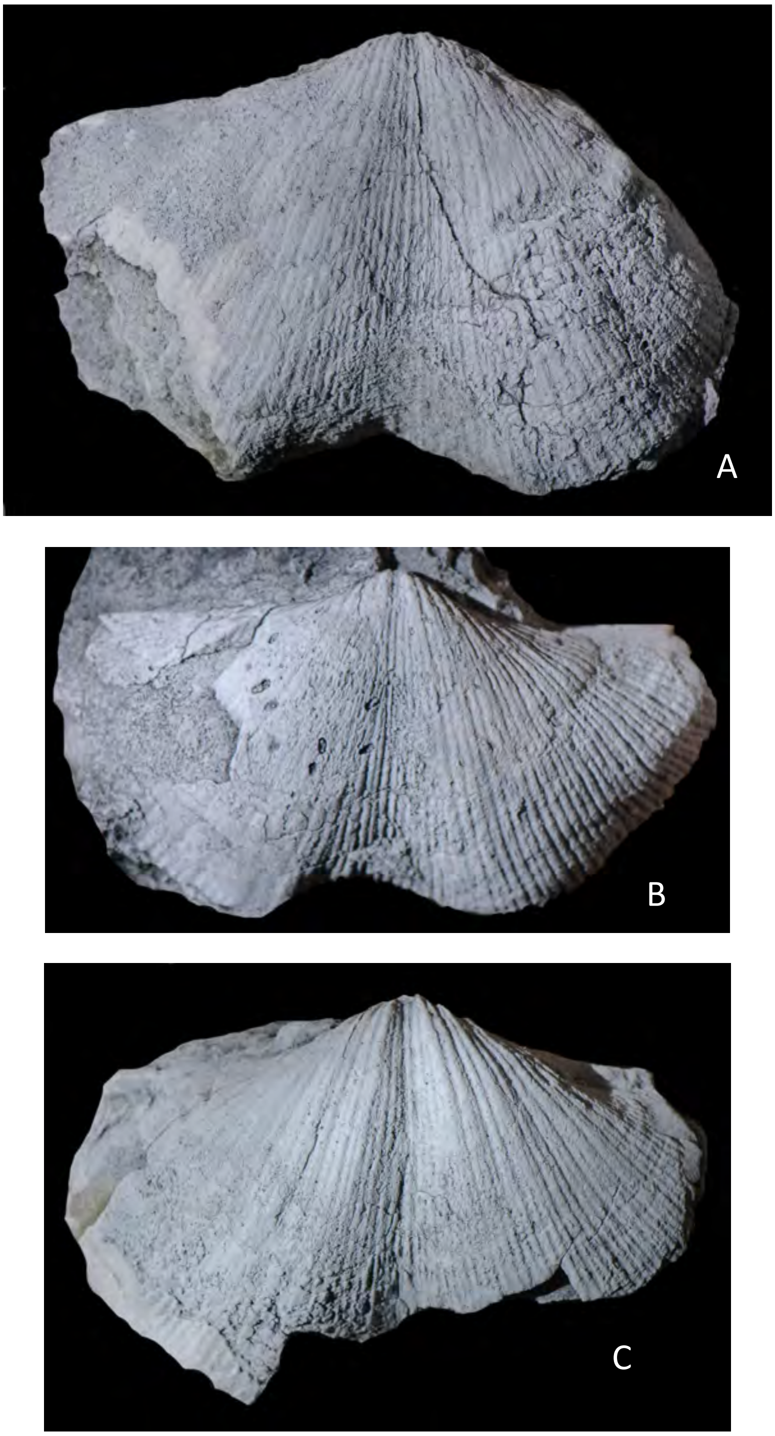

Fig. 228. *Fasciculatia striatoparadoxa* (Toula). A, ventral valve GSC 140917 from C-4015. B, ventral valve GSC 140918 from C-4015. C, ventral valve GSC 140919 from GSC loc. 58951. Trold Fiord Formation, Ellesmere Island. Specimens x1.

Amongst available material, the median septum in one dorsal valve extends at least as far as mid-length. The leached internal mould shows a wide and longitudinally laminated ctenophoridum, moderately high diverging crural plates and small subhorizontal upwardly concave socket plates. To each side of the mid-line are large subrectangular muscle field, tending to be less elongate in smaller specimens. The posterior floor is slightly thickened and bears fine pustules and radiating imprints from mantle canals. There are twenty one coils in one of the visible spiralia.

Resemblances: Possibly a specimen figured as *Spirifera* allied to *pennata* not Owen by Etheridge (1878, p. 633, pl. 29, fig. 1) is alled to *Fasciculatia striatoparadoxa*, but this needs confirmation (Fig. 229). It was collected from Dana Bay in north Ellesmere Island.

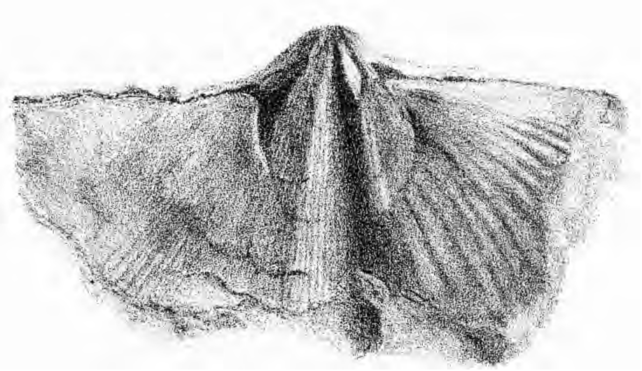

Fig. 229. Specimen figured as “*Spirifera* sp. (allied to *pennata* D. D. Owen)” by Etheridge (1878, p. 633, pl. 29, fig. 1) from north Ellesmere Island, that possibly belongs to *Fasciculatia striatoparadoxa* (Toula) or to *Betaneospirifer*, which seems less likely. The different width of apparent ribs either side of the figure is disconcerting.

The poor preservation for the type of *striatoparadoxa,* which is a broken ventral valve without any dorsal valve*,* tells against any confident assignment of specimens to Toula’s species. The neotype sourced from north of Kapp Waern, Nordforden, where Gobbett (1964, Fig. 4) shows Brachiopod Chert, and apparently no Spirifer Limestone. It certainly seems that the present suite is close at least externally to the set figured, without geographic or zonal specifics provided for each individual figure, by Lee et al. (2016) from the Hotvinden Member of Spitsbergen, and close in general appearance to the Spiriferenkalk specimens figured by Wiman (1914). The source of the Wiman material is not entirely clear. Although some have regarded the Spiriferenkalk as equivalent to the Vøringen Member, many of the well-controlled Productida he described come from younger beds, according to various Russian authorities, including Stepanov, Ustritsky and Sarytcheva, as well as Gobbett (1964) and Nakamura et al. (1992), and that may well pertain also to the spiriferids that he figured.

Numerous specimens from Spitsbergen have been assigned to *Spirifer striato-paradoxus* Toula (1874, pl. 1, fig. 2a-c). In this species the dorsal fold is deemed to be narrow-crested like that of present specimens from Canada. Few specimens show costation very clearly. *Spirifer striato-plicatus* Gobbett (1964, p. 136, pl. 17, fig. 7-9, pl. 18, fig. 1) from the Spirifer Limestone is more strongly plicate, and is further discussed herein, starting on p. 282. Two ventral valves assigned to *Spirifer ravana* (not Diener) from the Spirifer Limestone in Spitsbergen by Stepanov (1937b, pl. 7, fig. 5, 6) appear to differ from the species. They have six to seven costae in 10mm, with costae of less regular strength in his so-called *condor* [not d’Orbigny] (Stepanov 1937b, p. 141, pl. 7, fig. 3), which has also been regarded as *striatoparadoxus* by some authorities. Some of Stepanov's specimens are more plicate than *striatoparadoxus*, and appear to belong to *striatoplicatus* Gobbett (see p. 282).

Permian shells from the Wegener Halvo Formation in central east Greenland that were assigned to *Spirifer striato-paradoxus* by Dunbar (1955, p. 131, pl. 23, fig. 1-7, pl. 24, fig. 1-5, pl. 28, fig. 2-6; 1961, p. 229, Fig. 2.5, 6) usually have small alate ears and a high broad round-crested fold (Dunbar 1955, pl. 23, fig. 1, 2, pl. 24, fig. 3) rather than narrow dorsal fold, although those of pl. 23, fig. 5 and pl. 24, fig. 1, repeated in Dunbar (1961, Fig. 2.5), have narrower fold, though not as extreme as that of Spitsbergen or Canadian specimens. Most shells are slightly less transverse, the sulcus is slightly more U-shaped and exaggerated, and costae on specimens are slightly coarser, and bifurcate conspicuously, compared with various specimens assigned to *striatoparadoxa*. They were renamed *greenlandica* by Waterhouse (2004a, pp. 95-99; 2016, Fig. 196A, B) and Fig. 234 herein. The crest of the dorsal fold of most of the specimens assigned to *striatoparadoxa* from Canada has a much narrower and slightly higher dorsal crest than in *greenlandica*, and fascicles are less conspicuous, differences that also apply to the Spitsbergen specimens figured by Wiman (1914) and Lee et al. (2016, Fig. 9C, G). A ventral valve at the top of

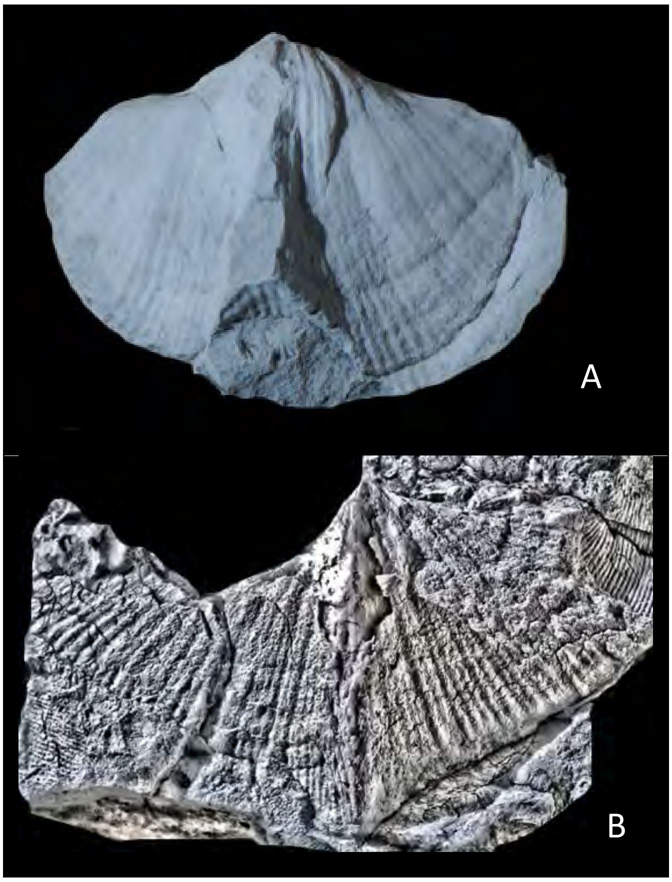

Fig. 230. *Fasciculatia striatoparadoxa* (Toula) A, dorsal view of specimen GSC 140921 with valves conjoined, from C-4015, Trold Fiord Formation, Ellesmere Island, x1. B, dorsal valve GSC 140987 from same locality, x1, reproduced by local equalization.

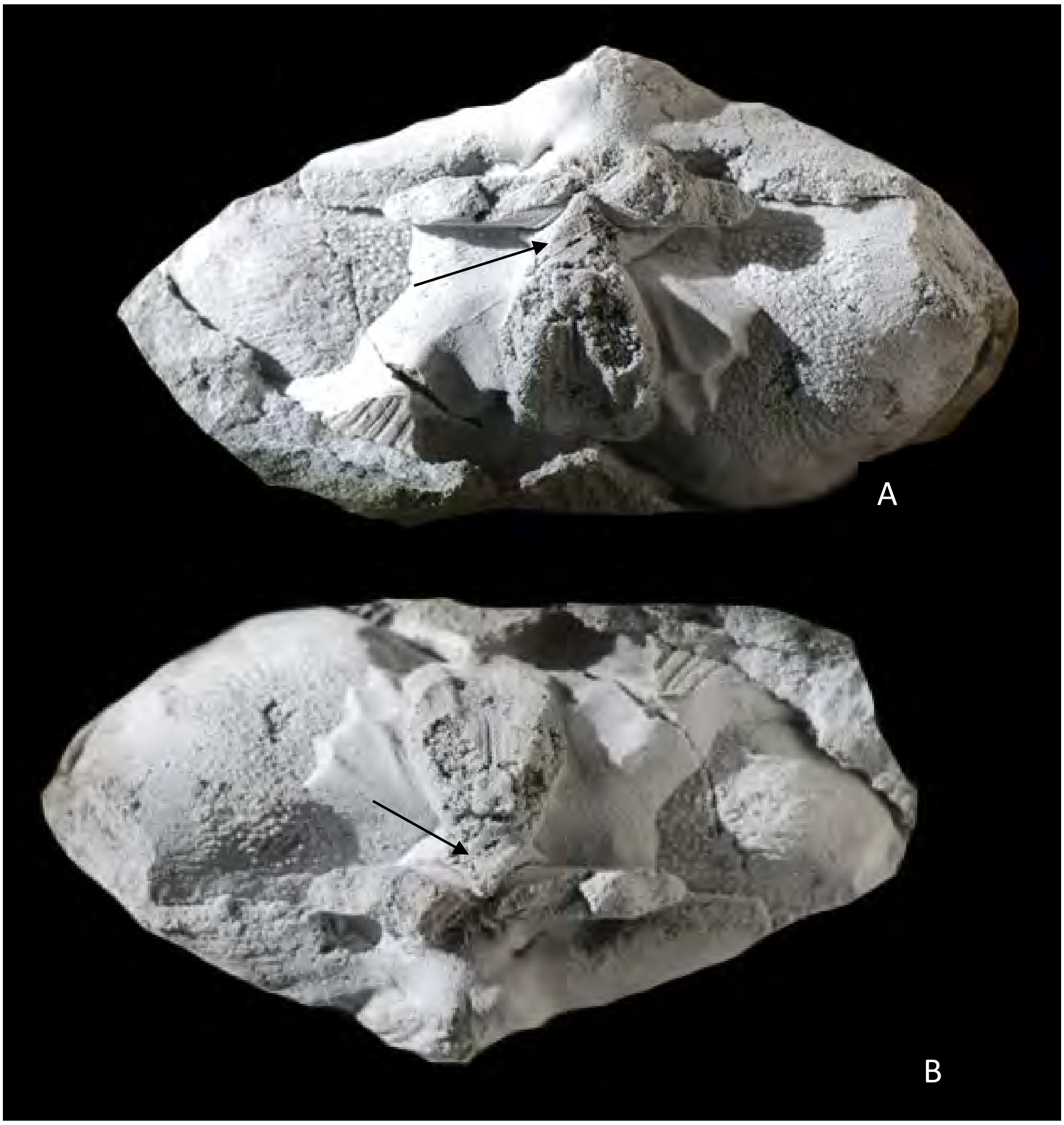

Fig. 231. *Fasciculatia striatoparadoxa* (Toula), posterior view of specimen GSC 140921 with valves conjoined. A, dorsal valve on top, B, dorsal valve below. The arrow points to the dorsal side of the subdelthyrial connector plug. From C-4015, Trold Fiord Formation, Ellesmere Island, x1.5. Further figures are provided in Waterhouse (in press, Fig. 30-32).

the Hotvinden Member that was figured from Spitsbergen by Nakamura et al. (1992, pl. 4, fig. 8) is much closer to the Greenland specimens than other specimens from Spitsbergen in its wide sulcus, and that of Nakamura et al. (1992, pl. 5, fig. 11), possibly from uppermost Hotvinden beds, is similar, so that these Spitsbergen specimens appear to belong to *greenlandica* and are of much the same age, to judge from stratigraphic position and associated species. But adequate understanding of *striatoparadoxa* is frustrated by the poor preservation of the neotype, and ignorance about its precise geographic and stratigraphic source. For all that is known, the designated neotype came from equivalents of the upper Hotvinden Member, and therefore possibly matched *greenlandica.* And the material designated *striatoparadoxa* herein, and including the Wiman material, may belong to a separate and possibly unnamed species, with its narrower fold and less fasciculated ribbing. That calls for close collection and careful re-evaluation of Spitsbergen material, with careful documentation of stratigraphic sequencing of specimens.

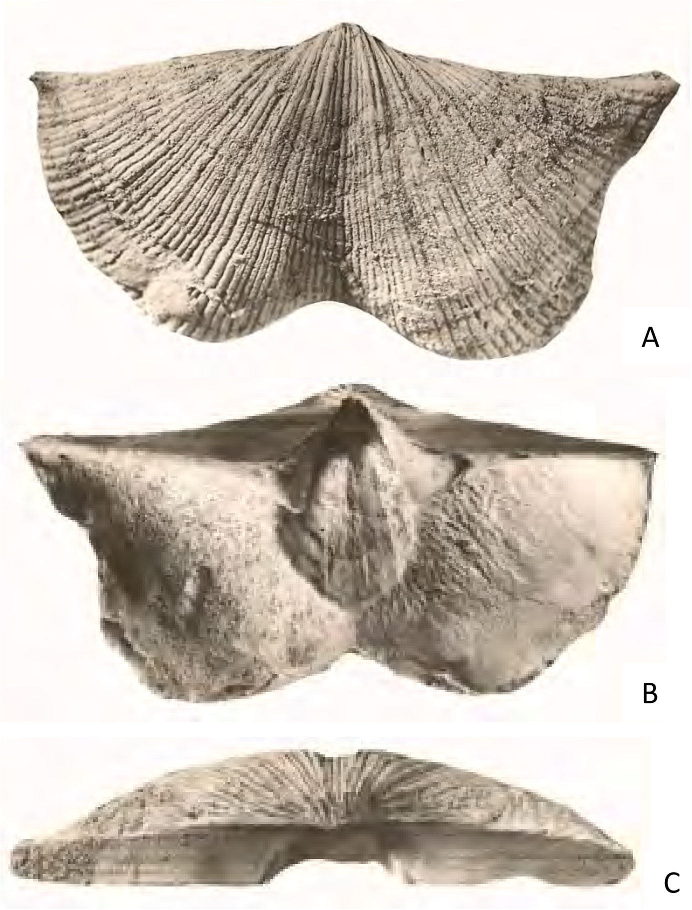

Fig. 232. *Fasciculatia striatoparadoxa* (Toula) A, external, internal and posterior views of, interior of ventral valve GSC 36937 from C-13356, Trold Fiord Formation, Melville Island. B shows vascular pattern. Identity is not completely secure but B appears to faintly indicate a subdelthyrial connector plate. Photographs from Miller (1974).

A further cause for concern is the nature of the delthyrial construct. This is known for *greenlandicus* and *striatoplicatus* type material, but is not known for *striatoparadoxus* type material.

According to Lee et al. (1916), the species *striatoparadoxa* ranged from Kungurian to Wuchiapingian. That is an unusually long range for one species, and spiriferid species rarely show such lengthy time ranges, including those that have by modern standards been thoroughly examined and explored, such as those of the Glass Mountains in Texas, United States (Cooper & Grant 1976a), and the species of the east Australian Permian (Waterhouse 2011, Fig. 5, 6), with much the same rigour applied in New Zealand, and the Salt Range and Himalayas, let alone the lengthy Carboniferous and Permian sequences of Canada, now largely monographed (Nazer 1977, Shi & Waterhouse 1996, Waterhouse 2018a, b, this study, and Waterhouse & Waddington 1982). In this survey, it is suggested that the real time range for the shells called *striatoparadoxa*, as for the Lee et al. material, was Roadian to Wordian. Some uncertainties remain, because Lee et al. (2019) figured material from the Hotvinden Member, without saying where in the member specimens came from, an important matter because the member ranges from Roadian into Wuchiapingian. Earlier ascriptions are judged to belong to *Betaneospirifer striatoplicata* (Gobbett), and younger ones to *greenlandica* Waterhouse. Even within these time limits, the specific limits and generic affinities of shells identified as *Fasciculatia striatoparadoxa* in Lee et al. present difficulties. Two specimens figured as this species in Lee et al. (2016, Fig. 3D-F) show no connector plate. Sections through the umbonal section (Lee et al. 2016, Fig. 7A-C) show umbonal callus, but are not analysed. Possibly a connector plate is present in Fig. 9E, but no analysis was offered. The internal moulds of Fig. 10E – G also need analysis and clarification, because an umbonal callosity and underlying callus is not clearly indicated, and one is left to wonder if some of specimens ascribed to *Fasciculatia* could prove to belong to a neospiriferid, such as *Kaninospirifer*. Several species of *Kaninospirifer* have been described from northern Russia, but only one, the type species, is close in shape and size and ornament, recorded as *Spirifer kaninensis* Licharew (1943, p. 279, Fig. 1-4; Stepanov, Kulikov & Sultanaev, 1975, p. 63; 1983, p. 22, pl. 3, fig. 1-3, pl. 4, fig. 1; Kalashnikov, 1986, pl. 125, fig. 9, pl. 126, fig. 5, 6; 1996, p. 51, pl. 9, fig. 6, 7, pl. 10, fig. 1, 2, text-fig. 6; Grunt, 2006b, p. 153, pl. 14, fig. 1, pl. 15, fig. 1, 2) and Waterhouse (2016, pp. 204-207, Fig. 250, 252, 253). This species shows similar anterior fading and broadening of the plicae. The main and consistent difference lies in the nature of the dorsal fold, which is broadly rounded in *kaninensis*, as compared with the higher and narrower fold in the present species. In a number of specimens, the inner plicae are a little better defined and broader, and outer plicae or fascicles less distinguished. Furthermore, the dental plates may be low in *kaninensis*, whereas they tend to be high in *striatoparadoxa*, but this difference is not apparently consistent, some *kaninensis* having moderately high dental plates. No *Kaninospirifer* is known to have the same delthyrial construct as *Fasciculatia*, because they lack any sign of a subdelthyrial connector plate and underlying callus.

Logan & McGugan (1968, p. 1136, pl. 143, fig. 7, 8, pl. 144, fig. 1-13) reported *Spirifer striato-paradoxus* from the Range Canyon Formation of Alberta, Canada, but silicified interiors show no sign of the connector callosity, and the specimens seem more likely to belong to Neospiriferinae, though included in synonymy of *striatoparadoxus* by Lee et al. (2016). Licharew & Kotlyar (1978, pl. 18, fig. 1) figured a ventral valve as *striatoparadoxus* from the Capitanian Chandalaz Formation in South Primoyre, east Russia, but the valve is elongate with moderately well-defined plicae. The shape differs considerably from that of *striatoparadoxa*, and the lack of internal detail means that the specimen could well prove to be neospiriferid, but requires confirmation from clarification of internal morphology.

Lee et al. (2016, p. 123) took a remarkably broad view of *striatoparadoxa*. They not only included the Logan-McGugan specimens with their very different delthyrial apparatus in this species, and differently shaped Chandalaz material of Licharew-& Kotlyar, but claimed that *Neospirifer sulcoprofundus* Liu & Waterhouse (1985, p. 85, pl. 9, fig. 9, fig. 5, 8, 11, pl. 10, fig. 2, 3, 6, 8, pl. 11, fig. 5, 6, 9, pl. 12, fig. 1, 3) from Neimongol (Inner Mongolia) was a junior synonym of *striatoparadoxa*. It is extremely difficult to accept this proposal. The Neimongol specimens are much more transverse, with almost straight rather than bulging anterior lateral margins, and more narrowly alate, and extended and upturned cardinal extremities, more emphasized plicae, and few bifurcate costae, counted

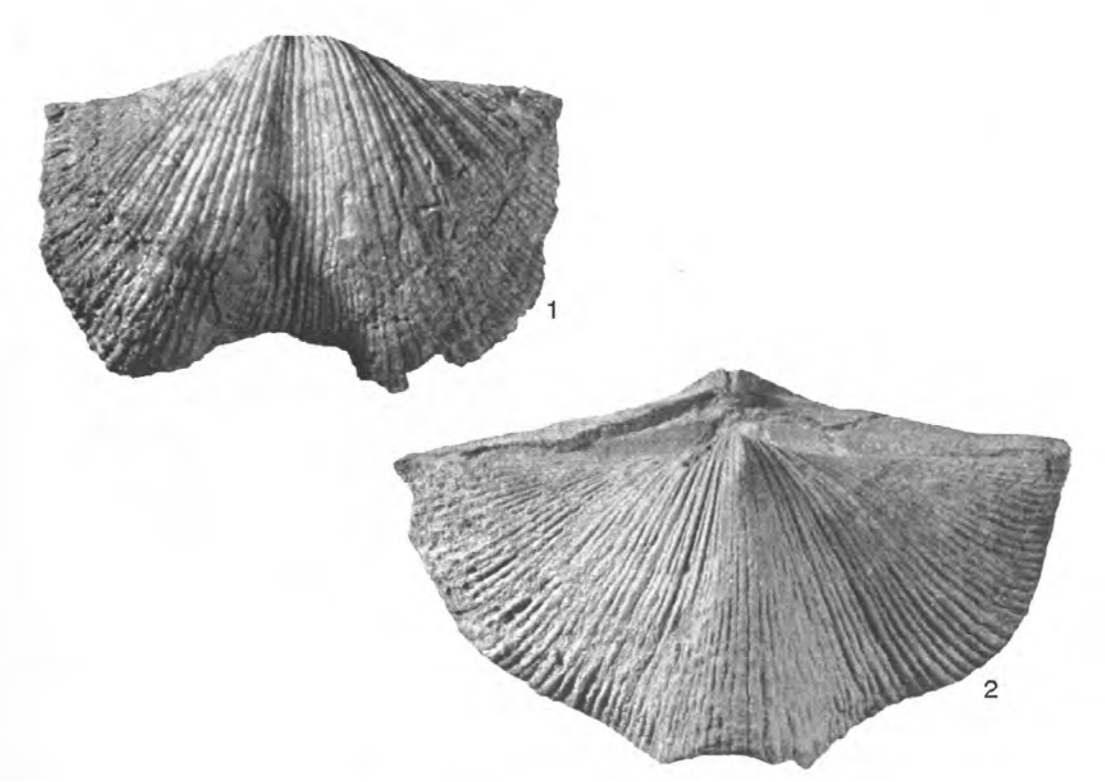

Fig. 233. *Fasciculatia greenlandica* Waterhouse, ventral and dorsal aspects of holotype, figured by Dunbar (1955) from Foldvik Group, northeast Greenland, x1. Note the broad dorsal fold and wide sulcus, with especially well defined dorsal fascicles, which suggest specific differences from shells ascribed to *striatoparadoxa* by Wiman (1914), Lee et al. (2016) and herein, although adequate comparison with the poorly preserved neotype of *striatoparadoxus* is not possible. Possibly *greenlandica* is really the same as *striatoparadoxa*, and the Wiman and other material belongs to a species of Roadian-Wordian age, older than the Greenland material (Wuchiapingian), and, apparently yet unnamed.

Fig. 234. *Neospirifer sulcoprofundus* Liu & Waterhouse, ventral aspect of holotype, CCGBH124. See also Fig. 237A. From Zhesi Formation, Inner Mongolia, x1. (Liu & Waterhouse, 1985). This is now *Imperiospirifer* Archbold & Thomas.

Fig. 235. *Neospirifer sulcoprofundus* Liu & Waterhouse, posterior aspects of two internal moulds, CCGBH124, holotype, x 0.6 and CCGBH126, x1. Note the absence of a subdelthyrial or connector plug from both specimens. From Zhesi Formation, Inner Mongolia, x1. (Liu & Waterhouse, 1985). Both show the striking upturn of the lateral flanks, as in *Imperiospirifer* Archbold & Thomas, a fact noted by those authors in referring the species to *Imperiospirifer*, though ignored by Lee et al. (2016).

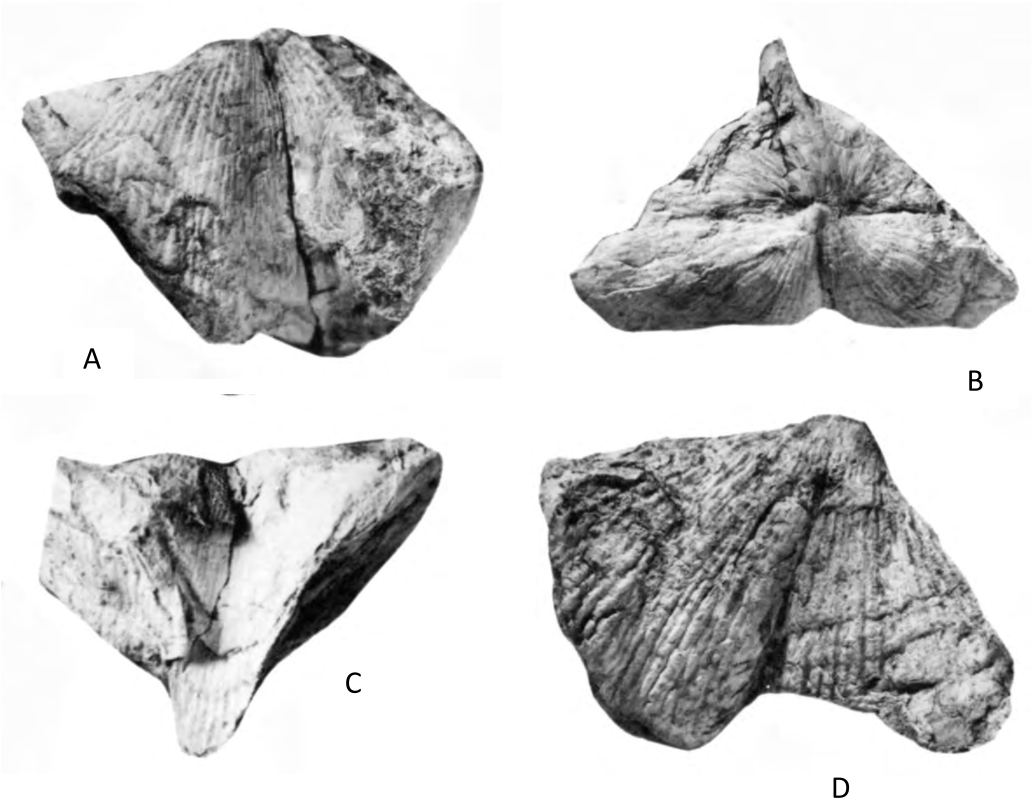

Fig. 236. *Neospirifer adpressum* Liu & Waterhouse. A, ventral aspect of holotype, 0.9. B, C, posterior and anterior aspects of specimen with valves conjoined, CCGBH 129, x1. D, ventral aspect of specimen ascribed to *sulcoprofundus*, likely to belong to *adpressum*. CCGBH 126, x1. Zhesi Formation, Inner Mongolia. (Liu & Waterhouse, 1985). These possibly belong to *Fasciculatia*.

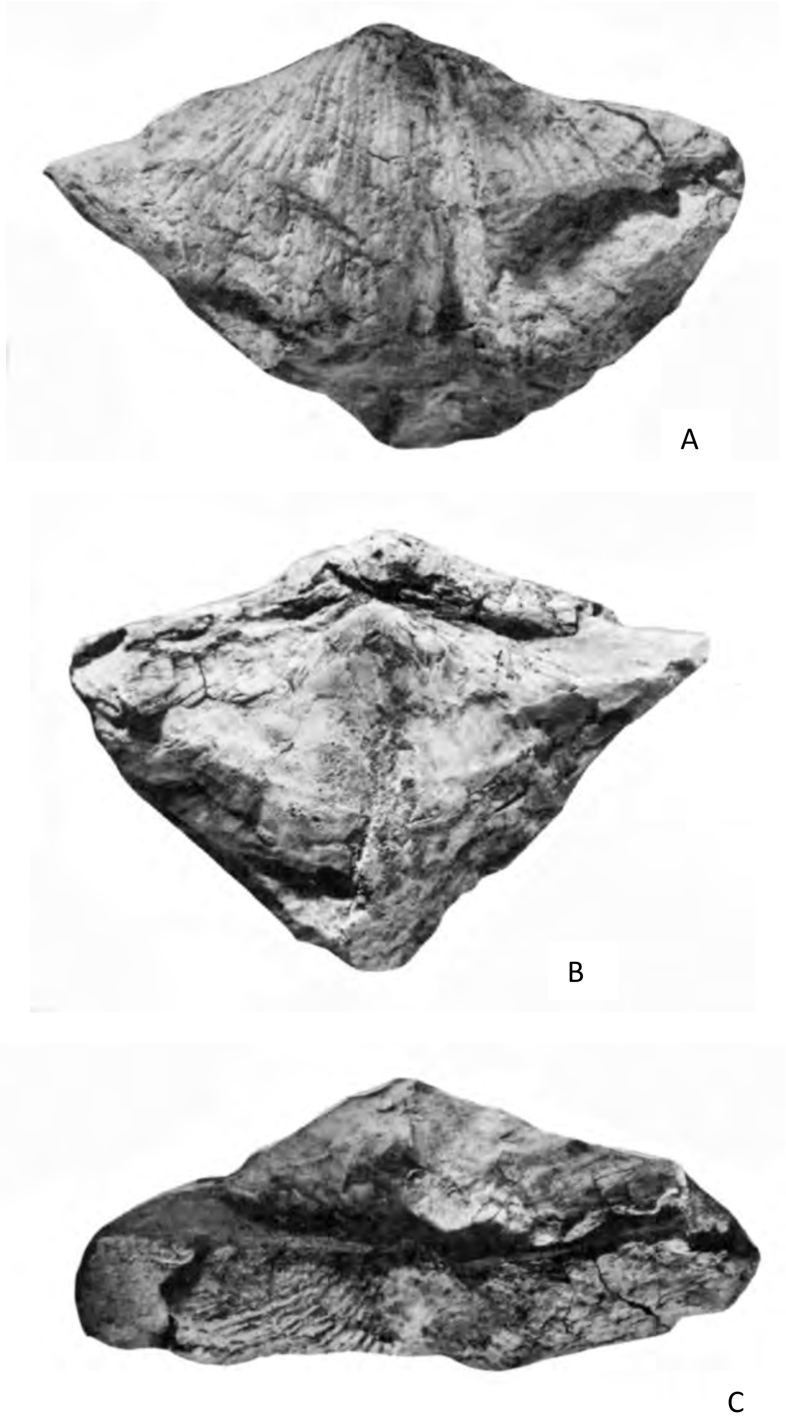

Fig. 237. *Imperiospirifer sulcoprofundus* (Liu & Waterhouse), ventral, dorsal and posterior aspects of CCGBH124. From Zhesi Formation, Inner Mongolia, x1. (Liu & Waterhouse, 1985).

at four or five in 5mm anteriorly. Often the sulcus is narrow and groove-like in the Mongolian specimens, and the dorsal fold distinctly higher anteriorly. Internally the dental plates were described as scapular-shaped and resting on short high rather than low adminicula, and the delthyrium was closed by a plate with growth ridges, forming a neodeltidium as in Neospiriferinae, and not equivalent to the connector plug of *Fasciculatia*, which lacks growth ridges. Some figures are repeated herein, for readers to assess the reliability of the Lee et al. synonymy. Probably the other specimens presumed to belong to *striatoparadoxa*, by Lee & Gu (1976, pl. 176, fig. 1, 11), Lee et al. (1980, pl. 177, fig. 6, 9), and Wang & Zhang (2003, pl. 136, fig. 1-4, pl. 37, fig.11, 12) may also be dismissed from synonymy. One specimen figured by Liu & Waterhouse (1985, pl. 11, fig. 2, 3) was excluded without explanation by Lee et al. (2016), but is transverse with plicae and strong plicae as in other specimens. Another specimen that does approach *striatoparadoxa* in shape was figured in Liu & Waterhouse (1985, pl. 10, fig. 3), refigured herein as Fig. 236D. The particular specimen is much closer to *Neospirifer adpressum* Liu & Waterhouse (see Fig. 236A-C), a more elongate shell compared with *striatoparadoxa*, with fuller antero-lateral margins, and specifically distinguished from *striatoparadoxa* by its deep narrow anterior sulcus and high narrow anterior fold, and stronger costae.

Archbold & Thomas (1993) suggested that the species *sulcoprofundus* might belong to their genus *Imperiospirifer* from Western Australia, because it displays similar upturned lateral flanks, but this proposal was overlooked or ignored by Shi et al. (2016). However the proposal appears reasonable from what is known of the morphology of type *Imperiospirifer* and the Liu-Waterhouse species from Mongolia. The species *sulcoprofundus* Liu & Waterhouse may be placed in *Imperiospirifer.*

Family **NEOSPIRIFERIDAE** Waterhouse, 1968b

Subfamily **NEOSPIRIFERINAE** Waterhouse, 1968b

Genus ***Betaneospirifer*** Gatinaud, 1949

Diagnosis: Transverse shells with wide hinge, neodeltidium over delthyrium, no subdelthyrial connector plate. Numerous costae, well defined plicae. Adminicula, dental and crural plates.

Type species: *Spirifera moosakhailensis* Davidson, 1862, p. 28 from Lopingian (Wuchiapingian) of Salt Range, Pakistan, OD.

Discussion: As shown below with illustrations, the ventral interior of shells ascribed to the species *striatoplicatus* by virtue of their external appearance differs from that of shells ascribed to *striatoparadoxa*. The latter form has a subdelthyrial umbonal callosity or plug under the delthyrium, whereas *striatoplicatus* has no such callosity. Lee et al. (2016, p. 130) claimed that Angiolini & Long (2008) had indicated that the two species “have nearly identical ventral internal structures”, but the interior of the two differ substantially. In fact Angiolini & Long (2008) offered limited comment on internal structures of *striatoplicatus,* unsurprisingly, because the figures suggest no reliable internal morphology was revealed in their material, and in tersely discussing *striatoparadoxa*, provided no information on delthyrial apparatus (see Angiolini & Long, 2008, p. 93), but did note that *Fasciculatia* had stronger dental plates than in *Kaninospirifer*. Their remarks on the interior of *striatoplicatus* were limited to muscle field shape (described as rounded), dental plates (described as well developed), and adminicula (described as slightly diverging). Nor did Lee et al. provide any analysis of the interior from reported observation. There are a number of aspects of internal morphology which were left unmentioned by Angiolini & Long (2008) and Lee et al. (2016).

The holotype of *striatoplicatus* Gobbett (1964, pl. 17, fig. 9) shows a ventral interior that lacks the thickened connector plate typical of *Fasciculatia*, and therefore points a position with Neospiriferidae. That so many other specimens are known only from only external appearance is unfortunately all too typical of boreal faunas, and explains why paleontological progress has been rather slow, with many remaining uncertainties. The present suggestions are premised on external and limited internal similarities, and strongly need underpinning by further preparation of Arctic specimens.

Unlike the family affinities of *Fasciculatia*, the family position of *striatoplicatus* is neospiriferid, but its generic affinities are approximate only, with scope for further analysis of species assigned to *Betaneospirifer.* Typical *Betaneospirifer* is believed to have a delthyrial cover plate or neodeltidium, not yet found in present Canadian or Spitsbergen specimens. The posteriorly fused dental plates, often with low median callus, recalls the arrangement in members of Neospiriferidae (see serial sections in Waterhouse 1968b, text-fig. 8).

Betaneospirifer striatoplicatus (Gobbett, 1964)

Fig. 43A, B, 238, 239

1875b *Spirifer cameratus* [not Morton] – Toula, p. 240, pl. 7, fig. 3a, b.
1908 *S. cameratus* (not Morton) – Whitfield, p. 54, pl. 3, fig. 3, 4.
1916 *Spirifer fasciger* (not Keyserling) - Tschernyschew & Stepanov, p. 47, pl. 9, fig. 3a, b.
? 1936 *Spirifer moosakhailensis* (not Davidson) – Stepanov, pp. 122, 127, pl. 5, fig. 4.
1937b *S. moosakhailensis* (not Davidson) – Stepanov, p. 140, pl. 7, fig. 1, 2.
?1937b *S. condor* [not d'Orbigny – Stepanov, p. 141, pl. 7, fig. 3.
1950 *S. ravana* [not Diener] – Frebold, p. 57, pl. 4, fig. 3, 3a, 6.
1950 *S*. cf. *moosakhailensis* [not Davidson] – Frebold, p. 60, pl. 4, fig. 1, 1a.
1964 *Spirifer striato-plicatus* Gobbett, p. 136, pl. 17, fig. 7-9, pl. 18, fig. 1.
?1971 *Neospirifer* cf. *groenwalli* – Stehli & Grant, p. 517, pl. 65, fig. 37-41.
cf. 1972 *Neospirifer permicus* Ifanova, p. 133, pl. 9, fig. 11, 12.
1986 *N*. cf. *fasciger* [not Keyserling] – Kalashnikov, pl. 116, fig. 6a, b.
cf. 1990 *N*? *permicus* – Kalashnikov et al., pl. 6, fig. 1a, b, v, pl. 74, fig. 4.
cf. 1998 *N. permicus* – Kalashnikov, p. 48, pl. 24, fig. 6, aff. pl. 29, fig. 6 (part, not pl. 16, fig. 3 = aff. *Fasciculatia*?).
2008 *Fasciculatia striatoplicata* – Angiolini & Long, p. 93, Fig. 8A, B, F, ?G, ?H.

Diagnosis: Wide hinge, well formed sulcus and moderately high fold, plicae well developed and persist to anterior margin, costae narrow and well defined. No connector plate.

Holotype: Specimen figured by Gobbett (1964, pl. 17, fig. 8, 9) from Spirifer Limestone, Spitsbergen, OD.

Material: A dorsal valve from GSC loc. 58977, Great Bear Cape Formation, Ellesmere Island.

Fig. 238. *Betaneospirifer striatoplicatus* (Gobbett) as figured from Great Bear Cape. Tschernyschew & Stepanov 1916.

Description: These specimens are characterized by their well-defined plicae, for which the four inner pair are well developed, and becoming broad and low anteriorly. Fine costae divide frequently, but fascicles are inconspicuous or absent. A dorsal valve from GSC loc. 58977 shows a well-defined fold and moderately well-defined plicae in four pairs, as well as strong costae. A median groove passes along the fold and is underlain as show by decortication by a low median septum, extending apparently to mid-length.

Resemblances: *Spirifer striatoplicatus* Gobbett (1964) from the Spirifer Limestone of Spitsbergen and Bjørnøya is moderately plicate, and one paratype more broadly plicate. The ventral delthyrial region lacks a connector plate, as figured for the holotype. Plicate specimens from Spitsbergen were figured as *Spirifer moosakhailensis by* Stepanov (1936, pl. 5, fig. 4) and Stepanov (1937b, pl. 7, fig. 1, 2). That of Stepanov (1937b, pl. 7, fig. 1) came from the Spirifer Limestone and the specimen figured in Stepanov (1937b, pl. 7, fig. 2) came from Cape Starotsin. They are firmly plicate, but broken and incomplete. Further material was figured from these levels by Stepanov (1937b), as in the synonymy, and all are moderately plicate and apparently conspecific, although those from the Spirifer Limestone called *S. ravana* by Stepanov (1937b, pl. 7, fig. 5, 6) approaches *Kaninospirifer*. Material from the Vøringen Member recorded by Angiolini & Long (2008, pl. 8, fig. A, B, F-H) has strong narrow and comparatively high plicae, although for some unexplained reason their Fig.8 F was left out of synonymy for so-called *groenwalli* by Lee et al. (2016), and two specimens (pl. 8, fig. G, H) are badly worn. Unfortunately, internal morphology has not been determined for any of the Angiolini-Long specimens. The difference in the present account from that of Lee et al. (2016) centres not on the species name, regarded as simply requiring confirmation, or on time range, regarded as consistent, nor very much on the present suggestion that *permicus* Ifanova, as explained shortly, and even shells ascribed to *subfasciger* Licharew should be incorporated: it is the difference in generic affinities and the significance attached to differing delthyrial constructs.This points to the need for much more thorough examination of various specimens that have to be identified mostly by external appearance, because of inadequate attention to the internal features of various taxa. At present, the possibility remains that large neospiriferine and spiriferine specimens have been assigned to a single species, instead of being discriminated through their internal morphology and subtle aspects of their exterior.

Fig. 239. *Betaneospirifer striatoplicatus* (Gobbett), dorsal valve GSC 140726 from GSC loc. 58977, Great Bear Cape Formation, Ellesmere Island, x1. See Fig. 43A, B.

Tschernyschew & Stepanov (1916) figured a comparatively complete ventral valve from the Great Bear Cape Formation of Great Bear Cape, and it is firmly plicate like the figured ventral valve of Gobbett (1964). It also strongly approaches the material described as *Neospirifer permicus* Ifanova (1972) from Kungurian beds of Russia. The holotype was figured by Ifanova (1972, pl. 9, fig. 11) from Talbeisk beds (Kungurian) of the Petchora Basin. A specimen of Kalashnikov (1998, pl. 24, fig. 6a, b) is close to *permicus*, and that of Kalashnikov (1998, pl. 29, fig. 6), regarded as aff. *permicus*, is moderately close. These specimens all came from the Levorkut beds of Petchora Basin. Ifanova's specimens are also close to *Spirifer subfasciger* Licharew (1934b, p. 120, pl. 1, fig. 11, 13, pl. 4, fig. 1-8), including varieties, also reported as *Neospirifer subfasciger* by Zavodowsky (1970, p. 150, pl. 76, fig. 3, 4). This species was named for small shells from the Kolyma River of northeast Russia, from possibly Hivatch beds of Late

Permian age, and the identification needs to be underpinned by further material and clarification of the interior. The Ifanova form could well be closely allied, if not conspecific, with Gobbett's species, judged by shape, size and plication, and assignment of the species to *Neospirifer*. A large number of species from northeast Russia were ascribed to *Neospirifer* by Zavodowsky (1970), and *subfasciger* is readily distinguished, Zavodowsky reporting the species from Omolon beds of northeast Russia. Of the numerous species described by Zavodowsky, only *N. drabini* Zavodowsky (1970, p. 160, pl. 92, fig. 5a, b) from Hivatch beds comes close. Given that it looks moderately like *Betaneospirifer subfasciger,* comes from the same beds, and is based on only one specimen, it seems likely that it is synonymous with *subfasciger*. *Neospirifer subfasciger* [not Licharew] of Kalashnikov 1998, pl. 11, fig. 3, 5a, b, 6) comes from faunas of Sakmarian age, and although somewhat similar, is not rated as conspecific. *Neospirifer subfasciger*? of Gobbett (1964, p. 141, pl. 17, fig. 10, 11) from the Cora Limestone of Bjørnøya and Upper Wordiekammen Limestone of Spitsbergen is also small and strongly plicate. Gobbett noted the similarity to some small and plicate specimens figured by Wiman (1914, pl. 5, fig. 6-13) as *Spirifer fasciger* from the Cora Limestone, and the ventral valve appears to have a median septum, as in *Septospirifer.* Ustritsky (1979, table 1) identified *Neospirifer subfasciger* (Licharew) from both the upper Starotsin Suite, and Selanderneset Suite in Spitsbergen, which was applied to more easterly outcrops largely equivalent to the Svenskeega and Hotvinden Members. Ustritsky provided no systematic description or illustration of his material.

Fragmentary specimens from the Sabine Bay Formation figured by Stehli & Grant (1971) need closer examination, to determine the nature of the interior. Plicae are moderately well defined and persistent, suggesting possible *Betaneospirifer*.

Betaneospirifer politus n. sp.

Fig. 240 – 244A, 245B, 246, 247

?1937b *S. subfasciger* [not Licharew] – Stepanov, p. 142, pl. 7, fig. 4.
1971 *Neospirifer* cf. *striatoparadoxus* [not Toula] – Brabb & Grant, p. 17, pl. 2, fig. 12-14.

Derivation: politus – polished, accomplished, Lat.

Diagnosis: Medium-small, well formed sulcus and high fold, plicae only moderately developed, with inner four pairs strong, and innermost two coupled each side of the sulcus. Internal features neospiriferine.

Holotype: Ventral valve GSC 140927 from C-4015, Trold Fiord Formation (Wordian), Ellesmere Island, illustrated as Fig. 240A, B, 246, here designated**.**

Material: A dorsal valve from GSC loc. 58977, Great Bear Cape Formation, Ellesmere Island. A specimen with valves conjoined and a dorsal valve from GSC loc. 26406, Assistance Formation, Devon Island. One ventral valve from C-4025 and three ventral valves from C-4077, Assistance Formation, and a ventral valve from C-4037, Trold Fiord Formation, Ellesmere Island. An incomplete specimen with valves conjoined from GSC loc. 53931, middle Takhandit Formation, Yukon Territory.

Description: These specimens are characterized by their moderately defined plicae, for which the four inner pairs are well developed, and become broad and low anteriorly. Fine costae divide frequently. The umbonal angle for the ventral valve measures between 105º and 110º. the sulcal angle measures close to 30º, and the fold is upstanding with moderately broad and well-rounded crest. The ribs show limited fasciculation, and are involved in well developed plicae, though not as strong as those of *striatoplicatus* Gobbett.

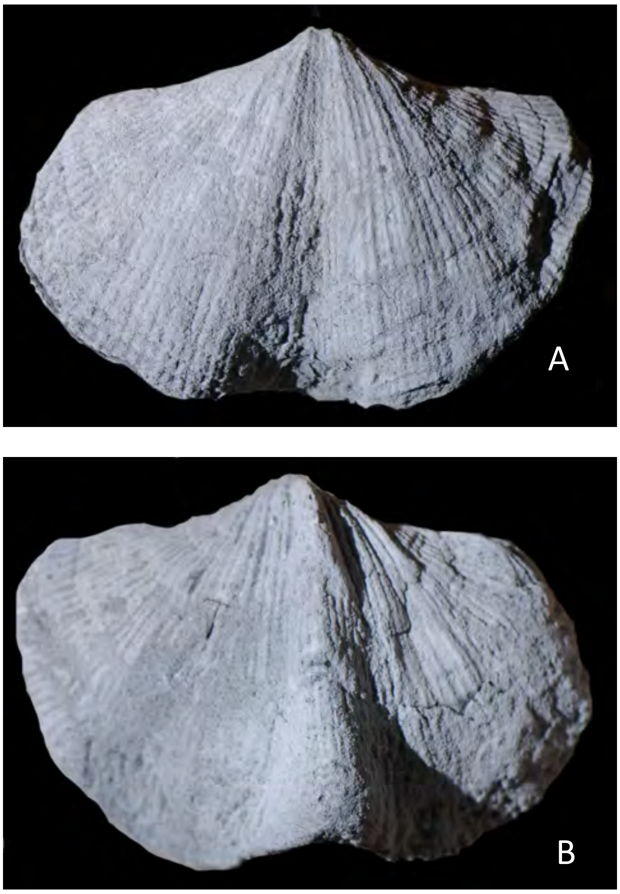

Fig. 240. *Betaneospirifer politus* n. sp. A, B, ventral and dorsal views of specimen GSC 140914 with valves conjoined, holotype, from C-4015, Trold Fiord Formation, Ellesmere Island, x1. This specimen was later leached in dilute HCl.

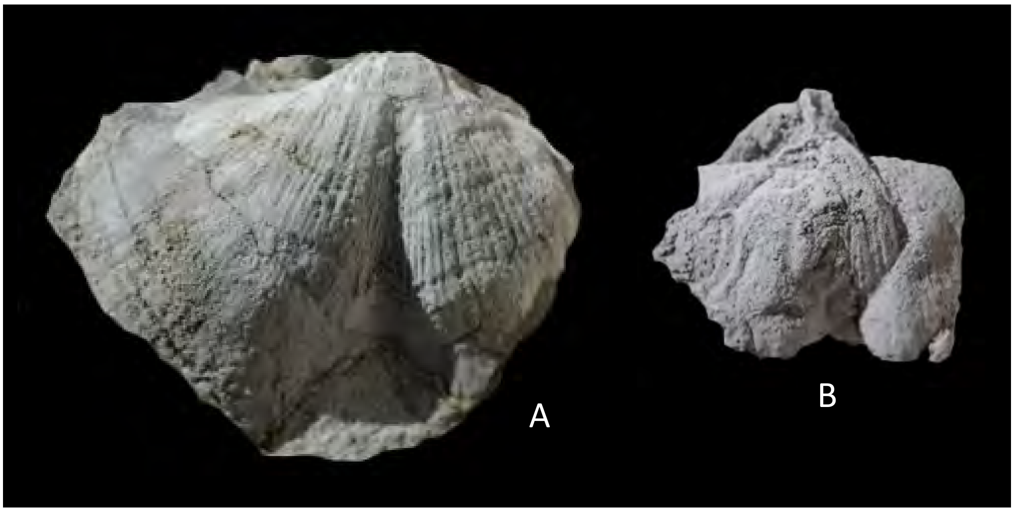

Fig. 241. *Betaneospirifer politus* n. sp. A, ventral valve GSC 140927 from C-4077, Assistance Formation, Ellesmere Island. B, leached posterior internal mould GSC 140928. From GSC 53931, Takhandit Formation, Yukon Territory. Specimens x1.

Fig. 242. *Betaneospirifer politus* n. sp., ventral valve from GSC 140929, GSC loc. 26406, Assistance Formation, Devon Island, x2.

Short well spaced adminicula are developed. A large internal mould of a specimen with valves conjoined from GSC loc. 26406 is 84mm wide, 59mm long and 40mm high, and displays the delthyrial construct that is normal for Neospiriferidae. The leached internal mould of a specimen with valves conjoined from GSC loc. 53931 shows plication, and high dental plates which joinr medianly and rest on short adminicula partly buried in secondary shell. The ventral muscle field is broad with narrow adductor ridges and broad diductor scars crossed by oblique ridges and grooves parallel to the oblique anterior margins. No subdelthyrial or connector plug, let alone a connector plate, is developed in this specimen, unlike the delthyrial arrangement in *Fasciculatia greenlandica*. A pleromal ridge is well developed along the junction between each dental plate and adminicula, and the two ridges merge posteriorly into a single ridge. Unless such morphological attributes are to be dismissed as of no taxonomic or phylogenetic significance, they indicate that the species is more neospiriferid than spiriferid, and so unlikely to belong to *Fasciculatia*.

Fig. 243. *Betaneospirifer politus* n. sp., leached internal mould of ventral valve GSC 140927 (see Fig. 241A), tilted to show delthyrial area. From C-4077, Assistance Formation, Ellesmere Island, x1.5. This illustates the way in which the dental plates fuse under the upper delthyrium, with growth lines, and may support a small very low callosity.

Resemblances: Small comparably plicate specimens were described by Brabb & Grant (1971) from the lower unit of the type Takhandit Formation. *Betaneospirifer striatoplicatus* (Gobbett) as described previously has stronger plication and better defined sulcus. *Fasciculatia striatoparadoxa* (Toula) is more transverse with tented fold and less developed plicae, and *F. groenwalli* (Dunbar) as interpreted herein, has tented posterior plicae which fade anteriorly, as in *striatoparadoxa* and fine ribs. *F. greenlandica* Waterhouse is closer in plication but has firm stronger ribs, many fascicles, and wider fold. These latter three species have a thickened subdelthyrial connector plate, unlike the arrangement in *politus*.

Fig. 244. A, *Betaneospirifer politus* n. sp., ventral valve interior 140927, from C-4077, Assistance Formation, Ellesmere Island, x2. The dental plates unite medianly in a low callosity crossed by growth ridges. B, *Fasciculatia striatoparadoxa* (Toula), ventral interior GSC 140921 for comparison, from C-4015, Trold Fiord Formation, Ellesmere Island, x2. The junction between dental and adminicula plates is spanned by a subdelthyrial connector plate. Both are internal moulds. c = connector plug, d = dental plate, p = pleromal ridge between adminiculum and dental plate, forming slender umbonal callosity.

Fig. 245. A, *Fasciculatia striatoparadoxa* (Toula), tilted posterior aspect of ventral internal mould GSC 140921, showing connector plug, arrowed. From C-4015, Trold Fiord Formation, Ellesmere Island, x2. B, *Betaneospirifer politus* n. sp., tilted posterior aspect of ventral valve interior GSC 140927 for comparison, from C-4077, Assistance Formation, Ellesmere Island, x2.

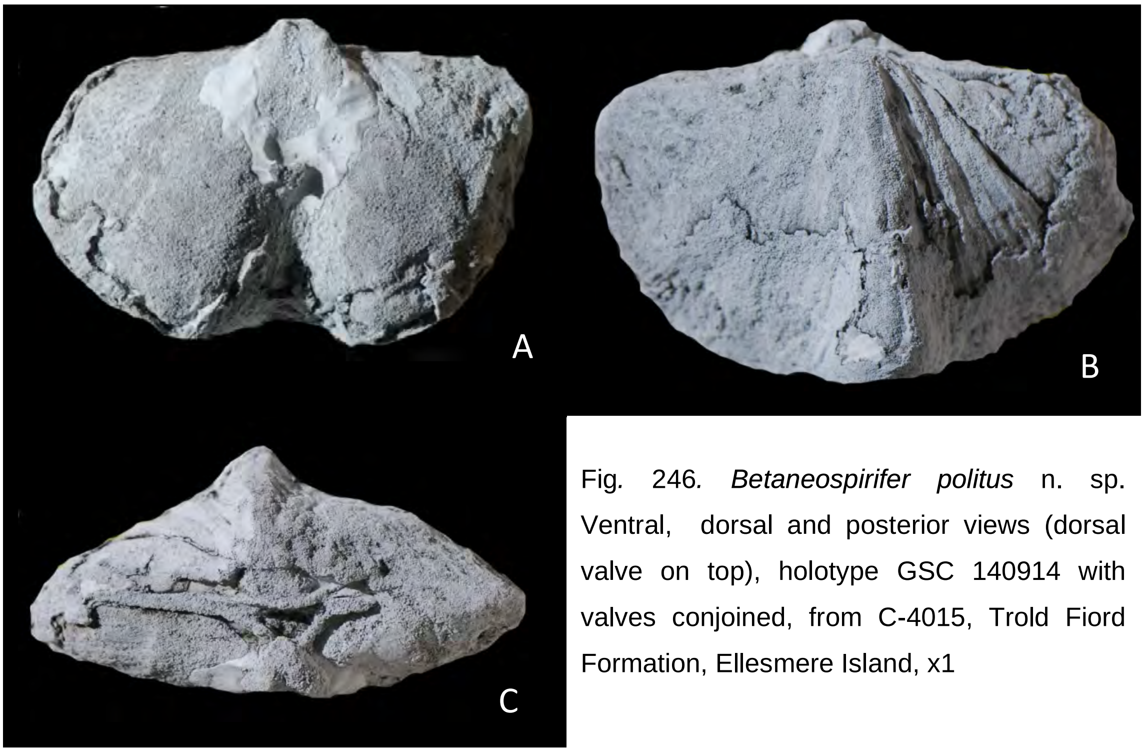

Fig. 246. *Betaneospirifer politus* n. sp. Ventral, dorsal and posterior views (dorsal valve on top), holotype GSC 140914 with valves conjoined, from C-4015, Trold Fiord Formation, Ellesmere Island, x1

Fig. 247. *Betaneospirifer politus* n. sp., internal ventral mould GSC 140920 from C-4037, Trold Fiord Formation, Ellesmere Island, x1.

Subfamily **CARTORHIUMINAE** new subfamily

Diagnosis: Transverse to elongate closely costate and weakly plicate shells with extended umbones and subrounded outline. Dental plates, adminicula, crural plates, noconnnector plate or tabellae, as a rule no delthyrial cover plate.

Name genus: *Cartorhium* Cooper & Grant, 1976a, p. 2191, here designated.

Discussion: This group is named for genera sharing a distinctive outline, with prominent ventral umbo, and displaying many of the attributes of Neospiriferidae, as evaulated by Cooper & Grant (1976a), although there are also strong similarities to Choristitinae Waterhouse in shape and internal plates, leaving the position open for further evaluation. Genera to be included in the group include *Cartorhium* Cooper & Grant, *Lepidospirifer* Cooper & Grant, *Ovispirifer* Waterhouse, and *Simplicatasia* n. gen., as further discussed on the following page. A figure of *C. chelonatum* by Cooper & Grant (1976a, pl. 613, fig. 35) shows exceptionally large pleromal plates, not connector plate.

Genus ***Simplicitasia*** new gen.

Derivation: simplicitas – simplicity, plainness, Lat.

Diagnosis: Transversely suboval with obtuse cardinal extremities, sulcus and fold, broad simple ribs, subdued if any plicae, capillate micro-ornament, high well-formed dental plates, short diverging adminicula, no tabellae. No umbonal callosity or subdelthyrial connector plate.

Type species: *Spirifer osborni* Harker, 1960, p. 63 from Assistance Formation (Roadian), Devonian Island, here designated.

Discussion: *Spirifer osborni* is a comparatively rare species found at mostly Devon Island and rarely in Spitsbergen and Yukon Territory, and possibly British Columbia. No dorsal valves and no internal details were originally available for any material from the Sverdrup Basin. A silicified ventral valve has been largely etched free of enclosing matrix, and found to have the interior characteristic of Spiriferoidea and Trigonotretoidea, with diverging dental plates supported by shorter diverging adminicula. Reference to any subdivision within Spiriferoidea is not clear, but there is no sign of a subdelthyrial or connector plate, nor substantial umbonal callosity, which would suggest Neospiriferidae (see Waterhouse 2016). Relating the genus to a particular strand within this family must be conjectural, largely because the ornament has become simple, and plicae likely to have typified ancestral stock reduced to very low remnants in a few specimens.

In shape, the present form comes close in some aspects to *Cartorhium* Cooper & Grant (1976a, p. 2191) from the Cisuralian and Guadalupian of the Glass Mountains in Texas, but members of this genus are more strongly plicate and have finer costae. There is also some approach to *Ovispirifer* Waterhouse, 2004a from the upper Wargal Formation of Pakistan, deemed to be of lower Guadalupian age by Gourvennec & Carter (2006, p. 2784) in the *Revised Brachiopod Treatise*, but well established as being of Wuchiapingian age (Waterhouse 2010b). This genus has higher dorsal fold, and stronger though low dorsal plicae. To some extent the type species externally approaches *Zhejiangospirifer* Liang, 1982, 1990 from China, of early Lopingian age (not Cisuralian as stated by Carter 2000a, p. 1786), although in detail the costation-plication is not the same. The Chinese genus, as also studied by Shen, Shi & Archbold (2003), lacks dental plates, and so may be readily distinguished. Although placed in Tangshanellinae Carter, 1994 in the *Revised Brachiopod Treatise*, the ornament of *Zhejiangospirifer* is much closer to that of Pustuloplicinae Waterhouse, 2004, a brachythyrid subfamily, given the presence of nodes in its micro-ornament, although the costation is quite different, suggesting considerable differentiation. Although questioned by Gourvennec in Gourvennec & Carter (2007, p. 2789), the Waterhouse position found some cautious support from Angiolini et al. (2011) and the affinities were elaborated and objections resolved in Waterhouse (2016, pp. 106-111). On the other hand, Shen (2017, p. 778) classed the genus as Choristitinae Waterhouse, quite a stretch for a genus characterized by nodes and no dental plates, in severe contradistinction to all known members of Choristitinae and indeed all Choristitioidea.

Simplicitasia osborni is externally very close to the Upper Carboniferous genus *Larispirifer* Enokian & Poletaev, in Poletaev, 1986 reported widely from Russia. The type species has a less prominent umbo, higher fold, higher ventral interarea, and the adminicula are short, thick and parallel, whereas those of *osborni* are thin and diverge widely. Moreover dental plates of *Larispirifer* are aligned with adminicula, rather than diverging widely (Poletaev 1986, fig. 5A). There are slight differences in the ribbing, because ribs in type *Larispirifer* are more clearly paired and bifurcate as a rule, whereas ribs are more varied in *osborni* and may occur in twos or threes, or be solitary, and the suggestion of plicae is more restricted. Carter (2006a, p. 1771) classed *Larispirifer* as Spiriferinae, comparing the genus with *Spirifer* (*Mesochorispira*) Carter, 1992, which differs in having divergent adminicula. Like *Larispirifer*, *Simplicitasia* lacks a subdelthyrial connector plate, and so is regarded as differing from Spiriferinae.

The genus also resembles in external shape and ornament the genus *Purdonella* Reed, 1944, based on *Spirifer nikitini* Tschernyschew, 1902 from the early Cisuralian of the Urals. As shown by Poletaev (1986), *Purdonella* has a subdelthyrial connector plate, and adminicula are subparallel and of moderate length, pointing to a position within Choristitoidea Waterhouse.

Simplicitasia osborni (Harker, 1960)

Fig. 248– 251

1960 *Spirifer osborni* Harker in Harker & Thorsteinsson, p. 63, pl. 20, fig. 15-17.
1961 *S. osborni* – Nelson, pl. 3, fig. 3a-c.
cf. 1963 *S. osborni* – McGugan, p. 624, pl. 77, fig. 1, 2.
1964 *S*? cf. *osborni* – Gobbett, p. 139, pl. 18, fig. 6.
cf. 1968 *S. osborni* – Logan & McGugan, p. 1137, pl. 143, fig. 9-11.

Diagnosis: Large shells with numerous coarse costae, increasing by branching on both valves, shallow sulcus and well-rounded lateral and anterior margins. No preserved neodeltidium, dental plates and adminicula spiriferiform, no connector or subdelthyrial plate. No tabellae.

Holotype: GSC 13744 figured by Harker & Thorsteinsson (1960), from GSC. loc. 26406, Assistance Formation (Roadian), Devon Island, OD.

Additional material: Specimen with valves conjoined and five ventral valves from GSC loc. 26406, Assistance Formation, Devon Island, one ventral valve from C-1410, an undocumented locality**,** apparently from the Assistance Formation, and fragment from C-4004 and ventral valve from C-4026, Trold Fiord Formation, Ellesmere Island. A fragment of the external mould of a ventral valve and part of an internal ventral mould from JBW 631, Takhandit Formation, Yukon Territory, might belong to the genus and species. A specimen with valves conjoined comes from

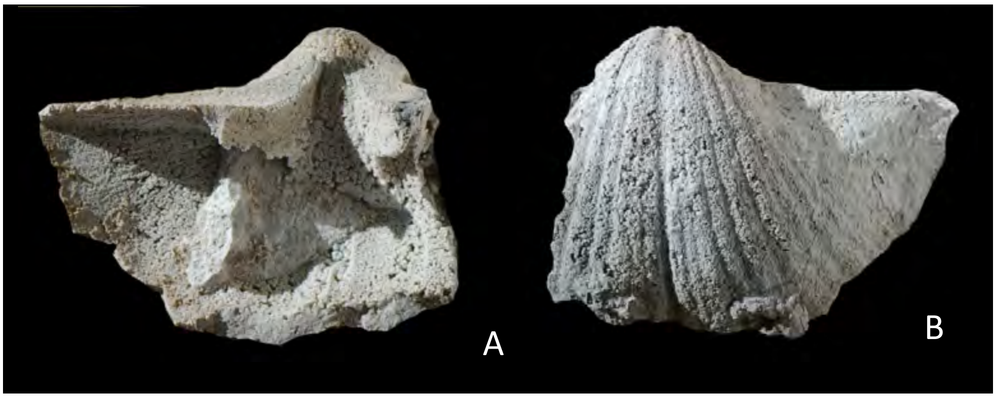

Fig. 248. *Simplicitasia osborni* (Harker). A, B, internal and external views of silicified ventral valve GSC 140924 after leaching in dilute HCl. From GSC loc. 26406, Assistance Formation, Devon Island, x1.

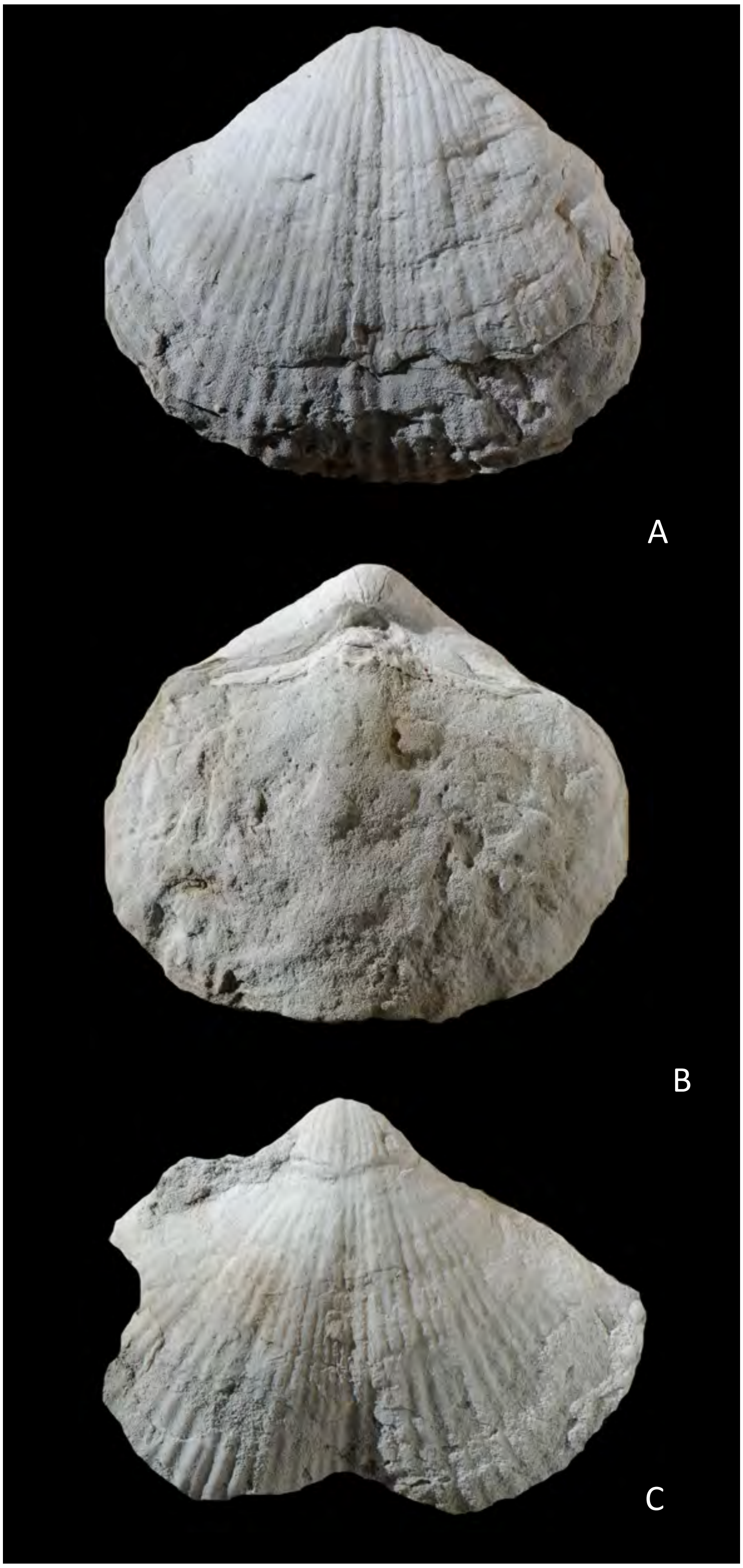

Fig. 249. *Simplicitasia osborni* (Harker). A, B, ventral and dorsal aspects of specimen GSC 140922 with both valves conjoined. C, ventral valve GSC 140923. Specimens x1, from GSC loc. 26406, Assistance Formation, Devon Island, x1.

an unknown locality, possibly in the Assistance Formation.

Dimensions in mm: both valves

Width	Length	Height	Umbonal angle	Hinge width	Sulcal angle	Delthyrium angle
78	65	37	110º	50	8º and 20º	70º

Description: The description is provided in Harker & Thorsteinsson (1960), and further information is contained in the measurements, and figures. The umbonal angle is 95º, and is incurved, the sulcus is narrow, commencing at the beak and widening at an angle between 15º and 20º, and occupied medianly by a well defined median groove, opposed to a dorsal fold with low broadly rounded crest and slightly recessed anterior margin, with visible trail. The ventral interarea is well defined with growth increments parallel to the hinge, concave under the umbo, and opposed to a much lower dorsal interarea. The delthyrium is open, without any delthyrial or subdelthyrial plate, and is bordered each side by a low dental ridge, without any umbonal callosity. A stegidium or neodeltidium was either never present or has been lost, as is often the case. Costae are low and broad, with narrowly rounded crests, increasing by branching and not noticeably differentiated. Two very low and broad plicae are present on two of the ventral valves, developing close to the umbonal tip, but not defined in the other specimen from GSC loc. 26406. A conjoined specimen from unknown locality has a broad and raised anterior fold (Fig. 250B). It thus differs from other specimens in this regard, though the fold of other specimens is clearly worn. In addition, the sulcus has a median rib, unlike the sulcus of the other specimens. A low fold is also present on a specimen that was figured by Nelson (1961, pl. 3, fig. 3b) from the Takhandit Formation.

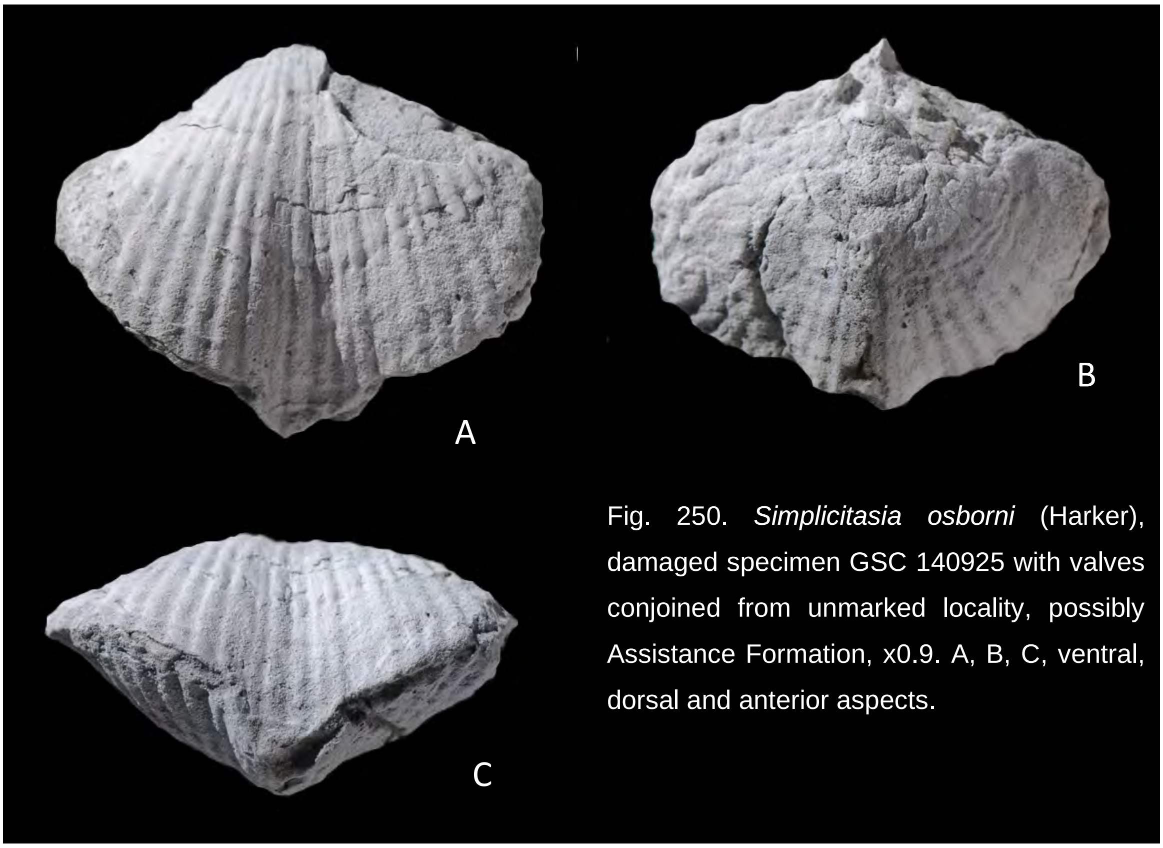

Fig. 250. *Simplicitasia osborni* (Harker), damaged specimen GSC 140925 with valves conjoined from unmarked locality, possibly Assistance Formation, x0.9. A, B, C, ventral, dorsal and anterior aspects.

Dental plates are large, inwardly concave and scapular-shaped, diverging at 110º, with terminal teeth broken off. They are supported by low diverging adminicula which are shorter than the dental plates, and largely buried in secondary shell, with broad infilling between the plates that is smoothly concave. There is no umbonal callosity. Adductor ridges divided by a narrow groove are narrow, and much broader diductor scars lie to each side, bearing only remnants of fine longitudinal grooves and ridges. The lateral floor has fine pits but is not well preserved. Little is shown of the dorsal interior, but there is a raised mound of shell over the floor posterior, and signs of a slender median septum. No tabellae are present. Traces of the spire are preserved in the matrix infilling one of the large ventral valves. The specimen from the uncertain locality is damaged posteriorly, but has crural plates and no tabellae.

Resemblances: Gobbett (1964) figured two ventral valves as *osborni* from the Brachiopod Chert at Bellsund, Spitsbergen. Dunbar (1955, p. 158, pl. 31, fig. 4-11) described a rather similar-looking species as *Choristites søderberghi* (now rendered “*Choristites*” *soederberghi*) from the Late Permian of central east Greenland, with similar general outline and similar costae, and faint suggestion of subdued plicae. The hinge is wider in this species, with stronger sulcal groove, slightly finer and more prominently bifurcate costae, and other minor differences. No dorsal valve was known to Dunbar (1955) in describing *soederberghi*, and no ventral interior has been available. So pending discovery of the interior, the species is provisionally retained as “*Choristites*”.

Fig. 251. *Simplicitasia osborni* (Harker), damaged ventral valve GSC 140926 showing impressions from the ventral muscles. JBW 631, x1. Middle Takhandit Formation.

Logan & McGugan (1968, p. 1137, pl. 143, fig. 9-11) allocated a few ventral valves to *Spirifer osborni* from the Mt Greene beds of the Ishbel Group of the Rocky Mountains in British Columbia, and McGugan (1963, p. 624, pl. 77, fig. 1, 2, text-fig. 3) reported specimens from the Telford Formation in British Columbia. The text-figure showed cross-sections of a ventral valve, admittedly with a rather peculiar curl to the dental plates. Their reports made it clear that the plates suggested a spiriferoid rather than choristitoid interior. Somewhat allied material was recorded as *Spirifer nikitini* Tschernyschew by Logan & McGugan (1968, p. 1136) from the Telford Formation in British Columbia, as spiriferiform specimens characterized by costae finer than those of *osborni,* and substantially older than *osborni.* Specimens were figured as *Choristites søderberghi* Dunbar by McGugan (1963, p. 624, pl. 76, fig. 9-11), with reference to pl. 6, fig. 1-11, which was not actually provided in the article. Logan & McGugan (1968, p. 1137) referred to an unpublished M. Sc. thesis at the University of Calgary by Gorveatt in 1967 on the Telford material identified as *nikitini*, which showed that dental plates were short and subparallel to divergent, and in many respects close to those of *osborni*. The species *Spirifer nikitini* Tschernyschew (1902, p. 542, pl. 10, fig. 1a-d, 2a-d, pl. 13, fig. 1) from the Schwagerinen-Kalk of the Urals is externally close to *osborni* (especially involving specimens figured in Tschernyschew 1902, pl. 10), but has finer and more numerous costae.

A ventral valve was figured as *Spirifer nikitini* from the Great Bear Cape Formation at Ellesmere Island by Tschernyschew & Stepanov (1916, p. 47, pl. 10, fig. 2), with no internal detail available. It appears to be close in shape and ribs are broader than those characteristic of *nikitini*, though approaching that of Tschernyschew (1902, pl. 13, fig. 1), and shares a narrow ventral umbo to suggest a possible purdonellid, as discussed on p. 261.

Choristites søderberghi of Nakamura (1992, et al., p. 94, pl. 5, fig. 80) from Spitzbergen might be related, but is poorly preserved, and first-hand examination is required for identification.

Subfamily **SEPTOSPIRIFERINAE** Waterhouse, 2016

Genus ***Gobbettifera*** Waterhouse, 2004a

Diagnosis: Small with plicae high and angular posteriorly, fading anteriorly, sulcus and fold well developed and angular, costae fine and persistent. Delthyrium open, no neodeltidium or subdelthyrial connector plate, adminicula and dental plates present, and short high to low ventral median septum in early maturity, and lost in later maturity to varying degree. Dorsal valve with crural plates, low often posterior dorsal septum, no tabellae.

Type species: *Gobbettifera angulata* Waterhouse, 2004a, p. 102 from Assistance Formation (Roadian), Devon Island, OD.

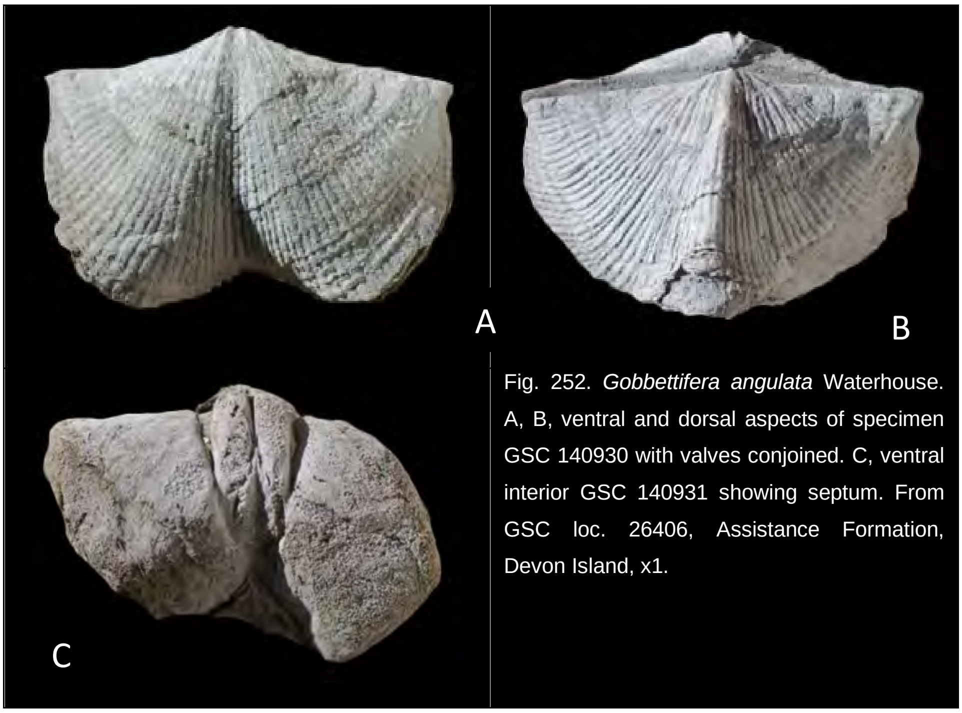

Fig. 252. *Gobbettifera angulata* Waterhouse. A, B, ventral and dorsal aspects of specimen GSC 140930 with valves conjoined. C, ventral interior GSC 140931 showing septum. From GSC loc. 26406, Assistance Formation, Devon Island, x1.

Discussion: This genus has proved controversial. Gourvennec in Carter & Gourvennec (2006, p. 2781) judged *Gobbettifera* to be a junior subjective synonym of *Septospirifer*, and certainly the two are close, with somewhat similar ornament though more exaggerated in *Gobbettifera*, and a ventral septum in both genera. The ventral plicae fade more quickly in *Gobbettifera*, and tend to be incorporated anteriorly in an increasingly broad sulcus, which in larger specimens becomes very deep or high, and the dorsal valve is more angular in cross-profile with narrow crest. Dorsal plicae are lower and also fade quickly, differences which could be specific, or arguably generic. The cardinal extremities become alate in late maturity. Lee et al. (2016, Fig. 13B-D) ascribed a shell with wide acute but not acute cardinal extremities as *Gobbettifera angulata*, but did not determine the nature of its interior, and the nature of the plication could possibly suggest *Fasciculatia striatoparadoxa* rather than *angulata*, although this is in no way certain.

Internally, the ventral septum of *Septospirifer* extends for the length of the ventral adductors, whereas the septum in many *Gobbettifera* is distinctly shorter. The septum in some large specimens at advanced maturity formed no more than a short posterior projecting ridge, reflected on the ventral side of the callus infilling the junction below the join of the adminicula and dental plates, to demonstrate that the ontogeny in *Gobbettifera* and *Septospirifer* followed different trajectories, likely to have evolved one from the other, and as assessed by Gourvennec, conceivably members within one evolving genus.

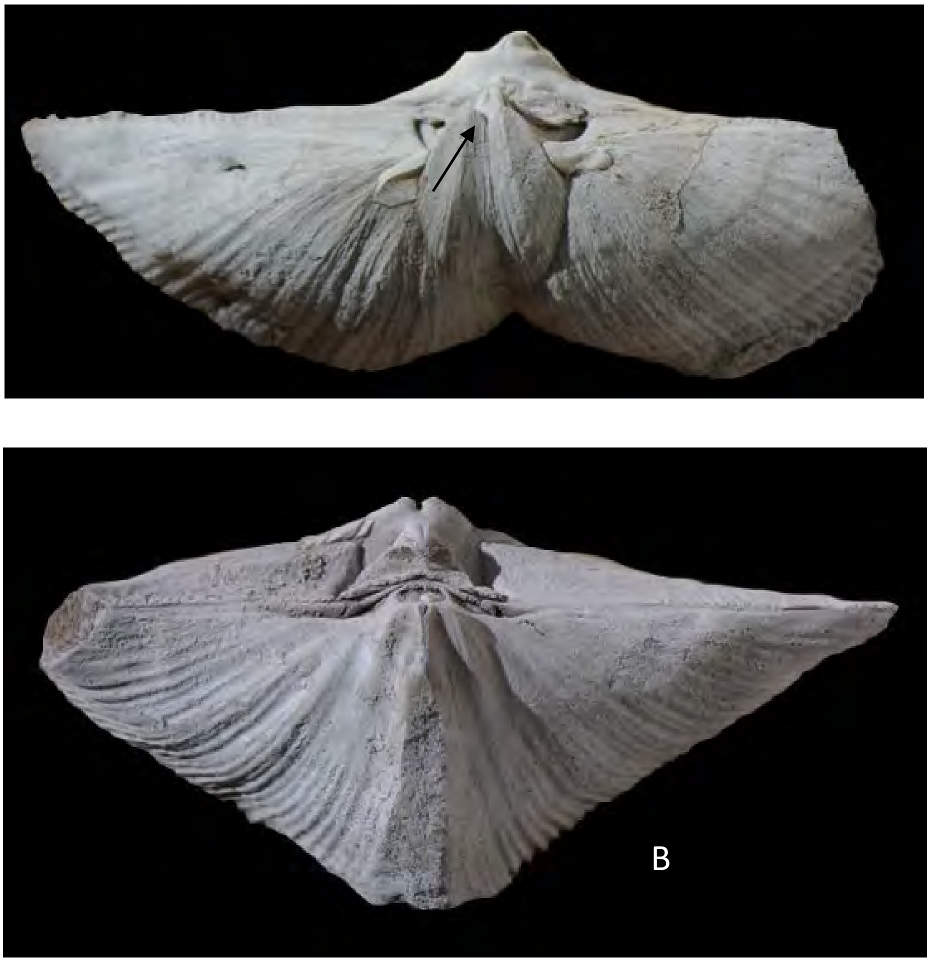

Fig. 253. *Gobbettifera angulata* Waterhouse. A, B, dorsal posterior and dorsal aspects of specimen GSC 140932 with valves conjoined, at early maturity, showing apical ventral septum, reduced in size compared with immature specimens. Arrow in A points to notch, left after leaching shell away in acid, and clearly present in B. From GSC loc. 26406, Assistance Formation, Devon Island, x1.5.

On the other hand, Lee et al. (2016) regarded *Gobbettifera* as congeneric with *Fasciculatia* Waterhouse 2004a. They acknowledged the presence of a posterior ventral septum (Lee et al. 2016, Fig. 11E), as figured by Waterhouse (2004a, Fig. 25A, B), and further illustrated in Waterhouse & Chen (2007, text-fig. 11A, p. 49), a reference left out of their synonymy. Evidently Lee et al. attached no significance to any septum, because it was not treated as a critical character state in their cladistic study (Lee & Shi 2016), and they did not explain such an apparent deviation from type and other *Fasciculatia.* As well they did not take account of the delthyrial apparatus, and lack of a subdelthyrial connector plate, nor attach any significance to the tented fold and channelled sulcus and alate cardinal extremities. One of the dangers of embarking on cladistic studies on the basis of an insufficient number of character states is that the treatment of genera becomes limited to those character states, and sets aside any information provided by unprocessed data, and rejects any study that takes account of differences that were not assessed.

The type species is so far known only from the Canadian Arctic Archipelago and the Yukon Territory. The youngest *Septospirifer* has been figured by Bamber & Waterhouse (1971, pl. 17, fig. 5) from the lower Takhandit Formation, in the basal member, distinctly older than the Assistance Formation. It has a long and well developed ventral median septum, as in type *Septospirifer*, known from the underlying Early Permian Jungle Creek Formation.

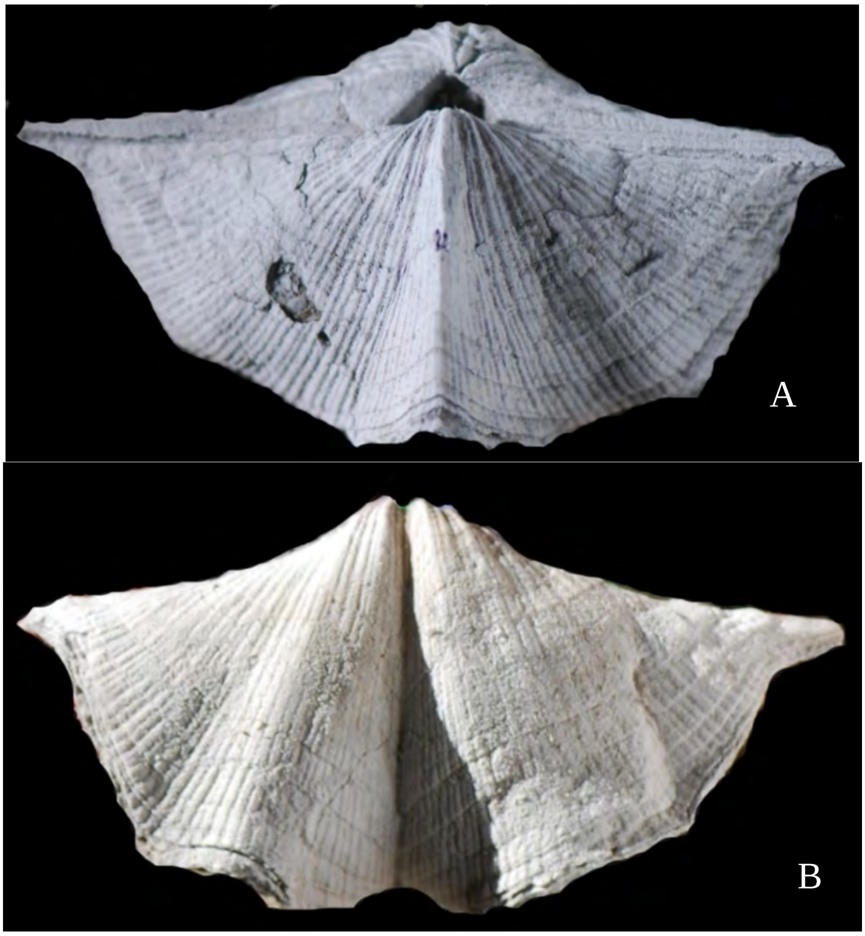

Fig. 254. *Gobbettifera angulata* Waterhouse. A, B, dorsal and ventral views of exterior, GSC 136656, x1.2, at late maturity. From Assistance Formation, Canada, x1.

Gobbettifera angulata Waterhouse, 2004a

Fig. 252 - 258

1960 *Spirifer striato-paradoxus* [not Toula] – Harker & Thorsteinsson, p. 67, pl. 19, fig. 1-7.
1970 *S. striato-paradoxus* [not Toula] – Bamber & Copeland, p. 360, pl. 14, fig. 9.
2004a *Gobbettifera angulata* Waterhouse, p. 102, text-fig. 24.6, 7, 25.
2007 *G. angulata* – Waterhouse & Chen, p. 22, text-fig. 11A.
2016 *Fasciculatia angulata* – Lee et al., p. 127, Fig. 2C, D, 6, 11, 12, 13A-F.
2016 *G. angulata* – Waterhouse, p. 202, Fig. 24.
2018a *G. angulata* – Waterhouse, p. 351.

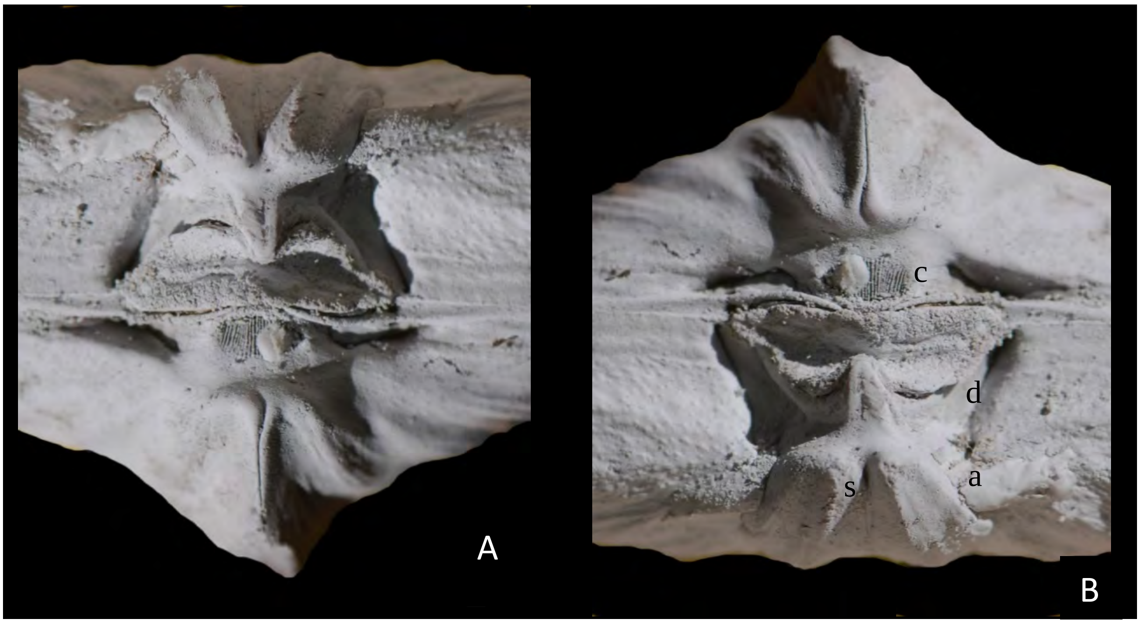

Fig. 255.*Gobbettifera angulata* Waterhouse, posterior aspect of GSC 140932 from GSC loc. 26406, Assistance Formation of Devon Island, showing adminiculum (a), dental plate (d), reduced median septum (s) and ctenophoridium (c). A, ventral valve on top, B, ventral valve below, x 3.

Diagnosis: Small to medium size, emphasized angular or tented fold and well defined sulcus becoming deep anteriorly, with narrowly channelled floor as a rule, plicae fading anteriorly and merging over anterior ventral valve. Ventral interior with low median septum, becoming relatively short with increased maturity.

Holotype: GSC 13748 from GSC loc. 26406, Assistance Formation, Devon Island, figured by Harker & Thorsteinsson (1960, pl. 19, fig. 1-3) and Waterhouse (2004a, Fig. 24.6, 7), OD.

Material: A very large collection of mostly conjoined specimens from GSC loc. 26406, Assistance Formation, Devon Island. One dorsal valve comes from C-4002 and a ventral valve from C-4016, both from Assistance Formation, Ellesmere Island.

Description: The species has been described in Harker & Thorsteinsson (1960), Waterhouse (2004a) and Lee et al. (2016). Lee et al. (2016) drew attention to two important facets in specimens ascribed to the species. They noted that Harker & Thorsteinsson (1960, p. 67) had recorded an arched deltidium. No such feature was figured, and none has been observed in any of the other studies. In present material, there is no deltidium or neodeltidium preserved, but the dental plates fuse under the umbo at the top of the delthyrium, with marked growth lines, and so close off the delthyrium, as shown in Fig. 255 and 256. Lee et al. also noted that the collections included some strongly transverse specimens which tended to have alate cardinal extremities, short and strongly geniculate sulcal tongue and relatively low fold. A specimen with alate cardinal extremities was figured by Waterhouse (2016, Fig. 247B, C), as reproduced herein as Fig. 254. The figure shows well the angular nature of the fold and sulcus, and the specimen, as is true of many others, does not have an anterior geniculate sulcus.

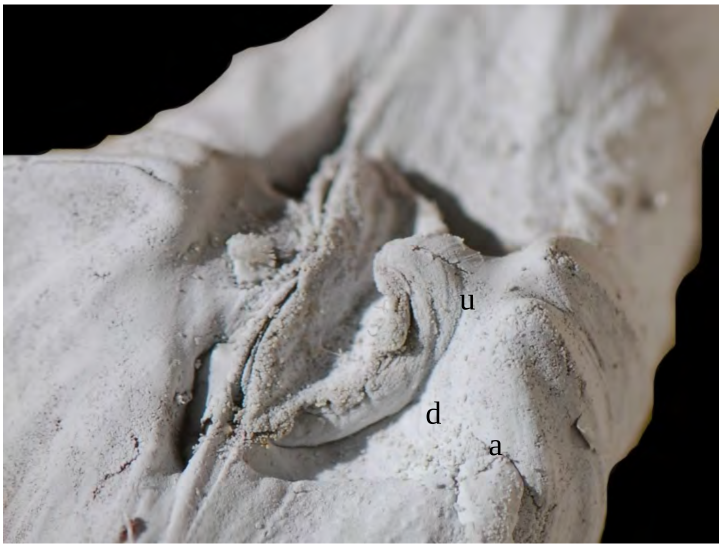

Fig. 256.*Gobbettifera angulata* Waterhouse, oblique posterior aspect of GSC 140932 from GSC loc. 26406, Assistance Formation of Devon Island, showing adminiculum (a), dental plate (d) and umbonal delthyrial closure (u), x 4.

Micro-ornament is not well preserved, but on one specimen is dominated by commarginal growth laminae that become sublamellar towards the anterior margin. Radial lira are only visible over parts of the shell.

One ventral valve at early maturity has only a short posterior septum, but the two ventral adductor scars are raised on a high ridge to each side, as shown in Fig. 258A. In other specimens the septum is larger and better developed (Fig. 257), and adductor ridges are comparatively low.

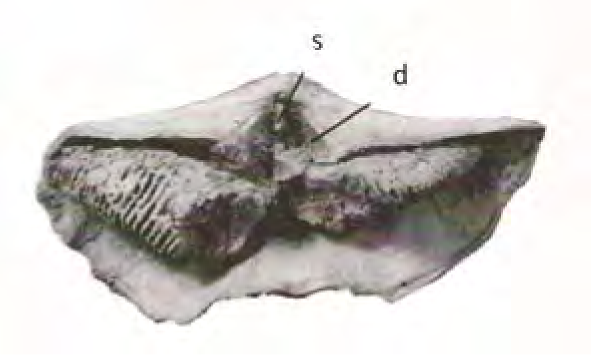

Fig. 257. *Gobbettifera angulata* Waterhouse, ventral valve GSC 9822 from GSC loc. 26406, Assistance Formation of Devon Island, showing dental plate (d), median septum (s) and spiralia. (Waterhouse 2004a, Waterhouse & Chen 2007).

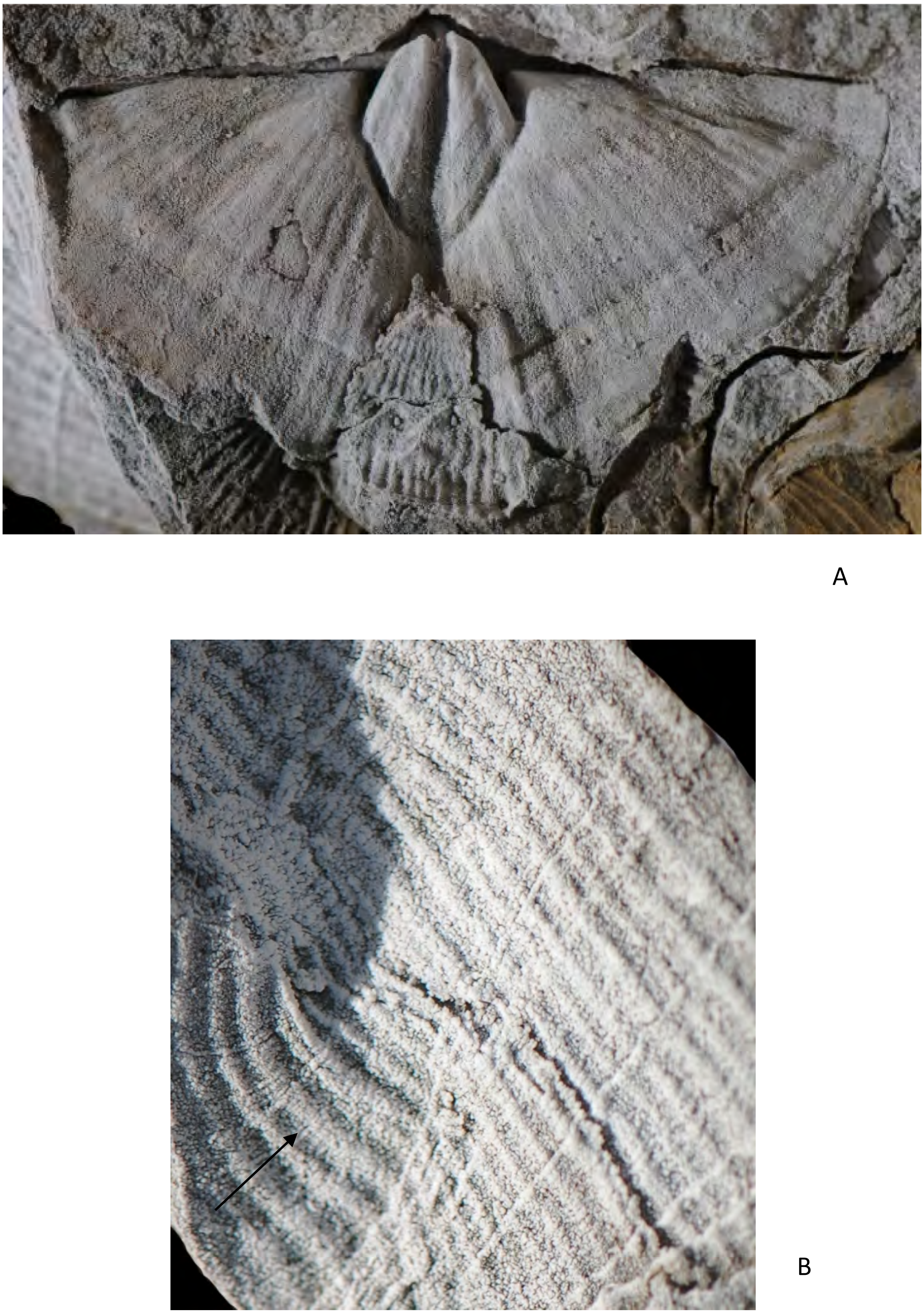

Fig. 258. *Gobbettifera angulata* Waterhouse. A, ventral internal mould GSC 141169, x 2.5, showing high adductor scars each side of short posterior septum. B, ventral external mold of part of GSC 141170, showing micro-ornament, with arrow pointing to rarely visible fine radial lira, x4. From C-4016, Assistance Formation, Ellesmere Island

On the validity and affinities of Kaninospiriferinae Kalashnikov, 1996

Knowledge of the delthyrial apparatus and mantle canal system in Kaninospiriferinae Kalashnikov has long been incomplete, so that the subfamily has not been easy to justify. To one authority, a critical factor was that plicae faded anteriorly in mature specimens (Grunt 2006b), and Waterhouse (2004a) suggested that one feature could be that dental plates were low, at least in a number of specimens assigned to the type species of *Kaninospirifer*. But the height of the dental plates may be somewhat variable, as also assessed by Lee et al. (2016). The family group was not recognized by Carter (2006a, p. 1799). He mistakenly claimed in the *Revised Brachiopod Treatise* that the genus lacked adminicula, an interpretation forwarded by Shi et al. (2002). Lee et al. (2016, p. 122) later allowed that the genus did have adminicula, but they allocated species to *Kaninospirifer* on the basis of having low adminicula, in defiance of the actual structure in type specimens of the genus. They also stated that their phylogenetic analysis did not support recognition of a separate subfamily group, but this was on the basis of simplistic and traditional (time-free, space-free) cladistics, based on an inadequate number of character states – including some erroneous interpretations, which must detract from any value that may be found for the analysis (Lee & Shi 2016).

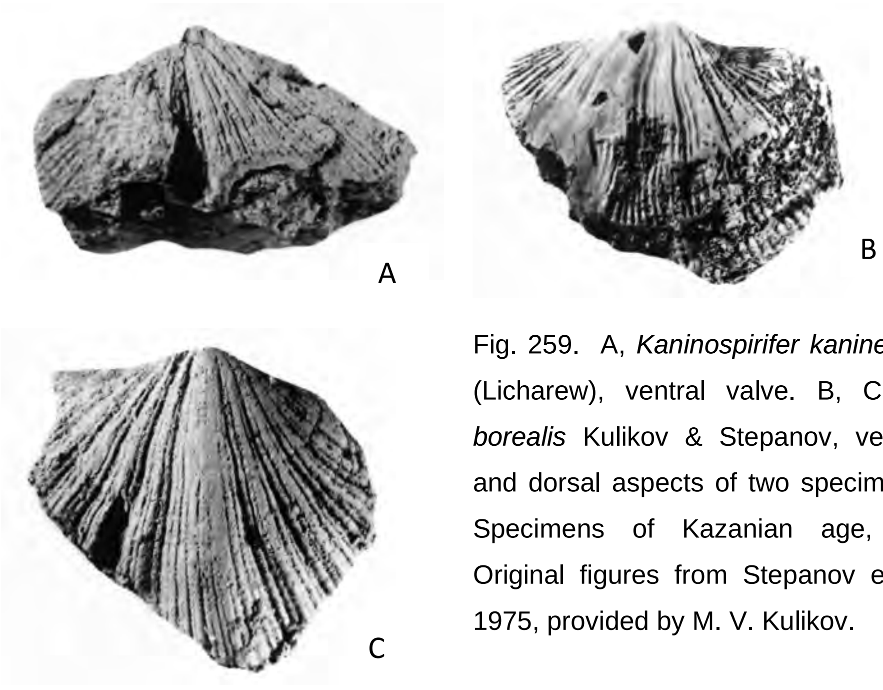

Fig. 259. A, *Kaninospirifer kaninensis* (Licharew), ventral valve. B, C, *K. borealis* Kulikov & Stepanov, ventral and dorsal aspects of two specimens. Specimens of Kazanian age, x1. Original figures from Stepanov et al. 1975, provided by M. V. Kulikov.

Kalashnikov (1998) pointed out that *Imperiospirifer* Archbold & Thomas (1993) from Western Australia showed considerable approach, and Waterhouse (2004a, p. 129) added two further genera from Western Australia, *Quadrospira* Archbold, and *Wadispirifer* Waterhouse. *Quadrospira* is strongly plicate, like the specimens assigned to *Kaninospirifer borealis* (See Fig. 259B, C), but also approaches Arctic *Betaneospirifer* such as *striatoplicatus* and *B*. *permicus*. Species close to all three of these genera were also reported and described from the Himalayas in India, Nepal and Tibet by Waterhouse (2004a, pp. 134-142), with distribution largely confirmed and elaborated by Lee et al. (1916), except they left out *Wadispirifer* Waterhouse, 2004a, p. 138. This genus was based on the large species

Neospirifer grandis Archbold & Thomas (1986a, p. 143), and displays very low dental plates (Archbold & Thomas 1986a, Fig. 11 E, F), approaching those of topotype *Kaninospirifer* figured by Kalashnikov (1998).

Gourvennec in Gourvennec & Carter (2006, p. 2784) synonymized *Wadispirifer* with *Betaneospirifer*, regardless of the information that *Betaneospirifer* always has well developed dental plates, and much stronger plicae. He was modest in his assessment, for he is an expert on Devonian not Permian brachiopods, but had con--sulted with Lucia Angiolini, who by that time had contributed to studies of some fossils from Pakistan and Oman, and was later to establish her Arctic Permian expertise in an article with S. Long (2008) on brachiopods from Spitsbergen. To Lee et al. 2016, the southerly group of genera belonged to a separate group, based on cladistic analysis. But, as indicated, the analysis was inadequate, with consideration of only a few character states, roughly half the number deemed essential for any provisional assessment of relations deemed necessary by Waterhouse (2016) in an overview of the Spiriferida. Their cladistic analyses, based on few characters, and inevitably setting aside considerations of time and space, were supposed to substitute for careful and wide-ranging true phylogenetic analysis. Traditional and oversimplistic cladistics has been critically analysed and rejected for widespread applications by Lazarus & Protheroe (1971). Furthermore, readers should be careful in assuming that the *Revised Brachiopod Treatise* is infallible. In numerous studies, Lazarev has revised and indeed demolished various aspects of the *Treatise* section of Productidina (see Waterhouse 2013, 2018a), and Schemm-Gregory (2008, p. 410) was forced to dismiss much of the study on older Spiriferida in the *Revised Brachiopod Treatise*. Perhaps the only way to defend many aspects of its classification is to present selected cladograms, which omit analysis of many characters, and confuse or conflate others. However one may choose to apply terminology, in his usage Waterhouse distinguished fascicles made up of very few costae that have limited if any affect on the inner shell. Plicae consist of larger plications of the shell, and often carry more costae. Type *Fasciculatia* is fasciculate as well as being weakly to broadly plicate. *Kaninospirifer* is plicate and costate. Lee et al. (2016) asserted that such ornament varied amongst species and genera, which certainly seems likely. But they misidentified *Gobbettifera* as belonging to *Fasciculatia,* when it not only has plicae but many ventral valves possess an internal septum not found in *Fasciculatia*, and lacks a subdelthyrial connector plate underlain by callus, which is developed in *Fasciculatia*, and has alate cardinal extremities. A Neimongol species of *Imperiospirifer* and a Canadian species possibly belonging to *Betaneospirifer*, were wrongly synonymized with *Fasciculatia.* On the other hand, they were probably correct in identifying *striatoparadoxus* Toula, 1873, 1875b as a member of *Fasciculatia*, as earlier mooted by Angiolini & Long (2008).

So where does that leave Kaninospiriferinae? I suggest at best that it stands as a group yet to be completely defined, and potentially with member genera prominent in the Middle Permian of temperate paleolatitudes, which involves the present Arctic, and for the southern paleohemisphere, Western Australia and Himalaya of India, Pakistan, Nepal, Tibet and Bhutan. The genus allegedly had high dental plates and low adminicula according to an uncheckable identification with this genus and species from Gansu Province in northwest China by a student in an unpublished thesis (Li 2009). Lee et al. (2016, Fig. 3A) figured an internal view of a Gansu specimen, but provided no external or dorsal view, nor even evidence over the age. The identification may be right, it may be wrong, but how to tell? Why they ignored the data from Kanin Peninsula is difficult to justify, but the assertion of adminicular height seems to have been crucial for their distinction of genera and assignment of species. The reports of *Kaninospirifer* from nearby Mongolia by Pavlova (1991) and Shi, Shen & Tazawa (2002) lack full documentation of the morphological features, and can hardly be regarded as a substitute for type material. Dental plates are certainly low and adminicula normal in a much more reliable figure provided by Kalashnikov (1998, Fig. 6), repeated in Waterhouse (2016, Fig. 252, p. 205), and quoted in Waterhouse (2004a, p. 131), from the Kazanian of Kanin Peninsula, as essentially topotype material (see Fig. 260). Even the diagnosis for the genus by Lee et al. (2016) that *Kaninospirifer* had deep dental flanges implies a lesser than normal development of dental plates, though in fact the dental plates are higher than flanges. They vary in height in the few figured *Kaninospirifer* from Kanin Peninsula, leading to the conclusion is that the height varied – apparently low as a rule, but variable, and even the variation may be considered as a morphological character.

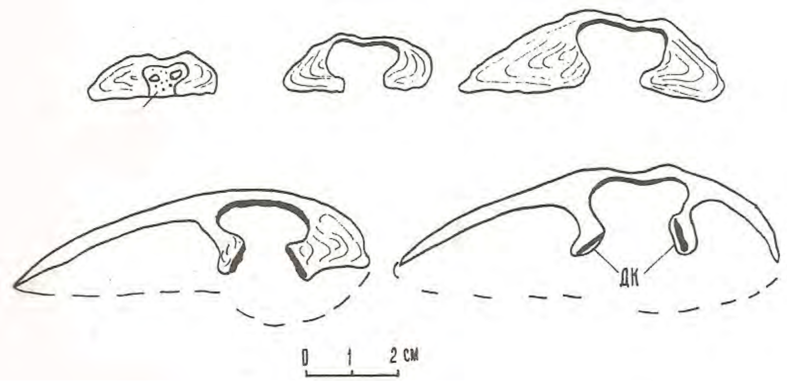

Fig. 260. *Kaninospirifer kaninensis* (Licharew), transverse sections of the ventral valve showing moderately high adminicula and low but only anterior dental plates (DK). From Guadalupian of Kanin Peninsula, Russia. (Kalashnikov 1998).

The three genera first recognized in Western Australia differ to a small extent from *Kaninospirifer. Neospirifer hardmani* Archbold & Thomas (1986a) has a rather generalized morphology that includes in some specimens a small delthyrial plate, its nature not fully explained by those authors, but possibly equivalent to a cover plate, as it was stated to be overhanging (see also Waterhouse 2004a, pp. 130, 134). Some *Quadrospira* have a small build-up of apical callus. Unlike the arrangement in many neospiriferid species, dental plates are reduced to flanges, at least in some to many specimens. *Wadispirifer amplus* (Archbold & Thomas) has what appears to be two small deltidial plates. All but *Wadispirifer* have a narrow high fold, whereas that of *Wadispirifer* is broad anteriorly with rounded crest, closer to that of *Kaninospirifer*, and all genera have plicae that are well defined posteriorly, and gradually fade anteriorly and tend to be partly incorporated in a large inner pair of ventral plicae, lending support to the observation by Grunt (2006b) for fading plicae, although plicae are more persistent in some species of *Quadrospira*. Thus these genera considerably approach *Kaninospirifer*, especially in ornament, and in the varying but often reduced dental plates, the lack of connector plate and feeble development of a possible cover plate or deltidial plates in one early form (*hardmani*), and modest umbonal callus in some specimens. The group began in Sakmarian or Asselian faunas of Western Australia, and spread in the later Permian in south Asia, and possibly reached Mongolia in mid-Permian. In north Russia, *Kaninospirifer* appeared in mid-Permian especially Kazanian times, and showed some features of the southerly genera in the tendency towards reduced dental plates, certainly to varying extent, minor umbonal callus, gradual loss of a cover plate, and overall similar major ornament. *Kaninospirifer* has a broad round-topped fold, as in *Wadispirifer*. Whether *Kaninospirifer* itself started in east Australia and New Zealand as *K. crassicostatus* Waterhouse (2010a, p. 76) remains contentious – Lee et al. dismissed the claim on the basis that the adminicula were too high, which may be regarded as incorrect, and dismissed the significance of plication as being unimportant, whereas Waterhouse had marked it as significant. Given the weak plication shared by *Spirifer hardmani* Foord, 1890 and *crassicostatus* Waterhouse, 1983d, a separate genus for the two may well be justified. No individuals and no species developed a ventral median septum, or a connector plate or connector plug.

But it is quite true that uncertainties remain. The micro-ornament is seldom well preserved, though if of a general spiriferin, trigonotretid or neospiriferid nature, is hardly likely to convey other that generalized information, because variation and permutations as a rule seem to have been more dependent on local ecological rather than genetic factors. The variations in fold profile and dental plates seem compatible with the development of the family group. Moreover, the origins for the west Australia components would appear to have been from neospiriferin stock, growing in size, changing in ornament, reducing the size of dental plates and cover plate, differences able to be preserved in descendent stock. A separate origin for *Kaninospirifer* is theoretically possible, but will require much more analysis, and at present, no separate sources for progenital stock are known. If it arose from neospiriferin stock, it mimicked the southern genera in size and ornament, also reduced the size in many individuals of the dental plates, lost the cover plate, and developed minor umbonal callus. Or did it arise from stock previously located as in Oman or Mongolia, that had migrated from Western Australia, through the Himalayan realm? That would certainly not be extraordinary, given that a number of other genera and subfamilies found in the southern Permian paleohemisphere are found also in the Arctic. Many other taxa are shared between the two realms: *Echinalosia, Wyndhamia, Wimanoconcha, Cimmerella, Magniplicatina, Himathyris, Oviformia*, *Sulcicosta* to name a few. Any cladistic or morphologic analysis that fails to explain such a remarkable agreement in morphologies is clearly oversimplistic and incomplete. No cladistic analysis can offer a satisfactory analysis without 1, processing the full range of aspects of morphological detail; 2, tracking development within species and genera; and 3, providing rigorous attention to age. As practised at present, cladistics are not a satisfactory or accurate alternative to rigorous phylogenetic analysis, based on careful attention to numerous character states, and to time control, and to geographic distribution.This could be rectified by taking care to assess an adequate number of character states, and giving full value to the significance of chronologic information, and perhaps more arguably, geographic information.

Lee et al. (2016) concluded that *Kaninospirifer* belonged in Neospiriferinae, which is acceptable, although this is a rather broad category, and tribal and subtribal distinctions are achievable. They regarded *Neospirifer* as a member of Trigonotretidae, and a member of Spiriferoidea King. Such is largely the view of the *Revised Brachiopod Treatise*, but analysis suggests the need for substantial modification, as discussed in Waterhouse (2016), based on the nature of the delthyrial apparatus and vascular pattern, and on the history of development through time, which of course is dismissed as unimportant in cladistic analysis, following the initial application of simple cladistics to biological development, set forward by Hennig (1966), who strongly deprecated any value being attached to paleontology, with its record of change through time and its inamenability to simple cladistics, though such “flaws” were not admitted. In 2016, Waterhouse proposed that Angiospiriferidae Legrand Blain, with its unusual pattern of coarsely reticulate mantle canals, numerous simple plicae, and large ventral umbonal callosity, of Early Carboniferous age, evolved in later time into Trigonotretidae, through the gradual introduction of costation, and then in turn into Aperispiriferinae, with retention of the unusual mantle canal system, lack of connector plate, and presence of large umbonal callosity. *Angiospirifer* itself was deemed to have a small convex deltidium, and a very small posterior subdelthyrial plate (Legrand-Blain 1985), apparently lost from Trigonotretidae. Neospiriferidae overlapped and preceeded Trigonotretidae in age, had much more developed and fewer plicae and close costation, no ventral umbonal callosity, differed in mantle canal system, lacked a connector plate, and developed a distinctive delthyrial cover plate or neodeltidium, presumably by modification of a stegidial plate. It either evolved from the spiriferid Subfamily Spiriferalariinae, with similar plication and costation, no umbonal callosity, a delthyrial cover plate or stegidial plates, and loss of a subdelthyrial connector plate, or developed within Trigonotretoidea, retaining internal features but developing a more costate exterior.

Lee et al. (2016, Table1) pointed out that some spiriferoid genera inhabited seemingly disparate paleolatitudes. Documentation is meagre, the generic identifications of very mixed reliability, and the paleolatitudinal range, if based on paleomagnetic measurements, subject to wide fluctuations of tens of degrees latitude – within the margin of error posited for each genus. Moreover, it has been shown that genera do not obey any invented rules of latitudinal restrictions, but move, often from zone to zone, from one faunal province to another, across great distances from far afield, including in the Yukon Territory, from the paleotropics, and even from high southerly paleolatitudes of a different hemisphere (Waterhouse 2018a, pp. 452-454, Fig. 379).

Superfamily **SPIRIFERELLOIDEA** Waterhouse, 1968b

Family **SPIRIFERELLIDAE** Waterhouse, 1968b

Discussion: Numerous species have been assigned to *Spiriferella*, nearly sixty by the early 1980's according to Waterhouse & Waddington (1982, Table 22), and many more since added, with a few related species allocated to *Eridmatus, Timaniella* and *Elivina*. Within that substantial corpus, it has been possible to recognize different family groups (Waterhouse 2016), Spiriferellinae, Timaniellinae for highly transverse spiriferellids, and Elivinidae for spiriferelloids that lack fine external pustules (as shown by first-hand examination of the types of *Elivina* at the Geological Survey of India, Kolkata, India), and differing in the nature of plication, sulcus and fold. It is necessary to challenge various claims for pustulation in *Elivina* that have been made by authorities who have never examined the types at first hand in Kolkata, or even inspected the material kept at the Smithsonian Institution at Washington D.C., where Cooper & Grant (1976a) stated that their *Elivina* was normally without pustules. That still leaves a formidable number of species in the Subfamily Spiriferellinae, and a number of lineages can be recognized, a minor but distinctive one based on the lack of a dorsal channel along the dorsal fold (*Plicatospiriferella, Arcullina*), which may be rated as a tribe, and several lineages of lesser deviation, but with more species. These include a succession of species dominated by *S. draschei* (Toula), in which the sulcus is particularly wide and involving S. *pseudodraschei* Einor, *S. oregonia* n. sp., *S. sulcoconstricta* n. sp., a cluster with wide hinge and broad dorsal fold channel (*Alispiriferella*), and a very large group that involved many *Spiriferella* species as well as *Eridmatus* and *Bamberina.*

In the following account, the species are informally grouped according to these proposals, with the best known or most prominent taxon mentioned first.

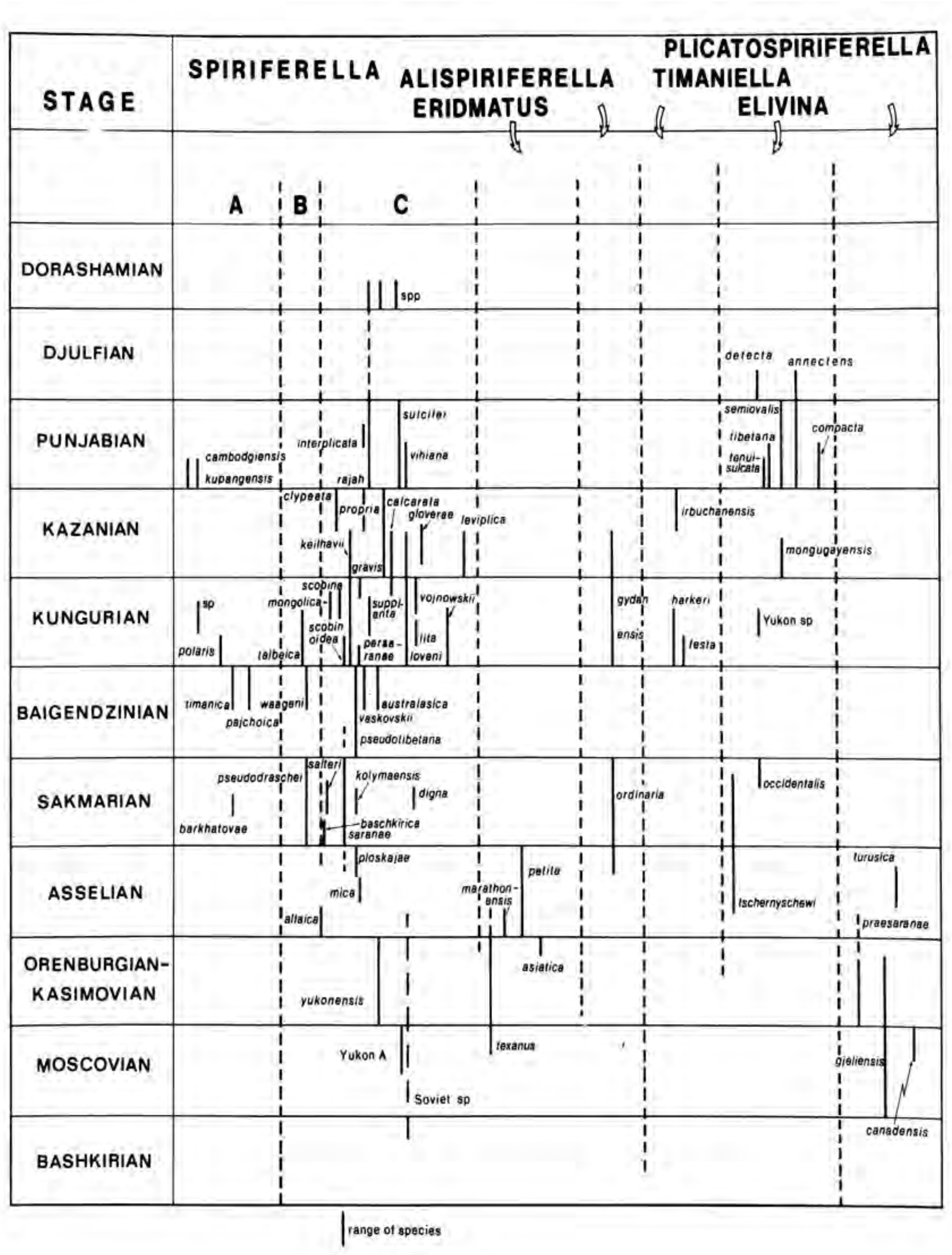

Fig. 261. The evolution of Spiriferellinae (now Spiriferellidae) as envisaged by Waterhouse & Waddington (1982). This tabulation, designed as a replacement for Fig. 22 in that study, was set aside or lost by the editorial staff. But the ranges and identifications are in substantial need of updating and correction.

Subfamily **SPIRIFERELLINAE** Waterhouse, 1968b

Genus ***Spiriferella*** Tschernyschew, 1902

Diagnosis: Medium-sized with moderately to highly convex ventral valve, strongly thickened internally, less convex and thinner dorsal valve, moderately wide hinge and incurved ventral umbo, normally with sulcus, narrowly channelled fold and plicae that are often costate, micro-ornament of cancellate radial and commarginal fila and pustules. Delthyrial apparatus varied, often with neodeltidium, or deltidial plates and/or stegidial plates, or/and large umbonal callosity. Ventral interior heavily thickened, short dental plates and adminicula, dorsal crural plates and well developed ctenophoridium, denticulate hinge.

Type species: *Spirifer saranae* de Verneuil, 1845 from Artinskian of Ural Mountains, OD.

Discussion: Members of Spiriferellinae in the Canadian Arctic and Yukon Territory were extensively reviewed by Waterhouse & Waddington (1982). The species as then interpreted by those authors certainly need updating andrevision. One important aspect relevant to the genus *Spiriferella*: Carter (2006, Fig. 1198, 1a-d) figured non-type Sakmarian material as the type, which in fact comes from the Artinskian.

Spiriferella arctica (Haughton, 1858)

Fig. 262, 263

1858 *Spirifer arctica* Haughton, p. 243, pl. 9, fig. 1.
1916 *Spiriferella saranae* [not Verneuil] – Tschernyschew & Stepanov, p. 50, pl. 9, fig. 1, pl. 11, fig. 1.
1916 *S. keilhavii* [not von Buch] – Tschernyschew & Stepanov, p. 52, pl. 11, fig. 2, 3.
1916 *S. parryana* [not Toula] – Tschernyschew & Stepanov, p. 54, pl. 11, fig. 4, pl. 12, fig. 1, 2, 3.
1955 *Spiriferella* (?) sp. undet. Dunbar, p. 145, pl. 27, fig. 15, 16,
1960 *Spiriferella saranae* ([not Verneuil] – Harker & Thorsteinsson, p. 71, pl. 22, fig. 3, pl. 23, fig. 8 (part, not fig. 22, fig. 1, 2 = *S. angulata* n. sp., fig. 4-8 =? immature *separata*?, pl. 23, fig. 3, 4 = *sulcoconstricta* n. sp.).
1971 *Spiriferella* sp. Bamber & Waterhouse, pl. 17, fig. 9, 11 (part, not fig. 4 = *angulata*).
1982 *Spiriferella pseudotibetana* [not Stepanov] – Waterhouse & Waddington, p. 20, pl. 4, fig. 12-14, 16, 17, pl. 5, fig. 1, text-fig. 15.
1982 *S. arctica* – Waterhouse & Waddington, p. 26, pl. 8, fig. 8.

Diagnosis: Medium size and subequilateral to weakly transverse, with broad hinge, up to six pairs of plicae bearing anterior costae over inner pairs, sulcus moderately defined with low anterior median rib, and often well formed subplicae. Dorsal fold with well formed but not wide median channel. Delthyrium open, without conspicuous neodeltidium or stegidial plates.

Lectotype: Specimen 95:1905/3 M'Clintock collection, National Museum of Ireland, Dublin, figured by Haughton (1858, pl. 9, fig. 1) and Waterhouse & Waddington (1982, pl. 8, fig. 8) and herein as Fig. 262, from Bathurst Island, SD Waterhouse & Waddington (1982, p. 28).

Material: A ventral valve from GSC loc. 57720, examined by Miller (1974), and ventral valve from C-4018, from the Great Bear Cape Formation, Ellesmere Island. A number of specimens from the lower two zones of the Takhandit Formation in Yukon Territory (Waterhouse & Waddington 1982).

Description: The type specimen is preserved as a ventral valve with incurved umbo, wide hinge, high interarea, six pairs of plicae with traces of anterior costae on the two inner plicae pairs, and suggestions of a subplication along the inner side of the plicae pair bordering the sulcus anteriorly. Miller (1974, pl. 16, fig. 1, 2) figured a ventral valve from GSC loc. 57720. A well preserved ventral valve was figured from C-4018 in the Belcher Channel, now Great Bear Cape, Formation of Ellesmere Island by Waterhouse & Waddington (1982). Further material from GSC 26407 of the Belcher Channel Formation, now revised to Great Bear Cape Formation, was figured by Harker & Thorsteinsson

(1960, pl. 22, fig. 1-3, pl. 23, fig. 8). The latter figure shows a typical specimen. That of pl. 22, fig. 1, 2 shows an exceptional deep and well developed sulcus, and certainly deviates from the norm, having a sulcus that is V-shaped rather than subconcave in section. It is recognized as a separate species, *angulata* n. sp. The new species approaches a slightly younger taxon recognized as *sulcoconstricta* n. sp. (see p. 317), and also S. *draschei* (Toula).

Tschernyschew & Stepanov (1916) figured a number of specimens from what is now the Great Bear Cape Formation of Ellesmere Island, and these are regarded as conspecific. They vary a little, but include specimens close in shape to the type specimen, with median sulcal rib and sulcal subplicae. Some are more costate. Lee et al. (2019) treated the *parryana* specimens of Tschernyschew & Stepanov (1916) as belonging to *loveni* Diener, as did Dunbar (1955, pp. 145, 146), but this is rejected, because shape differs considerably. Some similarities lie with *Spiriferella borealica* Kalashnikov (1998, p. 58, pl. 20, fig. 5, pl. 21, fig. 1-5, text-fig. 9) from the Talatin Suite in Russia, of upper Artinskian age. The two taxa are of similar shape, and *borealica* has a similar number of simple plicae, and a median sulcal costa. Subplicae are present rarely, the ventral interarea appears to be a little higher and the fold channel is absent (pl. 20, fig. 5, pl. 21, fig. 4b), suggesting that the species belongs to *Arcullina* (see p. 331).

The geographic range of the species is further expanded by including material from the lower Takhandit Formation of the Yukon Territory, figured by Bamber & Waterhouse (1971) and Waterhouse & Waddington (1982, pl. 4, fig. 12-14, 16, pl. 17, fig. 1). Dorsal valves are included, and like the Harker-Thorsteinsson material, display a distinctive dorsal fold channel.

Fig. 262. *Spiriferella arctica* (Haughton) from Bathurst Island, possibly Great Bear Cape Formation, x1. Plaster duplicate of lectotype, courtesy of the National Museum of Ireland.

The lectotype approaches material from the Ey zone of the middle Jungle Creek Formation of Yukon Territory that was figured as *Spiriferella saranae* by Waterhouse & Waddington (1982, pl. 4, fig. 5-11), but has slightly broader sulcus. It is very close to *S. yukonensis* Waterhouse & Waddington (1982) of the middle Jungle Creek Formation (Asselian, Sakmarian), but the sulcus is slightly shallower and wider anteriorly, with weaker sulcal subplicae.

The taxon was reported from Novaya Zemlya by Licharew & Einor (1939, p. 135, pl. 22, fig. 4, 5), and the figures suggest specimens that are close, but a little more transverse.

There is some resemblance to a form named *Spirifer* (*Spiriferella*) *keilhavii pseudosaranae* by Einor in Licharew & Einor (1939, p. 218, pl. 24, fig. 6-9) and *S. saranae wimani* [not Grabau] of Licharew & Einor (1939, pl. 22, fig. 7, pl. 23, fig. 2-5). These shells are found in Lower Permian beds of Novaya Zemlya. External moulds and shells assigned to Einor's form by Waterhouse & Waddington (1982) show limited approach, but internal moulds have much wider sulcus. These specimens came from the lower middle Jungle Creek Formation.

Wiman (1914, p. 38, pl. 3, fig. 2-26) figured a number of specimens from Spitsbergen as *Spiriferina draschei* (Toula). Those of fig. 3-8 are small, from the Corakalk and may be set aside. One or two have a number of plicae (fig. 9), suggestive of possible *Undulatina keilhavii* (see p. 335). Others show a moderately well formed sulcus and somewhat costate plicae, approaching *arctica*, and ventral views indicate a well developed neodeltidium, occupying a third to more than half of the delthyrium. Possibly they belong to *Spiriferella arctica* (Haughton), but they have a wider sulcus, and could prove to be *separata* (p. 310).

Source of the species: The source was given by Haughton (1858) as Cape Lady Franklin, Bathurst Island, but according to W. W. Nassichuk (in Waterhouse & Waddington 1982), no Permian rock has been found there over more recent years. Dr Nassichuk considered the formation most likely to have been the source to have been Belcher Channel Formation, which would now be Great Bear Cape Formation. This is consistent with the age of *Spiriferella arcticus*, and points in the context of overall succession and faunas to an upper Cisuralian age.

A second specimen mentioned but not figured by Haughton (1858) came from Hillock Point, Melville Island, where Trold Fiord Formation is exposed. This specimen has not been reassessed.

Fig. 263. *Spiriferella arctica* (Haughton), ventral valve GSC 30771 from C-4018, Great Bear Cape Formation, Ellesmere Island, x1. (Waterhouse & Waddington 1982).

Spiriferella cf. ***vojnowskii*** Ifanova, 1972

Fig. 264

cf. 1972 *Spiriferella vojnowskii* Ifanova, p. 139, pl. 12, fig. 6, 7, pl. 13, fig. 1, 2.
1982 *S*. cf. *vojnowskii* – Waterhouse & Waddington, p. 26, pl. 7, fig. 12-14.

Diagnosis: Medium size, subrounded weakly oval shells with long posterior walls generally concave in outline and diverging at some 120º, three or less commonly four prominent plicae pairs on each valve and finer lateral plicae in some specimens, plicae costae or smooth, sulcus well formed but neither unusually deep nor wide, may have median rib, other costae developed as a rule, fold well formed, with narrow median groove and lateral ribs. Pustules well developed, but variable. Dental plates well formed, muscle field with bordering ridges.

Holotype: Specimen figured by Ifanova (1972, pl. 12, fig. 6a, b, v) from Kungurian beds, west and southwest Petchora Basin, OD.

Description, Resemblances: A few specimens were compared with *vojnowskii* in Waterhouse & Waddington (1982). They came from C-6174 in the Kandik River in the Yukon Territory, from beds belonging possibly to the upper Jungle Creek Formation, or conceivably lower Takhandit Formation. The specimens have a median sulcal costa with low numerous ribs over the anterior plicae. Posterior umbonal walls are concave in outline. A short cover plate is developed (Waterhouse & Waddington 1982, pl. 5, fig. 4, 6).

Spiriferella vojnowskii Ifanova (1972) agrees in shape, plication, and dorsal fold with the Canadian material. Three or four plicae are prominent on the ventral valve, and the one figured dorsal valve has three wider plicae and three lateral costae. One specimen is more costate than others. Pustules are moderately well developed. Only a few specimens were figured by Ifanova (1972), and the Canadian material shows more variation, but agrees in essential detail, although the posterior walls are less divergent. The species is close to *arctica*.

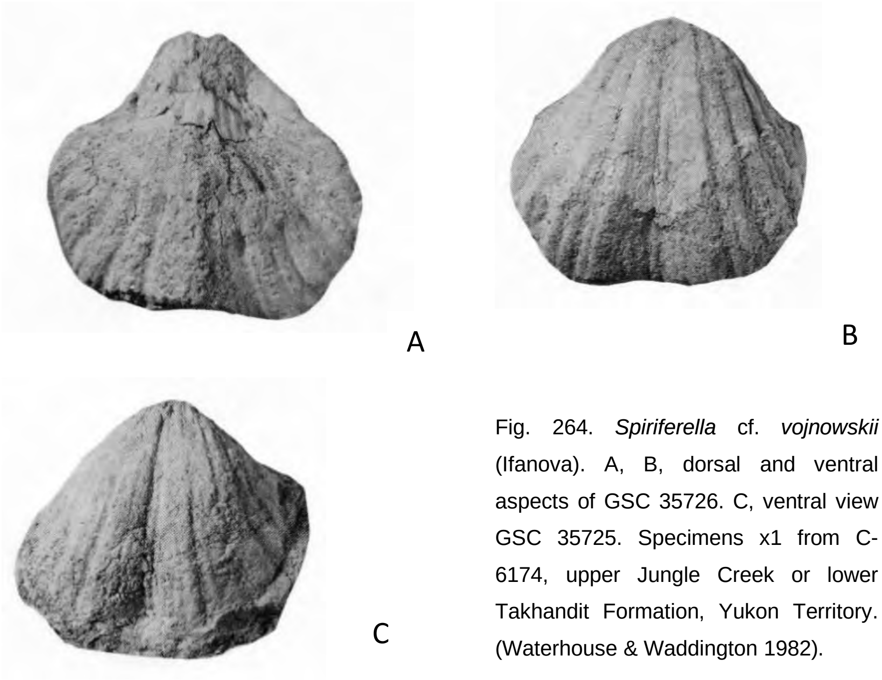

Fig. 264. *Spiriferella* cf. *vojnowskii* (Ifanova). A, B, dorsal and ventral aspects of GSC 35726. C, ventral view GSC 35725. Specimens x1 from C-6174, upper Jungle Creek or lower Takhandit Formation, Yukon Territory. (Waterhouse & Waddington 1982).

Spiriferella saranaeformis Fredericks, 1916

Fig. 265

1916 *Spiriferella rajah saraneformis* forma *vera* Fredericks, p. 87, pl. 5, fig, 3, 5, 9.
1939 *Spirifer* (*Spiriferella*) *rajah saranaeformis* – Licharew & Einor, p. 149, pl. 25, fig. 1, 4.
1978 *S. rajah* [not Salter] – Licharew & Kotlyar, pl. 18, fig. 6a, b.

Diagnosis: Large elongate, high interarea, moderately wide dorsal channel, plicae few and anteriorly costate.

Lectotype: Specimen figured by Fredericks (1916, pl. 5, fig. 3a-c) from near Vladivostok, here designated.

Material: Two conjoined specimens from C-6136, Cache Creek, Yukon Territory. Formation uncertain.

Dimensions in mm:

GSC	Width	Length	Height (both valves, squashed)
30803	59	67	26
	52	61	25

Description: Specimens are large and elongate, but the dimensions are indicative only, with some breakage and crushing. The ventral interarea is high and moderately concave under the beak. The sulcus is well formed and subevenly concave, and the fold broad anteriorly with well defined median channel. There are five pairs of ventral plicae, the outer two slender and simple, the inner three becoming costate anteriorly, and the sulcus developed as many as fourteen ribs anteriorly, with a pair along the mid-line. The dorsal fold is narrow posteriorly, flares anteriorly, and may develop a wide channel towards the anterior margin.

Resemblances: These two specimens are close in many respects to *saranaeformis* Fredericks in their large size, elongate outline, high ventral interarea, and costate plicae. The sulcus is also close, but the fold as far as it is preserved on the one figured dorsal valve has a narrower channel. Comparable material was figured in Licharew &

Einor (1939), and in one specimen the dorsal channel is better developed, but narrow, and the other specimen shows a wider channel close to that of present material. Their reference included forma *lata* of Fredericks (1916, pl. 5, fig. 6), a broken and wide specimen, which appears to be like *S. grandis* Kotlyar in Licharew & Kotlyar (1978, pl. 18, fig. 7, 8). The specimen figured as *rajah* [not Salter] in Licharew & Kotlyar (1978) shows a moderately well developed dorsal channel. The type material came from the lower Barabash Suite, regarded as Kazanian, but apparently is found within the fusuline range of *Yabeina*. The age for the Canadian material is not known.

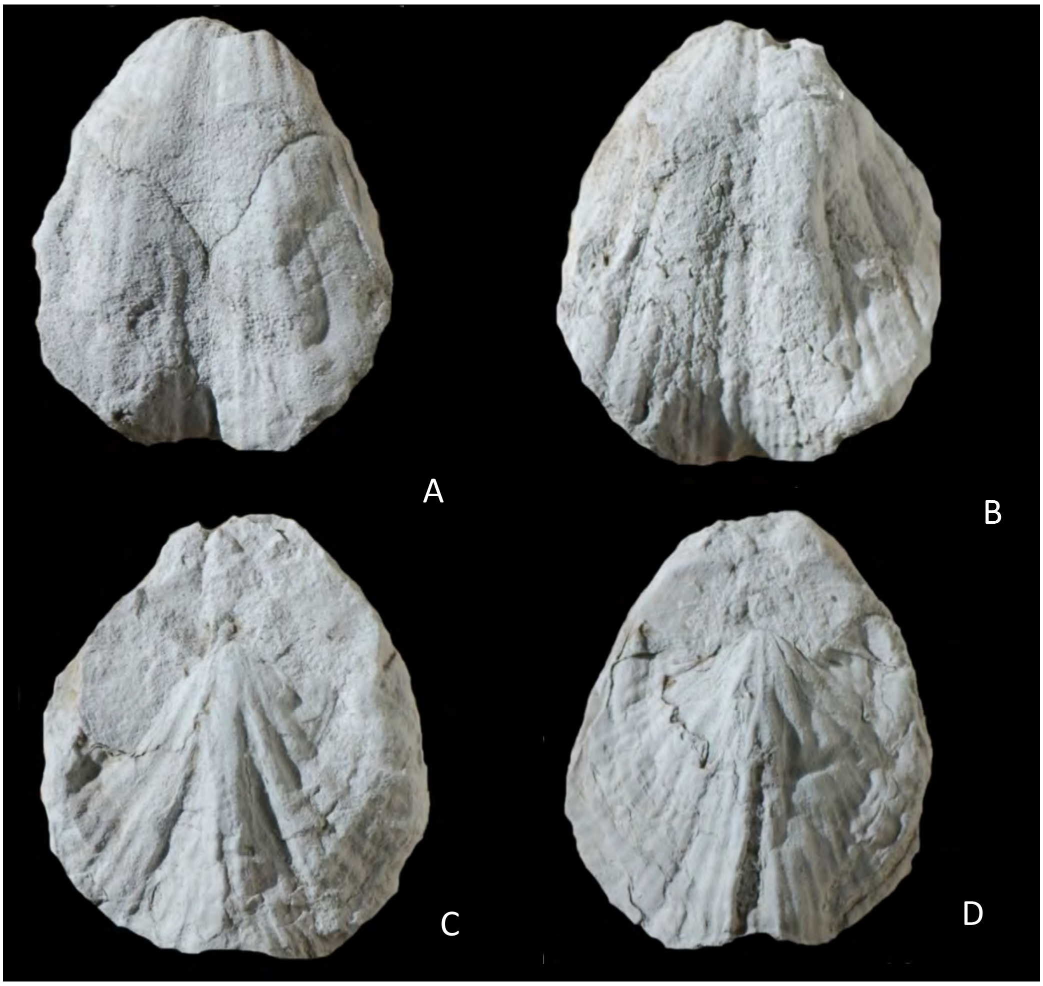

Fig. 265. *Spiriferella saranaeformis* Fredericks. A, D, ventral and dorsal aspects of GSC 141164. B, C, ventral and dorsal aspects of GSC 30403. From C-6136, Cache Creek, Yukon Territory, x1.

Spiriferella separata n. sp.

Fig. 266– 269

cf. 1914 *Spiriferina draschei* [not Toula] – Wiman, p. 38, pl. 3, fig. 10-26 (part, not fig. 2, 9 = *keilhavii*?, 3-8 = n. det**.)**
1960 *Spiriferella saranae* [not de Verneuil] – Harker & Thorsteinsson, p. 71, pl. 22, fig. 4-8, (not pl. 22, fig. 1, 2 = *angulata*, pl. 22, fig. 3 = *arctica*, pl. 23, fig. 3, 4 = *sulcoconstricta,* pl. 23, fig. 8 = *arctica*).
aff. 1960 *S. keilhavii* [not von Buch] – Harker &Thorsteinsson, p. 72, pl. 22, fig. 9-11 (part, not pl. 23, fig. 1, 2 = *sulcoconstricta*).
1968 *S. keilhavii* [not von Buch] – Nelson & Johnson, p. 736, pl. 96, fig. 7, 8, 12, text-fig. 3e, 8a, 9, 13b.
?1968 *S. rajah* [not Salter] subsp. A – Nelson & Johnson, p. 731, pl. 94, fig. 7-11 (part, not pl. 94, fig. 1-3 = *sulcoconstricta*, fig. 4-6 = *draschei*, fig. 12 = *gydanensis*, fig. 14, 15? = *angulata,* pl. 96, fig. 10 = n. det.).
?1971 *S.* aff *keilhavii* – Bamber & Waterhouse, p. 165, pl. 20, fig. 7.

?1978 *S. loveni* [not Diener] – Waterhouse et al., pl. 2, fig. 2.
1982 *S*. ?*loveni* [not Diener] – Waterhouse & Waddington, p. 22, pl. 5, fig. 3-6, 9-13, 15-17 (part, not fig. 2, 7, 8, 14, text-fig. 16b, d, f, 17, 18 = *Canalisella* spp. see pp. 324, 328, pl. 6, fig. 1, 2 = *Undulatina* sp.

Derivation: separio – different, Lat.

Diagnosis: Three or four plicae pairs prominent, pustules well developed, small neodeltidium, sulcus narrow but well defined, costae well developed over plicae, sulcus and fold.

Holotype: Specimen GSC 30786 from GSC loc. 26406, Assistance Formation (Roadian), Devon Island, figured by Waterhouse & Waddington (1982, pl. 5, fig. 15-17) and herein as Fig. 266B-D, here designated.

Material: Well over twenty specimens were recorded in Waterhouse & Waddington (1982, p. 20) from the middle biozone of the Takhandit Formation in Yukon Territory, of Roadian age, especially from GSC loc. 52744, and a broken ventral valve from JBW 631, both from mid-Takhandit Formation. More than ten specimens came from the Assistance Formation at GSC loc. 26406 of Devon Island, a few specimens from C-4072, Van Hauen Formation, and two ventral valves from GSC loc. 58973, Assistance Formation, Ellesmere Island. Rare specimens from C-6639 in unnamed sandstone in the Richardson Mountains of Yukon Territory.

Description: Medium to large-sized subequilateral shells with three or four prominent inner plicae, usually costate over much of length, with fine subplicae or costae laterally, totalling six or seven pairs in all. Posterior umbonal walls diverge at close to 90°, straight, weakly convex or rarely slightly concave in outline. Pustules well developed. Some specimens have a median sulcal costa, and others have two median ridges. The fold has a shallow distinct median groove. A small deltidial or neodeltidial plate lies over the posterior delthyrium, which is not a pseudodeltidium because it is often detached from single valves, and reveals a median groove in some specimens. Dental plates high, adminicula short and passing into high ridges along the border of the ventral muscle field. The specimens were described in Waterhouse & Waddington (1982), as in the synonymy. Different specimens from the older beds in the basal Takhandit Formation include specimens with fewer costae (GSC loc. 57242, 57259, JBW 519) as figured by Waterhouse & Waddington (1982, pl. 4, fig. 12-16, 17) and Bamber & Waterhouse (1971, pl. 17, fig. 9, 11), and are placed in *arctica* Haughton.

Resemblances: One ventral valve figured by Harker & Thorsteinsson (1960, pl. 22, fig. 9-11) from the Assistance Formation on Devon Island at GSC loc. 26406 has posterior walls weakly concave in outline, a median sulcal costa, numerous costae, and well formed delthyrial plate, sited just below the dental tracks. Although close in outline to that of *vojnowskii,* the Assistance specimen has broad inner plicae, and more costae and wider sulcus, and has a well-developed neodeltidium. It is interpreted as likely to belong to *separata,* and is close to the specimen of Fig. 266B, although a little more strongly costate. The specimens shown in Harker (1960, pl. 22, fig. 4-8) are small and paucicostate. From their size and shape, they are judged to be immature *separata*.

A specimen figured by Brabb & Grant (1971, p. 17, pl. 1, fig. 13-17) from the lower sandstone unit of the type Takhandit Formation in Alaska was included in synonymy of *pseudotibetana* by Waterhouse & Waddington (1982). It is small, and so potentially could have developed into one of several different species, certainly including *separata*. One feature is the presence of three costae in the anterior sulcus. Specimens figured as *keilhavii* by Nelson & Johnson (1968) have a wider sulcus than in *keilhavii*, and have a neodeltidium. There are up to seven pairs of plicae with differentiated costae. They come from the Takhandit Formation, possibly middle Takhandit, and material was also figured in Bamber & Waterhouse (1971) from the *Dyoros modestus* Zone in this formation.

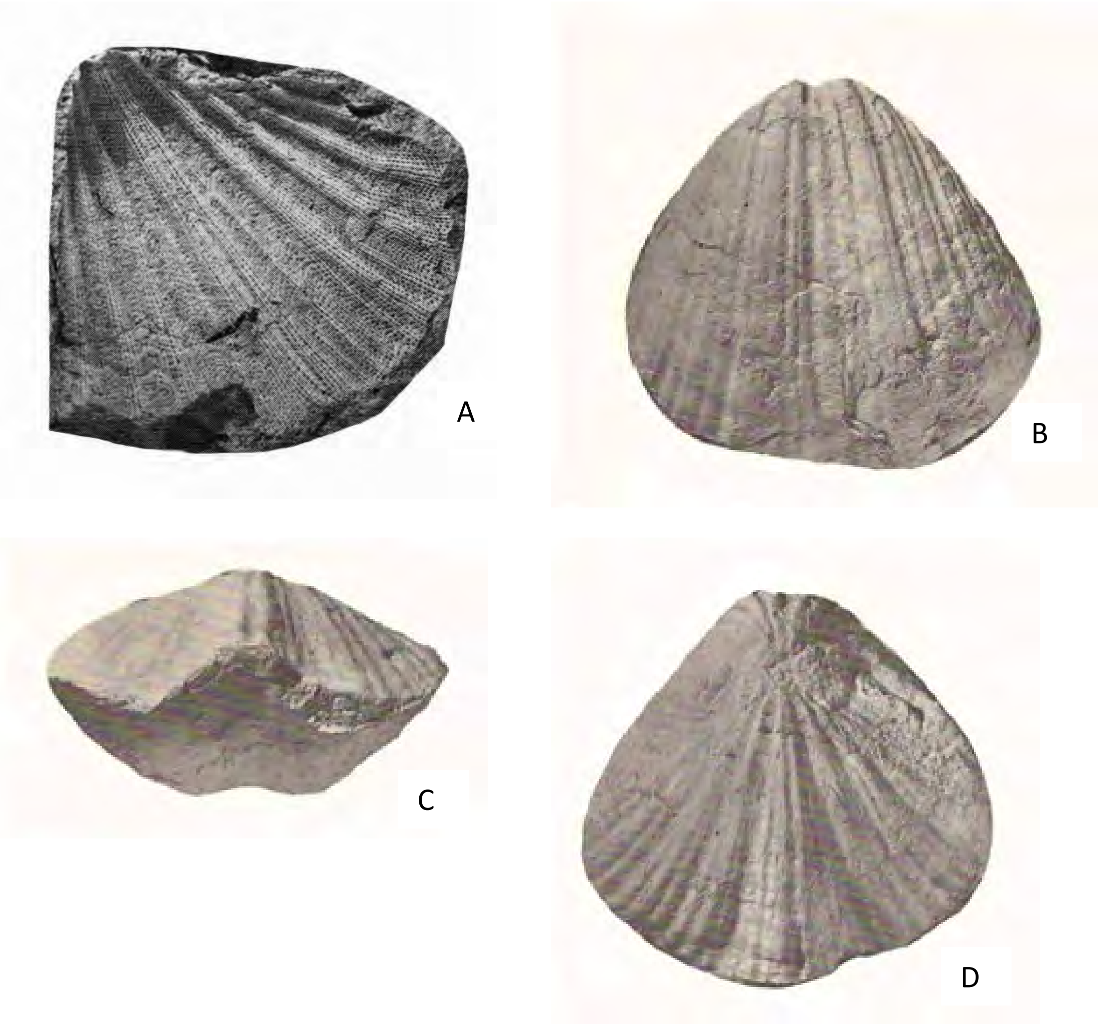

Fig. 266. *Spiriferella separata* n. sp. A, well developed ventral micro-ornament on external mould, GSC 35706 x2 from GSC loc. 52744, mid-Takhandit Formation, Tatonduk River. B-D, ventral, anterior and dorsal aspects of holotype, GSC 30786 x1 from C-4024, Assistance Formation, Ellesmere Island. (Waterhouse & Waddington 1982).

Fig. 267. *Spiriferella separata* n. sp., ventral valve GSC 140933, x1.5, fromGSC 58973, Assistance Formation, Ellesmere Island.

These Canadian specimens are close to two Russian species. *Spiriferella pseudotibetana* Stepanov (1937a, p. 34, pl. 1, fig. 7, pl. 3, fig. 1-3, pl. 10, fig. 1), initially described from the Krasnoufimian of Kolwa Peninsula, displays three well formed plicae pairs and few lateral costae, and rather strong costae, two or three on inner plicae and in some specimens, including a broad prominent median costa. Other shells from the same beds were ascribed to different varieties of *saranae* by Stepanov (1937a, pl. 2), involving *mongolica* (fig. 5b) and *drasche*i (fig. 6b, 10b). Overall shape is like that of the Canadian material, and some specimens have only plicae, without costae. The dorsal fold points to a position with *Arcullina*, being rounded, unlike the channelled fold of the Canadian specimens, and is narrower and slightly higher than in the Canadian specimens. None of the Canadian specimens show such strong costae, not that they are featured in all of the Kolwa specimens.

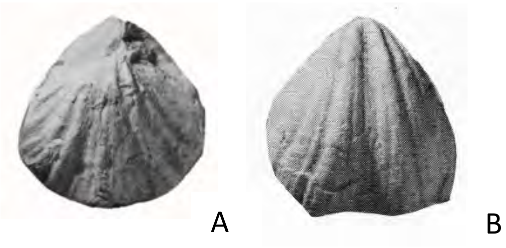

Fig. 268. *Spiriferella separata* n. sp. A, B, dorsal and ventral views of GSC 35704 x 1 from GSC loc. 57244, Takhandit Formation, Yukon Territory. (Waterhouse & Waddington 1982).

Another Russian species was named *Spiriferella vojnowskii* by Ifanova (1972), from the Kungurian beds of Petchora Basin, and this largely agrees in shape, plication, and dorsal fold with the Canadian material, although it tends to be broader. Three or four plicae are prominent on the ventral valve, and the one figured dorsal valve has three wider inner plicae and three lateral costae. One specimen is more costate, another less so. Pustules are only moderately well developed. Only a few specimens were figured by Ifanova (1972), and the Canadian material assigned to the present species consistently has more narrowly diverging and higher ventral umbonal walls, as a rule not concave in outline, and is less transverse. As a rule, costae are better developed. Some detail is not available for the Russian taxon, concerning the delthyrial cover and the ventral interior. The differences appear to have been relatively consistent, and suggest that *separata* could have evolved from *vojnowskii*, itself close to *arctica*.

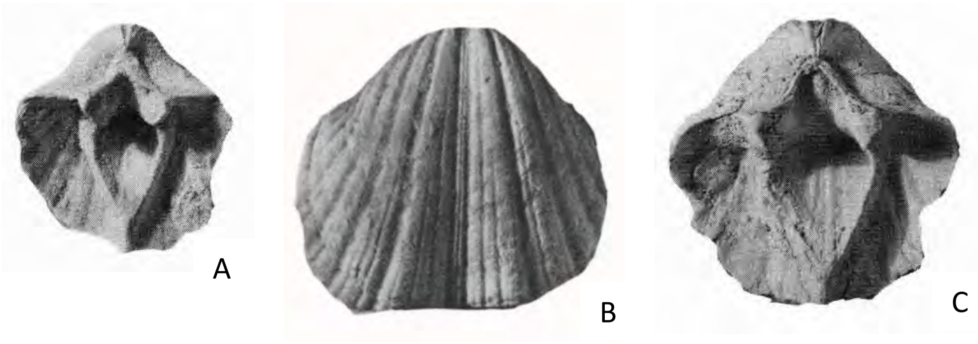

Fig. 269. *Spiriferella separata* n. sp. A, ventral valve interior GSC 30791. B, C, ventral exterior and interior GSC 30789. Specimens x1 from GSC loc. 26406, Assistance Formation, Devon Island. (Waterhouse & Waddington 1982).

Some specimens figured as *keilhavii* by Wiman (1914, pl. 3, fig. 3, 4, 10, 11, 18, 19, 24, 26, and possibly ventral valves showing the interior (fig. 1212-17, 22-23, 25) might belong to *separata*, agreeing in shape and sulcus but mostly with fewer costae. They come from the Spiriferenkalk and show well developed neodeltidium.

Spiriferella protodraschei Lee & Shi (2019, p. 30, Fig. 5A, B, 9A, 17, 18A-G) from the Kapp Starotsin Formation of Spitsbergen has a shallow sulcus of moderate width and dorsal fold with unusually narrow crest, described as angular, yet with a shallow and narrow median channel. Spiralia are ventrally directed. It does not, in terms of morphology or age, appeal as a precursor to the species *draschei*, but shows some approach to the new species *separata,* without being so firmly costate or having such a well defined dorsal fold channel, well developed pustules, conventional spiralia and wide anterior fold.

A separate clade of species:

Spiriferella draschei (Toula, 1875b)

Fig.270A, B, 271A

1875b*Spirifer draschei* Toula, p. 239, pl. 7, fig. 4a-c.
?1878 *Spirifera* cf. *grimesi* (not Hall) – Etheridge, p. 628, pl. 25, fig. 5.
?1878 *Spirifera ovalis* (not Phillips) – Etheridge, p. 629.
?1878 *Spirifera* Etheridge, p. 629.
1961 *Spiriferella saranae* [not de Verneuil] – Nelson, pl. 4, fig. 1a-c.
1962 *S. draschei* – Dunbar, pl. 2, fig. 9-11 (part, not fig. 12-14 = *angulata*).
1968 *S. rajah* [not Salter] subsp. A – Nelson & Johnson, p. 731, pl. 94, fig. 4-6 (part, see pp. 310, 317). Pl. 94, fig. 5 is not explained in the caption but appears to be associated with fig. 4 and 6].
1972 *S. draschei* – Ifanova, p. 136, pl. 11, fig. 4-7.
1982 *S. keilhavii* [not von Buch] – Waterhouse & Waddington, pp. 28, 27, and 26 (in that order, the pages having disarranged by the printer), pl. 4, fig. 15?, pl. 6, fig. 8, 9 (part, not pl. 6, fig. 3, 4 = *Undulatina*? sp.; not pl. 6, fig. 5-7, 10, 11, ?12, ?13, 14. Text-fig. 16 e, g, ?h, i = *sulcoconstricta*).
2019 *Spiriferella draschei* – Lee et al., p. 25, Fig. 4I, J, 5C, D (part, not 9A, 14-16 = *sulcoconstricta*).

Diagnosis: Medium to large commonly elongate shells with incurved ventral umbo and steep lateral flanks, bearing weakly costate or simple plicae. Sulcus wide with angle close to 30ºand even up to 40º, with up to sixteen sulcal costae. Fold narrow and high posteriorly, flaring anteriorly, with distinct shallow median groove, numerous small pustules in types. Dental plates high, adminicula short, apical callus well developed.

Type species: Specimen figured by Toula (1875, pl. 7, fig. 4a-c) from Kapp Starotsin Formation of Spitsbergen, SD Gobbett 1964, p. 154.

Material: Specimens were described in Waterhouse & Waddington (1982) from the Trold Fiord and Degerböls Formations.

Discussion: The species *Spiriferella draschei*((Toula) has been widely reported from present high latitudes of the northern hemisphere. The nature of the species was partly rectified by Lee et al. (2019). But problems remain. Lee et al. (2019) stated they had illustrated specimens that fall into two suites, but provided no specific information on relevant stratigraphy or the particular differences. Specimens from Arctic Canada also form two distinctive suites. One suite has a broad sulcus and many sulcal costae, like the type material described by Toula (1875b), and comes from the Takhandit Formation (Nelson 1961) and Trold Fiord Formation and approximate equivalents. A second group possesses a sulcus narrower by 10º to 15º or more, and has fewer sulcal costae. Unlike the Spitsbergen material, the pustules are moderately strong in both suites. The assignment of Canadian specimens to *draschei* by Lee et al. (2019) is therefore considerably revised, and modified to the extent that only a few of the specimens, which come from the Trold Fiord and Degerböls Formations, are assigned to the species, and even these differ in what is regarded as minor ways from the types. Of course, it may well be argued that the width of the sulcus varied considerably within a species, or at least within this species. But it is considered that this variation is best assessed by discriminating two forms, or two extremes, and then examining if there be any consistent differences in age, or local age, and stratigraphic preference. The preliminary discrimination suggests that the narrow sulcus was most prevalent especially in the older sediments ie. lower middle Takhandit Formation of the Yukon Territory and Assistance Formation of the Sverdrup Basin. No other species of *Spiriferella* or found amongst allied genera is known to show such wide variation in the nature and width of the sulcus.

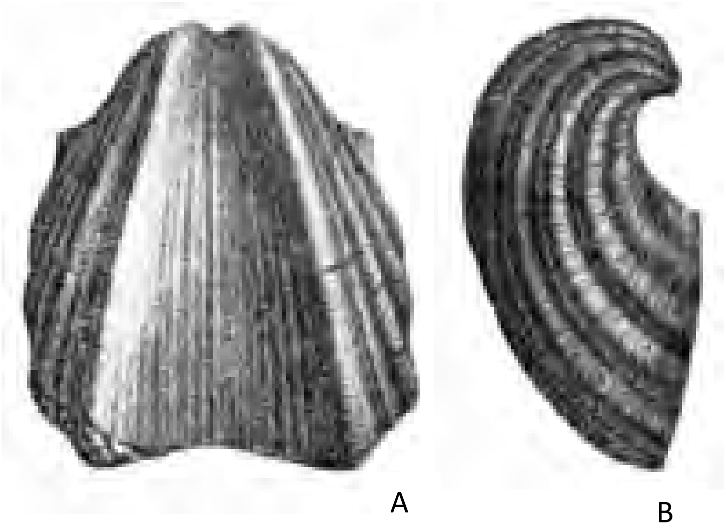

Fig. 270. *Spiriferella draschei* (Toula), original figures for holotype from Spitsbergen, x1. (Toula 1875b).

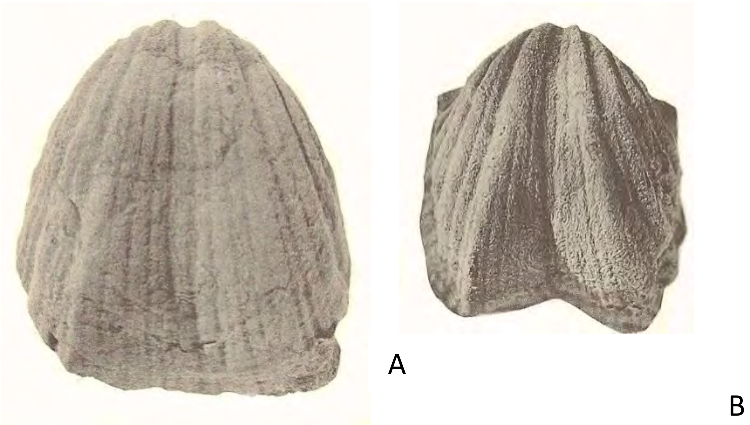

Fig. 271. *Spiriferella draschei* (Toula). A, ventral valve UA 520, from Yukon Territory, x1. B, *S. angulatus* n. sp., ventral valve UC F1134, but approaching *draschei*, from “high Takhandit Formation equivalents at Peel River”, Yukon Territory, x1.(Nelson & Johnson 1968).

A particularly interesting species was named *protodraschei* by Lee & Shi (2019, p. 30) from the Vøringen Member of Spitsbergen, which has a well developed delthyrial cover plate or neodeltidium, a few strong broad ventral plicae with narrow trench-like interspaces, narrow dorsal channel, and numerous small pustules, as well as postero-ventrally oriented spiralia. Lee & Shi (2019, p. 33) speculated that the species exhibited primitive characteristics (as plesiomorphs) of *draschei*, which may be found at the same stratigraphic level. The sulcus is not particularly wide, and if there was any relationship to the *draschei* lineage, the species was remarkably deviant, with sulcus far less developed than in specimens now discriminated as *sulcoconstricta, pseudodraschei*, or *oregonia* (see below), which are much closer to *draschei*, but received no consideration. They also claimed the spiralia were unique in their orientation, but perhaps that is because they only considered the range of species from Spitsbergen.

Spiriferella angulata n. sp.

Fig. 271B, 272

1937b *Spiriferella draschei* [not Toula] – Stepanov, pl. 8, fig. 9, 10.
1960 *Spiriferella saranae* [not Verneuil] – Harker & Thorsteinsson, p. 71, pl. 22, fig. 1, 2 (part, not fig. 3 = *arctica*, fig. 4-8 = *separata,* pl. 23, fig. 3, 4 = *sulcoconstricta,* fig. 8 = *arctica*).
1962 *S. draschei* [not Toula] – Dunbar, pl. 2, fig. 12-14 (part, not fig. 9-11 = *drasche*i).
cf. 1968 *S.rajah* subsp. A [not Salter]– Nelson & Johnson, pl. 94, fig. 14, 15. (See also synonymies on pp. 310, 317, 321).
1971 *Spiriferella* sp. Bamber & Waterhouse, p. 168, pl. 17, fig. 4.
cf. 1982 *S. keilhavii* [not von Buch] – Waterhouse & Waddington, pl. 4, fig. 15.
2008 *S. keilhavii* [not von Buch] – Angiolini & Long, p. 93, Fig. 9C-G, ?H (part, not fig. 9A, B = *keilhavii*).
?2008 *S. loveni* [not Diener] – Angiolini & Long, p. 96, Fig. 9I, J (part, not Fig. 10A = *keilhavii*).
2008 *Eridmatus* sp. – Angiolini & Long, p. 96, Fig. 10B-D, ?F. (Fig. 10E indet. or exceptional *angulata*).

Derivation: angulatus – with corner or angle, Lat.

Diagnosis: Medium size, subelongate with five to six pairs of plicae, moderately costate, well developed neodeltidium. Sulcus well defined with angular floor. Fold with distinct but narrow median channel.

Holotype: GSC 13762 from GSC loc. 26407, Great Bear Cape Formation, Devon Island, figured by Harker & Thorsteinsson (1960, pl. 22, fig. 1, 2), here designated.

Description: This species is moderately large in size and is found in late Artinskian faunas of the Arctic, in Canada, northeast Greenland and Spitsbergen. The ventral umbo is incurved, and the ventral valve highly arched, and the sulcus is well developed, with angle close to 25°, and a somewhat angular floor profile. The fold broadens anteriorly, with distinct but narrow median channel. The ventral interarea is concave and moderately high, with well developed neodeltidium. Costae are well developed over especially the anterior shell of both valves, and a number of specimens display a median sulcal costa. It has been necessary to construct a description from various described collections, which all share the distinctive number of plicae, highly incurved profile, angular sulcus, and fold with narrow channel, becoming moderately wide anteriorly, with moderately wide median channel. Most specimens come from the upper Artinskian or lower Kungurian faunas, but the source of some Yukon material is insecure.

Resemblances: The ventral valve figured from Grinnell Peninsula of Devon Island by Harker & Thorsteinsson (1960) is inflated with well defined sulcus that is V-shaped in profile. It came from what is now called Great Bear Cape Formation. It shares the sulcal profile with a specimen described from C-47947 as figured by Waterhouse & Waddington (1982, pl. 4, fig. 15), but its sulcus is wider. It is not known to me whether C-47947 comes from the Great Bear Cape Formation or the Degerböls Formation. A specimen figured by Nelson & Johnson (1968) is also close: it came from somewhere in the Takhandit Formation of Yukon Territory. The most convincing similarities are shown by specimens figured from the Mallemuk Mountain Group of northeast Greenland by Dunbar (1962), and especially from the Vøringen Member of Spitsbergen by Angiolini & Long (2008). The sulcus is narrower than that of *draschei* Toula, and displays characteristic angular floor as a rule and fewer costae. The species has a well developed medium-sized neodeltidium, and wider more angular sulcus than in *keilhavii*. Species belonging to *Eridmatus* mentioned by Angiolini & Long (2008) seem to be more elongate with extended and subparallel lateral margins, but lateral margins are lost, and they may well belong to the species.

Spiriferella protodraschei Lee & Shi in Lee et al. (2019, p. 30, Fig. 18A-G), from the Vøringen Member in Spitsbergen has a narrower sulcus and high narrow-crested fold with slender median channel, and tends to be transverse.

Fig. 272. *Spiriferella angulata* n. sp. A, C, ventral valve GSC 13762, holotype, from loc. 26407, Great Bear Cape Formation, Devon Island, x1. B, ventral valve GSC 26998 from basal Takhandit Formation, Yukon Territory, x1. (Harker & Thorsteinsson 1960, Bamber & Waterhouse 1971).

Spiriferella sulcoconstricta n. sp.

Fig. 273 - 275

?1960 *S. saranae* – Harker & Thorsteinsson, p. 71, pl. 23, fig. 3, 4 (part, not pl. 22, fig. 1, 2 = *angulata*, fig. 3 = *arctica*, fig. 4-8 = *separata*).
1960 *S. keilhavii* [not von Buch] – Harker & Thorsteinsson, p. 72, pl. 23, fig. 1, 2 (part, not pl. 22, fig. 9-11 =*separata*).
1968 *S. rajah* [not Salter] subsp. A – Nelson & Johnson, p. 731, pl. 94, fig. 1-3, 13 (part, not pl. 94, fig. 4-6 = *draschei*, fig. 7-11 = *separata*, fig. 12 = *gydanensis*, fig. 14, 15 = *angulata*).Pl. 96, fig. 10 = n. det.
1968 *S. rajah* [not Salter] subsp. B – Nelson & Johnson, p. 736, pl. 95, fig. 1-3; pl. 96, fig. 1-3, 11. Text-fig. 4d, 8b, 13c.
1971 *Spiriferella* sp. Bamber & Waterhouse, p. 174, pl. 19, fig. 12.
1978 *S. loveni* [not Diener] – Waterhouse et al., pl. 2, fig. 3 (part not fig. 4 = *Undulatina* sp., fig. 5, pl. 1, fig. 8 =*Canalisella*; not pl. 2, fig. 2 = *separata*).
1982 *S. keilhavii* – Waterhouse & Waddington, pp. 28, 27, and 26 (in that order, the pages having disarranged by the printer), pl. 6, fig. 5-7, 10-14 (part, not pl. 4, fig. 15 = possible *angulata*, pl. 6, fig. 8, 9 = *draschei*). Text-fig. 16e, g, (part not h = *draschei*), text-fig. 19 = *arctica*).

Derivation: sulcus – furrow, constrictus – hemmed in, Lat.

Diagnosis: Elongate shells with incurved ventral umbo and sulcus well defined and of moderate width, sulcal angle close to 15° to 20° as a rule, variably with median costa or emphasized groove, low to moderate number of sulcal costae. Lateral slopes high, not steep, with four to five pairs of plicae which are costate for much of their length. Fold moderately defined, with well formed but narrow median groove, five to six pairs of plicae laterally. Arched cover plate over delthyrium.

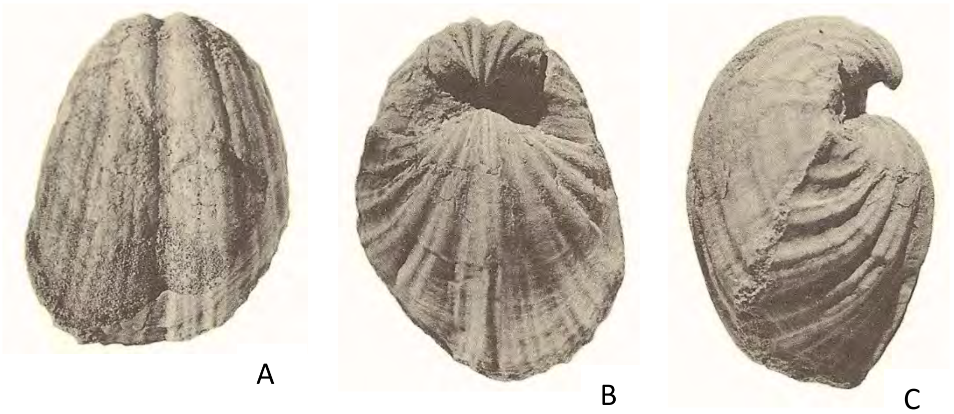

Fig. 273. *Spiriferella sulcoconstricta* n. sp. A, B, dorsal and lateral aspects of UA 521. C, ventral valve UC F1134. Specimens from Yukon Territory, x1. (Nelson & Johnson 1968).

Holotype: Specimen GSC 35653 from C-4081, Assistance Formation (Roadian), Ellesmere Island, figured in Waterhouse & Waddington (1982, pl. 6, fig. 5-7) and herein as Fig. 275, here designated.

Material: More than thirty specimens were available as summarized by Waterhouse & Waddington (1982, p. 27), referring to specimens from C-4016 and C-4081 of the Assistance Formation on Ellesmere Island, including conjoined specimens and ventral and dorsal valves. Some ventral valves come from the *Neochonetes culcita* Zone of the Takhandit Formation at Tatonduk River, Yukon Territory, and more were described as *Spiriferella rajah* from the upper Takhandit Formation at West Mount Burgess (sp. B) and the same formation exposed by Tatonduk River (sp. A), by Nelson & Johnson (1968). The species was more common in the Roadian than Wordian.

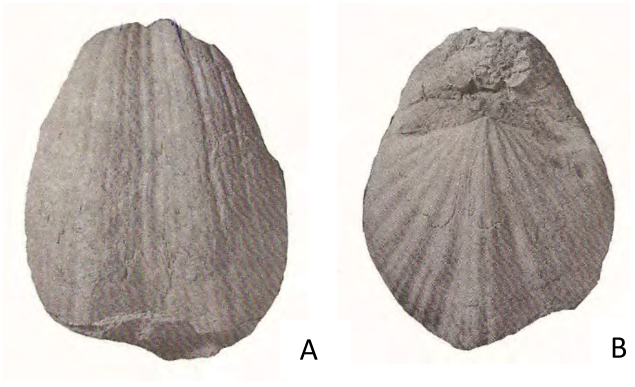

Fig. 274. *Spiriferella sulcoconstricta* n. sp. A, B, ventral and dorsal aspects of GSC 35645 x1 from C-4016, Assistance Formation, Ellesmere Island. (Waterhouse & Waddington 1982).

Description, Resemblances: The species is described from Canada under several headings by Harker & Thorsteinsson (1960), Nelson & Johnson (1968) and Waterhouse & Waddington (1982) as summarized in the synonymy. Although some detail is not known, it has been deemed important for local stratigraphy and biostratigraphy and paleobiology to discriminate between the Trold Fiord specimens which are like the Toula species called *draschei,* and the present suite, mostly from the Assistance Formation and middle Takhandit Formation, and so with differing at least local acmes. Unlike *draschei*, the Assistance specimens have a much narrower sulcus, with angle reduced by 10ºto 20º, and fewer sulcal costae. The lateral flanks are more gently sloping, longer and more subparallel. Even the very large specimen described by Nelson & Johnson (1968, pl. 95, fig. 1) has only eight costae in the sulcus. Nelson & Johnson (1968) provided thin sections, and sketches of the ventral interior, and illustrations of the micro-ornament in their study. *Spiriferella angulata* n. sp. from the Great Bear Cape Formation and allied faunas of Spitsbergen and Greenland is moderately close, and may have been ancestral. It has a somewhat similar sulcus that is more V-shaped in profile, and less parallel and shorter lateral margins.

There is some similarity to the sulcus in ventral valves figured as *Spirifer (Spiriferella) keilhavii sulcifer* Shumard, 1858, 1859 by Licharew & Einor (1939, p. 143, pl. 24, fig. 4, 5) from the Lower Permian of Novaya Zemlya, but little is known of these particular specimens. The species *sulcifera* Shumard is of Wordian age and was retained in *Spiriferella* by Cooper & Grant (1976a). *S. saranaeformis* Fredericks, 1916 is much larger with high ventral interarea and slightly less prominent sulcus, but shows similarities in shape and costation (see p. 309).

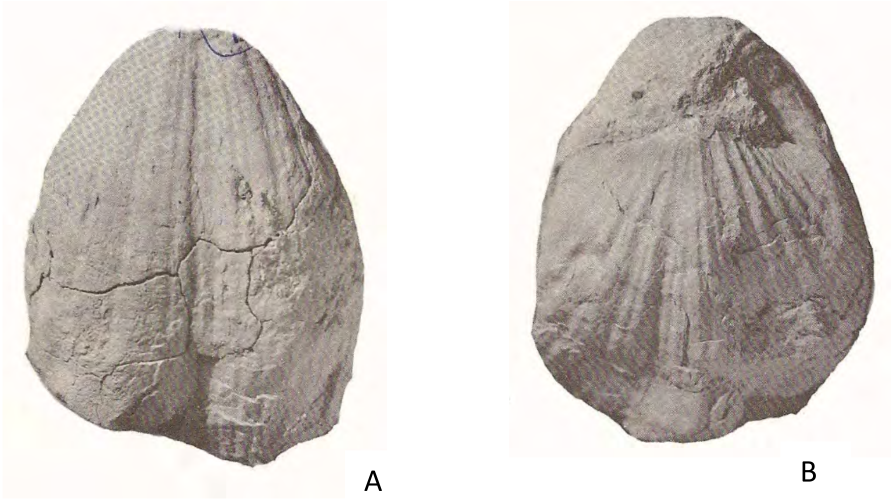

Fig. 274. *Spiriferella sulcoconstricta* n. sp. A, B, ventral and dorsal aspects of GSC 35653 holotype, x 1 from C-4081, Assistance Formation, Ellesmere Island. (Waterhouse & Waddington 1982).

There is limited similarity to *Spiriferella protodraschei* Lee & Shi in Lee et al. (2019, p. 30, Fig. 18A-G), based on two specimens from the Vøringen Member in Spitsbergen. The sulcus in *protodraschei* is distinctly narrower than that of many *sulcoconstricta*, and was not measured by Lee & Shi, but its angle is estimated to be close to 15º on the paratype. The shell has a wide hinge and four or five pairs of plicae, and narrow fold, numerous small pustules, limited costae, high dental plates and high umbonal callus. Lateral flanks are much broader than those of *sulcoconstricta*, and plicae are broad with well rounded crests. Lee & Shi in Lee et al. (2019, p. 30) mentioned a solid pseudodeltidium, shown in Fig. 1E-H, but the appearance and consideration of the nature of the delthyrial cover in Spiriferelloidea and Spiriferida in general suggests it was a single stegidial plate or a modified form of deltidium, not visibly formed by a pair of conjunct deltidial plates (Williams & Brunton, 1997, p. 428). It is called a neodeltidium herein, to signify a slight modification of the normal deltidium. The true strophomenatan pseudodeltium does not show such variation in size, and developed unhampered by a delthyrial pedicle in its ancestry.

Spiriferella oregonia n. sp.

Fig. 276

1957 *Spiriferella draschei* [not Toula] – Cooper, p. 56, pl. 11C, fig. 7-18.

Derivation: Named for Oregon.

Diagnosis: Shell of moderate length, with diverging lateral margins. Ventral sulcus well defined, with angle of 25º; high ventral interarea. Costae and plicae are exceptionally well defined.

Holotype: Specimen USNM 125406 figured by Cooper (1957, pl. 11C, fig. 7-10) and herein as Fig. 276A-C, here designated.

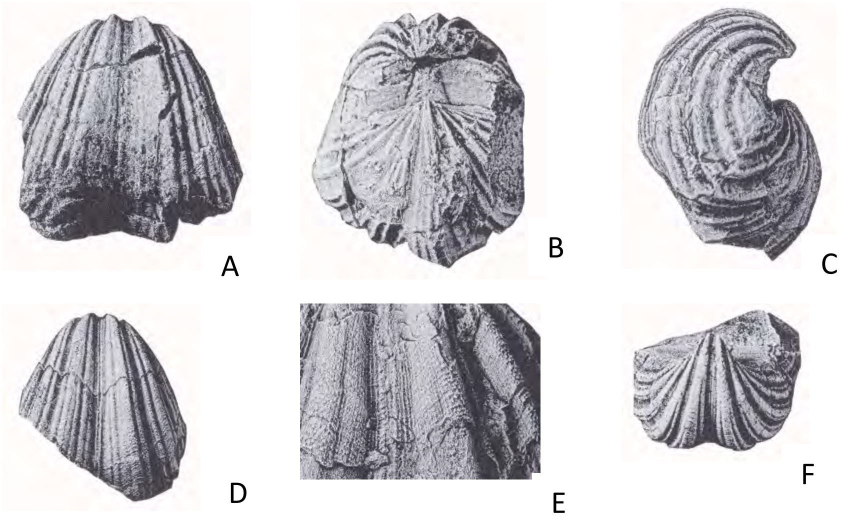

Fig. 276. *Spiriferella oregonia* n. sp. A-C, ventral, dorsal and lateral aspects of holotype, USNM 125406, x1. D, F, ventral and posterior aspects of ventral valve USNM 125401, x1. E, micro-ornament on USNM 125402, x3. From Coyote Butte Formation, Oregon. (Cooper 1957).

Description: Cooper (1957, p. 56, pl. 11C, fig. 7-18) referred well preserved specimens from the Coyote Butte Formation of Oregon to *Spiriferella draschei*, but the sulcus, although well formed, is narrower than in *draschei* and approaches that of *sulcoconstricta*, but the shell is less elongate and the lateral margins diverge more. Indeed, the sulcus and plicae are more crisply defined than those features in either *sulcoconstricta* or *pseudodraschei*, and the shape is pentagonal, the shell widening forward with maximum width close to the anterior margin, and the ventral interarea is particularly high. These features are used to diagnose a separate species. A well developed delthyrial plate or neodeltidium lies across the umbo (Cooper 1957, pl. 11, fig. 14), and papillae are well developed. At least eight costae lie within the sulcus, with a median or double rib.

Although Cooper (1957) assigned a mid-Permian age on the basis of the age range known to him for productids from the Glass Mountains of Texas, a Lower Permian age has been preferred by Bamber & Waterhouse (1971) and Waterhouse (2018a), because the Coyotte Butte brachiopods are closely allied or identical with the Jungle Creek faunal sequences described from the sequences in Yukon Territory. This would render the age of *Spiriferella oregonia* significantly older than *draschei*. The species is much closer to *draschei* and older than the supposed ancestor called *S. protodraschei* Lee & Shi.

Genus ***Alispiriferella*** Waterhouse & Waddington, 1982

Diagnosis: Transverse alate shells with wide hinge, well defined ventral sulcus and channel along crest of the dorsal fold, subalate cardinal extremities and simple plicae. Shell thickening substantial.

Type species: *Spiriferella ordinaria* Einor in Licharew & Einor, 1939, p. 140 from early Permian faunas of Novaya Zemlya, OD.

Discussion: This genus is moderately like *Timaniella*, but has simpler costae, greater length, and more thickening in the ventral valve, suggesting a close relationship to Spiriferellinae.

Alispiriferella gydanensis (Zavodowsky, 1968)

Fig. 277

1968 *Spiriferella gydanensis* Zavodowsky, p. 159, pl. 46, fig. 1.
1968 *Spiriferella rajah* [not Salter] subsp. A – Nelson & Johnston, pl. 94, fig. 12 (part, see also pp. 310, 316, 317).
1970 *S. gydanensis*– Zavodowsky, p. 162, pl. 75, fig. 1a, b, 5a, b, pl. 78, fig. 3.
1982 *Alispiriferella gydanensis* – Waterhouse & Waddington, p. 31, pl. 7, fig. 1-4.
?2005 *A. gydanensis* – Klets, pl. 18, fig. 1-10.

Diagnosis: Equidimensional shells with alate cardinal extremities, feebly costate ventral plicae, non-costate dorsal plicae. Fold with broad median channel and no costae.

Holotype: Specimen figured by Zavodowsky (1968, pl. 46, fig. 1; 1970, pl. 75, fig. 1) from the Omolon Horizon (Wordian) of Kolyma River region, northeast Russia, OD.

Canadian material: More than twenty specimens were recorded from C-10908, in the *Neochonetes culcita* Zone of White Mountains in the Yukon Territory, and more than ten specimens from Assistance Formation localities, including GSC 58968 and 58973 on Ellesmere Island, with one conjoined specimen from C-5995 in the Trold Fiord Formation on Ellesmere Island**.**

Description, Resemblances: The figured Canadian specimens are distinctly alate, as is typical of *Alispiriferella*, although one (Waterhouse & Waddington 1982, pl. 7, fig. 1) has apparently rounded cardinal extremities, probably due to wear. All of the Zavodowsky specimens except that figured in Zavodowsky 1970, pl. 75, fig. 5b are close but less alate. That raises the possibility that the Canadian specimens belong to a different more alate taxon, with slightly fewer sulcal ribs, but it would be preferable to check the nature of the Russian specimens first. They display a broad sulcus and fold like that of the Canadian material, and similarly little inflated dorsal valve. It is considered that the differences are possibly to have been due to differing modes of preservation or infraspecific variation.

Klets (2005) assigned to this species a number of specimens from the Lower Permian Khanalichan Suite of south Verchoyan, which show extended hinge and alate cardinal extremities, and strong pustules. The specimens are older than the types and present material, so they are therefore assigned to the species with some reservations, especially as short ribs appear in the dorsal fold channel.

Waterhouse & Waddington (1982, p. 32) noted the resemblance of some specimens described by Miloradovich (1936) from Novaya Zemlya and Stepanov (1937b) from Spitsbergen to *gydanensis,* and especially that figured by Stepanov (1937b, pl. 7, fig. 10) has moderately prominent ears. But a dorsal valve assigned to the same species (*parryana* = *loveni*) by Stepanov (1937b, pl. 7, fig. 11) has a narrower fold than in *gydanensis*. On the other hand, a dorsal valve figured in the suite described by Miloradovich (1936, pl. 4, fig. 8) has a wide channel in the dorsal fold, suggestive of Zavodowsky's species. His ventral valves are all incomplete, with what could be broken or worn lateral margins.

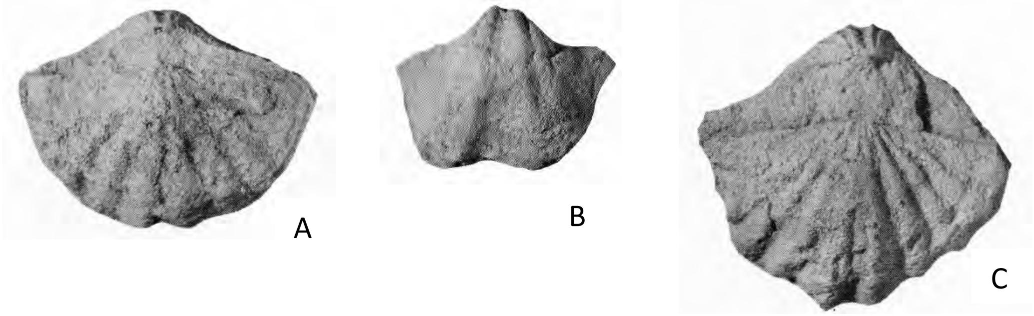

Fig. 277. *Alispiriferella gydanensis* (Zavodowsky). A, dorsal view of specimen with valves conjoined, GSC 35731 x1. B, ventral valve GSC 35730 x1.5. C, dorsal view of specimen with valves conjoined, GSC 35728 x1. From GSC loc. 58968, Assistance Formation, Ellesmere Island. (Waterhouse & Waddington 1982).

Genus ***Bamberina*** Waterhouse, 2004a

Diagnosis: Small shells with steep posterior walls, narrow hinge, moderately inflated ventral valve and little inflated dorsal valve, sulcus deep and V-shaped in section with median groove, fold low, with two medial costae separated by groove, additional costae anteriorly, but low throughout. Few plicae and lateral costae, scattered pustular micro-ornament. Short internal plates, little or no secondary thickening.

Type species: *Elivina*? *annectens* Cooper & Grant, 1976a, p. 2242 from Bell Canyon Formation (upper Wordian, Capitanian) of Glass Mountains, Texas.

Discussion: The micro-ornament is pustular, unlike that of *Elivina* Fredericks, 1924 and its type species, *Spirifer tibetanus* Diener, 1897, which, as inspected at the Geological Survey of India, Kolkata, lacks the pustules so typical of Spiriferellidae. (See Waterhouse 2004a, p. 219; 2016, p. 215).

Bamberina cordiformis (Waterhouse & Waddington, 1982)

Fig. 278

1971 *Spiriferella draschei* [not Toula] – Brabb & Grant, p. 17, pl. 2, fig. 26-28, 34, 35.

1971 *Spiriferella* sp. Bamber & Waterhouse, p. 178, pl. 21, fig. 16.
1982 *Elivina cordiformis* Waterhouse & Waddington, p. 34, pl. 34, pl. 8, fig. 1-7, text-fig. 16j.
?1988 *E. cordiformis* – Abramov & Grigorieva, p. 161, pl. 29, fig. 6-8.
2004a *Bamberina cordiformis* – Waterhouse, p. 219.

Diagnosis: Distinguished by highly incurved ventral posterior, wide sulcus, and low plicae fading anteriorly into several costae, sulcus deep and angular.

Holotype: GSC 27034 from unnamed sandstone, GSC loc. 53838, *Dyoros modestus* Zone, McDougall Pass, north Richardson Mountains, figured by Bamber & Waterhouse (1971, pl. 21, fig. 16), Waterhouse & Waddington (1982, pl. 8, fig. 1-5) and herein as Fig. 278A-C, OD.

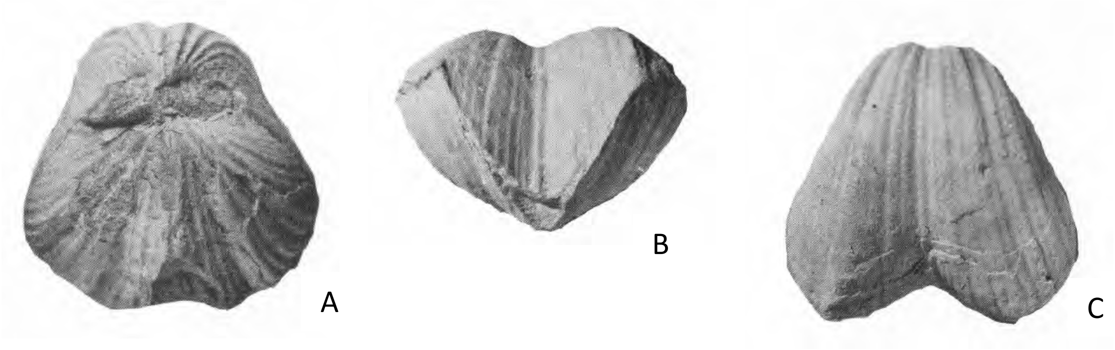

Fig. 278. *Bamberina cordiformis* (Waterhouse & Waddington). A, B, C, dorsal, anterior and ventral aspects of holotype, GSC 27034 from GSC loc. 53838, unnamed sandstone, *Dyoros modestus* Zone, Richardson Mountains, x1. (Waterhouse & Waddington 1982).

Resemblances: *Spiriferella draschei* [not Toula] of Brabb & Grant (1971) is a rather similar specimen from the lower part of the upper limestone unit in the type Takhandit section, whilst having a narrower sulcus anteriorly. Otherwise it displays much the same shape apart from being slightly less transverse, and displaying strong costae. The holotype of *draschei* has a broader less V-shaped sulcus, compared with type *cordiformis* and with the Alaskan material.

Abramov & Grigorieva (1988) recorded the species *cordiformis* from the Echi Suite of northeast Russia, which is somewhat older than the Canadian occurrence, and differs in some respects, to the extent that the identification requires further analysis: indeed it shows some approach to the Jungle Creek specimens identified as *Spiriferella pseudodraschei* in Waterhouse & Waddington (1982). *Eliva timorensis* Archbold & Bird (1989, text-fig. 9A-N) is similar in a number of respects to *cordiformis*, as discussed in Waterhouse (2004a, p. 220). It came from the Maubisse Formation of west Timor, equivalent to the Basleo Formation of Wuchiapingian age.

The V-profile of the sulcus is to lesser degree mirrored in the specimens noted previously as *Spiriferella angulata* n. sp. from the Great Bear Cape Formation, but the overall shape differs considerably, with maximum width placed well forward in *Bamberina cordiformis*. Texan material assigned to *Bamberina* also have a narrow almost trenched ventral sulcus.

Genus ***Canalisella*** Waterhouse, 2004a

Diagnosis: Close to *Spiriferella*, hinge variable in width and alate to obtuse cardinal extremities, fold traversed by deep moderately wide channel for full length, plicae usually number four to six pairs, well formed, with few or no costae.

Type species: *Spiriferella leviplica* Waterhouse & Waddington, 1982, p. 26 from Van Hauen Formation (Wordian) of Canadian Arctic Archipelago, OD.

Discussion: This genus is close to *Spiriferella* and was synonymized with that genus by Gourvenec (2006, p. 1786) and Lee et al. (2019), but it tends to have better-defined dorsal channel along the fold, and its plicae are simple as a rule, with few or no costae. It also comes close to *Alispiriferella* Waterhouse & Waddington, but members of that genus have a wide hinge at maximum width with alate cardinal extremities, and the fold tends to be higher and the dorsal channel is more strongly developed. It appears possible that *Canalisella* evolved from *Alispiriferella*, but there are substantial differences between the two genera.

The uncertainties surrounding this taxon centre partly on the nature of the relationship to *Spiriferella loveni*. At one extreme, specimens assigned to *loveni* may display so much variation over their outline, width of hinge, nature of cardinal extremities, number of plicae, and extent of costation, that they should incorporate the species *leviplica*. Here the genus is interpreted as involving at least three species, *loveni* and *leviplica* in the Arctic, as well as a hitherto neglected taxon, *aldrichi* Etheridge (see below). In addition, without necessarily including all related species, there are several species in Neimongol (Inner Mongolia).

A species described as *Arcullina*? *enokiana* Lee & Shi in Lee et al. (2019, p. 40, Fig. 5K, L, 19, 22) from the Kozhim Formation of the northern Urals in Russia is large, with largely simple strong plicae in five or six pairs, a median sulcal costa and moderately well-defined fold channel, unlike the fold in *Arcullina*. Pustules were described as relatively large. It shows considerable approach to *Canalisella*.

Canalisella leviplica (Waterhouse & Waddington, 1982)

Fig. 279, 280

?1937 *Spiriferella parryana* – Frebold, p. 45, pl. 11, fig. 6.
1978 *S. loveni* [not Diener] – Waterhouse et al. pl. 1, fig. 8, pl. 2, fig. 5 (part, not fig. 2 = *separata,* not fig. 4 = *Undulatina* sp.).
1982 *S. loveni* [not Diener] – Waterhouse & Waddington, p. 22, pl. 5, fig. 7, 8 (part, not fig. 2, 14 = *loveni*?, 3-6, 9-13, 15-17 = *separata*).
1982 *S. leviplica* Waterhouse & Waddington, pp. 26, 29 (left hand column), pl. 7, fig. 6-11 (part, not fig. 5 = *loveni*?).
2004a *Canalisella leviplica* – Waterhouse, p. 217.
2016 *C. leviplica* – Waterhouse, p. 217, Fig. 270A, C, D, F.

Diagnosis: Moderately large, weakly transverse, high ventral interarea, low arching neodeltidium or cover plate, three to five pairs of ventral plicae and three to five pairs of dorsal plicae, plicae well spaced and simple without costae, fold well defined posteriorly, high to low and broad anteriorly, with prominent median sulcus. Sulcus often bearing a median rib. Spiralia directed ventrally in at least one specimen, but this has not been verified or contradicted for other material, and may be a sport.

Holotype: GSC 30799 from C-4074, Van Hauen Formation, Ellesmere Island, figured by Waterhouse & Waterhouse (1982, pl. 7, fig. 6-8) and herein as Fig. 279A-C, OD.

Material: The species was recorded in Canada from C-4068, C-4069, C-4070 and C-4074 in the Van Hauen Formation and and C-4095 in the Degerböls Formation of Ellesmere Island.

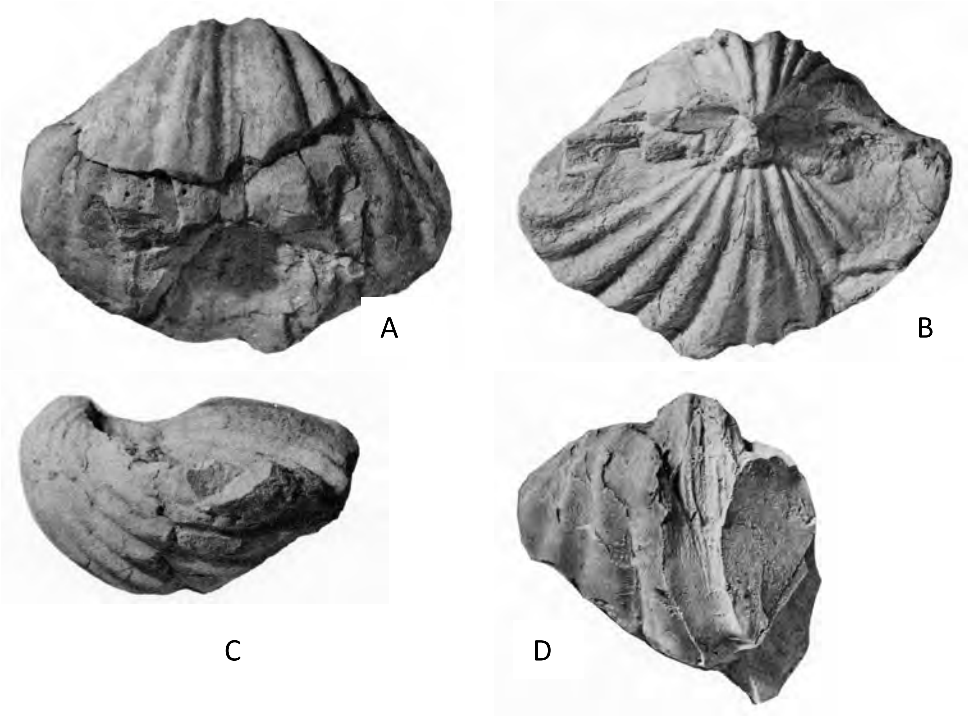

Fig. 279. *Canalisella leviplica* (Waterhouse & Waddington). A, B, C, ventral, dorsal and lateral aspects of holotype, GSC 30799 x1. D, internal mould of ventral valve, GSC 30978, x1.5. From C-4074, Van Hauen Formation, Ellesmere Island. (Waterhouse & Waddington, 1982).

Resemblances: The species came from the Van Hauen Formation and Degerböls Formation, No further material is available. This species is very close to some specimens of *Spiriferella loveni* as interpreted by Waterhouse & Waddingon (1982), to judge from figures, apart from having a lower and wider fold. Although some specimens ascribed to *leviplica* do not have a median rib along the ventral sulcus, a median rib is present in the sulcus of the holotype. A median rib is present also in some paucicostate specimens assigned to *Spiriferella keilhavii* [not von Buch], as for example in the Spitsbergen specimens figured as *draschei* and *keilhavii* by Stepanov (1936, pl. 5, fig. 2, 3). In addition, a median sulcal rib is also present in paucicostate specimens assigned to *S. keilhavii parryana* by Stepanov (1937b, pl. 7, fig. 10, 11) from the Productus beds of Cape Starotsin in Spitsbergen, though these do appear to have a wide hinge, perhaps through breakage and loss of the anterior lateral shell, to suggest *loveni*. The ventral valves have four or five pairs of plicae. A shell assigned to Stepanov (1937b, pl. 7, fig. 8) to *S. lita* Fredericks looks somewhat similar, with two median sulcal ribs and more lateral costae. Miloradovich (1936, pl. 1, fig. 1-3, pl. 2, fig. 1, 2, pl. 4, fig. 1-4) illustrated a number of specimens as *parryana* from Novaya Zemlya. One or two have a median sulcal rib, but most do not and others have more costae than in the present form, and as noted, a dorsal valve has a prominent fold channel, approaching that of *Alispiriferella gydanensis*. They were included in synonymy of *keilhavii* by Dunbar (1955), but this must be rejected. A specimen described by Frebold (1937, pl. 11, fig. 6) from Spitsbergen is transverse with obtuse cardinal extremities, and is possibly related, though the amount of lateral breakage is not known. The plicae on specimens figured as *S. keilhavii* by Frebold (1937, p. 45, pl. 11, fig. 7, 8) and *S. saranae* by Frebold (1937, p. 46, pl. 11, fig. 9) are simple, suggestive of *leviplica*, but are more numerous, approaching those of the species *keilhavii* von Buch.

Elivina sinensis Liu & Waterhouse (1985, p. 34, pl. 9, fig. 1-4, 6, 7, pl. 10, fig. 1, 4, 5, 7, 9) from Inner Mongolia is an interesting ally of the species under discussion. It has largely simple plicae, and well defined dorsal

Fig. 280. *Canalisella leviplica* (Waterhouse & Waddington), dorsal and anterior views of GSC 30795 x 2 from GSC loc. 26406, Assistance Formation, Devon Island. (Waterhouse & Waddington 1982). The anterior aspect shows ventrally directed spiralia, presumably a sport, and is also found in *Arcullina* (sic = *Canalisella*) *enokiana* Lee & Shi. (Waterhouse & Waddington 1982).

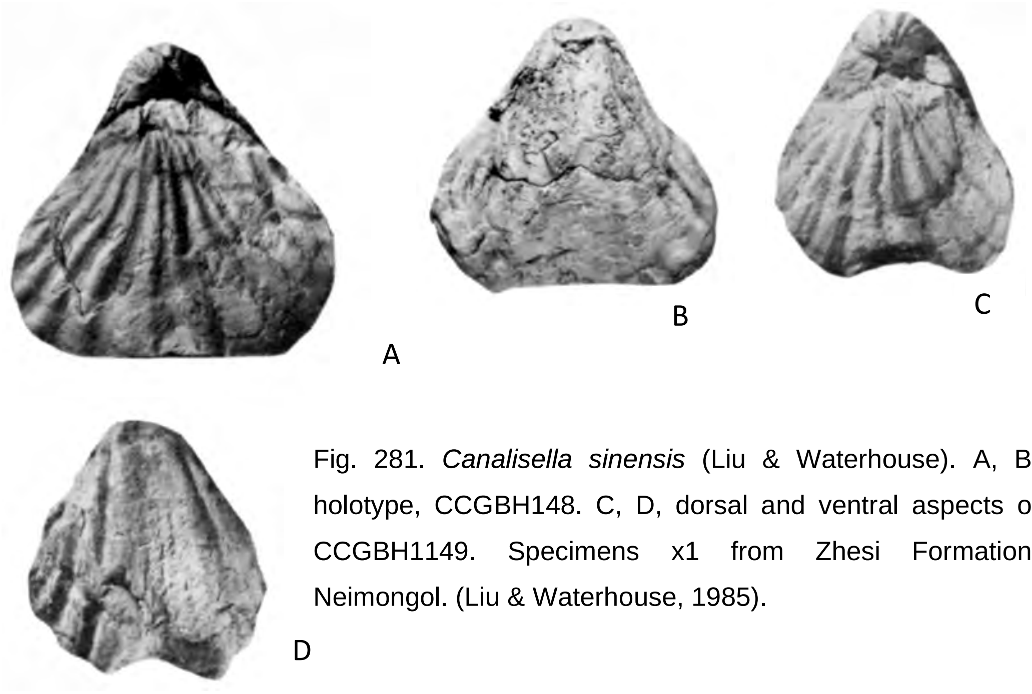

Fig. 281. *Canalisella sinensis* (Liu & Waterhouse). A, B, holotype, CCGBH148. C, D, dorsal and ventral aspects of CCGBH1149. Specimens x1 from Zhesi Formation, Neimongol. (Liu & Waterhouse, 1985).

fold channel, and the shape is subtriangular, with high ventral interarea and short hinge. Pustules are weakly developed, found especially in interspaces and are radially aligned, showing that the generic affinities are not with *Elivina*. Some specimens bear long costae, which are lacking from other specimens. This species appears to be allied to both *loveni* as outlined by Lee et al. (2019), and *leviplica*, and supports the desirability of having a separate genus for such distinctive forms. As well, *Spiriferella wangi* Liu & Waterhouse (1985, p. 31, pl. 7, fig. 9, pl. 8, fig. 1-5, 7, 8) from the same region is allied, as a much larger form, with very high and much wider ventral interarea, and up to seven pairs of plicae in the dorsal valve, and few costae. Large pustules cross five or six growth increments. Other variants of the overall suite are described in Liu & Waterhouse (1985), suggesting that this region was a centre of evolution for the group. Similar-looking specimens from Mongolia have been referred to *Spiriferella persaranae* Grabau (1931) but the holotype of this species (Grabau 1931, pl. 19, fig. 4, 4a) has more costae, approaching, as noted by Grabau (1931, p. 57), *Spiriferella salteri*, and with six sulcal costae (Grabau 1931, Fig. 61).

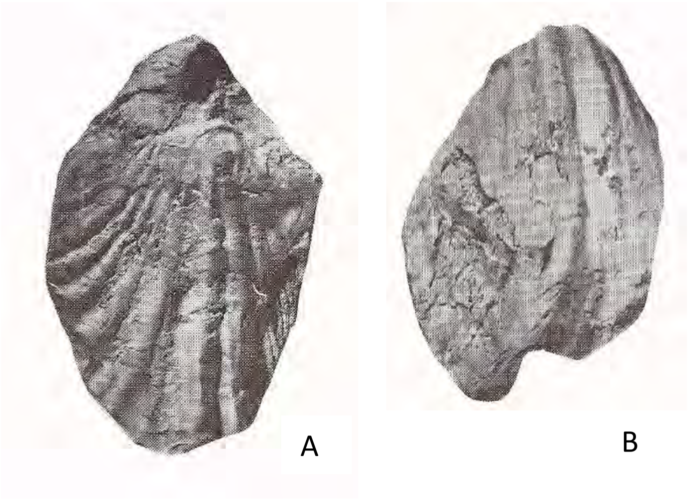

Fig. 282. *Canalisella wangi* (Liu & Waterhouse). A, dorsal aspect of holotype, CCGBH135. B, ventral aspect of CCGBH137. Specimens x1, from Zhesi Formation, Inner Mongolia. (Liu & Waterhouse 1985).

From the Talatin Suite of northeast Russia, *Spiriferella borealica* Kalashnikov (1998, p. 59, pl. 20, fig. 5, pl. 21, fig. 1-5, text-fig. 9) show similarities to *Canalisella* in its largely simple plicae and narrow median sulcal ribs, but the dorsal fold appears to be rounded in Kalashnikov (1998, pl. 20, fig. 5), and possibly in the somewhat distorted specimen of Kalashnikov (1998, pl. 21, fig. 3b). The shell is elongate with a prominent sulcal rib and high ventral interarea. The specimens approach the Great Bear Cape ventral valve figured by Tschernyschew & Stepanov (1916, pl. 12, fig. 1-3), but for this and other Great Bear Cape specimens the dorsal valve is poorly known.

Discussion: The text explaining and comparing the species *leviplica* was substantially garbled in the publication, after the proofs were checked to returned to the editor. As a result, the proposal, diagnosis, etymology and holotype were provided, but the description and comparisons jump to the left-hand column of page 29.

Canalisella? aldrichi (Etheridge, 1878)

Fig. 283

1878 *Spirifera aldrichi* Etheridge, p. 634, pl. 29, fig. 2.

Diagnosis: Spiriferellid shells with simple plicae, moderately wide hinge, sulcus along median dorsal fold bearing a median rib.

Holotype: Specimen B 4671 (or 89168), Natural History Museum, London, figured as above by Etheridge (1878), by monotypy.

Material: A dorsal valve from Dana Bay, Ellesmere Island.

Taxonomy and Nomenclature: A single dorsal valve was described and figured as *Spirifera aldrichi* by Etheridge (1878, p. 634, pl. 29, fig. 2) from Ellesmere Island. The text recorded seven pairs of simple plicae, and a median rib in the dorsal valve. No specimens of *Canalisella leviplica* shows a median rib along the dorsal median sulcus.

Whitfield (1908, p. 52) associated the species with his *Syringothyris*, but the fold in the two types differs considerably.

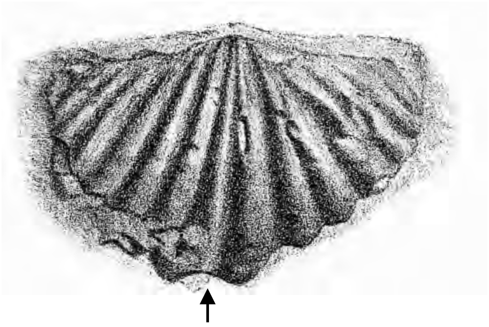

Fig. 283. *Spirifera aldrichi* Etheridge, original figure from Ellesmere Island, x1. Arrow points to median rib. This taxon appears to have belonged to a distinct taxon, allied to *Canalisella* and characterized by have a median costa in the dorsal fold-channel.

Canalisella loveni (Diener, 1903)

Fig. 284, 285B, E

1873 *Spirifer* sp. indet. Toula, p. 273, pl. 2, fig. 1, 2.
1875b *Spirifer parryanus* [not Hall] – Toula, p. 256, pl. 7, fig. 8a-d.
1903 *Spririfer loveni* Diener, p. 17.
1936 *Spiriferella keilhavii* [not Toula] – Stepanov, p. 123, pl. 5, fig. 2, 3.
1937 *S. parryana* [not Hall] – Frebold, p. 45, pl. 11, fig. 6.
1937b *S. keilhavii keilhavii* [not von Buch] – Stepanov, p. 146, pl. 7, fig. 9.
1937b *S. keilhavii parryana* – Stepanov, p. 147, pl. 7, fig. 10, 11.
1938 *S. parryana* – Frebold *in* Frebold & Noe-Nygaard, p. 23, pl. 1, fig. 10, 11.
1962 *S.* (?) *parryanus* – Dunbar, p. 9, pl. 1, fig. 11-15.
1964 *S.* aff. *interplicata* [not Rothpletz] – Gobbett, p. 155, pl. 20, fig. 4-6.
1982 *S. loveni* – Waterhouse & Waddington, p. 22, pl. 5, fig. 2, 14, pl. 6, fig. 2? (part, not pl. 5, fig. 3-6, 9-13, 15-17 = *separata*, fig. 7, 8 = *leviplica*, pl. 6, fig. 1 = *Undulatina* sp.).
1982 *S. leviplica* [not Waterhouse & Waddington] – Waterhouse & Waddington, p. 26, pl. 7, fig. 5? (part, not fig. 6-11 = *leviplica*).
1992 *S. saranae* [not de Verneuil] – Nakamura et al., pl. 2, fig. 2, ?5.
2004a *Canalisella loveni* – Waterhouse, p. 218.
2019 *S. loveni* – Lee et al., p. 20, Fig. 4E-H, Fig. 11, 12, 13.

Diagnosis: Subequidimensional to weakly elongate shells with wide weakly alate cardinal extremities in adult shells, delthyrium open or rarely with neodeltidium, pair of median costa as a rule, plicae number four to seven pairs, most specimens with few or no costae, fold low and with prominent median groove, pustules, short adminicula.

Lectotype: Specimen figured by Toula (1875b, pl. 1, fig. 8a-c) from Lovenberg, Spitsbergen, SD Lee et al. (2019, p. 20). Refigured in Lee et al. (2019, Fig. 4E, F, G, 12D, E) and herein, Fig. 285B.

Material, Description: Some ventral valves in the study by Waterhouse & Waddington (1982) come close to the lectotype of *loveni*, being weakly transverse with with hinge. One specimen comes from the Trold Fiord Formation at C-4015, and a ventral and a dorsal valve comes from the Degerböls Formation at C-4095, Ellesmere Island. Small specimens with four pairs of costate plicae from the Takhandit Formation are close to the original specimens as figured by Toula (1875b), but equally could be young specimens of another species. Equidimensional small shells described by Harker & Thorsteinsson (1960) from the Assistance Formation have four or five pairs of simple plicae, and are regarded as immature specimens of *separata*.

In the synonymy provided by Lee et al. (2019, p. 20), some specimens referred to *loveni* differ substantially from the types. For example, the specimen figured as *Spiriferina draschei* by Wiman (1914, p. 38, pl. 3, fig. 11) is large with few costae, but has a shape and wide sulcus like that of the associated specimens (Wiman 1914, pl. 3, fig. 2, 9, 10, 12-26) and approach the Canadian species *Spiriferella separata* n. sp., although with fewer costae. There is also some approach to *S. arctica* (see p. 308). *Spiriferella parryana* of Tschernyschew & Stepanov (1916, p. 54, pl. 11, fig. 4a-c, pl. 12, fig. 1-3) was included in *loveni* by Lee et al., but this was firmly denied by Dunbar (1955, p. 145) in pointing out that that of pl. 11, fig. 4a-c differed substantially, whereas that of pl. 12, fig. 1-3c was regarded as acceptable. None are transverse as typical *leviplica*, and the shells are assigned to *Spiriferella arctica*.

Fig. 284. *Canalisella loveni* (Diener), dorsal valve GSC 140934 from C-4095, Degerböls Formation, Ellesmere Island, x1. This dorsal valve is wide with broad hinge as in *loveni*, and apparently not as elongate as usual, but the anterior margin is incomplete.

The thin sections and valves figured from Spitsbergen as *S. parryana* by Miloradovich (1936, p. 73, pl. 1, fig. 1-3, pl. 2, fig. 1, 2, pl. 4, fig. 1-9) have more costae than normal for the species as here understood, and the dorsal valve as in pl. 4, fig. 8 though preserved only posteriorly is deep and comparatively wide, suggesting a possible position in *Alispiriferella* as discussed on p. 322. Three small specimens figured from Greenland by Dunbar (1955, pl. 27, fig. 1-3) have simple plicae, and two especially have posterior walls less concave in outline than the other shells from the same region that were figured by Dunbar, but the specimens are few and variation within the plexus of shells referred to *Undulatina laticostata* n. sp. (see p. 341) cannot be ruled out, not to mention the fact that the specimens are small and immature, and so presumably would have matured into shapes like those of the accompanying shells. Lee et al. (2019) referred most of the Greenland specimens to *loveni*. Some of the Spitsbergen-Bjørnøya specimens figured by Lee et al. (2019) are more transverse than others, showing an approach to *Canalisella leviplica*, but the cardinal extremities are not preserved, and they are provisionally grouped with the others, because they come from the same general region, although individual localities and detailed stratigraphic data were not provided by Lee et al. 2019. Overall the specimens assigned to *loveni* are more elongate than shells assigned to *Canalisella leviplica*. The small specimen from the upper middle Takhandit Formation at GSC loc. 53929 in the *Dyoros modestus* Zone, figured as *Spiriferella* aff. *keilhavii* by Bamber & Waterhouse (1971, p. 165, pl. 20, fig. 7) could belong, but seems through shape to be more likely to belong to a paucicostate specimen of *Spiriferella separata*. A small specimen from the Yukon Territory figured by Nelson & Johnson (1968, pl. 94, fig. 7-9) was allocated to *loveni* by Lee et al. (2019), but the small size inhibits confident identification, and the specimen seems likely to represent an immature shell related to associated and larger specimens assigned to *sulcoconstricta* n. sp. Lee et al. stressed that *loveni* from Spitsbergen had two sulcal ribs, although a number of their illustrations suggest a single rib. They discriminated two populations in the text, probably under the influence of different substrates, but did not specify the differences or itemize the figures.

Discussion: Dunbar (1955) assessed *keilhavii* and *loveni* as belonging to the same species, regarding the figures of the types as illustrating two extremes of one species. Lee et al. (2019) separated the two. They regarded *keilhavii* as limited to subequidimensional shells with six or seven pairs of plicae (or even eight or nine, judged from figures), and two sulcal costae, and allowed some degree of costation. The dorsal fold was stated to expand anteriorly, as shown in the original figure, but they were not able to collect any more dorsal valves. Their synonymy for *keilhavii* included very few specimens. *S. loveni* was regarded as having four to six plicae pairs, sulcus with two costae, and low generally wide fold and deep median groove. Weakly alate cardinal extremities were illustrated, and the shape regarded as slightly transverse to elongate. Only a very few of the illustrated specimens displayed costae. A rudimentary if any “pseudodeltidium” ie. neodeltidium was said to be developed, with stegidia. Such variation in development and size is not seen in the true pseudodeltidium of Strophomenata. Dental supports were described as flanges, adminicula short, and pustules unremarkable. Some of these aspects were not determined for *keilhavii*.

Some facets of the diagnosis in Lee et al. (2019) correct aspects of the original illustrations, which were probably inaccurate. The ventral valve lectotype of *loveni*, kept at the Naturhistorisches Museum of Wien, in Austria, has four pair of coarse simple plicae, with two medial sulcal costae (Lee et al. 2019, Fig. 12D), whereas Toula’s figure suggests five pairs of plicae and a median sulcal costa. The shell is obviously broken around the margins, but various other figures provided by Lee et al. show a weakly transverse to subelongate ventral valve with broad hinge, wider and more alate in possibly better-preserved ventral valves from the Kapp Starotsin Formation of Spitsbergen. Dorsal valves, again best preserved from Spitsbergen, tend to be weakly alate. They are not particularly close to the dorsal valve figured by Toula (1875b), but are closer to specimens figured by Toula (1873).

To encompass specimens that differed from type *loveni*, a new species was recognized by Waterhouse & Waddington (1982). These involved forms more transverse than type *loveni* and most of the specimens illustrated by Lee et al. (2019), with stronger dorsal fold channel, and little sign of costae, other than two sulcal costae in some specimens, unlike figures of the original types of *parryana* = *loveni*. The cardinal extremities are obtuse in *leviplica*, rather than weakly alate, and shorter than maximum width. Pustules are strong, and at least in one specimen, the spiralia are directed longitudinally rather than laterally, although there may be reservations about the value of this observation, as reflecting a sport, rather than general arrangement. There are differences between *loveni* and *leviplica*, possibly of infrasubspecific rank in reflecting a degree of geographic separation. Should it prove necessary to synonymize the two, that would simply mean that the name of the type species for *Canalisella* has to be changed. The generic validity I find to be satisfactory, given the occurrence of a number of species widely through the northern paleotemperate latitudes, all characterized by comparatively few and simple plicae with few or no costae and consistently with a well defined channel along the dorsal fold. The subdivision of various Greenland specimens figured by Dunbar (1955) between *keilhavii* and *loveni* by Lee et al. (2019) clouds the clear distinction between the two genera, as does the synonymizing of *Canalisella* with *Spiriferella*. The figures and morphologies show that *loveni* and allies are readily distinguished from *Spiriferella*.

Tribe **ARCULLINAINI** (**ARCULLININI**) new tribe

Name genus: *Arcullina* Waterhouse, 1986a, p. 4 from Kapp Starotsin Formation, Spitsbergen, here designated.

Diagnosis: Includes genera with rounded dorsal fold, lacking a median channel. Plicae often numerous.

Discussion: This tribe (see Fig. 261A) is distinguished by its tendency to have numerous plicae, and a rounded dorsal fold, in contrast to the channelled fold normal for *Spiriferella* and allied genera, which include *Eridmatus, Bamberina, Canalisella,* and *Alispiriferella*. But the pattern of evolution within Arcullinaini has been complex. The late Carboniferous genus *Plicatospiriferella* Waterhouse & Waddington, found in Yukon Territory and northeast Russia, has a rounded dorsal fold and a high number of plicae. A cluster of species found in the late Carboniferous of northeast Russia is like *Plicatospiriferella* in its high number of plicae, but has a channelled dorsal fold. It is believed that these species, mentioned shortly, and here named *Undulatina* n. gen. were associated with *Plicatospiriferella*, and possibly constituted the original source, giving rise to *Plicatospiriferella* through change in the dorsal fold, and retention of the distinctively high number of plicae. This group of species persisted into Permian time as the distinctive species *Undulatina keilhavii* (von Buch) and possibly *Tintoriella* Angiolini. That complicates the normal model of simple trends in the evolution of species and genera, with reversion and change incorporated in an association of genera, but is believed to reflect the reality of development. It is interpreted as demonstrating that jumps could occur for primary features, rather than simply involve a linear development of progressive change to one morphological feature in one direction. The latter option is of course favoured by simplistic computer programs and unrefined cladistics and genetics, but the fossil record suggests that evolution was more complex.

Genus ***Arcullina*** Waterhouse, 1986a

Diagnosis: Fold rounded rather than grooved, neodeltidium well developed, plicae simple, pustules coarse dense.

Type species: *Spiriferina polaris* Wiman, 1914, p. 39 from Vøringen Member (Kungurian) of Kapp Starotsin Formation, Spitsbergen, OD.

Discussion: This genus has been further clarified by Lee et al. (2019, p. 36) with the demonstration that a plate across the delthyrium could be well developed in the type species, and that pustules were relatively coarse, at least in a few species of approximately middle Permian age in the Arctic.

Several species have been described or redescribed as *Arcullina* from the southern paleohemisphere. They have a rounded dorsal fold without sign of a median groove, but some differ from *Arcullina polaris* in various respects, notably in the strength of the pustules, and sulcal costation. For some forms the delthyrial structure and the nature of the pustules are features yet to clarified. Overall these difficulties reflect back on the circumscription for the genus, as for so many genera, and underline the need for caution against insisting that locally developed features defined the genus, rather than allowing for variation around one or more central features and across the globe. Extraordinarily, there have been studies on species and genera that only make comparisons with other local genera and species, instead of world-wide. Global assessments for Spiriferellidae showed that pustules for example reflected ecologic conditions (Waterhouse & Waddington 1982).

A few species ascribed to *Arcullina* are found in the Himalayan region, of Lopingian age. They include *Spiriferella qubuensis* Zhang in Zhang & Jin, 1976, p. 212, pl. 18, fig. 1-5 from the lower Qubuerga Formation of southern Tibet, which lacked dorsal valves but included according to Zhang a specimen figured as *S. salteri* not Tschernyschew, with both valves complete and an entire dorsal fold. Type *S. salteri* has a channelled dorsal fold (Tschernyschew 1902, pl. 6, fig. 5). Further material has been recorded in the synonymy by Waterhouse (2004a, p. 212), including an external mould that shows well developed pustules. Shen et al. (2003a) considered the species to be a junior synonym of *S. nepalensis* Legrand-Blain (1977), but *nepalensis,* replicates of which with further specimens were kindly sent to me by Dr M. Legrand-Blain, is typical *Spiriferella* with channelled dorsal fold. Indeed, the material assigned to *qubuensis* by Shen et al. (2001) is much closer to *nepalensis* than to *Arcullina qubuensis*. A distinctive elongate form assigned to *Arcullina* is *oblata* Waterhouse (1978, pl. 14, fig. 15-18, pl. 24, fig. 3), with other figured material such as so-called *rajah* (not Salter) of Waterhouse (1978, pl 14, fig. 9, 10, pl. 24, fig. 2), and so-called *S. tibetana* [not Diener] of Waterhouse (1966, pl. 12, fig. 3, 4, pl. 13, fig. 1, 2, 4) from the Changhsingian Nisal Member of northwest Nepal. Shells are elongate with attenuated umbo and simple plicae, and two prominent sulcal costae. Pustules were described as fine. *A. angiolini* Waterhouse (2004a, p. 215, pl. 9, fig. 1-4, text-fig. 36) is of interest is that it comes from very late Changhsingian beds, just below the start of the Triassic with *Otoceras woodwardi.* Preservation is far from ideal, but the species has a round-crested fold.

From beds of Timor, probably equivalent to Basleo beds, of Wuchiapingian age, *Spirifer kupangensis* Beyrich (1864, p. 78, pl. 1, fig. 6a-c) has an entire dorsal fold, narrow hinge and large simple plicae, and median and flank ribs lie in the sulcus. Somewhat similar shells were misidentified as *Elivina tibetana* [not Diener] from beds of Wuchiapingian age in the Yarlung-Tsangpo suture zone of Tibet by Shen et al. (2003b, pl. 4, fig. 7-10). These specimens have a few plicae well rounded in cross-section, not at all like those of *Elivina*, and unlike *Elivina*, have pustules. Broili (1915, pl. 21, fig. 17a, b, 18) figured what appears to be an unusual form of *Arcullina* from Letti in the Indonesian archipelago, with slender plicae and fine costae.

From the Sakmarian Ko Yoa Noi Formation of southern Thailand, *Arcullina modestus* (Waterhouse, 1981b, pl. 23, fig. 2-9, pl. 24, fig. 1-11, pl. 25, fig. 1, 2) is weakly transverse with simple plicae and two sulcal costae, and narrow round-crested fold. Pustules vary in strength, and some at least are well developed. A delthyrial closing plate spans the delthyrium, lying a little below the interarea to each side, and rimmed by the dental tracks (Waterhouse 1981, pl. 24, fig. 6, 8, 11, pl. 25, fig. 2).

Arcullina etheridgei (Archbold & Thomas, 1985a, text-fig. 2N-V) from the Coolkilya Greywacke of the Carnarvon Basin in Western Australia is of Roadian age, and comes moderately close in several aspects to *A. polaris*, as noted by its authors. Shells tend to be elongate, with substantial ventral thickening, and a median sulcal costa is developed, and a single costa lies along each sulcal flank. The delthyrium is filled by a massive callosity.

In the McLean Peak Formation of Baigendzinian age in the upper Takitimu Group of New Zealand, *Arcullina humilis* Waterhouse (2001, pl. 6, fig. 1, 14, 15, 17-21, text-fig. 7d, e), has narrow sparsely costate plicae, a high ventral interarea, and rounded dorsal fold. Pustules are not large, and there is no apparent delthyrial plate, so that either these features varied on southern taxa, or indicate a different lineage within the genus.

Arcullina? *enokiani* Lee & Shi (2019, p. 40, Fig. 5K, L, 19, 22) is based on material originally segregated and named by a Russian but never published from the Kozhim Formation in northwest Russia. The shells are large with prominent simple plicae, number five or six pairs, no costae, and large and dense pustules. The nature of the delthyrium is not exposed. Lee & Shi (2019) remarked on the unusual orientation of the spiralia. Indeed Waterhouse & Waddington (1982) had figured a specimen they ascribed to *loveni* (now *leviplica*) with the same longitudinally directed spiralia. The chief point of interest is the presence of a channelled dorsal fold, which is unlike the fold found so far in any other species ascribed to *Arcullina*. Principal reasons for the placement by Lee et al. of *enokiana* appear to have been the simple plicae and the large pustules. But species of other genera have simple plicae, especially *Canalisella*, and large pustules have been observed on species not related to *Arcullina*, such as so-called *loveni* – now *Spiriferella separata* – recorded in Waterhouse & Waddington (1982, pl. 5, fig. 12, 13), and shown in Fig**.** 266A. If the nature of the dorsal fold proves to have been variable, then various species allocated to *Arcullina* will need to be reassessed and possibly assigned to new taxa. Such a step appears premature at present, and a strong question lies against the generic assignment of *enokiana* to *Arcullina*. The transverse outline of at least small specimens in early maturity is suggestive, and even the larger specimens that were supposedly elongate as figured in Lee & Shi (2019) have lost their lateral margins, leaving the shape only unreliably indicated, although even so, the specimen in Lee & Shi (2019, Fig. 22H) appears to have been transverse. The species is judged to belong to *Canalisella*, with which it agrees in all known attributes, other than large size and moderately elongate outline.

An earlier ally is *Plicatospiriferella* Waterhouse & Waddington, 1982, with rounded fold and numerous plicae with rounded species, known as two species from the Late Carboniferous of Yukon Territory in Canada (Waterhouse 2018a), and at least one species from the Middle Carboniferous of southern Verchoyan, figured as *Plicatospiriferella grata* Klets (2005, pl. 15, fig. 1-4). Other specimens from that region were included as *grata* (Klets 2005, pl. 15, fig. 5-9), but have a channelled dorsal fold, and further Middle and Upper Carboniferous forms were extensively figured, characterized by numerous simple plicae, and channelled fold (see below).

Tintoriella rajah (Salter in Salter & Blanford, 1865) was shown as having a rounded fold by Carter (2006a, Fig. 1865.3a), but the figure is unreliable. It was reproduced from a study by Davidson (1866) and is inaccurate, as may be verified from the specimen kept at the Natural History Museum. Its dorsal fold is channelled.

Arcullina polaris (Wiman, 1914)

1855 *Spirifer keilhavii* [not von Buch] – Salter, p. 386, pl. 36, fig. 11 (part, not pl. 36, fig. 9, 10).
1914 *Spirifer polaris* Wiman, p. 39, pl. 4, fig. 1-25, pl. 5, fig. 1-5.
1937b *Spiriferella polaris* – Stepanov, p. 150, pl. 8, fig. 6-8 (part, not fig. 5 = *lita*?)
1937 *Spiriferella polaris* – Frebold, p. 47, pl. 11, fig. 1, 1a, 1b.
1968 *Spiriferella saranae* [not de Verneuil] – Nelson & Johnson, p. 729, pl. 93, fig. 3-10, pl. 96, fig. 9?, text-fig. 4f, 5a, 13f (Pl. 93, fig. 1, 2 = suggests aspects of *sulcoconstricta*?).
1970 *Spiriferella polaris* – Barchatova, p. 176, pl. 20, fig. 7.
?1971 *Spiriferella* sp. Bamber & Waterhouse, p. 174, pl. 19, fig. 8.
?1986 *Spiriferella polaris* – Kalashnikov, p. 93, pl. 123, fig. 3-5.
1986a *Arcullina polaris* – Waterhouse, p. 4.
1992 *Spiriferella polaris* – Nakamura et al., pl. 1, fig. 8.
1998 *A. polaris* – Kalashnikov, p. 61, pl. 16, fig. 1, 2, pl. 17, fig. 5-7, pl. 18, fig. 1.
2006a *A. polaris* – Carter, p. 1805, Fig. 1198, 3a-d.
2019 *A. polaris* – Lee et al. p. 36, Fig. 5I, J, 7A, 19-21.

Diagnosis: Slightly elongate shells with delthyrial covering plate, deep angular sulcus rarely costate, and high fold with narrow crest, lacking median channel. Plicae simple, well spaced on ventral valve, more angular on dorsal valve, pustules swollen. Dental plates well developed, short median septum.

Lectotype: Specimen figured by Wiman (1914, pl. 4, fig. 23-25) from the Spiriferenkalk (= Vøringen Member of Kapp Starotsin Formation), Spitsbergen, SD Gobbett (1964, p. 150).

Material, Description: From Arctic Canada, specimens were described principally by Nelson & Johnson (1968) from the Takhandit Formation, conceivably the lower or perhaps middle Takhandit, with rare specimens recorded from Tatonduk River in Bamber & Waterhouse (1971) at GSC loc. 53932 in the *Neochonetes culcita* Zone, in the middle part of the formation. The ventral valves have broad comparatively low largely simple plicae, with a sulcal rib or central groove, and often a lateral costa on each side. Cardinal extremities and details of the delthyrium are not preserved. No dorsal valves are preserved, so that the identification is not fully secure.

Lee et al. (2019, p. 36) tentatively included a ventral valve as *Spiriferella saranae* by Harker & Thorsteinsson (1960, pl. 23, fig. 8) as belonging to the species *polaris*, but anterior costae are moderately developed over the plicae, even though the specimen is small. It appears to belong to *Spiriferella arctica* (Haughton), and lies on a block from the Belcher Channel Formation, now revised to be part of the Great Bear Cape Formation. They excluded the figures of Stepanov (1937b, pl. 8, fig. 5, 6) from synonymy, without explanation, but probably because fig. 6 is more costate, and fig. 5 because it is small and arguably approaches *S. lita* Fredericks.

***Arcullina*? sp.**

1971 *Spiriferella* sp. Stehli & Grant, p. 518, pl. 64, fig. 36-43.

Material: Five silicified ventral valves from Sabine Bay Formation, Axel Heiberg Island, Canadian Arctic Archipelago, described by Stehli & Grant (1971).

Description: The specimens are small and now transverse, thanks to breakage, with wide subalate hinge, five pairs of plicae with rounded crests, and signs of faint anterior costae on one specimen, a well-formed narrow sulcus, bearing a median costa in one specimen and three fine costae in another. The deltidial closing plate is well developed over the upper third of the delthyrium. Dental plates are high.

Resemblances: No dorsal valves are available, but the strong neodeltidium and indication that pustules were comparatively well developed, judged from the figures, as well as simple plicae, suggest that the specimens belong to arctic *Arcullina*. In *A. polaris*, the plicae in some shells have narrower and higher crests, and two costae extend along the sulcus. The present specimens are comparatively well preserved, and show a hinge that lay at maximum width, like that of *Arcullina digna* (Barchatova, 1968). Lee et al. (2019) stressed that the hinge of *polaris* was at less than maximum width, but their specimens as figured in Lee et al. (2019, Fig. 21) are manifestly incomplete around the cardinal extremities, except for Lee et al. (2019, Fig. 21V), which has the hinge at maximum width, with cardinal extremities less pointed than those of the specimens from the Sabine Bay Formation.

Genus ***Undulatina*** n. gen.

Derivation: unda - wave, Lat.

Diagnosis: Relatively large number of simple plicae, numbering six to ten pairs. Dorsal fold with median channel.

Type species: *Spirifer keilhavii* von Buch, 1847, p. 74, from Miseryfjellet Formation (Kungurian or early Roadian), Bjørnøya, here designated.

Discussion: This is a highly distinctive form characterized by a relatively high number of simple rarely costate plicae.

Undulatina keilhavii (von Buch,1847)

Fig. 285A, C, D, F

1847 *Spirifer keilhavii* von Buch, p. 74, pl. 1, fig. 2a, b.
1901 *S. keilhavii* – Frech, pl. 56c, fig. 1b, c.
1914 *Spiriferina keilhavii* – Wiman, p. 36, pl. 2, fig. 25-30, pl. 3, fig. 1.
1914 *Spiriferina draschei* [not Toula] – Wiman, p. 38, pl. 3, fig. 2?, 9? (part, not fig. 3-8, n. det., 10-26 = indet., possibly *separata* or more doubtfully *arctica*?).
1955 *Spiriferella keilhavii* – Dunbar, pl. 27, fig. 8, 9, 13, 14 (part, remainder = *laticostata*).
?2008 *Spiriferella keilhavii* – Angiolini & Long, p. 93, Fig. 9A, B (part, not 9C-G, ?H = *angulata*).
?2008 *Spiriferella loveni* [not Diener] – Angiolini & Long, p. 96, Fig. 10A (part. not 9I, J = *angulata*).
2008 *Eridmatus* sp. Angiolini & Long, Fig. 10F (part, see p. 316 for further synonymy).
2019 *Spiriferella keilhavii* – Lee et al., p. 17, Fig. 4A-D, 9A, 10.

Diagnosis: Moderately large subequidimensional to weakly transverse shells with low ventral interarea, seven pairs and up to eight or even nine pairs in some specimens of plicae on each valve at maturity, narrow laterally, inner pair of plicae may be strongly divided with costate inner pair of subplicae, weakly to moderately costate, only a small or no rigid neodeltidial or stegidial cover, median groove along most of the fold. Thick umbonal callus.

Lectotype: The dorsal valve refigured from von Buch (1847) by Frech (1901, pl. 57c, fig. 1b) from Productus Sandstone at Mt Misery (= Miseryfjellet Formation), Bjørnøya, was selected by Licharew & Einor (1939). Lee et al. (2019, p. 17) stated that this lectotype has been lost, and so replaced it with a ventral valve refigured from von Buch (1847) by Frech (1901, pl. 57c, fig. 1c) and Dunbar (1955, pl. 27, fig. 8), as repeated by Lee et al. (2019, Fig. 4C, 10A) and herein as Fig. 285A.

Discussion: *Spiriferella keilhavii* has been widely reported in the literature, but Lee et al. (2019) restricted the synonymy to specimens that agree closely with the von Buch illustrations, featuring subequidimensional proportions, a degree of costation, and seven pairs of plicae, seldom less, whereas some figures suggest as many as nine or even ten pairs. Difficulty arises with small specimens, not at full maturity, for these will not display the full number developed at maturity, but that is a problem with various taxa, and it is normal to associate small specimens with more mature specimens from the same locality. The inner plicae are narrow. The fold is narrow posteriorly, and flares anteriorly, whereas the sulcus does not become so broad in front. The species was particularly typical of the Miseryfjellet Formation of Bjørnøya, according to Lee et al. (2019), and regarded as being of Kungurian age, and their contention that the species was represented in somewhat younger occurrences in east Greenland is now revised, with assignment of those specimens to a new species*, Tintoriella laticostata*. One ventral valve figured by Angiolini & Long (2008, Fig. 9A, B) from the Vøringen Member of Spitsbergen has a high number of plicae in eight pairs, and a narrow sulcus, approaching that of *keilhavii*, and another ventral valve figured as *S. loveni* (not Diener) by Angiolini & Long (2008, Fig. 10A) is similar. Both are more elongate that the shells from Bjørnøya.

No specimens of *keilhavii* were to be found in Arctic Canada, according to Lee et al. (2019). A large specimen from the Assistance Formation of Devon Island, as figured by Harker & Thorsteinsson (1960, pl. 22, fig. 9-11) has seven pairs of plicae. Costae cover some of the valve. But the Assistance specimen has much broader inner plicae than developed in the original figured type of *keilhavii* and also displays the remains of a well developed

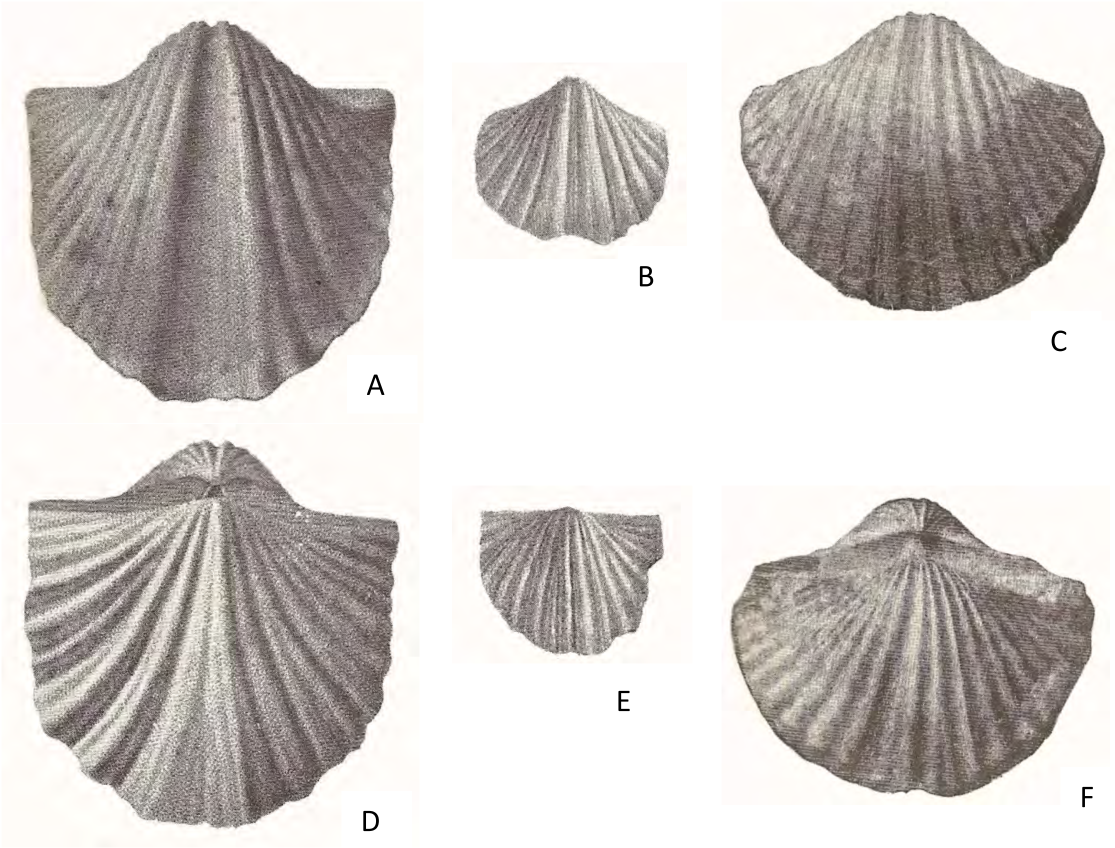

Fig. 285. A, D*, Spirifer keilhavii* von Buch, 1846, original figures of the ventral and dorsal aspects. B, E, *Spirifer parryanus* Toula, 1875b, original figures of the ventral valve and dorsal valve, now the types for *loveni* Diener. The specimen has now been lost. C, F, *S. keilhavii* ventral and dorsal aspects as figured by Wiman (1914).

delthyrial plate,which is set into the interarea lying below the dental flanges developed from the teeth at the edges of the dental plates, and is assigned to the new species *Spiriferella separata*. Associated small specimens look like immature *keilhavii*, but could be the immature representative of *separata*. It is particularly difficult to ascertain the specific affinities of juvenile and immature examples of many taxa, including those of *Spiriferella*.

Frebold (1931) and Dunbar (1955) regarded the species *keilhavii* von Buch as the senior synonym of *parryanus* Toula, 1875b, and this was opposed by Waterhouse & Waddington (1982). To separate the two decisively depends on the reliable refiguring of the initial type of *Canalisella loveni* (= *parryanus* Toula), and this has been accomplished by Lee et al. (2019). The types of both taxa have an ornament dominated by plicae, with the entry of strong costae commencing towards the anterior margin. The original figures for *keilhavii* are based as for *S. loveni* on drawings, and so may have reservations attached, but the photographs provided by Wiman (1914) and Lee et al. (2019) from the same type area of Bjørnøya provide reassurance that *keilhavii* has a high number of narrow plicae, and narrow sulcus and well defined dorsal fold channel. The difficulty confronting students of the species is to decide where to allocate specimens in which costae are more pervasive, as is commonly the case, and other specimens in which costae are reduced to a minimum, or even entirely absent. Waterhouse & Waddington regarded these latter specimens as representative of *parryanus* = *loveni*, whereas Dunbar treated all as incorporated within *keilhavii*.

Large ventral valves were figured as *keilhavii* from Bjørnøya by Gobbett (1964), and have been referred to *Timaniella wilckzeki* (Toula) by Lee et al. (2019), on account of their transverse outline and numerous costae.

Undulatina verchoyanica n. sp.

2005 *Plicatospiriferella grata* [not Klets] – Klets, p. 198, pl. 5, fig. 6-10.

Derivation: Named from the Verchoyan region.

Diagnosis: Small elongate shells with six or seven pairs of plicae, no costae, moderately distinct pustules, well defined fold channel.

Holotype: Specimen no. 29-21, figured by Klets (2005, pl. 15, fig. 8a, b) from Tilakhsk Suite of Middle Carboniferous age in south Verchoyan, here designated. Kept at Khabarovsk Geological Museum FGUGP (Federal Geological Unitarian Geophysical office, Dalgeophiza), Far East Russia.

Resemblances: This species was included in *Plicatospiriferella grata* Klets, 2005 from the same beds, but has a moderately defined median channel along the dorsal fold, whereas *grata* has a round-crested fold. Dorsal valves in particular are more transverse than those of *grata*, and a transverse ventral valve is also transverse and has a median sulcal costa, not seen in another smaller specimen, and has alate cardinal extremities, like those of a dorsal valve. The species is much less costate than shells of *Tintoriella laticostata* n. sp. (see below) and differs also in alate shape from *Undulatina keilhavii* (von Buch). Another Middle Carboniferous form named *Plicatospiriferella akachanica* Klets (2005, p. 200, pl. 16, fig. 1-5) from the Mishkin Suite of southern Verchoyan has six to seven pairs of plicae, as well as a few strong costae. No specimens are shown to be alate. The species has a channelled fold, and is recognized as a species within *Undulatina*.

Shells assigned by Klets (2005) to *Plicatospiriferella ploskajae* (Zavodowsky, 1970) and *P. costata* Klets, 2005 have only four or five pairs of plicae and so are readily distinguished from the present form and do not belong to the genus, being much closer to *Spiriferella*.

Undulatina kletsi n. sp.

2005 *Plicatospiriferella* sp. Klets, p. 200, pl. 16, fig. 10-13.

Derivation: Named for A. G. Klets.

Diagnosis: Transverse weakly alate shells with at least ten pairs of narrow costae-like plicae, and two sulcal costae.

Holotype: Specimen 321-1, figured by Klets (2005, pl. 16, fig. 12a, b) from lower Akachan beds (Upper Carboniferous), southern Verchoyan, here designated. Kept at Khabarovsk Geological Museum FGUGP (Federal Geological Unitarian Geophysical office, Dalgeophiza) ,Far East Russia.

Resemblances: This species is readily distinguished by its unusually fine and moderately numerous plicae, compared with those of *Undulatina verchoyanica* n. sp. This latter species also has a single if any sulcal rib, whereas the present and younger species has two narrow sulcal costae. No Permian species comes very close.

***Undulatina*?** sp.

Fig. 286

1978 *Spiriferella loveni* [not Diener] – Waterhouse, Waddington & Archbold, pl. 2, fig. 4.
1982 *Spiriferella ?loveni* [not Diener] – Waterhouse & Waddington, p. 22, pl. 6, fig. 1 (part, not fig. 2 = *loveni*, pl. 5, fig. 7, 8, 14 = *loveni*, fig. 3-6, 9-13, 15-17, Fig. 16b, d, f, 17, 18 = *separata*).
1982 S. *keilhavii* [not von Buch] – Waterhouse & Waddington, p. 28, pl. 6, fig. 3, 4 (part, not fig. 5-7, 10-14 = *sulcoconstricta*, not fig. 8, 9 = *draschei*).

Material: A ventral valve from GSC loc. 76029, Devon Island, and a possible second ventral valve from C-4015, Ellesmere Island, both in Trold Fiord Formation. A conjoined specimen from GSC loc. 58973, Assistance Formation, might be related. Other specimens from the Trold Fiord Formation are not available for study.

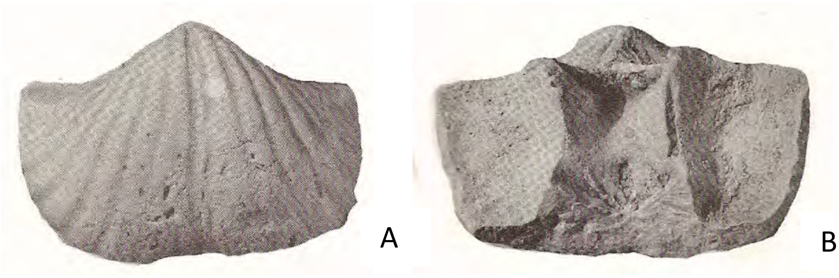

Fig. 286. *Undulatina*? sp. A, B, external and tilted anterior aspects of ventral valve GSC 35727 x1 from GSC loc. 76029, Trold Fiord Formation, Cameron Island. (Waterhouse & Waddington 1982).

Description, Resemblances: A ventral valve from GSC loc. 76029 (Waterhouse & Waddington 1982, pl. 6, fig. 3, 4) has a narrow sulcus and seven pairs of simple plicae, and the neodeltidium is small. It might be a descendent of *Undulatina keilhavii* (von Buch), given its general appearance. An unusual specimen from GSC loc. 58973 in the Assistance Formation (Waterhouse & Waddington 1982, pl. 6, fig. 1) has seven pairs of simple plicae over the dorsal valve, and a narrow fold channel. It seems possible that these specimens represent middle Permian survivors of *Undulatina,* and the same taxon may prove to represented elsewhere by lingering stock. On the other hand, the simple plicae suggest an approach to multiplicate *Canalisella*, pointing to the need for analysis of further material.

Several specimens from Spitsbergen may prove to have been related. They were figured as *Spiriferella saranae* (Frebold, 1937, p. 45, pl. 11, fig. 7, 8) and *S. keilhavii* (Frebold, 1937, p. 46, pl. 11, fig. 9). The specimens have seven pairs of well-formed simple (ie. non costate) plicae. The specimen referenced as *keilhavii* by Frebold is particularly close and came from the top of Festung section, at level 5.

Genus ***Tintoriella*** Angiolini, 1996

Fig. 287, 288

Diagnosis: Transverse shells with comparatively large number of broad costate plicae pairs, as a rule numbering seven to eight pairs. Otherwise close to *Spiriferella*, with channelled dorsal fold.

Type species: *Spirifera rajah* Salter, 1865, p. 59 from *Lamimargus himalayensis* Zone (Wuchiapingian) in northwest India, OD.

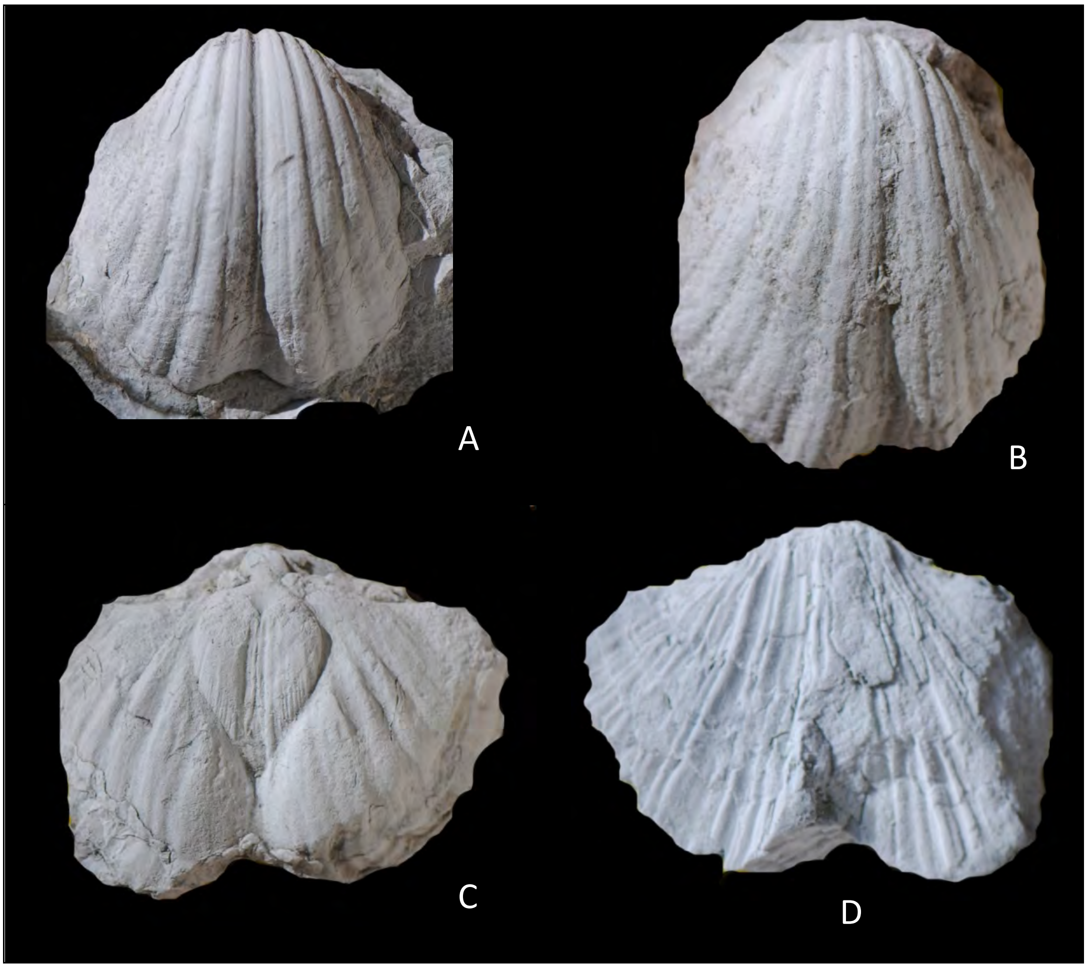

Fig. 287. *Tintoriella rajah* (Salter). A, Ventral valve GSC 141166 from Mandakpal (Wuchiapingian), Kashmir. B, ventral valve GSC 141165 from Nisal Member (Changhsingian), Dolpo, Nepal. C, D, ventral internal mould and dorsal internal mould GSC 141167 from Mandakpal, Kashmir. Specimens x1.

Discussion: *Tintoriella* Angiolini, 1996, p. 193, type species *Spirifera rajah* Salter in Salter & Blanford, 1865, p. 59 comes from a Wuchiapingian fauna of the Himalaya, as correctly stated by Carter in Gourvennec & Carter (2006, p. 2786). The type species of this genus is well known, with a large number of studies summarized in a synonymy provided in Waterhouse (2004a, p. 200). Ventral valves of *rajah* look somewhat similar to those of the Greenland *Spiriferella* described by Dunbar (1955), with a high number of well-rounded plicae, bearing costae, admittedly narrower than those of the Greenland species and with a more elongate shell. For the dorsal valve, a critically inaccurate illustration was provided by Carter in Gourvennec & Carter (2006, p. 2787, Fig. 1875.3b), reproducing a figure proferred by Davidson (1866, pl. 2, fig. 3) to show a rounded dorsal fold. This is wrong. The specimen is still extant at the Natural History Museum, London, and is registered as B 82086. It has been examined by the writer, and shows a shallow median channel along the dorsal fold. The holotype, refigured from Salter (1865) by Waterhouse (2016, Fig. 269), also displays a dorsal channel.

Tintoriella was proposed on bases that do not fully withstand critical evaluation, Angiolini (1996, 2001) having relied on non-type material of a different and older species for assessing type *Spiriferella*, and assessing the nature of the neodeltidium (which she called pseudodeltidium) and presence of an umbonal callosity as being significant, although as shown by Waterhouse (2016, pp. 215, 216) these features remain of contentious systematic value, in view of the considerable variability displayed by at least some species. These areas of uncertainty are acknowledged, together with the unknown nature of several facets of morphology for the Greenland material. The range of variability and internal detail is much better known for *rajah*, given that it has been studied and figured by a number of authors from a variety of lithofacies. Waterhouse (1978, 1983) and Gupta & Waterhouse (1978) have shown that the species ranged from Wuchiapingian into Changhsingian faunas of the Himalaya. Some reports have been deemed questionable, as assessed in Waterhouse (2004a, p. 201), and *Spiriferella subsalteri* Shen et al. (2003a) may well be synonymous, as an incompletely circumscribed taxon for which the dorsal valve was apparently not deemed to be essential for the delination of the species.

Fig. 288. *Tintoriella rajah* (Salter), ventral valves GSC 141168 and 141169 from Mandakpal, (Wuchiapingian), Kashmir, x1.

The overall external appearance of both ventral and dorsal valve, and ornament, sulcus and fold suggest that *rajah* and the Greenland species are likely to be congeneric, with differences in umbonal callosity and pustulation reflecting differences in paleolatitude and environment, and differences in shape and costal width due to specific differences. Tentatively therefore, and acknowledging the need for further evaluation of the neodeltidium, the Greenland species is referred to Angiolini's genus. At the same time, it must be allowed that Shi & Shen (1997), Shen et al. (2001) and Shi, Shen & Zhan (2003, p. 1062) have discounted the validity of *Tintoriella*, preferring to retain *rajah* in *Spiriferella*. But the Himalayan and Greenland forms are not typical *Spiriferella*, having more plicae than usual.

Undulatina keilhavii (von Buch) and the newly recognized species *Tintoriella laticostata* n. sp. both differ from *Spiriferella saranae* (de Verneuil) and a host of allied species in the development of two to four additional pairs of plicae. This is not a great difference, but helps to mark out the species as an exceptional variation from the arrangement typical of *Spiriferella*. Because its inner plicae are broad with numerous costae as a rule, and the outer ribs are slender and simple, the species *rajah* and *laticostata* n. sp. are distinguished from *keilhavii* to generic level, but are believed to have evolved from *keilhavii*. The latter species is much closer to Upper Carboniferous species from northeast Russia, as described previously.

Tintoriella laticostata n. sp.

Fig. 289

1931 *Spiriferella keilhavii* [not von Buch] – Frebold, p. 28, pl. 5, fig. 7-9.
1955 *S. keilhavii* – Dunbar, p. 139, pl. 25, fig. 1-9, pl. 26, fig. 1-11, pl. 27, fig. 1-14.
1961 *S. keilhavii* – Dunbar, p. 229, pl. 2, fig. 9, 10.
cf. 1992 *Spiriferella* sp. Nakamura et al., pl. 5, fig. 10.
2019 *S. loveni* [not Diener] – Lee & Shi in Lee et al., pp. 17, 20 (part).
2019 *S. keilhavii* [not Buch] – Lee & Shi in Lee et al., p. 17 (part).

Derivation: late – broad, costa – rib, Lat.

Diagnosis: Moderately large and transverse shells with a high number of plicae pairs, and numerous broad-crested costae, sulcus narrow and grading into lateral flanks, fold moderately broad, low, and costate with narrow median channel. No stegidial cover plate. Pustules small but well defined.

Holotype: Specimen figured by Dunbar (1955, pl. 25, fig. 4, 5) from Wegener Halvo and Schuchert Dal Formations, central east Greenland, here designated.

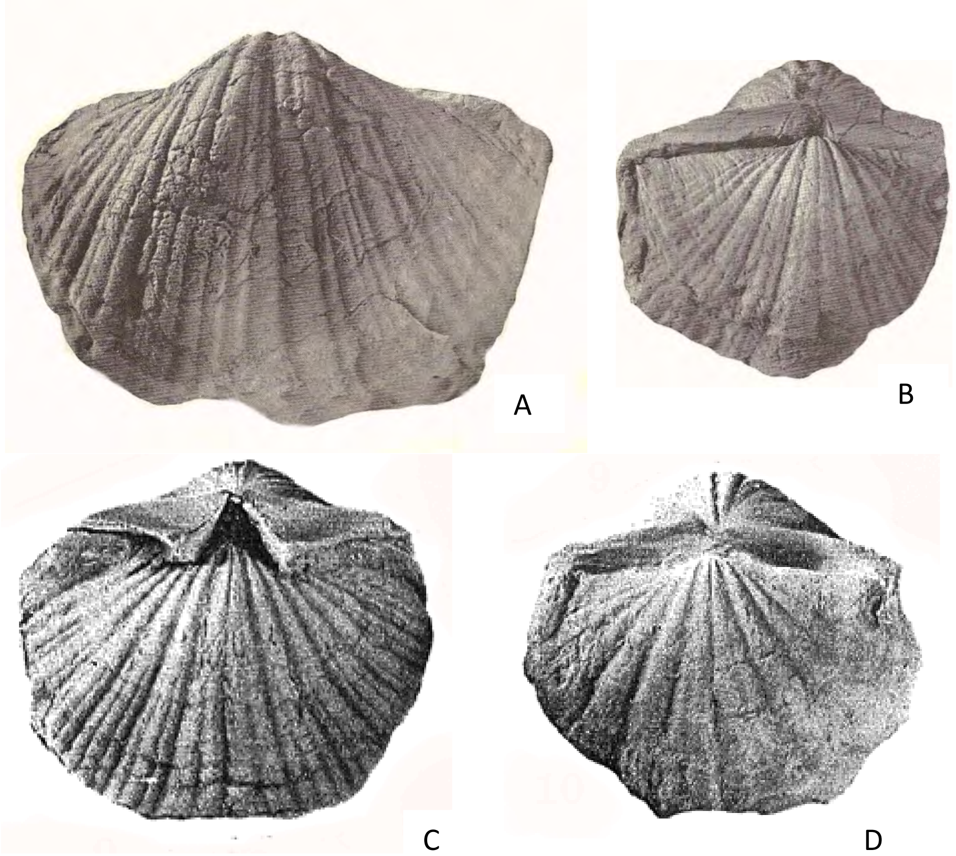

Fig. 289. *Tintoriella laticosta* n. sp. A, ventral valve. B, dorsal valve. C, D, dorsal and ventral aspects of a conjoined specimen. Specimens figured by Dunbar (1955) from the Kap Stosch Group Group of east Greenland. Specimens x1.

Discussion: Dunbar (1955) referred these specimens to *Spiriferella keilhavii* (von Buch), and the specimens are close to that species in terms of having numerous plicae pairs and in lacking a delthyrial cover, and in having a comparatively narrow and shallow sulcus and low fold, though less sharply defined than the equivalent features in *keilhavii*. The prime difference from *Undulatina keilhavii* lies in the much more prominent and consistent costation in the Greenland specimens. The fold channel is shallow. Internally, the adminicula are shown for only one specimen amongst the Greenland suite (Dunbar 1955, pl. 26, fig. 4), as short and continuing into distinct rims flanking the adductor field, not as long as in the Russian types for *Spiriferella*, and so closer to those of *Tintoriella* (cf. Waterhouse 1978, pl. 4, fig. 3). It would thus seem possible that the Greenland form, being of consistent morphology, and being younger than *keilhavii* (Lopingian as opposed to chiefly upper Cisuralian), evolved from *keilhavii*, and migrated into equivalent paleolatitudes of the southern hemisphere such as the Himalayan region to give rise to the species *rajah*.

Lee & Shi in Lee et al. (2019, p. 20) subdivided the suite of Greenland shells between *Spiriferella keilhavii* and *S. loveni*, referring the specimens figured by Dunbar (1955, pl. 26, fig. 1-11, pl. 27, fig. 1-5, 10, 11) to *loveni*, and the others to *keilhavii.* This is rejected: the mature shells are similar to each other, and readily distinguished by their broad costation. All differ substantially from the paucicostate and elongated specimens which Lee & Shi treated as *loveni* from the Kapp Starotsin Formation of Spitsbergen and Miseryfjellet Formation of Bjørnøya, and from *keilhavii* of Bjørnøya. Several small and paucicostate ventral valves were figured from the Greenland fauna by Dunbar (1955, pl. 27, fig. 1-5), and these appear to have been immature specimens, at a growth stage preceeding that when costae became well developed

Subfamily **TIMANIELLINAE** Waterhouse, 2016

Diagnosis: Constituent genera highly transverse with alate extremities.

Genus ***Timaniella*** Barchatova,1968

Diagnosis: Highly transverse with extended cardinal extremities, fold with wide median cleft; lateral plicae in several pairs and may be costate.

Type species: *Timaniella festa* Barchatova, 1968 from Kungurian-Roadian of Timan, north Russia, OD.

Discussion: *Alispiriferella* comes close in some respects, though tending to be more elongate, but it has heavy posterior thickening in the ventral posterior, as in members of Spiriferellinae.

A number of the specimens assigned by Lee et al. (2019) to *Timaniella wilckzeki* (Toula) approach the timaniellin genus described as *Rhombospirifer* Duan & Li, 1985 from the Cisuralian of Inner Mongolia, but the latter form has a broader fold with wide anterior channel.

Timaniella harkeri Waterhouse, 1971

Fig. 290, 291

1960: *Pterospirifer*? sp. Harker & Thorsteinsson, p. 69, pl. 21, fig. 1-14.
1971b *Timaniella harkeri* Waterhouse, p. 220, pl. 26, fig. 10-21.
1978 *T. harkeri* – Waterhouse, Waddington & Archbold, pl. 3, fig. 1, 2.
1982 *T. harkeri* – Waterhouse & Waddington, p. 32, pl. 2, fig. 9-18, text-fig. 21.
2016 *T. harkeri* – Waterhouse, Fig. 227A-C.
2019 *T. harkeri* – Lee et al., p. 44, Fig. 23, 27, 28.

Diagnosis: Shells with wide cleft in dorsal fold, four to six pairs of simple or weakly costate plicae. Fine radial and commarginal lira and pustules.

Holotype: GSC 26427 from GSC loc. 52705 in middle Permian sandstone of White Mountains, north Yukon Territory, figured by Bamber & Waterhouse (1971, pl. 26, fig. 14, 22), OD.

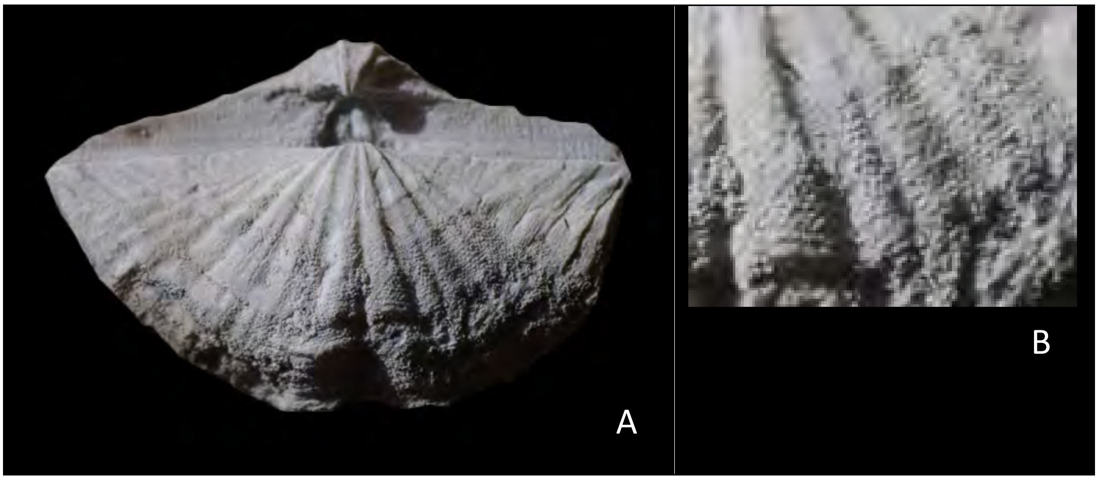

Fig. 290. *Timaniella harkeri* Waterhouse. A, dorsal aspect of specimen GSC 140935, from GSC loc. 26406, Assistance Formation, Devon Island, x1.5. B, panel showing pustules over parts of the shell, x4.

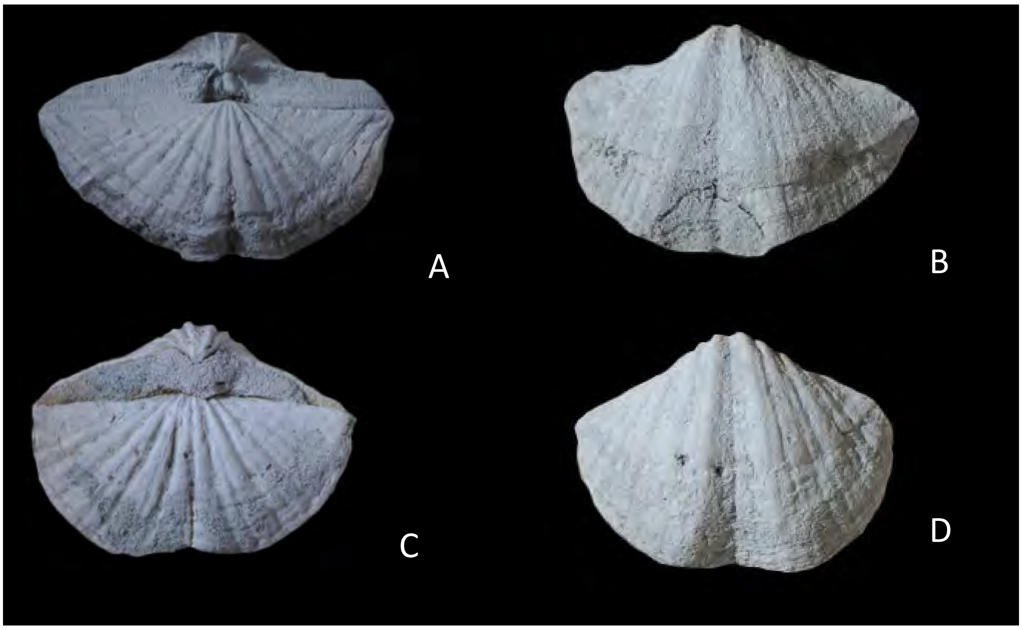

Fig. 291. *Timaniella harkeri* Waterhouse. A, B, dorsal and ventral aspects of GSC 140936. C, D, dorsal and ventral aspects of GSC 140937. From GSC loc. 26406, Assistance Formation, Devon Island, x1.

Material: Specimens are abundant in the Assistance Formation at GSC loc. 26406 of Devon Island, and have been listed from other correlative levels in Waterhouse & Waddington (1982, p. 32), including GSC loc. 58973, C-4016, C-4019, C-4023, C-4080 and C-4081 of Ellesmere Island. A further seven ventral valves come from C-4036, ?Assistance Formation, and one ventral valve and one dorsal valve come from C-4074 in the Van Hauen Formation of Ellesmere Island. Bamber & Waterhouse (1971) recorded occurrences at GSC loc. 52702 and 52705 at White Mountains. The zone is possibly equivalent to the middle Takhandit Formation. Waterhouse & Waddington (1982) listed material from C 10904 and C 11868, regarded as likely to be correlative with the middle Takhandit Formation.

Description, Resemblances: The species has been described and compared in Waterhouse (1971b), Waterhouse & Waddington (1982) and Lee et al. (2019). It was noted that material from the Cache Creek Group near Kamloops, British Columbia, and described as *Spiriferella* sp. by Crockford & Warren (1935) showed some similarities.

Spirifer vercherei [not Waagen] of Fredericks (1925, p. 25, pl. 3, fig. 108-110) from South Primoyre was tentatively included in *harkeri* by Waterhouse & Waddington (1982), and is close in various respects. The species *Timaniella harkeri* was listed in a large fold-out table with *Muirwoodia mammata* for South Primoyre in Kotlyar (1978), and shown as Ufimian-Kazanian, but also as matching *Neoschwagerina* and *Yabeina*. (ie principally Word and Capitanian). Internal moulds were figured by Licharew & Kotlyar (1978, pl. 18, fig. 2, 3) from the Chandalaz Suite.

Suborder Delthyrisidina (Delthyridina) Ivanova, 1972

Infrasuborder Delthyrisimorphi (Delthyrimorphi) Ivanova, 1972

Superfamily **ELITAOIDEA** (**ELYTHOIDEA**) Fredericks, 1924

Family **TORYNIFERIDAE** Carter, 1994

Subfamily **SPIRELYTHAINAE (SPIRELYTHINAE)** Waterhouse, 2016

Diagnosis: Distinguished from Toryniferinae by lack of 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: Unlike *Torynifer*, a ctenophoridium is well developed, and a cardinal plate is absent from *Spirelytha* and allies.

Tribe **SPIRELYTHAINI (SPIRELYTHINI**) Waterhouse, 2016

Diagnosis: Ornament of double-barrelled spines. Ventral valve with dental plates, adminicula, low well defined median ridge, subdelthyrial plate and pleromal ridges. Dorsal valve with ctenophoridium, crural plates, low median ridge.

Discussion: Tribe Kletsiaini Waterhouse, 2016, p. 336 is distinguished by presence of a cruralium.

Genus ***Spirelytha*** Fredericks, 1924

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, dental plates and adminicula, subdelthyrial connector plate. Dorsal interior with very short or negligible median septum, socket plates and no tabellae or cardinal plate.

Type species: *Spirelytha pavlovae* Archbold & Thomas, 1984b, p. 313 (nom. nov. pro *Spirifer scheii* Tschernyschew in Tschernyschew & Stepanov, 1916, p. 45, not Meyer 1913) from Store Björnekap (Great Bear Cape), Ellesmere Island, Arctic Canada.

Discussion: The type species of *Spirelytha* is comparatively obscure, having been based on *Spirifer scheii* Tschernyschew in Tschernyschew & Stepanov (1916), not *Spirifer scheii* Meyer, 1913. Potentially, the morphology was clarified by Archbold & Thomas (1984b, p. 313), in speculating that silicified material from Axel Heiberg Island probably belonged to the genus and species. This had been described as *Spirelytha* for ventral valves, and *Permophricodothyris* for dorsal valves by Stehli & Grant (1971). The ventral valves show a median septum and long adminicula with a posterior connector plate, and the dorsal valves show crural plates and very low if any median septum, with no tabellae.

Spirelytha pavlovae Archbold & Thomas, 1984

Fig. 292

1916 *Spirifer schei* [not Meyer] – Tschernyschew & Stepanov, p. 45, pl. 9, fig. 5, 6, 7.
1924 *Spirelytha schei* – Fredericks, p. 304.
1969 *S. schei* – Pavlova, p. 81.
1984b *Spirelytha pavlovae* Archbold & Thomas, p. 313.

Diagnosis: Transverse shells with shallow median groove.

Lectotype: The specimen figured as *Spirifer schei* by Tschernyschev & Stepanov (1916, pl. 9, fig. 5-7) from Great Bear Cape, Ellesmere Island, SD Archbold & Thomas (1984b, p. 313).

Discussion: The type material for the genus came from Canada, not from Siberia as in Carter & Gourvennec (2006b, p. 1868) for the *Revised Brachiopod Treatise*. No further material has become available. Adminicula are of uncertain length, and possibly were short, but require elucidation.

Fig. 292. *Spirelytha pavlovae* Archbold & Thomas, ventral, lateral and posterior aspects of ventral valve lectotype, from Great Bear Cape Formation, Arctic Canada, x1. (Tschernyschev & Stepanov 1916).

Spirelytha svartevaegensis Waterhouse, 2016

Fig. 293

1971 *Spirelytha* cf. *S. schei* [not Meyer or Tschernyschew] – Stehli & Grant, p. 518, pl. 63, fig. 3, 5, 6, 9.
1971 *Permophricadothyris*? sp. Stehli & Grant, p. 518, pl. 63, fig. 4, 8, 14-16, 18-20.
1984b *S. pavlovae* [not Archbold & Thomas] – Archbold & Thomas, p. 313.
2016 *Spirelytha svartevaegensis* Waterhouse, p. 331, Fig. 447.

Diagnosis: Transverse with shallow anterior sulcus but no median groove, and no clearly defined dorsal fold or dorsal median ridge, ventral median septum long and well defined. Adminicula exceptionally long.

Holotype: USNM 166288 from Sabine Bay Formation (Kungurian), below Svartevaeg Cliff, north Axel Heiberg Island, Canada, figured by Stehli & Grant (1971, pl. 63, fig. 3, 5, 6, 9) and Waterhouse (2016, Fig. 447A, C) and Fig. 293A, B herein, OD.

Description: The species had been described under two headings by Stehli & Grant (1971). They allocated a ventral valve to *Spirelytha*, and dorsal valves from the locality to *Permophricodothyris*?, but as pointed out by Archbold & Thomas (1984b), the two sets of valves are compatible with each other and belong to one species, and the species was named by Waterhouse (2016, p. 334). Spines are double-barrelled, though poorly preserved, and no delthyrial cover plate is preserved. Dental plates are high, and adminicula exceptionally long. The dorsal valve has socket and inner hinge plates, and no indication of tabellae, and the cardinal process, if present, is small and obscure. A slender median ridge is present in the dorsal valve (Stehli & Grant 1971, pl. 63, fig. 20).

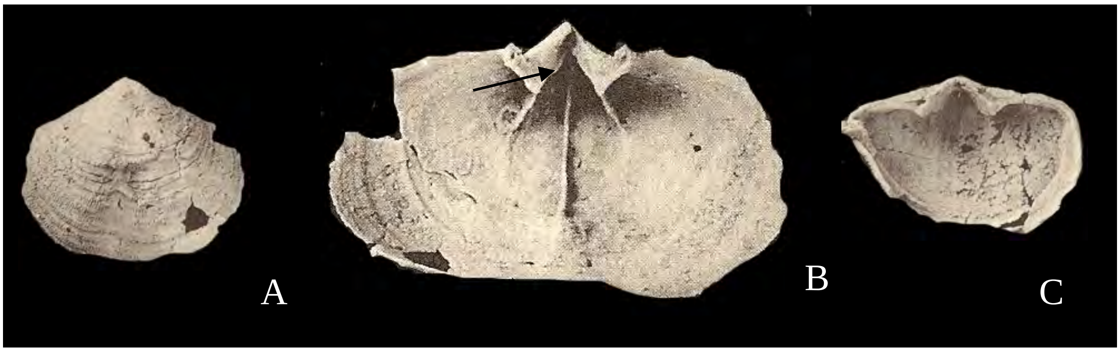

Fig. 293. *Spirelytha svartevaegensis* Waterhouse. A, B, ventral valve exterior and interior, holotype USNM 166288, x1.5, x3. C, dorsal interior, x1.5. From Sabine Bay Formation, Axel Heiberg Island. Note the indications of pleromal ridges (arrowed). (Stehli & Grant 1971).

Resemblances: This species is found in the Sabine Bay Formation. The ventral valve is less transverse than that of *Spirelytha pavlovae* from Great Bear Cape, with lower ventral interarea, shorter hinge, and shallower ventral sulcus, and without the median groove of the lectotype in *pavlovae*. Adminicula are long. Further aspects of the morphology cannot be compared, and clearly the reliance on only one figured ventral valve for understanding of *pavlovae* places limits on understanding any variability in the species. *Spirelytha kislakovi* Klets (1987, 2005, pl. 25, fig. 1-7) from an Early Permian suite of south Verchoyan is similar in its lack of dorsal fold. The present species is partly characterized by its adminicula, which are much longer than those found in many species ascribed to *Spirelytha*, such as those described from Western Australia by Archbold & Thomas (1984b) or the forms recorded from northeast Russia by Klets (2005). *Spirelytha grandis* Klets (2005, pl. 26, fig. 1-5) from the Middle Permian Marshrutninsk Suite of northeast Russia lacks tabellae and has a dorsal valve close to that the present species, but adminicula are short and widely divergent, and the ventral median ridge is long and sturdy. Specimens figured as *S. fredericksi* Archbold & Thomas by Klets (2005, pl. 26, fig. 6-11) have well developed double-barrelled spine bases, ventral adminicula and median septum, low median dorsal ridge and no sign of tabellae. A shallow sulcus and low dorsal fold are present. The specimens come from the Early Permian Sigskar Suite of South Verchoyan.

Spirelytha sp.

Fig. 294

Description: A ventral valve from GSC loc. 58951 from the Trold Fiord Formation of Ellesmere Island is wide as judged from growth lines (the lateral margins are broken) and little inflated, with a shallow median groove passing into a wider shallow sulcus anteriorly, and narrow commarginal rugae, each of which bears a row of double-barrelled spines. The delthyrium is wide with an angle of 50º, and the interarea to each side is narrow. Small teeth are supported by low dental plates, resting in turn on short adminicula.

Resemblances: The specimen is not as transverse as *Spirelytha pavlovae* Archbold & Thomas (1984b) from the Great Bear Cape Formation, but is of somewhat comparable low inflation and has a similar median groove posteriorly and sulcus in front*. S. svartevaegensis* Waterhouse from the Sabine Bay Formation is also transverse, lacks the ventral groove, and has distinctly longer adminicula.

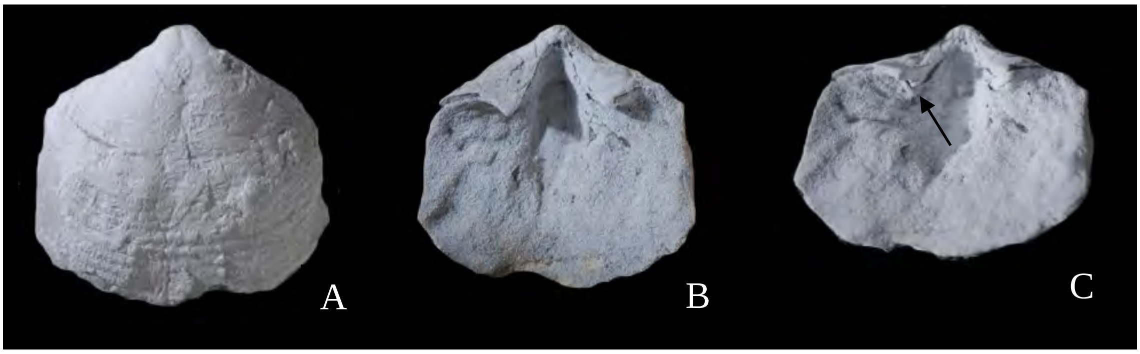

Fig. 294. *Spirelytha* sp. A, B, C, external, internal and tilted internal aspects of GSC 36896 from GSC loc. 58951, Trold Fiord Formation, Ellesmere Island, x2. Arrow in C points to dental plate and adminiculum.

Family **PHRICODOTHYRISIDAE** (**PHRICODOTHYRIDAE)** Caster, 1939

Subfamily **PHRICODOTHYRISINAE** (**PHRICODOTHYRINAE**) Caster, 1939

Genus ***Catatonaria*** Waterhouse, 2013

Diagnosis: Biconvex with anterior commissure weakly uniplicate as a rule, varying to rectimarginate, weak or no sulcus or fold, shell covered by regular commargons bearing each a single row of very short double-barrelled spines, may have fine pustules or spinules as well. Delthyrium may be bordered by low deltidial plates, but not in all specimens. No adminicula or tabellae, median septa low or absent. Spiralia directed posterolaterally.

Type species: *Neophricadothyris catatona* Cooper & Grant, 1976a, p. 2250, from Lenox Hills, Hueco Canyon, Bone Spring and Skinner Ranch Formations (mid-Cisuralian) of Glass Mountains, Texas, OD.

Discussion: The type and associated species from the Glass Mountains of Texas did not have the nature of the spiralia described, and in this study, it is assumed that they are congeneric with what appears to be an allied species from Canada with posterolaterally directed spiralia. Like the Texan type, the Canadian species has very short double-barrelled spines in single rows along each commargon, and like some of the Texan specimens the deltidial plates close the delthyrium, rather than border it each side. Much remains to be described over aspects of spine detail and variation in the subfamily. So far, no further occurrences are known beyond the confines of west Texas and Canada.

Catatonaria transversaria n. sp.

Fig. 295 –301

1960 *Squamularia asiatica* [not Chao] – Harker & Thorsteinsson, p. 64, pl. 18, fig. 12-15, text-fig. 5.

Derivation: transversa – across, Lat.

Diagnosis: Weakly transverse and moderately inflated shells as a rule, some specimens more elongate, some specimens less inflated, with highly incurved ventral beak, short hinge and comparatively wide but short double-barrelled spines.

Holotype: GSC 140939 from GSC loc. 26406, Assistance Formation (Roadian), Devon Island, illustrated herein as Fig. 295B, here designated.

Material: Two ventral valves from C-4002, four ventral valves and a specimen with valves conjoined from C-4019, one ventral valve from C-4025, three specimens with valves conjoined and possible dorsal valve from C-4024, and a ventral valve and specimen with valves conjoined from C-4081, all from the Assistance Formation at Ellesmere Island, as well as ten specimens with valves conjoined and ventral valve from GSC loc. 26406, Assistance Formation, Devon Island. From the Trold Fiord Formation comes a ventral valve from GSC loc. 58951, single ventral valves from C-4014, C-4026 and C-4034, two ventral valves each from C-4017 and C-4021, and a ventral and a dorsal valve from C-4004, Ellesmere Island, as well as a ventral valve from C-4074, Van Hauen Formation, Ellesmere Island. Three ventral valves from JBW 631, Takhandit Formation.

Dimensions in mm: both valves

Width	Length	Height	Umbonal angle	Hinge width	
40	33	?23	70°	24	holotype
29	?26	13		17	
32	30	17	75°	13	
35.5	30.5	24	80°	21	

Description: Shells of moderate size for genus, transverse as a rule, rarely elongate, ventral umbo incurved and umbonal walls long, straight or very slightly concave in outline, cardinal interarea well formed, gently concave and short, interrupted by broad delthyrium with angle of 45°, bordered by low flanges. The ventral umbo protrudes a little posteriorly, and has an angle of between 90° and 100°. The dorsal interarea is low with notothyrium obscure. The ventral valve is generally twice as high as the dorsal valve, but may be even higher, and some specimens are more elongate, and a few are less inflated and moderately transverse. Apart from a slight reduction medianly in convexity there is no ventral sulcus in some shells, but others have a shallow depression commencing well in front of the umbo, and contained within an angle of 20°. The dorsal valve lacks a fold. Both valves are covered by commargons, weakly convex and each separated by a weak depression or abrupt edge of a growth lamellum. Each commargon bears a single row of comparatively wide double-barrelled spines, six to eight in 5mm anteriorly, except for one or two anterior commargons that have two rows of smaller single-barrelled spines. The double-barrelled spines lie close to the anterior margin of some commargons, with two or three rows of slender single-barrelled spines behind them, and some commargons have only single-barrelled spines. The anterior margin is rectilinear.

The delthyrium is closed under the beak by a small plate, almost flat or gently convex with a median ridge, differing in different shells, and probably formed from two deltidial plates. Teeth are carried on low but distinct dental plates, without any supporting adminicula. The muscle field is large and elongate, and medianly depressed in two long adductor scars. To each side, the diductor scars are broader and less impressed, and both sets are deeply striated longitudinally. The muscle field is divided by a low median ridge, which is higher in some specimens over the posterior third of the shell length, but this vanishes with increase in size, and secondary thickening comes to bury the internal signs of external commargons visible in less mature specimens. The posterior shell each side of the muscle field bears shallow evenly spaced pits, and in some shells, the worn or partly decorticated shell shows radiating slender ribs, not visible externally. One ventral valve from JBW 631 shows a network of high ridges posteriorly each side of the muscle field (Fig. 297).

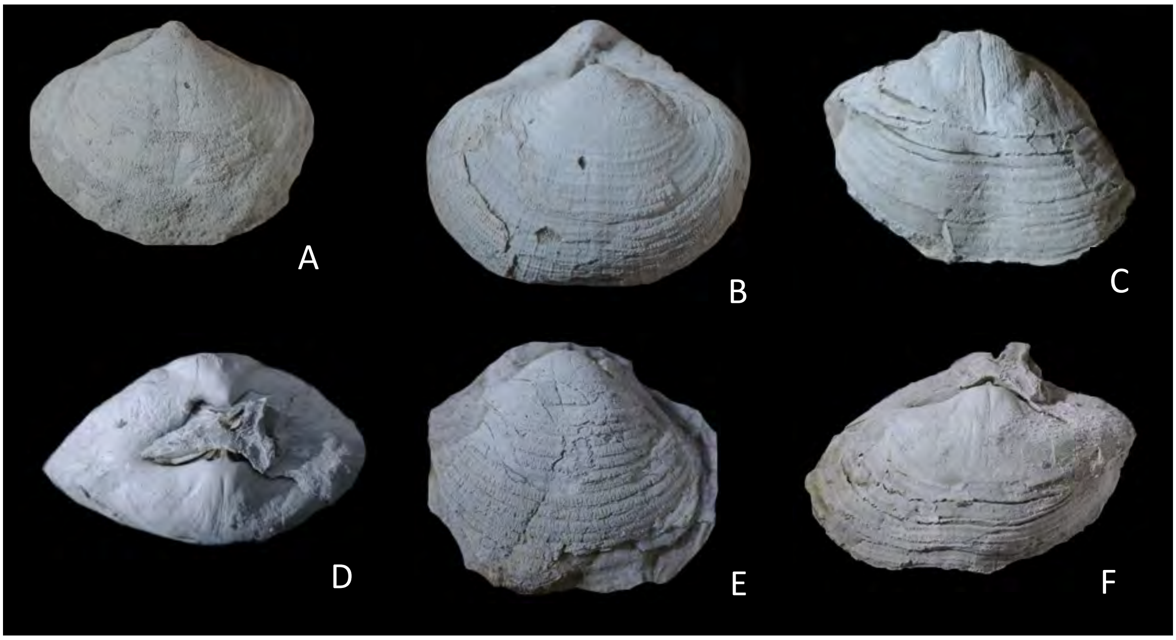

Fig. 295. *Catatonaria transversaria* n. sp. A, ventral view of specimen with valves conjoined, GSC 140938. B, dorsal aspect of specimen with valves conjoined, holotype, GSC 140939. C, D, F, ventral, posterior (ventral valve on top) and dorsal aspects of internal mould, GSC 140940. Specimens from GSC loc. 26406, Assistance Formation, Devon Island. E, ventral valve GSC 140942 from C-4004. Trold Fiord Formation, Ellesmere Island. Specimens x1.

In the dorsal valve, the ctenophoridium has vertical blades, recessed medianly and lower and finer to each side in at least one specimen. Socket plates lie to each side, with crenulate sockets. A very low and slender median ridge extends for half of the length of the shell in less mature specimens, but disappears with increased maturity and thickening of shell. To each side the shell is depressed, with a smooth portion posteriorly, and shallow grooves and low ridges arranged are longitudinally in front, which become exaggerated with increased maturity, whilst the median ridge broadens but remains comparatively low. Harker & Thorsteinsson (1960, text-fig. 5) provided some cross-sections. There are twelve coils in the spire of one specimen, eighteen in another, and spiralia are directed postero-laterally.

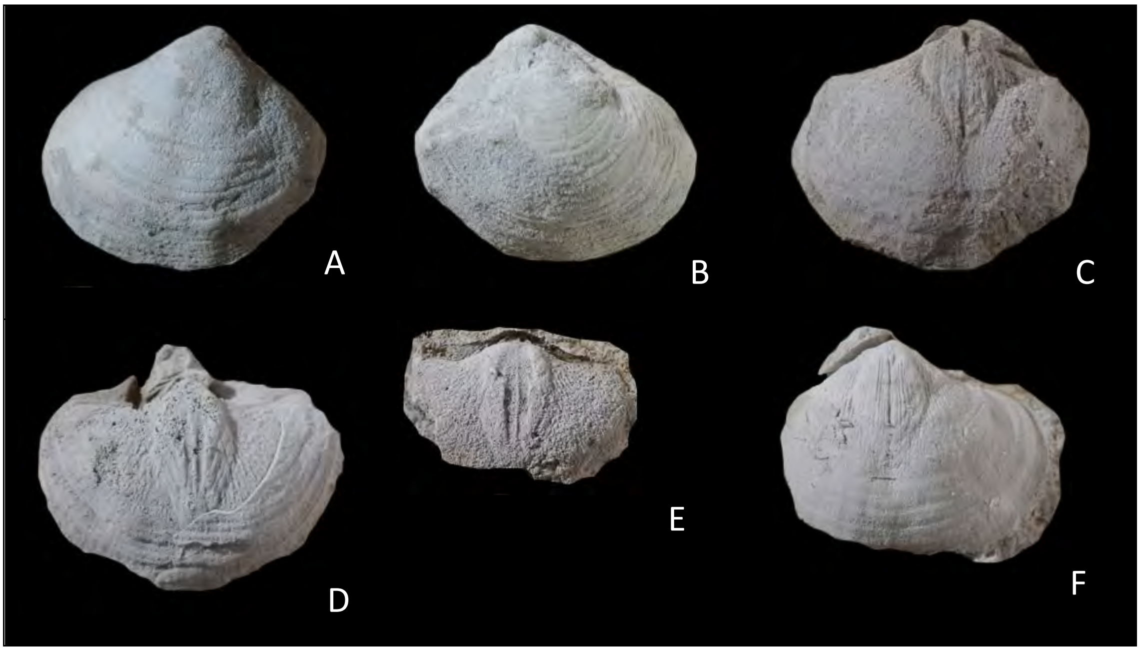

Fig. 296. *Catatonaria transversaria* n. sp. A, B, ventral and dorsal views of specimen with valves conjoined, GSC 140943. C, D, ventral and dorsal views of specimen GSC 140944 with valves conjoined, leached to show interior. E, dorsal internal mould GSC 140945. From GSC loc. 26406, Assistance Formation, Devon Island. F, leached ventral internal mould GSC 140946 from C-4081, Assistance Formation, Ellesmere Island. Specimens x1.

Resemblances. Some of the specimens described as *Neophricadothyris catatona* Cooper & Grant (1976a, pl. 636, fig. 1-25) are of much the same shape as the Canadian species, but have a shallow sulcus and low fold in a number of specimens, and with very narrow commargons. The type species has unusually short double-barrelled and fine single--barrelled spines along single rows. It comes from the Skinner Ranch Formation of early Permian age, and because of its spination, was distinguished as type species for *Catatonaria* Waterhouse, 2016, p. 344. As a rule, the delthyrium is open and is bordered in some specimens by low deltidial plates, but other specimens lack these plates, like the present species, or have a deltidium. *Neophricadothyris crassibecca* Cooper & Grant (1976a, pl. 638, fig. 1-33) from the Road Canyon Formation also has short fine spines and low deltidial flanges, and is judged to be congeneric.

Bullarina bullata (Cooper & Grant, 1976a, pl. 635, fig. 1-64, pl. 649, fig. 20-24) from upper Cisuralian as well as early Guadalupian (Road Canyon) beds of the Glass Mountains in Texas is a much narrower shell than the Canadian species, with prominent deltidial plates bordering the delthyrium in some specimens and a well-formed

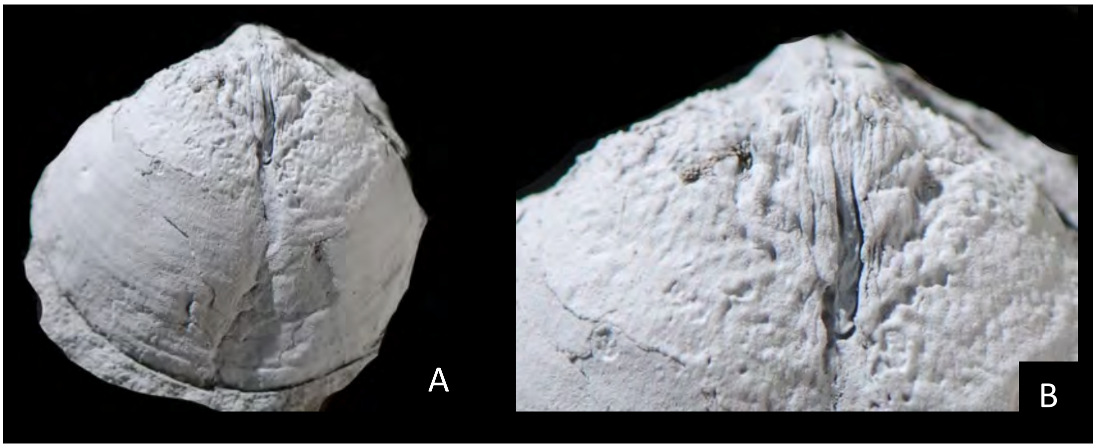

Fig. 297. *Catatonaria transversaria* n. sp. A, B, ventral internal mould, GSC 140947. A, entire valve, x1. B, enlargement of posterior showing muscle impressions and posterior complexly ridged shell surface, x4. Specimen from JBW 631, Takhandit Formation.

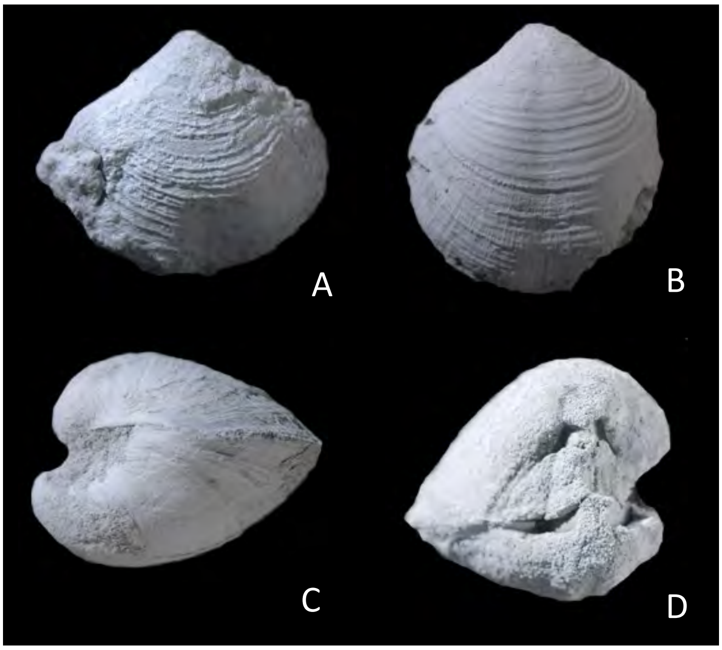

Fig. 298. *Catatonaria transversaria* n. sp. A, ventral valve GSC 140988 with well developed commarginal laminae. B, ventral valve, GSC 140995, x1. C, D, conjoined swollen specimen GSC 140996, C, lateral aspect, shell with dorsal valve on top. D, posterior aspect, specimen leached, ventral valve on top, x1.5. From GSC loc. 26406, Assistance Formation, Devon Island.

convex deltidial plate in other specimens. It was distinguished as genus *Bullarina* by Jin & Sun (1981), on account of the posterolaterally directed spiralia. Unlike *Catatonaria*, double-barrelled spines are frequently developed in a double rather than single row along each commargon, and deltidial plates or deltidium are well developed. The

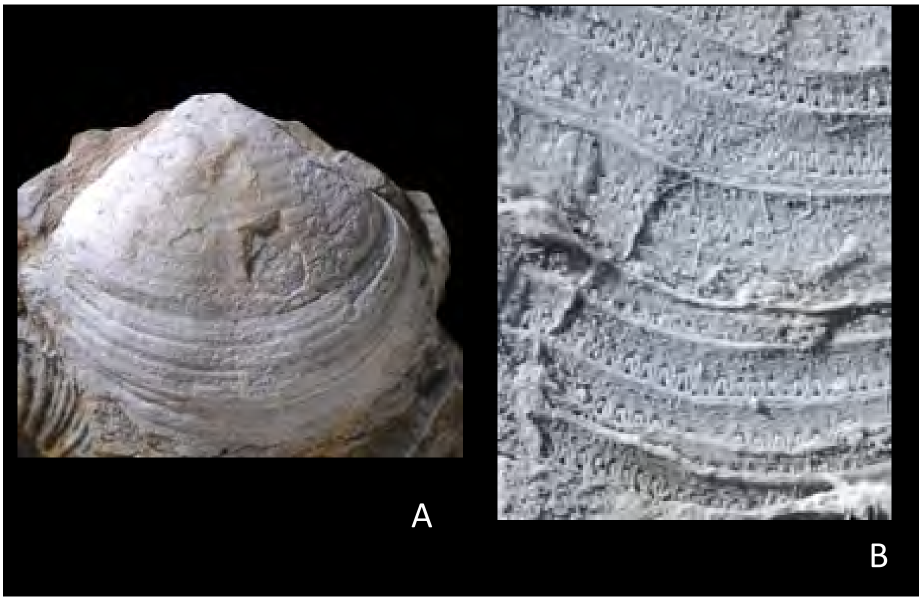

Fig. 299. *Catatonaria transversaria* n. sp. A, ventral valve GSC 140998 from GSC loc. 26406, Assistance Formation, Devon Island, x2. B, external mould GSC 140948 showing bases of single and double-barrelled spines on ventral valve, from GSC loc. 26406. Assistance Formation, Devon Island, x4.

dental supports are comparatively high, and a low median septum is present in each valve. Carter (2006c, p. 1866) stated that the type species was of Lopingian age, but the source formations, named as Bone Spring, Hess, Cathedral Mountain and Road Canyon Formations, are upper Cisuralian and lower Guadalupian in age. The well-rounded species *conara* Cooper & Grant (1976a) from the lower Word Formation (now Roadian Stage) also has two rows of spines over a number of commargons, as does *cordata* Cooper& Grant (1976a) from the Road Canyon Formation, a shell with moderately rounded outline, less transverse than the present species.

Fig. 300. *Catatonaria transversaria* n. sp., leached specimen GSC 141005 with valve conjoined showing posterolaterally oriented spiralia. Specimen from C-4034, Trold Fiord Formation, Ellesmere Island, x2.

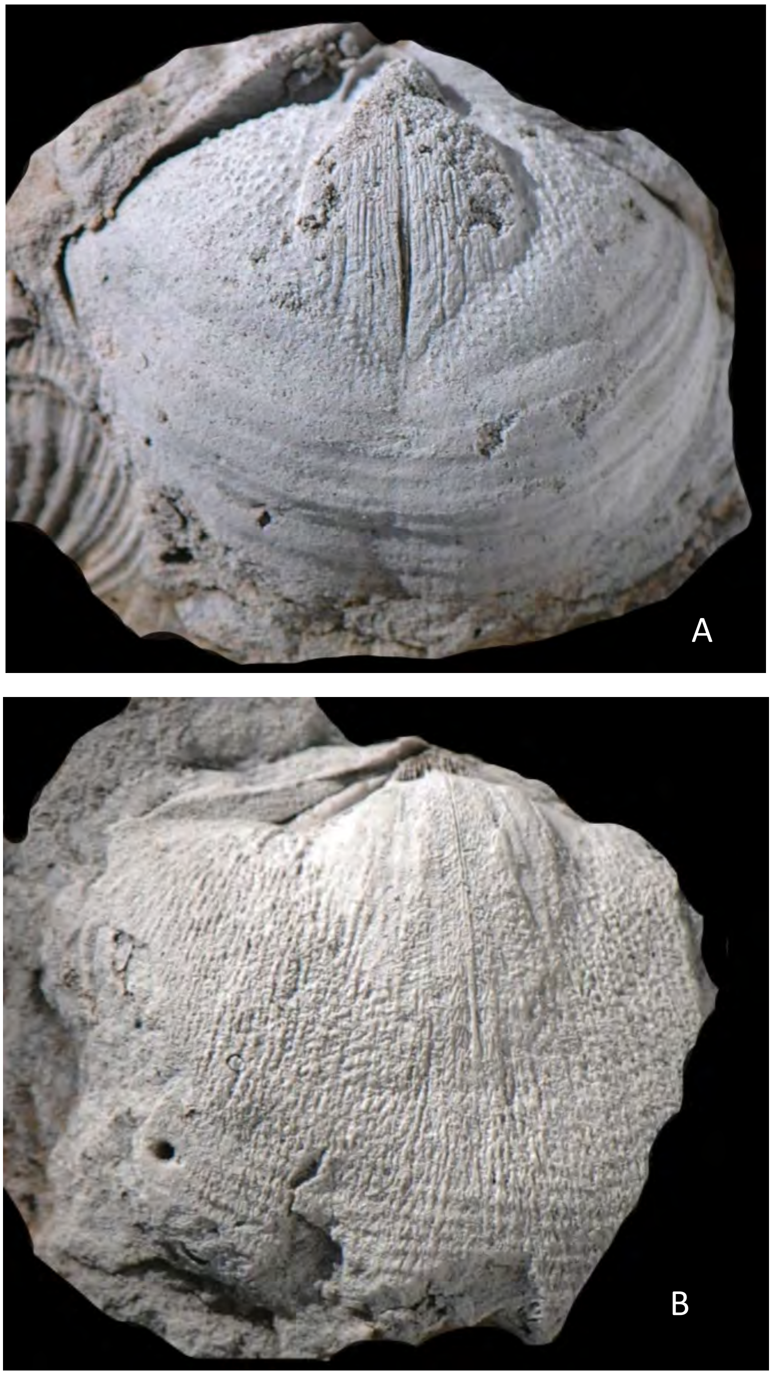

Fig. 301. *Catatonaria transversaria* n. sp. A, internal mould of ventral valve GSC 140997. B, internal mould of dorsal valve, GSC 140994. From GSC loc. 26406, Assistance Formation, Devon Island, x3.

The distinctive transverse species described as *Neophricadothyris transversa* Cooper & Grant (1976a, pl.639, fig. 1-27) may also display slight fold and sulcus, has fine commargons, and is well inflated. The spiralia are parallel to the hinge, and so approach those of *Phricodothyris* George, 1932, rather than those of the present form. It comes from the Neal Ranch Formation of Asselian age, and has short spines as in *Catatonaria catatona*. Like some of the other species it has low deltidial plates that fuse under the umbo, less conspicuous than those of *Bullarina bullata* (Cooper & Grant, 1976a).

The present species is more transverse than *Phricodothyris lenaensis* Abramov & Grigorieva (1983, p. 140, pl. 32, fig. 10-12, Fig. 55; Solomina 1978, p. 120, pl. 11, fig. 10, 11; Klets 2005, p. 152, pl. 28, fig. 4-8) from the upper Carboniferous Etiken level of Southern Verchoyan. Specimens ascribed to *Neophricadothyris asiatica* (Chao) from various upper Carboniferous and Permian faunas by Gobbett (1964, pl. 17, fig. 1-3; Ifanova 1972, pl. 13, fig. 5-10; Kalashnikov 1998, pl. 28, fig. 3, pl. 31, fig. 7, 8) are less transverse as a rule and inflated, approaching a Sakmarian species from the Callythara Formation of Western Australia, called *P. occidentalis* Archbold & Thomas, 1984b.

Infrasuborder AMBOCOELIAIMORPHI (AMBOCOELIIMORPHI) Waterhouse, 2016

Superfamily **AMBOCOELIAOIDEA** (**AMBOCOELIOIDEA)** George, 1931

Family **AMBOCOELIAIDAE** (**AMBOCOELIIDAE)** George, 1931

Subfamily **CRURITHYRISINAE** (**CRURITHYRINAE)** Waterhouse, 2016

Diagnosis: Members of this subfamily have a well-developed cardinal plate and several coils in the spiralia. Dorsal muscle scars are placed side by side, not fore and aft as in Ambocoeliinae.

Genus ***Orbicoelia*** Waterhouse & Piyasin, 1970

Diagnosis: Ventribiconvex, dorsal valve gently convex, weak or no sulcus, micro-ornament of uniramous spinules, knob-like cardinal process which is not tuberculate, small distinct cardinal plate, dorsal adductor scars placed side by side. Spiralia simple with several coils.

Type species: *Orbicoelia fraterculus* Waterhouse & Piyasin, 1970, p. 145 from Khao Phrik Limestone (Roadian) of Thailand, OD.

Discussion: *Orbicoelia* was first described from Thailand, and has been widely recognized, even in very early Triassic deposits (Chen et al. 2006).

Orbicoelia*? *aquilonia (Stehli & Grant, 1971)

Fig. 302

1971 *Crurithyris aquilonia* Stehli & Grant, p. 514, pl. 64, fig. 1-16.
?1971 *Crurithyris* sp. Bamber & Waterhouse, p. 178, pl. 21, fig. 17, 18.

Diagnosis: Small and biconvex with moderately prominent ventral umbo, well rounded cardinal extremities.

Holotype: GSC 26168 from Sabine Bay Formation (Kungurian), Axel Heiberg Island, figured by Stehli & Grant (1971, pl. 64, fig. 1-6) and Fig. 302B herein, OD.

Description, Discussion: The species was described by Stehli & Grant (1971) and compared with three other species. Although the generic position cannot be confirmed for *aquilonia*, because of the poor preservation of several critical features, involving the spiralia, other major features such as shape, open delthyrium, and possible ornament of fine uniramous spines suggest *Orbicoelia*. Stehli & Grant (1971) stated that fine radial costellae were apparently present, but cautioned that the apparent ribs might have resulted from silicification (cf. Balinski, 1975). *Crurithyris* sp. recorded by Bamber & Waterhouse (1971, pl. 21, fig. 17, 18) is shaped like *aquilonia* and comes from rocks of Wordian age in the Richardson Mountains at GSC loc. 53848. It shows distinct pustules or spinules, apparently all of much the same diameter, over the ventral valve, as in *Orbicoelia*. *Crurithyris* George, 1932 on the other hand has spinules of two different diameters (Brunton 1976, p. 768, 1984). The Yukon specimen was considered in Bamber & Waterhouse (1971) to show some approach to *Crurithyris arcuata* (Girty) from the Phosphoria Rock Complex of Idaho, Wyoming and Montana (Girty, 1910, p. 35, pl. 6, fig. 15-17, 1927; Branson 1930, p. 36, pl. 11, fig. 12-14), but this species has a narrow dorsal sulcus. *Crurithyris edemskyi* Grunt (2006b, p. 157, pl. 13, fig. 7, 8) from Ufimian faunas of Kanin is somewhat similar in shape, but its dorsal interior is not known.

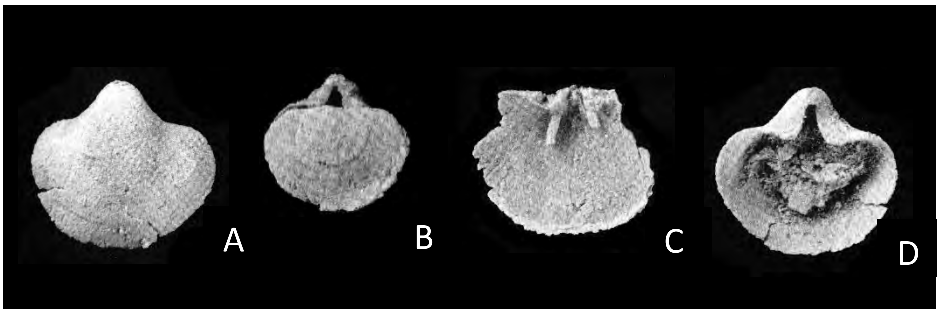

Fig. 302. *Orbicoelia*? *aquilonia* (Stehli & Grant). A, D, external and internal aspects of ventral valve, USNM 166301. B, dorsal aspect of specimen with valves conjoined, holotype GSC 26168. C, internal aspect of dorsal valve, USNM 166299. Specimens x3, from Svartevarg cliffs, Axel Heiberg Island. (Stehli & Grant 1971).

Order SPIRIFERINAIDA (SPIRIFERINIDA) Ivanova, 1972

Suborder SPIRIFERINAIDINA (SPIRIFERINIDINA) Ivanova, 1972

Superfamily **PENNOSPIRIFERINAOIDEA** (**PENNOSPIRIFERINOIDEA)** Dagys, 1972

Family **RETICULARIINAIDAE** (**RETICULARIINIDAE)** Waterhouse, 1975

Diagnosis: Transverse with fine plicae and well-defined sulcus and fold; micro-ornament of coarse hollow spines. In the dorsal valve the crural plates often unite to form a small cardinal plate with median ridge, and varying development of tabellae, as is also seen in some Paraspiriferinidae.

Genus ***Reticulariina*** Fredericks, 1916

Diagnosis: As in diagnosis, without exceptional shape or features.

Type species: *Spirifer spinosus* Norwood & Pratten, 1855, p. 71 from Chesterian of Illinois, United States, OD.

Reticulariina? sp. A

Fig. 303

Material, Description: A ventral valve from GSC loc. 57720, Great Bear Cape Formation, has five pairs of plicae and a narrow sulcus bearing a median rib. There are signs of comparatively large punctae aligned in a single row along the crest of each plication, and others on the flanks and within the interspaces, and a row lies along the sulcus. Tschernyschew & Stepanov (1916, p. 56) recorded a punctate shell as *Spiriferina cristata* Schlotheim from Great Bear Cape that may prove to be related. They did not figure the specimen.

Fig. 303. *Reticulariina*? sp. A, ventral valve GSC 36948 from GSC loc. 57720, Great Bear Cape Formation, Ellesmere Island, x5.

Genus ***Gjelispinifera*** Ivanova, 1975

Diagnosis: Well developed spines arranged in one or two rows along crests of plicae and in the type species along floor of sulcus. Otherwise like *Reticulariina*.

Type species: *Gjelispinifera gerasimovi* Ivanova, 1975, p. 86 from Gzhelian of Moscow Basin, OD.

Gjelispinifera punctuata n. sp.

Fig. 304 – 307

Derivation: punctum – puncture, a prick, Lat.

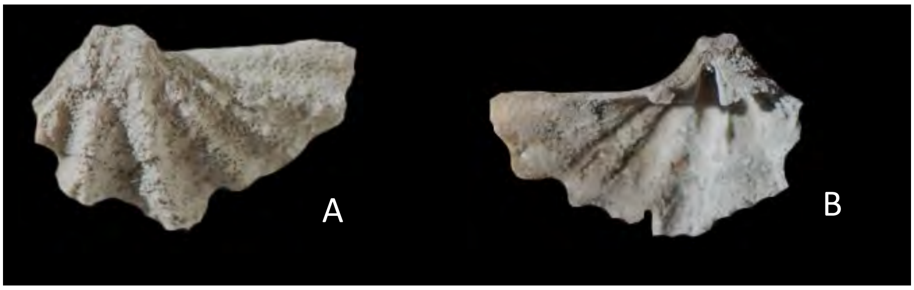

Fig. 304. *Gjelispinifera punctuata* n. sp. A, B, exterior and interior of ventral valve GSC 140952 from GSC loc. 53846, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory, x 4.

Fig. 305. *Gjelispinifera punctuata* n. sp. A, dorsal valve, external and internal aspects, GSC 140983, x4. From GSC loc. 53846, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory.

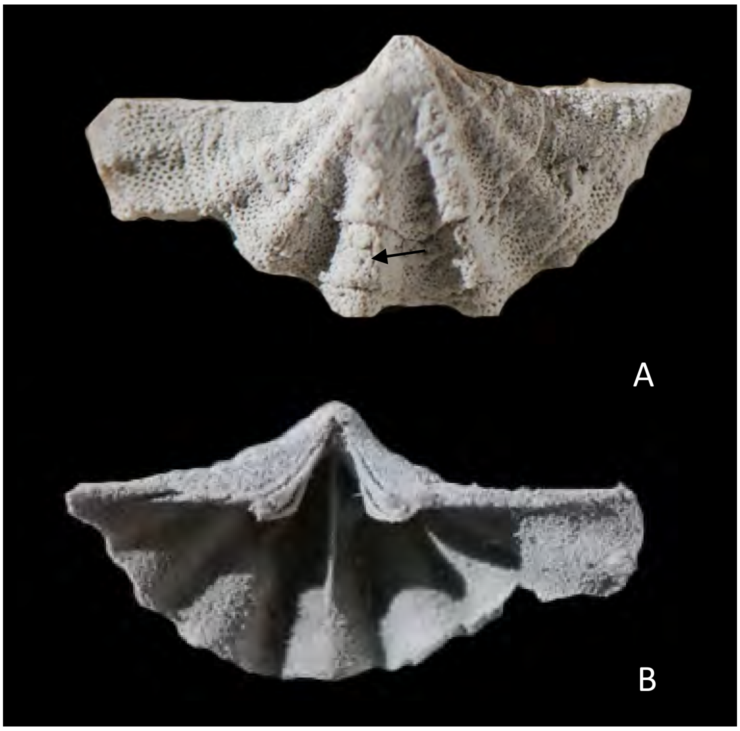

Fig. 306. *Gjelispinifera punctuata* n. sp. A, B, external and internal aspects of ventral valve GSC 140951 holotype, with row of spines along the crest of each plication, with one spine arrowed, x4 approx. From GSC loc. 53846, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory.

Diagnosis: Transverse with coarse spines aligned in single row along the crest of the fold and crests of the plicae, no coarse spines along floor of sulcus nor interspaces, shell finely punctate.

Holotype: Specimen GSC 140951 figured herein as Fig. 306A, B from GSC loc. 53846, Richardson Mountains, north

Yukon Territory, *Dyoros modestus* Zone, here designated.

Material. Four ventral valves and four dorsal valves, silicified, from GSC loc. 53846, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory.

Description: Specimens transverse, a ventral valve measuring 25mm, an estimated 9mm long, and 4mm high, and a dorsal valve measuring 15mm wide, 7.5mm long and 3.5mm high. Ventral umbo prominent, umbonal angle of 80º to 85º, posterior walls sweeping out to obtuse cardinal extremities at maximum width of shell. Delthyrium open with angle of 40º to 45º, interarea gently concave, moderately high, marked by horizontal growth striae. The dorsal interarea is much lower, planar, and with a wide notothyrium for which the angle measures 110º to 120º. The sulcus commences at the umbonal tip and widens at an angle of 25º, with a narrow trough-like floor, and the dorsal fold has a narrowly rounded crest and is only slightly higher than the plication to each side. Ventral plicae number four pairs, with narrow crests and groove-like interspaces. Dorsal plicae are similar in style and number. A row of coarse open spines, up to two in 1mm, lies along the crest of the fold and along the crest of each plication in each valve, but there are none along the sulcus or interspaces. Commarginal laminae are prominent over the anterior of dorsal and ventral valves. The shell is finely punctate, with 150 to 180 punctae in 1 square mm. The delthyrium is bordered by dental tracks each leading to a low tooth, and supported by inwardly converging low dental plates which rest posteriorly on short high adminicula diverging to the floor of the valve. A low median septum extends over less than the posterior half of the valve. Dental sockets are enclosed by horizontal socket plates and high inwardly converging crural plates, which are joined by a subhorizontal cardinal plate with low rounded median ridge. It may rest above the floor of the valve, or be sessile. Two long tabellar ridges lie over the floor of the valve directly under each crural plates, but are not contact with anterior crural plates. There is no median septum. Muscle scars are not visible in either valve.

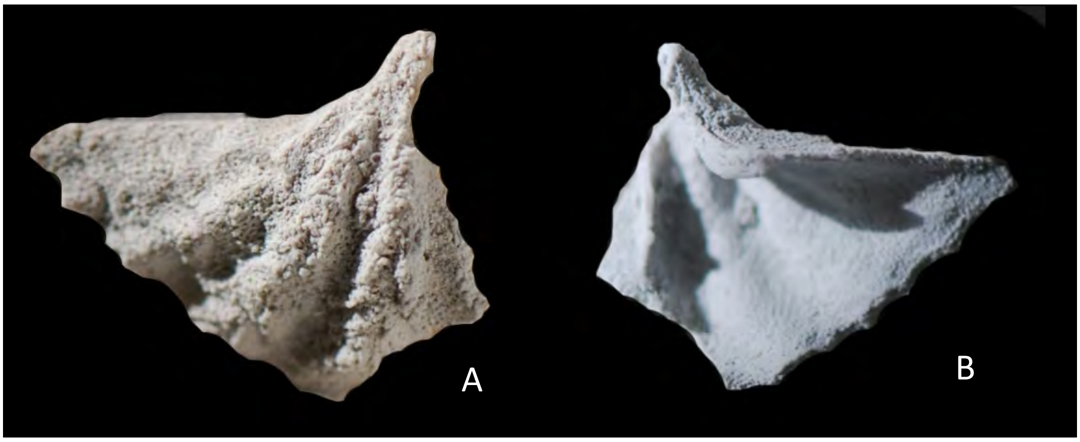

Fig. 307. *Gjelispinifera punctuata* n. sp. A, B, external and internal fragment of ventral valve GSC 140950, x5. B show median septum and slender dental plates. From GSC loc. 53846, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory.

Resemblances: *Gjelispinifera gerasimovi* Ivanova, 1975, p. 86 from the Gzhelian Stage of the Moscow Basin in Russia has one or two more pairs of plicae, and narrower ventral sulcus. Large spinules lie in a row along the floor of the ventral sulcus, unlike the arrangement in the present species. In the present species a short thick plate lies immediately in front of the cardinal process, connected laterally to the outer hinge plates and extending forward as a low ridge each side. The plate may bear a low rounded ridge. A similar cardinal plate is well figured by Cooper & Grant (1976b, pl. 720, fig. 59) for *Paraspirifera cellulana*, and in pl. 721, fig. 37, 39, 40 for *P. formulosa*.

Family **PARASPIRIFERINAIDAE** (**PARASPIRIFERINIDAE**) Cooper & Grant, 1976b

Genus ***Paraspiriferina*** Reed, 1944

Diagnosis: Small strongly biconvex with well rounded cardinal extremities and well-defined sulcus. Fold and plicae, fine closely spaced commarginal laminae and short hollow spinules or papillae. Dorsal tabellae, punctae fine.

Type species: *Spiriferina* (*Paraspiriferina*) *ghundiensis* Reed, 1944, p. 252 from Wargal Formation (Wuchiapingian, Lopingian Series, not Guadalupian as in Carter 2006c, p. 1914), Pakistan, OD.

Paraspiriferina mcdougallensis n. sp.

Fig. 308, 309

Derivation: Named from McDougall Pass, north Richardson Mountains in Yukon Territory.

Diagnosis: Very small shells with four pairs of plicae, no outstanding deltidial plates.

Holotype: GSC 140954, figured as Fig. 308A, B from GSC loc. 53846, *Dyoros modestus* Zone, unnamed sandstone, McDougall Pass, north Richardson Mountains, here designated.

Material: One dorsal valve, four ventral valves and one specimen with valves conjoined from GSC loc. 53846, and two ventral valves from GSC loc. 53848, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory. One ventral valve from C-4004, Trold Fiord Formation, Ellesmere Island.

Description: Specimens small, the conjoined specimen measuring 6mm in width, 5.6mm in length and 5.8mm in height. The ventral umbo has an angle of 95° and is well extended but only slightly incurved, and the posterior walls with backward concave outline pass laterally to the markedly obtuse cardinal extremities. Maximum width lies a little in front, close to mid-length. The ventral interarea is five sixths of the width, and high, with light horizontal grooves. An open narrow delthyrium widens at an angle of 25°, and shows no sign of deltidial or stegidial plates of the sort reported for Glass Mountains specimens assigned to *Paraspiriferina* by Cooper & Grant (1976b), but not mentioned or shown in illustrations for the type species by Reed (1944). The dorsal interarea is very low and almost planar with wide and open notothyrium. The sulcus commences at the beak and widens at a steady angle close to 20°, and has a narrow but rounded floor. The dorsal fold is higher and more prominent than the plicae, with rounded only moderately wide crest. Plicae number four pairs on the ventral valve, including a short outermost pair, and the dorsal plicae number three pairs. Both valves are crossed by low commarginal laminae, numbering five to seven in 1mm anteriorly on the ventral valve, and the shell is covered by dense tiny pustules, in a row along each commargon, as many as eight in 1mm across the anterior ventral shell.

Teeth are supported by scapular-shaped dental plates, which are supported by high and short adminicula. The median septum extends for a variable length from the posterior wall, a little less to more than half of the shell

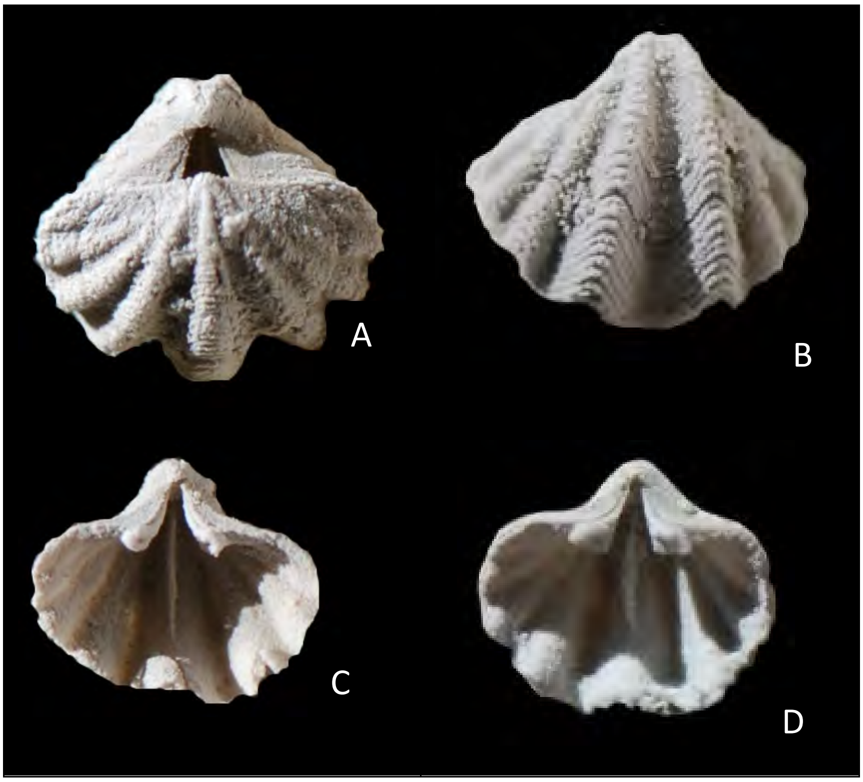

Fig. 308. *Paraspirifer mcdougallensis* n. sp. A, B, dorsal and ventral aspects of GSC 140954 holotype with valves conjoined. C, internal aspect of ventral valve GSC 140955. D, ventral interior of specimen GSC 140956. Specimens x6, from GSC loc. 53846, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory.

length. Muscle scars are not clearly defined. The dental sockets are well formed, with high inward sloping crural plates along the inner side, extending almost to the floor of the valve, and underlain by low tabellae which extend well forward. The posterior crural plates converge to fuse medianly and bear a low median ridge. In another and larger dorsal valve, the converging plates extend further forward. These details were displayed on a dorsal valve from GSC loc. 53846 that has now crumbled.

Resemblances: The type species of the genus, described as *Spiriferina* (*Paraspiriferina*) *ghundiensis* Reed (1944, p. 252, pl. 33, fig. 1, a-c, 2, a-c), has more plicae, a low median swelling in the posterior ventral interior, and long stronger median septum. From the Neal Ranch Formation of Asselian age in the Glass Mountains of Texas, *Paraspiriferina amoena* Cooper & Grant (1976b, pl. 720, fig. 1-35) is close in the number of plicae but has lower ventral interarea. All the other Glass Mountains species have more plicae, and are larger. Some of the species have stegidial plates preserved along the sides of the delthyrium, but nothing comparable is seen in present specimens. *Spiriferina multiplicata* so named by Sowerby (1829) [in the Sedgwick Trans. Geol. Soc. 2nd ser. 3: 119] was first described, illustrated and therefore validated under the genus *Trigonotreta* by King (1850, p. 129, pl. 8, fig. 15-18) from the

Magnesian Limestone of England, and as reported below (p. 362), has been confused with an entirely different genus by Shen & Clapham (2009). It is smaller and more transverse than the Canadian species, with slightly narrower sulcus and narrower and higher dorsal fold. The species also includes the specimen recorded as *Trigonotreta jonesiana* King (1850, p. 129, pl. 8, fig. 19).

Fig. 309. *Paraspiriferina mcdougallensis* n. sp A, ventral valve GSC 140984. B, dorsal interior GSC 140957 x6 from GSC loc. 53846, unnamed sandstone unit, McDougall Pass, Richardson Mountains, Yukon Territory.

Paraspiriferina stoschensis n. sp.

1931 *Spiriferina multiplicata* [not King] – Frebold, p. 10, pl. 1, fig. 12-14.
1955 *Spiriferina multiplicata* [not King] – Dunbar, p. 147, pl. 29, fig. 1-9.

Derivation: Named from Cape Stosch, east Greenland, source of some of the material.

Diagnosis: Small transverse shells with up to seven pairs of dorsal plicae that curve outward slightly, high ventral interarea. Very fine spinules apparently developed along anterior margin of each lamination (Dunbar 1955, pl. 29, fig. 9).

Holotype: Specimen figured by Dunbar (1955, pl. 29, fig. 1-3) from white blocks at Kap Stosch, east Greenland, here designated.

Description, Resemblances: The material has been described by Frebold (1931) and Dunbar (1955). The Greenland specimens were referred to *multiplicata* King (1850, p. 129, pl. 8, fig. 15-18) from the Magnesian Limestone in England, but the English specimens are very small and not convincingly conspecific, having only three to five plicae pairs. Micro-ornament in the Greenland material was described as consisting of numerous irregularly spaced lamellose growth varices, and the shell as punctate, indicating a position within *Paraspiriferina*. Low deltidial flanges lie each side of the delthyrium. The species is distinguished from *Paraspiriferina mcdougallensis* n. sp. described from the *Dyoros modestus* Zone in being more transverse with more plicae and a slightly higher ventral interarea, whereas the type species of the genus is transverse with slightly channelled crest to the dorsal fold, and more plicae.

Paraspiriferina? sp.

Fig. 310

Material: An internal mould with valves conjoined from GSC loc. 26406, Assistance Formation (Roadian), Devon

Island.

Dimensions in mm: both valves

Width	Length	Height
18	21-23?	19.5

Description: An inflated internal mould with valves conjoined from the Assistance Formation at GSC loc. 26406 has seven pairs of narrow plicae on each valve, well defined sulcus widening at 20º, and long median septum. Plicae are finer and more numerous than is normal for *Spiriferellina*. The lack of micro-ornament means that the identification is no more than provisional, but the similarity of the present specimen to material described by Dunbar (1955) suggests a possible approach to *Paraspiriferina*, and described above as a new species, although the Greenland specimens are more rounded in shape.

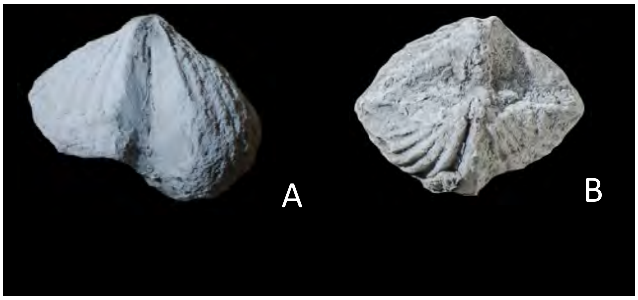

Fig. 310. *Paraspiriferina*? sp. A, B, ventral and dorsal aspects of specimen GSC 140949 with valves conjoined, from GSC loc. 26406, Assistance Formation, Devon Island, x1.

Genus ***Costasulculus*** n. gen.

Derivation: costa – rib, sulcus – groove, Lat.

Diagnosis: Small punctate and plicate shells, with closely-spaced commarginal growth lamellae and commarginal rows of fine spines, distinguished by the presence of costae traversing sulcus and fold. Ventral valve with median septum and adminicula and dental plates; dorsal valve with crural plates supported by high tabellae.

Type species: *Costasulculus claphami* n. sp. from Wuchiapingian of Hydra, Greece, here designated.

Discussion: The genus is very close to *Paraspiriferina* in having four or five pairs of strong plicae, micro-ornament of fine commarginal growth laminae each with a fringe of fine spinules, and the full complement of internal plates found for *Paraspiriferina*. What distinguishes the genus is the presence of a pair of firm costae extending for much of the length of the sulcus and fold. Similar costae lie over the anterior fold in a Carboniferous specimen figured by Sowerby (1829, pl. 562, fig. 4).

Costatisulcus claphami n. sp.

2009 *Paraspiriferina multiplicata* ([not Sowerby or King] – Shen & Clapham, p. 735, pl. 6, fig. 22-25, pl. 7, fig. 1-4.

Derivation: Named for M. E. Clapham.

Diagnosis: Small punctate shells with six pairs of plicae, very fine commarginal laminae and hair-like spines. A pair of costae traverses most of the length of the sulcus and a strong costa lies each side of the median fold. High dental plates, adminicula and tabellae and crural plates.

Holotype: NIGP143614, figured by Shen & Clapham (2009, pl. 5, fig. 22-25) from Episkopi Formation (Wuchiapingian), Hydra, here designated.

Description, Resemblances: The species has been described and well illustrated. The sulcal and fold costae are well developed, and largely consistent between specimens. The dorsal fold costae lie one each side of a median plication forming the crest of the fastigium. The commarginal laminae are very narrow, and it was noted that the dorsal valve has lost the fine hair-like spines, though these were probably present and presumably have been worn away. The dorsal interior displays high crural plates and tabellae, without any sign of the posterior small plate bearing a median ridge that is prominent in the specimens of *Paraspiriferina* from Canada and the United States.

The Hydra specimens look somewhat like one of the specimens allocated to *Spirifer octoplicata* by Sowerby (1829, pl. 562, fig. 4) from the Early Carboniferous of Derbyshire. This specimen has strong plicae, fine commarginal laminae, and short costae over the anterior lateral fold. Two other specimens (Sowerby, 1929, pl. 562, fig. 2, 3), do not show the anterior costae, but are smaller. Davidson (1861, p. 267, pl. 4, fig. 10, 12) believed that the species was identical with *Spiriferina cristata* (Schlotheim), and in compiling a lengthy synonymy, Shen & Clapham (2009) allocated the Hydra specimens to *Paraspiriferina multiplicata* (Sowerby), omitting the critical study by King (1850). The Derbyshire specimens are very much older than the Hydra specimens, and the Sowerby material differs from the present form in having better defined commarginal laminae and shorter submedian costae.

Family **SPIRIFERELLINAIDAE** (**SPIRIFERELLINIDAE**) Ivanova, 1972

Genus ***Spiriferellina*** Ivanova, 1972

Diagnosis: Small shells with strong plicae, micro-ornament of fine well spaced spines.

Type species: *Terebratulites cristatus* Schlotheim (alt. von Schlottheim), 1816, p. 28, from Zechstein (Wuchiapingian) of Germany, OD.

Spiriferellina cristata (Schlotheim, 1816)

Fig. 311

1816 *Terebratulites cristata* Schlotheim, p. 28, pl. 1, fig. 3a-c.
?1845 *Spirifer octoplicatus* (not Sowerby) – Robert, pl. 19, fig. 1.
1850 *Spirifer cristata* – King, p. 127, pl. 8, fig. 9-14.
1849 *S. cristatus* – Koninck, pl. 11, fig. 6.
1861 *S. cristata* – Geinitz, p. 88, pl. 16, fig. 8-11.
1955 *Punctospirifer cristata* – Dunbar, p. 149, pl. 29, fig. 13-20.
1959b *Spiriferellina cristata* – Campbell, p. 358, pl. 59, fig. 1-9, pl. 60, fig. 3.
1971 *Spiriferellina* cf. *cristata* – Stehli & Grant, p. 519, pl. 64, fig. 24-30.

Diagnosis: Small with modest sulcus and fold, four to five pairs of well developed plicae bearing well rounded crests on each valve, and micro-ornament of fine dense pustules.

Lectotype: Specimen figured as *Terebratulites cristatus* Schlotheim (1816, p. 28), figured by Campbell (1959b, pl. 60, fig. 3), from Zechstein of Thuringia, SD.

Description: The micro-ornament consists of tiny and crowded pustules over the entire shell, and shape and plication are close to features typical of *Spiriferellina*, as revised by Campbell (1959b).

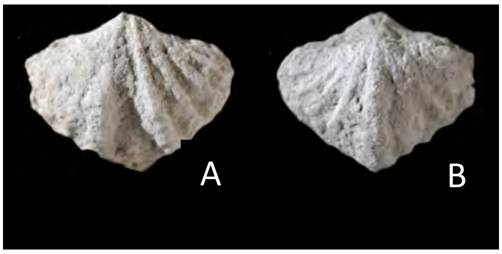

Fig. 311. *Spiriferellina cristata* (Schlotheim). A, ventral aspect and B, dorsal aspect of specimen GSC 140958 with valve conjoined, from C-4095, Degerböls Formation, Ellesmere Island, x1.

In addition to the synonymy, unfigured specimens have been assigned to *cristata* from the Arctic Permian with varying grades of confidence by Toula (1875b, p. 258), Wiman (1914, p. 33), Frebold (1937, p. 44) and Gobbett (1964, p. 176). *Spiriferellina* cf. *cristata* of Stehli & Grant (1971, pl. 64, fig. 24-30) from the Sabine Bay Formation has a narrower and low dorsal fold and narrow sulcus.

Suborder SYRINGOTHYRISIDINA (SYRINGOTHYRIDIDINA) Grunt, 2006b

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 developed in some forms. Shell penetrated by punctae or by taleolae.

Superfamily **SYRINGOTHYRISOIDEA** (**SYRINGOTHYRIDOIDEA)** Fredericks, 1926a

Family **SYRINGOTHYRISIDAE** (**SYRINGOTHYRIDIDAE)** Fredericks, 1926a

Subfamily **SYRINGOTHYRISINAE** (**SYRINGOTHYRIDINAE**) Fredericks, 1926a

Genus ***Syringothyris*** Winchell, 1863

Syringothyris? ***arcticus*** Whitfield, 1908

Fig. 312

1908 *Syringothyris arcticus* Whitfield, p. 53, pl. 3, fig. 5-8.

Diagnosis: Small shells with well defined sulcus and fold, seven or eight pairs of plicae.

Lectotype: Specimen figured by Whitfield (1908, pl. 3, fig. 6) from Cape Sheridan, here designated.

Material: An incomplete dorsal mould from C-4026, Trold Fiord Formation, Ellesmere Island.

Description: The specimen is broken, and shows a moderately wide low fold with rounded crest, several lateral plicae, a broad notothyrium, well developed ctenophoridium, and dental sockets. There is a low median ridge and two pairs of subrectangular longitudinally striate adductor impressions. A fragment of the external mould shows closely punctate shell, eight to ten punctae in 1mm.

Resemblances: The identification is based on a broken internal mould of a dorsal valve, and there can be little security about the generic or specific placement. The shape, height and width of the fold and inner plicae agree with the attributes of the material figured for the species described as *Syringothyris arcticus* Whitfield, but the critical ventral valve is not available for the present study. Whitfield reported that his material displayed a syrinx, so his species is provisionally referred to *Syringothyris*. But this genus is considered to be of principally Lower Carboniferous age, and was recorded as only doubtfully ranging into Upper Carboniferous (Carter 2006c, p. 1898), so that further enquiry is needed. The report of a syrinx has to be verified before the species can be allocated to a genus with any confidence. Perhaps the so-called syrinx was a rod of calcite, called a syrellum, as in *Orulgania* Solomina & Chernyak or *Syrella* Archbold. Previously Wiman (1914, p. 51, pl. 8, fig. 5-7) had recorded a species described as *Syringothyris spitzbergianus*, and Gobbett (1964) reported that the source was not known. Indeed Stepanov (1937b, p. 153, 181, pl. 9, fig. 1, 4) reassigned *arcticus*, with a query, to *Pseudosyrinx*, in reporting possible occurrences from the Spirifer Limestone of Spitsbergen. However, the dorsal fold of his specimen has a broad median channel, unlike the arrangement in Wiman's species. Gobbett (1964, p. 172, pl. 23, fig. 4, 5) also recorded the possible occurrence of *arcticus*?, as *Pseudosyrinx*, from the Spirifer Limestone and as well from the Brachiopod Chert of Spitzbergen, though his specimen shows finer plicae than in Whitfield's species.

Fig. 312. *Syringothyris*? *arcticus* Whitfield, posterior aspect of dorsal valve GSC 140959, showing interarea and notothyrium. Specimen from C-4026, Trold Fiord Formation, Ellesmere Island, x2.

Subfamily **PERMOSYRINXINAE** Waterhouse, 1986a

Genus ***Sulcicosta*** Waterhouse, 1983c

Diagnosis: Transverse shells with moderately high ventral interarea, delthyrium closed by a subdelthyrial connector plate, sulcus well defined and costate, fold moderately high and costate, plicae numerous, micro-ornament of shallow elongate grooves extending in front of tiny spinules, shell densely punctate. Dental plates high, adminicula high and short, without syrinx, muscle field short with calcite rod, called a syrellum, posteriorly. Dorsal ctenophoridium, short socket plates, low crural plates, low median ridge. Shell punctate.

Type species: *Pseudosyrinx plicata* Armstrong (1970b, p. 142, pl. 2, fig. 6-11) from poorly dated possibly Middle Permian of New South Wales, Australia, OD.

Discussion: Amongst the suite of Canadian specimens, the small ventral valves carry two ribs along each of the outer sides of the sulcus, close to the bordering sulcus. This suggests the possibility that the Canadian species belongs to *Sulcicosta* Waterhouse, 1983c, a genus found in the Early and Middle Permian of east Australia. In some larger specimens from Canada the sulcus is faintly costate, in others it appears to be smooth. Unlike some Australian species classed in that genus, the fold of mature dorsal valves in the present form carries no suggestion of costae, although very small specimens show signs of a median groove and lateral costae, which possibly have been worn away from larger specimens. In that respect, the Canadian form appears to fall between *Sulcicosta* and *Permasyrinx* Waterhouse. *Permasyrinx* is a genus represented by a number of species in east Australia (Armstrong 1970b, Waterhouse 1986b, 2015a), typified in part by having a smooth sulcus and smooth fold. So the affinities of the Canadian species are mixed, the ventral valve and immature dorsal valve like that of *Sulcicosta*, the mature dorsal valve apparently closer to that of *Permasyrinx*. *Subansiria* Sahni & Srivastava, 1956 as described first from the Himalaya of India is another possibly related genus. It was discussed in Waterhouse (2015a, pp. 207, 208), and the uncertainties mentioned in that report have still not been clarified. In general appearance, the type species of *Subansiria* comes close to the Canadian material, without including sulcal costae, but aspects of its morphology are poorly known, and it possibly has perideltidial areas, which are lacking from the Canadian form and from *Sulcicosta* and *Permasyrinx*. *Verkhotomia* Sokolskaya, 1963, p. 280, based on type species *V. pleonoides* Sokolskaya, is in some respects like the Canadian form in that the ventral sulcus is costate, and the dorsal fold smooth. The genus differs in shape, being much more elongate, and it is of Tournaisian to Visean in age, so the Canadian form is considered unlikely to be congeneric. *Tumarinia* Solomina & Grigorieva (1973, p. 35) may have sulcal ribs, but has a taleolate rather than punctate shell.

Sulcicosta transmarinus n. sp.

Fig. 313 – 316

Derivation: transmarinus – from over the sea, Lat.

Diagnosis: Small weakly transverse shells with well defined sulcus and fold and high number of narrow plicae, diminishing laterally.

Holotype: Specimen GSC 140963 from GSC loc. 26406, Assistance Formation, illustrated in Fig. 313D, here designated.

Material: Four ventral valves and two dorsal valves from loc. C-1410, Ellesmere Island, four ventral valves, four dorsal valves and two specimens with valves conjoined from GSC loc. 26406, Assistance Formation, Devon Island.

Description: The shell has been silicified and slightly worn. A broken ventral valve suggests an original width close to 55mm, length of 29mm or more, and height close to 12mm. An incomplete dorsal valve suggests an original width of 48mm, length of more than 27mm and height of at least 9mm. The specimens with valves conjoined are distorted, but suggest that the ventral valve was approximately twice as high as the dorsal valve. The ventral umbo is prominent with an umbonal angle of 110°, and concave posterior walls sweep out to cardinal extremities which lie at maximum width and are now obtuse. The ventral interarea is moderately high and concave in section, with delthyrium of 50° and low deltidial plates, whereas the dorsal interarea was probably low, but nowhere exposed, and the dorsal umbo broad and low. The sulcus is well formed, with concave floor and sinal angle close to 30°. In some specimens it is now smooth, possibly having been worn so, but in others bears a low median rib, joined in front by one then two pairs of lateral ribs, best preserved in small specimens, and some mature specimens carry indications of two ribs lying each side of the sulcus close to the bordering plication. The fold has an angle slightly less than 20°, with rounded crest and steep flanks, although a weak median channel is suggested in some specimens, and there are no costae visible in large

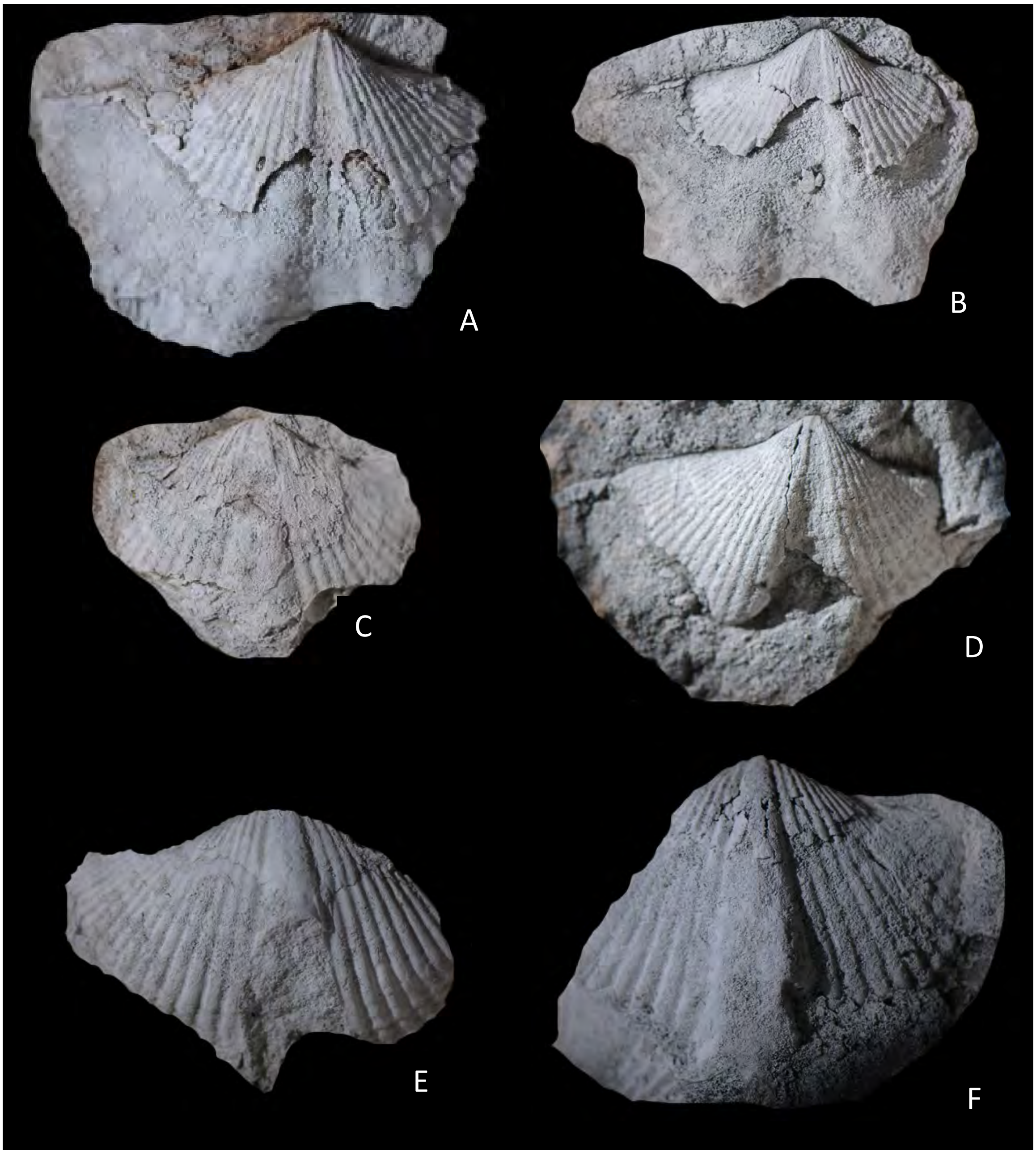

Fig. 313. *Sulcicosta transmarinus* n. sp. A, ventral valve GSC 140960 from loc. C-1410. B, ventral valve GSC 140961 from GSC 26406. C, dorsal valve GSC 140962 from loc. C-1410. D, ventral valve GSC 140963 holotype from loc. C-1410, showing sulcal costae, as also suggested in A and B. E, dorsal valve GSC 140964 from GSC loc. 26406. F, dorsal valve GSC 140965 from GSC loc. 26406. Specimens from Assistance Formation, x1.5.

dorsal valves. But the fold in small specimens (Fig. 316A, B) carries a median groove, and two low costae appear each side a few mm in front of the umbo, and it appears that these are worn away in larger specimens with increased maturity. There are usually twelve and up to sixteen pairs of narrow round-crested plicae and narrower interspaces over the ventral valve, with smooth lateral shell, and a roughly comparable number of plicae on the dorsal valve, with one dorsal valve displaying thirteen pairs. They commence posteriorly, and extend to the anterior margin with no increase by branching or intercalation. The shell has been imperfectly silicified, and shows signs of punctae, and unreliable traces of the external surface show elongate ridges and grooves.

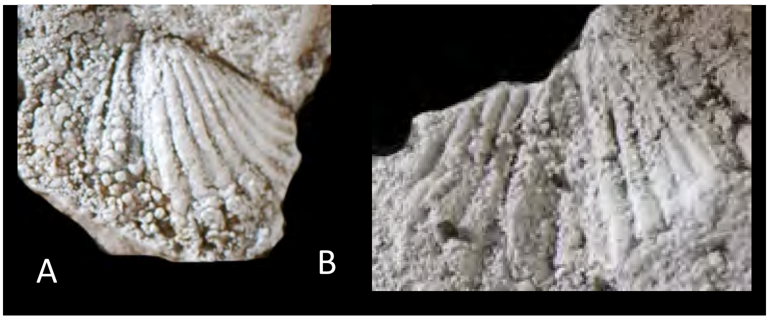

Fig. 314. *Sulcicosta transmarinus* n. sp. A, tiny ventral valve GSC 140966 x4 from GSC loc. 26406, Assistance Formation, Devon Island. Costae are visible in the sulcus. B, small ventral external mould GSC 140967 from loc. C-1410, Assistance Formation, x4.

Little is exposed of the interior. One specimen from C-1410 suggests the presence of a connector plate between dental plates and adminicula, and others indicate there was no high ventral median septum. The dorsal interior is obscure, and no specimens show any median septum.

A ventral valve from GSC loc. 52707 in the *Neochonetes culcita* Zone of the Richardson Mountain was figured as ?*Pseudosyrinx* sp. in Bamber & Waterhouse (1971, pl. 19, fig. 2) might be identical but needs inspection.

Resemblances: The type species of *Sulcicosta, Pseudosyrinx plicatus* Armstrong (1970b, p. 142, pl. 2, fig. 6-11) from poorly dated possibly Middle Permian of New South Wales, Australia, is close to the present form in overall size and proportions, with a roughly comparable number of fine plicae. The sulcal costae are low, numbering three, and costae over the fold are well defined, unlike the arrangement in any of the mature Canadian specimens. The ventral interarea is comparatively high. *Sulcicosta pelicanensis* (Armstrong, 1970b, p. 152, pl. 4, fig. 11, 12, pl. 6, fig. 4) from the *Streptorhynchus pelicanensis* bed of the north Bowen Basin, Queensland, slightly younger than the Canadian species, and of Capitanian or probably early Wuchiapingian age, is elongate with fine plicae and well defined costae over both sulcus and fold. From the Dresden Limestone of Sakmarian age in the southeast Bowen Basin, *S. costata* Waterhouse (1987, p. 14, pl. 1, fig. 1, pl. 3, fig. 5) has some ten pairs of narrow plicae, with faint sulcal costae in two or three pairs, and the dorsal valve, not preserved for its anterior half, lacks visible costae, although it does have a well defined median groove. *S. dolosus* Waterhouse (1987, p. 15; Armstrong 1970b, pl. 2, fig. 6, 7) is elongate with fine plicae and smooth sulcus and costate fold. It is of upper Guadalupian age in the Bowen Basin.

Fig. 315. *Sulcicosta transmarinus* n. sp., posterior aspect of ventral valve GSC 140972, showing interarea and delthyrium. Specimen from loc. C-1410, x2.

The species described as *Syringothyris arcticus* Whitfield (1908, pl. 3, fig. 5-8) has fewer plicae and longer straighter posterior walls, compared with those of the present species. There is no sign of sulcal costae. A ventral valve and dorsal valve from the middle Takhandit Formation in the Yukon Territory were regarded in Bamber & Waterhouse (1971, pl. 19, fig. 11) as close to *Pseudosyrinx wimani* Gobbett, 1964, pl. 23, fig. 1-3 from the Spirifer limestone of Spitsbergen, but they are more likely to be conspecific with *Nahoniella prolata*, described shortly. Gobbett's species, named to include *Spirifer tastubensis* Wiman, 1914, pl. 7, fig. 5-8, not of Tschernyschew 1902, has a higher ventral interarea, and wider sulcus and wider less sharply defined fold with no sulcal or fold costae.

Species of *Permasyrinx* in east Australia range from Cisuralian to Guadalupian, but plicae are as a rule fewer and stronger, and the sulcus and fold less sharply defined. The type species of the genus, *Permasyrinx procera* (Armstrong, 1970b, pl. 2, fig. 12-15; Waterhouse 1987a, pl. 1, fig. 10-12, 19), has fewer plicae and slightly wider sulcus and fold, and these differences apply widely. Some east Australian species are also distinctly more transverse. The species *Subansiria nobilis* Armstrong (1970b, p. 155, pl. 5, fig. 1-10, pl. 6, fig. 1, 2, 7-9) has even more plicae, and a transverse shell, but its fold is medianly sulcate, suggesting *Cyrtella* Fredericks, 1924. Waterhouse (1987a, p. 13, pl. 2, fig. 20, 22-24, pl. 3, fig. 1, 2) recorded the species from the Oxtrack and Flat Top Formations of the southeast Bowen Basin in Queensland, of Roadian and Wordian age respectively. The species *Permasyrinx granulata* (Armstrong, 1970b, p. 153, pl. 3, fig. 1-4, ?5, 6-12, pl. 4, fig. 1, pl. 5, fig. 11, 1, pl. 6, fig. 3, 5, text-fig. 5; Waterhouse 2015a, p. 212, Fig. 163F, 164-169) is moderately close in shape, sulcus and fold, but has slightly fewer and broader plicae. It comes from Sakmarian extending into what used to be termed lower Artinskian ie. Aktastinian faunas in the Tiverton Formation of the Bowen Basin in Queensland, although Aktastinian tends now rightly to be regarded as upper Sakmarian. One of the species that is closest in shape and plication was described as *Pseudosyrinx allandalensis* by Armstrong (1970b, p. 140, pl. 1, fig. 1-3, 5, 6 [not fig. 4, 7 = *archboldi* Waterhouse, 2015a, p. 215, Fig. 170]. The species is of Asselian age, and comes from the Allandale Formation of the Hunter Valley, New South Wales, with similar material from the south Sydney Basin in New South Wales and Tasmania (Waterhouse 2015b, p. 18). *P. allandalensis* is comparatively close to *P.*? *acuta* (Etheridge), described as *Spirifera bisulcata* Sowerby var. *acuta* Etheridge Snr. (1872, p. 329, pl. 16, fig. 1), and reassessed in Waterhouse (2015b, p. 26, Fig. 7A-C), with synonymy. This species is of Asselian (basal Permian) age. It shows the micro-ornament typical of *Permasyrinx*, but there is uncertainty about the nature of the mature dorsal fold, which is not preserved. The species seems closer to the Canadian form than any other Australian species assigned to *Permasyrinx*, as far as known, because its sulcus and fold are more sharply defined, and has eleven to twelve pairs of slender plicae, but unlike *Sulcicosta* definitely lacks sulcal costae. It comes from the Rammutt Formation at Gympie, southeast Queensland.

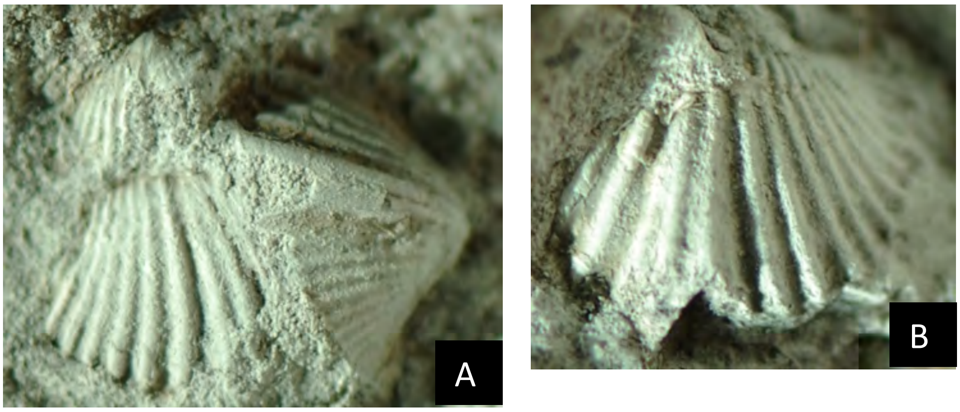

Fig. 316. *Sulcicosta transmarinus* n. sp. A, tiny ventral valve GSC 140968 and two dorsal valves GSC 140969 and 140970 from GSC loc. 26406, Assistance Formation, Devon Island. A channel passes along the dorsal fold. B, dorsal valve GSC 140971 with fold channel and a second costation appearing outside the bordering costae of the fold. From same locality. Specimens x4.

Genus ***Cyrtella*** Fredericks, 1924

Diagnosis: Strongly transverse, ventral interarea high and perideltidial areas developed as a rule, numerous ribs (or fine plicae), dorsal fold with well developed median channel, micro-ornament of fine papillae.

Type species: *Cyrtia kulikiana* Fredericks, 1916, p. 43 from Early Permian of Russia, OD.

Cyrtella sp.

Fig. 317

Material: A specimen with valves conjoined from C-4024, Assistance Formation, Ellesmere Island.

Description: The shell is transverse, measuring 34mm wide, 13mm long and high, with wide hinge, acute cardinal extremities, and broad little extended ventral umbo, for which the umbonal angle measures 110º. The interarea is wide, but not high, without a visible perideltidium, possibly because preservation is not good, and open delthyrium measuring just under 50º. The dorsal interarea is very low. The sulcus is well defined, its angle measuring 25º, with suggestions of a discontinuous median rib, and the fold is also well defined, with an angle of 20º, and shallow channel traversing the crest. Some fourteen pairs of narrow plicae lie over the ventral valve, and several low growth steps are developed anteriorly. The poorly preserved shell surface appears to be covered in tiny weakly elongate papillae, six to eight in 1mm posteriorly, and the shell is penetrated by small punctae, two to three in 5mm.

Resemblances: This specimen resembles various genera in shape. *Pterospirifer* Dunbar, 1955 for example is similarly transverse, but is not punctate. In some respects, the shape is close to that of *Licharewia*, and has fine micro-ornament of fine papillae, but unlike that genus and its allies, the shell of the present specimen is pierced by punctae. Type

Cyrtella is similarly transverse with a shallow groove along the dorsal fold, though the interarea is lower in the present specimen than in normal *Cyrtella*, perhaps because the specimen is immature, and there is no sign of a perideltidium, although this could reflect indifferent preservation, or geographic variation. Type *Cyrtella* has a micro-ornament of fine papillae as is obscurely implied by Fredericks (1916, pl. 2, fig. 4b).

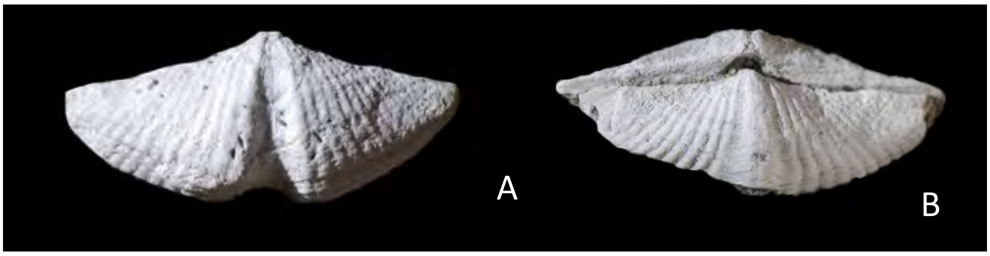

Fig. 317. *Cyrtella* sp. A, B, ventral and dorsal aspects of specimen GSC 140973 with valves conjoined from C-4024, Assistance Formation, Ellesmere Island, x2.

Superfamily **LICHAREWIAOIDEA** (**LICHAREWIOIDEA**) Slusareva, 1958

Diagnosis: Large transverse spiriferiform shells, taleolate, with few or no punctae except after secondary leaching or imperfect replacement of shell by silicification, numerous plicae and smooth sulcus and fold, may have fine pustules. Adminicula support dental plates, subdelthyrial connector plate, no ventral median septum, no tabellae.

Discussion: It is believed from examination of some Russian species and genera, including *Licharewia* itself, that the shell of Licharewioidea is densely taleolate, the taleolae replacing the pores of Syringothyrisoidea, as reported with illustrations of type species in Waterhouse (2018a). Carter (2006c, p. 1908) claimed that shell could be sparsely punctate, probably relying on a report by Grigorieva & Solomina (1973) who reported punctae. This appears to be highly exceptional, because topotypes of type and allied species and genera examined by the writer show the shell is normally pierced by numerous taleolae.

Family **LICHAREWIAIDAE** (**LICHAREWIIDAE**) Slusareva, 1958

Diagnosis: As for superfamily.

Discussion: Carter (2006c, p. 1906) treated Licharewiidae as a family with Syringothyridoidea, and Grunt (2006b, p. 158) placed the family as a 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, and this potential relationship invites further enquiry.

Genus ***Licharewia*** Einor, 1939

Diagnosis: Transverse biconvex shells with coarse plicae, well formed sulcus and fold and micro-ornament of short subelongate striae and ridges. Well developed adminicula, dental plates and subdelthyrial connector plate, low dorsal septum.

Type species: *Spirifer stuckenbergi* Netschajew, 1900, p. 18 from Kazanian of Russia, OD.

Discussion: *Licharewia* is close in many respects to *Olgerdia* Grigorieva, 1977, p. 50, but *Olgerdia* is distinguished by the presence of pleromal tissure which swells medianly to form connecting tissue between the adminicula and dental plates of the ventral valve, blocking at least part of the delthyrium, but lying well below the interarea. The type species of *Olgerdia* has dental plates rather than just dental flanges as claimed in a diagnosis in the *Revised Brachiopod Treatise*, and comes from the Omolon Suite, which is older that the Lopingian age (Late Permian) allocated by Carter (2000c, p. 1908). Klets (2005, Fig. 18, Table 2) showed the suite as underlying the Gijigin and Hivatch suites, and as matching upper Kazanian. Carter (2000c, p. 1908), a leading expert on Lower Carboniferous brachiopods from North America, had in the *Revised Brachiopod Treatise* even referred the Kazanian Stage of Russia to the Lopingian Series, whereas the Kazanian has long been known to match part of the underlying Guadalupian Series (Waterhouse 1976b, 1983b).

Licharewia sp.

Fig. 318, 319

cf. 1971 ?*Pseudosyrinx* sp. – Bamber & Waterhouse, pl. 19, fig. 2.

Diagnosis: Weakly transverse shells with ten to thirteen pairs of plicae.

Material: Two ventral valves and dorsal valve from GSC loc. 26406, Assistance Formation, Devon Island.

Dimensions in mm: internal mould

Width	Length	Height
74	35	28

Description: The internal mould is transverse with broad little extended ventral umbo, hinge at maximum width, alate cardinal extremities and eight pairs of plicae, followed laterally by at least one further pair of slender ribs, and smooth outermost shell. The interarea is transversely striate, and interrupted by a triangular delthyrium with concave sides diverging at close to 35º. It is underlain by a gently convex subdelthyrial connector plate bearing growth laminae parallel to the concave anterior margin, and marked by a few longitudinal grooves medianly. The low dental plates converge inwards, supported by high adminicula which are subparallel and extend almost to mid-length. The muscle field lies between the adminicula, and bears a median groove separating almost smooth adductor ridges, bordered each side by much wider diductor scars with fine longitudinal grooves and ridges. The posterior floor of the valve to each side is thickened, masking the external plicae, and marked by fine dense pustules and pits.

Resemblances: A reported species from Bjørnøya (Bear Island), Spitsbergen, described as *Spirifer capensis* von Buch (1847, Fig. 1a-d) is rather similar in general appearance, though the ventral sulcus is slightly wider, and the posterior lateral margins without ribs are slightly more extensive. But the species is of Devonian age, as pointed out to me by Tatjana Grunt.

Licharewia stuckenbergi (Netschajew, 1900, p. 18) from the Kazanian of west Russia is very close from its ventral aspect, but has a slightly more subdued dorsal fold with narrower crest. Other Russian species differ slightly in shape and in the fineness of the plicae.

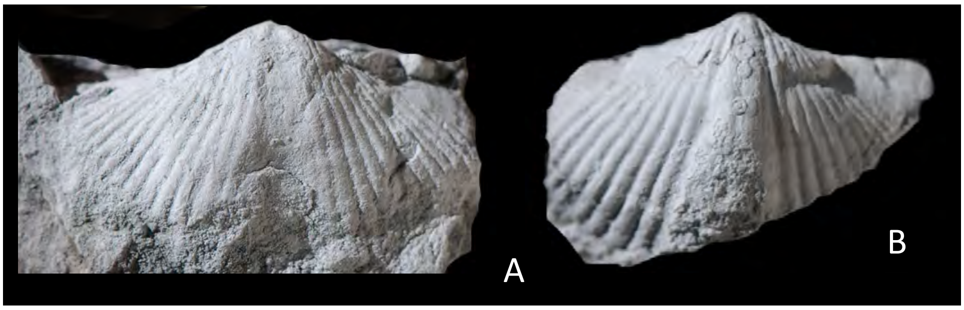

Fig. 318. *Licharewia* sp. A, ventral valve GSC 140975. B, dorsal valve GSC 140976 from GSC loc. 26406, Assistance Formation, Devon Island, x1.5.

This species shows some external similarity to what was identified as *Licharewia spitsbergiana* Gobbett, (1964, p. 143, pl. 19, fig. 2-6, text-fig. 21), from the Spirifer Limestone (Gobbett, 1964, p. 143), and rarely Brachiopod Chert (Gobbett 1964, caption to pl. 19). But the ventral muscle field is broad in the holotype of *spitsbergiana* as figured by Gobbett (1964, pl. 19, fig. 3), and the lateral sulcus bears plicae. Allied material was figured by Nakamura et al. (1992, pl. 2, fig. 8a, b) from unit 7-2 of Festningen in Spitsbergen. Probably the species *spitsbergiana* Gobbett does not belong to *Licharewia*, given its broad ventral muscle field. Whether it was punctate or taleolate is not known.

Fig. 319. *Licharewia* sp., ventral valve and tilted posterior aspect, GSC 140974 from GSC loc. 26406, Assistance Formation, Devon Island, x2. The arrow points to the dorsal side of the subdelthyrial connector plate.

Stehli & Grant (1971, p. 517, pl. 65, fig. 10, 11, 18-20, 25-28, 32) recorded a few fragments as *Licharewia* from the Sabine Bay Formation on Melville Island, but they are too small and incomplete to allow generic placement. No report was made of the micro-ornament, but figures suggest that the surface was possibly papillose.

Genus ***Nahoniella*** Shi, 1998

Diagnosis: Transverse and biconvex, sulcus with well defined borders, prominent fold with round crest and sharply distinguished from lateral shell, numerous plicae, and micro-ornament of tubercles without grooves. Connector plate large, adminicula short, wide ventral muscle field, ovarian impressions poorly developed or absent. Shell taleolate rather than punctate.

Type species: *Yukonella plana* Shi & Waterhouse, 1996, p. 128 from *Jakutoproductus verchoyanicus* Zone (lower Artinskian), Jungle Creek Formation, Yukon, Canada, OD.

Discussion: Specimens of the type species described by Waterhouse (2018a, p. 400) have dense taleolae in the shell, and it is deemed likely that the taleolae are also present in the original type material. Carter in Carter & Gourvennec (2007, p. 2789) interpreted the genus as belonging to Pterospiriferinae Waterhouse, but a licharewioid affinity is indicated by the moderately long adminicula and especially by the taleolate shell (Waterhouse 2018a, p. 400). The ventral muscle field is wide in type *Nahoniella* (see Shi & Waterhouse 1996, pl. 23, fig. 3)

Nahoniella prolata n. sp.

Fig. 320 – 322

1878 *Spirifera* sp. allied to *granulifera* [not Hall] – Etheridge, p. 634, pl. 29, fig. 4 (not 3 as in caption).
1937b *Pseudosyrinx* (?) *arcticus* [not Whitfield] – Stepanov, pl. 9, fig. 4.
1971 *Pseudosyrinx* cf. *wimani* [not Gobbett] – Bamber & Waterhouse, pl. 19, fig. 11.

Derivation: prolatus – delay, Lat.

Diagnosis: Large transverse shells with strong simple plicae and broad sulcus and fold, without median groove. Micro-ornament apparently of closely spaced growth laminae bearing row of slightly elongated pustules along each anterior margin. Shell taleolate. Broad ventral muscle field.

Holotype: Specimen GSC 140977 from C-4095, Degerböls Formation (Wordian), Ellesmere Island, Fig. 320A, here designated.

Material: Specimen with valves conjoined, ventral valve and fragment from C-4095, Degerböls Formation, and dorsal valve from C-4026, Trold Fiord Formation, Ellesmere Island.

Dimensions in mm:

Width	Length	Height	Height
96	43	13 ventral valve	
99 est.	45.5	18 ventral valve	25 both valves

Description: Shells transverse, ventral umbonal angle of 110°, cardinal angle alate, with hinge at maximum width. Ventral sulcus well formed and smooth with bordering pair of plicae diverging at 33°, dorsal fold also well formed with round crest, angle slightly less than 20°. Wear may produce a shallow median groove. Plicae narrow and numerous, numbering fourteen pairs, with round crests and evenly concave interspaces. Micro-ornament poorly preserved, but in

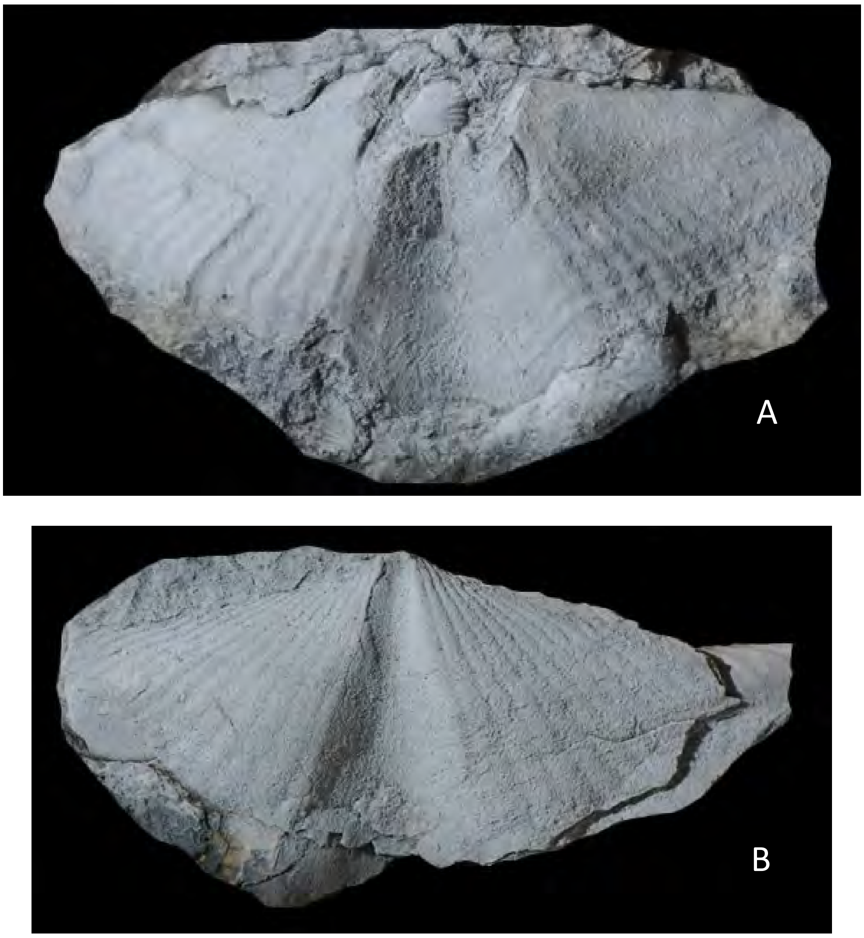

Fig. 320. *Nahoniella prolata* n. sp. A, ventral valve GSC 140977, holotype, with undescribed rhynchonellid (s. l.). B, ventral aspect of specimen GSC 140978 with valves conjoined. Specimens x1 from C-4095, Degerböls Formation, Ellesmere Island.

places the shell suggests closely spaced growth laminae, each bearing a row of slightly elongate pustules along the anterior margin. Patches over the surface display small pits, due probably to weathering, and the entire surface is covered by dense taleolae numbering about ten in one mm. As well there are poorly understood coarser protuberances of shell over some part of the worn shell. The dorsal interarea is well formed and low, whereas the ventral interarea is moderately high and very gently concave with greater curvature under the beak. The ventral muscle field is very wide, and the adminicula short and widely diverging. The posterior shell is thick, reaching 10mm at the hinge even well away from the umbo. A long dorsal median septum extends for half of the length of the valve.

Resemblances: A dorsal valve figured in Bamber & Waterhouse (1971, pl. 19, fig. 11) could belong to the species, but needs to be examined with regard to punctation. It was identified as *Pseudosyrinx* cf. *wimani* Gobbett, and came from GSC loc. 57244 in the middle Takhandit Formation. The shell figured as *Pseudosyrinx* (?) *arcticus* by Stepanov (1937b, pl. 9, fig. 4) from the Productus beds has a prominent dorsal fold, approaching that of *Nahoniella*, but the specimen is small and so difficult to compare.

Fig. 321. *Nahoniella prolata* n. sp., dorsal valve GSC 140979 from C-4026, Trold Fiord Formation, Ellesmere Island. Specimen x1.

Nahoniella plana (Shi & Waterhouse, 1996, p. 128, pl. 22, fig. 21-25, pl. 23, fig. 1-7, Fig. 44, 45) from the *Jakutoproductus verchoyanicus* Zone at the top of the Jungle Creek Formation in the Yukon Territory is close, but has less attenuated cardinal extremities and narrower sulcus and narrower plicae. Somewhat similar fragments were reported from the *Ogilviecoelia shii* Zone (Asselian) of the Jungle Creek Formation in Waterhouse (2018a, p. 401, Fig. 345A). Another Jungle Creek species was described as *N. decorus* Waterhouse (2018a, p. 400, Fig. 344, 345B – see also Bamber & Waterhouse 1971, pl. 11, fig. 9, 11), from the Gzhelian faunas at the base of the formation. These specimens are closer to the present form in outline and plication, without the ventral valve being quite as transverse, and with high fold becoming broad anteriorly. The present species is allied to *Spirifer loveni* [not Diener, 1903] of Wiman (1914, p. 50, pl. 7, fig. 12, 13, pl. 8, fig. 1-4) and renamed *Licharewia wimani* by Gobbett (1964, p. 145), agreeing in general shape and ornament, and possibly interior. One difference is that the fold in present material is narrower than in Wiman's original material, as in Wiman (1914, pl. 8, fig. 2), which shows an angle of 35°, compared with less than 20° for the present specimens. Gobbett (1964, p. 146) reported a thick delthyrial (= connector) plate and stated that the species was larger than other *Licharewia* species, with large apical angle and moderately convex ventral valve with more erect umbonal angle. A specimen was recorded from the Brachiopod Chert. A ventral valve figured by Wiman (1914, pl. 8, fig. 4) shows low dental plates, a broad subdelthyrial connector plate, and broad ventral muscle field like that of the material from C-4095. Wiman (1914) noted that Frech had proposed the name *arctica* for his *Spirifer loveni*, but pointed out that this name had been preempted by *arcticus* Haughton, 1858, named for a species now referred to *Spiriferella*. Nakamura et al. (1992, Fig. 1) recorded the species as *Licharewia* from the middle Hotvinden Member of Spitsbergen. The muscle field is wider than in *Licharewia* sp. described above from the Sverdrup Basin.

The fragments figured as *Tumarinia* cf. *T. wimani* by Angiolini & Long (2008, p. 97, Fig. 8D-E) from the Vøringen Member of Spitsbergen indicate much more triangular shells with less widely divergent postero-lateral walls. They allowed that the specimens were also close to *Yukonella* Shi & Waterhouse, oblivious of the fact that the name had been replaced by *Nahoniella* Shi. Angiolini & Long (2008) said it differed "only" in the micro-ornament, lack of ovarian impressions, and shorter adminicula. But the sulcus in their material is costate, and the form is referred herein to *Yukonospirifer* Shi & Waterhouse, as discussed on p. 265.

Spirifera sp. allied to *granulifera* (not Hall) of Etheridge (1878, p. 634, pl. 29, fig. 4, not 3 as in the plate caption) might be allied to this species. It had some twelve to thirteen pairs of plicae and a prominent simple median dorsal fold, and Whitfield (1908, p.52) had also noted a degree of similarity to his *Syringothyris*. It has a broad dorsal fold and the innermost two plicae on one side each divide into two, whereas the pair on the other side do not divide. Etheridge’s specimen came from Dana Bay in northern Ellesmere Island.

Fig. 322. *Nahoniella prolata* n. sp., dorsal valve figured as *Spirifera* sp. allied to *granulifera* Hall, by Etheridge (1878, pl. 29, fig. 4).

Licharewia spitsbergiana Gobbett (1964, p. 193, pl. 19, fig. 2-6, text-fig. 143; Nakamura et al., 1992, pl. 2, fig. 8a, b) is allied, with its wide ventral muscle field and widely spaced adminicula, and is readily distinguished by the way in which one or two plicae lie within the edges of the sulcus, to mark perhaps a deviation from typical *Nahoniella*. There are fewer plicae at ten to thirteen each side of the sulcus, and the shell is smaller. Gobbett (1964, p. 143) reported the species from the Spirifer Limestone of Spitsbergen, and found a specimen in the Brachiopod Chert. Nakamura et al. (1992, p. 88, Fig. 1) recorded the species from unit 7-2 of Festningen in Spitsbergen, and tabulated it as occurring in the lower Hotvinden Member (former Brachiopod Chert). The ribs in *spitsbergiana* number five to six in 10mm, compared with three in 10mm for *wimani*. Angiolini & Long (2008, Fig. 11A-C) assigned what appears to be allied material from the Vøringen Member to *Pseudosyringothyris borealis* Gobbett, but this species has much finer ribs. Angiolini & Long (2008) noted the presence of a subdelthyrial (= connector) plate, and commented that secondary fibres in the callus showed spiral convolutions.

DISCUSSION OF BRACHIOPOD ZONES AND CORRELATIONS IN ARCTIC CANADA

Fossil occurrences are summarized in Tables 7, 8, pp. 427 – 432.

SVERDRUP BASIN, CANADIAN ARCTIC ARCHIPELAGO

NEAR-SHORE FORMATIONS

Raanes Formation

The Raanes Formation rests on the Belcher Channel Formation, and was thought by W. W. Nassichuk to grade basinward into the Van Hauen Formation. The type section was provisionally designated by W. W. Nassichuk and formally consolidated by Beauchamp (1994) and Beauchamp & Henderson (1994) as exposed three miles northeast of Blind Fiord on Ellesmere Island. Brachiopods from some eleven stations collected through an estimated 950ft at the type section were examined by the writer in 1974, and the list suggests a possible correlation with the Sakmarian middle Jungle Creek Formation in the Yukon Territory (Waterhouse 1974). The fossils are dominated by species of *Kutorginella*, reticulariid, paucispiniferiid, *Kochiproductus*, aff. *Harkeria*?, *Arcullina*, *Cyrolexis,* and *Cleiothyridina*, as well as a large linoproductiform species at C-10527, collected 920ft to 950ft above the base. Examination of this latter species could be helpful for a close age assignment from a brachiopod perspective. On the whole the fossil lists look very like those of the Jungle Creek and to less extent the lower Takhandit faunas of the Yukon Territory**.** Faunal lists are of limited value, and clearly the fauna needs to be reassessed, but no brachiopods from the formation are available for the present study. At that time Nassichuk was convinced of the formation being little older than the Assistance Formation, but the formation has been shown as upper Sakmarian in age by Beauchamp et al. (2009), and the conodonts were assigned to two successive zones P6a and P6b, matched with zones found in the Aktastinian of Russia as described by Movshovich et al. (1979). Ammonoids included *Neoshumardites, Paragastrioceras jossae, Uraloceras involutum*, and *Metalogeceras crenatum* (Nassichuk et al. 1965). No *Jakutoproductus* has been found, whereas this genus helps delineate an Aktastinian zone (possibly lower Aktastinian) in the upper Jungle Creek Formation (Shi & Waterhouse 1996).

Great Bear Cape Formation

Some of the available Great Bear Cape material was collected from Grinnell Peninsula of Devon Island, in the uppermost part of what used to be called the Belcher Channel Formation, composed of limestone with fusulines, (Harker & Thorsteinsson 1960, Fig. 1, 3) in unit 3. Renamed Great Bear Cape Formation by Beauchamp & Henderson 1994), the beds were shown as lower to middle Artinskian in Beauchamp et al. (2009, Fig. 1). The fusulines and brachiopods towards the top of the Great Bear Cape Formation match those of the second lowest faunal zone in the Takhandit Formation of the Yukon Territory. The lower Takhandit Formation overlies the Jungle Creek Formation which contains early Permian fusulines (Ross in Bamber & Waterhouse 1971), and a scattering of ammonoids especially from the Peel River, and numerous early Permian brachiopods (Shi & Waterhouse 1996, Waterhouse 2018a).

That places a maximum possible age of upper Aktastinian for lower Takhandit, and allows correlation with the Baigendzinian in the Urals, permitted by the fusulines, and supported by the brachiopods. No collections of brachiopods from the older parts of the Great Bear Cape Formation are available for assessment in the present study, so that whether the brachiopods were the same or differed throughout the formation is yet to be clarified.

The fossils available from the upper Great Bear Cape beds in the present study involve possible *Derbyia semicircularis* n. sp., allied to a chiefly Roadian species in the basin, but found at least as an allied form in the second Takhandit zone of the Yukon Territory, *Krotovia*? sp. A, *Guangia pustulata* (Keyserling), *Thamnosia sangminlee* n. sp., *Thuleproductus subarcticus* Sarytcheva*,* found in upper Artinskian, Kungurian and reportedly younger levels of Russia and Spitsbergen, *c*horistitid gen. & sp. indet*.,* *Fasciculatia groenwalli* (Dunbar), first described from the Kim Fjelde Formation of the Mallemuk Mountain Group in northeast Greenland, and found in the Vøringen Member of Spitsbergen and Bjørnøya*,* *Betaneospirifer striatoplicatus* Gobbett, first described from the Vøringen Member (early Kungurian) of Spitsbergen, and matching *B*. cf. *permicus* (Ifanova), a species from the Levorkut beds of Petchora Basin, of Kungurian age according to Kalashnikov (1998), *Spiriferella arctica* (Haughton), *Spiriferella angulata* n. sp., also found in northeast Greenland and the Vøringen Member of Spitsbergen, *Spirelytha pavlovae* Archbold & Thomas and *Reticulariina* sp.

Limited weight can be placed on any assessment of the figures of brachiopods described from the Great Bear Cape Formation by Tschernyschew & Stepanov (1916). A number were not figured, but based on the text and figures, a tentative faunal list may be compiled, as follows: A chaoellin or spinarellin (not figured); *Marginifera typica septentrionalis* (not Tschernyschew, 1902) as figured by Tschernyschew & Stepanov (1916, pl. 7, fig. 1) is moderately close to *Liosella delicatula* Dunbar from the Assistance and Trold Fiord Formations, but inadequately known. *Retimarginifera* or *Uraloproductus* but not clear (pl. 8, fig. 1), a genus found in the Jungle Creek Formation and rarely in younger beds, including Takhandit Formation; *Productus tartaricus* (pl. 8, fig. 2) which is possibly *Liosella*; *Tubersulculus* (based on reference to Tschernyschew 1902 figures, but not confirmed by the figure pl. 6, fig. 1); productid *frami* Tschernyschew & Stepanov, which may prove a critical form, looking like *Striapustula*; *Waagenoconcha* or *Balkhasheconcha*? (pl. 6, fig. 2-4); *Cimmeriella* (pl. 8, fig. 4); magniplicatinin (unfigured specimens called *koninckianus* and *cancriniformis* by Tschernyschew & Stepanov); *Kuvelousia* or *Megousia* (pl. 7, fig. 5, 6); *Kochiproductus* (pl. 7, pl. 8, fig. 5), possibly *K*. *freboldi* Stepanov; *Derbyia,* possibly *D. semicircularis* n. sp. (pl. 10, fig. 1); phricodothyrid? more elongate than *Catatonaria transversaria* n. sp. (pl. 9, fig. 8); *Spirelytha pavlovae* Archbold & Thomas [= *schei* Tschernyschew & Stepanov 1916, pl. 9, fig. 5, not Meyer, 1913]; *Betaneospirifer striatoplicatus* Gobbett (pl. 9, fig. 3); *Fasciculatia groenwalli* (Dunbar) (pl. 9, fig. 4); *Purdonella* or aff. *Simplicitasia osborni* from the Assistance Formation, but with narrower shell than in the latter form (pl. 10, fig. 2); *Spiriferella arctica* (Haughton) (pl. 11, fig. 2, 3, 4, pl. 12, fig. 1-3); *Spirifernaella*?; spiriferinid; *Stenoscisma* sp., and *Rhynchopora* sp., none of them figured, and *Notothyris* sp. (pl. 12, fig. 5, 6). Tschernyschew & Stepanov (1916) stated that the shell was punctate, so that any similarity to *Cyrolexis* is superficial.

These identifications are conjectural to a degree, given the lack of detail in text or figures about spine distribution and nature of dorsal ears – like so many other paleontological reports on Arctic Permian faunas. But as it stands, the putative list strongly weighs against the assessments by Tschernyschew & Stepanov (1916) and Dunbar

(1955) that the fauna was of Asselian-Sakmarian age, and like those of the Urals described by Tschernyschew (1902). The fauna is of Baigendzinian age and approaching those of Middle Permian age, based on the affinities of the fossils world-wide, which show that many components of the classic Kungurian faunas are allied to those of Roadian and Wordian, and there are some approaches of Great Bear Cape fossils to fossils of the Trold Fiord and Assistance Formations. Given the nature of the Great Bear Cape fauna, and its stratigraphic position, it would appear to be of late Artinskian age, and older than the Sabine Bay Formation of the Sverdrup Basin.

The formation was shown as lower and middle Artinskian by Beauchamp et al. (2009). Bamber & Waterhouse (1971) in matching the fusuline faunas of Grinnell Peninsula, Devon Island with those of the second brachiopod zone in Takhandit faunas of Yukon Territory had initially suggested that the faunas matched those of the Saranin (upper Baigendizinian – Licharew 1966) in Russia. But fresh assessments based on conodonts demand a slightly greater age, as Sarginian. Four conodont zones were recognized in the Great Bear Cape Formation of Ellesmere Island by Henderson in Beauchamp & Henderson (1994), P6b as in the upper Raanes Formation, P7 based on *Neogondolella biselli* and *Sweetognathodus whitei* partial range Zone, in beds from 59 to 122m above the stratotype base, and P8, based on *Neostreptognathodus pequopensis* and *N. clarki* concurrent range Zone, allied to an upper Sarginian zone in Russia (Movshovich 1984). This zone is overlain by the *N. prayi* and *N. ruzhencevi* Zone (P9) in the upper five metres, allocated a top Artinskian or lower Kungurian age by Henderson in Beauchamp & Henderson (1994). The fossil localities at Grinnell Peninsula as discussed in Harker & Thorsteinsson (1960) came from 65ft below the top.

Sabine Bay Formation, *Paeckelmannella calignea* Zone

Brachiopod content:

The fauna from the Sabine Bay Formation collected at the Svartevarg Cliffs of Axel Heiberg Island was described on the basis of silicified material by Stehli & Grant (1971), and includes *Fissulina delicatula* n. gen., n. sp., a distinctive *Hustedia* sp., *Martinia stehlii* n. sp., *Paeckelmannella calignea* Stehli & Grant, *Betaneospirifer*? (with some similarities to *striatoplicatus*, but inadequately known), *Spirelytha svartevargensis* Waterhouse, *Anomaloria* sp., *Orbicoelia*? *aquilonia* (Stehli & Grant), *Licharewia*? sp. and reported *Callispirina*. *Fissulina delicatula* and *Paeckelmannella calignea* are distinctive species, restricted to the formation, and *Martinia stehlii*, *Arcullina* sp., *Spirelytha svartevargensis* and *Orbicoelia*? *aquilonia* are characteristic, the first mentioned represented in the Kapp Starotsin Formation and type lower Takhandit Formation, and the last mentioned possibly found in unnamed sandstone unit of McDougall Pass in the Richardson Mountains at GSC 53848, which matches the lower Trold Fiord Formation. Several other species were described by Stehli & Grant (1971), but their specific alliances need further study. They include shells identified as *Liosotella* (better *Anemonaria*) *pseudohorrida* (Toula), *Cleiothyridina* cf. *pectinifera* (Sowerby) and *Spiriferellina* cf. *cristata* (Schlotheim).

***Paeckelmannella calignea* Zone:**

For the biozone, the name *Paeckelmannella calignea* is proposed. This is a prominent and well-preserved species.

Age and correlation:

The Sabine Bay fauna is correlated with part of the Kungurian Stage of Russia, and part of the upper Cathedral

Formation of the Glass Mountains in Texas. The age is based largely on stratigraphic position and overall nature of the fauna, which shows only limited, and somewhat uncertain links with that of the overlying Assistance Formation, of Roadian age. The Sabine Bay rocks and *Paeckelmannella calignea* Zone are represented in the Yukon Territory by disconformity or a paraconformable break in sedimentation, or by thin beds which so far have not yielded fossils. In Beauchamp et al. (2009), the formation was shown as lower middle Kungurian. The basic high diversity of the brachiopods involving such genera as *Fissulina, Leiorhynchoidea, Orthotichia, Anomaloria, Orbicoelia*, *Callispirina* and *Glossothyropsis* as described by Stehli & Grant (1971) with some revision in the present study, suggest a possible match with the Nevolin level, or lower Irenian (lower upper Kungurian) Permian levels in northwest Russia, in which faunas were also diverse, both reflecting relatively warm and favourable climate that was probably world-wide.

Assistance Formation, *Neochonetes culcita* Zone

Brachiopod content:

Species limited to this formation in the Sverdrup Basin include *Orbiculoidea ornata* n. sp., *Arctitreta pearyi* Whitfield, *Dyoros gentilis* n. sp., *Pleurohorridonia?* sp., *Kutorginella minuta* n. sp., *Thamnosia* ? aff. *sangminlee* n. sp., *Thuleproductus arcticus* (Whitfield), *Gruntoconchinia* sp., *Schrenkiella truncata* n. sp., *Callaiapsida ustritskii* n. sp., *Gobbettifera angulata* Waterhouse, *Spirigerella inflata* n. sp., *S. plana* n. sp., *Reticulariina*? sp., *Cyrtella* sp. and *Licharewia* sp.

Species shared with the Trold Fiord Formation include *Derbyia semicircularis* n. sp., *Arctitreta triangularis* (Wiman), *Echinaria tardus* n. sp., rare *Patellamia confinis* Waterhouse, *Balkhasheconcha thorsteinssoni* n. sp., possible *Liosella delicatula* Dunbar, but definitely in Trold Fiord Formation, *Magniplicatina*? sp. B, and *Stenoscisma opitula* (Grant), which is most common in the Assistance beds. *Dzhiremulia conlustras* Waterhouse was a principal genus in the Assistance Formation, and is found rarely in the Trold Fiord and Van Hauen beds. Other species ranging further beyond Assistance and Trold Fiord formations involve *Kochiproductus freboldi* Stepanov and *Ametoria nassichuki* n. sp. also in the Degerböls Formation, *Anemonaria pseudohorrida* (Wiman) and *A. robusta* n. sp., also in the lower and middle Takhandit Formation, *Harkeria studiosa* Waterhouse, rare in the Trold Fiord Formation and more common in the Assistance and Van Hauen Formations, *Lineabispina ellesmerensis* Waterhouse, prominent in the Assistance beds but found rarely in the Trold Fiord, Van Hauen and possibly Takhandit Formations, *Rhynchopora taylori* Girty in the Assistance and Trold Fiord Formations as well as Takhandit 3 and middle zone of the Richardson Mountains, *Svalbardathyris kotlukovi* (Stepanov) found in Assistance, Trold Fiord, and rarely in the Degerböls Formations. *Simplicitasia osborni* (Harker) n. gen. is found in the middle zone of the Takhandit beds, as well as Assistance and Trold Fiord Formations. *Martinia*? sp. A is found in Assistance, Trold Fiord, and possibly middle Takhandit beds. *Canalisella leviplica* (Waterhouse & Waddington) occurs occasionally in Assistance and Trold Fiord beds and is typical of the Van Hauen beds, and *Alispiriferella gydanensis* (Zavodowsky) is shared with Assistance, Trold Fiord, and Takhandit zone 4, whereas *Catatonaria transversaria* Waterhouse n. sp. is shared between the Assistance and Trold Fiord formations and is rare in the Van Hauen beds.

A few other species are not found in the Trold Fiord Formation, but occur in the Yukon Territory. These include *Neochonetes culcita* n. sp., which is shared with the mid-Takhandit Formation and the lowermost zone of the north Yukon. *Cancrinella arctica* (Waterhouse) is moderately widespread, common in the Assistance Formation, and also in the Richardson Mountains, *Betaneospirifer politus* n. sp, also in mid-Takhandit Formation, zone 3, and *Spiriferella separata* n. sp. in the Assistance Formation and Takhandit zone 4, and C-6639 of uncertain age in the Richardson Mountains. *Spiriferella sulcoconstricta* is found in the Assistance and possibly middle Takhandit Formation (zone 3). *Sulcicosta transmarinus* n. sp. is shared between the Assistance Formation, and middle of three zones in the Richardson Mountains.

***Neochonetes culcita* Zone:**

The brachiopods of the Assistance Formation are referred the *Neochonetes culcita* Zone. The nominate species is selected because it is also present in the middle Takhandit Formation (level 3) of the Yukon Territory and Richardson Mountains, to facilitate correlation. Like a number of other species, *Lineabispina ellesmerensis* Waterhouse was at an acme in this level in the Assistance Formation, and has been found rarely in the Takhandit Formation, and rarely in the Trold Fiord and Van Hauen Formations.

Age and correlation:

The ammonoids *Sverdrupites* and *Daubichites* are regarded as critical for dating the rocks and faunas. They outweigh the preference for a Kungurian age expressed by Brabb & Grant (1971) for the lower unit of the type Takhandit Formation in Alaska, before the consolidation of the Roadian Stage concept. In Beauchamp et al. (2009, Fig. 2), the formation was shown as Roadian, even though the figure showed the principal conodont for all but the upper part as *Mesogondolella idahoensis*, which is normally regarded as an index for Kungurian faunas, as shown in Henderson (2018, p. 120). As well, the subspecies *idahoensis lamberti* from the basal Assistance Formation was regarded as post-Kungurian by Henderson & Mei (2003), but is now treated as a full species typifying a full zone of late Kungurian age (Henderson 2018), which means that the basal beds of the Assistance Formation are Kungurian. It has to be recalled that the Kungurian Stage especially is named not after United States sequences, where Waterhouse (1983e, pp. 218, 219) wished to placed the stratotypes, but in Russia, yet in practical terms, the upper Kungurian Stage is based on conodonts and stratigraphic sequences in the United States. In the United States, the type exemplars for *idahoensis* are in Idaho and Wyoming, not in Texas where faunas are of different appearance, being much more paleotropical in their affinities. No known Assistance brachiopods studied in the present report support such a late Kungurian age, which possibly means that no collections were provided for study, or that there has been a failure to distinguish between brachiopods of the two stages. In the absence of confirmatory evidence for any Kungurian input, the Assistance brachiopods of this study are regarded as entirely Roadian in age, and possibly no specimens examined in this study came from with beds with *lamberti*.

Trold Fiord Formation, *Cameronovia milleri* Zone

Brachiopod content:

The species limited to this formation, as far as known, include streptorhynchid, *Horridonia grandis* Waterhouse, *Sowerbina* sp., *Sowburia* cf. *rudis* (Dunbar), *Wimanoconcha feildeni* (Etheridge), *Tubersulculus*? sp., *Echinalosia* *pondosus* n. sp., *Wyndhamia sphenarctica* Waterhouse, *Arcticalosia unispinosa* (Waterhouse), *Melvillosia canadense* Waterhouse, *Liosella vadosisinuata* (Dunbar), *Liosotellina costellata* n. sp. (though the matrix looks like Assistance Formation), *Liraria borealis* n. sp., *Globiella hemisphaerium* (Kutorga), *Magadania attenuata* n. sp., *Stenoscisma* sp., *Cleiothyridina maynci* Dunbar, *Himathyris arctica* n. sp., *Callaiapsida* sp., *Canalisella loveni* (Diener), *Spirelytha* sp., *Spiriferellina*? sp. and *Syringothyris*? *arcticus* (Whitfield).

Trold Fiord species shared with the Assistance Formation were summarized previously on p. 381. A number of species are shared with the Degerböls Formation, including *Thuleproductus crassauritus* Sarytcheva & Waterhouse, *Patellamia sulcata* Waterhouse, *Liosella spitzbergiana* (Toula), *L. delicatula* Dunbar, *Kuvelousia sphiva* Waterhouse, and *Nahoniella prolata* n. sp. *Pleurohorridonia platys* n. sp. is found in these beds and the middle zone or *Dyoros modestus* Zone of the three zones in the Richardson Mountains zone, and *Thamnosia* sp. in the Degerböls and uppermost Takhandit zone. *Grumantia kempei* (Andersson) is found in the Trold Fiord and Degerböls Formations, as well as the upper two Permian zones in the Richardson Mountains. *Cameronovia milleri* Waterhouse is known, found also in the upper Takhandit Formation of the Yukon Territory, and in the uppermost Permian zone of the Richardson Mountains. *Fasciculatia striatoparadoxa* (Toula) may be shared with the Van Hauen Formation, and middle or *Dyoros modestus* Zone of the Richardson Mountains. *Spiriferella draschei* (Toula) is shared between the Trold Fiord and Degerböls Formations, and, according to Nelson & Johnson (1968), equivalents of the uppermost Takhandit Formation at Peel River.

Cameronovia milleri Zone:

A number of prospective species are available as name givers for the zone, but *Cameronovia milleri* Waterhouse is selected because it is distinctive, and is found also in beds believed to be correlative in the Richardson Mountains and Takhandit Formation of Yukon Territory.

Age and correlation:

Most of the fauna would appear to be of Wordian age, which conforms with stratigraphic position above Roadian faunas, and with rare ammonoids described by Nassichuk. Although *Horridonia grandis* Waterhouse from C-13356 is very close to *Horridonia horrida* (Sowerby) of Wuchiapingian age in England, it appears to have been a precursor species and therefore older than *Horridonia horrida* Sowerby, in view of its simpler dorsal ear spines. Unfortunately, no stratigraphic information in terms of relative position of collections from the Trold Fiord Formation has been provided to me, so it is not possible to see if the Trold Fiord faunas occur in a sequence of faunas, a severe handicap to their interpretation. According to Nakamura et al. (1992), Dr Liao Zhuoting from Nanjing, China, was able to subdivide the Trold Fiord brachiopods into several biozones, and he argued for a Capitanian age for the younger three levels, based on comparison of some unspecified conodonts, before the Word/Capitan boundary was rearranged (Wardlaw 2000). The species identified as *Haydenella wilczeki* (Toula) as characterizing a zone at the top of the Kapp Starotsin Formation in Spitsbergen certainly has no clear match in the Trold Fiord Formation of Arctic Canada. Nor does the underlying *Pterospirifer alatus* Zone of the Kapp Starotsin Formation show any particular tie, although it does contain a number of persistent species that are found in the Trold Fiord beds, but with no clear zonal allegiance. It is therefore concluded that the species described herein must have come from relatively low in the Trold Fiord Formation, and that they are mostly if not entirely of middle Guadalupian (Wordian) rather than Capitanian or Lopingian age. Although several brachiopods suggested links with Texan species of upper Guadalupian age, that used to be classed as Capitanian, as in Waterhouse & Waddington (1982), some of these levels, involving the Manzanita, Hegler and lower Pinery members, have been transferred to the Wordian Stage (Wardlaw 2000). As well, a few Productida are related to genera from Russia, including northeast Russia, involving the genera *Magadania* and *Globiella*, and these are of Kazanian, ie. Wordian, age.

The Wordian age is in accord with the assessment of the age in Beauchamp et al. (2009), who preferred a Wordian age for the lower Trold Fiord Formation.

An intriguing challenge:

Although the brachiopods of the Trold Fiord Formation appear to conform with conodont evidence for a Wordian age, there are some exceptional occurrences which call for closer enquiry. These involve the suite of strophalosioid genera and species from at localities GSC loc. 35316 and 53520 on Melville Island, GSC loc. 76029 on Cameron Island, and GSC loc. 52542 on Ellesmere Island. The strophalosioids are not found elsewhere in the Sverdrup Basin, nor in the Yukon Territory, and might be interpreted as typifying a distinctly younger fauna, conceivably of Capitanian age, even though accompanied by (possibly persisting) Wordian brachiopods. Thi is a matter beyond any possibility for me to explore futher.

OFFSHORE FORMATIONS

Van Hauen Formation

Brachiopod content:

Few species are described from the Van Hauen Formation. They include *Harkeria studiosa* Waterhouse, shared with the Assistance Formation and less with the Trold Fiord Formation, and *Lineabispina ellesmerensis* Waterhouse, found principally in the Assistance Formation, and possibly Trold Fiord Formation (C-4072) and middle Takhandit biozones. *Martinia*? sp. B is shared between the Van Hauen and middle Takhandit Formation, and *Fasciculatia striatoparadoxa* (Toula), and *Canalisella leviplica* (Waterhouse & Waddington) are present, the former also possibly in the Assistance Formation and chiefly in the Trold Fiord Formation and middle zone of the Richardson Mountains, the latter also in the Degerböls and Assistance Formations, though it is most characteristic of the Van Hauen Formation. *Catatonaria transversaria* n. sp. is rare in the Van Hauen Formation and more common in the Assistance and Trold Fiord beds. Information about the height above base or below top of the formation for the collections is not available to me. In preliminary surveys of the faunas in Canada by the writer, it was noted that what is now called *Dyoros modestus* n. sp. was found at several stations.

Brachiopod zone:

There has not been sufficient data available to me on the stratigraphic sucession of brachiopods to allow recognition of biozones in the Van Hauen Formation. The most prominent of fossils is *Canalisella leviplica*, but not enough is known about brachiopods from the formation. It is likely that fossils from two zones are present, equivalent to the Assistance

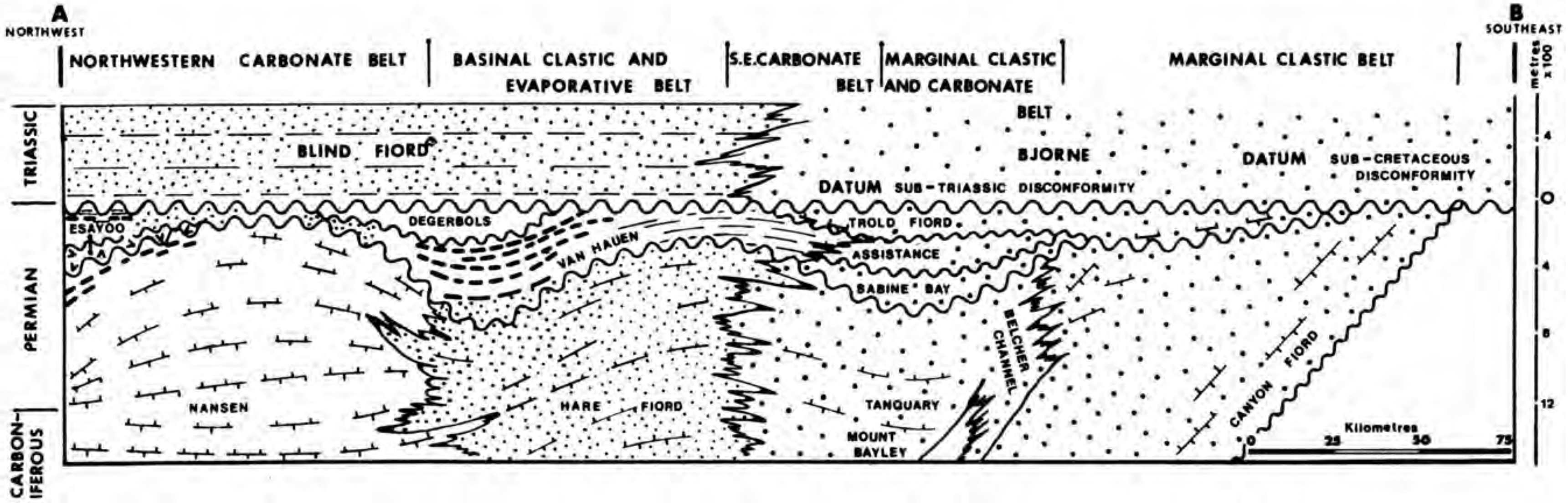

Fig. 320. Permian formations of the Canadian Arctic Archipelago, from Nassichuk et al. (1973 fig. 2) repeated in Waterhouse (1976b, Fig. 27). The present classification is shown in Fig. 2, p. 14. As shown in this report, available brachiopods tend to support some degree of correlation between Assistance and Van Hauen beds, and the Trold Fiord brachiopods appear to match those of Degerböls, rather than the newer arrangement suggest in Fig. 2.

Formation *and Dyoros modestus* Zone, with any match with the Trold Fiord beds less certain, and only one species, *Canalisella leviplica*, possibly pointing to a tie with Degerböls Formation.

Age and correlation:

The Van Hauen Formation is regarded as an offshore and deeper water equivalent of the Assistance and Trold Fiord Formations amongst possibly others in the Sverdrup Basin (see Fig. 1, 2, 321). There is a slight difference between earlier and later interpretations, as suggested in the figures, earlier proposals considering that the Trold Fiord Formation was possibly younger on the whole, and indeed, the available fossils do not contradict this possibility, because a number of fossils confirm a relationship with Assistance faunas and with Takhandit zones 3 to 4 in the Yukon Territory. What is needed for further elucidation is collection of a sequence of fossils, if such be available, through the formation.

Beauchamp et al. (2009, Fig. 2) showed the age at the base as upper Kungurian, ranging upwards through Roadian, Wordian, Capitanian and Wuchiapingian, with gaps present. The available brachiopods are mostly of Roadian and to lesser extent Wordian age.

Degerböls Formation, *Patellamia sulcata* Zone

Brachiopod content:

Thre are few unique species in this faunal assemblage, apart from a specimen of the choristitid *soederberghi* Dunbar. One striking species is *Patellamia sulcata* Waterhouse, a species also found rarely in the Trold Fiord Formation. Other species shared between the Trold Fiord Formation and Degerböls Formation involve *Pleurohorridonia platys* n. sp., also found in the *Dyoros modestus* Zone of the Takhandit Formation, *Waagenoconcha* sp., *Kuvelousia sphiva* Waterhouse, *Spiriferella draschei* (Toula) and *Nahoniella prolata* n. sp. *Kuvelousia perpusillus* n. sp. may have come from this formation, though this is not confirmed. *Liosella spitzbergiana* (Toula) is shared with the Assistance and Trold Fiord Formations. *Canalisella leviplica* (Waterhouse & Waddington) is typical of the Van Hauen Formation, but has been found in the Degerböls Formation at C-4095. *Rhynchopora taylori* Girty is shared with the Assistance, Trold Fiord, Takhandit beds (zone 3) and *Dyoros modestus* Zone of the north Richardson Mountains. *Ametoria nassichuki* is shared with the Assistance, Trold Fiord and Degerböls Formations. *Grumantia kempei* (Andersson) is found at GSC loc. 35760 of possible Degerböls Formation, as well as the Trold Fiord Formation and *Dyoros modestus* and *Cameronovia milleri* zones of the northern Yukon Territory. *Thamnosia*? sp. is possibly shared with the Trold Fiord Formation and zone 4 of the Takhandit Formation.

***Patellamia sulcata* Zone:**

The zone is named after *Patellamia sulcata* Waterhouse*,* as a most distinctive although not restricted species, signifying an acme zone.

Age and correlation:

Most of the species are shared with the Trold Fiord Formation, and the fauna may best be regarded as an offshore equivalent, not the same because so many Trold Fiord species are absent. This agrees partly with the assessment of a

Wordian-Capitanian age in Beauchamp et al. (2009), but no brachiopod species is clearly Capitanian in age. The brachiopods collected in sequence from some fifteen localities from C-10455 serially through to C-10470 through the type section of the Degerböls Formation by W. W. Nassichuk at Van Hauen Pass of Ellesmere Island were examined by the writer in 1974, and suggest a comparatively uniform fauna, with *Derbyia* [= *semicircularis* n. sp.]*, Anemonaria, Kuvelousia sphiva* Waterhouse, *Stenoscisma* [= *opitula* ((Grant)], *Fasciculatia striatoparadoxa* (Toula), *Canalisella* [= *leviplica* (Waterhouse & Waddington)], and *Phricodothyris* [probably *Catatonaria transversaria* n. sp.] prominent. Likely but unverified identifications are suggested in square brackets. Certainly, the faunal lists suggest little clearly marked change throughout the succession, and anticipated the conclusions of the present evaluation in pointing to correlation with the lower Trold Fiord Formation and a Wordian age (Waterhouse 1974). A brief report on subsurface brachiopods by the writer in Brideaux et al. (1975, p. 17) conveys little. If the formation is really Capitanian, then the present study has failed to distinguish the constituent brachiopods from those of Wordian age. This question is briefly discussed on p. 409.

Blind Fiord Formation

Fig. 321. Lower Blind Fiord Formation, Axel Heiberg Island, showing source of late Permian *Krotovia*? sp. B, overlain by basal Triassic with *Hindeodus parvus*. (Waterhouse 1972b).

The basal Blind Fiord Formation exposes laminated black to dark grey shale and siltstone, distally grading into non-siliceous shale (Beauchamp & Baud 2002). Latest Changsingian conodonts were described from the basal beds by Henderson & Baud (1997), with the basal Triassic conodont *Hindeodus parvus* appearing 31.75m above the base, and a few metres of underlying strata also containing indications of earliest Triassic. A Permian brachiopod *Krotovia*? sp. B was collected 19.5m above the base of the Blind Fiord Formation in northeast Axel Heiberg Island, and described by Waterhouse (1972b), as repeated on p. 99, Fig. 70B, and evidently was of late Changhsingian age. A later attempt to collect more from the locality was frustrated by snow, but it obviously would be interesting to learn if there were further macro-fossils in these late Permian sediments.

YUKON TERRITORY, MACKENZIE DISTRICT

TAKHANDIT FORMATION

Type section, Alaska (Roadian and Wordian)

The faunas of the Takhandit Formation at its type section in east Alaska have been summarized and illustrated in Brabb & Grant (1971). The lower sandstone unit includes shells identified with *Productus arcticus* Whitfield, but shells are broad with ears and trail lost, and so not clearly identical. Other species included reported *Kuvelousia weyprechti* (Toula), *Lineabispina ellesmerensis* Waterhouse (identified as *Linoproductus schrencki* in Brabb & Grant 1971), which is a distinctive form prominent in the Assistance Formation of the Sverdrup Basin, possible *Magniplicatina* aff. sp. B and "*Martinia* sp. undet.". The upper limestone unit includes possible *Grumantia kempei* (Andersson), *Kuvelousia sphiva* Waterhouse, *Cameronovia milleri* Waterhouse and possible *Betaneospirifer politus* n. sp., species which are mostly found in the Trold Fiord Formation of the Sverdrup Basin. Species shared between the two units are *Anemonaria pseudohorrida* (Wiman), also found in the lower and middle Takhandit, Trold Fiord and Assistance Formations, so-called *Yakovlevia*, in need of confirmation, *Rhynchopora* aff. *taylori* Girty [identified as *R. kochi* Dunbar], and *Catatonaria transversaria* n. sp. These assessments are of course provisional, with caution required from incomplete preservation and brief description, and allowance tolerated for partial if not full identity. But they do suggest an equivalent between the lower sandstone unit with the Assistance Formation, and close approach of the fauna from the overying limestone unit with faunas from the Trold Fiord Formation.

Two lower biostratigraphic units in Takhandit Formation of the Yukon Territory

The name Takhandit has been applied in the Yukon Territory to sediments of somewhat greater duration than displayed by the type section of the formation in nearby Alaska. Five successive faunas were recognized in the rocks exposed by the Tatonduk River sections, each represented by a number of GSC fossil localities, with brachiopods listed and illustrated by Bamber & Waterhouse (1971, pl. 17-22, Tables 18, 23) and localities detailed and arranged in stratigraphic order by Bamber (1972), numbered from zone 1 (at the base) serially to zone 5 at the top. The Yukon identifications are in need of revision, but collections are not available for the present study, other than a few specimens from the higher beds, and a useful collection from the middle Takhandit level at JBW 631. The lower two faunas, called Fa and Fs in Bamber & Waterhouse (1971), mark a modest and only gradual change from the underlying faunas of the Jungle Creek Formation, which have been described by Bamber & Waterhouse (1971), Shi & Waterhouse (1996) and Waterhouse (2018a). The basal Fa (now Fr) fauna, assigned to the *Rigrantia laudata* Zone (see pp. 421-2), retains strong links with the underlying upper Jungle Creek Formation, including *Rigrantia*, a choristitid and *Septospirifer*. On the other hand, *Anemonaria* was recognized, a genus which became more prominent in Middle Permian faunas of northern Canada. The overlying Fs fauna in the second of the five Takhandit zones includes reported *Derbyia, Karnellia*? *bullocki* (Nelson & Johnson), possible *Svalbardoproductus subarcticus* (Sarytcheva) and *Anemonaria* cf. *pseudohorrida* (Wiman). *Spiriferella arctica* (Haughton) is shared by both zones and is found in the Great Bear Cape Formation. Specimens supposed in Bamber & Waterhouse (1971) to be close to spiriferid *striatoparadoxa* [possibly *Fasciculatia groenwalli* (Dunbar)], and what is now called *Simplicitasia osborni* (Harker) were not illustrated and their identifications need to be further assessed. Rare *Reticulatia* and *Yukonospirifer* suggest close links with the upper Jungle Creek Formation. The most striking component of the fauna is offered by large specimens identified with *Linoproductus* or allied member of the Linoproductinae as figured in Bamber & Waterhouse (1971, pl. 18, fig. 8, 9), deemed highly characteristic of the fauna. Critical for understanding the age and nature of the lower Takhandit faunas is the presence of fusulines from the two faunas, which were described by Ross (1967) and further discussed by Mamet & Ross in Bamber & Waterhouse (1971). From the Fa (now Fr) fauna, *Schwagerina* was deemed to indicate a late Wolfcampian age, equivalent to Lenox Hills beds in the Glass Mountains of Texas, but Mamet & Ross conceded that the fossil may have been derived. *Schwagerina hyperborea* (Salter) was considered to point to the lower Leonard of Texas. The fusuline is found with other fusulines in the upper Belcher Channel Formation, now renamed Great Bear Cape Formation, on Devon Island, immediately below the Assistance Formation (Thorsteinsson in Harker & Thorsteinsson, 1960), with GSC loc. 26407 and 26470 in the top 65ft of the formation at Grinnell Peninsula, and this remains the most likely of correlations, feasibly suggesting from known age range of the fossils and stratigraphic sequence a broadly lower Leonardian or upper Artinskian correlation. That would imply a time-gap and fossil-gap in the middle Takhandit Formation of the Yukon Territory, below the equivalents of the type Takhandit section of Alaska, and involving most or all of the Kungurian Stage.

Given the absence of these beds from the type Takhandit of Alaska, and the fact that these beds are overlain by a cryptic disconformity with a substantial slice of missing Kungurian time, rocks and faunas, the lower part of the Takhandit Formation so-named in Yukon Territory should arguably be granted a new name. Or even scrapping Takhandit in favour of a total replacement name, based on the sequences exposed along the Tatonduk River valley or Ogilvie Mountains in Canada. Either of these steps would conform with the recommendations by the Code of Stratigraphic Nomenclature.

Middle and upper Takhandit biozones

Neochonetes culcita Zone

Brachiopod content:

The younger Takhandit faunas were divided into three: named Fps, Ft and Gc in Bamber & Waterhouse (1971). The so-called *Pseudosyrinx* of the Fps Zone is now regarded as close to *Licharewia*, and is accompanied by *Neochonetes culcita* n. sp., with *Anemonaria, Magniplicatina?* sp. A and *Betaneospirifer politus* n. sp., as well as the significant and distinctive species *Lineabispina ellesmerensis* Waterhouse and *Spiriferella sulcoconstricta* n. sp. shared with the Assistance Formation.

A collection from JBW 631 in the middle Takhandit Formation in the Ogilvie Mountains has yielded *Grumantia*? sp., *Neochonetes culcita* n. sp., *Fimbrininia* sp., *Guangia* sp., *Balkhasheconcha thorsteinssoni* n. sp., *Retimarginifera* sp., *Harkeria studiosa* Waterhouse, *Cimmeriella* sp. A, *Cimmeriella coyneae* n. sp., *Magniplicatina phosphatica* (Girty), *Stenoscisma opitula* (Grant), *Martinia*? sp. B, *Betaneospirifer politus* n. sp., possible *Simplicatasia* *osborni* (Harker) and *Spiriferella separata* n. sp. Some are small, some not well preserved, and most are found also in the Assistance Formation of the Sverdrup Basin, with a few ranging into the overlying zone in the Takhandit Formation and equivalents in the north Richardson Mountains.

***Neochonetes culcita* Zone:**

The zone is named *Neochonetes culcita* as a range zone, enabling ready correlation with the Assistance Formation of the Sverdrup Basin. *N. culcita* is also found in the Richardson Mountains. *Lineabispina ellesmerensis* is also a wide-ranging Canadian Arctic species, most prominent in the Assistance Formation.

Age and correlation:

Correlation with the Assistance Formation enforces a Roadian age, thanks to the Roadian ammonoids found in that formation.

Upper middle Takhandit Formation, *Dyoros modestus* Zone

Brachiopod content:

The overlying *Thamnosia* (Ft) Zone in Bamber & Waterhouse (1971) is rather meagre, and a revised list includes *Dyoros modestus* n. sp., *Thamnosia?* sp., ?*Rugivestis* sp., anidanthid, *Harkeria studiosa* Waterhouse, which is found in the Assistance and van Hauen Formations, and rarely in the Trold Fiord Formation. *Oviformia bamberi* (Waterhouse) and *Spiriferella separata* n. sp. are both shared with the Assistance Formation.

***Dyoros modestus* Zone**:

The zone is named after *Dyoros modestus* n. sp., as providing a convenient link with the faunas of the north Richardson Mountains to the north.

Age and correlation:

This fauna in the Takhandit Formation intervenes between faunas correlative with the Roadian Assistance Formation and the Wordian Trold Fiord Formation. There is no clear sign of this fauna in the type Takhandit of Alaska, but on the other hand much the same fauna is found in a similar stratigraphic position in the Richardson Mountains, and in the offshore Van Hauen Formation of the Sverdrup Basin. A collection from C-4063 5.8 miles south of peak 3550ft west of Trold Fiord, slightly younger than the Assistance Formation, included a smooth chonetoid, possibly signalling that the zone is represented, but no collections have been available for the present study. Provided that there has been no collecting failure or inadvertent mixing of faunal collections, this may indicate a slight faunal gap and pause in sedimentation in the Sverdrup Basin near-shore sequence, or perhaps local faunal diversification.

The standard sequences in the Glass Mountains are complex and varied, and the rearrangement of stages for international paleochronology readily accommodates an additional faunal zone for brachiopods within the Roadian Stage, because this has been extended beyond the Road Canyon Formation of Cooper & Grant (1972) to incorporate the China Tank and Willis Ranch Members of the Word Formation, as classed by Cooper & Grant (1972), and equivalent to the lower and middle Word Formation of King (1931). Similarly the sequences of lower Guadalupian in Russia and east Australia – New Zealand can accommodate potential matches with this zone.

Uppermost Takhandit Formation, *Cameronovia milleri* Zone

Brachiopod content:

The *Cancrinelloides* (Gc) Zone of Bamber & Waterhouse (1971) is renamed after *Cameronovia milleri* Waterhouse, and includes *Grumantia kempei* (Andersson), *Kuvelousia sphiva* Waterhouse, *Magniplicatina, Cancrinella arctica* (Water-

Stage	mid-Yukon	Richardson Mts	Offshore Sverdrup Basin	Nearshore Sverdrup Basin
Changhsingian **Wuchiapingian** **Capitanian**			Blind Fiord Black Stripe-	Lindström upper Trold Fiord
Wordian	Takhandit 5 *Cameronovia milleri* Z	*Cameronovia milleri* Z	Degerböls F *Patellamia confinis* Z	Trold Fiord F *Cameronovia milleri* Z
Roadian	Takhandit 4 *Dyoros modestus* Z	*Dyoros modestus* Z	Van Hauen F *Dyoros modestus* Z	basal Trold Fiord F *Dyoros modestus* Z
Roadian	Takhandit 3 *Neochonetes culcita Z*	*Neochonetes culcita Z*	Van Hauen F *Canalisella leviplica*	Assistance F *Neochonetes culcita Z*
Kungurian	sedimentary break		Van Hauen F no brachiopods described	Sabine Bay F *Paeckelmannella calignea Z* gap
upper Sarginian	Takhandit 2 *Schwagerina jenkinsi, Spiriferella arctica*			Great Bear Cape F *Schwagerina jenkinsi* *Spiriferella arctica*
lower Sarginian	Takhandit 1 *Schwagerina* *Rigrantia laudata Z*			Great Bear Cape F
Aktastinian	upper Jungle Creek F *Jakutoproductus verchoyanicus*			?Belcher Channel F

Table 1. Showing distibution and correlation of late early Permian, Middle Permian and Late Permian brachiopod zones with *Schwagerina* (fusuline) zone at base in the northern Yukon Territory and Sverdrup Basin of the Canadian Arctic Archipelago. Z = Zone, F = Formation. The Degerböls has been placed to accord with Fig. 1 and 321.

house, *Wellerella* and *Spiriferella sulcoconstricta* n. sp. *Cancrinella* sp. undet. of Brabb & Grant (1971) from the upper unit of the type Takhandit Formation in Alaska belongs to *Cameronovia milleri*, and is equivalent to the uppermost Takhandit faunas of the Yukon Territory.

***Cameronovia milleri* Zone:**

The zone is named after the distinctive fossil *Cameronovia milleri* Waterhouse, which provides a strong link with the Richardson Mountains and Trold Fiord Formation of the Sverdrup Basin.

Age and correlation:

A Wordian age is preferred. There are no brachiopods which clearly indicate a Capitanian as opposed to a Wordian age, and none that clearly suggest a Wuchiapingian age.

RICHARDSON MOUNTAINS

In the northern Richardson Mountains of northern Yukon Territory and Mackenzie District, a succession of faunas is found, and some material is examined in this study. Three successive zones were recognized in Bamber & Waterhouse (1971, pp. 176, 178, 180, 182), and rocks and fossil occurrences are presented in Bamber & Waterhouse (1971, Fig. 10), with stratigraphic sections and fossil localities detailed by Bamber (1972). The potential value for biozonal subdivision of this region for Middle Permian Arctic Permian faunas should not be underestimated, and the good preservation of silicified fauna offers useful information relevant to both the Takhandit Formation further south, and faunas of the Sverdrup Basin to the north. Remembering that the present and past surveys were based on preliminary work, much remains to be learned, and close study of the rocks and faunas should be of considerable interest.

Lower beds, *Neochonetes culcita* Zone

Brachiopod content:

The lower zone, then named Fn after *Neochonetes*, now *N. culcita* n. sp., was matched with the Fps Zone of the Takhandit Formation by Bamber & Waterhouse (1971). At section 116P-9 in the Rat River area, *Neochonetes* was reported and figured, together with shells compared with *Anemonaria pseudohorrida* (Wiman), found in GSC loc. 53826-53828. Further north at section 116P-1 at Scho Creek, *Neochonetes* was found with possible *Cancrinella arctica* and *Pterospirifer*. *Timaniella harkeri* Waterhouse came from GSC loc. 52705 in the sandstone unit at section 116P-6 of the Richardson Mountains (Bamber & Waterhouse, 1971, p. 220), with further occurrences reported in nearby localities, and characteristic of Assistance faunas in the Sverdrup Basin. At White Mountains, C-10980 from a fault slice has yielded *Alispiriferella gydanensis* (Zavodowsky), shared with the Omolon horizon of the Kolyma River area in northeast Russia, and localities in the Assistance Formation at Ellesmere Island (GSC loc. 58968, 58973, and C-3995), and Trold Fiord Formation of the Sverdrup Basin. Provisionally**,** the beds are assigned to the *Neochonetes culcita* Zone.

***Neochonetes culcita* Zone:**

The zone is named after *Neochonetes culcita.* This species is found also in the middle Takhandit Formation and Assistance Formation.

Age and correlation:

Several species point to correlation with the Assistance Formation and Roadian age.

Middle beds, *Dyoros modestus* Zone

Brachiopod content:

The overlying faunas of the northern Richardson Mountains were considered to be typified by a smooth chonetid, called *Lissochonetes*, and reassigned herein to *Dyoros* Stehli, 1954 (see Bamber & Waterhouse 1971, pl. 21, fig. 4-7 and this study, p. 46). This species, now named *Dyoros modestus* n. sp., is found also in the Van Hauen Formation and Takhandit Formation zone 4, and possibly at one station in the Trold Fiord Formation. The fauna also includes *Pleurohorridonia platys* n. sp. (also Trold Fiord and Degerböls Formations of the Sverdrup Basin), *Anemonaria robusta* n. sp. (also in Assistance and Trold Fiord Formations of Sverdrup Basin), *Megousia tortus* n. sp., *Martinia*? sp. A, *Bamberina cordiformis* (Waterhouse & Waddington), and *Orbicoelia*?, which somewhat resembles *O*.? *aquilonia* (Stehli & Grant) found in the Sabine Bay Formation. The faunas were found at Fish Creek section (116P-6) (GSC loc. 52702-52703) and in the Symmetry Mountain section (116P-11) at GSC loc. 53839-53848 in unnamed sandstone and GSC loc. 53837 and 53838 in unnamed shale. There was a reported but anomalous or exceptional lingering occurrence of *Timaniella harkeri* Waterhouse in Waterhouse & Waddington (1982, p. 32), but the locality was not documented in Bamber (1972), and there must be some uncertainty about the source. From GSC loc 53846, McDougall Pass, *Grumantia kempei* (Andersson), *Dyoros modestus* n. sp., *Liosella* sp., *Megousia tortus* n. sp., *Rhipidomella transfigona* n. sp., *Rhynchopora taylori* Girty, *Cyrolexis* sp., *Hustedia troelseni* Dunbar, *Martinia*? sp. B, and very incomplete so no more than possible *Fasciculatia striatoparadoxa* (Toula). *Gjelispinifera punctuata* n. sp. and *Paraspiriferina mcdougallensis* n. sp. (also Trold Fiord beds) have been described in this report, with *Megousia tortus* and *Paraspiriferina* also from the nearby fossil locality of GSC loc. 53848. Further collections at McDougall Pass in section 116P-9 have yielded *Dyoros modestus* n. sp., *Magniplicatina, Cancrinella arctica* (Waterhouse), *Kuvelousia, Cimmeriella* sp. (also in the Assistance Formation), *Orbicoelia*? and other species are found at GSC loc. 53822-53825. Similar fossils are found in the Scho Creek section of 116P-1, at GSC loc. 53876. *Cancrinella arctica* (Waterhouse) ranges through the *Dyoros modestus* and *Cameronovia milleri* Zones of the Richardson Mountains, and Assistance Formation of the Sverdrup Basin.

***Dyoros modestus* Zone:**

The zone is named after *Dyoros modestus*.

Age and correlation:

Although a number of species indicate links with Assistance faunas, some indicate a fresh input of new species not known in that fauna, including *Dyoros modestus* and *Megousia tortus.* These are considered to signify significant new faunal elements joined with surviving Assistance fossils. An ammonoid *Neogeoceras* has been reported in Nassichuk et al. (1965).

Uppermost beds, *Cameronovia milleri* Zone

Brachiopod content:

The zone is represented by *Kuvelousia sphiva* Waterhouse and *Cancrinella arctica* (Waterhouse) at the Scho Creek section 116-P1, GSC localities 53872-53875, and in the Symmetry Mountain section 116P-11 (GSC loc. 53850-53852), Fish Creek section 116P-6 (GSC loc. 52710), and section 116P-9 at McDougall Pass (GSC loc. 53821), the latter locality with *Cameronovia milleri*. In the Symmetry Mountain section, *Cancrinella* is present at GSC loc. 53850. There are a number of other fossils, *Grumantia kempei* (Andersson), and various taxa not fully identified, involving horridoniid, *Waagenoconcha, Magniplicatina*, possible *Wellerella*, and possible *Pterospirifer. Neochonetes* is present (Bamber & Waterhouse, 1971, pl. 22, fig. 5 - 7), but specific identity cannot be fully explored, because the sample is inadequate.

***Cameronovia milleri* Zone:**

The topmost zone is named after *Cameronovia milleri*, and is shared with the upper Takhandit Formation of the Tatonduk River to the south, and with the Trold Fiord Formation of the Sverdrup Basin.

Age and correlation:

Grumantia kempei (Andersson) and *Kuvelousia sphiva* Waterhouse reinforce correlation of the *Cameronovia milleri* beds with the faunas of the Tatonduk River and Trold Fiord Formation in the Sverdrup Basin. *Pterospirifer* invites comparison with *P. alatus* (von Schlotheim), which was reported from the second to top biozone of the Kapp Starotsin Formation at Spitsbergen (cf. Nakamura et al. 1992, pl. 5, fig. 1-3), but the Yukon specimen does not show the extreme alation of the Spitsbergen or Zechstein specimens, so that the similarity may be no more than generic. Setting aside the possible implications of that genus, the fauna is judged to be of Guadalupian age, most likely Wordian, based on brachiopod affinities.

TRANS-ARCTIC CORRELATIONS

YUKON TERRITORY, SVERDRUP BASIN

According to fusulines, the lower Takhandit Formation is of Baigendzian age (Waterhouse 1971), or Aktastinian (Ross 1967, in Mamet & Ross in Bamber & Waterhouse 1971, p. 205). To Waterhouse, the presence of the *Schwagerina jenkinsi* assemblage provides a clear and strong tie with the classic Baigendzinian faunas of Russia, and the large linoproductid found in the Fs fauna, second Takhandit zone, reinforces a Baigendzinian age. There were presumptions on the part of American ammonoid experts such as Furnish & Glenister (1960) that the classic Artinskian ammonoids persisted into classic Kungurian of Russia, which therefore could not be differentiated, but this seems to have been based merely on the lack of ammonoid evidence from the Kungurian, and the presumption has not found support from foraminifers, brachiopods or conodonts, nor in later overviews of Permian ammonoid distributions (Leonova 2016). *Schwagerina* is not known in the world standard Kungurian Stage of Russia, and if conditions were similar at that time in the Yukon Territory, there would have been a faunal as well as stratigraphic break within the Takhandit Formation between the Fs and Fps zones. The type Takhandit in Alaska commenced at the Fps Zone, of Roadian age, above a stratigraphic break preceeded in the Yukon by beds assigned to the lower Takhandit Formation. The Sabine Bay Formation in the Sverdrup Basin which occupies part of this interval includes non-marine sediment, as well as a marine interval regarded herein as equivalent to Nevolin in Russia, followed by a late Kungurian interval at the base of the Assistance Formation, correlated with the *lamberti* conodont Zone (Henderson 2018).

The *Neochonetes culcita* Zone is now substituted for the *Pseudosyrinx* or Fps Zone of Bamber & Waterhouse (1971) and is regarded as Roadian, or early Guadalupian Series, on the basis of brachiopod correlation with the Assistance Formation of the Sverdrup Basin to the north. Nassichuk (1970) and Nassichuk et al. (1965) showed that Assistance ammonoids could be matched with those of the Road Canyon Formation of the Glass Mountains, Texas. Although they considered the age to be Baigendzinian, Waterhouse in Bamber & Waterhouse (1971, p. 170) argued for a Ufimian age, and the age is now consolidated as Roadian Stage, at the base of the Guadalupian Series, or Middle Permian.

The overlying former Ft (*Thamnosia*) Zone, now named after *Dyoros modestus* n. sp., is stratigraphically younger, and matches the former Fl or now *Dyoros modestus* Zone of the Richardson Mountains to the north. A Wordian age was favoured from brachiopod evidence by Bamber & Waterhouse (1971, p. 182), with support provided by an ammonoid from the *Dyoros modestus* Zone (or just above) at Scho Creek, which was identified as *Neogeoceras* in Nassichuk et al. (1965). The Roadian Stage has been expanded beyond the limits of the Road Canyon Formation to incorporate the lower members of the Word Formation, so that the zone is now regarded as upper Roadian Stage.

The uppermost Takhandit faunas from both the type section (Brabb & Grant 1971) and Tatonduk River (Bamber & Waterhouse 1971, p. 182) were regarded as Kazanian, and now equated to Wordian of the present internal time scale. The ammonoid *Neogeoceras macnairi* Nassichuk et al. (1965) came from the Trold Fiord Formation of the Sverdrup Basin, and was regarded as Guadalupian. According to Liao Zhuo-ting as quoted in Nakamura et al. (1992, p. 83), conodonts from the upper Trold Fiord Formation indicate a Capitanian age, but Beauchamp et al. (2009) indicated that the lower Trold Fiord Formation was Wordian, and that is in accord with the present survey. *Horridonia grandis* Waterhouse, from the Trold Fiord Formation though without available documentation on stratigraphic position, shows ties with *Horridonia horrida* Sowerby from England, and this is of Wuchiapingian (Lopingian) age, but the detailed arrangement of spines suggests that the Canadian species preceeded *horrida*, and could have been of Guadalupian age.

GREENLAND

Amdrups Land, northeast Greenland

A small brachiopod fauna has been described and illustrated from the Mallemuk Mountain Group, of northeast Greenland by Dunbar (1962): there have been other accounts, but his article provides a useful if long outdated summary. Although Dunbar indicated a generalized correlation with the Brachiopod Chert of Spitsbergen, the faunas from two levels, G and H, match elements of the Vøringen Member on Spitsbergen, and this appears to have been supported by Lee et al. (2016) with the description of one particular fossil from the Vøringen Member that is shared with northeast Greenland, and by the listings of several species in Nakamura et al. (1992). Dunbar identified material with *Yakovlevia* (?) *impressus* (Toula) though Gobbett (1964) and Angiolini & Long (2008) made no reference to Dunbar's report. The species *impressus* was interpreted as a new genus *Archboldevia* by Angiolini & Long (2008), and restricted to the Vøringen Member. It is very close to *Yakovlevia* itself (Waterhouse 2013, p. 343). Gobbett (1964, p. 114) stated that *impressus* was limited to the Spirifer Limestone. So-called *Muirwoodia weyprechti* (Toula) was reported but not

Taxon	**Takhandit zones 1 & 2**	**Great Bear Cape Formation**	**Vøringen Member**	**Amdrup G, H faunas**
Derbyia semicircularis n. sp.	aff.	aff.		
Sowburia granulifera (Toula)			x	x
Karnellia? *bullocki* (Nelson & Johnson)	x			
Svalbardoproductus subarcticus (Saryt.)	x	x	x	**x**
Thamnosia sangminlee n. sp.		x	**?**	
Rigrantia laudata n. sp.	x			
Kochiproductus freboldi Stepanov	?	?	**?**	
Krotovia? sp. A		x		
Guangia pustulata (Keyserling)		x		
Anemonaria pseudohorrida (Wiman)	?			
Kuvelousia weyprechti (Toula)			?	x
Archboldevia impressus (Toula)			x	**x**
Linoproductid	x			
Rhynchopora taylori (Girty) *nikitini* Tsch.	?		**?**	
Pinegathyris amdrupi (Dunbar)			**x**	x
"*Choristites*"	x			
"*Choristites*?" sp. indet.		x		
Fasciculatia groenwalli (Dunbar)		x	x	x
Yukonospirifer sp.	(sp. A)		(sp. B)	
Betaneospirifer striatoplicatus (Gobbett)		x	x	
Septospirifer sp.	x			
Spiriferella arctica (Haughton)	x	x		
S. angulata n. sp.	x	x	x	x
Arcullina polaris (Wiman)	level ?		x	
Undulatina keilhavii (von Buch)			x	
Timaniella wilckzeki (Toula)			x	
Spirelytha pavlovae Archbold & Thomas		x		
Reticulariina? sp. A		x		

Table 2. Some of the brachiopods from late Artinskian and early Kungurian levels in Arctic Canada, Greenland and Spitsbergen-Bjørnøya.

figured by Dunbar (1962). His *Sowerbina granulifera* (Toula), now referable to *Sowburia,* has four rows of spines on the ventral valve, and Angiolini & Long (2008) included Dunbar's material in their synonymy for the species, which they wrongly identified as *Bruntonaria*. Both Angiolini & Long (2008) and Nakamura et al. (1992) showed the species as coming from the Vøringen Member. So-called "*Waagenoconcha*" *irginaeformis* Stepanov was reported but not figured. The Greenland specimen *Dictyoclostus neoinflatus* Licharew of Dunbar (1992, pl. 1, fig. 8, 9) from level H has swollen lateral flanks, suggestive of *Svalbardoproductus subarcticus* (Sarytcheva), and although the ears are no longer preserved, the specimen seems likely to belong to that species. It is also found in the Great Bear Cape Formation and Vøringen Member. Gobbett (1964, p. 91) referred Licharew's species to *Thamnosia arcticus* (Whitfield) and claimed that in Spitsbergen it was limited to the Spirifer Limestone. Dunbar's reported *Spiriferella draschei* (Toula) from level G looks much more like *S. angulata* than *draschei*, given its well developed ventral sulcus of only moderate width (Dunbar 1962, pl. 2, fig. 12-14). *Spiriferella parryana* (= *Canalisella loveni*) of Dunbar (1962, pl. 1, fig. 15) from horizon G is indeterminate. It has some five pairs of plicae but broken around the edges, and possibly at not full maturity. It was included in the synonymy of *loveni* by Lee et al. (2019, p. 20), but their Svalbard material was not documented with regard to any stratigraphic information for individual figures, other than a than a broad Kapp Starotsin Formation, with generalized distributions also shown in minutely scaled maps and indefinite boundaries (Lee et al. 2019, Fig. 8). *Neospirifer groenwalli* Dunbar (1962, pl. 2, fig. 6-8) from Horizon G has fine ribs, counted at eight in 10mm anterorly by Dunbar, comparable in number to those of specimens figured by Tschernyschew & Stepanov (1916, pl. 9, fig. 4) from the present Great Bear Cape Formation and Gobbett (1964, pl. 18, fig. 2) from the Vøringen Member of Spitsbergen. The Gobbett specimen is close in the profile of its fold, broad base, narrow crest, but Dunbar's specimen has narrower cardinal extremities, whereas the anterior lateral margins of the other specimens bulge more. However a large specimen assigned to *groenwalli* by Lee et al. (2016, p. 129, Fig. 13G-I) also bulges anterolaterally. This specimen has better developed plicae than in other shells, but costae are fine, at nine to ten in 10mm on either valve (measured for mid ventral valve and anterior dorsal valve) and the fold is similar. Of course, all of these identifications suffer from the lack of information about internal detail, but provisionally, all are referred to *Fasciculatia groenwalli* (Dunbar). Lastly, in Dunbar's account, the highly distinctive transverse species assigned to *Athyris amdrupi* Dunbar, 1962, pl. 2, fig. 1-5 from Horizon H was also listed and figured from the Vøringen Member at Skansbukta Bay by Nakamura et al. (1992, p. 78, pl. 1, fig. 7), with Dunbar's synonymy including reference to figures in Wiman (1914) and Frebold (1950). The species is transverse and shape like *Pinegathyris* Grunt, 1988, with a time range given as Kungurian to Kazanian in Alvarez & Rong (2002).

Allowing for uncertainties due to incomplete descriptions and preservation, it does seem highly likely that the Amdrup G and H levels of northeast Greenland correlate with the Vøringen Member of Spitsbergen and Bjørnøya, and show strong similarities to specimens from the Great Bear Cape Formation of the Canadian Arctic.

Table 2 lists some of the prominent species, as verified by figures or descriptions. Additional and significant species recorded for the Vøringen Member in Gobbett (1964, p. 21) include [with generic names adjusted] *Arctitreta macrocardinalis* (Toula), *Sowerbina timanica* (Stuckenberg), *Stenoscisma spitzbergiana* (Stepanov), *Arcullina polaris* (Wiman), and further species, close to the list provided by Nakamura et al. (1992, p. 78). It is likely that

Balkhasheconcha is present, possibly also in Canada. Many more species, belonging to such genera as *Kochiproductus* and *Anemonaria*, are found in the lower Takhandit Formation (Bamber & Waterhouse 1971) and Great Bear Cape Formation (Tschernyschew & Stepanov 1916), as outlined on p. 379. But whilst this tabulation of species is incomplete, it does show that the Great Bear Cape and lower Takhandit Formations retained Cisuralian genera, inherited from the Jungle Creek Formation, that were lost in the Vøringen and Amdrup formations, except for *Yukonospirifer.* And it shows that a number of new forms entered the latter two formations. On the other hand, the faunal levels share a number of species. This suggests that the Canadian faunas are slightly older, and that the Greenland-Spitsbergen faunas witnessed the significant loss of various Cisuralian genera, and the significant introduction of new forms, regarded herein as signalling the start of the Guadalupian Series and Kungurian Stage, which would point to a Saranin or preferably Filippovian age for the Vøringen and Amdrup G, H faunas.

Central east Greenland

A prime question concerns the age and correlation of the Permian brachiopods from central east Greenland, described and well illustrated by Dunbar (1955). The collections came from various levels and facies, but Dunbar was convinced that all were of the same age, with facies complex and interdigitating – a matter supported by Stemmerick & Piyasecki (1991), though still warranting some caution. Grunt & Blomeier (2013) separated the Posidonia Shale and Productus Limestone as being older. Dunbar's interpretation on age were what could now be regarded as a little inconsistent. He favoured a Kazanian age, and correlated the fauna with the Spirifer limestone of Spitsbergen, and disparately, it appears, with the lower Zechstein and Magnesian Limestone faunas of Germany and England, gaining bivalve support from a study by Newell (1955). The critical ammonoids *Medlicottia malmquisti* and *Godthaabites kullingi* were initially described by Frebold (1932) from the Martinia-kalk in Greenland. Miller & Furnish (1940) analysed *Godhaabites* and reidentified it as *Cyclolobus*, of Late Permian age, as reinforced in Nassichuk et al. (1965). Grant (1968, p. 6) did not accept the young age, and assigned the ammonoid to the Guadalupian, and Brabb & Grant (1971) considered that the upper Takhandit brachiopods matched those of central east Greenland, with *Godthaabites*. Waterhouse (1972a) also expressed reservations, stressing that the suture of *Godthaabites* was more primitive that the sutures in *Cyclolobus* and *Krafftoceras*, and so regarded the genus as a precursor and possibly older form. Figures of sutures were presented, though to me now the differences between mature *Godthaabites* and *Cyclolobus* do not seem very striking. Furnish & Glenister (1970) as experts on Upper Paleozoic ammonoid sutures were convinced that the Greenland *Godthaabites* compared with a primitive cyclolobid called *Krafftoceras* in Ruzencev & Sarytcheva (1965), which is found in the *Araxoceras* Zone (then Dzhulfian, now Wuchiapingian) in Armenia. Later Zakharov (1983) described *Godthaabites ruzhencevi* from Djulfian (Wuchiapingian) of the Transcaucasus. The relevant Salt Range faunas with *Cyclolobus* are now firmly held to be of Wuchiapingian age, thanks to major clarification of the Late Permian in China, with rejection of the Glenister-Furnish opinion that demanded *Cyclolobus* be of latest Permian age. The improved understanding was based on the record of *Codonofusiella*, a Wuchiapingian fusuline from below the *Cyclolobus* occurrences (Tayyab et al. 1981), reassessments and new Himalayan studies on brachiopods (Waterhouse 1978, Waterhouse & Chen 2007), and the discovery of significant conodonts (Wardaw & Mei 1999; Mei & Henderson 2002) and palynomorphs (Foster & Archbold 2001), as summarized by Waterhouse (2010, p. 268). But this still leaves a question over the age of the

Greenland faunas. Are the faunas all of Wuchiapingian age, as implied by the interpretation that *Godthaabites* matched *Krafftoceras* in age, and the conclusion by Dunbar (1955) that all the faunas he had described from central east Greenland belonged to one biostratigraphic unit. Or were there several separate faunas that could be teased out and arranged in a stratigraphic succession, with at least some older than the *Godhaabites* level, by a zone or even a stage in duration? Or is *Godthaabites* Guadalupian?

Stemmerick (1988) accepted Dunbar's assessment that all belonged to one faunal zone, and this was endorsed by an assessment of conodonts by Rasmussen et al. (1990). These authors reported widespread occurrences of *Neogondolella rosenkrantzi,* confirming an unacknowledged report by Sweet (1973, p. 641), and now consolidated as Wuchiapingian, or lower Lopingian, according to Henderson (2018). The conodonts also included reported *Xaniognathus abstractus*, and *Merrillina divergens* and came from the lower Ravnefjeld Formation, equivalent to the Posidonia Shale and Martinia beds, and embracing the source of *Godthaabites*, which would deny any caution expressed about a late Permian age, but ensure a lower Wuchiapingian rather than Changhsingian age. Rasmussen et al. concluded that the conodonts suggested correlation with the top of the Phosphoria and Park City Formations of western United States, the Cherry Canyon and Bell Canyon Formations of Texas, and Zechstein 1 of northern Europe. Kozur (1994) assigned the conodonts of the Foldvik Creek Group to Djulfian (approximately Wuchiapingian), and regarded the Schuchert Dal Formation as close or slightly younger in age (Kozur 1998). He reinterpreted *Merrillina divergens* of Rasmussen et al. (1990) as *M. praedivergens* Kozur & Mostler and told me he had found *M. divergens* in early Wuchiapingian beds in northwest Iran, in the *Codonofusiella* beds of Wuchiapingian age (Heinz Kozur, pers. comm., e-mail 24.9.03). Henderson (2018, p. 130) showed *divergens* as short-lived and limited to the early Wuchiapingian in the Tethyan realm. A Wuchiapingian (lower Lopingian) correlation was tabulated without discussion by Stemmerik & Worsley (2005) and Sørenson et al. (2007), implying the matter is now settled beyond debate.

Yet another interpretation of the Greenland Permian was offered by Shen (2016, Fig. 2). In a table he showed the Greenland Permian as arranged in two biozones, named after *Pterospirifer alatus* (Schlotheim) and *Haydenella wilczeki* (Toula), and correlated with the Wuchiapingian and Changhsingian stages respectively. No explanation was provided. I am not aware of any formal description of *Haydenella* from Greenland, but possibly one or other of the productids described by Dunbar (1955) could prove allied, such as the shells described as *Liosotella hemisphaerica* Dunbar (1955, p. 74, pl. 4, fig. 1-21). Ventral ribs are strongly developed in the Greenland material, and spine detail lacks clarity, but Dunbar denied the presence of dorsal spines, and there are no strut spines. There are signs of an umbonal slope row and rare hinge spines. (See p. 151). I am not aware of any evidence for a Changhsingian age. The “white blocks” of limestone found in early Triassic beds east of Kap Stosch could be Changhsingian, but Dunbar (1955, p. 28) listed much the same brachiopod content, whereas Newell found a number of additional bivalves

My assessment is that the brachiopods of central east Greenland or at least the bulk of them form a distinctive assemblage, of early Wuchiapingian age. Although some of the species are to be found in older faunas of Alaska, Yukon Territory and Canadian Arctic Archipelago and Spitsbergen, most of them are restricted in age and distribution. They include *Fissulina stoschensis* (Dunbar), *Capillonia toulai* (Dunbar), *Marginifera nathorstfjordensis* Dunbar, *Gruntoconchinia payerinia* n. gen., n. sp., *Pleurohorridonia scoresbyensis* Dunbar, *Sowburia maynci* (Dunbar), *Harkeria* *greenlandica* (Dunbar), *Kochiproductus* (*Dunbarovia*) *pleuricostatus* Dunbar, "*Liosotella*" *hemisphaerica* Dunbar [now possibly *Haydenella*], *Rhynchopora abnormalis* Dunbar, *R. kochi* Dunbar, *Stenoscisma kochi* Dunbar, *Cleiothyridina pectinifera* (d'Orbigny)*, *Pterospirifer alatus* (Schlotheim)*, *Fasciculatia greenlandica* Waterhouse, *Martinia greenlandica* Dunbar, *Tintoriella laticostata* n. sp., *Odontospirifer mirabilis* Dunbar, *Paraspiriferina stoschensis* n. sp., *Dielasma elongatum* Schlotheim*, and *D. stoschensis* Dunbar. A few species as asterisked are shared with the Zechstein of northern Europe, and others with the upper faunas of the Kapp Starotsin Formation, as elaborated by Nakamura et al. (1992). There is a scattering of reports from elsewhere, some regarded as correct, others to be tested. One of the most distinct species was described as *Strophalosia pulchella* Dunbar, now referred to *Craspedalosia*, and this is possibly present at Bjørnøya, although that needs confirmation, because a somewhat similar looking species from the Trold Fiord Formation of Arctic Canada has been found to be distinguished by possessing dorsal spines, and so has been named as separate genus, *Melvillosia*. Given the uncertainties, and acknowledging the need for more first hand study and revision of the species, it does appear that this Dunbar fauna marks a template for early Wuchiapingian brachiopods of the Permian Arctic.

SPITSBERGEN

No Arctic sequences of Permian rocks and faunas have been more closely studied than those of Spitsbergen, and the Canadian faunas show much in common, although the reservation that marine faunas in those times travelled freely and developed local signatures, with variations in inception and duration, and even exclusion needs to be kept in mind. The substantial study of brachiopods by Gobbett (1964) remains the bedrock of recent understanding, but that study has been modified by subsequent developments concerning stratigraphy, age and the time value of fossil groups, quite apart from the substantial revisions to systematic hierachy. Gobbett (1964) referred the Spirifer Limestone (by then more limited than the Spiriferenkalk of Wiman 1914) and Brachiopod Chert to a Svalbardian Stage as named by Stepanov (1957), regarded as possibly matching Kungurian to Kazanian, possibly matching a faunal gap or meagre representation in western Russia, though that is widely regarded as unlikely. Nakazawa (1999) regarded the bivalves as Kungurian in the main, allowing that such an age was a little older than that indicated by brachiopods.

Brachiopods from the Vøringen Member

Cutbill & Challinor (1965) renamed the rocks formerly known as Spiriferenkalk, and later Spirifer Limestone and Brachiopod Chert as Kapp Starotsin Formation, subdivided into three units: Vøringen Member, Svenskeegga Member later spelled Svenskeega, as in Grunt & Blomeier 2016), and Hotvinden Member. An elaborate time-chart and summary of brachiopod occurrences was issued by Nakamura et al. (1992, Fig. 3), on the basis of close collecting through the Kapp Starotsin Formation, and recognized a succession of zones. Stemmerik (1988) disagreed with the Nakamura et al. (1987) biozonation, ascribing the causes to local ecological factors, as if all zonation did not have ecological input, and as if ecology and biostratigraphy did not reflect climatic and other temporal factors. In spite of Stemmerik's objections, the Nakamura et al. proposals remain reasonable approximations,

The basal Vøringen Member possessed one brachiopod zone, named after *Sowerbina timanica* Stuckenberg, later misidentified with *Bruntonia maynci* (Dunbar) by Angiolini & Long (2008) – see p. 60 herein – and now renamed

Sowerbina longi n. sp. Nakamura et al. (1992) listed fifteen species from Inner Isfjorden, *Horridonia timanica* Stuckenberg, *H. granulifera* (Toula), *Yakovlevia impressa* (Toula), *Muirwoodia mammata* (Keyserling), *Chaoiella neoinflata* (Licharew), *Neospirifer grønwalli* Dunbar, *Spiriferella polaris* Wiman, *S. draschei* (Toula), *S. keilhavii* (von Buch), *Waagenoconcha irginae* (Stuckenberg) , *W. arctica* Nakamura n. sp., *Pseudosyrinx wimani* Gobbett, *Athyris amdrupi* Dunbar, *Derbyia grandis* Waagen and *Streptorhynchus macrocardinalis* Toula, arranged in order of stratigraphic appearance. Some species were shared with the overlying zones, *Muirwoodia duplex* Wiman with the *Paeckelmannella* Zone, and *Streptorhynchus kempei* Andersson and *Anemonaria pseudohorrida* Toula with the *Megousia weyprechti* Zone. The list is not exactly identical with the list provided by Gobbett (1964, p. 21) for the same beds at Isfjorden, but is close and includes many of the same significant species. Angiolini & Long (2008) provided a further valuable insight into Vøringen brachiopods, describing *Neochonetes, Anemonaria pseudohorrida* (Toula), *Archboldevia impressus* (Toula), *Thamnosia arctica* (Whitfield) [= *Thuleproductus subarcticus* Sarytcheva], *Bruntonia maynci* (not Dunbar) [= *Sowerbina longi* n. sp.], *Bruntonia rudis* (Dunbar) [=*Sowburia*], *B. granulifera* (Toula) [=*Sowburia*], *Tityrophoria* sp. ind. [?], *Kochiproductus* cf *plexicostatus* (not Dunbar) [possibly *K. freboldi* Stepanov], *Waagenoconcha* sp., *Linoproductus* sp., *Kuvelousia weyprechti* (Toula) [= sp. indet.], *Arctitreta* aff. *kempei* (Andersson) [*Grumantia*?], *Stenoscisma spitzbergiana* (Stepanov), *Fasciculatia striatoplicata* (Gobbett) [= *Betaneospirifer*], *Spiriferella keilhavii* (von Buch) [= *Undulatina*]*,* and also *S. loveni* (Diener [= *keilhavii*], *Eridmatus* sp. [*Spiriferella angulata* n. sp.], phricodothyrid, *Tumarinia* cf. *wimani* (not Gobbett) [= *Yukonospirifer* sp.], *Pseudosyringothyris borealis* (not Gobbett) [= *Nahoniella*]. Angiolini & Long (2008) recorded material close to *Timaniella magniplicata* Abramov & Grigorieva of Artinskian-Kungurian age, in accord with the preferred age for the Vøringen Formation, and this species is probably that rendered as *T. festa* Barchatova in Grunt & Blomeier (2013), and shown to be *T. wilckzeki* (Toula, 1873) by Lee et al. (2019). Possible links with the Assistance Formation of the Sverdrup Basin are suggested by the identification of Whitfield's species *Productus arcticus* in Angiolini & Long (2008), but there are indications of very large ears, suggestive of the genus *Svalbardoproductus* Ustritsky, with strong ribs as in *subarcticus* Sarytcheva, reported from the Vøringen Member by that author and Ustritsky (1979), and present in the Great Bear Cape Formation of Canada. Some of the specimens assigned to *Spiriferella* by Angiolini & Long (2008) approach *S. angulatus* n. sp., found also in the lower Takhandit Formation of Yukon Territory. A number of their identifications had to be based on incomplete or distorted material, conveying little information that is reliable. But some of the specimens assigned to *Fasciculatia striatoplicata* (Gobbett) by Angiolini & Long (2008, Fig. 8A, B, F) are strongly plicate with well defined sulcus and narrow-crested fold, broadening anteriorly, just as in Gobbett's species. Gobbett's species belongs to *Betaneospirifer*, not *Fasciculatia*, as elaborated in this study (p. 282), and approaches the Great Bear Cape ventral valve identified as *Spirifer fasciger* Keyserling by Tschernyschew & Stepanov (1916, pl. 9, fig. 3a, b). *B. permicus* (Ifanova), originally described from the Talbeisk Formation of Russia, of Kungurian age, is also close.

Comparison with Canada

The few brachiopods described in this report from the Great Bear Cape Formation that have been definitely reported from the Vøringen Member, involve possible *Thamnosia sangminlee* n. sp., *Svalbardoproductus subarcticus*

(Sarytcheva), *Fasciculatia groenwalli* (Dunbar) and *Betaneospirifer striatoplicatus* (Gobbett). *Yukonospirifer* is present in the Vøringen Member as well as zone 2 in the Takhandit Formation. Possible *Derbyia semicircularis* n. sp. and *Arcullina polaris* (Wiman) appear to have been long-ranging, and therefore of reduced significance. No distinctive species reported in Nakamura et al. (1992) or Angiolini & Long (2008), such as *Streptorhynchus macrocardinalis* (Toula), *Archboldevia impressus* (Toula), *Stenoscisma spitzbergiana* (Stepanov), *Pinegathyris amdrupi* (Dunbar) and *Undulatina keilhavii* (von Buch) have been pinpointed in the Great Bear Cape Formation, or the Takhandit Formation of Yukon Territory, and uncertainty surrounds other reported occurrences, involving horridoniids, *Kochiproductus*, anidanthids, because none of the descriptions are adequate in terms of detailed morphology. That applies even more pervasively to the monograph on the Great Bear Cape fauna by Tschernyschew & Stepanov (1916). To focus on what is known of the reasonably definite aspects of the brachiopods from the Great Bear Cape Formation, it has to be said that many differ substantially from those of the Vøringen Member, implying a possibly slight difference in age. Amongst the brachiopods from the two basal faunal assemblages of the Takhandit Formation in Canada, the lower zone includes *Derbyia semicircularis* and *Anemonaria pseudohorrida* as links to Vøringen fossils, but ranging well beyond. As well, there are a number of generalized possible similarities that need closer analysis. None of the genera that help distinguish these two lower Takhandit zones, involving *Septospirifer* and so-called *Linoproductus* and *Choristites*, are as far as known to be found in the Vøringen Member. The second Takhandit zone also includes *Karnellia*? *bullocki* (Nelson & Johnson) and *Spiriferella arctica* (Haughton). Given that this zone shares a distinctive fusuline assemblage with the upper Great Bear Cape Formation, the tie between the faunas seems unchallengeable, and the correlation with Vøringen still open for closer scrutiny. At present, it seems possible that the Vøringen faunas, or some of them, perhaps those found with particular conodonts, match an unfossiliferous part of the sequences in Yukon Territory, as early Kungurian (sensu Wardlaw 2000), possibly Saranin or Filippovian (basal Kungurian in classic terms) and conceivably represented by brachiopods not yet adequately analysed, or segregated, or collected, from the Great Bear Cape Formation. Theoretically, it would have been this level that could have lacked some of the characteristic species of the older faunas, and seen the entry of such forms as *Undulatina keilhavii* (von Buch). The Saranin level is a Russian stratigraphic level that is yet to find a clear match in the Spitsbergen or Canadian sequence, but in Russia its brachiopods seem meagre and Artinskian in attributes, and Foraminifera, ostracods and bryozoa more significant. The Great Bear Cape faunas are only moderately close to those of the Vøringen Member, being slightly older at upper Sarginian, compared with a basal or near basal Kungurian age for the Spitsbergen faunas. Such a correlation is moderately close to but more refined than the age suggested by Nakamura et al. (1992), but they decidedly opted for a Kungurian age, and drew attention to the similarity of the Vøringen faunas to the faunas from Amdrup G and H and Holm Land of north east Greenland, now placed in the Mallemuk Mountain Group. Their coupling of Kungurian with Roadian (Nakamura et al. (1992, Fig. 3) may be set aside.

Svenskeegga Member, Lower Hotvinden Member: brachiopods and age

Not many distinctive brachiopods were listed from the Svenskeegga Member by Nakamura et al. (1992). It was considered to be typified by *Paeckelmannella*, which acted as name for the zone, which extended into the lower

Hotvinden Member, and sharing a few species with older and younger beds, and including *Wimanoconcha wimani* (Fredericks) and *Thuleproductus crassauritus* Sarytcheva & Waterhouse, *Muirwoodia duplex* (Wiman), *Magniplicatina janischewskiana* (Stepanov), *Svalbardathyris kotlukovi* (Stepanov), “*Licharewia” spitsbergiana* Gobbett [with much broader ventral muscle field than in *Licharewia*] and supposed *Stepanoviella curvata* (Tolmachev). [Some generic names adjusted]. The lower Hotvinden Member was characterized by *Megousia* [now *Kuvelousia*] *weyprechti*, with restricted species *Chonetina spitzbergiana* Gobbett. These two zones represent comparatively depauperate levels compared with the highly diverse faunas of the Canadian Arctic, as represented in the Assistance and Trold Fiord and middle and upper Takhandit Formations. Nakamura et al. (1992) correlated the lower *Paeckelmannella* Zone with lower Wordian of the world standard, and with the Assistance Formation in Fig. 3, but as Trold Fiord Formation in their text (p. 84). The third or *Megousia weyprechti* Zone was correlated with Wordian and Capitanian, and with the lower Trold Fiord Formation of the Sverdrup Basin.

Reassessment of the data provided by Nakamura et al. (1992) provisonally confirms their suggested correlation between their lower *Paeckelmannella* zone, and Trold Fiord Formation, with *Thuleproductus crassauritus* a prominent guide fossil. *Paeckelmannella* itself is very close to a species *calignea* from the Sabine Bay Formation, and appears to have been a long-ranging species. Several of the Kapp Starotsin brachiopods suggest a Trold Fiord match, extending through the Svenskeegga Member into the lower Hotvinden Member. They include *Grumantia kempei* (Andersson), *Thuleproductus crassauritus* Sarytcheva & Waterhouse, *Wimanoconcha wimani* (Fredericks), *Fasciculatia striatoparadoxa* (Toula) as in this study (but see p. 266), possibly *Spiriferella draschei* (Toula) and *Spiriferellina cristata* (Schlotheim). That is not a large number, for many species are in common between the Assistance and Trold Fiord Formations, and so confidence must be limited, but provisionally, the fossil occurrences and affinities do suggest that the Svenskeegga and lower Hotvinden Members are correlative with the Trold Fiord Formation. No species are so far as known in the Kapp Starotsin Formation that are restricted to the Assistance Formation, although it must be allowed that there are earlier reports of various species ranging from Vøringen Member into Svenskeegga Member, reports that need to be checked. The suggestion that the Svenskeegga and lower Hotvinden match the lower Trold Fiord faunas is far from being other than provisional, because much more clarification is needed for many of the brachiopods from Spitsbergen and Bjørnøya. Nor, with the same cautions, is there any sign of Capitanian brachiopods. What tells against any assessment is the lack of detail for spine distribution for Productida, and lack of adequate information on internal morphology for some Spiriferida, which prevents any confident correlation with the Canadian faunas.

Younger Hotvinden Member

Two zones, based on *Pterospirifer alatus* (Schlotheim) and *Haydenella wilckzeki* (Toula) were recognized at Festningen for the upper Hotvinden Member, and these are dominated by a number of brachiopods that have been identified by Nakamura et al. (1992) with brachiopods described from central east Greenland by Dunbar (1955). The *Pterospirifer alatus* Zone was equated by Nakamura et al. (1992) with uppermost Trold Fiord and Capitanian, and including reported *Choristites soederberghi* Dunbar, followed by a *Haydenella wilczeki* Zone, the nominate species left unfigured, with another reported species of *Haydenella*. Neither species is represented in the Trold Fiord Formation according to the chart in Nakamura et al. (1992), though stated to be present in the text (p. 83). Dr Zhuoting Liao was quoted that the upper half of the Trold Fiord Formation had yielded Capitanian conodonts.

Most of the species listed for the *Pterospirifer* zone by Nakamura et al. (1992) are shared with the Greenland faunas described by Dunbar (1955) from central east Greenland, and are therefore likely to be of Wuchiapingian age. According to Nakamura et al. (1992), the zone in Spitsbergen includes such outstanding species as *Pleurohorridonia scoresbyensis* Dunbar, *Pterospirifer alatus* (Schotehem) and *Odontospirifer mirabilis* Dunbar, all found in the Wuchiapingian beds of central east Greenland. The overlying *Haydenella* Zone involves a number of different species shared with the Wuchiapingian of central east Greenland. There is no reason why they should not, from available evidence, be regarded as both having a Wuchiapingian age, and no obvious reason why the *alatus* zone should be considered to be Capitanian, except from a rather naive desire to fill out the column of stages. The two upper faunas recognized by Nakamura et al. (1992) have no recognizable counterpart in Canada. Subject to the need for verification from detailed systematic study, these faunas appear to be of Wuchiapingian age, beyond any relevance to most of the brachiopod faunas in the Canadian sequence. That apparently leaves a faunal gap in Spitsbergen, equivalent to the Capitanian Stage, but as discussed shortly, the faunas have not been systematically described in modern terms, and there are other possibilities. However it may be relevant to the claims by Bond et al. (2013), who noted a substantial change to the faunas of the middle and upper Hotvinden Member. Their assertions were not explained in detail, and claims of input from Triassic forebears left unsubstantiated. But it may be speculated that they were referring to the faunal change between the so-called *Megousia weyprechti* and *Pterospirifer alatus* zones. That change in fauna would have been especially marked if the two faunas were separated by a pause in accumulation of rocks and faunas.

A different view has been expressed by Shen (2016, Fig. 2). He accepted the identification of *Haydenella wilczeki* forwarded by Nakamura et al. (1992), and matched that species with an unspecified occurrence in what he stated to be Late Permian in northeast Greenland. Shen (2016) matched the *Pterospirifer alatus* Zone with the Wuchiapingian Stage, and *Haydenella wilczeki* with Changhsingian. It would be of great interest to clarify the affiniites and age of the latter species.

It seems a pity that Nakamura et al. (1992) overlooked or ignored the study on Spitsbergen by Ustritsky (1979), because it concerned the same rocks and faunas, and yet was so different in many of its conclusions, that any reader unfamiliar with the region is left perplexed about which is the preferable version. Ustritsky (1979) tabulated the occurrences of brachiopod species throughout the Kapp Starotsin Formation and incorporated what he called the Selanderneset beds and faunas, which are found in on the SW coast of Nordaustlandet at Selanderneset. Grunt & Blomeier (2013) matched beds of this name with the upper Hotvinden Member, above what has been called the Palanderbukta Member, correlative with the Svenskeegga and lower Hotvinden Members. Ustritsky's summary was based on intensive collecting by a large team from Leningrad, now St Petersburg. The faunal list shows limited agreement with the subdivisions in Nakamura et al. (1987, 1992), and drew attention to some major facies differentiation. Moreover, Ustritsky used a number of taxonomic names that needed to be substantiated through description and illustration. Unfortunately, faunal lists that preceed rather than follow extensive systematic description can only regarded with misgivings. Ustritsky (1979) ascribed the lower (ie. Vøringen) beds to Kungurian, with support from Foraminifera, although he allowed that some forms pointed to Kazanian and Ufimian. The bulk of the faunas was considered to match those of the Assistance Formation in Canada, and to be of Ufimian age, and pre-Kazanian. The Selanderneset or upper level faunas were matched with those of Greenland and Zechstein, which is in reasonable accord with Nakamura et al., but discrepantly, with the Baikur Suite of Taimyr, of Wordian-Capitanian age. He recognized *Spitzbergiana* Kotlyar, found also in Omolon Plateau of northeast Russia, and in Ufimian of Russia and in Novaya Zemlya. The zone based on *Haydenella wilckzeki* (Toula) was not verified, presumably because of collecting in a different area. The Foldvik Creek Group of northeast Greenland, with the brachiopod and bivalve faunas described by Dunbar (1955) and Newell (1955) and the ammonoid *Godhaabites*, was correlated by Ustritsky (1979), apart from some of the lower zone, with the lower half of the Zechstein Group. The upper zones were also shown as correlative with the Foldvik Creek Group of east Greenland, and all, as I understand his article, with Ufimian, which seems unacceptable.

Additional input was provided by Nakreem (1991, 1994) and Nakreem et al. (1992), with the report of a late Artinskian-Kungurian age for the Vøringen Member, and overall late Artinskian to Kazanian age (ie. Baigendzinian – Wordian) for the overall Kapp Starotsin Formation. The Vøringen Member was considered to contain Artinskian conodonts *Neostreptognathodus pequopensis, N. clarki* and *N. ruzhencevi*. According to Henderson (1994, 2018), the first two of these conodont species overlap in his zone P8 in the upper Great Bear Cape Formation, and P9 conodont zone at the top of the Great Bear Cape Formation. According to Nakreem, the upper Kapp Starotsin Formation yielded specimens of *Mesogondolella idahoensis*, which was considered by Nakreem to have a range of Kungurian and Ufimian, although the time range of this form has been questioned elsewhere, as in Henderson & Mei (2002), and revised subsequently (Henderson 2018) to indicate a Kungurian age, so that the identification seems unlikely**.**

Lee et al. (2016, p. 126) evaluated the age of the Kapp Starotsin Formation as Kungurian to questionably Capitanian, without giving reasons. In 2019, Fig. 2, Lee et al. showed the Vøringen Member as middle and lower Kungurian equivalent to and also older than the Sabine Bay Formation of Canada. The Kapp Starotsin Formation above the Vøringen Member was shown as ranging from upper Kungurian seamlessly into lower Wuchiapingian. An article by Wignall et al. (1998) argued for a Permian/Triassic transition, and complete Late Permian, in an article criticized by Angiolini & Long (2008, p. 77), although it would seem that Shen (2016) took a different view. He strongly supported a Late Permian age for the *Haydenella wilczeki* Zone of Nakamura et al. (1992), an interpretation discounted by Lee et al. (2016, 2019).

Angiolini & Long (2008) asserted that the Vøringen Member was late Artinskian-Kungurian, and correlated the Vøringen brachiopods with the brachiopods from lower Takhandit beds of Alaska. The Alaskan Takhandit was stated to range from Artinskian to Wordian. Their assertions were incorrect. In response, the lower part of the type Takhandit Formation is correlative with the Assistance Formation, and this is of Roadian age, distinctly younger than upper Artinskian and Kungurian. In concession, perhaps it has to be allowed that the faunas themselves may seem muddled to some authorities unfamiliar with Arctic faunas of Canada and Russian studies. The brachiopods do indeed approach aspects of the Kungurian and even upper Artinskian of the Petchora Basin, as analysed in this study from Ifanova (1972) and Kalashnikov (1990), and Kungurian in the studies by Grunt (2006a, b). That I suggest is because there was a large Arctic realm, in which benthonic faunas of an Arctic biome migrated to and fro through time across and around the basin, with pockets of advanced evolution, and pockets of conservatism and slow change. So prime value is placed on more mobile life forms that survived for only a brief interval.

Bjørnøya

The small island of Bjørnøya south of Spitsbergen exposes rocks of the Hambergfjellet Formation, separated by a gap in deposition from the overlying Miseryfjellet Formation. According to Lee et al. (2019, Fig. 2), the lower unit is of Artinskian age and correlated with the Great Bear Cape Formation of Canada, but extending higher, and the upper formation is separated by a depositional gap, and matches the lower middle Kapp Starotsin Formation, roughly equivalent to Svenskeegga and perhaps lower Hotvinden Member. At the behest of Brian Harland of Cambridge University, I examined the brachiopod collections, which are extensive and were housed in off-campus storage at Madingley Rise in the early 1990's. Fossils were collected at measured stratigraphic intervals and numbered through both formations. The lower Hambergfjellet fauna (K 3914 – 3951) in red limestone included a linoproductid, *Striapustula* cf. *singletoni* (Gobbett), *Arcullina* and *Tiramnia*, and the middle part of the formation (K 3836 – 3913) included large linoproductid, *Anemonaria* cf. *pseudohorrida* (Toula), *Kochiproductus,* and *Striapustula* cf. *spitsbergiana* (Gobbett). These fossils support the correlation in Lee et al. with Great Bear Cape Formation and more particularly the lower Takhandit Formation of Yukon Territory. The upper fossil collections (K 3796 – 3834) from the Hambergfjellet Formation were thought to include *Svalbardia capitolinus* (Toula), *Kochiproductus, Thuleproductus* cf. *arctica* (Whitfield), *Muirwoodia duplex* (Wiman) and other productids that suggest a possible very late Artinskian or early Kungurian age. From the overlying Miseryfjellet Formation, brachiopods from the basal beds (K 3696 – 3794) included *Grumantia kempei* (Andersson), "*Craspedalosia pulchella* (Dunbar)", *Wimanoconcha wimani* (Fredericks), *Thuleproductus crassauritus* Sarytcheva & Waterhouse, *Kuvelousia, Cyrtella* and *Simplicitasia osborni* (Harker). The upper localities (K 3642-3695) include specimens identified with *Grumantia kempei* (Andersson), *Sowburia*, *Kuvelousia sphiva* Waterhouse, *Alispiriferella gydanensis* (Zavodowsky), *Spirifernaella*, and "*Craspedalosia pulchella* (Dunbar)". This latter species with some of the others make it seem unlikely that all of the formation is as old as Kungurian, but specimens were not examined in detail, and may well prove to have dorsal spines as in *Melvillosia* rather than *Craspedalosia*. Gobbett (1964, p. 38) provided a list of a few fossils from the northern part of the island, and also included *Craspedalosia pulchella* (Dunbar). All of these identifications and certainly all those listed by me need verification, and are not full consistent with ranges known for species elsewhere. A number suggest a Roadian and more likely Wordian age. Reports on a few spiriferiforms are provided by Lee et al. (2016, 2019), but these lack detailed stratigraphic and geographic information with regards to source.

ENGLAND

The faunas of the Magnesian Limestone of England, somewhat like the lower Zechstein of Germany, have long had close attention, but show unusual features, due perhaps to age, perhaps in part to the somewhat saline and dolomitic environments prevailing in a semi-enclosed sea. On the one hand, aspects of the faunas do not closely resemble those of Canada. For example, *Streptorhynchus* is found instead of *Arctitreta*, Linoproductidina are poorly represented, and members of the Spiriferellidae absent. On the other hand, Horridonioidea are diverse, a number of strophalosioids are present, and a few Arctic elements such as *Spiriferellina* are found.

NORTH EAST RUSSIA

Two particular studies of the rocks and faunas from the Permian of northeast Russia by Klets (2005) and Biakov (2010) offer valuable insights into the development of the Arctic faunas. They marked a return to the thorough and wide-ranging research that previously was achieved by Gobbett (1964) in Spitsbergen and Grunt (2006a, b) in Kanin Peninsula, and reinforced by Abramov with support from Grigorieva in extensive studies on Verchoyan of northeast Russia, as a marked advance over any brief focus on particular problems. Both studies by Klets and Biakov are particular instructive through offering clear information on the nature of late Permian marine faunas from the Arctic realm, especially in northeast Russia. Klets (2005, p. 60) recognized two late Permian horizons, Dupgalaksk *Cancrinelloides obrutschevi* Zone, followed by the Kalpirsk *Crassispirifer monumentalis* Zone. The presence of two brachiopod genera in the latter zone is particularly striking. Both are Strophalosioidea, one named *Subtaeniothaerus* Solomina, 1988, the other *Marginalosia* Waterhouse, 1978. *Subtaeniothaerus* is very close to *Biplatyconcha* Waterhouse, 1983a, as a very large and distinctive genus. It is distinguished from *Biplatyconcha* by having slightly more differentiated, less uniform ventral spines, a difference treated by Waterhouse (2013) as valid, but obviously open to further enquiry, and quite possibly amounting to a specific rather than generic difference. *Biplatyconcha* is restricted to Changhsingian faunas in Nepal (Waterhouse 1978, Waterhouse & Chen 2007), and is found mostly in the Nisal Member of the Senja Group in west Nepal. *Marginalosia* was prominent in the late Changhsingian Pig Valley Member in limestones (Waterhouse 1964, 2002a, p. 137) and also in the Changhsingian Nisal Sandstone Member of Nepal (Waterhouse 1978; Waterhouse & Chen 2007). In northeast Russia, the latest Permian zones and levels are also of Lopingian (Late Permian) age. There is no sign of these particular two brachiopods in the Sverdrup Basin or Yukon Territory, Greenland or Spitsbergen. At least in the case of the faunas with *Biplatyconcha* and *Marginalosia*, that seems likely to signify that these particular rocks from northeast Russia were of advanced Lopingian – or Changhsingian – age. The Russian sequences in northeast Russia lack any sign of brachiopods assigned to *Haydenella,* possibly because temperatures were too low.

As for *Cancrinelloides* found in the Dupgalask fauna of northeast Russia, deemed to be of Capitanian age, its absence from Sverdrup or Yukon faunas has more ambivalent possibilities. It may be due to an age factor. On the other hand, *Cancrinelloides* is very limited in distribution, with no southern hemisphere equivalents, and perhaps its geographic extent was limited even in Arctic faunas. But its absence at its simplest implies an absence of brachiopod faunas of Capitanian age. Not many other brachiopods were listed from the fauna: they included *Strophalosia sibirica* Licharew, which possibly belongs to *Echinalosia*, *Wimanoconcha wimani* (Fredericks), a report that would repay further enquiry, *Bajtugania boguchanica* Solomina*, Tumarinia zavodowskyi* Grigorieva, *T. ganelini* (Grigorieva) and *Brachythyrina sibirica* Tschernyschew. There is little similarity to any fauna from Arctic Canada or Spitsbergen, which may imply that the faunal level in terms of brachiopods is absent from those regions. On the other hand, the Wuchiapingian equivalents of northeast Russia differ considerably from Wuchiapingian of Greenland and Spitsbergen, possibly signifying a different faunal province, although the Wuchiapingian was such a long stage with several diverse bizones in succession that different time spans may have been involved.

The underlying rocks and faunas in northeast Russia occupy a stratigraphic position close to that of the Assistance and arguably lower Trold Fiord Formations of the Sverdrup Basin, and much of the Takhandit Formation in Yukon Territory. Klets (2005, p. 60) assigned them to a Depenjin Horizon and Kazanian Stage, with three biozones, named after *Mongolosia russiensis*, *Terrakea*, and *Tumarinia zavodowsky*. Significantly, *Sverdrupites* is found in the two lower zones, with *Daubichites* as well in the middle zone, and shells identified with what is now *Wimanoconcha wimani* (Fredericks) was reported from two upper zones. It would appear to be this part of the sequence that matches at least some of the rocks and faunas discussed in the present study.

The underlying segment in northeast Russia, assigned mostly to Kungurian and Ufimian, and classed as the Tumarin Horizon, is also divided into three zones, with the lower two signalled by *Epijuresanites* and by *Popanoceras* and *Neouddenites* with other ammonoids. The brachiopods include species assigned to *Anidanthus, Megousia*, and *Rhynchopora*, but apart from *Magniplicatina janischewskiana* there are few direct links with the Canadian faunas, though there may be approaches to the early Takhandit faunas. Further down the sequence is *Jakutoproductus*, just as in the upper Jungle Creek Formation of Yukon Territory.

In the study by Biakov (2010, p. 24), further refinements were achieved. The faunas and rocks of the Guadalupian and Lopingian Series were grouped as the Omolonian and Kolymian levels. The Omolonian, equated with Roadian and Wordian in the world standard, was divided into four brachiopod-bivalve zones, featuring *Terrakea* (s. l – see Waterhouse 2013), *Magadania* and *Omolonia*, indicative of the overall nature and replacement of zonal assemblages of the sort to be expected elsewhere in the Arctic, with *Magadania* pointing to ties with Canada. The Kolymian Series involved Capitanian equivalents at the base, typified by *Cancrinelloides obrutshewi*, not known in Canada, and the overlying Lopingian is subdivided in two with further bivalve subzones and *Stepanoviella paracurvata*, a species described by Zavodowsky (1970, p. 109, pl. 89, fig. 1-6). A lower Gijigin level matched Capitanian, and Hivach level matched the Lopingian. Biakov found that in the latest Permian after Capitanian, bivalves replaced and dominated brachiopods in shallow water communities. The bivalves were far more numerous throughout the succession than was been the case in northern Canada, where bivalves are extremely rare – with the only known instance of relative prominence occurring in the Blackie Formation, of Bashkirian age (Waterhouse 2018b), and a modest degree of diversity during the Early Permian (Shi & Waterhouse 1996, Waterhouse 2018a).

The overall fit of the sequences with those of the Canadian north seems best with the Omolonian of Biakov (2010) and Depenjin Horizon and Kazanian Stage of Klets (2005). Even the Capitanian correlation suggested by Dr Liao as quoted by Nakamura et al. (1992) may require caution, because neither the Spitsbergen nor Canadian sequences have any *Cancrinelloides*, as far as is known. That would mean that the middle and upper Takhandit Formation, and the Assistance and lower Trold Fiord Formations of the Sverdrup Basin, were Roadian and Wordian in age.

SUMMARY OF YOUNGER PERMIAN STAGES THROUGHOUT THE ARCTIC AS RELEVANT TO ARCTIC CANADA

Brachiopod faunas are variously developed across the Arctic, and following text discusses where they are best displayed.

Aktastinian: Undoubtedly the Urals into northwest Russia provides extensive and varied faunas. The Canadian segment is well represented and diverse in the Yukon Territory, monographed for the older beds (upper Jungle Creek Formation), with younger Aktastinian brachiopods of the lower Takhandit Formation in the Yukon and Great Bear Cape Formation incompletely known.

Kungurian: Nothing matches of Kungurian of northwest Russia for comprehensive studies and completeness of succession, even though fusulines, ammonoids and conodonts are rare or missing from that region. The Canadian sequences are incomplete, with no Kungurian yet recognized in Yukon Territory, and younger Kungurian marine beds recognized only as part of the Sabine Bay Formation (brachiopods) and lower Assistance Formation (conodonts). It is suggested that part of the gap is filled by the Kungurian Vøringen Member of Spitsbergen.

Roadian: With conodonts, ammonoids, and numerous brachiopods, the Assistance Formation is one of the most significant exemplars for Roadian Stage in the Arctic, with much of its brachiopod component extending in the Yukon Territory and MacKenzie District. In the latter regions two brachiopod zones are clearly discriminated, with a diverse range of genera.

Wordian: The Wordian Stage is also well represented in both the Sverdrup Basin (lower Trold Fiord Formation) and upper Takhandit Formation of Yukon Territory and unnamed sandstones of the Richardson Mountains in the Yukon and Mackenzie District, as far as brachiopods are concerned. There are conodonts, but few ammonoids and no fusulines. Elements of both Roadian and Wordian are developed in Spitsbergen but require much revision and stratigraphic clarification. Kazanian faunas of mainland Russia have been closely studied but lack or are thinly represented by fusulines, ammonoids or conodonts.

Capitanian: Development of this stage in the Arctic is poorly understood, and is therefore a major challenge. Although conodonts indicate the presence of the stage in the upper Trold Fiord Formation, no Capitanian brachiopods have been definitely recognized, in distinction to rich sequences with abundant fusuline support in South Primoyre, and more meagre development in northeast Russia. Part of the difficulty stems from ignorance of what form the brachiopods will take. In eastern Australia and New Zealand, brachiopod genera assigned to the Capitanian Stage are much like those of the underlying Wordian, but differ specifically. In the Glass Mountains of Texas, the Capitanian brachiopods show a rich proliferation of genera (Cooper & Grant 1969 – 1976b). In Spitsbergen, the *Pterospirifer alatus* Zone could possibly represent Capitanian, as it changes markedly from underlying brachiopods of the so-called *Kuvelousia weyprechti* Zone, and several species come close to those of the overlying *Haydenella wilckzeki* Zone, which is dominated by taxa found in the Wuchiapingian of northeast Greenland, according to Nakamura et al. (1992). Or are the faunas Wuchiapingian? The distinction between the two zones in Spitsbergen was made on the basis of a few critical species (eg. *Pterospirifer, Haydenella*), but overall species compositions were said to be the same, whereas they would have been expected to differ more, were two stages represented.

Wuchiapingian: The fauna monographed by Dunbar (1955) from northeast Greenland stands out as a prime assemblage of Wuchiapingian brachiopods for the Arctic, probably lower Wuchiapingian. They show little in common with Wuchiapingian brachiopods of northeast Russia or South Primoyre, but the stage was a lengthy one, with potentially a number of zones developed, to judge from the studies of conodonts in China, and the macro-faunal successions of the Salt Range and Himalaya, suggesting that the rocks and fossils of the Arctic provide a very incomplete record of the Wuchiapingian Stage.

Changhsingian: There are no satisfactory assemblages of Changhsingian brachiopods known for the Arctic beyond northeast Russia, and even these appear to represent only one zone, in contrast to the faunal succession in the volcanic arc complex of New Zealand, and developed to lesser extent in the Gympie region of southeast Queensland, not to mention the thick and diverse sequences of the Himalaya in northern Nepal.

SUMMARY OF PALEOGEOGRAPHIC AND PALEOCLIMATIC IMPLICATIONS

Many of the genera found in the Early Permian Jungle Creek Formation of the Yukon Territory vanished from Arctic Canadian faunas by the start of the middle Takhandit Formation, and correlative Assistance Formation, and slightly older Sabine Bay Formation. Genera that disappeared from the Canadian Arctic fossil record included the strophomenoid genera *Orthotetes*, chonetid genera *Komiella*, *Chelononia, Chonetinella*, *Fascichonetes, Rugaria, Rugoschonetes*, *Sulcirugaria*, *Leurosina, Lissochonetes,* productiform genera *Jakutoproductus, Tuberculatella, Inflatusia, Sangredonia, Bailliena, Karnellia, Tityrophoria, Svalbardoproductus, Reticulatia, Rigrantia, Dutroproductus, Antiquatonia, Chaoiella, Nassichukia*, *Gemmulicosta, Tityrophoria, Calliprotonia, Juresania*, *Heteralosia, Yukonalosia, Ramaliconcha, Paucispinifera, Kozlowskia, Rugivestigia*, *Anidanthus*, *Protoanidanthus, Lineacrassus*, *Praeschrenkiella*, *Compressoproductus*, *Commarginalia*, *Rugivestis, Costispinifera*, rhynchonelliform genera *Orthotichia, Rhynoleichus, Septacamera, Camerisma, Yanzania*, *Composita*, *Eumetria*, *Hustedia* and spiriferiform genera *Triramnia, Martiniopsis*, *Brachythyris*, *Meristorygma, Ala*, *Junglelomia, Ettrainia*, *Purdonella*, *Tegulispirifer*, *Neospirifer*, *Lepidospirifer*, *Septospirifer, Eridmatus, Plicatospiriferella*, *Triramus*, *Ogilviecoelia*, *Zaissania*, *Tumarinia*, *Yukonospirifer* and the terebratuliform genera *Dielasma* and *Cryptacanthia*. This amounts to more than seventy genera, without the list being fully complete. Not that all were to be found at the top of this succession: the genera came and went throughout the succession, but their vanishing marked the end of a flourishing of early Permian genera. About forty genera persisted*:* *Orbiculoidea*, *Arctitreta*, *Dyoros*, *Fimbrininia*, Sowerbina, Kutorginella*, Thamnosia, Echinaria*, Tubersulculus*, Krotovia, Guangia, Kochiproductus, Waagenoconcha, Wimanoconcha, Echinalosia, Balkhasheconcha*, Paucispinifera, Anemonaria, Liosella*, *Retimarginifera*, *Kuvelousia, Dzhiremulia, Harkeria*, *Cimmeriella*, *Schrenkiella**, *Magniplicatina*, *Rhipidomella**, *Rhynchopora*, *Stenoscisma*, *Callaiapsida*, *Cleiothyridina*, *Martinia, Pterospirifer, Fasciculatia*, *Spiriferella, Alispiriferella, Timaniella, Arcullina, Spirelytha, Spiriferellina,* and *Nahoniella.* The asterisked genera went extinct elsewhere, and in Canada were unusual holdovers*.* The full documentation is incomplete, because the faunas from the lower Takhandit Formation are yet to be fully described. New genera to appear in the Canadian Arctic through evolution and migration included *Grumantia*, *Fissulina*, *Neochonetes*, *Horridonia*, *Pleurohorridonia*, *Sowburia*, *Thuleproductus*, *Ametoria*, *Patellamia*, *Gruntoconchinia*, *Wyndhamia*[1], *Arcticalosia*, *Melvillosia*, *Megousia*, *Liraria*, *Lineabispina*, *Magadania*, *Kolymaella*, *Cameronovia*, *Cancrinella*, *Svalbardathyris*, *Himathyris*^{i}, *Spirigerella*, *Oviformia*^{i}, *Paeckelmannella*, *Simplicitasia*, *Betaneospirifer*, *Gobbettifera, Undulatina, Tintoriella*^{i}, *Canalisella*, *Catatonaria*, *Orbicoelia*, *Reticulariina*, *Gjelispinifera*, *Paraspirifer*, *Sulcicosta*^{i}, *Cyrtella* and *Licharewia*. Not counting the few unresolved genera, this amounts to forty genera, no small part of the total. The superscript ^{i} marks genera with strong links to forms from the southern paleohemisphere.

No such massive faunal turn-over is found lower or higher in the column for the Permian until the end of the period, anywhere in the world where there was a reasonably complete geological and faunal succession. That excludes the United States which lacks much of the Lopingian Series and so gives a misleading impression of a post-Capitanian collapse of marine life. The great change was an early Kungurian event, rated as late in the Early Permian, although in fact the event should have closed off the Early Permian and been followed by the Middle Permian, but historical treatment of the Permian Period and flawed understanding of Permian biota beyond conodonts has prevailed, and so retained the present classification and retarded proper evaluation. The loss of life was notable across many parts of the globe, including the well-known regions of Russia and Australia, and almost coinciding with the classic Artinskian-Kungurian boundary, now masked by insistence that Kungurian was Early rather than Middle Permian (cs. Waterhouse 1983e, p. 218, 2004a). (Some uncertainty remains about the faunal affinities of the Saranin level at the top of the classic Artinskian and Baigendzinian levels. Brachiopods are few, but are like those of underlying rather than overlying faunas). The supposed faunal catastrophe between the Capitanian and Wuchiapingian was minor in comparison, exaggerated in its apparent loss of life by the withdrawal of seas and loss of shelf-space over much of the world. Of course the record in the Yukon Territory is complicated by the stratigraphic and faunal disruption from late Artinskian to late Kungurian, with the gap partly filled by the Sabine Bay Formation and early Assistance Formation in the Sverdrup Basin.

In Arctic Canada, as elsewhere, the new and incoming genera after Artinskian time marked a refreshment of life, highlighted by Stepanov (1973), a vastly experienced Russian authority. A few incoming taxa may have stemmed from older genera poorly or imperfectly known in older faunas, such as “*Chorististes*” *soederberghi*, but most form part of a newly resurgent Kungurian and Middle Permian assemblage of the Arctic, shared with such regions as Spitsbergen and Greenland, and extensive tracts of northern Russia, as in Australia and New Zealand. Within the vast northerly biome, the entry into Canada of several genera otherwise limited to north and northeast Russia, such as *Globiella*, *Magadania* and *Kolymaella*, is noteworthy. A few genera migrated from the paleotropical realm exemplified by west Texas, such as *Ametoria*, and perhaps *Orbicoelia* from Asia.

At the other extreme is the entry of a few genera having marked affinities with east Australia and New Zealand, involving *Echinalosia* (though known in older Canadian faunas), and more distinctively, other strophalosioids such as *Wyndhamia* and a likely descendent, *Arcticalosia. Cameronovia* of the Arctic and *Filiconcha* of Queensland and New Zealand were closely related, both appearing first in Wordian faunas. *Cyrolexis*, *Himathyris* and *Spirigerella* also appeared, typical especially of the southern warmer bitemperate climatic zone as in India-Pakistan-Nepal-southern Tibet and Western Australia. *Spirigerella* marks an unexpected appearance, because the genus is not known elsewhere in such regions as Greenland and Spitsbergen, nor in the Zechstein of northern Europe. The appearance of *Himathyris* *arctica* in the Trold Fiord Formation is particularly striking, because the only other known of the genus (so far) is that of *Himathyris gerardi* (Diener) in the Wuchiapingian of the Himalaya, where faunas belonged to a southerly paleotemperate form. The ages of these two occurrences indicate two-way traffic, from in this case the Arctic, where *Himathyris* first appeared, to Gondwana. *Oviformia* and *Sulcicosta* entered the succession, having first appeared in the basal Permian of east Australia. Moreover, cool-water genera entered the paleotropical faunas of Texas, such as members of Paucispinauriidae and Trigonotretidae.

The inadequacy of antitropical as opposed to paleotemperate and polar designations

In recent articles on the distribution of Permian faunas, authors have used the term antitropical, obviously meaning a paleofauna found in non-paleotropical waters. The concept is far from new, having been expressed conceptually during and after early days of the study of rocks and faunas in especially eastern Australia, but I do think that use of the word antitropical is misleading, and inaccurate, and so should be either replaced or heavily qualified.

Understanding of the term antitropical and its application to Permian faunas and their distribution was summarized by Shi & Grunt (2000), using paleogeographic reconstructions offered by Briggs (1995), and further elaborated by Shi et al. (2002, Fig. 3), as replicated in Fig. 320. The broad overall concept is acceptable, although the division of world Permian marine faunas into divided into three huge faunal realms, tropical, southern antitropical (Gondwanan realm) and northern antitropical (Boreal Realm), is not as refined as the division into five, tropical or paleotropical and subtropical, divisible into several distinctive units, northern and southern paleotemperate, and northern and southern polar, that was demonstrated well before in a computer-refined survey of all-then-known Permian brachiopods by Waterhouse & Bonham-Carter (1972, 1975). A major reservation has to be attached to the term tropical – or antitropical, because this term carries implications with regards temperature, paleolatitudes, and length of day and night, and presence and length of seasons. The proposed reconstruction is based on three regions not closely governed by paleolatitude or day-length or seasonality. The distribution for so-called paleotropical offered by Shi & Grunt (2000, Fig. 3) shows a region that varies hugely in scope, from paleolatitudes of ca. 25° to palaeolatitudes of ca. 45°, or a little more, as represented in Fig. 322. There is no way that such deviation should be covered in any term such as tropical,: it simply does not fit. Tropical should be limited to a zone within 10-15° paleolatitude. Perhaps it would have been more appropriate if the concept had ascribed the so-called tropical segment to a geographic counterpart to boreal and austral – such as medial or midian, or even that long familiar term, Tethyan, which would allow greater flexibility with regards to paleolatitudes and other criteria. The term tropical equates to some degree with equatorial, but such a term appears inappropriate for any region embracing the range of paleolatitudes shown in Fig. 322. Tropical should be used in a context of polar and temperate, subpolar and subtropical, not intermixed with geographic terms.

As one attempted gloss, part of the expanded paleotropical realm was designated as a transitional zone off the western seaboard of the United States. This deeply invades an area in the paleotropics. It seems more like a tectonic complex, with distributions altered after accumulation, through which belts of rocks and faunas with differing temperature and paleolatitudinal allegiances have been tectonically brought into juxtaposition. A second so-called x

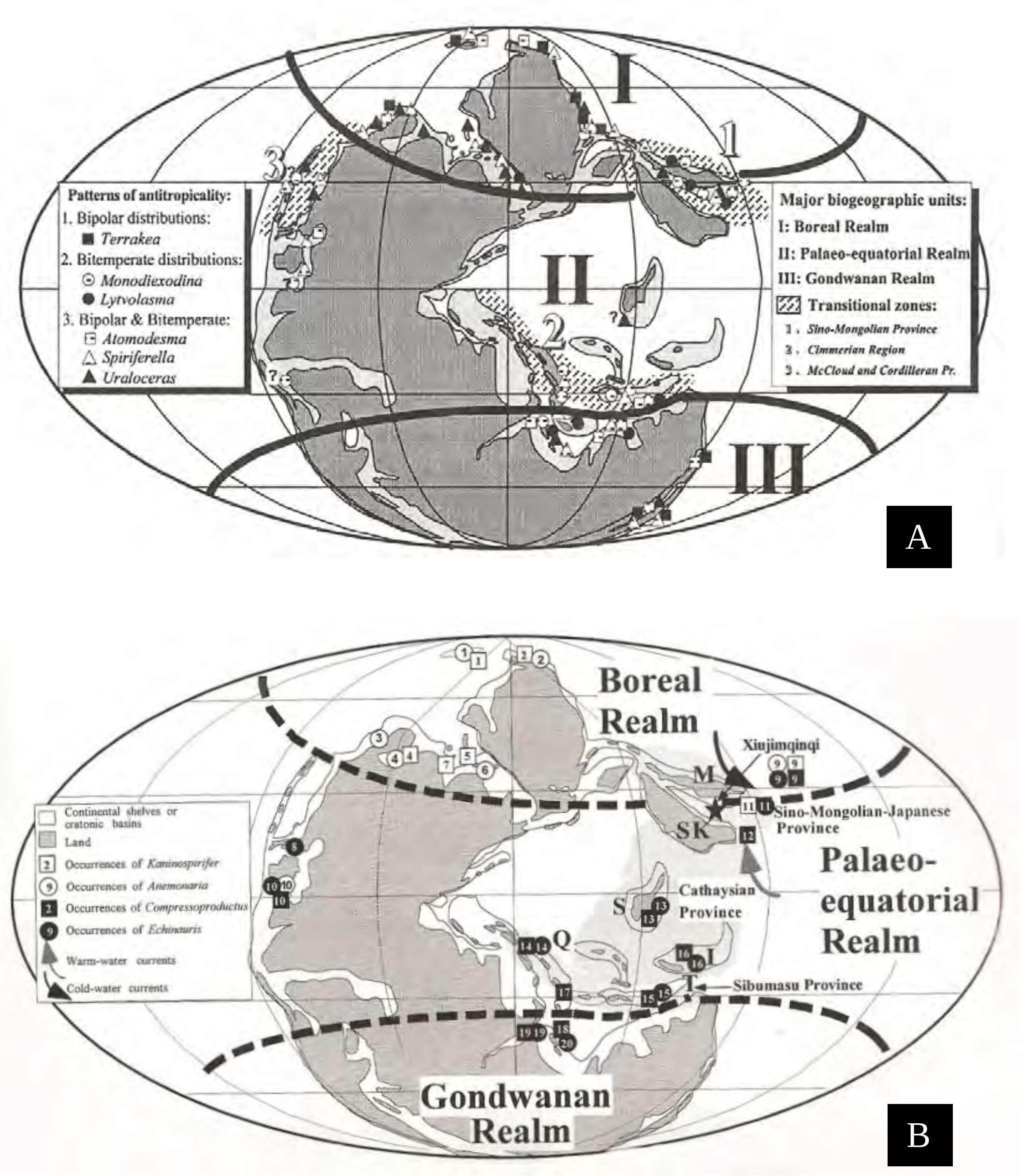

Fig. 322. Permian faunal realms according to (A), Shi & Grunt (2000, Fig. 3) and (B), Shi et al. (2002, Fig. 3). The diagrams are deemed oversimplistic, and in places incorrect. For example, the western part of the Canadian Rockies was not paleotropical during Permian time, and the palaeoequatorial realm is far too large, judged from faunal distributions of various phyla, involving fusulines, corals, brachiopods, molluscs and conodonts. The top of the diagrams showing northeast Russia should be discriminated as a subpolar region, based on the faunas and rocks of Omolon and Kolyma, and the segments of east Australia and parts of New Zealand were highly distinctive in terms of rocks and faunas, as a south polar realm. (Other parts of New Zealand were subtropical – Waterhouse, 2004a).

to the Vøringen Member. It is very close to *Yakovlevia* itself (Waterhouse 2013, p. 343). Gobbett (1964, p. 114) stated that *impressus* was limited to the Spirifer Limestone. So-called *Muirwoodia weyprechti* (Toula) was reported but not figured by Dunbar (1962). His *Sowerbina granulifera* (Toula), now referable to *Sowburia,* has four rows of spines on the ventral valve, and Angiolini & Long (2008) included Dunbar's material in their synonymy for the species, which they (1981), in which it is clearly shown that central and northern Tibet developed moderately close to southern Tibet. They did not belong to the far away paleotemperate latitudes of the northern hemisphere (Waterhouse 1987b). These areas were no more transitional than any other area on the globe which adjoins other areas. Tibet belonged to Gondwana during the early Permian, and formed part of the Tethys as the Tethys expanded and climates changed in the later Permian. It is always going to be difficult to summarize the great complexity of rocks and faunas through any geographic terminology in a single generalized map for an entire period. That is partly why the term paleotropical should both be narrowly defined, and regarded with caution, especially when authors offer only an anecdotal account of faunal distributions, rather than any comprehensive overview that hopefully will be undertaken to update and go far beyond the analyses in Waterhouse & Bonham-Carter (1975).

In terms of northern Canada, the faunal affinities are largely with those of other northern paleotemperate faunas, rather than a weakly delimited north polar zone, found in northeast Russia. Arctic Canada was antitropical. It was also antipolar. In positive terms, it was temperate. The Yukon and Sverdrup Basin faunas were the counterparts of the paleotemperate faunas of the southern hemisphere, as represented in Oman, Pakistan, India, Nepal, Western Australia etc, rather than with those of the southern paleopolar regions of east Australia and parts of New Zealand involving the volcanic arc and bordering shelf and incipient trench. The situation was indeed more complex and changeable, as analysed in part by various studies, rendering any use of the word antitropical little better than a reflection on the inadequacy of the terminology.

Local evolution

The input from local evolution in the Canadian Arctic Permian was not minor, involving as far as known not only *Arcticalosia*, but apparently *Patellamia*, derived from an member of Wimanoconchinae, possibly such as *Villaconcha planiconcha* Waterhouse, 2018 from the early Asselian of Yukon Territory, *Lineabispina,* allied to a Pennsylvanian genus from United States, and *Cameronovia*, a Wordian ally of the Wordian-Chanhsingian genus *Filiconcha* from east Australia and New Zealand. *Gobbettifera* offers an example of local evolution from a largely local genus *Septospirifer,* so close indeed that generic distinction is contentious.

Survival of Early Permian taxa

One of the particular aspects of the Canadian brachiopods from the Arctic centres on the survival into Middle Permian of several genera that elsewhere are considered to have perished by the end of Cisuralian or Early Permian time. These genera include *Fimbrininia*, *Kutorginella, Echinaria, Balkhasheconcha,* and *Schrenkiella*. *Lineabispina* is an outstanding genus that appears to be a relict of predominantly Carboniferous forms placed in Gigantoproductidae. This genus is also present across the border in Alaska, and it would seem likely that there are close links, as yet unexplored, with the largely undescribed Permian brachiopod faunas of Alaska. Such includes *Bamberina*, known in the type sequence of the Takhandit Formation just across the border, and found elsewhere in in the Glass Mountains of Texas, and possibly

Wuchiapingian of west Timor (Archbold & Bird 1989). A larger number of distinctive genera are shared with other Arctic faunas, including *Arctitreta* and *Grumantia* (if valid), *Fissulina, Gruntoconchinia*, *Kuvelousia*, *Globiella*, *Magadania, Kolymaella, Cancrinella*, *Svalbardathyris*, *Simplicatasia* and *Nahoniella.*

Links with Texas

There are several genera with strong links to the paleotropical Permian faunas from the Glass Mountains of Texas, as described by Cooper & Grant (1975). These include *Ametoria* and *Lirararia*, genera only known so far in Texas and in northern Canada.

Distinctive Features

The faunas discussed in this report have some unusual attributes. They are normal in their Strophomenaata (Strophomenata), and have a high diversity of Productusiformi (Productiformi) especially Productusidina (Productidina), with a modest number of Strophalosiaidina that are missing from many Arctic faunas. A few Rhynchonellaida and Athyrisida, a moderate number of Spiriferida, including many Spiriferellaidae and a few Delthyrisidina (Delthyridina) make up the rest of the Brachiopoda. Unlike many regions, there are no Terebratulaida, and an unusual scarcity of Bivalvia and Gastropoda.

CLIMATIC CHANGE: ISOCHRONOMETRY FOR THE CANADIAN, RUSSIAN AND AUSTRALASIAN FAUNAS

The faunal changes in the Canadian sequences accord well with the climatic and ensuing faunal changes known to have occurred in east Australia and New Zealand. In those regions, proxies are provided for very warm climate by coal measures (Loughnan 1973, 1975; Waterhouse 1964b, 2015a) and for cold temperatures by tillites, drop stones and other signs of glaciation (McClung 1975, Fielding et al. 2008, Waterhouse 1964b, c, 2015a). The stratigraphic level correlative with the Great Bear Cape Formation involves the Greta Coal Measures in east Australia, at a time exceptional for east Australia, as representing times warm and wet enough to allow great forests to flourish. Correlative marine faunas in the upper Takitimu Group of New Zealand, involving the *Echinalosia conata* Zone and *Attenuocurvus altilis* fauna (Table 4), when genera from the southern bitemperate biome entered the otherwise colder succession of the New Zealand volcanic arc, involving such genera as *Spinomartinia, Attenuocurvus, Arcullina, Taeniothaerus*. Several of these genera in cooler times are found in Western Australia, which occupied a position of much lower paleolatitudes in the paleotemperate climatic zone of the southern hemisphere, compared with this segment of New Zealand. In other words, during warmer climatic intervals, faunas migrated polewards into higher paleolatitudes, from Western Australia or equivalents into New Zealand. Signs of warm temperatures in the Canadian sequences are reflected in the presence of fusulines in the upper Great Bear Cape Formation, and in the lower Takhandit Formation of the Yukon. Fusulines are especially typical of the paleotropics. No fusuline has ever been found in the whole of the Australian Permian, as a reflection of control of biotic distribution by climate, and conodonts are rare (Nicoll 1976). There was a decline in faunal abundance over parts of the globe, deemed herein to have been caused by higher temperatures, and the abundance of silica and animals with siliceous components reflects higher rather than lower temperatures.

Russia marine level	**Queensland, New Zealand**	**Yukon Territory**	**Sverdrup Basin**	**International Stage**
	Echinalosia ovalis Mangarewa 2 F Flat Top (Qld)	gap	upper Trold Fiord F	Capitanian
Kazanian	*Pseudostrophalosia blakei* Mangarewa 1 F Ingelara (Qld)	*Cameronovia milleri* Takhandit 5 F	*Cameronovia milleri* lower Trold Fiord F	Wordian
?Ufimian	*Echinalosia maxwelli* Letham Burn F Oxtrack F (Qld)	*Dyoros modestus* Takhandit 4 F	*Dyoros modestus* Van Hauen low Trold Fiord? F	Roadian
Ufimian	*Echinalosia discinia* Letham 3, Brae F (Qld), Wandrawandian (NSW)	*Sulcicosta transmarinus* Tahandit 3	*Sulcicosta transmarinus* Assistance F	Roadian
Nevolin	*Wyndhamia typica*			Kungurian
Filippovian	*Megousia solita* Letham 1 Mbr Snapper Point F (NSW)	gap	gap	Kungurian
Saranin	*Attenuocurvus altilis* Elbow Creek F	gap	lower Assistance F	Kungurian
Sarginian	*Echinalosia conata* McLean Peaks F	*Schwagerina jenkinsi* Takhandit 2	*Schwagerina jenkinsi* Great Bear Cape F	Upper Artinskian (Baigendzinian)
Sarginian	*Spinomartinia adentata* Brunel, Chimney Peaks F	*Rigrantia laudata* Takhandit 1	Great Bear Cape F	Upper Artinskian (Baigendzinian)
Aktastinian	*Notostrophia homeri* *N. zealandicus* Brunel F	*Jakutoproductus verchoyanicus* Z Jungle Creek F	Jungle Creek F	Lower Artinskian (Aktastinian)

Table 3. See next page for caption.

Table 3. Correlation between the Canadian Permian with high latitude southerly Permian at the Artinskian – Kungurian interface. F - formation, Mbr member.

The overlying succession in east Australia above the coal measures was marked by the sudden return of glacigene sediment, accumulated largely under marine conditions, as if the crust had been depressed below sea-level by the weight of ice, and accompanied by cold-water marine faunas, often dominated by the bivalve *Eurydesma* or its derivative genus *Glendella* Runnegar. There are several levels of tillite and other glacigene deposits in east Australia and New Zealand, but these are limited to shallow water environments apart from drop-stones. Glacial sediments tend to be associated with faunas of particular attributes, limited in the range of genera and species, characterized as rule by thick shell of calcium carbonate with no aragonite (cf. Lowenstam 1964a, b). Such faunas are also found in off-shore and deeper water deposits, where there is no sign of tillite (Waterhouse 2015), and these faunas provide a much more complete record of cold climatic episodes than just the record of tillite accumulation on land and shallow waters itemized and to some extent miscorrelated by Fielding et al. (2008), because these are all too readily removed by later erosion. In Queensland, the eurydesmid bivalve *Glendella dickinsi* Runnegar dominates a fauna of low diversity (Waterhouse & Jell 1983), matched in New Zealand by a low diversity fauna with a few brachiopod species, that includes *Anidanthus solitus* (Waterhouse, 1968a) followed by further low diversity mollusc faunas, above spectacular glacigene laharic deposits (Waterhouse 2004a), all in the Caravan Formation. Then follows the Letham Formation with *Wyndhamia dalwoodensis* Booker, which is well represented especially in New South Wales, Australia. The level is followed by successive and alternating intervals, one set suggesting ameliorating conditions, through the absence of glacigene sediment, and greater diversity of biota, the other set recording reduced faunal diversity, associated with some evidence for glacial episodes.

One intriguing match with the *Pseudostrophalosia clarkei, Marginalosia minima* and *Ingelarella costata* Zones of Queensland-New Zealand, with cold-water faunas, suggesting a possible match with coarse clastic deposits of the Gijigin horizon, which some have interpreted as tillite. Preferred ages are discrepant however, the Australian zones arguably Capitanian, the Gijigin level, possibly as young as Wuchiapingian. In the Jungle Creek Formation of the Yukon Territory, a succession of faunas has been described by Shi & Waterhouse (1996) and Waterhouse (2018a, Fig. 379). For the lower part of the formation, five members were recognized, each characterized by both lithology and faunal content. The basal unit, Member A with warm-water faunas, was correlated with Gzhelian or Upper Carboniferous of Russia, with a series of cyclothemic sedimentary cycles. The overlying four members were correlated provisionally with the Asselian Stage. Each member showed varying input of genera from, on the one hand, northern Russia, and on the other, warmer water faunas of the mid-west and southern United States. The record is not simple, because Member D is exceptional in having a high percentage of dolomite in the sediment, and this and the shallow depths at which the sediment accumulated probably affected the faunal composition. But at the same time, the presence of dolomite implies warm conditions, and dolomite is never found in the Permian cold-water sediments of east Australia or New Zealand.

A break-down of geographic origins for the faunas surveyed in the present study is yet to be undertaken. But

Russia stratigraphic level	**Yukon Territory**	**Sverdrup Basin**	**International Stage**
	gap	upper Trold Fiord	Capitanian
Kazanian	*Cameronovia milleri* Takhandit 5	*Cameronovia milleri* lower Trold Fiord F	Wordian
Ufimian	*Dyoros modestus* Takhandit 4 *Neochonetes culcita* Takhandit 3	*Neochonetes culcita* Assistance F	Roadian
Elkin	gap	lower Assistance F	Kungurian
Nevolin	gap	*Paeckelmannella svartevargensis* Sabine Bay F	Kungurian
Filippovian	gap	gap	Kungurian
Saranin	gap	gap	Kungurian
Sarginian	*Schwagerina jenkinsi* Takhandit 2	*Schwagerina jenkinsi* Great Bear Cape F	Upper Artinskian (Baigendzinian)
Sarginian	*Rigrantia laudata* Takhandit 1	Great Bear Cape F	Upper Artinskian (Baigendzinian)
Aktastinian	*Jakutoproductus verchoyanicus* Z Jungle Creek F	Jungle Creek F	Lower Artinskian (Aktastinian)

Table 4. International and Russian correlations for the Canadian zones and rocks of the Sverdrup Basin and Yukon Territory.

the record will be incomplete, because whereas there were few significant breaks in sedimentation for the Jungle Creek Formation, which lasted from Gzhelian, Asselian, Sakmarian and Aktastinian time, there appears to have been significant pauses in sedimentation in nortern Canada, especially duringthe Kungurian Stage. In the Sverdrup Basin, no marine brachiopod faunas are recognized for the equivalents of the Saranin, Filippovian and Elkin levels in the Kungurian Stage of western Russia, although possibly the Vøringen level of Spitsbergen and Bear Island may prove to be Saranin or Filippovian. The diversity and affiliations for the brachiopods from the Assistance and Trold Fiord Formations are of limited value, because of the limited information about stratigraphic succession, and it appears that no brachiopods come from the basal Assistance Formation, with its *Neogondolella lamberti* Zone of latest Kungurian age (Henderson 2018). Collections in sequence have been carefully made from these formations by Prof. C. M. Henderson (pers. comm.) and examined by Liao Zhuoting, but I have not seen them. However a sequence from the type Degerböls Formation has been briefly inspected by the writer (see p. 386), and shows no marked faunal change in brachiopods throughout the formation. According to Beauchamp (1994), drop-stones are found in the Assistance and Trold Fiord Formation, whereas I have seen none in the correlative Takhandit Formation. Reid et al. (2007) judged that the Wordian carbonates had accumulated under conditions colder than those of the Kungurian and Artinskian.

In an overview of Arctic Permian faunas, Stemmerik & Worsley (2003, Fig. 2) have estimated that the mid-Permian rocks were deposited during progressive cooling. According to them, the Great Bear Cape Formation was deposited under cool conditions, the Sabine Bay, Assistance and Trold Fiord Formations was deposited under cold conditions, and the upper Trold Fiord Formation accumulated under very cold conditions. The faunal affinities when based on world-wide rathan regional assessments do not agree with these assessments. Fusulines in the upper Great Bear Cape Formation certainly do not betoken cool conditions, but point to a warm environment, no cooler than subtropical. The Sabine Bay basic faunal diversity was moderately high, suggestive of warm conditions. The Assistance faunas could be regarded as solidly temperate, cool at best, but tending overall warm, given the presence of conodonts, which are rare to absent in deposits of higher paleolatitudes. The lower Trold Fiord

Formation	Faunal attributes	Temperature assessment
Trold Fiord Takhandit zone 5	Brachiopods of moderate diversity, and include several genera otherwise confined or largely confined to northeast Russia and east Australasia, but most genera are like those from paleotemperate regions. The fauna matches that of the warmer intervals in the New Zealand succession.	Cold, but nowhere near as cold as correlative faunas of east Australasia. No tillites or varves.
Takhandit zone 4	Brachiopods of paleotemperate affinites like those of Assistance Formation. Warmer than overlying Trold Fiord Formation and underlying Takhandit zone 3.	cool.
Assistance middle Takhandit zone 3 and Richardson Mts	Some conodonts and ammonoids. Brachiopods of modest diversity, less than that of Sabine Bay and Great Bear Cape formations, and of paleotemperate affinities.	cooler than underlying faunas but not cold.
Basal Assistance	Brachiopods not known. Conodonts present.	warm temperate.
Sabine Bay	Brachiopods incompletely known, but include genera found only elsewhere from subtropical to tropical conditions.	warm temperate.
gap	fauna not known. Faunas in Greenland and Spitsbergen-Bjørnøya probably cool to cold.	
Great Bear Cape, lower Takhandit beds zones 1, 2	Exceptional in presence of fusulines, limited to subtropical and tropical conditions. Fauna otherwise poorly known, but includes brachiopods lingering from earlier warm-water faunas, such as *Linoproductus* s.l. and *Septospirifer.*	marginal subtropical, warm to very warm.

Table 5. Temperature estimates for the Kungurian to Wordian faunas of northern Canada.

Formation indicates cooling, with incoming of some cold-water indices found in east Australasia, and northeast Russia, though the high diversity cannot be rated as more than equivalent to high temperate paleolatitudes. No brachiopods from the younger Trold Fiord have been available for assessment, but even at an extreme, the environment would have been no less than barely subpolar, although a high latitude paleotemperate climate is far more likely, reserving a subpolar designation for northeast Russia.

It has been argued that the change in the character of rocks and faunas in northern Canada indicate a northerly shift under plate tectonics, and this may well be correct. But care should be taken to disentangle the affect of massive climatic shifts as well, with earth climate world-wide changing from warm, perhaps very warm, to substantial cooling. The change was not uniformly in one direction, which challenges the concept that it was due solely to northerly crustal displacement, but rather reflected oscillations between warm and cool to cold, though far from ever being glacial.

Beyond Canada, the Kapp Starotsin faunas of Spitsbergen offer promise, judged from preliminary assessments by Nakamura et al. (1992) and Ustritsky (1979), and it is to be hoped that henceforth, careful attention and documentation in terms of measured sequences of species, missing from some recent articles, is provided in studies on the Kapp Starotsin and other brachiopod successions. In the Yukon Territory, documentation of the sequences in the Takhandit Formation and unnamed sandstones of the North Richardson Mountains has been provided by E. W. Bamber (Bamber & Waterhouse 1971, Bamber 1972).

APPENDIX

Superfamil**y PRODUCTOIDEA (PRODUCTOIDEA)** Muir-Wood & Cooper, 1960

Family **RETARIAIDAE (RETARIIDAE**) Muir-Wood & Cooper, 1960

Subfamily **RIGRANTIINAE** Lazarev, 2000

The tribe Rigrantiini is elevated to subfamily level, based on the diversity of genera within the group.

Tribe **RIGRANTIAINI (RIGRANTIINI)** Lazarev, 2000

Tribe Antiquanoniaini is distinguished by the lack of a dorsal furrow across the inner dorsal ears (Waterhouse 2013, p. 124).

Genus ***Rigrantia*** Lazarev, 2000

Diagnosis: Ventral ridge at base of umbonal slopes, furrow between disc and dorsal ears. Ventral spines in hinge row and over disc and trail, and as a rule along the umbonal slope ridge. No dorsal spines, but well developed pits. Disc, especially that of ventral valve, reticulate.

Type species: *Antiquatonia planumbona* Stehli, 1964, p. 316 from Bone Spring Formation of western United States, OD.

Discussion: This genus and related form *Bicarteria* Lazarev, 2000 was discussed with their permutations in Waterhouse (2013). Waterhouse (2013, pp. 123, 124) pointed out that *Pseudantiquatonia* Zhan & Wu, 1982 from the Xiala Formation of Wordian age in central Xizang (Tibet) appears to be allied. It was noted that a dorsal ear groove is present, as in *Rigrantia*. This undoubtedly places the genus within Rigrantiaini, and the genus was distinguished from *Rigrantia* by the lack of dorsal pits. Brunton et al. (2000) had placed the genus in Tyloplectiini Termier &

Termier, but *Tyloplecta* has no dorsal ear furrow, and has distinct nodes at the intersections of costae and commarginal rugae, as also pointed out by Shen (2017, p. 713, pl. P9, fig. 1-5, 9, 10). Shen claimed that no ridge was present at the base of the ventral umbonal slope, but several figures show a row of such spines, and a few suggest a ridge. The ridge may be absent or weakly developed in various specimens assigned to *Rigrantia*, but the dorsal groove is the critical factor, and Shen (2017) did not report or not notice the feature, and seems to have been unaware of the significance of the groove, as well highlighted by Lazarev (2000).

An interesting development in the tribe was reported by Waterhouse (2018a, p. 83) in the lower Jungle Creek Formation, in which the ventral ear ridge is very low, or virtually absent, though the dorsal ear furrow is present. The umbonal slope row of ventral spines passes forward into several rows, and the genus is distinguished as *Dutroproductus*, with type species *D. dutroi* Waterhouse. *Dutroproductus* differs from *Rigrantia* in the same way that *Thamnosia* Cooper & Grant (1969) differs from *Kutorginella* Ivanova (1951).

Rigrantia laudata n.sp.

Fig. 324

1971 *Antiquatonia* sp. Bamber & Waterhouse, p. 172, pl. 18, fig. 5-7.

Derivation: laudator – praiseworthy, Lat.

Diagnosis: Large shells, wide hinge hinge, posteriorly reticulate with hinge row spines becoming large lateraly, well spaced spines over ventral disc and trail, pits well developed over dorsal disc. Spines at base of ventral umbonal slopes feebly developed or absent.

Holotype: GSC 26990 from GSC loc. 57242, figured by Bamber & Waterhouse 1971, pl. 18, fig. 5, and herein as Fig. 324A, here designated.

Material: A number of specimens from the basal Takhandit Formation at various localities.

Description: Specimens moderately large for the species, weakly transverse with hinge at maximum width, large ears, convex on the ventral valve and concave in the dorsal valve. The ventral umbo is incurved and broad with angle close to 110°, and posterior walls are convex and high. A broad shallow sulcus with ill-defined borders commences over the anterior disc and continues to the anterior margin, with angle of 30° as measured from the start of the sulcus. The disc curves smoothly into the trail, which is twice as long as the disc. The dorsal disc is very gently concave, so that the visceral disc is thick, and the disc curves abruptly into the long trail. A narrow fold commences over mid-disc, and becomes moderately high over the anterior disc. Ribs are well developed over most of the valve, missing only from the posterior outer ears. They number eight in 10mm over mid-valve, and six to seven in 10mm anterior, the ribs becoming slightly differentiated over the trail, some strong, others finer, with occasional forking, especially over the posterior trail. Ribs are very fine over the dorsal umbo, as many as sixteen in 10mm, and become fewer and stronger at eight in 10mm at the anterior disc, and increase by intercalation. Narrow growth rugae are prominent over the ventral disc, six or seven in 10mm, but are fine and inconspicuous over the dorsal disc. A low ridge is developed along the base of the umbonal slopes, and a narrow deep groove lies along the inner side of the dorsal ears. Ventral spines form a row just in front of the hinge and become sturdy well away from the umbo, about 1.5mm in diameter. Spines are fine, erect and rare over the disc, and scattered over the trail, close in strength to those of the outer hinge row. The effect on the ribbing varies: a spine may lie across two ribs, with only one thickened rib proceeding forward from the base of the spine, or in other instances, a spine emerging from a single rib may be followed anteriorly by two ribs. Spines are feebly if at all developed along the base of the ventral umbonal slopes. The dorsal valve does not display any clearly developed spines, but there are a number of clearly developed slightly elongate pits.

Resemblances: The type species of *Rigrantia, Antiquatonia planumbona* Stehli, 1954, p. 316 from the Bone Spring Formation of Texas, has more prominent commarginal ornament on both valves, and prominent spines along the base of the umbonal slopes. Lazarev (2000) reassigned to *Rigrantia* the species from the Permian of Texas described as *Antiquatonia* by Cooper & Grant (1975). From the Skinner Ranch Formation, *A. hessensis* (King, 1931, p. 68, pl. 11, fig. 6; Cooper & Grant 1975, p. 1090, pl. 391, fig. 6-17) is more transverse with finer ribs and other differences. *R. inflativentra* (Cooper & Grant, 1975, p. 1091, pl. 386, fig. 2-9) displays well developed dorsal commarginal rugae, and coarse anterior ventral spines, and *R. costella* (Cooper & Grant, 1975, p. 1090, pl. 453, fig. 30-33) from the Lenox Hills Formation (Neal Ranch beds of Ross 1963) is another transverse shell with fine costae and weak umbonal slope spines. The dorsal valve is not known. Another Lenox Hills species, *R. regularis* (Cooper & Grant, 1975, p. 1093, pl. 391, fig. 1-5) is closer to the present form in the ventral valve (its dorsal valve is not known) and has feeble umbonal slope spine row, with shallower sulcus and shorter disc. The Oregon species named *Antiquatonia cooperi* by Shi (1990, p. 490) and described by Cooper (1957, p. 35, pl. 5C, fig. 18-22) has a deeper sulcus and higher fold, and more transverse dorsal disc, with large ears. It clearly belongs to *Rigrantia*, with its deep furrow along the inner side of each dorsal ear. The Canadian specimens assigned to this species in Shi & Waterhouse (1996, p. 13, fig. 3-11) from the so-called *Yakovlevia* Zone in the middle Jungle Creek Formation tends

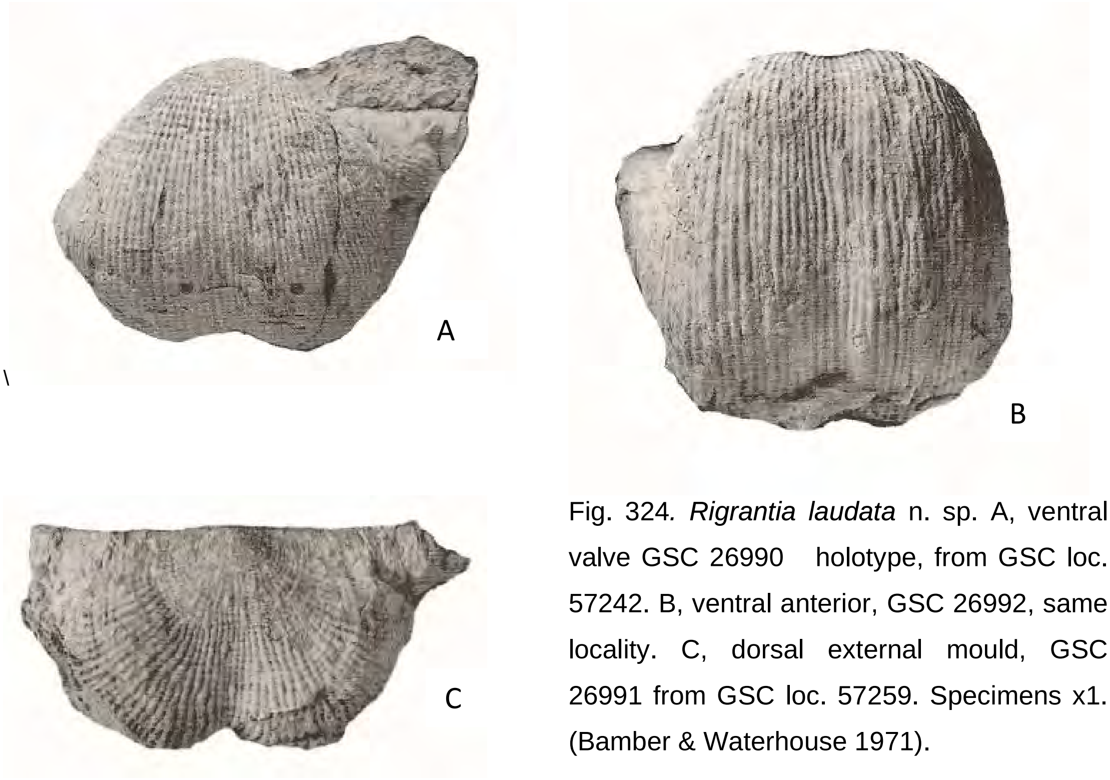

Fig. 324. *Rigrantia laudata* n. sp. A, ventral valve GSC 26990 holotype, from GSC loc. 57242. B, ventral anterior, GSC 26992, same locality. C, dorsal external mould, GSC 26991 from GSC loc. 57259. Specimens x1. (Bamber & Waterhouse 1971).

to have higher fold and better developed sulcus and more rugose dorsal disc. None show the dorsal ear cleft, and such was not described in the text. Yole (1963, pl. 2, fig. 18) identified a ventral valve with Cooper's species from Formation B of Vancouver Island, but the hinge and umbonal slope spines are not revealed, and no dorsal valve was figured. Otherwise the specimen looks moderately close.

TABLE 6. FOSSIL LOCALITIES FOR GSC FIELD STATIONS

C-12 No data. Possibly Trold Fiord Formation.

C-462 Collected by W. W. Nassichuk, three miles NW of Tingmisut Lake, bearing 335º, Sabine Peninsula, Melville Is-land. Assistance Formation.

C-463 Collected by W. W. Nassichuk, four miles NW of centre of Tingmisut Lake, bearing 310º, Sabine Peninsula, Melville Island. Assistance Formation.

C-464 Collected by W. W. Nassichuk, photo A 16763-171, sixteen miles SW of centre of Tingmisut Lake, bearing 335º, Sabine Peninsula, Melville Island. Assistance Formation.

C-465 Collected by W. W. Nassichuk, six miles west of Tingmisut Lake, Sabine Peninsula, Melville Island. Assistance Formation.

C-1410 Detail not known. Lithology and species are close to those of Assistance Formation.

C-1872 Five miles southeast of Tingmisut Lake, on east side of the west arm of Weatherall Bay, Melville Island. Assist-ance Formation.

C-1886 12km northwest of Yelverton Pass summit, Ellesmere Island. Trold Fiord Formation.

C-3993 Collected by W. W. Nassichuk from creek southwest side of Mount Bridgman, Ellesmere Island, Degerböls Formation.

C-3995 As above. Trold Fiord Formation.

C-3996. Ellesmere Island, creek on southwest side of Mt Bridgman. Trold Fiord Formation. Collected by W. W. Nassichuk.

C-3997 No data. Possibly Trold Fiord Formation, Ellesmere Island.

C-3998 No data. Possibly Great Bear Cape or Degerböls Formation, Ellesmere Island.

C-4002 79º30'N, 83º25'W. Assistance Formation.

C-4003. Isolated outcrop north of Gap Lake, Ellesmere Island. 80º05'00"N, 83º25'00"W. Assistance Formation. Collected by W. W. Nassichuk.

C-4004 79º30'N, 83º25'W. Stated to be Trold Fiord Formation. But looks like Assistance Formation (p. 146).

C-4005 No detail. Probably Trold Fiord Formation of Ellesmere Island.

C-4006 North side of Gap Lake, Ellesmere Island, 79º30'N, 83º25W. Trold Fiord Formation. Collected by W. W. Nassichuk.

C-4007 Stream northwest of major drainage, 4km north of Oesle Fiord, Ellesmere Island. Assistance Formation.

C-4008 Collected by W. W. Nassichuk from stream NW of major drainage 2.5 miles north of head of Vesle Fiord. Ellesmere Island. Trold Fiord Formation.

C-4014 25 miles SE of Cape Lockwood, East Cape, Ellesmere Island. 80º05’N, 81º45’W, Trold Fiord Formation.

C-4015 80º05’N, 81º45’W, Trold Fiord Formation.

C-4016. Ellesmere Island, 25 miles SE of Cape Lockwood, East Cape. 80º5’0” N, 81º5’0” W. Assistance Formation. Collected by W. W. Nassichuk.

C-4017 Collected by W. W. Nassichuk from 25 miles SE of Cape Lockwood, East Cape, Ellesmere Island, 80º05’N, 81º45’W, Trold Fiord Formation.

C-4018 80º05’N, 81º45’W, Ellesmere Island, collected by W. W. Nassichuk. Originally deemed Belcher Channel Formation, now probably Great Bear Cape Formation.

C-4019 Collected by W. W. Nassichuk from 25 miles SE of Cape Lockwood, East Cape, Ellesmere Island, 80º05’N, 81º45’W, Assistance Formation.

C-4020 80º05’N, 81º45’W, Ellesmere Island. Trold Fiord Formation Collected by W. W. Nassichuk.

C-4021 80º05’N, 81º45’W, Ellesmere Island. Trold Fiord Formation. Collected by W. W. Nassichuk.

C-4022 No data. Possibly Degerböls or Great Bear Cape Formation, Ellesmere Island.

C-4023 80º05’N, 81º45’W, Ellesmere Island. Assistance Formation. Collected by W. W. Nassichuk.

C-4024 80º05’N, 81º45’W, Ellesmere Island. Assistance Formation. Collected by W. W. Nassichuk.

C-4025 Collected by W. W. Nassichuk from 25 miles SE of Cape Lockwood, East Cape, Ellesmere Island, 80º05’N, 81º45’W. Assistance Formation.

C-4026 Collected by W. W. Nassichuk from Ellesmere Island, 80º05’N, 81º45’W. Trold Fiord Formation.

C-4028 Collected by W. W. Nassichuk from isolated outcrop 25 miles SE of Cape Lockwood, Ellesmere Island, 80º05’N, 81º45’W. Assistance Formation.

C-4034 Trold Fiord Formation, Ellesmere Island, fide Miller (1974).

C-4036 25 miles SE of Cape Lockwood, Ellesmere Island. ?Assistance Formation.

C-4037 25 miles SE of Cape Lockwood, Ellesmere Island, 50ft above 4036. Trold Fiord Formation.

C-4064 No data. Possibly Assistance Formation, Ellesmere Island.

C-4065 No data. Possibly Assistance Formation, Ellesmere island.

C-4066 Creek two miles north of headland of Blind Fiord, Ellesmere Island. Collected by W. W. Nassichuk. Possibly Assistance Formation.

C-4067 Creek 2 miles N of head of Blind Fiord on west side of major drainage, Raanes Peninsula, Ellesmere Island. Originally assigned to Belcher Channel Formation, now Great Bear Cape Formation?. Collected by W. W. Nassichuk.

4068 Eight km south of Blind Fiord, Ellesmere Island. Van Hauen Formation. Collected by W. W. Nassichuk.

C-4069 same as 4067.

C-4070 same as 4067.

C-4072 5km north of head of Blind Fiord, Ellesmere Island. Van Hauen Formation. Collected by W. W. Nassichuk.

C-4073 Van Hauen Formation. Collected by W. W. Nassichuk.

C-4074 5km north of head of Blind Fiord, Ellesmere Island. Trold Fiord Formation. Collected by W. W. Nassichuk.

C-4075 Van Hauen Formation, Ellesmere Island. Collected by W. W. Nassichuk.

C-4077 No data. Apparently Assistance Formation, Ellesmere Island.

C-4080 8km southwest of head of Trold Fiord, Ellesmere Island. Assistance Formation.

C-4081 8km southwest of head of Trold Fiord, Ellesmere Island. Assistance Formation.

C-4091 9 miles NE of Van Hauen Pass, north side of Hare Fiord, west of peak 2950, Ellesmere Island. ?Degerböls Formation.

C-4095 Collected by W. W. Nassichuk at section between Mount Schuchert and Mount Barrell, Krieger Mountains, Ellesmere Island. Degerböls Formation.

C-6136 Upper Cache Creek, Yukon Territory, NTS 117A, 68º07'30''N, 136º22'W.

C-6167 No data. The specimen has been through fire, and otherwise looks as though sourced from the Assistance Formation.

C-6174 North-trending ridge at headwaters of Kandik River. 65º48'N, 120º21'W.

C-6639 Blow River area, south of Cottonwood Creek, Yukon Territory. Unnamed crinoidal grainstone, probably matching middle Takhandit Formation.

C-10904 68º01'N, 136º36'W. Unnamed Permian clastics.

C-10908 White Mountains. Fault slice on north flank of White Mountain uplift; 68º01'N, 136º36'W. Unnamed Permian carbonate in section 117A 30. Coll. D. K. Norris.

C-11868 Sadlerrochit Formation, divide between headwaters of Gravel and Timber Creeks, north flank of Old Crow Basin. Section 117A29. Lisburne Group.

C-13356 Collected through 100ft interval by Atlantic Richfield on west side of Hecla Bay, Melville Island. Trold Fiord Formation.

C-23614 No data. ?Degerbols Formation.

C-47947 Talus from supposed Degerböls Formation, eastern Bjorne Peninsula, 77º36'N, 86º10'W. Collected by R. Thorsteinsson. Presumably Great Bear Cape Formation.

GSC FOSSIL LOCALITIES

25986 Collected by H. R. Grenier from probable Trold Fiord Formation, Cameron Island.

25903 Collected by E. T. Tozer from disintegrated outcrop on top of cuesta ridge facing south, three miles north of lake on west side of Weatherall Bay, Melville Island. Assistance Formation.

25993 As for GSC 25986.

25994 As above.

25995 As above.

26406 Collected by P. Harker & R. Thorsteinsson from northern Grinnell Peninsula, Devon Island, Assistance Formation.

26407 Great Bear Cape Formation, originally classed as Belcher Channel Formation, as in Harker & Thorsteinsson (1960, Fig. 3). Collected by those authors from Devon Island.

32201 Collected by R. Thorsteinsson from probable Trold Fiord Formation, Svartevarg cliffs, north coast of Axel Heiberg Island.

35316 Collected by R. Thorsteinsson, Sabine Peninsula, Melville Island, from talus. Trold Fiord Formation.

35317 Collected by R. Thorsteinsson from Trold Fiord talus above Assistance Formation, Sabine Peninsula, Melville Island.

35320 Collected by R. Thorsteinsson & E. T. Tozer from Sabine Peninsula near Hillock Point, Melville Island. Probably Trold Fiord Formation. See Tozer & Thorsteinsson (1964, p. 108).

36760 No data, but lithology suggests Great Bear Cape or probably Degerböls Formation.

37161 Collected by R. Thorsteinsson & E. T. Tozer, from probable Trold Fiord Formation above Assistance Formation, north of Tingmisut Lake, Melville Island. See Tozer & Thorsteinsson (1964, p. 107).

36770 No data. Possibly Assistance Formation.

43847 Unnamed sandstone and limestone at McDougall Pass, Symmetry Mountain, Richardson Mountains, north Yukon Territory. Collected by E. W. Bamber. See Bamber (1972, p. 143).

47849 **No data**.

47856 Collected by R. Thorsteinsson at Van Hauen Pass, Ellesmere Island. Degerböls Formation, Ellesmere Island.

52542 Collected by R. Thorsteinsson, from west snout of glacier between Caledonian Bay and East Cape, 21ft above base of Trold Fiord Formation, Ellesmere Island.

52702 Permian sandstone, White Mountains East, section 116P-6. See Bamber (1972, p. 131).

52705 Collected by E. W. Bamber at section 116P-6, White Mountains, 1450 ft above Devonian. See Bamber (1972, p. 132).

57242 Collected by E. W. Bamber at section 116C-2, west Tatonduk River, Yukon Territory. See Bamber (1972, p. 11).

52744 No data. Apparently middle Takhandit Formation of Yukon Territory.

52755 Sheep Mountain, section 116F-1, 4 miles east of Tatonduk River, upper Takhandit Formation. See Bamber (1972, p. 26).

57259 Collected by E. W. Bamber at section 116C-2, west Tatonduk River, Yukon Territory. See Bamber (1972, p. 11).

53821 Collected by E. W. Bamber at section 116P-6 44 feet below top of fomation of unnamed sandstones, White Mountains, north Yukon Territory.

53822 Collected by E. W. Bamber from three miles north of Horn Lake, 1362 feet below top of measured section, northern Richardson Mountains.

53823 Collected by E. W. Bamber from three miles north of Horn Lake, 1375 feet below top of measured section, northern Richardson Mountains.

53828 Collected by E. W. Bamber from unnamed sandstone at McDougall Pass, 516 feet above base, near Scho Creek, section 116P-9, northern Richardson Mountains. See Bamber (1972, p. 137).

53834 Collected by E. W. Bamber from Symmetry Mountain, in talus 680 feet above top of Devonian, northern Richardson Mountains.

53846 Collected by E. W. Bamber in 1962; McDougall Pass, unnamed sandstone unit, Richardson Mountains. See Bamber (1972, p. 143).

53847 Collected by E. W. Bamber from same section as GSC loc. 53834, ca. 2500 feet above top of Devonian. See Bamber (1972, p. 143).

Table 7 - BRACHIOPODS FROM THE YOUNGER PERMIAN IN THE SVERDRUP BASIN

Taxon	Formation					
	Great Bear	Cape Sabine Bay	Assistance	Trold Fiord	Degerbols	Van Hauen
	G	S	A	T	D	V
Orbiculoidea ornata n. sp.			A			
Derbyia semicircularis n. sp.			A	T		
Streptorhynchid gen. & sp. indet.				T		
Arctitreta pearyi Whitfield			A			
A. triangularis (Wiman)			A	T		
Grumantia kempei (Andersson)				T	D	
Fissulina svartevargensis n. gen., n. sp.		S				
Neochonetes culcita n. sp.			A			
Dyoros gentilis n. sp.			A			
D. modestus n. sp.						V
Horridonia grandis Waterhouse				T		
Pleurohorridonia? sp.			A			
P. platys n. sp.				T	D	
Possible gerontic specimen of *P. platys*				T		
Sowerbina? sp.				T		
Sowburia cf. *rudis* (Dunbar)				T		
Kutorginella minuta n. sp.			A			
Thamnosia sangminlee n. sp.	G					
Thamnosia aff. *sangminlee* n. sp.			A			
Thamnosia? sp.				T	D	
Svalbardoproductus subarcticus (Sarytcheva)	G					
Thuleproductus arcticus (Whitfield)				A		
T. crassauritus Sarytcheva & Waterhouse				T	d?	
Kochiproductus freboldi Stepanov			A	T		
Echinaria tardus n. sp.			A	T		
Ametoria nassichuki n. sp.			A	T	D?	
Tubersulculus? sp.				T		
Krotovia? sp. A	G					
Krotovia aff. *licharewi* (Frebold)			A?			
Guangia pustulata (Keyserling)	G					
Waagenoconcha sp.					D	
Gruntoconchinia sp.			A			
Wimanoconcha wimani (Fredericks)				T		

	Formation					
Taxon	Great Bear Cape	Sabine Bay	Assistance	Trold Fiord	Degerbols	Van Hauen
W. feildeni (Etheridge)				T		
Patellamia confinis Waterhouse			A?	T		
P. sulcata Waterhouse				T	D	
Balkhasheconcha thorsteinssoni n. sp.			A			
Echinalosia pondosus n. sp.				T		
Wyndhamia sphenarctica Waterhouse				T		
Arcticalosia unispinosa (Waterhouse)				T		
Melvillosia canadense Waterhouse				T		
Anemonaria pseudohorrida (Wiman)			A	T		
A. robusta n. sp.			A	T		
Liosella spitzbergiana (Toula) n. gen.			A	T	D	
L. delicatula (Dunbar)			a?	T		
L. vadosisinuata (Dunbar)				T		
Liosotellina multicostella n. gen., n. sp.			T?			
Kuvelousia sphiva Waterhouse			a?	T	D	
K. perpusillus n. sp.			a?		D?	
Liraria borealis n. sp.				T		
Globiella hemisphaerium (Kutorga)				T?		
Cimmeriella sp.			a			
Cimmeriella? sp.				T		
Dzhiremulia conlustras Waterhouse			A	T	D	V
Harkeria studiosa Waterhouse			A	t		
Schrenkiella truncata n. sp.			A			
Lineabispina ellesmerensis Waterhouse			A	t		v
Magadania attenuata n. sp.				T		
Magadania? sp.				T	D?	
Cameronovia milleri Waterhouse				T		
Cancrinella arctica (Waterhouse)			A			
Magniplicatina janischewskiana (Stepanov)			A			
Magniplicatina? sp.				T		
Rhynchopora taylori Girty			a	t		
Stenoscisma opitula (Grant)			A	T		
Stenoscisma sp.			A			
Callaiapsida ustritskii n. sp.			A			
Callaiapsida sp.				T		
Hustedia sp.		S				

	Formation					
Taxon	Great Bear Cape	Sabine Bay	Assistance	Trold Fiord	Degerbols	Van Hauen
Cleiothyridina maynci Dunbar				t		
Svalbardathyris kotlukovi (Stepanov)			A	T	d	
Himathyris arctica n. sp.				T		
Spirigerella inflata n. sp.			A			
S. plana n. sp.			A			
Hustedia sp.		S				
Oviformia bamberi (Waterhouse)			a	t		
Martinia stehlii n. sp.		S				
Martinia? sp. A			A	t		
Martinia? sp. C			A			v
Choristites? sp.	G					
“Choristites” soederberghi Dunbar					d?	
Paeckelmannella calignea Stehli & Grant		S				
Fasciculatia groenwalli (Dunbar)	G					
Fasciculatia striatoparadoxa (Toula)				T		v
Betaneospirifer? *striatoplicatus* (Gobbett)	G					
B. politus n. sp.		?	A			
Simplicitasia osborni (Harker)			A	t		
Gobbettifera angulata Waterhouse			A			
Spiriferella arctica (Haughton)	G					
S. separata n. sp.			A			v
S. draschei (Toula)				T	D	
S. angulata n. sp.	G					
S. sulcoconstricta n. sp.			A			
Alispiriferella gydanensis (Zavodowsky)			A	t		
Canalisella leviplica (Waterhouse & Waddington)				t		V
C. loveni (Diener)				t		
C. aldrichi (Etheridge)				T		
Arcullina sp.		S				
Undulatina sp.			a?	T		
Timaniella harkeri Waterhouse			A			v
Spirelytha pavlovae Archbold & Thomas	G					
S. svartevargensis Waterhouse		S				
Spirelytha sp.				T		
Catatonaria transversaria n. sp.			A	T		V
Orbicoelia? *aquilonia* (Stehli & Grant)		S				

Taxon	Formation					
	Great Bear Cape	Sabine Bay	Assistance	Trold Fiord	Degerbols	Van Hauen
Reticulariina? sp. A	G					
Paraspiriferina? sp.			A			
Paraspiriferina mcdougallensis n. sp.				t		
Spiriferellina cristata (Schlotheim)					D	
Syringothyris? *arcticus* Whitfield			A?			
Sulcicosta transmarinus n. sp.			A			
Cyrtella sp.			A			
Licharewia sp.			A			
Nahoniella prolata n. sp.				T	D	

Table 7. Brachiopod taxa from formations of the Sverdrup Basin, Canadian Arctic Archipelago. Uncertain occurrences queried, minor occurrences in lower case. *Krotovia*? sp. B is found in the lower Blind Fiord Formation, of late Permian age.

Table 8 - BRACHIOPODS FROM THE YOUNGER PERMIAN OF YUKON TERRITORY

Taxon	Faunal association				
	Sverdrup Basin				Yukon Territory
Grumantia kempei (Andersson)			T	D	R2,3
Grumantia? sp.					K3
Neochonetes culcita n. sp.		A			K3, R2
D. modestus n. sp.				V	R2
Peurohorridonia plana n. sp.			T	D	R2
Karnellia? bullocki (Nelson & Johnson)					K2?
Thamnosia? sp.			T	D	K4
Svalbardoproductus subarcticus (Sarytcheva)	G				?K2
Rigrantia laudata n. sp.					K1
Kochiproductus freboldi Stepanov		A	T		K3
Guangia sp.					K3
Balkhasheconcha thorsteinssoni n. sp.		A	t		k3

Taxon			Faunal association		
		Sverdrup Basin			Yukon Territory
Anemonaria pseudohorrida (Wiman)		A	T		K1, 3
Anemonaria robusta n. sp.		A	T		R2
Anemonaria sp.					R2
Retimarginifera? sp.					k3
Megousia tortus n. sp.					R2
Kuvelousia perpusillus n. sp.		a?		D?	K5?
Cimmeriella sp.		a			K3
C. coyneae n. sp.					K3
Harkeria studiosa Waterhouse		A	t	V?	k3
Lineabispina ellesmerensis Waterhouse		A	t	v	K3
Cameronovia milleri Waterhouse			T		R3
Kolymaella sp.					K3
Cancrinella arctica (Waterhouse)		A			R2,3
Magniplicatina janischewskiana (Stepanov)		A			K3
M. phosphatica (Girty)					K3
Rhipidomella transfigona n. sp.					R2
Rhynchopora taylori (Girty)		a	t		K1, R2
Stenoscisma opitula (Grant)		A	T		k3
Hustedia troelseni Dunbar					R2
Martinia stehlii n. sp.	S				=K3
Martinia? sp. A		A	t		R2
Martinia? sp. B					K3
Martinia? sp. C		A		v	K4
Yukonospirifer sp.					K2
Fasciculatia striatoparadoxa (Toula)			T	v	R2
Betaneospirifer politus n. sp.		A			K3
Simplicitasia osborni (Harker) n. gen.		A	T		K3
Spiriferella arctica (Haughton)	G				K1,2
S. saranaeformis Fredericks	Jungle Creek or Tahkhandit?				
S. separata n. sp.		A		v	K3, R
S. draschei (Toula)			T	D	K (possibly upper)
S. angulata n. sp.	G				?K1 or 2
S. sulcoconstricta n. sp.		A			K3, 5
Bamberina cordiformis (Waterhouse & Waddington)					=K4 or 5
Arcullina polaris (Wiman)					K3?
Timaniella harkeri Waterhouse		A			White Mts, uncertain zone, probably K3

Catatonaria transversaria n. sp.	A	T	v	K3

Taxon	Faunal association				
	Sverdrup Basin				Yukon Territory
Orbicoelia? *aquilonia* (Stehli & Grant)	S				R2
Gjelispinifera punctuata n. sp.					R2
Paraspiriferina mcdougallensis n. sp.			t		R2

Table 8. Brachiopod taxa from faunal levels and zones in the Yukon Territory. K = Takhandit Formation, the number indicating the zonal number from bottom (1) to top (5). =K equivalent in type section of Alaska. R = assemblage in Richardson Mountains of northern Yukon, zones numbered from 1 at base to 3 at top. Uncertain occurrences queried, minor occurrences in lower case. Sverdrup occurrences are also listed, keyed as in Table 7.

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