

**INGELARELLOIDEA (SPIRIFERIDA: BRACHIOPODA) FROM AUSTRALIA AND
NEW ZEALAND, AND RECLASSIFICATION OF INGELARELLIDAE AND
NOTOSPIRIFERIDAE**

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Abstract

Ingelarellid and Notospiriferid brachiopods are separated from Martiniids and classed in Delthyridina, as Superfamily Ingelarelloidea. Three morphological terms are proposed: **globons** (plural): swollen hollows or exopunctae found within primary shell layer of some Notospiriferidae, **mesopunctae** (plural) pores that pass through the outer primary shell layer to penetrate deeply into the secondary layer, without reaching the interior, and **tigillum** (singular), proposed for an internal ridge of thickening along the ventral mid-line in front of the muscle field. These features have classificatory significance. Ingelarellid brachiopods are discussed, including revised determinations for New Zealand and east Australian species that affect the age of formations, and a summary is provided for stratigraphic implications of significant *Tomioopsis* species in the late Early and Middle Permian. It is shown that *Martiniopsis* does not come from North Auckland, New Zealand, on available evidence, counter to one claim. Morphological analyses establish that New Zealand and east Australian species now referred to *Martiniopsis* did not evolve directly from east Australia - New Zealand *Tomioopsis* stock, but from two separate lineages, including new genus *Tigillumia*, type species *M. biparallela* Waterhouse, 1987a. The genus *Tomioopsis* with a large number of Carboniferous to Permian species is subdivided into subgenera, *Tomioopsis* Benedictova, *Ambikella* Sahni & Srivastava, *Ingelarella* Campbell, and new subgenera *Johndearia*, type species *Ingelarella isbelli* Campbell, 1961, and *Geothomasia*, type species *Tomioopsis teichertii* Archbold & Thomas, 1986. *Roespiriferinae* is proposed as a new subfamily, based on *Roespirifer* Waterhouse & Piyasin, 1970, and distinguished by the micro-ornament of low solid spinules and lack of grooves. Notospiriferidae Archbold & Thomas, 1986 is recognized as a family, apparently restricted to Late Paleozoic of Australia and New Zealand, and evolved from Ingelarellidae. Three subfamilies are recognized, Notospiriferinae, Glendoniinae and Mesopunctiinae new. New genera *Papulinella*, type species *Notospirifer hillae* Campbell, 1961, *Monklandia*, type species *M. gympiensis* n. sp., *Wairakispirifer*, type species *N. microstriatus* Waterhouse, 1964, and *Mesopunctia*, type species *N. macrospinosus* Waterhouse, 1968, are proposed. *Kelsovia* Clarke, 1990 is probably a junior synonym of *Tabellina* Waterhouse, 1987a.

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INTRODUCTION

This paper discusses east Australian and New Zealand brachiopods of Ingelarelloidea, focussing on subgenera in *Tomioopsis* and stratigraphic implications, and on the classification and interrelationships of Notospiriferidae. Stratigraphic successions for most of the fossils discussed are outlined for the Bowen Basin by Dear (1972), McClung (1981) and Waterhouse (1987b, 1989), Gympie district, southeast Queensland by Waterhouse & Balfe (1987), west Nelson, New Zealand by Campbell et. (1998) and Wairaki Downs, New Zealand by Waterhouse (1998).

Locality descriptions, repositories

New Zealand fossil collections are coded by letter and number in the archival Fossil Record File of the Geological Society of New Zealand. This is arranged numerically within each sheet district of the 1:50 000 New Zealand Infomap 260 series, coded by letter and number. Collections within the range of D44/f108-137 are also assigned a GS locality number and are kept at the Institute of Geological and Nuclear Sciences (IGNS), Lower Hutt, where significant specimens carry the prefix BR in the registry of brachiopods. The Department of Geology, University of Otago, Dunedin, holds the collections D44/f304-365, and important specimens are serially numbered with prefix OU. Collections in Australia are housed at departments of geology as follows: UQ University of Queensland, Brisbane, ANU Australian National University, Canberra, UNE University of New England, Armidale. UQ locality numbers are prefixed by L. Material prefixed GSC is from Geological Survey of Canada, Institute of Sedimentary & Petroleum Geology, Calgary, QM Queensland Museum, Brisbane, GSQ Geological Survey of Queensland, Brisbane. OD means by original designation.

Morphological terms

globon (s): proposed for the swollen exopunctae peculiar to species within Notospiriferidae. These are globose or subglobose cavities within the primary shell layer, as described by Campbell (1959) and Armstrong (1970). They differ in size and shape from the linear narrow and shallow grooves or hollows in quincunx found in many Ingelarelloidea and in Martinioides.

mesopunctum (ae): a term proposed for pores that pierce the external or primary layer of shell at the anterior end of surface grooves, and enter the secondary shell, without penetrating to the inner surface. They are found in Subfamily Mesopunctiinae. Endopunctae fully penetrate the secondary layer, and exopunctae are limited to the primary layer.

tabella (ae): name proposed by Waterhouse (1971) and used by Archbold & Thomas (1986) for dorsal internal plates that support crural plates. Equivalent to "dorsal adminicula" of authors. Adminicula are plates with a different function, supporting the dental plates and found only in the ventral valve.

tigillum (l): applied to a ridge along part or all of the interior ventral valve in front of the muscle field, apparently strengthening the valve, and found variously in sulcate or non-sulcate shells, that externally may carry a median ridge, or two lateral subplicae, or be essentially smooth apart from micro-ornament. Found in some genera or subgenera of Ingelarellidae. From Latin *tigillum*, meaning a small bar of wood, or little beam.

SYSTEMATIC STUDIES

Suborder DELTHYRIDINA Ivanova, 1972

Superfamily INGELARELLOIDEA Campbell, 1959

[nom. transl. hic ex Archbold & Thomas 1986, ex. Ingelarellinae Campbell, 1959]
Archbold & Thomas (1986) rejected links between Ingelarellidae and Reticularoidea suggested by Sarytcheva et al. (1963), Waterhouse (1971, 1978) and Grant (1976), and left the superfamilial relationships as indeterminable. Carter et al. (1994, p. 340) classed Martiniopsidae, Ingelarellidae and Gerkispiridae within Martinioidea Waagen, 1883, but these families involve genera with well formed internal plates, whereas Martiniidae Waagen, 1883 lacks internal plates (Waterhouse 1968). Martiniidae appears to have descended from Ambocoelioidea George, 1931, whereas Ingelarellidae, together with Gerkispiridae, have, it is here proposed, stemmed from within Delthyridina, a position ultimately close to that shown in Russian studies, eg. Sarytcheva et al. (1963, p. 305). Ingelarellids show comparable internal plates, what appears to be allied cardinal process, and an external micro-ornament not identical with, but apparently developed from fimbriate, finely pustulose or granular micro-ornament developed in Devonian Delthyridina.

Family INGELARELLIDAE Campbell, 1959

[nom. transl. Archbold & Thomas 1986 ex Ingelarellinae Campbell]

Subfamily INGELARELLINAE Campbell, 1959

The classification of Spiriferida that was set out by Carter et al. (1994) must be questioned in one major aspect. They recognized Family Martiniopsidae Kotlyar & Popeko, 1967 as distinct. Having examined type *Martiniopsis* at the Geological Survey of India, Calcutta (Waterhouse 1965), and type *Ingelarella* at the University of Queensland, and many other species identified with these genera, I find it impossible to distinguish the two to even subfamilial level, and Archbold & Thomas (1986) came to the same conclusion. The diagnosis provided by Carter et al. (1994, p. 340) for Martiniopsidae "micro-ornament usually weakly to strongly capillate" does not apply to *Martiniopsis*. Instead, the micro-ornament of *Martiniopsis*, as described by Waterhouse (1965, p. 168), is identical to that of *Ingelarella*, and largely, *Tomiopsis* Benediktova and probably *Ambikella* Sahni & Srivastava. Therefore Martiniopsidae and Ingelarellidae are regarded as synonymous. Ingelarellidae has priority over Martiniopsidae.

Ingelarella does not appear to be a valid genus, being a junior synonym probably of *Tomiopsis* Benediktova, 1956, and almost certainly of *Ambikella* Sahni & Srivastava, 1956. *Tomiopsis* was first proposed for a vertebrate in 1893 by Cope, but its application as a name for a brachiopod genus has been "validated" through appeal of Archbold & Thomas in 1984 to the International Committee on Zoological Nomenclature. The genus *Tomiopsis* is of Early Carboniferous age, and is like *Martiniopsis* in internal plates. Differences in micro-ornament seem to be no more than subtle, with infrasubspecific variations that reflect growth conditions. *Ambikella* was based on a deformed specimen, and had been wrongly interpreted until Waterhouse (1965) showed that the genus was in fact close to *Martiniopsis* Waagen, and probably identical with *Ingelarella* Campbell. The one area of uncertainty with

regard to *Ambikella* lies with the micro-ornament, not well preserved, but consisting of fine external grooves in quincunx, as is clearly visible in other Himalayan material (eg. Waterhouse 1978, p. 58, Singh & Archbold 1993, p. 66), and in well preserved external moulds from Late Permian in the Manang district of Nepal.

Any suggestion of identity between *Ingelarella* and *Tomiopsis* or *Ambikella* has met with considerable resistance from a few Australian workers. McClung (1978) virtually refused to even consider the possibility, raising flimsy objections, apparently on the grounds that *Ingelarella* was an Australian genus, no matter what its validity. Archbold & Thomas (1986) misrepresented *Ingelarella* by claiming that several of its species possessed small c-shaped protuberances at the posterior end of surface grooves, a feature not seen in *Tomiopsis* or *Ambikella*. Later Archbold in Singh & Archbold (1993, p. 66) asserted that the type species *angulata* was too worn to allow surety. But this assertion is rejected, and seems less than objective. The type and topotype material of *angulata* that I have examined is reasonably well preserved. Because the matrix is somewhat calcareous, shells exfoliate below the surface when cracked out of enclosing rock. To observe the true micro-ornament, the matrix with attached shell was carefully detached in small flakes, and leached in dilute HCl under close control. The solution was checked at intervals while the shell was being etched away, until the micro-ornament became clearly revealed. This procedure uncovered surface grooves, with no spines or raised crescentic rims at the posterior ends of the grooves. These flakes were preserved with the topotype material at the University of Queensland in the type collections, and kept and labelled in a small enclosed box. If somehow they have been lost, there is more topotype material available for processing. Evidently Dr. Archbold did not find or notice the material I had processed, and failed to take steps to prepare further material. Based on careful preparation and observation, I conclude that topotypes of *Ingelarella angulata* Campbell, 1959 have elongate surface grooves, with no c-spines (Waterhouse 1986, p. 110; 1987). Parfrey (1988, p. 18) examined large collections of topotype *angulata*, and also concluded that the micro-ornament consisted of shallow grooves arranged in quincunx. She asserted that c-spines were definitely not developed. Therefore Archbold's claims must be set aside. Moreover McClung (1978) has proposed that *angulata* grades into *ingelarensis*, and many *ingelarensis* are known to show surface grooves, entirely lacking c-spines. The c-spines observed by Armstrong (1970) are developed in different species, including *Ingelarella ovata* Campbell, and *I. profunda* Campbell, now referred to *Homevalaria* Waterhouse, 1986. In addition Armstrong (1969) also compared non-topotype specimens that show spines to *Ingelarella angulata*, but these are reassessed as belonging to a different genus, *Monklandia*, a Notospiriferid.

It appears that *Ingelarella* is identical in most respects with *Ambikella*, and neither type species is known to display any profound difference from *Tomiopsis*. *Tomiopsis* was named a few months before *Ambikella*. Over recent years, *Tomiopsis* has been used in preference. There remains a second option which biologically may be preferable - the abandonment of *Tomiopsis*, *Ambikella* and *Ingelarella* in favour of *Martiniopsis*, as favoured by Runnegar & McClung (1975) and Dickins (1989) for example, and first suggested by Waterhouse (1968, p. 57). This appears defensible,

in so far as the present study shows that some morphological attributes, such as plication and to some extent definition of sulcus and fold, reflect geographic, environmental and specific rather than generic differences. This text points to several collections that involve clines from plicate to smooth and deeply to scarcely sulcate shells, such as *Tomioopsis dissimilis* and *T. havilensis* - *T. costata*. But at the same time, it has been found that there are internal differences in magnitude and arrangement of plates and internal ridging which indicate that species assigned to *Martiniopsis* have evolved from lineages not known amongst *Tomioopsis*.

Genus *Tomioopsis* Benedictova, 1956

TYPE SPECIES: *Tomioopsis kumpani* Benedictova, 1956.

ASSOCIATIONS OF MORPHOTYPES THROUGH TIME IN AUSTRALIA AND NEW ZEALAND: *Tomioopsis* species are very numerous and specifically diverse in east Australia, especially Queensland and New South Wales. At first sight they form a bewildering plexus of species, with several formations containing two to four named species. This number has been reduced a little through the recognition of *Homevalaria* Waterhouse, 1986, with distinctive micro-ornament, *Tabellina* Waterhouse 1987a, and a new genus *Monklandia*, regarded as Notospiriferid. Furthermore, in this study, it is shown that contemporaneous individuals from single collections that have been subdivided between plicate species and relatively smooth non-plicate but sulcate species should apparently be grouped into single species. Examples include *angulata* and *ingelarensis*, as argued by McClung (1978), and *costata-havilensis* and *plicapapilana*, as well as other species shown here to vary within single suites, such as *mantuanensis* and *dissimilis*. Even so, there still remains more than 25 species, as well as a number of intervals not occupied by tightly delimited taxa. This occurs despite the overall low faunal diversity in east Australian Permian (Waterhouse & Bonham-Carter 1975), and strongly suggests that *Tomioopsis* was well adapted to low temperatures, and speciated rapidly.

An overall survey of the species in east Australia and New Zealand reveals three major clusters. There is an Early Permian (Cisuralian) association of species characterized on the whole by deep ventral sulcus, faint to moderate plicae, subparallel adminicula of moderate length, no tigillum, comparatively short tabellae and moderate shell thickening. There is a large Cisuralian, Guadalupian and Lopingian suite with generally well formed ventral sulcus, moderate to long adminicula, tigillum, and tabellae of moderate to considerable length, displaying stronger tendency to develop thick secondary tissue. In late Cisuralian into Lopingian, another suite developed with reduced sulcus and low fold, low or no plicae, generally well spaced medium-length to short internal plates, low tigillum and thick secondary shell in the ventral valve. Within this suite strong dorsal thickening developed in some species. McClung (1978, pl. 2, p. 31) showed a somewhat similar threefold association with some assumptions on substrate.

Tabulation through time of three major associations treated as subgenera of *Tomioopsis* in east Australia and New Zealand.

Lopingian		
<i>Ingelarella</i>		<i>Johndearia</i>
<i>antesulcata, furca</i>		<i>isbelliformis</i>
<i>parallela</i>		
Guadalupian		
<i>havlensis-costata</i>		<i>pelicanensis</i>
<i>mantuanensis</i>		
<i>oviformis-angulata</i>		<i>isbelli, dissimilis</i>
<i>ingelarensis, angulata</i>		<i>magna</i>
<i>ingelarensis confusa</i>		
Cisuralian		
<i>subplicata</i>		<i>undulosa</i>
		<i>brevis</i>
<i>plica-paraplana</i>		
<i>sulcata</i>	<i>Ambikella</i>	
	<i>branxtonensis</i>	
	(?-) <i>symmetrica</i>	
<i>elongata</i>	<i>konincki</i>	
	<i>postglabra</i>	
	<i>regina</i>	

A few species do not fit within these associations. So-called *Ingelarella etheridgei* McClung (= *strzeleckii* de Koninck) and possibly allied *I. davidi* McClung from the Elderslie Formation are transverse forms with well formed sulcus and fold, a number of narrow plicae, subplicae in the sulcus of *davidi* and short tabellae, in some shells crossing inner plicae. Their micro-ornament is not described, so that affinities remain uncertain, pending an adequate description.

Species of *Tomioopsis* have been described from the Permian in Western Australia by Archbold & Thomas (1986). The older species *notoplicatus* (Carrandibby Formation), *woodwardi* (Poole Sandstone, Nura Nura, Fossil Cliff), and *rarus* (High Cliff Sandstone) are subelongate forms moderately close to *Ambikella fructiformis-siangensis* of the Early Permian in India, showing adminicula that tend to be close-set, subparallel and within the sulcus anteriorly, and not much thickening of secondary shell and no tigillum. Tabellae are moderately developed, though in some specimens they diverge widely and are short. Younger species *pauciplicatus* (Madeline Formation), *teichertii* (Wandagee Formation), *globosus* and *balgoensis* (Lightjack Formation), and *hardmani* (Upper Marine beds, Port Keats Group) seem to have evolved from the earlier set of species at the time of Byro Group deposition (late

Cisuralian), and persisted into the Late Permian. These five are similar to each other in their transverse outline, low broad ventral umbo, rounded lateral flanks, moderately well defined sulcus and fold, and subdued if any plicae. Adminicula are moderately long and generally subparallel and secondary thickening not great. Tabellae are generally short and widely diverging, although they are slightly longer and more subparallel in some specimens. These form a completely different grouping from *Tomioopsis* in east Australia and New Zealand, and from species found further afield.

The type species of *Tomioopsis* is *T. kumpani* (Yanischevsky) from the Early Carboniferous of Kuznetz Basin, and slightly younger forms *T. plicata* (Monachova) and *T. plicata plana* Sokolskaya are close. These differ in detail from east Australian associations. Plicae are low and close-set and shell is thin, so that even juvenile and early mature specimens from New Zealand and east Australia have thicker ventral valve posteriorly. Adminicula pass virtually along the crest of the sulcus, whereas they lie a little more within the sulcus in the early Permian species of east Australia. In the dorsal valve, the dorsal myophragm is longer and thicker, beginning at the base of the cardinal process. Tabellae are short, and lie either along the fold edge, or more laterally. Overall appearance of these Carboniferous *Tomioopsis* is most like that of *Monklandia gympiensis*, an unusual genus and species at Gympie, Queensland, with micro-ornament of small crescentic spines, not seen in *Tomioopsis*.

Given these differences, it is proposed to recognize several subgenera within *Tomioopsis*, that embrace overall related suites of species, distinguished from other subgenera by relatively minor, but generally consistent characters.

***Tomioopsis* Benedictova, 1956**

TYPE SPECIES: *Tomioopsis kumpani* Yanischevsky, 1935.

DIAGNOSIS: Spiriferidan shells with interareas, open delthyrium, rounded cardinal extremities, ventral sulcus with subplicae, median costa, or smooth, dorsal fold with rounded or grooved crest, plicae of varying number and strength, micro-ornament of narrow shallow grooves, generally in quincunx, as well as concentric growth increments and lamellae. Ventral interior includes high dental plates bearing teeth, supported from floor of valve by adminicula, adductors narrow and generally raised, tigillum present or absent. Dorsal interior with laminate "cardinal process", dental sockets, crural plates well formed, supported by subvertical tabellae of varying length and disposition. Adductors developed, divided by low myophragm of varying strength and length. Shell taleolate.

Subgenus *Tomioopsis* Benedictova, 1956

DIAGNOSIS: Shell thin, plicae low and narrow, may be moderately numerous (ie. 6 pairs), sulcal subplicae well developed in several species, median channel along dorsal fold. Adminicula of moderate length and spacing, diverge weakly forwards, tabellae short, may diverge into interspace between inner two pairs of plicae. Myophragm broad and commences in front of cardinal laminae in type species.

DISCUSSION: A suite of typical *Tomioopsis* of Zabaikal is described by Kotlyar & Popeko (1967), *kumpani* and *plicata* from the upper Lower Carboniferous Gutai Suite, *mergensis* Sokolskaya from the Gutai Suite and mid- Carboniferous Tuthaltui Suite, and *T. rhombiformis* Kotlyar from this suite, all typical *Tomioopsis*, and of interest in

showing moderately strong concentric growth steps and wrinkles. *T. kokpectensis* Sokolskaya, 1959 from the Kokpecten Suite of east Kazakhstan may be upper Carboniferous to as young as early Permian (Sarytcheva 1968).

Subgenus *Ambikella* Sahni & Srivastava, 1956

TYPE SPECIES: *Ambikella fructiformis* Sahni & Srivastava, 1956 (= *Tomioopsis siangensis* Singh & Archbold, 1993).

DIAGNOSIS: Inflated moderately large shells with well formed sulcus, fold, plicae present or absent, much more open and coarser than in *Tomioopsis (Tomioopsis)*, shell thicker than in *Tomioopsis (Tomioopsis)*, but not very thick. Adminicula well formed, moderately long, weakly diverging, no tigillum, tabellae short and diverging, or moderate in length and weakly diverging or subparallel.

DISCUSSION: *Ambikella* is reinterpreted following Waterhouse (1965) and Singh (1978). The holotype is badly deformed, and micro-ornament imperfectly preserved, but Singh argued strongly for its validity. A scattering of early Permian specimens from the Himalaya, as summarized by Waterhouse (1965) is reinforced by description of *Tomioopsis siangensis* Singh & Archbold (1993) from the Garu Formation, Siang district, eastern Himalaya, although the authors only illustrated external detail and not the full exterior. This species appears very close to *fructiformis* from nearby Sikkim. The authors did not compare the two closely, seemingly because *fructiformis* was deformed, and came from a different area. Nonetheless the two are similar in age, geographic distribution and morphology, and it certainly appears from well known species in east Australia and New Zealand that ranges do vary somewhat and that species were widely dispersed. Here the two are regarded as synonymous, because there is no significant difference in size, shape, shell thickness and internal plates, except that *fructiformis* is deformed. It also lacks plicae, but it is clear from examination of many species that the presence and strength of plication is variable in many *Tomioopsis* species. Specimens figured as ?*Enteleles* sp. and ?*Spiriferella* sp. from the Agglomeratic Slate of Kashmir by Bion (1928, pl. 1, fig. 6, pl. 2, fig. 7) appear generically close. Even at first glance, *Ambikella* differs from *Tomioopsis (Tomioopsis)* in its larger size, plication that is either stronger and more open, or faint to absent, and thicker shell.

Many scattered species also show comparable morphology - only moderate thickening, well formed adminicula and tabellae, and no tigillum. In east Australia, *Tomioopsis regina* Waterhouse, 1987a from the Fairyland Formation of southeast Bowen Basin, and *T. postglabra* Waterhouse, 1987a from the Dresden Formation of the same area appear to be close, with *Ingelarella symmetrica* Campbell from the Tiverton Formation, north Bowen Basin. From the early Cisuralian of the Sydney Basin, *konincki* Etheridge and *branxtonensis* Etheridge have rather short tabellae and lack a tigillum. The species *branxtonensis* Etheridge, 1919 approaches *symmetrica* in its plates and strong secondary thickening, and may prove to be senior synonym, although much smaller and more transverse. From Western Australia three species *notoplicatus*, *woodwardi* and *rarus* named by Archbold & Thomas are close to type *Ambikella* as subelongate shells with long adminicula, moderate to short tabellae and no tigillum.

Some younger Permian species show a strong approach to early Permian

Ambikella in the development of internal plates and lack of tigillum. Thus *Mentzelia punjabica* Reed, 1944 from possibly the Kalabagh Member in the Salt Range displays little thickening, long subparallel adminicula with sulcus commencing anteriorly and no tigillum. Of early Late Permian in age, it could have been derived from *Ambikella* stock. The same is true of *T. himalayanicus* Waterhouse, 1978 from the Calcareous Sandstone or Gungri Formation of the Spiti region. Comparatively rare *Tomioopsis* from the Late Permian Pija Shale Member and Galte Member of western and central Nepal (Waterhouse 1978, p. 58) shows well preserved micro-ornament, but unfortunately internal plates are not well known.

Tomioopsis harringtoni Archbold & Thomas (1986) from the Bonete Formation, east Argentina, shows moderate thickening, and its short diverging tabellae suggest *Ambikella*.

Several high latitude species of the northern hemisphere come close in ornament and internal plates. *Tomioopsis tricostata* Kotlyar in Kotlyar & Popeko (1967, pl. 53, fig. 1-5) from the Harashibir Suite of mid-Carboniferous age in east Zabaikal has few sturdy plicae, wide sulcus and high fold, widely diverging adminicula, no tigillum and short tabellae, with some shell thickening, marking an approach towards *Ambikella*. The Upper Carboniferous *T. convexa* Kotlyar in Kotlyar & Popeko (1967) from the Shazagaitai Suite of Zabaikal also involves *Ambikella*-like material. The Upper Carboniferous *T. larini* Abramov, 1970 of Verchoyan, east Siberia has well developed plicae, wide sulcus and fold, with sturdy adminicula, no tigillum and subparallel moderately well developed tabellae (Kotlyar & Popeko 1967, Abramov & Grigorieva 1983). The shell size is comparatively small. *T. titovi* Zavodowsky (1970, pl. 18, fig. 1-2) of the Early Permian Burgali Horizon, northeast Siberia, has few moderately strong plicae and short tabellae, strongly suggestive of *Ambikella*, especially *konincki* from east Australia. Ventral valves named *T. kolymaensis* Zavodowsky and *T. popowi* Zavodowsky show moderate adminicula and probably are close, but the dorsal valve was not illustrated. Both also come from Burgali beds.

Unnamed individuals of *Tomioopsis* reported from the younger Permian Bochar Suite of Kolyma-Omolon Massif by Abramov & Grigorieva (1988, p. 30, fig. 7, 8, 11) are of average size with comparatively thick shell and strong plicae, and adminicula and tabellae are of moderate length. Although shell thickening is not great, they would not look out of place in an east Australian collection, the plicae being strong as in *Ingelarella*, the interior obscure as far as the tigillum is concerned, so that subgeneric affinities are obscure. An Early Permian *Tomioopsis* from the Akachan Suite of south Verchoyan shows moderately long tabellae, with only thin shell (Abramov & Grigorieva 1988, pl. 31, fig. 12), but just one dorsal valve is figured.

Tomioopsis ovulum Waterhouse (1971) from Asselian of western Canada also shares some of the attributes, possessing wide low ventral umbo, low or no plicae, moderately long adminicula, no tigillum and comparatively long tabellae, at 0.3 to 0.4 of dorsal valve length. The small *T. petrenkoi* Czarniecki (1969) from Treskelodden beds of Spitsbergen is also close.

Ambikella thus appears to have a subgenus ranging widely over moderately high temperate latitudes of the Arctic and Gondwana in the Late Carboniferous and

Early Permian especially, and possibly persisting into Late Permian in the Himalaya - Salt Range and northeast Siberia.

Tomioopsis (Ambikella?) bamberi n. sp.

1971 *Tomioopsis magna* (not Campbell); Waterhouse, p. 77, pl. 17, fig. 1, 2, 4, 5, 9, 10.

ETYMOLOGY: Named for E. Wayne Bamber.

HOLOTYPE: GSC 24832 figured by Waterhouse (1971, pl. 17, fig. 1, 2, 4, 10), here designated, from Tingmisut Lake, Melville Island, Canada.

DIAGNOSIS: Specimens large, sulcus broad anteriorly, bulges anteriorly, absent from posterior shell, fold wide with low broad median depression, low plicae may be present anteriorly. Adminicula long, subparallel, no tigillum, tabellae long and diverge forward, shell thick posteriorly, taleolate.

DISCUSSION: There does not appear to be any species known from the northern hemisphere that comes close, and the tabellae are unusually long for *Ambikella*, and the ventral shell moderately thick. There is a strong external similarity to the late Cisuralian early Guadalupian species *Tomioopsis (Johndearia) magna* (Campbell, 1961) of east Australia, but the shape is more transverse, internal plates are longer and secondary thickening less, and tigillum not apparent, although thick posterior shell is developed, so that the species does approach *Johndearia* in that respect. The species *magna* is found in the lower Moonlight Sandstone Member with *Pseudostrophalosia blakei* Dear, in the *Etheripecten plicata* Zone of Waterhouse & Jell (1983, pl. 2, fig. 6, 7, 13) in the north Bowen Basin of Queensland. McClung (1978) reported the species in the Sydney Basin from the Wandrawandian and Elderslie beds, which appear a little older. Specimens that show the ventral fold in the sulcus typical of *magna* appear sporadically through the late Cisuralian and Guadalupian of east Australia.

The species *magna* shows considerable approach to *Tomioopsis belfordensis* (McClung 1978, pl. 11, fig. 6-13) from the Belford Formation of the north Sydney Basin. Some of the Belford specimens have subplicae in the sulcus and some show a faint anterior sulcal swelling. There is a dorsal groove and up to 4 pairs of plicae, but most lack plicae. McClung (1978) reported that adminicula extend for no more than a third of the length of the valve, and tabellae to almost one third valve length, but they seem to be nearer a fourth or mostly fifth of the length of internal moulds. Tabellae are close to those of *magna*, especially in larger specimens. The obscure specimen ascribed to *oviformis* (not M'Coy) by McClung (1978, pl. 14, fig. 14) from the Belford Formation is possibly conspecific.

Clarke (1987) in observing that his Tasmanian material ascribed to *magna* showed coarse grooves, claimed that micro-ornament has not been elaborated for other *magna* material, and dismissed the Canadian material now referred to *bamberi* as having abraded shell surface. He omitted to point out that Waterhouse (1971, p. 781) had described surface grooves for the Canadian specimens, 0.3-0.5mm long, spaced 3-4 in 1mm along concentric rows. Clarke provided no measurements or counts for the surface grooves on his *magna*.

Subgenus *Ingelarella* Campbell, 1959

TYPE SPECIES: *Ingelarella angulata* Campbell, 1959.

DIAGNOSIS: Large shells, broad sulcus and wide fold with rounded or grooved crest, lateral shell smooth or moderately to strongly plicate, adminicula and tabellae comparatively long and subparallel, secondary thickening especially marked in ventral posterior and forms a ridge or tigillum along mid-line in front of muscle field.

DISCUSSION: *Ingelarella* is distinguished from *Tomiopsis* (*Tomiopsis*) by having fewer stronger plicae, thicker shell and plates and longer tabellae. It is not clear whether *Tomiopsis* (*Tomiopsis*) has a tigillum or not. *Ingelarella* is distinguished from *T. (Ambikella)* by its generally longer tabellae, thicker shell, and tigillum. The tigillum is well developed in plicate shells such as *angulata*, *globosa* and *oviformis*, regarded as probably synonymous, but is also seen in non-plicate shells such as those referred to *ingelarensis* Campbell. Species regarded as belonging to *Ingelarella* include *undulosa*, *subplicata*, *angulata*, *ingelarensis*, *mantuanensis*, *havigensis*, *costata*, *parallela*, *antesulcata* and *furca* in east Australia and New Zealand. No species from further afield is definitely known to be allied, but *Notospirifer bazardarensis* Grunt, 1993 from the Tashkazyk Formation, of Early Permian age in the Pamirs, has coarse plicae and possibly a tigillum. As well, Upper Permian *Tomiopsis* from Verchoyan described by Abramov & Grigorjeva (1988) might be allied, but are not well known.

Two east Australian species that show comparable internal plates and overall shape, with well formed sulcus and fold, *ovata* Campbell and *profunda* Campbell, are distinguished by the development of slender crescentic elevations behind the surface grooves. Both have a low tigillum and so may have arisen from *Ingelarella* close to *elongata* McClung & Armstrong, which has tigillum and long tabellae. They are distinguished as *Homevalaria* Waterhouse, 1986. Specimens that come close in overall morphology are found widely in east Australia, and have been referred to *ovata*, but the nature of micro-ornament and interior are generally not established. Late Permian ventral valves found in the Hilton Limestone Formation of New Zealand could prove to be allied, but micro-ornament and dorsal valve are not preserved.

***Tomiopsis (Ingelarella) paraplana* new name**

not 1959 *Tomiopsis plicata plana* Sokolskaya, p. 62, pl. 3, fig. 2-4.

1960 *Ingelarella plana* Campbell, p. 1112, pl. 136, fig. 1-7.

1982 *Tomiopsis plana* (Campbell not Sokolskaya); Waterhouse, p. 116.

1983 *T. plana* (Campbell not Sokolskaya); Waterhouse, p. 159, pl. 2, fig. 10, pl. 3, fig. 1-4.

HOLOTYPE: UQF 15686, figured by Campbell (1960, pl. 136, fig. 6a-c) from Cattle Creek, 2 miles from junction with Consuelo Creek, Cattle Creek Formation, south-west Bowen Basin, Queensland.

DESCRIPTION: The species has been described as *plana* by Campbell (1960) and Waterhouse (1983). Internal plates are comparatively short, secondary thickening is moderate, and a tigillum is developed.

DISCUSSION: The name *plana* allocated by Campbell to an Australian species now regarded as *Tomiopsis* is a homonym for a subspecies proposed earlier by Sokolskaya. The name is therefore changed. In my opinion, the Cattle Creek species is probably conspecific with more plicate specimens named as *Ingelarella plica* Campbell, 1960 from the same locality. Internal plates are much the same on both forms, but the two differ externally in the degree of plication and the nature of the dorsal fold. *Ingelarella*

sulcata Waterhouse, 1964 from Brunel Formation, Takitimu Group, New Zealand, is allied, and shows a very strong tigillum, and rather steep walls for the fold.

***Tomioopsis (Ingelarella) undulosa* (Campbell, 1961)**

1961 *Ingelarella undulosa* Campbell, p. 180, pl. 26, fig. 4-9.

?1968 *Ambikella confusa* not Waterhouse; Waterhouse, p. 60, pl. 10, fig. 7, pl. 14, fig. 9, pl. 15, fig. 7 (not pl. 10, fig. 9-12, pl. 15, fig. 3, pl. 18, fig. 1, text-fig. 7B = *confusa*).

1968 *Ambikella cf. undulosa* (Campbell); Wass & Gould, pl. 15, fig. 17.

1975 *Martiniopsis undulosa* (Campbell); Runnegar & McClung, pl. 31.1, fig. 28, 29.

1978 *Ingelarella undulosa* Campbell; McClung, p. 47, pl. 8, fig. 1-3, 7.

1978 *Ingelarella* sp. nov. A McClung, p. 50, pl. 8, fig. 4-6.

1978 *Ingelarella cessenockensis* McClung, p. 49, pl. 2, fig. 10, 11, pl. 10, fig. 4-15, 18, 19.

1988 *Ingelarella undulosa* Campbell; McLoughlin, pl. 1, fig. 1.

HOLOTYPE: UNE F 5840, figured by Campbell (1961, pl. 26, fig. 8) OD from lowest of 3 *Tomioopsis* beds about 5km SSW of Homevale Homestead, north Bowen Basin, Queensland. Holotype of *cessenockensis*: specimen UNE F 12504 figured by McClung (1978, pl. 10, fig. 7, 8) OD from Elderslie Formation, Sydney Basin, New South Wales. DIAGNOSIS: Large shells with shallow sulcus, groove-like posteriorly, fold broad, lateral slopes generally not plicate, adminicula generally moderate in length and well to moderately spaced, tabellae long.

MATERIAL: Six specimens from GS 6070 (D44/19621) as described in Waterhouse (1968), Wairaki Downs, New Zealand. Six ventral valves, two dorsal valves and one specimen with valves conjoined preserved as internal moulds from UQ L 3762, 60km south of Springsure, Freitag Formation, southwest Bowen Basin, Queensland.

DESCRIPTION: Specimens from Freitag Formation moderately large, sulcus broad and shallow, fold low with rounded crest, no or very faint lateral plicae. Adminicula little more than 0.25 length of internal mould, variable in spacing, sited close together or far apart, subparallel, tigillum low and long. Tabellae about 0.3 length of dorsal mould, diverging, only moderately close-set. Secondary thickening considerable in ventral valve.

RESEMBLANCES: The species *undulosa* was described by Campbell (1961) from siltstone probably below Moonlight Sandstone Member of north Bowen Basin.

A suite of well preserved specimens from the Freitag Formation of southwest Bowen Basin endorses the identification of that species from the Freitag by McLoughlin (1988). A well preserved ventral valve UQF 65495 shows that the posterior external umbonal region has a narrow groove that continues well forward. Such a feature is not immediately apparent in the Campbell material, because figured ventral valves are internal moulds, but a narrow median external groove could be present. The tigillum is shown in one specimen (Campbell 1961, pl. 26, fig. 4b). The groove persists well forward in very large *undulosa* from the Freitag Formation, and a low tigillum is present. Posterior thickening is substantial, and the plates in front relatively short.

The ventral groove is close to that seen in *Tomioopsis ingelarensis confusa* (Waterhouse), which is very close otherwise to *T. ingelarensis* (Campbell), but the *ingelarensis* suite is distinguished from *undulosa* by its different fold, sulcus and spac-

ing of internal plates. *T. ingelarensis confusa* (Waterhouse) is based on material from the *Echinalosia maxwelli* Zone in the lower Mangarewa Formation, Wairaki Downs, and closely allied material has been described from the same zone in the Otrack Formation of the southeast Bowen Basin, Queensland, by Waterhouse (1987a, pl. 9, fig. 4-7, 9, 12). Compared with type *confusa*, *undulosa* specimens are moderately transverse, with a wide sulcus. The dorsal fold is low, broad and gently rounded, but is more prominent than in *confusa*. Adminicula lie further apart and are relatively shorter than in *confusa*, and tabellae are shorter and subparallel.

Specimens were also reported as *confusa* from the Letham Formation, Wairaki Downs, at GS 6070 (D44/f9621) by Waterhouse (1968). Additional Letham specimens, restricted to ventral valves, are also available for study. Compared to *Tomioopsis (Ingelarella) ingelarensis* and *T. (l.) ingelarensis confusa*, they tend to be transverse, rather than weakly transverse to elongate as in the types of *confusa*, and have wider ventral muscle field, and deeper exopunctae posteriorly, compared with type *confusa*. Adminicula are more parallel than in type *confusa* in small specimens, but in larger ones, lie further apart and diverge a little more. No dorsal valves are known from the additional Letham collections. The small size of the specimens, and the lack of information about the dorsal valve means that the identity of the Letham suite is difficult to determine with full security. But the additional information about the nature of *undulosa* enables the Letham specimens to be regarded as possible small specimens of this species. No other small specimens show such a close approach.

Tomioopsis cessenockensis McClung, 1978 is found throughout the Elderslie Formation, Sydney Basin, overlapping *brevis* in its range. It shows many similarities to *undulosa*, including wide shallow sulcus and wide often low dorsal fold. Internal plates are apparently moderately short, although this is partly because they have been buried in substantial secondary thickening. The principal difference from type *undulosa* lies in the marginally more closely spaced and slightly shorter adminicula. Arguably *cessenockensis* might be regarded as a subspecies of *undulosa*, especially if it is deemed desirable to enforce a stratigraphic separation between *brevis* and *undulosa*, but objectively and practically in terms of species delineation, it should be regarded as a full and junior synonym. The difference in placement of adminicula may be a variant, because such differences have also been observed amongst collections of *ingelarensis* and *mantuanensis*. In the Freitag Formation, there is a mixture of specimens, some resembling *cessenockensis*, others like typical *undulosa*. Similar overlap occurs in the upper Elderslie Formation, according to McClung (1978).

A ventral valve was figured as *undulosa* from south Marulan, New South Wales, by Wass & Gould (1968), and looks moderately close. The age was not precisely determined, but was judged to be equivalent to upper Branxton Formation or lower Nowra Sandstone of the Sydney Basin. McClung (1978) described the species from the upper Elderslie Formation, north Sydney Basin, and reported it from the Wandrawandian Formation, south Sydney Basin. *Ingelarella* n. sp. A of McClung (1978, pl. 8, fig. 4-6) comes from upper Elderslie Formation, and differs from *undulosa* only in having slightly shorter internal plates and thinner shell. Specimens figured from the Eight Mile and Tunnel Blocks south of Warwick, south Queensland, described as

Martiniopsis (Ambikella) ingelarensis by Dickins (1981, p. 31, pl. 4, fig. 20-24, pl. 5, fig. 1-17) are moderately close to *undulosa*.

STRATIGRAPHY: The Freitag Formation is a unit of medium to coarse sandstone below the Ingelara Formation, and its fauna has generally been lumped with the Ingelara fauna. McClung (1978) referred the upper Freitag to the *isbelli* Zone, and later (1981) referred the entire formation to the *isbelli* Zone, but *isbelli* has never been described from either the Freitag or Ingelara Formation. The present study shows that at least in one area, part of the formation is distinctly older, and is to be matched in *Tomiopsis* terms with the *undulosa* rather than *ingelarensis* or the *isbelli* level, confirming the proposal by McLoughlin (1988). Freitag *Wyndhamia* and *Paucispinauria* species differ from Productidan species found with *isbelli* and a similar *Wyndhamia* occurs at GS 6070 in the lower Letham Formation, Wairaki Downs. Runnegar & McClung (1975) recognized an *undulosa* Zone as following the *brevis* Zone, and succeeded by the *isbelli* Zone, the succession said to be well exemplified in Tasmania, but where it is so far unverified by systematic study. The species *brevis* is nowhere known in the Bowen Basin.

***Tomiopsis (Ingelarella) subplicata* (Waterhouse, 1968)**

1968 *Ambikella dissimilis subplicata* Waterhouse, p. 69, pl. 12, fig. 7, 9, 10, pl. 13, fig. 1, 2, 4, 7, text-fig. 2A.

cf. 1978 *I. cf. costata* not Waterhouse; McClung, p. 54, pl. 14, fig. 4-13.

cf. 1978 *I. oviformis* (not M'Coy); McClung, p. 42, pl. 4, fig. 15, 16 (not pl. 15, fig. 1-6 = *oviformis* M'Coy, pl. 14, fig. 14 = *magna* Campbell).

HOLOTYPE: BR 1357, GS 9697 (D44/f9001) OD from *Lethamia ligurritus* Subzone, upper *Echinalosia discinia* Zone, Letham Formation, Wairaki Downs.

DIAGNOSIS: Medium-sized shells with sulcate fold, 2 subplicae in sulcus, 3-4 pairs of lateral plicae. Adminicula and tabellae 0.3 or more of valve length and only moderately spaced.

MATERIAL: Individual specimens with valves conjoined valves from D44 at f326, f307, f308, f315, f312, and possibly f321, lower *Echinalosia discinia* Zone, 4 specimens with valves conjoined and 3 ventral valves from f109 (GS 15208 - BR 2360-2362), individual specimens from f108 (GS 15207), and possibly f331, *Lethamia ligurritus* Subzone, *Echinalosia discinia* Zone, Letham Formation, Wairaki Downs, New Zealand.

DIMENSIONS IN MM: Internal moulds from D44/f109

Width	Length		Height both	Adminicula		Tabellae	
	Ventral	Dorsal		L	apart	L	apart
24	19	18	8	10	4.5	6	2
24	23	19	10	8	4.5	7.5	4
38			23	16.5	5.5	8	4
45	+29	19	11	6	8	5	

DESCRIPTION: Specimens small, moderately inflated, ventral beak incurved, moderately prominent, umbonal angle 90-110°, interarea high, concave. Dorsal valve less

inflated, dorsal umbo very broad, interarea low. Ventral sulcus well formed, widens at 35-40° in internal mould, well developed pair of subplicae commencing within sulcus about 10mm from umbonal tip. Fold high and wide, with posterior depression, fold may lose median depression anteriorly. Ventral plicae in 3-4 pairs, dorsal plicae in 4 well defined pairs. Micro-ornament of short elongate grooves.

Dental plates high, supported by subvertical adminicula, ventral adductor scars narrow, diductor scars wide with strong oblique grooves, tigillum well developed. Cru-ral plates low and diverge widely, supported by subvertical tabellae, extending for less than 0.3-0.35 of valve length.

DISCUSSION: These Letham Formation specimens are identified with *subplicata* Waterhouse, here raised to full species status. As noted by Waterhouse (1968), the species differs from *dissimilis* Waterhouse, 1964 in the shell shape, length and spacing of adminicula and tabellae, and lack of substantial posterior thickening in the ventral valve.

Specimens figured as *Ingelarella oviformis* by McClung (1978) from the Fenestella Shale, north Sydney Basin, are close to *subplicata* in appearance, including sulcus, fold and internal plates, although there are suggestions of a fifth pair of plicae on the ventral valve, which is unusual. So-called *I. cf. costata* (not Waterhouse) of McClung (1978) from the same beds are larger specimens with thickened shell, very close externally, and of greater maturity and size than type *subplicata*, insofar as they can be interpreted from internal moulds. The similarity to *costata* Waterhouse is judged to be superficial. Specimens that lack plicae were figured from the same beds by McClung (1978, pl. 10, fig. 16, 17, pl. 11, fig. 1-5) as *I. ingelarensis* Campbell.

The New Zealand specimens of *subplicata* are close to *Tomioopsis (Ingelarella) angulata* (Campbell, 1959), but the posterior walls diverge less. An additional pair of plicae is often visible on *angulata*. The ventral muscle field is more emphasized than in Campbell's species, with different diductor and adductor scars. The adminicula and tabellae are distinctly shorter in *angulata*, generally extending for about 0.2-0.25 of valve length, although a few individuals have longer plates. The type species *Ingelarella angulata* comes from the Ingelara Formation, ranging into the lower Peawaddy Formation (Campbell 1953, 1959) of southwest Bowen Basin, and ranges into the Barfield Formation of southeast Bowen Basin (Parfrey 1988, Waterhouse 1987a). Specimens were compared to *angulata* from the Muree Formation of the north Sydney Basin by McClung (1978, pl. 15, fig. 7-14). These are accompanied by *oviformis* M'Coy, 1847 (McClung 1978, pl. 15, fig. 5, 6 and Mt Vincent - fig. 2-5), and the two suites appear to be separated on size, with smaller specimens allocated to *angulata*. Not only are his specimens probably *oviformis*, but there must be the strong possibility that *angulata* itself is a junior synonym of *oviformis*. Specimens of *oviformis* are also recorded from an unspecified part of the Belford Formation by McClung (1978, pl. 15, fig. 1). Older specimens referred to *angulata* by McClung (1978, pl. 14, fig. 15-16) from the Belford Formation and Fenestella Shale are not *angulata*, but *subplicata* Waterhouse. As well, *globosa* Campbell, 1961 from the Barfield Formation, southeast Bowen Basin, is conspecific with *angulata* according to Waterhouse (1987a). Thus a substantial array of individuals is now known for the corpus. In the

Bowen Basin, *angulata* and *globosa* occur with *Pseudostrophalosia ingelarensis*, possibly ranging into lower *Echinalosia ovalis* beds in the poorly dated lower Peawaddy Formation. In the Sydney Basin, *oviformis* is found chiefly in what are said to be *ovalis* equivalents, but ranges lower into the Belford Formation, under poor age control.

The suggestion by Waterhouse (1987a) that *Tomioopsis globosa* (Campbell) was a junior synonym of *T. angulata* was not accepted by Parfrey (1988), who stated that the plicae were deep in *globosa*. Both taxa show a comparable distribution of plicae, subplicae, and sulcate fold, and allocating specific significance to this degree of difference may not be warranted. Parfrey also stated that the tabellae bend inwards at the anterior end in *globosa*. This is not yet demonstrated to be consistent, the tabellae in suites of *angulata* figured by McClung (1978, pl. 1) also suggesting an anterior straightening, or weak convergence. There is little doubt that the *Tomioopsis* plexus of species requires further analysis for lateral and vertical variation, and it appears probable that some species will be found to be extreme or even modest variants of previously named forms. The species *globosa* appears to offer one example.

The relationship of these plicate shells assigned to *subplicata* and *angulata* to *Tomioopsis ingelarensis* stock remains an open question. McClung (1978) has demonstrated that *ingelarensis* appears to grade into *angulata*, although it is true that *angulata* at maturity is generally somewhat smaller, and the ventral umbo is broader and projects less posteriorly, and posterior walls extend less laterally. Possibly the width of the two would be closer if allowing for the plication. Specimens that are close to *subplicata* in the Fenestella Shales are accompanied by non-plicate specimens that are close in internal plates, although the fold may be a little narrower. These were referred to *ingelarensis* Campbell by McClung (1978, pl. 10, fig. 16, 17, pl. 11, fig. 1-5). The species *subplicata* is like *ingelarensis* in having a broad ventral umbo and long posterior ventral walls. Whether it should be regarded as a plicate *ingelarensis*, or whether the Fenestella Shale and Wandrawandian non-plicate specimens should be regarded as non-plicate *subplicata* requires further study: I have no material to hand and McClung figured only internal moulds, making full study difficult. In the meantime, *ingelarensis* is treated as a long-ranging species that persisted through the *subplicata*, *ingelarensis confusus* and *angulata* levels.

There is some approach to *Notospirifer bazardarensis* Grunt (1993) from the Early Permian Tashkazyk Formation of the Pamirs, a plicate form with well spaced ventral adminicula, short tabellae, and sinus in the dorsal fold. This was initially identified as *Ingelarella*, then later referred to *Notospirifer* because of the absence of a dorsal medium septum - a somewhat baffling interpretation. The external micro-ornament consists of long shallow surface grooves, as in *Ingelarella* and *Tomioopsis*.

***Tomioopsis (Ingelarella) havilensis* (Campbell, 1960)**

1960 *Ingelarella havilensis* Campbell, p. 1120, pl. 139, fig. 3-6.

1965 *I. ingelarensis* not Campbell; Waterhouse & Vella, p. 68, pl. 4, fig. 1, 4 (not fig. 2, 3, 5, ?6 = *pelicanensis*).

1965 *I. dissimilis* not Waterhouse; Waterhouse & Vella, p. 69, pl. 5, fig. 2.

1969 (not named) Waterhouse, text-fig. 5.

1982 *Tomioopsis ingelarensis* (not Campbell); Waterhouse, p. 56, pl. 23, fig. e, j.

1983 *Martiniopsis havilensis* (Campbell); Dickins, text-fig. 3A-F.

1989 *Martiniopsis havilensis* (Campbell); Dickins, p. 76, pl. 4, fig. 15-17, pl. 5, fig. 1-4, ?5, 12-14 (not pl. 4, fig. 8-14 = *costata* (Waterhouse), not pl. 5, fig. 6-11 = aff. *costata*).

1996 *Tomioopsis havilensis* (Campbell); Waterhouse, p. 44.

1998 *T. mantuanensis* (not Campbell); Campbell et al., p. 77.

This species is possibly present at D44, f339, and is visible in coarse sandstone of the topmost Mangarewa unit (*Terrakea elongata* Zone) just below limestone on the south side of a tiny creek north of the last major east tributary of Letham Burn, Wairaki Downs.

The distinctive species *havilensis* is recognized in the Middle Permian Flowers Formation of northwest Nelson. It is characterized by broad ventral sulcus bearing a median groove and well developed tigillum. The moderately short moderately spaced adminicula approach those of *ingelarensis*, but this species has a different sulcus. Shells are laterally smooth or plicate. As recognized by Dickins (1983), the species *havilensis* characterizes the topmost marine invertebrate faunas of the Bowen Basin. It is not known in New South Wales, nor in Tasmania (Waterhouse 1996). In the northern Bowen Basin, the species *havilensis* follows *pelicanensis* (Dear 1972), but in the Flowers Formation of northwest Nelson, the two species seem to occur together. Dickins (1989) assigned to *havilensis* specimens from the Black Alley Shale (Dickins 1989, pl. 4, fig. 15) and MacMillan Formation (Dickins 1989, pl. 4, fig. 16, 17, pl. 5, fig. 3, 4). One specimen is a little closer to *pelicanensis* (Dickins 1989, pl. 5, fig. 5). Specimens from the upper Blenheim Subgroup at Parrot Creek, north Bowen Basin, appear moderately similar to *havilensis* (Dickins 1989, pl. 5, fig. 12, 13). As well, detail of surface ornament on another specimen was figured by Dickins (1989, pl. 5, fig. 14), presumably belonging to the species.

Dickins (1989, p. 77) commented on some approach by *havilensis* to *Martiniopsis woodi* Waterhouse from the AG4 limestone block near Artherton. None of the shells figured by Dickins (1989) confirm his claim, and no *M. woodi* specimens carry the characteristic ventral furrow, heavy posterior thickening, or tigillum characteristic of *havilensis*. Conceivably the species *havilensis* might have undergone numerous changes into *woodi*, but against this is the similarity between *woodi* and Salt Range *M. inflata* Waagen, implying origin from further afield. A New Zealand species that is much closer to *havilensis* is *Ambikella* (now *Tomioopsis*) *furca* Waterhouse (1967b, fig. 34-36, 37, 39), evidently a descendent species found in a carbonate lens at Wairoa Gorge in the lower Te Mokai Group of east Nelson.

***Tomioopsis (Ingelarella) costata* (Waterhouse, 1964)**

1964 *Ingelarella costata* Waterhouse, p. 159, pl. 31, fig. 6, 9-15, pl. 32, fig. 1-3, pl. 35, fig. 2, 3, text-fig. 75, 76.

1968 *Ambikella costata* (Waterhouse); Waterhouse, p. 67, pl. 12, fig. 2-5, 11.

1989 *Martiniopsis havilensis* (not Campbell); Dickins, p. 54, pl. 4, fig. 8-14, aff. pl. 5, fig. 6-11 (not pl. 4, fig. 15-17, pl. 5, fig. 1-4, 5?, 12-14 = *havilensis*).

HOLOTYPE: BR 613, figured by Waterhouse (1964, pl. 31, fig. 6, 11, 13, 15, pl. 35, fig. 2, 3) OD from upper Mangarewa Formation, Wairaki Downs, New Zealand.

DIAGNOSIS: Moderately inflated shells with incurved ventral beak, wide sulcus that may bear costa, as well as two sulcal subplicae and deep median groove, well formed tigillum. Plicae high, gently rounded, curving outward, surface grooves long. Dental plates low, adminicula moderately long, dorsal tabellae moderately short, well-spaced. DISCUSSION: Dickins (1989, pl. 4, 5) has figured an interesting suite of specimens from the upper Blenheim Subgroup of the Bowen Basin. Several look to be very close to *Martiniopsis havilensis* (Campbell), as determined by Dickins. But some of the specimens are strongly plicate and look like *Tomiopsis costata* (Waterhouse). They show the tigillum which is a feature of both *havilensis* and *costata*. Although the types of the two species, and indeed entire suites of *havilensis* and *costata* look very different, one being non-plicate, the other strongly plicate, specimens from the upper Blenheim Subgroup figured by Dickins (1989) suggest that the two may represent bimodal extremes of one variable form. The plicate specimens figured by Dickins (1989) include several from the Tay Glen Crossing, just below the MacMillan Formation (pl. 4, fig. 8-14).

Specimens from the Exmoor Formation figured as *Martiniopsis havilensis* (not Campbell) by Dickins (1989, p. 77, pl. 5, fig. 6-11) from the north Bowen Basin are worn, with 3 pair of plicae, low umbones and narrow sulcus. Other than being rather transverse, they look moderately close to *costata*, but are poorly preserved and their specific affinities obscure. The species *Tomiopsis angulata* (Campbell, 1959) from the Ingelara Formation is also close but has wider deeper sulcus and higher umbones with less widely diverging ventral posterior walls.

The internal moulds from the Fenestella Shale and lowest Belford Formation that were compared with *costata* by McClung (1978, p. 54, pl. 14, fig. 4-13) do not appear to belong to *Tomiopsis costata*. They show stronger ventral posterior thickening, less pronounced outer plicae, and different much wider sulcus and fold. Only internal moulds were figured, causing difficulty in determining the species, but the specimens suggest large and fully mature individuals with thick shell, close to *subplicata* Waterhouse.

Subgenus *Johndearia* n. subgen.

ETYMOLOGY: Named for the late John Dear, Queensland geologist. John produced an outstanding study of Bowen Basin Permian Productida, and an overview of Bowen Basin stratigraphy, before moving into consulting geology.

TYPE SPECIES: *Ingelarella isbelli* Campbell, 1961.

DIAGNOSIS: Large specimens with secondary thickening marked in ventral valve, also strong in dorsal valve of some species, valves tend to be weakly or non-plicate, and sulcus and fold may be subdued. Internal plates usually appear well spaced and short, as largely buried in secondary thickening, tigillum present.

DISCUSSION: Species of the subgenus range from upper Cisuralian into Lopingian in east Australia and New Zealand. The oldest known species *brevis* Armstrong & McClung presumably arose from *plica-paraplana* or perhaps *sulcata* stock, in so far as *brevis* shows comparatively well spaced and not very long internal plates, and a tigillum is developed, in some specimens high just in front of the muscle field. The species *brevis* shows the steep walls of the fold seen in *sulcata*.

***Tomioopsis (Johndearia) sp. aff brevis?* (McClung & Armstrong, 1975)**

1964 *Ingelarella* sp. A Waterhouse, p. 157, pl. 31, fig. 4, 5.

Specimen BR 830 from GS 6070 (D44/f9621), lower Letham Formation, Wairaki Downs, New Zealand, is transverse, with prominent dorsal fold showing steep lateral walls, slightly sulcate anteriorly, well defined sulcus with weak subplicae, and low plicae laterally. Tabellae are of moderate length ca. 0.25 of dorsal valve, well spaced, and diverge anteriorly.

There is a measure of similarity of this specimen to unusual specimens amongst the suite described as *Martiniopsis brevis* McClung & Armstrong, 1975 as reviewed by McClung (1978). The low and steep flanks of the dorsal fold, particularly characteristic of *brevis*, are also shown by the Letham specimen. Several individuals show comparable dorsal fold and plicae (McClung 1978, pl. 5, fig. 3, 6, pl. 6, fig. 3, 4, 6, pl. 7, fig. 2, 11, 13). Internally, the tabellae of most specimens of *brevis* are distinctive, being characteristically short and widely diverging, unlike those of the Letham specimen. But there are a number of associated individuals with longer, less widely diverging tabellae, such as those figured by McClung (1978, pl. 6, fig. 3, pl. 7, fig. 2, 11). This opens the possibility that the Letham specimen is a rare form of *brevis*, but more material is required to explore that possibility. The species *brevis* characterizes a level low in the Maitland Group, Sydney Basin (Runnegar & McClung 1975), and is reported from the Elderslie Formation, lower Fenestella Shale, Snapper Point Formation and lower Wandrawandian Siltstone. It is listed from Tasmania, but has not been found in the Bowen Basin.

***Tomioopsis (Johndearia) dissimilis* (Waterhouse, 1964)**

1964 *Ingelarella dissimilis* Waterhouse, p. 162, pl. 32, fig. 4-8, 10, 11, pl. 35, fig. 6.

1978 *Ingelarella singletonensis* McClung, p. 54, pl. 2, fig. 12, 13, pl. 13, fig. 13, 14, pl. 14, fig. 1-3.

1978 *I. warneri* McClung, p. 52, pl. 13, fig. 1-10.

1987a *Tomioopsis dissimilis* (Waterhouse); Waterhouse, p. 36, pl. 10, fig. 5-9, 11-13, pl. 11, fig. 1.

HOLOTYPE: BR 836 figured by Waterhouse (1964, pl. 32, fig. 4, 5, 7, 8) OD unit 3 in Mangarewa Formation (lower *Echinalosia ovalis* Zone), Wairaki Downs. Holotype for *singletonensis*, UNE F14132, McClung (1978, pl. 14, fig. 1, 2) OD from Mulbring Formation, Sydney Basin; for *warneri* UNE F12343, McClung (1978, pl. 13, fig. 2, 5,) from Bickham Formation, Sydney Basin.

In Wairaki Downs, this species was described first from GS 7352 (D44/f9870), which falls at the top of unit 3 in the middle Mangarewa Formation, lower *Echinalosia ovalis* Zone. Rare specimens from D44/f111 (GS 15227) are possibly conspecific. Additional D44 material comes from a younger part of the zone in Mangarewa unit 4 at GS 3616 (f9870), f121? (GS 15217) and f318.

Initially, on the basis of a few specimens, the species was thought to be characterized by its transverse shell with low umbones, weakly plicate or smooth and sulcate ventral valve, and more plicate dorsal valve, and wide dorsal fold. The adminicula are short and spaced far apart, and the tabellae are also short and well spaced. To these diagnostic features should be added the substantial posterior sec-

ondary thickening in the ventral valve and presence of low tigillum.

In essential external and internal detail, *Ingelarella singletonensis* McClung, 1978 from the Mulbring Formation, Sydney Basin, appears to be conspecific. The differences in size and other criteria are deemed simply individual and geographic. Overall age is much the same, though type *dissimilis* enters the succession a little earlier in New Zealand and persists upward to match the limited range in the Sydney Basin.

Another suite of specimens is not quite so close, being smaller, with very heavy secondary thickening in the ventral valve, and reduced ventral muscle field and rather low and often short tigillum. These were called *Ingelarella warneri* by McClung (1978, p. 52, pl. 13, fig. 1-10). The short plates and generally transverse shape with broad shallow sulcus and moderately defined fold, with low plicae in some specimens, strongly suggest an alliance to *Tomioopsis dissimilis* stock, and they may at best be regarded as a subspecies. They are found in the Porcupine Formation and also Bickham Formation of the Murrurundi - Gunnedah area of the north Sydney Basin. The Porcupine Formation is approximately correlative with the Muree Formation, according to McClung.

Specimens from the lower Flat Top Formation of the southeast Bowen Basin were assigned to *dissimilis* by Waterhouse (1987a). Some of these agree closely with the New Zealand specimens in external transverse shape, adminicula and tabellae. Others are notably elongate. They are further typified by very heavy thickening along the internal ventral posterior (eg. Waterhouse 1987a, pl. 10, fig. 7, 8, 12), with low broad rounded tigillum in some specimens. These strongly approach the species *Ingelarella isbelli* Campbell (1961, pl. 25, fig. 1-5) from the Moonlight Sandstone Member and lower Blenheim Formation of the north Bowen Basin. Typically, individuals of Campbell's species are subrounded to elongate, with wide sulcus bearing subplicae, and prominent usually rounded fold. Lateral plicae are generally absent, or very low. Within the ventral valve, secondary thickening is very heavy along the hinge, and adminicula are short and well spaced, and the tigillum is of moderate length and comparatively well developed. Although the types of *T. dissimilis* are more transverse, with low plicae and inconspicuous subplicae in the ventral sulcus, and sulcate dorsal fold, they do share the heavy posterior ventral thickening, and short well spaced adminicula. The specimens examined from the lower Flat Top Formation by Waterhouse (1987a) strongly suggest that the *dissimilis* suite ranges from elongate, non-plicate specimens to transverse more plicate specimens, all with posterior ventral thickening, and short well spaced adminicula. It may therefore appear that *dissimilis* Waterhouse, 1964 should be synonymized with *isbelli* Campbell, 1961. However the two overlap at the extremes, in some, but not all features. No dorsal valves so far assigned to *dissimilis* show much secondary posterior thickening, and the tabellae are short, well spaced, and straight in outline, diverging forward. By contrast, dorsal valves in material so far assigned to *isbelli* carry substantial secondary thickening posteriorly, and the tabellae, although short and well spaced, are typically curved in outline, as emphasized by McClung (1978), and generally converge anteriorly. This very characteristic feature has not been observed in any of the New Zealand or

Flat Top specimens. Therefore the two are left distinct, but may be regarded as possibly related, certainly at superspecies level, and possibly contemporaneous.

The species *isbelli* was originally described from the lower Blenheim Formation, and Moonlight Sandstone Member of the north Bowen Basin (Campbell 1961, Dear 1972, Runnegar & McClung 1973, Waterhouse & Jell 1983), and from Tasmania by Clarke (1987). McClung (1978) reported the species from the Belford and Muree Formations of the north Sydney Basin, and various other levels, not all sustainable. McClung (1978, p. 42) suggested that one specimen of Morris (1845, pl. 16, fig. 3) from New South Wales or Tasmania, locality and stratigraphic level not known, belongs to *isbelli*. A prime question concerns the particular species of *Terrakea*, *Echinalosia* or *Wyndhamia* to be found with *isbelli*. According to Runnegar & McClung (1975, table 31.2) the *isbelli* Zone is accompanied by *Wyndhamia preovalis*, *minima*, *enorme*, *jukesi-dalwoodensis*, *Terrakea dickinsi* and *T. brachythaera-solida*, an absurd range of species, with not one accurately identified. Dear (1972, p. 10) listed *isbelli* with *Pseudostrophalosia blakei*, *Terrakea elongata exmoorensis* and *Tomioopsis magna* as helping to typify his Exmoor fauna. Waterhouse & Jell (1983, table 8, p. 243) largely confirmed this, listing and figuring rare *Tomioopsis isbelli* with *Ps. ingelarensis* (~*blakei*) and *Terrakea exmoorensis*, also found with *T. magna*, in a *Ps. ingelarensis* (now *blakei*) faunal assemblage in the upper Moonlight Sandstone Member, or Exmoor fauna of Dear (1972). This association thus appears to be valid for the Bowen Basin.

The range of *dissimilis* differs a little in different regions. It first appears in basal Flat Top Formation, in the topmost *Pseudostrophalosia blakei* Zone, certainly here overlapping *isbelli* in range. In New Zealand it appeared first in the overlying *Echinalosia ovalis* Zone, and persisted, rarely, throughout the duration of that zone. In the Sydney Basin, it appears to be represented as *warneri* in the early supposed equivalents of the *ovalis* Zone in the Porcupine Formation (Gunnedah region), and is found in higher supposed equivalents of this zone in the Mulbring Formation of the Hunter Valley. Still further south, according to Clarke (1987), *isbelli* is found in the *Echinalosia ovalis* Zone of Malbina E Formation.

The specimen figured as *Ingelarella dissimilis* by Waterhouse & Vella (1965, pl. 5, fig. 2, Waterhouse 1969, text-fig. 1) from the Flowers Formation, west Nelson, New Zealand, is reassessed as being different from *dissimilis*. It shows considerable approach in transverse shape, plication, subplication, grooved sulcus and moderately short, moderately spaced admicula to specimens from the top of the German Creek Coal Measures and topmost Blenheim Group in the north Bowen Basin, identified by Dickins (1983, text-fig. 3 C, E) with *Martiniopsis* (now *Tomioopsis*) *havlensis*. *Tomioopsis (Johndearia) pelicanensis* (Campbell, 1960)

1960 *Ingelarella pelicanensis* Campbell, p. 1119, pl. 135, fig. 4-5, pl. 140, fig. 5. (See Taxonomy).

1964 *I. pelicanensis*? Campbell; Waterhouse, p. 165, pl. 32, fig. 12, 14, 16, pl. 33, fig. 2.

1964 *I. pelicanensis* Campbell; Hill & Woods, pl. P9, fig. 1, 2.

1965 *I. ingelarensis* not Campbell; Waterhouse & Vella, p. 68, pl. 4, fig. 2, 3, 5, 76 (not pl. 4, fig. 1, 4 = *havlensis*).

1972 *I. pelicanensis* Campbell; Hill et al., pl. P9, fig. 1, 2.

1998 *Tomiopsis ingelarensis* (not Campbell); Campbell et al., p. 77.

DISCUSSION: Northwest Nelson specimens assigned to *Ingelarella ingelarensis* by Waterhouse & Vella (1965) must be re-evaluated. They show the short well-spaced adminicula and overall shape typical of *Tomiopsis pelicanensis* from the upper Blenheim Formation of north Bowen Basin, Queensland, and upper Mangarewa Formation of New Zealand (Waterhouse 1964).

TAXONOMY: In the text Campbell (1960) inadvertently used the generic name *Homevalia* for *pelicanensis* instead of *Ingelarella*, correctly used in the caption. This was an oversight, and originated from an earlier intention to name the genus after material from near Homevale station. Fire at the university department destroyed his material, so he had to substitute specimens from the extended Ingelara Formation (Prof. K. S. W. Campbell, pers. comm.). To commemorate his original intention, I used the name *Homevalaria* for Homevale material (Waterhouse 1986) for species that differ slightly from *Ingelarella* and *Tomiopsis* in having low arcuate spines at the posterior end of surface grooves.

***Tomiopsis (Johndearia) isbelliformis* Waterhouse, 1978**

1978 *Tomiopsis isbelliformis* Waterhouse in Waterhouse & Mutch, p. 522, text-fig. 12-15, 17, 18.

HOLOTYPE: BR 2231, figured by Waterhouse (1978, text-fig. 14) OD from Hilton Limestone Formation, Wether Hill Station, Southland.

DIAGNOSIS: Transverse shells with wide shallow sulcus and short well spaced adminicula; dorsal valve with low fold and plicae.

MATERIAL: Seven ventral valves from D44/f376, Hilton Limestone Formation, Coral Bluff, Wairaki Downs.

DESCRIPTION: Specimens small and not well preserved. Shell transverse, with broad umbo not extended far posteriorly, umbonal angle over 120°, hinge wide, cardinal extremities rounded. Sulcus shallow, apparently commences a little in front of umbo, floor moderately broad, without groove or subplicae, no lateral plicae. Micro-ornament not preserved. Adminicula short, well spaced, diverging at 40° approximately, supporting high probably short dental plates. Muscle field wide, myophragm posteriorly in some specimens, two adductor ridges in one small specimen, but adductors poorly distinguished in larger shells. Substantial secondary thickening developed near hinge each side of adminicula.

RESEMBLANCES: These specimens show the transverse little inflated outline, shallow broad simple ventral sulcus, and short well spaced adminicula that characterize *Tomiopsis isbelliformis* Waterhouse from the Hilton Limestone Formation in the "Nemo" block of Wether Hill Station. The species is a distinctive one. Present material differs a little in being smaller, with slightly variable muscle field, and slightly variable sulcus in different specimens.

DISCUSSION: This Late Permian species shares the short well spaced plates and negligible sulcus of *Johndearia*, but is not typical, in that a tigillum is not perceptible, and secondary thickening is considerable but not great.

Subgenus *Geothomasia* n. gen.

ETYMOLOGY: Named for George A. Thomas, brachiopod specialist especially on Permian of Western Australia.

TYPE SPECIES: *Tomiopsis teichert* Archbold & Thomas, 1986.

DIAGNOSIS: Medium-small transverse shells with well formed sulcus and fold extending from umbones, low plicae, sulcus may carry groove and/or suggestions of subplicae, fold entire. Shell comparatively thin, adminicula thin, often subparallel and extending close to centre of sulcus anteriorly, no tigillum, tabellae short to moderate in length, often widely diverging.

DISCUSSION: The younger species of *Tomiopsis* named by Archbold & Thomas (1986) from the Permian of Western Australia appear closely allied, especially *teichert*, *balgoensis*, *hardmani*, *globosus* and *pauciplicatus*. The species, named from a succession of formations, share attributes and even though adminicula and tabellae may differ throughout, individuals within each suite displays the characteristic medium-length thin close-set subparallel adminicula and widely diverging short tabellae. They evolved from older Permian *Tomiopsis* (*Ambikella*).

Genus *Martiniopsis* Waagen, 1883

McClung (1978) and Campbell (1992) asserted that the large size and thick shell of New Zealand *Martiniopsis* ruled out any relationship to type *Martiniopsis*. They offered nothing to support any generic significance for these criteria. A careful analysis shows that the three New Zealand species (Waterhouse 1964, 1967b, 1982) and the one east Australian species (Waterhouse 1987a) assigned to *Martiniopsis* appear to have arisen from different strands, not closely related to any of the *Tomiopsis* species. Internally, the two younger species *woodi* Waterhouse and *patella* Waterhouse assigned to *Martiniopsis* in New Zealand resemble *Ingelarella* with long internal plates, but lack the tigillum of *Ingelarella*. *Ingelarella* is deeply sulcate and generally plicate, unlike *Martiniopsis*. *Johndearia*, which more closely approaches *Martiniopsis* externally, with very low or no plicae, and only a shallow though often broad sulcus, differs more internally, displaying short to medium-length widely spaced plates, low tigillum, and heavy thickening. *Ambikella* is closer overall in shell thickness and lack of tigillum, but is sulcate, usually plicate, and has shorter tabellae. Thus New Zealand *Martiniopsis* belong to a completely different association.

The older New Zealand *Martiniopsis*, *M. adminiculata* Waterhouse from the Brunel Formation of the Takitimu Group, and *M. biparallela* Waterhouse from the Brae Formation, Bowen Basin, have long close-set adminicula, strong tigillum or median ridge, and comparatively long tabellae. They are like no *Tomiopsis* known to me. If these *Martiniopsis* arose from *Tomiopsis-Ingelarella* etc stock, rather than from Gondwana *Martiniopsis*, then marked morphological changes were involved, that conflict with principles of parsimony. After all, the types of *Martiniopsis* do come from Gondwana and so were in the southern hemisphere during Permian times. They are similar externally to the Australian - New Zealand species assigned to *Martiniopsis*, and display moderately long internal plates. There is little commonality in the nature of the enclosing matrix for the various *Martiniopsis*, which varies through breccia, various kinds of carbonate, and shale-mudstone, so that the differences are not due

to substrate or bottom facies, or water depth. Their presence strongly suggests warm-water affinities (cf. Campbell 1959), as supported by the affinities of accompanying fauna. *Tominiopsis* characterized faunas with colder-water affinities, and it is clear from wide-ranging statistical studies that warm- and cold-water faunas alternated throughout the New Zealand Permian (Waterhouse & Bonham-Carter 1975). Campbell (1992) indicated that he considered New Zealand Permian possessed only cold-water faunas, but that thesis is denied by statistical overviews and detailed analyses.

Martiniopsis* cf. *woodi Waterhouse, 1964

cf. 1964 *Martiniopsis woodi* Waterhouse, p. 148, pl. 30, fig. 3-5, 8, pl. 37, fig. 2, 3, text-fig. 71, 72A, B.

1968 *Martiniopsis woodi* Waterhouse (?); Waterhouse, p. 57, part.

1992 Martineacea fam. et gen. indet. Campbell, p. 56. text-fig. 2A (text-fig. 2B, C uncertain).

MATERIAL: Three specimens figured by Campbell (1992), supposedly from Wether Hill Limestone (=Hilton Limestone Formation), Wether Hill Station, according to Campbell (1992), more likely from east side of Wherowhero Point, Orua Bay, North Auckland, PO 4, near f5705 but at least 3m higher in the succession.

DESCRIPTION: Three specimens that were studied by Campbell (1992) are re-examined. Specimen BR 1332 (Campbell 1992, text-fig. 2A) is of moderate size, with extended umbo, concave posterior walls, low growth wrinkles anteriorly, and definite dental plates and adminicula, not reported by Campbell. The surrounding matrix contains mafic dark green fine-grained water-rounded pebbles that partly stand up above the etched matrix. There are also prominent fragments of prismatic shell up to 0.8 cm long and over 3mm thick.

Specimen BR 1333 is more globose in shape, with posterior walls less concave in outline. It was thought to be a dorsal valve by Campbell, but there is a very shallow anterior sulcus, as is common for *Martiniopsis*, and this firmly indicates a ventral valve. The specimen is misoriented in the figure, and the vertical axis has been inclined 20° to the right. Broken bryozoans are visible in the light-coloured matrix and the surface is mottled. As no plates are visible, and as the shape is unusual and the specimen little inflated, it need not be identical with either of the other two specimens.

Specimen BR 1334 is a small ventral valve, also wrongly oriented by Campbell (1992, text-fig. 2C). The specimen approaches BR 1332 in shape, and shows a concave interarea and adminicula. No pebbles or Bryozoa or prisms are seen in the matrix, which is light grey in colour.

RESEMBLANCES: These specimens are varied. Two show adminicula, and the attribution of the specimens to Martineaceae (sic = Martiniacea, now Martinioidea) fam. and gen. indet. by Campbell (1992) seems inappropriate. From shape and internal attributes, and lack of any complex spine bases, the best preserved specimen BR 1332 clearly falls within Ingelarellidae.

The comparison by Waterhouse (1968) with *Martiniopsis woodi* is not unrealistic. BR 1332, the most complete specimen, does show the concave posterior umbonal walls seen also in the holotype of *M. woodi*, and is moderately close to an unfigured

paratype in the IGNS collections (not BR 575 as in the 1968 text). Its adminicula are spaced somewhat as in this species and the specimen shows similar very subdued concentric wrinkles. There are three reasonable choices open: to leave the specimen as open specifically, call it "*Martiniopsis* sp. indet. aff. *woodi* Waterhouse," or allow that a distant match with *woodi* is possible. The latter approach was taken by Waterhouse (1968) in searching for correlation potential, and to a paleontologist familiar with the degree of variation amongst species of the Ingelarellidae, the decision is not unreasonable.

DISCUSSION: The "revision" of these specimens by Campbell (1992) was not reliable. The main thrust of the Campbell article seems to have been to claim that Waterhouse (1968) misrepresented the affinities of the specimens and that the brachiopods he mentioned could not have come from North Auckland. Instead, he claimed, they had been wrongly labelled, and probably came in fact from Wether Hill Limestone, Wether Hill Station, Southland. Externally, the specimens somewhat resemble *Spinomartinia spinosa* Waterhouse from the Wether Hill and Nemo blocks of Wether Hill Station, and some specimens had been collected early enough from Wether Hill for them potentially to have become mislabelled by the time I started work on New Zealand Permian brachiopods. As I did not collect them, I cannot answer for their source with complete certainty. They were probably in NZGS collections, and labelled as to GS locality, I would think in Dr J. Marwick's handwriting, by the time I joined the New Zealand Geological Survey on permanent staff in January 1954. Campbell (1992) stressed that there were no fusulines in the matrix, and because the brachiopods were assigned the same fossil locality number as fusulines, considered or at least implied that the lack of fusulines proved the brachiopods had been wrongly located. But in those days, fossil localities were not allocated freely, and recollections and often nearby collections were either given the same number, or left unnumbered. I believe that specimen BR 1332 came from a low limestone bluff, above high-tide level, just north of the fusulines. That is where I collected a large fragment (never figured) of what appeared to be the same species, when in the area with Messrs. S. N. Beatus and F. Bowen, NZGS, ca 1961. Dr Marwick was familiar with my study, and we probably discussed the location, but unfortunately I now have no recollection of whether we talked about the site, or what he said. However, had he indicated any doubt about provenance, I would have certainly recorded it, and had Dr Marwick denied the occurrence, that would have promoted an effort to correctly source the material by talking with the field geologists at NZGS. Sir Charles Fleming was my colleague and superior, and certainly would have raised questions had there been any doubt about source, as he kept in close touch with my work, and was keenly interested in North Auckland Permian.

The only remotely comparable spiriferid from Wether Hill is *Spinomartinia* Waterhouse, 1968, but these specimens lack adminicula and so are readily distinguished. Both the Wether Hill and Nemo limestone blocks have been thoroughly searched by me for brachiopods, and no *Martiniopsis* is known, the report by me in Waterhouse (1968) being an error, based on misidentified *Spinomartinia*. *Martiniopsis* from Coral Bluff and from Wairaki Breccia-Conglomerate, Wairaki Downs (Waterhouse

1998) were not then known, and anyway, differ substantially at specific level and have different enclosing matrix. *Martiniopsis woodi* had however by that time been collected from Arthurton. No other *Martiniopsis* was then known, and there was no overseas Permian material in NZGS collections. (Even if there had been, the presence of atomodesmatid fragments in the matrix and low concentric wrinkles suggest that the specimen came from New Zealand.)

The matrix of the specimen BR 1332 under question strongly supports a North Auckland origin. It is of light-coloured carbonate, bearing small rounded mafic pebbles that stand out from the matrix. What seems to be exactly the same sort of pebble, etched by nature from similar light-coloured matrix, is common in the limestones of Orua Bay, North Auckland, as I verified in October 1997. This is a very distinctive phenomenon, and is not displayed for any of the other *Martiniopsis* - or indeed any Permian limestone samples from New Zealand (or any overseas material that I am familiar with through field work in Texas, Canadian Arctic, Rockies, Himalaya, Zechstein, Urals, Andes, Armenia, Mexico, Thailand, Alps). BR 1332 is the specimen that looks particularly like *Martiniopsis woodi*. Although complete certainty is lacking, it seems very likely that this specimen came from North Auckland, and belongs to *Martiniopsis*, and is acceptably compared to *Martiniopsis woodi*. This is supported by my own find of *Martiniopsis* at the low cliff.

The other two specimens do not have the distinctive pebbles, and are not so close to *woodi* in appearance, one in particular (BR 1333) being so obscure that it is difficult to decipher what genus is involved. The matrix for both is lightly coloured and like that found in Orua Bay. The matrix is slightly lighter than that found in the Hilton Limestone blocks of Wether Hill Station, and different from the matrix surrounding *Martiniopsis woodi* at Arthurton, south Otago, or *M. patella* at Wairaki Downs, Southland.

STRATIGRAPHY: Despite the account in Campbell (1992), the limestones of Marble Bay, Orua Bay and other localities in North Auckland are not all characterized by the presence of Fusulines. He may have been misled by the study of Marble Bay geology by Spurlin & Gregory (1981), which stated that fossils are numerous, with many kinds, and that widespread alteration of limestone still has left "ghosts" of corals and other forms. In fact there are a variety of carbonates, and the bulk show no fusulines, no corals, and no molluscs or brachiopods. Some layers do have a shell mash of bivalves or brachiopods in fragments no larger than 1-2cm across. Campbell (1992) stated that he relied on collections of samples at the University of Auckland, as if museum collections sufficed as a substitute for field-work. Given the nature of the work by Spurlin & Gregory (1981), and the need for substantial reassessment proved by Ramsay & Moore (1985, 1986), which I would strongly endorse from my own field-work, there is no reason to suppose that the Auckland University collection was adequate.

Genus *Tigillumia* n. gen.

ETYMOLOGY: *tigillum* - small bar of wood, small beam, Lat.

TYPE SPECIES: *Martiniopsis biparallela* Waterhouse, 1987a.

DIAGNOSIS: Shells externally like *Martiniopsis* with no plicae, shallow or no sulcus,

generally no fold, micro-ornament of shallow elongate exopunctate grooves in quincunx. Adminicula long and close-set, enclosing narrow muscle field rimmed anteriorly each side by high ridges which join anteriorly along mid-line. Tabellae of moderate length, moderately spaced.

DISCUSSION: Unlike type *Martiniopsis* and various other species, the adminicula of the ventral valve are very close-set and long, and there is a well formed median ridge or what is here termed tigillum in the ventral valve. The type species of *Tigillumia* comes from the Roadian (Guadalupian) Brae Formation of southeast Bowen Basin, and another species *Martiniopsis adminiculata* Waterhouse, 1982 is known from the mid-Cisuralian Brunel Formation of New Zealand.

Revised list of McClung identifications

Only two monographs have been issued on Ingelarellidae, by Campbell (1961) on species from the Bowen Basin, and by McClung (1978) on species mostly from the Sydney Basin. Campbell's species in his monograph and other studies withstand close scrutiny, apart from the doubts raised by McClung over possible gradation between *ingelarensis* and *angulata*, and the possibility that *globosa* represents a variant of *angulata*. Neither proposal incidentally was validated by Parfrey (1988) in her careful evaluation of the taxa. In addition, *angulata* Campbell may prove to be a junior synonym of *oviformis* M'Coy, and *symmetrica* Campbell a junior synonym of *branxtonensis* Etheridge, suggestions that require further appraisal, insofar as the types come from different basins, and involve a rather comprehensive approach to the delimitation of species, extending beyond tight morphological confines, as warranted by an extensive overview of the variation displayed by large contemporaneous suites of *Tomioopsis*. The erection of various species in the monograph by McClung (1978) is more difficult to accept. By focussing on internal moulds, he neglected details of micro-ornament, preferring to accept that all species were characterized by grooves and small spines, although this was nowhere substantiated by any of his descriptions or illustrations. His focus on internal moulds also meant that overall external shape was misrepresented, because umbones were lost, and generally, no allowance made for the thickness of posterior shell. McClung also seemed determined to force New Zealand stratigraphy into the model offered by the Sydney and Bowen Basins, in which fossiliferous marine sedimentation ceased towards what is now recognized as the end of the Guadalupian (Middle Permian). But, whereas marine sediments are followed by non-marine coal measures in the Sydney and Bowen basins, marine sedimentation continued in New Zealand, where there are no non-marine Permian rocks, other than possibly in west Nelson. Nonetheless, to enforce his view, McClung discounted morphological differences, and synonymized Late Permian New Zealand species with mid-Permian species, notably *mantuanensis*. The facts that New Zealand displayed no coal measures, and that its Late Permian faunas differed substantially from those found with New Zealand and Australian *mantuanensis*, and yet overlay *mantuanensis* faunas (Waterhouse 1998) held no significance for McClung. In addition, McClung (1978) erected a large number of new species. Unlike those named with cooperation of John Armstrong, his proposed taxa appear to be variants of species already named, chiefly from the Bowen Basin, by Campbell

(1960, 1961). McClung's work therefore needs to be re-evaluated, and its chief importance lies in indicating some of the variation that may be displayed over a considerable geographic area, and to some extent through short time intervals, within the abundant and rapidly diversifying genus *Tomiopsis* and its constituent subgenera.

McClung	Revised identification
(all <i>Ingelarella</i>)	<i>Tomiopsis</i> , subgenera <i>I.</i> - <i>Ingelarella</i> , <i>J.</i> - <i>Johndearia</i> , <i>A.</i> - <i>Ambikella</i> . <i>M.</i> - <i>Monklandia</i>
<i>oviformis</i> (M'Coy)	<i>T. (I.) oviformis</i>
<i>strzeleckii</i> (de Koninck)	<i>M. gympiensis</i> n. gen., n. sp.
<i>konincki</i> (Etheridge)	<i>T. (A.) konincki</i>
<i>branxtonensis</i> (Etheridge)	<i>T. (A.) branxtonensis</i>
<i>elongata</i> (McClung & Armstrong)	<i>T. (I.) elongata</i>
<i>ovata</i> Campbell	<i>Homevalaria ovata</i>
<i>profunda</i> Campbell	<i>H. profunda</i>
<i>brevis</i> (McClung & Armstrong)	<i>T. (J.) brevis</i>
<i>undulosa</i> Campbell	<i>T. (I.) undulosa</i>
<i>magna</i> Campbell	<i>T. (J.) magna</i>
<i>etheridgei</i> McClung	gen.? <i>strzeleckii</i> (de Koninck)
<i>davidi</i> McClung	gen.? <i>davidi</i>
<i>cessnockensis</i> McClung	<i>T. (I.) undulosa</i> (Campbell)
<i>ingelarensis</i> Campbell	<i>T. (I.) ingelarensis</i>
<i>belfordensis</i> McClung	<i>T. (J.) magna</i> (Campbell)
<i>isbelli</i> Campbell	<i>T. (J.) isbelli</i>
<i>warneri</i> McClung	<i>T. (J) dissimilis</i> (Waterhouse) subsp. or var.
<i>mantuanensis</i> Campbell	<i>T. (I.) mantuanensis</i>
syn. <i>parallela</i> Waterhouse	<i>T. (I.) parallela</i>
syn. <i>furca</i> Waterhouse	<i>T. (I.) furca</i>
syn. <i>woodi</i> Waterhouse	<i>Martiniopsis woodi</i> Waterhouse
<i>singletonensis</i> McClung	<i>T. (J.) dissimilis</i> Waterhouse
cf. <i>costata</i> Waterhouse	<i>T. (I.) subplicata</i> Waterhouse
<i>I. angulata</i> Campbell	<i>T. (I.) angulata</i> (? = <i>oviformis</i>)
<i>excelsus</i> (Waterhouse)	<i>Notospirifer?</i> <i>excelsus</i> Waterhouse

Virtually all of the McClung species are junior synonyms, or, charitably, regarded as subspecies of earlier taxa.

Stratigraphic Implications

Species of *Tomiopsis* s. l. are numerous enough in east Australia and New Zealand to encourage a zonation on species ranges and overlaps. For the late Cisuralian and Guadalupian Runnegar & Armstrong (1975) proposed four successive zones, *brevis*, *undulosa*, *isbelli* and *mantuanensis*. This may be extended and subdivided, now that more species are known, and others assessed as closely related.

1. *brevis*: Much as in Runnegar & McClung, in Tasmania and the Snapper Point and Elderslie Formation of Sydney Basin, this species is still not known in Queensland, but may be questionably represented in the lower Letham Formation of Wairaki Downs, New Zealand.

2. *undulosa*: The viability of this as a separate zone remains an open question. The species occurs below the Moonlight Sandstone Member in the north Bowen Basin, and in the Freitag Formation, southwest Bowen Basin, where *brevis* is not found. In the Sydney Basin, McClung (1978) reported *undulosa* in the middle Wandrawandian Formation and possibly upper Elderslie. A closely allied form *cessnockensis* overlaps both *brevis* and *undulosa* (McClung 1978, p. 50). Differing only in having more closely spaced adminicula, it may be a subspecies, if not a full synonym of *undulosa*. Therefore the separation between *brevis* and *undulosa* is not clear in parts of both the Sydney and Bowen Basin, given the lack of stratigraphic data in McClung (1978), but possibly *brevis* entered first and was then joined by *undulosa* s.s. Possible small specimens belong to *undulosa* in the lower Letham Formation, New Zealand. A different arrangement was suggested for Tasmania by Clarke & Farmer (1976), in which *plica* preceded and overlapped *brevis* and was followed by a discrete *undulosa*. This cannot be accepted of course until verified by systematic documentation.

3. *subplicata*: This species is found in the upper Letham Formation of New Zealand, and apparently in the Fenestella Shale of the north Sydney Basin. A co-occurring species in the Fenestella Shales is either smooth *subplicata* or *ingelarensis* Campbell s.l.

4. *confusa*: a subspecies at best of *ingelarensis*, this is found as part of the *Echinalosia maxwelli* Zone in the basal Mangarewa Formation of New Zealand and Otrack Formation of the Bowen Basin. Possibly the zone is represented also in the Fenestella Shale and part of the Wandrawandian Formation of the Sydney Basin.

5. *magna* and *angulata*: The species *magna* is present in the lower Moonlight Sandstone Member of the north Bowen Basin, and *belfordensis* McClung of the Belford Formation, north Sydney Basin, is a probable synonym. This species may represent a shallow-water coarse substrate time equivalent of *angulata* (and type *ingelarensis*) in coarse and fine sediments of the Ingelara Formation (and lower Peawaddy beds?) of the southwest Bowen Basin, and fine-grained Barfield Formation of southeast Bowen Basin. The species *angulata* also approaches *oviformis* of the Belford and Muree Formation. These various species may be crudely contemporaneous, and *magna* may range into younger sediment.

6. *isbelli* and *dissimilis*: These are two variable but somewhat similar species, apparently close in age range. The species *isbelli* is found in the upper Moonlight Sandstone Member of north Bowen Basin, and reported and in some instances verified by McClung (1978) from the Belford and Muree Formations, Bickham and Porcupine Formations of north Sydney Basin, and Nowra Sandstone, Berry Formation and Gerringong Volcanics of south Sydney Basin and in Malbina E Formation and other beds of Tasmania (Clarke 1987). The allied species *dissimilis* is found in Mangarewa units 3 and 4 and in the lower Flat Top Formation of southeast Bowen Basin. The species *singletonensis* from the Mulbring Formation is regarded as conspecific. Overall the *dissimilis-isbelli* assemblage requires further disentangling, and may represent only one zone, with different species characterizing parts in different succession in different regions. It may overlap part of the *angulata-oviformis-magna* plexus.

7. *mantuanensis*: The species *mantuanensis* occurs in the Mantuan Member, upper Peawaddy Formation, and in a separate layer of the Blenheim Formation (Waterhouse

& Jell 1983) in the west and Bowen Basin, and in the lower middle Flat Top Formation of the southeast basin. In the Sydney Basin, *mantuanensis* supposedly overlaps *isbelli* in the Nowra and Berry and Muree Formations (McClung 1978), and it overlaps *dissimilis* in Mangarewa unit 4, above unit 3 with only *dissimilis*.

8. *havigensis* - *pelicanensis*: These species occur above *mantuanensis* in the north Bowen Basin and in the topmost Mangarewa Formation of New Zealand, together with *costata*, which appears to be a plicate *havigensis*. The two name species also occur in the Flowers Formation of west Nelson.

The preceding review shows that species overlap somewhat and appear to have different overlaps or exclusions in different regions. Further difficulty stems from inadequate stratigraphic data and systematic descriptions, so that whereas New Zealand and some of the Bowen Basin are moderately well known, the Sydney Basin and Tasmania are under poor control. For Tasmania, very few species have been illustrated and described, so that lists as in Clarke & Banks (1975) and Clarke & Farmer (1976) largely have to be set aside until verified. The stated ranges and comparisons in McClung (1978) on Bowen Basin and New Zealand occurrences seldom withstand close scrutiny, and that leaves open the reliability of statements on the Sydney Basin. Whilst these may be more acceptable because he worked directly on Sydney Basin material, his concentration on internal moulds and failure to analyse or figure various identifications leave many unanswered questions.

There are intriguing compatibilities and incompatibilities with ranges of Productida. For example *isbelli* is found with *Pseudostrophalosia blakei* in the north Bowen Basin, yet is reported with *Echinalosia ovalis* in Tasmania. In the north Bowen Basin *ovalis* forms a separate zone with *mantuanensis*, just as in the southwest Bowen Basin. Because Productida are more numerous than *Tomioopsis* s. l., they may be preferable for close subdivision and correlation, but of course a broad approach that considers a range of taxa will reduce the risk of miscorrelation. Both *Tomioopsis* and Productida such as *Echinalosia*, *Wyndhamia*, *Pseudostrophalosia*, *Terrakea* and *Paucispinauria* appear to be revealing time-shifts and overlaps, apparently related to bottom-facies and especially temperature and paleolatitude.

Subfamily **RORESPIRIFERINAE** n. subfam.

NOMINATE GENUS: *Rorespirifer* Waterhouse & Piyasin, 1970.

DIAGNOSIS: Identical with Ingelarellinae in shape and internal features, distinguished by micro-ornament, which consists of small solid spinules rather than elongate grooves.

DISCUSSION: *Rorespirifer* is a Kungurian or slightly younger genus from paleotropical (southern subtropical) faunas of south Thailand. The micro-ornament is readily distinguished from that of *Martiniopsis*, *Tomioopsis* and related forms, in that surface grooves are lacking. Archbold & Thomas (1986), without examining the types, declared that Waterhouse & Piyasin (1970) had misinterpreted the micro-ornament, and that the preservation of *Rorespirifer* micro-ornament was poor. There is little to commend in an approach by which paleontologists refuse to examine type material, dismiss textual studies by authors that indicate new morphology, assert preservation is poor without having seen the preservation rather than accept observations, and fail to examine illustrations carefully. The enlarged figure in Waterhouse & Piyasin (1970,

pl. 29, fig. 15) shows small solid papillae or tiny solid spines aligned and close-set along concentric growth rows, with a little more spacing between rows, just as described in the text. The pattern is a little irregular and is a natural biological one, not caused by vagaries of preservation. The spinules are so fine that it is difficult to adequately represent them on a photograph, due to problems from depth of field and a convex shell surface. But the spinules are there, and by the standards of technology then available, the figure is of high standard, thanks to the skill of Mr Brian Donovan our photographer. Grant (1976, pl. 62, fig. 8) also showed papillae in one of his specimens, and acknowledged his Thai material showed tiny pustules. Perhaps some of the difficulties raised by Archbold & Thomas (1986) arose from their lack of familiarity with silicified material that has been etched from limestone. Grant ascribed his species to *Martiniopsis trimmata* Grant, because he misconstrued the nature of *Martiniopsis* ornament.

Balinski (1975) pointed out that finely costate shells could assume the appearance of being finely spinose after removal of the primary layer. Although his studies are not directly applicable to *Martiniopsis* or *Roespirifer*, it may be suggested that perhaps the papillae of *Roespirifer* represent taleolae, left protruding after removal of the primary layer. Against this, the outer surface as now preserved shows very fine and close-set delicate growth increments, which appear to represent the external surface. The surface also shows coarser bands, which are also repeated without the fine increments on the inner layer. Furthermore, the papillae are very much more closely spaced and aligned than the taleolae described and figured in *Tomiopsis* s. l. by Campbell (1959, pl. 56, fig. 14) or in *Martiniopsis* (Waterhouse 1964, pl. 37, fig. 3, 1965). Therefore it is concluded that the micro-ornament for *Roespirifer* is distinctive and as described by Waterhouse & Piyasin (1970).

AGE: Grant (1976) argued that the Thai Rat Buri limestone brachiopods indicated an Artinskian age, in contrast to a Kungurian or even Kazanian -Wordian s. l. age preferred by Waterhouse & Piyasin (1970, Waterhouse 1973). Grant stressed a close match with faunas from Bitauini, Timor, and Amb Formation of the Salt Range, which he, unlike me, regarded as Artinskian. My views were based on brachiopod evidence rather than ammonoids, and appear to have been confirmed, or strongly supported by conodonts. The Bitauini includes the Kungurian conodont *Vjalovognatus shindyensis*, and Amb has comparable or younger conodonts (Dr H. Kozur, pers. comm., Wardlaw 1997, Nicoll & Metcalfe 1997).

Family NOTOSPIRIFERIDAE Archbold & Thomas, 1986

[nom transl. hic ex Notospiriferinae Archbold & Thomas, 1986]

This family involves a group of mostly if not entirely east Australian and New Zealand shells. Campbell (1959, 1960, 1961) recognized a number of species in east Australia, which he ascribed to *Notospirifer* Harrington, and McClung & Armstrong (1978) made a critical advance in being first to subdivide Notospiriferid shells by recognizing a separate genus *Glendonina*. Armstrong (1969, 1970) offered valuable studies of micro-ornament, and Clarke (1987, 1990, 1992a, b) carefully described three additional genera from the Permian of Tasmania. In the following text a substantial re-interpretation is offered on the basis of both new material and re-appraisal of former

collections, especially from Wairaki Downs, New Zealand, and the Bowen Basin and Gympie area, Queensland.

Members of Notospiriferidae are close to members of Ingelarellidae in shape and plication, but do not include non-plicate members. The interior of the ventral valve is largely identical to that of Ingelarellidae, although no tigillum is developed, and the dorsal valve is close, but typically displays short or no tabellae, in contrast to the well-formed moderately short to long tabellae of all Ingelarellidae. The micro-ornament also offers a critical difference. In Ingelarellidae, surface grooves are developed en echelon, with variably raised margins, and rarely edged posteriorly by a slender crescentic rim, as in *Homevalaria*. In *Roespirifer*, tiny solid spinules are developed. In Notospiriferidae, micro-spines are better developed, and surface grooves are deeper and of three kinds. Notospiriferinae has very small spines and deep swollen exopunctae, here called globons. Glendoniinae has higher spines, prolonged posteriorly in some genera, and shallow narrow grooves more as in Ingelarellinae. Mesopunctiinae has small or no micro-spines, shallow narrow grooves, and mesopunctae, which are cylindrical deep pores that penetrate the outer part of the main lamellar layer or secondary layer of shell from the anterior end of the groove. As well, the various genera in all three subfamilies may be discriminated from each other generally by external shape, involving number and shape of plicae, and nature of the sulcus and fold.

The entire family is known only from Late Paleozoic of Gondwana in east Australia and New Zealand. Clarke (1992b) has suggested that the centre of its radiation occurred in Tasmania, and this appears to be true in so far as *Farmerella* and *Birchsella* are reliably reported only from Tasmania, together with some species of *Notospirifer* and *Glendonia*. But *Kelsovia* named by Clarke from Tasmania is probably a junior synonym of the Queensland genus *Tabellina*, and many more species of *Glendonia* and *Notospirifer* have been described from the Sydney and Bowen Basins, compared with Tasmania. Genera *Monklandia*, *Papulinella*, *Wairakispirifer* and *Mesopunctia* are found in Queensland and New Zealand (Gympie, southeast Queensland, was once part of New Zealand or vice versa) and are unknown from Tasmania. Thus it appears that evolution proceeded in several centres simultaneously, with Queensland showing the highest diversity of species and genera.

The origin of the family, to judge from the fossil record and geographic dispersion, probably occurred in the Late Carboniferous, possibly in Queensland. The plicate nature of the shell points to an origin from *Tomiopsis* (cf. Clarke 1992b). The lack of tigillum and short or no tabellae suggests a source from the Late Carboniferous and Permian subgenus *Ambikella*. No genus or species is known to have reverted to a non-plicate form.

Subfamily NOTOSPIRIFERINAE Archbold & Thomas, 1986

Notospirifer Harrington, 1955 and *Farmerella* Clarke, 1992b were included in Notospiriferinae by Carter et al. (1994, p. 341) and stated to be characterized by a micro-ornament of "quincunxially arranged grooves and ridges, with anteriorly directed spinules at the posterior ends of short grooves, and with deep elongate globose pits extending into the secondary layer under (the) spinules". This conforms with the inter-

pretation offered in error by Waterhouse (1967a, text-fig. B, p. 277). However Armstrong (1970, p. 293, text fig. 4) demonstrated that the pits passed forward into the shell from the anterior groove, and quoted articles by Waterhouse (1964, p. 172) and Waterhouse & Vella (1965, p. 70) in support. So the diagnosis of *Notospiriferinae* by Carter et al. (1994) needs amending. Archbold & Thomas (1986) were not clear about the micro-ornament and the depth of the pits within the subfamily, but Clarke (1992b, text-fig. 1) provided description and diagrams that support the Armstrong view, especially for *Notospirifer* and *Glendonina*, although he evidently did not appreciate the presence of "pits" leading further into the shell in some species.

Genus *Notospirifer* Harrington, 1955

The actual micro-ornament of *Notospirifer* remains a little uncertain with regard to the type species, *N. darwini* (Morris), because the types are not well preserved and no external detail has ever been figured. Campbell (1959, 1960, 1961) in his descriptions of the types and other species made no mention at all of micro-spines. Waterhouse (1964, 1967a, 1968) suggested that the surface of many Queensland *Notospirifer* described by Campbell has been worn, as is the case for chonetids, and that the abraded nature of the shell was obscuring the real surface ornament. The first clear indications of spines in any member of the family Notospiriferidae were provided by the description of spinules in *N. spinosa* from west Nelson by Waterhouse & Vella (1965). Then spines were found in material collected by Waterhouse (1967a) in company with Prof. Ken Campbell, in possible topotype material of the type species at Glendon, north Sydney Basin, in the Muree Sandstone. Now that species assigned to *Notospirifer* have been subdivided between a number of genera, the original determination as *Notospirifer* of course has to be reconsidered. Armstrong (1969, p. 199) found a topotype UQ F 56154 from Glendon that came much closer in shape to the original *darwini*, and reported the presence of swollen exopunctae, that is globons, and low knobs, rather than shallow grooves and small spines. No illustration of the "knobs" was provided. In type *Notospirifer*, the tabellae are very tiny, and placed next to the fold (Waterhouse 1967, Armstrong 1969). Campbell (1959, p. 342) stated the adminicula were very weak or absent and "if present, very short", and Armstrong (1969, p. 199) recorded very short tabellae. The lectotype is poorly preserved, and the nick in the cast that is lectotype might have originated from a short tabellar plate, or where the crural plate abutted the posterior wall, although the latter possibility would be very unusual. Although Clarke (1987) asserted that tabellae were missing, his statements are not confirmed by other authors or by the types, and he himself does not appear to have found or described additional topotype material.

Armstrong (1969) and Waterhouse (1967a) stressed the significance of two sulcal subplicae in the ventral valve of *Notospirifer darwini*, a feature rarely seen in Notospiriferidae. *Notospirifer gentilis* Waterhouse (in Waterhouse & Jell 1983, pl. 3, fig. 1-5) from the Glendoo Sandstone Member, north Bowen Basin, is one of the few species to display the same feature. Its micro-ornament comprised small close-set subrounded globons, and it is far from clear that spines are present. There are no tabellae. This species may be regarded as a close ally of *darwini*, distinguished by its low plicae.

A more distant ally is *Notospirifer excelsus* Waterhouse (1968, pl. 15, fig. 1-3) from the *Plekonella multicosata* Zone of the Arthurton Group, New Zealand. This has numerous small subglobular globons in front of short crescentic spinules (Waterhouse 1968, pl. 15, fig. 6), the globons shown as larger and longer in the upper left of the figure. The sulcus has two subplicae passing anteriorly into a median sulcal swelling, not observed in other Notospiriferidae. The dorsal valve is not known. The species may be referred to *Notospirifer*, but the possibility seems strong that it represents a separate new genus, with distinctive sulcus and micro-ornament, and as noted by McClung (1978), it is unusually elongate for a Notospiriferid. Indeed McClung claimed that the species belonged to *Ingelarella*, misrepresenting the globons as radially elongate surface grooves, and claiming that the spines were those typical of *Ingelarella*. But he never described or figured any such spines for his extensive material, and I have never seen such micro-ornament on any species of *Ingelarella* or *Tomiopsis* that I have examined in various institutions in Britain, Canada, Russia, India, Australia and New Zealand.

To judge from available evidence, it appears that *Notospirifer* is likely to have constituted a small set of species of late Cisuralian to Guadalupian age with a descendent ally of Lopingian age. It may be defined by its sulcal subplicae, generally transverse outline with low lateral plicae and globons in the primary layer and short to no tabellae. The presence of spines is well established only for *N. excelsus*.

Genus *Farmerella* Clarke, 1992

Farmerella Clarke, type species *F. exopora* Clarke, 1992b displays globons and tiny blunt micro-spines. In having a prominent median subplication in the sulcus, it was described as homeomorphic with *Glendonina* McClung & Armstrong by Clarke (1992b), but is externally distinct with more numerous and subangular crowded lateral plicae. Internally tabellae are short or absent. The genus is known so far only from Cisuralian of Tasmania.

Genus *Papulinella* n. gen.

ETYMOLOGY: papula, pustule, pimple, Lat.

TYPE SPECIES: *Notospirifer hillae* Campbell, 1961.

DIAGNOSIS: Small transverse shells with non-costate, non-plicate sulcus, moderately developed fold with or without median groove, low lateral plicae. Micro-ornament of small spinules with short or no posterior buttresses, narrow anterior grooves passing into globons bordered generally by ridges. Interior as for family, tabellae generally not developed.

DISCUSSION: It is *Notospirifer hillae* Campbell that has provided the template for *Notospirifer*, thanks to detailed study and fine illustrations of the types by Armstrong (1970). But there is a clear external difference between *N. darwini* and *hillae*, in that the latter species lacks the two sulcal subplicae well developed in *darwini* and *gentilis*. An exact comparison of micro-ornaments awaits further study. No truly external micro-ornament has yet been figured for *darwini*, and no full comparison between what were described as "knobs" of *darwini*, and the "knob-like spines" of *hillae* has been published by Armstrong (1969, 1970). Even if these prove identical, the difference in sulcus suffices to separate the two, although there might be reason to downgrade

Papulinella to a subgenus. The species *Notospirifer excelsus* Waterhouse, 1968 as described above shows a micro-ornament somewhat different from *hillae* in its small well defined c-shaped spinules and small subelongate globons apparently with less developed bordering rims. But this is not the type species.

Papulinella hillae was described from the Tiverton Formation of north Bowen Basin by Campbell (1961) and a subspecies *plicata* named from the same beds. The species has also been recognized in the southwest Bowen Basin by Dear (1972) and in the Rose's Pride and Elvinia Formations of the southeast basin by Waterhouse (1987a). Fragmentary material has been reported from the Brunel Formation, Takitimu Group, New Zealand by Waterhouse (eg. 1968). Waterhouse described what appears to be comparable micro-ornament, consonant with the genus *Papulinella*, but better material is required to establish the species. *Notospirifer paraextensus* Waterhouse (1987a) from the Fairyland Formation of the southeast Bowen Basin has crowded globons, but the presence of spines is not established. However the close spacing and depth of the globons suggest a closer relationship to *hillae* rather than *Notospirifer darwini*, and the sulcus is like that of *hillae*.

Subfamily GLENDONIINAE Clarke, 1992

This subfamily was distinguished by its "micro-ornament of quincunxially arranged shallow elongate grooves terminated anteriorly by low elongate spinules and shallow elongate pits", according to Carter et al. (1994, p. 341). The subfamily thus was diagnosed as differing from Notospiriferinae in the position of the spines, placed behind the grooves in Notospiriferinae, and in front in Glendoniinae. But the grooves in *Glendonia* in fact lie in front of the spines, not behind (cf. Clarke (1987, p. 70).

Genera include *Glendonia* McClung & Armstrong, 1978, *Birchsella* Clarke, 1987, *Kelsovia* Clarke, 1990, which appears to be junior synonym of *Tabellina* Waterhouse, 1987a, and a new genus *Monklandia*. The globons of Notospiriferinae, and the mesopunctae of Mesopunctiinae are lacking.

According to Carter et al. (1994), *Homevalaria* Waterhouse, 1986 also belonged to Glendoniinae, though in my opinion, the presence of well developed tabellae point to placement of *Homevalaria* within the Ingelarellidae. Excellent illustrations of the micro-ornament in *Homevalaria* are provided by Armstrong (1970, text-fig. 1A, E), and also Campbell (1961, pl. 24, fig. 9).

Genus *Glendonia* McClung & Armstrong, 1978

This genus is characterized by its strong subplication in the ventral sulcus, and weakly grooved dorsal fold or fastigium. Lateral plicae are comparatively high and strong. Microspines are generally well formed and suberect, not prolonged posteriorly. Tabellae may be comparatively well developed. Species were described from late Cisuralian and early Guadalupian of the Sydney and Bowen Basins by McClung & Armstrong (1978).

Clarke (1987, 1992b) seemed to think that a wide range of morphologies should be referred to *Glendonia*, but the species he discussed show different characteristics, and some are now referred variously to *Monklandia*, *Wairakispirifer* and *Mesopunctia*. It is clear that he failed to understand the nature of mesopunctae or "pits" described by Armstrong (1970) and Waterhouse (1964). He also discounted

the significance of the central costa along the sulcus of *Glendonia*, referring to *Glendonia* various species that not only differed in the nature of micro-ornament, but lacked a median sulcal rib. For example he referred a Glendoo specimen described by Waterhouse (1967a, pl. 13, fig. 4-7, 12) to *Glendonia*, but this has the two sulcal subplicae typical of *Notospirifer* and *Monklandia*, rather than the central sulcal plication typical of *Glendonia duodecimcostata* (M'Coy).

Genus *Birchsella* Clarke, 1987

Birchsella differs from *Glendonia* in lacking a sulcal subplication and having a strongly thickened ventral interior, subdued plicae, and small blunt microspines, buttressed posteriorly, with very short and shallow narrow surface grooves. The genus is so far known only in the lower Guadalupian of Tasmania. Adminicula are buried in secondary thickening, and no tabellae are developed.

Genus *Tabellina* Waterhouse, 1987

(syn. *Kelsovia* Clarke, 1990)

Tabellina Waterhouse, 1987, type species *Ingelarella denmeadi* Campbell, 1961 from the Fairyland Formation of southeast Bowen Basin, has strong and numerous plicae and is shaped like members of Notospiriferidae. Tabellae are very short. Micro-ornament is poorly known for the type species. Although Campbell reported normal Ingellarellid grooves in quincunx, the micro-ornament is obscured on his and my material from the Fairyland Formation. Specimens very close to the type species were described by Parfrey (1986) as *Notospirifer undulatus* Parfrey, and recorded as displaying short grooves, and low spinules, suggestive of Glendoniinae. Tabellae are very short in Parfrey's species, and her specimens came from Camboon Andesite, from beds close in age to the Fairyland Formation a few tens of km to the south.

Clarke (1990, p.72) tentatively compared Parfrey's species with *Kelsovia superba* Clarke from the Swifts Jetty Sandstone, northern Tasmania, whilst stressing the need for caution because of what he considered was the uncertain nature of the micro-ornament in *undulatus*. In 1992b he firmly regarded *undulatus* as a member of *Kelsovia*.

Kelsovia Clarke, 1990 from the Swifts Jetty Sandstone, Tasmania, is probably a junior synonym of *Tabellina*. It shares a broad prominent dorsal fastigium or fold, and has 4-5 pair of dorsal plicae, and short widely diverging tabellae. The species displays a high, long dorsal median septum, but this is not considered to be of more than specific importance. The micro-ornament consists of sturdy low crescentic elevations that are posteriorly prolonged, and shallow elongate exopunctae. Mesopunctae are absent. Clarke (1990, 1992a, b) failed to make any comparison with *Tabellina*, despite the obvious similarities in shape, prominent fold and short tabellae.

Another species *Tabellina cracowensis* Waterhouse (1987a, pl. 7, fig. 11-14) was described as having a micro-ornament of shallow elongate grooves, without exopunctae. This species has few plicae and has short tabellae. It needs to be re-examined, but appears to be congeneric.

Tabellina armstrongi n. sp.

1978 *Notospirifer*? n. sp. McClung & Armstrong, p. 4, pl. 2, fig. 21-25.

1990 *Kelsovia* Clarke, p. 72.

ETYMOLOGY: Named for John Armstrong.

HOLOTYPE: GSQ F12287, figured by McClung & Armstrong (1978, pl. 2, fig. 24, 25) from Cattle Creek shale, southwest Bowen Basin, here designated.

DIAGNOSIS: Medium-sized shells with moderately high fold and wide sulcus, 2 pairs of ventral plicae and 3 pairs of dorsal plicae.

DISCUSSION: This species displays very short widely diverging tabellae, and micro-ornament of thick low crescentic spinules with deep narrow grooves in front (McClung & Armstrong 1978, pl. 2, fig. 25). It is distinguished from *Tabellina denmeadi* (Campbell) and *T. superba* (Clarke) by the comparatively low fold and few plicae. The new form is closest to the slightly older species *T. cracowensis* Waterhouse (1987, pl. 7, fig. 11-14) from the Elvinia Formation of the Bowen Basin. This has none to 2 or 3 pairs of plicae, and its fold is higher and the sulcus deeper.

Genus *Monklandia* n. gen.

ETYMOLOGY: Named from Monkland beds, district of Gympie, applied to the principal gold-bearing levels of the upper Rammutt Formation. The name Monkland has also been applied to the Monkland and Great Monkland claims and Monkland road.

TYPE SPECIES: *Monklandia gympiensis* n. sp.

DIAGNOSIS: Large strongly plicate shells with broad shallow sulcus bearing 2 subplicae and flat fold with median groove, micro-ornament of fine grooves passing forward from c-spines, shell thin with thin primary layer. Admnicula moderately long, tabellae short, longer than usual for Notospiriferidae.

DISCUSSION: The lack of globons and mesopunctae distinguish this genus from members of the Notospiriferinae and Mesopunctiinae. Within Glendoniinae, *Glendonia* McClung & Armstrong has a strong sulcal median plication, and *Birchsella* Clarke shows considerable thickening in the posterior ventral valve. *Tabellina* Waterhouse is moderately close but is distinguished by its much more prominent fold and deep simple sulcus. All three of these genera lack two subplicae from the ventral sulcus. In addition the tabellae are longer in *Monklandia*, and unusually long for the family. *Homevalaria* Waterhouse, here regarded as a member of Ingelarellidae, has much thicker shell, longer tabellae and micro-ornament of shallow narrow surface grooves, in front of straight or c-shaped delicate raised crescents. The sulcus is deep and simple and plicae few and strong, so that overall appearance differs considerably.

Monklandia gympiensis n. sp.

1872 *Spirifera undifera* var. *undulata* (not Roemer); Etheridge Snr, p. 330, pl. 16, fig. 3-5.

1892 *Spirifera strzeleckii* not de Koninck; Etheridge Jnr, p. 234, pl. 10, fig. 5, 6 (not pl. 10, fig. 7).

1978 *Ingelarella strzeleckii* (not de Koninck); McClung, p. 43, pl. 3, fig. 20-26.

1987 "*Notospirifer*" *strzeleckii* (not de Koninck); Waterhouse & Balfe, p. 30, pl. 1, fig. 6, 7.

HOLOTYPE: QM F 946, figured by Etheridge Snr (1872, pl. 16, fig. 3), Etheridge Jnr (1892, pl. 10, fig. 6) and McClung (1878, pl. 3, fig. 24) from Monkland beds, Lady Mary Reef, Gympie, here designated.

DIAGNOSIS: Transverse shells with 4 to usually 6 pairs of narrow plicae, wide very shallow ventral sulcus with 2 subplicae, flat-topped wide low fold bearing median

groove.

DESCRIPTION: This species has been described by McClung (1978). It is a very distinctive transverse shell with strong but narrow plicae in 4, 5 or mostly 6 pairs, broad very shallow flat-floored sulcus with 2 sulcal costae, and wide low fold with median groove. Adminicula extend for about 0.2 of the length of the valve, and tabellae for almost 0.2 of length, passing forward each side of the fold, or cutting across the inner pair of plicae. The critical feature lies in the micro-ornament. This consists of very slender shallow grooves, about 5 in 1mm, overlapping to number 10 per mm, about 0.7mm long, each arising in front of a slender c-shaped spine. The grooves taper anteriorly and may radiate laterally forward from the centre of the interspaces. Outer shell thin, not deeply penetrated by grooves, no globons or cylindrical mesopunctae.

RESEMBLANCES: McClung (1978) could find no species that resembled this distinctive form. Although he did not describe the micro-ornament, he referred the Monkland material to *Ingelarella*. It is possible that if he had observed the micro-ornament, he would have regarded it as typical of *Ingelarella*. From the Tiverton Formation of the north Bowen Basin, *Notospirifer* (now *Papulinella*) *hillae* Campbell, 1961 is moderately close but has higher plicae, higher fold, deeper sulcus, no subplicae, globons, and short or no tabellae. The species named *Martiniopsis subradiata* var. *konincki* Etheridge Jnr (1892) from the Allandale Formation, north Sydney Basin, as revised by McClung (1978) is similar in that plicae are narrow and 3-4 pairs in number, and the sulcus is moderately broad with 2 subplicae, and dorsal fold wide, rarely with a median furrow. It is moderately inflated with narrower less flat-floored sulcus, weaker subplicae, fewer plicae, narrower higher dorsal fold, generally with rounded crest. Tabellae are short. Overall shape suggests *Tomiopsis* (*Ambikella*), but micro-ornament is poorly known.

DISCUSSION: McClung (1978, p. 43) cited a Gympie specimen figured by Etheridge Snr (1872) as lectotype of *Spirifer strzeleckii* de Koninck. This is improper. Although de Koninck (1877) had referred Etheridge's specimens to *strzeleckii*, he had based the description and definition of his species *strzeleckii* on completely different specimens, obtained from Guadalupian beds of the Hunter Valley, New South Wales, rather than Cisuralian beds of Gympie. Thus even though de Koninck's specimens were later lost by fire, the Etheridge specimens cannot be considered available as replacement types, because they differ so much from de Koninck's species. Campbell (1960, p. 1111) came to the same conclusion. He stated "I am convinced they are definitely not conspecific with either of the types [of *strzeleckii*] figured by de Koninck, and since they do not appear to have been used in drawing up the original description, they do not qualify as syntypes." McClung (1978) did not explain why he ignored Campbell's careful assessment. I conclude that McClung's redefinition of *strzeleckii* was inappropriate, and that the Gympie specimens cannot be ascribed to *strzeleckii* de Koninck. The correct procedure is to refer the Gympie specimens to a new species.

Of the two specimens figured as *strzeleckii* by de Koninck (1877), that of de Koninck (1877, pl. 12, fig. 1, 1a) is clearly identical with *Ingelarella etheridgei* McClung

(1978). The other specimen (de Koninck 1877, pl. 14, fig. 1, 1a) has a grooved dorsal fold and is somewhat like a transverse version of *oviformis* M'Coy, 1847, although no particular match has been found. I here designate the first figured specimen de Koninck (1877, pl. 13, fig. 1, 1a) as lectotype of the species *strzeleckii* de Koninck. In view of its destruction by fire, the specimen figured by McClung (1978, pl. 9, fig. 3, 6), UNE 14263, is proposed as neotype. This replaces the name *etheridgei* McClung, 1978 with *strzeleckii* de Koninck, and should enable ready recognition of de Koninck's species. *Ingelarella davidi* McClung, 1978 from the same formation is possibly allied, McClung allowing that the distinction between the two was "somewhat arbitrary." The generic positions of *strzeleckii* and *davidi* require clarification, because McClung did not describe micro-ornament, preventing full assessment.

***Monklandia glendonensis* n. sp.**

1967a *Notospirifer darwin?* (not Morris), Waterhouse, p. 274, pl. 13, fig. 4-7, 12.

1969 *Ingelarella* sp. cf. *angulata* not Campbell; Armstrong, p. 200, pl. 2, fig. 5-7, 14, 15.

1987 *Glendonina duodecimcostata* (not M'Coy); Clarke, p. 282.

1992b *G. duodecimcostata* (not M'Coy); Clarke, p. 76.

ETYMOLOGY: Named from Glendon, Hunter Valley, type locality.

HOLOTYPE: UQF 56157, figured by Armstrong (1969, pl. 2, fig. 5, 7, 14, 15) from Muree Formation, Glendon, north Sydney Basin.

DIAGNOSIS: Small transverse shells with moderately prominent umbones, 3-5 pair of low plicae, 2 sulcal subplicae and median dorsal furrow along fold crest, micro-ornament of small spines and elongate grooves. Adminicula short, well spaced, tabellae moderately long for family, short, widely diverging or subparallel.

DISCUSSION: This species is described by Armstrong (1969) and Waterhouse (1967a), the latter offering a careful comparison and contrast with *Notospirifer darwini* (Morris), which has lower broader ventral umbo, wider sulcus, slightly broader plicae, usually in 3 pairs, micro-ornament of globons and very short tabellae. One of Armstrong's figured specimens (1969, pl. 2, fig. 6), although regarded as conspecific, was not detailed by published registration number and shows comparatively long tabellae extending along the interspace each side of the fold. The holotype is chosen because its micro-ornament was well illustrated by Armstrong (1969). The ventral valve is figured by Waterhouse (1967a).

Monklandia gympiensis from the Rammutt Formation of the Gympie district, southeast Queensland, has thinner shell, and several individuals show more plicae. Sulcus, fold and adminicula are close overall but the sulcus is slightly deeper and fold higher and narrower in the new species. The tabellae are like those of the topotype in Armstrong (1969, pl. 2, fig. 6) rather than in the holotype or the specimen figured by Waterhouse (1967a).

Armstrong considered that he had five specimens of this form. He compared it with *Tomioopsis (Ingelarella) angulata* (Campbell), but the Glendon specimens all show lower broader ventral umbo, narrower sulcus and fold, and shorter tabellae compared with *angulata*. The micro-ornament of *angulata* lacks spines, judged from topotypes described by Parfrey (1988) and Waterhouse (1987a). Armstrong (1969, p. 203) thought that the specimen *darwinia?* of Waterhouse (1967a) might be closely

allied to so-called "*Spirifer*" *duodecimcostatus* M'Coy, but expressed some hesitation, and there was certainly no similarity to *Spirifer*, inverted commas or not. Clarke (1987, 1992b) insisted that the specimen was *Glendonina duodecimcostata*, but this is a more transverse species with bolder plicae, higher fold and deeper sulcus bearing a strong median subplication.

Subfamily **MESOPUNCTIINAE** n. subfam.

New Zealand and Queensland material assigned to Notospiriferidae include species characterized by shell, especially in projecting growth lamellae, which is strongly punctate internally (see Armstrong 1970, Waterhouse 1964, 1968, 1982). These punctae are shown by shell sections (Waterhouse 1964, pl. 37, fig. 4, 6), and also demonstrated in natural casts, wherein the punctae are filled by cores of matrix (Waterhouse 1968, pl. 14, fig. 10, pl. 15, fig. 6). These punctae are much deeper than found in the type species described for Notospiriferinae or Glendoninae, but do not open into the body cavity.

The constituent genera of Mesopunctiinae differ externally from other Notospiriferidae. *Wairakispirifer* lacks spinules and has moderately well formed plicae that grade evenly from the sulcus, and the sulcus is evenly concave with no sulcal subplication or subplicae, and the crest of the fold is rounded. *Mesopunctia* is close to *Wairakispirifer* but has high fold and low spinules. Its pits are moderately deep and crowded, approaching those of *Notospirifer*, but deeper and more cylindrical. Both genera differ externally from *Notospirifer* with its subplicae, *Farmerella* with its numerous strong plicae, *Glendonina* with its sulcal subplication, *Tabellina* with its broad high fold much stronger than lateral plicae, *Birchsella* with moderately wide sulcus and fold, and heavy internal thickening of ventral valve, and *Monklandia* with sulcal subplicae.

Genus ***Wairakispirifer*** n. gen.

ETYMOLOGY: Wairaki - place name, spirifer - brachiopod genus.

TYPE SPECIES: *Notospirifer microstriatus* Waterhouse, 1964.

DIAGNOSIS: Small transverse little inflated shells, with well formed ventral sulcus, no subplicae or median rib in sulcus, low wide rounded dorsal fold, well formed lateral plicae, micro-ornament of fine grooves in quincunx, no spines, mesopunctae restricted to anterior shell, penetrating to inner shell (Waterhouse 1964, pl. 37, fig. 6, Armstrong 1970, p. 293), narrowing at surface. Adminicula well formed, little posterior thickening. No tabellae in the type species.

DISCUSSION: The species *microstriatus* is characterized by its small size, low well formed plicae, moderately developed sulcus without subplication, mesopunctae especially well displayed in anterior lamellae, and absence of tabellae. Briggs & Campbell (1993, p. 325) referred the type species *microstriatus* to *Glendonina* McClung & Armstrong, 1978, and the same assertion was made by Clarke (1992b, p. 76) in referring to an article by H. J. Campbell & Clarke, as yet unpublished. *Glendonina* is readily distinguished from *Wairakispirifer*. It has a strong median plication along the sulcus, deeply grooved fold, and well developed spinules, and lacks mesopunctae. ***Wairakispirifer microstriatus*** (Waterhouse, 1964)

1964 *Notospirifer microstriatus* Waterhouse, p. 170, pl. 33, fig. 1, 8, 13, pl. 34, fig. 1,

2, pl. 36, fig. 2, text-fig. 79B (not pl. 33, fig. 5-7, 9-12, pl. 37, fig. 4, 6, text-fig. 78, 79A, C, D, E = *Mesopunctia macropustulosus*).

1987a *N. microstriatus* Waterhouse; Waterhouse, p. 39, pl. 11, fig. 3.

HOLOTYPE: BR 707 figured by Waterhouse (1964, pl. 33, fig. 1, 8, 13) OD from lower Mangarewa Formation, *Echinalosia maxwelli* Zone, Wairaki Downs, New Zealand.

DISCUSSION: This species is found in the *Echinalosia maxwelli* Zone of the Mangarewa Formation, and the Oxtrack Formation of southeast Bowen Basin, Queensland. The species was reported from locality GS 7807 (D44/f9878) in the Caravan Formation, Wairaki Downs (Waterhouse 1998) by Waterhouse (1968, p. 75, text-fig. 6A), because of general overall appearance, but greater inflation was noted, and grooves and ridges were reported. The exterior is now largely lost and it cannot be determined whether spines were present or not. Preservation is poor, and the identification should be left at Notospiriferid gen. & sp. indet.

Genus *Mesopunctia* n. gen.

ETYMOLOGY: meso - median (re depth of punctae), punctum - pore, Lat., ending rearranged.

TYPE SPECIES: *Notospirifer macrospinosus* Waterhouse, 1968.

DIAGNOSIS: Small transverse shells with rounded few plicae and smooth sulcus, rounded fold, micro-ornament of small blunt crescentic spines, weakly prolonged posteriorly, mesopunctate. Ventral interior as for family, tabellae short or absent.

DISCUSSION: This genus is characterized by wide deep mesopunctae, which pass through the primary shell layer and into, but not through the inner layer, best seen over anterior shell and growth lamellae. They do not penetrate to the inner surface, and have parallel sides, so that they were cylindrical. Tiny rather blunt and thick spines are present.

Mesopunctia macropustulosus (Waterhouse, 1968)

1964 *Notospirifer microstriatus* Waterhouse, p. 170, pl. 33, fig. 5-7, 9-12, pl. 37, fig. 4-6, text-fig. 78, 79A, C, D, E (not pl. 33, fig. 1, 8, 13, pl. 34, fig. 1, 2, pl. 36, fig. 2, text-fig. 79B = *Wairakispirifer microstriatus*).

1968 *N. macropustulosus* Waterhouse, p. 76, pl. 14, fig. 2, 3, pl. 18, fig. 2, 4, text-fig. 6E.

1983 *N. macropustulosus* Waterhouse; Waterhouse & Jell, p. 246, pl. 3, fig. 6.

1987a *N. macropustulosus* Waterhouse; Waterhouse, p. 39, pl. 8, fig. 9, 13, 15, 17, pl. 9, fig. 10, pl. 11, fig. 9, 11.

This species has been described from the *Echinalosia ovalis* and *Terrakea elongata* Zones of the Mangarewa Formation, Wairaki Downs, and from the lower Blenheim Formation, north Bowen Basin, and Flat Top Formation, southeast Bowen Basin, within the *Echinalosia ovalis* Zone. Additional D44 specimens are found in the *elongata* Zone of Wairaki Downs at f132 (GS 15221), f338, f335, f355, ?f359, f356, and f361. The micro-ornament consists of fine elongate grooves, and small broad pustules at their posterior ends, the grooves entering short punctae anteriorly. In BR 723 from GS 6072 (Waterhouse 1964b, pl. 33, fig. 6, 7, 9) there are thick tubes of matrix that filled the mesopunctae. These tubes are mostly deep and parallel-sided, not swollen.

Mesopunctia extensa (Campbell, 1961)

1961 *Notospirifer extensus* Campbell, p. 187, pl. 28, fig. 1-4.

1970 *N. extensus* Campbell; Armstrong, p. 289, text-fig. 1C, 2, 3D-H.

This species was described from beds of uncertain age in the southwest Bowen Basin by Campbell (1961), and Dear (1972, p. 8) attributed the species to the lower part of the Stanleigh Formation, with *Taeniothaerus*, *Pseudostrophalosia brittoni*, and other species. The micro-ornament and punctation were carefully examined from the types by Armstrong (1970), and he established the presence of punctae passing through the primary layer and entering the inner layer, indicating *Mesopunctia*. This is the oldest species so far known for Mesopunctiinae, and is of mid-Cisuralian age.

Mesopunctia tweedalei (Campbell, 1961)

1961 *Notospirifer extensus tweedalei* Campbell, p. 188, pl. 28, fig. 5-8.

1983 *N. extensus tweedalei* Campbell; Waterhouse, p. 160, pl. 3, fig. 5-8.

This species comes from the *Tomiopsis (Ingelarella) plica* Zone in north Bowen Basin. Micro-ornament is not well known, the types and others displaying small moderately deep pits, that might have been affected by wear. The form is close to *extensa* in outline and shows the *Mesopunctia* proportions of plicae and sulcus-fold. The taxon is allocated full species rank, and is slightly younger than *M. extensa*.

Mesopunctia spinosa (Waterhouse & Vella, 1965)

1965 *Notospirifer spinosus* Waterhouse & Vella, p. 70, pl. 4, fig. 4-13.

1978 *N. spinosus* Waterhouse & Vella; Suggate et al. 1978, text-fig. 4.7, fig. 15, 16.

1981 *N. spinosus* Waterhouse & Vella; Speden 1981, pl. 7, fig. 15, 16.

1998 *Glendonia duodecimcostata* (not M'Coy); Campbell et al. p. 292.

This species was described from the Flowers Formation of northwest Nelson. It is shaped rather like *Wairakispirifer*, especially because compaction and distortion have reduced the height of the plicae, and has little posterior thickening. Unlike *Wairakispirifer*, it has well developed microspines behind well formed surface grooves, and at least anterior mesopunctae. Most specimens show no tabellae. Waterhouse & Vella (1965) overlooked the presence of a faint rise in the median sulcus in a few specimens. This recalls the slightly older species *Glendonia duodecimcostata* (M'Coy, 1847) from the Muree Sandstone near Raymond terrace, north Sydney Basin (Armstrong 1969) and lower Moonlight Sandstone Member of north Bowen Basin (Waterhouse & Jell 1983, pl. 2, fig. 10, 14). According to McClung & Armstrong (1978), the species *duodecimcostata* occurs in a range of roughly middle Permian zones in east Australia, though further scrutiny might reveal lumping of species. Indeed *spinosus* appears to have been referred to that species in Campbell et al. (1998), but M'Coy's species is readily distinguished by its prominent sulcal subplication, and lack of mesopunctae.

Mesopunctia minuta (Campbell, 1960)

1960 *Notospirifer minutus* Campbell, p. 1121, pl. 140, fig. 6-8.

1970 *N. minutus* Campbell; Armstrong, p. 291, text-fig. 1A, D, 4.

LECTOTYPE: UQ F15829A/B, figured by Campbell (1960, pl. 140 (not 139), fig. 6-8), subsequently designated by Clarke (1987).

DISCUSSION: This species comes from the upper Blenheim Formation in the north Bowen Basin, and a ventral valve compared to this species from the upper Moonlight Sandstone is somewhat older, and so requires more material for adequate assess-

ment. Armstrong (1970) described and illustrated mesopunctae in the species. The species is close to the contemporaneous species *Mesopunctia macropustulosus* Waterhouse in appearance, but has a median cleft along the dorsal fold, and shows small but distinct tabellae (Waterhouse 1987a, p. 40). The species *macropustulosus* is found in the *Echinalosia ovalis* and *Terrakea elongata* Zones of New Zealand, and in the *E. ovalis* Zone of the Bowen Basin, and is then replaced by *M. minutus* in the *T. elongata* Zone of the Bowen Basin.

Clarke (1987, p. 279, text-fig. 14) reported this species from Malbina Formation Member E in Tasmania, but the dorsal fold is much more massive in his figure and globons rather than mesopunctae are present. He failed to appreciate that type *minutus* differs considerably from *Notospirifer* in the nature of its micro-ornament, as clearly shown by Armstrong (1970).

***Mesopunctia microspinosa* (Waterhouse, 1968)**

1968 *Notospirifer microspinus* Waterhouse, p. 78, pl. 14, fig. 4-6, 10.

HOLOTYPE: BR 1250, figured by Waterhouse (1968, pl. 14, fig. 5, 6, 10) OD from *Plekonella multicostata* Zone, Arthurton Group, near Arthurton, New Zealand.

DISCUSSION: This species has a dense array of small spines over the shell surface, and very fine short grooves are present, with details and dimensions described in Waterhouse (1968, pp. 78, 79). There is no median subplication, or pair of subplicae in the sulcus, and plicae are few and the fold and sulcus narrow and even more emphasized than in *Mesopunctia macrospinus*. Adminicula are short and tabellae minute. Mesopunctae are preserved on anterior lamellae as deeply penetrating cylinders of matrix, similar to those of *macrospinus*.

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