

**LATE PALEOZOIC
BRACHIOPODA AND MOLLUSCA
FROM WAIRAKI DOWNS, NEW ZEALAND**

J. B. WATERHOUSE



LATE PALEOZOIC

BRACHIOPODA AND MOLLUSCA

CHIEFLY FROM WAIRAKI DOWNS, NEW ZEALAND

**With notes on Scyphozoa and Triassic ammonoids
and new classifications of Linoproductoidea (Brachiopoda)
and Pectinida (Bivalvia)**

J. B. WATERHOUSE

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Prologue

The most closely studied Permian sequence of New Zealand lies at Wairaki Downs, western Southland. Here macro-invertebrate fossils are common, but not very well preserved. The very facts of their limited occurrence and difficult preservation in complex stratigraphy has impelled a close study of related faunas, especially in Australia, Himalaya, and world standard Permian, in order to unravel the New Zealand Permian correlations. So the humble Wairaki Downs Permian assumes some importance, not for what it contains, but the further enquiry it has stimulated. Thus in the present work, major brachiopod and bivalve groups are reassessed on a world-wide basis, unconstrained by geographic limits, or time.

Concomitantly, my fascination has grown in tracking the different views on evolution of brachiopod and molluscan groups, and seeking to understand the causes of the differences. It appears that interpretations often reflect fashionable world or local philosophies, and these are briefly outlined especially for bivalves in demonstrating the relation between individual studies and differing classifications. Although I have avoided taking further steps into "the psychology of the individual" some readers may even find a field open for such speculation! It does suggest the need for mature consideration and caution in assessing publications - in short, to retain scientific caution against the modern pressures of ambition and haste, and avoid the spurious assumption that the "latest work" is necessarily "the best" - many examples in New Zealand and east Australian work suggest the opposite. Some studies by paleontologists are simply background static against serious advance. The fundamentals remain valid - check the original source, check the specimens, check the field occurrence - accept nothing without questioning, no matter how great the reputation, and how recent the publication.

Other publications in the Earthwise series.

1998: *Ingelarelloidea* (Spiriferida: Brachiopoda) from Australia and New Zealand, and reclassification of *Ingelarellidae* and *Notospiriferidae*. *Earthwise 1*: 1-46.

1999: Some Permian Spiriferidan species (Brachiopoda) from New Zealand and Queensland. *Earthwise 2*: 1-16.

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Front cover: *Ingelarella subplicata* (Waterhouse) from Letham Formation, Wairaki Downs, internal mould showing adminicula (below) and tabellae (above).

**Late Paleozoic Brachiopoda and Mollusca, chiefly from Wairaki Downs,
New Zealand .**

**With notes on Scyphozoa and Triassic ammonoids, and new classifications of Linoproductoidea
(Brachiopoda) and Pectinida (Bivalvia).**

J. B. WATERHOUSE

Abstract

Significant new occurrences of Brachiopoda and Mollusca are described from the New Zealand Permian, especially Wairaki Downs area, and from related faunas of east Australia.

Amongst Brachiopoda, considerable adjustment is outlined for Linoproductoidea, Strophalosiidina and Ingelarelloidea. Some related taxa from Western Australia, Canada, Ireland, Nepal, Russia and United States are also reassessed. Newly named brachiopod genera are *Archboldina*, type species *Pustula micracantha* Hosking and *Lazarevonia*, type species *Krotovia arcuata* Waterhouse (Superfamily Productelloidea), *Callyconcha*, type species *Comuquia australis* Archbold (Superfamily Productoidea), *Nambuccalinus*, type species *Lyonia bourkei* Briggs, *Pinegeria*, type species *Terrakea? pinegensis* Grigorieva, *Spargospinosa*, type species *Terrakea belokhini* Ganelin, and *Regrantia*, type species *Striatifera linoproductiniformis* Cooper & Grant (Superfamily Linoproductoidea), *Bruntonaria*, type species *Dasyalosia lamnula* Brunton, *Capillaria*, type species *Strophalosia preoivalis warwicki* Maxwell, and *Melvillosia*, type species *Melvillosia canadense* n. sp. (Superfamily Strophalosiidae), and *Trigorhium*, type species *Neospirifer amphigyus* Cooper & Grant (Superfamily Spiriferoidea). New Productidin tribes are Lethamini, name genus *Lethamia* Waterhouse (Family Productellidae), Lyoniini, name genus *Lyonia* Archbold, Filiconchini, name genus *Filiconcha* Dear, Magniplicatinini, name genus *Magniplicatina* Waterhouse, Cookilellini, name genus *Cookilella* Archbold, and Undariini, name genus *Undaria* Muir-Wood & Cooper (Family Linoproductidae) and and Arcticalosiini, name genus *Arcticalosia* Waterhouse, Family Strophalosiidae. Subfamily Echinalosiinae, name genus *Echinalosia* Waterhouse, is proposed within Strophalosiidae. Figures are provided for some Asian types of which species are now found in Australia.

A number of new bivalves are recorded. New genera include *Manimanina*, type species *Posidoniella malimanensis* Gonzalez (?Family Atomodesmidae, Pterida?), and *Newellipectinia*, type species *Aviculopecten americanum* Newell & Boyd, *Vanvleetia*, type species *A. vanvleeti* Beede, *Furcatia*, type species *Etheripecten petulantus* Waterhouse, *Strebloboyardia*, type species *Aviculopecten? montpelierensis* Girty, *Pectengonzalez*, type species *Obliquipecten granti* Newell & Boyd, *Lionicula*, type species *Streblochondria? lionensis* Fleming, and *Zelotypia*, type species *Maccoyella incurvata* Waterhouse for Aviculopectinidina. New family groups are Subfamily Manimanininae, name genus *Manimanina* Waterhouse (?Family Atomodesmidae), Subfamily Undopectininae, based on *Undopecten* Waterhouse (Family Aviculopectinidae), Tribe Aucellinini, name genus *Aucellina* Pompeckj (Family Chaenocardiidae), Subfamily Limatulinae, based on *Limatulina* de Koninck (Family Streblochondriidae), Subfamily Orbiculopectininae with Tribes Orbiculopectinini, based on *Orbiculopecten* Gonzalez and Eocamptonectini, based on *Eocamptonectes* Newell (Family Dellopectinidae), Tribe Furcatiini, name genus *Furcatia* Waterhouse (Family Huanopectinidae), Family Dolponellidae, based on *Dolponella* Waterhouse (Superfamily Eurydesmidae) and Subfamily Plesiocyprinellinae, based on *Plesiocyprinellina* Mendes (Family Megadesmidae). Order Pectinida is subdivided into three suborders, Pectinidina Waller, Aviculopectinidina new and Monotidina new.

Several gastropods are revised, with a new tribe Spirovallinii based on *Spirovallum* Waterhouse (Family Eotomariidae).

New Triassic ammonoid taxa are *Beaumontaria*, type species *B. grebneffi* n. sp. (Family Ceratitidae), *Kakaria*, type species *Prospiringites coombsi* Kummel (Family Parapopanoceratidae), *Simplicites*, type species *Leiophyllites marshalli* Browne, and Subfamily Indirigophyllitinae (Family Ussuritidae).

As well as new discoveries and new descriptions, attention is devoted to the contributions by several paleontologists from New Zealand, Australia and North America, where their work has affected understanding of New Zealand Permian stratigraphy and systematic fossil studies.

Keywords Permian, Triassic, New Zealand, Bowen Basin, Sydney Basin, Brachiopoda, Gastropoda, Bivalvia, Ammonoidea, classification of brachiopod and bivalve groups

New Taxa. Brachiopoda Ordinal group: Lytoniida. Family group: Subfamily Echinalosiinae, Tribes Lethamiini, Lyoniini, Filiconchini, Cookilellini, Magniplicatinini, Undariini, Echinalosiini and Arcticalosiini. Genera *Callyconcha*, *Archboldina*, *Lazarevonia*, *Nambuccalinus*, *Pinegeria*, *Regrantia*, *Spargospinosa*, *Bruntonaria*, *Capillaria*, *Melvillosia*, and *Trigorhium*. Species, subspecies: *Paucispinauria paucispinosa wardenensis*, *Saetosina dawsonensis*, *Magniplicatina heywoodi*, *Echinalosia conata*, *E. floodi*, *E. discinia briggsi*, *E. ovalis tasmantia*, *Melvillosia canadense*, *Wyndhamia typica crassispina*, *W. clarkeina*, *Acanthalosia? parfreyi*, *Marinurnula ovata*. **Bivalvia** Ordinal groups: Suborder Aviculopectinidina, Suborder Monotidina. Family group: Malimanininae, Undopectininae, Aucellinini, Limatulinae, Orbiculopectininae, Orbiculopectinini, Eocamptonectini, Dolponellidae, Plesiocyprinellinae. Genera: *Malimanina*, *Newellipectinia*, *Vanvleetia*, *Furcatia*, *Strebloboyardia*, *Pectengonzalez*, *Zelotypia*. Species: *Aphanaia proiectus*, *A? glabra*. **Gastropoda** Family group: Spirovallini. **Ammonoidea** Family group: Indirigophyllitinae. Genera *Beaumontaria*, *Kakaria*,

Simplicites. Species: *Beaumontaria grebneffi*.

Major reclassifications: Superfamily Linoproductoidea, Family Strophalosiidae, Pectinida, Late Paleozoic Pholadomyida

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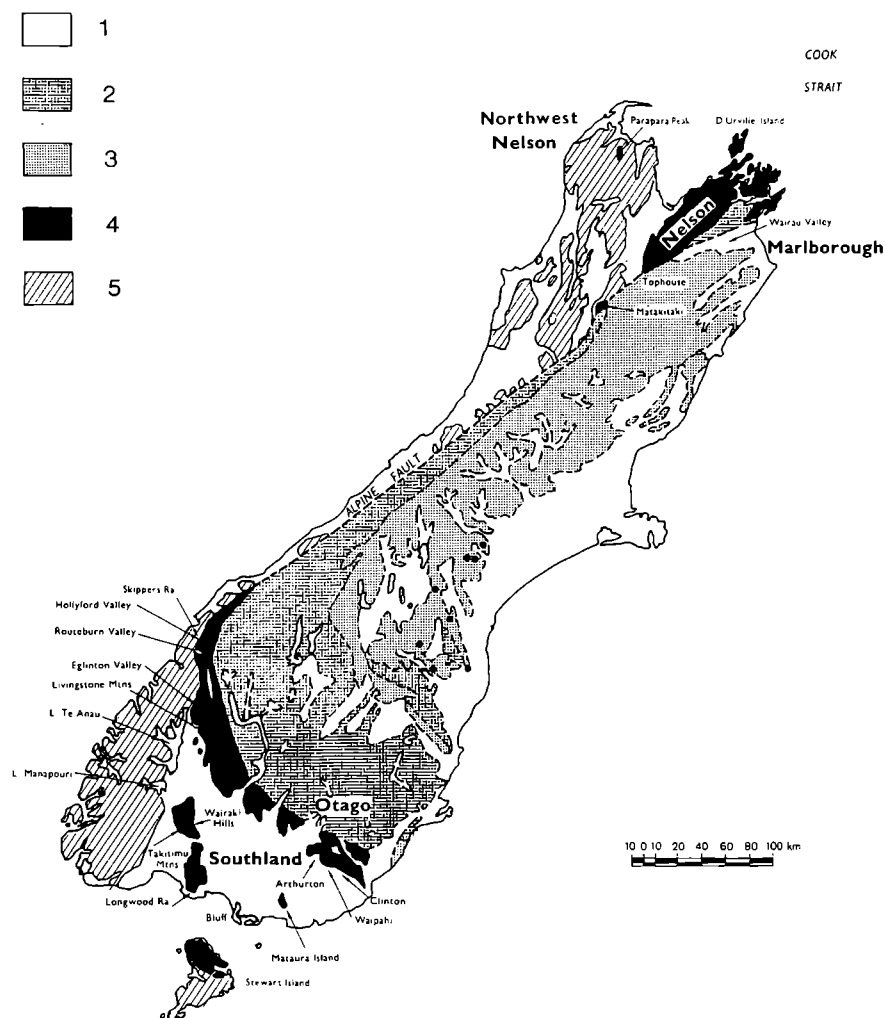
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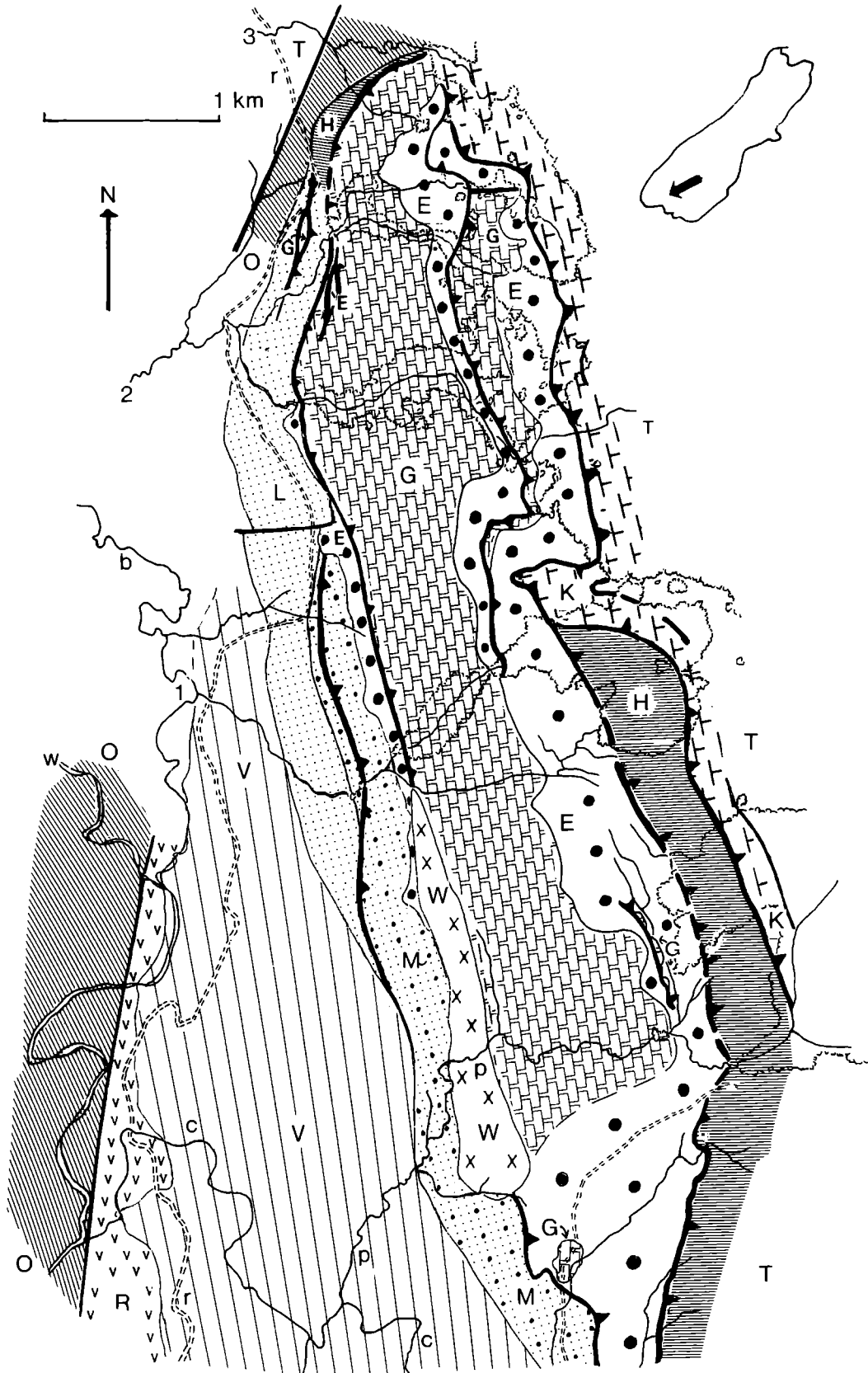
INTRODUCTION

This monograph describes new collections of Permian Brachiopoda and Mollusca, the bulk made by the writer, as well as substantial collections at the Department of Geology, University of Otago. These come mostly from the Wairaki Downs, western Southland, New Zealand (text-fig. 1, table 1). Previous work is revised where relevant, and related Permian species of east Australia, especially from the Sydney and Bowen Basins, are re-examined, with mention of some west Australian, Canadian, Irish, Nepalese, Russian and United States taxa where relevant. Systematic summaries are also provided for some middle Triassic ammonoids from New Zealand.

Considerable attention is focussed herein on the classification of some major groups of invertebrate fossils that are particularly significant in Permian collections from east Australia and New Zealand, and are important world-wide. These groups include the Linoproductoidea and Strophalosiidae (Brachiopoda), which are substantially changed from the study offered in the revised brachiopod treatise by Brunton, Lazarev, Grant & Jin (2000). Revision is found to render the classification more logical, and much more accurate, because there are many objective errors in the revised brachiopod treatise. As well, Late Paleozoic and Mesozoic members of Pectinida, involving Aviculopectinidina and some Monotidina are revised on a world-wide basis, with close attention to the views of Professors Newell & Boyd, and contrary views by Drs M. M. Astafieva, M. R. W. Amler and Prof. K. Nakazawa. In addition the Late Paleozoic Pholadomyida are reviewed, building on the classification by Morris, Astafieva & Dickins (1991).



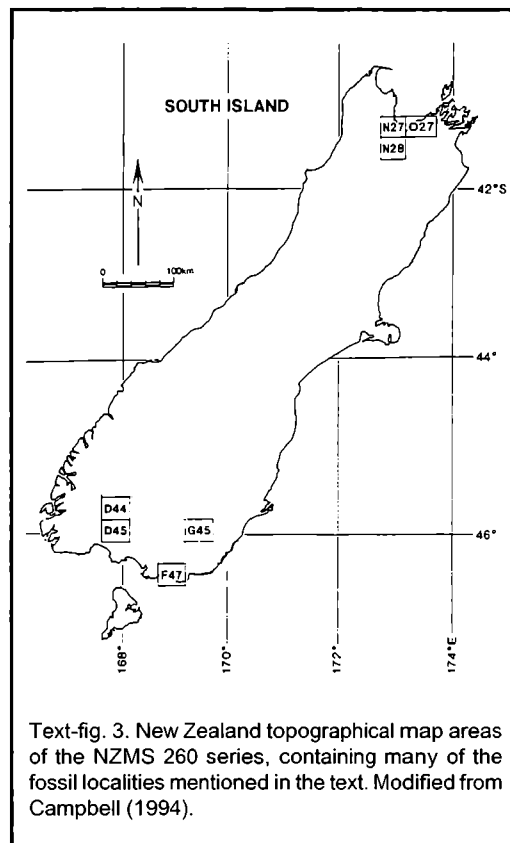
Text-fig. 1. South Island, New Zealand, showing approximate distribution of rocks, with place names mentioned in text. Wairaki Downs lies west of Wairaki Hills, north of Ohai. Adapted from Suggate et al (1978, p. 148). 1, largely post Permian, mostly Cretaceous-Recent. 2, Haast and Otago Schist of metamorphosed Carboniferous - Triassic. 3, "Torlesse" mostly Permian and Triassic, minor Carboniferous. 4, Carboniferous, Permian and Triassic (including Maitai Supergroup, Brook Street, Dun Mountain, Croisilles and Patuki rocks). 5, Pre-Permian sediment as well as igneous rock of varying age.



Text-fig. 2. Simplified Permian and Mesozoic geology of Wairaki Downs, west of Wairaki Hills at 167°57'E, 45°47'S. Formations: E, Elsdun Formation (Jurassic); G, Glendale Formation (Lopingian); H, Coral Bluff Assemblage, with Hilton Limestone (Lopingian) and Old Wairaki Hut Formation (Cisuralian or ?Triassic); K, Wairaki Breccia-Conglomerate (late Lopingian); L, Letham Formation (late Cisuralian); M, Mangarewa Formation (Guadalupian); O, Old Wairaki Hut Formation (late Cisuralian, or early Triassic?); R, Elbow Creek Formation (late Cisuralian); V, Caravan Formation (late Cisuralian); W, Weetwood Formation (Mesozoic igneous). Geographic features: b, Letham Burn; c, Elbow Creek; p, Productus Creek; t, track from Beaumont Station to Barrett's hut; w, Wairaki River; 1, 2, 3 major east tributaries of Letham Burn. Major thrusts shown by heavy lines with diamonds. Map prepared from aerial photograph no. 5215 (1978). From Waterhouse (1998a, b).

Table 1 . Stratigraphic succession and biozones for Permian at Wairaki Downs and Takitimu Mountains.

Sedimentary unit	Biozone	Correlation
Wairaki Breccia-Conglomerate	<i>Wairakiella rostrata</i>	Lopingian
Hilton Limestone	<i>Spinomartinia spinosa</i>	Series
Glendale Formation	<i>Plekonella multicostata</i>	
	rock and faunal gap	
Mangarewa unit 8	<i>Terrakea elongata</i>	Guadalupian
Formation		
7	<i>Echinalosia ovalis</i>	Series
6		
5	<i>Pseudostrophalosia? cf blakei</i>	
Letham Burn Member	<i>Echinalosia maxwelli</i>	
4		
Letham Formation		
3	<i>Echinalosia discinia</i>	Cisuralian
2		
1	<i>Spiriferella supplanta</i> fauna	Series
Caravan Formation	Anidanthin sp. indet. fauna	
Elbow Creek Ftm	<i>Attenuatella altilis</i> fauna	
Old Wairaki Hut Ftm	Triassic or late Cisuralian? infaunated or successive	
McLean Peaks Ftm	<i>Echinalosia conata</i>	
	<i>Spinomartinia? adentata</i>	
Chimney Peaks Ftm		
Brunel Formation	<i>Terrakea dickinsi</i>	



Text-fig. 3. New Zealand topographical map areas of the NZMS 260 series, containing many of the fossil localities mentioned in the text. Modified from Campbell (1994).

The stratigraphy, succession and history of geological study in the Wairaki Downs is studied in an accompanying monograph, planned as volume 4 of the current series. In that study, biozones and correlations with the international Permian standard (tables 2, 3), and sequences of the remainder of the New Zealand Permian, and east Australia (table 4), are reviewed, together with available data on radiometry. Preliminary summaries of stratigraphy and correlation were provided by Waterhouse (1997b, 1998a, b). In conformity with the International Guide to stratigraphic nomenclature (Salvador 1994), the stratigraphic nomenclature follows those works, as they have priority over names used in a different and redundant sense by Landis et al (1999). That study interpreted the geology of Wairaki Downs according to a structural model, and its maps and understanding of stratigraphy and structure have proved too inaccurate to allow comprehension of the biozonal succession.

SYSTEMATIC STUDIES

Permian Brachiopoda and Mollusca from the Wairaki Downs of New Zealand have been systematically studied by Fletcher (in Fletcher et al 1952) and Waterhouse (eg 1963a, b, 1964b, 1965a, 1968a, 1979c, 1980a, c, 1982a, b, 1998c, 1999b). Promises of other paleontological studies in Landis (1987) and Campbell, Owen & Landis (1995) have not yet been kept. The collections have been expanded since 1976 by the writer, with the discovery of new forms, new fossiliferous levels, and additional material. Some species and a number of genera are described from beyond Wairaki Downs.

Locality records, repositories

The distribution of the formations is shown in Text-fig. 1, 2, and more detailed locations are mapped and figured in the companion volume. Data on sediment type and association of fossils are provided in Mutch (1972) and Waterhouse (1964a, 1973b, 1977, 1979b, 1982a, b). Collections within the range of D44/f108-137, 374-377, 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 Brachiopod registry), and TM (type Bivalvia, Gastropoda). The Department of Geology, University of Otago, Dunedin, holds the

Table 2. International standard for Permian stages (Wardlaw 2000) based on conodonts, and principal subdivisions of benthonic faunas, summarized in Waterhouse (1976b, table 1, p. xiv), and based primarily on fusulines and brachiopods.

Series	Stage	"Substage" or level
Lopingian	Changhsingian	
	Wuchiapingian	
Guadalupian	Capitanian	Hegler etc Appel Ranch
	Wordian China Tank	Willis Ranch
	Roadian	
Cisuralian	Kungurian	lower Ufimian Irenian (minor Elkin level) Irenian (Nevolin fauna) Filippovian Saranin
	Artinskian	Sarginian Aktastinian
	Sakmarian	Sterlitamakian Tastubian
	Asselian	Kurmaian Uskalikian Surenan

collections D44/f304-365, and important specimens are serially numbered with prefix OU. All of the localities are recorded in the national archival Fossil Record File of the Geological Society of New Zealand, which is arranged numerically within each sheet district of the 1:50 000 New Zealand Infomap 260 series (text-fig. 3).

In Australia, the convention for many institutions is to indicate the fossil locality number with prefix L and the fossil serial number with prefix F on the actual specimen or enclosing matrix, with no further guidance as to institution. Collections are registered serially by number in each institution and Briggs (1998) has provided detailed descriptions of localities. Here I add prefixes as summarized below, but these prefixes are not on the actual specimens.

UQ - Department of Geology, University of Queensland, Brisbane, (now transferred to the Queensland Museum), QM - Queensland Museum, Brisbane, GSQ Geological Survey of Queensland, Brisbane, UNE - University of New England (types now transferred to Australian Museum), AM - Australian Museum, Sydney, SUP - Department of Geology, University of Sydney, Sydney, GST - Geological Survey of Tasmania, Hobart, GSWA - Geological Survey of Western Australia, Perth.

Further references are made to other institutions. BB - Natural History Museum, London, SM - Sedgwick Museum, Cambridge, GSI - Geological Survey of India, Calcutta, USNM - United States National Museum, Washington, D.C., GSC - Geological Survey of Canada, Calgary.

MATERIAL: The heading Material in the text refers to new or additional material reinforcing collections described in previous systematic studies, unless otherwise stated. Further Permian collections at the Geological Institute in Lower Hutt and Department of Geology, University of Otago, remain to be examined. They come mostly from the Letham and Mangarewa Formations of the Wairaki Downs Group, and the Wairaki Breccia-Conglomerate.

ABBREVIATIONS: OD - by original designation; SD - by subsequent designation. Abbreviations used for Dimensions are: L - length, W - width, H - height.

Subspecies

Herein, subspecies are regarded as entities essentially identical with the full species. They may differ to slight degree in age range or geographic extent, and generally show a preponderance of a feature or features less common in the types.

Morphology in articulate brachiopods

The revised brachiopod treatise has provided a glossary and explanation for morphological terms (Williams, Brunton & MacKinnon 1997), with emphasis on Lower Paleozoic and Tertiary-Recent brachiopods.

Table 3. Putative correlations for New Zealand biozones and faunas with International standard for Permian stages

Series	Stage	New Zealand biozone
	Changhsingian	<i>Wairakiella rostrata</i> <i>Marginalosia planata</i> <i>Spinomartinia spinosa</i>
Lopingian	Wuchiapingian	<i>Plekonella multicosata</i> <i>Martiniopsis woodi</i> (likely faunal gap)
	Capitanian	(possible faunal gap) <i>Yabeina-Lepidolina</i> fauna (possible faunal gap) <i>Terrakea elongata</i>
Guadalupian		<i>Echinalosia ovalis</i> <i>Pseudostrophalosia?</i> cf <i>blakei</i> fauna
	Wordian	<i>Echinalosia maxwelli</i>
	Roadian	<i>Echinalosia discinia</i> <i>Spiriferella supplanta</i> fauna Anidanthin sp. indet. fauna <i>Attenuatella altilis</i> fauna
Cisuralian	Artinskian	(? Old Wairaki Hut Ftm) <i>Echinalosia conata</i> <i>Spinomartinia?</i> <i>adentata</i> <i>Terrakea dickinsi</i>
	Sakmarian	Gondor Ftm fauna Dunton Peak fauna
	Asselian	<i>Neoplatyteichum impressa</i> faunule

COSTAE, COSTELLAE. Williams, Brunton & Mackinnon (1997, p. 335) proposed changing the definition of costae-costellae from "an arbitrary use to imply a relative coarseness in texture." In their redefinition, costae arise at the margin of the bryophic shell, and costellae arise by splitting from costae, or by intercalation. This is feasible. Equally, others might prefer, and surely should prefer, to provide detailed analysis of the mode of increase. Thus we are no further ahead. In the meantime, the established terminology is retained. There are difficulties not adequately addressed in the proposal to change the terminology.

1. It destroys some 40 years of descriptions, and abandons the term capillae.
2. It ignores the common fact that much material will not be preserved well enough to show whether costae are increasing or not, and the new nomenclature is too inflexible to cope.
3. Costae and capillae are used in other phyla, and cannot be adapted to the new proposals.
4. Many brachiopods have radial ornament limited to the shell margin, with smooth posterior. The nomenclature for these shells is not addressed.

The merit of the proposal lies in pointing to the need for analysing the mode of increase and change to radial ornament, and this is not fully met by the proposed changes to definitions of words. To meet the requirements for nomenclatural stability, and to meet the meritorious part of the argument, it is proposed to retain the terms costae, costellae and capillae as in common use. To cover the mode of increase, it is suggested that fissicostae (or fissicostellae) be applied, where known and where relevant, to ribs that increase by splitting. And intercostae - or intercostellae - may be applied where the ribs increase by intercalation. This will avert confusion, and retain whatever merit is attached to the definitions of costae-costellae and capillae as in Muir-Wood & Cooper (1960).

INTERNAL PLATES

Confusion remains over internal plates. For instance the adminicula of *Syringothyris* were called dental plates (Williams, Brunton & Mackinnon 1997, text-fig. 355): the authors were ill-at-ease with the Australian concept of adminicula devised for Spiriferida. Similarly tabellae, the dorsal equivalent, remained an unfamiliar and, to them, new and therefore unacceptable concept. Sometimes the clumsy and repetitive term "dorsal adminicula" is used, implying the need for "ventral adminicula," although further confusion is often caused by omission of the term "ventral". I prefer to use tabellae for dorsal plates, and adminicula for the different ventral

plates, because such applications are precise and concise, and unambiguous. By contrast, ventral and dorsal interareas are acceptable, because the terms apply to two parts of one functional structure.

As well, the term “inner hinge plates” is used in the revised brachiopod treatise for plates sited far in advance of the hinge. Campbell (1965, p. 10) notwithstanding, the reservations expressed by that great brachiopod expert J. Allan Thomson (1927, p. 87) about the inappropriate use of hinge plate, as opposed to the true use of the term for posterior horizontal plate seen in *Magellania*, for me remain valid. In describing brachiopod internal plates, neutral terms should be preferred. If a plate is nowhere near the hinge, and does not relate to the hinge, it should not be called a hinge-plate. Otherwise terms become misleading. If a “hinge-plate” migrated in position, or changed in function, it should not be called a hinge-plate, because it is no longer a hinge-plate, and anyway, claims about change and ontogeny often are subjective, and potentially will be overturned by further study.

The nomenclature of internal dorsal plates thus remains in some confusion. Reservations have been expressed about attempts to insist on one special definition of “crural plates”. Chatterton (1973) commented on a different usage by Pitrat (1965). Grant (1976, p. 49, see pl. 7 etc) used crural plate for a plate attached to what he called the socket plate and stated that it “is called the “crural plate” because the brachiophore extends forward from the upper part of that plate”. Cooper & Grant (1974) introduced further specialist terms, omitted by Williams, Brunton & MacKinnon (1997), perhaps because these authors have not been engaged in recent years with systematic description of such brachiopods.

Overall, the questions posed by Campbell (1965, pp. 9-14) over homologies and analogies amongst dorsal internal plates raise the need for further analysis and study of ontogenetic development, somewhat neglected in the revised brachiopod treatise. This lack again, to me, reinforces the need for neutral terms. Some authors have made it clear that any difference from their views was to be deplored. But a long-lasting failure to use “adminicula” and a preferred use of “pedicle valve” against the correct “ventral valve” shows that no-one achieves infallibility, and it is clearly scientific, courteous and tolerant to avoid derisory comments on other studies, especially in a treatise, and to be cautious in rejecting differing applications of names for morphological parts.

Otherwise the section on morphology in the revised brachiopod treatise raises comparatively few problems. It is primarily the misinformation on age, synonymies and generic definitions for Productida that are matters of graver concern (Waterhouse 2000c, d, e).

Brachiopod terms used herein

adminicula - plates in Spiriferida, supporting dental plates from floor of ventral valve.

globon - swollen hollow chamber formed by exopunctae in some Notospiriferidae, especially *Notospirifer*.

mesopunctae - hollow pores that extend through outer shell layer into main shell layer, but do not reach interior, unlike endopunctae (as in *Mesopunctia*, *Wairakispirifer*).

tabellae - plate in dorsal valve supporting crural plate from floor of valve.

tigillum - thickened shell along mid-line of ventral valve in front of muscle field, in Ingelarellidae.

Guides to major classification of articulate brachiopods

Chonetidina - Follows Racheboef 2000.

Productelloidea - In need of recognition and major revision.

Linoproductoidea - Substantially revised herein.

Strophalosiidae - Some modification to Brunton, Lazarev, Grant & Jin 2000.

Spiriferoidea - Substantially follows Carter et al 1994.

Ingelarelloidea - Largely follows Waterhouse 1998c.

Morphology for Bivalvia

A discussion of ligament types, especially relevant to Pectinida, is provided in the introductory sections on Aviculopectinidina (see text-fig. 9, 10).

alivincular - external ligament with median resilifer.

canalivincular - channelform ligament, concave, with only growth markings.

duplivincular - ligament in which grooves form chevrons.

lativincular - ligament with very wide resilifer, previously termed alivincular or transitional ligament.

lineavincular - ligament in which grooves for fusion layers lie subparallel to hinge, previously included as duplivincular ligament, but grooves do not form chevrons.

platyvincular - ligament in some Pectinida without resilifer, broad and somewhat concave, previously termed transitional ligament.

pseudotrabeculae - ridges radiating from under umbo across ligament area on some Aviculopectinidina.

replivincular - ligament in which chevrons of duplivincular ligament are truncated and relict, but still converge or slant towards umbo.

Guides to major classification of Bivalvia

Pectinida - Substantially modified from Newell & Boyd 1995.

Pholadomyida - Builds on Morris et al 1991.

Phylum COELENTERATA Frey & Lenckart, 1847
 Class SCYPHOZOA Gotte, 1887
 Subclass CONULATA Moore & Harrington, 1956
 Order CONULARIIDA Miller & Gurley, 1896
 Superfamily **CONULARIOIDEA** Walcott, 1886
 Family **CONULARIIDAE** Walcott, 1886
 Subfamily **PARACONULARIINAE** Sinclair, 1952
 Genus ***Paraconularia*** Sinclair, 1940
Paraconularia sp.
 Pl. 1, fig. 1

MATERIAL: A specimen OU 2600 from D44/f35, Glendale Formation, Wairaki Downs.

DESCRIPTION: Specimen shows two faces, with corner grooves which disrupt costae, numbering 9-10 in 5mm, some ending with swollen tubercle, but surface worn, suggestion of fine lines parallel to costae. Well defined groove in middle of face.

RESEMBLANCES: The specimen differs in shape and density of costae from *Paraconularia derwentensis* (Johnston), as described by Waterhouse (1979c) from the Letham Formation, and from *P. ornata* Waterhouse of the *Plekonnella multcostata* Zone in the Arthurton Group. The number of costae, shape, and face groove are somewhat closer to features seen in the Late Triassic species *P. matauraensis* Waterhouse, 1979d.

Phylum BRACHIOPODA Dumeril, 1806
 Order PRODUCTIDA Sarytcheva & Sokolskaya, 1959

Russian authorities were first to appreciate the currently accepted rank of productids, against considerable resistance from many western paleontologists. For instance Cooper & Grant (1975) persisted in referring productidins to Order Strophomenida Opik, a matter of historical record expunged from the brief historical introduction to Productida in the revised brachiopod treatise. Brunton, Lazarev & Grant (2000, p. 351) did allow that Waterhouse (1978, p. 20) recognized the full ordinal status of Productida, and this was also true of Waterhouse (1975, p. 4). This was because I gave high value to the Russian work. Brunton, Lazarev & Grant (2000) further stated that Waterhouse (1978) recognized two subdivisions, Productidina and Strophalosiidina, but in fact Waterhouse (1975, 1978, p. 23) recognized three, because Chonetidina was included. Many authors, including Cooper & Grant (1974) and Williams, Harper & Grant (2000) allow Lyttoniidina (formerly Oldhaminidina) as well, but I consider that this is a separate order, now named Lyttoniida (after Oldhaminida Waterhouse 1983).

Suborder CHONETIDINA Muir-Wood, 1955
 Superfamily **RUGOSCHONETOIDEA** Muir-Wood, 1962
 Family **RUGOSCHONETIDAE** Muir-Wood, 1962
 Subfamily **RUGOSCHONETINAE** Muir-Wood, 1962
 Genus ***Neochonetes*** Muir-Wood, 1962

Archbold (1981b, p. 113) pointed out that *Neochonetes beatusi* Waterhouse from the Mangarewa Formation "was a large species with hinge spines at a low angle and a gentle broad sulcus that might be a migratory descendent of the *N. granulifer* stock". This stock includes the type species. He recognized no comparable species anywhere in Australia, including the chonetid-rich faunas of Western Australia, where species tend to have maximum width placed in front of the hinge, and hinge spines emerge at a higher angle. The type species of *Neochonetes*, *N. dominus* (King 1938, pl. 36, fig. 3-6) from Upper Carboniferous of Texas, has shallow sulcus and spines emerging at a low angle. Internally, well developed lateral septa lie between the adductors in the dorsal valve, much as in the New Zealand species *beatusi*, eg BR 1444 from GS 9697 (Waterhouse 1982a, pl. 5, fig. f). Vascular trunks appear to be developed on the ventral valve in *beatusi* as in *dominus* (see Chacon-Martinez & Winkler Prins 2000).

For the subgenus *Sommeria* Archbold 1981b, altered to *Sommeriella* Archbold, 1982, the diagnosis shows that it is based on features that vary even within the type species, and are not unique. The sulcus is described as *usually* conspicuously developed, but it is by no means profound, and there is *often* a dorsal fold, the ventral valve is more convex (how much not stated), and spines emerge at 40-45°. The maximum width of the shell *usually* lies anterior to the hinge. His figures (Archbold 1981b, text-fig. 6J, K, R) show that some specimens are alate and transverse with maximum width at the hinge, counter to the general rule. The diagnosis delineates low-ranking and somewhat variable discriminants for a superspecies within the genus

Neochonetes, and arguably this qualifies as a subgenus. On the other hand, vascular trunks do not appear to be developed in the ventral valve, according to the figures provided by Archbold (1981b). and this suggests a significant difference from *Neochonetes dominus*.

Neochonetes beatusi Waterhouse, 1964b

1964b *Neochonetes beatusi* Waterhouse, p. 18, pl. 1, fig. 3-6.

1982a *N. beatusi* Waterhouse; Waterhouse, p. 28, pl. 5, fig. c-f, pl. 6, fig. a, b.

HOLOTYPE: BR 743, figured by Waterhouse (1964b, pl. 1, fig. 4) OD from D44/f9870 (GS 7352), lower *Echinalosia ovalis* Zone, Mangarewa Formation, Wairaki Downs.

DISCUSSION: Four chonetid taxa have been described from the Middle to Late Permian of east Australia and New Zealand, *Neochonetes beatusi* Waterhouse, *Lissochonetes semicircularis* Campbell (1953, pl. 1, fig. 10-13, Hill & Woods 1964, Dear 1971, pl. 2, fig. 9, Hill et al 1972, Waterhouse 1986b, pl. 2, fig. 33-35, pl. 3, fig. 1-4, pl. 15, fig. 2-5, Parfrey 1988, pl. 2, fig. 11-13), *L. semicircularis solida* Dear (1971, pl. 2, fig. 1-8), and *Capillonia brevisulcus* (Waterhouse, 1964b, 1973a, 1982a). External ornament on *beatusi* shows well developed ribbing, characteristic of *Neochonetes*. The other east Australian and New Zealand species are comparatively smooth.

Additional chonetid material from the Letham Formation is only moderately well preserved, leading to some uncertainty over identification. A very few specimens at D44/f108 (GS 15208) and D44/f110 (GS 15207) show costae crossed by low growth lines, suggestive of *Neochonetes*. But even these specimens appear to be smooth - possibly due to wear - over the posterior ventral valve. Specimens from the lower *Echinalosia discinia* Zone at D44/110 (GS 15207) and D44/f307, ?f313, f314, f312, f326, f328, f330, and f331 are probably *beatusi*. A number of individuals of likely *beatusi* are found in the *Lethamia ligurritus* Subzone at D44/f108 (GS 15208), ?f109 (GS 15209), f113 (GS 15212), f115 (GS 15210), f1001 (GS 9697), f305 and f319.

The suites vary somewhat in shape, and other than variably preserved ornament, no truly consistent and reliable feature can be discerned that would allow a firm discrimination of morphotypes consistent with age. As well, internal differences are not clear for many specimens. Therefore rather similar specimens are provisionally aggregated as *beatusi*, implying that it was a wide-ranging, facies-tolerant species, which persisted through the *Echinalosia discinia* and *E. ovalis* zones.

Subfamily **SVALBARDIINAE** Archbold, 1982
Genus ***Capillonia*** Waterhouse, 1973

TYPE SPECIES: *Lissochonetes brevisulcus* Waterhouse, 1964.

DISCUSSION: This genus was distinguished by Waterhouse (1973a) from *Lissochonetes* Dunbar & Condra by its dorsal ornament of fine capillae and smooth ventral valve, apart from growth lines on both valves. As noted by Archbold (1981b, p. 4), there must be some reservations over the dorsal capillae, and perhaps it is not really possible to tell if there has been very slight weathering of an originally smooth surface to produce an ornament of fine growth lines and faint capillation: ultrastructure study may be needed to be sure. Whether there are further distinctions remain a little uncertain, because not all chonetid genera are fully known.

Archbold (1983a) and Parfrey (1988, pl. 2, fig. 11-13) referred to *Capillonia* the species *semicircularis* Campbell, 1953, from the lower Peawaddy Formation of southwest Bowen Basin. This species was also recorded from the Barfield Formation and lower Flat Top Formation by Dear (1971) and Waterhouse (1986b) with provisional comparison to *Capillonia*. To judge from well preserved Flat Top material, *solida* comes generically close to *Capillonia brevisulcus*, although its outline is less semicircular, with less prominent lateral extremities, and in turn is difficult to separate from *semicircularis*, by other than degree of maturity (Waterhouse 1986b). Campbell's species was recorded by McClung (1983, text-fig. 12:2) as "*Lissochonetes*", for it seems that he did not accept genera proposed after the 1965 brachiopod treatise.

The type species of *Lissochonetes*, *Chonetes geinitzianus* Waagen, 1884 from United States has smooth valves, apparently fewer hinge spines, and less defined lateral septa, with different ontogenetic development.

Tivertonia Archbold, 1983, type species *Lissochonetes yarrolensis* Maxwell, 1964 is close in number of spines to type *Capillonia*, but tends to be less alate with maximum width placed near mid-length. Just how reliable these criteria are for generic distinction remains to be established, because Archbold (1983a, 1986b) figured mostly incomplete specimens, and worn chonetid specimens often lose the hinge spines and cardinal extremities. If the shape does not offer a consistent distinction, then the genus may have to lapse into synonymy. Archbold also stressed the shortness of hinge spines, but provided no figures or textual description to confirm that the full length of the spines in mature specimens had been accurately determined. Archbold in Waterhouse (1986b, p. 22) elaborated his diagnosis of *Tivertonia*, but even so Shi in Shi & Waterhouse (1991) pointed out the need to further explain the genus. Figures so far available suggest that the differences between *Tivertonia yarrolensis* and *Capillonia brevisulcus* could prove to be of only specific rank, although *C. brevisulcus*, like *C. semicircularis solida*, appears to have heavier marginal ridging in the dorsal valve.

Capillonia brevisulcus (Waterhouse, 1964)

Pl. 1, fig. 2 - 8, 9

1925 *Chonetes* cf *vishnu* (not Salter); Marwick, p. 362, text-fig. 2, 3.1956 *Chonetes* aff *vishnu* (not Salter); Marwick in Wood, p. 47.1964b *Lissochonetes brevisulcus* Waterhouse, p. 21, pl. 1, fig. 7-11, pl. 2, fig. 1-8, pl. 3, fig. 1-12, pl. 31, fig. 3-4, text-fig. 2A, 3-5.?1969 *Lissochonetes* sp. Runnegar & Ferguson, pl. 5, fig. 8.1973a *Capillonia brevisulcus* (Waterhouse); Waterhouse, p. 37.1978 *C. brevisulcus* (Waterhouse); Waterhouse & Mutch, p. 517, text-fig. 3-6.1978 *C. brevisulcus* (Waterhouse); Suggate et al, text-fig. 4.7, fig. 6, 10.1981 *C. brevisulcus* (Waterhouse); Speden, pl. 7, fig. 6, 10.1982a *C. brevisulcus* (Waterhouse); Waterhouse, p. 29, pl. 6, fig. c.2000 *C. brevisulcus* (Waterhouse); Racheboeuf, p. 415, text-fig. 271.2a-c.

HOLOTYPE: BR 917, figured by Waterhouse (1964b, pl. 2, fig. 4, pl. 3, fig. 2, 3) and also by Suggate et al (1978), Speden (1981) and Racheboeuf (2000, text-fig. 271.2a) OD from G45/f8458 (GS 1256), *Spinomartinia spinosa* Zone, Bagrie Formation, Arthurton Group, near Clinton.

DIAGNOSIS: Transverse shells with alate cardinal extremities, shallow anterior ventral sulcus, low anterior dorsal fold, dorsal valve may display faint traces of capillae.

MATERIAL: Some 23 ventral valves, 2 dorsal valves, and 17 specimens with valves conjoined from D44/f363, including OU 18264-8, one ventral valve from D44/f364, and 4 ventral valves, one possible dorsal valve, and 2 specimens with valves conjoined from D44/f117 (GS 15228), 2 ventral valves, one dorsal valve and a specimen with valves conjoined from D44/f9884 (GS 7813), all from equivalent *Plekonella multicostata* Zone, Glendale Formation, Wairaki Downs. A possible but well worn ventral valve and 3 dorsal valves from D45/f7578, *Spinomartinia spinosa* Zone, Hilton limestone, Wether Hill Station.

DESCRIPTION: The material from D44/f363 is well preserved, as natural internal and external moulds. Where not worn, the ventral valve is smooth apart from very faint growth lines, but several specimens are worn to appear costate. The dorsal exterior is largely smooth, apart from low growth-lines, and some specimens suggest traces of capillae. The shallow anterior ventral sulcus and dorsal fold are typical of the species. Internal detail is well displayed, but the cardinal row of spines along the hinge are broken short at the hinge. Specimens from f117 are not so well preserved, the external moulds being broken, but some suggest a smooth exterior.

The ventral valve BR 2381 from D45/f7578 is small, and has no sulcus, but matches other specimens of comparable size. Dorsal valves are a little larger and show dental sockets and low anterior broad fold. None show the exterior clearly. A chonetid specimen BR 2218, previously described as *brevisulcus* from the Nemo block by Waterhouse & Mutch (1978, text-fig. 4), shows a medianly convex venter with slight anterior median flattening, suggestive of *Capillonia*. A wide anterior sulcus is present on another Wether Hill *Capillonia* BR 2217 figured by Waterhouse & Mutch (1978, text-fig. 3).

DISTRIBUTION: *Capillonia brevisulcus* is most abundant in the *Spinomartinia spinosa* Zone of the Arthurton Group, and has been found near Wether Hill Station in the so-called Nemo Formation of Mutch (1972, in Waterhouse & Mutch 1978). It is rarely present in the older *Plekonella multicostata* Zone, and more doubtfully found in the *Martiniopsis woodi* Zone of the Arthurton Group. There are reports of the species from the upper Pine Bush Formation and Titiroa Limestone of the Kuriwao Group, Matura Island, and in the Tramway Formation of Annear Stream, east Eglinton River (Waterhouse 1964a). Possible *Capillonia brevisulcus* has been noted by Waterhouse & Balfe (1987, p. 27) in the upper South Curra Limestone of the Gympie Basin, southeast Queensland, figured as *Lissochonetes* sp. by Runnegar & Ferguson (1969).

Family **ANOPLIIDAE** Muir-Wood, 1962
Subfamily **ANOPLIINAE** Muir-Wood, 1962

Meagre material from New Zealand belongs to this subfamily, judged from the swollen ventral valve, and might belong to one of the anopliid genera that are of Permian age and found in Western Australia (Archbold 1980a, 1981c), southeast Asia and Himalayas, and in high northern latitudes. The genera include *Demonedys* Grant, 1976 and *Glabriconetina* Waterhouse, 1978, as in Racheboeuf (2000, p. 384) and to lesser degree *Tornquistia* Paeckelmann, 1930. But the lack of knowledge about internal septation and other facets of the New Zealand material means that only a generalized designation is possible.

Archbold (1981c, p. 28) pointed out that *Quinquenella* Waterhouse, 1978 shared a number of attributes with *Glabriconetina* Waterhouse, 1975, 1978. Both genera are found in the Late Permian Senja Formation of Nepal, considered to be of Changhsingian age, and fuller knowledge of the morphologies would be clearly desirable. However Archbold (1981c) may have misjudged the contours and shape of the ventral valve in *Glabriconetina*, which is swollen more than perhaps he realized. *Quinquenella* has a broader

only slightly convex ventral valve, with faint if any median swelling. This is verified also for species of *Quinquenella* recognized by Archbold (1981a, c) in Western Australia and Irian Jaya. Racheboeuf (2000, p. 384) recognized both *Glabriconetina* and *Quinquenella*. Archbold (1981a) made *Quinquenella* the name genus of a new subfamily, and considered that any similarity to Reticonetidae Muir-Wood, 1962 was superficial. He provided an illuminating discussion of similarities to Undulellinae Cooper & Grant, 1975, and to possible species of *Svalbardia* Barkhatova. Both Quinquenellinae and Undulellinae were classed in Rugosochonetidae by Racheboeuf (2000), but some question remains about the aptness of these relationships, which is stressing overall shape and ornament, rather than internal features of the dorsal valve. I consider that the several septa in the dorsal valve suggest an alliance with Anopliidae rather than Rugosochonetidae, and would place the two subfamilies in Anopliidae (Waterhouse 2000c). This accords with the definition of Rugosochonetidae by Martinez-Chacon & Winkler Prins (2000, p. 220).

Anopliin? gen. & sp. indet.

Pl. 1, fig. 9, text-fig. 4

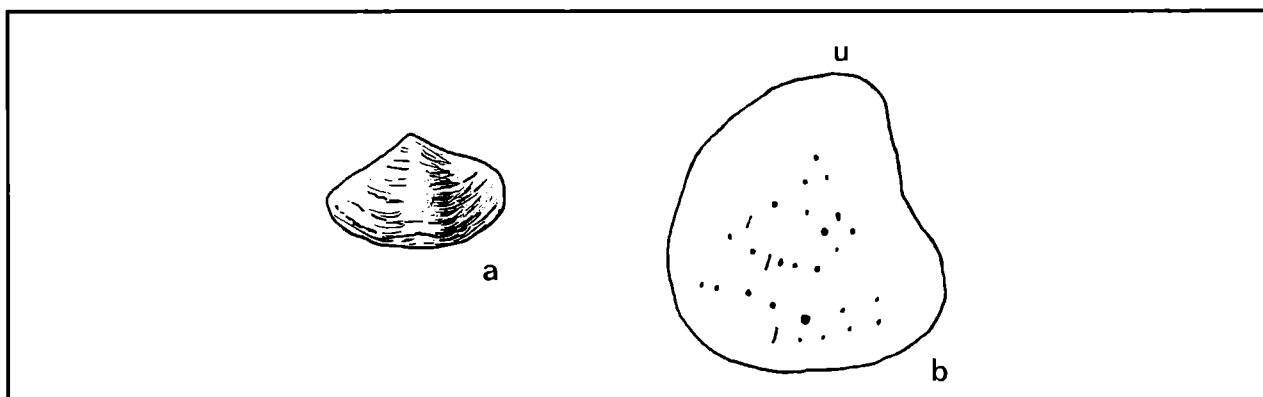
DIAGNOSIS: Small transverse shell, ventral valve swollen medianly.

MATERIAL: An obscure ventral valve BR 2380 from D45/f7578, *Spinomartinia spinosa* Zone, Hilton limestone, Wether Hill Station.

DIMENSIONS IN MM: approximate

Valve	Width	Length	Height
ventral	12	6.8	?2.5

DESCRIPTION: Ventral valve small, transverse with cardinal extremities subalate in early growth phases, becoming bluntly obtuse, valve medianly swollen, without forming fold or sulcus, surface originally smooth, but wear has produced lineations along small internal aligned pustules.



Text-fig. 4 A - Anopliin gen. & sp. indet, sketch of distorted BR 2380 from D44/f7578, Hilton limestone, x 2 approx. B - *Echinalosia conata*, OU 18753, fragment of ventral external mould from D45/f7115, illustrating distribution and thickness of spine bases. u - approximate position of umbo, x 2. From a photograph, as specimen mislaid.

RESEMBLANCES: This specimen is distinguished from *Capillonia brevisulcus* (Waterhouse, 1964b) by the medianly swollen ventral valve. Two dorsal valves found nearby are slightly larger, transverse, with abruptly obtuse cardinal extremities and low broad fold anteriorly, and are likely to be *Capillonia*. There is considerable approach to *Glabriconetina kuwaensis* Waterhouse, 1978 from the Late Permian (Changhsingian) Kuwa Member of west Dolpo, but the full generic position of the Wether Hill material depends on the internal septation, as yet not known.

From Stephens Island a ventral valve BR 1635 was identified as Chonetidae gen. indet. by Campbell et al (1984, text-fig. 6.5). It is well arched, but not medianly swollen, and so is readily distinguished from any of the other species so far known in New Zealand.

Suborder PRODUCTIDINA Waagen, 1883

Species described from east Australia and New Zealand are listed in Table 8.

Superfamily **PRODUCTELLOIDEA** Schuchert, 1929

[nom. transl. hic ex Productellidae Schuchert in Schuchert & Le Vene 1929, p. 17]

It is time to recognize that the Productoidea Gray, as set out by Muir-Wood & Cooper (1960), Muir-Wood (1965) and Brunton, Lazarev, Grant & Jin (2000) contains very disparate families. The Productelloidea should exclude the groups that display specialized halteroid and strut spines (as defined by Waterhouse 1981, p.

58), reticulate ornament, and substantial internal marginal structures such as seen in Dictyoclostidae, Productidae, and the various marginiferids which were dispersed in disparate groupings within Productoidea by Brunton, Lazarev, Grant & Jin (2000). More study is still required to elucidate the superfamily, and other than proposal of a new tribe, relationships may be regarded as provisional. Waterhouse (1981, p. 74) used the superfamily with a query, but offered no discussion.

?Family **PRODUCTELLIDAE** Schuchert, 1929

Study especially on Devonian and Carboniferous members of Productidina by Lazarev (1986, 1987, 1990) has led to some radical changes amongst family group associations. Not all are clear, and there has been on-going change in the arrangements, from Lazarev 1986 to the revised brachiopod treatise (Brunton, Lazarev, Grant & Jin 2000). One is left with the impression that the fluidity may not yet have stabilized. The Lazarev insights have been most valuable (eg Lazarev 1990), with further advances by Brunton, Lazarev, Grant & Jin (2000), but there remain, and have even grown, substantial inconsistencies and flaws, exacerbated by the need for accurate input from Gondwana faunas. Here, interest centres on the family relationships of the New Zealand genus *Lethamia*, which was initially described from the Letham Formation of Wairaki Downs, and has since been recognized widely in east Australia (Briggs 1998, Waterhouse 1986b), with a close ally *Wooramella* Archbold in Hogeboom & Archbold (1999) in Western Australia.

Subfamily **TUBERSULCULINAE** Waterhouse, 1971

Tubersulculinae are characterized by moderately numerous ventral spines that are fine and emerge with only slightly or non-swollen bases, and are moderately to well aligned concentrically. Internally marginal structures are developed only in the ventral valve in front of the hinge: there are various other characteristics, including two series of papillae in the fully mature dorsal valve. Costispiniferini Muir-Wood & Cooper, 1960 appears to be distinguished by its coarse or coarse and fine ventral spines, rather scattered to very weakly arranged concentrically, tendency to ribbing, heavy interior marginal structures crossing inside ears of both valves, dorsal spines, and very large few anterior dorsal papillae. The synonymy of Tubersulculinae with Costispiniferini, proposed by Brunton, Lazarev, Grant & Jin (2000, p. 434), seems unlikely, and the possibility remains that Costispiniferini may have to be restored to Marginiferidae Muir-Wood & Cooper, as characterized by cardinal process, heavy marginal structures, overall build, and spine nature and pattern. Tubersulculinae are much closer to Productellidae.

Tribe **LETHAMIINI** new

NAME GENUS: *Lethamia* Waterhouse, 1973.

DIAGNOSIS: Shells with slender body corpus, spirally curved ventral valve, no geniculation for trail. Ventral spines numerous, moderate to fine, tend to be concentrically aligned, no swollen or posteriorly prolonged bases, light concentric wrinkles. Dorsal spines fine and erect, numerous, light concentric wrinkles. Ventral interior with dense papillae, few slightly larger papillae anteriorly, low posterior marginal ridge. Dorsal valve with trifid cardinal process and septum developed anteriorly, fine dense papillae and array of moderate-sized papillae anteriorly.

DISCUSSION: *Lethamia* is a well known genus, its type species described by Waterhouse (1982a), and additional species described from eastern Australia by Briggs (1998) and Waterhouse (1986b). The illustrations are particularly good, both for the type species, and for Australian species. Yet Brunton, Lazarev, Grant & Jin (2000, p. 436) claimed the genus was poorly defined, queried its occurrence in Australia, and provided no figures, although I believe that when I provided Dr Brunton with excellent negatives for the treatise, in 1990, I pointed that out that further negatives would be provided if required, or could be sought from the New Zealand Geological Survey archives at Lower Hutt. This illustrates the unreliability of the section on Productidina in the revised brachiopod treatise. If the authors believed their text, it is surprising that they never tried to clarify matters with me. As Lazarev (1986, 1990) and Brunton, Lazarev & Grant (1995) kept changing their interpretation of *Lethamia* so often, it may be that the authors could not fit *Lethamia* into their various schemes. But of course that need not imply a motive for suggesting that the genus was poorly known, obscure, and badly figured: rather a lapse occurred, and documentation (Waterhouse 1982a, 1986b) was overlooked or mislaid, and negatives neglected. Several other Gondwanan genera were subject to comparable carelessness. Fortunately Briggs (1998) provided a more meticulous appraisal of *Lethamia*, reinforced by a study by Archbold in Hogeboom & Archbold (1999) on an allied form.

HISTORICAL REVIEW: The genus *Lethamia*, first described from Wairaki Downs, was placed by Waterhouse (1982a, pl. 9, fig. c-i, pl. 10, fig. a-j) as a member of Subfamily Tubersulculinae Waterhouse, in Bamber & Waterhouse, 1971. *Tubersulculus* Waterhouse, 1971 had been named for a Canadian type species, *T. maximus* Waterhouse, 1971, that was shown to differ from *Krotovia* in possessing a ventral sulcus, dorsal fold, and tubiform trail. The type species of *Krotovia* is the Early Carboniferous species *Productus spinulosus* Sowerby.

The subfamily Tubersulculinae was originally referred in turn to Overtoniidae Muir-Wood & Cooper, 1960, a family which, according to Muir-Wood & Cooper (1960), incorporated *Krotovia* and *Levipustula*. Archbold (1984) considered that Tubersulculinae could not be distinguished from Overtoniidae, and put *Lethamia* in that family. Later Archbold in Hogeboom & Archbold (1999) recognized the subfamily as a member of Overtoniidae. Briggs (1998) also accepted the initial Waterhouse classification and referred *Lethamia* to Tubersulculinae, within Overtoniidae.

In his preliminary studies, Lazarev (1986, p. 28, 1990, p. 112) recognized the subfamily Tubersulculinae, and referred to it the genera *Fimbrinia* Cooper, 1972 (= *Fimbriaria* Muir-Wood & Cooper, 1960), *Scoloconcha* Gordon, 1966, and *Tuberculatella* Waterhouse, 1982 (see d). *Fimbrinia* is very different from *Tubersulculus*, bearing strong concentric bands, but *Tuberculatella* has dorsal spines and pits, and swollen ventral spine bases, suggestive of Tubersulculinae. Surprisingly, Tubersulculinae was included in Sentosiidae McKellar, 1970 by Lazarev (1986), and just as curiously, *Krotovia* and *Lethamia* (with a query) were transferred to Sentosiinae McKellar. *Levipustula* was made name bearer of a subfamily within Juresaniidae Muir-Wood & Cooper by Lazarev (1986, p. 29) and then shifted to Yakovleviidae Waterhouse by Lazarev (1990, p. 146), both suggestions particularly unlikely. An even more radical step was the transference by Lazarev (1986) of Overtoniidae and Sentosiidae to Superfamily Echinoconchoidea Stehli. *Sentosia* shows fine concentric bands with fine spines on both valves, and obviously is an echinoconchoid, and unrelated to *Lethamia* or *Krotovia*. His error possibly arose in part from a study by Brunton (1966) which misidentified an echinoconchoid species *lamellosa* Brunton with *Krotovia*. *Overtonia* Thomas displays elaborate ornament in bands, as well as some degree of internal compatibility, but is not echinoconchoid.

In Brunton et al (1995), *Levipustulini* was recognized as a tribe within Plicatiferinae, and ascribed erroneously to Muir-Wood & Cooper, 1960, and regarded as a member of Productellidae. Brunton et al (1995) downgraded Overtoniidae to a tribe, and moved it to membership of the Productellidae Schuchert, a marked improvement on Lazarev (1986, 1990). Tubersulculinae was dropped. Sentosiidae remained in Echinoconchoidea with *Lethamia* as a member that was obviously out of place. Brunton et al (1995) and Brunton, Lazarev, Grant & Jin (2000) also recognized a new tribe Krotoviini, with a brief diagnosis, noting concentric ornament weak or lacking, ventral profile an ideal spiral, and shallow corpus cavity. These generalizations hardly qualify as diagnostic, leaving the tribe in limbo. Close comparison with *Tubersulculus* was avoided by the facile synonymizing of Tubersulculinae with Costispiniferinae. Some internal differences between *Krotovia* (see Brunton 1966) and *Tubersulculus* are found, mainly in the dorsal valve, including the notable absence of medium-sized internal pustules from the dorsal valve of *Krotovia*, but present in *Tubersulculus*. These differences probably reflected the immature state of Brunton's small specimens. The presence of a curious anterior ventral fold in mature *Tubersulculus* offers a ready distinction at generic but not family-group level from *Krotovia*, but the lack of ontogenetic studies and even assessments of maturity by Brunton (1966) has meant that *Krotovia* remains a poorly known genus, of uncertain tribal distinction.

In 1997, text-fig. 1, Brunton & Lazarev indicated that Tubersulculinae Waterhouse was to be synonymized with Costispiniferini, and showed that Costispiniferini sourced from Early Carboniferous Krotoviini. Costispiniferini was regarded as a tribe within Overtoniinae, treated in turn as a member of Productellidae. Evidently *Lethamia* was still viewed as a member of Sentosiinae, because it was excluded from the large assembly of genera within Productellidae. Yet *Lethamia* spines are not as numerous nor in bands like the patterns seen in Sentosiinae. Nor is there any close relationship between Costispiniferini and *Lethamia*. Furthermore, a tie between Costispiniferini and Tubersulculini seems highly questionable. The essential attributes of Costispiniferini involve close-spaced coarse irregularly arranged spines on both valves, (and in some species fine as well), weakly arranged in concentric rows, with no or very low concentric rugae or lamellae, and varied amount of ribbing. Comparable radial ornament is never seen in *Krotovia*, *Tubersulculus*, *Onopordumaria*, *Lethamia* and allies. Internally, posterior ventral marginal ridges and high ridge across the dorsal ears are developed in *Costispinifera*. Moreover this genus displays a different cardinal process, and different dorsal internal pustules arrayed mostly in a single row. The internal features of *Costispinifera* are shared with *Echinauris* Muir-Wood & Cooper, but not with *Echinaria* Muir-Wood & Cooper, which although included by Brunton & Lazarev (1997) in Costispiniferini, is quite different internally and externally. *Echinauris* lacks the radial ornament of *Costispinifera* but shares its strong ventral spines.

Krotoviini is closer to Lethamiini in its spine pattern, especially *Krotovia*. The other supposedly associated genus *Scoloconcha* Gordon, 1966 has different spines and very heavy posterior marginal ridge in the dorsal valve. Neither shows clearly developed fine internal pustulation, though there is some, suggesting either little advance in ontogenetic development, or immaturity of the interiors that were figured. The cardinal process of *Krotovia* is quadrifid, that of *Scoloconcha* trifid. There are fine spines in *Krotovia*, which arise from low tubercles. Compared with *Lethamia*, concentric ornament is more prominent in the type species *Krotovia spinosa* (Sowerby), especially on the dorsal valve (see Brunton 1966, pl. 12, fig. 1, 14, 16-18). Concentric spines are even more prominent in *K. lamellosa* Brunton, but this species shows coarse and fine spines over the ventral lamellae, as in echinoconchoids, and does not belong to *Krotovia*. In spite of the revised brachiopod treatise, *Krotovia* is very close to *Tubersulculus*, and Krotoviini remains a very tenuous concept, resting on the basis of a flawed assessment of Tubersulculinae and an unjustified exaggeration of the significance of the difference in ventral valve profiles between *Krotovia* and *Tubersulculus*.

Levipustulini Lazarev was suggested by Brunton, Lazarev, Grant & Jin (2000) as an alternative host for *Lethamia*, if the trail proved to be geniculate. This sort of guesswork was used as a substitute for actually reading the literature! It clearly is not geniculate in *Lethamia*, as described by Waterhouse (1982a, 1986b)

and Briggs (1998). By contrast, *Levipustula* Maxwell has a short geniculate trial, and the ventral spines bases are slightly swollen and posteriorly prolonged. There is weak concentric ornament, two orders of internal pustules and trifid cardinal process. The tribe was placed in Subfamily Plicatiferinae Muir-Wood & Cooper by Brunton, Lazarev, Grant & Jin (2000, p. 453). Plicatiferinae includes geniculate shells with strong concentric rugae as a rule, ventral spines only, and relationship to *Levipustula* and allied genera requires further consideration.

ALLIED GENERA: *Stictozoster* Grant, 1976, type species *S. leptus* Grant from the Wordian limestone of Ko Muk, south Thailand, is allied to *Lethamiini*, with fine spines on both valves. Its marginal ridges are very feebly developed, and internal pustules are small or in two series. *Wooramella* Archbold, 1999 is very close to *Lethamia*.

Undellaria Cooper & Grant, 1975, type species *U. magnifica* Cooper & Grant, is possibly related, with fine erect spines, a little crowded over the ventral ears, and rare on the dorsal valve. The spines are even less concentrically aligned than in *Lethamia*. Internal detail is close, including the fine internal papillation and stronger anterior dorsal pustules. The genus was placed in Linoproductidae Stehli by Cooper & Grant (1975), and in Subfamily Auriculispiniinae Waterhouse, Family Linoproductidae by Brunton, Lazarev, Grant & Jin (2000). There is no radial ornament and such placement seems unlikely.

Tuberculatella Waterhouse, 1982, type species *T. tubertella* Waterhouse, is close in its spine arrays, but ventral spines arise from swellings, and the dorsal valve bears large dimples. Internal pustulation is somewhat similar, with dense fine papillae and more obvious but small dorsal papillae as well. This genus was overlooked by Brunton, Lazarev, Grant & Jin (2000), as far as I can discover - it is certainly absent from the index. But it has featured as an important zonal key in Argentina (Sabattini & Pagani 2000). It shows an approach to *Avoniinae* Sarytcheva, 1960.

Possibly *Onopordumaria* Waterhouse, 1971, type species *O. punctura* Waterhouse from Moscovian of Canada may be allied to *Lethamiini* but has relatively larger internal papillae and could belong to *Costispiniiferini*. This is further suggested by the strong posterior and lateral ridge in the dorsal valve, continuing around the margin, and indication of a ventral marginal ridge (or growth rugae?). The Late Carboniferous type species of this Canadian genus is very close to the poorly defined *Echinauriella* Lazarev in Brunton & Lazarev (1997) from the Transcaucasus mid-late Permian. A cincture and heavy posterior dorsal marginal ridge are visible in the type species *Krotovia jisuenseformis* Sarytcheva in Ruzencev & Sarytcheva (1965), of late Guadalupian or early Lopingian age. (The wrong reference, authorship and age were given for *jisuensiformis* by Brunton, Lazarev, Grant & Jin 2000, p. 434).

Genus *Lethamia* Waterhouse, 1973

A low ridge lies along the dorsal hinge, and passes across the posterior lateral shell (Waterhouse 1982a, pl. 8, fig. e).

Waterhouse (1981, p. 74) drew attention to the close similarity of *Pustula senticosa* Hosking, 1933 from the Callytharra Formation of Western Australia to *Lethamia*, although Grant (1976, p. 12) and Archbold (1984, p. 83) preferred to assign the species to *Stictozoster* Grant. However the species *senticosa* displays much coarser spines less aligned in concentric rows than seen in the type species of *Stictozoster*, *S. leptus* Grant from the Rat Buri Limestone. Eventually *senticosa* was made the type of new genus *Wooramella* by Archbold in Hogeboom & Archbold (1999), and Archbold allowed that it was "remarkably similar" to *Lethamia* (p. 261). Earlier, in contrasting *senticosa* with *Lethamia*, Archbold noted that the dorsal septum was delicate, thin, and not raised anteriorly as in *Lethamia ligurritus*. "The large size of the only available dorsal valve of *senticosa* ... indicated that the specimen was not a juvenile" (Archbold 1984, p. 83). Waterhouse (1986b, p. 35) commented that "the median septum in type *Lethamia* is slender and it is not until late maturity that it became thick with a terminal pillar or fork. Archbold (1984) misrepresented the dorsal median septum of *Lethamia* as being always massive and raised anteriorly: this is not so." Archbold in Hogeboom & Archbold (1999, p. 261) objected, but the Waterhouse statement seems logical. Archbold further objected that Waterhouse had not described juvenile or figured juvenile *Lethamia* - but immature specimens were certainly involved in the circumscription of *ligurritus* by Waterhouse (1982a, p. 40), the text stating that the septum increased anteriorly in width and height, thus demonstrating that small specimens had been studied. The specimen BR 953 figured by Waterhouse (1982a, pl. 8, fig. h) is immature. The fact that Archbold has reassessed his reference of *senticosa* to *Stictozoster*, and accepted that *senticosa* is very close to *Lethamia*, as originally argued by Waterhouse (1982a) in contrast to Grant (1976), may be regarded as a valuable clarification. He did not discuss the family group relationships proposed by Brunton & Lazarev (1997), and retained a relationship to *Tubersulculinae* and *Overtoniidae*.

Lethamia sp.
Pl. 1, fig. 12

MATERIAL: Obscure ventral valve BR 2272, a second even more obscure specimen BR 2271 and dorsal valve BR 2274 from D44/f123 (GS 15226), *Pseudostrophalosia?* cf. *blakei* fauna, lower Mangarewa Formation, Wairaki Downs.

DIMENSIONS IN MM: approximate

Specimen	Width	Length	Height
BR 2272	20	27	10.5

DISCUSSION: Material poorly preserved, and external ornament and hinge details largely lost. The pattern of fine internal pustules suggests a relationship to *Lethamia*. The ventral valve BR 2272 is more elongate and inflated than normal for *Lethamia ligurritus* Waterhouse from the upper Letham Formation. Another possible ventral valve BR 2271 is only gently convex but identity is obscure.

Lethamia? collina Waterhouse, 1982a
Text-fig. 5a, b

1956 *Productus* sp. Marwick in Wood, pp. 46, 48.

1964b *Horridonia* n. sp. Waterhouse, p. 58, pl. 8, fig. 11, pl. 9, fig. 1, 2, text-fig. 21.

1978 *Horridonia* sp. Waterhouse & Mutch, p. 519.

1978 *Horridonia* n. sp. Suggate et al, text-fig. 4.5, fig. 6.

1981 *Horridonia* n. sp. Speden, pl. 5, fig. 6.

1982a *Lethamia collina* Waterhouse, p. 43, pl. 10, fig. a, text-fig. 17G (not pl. 10, fig. b = indet).

HOLOTYPE: BR 51, figured by Waterhouse (1964b, pl. 8, fig. 11, pl. 9, fig. 1, 2, text-fig. 21), Suggate et al (1978) and Speden (1981) OD from G45/f8612 (GS 5078), *Plekonella multicosata* Zone, Bagrie Formation, Arthurton Group, near Arthurton.

DIAGNOSIS: Shell transverse, ventral umbo enrolled, anterior shallowly sulcate, hinge wide, dorsal valve gently concave with short anterior swelling or fold, visceral disc thick. Ventral spines erect and moderately large over posterior lateral shell and ears, scattered body spines. Dorsal spines not known.

MATERIAL: Three obscure ventral valves from D44/f376 (OU 18738-39), *Spinomartinia spinosa* Zone, Hilton Limestone, Wairaki Downs.

DESCRIPTION: One specimen has umbonal angle of 90°, low posterior umbonal walls, moderately wide hinge, obtuse cardinal extremities, high and arched valve, convexity exaggerated by distortion, anterior median shell flattened, not sulcate, low concentric wrinkles 1-2 per mm, apparently low close-set body spines, up to 1.5mm apart anteriorly, in rows just over 1mm apart anteriorly. Other specimens gently convex and obscure.

RESEMBLANCES: The figured specimen is close to mature *Lethamia collina* in shape, although smaller, and the others could be immature specimens. They show thin shell and apparently fine spines in quincunx as in *Lethamia*, but various significant details remain unknown.

The specimen BR 2222, recorded but not figured from GS 5873, D45/f7572 as *Horridonia* sp. in Waterhouse & Mutch (1978) from the Nemo limestone block, Wether Hill Station, has thick shell, wide umbo, and two large erect spine bases postero-laterally, with erect anterior spines.

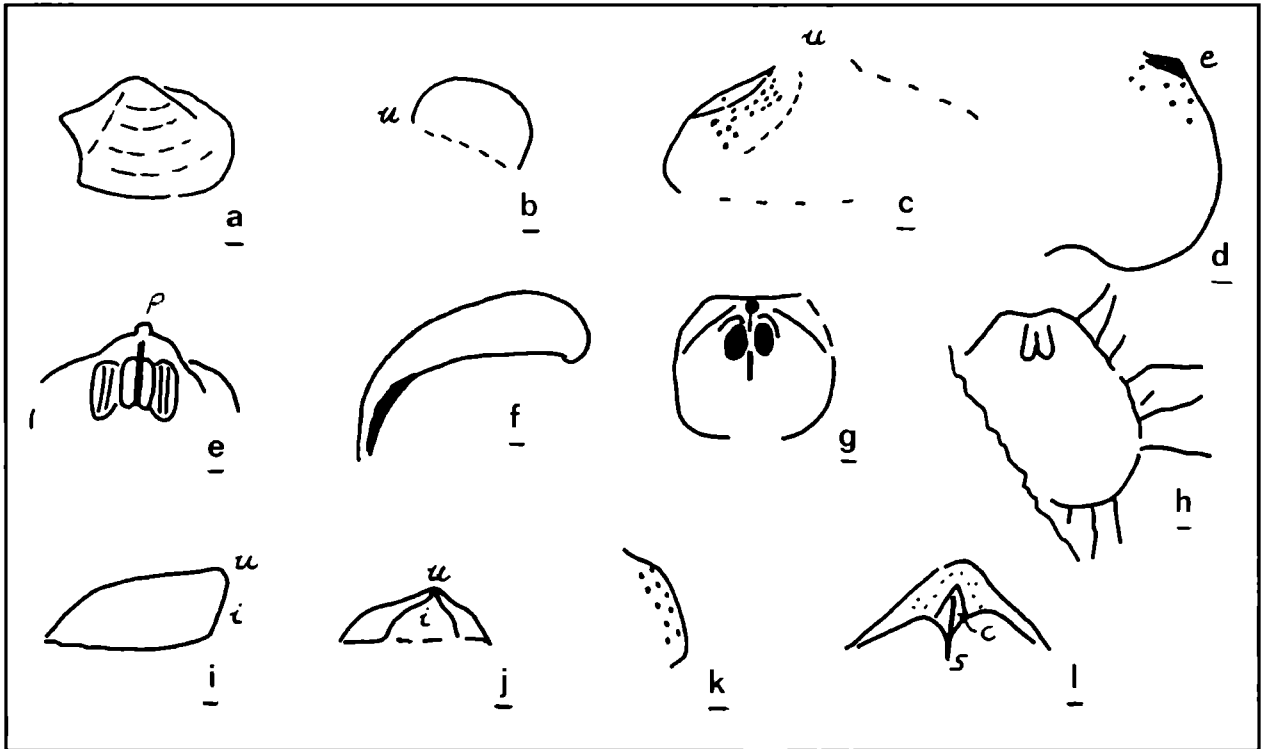
The ventral spines in this species differ somewhat from the largely even sized evenly spread spines seen in the type species of *Lethamia*. Specimen BR 50 from GS 5078 (G45/f8612) in AG4 Formation, Arthurton Group, shows scattered erect body spines on the ventral valve, with more closely spaced, more sturdy erect spines over the ears and posterior lateral slopes. A large spine with diameter of just over 1mm is present laterally on the incomplete ventral exterior. The spine pattern was illustrated for BR 755 from the same locality in Waterhouse (1982a, text-fig. 17G). The spines lie in a row along the hinge, and continue or are offset from a row continuing laterally. Two large spines lie on the posterior median shell. Anterior moderately thick body spines lie in irregular concentric rows. BR 51 (see Waterhouse 1964b, pl. 8, fig. 11, pl. 8, fig. 1, 2) from GS 5078 has two prominent spines posteriorly.

Another specimen BR 49 from GS 5078, figured by Waterhouse (1982a, pl. 10, fig. b), is elongate with narrow non-sulcate venter, and may belong to a different taxon.

Briggs (1998) suggested a possible relationship to *Lethamia condaminensis* Briggs from his *Echinalosia voiseyi* Zone of the Condamine block, south Queensland, and allowed that *collina* might be a senior synonym. Both species are based on poorly preserved material, and it seems that ventral spinosity is even less well known for *L. condaminensis* than for *collina*. Archbold in Hogeboom & Archbold (1999) noted that *condaminensis* closely approached *Wooramella* Archbold in the wide ears. That is also true for *collina*. Unfortunately neither *collina* or *condaminensis* are well enough preserved to show if the hinge had alar extensions like those of *Wooramella*.

GENERIC RELATIONSHIPS: The species *Lethamia? collina* Waterhouse is characterized by inflation, broad incurved ventral umbo, low sulcus and fold and geniculate trail, with low anterior ribs. It comes from the *Plekonella multicosata* and *Spinomartinia spinosa* Zones of the Arthurton Group, as well as the *S. spinosa* Zone of Wairaki Downs and Wether Hill. The types have a relatively thick ventral valve with low anterior marginal ridge.

The original attribution of the *collina* types by Waterhouse (1964b) was to *Horridonia*. *Horridonia* has cardinal spines along both the ventral and dorsal valves, whereas the present form appears to have ventral cardinal spines only, and those spines are not very strongly developed. Admittedly the pattern of dorsal spines in *collina* is poorly established, and the presence or absence of dorsal cardinal spines for *collina* is interpreted only from the ventral hinge (along which the presence of dorsal spines would be expected to be indicated by pits) and internal dorsal mould. The Arctic Permian genus *Tityrophia* Waterhouse, 1971 has a row of ventral hinge spines and no dorsal hinge spines, but this genus also displays better developed costae and a distinct ventral sulcus, with no widespread dense pitting internally.



Text-fig. 5. Productidina and *Stenoscisma* from Wairaki Downs etc.

- a, b. *Lethamia? collina* Waterhouse ventral valve OU 18739 from Hilton limestone, D44/f376, ventral and lateral views of deformed specimen, x 1. u - umbo.
- c. *Terrakea exmoorensis* Dear OU 18740 from Letham Formation D44/f321, x1, broken, showing numerous crowded spine bases on posterior lateral flanks of ventral valve. u - umbo.
- d. *Paucispinauria paucispinosa wardenensis* n. subsp. showing position of posterior lateral spine bases. UQF 65413 from UQL 3758, Freitag Formation, Bowen Basin, Queensland, x 1. Small ear e has no spines.
- e. *Echinਾਲosia conata* n. sp. OU 18745 from D45/f7115, Takitimu Group, showing projection of matrix p indicating hole into umbonal shell between teeth, suggesting a peduncle, muscle scars in front, x 1.2.
- f. *Marginalosia?* sp. section of specimen with valves conjoined, BR 2389 from D45/f7578, Hilton limestone, x 1, showing thickened anterior dorsal trail, ventral valve on top.
- g. *Etherilosia?* sp. dorsal interior OU 18757 from D44/f9604, Brunel Formation, Takitimu Group, x 3. Showing cardinal ears, with anterior ridges, cardinal process as solid circle and muscle scars black.
- h. *Etherilosia?* sp. OU 18756 from same locality, showing internal mould of ventral valve with posterior adductors and radiating slightly rhizoid spines, x 3.
- i, j, k. *Megasteges?* sp. ventral valve OU 18758 from Hilton Limestone, D44/f376 x 2, showing i - lateral profile, x 1.25, j - posterior view with interarea i, x 1, and k - lateral spine bases on right side, x 1. l - interarea, u - umbo.
- l. *Stenoscisma?* sp. OU 18302 from Hilton Limestone, D44/f376, posterior view of ventral valve with posterior shell, anterior internal mould, x 1. c - camarophorium with medium ridge and s - median septum in front.

Hill (1950) described a species *Horridonia mitis* from the early Permian of southwest Bowen Basin. This has a shell surface which is largely smooth apart from spines and so approaches the present form. But Waterhouse (1986b) found that the ventral spines in *mitis* formed a row along each umbonal slope, and reinterpreted the form as a new genus *Azygidium*, within Marginiferini. *Azygidium* was synonymized with *Anemonaria* Cooper & Grant, 1969 by Briggs (1998, p. 143). Briggs claimed that a zygidium was developed in *Azygidium*, in dispute with Waterhouse (1986a) who had stated none was present. Yet Briggs was uncertain, for he then added "if the absence of a zygidium is confirmed, retention as a separate subgenus may be justified" (1998, p. 145). His figures (1998, fig. 72, A, B) purporting to show a zygidium seem unconvincing, and do not suggest a zygidium. Further the species *mitis* shows other differences from *Anemonaria*, including a lack of costellae and different arrangement of ventral spines. *Anemonaria* is typified in part by the presence of sturdy strut spines in one or two pairs on the lateral and anterior flanks of ventral valves (Cooper & Grant, 1975, pl. 408, fig. 1-5, 22, 24, 25). Similar spines are seen in Russian and Canadian Arctic species of *Anemonaria* (Sarytcheva 1977, Shi & Waterhouse 1996). In *Azygidium mitis*, there are more body spines over the ventral

valve than in *Anemonaria*, and the two pairs of strut spines found in *Anemonaria* do not appear to be developed. Only one of the various ventral valves figured by Hill (1950) and Waterhouse (1986b) suggest the presence of a single strut spine (Waterhouse 1986b, pl. 9, fig. 1), and this spine seems in fact to be the last of the umbonal slope row. Thus the spine pattern supports Waterhouse's initial view that *mitis* was separable from the otherwise somewhat similar genus *Anemonaria*. Such detail was overlooked by Briggs (1998), and given his uncertainty about what constitutes a zygidium, his views may be set aside.

The genus *Azygidium* was recognized as valid by Brunton, Lazarev, Grant & Jin (2000, p. 444) as a member of Paucispiniferini, but I would prefer that this tribe was reserved solely for Marginiferidae with large strut spines, as defined by Waterhouse (1981). *Azygidium* is closer to Marginiferini Stehli, whereas *Anemonaria* belongs to Paucispiniferini.

Genus *Archboldina* new

DERIVATION: Named for Neil W. Archbold.

TYPE SPECIES: *Pustula micracantha* Hosking, 1933, here designated.

DIAGNOSIS: Small shells transversely oval in shape, ventral valve gently to moderately convex, dorsal valve concave, no geniculation, cardinal extremities weakly acute to obtuse. Spines uniform and evenly arranged over ventral valve, of moderate diameter, rare on outer ears, weakly aligned in concentric rows, but some irregular, bases slightly if at all swollen, erect to subprostrate. Dorsal spines fine, scattered and moderately well spaced, rare on posterior ears. Concentric laminae fine, subevenly spaced, not prolonged or uneven, slightly stronger on dorsal valve. Cardinal process bifid, short median septum, thick at maturity, strong marginal ridge around entire disc.

DISCUSSION: The type species comes from the Callytharra Formation (Sakmarian) of Western Australia, and has been previously assigned to *Pustula* and *Krotovia*, two determinations readily set aside, and then *Dyschrestia* Grant, 1976 by Archbold (1984). The type species of the latter genus, *D. spodia* Grant from the mid-Permian Rat Buri Limestone of southern Thailand, has thicker body cavity and less well developed marginal ridge (see Grant 1976, pl. 22, fig. 7) - indeed Grant recorded none at all. Ventral spines are of several diameters, including a number thicker than in *micracantha*, Grant (1976) noting thick and thin spines, including a cluster on the flanks in front of the ears, with spacing somewhat irregular. As well, growth lamellae are very ragged and irregular with uneven anterior margins, on both valves. Thus *micracantha* is only similar to that of *Dyschrestia* in general appearance and size, with substantial differences in detail between the two forms in spine distribution patterns, growth lamellae and interior.

Piatnitzkya Taboada, 1993 from Early Permian of Argentina is moderately close in appearance, with slightly more prominent spine bases, no ventral ears and flatter dorsal valve with geniculate trail. It was acceptably classed in Levipustulini Lazarev by the revised brachiopod treatise, and the suggestion that it might have fine ribbing by Brunton, Lazarev, Grant & Jin (2000, p. 453), counter to the description and illustrations, is rejected by Dr Taboada (pers. comm., email, Dec., 2000). Other levipustulin genera also come moderately close. *Bulahdelia* Roberts of upper Visean age in Australia is close in general appearance to the new form, with strong dorsal internal ear baffles, and dorsal spines only anteriorly in lamellose bands. *Lanipustula* Klets, 1983 from the Transbaikal and Mongolia Lower Carboniferous is also close in general appearance, with scattered dorsal spines, moderately well defined adductor scars, buttress plates and posterior ventral spine bases prominent internally.

The family position of *Archboldina* is difficult to ascertain. The marginal ridge and substantial dorsal endospines point to Tribe Costispiniferini. The shape and ornament resemble aspects of *Lethamia* and *Wooramella*. *Wooramella* is more alate with smooth ears and more concentrically arranged spines. Its dorsal interior is poorly known, but is deemed to have a slender dorsal septum. *Lethamia* also has distinctly finer spines, with more on the ears, and much finer dorsal endospines anteriorly, and less well developed dorsal interior comarginal ridge. Provisionally the genus is regarded as an ally of these forms, but this may prove incorrect.

Subfamily **OVERTONIINAE** Muir-Wood & Cooper, 1960
Tribe **AVONIINI** Sarytcheva, 1960

[nom. transl. Brunton, Lazarev & Grant 2000, p. 452 ex Avoniinae Sarytcheva]

Genus *Lazarevonia* new Pl. 2, fig. 1 - 9

DERIVATION: Named for Stanislav Lazarev.

TYPE SPECIES: *Krotovia arcuata* Waterhouse, 1978, here designated.

DIAGNOSIS: Small concavo-convex shells with narrow body corpus, large ears and no geniculation, no interareas. Ventral spines sited on short ribs or elevations, at the posterior or anterior end or middle, elevations may widen forward or remain with parallel sides, ears smooth, concentric ornament very weak. Dorsal valve with many round to weakly elongate pits, weak concentric laminae, scattered erect fine spines, trail weakly or non-geniculate. Ventral adductor scars smooth or with growth lines parallel to anterior margin, diductors placed well forward, valve floor covered closely with pustules of one order in size, no marginal ridge. Dorsal anterior adductor scars smooth, triangular in outline, posterior lateral elements obscure. Short median septum extends to mid-length, brachial ridges extend well forward and enclose large area. Very low and narrow marginal ridges pass inside the ears and around the margin. Floor of valve marked by small close-set pustules posteriorly, becoming larger and spaced further apart anteriorly, not in large row or two across anterior disc, none over trail.

DISCUSSION: Four Lower Carboniferous genera of Avoniini Sarytcheva are similar in some respects. *Avonia* Thomas is a poorly known form, distinguished by better formed costae. *Quasiavonia* Brunton, 1966, type species *Productus aculeatus* Sowerby has sparse spines with subdued bases ventrally, and more low concentric ornament. *Onavia* Lazarev in Brunton & Lazarev 1997, type species *O. barunkhurensis* Lazarev from Mongolia, is close in dorsal valve, with pits and spines but somewhat stronger concentric ornament, and close in ventral muscle field, but the posterior ventral marginal ridge is stronger, ventral spine basal swellings somewhat weaker and concentrics stronger. The dorsal interior is poorly known, but moderately close as far as revealed. *Barunkhuraya* Lazarev in Brunton & Lazarev (1997) is close externally in ventral attributes, apart from stronger concentric ornament, but lacks dorsal spines.

Other genera do not come so close. *Tuberculatella* Waterhouse (1982d, text-fig. 2) from Late Carboniferous of Thailand is moderately similar, with ventral spine bases less elongated, different ventral muscle field, and two orders of interspersed tubercles internally. The dorsal muscle field and median septum are similar, and the dorsal exterior also close, with hollows, erect spines and comparatively weak concentric growth ornament. *Dalinuria* Li & Gu, type species *L. liaoningensis* Li & Gu (1976, pl. 135, fig. 1-13) from Middle Permian of Mongolia is close in general appearance but has bolder concentric ornament and lacks basal elongate spine swellings on the ventral valve.

Productidin, family, gen. & sp. indet.
Pl. 1, fig. 13

A dorsal valve BR 2345 from D44/f121 (GS 15217), *Echinalosia ovalis* Zone, Mangarewa Formation, Wairaki Downs, has deeply concave disc with maximum width at mid-length, and subgeniculate trail, obscured by other shell material. There are faint traces of costae, coarse concentric wrinkles, and a few scattered anterior erect spines.

Superfamily **PRODUCTOIDEA** Gray, 1840
Family **MARGINIFERIDAE** Stehli, 1954
Subfamily **MARGINIFERINAE** Stehli, 1954
Tribe **INCISIINI** Grant, 1976

[nom. transl. Brunton, Lazarev & Grant 1995 ex Incisiidae Grant]

The emphasis by Brunton, Lazarev, Grant & Jin (2000) and Grant (1976) on Incisiiii having an outline that is commonly anteriorly bilobate is rejected, that feature pertaining only to *Incisius* and its possible senior synonym *Cyrtalosia* Termier & Termier. Thus *Comuquia* Grant, 1976 which was classed according to the revised brachiopod treatise in Costispiniiferini, is much closer to *Incisius* Grant and allies in shape, ornament and interior.

Genus **Callyconcha** new

DERIVATION: cally - Callytharra Basin, concha - shell, Lat.

TYPE SPECIES: *Comuquia australis* Archbold, 1984, here designated.

DIAGNOSIS: Dorsal valve deeply concave, no dorsal spines, few ventral spines, concentric lamellae especially prominent on ventral valve.

DISCUSSION: This genus is close to *Comuquia* Grant but lacks dorsal spines and has very few ventral spines. A pair of spines flanks the beak and a row of up to three spines lies laterally. *Comuquia* has more ventral spines anteriorly and laterally and spines are long. There are few lamellae. Dorsal spines on *Comuquia* are short, following growth lines around the anterior margin of the adult shell.

Another ally is *Rhytisia* Cooper & Grant, 1975, with more numerous ventral spines and low concentric rugae, and no dorsal spines. These and other genera share moderately developed marginal ridges and small bifid cardinal process.

Several described species approach the new genus. *Comuquia himalayensis* Jin & Sun (1981, pl. 4, fig. 17-26) from early Permian Laisala Limestone of south Tibet is similar, with few ventral spines and not very lamellate, though specimens are abraded. *Productus (Marginifera) aequivocalis* Reed (1930b, pl. 2, fig. 5) from Tibet has a subglobose ventral valve that is "smooth apart from a few widely separated and irregularly distributed low pustules which occur on the lateral slopes." The dorsal valve is not known.

Superfamily LINOPRODUCTOIDEA Stehli, 1954

A new classification for this family is summarized in Table 4. It differs substantially from that in the revised brachiopod treatise. In the treatise, the superfamily was divided by Brunton, Lazarev, Grant & Jin (2000) into two families with many subfamilies and tribes. Although some of the main outlines are acceptable, overall relationships are obscured by having numerous subfamilies and tribes that are not arranged in any meaningful way, and the authors compounded difficulties by overlooking published genera, by incorporating a number of genera that do not belong, offering unacceptable synonymies, and misrepresenting both the taxonomy and content of important constituents. To some extent the better illustrated and more objectively presented strategies of Muir-Wood & Cooper (1960) were preferable.

What may cause most surprise, apart from evidence of so much objective error, as briefly indicated by Waterhouse (2000c, d, e), is the inclusion by Brunton, Lazarev, Grant & Jin (2000, p. 546ff) of two Devonian groups that show few palpable links with Linoproductoidea. These were Devonoproductinae Muir-Wood & Cooper, and Eoproductellinae Lazarev. They do show some approach in the presence of radial ribs. But teeth and sockets, common presence of interareas, nature of cardinal process and muscle impressions are some of the attributes that show strong differences from Linoproductoidea, and much closer relationships to other Devonian genera. Such genera were lumped, contentiously, in the Linoproductoidea in the revised brachiopod treatise, evidently because they were viewed as Devonian forebears. They may well have been forebears, but even the simplest of hierarchical and cladistic analyses would tend to separate them morphologically. At present the model seems intuitive rather than well documented, notwithstanding the claims in Lazarev (1987, 1990). I prefer to keep Linoproductoidea as a well defined group, and separate from its ancestors. The emphasis on vertical ties by Lazarev (1990) seems to me to obscure many demonstrable similarities and relationships, and to conceal the critical morphological gap between ancestors and descendants.

Table 4. Classification of the Linoproductoidea.

- Superfamily Linoproductoidea Stehli, 1954
 - Family Linoproductidae Stehli, 1954
 - Subfamily Linoproductinae Stehli, 1954
 - Tribe Linoproductini Stehli, 1954
 - Subtribe Linoproductinai Stehli, 1954
 - Subtribe Fluctuariinai Nalivkin, 1979
 - Subtribe Schrenkiellinai Lazarev, 1990
 - Tribe Stepanoviellini Waterhouse, 1975
 - Subtribe Stepanoviellinai Waterhouse, 1975
 - Subtribe Lamiproductinai Liang, 1990
 - Subfamily Anidanthinae Waterhouse, 1968
 - Subfamily Gigantoproductinae Muir-Wood & Cooper, 1960
 - Tribe Gigantoproductini Muir-Wood & Cooper, 1960
 - Tribe Semiplanini Sarytcheva, 1960
 - Subfamily Proboscidellinae Muir-Wood & Cooper, 1960
 - Subfamily Striatiferinae Muir-Wood & Cooper, 1960
 - Tribe Striatiferini Muir-Wood & Cooper, 1960
 - Tribe Compressoproductini Jin & Hu, 1978
 - Family Kansuellidae Muir-Wood & Cooper, 1960
 - Subfamily Kansuellinae Muir-Wood & Cooper, 1960
 - Subfamily Auriculispininae Waterhouse, 1975
 - Tribe Auriculispinini Waterhouse, 1975
 - Tribe Lyoniini Waterhouse, new
 - Tribe Filiconchini Waterhouse, new
 - Tribe Siphonosiini Lazarev, 1990
 - Tribe Undariini Waterhouse new
 - Subfamily Paucispinaurinae Waterhouse, 1986
 - Tribe Paucispinaurini Waterhouse, 1986
 - Tribe Coolkilellini Waterhouse new
 - Tribe Magniplicatinini Waterhouse, new
 - ?Family Monticuliferidae Muir-Wood & Cooper, 1960
 - Subfamily Monticuliferinae Muir-Wood & Cooper, 1960
 - Subfamily Tongluellinae Liang, 1990

Family LINOPRODUCTIDAE Stehli, 1954

This family was defined as characterized by deep corpus cavity, distinct trails, and commonly no dorsal

spines by Brunton, Lazarev, Grant & Jin (2000). More weight should be given to the prime characteristic of the family, which lies in the distinct well defined close-set ribbing, with moderately numerous ventral spines, few if any thick, and virtually all erect or suberect, without prolonged bases. Few genera have dorsal spines. The depth of the body cavity is variable, and not as significant as claimed in the revised treatise.

The revised brachiopod treatise included Linoproductinae, Anidanthinae, "Grandaurispininae" (a junior synonym of Paucispinaurinae) and Siphonosiinae in Linoproductidae. Here the family is altered, principally by excluding "Grandaurispininae" and Siphonosiinae, and recognizing Stepanoviellini Waterhouse, 1975, and including Gigantoproductinae, Striatiferinae and Proboscidellinae, moved from Monticuliferidae. As well genera are substantially reassigned on the basis of tighter and more consistent morphological constraints.

Subfamily **LINOPRODUCTINAE** Stehli, 1954

[syn. Ovatiinae Lazarev, 1990]

Ventral spines only in most genera, often large, deep or shallow body cavity, both valves with fine close-set radial ornament, concentric ornament inconspicuous.

Tribe **LINOPRODUCTINI** Stehli, 1954

[nom. transfer. hic ex Linoproductinae Stehli]

Ventral spines, with well developed row along hinge.

Subtribe **LINOPRODUCTINAI** Stehli, 1954

[nom. transfer. hic ex Linoproductinae Stehli]

Shells oval in outline, transverse or elongate, ventral umbo prominent, ears developed, venter arched. Spines evenly distributed or rare over ventral valve, development symmetrical and shell free-living. Constituent genera include *Linoproductus* Chao, *Balakhonia* Sarytcheva, *Marginovatia* Gordon & Henry, *Ovatia* Muir-Wood & Cooper, *Teleoproductus* Li Li and *Linoprotonia* Ferguson. Genera *Bandoproductus* Jin & Sun, *Coolkilella* Archbold, *Kasetia* Waterhouse and *Mistoproductus* Yang De-li, placed in association by Brunton, Lazarev, Grant & Jin (2000), should be excluded.

Subtribe **FLUCTUARIINAI** Nalivkin, 1979

[nom. transl. hic ex Fluctuariinae Nalivkin, 1979]

Elongate shells close to Linoproductinai, with differentiated ribs and with concentric wrinkles. *Fluctuaria* Muir-Wood & Cooper.

Subtribe **SHRENKIELLINAI** Lazarev, 1990

[nom. transl. hic ex Shrenkiellinae Lazarev, 1990. The family group unit was proposed as a nomen nudum with no diagnosis, discussion or indication of name genus in an informal document by Lazarev 1986. Brunton, Lazarev, Grant & Jin (2000) mistakenly indicated the date of the taxon as Lazarev 1986]

Medium-sized to large transverse shells with long hinge, inconspicuous ventral umbo, and medianly flattened ventral disc, hinge spines in row near hinge margin only. *Shrenkiella* Barchatova and *Striatospica* Waterhouse belong here. The revised brachiopod treatise (2000, pp. 562, 563) included *Dictyoclostoidea* Jin & Hu and *Permundaria* Nakamura, Kato & Choi, of uncertain affinities. The row of conspicuous hinge spines is also found in *Linoproductus*, as well illustrated by Cooper & Grant (1975), so that the group is very close to Linoproductinai in spine pattern, and close to Stepanoviellini in shape.

Tribe **STEPANOVIELLINI** Waterhouse, 1975

[nom. transl. hic ex Stepanoviellinae Waterhouse, 1975, p. 12]

This group, lumped in the revised brachiopod treatise with Linoproductinae, is recognized for Linoproductinae of small to medium size, that have an extended hinge in many genera, inconspicuous ventral umbo, transverse outline, and few, generally only ventral spines, rarely with dorsal spines (*Stepanoviella*), sometimes wide hinge. Costellae well and often closely developed, may be differentiated, on both valves. In several genera the body corpus is shallow.

Linoproductini are less transverse with more prominent umbones and higher posterior walls and often better developed ears.

Subtribe **STEPANOVIELLINAI** Waterhouse, 1975

[nom. transfer. hic ex Stepanoviellinae]

Radial ornament linear and simple. Constituent genera include *Stepanoviella* Zavodowsky, *Chianella* Waterhouse, *Cimmeriella* Archbold & Hogeboom, *Globiella* Muir-Wood & Cooper, and *Liraria* Cooper &

Grant, Brunton, Lazarev, Grant & Jin (2000, p. 544) suggested that *Pseudohaydenella* Liang was possibly a synonym of *Chianella*, but it is difficult to be sure from the figures. The constituent genera were scattered amongst Linoproductidae (mostly Linoproductinae) and Monticuliferidae (Auriculispinae) by the revised brachiopod treatise.

Subtribe **LAMIPRODUCTINAE** Liang, 1990

[nom. transl. hic ex Lamiproductidae Liang, 1990, p. 466]

Characterized by branching and erractic costellae, crossed by fine growth cinctures, scattered fine erect body spines and few spines along hinge of ventral valve.

DISCUSSION: Liang (1990) proposed Lamiproductidae for a single genus *Lamiproductus* Liang from Zhejiang Province of China. He stressed the "dendritic" ribs. Unrealized by Jiang (1990), genus *Asperlinus* Waterhouse & Piyasin, 1970, type species *Productus asperulus* Waagen, 1884 from the Chhidru Formation of the Salt Range Pakistan is closely related, and possibly senior synonym. The exterior is very close at generic level, and the interior of the dorsal valve has comparable marginal ridges and septum (cf Waagen 1884, reproduced in Brunton, Lazarev, Grant & Jin 2000, text-fig. 376.4d, with Liang 1990, pl. 35, fig. 11).

Brunton, Lazarev, Grant & Jin (2000) ignored Lamiproductidae and synonymized *Lamiproductus* with *Pseudohaydenella* Liang, 1990. *Asperlinus* was recognized separately. *Pseudohaydenella* was very poorly figured by Liang, and seems to be more convex than *Lamiproductus*, so that the proposed synonymy remains questionable. In turn Brunton, Lazarev, Grant & Jin (2000) suggested that *Chianella* Waterhouse might prove to be senior synonym for *Pseudohaydenella*. That remains open for further enquiry. Here it is proposed to recognize Lamiproductinae as a subtribe, with *Asperlinus* and *Lamiproductus*.

Subfamily **ANIDANTHINAE** Waterhouse, 1968

Members of Anidanthinae have the well defined costellae of *Linoproductus*, with inconspicuous spines limited to the ventral valve. The dorsal valve is lamellate to varying degree.

Briggs (1998) followed various authors, including a few cited in Briggs (1998, p. 198), in elevating the group to a full family. He did not refute the appraisal by Brunton et al (1995, p. 931) that the rank should be retained at the original subfamily level, within Linoproductidae, but that lead is followed herein. Genera included in the subfamily are *Anidanthus* Booker, *Akatchania* Kletz, *Fusiproductus* Waterhouse, *Kuvelousia* Waterhouse, *Nothokuvelousia* Waterhouse, *Megousia* Muir-Wood & Cooper, *Protoanidanthus* Liao (possibly a synonym of *Fusiproductus*), and *Protoanidanthus* Waterhouse. *Zia* Sutherland & Harlow is regarded as Productidae, counter to the revised brachiopod treatise: it lacks dorsal lamellae and differs in many other respects.

Genus **Protoanidanthus** Waterhouse, 1986

TYPE SPECIES: *Protoanidanthus compactus* Waterhouse, 1986.

DIAGNOSIS: Small anidanthids lacking alae from dorsal ears, ventral ornament of costellae and spines in hinge row and scattered body spines, dorsal ornament of radial ribs and concentric lamellae.

DISCUSSION: Extraordinarily, this genus was left out of the revised brachiopod treatise by Brunton, Lazarev, Grant & Jin (2000) but is regarded as valid and has been well circumscribed by Briggs (1998). The genus is also present across the Arctic, as reviewed by Shi & Waterhouse (1996) and Waterhouse (1986b).

***Protoanidanthus?* sp.**

MATERIAL: A ventral valve OU 18742 from D45/f7112, *Echinalosia conata* Zone, upper Takitimu Group, Mt Wilanda, Wilanda Downs Station near Ohai, western Southland.

DESCRIPTION: A small ventral valve has costellae and spines. The well developed anidanthin muscle field suggests that the specimen is mature. Specimens of *Protoanidanthus* tend to be small and are often less transverse than other forms. No reliable occurrences of the genus are yet known for New Zealand.

Anidanthin gen. & sp. indet.

1993 Anidanthid cf *Megousia solita* not Waterhouse; Briggs & Campbell, p. 326, text-fig. 3:11, 12.

An obscure ventral valve BR 2320 from D44/f9878 (GS 7807) of the Caravan Formation, Wairaki Downs, was regarded as close to *Megousia solita* by Briggs & Campbell, but it shows little similarity to that species. Admittedly, the comparison makes good sense stratigraphically, and in so far as it appears to support the claim by Waterhouse (1982a) that the locality contained brachiopods little older than fossils from the basal Letham Formation, against vigorous protestations in favour of a greater age by Mutch (1966) and Houghton

(1981), perhaps the identification should be allowed to stand unchallenged. But in reality, little weight can be attached to claims that internal features show considerable approach to *Megousia solita*, and preservation seems, from the figures, to be so poor that specific identification is speculative. The figures in Briggs & Campbell (1993) certainly do not suggest a species close to *Megousia solita* as figured by Waterhouse (1968b, pl. 154, fig. 1-6, 8-10) and Briggs (1998, text-fig. 98), and Briggs (1998, p. 207) did not include the material in the synonymy of *solita*. The material was loaned to Dr Briggs, and has never been returned, despite numerous requests.

Specimens from the Stephens Group on Stephens Island that were initially ascribed to *Anidanthus* sp. by Campbell et al (1984, text-fig. 16:11-13) were referred to *Megousia solita* by Briggs & Campbell (1993, text-fig. 3:1-10) and Briggs (1998, p. 207). A more careful appraisal is required, because the smaller dorsal ears and finer costellae of these specimens indicate differences from *Megousia solita*.

Briggs (1998) asserted that the species *Nothokuvvelousia aurifera* Waterhouse, 1986b from Rose's Pride Formation, southeast Bowen Basin, was identical with *Megousia solita* Waterhouse, 1968b. In the types and other specimens of *Megousia solita* from the Wandrawandian Formation of the south Sydney Basin, the dorsal lamellae are much longer, the dorsal ears long, and costellae much coarser at 7-8 in 5mm posteriorly, 10 in 5mm anteriorly, compared with 10-12 in 5mm posteriorly and 14 in 5mm anteriorly in *aurifera*. There is no compelling reason to synonymize the two, and as Briggs (1998) seems to have relied on this misidentification to change the age of the Rose's Pride Formation, his age must also be corrected.

DISCUSSION: Briggs & Campbell (1993, pp. 325, 326) considered that the Stephens beds belonged to the Dun Mountain-Maitai Terrane, and they considered that the block had been derived from the Brook Street Terrane, pointing to terrane convergence during "the period (sic) of Stephens Formation (sic) deposition." It will be obvious to the perspicacious reader that since allegedly the same *Terrakea* species, and *Megousia solita* are found in the Sydney Basin, other solutions seem possible, and it should be allowed further that the species may well have dwelled in more than one terrane, especially as kindred species range through basins in New South Wales and Queensland, and into New Zealand. The source of Stephens detritus and reworked fossils remain an important issue for enquiry. Other fossil and regional stratigraphic evidence, both for the Permian and the Triassic fossils in the lower Te Mokai (earlier, "Stephens") Group, do support derivation from Brook Street Terrane, insofar as the fossil suites are absent from Maitai Terrane, and have allied species in former Brook Street Terrane in the Wairaki Downs area.

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

Gigantic, large, or medium-sized shells, hinge at greatest width, shallow corpus cavity, fully covered with close-set ribs, generally narrow interspaces, spines rare, on ventral valve only, erect, may be surrounded by smooth circular area but not prolonged posteriorly in *Globosoproductus*, cardinal process pit present as a rule.

The summary present by Brunton, Lazarev, Grant & Jin (2000, p. 550 ff) is modified, because *Kansuella* and allies must be excluded. Gigantoproductinae are related to Linoproductidae, to judge from ornament involving ribs and distribution and nature of spines, not Monticuliferidae as claimed in the revised brachiopod treatise. The emphasis on shallow body cavity in the treatise is regarded as misplaced.

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

Genera include *Gigantoproductus* Prentice, *Beleutella* Litvinovich, *Datangia* Yang De-Li, *Globosoproductus* Litvinovich & Vorontsova, *Serbarinia* Morozov, *Titanaria* Muir-Wood & Cooper, *Xinjiangiproductus* Yao & Fu.

Tribe **SEMIPLANINI** Sarytcheva, 1960

Semiplanus Sarytcheva, *Latiproductus* Sarytcheva & Legrand-Blain, *Semiplanella* Sarytcheva & Legrand-Blain, *Talasooproductus* Litvinovich & Vorontsova.

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

Genus *Proboscidella* Oehlert is an unusual mostly Visean (Early Carboniferous) genus with bifid cardinal process, unlike that of Striatiferinae. The nature of the spine bases was not analysed by Muir-Wood & Cooper (1960) or the revised brachiopod treatise (2000), so that placement of the subfamily is provisional. There is some approach, apparently through convergence, with *Siphonosia* Cooper & Grant and *Undaria* Muir-Wood & Cooper. These have posteriorly prolonged spine bases and are classed in a different family, but closer scrutiny is required.

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

The subfamily is transferred from Monticuliferidae (revised brachiopod treatise 2000, p. 560) to Linoproductidae, in view of the nature of the ornament, involving radial ribs and ventral spines. Two tribes are recognized, differing in shape, but sharing an unusual cardinal process with single myophore lobe.

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

Genus *Striatifera* Chao. Spines are inconspicuous, hinge wide, and body corpus shallow.

Tribe **COMPRESSOPRODUCTINI** Jin & Hu, 1978

[nom. transl. hic ex Compressoproductinae Jin & Hu]

This group is characterized by fine radial ornament, few and erect ventral spines found especially near hinge and moderately high body corpus. Shells may become assymmetric from nestling in host. The tribe is close to Linoproductidae, not Monticuliferidae as in the revised brachiopod treatise (2000, p. 546). Genera are *Compressoproductus* Sarytcheva, *Fallaxoproductus* Li, Gu & Li, *Sarytchevinella* Waterhouse and *Regrantia* n. gen. The high and often narrow ventral valve and fine radial ornament are reminiscent of other linoproductids, such as *Proboscidella* Oehlert and *Striatifera* Chao, of Carboniferous age, with narrow short spine bases as in Linoproductidae.

Fluctuaria Muir-Wood & Cooper, Subtribe Fluctuariinai, shows an approach in shape to *Compressoproductus*. *Undaria* Muir-Wood & Cooper also shows some approach, but its elongate ventral spine bases suggest a source from Auriculispininae.

Genus ***Regrantia*** new

DERIVATION: Named for Richard E. Grant.

TYPE SPECIES: *Striatifera productiniformis* Cooper & Grant, 1975, here designated.

DIAGNOSIS: Moderately large asymmetric shells tending to be somewhat subtriangular in outline with prominent ventral umbo and short well defined asymmetric hinge, very convex ventral valve and gently concave dorsal valve, deep body corpus. Ornament of fine radial ribs, wrinkles over both valves and moderately developed spines, clustered postero-laterally and scattered irregularly over ventral valve, no dorsal spines. Dorsal interior with blade-like septum passing forward from simple cardinal process bearing single myophore lobe.

DISCUSSION: This genus is based on the fully described and well illustrated species from the Neal Ranch Formation of the Glass Mountains, Texas. It is readily distinguished from *Striatifera*, of Early Carboniferous age, by its short straight hinge, lacking from *Striatifera*, and more prominent spines, different shape, greater inflation, and regular wrinkles and many other features. It falls closer to *Compressoproductus*, but has a well developed although short hinge and more ventral spines. The two share the posterior lateral cluster of spines, and wrinkles and other features, and thus are regarded as contribal. *Sarytchevinella* Waterhouse has short hinge, without the ears and with fewer spines and no postero-lateral cluster, and its shape differs. *Fallaxoproductus* Li, Gu & Li lacks wrinkles from the ventral valve. *Compressoproductus planus* Waterhouse, 1978 from the Lopingian of the Himalaya belongs to this genus.

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

[nom. transl. Brunton, Lazarev & Grant, 1995, p. 929 ex Monticuliferinae Muir-Wood & Cooper, 1960]

This family is typified by small round swellings over the ventral exterior, called monticules. According to Muir-Wood & Cooper (1960, p. 15) "Interrupted capillae appear in *Monticulifera* n. gen. as 4 or 5 short elevated lines on the anterior side of the rounded nodes covering the shell. These nodes are designated monticules. These may bear spines as in *Krotovia*, and usually the shell is nodose when the spines are stripped off. Radial alignment of spine ridges simulate costae and the ridges may actually fuse to form true costae". The spines appear to be erect, and may arise from the middle of the swelling, and the ribs continue forward into the monticule and persist in front. The nature of the "spine ridges" as distinct from costae was not explained by Muir-Wood & Cooper. The ventral muscle field is somewhat raised anteriorly, and the cardinal process broad and bifid, and a ginglymus may be developed.

DISCUSSION: Monticuliferidae, elevated to full family, was regarded as standard bearer for many mostly Permian genera in the revised brachiopod treatise. Here is it treated as an unusual, and possibly challengeable member of Linoproductoidea. Most of the genera here separated from Monticuliferidae differ in their ventral ornament. They display some to many spines that are prostrate to suberect, and emerge from short to moderately large swollen bases, always at the anterior end of the swelling. The spine base is prolonged posteriorly, whereas there has been no evidence so far published to indicate that the spine base is posteriorly prolonged in *Monticulifera* or its allies. As well, the swelling in these genera differs in the relationship to ribs. One to three ribs may enter the swelling from the posterior side, one or none may lie in front, whereas the swellings in *Monticulifera* seems to have no effect on the number of ribs. The raised muscle field of *Monticulifera* is not seen in the other genera, and these also generally have a higher cardinal process, though this is not invariant. A ginglymus may be developed in Monticuliferidae, as amongst the larger and more transverse gigantoproductins s. l.

The report in Muir-Wood & Cooper (1960) is inadequate because of the failure to properly examine the nature of the monticules and spines bases, due to overreliance on silicified material, and no subsequent study has provided clarification. I am assuming that the monticules do not enclose a cavity between external monticule and internal valve floor. If they are separated from the floor of the valve by a layer of shell, then Monticuliferidae could possibly embrace the genera here referred to Kansuellidae. But that is ruled out by further attributes of the two families. Members of Monticuliferidae may lack radial ornament, and have an unusual ventral muscle field, elevated anteriorly. The unusual ginglymus and muscle field are well illustrated by Liang (1990, pl. 37, fig. 3, 5).

Amongst other Productida, there are some similarities in wide transverse hinge, whorl profile, geniculate trail and overall shape, fine radial ornament, ginglymus and anteriorly raised ventral muscle field to *Yakovlevia* and allies. None of these show monticules, and a few large spines are developed in *Yakovlevia* itself. Allied genera are *Duarteia* Mendes and *Sajakella* Nasikova, and are classed in Yakovleviini Waterhouse. Brunton, Lazarev, Grant & Jin (2000, p. 465) placed *Inflatia* Muir-Wood & Cooper and *Tenaspinus* Brunton & Mundy in the group, but they differ in details of shape and ornament. The family group relationships of both Yakovleviini and Monticuliferidae require further study.

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

Monticulifera Muir-Wood & Cooper, *Zhenania* Ding and ?*Chilianshanina* Yang & Ting are characteristic, with capillae and with monticules on the ventral valve, from which spines emerge.

Subfamily **TONGLUELLINAE** Liang, 1990

Tongluella Liang and *Paramonticulifera* Tong, said to be senior synonym, lack capillae. Monticules well developed.

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

[nom. transl. hic ex Kansuellinae Muir-Wood & Cooper, 1960, p. 336]

This family is typified by having some to many ventral spines which emerge anteriorly from a slight to considerable swelling, through which the hollow spine base is prolonged posteriorly. One, two or rarely three costae or ribs may pass forward into the swollen spine base, and none to one rib may continue forward from the swelling. Concentric wrinkles are often developed. The ventral muscle field is set into the shell and not raised anteriorly above the floor.

DISCUSSION: Members of this newly distinguished family are characterized by swollen and posteriorly prolonged spine bases over the body of the ventral valve. Costellae or capillae cover both valves, and tend to be less close-spaced than in Linoproductidae. Concentric wrinkling is subdued to well developed on both valves as a rule. Emphasis on shallow to very shallow body cavity and on lack of dorsal spines is downplayed, despite Brunton, Lazarev, Grant & Jin (2000, p. 536). Furthermore, the stress laid by them on lack of marginal structures as "normally absent" applies widely in the superfamily and does not help distinguish between Linoproductidae and Monticuliferidae, or Kansuellidae as here delineated. The member subfamilies and tribes are considerably altered from the scheme set out in the revised brachiopod treatise, because that scheme was inconsistent and ignored morphological ties.

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

This unusual subfamily differs from most of the related and generally younger members in being large and transverse, very close to Gigantoproductinae in size and shape, to the extent that the revised brachiopod treatise did not distinguish the subfamily. However the spine bases, ribbing and development of concentric ornament help distinguish *Kansuella* from *Gigantoproductus* and allies.

Constituent genera are *Kansuella* Chao, better figured by Chao (1928) and Brunton, Lazarev, Grant & Jin (2000, text-fig. 389) than by Muir-Wood & Cooper (1960), and *Kueichowella* Yang Shi-pu. These are large forms. The newly developed ornament of concentric wrinkles and prolonged ventral spines were retained with size reduction in younger forms.

Subfamily **AURICULISPININAE** Waterhouse, 1986

Medium-sized with ovally transverse outline, spines of ventral valve close to hinge, may be crowded on ears, scattered over rest of valve, where characterized by short elongate gently swollen bases, each spine base directed posteriorly within shell. Dorsal spines rare or absent. Costellae well developed, not as linear, broad-crested or crowded as in Linoproductidae as a rule, concentric wrinkles present to well developed. Body corpus narrow to deep.

Brunton, Lazarev, Grant & Jin (2000, p. 537) presented a different model, writing of elongate shells, some of which have been transferred to Linoproductidae. They regarded the absence of marginal structures as diagnostic as a rule, but other groups share this feature. They also observed that teeth and sockets were

absent. That is also true of other Linoproductoidea, so that the helpfulness or even relevance of this point is not immediately clear, to me at least. It was possibly added as an unnecessary discriminant from Eoproductellinae.

Tribe **AURICULISPININI** Waterhouse, 1975

[nom. transfer. hic ex Auriculispininae Waterhouse, 1975, p. 57]

This tribe encompasses normally transverse genera with variable number of spines near hinge, often crowded on ears. Constituent genera are *Auriculispina* Waterhouse, *Costatumulus* Waterhouse and *Platycancrinella* Waterhouse. The latter genus was synonymized with *Cancrinella* Frederiks by Brunton, Lazarev, Grant & Jin (2000, p. 533) but it lacks dorsal spines and has different more transverse less inflated shape and more gently concave dorsal valve and large ears. *Cancrinella* differs in shape, has different ventral hinge spines, and has many dorsal spines. The two are not synonymous, and belong to different subfamilies.

There is some uncertainty about other genera allocated to the subfamily in the revised brachiopod treatise. *Linoprotonia* Ferguson, an early Carboniferous form has many ear-spines but is otherwise linoproductid. *Teleoproductus* Li Li was assigned to the subfamily in the revised brachiopod treatise (2000, p. 544) but might be linoproductid. *Vitiliproductus* Jin & Liao is obscure with tetrathedral elevations over the ventral valve, suggestive of *Monticulifera*: it was assigned with a query to Auriculispininae by the revised brachiopod treatise but the genus needs to be more closely examined.

Genus ***Auriculispina*** Waterhouse, 1975

TYPE SPECIES: *Cancrinella levis* Maxwell, 1964.

DIAGNOSIS: Thin-bodied transversely oval shells with maximum width at mid-length and small poorly differentiated ears, ornament of costellae and low wrinkles, no dorsal spines, ventral spines dense postero-laterally, arranged in quincunx over disc and anterior, generally with swollen and posteriorly prolonged bases.

DISCUSSION: The type species comes from the lower Burnett Formation of the Yarrol Basin. It has posteriorly thickened ventral wall and deeply inset ventral adductors. Only the type species has been known, up to now.

Auriculispina capillata (Waterhouse, 1988)

1988 *Terrakea capillata* Waterhouse in Foster & Waterhouse, p. 156, text-fig. 8d-h.

1991 *Lyonia capillata* (Waterhouse); Archbold & Dickins, p. 4.

1993a *Costatumulus capillata* (Waterhouse); Archbold, p. 315.

1995b *C. capillata* (Waterhouse); Archbold, p. 106, text-fig. 6A-L.

1996 *C. capillata* (Waterhouse); Archbold & Dickins, p. 129.

1998 *C. (?) capillata* (Waterhouse); Briggs, p. 157.

HOLOTYPE: GSWA F47193, figured by Foster & Waterhouse (1988, text-fig. 8e) and Archbold (1995b, text-fig. 6K, L) OD from Calytrix Formation, Grant Group, Canning Basin, Western Australia.

DIAGNOSIS: Small thin-bodied shells with small ears, maximum width at mid-length, fine costellae and subdued crowded wrinkles. Ventral postero-lateral shell including ears have numerous crowded spines, extending well forward, body spines with short posteriorly prolonged bases.

DISCUSSION: This species is smaller than *Auriculispina levis* (Maxwell), with more and lower wrinkles, fewer posterior lateral spines that extend further forward along the lateral flanks, and other differences.

The species has been variously misunderstood in the past. Waterhouse (in Foster & Waterhouse 1988) thought it might belong to *Terrakea*, from the nature of the ventral ornament, but was mistaken in reporting dorsal spines. This was corrected by Archbold (1995b) in finding that dorsal spines were absent.

But that did not end the misconceptions. Initially, Archbold & Dickins (1991) revised the species as belonging to *Lyonia* Archbold. This attribution is also inappropriate, because *Lyonia* has a different arrangement of spines along the ventral hinge, and Briggs (1998, p. 157) also pointed out this discrepancy.

Then *Costatumulus* became the favoured genus, and Archbold (1993a, 1995b) in emphasizing that Waterhouse had misidentified the genus, put aside any reference, even in his synonymy, to *Lyonia*, although it was acknowledged as wrong by Archbold & Dickins (1996). Briggs (1998) also favoured a probable relationship with *Costatumulus*. This genus has one or two rows of hinge spines. By contrast, *capillata* has a burst of spines over the posterior lateral ventral valve. This prime feature, with attributes of ornament and shape, means that *capillata* can be accommodated in *Auriculispina* Waterhouse, 1975, based on *Cancrinella levis* Maxwell, 1964 from the lower Burnett Formation of the Yarrol Basin, Queensland. The species *levis* is close in shape and costation, and has a very large number of spines over the ventral ears, and the spines cluster does not extend so far laterally forward as in the west Australian species. Dorsal spines are missing, and ventral spine bases less conspicuous than in *capillata*.

Archbold & Dickins (1991, p. 4) complained with regard to this and other brachiopod species recorded by Foster & Waterhouse (1988) about "the lack of complete faunal description" to excuse their own (Archbold-Dickins) failure "to assess the biostratigraphic importance". They failed to point out that the Foster - Waterhouse material came from a core cutting, and so was of necessity meagre. The material nonetheless suffices to rule out the generic determinations made in Archbold & Dickins (1991, 1996) and Archbold (1993a, 1995b), and indicates, as we said, an Early Permian age. Overall, the initial determinations by Foster & Waterhouse (1988) have proved to be of more value than some of the revisions, involving both *capillata*, and *Strophalosia*, as discussed later.

Genus ***Platycancrinella*** Waterhouse, 1983
Pl. 2, fig. 10 - 20

TYPE SPECIES: *Platycancrinella grandauris* Waterhouse, 1983.

DIAGNOSIS: Ventral valve transverse and gently convex with large ears, acute cardinal extremities, dorsal valve gently concave, body corpus narrow, trail subgeniculate, low. Both valves closely costellate, numerous erect spines over ears, ventral body spines close-spaced with swollen bases posteriorly over much of the disc, and may be prostrate, anterior spines generally erect. No dorsal spines, well developed short hollows, wrinkles moderately developed on both valves. Internally, ventral muscle imprints light, dendritic posteriorly, posterior wall little thickened. Dorsal median septum long and broad posteriorly.

DISCUSSION: This genus was described from the Lopingian (Late Permian) Pija Member, Senja Formation, north Nepal, by Waterhouse (1983b). It was synonymized with *Cancrinella* by Brunton, Lazarev, Grant & Jin (2000), but is readily distinguished from that genus by the lack of dorsal spines (see Waterhouse 2000c, d) and by the lack of well formed rows of hinge spines.

The genus is very closer to *Auriculispina* Waterhouse, 1975, type species *Cancrinella levis* Maxwell, 1964, from the early Cisuralian or Late Carboniferous lower Burnett Formation of the Yarrol Basin, Queensland. *Auriculispina* has much the same ornament, apart from differences such as finer ventral spine bases and no erect spines, and significantly, somewhat fewer ear spines. The ears are much larger in *Platycancrinella*, so that overall shape is different, and this is regarded as prime discriminant. Amongst minor attributes, the dorsal median septum is longer and narrower than in *Auriculispina levis*, and the posterior wall of the ventral valve is much less thickened than in the type species, with lightly impressed adductor field, dendritic posteriorly, whereas *Auriculispina levis* has a much thickened ventral posterior wall and high striate adductor platform.

Platycancrinella transversa (Briggs, 1998)

1985 *Auriculispina levis* (not Maxwell); Briggs, p. 99.

1998 *Magniplicatina transversa* Briggs, p. 187, text-fig. 91.

DISCUSSION: This species was described from a number of localities in New South Wales and Queensland, in beds judged by Briggs to be equivalent to his *warwicki* Zone. The type material came from the Colrairie Mudstone, near Kimbriki. As well as costellae and wrinkles, it has large ears with numerous ventral spines, posterior ventral disc spines with large bases, and anterior erect spines, much as in *Platycancrinella grandauris*. Ventral thickening is slight, and muscle scars are lightly impressed, and dorsal septum long. The species differs from *Magniplicatina* in its larger ears and absence of 1-3 well defined row of spines along the ventral hinge. *Auriculispina* is closer, but has small ears, different spines, and thickened posterior ventral walls with different adductor scars, and other features.

Genus ***Costatumulus*** Waterhouse, 1983

TYPE SPECIES: *Auriculispina tumida* Waterhouse in Waterhouse, Briggs & Parfrey, 1983, considered by Briggs (1998, p. 155) to be a junior subjective synonym of *Productus cora* var *farleyensis* Etheridge & Dun, 1909, as accepted herein.

DIAGNOSIS: Large shells with swollen venter, well defined ears, double row of hinge spines without cluster of spines over ears, fine costellae, ventral spine bases short, slightly swollen, arising from spine ridges, dorsal valve without spines. Ventral adductor scars initially elongate, triangular, and smooth, later becoming subtriangular and posteriorly striate, and ultimately elongate-oval and completely dendritic, according to Briggs (1998).

DISCUSSION: Briggs (1998, p. 145) rejected Auriculispininae, and referred *Costatumulus* to Linoproductidae, but offered no rebuttal of Brunton & Lazarev (1997) or Brunton et al (1995).

As shown in the following discussion of New Zealand material, the genus is proving to be widespread in distribution, with likely occurrences both throughout much of Gondwana and also in the Arctic and even Texas.

***Costatumulus?* sp.**
Pl. 1, fig. 10

MATERIAL: One ventral valve BR 2262 from D44/f109 (GS 15208), *Echinalosia discinia* Zone, upper Letham Formation, and another BR 2400 from D44/f123 (GS 15226), *Pseudostrophalosia?* cf *blakei* fauna, lower Mangarewa Formation, Wairaki Downs.

DIMENSIONS IN MM:

Specimen	Width	Length	Height	Umbonal angle
BR 2262	23	22.5	15	110°

DESCRIPTION: Ventral valve BR 2262 highly vaulted, umbo massive, little extended beyond hinge, hinge at maximum width with small gently convex ears, cardinal angle about 90°, and valve also wide well forward. Venter convex, no median sulcus. Ornament of fine costellae, 10-12 in 5mm anteriorly. Very low wrinkles lie on lateral flanks and anteriorly. The arrangement of spines along the hinge not entirely clear, possibly one row near umbo, 2 rows on outer ears. Body spines arranged in quincunx, bases wider than ribs, 2.5mm long, raised. Adductor scars weakly impressed and striate, diductors small and weakly impressed. Ventral valve BR 2400 from D44/f123 somewhat similar in shape and low wrinkles, 9-10 costellae in 5mm anteriorly, spine bases broader than on other specimen, less than 2mm long, ears small, hinge spines obscured.

DISCUSSION: *Costatumulus* is known from only Early Permian faunules of east Australia, as somewhat larger species, *C. farleyensis* (Etheridge & Dun) and *C. meritus* Waterhouse, as well as Early Permian occurrences further afield as *C. irwinensis* (Archbold) in Western Australia, and species in the eastern Himalaya (Singh & Archbold 1993) and Argentina (Taboada 1998). The genus is possibly present in Arctic Canada (see Shi & Waterhouse 1996, pl. 17, fig. 16, 17), and also in the Taylor Ranch Member of the Hess Formation in the Glass Mountains, Texas, as *Linoproductus undatus* Cooper & Grant (1975, pl. 433, fig. 27-43). Younger occurrences are known for the Carnarvon Basin, Western Australia, where Archbold (1993a) listed *Costatumulus* sp. from the *Echinalosia prideri* Zone, and *C. bellus* (Etheridge) from the *Fusispirifer wandageensis* Zone. *C. bellus* (see Archbold 1983b, text-fig. 1Q-X, text-fig. 2A, B) is small for the genus and slightly more transverse than the New Zealand form, with strong costae.

Tribe **LYONIINI** new

NAME GENUS: *Lyonia* Archbold, 1983.

DIAGNOSIS: Transverse shells with wide hinge and single to double row of erect ventral spines along hinge, scattered body spines with weakly to moderately prolonged slightly swollen bases. Body cavity shallow, both valves with well defined costellae.

DISCUSSION: This tribe is recognized for a distinctive subset of Auriculispiniinae, characterized by shape and ornament. *Lyonia* is particularly close in shape to *Bandoproductus*, but has dorsal spines. This, with many other examples, helps demonstrate that presence or absence of dorsal spines in some stock may not be significant to other than generic level.

CONSTITUENT GENERA: *Lyonia* Archbold, *Canocrinelloides* Ustritsky, *Bandoproductus* Jin & Sun, *Nambuccalinus* Waterhouse.

Genus ***Bandoproductus*** Jin & Sun, 1981

TYPE SPECIES: *Bandoproductus hemiglobicus* Jin & Sun, 1981.

DIAGNOSIS: Transverse large shells with closely costate valves, spines only on ventral valve, row along hinge and scattered body spines.

DISCUSSION: This genus is found in south Asia (Waterhouse 1982e), and east Australia (Waterhouse 1986b, Waterhouse & Balfe 1987, Briggs 1998) and is represented in New Zealand by a single fragment.

***Bandoproductus?* sp.**

1964a *Linoproductus* sp. Waterhouse, p. 171.

1982a ?*Linoproductus* sp. Waterhouse, p. 44.

MATERIAL: A posterior fragment of a ventral valve BR 1501 from D44/f9604 (GS 5885), *Terrakea dickinsi* Zone, Brunel Formation, Takitimu Group.

DISCUSSION: The narrow protruding umbo of this specimen and the close-set costellae suggest *Bandoproductus*. Preservation is poor, but the large ears suggest the presence of large erect spines in a row

close to the hinge. Species in east Australia tend to be of earlier Permian age, as far as is known.

Genus ***Nambuccalinus*** new

DERIVATION: Named from Nambucca, New South Wales.

TYPE SPECIES: *Lyonia bourkei* Briggs, 1998, here designated.

DIAGNOSIS: Large transverse shallow-bodied shells with maximum width at hinge, large ears, acute cardinal extremities, dorsal valve moderately concave. Both valves covered by costellae, prominent 2-3 rows of long erect sturdy spines along ventral hinge, scattered subprostrate body spines with short elongate bases, no dimples. Dorsal valve with numerous fine erect spines, absent from ears, no dimples. Concentric growth ridges and wrinkles fine and close-set over both valves. Muscle scars lightly impressed in both valves, short medium septum and low cardinal ridges in dorsal valve.

DISCUSSION: From overall shape and dimensions this form is a member of Lyoniini, but is distinguished from all but *Lyonia* in the presence of dorsal spines. *Lyonia* is close, but has only one row of cardinal spines, far fewer dorsal spines, and numerous pits over the dorsal exterior, to mention some of the more conspicuous differences. No species of any of the other genera show so many hinge spines, although *Bandoproductus macrospina* Waterhouse has a few extra spines near the hinge as noted by Briggs (1998). But in other respects, including detail of the interior, described in further detail by Briggs (1998), the new genus is an ally of *Lyonia*. Briggs (1998) regarded the species *bourkei* as Asselian, but a Late Carboniferous age cannot be ruled out in view of SHRIMP evidence (Waterhouse 2000b).

Tribe **FILICONCHINI** new

NAME GENUS: *Filiconcha* Dear, 1969.

DIAGNOSIS: Weakly transverse shells with flat ventral disc, subrectangular outline. Ventral body spines numerous with elongate bases, spines few and not organized in row close to hinge.

DISCUSSION: *Filiconcha* Dear with dorsal spines and *Spitzbergenia* Kotlyar without dorsal spines are close but not identical in shape to *Lyonia* and allies. The difference lies chiefly in the development of hinge spines.

Genus ***Filiconcha*** Dear, 1969

TYPE SPECIES: *Filiconcha hillae* Dear, 1969.

DIAGNOSIS: Transverse ovals subrectangular shells with short geniculate trail, radial costellae, ventral spines few on ears, bearing short posteriorly prolonged spine bases over body of valve, dorsal spines numerous and erect. Ventral interior with thick posterior wall and distinctive striate adductor platform, cardinal process squat and broad, numerous dorsal pustules anteriorly behind short trail.

DISCUSSION: Briggs (1998, p. 197) offered a brief description of the genus *Filiconcha*, but failed to offer an adequate distinction from *Terrakea*. The distinction between the two genera is marked, involving for *Filiconcha* the homogeneity of ventral spines, short spine bases and short trail, and rectangular linearly striate adductor platform and thick posterior wall in the ventral valve. Dorsally the cardinal process, medium septum and anterior pustulation all differ, as elaborated by Dear (1969) and Waterhouse (1976a, 1986b).

Brunton, Lazarev, Grant & Jin (2000, p. 539) neglected to record the presence of *Filiconcha* in New Zealand, but overall the revised brachiopod treatise is unreliable over distributions, at least for Permian Productida (Waterhouse 2000e), and perhaps distributions are a task too formidable for a treatise to attempt.

Filiconcha auricula Waterhouse, 1976

1976a *Filiconcha auricula* Waterhouse, p. 238, text-fig. 4, 3-14.

1978 Fam. & gen. indet. Waterhouse & Mutch, p. 519, text-fig. 8, 9.

1978 *Terrakea* sp. Waterhouse & Mutch, p. 521.

1998 *Filiconcha auricula* Waterhouse; Briggs, p. 197.

HOLOTYPE: BR 1703 from G45/f7689 (GS 11139) OD, possibly *Spinomartinia spinosa* Zone, Arthurton Group, near Arthurton.

DESCRIPTION: The fragment BR 2225 from D45/f7592 (GS 5863), Hilton limestone, Wether Hill Station, is now believed to belong to this species. It shows moderately close-set spines with distinct short elongate bases, and was recorded as *Terrakea* sp. by Waterhouse & Mutch (1978). Obscure specimens, recorded by Waterhouse & Mutch (1978, p. 519, text-fig. 8, 9) from the same rocks as Fam. & gen. indet., possibly

belong here, agreeing in shape, but with ornament largely lost, although I did observe faint traces of ribs on the specimens. A ventral fragment BR 2401 from D45/f7578 shows ornament moderately well over the middle and anterior valve. The species has also been observed in the Hilton limestone exposed in headwater creeks of Pleasant valley, Aparima River.

DISCUSSION: The holotype and other specimens came from a loose boulder. The species that accompany the holotype and the nature of the matrix suggest that the block may have come from the *Spinomartinia spinosa* Zone, rather than the *Plekonella multicostata* Zone as interpreted by Waterhouse (1976a).

Tribe **SIPHONOSIINI** Lazarev, 1990

[nom. transl. hic ex Siphonosiinae Lazarev, 1990. The name was proposed as a nomen nudum by Lazarev 1986]

The revised brachiopod treatise recognized one genus in this group. Cooper & Grant (1975, p. 1188) discussed *Siphonosia* in general terms, carefully comparing it with *Proboscidella* Oehlert. Brunton, Lazarev, Grant & Jin (2000, p. 535) opted for a linoproductid relationship, but gave no reason: presumably the high body corpus weighed in favour of this position. Figures in Cooper & Grant (1975, pl. 466, fig. 5, 12, 14, 15, 24, 21, 24) indicate suberect to subprostrate body spines, and scattered erect body spines over the ventral valve, with only weak indications of a possible alliance to Auriculispiniinae. This is strengthened by the development of a dense array of erect sturdy ear spines on the ventral valve. Thus inspection of specimens seems to be necessary for full appraisal.

Tribe **UNDARIINI** new

NAME GENUS: *Undaria* Muir-Wood & Cooper, 1960.

DIAGNOSIS: Asymmetric shells with moderately developed irregular hinge, fine diversified ribs and erect and prostrate ventral spines with prolonged slightly swollen bases, no dorsal spines. No long tubiform trail or heavy dorsal marginal ridge.

DISCUSSION: The genus *Undaria* Muir-Wood & Cooper looks somewhat similar to *Siphonosia* Cooper & Grant but much less extreme in its development. The ventral valve, especially as shown in original figures by Muir-Wood & Cooper (1960, pl. 118, fig. 3-11, note fig. 5), appears to have elongated spine bases, indicating a relationship to Auriculispiniinae. The genus lacks dense ear spines, but variation in number of ear-spines is common in the subfamily. The genus was carefully compared with *Siphonosia* by Cooper & Grant (1975) and appears to have arisen independently from Auriculispiniini. The two tribes Siphonosiini and Undariini appear to represent extreme, independent, and presumably "dead-end" developments.

Subfamily **PAUCISPINAURIINAE** Waterhouse, 1986

[syn. Grandaurispiniinae Lazarev, 1990]

TAXONOMY: Paucispinariinae was proposed by Waterhouse (1986a, June, p. 2) at the same time as Grandaurispiniinae Lazarev (1986, June, p. 32) was listed, but not proposed or discussed. Disturbingly, Brunton, Lazarev, Grant & Jin (2000, p. 533) presented an incorrect account. They claimed that Paucispinariinae had not been proposed until September, 1986 (Waterhouse 1986b, p. 37). They also did not acknowledge that the Lazarev proposal was in a list, with no typical genus or other genus indicated, and no diagnosis or explanation. Lazarev (1986) did not provide a description or definition that stated in words characters that purported to differentiate the taxon. The International Commission for Zoological Nomenclature (2000, article 13.1, p. 17) states that to be available, every new family-group name published after 1930 must satisfy the provisions of Article 13.1. Article 13.1 (p. 17) states "every name... must be accompanied by ... a.. description or definition that states in words characters that are purported to differentiate the taxon..." Grandaurispiniinae Lazarev (1986) did not conform to this rule. By contrast, Waterhouse (1986a) did provide a brief explanation, and indicated both the name genus and allied genera. The proposal was reinforced shortly afterwards by Waterhouse (1986b) and Shi & Waterhouse (1996, p. 100). It thus seems to me that the Waterhouse proposal should outweigh a nomen nudum, and that it gained further weight by being reinforced shortly afterwards. And most importantly, the proposal of June 1986 did conform with the code of Zoological Nomenclature. Lazarev (1990) and Brunton, Lazarev, Grant & Jin (2000) misrepresented the situation. The Lazarev name does not and never did have priority.

Indeed, some question remains over whether Lazarev's article of 1986 was a publication. It came to me with numerous hand-written insertions and corrections, as part of the procedures involved in submitting for a higher degree, as shown in the reference for Lazarev 1986. There is no indication I can find that it was ever offered for sale. It is not quoted nor referenced in the authoritative summary of the classification of Productida by Brunton, Lazarev & Grant (1995), with reference instead to the finished study by Lazarev (1987), although the date of 1986 was attached, contentiously, to the name. As the Lazarev name was only listed in what seems to be an informal summary, equivalent to a doctoral thesis, dated 1986, with no

diagnosis or explanation or discussion, *Grandaurispininae* Lazarev, 1986 appears to rate as a nomen nudum. Nor was a discussion or diagnosis provided in Lazarev 1987. Not until 1990 did Lazarev (1990, p. 130) provide validation, and its validity dates from 1990. Prior mentions carry no standing, according to the rules of zoological nomenclature, yet Brunton, Lazarev, Grant & Jin (2000) kept referring to Lazarev, 1986.

FAMILY RELATIONSHIPS: The assignment of *Grandaurispininae* Lazarev, 1990 (junior synonym of *Paucispinaurinae* Waterhouse, 1986) to *Linoproductidae* cannot be sustained. *Linoproductidae* have better defined closer-set radial ribs, and ventral body spines that do not have prolonged bases. Certainly a number of the *paucispinaurin* genera have a thick body cavity as in *Linoproductinae*, but this is regarded as of lesser importance. Brunton, Lazarev, Grant & Jin (2000, p. 533) mentioned that the subfamily comprised *linoproductids* with thin spines also on the dorsal corpus. The significance of dorsal spines at subfamily level is questionable, because so many otherwise similar genera differ only in the presence or absence of dorsal spines. The revised brachiopod treatise also added for the diagnosis "marginal structures, series of trails absent." Such criteria do little to distinguish members of the subfamily from other *Linoproductoidea*.

Constituent genera are listed below. *Holotricharina* Cooper & Grant, 1975 was included by Brunton, Lazarev, Grant & Jin (2000, p. 535) but is probably a marginiferid in view of its ornament and interior, even though Cooper & Grant (1975) recorded a *linoproductinid* cardinal process. As well, *Lyonia* and *Stepanoviella* are here assigned to *Linoproductidae*, and *Platycancrinella* to *Auriculispininae*.

Tribe **PAUCISPINAURIINI** Waterhouse, 1986

[nom. transfer. hic ex *Paucispinaurinae* Waterhouse, 1986]

DEFINITION: This tribe incorporates shells often with thick visceral cavity and ventral and dorsal spines. Shape generally weakly transverse to subelongate, with well inflated ventral valve and high posterior shoulders. Concentric wrinkles weakly developed.

CONSTITUENT GENERA: *Paucispinauria* Waterhouse, *Spargospinosa* Waterhouse, *Terrakea* Booker, *Grandaurispina* Cooper & Grant, *Saetosina* Waterhouse and *Pinegeria* Waterhouse.

Genus ***Paucispinauria*** Waterhouse, 1983

TYPE SPECIES: *Terrakea concava* Waterhouse, 1964b.

DIAGNOSIS: Shells with narrow to moderate body corpus, variably geniculate trail and comparatively few spines on ears, lacking cluster of crowded spines found on ears and/or on posterior lateral slopes, anterior dorsal spines may be very coarse.

DISCUSSION: *Paucispinauria* is a distinctive genus, proposed by Waterhouse (1983b) for shells characterized by its few ear spines, especially on the ventral valve. Some spines over the dorsal trail tend to become very large. Unlike *Terrakea* (eg *pollex*, *brachythaera*, *elongata*, *dickinsi*, *exmoorensis*), *Paucispinauria* includes species that are not deep-vaulted and do not have a very long trail and high lateral walls for the ventral valve. In the Bowen Basin and New Zealand, species of *Paucispinauria* often alternate with species of *Terrakea*. The oldest species so far known is *P. geniculata* Waterhouse, 1986b from the Elvinia Formation of the southeast Bowen Basin, and the youngest named species is *P. verecundum* (Waterhouse) from the Glendale Formation of Wairaki Downs and upper Arthurton Group near Arthurton, New Zealand, and possibly South Curra Limestone of southeast Queensland. Unlike *Terrakea*, the genus is not known further afield, but has a close ally in the Russian Arctic.

Briggs (1998) discounted this genus with the claim that the number of ear spines varied considerably. I have not been able to substantiate his claim, and his own figures of various species do not verify his assertions. Thus his figures of *geniculata*, *concava* and *paucispinosa*, referred previously by Waterhouse (1986b) to *Paucispinauria*, show few ear-spines, compared with the many ear spines in species correctly referred to *Terrakea*. The consistency of this morphology, and the stratigraphic consistency and value, show that the genus should be discriminated. It was recognized as valid by Brunton, Lazarev, Grant & Jin (2000, p. 535), with good figures, in contrast to their ineffectual figures provided for *Terrakea*.

Paucispinauria paucispinosa wardenensis n. subsp.

Pl. 1, fig. 18 - 21, text-fig. 5d

1909 *Productus brachythaerus* (not Morris); Etheridge & Dun, p. 5, pl. 43, fig. 6 (not pl. 42, fig. 1, 4, 6, 8, pl. 43, fig. 8-11 = *Terrakea brachythaera* (Morris), largely fide Briggs 1998).

1930 *Terrakea leve* Booker, pp. 70-71 AMF 1158 only, fide Briggs 1998 (not pl. 2, fig. 3, 4 = *T. brachythaera* (Morris)).

?1981 *T. cf dickinsi* not Dear; Dickins, p. 30, pl. 4, fig. 6-10.

cf 1982a *Terrakea concava* not Waterhouse; Waterhouse, p. 49, pl. 10, fig. k.

1988 *Terrakea* sp. McLoughlin, pl. 1, fig. 2, 3.

1998 *T. concava* not Waterhouse; Briggs, p. 170, text-fig. 84.

DERIVATION: Named from Warden Head, south Sydney Basin, New South Wales.

HOLOTYPE: UQF 75333 figured by Briggs (1998, text-fig. 84G) from UQL 5156, Wandrawandian Formation, Warden Head, south Sydney Basin, New South Wales, here designated.

DIAGNOSIS: Moderately large subtransverse to elongate specimens without ventral sulcus, spines few over ventral ears, missing from outer extremities, and with short bases over rest of ventral valve, emerge at high angle. Dorsal spines very fine over disc, large and few over geniculate trail. Differs from *paucispinosa* in more vaulted disc, slightly fewer dorsal spines and shorter ventral spine bases.

MATERIAL: Three ventral valves and dorsal valve with a number of other specimens from UQL 3758, 60km south of Springsure, Bowen Basin. Additional ventral valves UQF 75055 and 75056 were figured by McLoughlin (1988).

DIMENSION IN MM: Ventral valve (approximate)

UQF	Width	Length	Height
65423	31	25	11
65524	36	+29	17
65423	50	45	~28
Dorsal valve			
65483	43	30	18

DESCRIPTION: Specimens large at maturity with broad umbo measuring 100° in Freitag specimen UQF 65423, 70° in another, posterior walls high and gently convex in outline, maximum width at hinge, rounded cardinal extremities, ears large but poorly defined. Posterior ventral valve gently convex medianly, valve becomes flattened and develops very shallow if any median depression in front. Dorsal valve broad with wide hinge, narrow poorly defined ears with subacute rounded extremities, gently concave visceral disc, and high geniculate trail. Costellae cover both valves, as fine as 10 in 5mm on UQF 65423, 12 in 5mm on dorsal disc, and 7 in 5mm on trail, where become impersistent. Ventral spine bases up to 4mm apart along rows 2.5mm apart, more irregularly distributed on anterior of large specimens, 2-3mm apart and up to 8-9mm between rows, emerge at high angle of 45-50° over disc and suberect on larger specimens in front, measure almost 1mm in diameter anteriorly on UQF 65423, and emerge from short swollen base up to 2.2mm long. Spines measure 1.4mm in diameter over anterior of largest specimen and emerge directly from shell with no posteriorly extended base, but bases slightly swollen. Dorsal spines moderately close-set and only 0.5mm in diameter over anterior disc, large and erect over trail, up to 2mm in diameter; a few dimples and growth irregularities also present. Fine growth increments are also developed, 6-8 in 1mm, and varying in strength.

One Freitag specimen has faintly raised striate adductors, no visible diductors, and valve bearing long channels or hollow tubes from spine bases posteriorly; anteriorly, the external ornament is visible because of thinness of the shell. Muscle scars are also faint in the specimen of intermediate size, with very faintly impressed round diductors. The large specimen has short posteriorly placed adductor scars with striae and divided by a posterior myophragm, from which ridges and grooves pass obliquely back. Diductors large, extend almost as far back as adductors, striate part extends in front of adductors in small specimens but not in large UQF 65423. Posterior floor thickened, without hinge ridge, fine pustules anteriorly and hollow bases of spines. Dorsal interior not known.

RESEMBLANCES: It is considered that the ventral valves from GS 6070 (D44/f9621) of the lower Letham Formation in Wairaki Downs, that were assigned to *Terrakea concava* (not Waterhouse) by Waterhouse (1982a) and Briggs (1998), probably belong to this subspecies. One specimen was described as elongate, and two as transverse with rounded venter: all are small. The body spines have very short bases, one of the characteristics of this species, and are highly inclined from the shell. The dorsal valve is geniculate. The GS 6070 material may be regarded as *Paucispinauria paucispinosa* cf *wardenensis*.

Various specimens ascribed by Briggs (1998) to *Terrakea concava* and reallocated to *Paucispinauria paucispinosa wardenensis* were reported from his upper so-called *Echinalosia maxwelli* and *E. davidi* Zones, which equate with the *E. discinia* Zone sensu stricto, including faunas of the Branxton Subgroup, upper Elderslie Formation, Wandrawandian Formation and Fenestella Shale of the Sydney Basin. As well, Briggs (1998) referred to a number of specimens only by locality, with no description or illustration, and these need to be re-examined for adequate assessment. Non-type specimens recorded by Briggs (1998) from UNE localities are no longer in those collections: according to records, they have been borrowed, and not returned.

Paucispinauria paucispinosa Waterhouse (1986b, pl. 12, fig. 12-16) from the Brae Formation of south-east Bowen Basin is a large transverse or elongate thin-bodied form with few well spaced body spines and very few or no ear spines on the ventral valve. The types, further discussed below, thus differ in inflation and profile, but they share the smoothness of the outer ventral ears, and the possibility seems high that *wardenensis*

and *paucispinosa* are very close to each other. In the present model, *paucispinosa paucispinosa* is found chiefly in the Brae Formation of the southeast Bowen Basin. Individuals of *paucispinosa* have been observed in UNE collections from the Sydney Basin. Briggs (1998) also reported the species in the Sydney Basin (Branxton Subgroup, Belford Formation, Wandrawandian Formation), without adequately documenting or illustrating the specimens. Briggs (1998, text-fig. 85B) referred Oxtrack Formation specimens to this species, but the Oxtrack shells have more ear spines. The Drake Volcanics specimen of Briggs (1998, text-fig. 85B) is a dorsal valve, difficult to identify, but more geniculate than is usual for *paucispinosa*.

Paucispinauria concava (Waterhouse, 1964b) from the Letham Burn Member, lower Mangarewa Formation, Wairaki Downs, and also the Oxtrack Formation, southeast Bowen Basin, is close to *wardenensis*. The types of *concava* are more transverse with finer ventral spines 0.5mm wide, 2mm apart along rows 1.5mm apart, and up to 0.7mm in diameter and 3mm apart anteriorly. No ventral valves are as tumid, high and incurved as the present suite, so that overall shape is different, and many valves of *concava* are gently sulcate medianly, more than the present material or the Briggs figured specimens. Costellae and spine bases are close in all suites, but the outer ventral ears of the new form, including the Briggs "*concava*" material, generally lack spines, whereas 1-3 spines are developed on the outer ventral ears of typical *concava*. The dorsal valve of *P. concava* is concave and usually grades imperceptibly into the trail although a few are geniculate, possibly by deformation, and anterior spines are up to 1mm in diameter over trail, mostly in one prominent row. Internally, diductors are better defined and more anteriorly placed, and internal spine bases more prominent. The Freitag suite can thus be distinguished from the lower Mangarewa-Oxtrack specimens. An initial appraisal of Sydney Basin collections from various stations at University of New England suggests a flux of morphotypes, to imply that distinctions found in geographically distinct regions of Bowen Basin and New Zealand became blurred in the Sydney Basin, where faunal diversities were lower, and species ranges more prolonged and heterochronous (Waterhouse 2000a).

Paucispinauria solida (Etheridge & Dun, 1909) is suboval in shape and generally not sulcate, with more concave dorsal valve. Ventral spine bases are longer, and ear spines more numerous. Other observations are summarized below.

Table 5. Succession of important linoproductid and strophalosiid species for Middle Permian, showing some discrepancies between Sydney Basin, New Zealand and southeast Bowen Basin (Waterhouse 2000a). Subspecies grouped with species. See also Table 6.

South Sydney Basin	North Sydney Basin	SE Bowen Basin	Wairaki Downs
Kulnura marine band			Mangarewa 8 <i>T. elongata</i> & <i>clarkei</i>
<i>Ps. clarkei</i>			
Broughton <i>E. wassi</i> & <i>T. brachythaera</i>	Mulbring <i>E. runnegari</i>	Flat Top	Mangarewa 6,7 <i>E. ovalis</i> &
Berry <i>E. ovalis</i> & <i>runnegari</i> & <i>brachythaera</i>	Muree <i>ovalis</i>	<i>ovalis</i> & <i>brachythaera</i>	<i>P. solida</i>
Nowra	Belford	Barfield	Mangarewa 5 <i>exmoorensis</i> & cf <i>blakei</i>
<i>E. ovalis</i>	<i>ovalis?</i>	<i>Ps. blakei</i>	
Wandrawandian <i>E. maxwelli</i>	Belford <i>maxwelli</i> & <i>P. concava</i>	Oxtrack <i>maxwelli</i> & <i>concava</i>	Letham Burn M <i>maxwelli</i> & <i>concava</i>
	Fenestella Shale <i>E. denisoni</i>	Brae <i>denisoni</i>	Letham 2,3 <i>denisoni</i>
<i>E. discinia</i> & <i>P. paucispinosa</i>	<i>E. discinia</i> & <i>paucispinosa</i>	<i>E. discinia</i> & <i>paucispinosa</i>	<i>E. discinia</i> & <i>exmoorensis</i>
Snapper Point <i>W. typica</i>	Elderslie <i>typica</i> & <i>E. floodi</i> & <i>T. exmoorensis</i>		Letham 1 <i>typica</i> & <i>paucispinosa</i> Caravan <i>exmoorensis?</i>

E. - *Echinalosia*, *W.* - *Wyndhamia*, *Ps.* - *Pseudostrophalosia*, *T.* - *Terrakea*, *P.* - *Paucispinauria*

DISCUSSION: Perplexingly, Briggs (1998) compared *paucispinosa* to *Terrakea elongata* (Etheridge & Dun), a species that is much more vaulted, with incurved ventral umbo and numerous ventral ear spines, as well

as other differences, leading to the possibility that he was either misinterpreting either *elongata* or *paucispinosa*, or possibly both species. I prefer to retain *paucispinosa paucispinosa* for rather transverse shells, large at maturity, with very few ventral ear spines. Shells of more varied shape, more vaulted, less transverse, but with similarly few ear spines, are referred to *P. paucispinosa wardenensis*. The Oxtrack specimens assigned by Briggs (1998) to *paucispinosa* are excluded because they are more vaulted with larger spines on the trail and slightly more ventral ear spines, including spines on the outer ears, whereas the outer ears of *paucispinosa* lack spines. As shown in the original analysis, the species and some other ornament details of ornament differ a little between the Oxtrack and type lower Mangarewa suites, and this is regarded as ecologic variation.

Briggs (1998) allocated material from the middle Belford Formation of the north Sydney Basin (UQL 5137) to *paucispinosa*, but it is better identified with *concava*, judged from its morphological attributes, including ventral ear spines.

BIOSTRATIGRAPHY: Biostratigraphic implications are complex (table 6). The subspecies *wardensis* is accompanied in the Freitag Formation by *Wyndhamia typica crassispina*, *Aperispirifer archboldi*, and *Ingelarella undulosa*. These are also found in the basal Letham Formation of Wairaki Downs. In Wairaki Downs the upper Letham Formation has a different faunal assemblage, including *Echinalosia discinia*, *Terrakea exmoorensis*, *Lethamia*, *Aperispirifer lethamensis* and *Ingelarella subplicata*. Elements of this fauna also appear in the Brae Formation of the southeast Bowen Basin, including *discinia* and *Lethamia*, with *Paucispinauria paucispinosa paucispinosa*. The Sydney Basin has slightly different occurrences. *Wyndhamia typica typica* lies in the lower Elderslie Formation, approaching *W. typica crassispina*, and accompanied by *Aperispirifer archboldi*, *Ingelarella undulosa* and *Johndearia brevis*. But shells close to *paucispinosa wardenensis*, found with *Wyndhamia* in the lower Letham Formation and Freitag Formation, are found higher in the Branxton Subgroup, in the Fenestella Shale. Here they are accompanied by *Aperispirifer lethamensis*, *Ingelarella subplicata* and *Echinalosia discinia*. There thus appears to have been a complex and not temporally rigid distribution of species, reflecting paleolatitude and perhaps substrate, with implications of individualistic dispersion. Further, whereas *discinia* is accompanied by *Paucispinauria paucispinosa paucispinosa* in the Brae Formation, *discinia* is found with *Terrakea exmoorensis* in the upper Letham Formation. The Elderslie Formation at the top has *exmoorensis* ("*rylstonensis*"), followed narrowly by *paucispinosa wardenensis* within a very small stratigraphic interval. But in the Letham Formation, *paucispinosa wardenensis* is succeeded by *exmoorensis*. These variations appear natural and involve very small time intervals, over substantial geographic domains, as part of the outcome of competitive hegemonies between closely allied taxa (Tables 4, 6).

It should be noted that these assessments substantially alter the misconceptions in Briggs (1998) and bring the New Zealand succession into much closer alignment with the succession of species in the Sydney and Bowen Basins. The sequence in the Sydney Basin, to judge from preliminary assessment of collections, is very diverse, the beds containing a plexus of *Paucispinauria*, represented in the Bowen Basin and New Zealand by more restricted and better defined levels.

***Paucispinauria solida* (Etheridge & Dun, 1909)**

Pl. 1, fig. 22 - 27, pl. 3, fig. 1 - 6

1892 *Productus brachythaerus* (not Morris); Etheridge, p. 252, pl. 44, fig. 14.

1909 *Productus* (?) *solida* Etheridge & Dun, p. 303, pl. 43, fig. 1-4.

1964 *Terrakea solida* (Etheridge & Dun); Hill & Woods, pl. P6, fig. 3-7.

1964b *T. elongata* (not Etheridge & Dun); Waterhouse, p. 81, pl. 15, fig. 1-6, pl. 16, fig. 1, 7, text-fig. 26-30.

1971 *T. solida* (Etheridge & Dun); Dear, p. 19, pl. 5, fig. 6, 7, pl. 6, fig. 1-7.

1972 *T. solida* (Etheridge & Dun); Hill, Playford & Woods, pl. P6, fig. 3-7.

1983 *T. brachythaera* (not Morris); Waterhouse & Jell, p. 242, pl. 1, fig. 14, 16-18, pl. 2, fig. 1 (not pl. 9, 11, 12, 13, 15 = *T. exmoorensis* Dear).

1989 *T. solida* (Etheridge & Dun); Dickins, p. 75, pl. 4, fig. 1-7, text-fig. 4a-h.

1998 *T. solida* (Etheridge & Dun); Briggs, p. 183, text-fig. 90A-H.

LECTOTYPE: AMF 35478 figured by Etheridge & Dun (1909, pl. 43, fig. 1, 2) and Dickins (1989, text-fig. 4a-d) from Mantuan Member, southwest Bowen Basin, Queensland, SD Dear (1971).

DIAGNOSIS: Specimens large, disc moderately inflated, swollen ventral valve as wide as long, venter may be flattened weakly, and trail weakly sulcate, geniculate, spines coarse on both valves, spine bases short, ventral ear spines few but more than on *paucispinosa* or *concava*, costellae may be coarse, posterior shell thick in ventral valve.

MATERIAL: From D44, nearly 50 ventral valves, 15 dorsal valves and 19 specimens with valves conjoined from f111 (GS 15227, with BR 2260, 2261, 2355, 2383), 14 ventral valves and 4 dorsal valves from f344, 6 ventral valves, single dorsal valve and specimen with valves conjoined from f346, and a few specimens

from f345, lower *Echinalosia ovalis* Zone, 25 ventral valves, 11 dorsal valves and 4 specimens with valves conjoined from f119 (GS 15215 - BR 2354), 21 ventral valves, 8 dorsal valves and 8 specimens from f120 (GS 15216), 22 ventral valves, 2 dorsal valves and a specimen with valves conjoined from f121 (GS 15217), 6 ventral valves and a dorsal valve from f122 (GS 16218), 3 ventral valves and fragments from f129 (GS 15214), 25 ventral valves, and 5 dorsal valves from f130 (GS 15220), and a few from f125 (GS 15213), 3 ventral valves and 2 dorsal valves from f326, a few valves from f347-350, and f9480, upper *E. ovalis* Zone, Mangarewa Formation, Wairaki Downs. Numbers understated, and some specimens counted as ventral valves may really be specimens with valves conjoined, the dorsal valve being hidden in matrix.

DESCRIPTION: Specimens large for New Zealand collections, one specimen measuring 37mm wide, 32mm long and nearly 20mm high, another 31mm wide, 32mm long and 22mm high. Ventral umbo incurved, umbonal angle 80°, posterior walls moderately high, persisting to lateral flanks, maximum width placed a little in front of mid-length. Ventral ears large and convex, with broadly obtuse cardinal extremities. Venter fully arched, without sulcus in most specimens, although some specimens medianly flattened, curving evenly into trail. Dorsal valve gently concave over disc, ears less well defined than in ventral valve, trail geniculate and moderately high, generally no median fold. Costellae on both valves number about 12-14 in 5mm over middle and anterior of ventral valve, 14 in 5mm on dorsal exterior, increase by splitting, crossed by fine and faint growth increments, and low concentric swellings over ventral valve, more prominent on dorsal valve, spaced up to 1mm apart, numbering about 18-20. Ventral spines with recumbent bases, up to 1.5mm wide and each arising from 2-3 costellae, persisting for 2.5 to 3.5mm, some spine bases over 10mm long, spines emerge generally at angle close to 35°, well spaced anteriorly. Spines over ears few, a row of 2-4 near hinge, similar number along staggered row in front, and 1-2 spines near anterior lateral edge, all erect and sturdy. Dorsal spines over disc fine and erect, but generally lost from mature specimens, lie in 3-4 rows over trail, suberect and sturdy, up to 1mm across, varying in size, and somewhat irregularly disposed, thin, and rare over dorsal ears.

Ventral adductors moderately impressed posteriorly, raised anteriorly in mature specimens, irregularly scored by sublongitudinal markings, overlapped for half length by very large and striate diductor impressions. Posterior shell strongly thickened to more than 4.5mm in a D44/f344 specimen that is 34mm wide and 29mm long, anterior shell scored by spine bases. Cardinal process lies in plane of commissure, poorly known, apparently bifid, supported by broad septum that persists to beyond mid-length. Posterior dorsal adductor scars small, with irregular markings, faintly impressed, anterior adductors better defined, weakly raised, tend to be almost smooth. Brachial imprints obscure, low posterior marginal ridge close to hinge, and anterior disc bordered by low broad marginal ridge.

VARIATION: Specimens from D44/f121 (GS 15224) from high in the zone close in these details, small, but disc thick in one well preserved specimen, as in typical *solida*. Spine bases up to 3.5mm long, 1mm wide, ears not well defined. The few specimens from D44/f129 (GS 15214), in lithology like that of GS 3616 (D44/f9478), are narrow and elongate, like the elongate specimens from GS 3616, but do not show ear spines well. Dorsal spine bases are up to 1.7mm across, and concentric wrinkles are prominent in specimens from D44/f344, f122 (GS 15218), and f130 (GS 15220).

RESEMBLANCES: In overall shape, swollen venter, thick disc, wrinkled dorsal valve, and geniculate trail, the present specimens are like those figured as *Terrakea solida* by Dear (1971, pl. 5, fig. 6, 7, pl. 6, fig. 1-7), Hill & Wood (1964) and Hill et al (1972) from the Mantuan Member of the upper Peawaddy Formation of the southwest Bowen Basin. The Mantuan specimens are larger than the New Zealand examples, and have slightly coarser costellae and spines, as is to be expected from greater size, the differences in size being ascribed to environmental parameters. There are some comparably large New Zealand specimens (eg from D44/f344) but these do not show external ornament. In *solida*, the ears are large in some specimens, and apparently small in others, and the maximum width generally lies at the hinge until late in ontogeny. Dorsal wrinkles are less prominent in the Queensland types than in New Zealand material. Etheridge & Dun (1909, p. 303, pl. 43, fig. 1-4) in naming the species stressed the thick nature of the posterior shell, but this is not a reliable specific feature in that thick shell is also present in other species, especially of late Middle Permian age in east Australia. Dear (1971) redefined and helped to clarify the species. The most critical aspect is the nature of the ear spines. These are not fully described in any text, but from what can be seen in Dear's figures (eg pl. 6, fig. 1b, c), the ear spines seem sturdy, not densely clustered, and lie in four rows on his figured specimen. GSQF 11730 of Dear (1971, p. 20) has very few ear-spines. In a lateral view of a ventral valve figured by Hill et al (1972, pl. P6, fig. 3) spines over the ears and lateral flanks are few. In other specimens the spines form a single or double row inside the ventral ears, and some posterior spines are very coarse. A specimen that I have from the Mantuan Member shows large erect spines, well spaced over three rows, and identical with the spines on New Zealand material. The ear spines are thus much less dense and clustered than in *exmoorensis*, *brachythaera*, or *elongata*.

Specimens from the Blenheim Formation of north Bowen Basin, ascribed to *Terrakea brachythaera* from a band with *Echinalosia ovalis* between the *Pseudostrophalosia blakei* - *Terrakea exmoorensis* Exmoor fauna and *Ps. clarkei* Scottville fauna apparently belong to *Paucispinauria solida*. Waterhouse & Jell (1983, p. 242, pl. 1, fig. 14, 16-18, pl. 2, fig. 1) described the specimens as differing from others (ie *Terrakea exmoorensis*) in the sequence. "Ventral spines emerge from the disc at a moderately high angle, and spines

over the outer ears near the umbones are not numerous but are well developed and close-set in two or three rows along the outer umbonal slopes and over the lateral inner ears " (Waterhouse & Jell 1983). This description strongly suggests a close similarity to *solida*.

McClung (1983, text-fig. 19) figured three internal moulds from locality LD 96 in the Denison Trough, southwest Bowen Basin as *Terrakea solida*. The lack of data on the exterior makes any specific identification hazardous.

From Port Puer, Tasmania, a silicified internal mould illustrated as *Terrakea brachythaera* by Morris (1845, pl. 14, fig. 4a-b), de Koninck (1847, pl. 16, fig. 1c-d) and Etheridge (1880, pl. 14, fig. 44, 45) was considered to be *solida* by Hill (1950, pl. 2, fig. 2a-d). Clarke (1987) assigned the specimen to *brachythaera*, but lack of external ornament prevents confidence, and Briggs (1998) did not accept the identification, with no reason given.

Dickins (1989, p. 75) stated that he could see no difference between the types of *solida* and material from the Otrack Formation, or *Terrakea elongata* figured by Dear from the north Bowen Basin. He provided no synonymy for the species. Such caution is unwarranted in one sense, insofar as the species from Mantuan, Otrack and north Bowen Basin (Blenheim Formation) beds are distinguishable. But it is true that the types are very poorly preserved indeed, and really the best guide to what species is involved is indicated by the source of the material, because in each case, it has been possible for Dear (1971) and Waterhouse & Jell (1983) to collect and examine and describe many topotype specimens long after the original descriptions. Substantial Otrack collections identified with the Mantuan species by Dickins show no specimens with thick posterior valves and they were deemed to belong to *Paucispinauria concava* by Waterhouse (1986b). On the other hand, *Terrakea elongata* from the northern Bowen Basin involves somewhat thickened ventral valves, suggestive of *solida*, as reported by Waterhouse (1964b). The best approach is surely that offered by Dear (1971), who attempted synonymies and overviews, rather than avoiding any attempt to resolve the problem. His studies have helped to show that *solida* sensu Dear is a useful species, even if its taxonomic validity remains open to challenge. It is Dr John Dear, along with Prof. K. S. W. Campbell, and Drs G. Maxwell and S. M. Parfrey, who have done so much to clarify the systematics and stratigraphic ranges of Queensland Permian brachiopod species and genera.

The New Zealand and Bowen Basin specimens are close to *Paucispinauria concava* (Waterhouse, 1964) from the lower Mangarewa Formation, though the type collections of *concava* include many sulcate ventral valves, less or non-geniculate dorsal valves, thinner body cavity, and ears on both valves less prominent. Concentric growth increments are more conspicuous, and growth wrinkles less evident on the dorsal valve of typical *concava*. Costellae were counted at 10 in 5mm anteriorly on the dorsal valve, and 10-12 at 10mm from the umbo in the ventral valve, with similar density anteriorly. One or two costellae pass into spine bases up to 3mm long, and ventral spines up to 0.7mm thick. Ventral spines in *P. concava* emerge from the shell at a high angle of 45-50° from the surface of the shell, a characteristic feature of the species first drawn to my attention by Professor Dorothy Hill in 1955. Dorsal spines are up to 1mm thick on the trail, much as in present material. The present material is close in some of these respects to the suite described as *Paucispinauria concava* from the Otrack Formation of the southeast Bowen Basin (Waterhouse 1986b). These have comparatively large ventral ears, broader ventral umbones, dorsal valve often geniculate and wrinkled, and costellae numbering 13-15 in 5mm. Ventral spines are slightly finer, and dorsal spines include a few thick ones anteriorly.

The species *solida* is especially characteristic of the Mantuan Member of the Bowen Basin, and reported unreliably also from wells and cores, and probably mistakenly from the *pelicanensis* bed in the north Bowen Basin by Dear (1971, p. 21), where *Terrakea elongata* is present (Waterhouse 1982a, pl. 12, fig. a). Alleged occurrences from the Ingelara and Freitag beds of the southwest Bowen Basin reported by Dear (1971) cannot be sustained (Waterhouse 1982a). Poorly preserved specimens from the South Curra Limestone of Gympie that were compared to *solida* by Runnegar & Ferguson (1969, pl. 5, fig. 1-4) require more material to allow full understanding. They might be closer to *Paucispinauria verecunda* Waterhouse. Telford (1971, pl. 16, fig. 4) illustrated a dorsal valve as *solida* from the Cataract River Formation near Drake, northern New South Wales.

Paucispinauria paucispinosa Waterhouse (1986b, pl. 12, fig. 12-16) in the Brae Formation of southeast Bowen Basin is characterized by its low inflation and well spaced body spines, with very few spines over the ventral ears.

Terrakea elongata (Etheridge & Dun, 1909) has been described by Waterhouse (1964b) from GS 3616 (D44/f9478) to the north of most of the Wairaki Downs localities with *solida*. Dear (1971, p. 21) noted considerable approach of these specimens to *solida*, but considered they should be identified with *T. elongata*, in view of the characteristic shape. The ear spines of these New Zealand specimens, as for the types, are poorly known except for the right ear in BR 183 (Waterhouse 1964b, pl. 15, fig. 2, 3), which suggests few spines, as in *solida*. The shape of these GS 3616 specimens, like those from D44/f129 (GS 15217) and f339, and some from D44/ f111, 119 and 130 (GS 15822, 15210, 15220) is like that of *Terrakea elongata*, but the stratigraphic position suggests that they belong to a subset of narrow *Paucispinauria solida*, but external data on the ventral ears is required for confirmation. The appearance and ornament on the better exposed dorsal valves are typical of *solida*.

DISCUSSION: Clarke (1987, p. 266, text-fig. 3M-N) noted that a suite from Malbina Formation member E at Mount Dromedary, and also the specimen figured as *brachythaera* from Point Puer, Tasmania, by Morris

(1845, pl. 14, fig. 4a, b) closely approach *solida* in details of posterior thickening. They were included as *Terrakea brachythaera* (Morris), described by Clarke (1987, p. 266, text-fig. 3) from Malbina E of Tasmania. The ventral ear spines for the Tasmanian *brachythaera* were described by Clarke as dense and suberect, which agrees with what is believed to be typical *brachythaera* (Waterhouse 1964b), and the figured dorsal valves show prominent pits, often seen in *brachythaera*.

Paucispinauria verecunda (Waterhouse, 1982a)

1971a *Terrakea* n. sp. Waterhouse, p. 348, text-fig. 1.

1982a *Terrakea verecundum* Waterhouse, p. 50, pl. 12, fig. b-e, g, i, k, text-fig. 17L, M.

HOLOTYPE: BR 1181, figured by Waterhouse (1982a, pl. 12, fig. b, c, d, g, i, k, text-fig. 17L, M) OD from G45/f8592 (GS 5077), *Plekonella multicostata* Zone, Bagrie Formation, Arthurton Group, near Arthurton.

DESCRIPTION: The spines on the ventral ears are very few, as figured by Waterhouse (1982a, text-fig. 17L) for the holotype. The spines on the external ear of the specimen BR 1496 from the Glendale Formation, Wairaki Downs, at D44/f9951 (GS 9397) are also few in number (Waterhouse 1982a, pl. 12, fig. e), and body spines have comparatively short spine bases. Costellae number 12-14 in 5mm, and 8 in 5mm at the anterior margin, and the trail is short.

RESEMBLANCES: This species is readily distinguished, as shown in Waterhouse (1982a). Conjecturally, specimens from the upper South Curra Limestone of Gympie may prove to be conspecific, but more material is required to circumscribe specific characters. They were figured by Runnegar & Ferguson (1969, pl. 5, fig. 1-4) as *Terrakea* cf. *solida*, but differ substantially from this species in shape, showing the moderate inflation and transverse outline with large ears seen in *P. verecunda*. Critically, ventral ear spines are not well preserved. The material is kept in the University of Queensland collections at the Queensland Museum.

Another species with few ear spines *Paucispinauria paucispinosa* Waterhouse (1986b, pl. 12, fig. 12-16) from the Brae Formation, southeast Bowen Basin, is close and has a slightly lower ventral valve.

Genus *Spargospinosa* new

DERIVATION: spargo - scatter, throw, spina - thorn, Lat.

TYPE SPECIES: *Terrakea belokhini* Ganelin in Sarytcheva, 1977, here designated.

DIAGNOSIS: Shells with inflated body corpus, geniculate trail, ornament of fine radial ribs, rare erect spines along ventral hinge, ear spines few, body spines scattered and few especially anteriorly, bases may be prolonged or not externally. Dorsal spines erect, mostly around margin and over trail, may be large, also dimples that are often elongate anteriorly, light concentric growth lines and wrinkles. Interior with thickened posterior ventral wall, striate posterior lateral floor, inset ventral adductor platform.

DISCUSSION: Shells described as *Terrakea* from the Russian Arctic in Sarytcheva (1977) belong to a distinctive subset, involving *T. borealis* Ganelin, *T. grandis* Ganelin, *T. belokhini* Ganelin and *T. korkodonensis* (Likharev). They are close to *Paucispinauria* in the paucity of posterior lateral ventral spines, but mature specimens have generally fewer spines along the ventral hinge, and fewer body spines with prolonged bases less regularly dispersed over the disc and trail, and smaller ears, higher posterior walls and less transverse outline. Dorsal spines are slightly fewer but may be moderately numerous, erect and thick over the trail. The trail is more strongly and consistently geniculate in the Russian suite. The two suites differ from each other more than *Grandaurispina* differs from *Terrakea*.

In shape the species come close to *Coolkilella* Archbold, 1993 (see b) from Western Australia, but this genus lacks dorsal spines.

Genus *Terrakea* Booker, 1930

Terrakea is restricted to species which have a cluster of specialized variably stout erect spines over the posterior shoulders and ears of the ventral valve. *Paucispinauria* has few to no ventral ear spines, no cluster of strong spines on the posterior lateral slopes, and generally displays stout spines over the dorsal trail. *Saetosina* has numerous close-spaced fine spines, with no stout strut or halteroid spines on either valve.

Grandaurispina Muir-Wood & Cooper, 1960, type species *G. kingorum* Muir-Wood & Cooper, 1960, is regarded as a close ally of *Terrakea* Booker, 1930, as discussed by Waterhouse (1971a). A careful appraisal of the thorough survey of *kingorum* and associated species of the Glass Mountains, west Texas, by Cooper & Grant (1975, p. 1159-1173) confirms that *Grandaurispina* is identical with *Terrakea* except for its thicker and probably longer ventral spines over the ears and posterior lateral slopes. Kotlyar (1989, p. 212) pointed out that the two were very close. Briggs (1998, p. 163) also considered that the two were similar, and noted that various Glass Mountains species described as *Grandaurispina* by Cooper & Grant (1975) were indistinguishable from *Terrakea*, but the types could be distinguished by thicker ventral ear spines.

That *Terrakea* has been considerably misrepresented is illustrated nowhere better than by Yancey (1978), who claimed to reassess the species *Terrakea arctica* Waterhouse, 1971 and evaluate it as an overtoniid. He apparently overlooked the presence of internally prolonged spine bases, the presence of costellae and dorsal spines, the difference in cardinal process and other features in *arctica*, and the absence of those features from overtoniids. A number of authors have preferred to evade any analysis, and ignored *Terrakea* in favour of *Grandaurispina*. Yet the shape, including hinge and trail, the ornament of costellae, ventral spines including dense cluster of ear spines, and erect and prostrate body spines, and erect dorsal spines, the musculature, cardinal process, nature and variation in the dorsal medium septum, dorsal hinge ridge, brachial ridges, pustulation and other features are all shared between *Terrakea* and *Grandaurispina*. *Grandaurispina* can be best considered as a small group of specialized species, characterized by thick posterior lateral ventral spines, and found in association with *Terrakea*.

***Terrakea dickinsi* Dear, 1971**

1964b *Terrakea* n. sp. aff *pollex* Waterhouse, p. 64, pl. 10, fig. 1-5, text-fig. 23A, 24A.

1971a *T. pollex* n. subsp. Waterhouse, pl. 2, fig. 16.

1971 *Terrakea dickinsi* Dear, p. 15, pl. 4, fig. 2-9.

1980 *T. dickinsi* Dear; Runnegar, text-fig. 191, fig. 4, 5.

1982a *T. pollex aurispina* Waterhouse, p. 47, pl. 11, fig. a-d, f-i, text-fig. 17H, J, K.

1983a *T. dickinsi* Dear; Waterhouse, p. 157, pl. 1, fig. 3.

?1986b *T. cf dickinsi* Dear; Waterhouse, p. 50, pl. 11, fig. 28-32, pl. 15, fig. 14.

1998 *T. dickinsi* Dear; Briggs, p. 166, text-fig. 82.

HOLOTYPE: GSQF11710, *dickinsi*, figured by Dear (1971, pl. 4, fig. 2) OD from upper Tiverton Formation, Bowen Basin, Queensland. For *aurispina*, BR 217 figured by Waterhouse (1964b, pl. 10, fig. 1-3, text-fig. 23A, 24A) OD from D44/f9604 (GS 5885), *Terrakea dickinsi* Zone, Brunel Formation, Takitimu Group, Wairaki Gorge.

DISCUSSION: The subspecies *aurispina* Waterhouse is deemed conspecific with *Terrakea dickinsi* Dear. Unlike *T. pollex* Hill, it is large with comparatively broad venter, rather than narrow thumb-like shape. Although Waterhouse (1964b, p. 67, 1982a, p. 47) noted that collections of *pollex* contained specimens ranging into the *dickinsi-aurispina* shape, the collections he examined came from various localities and included non-type material. The type species of *pollex* was revised by Waterhouse (1986b, pl. 11, fig. 19-27). It comes from the Fairyland Formation near Cracow, southeast Bowen Basin, and has many ear spines. Geniculation develops at a very small size. Specimens from the Tiverton Formation in the northern Bowen Basin have been often listed as *T. pollex*, but a preliminary look through extensive collections made by the writer at Homevale (including UQL 4515, 4519, Waterhouse, Briggs & Parfrey 1983, text-fig. 1) suggests that these commence geniculation at a slightly larger size, have slightly fewer spines over the ventral ears and anterior lateral slopes, and have longer ventral spine bases. They appear to constitute a new species.

Paucispinauria geniculata Waterhouse (1986b, pl. 12, fig. 4-11) with few ear spines comes from the Elvinia Formation of the southeast Bowen Basin. What may prove to be allied material occurs, not abundantly, below the *Taeniothaerus* zone near Homevale, as at UQL 4510 (Waterhouse, Briggs & Parfrey 1983, text-fig. 1).

STRATIGRAPHY: *Terrakea dickinsi* is characteristic of the upper Cattle Creek Formation and upper Tiverton formations of the Bowen Basin. Waterhouse (1986b, p. 50, pl. 11, fig. 28-32, pl. 15, fig. 14) compared specimens from the Rose's Pride Formation of south Bowen Basin to this species, and Briggs (1998) agreed the species was in the Rose's Pride beds, but left out the Waterhouse reference from synonymy, without explanation. Possibly the species ranges into slightly older beds (with *Pseudostrophalosia brittoni*) but it is also possible that the Rose's Pride Formation has condensed faunas from two zones. A very few southerly occurrences of *dickinsi* were itemized by Briggs (1998, p. 168), but must be discounted until verified by description or illustration, or at least, deposited in curated collections that are available for inspection.

***Terrakea exmoorensis* Dear, 1971**

Pl. 1, fig. 16, 17, text-fig. 5c

1905 *Productus* sp. indet. Etheridge, p. 67, pl. 18, fig. 4, 5.

1964 *Terrakea cf fragilis* (not Dana); Hill & Woods, pl. P5, fig. 9, 10.

1971 *Terrakea elongata exmoorensis* Dear, p. 18, pl. 5, fig. 3-5.

1972 *T. elongata exmoorensis* Dear; Hill et al, pl. P5, fig. 9, 10.

1983 *T. elongata exmoorensis* Dear; Waterhouse & Jell, p. 242, pl. 1, fig. 10.

1983 *T. brachythaera* (not Morris); Waterhouse & Jell, p. 242, pl. 1, fig. 9, 11-13, 15 (not pl. 1, fig. 14, 16-18, pl. 2, fig. 1 = *solida* Etheridge & Dun).

1998 *T. exmoorensis* Dear; Briggs, p. 179.

1998 *T. rylstonensis* Briggs, p. 168, text-fig. 83.

HOLOTYPE: GSQF 5537, *exmoorensis*, figured by Dear (1971, pl. 5, fig. 5, fig. 3) and Hill & Woods (1964, pl. P5, fig. 9, 10; Hill et al 1972, pl. P5, fig. 9, 10) OD from basal Blenheim beds, north Bowen Basin, Queensland. For *rylstonensis*, AMF 45480, figured by Briggs (1998, text-fig. 83C) OD from Snapper Point Formation, south Sydney Basin.

DIAGNOSIS: Subelongate to subquadrate or moderately transverse shells with broad gently convex venter, moderate to long subgeniculate or arched trail, ornament of numerous erect spines over umbonal and adjoining posterior lateral slopes, many fine body spines with short or moderately long bases, dorsal valve may be somewhat dimpled, generally with many erect not very wide spines.

NEW ZEALAND MATERIAL: From D44, one ventral valve and one dorsal valve from f304, one specimen with both valves from f313, single ventral valves from f314, and f315 in the lower *Echinalosia discinia* Zone, one ventral valve from f317, two ventral valves and a dorsal valve from f323, one ventral valve BR 2267 and one dorsal valve from f9001 (GS 9697), and a few individuals from f115 (GS 15210, BR 2268), f126 (GS 15225, BR 2244), f319 (OU 18740), f321, f322, f324 from the *Lethamia ligurritus* Subzone, in the upper *E. discinia* Zone, Letham Formation, Wairaki Downs. Six ventral valves, four dorsal valves from D44/f123 (GS 15226), including BR 2264, *Pseudostrophalosia? cf blakei* fauna, lower Mangarewa Formation, Wairaki Downs.

DIMENSIONS IN MM: Letham specimen

BR	Locality	Width	Length	Height
2244	f126	26.7	25	14

DESCRIPTION: For Letham material, venter well arched, flattened medianly or gently convex, narrow umbo with angle of 80°, moderately distinct and rather convex ventral ears, maximum width of valve lies in front of mid-length. Dorsal disc moderately concave (f321) or flat (f319). Costellae on ventral valve fine with long fine spine bases as a rule, although some bases very short, spines numerous but not crowded over lateral flanks and ears. Spines close-spaced posteriorly over dorsal valve from f319, fine and numerous anteriorly, few and a little thicker anteriorly on trail.

For D44/f123 material, ventral valve vaulted, umbo incurved, ears moderately large with numerous spines crowded over inner ears, spine bases long over visceral disc. Dorsal valves with subulate cardinal extremities, subgeniculate trail, fine costellae, up to 16 in 5mm, concentric wrinkles, numerous pits, and fine erect spines. Cardinal process broad, lying in plane of disc, posterior marginal ridge.

RESEMBLANCES: The New Zealand material is identified with *Terrakea exmoorensis* Dear from the Moonlight Sandstone Member at the base of the Blenheim Formation in the north Bowen Basin, sharing critical attributes of shape and spinosity in both valves, including wide lateral slopes, many erect ventral ear and umbonal slope spines, a little more variable ventral spine bases, fine ventral trail spines, comparable dorsal spines and geniculate or subgeniculate trail. The *discinia* Zone suite of *Terrakea* in New Zealand is moderately like *Terrakea exmoorensis* in shape, but has slightly fewer ventral ear spines and only inconspicuous dorsal pits, external ventral spine bases usually short but may be internally prolonged, and in some specimens, less geniculate trail than in some but not all *exmoorensis* specimens.

Dear distinguished his taxon as a subspecies on the basis of size, smaller than *elongata*, and less thickened umbonal walls. These are valid observations. From a biostratigraphic point of view, it seems more convenient to regard the taxon as a full species falling within the *brachythaera* superspecies plexus, with *elongata* regarded as a companion, younger species, and Briggs (1998) also treated the form as a full species. Many specimens of *exmoorensis* are not particularly elongate, but the ventral valves are highly vaulted, and the visceral disc moderately thick. There needs to be further enquiry into the circumscription of the species, which will be aided by the fact that there are numerous specimens from the type area. Briggs (1998) considered that the species was characterized in part by fine and numerous spines on the disc. Waterhouse & Jell (1983) assigned many specimens from the Exmoor faunas of the Moonlight Sandstone Member to *Terrakea brachythaera* (Morris) and the preceding synonymy segregates them and suggests they should be regarded as *exmoorensis*.

The New Zealand suite from the *Echinalosia discinia* Zone agrees with *Terrakea rylstonensis* Briggs (1998) in spinosity, ventral ears and dorsal valve, but includes a greater range of profile for the ventral valve, some being like the Australian examples, others being comparatively higher, with steeper posterior lateral flanks and flatter venter. If the permissible morphological range for *rylstonensis* is enlarged to incorporate such variation, it would also overlap many specimens of the *exmoorensis* suite. There is some need for caution, in so far as *rylstonensis* is poorly preserved, with dorsal exterior not figured. But it is believed that *rylstonensis* was described from only part of the available collections and was too narrowly circumscribed. The species *exmoorensis* is here regarded as senior synonym to *Terrakea rylstonensis* Briggs. Briggs (1998) offered an extended "diagnosis" but no description, and no indication of critical differences from other species. The present understanding of *rylstonensis* is based partly on the Briggs study and partly on UNE material from the Sydney Basin, not mentioned by Briggs. The species comes very close to *Terrakea exmoorensis* Dear, 1971, originally described from the Blenheim Formation of the north Bowen Basin. Dear's species is represented in the type area by an abundance of material and shows comparable attributes in the steep posterior walls, broad venter, subgeniculate trail, and overall distribution and nature of spines on both

valves. Both forms are moderately close to the older species *Terrakea dickinsi*, but have more posterior ventral spines. The most obvious difference between *exmoorensis* and *rylstonensis* lies in the longer trail and greater inflation of some specimens of *exmoorensis*, and this is not regarded as critical, both in its own right, and because many *Terrakea* found with elongate *exmoorensis* have shorter trails, or are broad. The *rylstonensis* suite from the Snapper Point Formation appears to be of more limited morphological range, within the range of variation shown by *exmoorensis*. Type *exmoorensis* is found in the *Pseudostrophalosia blakei* Zone, whereas *T. rylstonensis* is found in the distinctly older *Echinalosia discinia* Zone of the Sydney Basin, although a preliminary survey of UNE collections suggests that material close to *rylstonensis* s.s. ranges above the *discinia* Zone in the Sydney Basin. Even so there are complications, because *discinia* is not found in the north Bowen Basin, nor *blakei* in the Sydney Basin: nonetheless, *blakei* is believed to be younger. Possibly the two species overlapped or varied in range. In New Zealand it appears that both *discinia* and rare *blakei* are found with *exmoorensis*.

The Letham specimens show some approach to ventral valves of *Paucispinauria* misreported as *concava* by Waterhouse (1982a, pl. 10, fig. k) from GS 6070 in the lower Letham Formation. These specimens such as BR 215 and 757 are vaulted with moderately small ears, BR 757 being unusual in showing low concentric wrinkles, as well as long spine bases. The number of ear spines is few, and the GS 6070 specimens are now deemed close to *Paucispinauria paucispinosa wardenensis* Waterhouse.

Briggs (1998, in Briggs & Campbell 1993) considered that re-worked *Terrakea* from the Stephens Group of northeast Nelson at GS 12643 (P25/f001) approached *Terrakea rylstonensis* Briggs, 1998. These specimens (Campbell et al (1984, text-fig. 4: 3, 4; Briggs & Campbell 1993, text-fig. 3:13-19) have a slightly more arched venter, fewer posterior lateral ventral spines that impinge less on the umbonal slopes, and thicker dorsal trail spines than in *rylstonensis*, so that comparison is not particularly close.

***Terrakea* cf *exmoorensis* (Dear, 1971)**

Pl. 1, fig. 14, 15

1982a *Terrakea* sp. Waterhouse, p. 48, pl. 10, fig. h, j.

1993 *Terrakea* sp. Briggs & Campbell, p. 329, text-fig. 3.20.

1998 *Terrakea* cf *rylstonensis* Briggs, p. 168.

Poorly preserved *Terrakea* comes from the Caravan Formation at D44/f9878 (GS 7807), Wairaki Downs. The specimens were deemed by Briggs & Campbell (1993) to be identical with a Sydney Basin species later named *Terrakea rylstonensis* Briggs, 1998, as discussed above. The specimen figured in Briggs & Campbell (1993, text-fig. 3.20) is very poorly preserved, and suggests that posterior lateral spines were numerous. The more complete and better illustrated internal moulds figured by Waterhouse (1982a) have a more rounded less transverse disc than in shells figured as *rylstonensis*. These specimens have been removed from the type collections at IGNS, and have never been returned by Dr Briggs, despite requests. Thus no further examination is possible. But the illustrations in the various articles shown in the preceding synonymy suggest that the Caravan material may be provisionally assigned to *rylstonensis* and therefore *exmoorensis*. It was omitted from synonymy of *rylstonensis*, without explanation, by Briggs (1998), yet was mentioned in a discussion of occurrences, as cf *rylstonensis*.

***Terrakea brachythaera* (Morris, 1845)**

1845 *Productus brachythaerus* not Sowerby; Morris, p. 284, pl. 14, fig. 4c (not pl. 14, fig. a, b = gen. & sp. indet.).

1847a *P. subquadratus* not Morris; de Koninck, p. 241, pl. 16, fig. 1a, b (not c, d indet.)

1847b *P. brachythaerus* not Sowerby; de Koninck, p. 102, pl. 16, fig. 1a, b (not c, d indet.)

1847 *P. fragilis* Dana, p. 143.

1849 *P. fragilis* Dana; Dana p. 686, pl. 2, fig. 7.

1877 *P. brachythaerus* not Sowerby; de Koninck, p. 198, pl. 10, fig. 4, 4a, pl. 11, fig. 1.

1888 *P. brachythaerus* Sowerby (?); Johnston, pl. 14, fig. 2-4?

?1892 *Productus* sp. indet. Etheridge, pl. 13, fig. 3 fide Briggs 1998.

*1901 *Productus brachythaerus* not Sowerby; Frech, pl. 57d, fig. 1a, b.

*1909 *P. brachythaerus* not Sowerby; Etheridge & Dun, p. 5, pl. 42, fig. 1, 4, 6, 8, pl. 43, fig. 8-11 (not pl. 43, fig. 6 = *Paucispinauria paucispinosa wardenensis* Waterhouse).

*1909 *Productus brachythaerus* var *elongatus* Etheridge & Dun, p. 7, pl. 42, fig. 2, 3 fide Briggs 1998 (not pl. 43, fig. 5, 7 = *elongata* (Etheridge & Dun)).

1930 *Terrakea brachythaera* (not Sowerby); Booker, pl. 1, fig. 2, 5.

*1930 *Terrakea fragile* (Dana); Booker, p. 71, pl. 1, fig. 1, 3, 4, pl. 2, fig. 1, pl. 3.

1930 *T. leve* Booker, p. 70, pl. 2, fig. 3, 4, text-fig. 1a (part = *P. paucispinosa wardenensis* Waterhouse).

*1930 *T. elongata* (Etheridge); Booker, p. 74, pl. 1, fig. 6.

1950 *Productus brachythaerus* Morris not Sowerby; Hill, p. 18, pl. 2, fig. 1.

1960 *T. brachythaerum* (Morris); Muir-Wood & Cooper, p. 315, pl. 119, fig. 14-17, 21, 22.

1960 *T. fragile* (Dana); Muir-Wood & Cooper, p. 119, pl. 119, fig. 13, 18-20, 23.

!1964 *T. cf brachythaerus* (Morris); Hill & Woods, pl. P6, fig. 2 (not fig. 1 = *Saetosina multispinosa* (Dear)).

- 1965 *T. brachythaerum* (Morris); Muir-Wood, p. 503, text-fig. 375.2a-d.
 1965 *T. fragile* (Dana); Muir-Wood, p. 375, text-fig. 375.2e-f.
 *1969 *Terrakea* sp. Wass & Gould, p. 226, pl. 14, fig. 19.
 *1969 *T. solida* (not Etheridge & Dun); Wass & Gould, p. 215.
 !1971 *T. multispinosa* (not Dear); Dear, p. 18, pl. 7, fig. 10 (not pl. 7, fig. 1-9, 11 = *S. multispinosa* (Dear)).
 !1972 *T. multispinosa* (not Dear); Hill et al, pl. 2, fig. 2 (not fig. 1 = *S. multispinosa* (Dear)).
 1986b: *T. brachythaera* (Morris); Waterhouse, p. 50, pl. 12, fig. 1-3.
 *1987 *T. brachythaera* (Morris); Clarke, p. 266, text-fig. 3A-P (not text-fig. 3Q fide Briggs 1998, species not stated).
 *1998 *T. etheridgei* Briggs, p. 172, text-fig. 86.
 1998 *T. brachythaera* (Morris); Briggs, p. 176, text-fig. 87.
 !1998 *T. quadrata* Briggs, p. 181, text-fig. 89.
 2000 *T. brachythaerum* (Morris); Brunton, Lazarev, Grant & Jin, p. 534, text-fig. 372.2a-d.
 2000 *T. fragile* (Dana); Brunton, Lazarev, Grant & Jin, text-fig. 372.2e, f.
 *Includes material identified by Briggs (1998) with *etheridgei*, here regarded as a subspecies, if not a variety of *brachythaera*.
 ! includes material identified by Briggs (1998) with *T. quadrata*, here regarded as a subspecies.

NAME: Until the revision by Briggs (1998), *Terrakea brachythaera* (Morris) proved to be a very poorly known species based on a neotype rather unfortunately selected by the International Commission for Zoological Nomenclature (Op. Int. Zool. Nom. 486, 1957) in response to a submission by Maxwell (1956) to suppress the specific name *brachythaerus* G. B. Sowerby (1844) in favour of *brachythaerus* Morris (1845). The difficulty had been that *Terrakea* was envisaged as a productid, whereas Sowerby's specimen was a strophalosiid. But the designation of a poorly preserved specimen as lectotype left the species - and therefore genus - under a cloud of uncertainty.

HOLOTYPE, LECTOTYPES: For *brachythaera*, BB 9466, figured by Morris (1845) as above. This was refigured, inaccurately, by de Koninck (1847b, pl. 16, fig. 1a, b - c, d in text, p. 103) and by Hill (1950, pl. 2, fig. 1). The Hill figure shows the ventral aspect of an internal mould, now regarded as lectotype. But the figures in Morris (1845) and de Koninck (1847a, b) show the ventral ears, probably not well because the right ear in Morris has many spine bases, and the left ear features a row along the hinge. Presumably the posterior part of the specimen was later separated from the visceral disc, and I have not seen it at the Natural History Museum. For *fragile*, USNM 3633d figured by Dana (1849, pl. 2, fig. 7) SD Muir-Wood & Cooper (1960, p. 421) from Broughton Formation, Sydney Basin, New South Wales. For *leve*, a lectotype is selected as AMF 1158 from Mulbring, figured by Etheridge & Dun (1909, pl. 43, fig. 6), as explained in Discussion. For *etheridgei*, SUP 25553 from South Marulan, Sydney Basin, figured by Briggs (1998, text-fig. 86A) OD. For *quadrata*, AMF 96272 from Flat Top Formation, Bowen Basin, Queensland, figured by Briggs (1998, text-fig. 89C, D, E) OD.

TYPE LOCALITY: Various sources for the lectotype BB9466 have been suggested, after Morris (1845) had indicated that the species was known from "Illawarra" (south coast, New South Wales), Raymond Terrace (north Sydney Basin), and various localities in Tasmania. Hill (1950, p. 19), followed by Waterhouse (1964b), who had both examined the type at the Natural History Museum, London, had stated Illawarra, south Sydney Basin. Clarke (1987) forcefully asserted that the type comes from the Muree Sandstone, probably, at Raymond terrace, north Sydney Basin, attacking Waterhouse, and not mentioning Hill. However Briggs (1998, p. 178) contradicted Clarke, and on the basis of a Waterhouse observation on the nature of matrix, concluded that the type had come from the Broughton Formation at Gerringong, which would match "the Illawarra district." I confirmed the observation on the nature of the matrix at the Natural History Museum in June, 2000.

SUITES OF SPECIMENS: Three substantial suites have been ascribed by some authors to the species *brachythaera* from New Zealand, Tasmania and south Sydney Basin. The New Zealand suites (Waterhouse 1964b, Waterhouse & Vella 1965) have been accepted as typical *brachythaera*, but I believe they are best regarded as *elongata*. The specimens figured and described as *brachythaera* by Clarke (1987, text-fig. 3A-Q) from Malbina Formation Member E at Mt Dromedary, Tasmania, are like *Paucispinauria solida* in shape, having a somewhat convex venter and generally transverse outline. Clarke (1987, p. 266) reported that spines were dense and suberect on the ventral ears. This is not clearly indicated on any of his figures, but is surely clear enough in meaning: his specimens do not have the rather few ear spines found in *solida*, but the ear spines are "dense and suberect", as in *brachythaera*. Unfortunately no figure of the ear spines was provided, nor any counts, but from available evidence, the Tasmanian specimens are the same as *brachythaera* Morris. Briggs (1998) regarded the Tasmanian material as belonging to *Terrakea etheridgei* Briggs, here regarded as a subspecies, or preferably a series of variants of *brachythaera*. Interestingly, Clarke (1987) evaluated a second specimen figured by Morris (1845, pl. 14, fig. 4a, b) as also belonging to *brachythaera*. This specimen came from Port Puer, Tasmania, and Clarke (1987) noted that it looked also like *solida* Etheridge & Dun. However this was not accepted by Briggs (1998), and he did not comment on any specific relationship, as far as I am aware.

Yet another suite was named *Productus fragilis* Dana, 1847, from the south Sydney Basin near

Wollongong. These specimens are kept at the Smithsonian Institute, Washington DC. They have been deemed to not show the ventral ear ornament (Dr G. A. Cooper in Waterhouse, 1964b). The specimens were compared with the type of *brachythaera* by Waterhouse (1964b, p. 80), and note was made of the strongly geniculate trail in *fragile*, as observed by Booker (1930). The geniculation may have been exaggerated by deformation, and Waterhouse (1964b) considered that the trail had been broken from the lectotype of *brachythaera*. Inspection of the plaster casts of Dana's specimens that are kept at IGNS, Lower Hutt, shows little of the crucial ventral ear spines, but affirms that the venter is well rounded and arched more than in *elongata* (specimen USNM 3633b, Muir-Wood & Cooper 1960, pl. 119, fig. 19, 20). Muir-Wood & Cooper (1960, pl. 119, fig. 13, 18-20, 23) figured some of Dana's types, including the lectotype and a number of specimens ascribed to *Terrakea brachythaera* from the same locality (pl. 119, fig. 14-17, 21, 22). In two of their figures faint nodes on the shell appear to suggest numerous close-set and moderately fine ear spines

Table 6. Showing slightly discrepant ranges for key species in the late Cisuralian and Guadalupian of Sydney Basin, Bowen Basin and New Zealand (Waterhouse 2000a).

Bowen Basin SW	Basin SE	N	NZ	Sydney Basin
		<i>elongata clarkei</i>	<i>elongata clarkei</i>	<i>clarkei</i>
<i>solida ovalis</i>	<i>brachythaera ovalis</i>	<i>solida ovalis</i>	<i>solida ovalis</i>	<i>brachythaera ovalis</i>
		<i>exmoorensis</i>	<i>exmoorensis</i>	<i>exmoorensis- brachythaera ovalis?</i>
<i>blakei</i>		<i>blakei</i>	? <i>blakei</i>	
	<i>concava maxwelli</i>		<i>concava maxwelli</i>	<i>concava maxwelli</i>
	<i>paucispinosa discinia</i>		<i>exmoorensis discinia</i>	<i>paucispinosa discinia</i>
<i>paucispinosa typica, floodi?</i>			<i>paucispinosa typica</i>	<i>exmoorensis typica floodi</i>
			<i>exmoorensis?</i>	

Major Productidin species in the lower Middle Permian of the Bowen and Sydney Basins and New Zealand, illustrating a degree of heterochroneity between significant forms in different basins, especially between the Sydney Basin and New Zealand with the Bowen Basin (Waterhouse 2000a). Species belong as follows: *Paucispinaria paucispinosa*, *concava* and *solida*; *Terrakea exmoorensis* and *brachythaera*, *Echinalosia floodi*, *discinia*, *maxwelli* and *ovalis*, *Wyndhamia typica*, *Pseudostrothalosia blakei* and *clarkei*.

(pl. 119, fig. 16, 20), though inspection of the plaster moulds, which are possibly flawed, suggests this is at best conjectural. Compared with the New Zealand upper Mangarewa specimens of *elongata*, the Wollongong specimens have gently convex venter and ventral spines spaced further apart, and dorsal spines apparently less erect, and appear close in these respects to typical *T. brachythaera*. The Clarke (1987) specimens from Tasmania look very close in shape to the Dana specimens from Wollongong, but show prominent elongate pits over the dorsal valve with ventral body spines seemingly as thin as in *T. fragile*. Some specimens from the Broughton Formation of the south Sydney Basin look like *elongata*. I have in my notes reference to Booker's specimens from Pringle Bay which are narrow and elongate, suggestive of *elongata*. Further enquiry may establish whether these are a variation of *brachythaera*, or *elongata*, or whether *elongata* should be regarded as a subspecies, if that, of *brachythaera*.

Booker (1930) described and illustrated a number of specimens from the Sydney Basin, ascribing individuals to *Terrakea brachythaera*, *T. fragile*, *T. elongata* and *T. leve*. Some specimens, although decorticated, suggest a likely cluster of inner ear spines as implied for *fragile*, eg *T. brachythaera* Booker (1930 pl. 2, fig. 2, 5 (=4), from Jamberoo. Stratigraphic and locality details are not given in modern terms by Booker (1930). All taxa have been deemed conspecific by Waterhouse (1964b). Brunton, Lazarev, Grant & Jin (2000) continued to regard *fragile* as a valid species, but have given no supporting evidence, and have not refuted the data that show *fragile* to be conspecific with *brachythaera*.

The preceding interpretation of *brachythaera* comes close to the view for the species expressed by Briggs (1998), who focussed on material from the Broughton Formation. His figures show a moderately inflated ventral valve, geniculate dorsal valve and moderately numerous ear spines. Broughton material is particularly transverse, and ventral spines comparatively fine. Briggs appears to have defined and discussed *brachythaera* in unrealistically restricted terms, and his diagnosis and assessments are contradicted by the specimens referred in his synonymies to *brachythaera*. For example, many of the Dana specimens are not very transverse, and the New Zealand material that he insisted was *brachythaera* differs even more strongly

in shape, variability, height and spine details. When a wider range of morphologies is incorporated, it seems that two other Briggs species fall close enough to *brachythaera* to be incorporated within the species. *Terrakea etheridgei* Briggs comes from various levels in New South Wales, including the Nowra Sandstone, Muree Formation, Mulbring Formation of the Sydney Basin, and Porcupine Formation, Gunnedah Basin, South Marulan etc. The species was allowed by Briggs to be close to *brachythaera*, but said to be distinguished by its slightly narrower disc, and stronger spines anteriorly on both valves. But the arched shape and ear spines are close to *brachythaera*. *T. quadrata* Briggs from Queensland is also very close in size and shape and spinosity, and distinguished by its quadrate rather than oval outline, sturdier spines and greater thickening of the shell which naturally was accompanied by more impressed muscle scars and thicker septum. Briggs allowed that it did look like *brachythaera*, and it is here regarded as a contemporaneous subspecies, or perhaps variant. The figured specimens figured by Briggs (1998) are clearly slightly crushed, altering the steepness of posterior lateral walls.

In summary it appears from available evidence that the species *Terrakea brachythaera* is senior synonym and conspecific with *T. fragile* and *T. leve*, *T. quadrata* and *T. etheridgei*. It characterized Malbina E of Tasmania and correlative Gerringong and ?Mulbring-Muree beds of the Sydney Basin. It displayed a generally but not uniformly transverse ventral valve with gently arched and anteriorly weakly sinuate ventral valve, and geniculate dorsal valve with moderately long trail. A burst of fine ear spines is developed on the inner ventral ears. From available evidence involving faunal succession and other brachiopod and molluscan species, contemporaneous faunas of parts of the Bowen Basin in Queensland, and in middle Mangarewa Formation of New Zealand included *Paucispinauria solida*, rather than *T. brachythaera*. Yet in parts of the Bowen Basin, *brachythaera* did penetrate, found rarely in the Flat Top Formation (southeast Bowen Basin) as *T. quadrata* Briggs (= *brachythaera*). In the north Bowen Basin and New Zealand, overlying faunas involve a species *T. elongata*, descended from *brachythaera*, with strong burst of ear spines, and more spinose venter and dorsal valve. The venter may be weakly flattened, and the trail long. Because of uncertainties over some of the ranges and correlations in the Sydney Basin, it is possible that typical *brachythaera* persisted there with range overlapping that of *elongata*.

DISCUSSION: Booker (1930) described his species *leve* from Mulbring and Jamberoo, New South Wales, and figured material from an "unknown locality". According to Fletcher (1971), the material figured by Booker (1930, pl. 2, fig. 3, 4, text-fig. 1a) is lost. Specimens cited in the original description by Booker (1930, p. 71) are available as types, involving AMF 1158, from Mulbring, and AMF 10943 and 100945 from Jamberoo, as figured by Etheridge & Dun (1909, pl. 43, fig. 6, 9, 11). All were cited as syntypes by Fletcher (1971). The Mulbring specimen F 1158 figured by Etheridge & Dun (1909, pl. 43, fig. 6) is selected as lectotype.

***Terrakea elongata* (Etheridge & Dun, 1909)**

1909 *Productus brachythaerus elongatus* Etheridge & Dun, p. 299, pl. 43, fig. 5, 7 (not pl. 42, fig. 2, 3, 7 = *brachythaera* (Morris)).

1930 *Terrakea elongata* (Etheridge & Dun); Booker, p. 74 (not pl. 1, fig. 5 = *T. brachythaera* (Morris)).

1964b *T. brachythaera* (not Morris); Waterhouse, p. 73, pl. 12, fig. 1-8, pl. 13, fig. 1-12, pl. 14, fig. 1-13, pl. 37, fig. 1, text-fig. 23C, 24D, E, 26-31.

1965 *T. brachythaera* (not Morris); Waterhouse & Vella, p. 64, pl. 2, fig. 2, 5-10, pl. 3, fig. 3.

1971 *T. elongata* Booker (sic); Dear, p. 16, pl. 4, fig. 10-12, pl. 5, fig. 1, 2.

1978 *T. brachythaera* (not Morris); Suggate et al, text-fig. 4.5, fig. 4, 5, 11.

1981 *T. brachythaera* (not Morris); Speden, pl. 5, fig. 4, 5, 11.

1982a *T. brachythaera* (not Morris); Waterhouse, p. 49, pl. 11, fig. e, text-fig. 30.

1982a *T. elongata* (Etheridge & Dun); Waterhouse, pl. 12, fig. a.

cf 1983 *T. cf brachythaera* (Morris) form B; McClung, p. 76, text-fig. 18, 1-5.

1998 *T. elongata* (Etheridge & Dun); Briggs, p. 179.

LECTOTYPE: AMF 35475 (originally F 2374) figured as *Productus brachythaerus elongatus* by Etheridge & Dun (1909, pl. 43, fig. 5), SD Waterhouse (1964b, p. 82), from Scottville Member, Bowen Basin, Queensland. Briggs (1998) criticized Waterhouse (1964b) for stating that the two figures of Etheridge & Dun (1909) were of the same specimen. He claimed there were two specimens, and that one could not found, as is also implied by Fletcher (1971, p. 52). Dear (1971) also believed that the two figures were of one specimen, and Dear (1971, p. 16) referred specifically to one specimen in discussing its source locality, so that the matter invites further investigation.

DIAGNOSIS: Narrow and elongate varying to broad less elongate shells with long ventral spine bases over disc, crowded dorsal spines, close-set sturdy costellae, and numerous spines clustered over inner ears and outer umbonal slopes.

DISCUSSION: This taxon is interpreted as a close ally of *Terrakea brachythaera*, distinguished by its larger size and thicker shell, indicating favourable conditions of growth. I hesitate between treating it as a species, or subspecies of *brachythaera*. It is found chiefly in the north Bowen Basin. The original types of *elongata* are large and elongate shells with high visceral cavity (Etheridge & Dun 1909), shown by Dear (1971, 1972) to

have come from the upper Blenheim Formation, especially Scottville Member, in the north Bowen Basin. Waterhouse (1982a, pl. 12, fig. a) figured a Queensland specimen of *elongata* to show a moderately dense cluster of strong, uniform spines over the inner ventral ears. The specimen came from Clermont, probably from the *pelicanensis* bed. Earlier Waterhouse (1964b, p. 84) remarked on the somewhat flattened visceral disc.

It has long been suggested that this taxon is very close to the New Zealand material from the upper Mangarewa and Flowers Formations (eg Waterhouse 1964b, 1982a, 1986b, p. 50). The type material differs from New Zealand material chiefly through its larger absolute size, and somewhat longer trail. The New Zealand specimens are close in overall proportions, and are similarly characterized by a particularly strong brush of spines on the inner ventral ears.

Probably the specimens figured by McClung (1983, text-fig. 18) as *Terrakea cf brachythaera* from interval E in the GSQ Eddystone 1 core belong to *elongata*. They show an *elongata*-like development of body spines and ventral ear-spines are moderately numerous. The Eddystone E fauna looks to be close to that of the upper Blenheim Formation in north Bowen Basin. Specimens of *Terrakea* were also reported from interval C by McClung (1983, p. 76, text-fig. 17) but only internal moulds were figured, making specific affinities difficult to determine. They were referred to *elongata* by Briggs (1998), but this seems likely to be in error, even though it supported his correlations.

Genus *Saetosina* Waterhouse, 1986

TYPE SPECIES: *Terrakea multispinosa* Dear, 1971.

DIAGNOSIS: Medium-large transverse or elongate shells with fully arched venter and large ventral ears, dorsal valve geniculate, flat posteriorly, body cavity high. Ornament of uniformly fine spines on both valves, crowded on ventral ears, and comparatively fine costellae.

DISCUSSION: *Saetosina* Waterhouse, 1986 was discountenanced by Briggs (1998) and Brunton, Lazarev, Grant & Jin (2000), but its distinctively fine spination and lack of thick halteroid and strut spines from the ventral valve, and absence of thick erect spines from the anterior dorsal valve provide valid generic distinctions. These features are nowhere matched in any of the species assigned to *Terrakea* or *Paucispinauria*. The type species, *Terrakea multispinosa* Dear, 1971 from the Flat Top Formation of southeast Bowen Basin, has numerous ventral ear spines, pointing to derivation from *Terrakea* stock. Inconsistently, Briggs (1998) recognized *Grandaurispina* on the basis of its thick ventral ear spines.

Saetosina dawsonensis n. sp.

1986b *Saetosina multispinosa* (not Dear); Waterhouse, p. 54, pl. 13, fig. 6, 7 (not pl. 13, fig. 8 - 12 = *S. multispinosa*).

1988 *Terrakea multispinosa* not Dear; Parfrey, p. 14, pl. 2, fig. 22, 3, fig. 6-10.

1998 *T. multispinosa* not Dear; Briggs, p. 181 (not text-fig. 88 = *S. multispinosa*).

DERIVATION: Named from Dawson River near type locality.

HOLOTYPE: GSQF 12991 figured by Parfrey (1988, pl. 3, fig. 9) from Barfield Formation, south Bowen Basin, Queensland, here designated.

DIAGNOSIS: Costellae moderately coarse and spines fine but not very crowded, except for ventral ears, on both valves.

DESCRIPTION: Shells large and transverse, one ventral valve measuring about 43mm wide and 29mm long, another 37mm wide and 28mm long, with broad ventral umbo and posterior walls diverging at about 110-125°, valve strongly convex. Dorsal valve with gently concave almost flat disc, well defined large ears with bluntly acute extremities, and high geniculate trail. Both valves costellate, range from 6-9 rarely 10 in 5mm at start of dorsal trail, and may become coarser anteriorly. Ventral spines uniformly fine with short narrow bases, arranged in quincunx up to 3mm apart, dorsal spines moderately fine, and comparatively few, reaching diameter of 0.3-0.5mm.

DISCUSSION: This species was described by Parfrey (1988) from several localities in the Barfield Formation, south Bowen Basin, and had also been reported from these beds by Briggs (1998) and Waterhouse (1986b), as *multispinosa*. Dimensions were provided by Waterhouse (1986b, p. 55) from a thesis by Dr S. M. Parfrey, and the + sign, shown by Waterhouse, indicates incomplete dimensions where, as Parfrey (1988) noted, the trail was incomplete. The Barfield specimens are transverse and geniculate, whereas most of the typical *multispinosa* from the overlying Flat Top Formation tend to be elongate, and less geniculate, but there is variation. The distinctive features lie in the costellae and spine numbers. The costellae range from 6-9, rarely 10, in 5mm at the start of the trail on the dorsal valve of *dawsonensis*, compared with costellae counts of 15-16 in 5mm on dorsal valves of *multispinosa* according to Dear (1971, p. 19) and 15-18 in 5mm according to Briggs (1998, p. 181). Waterhouse (1986b, p. 55) gave many measurements for *multispinosa* from the

Flat Top Formation, that indicate a range of 11-18 in 5mm, mostly at 16 or 17 in 5mm, and noted that more occur in material from finer clastics. For the ventral valve Waterhouse (1986b) measured mostly 12-17 costellae in 5mm at 20mm from the umbo for *multispinosa*, with two at 7 and 9. Costellae may become coarser on the trail. Spines on the new species may be as fine as those of *multispinosa*, but are much fewer in number, especially on the dorsal valve. Spines may reach a diameter of 0.3-0.5mm, whereas the numerous spines of *multispinosa* generally measure only 0.2-0.3mm, also confirmed by Briggs (1998). The crowded spines seen over the anterior trail of *multispinosa* are lacking from the new form, perhaps because no known specimens become so large and elongate.

Genus *Pinegeria* new

DERIVATION: Named from Pinegi River, north Russia.

TYPE SPECIES: *Terrakea? pinegensis* Grigorieva in Sarytcheva, 1977, here designated.

DIAGNOSIS: Suboval shells with moderately short hinge, vaulted ventral valve with very small ears, deeply concave dorsal valve, short geniculate trail. Costellae very well defined and close-set on both valves, increasing by intercalation. Spines fine and erect posteriorly on ventral valve, suberect with posteriorly prolonged bases over visceral disc, erect, broad and crowded over not only small ears but around lateral and anterior margins; scattered, fine and erect on dorsal valve. Low concentric wrinkles especially on dorsal valve.

DISCUSSION: The type species comes from the Pinegi River, Russian Arctic. It has the suberect spines with prolonged bases that help characterize *Terrakea*, to which the species was originally referred, but differs from that genus in the very small ears and development of numerous erect spines around the lateral and anterior margins, and relatively strong ribs. It is distinguished from *Paucispinauria* by the well defined ribs, and array of erect marginal spines on the ventral valve, and small ears.

Coolkilella Archbold, 1993 is moderately close in shape but has a different spine pattern, including prolonged bases, and there are fewer ventral spines anteriorly and no dorsal spines.

Tribe **COOLKILELLINI** new

NAME GENUS: *Coolkilella* Archbold, 1993.

DIAGNOSIS: Small compact shells with moderately thick body cavity, long ventral spine bases, few hinge spines, no dorsal spines, closely costellate. Dorsal valve geniculate, may be pitted.

DISCUSSION: This is a minor association, involving *Coolkilella* Archbold, *Magadania* Ganelin, and *Kasetia* Waterhouse. All are similar to each other, and very close to *Paucispinauria* and allies, but distinguished by the absence of dorsal spines. *Coolkilella* Archbold (1993b, 1996) comes very close to, and even could prove to be a junior synonym of the poorly known north Russian genus *Magadania* Ganelin in Sarytcheva (1977). Brunton, Lazarev, Grant & Jin (2000, p. 530) also noted that *Coolkilella* approached *Kasetia* Waterhouse, 1981, which is a more compact shell with valves covered by low wrinkles, and spinose ventral ears, somewhat distinct from other members of the tribe.

These genera are judged to belong to Paucispinaurinae, not Linoproductinae as claimed by Brunton, Lazarev, Grant & Jin (2000), because they share elongate ventral spine bases.

Tribe **MAGNPLICATININI** new

NAME GENUS: *Magniplicatina* Waterhouse, 1983.

DIAGNOSIS: Body corpus shallow, concentric wrinkles strongly developed. Otherwise close to Paucispinaurini in costation, ventral spines in hinge row or rows, fine, body spines mostly erect but may have prolonged hollow bases, dorsal spines absent or numerous and erect. Interior much as in Paucispinaurini.

DISCUSSION: *Cancrinella* Frederiks and *Magniplicatina* Waterhouse are very close to *Paucispinauria*, *Terrakea* and allies, and are distinguished by strong concentric wrinkles and slender body corpus. Grigorieva, Ganelin & Kotlyar in Sarytcheva (1977, p. 127) mentioned a new subfamily Cancrinellinae, but did not define or discuss the subfamily. Ventral adductors are dendritic throughout ontogeny (Shi & Waterhouse 1996, p. 96).

Cancrinella and *Magniplicatina* are close to Auriculispinae Waterhouse, 1986 but spine bases are generally more elongate and wrinkles are stronger. Ventral adductor scars are striate and subelongate rather than dendritic at early into full maturity in several Auriculispinae. Although Briggs (1998) has in general discounted the value of muscle impressions and their nature, size and shape, the imprints appear to offer clear and consistent differences in shape and markings along different ontogenetic paths. Of course, as Waterhouse (1964b) showed, there may be convergence from different stocks in late ontogeny.

Brunton, Lazarev, Grant & Jin (2000, pp. 533, 543) assigned *Cancrinella* to Grandaurispiniinae (ie Paucispinaurinae) and *Magniplicatina* to Auriculispiniinae, but the two genera are so close that the difference in dorsal spinosity would seem to be of generic importance only. *Magniplicatina* is now known to be widespread in the northern hemisphere, including Glass Mountains, Texas. Such species were assigned to *Cancrinella* by Cooper & Grant (1975), until changed in the revised brachiopod treatise.

Genus *Magniplicatina* Waterhouse, 1983
Magniplicatina undulata Waterhouse, 1986

1950 *Cancrinella farleyensis* (not Etheridge & Dun); Hill, p. 14, pl. 7, fig. 7, pl. 8, fig. 2, 3 (not pl. 8, fig. 1, 4-6 = *Costatumulus farleyensis* (Etheridge & Dun)).

1964 *Cancrinella farleyensis* (not Etheridge & Dun); Hill & Woods, pl. P6, fig. 12 (not 13-16 = *Costatumulus farleyensis*).

1964b *Cancrinella* aff *farleyensis* (not Etheridge & Dun); Waterhouse, p. 61, pl. 9, fig. 3, text-fig. 22.

1972 *Cancrinella farleyensis* (not Etheridge & Dun); Hill et al pl. P6, fig. 12 (not fig. 13-16 = *Costatumulus farleyensis*).

1986b *Magniplicatina undulata* Waterhouse, p. 45, pl. 9, fig. 17-20.

1998 *M. undulata* Waterhouse; Briggs, p. 188, text-fig. 92.

HOLOTYPE: UQF 74019 figured by Waterhouse (1986b, pl. 9, fig. 19) OD from *Echinalosia curvata* Zone, Elvinia Formation, southeast Bowen Basin, Queensland.

DISCUSSION: Material reported from the *Terrakea dickinsi* Zone, Brunel Formation, lower Takitimu Group, at D44/f9604 (GS 5885), D44/f9957 (GS 9276) and D44/f9958 (GS 9277) by Waterhouse (1964b) is assigned to the species *Magniplicatina undulata*. Waterhouse (1964b, p. 62) had noted that the Takitimu material was especially close to material from the Cattle Creek Formation of the southwest Bowen Basin, which Briggs (1998) later included in *M. undulata*. The species *farleyensis* is now discriminated as belonging to the genus *Costatumulus* Waterhouse.

Magniplicatina halli (Waterhouse, 1982)
Pl. 3, fig. 7, 8

1982a *Cancrinella halli* Waterhouse, p. 45, pl. 10, fig. e-g, i, pl. 23, fig. g, h.

1986b *Magniplicatina superba* Waterhouse, p. 45, pl. 9, fig. 21-27, pl. 10, fig. 1-4, text-fig. 9.

1998 *M. perfecta* (not Waterhouse); Briggs, p. 191, text-fig. 93C, D, G (not fig. 93A, B, E, F, H = *M. perfecta*).

2000 *M. halli* Waterhouse; Brunton, Lazarev, Grant & Jin, p. 543, text-fig. 378.2a-c.

HOLOTYPE: BR 950, *halli*, figured by Waterhouse (1982a, pl. 10, fig. e, 1) OD from D44/f9001 (GS 9697), *Echinalosia discinia* Zone, Letham Formation, Wairaki Downs. UQF 70078, *superba*, figured by Waterhouse (1986b, pl. 10, fig. 2-4) OD from *E. discinia* Zone, Brae Formation, southeast Bowen Basin.

DIAGNOSIS: Little inflated, transverse shells with moderately strong close-set wrinkles, 2 rows of ventral hinge spines, and fine costellae, about 20 or more in 5mm.

MATERIAL: Specimens from D44/f307, f306, f314 from the lower *Echinalosia discinia* Zone, and from D44/f324 and f9001 (GS 9697) of the *Lethamia ligurritus* Subzone, Letham Formation, Wairaki Downs.

DISCUSSION: *Magniplicatina superba* Waterhouse from the Brae Formation of the southeast Bowen Basin is reassessed as being synonymous with *M. halli*. It has a broad gently convexo-concave disc, moderately strong wrinkles, and costellae of comparable density, distinctly finer than in *M. perfecta* Waterhouse or *M. magniplica* (Campbell). Ventral spine bases may be long. The double row of spines along the hinge deemed to be diagnostic for the Brae specimens has now been uncovered on specimens from the *Lethamia ligurritus* Subzone. Some *superba* specimens are rather transverse with lower wrinkles than in many but not all specimens of *halli*.

A specimen from the middle Fenestella Shale of Sydney Basin that was regarded as having affinities with *Magniplicatina perfecta* by Briggs (1998, text-fig. 93G) falls close to *halli*, agreeing in shape, and having fine costellae. Ventral spines are a little more numerous than usual. Other figured specimens (Briggs 1998, text-fig. 93 C, D) from Ulladulla, south coast of New South Wales, are more obscure, but are possibly conspecific.

Specimens allocated to *perfecta* by Briggs (1998, text-fig. 95B, F, H) from the Nowra Formation etc vary in some attributes but fall close to *perfecta*, although they have rather long spine bases compared with type *perfecta*, and perhaps are variants. They presumably occur with *Echinalosia robusta*, now regarded as *E. maxwelli*. *M. perfecta* Waterhouse (1986b, pl. 10, fig. 6-11) from the Oxtrack Formation of the Bowen Basin, is also associated with *E. maxwelli*. It is a species that has coarse costellae, 13-15 in 5mm, and wrinkles may be strong anteriorly, and crests tend to be angular, rather than rounded. Ventral spines are

often erect. The Otrack specimens are only gently concavo-convex and rather transverse, unlike the more arched shell typical of *M. magniplica* and *M. halli*.

***Magniplicatina magniplica* (Campbell, 1953)**

Pl. 3, fig. 9 - 11, text-fig. 6

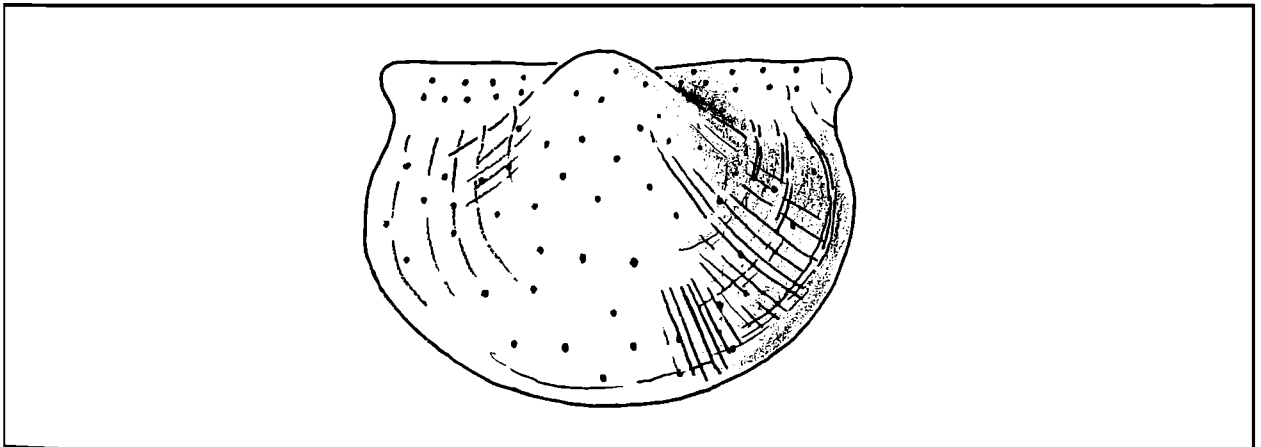
- 1953 *Cancrinella magniplica* Campbell, p. 7, pl. 1, fig. 1-5.
 1953 *C. cf magniplica* Campbell; Campbell, p. 7, pl. 1, fig. 6-8.
 1953 *Cancrinella* sp. Campbell, p. 7, pl. 1, fig. 9.
 1964b *Cancrinella magniplica* Campbell; Waterhouse, p. 62, pl. 9, fig. 4-8.
 1964 *C. magniplica* Campbell; Hill & Woods, pl. P6, fig. 17.
 1966 *Cancrinella gyrandensis* Wass, p. 97, pl. 3, fig. 1-5.
 1971 *C. magniplica* Campbell; Dear, p. 13, pl. 4, fig. 1.
 1971 *C. gyrandensis* Wass; Dear, p. 14.
 1972 *C. gyrandensis* Wass; Hill et al, pl. P6, fig. 17.
 1986b *Magniplicatina magniplica* (Campbell); Waterhouse, p. 48, pl. 10, fig. 5.
 1988 *M. magniplica* (Campbell); Parfrey, p. 13, pl. 2, fig. 9, 20, 21.
 1998 *M. magniplica* Campbell (sic); Briggs, p. 194, text-fig. 72C, 94A-F.
 1998 *M. perfecta* not Waterhouse; Briggs, p. 192 (part).

HOLOTYPE: UQF 14214, *magniplica*, figured by Campbell (1953, pl. 1, fig. 1, 2) OD from "Ingelara mudstone bed" (= lower Peawaddy Formation?), Bowen Basin, Queensland. For *gyrandensis*, UQF 43422 figured by Wass (1966, pl. 3, fig. 1-3) OD from Barfield Formation, Bowen Basin.

DIAGNOSIS: Shells with 10-13 costellae in 5mm, moderate to strong round-crested wrinkles, 1-2 rows of hinge spines.

MATERIAL: About 10 ventral valves and a few dorsal valves from D44/f123 (GS 15226), *Pseudostrophalosia?* cf *blakei* fauna, Mangarewa Formation, Wairaki Downs.

DESCRIPTION: Specimens including BR 2340, 2341, 2384, 2385 from unit 5 in the lower Mangarewa Formation at D44/f123 are comparatively numerous. They are subrectangular in shape and some are highly arched, whereas others are less inflated. They display moderately coarse costellae, varying from 13-15 in 5mm. Spines lie in a double row along the ventral hinge. Over the visceral disc and trail, a number of spines are erect, with no extended bases, and others show long recumbent bases. Wrinkles are low and crowded posteriorly, and are well spaced in front with rounded crests and often angular troughs. They are moderately high across the venter, but are not strong anteriorly.



Text-fig. 6. *Magniplicatina magniplica* (Campbell). Diagrammatic sketch of ventral valve BR 2340 from D44/f123, Mangarewa Formation, showing some of the spines bases, costellae and wrinkles, x 2 approx.

RESEMBLANCES: The material from D44/f123 compares moderately well with *Magniplicatina magniplica* (Campbell) in strength of ribs and spine bases. Some specimens have strong wrinkles but most have low wrinkles that are closer-set. They also resemble *M. halli* (Waterhouse) but have coarser ribs. The hinge has two rows of spines, but this feature is not well shown in type *magniplica*, which is mostly crack-out material that shows the true exterior poorly.

DISCUSSION: Material described by Waterhouse (1964b) from D44/f9621 (GS 6070), *Spiriferella supplantata* fauna, lower Letham Formation, Wairaki Downs was reassigned by Briggs (1998) to *Magniplicatina perfecta* Waterhouse, 1986b. He distinguished *perfecta* from *magniplica*, stating that the rugae were less pronounced across the middle part of the shell and had more angular crests and troughs, and noted that spine ridges

arose from fewer costellae (1-3, usually 1) compared with *magniplica* (2-4, usually 3) in *magniplica*. This seems to be true of one of GS 6070 specimens (pl. 9, fig. 5, 7, 8). But the other specimen has rugae that are high across the venter, with rounded crests, and spine bases arise from 4 costellae, as deemed typical of *magniplica* by Briggs. Even in Campbell's type material, these aspects vary somewhat, which was why the GS 6070 was compared with *magniplica* in the first place, even though the age seemed discrepant. Because of the sparsity of GS 6070 material, identity is difficult to decipher. But the material does fall very close to *magniplica*. Specimen BR 2341 and an unnumbered specimen come very close indeed in the strength of wrinkles to the specimen figured by Campbell (1953, pl. 1, fig. 7, 8) which is regarded as highly typical, although not from the type locality. Other GS 6070 specimens have lower wrinkles, but still compare with the suite originally figured by Campbell (1953).

***Magniplicatina heywoodi* n. sp.**

1983 *Cancrinella magniplica* not Campbell; McClung, p. 75, text-fig. 16.

1986b *Magniplicatina halli* (not Waterhouse); Waterhouse, p. 49, pl. 10, fig. 12-14.

1998 *M. perfecta* not Waterhouse; Briggs, p. 192 (part).

DERIVATION: Named for Philip Heywood, Theodore.

HOLOTYPE: UQF 74025 figured by Waterhouse (1986a, pl. 10, fig. 14), here designated, from UQL 4585, *Echinalosia ovalis* Zone, Flat Top Formation, southeast Bowen Basin, Queensland.

DIAGNOSIS: Moderately inflated somewhat compressed specimens, wrinkles close-set and low but crossing venter posteriorly with somewhat angular rounded crests, becoming much higher and spaced further apart anteriorly, troughs tend to be subangular. Generally several rows of spines along ventral hinge area, ventral body spines mostly arise from 2 posterior costellae, bases generally up to 2-5mm long, costellae fine, may be more than 20 in 5mm anteriorly.

MATERIAL: Specimens from D44/f119, f121, f122, and f130 (GS 15215, 15217, 15218, 15220), *Echinalosia ovalis* Zone, Mangarewa Formation, Wairaki Downs.

DESCRIPTION: Shells of average size, weakly transverse, with hinge at maximum width, weakly produced cardinal extremities, ventral valve very convex without sulcus and broad umbo with angle close to 100°, dorsal valve concave and curving into moderately high trail. Ornament of fine costellae and moderately well developed concentric rugae on both valves, rugae especially pronounced postero-laterally, variable in cross-profile, with interspaces generally angular, some evenly concave. Costellae fine at 20 or so in 5mm anteriorly on ventral valve, 14-17 in 5mm at 20mm from dorsal umbo. Erect spines lie in 2 to usually 3 or 4 rows along the ventral hinge, spine bases over disc 1-5mm long, often formed by convergence of two costellae. No dorsal spines.

RESEMBLANCES: Specimens from the Flat Top Formation that were referred to *Magniplicatina halli* by Waterhouse (1986b, p. 49, pl. 10, fig. 12-14) come very close to that species in detail of costellae. As observed by Waterhouse (1986b, p. 49), there are 3 rows of spines along the hinge in Flat Top specimens, and spine bases are 1-2mm long. The specimens are more arched than the types of *halli* or *superba*, and have a wide hinge and moderately defined wrinkles, which tend to be fine posteriorly, and abruptly become larger. Crests and interspaces of wrinkles may be subangular. Thus the species combines attributes of preceding species, with fine costellae like *halli*, and wrinkles showing attributes of *perfecta*. The Flat Top specimens figured by Waterhouse (1986b) were referred to *M. magniplica* by Briggs (1998, p. 195). They agree with this species in shape and inflation, but have lower less round-crested wrinkles and different spine details and finer costellae.

Somewhat allied Wairaki Downs specimens that compare in shape and inflation and wrinkles with *Magniplicatina heywoodi* are found in the upper *Echinalosia ovalis* Zone but the nature of hinge spines is not certain.

A specimen figured as *Cancrinella magniplica* by McClung (1983, p. 75, text-fig. 16) from level E, Eddystone GSQ 1, western Bowen Basin, has low wrinkles and fine costellae, and could be allied, but no data was provided on details of ventral hinge spines.

The specimens figured as *Magniplicatina perfecta* by Briggs (1998, text-fig. 93 A, E) from Copper Point, New South Wales, have long spine bases, well inflated shell and moderate wrinkles, like *heywoodi-perfecta*. The coarse costellae indicate *perfecta*. The specimen of Briggs (1998, text-fig. 93B, H) is similar, with few hinge spines apparently, and the specimen in Briggs (1998, text-fig. 93F) has at least 3 spine rows along the hinge. These all come from a locality in a Nowra Sandstone correlative, and suggest ties with the Otrack Formation of southeast Bowen Basin, from which type *perfecta* were described.

Suborder STROPHALOSIIDINA Waterhouse, 1978

AUTHORSHIP: THE SCHUCHERT- WAAGEN PROBLEM: Brunton, Lazarev & Grant (1995, p. 931) ascribed Strophalosiidina to Waagen (1883), but this was erroneous, because Waagen (1883, p. 613) placed

Strophalosia King as a member genus of Chonetinae, not in a distinct subfamily. In the revised treatise, Brunton, Lazarev, Grant & Jin (2000, p. 565) wrongly claimed that Strophalosiidina was “nom. transl. Brunton, Lazarev & Grant, 1995, p. 931, ex Strophalosiinae SCHUCHERT, 1913a, p. 391...” This statement was not truthful. The 1995 article never referred to Schuchert (1913) in connection with Strophalosiidina. They could have corrected their mistaken attribution to Waagen, but did not. They were aware of it, or at least Dr Brunton was, because I wrote to him about it, and he allowed that the ascription to Waagen was an error. Even this view seems to have been later forgotten. They were not free to ascribe Strophalosiidina to Schuchert, Waagen, or Lazarev. The name and concept had already been conceived for the first time, and authored, and had been in use for 25 years.

Paleontologists should not be satisfied with work that misrepresents earlier studies, and it is particularly regrettable for a treatise, which should set out to be an objective work summarizing knowledge, and with no personal agenda. As I understand, Dr R. E. Grant wrote by and large the strophalosiid section of the 1995 article (Dr Stas Lazarev, pers. comm., 1996), and in conversation with me he sometimes, and perhaps for argument's sake, championed the ascription of ordinal names to the authors of family groups, following the attitude of his colleague Dr G. A. Cooper. Such academic arguments were disregarded in print, with, for example, the proposal of Suborder Spiriferinidina by Cooper & Grant (1976). My stance is that those who conceive and publish the concept first are obviously the real authors. There was no requirement to ascribe Spiriferinidina to Davidson just because he authored Spiriferinidae in 1884. Later it was realized that Spiriferinidina Ivanova, 1972 preceded Cooper & Grant's proposal. Without hesitation, Carter et al (1994) followed proper procedures, and ascribed Spiriferinidina to Ivanova. But Brunton, Lazarev, Grant & Jin probably would have reacted differently, ignored and misrepresented the previous work, and declare Davidson authored the suborder, which he certainly never did.

Dr Grant died before the 1995 article was published, and presumably did not write the treatise item about Strophalosiidina. He apparently did write all or much of the strophalosiid section in Brunton et al (1995), and possibly had forgotten, or was unaware of the prior and firm proposal of Strophalosiidina by both Waterhouse and Lazarev, because no mention was made. That implies that Grant thought that Strophalosiidina was a new concept, and he wished to ascribe it to Waagen, whom he mistakenly thought had authored the family group. He was not right, and he was not free to disregard earlier work.

There are further difficulties with Brunton, Lazarev, Grant & Jin (2000). Whereas some experts have preferred to grant authorship of ordinal groups to the author of the family, none have never to my knowledge done that by seeking to displace an author of an ordinal group already proposed. Waterhouse was the first to visualize Strophalosiidina as an ordinal group, and so named and authored it. He was independently followed some years later by Lazarev (eg 1987, 1989), and he named it as well, with his authorship. If the name is to revert to Schuchert, following the lead of Brunton, Lazarev, Grant & Jin (2000), and not, as they claimed, Brunton, Lazarev & Grant (1995), then a similar procedure must - or might - be followed for other ordinal groups, from principles of consistency and fairness. Here are some of the changes that would need to be made to the revised brachiopod treatise.

Order Strophomenida Opik, 1934 becomes Strophomenida King, 1846
 Suborder Productidina Waagen, 1883 becomes Productidina Gray, 1840
 Suborder Chonetidina Muir-Wood, 1955 becomes Chonetidina Bronn, 1862
 Suborder Lytoniidina Williams, Harper & Grant 2000 becomes Lytoniidina Waagen, 1883
 Suborder Orthidina Schuchert & Cooper, 1932 becomes Suborder Orthidina Woodward, 1852
 Order Spiriferinida Cooper & Grant, 1976 becomes Order Spiriferinida Davidson, 1884

And the list continues, not only for Brachiopoda, but all other Animalia. It may be pointed out that anyone in future, at any time, can destabilize the literature, if the Brunton, Lazarev, Grant & Jin procedure is accepted.

THE WATERHOUSE VERSION: After Waterhouse (1975) had briefly mentioned Strophalosiidina as a new suborder, followed later by a fuller discussion in Waterhouse (1978), Lazarev (1986) independently erected the same suborder. Waterhouse (1978, p. 20 ff) pointed out that he recognized three main categories for Productida, namely Chonetidina, Productidina and Strophalosiidina, and listed and discussed various component superfamilies and families, with discriminants outlined. The diagnostic features had already been discussed, as in Waterhouse (1964b) etc. The distinctions between the three suborders were regarded as buttressed by the discussions, and the classification expressed the meaning of the distinctions. The proposal was a culmination of years of published study, and was original, a step beyond prevailing views. It was accepted widely, as for instance in studies by Archbold (1986c) and Briggs (1998).

According to Brunton, Lazarev, Grant & Jin (2000, p. 565), they used the suborder “sensu Lazarev, 1989, non Waterhouse, 1978” (font changed). This is shown to be inaccurate even in the same treatise by Brunton, Lazarev & Grant (2000, p. 351). They acknowledged that Cooper & Grant (1975) had “retained the Productidina with four superfamilies (Strophalosiacea, Aulostegacea, Richthofeniacea, and Productacea)”... and that Waterhouse (1978) had recognized.... “Strophalosiidina (divided into Strophalosiacea, Richthofeniacea, and Aulostegacea..)”. The three subdivisions of Strophalosiidina used by Waterhouse (1975, 1978) are the same as those recognized by Brunton, Lazarev, Grant and Jin (2000)! So by and large, the revised brachiopod treatise does not differ from Waterhouse (1978), other than for matters still under contention, and various improvements and changes. All recognized orders and suborders have endured such changes during the revised brachiopod treatise studies.

Critically, Schuchert (1913, p. 389) presented quite a different model. Chonetinae, Productinae and Strophalosiinae were grouped as Productidae. But Richthofeniidae were placed in a separate family. If the Waterhouse proposal had to be set aside because it was allegedly imperfect, why was Schuchert's separation of Strophalosiinae as a subdivision of Productidae, and Richthofeniidae deemed preferable?

The implication by Brunton, Lazarev, Grant & Jin (2000, p. 565) that Waterhouse (1978) presented an unsatisfactory version of Strophalosiidina is not correct. The further implication that Lazarev had provided the version exactly like that in the revised treatise is irrelevant, and any reader not too dismayed with the goings on may investigate the claim from the original paper. They will find it untrue. In 1987 Lazarev (p. 48), in his first discussion of his Strophalosiidina, included only Strophalosiacea and Lyttonioidea! Lyttonioidea [Lyttonioacea] is excluded from Strophalosiidina, by the revised brachiopod treatise, as by Waterhouse (1978). Richthofeniacea were not even mentioned by Lazarev (1987). He repeated this in Lazarev (1990, p. 77), and mentioned casually Aulostegacea, and Scacchinellacea (a group within Aulostegoidea), but still nothing of Richthofenioida. Thus the original understandings of the *Strophalosi* group in Schuchert (1913) and Lazarev (1987, 1990) were far removed from Strophalosiidina as understood by both the revised brachiopod treatise, and by Waterhouse (1975, 1978). Yet the revised brachiopod treatise adopted Schuchert, stated Lazarev had given a correct version as followed in the treatise, and dismissed Waterhouse, whom in fact they followed.

It may be time to regularise procedures. I suggest, in the interests of nomenclatural stability, and pending a clear decision by the International Committee for Zoological Nomenclature, that authorial names of members of ordinal groups be retained as first proposed. They may be upgraded from family group authorship, or ascribed to the author first publishing the concept. Once proposed, the name and author must stand. The rules of priority should stand inviolate.

A further potential source for destabilization stems from the possibility that authors will approach ICZN to ratify a suspension of the code or normal procedures, without properly advising all concerned. Given these days of great disparity in resources and accessibility to published and electronic media, it should be mandatory for such applicants to advise those authors originally involved, before the application is considered by ICZN. Otherwise the potential is there for future changes to continue to destabilize zoological nomenclature.

Superfamily **STROPHALOSIOIDEA** Schuchert, 1913
Family **STROPHALOSIIDAE** Schuchert, 1913

This family is important for correlation of Permian sequences in east Australia and New Zealand, and some of the changes from the correlation scheme proposed by Briggs (1998) are summarized in Table 7, with overall summary of species and genera in Table 8.

Four subfamilies are recognized for this family, Strophalosiinae, Dasylosiinae, Mingenewiinae and Echinalosiinae.

Subfamily **STROPHALOSIINAE** Schuchert, 1913

The genus *Strophalosi* King, 1844, type species *S. gerardi* King, lacks dorsal spines, as first shown by Waterhouse (1964b) and confirmed by Brunton (1966). *Heteralosi* King, 1938, type species *H. slocomi* King, was proposed for species thought to be distinguishable from *Strophalosi* through the absence of dorsal spines. Some authors have persisted in allowing validity to *Heteralosi*, viewing with suspicion a Gondwanan genus, *Strophalosi*, based on a Himalayan form, found so long ago, and buttressed by few additional specimens (Waterhouse 1983b) from high in the Permian. Regrettably, it seems that only Howard Brunton and I have bothered to examine the type specimens of *Strophalosi gerardi*. Grant (1976) and Archbold (1986c) continued to use *Heteralosi*, but offered no valid distinction of generic significance between the two genera, as Briggs (1998) underlined. Brunton, Lazarev, Grant & Jin (2000, p. 568) provided no difference between the two. They noted ventral spines were "bidirectional" and both valves may be lamellose in *Heteralosi* - but the same is true for *Strophalosi*. It is possible that there are distinctions, but no authority has yet justified any worthwhile distinction. Protestations that *Heteralosi* is Late Carboniferous and Permian, and from United States rather than just Permian - and Indian - need to be underpinned by firm morphological distinctions. Otherwise, *Heteralosi* will have to lapse. This certainly seems to be the conclusion to be drawn from an analysis by Brunton (1966, p. 188). He could see no difference between the types of the two genera, other than age, but warned that he could not compare the interiors adequately. He regarded "the question as to whether *Heteralosi* should be treated as junior synonym of *Strophalosi* is, therefore, one of opinion regarding size and geographical distribution". On the contrary, these parameters do not appear to be significant discriminants, and even Brunton, Lazarev, Grant & Jin (2000) did not overtly ascribe any significance to these factors.

Genus **Coronalosia** Waterhouse & Gupta, 1978

TYPE SPECIES: *Coronalosia blijniensis* Waterhouse & Gupta, 1978.

DIAGNOSIS: Medium-sized shells with gently convex ventral valve, gently concave dorsal valve, wide hinge,

spines few and well spaced over most of ventral exterior, most spines comparatively fine and subprostrate, rarely suberect. Thicker spines lie in row along hinge, sturdy laterally, lumen opens internally, spines also around margin also may open into interior in one or more rows. Dorsal exterior without spines, fine growth increments and finely striate radially.

DISCUSSION: The description of this genus was badly compromised by editorial muddlement to the text, where the Discussion on a preceding chonetid was inserted after the genus name; the species name became *blijniensis*, from *bijniensis*, and may as well stand, courtesy of the printer, and the numerous photographs were very badly reproduced, as justly noted by Brunton, Lazarev, Grant & Jin (2000, p. 565). Therefore some illustrations are reproduced here.

Because there has been considerable difficulties at the Geology Department, Panjab University, Chandigarh, the few specimens retained by me for further study have been housed at the Canterbury Museum. Attempts to discuss the matter with Panjab University never received any response, and obviously the specimens could not be entrusted to the mail in the dubious hope that they will arrive and be properly curated.

The nature of the ventral spines with well formed row along the hinge are reminiscent of Devonian strophalosiiform genera, lumped as Araksalosiidae Lazarev in the revised brachiopod treatise.

As Briggs (1998, p. 66, 67) noted, *Strophalosia irwinensis* Coleman, 1957 (Archbold 1986c, 1991) and *S. jimbaensis* Archbold, 1986 from Western Australia have prostrate spines over the disc and a distinct row of coarser postero-laterally directed spines along the posterior margin. The ventral spines are regularly distributed and become large anteriorly in *irwinensis*. Fine capillae lie on the dorsal exterior, and a few valves have dimples. *S. jimbaensis* has prostrate varying to suberect uniform ventral spines, largely of one diameter, and dorsal capillae. The west Australian species belong to *Coronalosia*.

Liveringia Archbold, 1987, type species *L. magnifica* Archbold, 1987, is also related, with a row of ventral spines close to the hinge, rare spines on the outer ventral ears, and capillae and dimples on the dorsal valve.

***Coronalosia blijniensis* Waterhouse & Gupta, 1978**

Pl. 4, fig. 17 - 21

1978 *Coronalosia blijniensis* Waterhouse & Gupta, p. 417, pl. 1, fig. 4, pl. 2, fig. 1-6, pl. 3, fig. 1-6.

DERIVATION: The name *blijniensis* was published, I think as a printer's error, derived from the proposed name *bijni*, which is an Indian place-name in the Garwhal Himalaya, and applied to a tectonic unit. The name arguably should be corrected as a justifiable emendation (International Commission for Zoological Nomenclature 2000, article 33.2.2). But the incorrect spelling has been used widely, by Gupta in Waterhouse & Gupta (1979), Archbold (1986c), Briggs (1998) and the revised brachiopod treatise, and it is suggested that the name be accepted.

HOLOTYPE: Specimen CASGF 526, figured by Waterhouse & Gupta (1978, pl. 2, fig. 1) OD from Early Permian Bijni tectonic unit, Garwhal Himalaya, India.

DISCUSSION: *Echinalosia voiseyi* Briggs (1998, p. 105, text-fig. 56)

from Gilgurry Mudstone, south Queensland, is outstanding amongst Australian members ascribed to *Echinalosia* by Briggs (1998). The ventral valve has fine numerous prostrate spines 0.2mm thick, and less numerous semi-recumbent ear spines reaching 0.25mm in diameter. Three laterally directed semi-recumbent spines up to 0.6mm in diameter form an erratic row near the posterior margin each side of the umbo. It is this feature that recalls the arrangement in *Coronalosia blijniensis* of the Garwhal Himalaya. In the Indian species, the hinge spines are more numerous and open internally. Unlike the Indian species, the dorsal valve of *voiseyi* is very finely spinose, and low fine growth lamellae are dominant, with no radial capillae, and the hinge very wide. The species *voiseyi* is very poorly known, and conservatively, is retained in *Echinalosia*.

SOURCE OF TYPE MATERIAL: Doubts have been raised in some circles about the reliability of source of Professor V. J. Gupta's material. However *Coronalosia blijniensis* undoubtedly came from the Indian Himalaya, and Bijni Tectonic Unit. The material was in fact discovered by an Australian team, including Drs Conaghan, Powell and Talent, and was later collected by (or for?) Prof. Gupta. It has been possible for me to check Gupta's Carboniferous, Permian, and Triassic macro-invertebrate collections against the numerous collections kept at the Geological Survey of India, Calcutta, and my own very substantial collections, now mostly at the Queensland Museum.

Genus *Etherilosia* Archbold 1993

Archbold (1993b) proposed the genus *Etherilosia* for *Strophalosia etheridgei* Prendergast, 1943, a small form with relatively large ventral attachment scar and rhizoid spines, as stressed by Archbold (1995a, p. 100). The genus might be regarded as suspect by some workers, because, as allowed by Archbold (1986c, pp. 104-105), Waterhouse (1959b, 1964b, 1982a) had established that small *Echinalosia* - and probably other Strophalosiidae - passed through an early growth stage in which the scar of attachment was relatively

large, and early ventral spines mildly rhizoid. Archbold (1986c) placed some stress on the well developed brachial ridges in Prendergast's species, which would suggest some degree of maturity, and this seems to be confirmed by the nature of the cardinal process. Briggs (1998, p. 66) pointed out that species assigned by Archbold (1986c) and Cooper & Grant (1975) to *Heteralosisia* could be placed in *Etherilosia*. The genus was classed in Strophalosiinae by Brunton, Lazarev, Grant & Jin (2000, p. 565).

***Etherilosia?* sp.**

Pl. 5, fig. 4, 5, text-fig. 5g, h

MATERIAL: Two specimens OU 18756-7 from D44/f9604 (GS 5885), *Terrakea dickinsi* Zone, Brunel Formation, Wairaki Gorge.

DIMENSIONS IN MM:

Specimen OU	Width	Length	Height	Hinge length
18756	9.5	9.5	1.5	4.7
18757	5.5	4.5	1.5	4.8

DESCRIPTION: A small specimen OU 18757 with valves conjoined shows a convex ventral valve with wide hinge and small well-formed ears, bearing 1-2 spines. Apparently erect spines are indicated around the anterior ventral margin. The dorsal valve appears to be without spines, although this is not certain. It has a narrow convex nepionic portion, and is otherwise very gently concave. Anteriorly, the shell appears to curve sharply ventrally, suggestive of a low geniculate trail. The dorsal cardinal process appears to be bifid, and supported by a ridge in front of the dental socket. Adductors are small and ovally subtriangular, occupying most of the nepionic part of the dorsal valve, which is only 3mm wide and 2mm long (compare with dimensions as measured above), posterior elements not clearly indicated. A low but clearly developed medium septum extends from just in front of the cardinal process for more than two thirds of the length of the valve. There are small pits and pustules, but no sign of brachial ridges. Several of these attributes indicate maturity.

A larger elongate specimen OU 18756 of irregular outline is a poorly preserved ventral valve with flat disc and steeply inclined margin. The hinge is short and interarea inclined steeply forward dorsally. Around the periphery is an array of spines, several rhizoid.

DISCUSSION: In *Echinalosisia maxwelli*, adnate specimens 6-10mm in width, much larger than the present dorsal valve, have a very slender dorsal medium septum that is subdivided into two low ridges, and smaller shells have no medium septum (Waterhouse 1964b, 1982a). A trail does not develop until specimens reach a larger size.

Subfamily **MINGENEWIINAE** Archbold, 1980

NAME GENUS: *Mingenewia* Archbold, 1980.

DIAGNOSIS: Ventral valve variably spinose, dorsal valve characterized by lamellae bearing radial filae to varying degree. Interior strophalosioid or unusual with ventral median septum.

DISCUSSION: Archbold (1980b) erected this subfamily for a single unusual genus, based on a single species, characterized by absence of spines and presence of dorsal lamellae, ventral septum, and high terminations to the brachial ridges. Here the dorsal lamellae with radial filae are regarded as the prime diagnostic feature. Other features are regarded as generic, and collections of the type species at the Natural History Museum, London, suggest that development of the ventral septum is variable. This means that the distinctive genus *Craspedalosisia* Muir-Wood & Cooper, 1960, pl. 6, fig. 1-9) may be included in the subfamily. *Craspedalosisia* lacks a ventral septum and has ventral recumbent tapering spines and erect sturdy sinuous spines. Dorsal spines are absent, except on Canadian material described by Waterhouse (1969d).

Genus ***Melvillosia*** new

DERIVATION: Named from Melville Island, Canadian Arctic Archipelago.

TYPE SPECIES: *Melvillosia canadense* n. sp., here designated.

DIAGNOSIS: Close to *Craspedalosisia*, distinguished by presence of rare dorsal spines.

Melvillosia canadense n. sp.

1969d *Craspedalosisia pulchella* not Dunbar; Waterhouse, p. 38, pl. 7, fig. 5, 7, 9, 12, pl. 10, fig. 14.

DERIVATION: Named from Canada.

HOLOTYPE: Specimen GSC 23828 from GSCL 35320, in unit B formation (Guadalupian), Melville Island, Canadian Arctic Archipelago, here designated.

DIAGNOSIS: Shell triangular in shape. Ventral spines in moderately thick erect series and slender prostrate series. Rare dorsal spines. Lamellae not numerous.

DESCRIPTION: Specimens of moderate size, holotype measuring 28mm in width, over 30mm in length and nearly 11mm in height, subtriangular in outline, with small cicatrix on ventral umbo of one specimen, not on another, ventral valve convex, high steep posterior walls diverging anteriorly at 110° to anterior third of shell length. Dorsal valve with small convex posterior, otherwise concave, with short trail, ears tiny in both valves. Ventral interarea high and weakly concave, dorsal interarea low. Ventral spines dense, of erect halteroid spines, about 1mm in diameter, scattered over disc and trail and clustered on outer disc near inner ears and anterior umbonal slopes, also semi-recumbent spines about 0.3mm in diameter, with slightly swollen bases. Sublamellate growth lines, and traces of radial capillae. Dorsal valve with well developed concentric lamellae, bearing radial capillae, pits and rare anterior sturdy suberect spines.

DISCUSSION: The species was described with further detail by Waterhouse (1969d). *Craspedalosis pulchella* (Dunbar, 1955, pl. 7, fig. 11-22) from Greenland has finer erect ventral spines, as well as fine subprostrate spines, more numerous dorsal lamellae, and no dorsal spines. Somewhat obscure specimens were described from the Spirifer Limestone of Spitsbergen by Gobbett (1964, pl. 2, fig. 6-10), and might belong to a separate species. The type species of *Craspedalosis*, *Orthothrix lamellosa* Geinitz from the Zechstein of north Europe, has a number of concentric lamellae and a tangle of ventral spines in at least two orders, with no dorsal spines.

Subfamily **ECHINALOSIINAE** new

NAME GENUS: *Echinalosia* Waterhouse, 1967.

DIAGNOSIS: Shells distinguished from other members of family by possessing erect spines of one series over dorsal valve, dorsal valve lacking well formed capillate lamellae, fine concentric lamellae developed to varying degree, radial filae generally weak or absent. Ventral valve generally with attachment scar, two series of spines, interareas, teeth and sockets developed.

DISCUSSION: This is the most diverse and numerous of strophalosiid subfamilies. There are several separate tribes, which possibly stem from separate Devonian sources amongst the genera classed in Araksalosiinae Lazarev. The present step is conservative, with the strong possibility that the group is polyphyletic.

CONSTITUENT GENERA: *Echinalosia* Waterhouse, *Wyndhamia* Booker, *Costalosiella* Waterhouse, *Crossalosis* Muir-Wood & Cooper, *Hontorialosis* Martinez Chacon, *Marginalosis* Waterhouse, *Notolosis* Archbold, *Pseudostrophalosis* Clarke, *Capillaria* Waterhouse.

Genus **Echinalosia** Waterhouse, 1967

This genus is characterized by comparatively little thickened dorsal valve, ventral spines of two series, thin prostrate and thicker more erect spines distributed usually closely over the ventral valve, fine usually erect and in some species scattered prostrate dorsal spines, all of much the same diameter. The arrangement of the spines is quite different from that in *Wyndhamia*, *Pseudostrophalosis*, and other genera. Brunton, Lazarev, Grant & Jin (2000, p. 571) failed to adequately interpret the spine pattern, and could only rely on shape and size, aspects that are less importance.

Clarke (1969, 1970) regarded most east Australian strophalosiid species as referable to *Wyndhamia*, and denied validity to *Echinalosia*. In this he was followed by Runnegar & McClung (1975). Dickins (1969, p. 89) stated that he found considerable difficulty in separating various species of *Echinalosia*, which he called *Strophalosis*. *Strophalosis* is a genus based on *Strophalosis gerardi* King, and lacks dorsal spines (Waterhouse 1964b, 1967a, Brunton 1966). Dickins also referred *Wyndhamia* to *Strophalosis*. In 1989, p. 75, Dickins without explanation of why he took to long to recognize *Echinalosia*, switched to using *Echinalosia*. But he continued to assert that various species within the genus were suspect. For a time only Dear (1971) stood out against the numerically dominant publications, not to mention the imposition of editorial and refereeing censorship. It took several decades for authors to realize the distinctions between *Wyndhamia* and *Echinalosia* (eg Clarke 1987, McClung 1983, Dickins 1989). Archbold (1986c), Parfrey (1988), and Briggs (1998) helped to consolidate the differences between genera, and like Dear, they countenanced the recognition of many species.

SPECIES ASSOCIATIONS: Several lineages are emerging from current studies of *Echinalosia* in east Australia and New Zealand. The most prominent centres on the species *maxwelli*, characterized by moderately sturdy generally erect to subrecumbent spines mixed with finer prostrate spines on the ventral valve, and deeply concave dorsal valve. This includes *curtosa*, *dejecta*, *denisoni*, *curvata*, *floodi*, *maxwelli*, *ovalis*

and various minor clusters treated as species by Briggs (1998). A fine-spined group includes *discinia*, *telfordi* and *runnegari*. The species *preovalidis* and *curvata* may have been ancestral, and *voiseyi*, an exceptional species with few spines and large posterior lateral ventral spines a possible derivative, unless it has been derived from stock allied to *Coronariosia*. The species *mcclungi* is possibly an offshoot from the *dejecta* suite. An unusual species is described below as *conata*, and its dorsal external ornament of concentric laminae strongly implies a separation from the other species, possibly to generic level.

***Echinalosia conata* n. sp.**
Pl. 3, fig. 12 - 22, text-fig. 5e

1964b *Strophalosia prideri* not Coleman; Waterhouse, p. 213.

1982a *Echinalosia prideri* (not Coleman); Waterhouse, p. 31, pl. 23, fig. i, text-fig. 19A, B.

1982a ?*Taeniothaerus* cf *miniliensis* not Coleman; Waterhouse, p. 41.

1998 *Echinalosia* cf *mcclungi* (not Briggs); Briggs, p. 80 (part, not text-fig. 41 = *mcclungi*).

DERIVATION: conatum - enterprise, endeavour, Lat.

HOLOTYPE: Specimen OU 18750, pl. 4, fig. 21, from D45/f7112, *Echinalosia conata* Zone, McLean Peaks Formation, Takitimu Group, Wilanda Downs.

DIAGNOSIS: Ventral valve moderately convex, at full maturity developing high massive posterior walls, broad somewhat flattened disc and anterior trail, hinge wide, maximum width near mid-length. Dorsal valve gently concave with trail at high angle. Ventral spines erect, moderately close-set, but very unevenly spaced, sometimes emerging close to each other, diameter varies, but not a clear division into two orders, prostrate spines rare; posterior row of large spines set just in front of hinge, surface also covered by low concentric rugae, and uncertainly, by filae, suggested within shell. Dorsal lamellae short, with erect spines and filae visible on some specimens. Ventral teeth small, close-set, not thickened, no median septum, ventral adductors large and high. Dorsal cardinal process small and brachial ridges inconspicuous, medium septum poorly if at all developed.

MATERIAL: About 12 ventral valves and 3 dorsal valves (OU 18744-18754) from D45/f7112 at Mt Wilanda. Previous material includes a ventral valve from D44/f9559 (GS 5613), and another from D44/f9755 (GS 6612), *Echinalosia conata* Zone, McLean Peaks Formation, Takitimu Range.

Specimen	DIMENSIONS IN MM: Ventral valves					
	Width	Length	Height	Hinge	Adductor scars	
OU					W	L
18745	20	22	6	?15	4.5	8
18747	34	31	12.5	30.5	6	11
18754	21	17	4.5	17	3.2	4.2
18749	19	?18.5	9.5	17.5	3.7	6.8
18746	22.5	21.5	18.3	18		
18744	28	22.5	15.5	19	5	?9
		Dorsal valve				
18750	29	18	4.5	?22		

DESCRIPTION: Ventral valve with moderately high posterior walls, diverging forward at 60-90°, ventral umbo pointed and without any conspicuous cicatrix, visceral disc variable from gently convex to broad and somewhat flattened, developing a shallow sulcus over mid-anterior length, sulcus may fade from some large specimens over trail. Posterior lateral part of shell generally large and gently convex, with small ears occasionally discriminated, cardinal extremities bluntly obtuse, hinge wide, cardinal interarea moderately high and gently concave. Dorsal valve transverse, gently concave, with posterior lateral ears and subgeniculate trail, low eccentric fold may be present anteriorly, or absent, interarea low. Ventral valve with low concentric growth undulations; low filae not clear on few available exteriors, but suggested, perhaps as part of shell structure. Spines prominent along row in front of hinge, erect and comparatively thick at 1mm diameter, on some specimens a prominent spine has swollen base 1.5mm in diameter towards posterior wall. Spines scattered in irregular subquincunxial pattern over rest of valve, generally 0.3 to 0.8mm in diameter, and unevenly spaced to the extent that sometimes close-set pairs are visible. Prostrate spines rare, 0.5mm in diameter. Posterior external fragment from GS 5613 has low spine bases 1.5-2mm apart along rows 1.5mm apart and concentric growth wrinkles. Posterior spine bases are less than 1mm apart. Dorsal nepionic shell about 5mm wide, almost smooth. Rest of dorsal valve ornamented by bands, numbering 8 in OU 18750, of 4-6 prominent growth lirae about 1mm across, separated by wider bands up to 2.5mm across, which are smooth or have faint radial capillae, 2-3 in 1mm, and bearing erect spines 0.2-0.25mm in diameter, irregularly spaced, about 1mm or more apart.

Ventral teeth close-set, without heavy callus, diverging laterally forward from hinge. Ventral adductor platform raised, long, generally almost smooth, often divided by fine median ridge or myophragm, replaced in

some shells by groove, and not found in largest specimens; shell behind muscle field half encloses short cavity under umbo, suggestive of open peduncle, but exterior shows no gap, indicating it was closed off in advanced maturity. Myophragm replaced by double ridge with median groove in one large shell and in this specimen posterior scars subdifferentiated. Diductors of moderate size, generally commencing at posterior third of adductor platform, marked by longitudinal striae; diductor impressions well defined in large specimen and bearing deep parallel striae. Floor of valve marked by a few open spines in early and early mature growth stages, and anterior floor has low pits and pustules, generally aligned. In large specimen, floor in front of muscle field has incised elongate irregular pits, and trail surface comparatively smooth.

Dorsal cardinal process projects in plane of disc, small, not very long, supported laterally by two short cardinal ridges, and short anterior ridge along mid-line. Muscle field with posterior-lateral triangular elements and more roundly triangular raised anterior inner elements. Septum not apparent in front of scars, and brachial ridges obscure. Anterior floor with fine pits.

RESEMBLANCES: No species appears to be similar. Two poorly preserved ventral valves, misinterpreted in part by Waterhouse (1964b, 1982a), have been previously described from the upper Takitimu Group at GS 5613 and 6612, apparently from the McLean Peaks Formation. They have short hinge and small ears with no sulcus. In early work I was misled by incorrect labelling. An external cast that I thought was *Taeniothaerus* from GS 5613 fits onto the internal mould mislabelled GS 5612. I believe Dr D. J. C. Briggs may have first noticed this, and added to the specimen a note that pointed out the match. The external fragment suggests rather fine close-set spines 1-1.5mm apart, with growth steps.

Briggs (1998, p. 81) re-examined the two specimens and whilst allowing for the poor preservation, confidently compared them to *Echinalosia mcclungi* Briggs (1998) from the Pebbly Beach Formation, south Sydney Basin, and listed from various other localities, including Elderslie Formation of the north Sydney Basin. Its range was said to be upper *Echinalosia preoivalis* Zone, but this has not been adequately established, partly because no well preserved *preoivalis*, or other species characteristic of the zone, have been described with *mcclungi*. He misrepresented the nature of the ventral spinose ornament for the New Zealand material, and indeed completely misinterpreted the species: there is little similarity to *mcclungi*, which lacks dorsal concentric ornament. The species *mcclungi* often has a short hinge and moderately thickened dorsal valve, explaining the initial reference by Briggs (1987, p. 138) to *Wyndhamia*. Lateral posterior spines are thick with open lumen, unlike the spines in *conata*, and dorsal spines of *mcclungi* are erect and few. Obscure specimens of *mcclungi* from UNEL 1348 show scattered spines along rows, and flat dorsal valve, with no apparent radial capillae and no concentric ornament, unlike *E. conata*. Briggs also reported the species from UNEL 845, but no strophalosiids are present in the collection, possibly having been removed and never returned. The generic affinities of *mcclungi* are obscure, but the nature of the extended ventral umbo, aspects of ventral spines, thickened dorsal valve and possibly the dorsal spines suggest *Acanthalosia*. This requires confirmation from re-examination of the dorsal spines, which were mentioned by Briggs as including a few erect spines and "perhaps" some interspersed finer spines.

Crossallosia Muir-Wood & Cooper, 1960, type species *Productus buchianus* de Koninck, 1847, has prominent laminae on the dorsal valve, but overall ornament and shape differ.

Archbold (1987, p. 34) was misled by my earlier observations into including the Takitimu specimens in his new species *Echinalosia denisoni* Archbold, a species discussed herein under that name.

BIOSTRATIGRAPHY: A significant stratigraphic succession of three strophalosiid species is found in the upper Takitimu Group and lower Letham Formation. These species were originally identified as *Wyndhamia dalwoodensis* Booker, now *Wyndhamia typica wardenensis*, from the lower Letham Formation, *Strophalossia prideri* Coleman, now *Echinalosia conata*, from the McLean Peaks beds of the higher Takitimu Group, and ?*Wyndhamia* sp. aff *jukesii* (Etheridge), now *Wyndhamia?* sp., from the supposed upper Brunel Formation in the Takitimu Group (Waterhouse 1964b, 1982a, H. J. Campbell in Campbell et al 1990, fig. 7). The identification of these forms has now been substantially clarified, and the overall implications of the initial studies have been reinforced by the discovery and description of further distinctive genera and species. Together with the strophalosiids, other brachiopod species, strongly supported by several gastropod species, help delineate two zones above the *Terrakea dickinsi* Zone, that have no species in common with the abundant faunas of east Australia. Given the strong ties above and below the two biozones, it therefore seems likely that the two biozones were represented by unconformity or non-marine conditions in east Australia, unless the *Wyndhamia?* proves to be conspecific with *mcclungi* Briggs, found in the Pebbly Beach Formation of the south Sydney Basin.

Echinalosia floodi n. sp.
Pl. 4, fig. 1 - 5, cf pl. 5, fig. 17

?1981 *Echinalosia preoivalis* (not Maxwell); Dickins, p. 30, pl. 4, fig. 1, 2, 4, 5.

DERIVATION: Named for Peter G. Flood.

HOLOTYPE: AMF 117369, pl. 4, fig. 2, from UNEL 1012, lower Elderslie Formation, north Sydney Basin,

New South Wales, here designated.

DIAGNOSIS: Small shells with weakly to moderately concave dorsal valve, low geniculate trail, scattered ventral thick and thin erect spines and few fine prostrate spines, fine dorsal spines.

MATERIAL: Some 9 ventral valves and 9 dorsal valves from UNEL 1012, two ventral valves from UNEL 990, and 5 ventral valves and a specimen with valves conjoined from UNEL 1013/2, lower Elderslie Formation, Sydney Basin, New South Wales.

DESCRIPTION: Shell small, concavo-convex, ventral valve convex with low steep posterior wall, umbo bluntly pointed or broad, outline weakly transverse to subelongate, hinge wide, up to maximum width of shell, with moderately low interarea in plane of commissure and blunt cardinal extremities. Venter generally gently arched, may be weakly flattened in shells from UNEL 1013, but never sulcate. Maximum width close to mid-length. Dorsal valve gently concave with low geniculate trail, interarea at almost right angle to commissure, valve might show faint median rise anteriorly. Ventral spines scattered and well spaced, erect, 0.5–0.8mm in diameter, about 2.5mm apart along rows 2–4mm apart. Posteriorly spines also erect and 0.5mm in diameter, 2mm apart. Rare spines up to 1mm in diameter. A few subprostrate spines, and short posterior ridges and fine concentric lamellae and ridges, no radial capillae. Dorsal valve UNEF 14341 has fine erect spines of even diameter 2mm apart at start of trail, 1.5mm between rows, low concentric ridges and very faint radial capillae, 7–8 per mm.

Ventral adductor platform divided by low myophragm posteriorly, moderately short, with shallow overlapping diductor scars and small close-set teeth. Dorsal cardinal process small, slender, erect, median septum extends for half to 0.75 length and moderately sturdy. Dorsal adductor scars with large anterior division and obscure posterior division, hinge ridge in larger specimens, and low ridge around trail, but brachial impressions obscure.

DIMENSIONS IN MM:

Specimen	Width	Length	Height	Hinge width	UNEL
	23	25.5	12.5	20.5?	1012
AMF 117369	24	26	11	19.5	1012
AMF 117367	27	23	7		1012
	28	23	9	23.5	1012
	31	28.5	13.5		1013/2
	33	28	9.5	26	1013
	33	25	9?	24	1013
	24	17	3	20	1012
UNEF14399	33	23	7	26	1012
UNEF14307	30.5	25.5	6	25	1012

RESEMBLANCES: Although assigned to *Echinalosia maxwelli* (Waterhouse), and earlier, to *E. preovalis* (Maxwell), by Briggs (1998, p. 83), the *Echinalosia* specimens from the lower Elderslie Formation have much less concave dorsal valve, less convex ventral valve and different spine pattern with fewer prostrate ventral spines than in these species. The species *mcclungi* Briggs (1998) from the Pebbly Beach Formation of the south Sydney Basin has a short hinge, elongate ventral umbo and different spine pattern with more diverse ventral spines that are coarse laterally, and generally a flatter dorsal valve. *E. preovalis* (not Maxwell) of Dickins (1981) from Warwick, Eight Mile and Tunnel blocks could be allied to *floodi*, but no dorsal valve was described or figured. Briggs (1998) referred the Warwick specimens to *E. discinia* Waterhouse, but shape and muscle field differ from this species. As well, material from the Freitag Formation in GSQ cores shows attributes of the new species, as discussed for *Wyndhamia typica crassispina*.

BIOSTRATIGRAPHY: This species is accompanied by *Paucispinauria paucispinosa wardenensis* n. subsp. at UNEL 1012, and *Aperispirifer archboldi* Waterhouse (eg UNEF 12789) at UNEL 1018, 1118 and 1024. It appears to be older than the zones of *Echinalosia maxwelli* and younger than the *Echinalosia preovalis* - *Terrakea dickinsi* - *Ingelarella plica* faunas.

Echinalosia discinia Waterhouse, 1986b Pl. 4, fig. 6, 7, 10 - 12

1929 *Strophalosia gerardi* not King (?); Booker, pl. 1, fig. 6-7 fide Briggs 1998.

1954 *Strophalosia ovalis* (not Maxwell); Maxwell, p. 548, pl. 57, fig. 14 (not pl. 57, fig. 4-9, 13 = *Echinalosia ovalis*; pl. 57, fig. 10-12 = *Pseudostrophalosia crassa* Briggs syn. *clarkei* (Etheridge)).

1986b *Echinalosia discinia* Waterhouse, p. 28, pl. 4, fig. 7, 8, 10-17 (not pl. 4, fig. 9 = *E. denisoni* Archbold).

1998 *E. maxwelli* (not Waterhouse); Briggs, p. 81, text-fig. 42.

1998 *E. davidi* Briggs, p. 83, text-fig. 43.

1998 *E. discinia* Waterhouse; Briggs, p. 86, text-fig. 45A, B, F, ? C, D, E, G, H.

HOLOTYPE: UQF 70303, *discinia*, figured by Waterhouse (1986b, pl. 4, fig. 12) OD from Brae Formation, southeast Bowen Basin. For *davidi*, UQF 75224 figured by Briggs (1998, text-fig. 43A, B) OD from Fenestella Shale, Sydney Basin.

DIAGNOSIS: Hinge moderately to very wide, interareas moderately high, dorsal disc gently concave, dorsal and ventral spines numerous, comparatively fine, dorsal growth lamellae conspicuous, ventral adductors of intermediate length, wide, posteriorly placed.

MATERIAL: A few specimens come from localities within the lower *Echinalosia discinia* Zone at D44/f110 (GS 15207), ?f307, f310 and in the upper zone, *Lethamia ligurritus* Subzone at D44/f109 (GS 15209 - BR 2261), f320-323, and f116 (GS 15211), Letham Formation, Wairaki Downs.

RESEMBLANCES: Specimens agree with the Queensland species described by Waterhouse (1986b) in profile, spines slender to moderate in width, well developed dorsal lamellae, and muscle scars. The one marked difference is that the Brae specimens have a very wide hinge, whereas the hinge in some Letham specimens is narrower. The ventral spines of specimen BR 2270 from D44/f110 (pl. 3, fig. 6) are mostly prostrate and 0.4 in diameter; dorsal spines are erect and fine at 0.25-0.3mm. Cardinal extremities appear to be smooth.

Specimens from the upper Elderslie Formation, lower Fenestella Shale and Wandrawandian Formation, especially older beds, of the Sydney Basin that were confused with *Echinalosia maxwelli* by Briggs are deemed to belong to this species. Unlike *E. maxwelli*, the Sydney Basin specimens have prostrate ventral spines 0.3mm in diameter, and erect spines 0.4-0.5mm in diameter, according to Briggs (1998). The erect spines in type *maxwelli*, based on numerous specimens (over 500 were examined in the original description) measure 0.8 -1mm in diameter, and the prostrate spines are 0.3-0.5mm in diameter. The Sydney Basin specimens do look somewhat like *maxwelli* - but as first noticed by Waterhouse (1964b, p. 40), the erect spines are distinctly finer. There are other differences from *maxwelli*: like *discinia*, the Sydney Basin shells are more disc-like than *maxwelli*, and the ventral interareas are higher, and the ventral adductors longer, as in *discinia*. The shells differ from type *discinia* in having more prostrate spines, and may be distinguished as a subspecies, proposed below.

Echinalosia davidi Briggs is also regarded as conspecific. It also has comparable fine ventral spines, mostly prostrate, with a diameter of 0.3-0.45mm. Like type *discinia*, the valve is little inflated, subrounded to oval, with moderately high interarea, moderately long ventral adductors, and smooth ventral extremities. It differs from *E. maxwelli* which has a lower ventral interarea, shorter adductors and slightly more spinose cardinal extremities and thicker erect and suberect ventral spines. The appearance of *davidi* is different from *discinia*, but the difference is ranked only as subspecific, as explained below. The form is found in the Wandrawandian Formation, Fenestella Shale and Branxton Subgroup, above the shells mistakenly ascribed by Briggs (1998) to *E. maxwelli*. Some specimens from the Letham Formation (eg D44/f110) show ornament typical of *davidi*.

In describing additional material of *Echinalosia discinia*, Briggs (1998) drew attention to the thicker ventral spines found in specimens of the upper Brae Formation, above the type locality, at UQL 4108 and 4534. He judged that this required the specimens to be reassigned to his *E. robusta*, shown below to be junior subjective synonym of *E. maxwelli*. If correct, it marks a significant evolutionary change, all the more intriguing because accompanying macro-fossils are all identical with species from the middle Brae Formation, accompanying type *discinia*. Unfortunately Briggs provided no independent documentation or figures, the only figure being given by Waterhouse (1986b, pl. 4, fig. 9). This is now assigned provisionally to *E. denisoni* Archbold as discussed below, not *maxwelli*. Such an identification is consistent with the known range of accompanying species.

STRATIGRAPHIC IMPLICATIONS: The species *discinia* s.l. is found in the Brae Formation, southeast Bowen Basin, upper Elderslie Formation and Fenestella Shale, north Sydney Basin, and lower Wandrawandian Formation of the south Sydney Basin, and upper Letham Formation, New Zealand. It was also reported from UNEL 1189-1192 in the upper Wandrawandian Formation by Briggs (1998), but these collections, borrowed by Dr Briggs, could not be found at the University of New England. The species is not known so far from the poorly controlled Middle Permian of Tasmania.

EVOLUTIONARY RELATIONSHIPS: This species is characterized by fine spines, and likely descendents are *Echinalosia runnegari* Briggs and *E. telfordi* Briggs. *E. preovalis* (Maxwell) might represent a forebear.

***Echinalosia discinia briggsi* n. subsp.**

1998 *E. maxwelli* (not Waterhouse); Briggs, p. 81, text-fig. 42.

DERIVATION: Named for David J. C. Briggs.

HOLOTYPE: UQF 75219 figured by Briggs (1998, text-fig. 42A), here designated, from Wandrawandian Formation, Warden Head, south Sydney Basin, New South Wales.

DIAGNOSIS: Shells with distinctive well spaced pattern of prostrate and erect spines on ventral valve.

DISCUSSION: This subspecies is like *discinia* in the spine dimensions, height of ventral interarea, length of ventral adductors, and overall shell shape and height. In the south Sydney Basin it occurs in a stratigraphic interval judged equivalent to that of allied subspecies.

***Echinalosia discinia davidi* Briggs, 1998**
Pl. 4, fig. 6

1929 *Strophalosia gerardi* King (?); Booker, pl. 1, fig. 6-7 (fide Briggs 1998).
1998 *E. davidi* Briggs, p. 83, text-fig. 43.

HOLOTYPE: UQF 75224 figured by Briggs (1998, text-fig. 43A, B) OD from Fenestella Shale, Sydney Basin, New South Wales.

DIAGNOSIS: Ventral spines mostly prostrate.

DISCUSSION: This form is found at very few localities. Some Letham specimens from New Zealand show the same spine pattern.

***Echinalosia discinia discinia* Waterhouse, 1986a**

1954 *Strophalosia ovalis* not Maxwell; Maxwell, p. 548, pl. 57, fig. 14 (not pl. 57, fig. 4-9, 13 = *Echinalosia ovalis*, not pl. 57, fig. 10-12 = *Pseudostrophalosia crassa* Briggs syn. *clarkei* (Etheridge)).
1986b *Echinalosia discinia* Waterhouse, p. 28, pl. 4, fig. 7, 8, 10-17 (not pl. 4, fig. 9 = *E. denisoni* Archbold).
1998 *E. discinia* Waterhouse; Briggs, p. 86, text-fig. 45A, B, F, ? C, D, E, G, H.

DISCUSSION: Details are provided above. Although Briggs (1998) considered the preceding three forms provide a stratigraphic succession, too few localities are available to confirm this as yet, and even in the successions of the north Sydney Basin that Briggs emphasized, very few localities were recorded, and none showed all three subspecies in succession. For the south Sydney Basin, misidentified *maxwelli* was supposedly followed by *davidi* and *discinia* at brief intervals in few localities. Collections at the University of New England have many specimens that were not mentioned by Briggs (1998), and these suggest that the Briggs (1998) succession of morphotypes was achieved by setting aside a great deal of material. Initial studies of accompanying Productida and Spiriferida do not confirm any significant stratigraphic difference.

***Echinalosia denisoni* Archbold, 1987**
Pl. 4, fig. 8, 9

1983 *Echinalosia* sp. nov. McClung, p. 71, text-fig. 13: 1-12.
1986b *E. discinia* not Waterhouse; Waterhouse, p. 28, pl. 4, fig. 9 (not pl. 4, fig. 7, 8, 10-17 = *E. discinia*).
1987 *E. denisoni* Archbold, p. 34.
1998 *E. denisoni* Briggs, p. 98 (part, not text-fig. 51 = sp. indet.).
1998 *E. bookeri* Briggs, p. 86, text-fig. 44.

HOLOTYPE: GSQF 12465, *denisoni*, figured by McClung (1983, text-fig. 13:12) OD from "interval C", GSQ Eddystone 1, Bowen Basin, Queensland. For *bookeri*, UQF 75231 figured by Briggs (1998, text-fig. 44B, E) OD from Branxton Subgroup, northern Sydney Basin, New South Wales.

DIAGNOSIS: Medium small shells, ventral valve moderately convex, dorsal valve moderately concave, hinge short, ventral interarea high, ventral muscle field long. Ventral spines coarse, variably erect and prostrate, dorsal spines rather few, moderately coarse.

MATERIAL: A possible specimen OU 18276 from D44/f320, upper Letham Formation, Wairaki Downs.

DESCRIPTION: Specimen as figured immature, has posterior erect spines up to 0.5-0.6mm in diameter, slightly thicker than in *Echinalosia discinia* material at comparable size found in the same beds, and close to spines on first formed part of *denisoni*, which develops much thicker spines anteriorly.

DISCUSSION: The species *denisoni* was proposed for an *Echinalosia* reported from interval C in GSQ Eddystone 1, Denison Trough, Queensland, by McClung (1983). The species is characterized by large few spines on both valves. McClung's interval C was said to include *Ingelarella* cf. *undulosa* Campbell, obscure *Terrakea* and *Sulciplica* cf. *phalaena* (Dana). It is overlain by a fauna from interval D that was correlated by McClung (1983) with the Ingelara Formation, containing species such as *Ingelarella angulata* Campbell and possible *I. ingelarensis* Campbell. The species *denisoni* was possibly ancestral to *maxwelli* and *ovalis*, judged from shape and ornament.

At only two localities, in the Branxton Subgroup and Fenestella Shale according to Briggs (1998), distinctive specimens were found roughly between species now identified as *discinia*, or within the top of its range, and *maxwelli* (= *robusta*). These were assigned a distinctive species *Echinalosia bookeri* Briggs (1998, text-fig. 44), characterized by thick prostrate as well as erect ventral spines, few fine prostrate spines, high ventral interarea and long ventral adductors. The comparatively short hinge, high ventral interarea, long ventral adductors, stout prostrate and some thick erect ventral spines, are features shared with *E. denisoni* Archbold, 1987 from "interval C" of the GSQ Eddystone 1 core, Denison Trough. Briggs (1998, p. 86) described the dorsal spines of *bookeri* as rare and only 0.25mm in diameter, but some dorsal spines are at least 0.6mm in diameter, as is also illustrated in his figures. The dorsal spines of *denisoni* were described by Briggs (1998, p. 99) as moderately numerous and up to 0.3mm in diameter, but the types do not have many dorsal spines, and they measure close to 0.6-0.8mm in diameter in topotypes, as illustrated by McClung (1983, text-fig. 13:10, 12). There are some differences: the *bookeri* specimens are more gently concavo-convex, and have more large prostrate spines on the ventral valve, but the two are very close and differences are judged to be infrasubspecific. In the Sydney Basin, *bookeri* falls within the *Echinalosia discinia* Zone, at the upper end of its range, or possibly just above *discinia*. In the Denison Trough, *denisoni* was found above *Glendella dickinsi*, and below apparent equivalents of the Ingelara Shale at interval D of McClung (1983). McClung (1983) reported, without confirmation from figures or description, that *Ingelarella cf undulosa* was found in interval C, indicating possible correlation with either *discinia* or *typica* biozone.

A ventral valve figured as *Echinalosia discinia* by Waterhouse (1986b) has thick subprostrate and a few thick erect spines, with rare thin prostrate ventral spines, unlike associated specimens, and may be placed in the same species. It comes from the Brae Formation, southeast Bowen Basin, and is found at UQL 4108, close to the top of the formation and above all figured *discinia* (Waterhouse 1986b, pl. 4, fig. 9). Whether other *Echinalosia* from this locality also belong to *denisoni* requires re-examination of the collection, but Briggs (1998) considered the material from the locality all belonged to one species, as discussed for *discinia* herein. A higher locality UQL 4534 also has *Echinalosia* (Waterhouse 1986b, table 12, p. 213) that need to be re-examined: Briggs wrote that the specimens were conspecific with those from UQL 4108.

Other material assigned by Briggs (1998) to *Echinalosia denisoni* is probably not conspecific. This includes unfigured, undescribed material from above the Moonlight Sandstone Member at UQL 4650 that has to be discounted because it is uncheckable, pending discovery of further material, or retrieval of the specimens that he examined. His figures of specimens ascribed to *denisoni* from DM Narrabri 1 show specimens with flatter dorsal valve internally, shorter ventral adductors, and fine ventral spines of more variable diameter. Nor can the Briggs assertion be sustained that *Echinalosia ovalis* of Waterhouse & Jell (1983, pl. 1, fig. 1-6) belonged to *denisoni*, although details of ventral muscle field and interarea and concavo-convexity are close. Spines on both valves of the Waterhouse-Jell material differ considerably from those of *denisoni*, as acknowledged by Briggs (1998, p. 99) in noting that its ventral spines were finer and more numerous than in *denisoni* and dorsal spines much more numerous than in *denisoni*. His other comments may also be rebutted. Finally, the reference by Briggs (1998, p. 99) to Blenheim Formation shells figured by Etheridge (1880, pl. 10, fig. 24, 25 - GSQF 1461-1462, 1471) seems difficult to sustain: the identification with *clarkei* seems preferable.

***Echinalosia maxwelli* (Waterhouse, 1964)**

1964b *Strophalosia maxwelli* Waterhouse, p. 32, pl. 4, fig. 6-11, pl. 5, pl. 6, pl. 7, fig. 1-3, pl. 36, fig. 5, 6, text-fig. 7a, c, e, 8b, 9a-m, 10a, b, 11, 12a-d, 13, 14.

1964 *Strophalosia clarkei* var *minima* Maxwell; Hill & Woods, pl. P4, fig. 14 (not pl. P4, fig. 13a, b = *Marginalosia? minima* (Maxwell)).

1972 *Echinalosia minima* Dear (sic); Hill et al, pl. P4, fig. 14 (not pl. P4, fig. 13a, b = *M. ? minima* (Maxwell)).

1982a *Echinalosia maxwelli* (Waterhouse); Waterhouse, p. 32, pl. 19, fig. a-d, pl. 23, fig. a-d, text-fig. 20-23A, 28. (See for fuller synonymy).

1986b *E. maxwelli* (Waterhouse); Waterhouse, p. 30, pl. 4, fig. 18-22, pl. 5, fig. 1, 2.

1998 *E. robusta* Briggs, p. 88, text-fig. 46.

2000 *E. maxwelli* (Waterhouse); Brunton, Lazarev, Grant & Jin, p. 571, text-fig. 405.2a-d.

HOLOTYPES: BR 253, *maxwelli*, figured by Waterhouse (1964b, pl. 4, fig. 8, 9, pl. 5, fig. 5, pl. 6, fig. 5) OD from D44/f9672 (GS 6323), *Echinalosia maxwelli* Zone, lower Mangarewa Formation, Wairaki Downs. For *robusta*, UQL 75235 figured by Briggs (1998, text-fig. 46A) OD from middle Belford Formation, Sydney Basin, New South Wales.

DIAGNOSIS: Medium-sized suboval, transverse to elongate, moderately high shells, comparatively low interareas and short posteriorly placed ventral adductors, ventral spines of variable density and spacing, prostrate spines 0.3-0.4mm diameter, erect spines 0.8 to usually 1 mm diameter. Dorsal spines variable in spacing and number, generally 0.2-0.3 diameter.

DISCUSSION: The original description of the species *maxwelli*, later to be made type species of the widespread genus *Echinalosia*, was based on over 500 specimens that were very well preserved, well illustrated and represented by numerous numbered specimens at IGNS, Lower Hutt. Many more specimens have been

collected. It was found that the species exhibited a range of shapes and ornament even within the type locality, and these were measured and discussed. It is this degree of variation that mandates a degree of caution in assessing the validity of *Echinalosia* species erected by Briggs (1998), illustrated by few figures, based on few and generally unstated numbers of specimens, with supplementary collections in disarray because they do not appear to have been returned to institutions. This is reinforced by misgivings over the emphasis on size by Briggs in his work. Variations in shell size of 10-20% are here not regarded as specifically significant, either for Productida, or indeed for most biota, yet to Briggs, this was a prime criterion.

It is considered that Briggs (1998) substantially misinterpreted the nature of *Echinalosia maxwelli*. He referred to the species a suite of specimens which look somewhat similar to one form of the type species, but are lower, with proportionately higher ventral interarea, longer ventral adductors, smoother cardinal extremities, and distinctly thinner spines. This is now referred to a subspecies of *E. discinia*. He separated from *maxwelli* specimens he called *robusta* that although a little larger than type *maxwelli*, have comparably thick erect ventral spines, ca 1mm in diameter, comparable prostrate spines (0.35-0.45mm in *robusta*, 0.25-0.4 in type *maxwelli*), and dorsal spines one one slightly variable series, (0.15 recumbent grading into 0.25 erect in *robusta*, mostly 0.2 mm, ranging from 0.15-0.3 recumbent, 0.25-0.3 erect in type *maxwelli*) and relatively low ventral interarea, and relatively short posteriorly placed ventral adductor scars. Differences between the suite of type *maxwelli*, and especially the large suite of specimens available from the Oxtrack Formation that were regarded as *robusta* by Briggs (1998) are present, but are judged to be minor. They have been assessed and statistically summarized in Waterhouse (1986b), and overall, the variation appears to be less than the variations displayed with the large and well preserved type collections of *Echinalosia maxwelli* from a single locality. For *maxwelli*, the specimens occur in over 50 layers, and even within individual layers, there is variation; as well the specimens trend differently from layer to layer. Species splitters might wish to recognize at least four species amongst the *maxwelli* types. Were this practise followed, it would be very difficult to trace fossil species very far, and correlation would be difficult, and delineating major evolutionary trends would become increasingly precarious. Nonetheless that possibility remains as future potential, but even so, it may not be possible to justify a number of Briggs' species.

The form *robusta* was recognized in the Belford Formation and Branxton Subgroup of the Sydney Basin, and Oxtrack Formation of the southeast Bowen Basin and other stations by Briggs (1998). He considered that *maxwelli* was followed stratigraphically by *discinia*, then by *robusta*, but this order is deemed wrong, with *maxwelli* (= *robusta*) following *discinia*.

***Echinalosia ovalis ovalis* (Maxwell, 1954)**

Pl. 4, fig. 13 - 16

1872 *Productus* or *Strophalosia* Etheridge Snr, p. 334, pl. 18, fig. 4, 4a.

1892 *Strophalosia clarkei* (not Etheridge Snr); Etheridge, pl. 13, fig. 14 (not pl. 13, fig. 13 = *Pseudostrophalosia clarkei* (Etheridge), not pl. 13, fig. 12, 16, 17, pl. 14, fig. 19 = *Ps. crassa* Briggs syn. *clarkei* (Etheridge)).

1892 *Strophalosia gerardi* (not King); Etheridge, p. 260, pl. 40, fig. 8; pl. 40, fig. 7 = *Echinalosia glabra* Briggs syn. *ovalis* (Maxwell) (not pl. 12, fig. 23-25, pl. 13, fig. 13 = *Ps. clarkei*).

1954 *Strophalosia ovalis* Maxwell, p. 548, pl. 57, fig. 4-9, 13 (not pl. 57, fig. 14 = *E. discinia* Waterhouse, not pl. 57, fig. 10-12 = *Ps. crassa* syn. *clarkei*).

1964 *S. ovalis* Maxwell; Hill & Woods, pl. P4, fig. 16, pl. P5, fig. 1, 2.

1970a *Wyndhamia clarkei* (not Etheridge); Armstrong, pl. 3, pl. 4, fig. 1-5, pl. 5, fig. 1-4.

1972 *Echinalosia ovalis* (Maxwell); Hill et al, pl. P4, fig. 16, pl. P5, fig. 1, 2.

1975 *Wyndhamia ovalis* (Maxwell); Runnegar & McClung, pl. 31.2, fig. 1-3?

1980 *Echinalosia ovalis* (Maxwell); McClung, pl. 19.1, fig. 3.

1982a *E. ovalis* (Maxwell); Waterhouse, p. 37, pl. 7, fig. a-f.

1983 *E. ovalis* (Maxwell); Waterhouse & Jell, p. 241, pl. 1, fig. 1-6.

1998 *E. ovalis* (Maxwell); Briggs, p. 103, text-fig. 55.

?1998 *E. hanloni* Briggs, p. 90, text-fig. 47.

1998 *E. wassi* not Briggs; Briggs, p. 96 (not text-fig. 50 = *E. wassi*).

HOLOTYPE: UQF 15630, *ovalis*, figured by Maxwell (1954, pl. 57, fig. 5-7) OD from Mantuan Member, Peawaddy Formation, Bowen Basin, Queensland. For *hanloni*, UQF 75247 figured by Briggs (1998, text-fig. 47B) OD from Muree Formation, Sydney Basin, New South Wales.

DIAGNOSIS: Large specimens with swollen generally transverse ventral valve, interarea low to usually high, dorsal valve deeply concave, ventral adductor platform long. Ventral spines of fine prostrate and semi-prostrate series and semi-erect or erect series twice as thick with other thicker spines, varied in distribution, dorsal spines mostly thin and erect, variable in distribution.

MATERIAL: From D44, a provisional 100 ventral valves, 22 dorsal valves and 37 specimens with valves conjoined from f111 (GS 15227), including BR 2260, 11 ventral valves and 4 dorsal valves from f344, 2 ventral valves, a dorsal valve and 2 specimens with valves conjoined from f346, in the lower *Echinalosia ovalis* Zone, some 28 ventral valves, 9 dorsal valves and 16 specimens with valves conjoined from f119 (GS 15215), about 21 ventral valves, 3 dorsal valves and 3 specimens with valves conjoined from f120 (GS

15216), 40 ventral valves, 6 dorsal valves and 5 specimens with valves conjoined from f121 (GS 15217), 15 ventral valves from f122 (GS 15218), 14 ventral valves, 5 dorsal valves and 9 specimens with valves conjoined from f130 (GS 15220), and a few individuals from f124 (GS 15219), f125 (GS 15213), f129 (GS 15214), f348, f349, f350, f351, and 7 ventral valves from f360 in the upper *E. ovalis* Zone, Mangarewa Formation, Wairaki Downs. Specimens counted as ventral valves may prove to have dorsal valve attached but hidden in matrix, overall numbers understated.

DESCRIPTION: Specimens large, moderately transverse to subelongate in outline, ventral umbo prolonged, umbonal angle of 70° to 130°, venter variably weakly sulcate, flattened medianly, or arched. Hinge shorter than maximum width, cardinal extremities rounded, maximum width placed near mid-length, interarea with narrow delthyrium, generally of only moderate height, although relatively high in specimens from f121, f122, and f130. Dorsal valve deeply concave, trail geniculate, subgeniculate, or may curve more evenly from disc, low fold visible anteriorly in a few specimens. Ventral spines arranged more or less in quincunx, of uneven strength and diameter, subhorizontal or erect, over 2.5mm apart along rows anteriorly, rows 2.2mm and rarely up to 3mm apart anteriorly. Spines up to 1mm in diameter, more than twice diameter of thin recumbent spines. Dorsal spines thin, erect, less than 0.2mm in diameter. Growth lines and growth lamellae moderately developed, 2-3 per mm over ventral valve anteriorly, 3 or 4 per mm and more prominent on dorsal valve. Capillae not visible, but fine surface detail obscure.

Ventral teeth well developed, posterior wall internally thickened and pitted. Ventral adductor scars long, triangular in outline, divided by low ridge, marked by low growth ridges, raised anteriorly, impressed in posterior wall posteriorly. Diductor scars overlap anterior third of adductors, oval, marked by longitudinal ridges and grooves, impressed. Dental sockets small, cardinal process projects posteriorly in plane of disc, with swollen lateral and median lobes, supported anteriorly by high median septum without antron, narrow between adductors, high in front, and slender, extending just past mid-length. Dorsal adductor scars with small posterior divisions immediately in front of sockets, steeply inclined forwards, anterior divisions large. Brachial ridges pass from in front of sockets to encircle disc, anterior part not clear. Pallial pits small.

Material from higher localities in the zone are mostly small and not well preserved, being crowded together, and few show the height of the ventral interarea, though several have a long ventral adductor platform. Ventral spines are coarse and well spaced, even in specimens from f120.

RESEMBLANCES: The red mudstones south of Productus Creek in Mangarewa unit 6 include *Echinalosia* with high ventral interarea and long ventral adductor scars, features that help characterize the species *ovalis*. Individuals vary in the development of spines, which are often coarse, and the ventral valves are very convex, presumably in response to difficulties of achieving stability. The specimens are thus moderately different externally from *Echinalosia maxwelli*, although of comparable size and variable shape, and ventral spines may be very slightly thicker, and dorsal spines a little less prominent and finer in *ovalis*. The most consistent difference lies in the higher ventral interarea and length of the ventral adductor scars, nearly twice as long in proportion to the shell length than in *E. maxwelli*. In the dorsal valve, the posterior adductors are more laterally placed, and brachial ridges more defined, and dorsal septum slightly longer, but type *maxwelli* is better preserved, so that these comparisons have not been fully validated by comparably well preserved suites.

Type *Echinalosia ovalis* (Maxwell) from the Mantuan Member of the Peawaddy Formation of southwest Bowen Basin is larger than New Zealand material and includes specimens with high ventral interarea, although others have a low interarea. Large erect and suberect ventral spines vary from 0.7 to 1.5mm in diameter, spaced about 2mm apart anteriorly, along rows 2-3 or rarely 4mm apart. Spines are very varied in distribution, and also differ in the degree of erection: some lie vertical, many lie subprostrate. Much thinner prostrate spines are also present in an apparently irregular pattern and highly variable in different individuals, and even different parts of the one valve. Internally, the ventral adductors are proportionately long and anteriorly high, and comparable with those of the present material. There is a little variation, but specimens with short ventral adductors are rare. Size and concomitant spine spacing may reflect favourable ecological conditions, rather than point to a reliable morphological distinction. Briggs (1998) regarded *ovalis* as characterized by its large size with spines fine and of two series on the ventral valve, both uniform in diameter beyond the umbonal region. But he allowed that prostrate spines were 0.4mm in diameter, compared with "high-angle recumbent to suberect spines 0.9mm in diameter", with further observations. He illustrated good examples, but these only represent some of the range of individual variation and collections show a much wider range in pattern of spinosity. To Briggs (1998), the species was limited to the Peawaddy Formation and Flat Top Formation, and Condamine beds near Warwick (UQL3536).

From the lower Blenheim Formation of the northern Bowen Basin, Waterhouse & Jell (1983, pl. 1, fig. 1-6) reported specimens that were considered to belong to *Echinalosia ovalis* (Maxwell). They are small compared with type *ovalis*, and have a long ventral adductor platform, but the ventral interarea is moderately low. Thus these appear to be very close to some of the present specimens. Accompanying species at this level in the north Bowen Basin include *Paucispinauria solida*, *Ingelarella mantuanensis*, and *Marinurnula mantuanensis*, similar to species found in this fauna in New Zealand and in the Mantuan Member of the southwest Bowen Basin. The fossils are found in a thin band above beds with *Pseudostrophalosia blakei*, and below beds with *Pseudostrophalosia clarkei*. Similarly in the southeast Bowen Basin, shells ascribed to *E. ovalis* by Waterhouse (1986b, pl. 5, fig. 3-8) come from the middle Flat Top Formation, found above *Ps.*

blakei. These have a moderate to high ventral interarea and ventral adductors are long in some specimens, shorter in others. One specimen with valves conjoined was adjudged to be this species *ovalis* from Fossil Ridge, southeast Bowen Basin, by Maxwell (1954, pl. 57, fig. 14). It is difficult to interpret but may be *maxwelli*, or more probably, as Briggs (1998) also suggested, *discinia*, to judge from its wide hinge and gently concave dorsal valve.

Closely comparable *ovalis* material, including specimens with high ventral interarea and some with long ventral adductors were recorded from Mangarewa unit 7c (GS 3616 - D44/f9478) by Waterhouse (1982a, pl. 7, fig. a-f). Telford (1971, pl. 16, fig. 6) reported the species from the Cataract Formation and Gilgurry Mudstone near Drake, northern New South Wales, but verification is required.

Dickins (1989, p. 75) considered *Echinalosia ovalis* to be "quite long ranging, from the base of the Blenheim Subgroup and possibly through Fauna 1V" but his view of *Echinalosia* species remains unquantified, and as a result his qualitative descriptions such as "rather" and "not particularly" are difficult to decipher, given the lack of measurements. He compared specimens from a Sydney Basin bore DM Camden to the species *E. ovalis* (Dickins 1989, pl. 3, fig. 7-9), and stated that the species occurs in the Kulnura marine tongue in the north Sydney Basin. The description and comparison lack detail, but the specimens are *Wyndhamia* or more likely *Pseudostrophalosia*, not *Echinalosia*. They show prominent ventral lamellae and close-set coarse spines on both valves, approaching the shells misidentified as *Wyndhamia cf. ingelarensis* by McClung (1983) from interval E, GSQ Eddystone 1 core, Bowen Basin, but different in shape. Large *clarkei* are somewhat like the Kulnura specimens at late maturity. Briggs (1998) indicated a new species *Pseudostrophalosia crassa* in the upper Tomago Coal Measures at this level. The ventral spines are a little coarser and more close-set than in figured ventral valves of *clarkei*, but there seems to be gradation between *crassa* and *clarkei*.

Echinalosia hanloni Briggs (1998, text-fig. 47) from the Muree Formation, north Sydney Basin, is overall close to *E. ovalis* in size, high ventral interarea, long ventral adductors and sturdy spines. The types are distinguished by their subprostrate thick ventral spines, imparting a distinctive appearance, so that a subspecific rank would be acceptable. Briggs recorded the ventral spines as constituting a single recumbent series, but it would be more accurate to describe thin prostrate spines as comparatively rare, and thick spines as subprostrate (see Briggs 1998, text-fig. 47A, D). He also misunderstood the nature of the dorsal spines, writing that all were of one recumbent series. In fact, many are suberect to erect (Briggs 1998, text-fig. 47E). Thus *hanloni* is not as distinctive as Briggs claimed, and the form clearly falls within the ambit of an *ovalis* plexus, explaining why Runnegar (1980) and McClung (1980) referred the specimens to Maxwell's species. Briggs (1998, p. 91) recorded *hanloni* from the Muree, Mulbring and Porcupine Formations, Nowra Sandstone and from South Marulan, stations that appear likely to be correlative, though many have not been verified by documentation. He also stated that the species was found also in the Belford Formation of Sydney Basin and Oxtrack Formation. These occurrences were not documented or illustrated.

Echinalosia wassi Briggs (1998) was proposed for moderately large moderately high shells with deeply concave dorsal valve, moderately high ventral interarea and moderately long ventral adductors. The ventral ornament includes fine prostrate spines, and thicker prostrate and erect spines 0.8-1.2mm in diameter which are especially developed postero-laterally, including a few on the ears (Briggs 1998, text-fig. 50B, C). These posterior lateral spines are somewhat reminiscent of *Pseudostrophalosia*, but not as clustered. There are erect or recumbent not very numerous dorsal spines 0.25mm in diameter posteriorly, and reaching 0.4mm diameter anteriorly. Overall aspects of the species are close to those of *E. ovalis*, differing in wide hinge and very low ventral umbo. It is kept separate, but perhaps should be rated as a subspecies or even variant, pending inspection of substantial collections. There is some similarity to *E. mcclungi* Briggs in the scattered and varied ventral spines, thick posterior lateral ventral spines and few dorsal spines. *E. wassi* was described from various New South Wales, including the Broughton Formation (Kiama Sandstone Member) of the south Sydney Basin, where it is associated with *Terrakea brachythaera*. This points either to a Sydney Basin equivalent of the *Pseudostrophalosia clarkei* - *Terrakea elongata* Zone in New Zealand and north Bowen Basin, or more likely to a localized Sydney Basin subdivision of the *brachythaera* range zone. Briggs (1998) regarded the upper Mangarewa shells of Wairaki Downs at GS 3616 as conspecific with *wassi*, but the New Zealand specimens look much closer to those of type *ovalis*. There are slightly fewer erect spines than in *wassi*, and the extensive suites of New Zealand shells here identified with *ovalis* do not show the large posterior lateral ventral spines, wide hinge, high interarea and low ventral umbo typical of *wassi*.

Echinalosia runnegari Briggs (1998, text-fig. 49) from the Mulbring Formation of north Sydney Basin is comparatively low and broad, with both orders of spines on the ventral valve prostrate, comparatively smooth dorsal and ventral ears, and moderately numerous fine erect and rare scattered prostrate dorsal spines. The broad shallow disc, rather low ventral interarea, comparatively smooth ears and posteriorly placed short muscle field, at least in figured material (for descriptions provide little data) suggest a distinct species, within the age range of either or both *E. ovalis* or *wassi*.

***Echinalosia ovalis glabra* Briggs, 1998**

1892 *Strophalosia gerardi* King?; Etheridge, p. 260, pl. 40, fig. 7 fide Briggs 1998 (not pl. 12, fig. 23-25, pl. 13, fig. 33 = *Pseudostrophalosia clarkei* (Etheridge), pl. 40, fig. 8 = *ovalis ovalis* (Maxwell)).

1971 *Echinalosia ovalis* (Maxwell); Dear, p. 9 fide Briggs (part).

1986b *E. ovalis* (Maxwell); Waterhouse, p. 31, pl. 5, fig. 3-8.

1998 *E. glabra* Briggs, p. 103, text-fig. 54.

HOLOTYPE: UQF 27677 figured by Briggs (1998, text-fig. 54B) OD from Flat Top Formation, southeast Bowen Basin, Queensland.

DIAGNOSIS: Moderately large shells with moderate to wide hinge, and moderate to high interarea, ventral spines rather fine, erect series 0.5-0.6mm diameter and slightly thicker in array near each ear, dorsal valve deeply concave posteriorly, medium to long ventral muscle field.

DISCUSSION: *Echinalosia glabra* Briggs from the Flat Top Formation of the southeast Bowen Basin is close to *E. ovalis*. It has rather slender spines over much of the ventral valve, and although Briggs (1998, p. 103) stated that the erect spines were only 0.2mm thick, many are 0.5mm in diameter, some even thicker, and erect spines near the posterior lateral margins are even broader, trending towards *E. wassi* Briggs from the Broughton Formation of south Sydney Basin. Briggs (1998) included one specimen of Waterhouse (1986a, pl. 5, fig. 6, 7) in *deari*, because of shape: this might be correct but needs to be established from external spinosity, because shape varies in these taxa. There is some approach to *E. runnegari* Briggs, 1998, but that species is less inflated and has smooth ventral ears without coarse posterior lateral spines, and short ventral muscle field, unlike the long *ovalis*-like scars of *glabra*.

***Echinalosia ovalis tasmantia* n. subsp.**

1969 *Wyndhamia ovalis* (Maxwell); Clarke, p. 45, pl. 8, fig. 6.

1987 *Echinalosia ovalis* (Maxwell); Clarke, p. 264, text-fig. 2A-L.

1998 *E. hanloni* (not Briggs); Briggs, p. 91.

HOLOTYPE: GST 14006 figured by Clarke (1987, text-fig. A, B) from Malbina Member E, Tasmania, here designated.

DIAGNOSIS: Medium-sized shells with convex ventral valves, moderately high ventral interarea, long to medium-length ventral adductor scars, ventral spines close-set, erect and suberect spines generally 0.6-0.8mm thick, and thinner prostrate spines, dorsal spines scattered, erect, 0.3-0.5mm thick.

DESCRIPTION: The material has been described by Clarke (1969, 1987). Shells are of moderate size with vaulted ventral valve, moderately wide hinge and angular cardinal extremities, and wide dorsal valve. Ventral spines close-set, in two orders, but erect spines are comparatively fine, and dorsal spines scattered and fine. Ventral adductor platform long, and diductor scars large and well-formed. Dorsal cardinal process sturdy, brachial ridges well defined, anterior marginal ridge thick.

DISCUSSION: Material from the Malbina E beds in Tasmania that had been identified with *ovalis* by Clarke (1987, text-fig. 2A-L) was referred to *hanloni* by Briggs. The Clarke figures do not show long semirecumbent thick ventral spines such as supposedly typify *hanloni*. The Tasmanian material is interpreted as constituting a geographic subspecies of *Echinalosia ovalis*, characterized by the comparatively convex ventral valve and comparatively fine ventral spines.

Genus *Capillaria* new

DERIVATION: capilla - fine, thread - Lat.

TYPE SPECIES: *Strophalosia preovalis* Maxwell var *warwicki* Maxwell, 1954, here designated.

DIAGNOSIS: Small strophalosiids with narrow hinge, poorly formed or no lateral ears, distinguished by moderately well developed radial capillae on dorsal valve, concentric ornament inconspicuous. Ventral spines of two orders, scattered and thick erect spines tend to be developed laterally, dorsal spines erect and few, dorsal exterior with a few dimples.

DISCUSSION: This genus is close to *Echinalosia*, and distinguished by its clearly developed dorsal capillae, with different inflation and high posterior walls. The type species was described and illustrated most effectively by Briggs (1998), with clarification of taxonomy and morphology. The species comes from Briggs' *warwicki* Zone, judged by Briggs (1998) to underlie his extended *preovalis* Zone. No comparable species is found in east Australia or New Zealand. Dorsal capillation also is developed in *Coronalosia* Waterhouse & Gupta, and in *Craspedalosia* Muir-Wood & Cooper of Strophalosiinae, but does not appear to indicate any close relationship.

Genus *Marginalosia* Waterhouse, 1978

TYPE SPECIES: *Echinalosia? kalikotei* Waterhouse, 1975.

DIAGNOSIS: Large Strophalosiidae with interareas, ventral umbonal scar small, dorsal valve geniculate, ventral spines fine, largely but not entirely uniform in diameter, numerous, seldom differentiated and without swollen bases; dorsal spines numerous, fine to as thick as ventral spines, uniform and erect, external pits common. Ventral interior with posterior marginal ridge, dorsal interior with anterior marginal ridge and thickened trail.

DISCUSSION: The genus *Marginalosia* was established for a Late Permian (Changhsingian) species of west Nepal, and includes also the Changhsingian species *Strophalosia planata* Waterhouse, 1964b from the Pig Valley limestones of the lower Te Mokai Group, east Nelson. It was suggested that the Arctic species *S. ? bajkurica* Ustritsky (in Ustritsky & Chernyak 1963) from Taimyr Peninsula might be allied, as this shows a heavy marginal ridge in the ventral valve. The species is from the upper Baikur fauna, approximately correlative with the Gijigin tillite level (Likharev 1966, Waterhouse 1976b, p. 58, table 15). Brunton, Lazarev, Grant & Jin (2000, p. 573) treated the genus as comparatively late in the Permian, as supposed Capitanian in R. E. Grant terms, which often turns out to be Wuchiapingian or younger.

Notolosia Archbold (1986c) from Western Australia has dorsal marginal ridge and fine ventral spines suggestive of *Marginalosia*, but lacks dorsal pits, and its spine pattern is closer to that of *Pseudostrophalosia*.

One late Guadalupian (Middle Permian) species hitherto assigned to *Echinalosia* shows a strong approach to Late Permian species of *Marginalosia*, and on available evidence appears ancestral. It is referred to *Marginalosia* with a query. Perhaps it is implying a slightly younger age for the particular beds than hitherto realized, or means, as here adopted, that the range of the genus must be slightly extended.

***Marginalosia? minima* (Maxwell, 1954)**

1954 *Strophalosia clarkei* var *minima* Maxwell, p. 547, pl. 56, fig. 9-11.

1964 *Strophalosia clarkei* var *minima* Maxwell; Hill & Woods, pl. P4, fig. 13a, b (not pl. P4, fig. 14 = *Echinalosia maxwelli* (Waterhouse)).

1965 *Strophalosia minima* Maxwell; Waterhouse & Vella, p. 62, pl. 2, fig. 4.

1971 *Echinalosia minima* Dear (sic); Dear p. 7, pl. 3, fig. 11-16.

1972 *E. minima* Dear (sic); Hill et al, pl. P4, fig. 13a, b (not pl. P4, fig. 14 = *E. maxwelli* (Waterhouse)).

1980 *E. minima* (Maxwell) or *E. maxwelli* (Waterhouse); Runnegar, photo 19.1, fig. 2.

1998 *E. minima* (Maxwell); Briggs, p. 99, text-fig. 52.

HOLOTYPE: UQF16262 figured by Maxwell (1954, pl. 56, fig. 9, 10), Hill & Woods (1964, pl. P4, fig. 13a, b) and Hill et al (1972, pl. P 4, fig. 13a, b) OD from upper Blenheim Formation, north Bowen Basin, Queensland.

DIAGNOSIS: Moderately large generally transverse shells with wide hinge, weak or no sulcus, ventral spines of mostly uniform size, erect to suberect as a rule, closely spaced along concentric rows, concentric lamellae moderately developed. Dorsal valve gently concave, numerous erect spines and fine concentric lamellae. Internally, a posterior ridge prominent in ventral valve, and ridge developed around dorsal valve which is weakly thickened anteriorly. Body cavity moderately thin.

DESCRIPTION: Suites of specimens from UQL 1384 and 1385, upper Blenheim Formation, north Bowen Basin, also described by Maxwell (1954), have been re-examined. There is some variation: some ventral valves carry a shallow anterior sulcus, a very few have a short hinge. A very few spines are subprostrate, but of much the same dimensions as the erect spines, and bases are not swollen. Some dorsal valves have a median fold, and one or two have a short hinge. Pits are moderately developed over the dorsal exterior (see also Briggs 1998, text-fig. 52C).

RESEMBLANCES: This species was identified from the Flowers Formation of northwest Nelson by Waterhouse & Vella (1965), on the basis of the outline and wide hinge and nature of the adductor scars in the ventral valve. The critical nature of the spines remains unknown, and it appears that no further material was found in later field studies (Dr H. J. Campbell, IGNS, pers. comm.).

A number of specimens from the Kulnura marine tongue, Tomago Coal Measures, New South Wales, were assigned by Dickins (1989) to *Echinalosia cf minima* "Dear" - meaning Maxwell as designated by Waterhouse & Vella (1965) who were first to review the standing of *minima*. The Kulnura shells were said to differ from the *ovalis* shells by lacking a ventral muscle platform. This statement is not supported by the figures, because that of pl. 3, fig. 2, assigned to *cf minima*, clearly shows a ventral adductor platform, and this has been verified by first hand inspection, courtesy of Dr Clinton Foster, AGSO, Canberra. Moreover the small specimens have been figured at incorrect scales, those of Dickins (1989, pl. 3, fig. 2, 11) being larger than indicated by 20-30%. They may not be same species as the large *Pseudostrophalosia* shells (fig. 10, 12-21). The specimen of Dickins (1989, pl. 3, fig. 1) has long hollow spine bases as in *Pseudostrophalosia clarkei*, but the presence of costellae suggests a closer relationship to *Terrakea*. It is shown at about 1.5 natural size, not x2 as in the figure caption.

GENERIC RELATIONSHIPS: The taxon *minima* was regarded as related to *clarkei* (Etheridge) by Maxwell (1954) and assigned to *Wyndhamia* in initial studies by Briggs (1987), but Waterhouse (1964b) and Dear

(1971), followed eventually by Briggs (1998), treated the form as a ally of *Echinalosia maxwelli*. Re-appraisal of the topotype material indicates that the species shows many attributes of *Marginalosia*, including the comparatively uniform and mostly erect ventral spines, strong inner posterior lateral marginal ridge, moderately developed dorsal marginal ridge, and a degree of dorsal thickening anteriorly. These features are more strongly developed in younger species of *Marginalosia*, including the type from the Himalaya, and also *M. planata* (Waterhouse) from New Zealand.

TAXONOMY: Dear (1971) used the varietal name *minima* of Maxwell for the same specimens figured and named by Maxwell (1954), and this was applied to a full species, which he ascribed to himself. This was followed by Hill et al (1972) and Dickins (1989, p. 75). However Waterhouse & Vella (1965, p. 62) were first to elevate *minima* to full species rank, and related *minima* to *maxwelli* and *ovalis*, in a lineage later called *Echinalosia*. They ascribed the species *minima* to Maxwell, and this authorship should stand, insofar as Waterhouse & Vella may be regarded as first principal revisers. This treatment is confirmed by the International Commission for Zoological Nomenclature (2000), which stated that varieties named before 1960 may be treated as of specific rank, with the name attributed to the original author.

Briggs (1998, 101) presented a very inadequate summary of the taxonomy, failing to refer to the first demonstration that *minima* was to be ranked as a full species, and criticizing Dear (1971) for not following the 1985 ICZN ruling (Article 45g) that varieties may be regarded as of subspecific rank - the same unjustified criticisms were levelled at other workers as well. The 1985 rulings were made as revisions to earlier dicta (Stoll et al 1961) which implied that varieties were open to revision by later workers, and need not be deemed to have formal taxonomic standing. This was interpreted by various authorities, such as Prof. D. Hill and Sir Charles Fleming, as implying that varieties were available for renaming at full specific rank. Dear, in the late 1960's and early 1970's when he made his studies, followed the then prevailing procedures, as carefully monitored by Professor Dorothy Hill. Briggs seemed to have expected Dear to somehow anticipate the procedural change - and similarly misrepresented other workers, who had also observed the current ICZN rules, until the ICZN changed the rules. In addition, allowance must be made for the time that elapses between submission of an manuscript and final appearance of the published work.

***Marginalosia?* sp.**

Pl. 5, fig. 1 - 3, text-fig. 5f

DIAGNOSIS: Shells with comparatively gently concave dorsal disc, strongly geniculate trail, thick body cavity.

MATERIAL: Five ventral valves and 5 dorsal valves (BR 2382, 2386, 2387) as well as two broken specimens (BR 2388) with valves conjoined from D45/f7578, *Spinomartinia spinosa* Zone, Hilton limestone, Wether Hill Station. Poorly preserved specimens from Coral Bluff possibly are conspecific, but no completely convincing material is available amongst the 5 ventral valves and 2 dorsal valves, with other fragments, from D44/f376.

DIMENSIONS IN MM: From D45/f7578.

Specimen	BR	Width	Length	Height
dorsal	2386	28	20.5	8.5
dorsal	2382	32.5	26	9
ventral	2388	36	30	17

DESCRIPTION: Wether Hill material variably preserved, and does not show ornament well, or much of internal morphology. Ventral valve transverse and convex, umbo broad without cicatrix. Dorsal valve transverse and gently concave over visceral disc, with convex nepionic part almost 5mm wide and 2.5mm long in one specimen, trail geniculate. Cardinal extremities in dorsal valve usually bluntly obtuse at angle close to 100°, or with tiny ears, and ventral valve has small ears. Hinge long and straight, but cardinal areas not exposed. Ventral sulcus absent or variably represented by very shallow mid-length or anterior depression. Very low dorsal fold commences about mid-length, narrows over trail. Ventral ornament of fine spines arranged in quincunx, rows about 1.5mm apart with up to 2.5 to 3mm between spines posteriorly, and maintain similar pattern anteriorly, or may become slightly more closely spaced. Some spines adpressed against the shell: preservation imperfect, but it appears all visible spines are of one diameter, close to 0.4mm. Low growth rugae 1 to 1.5mm apart cover valves. Dorsal exterior poorly preserved, but one partly buried specimen suggests moderately large erect spines apparently up to 0.5mm in diameter, perhaps 2mm apart in quincunx, though poorly exposed, and growth wrinkles 1-1.5mm apart anteriorly, as well as finer increments, and moderately large pits with complex shell structure. Another specimen suggests fine radial capillae, 3-5 in 1mm, increasing by intercalation, unless due to fibrous shell structure.

Little of the interior is visible, but ventral adductors appear to be elongate and not markedly if at all dendritic, adductor platform not very high. Small pits cover the floor, and a low marginal ridge appears anteriorly around the trail.

The dorsal interior is also obscure. The cardinal process is largely broken, and little is left of the socket ridges. The medium septum appears to be less than half the length of the valve. The anterior visceral disc

carries fine slightly elongate aligned pits, about 3 in 1 mm, and low growth increments, 5 in 1 mm. The start of the trail is marked by strong thickening and the trail is thickened to 2.3 mm from shell 0.8 mm thick posteriorly in a specimen about 30 mm long. The ventral valve is 1.7 mm thick posteriorly and 0.8 mm thick anteriorly in the same specimen.

RESEMBLANCES: Ornament is too obscure to allow full identification, but the material apparently belongs to *Marginalosia*. The type species *Marginalosia kalikotei* (Waterhouse, 1975, pl. 1, fig. 4-7; 1978, pl. 7, fig. 21-26, pl. 8, fig. 1-15, pl. 9, fig. 13) is moderately close with comparable ornament, including dorsal pits, signs of capillae, and thickened dorsal valve, but the dorsal valve is more concave, and the trail, although geniculate, is longer and inclined at a lower angle from the visceral disc. The species comes principally from the Nisal Member and ranges as high as the Luri Member (Waterhouse 1978, pl. 10, fig. 2) of the Senja Formation in west Dolpo, Nepal Himalaya. It is also possibly present in east Dolpo (Waterhouse 1966a, pl. 3, fig. 5).

The New Zealand species *Marginalosia planata* (Waterhouse 1964b, pl. 7, fig. 4-11, pl. 8, fig. 1, 2) from the Pig Valley Formation, Te Mokai Group, east Nelson, is close in shape and has more lamellose dorsal valve, with concave disc and less conspicuously geniculate trail, although coming close. Some Nelson specimens have a shorter hinge, higher ventral interarea, and more oval outline than in the Wether Hill material, but others are comparable.

BIOSTRATIGRAPHY: H. J. Campbell et al (1995) claimed, without providing any proof, that the Permian fauna in the east Nelson carbonates with *Marginalosia planata* were older than the *Martiniopsis woodi*, *Plekonella multicostata* and *Spinomartinia spinosa* Zones of the local New Zealand Puruhuan Stage. But typical *Marginalosia* appears to be restricted to Late Permian faunas in Nepal, Australia and Taimyr Peninsula, and the age of *planata* is likely to be Late Permian as well, as reinforced by *Nakimusiella* (Waterhouse 1999b) and other fossils. The allied, but rather distinctive species *minima* is somewhat older, coming from the *Terrakea elongata* Zone, below the *Plekonella multicostata* Zone. The summary of New Zealand Permian biozones by H. J. Campbell (1999) abandoned without comment the Campbell et al (1995) proposals, to accept the late Permian correlation for the *Marginalosia planata* Zone, as post-dating the *Spinomartinia spinosa* Zone.

Genus *Wyndhamia* Booker, 1929

TYPE SPECIES: *Strophalosia (Wyndhamia) dalwoodensis* Booker, 1929, junior subjective synonym of *Productus (Branxtonia) typica* Booker, 1929.

DIAGNOSIS: Large concavo- or plano-convex Strophalosiidae with small ventral cicatrix, ventral spines in recumbent to inclined series predominant over disc, with rare to very rare more slender generally prostrate spines, ear spines rare to absent. Dorsal valve weakly concave to almost flat, developing several anterior trails that are melded into a massive wedge, sparse suberect spines. Teeth strong, may have bulbous callosities at maturity, ventral adductors long, dorsal valve strongly thickened anteriorly, sharply geniculate, raised anterior ridge.

DISCUSSION: Although proposed so long ago, and used frequently in Australian studies on Permian strophalosiids, understanding of this genus has remained clouded until substantially clarified through the studies by Briggs (1998). Briggs argued that the generic characteristics centred principally on the essential absence of spines ("largely absent") from the ears, and the presence of a single recumbent series over the ventral disc. No ornament for the lateral margins of the ventral valve was mentioned.

However the only figure provided by Briggs (1998, text-fig. 64A) for the ventral exterior shows a very few spines on the ventral ears, and a very few prostrate and subprostrate spines, and even an erect one that is only half the diameter of most ventral spines. He thus partly misdiagnosed the genus, but came closer than any previous worker in revealing its significant discriminants. The specimen figured as *Wyndhamia valida* Booker (1929, pl. 2, fig. 1-3) shows very fine as well as thicker erect spines near the middle of the ventral valve.

Several specimens of *Wyndhamia typica* are kept at the University of New England, from UNEL 1171 in the Elderslie Formation of the Lochinvar Anticline, north Sydney Basin. UNEF 14292 shows some semiprostrate spines on the ventral exterior both laterally and posteriorly. Some ventral valves lack ear spines, others have a few, including ventral valves of *typica* on a large slab from UNEL 928, Snapper Point Formation, south Sydney Basin.

The only other species that was considered by Briggs (1998) to belong to *Wyndhamia* was the Tasmanian species *jukesii* Etheridge. Despite Briggs' presentation, fine prostrate spines are present rarely on the ventral valve of *jukesii*, as well as thicker spines, as figured for Berriedale specimens by Clarke (1969, pl. 8, fig. 1, 3). This strongly indicates that *Wyndhamia* is characterized partly by a paucity, but not absence of ear spines, and a paucity, but not absence of fine as well as thick ventral spines. In his diagnosis for *Wyndhamia*, Briggs drafted too rigid a definition, and ignored what specimens displayed. The anterior internal marginal ridge of the dorsal valve in *Wyndhamia typica* and *W. jukesii* carries large pustules, but again Briggs (1998) stated this was invariable, whereas in fact specimens can be found with no pustules. From the Elderslie Formation, UNEF 14296 is a well preserved dorsal valve that has no large pustules on the dorsal anterior marginal ridge, and the same is true of F 14301. In addition, the dorsal exterior tends to be dimpled, and the

inner ventral valve, especially of *typica*, is pocked by pits, and occasional ridges. All three of these criteria are of uncertain significance.

***Wyndhamia* ? sp.**

1964b ?*Wyndhamia* sp. aff *jukesii* (not Etheridge); Waterhouse, p. 48, text-fig. 16, 17.

1982a ?*Wyndhamia jukesii* (not Etheridge); Waterhouse, p. 39, pl. 7, fig. g, i, k.

DIAGNOSIS: Small shells with gently convex ventral valves, low posterior walls, ventral spines few and suberect, rarely prostrate and slender, absent postero-laterally and from ears, ventral adductor platform small, low and broad. Dorsal valve with flat disc, ornamented by scattered erect spines and heavy concentric ornament with pits.

DESCRIPTION: Material was described by Waterhouse (1964b, 1982a) and suffices to indicate a possibly new species, left unnamed until the nature of ventral spinosity can be verified. The ventral valve is distorted or irregular or assymmetric, and the hinge may vary in length each side of the umbo. The ventral spines are so far known to be well spaced, mostly thin and erect, none present postero-laterally, very seldom thin and prostrate. Dental callosities not developed. The exterior of the dorsal valve is almost flat, but wedge-like thickening is not substantial. Dorsal spines are moderately thick, erect, close-spaced anteriorly, and absent posteriorly, probably removed by wear. Capillae are lacking. The dorsal interior has a thick anterior internal ridge (Waterhouse 1982a, pl. 7, fig. k - not j as in caption), but the papillae are not very large.

RESEMBLANCES: These specimens are distinctive. Unlike *Wyndhamia jukesii* (Etheridge, 1880) from Tasmania, they have only low ventral posterior walls and less tangled thinner and erect ventral spines, with almost none found to be prostrate. Although Briggs (1998) assigned *jukesii* to *Wyndhamia* partly on the basis of the alleged absence of ventral prostrate spines, such are clearly shown to be present on probable topotype *jukesii* by Clarke (1969, pl. 8, fig. 1, 3). *Wyndhamia typica* is readily distinguished by its larger size, more vaulted ventral valve, coarser ventral spines with some prostrate, and a very few ear spines.

Aspects of the scattered ventral spines and irregular shape recall features of *Echinalosia mcclungi* Briggs (1998) from the Pebbly Beach Formation of the south Sydney Basin. This is an unusual species for *Echinalosia*, as allowed by Briggs (1998), with posteriorly directed ventral umbo, high reclined ventral interarea, and slightly thickened dorsal valve. Unlike the Takitimu form, prostrate ventral spines, dental callosities and large postero-lateral ventral spines are developed on *mcclungi*, with elongate ventral adductors. Some aspects suggest an approach to *Acanthalosia*, but the dorsal spine pattern was not clearly illustrated and requires clarification. Dorsal spines on the New Zealand form are large and erect.

Acanthalosia? ardua (Waterhouse) from the underlying Brunel Formation is readily distinguished by its more transverse shape, with ventral sulcus, and different ventral spines and presence of capillae, although the dorsal exterior shows some approach in being dimpled: it also has scattered erect and some prostrate spines. The dorsal valve of *Echinalosia conata* Waterhouse from the McLean Peaks Formation is deeply concave with concentric laminae and spines are more numerous. The shells are more transverse and arched with large long ventral adductor platform.

DISTRIBUTION: Early collections of this species were found in a cluster in what H. J. Campbell in Campbell et al (1990, text-fig. 6) later mapped as upper Brunel Formation, although the rocks to me differ from typical Brunel beds, and the youngest station occurs towards the top of the overlying Chimney Peaks Formation.

***Wyndhamia typica typica* (Booker, 1929)**

1877 *Productus clarkei* not Etheridge Snr; de Koninck, p. 203, pl. 11, fig. 11? (not pl. 19, fig. 5 = *Pseudostrophalosia clarkei* (Etheridge)).

1880 *Strophalosia clarkei* (not Etheridge Snr); Etheridge, p. 27, pl. 9, fig. 21, pl. 10, fig. 22 (not pl. 9, fig. 18, 19, 20, pl. 10, fig. 23-25, pl. 12, fig. 23 = *Ps. clarkei*).

1929 *Strophalosia (Wyndhamia) dalwoodensis* Booker, p. 25, pl. 1, fig. 1-5, pl. 3, fig. 5, 7.

1929 *S. (Wyndhamia) valida* Booker, p. 26, pl. 2, fig. 1-5, pl. 3, fig. 4, 6.

1929 *Productus (Branxtonia) typica* Booker, p. 30, pl. 3, fig. 1-3.

1950 *Strophalosia clarkei* (not Etheridge Snr); David, pl. 34b.

1954 *Strophalosia typica* (Booker); Maxwell, p. 545, pl. 55, fig. 8-14.

1957 *S. clarkei* (not Etheridge Snr); Coleman, pl. 18, fig. 1, 2.

1960 *Wyndhamia dalwoodensis* Booker; Muir-Wood & Cooper, p. 89, pl. 5, fig. 11-13. Plate explanation states "*Branxtonia typica* Booker = *Wyndhamia typica* Booker. (Not pl. 5, fig. 7, 9, 10 = *W. clarkeina* Waterhouse).

1960 *Wyndhamia valida* Booker; Muir-Wood & Cooper, p. 90.

1965 *W. dalwoodensis* Booker; Muir-Wood, p. 452 (not fig. 307.3a-c = *W. clarkeina*).

1969 *W. dalwoodensis* Booker; Clarke, p. 43, pl. 8, fig. 4 (not pl. 8, fig. 5 = *W. jukesii* (Etheridge)).

1998 *Wyndhamia typica* (Booker); Briggs, p. 125, text-fig. 64.

1998 *Pseudostrophalosia clarkei* (not Etheridge); Briggs, p. 118 (part).

2000 *Wyndhamia dalwoodensis* Booker; Brunton, Lazarev, Grant & Jin (not text-fig. 405.3a-c = *W. clarkeina*)

LECTOTYPES: AMF 41763, *typica*, from Elderslie Formation, north Sydney Basin, New South Wales, figured by Booker (1929, pl. 3, fig. 1-3), Maxwell (1954, pl. 55, fig. 9, 10 - not 11, 12 as in caption) and Muir-Wood & Cooper (1960, pl. 5, fig. 11-13) SD Maxwell (1954, p. 545), as in Briggs (1998, p. 126). For *dalwoodensis*, AM specimen figured from same locality by Booker (1929, pl. 1, fig. 2) SD Waterhouse (1964b, p. 50). For *valida*, figured type material supposedly missing according to Fletcher (1971, p. 57), but this seems unlikely as I saw the material (see Waterhouse (1964b, p. 51). Specimen figured by Booker (1929, pl. 2, fig. 1-3), here selected.

DISCUSSION: There has been a confusing decoupling of generic and species names, involving *Strophalosia* (*Wyndhamia*) *dalwoodensis* Booker, 1929, and *Productus* (*Branxtonia*) *typica* Booker from Branxton, north Sydney Basin, thanks to poorly co-ordinated studies by Maxwell (1954) and Muir-Wood & Cooper (1960), as interpreted by Briggs (1998, p. 123). His work was not assessed by Brunton, Lazarev, Grant & Jin (2000), probably because their work was in press at the time. The specimens were stated to be 2250ft below the Muree beds, and judged to be from the basal Branxton or Elderslie Formation by Maxwell (1954, p. 545), presumably from Australian Museum records, which were not published by Booker (1929). Briggs (1998) found further specimens by following a map provided by Raggatt & Booker (1929, pl. 6). The specimens ascribed to *dalwoodensis* have a comparatively wide hinge, and a moderately well developed anterior ventral sulcus. The internal moulds indicate strong dimples (as elevations) for the exterior, but none show the external ornament. According to Waterhouse (1964b, p. 51), dental callosities were not developed. However Briggs (1998, p. 126), although mentioning no callosities in his description of *typica*, considered that the lack of plate-like callosities from a New Zealand specimen indicated a difference from *typica*, and callosities are figured for a Capertree specimen by Briggs (1998, text-fig. 64H). *W. valida* from the same beds is better preserved, and appears to have been comparable in shape, with wide hinge and slightly less developed ventral sulcus. The spines are coarse and well spaced on the ventral valve, and even posteriorly are about 2mm apart. *Branxtonia typica* Booker, also from the same beds, is based on an internal mould with hinge lost, showing coarse spine bases and ventral sulcus. This is the species that has "naming rights", because Maxwell (1954) synonymized *dalwoodensis* and *valida* with *typica*, and Muir-Wood & Cooper (1960) synonymized *Branxtonia* with *Wyndhamia*. Logically, they may not have been free to do so: arguably the designation of *typica* as type may have carried with it the mandatory and consequent synonymizing of *Wyndhamia* with *Branxtonia*. The discussion by Muir-Wood & Cooper (1960, pp. 89, 90) was inadequate in this regard. They chose *Wyndhamia* over *Branxtonia* as name bearer without giving reasons, and ignored the previous designation of *typica* as type species by Maxwell (1956). They recognized *dalwoodensis* and *valida* as species, but not *typica*, which was regarded, against ICZN rules, as a synonym of *dalwoodensis*. Briggs (1998) failed to address this oversight, and the problem was perpetuated by the revised brachiopod treatise, which regarded *typica* as a synonym of *dalwoodensis*, and treated *valida* as a separate species.

Muir-Wood & Cooper (1960, pl. 5, fig. 7, 9,10) assigned specimens from the Permian of Tasmania to *dalwoodensis*, but gave no details on stratigraphy or location. The specimens are distinguished by the high number of prostrate fine spines on the ventral valves, but otherwise look close to *Wyndhamia typica*. They are here named as a separate species. Muir-Wood & Cooper (1960, pl. 5, fig. 11-13) also refigured the type specimen of *Branxtonia typica* Booker, and Maxwell (1954, pl. 55, fig. 8-14) also refigured this (fig. 9, 10, not 11, 12 as in caption) and other specimens like *typica*.

***Wyndhamia typica crassispina* n. subsp.**

Pl. 5, fig. 12 - 16, 17?

1964b *Wyndhamia dalwoodensis* Booker; Waterhouse, p. 50, pl. 8, fig. 3, 4.

1998 *Pseudostrophalosia clarkei* (not Etheridge Snr); Briggs, p. 116, text-fig. 29 (part, text-fig 61 = *clarkei*).

DERIVATION: *crassa* - thick, *spina* - thorn, spine, Lat.

HOLOTYPE: UQF 65481, figured in pl. 5, fig. 14 -16, from UQL 3759, Freitag Formation, southwest Bowen Basin, Queensland, 60km south of Springsure, here designated.

DIAGNOSIS: Large shells with convex ventral valve and very gently concave dorsal valve, thickened anteriorly into wedge. Ventral spines fine and close-set to width of 20-25mm, then becoming large in patches, sometimes mid-valve or around periphery and especially posterior periphery, moderately close-set around periphery.

MATERIAL: One specimen with valves conjoined, 3 internal moulds and 2 external moulds of ventral valves, one dorsal external mould of doubtful relationship from UQL 3759, Freitag Formation.

DIMENSIONS IN MM: Ventral valves from UQL 3759

UQF	Width	Length	Height
65426	37	40	12
65481	48	45	19

DESCRIPTION: Shells large, moderately inflated, width and length of comparable dimensions, maximum width lies near mid-length, hinge with low ventral interarea, small moderately defined lateral ears and obtuse cardinal extremities, one specimen lacks ears. Venter either convex or flattened, and very weakly or indefinitely sulcate. Dorsal valve gently concave, interarea not preserved. Ventral ornament of fine close-set spines 0.4mm diameter over first formed shell up to width of about 15-25 mm, then becoming larger, most spines subuniform in diameter, 0.6-1mm in diameter, rarely over 1mm, 1.5 to 2mm apart along rows 2-3mm, rarely 5mm apart anteriorly, somewhat irregular, mostly suberect; may revert to finer in front or in patches, a very few spines fine or prostrate on some specimens, spines worn from posterior shell; spines variably rare, or moderately strong, erect, in 2-3 rows over the posterior slope in front of small ears; ears themselves have few or no spines, judged from well preserved external moulds; growth wrinkles prominent anteriorly. There is no cluster of posterior lateral ventral spines but sparse strong spines are scattered posteriorly in a pattern that varies in each specimen.

A gently concave and non-geniculate dorsal valve shows spines fine up to 0.4mm in diameter posteriorly and close-set along concentric rows, with band of stronger spines around periphery in 3-4 rows and 0.5-0.6mm in diameter, lamellae also conspicuous. But I feel cautious over the identity, even though the specimen is given a Freitag locality, and note a strong approach to *Echinalosia floodi* n. sp. (pl. 5, fig. 17).

Ventral teeth very close-set and large, with no lateral buttress or callosity, muscle adductor platform posteriorly placed, high, long, comparatively smooth with myophragm, diductor impressions very large and broad, striated. Low and broad marginal ridge lies across ears. Anterior floor on F 65481 carries several impressions of prostrate spines or ridges not visible externally, and also pits internally opposed to large erect external spines. Dorsal valve (definitely *Wyndhamia*) has broad short cardinal process in plane of disc, and dental sockets. Medium septum extends almost to anterior third of length, dividing large anterior and posterior elements of adductor scars. Brachial ridges obscure. Crest of anterior marginal ridge not preserved.

RESEMBLANCES: Booker's species *typica* looks close to the Freitag form. The ears are slightly more prominent and have fewer spines, the shape slightly more transverse and less inflated, the hinge wider, the sulcus slightly deeper. These differences are not profound, and some degree of variation was indicated amongst the *dalwoodensis* suite by Waterhouse (1964b, p. 51), and *typica* material at the University of New England shows more variation. The figure of the ventral exterior by Briggs (1998, text-fig. 64A) indicates mostly uniform subprostrate spines, and apart from a very few thin prostrate spines, there are a very few sturdier erect spines around the periphery, on one ear, and on the flanks. UNE material from L1171 show more thin prostrate spines (eg F 14292) and rarely, a few ear spines. In the Freitag suite, posterior body spines are finer, and slightly closer together, and there are few prostrate spines, and relatively sturdy peripheral spines, arranged in concentric rows anteriorly, and few ear spines. Thus overall the spinose ornament is close but not identical on the Sydney and Bowen Basin forms, but the difference is neither great nor consistent. The external dorsal mould from the Freitag Formation, to which some doubt is attached over specific and generic relationships, lacks external pits, but shows similar concentric lamellae and slightly more prominent, more numerous dorsal spines. The similarities in ventral spinosity, including few prostrate ventral spines and few ear spines, are taken to indicate specific similarity, and the slight difference in size of lateral spines is interpreted as indicating subspecific difference. The ventral muscle scars and long dorsal septum and massive cardinal process are shared, together with moderately long hinge and shell shape, but the Queensland specimens are more vaulted, and ventral ears are smaller, and dental callosities are missing from the Queensland material. The nature of the dorsal marginal ridge, which is strongly papillate in some but not all *typica*, is not preserved for the Queensland species. The difference between the various suites is not great.

The New Zealand specimen BR 776 from GS 6070 (D44/f9621), lower Letham Formation, that was identified with *Wyndhamia dalwoodensis* (now *typica*) by Waterhouse (1964b) shows two critical attributes of the Freitag form, in having a hinge somewhat shorter than in *Wyndhamia typica*, and in the arrangement of the ventral spines as far as they can be determined, which are fine and close-set posteriorly, and variable in diameter, including large spines anteriorly. There is no lateral cluster of ventral spines, and one or two large erect spines lie near or on the ears. A very few of the thick spines are subprostrate and there are no elongate slender prostrate spines. The New Zealand form is weakly sulcate anteriorly, more like some but not all *typica*. It also shows the heavy posterior ventral marginal ridge seen in *typica*, but lacks the internal dimpling and has no large dental callosities. Overall, it is close to *crassispina*, and may be regarded as belonging to that taxon. Briggs (1998, p. 126) could not match the material with any east Australian species.

STROPHALOSIIDS IN THE FREITAG AND ALDEBARAN FORMATIONS: The present species is probably the same as that identified with *Pseudostrophalosia clarkei* (Etheridge) by Briggs (1998, text-fig. 29, p. 46, p. 118) from what was recorded as beds close to Freitag Formation in GSQ cores in the Denison Trough of the Bowen Basin. None of the core material was figured or described by Briggs, and so his report is of low value, being uncheckable, even though the identification was critical for his overall revolutionary correlation scheme. Dr S. M. Parfrey, Department of Mines and Energy, Queensland, has written that the core material mentioned by Briggs is all poorly preserved, fragmentary, and in no way segregated or labelled (in litt., 6 July, 1999). Therefore with Dr Parfrey's help, the core material was re-examined and checked against the Briggs identifications at the core shed in Zillmere, Brisbane.

I. Eddystone 1 at GSQL 2115, in undifferentiated Permian below Ingelara Formation and above GSQL 2114 with *Glendella dickinsi*.

Two poorly preserved dorsal valves are weakly concave, one not strongly thickened, with posterior marginal ridge, but not specifically identifiable. A conjoined specimen, ventral valve arched, some prostrate spines up to 0.8mm in diameter and other erect spines 1mm in diameter, closely spaced even anteriorly. The dorsal valve is concave with fine dense erect spines and the valve is not thickened, or flat internally or externally. Two other specimens have moderately thick disc and close-spaced spines.

These specimens cannot be securely identified. They apparently include *Wyndhamia* rather than *Pseudostrophalosia*, and *Echinalosia* akin to *floodi* n. sp. The available material does not confirm the identifications by Briggs (1998) with *clarkei* and that identification must be set aside.

2. GSQ Emerald NS 9R, Aldebaran Sandstone correlative, below Freitag Formation, GSQ 2578-86. *Pseudostrophalosia clarkei* was reported from these localities. None of these specimens are now present in the collections, and they have, at best, been misplaced, and could not be found at the GSQ collections. This report therefore cannot be checked, was possibly erroneous, and must be set aside.

3. Planet Warrinilla North 1, GSQ 481 in Aldebaran Sandstone below Ingelara and possibly Freitag or equivalent.

Specimen GSQF 7778 is present with thickened probably wedge-shaped dorsal valve and gently convex ventral valve with apparent sulcus and long ventral muscle field suggestive of *Wyndhamia typica crassispina*, although preservation of ornament is poor. Three internal moulds are poorly preserved, but allied. There is also a fragmentary ventral valve showing anterior close-spaced suberect spines. Briggs (1998) recorded the species as *Echinalosia hanloni*, which may be discounted.

4. AAO Glentulloch 1, upper Aldebaran Sandstone, GSQ 239.

Some 8 specimens have gently convex ventral valve with erect or suberect spines 0.6-0.9mm in diameter, closely set along well spaced rows, or less regular. Dorsal valves apparently wedge-shaped and moderately concave externally. Most specimens show no prostrate spines, but external ornament is not well preserved, and such spines are possibly present on one ventral valve fragment. One specimen shows a visceral disc that is 11mm thick. These specimens were presumably identified as *Pseudostrophalosia clarkei* by Briggs (1998), but are not typical of that species, and strongly approach *Wyndhamia typica crassispina*.

Other specimens may belong, as in Briggs (1998), to *Echinalosia* sp. indet., possibly allied to *E. floodi* n. sp. They have a thick visceral disc and high ventral muscle platform (GSQF3699, 3585, 3588, 3587) and the dorsal valve is weakly concave with low fold (GSQF3587). Spines are dense and fine along the hinge. The specimens have been labelled as *Echinalosia ovalis*, but this is not correct.

The present material from the Freitag Formation provides much more reliable and verifiable information on the nature of Freitag strophalosiids. Compared with *clarkei*, the present material is somewhat similar in shape and profile, but is substantially larger, a criterion deemed very important to Briggs (1998), with, most critically, more coarse spines anteriorly and postero-laterally on the ventral valve, distinctly fewer ventral ear spines, and coarser dorsal spines (0.5mm diameter) compared with those of *clarkei* (0.1-0.15mm diameter), using the *clarkei* measurements provided by Briggs (1998). In the Freitag material, prostrate spines are very few, whereas in *clarkei* prostrate spines are numerous. Further differences could be enumerated between the Freitag internal details and those conveyed by Briggs (1998) for *clarkei*, but *clarkei* is rather more variable than allowed by Briggs, to judge from better material, and I discount aspects of his emphasis on shallow long adductors and other attributes.

There is a closer approach to *Pseudostrophalosia crassa* Briggs, 1998 in the coarseness of lateral and anterior spines, but as Briggs (1998, text-fig. 29, p. 46) indicated, *crassa* occurred much higher in the same core at GSQ 2117. In my opinion the division between *crassa* and *clarkei* is a delicate one, and there may be gradation between the two, and this is illustrated by his figure of *clarkei* "with exceptionally coarse spines" (Briggs 1998, text-fig. 61D) that is identical with *crassa*. Briggs (1998) in his specific diagnosis (he provided no description) of *clarkei* avoided mention of ear spines, and none of his figures reveal the ventral ears clearly. Nonetheless by classing *clarkei* in *Pseudostrophalosia*, he implied that ventral ear spines are numerous. In topotype *crassa*, ventral ear spines are crowded. Even allowing for a variable *clarkei*-*crassa* flux, the new species differs in size, somewhat sulcate ventral valve, and the arrangement and numerical proportions of fine and coarse ventral spines, and few ear spines.

The new subspecies is moderately close in shape and size to *Pseudostrophalosia brittoni* (Maxwell, 1954, Clarke 1970, Waterhouse, Briggs & Parfrey 1983, Waterhouse 1986b) from the Tiverton and possibly Rose's Pride Formation of the Bowen Basin. Spines are moderately fine posteriorly on the ventral valve and coarse anteriorly. Specimens of *brittoni* are often ventrally sulcate, and internally, dental callosities are large and the ventral adductor platform very high. There are large ear spines, a brush of posterior-lateral spines and fine prostrate spines on the ventral valve. The dorsal valve is more concave and less thickened.

Pseudostrophalosia blakei (Dear, 1971) from the lower Blenheim Formation of north Bowen Basin is smaller, and has more fine spines of uniform diameter over the ventral valve. It is known from a large range of specimens that variably include forms with narrow and wide hinges, sulcate and convex ventral valves, and posteriorly, many ventral spines are prostrate.

STRATIGRAPHIC DISTRIBUTION: The species *Wyndhamia typica* (Booker) is found in the Elderslie and Snapper Point Formations of the Sydney Basin, Briggs (1998, p. 125) put in synonymy a specimen figured as a dorsal interior of *clarkei* by Etheridge (1892, pl. 13, fig. 15) as coming from "the Bowen River Coal Field." Although not explained by Briggs (1998), the specimen was probably included as *Wyndhamia* because it has a thick marginal ridge shown as dimpled over the surface. It seems likely that it really is *clarkei*, and that the

dimpling is less diagnostic than supposed by Briggs. *W. typica crassispina* is found in the upper Aldebaran and Freitag Formations of the southwest Bowen Basin and lower Letham Formation of New Zealand, and is very closely related to *typica*. The Freitag and lower Letham faunas share critical species of *Aperispirifer* and *Tomiopsis* with the Elderslie and Snapper Point Formations, and are deemed correlative. This in turn, given the variability displayed by individuals assigned to Elderslie specimens of *typica*, suggest variability in a widespread species.

***Wyndhamia clarkeina* n. sp.**

- 1960 *Wyndhamia dalwoodensis* not Booker; Muir-Wood & Cooper, p. 90, pl. 5, fig. 7, 9, 10.
 1965 *W. dalwoodensis* not Booker; Muir-Wood, p. 452, text-fig. 307. 3a-c.
 1969 *Wyndhamia dalwoodensis* not Booker; Clarke, p. 43, pl. 8, fig. 4 (not 5 = *W. jukesii* (Etheridge)).
 1998 *W. jukesii* (not Etheridge); Briggs, p. 126 (part).
 2000 *W. dalwoodensis* not Booker; Brunton, Lazarev, Grant & Jin, p. 574, text-fig. 405. 3a-c.

DERIVATION: Named for Michael J. Clarke.

HOLOTYPE: USNM 112138d, figured by Muir-Wood & Cooper (1960, pl. 5, fig. 10), Muir-Wood (1965, text-fig. 307. 3a) and Brunton et al (2000, text-fig. 405. 3a) from Collinsville Road Quarry near Granton, Hobart, Tasmania, here designated.

DIAGNOSIS: Shells with a number of fine prostrate spines as well as sturdy spines over anterior ventral valve. Dorsal anterior marginal ridge not strongly dimpled in available material. Otherwise close to *Wyndhamia typica*.

DESCRIPTION: Large *Wyndhamia* close to type species *W. typica* in shape with wide hinge and fewer dimples on dorsal valve, few ventral ear spines, distinguished by possessing slender prostrate spines over ventral anterior. Spines may be rare on dorsal valve.

A ventral valve figured as *dalwoodensis* by Clarke (1969) is included as *clarkeina*, although the exterior ornament is not certain. The locality was given as a correlate of Malbina A at Arcadian siding in the Maydena area (see Waterhouse 1970a) and uppermost Cascades Group, that is Grange Mudstone (Clarke 1969, p. 49).

DISCUSSION: This species has served as "typical *Wyndhamia*", allegedly belonging to *dalwoodensis* (sic = *typica*) for brachiopod treatise studies, but is unusual for *Wyndhamia*, and differs from *dalwoodensis* or *typica* in possessing a number of slender prostrate spines anteriorly on the ventral valve. Otherwise the species is shaped much like *typica*, and lacks ear spines, as far as can be seen. The difference could qualify the taxon for being a subspecies of *typica*, but the spine pattern differs significantly from other species so far described for *Wyndhamia*.

Material is not scarce in Tasmania. Clarke (1969) reported the species as *dalwoodensis* from a Malbina A correlate at Maydena siding, Tasmania, and Waterhouse (1970a, p. 388) reported the species at the same general level at Malbina A, B, and underlying Grange Mudstone.

Genus *Pseudostrophalosia* Clarke, 1970

TYPE SPECIES: *Strophalosia brittoni* Maxwell, 1954.

DIAGNOSIS: Ventral valve with closely spaced fine and coarse often recumbent and also erect spines, including erect cluster over postero-lateral slopes entering on to ears, dorsal valve gently concave and usually wedge-shaped and thick anteriorly, with fine mostly erect spines, dorsal marginal ridge smooth or finely pustulose.

DISCUSSION: This genus was proposed by Clarke (1970) for a single specimen named *Strophalosia brittoni* Maxwell, 1954, supposedly distinguished by its dendritic posterior adductor impressions. Only one internal mould of a ventral valve was known to Clarke, and the ventral exterior, and dorsal exterior and interior not known. Another slightly crushed specimen with dendritic posterior adductor impressions, otherwise undescribed, was reported by Clarke (1970) from the Berriedale Limestone in Tasmania, and less specific reference to this material was offered by Clarke (1969, p. 48). This lack of description naturally made the genus very difficult for other authors to circumscribe, especially because no one else has ever agreed with Clarke's focus on dendritic adductor muscle scars. Archbold (1987, p. 20), Waterhouse (1982a, p. 39) and Brunton, Lazarev, Grant & Jin (2000, p. 574) suggested that *Pseudostrophalosia* was a synonym of *Wyndhamia*, and Waterhouse (1982a) stressed that *Wyndhamia enorme* Clarke, 1970, based on various ventral valves associated with *brittoni*, was the same as *brittoni*.

Taking up a suggestion by Waterhouse (1986b, p. 28) that a brush of posterior lateral spines might be significant as a discriminant for *Pseudostrophalosia*, Briggs (1998) was first to firmly discriminate the genus on its spinosity and demonstrate other differences from both *Echinalosia* and *Wyndhamia*. Brunton, Lazarev,

Grant & Jin (2000, p. 574) ignored the Briggs (1998) revision, but perhaps this was because their study was already in press. Here the Briggs analysis is largely followed at generic level, although it has been found that his interpretation of various species and stratigraphic distribution cannot withstand scrutiny. Unfortunately it has not been possible to confirm the significance of the nature of the anterior marginal ridge, known to be heavily papillate in some type *Wyndhamia typica*, and faintly if at all papillate in type *Pseudostrophalosia*.

The genus *Pseudostrophalosia* is represented in Western Australia by *Wyndhamia colemani* Archbold, 1987 from the Madeline Formation, with closely-spaced ventral ear and posterior lateral slope spines. *Arcticalosia multispinifera* (Prendergast, 1943) from the Nooncanbah, Wandagee and Cundlego Formations of the Carnarvon Basin, Western Australia, looks somewhat similar but has fine ventral spines of one diameter, as in the type of the genus, *A. unispinosa* (Waterhouse, 1969) from the Canadian Arctic.

***Pseudostrophalosia?* cf *blakei* (Dear, 1971)**

Pl. 5, fig. 6 - 11

cf 1971 *Wyndhamia blakei* Dear, p. 9, pl. 2, fig. 10-11, pl. 3, fig. 1-4.

cf 1971 *W. ingelarensis* Dear, p. 12, pl. 3, fig. 5-9 (not fig. 10 = *Acanthalosia deari* (Briggs)).

cf 1983 *W. ingelarensis* Dear; Waterhouse & Jell, p. 241, pl. 1, fig. 7, 8, pl. 6, fig. 1.

cf 1998 *Pseudostrophalosia ingelarensis* (Dear); Briggs, p. 118, text-fig. 62A-C (not D-I = *P. clarkei* (Etheridge)).

HOLOTYPE: GSQF 11623, *blakei*, figured by Dear (1971, pl. 2, fig. 10) OD from lower Blenheim Formation, north Bowen Basin, Queensland. UQF 15651, *ingelarensis*, figured by Dear (1971, pl. 3, fig. 5) OD from Ingelara Formation, southwest Bowen Basin, Queensland.

DIAGNOSIS: Dorsal valve flat to moderately concave, ventral sulcus of variable strength, ventral interarea low, often narrow, ventral spines numerous, recumbent and mostly erect, of subuniform diameter, dorsal spines fine. Ventral adductor platform high, short to moderate in length, posteriorly placed.

MATERIAL: Over 10 ventral valves, 5 dorsal valves, and one specimen with valves conjoined from D44/f123 (GS 15226), including BR 2239, 2271, 2273, 2275, 2276, *Pseudostrophalosia?* cf *blakei* faunule, lower Mangarewa Formation, Wairaki Downs.

DIMENSIONS IN MM:

Specimen	Width	Length	Height	Hinge length
BR 2271	27	24+	5	14.5

DESCRIPTION: New Zealand specimens are not very well preserved, having been considerably weathered. Ventral valves convex, posterior slope high and steep, hinge of only moderate width, ventral interarea low, one specimen with broad and well defined sulcus, another medianly flattened, others convex with no sulcus. External ornament obscure, and shows close-set suberect spines and uneven pits in concentric rows, with anterior irregular rugae, and a few adpressed spines on ventral valve, most spines appearing to be of similar diameter. Posterior umbonal slopes or ears not preserved. On BR 2771 spines over the posterior disc are only 0.4mm in diameter, but reach 0.6-0.7mm in diameter anteriorly, where close-set, all erect to subprostrate and of similar diameter. Erect spines on a fragment of external mould BR 2275 are 0.6-0.7mm in diameter, some of same diameter prostrate, with a very few 0.4mm in diameter prostrate and pressed against shell exterior in front of base to leave short groove, spaced approximately 1.5 to 2.5mm apart along rows 1.5-2mm apart, low concentric growth lines, no radial capillae. Ventral adductor scars high, short and posteriorly placed.

The dorsal valves are poorly preserved, and show dental sockets, cardinal process and long median septum. Some valves are very gently concave, others more concave, especially BR 2339, leading to uncertainty whether only one species is present or two, because the amount of deformation is hard to assess. Flatter individuals bear fold anteriorly, subgeniculate, sublamellate, pitted, rugose anteriorly, and bearing very fine erect spines 0.2mm in diameter in BR 2276 and 9-11 concentric growth-lines per mm, no radial capillae. The nepionic part is flat, concave, or strongly convex. Preservation does not show if dorsal valve wedge-shaped.

RESEMBLANCES: These specimens are compared to *Pseudostrophalosia blakei* (Dear) from the Moonlight Sandstone Member, lower Blenheim Formation, north Bowen Basin on the basis of what morphology is available for comparison: there are details critical for generic placement that are missing, so identification relies chiefly on shape and nature of spines over most of the shell, but not the posterior lateral slopes. The types of *Pseudostrophalosia blakei* have been examined at the Geological Survey of Queensland at Zillmere, Brisbane. The figures in Dear (1971) suggest posterior prostrate spines on the ventral valve, but these are not so evident on the actual specimens, which are rather worn interiors. Thus the unfigured GSQF 11776 (see Dear 1971, p. 9) has rare prostrate spines, and numerous spines on the ventral ears and posterior lateral shell. Another fragment GSQF 11777 has a few grooves indicative perhaps of prostrate spines and mostly crowded uniform erect spines on the ventral valve. The overall typical shape of the ventral valves in

the Dear type collection is subtriangular with large ears, but this shape is not necessarily diagnostic, amounting to a local variant, and there are innumerable more transverse specimens in the same beds. Ventral spines are about 1.2 to 1.5mm apart and 0.6mm wide on a shell 30mm long. On other specimens spines may be 0.7mm in diameter 2.5-3mm apart along rows 1.5mm apart, subevenly spaced. There are occasional ribs. These externals do not show conspicuous prostrate spines, but show overall an ornament of mostly close-set, uniform, suberect spines. The ornament of the D44/f123 suite is close as far as can be interpreted. The ventral muscle field is moderately long (cf Dear 1971, pl. 3, fig. 2) and some ventral interiors carry ventral grooves reminiscent of *clarkei*. The dorsal spines in D44/f123 specimens are comparable to those of type *blakei*. The nature of the dorsal marginal ridge is not fully clear, but it appears papillate (Dear 1971, pl. 3, fig. 3).

In shape, including gently concave dorsal valve, the D44/f123 specimens fall close to *Wyndhamia ingelarensis* Dear, found in the Ingelara Formation of southwest Bowen Basin, and the Barfield Formation of southeast Bowen Basin. The ornament is not known to be completely similar, because the dense array of posterior lateral spines reported for *ingelarensis* and *blakei* is not preserved on New Zealand material. The types of *ingelarensis* are massive, with ventral sulcus and wide hinge, and wide ventral muscle field. Waterhouse & Jell (1983) and Waterhouse (1986b, p. 34) suggested that *ingelarensis* overlapped in its morphology with *Wyndhamia blakei* Dear, first described from the north Bowen Basin, and the two holotypes cited by Dear (1971, pl. 4, fig. 5 for *ingelarensis*, and pl. 2, fig. 10 for *blakei*) are obviously close in size, shape and ornament, with some slight differences in spine density and diameter. Within the limits of observation, the spine pattern in *blakei* is very like the overall pattern found in *ingelarensis* (compare Dear 1971, pl. 3, fig. 1a, 1b for *blakei*, with Dear 1971, pl. 3, fig. 5a for *ingelarensis*). It was concluded that the specimens form a somewhat variable suite, but possibly could prove to be separable (Waterhouse & Jell 1983, p. 241). Confusing the issue is the observation that some Barfield specimens have been described as having deeply concave dorsal valves, but these are now separated as *Acanthalosia? parfreyi*. The New Zealand dorsal valves fall close to the large *ingelarensis* with weakly concave dorsal valves, rather than the small *blakei* (and type *ingelarensis*) specimens which have wedge-shaped dorsal valves, flat externally.

The narrowness of the *blakei* hinge has been stressed by some authors, but *blakei* figured by Waterhouse & Jell (1983, pl. 1, fig. 7, 8) from beds close to the type locality have wide hinge and no dorsal fold. Both *blakei* and *ingelarensis* are close in many attributes, and notably have fine close-set ventral spines. The obvious differences in shape etc may be interpreted as reflective of different substrates. That in turn may be deemed to signify different species. But against that interpretation, large collections of *blakei* show considerable variability sufficient to embrace the *ingelarensis* corpus in terms of sulcus, hinge width, ventral muscle field, and to split such collections as separate taxa seems impractical. So although further enquiry is needed on these matters of taxonomic validity, the Australian holotypes of *blakei* and *ingelarensis* appear to overlap in age range, and fall very close to each other. The selection of small specimens as holotypes is unfortunate because fully grown specimens have to be assessed for specific delineation. Only small *blakei* were figured by Dear (1971), in contrast to some large *ingelarensis* which clearly differ in size and massive posterior, and that conveys a misleading impression of the two taxa.

In describing a suite of specimens from interval E in a core in the Bowen Basin called GSQ Eddystone 1, McClung (1983, pl. 15) stated that his specimens were assigned to *ingelarensis* rather than *blakei* because the ventral valve was more strongly sulcate and more transverse, and lacks well developed brachial ridges. However his figures show that the suite varies considerably in these attributes, negating the significance attached to them, and one of Dear's original *blakei* specimens (1971, pl. 3, fig. 2) is strongly sulcate. Spines in McClung's ventral valves are slightly wider than usual for *blakei* or *ingelarensis*, and Briggs (1998) assigned McClung's suite to *Pseudostrophalosia crassa* Briggs. This is consistent with accompanying brachiopod species, which include *Johndearia pelicanensis* (Campbell) and *Ingelarella cf havilensis* Campbell (so-called *I. mantuanensis* of McClung) and *Notospirifer minutus* Campbell, to confirm a correlation with the *Terrakea elongata* Zone. Briggs (1998) thought the beds were part of the Ingelara Formation, but although the facies may be comparable, the Ingelara fauna is quite different, and older.

In summary, from a survey of the literature, it appears probable that Waterhouse & Jell (1983) were correct to synonymize the two names, and regard *blakei* as a characteristic species, involving wide to narrow shape and hinge, convex or sulcate ventral valve, moderately high ventral interarea, and comparatively fine and close-set rather uniform spines over both valves, with close-set irregular spines prominent in early growth stages. The species *blakei* is represented by a very large suite of material at its type locality, and the full range of variation is scarcely conveyed in the few illustrations so far published.

Compared with New Zealand *Echinalosia discinia* Waterhouse, the dorsal valve of material from D44/f123 is much less concave, and the ventral posterior walls higher and steeper, and ventral spines slightly thicker and more recumbent than on most specimens, though examples of *discinia* do show recumbent ventral spines. *E. maxwelli* (Waterhouse) also has a much more concave dorsal valve, larger ventral spines, with other differences and *E. ovalis* (Maxwell) is readily distinguished by its long ventral muscle field, high ventral interarea and other differences.

DISCUSSION: Briggs (1998) kept the two species *blakei* and *ingelarensis* separate. He diagnosed *blakei* as medium-sized, slightly elongate, with narrow hinge and distinctive outline, low and high angle recumbent spines of two orders on the ventral valve, both reaching 0.75mm in diameter and dorsal valve with numerous suberect spines and fine shallow dimples. No figures were provided. Somewhat incon-

sistently, the specimens figured by Waterhouse & Jell (1983) were included in synonymy, although they are transverse, with hinge up to almost 0.9 maximum width of the valve, and overall shape not conforming with Briggs' diagnosis. Large suites of *blakei* do not conform with the Briggs definition, differing in shape and ornament, so that his diagnosis is inapplicable. The species *ingelarensis* was distinguished by Briggs in part by its large transversely oval to subcircular outline with fine (0.3 up to 0.4mm) and coarse semi-recumbent spines about 0.5mm in diameter, and some complexity noted in spine distribution. But these spine attributes must be discounted. As Briggs pointed out, the species was difficult to interpret, because of the unfavourable enclosing matrix. He therefore used material for the best illustrations of *ingelarensis*, and no doubt for his description, from UQL 3135 in the north Bowen Basin, found above the main *clarkei* band. Accompanying fossils at UQL 3135 include the very distinctive and short-ranging brachiopods *Terrakea elongata* and *Johndearia pelicanensis* which establish a close link to other *Pseudostrothalosia clarkei* faunas, and differ strongly from the species found in the Ingelara Shale with type *Pseudostrothalosia ingelarensis*. The material of genuine Ingelara Formation *P. ingelarensis* prepared and figured by Briggs (1998, text-fig. 62A-C) shows nothing of the posterior spines, but indicates an array of closely spaced rather uniform suberect spines. Anteriorly, erect spines are up to 0.6mm in diameter, with thinner prostrate spines perhaps half as thick, but overall spines tend to be uniform in size, crowded and erect, or suberect. This is the pattern that is found on *blakei*. Insofar as *blakei* is much more variable than allowed by Briggs, and may have a wide hinge, and shares a sulcus and short hinge and low ventral interarea with some *ingelarensis*, the validity of *blakei* stands or falls on the nature of the ventral ornament, shown as consisting of variably semirecumbent to suberect spines about 0.55-0.6 to 0.75mm in diameter in *blakei*, and apparently erect in *ingelarensis* at 0.5-0.75mm in diameter. Differences seem to be of low significance.

According to Dickins (1989, p. 75), *blakei* was to be distinguished by its narrow shell "especially at its posterior end," whereas the type and other *ingelarensis* had a "relatively wider less convex" ventral valve. But these alleged differences do not hold true, as may be seen in examining the original collection of *blakei* figured by Dear (1971, pl. 3, fig. 2, 4), and *ingelarensis* (Dear 1971, pl. 2, fig. 6), let alone from examination of unfigured and numerous topotypes. The convexity of the shells also varies.

Table 7. Summary of some of the changes to identifications by Briggs (1998) that affect correlations

Linoproductidae

Paucispinauria concava (not Waterhouse) was reported with so-called *maxwelli* by Briggs in the Sydney Basin. The Sydney Basin material is not conspecific, and is referred to *Paucispinauria paucispinosa wardenensis* n. subsp. Real *concava* in the Otrack Formation was confused with *P. paucispinosa*, which has much fewer ear spines than type *concava* or Otrack specimens.

Terrakea rylstonensis Briggs from the Snapper Point Formation, south Sydney Basin, is synonymized with *T. exmoorensis* Dear.

Strophalosiidae

Echinalosia maxwelli (Waterhouse) and *E. preovalis* (Maxwell) reported from the lower Elderslie Formation, Sydney Basin, by Briggs (1998) and others are recognized as a different species *E. floodi* n. sp., removing prime evidence for a long maintained miscorrelation between Cattle Creek Formation of the southwest Bowen Basin and lower Elderslie Formation.

Echinalosia hanloni Briggs: recognized as separate species by Briggs (1998) but regarded here as very close to *E. ovalis* (Maxwell). Oversplitting of the species will delineate minor taxa of minor correlation value, and possibly of little temporal significance. Does not appear to be reliably found below *E. ovalis* in surface outcrops.

Echinalosia robusta Briggs: named by Briggs for specimens in the Belford and Otrack Formations respectively. On the basis of ornament, synonymized with *E. maxwelli* (Waterhouse).

Echinalosia davidi Briggs: supposedly younger than *E. discinia*, is regarded as synonymous with *discinia*.

Echinalosia maxwelli (Waterhouse): recognized by Briggs (1998) for shells from the upper Elderslie Formation and Fenestella Shale. Wrongly identified, because the specimens have much finer spines than *maxwelli*, and are referred to *E. discinia briggsi* n. subsp. The species *maxwelli* occurs above, not below *E. discinia*.

Pseudostrothalosia ingelarensis (Dear): figured from the upper Blenheim Formation, north Bowen Basin, by Briggs (1998, text-fig. 62E-I), above *P. clarkei*. The illustrated specimens are conspecific with *clarkei*, and differ from type *ingelarensis* in ornament, dorsal valve and other features.

Echinalosia denisoni Archbold: misidentified by Briggs (1998) with specimens moderately high in the Blenheim Formation, above the Moonlight Sandstone Member. The identifications cannot be sustained. The types of *denisoni* are found with *Johndearia undulosa*, found below the Moonlight Sandstone.

E. bookeri Briggs: found in the Branxton Subgroup and Fenestella Shale, just above *J. undulosa* in the Sydney Basin. Junior synonym of *E. denisoni*.

E. maxwelli (Waterhouse), confused with *E. discinia* Waterhouse in the Fenestella Shale and Wandrawandian Formation of Sydney Basin.

Pseudostrothalosia crassa Briggs: hard to distinguish objectively from *clarkei* in stratigraphic sense. Claimed by Briggs (1998, text-fig. 29) to be in supposed Ingelara Formation in GSQ Eddystone 1, but accompanying brachiopods demonstrate *Terrakea elongata* - *Ingelarella havilensis* level of north Bowen Basin, well above Ingelara Shale: the brachiopod was acceptably identified, but the formation was not.

Pseudostrothalosia clarkei (Etheridge Snr): reported by Briggs (1998, text-fig. 29) in Freitag Formation below Ingelara Formation but the only well preserved material found at this level differs from *clarkei* in its stronger ventral and dorsal spines, higher more inflated ventral valve, wider and larger size, ventral ears with few spines, sparsity of prostrate ventral spines etc, indicating that the genus is *Wyndhamia* not *Pseudostrothalosia* (= *typica crassispina* n. subsp.)

Pseudostrophalosia clarkei (Etheridge Snr, 1872)

- 1872 *Productus clarkei* Etheridge Snr, p. 334, pl. 17, fig. 2a, b, pl. 18, fig. 4, 4a.
 1880 *Strophalosia clarkei* (Etheridge Snr); Etheridge, p. 27, pl. 9, fig. 18a, 19, 20, pl. 10, fig. 23-30, pl. 12, fig. 33 (pl. 10, fig. 26-30 = *Pseudostrophalosia crassa* Briggs = syn. *clarkei*).
 1880 *S. gerardi* not King; Etheridge, p. 32, pl. 12, fig. 34-37, pl. 13, fig. 38.
 1892 *S. clarkei* (Etheridge Snr); Etheridge, p. 285, pl. 13, fig. 12, 13, 16, 17, pl. 14, fig. 19 (pl. 13, fig. 12, 16, 17, pl. 14, fig. 19 = *Ps. crassa* syn. *clarkei*, not pl. 13, fig. 14 = *Echinalosia ovalis* (Maxwell) fide Briggs).
 1892 *S. gerardi* not King; Etheridge, p. 260, pl. 13, fig. 18, pl. 14, fig. 18 (not pl. 40, fig. 7 = *Echinalosia ovalis glabra* Briggs).
 1929 *S. clarkei* (Etheridge Snr); Reid, text-fig. 28.
 1954 *S. clarkei* (Etheridge Snr); Maxwell, p. 546, pl. 56, fig. 1-7.
 1954 *S. brittoni* var *gattoni* Maxwell, p. 544, pl. 55, fig. 4-7.
 1954 *S. ovalis* not Maxwell, p. 548, pl. 57, fig. 10-12 fide Briggs 1998 (not pl. 57, fig. 1-9, 13 = *E. ovalis*).
 1964 *S. clarkei* (Etheridge Snr); Hill & Woods, pl. P4, fig. 11, 12.
 1964b *Wyndhamia clarkei* (Etheridge Snr); Waterhouse, p. 51, pl. 8, fig. 5-9, pl. 37, fig. 5, text-fig. 7i, j, 8c, 15a-c, 18, 19.
 1964b *Wyndhamia clarkei gattoni* (Maxwell); Waterhouse, p. 54.
 1965 *Wyndhamia clarkei* (Etheridge Snr); Waterhouse & Vella, p. 63, pl. 2, fig. 3.
 1971 *Wyndhamia clarkei gattoni* Dear (sic); Dear, p. 12.
 1972 *W. clarkei* (Etheridge Snr); Hill et al, pl. P4, fig. 11, 12.
 1983 *Wyndhamia cf ingelarensis* not Dear; McClung, p. 73, pl. 15, fig. 1-21 (= *Ps. crassa* syn. *clarkei*).
 1989 *Echinalosia cf minima* not Dear; Dickins, p. 75, pl. 3, fig. 12-21 (not pl. 3, fig. 1-11 = *Terrakea* sp.?)
 1998 *Pseudostrophalosia clarkei* (Etheridge Snr); Briggs, p. 116, text-fig. 61.
 1998 *Ps. crassa* Briggs, p. 119, text-fig. 63.
 1998 *P. ingelarensis* (not Dear); Briggs, p. 118, text-fig. 62D-I (not text-fig. 62A-C = *Ps. ingelarensis* (Dear) -*blakei* (Dear)).

LECTOTYPE, HOLOTYPE: QMF 2887, *clarkei*, figured by Etheridge Snr (1872, pl. 17, fig. 2) and Maxwell (1954, pl. 56, fig. 5, 6) SD Maxwell (1954, p. 546) from Collinsville area, north Bowen Basin, Queensland, believed to be from lower part of Big Strophalosia band, Gattonvale. For *gattoni*, UQF 15655 figured by Maxwell (1954, pl. 55, fig. 4-6) OD from similar position. For *crassa*, GSQF 12493 figured by McClung (1983, text-fig. 15.16) and Briggs (1998, text-fig. 63A) OD from fauna E, GSQ Eddystone 1 core, correlative with Scottville Member or younger Blenheim Formation, north Bowen Basin.

DIAGNOSIS: Moderately large shells, inflation low, posterior ventral valve gently convex and posterior walls low, venter ornamented by generally fine erect to suberect and prostrate spines of two orders, varying to moderately coarse, margins bear stronger erect spines, dorsal valve almost flat externally, wedge-shaped, spines rather variable, fine and close-set, or scattered, occasionally thick, generally erect.

MATERIAL: Two or three dorsal valves and single ventral valves from D44/f132 (GS 15221), 338 (BR 2399) and 355, and specimens from two further unregistered localities, *Terrakea elongata* Zone, Mangarewa Formation, Wairaki Downs.

RESEMBLANCES: Wairaki Downs material is sparse, and not completely identical with the *clarkei* types. It is believed that they represented specimens that grew under the stress of current-swept coarse substrate, therefore developing thick shell, and rather sturdy spines less dense than usual. This is of course contentious, and the uncertainty could be expressed by use of a query. Briggs (1998) did not accept the identification, because of the height and width of ventral adductor platform, thin dental callosities, and unusual brachial ridges. But these objections seem ill-judged. The variety *brittoni gattoni* Maxwell was accepted as *clarkei* by Briggs (1998) and has a very high and wide muscle platform, as do many specimens of *clarkei* - Briggs incorrectly regarded specimens not fully mature as representing the mature *clarkei* adductor platform. A number of *clarkei* ventral valves lack dental callosities. The brachial ridges are unusual in an outstanding and well preserved valve from New Zealand, as compared with the worn dorsal valve figured by Briggs. The unusual feature in the New Zealand specimen concerned a "tight anterior hook". A similar feature is seen on a very few dorsal valves at a stage of late maturity, including material from UQL 3135. Briggs suggested that the New Zealand specimens belonged to *hanloni* Briggs, a subjective synonym of *ovalis*, but there are many obvious differences in shape, valve thickness, valve concavity, muscle field, outline of brachial ridges etc. Briggs (1998) asserted that the lack of data of spines prevents even generic identification. In fact spines are known on both valves - for example BR 222 from GS 6071 shows the burst of lateral flank spines typical of the genus, and dorsal valves show rare spines, likely to have been reduced in number by sedimentary stress and subsequent burial (eg Waterhouse 1982a, pl. 7, fig. h, j). As for the dismissal of the wedge-shape of the dorsal valve, no matter what Briggs asserted, there are very substantial populations of *Echinalosia* in both New Zealand and Australia that never have wedge-shaped dorsal valves. This includes type *maxwelli* with thousands of specimens, and *Echinalosia* in the middle Mangarewa Formation, again with thousands of specimens. *Pseudostrophalosia* is represented by huge numbers of specimens in the *blakei* and *clarkei*

bands of the north Bowen Basin, and these have wedge-shaped dorsal valves. None of these beds has been examined in the field by Briggs. Dear (1971), who worked without a deliberate correlation agenda and therefore made objective assessments, was satisfied that the New Zealand material was identical with *gatonii* Maxwell, now regarded as *clarkei*.

The sparse examples from west Nelson are characteristic in terms of ventral interior and overall shape.

Table 8. Species list for Productida from east Australia and New Zealand Permian

- Genus *Lethamia* Waterhouse
Lethamia rara Briggs, *L. hillae* Waterhouse, *L. condaminensis* Briggs, *L. ligurritus* Waterhouse, *L. ? collina* Waterhouse
 Genus *Azygidium* Waterhouse
Azygidium mitis (Hill)
 Genus *Nambuccalinus* Waterhouse
Nambuccalinus bourkei (Briggs)
 Genus *Bandoproductus* Jin & Sun
Bandoproductus hastingsensis Briggs, *B. youdalensis* Briggs, *B. walkomi* Briggs, *B. macrospina* Waterhouse
 Genus *Costatumulus* Waterhouse
Costatumulus farleyensis (Etheridge & Dun) [syn. *C. tumida* Waterhouse], *C. prolongata* Waterhouse, *C. meritus* Waterhouse
 Genus *Auriculispina* Waterhouse
Auriculispina levis (Maxwell)
 Genus *Platycancrinella* Waterhouse
Platycancrinella transversa (Briggs)
 Genus *Terrakea* Booker
Terrakea pollex Hill, *T. dickinsi* Dear, [syn. *T. dickinsi aurispina* Waterhouse], *T. exmoorensis* Dear [syn. *T. rylstonensis* Briggs], *T. brachythaera* (Morris) [syn. *T. etheridgei* Briggs, *T. quadrata* Briggs, *T. fragile* Dana, *T. leve* Booker], *T. elongata* (Etheridge & Dun)
 Genus *Paucispinauria* Waterhouse
Paucispinauria geniculata Waterhouse, *P. concava* (Waterhouse), *P. paucispinosa* Waterhouse, *P. paucispinosa wardenensis* Waterhouse, *P. solida* (Etheridge & Dun), *P. verecunda* (Waterhouse)
 Genus *Saetosina* Waterhouse
Saetosina multispinosa (Dear), *S. dawsonensis* Waterhouse
 Genus *Magniplicatina* Waterhouse
Magniplicatina undulata Waterhouse, *M. perfecta* Waterhouse, *M. halli* Waterhouse [syn. *M. superba* Waterhouse], *M. magniplica* (Campbell) [syn. *Cancrinella gyrandensis* Wass], *M. heywoodi* Waterhouse
 Genus *Filiconcha* Dear
Filiconcha hillae Dear, *F. auricula* Waterhouse
 Genus *Protoanidanthus* Waterhouse
Protoanidanthus compactus Waterhouse, *P. gosforthensis* Briggs, *P. pokolbinensis* Briggs
 Genus *Anidanthus* Whitehouse
Anidanthus cessnockensis Briggs, *A. springsurensis* (Booker), *A. paucicostatus* Waterhouse
 Genus *Megousia* Muir-Wood & Cooper
Megousia solita Waterhouse, *M. crenulata* Briggs
 Genus *Nothokuvulousia* Waterhouse
Nothokuvulousia aurifera Waterhouse
 Genus *Lipantheris* Briggs
Lipantheris sparsispinosus Briggs, *L. anotos* Briggs
 Genus *Taeniothaerus* Whitehouse
Taeniothaerus farleyensis Briggs, *T. homevalensis* Briggs [syn. *T. lakismatos* Briggs], *T. subquadratus* (Morris) [syn. *Aulosteges acanthophorus* Fletcher]
 Genus *Megasteges* Waterhouse
Megasteges randsi (Hill)
 Genus *Strophalosia* King
Strophalosia concentrica Clarke, *S. subcircularis* Clarke [syn. var. *tumida* Clarke, var. *brevicardinalis* Clarke, *Costalosia apicallosa* Clarke, *Wyndhamia? irregularis* Clarke], *S. yalwalensis* Briggs
 Genus *Echinalosia* Waterhouse
Echinalosia curtosa Waterhouse, *E. dejecta* Waterhouse, *E. preovalis* (Maxwell), *E. curvata* Waterhouse, *E. ? conata* Waterhouse, *E. discinia* Waterhouse [syn. *E. davidi* Briggs], *E. denisoni* Archbold [syn. *E. bookeri* Briggs], *E. maxwelli* (Waterhouse) [syn. *E. robusta* Briggs], *E. ovalis* (Maxwell) [syn. *E. hanloni* Briggs], *E. ovalis glabra* Briggs, *E. ovalis tasmanitia* Waterhouse, *E. wassi* Briggs, *E. runnegari* Briggs, *E. telfordi* Briggs, *E. ? voiseyi* Briggs
 Genus *Capillaria* Waterhouse
Capillaria warwicki (Maxwell) [syn. *E. warwickensis* Waterhouse]
 Genus *Acanthalosia* Waterhouse
Acanthalosia domina Waterhouse, *A. concava* (Maxwell). [syn. *A. domina stanthorpensis* Waterhouse], *A. ? ardua* (Waterhouse), *A. deari* (Briggs), *A. ? parfreyi* Waterhouse
 Genus *Marginalosia* Waterhouse
Marginalosia? minima (Maxwell), *M. planata* (Waterhouse)
 Genus *Wyndhamia* Booker [syn. *Branxtonia* Booker]
Wyndhamia jukesii (Etheridge), *W. typica* (Booker) [syn. *W. dalwoodensis* Booker, *W. valida* Booker], *W. typica crassispina* Waterhouse, *W. clarkeina* Waterhouse
 Genus *Pseudostrophalosia* Clarke [?syn. *Notolosia* Archbold]
Pseudostrophalosia brittoni (Maxwell), *Ps. blakei* (Dear) [syn. *W. ingelarensis* Dear], *Ps. clarkei* (Etheridge Snr) [syn. *Ps. crassa* Briggs]

DISCUSSION: In revising the types of *clarkei*, Briggs (1998) noted that there were fine body spines, 0.4mm in diameter, becoming 0.5mm in diameter anteriorly, and coarse medium to high angle recumbent spines 0.6mm in diameter medianly and 0.8-1mm in diameter anteriorly. But ventral erect spines more than 1mm thick are visible on material figured as *clarkei* by Briggs (1998, text-fig. 61D), and were mentioned as "very coarse" on the posterior-lateral flanks. Briggs emphasized that the ventral umbo was lightly thickened with lightly impressed diductor scars and adductors sited on low platform, but these features indicate a degree of immaturity in the material he described. Material from UQL 3135, just above the *clarkei* bed, Capella block, and accompanied by *Johndearia pelicanensis* (Campbell), a key species for this level, shows irregularly scattered erect spines over the venter, about 1mm in diameter, as well as fine erect spines, and the array is rather diverse. In other ventral valves the spines are slightly finer and recumbent. One large ventral valve nearly 40mm wide has fine erect and very closely spaced spines 0.7mm in diameter, with a large burst of thick erect spines up to 1.3mm in diameter laterally. Overall, spacing and diameter and angle of emergence is much more variable than indicated by Briggs. Dorsal spines are fine and erect mostly, and variable in density and distribution from specimen to specimen. Internally, the ventral adductor platform is also variable, and is often substantially higher than figured by Briggs, and varies from narrow to moderately wide. A slender myophragm is present in several specimens. In some specimens there are no dental callosities.

Pseudostrophalosia crassa (1998, p. 119, text-fig. 63) comes from beds of almost identical or perhaps slightly younger age (though miscorrelated by Briggs), to judge from associated brachiopod and molluscan species, which include *Terrakea elongata* (Etheridge & Dun), *Ingelarella havilensis* Campbell and *Aperispirifer parfreyi* Waterhouse shared with type *clarkei* beds. The species *crassa* was said to be distinguished principally by its fine low-angle recumbent and coarser low to high angle recumbent series. Briggs noted that the maximum diameters of these series varied widely, from 0.3 to 0.6mm respectively in some specimens, to 0.6mm and 1mm in others. Coarse spines form a loose group laterally. The ventral adductor platform, well illustrated by McClung (1983), is relatively wide and long.

At first sight, *Pseudostrophalosia crassa* differs from *clarkei* in its coarser spines and larger higher ventral adductor platform, and other aspects. But there appears to be an intergradation between the extremes. Even amongst the specimens selected by Briggs, the specimen of *clarkei* figured by Briggs (1998, text-fig. 61D) approaches *crassa*, and study of large suites of *clarkei* from the north Bowen Basin show a wide range of ventral spine patterns, density and thickness even amongst single collections. They also show that the ventral adductor platform may be high, and sometimes wide. Although it may be desirable to separate the coarse from the fine-spined shells, it appears to be in practise very difficult, and does not lead to any unambiguous biostratigraphic conclusion. In GSQ Eddystone 1, specimens show coarser spines in progressing up the core (Briggs 1998), but there is no confirmation for this trend from other sections. Potentially, it should prove possible to subdivide *clarkei* into three associations, a basal association that includes the types, a younger level characterized, in the north Bowen Basin, by *Johndearia pelicanensis* (Campbell), and a topmost level characterized by *Ingelarella havilensis* Campbell, with *Marginalosia? minima* prominent (Dear 1972, p. 11). The *crassa* form is accompanied by *havilensis* in GSQ Eddystone 1, and variably spinose *clarkei* are accompanied by *pelicanensis*. This remains a field for further enquiry, and at present it is difficult to put boundaries between the different kinds of shell assigned to *clarkei*. In the preceding synonymy, some ascriptions rely on Briggs (1998). But the claim that the specimens figured as *clarkei* by de Koninck (1877, pl. 10, fig. 5) from the Patterson River or near Branxton seems dubious.

TAXONOMY: Dear (1971) validated and claimed authorship for the name *gattoni* as a subspecies of *clarkei*, after Maxwell (1954) had proposed it as variety. The subspecies *gattoni* was distinguished by its highly arched subcircular ventral valves and large dental callosities. Dear noted that New Zealand material described as *clarkei* from the upper Mangarewa Formation by Waterhouse (1964b, pl. 8, fig. 5-9) was close to *gattoni*. This was initially pointed out by Waterhouse (1964b, p. 54), in revising the Maxwell types, and in asserting that *gattoni* was close to *clarkei*, not *brittoni*. The form *gattoni* is found with *clarkei*, in the lower Big Strophalosia band, and it is probably best regarded as of infrasubspecific rank. The figured New Zealand material involved a specimen at late maturity- or even gerontic, according to the growth development stages analysed by Waterhouse (1982a) for closely related material. Associated material is less distinct.

Dickins (1989) took a view contrary to that of Maxwell (1954), Dear (1971) and Waterhouse (1964b), and regarded *gattoni* as a subspecies of *Echinalosia minima*. No evaluation or analysis was offered, and his interpretation is rejected.

STRATIGRAPHIC DISTRIBUTION: The species *clarkei* is restricted to the upper Blenheim Formation of the north Bowen Basin, and the upper Mangarewa Formation and Flowers Formation of New Zealand. Accompanying species are also identical, including *Terrakea elongata*, *Ingelarella havilensis*, and *Johndearia pelicanensis*. Briggs (1998) claimed that *clarkei* is present also in the Freitag Formation and Aldebaran Formation of the Denison Trough, southwest Bowen Basin, but his lists cannot be substantiated. Many of the specimens to which he referred cannot be found in collections, and what does remain in no way sustains his identifications. They are specifically discussed under the description for *Wyndhamia typica crassispina*. On the basis of these flawed assertions, Briggs (1998) severely miscorrelated the formations of the Bowen Basin, and regarded *clarkei* as older than *ingelarensis* and *ovalis*. To help sustain this concept, he misreported *ingelarensis* as occurring above *clarkei* in the north Bowen Basin, at UQL 3135 for example (Briggs 1998, text-fig. 62E-G), but the particular specimens are in fact *clarkei*.

Genus *Notolosia* Archbold, 1986

Notolosia Archbold, 1986, type species *N. dickinsi* Archbold, 1986, from the Hardman Member of the Canning Basin, Western Australia, was proposed as a subgenus of *Echinalosia*. The type species has a large ventral cicatrix on the umbo, circular to subcircular outline, and some long thick semi-recumbent spines. The moderately fine evenly spaced mostly subprostrate with some erect ventral spines and strong dorsal marginal ridge suggest attributes of *Marginalosia*, but the pits common on the dorsal valve seem to be lacking.

Although the genus was interpreted as a close ally of *Echinalosia*, the thickened wedge-shape of the dorsal valve, and the distribution of ventral spines, with close-set cluster on the ventral ears (see Archbold 1986c, text-fig. 7N, O, S) show that the *Notolosia* is closely allied to *Pseudostrophalosia* Clarke. I am not sure that it will be possible to distinguish the two on other than specific parameters.

Tribe **ARCTICALOSIINI** new

NAME GENUS: *Arcticalosia* Waterhouse, 1986.

DIAGNOSIS: Strophalosiidae with uniformly fine and generally erect spines of one order over the ventral and dorsal valves.

DISCUSSION: Unlike Echinalosiini, ventral and dorsal spines are of one order. In Echinalosiini the ventral spines are of two orders, although one series, especially the fine ones, may become rare, and may be variably erect and prostrate, with a few scattered dorsal spines moderately thick.

The tribe is rare, with so far two genera, *Arcticalosia* and *Orthothrix* Geinitz, best known in but not limited to higher latitudes of the northern hemisphere. *Strophalosia multispinifera* Prendergast from the Nooncanbah, Cundlego and Wandagee Formations and Nalbia Sandstone, Canning and Carnarvon Basins, Western Australia, appears typical of *Arcticalosia*. As Archbold (1987, p. 20) noted, *Wyndhamia colemani* Archbold from the Madeline Formation and elsewhere in Western Australia also has ventral spines of mostly one diameter, but a few very thin spines amongst the coarse ones are shown in his fine illustrations (eg Archbold 1983b, pl. 1, fig. B, C, E, N), ruling out placement with *Arcticalosia*. With its dense cluster of posterior lateral ventral spines, it may be placed in *Pseudostrophalosia*.

Genus *Orthothrix* Geinitz, 1847

TYPE SPECIES: *Orthis excavata* Geinitz, 1842.

DISCUSSION: The type species comes from the Zechstein of north Europe, of Wuchiapingian age, not Roadian-Kazanian as claimed by Brunton, Lazarev, Grant & Jin (2000, p. 574). The type species is subtriangular in shape, with uniform subprostrate to suberect ventral spines and fine closely spaced subprostrate dorsal spines.

The distinctive species *Echinalosia simpsoni* has been described from the Mingenew Formation in the Perth Basin of Western Australia by Archbold (1996, p. 22, pl. 3A-V), and may be reassigned to *Orthothrix*. It is characterized by a somewhat variable shape, with a number of specimens that are distinctively subtrigonal in outline, and a number that are sulcate. The ventral spines are very fine, subaligned along concentric rows, and mostly if not entirely erect. Dorsal spines are fine, numerous and close-set.

Subfamily **DASYALOSIINAE** Brunton, 1966

This subfamily is restricted to genera with two series of crowded spines on both the dorsal valve and ventral valve. By contrast, Echinalosiinae has one series of spine, variably spaced and erect or prostrate or both on the dorsal valve. The type species of *Dasyalosia*, *Spondylus goldfussi* Muenster from the European Zechstein, is an unusual genus with vermiform tangled spines on both valves. Ventral spines include long rhizoid spines and rare straight prostrate spines. Dorsal spines are rhizoid and tapered, with a row around the margin, and slender more prostrate spines are visible in figures. The dorsal valve is lamellose anteriorly. The vermiform nature need not be a family group character, because similar spines are developed on another Zechstein form *Craspedalosia*, which has lamellate non-spinose dorsal valve, placed in Mingenewiinae Archbold. Two genera deemed to be allied to *Dasyalosia* are *Acanthalosia* Waterhouse, of ?Late Carboniferous and early Permian age, and *Bruntonaria* n. gen. of Visean (Lower Carboniferous) age. These have two series of spines on each valve, usually less tangled than in *Dasyalosia*, although those of *Acanthalosia* show some degree of entanglement, especially on the type species.

Genus *Acanthalosia* Waterhouse, 1986

TYPE SPECIES: *Acanthalosia domina* Waterhouse, 1986.

DISCUSSION: This genus is represented by several species in Queensland, and one possible species in New Zealand. It is characterized by its complex array of crowded spines, involving at least two series on each valve, though not realized by Brunton, Lazarev, Grant & Jin (2000, p. 569). The ventral spine pattern is dominated by close-set dense and interspersed erect and prostrate spines.

Acanthalosia? ardua (Waterhouse, 1982)

1964b *Strophalosia* aff *preovalis* Waterhouse, p. 29, pl. 4, fig. 3-5.

1982a *Echinalosia ardua* Waterhouse, p. 30, pl. 6, fig. d-i.

HOLOTYPE: BR 1476, figured by Waterhouse (1982a, pl. 6, fig. f) OD from D44/f9947 (GS 9276), *Terrakea dickinsi* Zone, Brunel Formation, Takitimu Group, Wairaki Gorge.

DISCUSSION: This is a distinctive species with concave dorsal valve. The ventral interarea is of moderate height. Capillae, growth lamellae and deep elongate pits are prominent on the dorsal exterior. The dorsal valve is not smooth as in *Strophalosia*, and not strongly wedge-shaped as in *Wyndhamia* and allies, but OU 18775 shows a somewhat thickened dorsal valve anteriorly, made up of two layers of thick shell, each made up of fine layers.

The nature of the external ornament is not clear, but examination of topotype and allied material at IGNS, Lower Hutt, indicates a mix of erect and prostrate spines on both dorsal and ventral valve, as in *Acanthalosia*. Amongst topotype material, BR 1502 is a deeply sulcate ventral valve with suggestions of prostrate and fine erect spines 2mm apart along rows. BR 2368 involves a ventral external mould with many prostrate spines 0.5mm in diameter and coarser erect spines, 0.8mm in diameter. This specimen is on the same block as BR 1477 in Waterhouse (1982a, pl. 6, fig. e). BR 1504 is a small dorsal valve with markings that might be prostrate spines, but seem more likely to be some attached animal. BR 1527 is another small dorsal valve showing erect spines and a very few possibly prostrate spines. Amongst material at IGNS from GS 5885, BR 1523 is a small ventral valve showing erect and subprostrate spines. BR 382 is an external mould of a mature ventral valve, showing scattered moderately sturdy erect spines 0.6-0.8mm thick, and a number of finer prostrate spines. BR 2369 is a small dorsal valve showing tiny erect spines with none prostrate. The figured dorsal exterior and interior of BR 384 (Waterhouse 1964b, pl. 4, fig. 4, 1982a, pl. 6, fig. g) shows a very pitted uneven surface, with tiny fine erect spines and what may be coarser adpressed spines, to some extent the reverse of what is typical of other species of *Acanthalosia*, but suggestively close. Overall the generic position remains obscure, in the absence of mature external moulds, but most of the available external moulds suggest a possible relationship with *Acanthalosia*.

There is no clear match for this species in east Australia, despite an extensive search for comparable material amongst undescribed collections, as well as in the literature. Whether this is because the species represents a geographic or temporal isolate, or a facies-modified form, remains to be determined. Briggs (1998, p. 109) suggested that the New Zealand species might belong to *Acanthalosia* Waterhouse, 1986 in terms of overall shape, and his observations of ornament on an unfigured ventral valve from GS 9276. No reference number was quoted, so that his observation remains untestable, and the most critical attribute for *Acanthalosia* lies in the two series of dorsal spines, which was not determined by Briggs (1998). Briggs (1998) considered that *ardua* was possibly conspecific with *A. concava* (Maxwell, 1954). This may prove correct, but from available data, based on insufficient material, the Australian species is more elongate, with maximum width lying well forward, much longer and higher ventral adductor scars and more concave dorsal valve. Thus it appears that the two species are separable. The species *concava* occurs widely in Queensland according to Briggs (1998, p. 111), and is found in the Cattle Creek Formation in what Briggs termed upper *Echinalosia preovalis* Zone, not clearly defined.

Another species of *Acanthalosia* was recorded from the Cattle Creek Formation of Queensland by Briggs (1998, text-fig. 58) as *Acanthalosia* sp. Enough of the material examined by Briggs is intact at GSQ, Zillmere, to indicate a distinctive new species characterized by very fine spines on both valves, and deeply concave dorsal valve. The rubber latex mould of the specimen illustrated by Briggs (1998) was returned, without the original rock mould, to the Geological Survey of Queensland at Zillmere (Dr. S. M. Parfrey, pers. comm.)

Wyndhamia sp. of Begg & Ballard (1991, text-fig. 5, 6) from the Mantle Volcanics Formation of western Southland, New Zealand, shows only erect spines, apart from one inclined spine, on the small external mould of the dorsal exterior. Pustules are prominent, and the convex nepionic shell is larger than in *ardua*. Although not stated in the text, the material is kept at Otago University.

Acanthalosia deari (Briggs, 1998)

1971 *Wyndhamia ingelarensis* not Dear; Dear, p. 12, pl. 3, fig. 10 (not fig. 5-9 = *Pseudostrophalosia ingelarensis* (Dear)~ *blakei* (Dear)).

1983 *Echinalosia maxwelli* (not Waterhouse); McClung, p. 72, text-fig. 14:1, 2, 6.

1983 *Wyndhamia ingelarensis* not Dear; McClung, p. 73, text-fig. 14: 3-5, 7, 8.

1986b *Wyndhamia blakei* not Dear; Waterhouse, p. 33, pl. 5, fig. 24, 29, 30, pl. 6, fig. 1, 2, pl. 15, fig. 10 (not pl. 5, fig. 25, 26?, 27?, 28 = *A.? parfreyi* Waterhouse).

1998 *Echinalosia deari* Briggs, p. 101, text-fig. 53.

HOLOTYPE: UQF 73991 figured by Waterhouse (1986b, pl. 5, fig. 24, 29) OD from lower Flat Top Formation, southeast Bowen Basin, Queensland.

DIAGNOSIS: Small shells with comparatively short hinge, dorsal valve almost flat posteriorly, and weakly concave overall, ventral shoulders massive. Ventral spines comparatively close-set and of two orders, dorsal spines close-set, mostly erect but with scattered thin prostrate spines.

DISCUSSION: The topotype material of this species, as figured by Waterhouse (1986b), has crowded ventral spines of two interspersed series (Waterhouse 1986b, pl. 5, fig. 24, 29), and a dorsal valve showing numerous crowded mostly erect spines, with scattered prostrate spines (Waterhouse 1986b, pl. 5, fig. 29). A dorsal valve, with few if any prostrate spines, and many crowded erect spines is figured by McClung (1983). A dorsal exterior illustrated by Briggs (1998, text-fig. 53B) from the same locality (GSQLD 96, Catherine Sandstone, southwest Bowen Basin) has rare prostrate spines as well as erect spines. Overall, this material may be deemed as a species of *Acanthalosia*, marked by its prostrate as well as erect spines on the dorsal valve, and two series of crowded spines on the ventral valve.

SYNONYMY: The synonymy is modified from Briggs (1998). He excluded without explanation topotype specimens figured by Waterhouse (1986b, pl. 6, fig. 1, 2, pl. 15, fig. 10), and included a younger Flat Top Formation specimen that has a short hinge. A short hinge is also seen in topotype *Echinalosia maxwelli* (Waterhouse, 1964b, pl. 4, fig. 10, pl. 6, fig. 6), showing that the feature need not be diagnostic.

***Acanthalosia? parfreyi* n. sp.**

1986b *Wyndhamia blakei* not Dear; Waterhouse, p. 33, pl. 5, fig. 25?, 26, 27?, 28 (not pl. 5, fig. 24, 29, 30, pl. 6, fig. 1, 2, pl. 15, fig. 10 = *Acanthalosia deari* (Briggs)).

1988 *Echinalosia* sp. Parfrey, p. 12, pl. 2, fig. 14-17, 19.

?1988 *Wyndhamia* sp. Parfrey, p. 13, pl. 2, fig. 18.

1998 *Echinalosia deari* not Briggs; Briggs, p. 101.

DERIVATION: Named for Susan M. Parfrey.

HOLOTYPE: GSQF 12983 figured by Parfrey (1988, pl. 2, fig. 14, 19), from GSQL 2734, Barfield Formation, southeast Bowen Basin, Queensland, here designated.

DIAGNOSIS: Suboval weakly elongate to transverse shells with convex ventral valve, moderately concave dorsal valve, interareas low and hinge narrow, ventral spines dense, coarse and well spaced, erect and suberect, with few very thin prostrate spines, spines not crowded laterally or posteriorly, dorsal spines fine, erect and subprostrate.

DESCRIPTION: The ventral valve is transverse to subelongate and gently convex with very broad ventral umbo and usually no sulcus, although a few shells have median flattening, and others display a narrow sulcus. The dorsal valve is moderately concave, without long trail, and is moderately thickened. Shells have a rather narrow hinge, low ventral interarea and very low dorsal interarea. Ventral ornament consists of growth lines and short lamellae, and complex spine pattern, involving mostly coarse erect spines, often with swollen bases, suberect spines, and some thin prostrate spines especially laterally. Dorsal spines are less well known, but appear to include sturdy erect spines and finer spines, some suberect, others prostrate. Concentric laminae and growth lines are moderately prominent, and fine dimples are visible.

The ventral adductor field is small and posteriorly placed, and becomes long and high at late maturity.

RESEMBLANCES: The present species is represented by comparatively few specimens, but is distinctive in shape, and differs from *Pseudostrophalosia* and *Echinalosia* in the nature of its ornament. It is closer to *Echinalosia* but appears to have diverse dorsal spines. The overall profile and massive ventral valve with low steep posterior ventral posterior walls and thick erect ventral spines mark a distinctive form, not entirely clear in its generic position. Most of the specimens were included by Briggs (1998) in *Echinalosia deari* Briggs, but this species, based on a suite of specimens from the overlying lower Flat Top Formation, has a much less convex ventral valve and more gently concave dorsal valve, with much more crowded spines. Specimens of *parfreyi* figured by Waterhouse (1986b, pl. 5, fig. 25, 27) come from the Barfield Formation as far as known, but fig. 25 from UQL 2573 looks moderately like *deari*.

Acanthalosia concava (Maxwell, 1954) is similar in its deeply concave dorsal valve. Although it has a more prominent ventral umbo, wider hinge and elongate outline, with other differences, it approaches the new form in its dorsal concavity, thickening and thick ventral spines.

A species of *Pseudostrophalosia* is found in the correlative Ingelara Shale, originally described as

Wyndhamia ingelarensis Dear, 1971, and this form is larger with generally wide hinge, less concave dorsal valve, and most critically, an array of postero-lateral spines and close-set erect spines of mostly one diameter over the ventral valve; dorsal spines are fine and erect. Some attributes of the new form suggest, as noted by Parfrey (1988), the species *Echinalosia preoivalis* (Maxwell). But unlike that species, there are rather coarse spines on both valves over 1mm wide anteriorly and 3-4 mm apart anteriorly even on the comparatively small holotype.

There appear to be two lineages in species referred to or possibly linked to *Acanthalosia*. One has little incurved ventral umbo and comparatively flat and moderately thickened dorsal valve, including *domina* and *deari*, and perhaps *mcclungi*, if allied. The other shows more concave less thickened dorsal valve, involving *concava* and *ardua*, with *parfreyi* somewhat but not entirely similar.

Genus *Bruntonaria* new

DERIVATION: Named for C. Howard C. Brunton.

TYPE SPECIES: *Dasyalosia panicula* Brunton, 1966, here designated.

DIAGNOSIS: Shell small, concentric lamellae moderately to well developed. Ventral spines dense, long, mostly subprostrate, some thick, and also short or broken erect spines, all somewhat similar in diameter. Dorsal spines dense, in suberect and prostrate series.

DISCUSSION: *Dasyalosia panicula* Brunton and *D. lamnula* Brunton from Visean of County Fermanagh, Ireland, differ from the Permian genus *Dasyalosia* Muir-Wood & Cooper in having much less tangled and vermiform spines, stronger lamellae and long ventral adductor scars. The cardinal process is low in the type species, probably reflecting immaturity. Many ventral spines curve forwards and are only weakly if at all deflected. Dorsal spines show two series: details are described and illustrated by Brunton (1966). The Irish species come much closer to *Acanthalosia* Waterhouse than to *Dasyalosia*. As well illustrated by Briggs (1998, text-fig. 57) and Waterhouse (1986b, pl. 5, fig. 9-18, pl. 15, fig. 8), the ventral valve of *Acanthalosia* has prostrate spines that are much finer and more prostrate than in *Dasyalosia*, and the erect spines are more sturdy and less curved, but may be tangled. Dorsal prostrate spines are also more prostrate and slender, and erect spines moderately thick, but not curved forward. In addition, lamellae are less developed, and the dorsal valve tends to be somewhat thickened. There are various internal differences as well.

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

Briggs (1998, pp. 131-133) elaborated the assessments of Coleman (1957) and Waterhouse (1983e, p. 192) that aulostegids appear to be more closely related to productids than strophalosiids, and firmly classed Aulostegoidea in Productidina Waagen, as distinct from Strophalosiidina Waterhouse. There are strong reasons for supporting this stand, but first a full analysis must take account of approaches to Echinoconchoidea amongst Productidina and certain strophalosiid groupings. Such broad reviews were not provided by Briggs (1998) in his well reasoned, but too circumscribed analysis. Pending such revision, the Aulostegoidea is left associated with Strophalosiodea.

Family **AULOSTEGIDAE** Muir-Wood & Cooper, 1960 Genus *Megasteges* Waterhouse, 1975

TYPE SPECIES: *Megasteges nepalensis* Waterhouse, 1975.

DIAGNOSIS: Large shells, ventral valve asymmetric, high interarea and elytridium, ventral sulcus, sessile and erect spines. Dorsal valve convex near hinge, concave anteriorly, geniculate, ornamented by pustules with small erect spines. Ventral muscle field with long narrow adductors surrounded completely or partly by diductors, cardinal process with two anterior septa and medium septum, dendritic adductors.

DISCUSSION: *Megasteges* as proposed by Waterhouse (1975) is rather like *Fusispirifer* in distribution, found widely in marine beds of eastern Gondwana in Asia and Australasia. Originally described from Nepal, the genus was recognized in Western Australia, as summarized by Archbold (1993b), and in the Bowen Basin by Briggs in Waterhouse (1986b) as *Aulosteges randsi* Hill, 1950. It is possibly represented in New Zealand by a dorsal valve figured as "Aulostegidae genus indet." from the Queens Beach Member, Stephens Subgroup, Stephens Island (Campbell et al 1984, text-fig. 6.14). In addition a worn specimen comes from the Hilton Limestone of Wairaki Downs.

Megasteges? sp.

Pl. 5, fig. 18, text-fig. 5i, j, k

MATERIAL: A single worn ventral valve OU 18758 from D44/f376, *Spinomartinia spinosa* Zone, Hilton Limestone, Wairaki Downs.

DIMENSIONS IN MM:

Width	Length	Height
17.5	17.5	9.5

DESCRIPTION: Specimen worn, small, asymmetric, umbo placed to one side of mid-line, not showing any cicatrix, umbonal walls diverge at 115°, posterior truncated by wide interarea subvertical to commissure, but detail obscure, posterior umbo swollen, shell contracted in front, then swollen again. Anterior shell depressed medianly. Surface ornament of scattered erect spines laterally, fine concentric growth lines, and short costae around anterior margin.

RESEMBLANCES: The generic and even familial position of this specimen are not established, but overall shape and not very well preserved spines suggest *Megasteges*. The size and shape are particularly like *Aulosteges* sp. recorded by Grant (1970, pl. 1, fig. 21) from the Khisor Member (white sand) of the topmost Chhidru Formation, Salt Range, and Grant's form could be *Megasteges*. It is a small distorted specimen showing vestiges of spines. Neither this nor the New Zealand specimen are very well preserved, so that similarity is of low value, but nonetheless striking.

A moderately close species is the west Australian *Megasteges fairbridgei* (Coleman 1957, pl. 2, fig. 5-12) from the Hardman Member of the Kimberley area, and also near Port Keats, in the Cherrabun Member of Late Permian age (Archbold 1988, 1993a), here regarded as matching the Kufri faunas of the lower and middle Chhidru Formation, Salt Range. Archbold (1986a) noted a close approach to *Aulosteges baracoodensis* var *septentrionalis* Etheridge, 1907 and *Aulosteges reclinis* Coleman (1957, pl. 6, fig. 1 non cet.) A small specimen and the posterior part of larger ventral valves of *fairbridgei* are similar to the present specimen in shape, and show elevated coarse spine ridges, as suggested on the present specimen. A sulcus develops anteriorly. *Megasteges nepalensis* Waterhouse from the Senja Formation of Late Permian Changhsingian age in west Nepal is close in general appearance, but the ventral valve is more sulcate and no costae are present.

Order LYTTONIIDA new

DIAGNOSIS: Ostreiform inequivalve brachiopods with the dorsal valve represented largely by lobate brachidial plate. Spinose projections rare, limited to ventral valve and not comparable to spines of Productida, ventral valve with posterior flap, no interarea or teeth, hinge line normally covered by ventral shell, articulatory structures not comparable to those of Productida or other brachiopod orders. Secondary shell layer pseudopunctate.

DISCUSSION: Lytoniid brachiopods, in comparison with other brachiopods, are bizarre. They appear to have evolved from Productida, probably Strophalosiida, but differ so much from that order in so many ways that they should be separated as a discrete order. Despite excellent studies of the group, summarized and furthered by Termier & Termier (1949), Cooper & Grant (1974), Williams (1965, p. 511-521) and Williams, Harper & Grant (2000), details of morphology, shell structure growth of the shells, shell morphology and classification remain open to "fundamental revision" (Williams, Harper & Grant 2000, p. 619). Separation as an order does not imply the group did not evolve from Productida, a possibility that seems to have been endorsed by the discovery of a calcified ptychophorous brachidium in the strophalosioid *Falater* by Grant (1972). But the assignation as Order does indicate the greatness of the morphological gap.

TAXONOMY: Lytoniida Williams, Harper & Grant, 2000 was proposed as a new suborder, or accurately as a replacement name for Oldhaminidina Williams, 1953, 1965. The authors preferred to adjust the name to tie with the name Lytoniidae (p. 630), which had previously been set aside because of nomenclatural confusion. The renaming of the order follows a similar adjustment, after Waterhouse (1983d, p. 130) proposed Order Oldhaminida.

Order ORTHOTETIDA Williams, Brunton & Wright, 2000
 Suborder ORTHOTETIDINA Williams & Brunton, 2000
 Superfamily ORTHOTETOIDEA Waagen, 1884
 Family SCHUCHERTELLIDAE Williams, 1953
 Subfamily STREPTORHYCHINAE Stehli, 1954
 Genus *Notostrophia* Waterhouse, 1973

TYPE SPECIES: *Notostrophia homeri* Waterhouse, 1973 OD.

DISCUSSION: In 1973a, Waterhouse speculated that the shell of this genus was pseudopunctate, and this invited forthright comment from Williams & Brunton (2000, p. 470). Those authors chose to ignore, or overlooked, the fact that Waterhouse had revised his assessment of the shell in the type species (Waterhouse 1982a, p. 28) and for an Australian species (Waterhouse 1986b, p. 21). This underlines the need for care in using the revised brachiopod treatise, because some of its authors have not kept abreast of the literature, especially for Gondwanan studies.

With regard to their criticism, Williams & Brunton (2000) chose to stigmatize the Waterhouse terminology as "idiosyncratic". Perhaps so. Sometimes idiosyncrasy can be better than following the fashion. Both of the critics for many years used the terms pedicle and brachial valves, while I was apparently idiosyncratic enough to use ventral and dorsal. They did not use the term adminicula, I did. Now the revised brachiopod treatise, including articles by those authors, uses ventral, dorsal, and adminicula. Terms like pedicle valve, and brachial valve, are abandoned. Sometimes even people stigmatized as idiosyncratic can be right to stand out against prevailing fashions.

Order RHYNCHONELLIDA Kuhn, 1949
 Suborder RHYNCHONELLIDINA Kuhn, 1949
 Superfamily **WELLERELLOIDEA** Likharev, 1956
 Family **WELLERELLIDAE** Likharev, 1956
 Genus ***Plekonella*** Campbell, 1953
Plekonella n. sp.
 Pl. 5, fig. 19 - 22, 24

Two moderately well known species in the lower Middle Permian of New Zealand are *Plekonella acuta* Campbell, and *P. southlandensis* (Fletcher). *P. acuta* is typified by its triangular outline with long straight or concave posterior walls and 2 costae in the sulcus, and 3 ribs on the fold. In Australia, it is found in the lower Peawaddy Formation and Mantuan Member of the southwest Bowen Basin (Dear 1971), the upper Barfield Formation of southeast Bowen Basin (Parfrey 1988), and Abels Bay Formation of south Tasmania (Clarke 1987). In New Zealand, *P. acuta* was reported by Waterhouse (1964b) from various stratigraphic intervals, including the *Spiriferella supplantata* Zone, the *Echinalosia maxwelli* and *Terrakea elongata* Zones, and also in the *Marginalosia planata* Zone, of much younger age.

The other species *Plekonella southlandensis* has 3-5 costae in the ventral sulcus, and 4-6 costae on the fold, and lateral costae that branch. It is broad in outline, with short widely diverging posterior walls. It is found typically in the upper *Echinalosia ovalis* Zone of the Mangarewa Formation in New Zealand, and in the Flat Top Formation of the southeast Bowen Basin.

At Wairaki Downs, Letham Formation *Plekonella* comes from D44 localities at f110 (GS 15207), f307, f310, f311, f306, f314, f312, f328 and f331 from the lower *Echinalosia discinia* Zone and D44/f108-109 (GS 15208-15209), f115 (GS 15210), ?f305, f317, f322, f323, ?f324 in the upper *E. discinia* Zone. Specimens look mostly like *P. acuta*, with 2 sulcal costae, and long posterior walls. But there is variation, with more costae occurring in the sulcus and fold of some specimens, and branching costae laterally. From the *Lethamia ligurritus* Subzone (upper *E. discinia* Zone) at f108, individuals have 2-4 costae in the sulcus. Individuals are more varied from GS 9697 (D44/f9001) and f319, and 2-4 sulcal costae are seen in specimens from f322, and 4-5 in the sulcus on specimens from f321, whereas only 2 sulcal costae are seen in samples from f323 and f116 (GS 15211).

Specimens from GS 6070 (D44/f9621) at the top of unit 1 in the lower Letham Formation also show a mix of morphologies. At least 8 ventral valves, 4 dorsal valves, and 2 specimens with valves conjoined are like *Plekonella acuta*, as recorded by Waterhouse (1964b). But one ventral valve and 6 dorsal valves show the branching costae not regarded as normal for *P. acuta*. Also, one specimen with valves conjoined, BR 799 from GS 7343 (D44/f9861) from the lower part of unit 4 (*Echinalosia maxwelli* Zone), is large with several sulcal costae and lateral branching costae, somewhat as in *southlandensis*.

The Letham specimens could be identified as mixed *Plekonella acuta*, and *P. southlandensis*. But the specimens with 3-5 costae in the venter differ from typical *southlandensis* in having long posterior walls often concave in outline, and so approach *P. acuta* in shape. Also, the sulcus and fold commence well in front of the umbones, and costae increase by intercalation well forward, whereas costae in the sulcus of *southlandensis* commence close to the umbo.

In specimens from D44/f123 (GS 15226) from the lower Mangarewa Formation, the outer ribs bifurcate. The sulcus displays 2 or 3 ribs commencing near the umbo, and more may appear anteriorly, increasing by intercalation. These fall close to *Plekonella southlandensis* (Fletcher), as figured herein, but they are not fully identical.

Conceivably the Letham collections come from a variable suite of a new species, characterized by 2-5 costae in the venter, and long posterior walls. And possibly the D44/f123 examples indicate another morphotype. But further material is desirable to establish this possibility. As a holding measure until collections can be remeasured and reassessed, the forms narrowly typical of *acuta* and *southlandensis* are identified as those species, and the others discriminated as *Plekonella* n. sp.

A degree of variation is displayed by a suite of *Plekonella*, identified as *acuta*, by McClung (1983, text-fig. 10) from GSQ locality LD 96 in the Denison Trough, Bowen Basin, Queensland. Some show more than two sulcal costae (text-fig. 10.7, 11). The correlation was not accurately determined by McClung (1983), but may fall close to the Catherine Sandstone. Another so-called *acuta* specimen (McClung 1983, text-fig. 10.5) from interval F (= *Terrakea elongata* Zone), GSQ Eddystone 1, west Bowen Basin, is like *Plekonella southlandensis* (Fletcher).

Plekonella? sp.

MATERIAL: Two dorsal valves from D45/f7578, *Spinomartinia spinosa* Zone, Hilton limestone block, Wether Hill Station. Obscure dorsal valve from same zone at D44/f9479, Hilton Limestone, Wairaki Downs.

DESCRIPTION: A poorly preserved specimen from D45/f7578, preserved as an internal mould 8.5 mm wide, has scarcely any dorsal fold other than a broad median swelling, and costae are low, numbering 4-5 pair. Dental sockets denticulate, medium septum extends for half the length of valve. Cardinal plate broad, and bears broad oval median ridge. Another specimen from D45/f7578 is just over 7mm wide and has a more raised dorsal fold, damaged, but possibly bearing 4 costae, with 2 costae to each side. A medium septum is present but cardinalia are not revealed.

The Coral Bluff dorsal valve from D44/f9479 shows a very low fold with 3 costae, the median one bifurcating at the anterior margin. There are a few lateral costae, but the full number is obscured by poor preservation. The median septum extends almost to mid-length. Part of dental socket also present.

Suborder STENOSCISMATIDINA Waterhouse, 1981

Sapel'nikov & Mizens (1989) independently proposed the same suborder.

Superfamily **STENOSCISMATOIDEA** Oehlert, 1887

Family **STENOSCISMATIDAE** Oehlert, 1887

Genus ***Stenoscisma*** Conrad, 1839

Stenoscisma? sp.

Pl. 5, fig. 23, text-fig. 5l

MATERIAL: Three complete ventral valves, including BR 2350, 2 dorsal valves from D44/f9479 (GS 3615), ventral and dorsal valve from same locality (s.l.), D44/f376, OU 18301-2, *Spinomartinia spinosa* Zone, Hilton Limestone, Wairaki Downs.

DIMENSIONS IN MM:

Specimen	Width	Length	Height
BR 2350	25	?23	6.5 ventral
OU 18302	25	17	6 ventral
OU 18301	22	21	7.5 dorsal

DESCRIPTION: Valves subpentagonal, umbo extended, incurved, umbonal angle 90-100°, posterior walls gently concave in outline, maximum width lies a little in front of mid-length. Inflation varies from low to moderate, presumably depending on degree of maturity of specimens, dorsal valve transverse and less inflated. Inflated ventral valve has anterior sulcus, not seen in less inflated shells, and measured dorsal valve suggests low fold or rise over mid-length. No costae visible and probably absent although the fact that the anterior is poorly preserved in several specimens means uncertainty remains. Low concentric growth rugae and faint growth lines.

Ventral spondylium well developed, sides concave inwards, irregularly marked by low growth lines parallel to anterior edge, sessile on thickened posterior floor, supported anteriorly by low median thick ridge. A slender ridge appears to lie along middle of spondylium in the most inflated specimen, but could be caused by fracture. This specimen carries low radiating pallial lines on floor of valve in front of spondylium, low median ridge and scattered pallial pits. Shell much thickened posteriorly.

Dorsal valves more obscure internally. Specimen OU 18301 has long slender median septum extending more than third of shell length from umbo and shows posterior part of septalium. A second very obscure specimen shows dental sockets and part of septalium on high median septum.

DISCUSSION: The genus cannot be fully determined, because of uncertainty about the dorsal interior and anterior costation. *Stenoscisma papilio* Waterhouse, 1964 from the *Plekonella multcostata* Zone of the Kildonan Member, Bagrie Formation, Arthurton Group has a little inflated ventral valve and is medianly costate, *Stenoscisma* sp. of Waterhouse (1982a, p. 52) from the same zone is inflated with strong anterior costae. *Stenoscisma glabra* Waterhouse, 1986 from the Brae Formation of the southeast Bowen Basin, Queensland, is even less inflated than the Coral Bluff material, and lacks costae and well formed sulcus.

The material is moderately close to *Psilocamara* Cooper in its ventral valve, but the dorsal interior, although not completely clear, seems different. *Psilocamara saginatum* Waterhouse, 1964 is found in the *Notostrophia zealandicus* Subzone of the lower Takitimu Group, and is readily distinguished from the Coral Bluff specimens by its higher ventral valve with well formed sulcus. A likely ventral valve of *Psilocamara* OU 18759 has been found at Wilanda Downs (D45/f7115), as figured herein (pl. 5, fig. 25).

Order SPIRIFERIDA Waagen, 1883

Suborder SPIRIFERIDINA Waagen, 1883

Superfamily **MARTINIOIDEA** Waagen, 1883

Family **MARTINIIDAE** Waagen, 1883

Subfamily **MARTINIINAE** Waagen, 1883

Genus ***Spinomartinia*** Waterhouse, 1968

This genus has been discussed by Shi & Waterhouse (1996, p. 148) and Waterhouse (1981, 1999b, p. 4), in relation to *Martinia* M'Coy, *Tiramnia* Grunt and *Heteraia* Cooper & Grant, all regarded as closely related, and referable to Martiniidae, as indicated by the critical lack of adminicula from the ventral valve. Elivellinae Carter, 1994 has been regarded as a subfamily within Martiniidae, but here it is preferred to regard Elivellinae as falling within Spiriferoidea, because constituent genera have adminicula.

Spinomartinia? adentata (Waterhouse, 1964)

Pl. 5, fig. 26, 27, text-fig. 7a

1964b *Martinia adentata* Waterhouse, p. 114, pl. 21, fig. 10-14, text-fig. 53A, B, 54.

1999b *Spinomartinia? adentata* (Waterhouse); Waterhouse, p. 5.

HOLOTYPE: BR 670, figured by Waterhouse (1964b, pl. 21, fig. 10, 11, 13, 14, text-fig. 53A, B) OD from D44/f9511 (GS 5296), *Spinomartinia? adentata* Zone, upper Brunel Formation (?), Wairaki river valley.

MATERIAL: Three ventral valves and fragments from D44/f378, lower McLean Peaks Formation, Spense Burn, Aparima Valley.

DIMENSIONS IN MM: Ventral valve

Specimen	Width	Length	Height
OU 18761	29	30	12 distorted
OU 18760	32	37	19

DESCRIPTION: The specimens are moderately well preserved. The larger specimen is more elongate than the types, but accompanying specimens each differ in outline, pointing to some variability, although all are elongate. As they are preserved in fine sandstone it was hoped that the nature of micro-ornament might be determined (Waterhouse 1999b), but leaching of one specimen in dilute HCl revealed that the surface is mostly covered in a dense web of burrowings, obscuring micro-ornament. The shell shows an outer white fibrous layer, with fibres vertical to the exterior, and an inner translucent brown crystalline layer, half to a third of the valve thickness. The outer fibrous layer in the large measured specimen appears to be covered by a very thin external layer which seems to be made up of fine radial lathes, that bear or form close-set fine growth increments, about 3-4 per mm. No spines are visible. In patches the outer layer is slightly worn, to reveal the ends of the fibres, which look like the "exopunctae" reported for *Martinia* by early workers. It thus appears from this material that Cooper & Grant (1976) could have been right to dismiss the reported exopunctae as a weathering effect, even though challenged by Waterhouse (1999b). Yet that may not explain why the exopunctae of *Martinia* appear to be arranged so regularly in quincunx.

Ventral adductors divided by fine thin low median ridge, and marked by fine growth grooves directed postero-laterally over the scars. To each side lie wide diductor impressions scored by 5-6 radial grooves, with finer radial markings. Delthyrium appears closed, at least under umbo, by low plate joining posterior part of low dental plates.

Spinomartinia spinosa Waterhouse, 1968

Pl. 6, fig. 1 - 4, text-fig. 7 b

1968a *Spinomartinia spinosa* Waterhouse, p. 53, pl. 8, fig. 4, 5, 9-11, pl. 9, fig. 1-8, pl. 17, fig. 4.

cf 1969 *Martinia* sp. Runnegar & Ferguson, p. 278, pl. 5, fig. 12, 13.

1978 *S. spinosa* Waterhouse; Waterhouse in Waterhouse & Mutch, p. 522, text-fig. 16, 19-25.

1978 *S. spinosa* Waterhouse; Suggate et al, text-fig. 11, 3, fig. 8-10.

1981 *S. spinosa* Waterhouse; Speden, pl. 8, fig. 8-10.

1999b *S. spinosa* Waterhouse; Waterhouse, p. 6.

HOLOTYPE: OU 2413, kept at University of Otago, figured by Waterhouse (1968a, pl. 9, fig. 2-4), Suggate et al (1978) and Speden (1981) OD from G45/f8498 (GS 1456), *Spinomartinia spinosa* Zone, Trig DD Formation, Arthurton Group near Clinton.

DIAGNOSIS: Large oval to rounded shells with prominent ventral umbo and inflated ventral valve, dorsal valve less inflated, with broad umbo.

DISCUSSION: This species was originally described from the Arthurton Group near Clinton, south Otago. Additional material was described by Waterhouse (1999b) from Hilton limestone at D45/f7578 (BR 2391-2), Wether Hill Station, and D44/f376, including OU 18278-18280, Wairaki Downs. Two well preserved ventral valves OU 2575/2026 and a dorsal valve come from D45/f7000, Wether Hill Station, and some ventral valves are found in basal sandy beds in the headwaters of Pleasant Creek, Aparima River, at D44/f379. Possibly allied material was figured from the upper South Curra Limestone of the Gympie Basin, southeast Queensland, by Runnegar & Ferguson (1969).

Superfamily **SPIRIFEROIDEA** King, 1846
 Family **SPIRIFERIDAE** King, 1846
 Subfamily **SPIRIFERINAE** King, 1846
 Genus **Fusispirifer** Waterhouse, 1966

TYPE SPECIES: *Spirifer nitiensis* Diener, 1897.

SUBFAMILY: Poletaev (1997) indicated that this genus has the apical apparatus and costal development of Spiriferinae, whereas previously the genus has been regarded as a member of Neospiriferinae, including the study by Carter et al (1994).

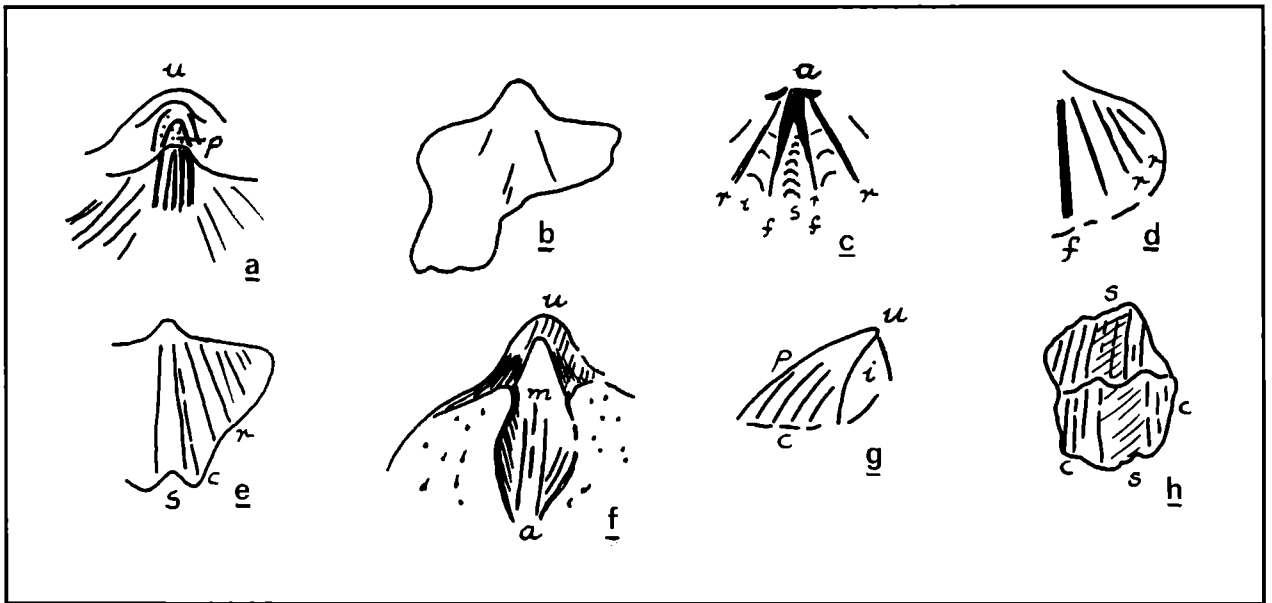
Fusispirifer? sp.
 Pl. 6, fig. 8, 9

1968a *Aperispirifer* sp. B Waterhouse, p. 36, pl. 3, fig. 10, 14.

1999b *Fusispirifer?* sp. Waterhouse, p. 8.

MATERIAL: Several fragments of ventral valves from D44/f9479 (GS 3615) and D44/f376 (OU 18762-3), *Spinomartinia spinosa* Zone, Hilton Limestone, Wairaki Downs.

DISCUSSION: *Fusispirifer* was first named from Himalayan material and is moderately common in Western Australia and throughout the lower and middle Permian of the Bowen Basin (Waterhouse 1987a, pp. 22-24), and Malbina Formation Member E of Tasmania (Clarke 1987, p. 267, text-fig. 5A-E). The genus is rare in New Zealand, as obscure fragments from Coral Bluff, Wairaki Downs, and was identified for Dr H. J. Campbell, IGNS in the Parapara Group of west Nelson (Campbell, Smale et al 1998).



Text-fig. 7. Diagrams of Spiriferida

- a. *Spinomartinia? adentata* (Waterhouse) from Takitimu Group, D44/f378, OU 18761, ventral valve leached mould, showing p - small plate under u - umbo, x 3.
 b. *Spinomartinia spinosa* broken ventral valve OU 18280 from D44/f376, Hilton Limestone, x 1.2.
 c. *Alispiriferella* sp. dorsal valve OU 18285 from D44/f363, Glendale Formation, x 3, showing s - wide sulcus in f - fold, r - rib, i - interspace, a - interarea, x 4.
 d. *Arcullina humilis* OU 18767 from D45/f7115, Takitimu Group, dorsal costal diagram showing narrow round-crested fold f, with narrow lateral plicae r, x 1.
 e. *A. humilis* OU 18764 from same locality, ventral costal diagram. s - sulcus, r - plication, c - branching costa, x 1..
 f. *Ingelarella* or *Homevalaria* sp. OU 18769 from D44/f376, Hilton Limestone, ventral internal mould with deep sulcus, showing m - high muscle field, with a - adductors and u - umbo, x 1.
 g. Syringothyrididae gen. & sp. indet. A OU 18300 from D44/f376, Hilton Limestone, oblique lateral posterior view of finely punctate fragmentary ventral valve, with c - costae, i - interarea, p - lateral edge of sulcus, u - umbo, x 2.
 h. *Sulcicosta* sp. BR 2363 from D44/f111, Letham Formation, punctate fragment of ventral internal mould with sulcus s cracked and displaced across middle, and low costae c in sulcus and on flanks, x 1.

Genus **Transversaria** Waterhouse & Gupta, 1983

TYPE SPECIES: *Fusispirifer marcouiformis* Jin in Zhang & Jin, 1976.

DIAGNOSIS: Transverse spiriferids with alate cardinal extremities and fine costae or costellae, no develop-

ment of plication or fasciculation except faintly at beak, sulcus narrow, well formed, fold and fastigium high, delthyrial plate.

SYNONYM: *Latispirifer* Archbold & Thomas, 1985, type species *L. callytharrensensis* Archbold & Thomas, 1985.

DISCUSSION: Carter et al (1994, p. 346) synonymized the genus *Transversaria* Waterhouse & Gupta, 1983 with *Fusispirifer*. The type species of *Transversaria* is *Fusispirifer marcouiformis* Jin in Zhang & Jin (1976, pl. 12, fig. 9-11, pl. 13, fig. 1, 2, 21-23) OD from the *Taeniothaerus* assemblage in the Permian Shilong Group of south Tibet. As is clear from the Jin description, provided in translation by Waterhouse & Gupta (1983, p. 240) and the original figures, *marcouiformis* lacks plicae - or at best the plicae are so subdued that their presence was denied by Jin, and do not appear on the illustrations. Therefore the genus is readily distinguished from *Fusispirifer* (Waterhouse 1999b) and resembles *Spirifer* and allies quite closely, apart from transverse outline.

Archbold & Thomas (1985b, p. 270, 1987, p. 177) claimed that *Fusispirifer marcouiformis* had been based on two species and claimed that the lectotype of the species, as selected by Waterhouse & Gupta (1983) belonged to *Fusispirifer*, whereas the other specimens belonged to *Latispirifer* Archbold & Thomas 1985, a genus described from the Carnarvon and other Permian basins of Western Australia. The lectotype of *marcouiformis* was misinterpreted by Archbold & Thomas (1985b). They stated that it was only an internal mould: in fact the ventral exterior is also preserved and figured: it lacks external plicae. The figures in Zhang & Jin (1976, pl. 13, fig. 1 and 23) show the posterior exterior of the ventral valve, and are not internal moulds. They show shell split off from the internal mould. I saw the material at Nanjing in 1980. The other figured specimen which was considered to be *Latispirifer* by Archbold & Thomas (1987) is a larger individual of the same species. Therefore *Transversaria* appears to be valid, and a senior synonym of *Latispirifer*. The interpretations made by Archbold & Thomas (1985b) to defend their genus have to be set aside, and in fact help demonstrate that *Latispirifer* is a junior synonym.

Subfamily **NEOSPIRIFERINAE** Waterhouse, 1968

Genus ***Neospirifer*** Frederiks, 1924

Neospirifer arthurtonensis Waterhouse, 1968

Pl. 6, fig. 5 - 7

1968a *Neospirifer arthurtonensis* Waterhouse, p. 28, pl. 2, fig. 14, 16, pl. 3, fig. 1-9, pl. 17, fig. 1, 3, text-fig. 7C, D, 9A, 10-13.

1976a *N. arthurtonensis* Waterhouse; Waterhouse, p. 244, text-fig. 6.5, 7.7.

1999b *N. arthurtonensis* Waterhouse; Waterhouse, p. 9.

HOLOTYPE: BR 521, figured by Waterhouse (1968a, pl. 3, fig. 1) OD from G45/f8613 (GS 5079), *Martiniopsis woodi* Zone, Bagrie Formation, Arthurton Group, near Arthurton.

DIAGNOSIS: Small shells with prolonged ventral umbo, sulcus deep and U-shaped in section, persistent plicae with coarse costae.

DISCUSSION: Material was recorded by Waterhouse (1999b) from D44/f363, equivalent *Plekonella multicosata* Zone, Glendale Formation, Wairaki Downs, and is figured herein.

The taxon *arthurtonensis* is one of the species recognized as valid *Neospirifer* in a world review by Poletaev (1997).

***Neospirifer?* sp.**

1999b *Neospirifer?* sp. Waterhouse, p. 10.

DISCUSSION: Material was described by Waterhouse (1999b) from D44/f9479 (GS 3615) and f376, *Spinomartinia spinosa* Zone, Hilton Limestone, Wairaki Downs.

Neospirifer mossburnensis Waterhouse, 1999

1967b *Neospirifer* sp. Waterhouse, p. 91, text-fig. 28.

1982 *Trigonotreta? nelsonensis* (not Waterhouse); Hyden et al, text-fig. 2a-d.

1999b *Neospirifer mossburnensis* Waterhouse, p. 11.

HOLOTYPE: Specimen OU 2590 figured by Hyden et al (1982, text-fig. 2a-d) OD from E44/f001, Stephens Subgroup, near Mossburn, reworked from Permian.

DIAGNOSIS: Transverse shells with broad inner plicae and fine costae.

DISCUSSION: This species is represented by scattered valves in the *Wairakiella rostrata* Zone, Wairaki Brec-

cia-Conglomerate, Wairaki Downs. A number of specimens are well preserved, but remain to be figured.

Subfamily **TRIGONOTRETINAE** Schuchert, 1893
Genus *Trigorhium* new

DERIVATION: tri - three,

TYPE SPECIES: *Neospirifer amphigyus* Cooper & Grant, 1976, here designated.

DIAGNOSIS: Large transverse shells with alate cardinal extremities, well formed sulcus and fold, open delthyrium with large apical callosity. Plicae high, 5-6 pairs, primary costa much higher than other costae, usually one costa each side, and these tend to split in pairs anteriorly. Sulcus with median plication and subplication or fascicle to each side in large shells, comprising dominant central rib and finer lateral rib each side. Concentric laminae moderately well defined.

DISCUSSION: The type species was figured by Cooper & Grant (1976, p. 2174, pl. 502, fig. 11, pl. 593, fig. 1-15, pl. 594, fig. 1-11) from the China Tank Member of the Word Formation, Glass Mountains, Texas, and ranging into Appel Ranch Member. It was ascribed to *Neospirifer*, but has high primary ribs in the plicae, and open delthyrium with apical callosity, characters which point to Trigonotretinae, not Neospiriferinae. In overall appearance, the species comes moderately close to *Trigonotreta* Koenig. The cardinal extremities may be alate in this genus, as for example in *T. dickinsi* Archbold & Thomas (1986a) from the Noonkanbah and Wandagee Formations of Western Australia, and some forms have as many costae in the rib bundles. The most distinctive feature of the new form lies in the presence of fascicles over the floor of the sulcus (see Cooper & Grant 1976, pl. 593, fig. 1 (holotype), pl. 594, fig. 7, 8), never seen in species so far ascribed to other members of Trigonotretinae, or Neospiriferinae. Plicae may enter the sulcus in *Aperispirifer* and allies, by anterior widening of the sulcus, but such are laterally placed, whereas those of *Trigorhium* are medianly placed.

Genus *Aperispirifer* Waterhouse, 1968

TYPE SPECIES: *Aperispirifer lethamensis* Waterhouse, 1968.

DIAGNOSIS: Large generally transverse or rarely elongate shells with weakly alate cardinal extremities. Sulcus well defined posteriorly, may broaden and deepen or become shallow anteriorly. Ornament of fasciculate costae with round or angular crests, primary costa not prominent, bundles may fade anteriorly or persist to margin. Concentric laminae may be very prominent, especially on the type species. Delthyrium open, rimmed by dental tracks, floor of shell under delthyrium occupied by callosity of small to large size. Teeth supported by dental plates and adminicula, dorsal valve with unsupported crural plates, not extending to floor.

DISCUSSION: This genus is distinguished from *Trigonotreta* Koenig by its costae: *Trigonotreta* has higher plicae, with the median costa high and prominent, at least posteriorly, and there appears to be scope for subdividing the genus. As discussed below, *Aperispirifer* is very close to *Lepidospirifer* Cooper & Grant, and the differences between them might by some be considered as minor and geographic. No species has been described as yet from beds older than Kungurian in New Zealand or east Australia, and the youngest known species is of late Lopingian age.

Species of east Australia and New Zealand are shown in Table 9.

Aperispirifer archboldi Waterhouse, 1999
Pl. 6, fig. 10

1964b *Neospirifer wairakiensis* not Waterhouse; Waterhouse, p. 127, pl. 23, fig. 5, 7, 8-10, pl. 24, fig. 1-3, pl. 25, fig. 2-4, 6, 7, text-fig. 61A, 62, 63 (not pl. 23, fig. 4, 6, pl. 25, fig. 1, 5, pl. 35, fig. 4, text-fig. 56-60, 61B = *Aperispirifer wairakiensis* (Waterhouse)).

1968a *Aperispirifer wairakiensis* (Waterhouse); Waterhouse, p. 35.

1978 *N. wairakiensis* not Waterhouse; Suggate et al, text-fig. 4.5, fig. 10, 13.

1981 *A. wairakiensis* (not Waterhouse); Speden, pl. 5, fig. 10, 13.

1982a *Aperispirifer wairakiensis* (not Waterhouse); Waterhouse, p. 54, pl. 15a.

1999b *Aperispirifer archboldi* Waterhouse, p. 12.

HOLOTYPE: BR 814, figured by Waterhouse (1964b, pl. 23, fig. 5, 1982a, pl. 15, fig. a), Suggate et al (1978, text-fig. 4.5, fig. 10) and Speden (1981, pl. 5, fig. 10) OD from D44/f9621 (GS 6070), *Spiriferella supplanta* faunule, Letham Formation, Wairaki Downs.

DIAGNOSIS: Moderately large, not very transverse specimens with heavy secondary callus, plicae moderately persistent, ribs coarse with rounded crests, sulcus broad anteriorly.

DISCUSSION: The species is restricted to the *Spiriferella supplantata* faunule in the basal Letham Formation in New Zealand. Few *Aperispirifer* have been described from the Middle Permian of east Australia at this level. But a small dorsal valve UQF 65496 from the Freitag Formation from the southwest Bowen Basin has a broad low fold, comparable to that seen in BR 476 (Waterhouse 1964b, pl. 24). Costae are finer than in the Letham specimens. I have also observed specimens of this species from the Elderslie Formation, Sydney Basin, in collections from UNEL 1022 and 990 (UNEF 14331).

The round-crested costae and strong lamellae of this species show some approach aspects of *Lepidospirifer* Cooper & Grant, found in the Cathedral Mountain Formation (Kungurian Stage) and Road Canyon Formation (Roadian Stage) of Glass Mountains, Texas.

***Aperispirifer lethamensis* Waterhouse, 1968**

1968a *Aperispirifer lethamensis* Waterhouse, p. 38, pl. 3, fig. 13, pl. 4, fig. 1-7, pl. 5, fig. 2-4, 6, 7, pl. 6, fig. 3, text-fig. 11-13, 14A-C (not pl. 3, fig. 15, pl. 5, fig. 1, 5, 8, pl. 6, fig. 2, text-fig. 11-13, 14D, 15 = *A. parfreyi* Waterhouse)

1978 *A. lethamensis* Waterhouse; Suggate et al, pl. 4.6, fig. 10-12.

1981 *A. lethamensis* Waterhouse; Speden, pl. 6, fig. 10-12.

1982a *A. lethamensis* Waterhouse; Waterhouse, p. 91, text-fig. 29c.

1999b *A. lethamensis* Waterhouse; Waterhouse, p. 13.

The species *Aperispirifer lethamensis* is based on material from the *Echinalosia discinia* Zone, *Lethamia ligurritus* Subzone, Letham Formation, Wairaki Downs. Lateral plicae are present in the sulcus but are fainter than in *wairakiensis* and the ventral umbo is moderately broad. In southeast Bowen Basin the approximately correlative Brae Formation contains *Neospirifer concentricus* Waterhouse (Table 9).

***Aperispirifer wairakiensis* (Waterhouse, 1964)**

1964b *Neospirifer wairakiensis* Waterhouse, p. 127, pl. 23, fig. 4, 6, pl. 25, fig. 1, 5, pl. 35, fig. 4, text-fig. 56-60, 61B (not pl. 23, fig. 5, 7, 8-10, pl. 24, fig. 1-3, pl. 25, fig. 2-4, 6, 7, text-fig. 61A, 62, 63 = *A. archboldi* Waterhouse).

1968a *Aperispirifer wairakiensis* (Waterhouse); Waterhouse, p. 35.

1999b *A. wairakiensis* Waterhouse; Waterhouse, p. 14.

In New Zealand, this species is restricted to the Letham Burn Member, lower Mangarewa Formation, in the *Echinalosia maxwelli* Zone (Table 9). In the correlative *E. maxwelli* Zone of the Oxtrack Formation of the southeast Bowen Basin, *Aperispirifer ovalis* Waterhouse (1987a) is present, readily distinguished from *Aperispirifer wairakiensis* by its narrower more elongate shell, but showing comparable plicae, which are angular in cross-profile, fading anteriorly, with inner pair lying well within the sulcus. Arguably the similarity in plicae on both forms, and difference in shape, could mean that *ovalis* is a subspecies of *wairakiensis*.

Specimens described as *Neospirifer* sp. by Campbell (1953) and *Neospirifer* sp. B by Hill & Woods (1964, pl. P8, fig. 5) from the Ingelara Formation (s.l.) of the Denison Trough, southwest Bowen Basin, and later ascribed to *N. wairakiensis* in Hill et al (1972, pl. P8, fig. 5) were named *A. wairakiensis hillae* Waterhouse (1999b, p. 14). The ventral umbo is prolonged posteriorly, with high costae, and the shell has a rhomboid shape, pointing to *Aperispirifer wairakiensis*. Plicae are more persistent, the sulcal subplicae only moderately developed, and the sulcus broad and deep anteriorly, compared with *A. wairakiensis*. In these regards the specimens approach *A. parfreyi*, and have moderate concentric laminae. There is also a close approach to *A. lethamensis*. The stratigraphic position of the Campbell specimens is not clear, as although Hill stated Ingelara Formation, the matrix is shale, suggesting lower Peawaddy Formation. Parfrey (1988, p. 32, text-fig. 10) showed its range as starting above Ingelara and only uncertainly in lower Peawaddy, so it is possibly mostly Catherine Sandstone.

Table 9. Succession of *Aperispirifer* and *Neospirifer* (*N*) in southeast Bowen Basin and New Zealand.

SE Bowen Basin Formation	Species	SW Bowen Basin Formation	Species	Formation & unit	New Zealand Species
Flat Top	<i>parfreyi</i>	Eddystone E, F	<i>parfreyi</i> var.	8b aff.	<i>parfreyi</i>
Barfield	<i>parfreyi</i>	Mantuan	<i>parfreyi</i>	Mangarewa7b	<i>parfreyi</i>
		L. Peawaddy		6	<i>parfreyi</i>
		Catherine	<i>wairakiensis hillae</i>		
		Ingelara		5	
Oxtrack	<i>ovalis</i>			4	<i>wairakiensis</i>
Brae	<i>N. concentrica</i>			Letham 3	<i>lethamensis</i>
-	-			2	-
-	-	Freitag	<i>archboldi</i>	1	<i>archboldi</i>

***Aperispirifer parfreyi* Waterhouse, 1999**

1952 *Spirifer* aff *tasmaniensis* (not Morris); Fletcher in Fletcher et al, p. 15, pl. 1, fig. 2.

1964b *Neospirifer* sp. A Waterhouse, p. 134, pl. 26, fig. 1.

1964 *Neospirifer* sp. A Hill & Woods, pl. P8, fig. 2-4 (not pl. P8, fig. 5 = *A. wairakiensis hillae* Waterhouse).

1968a *Aperispirifer lethamensis* not Waterhouse; Waterhouse, p. 38, pl. 3, fig. 15, pl. 5, fig. 1, 5, 8, pl. 6, fig. 2, text-fig. 11-13, 14D, 15 (not pl. 3, fig. 13, pl. 4, fig. 1-7, pl. 5, fig. 2-4, 6, 7, pl. 6, fig. 3, text-fig. 11-13, 14A-C = *A. lethamensis* Waterhouse).

1972 *Neospirifer wairakiensis* not Waterhouse; Hill et al, pl. P8, fig. 2-4 (not pl. P8, fig. 5 = *A. wairakiensis hillae*).

1983 *Trigonotreta* sp. D McClung, p. 66, text-fig. 9, ?2, 5, 6 (not 1, 3, 4, 7 = *A. wairakiensis hillae?*).

1987a *A. lethamensis* not Waterhouse; Waterhouse, p. 21, pl. 5, fig. 1-3, 5-8, 10.

1988 *A. wairakiensis* (not Waterhouse); Parfrey, p. 17, pl. 3, fig. 14, 18, 20, 21, 23-25, pl. 4, fig. 1.

1999b *A. parfreyi* Waterhouse, p. 15.

HOLOTYPE: UQF 69977, figured by Waterhouse (1987a, pl. 5, fig. 1, 3) OD, from Barfield Formation, south-east Bowen Basin, Queensland.

DIAGNOSIS: Transverse shells with subrectangular outline, ventral umbo only moderately high, sulcus well defined, fold high and narrow-crested, plicae raised, persistent, pair of plicae incorporated in sulcus, costae moderately high.

DISCUSSION: This species is characteristic of the Barfield and lower Flat Top Formations of southeast Bowen Basin, Mantuan Member, west Bowen Basin, and a narrow zone with *Echinalosia ovalis* and *Paucispinauria solida* in the Blenheim Formation of the north Bowen Basin. In New Zealand it is typical of the upper Mangarewa Formation, Wairaki Downs, in the *Echinalosia ovalis* Zone. Allied specimens are found in the topmost Mangarewa Formation, *Terrakea elongata* Zone, and in the correlative GSQ core of Eddystone, level E (McClung, 1983) and possibly F, although the figured specimen is a narrow internal ventral mould, not very informative. Indeed no well preserved *Aperispirifer* has yet been described from the *elongata* Zone.

Genus ***Lepidospirifer*** Cooper & Grant, 1969

TYPE SPECIES: *Lepidospirifer angulatus* Cooper & Grant, 1969.

DISCUSSION: *Lepidospirifer* is very close indeed to *Aperispirifer* Waterhouse, 1968. It has an open delthyrium with small apical callosity normally fused to the floor of the valve rather than extending forward as a platform, costellae, plicae and prominent growth lines which were stressed as highly significant by Cooper & Grant (1969), but are like those of *Aperispirifer*. Differences from *Aperispirifer* that involve slight differences in outline and prominence of the ventral umbo may be discounted, because *A. ovalis* Waterhouse is shaped like *Lepidospirifer* species. The ribs of *Lepidospirifer* tend to be close-set with round crests, whereas those of *Aperispirifer* are spaced slightly further apart and may have angular crests. As well, the apical callosity is smaller in *Lepidospirifer*. Thus there are differences, but some authorities may discount their generic significance and regard *Lepidospirifer* as a subgenus or as a small cluster of geographically isolated species within *Aperispirifer*. Certainly the ornament in *Neospirifer* shows as much or more variation, and *Trigonotreta* is highly variable, although in this case, there is room for generic or subgeneric distinctions.

Whatever the generic validity, it appears that *Lepidospirifer* is a member of Trigonotretinae, and marked an outpost of the subfamily in the paleotropical realm of Texas in the Permian. It was best developed in the Cathedral Mountain Formation, of Kungurian age, with one species persisting into Roadian. Poletaev (1997) included the genus in Neospiriferinae. He stressed the lack of vascular channels, but this was most likely a reflection of the silicified shells examined by Cooper & Grant, and possibly the thinness of the shell that grew in paleotropical conditions. He also stressed the tiled nature of the ornament, but this is seen as well in some species of *Aperispirifer*, and is judged to be a specific and ecologic feature.

Genus ***Sulciplica*** Waterhouse, 1968

TYPE SPECIES: *Sulciplica transversa* Waterhouse, 1968.

DISCUSSION: Shi et al (1997) pointed out that this genus had a notable and suggestive biogeographic distribution in the Permian, centred in east Australia, and extending to New Zealand, Perth Basin of Western Australia (Archbold 1995a) and the Shan-Thai terrane of southeast Asia. The only species reliably known in New Zealand is *Sulciplica vellai* Waterhouse, 1999b from the Flowers Formation of northwest Nelson. An additional possible species was misidentified as ?*Notospirifer* sp. by Campbell et al (1984, p. 277, text-fig. 6.7) from the Stephens Subgroup, Stephens Island, east Nelson.

Family **SPIRIFERELLIDAE** Waterhouse, 1968

Permian Spiriferellidae are most abundant in the Arctic and Himalaya, rare in paleotropics, and completely absent from eastern Australia. A number of species are found in Western Australia. New Zealand also hosts a number of species, with comparatively high generic diversity.

Genus ***Spiriferella*** Chernyshev, 1902

Spiriferella sp. A

Pl. 6, fig. 13

DISCUSSION: A ventral valve OU 18285 and other fragments from D44/f376, *Spinomartinia spinosa* Zone, Hilton Limestone, Wairaki Downs. Sulcus well defined, sides diverge at 15-17°. Costae low, subequal, rounded crests, 3 pairs of very low and scarcely perceptible plicae. Muscle field elongate and posterior shell very thick.

Spiriferella sp. B

Pl. 6, fig. 11, 16

1968a *Spiriferella* sp. Waterhouse, p. 50.

1982a *Spiriferella* sp. Waterhouse, p. 54.

1999b *Spiriferella* sp. Waterhouse, p. 19.

DISCUSSION: This material, consisting of worn ventral valves, is figured for the first time. Waterhouse (1982a, p. 102) quoted a personal communication from Profs. J. D. Campbell and C. A. Landis who collected the material that it came from the Glendale Limestone, confirming the record by Force (1975, p. 376) of a fossil in conglomerate in the Glendale Limestone. The shells are so worn that they may not necessarily have sourced from the Glendale. Now outcrop is very poor due to plant growth. Even if it had been reworked from older Permian, the ultimate source remains unclear. *Arcullina humilis* from the upper Takitimu Group has narrower plicae and narrower umbo, *Spiriferella supplantata* from the lower Letham Formation is perhaps closest, and *Alispiriferella* sp. from the lower Glendale Formation is more transverse with wide inner plicae.

Genus ***Arcullina*** Waterhouse, 1986

TYPE SPECIES: *Spiriferella polaris* Wiman, 1914.

DIAGNOSIS: Spiriferellidae characterized by simple dorsal fold without median groove and generally no costae. Plicae well developed, often smooth, median or lateral costae or both sets in sulcus, secondary thickening generally heavy in ventral valve.

DISCUSSION: This genus was erected by Waterhouse (1986a) for species tabulated in column A of *Spiriferella* in Waterhouse & Waddington (1982). Of the species assigned, a median groove has been reported for the species *australasica* Etheridge by Archbold & Thomas (1985a), not realized by Waterhouse & Waddington, so this species should be transferred. Other species may be added to the genus, including some noted below. The primary character is generally reinforced by the other attributes noted in the diagnosis. Several species in north Russia were described as *Arcullina* by Kalashnikov (1998) and Grunt et al (1998).

Arcullina humilis n. sp.

Pl. 6, fig. 12, 14, 15, 17 - 21, text-fig. 7d, e

DERIVATION: *humilis* - lowly, Lat.

HOLOTYPE: OU 18766, figured in pl. 5, fig. 14, from D44/f7115, ?McLean Peaks Formation, Wilanda Downs, here designated.

DIAGNOSIS: Small shells with heavy internal ventral thickening, low narrow sparsely costate plicae, very high ventral interarea, no dorsal median groove.

MATERIAL: A dorsal valve and 5 ventral valves from D44/f7115, *Echinalosia conata* Zone, McLean Peaks Formation, Wilanda Downs.

DIMENSIONS IN MM:

Specimen	Width	Length	Height	Hinge	Adductor	Platform
OU				W	W	L
18765	28	32	+15	27	11.5	14.5
18766	26	24	13			
18764	26	19	+7			

DESCRIPTION: Specimens small but at maturity to judge from thick shell, usually slightly elongate, with

wide hinge and blunt cardinal extremities. The ventral interarea is very high, gently concave, marked by horizontal and radial grooves and ridges, with open delthyrium blocked by a swollen umbonal callosity with rounded crest in one specimen and divided crest in the other. Ventral sulcus well formed, angle close to 30°, floor concave, without prominent median costa, a prominent rib each side; plicae number 5 pair, grading evenly in size to flanks, bearing no costae for 12-15mm, then becoming subdued with suggestions of 2 costae for some, as well as costa on sulcal flanks of innermost pair of plicae, further 2-4 fine costae laterally beyond plicae. Fine concentric growth-lines present anteriorly. There are poorly preserved traces of fine radial threads, 3-4 per mm antero-laterally, and 5-6 fine growth filae per mm in the same area, with unreliable suggestions of tiny pustules limited to single growth lamellae. (Waterhouse & Waddington (1982, p. 10) showed that pustules limited to one growth lamellum suggest cold waters, as opposed to warmer waters, where pustules span up to four growth lines). The dorsal valve has a narrow and low median fold, with no median groove, and some 5 pair of plicae, the inner pair broadening and costate, the others non-costate, fine radial and concentric threads and small pustules each spanning only single filum.

Dental plates scapular-shaped, converging ventrally at close to 90°, supported by short adminicula largely buried in secondary shell and bearing teeth. Muscle field moderately large with striate adductors and diductor scars to each side, varying in detail; valve floor to each side lightly pustulose in one specimen and pitted in the other. Secondary thickening considerable, reaching thickness of 9mm between interarea and outer wall of posterior shell.

RESEMBLANCES: This species is distinguished by its small elongate size, thick posterior ventral shell, mostly simple plicae, with no central costa in the sulcus. The type species of *Arcullina*, *Spiriferella polaris* Wiman (1914, pl.4. fig. 1-22, pl. 5, fig. 1-5 - see Kalashnikov 1998 for synonymy and revision) from the Spiriferkalk of Spitsbergen has wide ventral plicae and higher more angular dorsal plicae. The shape is elongate and sulcus non-costate. *S. barchatovae* Waterhouse & Waddington (1982 - see Chernyshev, 1902 pl. 12, fig. 4, pl. 40, fig. 7) from Schwagerina beds of the Sula River in the Urals has simple plicae, well rounded fold, elongate shape and wide non-costate sulcus.

Arcullina etheridgei (Archbold & Thomas 1985a, text-fig. 2N-V) from the Coolkilya Greywacke of the Carnarvon Basin, of Roadian (Middle Permian) age, is close in having massive thickening in the ventral valve and comparatively simple plicae on many specimens, but specimens tend to be more elongate. A median rib is visible in the sulcus of several shells, and a single coarse costa passes along each sulcal flank. Archbold & Thomas (1985a) noted considerable approach to *polaris* Wiman, the type species of *Arcullina*.

Arcullina modesta (Waterhouse, 1981, pl. 23, fig. 2-9, pl. 24, fig. 1-11, pl. 25, fig. 1, 2) from the *Spinomartinia prolifica* Zone (Sakmarian or Artinskian) at Ko Yao Noi, Thailand, tends to be transverse with a central sulcal costa, and some specimens have more ribs, but several look close. There is much less secondary thickening.

DISCUSSION: As noted by Waterhouse & Waddington (1982, p. 10), the delthyrium of *Spiriferella* and allies is sealed by a plate. Under the plate, a callosity may develop (see Waterhouse & Waddington 1982, pl. 5, fig. 4 for *loveni*). The delthyrial plate is well shown for *loveni* by Kalashnikov (1998, pl. 17, fig. 5). No plate is visible in any of the present ventral valves, and either it may have been lost, or, with more potential classificatory significance, was never present. The only moderately well preserved *Spiriferella* in New Zealand is *S. supplanta* Waterhouse, 1964, but even these are not very well preserved in the umbonal region. They do not seem to have had a delthyrial plate. Archbold & Thomas (1985a) noted that the delthyrial plate was very small in *S. cundlegoensis* Archbold & Thomas, and small or absent in *S. australasica* (Etheridge), and they stated that the delthyrium in what is now *Arcullina etheridgei* (Archbold & Thomas) was completely infilled by a massive apical callus.

Genus *Nakimusiella* Shen, Archbold, Shi & Chen, 2001

TYPE SPECIES: *Nakimusiella selongensis* Shen et al 2001.

DIAGNOSIS: Variably elongate shells with obsolete sulcus, and simple costae, bifurcating near anterior margin in large specimens.

TAXONOMY: I apologise to Dr Shen and colleagues for using their name *Nakimusiella* before it was published by them. I misunderstood its publication date, which has been unduly delayed. The name was properly attributed, and technically was published by Shen et al in Waterhouse (1999b).

Nakimusiella oweni Waterhouse, 1999

1878 *Spirifer glaber* (not Sowerby); Hector, p. xii.

1967b *Spiriferella* n. sp. Waterhouse, p. 92, text-fig. 5G, 32.

1999b *Nakimusiella oweni* n. sp. Waterhouse, p. 20.

HOLOTYPE: BR 654, figured by Waterhouse (1967b, text-fig. 5G, 32) OD from N28/f7474 (GS 441), *Marginalosia planata* Zone, Pig Valley Limestone Formation, Te Mokai Group, east Nelson (see Waterhouse 1987c).

DIAGNOSIS: Small well inflated shells with plicae reduced to one anterior pair, costae low, sulcus narrow, v-shaped in section, fold low with median anterior groove.

DISCUSSION: This species was described from the Pig Valley Limestone at Wairoa Gorge, east Nelson, in the *Marginalosia planata* Zone. The Nelson form is apparently allied to the very distinctive genus *Nakimusiella* Shen et al This was described from the Late Permian Changhsingian Stage at the hill of Selong in south Tibet, and the generic tie reinforces a Late Permian age for the New Zealand Waitian Stage, based on rocks and faunas in the Pig Valley Formation.

Genus *Alispiriferella* Waterhouse & Waddington, 1982

TYPE SPECIES: *Spiriferella ordinaria* Einor in Likharev & Einor, 1939.

DIAGNOSIS: Transverse alate Spiriferellidae, subrectangular in outline, with wide well defined sulcus along crest of dorsal fold, costae simple, not complex or numerous. Interior as in *Spiriferella*.

DISCUSSION: This genus was named for two Arctic species, *Alispiriferella ordinaria* (Einor) found in Novaya Zemlya and Arctic Canada in beds of Cisuralian age, and *A. gydanensis* (Zavodowsky) from Late Permian Omolon horizon of Kolyma Peninsula, and in Guadalupian of Arctic Canada and Spitsbergen.

Alispiriferella n. sp.
Pl. 7, fig. 1 - 3, text-fig. 7c

1999b *Alispiriferella* n. sp. Waterhouse, p. 21.

DIAGNOSIS: Specimens from D44/f363, including OU 18285-7, weakly transverse, cardinal extremities extended, ventral valve well inflated, sulcus well defined, dorsal valve little inflated, fold very low and broad, costate, with shallow median groove that is wide anteriorly, 5 pairs of weakly costate plicae on each valve.

DISCUSSION: Material described by Waterhouse (1999b) from the lower Glendale Formation, Wairaki Downs, is figured.

Suborder DELTHYRIDINA Ivanova, 1972
Superfamily **INGELARELLOIDEA** Campbell, 1959

[nom. transl. Waterhouse 1998c, ex Ingelarellinae Campbell, 1959]

Waterhouse (1998c, p. 3) considered that Ingelarelloidea may have stemmed from within Delthyridina. They possess comparable internal plates, what appears to be allied ctenophorium, and an external micro-ornament not identical with, but apparently developed from that of Devonian Delthyridina, which displays fimbriate, finely pustulose or granular arrays. Previously Pitrat (1965) and Carter et al (1994) had associated the family with Martiniidae within Martinoidea.

Family **INGELARELLIDAE** Campbell, 1959

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

This family is subdivided into two subfamilies, Ingelarellinae Campbell, 1959 characterized by micro-ornament of fine surface grooves en echelon, with no or faint spine development, and Roespiriferinae Waterhouse, 1998 (see Waterhouse 1998c), characterized by tiny spinules in concentric close-set rows. In both subfamilies the internal plates are well developed, including adminicula and tabellae.

Subfamily **INGELARELLINAE** Campbell, 1959

DIAGNOSIS: Spiriferidan shells with interareas, open delthyrium, rounded cardinal extremities, ventral sulcus variably 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, may be weakly rimmed posteriorly, 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 (Waterhouse 1998c).

DISCUSSION: Members of New Zealand and east Australian Ingelarellinae were reassessed in an overview by Waterhouse (1998c) and it was shown that type *Martiniopsis*, examined at the Geological Survey of India, Calcutta, and type *Ingelarella* at the University of Queensland, and many other species identified with these genera (Waterhouse 1965b), belong to the same subfamily, as endorsed by Archbold & Thomas (1986b). This runs counter to Carter et al (1994, p. 340) and Kotlyar & Popeko (1967), who distinguished Martiniopsidae

as characterized by “micro-ornament usually weakly to strongly capillate.” That description does not apply to *Martiniopsis*. Instead, the micro-ornament of *Martiniopsis* is identical to that of *Ingelarella*, and largely, *Tomiopsis* Benediktova.

In revising the subfamily, Waterhouse (1998c, pp. 27, 28) found that the earlier work on east Australian species by McClung (1978) was in considerable need of revision (Table 10). McClung referred many species to one genus, *Ingelarella*, which he misinterpreted as displaying different micro-ornament from *Tomiopsis*, and described a number of new species from the Sydney Basin. It appears that most of his newly proposed taxa were infrasubspecific variants of species already named from the Bowen Basin by Campbell (1960, 1961) and some named from New Zealand by Waterhouse (1964b, 1968a).

Genus *Martiniopsis* Waagen, 1883

It was shown by Waterhouse (1998c, p. 23) that *Martiniopsis* differed from lineages of *Tomiopsis* and *Ingelarella* through its shallow or no sulcus, no plicae, well developed adminicula and tabellae, and lack of tigillum. A tigillum is a bar of thickening along the mid-line in the ventral valve, extending in front of the adductor field. *Johndearia* is close externally to *Martiniopsis*, but is distinguished by its thick shell in the ventral valve, comparatively short and well spaced adminicula and tabellae, and presence of low tigillum.

Martiniopsis is present in New Zealand, but no true *Martiniopsis* are yet known from the Permian of east Australia. The nature of *Martiniopsis* and its distribution was misunderstood by McClung (1978), followed by Campbell (1992).

Martiniopsis cf *woodi* Waterhouse, 1964b

cf 1964b *Martiniopsis woodi* Waterhouse, p. 148, pl. 30, fig. 3-5, 8, pl. 37, fig. 2, 3, text-fig. 71, 72A, B.
 1968a *Martiniopsis woodi* Waterhouse (?); Waterhouse, p. 57, part.
 1992 Martineaceae (sic) fam. et gen. indet. Campbell, p. 56. text-fig. 2A (text-fig. 2B, C uncertain).
 1998c *Martiniopsis* cf *woodi* Waterhouse; Waterhouse, pp. 24-26.

DISCUSSION: Campbell (1992) claimed that *Martiniopsis* reported from Orua Bay, North Auckland, had been misidentified by Waterhouse (1968a) and that the specimens probably came from Wether Hill Limestone (now Hilton limestone), Wether Hill Station, Southland. He identified them as Martineacea gen. & sp. indet. However Waterhouse (1998c) found that no *Martiniopsis* or “Martineacean” was known at Wether Hill station. Further, it was shown that Campbell had overlooked aspects of the morphology, including a failure to recognise the critical presence of adminicula and surface ornament that pointed to a likely identity with *Martiniopsis*, and it was also noted that there was no such family group name as Martineaceae. As well, it was found that the specimens had been misoriented by Campbell in the figures. One specimen BR 1332 figured by Campbell (1992, text-fig. 2A) appeared to be identifiable with *Martiniopsis woodi* Waterhouse, 1964b. Furthermore various aspects of the rock matrix of this specimen, involving colour and density and presence of small mafic pebbles standing out from the matrix, were found to be identical in appearance with rock at Orua Bay and Marble Bay, North Auckland. The unusual appearance is due to marine erosion of carbonate which contained mafic volcanic pebbles. Waterhouse (1998c, p. 26) concluded that the specimen had come from the east side of Wherowhero Point, Orua Bay, North Auckland, PO 4, near f5705 but at least 3m higher in the succession. This was in accord with discussions with Sir Charles Fleming and Dr J. Marwick over North Auckland Permian material during 1954-5. Incidentally, the specimen here assigned to *woodi* has pieces of *Atomodesma* prisms in the matrix, and these were first drawn to the attention of Sir Charles by Dr C. T. Trechmann, when, during a visit to New Zealand, he was shown the North Auckland material at the New Zealand Geological Survey, then at 156 The Terrace, Wellington. In the minds of Sir Charles, and Jack Marwick who collected the material, there was no doubt about its source. So the attempt to revise the North Auckland Permian material, without visiting the rocks in the field, consulting people who were involved, or learning about brachiopod morphology and nomenclature, has not clarified matters.

The species *woodi* is particularly close to the type species *M. inflata* Waagen, 1883 from the lower Chhidru Formation of Wuchiapingian (Late Permian) age in the Salt Range, Pakistan.

Martiniopsis patella Waterhouse, 1967b Pl. 7, fig. 4, 5

1967b *Martiniopsis patella* Waterhouse, p. 93, text-fig. 8, 29, 30, 31, 33.

HOLOTYPE: BR 827, figured by Waterhouse (1967b, text-fig. 8, 30) OD from D44/f9874 (GS 7356), *Wairakiella rostrata* Zone, Wairaki Breccia-Conglomerate, Wairaki Downs.

DIAGNOSIS: Large transverse *Martiniopsis* with short lateral margins, straight or concave posterior walls, broad weakly sulcate anterior margin, posterior ventral valve narrowly channeled medianly or smooth, adminicula and tabellae comparatively short and widely diverging.

MATERIAL: Three large ventral valves from D44/f374 (including OU 18288), and 2 dorsal valves including BR 2393 and a ventral valve BR 2394 with fragments and external moulds from D44/f9874 (GS 7356), *Wairakiella rostrata* Zone, Wairaki Breccia-Conglomerate, Wairaki Downs.

DIMENSION IN MM: ventral valves

Specimen	Width	Length	Height	Locality
BR 2394	51	38	15	f9874
OU 18288	63	54	20	f374

DESCRIPTION: Ventral valves from D44/f374 transverse, moderately inflated, ventral umbo prolonged, umbonal angle about 75° in one specimen and ?80° in the other, posterior walls concave. Ventral valve from GS 7356, the type locality, is less inflated and has broad umbonal angle of over 80°. Cardinal extremities well rounded, umbonal area smooth, narrow medium sulcus present anteriorly in one specimen from f374, and very shallow in another, and perhaps developed anteriorly in the third, which is however deformed; anterior shell lost from another specimen. Dorsal valves include BR 2393, the first known dorsal valve topotype, little inflated, very low fold with broad gently convex crest and low steep sides. Interarea in this specimen inclined about 30° from commissure, low, almost flat, marked by growth grooves, bearing wide open notothyrium near 90°. Surface of dorsal valves worn, not showing micro-ornament, but revealing low close-set concentric wrinkles, 4-5 in 5mm. Surface ornament on ventral valves comprises radially aligned grooves, usually short, varying 0.2 to 0.5mm in length, and about 7 in 7mm across the shell. The large specimen from f374 has fine burrows crossing the shell exterior, and the external mould forms a regular honeycomb pattern, presumably from an epiphyte.

Adminicula extend over posterior third of valve and diverge forwards at 35° in the topotype, and lie closer together in the specimens from f374. In dorsal valve, tabellae short and well spaced, thickened posteriorly, slightly convex inwards in outline, diverging forward at about 25°, diverging weakly from floor of valve to support crural plates. Dental sockets enclosed by socket plates, small ctenophoridium, low median septum not extending as far forward as tabellae, muscle scars lightly striated, and floor of valve with low dense pustules and pits. Anterior valve rimmed by low concentric ridges and grooves, reflecting wrinkled exterior of shell.

RESEMBLANCES: These specimens are close to the original types, showing comparable internal plates, external wrinkles, transverse shape with narrow lateral margins, and shallow anterior ventral sulcus. The holotype, a ventral valve, is medianly grooved posteriorly, unlike these specimens, and the present suite expands understanding of the species in showing more dorsal valves. There is some variation in inflation and prominence of ventral umbo and depth and presence of ventral sulcus posteriorly, and in the ventral muscle field.

Martiniopsis woodi Waterhouse, 1964 from the zone of that name in the Earnvale Member, Bagrie Formation, Arthurton Group is close, but has longer lateral margins, and long tabellae and adminicula.

Tomioopsis sp. in Hyden et al (1982, text-fig. 4) from the upper Stephens Subgroup near Mossburn shows some approach, but is narrower with slightly wider sulcus anteriorly. Adminicula are slightly more close-set and subparallel.

DISCUSSION: Collections made since the initial studies show that this distinctive species is relatively common in the Wairaki Breccia-Conglomerate, and additional well-preserved specimens, not examined here, are present at IGNS, Lower Hutt (Dr. H. J. Campbell, pers. comm.), and Department of Geology, Otago University.

Genus *Tigillumia* Waterhouse, 1998

TYPE SPECIES: *Martiniopsis biparallela* Waterhouse, 1987.

DIAGNOSIS: Shells externally like *Martiniopsis* with no plicae, shallow or no sulcus, generally no fold, micro-ornament of shallow elongate exopunctae in quincunx. Adminicula long and close-set, enclosing narrow muscle field rimmed anteriorly each side by high ridges which join anteriorly along mid-line to form tigillum. Tabellae of moderate length, moderately spaced.

Tigillumia mintyi Waterhouse, 1999

Pl. 7, fig. 6 - 11

1968a *Ambikella cf ingelarensis* Waterhouse, p. 60.

1968a *Ambikella parallela* (not Waterhouse); Waterhouse, p. 73, pl. 14, fig. 8 (not pl. 13, fig. 3, 5, 6, pl. 14, fig. 7 = *Ingelarella parallela* (Waterhouse)).

1999b *Tigillumia mintyi* Waterhouse, p. 22, text-fig. 1a-d.

HOLOTYPE: OU 18289, figured by Waterhouse (1999b, text-fig. 1a) OD, refigured pl. 6, fig. 6 herein, from D44/f376, *Spinomartinia spinosa* Zone, Hilton Limestone, Wairaki Downs.

DIAGNOSIS: Small transverse shells with moderately prominent beaks, ventral valve smooth or with shallow anterior sulcus, may be groove-like, ventral adminicula close-set, long, dorsal tabellae also close-set and long.

MATERIAL: Specimens come from the *Spinomartinia spinosa* Zone, D44/f376 (OU 18289-18298) and D44/f9479 (GS 3615), including BR 590, 2358, 2359, preserved as shells and internal moulds at Hilton Limestone, Coral Bluff, Wairaki Downs. Also in boulder of Tertiary conglomerate at Waituna Stream, D44/f9524 (GS 7803).

DIMENSIONS IN MM:

BR	Width	Length	Height
2359	30	22	7.5

DISCUSSION: Photographs are provided for this species, described with line drawings by Waterhouse (1999b).

Genus *Tomioopsis* Benedictova, 1956

TYPE SPECIES: *Tomioopsis kumpani* Yanischevsky, 1935.

DIAGNOSIS: Shell thin, plicae low and narrow, may be moderately numerous at up to 6 pairs, sulcal subplicae well developed in several species, median channel along dorsal fold. Micro-ornament of grooves in quincunx, may be rimmed. Adminicula of moderate length and spacing, diverge weakly forwards, tabellae short, diverging widely to cross into interspace between inner two pairs of plicae. Myophragm broad and commences in front of cardinal laminae in type species.

DISCUSSION: Several subgenera were distinguished for *Tomioopsis* by Waterhouse (1998c). Differences appear to be consistent and well sustained in large populations, and so the subgenera are elevated to genus rank.

Genus *Ingelarella* Campbell, 1959

TYPE SPECIES: *Ingelarella angulata* Campbell, 1959.

DIAGNOSIS: Large shells, broad sulcus, may be subplicate or medianly costate, and wide fold with rounded or grooved crest, lateral shell smooth or moderately to strongly plicate, micro-ornament of shallow grooves in quincunx; adminicula comparatively long and subparallel, generally intrasulcal, tabellae long and subparallel, in first interspace between dorsal fold and innermost pair of plicae, 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 *Tomioopsis* by having fewer stronger plicae, thicker shell and plates and longer tabellae, which do not diverge forward so widely. It is not clear whether *Tomioopsis* has a tigillum or not. *Ingelarella* is distinguished from *Ambikella* Sahni & Srivastava, 1956 by its generally longer tabellae, thicker shell, and presence of a tigillum, which is lacking from *Ambikella*. The tigillum is well developed in plicate *Ingelarella* such as *angulata*, *globosa* and *oviformis*, regarded as probably synonymous, and a tigillum is also present in non-plicate shells such as those referred to *ingelarensis* Campbell.

Ingelarella undulosa Campbell, 1961

Pl. 7, fig. 18, 19, 21, pl. 8, fig. 1, 2

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

1968a *Ambikella cf ingelarensis* not Campbell; Waterhouse, p. 60, text-fig. 6B (part, GS 3615 material = *Tigillumia mintyi* Waterhouse).

1968a *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 = *I. confusa* (Waterhouse)).

?1968 A. 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 *I. cessnockensis* McClung, p. 49, pl. 2, fig. 10, 11, pl. 10, fig. 4-15, 18, 19.

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

1998c *Tomioopsis (Ingelarella) undulosus* (Campbell); Waterhouse, pp. 12-14.

HOLOTYPE: UNEF 5840, *undulosa*, figured by Campbell (1961, pl. 26, fig. 8) OD from lowest of three *Tomioopsis* beds about 5km SSW of Homevale Homestead, north Bowen Basin, Queensland. For *cessnockensis*, UNEF 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 moderately long and well spaced, tabellae also moderately long.

MATERIAL: Specimens from the Freitag Formation include 3 ventral valves and a dorsal valve from UQL 3759, single ventral valves from UQL 3761 and 3762 and a dorsal valve at UQL 3766. All have the same locality description, 60 km south of Springsure.

DISCUSSION: This species was described from the Freitag Formation, southwest Bowen Basin, Queensland, by Waterhouse (1998c), and compared to material from the *Spiriferella supplantata* fauna at GS 6070, lower Letham Formation, Wairaki Downs. The species incorporates *Tomioopsis (Ingelarella) cessenockensis* (McClung, 1978) from the Elderslie Formation, Sydney Basin.

Ingelarella subplicata (Waterhouse, 1968)

Pl. 7, fig. 12 - 17

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

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

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

1998c *Tomioopsis (Ingelarella) subplicatus* (Waterhouse); Waterhouse, pp. 14-16.

HOLOTYPE: BR 1357, D44/f9001 (GS 9697) 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 well spaced.

DISCUSSION: This species was discussed by Waterhouse (1998c) and shown to typify the *Echinalosia discinia* Zone of the middle and upper Letham Formation at Wairaki Downs, New Zealand. It is represented in the Fenestella Shale of the north Sydney Basin, as specimens variously misidentified by McClung (1978), and by many specimens in UNE collections.

Table 10. List of Ingelarellidae from east Australia and New Zealand.

McClung 1978 (all <i>Ingelarella</i>)	Revised identification
<i>oviformis</i> (M'Coy)	<i>I. - Ingelarella, J. - Johndearia,</i>
<i>strzeleckii</i> (de Koninck)	<i>A. - Ambikella. M. - Monklandia</i>
<i>konincki</i> (Etheridge)	<i>I. oviformis</i>
<i>branxtonensis</i> (Etheridge)	<i>M. gympiensis</i>
<i>elongata</i> (McClung & Armstrong)	<i>A. konincki</i>
<i>ovata</i> Campbell	<i>A. branxtonensis</i>
<i>profunda</i> Campbell	<i>I. elongata</i>
<i>brevis</i> (McClung & Armstrong)	<i>Homevalaria ovata</i>
<i>undulosa</i> Campbell	<i>H. profunda</i>
<i>magna</i> Campbell	<i>J. brevis</i>
<i>etheridgei</i> McClung	<i>I. undulosa</i>
<i>davidi</i> McClung	<i>J. magna</i>
<i>cessnockensis</i> McClung	<i>gen.? strzeleckii</i> (de Koninck)
<i>ingelarensis</i> Campbell	<i>gen.? davidi</i>
<i>belfordensis</i> McClung	<i>I. undulosa</i> (Campbell)
<i>isbelli</i> Campbell	<i>I. ingelarensis</i>
<i>warneri</i> McClung	<i>J. magna</i> (Campbell)
<i>mantuanensis</i> Campbell	<i>J. isbelli</i>
<i>syn. parallela</i> Waterhouse	<i>J. dissimilis</i> (Waterhouse) subsp. or var.
<i>syn. furca</i> Waterhouse	<i>I. mantuanensis</i>
<i>syn. woodi</i> Waterhouse	<i>I. parallela</i>
<i>singletonensis</i> McClung	<i>I. furca</i>
<i>cf. costata</i> Waterhouse	<i>Martiniopsis woodi</i> Waterhouse
<i>I. angulata</i> Campbell	<i>J. dissimilis</i> (Waterhouse)
<i>excelsus</i> (Waterhouse)	<i>I. subplicata</i> Waterhouse
	<i>I. angulata</i> (? = <i>oviformis</i>)
	<i>Notospirifer? excelsus</i> Waterhouse

Nearly all of the McClung species are junior synonyms, or, charitably, regarded as subspecies of earlier taxa. The species *etheridgei* and *davidi* are so poorly described that genus remains uncertain.

Ingelarella costata Waterhouse, 1964
Pl. 7, fig. 20

1964b *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.

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

1983a *Martiniopsis havilensis* (not Campbell); Dickins, text-fig. 3 C, D, E? (not text-fig. A, B, F? = *Ingelarella havilensis* Campbell).

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

1998c *Tomiopsis (Ingelarella) costata* Waterhouse; Waterhouse, p. 17.

DISCUSSION: This species is regarded as a plicate form of *havilensis*. It is found in the *Terrakea elongata* Zone of the upper Mangarewa Formation, and in the upper Blenheim Subgroup and just below the MacMillan Formation in the north Bowen Basin. Specimens from the Fenestella Shale and lower Belford Formation, supposed to be allied by McClung (1978), are reassigned to *Ingelarella subplicata* (see Waterhouse 1998c).

Ingelarella? sp.
Text-fig. 7f

MATERIAL: Six ventral valves including OU 18769 from D44/f376, *Spinomartinia spinosa* Zone, Hilton Limestone, Wairaki Downs.

DESCRIPTION: Valves broken and incomplete. Best preserved specimen displays incurved umbo and deep sulcus, no plicae posteriorly, anterior shell not preserved, so not known if plicate anteriorly. Umbo incurved, teeth born on scapular-shaped dental plates, supported by high adminicula diverging forward at about 25°, probably moderately long, but not certain as shell anterior lost. Muscle field broad and raised anteriorly, scars lightly impressed. Posterior shell thick and bearing pallial pits.

RESEMBLANCES: These specimens are distinguished by their deep sulcus and moderately well formed, moderately spaced adminicula. As far as they are preserved, they approach Early Permian species from the lower Tiverton Formation, north Bowen Basin, Queensland, such as *Ingelarella profunda* (Campbell, 1961), now placed in *Homevalaria* (see Waterhouse, 1986c). Critical micro-ornament is not preserved on the Wairaki Downs specimens, so that it is not possible to determine the genus.

Genus ***Johndearia*** Waterhouse, 1998

TYPE SPECIES: *Ingelarella isbelli* Campbell, 1961.

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

DISCUSSION: *Johndearia* was initially proposed as a subgenus of *Tomiopsis*. Species range from late Cisuralian into Lopingian in east Australia and New Zealand. The oldest known species *brevis* McClung & Armstrong presumably arose from *Ingelarella plica* 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*. It is possibly represented in the lower Letham Formation of New Zealand (Waterhouse 1998c, p. 19). Another species of *Johndearia* to be found in New Zealand is *dissimilis* Waterhouse, 1964b, found in the *Echinalosia ovalis* Zone of Mangarewa units 6 and 7, Wairaki Downs. This is apparently senior synonym for *Ingelarella warneri* McClung, 1978 (Bickham Formation, New South Wales), and allied to if not synonymous with *I. singletonensis* McClung, 1978 from the Mulbring Formation in the Sydney Basin. The species was also recorded from the Flat Top Formation, southeast Bowen Basin, by Waterhouse (1987a). *Johndearia pelicanensis* (Campbell) is found in the uppermost Mangarewa Formation and Flowers Formation of New Zealand, and in the north Bowen Basin, Queensland, in the *Terrakea elongata* Zone.

Johndearia isbelliformis (Waterhouse, 1978)
Pl. 8, fig. 3

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

1998c *T. (Johndearia) isbelliformis* Waterhouse; Waterhouse, p. 22.

HOLOTYPE: BR 2231, figured by Waterhouse (1978, text-fig. 14) OD from *Spinomartinia spinosa* Zone, Hilton limestone, Wether Hill Station.

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

DISCUSSION: Unlike older species of *Johndearia*, this species appears to lack a tigillum and has not very thick shell, marking significant changes in the stock (Waterhouse 1998c). Poorly preserved material was described from the Hilton Limestone at Coral Bluff by Waterhouse (1998c) and a broken specimen OU 18299 is figured herein.

Family **NOTOSPIRIFERIDAE** Archbold & Thomas, 1986

[nom transl. Waterhouse, 1998c ex Notospiriferinae Archbold & Thomas, 1986]

DISCUSSION: Members of Notospiriferidae are close to genera 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, but no tigillum is ever developed. The dorsal interior is close, but displays very short or no tabellae, in contrast to the well-formed to long tabellae of all Ingelarellidae. The micro-ornament offers a further 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 *Rorespirifer*, tiny solid spinules are developed. Notospiriferidae has sutured hollow micro-spines called c-spines by Waterhouse (1967d, p. 277, 1998c, p. 35, Armstrong 1969, p. 200), and surface grooves are deeper.

Building on studies by Campbell (1959), Armstrong (1970b) and Clarke (1991, 1992b), three subfamilies are recognized. Notospiriferinae has very small spines, not indeed visible in the type species and other forms of *Notospirifer*, arguably in part because of poor preservation, and deep swollen exopunctae, termed globons. These are globose or subglobose cavities within the primary shell layer, as described by Campbell (1959) and Armstrong (1970b). They differ in size and shape from the linear narrow and shallow grooves or hollows in quincunx found in many Ingelarellidae.

Glendoniinae has higher c-spines, prolonged posteriorly in some genera, and shallow narrow grooves. Mesopunctiinae has small or no micro-spines, shallow narrow grooves, and deep pores that penetrate the outer part of the main lamellar layer of shell. The various genera in all three subfamilies may be recognized generally from both details of micro-ornament and external shape, involving number and shape of plicae, and nature of the sulcus and fold.

The classification is as follows, with distribution in brackets:

Family Notospiriferidae Archbold & Thomas
 Subfamily Notospiriferinae Archbold & Thomas
 Genus *Notospirifer* Harrington (east Australia, New Zealand)
 Genus *Farmerella* Clarke (Tasmania)
 Genus *Papulinella* Waterhouse (Queensland, New Zealand)
 Subfamily Glendoniinae Clarke
 Genus *Glendonia* McClung & Armstrong (east Australia)
 Genus *Birchsella* Clarke (Tasmania)
 Genus *Tabellina* Waterhouse (east Australia) [syn. *Kelsovia* Clarke]
 Genus *Monklandia* Waterhouse (east Australia)
 Subfamily Mesopunctiinae Waterhouse
 Genus *Wairakispirifer* Waterhouse (Queensland, New Zealand)
 Genus *Mesopunctia* Waterhouse (Queensland, New Zealand)

Subfamily **MESOPUNCTIINAE** Waterhouse 1998

Members of this subfamily are characterized by shell, especially in projecting growth lamellae, which is punctate (see Waterhouse 1964b, 1968a, 1982a). These punctae are shown by shell sections (Waterhouse 1964b, pl. 37, fig. 4, 6), and also demonstrated in natural casts, wherein the punctae are filled by cores of matrix (Waterhouse 1968a, pl. 14, fig. 10, pl. 15, fig. 6). These punctae are much deeper than found in the species described for Notospiriferinae or Glendoniinae. The pores are termed mesopunctae to indicate that they penetrate deeply, more than exopunctae, and less than endopunctae.

Genus *Wairakispirifer* Waterhouse, 1998

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 apparently restricted to anterior shell, penetrating to inner shell (Waterhouse 1964b, pl. 37, fig. 6, Armstrong 1970b, p. 293), narrowing at surface. Adminicula well formed, little posterior thickening. No tabellae, at least in the type species.

Wairakispirifer microstriatus (Waterhouse, 1964)

1964b *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* (Waterhouse)).

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

1998c *Wairakispirifer microstriatus* (Waterhouse); Waterhouse, p. 40.

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

DISCUSSION: This species is found in the *Echinalosia maxwelli* Zone of the Letham Burn Member, Mangarewa Formation, and the Otrack Formation of southeast Bowen Basin. The species was reported from locality GS 7807 (D44/f9878) in the Caravan Formation by Waterhouse (1968a, 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 *Notospirifer* gen. & sp. indet.

Genus *Mesopunctia* Waterhouse, 1998

TYPE SPECIES: *Notospirifer macropustulosus* Waterhouse, 1968, from upper Mangarewa Formation, Wairaki Downs.

DIAGNOSIS: Small transverse shells with rounded few plicae and smooth sulcus, rounded fold, micro-ornament of small blunt crescentic c-spines, weakly prolonged posteriorly, moderately deep exopunctae and globons passing at least anteriorly and over lamellae into mesopunctae. Ventral interior as for family, tabellae short or absent.

DISCUSSION: This genus is characterized by wide deep mesopunctae, which pass through the outer or primary shell layer and into but not through the inner layer. They do not penetrate to the inner surface, and have swollen sides as in globons, or parallel sides so that they were cylindrical. Tiny rather blunt and thick spines are present.

Mesopunctia macropustulosus (Waterhouse, 1968a)

1964b *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*).

1968a *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.

1998c *Mesopunctia macropustulosus* (Waterhouse); Waterhouse, p. 41.

DISCUSSION: 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. It is then replaced by *Mesopunctia minuta* (Campbell, 1960) in the *T. elongata* Zone of the Bowen Basin. *M. minuta* is close to *M. macropustulosus* (Waterhouse) in appearance, but has a median cleft along the dorsal fold, and shows small but distinct tabellae (Waterhouse 1987a, p. 40). A comparatively large internal mould was compared to *minuta* by Wass & Gould (1968, pl. 15, fig. 1-5) from the South Marulan district of New South Wales. This has short widely diverging tabellae, a deep cleft in the dorsal fold, and two narrow subplicae close to the mid-line of the sulcus. Micro-ornament is not preserved, so it cannot be ascertained if the form represents a new species allied to *Notospirifer*, which is characterized by two sulcal subplicae (Waterhouse 1998c), as well as globons.

Clarke (1987, text-fig. 14) reported the species *minuta* from Malbina Formation Member E in Tasmania, but the dorsal fold of his material is more massive than in *minuta* or *macropustulosus*. The exopunctae are swollen.

Order SPIRIFERINIDA Cooper & Grant, 1976

Cooper & Grant (1976) were first to propose the Order Spiriferinida, and I believe that their proposal should be duely credited. Carter et al (1994) wished to translate the authorship from Ivanova (1972) after she was first to propose Spiriferinidina. Superfamilial group classification is not subject to the same rules as family groups. Classes and orders are very different concepts and authorship should be inviolate, and subject to strict priority of proposal, provided there is no substantial change in concept. Although it is acceptable for authors to disregard as they wish prior proposals, that does not mandate a freedom to substitute other authors.

Suborder SPIRIFERINIDINA Ivanova, 1972
 Superfamily SYRINGOTHYRIDOIDEA Frederiks, 1926
 Family SYRINGOTHYRIDIDAE Frederiks, 1926

As far as I know this ending is widely used (see Carter et al 1994), but the International Commission for Zoological Nomenclature (2000, p. 33) noted that omission of id would be permissible.

Subfamily PERMASYRINXINAE Waterhouse, 1986
 Genus *Sulcicosta* Waterhouse, 1983
Sulcicosta sp.
 Text-fig. 7h

A fragment of a ventral valve BR 2363 from the lower Mangarewa Formation at D44/f111 (GS 15227), *Echinalosia ovalis* Zone, Wairaki Downs, shows narrow plicae and some 4 low broad costae in the sulcus. The surface is finely punctate. This genus is represented by three species from Late Paleozoic of the Sydney and Bowen Basins of east Australia (Waterhouse 1983c, 1987a, p. 13ff).

Syringothyrididae gen. & sp. indet. A
 Text-fig. 7g

A very obscure valve OU 18300, probably ventral, from D44/f376, *Spinomartinia spinosa* Zone, Hilton Limestone, Coral Bluff, Wairaki Downs, might belong here but shows little of the interior or exterior, other than signs of high interarea, shallow broad sulcus, fine costae, and punctate shell.

Syringothyrididae gen. & sp. indet. B

MATERIAL: A ventral valve from D44/f374, *Wairakiella rostrata* Zone, Wairaki Breccia-Conglomerate, Wairaki Downs.

DESCRIPTION: Specimen about 25mm wide and 15mm long and at least 6mm high, transverse, with moderately high but obscure interarea and narrow cardinal extremities. Well formed sulcus, and at least 7 and probably 9 pairs of plicae present. Surface of shell densely punctate. Lack of information about ventral interior and dorsal valve means that the genus cannot be identified.

Order TEREBRATULIDA Waagen, 1883
 Suborder TEREBRATULIDINA Waagen, 1883
 Superfamily DIELASMATOIDEA Schuchert, 1913
 Family HETERELASMINIDAE Likharev, 1956
 Genus *Marinurnula* Waterhouse, 1964
Marinurnula ovata n. sp.
 Pl. 8, fig. 4 - 8

DERIVATION: ovum - egg, Lat.

HOLOTYPE: Specimen BR 2348 figured in pl. 7, fig. 4, 7, from D44/f109 (GS 15209), *Echinalosia discinia* Zone, Letham Formation, Wairaki Downs, here designated.

DIAGNOSIS: Shell of oval outline, distinguished from other species by having maximum width close to mid-height of shell outline.

MATERIAL: Material from D44 includes single internal moulds and specimen with valves conjoined from f9621 (GS 6070), *Spiriferella supplanta* faunule, 2 specimens with valves conjoined from f309, single specimens from f326 and f307, lower *Echinalosia discinia* Zone, 3 from f109 (GS 15209) with specimens BR 2348, 2349, single specimens from f9001 (GS 9676), f126 (GS 15225), and possibly f116 (GS 15211), f319, f320, f323, and f324, upper *E. discinia* Zone, Letham Formation, Wairaki Downs. One specimen with valves conjoined from f123 (GS 15226, BR 2347), lower Mangarewa Formation, Wairaki Downs.

DIMENSIONS IN MM:

Specimen	Locality	Width	Length	Height	Maximum width from posterior	Foramen width
BR 15209	f109	18.5	32	10	18	2
OU 18771	f307	16	23	5	9.5	2.2 (squashed)

DESCRIPTION: Specimens oval in outline with maximum width near mid-length. Umbonal foramen small, posterior walls high, ventral valve gently convex posteriorly, broad and almost flat over anterior half, with

slight median swelling, maximum height at hinge. Dorsal valve arched, without any sulcation, highest in front of hinge. Both valves marked by low concentric growth rugae. Ventral teeth not supported by plates. Muscle scars faint. Dental sockets small, crural plates rise just in front of socket plates directly from steep posterior floor of the valve.

RESEMBLANCES: The specimens are distinguished by their oval outline with maximum width near mid-height, and by the posterior position of the crural plates. *Marinurnula prima* Waterhouse (1987a, pl. 13, fig. 20, 21) from the ?Late Carboniferous Fairyland Formation of the southeast Bowen Basin has maximum width placed well forward. Another species with maximum width placed well forward is *M. mantuanensis* Campbell (1965, pl. 5, fig. 10-14, pl. 16, fig. 20, 21) from upper Barfield Formation or lower Flat Top Formation. Further specimens of this species were described from the Flat Top and Barfield Formations by Waterhouse (1987a, pl. 13, fig. 26, 29-31) and the lower Blenheim Formation of the north Bowen Basin (Waterhouse & Jell 1983, pl. 3, fig. 19).

The maximum width of the type species, *M. rugulata* Waterhouse, 1964b also is anteriorly placed.

***Marinurnula rugulata* Waterhouse, 1964**
Pl. 8, fig. 10

1964b *Marinurnula rugulata* Waterhouse, p. 177, pl. 34, fig. 6, 7, 8, text-fig. 81.

HOLOTYPE: BR 900, figured as above by Waterhouse (1964b) OD from G45/f8592 (GS 4651), *Plekonella multicosata* Zone, Arthurton Group, near Arthurton.

DIAGNOSIS: Elongate shells, widest in front of mid-length, little inflated, slightly incurved ventral umbo, shallow anterior sulcus, valves crossed by few strong concentric wrinkles; shell finely punctate.

MATERIAL: A ventral valve and specimen OU 18303 with valves conjoined, from D44/f364, equivalent *Plekonella multicosata* Zone, Glendale Formation, Wairaki Downs, preserved as internal and external mould.

DISCUSSION: The species was initially described from the *Plekonella multicosata* Zone of the Bagrie Formation, Arthurton Group, south Otago.

Phylum MOLLUSCA Linne, 1758
Class BIVALVIA Linne, 1758
Subclass PALAEOTAXODONTA Korobkov, 1954
Order NUCULIDA Dall, 1889
Pl. 8, fig. 9, 11, 12

Some Palaeotaxodont species are figured from the Letham and Mangarewa Formations, Wairaki Downs. Species are common, as will be shown in the lists provided in the accompanying volume. Species were described by Waterhouse (1965a).

Subclass PTERIOMORPHIA
Order PTERIIDA Newell, 1965
Suborder PTERIIDINA Newell, 1965
?Superfamily PTERINEOIDEA Miller, 1877
Family ATOMODESMIDAE Waterhouse, 1976

[nom. transl. Astafieva 1993 ex Atomodesminae Waterhouse, 1976. Johnston & Stevens (1985) proposed to "translate" (sic - correct?) Subfamily Atomodesminae Waterhouse to Atomodesmatinae. But desma is Greek, and the stem for the family group name is Atomodesm, not Atomodesmat. This is confirmed by the International Code Zoological Nomenclature (2000, p. 33). The correct ending was used by Waterhouse (1979a, 1980a)]

ORDINAL RELATIONSHIPS

The ordinal and subordinal positions of Atomodesmidae remain contentious. Cox in Cox et al (1969, p. 115) considered that *Atomodesma* belonged to Eurydesmatidae (= Eurydesmidae) and in the same bivalve treatise, Newell (1969a, p. 291) put *Eurydesma* and *Atomodesma* (p. 289) in Myalinidae. In the same volume, Newell in Cox (1969a, p. 317) placed *Aphanaia*, a close ally of *Atomodesma*, in Inoceramidae. It has taken years to at least clear some of the confusion prevailing amongst writers of that treatise.

Various authors place *Atomodesma* and allies with Inoceramoidea in Pteriomorphia with Pteriida and Pectinida. Some consider that *Posidoniella* provided ancestral stock for Atomodesmidae. This genus appears to have prismatic shell and right anterior ear (Dickins 1983b) with no anterior left ear, suggestive of Pectinida. The anterior of Atomodesmidae lacks, as far as I can decipher, any sign of asymmetric anterior auriculation, and does not approach *Posidoniella*. Kauffman & Runnegar (1975) referred *Atomodesma* to Inoceramidae, which was placed in Ambonychioidea. Johnston & Collom (1998) argued that the Inoceramidae

should be associated as a superfamily with Praecardiodea Newell, 1965 in Subclass Cryptodonta. They suggested that the line of small scars below the ligament helped to suggest kinship between Inoceramidae (including *Atomodesma*) and cardioloids. But a comparable arrangement is suggested in myalinids and pteriids (s. l.).

Here it is suggested that Atomodesmidae belong to the Pteriida. The ligament area is not myalinid, in so far as the grooves appear to be growth grooves, and parallel rather than intersect the ventral hinge margin. The shell is prismatic as is common for Pteriida, and the muscle scars and pallial line are largely pteriiform, with compact posterior adductor scar, posterior muscle retractor insertion areas, mantle retractor insertion pits, posterior pedalbyssal retractor muscle insertion areas, and what are interpreted as small anterior pedal byssal retractor areas, following Kauffman & Runnegar (1975, text-fig. 6). This arrangement is close to that reported for pteriiform bivalves such as *Pinctada* (see Newell 1938). Pectinida have a larger more complex muscle mass. I interpret Atomodesmidae as a sister family of Kolymiidae Kusnetzov, 1973, in which the anterior protruding wings have been retracted into the shell, to form the umbonal septum in each valve. With that morphological change, the shell was able to nestle differently on the substrate, and became able to develop an inequivalve habit.

By contrast, Astafieva (1993) allocated Kolymiidae, Atomodesmidae and Inoceramidae (with *Varvaria* Astafieva and *Permoceramus* Waterhouse) to three separate superfamilies, Pterineoidea, Ambonychioidea and Inoceramoidea. On the other hand Kauffman & Runnegar (1975) preferred a close relationship between *Permoceramus*, *Atomodesma* and *Kolymia*, referring all to Inoceramiidae, as members of Ambonychioidea, and not pteriiform. Here *Kolymia* and *Atomodesma* are regarded as closely allied at superfamily level, provisionally included as Pterineoidea. *Permoceras* appears to have arisen from an atomodesmid such as *Aphanaia* M'Coy, as discussed by Kauffman & Runnegar (1975). Or it may have arisen from *Malimanina* Waterhouse, as discussed below. And its relationship to Inoceramidae remains an open question.

An alternative path may be suggested. *Malimanina* is based on an Early Carboniferous bivalve that approaches *Maitaia*, but lacks an umbonal septum. Gonzalez (1998b) considered that the type species, so-called *Posidoniella malmanensis* Gonzalez, represented ancestral stock for atomodesmids, arising from *Posidoniella*, and developing in the middle Carboniferous a primitive umbonal septum. Unlike *Posidoniella*, *malmanensis* lacks a right anterior auricle. Otherwise, within the limits of what is known, it is moderately close to atomodesmids. Whether it formed ancestral stock or an independent development remains open for further study.

Subfamily **ATOMODESMINAE** Waterhouse, 1976

Genera characterized by umbonal plate or deck, below the channel-form ligament, shell mostly or entirely prismatic.

Historical Overview

Some early students of Permian Bivalvia, in what may be termed the first phase of systematic study, seem to have focused on describing local faunas with little reference to either the literature or collections from elsewhere. That is one possible explanation why three rather similar genera were proposed for large Permian bivalves with prismatic shell, namely *Atomodesma* Beyrich, 1864, *Aphanaia* de Koninck, 1877, and *Maitaia* Marwick, 1934, 1935. There certainly was a paucity of literature on Permian fossils available to Marwick (Fleming 1979). Yet it is true that Trechmann (1917) had already indicated possible relationships for New Zealand Permian faunas when assigning prismatic shells from Late Paleozoic in east Nelson to the Australian genus *Aphanaia*. Marwick never saw the types of the two earlier genera, knew nothing of *Atomodesma*, and misinterpreted the genus *Aphanaia* in naming his genus *Maitaia*, based on Late Permian material from east Nelson. Perhaps there may have been some attitude of wishing to have local genera for a country. If that sound fanciful, it is not. It was a very strong philosophy amongst distinguished New Zealand and Australian paleontologists, young and old, in the 1950's, as I know from first hand experience. That approach persisted for much longer amongst some individuals in Australia and New Zealand, as explained for ingelarellids by Waterhouse (1998c). The attitude remains still amongst some paleontologists who assert a North Atlantic hegemony over ammonoid and brachiopod genera and species (Waterhouse 1996b, p. 120, 2000c, d, e and this volume - see *Terrakea* and *Strophalosia*). Thus genera and species validly proposed by students of Gondwana fossils have been ignored or set aside in favour of taxa later from northern hemisphere faunas.

One motivation that impelled paleontological research after World War 2 was the desire to tighten the limits of genera, and ensure that a world-wide basis was used for diagnoses, in an attempt to get rid of junior synonyms. This was inspired by the example of Ernst Mayr, who reduced the number of living species and genera of birds through careful world-wide study. It came to be appreciated that *Aphanaia* (Dickins 1956, 1961a, p. 123) and *Maitaia* (Waterhouse 1958, 1959a, 1963a) showed the same overall attributes as *Atomodesma* Beyrich. This may be termed the second phase. As a young participant of that phase, I was particularly fortunate, because, despite the difficulties of post-war years in Europe, I was able to inspect at first hand the obscure and little known types of *Atomodesma* and *Aphanaia*, kept in museums of the Netherlands, Germany and England, and show for the first time that an umbonal septum or deck was developed in all three genera. As well, it was possible to peruse literature not available anywhere in New Zealand or Australia.

The third phase, as far as *Atomodesma* and allies were concerned, began with the attempt to tease out morphologic differences, and try to recognize strands of development and overall evolution, irrespective of national boundaries. The distinctness of the group was delineated by formal designation of a subfamily Atomodesminae Waterhouse, 1976, later upgraded to a full family, and several distinct morphological groups were differentiated as genera in New Zealand (Waterhouse 1979a) and Russia (Astafieva 1986, 1988, 1989, 1991b, 1993, Astafieva-Urbaitis & Astafieva 1984, Muromzeva 1979, 1984). A few paleontologists preferred to remain at phase 2. Dickins (1989) considered that Atomodesminae should be kept as a subfamily within Inoceramidae Giebel, 1852, with a query, and accepted the claim by Browne & Newell (1966) that *Atomodesma* showed multiple ligament pits. Waterhouse (1970b) preferred to regard the Browne-Newell material as exceptional, and proposed a new genus *Permoceramus*. This was accepted by Kauffman & Runnegar 1975, and was judiciously reviewed with underlining of alternative possibilities on classification by Newell & Boyd (1987, pp. 9, 10), but disregarded by Dickins (1989). *Permoceramus* was reported from Verchoyan, Siberia, by Muromseva (1979). Astafieva (1993) not only recognized *Permoceramus*, but named a companion genus *Varvaria* Astafieva, 1993 for *Permoceras sibiricus* Muromzeva, 1979 from the Late Permian Hauralakh Suite of Orulgan. Both were classed in Inoceraminae Giebel. A possible ally was reported from *Parafusulina* beds in the Kanokura Group, Japan, as *Isognomon* by Hayami (1960, text-fig. 6). Dickins (1989, p. 68) objected to the erection of new atomodesmid genera by Waterhouse (1979a), because this was "Contrary to the then current usage" and the proposals would "cause confusion". However Russian workers have been able to recognize the new genera in the Middle and Late Permian of Siberia, and the reference of all Atomodesminae to one genus *Atomodesma* by Dickins and to various subgenera with the genus by Kauffman & Runnegar (1975), seems ultracautious. The locus for research on the group has shifted from Australia and New Zealand to Russia, where the group is so diverse and so numerous there that it has possible to publish an entire monograph devoted to some of the genera and species found in Russia (Astafieva 1993).

Genus *Aphanaia* de Koninck, 1877
***Aphanaia proiectus* n. sp.**
 Pl. 8, fig. 13, 14, pl. 9, fig. 1 - 3

1963a *Atomodesma* sp. aff *mitchellii* (not M'Coy); Waterhouse, p. 706, pl. 100, fig. 8, 9, 10, pl. 101, fig. 1, pl. 105, fig. 8, fig. 9 indet.

DERIVATION: *proiectus* - stretched out, jutting, projecting, Lat.

HOLOTYPE: TM 7892, pl. 8, fig. 14, pl. 9, fig. 1, from D44/f137 (GS 15222), upper Mangarewa Formation, *Terrakea elongata* Zone, Wairaki Downs, here designated.

DIAGNOSIS: Large species with very high anterior walls, oblique outline, narrow anteriorly prolonged umbones, narrow umbonal septum, shell very thin.

MATERIAL: Six specimens with valves conjoined, 5 left valves and 3 right valves, with fragments, from D44/f137 (GS 15222), including BR 7892-7894, one specimen with valves conjoined and fragments from D44/f336, small left valve (BR 7895) from D44/f352, *Terrakea elongata* Zone, upper Mangarewa Formation, Wairaki Downs. Earlier material from D44/f9623 (GS 6072) and D44/f9868 (GS 7350), same zone and formation.

DIMENSIONS IN MM: GS 15222

Specimen	Length	Height	Width Right Valve	Width Left Valve
BR 7892	125	110+	33	46
BR 7893	+68	80+	24	30

DESCRIPTION: Specimens large, strongly prosogyre in outline, posterior wings large in small specimens, becoming proportionately reduced as specimens increase in size. Umbones long, strongly prosogyrous, with comparatively narrow umbonal angles of 57° to 65°, usually about 60°, much the same in each valve. Left valve distinctly more inflated than right valve. Anterior walls very high, gently concave in both outline and face, palpably higher on left valve compared with right valve, curving abruptly on to outer face. Valves most inflated below umbones, along opisthocline line curving concavely forwards, near anterior wall. Hinge prolonged posteriorly in small specimens, up to length of 60-65mm, when valves as high as long, and posterior wing well developed, but not discriminated from rest of valve. Posterior cardinal angle 130°, and posterior maximum length near mid-height. As specimens increased in size, the hinge stopped growing, and posterior cardinal angle increased by 10-20°, and shell becomes most prolonged posteriorly well below mid-height. Ornament of well spaced growth wrinkles, steep on ventral side, and 2-3 major (possibly annual) growth steps.

Interior visible on several specimens, and also figured by Waterhouse (1963a, pl. 100, fig. 8, 9). Hinge long and marked by few parallel grooves, with fine parallel lineations as well, but no vertical markings. Umbonal septum concave, set below hinge, with concave floor and narrow angle of 35-45°, as low as 33°, and generally about 40°. Muscle scars and pallial line not visible, perhaps because shell is unusually thin for

genus, usually close to 1mm, and up to 1.7mm thick, prismatic.

RESEMBLANCES: The type species of *Aphanaia* is *Inoceramus mitchellii* M'Coy (1847) from Glendon and Wollongong, Sydney Basin (see Dickins 1963, pl. 9, fig. 16, 17). The types are kept at the Sedgwick Museum, Cambridge, and look like small individuals and growth lines of early growth stages on large individuals of the present species, with closer-set and more regular wrinkles and large posterior, but the umbones are much less prominent and are broader. Specimens allied to *mitchellii* were reported from the upper Mangarewa Formation of New Zealand by Waterhouse (1963a) and these are now identified as immature individuals of the present species. A specimen from GS 7350 (Waterhouse 1963a, pl. 100, fig. 10) is almost smooth, unlike other specimens, but has a large growth step around the margin. Less well preserved specimens of uncertain identity were figured for shell structure from the middle Mangarewa Formation at GS 3616 (Waterhouse 1963a, pl. 105, fig. 9).

Aphanaia tivertonensis Waterhouse (1979a, pl. 1, fig. 3, 6, 7, pl. 2, fig. 3 - also Kauffman & Runnegar 1975, pl. 2, fig. 1-7, pl. 3, fig. 2, 4-6, text-fig. 1A, C, D, E), from the Tiverton Formation of the north Bowen Basin has more incurved, less projecting umbones, larger posterior wings, and wider umbonal septum.

Aphanaia otamaensis Waterhouse (1979a, pl. 2, fig. 4-8) from the Waipahi Group, Rai Group, and Takitimu Group (Brunel or Chimney Peaks Formation) of New Zealand has high anterior walls, but the umbones are low, and the umbonal septum very large with wide angle. A specimen close to this form, previously misidentified as *Maitaia trechmanni* by Dr. I. G. Speden in Johnston (1977), has been identified by Waterhouse (1982c) from the Rai Group of east Nelson. Speden's misidentification encouraged considerable miscorrelation on the part of Johnston in his mapping programme, and the rocks in question are, as originally supposed by Waterhouse (1964a), and affirmed by the fossil, considerably older than the Tramway Formation, not correlative. (The Rai unit of Waterhouse (1964a) is regarded as valid, although abandoned by Johnston (eg. 1981): he misrepresented the type section as being in the Rai Valley, whereas it was proposed for Lee River rocks.)

The species described as *Atomodesma obliquatum* Waterhouse (1963a, pl. 100, fig. 5-7) from the *Echinalosia maxwelli* Zone in the lower Mangarewa Formation is close in general appearance, with prominent umbones and outline changing during ontogenetic development in which the posterior wing becomes reduced proportionately with increase in size. Umbones are broader and less extended, and the umbonal septum is wider, with angle at 50°, and posterior wing larger at maturity. The species is assigned now to *Maitaia*, because valves are subequal or equal in width.

Aphanaia gigantea de Koninck (1877, pl. 21, fig. 6), also figured by Waterhouse (1958, text-fig. 16; 1979a, pl. 3, fig. 3, 4, pl. 4, fig. 1-5), has prominent beaks, high anterior walls and extremely reduced posterior wing. Specimens are less inflated than the new form, and show concentric wrinkles. Well preserved specimens appear to be equivalve, so that the species was considered to belong to *Maitaia* Marwick by Waterhouse (1979a). Astafieva (1991a) pointed out that small specimens assigned to *gigantea* by Waterhouse (1979a) strongly approached the genus *Cigarella muromsvevae* Astafieva.

Aphanaia judomensis Astafieva (1993, pl. 6, fig. 6-8, pl. 13, fig. 8, 9) from the Ufimian of southern Verchoyansk, east Siberia, has large posterior wing and very prominent umbones, somewhat as in small specimens of the present species, but no large specimens are known for the Russian species. The posterior wings are small on mature *A. proiectus*.

***Aphanaia? glabra* n. sp.**

?1980a ?*Maitaia* sp. Waterhouse, p. 108, text-fig. 2.7, 3.2.

1985 *Maitaia obliquatum* (not Waterhouse); Johnston & Stevens, p. 747, text-fig. 2. 1-9.

DERIVATION: *glabra* - smooth, Lat.

HOLOTYPE: TM 5893, figured by Johnston & Stevens (1985, text-fig. 2.4), from N29/f75, GS 13308, Kaka Formation at Speargrass Creek, Nelson, here designated.

DIAGNOSIS: Medium-sized inflated shells with thick prismatic shell, no posterior wings, high anterior wall, large growth steps but few wrinkles, umbonal plate angle 50°.

DESCRIPTION: This species is of moderate size, up to 70-80mm long though not complete, with one specimen 120mm long. All specimens are of separate valves, both are well inflated, with relative inflation not certain. Valves prosocline with weakly prosogyrous umbones, tweaked forwards terminally, steep high anterior wall and hinge of moderate length, with no defined posterior wing. Valves comparatively smooth, apart from 1 - 3 growth steps, fine wrinkles and strong rugae irregularly developed on some specimens. Ligament concave with usual markings, and umbonal deck with angle of 50°. The shell in a specimen some 47-48mm high is up to 8mm thick.

RESEMBLANCES: Specimens from the Kaka volcanics at Speargrass Creek, south Nelson, that were misidentified as *Maitaia obliquatum* by Johnston & Stevens (1985), show very high anterior walls, suggestive of *Aphanaia* rather than *Maitaia*, although none of the specimens clearly demonstrate that the species was

inequivalved, because none are conjoined. There is no distinct posterior wing, and both valves are high. In lacking a posterior wing, they approach *Mytilidesmatella* Waterhouse and *Cigarella* Astafieva, but overall shape and high anterior wall suggest *Aphanaia* de Koninck.

There is considerable approach to shells identified as ?*Maitaia* by Waterhouse (1980a) from D44/f9960 (GS 9279) - TM 5668 - and D44/f9961 (GS 9280), including TM 5749, from the *Spinomartinia? adentata* Zone in the Takitimu Group of the Takitimu Range. The umbonal deck in these specimens has a septal angle of 50° and specimens are comparatively smooth with a few growth steps. From a preliminary assessment, these occurrences are close in age, possibly slightly older, than occurrences of *Aphanaia otamaensis* in the Takitimu Group (Waterhouse 1979a).

Maitaia obliquatum (Waterhouse, 1963) from the *Echinalosia maxwelli* Zone in the Letham Burn Member, Wairaki Downs, is less inflated and more rugose, with thinner shell and more defined posterior wing. *Aphanaia proietus* Waterhouse from the *Terrakea elongata* Zone of the upper Mangarewa Formation, Wairaki Downs, is larger with thinner shell, posterior wing, more rugae, and narrower umbonal septum. *A. mitchellii* (M'Coy, 1847) differs also in shape, with posterior wing and rugae. From the Tiverton Formation of the northern Bowen Basin, Queensland, *A. tivertoni* Waterhouse, 1979 is moderately close in its umbonal septum and high anterior walls and similar prosogyrous umbones and lack of posterior wing, but the shell is ornamented by regular concentric rugae. This is the closest of named species from New Zealand and east Australia, and is of Sakmarian (?Tastubian) age. *A. otamaensis* Waterhouse (1979) is also close in shape, but has broad umbonal deck and irregular strong concentric rugae. It is found in the Waipahi, Takitimu and Rai Groups.

Genus *Maitaia* Marwick, 1934, 1935

More species of *Maitaia* are now found in Russia than in New Zealand, Astafieva (1989) having described four species, and added another in 1993. But there does not appear to be the same overwhelming abundance of individuals in Russia compared with *Maitaia* in the Tramway Formation of New Zealand (Waterhouse 1964a).

Maitaia trechmanni Marwick, 1934

1934 *Maitaia trechmanni* Marwick, p. 948.

1935 *Maitaia trechmanni* Marwick, p. 295, pl. 34, fig. 1-3.

cf 1976a *Maitaia trechmanni* Marwick; Waterhouse, p. 248, text-fig. 7. 2.

1980a *M. trechmanni* Marwick; Waterhouse, p. 109, text-fig. 2.9, 3.3, 3.4 (see for synonymy and discussion).

A few fragments come from D44/f117 (GS 15228), lower Glendale Formation, Wairaki Downs, equivalent to the *Plekonella multicosata* Zone of the Artherton Group. One fragment shows the broad and well formed umbonal deck characteristic of *Maitaia trechmanni*, and a small specimen is compatible in outline. This material is not specifically diagnostic in itself, but differs in its septum from that of *Trabeculatia trabecula* (Waterhouse) from the *Spinomartinia spinosa* Zone, and also from *Mytilidesmatella woodi* (Waterhouse).

Genus *Mytilidesmatella* Waterhouse, 1979

TYPE SPECIES: *Atomodesma woodi* Waterhouse, 1963.

DIAGNOSIS: Large equivalved shells with anteriorly placed umbones, no anterior ear, no posterior wing, no radial rugae, low concentric rugae. Anterior face low. Umbonal septum large and long, posterior adductor prominent with second scar along pitted pallial line closer to umbo, in position of posterior byssal retractor scar of Kauffman & Runnegar (1975, text-fig. 6), but shaped like the posterior adductor scar.

DISCUSSION: This genus is represented by only one species in New Zealand. The type material comes from a long lens or block of limestone in the Artherton Group, with several other mostly unregistered localities in the same block. The species possibly occurs in the Waimahaka Limestone in the Kuriwao Group of Southland, as described herein.

Astafieva (1989, 1993, p. 99) has assigned *Kolymia acuta* Lyutkevich & Lobanova from Pai Hoi, and also Delejin Horizon of Verchoyan, Siberia, to *Mytilidesmatella*. She proposed that the genus be treated as a subgenus of *Maitaia* Marwick. There certainly are strong similarities to *Maitaia* in shape, but to me the internal differences warrant full generic separation.

Dickins (1989, text-fig. 3) asserted that *Mytilidesmatella* could not be distinguished from *Maitaia trechmanni*, but there are considerable differences in the development of posterior wing, posterior musculature, and umbonal deck. Unlike various Russian authorities, supported by the writer, Dickins (1989) assigned all *Atomodesminae*, and also *Permoceramus* Waterhouse to one genus.

?*Mytilidesmatella woodi* Waterhouse, 1963

Text-fig. 8

?1956 *Maitaia trechmanni* not Marwick; Wood, p. 44, text-fig. 23A, D.

?1963a *Atomodesma woodi* Waterhouse, p. 708, pl. 101, fig. 2-5, pl. 102, fig. 1, 4, pl. 105, fig. 12.
 ?1979a *Mytilidesmatella woodi* (Waterhouse); Waterhouse, p. 13.

HOLOTYPE: TM 3645, figured by Waterhouse (1963a, pl. 101, fig. 4) OD from G45/f8613 (GS 5079), Otaria Formation, Arthurton Formation, near Arthurton.

DIAGNOSIS: Large little inflated shell with low wrinkles, colour stripes on well preserved specimens.

PRESENT MATERIAL: Three specimens including OU 18776 from F47/f43 Waimahaka Limestone, at debouchement of Titiroa Stream on to Matura River flood plain, southern Southland. Seven specimens, including OU 18777, from a carcass disposal pit in more deeply weathered carbonate, close by at F47/f44.

DESCRIPTION: Specimens large, up to 15cm in longest dimension, and comparatively smooth, with very subdued wrinkles and no well defined posterior wing, although the posterior shell is extensive and body cavity thin. The specimens from the carcass pit are more fragmentary and have now decayed badly so the description relies on notes. The notes can no longer be checked against the material, and so are of interest only in suggesting the need for further enquiry. The shells were little inflated with broad umbonal angle of 80-85°, low anterior wall with no ear, and gently inflated posterior, lacking a differentiated wing. Ornament composed of a few low broad wrinkles, strongest near the hinge. Striated ligament area well developed, umbonal deck broad with an angle of 75°, not constricted by ligament area under the beak, gently concave and divided from the anterior wall so that it projects slightly as a short flange. Full extent of the umbonal septum not preserved. One internal mould showed a well formed bean-shaped posterior adductor scar, a faintly impressed pallial line, and faintly impressed subrounded scar near the umbo.

RESEMBLANCES: The morphology as far as it was preserved was like that of *Mytilidesmatella woodi* (Waterhouse) from the Otaria Formation, Arthurton Group. The low inflation, lack of well defined posterior wing, low wrinkles, umbonal septum as far as it was preserved, and apparent double muscle scar all fall within the ambit of the unusual aspects of *woodi*. Complete identity with *woodi* cannot be established because the full extent of the umbonal septum was not determined. Of course, now that the material has disintegrated, the present account lacks checkability, and can only serve as a pointer to the need for confirmation.

Mytilidesmatella acuta (Lytkevich & Lobanova, 1960, pl. 21, fig. 1, 2; Astafieva 1993, pl. 7, fig. 2) from the Delenjii Suite, Pai Hoi, Siberia, is small with stronger wrinkles and narrower umbones.

Dickins (1989, p. 69, text-fig. 3) figured a specimen TM 6846 that he stated was *Atomodesma trechmanni* Marwick, but also identical with *Mytilidesmatella woodi* (Waterhouse). Evidently the source or formation was not known, for no stratigraphic or locality detail was provided, but that was regarded as unimportant, the critical factor being, to him, that it came from New Zealand, and therefore belonged to the one species *trechmanni* that he recognized in terms of specific name, the morphology being regarded as unimportant. The specimen is an internal mould, with valves splayed open. His figure shows the umbonal end of a septum, and does not clearly indicate whether the septum is long or short. Dickin's comment seems to have been based on misunderstanding of morphology and preservation, as well as disregard for the need of stratigraphic and locality data.



Text-fig. 8. ?*Mytilidesmatella woodi*, right valve OU 18776 from F47/f43, Waimahaka Limestone, Matura River, x 1. More informative material that showed internal detail from a nearby pit at F47/f44 has since decayed, so that identification of the species and genus is provisional only.

New Zealand species ascribed to *Trabeculatia* by Waterhouse (1979a), *marwicki* and *trabecula*, are more inflated with strong wrinkles, smaller umbonal septum, and single posterior adductor scar. The hinge is thickened to suggest a ligament as displayed in some Inoceramidae. Three species of *Trabeculatia* have been described from the Middle Permian Delenjin and Dulgalkh suites of Verchoyan by Astafieva (1986, 1993). *Maitaia obliquata* (Waterhouse) and *M. trechmanni* Marwick also have moderately high anterior with differentiated posterior wing, smaller umbonal septum and single adductor scar. *Aphanaia mitchellii* (M'Coy) is well inflated and inequivalved, and *A. otamaensis* Waterhouse has a very high anterior wall with very broad umbonal septum. An Australian species that comes close to *Mytilidesmatella woodi* is *Maitaia gigantea* (de Koninck, 1877 - see Waterhouse 1979a, p. 10) from sandstone at Branxton, north Sydney Basin, New South Wales. This species lacks a posterior wing and has large but low wrinkles. One adductor scar is known, and the shell is very thin. It seems possible that *Mytilidesmatella* evolved from this Middle Permian species, placing a lower limit on the age of *Mytilidesmatella*. Astafieva (1991) judged that *gigantea*, or some of the material assigned to that species by Waterhouse (1979a), might belong to *Cigarella*.

incerte sedis

Family **ATOMODESMIDAE** Waterhouse, 1976?

Subfamily **MALIMANININAE** new

NAME GENUS: *Malimanina* Waterhouse n. gen.

DIAGNOSIS: Shells lacking umbonal deck or plate, displaying prismatic shell layer, channel-form ligament.

DISCUSSION: This subfamily differs from members of Atomodesminae in lacking an umbonal plate or deck. Associating *Malimanina* with *Atomodesma* might imply that the umbonal deck evolved from a simpler form without a deck. Some aspects of musculature, hinge, shell symmetry and structure in *Atomodesma* and allies suggest an origin from Pteriida, in which the anterior wings moved posteriorly to become tucked under the umbones and form umbonal decks. But Malimanininae suggests a different developmental path.

Genus ***Malimanina*** new

DERIVATION: Maliman, San Juan Province, Argentine.

TYPE SPECIES: *Posidoniella malimanensis* Gonzalez, 1998, here designated.

DIAGNOSIS: Small shells with terminal umbones, almost or fully equivalve, prismatic layer, ornament of strong concentric rugae, no anterior ear, ligament channel-form with no umbonal septum. Muscle scars poorly known, but row of small rounded scars extend along pallial line, and small radially elongated scars from mantle insertions lie behind pallial line.

DISCUSSION: This genus is distinguished from genera referred to Atomodesminae by the lack of an umbonal plate or deck. Of genera so far ascribed to Atomodesminae, *Intomodesma* Popov from Middle to Late Permian of northeast Russia is closest in its ornament of strong concentric rugae, but the type species *I. costata* Popov has an umbonal deck (Kauffman & Runnegar 1975).

Gonzalez (1998b) ascribed the type species to *Posidoniella* de Koninck, 1885, also of Early Carboniferous age. This genus also has an elongate channel-form ligament, not as high as in *Atomodesma* and allies, or the new genus. *Posidoniella* is further characterized by a well developed anterior auricle and byssal notch in the right valve, well shown by Dickins (1983b, pl. 1, fig. 1-5). These attributes with hinge and reported prismatic shell suggest a pectinid relationship for *Posidoniella*, close in many respects to Eurydesmidae, apart from the fact that *Eurydesma* lacks prismatic shell.

From Westphalian Kuttung rocks of New South Wales, Campbell (1961b) figured a specimen as *Posidonia* that showed atomodesmid hinge with no umbonal septum, and Runnegar (1972) noted that it may have been ancestral to *Atomodesma*, although noting that the beaks were subterminal.

Malimanina arguably marks the earliest known member of Atomodesmidae, at a phase before the development of the distinctive umbonal deck. Gonzalez (1998b, p. 176) observed that poorly preserved Middle Carboniferous *Atomodesma* s.l. described from the *Levipustula* Zone of Patagonia exhibited a rudimentary umbonal deck (Gonzalez 1983). These shells also display coarse concentric wrinkles and subquadrate outline. In New Zealand, indeterminate ?atomodesmid specimens are found in clastic sediments associated with stage 2 spilites of the Patuki Group on D'Urville Island. These are dated as Middle to Late Carboniferous by Sivell & McCulloch (2000), correcting implications of a much younger, Permian, age, preferred by Kimbrough et al. (1992).

Superfamily **PTERIOIDEA** Gray, 1847
 Family **PTERINIIDAE** Miller, 1877
 Genus ***Merismopteria*** Etheridge, 1892
Merismopteria macroptera (Morris, 1845)
 Pl. 9, fig. 5

- 1845 *Pterinea macroptera* Morris, p. 276, pl. 13, fig. 2, 3.
 1849 *Cypricardia acutifrons* Dana, p. 702, pl. 8, fig. 4.
 1877 *Pterinea macroptera* Morris; de Koninck, p. 305, pl. 16, fig. 12, 12a.
 1877 *Avicula sublunulata* (Morris); de Koninck, p. 242, pl. 16, fig. 4.
 1892 *Merismopteria macroptera* (Morris); Etheridge, p. 271.
 1960a *Merismopteria macroptera* (Morris); Dickins, p. 387, pl. 63, fig. 6-12.
 1965 *Merismopteria* sp. aff *macroptera* (Morris); Waterhouse & Vella, p. 75.
 1981 *Merismopteria* sp. Dickins, pl. 2, fig. 16.
 1983 *Merismopteria macroptera* (Morris); Waterhouse in Waterhouse & Jell, p. 248, pl. 3, fig. 25, 28.
 cf 1984 *M. macroptera* (Morris); Muromzeva, p. 57, pl. 23, fig. 13, 14, 18-21.
 1987b *M. macroptera* (Morris); Waterhouse, p. 145, pl. 1, fig. 28.
 1988 *M. macroptera* (Morris); Waterhouse, p. 171, pl. 1, fig. 10, pl. 2, fig. 1, 3.
 1992a *M. macroptera* (Morris); Clarke, p. 38, text-fig. 18C-I, 22A-F, 23.

The external mould of a right valve OU 18305 comes from D44/f344 in the lower *Echinalosia ovalis* Zone, Mangarewa Formation, Wairaki Downs. The species is common in the Middle Permian of east Australia, with synonymy summarized in Waterhouse & Jell (1983). This is the first report of the species in Wairaki Downs, and the species also occurs in the Flowers Formation of northwest Nelson (Waterhouse & Vella 1965, p. 75).

INTRODUCTION TO ORDER PECTINIDA

The Newell Contribution

Leading studies of Late Paleozoic bivalves have been conducted by Professor Norman Newell for more than 60 years, a remarkable record. Would that it were emulated more often. I have the impression that publications by many of the significant contributors to paleontology extend for up to 30 years, and some over 40 years, until death, loss of research facilities, or loss of interest intervenes. Sixty years plus is outstanding. It is by no means intended as a depreciation of the esteem he deserves, when I point out that Professor Newell has not always evaluated his own work very accurately, or followed his own precepts. In systematics and taxonomy, he has made frequent reference to the need for modern population studies of fossils, and urged the suspension of or at least strong reservations over taxa proposed by others, until they can be validated through extensive study of variation amongst fossil populations. Yet his own named taxa are generally based on a few specimens, sometimes well preserved, others obscure in terms of hinge and internal detail. Although he has had access to silicified material from the Glass Mountains, the measurements given in his descriptions of this material are few, and statistical studies rare. There is some justification for being wary of making so-called population studies from such collections, and perhaps he refrained from such studies with good reason. The Glass Mountains material came from blocks, with an uncontrolled number of "populations", no better than the Foraminiferal collections analysed statistically and spuriously as being "population" based, inferring samples of co-existing specimens, when in fact they lump numerous successive populations. The fact is that Professor Newell has concentrated his effort, especially after his two early monographs, to "classic" specimen-centred palaeontology, closely studying and comparing a few well preserved specimens, often collected by others, and patiently devising and testing their classification and description, with little use of field evaluation, numerical studies or modern biological procedures in which large numbers of many criteria are statistically analysed. Without denying that there is a great need for biometric studies, it may be suggested that Newell's work has focussed on what was needed most throughout the twentieth century - a preliminary systematic overview of available fossil material. No apology is needed for the corpus of his work. It stands as a fine and cherished achievement. There is no need for any pretence that it has used biometric methods. Nor, by the same standard, is there any justification for dismissing the work of colleagues, just because they have followed his example and made limited use of statistical or biometric techniques.

Paleontologists may not realize that Professor Newell in choosing to work mostly on Late Paleozoic bivalves has faced considerable difficulties. It has scarcely been possible for him to trace the detailed development of bivalve genera and species, and higher categories, through successive biozones, because bivalves are comparatively rare throughout the Permian especially of the United States. Indeed, he never refers to biozones - a revealing omission. Even the huge volumes of carbonate dissolved for fossils by Dr G. A. Cooper, principally for brachiopod studies, and shared with Professor Newell, have yielded comparatively few bivalves, not all well preserved. This stands in contrast with successions in Australia and New Zealand where bivalves make up a substantial part of successive macrofaunal biozones, and where species of *Maitaia*, *Trabeculatia*, *Etheripecten*, *Deltopecten*, *Eurydesma*, *Myonia* and *Vacunella* can be overwhelmingly abundant. Professor Newell has not enjoyed such luxury. What he has been able to do is elucidate details of morphology, and circumscribe some species in detail, to overcome difficulties caused by the presence of comparatively few species, and the low potential to conduct detailed evolutionary studies of related and evolving taxa through a number of successive biozones.

Prof. Newell has remained intellectually adventurous and at the forefront of exploring more profound and some would say intellectually daring schemes of classification, and in evaluating other proposals. His views on major relationships have been severely challenged by Waller (1978), over the fundamental boundaries between Pteriida, Pectinida and Ostreida. In this debate, I agree with Newell & Boyd (1995, p. 35)

when they argued that original shell composition and microstructure were less significant taxonomically than details of morphology, whilst allowing for judicious appraisal (Newell & Boyd 1990). A fine example was offered in the analysis of the shell structure in *Pseudomonotis* from Western Australia, in which the entire shell was found to be composed of calcite rather than aragonite, unlike other pseudomonotids (Newell & Boyd 1989). Microstructure was shown to be like that of gryphaeid oysters, rather than the aviculopectiniform structure of other pseudomonotids. Their assertion agrees with observations on the calcite versus aragonite composition in shells of New Zealand Permian compared with North American Permian by Waterhouse (1982b). Newell & Boyd (1995, pp. 34-35) noted the Waterhouse observation, and also found that west Australian shells which possessed calcite, rather than aragonite, were in other respects closely similar to shells with aragonite. Although Newell & Boyd (1995), in contrast to their conclusion in 1989, dismissed temperature as a factor, because shells with aragonite and with calcite lived together in a wide range of temperatures today, it is clear that within major biotic groups, temperature did and does play a major role. The observations on variability in shell composition and structure offer a direct challenge to Waller's (1978) scheme, which attached unreserved classificatory significance to shell structure and composition.

Morphological discriminants

Within Pectinida Newell & Boyd (1995, pp. 29, 31) commented that there are difficulties in the mosaic distributions of characters and probabilities of sporadic convergence in details of ornament, notably in the shape of growth lines as they cross the intercostal troughs, and the way in which new ranks of costae are added. Both Newell (1938) and Waterhouse (1969b, 1982b) gave too much weight to these features, and I strongly agree with Newell and Boyd that caution is needed.

LIGAMENT TYPES (Text-fig. 9, 10)

Other features also need to be treated with care. The bivalve treatise (Trueman 1969, p. 62) cautioned that "It is difficult to utilize the ligament as a factor of importance in classification of the Bivalvia because of its adaptive characters", and within limits, this appears well justified, given the range of alivincular, duplivincular and channelform ligaments in what otherwise appear to be closely related forms. A tentative refinement of some of these categories will be used, as explained in the Introduction, in order to compress description and avoid ambiguity that has crept into bivalve diagnoses and descriptions. These terms are as follows.

lativincular - ligament with broad and often shallow resilifer, modified from normal alivincular hinge. Example - *Strebloboyardia*. This partly corresponds with what Newell & Boyd (1987, p. 5) called a transitional ligament, which they described as broad and elongate cardinal area covered by fibrous ligament and bearing a single elastic band along dorsal margin and supplementary band below the beaks (Newell & Boyd (1995, p. 13).

platyvincular - a planar or gently concave ligament with grooves and ridges, possibly of growth origin, or comparatively smooth, typically developed in *Deltopecten* or *Corrugopecten*. May be broadly triangular overall in outline. One of several kinds of "transitional" ligament, without narrow lateral areas.

canalivincular - channelform ligament, with no subdivisions through grooves or resilifer other than growth-steps. Examples *Dolponella*, *Maitaia*. Kauffman & Runnegar (1975, p. 45) proposed that the ligament was composed of a thick layer of fibrous ligament covered by a single outer lamellar sheet.

replivincular - ligament in which the normally complete chevrons of duplivincular ligament are reduced to short segments, generally inclined inwards towards the umbo, but truncated. Examples *Claraia*, *Halobia*.

lineavincular - ligament with parallel bands of fibrous and lamellar tissue. Example *Myalina*. Previously lumped with duplivincular ligament of chevron bands. This restricts the application of established terms as follows:

alivincular - resilifer central or subcentral, compact. Examples *Limopsis*, *Etheripecten*.

duplivincular - hinge of fibrous and lamellar bands shaped as chevrons. Examples *Arca*, *Pterinopecten*.

Classification

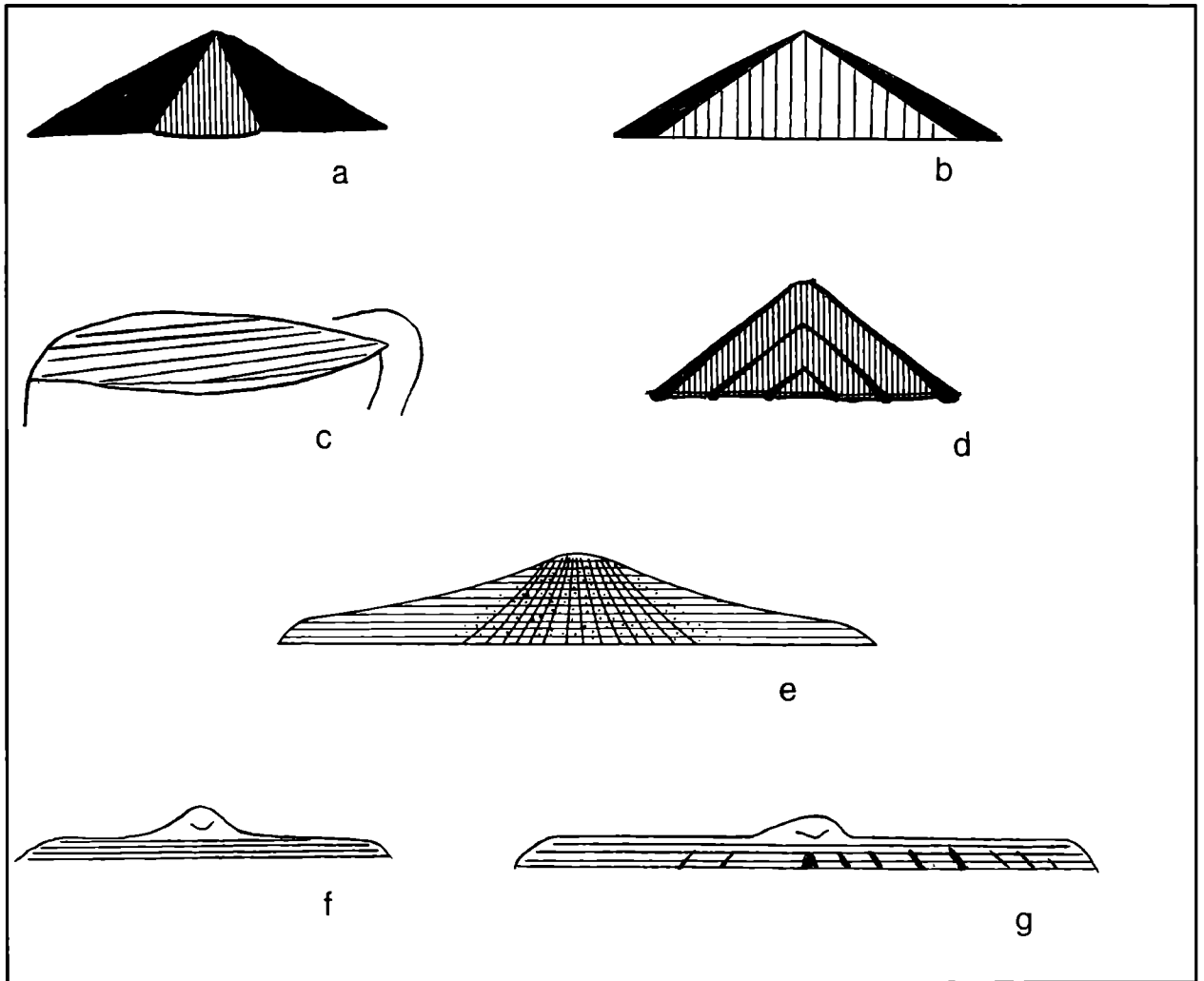
The overall classification for Upper Paleozoic Pectinida as set out by Newell & Boyd (1995) has many contentious assessments of genera, and seems to be demonstrably flawed in its recognition of many families based on a single genus, or rarely two genera. The preponderance of their family groups falls in these unlikely categories, and the high number of monogeneric families strongly suggests that criteria are being exaggerated in importance, and other criteria are not being given due weight. Their system thus seems threatened by its own patent flaws.

A different approach was endorsed by Astafieva (1994), with the recognition of ten families all within one superfamily Pectinoidea. A helpful summary of generic and familial attributes was provided in her studies, emphasizing structure of the ligament, ratio of convexities of the two valves, general character of sculpture and overall form and microstructure of the shell in each valve. Generic criteria were regarded as involving primarily the ratio of anterior and posterior auricles, and their shape, obliquity of shell and details of ornament. My own approach prefers more flexibility, and would allow some variation for instance in hinge length and nature of auricles, and in shell microsculpture - and even in ligament structure.

A new classification is proposed. Prime features for this new classification are relative degree of inflation of valves, relative length and definition of wings and auricles, nature of the mode of increase of costae, direction of growth lines, and the nature of the hinge. Paleogeographic parameters are deemed to

allow significant variation, especially in shell structure and composition. In view of the great diversity of Pectinida and the high number of genera, it has been decided to compress family group hierarchy, and limit the number of superfamilies and families, by making use of subfamilies and tribes. This enables relationships to be revealed, and avoid the clutter of numerous families, in no obvious pattern, in large superfamilies, and also avoid a large number of superfamilies, which invite ordering into closer and more distant relationships.

There are two areas of uncertainty, because important families are named from long-proposed but poorly known genera. Through laws of priority, Aviculopectinidae have to assume importance, with a debated right valve. Should the present nomenclature prove wrong, Acanthopectinidae or Limipectidae may have to be substituted. Secondly, Chaenocardidae are also a senior family, which, if wrongly interpreted, can be replaced by Streblochondriidae. The overall conceptual relationships will remain. The genera listed are not necessarily exhaustive, but even so the classification shows well the enormous contribution made by Professor Newell.



Text-fig. 9. Ligaments in Pectinida and other bivalves. Diagrammatic representations showing sections in right valves, extended from Trueman (1969, text-fig. 52).

a. Alivincular amphidetic ligament, as in *Etheripecten*. Black - lamellar and fusion layers of ligament; vertical rules - fibrous layer of ligament. b. Lativincular ligament, as in *Strebloboydia* and *Orbiculopecten*. Pattern as for a. c. Lineavincular ligament (*Myalina*). d. Duplivincular ligament, as in *Arca* and *Pterinopecten*. e. Platyvincular ligament of *Corrugopecten* with pseudotrabeclae below umbo. f. Canalivincular ligament for *Daonella*. g. Replivincular ligament as for *Claraia* and *Halobia*.

Classification of Suborder Aviculopectinidina

Superfamily Pterinopectinoidea Newell, 1938

Family Pterinopectinidae Newell, 1938

Subfamily Pterinopectininae Newell, 1938

Pterinopecten Hall, *Annulipecten* Ruzickia, Prantl & Pribyl, *Dunbarella* Newell, *Limanomya* Gray, *Lyriopecten* Hall, *Pseudoaviculopecten* Newell, *Pterinopectinella* Newell, *Ivanovipecten* Astafieva & Astafieva-Urbaitis, *Denguria* Newell & Boyd

Subfamily Claraiinae Gavrilova, 1996

Tribe Pseudoclaraiini Gavrilova, 1996

Pseudoclararaia Zhang, *Periclararaia* Li & Ding, *Claraioides* Fang, *Rugiclararaia* Waterhouse

Tribe Claraiini Gavrilova, 1996

Claraia Bittner, *Epiclararaia* Gavrilova, *Crittendenia* Newell & Boyd, ?*Chuluaria* Waterhouse (or Dolponellidae Waterhouse)

Family Halobiidae Kittl, 1912

Halobia Bronn, *Halobia* (*Zittelihalobia*) Polubotko, *H. (Parahalobia)* Yin & Hsu, *Daonella* Mojsisovics, *Aparimella* Campbell

Superfamily Aviculopectinoidea Meek & Hayden, 1864

Family Aviculopectinidae Meek & Hayden, 1864

Subfamily Aviculopectininae Meek & Hayden, 1864 [syn. Acanthopectinidae Newell & Boyd, 1995, Limipectininae Newell & Boyd, 1990]

Genera: *Aviculopecten* M'Coy, *Heteropecten* Kegel & Costa, *Limipecten* Girty, *Acanthopecten* Girty, *Fasculiconcha* Newell

Subfamily Undopectininae Waterhouse new

Genus *Undopecten* Waterhouse, *Hayasakapecten* Nakazawa & Newell, *Turbopecten* Astafieva, *Newellipectinia* Waterhouse

Family Etheripectinidae Waterhouse, 1982

Subfamily Etheripectininae Waterhouse, 1982

Tribe Etheripectinini Waterhouse, 1982

Genera: *Etheripecten* Waterhouse, [syn. *Paradoxipecten* Zhang], *Fletcheripecten* Waterhouse, *Vanvleetia* Waterhouse, *Glabripecten* Waterhouse, *Eumorphotis* Bittner, *Spyridopecten* Campbell & McKelvey, *Girtypecten* Newell, *Vnigripecten* Muromzeva, *Neptunella* Astafieva, *Chiron* Astafieva

Tribe Cassianoidini Newell & Boyd, 1995

Genus *Cassianoides* Newell & Boyd

Subfamily Annuliconchinae Newell & Boyd, 1995

Annuliconcha Newell

Family Oxytomidae Ichikawa, 1958

Genera: *Oxytoma* Meek and subgenera, *Arctotis* Bodylevsky, *Maccoyella* Etheridge [syn. *Mineostrea* Bonarelli], *Zelotypia* Waterhouse, *Meleagrinnella* Whitfield, *Pseudavicula* Hudleston

Superfamily Chaenocardioidea Miller, 1889

Family Chaenocardiidae Miller, 1889

Subfamily Chaenocardiinae Miller, 1889

Tribe Chaenocardiini Miller, 1889

Genera: *Chaenocardia* Meek & Worthen, *Obliquipecten* Hind, cf *Rutotia* de Koninck

Tribe Otapiriini Waterhouse, 1982

Otapiria Marwick

Subfamily Asoellinae Begg & Campbell, 1985

Tribe Asoellini Begg & Campbell, 1985

Asoella Tokuyama, *Etalia* Begg & Campbell

Tribe Aucellinini Waterhouse new

Aucellina Pompeckj

Family Streblochondriidae Newell, 1938

Subfamily Limatulinae Waterhouse new

Genus *Limatulina* de Koninck

Subfamily Streblochondriinae Newell, 1938 [syn. Saturnellinae Astafieva, 1994]

Genera: *Streblopteria* M'Coy, *Streblochondria* Newell, *Orbiculipecten* Gonzalez, *Striochondria* Waterhouse, *Saturnella* Astafieva

Subfamily Guizhoupectininae Astafieva, 1994

Genera: *Guizhoupecten* Chen, ?*Xinjangopecten* Yang & Chen, ?*Tianshanopecten* Feng,

?*Junggarochondria* Yang & Chen

Family Deltopectinidae Dickins, 1957

Subfamily Deltopectininae Dickins, 1957

Genera: *Deltopecten* Etheridge, *Squamuliferipecten* Waterhouse, *Corrugopecten* Waterhouse, ?*Adornatipecten* Astafieva, *Vorkutopecten* Guskov

Subfamily Cyrtorostrinae Newell & Boyd, 1995

Genera: *Cyrtorostra* Branson, *Clavicostra* Newell

Subfamily Orbiculopectininae Waterhouse new

Tribe Orbiculopectinini Waterhouse new

Orbiculopecten Gonzalez, *Lionicula* Waterhouse

Tribe Eocamptonectini Waterhouse new

Eocamptonectes Newell, *Strebloboydia* Waterhouse, *Pectengonzalez* Waterhouse

Superfamily Pseudomonotoidea Newell, 1938

Family Pseudomonotidae Newell, 1938

Subfamily Pseudomonotinae Newell, 1938

Genera: *Pseudomonotis* Beyrich, *Ps. (Trematiconcha)* Newell & Boyd, *Pachypteria* de Koninck, *Prospodylus* Zimmermann, *Pegmavalvula* Newell & Boyd, ?*Marinopecten* Termier et al

Subfamily Hunanopectininae Yin, 1985

Tribe Hunanopectinini Yin, 1985

Genera: *Hunanopecten* Zhang, *Fransonia* Newell & Boyd

Tribe Furcatiini Waterhouse new

Furcatia Waterhouse

Subfamily Leptochondriinae Newell & Boyd, 1995

Genus *Leptochondria* Bittner

Family Terquemidae Cox, 1964

Genera: *Paleowaagia* Newell & Boyd, *Terquemia* Tate, *Newaagia* Hertlein

Superfamily Euchondrioidea Newell, 1938

Family Euchondriidae Newell, 1938

Subfamily Euchondriinae Newell, 1938

Euchondria Meek, *Crenipecten* Hall

Subfamily Crenipectinellinae Astafieva, 1991

Crenipectinella Astafieva

incerte sedis

Family Posidoniidae Frech, 1909

Posidonia Bronn, *Rutotia* sensu de Koninck

Order PECTINIDA Newell & Boyd, 1995

[nom. corr. hic ex Pectinoidea Newell & Boyd]

DIAGNOSIS: Monomyarian rounded pteriomorphs, usually with auricles or wings, right valve commonly pleurothetic with byssal notch, at least in early growth stages; ligament duplivincular or replivincular, alivincular, lativincular, or canalivincular, amphidetic or opisthodetic, thin outer simple prismatic calcite layer in both valves or only right valve as a rule, may be absent, foliated calcite dominant in many taxa, crossed lamellar or nacreous aragonite in other taxa, especially in lower paleolatitudes.

DISCUSSION: Pectinida was proposed as a new order by Newell & Boyd (1995), without comparison to other orders, but with an ample definition that draws out the variabilities in shell composition and morphologies, as modified in the preceding text. The proposal is justified, because it enables members of the order to be sorted into several major groupings that share critical similarities, as summarized in the diagnosis, and differ from other major groupings. Even downscaling subfamilies and families to tribe level leaves a number of superfamilies that share common morphologies, and the most convenient way to illustrate this is through the introduction of suborders, within a larger association, the Order Pectinida.

The three prime suborders recognized are Aviculopectinidina, with external amphidetic ligament, generally wings and auricles, and costate or plicate ornament, Monotidina with opisthodetic ligament, reduced wings and often with little ornament, and Pectinidina Waller, with compressed internal amphidetic ligament and particular hinge structures, and variously ornamented.

Suborder AVICULOPECTINIDINA new

Right valve with well developed anterior auricle and byssal notch, ornament generally of plicae or costae, ligament amphidetic, external, generally duplivincular, replivincular, alivincular, platyvincular, lativincular or canalivincular, hinge rarely pseudotaxodont, hinge teeth small and generally absent. Superfamilies include Aviculopectinoidea, Chaenocardioidea, Pterinopectinoidea, Pseudomonotoidea and Euchondrioidea.

Superfamily PTERINOPECTINOIDEA Newell, 1938

[nom. corr. hic ex Pterinopectinacea Newell & Boyd, nom. transl. ex Pterinopectinidae Newell]

DIAGNOSIS: Shells with duplivincular, replivincular or canalivincular ligament, wings small to large, variously defined, right anterior auricle present.

Family PTERINOPECTINIDAE Newell, 1938

DIAGNOSIS: Ligament basically chevroned duplivincular, but shows reduction in Claraiinae to incomplete chevrons, typical of the "replivincular ligament" and even a simple channel-form canalivincular ligament. Shells generally little inflated, generally inequivalve, inequilateral, ornament generally costate, may be smooth, right anterior auricle and byssal notch, posterior wings large to small or missing.

DISCUSSION: The classification of this family was discussed by Waterhouse (2000f), with particular reference to Claraiinae Gavrilo. *Denguria* Newell & Boyd of Permian age shows a close approach to Claraiinae.

Family HALOBIIDAE Kittl, 1912

DIAGNOSIS: Weakly inflated equivalve byssally attached non-pleurothetic shells with radial costae and comarginal rugae especially in early ontogeny. Ligament seldom preserved, replivincular or canalivincular.

DISCUSSION: Halobiidae appear to be a Triassic group of Pterinopectinoidea, independent of Claraiinae. Dr B. Gruber in Campbell (1994, text-fig. 4.5) found that the hinge in a specimen of *Halobia* (*Halobia*) *areata* has a duplivincular hinge, modified to the replivincular state. This was reinforced by a ligament area in *Halobia* (*Zittelihalobia*) *hochstetteri* discovered by Campbell (1994). A specimen of *Daonella frami* was shown by Campbell (1994) to be canalivincular. Thus the ligaments are very like those recorded for various *Claraia*, as summarized by Waterhouse (2000f). One peculiar feature of *Halobia* is a fold or byssal tube anteriorly below the anterior ear, and this is arguably anticipated by a rather convex anterior left wing in various Pterinopectininae.

Campbell (1994) had interpreted the Halobiidae quite differently. He represented the ligament as multivincular, but the shallow resilifers converge and taper dorsally, just as in Claraiinae. He also proposed a new Halobioidea, which should have been ascribed to Kittl, and distinguished it only from "Pectinia" (ie Pectinidina) and "Ostreina" (ie Ostreida), without regard to various other Mesozoic and Late Paleozoic family groups.

Superfamily **AVICULOPECTINOIDEA** Meek & Hayden, 1864

This is the major superfamily within Late Paleozoic Pectinida. Shells vary from biconvex to planoconvex auriculate, posterior wings large and well defined, umbonal slopes steep, large right anterior auricle, deep byssal notch, may have well developed left anterior auricular sinus, ligament external and typically alivincular, hinge teeth generally absent or minor. Shell structure variously modified in different lineages and according to paleogeography.

Family **AVICULOPECTINIDAE** Meek & Hayden, 1864

Shell plicate or undulose, increase by branching on right valve, growth lines arch hingewards over costae and ventrally in interspaces. Hinge alivincular, without dental structures.

Subfamily **AVICULOPECTININAE** Meek & Hayden, 1864

Moderately inflated left valve with coarse generally plicate or subplicate ornament, and less inflated right valve on which ornament is more subdued and ribs increase by branching. To this subfamily is referred *Acanthopecten* Girty, 1903, which Newell & Boyd (1995) had proposed as sole member of Family Acanthopectinidae Newell & Boyd. *Acanthopecten* has an inflated left valve with strong radial plicae, and only moderately convex right valve with plicae that may be costate, as in the type species. Growth lines point ventrally in interspaces. Limipectininae Newell & Boyd, 1990 is also synonymized. It was proposed as a monogeneric subfamily distinguished by its nacreous shell layer. The genus *Limipecten* Girty is very close in most aspects to *Aviculopecten*, as affirmed by Dickins (1983b) and Waterhouse (1969b), and the shell structure as well as strong lamellar and complexly ribbed ornament suffice to distinguish a genus.

Genus ***Aviculopecten*** M'Coy, 1851

TYPE SPECIES: *Aviculopecten planoradiatus* M'Coy, 1851.

DISCUSSION: The type or neotype of the type species, SM 5988, SD Hind (1903, p. 66), has been figured by M'Coy (1851), Hind (1903), Newell (1938) and Waterhouse (1969b).

Fundamental differences have arisen over the morphology of *Aviculopecten*. In 1938 Newell misinterpreted various aspects of the left valve ornament (Waterhouse 1969b), and referred to the genus various species since discriminated as *Etheripecten*. Later, what appears to be further confusion has arisen from the Newell & Boyd (1995) claim that *Aviculopecten* is biconvex. They based this claim on the alleged similarity between the type species of *Aviculopecten*, based on an Early Carboniferous left valve, and a Permian species that displays a supposedly similar left valve, and convex right valve. They asserted that *Hayasakapecten* Nakazawa & Newell, 1968 was congeneric. Newell & Boyd (1995, p. 60) considered that *Pecten flexuosus* M'Coy (1844, p. 93, pl. 18, fig. 1) was conspecific with the type species. This is a convex right valve with plicae, which, if correctly interpreted by Newell & Boyd (1995), should be senior synonym and type species. M'Coy later renamed *flexuosus* as *docens*.

The Newell & Boyd view does not agree with the opinion of other workers. Hind (1903) proposed that the right valve of *A. planoradiatus* is probably *A. tabulatus* M'Coy (1844). Dickins (1981, p. 28) further examined the relevant material and literature and provided evidence on the nature of the right valve of *planoradiatus*. The right valve is virtually flat, with branching costae, as in *Heteropecten* Kegel & Costa. Dickins considered that *tabulatus* was a separate and different species, and that the right valve of *planoradiatus* had been misidentified as *tabulatus*. Dickins (1981) stressed that *Limipecten* was close to *Aviculopecten*, as claimed by Waterhouse (1969b). None of these assertions were refuted by Newell & Boyd (1995). Insofar as Hind and Dickins, and the writer were able to examine collections in England, rather than just assess figures and much younger species, their view should carry weight. Dickins in particular made an extensive enquiry, with previous documentation as a guide.

Genus ***Heteropecten*** Kegel & Costa, 1951

The ornament is distinctive and involves low broad ribs formed by plication of the shell in the left valve, narrow interspaces, and a modest amount of rib or plication splitting. The right valve is much less convex than the left. The genus is close to *Aviculopecten*, in which ribs are more elevated and less subdivided.

Heteropecten sp. or spp.
Pl. 5, fig. 24, pl. 9, fig. 4

A left valve TM 8199 from D44/f123 (GS 15226), *Pseudostrophalosia?* cf. *blakei* fauna, lower Mangarewa Formation, has broad flat-crested primary ribs, subdivided by grooves ventrally, with narrow interspaces. Growth-lines are mostly straight across the ribs, some arching dorsally, others ventrally and in the widest of interspaces, they arch ventrally. They arch dorsally over the crest of narrow median ribs. A more closely

ribbed specimen TM 5259 from D44/f9478 (GS 3616) with broad flat crests was reported by Waterhouse (1982a, pl. 1, fig. d, e). Another left valve TM 8197 found at D44/f344, lower *Echinalosia ovalis* Zone, Mangarewa Formation, Wairaki Downs, has slightly rounded crests and growth lines that are straight mostly, with some arching hingewards over the crests.

Subfamily **UNDOPECTININAE** new

NAME GENUS: *Undopecten* Waterhouse, 1982.

DIAGNOSIS: Shell upright, posterior wings large, shell biconvex, almost equivalve, ornament of plicae on both valves, resilifer well developed.

DISCUSSION: This subfamily includes *Undopecten*, *Hayasakapecten* Nakazawa & Newell, 1968, *Turbopecten* Astafieva, 1991 and *Newellipectinia* n. gen. All vary a little in nature of ornament but share inflated right valve and plicae on both valves. Aviculopectininae differ in having a less convex right valve with finer ornament. The genera are widely distributed, pointing to an early beginning. The biconvexity suggests Deltoplectininae, whereas the nature of the ligament and large size of the posterior wings suggest an alliance with Aviculopectininae. Growth lines follow the same course as in *Aviculopecten* etc. *Acanthopecten* is close especially to *Hayasakapecten*, but its right valve is flatter and right valve ornament subdued.

Genus ***Undopecten*** Waterhouse, 1982

TYPE SPECIES: *Pecten fittoni* Morris, 1845.

DISCUSSION: The same type species was nominated later as type for *Morrisipecten* Muromzeva & Guskov and for *Altaipecten* Tang & Chen. Waterhouse (1982b, p. 37) assigned the genus to Deltoplectinidae because of its biconvexity and identical ornament on both valves. But it was noted that a well formed resilifer was developed, and Newell & Boyd (1995, p. 41) reallocated the genus to Etheripectinidae. Waterhouse in Waterhouse & Jell (1983, p. 248-249, pl. 4, fig. 1-4, 6, 11, 14) discussed *Undopecten* and noted a considerable approach to a new species of mid-Permian age in the north Bowen Basin, called *Etheripecten plicatus* Waterhouse. This species has a plicate left valve and flat right valve, with no plicae.

It could be considered that *Undopecten* should be regarded as a very large member of Streblochondriidae, for it shares biconvex shell and resilifer. But the upright stance, large size, large posterior wings and very different outline and ornament provide significant differences.

Undopecten is allied to *Hayasakapecten* Nakazawa & Newell, 1968, a genus synonymized with *Aviculopecten* by Newell & Boyd (1995). The left valve of *Hayasakapecten* is only moderately like that of *Aviculopecten*, with more round-crested plicae, and the right valve is convex and plicate. A resilifer is developed, and growth lines arch ventrally in the interspaces.

Genus ***Newellipectinia*** new

DERIVATION: Named for Professor Norman D. Newell.

TYPE SPECIES: *Aviculopecten americanus* Newell & Boyd, 1995, here designated.

DIAGNOSIS: Biconvex upright shells with strong plicae, weakly ornamented wings other than costate right anterior auricle, resilifer well developed.

DISCUSSION: The type species comes from the Cathedral Mountain, Road Canyon, and Bone Spring Formations of the Glass Mountains, Texas. It has primary and secondary plicae that increase rapidly in strength, channelled interspaces, no costae, and a few hyote spines. Growth-lines arch hingewards over the plicae and ventrally in interspaces. The genus is very close to *Undopecten* Waterhouse, 1982, which has smooth auricles with low costae and closely costate plicae. *Hayasakapecten* Nakazawa & Newell, 1968, type species *H. shimizu* Nakazawa & Newell, 1968 has strong non-costate plicae and ribbed auricles, and the concentric sculpture produces a scaly or tuberculine appearance, and may extend as spinose projections ventrally, as in *Acanthopecten*. Newell & Boyd (1995) referred the species *americanus* to *Aviculopecten*, but the plicae of this genus are flat-crested and of different appearance, and the right valve is less inflated.

Family **ETHERIPECTINIDAE** Waterhouse, 1982

[nom. transl. Newell & Boyd (1995, p. 33) ex Etheripectininae Waterhouse, 1982]

DIAGNOSIS: Shells inequivalve, right valve comparatively flat, posterior wings large, umbonal slopes well defined, ornament primarily costate, not plicate, increase by intercalation, not branching on either valve, growth-lines swing hingewards in interspaces. Hinge alivincular, no teeth.

DISCUSSION: This family is close to *Aviculopectininae* in shape and hinge, but differs in ornament. As Newell & Boyd (1995, p. 33) wrote, "a majority of Upper Paleozoic multicostate pectinoids belong to this family". The elevation to family was not accepted by Nakazawa (1999), but allows subdivision of a large diverse group into subfamilies.

Subfamily **ETHERIPECTININAE** Waterhouse, 1982

Ornament of intercalate costae on left valve and branching costae on right valve, variably spinose.

Tribe **ETHERIPECTININI** Waterhouse, 1982

Ovally pectiniform in shape with large round-edged wings.

Genus ***Etheripecten*** Waterhouse, 1963

TYPE SPECIES: *Etheripecten striatura* Waterhouse, 1963.

DIAGNOSIS: Left valve convex, right valve flat or gently convex, alivincular ligament. Characterized by nature of ornament: left valve bearing costae in well differentiated orders, narrow primary costae of thickened ridges, further costae arising by intercalation as a rule, growth lines arch dorsally between costae, interspaces very wide. Right valve with simpler costae, opposing those of left valve, increasing by intercalation, growth lines tend to arch dorsally in interspaces. Inner shell layer may be aragonitic or calcitic.

DISCUSSION: Yin (1982, p. 346) objected to the diagnosis of *Etheripecten* because it involved aspects of the morphology of the right valve. "This is somewhat impractical because right valves are much rare in occurrence." This lack of right valves is a common difficulty in many faunas, world-wide, and in that regard the preservation of Australian and New Zealand material is particularly advantageous, with so many right valves to be found. So one's response has to be sympathetic. But if Yin's material was so incomplete, then clearly he could not adequately circumscribe taxa. It seems that he expected to be able to shape systematic and taxonomic procedures around the vagaries of preservation of his indifferent material, and to defend what seems to be a strange attitude, attacked Waterhouse for using the right valve to help circumscribe *Etheripecten*.

Newell & Boyd (1995) synonymized *Etheripecten* with *Heteropecten* Kegel & Costa, 1951, type species *Aviculopecten (Deltopecten) catherinae* Reed, 1930 (see Reed 1930a) of upper Carboniferous age. This synonymy is unacceptable, and is based on a flawed analysis. Even a glance at the type species of *Heteropecten*, of which numerous figures are provided by Kegel & Costa (1951) and Rocha-Campos (1970, pl. 1, 2), will show substantial differences in ornament. The left valve primary ribs of *Heteropecten* are broad like narrow plicae and the *Heteropecten* shell is undulose and thin. In type or other *Etheripecten*, the ornament is dominated by costae, which arise from somewhat thickened and only weakly undulose shell. There are examples of *Etheripecten* that do develop a more undulose shell, formed by plicae that affect the shell, including *Etheripecten plicata* Waterhouse in Waterhouse & Jell (1983). Even so, this ornament differs substantially from that of *Heteropecten*, because ribs with thickened shell are present as well. In addition, the interspaces are narrow in *Heteropecten*. By contrast, the interspaces are much wider than ribs in *Etheripecten*, imparting a very different appearance to the shell. In *Heteropecten*, there is generally no more than one additional order of rib, arising by intercalation. The left valve of *Etheripecten* has several orders of ribs, arising by intercalation, and ribs are slender. There are not many species of *Heteropecten*, and all show a consistent pattern of ornament. There are a large number of species of *Etheripecten* - and close allies, and even within substantial populations, individuals show little resemblance to *Heteropecten*. Whilst two species may theoretically represent two ends of a spectrum with a number of species that close the morphological gap, there are numerous Carboniferous and Permian species that look exactly like *Etheripecten*, and another much smaller cluster that fall close to *Heteropecten*. The gap remains. Why then force them into one genus? There are further differences. In the right valve, costae branch in *Heteropecten*, but are intercalated in *Etheripecten*, the growth lines arch ventrally between right valve costae in *Heteropecten*, and dorsally (hingewards) in *Etheripecten*. The byssal notch is much deeper under the right anterior auricle in *Etheripecten* than in *Heteropecten* (Waterhouse 1969b, 1982b). On these grounds, Waterhouse (1969b) suggested that *Heteropecten* was a descendent of *Aviculopecten* M'Coy, 1851. My conclusion is that the lumping of *Etheripecten* with *Heteropecten* is much more doubtful than the Newell-Boyd claim that *Aviculopecten* is biconvex. In 1938, Newell referred to *Aviculopecten* shells now distinguished as *Etheripecten* through differences in plication and costation on both valves. In 1995, Newell & Boyd changed their interpretation of *Aviculopecten* and lumped *Etheripecten* with *Heteropecten*. Yet for all the shifts in treatment, *Aviculopecten*, *Heteropecten* and *Etheripecten* remain valid and worthwhile genera.

Nakazawa (1999), like many other authors, has distinguished *Etheripecten* from *Heteropecten*. He stressed the broad and bifurcated ribs on the right valve of *Heteropecten*.

Genus *Fletcheripecten* Waterhouse, 1982

TYPE SPECIES: *Fletcheripecten heterosus* Waterhouse, 1982.

DIAGNOSIS: Shells very close to *Etheripecten*, with unusually prominent primary costae involving thickened shell, and only narrow shell plication.

DISCUSSION: *Fletcheripecten* is much closer than *Etheripecten* to *Heteropecten* at first sight, but shows strong primary ribs with wide interspaces, whereas the ribs of *Heteropecten* are narrow plicae or subplicae with flattish crests and often sharply curved edges, and interspaces are narrow. Growth lamellae in *Fletcheripecten* arch ventrally over left valve costae, and right valve ribs increase by intercalation, not branching, unlike the arrangement in *Heteropecten*. The subauricular byssal notch is deeper in *Fletcheripecten* than in *H. catherinae*. The species *Heteropecten laticostatus* Waterhouse, referred to *Heteropecten* by Newell & Boyd (1995), conforms well with *Fletcheripecten*, not *Heteropecten*. Nakazawa (1999) synonymized both *Fletcheripecten* and *Paradoxipecten* Zhang with *Etheripecten*. But there are so many species of *Etheripecten* - including many referred mistakenly to *Aviculopecten* and *Heteropecten*, that subdivision will help to delineate streams of evolutionary development.

Genus *Glabripecten* Waterhouse, 1982

TYPE SPECIES: *Glabripecten glaber* Waterhouse, 1982.

DIAGNOSIS: Left valve well inflated and erect, right valve gently convex, up to half as high as left, ornament of faint concentric growth lines, well formed resilifer.

DISCUSSION: This genus was interpreted as an unusual etheripectinid by Waterhouse (1982b), distinguished by its lack of ornament. It was noted that *Etheripecten leniusculus* (Dana, 1849) shows considerable approach, apart from having fine costae, with some other distinctions. However Newell & Boyd (1995) proposed that the form should be synonymized with *Streblopteria* M'Coy, 1851, in turn placed in Dellopectinidae Dickins. They gave no reasons. *Glabripecten* is not equally or subequally biconvex, unlike *Dellopecten* or *Streblopteria*, and the posterior wings are long, unlike those of *Dellopecten* or *Streblopteria*. As well, the *Glabripecten* hinge displays a small deep and well formed resilifer, whereas *Dellopecten* has a broad or no resilifer. To *Streblopteria* Newell & Boyd assigned a species *montpelierensis* Girty that was strongly biconvex, with small posterior wings, broad if any resilifer, and lamellar tooth and socket in the hinge. *Glabripecten* has large posterior wings, deep narrow resilifer and no tooth or socket. About the only point of similarity between "*Streblopteria*" sensu Newell & Boyd and *Glabripecten* seemed to lie in the comparatively smooth surface of the shell, and this is not deemed to indicate congenericity. *Glabripecten* is deemed valid, and a member of Etheripectinidae, not Dellopectinidae.

Genus *Vanvleetia* new

DERIVATION: Named from species name vanvleeti.

TYPE SPECIES: *Aviculopecten vanvleeti* Beede, 1903, here designated.

DIAGNOSIS: Left valve moderately convex, right valve less so, left anterior wing large with acute cardinal extremity and even larger posterior wing with obtuse cardinal margin. Right anterior auricle prominent and byssal notch deep. Ornament characteristic on left valve, strong primary subplicae with hyote spines opening ventrally and arranged in approximate concentric rows, median interstitial rib may be well developed and spinose, interspaces broad with fine radial threads crossed by low irregular concentric growth lamellae. Right valves scarce and poorly known, with more subdued radial ornament.

DISCUSSION: Newell (1938) remarked on the distinctive nature of this species. It was assigned to *Heteropecten* by Newell & Boyd (1995, p. 36) but is readily distinguished by its ornament, which is much closer to that of *Etheripecten*. It also approaches *Girtypecten* Newell, 1938, but lacks the strong concentric ridges of that genus and may have a smaller posterior left wing. The closest genus is *Fletcheripecten*, which is distinguished by having more solid primary ribs without hyote spines on the left valve.

Specimens belonging to *Vanvleetia* has been recorded from several levels in Middle to early Late Permian of United States, and are likely to belong to more than one species. The genus is represented in the Early Permian Jungle Creek Formation of the Yukon Territory, Canada, by *Etheripecten* sp. A of Shi & Waterhouse (1996, pl. 30, fig. 17, 18).

Tribe **CASSIANOIDINI** Newell & Boyd, 1995

[nom. transl. hic ex Cassianoididae Newell & Boyd]

The sole genus *Cassianoides* Newell & Boyd is distinctively subangular in shape with large posterior wings,

highly convex left valve, almost flat right valve, strong primary left valve ribs bearing hyote spines, and strong growth-lines arching hingewards over wide interspaces. The right valve has long anterior auricle and is ornamented by subdued ribs. Hinge alivincular.

Nakazawa (1999, p. 15) pointed out that species of this genus had previously been assigned wrongly to *Cyrtorostra* and *Cassianella*, including *Cassianella alta* Waterhouse, 1987 from the Flat Top Formation of the southeast Bowen Basin. *Cassianoides* has an unusual shape, and so is retained as distinct from Etheripectinini, but is obviously close to *Vanvleetia* and *Fletcheripecten*.

Subfamily **ANNULICONCHINAE** Newell & Boyd, 1995

[nom. transl. hic ex Annuliconchidae Newell & Boyd]

Only one genus is known, *Annuliconcha* Newell, 1938. Posterior wings large, ornament predominantly concentric with heavy concentric ribs at intervals, also fine radials. Right valves less convex with finer ornament. The genus is thus like both Aviculopectininae and Etheripectininae, and the latter group is deemed a more likely source because its radial ornament is much weaker than in Aviculopectininae. The large size of the posterior wings suggests that derivation from Streblochondrinae is unlikely. Newell (1938) noted that early growth phases resembled those of *Acanthopecten* and *Girtypecten*, and *Girtypecten*, a member of Etheripectininae, has strong concentric as well as radial ornament.

Family **OXYTOMIDAE** Ichikawa, 1958

DIAGNOSIS: Commonly strongly inequivalve, inequilateral, umbonal slopes subdued, large posterior wings, small right anterior auricle, deep byssal notch, ornament predominantly of fine, variable ribs, commonly stronger on left valve, oblique resilifer, hinge edentulous or with interlocking teeth and sockets, pallial line in series of pits, inner ostracum calcite, with crossed lamellar structure, outer ostracum of right valve prismatic.

DISCUSSION: Cox (1969b) pointed out that this Mesozoic family arose from Aviculopectinidae, as understood in the bivalve treatise. The large posterior wings and the comparatively fine ribs point strongly to derivation from Etheripectinidae, with internal modifications to musculature and hinge, and development of less clearly defined and larger posterior wings with gently convex umbonal slopes, and smaller right anterior auricle.

Genus **Zelotypia** new

DERIVATION: zelotypia - jealousy, Lat.

TYPE SPECIES: *Maccoyella incurvata* Waterhouse, 1959, here designated.

DIAGNOSIS: Medium-sized inequivalve inequilateral shells, left valve highly convex, prosogyrous umbo and no posterior wing. Right valve flat or concave. Hinge as in *Maccoyella* Etheridge.

DISCUSSION: Two Early Cretaceous species from Patagonia and New Zealand, *Mimetostreon bonarellii* Leanza and *Maccoyella incurvata* (Waterhouse) are distinguished from the type and other members of *Maccoyella* Etheridge, 1892 by their greater inflation, more swollen and convex left valve and flat to generally concave right valve, with loss of the posterior wings. By contrast, *Maccoyella* is unequally biconvex, gently inflated, with large posterior wings in each valve. Further differences, of minor significance, were enumerated by Waterhouse & Riccardi (1970). Those authors considered that the small swollen species potentially could have arisen independently through gryphaeation. This may well have occurred amongst Ostreida, but there are no well established examples amongst Aviculopectinidina that come to mind. The two species are so close in so many details that they appear to have been related.

As noted by Waterhouse & Riccardi (1970), *Mimetostreon* Bonarelli, 1921, shows some approach. This genus was based on *Avicula corbiensis* Moore, 1870, and has long been synonymized with *Maccoyella* Etheridge, 1892, which it closely resembles in hinge and ornament (see Cox 1969b, Waterhouse & Riccardi 1970 for references). The synonymy appears acceptable. The species *corbiensis* is not that well known, because of poor preservation of the type specimen, but is much less inflated and incurved than *bonarellii* or *incurvata* (Waterhouse & Riccardi 1970, text-fig. 3). The specimens figured as *corbiensis* are small, and generally incomplete, but some show a well developed posterior wing in the left valve (Etheridge 1907, pl. 61, fig. 5). Even so, Etheridge expressed slight caution about the identity of his material, which remains insecure because of the very poor state of preservation of the original type. For that, only the low inflation and higher number of costae provide criteria for comparison. To aff *corbiensis* Cox (1961, pl. 1, fig. 9-13) assigned West Australian specimens which lack posterior wings as far as can be seen and are moderately inflated, with feebly convex right valve. There is no sure conspecificity with *corbiensis*. Skwarko (1988, pl. 6, fig. 1-11) compared specimens to *corbiensis* from the Northern Territory of Australia which have very large posterior wings on each valve, and flat or weakly convex right valve.

The species *Oxytoma rockwoodensis* Etheridge, 1892 has been synonymized with *corbiensis* by various authors, and it is based on a small left valve with a number of costae and with a prominent posterior

wing. Thus *corbiensis* is known to differ from the new genus in its inflation, low curvature and high number of ribs, and it possibly differs in its large posterior wings. It agrees with the new form in its small size, and possibly little inflated, or even concave right valve.

Superfamily **CHAENOCARDIOIDEA** Miller, 1889

[nom. transl. hic ex Chaenocardiidae Miller]

DIAGNOSIS: Valves biconvex, equivalve to inequivalve, with relatively small posterior wings in each valve, weakly to well defined, right anterior auricle and byssal notch well developed. Ornament varies from coarse to fine, costae tend to increase by branching, but implantation also common, growth lines often arching ventrally in interspaces and hingewards over costae. Hinge generally amphidetic, ligament alivincular, lativincular, or platyvincular, some genera have one or two hinge teeth.

ORIGIN: An Early Carboniferous genus *Limatulina* de Koninck has small posterior wings and subequivalve shell, with left valve ornament close to that Etheripectinini, although growth lines follow the course normal for Aviculopectinidae.

Family **CHAENOCARDIIDAE** Miller, 1889

Shells normally pleurothetic, wings poorly defined, small to large right anterior auricle, ligament alivincular to semi-lativincular, asymmetric to normal amphidetic.

Subfamily **CHAENOCARDIINAE** Miller, 1889

Ligament alivincular to often semi-lativincular, and usually asymmetrically amphidetic.

Tribe **CHAENOCARDIINI** Miller, 1889

[nom. transf. ex Chaenocardiidae Miller]

DIAGNOSIS: Right anterior auricle well developed.

DISCUSSION: *Chaenocardia* is a Pennsylvanian genus with smooth almost biconvex valves, characterized by oblique retrocrescent shape, with semi-lativincular highly asymmetric amphidetic ligament, and single weakly developed anterior and posterior teeth.

Astafieva (1994) and Waterhouse (1982b) regarded *Chaenocardia* as a close ally of *Streblochondria* Newell, 1938. Such a relationship has long been resisted by Newell. The dispute was crystallized by Newell & Boyd (1995, p. 76) with the proposal that Chaenocardiidae was monotoideid, and included *Eurydesma* as a constituent genus. Monotoidea are ovoid shells, often without posterior wing or auricle, and with anterior right ear, and opisthodetic often transitional ligament. As far as I can judge, *Chaenocardia* and its possible ally *Obliquipecten* Hind have a distinct although small posterior wing in each valve (see for example Newell & Boyd 1995, text-fig. 55. 1b, 3b, 4, 6; text-fig. 61.1, 2, 3a, 5b). As well, the ligament does extend a little in front of the umbones (see Newell & Boyd 1995, text-fig. 55.3a), and is asymmetrically amphidetic (Newell 1938, pl. 16, fig. 5). The valves are much less inflated than most Eurydesmidae, Buchiidae and some Monotidae, and umbones are prosogyrous or orthogyrous, like Streblochondriinae. Moreover the feebly dentition is very like that of genera such as *Eocamptonectes* and allies, which are otherwise like Streblochondriidae. *Chaenocardia* is judged to be an unusual member of a large group of streblochondriiform bivalves, and somewhat unfortunately, acts as name-giver to the group.

THE QUESTION OF *Rutotia* de Koninck, 1885

TYPE SPECIES: *Pecten hemisphaericus* Phillips, 1836, SD Newell, 1969c, p. 339.

DESCRIPTION: The designated type species of *Rutotia* is based on a left valve with hinge slightly shorter than maximum shell length, and poorly differentiated wings with acutely obtuse cardinal extremities and the shell covered by light concentric ornament, figured by Phillips (1836, pl. 6, fig. 16). De Koninck (1885, pl. 39, fig. 6, 7) added a somewhat similar left valve with a few apparent low ribs, and showed the right valve in profile as being slightly less inflated. Ribs are not seen on any of the other figured specimens assigned by de Koninck (1885) to *Rutotia*. *Rutotia grandis* de Koninck (1885, pl. 39, fig. 1-3) has slightly shorter hinge and umbones more anteriorly placed, and lacks conspicuous radial ornament, or well defined wings, and is of similar relative inflation. The right valve was not shown to have a right anterior auricle or byssal notch. *R. phillipsi* de Koninck is a left valve of somewhat similar shape. *R. obesa*, *R. ornithocephala* and *R. ovalis* were figured as right valves, without an anterior auricle. Numerous figures were provided of various other specimens, allocated various species names, and representative of one or two to three species. The specimens, judged from these illustrations, show that de Koninck understood his new genus *Rutotia* as follows:

DIAGNOSIS for *Rutotia* sensu de Koninck: Shells medium to small in size, biconvex, right valve slightly smaller and less convex than left valve, umbones prominent, hinge short with bluntly obtuse to acutely obtuse cardinal extremities, wings poorly defined, umbonal slopes gentle, no auricles or visible byssal notch. Ornament of subdued growth lines or low rugae, or smooth. Ligament amphidetic, otherwise not known.

DISCUSSION: Newell (1938, p. 88) considered that *Pecten hemisphaerica* Phillips, as described by Hind (1903, p. 43, 47), had a well defined byssal notch, and was a synonym of *Streblopteria* M'Coy. He formally selected this species as lectotype in the bivalve treatise (Newell 1969c, p. 341). The action is regrettable, undermining de Koninck's work for no good reason. The right valves figured by de Koninck lack a byssal notch, and indicate a genus close to *Posidonia*, not close to *Streblopteria*, but Pectinida nonetheless, despite Newell (1938, p. 88) claiming that de Koninck's genus was not pectinoid (ie Pectinida). Through Newell's designation of a lectotype, we are left with having to interpret a left valve as figured by Phillips (1836), and a brief analysis by Hind (1903), which Newell (1938) admitted was far from clear. Even accepting Hind (1903), the anterior wings of Phillips' specimen have different outlines and are less clearly defined than in left valves of *Streblopteria*, so synonymy with *Streblopteria* must be discounted. Astafieva (1994) considered *Rutotia* was possibly valid, and an ally of *Chaenocardia* and *Streblochondria*. The poor definition of the wings suggest a clear difference from *Streblopteria*, and open the possibility of a relationship with *Chaenocardia*. If Hind was right. Without intensive research, it is difficult to be sure if Hind was right, and if he really did have specimens of *hemisphaerica*. De Koninck's profusely illustrated material indicates a close relationship with *Posidonia* Bronn, distinguished by less defined anterior wings, lower concentric ornament, and slightly greater inflation. They are the specimens that should have received the name *Rutotia*, and then the present uncertainty would have been avoided.

Tribe **OTAPIRIINI** Waterhouse, 1982

[nom. transl. hic ex Otapiriinae Waterhouse]

DIAGNOSIS: Right anterior auricle small.

DISCUSSION: *Otapiria* Marwick, 1935, type species *O. marshalli* (Trechmann) from the New Zealand Triassic, is close to *Chaenocardia* in its poorly defined wings and asymmetric amphidetic ligament, in which the resilifer is lativincular (Marwick 1935, pl. 36, text-fig. 28-32, 34, 35). The right anterior auricle is very small, and the byssal notch well formed. *Otapiria* carries fine radial ornament, or may be almost smooth. Waterhouse (1982b) erected Otapiriinae in the context of Permian *Chaenocardia*, *Streblochondria*, *Streblopteria* and *Pseudomonotis*. This assessment approached that of L. R. Cox in the bivalve treatise, who referred *Otapiria* to Aviculopectinidae (p. 339), in contrast to other authors such as Imlay (1969), Covacevich & Escobar (1979) and Begg & Campbell (1985), who referred *Otapiria* to Monotidae. These latter authors failed to appreciate the significance of the different hinges in *Otapiria* or *Monotis*; the ligament is opisthodetic in *Monotis*, and amphidetic in *Otapiria*. The trouble largely lay in their neglect of Late Paleozoic bivalves.

Subfamily **ASOELLINAE** Begg & Campbell, 1985

[nom. transl. hic ex Asoellidae Begg & Campbell]

DIAGNOSIS: Small shells, inequivalve, inequilateral, left valve convex, right valve gently convex to gently concave, posterior wings poorly defined or absent, right anterior auricle generally elongate and slender, or very small, byssal notch deep, ligament amphidetic, alivincular.

DISCUSSION: Family Asoellidae was proposed for Triassic genera and compared with Triassic families of Monotidina, especially Buchiidae and Monotidae, but closest relationships lie with Aviculopectinidina of Late Paleozoic age, which were largely ignored, other than Pseudomonotidae. The comparatively smooth shell surface - with traces of radials, the symmetry, hinge and right auricle suggest an approach to Chaenocardiidae and Streblochondriidae, not discussed by Begg & Campbell (1985). *Asoella* differs from Paleozoic members of these families by possessing gently convex umbonal slopes with posterior wings poorly defined or absent. *Chaenocardia* is slightly inequivalve, and has very small posterior wings and faint radial ornament. Most Streblochondriinae are biconvex, generally with better defined ornament, and with better defined wings, features which mark differences from *Asoella*. On the other hand the ligament is asymmetrically amphidetic in *Chaenocardia*, and in *Otapiria*, tending to be lativincular, whereas that of *Streblochondria* is symmetrically amphidetic and alivincular, and the hinge of Streblochondriidae lacks the few simple buttresses or teeth seen in *Chaenocardia*, and missing from *Asoella* and *Otapiria*. Although the uncertainties could be evaded by referred Asoellidae to a discrete family, ranking with the two rival sources, it is here suggested that the group may be classed provisionally with *Chaenocardia*. Like Astafieva (1994), I consider the strong obliquity in *Chaenocardia* to be exceptional, and allied forms such as *Otapiria* with very reduced wings, gently umbonal slopes and non-denticulate hinge help demonstrate an approach to *Asoella* and *Etalia*. One alternative would be to treat *Asoella* as a member or tribal unit within Otapiriinae.

Tribe **ASOELLINI** Begg & Campbell, 1985

[nom. transf. hic ex Asoellidae Begg & Campbell]

Members of Asoellini have a large right anterior auricle and moderately convex left valve.

Tribe **AUCELLININI** new

[not Aucellidae Fischer, 1887, nom. transl. Lausen 1897 ex. Aucellinae Fischer, 1887, suppressed by ICZN Opinion 492 (1957)]

NAME GENUS: *Aucellina* Pompeckj, 1901.

DIAGNOSIS: Small pleurothetic bivalves, left valve convex, right valve almost flat where known, very small anterior right auricle, posterior wings inconspicuous or absent, anterior left wing may be prominent, ligament alivincular, amphidetic.

DISCUSSION: The genus *Aucellina* looks like *Buchia* in general, and so has been classed in Buchiidae but the cardinal area extends well forward from the beak and the ligament is amphidetic, not opisthodetic. *Paraucellina* Pavlov, also of Cretaceous age, and *Bittneria* Broili, of Triassic age, may be allied but the right valves are not known according to the bivalve treatise. Begg & Campbell (1985) noted a possible relationship between *Aucellina* and *Asoella-Etalia*, and *Aucellina* is here placed in a separate tribe because of its more inflated left valve, smaller right anterior auricle and other differences.

Family **STREBLOCHONDRIIDAE** Newell, 1938

[nom. transl. Newell & Boyd, 1985 ex Subfamily Streblochondriinae Newell]

DIAGNOSIS: Shells biconvex, almost equivalve to inequivalve, upright to slightly prorescent, ovate, well defined umbonal slopes, posterior wings small, ornament variable, of close-set fine or no radial ornament and concentric threads to varying degree. Short amphidetic alivincular hinge, resilifer short and extended slightly outward.

According to Newell & Boyd (1995), the outer shell layer is antimarginal fibrous in both valves, but the shell structure is not known for all *Streblochondria*, nor for many other genera, so that its generic and familial significance is not yet known, and emphasis on its significance may prove unjustified.

PREVIOUS CLASSIFICATIONS: The classification of Streblochondriidae and genera regarded by other authors as related according to Newell & Boyd (1995) may be summarized as follows:

Superfamily Aviculopectinoidea Meek & Hayden, 1864

Family Streblochondriidae Newell, 1938

Genera: *Streblochondria* Newell, *Guizhoupecten* Chen

Family Deltopectinidae Dickins, 1957

Genera: *Deltopecten* Etheridge Jnr, *Streblopteria* M'Coy, *Crittendenia* Newell & Boyd, *Eocamptonectes* Newell

Superfamily Monotoidea Fischer, 1887

Family Chaenocardiidae Miller 1889

Genera: *Chaenocardia* Meek & Worthen, *Eurydesma* Morris, *Obliquipecten* Hind

This arrangement differed very substantially from proposals in an article by Astafieva (1994), which was mentioned in the references by Newell & Boyd (1995), but scarcely discussed.

Superfamily Pectinoidea Wilkes, 1810

Family Chaenocardiidae Miller, 1889

Subfamily Chaenocardiinae Miller, 1889

Genera: *Chaenocardia* Meek & Worthen, *Obliquipecten* Hind, subgenera *Obliquipecten* Hind, *Endocostapecten* Feng Qing-lai

Subfamily Streblochondriinae Newell, 1938

Genera: *Streblochondria* Newell, *Eocamptonectes* Newell, *?Pleuronectites* Schlotheim, *Streblopteria* M'Coy, with subgenera *Streblopteria* M'Coy and *?Rutotia* de Koninck

Subfamily Guizhoupectininae Astafieva, 1994

Genera: *Guizhoupecten* Chen, *Xinjangopecten* Yang & Chen, *?Tianshanopecten* Feng, *Junggarochondria* Yang & Chen

Subfamily Saturnellinae Astafieva, 1994

Genus *Saturnella* Astafieva

The fundamental difference between the two classifications lies in the different treatments of Chaenocardiidae. Newell & Boyd (1995) suggested that the hinge structure of this family was entirely different, because teeth were developed. Scrutiny of their figures may not convince every reader, in so far as the denticular structure seems very faint on some critical specimens - but the figures are supplemented by their

examination and description. Their interpretation of morphology is therefore accepted, but their classification is rejected.

Astafieva (1994) proposed two new subfamilies allied to *Streblochondriidae*. Of these, *Guizhoupectininae* is interpreted as a distinctive subfamily with coarse radial ornament and long anterior right ear, possibly close to *Deltopectinidae*. Following Astafieva (1994), some genera recognized by Chinese authorities are tentatively included, although this requires confirmation. *Saturnella* has strong concentric ornament, and was assigned a separate subfamily. Here the genus is retained as a member of *Streblochondriinae*.

On available evidence, taking into account known variabilities, it appears that the association of *Streblopteria* with *Streblochondria* should be retained, as in Amler (1994) and Nakazawa (1999, p. 11).

Genus *Streblopteria* M'Coy, 1844

Streblopteria M'Coy, 1851, type species *Meleagrina laevigata* M'Coy, 1844 of early Carboniferous age, lacks radial ornament and its hinge is not known. But it is so like *Streblochondria* and *Striochondria* in general morphology that it is likely to belong to the same subfamily. Indeed, a good case could be made for synonymizing all three genera. Newell & Boyd (1995, p. 50) offered a contentious interpretation for *Streblopteria*, interpreting it from a Guadalupian (Middle Permian) species, *montpelierensis* (Girty), rather than the Carboniferous type, and other species that resembled *Streblopteria* in all known detail. Although moderately close in external shape, *montpelierensis* apparently lacks a narrow deep resilifer, and has a short lamellar tooth in the right valve. Newell & Boyd (1995) allocated *Streblopteria* to *Deltopectinidae*, because *Deltopecten* was considered to share a transitional ligament (see Newell & Boyd 1987, pp. 3, 5, 1995, p. 13), or what is here called lativincular ligament for *montpelierensis* and platyvincular for *Deltopecten*. The presence of hinge teeth and lack of plicae from *montpelierensis* were not regarded as significant at family level. In fact, the supporting aspects of their argument, concerning ligament, biconvexity, and short posterior wings (which they overlooked) had long been deduced by Gonzalez (1978) and Waterhouse (1982b), but that work was not acknowledged.

Amler (1994, p. 139) described *Streblopteria* as acline to slightly opisthocline, anterior ears longer or equal to posterior ears, both valves smooth or with concentric ornament, right anterior ear strongly ribbed. It is assumed that there was a resilifer in the hinge, which was in all likelihood identical to that of *Streblochondria*. As in most studies, the genus was distinguished from *Streblochondria* solely by the lack of radial ornament from all but the auricles.

Newell in Hertlein et al (1969b, p. 339) synonymized *Rutotia* de Koninck with *Streblopteria*, but the posterior walls and wings are much less defined in this genus. No mention of Newell's proposed synonymy is to be found in Newell & Boyd (1995).

Streblopteria minauris Waterhouse, 1987b

1982b *Streblopteria parkesi* (not Fletcher); Waterhouse, p. 31, pl. 16, fig. e, f, j, pl. 17, fig. c (not pl. 16, fig. k = *Striochondria parkesi* (Fletcher)).

1987b *Streblopteria minauris* Waterhouse, p. 150, pl. 7, fig. 6-10, pl. 8, fig. 1, 3.

HOLOTYPE: UQF 70243, figured by Waterhouse (1987b, pl. 7, fig. 6) OD from Brae Formation, southeast Bowen Basin, Queensland.

DIAGNOSIS: Specimens well rounded in outline, ornament of faint growth-lines, no radial ornament, right anterior auricle moderately prominent, left anterior wing conspicuous with convex surface.

MATERIAL: Single valves from D44/f9001 (GS 9697), f321-323, *Echinalosia discinia* Zone, *Lethamia ligurritus* Subzone, Letham Formation, Wairaki Downs.

DISCUSSION: The right anterior auricle is smooth in specimens from the Brae Formation of Queensland and Letham Formation of New Zealand.

Streblopteria sp.

DIAGNOSIS: Little inflated smooth right valve, with well defined growth lamellae on right anterior auricle.

MATERIAL: Single right valve from D44/f344, lower *Echinalosia ovalis* Zone, Mangarewa Formation, Wairaki Downs.

DIMENSIONS IN MM:

Length	Height	Width
+21	20	?2.5

Genus *Striochondria* Waterhouse, 1983

TYPE SPECIES: *Streblochondria auriocosta* Waterhouse, 1982.

DIAGNOSIS: Small acline to slightly opisthocline shells, right valve gently convex, left valve more inflated, right anterior auricle bearing few to numerous costae, finer ribs on left anterior wing, both valves ornamented by sharply defined radial capillae, intercalate in both valves, and concentric lirae (see Waterhouse 1983c).

DISCUSSION: Only a few species are referable to this genus, which is found only in east Australia and New Zealand: *Streblochondria parkesi* Fletcher, *S. erecta* Waterhouse, *S. auriocosta* Waterhouse and *S. orbiculata* Waterhouse. It represents a distinct and minor off-shoot from *Streblochondria*. The ornament is like that of *Orbiculopecten* Gonzalez, but the ligament is alivincular, not lativincular.

The genus was misinterpreted by Astafieva (1994) as poorly preserved and indistinguishable from *Streblochondria*. Not so. The type species is well preserved, showing exterior and interior detail. The ornament is so delicate that it has not been well conveyed in photographs (Waterhouse 1982b, pl. 16, fig. 14 c, 1987b, pl. 8, fig. 8). Ornament on the right anterior auricle is coarse. The fine ornament allows ready distinction from *Streblochondria*, with its much coarser radial and concentric ornament, consistent with ornament on the right anterior auricle. The ornament differs by an order of magnitude, and is just as different as the coarse plicae of *Deltopecten* compared with the ribs of *Streblochondria*. As well, valves are more inequivalve. Shell structure may be different between the types of the two genera (foliate calcite in *Striochondria*, fibrous outer layer in *Streblochondria*), but this could reflect environmental differences.

Newell & Boyd (1995, p. 83) included *Striochondria* amongst a group of genera as unrecognizable because they were in most cases poorly illustrated, very small samples of worn or fragmented specimens with hinge characters and shell microstructure not demonstrated etc, etc. The claims are untrue and apply much better to *Crittendenia*, their own genus. They denounced the lack of population variation, but none of the species they described were adequately based on population studies.

Striochondria parkesi (Fletcher, 1929)

Pl. 9, fig. 6

1906 *Aviculopecten englehardti* not Etheridge & Dun; Etheridge & Dun, pl. 9, fig. 7?, pl. 14, fig. 6-8.

1929a *A. parkesi* Fletcher, p. 13, pl. 5, fig. 1-3.

1929a *A. englehardti* not Etheridge & Dun; Fletcher, p. 14, pl. 6, fig. 2, 3.

1982b *Streblochondria parkesi* (Fletcher); Waterhouse, p. 31, pl. 16, fig. k (not pl. 16, fig. e, f, j, pl. 17, fig. c = *Streblopteria minauris* Waterhouse). See for further synonymy and discussion.

HOLOTYPE: Specimen figured by Fletcher (1929a, pl. 5, fig. 2) OD, south Sydney Basin, New South Wales.

DIAGNOSIS: Well inflated, right valve with small posterior wing, ornament of fine capillae over valves, 0 - 2 costae on right anterior auricle.

MATERIAL: Right valve OU 18306 from D44/f352, and another OU 15221 from D44/f132, fragments from f339, *Terrakea elongata* Zone, upper Mangarewa Formation, Wairaki Downs.

DISCUSSION: Mangarewa specimens ascribed to *parkesi* from GS 3616 (D44/f9478), GS 7352 (D44/f9870), and Letham material from GS 9697 (D44/f9001) have one rib on the right anterior ear.

Striochondria orbiculata (Waterhouse, 1982)

Pl. 9, fig. 8

1982b *Streblochondria orbiculata* Waterhouse, p. 33, pl. 16, fig. g, pl. 17, fig. a, b, d, e.

HOLOTYPE: TM 3630, figured by Waterhouse (1982b, pl. 17, fig. a, d) OD from *Plekonella multicostata* Zone, Arthurton Group, near Arthurton.

DIAGNOSIS: Valves moderately inflated, anterior umbonal slope concave, short to long, posterior wings small, outline well rounded, ornamented by faint radial capillae, 0-4 ribs on right anterior auricle.

MATERIAL: A right valve TM 3567 from D44/f9626 (GS 6074), equivalent *Plekonella multicostata* Zone, Glendale Formation, Wairaki Downs.

DISCUSSION: A right valve from a carbonate band low in the Glendale Formation is assigned to *Striochondria orbiculata*. The band is a marker that may be traced from a little south of the Kowhai tree near Coral Bluff southwards to the headwaters of the first east tributary of Letham Burn.

Subfamily **GUIZHOUPECTININAE** Astafieva, 1994

Astafieva stressed that *Guizhoupecten* Chen was characterized by branching costae in the right valve, contrasting with intercalate right valve costae in *Streblochondria*. But the ornament is complex in *Guizhoupecten*, and species may show a mix of intercalate and branching costae. The shell is gently subplicate in the type species, and strongly plicate in *G. cheni* Newell & Boyd. As well Newell & Boyd (1995) described lamellar teeth along the hinge (Newell & Boyd, 1995, p. 57). Complex ornament was described for a species from the Bowen Basin, Queensland, by Waterhouse (1987b) with low plicae and very fine cancellate ornament, but no teeth are developed along the hinge. The presence or absence of teeth in the type species needs to be clarified. Here it is considered that the nature of mode of increase of ribs is diverse and complex, and the group is to be distinguished by its plication. It clearly mimics members of *Undopectinae* in its plicate biconvex shell and alivincular ligament, but has short posterior wings to suggest that the two may have developed in parallel. *Deltopecten* and allies are closer in wing length and include genera with complex ornament. Although the ligament may lack a resilifer, and be platyvincular in *Deltopecten* and allies, some externally identical specimens are alivincular: they differ from *Guizhoupecten* only in detail of ornament, and they lack hinge teeth. Given such variability of ligament amongst east Australian coarsely plicate and large shells assigned to *Deltopecten*, it is possible and perhaps likely that *Guizhoupecten* is a largely paleotropical member of *Deltopectininae*. A final decision should await careful reassessment of *Deltopecten* and allied suites of the east Australian Permian, to reveal exactly what variation occurs in the hinges of the coarsely plicate pectinids. In the meantime, Astafieva's subfamily is tentatively regarded as allied to *Streblochondriinae*.

Astafieva (1994) also included some obscure Chinese genera, dismissed as unrecognizable by Newell & Boyd (1995). I have not had the opportunity to examine them.

Subfamily **LIMATULININAE** new

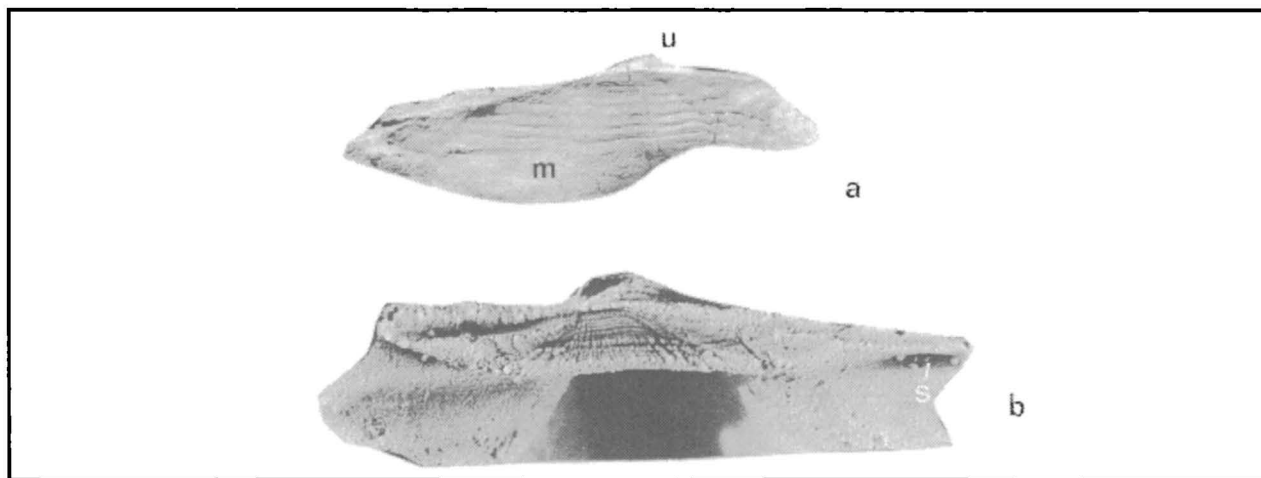
NAME GENUS: *Limatulina* de Koninck, 1885.

DIAGNOSIS: Ovoid retrocrescent with obtuse medium small posterior wings, irregular well spaced costae, increasing by intercalation, well formed right anterior auricle and byssal notch. Right valve almost as inflated as left valve. Ligament transitional and lativincular, resilifer elongate.

DISCUSSION: The genus *Limatulina* de Koninck, based on *Avicula radula* de Koninck, 1842 from the Lower Carboniferous Limestone at Vise, Belgium, was classed in *Aviculopectinidae* Meek & Hayden by Newell & Boyd (1981). It has a comparatively small posterior wing compared with *Aviculopecten* and *Etheripecten*, strongly retrocrescent outline, and broad low ribs suggestive of *Etheripecten*. The right valve is somewhat inflated, and the ornament is costate, not plicate or subplicate ventrally. These aspects suggest that *Limatulina* may have been derived from an ancestor with attributes of *Undopectininae* and *Etheripectinidae*, and was ancestral to *Streblochondriinae*, which appeared largely in the Late Carboniferous and flourished and diversified in Permian times. Members of *Streblochondriidae* also have a biconvex shell, generally with a more upright stance and more closely spaced ornament than in *Limatulina*.

Family **DELTOPECTINIDAE** Dickins, 1957
Subfamily **DELTOPECTININAE** Dickins, 1957

DIAGNOSIS: Large, biconvex or almost equally inflated, ornament of strong radial plicae or subplicae, plain or variably costate, growth-lines swing ventrally in interspaces, costae may increase by branching on right valve, some with strong concentric lamellae, without spines. Large right anterior auricle and deep byssal notch, large left anterior wing, posterior wings generally small. Ligament appears variable, some platyvincular, including type *Deltopecten*, individuals with broad shallow resilifer, others externally similar with small resilifer, indicating hinge alivincular or lativincular and transitional.



Text-fig. 10. Ligaments in Pectinida. a. Platyvincular ligament in *Deltopecten waterfordi* Dickins, right valve CPC 3921, figured by Dickins (1963, pl. 12, fig. 5) and Newell & Boyd (1995, text-fig. 35.1b). b. Lativincular ligament with pseudotrabeculae in *Cyrtorostra varicosata* Branson, USNM 38883, figured by Newell & Boyd (1995, text-fig. 45.2a). m - matrix, u - umbo.

DISCUSSION: The type species of *Deltopecten*, *illawarrensensis* Morris, 1845, is distinguished by large size and strong simple plicae. Dickins (1963) showed that the species *mittelli* Etheridge & Dun, 1906 was conspecific, and Newell & Boyd (1995) included *D. waterfordi* Dickins as the same species, though this seems doubtful, given differences in morphology and age. Well preserved hinges show a broad depression, but no well formed resilifer, as characterizing the platyvincular ligament. Otherwise the genus shows attributes of Aviculopectinidae in its growth lines and mode of increase of ribs, but differs from members of that family in the smallness of the posterior wings.

Waterhouse (1982b, pp. 34, 35) showed that various east Australian species externally close to *Deltopecten illawarrensensis* in size, ornament and auriculation appear to vary in details of the hinge. The right valve of the type of *limaiformis* Morris at the Natural History Museum, London, has a shallow resilifer, and AMF 2631 was figured to show a small resilifer (Waterhouse 1982b, pl. 18, fig. d). Yet other specimens appeared to lack a resilifer. Specimens of *D. waterfordi* such as CPL 3921 show a resilifer - in others, a resilifer is obscure or definitely missing. There thus appears to be variation in the nature of the hinge. Adding to the diversity, the hinge in *Corrugopecten* Waterhouse lacks a resilifer, but reveals a pattern of ridges radiating from under the umbo over the ligament, across the horizontal ridges and grooves, to the ventral margin (Waterhouse 1982b, text-fig. 4). The ribs converge under the umbo, but do not join to form chevrons. They are here termed pseudotrabeculae. The ridges look somewhat like the ridges and grooves called trabeculae by Johnston & Collom (1998) on the underside of the outer calcitic layer of the hinge in Inoceramidae. There is no apparent loss of shell on hinges of *Corrugopecten*, so that they appear to be of different unknown origin, related to ligament function. Similar pseudotrabeculae are seen in other *Deltopecten* or allied forms, with or without a resilifer, including *limaiformis* (Waterhouse 1982b, pl. 18, fig. d), *D. waterfordi* ("*illawarrensensis*" (Newell & Boyd 1995, text-fig. 35.3), and *D. media* Laseron (Dickins 1957, pl. 7, fig. 6).

RELATIONSHIPS: The alliance between *Deltopecten* and allies with *Streblochondria* was first proposed by Gonzalez (1978) and supported by Waterhouse (1982b). The tie is suggested by biconvexity, and the small size of the posterior wings. That shell is foliate calcite in type *Deltopecten*, and antimarginal fibrous in at least some *Streblochondria* and *Guizhoupecten* sets paleogeographic parameters, but cannot with any certainty be deemed to delineate superfamilial or even familial boundaries. Hinge details differ, because *Deltopecten*, as narrowly defined, lacks the well formed resilifer of *Streblochondria*, and yet shells externally similar have a narrow resilifer.

Such a link between *Streblochondria* and *Deltopecten* was opposed by Astafieva (1994) because of the nature of the *Deltopecten* hinge, which she understood was typified by no or only a very large shallow resilifer. However it is clear that she had little idea of the variation displayed for hinge amongst species assigned to *Deltopecten*. Whilst one may argue that *Deltopecten* must be restricted only to *illawarrensensis*, that leaves a number of externally close species which vary in the nature of their hinge. To merely assign them, or some of them, to a separate genus, would mean that we had *Deltopecten* with a constant hinge without deep resilifer, and a genus, arguably allied to *Guizhoupecten*, for species in which the hinge ranged from that of *Deltopecten*-type to alivincular: the family group implications may not need to be changed. Newell & Boyd (1995) claimed that only *D. illawarrensensis* (in which they lumped *waterfordi*) was known to lack the median resilifer. However this is not correct. Individual specimens of several species may lack the median deltoid resilifer, and some show not even a broad shallow resilifer. To Deltopectinidae, Newell & Boyd (1995) referred *Deltopecten*, *Streblopteria*, *Crittendenia* and *Eocamptonectes*. This seems a disparate assortment, in two different superfamilies, and three or four different tribes. It also departed from their preferred procedure of only referring a single genus to a family.

A supposed ally of *Deltopecten*, according to Newell & Boyd (1995), was the genus *Crittendenia* Newell & Boyd (1995, text-fig. 38), type species *C. kummeli* Newell & Boyd from *Meekoceras* beds of north-east Nevada. They pointed out a strong approach to *Pseudomonotis painkhanda*, *P. griesbachi* and *P. decidens* described by Bittner (1899) from the Scythian (Early Triassic) of the Himalaya, and in proposing their name offered no justification or means of discrimination at species level, nor were population studies deemed necessary. The nature of the hinge for the species and the genus was not determined by Newell & Boyd (1995), but the species were referred to Deltopectinidae. It is much more likely that *Crittendenia* belongs with Pterinopectinidae, Asoellinae or Eurydesmidae. Nakazawa (1996, attached footnote) stated that *Crittendenia* is a junior synonym of *Pseudoclaraiia* Zhang. It was treated as a member of Claraiinae Gavrillova, 1996, within Pterinopectinidae, by Waterhouse (2000f).

Genus *Corrugopecten* Waterhouse, 1982

TYPE SPECIES: *Corrugopecten multicostatus* Waterhouse, 1982.

DIAGNOSIS: Biconvex shells, right valve slightly less inflated than left, long right anterior auricle and deep byssal notch, smaller posterior wings, both valves with ornate plicate bundles of ribs in several orders, slightly simpler on right valve, crossed by strong laminae, arching hingewards in interspaces. Ligament area high with grooves and pseudotrabeculae, no resilifer pit.

DISCUSSION: *Corrugopecten* is not generically close to *Heteropecten*. Despite the claim by Newell & Boyd

(1995) that the two were identical, the genus does not look close in the ornament of its left valve, small size of the posterior wings, and the swollen nature of the right valve, to any of the known species of *Heteropecten* that conform with the types figured by Kegel & Costa (1951) or Rocha-Campos (1970). The ribs increase by branching (as in *Heteropecten*), but growth-lines arch hingewards, or pass straight across between costae over which they arch ventrally or dorsally. As well, *Corrugopecten* lacks a resilifer in the hinge (Waterhouse 1982b, text-fig. 4). The outer hinge carries strong growth grooves and ridges parallel to the hinge margin. Centrally, oblique ridges cut across to form pseudotrabeculae under the umbo. Left valve ornament of *Corrugopecten* is very complex, with bundled ribs over subplicate primaries. In the right valve the subauricular notch is very deep, and the valve is subconvex - more inflated than in *Etheripecten* or *Heteropecten*, less inflated than in *Deltopecten*. The right valve ornament is intricate, but less varied than in the left valve. The genus represents a very distinctive extreme, and should be recognized, because it differs so strongly from other genera, including *Heteropecten*. Newell & Boyd (1995) took such a broad view of *Heteropecten* that it would, according to their overview, display far more variables than many of the families they discriminated for single genera. Indeed they achieved a curious arrangement of extremely long-lasting few and variable species, very broad genera and very exclusive families. A number of their families are no more than genera, and some of their genera lump species of more than one family.

Genus ***Squamuliferipecten*** Waterhouse, 1986

TYPE SPECIES: *Pecten squamuliferus* Morris, 1845.

DIAGNOSIS: Weakly biconvex shells with subequal strong coarsely lamellate ribs on both valves.

DISCUSSION: *Squamuliferipecten* was synonymized with *Heteropecten* by Newell & Boyd (1995). The type and allied species of *Squamuliferipecten* (Waterhouse 1986a, 1987b) are biconvex unlike *Heteropecten*, the posterior wings are significantly smaller and ornament differs. The ligament area is broad with no ligament pit (Dickins 1957, p. 41, Etheridge & Dun 1906, pl. 2, fig. 5), or very shallow resilifer bearing pseudotrabeculate radiating ridges, not seen in *Heteropecten*. The genus is closest to *Deltopecten*, with aspects of the complex ornament suggestive of *Guizhoupecten*.

Subfamily **CYRTOROSTRINAE** Newell & Boyd, 1995

[nom. transl. hic ex Cyrtorostridae Newell & Boyd]

DIAGNOSIS: *Cyrtorostra* Branson is a widespread genus of Permian age, including Bowen Basin of Queensland. The valves are almost equally biconvex, umbones prosogyrate, posterior wings fairly small, right anterior auricle with deep byssal notch, and ornament of costae or bundles of costae that project beyond the margin as large spines, bundles marked internally as single channels on the shell interior. The costae more or less alternate with each other on the two valves. Ligament subexternal amphidetic, lativincular, with very broad resilifer, may be marked by pseudotrabeculae. Outer ostracum antimarginal fibrous.

DISCUSSION: *Cyrtorostra* was placed as sole member of Family Cyrtorostridae by Newell & Boyd (1995) with no indications of relationships with other Pectinidina. Here it is proposed that the group is allied to *Deltopecten* and Deltopectininae, sharing biconvexity, small posterior wings, and broad open resilifers, that may bear pseudotrabeculae. It differs in the nature of its more compact shape and greater relative inflation.

Clavicosta Newell, 1938 would seem to be closely allied, as a genus described as only one species (?) from the Late Carboniferous and Early Permian of United States. Yet Newell (1938) made no mention of *Cyrtorostra* in his initial description of *Clavicosta*, and Newell & Boyd (1995) made no mention of *Clavicosta* in describing Cyrtorostridae. However Cox (1969b, p. 346) in the bivalve treatise did note that *Cyrtorostra* was a possible descendent from *Clavicosta*. It was nonetheless classed in Oxytomidae, whereas *Clavicosta* was placed in Aviculopectininae by Newell (1969b, p. 337)..

Subfamily **ORBICULOPECTININAE** new

NAME GENUS: *Orbiculopecten* Gonzalez, 1978.

DIAGNOSIS: Small subequivalve upright shells with small posterior wings, fine radial and concentric ornament without coarse plicae, ligament lativincular with very wide shallow resilifer. Hinge denticulate or lacking teeth and sockets. No pseudotrabeculae, as far as is known.

Tribe **ORBICULIPECTININI** new

DIAGNOSIS: Hinge without teeth or sockets, size small to medium-sized.

DISCUSSION: Two genera are so far known in this tribe, found in moderately high paleolatitudes and of Carboniferous age.

DISCUSSION: The genus *Orbiculopecten* was referred by Gonzalez (1978) to *Deltopectininae*, but this was contradicted by Astafieva (1994), who seems to have misunderstood the genus, and opposed Waterhouse (1982b) rather than Gonzalez (1978) who had propounded the relationships, and indicated the shallowness of the resilifer. Figures of the hinge are perfectly clear (Gonzalez 1978, pl. 1, fig. 7, text-fig. 2C, D). *Orbiculipecten* differs significantly from *Deltopecten* and allies in lacking plicae or costate plicae. Gonzalez regarded *Orbiculipecten* as Late Carboniferous, giving rise to *Deltopecten* in the Early Permian. However a Late Carboniferous age for *Deltopecten* and allies seems possible (Waterhouse 1987b, 1989, 2000b), and further study is required to ascertain the full ranges of the two genera.

Streblochondria histion Campbell, 1962 from the Upper Carboniferous Kullatine rocks of northeast New South Wales may be referred to *Orbiculopecten*. It has ornament like that of the type species, and Campbell (1962) described the resilifer as broad and shallow - that is lativincular. His figures (Campbell 1962, pl. 12, fig. 11c, 12d) help confirm this, but it is not fully clear whether the ligament is platyvincular or lativincular.

Genus *Lionicula* new

DERIVATION: Named from Mt Lion, south-central Queensland.

TYPE SPECIES: *Streblochondria? lionensis* Fleming, 1969, here designated.

DIAGNOSIS: Medium-sized gently biconvex almost equivalve subequilateral shells with small posterior wings, large right anterior auricle with byssal notch, large anterior left valve wing. Left valve ornament of moderately strong sharply raised ribs, increase by branching or mostly by intercalation, some arising close to primary ribs, suggestive of incipient bundling, crossed by sharply defined concentric threads. Right valve ornament principally of slightly sturdier broad-crested ribs or subplicae, close-set with very narrow interspaces, increase by intercalation, crossed especially laterally by sharply raised growth threads. The growth threads arch variously over costae and interspaces, with some inconsistency. Ligament amphidetic, platyvincular.

DISCUSSION: This species differs from *Streblochondria* in the lack of resilifer. The lack of resilifer and overall shape and size point to a close relationship with *Orbiculipecten* Gonzalez, which is also close to *Streblochondria* in general shape and size. The South American genus is distinguished principally by its ornament, comprised of very fine radial threads on both valves, with increase by intercalation. The radials are crossed by fine concentric threads, intersecting to form delicate spine-like projections. Wings and auricle are somewhat more strongly ribbed relative to body ornament in *Orbiculipecten*, whereas ribs of the ear and wings of the new genus are no stronger than ribs at the ventral margin.

Lionicula comes from the upper Neerkol Formation, with reported *Auriculispina levis* (Maxwell), and judged to be Late Carboniferous or Early Permian in age.

Runnegar (1972) assigned Fleming's species to *Deltopecten*, but the species differs substantially from that genus in size and ornament, and lacks well defined plicae.

Tribe **EOCAMPTONECTINI** new

NAME GENUS: *Eocamptonectes* Newell, 1969.

DIAGNOSIS: Shaped overall like *Streblochondria*. Hinge lativincular, with wide resilifer and narrow raised area for lamellar and fusion layers to each side, teeth and sockets present.

DISCUSSION: Members of this tribe have been lumped with *Streblochondriidae* and other families, but they are distinguished by the broad resilifer and lativincular hinge, which points to a close alliance with *Orbiculopectinini*. Unlike members of this tribe, teeth and sockets are developed along the hinge. Three genera are so far known, from Permian paleotropics.

The wide resilifer, teeth and sockets are not found in species assigned to *Streblochondria*, *Striochondria* or species assigned by various authors to *Streblopteria*. *Chaenocardia* Meek & Worthen has a short hinge with moderately wide resilifer of a semilativincular hinge, and teeth, involving anterior right valve tooth and socket, and left valve anterior socket and tooth. Left valve wings are less clearly defined in *Chaenocardia*, and the overall shape more oblique. In this classification it is treated as a development independent of *Eocamptonectini*, but this invites further study, and arguably *Orbiculopectininae* should be allied with *Chaenocardiidae*. In the present analysis, *Chaenocardia* is regarded as distinguished by asymmetrically amphidetic ligament and poorly defined wings, and the resilifer appears to be narrower than in a lativincular hinge.

Genus *Eocamptonectes* Newell, 1969

The type species *Camptonectes papillatus* Girty is well illustrated by Newell & Boyd (1995, text-fig. 40.1-5). Internally the left valve has an anterior buttress below the hinge plate, and a short lamellar tooth lies at each end of the hinge, fitting into corresponding sockets in the right valve.

Genus *Strebloboyardia* new

DERIVATION: streblo - prefix for allied aviculopectinid bivalves, and named for Professor Don W. Boyd.

TYPE SPECIES: *Aviculopecten? montpelierensis* Girty, 1910, here designated.

DIAGNOSIS: Streblochondriiform acline shells, biconvex, umbones medianly placed, ornament of light and closely spaced concentric growth lirae and radial striae, anterior auricles slightly longer than posterior wings, byssal sinus shallow or missing from left anterior wing. Internally, short lamellar tooth at anterior end of wide shallow resilifer in right valve, with corresponding left valve socket; possible posterior socket and tooth as well. Hinge lativincular.

DISCUSSION: This genus is named for a species described by Girty (1910), Newell (1938) and Ciriacks (1963). Newell & Boyd (1995, text-fig. 37) referred the species to *Streblopteria*, but the left sinus is appreciably deeper in the type species of this genus, *S. laevigata* M'Coy, and the umbones more anteriorly placed. Hinge details remain unknown for *Streblopteria*, but it is assumed by most authors that the morphology is much like that of *Streblochondria* (Amler 1994, Astafieva 1994). This cautious appraisal appears more acceptable than the contention by Newell & Boyd (1995) that a species much younger than the type of *Streblopteria*, and of differing external appearance, was generically identical. The new form shows anterior dentition, and Newell & Boyd (1995) also noted a boss or knob "above the upper extremity of the byssal notch". They described the anterior left valve socket and right valve tooth, and indicated on their text-fig. 37. 1 a second left valve posterior socket, and a possible right valve buttress or tooth, unlabelled, on the opposing right valve. The dentition is different in *Eocamptonectes* Newell in Hertlein et al (1969), with anterior and posterior sockets in the right valve and anterior and posterior teeth in the left valve, but otherwise conforms to the same pattern. *Chaenocardia* Meek & Worthen, 1869 has a somewhat similar hinge, with anterior tooth and socket in each valve, the left tooth in front of the socket. The hinge is short with broad well formed resilifer and the right byssal notch very high. Because of its considerable asymmetric shape, and poorly defined small posterior wings, *Chaenocardia* is separated from Streblochondriinae and Eocamptonectini, but this arrangement is open to further resolution. Newell & Boyd (1995) separated Chaenocardiidae as a member of Monotoidea, whereas Astafieva (1994) and Waterhouse (1982b) treated it as closely allied to *Streblochondria*. That seems the better option, given what is known of morphologies and relationships, because the ligament clearly extends in front of the umbones in both *Chaenocardia* and *Obliquipecten*, and is amphidetic.

Genus *Pectengonzalez* new

DERIVATION: Named for C. R. Gonzalez.

TYPE SPECIES: *Obliquipecten granti* Newell & Boyd, 1995.

DIAGNOSIS: Upright little inflated shells with short hinge, large anterior right auricle, deep and high byssal notch, small but well defined left valve wings, subdued radial ornament and auricular costae, otherwise ornamented by low growth lines and steps. Ligament lativincular, asymmetrically amphidetic, tooth and socket at front of ligament in each valve. Shell structure not known.

DISCUSSION: Newell & Boyd (1995, p. 83) realized that the species *granti* showed differences from *Obliquipecten laevis* Hind, type species of the genus. Externally, the differences are substantial, involving much less obliquity, different right anterior auricle, and much better defined wings in the left valve of *granti*. Internally differences are even more significant. Newell (1938, pl. 8, fig. 5a, b) took great pains to reveal the left valve hinge of type *Obliquipecten laevis*, to reveal an amphidetic ligament, with well formed small resilifer extending in front of the umbo. There is no sign of teeth. Perhaps preservation or preparation allowed teeth to be masked, but overall the hinge looks very like that of *Streblochondria*, apart from a more forward position for the resilifer. Although Newell & Boyd (1995) considered that *granti* was close to *Chaenocardia*, some might prefer to associate *Obliquipecten* more closely with *Streblochondria*.

Pectengonzalez is distinguished from *Eocamptonectes* by details of ornament, shape and dentition. *Strebloboyardia* is closer, more inflated, with somewhat different shape, inflation, ornament, dentition and wider resilifer.

Superfamily PSEUDOMONOTOIDEA Newell, 1938

[nom. transl. Newell & Boyd (1995, p. 64) ex Pseudomonotidae Newell]

Left valve more convex than right, byssate in juveniles, suborbicular to irregular, bluntly rounded wings, divergent flat cardinal areas, and triangular median resilifer, juveniles retrocrescent to prorescentic and change in convexity and ornament with maturation, ornament intercalate-costate. Shell structure varies, inner ostracum may be crossed lamellar, right outer outer ostracum coarsely prismatic, left outer ostracum similar or homogenous; examples known with foliate calcitic outer ostracum, with further variations.

Family **PSEUDOMONOTIDAE** Newell, 1938
 Genus *Pseudomonotis* Beyrich, 1862
Pseudomonotis? sp. C

1982b *Pseudomonotis* sp. C Waterhouse, p. 41, pl. 22, fig. c.
 1993 Anidanthid Briggs & Campbell, p. 325.

The bivalve *Pseudomonotis* sp. C of Waterhouse (1982b) was reidentified by Briggs & Campbell (1993) as a brachiopod dorsal valve, within Anidanthidae Waterhouse. The figure of TM 5240 in Waterhouse (1982b) clearly indicates an asymmetric specimen, which rules out the chance of it being an anidanthin brachiopod, because these are bilaterally symmetrical. The description of the auricles by Waterhouse (1982b) confirms this, the anterior auricle being short with byssal retraction, and obtuse, the posterior auricle being large, gently convex, and with acute cardinal extremity. Such morphological attributes are certainly not indicative of brachiopods. Within members of the brachiopod subfamily Anidanthinae, the dorsal ears are mirror image of each other, and are concave externally, and have obtuse extremities. So the claim by Briggs & Campbell (1993) must be rejected. In addition, the dorsal valve of *Anidanthus* carries somewhat irregular concentric lamellae or ridges, much better defined and more regular than the concentric ornament of *Pseudomonotis?* sp. C. The costae of the bivalve show low swellings suggestive of projections, another feature not seen in Anidanthinae, which lacks dorsal spines. Because pseudomonotid bivalves show some attributes of brachiopod symmetry and a vague approach in ornament, it is possible to confuse the two at first glance, but with a little care, the two may be discriminated. Presumably the errors in Briggs & Campbell (1993) were caused by their misunderstanding of the differences in morphology between brachiopods and bivalves. Dr Briggs has never published on bivalves, and Dr H. J. Campbell never himself has never described brachiopods, apart from his intriguing article on North Auckland "Martinecae" (Campbell 1992), which is discussed under *Martiniopsis woodi* in this text. In Briggs & Campbell (1993), their brachiopod turns out to be a bivalve.

Briggs & Campbell (1993) noted that the caption for *Pseudomonotis* sp. C gave the locality as GS 9276, whereas the text stated that the locality was GS 9676. They stated that the real locality and level could not be determined. They neglected to mention that the locality in the text was accompanied by reference to the *Lethamia ligguritus* Zone (now Subzone), which includes GS 9676, and excludes GS 9276. This is further reinforced by listing of the species in the *Lethamia ligguritus* Zone, at GS 9676 in Waterhouse (1982b, p. 52). The species is not given in the list of species from GS 9276 (Waterhouse 1982b, p. 51). Thus the printing or editorial error of 9276 instead of 9676 is regrettable, but is adequately covered in any careful perusal of the text. The initial error was inadvertent, their errors somewhat perplexing, to say the least.

Subfamily **HUNANOPECTININAE** Yin, 1985

[nom. transl. hic ex Hunanopectinidae Yin]

Medium-small orbicular to weakly retrocrescent shells, inequivalve, left valve more inflated, valves concordant, posterior auricles small, left valve anterior wing relatively large with sinus, right anterior auricle large with deep narrow byssal notch. Ligament external, alivincular.

Tribe **HUNANOPECTININI** Yin, 1985

[nom. transf. hic ex Hunanopectinidae Yin]

Right valve smooth, left valve smooth or costellate, lamellar tooth in each valve.

Tribe **FURCATIINI** new

NAME GENUS: *Furcatia* Waterhouse n. gen.

DIAGNOSIS: Valves costate, no teeth in hinge.

DISCUSSION: *Furcatia* is known only from a Queensland species, which differs from *Hunanopecten* Zhang, 1977 and *Fransonia* Newell & Boyd, 1995 in having both valves costate and in lacking teeth. The Queensland form shares the characteristic large anterior left valve wing and alivincular hinge, unequally convex valves and short posterior wings.

Genus ***Furcatia*** new

DERIVATION: furca - split, two-pronged fork, Lat.

TYPE SPECIES: *Etheripecten petulantus* Waterhouse, 1987.

DIAGNOSIS: Small prosogyrous to upright inequivalve shells, left valve up to twice as convex as right valve, anterior right auricle moderately large, posterior wing small, anterior left wing very large, posterior wing small. Ornament distinctive, of narrow closely spaced and well defined ribs arising by branching on both valves, and also to lesser degree by implantation, crossed by well formed concentric ridges. Resilifer alivincular, no teeth.

DISCUSSION: This genus is distinguished from *Streblochondria* by its inequivalved nature, very large anterior left wing and by branching of ribs on the left as well as the right valve. Ribs are intercalate only in *Streblochondria* (Newell 1938, p. 82, Astafieva 1994). Astafieva regarded the mode of rib increase as significant to family group level, but various chaenocardioid genera appear to be rather variable in this regard, unlike members of Aviculopectinoidea. The large anterior left valve wing and inequivalved nature suggest a close alliance with Hunanopectininae Yin.

The species *petulantus* comes from the Elvinia Formation of Early Permian age in the southeast Bowen Basin. Waterhouse (1987b) allocated the species to *Etheripecten*, presumably because of the less convex right valve, but the species fits much better within Hunanopectininae.

Superfamily **EUCHONDRIOIDEA** Newell, 1938

[nom. transl. Nevesskaya et al 1971 ex Euchondriidae Newell]

Family **EUCHONDRIIDAE** Newell, 1938

This is a distinctive group bearing pseudotoxodont hinge with resilifer. Valves almost equally convex. Left valve costate with concentric crossed lamellar inner ostracum and homogeneous outer ostracum. Right valve ornamented by inconspicuous filae. Shell prismatic outer ostracum.

The group began in the Devonian, and so seems unlikely to have given rise to any member of the Aviculopectinoidea or Pterinopectinoidea (Newell 1938, text-fig. 17).

incerte sedis

Family **POSIDONIIDAE** Frech, 1909

Posidonia Bronn is an inequilateral shell with moderately to well defined not very large wings and umbonal slopes, no differentiated auricle at maturity, and subdued concentric ornament, of Carboniferous to Early Triassic age. Weigelt (1922) described the hinge as pterinopectinid, that is chevroned duplivincular, and reported that early growth stages revealed a small right anterior auricle and byssal notch, subsequently lost. That would imply a relationship to Pterinopectinidae, and Posidoniidae would become name-giver to the superfamily. Later Cox & Newell in the bivalve treatise (Hertlein et al 1969, p. 342) stated that the ligament area was narrow and hinge edentulous. Although Dickins (1983b, p. 59) endorsed Newell's 1938 interpretation, Rathmann & Amler (1992) referred *Posidonia* to Buchiacea, which implies an alivincular or modified hinge, rather than one that was duplivincular.

Few of the genera associated with *Posidonia* in the bivalve treatise are well known, and indeed Campbell (1994) dismissed the group from serious consideration. But the family name enjoys long priority, and so cannot be set aside just for convenience. Hopefully it will come to be better known, following the advances in understanding of genera such as *Claraia* and *Halobia*. Genera that lack an anterior right auricle and have amphidetic ligament and moderately developed wings may prove to belong to the same family, even if the hinge proves to be canalivincular.

As pointed out in a discussion under the heading of Chaenocardiidae, shells assigned to *Rutotia* de Koninck (1885) may be allied to *Posidonia*. This genus was described and illustrated by a substantial number of Carboniferous examples from Belgium, to indicate a biconvex form with less inflated right valve, short hinge and rounded or angular cardinal extremities, poorly defined wings and no right anterior auricle. Ornament is absent or restricted to light concentric lines as a rule. The hinge was not shown, but was apparently amphidetic. However Newell (1969c) sought to set aside the genus by synonymizing it with *Streblopteria*, nominating as type species a solitary left valve figured by Phillips (1836). This valve looks like *Rutotia*, but Hind (1903) had claimed to find more material that showed a byssal notch. His observations were far from clear, nor necessarily pertinent to Phillips' species, but Newell declared *Rutotia* was a synonym, even though de Koninck's own abundant material clearly is not *Streblopteria*. Nor is Phillips' type, because it has, even on the left valve, different umbonal slopes and less defined wings. The right valve remains uncertain for Phillips' species and therefore *Rutotia* remains in limbo.

Suborder **MONOTIDINA** new

Pectinid shells with opisthodontic ligament. Right anterior ear generally well developed, generally highly inequivalve, with little or no radial ornament.

DISCUSSION: Two superfamilies are recognized, Monotoidea and Eurydesmoidea.

Superfamily MONOTOIDEA Fischer, 1887

Shells with radial ornament, ligament opisthodontic, right anterior auricle generally small.

Family **DOLPONELLIDAE** new

NAME GENUS: *Dolponella* Waterhouse, 1978.

DIAGNOSIS: Subequivalve inequilateral apparently monomyarian shells with moderately developed right anterior auricle, no posterior wings, no left anterior wing, ornament of close-set fine radials of two-three intercalate orders, ligament external, canalivincular, no resilifer, opisthodontic.

DISCUSSION: *Dolponella* is known for a single species, *D. sulcata* Waterhouse, 1978 from the Nisal Sandstone of the Senja Formation in Dolpo, northwest Nepal. The valves are both convex with anteriorly placed prosogyrous umbones, and so look somewhat like *Cyrtorostra* Branson, but they differ in essential attributes from that genus in lacking posterior wings, having fine radial ornament, and possessing a channelform opisthodontic ligament. The arrangement of wings and opisthodontic ligament point strongly to a position within Monotidina rather than Aviculopectinidina, including Pseudomonotidae, which do come close in lateral sulcus and fine dense ribbing. The biconvexity and channelform ligament suggest an approach to Eurydesmidae, but the few known members of this family lack a well-formed discrete right anterior auricle and radial ornament. Nonetheless *Eurydesma* itself is close in general aspect, with one species *E. sacculus* (M'Coy, 1847) displaying a well formed broad sulcus laterally, and *E. sulcatum* Waterhouse, 1987, from Rose's Pride Formation, southeast Bowen Basin, being particularly close in the site and nature of its sulcus. But the right anterior ear and the ornament offer strong distinctions, judged to be at family level.

A Triassic genus that shows somewhat comparable ornament is *Chluaria* Waterhouse, 2000. This has a canaliform ligament apparently, and poorly developed or missing posterior wings, and a small right anterior auricle with larger byssal notch. Unlike *Dolponella*, the genus is markedly inequivalve. Although classed in Clariinae of the Pterinopectinidae by Waterhouse, the genus might have to be relocated, especially if the ligament can be interpreted as opisthodontic. *Praeamonotis* Waterhouse, 1987 from the Middle Permian of Bowen Basin, Queensland, could prove to be allied, but needs to have the hinge and auriculation checked.

Another genus that shows considerable approach is *Pseudavicula* Hudleston, based on *Lucina anomala* Moore of Cretaceous age, and revised by Dickins (1960b). A resilifer is developed.

Superfamily **EURYDESMOIDEA** Reed, 1932

[nom. transl. hic ex Eurydesmidae Reed]

DIAGNOSIS: Shells inequivalve to equivalve, inequilateral, hinge opisthodontic, canalivincular, or showing triangular shallow scooped resilifer, right anterior auricle developed or modified, hinge may have simple teeth, ornament reduced, generally no posterior wings.

DISCUSSION: Eurydesmidae and Buchiidae are referred to this superfamily, and Pergamiidae Cox shows many similarities. All have comparatively smooth shell, generally a small right anterior auricle, and opisthodontic hinge with resilifer or canalivincular. One genus, *Glendella* Runnegar within Eurydesmidae, is remarkably like members of Buchiidae apart from different right anterior auricle, having inflated left valve, almost flat right valve and short hinge. The genus was synonymized with *Eurydesma* by Newell & Boyd (1995), but no reasons were given, and *Glendella* is so distinctive that its recognition marks a valuable contribution to understanding the family.

ORIGIN: Newell & Boyd (1995) acceptably pointed to Chaenocardiidae as likely root-stock for Monotoidea (now Monotidina). *Chaenocardia* is oblique with short asymmetrically amphidetic ligament and comparatively smooth shell. They classed it in Monotoidea. Others retain *Chaenocardia* with its Paleozoic streblochondriin allies, but that is not deny its significance as potential source material. There are bound to be other alternatives, as might well be revealed from renewed study of European Early Carboniferous and also Chinese Pectinida.

Family **EURYDESMIDAE** Reed, 1932

CLASSIFICATION: Newell & Boyd (1995, p. 76) referred the genus *Eurydesma* Morris, 1845 to Monotoidea, which was deemed to replace Buchioidea Cox, 1953. Waller (1978) had earlier proposed Buchioidea Waller, but seemingly overlooked the availability of Monotoidea, and the procedure in formal nomenclature by which superfamilies retain authorship of the original proposer of any unit within the family group. Previously, Waterhouse (1980b, p. 8) stated that *Eurydesma* and *Glendella* should be regarded as related to Buchiidae

"at perhaps superfamily level," and now this seems to have independently supported by Newell & Boyd (1995). Although they put the concept forward as their own, I suspect it has been mooted by a number of authorities.

Dickins (1983b, p. 61) by contrast insisted that *Eurydesma* was a close ally of *Atomodesma*, and belonged with Ambonychiidae. Johnston & Collom (1998) disputed the relationship to Ambonychioidea, but did class Buchiidae and Eurydesmidae with Inoceramoidea Giebel, 1852. I am inclined to regard *Atomodesma* as remote from *Eurydesma*, given the obvious and substantial differences in symmetry, musculature, hinge and shell structure.

Many different authors have speculated about the position of *Posidoniella* de Koninck, 1885, which has been interpreted as a possible ancestor of *Atomodesma* - or *Eurydesma*, or various other significant genera. *Posidoniella* is not fully known, hampering an understanding of relationships. Yet overall shape and similarities would suggest a simple narrow ligament, likely to be opisthodontic and canalivincular. Runnegar (1972) stated he had examined well preserved *Posidoniella*, and recorded a prismatic outer shell layer, symmetrical byssal notches in each valve, and a duplivincular ligament - its nature not distinguished as chevroned or parallel layers as in the lineavincular ligament of *Myalina* etc. Nor did he indicate an amphidetic or opisthodontic nature. He failed to recognize an anterior right auricle, but Dickins (1983b, pl. 1, fig. 1-5) proved that one is present on the type species *P. vetusta* (Sowerby), reinforced by illustrations and description. Musculature remains unknown.

The biconvexity, opisthodontic ligament and small right anterior auricle possibly suggest a relationship to *Eurydesma*. On the other hand overall shape, hinge and prismatic shell have suggested a possible source for Atomodesmidae to some workers. Both *Eurydesma* and Atomodesmidae were well represented in cool to cold waters of Gondwana, under conditions favourable for prismatic shell, and at least simplistically, there is no clear reason for *Posidoniella* to have lost its prismatic shell in giving rise to *Eurydesma*, with its foliate calcite, although such an origin could be explained away by postulating additional evolutionary steps. I do not favour the suggestion that *Posidoniella* gave rise to both *Eurydesma* and *Atomodesma*, as argued by Dickins (1983b). Indeed, given the obvious gaps for the Carboniferous fossil record, ancestors for both may have been elsewhere. *Posidoniella* remains a possible, but to my mind, dubious source for Atomodesmidae, or, in rivalry with Chaenocardiidae, as an acceptable and even preferable source for Eurydesmiidae. It even approaches Triassic members of Pergamiidae, summarized below. The muscle scars of *Posidoniella* would offer critical evidence, as eurydesmiid scars are buchiid-aviculopectinid, whereas those of Atomodesmidae differ considerably in size, position and association.

MORPHOLOGY of EURYDESMIDAE: Stolickza (1871) and Runnegar (1970, 1979, p. 261) have stressed that the hinge of *Eurydesma* shows a tooth in the right valve and Dickins (1957) asserted that a tooth was present in each valve. But teeth as many morphologists understand the term are entirely internal. As stressed by Waterhouse (1987b, p. 139), the so-called tooth in *Eurydesma* is partly external, and carries on its anterior face growth-lines that are seen for example in the illustration in Newell & Boyd (1995, text-fig. 56.1, 2). The "tooth" would be better called an anterior buttress or condyle, modified from an anterior ear, and Newell & Boyd (1995) called the structure "an external tooth". Indeed, unlike Runnegar (1979), Dickins (1983b) later re-evaluated his terminology. In reporting a small anterior ear in the right valve of the type species of *Posidoniella*, *vetusta* Sowerby, of early Carboniferous age, Dickins concluded that the ear was analogous with the so-called dental process of right valves of *Eurydesma*. For *Eurydesma*, it would seem preferable to avoid the term tooth - whether internal or external, even although it was probably articulatory, because anatomically it seems to have originated from a modified right ear, and indeed remained a somewhat ear-like structure. Waterhouse (1980b) pointed out the intriguing similarity to the Triassic genus *Hokonuia* Trechmann, in which the elongate right ear butts into the interior of the left valve, although there is no articulatory function or connection to the left valve, as was first discovered by Waterhouse (1960b). There is also a ridge in *Eurydesma*, variably raised, that borders the lower anterior end of the channel-form ligament structure. This does not lock into an opposing socket and so may be called a ridge, although Waagen (1891) called it a tooth. Dana (1849) commented on the similarities between *Eurydesma* and *Meleagrinnella*, and Waagen (1891) reported for *Eurydesma* a "little wing" in the left valve that projected into the right valve. Etheridge & Dun (1910, p. 56) discounted the presence of true teeth and compared the anatomy with that of the pterioid genus *Meleagrinnella* (now *Pinctada*), calling the structures under the umbones cardinal folds, approaching little wings or ears. These authors of long ago thus showed a better understanding of the *Eurydesma* hinge than some of the more recent workers, such as Runnegar (1970, 1979) or Dickins (1957) in his early phase.

Newell & Boyd (1995) assigned *Eurydesma* to the Family Chaenocardiidae Miller, 1889, and regarded Family Eurydesmidae Reed as redundant. In *Chaenocardia*, the tooth is entirely internal, as far as can be judged, and so ranks as a true tooth. (The descriptions in Newell & Boyd are cursory in this regard, and their photographs good, but not completely revealing). *Chaenocardia* was shown as having a small low tooth in the left valve and socket in the right. The difference in shape, as well as dentition, suggests that *Eurydesma* should not be too closely associated. In my view, *Eurydesma* is monotidin, whereas the affinities of *Chaenocardia* appear allied to Streblochondriidae, as in Waterhouse (1982b) and Astafieva (1994), within Aviculopectinina. However there are certainly similarities, and *Chaenocardia*, according to one set of possible evolutionary pathways, may have been close to the cusp of evolutionary divergence that led to *Eurydesma*.

PALEOECOLOGY: The genus *Eurydesma* is found widely within and especially just above glacial diamictites

in Australia, Indian subcontinent, South Africa, South America, and it is also found rarely in New Zealand, in volcanic detritus. The enclosing sediment for *Eurydesma* world-wide frequently contains grit or rubble, although examples are known of *Eurydesma* in fine-grained rock (Waterhouse & Gupta 1982). Runnegar (1979, p. 281), in part of a study endorsed by Newell & Boyd (1995), proposed that live *Eurydesma* specimens under optimal conditions were "effectively floating on the substrate" and that the shells were advantaged by being composed of calcite, because the greater specific gravity of aragonite would have caused the shells "to sink slowly into the substrate as they were washed back and forth" (Runnegar 1979, p. 261). Such a model of *Eurydesma* moving shorewards and seawards, back and forth under tidal or wave action, half suspended above substrate or within a slurry of sediment, seems fanciful. Although more prosaic, a more static habit of being half or more buried in sand seems much more likely, Runnegar, Newell and Boyd notwithstanding, because otherwise the shells would be unable to resist being swept ashore, or out to sea. *Eurydesma* was semi-infaunal, rather than nektonic or drifting or floating. The entirely different habitats, and the different hinges reinforces the need for some classificatory distance between *Chaenocardia* on the one hand and *Eurydesma* on the other, and the understanding of morphology, classification and paleoecology by Runnegar, Newell and Boyd leaves much to be desired. Incidentally, in assessing the specific gravities of different shell material, account should also be taken of the different buoyancies prevailing under cool to cold icy sea, especially under the ice-sheets that seem to have prevailed for *Eurydesma* habitats. Under such conditions, crystallization of ice from sea would have raised salinity levels, and altered buoyancy, but such parameters were not addressed by Runnegar (1979). *Eurydesma* from its genetic make-up probably had little option but to build up shell from calcite under such conditions, and it developed thick shell to help stabilize and protect itself in sediment.

?Family **PERGAMIDIIDAE** Cox, 1969

DIAGNOSIS: Medium-sized, equivalve or subequivalve, inequilateral ovate monomyarian shells with anteriorly placed umbones, no differentiated posterior wings, may have small right anterior auricle, anterior byssal gape, little or no radial ornament, shell largely smooth other than growth lines. Ligament external to subexternal, with shallow posteriorly inclined resilifer, few if any simple teeth, inner ostracum nacreous only in *Semuridia* Melville.

DISCUSSION: Cox in Hertlein et al (1969, p. 313, 314) put this Triassic-Jurassic family in Pteriacea. Although the ligament may extend slightly in front of the umbones in *Krumbeckiella* Ichikawa, I believe that the hinge is essentially opisthodontic. The family appears very close to Dolponellidae and moderately close to Eurydesmidae.

There may be reservations about the inclusion of *Manticula* Waterhouse, an extraordinary genus with very high right valve, no right anterior auricle, thick outer ostracum with crossed lamellae, and simple short high ligament area with no resilifer. The peculiar hinge was illustrated by Waterhouse (1960b) and reproduced in the bivalve treatise (Hertlein et al 1969, text-fig. C44.3b), where it is wrongly ascribed to Wilckens. It took me several days of arduous collecting to at last find a hinge.

Order LIMOIDA Waller, 1978

Order Limoida was discriminated by Waller (1978) for bivalves previously referred to a superfamily, on the basis of shell structure and soft parts in living *Lima*, as distinguished from Ostreida. Waller (1978) allowed that his cladogram was not time-constrained, yet expressed the belief, perhaps more accurately termed hope - that the characters which justified the ordinal distinction appeared early in the evolution of Limoida. That assumption surely was vital to his thesis and classification, and yet was not tested. As a result, grave cautions remain unanswered. Were the characters sufficiently and consistently vital to always mandate ordinal as opposed to subordinal or superfamilial distinction? Did early members of Limoida display the same ordinal characters emphasized in living *Lima*? If they appeared later, does that vitiate the value placed on the characters, or demand more flexibility in classification? The lack of time constraints in the classification has meant a simplification and overstress on living features. Nonetheless the group is regarded as distinct to ordinal level by authorities, Newell (1999) stressing the characteristic muscle placements as analysed by Gilmour (1990).

Superfamily **LIMOIDEA** Rafinesque, 1815

Family **LIMIDAE** Rafinesque, 1815

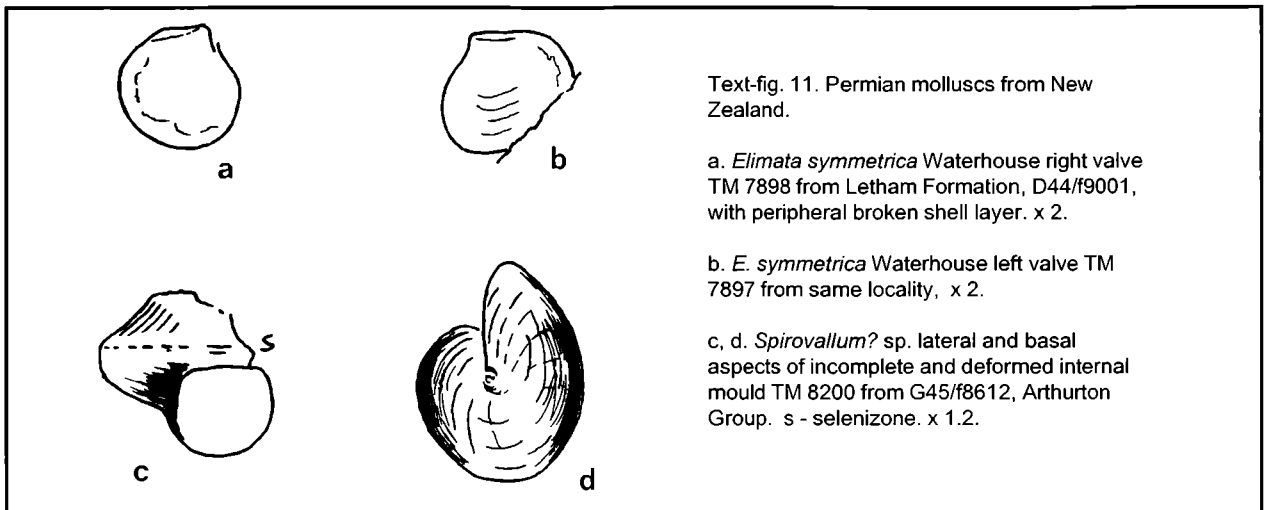
Genus ***Elimata*** Dickins, 1963

Elimata symmetrica Waterhouse, 1987

Pl. 9, fig. 7, text-fig. 11a, b

1987b *Elimata symmetrica* Waterhouse, p. 159, pl. 9, fig. 14-19.

HOLOTYPE: UQF 70737 figured by Waterhouse (1987b, pl. 9, fig. 14) OD from Brae Formation, southeast Bowen Basin, Queensland.



DIAGNOSIS: Small somewhat rounded shells with umbo medianly or anteriorly placed, umbonal slopes low.

MATERIAL: A left and right valve TM 7877, 7878 from D44/f9001 (GS 9697), a possible left valve from D44/f322, *Lethamia ligurritus* Subzone, upper *Echinalosia discinia* Zone, Letham Formation, Wairaki Downs.

DIMENSIONS IN MM: From GS 9697

Specimen	Length	Height	Width	Length of anterior
TM 7897	9	8.8	2	?4.5 (right valve)
TM 7898	11	8.8	?2	?6 (left valve)

RESEMBLANCES: These valves fall moderately close to the distinctive species *Elimata symmetrica* from the Brae Formation of southeast Bowen Basin, Queensland. They show very fine concentric lirae. A small anterior wing and smaller posterior wing are developed, well shown in TM 7898 from GS 9697.

Subclass ANOMALODESMATA Dall, 1889
Order PHOLADOMYIDA Newell, 1965

Two models of evolution

Characteristic of bipolar high latitude Permian marine faunas over Gondwana and Laurasia, Anomalodesmata are a significant component of Permian faunas in Wairaki Downs. Their morphology as preserved is comparatively simple, so that classification and relationships must be interpreted from comparatively few features, leading to ambiguities and alternative interpretations that are not readily reconciled. A difference of views arose in the 1960's. One view claimed that Australian Anomalodesmata were all closely related and represented local diversification from one root stock, and all were to be classified in one family. The other approach suggested that the so-called family was polyphyletic. Such questions often confront paleontologists. Did somewhat similar species and genera evolve and diversify more or less in situ from a common ancestry, or were there several subtly different streams present through inward migration of further genera?

Such a dilemma has arisen in the different origins postulated for Australian Permian Anomalodesmata, by two paleontologists working independently on the same faunas. Prof. Bruce Runnegar was then based at the University of Queensland and presented a Ph. D. on Anomalodesmata at the University of Queensland. He specialized on Bivalvia, had large Australian collections readily accessible, and collaborated first with Dr J. M. Dickins, another Permian bivalve specialist, and later, the eminent Late Paleozoic bivalve specialist, Prof. Norman Newell. His thesis was shaped in east Australia in the mid-sixties, and publications spanned an interval of some 10 years, from approximately 1965 to 1974. The nub of his scheme (Runnegar 1967, p. 29ff) lay in the belief that the Australian Permian Anomalodesmata were peculiarly Gondwanan, centred on Australia, and arose in the Permian Period, although the age was later extended into Late Carboniferous. The nature of the original root stock was never discussed. Apart from minor genera *Undulomya* and *Praeundulomya* classed in Pholadomyidae and Permophoridae, which he did not regard as pholadomyid, Runnegar (1974) placed all the relevant Permian Australian genera in one undivided family Megadesmidae. As well, *Vacunella* was probably meant to be included: it was omitted from any family, perhaps by oversight, because in other studies he made it clear that he believed *Vacunella* evolved from *Myonia* and was megadesmid. The family also included *?Crassiconcha* Nechaev, not explained, and some Brazilian genera.

My involvement with Bivalvia was much less specialized, as I was also studying other Mollusca, Brachiopoda, and stratigraphic problems, and thereby considering a broader canvas of evolution. Moreover for many years I could examine Australian material only in the course of visits to Australia, while I worked through New Zealand collections containing identical species. I was able to see at first hand the type collections of most of the type species of Australian "Megadesmidae", housed in England at the Sedgwick Museum and Natural History Museum, London, and in United States at the Smithsonian Institute and Yale

University. Thus I could examine M'Coy, Morris and Dana type material, which was not accessible to Runnegar in his early work. I was further able to examine the Early Carboniferous bivalves of especially England, and gain some familiarity with the Russian Permian bivalve assemblages. Two distinguished experts Dr. John Marwick and Sir Charles Fleming were colleagues while I worked at the New Zealand Geological Survey and willingly provided invaluable insight on the morphology, taxonomic procedures and philosophies and environments of very rich and well known Tertiary and Recent bivalves. In that I was fortunate indeed, because conchologists sometimes enjoy powerful advantages over aspects of paleontology, as was illustrated by the need for Boyd & Newell (1998) to recant on their new interpretation of Triassic Trigonoidea, so critical of Sir Charles Fleming, in the face of overwhelming evidence that Fleming was right, and they were wrong. Sir Charles knew the living and Tertiary examples: they did not. Whilst Drs Fleming and Marwick knew little of Pholadomyida, I was able to inspect *Pholadomya* at the Natural History Museum, London. Thanks to numerous discussions and extensive examination of British Carboniferous bivalves, my view came to be basically, that the association of Australian genera grouped by Runnegar in Megadesmidae were polyphyletic and sourced from several different early Carboniferous bivalve stock. Eventually I moved to the University of Queensland (1974-1990) and so gained readily access to large collections and field outcrops in east Australia.

At the start of this present study, I was expecting to have to withdraw my overall proposition that Megadesmidae were polyphyletic. There is little point in defending one's own past views if they are clearly wrong - the aim is to understand fossils, not to imbue them with one's own prejudices. The evidence against a polyphyletic view seemed to be mounting steadily, to favour the views of Professor Runnegar. Mello & Simoes (1996) had published cladistic analyses that supported the Runnegar interpretation, or so they declared. Moreover Morris et al (1991) stated that they accepted also the proposition that Australian megadesmids such as *Myonia* and *Vacunella* had arisen de novo, within Australia.

But a closer reading of those studies revealed that the support for the Runnegar thesis was based more on courtesy, than realistic appraisal. The cladistic analyses by Mello and Simoes strongly asserted that *Vacunella* was distinct from Megadesmidae, as I had long suggested, and as Runnegar had long opposed. The Morris et al (1991) article, based mostly on northern hemisphere fossils, in fact endorsed the polyphyletic claim, by dispersing Australian Pholadomyida amongst two superfamilies and three subfamilies, not counting *Undulomya* and *Praeundulomya*. In both articles the authors expressed support for Runnegar's credo - and then jeopardized that support by publishing evidence for polyphyletic origins.

Classification

Morris, Dickins & Astafieva-Urbaitis (1991) have offered a classification for Pholadomyida as follows:

- ?Superfamily Edmondioidae King, 1850
 - Family Edmondiidae King, 1850
 - Family Megadesmidae Vokes, 1967**
- Superfamily Pholadomyoidea King, 1844
 - Family Grammysiidae Miller, 1877
 - Subfamily Grammysiinae Miller, 1877
 - Subfamily Cuneamyinae Morris, Dickins & Astafieva-Urbaitis, 1991
 - Family Sinodoridae Pojeta & Zhang, 1984
 - Family Sanguinolitidae Miller, 1877
 - Subfamily Sanguinolitinae Miller, 1877*
 - Subfamily Pholadellinae Miller, 1877
 - Subfamily Alulinae Mailleux, 1937
 - Subfamily Undulomyinae Astafieva-Urbaitis, 1973*
 - Subfamily Chaenomyinae Waterhouse, 1966
 - Subfamily Vacunellinae Astafieva-Urbaitis, 1973**
 - Family Permophoridae van de Poel, 1959**

* in Australian Permian ** in New Zealand and Australian Permian

These authors offered a wide, but not exhaustive survey of various Late Paleozoic species and genera, and like previous workers, showed that constituent genera were long-lived and wide-ranging. The inclusion of Permophoridae is a radical and instructive departure from earlier work, and as far as I recall was suggested to me many years previously by Dr Dickins. Overall classification was based on careful evaluation of many characters, including shell structure.

The classification is accepted, with three emendations, based on detailed morphological assessments. The Megadesmidae is subdivided into three subfamilies: Megadesminae, Astartilinae Waterhouse, 1969, and Plesiocyprinellinae new. The family group name Tribe Myonini Waterhouse, 1969 is upscaled to subfamily, and associated with Edmondiidae. Vacunellinae Astafieva-Urbaitis, 1973 is placed within Chaenomyinae Waterhouse, 1966 as a tribe, and both are referred to Pholadomyidae.

- Superfamily Edmondioidae King, 1850
 - Family Edmondiidae King, 1850
 - Subfamily Edmondiinae King, 1850
 - Subfamily Myoniinae Waterhouse, 1969
 - Family Megadesmidae Vokes, 1967
 - Subfamily Megadesminae Vokes, 1967

- Subfamily Astartilinae Waterhouse, 1969
- Subfamily Plesiocyprinellinae new
- Superfamily Pholadomyoidea King, 1844
 - Family Grammysiidae Miller, 1877
 - Subfamily Grammysiinae Miller, 1877
 - Subfamily Cuneamyinae Morris, Dickins & Astafieva-Urbaitis, 1991
 - Family Sinodoridae Pojeta & Zhang, 1984
 - Family Sanguinolitidae Miller, 1877
 - Subfamily Sanguinolitinae Miller, 1877
 - Subfamily Pholadellinae Miller, 1877
 - Subfamily Alulinae Maillieux, 1937
 - Subfamily Undulomyinae Astafieva-Urbaitis, 1973
 - Family Pholadomyidae Gray, 1847
 - Subfamily Pholadomyinae Gray, 1847
 - Subfamily Chaenomyinae Waterhouse, 1966
 - Tribe Chaenomyini Waterhouse, 1966
 - Tribe Vacunellini Astafieva-Urbaitis, 1973
 - Family Permophoridae van de Poel, 1959

Historical overview

GENERA

Individuals of Anomalodesmata are abundant in the east Australian Permian. They are conspicuous in New Zealand only in late Cisuralian and Guadalupian faunas, and most species are identical with Australian forms. Excluding members of Undulomyinae and Permophoridae, some nine genera were proposed in the days of early paleontological exploration of east Australia by Sowerby 1838, Morris 1845, Dana 1847, 1849, M'Coy 1847 and de Koninck 1876-7. The principal genera in Australia now recognized include long proposed taxa *Myonia* Dana, *Megadesmus* Sowerby, *Astartila* Dana, and *Pyramus* Dana, joined by the more recently proposed but widely accepted form *Vacunella* Waterhouse. *Myofossa* Waterhouse was originally proposed from Western Australia. It was disregarded by Runnegar (1974), rejected by Runnegar & Newell (1971, p. 28), recognized in Argentina and Russia by Gonzalez (1977) and Muromzeva (1984), and elevated in significance as including several Lower Carboniferous species in Europe by Morris et al (1991). The genus was interpreted as a member of Sanguinolitidae by Waterhouse (1969c) and Muromseva (1984). Runnegar (1974) did not even recognize the family Sanguinolitidae, but it has been firmly restored by Morris et al (1991). *Pachymyonia* Dun has been granted value by Dickins (1957, 1963) and Waterhouse (1966b, 1969a, 1987b) and in Russian studies, but was firmly synonymized with *Myonia* by Runnegar (1967, p. 47) and Runnegar & Newell (1971, 1974). It was accepted by Morris et al (1991), and allocated, with a query, to Sanguinolitidae. A more restricted form is *Pleurikodonta* Runnegar, 1965 in east Australia, and identified by me amongst collections from west Nelson, New Zealand (Campbell et al 1998). *Cleobis* Dana is recognized, with some reservations, by most authors, and regarded as closely allied to *Megadesmus*, perhaps as a subgenus. *Myonia* (*Myomedia*) Waterhouse and *Oblicarina* Waterhouse are taxa that I believe to be valid, but there is not full agreement. *Australomya* Runnegar is listed in most overviews, and included with a query in Vacunellinae by Morris et al (1991). The genus is very poorly delimited, and arguably the type species is a slender species of *Vacunella*.

A number of these genera have now been described from high latitudes of Siberia (eg Astafieva-Urbaitis et al 1976). Muromzeva (1984) for example recorded species of *Megadesmus*, *Pyramus*, *Myonia* and *Pachymyonia*, and identified specimens, perhaps arguably, with the type species of *Myomedia* and *Myofossa*. Additional genera have been named, including *Praemyonia* Astafieva-Urbaitis, and *Cunavella* Astafieva-Urbaitis, genera not found in Australia, and not mentioned by Morris et al (1991). In South America, species are ascribed to *Pyramus*, *Myonia*, *Astartila* and *Australomya*. *Runnegariella* Simoes & Anelli has been considered to be a new member of the family in Brazil. Other South American allies are discussed below.

Newell (1956) on the basis of museum studies was dismissive of the early work, during the second phase of paleontological enquiry discussed for studies on Atomodesmidae, when much effort was devoted to reducing the number of genera. He recognized only four megadesmid genera in Australia, *Pachydomus* (now *Megadesmus*), *Myonia*, *Pyramus* and *Cleobis*, but his survey was not helped by a number of errors or oversights in interpreting morphological details of dentition and musculature.

Dickins (eg 1963) in various studies has allowed six or seven genera or subgenera. Like Fletcher (1929b, 1932), he maintained a conservative approach, and sought carefully for forebears amongst European stock. Innovative reappraisal was attempted by Runnegar (1965, 1967) and Waterhouse (1965c etc) in expanding the range of morphological detail for assessment. They attached significance to details of musculature, largely ignored by previous workers, as well as hinge, pallial sinus, and shape. Waterhouse recognized several new genera, of which *Vacunella* has proven to be widespread and significant, to the point of becoming name bearer for a family-group member. Runnegar (1974) enlarged the focus of study by investigating the Order Pholadomyida, undertaking the kind of extensive review of morphology through time that is necessary for classification, and this was elaborated with substantial changes and corrections for espe-

cially Late Paleozoic members by Morris et al (1991). Astafieva-Urbaitis (1973, 1981, 1988, 1990) has consolidated family group nomenclature, and substantially disproved the point-source origin of Australasian Anomalodesmata. Thanks to studies by Astafieva-Urbaitis, the focus of systematic studies during the 1970's and 1980's has shifted from east Australia to Russia, and South American studies are also proving highly relevant.

GENERIC RELATIONSHIPS

Interrelationships between the anomalodesmatan genera invite further study, as may be illustrated by the substantial differences between the overviews by Runnegar (1974) and Morris et al (1991). As well, differences in view have been expressed in particular about the relationships between *Myonia*, *Megadesmus* and *Vacunella*, and scholars should take care to read critically the articles for themselves, and be cautious in accepting and making statements about other studies, being careful to verify the original texts, and check species identifications back with the original types. Readers cannot always rely on the accuracy or fairness of all of the summaries. Thus Waterhouse (1969c, p. 100) wryly noted that an account in Runnegar (1967, table 2, p. 30) presented as the Waterhouse view only one of the several alternatives outlined in Waterhouse (1966b, p. 554-6). There was even a case in which an Australian reviewer asked to referee my manuscript for a New Zealand Geological Survey bulletin passed on unpublished data, without permission, to an Australian colleague, who promptly altered his own manuscript and published and criticized in an Australian publication my manuscript views on *Cleobis*, as if they had been published. Out of misguided solititousness, I froze onto views of a genus I had come to change my mind about, to justify that unwelcome and improper publication. A little sleuthing by any reader will reveal a reference to Waterhouse in press in a publication that preceded the Waterhouse publication by two years. No permission had been sought, or given. Even the admirable overview by Morris et al (1991, p. 56) suggested for the *Edmondia*-megadesmid relationship that a extensive discussion and summary was provided by Runnegar (1967, p. 29). Yet that page has no reference to *Edmondia*, and the Runnegar text (pp. 31, 32) argued for separation between the two in part because *Edmondia* seemed to display a *Mya* or *Corbula*-like internal resilifer. I suspect that only Morris, Dickins & Astafieva-Urbaitis would hold that view now - if indeed they really ever held it. There is, in the history of studies on Australian Pholadomyida, a surprizing amount of carelessness and inaccuracy, reminiscent of the study on Linoproductoidea in the revised brachiopod treatise. Despite urging acceptance of the Runnegar view of the *Edmondia*-*Myonia* relationship, Morris et al have come to very different conclusions, and have split Runnegar's Megadesmidae into several streams, which was precisely the opposite of Runnegar's view on classification. One can only wonder why the authors did not highlight or even admit the value of their own work as being opposed to the Runnegar model. It was as though they recoiled from any hint of "newness", or sought endorsement of their views by feigning a confirmation of some earlier studies.

THE VACUNELLA - MYONIA NEXUS

Whereas Waterhouse (1969a) distinguished *Myonia* from *Vacunella*, Runnegar (1967 etc) stressed a genetic relationship, asserting that *Myonia*, a near-surface infaunal bivalve, had evolved into a more specialized deep-burrowing form *Vacunella*. This was not consistent with Runnegar (1969) later ascribing his root-stock *Myonia* (*M. sulcata* Runnegar) to a new genus *Australomya*, which is obviously close to, if not identical with, *Vacunella*. Nonetheless his earlier view was endorsed without modification or caveat by Runnegar & Newell (1971, 1974).

Some recent studies subdivide genera between Megadesmidae (*Megadesmus*, *Astartila*, *Cleobis*, *Pyramus*), and Vacunellidae (*Vacunella*, *Australomya*, *Myonia*, *Pachymyonia*, *Praemyonia* and *Cunavella*) as in Muromzeva (1984) and Astafieva-Urbaitis (1990). Dickins (1981) relegated these clusters to subfamily level, which would approach the Runnegar overview, by placing all within a single Megadesmidae, but at least recognized the reality of separate streams. However Morris et al (1991) classed the two groups in different superfamilies, Edmondoidea and Pholadomyoidea, which certainly goes further than previous studies, and accords to some degree with and expands on the views of Astafieva-Urbaitis (1973) and Waterhouse (1988). Mello & Simoes (1996) in their cladistic study also emphasized a substantial morphological and therefore classificatory gap by failing to find synapomorphy between Megadesmidae and *Vacunella*. The various conclusions of these different authors is consolidated herein with a reassessment of morphological features, leading to a classification that builds on Morris et al (1991).

There has been scant acceptance of the proposal by Waterhouse (1969a) that at least subfamilial status should be used to differentiate between genera on the basis of dentition and small differences in musculature. *Myonia*, *Myomedia*, *Myofossa* and *Pachymyonia* lack teeth, *Megadesmus* and *Pyramus* have one tooth in the right valve, *Cleobis* a very small right tooth, but generically close to *Megadesmus*, and *Astartila* and *Pleurikodonta* may have a tooth or least a boss in each valve, and different anterior musculature, lacking the "isthmus" formed by a retractor scar or even complex behind the anterior adductor, and lacking muscle insertion pits over the internal flanks. I consider that Tribe Myonini, now Subfamily Myoniinae, is a useful association, and of course welcome the distinction of Vacunellidae, now Vacunellini. None of the surveys have been without flaws; my higher classifications in 1987b and 1988 failed to attend adequately to advances and discrepancies in Astafieva-Urbaitis (1973) and Runnegar (1974); Runnegar (1974) dismissed *Oblicarina* on faulty analysis, synonymized *Pachymyonia* with *Myonia*, ignored *Myofossa* and *Myomedia*, and offered a classification largely demolished by Morris et al (1991); Russian studies, which have greatly expanded the group, seem to be based heavily on external appearance, with internal detail not as well

preserved as in Australian fossils. South American studies, excellent on their own material, have failed to grasp the morphology of some east Australian genera, and overlooked the extensive Russian publications.

MONOPHYLETIC OR POLYPHYLETIC ORIGIN

The fundamental model advocated by Runnegar (1967, p. 32) was that the various genera “ had radiated rapidly from one or two ancestral forms in the late Carboniferous or early Permian.” This seems wrong: the claims by Dickins (1963, p. 45, 1981, p. 26) and Waterhouse (1966b, fig. 2) of early Carboniferous roots seem to be substantiated by Russian work and the age-ranges of genera such as *Myofossa* adduced by Morris et al (1991). Indeed Runnegar (1972) himself later described a small form *Pyramus barringtonensis* from the east Australian mid-Carboniferous. Given that there is such a limited range of morphological features and variation in the group, with substantial gaps and flaws of preservation in the fossil record - let alone gaps in the study of the group - there is clearly much to be said for further detailed studies, including shell ultrastructure and geochemical and genome analysis.

Superfamily **EDMONDIOIDEA** King, 1850

With some caution, Morris et al (1991) included Edmondiidae and Megadesmidae within one superfamily. This endorses and elaborates a view expressed by de Koninck (1876-7), sustained by Dickins (1957, 1963) and Waterhouse (1966b, 1969a), and firmly endorsed by Astafieva-Urbaitis (1973). Runnegar (1965, 1966) at first followed these appraisals, but then (1967, pp. 31, 32) found some difficulties, not surprisingly, because he interpreted as one alternative the internal plate of *Edmondia* as signifying the presence of a resilifer as in *Mya* or *Corbula* (Runnegar 1967, p. 32), which is certainly nothing like anything in *Myonia* or *Megadesmus*. He therefore dissociated Megadesmidae (his Pachydomidae) from Edmondiidae. He also in early work had misunderstood the ligament of *Pholadomya*, omitting to note the compact and internal nature implied by the deep pit in the type species (Moesch 1875, Waterhouse 1969c).

Family **EDMONDIIDAE** King, 1850

Edmondiidae was regarded by Morris et al (1991) as including *Edmondia*, *Scaldia*, *Allorisma* and *Cardiomorpha*, united by various criteria, including suggestion of inner ridge or plate below the hinge, and escutcheon, without lunule, and no posterior gape. Photographs and text-figures of various Edmondiidae showing shape and hinge are provided by Waterhouse (1966b, pl. 13-15, 1969c) and Runnegar & Newell (1974).

Subfamily **MYONIINAE** Waterhouse, 1969

[nom. transl. hic ex Tribe Myoniini (nom. corr. hic ex Myoniides) Waterhouse, 1969a, pp. 21, 26]

HISTORY: Initially Waterhouse (1969a, 1988) had considered that the genera *Myonia*, *Myomedia*, *Myofossa*, and *Pachymyonia* fell within Tribe Myoniides (ie Myoniini). Waterhouse (1969c, p. 110), in an article written after Waterhouse (1969a), stated that *Myofossa* should be replaced in Sanguinolitidae, because it displayed a lunule, and Muromzeva (1984) also put the genus with *Ragozina* Muromzeva in that family. This was confirmed by Morris et al (1991).

Of the genera referred to Edmondiidae (Edmondiinae) by Morris et al (1991), *Cardiomorpha obliqua* is moderately close to Myoniinae, displaying thick shell, and inconspicuous internal rib. Its adductor and accessory muscle scars were described as being “rather similar” to those of megadesmids by Morris et al (1991, p. 57).

A very different view of the relationships of *Myonia* was asserted by Runnegar, in opposing any tie with *Edmondia*, and stressing a close link with *Megadesmus*. Runnegar (1967, pp. 31, 32) stressed that unlike *Myonia*, *Edmondia* displayed a *Mya* or *Corbula*-like internal resilifer. In 1974 Runnegar & Newell did not deny the Runnegar thesis that *Edmondia* had a *Mya* or *Corbula*-like resilifer, but severely criticized suggestions in Waterhouse (1965c, 1966b) that the internal plate of *Edmondia* was a hinge structure, failing to point out that Waterhouse was only quoting others, not undertaking an original analysis: it was not his thesis. Runnegar & Newell (1974) misconstrued Waterhouse's main point. This was not that the internal ossicle of *Edmondia* was part of the hinge, or bore a ligament as various other authors had claimed. It was that the internal ossicle of *Edmondia* was duplicated in genera such as *Myonia* by a ridge within the shell and below the hinge, whatever its function. Earlier this point had been appreciated by Runnegar (1966, p. 380): - “Waterhouse (1965 [=c], p. 378) has pointed out that a ridge that is sometimes present on the inner side of the nymphs of Australian genera is reminiscent of the inner plate of *Edmondia*.” The examples of *Edmondia* with a large ossicle (eg Waterhouse 1966b, pl. 15, fig. 2, 3, 1969c, text-fig. 6B) are to be set along side *Edmondia* with a small or subdued ossicle (Waterhouse 1966b, pl. 15, fig. 5). These latter examples have a structure very close to that seen in *Myonia* (see Runnegar 1967, pl. 5, fig. 15, Waterhouse 1969a, pl. 1, fig. 1, 3) and other Australian genera (see *Pyramus* in Waterhouse 1988, pl. 20, fig. 3). This simple point, although emphasized by Waterhouse, has been misrepresented in other studies, yet, whatever it means, seems valid. Morris et al

(1991, p. 57) also noted that the internal rib was "only just distinct" in *Cardiomorpha*, a member of Edmondiidae, and that *Cardiomorpha* muscle scars were comparable to those of megadesmids - in which they included *Myonia*.

The Waterhouse proposal is supported by the additional documentation of *Edmondia* provided by Runnegar & Newell (1974). The hinge plate in silicified Permian shells from Texas that were ascribed to *Edmondia* by Runnegar & Newell (1974, text-fig. 2) is clearly internal. It carries small adductor scars. I should have stressed that the analogous structures in *Pyramus* and *Myonia* are also clearly internal, relating to viscera, and not hinge. Therefore the clarification by Runnegar & Newell (1974) may add support to the contention by Dickins (1963) and Waterhouse (1966b etc) that *Edmondia* and *Myonia* are related - at relatively high level, as expressed by associating the two as separate families within Edmondioidae by Morris et al (1991). There are many similarities, and the classification urged by Runnegar & Newell (1971, 1974) and Runnegar (1974), which argues for strong separation between *Edmondia* and various megadesmids and *Myonia* etc is tenuous, given their insistence on ill-defined family parameters, and vague generic diagnoses that offer no clear generic distinctions between types. This point needs to be emphasized. Runnegar did not provide firm morphological limits for genera such as *Megadesmus*, *Myonia* and *Australomya*. From his account, the genera seem to occupy shadowy, indefinite, and interchangeable areas in complex clines of overlapping variables.

GENERA: The genera within Myoniinae involve large upright subrectangular shells, close to Edmondiinae in shape and escutcheon, but larger, with allied hinge lacking teeth. There is no large internal plate, unlike many but not all *Edmondia*, and accessory muscles are more numerous than known for any Edmondiinae (Waterhouse 1969c, Runnegar & Newell 1974). The constituent genera within Myoniinae have been described and amply illustrated especially by Runnegar (1967) and Waterhouse (1969a, 1988), the latter publication providing photographs at natural size of the numerous Dana type specimens.

DENTITION IN MYONIA: The hinge of *Myonia elongata* Dana, the type species of *Myonia*, is edentulous, as stated in a number of studies by Waterhouse (1965c, 1969a, 1987b, 1988), and well illustrated by Waterhouse (1969a, pl. 1, fig. 1, 3, 1988). Nor is a tooth visible in *Pachymyonia*. Runnegar (1965, p. 230, Runnegar & Newell 1971) stressed that the hinge of *Myonia* was "virtually edentulous," counter to the inexplicable view of Newell (1956) that a tooth was developed in each valve. Runnegar (1967, p. 32) noted that a specimen of *Myonia tayoensis* (Reed, 1930a) showed a small tooth in the right valve. A latex mould of this specimen, torn across the umbo, was figured by Runnegar (1967, pl. 13, fig. 14), and possibly but not clearly suggests a very broad triangular prominence under the umbo. Rocha-Campos (1970, p. 33) evaluated the hinge of this species as "apparently edentulous," but noted one specimen (his pl. 3, fig. 13) that indicated a projection under the umbo, which possibly represented a cardinal tooth. There must be reservations. If the types and accompanying species of *Myonia* in Australia show no right valve tooth, does a shell, apparently exceptional and from a distant country, necessarily belong to the same genus when it has a right valve tooth? To Runnegar, the answer was yes: the genus is *Myonia*, and the dentition is of little consequence. He regarded the dentition as variable in size and shape in various species and genera. I would prefer to research the South American form more fully before asserting that *Myonia* is variably denticulate or edentulous. If a right-valve tooth is a feature of *tayoensis*, should *tayoensis* or at least the specimen that shows the tooth be regarded as closer to *Pyramus* than to *Myonia*? Although *tayoensis* shows no clear pallial sinus, *Pyramus laevis* also does not often show a well-formed pallial sinus (Runnegar 1967, text-fig. 4, p. 36).

VALIDITY OF PACHYMYONIA: It is disconcerting to find that Runnegar (eg 1974) has persistently denied the value of *Pachymyonia* Dun, which is readily distinguished through shape by having a strong posterior carina, whereas *Myonia* has none. The stance seems inconsistent, because for other genera, Runnegar strongly emphasized shell shape. Other authors, such as Dickins (1963) and Muromseva (1984), have persisted in defending the validity of *Pachymyonia*. From a wide-ranging re-evaluation of Late Paleozoic species and genera, Morris et al (1991) suggested that *Pachymyonia* might fit best within Sanguinolitidae, and *Sanguinolites* itself shows strong external similarities. So why did Runnegar synonymize *Myonia* and *Pachymyonia*? The answer lies in what appears to have been a mistaken understanding of *Myonia* itself. Runnegar (1967) mistakenly asserted that *Myonia* was carinate. The type species of *Myonia* is *Myonia elongata* Dana, 1847, 1849, and this was redescribed by Runnegar (1967). He misinterpreted the species. He did not figure or examine the type specimens, but relied on material he had misidentified as *elongata* (Runnegar 1967, pl. 5, fig. 12-15, 18). That material belonged rather to *Myonia carinata* (Morris 1845, pl. 11, fig. 3, Waterhouse 1988, pl. 7, fig. 3), which carries a gently carinate posterior umbonal ridge, so that in shape the species *carinata* - as indicated by its specific name - is not the same as either *Myonia* or *Pachymyonia*. As shown by Waterhouse (1969a, pp. 28, 30, 1987b, p. 171, 1988, p. 180, pl. 7, fig. 1, 2, pl. 8, fig. 1, 2, pl. 9, fig. 1) with full illustrations and details of individual specimens registered by number in various institutions, including the original types, *Myonia elongata* Dana (1849, pl. 5, fig. 3), the type of *Myonia*, has no carination. The comparison is clearly made in Waterhouse (1988, pl. 7, fig. 1, 2 - lectotype, *elongata* and allies such as *valida*) with Waterhouse (1988, pl. 7, fig. 3 - *carinata*). The species *carinata* was therefore made type of the subgenus *Myomedia* Waterhouse, 1969a. Runnegar (1967) compounded the error by also misinterpreting *Myonia carinata*. Although that species is very distinctive, and limited to Middle Permian faunas, he managed to confuse it with Early Permian *Pachymyonia etheridgei* Dun (see Runnegar 1967, pl. 4, fig. 11-13). When scholars accept Runnegar (1967) on *Myonia*, they reveal failure to check the Runnegar

identifications with the actual types, or carefully peruse the literature. At the least, such workers should explain why the illustrated aspects of morphology of the type specimens are set aside in favour of statements that misrepresent morphology and taxonomy, and are at odds with studies by Dana (1849), Dun (1932), Fletcher (1932) and Waterhouse (1988).

Although Morris et al (1991) proposed to associate *Pachymyonia* with *Sanguinolites* (with a query), this is rejected, because *Pachymyonia* lacks a lunule, and has the same musculature as *Myonia*.

Family **MEGADESMIDAE** Vokes, 1967

As in Morris et al (1991), Megadesmidae are tentatively regarded as a member of Edmonдиоidea. The early Carboniferous edmondiid genus *Cardiomorpha* shares some attributes, and the hinge of *Scaldia* has a tooth, as well illustrated in Waterhouse (1966b). Three subfamilies are recognized herein, which share many attributes especially in terms of thick shell, strong tooth in right valve, minor or no posterior gape, escutcheon weakly to well developed, no lunule, and other criteria. They may have shared a common ancestry, from stock approaching the genus *Scaldia*, which has a simple hinge tooth in each valve.

Subfamily **MEGADESMINAE** Vokes, 1967

Mello & Simoes (1996) undertook a cladistic analysis of Megadesmidae, based on 26 characters, and recognized one clade that included *Megadesmus*, *Astartila*, *Pyramus*, *Myonia* and *Australomya*. This was distinguished from a group of South American genera, discussed below, and also from *Vacunella*. Morris et al (1991) took a different view, assigning the associated genera to three different families, in two different superfamilies. Mello & Simoes (1996) were aware of that work, and evidently considered their study more objective. Unfortunately, the reliability of their cladistic analysis lies under a cloud, because they stated that the genera were united a blunt tooth in the centre of the hinge of the right valve. As discussed above, there is no tooth in the types of *Myonia*, *Pachymyonia* or *Myomedia*, judged from specimens from the extensive Permian collections of eastern Australia or New Zealand, and types in the Smithsonian Institute, Sedgwick Museum and Natural History Museum. No tooth was described in the description or diagnosis of *Australomya* Runnegar, but this may have been because the hinge is concealed. But it cannot be assumed that a tooth is present, without proof. Overall morphology of this form strongly suggests that it would have a hinge like that of *Vacunella*. *Vacunella* has no hinge teeth.

Part of the difficulty confronting Mello & Simoes may have lain in the uncertainty over the nature of the hinge, because they had to rely on literature for an understanding of Australian types, only to find some degree of inconsistency that opened up ambiguities. As an example, Runnegar noted that a specimen of *Pyramus laevis* (Runnegar 1967, pl. 2, fig. 7) was "almost edentulous". Yet his figure clearly shows a tooth. Reading of his articles shows that this item has been consistently treated in a flexible manner. In 1972, he described an Early Permian species of *Megadesmus*, *M. pristinus* Runnegar, with a hinge that was "virtually edentulous" with no further explanation and with no figure provided. In short, to Runnegar, the dentition either did not matter that much, or varied considerably and inconsistently. Perhaps his approach was compatible with his view of the alleged dentition in *Eurydesma* (Runnegar 1970), as discussed previously herein.

I remain to be convinced that internal features were so variable and flaccid. But if the internal morphology is so variable, any cladistic analyses would have to be extremely sophisticated to be worth doing.

Another aspect of variation concerned the small pedal and retractor muscle scars. Runnegar (1967) emphasized that what was most significant for these was the number of scars, not their point of insertion or shape. The differences and variations were never illustrated or even documented in specific detail, and therefore have not been adequately validated. Wass (1972) concluded that the "anterior musculature has been shown to be almost continuously variable between *Astartila* and *Megadesmus*". He provided no illustrations, and itemized no specimens that verify such claims. If the claim was correct, one is left to wonder whether *Astartila* should be discriminated from *Megadesmus*, and what are the prime discriminants. The discriminants are not provided by Runnegar (1967). His diagnoses of *Pyramus* and *Myonia* allowed overlapping features and were not completely accurate, especially for *Myonia*, as noted by Waterhouse (eg 1987b, 1988). His main emphasis seemed to fall on size and shape, which is why his denial of *Pachymyonia* and *Oblicarina* seems anomalous, until it is realized that he misidentified type and other species.

The genera here regarded as members of Megadesminae are *Megadesmus*, *Megadesmus (Cleobis)*, and *Pyramus*. Simple statistical treatments imply that *Notomya* M'Coy is also valid (Waterhouse 1988), but morphologically the two look very close. They are united by their sturdy elongate shape, often large size, moderately to well defined escutcheon and tendency to develop posterior gape. *Megadesmus* displays valve overlap, and *Pyramus* has a pallial sinus. Further details are provided by Runnegar (1965, 1966, 1967) and Waterhouse (1969a, 1988).

Genus **Megadesmus** Sowerby, 1838 *Megadesmus?* sp.

1969a *Myonia compacta* not Waterhouse; Waterhouse, p. 65, pl. 14, fig. 2 (not pl. 15, fig. 2, 3, 5, 7, ?6 = *compacta*).

MATERIAL: One valve from D44/f315, lower *Echinalosia discinia* Zone, Letham Formation, Wairaki Downs.

DISCUSSION: Specimen inflated, with short hinge and incurved ventral umbo. The specimen appears identical with a specimen described as *Myonia compacta* by Waterhouse (1969a) from the Letham Formation at GS 6070 (D44/f9621). Individuals of *Myonia compacta*, including the holotype, are more elongate and less inflated, with less incurved umbones, and come from GS 7352 (D44/f9870) and GS 3616 (D44/f9478) in the *Echinalosia ovalis* Zone, and newly from D44/f111 (GS 15227) and D44/f346 from the lower *E. ovalis* Zone, and D44/f121 (GS 15217) from the upper *ovalis* Zone, all in the Mangarewa Formation of Wairaki Downs.

Subfamily **ASTARTILINAE** Waterhouse, 1969

DELINEATION: Astartilinae is a small cluster that stands a little apart from *Megadesmus* and its close allies, and the differences seem to be as great as the criteria used by Morris et al (1991) to delimit various subfamilies within their summary of Pholadomyoidea. The genera include *Astartila*, *Pleurikodonta*, and *Runnegariella*. They are united by their somewhat rounded as opposed to elongate outline with prolonged posterior shell seen in *Megadesmus*, *Cleobis* and *Pyramus*. They lack mantle insertion points over the internal valve, unlike *Megadesmus* and allies, or Myoniinae. None display valve overlap or any suggestion of pedal or posterior gape, and the pallial line is entire. The left "tooth" of *Astartila* described by Waterhouse (1965c, 1969a) may be no more than a prominence sited at the posterior side of the left valve socket, and jutting into a weak hollow in the hinge of the right valve, as also judged by Newell (1956). This prominence is better developed than in *Megadesmus* (see Waterhouse 1988, pl. 20, fig. 2), *Cleobis* and *Pyramus*. Conceivably, not all specimens ascribed to *Astartila* may display the prominence - indeed for most, the hinge is not revealed - but such specimens are yet to be found, prepared and illustrated. The types do display such a hinge. Another difference displayed by *Astartila* is in its anterior accessory musculature. The protractor-retractor complex in *Megadesmus* and *Pyramus* forms an isthmus extending posteriorly from the dorsal posterior margin of the anterior adductor. In the Dana types of *Astartila*, this isthmus is not developed, and instead there is an entirely discrete scar. Unfortunately, the details of musculature have been only photographed and figured for a number of individuals by Waterhouse (1969a, 1988): the illustrations in Runnegar are few in number, small-scaled, and diagrammatic.

HISTORY: Waterhouse (1969a, 1987b, 1988) considered that *Astartila* belonged to a discrete subfamily characterized by having a tooth in each valve, as illustrated for the original types of *Astartila* by Waterhouse (1988, pl. 18, fig. 4, 8, pl. 19, fig. 9) and Waterhouse (1969a, pl. 12, fig. 4, 7, 8). But no one else has agreed. When constructing this manuscript, I decided to set subfamily aside. But the more I looked into the matter, the less satisfied I became with the prevailing approach. Basically, this is because the types that I have examined remain open to study, reinforced and made accessible to further study through many good and detailed published photographs, with reference to curated specimens. Scholars have strongly asserted contrary views. But none have provided supporting documentation in the way of figures, or often even specifications of sample numbers. Few have even looked at the type specimens, other than Newell and me, and Newell evaluated the hinge as *having a tooth in each valve*. One is therefore left to weigh data against opposing, undocumented assertions, and clearly, the data must be preferred, no matter how many others think differently.

MUSCULATURE: Musculature was the focus of a somewhat mystifying account by Wass (1972) on shells he recorded as *Astartila* - or new genus - or *Megadesmus*, for he did not decide - from the Farley Formation, Sydney Basin. He emphasized his discovery of a small pedal protractor scar at the posterior end of the anterior adductor impression as marking a pronounced advance. Yet Runnegar (1967, p. 14) had stated that the scar was possibly present, and Waterhouse (1969a, p. 56) wrote of a "protractor probably attached to the adductor," in modifying an initial view that the small scar seemed to be absent. Earlier, Runnegar (1965, p. 245) judged that the anterior adductor was probably not fused to any protractor, but noted that the protractor could have been attached to the adductor, not to the shell. In short, Wass (1972) was inflating the importance of his own work, and ignoring other studies. Runnegar & Newell (1971, p. 32, footnote) referred in a derogatory way to Waterhouse (1965c) on this point, and ignored the Waterhouse (1969a) revision! They did refer to Runnegar (1965) but did not quote his view, preferring instead to quote only his amended view of 1967. Reviewing such publications for inconsistencies should be unnecessary, but constant denigratory misrepresentation leads to substantial misrepresentation of species and genera. There seems to have been such a concern to defend or conceal some of the earlier views that portrayals of genera and the work of others, and even summaries of their own earlier work, require discernment.

Wass (1972) claimed that Waterhouse (1969a) had used the presence of an escutcheon on *Megadesmus* to differentiate it from *Astartila*. A narrow slit each side of the calcified ligament was recorded for *A. cyclas* by Waterhouse (1969a, p. 57) and poorly formed, but present, in other species. The escutcheon is variously defined amongst students of bivalves. I relied on the experience of Recent and Tertiary bivalve experts Sir Charles Fleming and Dr J. Marwick in considering that the escutcheon has to be sharply delimited and not simply the opposing slopes of the valves above the hinge line and behind the umbones. Wass (1972, p. 319) summarized his views, stating that "*Astartila* ss. does not possess both pedal scars anterior to the umbones, has an umbonal carina, and an escutcheon is weakly developed or absent; *Megadesmus*

sometimes lacks an umbonal carina and has a well developed escutcheon with both anterior pedal muscles being well developed; *Astartila* as discussed (by Wass) ... has a reasonably well developed escutcheon, possesses both pedal scars anterior to the umbones and has an umbonal carina". So his text, allowing for its awkward syntax, questions some of his own assertions - he states that the *Astartila* escutcheon is weakly developed or absent - and that it is reasonably well developed. It does not have both pedal scars anterior to the umbones, and it does have both pedal scars. His work is bizarre. Whether his specimens were really referable to *Astartila*, or to *Megadesmus*, or even as Wass (1972) suggested " a subgenus of either *Astartila* or *Megadesmus*" remains unsure, but the likelihood seems strong that he was dealing with young *Megadesmus*, which he had confused with *Astartila*. As Runnegar (1965, p. 232) cautioned, juvenile specimens of *Megadesmus* are often difficult to separate from adults of *Astartila*. Clearly, Wass (1972) has shown that a proper evaluation of his material is still waiting. Workers on South American Megadesmidae have relied heavily on the Wass study (Prof. Mello, pers. comm.), which I find extraordinary. Which of the various alternative and self-contradictory views on *Astartila* does any reader accept, I wonder? And why?

Notwithstanding the Wass article, the illustrations of type material provided by Dana (1849), Newell (1956) and Waterhouse (1969a, 1988) - no others have contributed - suggest that *Astartila* shows objective differences from *Megadesmus* and *Pyramus* - and especially from *Vacunella* and its allies, and also *Myonia*. Given this morphological distance amongst a group displaying very conservative morphology, it appears that *Astartila* merits some degree of discrimination. That said, it would be desirable to clarify the nature and consistency of hinge structure, and confirmation of muscle arrangement within non-type material, and within species of different age, because Runnegar (1967, 1974) and Wass (1972) have asserted but not illustrated or even specified an intergradation in characters of hinge and musculature for the genera. I agree that claims should be checked from further material. In the meantime, the only verifiable data that has been provided should not be ignored.

Genus *Astartila* Dana, 1847
? *Astartila intrepida* Dana, 1847

?1847 *Astartila intrepida* Dana, p. 155.

?1988 *A. intrepida* Dana; Waterhouse, p. 196, pl. 7, fig. 4, pl. 17, fig. 3-6, 9, pl. 18, fig. 1-11, pl. 19, fig. 1-12, 15, pl. 20, fig. 1. (See for synonymy and typology.)

A small right valve TM 7907 about 16 mm long from D44/f121 (GS 15217), upper *Echinalosia ovalis* Zone, Mangarewa Formation, Wairaki Downs, apparently belongs to *Astartila intrepida* in terms of shape, ornament and dimensions, and shows low concentric growth lines. A low narrow ridge is developed along the posterior umbonal slope, whereas this is rounded in *Astartila*, but the ridge is interpreted as possibly due to deformation. Admittedly a ridge is present often in *Megadesmus*, so perhaps this is the correct identification. *A. intrepida* is common in the younger Middle Permian of the Sydney Basin, New South Wales, and is scarce in the Bowen Basin of Queensland.

Extensive figures and measurements of the Dana and relevant M'Coy types were provided by Waterhouse (1988).

Genus *Pleurikodonta* Runnegar, 1965

This genus was erected as a subgenus of *Astartila*, and elevated to full generic standing by Wass & Gould (1968), followed by Waterhouse (1987b, 1988). Hinge teeth were said to be feeble or missing, presumably because, as Runnegar pointed out, the valves possessed interlocking teeth around the margins, formed by ribs. Runnegar (1965) believed that his type species *P. elegans* was a new discovery. But in fact he overlooked several east Australian species that have been described by various authors from the Middle Permian - *Astarte gemma* Dana, 1847, *Venus? gregaria* M'Coy, 1847 and *Astartila subgemma* Fletcher, 1929b. All apparently are conspecific, and *elegans* must be relegated to synonymy of *gemma* Dana. But the genus remains valid, as a useful expansion of the Subfamily Astartilinae.

Genus *Runnegariella* Simoes & Anelli, 1995

Runnegariella is only slightly elongate, and has a large anterior, so it comes close in shape to *Astartila* and *Pleurikodonta*. The musculature includes what is called "protractor pedial (=pedal?) anterior" attached to the posterior part of the adductor scar, and the left valve shows a prominent condyle. The condyle is indicative of the *Astartila* hinge described by Waterhouse (1969a, 1988) in the Dana types. The overall outline differs strongly from that of *Astartila*, with the anterior convex along the dorsal side, whereas the short posterior dorsal margin is concave. The posterior ligament is small, and it is not clear if an escutcheon was differentiated.

Subfamily **PLESIOCYPRINELLINAE** new

NAME GENUS: *Plesioocyprinella* Holdhaus, 1918.

DIAGNOSIS: Medium-sized shells compared with Megadesminae, often subtriangular in shape with posterior carina, small or no posterior gape, hinge basically as in *Megadesmus*, with right tooth often large, and left valve may have anterior boss, typically without lunule and/or escutcheon, ligament opisthodetic, parinvicular, attached to short nymphs. No small accessory a and b scars.

DISCUSSION: Runnegar & Newell (1971) published an enthralling re-interpretation of bivalves from the Estrada Nova Formation in the Parana Basin, Brazil, advocating that a fauna diversified in isolation, with a number of genera evolved from Megadesmidae. Genera included *Plesioocyprinella* Holdhaus, *Casterella* Mendes, *Jacquesia* Mendes, and *Ferrazia* Reed. They were regarded as Megadesmidae by Runnegar & Newell (1971), although they are somewhat outstanding in shape, several showing a general approach to the Devonian genus *Grammysia*, and having a more massive hinge and other differences compared with *Megadesmus*. The genera *Plesioocyprinella*, *Casterella* and *Jacquesia* lack an escutcheon or lunule, and the hinge is slightly more elaborate than in *Megadesmus*. *Jacquesia* has a lunule and narrow poorly defined escutcheon. Mello & Simoes (1996) from cladistic analysis concluded that they were separable from *Megadesmus* and allies. *Megadesmus* and allies displayed accessory muscles that were not developed in the Parana Basin genera (Gilhardi & Simoes 1996). Mello & Simoes (1996) also contradicted the synonymizing of *Cowperesia* Mendes with *Pyramus* by Runnegar & Newell (1971, p. 35), and judged it to be allied to *Plesioocyprinella* and allies.

Superfamily **PHOLADOMYOIDEA** King, 1844

Several families and subfamilies were aggregated in Pholadomyoidea by Morris et al (1991) but they pointed out that Sanguinolitidae and Permophoridae shared some features, with the implication both differed from Pholadomyidae. Morris et al (1991) assigned *Vacunella*, *Myonia* and various other genera to Pholadomyoidea, as distinct from Megadesmidae which they allocated to Edmondioidae. This comes close to the position advocated by Astafieva-Urbaitis (1973) and Waterhouse (1969a). Several Australian Permian genera were placed in three subfamilies Sanguinolitinae, Undulomyinae and Vacunellinae within Sanguinolitidae.

Family **PHOLADOMYIDAE** King, 1844

Here it is proposed that Vacunellini and what is here regarded as its close ally Chaenomyinae be transferred from Sanguinolitidae, as in Morris et al (1991), to Pholadomyidae. *Vacunella* and *Chaenomya* lack a lunule and come very close in shape and hinge detail to early Mesozoic genera assigned to Pholadomyidae.

Subfamily **CHAENOMYINAE** Waterhouse, 1966

This subfamily incorporates posteriorly elongate bivalves with edentulous hinge, opisthodetic external ligament, ornament of comarginal growth-lines, ribs or rugae, moderate to large posterior gape and moderate to shallow pallial sinus.

Tribe **CHAENOMYINI** Waterhouse, 1966

Only one genus is known in the tribe, *Chaenomya*, with wide posterior gape, posterior external ligament, high but shallow pallial sinus (Meek & Hayden 1864, pl. 2, fig. 1) and no retractor scar above the posterior adductor (Waterhouse 1969a, text-fig. 8i), as confirmed by Runnegar (1974, text-fig. 5g). The absence of the scar presumably related to the particularly wide gape and unusual extrusion-retraction mechanism of the siphon. Morris et al (1991) treated Chaenomyinae as a subfamily within Sanguinolitidae, but it differs from Sanguinolitinae in the absence of a lunule. Morris et al (1991, p. 81) argued that *Chaenomya* was uniquely characterized by a very wide posterior gape that pointed to an unusual siphon formation. They stated that *Chaenomya* did not have a deep pallial sinus, which indicated substantial difference from members of the Undulomyinae. Although it may be true that the depth of the pallial sinus is not known for all members of Undulomyinae, the argument seems valid. The overall greater height and more barrel-shaped shell of *Chaenomya*, with its lack of lunule, appear to enforce this separation.

Chaenomyinae Waterhouse was elevated to family status by Runnegar (1974) and Runnegar & Newell (1974). *Argyromyra* Fischer, *Cosmomya* Holdhaus, and *Osteomya* Moesch were referred to Family Chaenomyidae by Runnegar (1974), but *Cosmomya* was reallocated to Sanguinolitinae by Morris et al (1991), and *Osteomya* was deemed to be closely related to *Plectomya*.

Waterhouse (1969a) had considered that the east Australasian genus *Vacunella* was a member of Chaenomyinae, but Runnegar (1974) and Runnegar & Newell (1974) dissociated *Chaenomya* from *Vacunella*. These authors preferred to regard *Vacunella* as a close associate of Megadesmidae, not Chaenomyidae, changing without remark from Runnegar's earlier assessment that *Vacunella* was closely related to *Pholadomya* (Runnegar 1966, p. 378). Runnegar's change of view was based on alleged ties between

Myonia and *Vacunella*, which suggested to him that *Vacunella* had evolved not from *Chaenomya* stock, but from myoniid stock, or allied megadesmid. That theme was developed by Astafieva-Urbaitis (1973) in distinguishing Family Vacunellidae, which included *Myonia*, and indeed *Chaenomya* - implying that she had overlooked the earlier proposals of Chaenomyinae and Myoniini. Her view was essentially espoused by Morris et al (1991), with the recognition of both Chaenomyinae and Vacunellinae within Sanguinolitidae. *Myonia*, ?*Australomya* and *Vacunella* were referred to Subfamily Vacunellinae by Morris et al (1991, p. 94), and Chaenomyinae was allocated only the genus *Chaenomya*. These authors presumably overlooked the earlier proposal of family group unit Tribe Myoniini, based on *Myonia*, by Waterhouse (1969a), which in their scheme, would preempt Vacunellinae, because it has priority as a family-group proposal.

On available information, *Chaenomya* evolved from within either Edmondioidae or Pholadomyoidae. The fossil record and hinge detail appear to render any derivation from Megadesmidae unlikely, and given that the lunule is variously defined amongst individuals of Sanguinolitidae, it does not appear difficult to envisage origin from within this group, especially under the broad association assembled by Morris et al (1991). The alternative, of separating Pholadomyidae and Edmondiidae from Sanguinolitidae on the basis of lunule has not commended itself to anyone.

Morris et al (1991, p. 82, text-fig. 33) drew attention to "*Chaenomya*" *jacunda* de Koninck (1885, pl. 1, fig. 1-8) from Visean of Belgium, a species which shows a wide posterior gape, well defined escutcheon, small lunule, and wide but shallow pallial sinus. Although assigned to *Sedgwickia* by Runnegar (1974), Morris et al suggested that the form belonged to an uncertain genus and subfamily, that possibly provided ancestral material for *Myonia*, *Vacunella* and even *Chaenomya*. There would seem to be some possible approach to *Praemyonia* Astafieva-Urbaitis, which is close in overall shape and inflation, and slightly better defined concentric ornament, and a possible lunule, judged from figures.

Tribe **VACUNELLINI** Astafieva-Urbaitis, 1973

[nom. transl. hic ex Vacunellidae Astafieva-Urbaitis, 1973]

This subfamily was separated for *Vacunella* and its very close allies, but it is very difficult to accept the thesis first promulgated by Runnegar (1967) and sustained by Astafieva-Urbaitis (1973) and Morris et al (1991) that *Myonia* was a forebear, and should be associated at subfamily level. Only Runnegar provided any analysis: others were content to accept Runnegar's conclusions. This is surprising, given that Morris et al had to so substantially revise the Runnegar (1974) overview of Pholadomyida, as well as correct a number of his misunderstandings over genera and species. The aspects of morphological similarity between *Myonia* and *Vacunella* involve size, ornament, including spicular shell, posterior external ligament, and many aspects of musculature, including somewhat similar accessory scars. There are minor differences in this regard, as analysed by Runnegar (1966, 1967) and Waterhouse (1969a), involving tiny imprints, called muscle a and b, present in *Myonia*, missing from *Vacunella*, and a posterior small complex on the pallial sinus, only in *Vacunella*, not *Myonia* (Runnegar 1966, text-fig. 1). As well as these possibly minor differences, there are substantial and obvious differences between *Vacunella* and *Myonia*. *Myonia* is an upright shell, more or less rhomboid to subrectangular in shape, with more or less orthogyrus umbones, short straight hinge, and no posterior gape. *Vacunella* is upwardly concave, with curved hinge, prosogyrous umbones, broader shape like a laterally squashed banana, pallial sinus and moderate posterior and usually anterior gape. The two look very different, and clearly *Vacunella* was much more adapted to a burrowing infaunal habit. Since habit and obvious morphologies are so different, there appears to be little reason for associating the two. This was confirmed by cladistic analysis (Mello & Simoes 1996), but unfortunately the particular data used for the cladogram was not provided.

Pachymyonia and *Myomedia* may be associated with *Myonia*, and differ from *Vacunella* in much the same way. Similarly the genera here deemed close to *Vacunella*, such as *Cunavella* Astafieva-Urbaitis, 1990, *Exochorhynchus* Meek & Hayden, 1864 and *Oblicarina* Waterhouse, show little approach to *Myonia* or allies in critical parameters of shape and gape. *Australomya* Runnegar, 1969 belongs here, if separable from *Vacunella*. All show modest to considerable posterior gape.

The fossil record does not support the claim by Runnegar (1974) and Runnegar & Newell (1974, text-fig. 8) that *Myonia* evolved into *Vacunella* by shells developing a deeper burrowing habit. It is true that *Myonia* and especially *Pachymyonia* are more common in older Permian of Australia, but early Permian *Vacunella* also are known (Runnegar 1969). It seems likely that *Vacunella* preferred a sandy substrate, found widely in Middle Permian of the Sydney and Bowen Basins rather than the more calcareous or gritty bottom conditions more common in earlier Permian, so that *Vacunella* is naturally more abundant in Middle Permian of east Australia. Both genera may have been present in at least Late Carboniferous faunas, for which the fossil record is very poor, or at least poorly understood, in east Australia. *Praemyonia* Astafieva-Urbaitis, 1988, recognized in Early and Late Carboniferous of Russia and North America, looks overall more like *Vacunella* than *Myonia*, but more needs to be demonstrated about the nature of the interior, and whether or not it has a lunule. *Cunavella* Astafieva-Urbaitis, 1990 is represented by a number of Middle Carboniferous to Permian species, and is clearly closer to *Vacunella* than to *Myonia*. This helps refute the Runnegar proposal of evolutionary trend that envisaged *Vacunella* stock postdating *Myonia*: if anything the reverse was true. It also underlines the longevity and very slow evolutionary change within Pholadomyida. The world picture, thanks to Russian work, shows that the 1960's model based on restricted east Australian studies was far too limited. Indeed, the overview of Anomalodesmata by Runnegar (1974) omitted, inexplicably, or

for geopolitical reasons, consideration of fossils from the former Soviet Union. The long sustained morphological separation between *Vacunella* and *Vacunella*-like stock on the one hand, and *Myonia* and allies on the other hand, and the array of species in both Russia and Australia that points to pre-Permian development, are factors deemed to encourage the recognition of two separate streams for *Myonia* and *Vacunella* and allies.

But where did Vacunellini spring from? The preponderance of genera are prosocline in outline, and tend to have a posterior umbonal ridge or at least subangular to sharply curved change in angle on the posterior slope. The very anterior position of the umbones would have tended to render a lunule redundant. The pallial sinus, although emphasized as deep by Runnegar (1966, 1967), is nowhere as deep as in *Pholadomya* species or many of the Mesozoic and Tertiary genera (Waterhouse 1969c), nor as deep as in a number of Undulomyiinae. A source may have lain in such early Carboniferous sanguinolitid forms as *Myofossa* or *Praemyonia*, but this far from the only possibility.

And what were the relationships with *Chaenomya*? Although *Chaenomya* is an outstanding species with peculiar mode of siphon extrusion as analysed by Morris et al, this seems to have been a "dead-end" and presumably evolved rapidly as an off-shoot from a genus very like *Vacunella* in shape, and presumably also without a lunule. A different view was expressed by Morris et al (1991) in suggesting that the Visean species "*Chaenomya*" *jacunda* de Koninck may have been ancestral. This species has a lunule. In evolutionary terms, and given considerations of diversity, biomass and morphological space, *Chaenomya* may be regarded as an exceptional form within the *Vacunella* framework, and under the constraints of nomenclatural procedures and rules of priority, this might be best expressed by calling *Vacunella* and allies a tribe, within Chaenomyiinae.

A further question centres on the relationship of the *Vacunella* association to Pholadomyidae. Triassic pholadomyids such as *Homomya* Agassiz and *Pachymya* Sowerby are very close to *Vacunella* in overall shape and many external attributes, and the pallial sinus of *Pachymya* is shallow, suggesting *Vacunella* should be associated with Pholadomyoidea.

Genus *Oblicarina* Waterhouse, 1967

Oblicarina Waterhouse, 1967c was assigned to Vacunellinae by Waterhouse (1987b). Although it resembles Sanguinolitidae in external shape, it has a moderately large posterior gape, and presumably well formed posterior sinus, as in Vacunellini. Etheridge (1892) did report a lunule, but one is not clearly developed. Runnegar (1974) considered that *Oblicarina* was based on a crushed *Vacunella curvata* (Morris), but several specimens are known for the type species *Chaenomya*? *carinata* Etheridge, 1892 (see Waterhouse 1987b, p. 175, pl. 11, fig. 5, pl. 14, fig. 4, 6) and consistently show not only strong posterior carination, but strong concentric wrinkles anteriorly and laterally, and smooth posterior dorsal face. Such features are not seen in *Vacunella*. Of course individuals of *Vacunella* may be crushed to become pseudocarinata, but do not transform into specimens with regularly disposed posterior carination or anterior wrinkles. The evaluation of one specimen may require great care, caution and good judgement. But when a number of specimens all show consistent carination and disposition of unusual growth wrinkles, the validity of the grouping is clear.

Two species from the Indian subcontinent have been assigned to *Globicarina*, on the basis of first-hand examination. *Mytilomorpha translata* Reed (1932, pl. 8, fig. 9, 10) has strong umbonal ridge and large posterior gape, and comes from early Permian of Kashmir. From the Lower Productus Limestone or Amb Formation of the Salt Range, *Sanguinolites*? *sphenoidalis* Reed (1944, pl. 56, fig. 2) has the prosocline outline, posterior carination and escutcheon typical of the genus.

Genus *Exochorhynchus* Meek & Hayden, 1864

This genus has been well reviewed by Astafieva-Urbaitis (1981). She showed that it was very close to *Vacunella*, but distinguishable through its shape and nature of umbones. Detail of accessory muscles remains obscure. Morris et al (1991) classed *Exochorhynchus* in Undulomyiinae Astafieva-Urbaitis, 1984, but overall shape and external details including escutcheon suggest such a separation from Vacunellini is unwarranted. The separation seems to have been premised solely on the unproven, and indeed unlikely assertion that *Vacunella* arose independently from *Myonia*-stock in Gondwana, and converged in morphology.

Morris et al (1991, p. 80) asserted that a species of *Exochorhynchus* originally described as *Allorisma barringtoni* Thomas, 1928 from Peru was apparently senior synonym to *Allorisma similis* Lyutkevich & Lobanova, 1960 from Taimyr Peninsula. This seems unlikely to judge from the various illustrations. The Russian form has been reported widely from Early Permian of Russia and Canada in beds of Sakmarian and perhaps Artinskian age, as summarized by Shi & Waterhouse (1996). The Peruvian specimens are accompanied by mid-Pennsylvanian ammonoids. Although Morris et al (1991) speculated that the collections had been mixed, there seems no reason why *Exochorhynchus* could not have ranged up from Late Carboniferous.

Genus *Praemyonia* Astafieva-Urbaitis, 1988

Several Russian species have been grouped in this genus, including species previously referred to *Allorisma* and *Tellinomorpha*, from Lower Carboniferous faunas. The shells are orthogyre, with strong regular concentric wrinkles, escutcheon, and distinct but narrow posterior gape. The hinge is curved.

Genus *Cunavella* Astafieva-Urbaitis, 1990

Several northern hemisphere species have been described from mid-Carboniferous to Cisuralian faunas, and the species are overall very close to *Vacunella*. It was suggested that *Vacunella etheridgei* (de Koninck) belongs to this genus.

Genus *Australomya* Runnegar, 1969

Australomya Runnegar, 1969 probably belongs to Vacunellini, but its validity remains questionable. The lack of detailed figures especially on musculature and articulation makes interpretation difficult, and *Australomya* remains a very poorly defined taxon, with no adequate diagnosis or clear distinction offered. Because the type species *hillae* Runnegar was characterized chiefly by its narrow extended shape, it naturally has a less extended posterior gape, and less developed posterior pallial sinus. Logically this might suggest *Myonia*, as noted by Waterhouse (1980a), but the overall shape appears to support an alliance with *Vacunella*. Confusingly, Runnegar (1969, p. 288) reported "an indistinct tooth in the right valve, but for all practical purposes edentulous" and the hinge was not figured or fully documented. Other species referred to *Australomya* by Runnegar (1969) were *Myonia* cf *waterhousei* Dun 1932, ?*Vacunella dawsonensis* Runnegar, 1967 and *Myonia sulcata* Runnegar, 1967. Runnegar (1969, p. 285) also suggested that ?*Sanguinolites amatopensis* Thomas from Peru might belong to *Australomya*. Morris et al (1991, p. 66) dismissed this suggestion and placed the species in *Myofossa* (*Ragozinia*).

Updating his view of *Australomya*, Runnegar (1974, p. 928-9) asserted that "Waterhouse's concept of *Vacunella* is an elongate shell with a shallow pallial sinus. In part this may be due to a different interpretation of the morphology of the type species (compare Waterhouse 1967c, fig. 2a; Waterhouse 1969a, fig. 15c with Runnegar 1966, fig. 1a; 1967, fig. 3c) and in part due to the fact he includes species such as *Australomya waterhousei* (Runnegar 1967) in *Vacunella* (Waterhouse 1969a, fig. 15) [Punctuation and key letters for reference dates slightly changed]. Runnegar's presentation is dubious, to say the least, and possibly reflected his need to justify *Australomya*. The diagrams of Waterhouse (1969a, text-fig. 15, p. 36, including 15c) show comparatively high shells, no more elongate than in Runnegar's text-figures. Runnegar's own figures of *Vacunella* include several specimens (Runnegar 1967, pl. 8, fig. 1, 7) that are as high as the specimen of Waterhouse (1969a, pl. 3, fig. 6) and one specimen (Runnegar 1967, pl. 9, fig. 15) of *Vacunella* that is much more elongate than any figured by Waterhouse (1969a). It is this sort of dissonance, or gap, between his text which explains his visualization and thinking, both about other people's work and the actual material as illustrated, that I find so disconcerting. As Waterhouse (1969a) showed in a number of photographs, the shape of the species varied considerably even within collections from any one locality. Nor does Runnegar's assertion that *Australomya sulcata* (Runnegar) was an elongate slender species withstand examination. His own figures (1967, pl. 7, fig. 2, 4, 6) show high short specimens that are moderately inflated (Runnegar 1967, pl. 7, fig. 3, 5) and even the holotype differs little in overall proportional dimensions from the holotype of *Vacunella curvata*. His analysis misrepresents the nature of the Waterhouse understanding, and misrepresents the nature of the Waterhouse figures - and overlooks, or misrepresents, his own figures! If shape is the all-important criterion, following the text in Runnegar (1974), then *sulcata* must be excluded from *Australomya*.

Another species said to be elongate and low was cf *waterhousei* Dun of Runnegar (1967). This species is represented by many comparatively high specimens, and some elongate shells of moderate inflation, as may be seen from perusing Runnegar (1967, pl. 10). This species has a posterior gape and shallow but distinct posterior sinus as in *Vacunella*.

The other species allocated to *Australomya* was *Vacunella? dawsonensis* Runnegar (1967, pl. 11, fig. 1-8). This is close to the type species *hillae* in shape, with shells ranging from slender to moderately inflated. But it has a distinct pallial sinus and posterior gape, which supposedly distinguished *Vacunella* from *Australomya*.

Here it is proposed to synonymize *Australomya* with *Vacunella*. The type species is variably elongate to high, slender as in *dawsonensis*, and distinguished by having weak if any pallial sinus. The overview by Runnegar (1974) is inaccurate and unsatisfactory. The species *dawsonensis* and *waterhousei* show no significant difference from *Vacunella*. The species *hillae* and *sulcata* do allegedly lack a pallial sinus (on the basis of few specimens) but may show posterior gape, and are not known to differ in aspects of musculature or hinge or shell structure from *Vacunella*. Uncertainties remain, because the type species was so incompletely described. The synonymy puts the onus on workers who wish to defend the genus to find some firm and consistent morphological difference to distinguish it from *Vacunella*.

An observation that *Australomya hillae* approaches species of *Sedgwickia* by Runnegar (1974, p. 932) opens up intriguing possibilities, although Runnegar himself preferred to regard the similarity as due to convergence. However Morris et al (1991, p. 61) showed that Runnegar had misinterpreted *Sedgwickia*, and had confused with that genus specimens of *Myofossa* Waterhouse. The holotype of the type species of *Sedgwickia*, *S. attenuata* M'Coy was judged to be so small and crushed that it was uninterpretable. They recommended that the species and genus be rejected as a nomen dubium.

Genus *Vacunella* Waterhouse, 1965

The genus *Exochorhynchus* Meek & Hayden, 1864 is close in appearance to *Vacunella*, but much more prosocline. Runnegar (1974) dismissed *Exochorhynchus* as based on deformed specimens, but it was recognized by Astafieva-Urbaitis (1981) in Russia, and by Shi & Waterhouse (1996) in Arctic Canada. Morris et al (1991, p. 80) allowed that *Exochorhynchus* showed considerable similarity to *Vacunella*, but considered this was by convergence, with *Vacunella* evolving independently from *Myonia*. The demonstration by Morris et al (1991) that a genus such as *Myofossa* can range from Early Carboniferous of Europe into Early Permian etc of Western Australia does not support that thesis. Morris et al (1991) placed *Exochorhynchus* in Undulomyiinae, whereas Waterhouse (1987b) put the genus in Vacunellinae, as is supported by the absence of the lunule. The obvious difference between the two genera, pending better understanding of musculature and shell structure, lies in the very anterior position of the umbones in *Exochorhynchus*. In this regard, *Sanguinolites etheridgei* de Koninck from east Australia has umbones placed well forward, although the upright shape is closer to that of *Vacunella*, and Astafieva-Urbaitis referred the genus to *Cuvanella*.

***Vacunella curvata* (Morris, 1845)**

Text-fig. 12

1845 *Allorisma curvatum* Morris, p. 270, pl. 10, fig. 1.1965c *Vacunella curvata* (Morris); Waterhouse, p. 377.1983 *V. curvata* (Morris); Waterhouse & Jell, p. 252, pl. 5, fig. 10. (See for synonymy and stratigraphic distribution).1987b *V. curvata* (Morris); Waterhouse, p. 173, pl. 14, pl. 14, fig. 7.1989 *V. curvata* (Morris); Dickins, p. 69, pl. 1, fig. 15.

LECTOTYPE: NHM PL 3692, figured by Morris (1845) SD Waterhouse (1965c), from Gerringong Volcanics (Broughton Formation), south Sydney Basin, New South Wales.

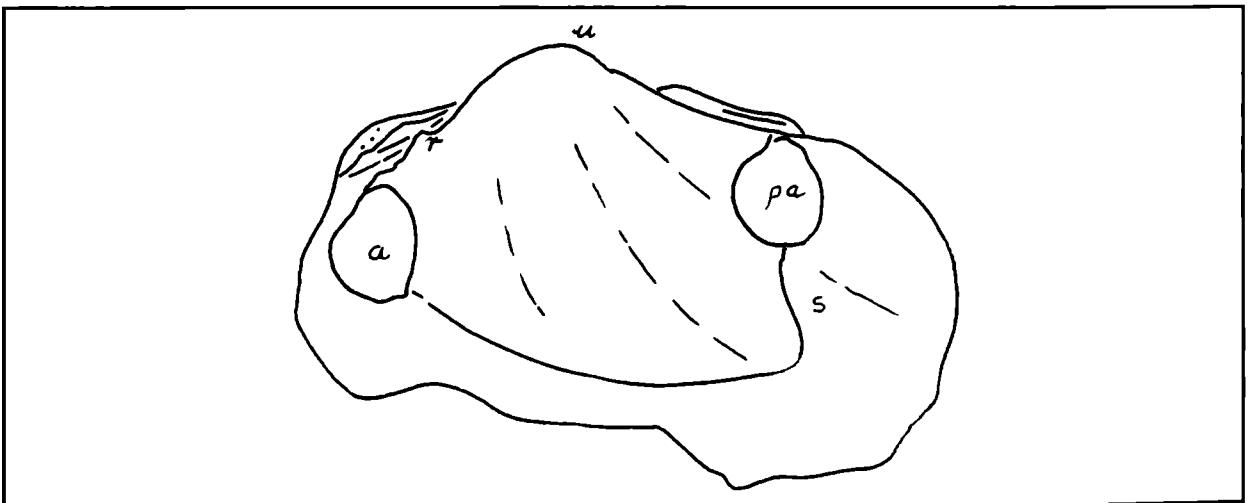
DIAGNOSIS: Large moderately inflated shells of variable height and length with substantial posterior gape, slight pedal gape, no carination, umbones placed towards anterior.

MATERIAL: One well preserved left valve TM 7899 and fragments from D44/f132 (GS 15221), *Terrakea elongata* Zone, Mangarewa Formation, Wairaki Downs.

DIMENSIONS IN MM:

Specimen	Length	Height	Width	Anterior length	Umbonal angle
TM 7899	88	?63	23	28	110°

DESCRIPTION: Moderately large, umbo broad, anteriorly placed, orthogyrous, anterior shell most extended below mid-height, posterior most extended at mid-height, umbonal ridge convex, sloping at 35° from hinge, weak sinus lies below umbo, sloping posteriorly, subvertical. Weak posterior gape. Ornament of moderately well defined growth lamellae, and 3 prominent growth steps. Anterior sublunular depression, posterior hinge long with prominent groove, affected by growth steps. Two tiny pedal muscle scars lie under umbo, prominent anterior retractor scar, and large adductor scar, pallial line weakly impressed, with posterior sinus, large diffuse posterior adductor, with dorsal accessory retractor scar.



Text-fig. 12. *Vacunella curvata* (Morris) internal mould of left valve TM 7899 from D44/f132, Mangarewa Formation, x 1. a - anterior adductor, pa - posterior adductor, r - anterior retractor, s - pallial sinus, u - umbo.

Class GASTROPODA Cuvier, 1797
 Order PROSOBRANCHIATA Milne-Edwards, 1848
 Suborder PLEUROTOMARIINA Cox & Knight, 1960
 Superfamily PLEUROTOMARIOIDEA Swainson, 1840
 Family EOTOMARIIDAE Wenz, 1938
 Subfamily EOTOMARIINAE Wenz, 1938
 Genus *Neoplatyteichum* Maxwell, 1964

TYPE SPECIES: *Neoplatyteichum dickinsi* Maxwell, 1964.

DIAGNOSIS: Turbiform gastropods, upper whorl moderately convex, five whorls preserved, selenizone moderately to weakly defined, concave, bordered by ridges, placed below upper third of whorl and above mid-height. Ornament of spiral threads and weak collabral lirae, deep sutures emphasized by low convex shelf at suture. Whorl below suture with weak shoulder to base, outer whorl may on some specimens be planar in spire, base anomphalous.

DISCUSSION: A number of species from Australasia that assigned to *Mourlonia* de Koninck come close to this genus in upper whorl profile. The type species of *Mourlonia*, *M. carinata* (Sowerby) has more expanding whorls and less convex upper whorl, and spiral threads in the selenizone (Dickins 1976).

Neoplatyteichum impressa (Waterhouse, 1966)
 Pl. 9, fig. 9

- 1966c *Mourlonia?* *impressa* Waterhouse, p. 178, pl. 1, fig. 1-4.
 1978 *M. impressa* Waterhouse; Suggate et al, text-fig. 4.5, fig. 9, 12.
 1981 *M. impressa* Waterhouse; Speden, pl. 5, fig. 9, 12.
 1986 *M. (Mourlonia) strzeleckiana* (not Fletcher); Dickins et al, pp. 297-8.
 1989 *M. (Mourlonia) strzeleckiana* (not Fletcher); Dickins, p. 69, pl. 2, fig. 12 (not fig. 13-18 = *Platyteichum loratum* Waterhouse).
 1993 *M. (M.) strzeleckiana* (not Morris); Johnston, p. 27.
 1996 *M. (M.) cf strzeleckiana* (not Morris); Johnston, p. 37.

HOLOTYPE: TM 3877, figured by Waterhouse (1966c, pl. 1, fig. 1-3), repeated in Suggate et al (1978), Speden (1981) and Dickins (1989, pl. 2, fig. 12) OD, from P26/f8513 (GS 9477), Croisilles Ophiolite Complex, Nelson.

DISCUSSION: The gastropod species named *Mourlonia?* *impressa* by Waterhouse (1966c) came from the Croisilles Ophiolite Complex (Waterhouse 1964a) near the road above Elaine Bay and Croisilles Harbour, northeast Nelson. The specimens were discovered by an extraordinary feat of alertness and good eyesight on the part of Mr Jack Stanley, Nelson. He was driving along the gravel road, and saw the specimens through the rear view mirror! We collected them together. Later, further material was collected by a party that included Drs C.A. Landis and M. R. Johnston, and was reidentified by Dr J. M. Dickins, apparently at the same locality. The party overlooked the earlier work, but I drew attention of the authors to *M?* *impressa* at the refereeing stage. Dickins identified the gastropod species as *Mourlonia strzeleckiana* (Morris), and he, with Johnston (1996) and other workers, claimed that the gastropod supported the thesis that the Croisilles rocks were a melange derived from oceanic crust, and reworked to incorporate what was claimed to be a "Late" Permian gastropod. Emplacement of the Croisilles rocks was deemed to be as late as Cretaceous according to Johnston (1993, 1996). Dickins (1989, p. 71) stated that "he had little doubt of the close relationship of *M?* *impressa* with the specimens of *M. (M.) strzeleckiana* described "... from the upper Blenheim rocks of the Bowen Basin.

There are major errors in the accounts by Dickins et al (1986), Dickins (1989), and Johnston (1993, 1996). The species *strzeleckiana* belongs to *Mourlonopsis*, not *Mourlonia*, and is of Middle Permian Guadalupian age, not Late Permian Lopingian age (see Jin et al 1997a, b, Wardlaw 2000). The Morris species is not at all close to the Croisilles gastropod, in that it is much larger and has more swollen whorls, with high-placed selenizone, and no sign of fine closely spaced spiral ribs. This is shown in present figures of the type specimen. The type is somewhat decorticated, but fragments of the original exterior remain, and these are smooth. Some specimens of *Mourlonopsis* do have faint traces of spirals according to Fletcher (1958), but none have ever been figured. I have examined collections of the species kept at the Australian Museum, Sydney, from Wollongong, Black Head (Gerringong), Wyro, Kiama etc in the south Sydney Basin. I was able to see faint spiral ribs in AMF 21278 from Black Head, Gerringong, and AMF 21295 and 21436 have faint suggestions. The ribs are low and well spaced, with only 6 over the upper whorl, compared with about 16 narrow closely spaced ribs over the much smaller upper whorl of *impressa*. Other specimens of *strzeleckiana* show no spiral ornament. Therefore the Croisilles gastropod cannot be convincingly identified with the Middle Permian species *strzeleckiana*. The geological interpretation of the Croisilles complex by Johnston (1993, 1996) and others is therefore jeopardized to some extent, because they relied, at least

partly, on the alleged Late Permian age of the gastropod to help prove that the Croisilles had been derived from the Dun Mountain ultramafic suite.

The species *impressa* is now referred to *Neoplatyteichum*. The type species, *Neoplatyteichum dickinsi* Maxwell (1964, pl. 4, fig. 18-24), is known so far only from the lower Rands Formation of the Yarrol Basin, and deemed to be Late Carboniferous by Maxwell and also Waterhouse (1987b, 1989), but possibly as young as Early Permian. The genus is not that close to *Platyteichum*, having a different whorl profile and less emphasized selenizone. The holotype (Maxwell 1964, pl. 4, fig. 18, 19) has well rounded whorl profile, though some other specimens suggest a tripartite subdivision of more planar surfaces, especially in Maxwell (1964, pl. 4, fig. 22). In the spire of the New Zealand form a somewhat similar appearance is suggested. The selenizone is not clearly defined on illustrations of *dickinsi* because the rims are low, though clearly seen on the actual specimens, formerly at the University of Queensland and now in the care of the Queensland Museum. In *N. impressa* the selenizone lies just above mid-height, and in *N. dickinsi* the selenizone is just above mid-height in the holotype, but somewhat higher (near upper third) in the specimen of Maxwell (1964, pl. 4, fig. 22). Spiral ornament is as fine as in the New Zealand form.

Mourlonia (Mourlonia) sp. reported by Runnegar (1969, pl. 18, fig. 15) from the Wasp Head Formation (or lower Conjola Formation) at the south end of the Sydney Basin, New South Wales, shows some approach. The age is basal Permian, possibly Asselian Stage, being accompanied by *Eurydesma* and *Ingelarella elongata*. It therefore is of the same age as the beds at Alum Rock, New England orogen, which has yielded a basal Permian SHRIMP age (Waterhouse 2000b). The Australian form has comparable spiral ornament and globose upper whorl, but the spire is broader, collabral ornament fainter, selenizone well defined by two rims, and possibly the outer whorl rounds more abruptly on to the base. It is not fully clear, but the selenizone seems, from the figure, to lie at the top of a median vertical band on the whorl that is better defined than in *M? impressa*. With only one specimen figured, it is difficult to know if these differences are meaningful, and to what extent they have been affected by distortion.

Mourlonia aifamensis Dickins & Skwarko (1981, pl. 6, fig. 10, 11, 14, 15) from the Lower Permian Aifat Formation of Irian Jaya has a raised selenizone well above mid-height and low somewhat fewer spiral ribs. It comes moderately close, and may be assigned to the same genus.

POSSIBLE AGE: From available evidence, the gastropod points to a likely basal Permian or Late Carboniferous age. The Croisilles complex is otherwise poorly dated, and radiometrically dated plagiogranites from the Croisilles rocks were intruded only in a late phase well after accumulation of the bulk of the rocks (Sivell & McCulloch 2000), so that plagiogranite ages stressed by Kimbrough et al (1992) are significantly too young to be relevant. Atomodesmid fragments are known, suggesting a likely time-frame of Late to Middle Carboniferous to possibly as young as Early Triassic. A more precise age is offered from radiometric dating of volcanics in the Patuki ophiolite suite. Sivell (1988) noted that some of the Croisilles volcanics compared closely with Stage 2 Patuki volcanics, and the latter have yielded a Late Carboniferous age from Nd-isotope data at 308 ± 12 Ma. In so far as younger Stage 3 Patuki rocks, of different geochemical signature and matched in the Croisilles suite, gave an value of 278 ± 4 Ma (Early Permian). An Early Permian to Late Carboniferous age for the Croisilles gastropod appears feasible.

Genus *Mourlonopsis* Fletcher, 1958

TYPE SPECIES: *Pleurotomaria strzeleckiana* Morris, 1845.

DISCUSSION: Dickins (1989) did not recognize the validity of this genus, referring the type species to *Mourlonia* de Koninck, 1883. Fletcher justified his genus on the basis of the height of the spire, and Dickins (1989, p. 69) disputed this, stating that the height of the spire seemed rather variable, without providing any justification, or citing any examples. *Mourlonopsis strzeleckiana* clearly has not only a higher spire, but a much more fully rounded upper whorl compared with the type species of *Mourlonia* (see Dickins 1976), and the ornament differs, *Mourlonia* having better defined spiral ornament than seen in *Mourlonopsis*. Dickins in his articles has taken a very conservative approach in gastropod classification, as noted by Batten (1967) in criticizing the Dickins approach. Dickins has never been able to refute Batten's analysis.

Mourlonopsis strzeleckiana (Morris, 1845)

Plate 10, fig. 2 - 4

1845 *Pleurotomaria strzeleckiana* Morris, p. 287, pl. 18, fig. 5.

1858 *P. strzeleckiana* Morris; Plews, pl. 3, fig. 4.

1951 *Mourlonia strzeleckiana?* (Morris); Campbell, p. 33, pl. 1, fig. 1, 2.

1952 *Pleurotomaria* aff *strzeleckiana* Morris; Fletcher, p. 17 (not pl. 2, fig. 1, 2 = *Platyteichum*).

1958 *Mourlonopsis strzeleckiana* (Morris); Fletcher, p. 129, pl. 9, fig. 9-11.

1963b *M. strzeleckiana* (Morris); Waterhouse, p. 122, text-fig. 2A, 21, 22, table 4.

HOLOTYPE: PL 3921 figured by Morris (1845) and herein, kept at Natural History Museum, London, by monotypy, from Illawarra or Glendon, Sydney Basin, New South Wales.

DISCUSSION: Through the kindness of the Natural History Museum, London, the type specimen of *Mourlonopsis strzeleckiana* can be refigured. The exterior is decorticated, but fragments of the original shell surface show that spiral ornament is minimal, in affirmation of the understanding of the genus and species according to Morris (1845), Campbell (1951), Fletcher (1958) and Waterhouse (1963b). A few fine spiral threads have been seen on some specimens (Fletcher 1958), and some are reported in the preceding discussion on *Neoplatytechum impressa*, but they are not comparable with the regular closely spaced numerous ribs of *impressa*. In addition, *strzeleckiana* is very much larger than *impressa*, although with a comparable number of whorls, and differs in whorl profile with more pronounced selenizone and other differences. Dickins (1989) misrepresented the species as characterized by well defined spiral ornament, and seemed to discount the various differences in whorl profile, position of selenizone, size, and other parameters. As a result he misidentified *Mourlonia impressa* Waterhouse, 1966c. The errors appear to have arisen from his confusion of a species of *Platytechum* (see below) with *Mourlonopsis strzeleckiana*. Correction to these misidentifications helps unravel the "Late" Permian or even much younger age assigned by Dickins et al (1986), Dickins (1989) and Johnston (1996) to the Croisilles ophiolite suite. They claimed that the Croisilles rocks were much younger than the Dun Mountain protolith. But reinterpretation of the gastropod, and geochemical studies summarized by Sivell & McCulloch (2000) show that Waterhouse (1964a) and Waterhouse & Sivell (1987) were right to regard the Croisilles as older, not younger, than the Dun Mountain protolith.

Genus *Platytechum* Campbell, 1953
***Platytechum loratum* Waterhouse, 1963**
 Pl. 9, fig. 10

1963b *Platytechum loratum* Waterhouse, p. 131, text-fig. 4, 37-50.

1987b *P. loratum* Waterhouse; Waterhouse, p. 180, pl. 12, fig. 4, 17.

1989 *Mourlonia (Mourlonia) strzeleckiana* (not Morris); Dickins, pl. 2, fig. 13-18.

HOLOTYPE: TM 3251 figured by Waterhouse (1963b, text-fig. 37, 39, 49) OD from D44/f9623 (GS 6072), *Terrakea elongata* Zone, Mangarewa Formation, Wairaki Downs.

DIAGNOSIS: Spire of variable height, lower than in some species, loosely to tightly coiled whorls in spire, spiral costae numerous, close-set, somewhat variable in number and definition, upper outer whorl more convex than some other species, selenizone prominent and sited above concave band of outer whorl, exposed in spire well above suture.

MATERIAL: This species is represented by many specimens, and is listed from many localities in the tables of occurrence, provided in the accompanying volume. A specimen OU 18310 is figured from D44/f310, lower *Echinalosia discinia* Zone, Letham Formation, Wairaki Downs.

RESEMBLANCES: *Platytechum loratum* differs in a number of ways from the type species *P. costatum* Campbell, 1953 from the Ingelara beds (s.l.) of the Denison Trough in central Queensland. The upper whorl above the selenizone is more convex towards the aperture as a rule, although not invariably, and the upper whorl has a well developed sutural shelf, rather than lapping on to the penultimate whorl. As well the lower aperture and growth-lines arch more forward below the selenizone. The selenizone is more prominent, and the concave band below the selenizone tends to be higher and more conspicuous than in the type species. Overlap of whorls is much less in the spire, so that the selenizone lies well above, rather than just above, the suture. The base has an open umbilicus in *loratum*, and may be covered in *costatum*.

DISCUSSION: Well preserved specimens were wrongly assigned by Dickins (1989, pl. 2, fig. 13-18) to *Mourlonopsis strzeleckiana* from the MacMillan Formation in the upper Blenheim Subgroup of the Blenheim area in the Bowen Basin, central Queensland. The whorls of the specimens are globular in the spire, and flattened over the body chamber above the selenizone, with steep subvertical segment below, and the selenizone is placed just above mid-height. Slender but firm collabral growth lirae and slightly stronger spiral ribs are well developed. By contrast, *Mourlonopsis strzeleckiana* lacks such distinct fine spiral ribs, and has weaker collabral ornament. The whorl profile of *Mourlonopsis* also differs, being more swollen in both spire and body whorl, and the selenizone is placed higher on the whorl, and is raised. The MacMillan Formation specimens may be referred to *Platytechum* Campbell, 1953. They are close in ornament to *P. coniforme* (Etheridge 1892, pl. 41, fig. 5; Waterhouse 1987b, pl. 12, fig. 13-16) from the lower Flat Top Formation, Bowen Basin. Etheridge's species varies somewhat in whorl profile, and may have more of the shelf below the seam, though this varies a little, and the spire whorls and the ornament are quite close. *Platytechum costatum* Campbell, 1953, from the Ingelara Formation is close to *coniforme*, or a junior synonym, as discussed by Waterhouse (1987b, p. 179). In that discussion, it was noted that changes in identification proposed by Dickins (1961b, in Malone et al 1966, p. 72) were induced by changes in his interpretation of correlations, and in turn, his correlations turned out to be incorrect.

The spire in Dickin's MacMillan specimens is particularly like that of *Platytechum loratum* Waterhouse, 1963b, showing the selenizone in the high spire and the concave band below the selenizone on the body whorl, and arched lower aperture. The ornament is sharply defined in the Australian specimens, and some

New Zealand individuals show comparable ornament, whereas the New Zealand types are slightly decorticated. Although some specimens of *loratum* have a more swollen body whorl, others are very close to the small suite figured by Dickins. Fossils from the MacMillan Formation include *Glyptoleda flexuosa* Waterhouse, *Vacunella curvata* (Morris), and *Ingelarella havilensis* Campbell, which are also found in the *Terrakea elongata* Zone in the upper Mangarewa Formation, Wairaki Downs.

The species *loratum* appears to have been long-lived and widespread in southern New Zealand, to judge from the record in the Letham and Mangarewa Formations of the Wairaki Downs, and extended into the Bowen Basin in the MacMillan Formation. However closer study is required to confirm the Letham occurrences, and detailed analyses may show different lineages and possibly different species. *Platyteichum loratum* was reported by Waterhouse (1987b, p. 180, pl. 12, fig. 4, 17) from the *Echinalosia ovalis* Zone in the Flat Top Formation, as specimens showing an open umbilicus and selenizone well exposed in the spire.

Genus ***Mellarium*** Waterhouse, 1960
Mellarium mutchi Waterhouse, 1960

1917 *Platyschisma* sp. Trechmann, p. 58, pl. 5, fig. 9.

1960a *Mellarium mutchi* Waterhouse, p. 272, text-fig. 3-12.

1960a *Mellarium* cf. *mutchi* Waterhouse; Waterhouse, p. 276, text-fig. 13, 14.

?1963b Family, gen. & sp. indet. Waterhouse, p. 609, text-fig. 3, 50.

HOLOTYPE: Specimen TM 2040, figured by Waterhouse (1960a, text-fig. 3-5) OD from D44/f9620 (GS 6066), Middle Triassic, north Wairaki Downs.

DIAGNOSIS: Turbiniform globular shells, ornamented by strong spiral costae and weak collabral growth striae, base cryptomphalous, slit sited above mid-whorl, one fifth of circumference, selenizone convex, inner aperture may be strongly thickened.

DISCUSSION: This is a very characteristic gastropod that may prove highly useful for correlation. Locality GS 6326 (D44/f9670), a few metres stratigraphically below the type locality of *Mellarium mutchi* at GS 6066, has yielded ammonoids described by Kummel (1960), as well as undescribed *Sturia*, identified by the writer. No *Daonella* are known. There are fragments of *Mellarium mutchi* from younger levels. The worn and deformed specimen compared with *mutchi* by Waterhouse (1960a) may be regarded as conspecific. It comes from the Countess Formation, regarded as Permian by Grindley (1958) and Hyden, Begg, H. J & J. D. Campbell (1982). The gastropod contradicts this, supporting a Middle Triassic or Anisian age, as reinforced by the bivalve *Permophorus obovata* Waterhouse, 1979d. A Triassic age also seems to have been accepted by Aitchison et al (1988).

So-called *Platyschisma* of Trechmann (1917) also looks like *Mellarium mutchi*, but is poorly preserved and requires further study, so that at present there is no reliable identification. It is found amongst limestone blocks in the Pig Valley Formation near the base of the Te Mokai Group, near the junction of Lee and Wairoa Rivers, east Nelson. Early Triassic ammonoids are also found (Owen 1991). As interpreted by Waterhouse (1993), all, including the *Mellarium*, have been reworked, probably from Brook Street Terrane, so that the age is younger than Anisian.

Genus ***Collabrina*** Waterhouse, 1978
Collabrina sp.
Pl. 9, fig. 12, 13

MATERIAL: One specimen from D44/f9621 (GS 6070), *Spiriferella supplanta* faunule, 2 specimens including OU 18308 from D44/f315, and single specimens from D44/f310 (OU 18309) and D44/f307, *Echinalosia discinia* Zone, Letham Formation, Wairaki Downs.

DISCUSSION: These specimens have a high spire and swollen upper whorl profile, reminiscent of *Platyteichum spiroloxum* Waterhouse, 1963 from the upper Takitimu Group, but, unlike that species, apparently devoid of spiral ribs. Other New Zealand genera of Permian age that fall moderately close, namely *Bicarinella* Waterhouse and *Spirovallum* Waterhouse, differ in having a concave upper whorl profile. *Mourlonia* (*Woolnoughia*) Dickins, 1963 from Early Permian of Western Australia has spiral ornament, and is phaneromphalous, with selenizone placed low on the whorl.

The overall appearance of the specimens suggests the high-spired genus *Collabrina* Waterhouse, a genus which displays collabral ornament, broad concave selenizone placed near mid-height, and anomphalous base. The type species *Collabrina lunulata* Waterhouse, 1978 comes from Late Permian of the Nepal Himalaya, and the genus has been found in the ?Late Carboniferous Fairyland Formation of southeast Bowen Basin, as *Collabrina parva* (Wass, 1967), according to Waterhouse (1987b).

Subfamily **NEILSONIINAE** Knight, 1956
Tribe **SPIROVALLINI** new

NAME GENUS: *Spirovallum* Waterhouse, 1963.

DIAGNOSIS: Selenizone sited on prominent peripheral flange, slit short, ornament comparatively simple and collabral with simple or bundled radial lirae. Base anomphalous.

DISCUSSION: Yochelson (1966) pointed out that *Nordospira* Yochelson, which is a close ally if not synonymous with *Spirovallum*, was distinguished from Eotomariidae and Pleurotomariidae by its selenizone and anomphalous base. Neilsoniinae are similar in being anomphalous with predominant collabral ornament, but are small with more elaborate selenizone that is deeply concave and bordered by underlying and rarely overlying spiral carina.

Genus ***Spirovallum*** Waterhouse, 1963

TYPE SPECIES: *Spirovallum liratum* Waterhouse, 1963.

DISCUSSION: This genus was proposed for two species from New Zealand by Waterhouse (1963b). In 1966 Yochelson erected a new genus *Nordospira* for two Arctic species, of which one, the type, appears very close to *Spirovallum*. The type species *N. henningsmoenae* Yochelson (1966, pl. 1, fig. 1-3) from the late Cisuralian Spiriferkalk at Tempelfjorden, Spitsbergen, is high-spired with radial ornament of fine collabral lirae, and narrow concave selenizone on a flange-like expansion near mid-whorl. The base is anomphalous. The most conspicuous difference between *Spirovallum* and *Nordospira* lies in the profile of the whorl above the slit-band, being flat to concave in *S. liratum*, and convex in *N. henningsmoenae*. This difference is not entirely consistent, because individuals of *Spirovallum* have flat to gently convex upper whorl. The selenizone in *Nordospira* has a concave surface unlike that of some *Spirovallum*, but this varies in *Spirovallum*, and although there are various differences, overall the two are very close, and some of the differences may be specific rather than generic.

In the second *Nordospira* species described from Alaska, *N. vostokovae* Yochelson (1966, pl. 1, fig. 4-6), less of the penultimate whorl is overlapped by the outer whorl. It has a lower spire and the upper whorl is more convex. Below the selenizone lies a concave band, somewhat higher than the selenizone, and then a well formed shoulder. Yochelson (1966) allowed the possibility of it belonging to a different genus, and this is deemed probable. Indeed *Nordospira yochelsoni* Sabattini, 1995 from the Early Permian *Tuberculatella* Zone of Argentina shows similar attributes, and latex moulds she kindly sent me suggest the species could be allied with the Alaskan species *vostokovae* as a distinct genus, of a different tribe. It has raised deeply concave selenizone, concave upper whorl, and fine radial threads. Dr Sabattini (e-mail 7 October 2000) has examined moulds of the Alaskan species and also believes that a separate, probably new genus is involved. It is moderately close to the middle or upper Carboniferous species *Peruvispira kempseyensis* Campbell (1962, pl. 12, fig. 1-4) from glacial rocks in New South Wales. This species has sharply defined radial lirae, concave upper whorl, and subplanar outer band below the selenizone, without the third peribasal carina typical of *Peruvispira*. In many respects her species is like *Pseudobaylea* Dickins, 1963, from Early Permian of Western Australia. This form was assessed by Dickins (1963) as a subgenus of *Platyteichum* Campbell, but differences are substantial. *Pseudobaylea* has a convex upper whorl profile.

Spirovallum* sp. aff *liratum Waterhouse, 1963

aff 1963b *Spirovallum liratum* Waterhouse, p. 607, text-fig. 2, 45-49, table 10.

HOLOTYPE: TM 3154, figured by Waterhouse (1963b, text-fig. 47-49) OD from D44/f9524 (GS 7803), *Spinomartinia spinosa* Zone, in a boulder of Hilton limestone in Tertiary conglomerate, southeast of Waituna Station, north Takitimu Mountains.

DIAGNOSIS: Selenizone sited at periphery, flat on early whorls, convex in later formed whorls, not bordered by prominent carina. Ornament of fine close-set radial threads.

MATERIAL: Six fragmentary specimens from D44/f376, *Spinomartinia spinosa* Zone, Hilton Limestone, Wairaki Downs.

DESCRIPTION: Specimens obscure, spire broad with estimated angle of 70-80° in two specimens, and the angle in the least deformed specimen about 75°, upper whorl convex below suture, then concave, selenizone lies at periphery on elevated ramp, bordered by low carina each side, gently concave with well defined lunulae, upper whorl ornamented by strong close-set lirae, about 5 in 1mm, arching forward, and inclined backwards from seam at about 60°. Base gently concave, apparently anomphalous, ornamented by lirae, gently convex. Penultimate whorl and earlier whorls overlapped to base of selenizone in the spire.

RESEMBLANCES: These specimens fall only moderately close to *Spirovallum liratum* Waterhouse, 1963b from a boulder in Tertiary conglomerate. The spire is broader, and the upper whorl is concavo-convex, not concave, and the lirae are slightly stronger, and selenizone concave. Insofar as the present specimens all come from one stratigraphic level, the differences may prove to be subspecific or specific. *Nordospira* Yochelson is close in the profile of its upper whorl, which is either flat or convex, and its selenizone has a concave surface.

***Spirovallum?* sp.**
Pl. 9, fig. 11, text-fig. 11c, d

MATERIAL: One specimen TM 8200, preserved as outer whorl and part of penultimate whorl, from G45/f8612 (GS 5078), *Plekonella multicosata* Zone, Arthurton Group near Arthurton.

DESCRIPTION: Specimen preserved as an internal and external mould. Upper whorl concave, slit-band placed below mid-height at the periphery, base convex and anomphalous. Surface a little worn, showing very faint radial ornament, and very weak closely spaced spiral ornament, selenizone narrow, very gently convex, bordered by two low carina.

RESEMBLANCES: This specimen compares in some respects with *Spirovallum liratum* Waterhouse (1963b, text-fig. 47-49) known from a boulder in Tertiary conglomerate, which also bears the key zonal species *Spinomartinia spinosa* Waterhouse. The present specimen comes from slightly older beds of the *Plekonella multicosata* Zone, and is distinguished by the fine spiral ornament.

Tribe **NEILSONIINI** Knight, 1956
Genus ***Peruvispira*** Chronic, 1949
***Peruvispira* sp. B**

1963b *Peruvispira* sp. B Waterhouse, p. 598, text-fig. 32, 33, table 5.

Three specimens from D44/f117 (GS 15228), Glendale Formation, Wairaki Downs, show the high spire, fine costellae and faint peribasal carina of this form. It was originally described from the *Plekonella multicosata* Zone of the Arthurton Group.

Class CEPHALOPODA Cuvier, 1797

Several Middle Triassic taxa are named here, and fuller accounts will follow in future publications.

Order CERATITIDA Hyatt, 1900
Suborder CERATITIDINA Hyatt, 1894
Superfamily **CERATITOIDEA** Mojsisovics, 1879
Family **BEYRICHITIDAE** Spath, 1934
Genus ***Beaumontaria*** new

DERIVATION: Named for Beaumont Station, near Ohai, western Southland.

TYPE SPECIES: *Beaumontaria grebneffi* n. sp., here designated

DIAGNOSIS: Moderately evolute shells with early whorls ovally triangular in section, broadening dorsally, developing into ovally subrectangular cross-section with well rounded ventral shoulders and convex to gently convex venter, no ventral keel; strongly tuberculated, the first stage with well defined ribs branching from umbilical nodes and recurving at ventral margin, second stage with broad ribs branching from bullate to spinose lateral tubercles, and marginal tubercles, no umbilical tubercles, mature body chamber with low or no ribs and no or only lateral bullae, markedly egressive. Suture beyrichitid ammonitic.

DISCUSSION: *Favriticeras* Bucher, 1992 from the Middle Anisian of United States is moderately close in appearance but has different distribution of bullae and nodes, and the saddles of the suture are less denticulate.

An overview of other genera reveals several that show external convergence, especially at the fully developed mature stage. Some species of *Frechites* Smith, 1932 look moderately close. *F. nevadanus* Mojsisovics, 1886 as figured by Smith (1914, pl. 15, fig. 6, pl. 64, fig. 1-14, pl. 65, fig. 1-13) and Silberling & Nichols (1982, pl. 19-25, pl. 10, pl. 11, fig. 1-6) displays prominent lateral bullae on heavy ribs that fork ventrally, to bear a row of smaller bullae along the edge of the broad venter. This species comes from the *Parafrechites meeki* Zone of the Humboldt Range, Nevada, the middle of the three Upper Anisian zones recognized by Silberling & Nichols (1982). The Nevadan specimens are much smaller than the New Zealand genus and are more heavily ribbed. Other North American species assigned to *Frechites* show some approach. From the upper Anisian *Frechites chischa* Zone of British Columbia, *Frechites hamatus* Tozer

(1994, pl. 64, fig. 9-11) has a row of bullae, with suggestions of low tubercles near the venter, but the venter is tabulate, bullae less prominent and ribs more conspicuous.

Nevadites Silberling & Nichols, 1982 is another genus that shows prominent tubercles, as in the type species *N. hyatti* (Smith) from Anisian of western United States. The shell is very evolute, and ribs more numerous and prominent, compared with the New Zealand form.

***Beaumontaria grebneffi* n. sp.**

Text-fig. 13

DERIVATION: Named for Andrew Grebneff.

HOLOTYPE: OU 3978, text-fig. 12A, B, from D45/f7906, in unnamed unit of North Etal Group (Campbell 1994, text-fig. 21), Beaumont Station, Southland, here designated.

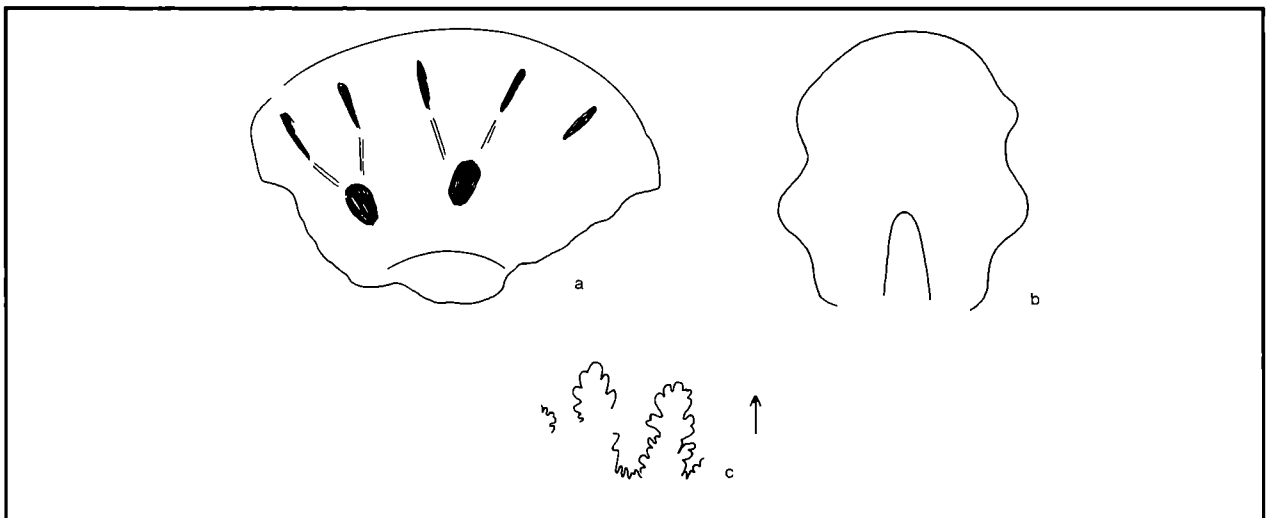
DIAGNOSIS: Large shells with whorl section trapezoidal at maturity, lateral bullae large, connected by two diverging ribs to large tubercles near ventral margin, outer whorl only with lateral bullae, early whorls with close-set ribs and row of umbilical bullae. Suture beyrichitid, saddles high, slender, deeply incised.

MATERIAL: More than 6 fragmentary specimens from D45/f7906, including OU 3978, OU 14636, 18364. Small specimens OU 14743 and 14954 from D45/f7995. OU 3253 and OU 14960 from D44/f9132 (Capil Formation of Begg 1981). OU 18383-19384 from D44/f9132, and further material from Middle Triassic of western Southland.

DIMENSIONS IN MM:

Specimen	D44	D	H	W	U
OU 14960	f9132	170	72	44	~60

DESCRIPTION: Shell distinctive, with heavy well spaced ribs and two rows of large bullae. One fragment is 18cm long, smooth aperturally, with umbilicus measuring 5.8cm across. Holotype OU 3978 shows a whorl 49mm high and 58mm wide, excluding knobs, subrectangular whorl-section, flanks steep and subparallel, venter broad, gently convex, a row of large tubercles aligned dorsal to the smooth venter, prolonged dorsally, up to 23mm apart along the row, and a second row closer to the umbilicus, roughly 28mm apart with higher rounded tubercles up to 15mm long. The dorsal lateral tubercles are linked by broad ribs diverging to ventral tubercles. In between these sets lies another ventral tubercle, prolonged into a rib dorsally, which fades before the umbilicus, and unconnected to dorsal bulla. The penultimate whorl is more rounded in section. Small specimens differ in appearance, being ornamented with close-set ribs raised along the umbilical edge, and no lateral or marginal tubercles. Specimen OU 1967 with whorl 10.5mm high has about 2-3 ribs in 5mm, raised at the umbilical edge, and forking just below tubercles. The whorls are ovally subtriangular in section, widest just below the umbilicus, with rounded venter. Specimen OU 3253 from D44/f9132 with whorl 12mm high has up to three ribs diverging ventrally from the umbilical tubercle, and they bend sharply from the aperture at the ventral margin. The umbilical row of tubercles persists in another specimen OU 3253 from D44/f9132 on a whorl 33mm high, and the ribs are straighter in outline, with two or three branching from a tubercle, and with occasional solitary rectiradiate ribs in between.



Text-fig. 13. *Beaumontaria grebneffi* n. gen., n. sp.

a, b. Lateral and whorl section diagrams of holotype OU 3978 from D45/f7906, showing two rows of tubercles joined by low broad ribs. x 1.

c. Part of ventral suture for OU 14636 from same locality, figured by Begg (1981, p. 203). x 1.

RESEMBLANCES: *Favreticeras rieberi* Bucher (1992, pl. 5, fig. 1-24, pl. 7, fig. 8, 9, text-fig. 13) from the middle Anisian *Balatonites shoshonensis* Zone, mainly in the Augusta Mountains of northwest Nevada, shows considerable approach, although the saddles are much less incised, and shells are much smaller, with two rows of bullae near the aperture in mature specimens, and a single umbilical row in smaller specimens. The whorls are more subrectangular to trapezoid in section, with marked ventral shoulders. Other species ascribed to *Favreticeras* by Bucher (1992) differ more in their tubercular ornament and ceratitic suture.

There is a superficial approach externally to *Paraceratites cricki* (see Silberling & Nichols 1982, p. 34, pl. 17, fig. 6-20) from the *Gymnotoceras rotelliformis* Zone of west United States. Mature specimens have two rows of prominent bullae and heavy ribs are developed, although not quite in the same pattern as in the present form. The American species is more closely ribbed at earlier growth stages, in which the dorsal row of tubercles lies at the umbilical wall, and the venter develops a low keel.

DISCUSSION: This species and genus will be more fully described and illustrated, with data on stratigraphy and age.

Suborder MEGAPHYLLITIDINA Shevyrev, 1983
Superfamily **NATHORSTITOIDEA** Spath, 1951
Family **PARAPOPANOCERATIDAE** Tozer, 1971

FAMILY RELATIONSHIPS: Tozer (1971, p. 1030) proposed this family as a member of Megaphyllitoidea, distinguished from Procarnitidae and Megaphyllitidae by long body chamber, and further from Megaphyllitidae with its occluded umbilicus (see Waterhouse 1999a, p. 52). Shevyrev (1986) appreciated that *Parapopanoceras* and allies were much more closely related to Nathorstitoidea Spath, 1951. He included Longobarditidae and Groenlanditidae as well, but these appear to have a dorsal siphuncle (Waterhouse 1994, p. 29, 1999a, pp. 17, 18). Nathorstitids have subdued but distinctive ornament, unlike the essentially smooth conch of *Parapopanoceras* and allies, and the venter is acute throughout ontogeny. But otherwise, the two share ventral siphuncle and long body chamber. The development of a sharp venter especially in late ontogeny of a number of parapopanoceratid species especially within *Beaumontites* Browne and *Stenopopanoceras* Popov suggest an apparent reversion to nathorstitids, and recall the sharp venter and high body chamber of Groenlanditidae and Longobarditidae. There must be some question over the ranking of Parapopanoceratidae, and perhaps it should be relegated to subfamily status within Nathorstitidae.

Genus *Kakaria* new

DERIVATION: Named from Kaka Point, southeast Otago, New Zealand, near fossil locality of type species.

TYPE SPECIES: *Prospingites coombsi* Kummel, 1965, here designated

DIAGNOSIS: Smooth shells developing eccentricumbilicate coiling after being tightly coiled, then reverting to regular coiling with moderately open umbilicus. Whorls remain broad, and venter convex throughout ontogeny. Suture ceratitic with numerous saddles and denticulate lobes, siphuncle ventral, body chamber ca 1.3 of circumference.

DISCUSSION: This genus is allied to *Amphipopanoceras* Voinova, type species *Popanoceras* (*Amphipopanoceras*) *dzeginensis* Voinova, 1947. Tozer (1994, in McLearn 1969) has stressed eccentricumbilicate coiling as a guide to *Amphipopanoceras*. Several figures of the type species *A. dzeginensis* Voinova, as in Popov (1961, pl. 22, fig. 7 (holotype), pl. 25, fig. 2) and Voizin & Tikhomirova (1964, pl. 47, fig. 2) from upper Anisian and Ladinian faunas of Siberia show a moderately broad form (width/diameter ratio about 0.5) with rounded venter and modest degree of eccentric coiling. The problem is that these specimens are only phragmocones, so that the nature of the full and mature conch is not illustrated. However Voizin & Tikhomirova (1964, pl. 47, fig. 3) furnished an illustration of *dzeginense* from the type locality that is of very different appearance, with high slender enveloping outer whorl and acute venter. Evidently the type species changed in its ontogeny from small comparatively broad and involute shells with well rounded venter, to eccentrically and slightly more openly coiled shells, and finally a more slender shell with enveloping outer whorl, acute venter and very narrow umbilicus. It is close in turn to other Siberian species *A. acutum* Popov, 1961 and *A. jakuschevi* Popov, 1961, showing that the shell shape with enveloping slender mature whorl, narrow umbilicus and tapered venter characterizes several species within a well delineated genus. Canadian species referred to *Amphipopanoceras* by Tozer (1994) are eccentricumbilicate, and more openly coiled at maturity than the Siberian species mentioned previously. The Canadian forms, including *selwyni* (McLearn), *inconstans* (Dagis & Ermakova), and *tetsa* (McLearn), show a tendency to develop a tapered and even acute venter: only *medium* (McLearn) amongst the Canadian species described by Tozer (1994) has a rounded venter, and this species is comparatively slender.

New Zealand specimens assigned to *Beaumontites* Browne, 1952 have generally a tapered outer whorl with narrowly rounded venter, and are eccentricumbilicate with comparatively open coiling. Thus both *Amphipopanoceras* and *Beaumontites* display eccentricumbilicate coiling. Eccentricity is more limited in *Kakaria* and the mature *Kakaria* shell is more openly coiled, with much broader venter.

Waterhouse (1996b, 1997) referred in passing to *coombsi* as *Neopopanoceras* or *Globopopanoceras*,

as a holding action to await publication of a name. *Globopopanoceras* Waterhouse, 1999, a new name to replace *Neopopanoceras* Spath not Schindewolf, is based on *Popanoceras* (*Parapopanoceras*) *haugi* Hyatt & Smith, 1905. The genus embraces parapopanoceratids that are openly and regularly coiled with whorls overlapping only a little (Waterhouse 1999a).

***Kakaria coombsi* (Kummel, 1965)**

- 1965 *Prosphingites coombsi* Kummel, p. 538, text-fig. 1-5, 6A, B.
 1971 *Stenopopanoceras coombsi* (Kummel); Tozer, p. 1016.
 1978 *Prosphingites coombsi* Kummel; Suggate et al, text-fig. 4.35, fig. 1, 2.
 1981 *P. coombsi* Kummel; Speden, pl. 9, fig. 1, 2.
 1996 *Stenopopanoceras coombsi* (Kummel); Paull et al, p. 582.
 1996a aff *Neopopanoceras* Spath (not Schindewolf) *coombsi* (Kummel); Waterhouse, p. 173.
 1997 *Globopopanoceras? coombsi* (Kummel); Waterhouse, pp. 402, 403.
 1999a *coombsi* Kummel aff *Globopopanoceras* Waterhouse, p. 54.

HOLOTYPE: Specimen OU 3863, figured by Kummel (1965, text-fig. 1, 2), Suggate et al (1978) and Speden (1981) OD, from H46/f096 and H46/f108, Potiki Siltstone, near Kaka Point, southeast Otago, New Zealand.

DIAGNOSIS: Moderately swollen evolute shells becoming eccentricumbilicate but retaining rounded venter.

MATERIAL: A large suite, kept at Otago University, from H46/f8674, Potiki Siltstone, Kaka Point. About 10 specimens collected by A. Grebneff from same place.

DESCRIPTION: Specimens moderately well preserved, evolute with globose inflated whorls and round venter. Surface shows very low growth wrinkles especially on umbilical side of whorl. Coiling somewhat variable in tightness, and small specimens about 12-13mm in diameter are as long as wide and tightly coiled, with very narrow umbilicus. The shell then develops eccentricumbilicate coiling to abruptly widen the umbilicus, and coiling then becomes regular again, with outer coils more openly coiled and narrower with increase in size. The venter remains rounded. Suture well displayed, saddles bulbous, crests entire, generally 4 pair to umbilical shoulder, lobes with generally 6-7 denticles, extending up flanks of saddles; auxiliaries vary in number and some lobes denticulate, others not. There are about 5 up to 7 saddles from median saddle to seam. Siphuncle ventral, length of body chamber up to 1.2 circumference.

RESEMBLANCES: This species has broad subglobose whorls with well rounded venter and lateral flanks. Externally they look close to *Globopopanoceras haugi* (Hyatt & Smith, 1905) from the Union Wash Formation of Inyo County, California, represented by plaster casts at the Department of Geology, University of Otago. The saddles are high and phylloid. Denticles are moderately strong in the species *coombsi*, and denticles are slightly stronger and fewer in the lobes of *haugi*, and climb higher up the flanks of the saddles. The aperture is lower and wraps more around preceding whorls in *coombsi*. Unlike *haugi*, the species *coombsi* displays eccentric coiling at a width of 13-15mm. The species therefore somewhat approaches the type species of *Amphipopopanoceras*, *A. dzegrinensis* Voinova, 1947, but this differs in its slightly narrower whorls, and late change in shell morphology through which the outer whorl becomes slender, high and tapered, to acute. Most Canadian species ascribed to *Amphipopopanoceras* by Tozer (1994) differ from both *dzegrinensis* and *coombsi* in having moderately tapered venters during later growth stages, and the overall shell is narrow, and the eccentric coiling persists so that shells gradually became more evolute, without the venter becoming acute. From New Zealand, *Beaumontites fraseri* Browne, with probably synonymous taxa *bartrumi*, *routi* and *tepingai*, also comprises narrow shells, that steadily uncoil in later growth stages, and develop narrow outer whorl with tapered venter.

DISCUSSION: The species *coombsi* approaches the Late Scythian genus *Prosphingites* only in general shape, subdued ornament and in having a multisellate suture. Unlike *Prosphingites*, whorls are eccentrically coiled, the body chamber is very long, the siphuncle is ventrally placed, and the saddles and lobes are much better defined and subphylloid in the suture. These attributes all point to a parapopanoceratid alliance.

AGE: Paull et al (1997) argued for a Scythian age for *coombsi*, on the basis that Kummel (1965) had dated the species as Scythian, and that his age was supported by a Scythian conodont species. However Tozer (1971) and Waterhouse (1997, 1999a) showed that Kummel had misidentified the genus to which *coombsi* belonged and showed that the species was of Middle Triassic age. Even Paull et al (1997) appreciated that *coombsi* was parapopanoceratid, not *Prosphingites*, but it seems they were not able to understand that the change in ammonoid identification demanded a change in age. The Middle Triassic age, urged by Waterhouse (1997), as opposed to the Paull, Coombs and Campbell preference for an Early Triassic age, is confirmed by my identification of two specimens of the Middle Triassic genus *Monophyllites* collected at the same locality by A. Grebneff. Therefore the conodont has been misidentified, or has a longer time range than previously realized, or has leaked into the *coombsi* beds. The Scythian age adduced by Kummel (1965) and defended by Paull et al (1996, 1997) is wrong.

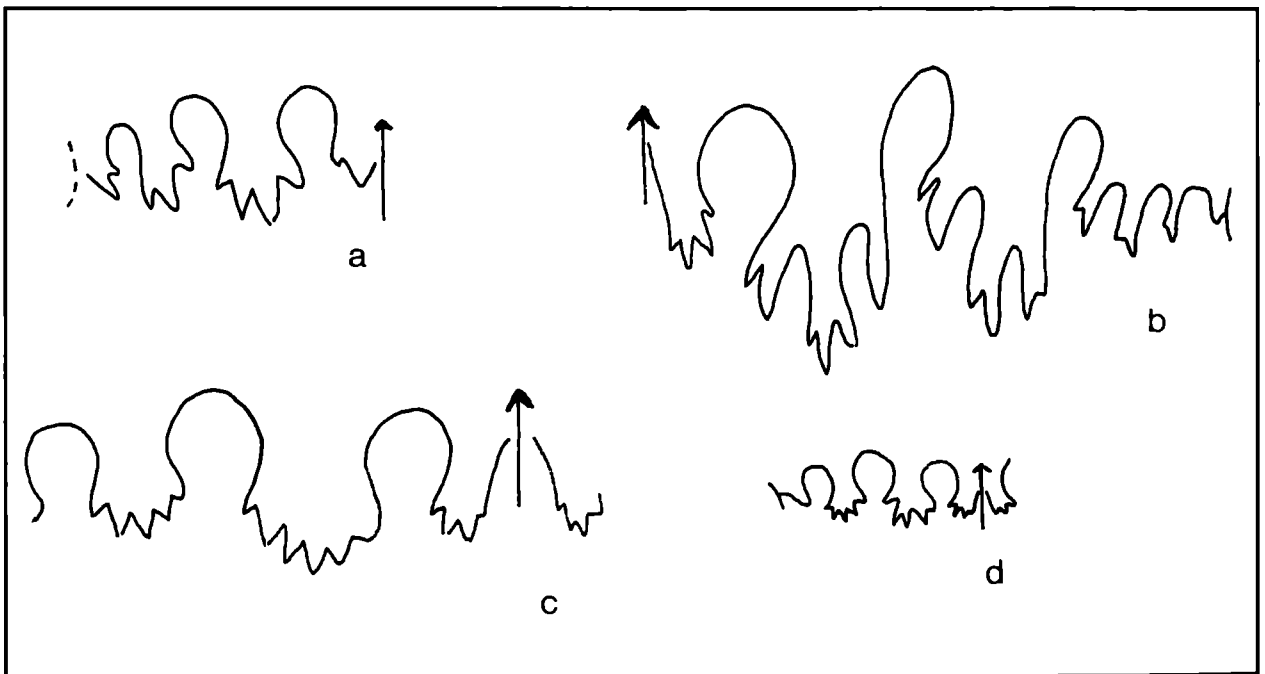
Order PHYLLOCERATIDA Arkell, 1950
 Suborder PHYLLOCERATIDINA Arkell, 1950
 Superfamily **USSURITOIDEA** Hyatt, 1900
 Family **USSURITIDAE** Hyatt, 1900
 Subfamily **USSURITINAE** Hyatt, 1900
 Genus *Simplicites* new
 Pl. 10, fig. 1, text-fig. 14

DERIVATION: simplex, simplicis - plain, Lat.

TYPE SPECIES: *Leiophyllites marshalli* Browne, 1952, here designated

DIAGNOSIS: Serpenticone species with ornament of light closely spaced collabral lirae, suture ussuritid, saddle crests swollen and weakly asymmetric, inclined dorsally, ventral sides plain, dorsal sides with deep cleft towards trough of lobes.

DISCUSSION: The species *marshalli* was referred to *Leiophyllites* Diener by Browne (1952) and Kummel (1960), as repeated by Suggate et al (1978) and Speden (1981), but the type species of *Leiophyllites*, *L. suessi* (Mojsisovics), lacks fine collabral lirae and the saddles in the ventral suture are more symmetric with shallower divisions at the base (text-fig. 13). *Leiophyllites*, with close allies *Durvilleoceras* Waterhouse and *Stenophyllites* Tozer, are classed in Leiophyllitidae Waterhouse, 1996, and allied to Flemingitoidea (Waterhouse 1996). By contrast, the new genus is a member of Ussuritinae, and allied to *Ussurites* Hyatt and *Monophyllites* Mojsisovics. The type species of *Ussurites*, *U. sichotus* (Diener 1895a, pl. 5, fig. 1), has a comparatively simple suture with first lateral saddle indented only on the ventral side, and second lateral saddle indented on the dorsal side (text-fig. 13). The dorsal indentations of the second lateral saddle are deeper and more numerous than in *marshalli*, as are those on the ventral side of the first lateral saddle. As well, the whorls are lower and more serpenticone in *marshalli*. The genus *Ussurites* includes a number of species with suture virtually identical with *sichotus*, including *arthaberi* (Welter), *yabei* (Diener), *kiepertii* Toulou, and *sokolovi* Popov.



Text-fig. 14. Sutural diagrams.

- a. *Simplicites marshalli* (Browne), holotype, x 3 approx., from Browne (1952, text-fig. 3).
 b. *Ussurites sichotus* (Diener) x 1 approx. From Spath (1934, text-fig. 100).
 c. *Leiophyllites taramelli* (Martelli) x 4.5 approx. From Spath (1934, text-fig. 104).
 d. *L. suessi* (Mojsisovics) x 1.5 approx. From Spath (1934, text-fig. 104).

Himalayan species of Middle Triassic age come close to *Simplicites*. *Monophyllites pradyumna* Diener (1895b, pl. 31, fig. 3, 4 - GSI 5908, 5909) is very close externally, and has a very close and slightly simpler suture. A specimen ascribed to this species from northwest Himalaya by Diener (1907, pl. 13, fig. 5) has higher whorls. *Monophyllites hara* Diener (1895b, pl. 31, fig. 9 - GSI 5914) also has higher more rectangular whorls and slightly more complex suture. *M. kingi* Diener (1895b, pl. 31, fig. 10) also has a very simple suture and more slender whorls. These various species are of Anisian age, with further detail discussed by Waterhouse in part 6 of the series on Himalayan Triassic ammonoids.

Subfamily **INDIRIGOPHYLLITINAE** new

NAME GENUS: *Indirigophyllites* Popov, 1961.

DIAGNOSIS: Distinguished from Ussuritinae Hyatt by its denticulate ventral saddle.

DISCUSSION: Ussuritinae are restricted to genera such as *Ussurites* Hyatt, *Monophyllites* Mojsisovics, *Simplicites* n. gen. and *Mosjvarites* Pompeckj, in which the ventral saddle has smooth sweeping lateral flanks without denticulations. By contrast, the ventral saddle in *Indirigophyllites* Popov and *Arctophyllites* Konstantinov, 1995 has denticulate flanks. In both subfamilies the external shell is ornamented by fine radial filae. The terminations of the serrations over saddles and lobes are swollen, as opposed to acute terminations in genera now dispersed amongst Danubitoidea and Proptychitoidea. Swollen terminations are not unique to Ussuritidae, also appearing in members of Acrochordiceratidae, Sturiidae and Cladiscitidae.

CONCLUSIONS

New Zealand

The array and range and distribution of the species described in this monograph both amplify and qualify the summaries of paleoecology and zonal character of the mid-Permian zones set forward in Waterhouse (1973b, 1977a, 1979b, 1982a, b). A number of species, especially amongst Mollusca, are found to range for more than one zone, and the distribution appears, notably for Brachiopoda, dependent on depth as well as substrate. The overall species distribution, taking into account the occurrences in east Australia as well as New Zealand, points to complex and variable, and somewhat individualistic lineages of evolution for a number of forms, with many shared and contemporaneous species, different ranges for some species, and different genera and different species at some horizons, in different basins and parts of basins (Waterhouse 2000a). Such a complex distribution invites closer study, with a view to elucidating both patterns of distribution, and evolution of new species. But it would be especially desirable, before adducing and interpreting such patterns, to acquire refined knowledge of the Sydney Basin species, to a level comparable with that now established for the Bowen Basin, Gympie Basin and New Zealand. Tasmania remains poorly known, because only some of the listed faunas have been described, and fossil lists unsupported by descriptions are of limited value.

For many of the New Zealand stations, collections involve few and often fragmentary individuals, and for others, many more specimens remain to be collected. There is good potential for further detailed systematic study, especially within the Mangarewa Formation, of some of the more abundant species, including polyzoans and microfossils.

Faunal distributions, and relationships

In this study it may be noted that no new genera have been described from the New Zealand Permian. There still remain some faunas to be examined, and at least one brachiopod genus requires study, involving supposed *Globiella* or allied form discovered and identified by Dr H. J. Campbell from the Dunton Range.

The large brachiopod, bivalve and gastropod assemblages of eastern Australia are also under substantial control, but there certainly are many more faunas and some genera to be clarified. Thanks especially to Dr N. W. Archbold, brachiopods of Western Australia have been intensively described, and Dr J. M. Dickins has dealt with a substantial number of bivalves and gastropods. Ammonoids have been closely examined for Western Australia, but the few known from east Australia require revision.

For Western Australia, one of the facets discovered by Archbold, with regard to the diversity of Strophalosiidae, has been endorsed in the present study. Now genera are known to include *Strophalosia*, *Coronalosia*, *Etherilosia*, *Echinalosia*, *Orthothrix*, *Mingenewia*, *Arcticalosia*, *Lialosia*, *Liveringia* and probably *Pseudostrophalosia*, unless *Noto* *rosia* is indeed separable. In Queensland, diversity is distinctly lower, even though species are abundant, with *Strophalosia*, *Echinalosia*, *Capillaria*, *Wyndhamia*, *Marginalosia*?, *Pseudostrophalosia* and *Acanthalosia*. New Zealand has only *Echinalosia*, *Etherilosia*?, *Pseudostrophalosia*, *Marginalosia*, *Acanthalosia*? and *Wyndhamia*. The unevenly known faunas of Tasmania include *Echinalosia*, *Wyndhamia* and *Strophalosia*.

Despite the diversity of Permian brachiopods for Australia and New Zealand, there has been a tendency to neglect or misrepresent these and other Gondwanan taxa in many northern hemisphere studies, as is especially evident in major overviews such as the revised brachiopod treatise for Productida. Yet increasingly, it appears that Gondwanan genera are present even amongst the paleotropical faunas of the Glass Mountains. Briggs (1998) has drawn attention to likely *Etherilosia* amongst species referred to *Heteralosia* by Cooper & Grant (1975), *Terrakea* is present (Kotlyar 1989, Briggs 1998, Waterhouse 1971), and *Magniplicatina* is recognized widely (Brunton, Lazarev, Grant & Jin 2000). It has been interesting to realize the presence of Trigonotretinae amongst Glass Mountains Spiriferida, including *Lepidospirifer* Cooper & Grant, very close to *Aperispirifer*, and *Trigorhium*, a new and distinctive genus derived from *Trigonotreta* stock. Such forms reinforce the presence of Wordian *Spiriferella* with Gondwanan and Arctic links.

In New Zealand, a few more northern genera have been discovered, such as *Arcullina* and *Alispiriferella*, hitherto best known from the Arctic, with *Arcullina* found in Thailand and Western Australia. As well, Himalayan and Gondwanan genera are known to include *Megasteges*, *Nakimusiella* and gastropod *Collabrina*.

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EXPLANATION OF PLATES

Plate 1

- Fig. 1. *Paraconularia* sp. OU 2600 from Glendale Limestone, x 1.
 Fig. 2 - 8. *Capillonia brevisulcus* (Waterhouse) from D44/f363, Glendale Formation. 2, external mould of specimen OU 18267 with valves conjoined, dorsal aspect, x 2. 3, external mould of specimen OU 18268 with valves conjoined, dorsal aspect, x 2. 4, ventral internal mould and cardinal area OU 18266, x 3. 5, 6, 7, ventral internal mould OU 18264, x 3 and x 1. 8, dorsal external mould OU 18265, x 1.
 Fig. 9. Poorly preserved shells from Hilton limestone, D45/f7578 with anopliin BR 2380 (top left) - see text-fig. 4A, *Capillonia brevisulcus* BR 2381 (base of figure) and dorsal valve of *Marginalosia?* sp. BR 2382 (top right), x 1.
 Fig. 10. *Costatumulus* sp. ventral internal mould BR 2262 from D44/f109, Letham Formation, x 1.
 Fig. 11. *Lethamia ligurritus* Waterhouse ventral internal mould BR 2263 from D44/f121, Letham Formation, x 1.
 Fig. 12. *Lethamia* sp. dorsal internal mould, BR 2274 from D44/f123, Mangarewa Formation, x 1.
 Fig. 13. Productidid gen. & sp. indet., dorsal external mould BR 2345 from D44/f121, Letham Formation, x 1.
 Fig. 14 - 15. *Terrakea cf exmoorensis* Dear. 14, ventral external mould, BR 2402 from D44/f123, lower Mangarewa Formation, x 2. 15, ventral external fragment BR 2403 showing ear spines from same locality, x 1.
 Fig. 16, 17. *Terrakea exmoorensis* Dear. 16, ventral valve BR 2268 from D44/f116, Letham Formation, x 1. 17, lateral view of ventral valve BR 2344 showing ear spines, some marked, from D44/f126, from Letham Formation, x 2.
 Fig. 18 - 21. *Paucispinauria paucispinosa wardenensis* n. subsp. from UQL 3758, Freitag Formation, southwest Bowen Basin, Queensland, x 1. 18, 21, internal mould of ventral valve UQF 65423, also small internal ventral mould UQL 65424 in fig. 21. 19, ventral internal mould UQF 65524. 20, dorsal exterior UQF 65483.
 Fig. 22 - 27. *Paucispinauria solida* (Etheridge & Dun) from Mangarewa Formation. 22, ventral valve BR 2255 from D44/f111, x 1. 23, fragment of ventral external mould OU 18271 showing posterior lateral spine bases, from D44/f344, x 1. 24, ventral internal mould BR 2354 from D44/f119, x 1. 25, elongate ventral valve OU 18274 from D44/f323, x 1. 26, ventral internal mould OU 18269 from D44/f360, x 0.5. 27, ventral internal mould OU 18272 from D44/f344, x 0.5.

Plate 2

- Fig. 1 - 9. *Lazarevonia arcuata* (Waterhouse). 1, latex cast of ventral exterior, UQF 73609 from UQL 4804. 2, latex cast of ventral exterior, UQF 73608 from UQL 4804. 3, latex cast of ventral exterior UQF 73610 from UQL 4792. 4, dorsal external mould, unregistered specimen. 5, ventral internal mould UQF 73613 from UQL 4805. 6, ventral internal mould UQF 73614 from UQF 4795. 7, dorsal aspect of internal mould UQF 73615 from UQL 4800. 8, 9, dorsal internal mould and latex cast UQF 73616 from UQL 4807.
 Specimens from the Pija Shale Member, Manang district, north-central Nepal. The types from Dolpo, west Nepal, were figured by Waterhouse (1978). Additional specimens, presented here, were badly reproduced in Waterhouse (1983b). All specimens x 2.
 Fig. 10 - 20. *Platycancrinella grandauris* Waterhouse. 10, 11, external mould and latex cast of holotype, ventral valve UQF 73620 from UQL 4794. 12, latex cast of ventral valve, unregistered specimen. 13, worn ventral valve, unregistered specimen. 14, worn ventral valve, unregistered specimen. 15, worn external mould of dorsal valve, unregistered specimen. 16, dorsal external mould UQF 73621 from UQL 4794. 17, internal mould of both valves, dorsal aspect with part of ventral external mould to right, UQF 73624 from UQL 4793. 18, ventral internal mould UQF 73622 from UQL 4794. 19, worn ventral valve UQF 73623 from UQL 4792. 20, dorsal internal mould UQF 73625 from UQL 4794, x 2. Stress lineations visible in fig. 14, 19.
 Specimens from Pija Shale Member, Manang, Nepal. These include the original figures of the species, poorly reproduced in Waterhouse (1983b). Specimens x 1, except fig. 20, x 2.

Plate 3

- Fig. 1 - 6. *Paucispinauria solida* (Etheridge & Dun) from Mangarewa Formation. 1, ventral external moulds showing few ear spines from D44/f111, including BR 2383, x 2. 2, dorsal external mould BR 2344 from D44/f126, x 0.75. 3, ventral anterior of internal mould OU 18270 from D44/f344, x 2. 4, 5, ventral and dorsal aspects of internal mould OU 18743 from D44/f339, x 2. 6, dorsal external mould OU 18273 from D44/f339, x 0.75.
 Fig. 7, 8. *Magniplicatina halli* (Waterhouse) from Letham Formation, ventral external mould and dorsal internal mould, bryozoa below, OU 18275, x 2.
 Fig. 9 - 11. *Magniplicatina magniplica* (Campbell) from lower Mangarewa Formation, D44/f123, x 1. 9, ventral internal mould BR 2341. 10, posterior ventral internal mould BR 2384. 11, anterior aspect of ventral internal mould BR 2385.
 Fig. 12 - 22. *Echinalosia conata* n. sp. from D44/f7115, Takitimu Group, x 1. 12, ventral internal mould OU 18749. 13, internal mould OU 18753 of mature ventral valve. 14, decorticated ventral valve OU 18746. 15, 16, anterior and ventral aspects of ventral internal mould OU 18747. 17, obscure ventral external mould OU 18748, showing spine bases. 18, ventral internal mould OU 18744. 19, dorsal external mould OU 18751. 20, ventral internal mould OU 18745. See text-fig. 5e. 21, dorsal external mould, holotype, OU 18750. 22, dorsal internal mould OU 18752.

Plate 4

- Fig. 1 - 5. *Echinalosia floodi* n. sp. from UNEL 1012, Elderslie Formation, Sydney Basin, x 2. 1, ventral external mould AMF 117370. 2, holotype ventral internal mould AMF 117369. 3, dorsal external mould AMF 117368 (formerly UNEF 145341). 4, 5, ventral and dorsal aspects of internal mould, valves conjoined, AMF 117367.
 Fig. 6, 7, 10 - 12. *Echinalosia discinia* Waterhouse from Letham Formation. 6, ventral external fragment BR 2270, = *E. discinia davidi* Briggs, from D44/f110, x 2. 7, ventral internal mould BR 2266 from D44/f110, x 1. 10, dorsal aspect of BR 2343 from D44/f116, x 1. 11, 12, internal mould of both valves, ventral and dorsal aspects OU 18755 from D44/f307, x 2.
 Fig. 8, 9. *Echinalosia denisoni* Archbold, dorsal exterior view of latex cast of both valves OU 18276 from D44/f320, Letham Formation, Wairaki Downs, x 1, x 2.
 Fig. 13 - 16. *Echinalosia ovalis* (Maxwell) from Mangarewa Formation. 13, ventral internal mould BR 2261 from D44/f121, x 2. 14, ventral internal mould BR 2260 from D44/f111, x 2. 15, exterior of ventral valve BR 2351 from D44/f111, x 2. 16, dorsal internal mould BR 2352 from D44/f111, x 2.
 Fig. 17 - 21. *Coronalosia blijniensis* Waterhouse & Gupta from Bijni tectonic unit, Garwhal Himalaya, India, x 1. 17, dorsal internal mould CASGF 589. 18, holotype, ventral internal mould with part of posterior external mould CASGF 526 showing hollow spine tubes

along hinge. 19, 20, dorsal internal mould CASGF 532 under different lightings. 21, unregistered ventral external mould showing large posterior lateral spines at upper left, but rest of hinge row lost. Material lodged at Canterbury Museum, some also figured by Waterhouse & Gupta (1978).

Plate 5

- Fig. 1 - 3. *Marginalosia?* sp. from D45/f7578, Hilton limestone, Wether Hill Station. 1, two interiors of worn dorsal valves BR 2386 and 2387, x 1. 2, specimen BR 2388 with valves conjoined, x 0.75, ventral aspect broken and showing dorsal valve in section - see text-fig. 4g. 3, lateral view of same specimen with umbo to right, x 0.75.
- Fig. 4, 5. *Etherilosia?* sp. from D44/f9604, Brunel Formation, Takitimu Group. Interior of ventral valve OU 18756 with radiating slightly rhizoid spines, below interior of dorsal valve OU 18757, x 2. See text-fig. 5g, h.
- Fig. 6 - 11. *Pseudostrophalosia?* cf *blakei* (Dear) from D44/f123, Mangarewa Formation. 6, ventral internal mould BR 2239, x 1. 7, ventral internal mould BR 2275, x 1. 8, ventral external mould BR 2275 showing fine adpressed spines, x 2. 9, dorsal external mould BR 2339, x 1. 10, 11, dorsal external mould BR 2276, x 1, x 2.
- Fig. 12 - 16, 17? *Wyndhamia typica crassispina* n. subsp. from UQL 3759, Freitag Formation, southeast Bowen Basin, Queensland, x 1. 12, ventral external mould UQF 65492. 13, ventral internal mould UQF 65480. 14, holotype, UQF 65481 with valves conjoined, ventral external mould. 15, 16, same specimen, ventral and dorsal aspects of internal mould. 17, dorsal external mould UQF 65482, identity questionable, and suggestive of *Echinalosia floodi* n. sp.
- Fig. 18. *Megasteges?* sp. from Hilton Limestone, D44/f376, Wairaki Downs. Worn ventral valve OU 18758 x 2. See text-fig. 5i, j, k.
- Fig. 19-22. *Plekonella* aff *southlandensis* (Fletcher) from D44/f123, Mangarewa Formation, showing branching ribs, x 1 approx. 19, ventral external mould BR 2356. 20, ventral and dorsal aspects of internal mould BR 2357. 21, ventral and dorsal aspects of internal mould BR 2396. 22, ventral and dorsal aspects of internal mould BR 2395.
- Fig. 23. *Stenosisma?* sp., dorsal valve BR 2350 from Hilton Limestone D44/f9478, x 1.
- Fig. 24. *Plekonella* n. sp., specimens including ventral valve BR 2390 and dorsal valve BR 2398 with left valve TM 8197 of *Heteropecten* sp. (left middle) on block from Mangarewa Formation at D44/f344, x 1.
- Fig. 25. *Psilocamara?* sp. ventral valve OU 18759 from D45/f7115, Takitimu Group, x 1.
- Fig. 26, 27. *Spinomartinia?* *adentata* (Waterhouse) from D44/f378, Takitimu Group, x 1. 26, posterior of ventral internal and external mould with small plate under umbo, OU 18761. See text-fig. 7a. 27, ventral valve OU 18760.

Plate 6

- Fig. 1 - 4. *Spinomartinia spinosa* Waterhouse from Hilton Limestone, x 1. 1, ventral valve OU 18773 from D44/f379, Pleasant Creek, Aparima Valley. 2, ventral valve BR 2392 from D45/f7578, Wether Hill Station. 3, dorsal valve BR 2391 from same locality. 4, internal mould of ventral valve OU 18278 from D44/f376, Coral Bluff, Wairaki Downs.
- Fig. 5 - 7. *Neospirifer arthurtonensis* Waterhouse from Glendale Formation, Wairaki Downs. Ventral and dorsal aspects of internal mould and dorsal external mould with part of ventral external mould, OU 18282 from D44/f363, x 2.
- Fig. 8, 9. *Fusispirifer?* sp. from Hilton Limestone, D44/f376, Wairaki Downs. 8, internal mould of ventral posterior fragment OU 18762, x 1. 9, fragment of posterior internal mould of ventral valve OU 18763, x1.
- Fig. 10. *Aperispirifer archboldi* Waterhouse from Freitag Formation, Queensland. Dorsal internal mould UQF 65496, from UQL 3762 as judged from matrix, x 1.
- Fig. 11, 16. *Spiriferella* sp. B, Glendale Formation?, Wairaki Downs, x 1. 11, ventral valve OU 2462. 16, leached ventral internal mould OU 2463. Well worn and reworked, possibly derived.
- Fig. 13. *Spiriferella* sp. A external mould of ventral valve OU 18285 from D44/f376, Hilton Limestone, Wairaki Downs, x 2.
- Fig. 12, 14, 15, 17 - 20. *Arcullina humilis* n. sp. from Takitimu Group D45/f 7115 x 1. 5 approx. 12, 15, ventral exterior OU 18764, shell and latex cast. See text-fig. 7e. 14, ventral valve OU 18766, holotype. 17, 20, latex cast and ventral internal mould, OU 18765. 18, 19, latex cast of dorsal exterior OU 18767 under different lightings, fold between f - f. See text-fig. 7d.

Plate 7

- Fig. 1 - 3. *Alispiriferella* sp. from D44/f363, Glendale Formation, Wairaki Downs. 1, ventral internal mould with part of exterior OU 18286, x 2. 2, 3, dorsal external mould OU 18287, x 1, x 2.
- Fig. 4, 5. *Martiniopsis patella* Waterhouse from Wairaki Breccia-Conglomerate, Wairaki Downs, x 1. 4, dorsal internal mould BR 2393 from D44/f 9874. 5, ventral valve OU 18288 from D44/f374.
- Fig. 6 - 11. *Tigillumia mintyi* Waterhouse from D44/f376, Hilton Limestone, Wairaki Downs. 6, holotype ventral valve OU 18289 x 1. 7, ventral internal mould OU 18298, x 2. 8, dorsal internal mould OU 18297 x 2. 9, ventral internal mould with heavy posterior thickening, OU 18294, x 2. 10, worn ventral valve OU 18770 with heavy posterior thickening, x 1. 11, ventral valve OU 18293, x 1.
- Fig. 12 - 17. *Ingelarella subplicata* (Waterhouse) from D44/f109, Letham Formation, Wairaki Downs, x 1. 12, ventral view of broken internal mould BR 2362. 13-16, ventral, anterior, dorsal and posterior aspects of internal mould BR 2360. Dorsal valve on top in fig. 14, 16. 17, ventral view of broken internal mould BR 2361.
- Fig. 19, 20, 22. *Ingelarella undulosa* Campbell from Freitag Formation, Bowen Basin, Queensland, x 1. 19, 20, ventral and dorsal aspects of internal mould of specimen with valves conjoined, UQF 65491 from UQL 3759. 22, internal mould of ventral valve UQF 65478 from UQL 3766.
- Fig. 21. *Ingelarella costata* Waterhouse dorsal valve OU 18768 from Mangarewa Formation, Wairaki Downs, at D44/f354, x 1.

Plate 8

- Fig. 1, 2. *Ingelarella undulosa* Campbell from Freitag Formation, Bowen Basin, Queensland, x 1. 1, internal mould of dorsal valve UQF 65489 from UQL 3759. 2, internal mould of dorsal valve UQF 65479 from UQL 3766.
- Fig. 3. *Johndearea isbelliformis* (Waterhouse) from D44/f376, Hilton Limestone, Wairaki Downs, worn fragment of ventral valve OU 18299, x 1.
- Fig. 4 - 8. *Marinumula ovata* Waterhouse from Wairaki Downs, x 2. 4, 7, ventral and dorsal aspects of holotype, internal mould of specimen with valves conjoined, BR 2348 from D44/f109, Letham Formation. 5, 6, ventral and dorsal aspects of specimen with valves conjoined OU 18771 from D44/f307, Letham Formation. 8, dorsal aspect of internal mould of specimen with valves conjoined BR 2347 from D44/f123, Mangarewa Formation.
- Fig. 9. *Nuculopsis imperta* Waterhouse TM 8198 from D44/f746, Letham Formation, Wairaki Downs, x 1.

- Fig. 10. *Marinurnula rugulata* Waterhouse from D44/f364, Glendale Formation, Wairaki Downs, internal mould, ventral valve OU 18303, x 2.
- Fig. 11. *Polidevcia* aff *antequadrata* Waterhouse TM 7900 showing muscle imprints, from D44/f132, Mangarewa Formation, Wairaki Downs, x 1.
- Fig. 12. *Nucundata* sp. TM 7901 from D44/f113, Mangarewa Formation, Wairaki Downs, x 1.
- Fig. 13, 14. *Aphanaia proiectus* n. sp. from D44/f137, Mangarewa Formation, Wairaki Downs, x 1. 13, left valve aspect BR 7893. 14, left valve aspect, holotype BR 7892.

Plate 9

- Fig. 1 - 3. *Aphanaia proiectus* n. sp. from D44/f137, Mangarewa Formation, Wairaki Downs. 1, holotype TM 7892 anterior aspect, left valve to right, x 1. See pl. 8, fig. 14. 2, anterior aspect of TM 7893, left valve to right, x 1. See pl. 7, fig. 13. 3, latex cast of TM 7894 showing umbonal deck under umbo of right valve, anterior to left, slightly tilted, x 2.
- Fig. 4. *Heteropecten* sp. from D44/f123, lower Mangarewa Formation, Wairaki Downs. Left valve TM 8199, showing the wide primaries typical of genus, x 1.
- Fig. 5. *Merismopteria macroptera* (Morris) from D44/f344, Mangarewa Formation, Wairaki Downs, external mould of right valve OU 18305 with part of interior, x 2.
- Fig. 6. *Striochondria parkesi* (Fletcher) from D44/f352, Mangarewa Formation, Wairaki Downs. Right valve OU 18306, x 2.
- Fig. 7. *Elimata symmetrica* Waterhouse right valve TM 7897 from D44/f9001, Letham Formation, Wairaki Downs, x 1. See text-fig. 10 b.
- Fig. 8. *Striochondria orbiculata* (Waterhouse) right valve TM 3567 from D44/f9626, Glendale limestone band, Wairaki Downs, x 2.
- Fig. 9. *Neoplatyteichum impressa* (Waterhouse) from P26/f8513, Croisilles ophiolite complex, Nelson, latex cast of holotype TM 3877, x 2. Note fine close-set costae, clearly displayed below selenizone.
- Fig. 10. *Platyteichum loratum* Waterhouse OU 18310 from D44/f310, Mangarewa Formation, Wairaki Downs, x 2.
- Fig. 11. *Spirovallum?* sp. TM 8200, anterior aspect of PVC cast, from G45/f8612, Arthurton Group, near Arthurton, x 1. See text-fig. 10c, d.
- Fig. 12, 13. *Collabrina* sp. OU 18308 from D44/f315, Mangarewa Formation, x 1, x 2.

Plate 10

- Fig. 1. *Simplicites marshalli* (Browne), OU 14651 from D44/f141 courtesy of Dr John G. Begg, IGNS.
- Fig. 2 - 4. *Mourlonopsis strzeleckiana* (Morris), holotype BB 3921, kept at Museum of Natural History, London, photographs supplied courtesy of museum, x 2. Tilted anterior, posterior and dorsal aspects.

Plate 1

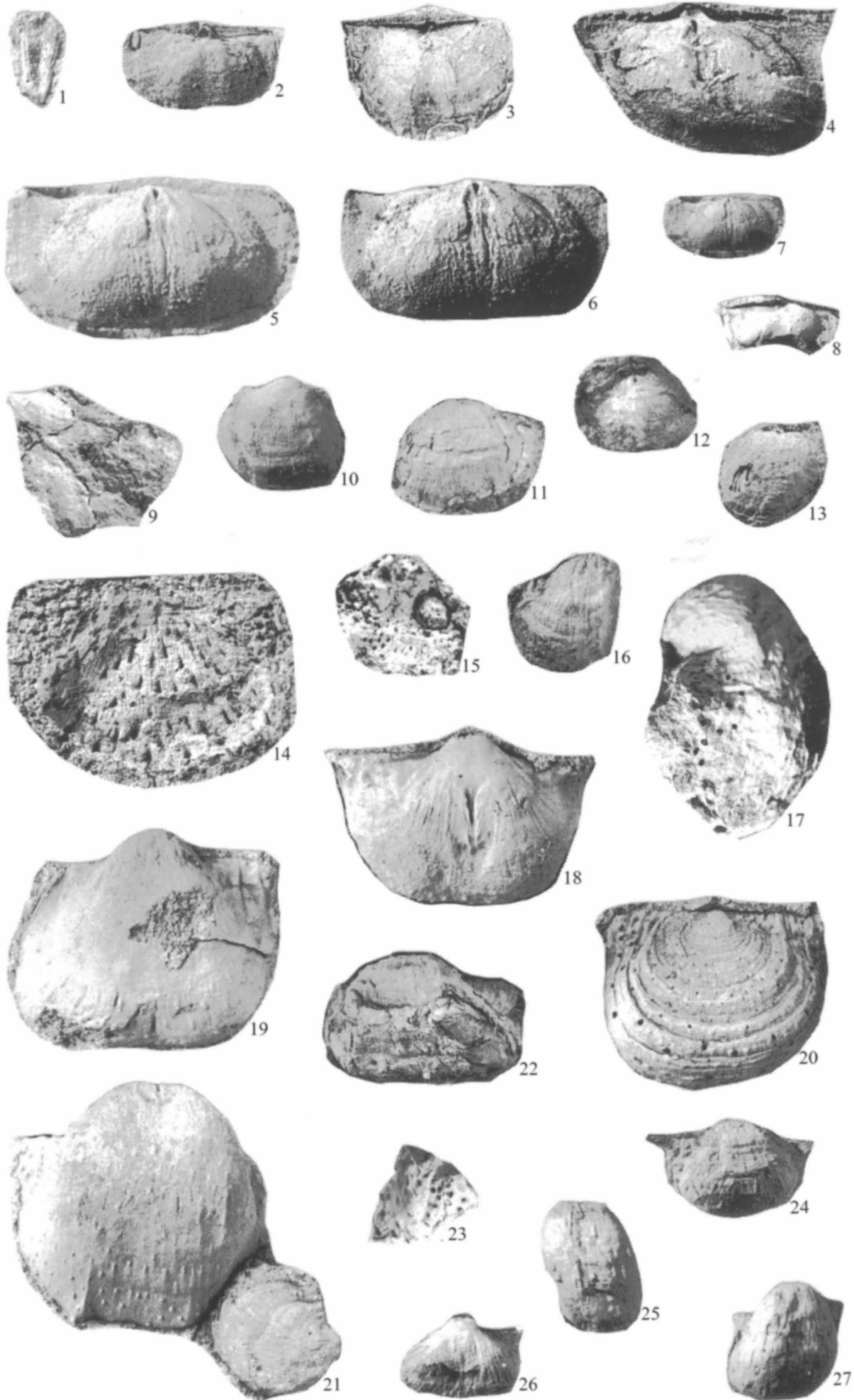


Plate 2

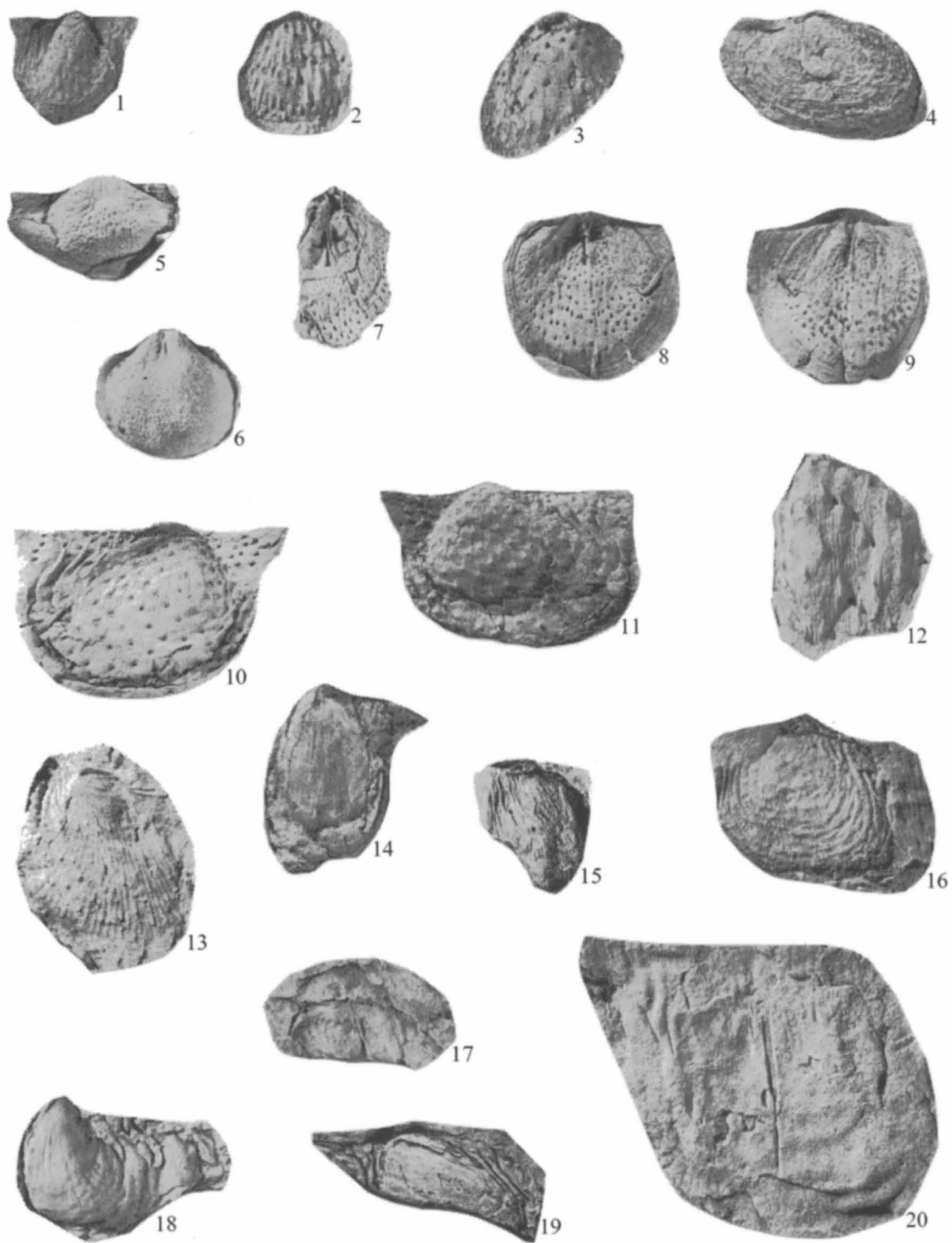


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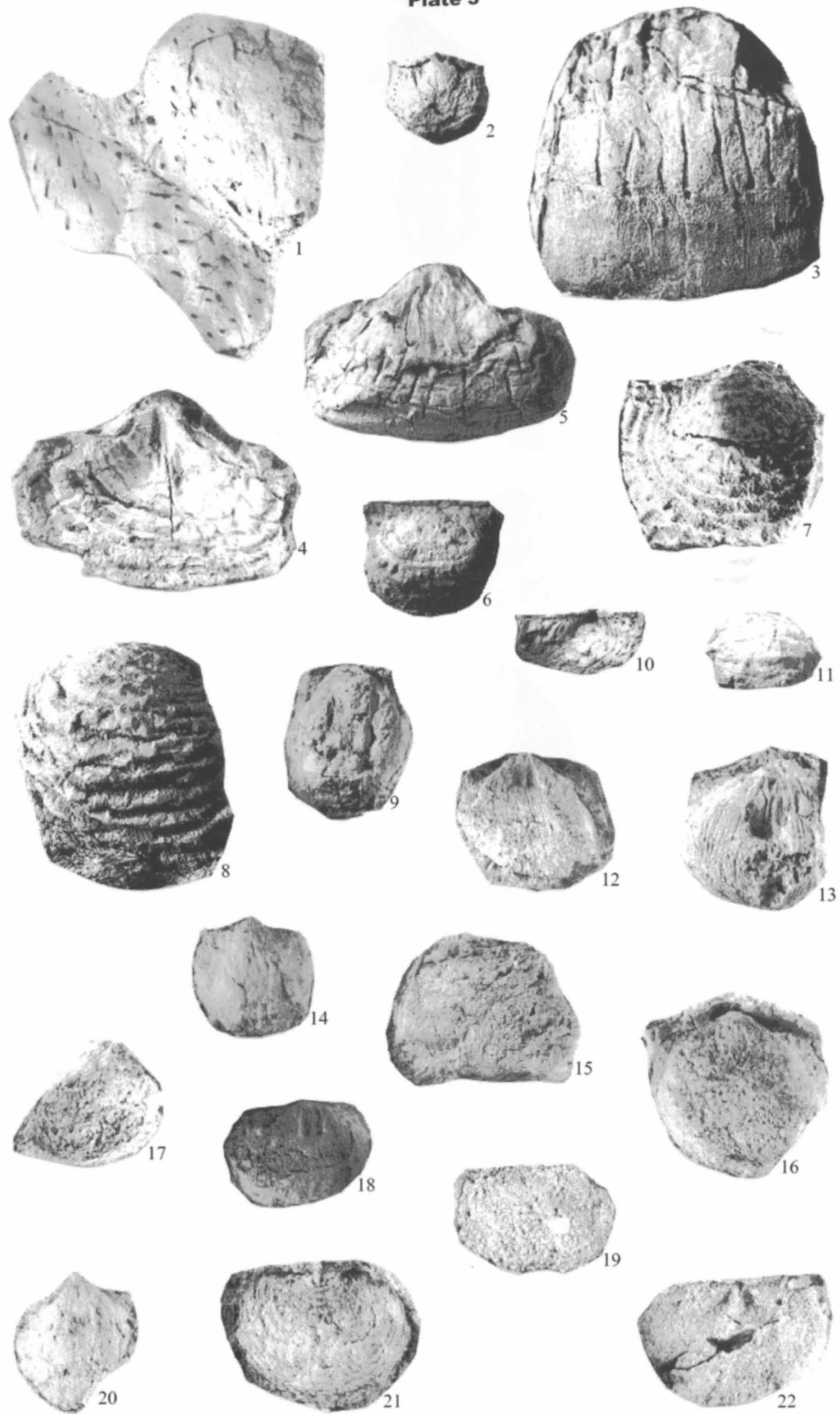


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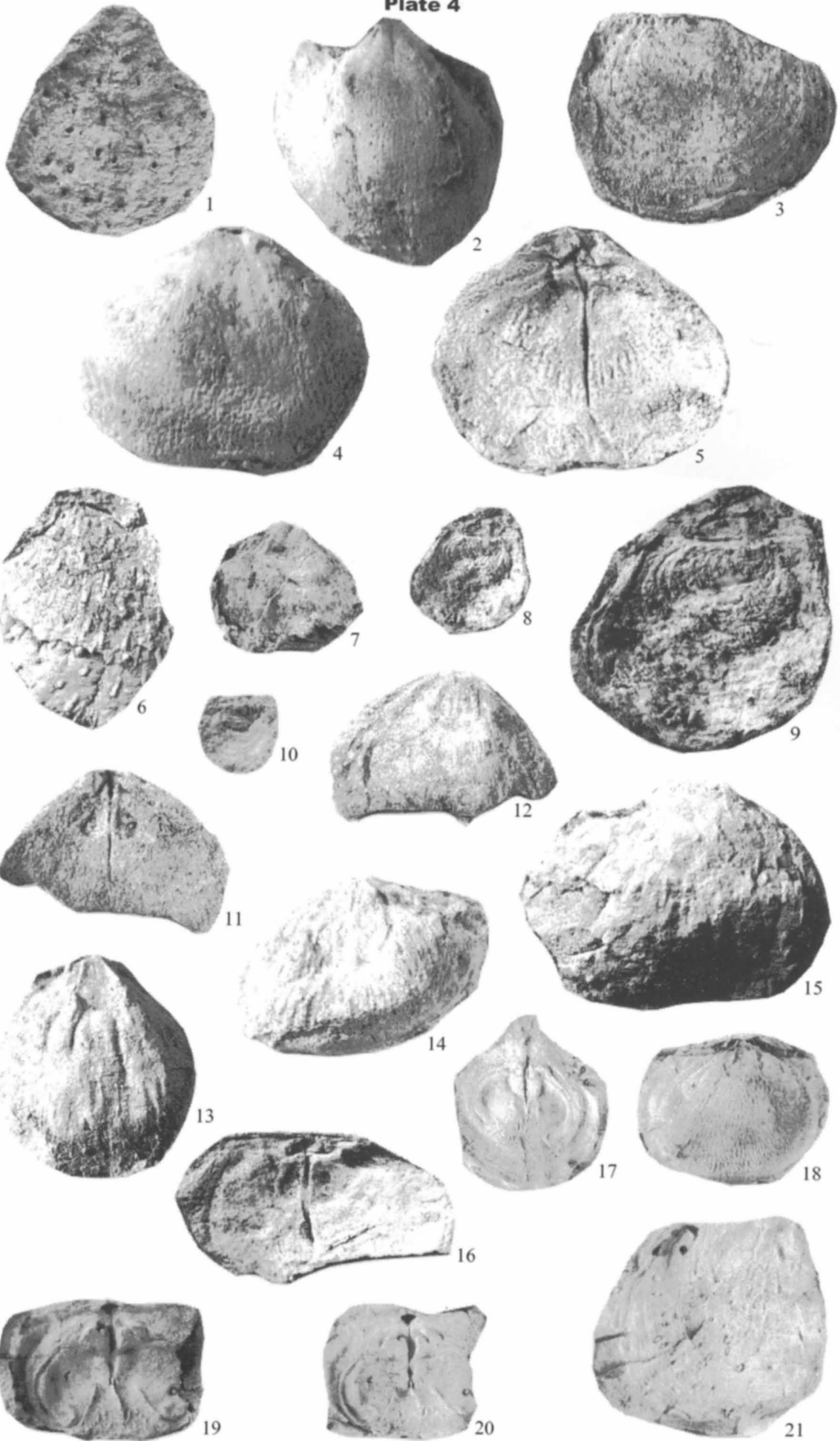


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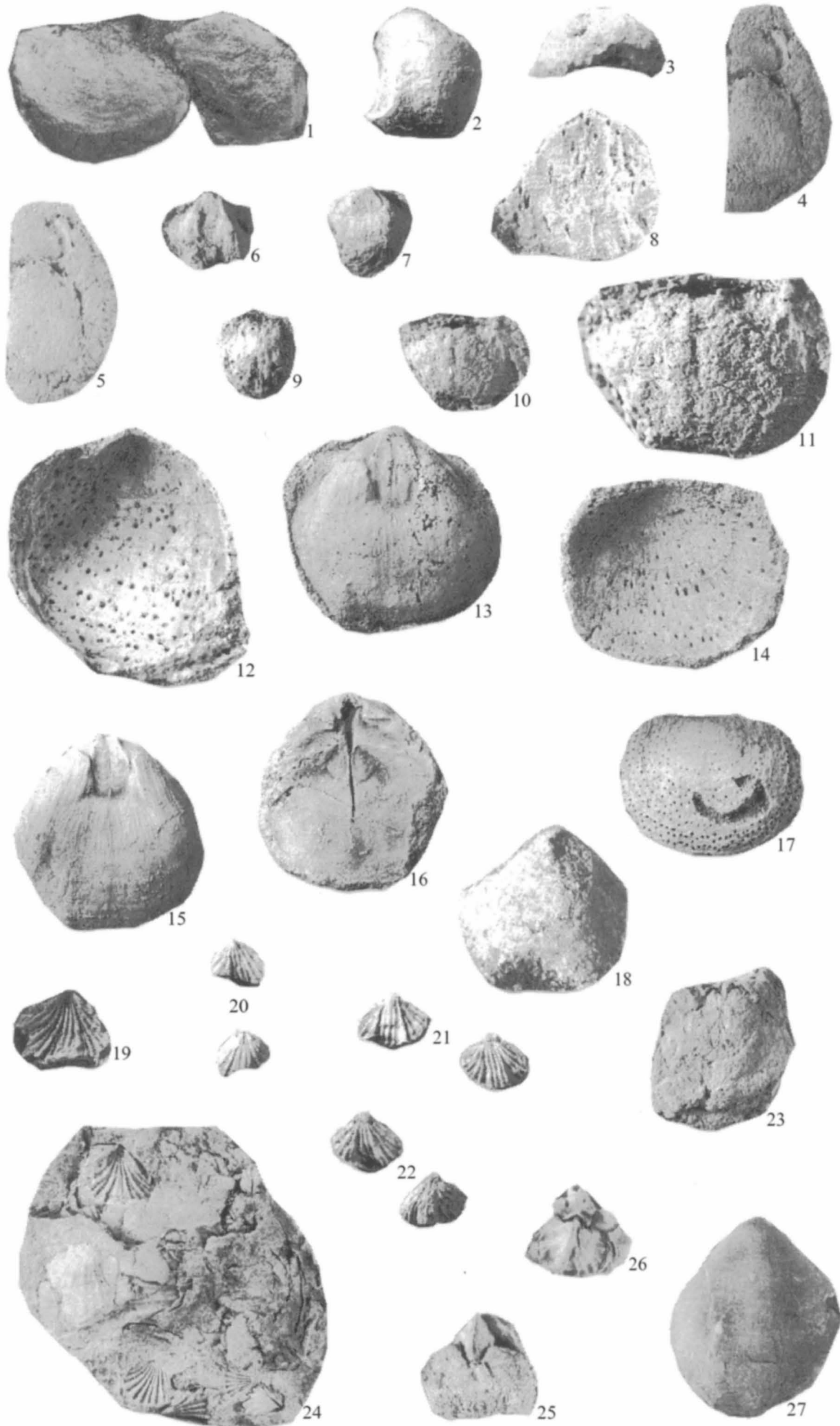


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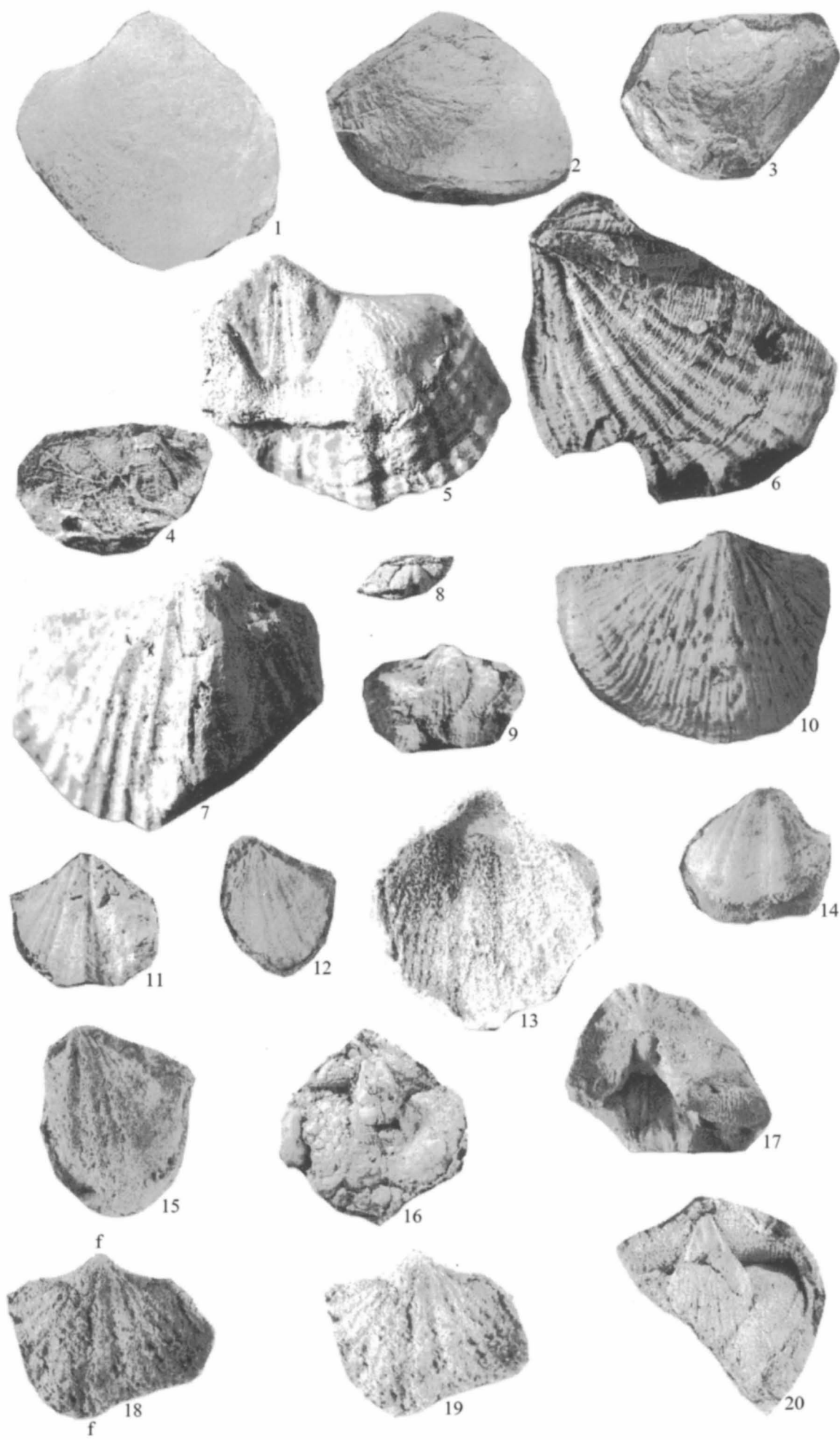


Plate 7



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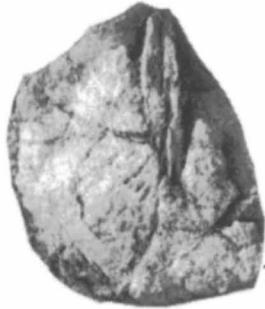
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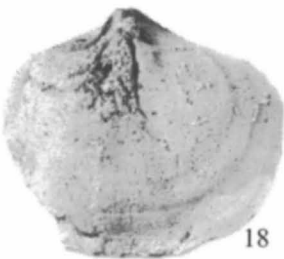
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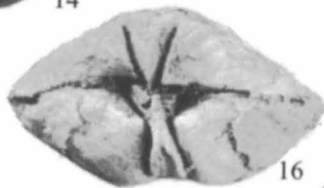
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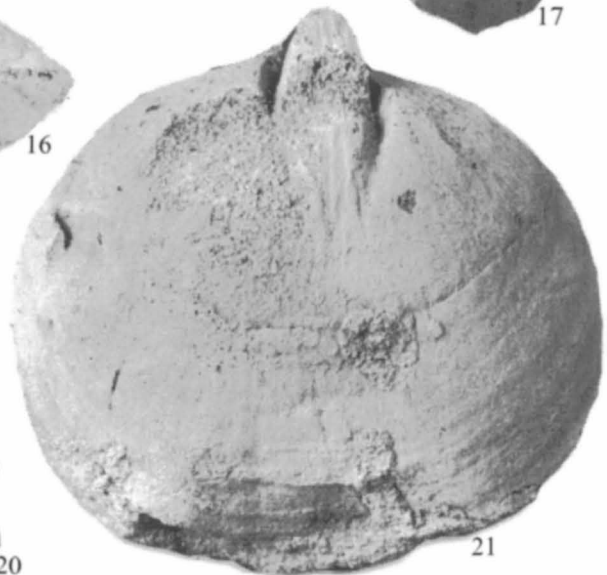
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Plate 8

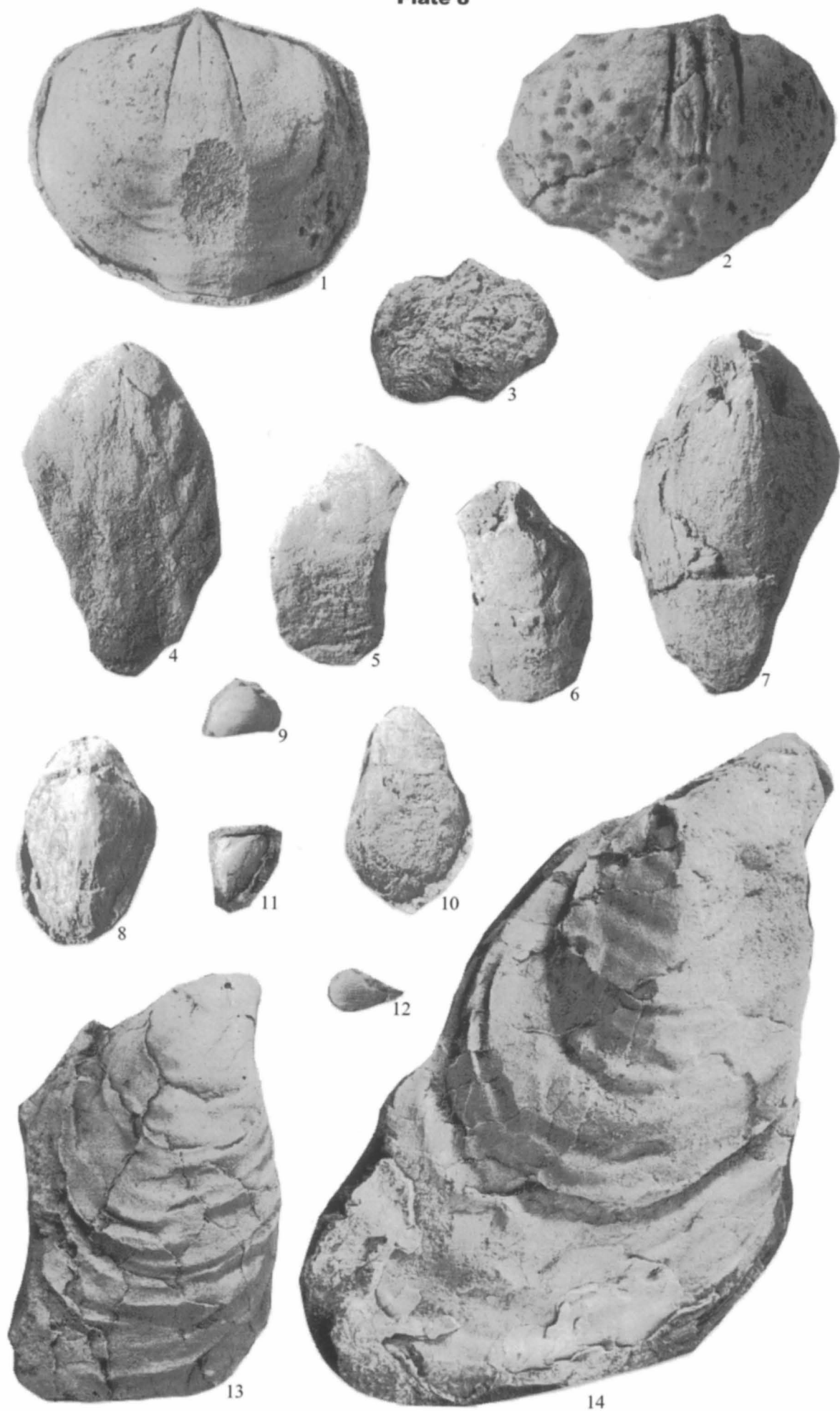


Plate 9

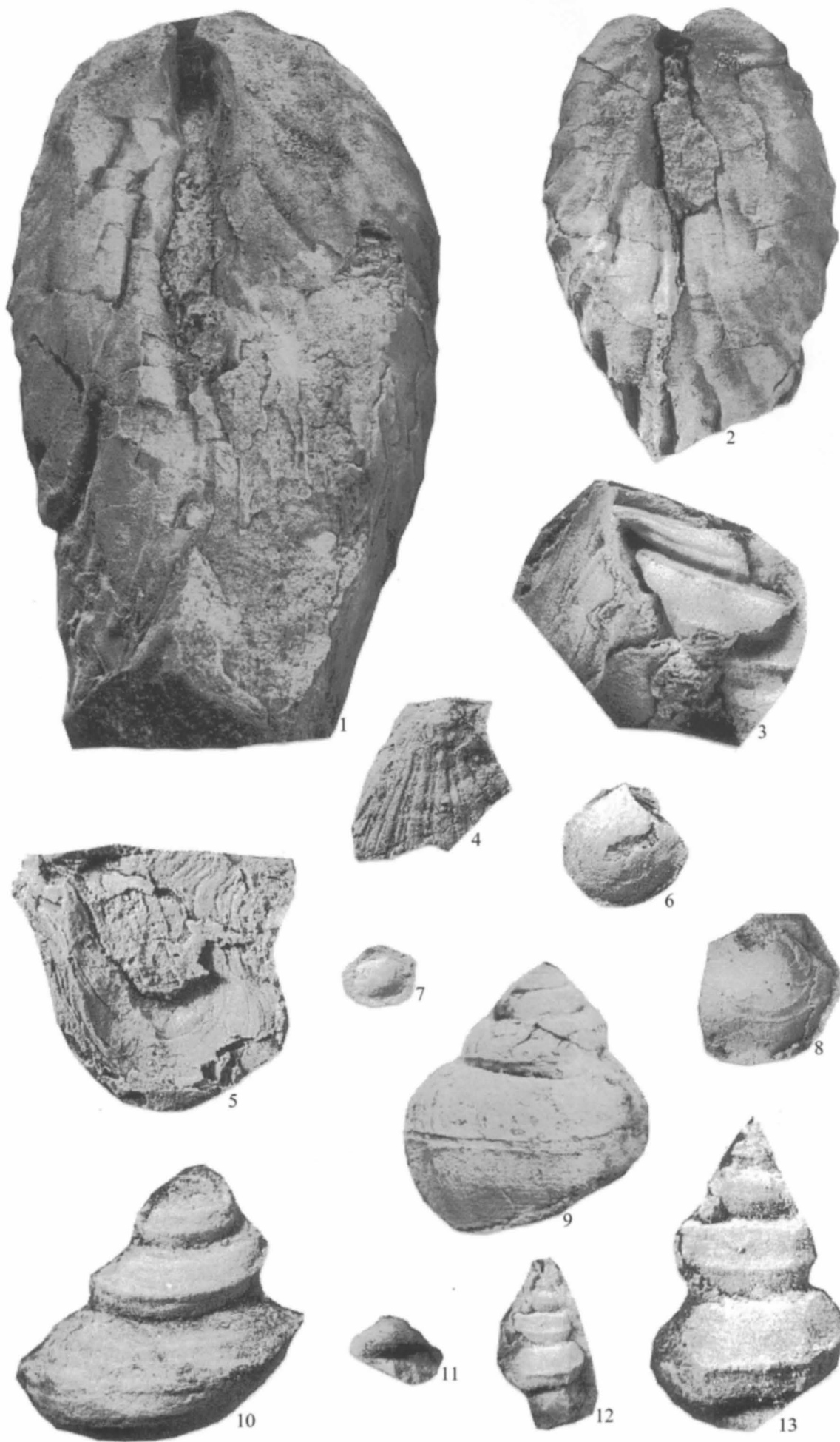


Plate 10

