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Earthwise volume 8

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PREFACE

Members of the Subclass Pteriomorphia are reviewed, with particular attention to those of Devonian to Cretaceous age. Many of the constituent groups were nestling or semi-epifaunal, remaining so throughout their history to the present day, but some developed an expanded anterior, changing in habit, to lie flat on the sea-floor with commissure horizontal, or be upright with commissure vertical, and develop a degree of mobility. Later there was a gradual reversion in several groups, with reduction and loss of the anterior extension and return to a bottom-hugging and often pleurothetic habit, a trend that had already started during the time of great proliferation in the Early Carboniferous and Permian. None of these regressive groups survived beyond the Cretaceous, leaving the specialised pteriomorphs to persist into the present with a number of their more primitive sister groups.

This study is dedicated to the memory of two former and fellow students of Pteriomorphia, the distinguished New Zealand paleontologists Jack Marwick and Sir Charles Fleming.

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Earthwise, 25 Avon Street, Oamaru 9400, New Zealand.

Cover: *Tesselarulina nobilis* (Koninck) from Early Carboniferous of Belgium. See p. 107.

Summary

The fossil record, classification and evolution of various members of Subclass Pteriomorphia are reviewed, with particular reference to Family Atomodesmidae (Superfamily Inoceramoidea), and the pectiniform bivalves of Superorder Pectinidia. This is divided into Pterinopectinida (new), Pectinida, Limida divided into Limidina, Aviculopectinidina and Monotidina, and Ostreida, divided into Etheripectinidina (new) and Ostreidina. A number of fossils demonstrate critical evolutionary change, occupying boundary or linking positions between major groups, including the Atomodesmidae-Inoceramidae relationship, the evolution of eurydesmids from chaenocardiids, and the diversification of subfamilies and families within Pterinopectinida, Aviculopectinidina and Etheripectinidina. It is confirmed that pterinopectens evolved into both etheripectens and aviculopectens, and some aviculopectens in the Late Paleozoic developed a shortened hinge, evolving into monotids, with change to the anterior right auricle. A somewhat comparable trend followed independently in an etheripectinin group in the later Mesozoic. Particular attention is paid to the origin of the Halobiidae, and to the disputed affinities of Pergamiidae Cox and *Manticula* Waterhouse, and the mystery group Aulacomyellinae Ichikawa. New genera are proposed from Devonian to Jurassic faunas of United States, members of Devonian and Early Carboniferous faunas of England, Scotland, Ireland and Germany, and from Carboniferous to Cretaceous faunas of Antarctica, Argentina, Australia, Canada, China, Mexico, Nepal and Russia.

New genera are proposed, including *Undosusia*, type species *Aphanaia tivertonensis* Waterhouse, 1979a (Family Atomodesmidae), *Enitoria*, type species *Rutotia grandis* Koninck, 1885 (Family Posidoniidae), *Pterinonova*, type species *P. eximius* Koninck, 1885, *Bradfordipecten*, type species *Pseudaviculopecten bradfordensis* McAlester, 1962, *Pterinoplica*, type species *Pterinopectinella spinifera* Newell & Boyd, 1995, *Tesseratia*, type species *Pterinopecten serbodowae* Fredericks, 1915, *Bifurcatatia*, type species *Aviculopecten meleagrinoides* M'Coy, 1851 and *Ornatipecten*, type species *Aviculopecten ornatus* Hall, 1883 (Family Pterinipectinidae), and *Natalissima*, type species *Pterinopecten* (*Pseudaviculopecten*) *casterorum* Fleming, 1957b, *Intercalatia*, type species *Aviculopecten exacutus* Hall, 1883 and *Yassapecten*, type species *Aviculopecten etheridgei* Koninck, 1877 (Family Natalissimidae), *Imposidonia*, type species *Posidonia elegantula* Waterhouse, 2000 and *Ralphimlaya*, type species *Aulacomyella neogeae* Imlay, 1940 (Family Halobiidae), *Undorugosa*, type species *Pecten* (*Aequipecten*) *wilczekiformis* Licharew, 1927, *Echiniferipecten*, type species *Clavicosta rugatula* Waterhouse, 1978 and *Carrollingeria*, type species *Aviculopecten carrolli* Hind, 1903 (Family Aviculopectinidae), *Confundopecten*, type species *Pecten limaeformis* Morris, 1845, *Burnettilina*, type species *Limipecten burnettensis* Maxwell, 1964 and *Elviniaria,* type species *Cyrtorostra limitans* Waterhouse, 1987 (Family Deltopectinidae), *Concentiolineatus*, type species *Streblopteria homevalensis* Waterhouse, 1987, *Tesselarulina*, type species *Aviculopecten wasserfallensis* Paul, 1937, *Redesdalia*, type species *Pseudamusium redesdalensis* Hind, 1903, *Astafievina,* type species *Lima sedgwicki* M'Coy, 1844, *Amleripecten*, type species *Streblopteria praetenuis* Koenen, 1879, and *Montorbicula*, type species *Streblopteria montgomeryi* Gonzalez, 2006 (Family Streblochondriidae), *Frigidusia*, type species *Manticula complanata* Crame, 1995 (Family Eurydesmidae), *Costellinaria*, type species *Aviculopecten subconoideus* Etheridge, 1876, *Inaequalitaria*, type species *Aviculopecten subquadratus* Bell, 1929, *Etheriplica*, type species *Etheripecten plicatus* Waterhouse (in Waterhouse & Jell, 1983), *Primaspina*, type species *Aviculopecten dawsonensis* Runnegar & Ferguson, 1969 and *Nodulipecten*, type species *N. hoskingi* n. sp. (Family Etheripectinidae), *Lineaspina*, type species *Annuliconcha dentatus* Newell & Boyd 1995 (Family Annuliconchidae), *Ciriacksia*, type species *C. ciriacksi* n.

sp., *Acerplica*, type species *Aviculopecten pincombei* Mitchell, 1924, *Stellaripecten*, type species *Pecten stellaris* Phillips, 1836, *Lamnipecten*, type species *Pecten dissimilis* Fleming, 1828, *Sinopectininia*, type species *Aviculopecten* (*Deltopecten*) *giganteus* Chao, 1927, *Fallaxopecten*, type species *Aviculopecten mccoyi* n. sp. and *Costatoplicatina*, type species *Pecten transversus* Sowerby, 1840 (Family Acanthopectinidae), *Pteropiria*, type species *Otapiria tailleuri* Imlay, 1967 (Family Otapiriidae), *Wallerobia*, type species *Enteropleura jenksi* Hopkin & McRoberts, 2005 and *Kotickia*, type species *Aulacomyella willeyi*, Kelly, 1991 (Family Bositridae) and *Ellesmerella*, type species *Posidonia areana* Tozer, 1961 (Family Aulacomyellidae), *Sedeoconcha*, type species *Pegmavalvula delicata* Newell & Boyd, 1970 (Pseudomonotidae), *Aprathichondria*, type species *Euchondria aprathensis* Rathman & Amler, 1992, *Velbertia*, type species *Euchondria vera* Drevermann, 1902, *Pellucipecten*, type species *Aviculopecten pellucidus* Meek & Worthen, 1860, and *Callytharrachondria*, type species *Euchondria callytharraensis* Dickins, 1963 (Family Euchondriidae). Newly named species are *Promytilus homevalensis*, *Intomodesma minisculus*, *Ciriacksia ciriacksi, Fallaxopecten mccoyi*, *Nodulipecten hoskingi* and *Eurydesma protrudus*.

New family Manticulidae is proposed within Ambonychoidea, Permoceraminae new subfamily is proposed for *Permoceramus* Waterhouse, 1970 in Family Atomodesmidae and Oretinae new subfamily is proposed for *Oretia* Marwick, 1953, in Family Pergamidiidae. New suborder Ambonychiidina is proposed for Ambonychioidea, Inoceramoidea and Alatoconchoidea. New superorder Pectinidia is proposed for pectiniform orders. New order Pterinopectinida is proposed for pterinopectiniform families, and new subfamilies Pterinopectinellinae and Tesseratiinae within Pterinopectinidae, new family Natalissimidae with subfamilies Natalissiminae and Pseudaviculopectininae within Pterinopectinoidea, new subfamily Chuluariinae within Claraiidae, and new subfamilies Echiniferipectininae and Spyridopectininae within Aviculopectinidae and Squamuliferipectininae within Deltopectinidae. Subfamily Streblopteriinae is proposed within Streblochondriidae. New subfamilies Echinorbinae and Mysidopterinae and Tribes Calcicanicularini and Echinorbini are proposed within Limidae. New suborder Etheripectinidina is erected, and Subfamily Heteropectininae and Girtypectininae are erected within Etheripectinidae, Subfamily Maccoyellinae within Family Oxytomidae, and Subfamilies Lamnipectininae and Costatoplicatininae within Acanthopectinidae. Bositridae new family is erected within Aulacomyelloidea, and Pegmavalvulinae within Pseudomonotidae.

List of contents

List of Tables

List of text-figures

Plate 1

Fig. 1, 2. "*Spyridopecten*" of Newell & Boyd not Campbell & McKelvey.
Fig. 3. *Deltopecten subquinquelineatus comptus* not Dana of Hosking (1931).
Fig. 4, 5. *Girtypecten sublaqueatus* (Girty).

Introduction

For any study of bivalves, a prime source of information is provided by the compilations of the Treatise series, published in 1969 and 1971. This is now considerably out of date, and replacements are under way. A very substantial study, with sweeping surveys of various groups and focus on shell structure has been provided by Carter (1990), and this work gives summaries of ideas then current on classification and relationships.

There have many substantial advances over recent years in classification and morphology, but at the same time there has been slippage in two important aspects. Regrettably, some authorities are proposing bivalve species and even genera even on the basis of a single valve, or at least single illustrated valve – and astonishingly, just exteriors. In syntheses, there has been some tendency to focus too heavily on trans-Atlantic faunas. Or at best, trans-Atlantic studies. Southern hemisphere faunas, whilst less diverse and less studied than those of the paleotropical and more northerly faunas, nonetheless include significant elements that contribute to understanding the overall evolutionary development of the subclass, and the incompleteness of studies that ignore southern faunas is worsened by neglect of faunas from China and even Siberia. The present survey is in no way complete, but examines some of the themes that are not fully settled, and also attempts to explore the somewhat neglected Devonian and Early Carboniferous pteriomorph bivalves. A number of new genera are proposed for species hitherto assigned to very broadly defined genera that clearly incorporate different morphological strands. Formalization of perceptions of different strands of species-links offers one of the pathways to resolving some of the complexities of evolutionary development. Just as genera based on a single species seem precarious until reinforced by other and congeneric species, family units based on a single genus may appear to be justified by “morphological space”, but are rendered more secure by the recognition of further genera. One consequence of such study is the inevitable complexification of the fossil record and the detection of new and hitherto unsuspected patterns of change, and closure or division of what were previously deemed to be simple evolutionary pathways. Some of yesterday’s clades now look too simplistic, and family trees have swollen and grown new branches, even though the gaps remain, to demand even closer study.

Acknowledgments

Many have helped with this study. I particularly and gratefully acknowledge the help from librarians, especially M. Dyer, Geological and Nuclear Science, Lower Hutt, New Zealand. Much help has been received from curators and scientists at museums and institutions, N. Hiller, Canterbury Museum, Christchurch, E. Fordyce and A. Grebneff, University of Otago, J. G. Begg, A. Beu, H. J. Campbell, J. S. Crampton and J. Simes, GNS Science, Lower Hutt, S. M. Parfrey, Queensland Museum, Brisbane, Yong Yi Zhen, Australian Museum, Sydney, G. R. Shi, Deakin University, D. Holloway, Museum of Victoria, Melbourne, the late J. M. Dickins, AGSO, Canberra, E. W. Bamber, Geological Survey of Canada, Calgary and Jean Dougherty, GSC, Ottawa, Bushra M. Hussaini, American Museum of Natural History, New York, M. Florence, Smithsonian Institute, Washington D.C., C. A. McRoberts, University of Syracuse, New York, M. A. Parkes, Natural History Division, National Museum of Ireland, Dublin, C. H. Holland, Trinity College, Dublin, J. Todd and Sarah Long, Museum of Natural History, London, E. M. Harper, Sedgwick Museum, Cambridge, Annelise Folie, Royal Belgium Institute of Natural Sciences, Brussels and M. M. Astafieva, Paleontological Institute, Moscow. Several paleontologists have greatly helped enquiries, D. W. Boyd, Laramie, M. Hautmann, Wurzburg, the late A. C. Rocha-Campos, Rio de Janiero, A. Biakov, Magadan, J. A. Grant-Mackie, Auckland, C.M. Waterhouse & M.E. Waterhouse, Sydney and T. A. Grunt, Paleontological Institute, Moscow.

Repositories

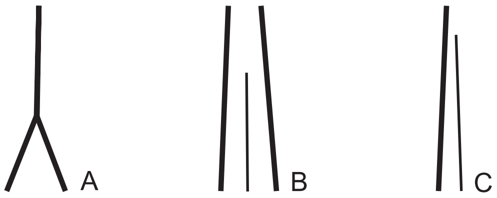
New Zealand collections are housed at AU – Department of Geology, Auckland University, FMo - Canterbury Museum, Christchurch, OU – Department of Geology, University of Otago, Dunedin, and TM - GNS Science institution in Lower Hutt. Australian collections are housed at the following institutions, with specimens catalogued by number and prefixes as follows: AMF - Australian Museum, Sydney, ANU – Geology Department, Australian National University, Canberra, CPC - Geoscience Canberra, GSQ – Geological Survey of Queensland, kept at Queensland Museum, MMF - Mining Museum, Sydney, SUP - Sydney University Department of Geology, Sydney, TMB - Tasmanian Museum, Hobart, UNE - University of New England, Armidale, UQF - Queensland Museum, Brisbane and UWA – University of Western Australia, Perth. Further afield, prefixes and institutions include AMNH – American Museum of Natural History, BGR – Slg der Bundesanstalt für geowissenschaften und Rohstoffe, Aussenstelle, Berlin, CASM E – Sedgwick Museum, Cambridge, DGM – Seçao de Paleontologia de Divisâo de Geologia e Mineralogia, Departamento Nacional de Producao Mineral, Rio de Janeiro, DGP – Departmento de Geologia e Paleontologia, Facultade de Filosofia, Ciências e Letras, Universidade de Sâo Paulo, GSC – Geological Survey of Canada, Ottawa, GSE. – Geological Survey office, Edinburgh, J. A. - Jacques Avias collection, University of Montpelier, IRSNB - Royal Belgium Institute of Natural Sciences, Brussels, NMI – National Museum, Ireland, Dublin, NHM (also BMNH) – Natural History Museum, London, OGC – Oil and Gas Commission, Dehra Dun, P – British Antarctic Survey, Cambridge, and USNM – Smithsonian Institution, Washington DC. Other specimens and localities are explained in the text.

Fossil localities of Australian material kept at the Queensland Museum, Brisbane, are serially numbered with prefix UQL, and New Zealand kept at GNS Science, Lower Hutt, are registered by number with prefix GS. Together with fossil localities from Nepal and Canada, they are described in Table 5 (p.192).

Morphological terms

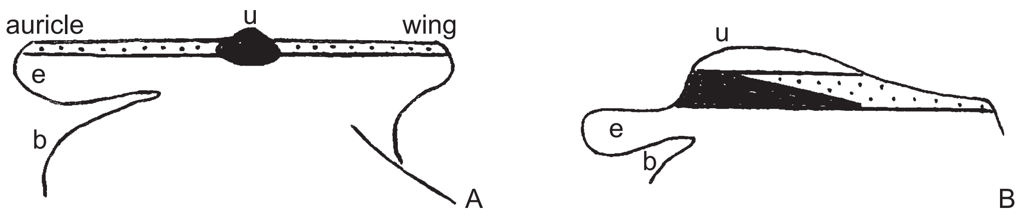
Three kinds of increase in ribbing are recognized (Text-fig. 1). Commonly, ribs increase by intercalation, or by branching. The terms branching and splitting are herein restricted to examples in which the strength of the ribs beyond the split are equal or subequal in strength. A third kind of increase occurs where the primary rib retains or increases its strength, and gives rise, on one flank or other, or close to the flank, to a very slender rib that gradually increases in strength. This kind of rib increase is termed **semicalate** if separate from but close to the primary rib, or **semifurcate** if in touch with the primary rib.

The terms procrescent, orthocrescent (acline) and retrocrescent are applied in the normal sense. Some shells change their growth habit, and become **bicrescent**. The shells commence as procrescent, and later in ontogeny, the anterior margin pushes forward, changing the shape of the shell as in some limoid species and genera.



Text-fig. 1. Mode of increase of ribs. A, bifurcation of primary rib. B, increase by intercalation, in which secondary rib commences between two primary ribs. C, example in which secondary rib branches from (semifurcation) or arises close to (semicalation) primary rib.

In descriptions of pteriomorphs for this study, the term **wing** (Text-fig. 2A) refers to the slender shell at the posterior dorsal and anterior dorsal margins of the valve, discriminated from the body of the shell by change in slope, and sometimes by different ornament. The **auricle** (Text-fig. 2A) is discriminated for the generally anterior right valve wing-like structure that is separated or partly separated from the umbonal slope and body of the shell by a byssal notch or infilling.



Text-fig. 2. Different kinds of ligament and cardinal extremities. A, hinge interior of Aviculopectinidina and Etheripectinidina, right valve, showing posterior wing and anterior auricle above byssal notch . B, Hinge in right valve of Monotidina (*Hokonuia*) with anterior ear above byssal notch, ear matches e in Fig. 2A and does not carry ligament on inner side. Ligament truncavincular, with resilifer placed at anterior end of the ligament. Black - resilifer, dots cover remaining ligament. b – byssal notch, e – interior of ear or auricle, u = umbo.

The auricle and wing in pteriomorphs carry the ligament on the inner side. Some pteriomorphs (in Monotidina) have an anterior **ear** in one or both valves, and the ear does not carry the ligament on its inner side (Text-fig. 2B). In Eurydesmidae an anterior **ear ledge** is recognised in which a modified and relict auricle in each valve is developed on the commissural side of a byssal channel or pseudolunule, probably occupied by a byssus. In such shells there appears to have been a withdrawal of the anterior wing-auricle posteriorly into the shell, so that the inner wing is represented by an anterior dorsal shelf, and a fold or tooth may develop on the shelf or at its posterior margin.

The ligament is described as **lineavincular** where it is traversed by deep grooves separated by ridges, and as **duplivincular** or **chevron** duplivincular where the ridges converge in a V under the umbo, and **multivincular** where there are mutiple ligament pits. The duplivincular ligament may loose its shape and become represented by a series of ridges inclined towards the umbo (**replivincular**), or be reduced to a narrow channel (**canalivincular** ligament). The **alivincular** ligament has a triangular ligament pit or resilifer, which may be very wide, occupying most of the length of the ligament (**lativincular**). In other alivincular-related genera, the resilifer may disappear, leaving a flat or **platyvincular** ligament, without resilifer. These terms are explained in Waterhouse (2001, p. 114, Text-fig. 9; Waterhouse & Chen 2006, Text-fig. 11). A new term is proposed for the ligament developed in Monotodea and Eurydesmatoidea – **truncavincular** – for ligaments that are anteriorly truncated, so that the resilifer, which occupies a median position in the normal alivincular ligament, is placed at the anterior edge of the ligament (Text fig. 2B). The truncavincular ligament is present in shells with an ear or ear ledge rather than auricle or wing.

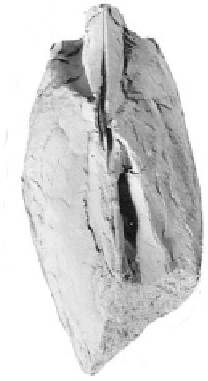
Epifaunal shells that lie on one or other valve have been termed pleurothetic. Some shells lie on the anterior face, which may become flattened: these are termed **anteroposited**. Pleurothetic shells that lie on the left valve are termed **sinistroposited**, and shells that lie on the right valve are termed **dextroposited**.

In shells identified as *Enteropleura*, a fine posterior ridge, or two ridges, have been treated as muscle tracks by various authors. But as the ridges extend as far as the posterior ventral margin, well beyond any muscle scar, that could not have been their cause or function, and they are regarded instead as slender strengthening ridges or carina.

A question over function and life style

The functional morphology of byssally attached bivalves was extensively discussed and illustrated by Stanley (1972), including close analyses of Pteriomorphia. But the habitat and mode of attachment and matters of mobility remain to be addressed for one aspect commonly observed in Late Paleozoic pteriomorphs belonging to a range of different genera in various families such as Aviculopectinidae, Deltopectinidae, and Etheripectinidae. It concerns the development of a very long anterior wing and anterior auricle, extending well beyond the anterior margin of the shell below the hinge. The right anterior auricle and left anterior wing are convex, and form a tube, open anteriorly (Text-fig. 3), whereas in some other groups the anterior wing-auricle couple close tight when the commissure is closed. It would seem that the wing-auricle projected so far forward as to make byssal attachment awkward, and arguably inefficient. The shells may have been mobile, but again, the large size of the wing contrasts with that of Pectinidae, known to be or have been mobile. The long anterior wing-auricle must have been advantageous, but precisely in what way requires further analysis. The great length of the hinge suggests that it acted as a stabilisation factor for the dorsal shell, and possibly the large auricle was important for the directing of water involved in feeding or motion.

Text-fig. 3. *Etheripecten leniusculus* (Dana), dorsal view, right valve to right, left valve to left, anterior at top of figure, showing left valve convex anterior wing and right valve convex auricle projecting anteriorly beyond body of shell, with gape in between. Original of *Pecten mitis* Dana, x1, USNM 4758. See Waterhouse (1988).



Abbreviations

OD – by original designation. SD – by subsequent designation. The nomination of a type species for a genus is by original designation unless otherwise indicated.

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

Nomenclature and endings

Superorders

Over recent years it has been found useful to recognise a category called superorder. This category is of high value, but instead of following the procedure of adding an appropriate ending to the root of the name used at other ordinal group levels such as suborder and order, an entirely different name is applied in bivalve studies, transferred from a higher category, or historic usage of order. Nowadays orders and suborders have a genus name root, and it is considered that ordinal names should all be similarly based on the one stem, and the application of such terms as “Superorder Palaeoheterodonta Newell, 1965” to the orders Actinodontida, Modiomorphida, Trigoniida and Unionida should be set aside as a non-conforming proposal. It is here suggested that either the superorder names be brought into harmony with other ordinal names, or that the present category of superorders be transferred to infra-subclass, because that allows more freedom. My preference is the first suggestion, because then orders fall in three categories, just like family rankings. It is understandable that authors have sought to preserve and sanction some of the charming medley of names invented for bivalve groups, but it may be timely to bring consistency into the categories of ordinal terminology. The question then arises about authorship. Should the author of the first proposal be attributed to all three ranks, following the procedure for family group names, or should each rank be authored specifically? Both systems have merit, and either system may be applied until and if the International Subcommission for Zoological Nomenclature decides to provide guidance. For simplicity, the name of the first attributed author is applied where name-change and rank shifts are involved, but this is provisional.

Ordinal ending – ida or oida?

Another source of perplexity is the deviation in endings for Order. A number of bivalve specialists add **oida** to the root of the genus. Brachiopod specialists add **ida**. One would hope in zoological nomenclature that specialists could achieve uniformity over such a matter, but in different fossil groups, the lead has been set by different specialists, and divergence has occurred, and stubbornness consolidated. On behalf of the -ida ending, it may be pointed out that five substantial volumes of the Treatise series on Phylum Brachiopoda have consistently used that ending, and no other studies on any single phylum can be matched in sheer volume or comprehensiveness. Many other major studies, including a number of recently published Treatise volumes, have used the -ida ending. The International Subcommission of Zoological Nomenclature (2000) provides no guidance on ordinal endings. The chief editor of the Treatise series, Kaesler (2006, p. xix), explained how a Colloquium on Zoological Nomenclature in 1958 voted “against the establishment of rules for naming taxa above family-group rank, because it was judged that such regulations would unwisely tie the hands of taxonomists”. Certainly, few would want that. But such a decision has hampered systematic and taxonomic students who would like to achieve consistency in terminal endings, and it is difficult to see how such consistency would interfer with progress and flexibility in classification.

On the understanding that -ida has been used widely, especially in Treatise series, the -ida ending is adopted for this study.

Methodology

An extremely useful approach over recent years has been cladistic analysis of character states, to determine major categories of associations. It has been decided, somewhat arbitrarily, for there can be little question that the hermeneutics of cladistics await substantive analysis, that major clades without convergence constitute orders, and these clades have been used to develop prime arrangements in Bivalvia. There is another methodology, older, but also of value, based on building up categories from below or “bottom up”. If several genera are closely linked in morphologies, they can make up a subfamily: if several subfamilies can be linked, they make up a family, and several families can be associated in superfamilies. These build into suborders, and suborders into orders, and so on. This approach has a circumscribed objectivity: there remains the need to judge the ranking of “morphological space” between categories, and the need remains to allow that not all groups were prolific and diverse enough to allow differentiation of every nomenclatural category, so that the number of categories may differ in different groups. Such failings underline the desirability of the independent approach towards classification that is offered by cladistics, but it cannot be said that cladistics have fulfilled their promise. Selection of characteristics remains open to partiality or bias. An example may be made of the cladogram presented for “Pectinida” by Newell & Boyd (1995, Fig. 16). There are patches of agreement with the bottom-up analyses presented in this report (Fig. 109), but there are also discrepancies. That is hardly surprising. Some families have been omitted – notably Oxytomidae, Monotidae and Buchiidae. Many character-states have been neglected, involving aspects of the hinge, its length, auriculation, nature of the right valve ornament and profile, and many aspects of ornament – even though this was virtually the main factor in discrimination used by Newell (1938) for genera (sometimes on only the left valve), genera that later were elevated in status to monogeneric families in Newell & Boyd (1995). Several types of ligament were lumped as “transitional”. Such partiality in treatment is a common flaw in innumerable cladistic studies. Furthermore the practise of cladistics has too often been based solely on soft-tissue characters with inadequate treatment of morphological attributes no longer found in living forms. Instead of relying solely on features of living material to provide the character states for analysis, it would be more objective to construct analyses in a time-controlled framework, with mutiple horizontal and vertical assessments. And that raises the problem of not being able to fully compare past and present character states. Given the complexity of biota and the unevenness of available data, it is hardly reasonable to expect that the application of simplistic formulae and selection no matter how judicious of character states will resolve major biological questions over classification: nor can the claim of “objectivity” be entertained without considerable tolerance.

But even if subjectivity were avoided, and all leading (!?) character-states were included, a problem remains. Whatever main features are chosen for emphasis in classification, it is clear that through time, their nature varies – with change to hinge, auriculation, wings, ornament, biconvexity and ligament, and shell structure. At present the construction of cladograms does not adequately take in account morphological drift and change. It moreover carries within its conclusions an interesting if unacknowledged premise that past taxa are grouped with living taxa because of their potential to develop a character seen in the living, but not in the past. The shell structure of *Lima* offers an example – it is now outstanding – it was not so different from other genera in the Paleozoic. This to me seems to be verging on the metaphysical. It may yet prove to be correct, and have strong implications for evolution. But I would like to see some evidence. In the “bottom-up” approach, a character-state that distinguishes a genus can have classificatory significance for a familial or ordinal group only if it is shared with the other genera, ancestral or descendent, that are placed in the same group. If such a character-state is not shared with preceeding genera, it should not feature in the circumscription of the group, except as a permitted variable. According to the “bottom up” approach, if the character-states are not known for ancestral genera, then they cannot be granted high significance in the classification of those genera, because extrapolation has to be carried into the realm of guess-work. Such an approach, I suggest, results at times in an overcircumscribed limitation to which character-states are to be assessed. In short, the two methodologies as now practised have a degree of incompatibility and a degree of uncertainty, and the need to reconcile them, as well as encouraging a modicum of compromise and a degree of incompleteness, underlines the desirability of recalibrating and improving cladistics, as well as softening the apparent rigidities of bottom-up techniques. No method escapes the need for a measure of further judgement. In the conclusions (p.187), the summary draws attention not only to the need to heavily modify published cladistic analyses, but to problems stemming from "bottom-up" study.

Ages, stratigraphic information

Without a great deal of research, reasonably precise ages and information on strata source cannot be provided. This has been all too evident in the Treatise series on Brachiopoda. Here no pretensions can be made – the data is of uneven reliablity, but where possible, is accurate: all too often reliance has to be placed on the original source, now long out of date. I am most familiar with Permian correlations, having been the first to propose the present arrangement for international stages and series (Waterhouse 1983c), and with Early to Middle Triassic stages etc, but largely rely on the correlations and ages given in publications, for all that some are well out of date.

Illustrations

Figures have been compiled from numerous sources. Some are marginal indeed, but illustrate significant species. Others have been kindly provided as acknowledged by various colleagues, and their photographs have been retained as sent, preferably with scale. For others without a scale, the size is indicated approximately.

SYSTEMATIC STUDIES

Phylum Mollusca
Class Bivalvia Linné, 1758
Infraclass Autobranchiata Grebben, 1894
Subclass Pteriomorphia Beurlen, 1944

An inclusive view of Pteriomorphia is adopted for this study, as in Waller (1998, Fig. 4) and Amler (1999, p. 238). Carter (1990) on the other hand recognised two classes, Pteriomorphia and Isofilibranchia (with Modiomorphida and Mytilida), closer to the classification in Waller (1978, pp. 349, 351).

Superorder Mytilidia Ferussac, 1822

[nom. transl. hic ex Mytillacés Ferussac, nom. subst. hic ex Isofilibranchia Iredale, 1939].

Constituent orders are Mytilida Ferussac, 1822 and Praecardiida Newell, 1965.

Order Mytilida Ferussac, 1822
Superfamily **MYTILOIDEA** Rafinesque, 1815
Family **MYTILIDAE** Rafinesque, 1815
Subfamily **MODIOLINAE** Keen, 1958

Diagnosis: Modioliform shells with beak slightly behind anterior margin in most genera, hinge margin smooth or marked by fine vertical striae, radial ornament usually absent or minor, periostracum fibrous hairy as a rule. Ligament opisthodetic, elongate and deep-set, supported by elongate nymph.

Genus ***Promytilus*** Newell, 1942

Type species: *Promytilus annosus annosus* Newell, 1942, p. 38 from upper Missourian Kansas City and Lansing Groups of Kansas.

Diagnosis: Shell thin, beaks subterminal to terminal, anterior lobe small and partly set off from rest of shell by broad sulcus extending from beaks to ventral margin sinuosity, umbonal ridge rounded and curved in outline, hinge line smooth.

Discussion: Newell (1942, p. 38) referred modioliform shells of Carboniferous to Permian in age to *Promytilus* Newell, 1942. *Promytilus* was defined as having terminal beaks, in distinction to *Volsellina* Newell, 1942, which was defined as having subterminal beaks, and the umbonal ridge was deemed to be almost straight in *Volsellina* and curved in *Promytilus*. But the species assigned to these two genera by Newell (1942) do not fully conform with his definitions, because two species ascribed by Newell to *Promytilus* have subterminal beaks, and one of the two species ascribed to *Volsellina* has curved umbonal ridges (Newell 1942, text-fig. 11). It is preferred to apply *Promytilus* to shells with ventral sulcus and curved posterior umbonal ridge, even though the beaks are not terminal (Waterhouse 1987), but possibly *Volsellina* may prove to be a cluster of species within *Promytilus*. In turn, both taxa named by Newell (1942), and especially *Volsellina*, may prove to be no more than Paleozoic forebears or close allies of the living genus *Modiolus* Lamarck, 1799. It is difficult to find any substantial difference to validate *Volsellina* other than age.

However Waller (2005, p. 10) took a different view. He stated that *Promytilus* was characterized by its anterior lobe in front of the beak, which is not true of the type species, as explained by the initial diagnosis of Newell (1942, p. 37) and confirmed by Soot-Ryen (1969). Nonetheless, it is not considered than the anterior position of the anterior lobe relative to the beak in many species assigned to *Promytilus* can justify a separate genus, and therefore Waller's statement should be modified but not entirely rejected, with the qualification that many rather than all *Promytilus* have an anterior lobe in front of the beak. Waller argued that *Promysidiella* Waller, 2005 evolved in a trajectory towards *Mytilus* during late Early Triassic time from *Promytilus*, last known in early Scythian. Nonetheless, the similarities in so many respects between *Promytilus* and the living *Modiolus* remain persuasive, suggesting that *Promytilus* provided or was part of the modiolid suite of genera, persisting to the present day, as well as giving rise, according to Waller's analysis, to mytilids in the early Mesozoic. But timing and trajectory are still under poor control. Waller (2005, p. 9) claimed that *Promysidiella* first appeared in the "early Anisian" Bithynian of Europe, but Bithynian is middle, not early, Anisian, following the Manasluan and Aegean substages (Table 1, p.16). *Mytilus eduliformis subpraecursor* Yin in Yang et al. (1979, pl. 2, fig. 14-16) from the Shichienfeng Group of Shansi Province, China, certainly looks close to *Mytilus* in shape, and was judged to be of late Scythian age, older than its proposed forebear, *Promysidiella*. Admittedly the interior is not shown in figures, but the byssal invagination stressed by Waller (2005) as typical for *Promysidiella* is lacking.

Australian species as a rule show fine discontinuous radial ridges. Newell (1942, p. 38) considered that such ridges in American species were due to corrosion of radially directed calcite prisms in the shell. This has not been confirmed for Australian species, and living mytilids and modiolinids have true external ridging.

Promytilus homevalensis new species

Text-fig. 4

Holotype: Specimen UQF 211901 from Early Permian (Sakmarian, early Artinskian) Tiverton Formation, Bowen Basin, Queensland, here designated.

Diagnosis: Small shells with pronounced sulcus and well curved posterior ridge, umbones subterminal, concentric growth lines and ridges crossed by irregular fine radial ridges and filae.

Material: Specimens from localities UQL 1626, 3127, 4512, 4519 and 4523, spanning the *Svalbardia armstrongi* Subzone and *Taeniothaerus subquadratus* Zone (see Waterhouse 2008),

Table 1. Lower and lower Middle Triassic stages.

Series	Subseries	Stage Himalaya	Stage Canada
Middle Triassic	Ladinian		
	Anisian	Illyrian	Illyrian
		Pelsonian	Pelsonian
		Bithynian	Bithynian
		Aegean	Aegean
		Manasluan	
Scythian (Lower Triassic)	Olenekian	Mesokantoan	Spathian
		Gangapurnan	Smithian
	Induan	Annapurnan	Dienerian
		Gangetian	Griesbachian
Lopingian (Permian)		Changhsingian	
		Wuchiapingian	

These subdivisions are based on ammonoid faunas. The Early Triassic is internationally subdivided into Induan and Olenekian, two very crude divisions that do not reflect the nature and evolution of the faunas. On the basis of seven monographic studies of Himalayan ammonoid assemblages, it was concluded by Waterhouse (2002c) that a fourfold subdivision was more natural, although less geopolitically acceptable, and that Tozer (1967) was correct in advocating such a subdivision. Himalayan subdivisions were preferred over Canadian ones, because the successions are much more complete, without so many missing zones and with richer faunas compared with the scattered and depauperate sequences of Canada. The Gangetian subdivision is of very long standing (Mojsisovics et al. 1895) and was validly proposed with well defined and characteristic ammonoid assemblages (Waterhouse 2002c). The often used Griesbachian Stage includes late Permian faunas (Kozur 1998, Fig. 1). The Manasluan Substage was introduced for rich faunas found above *Keyserlingites* faunas of the topmost Early Triassic, and found below *Paracrochordiceras* faunas of the Aegean Substage (Waterhouse 1999).

Tiverton Formation, Bowen Basin, Queensland.

Dimensions in mm:

Locality	Valve	Length	Height	Width
UQL 4519	left	38	22	9
UQL 4520	left	30	20.5	7
UQF 211901	right	39	28	8

Description: Shells of moderate size, equivalve, with subterminal umbones, umbonal ridge extending at 25-30° from the hinge and curving to lie approximately 50° from the hinge ventrally, anterior shell extends in front of umbones, and extensive sulcus extends from below umbo to posterior ventral margin. Hinge just over half of valve length, posterior margin rounded and extended. Concentric increments cover shell, about 12 per mm posteriorly, with growth steps and laminae, each with up to 20-22 increments, crossed by subfusc slightly erratic and impersistent radial ridges, increasing by intercalation. Ligament opisthodetic, canaliform, long and slender; no teeth.

The species will be further illustrated in a forthcoming study by G. R. Shi and the writer.

Discussion: The specimens described as *Promytilus cancellatus* by Maxwell (1964, pl. 3, fig. 4-6), also figured in Hill & Woods (1964b, pl. P11, fig. 10) and Hill, Playford & Woods (1972, pl. P11, fig. 10), have somewhat similar ornament and subterminal umbones, but lack the curved umbonal ridge and the prominent sulcus, thus approaching *Volsellina*. The species was referred to that genus by Waterhouse (1987, p. 137) in describing Maxwell's species from the Dresden Formation and lower Elvinia Formation of Sakmarian age in the southeast Bowen Basin of Queensland. Maxwell's types come from the Asselian Burnett Formation of the Yarrol Basin, Queensland. Clarke (1992, p. 34, Fig. 24G-I) reported Maxwell's species as *Promytilus* from the

Text-fig. 4. *Promytilus homevalensis* n. sp. Latex cast of holotype, right valve UQF 211907, from Early Permian Tiverton Formation, Bowen Basin, Queensland x 1.8.

Table 2: International subdivisions for the Permian Period, following Waterhouse (1983c) and Jin (1996).

Series	Stage
Lopingian	Changhsingian
	Wuchiapingian
Guadalupian	Capitanian
	Wordian
	Roadian
Cisuralian	Kungurian
	Artinskian
	Sakmarian
	Asselian

basal Bundella Formation and Tasmanites Shale of Tasmania, but the Tasmanian specimens are high, with umbones placed far from the anterior margin and no indication of radial threads.

Promytilus mytiliformis (Etheridge, 1892) from the Middle Permian Flat Top or Barfield Formation of the southeast Bowen Basin in Queensland is larger with less marked sulcus, stronger umbonal ridge and less conspicuous radials, compared with the present species. Etheridge's species was redescribed by Waterhouse (1980a, p. 106), in reporting the species as *Promytilus* from the Capitanian (Middle Permian) *Pseudostrophalosia clarkei* Zone of the Mangarewa Formation in New Zealand. The Tasmanian species called *Modiomorpha*? *ornatissima* by Johnston (1888, pl. 15, fig. 15) from Porter's Hill, Hobart, Tasmania, has a long hinge and less curved outline, as in *Volsellina*.

The present form is shaped like an Early Permian species identified as *Modiolus koneckii* Dickins (1963, pl. 8, fig. 6-11, text-fig. 9) from the Sakmarian and ? basal Artinskian Callytharra Formation, Fossil Cliff Formation and base of the Poole Sandstone in Western Australia, and differs mainly in the presence of fine low ribs. Dickins (1963) discussed the question of whether *Promytilus* should be distinguished from the living genus *Modiolus* Lamarck, and concluded that there appeared to be little difference, except for a better developed anterior lobe in *Modiolus*. That of the Tiverton species is not quite so prominent, but otherwise the species is close to *koneckii*.

Superorder Pteriidia Newell, 1965

[nom. corr. ex Eupteriomorphia Boss, 1982, nom. transl. hic ex Pterioida Newell, 1965].

Order Pteriida Newell, 1965

Suborders Pteriidina Newell, 1965, Pinnidina Waller, 1978, and Ambonychidina new suborder are referred to this order.

Suborder **AMBONYCHIIDINA** new suborder

This suborder is separated from Pteriidina, and is characterized by its opisthodetic ligament, and lack of anterior wings as a rule. Ligament normally duplivincular (lineavincular), platyvincular or multivincular, musculature heteromyarian or monomyarian. The members of the suborder differ considerably from Pteriidina in habit, being bottom-hugging epifauna or semi-infaunal to infaunal. Pinnidina are infaunal mytiliform or cuneiform shells with anterior umbones, with long linear ligament, edentulous hinge and dimyarian musculature, the anterior adductor small.

Three superfamilies are recognised in Ambonychiidina, Ambonychioidea and Inoceramoidea, as in Nevesskaya et al. (1971), and Alatoconchoidea Termier, Termier & Lapparent, 1973, is assessed as a superfamily. Alatoconchoidea shares a lineavincular ligament, and is distinguished by the large size, strong carination and exceptional shape.

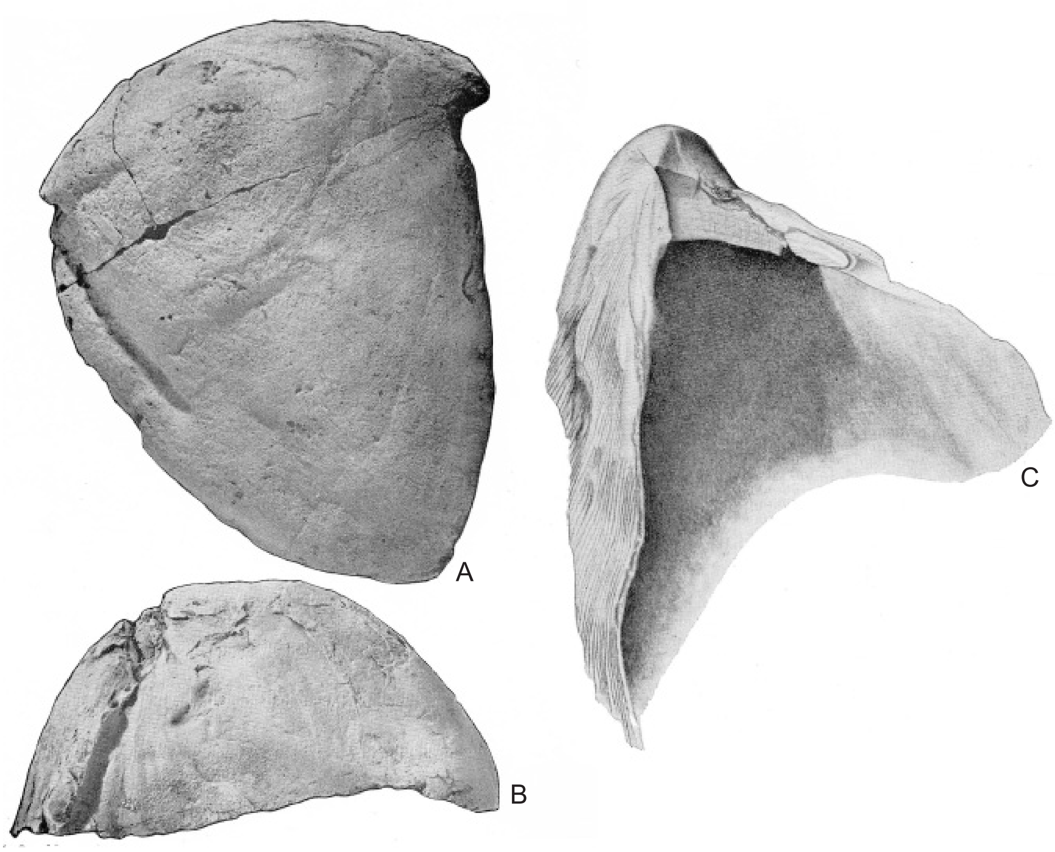
?Superfamily **AMBONYCHIOIDEA** Miller, 1877

Family **MANTICULIDAE** new family

Text-fig. 5 - 7

Name genus: *Manticula* Waterhouse, 1960, p. 428, from Upper Triassic of New Zealand, here designated.

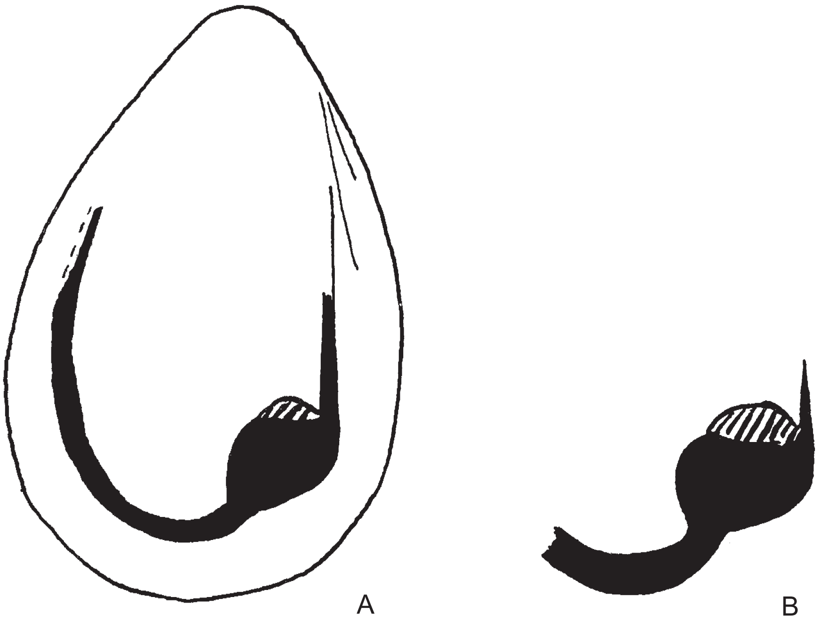
Diagnosis: Inequivalve, right valve very strongly inflated, left valve convex, inequilateral, shell surface marked only by faint growth lines and weak growth steps, umbones anteriorly placed, no byssal notch clearly present, ligament developed as triangular area, usually flat, internal at maturity with low linear grooves, no internal shelf or teeth, pallial line faint, anterior adductor small and faintly impressed, posterior adductor posteriorly placed, relatively small with dorsally



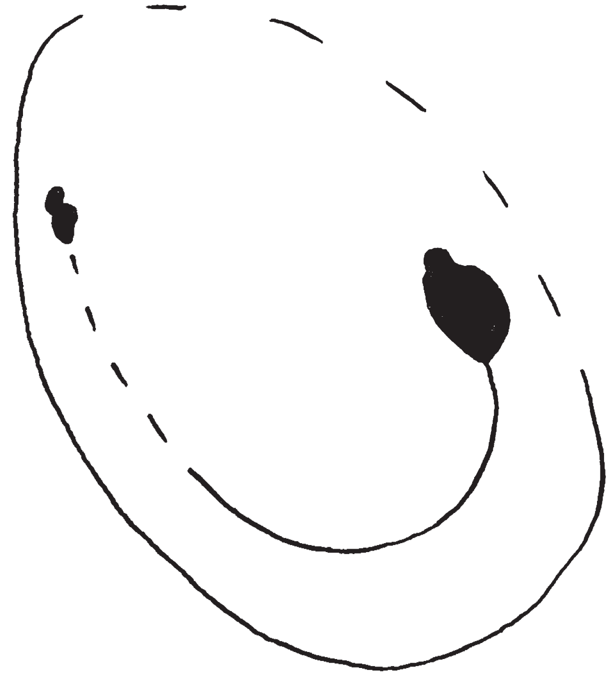
Text-fig. 5. *Manticula problematica* (Zittel). A, anterior view of highly inflated and slightly squashed right valve TM 2162, x 0.5. B, Posterior view of specimen TM 2171, showing inflated right valve and less inflated left valve, x 0.5. C, umbonal part of right valve, latex cast of TM 2159, x1. Specimens from Late Triassic of Nelson, New Zealand. See Waterhouse (1960).

attached posterior retractor. Shell of outer foliate lamellae and internally massive aragonitic CL structure, shell apparently calcitic, no prismatic layer.

Discussion: The type species of *Manticula* is *Mytilus problematicus* Zittel from Upper Triassic beds of New Zealand and New Caledonia, and has been studied especially by Zittel (1864), Trechmann (1918), Benichou (1960) and Waterhouse (1960). The shape is mytiloid, apart from grossly inflated right valve (Text-fig. 5). Cox (1969b, p. 314) ascribed the genus to Pergamiidae Cox, 1969b, and this was accepted without question by Crame (1995, p. 309) and Waterhouse & Gupta (1982). But *Pergamidia* Bittner, 1891 has an external amphidetic ligament, whereas the ligament in *Manticula* (see (Waterhouse 1960, Fig. 3, not Wilckens 1927 as claimed by Cox, 1969b) is opisthodetic and internal at maturity. The muscle scars, especially that of the posterior adductor (Text-fig. 6, 7), strongly suggest placement within Ambonychioidea or Pterioidea, and the lack of an outer layer of shell made up of prisms possibly favours an ambonychioid relationship. However no genus can be found that is very close to *Manticula*. Ambonychiidae are generally equivalved, with moderately short hinge lacking a resilifer and lineavincular in nature, and as a rule, a few simple teeth (Pojeta 1966) are sited on an inner anterior shelf. The muscle field is heteromyarian or usually monomyarian. The shell of Ambonychiidae may have an outer prismatic or homogeneous layer and inner ostracum of lamellar nacreous aragonite, especially in



Text-fig. 6. *Manticula problematica* (Zittel). Internal moulds of left valves x 1 showing posterior adductor impression with posterior retractor (cross-hatched) and part of pallial line. A, J.A. 9.277a. B, J.A. 9.892. From Late Triassic of New Caledonia, figured by Benichou (1960, pl. 17).



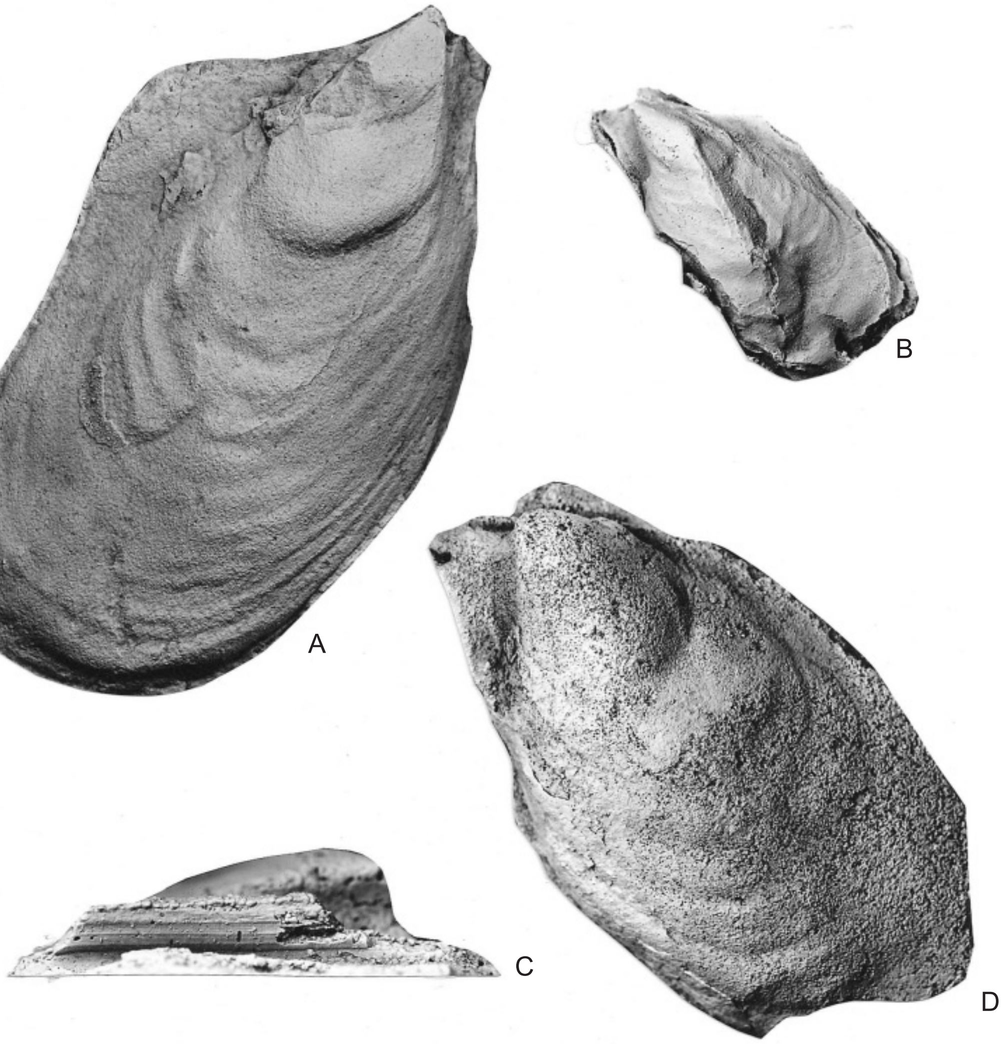
Text-fig. 7. *Manticula problematica* (Zittel). Internal mould of left valve showing posterior adductor impression, pallial line and anterior scar, sketch of specimen accompanying TM 14977, Upper Triassic of New Zealand, GNS reference collection, x1.

earlier forms, with crossed foliate structure appearing later. They are mostly of mid-Paleozoic age, commencing in the middle Ordovician and possibly ranging into Lower Mississippian, according to Newell & LaRocque (1969a). Family Myalinidae appeared in Carboniferous faunas and ranged into the Mesozoic Era according to Newell (1969a, p. 289). They more commonly lack hinge teeth, and have similar muscle field, but the shell includes thick prismatic layers as a rule. The genus *Manticula* is highly distinctive, and is allocated to a separate family, of uncertain affinities, because it has a somewhat distinctive shell composition and does not have a lineavincular ligament. It appears close in various respects to Myalinidae.

Waller (2005) interpreted *Manticula* from a study by Crame (1995) which referred a species from Cretaceous deposits of the Antarctic to the genus. He reported a small skewed anterior auricle in each valve and a very broad shallow ligament pit. Both Crame (1995) and Waller (2005) stressed a close relationship between *Eurydesma* and *Manticula*. Carter (1990) described foliate shell, and an irregular simple middle fibrous prismatic layer in *Eurydesma* somewhat like that of *Manticula problematica*, and noted that the prisms were differently arranged from those of myalinids, inoceramids or atomodesmids. Waller (2005, p. 8) also suggested that *Eurydesma* and *Manticula* had similar calcitic microstructures, including layers that are calcitic cross-foliated and a similar innermost aragonitic microstructure with CL structure described by Carter (1990, p. 203). But the two genera are not close in shape or interior. *Mytilus problematicus* Zittel, 1864 lacks the posterior groove seen in *complanata*, and lacks the fine and close-set growth-wrinkles and radial ribs over the umbones of *complanata*. The species *problematica* has a much more inflated valve, and this is the right valve. Avias (1953, pl. 24, fig. 1-3) and Crame (1995, p. 306) confused the orientation and valve identification for one specimen: their swollen so-called left valve is the right valve, and the small far less convex valve is the true left valve. Benichou (1960) studied large collections of the species from New Caledonia, and also found only the right valve to be swollen, and corrected the interpretation offered by Avias (1953). However not all specimens have been checked, and therefore it cannot be ruled out that some specimens developed an inflated left rather than right valve. The one reservation to be kept in mind is that the right-left combination of an Avias specimen was misinterpreted, and left and right valves figured by Crame (1995) were also misinterpreted (see p.124).

The ligament area, seldom seen in *Manticula problematica*, forms a small triangular striated area, at the level of the commissure in immature specimens and sunken well below in larger shells, with narrow margins each side that do not form part of the ligament as far as can be discerned. The presence of a resilifer is doubtful – obscure at best, and nothing like the resilifer that is found in a few specimens of *Eurydesma* (see Text-fig. 59A) or in *Pergamidia* or Pectinidia, because it occupies virtually all of the dorsal commissure. In *Ambonychia,* many myalinids, *Eurydesma* and other genera, a small internal shelf is present below and in front of the ligament. This is absent from *Manticula*.

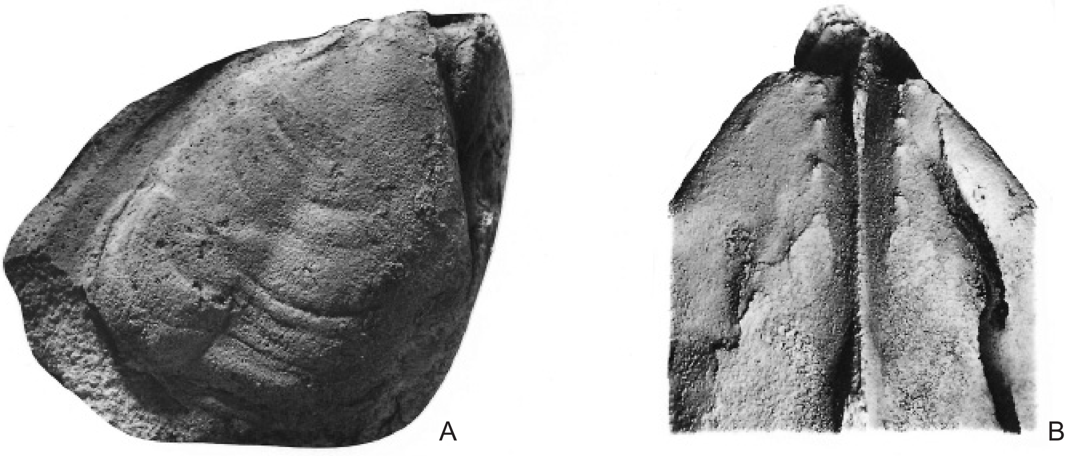
No *Manticula* has been found to clearly show the tiny auricular- or ear-flanges revealed for the Antarctic shells named *complanata* by Crame (1995), and no specimen has been found to indicate juvenile structures buried by later shell. That leaves open the possibility that the structures were resorbed in type *Manticula*, which remains to be proven, or that the small Antarctic specimens are not fact related to mature *complanata*, and the latter option has presumably been carefully explored and dismissed. Some specimens in the collections at GNS Science, Lower Hutt, show that the ligament is bordered anteriorly by a flange, forming both the anterior wall to the ligament and the exterior, including the commissure, of the shell, and this may be bent – whether by distortion or in its original state being uncertain. In *Eurydesma*, the ligament area is tapered under the umbo – unlike the arrangement in *Manticula*, which is highest at the anterior margin.



Text-fig. 8. *Kolymia* from Late Permian of Verchoyan, Siberia. A, *Kolymia verchoyanica* Lutkevich & Lobanova N179/11570, right valve x1. B, *K. merklini* Muromseva N186/11570a, left valve aspect, x1. C, *K. inoceramiformis* Licharew, N164/11570, showing part of ligament area of left valve, x5. D, left valve of same species N179/11570 x1. Material from V. A. Muromseva, 1978, kept at Paleontological Institute, Moscow, photographs supplied courtesy of K. A. Astafieva-Urbaiitis.

Crame (1995, pl. 2, fig. 3) figured a rubber peel from a left valve of *Manticula problematica* that claimed to show a deep subcentral resilifer, but the figure is unlabelled, and the text does not explain detail sufficiently to be convincing. Crame had to rely on a mould that showed the underside of the ligament area, and that is always difficult to interpret. The illustration suggests a flat triangular ligament area, terminated anteriorly (on the right side of the figure) by a ridge, in front of which is a broad bulge leading to the anterior margin (TM 7672). The assumption that the crest of the bordering ridge carried part of the ligament was noted as an unlikely conjecture in the analysis by Waterhouse (1960), and it remains unproven. The Crame specimen was inspected at GNS Science, Lower Hutt, and does not appear to confirm that a resilifer is present. Possibly, the anterior ridge and anterior groove marked the exit for a left valve byssus, because, with such a large right valve, the shell may have been pleurothetic, and left valve attached.

The species *complanata* has to some degree a hinge structure, anterior ears and shell structure approaching features of *Eurydesma,* as elaborated herein on p.123. That these similarities cannot be projected to *Manticula problematica* is shown by the muscle field. It is large, posteriorly subcentral, and subpectiniform in *Eurydesma* (Text-fig. 61). Very different musculature is found in *Manticula*, as figured in Text-fig. 6 and 7, with the posterior adductor much smaller, and sited close to the posterior-ventral margin, much as in Atomodesmidae, Myalinidae and Mytilida. *Manticula* also shows the posterior part of an entire pallial line, and signs of an anterior scar (Waterhouse 1960), suggesting a pterioid, ambonychioid or even mytilid affinity. This conflicts with the interpretation which assigns *Manticula* to Eurydesmidae (Carter 1990, Waller 2005). The muscle field is preserved as illustrated in some New Caledonian specimens. For New Zealand material, it was described by Waterhouse (1960) for specimens from GS 7615 (now R17/f8557) in the GNS type collection. There also suggestions of similar scars in TM 14927, and in a specimen from GS 4554 (GNS Reference collection), and in a left valve from Nelson.



Text-fig. 9. A, *Kolymia pterinaeformis* Popov, right valve UQF 70036, internal mould x1. B, *Kolymia* sp., N186/11570b, dorsal aspect of specimen with valves conjoined, showing pedal scars close to hinge x6. Specimens from Late Permian beds of Verchoyan. B kept at Paleontological Institute, Moscow. Photograph supplied by K. A. Astafieva-Urbaiitis.

Superfamily **INOCERAMOIDEA** Giebel, 1852

Amler (1999) referred Inoceramidae to Ambonychioidea Miller, but this is contrary to the rules of Zoological Nomenclature, because Inoceramidae Giebel, 1852 was proposed well before Ambonychiidae Miller, 1877. In the usage promulgated by McCormick & Moore (1969) in the Treatise, inoceramids were referred to Pterioidea. Nevesskaya et al. (1971) recognised both groups as separate superfamilies, and this is followed herein. Some doubt remains over the relationship between the two: they are close in many respects, and although the multivincular hinge in many Inoceramoidea suggests Pteriidina, there are as a rule differences in scale and number between the multivincular ligament pits of Inoceramoidea compared with those of Pterioidea.

Inoceramoidea are characterized by opisthodetic ligament and prismatic shell. The ligament is platyvincular or with mutiple ligament pits, and teeth are as a rule lacking.

Family **ATOMODESMIDAE** Waterhouse, 1976

Diagnosis: Medium to large shells, inequivalve to equivalve, inequilateral, umbones anteriorly placed, byssal notch or gape may be present in both valves but generally absent, ligament normally platyvincular external to semi-internal, posterior adductor scar moderate in size, no anterior adductor scar, pallial line discontinuous, pitted, shell of slender prisms.

Discussion: Neither the source nor descendents of Atomodesmidae are clearly established. Kolymiidae Kuznestov, 1973 is close in size, shape and prismatic shell to Atomodesmidae, but a small anterior wing is developed in each valve (Text-fig. 8, 9) and a prominent gape may be enclosed by the anterior wings of the two valves, whereas in atomodesmids, the two valves are often adpressed along the anterior commissure. The ligament is developed above the inner shell layer in Kolymiidae, whereas that of atomodesmiids is placed above the prismatic layer. That suggests Kolymiidae are like Retroceramidae Pergament in Koschelkina, which is shown to be close in the development of its ligament to the pterioid Isognomonidae (Crampton 1988), whereas atomodesmids are closer to the arrangement in the Inoceramidae. There are further differences between members of the two families. *Kolymia* (Text-fig. 9B) displays a very large pedal scar close to the hinge, with a row of pits extending anteriorly to the inner umbo, unlike musculature seen in atomodesmids. It has been speculated that the anterior adductor lay within the umbonal septum of atomodesmids, but this is uncertain. Recent studies on classification that were summarised in Amler (1999, p. 239) have ignored both Kolymiidae and Atomodesmidae, possibly because Kauffman & Runnegar (1975) had argued that *Atomodesma* and *Kolymia* were Late Paleozoic representatives of Inoceramidae. These authors preferred an economy of classification, as was fashionable for a few decades (see Waterhouse 2001, pp. 107, 108), and their approach has been overtaken by the diversification of biota recognized in current studies, both at family and higher level and at generic level amongst atomodesmids and kolymiids. The inoceramid *Tenuipteria* may well be like atomodesmids in its hinge, but its hinge was clearly modified from a multivincular ligament, and it appears that suppositions mustered by Kauffman & Runnegar do not counter the usefulness and objectivity of referring a compact group of Late Paleozoic genera to Atomodesmidae, with many genera recognized by Muromseva (1984), Astafieva (1993) and Biakov (1992, 2007), separate from a large diverse group of Late Mesozoic genera placed in Inoceramidae. Given the fossil record, it is still uncertain that atomodesmids gave rise directly to Inoceramidae, and if cryptic descendents did survive through the Triassic Period, their morphological affinities remain unestablished. Cox (1969c) recorded the supposed inoceramid *Parainoceramus* Voronetz as coming from Upper Triassic, but the diagnosis proferred by Cox (1969c, p. 320) does not necessarily apply to the type species of *Parainoceramus* (Speden 1970). As well, some supposedly inoceramid species from Siberia have been reassigned to Permian genera (Waterhouse & Chen 2006, p. 80), and Astafieva (1986) treated *Parainoceramus* as Permian and treated the type species as invalid, and referable to *Kolymia* Licharew (Astafieva 1993, p. 117).

In rebutting some of the assumptions in Kauffman & Runnegar (1975), Dickins (1983) provided an overview of the *Atomodesma* ligament as compared with that of other genera deemed to have been related. He noted that the ligament area of *Atomodesma* was relatively wide and opisthodetic, and, according to Kauffman & Runnegar (1975), would seem to have been composed of a thick layer of fibrous ligament covered by a single outer lamellar sheet. However, Dickins (1983, p. 60) suggested, the ligament instead might have involved several fibrous and lamellar sheets, or even a sheet in which there was no differentiation into fibrous and lamellar layers. Such possibilities are important, because ambonychiids and myalinids have lineavincular ligaments, in which alternating bands of fibrous and lamellar ligament are attached to deep grooves and ridges, in parallel rows (lineavincular) rather than in chevrons (duplivincular). Dickins rejected Pojeta's 1978 claim that (lineavincular) grooves are necessarily at an angle to the hinge-line. He showed that they may be parallel or oblique, and, as established by Waterhouse (1959a) for platyvincular ligaments in atomodesmids, the grooves may pass into prominent growth-lines over the outer shell. Moreover Dickins (1983) was able to point to members of ambonychiids, myalinids, arcoids and cyrtodonts that varied from their normal form of ligament, in developing a channel-form ligament without deep attachment grooves, and without resilifer, just as in atomodesmids. Moreover, it may be added, whereas the aforementioned groups varied and approached atomodesmids in the nature of their ligament, no atomodesmids show resilifer, or duplivincular or lineavincular ligaments. The ligament is semi- internal in Atomodesmidae and is internal in Ambonychiidae.

The source of the atomodesmids remains uncertain. Ambonychiids provide the most commonly preferred root. Carter (1990) noted the similarity of atomodesmids to ambonychiid genera *Cleionychia* Ulrich and *Amphicoelia* Hall of Ordovician and Silurian age respectively. Campbell (1961) figured as *Posidonia* a valve from the *Levipustula levis* Zone in Kuttung rocks of New South Wales that Runnegar (1972) suggested might have been ancestral to *Atomodesma* and *Kolymia*. The Campbell specimen is obscure, and poorly known. Genus *Amosius* Gonzalez & Waterhouse, 2004, type species *Eurydesma harringtoni* Gonzalez, 1972b from the lower *Levipustula levis* Zone of Serpukhovian or probably Bashkirian to Moscovian age in Argentina, has prismatic shell, platyvincular ligament, and anterior denticle. It would seem to be ambonychiid, and a somewhat similar but older member of the same or related genus, as yet undiscovered, may have provided the ancestral source for atomodesmids. As shown below, Atomodesmidae are represented in the Bashkirian-Moscovian fauna of Argentina, but add limited information about the nature of early Carboniferous or Devonian root-stock.

It was underlined by Dickins (1983, Fig. 1A) that the early Carboniferous genus *Posidoniella* Koninck, 1885 showed a right anterior auricle and byssal notch, like that of specimens ascribed to *Atomodesma mytiloides* Beyrich by Dickins (1963, pl. 10, fig. 5) from the younger Early Permian Wandagee and Norton Formations of the Carnarvon Basin and Nooncanbah Formation in the Fitzroy Basin in Western Australia. Unfortunately, Dickins did not determine whether or not the ligament underlay the "auricle" in his specimen, and it is difficult to be sure from his figure (1963, pl. 10, fig. 2) that the auricle is not merely a deflection of the anterior margin, because in that figure the ligament appears to stop under the anterior umbo. Unnoted by Dickins (1983), the left valve of *Posidoniella vetusta* Koninck (1885, pl. 31, fig. 8) shows a left anterior wing. That surely implies a pterioid relationship, differing from Kolymiidae, which do have a left valve anterior wing but no conspicuous right valve byssal notch. As a rule, and unlike Kolymiidae, atomodesmids do not have an anterior wing on either valve, and normally, do not show any gape (see for instance Kaufmann & Runnegar 1975, pl. 3, fig. 1; Muromseva 1984, pl. 7, fig. 9b, pl. 11, fig. 5b; Waterhouse & Chen 2006, text-fig. 9D), whereas in *Kolymia* and allies, the anterior lobes terminate with a large gape (see Muromseva 1984, pl. 18, fig. 3b; Astafieva 1993, pl. 13, fig. 5). Unfortunately *Posidoniella* is so poorly known internally that any purported relationship between *Posidoniella* and atomodesmids provides little firm information on the development of the group, and the need for caution remains, because the presence of a byssal notch and anterior right valve ear does not closely accord with aspects of *Atomodesma*. Carter (1990, p. 197) regarded *Posidoniella* as ambonychiid, whereas Runnegar (1979) regarded it as cyrtodontid. *Posidoniella* has calcitic regular prismatic and nacreous structure in the right valve, but the left valve shell structure is so far not known.

A more meaningful alliance has been established through *Malimanina* Waterhouse, 2001, p. 112, named for *Posidoniella malimanensis* Gonzalez, 1998 from Carboniferous of San Juan

Province, Argentina. The shell is characterized by strong concentric rugae and platyvincular ligament, with no umbonal deck or anterior wings. Small rounded pits extend along the pallial line, and small radially elongate scars from mantle insertions lie behind the pallial line. The shell is predominantly of calcite prisms. In all known attributes, the species accords with atomodesmids, except for the absence of an umbonal deck. Waterhouse (2001) therefore proposed a new genus, placed in a new subfamily, which was regarded as an early atomodesmid. The age of *Malimanina* was given as Tournaisian by Gonzalez (1994), which would rule out derivation of *Atomodesma* and allies from either *Amosius* by loss of the teeth and development of a umbonal septum, or from Kolymiidae, by movement of the anterior lobe and septum back under the umbones, as proposed by Waterhouse (2001, p. 107) in suggesting a pteriidin origin for Atomodesmidae. However this dating is now corrected to Serpukhovian-Bashkirian (C. R. Gonzalez, pers. comm.): here an age of Bashkirian into Moscovian is preferred. The origin of *Malimanina* remains obscure, and options remain open for derivation from an ambonychiid or pteriid source.

Atomodesma sp. B described by Gonzalez (1983, 1990) from the *Levipustula levis* faunas of Chubut, south Argentina, has a large furrow in each valve, looking close to *A. uniplicatum* Waterhouse, 1979a from the late Early Permian faunas of Western Australia. The two species stand out from remaining and younger species of *Atomodesma*, which have more and narrower furrows. Two other possible atomodesmids are also known in the *levis* faunas of Argentina, as well as a possible member of Kolymiidae (Gonzalez 1983, C. R. Gonzalez, pers. comm.). In New Zealand, large fragments of an unknown atomodesmid species have been found in the Croisilles ophioloid association, likely from isotopic evidence to be of Late Carboniferous in age (Waterhouse 1966, Fig. 4; 2002a, pp. 124-125). The species is subquadrate in shape, close to one of the Carboniferous species described by Gonzalez (1983), but lacks the strong rugae of the Argentinian form.

A summary of classification that expresses the evolution of the groups, is as follows:

Family Inoceramidae Giebel, 1853
    (Jurassic, Cretaceous) subfamilies
    (Triassic) no known Inoceramidae
Family Atomodesmidae Waterhouse, 1976
    (Triassic) doubtful (probably derived) occurrences of Atomodesminae in basal Triassic.
    (Permian, Carboniferous) Atomodesminae Waterhouse, 1976
    (mid- Carboniferous) Malmanininae Waterhouse, 2001
    Incerte sedis
    (Permian) Permoceraminae n. subfam.

For Permoceraminae, the fossil record favours a short-lived development of (or reversion to) multivincular hinge from Atomodesminae, and suggests that the Inoceramidae arose de novo in Mesozoic time. But gaps in the fossil record cannot be regarded as conclusive, and it might be equally if not more strongly argued, as by Russian authorities, that *Permoceramus* marked the commencement of Inoceramidae. The essential point is that the evolution of *Permoceramus* marked a substantial step, with the development, short-lived or not, of a new family-group. To not accept this suggests a scepticism about evolution, and infers that Atomodesmidae, Kolymiidae and Atomodesmidae and presumably Retroceramidae all formed a compact group, in which substantial changes in morphology were of no significance for classification.

Subfamily **MALIMANININAE** Waterhouse, 2001

Diagnosis: No umbonal plate, ligament channel-form.

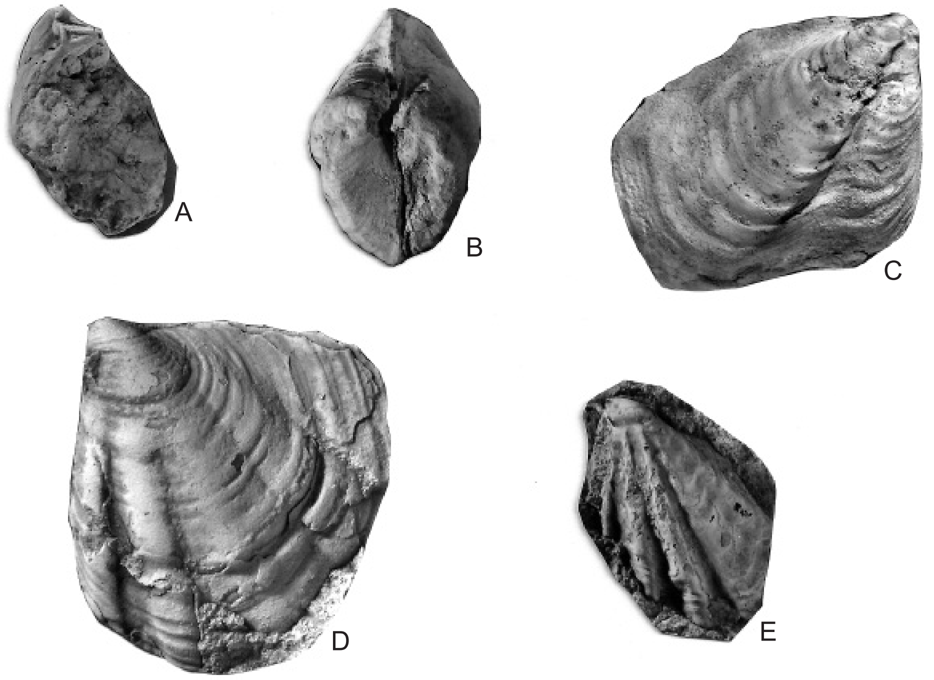
Discussion: Only the genus *Malimanina* Waterhouse, 2001, p. 112 is so far known, based on type species *Posidoniella malimanensis* Gonzalez, 1998, p. 177, from Carboniferous of Argentina. The internal structures of most other Carboniferous shells like atomodesmids in shape and ornament are not known. The question remains as to whether this genus marked a step in atomodesmid evolution towards *Atomodesma*, or was a side-shoot, involving loss of umbonal septum from atomodesmid stock. Further study is required to establish the relationship to the Early Carboniferous genus *Posidoniella* Koninck, 1885. This genus shows no indication of an umbonal septum, and it displays a small right valve anterior ear or auricle, byssal notch and a left valve anterior wing, suggesting a pteriiform source. If it was ancestral, then Inoceramoidea must be transferred to Pteriida, as in Waterhouse (2001).

Subfamily **ATOMODESMINAE** Waterhouse, 1976

Text-fig. 10

Diagnosis: Umbonal deck developed below platyvincular ligament.

Discussion: Members of Atomodesminae are most prominent in Permian high latitude to temperate paleolatitudes and extended widely over Gondwana and into North America. The genera recognised in Australia, Timor, Himalaya, and New Zealand are based on external appearance of ornament and shape, and on internal features. More emphasis has been placed on external appearance in Russian studies, following the analysis of Inoceramidae, for which taxa are well established, and particularly well justified for such distinctive forms as *Cigarella* Astafieva. Genera and species are most abundant in Siberia and New Zealand, with a much longer time range in



Text-fig. 10. *Atomodesma*. A, *A. elongatum* Wanner, plaster cast of specimen figured by Wanner (1922, text-fig. 13) as *A. variabile*, from Basleo, Timor, x1. B, C, dorsal aspect and right valve of *A. uniplicatum* Waterhouse, holotype USNM 124758 from Nooncanbah Formation, Western Australia, x 0.5. D, *A. elongatum* left valve from Ngawal Formation, Nepal x1. E, *A. multifurcatum* Wanner, left valve from Ngawal Member, Nepal, x1. A, now kept at Nationaal Natuurhistorisch Museum Naturalis, Leiden, D, E unregistered specimens kept at Queensland Museum, Brisbane.

New Zealand (possibly Late Carboniferous). Occurrences are more scattered in the Himalaya and Australia, and are moderately diverse in the Carboniferous of Argentina.

Genus ***Aphanaia*** Koninck, 1877

Text-fig. 11, 12

Type species: *Inoceramus mitchelli* M'Coy, 1847, p. 299, SD Dickins (1956, p. 23) from Middle Permian (Wordian) Branxton Formation, New South Wales.

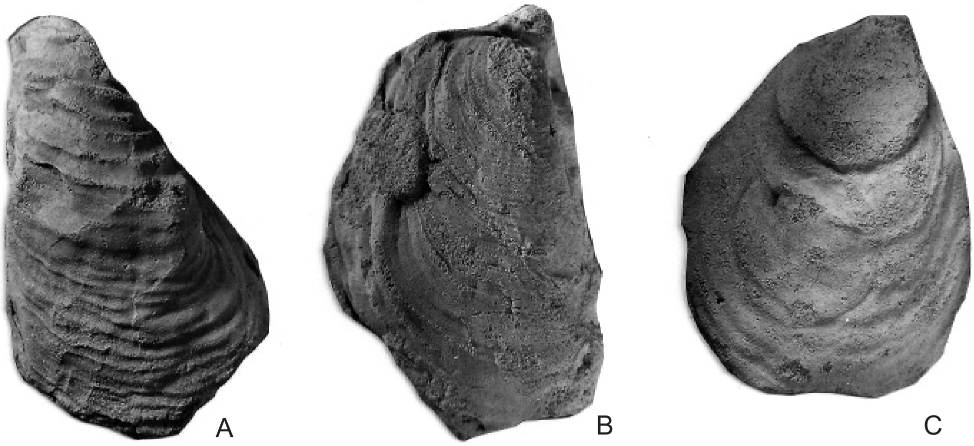
Diagnosis: Shells without radial grooves and plicae, characterized by left valve being more inflated than right valve, fine growth wrinkles of variable strength, may branch or terminate abruptly, growth steps usually prominent on right valve, no anterior auricle, posterior wings variably developed or absent.

Text-fig. 11. *Aphanaia otamaensis* Waterhouse, showing umbonal septum, ligament area, and prismatic shell. OU specimen from Early Permian of Southland, New Zealand, x2. See Waterhouse (1979a).

Discussion: The ligament of type *Aphanaia* is narrower and less well formed than in *Maitaia* Marwick, 1934, 1935, at least in the type species, but is better developed in some other species. Its growth habit often involves one to three major growth steps, especially in the right (smaller) valve (Dickins 1956, pl. 4, fig. 1). Specimens from one station in the Hunter Valley, New South Wales, vary considerably in the strength and spacing of commarginal ornament.

Atomodesma Beyrich, 1864 differs in being subequivalve to equivalve, with lateral grooves and ridges, and a strong tendency for the anterior face of each valve to form a platform (Waterhouse & Chen 2006, Fig. 9D), as shown in Text-fig. 10: it was anteroposited on the sea-floor. *A. uniplicatum* Waterhouse (1979a, pl. 1, fig. 1, 2, 4, 5) from the Nooncanbah Formation of Baigendzinian or Kungurian age in the Fitzroy Basin, Western Australia, is an upright virtually equivalved form with low umbones and one opposed sulcus in each valve. Younger species of *Atomodesma* developed one to several narrower grooves over each valve, the number of grooves increasing upwards through the stratigraphic column (Waterhouse & Chen 2006, text-fig. 8) to culminate in *A. multifurcatum* Wanner, 1922 of Late Permian age. Species that commenced slightly earlier, with fewer grooves, persisted.

The much older species *Atomodesma* sp. B *of* Gonzalez (1983) from Argentina has a very similar deep wide furrow anteriorly on each valve, and is likely to have pleurothetic, with no clearly developed platform on the anterior face. It thus links *Aphanaia* and *Atomodesma*, as the first representative of *Atomodesma.*



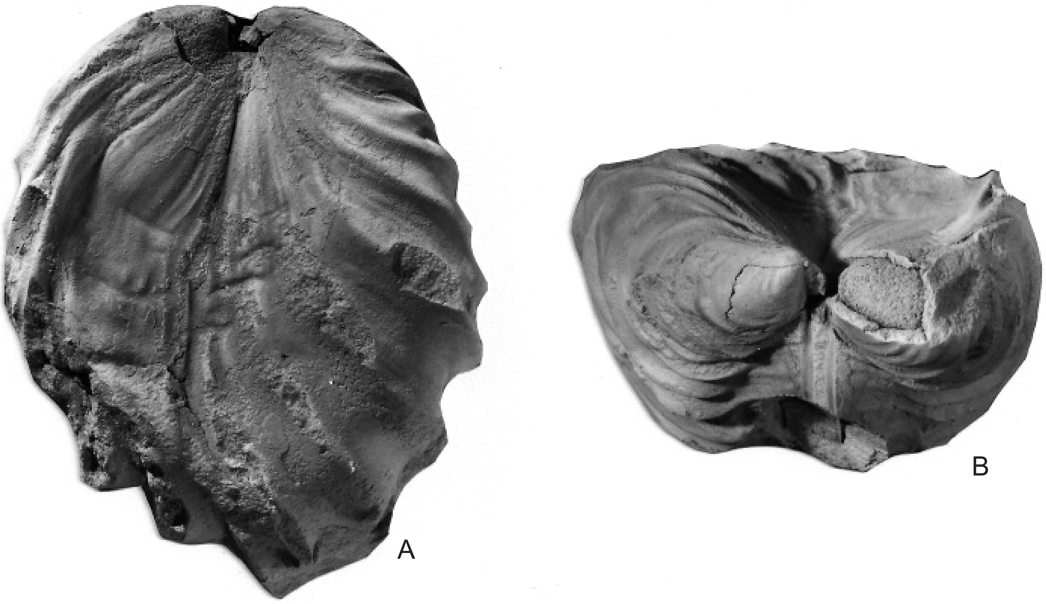
Text-fig. 12. Individuals of *Permoceramus brownei* Waterhouse (A, ?B) and C, *Aphanaia mitchelli* (M'Coy), showing variation in ornament. A, left valve of AMF 48885, with strong commarginal rugae. B, right valve aspect of AMF 2170, with irregular rugae and finer wrinkles. C, right valve of AMF unregistered specimen showing growth stop and very large posterior adductor scar. Specimens from Middle Permian (Roadian) of Hunter Valley, Australia, x1. See Dickins (1963) and Waterhouse (1979a).

Genus ***Intomodesma*** Popov, 1958

Text-fig. 13

Type species*: Intomodesma costata* Popov, 1958, p. 48 from Late Permian of Siberia.

Diagnosis: Equivalve to subequivalve shells with strong commarginal rugae, steeper on the ventral face.



Text-fig. 13. *Intomodesma turgida* Popov, dorsal and anterior aspects of CPC F211968 from Late Permian of Lena River area, Siberia, x1.5.

Discussion: This is a very striking genus, hitherto found in northern hemisphere faunas, Biakov (1991) stating that species in Siberia were restricted to Late Permian (Hivatch level, matched with late Tatarian), and there is a possibly Late Permian occurrence in Nevada, United States (Kauffman & Runnegar 1975). This presumably corrects a chart in Astafieva (1991b, Fig. 1) that shows *Intomodesma* as entering the Boreal realm in the Delenjin level, which she considered to be of Ufimian, that is Roadian or early Wordian (Middle Permian) age. In east Australia, two species are found in late Early Permian (upper Kungurian) and early Middle Permian (Roadian) faunas.

Intomodesma minisculus n. sp.

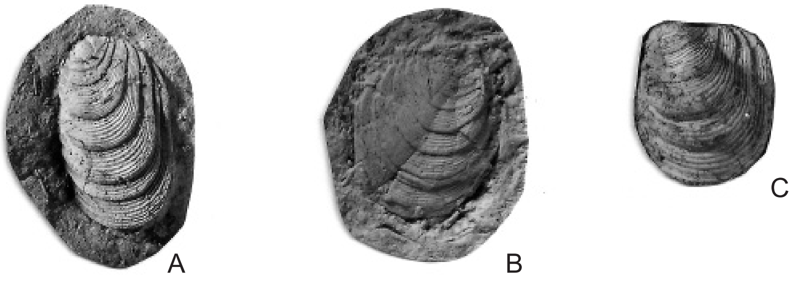
Text-fig. 14A

1987 *Aphanaia* sp. Waterhouse, p. 143, pl. 2, fig. 2-5, 8.

Derivation: minisculus – make small, Lat.

Holotype: UQF 70224 from upper Kungurian (upper Cisuralian) Brae Formation, southeast Bowen Basin, Queensland, figured by Waterhouse (1987, pl. 2, fig. 3), here designated.

Diagnosis: Very small for genus, with strong commarginal rugae and fine intervening laminae on interspaces. Right umbo more prominent than that of left valve. Both valves are moderately inflated.



Text-fig. 14. A, *Intomodesma minisculus* n. sp. left valve UQF 70223 from upper Cisuralian (Kungurian) Brae Formation, Bowen Basin, Queensland, x3. B, C, *Intomodesma* sp. B, right valve UQF 70673. C, left valve UQF 74318. From Guadalupian (Roadian) Oxtrack Formation of Bowen Basin, Queensland, x4. See Waterhouse (1987).

Description: Shells very small, up to 6mm long, 7mm high and 1.5mm wide, with further dimensions provided in Waterhouse (1987, p. 144). Moderately prominent umbo in right valve measuring 80^{o}, left umbo lower and broader up to 95^{o}, hinge short, shells procrescent and anterior face steep but not flattened, byssal gape in each valve, wider in right valve, no posterior wing. Ornament of six or seven prominent growth steps, steep on ventral side, dorsal treads have six or seven fine and regularly spaced growth laminae. Ligament area concave, with light striae parallel and vertical to hinge, small umbonal deck with dorsal and anterior sides subtending a right angle under umbo, anterior side curved, dorsal side straight. Posterior adductor scar with attached retractor scar on dorsal side. Pallial line not preserved.

Discussion: This species is distinguished by its very small size and presence of growth laminae over the major rugations. From the Late Permian of Siberia, *Intomodesma costata* Popov and *I. turgida* Popov from Siberia are much larger with 10-12 rugations and no visible growth laminae.

I. pterinaeformis (Popov, 1948) has a large posterior wing and *I. bicarinatum* (Muromseva, 1984) has extended umbones. The illustrations do not show growth increments like those of the present form, but fine growth increments are visible on some specimens (A. Biakov, pers. comm.).

A different species (Text-fig. 14B, C) showing similar ornament but with longer shell and lower broader umbones was recorded by Hill & Woods (1964b, pl. P11, fig. 5, 6), Hill, Playford & Woods (1972, pl. P11, fig. 5, 6) and Waterhouse (1987, pl. 2, fig. 10) from the Oxtrack Formation, lying above the Brae Formation in the southeast Bowen Basin, and of Roadian (early Middle Permian) age. None of the species of *Aphanaia*, *Trabeculataia, Maitaia* or *Mytilidesmatella* that are common in New Zealand and to less extent in Australia show comparable shape or ornament, even at early growth stages.

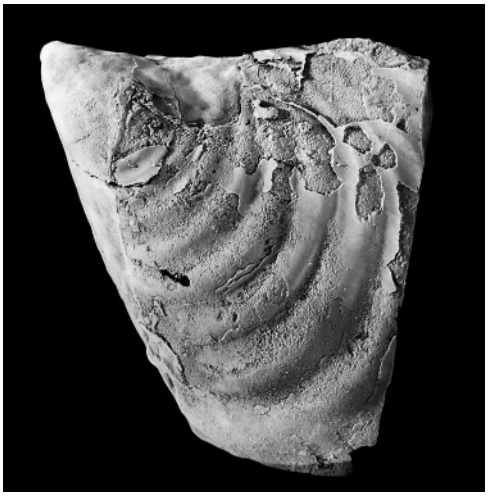
Genus ***Undosusia*** new genus

Text-fig. 15

Derivation: undosus - full of waves, Lat.

Type species: *Aphanaia tivertonensis* Waterhouse, 1979a, p. 4 from Early Permian (Sakmarian – early Artinksian) Tiverton Formation, Queensland, here designated.

Diagnosis: Large shells with terminal umbones, right valve less convex than left valve and with low growth-steps, broad but not flattened anterior face, no clearly defined posterior wings, both valves similarly ornamented by rolling strong undulations. Umbonal septum broad and moderately large, ligament area of moderate development, somewhat constricted, posterior umbonal scar large.



Text-fig. 15. *Undosusia tivertonensis* (Waterhouse), left lateral view showing rugations, holotype UQF 54214b from Early Permian Tiverton Formation, Early Permian of Queensland, x1. See Kauffman & Runnegar (1975) and Waterhouse (1979).

Discussion: This genus is close to *Aphanaia* Koninck, 1877 in being inequivalve, and is distinguished from that genus by its characteristic coarse growth undulations that steadily increase in amplitude on the left valve, slightly stronger and more regular than on the right valve. Growth stops on the right valve are inconspicuous. The genus that is closest in ornament is *Intomodesma* Popov, 1958, but the rugae of this genus have steep ventral sides and long gentle dorsal slopes, forming a step-like ornament, in contrast to the evenly undulating commarginal rugae of the present form. *Maitaia* Marwick has lower, more closely spaced commarginal wrinkles and expanses of smooth shell, whereas *Mytilidesmatella* Waterhouse, 1979a has few wrinkles or growth steps on either valve, and internally has a very large and long umbonal septum. *Trabeculatia* Waterhouse, 1979a shows small regular rugae on both valves, no growth steps and large posterior wings. The umbonal septum is small or moderately small, and the ligament area is narrow and tends to be internal. Both valves are identical in these three genera and judged from the equality of the two valves and regularity of ornament, they probably rested on the anterior face, rather than on the right valve, and were likely to have been attached by byssal threads, which have left little or no trace in the shell, without the development of a byssal gape. They were anteroposited, as opposed to the dextroposited stance of the pleurothetic *Aphanaia*. *Undosusia* was dextroposited as well, insofar as the right valve is slightly less inflated than the left, but there was probably a forward lean, because the anterior face is broad.

The type species was described by Waterhouse (1979a, p. 4, pl. 1, fig. 3, 6, 7; pl. 2, fig. 3) and as *Atomodesma* (*Aphanaia*) sp. by Kaufmann & Runnegar (1975, text-fig. C, D [not B, as in part of the caption], pl. 2, fig. 1-7, pl. 3, fig. 2, 4-6). Kaufmann & Runnegar (1975) noted that their material displayed attributes of both *Aphanaia* and *Intomodesma*. The species comes from the Tiverton Formation of the north Bowen Basin, and is mostly of Sakmarian age, but the collecting by B. Runnegar was not under close stratigraphic control, and the fossil collection possibly included specimens from several faunal horizons.

A number of species from the Late Permian faunas of northeast Siberia show somewhat similar ornament over the left valve, and A. Biakov has recognised new genera of which one has concentric rugations that may branch or die out, unlike those of the present genus, and the other is closer in left valve ornament, but is equivalve or very slightly inequivalve. *Maitaia bella* Biakov (1992, pl. 4, fig. 5) from the Gijigin Horizon of the Omolon Massif, in the *Cancrinelloides curvatus* Zone, has somewhat similar even undulations over the shell. Only the one valve has been figured in the studies, and the lack of figures of the interior and the opposing (right or left) valve does cause difficulty in helping to understand the taxon.

Subfamily **PERMOCERAMINAE** new subfamily

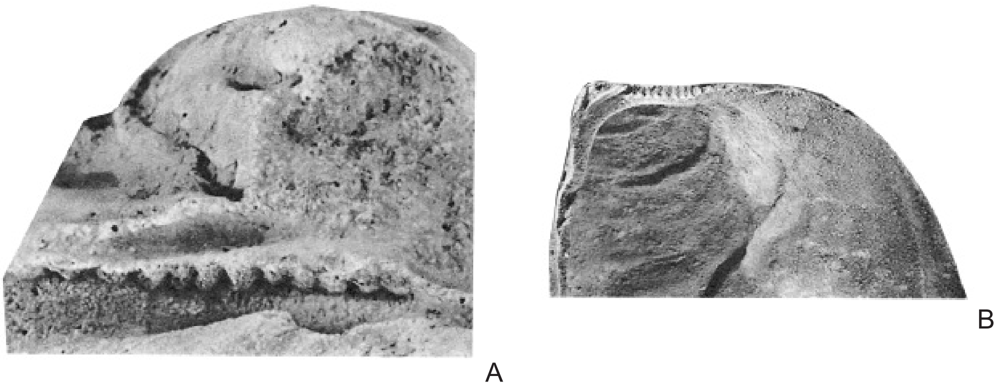
Text-fig. 12A, ?B, 16

Name genus: *Permoceramus* Waterhouse, 1970, p. 763 from the Middle Permian (Wordian) Branxton Formation of New South Wales, here designated.

Diagnosis: Inequivalve inequilateral shells with small umbonal septum and multivincular ligament.

Discussion: Very rarely, in Siberia, Japan and New South Wales, kolymiid or atomodesmid shells develop a multivincular hinge, like that of inoceramids and some pteriidins (Browne & Newell 1966, Waterhouse, 1970, Kauffman & Runnegar 1975). This was recognized through the description of genus *Permoceramus* Waterhouse, type species *P. brownei* Waterhouse, 1970. Hayami (1960) reported what may be *Permoceramus* from the Permian of Japan. A further genus *Varvaria* Astafieva-Urbaiitis & Astafieva, 1985, based on *Permoceramus sibiricus* Muromseva, 1979, has been compared with the Mesozoic genus *Retroceramus,* and assigned to Kolymiidae. *Permoceramus* has been accepted as indicative of a macro-evolutionary change from *Aphanaia* stock (Dickins 1983). Kauffman & Runnegar (1975) fulminated about “errors” of previous studies, but the morphological attributes and the fossil record require a more thoughtful appraisal, and it seems doubtful whether the uncertainties can be resolved without further study. One option would be to represent the fossil record and time sequence in classificatory terms as follows:

Inoceramidae Giebel, including Subfamily Inoceraminae of Jurassic and Cretaceous age, without umbonal septum, ligament normally multivincular, and Subfamily Permoceraminae new subfamily, characterized by umbonal septum and multivincular ligament. *Permoceramus* evolved from



Text-fig. 16. *Permoceramus brownei* Waterhouse, showing the multivincular ligament in AMF 51673 (formerly SUP 2171). A, left valve x4, B, right valve x1. From Middle Permian Muree Formation, Hunter Valley, New South Wales. See Browne & Newell (1966) and Waterhouse (1970).

Aphanaia, also of Permian age, with platyvincular ligament and umbonal septum. *Aphanaia* was a member of Atomodesminae (Carboniferous-Permian), within Family Atomodesmidae. Astafieva-Urbaiitis & Astafieva (1985) and Muromseva (1984) came close this approach. They set aside the view of Kauffman & Runnegar (1975) and placed *Permoceramus* in Inoceramidae, but retained atomodesmids in Myalinidae, and later Astafieva (1993, p. 76) recognised Atomodesmidae. *Varvaria* Astafieva-Urbaiitis & Astafieva, 1985, type species *Permoceramus sibirica* Muromseva, 1979, was assigned to Kolymiidae. This classification assumes that the fossil record does show the origin of Inoceramidae, but fails to establish survivorship of inoceramids through the Triassic Period. The alternative is to regard *Permoceramus* as a highly exceptional member of Atomodesmidae, as a valid subfamily, that perished during Permian time, and this choice is preferred, but only provisionally and with considerable reservations. It was later mimicked in Jurassic with true Inoceramidae. Once again, the fossil record fails to show ancestral stock for Inoceramidae, leaving matters uncertain.

Suborder Pteriidina Newell, 1965

In Pterioidea Gray, Nevesskaya et al. (1971) included Antioconchidae Eberson, Pterineidae Miller, Pteriidae Gray and ?Kochiidae Maillieux. As well, Kolymiidae Kutzneztov belongs to the superfamily. Many members of the Pterioidea are inequivalve, left valve more inflated than right valve, orbicular to strongly procrescent, with small or obsolescent anterior wings. There is a duplivincular, lineavincular or platyvincular ligament, often short in front of the umbo, and heteromyarian or monomyarian muscle scars with anterior muscle scar reinforced by a buttress in some genera. In most genera, dentition may be strong, actinodont or parallelodont, with variable number of small cardinals and commonly posterior laterals diverging from near umbones. Superfamily Bakevellioidea King, to which Nevesskaya et al. (1971, p. 15) allocated Bakevelliidae King, Cassianellidae Ichikawa, Isognomonidae Woodring and perhaps Dattidae Healey, is characterized by multivincular ligament.

Other genera lack multivincular ligaments, and have no internal teeth or anterior buttress, but a pteriidin affinity is indicated by aspects of the ligament (duplivincular, alivincular or channelform), anterior wings as a rule with byssal notch or gape to a degree, and dimyarian musculature. Two such families have been named, Posidoniidae Frech, 1909 and Pergamiidae Cox, 1969. They may be separable as a superfamily, which would imply that the chevron duplivincular hinge of Posidoniidae transformed into the alivincular hinge of Pergamiidae, but evidence for the relationship is not strong, and therefore the two families are recognised as separate entities within Pterioidea.

Amler (1999) included the Ambonychioidea (which included Inoceramoidea) with Pterioidea in Order Pteriida Newell. A degree of intimacy is well justified, because Kolymiidae Kuznetsov and Retroceramidae Pergament show attributes of both inoceramoids and pterioids, and their classification may be subject to further adjustment.

Superfamily **PTERIOIDEA** Gray, 1847

Diagnosis: Equivalve to subequivalve, comparatively upright, anterior wing small, posterior wing varies from large to absent, shell normally byssate. Ligament usually alivincular or duplivincular, teeth often present, musculature dimyarian as a rule.

Family **POSIDONIIDAE** Frech, 1909

Diagnosis: Small equivalve or subequivalve shells with small to large anterior and posterior wings, no marked byssal notch at maturity, dimyarian, ligament where known duplivincular, hinge edentulous.

Discussion: Of the genera assigned to Posidoniidae by Cox & Newell (1969, p. 342), only the Carboniferous form *Posidonia* is reliable. Some genera included in the family by Cox & Newell (1969) are now placed in the Mesozoic family Halobiidae Kittl, 1912, and others are Mesozoic forms with ligament and musculature largely unknown, with a number placed in Aulacomyellinae by Ichikawa (1958) and Kelly & Doyle (1991). As suggested by Waterhouse (2001, p. 134), Carboniferous species assigned to *Rutotia* Koninck, 1885 appear to be posidoniid, and are described as a new genus *Enitoria*.

Newell (1938)* classed *Posidonia* in Pterinopectinidae Newell, 1938, although Posidoniidae Frech, 1909 had long-acknowledged seniority, and later Rathman & Amler (1992) referred *Posidonia* to Buchiacea Cox, 1953, a placement that not only defied the rules of zoological nomenclature, but would seem to be most unlikely given the differences in ligament, musculature and auriculation. Cox & Newell (1969) included the family in Pectinacea. Campbell (1994) and Waterhouse (2001) regarded the genus as difficult to interpret, but the presence of dimyarian musculature and duplivincular ligament and lack of anterior auricle at maturity establish a pteriidin affinity. This view is consolidated by the close relationship to *Caneyella* Girty, a Carboniferous genus with long hinge, ribs and byssal attachment, and classed in Pterineidae Miller by Newell & LaRoque, 1969b, p. 298. Waller (2005) shifted the genus to Posidoniidae and Posidonioidea in Suborder Pteriidina Newell, 1965.

Nevesskaya et al. (1971) classed Posidoniidae as aviculopectinid, but Stanley (1972, p. 188) more acceptably noted the association of *Caneyella* with *Posidonia*, a view initiated by Girty (1909) and Weigelt (1922), but forcefully opposed by Newell (1938). Stanley (1972) regarded

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*Footnote: The date for publication of Newell's monograph is often quoted as 1937. This is because the title page of the study carries that year. But the page heading the section of plates carries the comment "Actual date of issue, July 28, 1938". Whether the text was really issued the year before remains moot, but would have been difficult to use in the absence of the plates. Newell, Cox & Hertlein (1969) date the Newell-proposed genera as 1938, but the references quote the work as 1937 (1938), which is unsatisfactory, and Newell et al. (1969) are followed.

Caneyella as transitional between Posidoniidae and Pterineidae, and here it is classed with Posidoniidae, following Waller (2005), as anticipated by Ramsbottom (1959).

Genus ***Posidonia*** Bronn, 1828

Type species: *Posidonia becheri* Bronn, 1828, p. 268 from Early Carboniferous of Germany.

Diagnosis: Small subequivalve to equivalve shells with weakly defined anterior and posterior wings, short-lived byssal notch early in ontogeny, ornament of commarginal low ridges or flanges, more rarely rugae, hinge short to long and without teeth, ligament chevron duplivincular, anterior adductor small, posterior adductor large.

Discussion: *Posidonia* is best known from Carboniferous deposits of north Europe, especially Germany, and excellent studies have been provided by Weigelt (1922, 1927). The genus has not been found in Permian deposits, an important matter from the point of view of the source for Mesozoic genera which were classed in Posidoniidae by Cox & Newell (1969).

Genus ***Enitoria*** new genus

Text-fig. 17

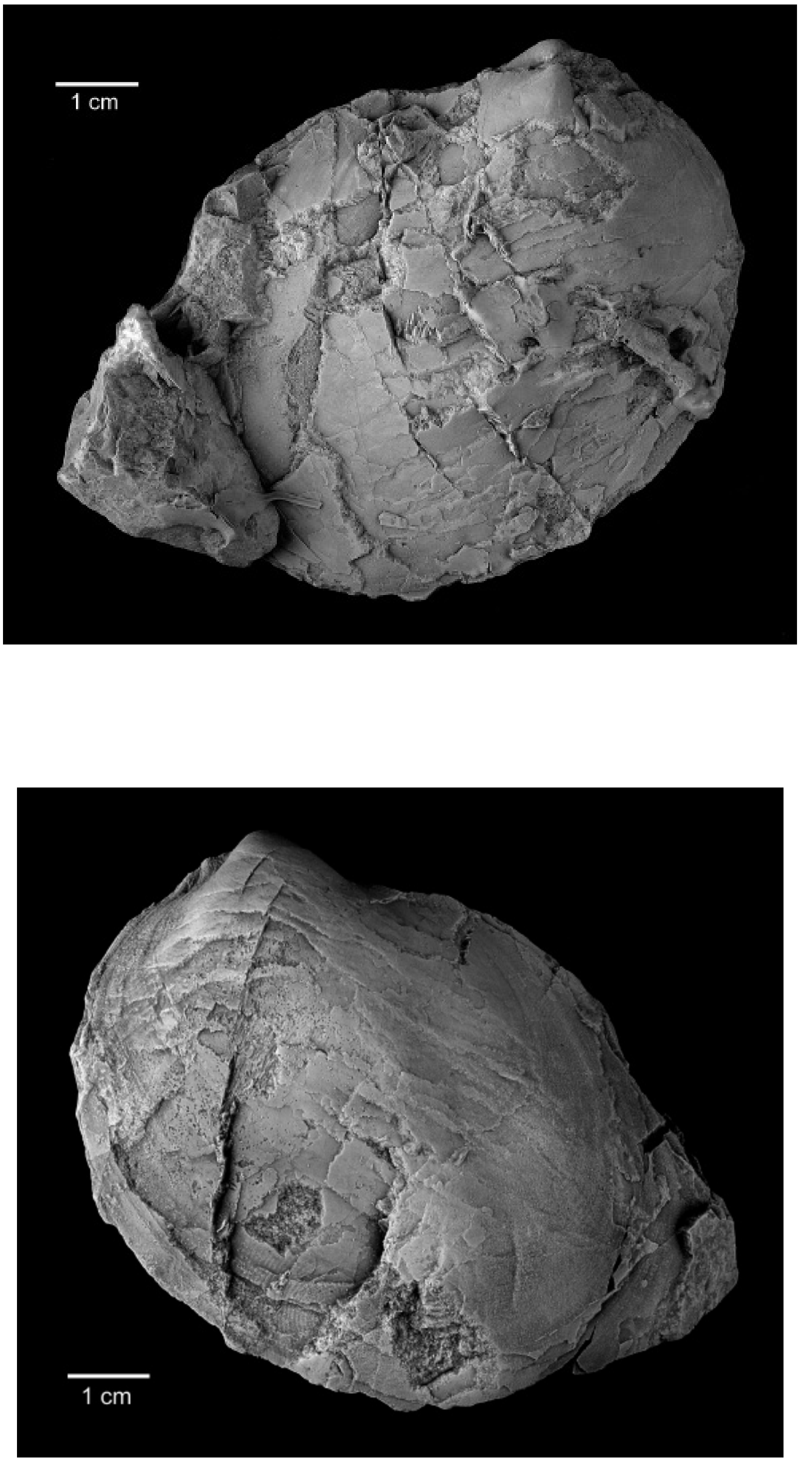
Derivation: enitor – mental exertion, Lat.

Type species: *Rutotia grandis* Koninck, 1885, p. 197 from Early Carboniferous (Visean stage 2) of Belgium, here designated.

Diagnosis: Large shells, inequivalve, with right valve less inflated than left valve, shell surface almost smooth, with low commarginal growth flanges, anterior and posterior wings similar in each valve, weakly developed and weakly distinguished from body of shell, cardinal extremities obtuse, ligament amphidetic, but not known in detail.

Discussion: The holotype of *Rutotia grandis* by monotypy is the sole figured specimen in Koninck (1885, pl. 39, fig. 1-3), registered as IRSNB a 4824. As described by Koninck (1885), *Rutotia* included *Pecten hemisphaericus* Phillips (1836, p. 212, pl. 6, fig. 6) from Early Carboniferous of England and Ireland. Hind (1903, p. 45, pl. 7, fig. 1-6) described further specimens of Phillips' species, and refigured the type specimen (pl. 7, fig. 2). He assigned the species to *Eumicrotis* Meek, but to judge from data provided by Hind (1903) it belongs to *Streblopteria* M'Coy, 1844, with comparatively smooth shell and long posterior wing, and Hind reported a small byssal notch. The one reservation is that Phillip's original figures shows low concentric rugae, that are normally finer in *Streblopteria*. Instead of citing one of Koninck's species as type of *Rutotia*, Newell (in Newell, Cox & Hertlein 1969, p. 339) sought to dispense with the genus by making Phillip's species the type, thereby synonymizing *Rutotia* with *Streblopteria* M'Coy. The Belgium species described by Koninck lack the right anterior auricle and very large posterior wings that characterize *Streblopteria* and the species *hemisphaerica.* The genus *Enitoria* is proposed in the sense intended for *Rutotia* by Koninck (1885) but blocked by Newell. It should be noted that Koninck also described several species of *Streblopteria* M'Coy, and clearly recognised the differences between his *Rutotia* and M'Coy's genus. He probably included Phillip's species because of some approach to *Rutotia* in general shape and ornament, and it clearly played no more than a minor role in the Koninck understanding of *Rutotia.*

The family affinities of *Enitoria* remain obscure, but the genus is pteriiform and apparently related to Posidoniidae, as suggested by Waterhouse (2001, p. 134). Amongst species of *Rutotia* described by Koninck (1885), a number of specimens are either smooth or possibly decorticated, and not all are figured or well enough preserved to identify generic position solely from inspection of the figures. Koninck's named species include *Rutotia lenticularis* , *R. obtusa*?, *R. ovalis* (?decorticated), *R. phillipsi* (smooth), *R. ornithocephala* (specimen figured in Koninck 1885, pl.



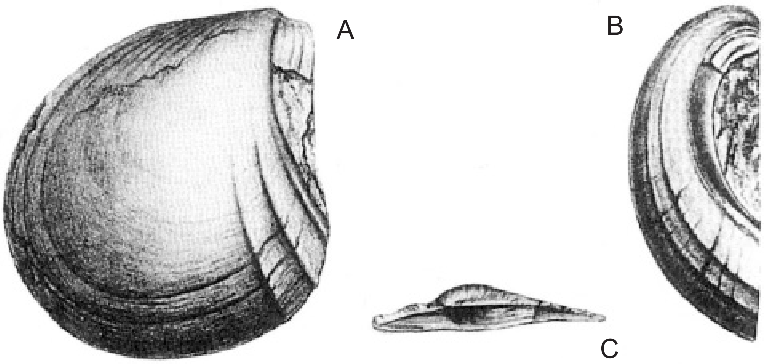
Text-fig. 17. *Enitoria grandis* (Koninck), A, right valve aspect, B, left valve aspect. figured as *Rutotia grandis* by Koninck (1885, pl. 39, fig. 1), IRSNB a 4824 from Early Carboniferous (Visean 2) of Belgium. Photographs courtesy of Annelise Folie, Royal Belgium Institute of Natural Science.

7, fig. 29 here nominated as lectotype), ?*R. amygdalina* (the specimen of Koninck 1885, pl. 13, fig. 24, 25 here nominated as lectotype), and *R. perobliqua* (decorticated?). *R. obesa?,* and *R. subcorrugata* have slightly more rugose shells, closer to *hemisphaericus*.

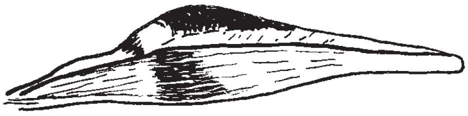
Family **PERGAMIDIIDAE** Cox, 1969

Text-fig. 18, 19

Pergamidiidae Cox, 1969b was placed as a member of Pterioidea together with Pterineidae Miller, ?Kochiidae Maillieux, Pteriidae Gray, Bakevelliidae King, Cassianellidae Ichikawa, ?Dattidae Healey, Inoceramidae Giebel, Isognomoniidae Woodring, Pulvinitidae Stephenson and Malleidae Lamarck. Even within such a formidable array of families, Pergamidiidae is exceptional, for it lacks teeth and mutiple resilifers, which help characterise most of these families. Nevesskaya et al. (1971) placed Pergamiidae in Ambonychioidea. Nonetheless, the family appears to be pteriidin, because of the presence of anterior wings and resilifer. *Pergamidia* Bittner, 1891, p. 103 comes from Late Triassic beds of Turkey and has a hinge and ligament that is amphidetic, as also noted by Waller (2005, p. 8), and lies within the right anterior wing, and has well developed resilifer. A large byssal gape lies in front, embraced by the anterior wings. This is well demonstrated by the description and figures in Bittner (1891) for the type species *Pergamidia eumenea* Bittner (1891, p. 103). A reproduced figure in Cox (1969b, Fig. C44.2b) shows the ligament extending well in



Text-fig. 18. *Pergamidia eumenea* (Bittner), right valve. A, lateral view and B, anterior view, and C, alivincular hinge, from Bittner (1891) and Cox (1969b, Fig. C44.2b) x 0.5. Upper Triassic of Turkey.



Text-fig. 19. *Pergamidea eumenea* (Bittner), rough sketch of right valve ligament with resilifer, x1, from Bittner (1891).

front of the right valve umbo, and an oblique resilifer extends back from under the umbo (Text-fig. 19). The presence of a resilifer and anterior wings suggests an approach to Pteriidae Gray, 1847, and the family is provisionally regarded as an ally, close to the position proposed by Cox (1969b).

Other genera referred to Pergamiidae by Cox (1969b) were *Manticula* Waterhouse and *Krumbeckiella* Ichikawa, and these have opisthodetic ligament and do not belong to the family. *Semuridia* Melville, 1956 was also placed in the family by Cox (1969b) and although more difficult to assess because detail of the anterior ligament is obscure, the presence of a resilifer, longitudinal posterior tooth, byssal gape and dimyarian musculature appears to confirm its position. The shell shows thick outer prismatic layer and an inner nacreous ostracum, Carter (1990) noting that this differed from *Manticula*, and approached shell material in *Posidoniella*.

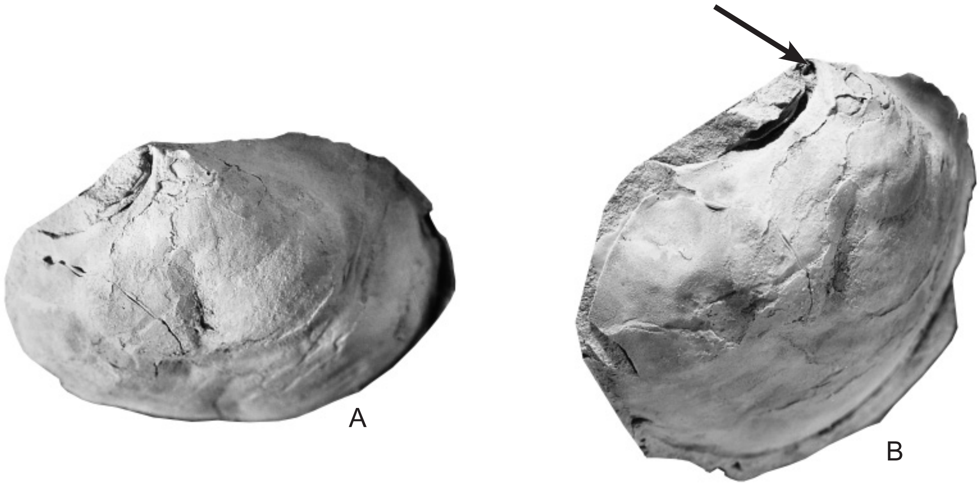
Whether or not the family should be allied with Posidoniidae remains uncertain, because of the difference in hinge, but the two do not differ substantially from each other in shape or ornament, and agree in musculature and lack of teeth. They are treated as stand-alone families, not yet fitting into to any major superfamily, and close study of shell structure may help clarify relationships.

Subfamily **ORETINAE** new subfamily

Text-fig. 20

Name genus: *Oretia* Marwick, 1953, p. 62 from Upper Triassic beds of New Zealand, here designated.

Diagnosis: Subequivalve inequilateral obliquely ovate shells, bicrescent, initially procrescent, with anterior extending forward in later growth stages, umbones anteriorly placed, no posterior wings, tiny anterior wing in each valve, ligament internal, canalivicular and largely opisthodetic, hinge edentulous, no resilifer or mutiple pits, muscles dimyarian, faintly impressed. Exterior smooth apart from low growth rugae or flanges. Shell of calcite, detail not known, not prismatic.



Text-fig. 20. *Oretia coxi* Marwick, left valve TM 5072, A, lateral and B, oblique anterior aspects, showing small anterior wing, arrowed. From Upper Triassic of Nelson, New Zealand, x 1.5. See Waterhouse (1979b).

Discussion: *Oretia* is a comparatively rare bivalve of late Triassic age found in New Zealand and New Caledonia, based on sole known species *O. coxi* Marwick (1953, pl. 4, fig. 2- 4, pl. 6, fig. 13, 14; Waterhouse 1979b, Fig. 1-11). The presence of a small anterior wing and shelf in each valve and anterior and posterior adductors point to pteriiform affinities, although the shell is subglobular and the shell apparently not prismatic. The right valve is slightly more inflated than the left (Waterhouse 1979b). Cox (1969f, p. 382) in the Treatise placed *Oretia* as “Family UNCERTAIN” at the end of a section on Pectinacea, and could point to no close affinities, but was not aware of detail on the hinge, ears or musculature.

No exactly similar shells have been encountered amongst Late Paleozoic and Mesozoic bivalves, but *Bittneria* Broili, type species *Avicula*? *efflata* Bittner (see Cox 1969e, p. 376) is a smooth shell with no posterior wing, and a small anterior wing. It is more upright than *Oretia*, and comes from the Upper Triassic of the South Tyrol, and might well belong to the subfamily. It was classed by Cox (1969e, p. 375) in Buchiidae, members of which do not have a left anterior wing. Unfortunately the right valve is not known for *Bittneria.*

In some respects *Oretia* is close to *Pergamidia,* as noted by Waterhouse (1979b), although Carter (1990, p. 204) considered it was not related. The smooth shell, lack of posterior wings, presence of anterior wings and lack of hinge teeth are shared characters. *Oretia* differs in having a less upright stance, in lacking a resilifer (TM 2282), and having a largely opisthodetic ligament and tiny anterior wings with much smaller if any anterior gape. It may be noted that *Semuridia* Melville also shows some approach. But relationships remain uncertain. The shell in TM 5708 is only 0.6mm thick, and for TM 2279 close to 2mm thick, with an outer ?foliate layer and inner hypostracum and no prismatic layer: further study of shell structure should help resolve the relationships of *Oretia*.

Superorder Pectinidia new superorder

Text-fig. 21

Diagnosis: Shells characterized in part by extended anterior, with anterior wing or auricle, which may be secondarily reduced. Ligament alivincular as a rule, with well formed resilifer; early family groups display a duplivincular ligament which evolved or retromorphed into a replivincular or canalivincular form in some families. Shell composition calcitic and/or aragonitic, thick prismatic shell reduced to outer layer. Musculature normally monomyarian, having changed from the dimyarian musculature normal for Pteriida.

Discussion: The principal focus of this monograph concerns the evolution and classification of pectiniform bivalves. It is proposed to divide the Eupteriomorphia of Boss, 1982 into two, leaving the superorder Eupteriomorphia (now Pteriidia) to include Order Pteriida with Suborders Ambonychidina, Pteriidina and Pinnidina. There have been a number of classifications for pectinomorphs, summarised well by Carter (1990) with the delineation of several orders, but the present treatment differs, because an additional order and new suborders are recognised. As well, the depiction of Order Limida and Order Ostreida as two depauperate orders with comparatively few families and superfamilies and no suborders is radically changed, with substantial expansion by incorporation of family groups allocated to Pectinida by Waller (1978), Carter (1990) and Amler (1999). These changes are based primarily on morphology, reinforced by the fossil record, rather than analysis of mostly living material. That may appear to downgrade the significance of soft tissue in bivalves, but on the other hand Russian zoologists have also segregated Pectinida from aviculopectens s. l., on the basis of soft tissue analysis. The classification is as follows:

Order Pterinopectinida new
Order Limida Waller, 1978
    Suborder Aviculopectinidina Starobogatov, 1992
    Suborder Monotidina Waterhouse, 2001

Suborder Limidina Waller, 1978

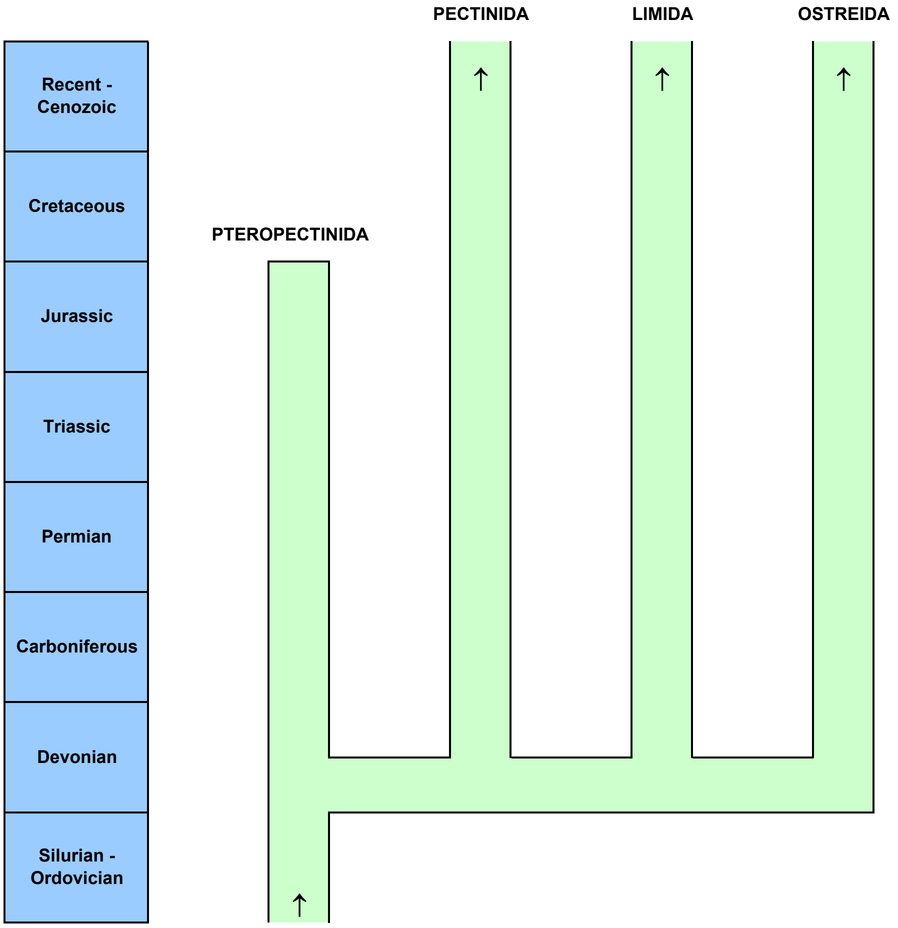
Order Ostreida Waller, 1978 (Ferussac, 1822)

Suborder Etheripectinidina new

Suborder Ostreidina Waller, 1978

Order Pectinida Nevesskaya, Scarlato & Starobogatov, 1971

The ordinal standing for limids is based on a cladistic interpretation of mainly soft-tissue morphology by Waller (1978, 1998) and other studies, as expressed by Amler (1999, p. 240). Waller (1978) showed Limida as a clade, and Ostreidina and Pectinidina as suborders of a separate clade. The character states that discriminate Limida include shell structure, aspects of the foot and tentacles, and muscle scars, relating to a life position with commissure vertical, in contrast to the horizontal commissure position common in some other pectiniform shells. Yet the distinctions are not overwhelming. Limids share with pectens the stomach type, and they share with many pectiniform shells an amphidetic alivincular hinge and ligament. Nevesskaya



Text-fig. 21. Major divisions amongst pectiniform bivalves. In this model Pectinida, Limida and Ostreida are considered to have shared a common aviculopectiniform ancestry, because of the shared nature of hinge, and sourced from Pterinopectinida. The alternative is that each arose separately, from within Pterinopectinida, which is arguably conveyed by the recognition of Limida and Pectinida as full orders. The Devonian and earlier fossil record is not good enough to trace the origins of all the major groupings.

et al. (1971) and Starobogatov (1992) regarded limids as being close to pectens and different from oysters, and Carter (1990) has described how the limid shell changed in composition and structure from Early Carboniferous time. The analysis that placed oysters close to pectens is not supported by the fossil record, which points to a source for oysters from etheripectinidin stock, much later than the commencement of pectens, as strictly defined. Nor does the fossil record support any supposition that aviculopectens were closer to pectens than to limids. But historic morphologies were not evaluated in the cladistic analyses of Limida and Ostreida.

Were classification to be based solely on “bottom up” analysis, building family and ordinal associations from the number of like rankings, it would be possible to take what some might consider to be a minimalist approach, ranking limids, pectens and oysters at subordinal level, and grouping Order Pectinida with Pteriida in one superorder. The morphological gaps between major components do not seem excessive: quite the reverse, and that appears to be consistent with a great diversification at species and genus level during especially late Paleozoic time. But this is a matter for general consensus, if possible, and herein the classifications summarized in Amler (1999) will be followed to the extent that ordinal rank is granted to Limida: once done, that imposes an arrangement for groups of similar rank throughout the pectens, and as a consequence, there is a need to gather the orders in a superorder: were the pectens, limids and oysters to be classed as suborders, they could be grouped as Order Pectinida. At the same time, the recognition of suborders within Limida and Ostreida might well be construed as favouring the present arrangement; although it is true that some might suggest that the suborders Aviculopectinidina, Monotidina and Etheripectinidina could rank the same as Limidina and Ostreidina. This study follows a pattern that is subjected to further enquiry in the concluding remarks (p. 190).

Because the two suborders Ostreidina and Limidina persist into the present, and can be subject to more extensive analysis than extinct fossil groups, the discussion on them follows that on the other suborders in their respective group.

Fossil record

The stratigraphic succession for pectiniform shells is at its best during Mesozoic time, especially in the Triassic when a succession of short lived genera and species ranged far and wide through marine conditions. That cannot be matched in the Paleozoic. Although the sporadic nature of the fossil record for Paleozoic Pectinidia is no worse than that for other major bivalve groups, there are gaps, particularly critical for understanding of the superorder, because evolution was so diverse and rapid. Parts of the record in some regions are good. The Early Carboniferous faunas of Ireland, United Kingdom, Belgium and Germany have been closely studied, although in need of considerable revision; and the Pennsylvanian Pectinidia of United States were scrutinized in an outstanding monograph by Newell (1938), followed by studies on some of the Permian representatives, culminating in Newell & Boyd (1995). A number of genera have been recorded from China and Russia, with high quality-studies by M. M. Astafieva, K. A. Astafieva – Urbaiitis, Zong-Jie Fang, Qing-lai Feng and Hongfu Yin. The main lack in these studies other than from Russia and Germany has been a failure to establish a full stratigraphically controlled succession of species and genera: there is nothing like the sequencing established for conodonts, fusulines or brachiopods. As one exception, east Australia offers a particularly fine and full record for Pectinidia during the Early and Middle Permian, reinforced by the Middle and Late Permian record in New Zealand. First monographed by Etheridge & Dun (1906), and reinforced in studies by Fletcher (1929) and Waterhouse (1982, 1987), the Australian Pectinidia show that many species were of limited time range, just as has been established for various Mesozoic pectiniform bivalves. The Australian Permian species did not commonly extend through much of a period, despite the implication of long time ranges for species conveyed by certain studies in United States. One fortunate aspect of the Australian bivalve record for the Permian Period is that specimens are numerous, allowing good control in studying intra-specific variation. Here and there apodicty is recorded in the fossil record, providing pointers for the course of evolution.

The beginnings of Pectinidia remain obscure. Many of the groups were discriminated by Early Carboniferous time, and some of these groups are represented meagrely through Devonian time. It remains unclear whether the groups – orders and superfamilies – appeared steadily during the Devonian or even Silurian Period, or whether there was a major and perhaps short-lived expansion, most likely in the Late Devonian Period: certainly major proliferation occurred during the Early Carboniferous.

Characteristics for classification

For classification, prime emphasis is placed on shape and what G. A. Cooper called "build" of the entire shell, the differences and similarities between right and left valves, including inflation and ornament, and development of wings and auricles, as well as the extent and nature of the ligament. The aspects reflect the habitat and modes of feeding and motion. Such procedures are not substantially at variance from other studies. For example, in tracing the origin and development of Halobiidae, Waller (2005) focused on external appearance and ornament, and allowed considerable ongoing change to auriculation, ornament, byssus, ligament and muscle field.

Significance is allowed to ligament. At first sight, the nature of the ligament appears to have been somewhat flexible, supporting the observation to that effect by Yonge (1978). In the Pectinidia, the ligament may be duplivincular, alivincular, lativincular, platyvincular or canaliform, supposedly without any perceptible pattern. But faunas from the southern paleohemisphere reveal two major overall trends in the nature of the ligament. As well established, the chevron-duplivincular ligament changes into alivincular, and various high-latitude southern occurrences show that the alivincular ligament can change to a platyvincular ligament, without a resilifer. In addition, Triassic fossils from the southern paleohemisphere show that a chevron duplivincular ligament could change into a canalivincular ligament, which occupies a long slender channel or trough. Thus some pattern is now imposed on the variation in ligament. Newell & Boyd (1995) used the term "transitional", but the term has been used over-flexibly, and specific designations have been been found to be more informative.

Shell structure and composition are highly significant, but also can be shown to vary, sometimes even within a genus, from calcite to aragonite, with occasional divergences from the norm of a prismatic external layer and internal nacre or calcite. The variation is probably in part systematic, but also in part environmental, and the classificatory claims based on excellent studies of variation between taxa at various levels still need to be validated by studies ranging through time and space on single taxa. Carter (1990) showed that within Paleozoic pteriomorphs "the replacement of nacre by other aragonitic structures and replacement of regular prismatic calcite by other calcitic structure represent grades in the evolution of shell micro-structure that were attained at different times in many different lineages" (Waller 1998, p. 28).

In attempting the classification, an effort has been made to amplify and consolidate the monogeneric family groups of Newell (1938) and Newell & Boyd (1995) by seeking lineages within those family groups that are characterized by different ornament and shape. It has been possible to justify their proposals with the recognition of additional genera and even subfamilies for several of their monogeneric units. In some cases, it is deemed desirable to downscale some proposed entities: it is not always rational to use a family or superfamily, when a subfamily or tribe will suffice. A much more structured classification can be achieved in this fashion, showing relationships and differences more clearly than studies which do not relate one family to another,

other than at a very general level, or recognise evolutionary lineages within families. It is also considered that recognition of suborders within orders provides a useful tool for conveying relationships, even though such a category has fallen out of favour, as implied in the summary of bivalve classification by Amler (1999).

Evolution of Pectinidia

The beginnings of the Pectinidia lie in younger Early Paleozoic time, followed by a critical late Middle Paleozoic change from endobyssate to epibyssate and free-swimming forms. By the Carboniferous Period, Pterinopectinida, Pectinida, Limidina, Etheripectinidina and Aviculopectinidina were clearly discriminated. Constituents of Monotidina were moderately well differentiated with two superfamilies by Permian time. There was strong proliferation of pectinidian genera and family groups during Early Carboniferous, slow deterioration through to the end of the Permian for Pterinopectinida, steady and inconspicuous development for Pectinida and Limidina, and varied development amongst Aviculopectinidina and Etheripectinidina, including moderate expansion amongst Etheripectinoidea and Pseudomonotoidea. The Permian-Triassic extinction put an end to a number of families, and further groups died out at the end of the Triassic Period. Drastic change occurred within the pterinopectens. The group had been slow decline, but gained renewed impetus after the great extinction. One group changed substantially in morphology but was able to exploit Early Triassic habitats, and contentiously, a second (halobiid) group reverted to Early Carboniferous pterinopectiniform morphological attributes: both families were very widespread with a succession of short-lived species and genera. Groups that survived within Etheripectinidina changed in shape, becoming less pectiniform, and more rounded in body with less distinct wings, displaying a strong tendency to reduce the anterior wing-auricle (Oxytomoidea), and loss of the anterior wing and auricle (Aulacomyelloidea). Pectinida remained inconspicuous. Members of Monotidina remained comparatively few, and for a time restricted to or concentrated in high southerly latitudes, until Late Triassic, with the expansion of new and very successful Monotidae, and other monotidins became conspicuous in the late Mesozoic, especially Cretaceous. Eventually, some Pectinida came to externally mimic etheripectinid members of the Etheripectinidina, and the other groups perished by the end of the Mesozoic.

In summary, Pectinidia evolved by developing anterior extensions. But through time, species and genera reverted, with shrinkage of the anterior in both Monotidina and some Etheripectinidina.

Order Pterinopectinida new order

Diagnosis: Pectiniform subequivalve shells, both valves as a rule subequally convex and hinge at or close to maximum length, ornament predominantly radial, usually increase by intercalation, but in other forms by branching on left valve, and increase by branching or less usually by intercalation on right valve, general appearance of ornament usually but not always similar on each valve, posterior wings moderate to large, seldom well delineated, anterior right valve auricle as a rule with byssal notch or infilled track. Ligament external, amphidetic and chevron-duplivincular, may be modified to canaliform in younger representatives, muscle field monomyarian.

Discussion: The order agrees with other major pectinidian groups in having a long hinge and usually posterior wings and anterior right valve auricle, but differs in the nature of the ligament. Comparisons and contrasts with the other orders are explained further in discussion of their attributes and provided in more detail in the study of individual family groups and genera. The order constituted the root stock for younger pectinidians, which developed a different ligament. Paleozoic members of the order are distinguished by the amphidetic duplivincular external ligament with chevron grooves and no resilifer from Order Pectinida with its internal resilifer and from Order

Limida which has an alivincular or platyvincular external ligament as a rule. Pterinopectinida are more readily distinguished from Monotidina, because the latter have a short hinge with small or no posterior wings and small right anterior ear, and the hinge is opisthodetic. Pterinopectinida is highly diverse, and there are a number of genera yet to be segregated. Younger members, just as for family groups in Order Limida, changed in shape and ligament, with a degree of convergence, traced in detail.

The order involves major families Leiopectinidae Krasilova of Silurian to Lower Devonian age, Pterinopectinidae Newell of mostly Devonian and Carboniferous age, ranging into Permian and reported from upper Silurian, Natalissimidae n. fam. (Devonian and Carboniferous), Claraiidae Gavrilova of Early Triassic age, and, it is here evaluated, Halobiidae Kittl, best known in Middle to Upper Triassic deposits, but persisting, it is here shown, into Late Jurassic faunas. Although others have favoured descent of Halobiidae from Posidoniidae, a proposal that cannot yet be fully denied or substantiated, the weight of available evidence favours a pterinopectiniform alliance.

The onset of the Mesozoic Era marked a major change in the evolution of the suborder, with Claraiidae becoming markedly inequivalved, the right valve being small and little inflated, and the hinge shortening, with small posterior wings and generally prominent right anterior auricle. Many members retained the duplivincular hinge, some show a replivincular hinge, and in others the ligament was contained in a single slender channel. This variation appears considerable, but possibly was affected by environment. Halobiidae retained the altered ligament, and changed substantially by losing the byssus and right anterior auricle, thus coming to resemble members of Aulacomyelloidea of the Order Ostreida.

The classification within the order is as follows:

- Superfamily Leiopectinoidea Krasilova, 1959
  - Family Leiopectinidae Krasilova, 1959
  - Family Rhombopteridae Korobkov, 1960
- Superfamily Pterinopectinoidea Newell, 1938
  - Family Pterinopectinidae Newell, 1938
    - Subfamily Pterinopectininae Newell, 1938
    - Subfamily Pterinopectinellinae new
    - Subfamily Tesseratiinae new
  - Family Natalissimidae new
    - Subfamily Natalissiminae new
    - Subfamily Pseudaviculopectininae new
- Superfamily Halobioidea Kittl, 1912
  - Family Claraiidae Gavrilova, 1996
    - Subfamily Claraiinae Gavrilova, 1996
    - Subfamily Pseudoclaraiinae Gavrilova, 1996
    - Subfamily Chuluariinae new
  - Family Halobiidae Kittl, 1912
- Superfamily and order not resolved
  - Family Permanomiidae Carter, 1990

The intriguing genus *Permanomia* Newell & Boyd (1970, p. 275) from mostly Middle Permian faunas of Texas shows a duplivincular ligament and unusual cloven-hoof-shaped muscle scar (Newell & Boyd 1970, Fig. 34C, G, H). Carter (1990) referred the genus to a separate new family, Permanomiidae, classed as an indeterminate superfamily of Order Pectinida by Amler (1999, p. 241).

Superfamily **LEIOPECTINOIDEA** Krasilova, 1959

[nom. transl. hic ex Leiopectinidae Krasilova 1959, p. 41].

Diagnosis: Generally slender equivalve or subequivalve shells with right anterior auricle, no byssal notch, short auricular crura internally.

Discussion: The superfamily ranged from Ordovician to Lower Devonian, and includes two endobyssally attached families, Rhombopteriidae Korobkov, 1960 and Leiopectinidae Krasilova, 1959. Rhombopteriidae Korobkov, 1960, based on *Rhombopteria* Jackson, 1890 of Ordovician-Silurian age, has two sets of ligament grooves and no byssal notch, and the left valve is more inflated than the right. It was placed in Pterioidea Gray by Amler (1999, p. 239), but it is preferred to treat the family as provisional root-stock for the order.

Superfamily **PTERINOPECTINOIDEA** Newell, 1938

Diagnosis: Shell attached by byssus, leaving byssal notch, no internal crura. Valves as a rule equal or subequal in inflation, usually similarly ornamented.

Discussion: Most upper Paleozoic pterinopectens fall within this group, but a small and hitherto neglected group Natalissiminae is exceptional in having comparatively flat or little ornamented right valve, with ornament differing from that of the left valve. From it were derived, it is believed, the Etheripectinidina and the Ostreidina.

Family **PTERINOPECTINIDAE** Newell, 1938

Diagnosis: Ligament duplivincular. Hinge long and wings large and weakly defined.

Discussion: The shell structure is simple prismatic in both valves, with regular simple prisms in the right valve and homogeneous or laminate in the left valve. The middle layer is nacreous, and inner layer nacreous to CL and CCL.

Subfamily **PTERINOPECTININAE** Newell, 1938

Diagnosis: Ornament predominantly radial, in various arrangements.

Discussion: Constituent genera include *Pterinopecten* Hall, *Newellipecten* Rûžićka, Prantl & Pribyl*, Dunbarella* Newell, *Denguiria* Boyd & Newell, *Vertumnia* Hall and *Lyriopecten* Hall. One genus called *Linanomia* Gray that was assigned to Pterinopectinidae by Newell (1969b, p. 334) possibly falls outside the subfamily. It is of Upper Devonian age, with short hinge and large byssal notch, and fine radial ribs. The ligament is not known, hindering discovery of relationships.

Genus ***Bifurcatatia*** new genus

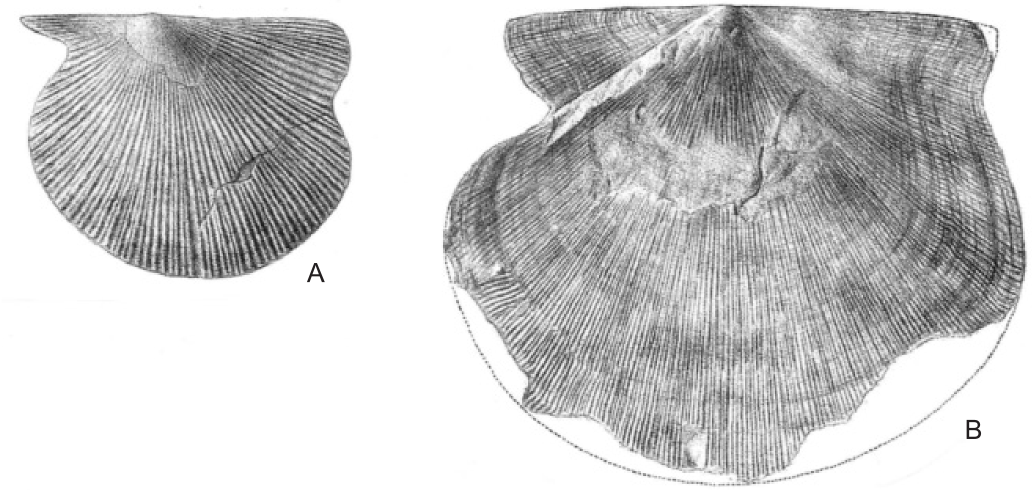
Text-fig. 22

Derivation: bi – two; furca – branch, Lat.

Type species: *Aviculopecten meleagrinoides* M'Coy, 1851, p. 96 from Early Carboniferous of Ireland and England, here designated.

Diagnosis: Small shells ornamented by fine ribs that increase on both valves by bifurcation.

Discussion: In most genera of Pterinopectininae the ribs on the left valve increase by intercalation, but in this genus, many of the left valve costae increase by branching, just as on the right valve. In other respects the genus is like other members of the subfamily in having a long hinge and large posterior wings, comparatively short left anterior wing and comparatively large right anterior auricle. The species *meleagrinoides* was figured by M'Coy (1851, pl. 16, fig. 3) and Hind (1903, pl. 17, fig. 20-23). *Pecten concavus* M'Coy, 1844, pl. 15, fig. 10, allocated to *Pterinopecten* by Hind (1903, p. 55, pl. 9, fig. 6, 7, refiguring the type in pl. 9, fig. 6) from Ireland and Northumberland, is congeneric. *Pecten radiatus* Phillips, 1836, pl. 6, fig. 8, also figured by Hind (1903, p. 55, pl. 9, fig.



Text-fig. 22. *Bifurcatatia radiatus* (Phillips) figured by Hind (1903, pl. 9 fig. 14) from Carboniferous of Ireland, kept at York Museum, x 0.8. B, *B. concavus* (M'Coy) figured by Hind (1903, pl. 9, fig. 6) from Northumberland, CASM E 1282, x 0.8.

12-16) from various localities in England, and also Ireland, has intercalate and branching ribs on the left valve, and *Pecten papyraceus* Sowerby (1823, p. 75, fig. 354), also figured by Hind (1903, p. 51, pl. 7, fig. 7-13) is apparently allied.

The new genus is moderately close in general appearance to *Dunbarella* Newell, 1938, p. 39 from Pennsylvanian faunas of United States, based on type species *D. whitei* (Meek) from Nebraska, but the ribs on Newell's genus are a little coarser, often with flat crests, and according to Newell the left valve ribs increase by intercalation. As well the byssal notch is better developed and the right anterior auricle better defined.

Subfamily **PTERINOPECTINELLINAE** new subfamily

Name genus: *Pterinopectinella* Newell, 1938, p. 41 from Upper Carboniferous of mid-west United States, here designated.

Diagnosis: Distinguished by presence of distinct bundles of bifurcate ribs on right valve. Left valve often spinose or nodose, right valve may be spinose. Right anterior auricle prominent and byssal notch high.

Discussion: This subfamily has distinctive right valve ornament in which ribs divide, and are associated in bundles. The left valve on most genera has lamellar spines, and another genus has nodose ribs: the right valve may be spiny or nodose. In other respects the genera are close to Pterinopectininae, but may have long right anterior auricle and large byssal notch, high anteriorly. The strong ornament, which may even involve plicae, is unusual for the order, and reappeared in the descendent Aviculopectinidae, so that remotely, an unknown member of the subfamily provided the source of that family. But the fossil record as far as known and the long hinge do not favour this possibility.

Genus ***Bradfordipecten*** new genus

Derivation: Named from Bradford County, Pennsylvania.

Type species: *Pseudaviculopecten bradfordensis* McAlester, 1962, p. 51, from Chemung beds (Upper Devonian) of Bradford County, Pennsylvania, here designated.

Diagnosis: Weakly inequivalve with only moderately long and moderately defined wings and distinct right anterior auricle. Ornament of coarse round-crested ribs or subplicae on both valves, those of right valve rarely split, and bearing growth laminae forming crescent-shaped scales, arching dorsally over ribs, left valve with broader ribs and a few fine costae arising by intercalation in the narrow interspaces, growth laminae low. Hinge duplivincular.

Discussion: The ornament of this species is unusually coarse, and is slightly different on the two valves. In the lamellar crescents that cross the rib crests of the right valve, the genus approaches *Pterinopectinella* Newell, 1938, but in this genus it is the left valve that is spinose. The left valve shows weak signs of nodes, and the genus is regarded as an early member of the subfamily. McAlester (1962, pl. 20, fig. 14, 15) regarded the type species as a member of *Pseudaviculopecten* Newell, but the ornament is much coarser and more differentiated on the two valves, and the posterior wings are not as well defined.

Pterinopecten mundus Whidborne, 1897, p. 137 from Upper Devonian Pilton Formation, Devon, England, is moderately high with long posterior hinge and large left posterior wing, and small anterior left valve wing with deep sinus. The left valve of Whidborne (1897, pl. 15, fig. 13, 13a – CASM E 300) has strong plicae with rounded crests and faint nodes, and is selected as lectotype. Secondary costae are more developed on the other figured specimen (pl. 15, fig. 12, 12a – CASM E 299). The species also has been reported from a very late Devonian fauna of Bergisches Land, western Germany, by Amler et al. (1990, p. 49, pl. 2, fig. 3) and Amler (1992, p. 414, pl. 1, fig. 9, 10), and the German specimen has strong and angular plicae and interspaces, and plicae often bear a semifurcate flank costa behind the crest, and posterior plicae are finer over the posterior wing. The generic position is close to that of *Bradfordipecten*, but no right valves have been described.

Genus ***Ornatipecten*** new genus

Derivation: ornate – with ornament; pecten - scallop, Lat.

Type species: *Aviculopecten ornatus* Hall, 1883, p. 37 from Hamiltonian (mid-Devonian) rocks of New York, here designated.

Diagnosis: Left valve ornamented by weakly nodose primary and intercalated secondary costae, crossed by low concentric ridges; right valve with bifurcate ribs in bundles.

Discussion: This genus is characterized by the well-spaced ribs in two orders, intercalate on the left valve, and narrowly bifurcate or rarely trifurcate ribs on the right valve. Low but distinct and well spaced concentric laminae are developed, with low nodes at intersections. *Pterinopectinella* and *Pterinonova* n. gen. have more prominent scaly spines, and the ribbing on the former genus is coarser, and on *Pterinonova* is semicalate. Whereas the right valve ribs are distinctly branched and strong in *Pterinopectinella*, the right valve ribs in the present genus are finer and more numerous, and the right valve ribs of *Pterinonova* are more differentiated and semicalate as well as branching. Hall (1883, pl. 2, fig. 7, 8, pl. 3, fig. 14, 1885, pl. 2, fig. 8), followed by Pojeta (1986, p. 102, pl. 58, fig. 5-8, pl. 59, fig. 4-9) in reporting the species from Michigan, both referred the species *ornatus* to *Aviculopecten*, but the long hinge and large weakly defined left valve wings point to pterinopectinid affinities. *Pterinoplica* n. gen. has shorter anterior auricle and left valve anterior wing, and more plicate spinose and diversely ribbed right and left valves.

Genus ***Pterinonova*** new genus

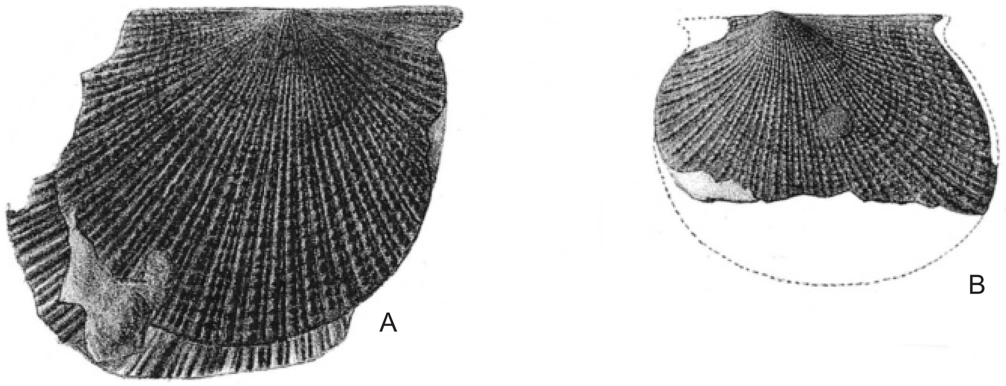
Text-fig. 23

Derivation: pterino – part of bivalve name; novo – make new, Lat.

Type species: *Aviculopecten eximius* Koninck, 1885, p. 211 from Early Carboniferous of Belgium, here designated.

Diagnosis: Shell with long hinge, very large posterior wings, smaller left anterior wing and right anterior auricle, shallow byssal notch. Characterized by well developed nodose primary ribs on left valve, with one or two more orders of non-spinose ribs increasing by semicalation and splitting to form weak bundles; right valve primary ribs weakly nodose, secondary and further ribs increase partly by intercalation and mostly by semicalation.

Discussion: The type species was described from Belgium by Koninck (1885, pl. 37, fig. 1, 2 – IRSNB 4873 and 4, 5 – IRSNB 4874), specimen IRBSN 4873 being nominated as lectotype. Hind (1903, p. 59, pl. 10, fig. 4, 5, pl. 11, fig. 13, 14) recorded the species from England and Ireland. He observed that ribs often occurred in pairs, and that a large one and a small one occurred close together, with an interval to the next pair. A number of the ribs are semicalate, by which a slender secondary rib arises close to the primary ribs on the anterior side (in this genus) and widens ventrally to gradually become as strong as the primary rib. The Hind material shows slightly more complex and finer ribbing than in the Belgium material. *Pterinopecten* sp. aff. *eximius* from the upper Devonian of Bergisches Land, Germany (Amler et al. 1990, pl. 2, fig. 1) is close, and is congeneric.



Text-fig. 23. *Pterinonova eximius* (Koninck). A, right valve (NHM) figured by Hind (1903, pl. 11, fig. 13) from County Dublin, Ireland, x1. B, left valve, figured by Hind (1903, pl. 10, fig. 4) x1, from Derbyshire. Kept at Sedgwick Museum. Specimens of Carboniferous age.

Pecten granosus Sowerby (1829, p. 144, pl. dlxxiv, fig. 2) from Early Carboniferous of England, also figured by Hind (1903, pl. 10, fig. 1-3, 6), is congeneric. *Pecten dumontianus* Koninck (1843, p. 134, pl. 4, fig. 3), from Belgium, also described by Koninck (1885, p. 214, pl. 37, fig. 3), is possibly congeneric, but only left valves were figured. A larger suite from England was ascribed to this species by Hind (1903, p. 65, pl. 8, fig. 4-8, pl. 14, fig. 1, 2) and these show the ornament typical of the genus on both valves, including mostly semifurcate right valve ribs. The primary ribs appear to be stronger and the secondary ribs fewer on the left valve compared with the Koninck material.

The genus is close to *Pterinopectinella* Newell 1938, p. 41, type species *N. welleri* Newell (1938, pl. 3, fig. 14, 18-24) from the Pennsylvanian of the United States, the left valve having spinose primary ribs and spinose secondary costae arising by intercalation, long posterior wing and relatively larger anterior wing. On the right valve of *Pterinopectinella*, with its large anterior auricle, deep high byssal notch and long posterior wing, the primary ribs branch into two ribs of equal size. The ribbing thus differs from that of the new genus, in which a few of the secondary ribs are intercalated, and most arise close to the primary ribs rather than in the middle of the interspaces and continue as slender secondary ribs for some distance before becoming large. *Pterinoplica* n. gen. is readily distinguished by its short anterior auricle and wing, by its plicae, and other differences.

Genus ***Pterinoplica*** new genus

Derivation: pterino – part of bivalve name; plica – fold, Lat.

Type species: *Pterinopectinella spinifera* Newell & Boyd, 1995, p. 29 from Cathedral Mountain Formation (Kungurian, Early Permian), Glass Mountains, Texas, here designated.

Diagnosis: Asymmetrically biconvex with spinose plicae on both valves, short right anterior auricle and left valve wing, posterior wings of moderate length.

Discussion: This genus differs from the Late Carboniferous genus *Pterinopectinella,* type species *P. welleri* Newell (1938, p. 41), in many respects. Newell's genus has long right anterior auricle and left anterior wing, and the right valve ornament consists of bifurcate weakly nodose broad ribs, whereas the right valve of the present form is ornamented by narrow plicae bearing two or three ribs, of which the primaries are moderately spinose, and even some of the posterior wing ribs are spinose. The left valve of *Pterinoplica* is ornamented by strongly spinose primary ribs, placed on subdued plicae and bordered by one or two lateral costae, with fine costae appearing in some interspaces. Newell & Boyd (1995) described the species *spinifera* as infracrescent, and noted that the byssal notch was bordered internally by a strong collar. It was stated that material came from both Leonardian and Guadalupian in the Glass Mountains, but most specimens were fragmentary.

Subfamily **TESSERATIINAE** new subfamily

Name genus: *Tesseratia* new genus from Early Permian of Urals, Russia, here designated.

Diagnosis: Ornament characterized by well spaced radial ribs crossed by strong commarginal ribs.

Discussion: This subfamily is proposed for pterinopectiform shells that have a distinctive ornament arranged in a network of radial and concentric ribs, unlike the predominantly radial ribs on genera of Pterinopectininae and Pterinopectinellinae. The ornament is close to that found in unrelated Streblochondriidae (*Tesselarulina*), and in the left valve of *Girtypecten* (Etheripectinidae).

Genus ***Tesseratia*** new genus

Text-fig. 24

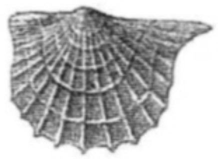
Derivation: tessera – a square, Lat.

Type species: *Pterinopecten serbodowae* Fredericks, 1915, p. 25 from Lower Permian of Urals and Timan, here designated.

Diagnosis: Pterinopectiniform shells characterized by tesselate pattern formed on both valves by strong and well spaced radial costae crossed by well spaced well defined concentric ribs. Hinge long, ligament duplivincular.

Discussion: This genus is distinguished by its highly distinctive ornament. The type species was described from the Lower Permian and Upper Carboniferous of the Urals and Timan (Fredericks 1915, Licharew 1927, Muromseva 1974, 1984). An allied species is represented in Early Carboniferous faunas of England as *Avicula tessellata* Phillips (1836, pl. 6, fig. 6), the holotype

Text-fig. 24. *Tesseratia tessellatus* (Phillips), as figured by Hind (1903, pl. 9, fig. 11), from Early Carboniferous of Little Island, Cork, Ireland, x1. Ornament on right valve is the same.



figured by monotypy, and Hind (1903, p. 63, pl. 9, fig. 8-11, holotype refigured in pl. 9, fig. 10 – BMNH L97118). Amler et al. (1990, p. 49) compared *A. tessellatus* to *Avicula austeni* Roemer, 1855, although their particular specimen has stronger umbonal slopes and long hinge with large anterior and posterior left valve wings. The species *austeni* belongs to a form yet to be fully circumscribed, but as figured by Whidborne (1897, p. 136, pl. 15, fig. 10, 11), appears to belong to *Tesseratia*. Amler et al. (1990) assigned the species to *Newellipecten* Rûžićka, Prantl & Pribyl, 1959, and Amler (1992, pl. 1, fig. 8) to *Newellipecten*?, but the type species of *Newellipecten*, *Aviculopecten niobe* Barrande of Early Devonian age, lacks the transverse ribbing of Phillips' species. The ornament is close to that of *Tesselarulina* gen. nov. (see p.106), but *Tesseratia* is pterinopectiniform, the other streblopteriid in shape and hinge.

Specimens figured as *Aviculopecten exacutus* Hall, 1884 from the Middle Devonian Hamilton Group of New York State, United States, were assigned by Newell (1938, pl. 2, fig. 1-3) to *Pseudaviculopecten* Newell, 1938, and have the tesselate ornament and duplivincular hinge typical of the new genus, but the figures show the species only at a very early growth stage. The type species of *Pseudaviculopecten* was cited as *Pecten princeps* Conrad, 1835 by Newell (1938, p. 38). This species has very fine radial ribs and inconspicuous concentric ornament, as illustrated for *princeps* by Conrad (1835) and Newell (1938, pl. 2, fig. 19, 20). *Pseudaviculopecten* is biconvex, and has intercalate ornament on both valves, and the right anterior auricle is well distinguished.

Roberts (1965, p. 76, pl. 12, fig. 9, 10) described a Visean species from near Gresford, northern New South Wales, Australia, that he considered to show some approach to what he called *Aviculopecten tesselatus* [sic] (Phillips). He noted differences, and pointed that the species also approached "*Pseudoaviculopecten exactus* (Hall)", according to a personal communication from J. M. Dickins. The correct specific name is *exacutus*, and Dickins must have been misled by the figures of Hall's species in Newell (1938, pl. 2, fig. 1-3), which are presented at a magnification of x5, and did not check the appearance of mature specimens. The Australian material lacks the strong concentric ribs of *tessellatus*, as noted by Roberts (1965, p. 76), and looks close to *Vertumnia* Hall, 1884, type species *Pterinea reversa* Hall, 1883, figured by McAlester (1962, pl. 24, fig. 1-7) and of Devonian age. The genus *Vertumnia* is unusual because the right valve is more inflated than the left, but this cannot be assessed for the Australian form, because no right valves were available. Roberts (1965) identified his specimens with ?*Girtypecten* Newell, 1938, but this genus differs considerably, with strong spinose radial ribs and moderately strong commarginal ribs.

Family **NATALISSIMIDAE** new family

Name genus: *Natalissima* n. gen. from Lower Devonian Reefton Group of New Zealand, here designated.

Diagnosis: Hinge less than maximum length of shell, valves subequally convex to strongly inequivalve, left valve more inflated, left valve wings small, right posterior wing small, anterior right auricle well developed, above deep byssal notch, wings clearly set off from body of shell by high umbonal slopes. Hinge duplivincular.

Discussion: Genera assigned to Pterinopectinidae have long hinge, often at maximum length, and low inflation with the wings and right anterior auricle weakly distinguished from the body of the shell. The present family is distinguished by the shorter hinge line, and better defined although smaller wings and right valve auricle. The name giver for the new family is selected from a newly named genus based on New Zealand material, because it shows most of the essential detail although muscle scars and shell structure are uncertain, aspects which also remain clouded for virtually all members in the superfamily.

The family is subdivided into two: one subfamily essentially biconvex, and the other with right valve much less inflated than the left valve. The latter subfamily gave rise, it appears, to Etheripectinidina. In that sense, it could also be classed as Etheripectinidina, but preserves the ligament of Pterinopectinida. The other subfamily, more arguably, provided the potential ancestry for Aviculopectinidina, given overall shape and development of wings and auricle. It could be classed as aviculopectinidin, but retains the duplivincular ligament. Evidence thus suggests that this was a “high energy” family, with ultra-high potential for rapid and significant change.

Subfamily **NATALISSIMINAE** new subfamily

Diagnosis: Distinguished by right valve less inflated with ornament differing from that of left valve.

Genus ***Natalissima*** new genus

Text-fig. 25

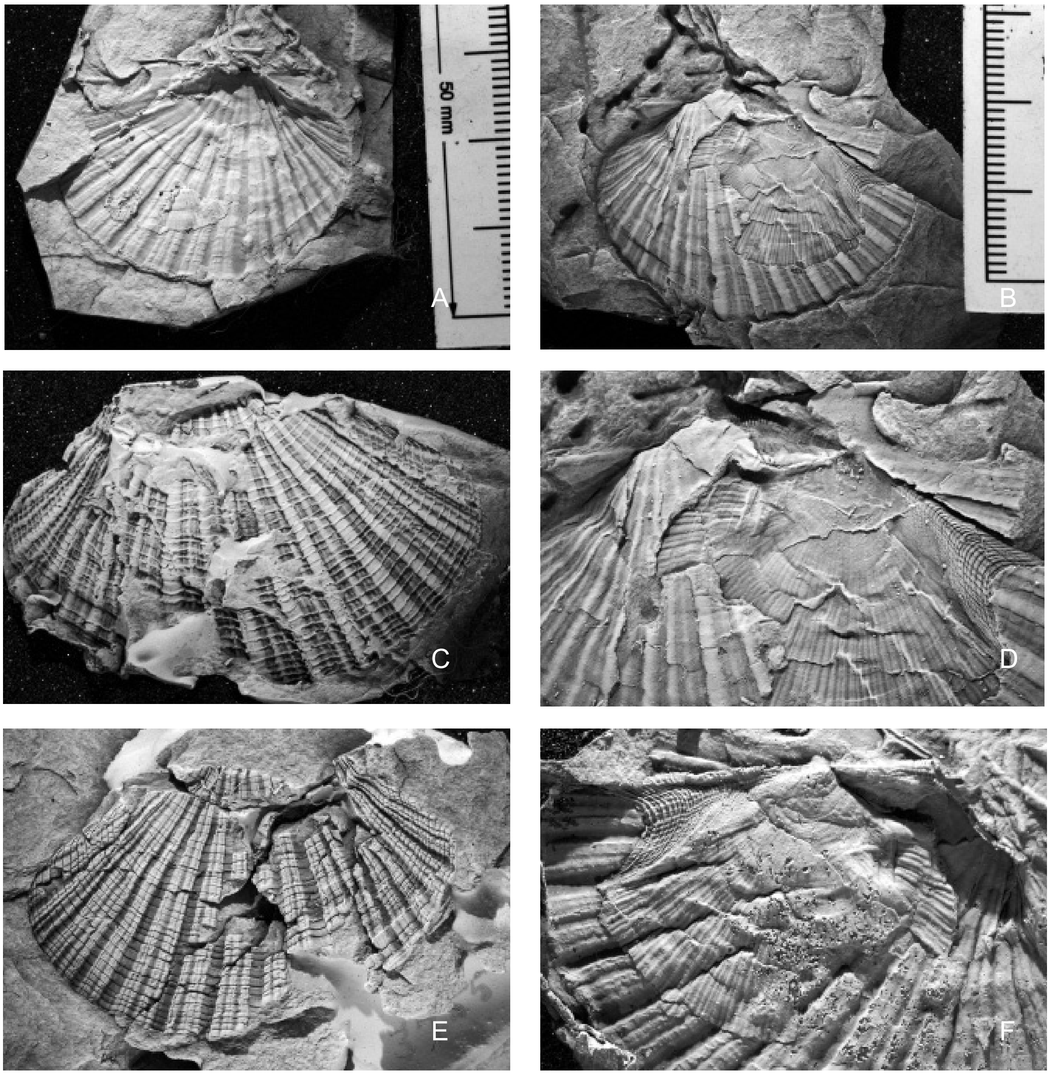
Derivation: natalis – of birth, Lat.

Type species: *Pterinopecten (Pseudaviculopecten) casterorum* Fleming, 1957b, p. 139 from Lower Devonian Reefton Group, New Zealand, here designated.

Diagnosis: Inequivalve, hinge short with well defined wings and deep sinuses, well developed right anterior auricle with narrow byssal slit; left valve ornament of costae in two or three orders, primaries prominent. Right valve little inflated, ornamented by uniform and fine costae.

Discussion: The type species has been described by Fleming (1957b, pl. 15, fig. 1-5) and Bradshaw (1999, Fig. 78A-I). It is a highly distinctive form with short hinge, well defined wings, well differentiated left valve ribs crossed by fine laminae, fine right valve ribs, and duplivincular ligament. Bradshaw (1999, p. 115) identified the species with *Lyriopecten* Hall, 1883, but the type species of this genus, *Avicula orbiculata* Hall in Miller, 1877, has a long hinge, weakly discriminated posterior wings and fine ribs, very close in many aspects to *Pterinopecten*. Bradshaw was persuaded of an alliance by the strong left valve primaries, which approached the ornament of several species identified with *Lyriopecten* by McAlester (1962) and Pojeta (1986). These species are much closer to type *Lyriopecten* in the length of hinge and poor definition of left valve wings, and showing a very large right valve byssal notch in the case of *L. anomiaeformis* Hall (McAlester, 1962, pl. 22, fig. 5). Fleming (1957b) came closer in his generic assessment, but *Pseudaviculopecten* Newell has much finer left valve ribbing, which is close to that of the right valve. *Yassapecten* n. gen. is close, with left valve ornament dominated by primary ribs and few if any secondary costae, and well spaced right valve ribbing, with other differences.

Ivanovipecten Astafieva & Astafieva-Urbaiitis (1994) , type species *I. myachkovensis* Astafieva-Urbaiitis comes from the Myachkovo horizon of the Moscow Basin, Russia, between Middle and Late Carboniferous in age, and Slovenia, and has a more inflated left valve with fine intercalated radial costae. The right valve is almost smooth, and moderately convex. The



Text-fig. 25. *Natalissima casterorum* (Fleming). A, B, D, F, holotype TM 2064. A, external mould, left valve. B, internal mould of left valve with attached exterior of right valve, D, enlargement of B, and F, latex cast of the specimen. C, E, latex cast and external mould of left valve TM 2063, x2 approx. From Lower Devonian Reefton Group, New Zealand. Photographs courtesy of John Simes, GNS Science. See Fleming (1957b).

posterior wings are distinct and of moderate length with deeply recessed sinus. The left anterior wing is well separated, and the right anterior auricle is similar, although the authors write nothing of a byssal notch. The hinge is duplivincular. Only one species is known.

Genus ***Yassapecten*** new genus

Derivation: yassa – Australian place-name; pecten – scallop, Lat.

Type species: *Aviculopecten etheridgei* Koninck, 1876, p. 89, from Lower Devonian of Yass, New South Wales, here designated.

Diagnosis: Medium in size, left valve wings of moderate length and definition, right valve wing and anterior auricle moderately long, byssal notch shallow, posterior sinuses comparately deep. Left valve costae well spaced and increase by intercalation, right valve costae comparatively simple and well spaced; growth increments fine and dense.

Discussion: The type species was redescribed from silicified material by Johnston (1993, p. 62, Fig. 41, 42) with a neotype ANU 36639 designated. Detail is well preserved, with chevron ligament and muscle scars. The species is close overall to *Pseudaviculopecten* as demonstrated by Johnston (1993), but the wings and auricle are less defined and are slightly larger than in *Pseudaviculopecten*, and the right anterior auricle is larger, with less of a byssal notch, and less convex. The ornament is simpler, with well spaced primary ribs and very fine further orders on the left valve, and simple ribs of one order on the right valve, whereas the right valve in *P. princeps* has crowded ribs of two or three orders. *Yassapecten* has very much simpler left valve ornament than in *Natalissima*, with fewer orders of costae, finer primaries and lower concentric lamellae.

Subfamily **PSEUDAVICULOPECTININAE** new subfamily

Name genus: *Pseudaviculopecten* Newell, 1938, p. 38 from Middle Devonian Hamilton Group of New York, here designated.

Diagnosis: Ornament similar on right and left valve. Hinge short, wings well defined, left valve more inflated than right valve.

Discussion: Members share the short hinge and well defined posterior wings with Natalissiminae, but have similar ornament on the two valves, and more inflated right valve.

Genus ***Intercalatia*** new genus

Derivation: inter – between; calathus – wicker basket, extended to woven intercalate canes, Lat.

Type species: *Aviculopecten exacutus* Hall, 1883, p. 8 from Middle Devonian Hamilton Group, New York, here designated.

Diagnosis: Ornament of fine intercalate costae in three differentiated orders on each valve, crossed by low growth laminae that may be prominent over first formed shell.

Discussion: The species *exacutus* Hall was well figured by Hall (1883, pl. 3, fig. 18-22), and by Pojeta (1986, pl. 58, fig. 1, 2, pl. 59, fig. 1-3) from the Upper Alpena Limestone and Four Mile Dam Formation of Michigan. The genus is distinguished from the otherwise similar form *Pseudaviculopecten* Newell by the ornament. In *Pseudaviculopecten*, the costae on both valves are fine and crowded and largely uniform, in two or three orders, with intercalation most common, but with some examples of branching on each valve, as may be discerned in figures of *Pseudaviculopecten* presented by McAlester (1962). McAlester (1962) described *Pecten striatus* Hall, 1843 and *Aviculopecten fasciculatus* Hall, 1883 and placed other species in synonymy from the Chemung rocks of New York, and showed them as closely related to the type species of *Pseudoaviculopecten, Pecten princeps* Conrad, 1835. There are a few finer costae, but most are of equal strength, unlike the more differentiated costae of *Intercalatia*. Growth-laminae are fine and close-spaced.

Superfamily **HALOBIOIDEA** Kittl, 1912

[nom. transl. by Campbell 1994, p. 64 ex Halobiidae Kittl, 1912, p. 5].

Diagnosis: Equivalve to strongly inequivalve shells with valves similar or differing in ornament, ligament duplivincular, replivincular or canalivincular, edentulous, monomyarian.

Discussion: This superfamily is proposed to incorporate two rather different families, apparently linked in the fossil record, as discussed for genus *Imposidonia* (p. 66). The families are of Mesozoic age, and neither is close to Paleozoic pterinopectinid families. Claraiidae has a little inflated right valve, reminiscent of Natalissiminae, but has a longer hinge and ill-defined posterior wings in many forms, and the ligament changed to replivincular or canalivincular. Halobiidae is much closer to Paleozoic pterinopectens in shape and long hinge, but lacks a right anterior auricle and has a canalivincular hinge. Putting the two together expresses the difference from Paleozoic forebears, and expresses the apparent kinship, but the morphological space between the two is considerable.

Campbell (1994, p. 64) was first to elevate Halobiidae to superfamily status, and he attributed the name to himself, which is clearly contrary to the rules for zoological nomenclature. He regarded the family as the only member of the superfamily, which may have some merit, but provided a misleading diagnosis, describing the ligament as alivincular, which it certainly is not, and regarding the family as a member of Ostreida, which seems extraordinary, given the differences in shape, attachment, right valve – left valve construct, shell structure and other parameters. No adequate reasons were provided to distinguish the family from Posidoniidae (see p. 34 herein) or various Mesozoic members of Aulacomyellidae (see p.171), or Bositridae (see p. 174). These families differ in their ornament and ligament, but come close in aspects of shape.

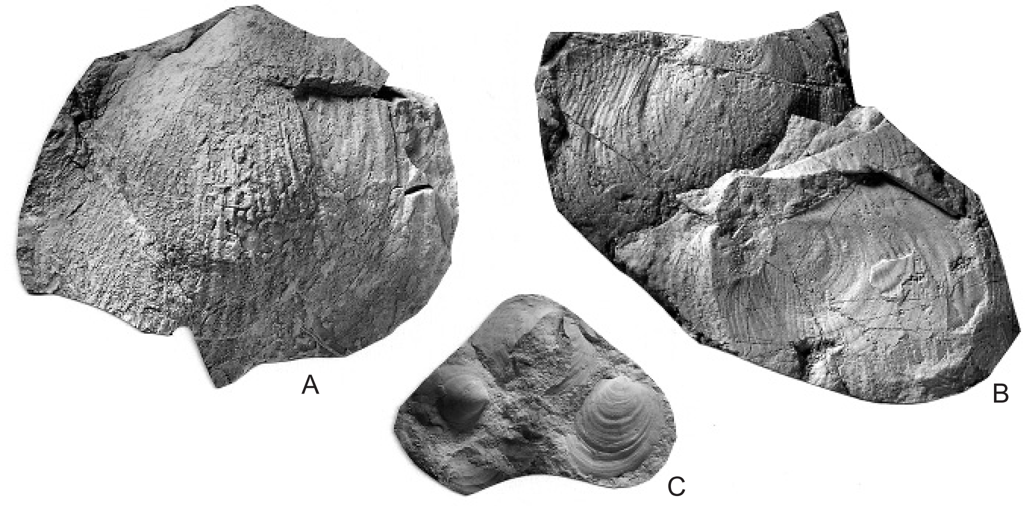
Family **CLARAIIDAE** Gavrilova, 1996

This family is distinguished from Pterinopectinidae by its convex left valve and more or less flat right valve, with well developed anterior auricle and varied byssal notch. Although Waterhouse (2000) reduced the family to subfamily level, it is judged to fully merit family status, especially in view of the other subdivisions within Pterinopectinoidea.

Subfamily **CLARAIINAE** Gavrilova, 1996

Text-fig. 26

Most claraiid genera appear to belong to this subfamily. Gavrilova (1996) stressed the nature of the ligament as showing more complete chevrons, but the ligament is often not visible, and indeed may be more variable than allowed by Gavrilova. Bøggild (1930, p. 30) observed regular prismatic structure in *Pseudomonotis clarai*. This is also true of *Claraia nakazawai* Waterhouse, 2000 from Early Triassic (Annapurnan – Dienerian) Sabche Member of central Nepal, in which the right valve has a thin outer prismatic layer.



Text-fig. 26. A, B. *Claraia nakazawai* Waterhouse from Sabche Member, Early Triassic (Annapurnan, Dienerian) of north-central Nepal, x 0.8. A, left valve FMo 3383. B, right valves FMo 3384 and 3385. C, *C. griesbachi* Bittner, block including FMo 3366 from Gangetian (Early Triassic) Pengba Member, north-central Nepal, x 0.8. See Waterhouse (2000).

Subfamily **PSEUDOCLARAIINAE** Gavrilova, 1996

This subfamily, based on *Pseudoclaraia* Zhang, 1980, was named for shells in which the chevrons became wavy posteriorly. It was pointed out by Waterhouse (2000, p. 178) that the ligament was only known for the type species: many species included in the same genus by Gavrilova (1996), including type material, do not show the ligament area, and another genus allocated to the subfamily, *Periclaraia*, does not show the ligament. Therefore it was suggested that the subfamily should be characterized by external parameters, involving a deep narrow byssal notch and comparatively well-formed convex left anterior wing as well as right anterior auricle. *Rugiclaraia* Waterhouse, 2000, based on *Posidonomya aurita* Hauer, 1850, was included in this group.

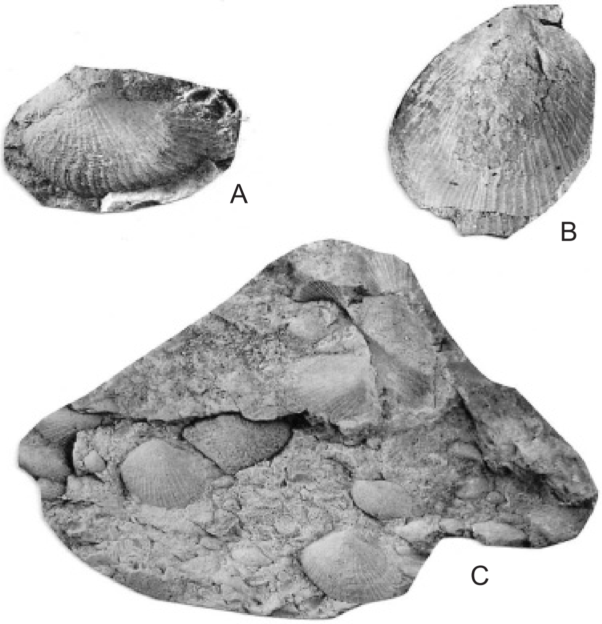
Subfamily **CHULUARIINAE** new subfamily

Text-fig. 27

Name genus: *Chuluaria* Waterhouse, 2000, p. 175 from Late Scythian (Mesokantoan Stage) Langpo Member of Nepal, here designated.

Diagnosis: Left valve swollen and right valve usually convex, wings poorly differentiated or as a rule absent, right anterior auricle slender and byssal notch short but may be high. Ligament area forms simple canalivincular groove, without chevrons, where known. Thin outer prismatic layer in right valve.

Discussion: *Chuluaria* is an outstanding genus with no anterior left valve wing, no separate left valve posterior wing, the left valve not being flattened or diminished in thickness other than gradually to the hinge, and poorly differentiated right valve posterior wing. Costae on *Chuluaria* are fine and well developed: and often bifurcate and remain associated in subdued clumps, without being raised into plicae: like ribbing in some species of *Claraia* and allies. It is of late Scythian age and the genus apparently ranged into early Anisian beds of the Himalaya. The



Text-fig. 27. *Chuluaria bragaensis* Waterhouse. A, left valve FMo 3409 x1. B, holotype right valve FMo 3414 x2. C, block, including FMo 3410 and 3411 x1. Specimens from Langpo Member, late Early Triassic (Mesokantoan – post-Spathian) of north-central Nepal. See Waterhouse (2000).

Arctic species *Halobia occidentalis* Whiteaves, reassigned to *Pseudomonotis* by Tozer (1961), is congeneric, and comes from Late Scythian *Wasatchites* beds of Canada and Spitsbergen. The slightly older form described as *Pseudomonotis occidentalis kindlei* McLearn from the Toad Formation of northeastern British Columbia, of Smithian age, which is equivalent to the much fuller Gangapurnan of the Himalaya, might prove to be allied. *Crittendenia* Newell & Boyd, 1995 is similar in many respects, with wider byssal notch, and the nature of the ligament is not known. It is a smooth genus with weakly defined or no wings, and found in Early Triassic of western United States, Himalaya and Pakistan. This genus is particularly notable for the scar of attachment on right valves, which are gently convex.

Family **HALOBIIDAE** Kittl, 1912

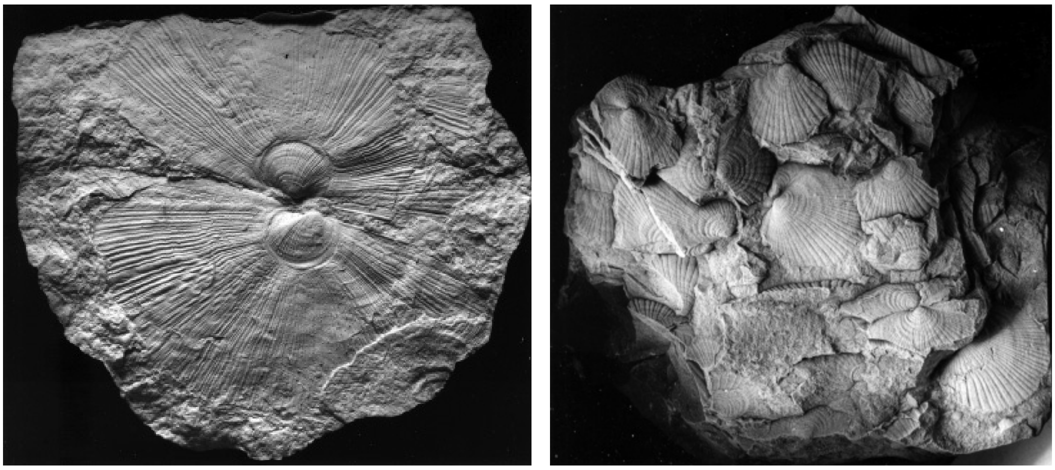
Text-fig. 28

Halobiidae are a Triassic group, interpreted in a number of studies as originating from the Carboniferous Family Posidoniidae. Here it is noted that a pterinopectiniform relationship is possible, given the evidence of the fossil record and morphological change. In the following discussion it is shown that such genera as *Bositra* and *Enteropleura* cannot be considered as ancestral, because they belong to Etheripectinidina. One possible source lies within Claraiidae, another within Posidoniidae.

Family relationship

Campbell (1994) and amongst others, Amler (1999, p. 241), regarded Halobiidae as belonging to a discrete superfamily “Halobioidea Campbell”. According to the international rules for zoological nomenclature, the superfamily should have been ascribed to Kittl, 1912. The superfamily grade was not adequately defended, but attributes of the group, involving subequivalve shells sharing similar ornament, with canalivincular hinge and lack of byssal notch, do make up an unusual association, and although the family is associated herein with Claraiidae because of evidence for relationship and similarity in aspects of ornament, this may require reassessment.

Although Cox & Newell (1969, p. 342) placed the Triassic genera *Daonella* Mojsisovics, *Halobia* Bronn and *Enteropleura* Kittl in Posidoniidae Frech, Waterhouse (2001, p. 117) preferred descent from Pterinopectinidae. But Waller (2005, p. 17) retained Cox & Newell’s view that



Text-fig. 28. A, *Aparimella* sp. B, *Halobia* sp. Photographs supplied courtesy of H. J. Campbell, GNS Science, without further documentation.

favoured relationship of Halobiidae to *Posidonia* and its probably precursor genus *Caneyella* Girty, 1909, a view endorsed in various studies, as in Encheva (1978) and Damborenea (1987). Both views projected lines of descent that involved substantial changes in morphology. Adopting the sequence of evolutionary progression proposed by Waller (2005), the changes may be summarized as follows:

Posidonia → *Bositra* → *Enteropleura* → *Daonella* → *Halobia*
duplivincular → alivincular → canalivincular
pteriiform → aviculopectiniform

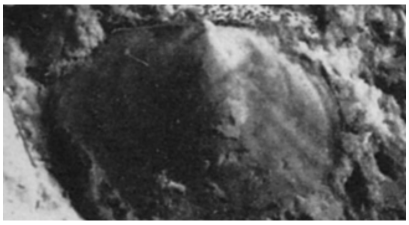
For other aviculopectiniform genera, evolution proceeded from pteriiform (heteromyarian, duplivincular, right anterior wing) to pterinopectiniform (monomyarian, duplivincular, right anterior auricle) to aviculopectiform (monomyarian, alivincular, right anterior auricle) by Early Carboniferous time. The thesis set forward by Waller (2005) proposes a separate and much later change, within Posidonioidea, in which the pterinopectiniform stage was elided. Of course such a stage may have been short-lived, but there is no evidence. Examples of alivincular ligaments turning into canalivincular ligaments appear to be unknown amongst Pectinidia, although there are many examples of alivincular ligaments becoming platyvincular. The alternative proposal is much simpler, proposing that the root-stock is provided by pterinopectiform bivalves. That has the advantage of reducing the three-stage changes to two. Moreover study on Claraiidae has established that the pterinopectinid duplivincular hinge was able to transform into a canalivincular ligament, and it would therefore be reasonable to regard Halobiidae, as restricted herein, to be a sister or descendent group parallel to various species and genera of Claraiidae, and never having passed through an aviculopectiniform and alivincular stage. In that way, the problematical jumps in morphology and difficulties of timing appear to be overcome. Of course, evolution has proceeded along so many different paths that possibilities cannot be ruled out without further analysis, nor indeed can yet a third option, of a source from within an etheripectinid or streblochondriid, be entirely set aside. Attention is therefore focused on the analysis presented by Waller (2005), which summarized what was known, based on an extensive survey of European and American literature and close examination of Middle Triassic fossils from Nevada. Here the evidence is reassessed, to discern if any alternative evolutionary trajectories can be gleaned, both from Waller's insights, and further information and material that has come to hand.

Waller (2005, p. 17) tracked a progression from *Posidonia* and precursor genus *Caneyella* (Posidoniidae), through a Middle Triassic genus *Bositra* into a sequence of genera *Enteropleura-Daonella-Aparimella-Halobia*. The linking genus *Bositra* is small, equivalve or subequivalve, somewhat rounded to oval in shape with subdued or no wings or auricles, and ornament of commarginal rugae and/or radial ribs. For such a progression, the ligament must have changed from duplivincular (*Caneyella*, *Posidonia*) to alivincular in *Enteropleura,* to "neomorphic" - or more specifically canalivincular for *Daonella* and *Halobia*. The life-style changed as well: from obligate byssally attached for *Caneyella* to facultative byssal attachment in *Posidonia,* then benthic possibly non-byssate reclining life-style in *Bositra, Daonella* and *Aparimella,* and more contentiously*, Halobia.* Waller argued that *Enteropleura* provided a convincing intermediary between the externally *Posidonia*-like *Bositra* and *Daonella*, which is clearly halobiid, pointing out that the commarginal wrinkles developed early in ontogeny, and radial ribs began later in ontogeny in *Enteropleura*. In *Daonella*, radial ribs commence at the umbo.

Bositra, Enteropleura (Text-fig. 29)

Both *Bositra,* which includes *Peribositria* Kurushin & Trushchelev, 1989 according to Waller (2005, p. 20), and *Enteropleura* have as far as known alivincular ligaments, and are monomyarian, significant differences from their supposed forebear *Posidonia*, to the extent that there have to

Text-fig. 29. *Enteropleura guembeli* (Mojsisovics), left valve x3 from Balatonitan beds of Vamos, Hegyesgyor, Wien Nr 168/1956, reproduced from Ichikawa (1958, pl. 23, fig. 7).



be questions about confamiliarity with *Posidonia*, notwithstanding the claim proferred by Ichikawa (1958) that *Enteropleura* arose from *Posidonia*. It has been suggested that unlike *Posidonia*, *Bositra* shows gapes (Jeffries & Minton 1965), but comparison between the extensive collections of *Bositra* and *Posidonia* at the Museum of Natural History, London, does not show convincingly consistent external distinctions apart from the presence of wings on *Posidonia*, and Kauffman (1981, p. 340) and Conti & Monari (1992, p. 205) did not accept the presence of gapes. That is not to deny the validity of subtle differences, but such may be poorly preserved, individual rather than universal, and obliterated by subsequent distortion. Objectively, the critical differences in the hinge and musculature between *Posidonia* (dimyarian, duplivincular) and *Bositra* (monomyarian, alivincular) cannot be readily discounted just because concentric rugae feature on both genera. Without any proven link, it seems difficult to justify classing *Bositra* as posidoniid, and the link to genuine Halobiidae as limited herein seems equally unproven. Rather *Bositra* may have evolved from a source close to *Otapiria* and allies, in which commarginal ornament may be predominant, the hinge short, the posterior wings undeveloped (p.166). The ligament is alivincular and muscle field monomyarian in *Bositra*, as in *Otapiria*. *Otapiria* is classed within Otapiriidae Waterhouse, treated herein as a member of Oxytomoidea. With allies in Otapirinae, it has a right anterior auricle, unlike *Bositra* and related genera now classed as a new group recognised as Bositridae.

Waller's proposal that *Enteropleura* preceeded *Daonella* may at first sight seem questionable, because the type species of *Enteropleura, Daonella guembeli* Mojsisovics, 1874 (SD Diener 1923, p. 52) is subcircular in outline, not attenuately oval, and has prominent umbo and displays little in the way of ornament, other than subdued commarginal rugae (see also Ichikawa 1958 and Text-fig. 29). Shells ascribed to *E. bittneri* Kittl, 1912, named for *Posidonomya* nov. spec. *of* Arthaber, 1896, Fig. 12 and refigured by Hopkin & McRoberts (2005, Fig. 3.13), and *Enteropleura* sp. A of Waller (2005) provide more satisfactory material for the chain of development as far as ornament is concerned, and the former actually shows, according to Arthaber (1896, p. 194, fig. 12), that the hinge is alivincular, although it must be allowed that the illustration is surely diagrammatic (Text-fig. 106). It is here believed that type *Enteropleura* does not fall within the chain of development towards *Halobia*, and that it has a hinge and musculature too different from *Posidonia* and *Halobia* to have been related – instead it is to be regarded like *Bositra* as a member of Bositridae, an aulacomyelloid family (p.174). *E. bittneri* Kittl and *Enteropleura* (sp. A) of Waller (2005) are judged to not belong to *Enteropleura,* being distinguished not only by ornament but by possessing a long low posterior wing. Because *bittneri* has a resilifer, as reported by Arthaber (1896), it lies outside the Halobiidae, and falls within Bositridae. The species is included within the new genus named *Wallerobia* (see p.176).

Halobia

Relying on the nature of the ligament revealed in Campbell (1994), Waterhouse (2001) was persuaded of a non-posidoniid source, proposing that Halobiidae had descended from Pterinopectinidae. The Pterinopectinidae include species remarkably like *Daonella* and *Halobia* in general shape, and for some species, ornament. The ligament is slender and horizontally striated, but rarely carries oblique thickenings (Campbell 1994, text-fig. 4.5), representing according to Waller (2005, p. 18) local knots of ligament. This suggested to Waterhouse (2001, p. 117) a close comparison with various forms of Claraiidae, an Early Triassic descendent from Pterinopectinidae, with ligament that varies from duplivincular to canaliform, and which may have "knots of ligament" to characterise what Waterhouse (2001) called a replivincular ligament. A replivincular ligament is one with relict chevron structure, transitional to canalivincular ligament. Of further significance for Halobiidae, it was demonstrated in a study of Claraiidae from the Himalaya by Waterhouse (2000) that the ligament in a number of specimens looks like that of *Halobia* and *Daonella.* Exceptionally the ligament shown in fine detail for one specimen of *Halobia* by Campbell (1994, pl. 3, fig. 3) shows uparching of growth ridges under the beak, to leave a small triangular hollow, with chevron-grooves composing the first formed part of the ligament under the umbo, and lineavincular grooves below. The triangular hollow in Campbell's figured *Halobia* is somewhat reminiscent of a small hollow figured by Boyd & Newell (2001, Fig. 3) below the beak of *Leptodesma falcata*, a pterineid genus with internal duplivincular ligament from the Permian of Texas. Conceivably the small hollow under the apex of the chevron grooves could have developed into a resilifer, and this resilifer-stage appears to have been elided or compressed in the growth of *Halobia* (and Claraiiidae), whereas a resilifer developed in Aviculopectinidina in earlier times from pterinopectin stock.

Halobia is characterized by a hollow tube, developed to varying width, that lies below what Campbell (1994, Fig. 3.3) termed an auricle, in front of the umbo. Members of Pterinopectinidae display a long anterior right valve auricle next to a byssal notch, and the anterior left valve in Pterinopectinidae carries a wing. Modification of the anterior pterinopecten hinge to form a tube below the anterior left wing and anterior right auricle would not seem to have been radical, and pterinopectens show concentric infillings of the first formed part of the byssal notch in the right valve, as for example in *Denguiria* Boyd & Newell, 1979. Waller (2005, p. 18) preferred to interpret the tube as an inhalant mantle canal, and provided several good reasons, though it should be noted that the support for his theory which was based on habitat would equally if not better apply to at least some Pterinopectinidae. In addition, the claim by Waller (2005) that the end of the tube would have been chipped if a byssus was involved does not seem fully convincing, because many bysally attached bivalves that I have inspected are not so chipped, and furthermore the anterior dorsal part of many specimens of *Halobia* is not just chipped but completely destroyed (Campbell 1994), which seems to amount to strong evidence that *Halobia was* byssally attached, if Waller's argument is accepted. It was claimed that because *Daonella* had no byssus, and yet descended from genera that were byssally attached, *Halobia* could not have reverted to a byssate form, but this cannot be entirely certain, given that evolutionary reversion has often occurred, as exemplified by Triassic ammonoids. Still, it is a reasonable assumption, to be countered only by very firm evidence. In this overview of pectiniform bivalves, it is shown how morphology developed first in the growth of the anterior shell, followed, through time, by reversion and reduction of that anterior shell: evolution was not unidirectional, and repetition and reversion were not uncommon, but occurred on a scale much larger than between two genera. In passing, Waller (2005, p. 18) objected to calling the shell dorsal to the tube an auricle, but this is to be rejected: whether the tube was for byssus or inhalant mantle tube, there is a separate and perceptible anterior segment of shell close to the dorsal commissure. It is a wing: it may be an auricle. Even the disagreement over the function of the tube is not critical, because its function fails to point to the source of the genus. *Posidonia* has a poorly defined anterior wing, with feeble if any byssal notch, reported only early in ontogeny for some specimens. Nor are byssal notches developed in *Bositra* or

Enteropleura. In *Halobia*, the tube commences very close to the anterior umbo. That is, loosely, close to where the byssus arises.

One genus that might shed further information on the nature of the anterior tube in *Halobia* and *Daonella* is provided by *Pterohalobia* Guo, 1985, p. 156 from the lower Middle Triassic fauna of Yunnan. Each valve has an extended anterior in the type species *P. productalata* Guo (1985, pl. 16, fig. 4-7), to suggest the possibility that an ally of Halobiidae developed extended anterior auricles, without a byssal tube and with shallow byssal notch in the right valve. The ornament is principally commarginal, with radial threads over the ears, and valves are equivalve and weakly inflated. The ligament groove is long and slender and the hinge edentulous (Guo 1985, p. 266). An allied form *Longidaonella* is of similar outline, and displays radial ribs. The specimens described as *Daonella productata* in manuscript by Hsu have extraordinarily long anterior wings (Chen & Liu 1976, p. 222, pl. 38, fig. 13-15) and were compared with *Daonella airaghii* Rieber (1968, pl. 2, fig. 16-19) from Europe: other elongate species include *D. caudata* Rieber and *D. elongata* Mojsisovics. It is true that both might be deemed pteriids not allied to Halobiidae, but available evidence is consistent with the relationships interpreted by Waterhouse (2001), and arguably support the byssal tube model advocated by Campbell (1994). Other taxa have been proposed, as *Perihalobia* Gruber, 1976 and *Indirigohalobia* Polubotko, 1984. These were considered to be distinguished by aspects of ornament and auricle, but were evaluated by Campbell (1994) as congeneric with *Halobia*.

Another Chinese genus that appears to be relevant to *Halobia* was named *Parahalobia* Yin & Hsu (in litt.) and formally published by Chen & Liu (1976, p. 224, pl. 39, fig. 7). The type species is *Parahalobia posidoniiformis* Yin & Hsu, a slender equivalve shell with long hinge and commarginal rugae and no radial ribs, from the younger Middle Triassic (ie. Ladinian). The figure indicates weakly defined moderately large anterior and posterior wings in each valve, with no anterior dorsal tube. Thus in ornament, it suggests *Bositra*, and in hinge and wing development, it suggests *Daonella* and especially *Aparimella* Campbell, from which it differs in the lack of radial ribs. It is not transitional between the two, because it is of Ladinian age. None of these Chinese occurrences seems to have been even mentioned by Campbell (1994) or Waller (2005).

The shell microstructure in *Halobia* and allies is pectinoid or pterioid, with outer simple prismatic layer, but shows an inner nacreous layer, more like that of pterioids, because as Carter (1990) noted, most pectinoids had developed aragonitic or calcitic cross-lamellae. Freneix (1972a, b) reported an outer prismatic layer and inner lamellar aragonitic layer in the shell of *Daonella indica* from Turkey, to support a pterioidean relationship, but Campbell (1994, p. 54) failed to find any trace of aragonite from powder camera x-ray analysis. He concluded that the shell was made up of three layers, an inner foliated layer, middle aragonite layer, and outer simple prismatic layer in material from Spitsbergen, New Zealand and New Caledonia. There are differences in shell make-up, and these may reflect paleoenvironment and paleolatitude, rather than generic and family-level difference.

McRoberts (2000, p. 599) rejected the claim by Johnston & Collom (1998) that Halobiidae could fall within their subclass Cryptodonta, pointing to lack of taxodont dentition, and nature of the ligament. McRoberts (2000) insisted that the ligament of Halobiidae was alivincular or duplivincular, but in *Halobia* and *Daonella*, it was clearly illustrated by Campbell (1994, pl. 3, fig. 1-4) to be usually canalivincular and rarely replivincular, though not so interpreted (Campbell 1994, Fig. 4.5), like that of some claraiid species (Waterhouse 2001).

Time ranges and sequence (Table 1)

Although the derivation and developmental sequence for Halobiidae proposed by Waller (2005) does involve several major and no more than provisional evolutionary jumps, it does accord with

Table 3. Succession of Early and lower Middle Triassic pteriomorphs in New Zealand and New Caledonia.

Stage	Ammonoid		Pteriomorph
	Murihiku terrane	Brook Street Maitai terrane	
Illyrian (Etalian = type Nelsonian local New Zealand stage)	*Beaumontites* sp., *Pleurofrechites, Sturia, Beaumontaria grebneffi, Gangadharites cultrata, Leiophyllites, ?Durvilleoceras, Indirigophyllites* *Sturia*	*Durvilleoceras woodmani, Phukungia, Longobardites*?* Ceratitoid*	*Daonella jadii* *Etalia johnstoni*
Pelsonian			
Bithynian (Malakovian local stage)	*Acerlecanites, Tardoria*, *Ussurites* cf. *arthaberi*		
Aegean			
Manasluan		*Stenopopanoceras* cf. *mirabile*	
Mesokantoan		*Pseudoflemingites, ?Eophyllites*	
Gangapurnan		Mixed faunas *Paranorites, Flemingites, Koninckites, Durvilleoceras*	
Annapurnan = false Nelsonian local stage			
Gangetian			

This table is based on reassessments of New Zealand ammonoids described in Marwick (1953) and New Zealand ammonoids recorded by Kummel (1959, 1965). New Caledonian* ammonoids studied by Campbell & Bando (1985) were reassessed in Waterhouse (2002a, pp. 135, 142, 143, 145, 2002c). Campbell (1994, 2004) has argued for different correlations, relying on a supposed late Scythian fauna misidentified by Kummel (1965), and ignoring its redetermination as Bithynian by Waterhouse (1999), based on critical Himalayan genera and identification of *Ussurites* cf *arthaberi* (see Waterhouse 2002b, p. 172). A further error was to confuse *Gangadharites cultrata* (Browne), a late Anisian genus and species (see Waterhouse 2002b, p. 16), with the mid-Anisian key *Anagymnotoceras varium* McLearn (see Waterhouse 1996, 1997). To further compound the medley of miscorrelation, a local Nelsonian Stage was proposed for a supposedly Scythian (Early Triassic) assemblage, with type section containing *Durvilleoceras woodmani* Waterhouse and ?*Phukungia*. The former ammonoid also possibly occurs in late Anisian assemblages in New Zealand and in New Caledonia (Waterhouse 2002a, p. 155), and stratigraphically occurs above the early Anisian ammonoid *Stenopopanoceras* cf. *mirabile* Popov, so it must be post-Scythian and no older than lower Anisian. Campbell assessed the age as Scythian because *Durvilleoceras* also occurs near Nelson ammonoid cemetery deposits with representatives of a mix of ammonoid zones: these remain undescribed, but have been assessed by the writer. In short, the New Zealand ammonoid evidence completely supports the assessment for the age of incoming *Daonella* argued by McRoberts (2000) and Waller (2005), and strongly contradicts the arguments for a much earlier entry in New Zealand, urged by Campbell (1994, 2004).

what is known about the sequence of generic appearances, provided one or two of his time-ranges are adjusted. *Posidonia* is mostly Early and Middle Carboniferous. It is not so far known reliably from Permian deposits (see p. 34).*Peribositria* Kurushin & Trushchelev (1989, p. 59) was described from lower "Smithian" or "Gangapurnan" fauna of Early Triassic age (Waterhouse 2002c), and type *Bositra* Gregorio, 1886, regarded as senior synonym by Waller (2005), comes from Jurassic beds. A specimen figured as *Posidonia mimer* (Oeberg) by Tozer (1961, pl. 28, fig. 6) from the *Meekoceras* beds of the Blind Fiord Formation (mid Scythian, Smithian Stage) in Arctic Canada is typical of *Bositra*, and has only faint suggestions of radial ornament and prominent commarginal rugae.

The genus *Enteropleura* Kittl which is believed to have descended from *Bositra* (sensu Waller 2005) is limited to the Middle Triassic *Shoshonensis* Zone in Europe, Nevada and China. *Balatonites shoshonensis* is of Pelsonian age, relatively high in the Anisian sequence (Silberling & Tozer 1968, Bucher 1992, Table 3), and above the Manasluan, Aegean and Bithynian substages and below the Illyrian substage (Waterhouse 2002b, p. 190; 2002c, p. 76) of the Anisian Stage. The zone was stated to be early middle Anisian by Waller (2005, p. 23), but this is not correct: it is late middle Anisian. Campbell (1994, 2004) has consistently applied a Bithynian (early middle Anisian) correlation to the first appearance of *Daonella* in New Zealand, older than the *Shoshonensis* Zone with *Enteropleura*. Such an age would destroy the evolutionary sequence proposed by Waller (2005), because it indicates that *Daonella* preceeded, not followed *Enteropleura*. But analysis of ammonoids accompanying first appearances of *Daonella* in New Zealand has shown that the New Zealand age is no older than Illyrian, uppermost Anisian (Waterhouse 2002c, p. 76; 2003), significantly younger than the age advocated by Campbell (2004). Identified ammonoid genera and species include *Gangadharites cultrata* (Browne), *Pleurofrechites, Beyrichites*, *Simplicites marshalli* (Browne), *Beaumontites* species, *Beaumontaria grebneffi* Waterhouse and *Indirigophyllites*, indicative of an Illyrian and even early Ladinian age (Table 3). Faunas and beds of the Bithynian Substage are also represented in New Zealand, with such ammonoids as *Stenopopanoceras* and *Ussurites* cf. *arthaberi* (Welter), and no *Daonella* are present with those particular ammonoids. That reinforces the validity of the sequence of genera postulated by Waller (2005).

Significance of *Aparimella*

A final caution is necessary. Triassic bivalves are rare or not so far studied, especially recently, in many faunas, and there was a substantial diversity plunge throughout especially Early and Middle Triassic faunas. The major evolutionary jumps between genera suggested by Waller (2005) have to be accompanied by caution. Even the apparent chain of ascent from *Daonella* through *Aparimella* to *Halobia* that was posited by Campbell (1994) has come into question from McRoberts (2000). Campbell (1994) had shown that *Aparimella* was found in rocks of intermediate age between those with *Daonella* and those with *Halobia*, and that *Aparimella* occupied an intermediate position between the two genera, having anterior and posterior wings (unlike *Daonella*), but lacking a tube (unlike *Halobia*). That is instructive, but age control for the species succession is not tight, and the New Zealand Triassic succession possibly has faunal gaps: there is considerable need for much closer review of the New Zealand faunas, which have not even been assembled into faunal zones. The disarray in New Zealand Triassic biostratigraphy is well but defiantly conveyed in the overview of New Zealand biostratigraphy in Cooper (2004), with confusion and miscorrelations over Triassic ammonoid and bivalve ages, an exceptional focus on local "stages," and little attention to biozones (Table 3).

In Canada, McRoberts (2000) pointed to a species of *Halobia* with poorly developed anterior auricle and external ornament like that of a slightly older species of *Daonella*. He argued that the species arose directly from *Daonella* and that the genus was polyphyletic. Again, time and fossil control are not completely under control. What if the *Daonella* species had evolved first into undiscovered *Aparimella*, retaining its distinctive ornament, and then evolved into *Halobia*? The point seems to be that uncertainty has already crept in to the trajectory postulated for the evolution of *Halobia*.

Additional genera (Text-fig. 30)

Additional genera fall very close to *Daonella* and *Halobia,* and indeed appear to preceed *Daonella*, to complicate the link-potential between Halobiidae and conceivable ancestral stock. As described below, *Wallerobia* n. gen. (p. 176) of Balatonitan – Pelsonian age is older than *Daonella* and/or *Aparimella*, and has radial ornament and slender posterior wing. But the presence of a resilifer is believed to place the genus outside the evolutionary history of Halobiidae. Another species, represented only by a left valve and so too incomplete to be named, falls apparently in Halobiidae – much more convincingly than *Peribostria* or *Bositra* – and has radial ribs and anterior and posterior wings. The right valve must have had a posterior wing and an anterior auricle or wing. This bivalve is found with the Bithynian ammonoid *Kyobratites vyassa* (Diener), and was figured by Waterhouse (2002b, pl. 3, fig. 8), from the Mukut Group of north-central Nepal (Table 4).

Text-fig. 30. Halobiidae aff. *Aparimella*?, left valve FMo 4582 from Mukut Group, middle Anisian (Middle Triassic) of north-central Nepal, x2. Photograph courtesy of N. Hiller, Canterbury Museum.

The specimen (Text-fig. 30) has radial ornament commencing below the umbo, little concentric ornament and long hinge. Where does this fit? It cannot be *Enteropleura*, and certainly is not *Bositra* or *Peribositria*. Could it have been more truly ancestral to *Halobia*? The most likely identification is with *Aparimella* Campbell, although the wings are more distinguished than in the species described by Campbell (1994). The Bithynian age of the species, if belonging to *Aparimella*, would theoretically cut out *Enteropleura* ss. and possibly even *Daonella* from any simple chain of development. It raises the possibility that *Aparimella* or ally developed early (from *Imposidonia* n. gen., as described shortly), and diversified less simply than along a single trajectory.

Two possible sources are known for *Halobia* and allies. *Imposidonia* n. gen. is based on a species with dense commarginal ribbing, as well as large posterior wings but with no anterior right auricle or left anterior wing, a long hinge, and possibly canalivincular ligament. The age is mid-Annapurnan (basal Dienerian), middle Scythian, older than other halobiids. Aspects of shape and ornament suggest possible derivation from the claraiid genus *Rugiclaraia*, most typical of the *Ophiceras* Zone in the early Scythian (Table 4), to suggest that Halobiidae could have evolved from Claraiidae in Early Scythian time. An alternative source is conjecturally possible, perhaps from *Posidonia*, through a genus *Praeamonotis* Waterhouse, 1987. This is based on a species *P. anticipata* Waterhouse (1987, p. 157, pl. 9, fig. 11-13) from the Wordian (Middle Permian) Flat Top Formation of the Bowen Basin in Queensland. Figures show incomplete right and left valves with low radial ornament and weakly defined posterior wings. A very narrow linear (canalivincular) ligament was reported. The text records feebly differentiated anterior wings in each valve, but these are not visible in the figures, leaving me as author somewhat dismayed at their inadequacy. If the wings were present, they do indeed suggest a Permian posidoniid (as classed in the 1987 study), and that will be need to be confirmed by searching out the additional material reported by Waterhouse (1987, table 18). From the information now available, it is deemed that *Imposidonia* provides a more likely source, partly through time-range proximity, but also from the nature of ribbing. *Halobia* and allies, as explained below, have weakly clumped splitting ribs, like that seen more feebly in genera and species of Claraiidae. *Praeamonotis* has simple ribs, that rarely split, but are not paired let alone clumped.

These reassessments and new finds fill out and indeed complicate the evolutionary development of Halobiidae, but do not resolve all possibilities. The genera classed as Halobiidae on available but inadequate information insofar as hinge detail and muscle scars are still poorly known for some genera and many species, include ?*Imposidonia*, *Aparimella, Daonella, Halobia, Parahalobia* and *Ralphimlaya* n. gen. *Pterohalobia* and *Longidaonella* remain uncertain but likely. From general features, these genera are subaviculopectiniform and emphatically not monotoid. They do not come close to Aviculopectinoidea, Streblochondrioidea, Pseudomonotoidea, Oxytomoidea or Euchondriidae, but remotely, could be a substantially altered off-shoot from the first two superfamilies, given the biconvexity and ornament. The possibility of a pterinopectiniform alliance seems to be more acceptable, given the close approximation in shape to pterinopectens, and the approximation of the ligament to that of many species of Claraiidae in the Early Triassic. From *Posidonia* the halobiids differ in musculature, hinge and auriculation, but there is an approach in ornament and ligament through *Praeamonotis*.

Several Mesozoic genera, including *Amonotis* Kittl (Triassic), *Didymotis* Gerhardt (Cretaceous), *Diotis* Simonelli (Jurassic), *Pseudodidymotis* Gillet (Cretaceous) and *Veldidenella* Alma (Triassic) were included in Posidoniidae in Cox & Newell (1969). They are mostly ribbed, and some appear to have amphidetic ligament, and may lack right anterior auricle and byssal notch. There is little reason to suppose that they were posidoniid, but some may prove to belong to Halobiidae, and some may have arisen from *Bositra*. *Posidonotis* Loracco was shown by Hayami (1988) to have the anterior right wing defined ventrally by a suture, and Waller (2005, p. 16) suggested it was pectinoidean. Ichikawa (1958, p. 188) referred this genus together with *Diotis*, *Didymotis* and *Pseudodidymotis* to a Subfamily Aulacomyellinae, characterised by radial ribs in part. *Aulacomyella* has a short hinge and reduced anterior compared with the other genera, and no right anterior wing or auricle. Some of the assigned genera could prove to be halobiid, but *Aulacomyella* itself has an opisthodetic ligament, as discussed on p. 171.

Imposidonia is ornamented only by commarginal ornament. The main members of Halobiidae, *Daonella, Aparimella* and *Halobia* are dominated by radial ornament, so that *Daonella*, the earliest of these forms, and the Nepal *Aparimella*? differ considerably in appearance. One of the features of the ornament lies in the “clumping” of costae in pairs, threes or more, largely if not entirely through splitting, to form low broad radial ribs, separated by very narrow interspaces. It

Table 4. Early and early Middle Triassic succession of ammonoid zones with pteriomorphs in Nepal, based on Waterhouse (2000, 2002c).

Stage	Ammonoid zone	Pteriomorphs
Bithynian	*Paradanubites kansa*	*Aparimella*? sp.
Aegean	*Paracrochordiceras anodosum*	
Manasluan	*Epiczekanowskites plexus*	Bositrid sp.
	Grambergia latiumbilicatus	
Mesokantoan	*Keyserlingites costatus*	*Chuluaria bragaensis, Crittendenia langpoensis, Cr. nammalensis*
	Eophyllites giganteus	*Chuluaria* sp. , *Crittendenia punjabiensis, Cr. nammalensis*
	Kariceltites manangensis	
	Ampletimoria welteri	
Gangapurnan	*Flemingites griesbachi*	*Imposidonia* sp.
	Nordophiceras erbeni	*Rugiclaraia* sp.
Annapurnan	*Pleurogyronites jomsomensis*	*Claraia kashmiriensis*
	Kingites elegans	
	Proptychites abundans	*Imposidonia elegantula*
	Gyronites frequens	*Claraia nakazawai, Pteroclaraia* sp., *Rugiclaraia*? sp. A, *Crittendenia painkhandana*
Gangetian	*Ophiceras tibeticum*	*Claraia griesbachi*
	Otoceras woodwardi	*Claraia dieneri, Pseudoclaraia*? sp.

is noteworthy that species of *Claraia* and *Chuluaria* also show, to lesser degree, bifurcated ribs associated in pairs.

Genus ***Imposidonia*** new genus

Derivation: im – different, opposite, Lat.; posidonia - bivalve genus.

Type species: *Posidonia elegantula* Waterhouse, 2000, p. 181 from Early Triassic (Annapurnan) Sabche Member of Nepal, here designated.

Diagnosis: Medium-sized equivalve or subequivalve shells with moderately long hinge, large weakly defined posterior wing in each valve, no anterior wing or auricle, no byssal notch or gape, ornament of commarginal ridges and narrow plicae. Ligament incompletely known, apparently canalivincular.

Discussion: In general appearance, from size and ornament and nature of umbones and valves, this genus looks close to the Carboniferous genus *Posidonia* Bronn, but it differs in that the hinge is longer, the posterior wings larger, and the anterior wings of *Posidonia* are lacking. In aspects of size, ornament and posterior wing, the genus looks very like *Rugiclaraia aurita* (Hauer), and *R. concentrica* (Yabe) from Europe and Asia, claraiid species that are especially abundant in the *Ophiceras* zones of upper Gangetian (Early Triassic) age, and persist into moderately young Early Triassic. The new genus differs in lacking a right valve auricle, and in having the right valve as inflated as the left valve. Given that the ligament of the new genus was apparently canalivincular, and given similarities of shape and ornament, it seems possible that the present genus evolved from *Rugiclaraia* stock, by change in mode of attachment, with loss of byssal notch and right auricle, and increased inflation of the right valve, the biconvexity restored by adopting a habit no longer dependent on a right valve byssus. Theoretically that amounts to a change from Claraiidae to Halobiidae. The timing of the change is at the end of the Gangetian Stage, with the new genus appearing in the second or *Proptychites abundans* Zone above the *Ophiceras tibeticum* Zone.

Imposidonia elegantula (Waterhouse, 2000)

Text-fig. 31, 32

2000 *Posidonia elegantula* Waterhouse, p. 181, Fig. 11A-G.

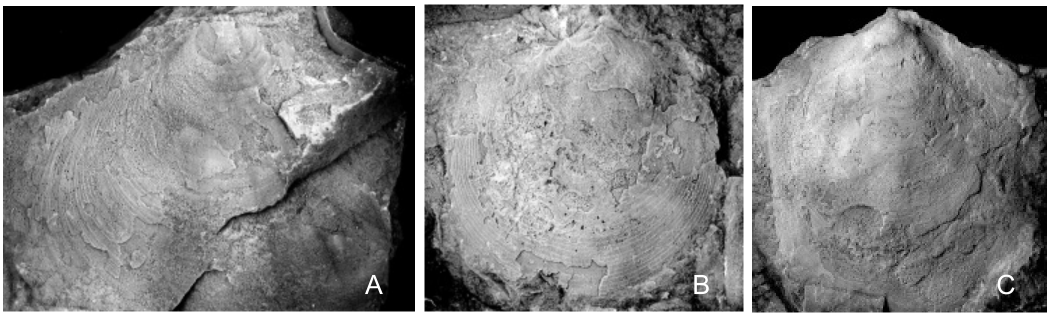
2004 *P. elegantula* – Waterhouse, pl. 12, fig. 6-12.

2005 *Claraia* Waller, p. 19.

Holotype: FMo 3429 from Sabche Member, Khangsar Formation, Manang district, Nepal, figured by Waterhouse (2000, Fig. 11A) and Waterhouse (2004, pl. 13, fig. 6), OD.

Description: The species was described by Waterhouse (2000), with figures re-issued in 2004. Ornament on both valves consists of slender commarginal ridges with narrow rounded crests, separated by broader concave interspaces. Over the body of the shell, the ridges may be very faintly arranged in low swells, and posteriorly, these become higher and narrower, but not on all specimens. Occasionally the ridges form very low rugations. There is a faintly impressed moderately large adductor scar placed behind the umbo and well in front of the posterior margin in one specimen, but the pallial line cannot be seen. The posterior hinge reveals a long linear ligament groove, but the ligament is not known anteriorly or under the umbo. Both valves have a thin outer layer of vertical prisms, especially on the right valve, and inner shell is thin and homogeneous, grading into a thin inner layer, with structure unknown.

Discussion: Waller (2005) claimed that *Posidonia* described by Waterhouse (2000) from the Himalayas was claraiid. This suggestion must be set aside, because Claraiidae have a well developed anterior right valve auricle and byssal notch, and neither are developed in the Himalayan shells assigned to *elegantula*. The only evidence that Waller (2005) provided was



Text-fig. 31. *Imposidonia elegantula* (Waterhouse). A, right valve FMo 3542 x 1.2. B, right valve FMo 3428 x1, holotype. C, left valve FMo 3529 x 0.8. Specimens from Early Triassic (Annapurnan – Dienerian) Jargeng Member, north-central Nepal, x1. Photographs courtesy of N. Hiller, Canterbury Museum. See Waterhouse (2000).

that commarginal flanges rather than corrugations indicate claraiid species. This is based on a misconception of claraiid ornament. Various species and genera of Claraiidae are rugose, including the very early Triassic species *Claraia griesbachi* (Bittner), as illustrated in Text-fig. 26. Of the species described from Nepal by Waterhouse (2000), *Posidonia* sp. A has commarginal rugae, but also has a large alate posterior wing and so could indeed be claraiid. The right valve is not known, hindering a secure identification. *Posidonia* sp. B and *P. elegantula* Waterhouse have fine and low commarginal ridges, and the right valves of *elegantula* emphatically lack a right anterior auricle and byssal notch, and so cannot be claraiid. There is a large posterior wing in each valve, poorly distinguished from the body of the shell, with the ventral posterior edge indicated by a small sinus. Some material suggests that the ligament is canalivincular – different from that normal for *Posidonia* or *Bositra-Peribositria*. Certainly the ornament, posterior wing and long hinge differ from features normal for *Bositra*. But the ornament does come close to that known for species of *Posidonia*. The type species of *Posidonia* has very narrow commarginal ridges, and amongst the Belgium species described by Koninck (1885, pp. 182-183), *P. constricta* and *P. obliqua* have narrow flange-like ridges, close to those of *elegantula*, although not as fine. The obvious and consistent difference that distinguishes the Nepal species is the comparatively long hinge and large poorly differentiated posterior wing in each valve and lack of anterior wing or auricle.

Text-fig. 32. *Imposidonia elegantula* (Waterhouse), right valve x1 showing ornament, from Sabche Member, north-central Nepal. Unregistered specimen kept at Queensland Museum, Brisbane.

Genus ***Ralphimlaya*** new genus

Derivation: Named for Ralph. W. Imlay.

Type species: *Aulacomyella neogeae* Imlay, 1940, p. 406 from Late Jurassic beds of La Casita and La Caja Formations of Mexico, here designated.

Diagnosis: Slender almost equilateral equivalve shells with long hinge and tiny umbones, ornament of fine weakly clumped costae crossed by low growth rugae, the ribs delimiting distinct anterior wing-like segment and broad posterior segment.

Discussion: The type species differs considerably from *Aulacomyella* Furlani, 1910, having a longer hinge, larger anterior shell, and much finer costae that are differently arranged. *Aulacomyella* is further discussed on p.171. The overall shape and ornament of Imlay's species strongly suggest halobiid affinities. The umbones are small, scarcely project dorsal to the hinge, medianly placed, and a growth-stop, or two stops, are developed close to the umbo within less than 5mm from the umbonal tip. The radial costae are slender and cover both valves. Ventrally they may be clumped at 4-6 on a low broad-crested rib, separated by slender slightly deeper interspaces, a feature also seen in species of *Daonella, Aparimella* and *Halobia*. Rarely, associated with the growth-stop, they may curve concave forward, or describe a double curve. The costae are crossed by slender close-set growth wrinkles over the median part of the shell, which become very fine commarginal laminae anteriorly and posteriorly. At what is judged to be the anterior dorsal margin, the radial ribbing, without commarginal rugae, outlines an anterior wing-like part of the valve, almost flat or even gently concave. The posterior part of the shell is also discriminated by the lack of commarginal rugae, and is larger and more vaguely defined, and is gently convex, grading evenly from the median shell, without any discrimination of a wing. The orientation of the valves, it should be noted, is based on analogy with halobiids: Imlay (1940) did not discriminate between right and left valves. In other respects the species was well described and measured (Imlay (1940, pl. 52, fig. 1-6, pl. 53, fig. 26), with holotype 21154 kept at the Museum of Paleontology, University of Michigan.

The recognition of a genus very close to the leading constituents of Halobiidae in Upper Jurassic deposits marks a so-called Lazarus-like reappearance of the family, at first sight. But several other genera may prove to be related, although none are so close to *Halobia* and allies. These are discussed on p. 64. The overall appearance of *Ralphimlaya* strongly suggests a genus derived from *Halobia* itself by loss of the anterior tube, but further study is required to consolidate the nature of the hinge and the structure of the shell. The age is given as early Tithonian by Cantú Chapa (1984), because of the association with *Virgatosphinctes mexicanus*.

Order Limida Waller, 1978

Although limids make up a comparatively small segment of the bivalve component of fossil and living shell-fish, Waller (1978) in an analysis of shared character states centred on soft tissue and living species depicted limids as a clearly separated group, pointing in his opinion to full ordinal standing. They were characterized as "monomyarian non-pleurothetic Pteriomorphia, having an outer calcitic fibrous-homogeneous ultrastructure and inner simple cross-lamellar aragonite" (Waller 1978, p. 351). Such a diagnosis does not discriminate the order clearly. There are other orders that include members of monomyarian and non-pleurothetic shells, and the shell structure is so particular that it does not apply to Mesozoic Limidae. More detail was provided by Waller (1998, pp. 24, 25), but again, the information was particularist, and leaves the reader with the impression that the order consists of a single family with various undoubtedly unusual attributes, extending at least from Recent to Upper Paleozoic. Scanning electron microsopy revealed a narrow medial wall of lamellar material within the fibrous resilium of *Lima lima*, but this wall was missing from other species and genera. Even older texts emphasized the distinctiveness of the family, Zittel (1937, p. 459) for instance referring to "shell substance fibrous, with minute tubules, not nacreous or prismatic". Waller (1998, p. 24) concluded that limids had never evolved the regular prismatic calcitic outer shell layers found in Ambonychioidea and Eupteriomorphia, but did treat the difference as plesiomorphic. The timing of the first Limida is still open to uncertainty. Carter (1990, p. 214) regarded the Ordovician Myodakryotidae Tunnicliff, 1987 as limid, whereas Waller (1998, p. 25) considered it to be a cyrtodontid stem group. That appears to be confirmed from the morphology as far as it is preserved, but the development of the posterior and anterior wings in the left valve of *Myodakryotus* does suggest potential for pectiniform development, though offering no persuasive evidence that it was necessarily or even potentially limid. Pojeta & Runnegar (1985, p. 327) regarded *Prolobella* Ulrich, 1894 as limid "for now", and suggested derivation from cyrtodonts in Caradocian time. *Prolobella* has an anterior wing and clavicle in front of the umbo and no teeth, suggestive of a pteriid. The evidence for beginnings so far is no more than flimsy, and clarification will require either improved techniques, or discovery of outstanding fossil material. That always remains a possibility, as witnessed by the description of outstandingly well preserved and diverse bivalve assemblages from east Australia and New Zealand by Johnston (1993) and Bradshaw (1999).

But to return to the uniqueness of Limida. The emphasis on this was expressed by Amler (1999, p. 240), in placing Limida with one family Limidae. It should not be overlooked that in some aspects of gross morphology, aviculopectens and chaenocardias come close to Limida, especially in the alivincular ligament, and development of biconvexity, wings and ornament. These are major features, and there must be some caution in considering that the similarities are outweighed by shell structure, not only in its own right, but because the shell structure in older limids is not the same as in living material, Carter (1990) showing that Carboniferous Limidae have outer irregular prismatic structure of calcite, with middle and inner layers of diffuse CL structure. Here it is suggested that the alivincular amphidetic hinge arose from the chevron duplivincular hinge during Silurian-Devonian time. Overall similarity in basic morphology indicate that limids split early from the early aviculopectens, probably after the time of separation of pectens, and were distinguished by the commissure-vertical life style from aviculopectens: there was divergence, not convergence. Whilst the nature of the foot, which can be rotated through 180° in modern limids, cannot be determined for past limids and other shell-fish, the posterior pedal retractor scars in Limida lie on the ventral or posterior side of the adductor scar, whereas they were claimed to be antero-dorsally placed in other bivalves (Morton, 1979), an observation not supported by numerous other pteriomorphs with postero-dorsal pedal retractors. The ordinal rank was accepted by Newell (1999) with stress on the differences in musculature demonstrated by Gilmour (1990), though it would seem that such differences developed over time, with gradual divergence of Limoidea. The ordinal ranking has been accepted by major students of pteriomorphs, with exclusion of other pteriomorphs that were recognised separately as Pectinida by Carter (1990), Newell & Boyd (1995) and Amler (1999). But the gross hard-part morphology and many aspects of soft parts is so like that of other pteriomorphs, especially when comparing Late Paleozoic contemporary members, that here Limoidea are regarded as one of several allied superfamilies, to render the order more significant in terms of diversity. The alternative procedure would be to allocate the sister groups to a separate Order Aviculopectinida. That can be readily done in the present scheme, but is not followed because, although uncertainties remain, it is preferred to issue a challenge to the current hegemony that hopefully will encourage a firm analysis, if not further enquiry.

Taxonomy: Amler (1999) assigned the authorship of Limida to Rafinesque (1815) in brackets, but here it is preferred to associate the order with Waller (1978) who clearly enunciated the concept in terms of modern understanding of what constitutes an order.

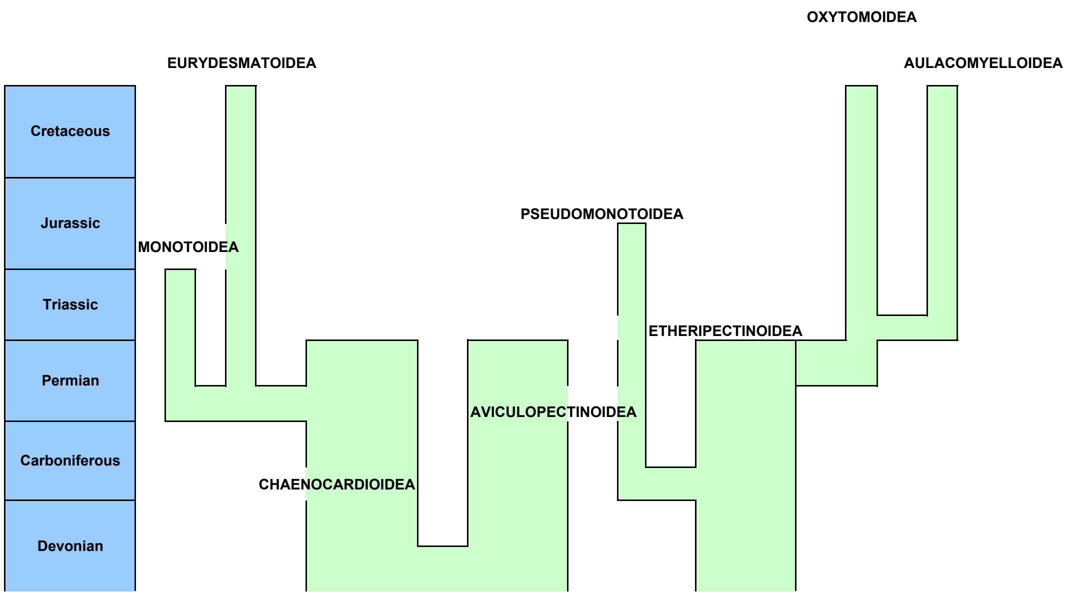
Suborder Aviculopectinidina Starobogatov, 1992

Text-fig. 33

[nom. transl. hic ex infra-suborder Aviculopectinoidinei Starobogatov, 1992, p. 23].

Diagnosis: Right valve anterior auricle and byssal notch generally well developed, large left valve wings, ornament generally of plicae or costae, ligament amphidetic, external, alivincular or platyvincular, rarely lativincular, hinge teeth small and generally absent.

Discussion: Aviculopectinidina arose from Pterinopectinida, retaining a monomyarian muscle field and developing an alivincular ligament, with lengthening of the hinge and enlargement of the anterior and posterior wings. Classification within the suborder was summarized in Waterhouse (2001) and Waterhouse & Chen (2006, table 8) and the nature of the different hinges illustrated in Waterhouse & Chen (2006, text-fig. 11). Building on and modifying those analyses, it is clear that aviculopectens form part of a major clade which excludes pectens. Members of Order Pectinida have a byssal notch, but the external ligament is largely obsolete, with the outer hinge connected by periostracum, and the resilium is internal and amphidetic, and the hinge may have simple teeth. The right valve may be more inflated than the left (Fleming 1957a).



Text-fig. 33. Superfamilies with Aviculopectinidina and Etheripectinidina.

Nomenclature

Starobogatov (1992) proposed the infra-suborder Aviculopectinoidinei to include Superfamilies Posidonioidea, Aviculopectinoidea, Euchondrioidea and Buchioidea, placing the group within Suborder Pterioidina (“Pterioidei”) as part of Order “Mytiliformii” (= Mytilida). Even though no recognition was granted to Pseudomonotoidea, Pterinopectinoidea or Chaenocardioidea, probably because these were incorporated in “Aviculopectinoidea”, his group embraced a broader range than the suborder as recognized herein. According to Starobogatov, the aviculopectens developed the anterior shell, and strengthened the fibrous layer of the ligament. It was considered that Order

Pectinida (“Pectiniformes”) evolved in a general way parallel to Mytilida, but arose in association with a different Suborder Unionidina and displayed a structure of stomach “sharply different” from that of Mytilidina. Of course the stomach is not preserved in Aviculopectinidina, and the pectinoid stomach type is one of a complex of different variations. Further discussion in Starobogatov (1992) centred on differences within Pectinida, between Pectinidina and Anomiidina, the latter treated as a superfamily Anomioidea Rafinesque by Amler (1999) within Ostreida. The Starobogatov (1992) classification downscaled many of the major groups recognised at ordinal-subordinal level by paleontologists – for instance *Arca* was placed in a superfamily within an infraorder Ostreoinei, whereas Waller (1980) recognised Order Arcida. *Lima* was placed as a superfamily in Order Pectinida, whereas Waller (1978) recognised Order Limida.

By contrast, Newell & Boyd (1995) treated aviculopectens as closely related to living pectens. Independently of Starobogatov (1992), Waterhouse (2001, p. 117) assigned them to a separate suborder Aviculopectinidina, to include Superfamilies Aviculopectinoidea, Pterinopectinoidea Newell, 1938, Chaenocardioidea Miller, 1889, Pseudomonotoidea Newell, 1938, Euchondrioidea Newell, 1938 and Posidoniidae of uncertain content and affinities. There was discussion, comparison, tabulation and illustration of the suborder. Buchioidea were specifically excluded, being treated as a component (changed to Eurydesmoidea) of Monotidina. In Waterhouse (2001), Aviculopectinidina is closer to what is used herein.

There are no pronouncements on the scope and authorship and few on endings for supra-family group categories in the current International Code for Zoological Nomenclature (2000). Judged from recent discussions in the literature, there are several ways in which the rank and content of suprafamilial categories are changed:

1. If the content and basic definition are subsequently elaborated, but not changed, the rank may be changed (up or down), and the authorship should be retained. This is fair and instructive, because understanding of category values will change over time, and nomenclature must be keep pace throughout the zoological kingdom.
2. If the rank is expanded in basic content to incorporate groups originally omitted, then the definition is altered, and the enlarged content may need to be coupled with the new author of the new content.
3. More commonly, definitions become confined, through splitting off of groups previously incorporated. The new group obviously has the name of its new author, and the authorship of the newly modified rump, especially if raised in rank, becomes open to question, but normally should be the original author.
4. If the definitions and scope are greatly changed, with gain and loss, the changes will be clarified by new authorship, to avoid confusion.

There is flexibility in promoting authorship. Promotion works well and fairly at family-group level, but the promotion of authorship from subfamily rank into ordinal group seems unwarranted. Some prefer to attribute a name to the first author to propose the ordinal unit, and others allocate each ordinal rank to the author who first proposed that ranking. The practise of automatically upscaling rank and retaining authorship is a matter for caution. On the one hand, it would seem fair to recognise the value of the contribution of the author who was first to recognise the rank of a group. On the other hand, the ongoing revision and improvement of understanding often leads to rank change, and the interest of taxonomists and systematists is hopefully focused on the biology, not the author. For that reason, recent studies have perhaps been overgenerous in granting authorship to scientists who had little or no concept of the modern divisions for which they are credited, but it does save argument. The questions over authorship will have to be finally resolved by the International Commission for Zoological Nomenclature, and arguably the task of adjustment will be all the easier by retaining until then the name of the first genuine proposer of whatever rank is involved.

Superfamily **AVICULOPECTINOIDEA** Meek & Hayden, 1864

Diagnosis: Shells biconvex, right valve may be less inflated, posterior wings small or large and well defined, anterior umbonal slope steep, large right anterior auricle, deep byssal notch, may have well developed left anterior wing sinus, ornament subequal on each valve, of plicae with or without costae; ligament external and typically alivincular, hinge teeth generally absent, minor if present.

Classification: The superfamily is subdivided into these constituents:

- Family Aviculopectinidae Meek & Hayden, 1864
    - Subfamily Aviculopectininae Meek & Hayden, 1864
    - Subfamily Undopectininae Waterhouse, 2001
    - Subfamily Spyridopectininae new
    - Subfamily Echiniferipectininae new
- Family Deltopectinidae Dickins, 1957
    - Subfamily Deltopectininae Dickins, 1957
    - Subfamily Squamuliferipectininae new
    - Subfamily Cyrtorostrinae Newell & Boyd, 1995

Family **AVICULOPECTINIDAE** Meek & Hayden, 1864

Diagnosis: Posterior wings large. Ornament normally of fine to coarse plicae, costate or smooth, growth-lines tend to point ventrally in interspaces, but vary. Hinge alivincular.

Discussion: The Aviculopectinidae were derived from Pterinopectinidina and retain the large posterior wings and subequally inflated valves, with ornament much the same on each valve. Shortening of the very long pterinopectiniform hinge with emphasized distinction of posterior wings with posterior sinus is seen in Natalissimidae, and members of Pseudoaviculopectininae have fine costae, as seen in members of Undopectininae Waterhouse. It appears possible that Undopectininae developed from Pseudaviculopectininae by becoming plicate and changing the ligament, and Aviculopectininae arose from Undopectininae by losing the costae and retaining the plicae. But this is not demonstrated by any known sequence of fossil appearances.

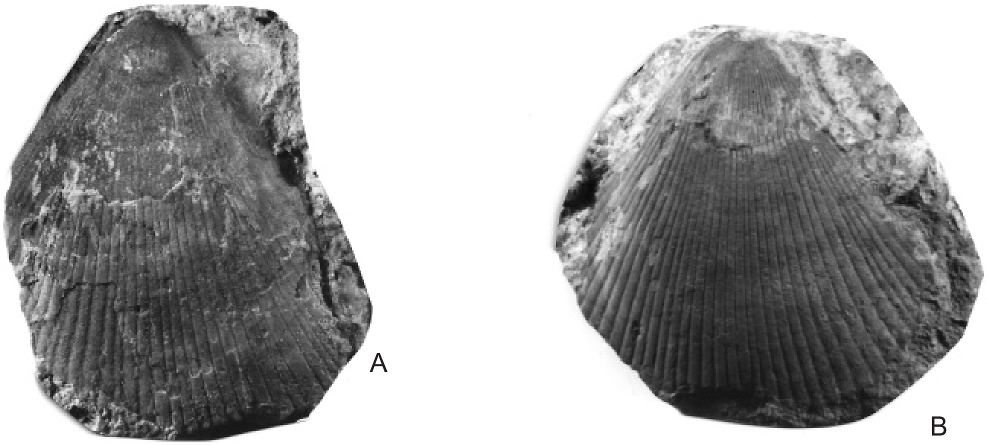
Subfamily **AVICULOPECTININAE** Meek & Hayden, 1864

Text-fig. 34

Diagnosis: Shells subequally biconvex, ornament of narrow plicae with varied development of growth lamellae.

Discussion: Hind (1903), the major revisor of British Carboniferous bivalves, and Dickins (1981, p. 28) interpreted the right valve of *planoradiatus*, the type species of *Aviculopecten*, as being flat or almost flat, whereas Newell & Boyd (1995) stated that the right valve was convex. The latter did not examine type collections, relying instead on previously published studies. They suggested that *Pecten flexuosus* M'Coy (1844, p. 93, pl. 18, fig. 1) exemplified the true right valve of *planoradiatus* although M'Coy had described this valve as only "slightly convex". The specimen is kept at the National Museum of Ireland, registered as NMING F 7379, from New Road, Armagh, County Armagh, and was re-appraised by Hind (1903, p. 69, pl. 13, fig. 1) as belonging to *Aviculopecten semicostatus* (Portlock, 1843, p. 436, pl. 36, fig. 9), the type of which is a left valve with a high number of closely-spaced ribs that plicate the shell. Dickins (1981) in his extensive examination of material housed in English institutions concluded that all the right valves were of low inflation. Thus the weight of published evidence goes strongly against the Newell-Boyd proposal.

But the Newell-Boyd proposal should not be firmly ruled out without further enquiry, and therefore the collections at the Natural History Museum, London, were re-examined. From that examination, it is clear that *Aviculopecten* is typified by sub-biconvex shells, with ornament composed of sturdy subplicae on both valves. The left valve holotype by monotypy of *planoradiatus* M'Coy (1851, p. 171; 1855, p. 489, pl. 3E, fig. 8) has numerous ribs with almost flat broad crests and narrow interspaces. Hind (1903, p. 67, pl. 12, fig. 1, 3) considered that the species was a junior synonym of *Pecten tabulatus* M'Coy (1844, p. 100, pl. 16, fig. 12), but Newell & Boyd (1995) rejected the suggestion, and Fang & Morris (1999, p. 149) pointed out that its right anterior auricle differed from that of true *planoradiatus*, without specifying the difference. The right anterior auricle of *tabulatus* M'Coy (1844, pl. 16, fig. 12) is prominent and convex, with anterior rounded margin and ribbed, close to but seemingly less convex than the anterior auricles in the right valves of *planoradiatus.* As well, M'Coy's right valve has a byssal notch higher and deeper than *tabulatus* figured in Hind (1903, pl. 12, fig. 4) and apparently shorter and narrower proximally than in *planoradiatus.* A right valve of *tabulatus* figured by Hind (1903, pl. 12, fig. 3) is broken short, but the anterior auricle figured by Hind (1903, pl. 12, fig. 4) is very long and not convex, and has a high byssal notch. Of course, much more needs to be known about infrasubspecific variation and differing preservation. The valve has flat-crested ribs, some bunched. Other *tabulatus* were figured by M'Coy (1855, p. 489, pl. 3E, fig. 8) and Hind (1903, p. 67, pl. 12, fig. 1-4). Hind (1903, p. 68) commented "The surface adorned by many simple unequal, smooth broad flattened radiating ribs, separated by almost linear grooves. The two valves are very similar. The anterior ears are obscurely radiate – the posterior ears have many radiating ribs but exhibit 2-3 stronger ribs near the upper border, the whole being continuously striated". In *Aviculopecten*, Hind (1903, pp. 69, 70) included *Pecten semicostatus* Portlock (1843, pl. 36, fig. 9; synonymized by Hind with *P. plicatus* Sowerby of Phillips, 1836, p. 212, pl. 6, fig. 21), *P. flexuosus* M'Coy (1844, pl. 18, fig. 1) and *A. docens* M'Coy (1855, p. 485, pl. 3E, fig. 6, 7). Hind (1903, p. 69, pl. 13, fig. 9-15)



Text-fig. 34. *Aviculopecten planoradiatus* M'Coy, left valves A, CASM E 5993, B, CASM E 5990 from Early Carboniferous of Derbyshire, England, x 2. Photographs courtesy of Sedgwick Museum, Cambridge. See Fang & Morris (1999) and Waterhouse (1969).

also figured *semicostatus*, with the hinge shown in Hind (1903, pl. 13, fig. 11). Some of these specimens have narrower ribs with more rounded crests than in *planoradiatus*, and are further discussed on p.157. Hind (1903) did not clearly describe the ligament, recording the hinge plate as diamond-shaped and obscurely striate longitudinally, but specimens show a small resilifer (eg. right valve NHM L45141). Specimens from Treak Cliff, Castleton, Derbyshire, have *planoradiatus* ribs with colour bands paralleling the dorsal margins. Plicae are higher and narrower in some specimens, eg. NHM L43579 from the top of Narrowdale Hill, near Hartington, Derbyshire, and NHM L43581 shows wide interspaces. NHM L13403 has the two valves, displaced, and the right valve is less inflated than the left, and is gently convex. *Aviculopecten docens* M'Coy, 1855 looks close but has ribs spaced further apart.

In summary, the collections at the Museum of Natural History, London, suggest that *planoradiatus* and allied species are unevenly biconvex, with strong ornament much the same on both valves, and a resilifer. Species limits and variation require further study.

These observations were made independently of a study by Fang & Morris (1999), who also examined the Natural History Museum material, and provided excellent illustrations of the nature of *Aviculopecten planoradiatus.* They came to very much the same conclusions, although they were more critical of the Newell & Boyd study.

A genus that is closely related to or identical with *Aviculopecten* is *Hayasakapecten* Nakazawa & Newell, 1968, type species *H. shimizui* Nakazawa & Newell, 1968, p. 70. This was named for inequilateral subequivalve shells, left valve more inflated than right valve, posterior wings larger than right anterior auricle and left anterior wing, ornament of simple radial ribs, concentric ornament moderately well developed, extending ventrally in interspaces, and well developed resilifer. The genus was recognized in the younger Permian (*Leptodus* beds) of the Tenjinnoki Formation of Japan, and was synonymized with the Early Carboniferous genus *Aviculopecten* by Newell & Boyd (1995). This synonymy was rejected by Fang & Morris (1999) and Waterhouse (2001), because *Hayasakapecten* shows ventrally directed spines in the interspaces, and is subequivalve. Nonetheless, the two genera are close to each other, as far as can be discerned from the few figures and the general description of *Hayasakapecten*, and the genus is placed in the same subfamily. Another member of the group, *Newellipectinia* Waterhouse, 2001, type species *Aviculopecten americanus* Newell & Boyd, 1995, from the late Lower Permian and early Middle Permian Bone Spring, Cathedral Mountain and Road Canyon Formations of United States, has a smaller anterior wing and auricle, much less extremely acute cardinal extremity for the anterior left valve wing, less ribbed wings and well developed and well spaced subregular subspinose projections over the left valve plicae, but not in the interspaces. As in the other genera, a resilifer is present. All genera are close to each other and are of Carboniferous to Permian age.

The revision of understanding of *Aviculopecten* has left a gap in the knowledge of internal musculature and pallial line. Recent understanding has been based on the careful presentation of internal detail as preserved in *Aviculopecten exemplarius* Newell (1938, pl. 4, fig. 10-12, Fig. 2.1, 2) from lower Pennsylvanian of Kentucky. As noted by Carter (1990), the pallial line is open dorsally and is not pitted, and there are two anteriorly placed pedal levator muscles. But *exemplarius* is definitely not *Aviculopecten*, and is close to *Heteropecten* Kegel & Costa, 1951 (p.144) in Etheripectinidae. Similarly the shell structure of aviculopectens is not firmly tied to accurately identified genera: Carter (1990, pp. 240-241) noted ancestral outer calcitic regular prisms, and mostly a mosaic, and/or foliate structure, but the shell structure of true *Aviculopecten* has not yet been examined. Observations on the shell of *Aviculopecten* by Newell (1938) are now known to relate to *Heteropecten* rather than *Aviculopecten* (p.147).

Subfamily **UNDOPECTININAE** Waterhouse, 2001

Text-fig. 35

Diagnosis: Shells biconvex, upright, posterior wings large, ornament of well-formed costate plicae on both valves, resilifer well developed as a rule, may be lativincular.

Discussion: This subfamily includes the costate and plicate genus *Undopecten* Waterhouse, 1982 of Permian age, based on *Pecten fittoni* Morris, 1845, p. 277, pl. 14, fig. 2 from Tasmania. *Morrisipecten* Muromseva & Guskov in Muromseva, 1984, p. 75 was proposed later with the same type species. *Altaipecten* Yang & Chen, 1985, p. 384, with type species *A. multicostatus* Yang & Chen from the Late Carboniferous of China is also regarded as synonymous. Newell & Boyd (1995, p. 41) claimed that “most known examples of *Undopecten* are right valves”, but this is not true of Australian material. *Turbopecten* Astafieva, 1991a, first described from the Tournaisian (basal Carboniferous) of Rudnyi Altai, is very close, with plicae and slightly different ribbing. Like other subfamilies of Aviculopectinidae, the genera have well developed resilifer, and are biconvex (Waterhouse 2001). *Acanthopecten*? sp. of Amler (1992, pl. 2, fig. 6) from the uppermost Devonian of the Velbert Anticline in the Rhine Schiefergebirge belongs to a distinctive form with very narrow interplicae and unusually small right anterior auricle and distinct commarginal ornament.

Text-fig. 35. *Undopecten fittoni* (Morris), latex cast AMF 19064 from Gerringong Volcanics (Middle Permian) of New South Wales, Australia, x1. See Waterhouse (1982).

Gonzalez (2002, p. 90) misunderstood *Undopecten* and its hinge and the intention behind the original proposal of the genus. Waterhouse (1982) had always drawn attention to the presence of a resilifer in *Undopecten*, and had distinguished it on the basis of its closely costate plicae: the relationship to Aviculopectinidae which also has a resilifer was clearly stated by Waterhouse (2001, p. 119), and Waterhouse (1982) had drawn attention to the biconvexity and plication, features shared with *Deltopecten*.

In developing plicae, the undopectinins could have been descendants from the upper Devonian Pseudaviculopectininae of Pterinopectinidina, and could have been fore-runners for the plicate and non-costate members of Aviculopectininae. As well, had such specimens lost the plicae, and developed less inflated right valves, they may have provided root-stock for

Etheripectinidae, although Natalissiminae offer an alternative source, that entails fewer significant changes. Neither of these possibilities can yet be buttressed by firm successions of generic change in the stratigraphic record, but hypothetically, Undopectininae offered significant root-stock for other Aviculopectinidae, and doubtfully for Etheripectinoidea.

Genus ***Undorugosa*** new genus

Derivation: undo – wave; ruga – wrinkle, Lat.

Type species: *Pecten* (*Aequipecten*) *wilczekiformis* Licharew, 1927, pp. 35, 104 from Artinskian of the Urals, Russia, here designated.

Diagnosis: Close to *Undopecten*, distinguished by regular concentric wrinkles over both valves.

Discussion: The species *wilczekiformis*, with lectotype selected by Lutkevich & Lobanova (1960) as that figured by Licharew (1927, pl. 3, fig. 7) and kept at the Central Geological Museum, St Petersburg, is a left valve from the Artinskian beds at Krasnoufimsk. It is very close to *Undopecten* in details of shape, ligament and ornament, and is distinguished from *Undopecten* by the development of low regular concentric wrinkles over both valves, roughly of the same spacing and strength as the radial plicae. The type species was described by Licharew (1927, pl. 3, fig. 4, 6, 7) and it is close to *Pecten (Aequipecten) keyserlingiformis* Licharew (1927, p. 103, pl. 3, fig. 1, 2, 3, 5). Muromseva (1984, pl. 28, fig. 10) figured similar material from the Sakmarian Stage of the Petchora Basin. Sakmarian specimens figured as *Aequipecten keyserlingi* Licharew (1927, pl. 2, fig. 9-12) from Krasnoufimsk, Russia, may be the same as *Pecten keyserlingianus* Stuckenberg, 1875, and show similar wrinkles, as confirmed by specimens described by Muromseva (1984, pl. 28, fig. 1-6) from Artinskian faunas of Timan.

The difference from *Undopecten* is not great, and subgeneric status would be appropriate.

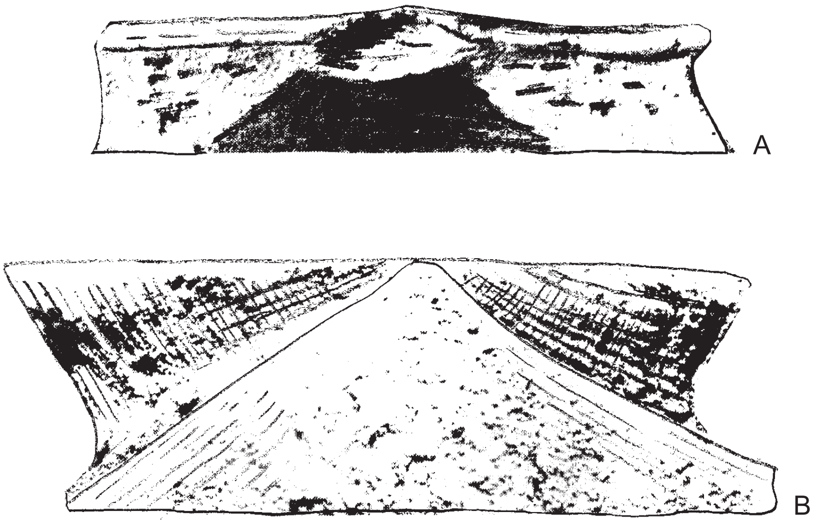
Subfamily **SPYRIDOPECTININAE** new subfamily

Text-fig. 36

Name genus: *Spyridopecten* Campbell & McKelvey, 1972, p. 36 from Westphalian Buckets Gap Formation of New South Wales, here designated.

Diagnosis: Subequally biconvex, ornament of fine branching and intercalated costae on both valves, may be feeble on right valve where tend to be weakly bundled, growth laminae moderately developed and close-set, anterior and posterior wings moderately high, subequal in length but not extending as far as as maximum shell length, very weak sinus and no byssal notch. Ligament alivincular, without crura or teeth. Shell composition not known.

Discussion: This subfamily is proposed for a highly exceptional genus, *Spyridopecten* Campbell & McKelvey. The type species of *Spyridopecten* is *S. montrosus* Campbell & McKelvey (1972, pl. 3, fig. 10-14, pl. 4, fig. 10-14) from the Buckets Gap Formation, and is dated as Serpukhovian, below *Levipustula levis* Maxwell, a key fossil to an extensive early Late Carboniferous (Bashkirian and ?Moscovian) Zone in Gondwana. *Spyridopecten* is characterized by the absence of byssal notch and by fine ribbing, especially feeble on the right valve. The right valve, in lacking a byssal notch, looks like the left valve, but Campbell & McKelvey were clearly confident in their assessment, and found that the right valve could be distinguished, at least in part, by its feeble ornament. In several respects, the genus recalls *Pernopecten* Winchell, 1865, a Mississippian to Permian form with high short wings and no byssal notch. This genus, as discussed by Newell (1938) and Newell & Boyd (1995), not only differs in ornament and the way in which the dorsal margin of the left wings extend well above the hinge, but has an internal resilifer and auricular crura. The genus belongs to Entoliidae Teppner, 1922, and is an early member of Pectinida (see p.183), whereas



Text-fig. 36. *Spyridopecten monstrosus* Campbell & McKelvey. A, left valve showing resilifer, ANU 21536, x6. B, dorsal part of right valve ANU 21538, x6. Modified from latex casts figured by Campbell & McKelvey (1972, pl. 4, fig. 11, 13). Specimens from Namurian of New South Wales.

the ligament of *Spyridopecten* is external and alivincular, like that typical of Aviculopectinidina. Spyridopectininae is judged to be close to Undopectinae in its dense costation, and different in the development of wings and auricle with reduced byssal development and reduced if any degree of plication.

Chiron Astafieva (1997) is allied. It is based on *C. mongolicus* (Lutkevich & Muromseva, 1962) from the Late Permian of Mongolia, and another species *C. fragilis* Astafieva (1997, Fig. 2) comes from the Lower Carboniferous of Gobi-Altai. Both species have wings slightly larger than in type *Spyridopecten*, and the ornament is stronger on the right valve than in *Spyridopecten*, and the costae are slightly more bunched and growth-laminae close-spaced and fine, but none of these differences seem very marked. The interior of *Chiron* is not known.

Newell & Boyd (1995, p. 39, Fig. 29.1a-c) identified as *Spyridopecten* a fine specimen (see Plate 1, fig. 1, 2) from the Upper Pennyslvanian Graham (Jacksboro) Shale (p. 39), also called Jacksboro Formation (p. 42) in Texas. It is little inflated with right valve weakly convex and less inflated than left valve, and both valves are ornamented by some 100 costellae in three ranks, increase by intercalation near mid-length, and ventrally by branching into pairs on the right valve and often threes to form low ventral bundles on the left valve. The shell is crossed by fine close-set laminae. The hinge is less than maximum length of shell, and the right anterior auricle has a rounded anterior margin, and is ornamented by radial costae over upper part, whereas the lower auricle is ornamented only by concentrics, with the anterior margin shallowly concave forward. The posterior wing on each valve has a concave posterior margin with acute cardinal extremity, and the anterior left valve wing is more convex next to the hinge.

The generic position is possibly new. The specimen is very close to *Spyridopecten* and *Chiron* in overall appearance, but the ribbing is more distinctive on both valves – and stronger than in *Spyridopecten* on the right valve. Ventral bundling is developed, approaching that seen in

Chiron and weakly developed in *Spyridopecten* (see Campbell & McKelvey 1972, pl. 3, fig. 13), but more restricted. Growth-laminae are comparatively well developed. The hinge is short as in *Spyridopecten*, and the left valve wings close to those of *Spyridopecten* in general features, and the right valve posterior wing is also close to that of *Spyridopecten*. But the right anterior auricle is divided in two, an upper part marked by radial ribs, with growth lines arching forward parallel to the rounded anterior margin, and a lower half, infilling a shallow byssal sinus, concave forward, and lacking radial ribs. There is no such distinction in *Spyridopecten*, in which the upper anterior auricle is much less rounded, and the same is true of *Chiron*. There thus considerable approach to *Costellinaria* n. gen. (see p.138) from the Early Carboniferous of Great Britain and Belgium, and elsewhere, and the generic position is not as clear as asserted by Newell & Boyd (1995). There is also considerable approach to *Pecten nexilis* Sowerby in Prestwich (1840, pl. 53, fig. 1, 2) and see Whidborne (1897, p. 129, pl. 16, fig. 5, 6, ?pl. 17, fig. 2, 3) from the Upper Devonian Pilton Formation of Devon, England. Sowerby's species was also reported from Upper Devonian of Bergisches Land, Rhine, Germany by Amler et al. (1990, p. 50, pl. 3, fig. 3, 4) and Amler (1992, pl. 2, fig. 4, 5). The species has fine ribs on the left valve, with branching and weak bundling, but intercalate ribs are not so evident. Concentric lamination is comparable. The right valve has fine ribs with slight central bundling but displays a large right anterior auricle with substantial byssal notch.

Family **ECHINIFERIPECTININAE** new subfamily

Name genus: *Echiniferipecten* n. gen., from Late Permian (Changhsingian) of Nepal, here designated.

Diagnosis: Small to large biconvex aviculopectiniform shells with wide hinge, large anterior and posterior wings and right anterior auricle, strong radial and spinose subplicae separated by wide interspaces, ligament alivincular with moderately well formed to lativincular resilifer.

Discussion: This new subfamily is based on three genera somewhat removed from Aviculopectininae and Undopectinae in ornament, although close in other respects. The ligament is closer to that of *Aviculopecten* than to that of *Deltopecten*, and no deltopectens are comparable in ornament. The name genus together with *Clavicosta* Newell, 1938 were originally regarded as close allies of *Cyrtorostra* Branson, which is also biconvex and has strong primary ribs that are often spinose. But *Cyrtorostra* has reduced posterior wings and pseudotrabeculae, and is closer to Deltopectinidae.

Newell (1938) suggested that *Clavicosta* had evolved from *Limipecten* Girty, but this genus has a flatter right valve with ornament differing considerably from that of the left valve.

Genus ***Echiniferipecten*** new genus

Text-fig. 37

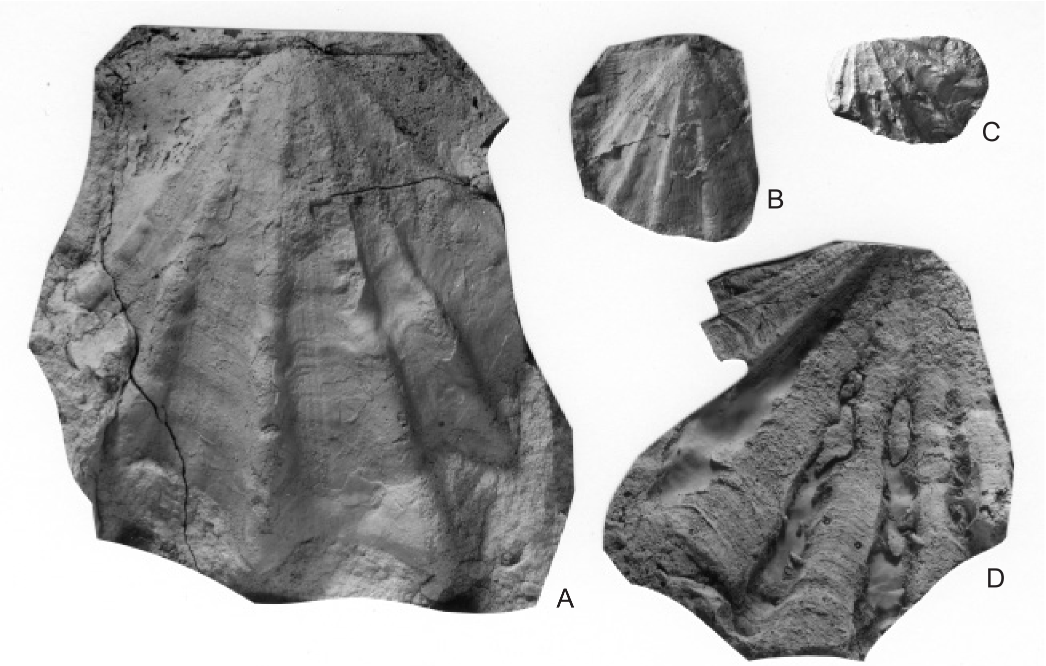
Derivation: echinus – sea-urchin; fera - to bear; pecten – scallop, Lat.

Type species: *Clavicosta* (?) *rugatula* Waterhouse, 1978, p. 103 from Late Permian (Changhsingian) Nisal Member, Senja Formation, west Nepal, here designated.

Diagnosis: Large biconvex shells with strong and spinose primary subplicae on both valves, separated by wide interspaces bearing several fine costae. Resilifer small and shallow.

Description: The species has been described as *Clavicosta* by Waterhouse (1978) and Waterhouse & Chen (2006) from the Dolpo and Manang districts of Nepal. The holotype UQF 69001 was figured in Waterhouse (1978, pl. 19, fig. 3, 4). A fragment from Manang, central Nepal, valve uncertain, shows a thin outer layer with well formed vertical prisms.

Discussion: The genus is represented in west and central Nepal north of the Himalayas, and



Text-fig. 37. *Echiniferipecten rugatula* (Waterhouse). A, internal mould of left valve UQF 69004, x 0.66. B, internal mould of small left valve UQF 69002, showing fine costae in interspaces. x 0.66. C, D, internal and external mould of right valve holotype, UQF 69001, x 0.3, x 0.66. From Nisal Member, Senja Formation, Nepal, of Changhsingian (Late Permian) age. See Waterhouse (1978).

material described by Reed (1931, pl. 6, fig. 11) as *Pseudomonotis* (*Eumicrotis*) *middlemissi* [not Diener] from the Chhidru Formation of the Salt Range, Pakistan, belongs to the genus. *Aviculopecten wynnei* Waagen var. of Reed (1944, pl. 54, fig. 9, 9a-c) is allied. According to figures in Waagen (1881, p. 320, pl. 23, fig. 9a-c), the primary ribs in the type lack scales which are developed in Reed's specimen, although secondary costae are sited close to the primary costa as in Reed's specimen. Waagen's species comes from the upper Wargal Formation of the Salt Range, Pakistan, of Late Permian (Wuchiapingian) age. It possibly belongs to a new genus, but the right valve is not known. *Aviculopecten hayasakai* Murata (1964, pl. 34, fig. 3-9) from the lower Kanokura Formation (Middle Permian) of Japan belongs to *Echiniferipecten*, with strong spinose scales on the primary ribs and three interstitial costae on the left valve, and similar but slightly less spiny ornament on the swollen right valve: secondary costae appear to be intercalate on both valves. A distinct new species is found in the Late Permian (Wuchiapingian) Port Keats Group in northern Western Australia.

This new genus is very close to *Clavicosta* Newell (1938, p. 79, pl. 13, fig. 1-5) from Pennsylvanian of United States. The genus has only two costae in interspaces, which carry tiny close-set scales. Primary ribs bear much larger spines spaced further apart, and commarginal laminae are low. The resilifer is lativincular and shallow (Newell 1938, pl. 13, fig. 3b). The genus *Cyrtorostra* Branson, 1930 is distinguished by its much smaller posterior wings, and hinge with lativincular resilifer marked by pseudotrabeculae, and is classed in a separate subfamily Cyrtorostrinae Newell & Boyd, 1995, placed as a member of Deltopectinidae Dickins (see p.95). The interspaces between primary ribs are swollen, unlike the concave interspaces of the present genus or *Clavicosta*.

Genus ***Carrollingeria*** new genus

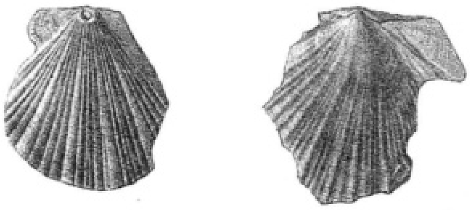
Text-fig. 38

Derivation: From species name.

Type species: *Aviculopecten carrolli* Hind, 1903, p. 97, from Early Carboniferous of England and Ireland, here designated.

Diagnosis: Characterized by broad simple primary ribs on each valve, hinge less than maximum length, right valve moderately inflated, right anterior auricle moderately developed with narrow byssal notch, left anterior and posterior wings not extended. Ornament much the same on each valve, some costae split on the right valve, intercalated on the left valve, ribs in three orders, primaries may carry fine radial threads over the crests.

Discussion: The type species was described by Hind (1903, pl. 17, fig. 24-27) and the material is kept at the Museum of Natural History, London. NHM L45059 has a comparatively deep byssal notch, and fine threads (micro-ribs) are present over the primary ribs. This specimen is proposed as lectotype. The broad primary ribs on the left valve are highly distinctive with flattened crests and characterize the genus, and these are separated by two further orders of ribbing. The right valve primary ribs are separated by finer secondary ribs. Six colour bands radiate from the umbo on some valves. Concentric growth laminae are fine. Although the species is small, and the primary ribs only moderately broad and comparatively low, and the hinge comparatively narrow, the ornament, and moderately large right anterior auricle suggest that this form was an early representative of the Echiniferipectininae, having evolved from Aviculopectininae. Compared with *Echiniferipecten* and *Clavicosta*, the shell is small with shorter hinge and less spinose primaries.



Text-fig. 38. *Carrollingeria carrolli* (Hind). A, left valve lectotype NHM 45059, figured by Hind (1903, pl. 17, fig. 26), from Early Carboniferous of Derbyshire, England, x1. B, right valve figured by Hind (1903, pl. 17, fig. 27) from Early Carboniferous of Limerick County, Ireland, kept at Geological Survey of Ireland, x1.

Hind (1903) compared the species with *Pecten murchisoni* M'Coy (1844, p. 97, pl. 18, fig. 3) and *P. ovatus* M'Coy (1844, pl. 14, fig. 11) from Early Carboniferous of Ireland. The species *murchisoni* was also figured by Koninck (1885, p. 219, pl. 36, fig. 21) as a specimen without secondary ribs, and by Hind (1903, p. 98, pl. 14, fig. 14, fig. 3-7, the type refigured in fig. 3). The left valve primary ribs are nodose, and the right valve ornament is composed of simple ribs, unlike that of *carrolli*.

The species *Aviculopecten ruthveni* M'Coy (1851, pp. 172, 185, 489, pl. 3e, fig. 4), refigured by Hind (1903, pl. 14, fig. 22) from Early Carboniferous of Ireland is somewhat similar in its left valve, with nodose primary ribs, but the right valve is not known. Left valves were also figured from the Early Carboniferous of Belgium by Koninck (1885, p. 213, pl. 37, fig. 10, 11, pl. 38, fig. 17, 18) and show small spinose laminae or nodes over the primary costae, and three orders of ribbing in all.

Pterinopectinella Newell, 1938, a genus which is common in Carboniferous faunas of Europe and North America, is characterized by the development of tubercles or small spines, especially on the left valve, and most species in *Pterinopectinella* have two orders of costae, and the right valve is almost flat with bifurcate ribs and long hinge in American species, including the type species *P. welleri* Newell (1938, pl. 3, fig. 14, 18-24). Its ligament is duplivincular.

Family **DELTOPECTINIDAE** Dickins, 1957

Diagnosis: Large, biconvex, ornament of radial plicae or subplicae, plain or variably costate, costae may increase by branching. Large right anterior auricle with deep byssal notch, large left anterior wing, posterior wings small in both valves. Ligament normally platyvincular, may be broadly concave, or bear a shallow median depression suggestive of a small resilifer.

Discussion: Reassessment of the nature of Aviculopectinidae as biconvex with ornament similar on each valve means that it is apparently very close to Deltopectinidae. Such a relationship was not considered by Newell & Boyd (1995) or Waterhouse (2001), for they stressed the differing nature of the ligament, considering that Aviculopectinidae were to be distinguished by the presence of a resilifer. But the variable nature of the ligament, involving absence or presence of a resilifer in various aviculopectiniform genera suggests that the nature of the inflation and ornament of the two valves offers a more consistent means of classification, and if the ligament is so variable, some might suggest that Deltopectinidae is not very different from Aviculopectinidae. Externally, members of the two families look similar in that both valves are convex to varying degree, and a number of genera are ornamented subequally with narrow plicae. It would appear that with increase in size and weight of shell amongst aviculopectinoid stock, the ligament became modified amongst genera presently assigned to deltopectens, and steps in this change are recorded within *Deltopecten* itself, in which the ligament occuped a shallow extended concave area, and in *Confundopecten* n. gen., which has a shallow depression or shallow resilifer below the umbones, not as flat as that of two other deltopectiniform genera, called *Squamuliferipecten* or *Corrugopecten*. There is one marked distinction which helps establish the difference between the two families. The posterior wings for each valve in *Aviculopecten* and allied genera are long, roughly counterbalancing the length of the right anterior auricle and left anterior wing. In *Deltopecten* and allied genera, the posterior wings are short – much shorter than the anterior auricle and wing. Because shells with differing ornament and different ligaments share this common distinction, it is deemed to be significant.

In the most widespread type of ligament found in Aviculopectinidina, a resilifer or pit lies between two grooved or flat areas, and the ligament is termed alivincular: the resilifer contains fibrous layers, and the ligament each side consists of fusion and lamellar layers. It is the fibrous ligament within the resilifer that provides a powerful mechanism for opening the valves, upon relaxation of the adductor muscles. The resilifer is not developed in the platyvincular hinge regarded as typical of Deltopectinidae. Was fibrous tissue present in the platyvincular hinge, and was it not normally in contact with the shell? It is likely that deltopectinid shells were so large and heavy that opening of the valves was a slower and more deliberate event, unlike that for Aviculopectinidae or Etheripectinidae. From those large shells, younger species evolved that were smaller, but retained features of the large parental stock. Possibly fusion or fibrous layers were seated in the platyvincular hinge, to constitute a profound difference from the alivincular ligament (Newell 1938, Trueman 1969), and such is suggested by the depth of grooves that traverse the ligament area in a number of species, such as "*Deltopecten*" (now *Squamuliferipecten*) *mitchelli* figured by Dickins (1957, pl. 7, fig. 8, pl. 8, fig. 10). Specimen AMF 25435 as figured shows deep wavy ligament grooves. Such a ligament may imply reversion to a lineavincular ligament allied to that seen in Myalinidae, and the best way of resolving the question would to find and section preserved ligament material from the species in question. In many Deltopectinidae, there are structural ridges called pseudotrabeculae (Waterhouse 2001, pp. 129, 131, text-fig. 10B) over the ligament significant for the strength of the hinge and ligament anchorage. Similar ridges are found in the allied Cyrtorostrinae Newell & Boyd, 1995.

To Deltopectinidae, Newell & Boyd (1995) referred the genera *Deltopecten*, *Streblopteria* M'Coy, *Crittendenia* Newell & Boyd and *Eocamptonectes* Newell, a very ill-assorted group. *Crittendenia* is clearly a member of Claraiidae Gavrilova, as explained by Nakazawa (1999) and Waterhouse (2000, 2001); *Streblopteria* is widely regarded as a member of Streblochondriidae Newell, and *Eocamptonectes* is very close, and apparently particularly allied to Orbiculopectininae Waterhouse, 2001. Deltopectinidae must, it appears, be restricted to *Deltopecten, Corrugopecten*, *Squamuliferipecten, Burnettilina* n. gen*., Confundopecten* n. gen. and *Adornatipecten*. The nature of the ligament for type *Deltopecten* itself remains unknown. In establishing the family as distinct from "Aviculopectinidae" (which in fact included etheripectinids, such as *Etheripecten, Primaspina* n. gen*.* and *Etheriplica* n. gen*.*), Dickins (1963) relied on material from the Tiverton Formation at Homevale, north-central Queensland, to demonstrate that one group of shells had what is now called an alivincular ligament, with well developed resilifer, in contrast to what he considered to be *Deltopecten* which lacks a resilifer, and displays what is now called a platyvincular ligament (Waterhouse 2001, p. 114, text-fig. 9, 10). This was to some extent an error. Dickins (1963) had misidentified as *Deltopecten limaeformis* specimens that belong to *Squamuliferipecten mitchelli* (Etheridge & Dun). The hinge, despite numerous assertions to the contrary, is not known for type *Deltopecten*. In a well preserved right valve of a different species believed to be congeneric, *D. waterfordi* Dickins (Dickins 1963, pl. 12, fig. 5, also Newell & Boyd 1995, Fig. 35.1b) from the Early Permian Callytharra Formation, Carnarvon Basin, Western Australia, a species very close in ornament to the type species, the ligament is formed in a very shallow scoop, set slightly below the outer dorsal edge of the shell, concave vertically and laterally (Waterhouse 1982, p. 35). In a companion species, *D. lyonsensis* Dickins (1957, pl. 7, fig. 3) from the Early Permian Lyons Group of the Carnarvon Basin, the ligament area also occupies a broad shallow scoop, concave vertically, gently concave along the hinge, and set just below the outer shell. Many authors, such as Astafieva (1994), Newell & Boyd (1995) and Gonzalez (2002, p. 90) have misrepresented the hinge of *Deltopecten* as being completely flat like that of the Tiverton Formation specimens described by Dickins (1957, 1963). Those specimens belong to *Squamuliferipecten*, not *Deltopecten*. In *Corrugopecten* and *Squamuliferipecten*, the ligament is flat or concave vertically and is planar laterally along the hinge, and may pass directly on to the outer shell or lie slightly below it. Whatever the significance, the hinge in the two examples for *Deltopecten* so far known is not quite the platyvincular hinge found in *Squamuliferipecten* or *Corrugopecten,* notwithstanding misrepresentations by authors who have overemphasized the invariant nature of the ligament, and did not take into account other morphological parameters here deemed significant for indicating interrelationships.

Subfamily **DELTOPECTININAE** Dickins, 1957

[nom. transl. Waterhouse 2001, p. 128 ex Deltopectinidae Dickins, 1957, p. 39].

Diagnosis: Small to large biconvex shells with well developed simple plicae, commarginal growth increments subdued, ligament where known forms broad scoop.

Discussion: This subfamily is restricted to genera with simple plicae and subdued growth increments. Shell structure is only known in detail for *Deltopecten lyonsensis* Dickins, 1957, p. 42 and is made up of concentric interlocking cross-foliae, presently of calcite, above thin massive hypostracum. One right valve revealed a thin outer prismatic layer. Carter (1990) noted that the inner foliate layer, making up most of the right valve, showed CF to CCF structure.

Deltopecten Etheridge 1892, type species *Pecten illawarrensis* Morris, 1845, p. 277, from possibly Harper's Hill, Hunter Valley, involves large biconvex shells ornamented by simple plicae, rarely with costae, and, to judge from related species from Western Australia, scoop-like ligament. No specimens have been described that show pseudotrabeculae, but there are few specimens that show the hinge. Although many species have been referred to *Deltopecten*, the genus is rare. Most species referred in recent years to *Deltopecten* belong in fact to *Squamuliferipecten*, having a different kind of plication, and having regular and well developed concentric laminae over both valves. Two species that show typically deltopectin ornament have been described as *D. lyonsensis* Dickins, 1957, and *D. waterfordi* Dickins, 1963 from Western Australia. Further afield, *Aviculopecten* cf. *mitchelli* of Reed (1932, p. 45, pl. 12, fig. 1, 1a) from the Agglomeratic Slate of Kashmir is possibly congeneric, whereas most Indian reports of *Deltopecten* refer in fact to *Squamuliferipecten*. From the Early Permian near Buenos Aires, Argentina, *Deltopecten harringtoni* Rocha-Campos & Carvalho, 1975 has steep-walled plicae with gently convex crests, possibly suggestive of *Deltopecten*, but more like *Aviculopecten,* and left valves assigned to this species by Rocha-Campos & Carvalho (1975, pl. 1, fig. 2) and Gonzalez (2002, text-fig. 8b) have moderately developed concentric laminae and a large left valve posterior wing, suggestive of Aviculopectinae.

Adornatipecten Astafieva, 1991a, type species *A. tarchanensis* (Muromseva & Turbanov) from the Lower Carboniferous of Mongolia, has very broad plicae, without strong concentric ornament, and was assigned to Deltopectinidae, implying a platyvincular hinge, though such is not clear from the text. The plicae are very like those of *Deltopecten,* and the posterior wings are short.

Evolution: The earliest known genus, *Adornatipecten* Astafieva, is of Tournaisian (basal Carboniferous) age, and may have arisen from aviculopectinid stock through the reduction on size of the posterior wings – aviculopectens are closer to source pterinopectens in having long posterior wings. The increase in shell size and change in hinge length presumably helped with the change in ligament from alivincular towards platyvincular.

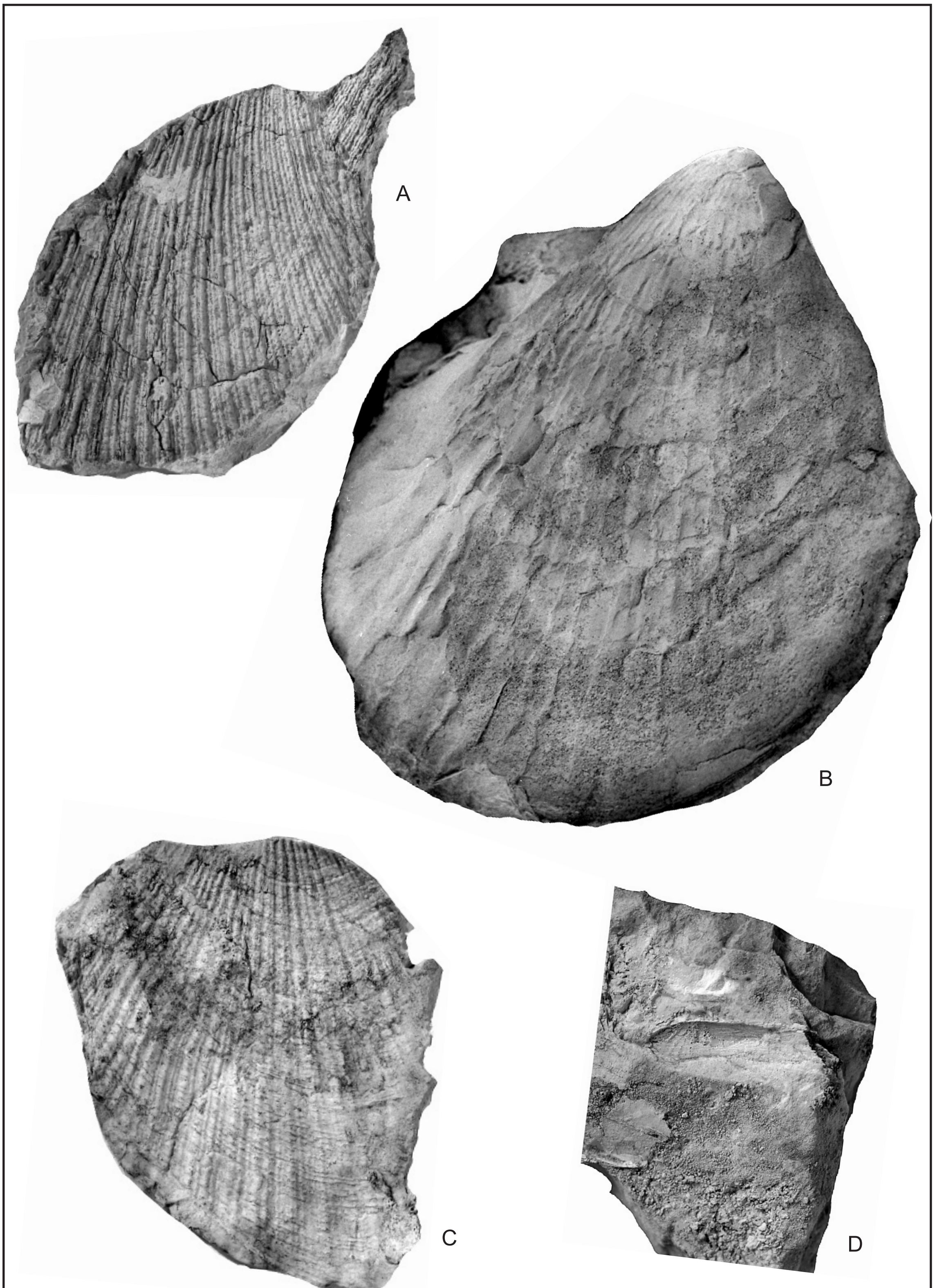
Subfamily **SQUAMULIFERIPECTININAE** new subfamily

Name genus: *Squamuliferipecten* Waterhouse, 1986, p. 6 from late Early Permian (Kungurian) of New South Wales, here designated.

Diagnosis: Biconvex, posterior wings short, ornament of plicae, with or without costae, strongly developed commarginal growth laminae. Ligament platyvincular, lativincular or weakly alivincular, often with pseudotrabeculae.

Discussion: The subfamily is distinguished from Deltopectininae by more elaborate ribbing, the presence of strong concentric laminae, and by the presence of pseudotrabeculae in the central ligament, not so far known in *Deltopecten*. Shell material for New Zealand *Squamuliferipecten* and *Corrugopecten* is not favourably preserved, having been partially replaced by zeolite (which suggests original cross-foliate aragonite – see Waterhouse 1982), and no outer prismatic layer is revealed.

Evolution: The oldest genus included in this group is of early Late Carboniferous age, found in east Australia and apparently Argentina. The species are gently plicate and elaborately costate, and although the classification implies that they arose, eventually, from *Adornatipecten* or allied genus, the linkage is not fully established.



Text-fig. 39. A, B, D. *Corrugopecten altoprimus* Waterhouse. A, latex cast of part of left valve, holotype TM 3551, x 0.9. B, decorticated left valve TM 3550, x 0.8. D, part of platyvincular ligament with pseudotrabeculae on TM 5232, a left valve x1. From Middle Permian (Wordian) Mangarewa Formation, New Zealand. C, *C. multicostatus* (Fletcher), latex cast of part of left valve from late Early? Permian at St George's Basin, New South Wales, x 0.6

Genus **Squamuliferipecten** Waterhouse, 1986

Type species: *Aviculopecten extensus* Fletcher, 1929, p. 6 from late Early Permian (Kungurian) of New South Wales, here designated. *A. extensus* is now judged to be junior synonym of *A. media* Laseron, 1910, p. 203.

Diagnosis: Large shells, biconvex with right valve less inflated than left, well developed right anterior auricle with byssal notch, well formed small posterior wings. Ornament of interlocking or opposed numerous subangular to rounded plicae on both valves, with a varying but small number of secondary ribs or costae, crossed by well formed close-set growth lamellae. Ligament platyvincular, may bear pseudotrabeculae.

Discussion: The right valve of *Squamuliferipecten* is convex but less inflated than the left valve. Both valves are plicate, the coarse ribs – ie. subplicae – being much coarser than the fine and usually much more differentiated ribs characteristic of Etheripectinidae. Plicae of *Deltopecten* have flat tops and steep flanks, whereas the crests of plicae in *Squamuliferipecten* are rounded with sloping flanks and concave interspaces, and concentric laminae are much more strongly developed in *Squamuliferipecten*. The ligament of *Squamuliferipecten* is planar rather than scoop-like, and has pseudotrabeculae. Most species referred in recent years to *Deltopecten* belong in fact to *Squamuliferipecten*, having a different kind of plication, and having regular and well developed concentric laminae over both valves. *Squamuliferipecten* is placed in Deltopectinidae because of the short posterior wings. But in lamination as well as strong plicae it approaches Lamnipectininae (see p.157), which is discriminated because of its flatter right valve, larger posterior wings and weaker finer right valve ornament.

An allied genus *Corrugopecten* Waterhouse, 1982, type species *C. altopriimus* Waterhouse, 1982, is characterized by very complex ornament on both valves (Text-fig. 39, 40, 41D), but is like *Squamuliferipecten* in hinge and inflation. It is chiefly of Middle Permian age in east Australia and New Zealand, whereas *Squamuliferipecten* is mostly of Early Permian age, and the late Early Permian species of *Squamuliferipecten,* called *S. media* (Laseron), is comparatively small.

Squamuliferipecten was referred to synonymy of *Heteropecten* Kegel & Costa, 1951 by Newell & Boyd (1995, p. 34), but in the type and other species of *Squamuliferipecten*, the posterior wings are significantly smaller, and the radial ribs are comparatively simple and stronger than those of *Heteropecten*, which are more diversified. The right valve of *Heteropecten* is considerably less inflated than the left, and has simpler ornament: the right valve of *Squamuliferipecten* is only slightly less convex than the left, and has ornament comparable to that of the left valve; both valves in *Squamuliferipecten* have strong concentric lamellae, much better developed than in *Heteropecten*. *Heteropecten* has a resilifer; the ligament in *Squamuliferipecten* is platyvincular, and also may have pseudotrabeculae, never seen in *Heteropecten*. There appears to be no objective evidence to justify synonymizing the two genera.

Squamuliferipecten mitchelli (Etheridge & Dun, 1906)

Text-fig. 41 A, B ,C

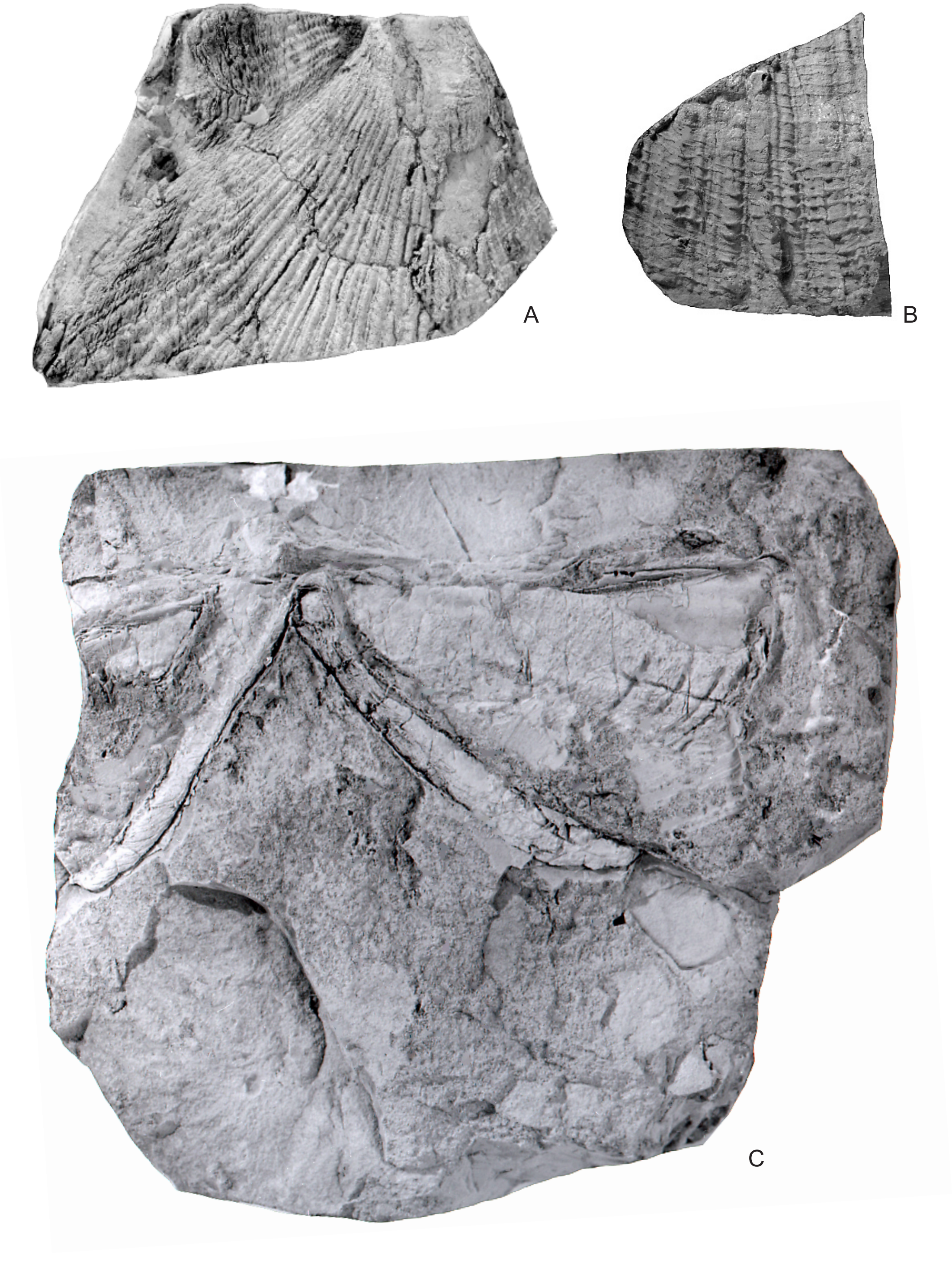
1849 *Pecten illawarrensis* [not Morris] - Dana, p. 705, pl. 9, fig. 9, 9a.

?1877 *Aviculopecten illawarrensis* – Koninck, p. 163, pl. 22, fig. 1.

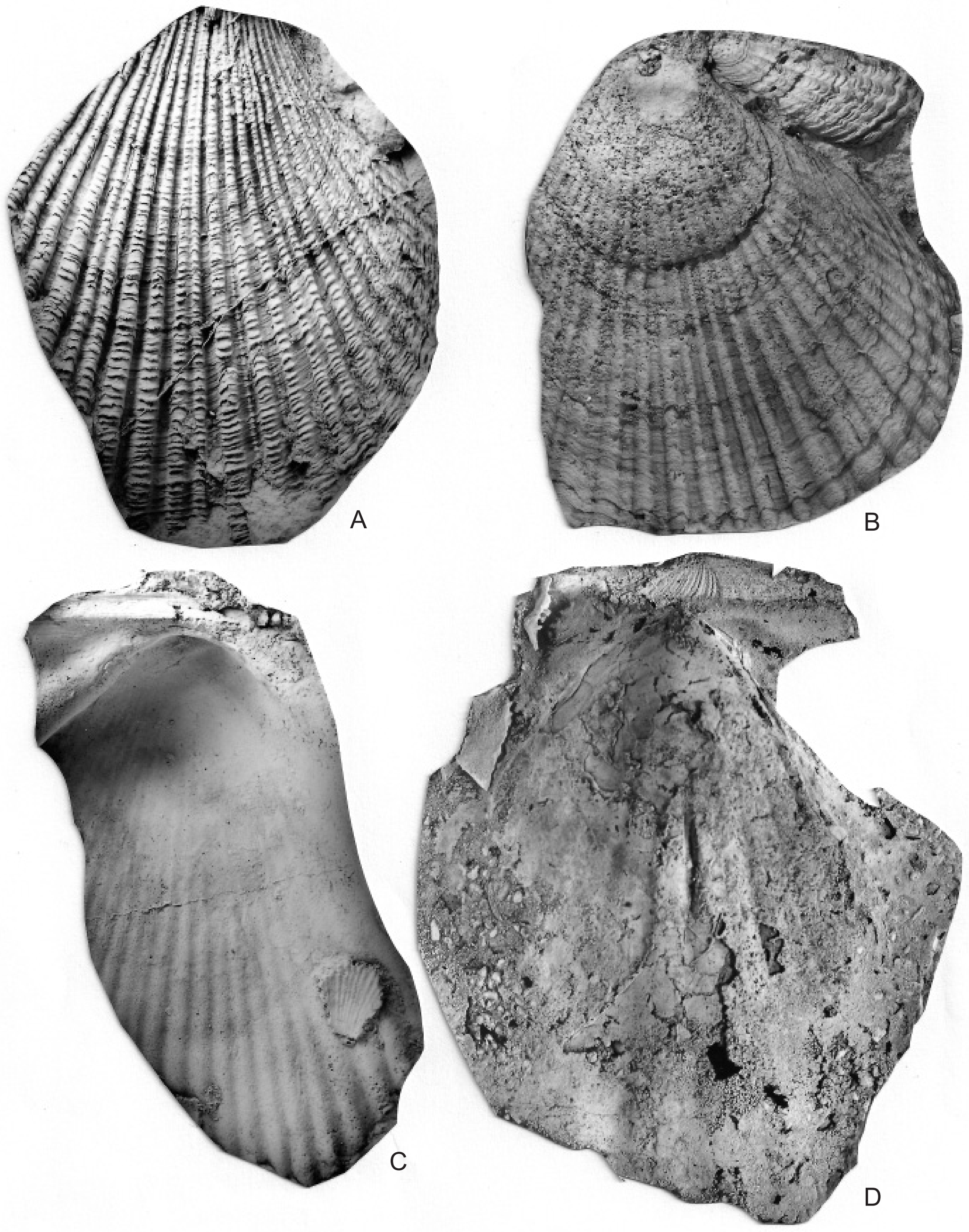
1892 *Deltopecten illawarrensis* – Etheridge, p. 269, pl. 41, fig. 3 (part, not pl. 43, fig. 2 = *Etheriplica* n. sp.).

1906 *A. mitchelli* Etheridge & Dun, p. 11, pl. 1, fig. 1-3, pl. 2, fig. 1, pl. 10, fig. 5, pl. 12, fig. 5, pl. 13, fig. 3, pl. 14, fig. 2, 3.

?1924 *A. mitchelli* - Richards & Bryan, pl. 20, fig. 2.



Text-fig. 40. A, C. *Corrugopecten altoprimus* Waterhouse. A, latex cast of posterior part of right valve TM 5230, x 0.6. C, right valve of holotype TM 3551, x 1.2. From Mangarewa Formation, New Zealand. B, *C.* cf. *multicostatus* (Fletcher), latex cast detail of left valve ornament from Early Permian (Artinskian) Takitimu Group, New Zealand, x1.



Text-fig. 41. *Squamuliferipecten mitchelli* (Etheridge & Dun), A, left valve, B, right valve, C, part of platyvincular ligament area of right valve. Latex casts of unregistered specimens kept at Queensland Museum, Brisbane, from middle Tiverton Formation (late Sakmarian, Early Permian) of Queensland, x1. D, *Corrugopecten* cf. *altoprimus* Waterhouse left valve part of platyvincular ligament with pseudotrabeculae, UQF 74352 from Wordian (Middle Permian) Flat Top Formation, Bowen Basin, Queensland, x1.

1928 *A. mitchelli* – Whitehouse, p. 282.

1929 *A. mitchelli* – Fletcher, p. 15.

1953 *“A.” mitchelli* – Kegel, p. 1, Fig. 1-3.

1957 *Deltopecten mitchelli* – Dickins, p. 40, pl. 7, fig. 8, pl. 8, fig. 10, text-fig. 8.

1963 *D. limaeformis* [not Morris] – Dickins, pl. 12, fig. 1, 2, ?3.

1964b *D. limaeformis* – Hill & Woods, pl. P11, fig. 11, 12.

1972 *D. limaeformis* – Hill, Playford & Woods, pl. P11, fig. 11, 12.

1987 *D. illawarrensis* – Waterhouse, p. 154, pl. 6, fig. 9 (part, not fig. 6 = *squamuliferus*).

cf. 1992 *D. illawarrensis* – Clarke, p. 41, Fig. 25A-I, 26A-F.

Lectotype: AMF 35304 figured by Etheridge & Dun (1906, pl. 1, fig. 1, 2) from Allandale Formation, north Sydney Basin, here designated.

Diagnosis: Biconvex shells with some 20 to 27 coarse ribs that may carry median groove, and rare secondary ribs. Concentric lamellae well developed and well spaced on both valves. The Tiverton specimen figured by Dickins (1963, pl. 12, fig. 3) is probably conspecific but has a larger number of secondary costae than usual.

Squamuliferipecten squamuliferus (Morris, 1845)

Text-fig. 42

1845 *Pecten squamuliferus* Morris, p. 278, pl. 14, fig. 1.

?1872 *Aviculopecten multiradiatus* Etheridge Snr, p. 327, pl. 13, fig. 1.

1906 *A. squamuliferus* – Etheridge & Dun, p. 8, pl. 1, fig. 4, pl. 8, fig. 4 (part, not pl. 2, fig. 4, 5 = n. sp.).

1906 *A. profundus* [not Koninck] - Etheridge & Dun, p. 9, pl. 11, fig. 4, 5.

1929 ?*A. squamuliferus* – Fletcher, p. 4.

1959 *A. squamuliferus* – Sahni & Dutt, p. 658, pl. 24, fig. 1, 2.

1982 ?*Corrugopecten squamuliferus* – Waterhouse, pl. 24, fig. e.

1987 *D. illawarrensis* [not Morris] – Waterhouse, p. 154, pl. 6, fig. 6 (part, not fig. 9 = *mitchelli*).

1987 *Squamuliferipecten squamuliferus* – Waterhouse, p. 157, pl. 7, fig. 1, pl. 8, fig. 10.

1987 *Squamuliferipecten* sp. Waterhouse, p. 155, pl. 6, fig. 2, 4.

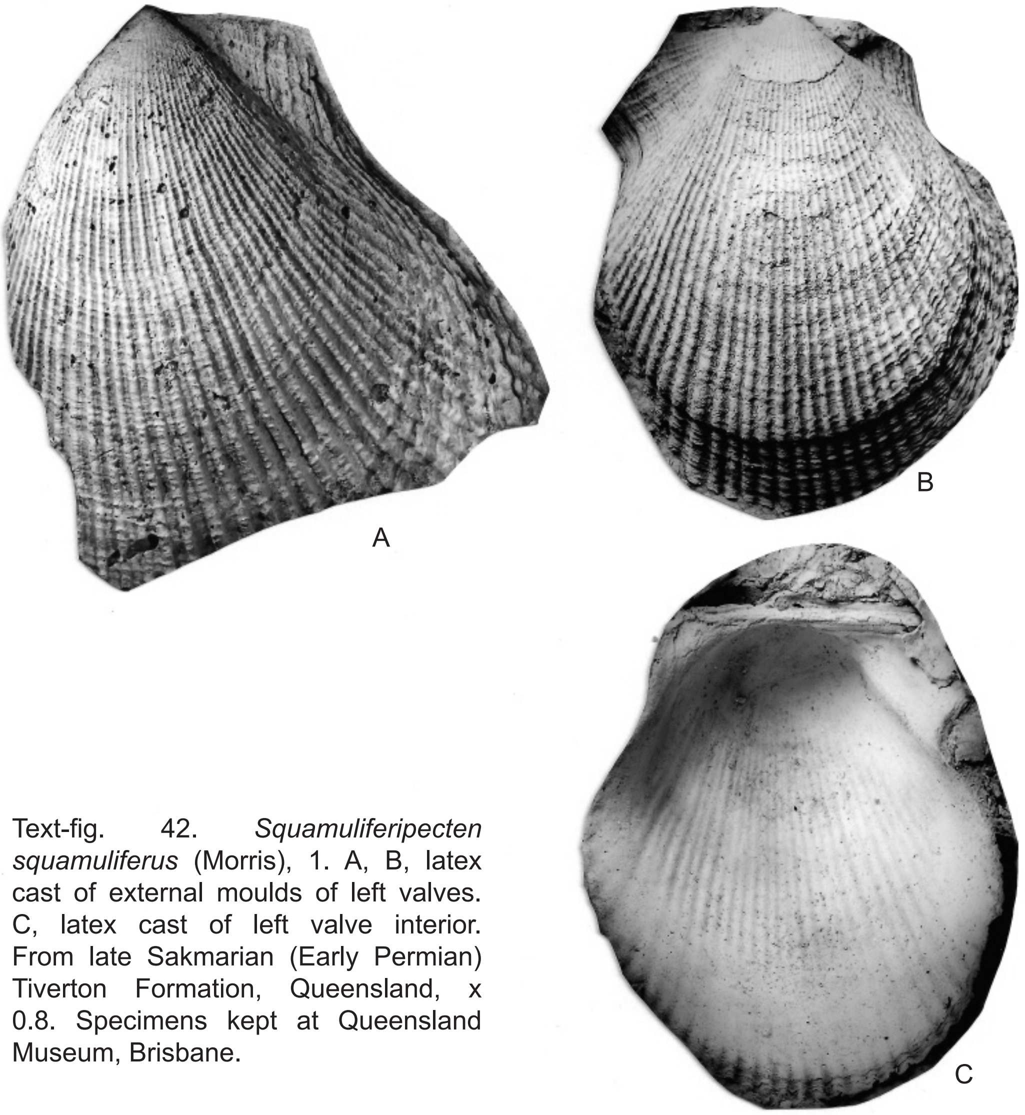
?1987 *D. limaeformis* - Waterhouse & Balfe, p. 30, pl. 1, fig. 10, 11.

Lectotype: NHM PL3685 from Mount Wellington, Tasmania, probably Cascades Group, figured by Morris (1845, pl. 4, fig. 1) and Waterhouse (1982, pl. 24, fig. e), SD Waterhouse (1982, p. 37). The probable locality exposes undifferentiated Cascades Group, which crops out on Huon Road, just past Turnip Fields Road in the Hobart suburb of Lenah Valley (M. R. Banks, pers. comm.). Holotype for *multiradiatus*, GSQ 17/1208 from the Rammutt Formation, Gympie, southeast Queensland, figured by Etheridge Snr (1872) and Waterhouse & Balfe (1987, pl. 1, fig. 10), by monotypy.

Diagnosis: Large shells, right valve a little less inflated than left valve, right anterior auricle very large, ornament of 40-50 round-crested plicae and secondary costae which are moderately numerous, concentric lamellae prominent.

Description: Shells large, left valve almost twice as wide as right valve, right anterior auricle very large with long deep byssal notch, left anterior wing moderately large with anterior margin convex in outline, posterior wing of each valve small, with generally sinuous posterior margin and rounded posterior cardinal extremity. Plicae number just over 40 up to 50, crests round, interspaces evenly concave, growth lamellae strongly developed, four to six in 5mm, little arched across interspaces and plicae, plicae tend to be broader in right valve and narrower on left valve, with interspaces narrower on right valve and wider on the left valve for some specimens. Interspaces may carry median ribs and some plicae have two costae ventrally. Five or six ribs on right anterior auricle, and the wings are firmly ribbed, with close-set growth lines. Hinge platyvincular.

Discussion: These specimens are larger than the type specimens from Tasmania, but have similar anterior right valve auricle and posterior wing, low inflation and a comparable number of similar but slightly narrower plicae. An allied specimen has been figured from the Farley Formation of



Text-fig. 42. *Squamuliferipecten squamuliferus* (Morris), 1. A, B, latex cast of external moulds of left valves. C, latex cast of left valve interior. From late Sakmarian (Early Permian) Tiverton Formation, Queensland, x 0.8. Specimens kept at Queensland Museum, Brisbane.

the Sydney Basin in the Hunter Valley, New South Wales, by Etheridge & Dun (1906, pl. 1, fig. 4), but another Farley specimen and a Ravensfield specimen (Etheridge & Dun 1906, pl. 2, fig. 4, 5) are small and have much finer costae, numbering close to 60, and the latter specimen AMF 35298 from Ravensfield has a platyvincular hinge. Given the nature of the hinge and ornament, they would appear to belong to a distinct species of *Squamuliferipecten*. Fletcher (1929, p. 5) referred the specimen figured by Etheridge & Dun (1906, pl. 1, fig. 4) “to my species *A. largis*”, but no description of this species appears to have been provided. Specimens from the Elvinia and Rose’s Pride Formations of southeast Bowen Basin, Queensland, were described by Waterhouse (1987), with a report of doubtful material from the Boughyard Member in that area. From the Manendragarh fauna of Peninsula India, Sahni & Dutt (1959) reported specimens that are moderately close to the present species, with 45 ribs in the right valve.

Etheridge & Dun (1906) and Fletcher (1929) considered that *Aviculopecten multistriatus* Etheridge Snr (1872, pl. 13, fig. 1) from the Gympie area of southeast Queensland, also figured by Waterhouse & Balfe (1987, pl. 1, fig. 10), should be synonymized with *squamuliferus*. The genus is probably *Squamuliferipecten*, and the number of plicae is close to 50, consonant with the number in *squamuliferus*. But many details are not known for the Gympie material.

Of other species, *Aviculopecten extensus* Fletcher (1929), the designated type species of *Squamuliferipecten*, is smaller, with 33-40 ribs and small posterior wings, and only moderately developed growth lamellae. The holotype AMF 19143 (Fletcher 1929, pl. 1, fig. 2, 3) from Ulladulla, south Sydney Basin, New South Wales, has few secondary ribs and rare tertiary ribs: the paratype (AMF 19144, Fletcher 1929, pl. 1, fig. 1) also comes from Ulladulla. The species is judged to be identical with *Aviculopecten media* Laseron (1910) from the "Wandrawandian Suite" at Burrier, south New South Wales. The type specimen AMF 20169 as figured by Laseron (1910, pl. 15, fig. 1; Fletcher 1929, pl. 7, fig. 3) does not show the hinge, but the left valve AMF 19504 ascribed to the species by Fletcher (1929, pl. 7, fig. 5) has a platyvincular hinge, as is possibly the case for AMF 19147 (Fletcher 1929, pl. 7, fig. 4), and a platyvincular hinge was figured for *media* specimen AMF 24054 by Dickins (1957, pl. 7, fig. 6, 7). The specimen AMF 19504 has some 27-28 mostly primary ribs, and although the caption stated that the hinge of the right valve is present, this is no longer true. *Aviculopecten gracilis* Fletcher (1929, p. 11, pl. 4, fig. 1-5, text-fig. 2), chiefly from Wyro, south Sydney Basin, was erected on the basis that its hinge lacked a resilifer, whereas that of *media* showed a resilifer. This does not appear to be correct, and the ligament area on both is platyvincular. One of the two specimens treated as *media* by Laseron (1910, pl. 15, fig. 2, 3) was reallocated to *gracilis* by Fletcher (1929, text-fig. 2), and this shows the hinge. The holotype of *gracilis* AMF 19160 (Fletcher 1929, pl. 4, fig. 1) clearly belongs to *Squamuliferipecten*. Both suites belong to *Squamuliferipecten*, and are close to, but smaller than, *S. extensus* (Fletcher), and the types of both *gracilis* and *extensus* come from Ulladulla. All three taxa are conspecific, and *media* Laseron has priority. None of the figured specimens shows well the exterior of the left valve.

Genus ***Burnettilina*** new genus

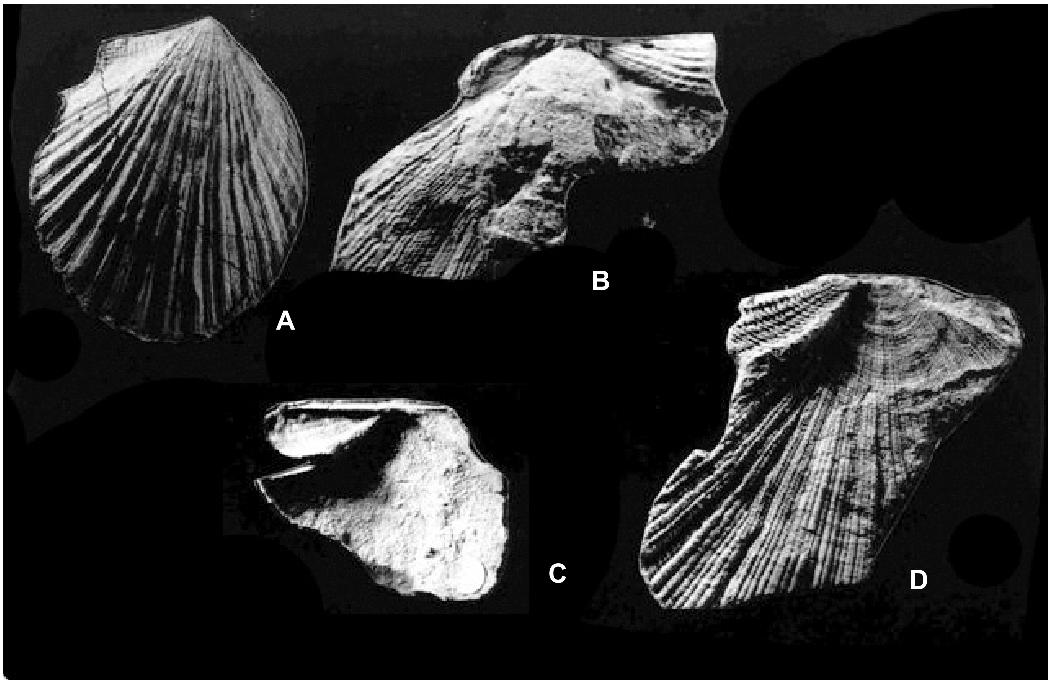
Text-fig. 43, 44

Derivation: Burnett district of Queensland.

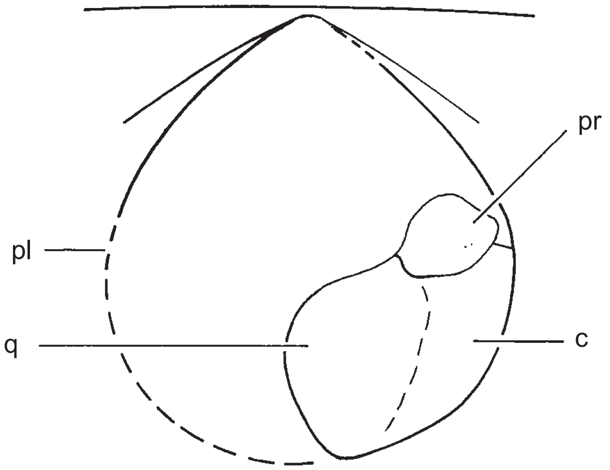
Type species: *Limipecten burnettensis* Maxwell, 1964, p. 14, from Late Carboniferous of Yarrol Basin, Queensland, here designated.

Diagnosis: Moderately small biconvex shells with long strongly costate right anterior auricle, both valves ornamented by gentle radial plicae and moderately strong varied costae, ligament platyvincular, may be lativincular edged by bourrelets in allied species.

Discussion: This genus is deltopectinid in being sub-biconvex with low plicae, but costae are strongly developed and diverse, and the shape more elongate and rounded than is usual for Deltopectinidae. It appears probable that *Orbiculipecten taboadai* Gonzalez (2002, Fig. 3-7) from the *Levipustula levis* Zone of Barreal, San Juan, Argentina, is congeneric or closely allied. This species has a hinge like that of *Orbiculopecten* Gonzalez, with lativincular resilifer bordered by bourrelets fore and aft, and valves are plicate and costate. There is a large adductor complex (Text-fig. 44), and a pallial line that closes under the umbo (Gonzalez 2002, text-fig. 4), which is exceptional amongst known Aviculopectinidina, and implies mobility approaching that of *Pecten*. The right anterior auricle is large above a deep byssal notch, and the posterior wings are short, most of the hinge lying in front of the beaks. The present genus is distinguished in part by its shape, with comparatively well defined and persistent posterior and anterior umbonal ridges, so that the outline is less rounded than that of *Orbiculipecten*, and the ornament involves strong auricular costae and moderately strong fine costae over both valves, sited on low plicae. Growth-lines are very fine, and concentric wrinkles inconspicuous, few, and variable. *Orbiculopecten* is characterized by very fine radial ribs and by moderately pronounced concentric growth lines and undulations: there are no plicae, and the costae may be missing near the umbones. There is some approach to *Undopecten* Waterhouse, 1982, a widespread genus with fine costae and plicae on



Text-fig. 43. *Burnettilina taboadai* (Gonzalez). A, left valve holotype IPI 2643 x 0.8. B, right valve IPI 2642, x l. C, right valve IPI 2225 left valve exterior IPI 2639 x 0.8. D, external mould of right valve IPI 2244, x 1. From middle Carboniferous Majaditas Formation, Barreal, Argentina. Photographs courtesy of C. R. Gonzalez, Tucuman. See Gonzalez (2002).



Text-fig. 44. *Burnettilina taboadai* (Gonzalez). Pallial line and muscle scars in left valve, x1, modified from Gonzalez (2002, text-fig. 4). From middle Carboniferous Majaditas Formation, Barreal, Argentina. Courtesy of C. R. Gonzalez, Tucuman. c – catch and q – quick adductor scar, pl – pallial line, pr - posterior retractor. See Gonzalez (2002).

both valves, but this genus has a well developed resilifer and comparatively long posterior wings. Because the posterior wings are short in *taboadai*, Gonzalez (2002) stating the posterior wings are only half as long as the anterior left valve wing and right anterior auricle, the species appears to be deltopectinin.

Burnettilina burnettensis (Maxwell, 1964)

1964 *Limipecten burnettensis* Maxwell, p. 14, pl. 1, fig. 14-17, pl. 2, fig. 4-11.
1964a *L. burnettensis* – Hill & Woods, pl. C13, fig. 7-8.
1973 *L. burnettensis* – Hill, Playford & Woods, pl. C13, fig. 7-8.
Holotype: UQF 27080a, b figured by Maxwell (1964, pl. 2, fig. 10, 11) from Upper Carboniferous Rands Formation, Yarrol Basin, Queensland, OD.

Description: The ornament consists of broad low plicae covered by fine ribs only 0.2-0.3mm wide, and the plicae are separated by interspaces which are often swollen, and may be traversed medianly by a stronger rib, so that overall the ornament is comparatively complex and not completely regular, with three orders of ribbing. Ribbing is weaker on the right valve, which is less convex. Ribs branch on the left valve UQF 43125 (Maxwell 1964, pl. 2, fig. 9), and in general ribs arise by both intercalation and branching. They are crossed by very sharply defined, almost vertical growth laminae. UQF 27086 shows a hinge (Maxwell 1964, pl. 1, fig. 17) with very weak vertical and longitudinal striae, but the lateral extremities are not visible, so that it is not clear if the hinge is platyvincular or lativincular. The posterior wing is often destroyed, but although it seems long in the specimen figured by Maxwell (1964, pl. 2, fig. 10), it appears that the wing was much shorter than the full anterior wing.

Discussion: There are differences in ornament between the species *taboadai* and *burnettensis*, involving less regular ribbing in the Queensland species, with more sharply defined concentrics, and finer costae over the right anterior auricle. The lativincular hinge in *taboadai* has extremely narrow bourrelets according to Gonzalez (2002, text-fig. 3), and none are seen in Maxwell's species.

Limipecten flexiauricularis Campbell, 1961, p. 466, pl. 61, fig. 9-16) from the *Levipustula levis* beds (Bashkirian, ?Moscovian) of Booral, New South Wales, has coarser and much less fasciculate ornament, with prominent broad primary and fewer secondary costae, crossed by closely spaced well developed laminae. Costae are intercalate on both valves. The right valve ornament is not clearly bundled, and shows broad primary and slender secondary ribs with narrow interspaces. The posterior wings of both valves are longer than in *taboadai* and shorter than in *burnettensis*, but the anterior left valve wing and right auricle are moderately long. Although the figured ligament appears to be platyvincular (Campbell 1961, pl. 61, fig. 11), Campbell described a shallow ill-defined and broad (lativincular) resilifer. The lack of plicae might prove to signify a different genus.

Genus ***Confundopecten*** new genus

Text-fig. 45

Derivation: confundo – mix, blend; pecten – shell-fish name, Lat.

Type species: *Pecten limaeformis* Morris, 1845, p. 277, from Early Permian (Sakmarian) rocks of Tasmania, here designated.

Diagnosis: Large subequally biconvex shells with long right valve auricle and anterior left valve wing, short posterior wings in each valve, ornament of strong close-set round-crested plicae with rare secondary ribs, weak commarginal laminae. Ligament plane with shallow and small median resilifer.

Discussion: The species *limaeformis* has been referred over many years to *Deltopecten* Etheridge & Dun, 1906. Dickins (1963) emphasized the lack of a resilifer in the *limaeformis* hinge, but Waterhouse (1982) cautioned that a number of specimens at the Museum of Natural History, London, showed a resilifer. Fang & Morris (1999) acknowledged the observations, and considered that further work might show "that the family Aviculopectinidae were better represented in the Gondwanan realm than previously realised". The overall aspect of the species *Pecten limaeformis* and another species represented by Allandale material, is certainly aviculopectinid in large size, swollen right valve and strong plicae on both valves, but the hinge is not identical to that of *Aviculopecten* and close allies *Hayasakapecten* and *Newellipectinia*, insofar as the resilifer is much shallower. One possibility is that the *Aviculopecten* ligament has been altered, with reduction in the size and depth of the resilifer. Another possibility is that the ligament of *Deltopecten* has evolved to develop a small and shallow resilifer. This alternative is favoured by the overall appearance of *limaeformis* and the Allandale material, because the posterior wings in both *limaeformis* and the Allandale species are much smaller than the anterior wing and auricle, whereas the posterior wings for the type species of *Aviculopecten, Hayasakapecten* and *Newellipectinia* are moderate in size to large – even larger than the anterior auricle and wing in some specimens. In view of this difference between aviculopectinids and deltopectinids, *limaeformis* is deemed to be deltopectinid.

Confundopecten limaeformis (Morris, 1845)

1845 *Pecten limaeformis* Morris, p. 277, pl. 13, fig. 1.
1888 *Aviculopecten limaeformis* – Johnston, pl. 14, fig. 1.
1982 *Deltopecten* aff. *limaeformis* – Waterhouse, p. 36, pl. 19, fig. a.
1987 *Deltopecten limaeformis* [not Morris] – Waterhouse, p. 153, pl. 6, fig. 1 (part, not pl. 5, fig. 12 = *latispatia* Waterhouse).

Lectotype: NHM PL3686 from probable equivalent of Berriedale Limestone, central Tasmania, figured by Morris (1845, pl. 13, fig. 1), SD Waterhouse (1987, p. 154).

Diagnosis: Large unequally biconvex shells with 34-40 well rounded slender plicae, including a few secondary ribs arising by branching.

Discussion: A large bivalve from the Early Permian of east Australia was described as *Pecten limaeformis* by Morris (1845, pl. 13, fig. 1) with type specimen NHM PL3686 most likely to have come from the probable equivalent of the Berriedale Limestone of central Tasmania. The same species was identified in the Tiverton Formation by Etheridge (1892, pl. 14, fig. 1) and Etheridge & Dun (1906, p. 23), as affirmed by Dickins (1963), but the Tiverton material belongs to a different species *mitchelli* Etheridge & Dun (1906). The species *limaeformis* is characterized by having a large number of relatively narrow plicae with round crests and interspaces of similar width, with some plicae branching into secondaries. For *limaeformis*, Etheridge & Dun (1906) reported 34 ribs, as against 36 estimated by Morris (1845), and 37 ribs are present in the specimen figured by Etheridge & Dun (1906, pl. 10, fig. 3, 4) from Ravensfield. The right valve aspect of the type specimen is well figured by Morris (1845, pl. 13, fig. 1), and the left valve is swollen.

Squamuliferipecten squamuliferus has a broader outline, less convex left valve and many more ribs and more prominent concentric laminae than *limaeformis* and platyvincular hinge. The holotype of *limaeformis* has 36 ribs, as counted by Morris (1845), varying between 34 and 40, whereas type *squamuliferus* has some 48 ribs. A shallow resilifer is developed in some Tasmanian and Sydney Basin specimens identified as *limaeformis*, including a right valve from the Eastern Marshes of Tasmania, kept at the Museum of Natural History, London, which is a possible topotype. The type specimen suggests a shallow resilifer on the left valve which seems slightly displaced from the right valve, with five or six grooves. NHM L70402, stated to be from

Gippsland, Victoria, has a shallow right valve chondrophore, deeper posteriorly, and low growth grooves. NHM L96922 has a weak left valve resilifer and shows pseudotrabeculae, made up of ridges and grooves radiating from the umbo, as well as growth grooves parallel to the commissure. Both valves are convex, the ribs are strong, with rare fine ribs, showing some tendency for right valve ribs to be slightly bunched (NHM PL408, from Bismarck Quarry, near Hobart), and there are faint traces of low concentric growth lamellae.

The species has been reported widely from the Early Permian of eastern Australia and also New Zealand, as summarized by Waterhouse (1987), but many accounts have to be revised if reliance is to placed on the discriminants shown by the type specimen: the number and nature of plicae (ca. 34-40), the weakly convex right valve and convex left valve and weak concentric growth laminae. For example, *limaeformis* of Etheridge & Dun (1906, pl. 10, fig. 3) was referred to (*Etheripecten*) *clarkei* fide Fletcher (1929, p. 28), and the specimen of Etheridge & Dun (1906, pl. 11, fig. 1, 2) from Maria Island, Tasmania*,* is placed in *Corrugopecten*. Johnston (1888, pl. 14, fig. 1) figured a likely specimen from Tasmania. Fletcher (1929, text-fig. 5) illustrated an internal mould, but the figure is indecipherable. Specimens from the Fairyland Formation of southeast Bowen Basin shows about 40 plicae (Waterhouse 1987, pl. 5, fig. 12, pl. 6, fig. 1), but are not well preserved, and the plicae in the specimen of pl. 5, fig. 12 are spaced further apart than usual. Specimens of *limaeformis* from the *Ingelarella plica* Zone of the Brunel Formation in New Zealand have some 35 plicae (Waterhouse 1982, pl. 19, fig. a).

The morphology of the hinge in allied material, probably belonging to a different species,

Text-fig. 45. *Confundopecten* sp. right valve internal mould showing small resilifer, AMF 24631 from Allandale Formation, New South Wales, of Asselian (Early Permian) age, x1. See Waterhouse (1982).

is well shown by the report and illustration of a left valve AMF 26431 from the Allandale Formation at Harper's Hill, New South Wales, by Waterhouse (1982, front cover and pl. 18, fig. d). This shows a moderately large shell with some 48 plicae (including costae) and small but well formed resilifer and fine pseudotrabeculae. It was identified at the Australian Museum as *Deltopecten limaeformis* (Morris, 1845), but has substantially more plicae than shown in *limaeformis*. A plicate left valve from the Marlborough Group, Tasmania, was figured with resilifer by Newell & Boyd (1995, Fig. 21.1), and possibly comes close to *limaeformis,* but possibly has fewer ribs – it could belong to *Heteropecten,* and has ribs much coarser than in *Etheripecten*.

Comparatively young specimens were figured by Dickins (1981) as *limaeformis* from the Eight Mile and Tunnel Blocks near Warwick, southeast Queensland. They look like Morris' species as far as preserved, but are very incomplete, and are judged to belong to *Squamuliferipecten extensus* (Fletcher) = *media* (Laseron).

Subfamily **CYRTOROSTRINAE** Newell & Boyd, 1995

[nom. transl. Waterhouse 2001, p. 130 ex Cyrtorostridae Newell & Boyd, 1995, p. 62].

Diagnosis: Biconvex with short posterior wings, ornament on each valve of high primary costae separated by swollen costate interspaces and bearing large spines which may be terminal, ligament alivincular to platyvincular ligament, may bear pseudotrabeculae.

Discussion: *Cyrtorostra* Branson, 1930 is biconvex, and has an alivincular or lativincular ligament. It is distinguished by ornament, which is highly specialized and more elaborate than found in Deltopectininae or Squamuliferipectininae. Newell & Boyd (1995) evidently regarded the genus as allied to Aviculopectinidae, and Waterhouse (2001) noted the presence of pseudotrabeculae within the broad resilifer, as in deltopectinids. The group is treated as a subfamily of Deltopectinidae, as suggested by Waterhouse (2001). Admittedly *Cyrtorostra* is like *Chaenocardia* and *Streblochondria* in its distinctive shape, but two considerations are believed to favour a closer association with deltopectinids, the rarity of chaenocardioids with plicae, and the absence of any chaenocardioid with pseudotrabeculae in the hinge. This is further supported by the recognition of a new cyrtorostrin genus with platyvincular ligament, like that of some deltopectinid genera. Cyrtorostridae was treated as monogeneric by Newell & Boyd (1995).

The genus *Cyrtorostra* is close in some aspects of ornament to *Clavicosta* Newell, 1938, p. 79, type species *C. echinata* Newell, 1938 of Upper Carboniferous age, and Waterhouse (2001) included the genus in the subfamily. But the two genera are not in the same family group, because *Clavicosta* and related genus *Echiniferipecten* have a longer hinge with large posterior wings and lack pseudotrabeculae. *Cyrtorostra* ranges from Lower to Upper Permian, being common in Late Permian faunas of the Salt Range, Pakistan, notwithstanding the claim by Newell & Boyd (1995) that the genus ranged only from Lower to Middle Permian.

Genus ***Elviniaria*** new genus

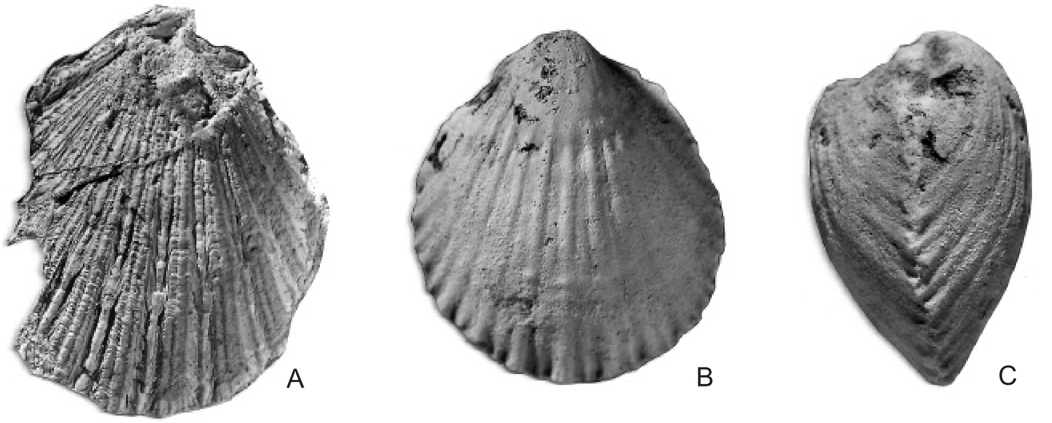
Text-fig. 46

Derivation: Named from Elvinia Formation, Queensland, source of the fossil material.

Type species: *Cyrtorostra limitans* Waterhouse, 1987, p. 158, from Early Permian (Sakmarian – lower Artinskian) of Bowen Basin, Queensland, here designated.

Diagnosis: Subequally biconvex orthocrescent shells with well developed costae over the swollen interspaces between primary costae, right anterior auricle smooth, ligament platyvincular.

Discussion: *Cytorostra limitans* Waterhouse (1987, p. 158) from the Elvinia and Tiverton Formations of the Bowen Basin in Queensland has up to three costae in each interspace, although the central interspatial costa remains prominent. *Cyrtorostra varicostata* Branson, 1930 from the



Text-fig. 46. *Elviniaria limitans* (Waterhouse). A, left valve latex cast UQF 51929 x1. B, C, left and anterior aspects (right valve to left) of UQF 51928, x2. Specimens from Early Permian (Sakmarian) Tiverton Formation, Bowen Basin, Queensland. See Waterhouse (1987).

early Middle Permian of mid-United States (Ciriacks 1963, Newell & Boyd 1995), the type species of *Cyrtorostra*, has only one interspatial costa, and is much more prosogyrous, with less inflated right valve. Ribs are present on the right anterior auricle and a resilifer is well developed in type *Cyrtorostra*.

Few species ascribed to *Cyrtorostra* have more than one rib over the swollen interspaces between the primary ribs. *C. arctica* Logan (1970) from the Assistance Formation of Roadian (mid-Permian) age on Devon Island, Arctic Canada, is an exception, and this species is also orthocrescent. Logan (1970) reported a shallow anteriorly directed resilifer below the beaks, even though one is not clearly visible in his figure (Logan 1970, pl. 122, fig. 3c). Unlike the present species, the right anterior auricle of the Canadian species has a strong costa. Some species ascribed to *Blanfordinia* Reed, 1944 from the Salt Range, India, have more than one interspatial rib, such as *B. trifurcata* Reed (1944, p. 315, pl. 55, fig. 10, 10a, 11, 11a) from the Wargal Limestone (Wuchiapingian, Late Permian) of Pakistan. The suite of species ascribed to *Blanfordinia* are procrescent like *Cyrtorostra* and probably congeneric with that genus, but the ligament is not revealed and the wings and anterior auricle obscure. *Oxytoma atavum* Waagen, 1881 from the Salt Range, nominated as type species of *Prooxytoma* Maslennikov, 1952, belongs to the same suite as *Blanfordinia*.

Superfamily **CHAENOCARDIOIDEA** Miller, 1889

Diagnosis: Shells biconvex, equivalve to slightly inequivalve with relatively small posterior wings in each valve as a rule. Right anterior auricle and byssal notch well developed. Ornament varies, coarse to fine, few genera plicate, ornament somewhat similar in general appearance on each valve as a rule, costae tend to increase by branching but implantation is also common, growth lines often arch ventrally in interspaces and hingewards over costae. Ligament external and amphidetic, alivincular, lativincular or platyvincular, some genera with few simple teeth.

Discussion: This is a superfamily of wide diversity, with a number of Early Carboniferous genera not previously recognised, to suggest that many Permian genera are relict or modified from earlier forms.

Classification: The classification of the family group is as follows:

Family Chaenocardiidae Miller, 1889
Family Streblochondriidae Newell, 1938
    Subfamily Streblochondriinae Newell, 1938
    Subfamily Guizhoupectininae Astafieva, 1994
    Subfamily Saturnellinae Astafieva, 1994
    Subfamily Streblopteriinae new
    Subfamily Orbiculopectininae Waterhouse, 2001
        Tribe Orbiculopectinini Waterhouse, 2001
        Tribe Eocamptonectini Waterhouse, 2001

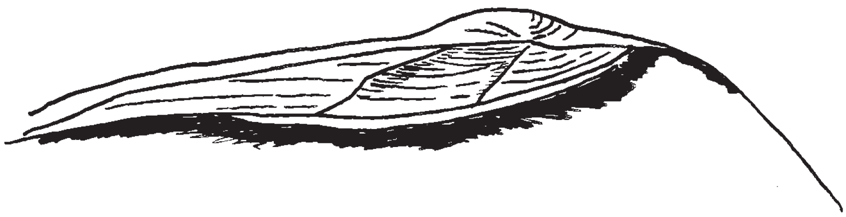
Evolution: Chaenocardioidea share with Deltopectinidae the short posterior wing of each valve and biconvex valves with somewhat comparable or identical ornament. Members are small, and much less strongly ornamented than most Deltopectinidae, or indeed most Aviculopectinidae, but do share an alivincular hinge with the latter family. The beginnings are not established: the fossil record indicates a Devonian age, and by Visean time genera and species were numerous. It is likely that Monotidina evolved from this superfamily, sharing some aspects of biconvexity and ornament, to suggest the possibility that nestling chaenocardioids lost the anterior wing and amphidetic ligament in Late Carboniferous or earliest Permian time.

Family **CHAENOCARDIIDAE** Miller, 1889

Text-fig. 47, 48

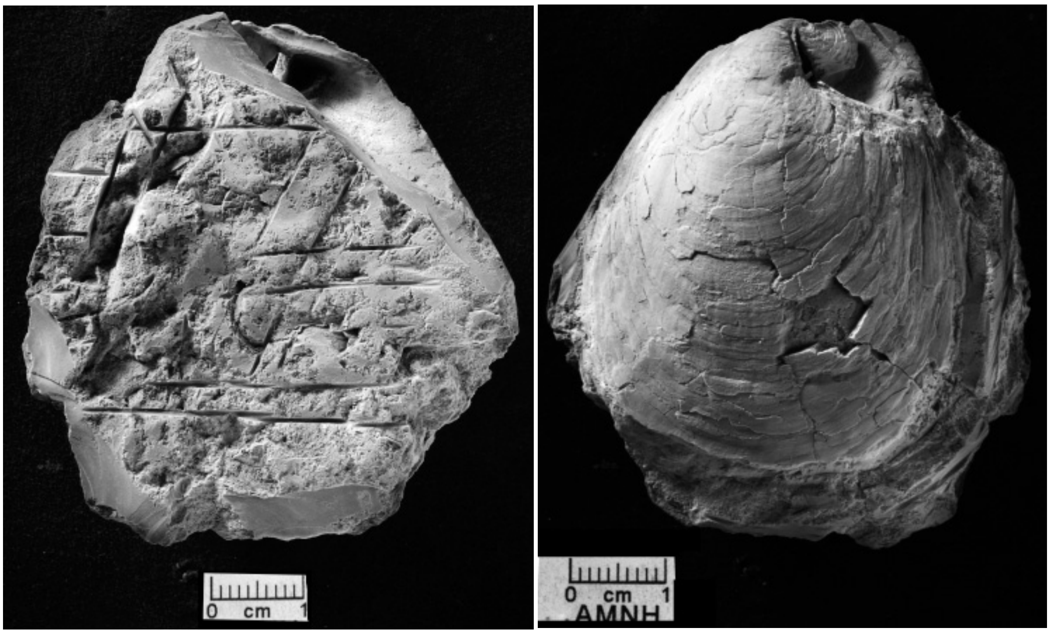
Diagnosis: Subequivalve little inflated comparatively smooth shells, hinge short, posterior wings small and right anterior auricle large, ligament asymmetrically amphidetic, simple tooth may be present.

Discussion: *Chaenocardia* Meek & Worthen, 1869 is a prosocrescent smooth gently biconvex shell with large anterior auricle, calcitic outer shell (Carter 1990), and short hinge, bearing a small left valve anterior tooth. It has been well figured by Newell & Boyd (1995, Fig. 55), and was described by them as having an opisthodetic, or almost opisthodetic, ligament. This is not substantiated by their illustrations. Their figure (55. 3a) was labelled as showing a socket in front of the umbo, yet this socket is marked by growth-grooves that clearly continue from the posterior hinge across a shallow resilifer. Since sockets do not have growth-grooves, their so-called "socket" must be part of the ligamental area, and the area clearly extends in front of the beak, so that the ligament is asymmetrically amphidetic, not opisthodetic. The same form of ligament is figured by Newell & Boyd (1995, Fig. 55.1a) for another left valve, and in both specimens the resilifer slopes back from



Text-fig. 47. *Chaenocardia ovata* (Meek & Worthen) left valve hinge with resilifer redrawn from Newell & Boyd (1995, Fig. 55.3a), x4. From Vanport Limestone, Ohio, kept at Chicago Field Museum.

under the tip of the umbo to the hinge. The figure of the right valve hinge in Newell & Boyd (1995, Fig. 55.5a) is more obscure: but the ligament appears to extend in front of the umbo. That is the implication from the figures, and confirmed by further specimens kept at the American Museum of Natural History, New York: the ligament is amphidetic, not opisthodetic, and *Chaenocardia* is a part of a small cluster of genera with asymmetrically amphidetic ligament and hinge tooth (Waterhouse 2001) that includes *Obliquipecten* Hind (Waterhouse 2001, p. 123). Newell & Boyd (1995) appear to have interpreted the genus as monotid in its affinities in so far as it was deemed to have an opisthodetic hinge. Given the presence of hinge teeth, *Chaenocardia* could prove to have been closely related to Eocamptonectini Waterhouse, 2001, which has slightly different hinge teeth, and short but more amphidetic hinge with wider resilifer and left valve anterior sinus, as discussed on p.108.



Text-fig. 48. *Chaenocardia ovata* (Meek & Worthen), right valve interior and exterior, AMNH 44054. From lower Pennsylvanian Blackthorn Asphalt Member, Atokan Formation, Oklahoma. Photographs supplied courtesy of B. M. Hussaini, American Museum of Natural History, New York. See Newell & Boyd (1995).

Chaenocardia and *Obliquipecten*, with *Endocostapecten* Feng, 1988 as a subgenus of the latter, were treated as members of Chaenocardiinae by Astafieva (1994). *Endacostapecten*, as described and figured by Feng (1988, pp. 634, 636, pl. 3, fig. 11-26) and based on *Streblochondria inequicostata* Yang & Chen (1985, pl. 3, fig. 4, 5) from Carboniferous beds of the Junggar Basin in China, is highly exceptional with internal ribbing and pits along the hinge, and its placement requires further study.

Family **STREBLOCHONDRIIDAE** Newell, 1938

Diagnosis: Shells biconvex, almost equivalve to inequivalve, slightly procrescent to orthocrescent as a rule, well defined umbonal slopes, posterior wings small, ornament variable. Short amphidetic alivincular ligament. Teeth rarely present.

Discussion: Newell & Boyd (1985) elevated Streblochondriinae to family level partly on the basis that the outer shell was fibrous on both valves, but this has not been established for all species, nor ruled out for genera and groups that were excluded by Newell & Boyd (1985) from the family (eg. *Chaenocardia* and *Saturnella* with allies). In shell so far studied, nacre is lacking, unlike primitive aviculopectens, and fibrous prisms are present in the outer shell (Carter 1990). Carter referred the family to Pectinoidea, a position which finds little support from gross morphology involving hinge, shape and ornament.

An extensive discussion by Astafieva (1994), although disparaged by Newell & Boyd (1995), recognized several subfamilies additional to Streblochondriinae, and new genera such as *Saturnella*. Newell & Boyd (1995) specified aspects in need of clarification in their dismissal of the work by a number of authors, especially those based on Chinese material. But in erecting various genera, Newell & Boyd (1995) failed to meet those specifications: they often did not describe shell structure or muscle field and other aspects for most of the pectinidian genera and species, including new taxa, that they recorded, and did not provide hinge-ligament data for several critical genera, and allowed considerable neglect of the nature of the right valve, following the lead set by Newell (1938) and endorsed by Yin (1982) with his extraordinary claim that the right valve was too rarely found to be taken into account. There is a degree of inconsistency in their rejection of genera described by other authors, because they excused themselves from the strictures levelled at other authors, and failed to apply the same criteria to their own work. Their own descriptions are highly useful, and their reiterated criticisms or neglect of other studies need not deflect from their own fine contributions.

Chaenocardiinae was incorporated by Astafieva (1994) and placed as family name-giver, following Waterhouse (1982). Several subfamilies were recognised for the family by Astafieva (1994) and Waterhouse (2001) and these are slightly rearranged in the present account, and regarded as belonging to Streblochondriidae. There appear to have been a number of evolving strands in Early Carboniferous faunas of Europe, and only some are formally named. The counter-argument, that evolution was erratic and diagnostic criteria highly variable and inconstant cannot be entirely gainsaid, but the way to establish such a possibility is through close attention to variations in order to unravel the lines of descent.

Subfamily **STREBLOCHONDRIINAE** Newell, 1938

Diagnosis: Ornament varied, hinge alivincular with small resilifer extended slightly outward, no teeth.

Genus ***Amleripecten*** new genus

Derivation: Named for M. R. W. Amler.

Type species: *Streblopteria praetenuis* Koenen, 1879, p. 329 from Kulm (Carboniferous) of Germany, here designated.

Diagnosis: Small shells, right valve ornamented by fine commarginal threads and narrow growth rugae with suggestions of fine filae over body of shell, becoming stronger and more persistent towards anterior margin, left valve ornamented by stronger radial costae over entire valve, increase by branching, commarginal growth lines subdued. Hinge short, posterior wings very small, right anterior auricle with one or more strong costae and weaker costae, byssal notch angular and well defined, left anterior wing large, well defined and weakly costate.

Discussion: This genus is distinguished by the strong difference in ornament on the two valves. It was described from the Kulm of Germany by Koenen (1879) and has been refigured by Amler (1994, Fig. 15, 16, 18, 19). Specimens were described from Aprath (cd 111α) of Germany by Rathmann & Amler (1992, p. 46, pl. 3, fig. 1, 3-10), clearly showing the disparate ornament of left valve close-set ribs and right valve concentrics. Notably in this material, the left valve anterior wing is strongly discriminated by the steep umbonal slope, and the posterior wing is short. The synonymy was discussed by Rathman & Amler (1992, pp. 446, 447).

Attributes of ornament in this genus suggest subfamilial differences from the other genera in Streblochondriinae.

Genus ***Concentiolineatus*** new genus

Text-fig. 49

Derivation: concentio - singing together; linea - linen thread, line, Lat.

Type species: *Streblopteria homevalensis* Waterhouse, 1986, p. 5, from Early Permian Tiverton Formation, Bowen Basin, Queensland, here designated.

Diagnosis: Weakly procrescent to slightly retrocrescent, anterior ears longer than or equal to posterior ears, both valves with concentric growth laminae, right anterior ear ribbed.

Discussion: The genus is not assigned to Saturnellinae Astafieva, because the concentric ornament is of laminae rather than rugae.

The nominated type species of this genus was originally referred to *Streblopteria* M'Coy, 1844, because, as in this genus, radial ornament was lacking, other than from the right anterior auricle. *Streblopteria* is based on *Meleagrina laevigata* M'Coy, 1851, p. 170, pl. 12, fig. 5, SD Meek & Worthen, 1866, p. 333. It is assumed that the ligament has a resilifer, as evaluated by Newell (1938, p. 88) and accepted by Amler (1994) and Waterhouse (1982, 2001, p. 126). M'Coy (1851) recorded a tooth in the hinge, but no such tooth was illustrated. Newell & Boyd (1995, Fig. 37) ascribed a Middle Permian species *Aviculopecten? montpelierensis* Girty to *Streblopteria*, and this species was referred to a separate and new genus *Strebloboydia* Waterhouse, 2001, p. 132, on the basis of age, differences in shape, including short posterior wings, and hinge. *Strebloboydia* has a tiny blunt right valve anterior tooth and left valve socket, and right valve auricular boss. The ligament is lativincular, so the genus is classed in Eocamptonectinii Waterhouse, 2001. The present species *homevalensis* has no hinge teeth, and approaches *Streblopteria laevigata* in showing fine but distinct concentric growth laminae over both valves, but differs in having a very much smaller and more clearly differentiated posterior wing, in contrast to the very large posterior wing developed on the left valve holotype of *laevigata* (see also Hind 1903, pl. 11, fig. 1-7, the type refigured in fig. 3). The large wing is a very distinctive feature of *Streblopteria*, and it appears, from examination of world-wide collections and literature, that the feature marks an unusual genus of limited geographic extent and time range. Possibly the long posterior wing was a throwback to, or persistence of, the long posterior wings characteristic of pterinopectens (see p. 35).

Several species of Early Carboniferous age close to *Concentiolineatus* were allocated by Amler (1994) to *Streblochondria,* such as *Pecten ellipticum* Phillips, 1836, pl. 6, fig. 15 (Amler 1994, Fig. 9) and doubtfully *Avicula sublobata* Phillips, 1836, pl. 6, fig. 25 (Amler 1994, Fig. 4, 5; Hind 1903, pl. 17, fig. 11-14), the latter species showing colour bands radiating from the right valve umbo. The original figure in Phillips (1836) suggests well spaced but fine radial costellae or even growth laminae, as in Hind (1903), not completely typical of *Redesdalia* (see p.102). The

Text-fig. 49. *Concentiolineatus homevalensis* (Waterhouse), holotype, right valve CPC 5177 from Early Permian (Sakmarian) Tiverton Formation, Queensland, x1. See Waterhouse (1987).

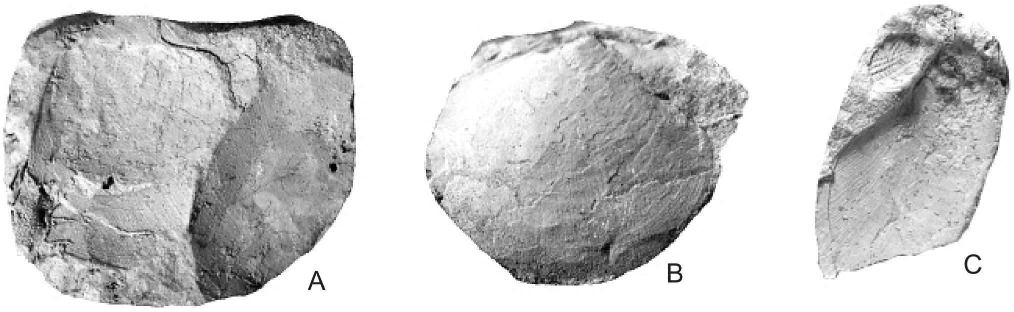
Early Carboniferous British species *Pecten deornatus* Phillips (1836, p. 213, pl. 6, fig. 26 – see Hind 1903, p. 100, pl. 18, fig. 10-14) - has fine concentric laminae as in the present genus, but shows moderate growth steps and possible radials as well.

The Late Carboniferous *Streblochondria granosostriata* Chao (1927, p. 41, pl. 2, fig. 17, 18) from China belongs to the genus. *Streblochondria regularis* Feng (1988, pl. 2, fig. 14-19, 21) from the middle to late Carboniferous Shiqiantan Formation of the Junggar Basin, China, is close and is extended anteriorly.

The poorly preserved Late Devonian species *Pleuronectites piltonensis* Whidborne (1897, p. 140, pl. 16, fig. 7-11) from the Pilton Formation of south England, is shown as smooth with costate right anterior auricle, and light commarginal ridges are suggested in pl. 16, fig. 11. The species was also figured from the Late Devonian of Velbert, west Germany, by Amler (1992, pl. 2, fig. 11-13) as *Streblopteria*. The so-named specimen from the Devonian of England shown by Amler (1994, Fig. 22) is apparently decorticated, and the right valve (Amler 1994, Fig. 20) obscure. Unlike *Streblopteria*, posterior wings are short. *Pleuronectites lepis* Whidborne (1897, p. 142, pl. 16, fig. 12, 13) shows commarginals on the left valve, and another ally was described as *P. hicksi* Whidborne (1897, p. 142, pl. 16, fig. 14).

The genus is widespread in Early Permian faunas of Gondwana. The east Australian species *Streblopteria biornata* Waterhouse (1987, pl. 6, fig. 3, 5, 8, pl. 14, fig. 2, 3) from the mid-Cisuralian (Sakmarian) Fairyland Formation of the southeast Bowen Basin, Queensland, has very fine auricular ribs, and is upright but longer and inflated. *S. minauris* Waterhouse (1987, pl. 7, fig. 2, 6-10, pl. 8, fig. 1, 3) from the upper Cisuralian (Kungurian) Brae Formation of the southeast Bowen Basin is somewhat rounded in outline and lacks auricular ribs.

Superficially the new genus approaches *Striochondria* Waterhouse, 1983b, which is characterized by very fine radial ribs (Text-fig. 50). *Striochondria* was dismissed as indecipherable by Newell & Boyd (1995) and as poorly preserved and no different from *Streblochondria* by Astafieva (1994). Such reports are misleading. The type species *Streblochondria auriocosta* Waterhouse was amply illustrated (Waterhouse 1982, pl. 13, fig. g, pl. 14, fig. c, e, f, pl. 15, fig. a-h, pl. 16, fig. h, pl. 21, fig. d, e, text-fig. 3) to show exquisitely fine radial filae (pl. 13, fig. g, pl. 14, fig. c, pl. 21, fig. e). These threads are far finer than those of *Streblochondria* at 4-8 in 1mm, compared with 1-2 per mm in *Streblochondria*. The only significant omission of the inaccurate concerns protested by Newell & Boyd (1995) is that shell structure has not been described for the



Text-fig. 50. *Striochondria auriocosta* (Waterhouse). A, left valve TM 3390, external mould. B, right valve OU 1378. C, external mould of right valve TM 3400. From early Middle Permian (Roadian) Letham Formation, New Zealand, x2. See Waterhouse (1982).

genus. The shell is present, and therefore available for description, but the muscle field remains unknown.

Striochondria is well represented in east Australia by such species as *S. engelhardti* (Etheridge & Dun), *S. auriocosta* (Waterhouse) and *S. erecta* (Waterhouse), of Middle Permian age, and is present in Argentina as *Streblochondria sueroi* Gonzalez (1969, pl. 1, fig. 10-15; Pagani 2005, Fig. 5A-H) from the Tepuel-Genoa Basin in Chubut. *Pecten undulosa* M'Coy, 1844, pl. 17, fig. 12 from the Early Carboniferous of Ireland has fine concentrics crossed by fine radial lirae, approaching those of *Striochondria* in the Permian of east Australia (Amler 1994, Fig. 11), but the ribs are stronger and spaced further apart, and concentric rugae are strong.

Genus ***Redesdalia*** new genus

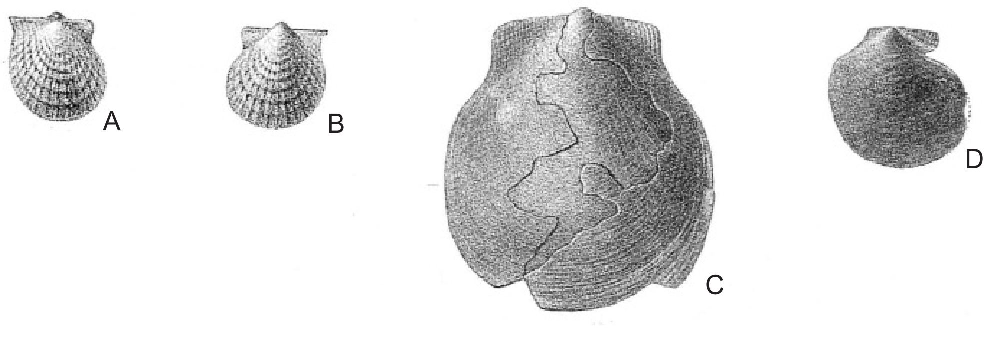
Text-fig. 51 C, D

Derivation: From Redesdale, north England, site of fossil species.

Type species: *Pseudamusium redesdalensis* Hind, 1903, p. 109 from Redesdale Ironstone, north England (Carboniferous), here designated.

Diagnosis: Little inflated biconvex inequilateral shells characterized by low inflation, weakly defined posterior wings, well formed right valve auricle and deep byssal notch, well rounded to oval outline, weak concentric ornament, well spaced subdued radial ornament variably present on especially left valve in some species.

Discussion: This genus is proposed for a number of species from the Early Carboniferous of England, Wales, Scotland and Ireland that are characterized by shape and ornament. *Streblochondria* Newell, 1938 is close, and distinguished by its stronger, denser and more regular ribbing, with greater inflation, better defined posterior wings, and less rounded more procrescent outline. Several Early Carboniferous species described from Ireland and United Kingdom belong to *Streblochondria*, including *Pecten planoclathratus* M'Coy (1844, p. 98, pl. 16, fig. 2). *Striochondria* Waterhouse, 1983b differs in similar ways, with fine close-set radial ribs. *Concentiolineatus* n. gen. is also allied, with no radial ornament except on the ears, and greater inflation, better defined posterior wings and less oval outline. *Streblopteria* M'Coy, 1851 lacks radial ribs over the shell



Text-fig. 51. A, B, *Tesselarulina nobilis* (Koninck), IRSNB a 4891, as figured by Koninck (1885, pl. 36, fig. 27, 28, 30) from Early Carboniferous of Belgium, x 0.9. C, *Redesdalia concentricolineatum* (Hind) as figured by Hind (1903, pl. 20, fig. 8), NHM left valve from Early Carboniferous of Castleton, England, x 0.9. D, *Redesdalia redesdalensis* (Hind) NHM right valve figured by Hind (1903, pl. 20, fig. 5) from Carboniferous Redesdale Ironstone, England, x 0.9.

other than the right anterior auricle, but is close in inflation and weakly defined posterior wings, which are unusually large.

The type species of *Redesdalia* was figured by Hind (1903, pl. 20, fig. 1-6) and the specimen figured by Hind (1903, pl. 20, fig. 5 – BNHM L47681) is here nominated as lectotype. The muscle field is visible in the Hind specimens: the upper third of the valves is smooth, and well spaced flat-topped radial ribs extend over the lower two thirds of the shell height, with traces of radial striae on some specimens. Ribs are present on the right anterior auricle. Amler (1994, Fig. 10) figured one of Hind's specimens that is less rounded and with stronger ribs than usual, and the left valve ribs fork but stay close to each other: branching is not clearly shown in Hind's figures. Various species are close in shape, and differ slightly in ornament, including *Pecten ellipticum* Phillips (1836, pl. 6, fig. 15; Hind 1903, p. 103, pl. 20, fig. 11-18), *P. gibbosum* M'Coy (1844, p. 93, pl. 18, fig. 5; Hind 1903, p. 106, pl. 21, fig. 12), *Avicula fibrillosum* Salter (1864, p. 65, pl. 1, fig. 2; Hind 1903, p. 106, pl. 16, fig. 16-22; Amler 1994, fig. 17), and *Pecten anisotum* Phillips (1836, p. 212, pl. 6, fig. 22; Hind 1903, p. 104, pl. 21, fig. 13-20; Amler 1994, fig. 7). *Pseudamusium concentricolineatus* Hind (1903, p. 111, pl. 20, fig. 7-10) has posterior wings of modest size, ribbed anterior auricle and low concentric laminae, and the shape and rare presence of low ribs suggest possible alliance with *Redesdalia*.

Pseudamusium simplex Dawson as figured by Bell (1929, p. 167, pl. 28, fig. 13-18) from the Early Carboniferous Horton Windsor Group of Nova Scotia, Canada, is apparently congeneric, and some Pennsylvanian species from United States seem to be closely allied, such as *Streblopteria oklahomensis* Newell (1938, pl. 14, fig. 8-12).

Newell (1938, p. 114) recorded several of the British and Irish species now included in the new form as "unresolved", confirming that in his view the species now placed in *Redesdalia* n. gen. differed or at least might differ from *Streblochondria* or *Streblopteria*.

Subfamily **GUIZHOUPECTININAE** Astafieva, 1994

Diagnosis: Medium-size equivalve shells, smooth or with comparatively strong ribs or plicae on both valves.

Discussion: Guizhoupectininae was distinguished because of the presence of intercalated ribs on the left valve and branching ribs on the right valve. *Guizhoupecten* Chen is a Permian genus from China and has been described from United States and Queensland by Newell & Boyd (1995) and Waterhouse (1987). Carboniferous genera from China were associated with the subfamily by Astafieva (1994), including *Xinjiangopecten* Yang & Chen, 1985, p. 381, type species *X. isocostatus* Yang & Chen 1985, pl. 3, fig. 9-15. This has ribs stronger than in *Streblochondria*, and stated to be intercalated in the left valve, with narrow interspaces, and the right valve is weakly inflated, and has similar but branching ribs. *Junggarochondria* Yang & Chen, 1985, p. 382, type species *J. xinjiangensis* Yang & Chen, 1985, pl. 3, fig. 8a-c is very inflated with thick ribs, small anterior right auricle and very small posterior wings, intercalate left valve ribs and branching right valve ribs. Another species was described as *J. inaequicostata* Yang & Chen (1985, pl. 3, fig. 4, 5), and the authors included *Avicula sublobata* Phillips, 1836 in the genus, pointing to specimens figured by Hind (1903, especially pl. 17, fig. 11), which has stronger ribbing than on the other illustrated specimens (Hind 1903, pl. 17, fig. 12-14). The species referred to *Junggarochondria* have a short hinge, and because the ligament area has not been illustrated, the relationship to Chaenocardiidae requires examination.

Astafieva (1994) tentatively included *Tianshanopecten* Feng (1988, pl. 2, fig. 1, 2, 6, 7) with numerous intercalated costae. This genus should be excluded – it is possibly etheripectinid, of small size, long posterior wings and strong but comparatively fine and diverse intercalated ribs, but the right valve is not known, rendering any further interpretation very difficult.

The development of strong radial ribs or even plicae is a striking feature, which may be of more practical use as a subfamilial discriminant than the mode of rib increase. In material with very fine ribbing, it becomes very difficult to clearly discern the mode of increase. Moreover in some shells the ribs increase by branching and by intercalation, and in *Guizhoupecten filae* Waterhouse (1987) from the mid-Permian Flat Top Formation of Bowen Basin, Queensland, or *G. cheni* Newell & Boyd (1995) from Guadalupian faunas of Texas, the ribs seldom increase in number, so that there is little or no branching.

Subfamily **SATURNELLINAE** Astafieva, 1994

Diagnosis: Distinguished by ornament of strong commarginal rugae, radial ornament absent or very faintly developed over body of shell, and stronger over right anterior auricle in some species.

Discussion. This subfamily is based on *Saturnella* Astafieva, a genus and species of Early Permian age in Mongolia. Astafieva (1994) considered that *Saturnella* or ally was derived from *Posidonia*, by retention into maturity of the byssal notch that was developed only in early growth stages of *Posidonia*, and gave rise to other members of the Streblochondriidae. Given the large number of streblochondriid genera and species in the Early Carboniferous, and rare Devonian occurrences, it has to be said that the fossil record does not support that hypothesis, and the differences in right anterior ear, byssal notch and also presence of two adductor scars in *Posidonia* suggest that *Posidonia* is pteriiform, and *Saturnella* aviculopectiniform. Low and regular growth rugae developed in a number of costate streblochondriid species, so that the subfamily stock may have been derived through suppression of ribbing, since ribbed forms were more common than rugose species without ribs. But no precise time can be pinpointed.

Genus ***Astafievina*** new genus

Text-fig. 52

Derivation: Named for M. M. Astafieva.

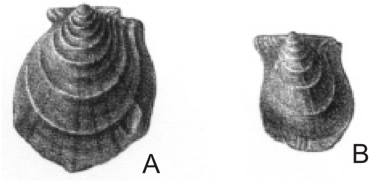
Type species: *Pecten sedgwicki* M'Coy, 1844, p. 99, from Early Carboniferous of Ireland, here designated.

Diagnosis: Characterized by few strong and concentric rugae on both valves, no strong radial ornament, right anterior auricle ribbed. Monomyarian, ligament alivincular.

Discussion: This genus comes from Early Carboniferous faunas of Ireland and England, and is characterized by its ornament of well spaced concentric ornament. *Posidonia* Bronn has much more regular and more closely spaced concentric rugae or flanges and lacks a byssal notch at maturity, or well formed right anterior auricle, whereas such is well shown by the holotype (through monotypy) from Little Island, Cork, of *Pecten sedgwicki*, as figured by M'Coy (1844, pl. 14, fig. 4 – NMING F 7410A, B) and further illustrated by Hind (1903, p. 101, pl. 16, fig. 28-33). The wings of the left valve are moderately prominent with deep sinus. Possibly the genus is related to or precursor to Annuliconchidae, but that requires further study and better stratigraphic control for species of *Astafievina* and Annuliconchidae. It is judged to be streblochondriid because ornament is similar on each valve.

The new genus is close in most respects to *Saturnella*, type species *S. aenigmata* Astafieva, 1994, p. 19 from Lower Permian rocks of Mongolia. This species is orthocrescent and further distinguished by the comparatively large right anterior auricle, which is costate. The species *Pecten auriculatum* M'Coy, 1844, p. 77, pl. 19, fig 5, also figured by Hind (1903, pl. 16, fig. 23-26), from Early Carboniferous of Ireland was deemed to be congeneric by Astafieva. Although

Text-fig. 52. *Astafievina sedgwicki* (M'Coy). A, B, NHM left valves as figured by Hind (1903, pl. 16, fig. 28, 29) from Early Carboniferous at Little Island, Cork, Ireland, and Narrowdale, Staffordshire, England, x1.



the right anterior auricle of M'Coy's species was said to be smooth by Hind (1903), the specimens figured by Hind (1903, pl. 16, fig. 23, and fig. 30-32 - NHM L24564) show ribs. Apart from the concentric rugae, the shell surface appears to be smooth, although M'Coy (1844, p. 88) noted the presence of very fine radial striae. Hind (1903) regarded *Pecten cingendus* M'Coy (1844, p. 90, pl. 17, fig. 11) as allied, and this has more closely spaced concentric rugae as in type *Saturnella*, and an unusually long posterior wing. Hind also regarded *Aviculopecten concentricocostatus* Koninck (1885, p. 237, pl. 31, fig. 6, 7, pl. 41, fig. 28-33) as possibly allied, but its generic position requires further study, and a right anterior auricle is not clearly figured.

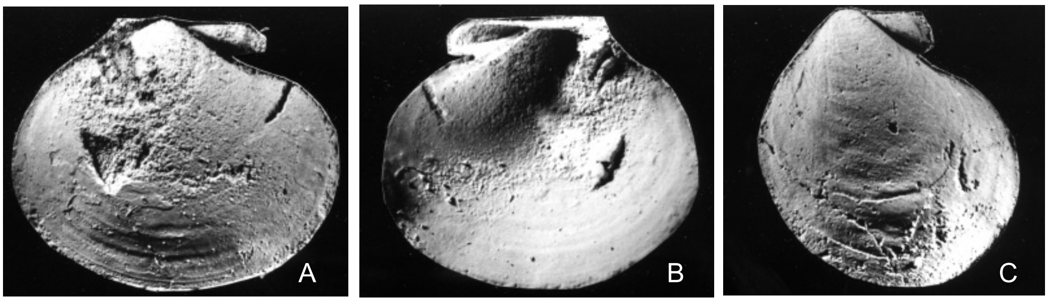
Genus ***Montorbicula*** new genus

Text-fig. 53

Derivation: mont - from montgomeryi, specific name; orbis – circle, Lat.

Type species: *Streblopteria montgomeryi* Gonzalez, 2006, p. 140 from Early Permian faunas of Patagonia, here designated.

Diagnosis: Suborbicular shells with fine commarginal wrinkles closely spaced on both valves, forming flanges close to the ventral margin, right anterior auricle and wings smooth, hinge platyvincular.



Text-fig. 53. *Montorbicula montgomeryi* (Gonzalez). A, right valve holotype, IPI 3758. B, interior of same specimen. C, right valve IPI 3786. From the Early Permian (Asselian) of Patagonia, as figured by Gonzalez (2006, Fig. 8), x 1.8. Photographs supplied by C. R. Gonzalez, Tucuman.

Discussion: *Streblopteria montgomeryi* Gonzalez (2006, p. 140, Fig. 8) from the Early Permian of Patagonia lacks auricular ribs and has a moderately deep byssal notch, and low commarginal rugae that are slightly irregular and apparently in two orders on the left valve. It lacks a resilifer, the area being described as triangular with posterior margin meeting the posterior dorsal margin at an obtuse angle. The lack of a well formed resilifer in the species *montgomeryi* Gonzalez matches aspects of the hinge in other aviculopectens, such as *Squamuliferipecten*, *Corrugopecten, Elviniaria, Calcicanicularia* and *Lionicula*, and such a ligament presumably arose independently in different groups, reinforcing the conclusion by Yonge (1978) that divergences appeared independently, parallel and reiteratively in different groups of Bivalvia. *Saturnella* Astafieva is close in appearance, but has resilifer and ribbed right anterior auricle and more regular and stronger concentrics especially on the left valve, and *Astafievina* n. gen. also has a resilifer and ribbed right anterior auricle, and is further distinguished by its coarse and higher but narrower well spaced concentric rugae.

Subfamily **STREBLOPTERIINAE** new subfamily

Name genus: *Streblopteria* M'Coy, 1851, p. 170 from Lower Carboniferous of Ireland, here designated.

Diagnosis: Distinguished by very long posterior wings and gentle umbonal slopes.

Discussion: Most chaenocardioids have very short posterior wings. At least two genera are exceptional, and are discriminated. *Streblopteria* was well figured as *Eumicrotis hemisphaericus* (Phillips, 1836, p. 212, pl. 6, fig. 16) by Hind (1903, pl. 7, fig. 1-6), as well as a further study of the type species *Meleagrina laevigata* M'Coy (1844, p. 80, pl. 12, fig. 5) by Hind (1903, p. 48, pl. 11, fig. 1-7). It has very light concentric wrinkles and rugae and is moderately inflated. A tooth was reported by M'Coy (1851, p. 170), but was doubted by Newell (1938, p. 88) and dismissed by Wilson (1962, p. 70). *Aviculopecten ornatus* Etheridge, 1873, p. 346, pl. 12, fig. 2 from the Lower Limestone Group, Scottish Midland Valley (P2 to basal E2) is also close to *Streblopteria*, but has very fine flexuous anterior striae (Wilson 1962, p. 70, pl. 5, fig. 18, 19). Several Belgium species were assigned to *Streblopteria* by Koninck (1885), but need revision.

Genus ***Tesselarulina*** new genus

Text-fig. 51A, B, 54

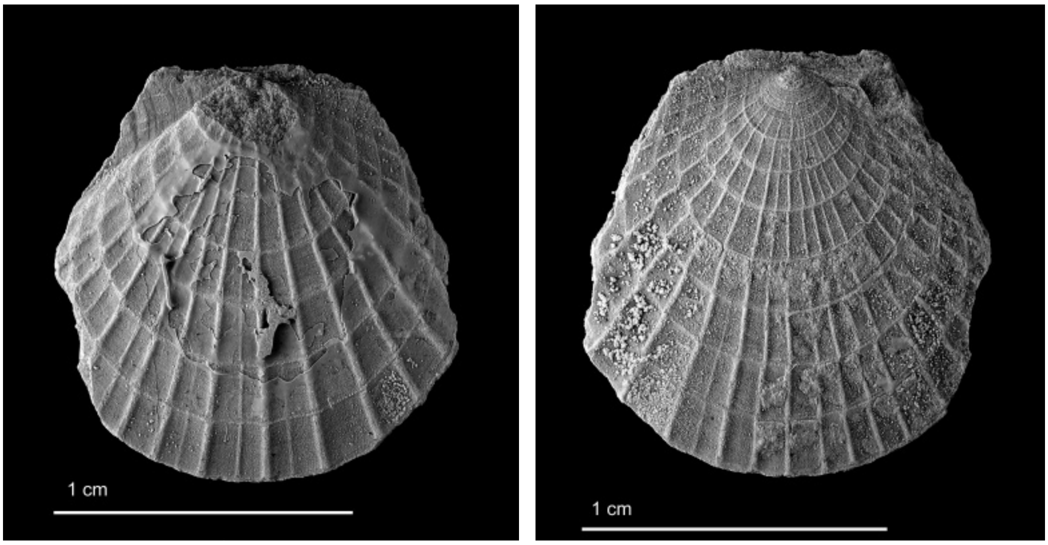
Derivation: tesserula – square paving stone, Lat.

Type species: *Aviculopecten wasserfallensis* Paul, 1937, p. 95 from Early Carboniferous of Germany, here designated.

Diagnosis: Shells characterized by lattice work of strong well-spaced costae crossed by strong well spaced concentric ridges on both valves. Posterior wings long and large.

Discussion: This genus is highly distinctive because of its ornament and shape. It is biconvex like members of Chaenocardioidea with short low posterior umbonal walls, well developed right anterior auricle and byssal notch, long anterior left valve wing, and firm radial ribs, including intercalated secondaries, slightly noded at intersections with the strong well spaced concentric ribs. The posterior wings are much longer than in most members of Chaenocardioidea. In shape the form is therefore very close to *Streblopteria* M'Coy, and this genus differs in being comparatively smooth.

Aviculopecten wasserfallensis Paul, 1937, pl. 33, fig. 25, 26, pl. 36, fig. 29 was described from the Richrather Limestone of Velbert, Bergisches Land, Germany. Paul (1941, p. 216) reassessed the genus as *Aviculopecten* (*Girtypecten*), and Richter & Amler (1994, p. 117, pl. 2, fig. 7-11, the type refigured as fig. 9 –BGR 6610) treated the species as a member of ?*Girtypecten*. The Permian genus *Girtypecten* Newell, 1938 has somewhat similar ornament on the left valve, apart from the development of large spines at the intersections of concentric and radial ribs, but the shape is etheripectinid, and its right valve is less ornate and much less inflated (p. 150) than the left valve, whereas the right valve ornament agrees with that of the left in the new genus. An upper Devonian Bergisches Land left valve figured as *Aviculopecten halli* (Whidborne) by Amler et al. (1990, p. 50, pl. 3, fig. 6) has a shorter hinge and subdued concentrics forming small nodes over the radial ribs: it appears to be congeneric. The original figures for *Pterinopecten hallii* in



Text-fig. 54. *Tesselarulina nobilis* (Koninck), IRSNB a 4891, left and right valves, supposedly as figured by Koninck (1885, pl. 36, fig. 27, 28, 30) from Early Carboniferous of Belgium; possibly holotype as figured by Koninck (1842) – compare with Text-fig. 51A, B. Photographs courtesy of Annelise Folie, Royal Belgium Institute of Natural Science.

Whidborne (1897, p. 134, pl. 15, fig. 2-6) are not so convincing and the material needs closer study.

From the Early Carboniferous of Belgium, *Pecten nobilis* is congeneric. The holotype by monotypy has been figured by Koninck (1842, pl. 3, fig. 21) and other individuals figured as *Aviculopecten* by Koninck (1885, p. 217, pl. 36, fig. 27, 28, 30 – IRSNB a 4891). This latter was figured to look like a streblochondriid or aviculopectinid genus by Koninck (1885), but the actual specimen is of different appearance with longer hinge and less clearly defined wings (cf. Fig. 51A, B, 54). From England, Hind (1903, p. 90, pl. 16, fig. 1-6) illustrated specimens with long hinge (pl. 16, fig. 1-3 - CASM E 718, CASM E 719) and very tiny specimens with short wings (pl. 16, fig. 4-6 - CASM E 722, CASM E 723). Hind (1903) considered that *Pecten cancellatum* M'Coy (1844, p. 89, pl. 14, fig. 9), *P. aequalis* M'Coy (1844, p. 89, pl. 15, fig. 13) and *P. cognatus* M'Coy (1844, p. 90, pl. 19, fig. 4) were conspecific. However *cancellatum* is illustrated as distinctive with stronger left valve ribs noded at intersections, and moderate but not very large posterior wing, suggestive of a different species and genus. *P. cognatus* appears to be congeneric and possibly conspecific, together with *P. aequalis*. *Aviculopecten fimbriatus* Hind (1903, p. 93, pl. 12, fig. 12, 13) from Early Carboniferous of England is congeneric. Other similar if not conspecific forms include *Pecten forbesi* M'Coy (1844, p. 93, pl. 15, fig. 20 - see Richter & Amler 1994, pl. 2, fig. 4) from Ireland and Germany, and *Aviculopecten blandus* Koninck (1885, p. 216, pl. 33, fig. 25, 26, pl. 36, fig. 29) from Belgium.

Pterinopectiniform shells characterized by tesselate pattern formed on both valves by strong and well spaced radial costae crossed by well spaced well defined concentric ribs are named *Tesseratia* n. gen. (see p. 49), which is represented in the Early Carboniferous of Britain by *Avicula tessellata* Phillips (1836, pl. 6, fig. 6). The ornament is close to that of *Tesselarulina* gen. nov., but the genus is pterinopectiniform with very long hinge, whereas *Tesselarulina* is more streblopteriin in shape and hinge.

Subfamily **ORBICULOPECTININAE** Waterhouse, 2001

Text-fig. 55

Diagnosis: Small suborbicular procrescent shells with long right anterior auricle, short hinge, longer in front of beaks than behind, ligament platyvincular or lativincular.

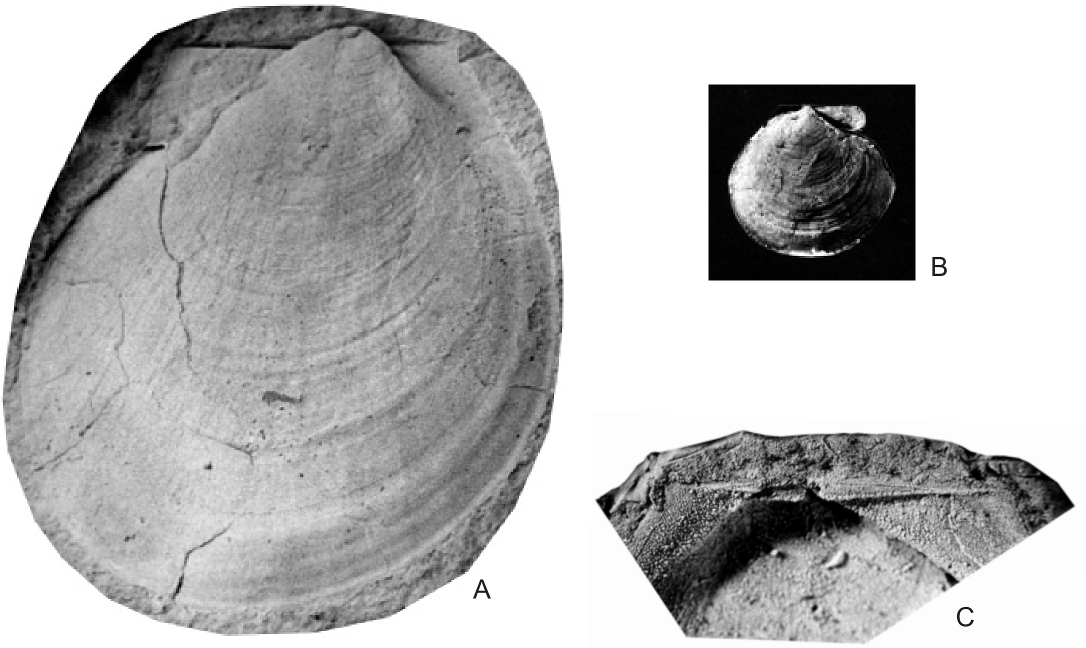
Tribe **ORBICULIPECTININI** Waterhouse, 2001

Diagnosis: Shells with lativincular or platyvincular ligament edged in front and behind by bourrelets, no hinge teeth.

Discussion: *Orbiculopecten* Gonzalez was referred by Gonzalez (1978) and Waterhouse (2001) to Deltopectinidae because of its lativincular ligament and biconvex valves with short posterior wings, but the shape of the genus seems more like that of Streblochondriidae. The tribe is from present knowledge limited to the Carboniferous *Levipustula levis* Zone or equivalents of Argentina and east Australia, and is characterized by a lativincular or platyvincular hinge, as treated in Waterhouse (2001). *Orbiculopecten* Gonzalez displays very fine filae with delicate spinose projections, whereas *Lionicula* Waterhouse, 2001 has much sturdier costae, with increase mostly by intercalation for both genera. The ligament is lativincular for *Orbiculopecten* and platyvincular for *Lionicula*. It is possible that each arose arose independently from streblochondriid species by dispensing with a resilifer, rather than radiate from a point source, perhaps in response to cool climatic conditions, so that the aggregating of genera with such hinges constitutes an interpretation to be tested.

Tribe **EOCAMPTONECTINI** Waterhouse, 2001

Diagnosis: Small shells with lativincular ligament and bordering areas, short behind the umbones, teeth and sockets present.



Text-fig. 55. *Orbiculopecten parma* Gonzalez. A, left valve PIL 11510, x3. B, holotype right valve PIL 11507, x 0.5. C, interior of left valve PIL 11509, x4. Specimens from Pampas de Tepuel Group, Chubut, Argentina. Photographs supplied by C. R. Gonzalez, Tucuman. See Gonzalez (1978).

Discussion: In the presence of teeth and wide resilifer the members of this tribe approach *Chaenocardia*, but have a more symmetrical amphidetic hinge with wider resilifer. Genera were all of paleotropical distribution, and include Permian forms *Eocamptonectes* Newell, *Strebloboydia* Waterhouse and *Pectengonzalez* Waterhouse. *Eocamptonectes* has left valve teeth and right valve sockets, *Strebloboydia* has a right valve tooth and knob, and *Pectengonzalez* has right valve tooth and socket anteriorly, and left valve tooth and socket. In these respects, there is some approach to *Chaenocardia,* and arguably they should be considered as a Permian subfamily descended from *Obliquipecten* Hind and *Chaenocardia* Miller.

Incerte sedis

Family **BINIPECTINIDAE** Feng & Liu, 1990

A very poorly known group called Binipectinidae Feng & Liu, 1990, based on *Binipecten* Feng & Liu, is streblochondriid in shape and ornamented by radial ribs. The hinge is exceptional, alivincular in juveniles, and with two triangular resilifers and ventral groove in adult shells. Only right valves were described, and Astafieva (1994) considered that the family could not be adequately interpreted without further information.

Suborder Monotidina Waterhouse, 2001

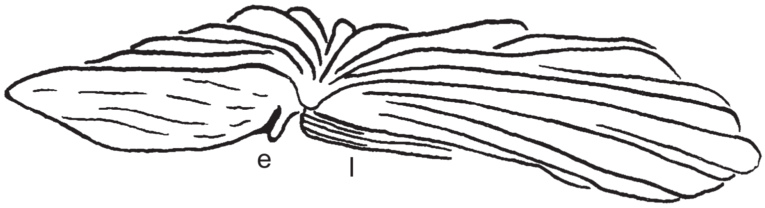
Text-fig. 56 - 58

Diagnosis: Shells with ligament opisthodetic or largely opisthodetic, anteriorly placed umbones and procrescent symmetry. Often inequivalve, may have well defined to little or no radial ornament, monomyarian. Right anterior ear poorly to generally well developed, together with left anterior wing if present placed in front of and below the ligament.

Text-fig. 56. *Monotis ochotica*, figured by Mojsisovics (1886, pl. 18, fig. 9), called var. *densistriata*, from Verchoyan, east Siberia, x1.

Discussion: Bøggild (1930, p. 260) showed that the outer shell in *Monotis salinaria* was composed of homogeneous calcite, lacking any distinct structure, and Carter (1990) reported foliate structure. Ando (1987, pl. 3) illustrated a number of *Monotis* shells, valve not known, with thick prismatic layers and Bøggild (1930, p. 260) reported regular prismatic structure in *Monotis substriata.* Carter (1990, p. 248) stated that *Monotis* lacks simple calcitic prisms from the outer right valve, unlike many aviculopectens, oxytomids, *Asoella, Pseudomonotis* or *Claraia*.

For a time, confusion prevailed in the classification of Mesozoic pteriomorphs. Virtually all pectiniform families other than pectens and limids were referred to an all-encompassing "Buchiacea" – including Monotidae, Oxytomidae, and various Mesozoic genera assigned in the Treatise to Aviculopectinidae, and this was accepted by many paleontologists. Those who had proposed other solutions were criticised or ignored, and it seemed that the age alone indicated the superfamilial position. Not even the code for zoological nomenclature was regarded – for Buchiacea did not have the priority enjoyed by Monotidae. Mesozoic pteriomorphs have to be analysed as closely as those of Paleozoic and Cenozoic age, and should be arranged according to morphological evidence in natural groupings.

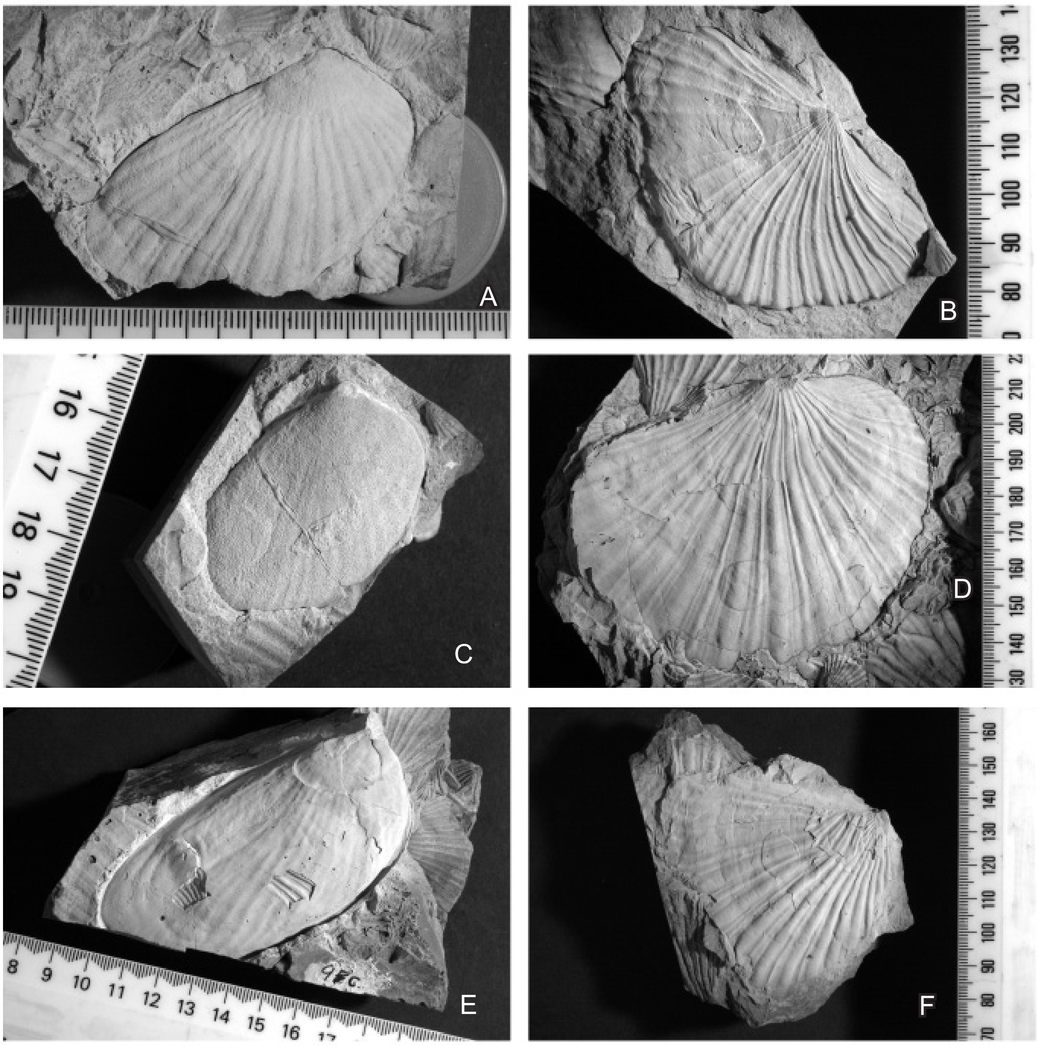


Text-fig. 57. *Monotis ochotica ochotica* (Keyserling), right valve redrawn from Ando (1987, Fig. 27), showing small anterior ear e in front of opisthodetic ligament l. Upper Triassic of Japan.

What discriminates Buchiidae, together with Monotidae and the Permian ancestors Dolponellidae and Eurydesmidae is that the ligament, often truncavincular, stops at the anterior end of the umbo. The dorsal anterior shell does not carry the anterior ligament, and a resilifer, if present, may commence under the umbo at the anterior edge of the ligament, instead of lying near mid-length, as in alivincular forms. The anterior shell thus differs substantially from that of Aviculopectinidina in lacking the large anterior wing and auricle, with ligament extending well in front of the umbones.

Starobogatov (1992) regarded Buchioidea as a member of infraorder Aviculopectinoinei, together with Posidonioidea Frech, Aviculopectinoidea Meek & Hayden and Euchondrioidea Newell. Here Posidonioidea is classed as Pteriida, and Buchioidea – which should possibly be replaced by Eurydesmoidea – in Monotidina. The opisthodetic as opposed to amphidetic nature of the ligament was regarded as of limited importance by Starobogatov, but the ligament for Monotidina is in harmony with other characteristics of gross morphology that help distinguish the suborder, and there is considerable difference between shells in which the ligament traverses the inner side of the anterior wings or auricles (Pterinopectinida, Pectinida, Aviculopectinidina, Limidina, Ostreida), and shells in which the anterior wing or auricle lies in front of and below the ligament, as is the case to varying degree in Monotidina.

There has to be some question about the relationship to aviculopectens, because the monotid ligament is so different in position, and is suggestive in some respects of the ligament in Ambonychioidea. There are essentially two arrangements between the anterior dorsal shell and ligament in shells classed as Monotidina. In one group Eurydesmatoidea, which includes *Eurydesma, Krumbeckiella*, *Frigidusia* n. gen., and at least some species identified as *Mysidiella*, the ligament stops virtually under the umbo (*Eurydesma, Mysidiella*), or extends very slightly beyond the umbo (*Krumbeckiella*?, *Frigidusia*) and lies in turn above a small to large internal shelf, sited below the commissure. There is little in the way of auricular development in any of these genera, but there may be a small anterior projection beyond the umbo in each valve, and this projection contains the internal shelf, and it may contain the short anterior end of the ligament, as illustrated by Krumbeck (1924) for *Krumbeckiella.* The shelf is believed to represent the inner auricle and anterior wing below the ligament in Aviculopectinidina. In *Eurydesma* the ligament is compressed below the umbo, and in *Frigidusia* a resilifer is present and extends slightly in front of the umbo. In *Monotis* and *Buchia,* the anterior right ear is more distinctive, and it lies entirely below and in front of the ligament, and involves the equivalent of the internal shelf. There is no left valve anterior wing or ear. The arrangement is especially well displayed in the Triassic genus *Hokonuia* Trechmann, in which the right anterior ear is very large, and projects into the body cavity, below the anterior end of the ligament, as figured by Waterhouse (1960, Fig. 25, text-fig. 2; repeated by Cox 1969e, Fig. C96. 4c,d). Clearly, a ligament along the right valve ear could have played no role in opening and closing of valves. In *Monotis*, the right anterior ear is tiny, yet may



Text-fig. 58. *Monotis* right valves, showing posterior muscle scar. A, *Monotis (Entomonotis) richmondiana* Zittel, AU 1445. B, *Monotis (Maorimonotis) maniapotoi* Grant-Mackie, AU 3027. C, *M. (Maorimonotis) routhieri* Grant-Mackie, AU 3025. D, *Monotis (Maorimonotis) maniapotoi* Grant-Mackie, AU 1725. E, *M. (Maorimonotis) routhieri* Grant-Mackie, AU 1789. F, *M. (Maorimonotis) awakinoensis* Grant-Mackie, AU 1878. Specimens from Upper Triassic of south Auckland. Photographs provided by J. M. Grant-Mackie, University of Auckland. See Grant-Mackie (1978a-c).

have a tooth-comb or pseudoctenolium, but there is none in *Maorimonotis* Grant-Mackie, 1978a. In Dolponellidae, there is a well-formed right anterior ear, and the ligament stops under the umbo. An exceptional arrangement has been figured for *Monotis ochotica* and *M. ochotica pachypleura* as identified by Nakazawa (1963, pl. 1, fig. 1-5), in which sketched reconstructions show the ligament as extending well in front of the resilifer in both valves and along the anterior auricle of the right valve. One photograph (pl. 1, fig. 3) appears to confirm Nakazawa's observation. This is completely at variance with the figures and specimens of monotids inspected in collections, and was not verified by the monograph of Japanese *Monotis* by Ando (1987). Whether the specimens are sports, or belong to a completely different genus and family, which judged from the figures seems likely, given the length of the right anterior auricle, will require inspection of the material.

The muscle scars are not entirely like those of Pectinida, Pterinopectinidina or Aviculopectinidina. In Monotidae they form a small postero-ventrally placed subrounded scar (Grant-Mackie 1978a, Fig. 20; 1978c, Fig. 53).

Eurydesmatoidea and Monotoidea are provisionally treated as allies, with the presumption that Monotoidea evolved from Eurydesmatoidea through specialization of a right anterior auricle from the shell underlying the anterior ligament, and reduction and compression of the ligament area. But differences in what is known of shell structure and muscle field indicate that the two could have arosen independently or diverged very early in their history. The "ideal" progenitor would seem to have been a biconvex, possibly byssally attached form with light radial ornament that became attached anterior face down on the substrate, to the extent that the anterior wing and auricle became redundant and largely lost. Aviculopectinid or especially chaenocardioid stock may have been involved, because these have the requisite basic shape and ornament and symmetry and attachment mode, and some even lost their resilifer. Within rare *Eurydesma*, the resilifer is present, and instead of being in the middle of the ligament area, is truncavincular, jammed against the anterior edge (Text-fig. 59A). *Chaenocardia*, as implied by Newell & Boyd (1995), approaches *Eurydesma* in having a subequivalved smooth shell with asymmetrically amphidetic ligament, and reduced posterior wings. That is not far from *Eurydesma*. The right valve has a tiny triangular tooth just below the anterior ligament in front of the umbo, on a slender shelf, and an obscure left valve tooth was reported by Newell & Boyd (1995). *Dolponella*, a Permian monotoid genus, is biconvex, lacks teeth and has long right anterior ear, and fine radial ornament. It is thus closer to streblochondriid genera apart from the opisthodetic and platyvincular ligament. So there is some evidence for two streams, lumped as Monotidina.

It may be considered that a limoid source is possible, because the hinge is short in these bivalves, and some are known to lack a resilifer, and have obsolescent or no anterior wings. The ostracum in limids consists of outer calcite and middle and inner layers of non-nacreous calcite, and adductor complex tends to lie towards the anterior, whereas it is posteriorly sited in *Eurydesma*, and given these and other differences, a close relationship is most unlikely.

A different account of monotid relationships was presented by Waller (1998, p. 29), in which they were deemed to have been part of Ostreida. Oxytomidae were included as monotid, quoting Begg & Campbell (1985). Waller (1998) claimed that monotids had sourced from pseudomonotids, on the basis that Newell & Boyd (1989) had demonstrated the presence of increasing calcite in a pseudomonotid species from Western Australia. It should not be overlooked that the presence of calcite in pectiniform shells had earlier been demonstrated by Dickins (1957) and Waterhouse (1982, pp. 10-13) for a much wider range of etheripectinids and deltopectinids in high paleolatitude faunas of Australia and New Zealand. Such observations reinforced the report by Dodd (1964) that the amount of calcite increases in *Mytilus* towards higher latitudes. Shell composition in pseudomonotids seems to offer no particular support for a relationship to monotids, and a relationship source must depend on other parameters. None are strikingly similar between pseudomonotids and monotids, and the great differences in shell shape (biconvexity, anterior hinge, resilifer) do not encourage a pseudomonotid source on further consideration. Moreover the dentition in the pseudomonotoid family Hunanopectinidae Yin is different from that of *Eurydesma*. It could be hypothesized that Pegmavalvulinae provided root stock, but members of this subfamily are not widespread and are not known before Permian times. Waller (1978, 1998) noted that the byssal notch widened distally rather than proximally as a pointer to linking pseudomonotids with monotids, but a number of pseudomonotids have proximal enlargement of the byssal notch, and the notch in various Aviculopectidina approach the sort displayed by monotids.

There are gross similarities to members of the Ambonychiidae, as monographed by Pojeta (1966). In these forms the shell is equivalve, inequilateral, with opisthodetic hinge, and typically deep grooves indicative of a lineavincular ligament. Anteriorly, a small internal plate with one or simple teeth is developed, and a byssal gape may be developed in both valves. The posterior adductor complex is comparatively small, with dorsal and ventral subdivision, and an anterior adductor may be developed. As a rule, prismatic structure is present in the shell. The similarities between ambonychiids and *Eurydesma* may be regarded as reflecting convergence, or as reversionary from aviculopectinoid stock. As a possibility here deemed to be remote, *Eurydesma* reflected a drastic approach in some aspects from ambonychiiform stock towards fringe members of Aviculopectinoida. The difficulty is finding an explanation for why there should have been such approach, given the very great difference in overall shell shape of ambonychiids from most aviculopectens, with their less inflated and more ornamented valves and much more developed anterior shell. It seems easier to visualize a change of shape and habitat by convergence with ambonychiids in stock that retained aspects of pectiniform ancestry in muscle scars and relict anterior ear-wing.

Johnston & Collom (1998) grouped a number of monotoid and other families in Superfamily Inoceramoidea Giebel, in turn regarded as a constituent of Order Praecardioida Newell, 1965. The constituent families included Buchiidae, ?Monotidae, ?Asoellidae, Pergamiidae, Eurydesmidae, and ?Posidoniidae. Such an array of different morphologies implies that evolution was so flexible that tracking the changes would have to be premised largely independently of shape, ligament, articulation and musculature. In addition, it is surprising that Kolymiidae Kuznetzov and Atomodesmidae Waterhouse were not included within the superfamily, presumably because they were lumped in Inoceramidae, in accord with a dated survey by Kauffman & Runnegar (1975). The Johnston-Collom scheme, so far as it was applied to the present genera and families, will at least need to be substantially modified, with Eurydesmidae and Buchiidae segregated because of their smooth or lightly ornamented shell, opisthodetic ligament and anterior hinge. Pergamiidae and Asoellidae are aviculopectiniform, and Posidoniidae are pteriiform. But members of the mostly Lower Paleozoic Praecardioidea Hoernes, treated as ancestral by Johnston & Collom (1998), are certainly close to Eurydesmoidea in shape and so remain as possible root stock.

Classification: The suborder is classified as follows:

Superfamily Eurydesmatoidea Reed, 1932
- Family Eurydesmidae Reed, 1932
- Family Buchiidae Cox, 1964

Superfamily Monotoidea Fischer, 1887
- Family Monotidae Fischer, 1887
- Family Dolponellidae Waterhouse, 2001

Superfamily **EURYDESMOIDEA** Reed, 1932

[nom. transl. Waterhouse 2001, p. 135 ex Eurydesmidae Reed, 1932, p. 50].

Diagnosis: Inequivalve to equivalve, inequilateral, ornament reduced, generally no posterior wing, ligament opisthodetic, external, platyvincular or with resilifer, right anterior auricle as a rule small or modified in a partly articulatory structure, independent of ligament, hinge may have simple large teeth and broad sockets, adductor large (see Waterhouse 2001, p. 137).

Discussion: Members of this superfamily are readily distinguished from Superfamily Monotoidea Fischer, 1887, which are subequivalved shells with well developed right anterior auricle, ornament of close-set radials in two or three orders in many shells, and external ligament that is platyvincular or has a shallow wide resilifer, and adductor complex that where known is compact.

Family **EURYDESMIDAE** Reed, 1932

Diagnosis: Often large, inequilateral, usually subequivalve shells with anterior "ear ledge" in each valve, usually no posterior wings, little ornament, anterior dorsal pseudolunular channel usually in each valve, external platyvincular or alivincular to truncavincular ligament, thickened hinge that may bear one or more feebly developed dental bosses and shallow sockets, smooth exterior.

Taxonomy: Reed (1932, p. 50) used the name Eurydesmidae, without any explanation, and in 1936, p. 16 referred to Eurydesmidae nov., again without any diagnosis or explanation. As far as can be discovered no author has yet defined the family, because the name was linked with the genus, and the definition regarded as obvious. Here the formal diagnosis is provided for the first time, with the name attributed by courtesy to Reed (1932).

Discussion: *Eurydesma* has been regarded as ambonychiid in affinities, and there are similarities in opisthodetic hinge, overall shape and ornament. But the posterior adductor is far larger than in ambonychiids, and like that of pectiniform genera. In addition, a pectinidian relationship is indicated by detail of the anterior hinge in *Eurydesma*, because somewhat similar structures are developed in undoubted pectiniform genera such as *Buchia* and especially *Maccoyella*. An alliance between Eurydesmidae and Pectinoidea was favoured by Runnegar (1970) and the genus was referred to Monotoidea by Newell & Boyd (1995), in relying on the nature of muscle field, pallial line and byssal scars, as illustrated by Runnegar (1970), and the presence of crossed foliae in the shell. The various attributes appear to be further removed from those of Pteriida. Newell & Boyd (1995) placed *Eurydesma* in Chaenocardiidae Miller. *Chaenocardia* has a large right anterior auricle, and a ligament that is asymmetrically amphidetic, the overall appearance strongly indicating a close relationship with Streblochondriidae Newell. Dickins (1961, p. 139) considered that Eurydesmidae was close to Mytilidae and Myalinidae and later Dickins (1983, p. 61) associated the genus with Ambonychioidea. Such an alliance is indeed supported by aspects of shape, ornament and anterior hinge, but these could have arisen by retromorphing from pectiniform stock. The *Eurydesma* ligament is external and lacks the deep grooves that indicate a lineavincular ligament, with segregated fusion and fibrous layers, as in the lineavincular and internal ligament of *Myalina*. Instead it is platyvincular, and shows considerable approach to the ligament in *Mysidiella* Cox, 1964 (pro *Mysidia* Bittner 1891 non Westwood, 1840), especially the species *Mysidiella imago* Hautmann (2001, pl. 4, fig. 5-11, text-fig. 16) from the Late Triassic of Iran. Such an alliance was first suggested by Koken (1904). The figured right interior of *M. imago* shows a narrow ligament and a deep byssal embayment, with shelf on the inner side bearing a prominent buttress, close to the arrangement in *Eurydesma*. Moreover Hautmann (2001) pointed out that the structure varied on the two valves, some right valves having the tooth, some left valves having the tooth – in other words the tooth was transposable in either valve. His instructive text was translated from German into English by Hautmann (2001, p. 42), and Waller (2005, p. 14) set aside the Hautmann translation to provide a fresh translation in English from the German text. Reassuringly this is almost word for word the same as Hautmann's English version, no doubt as a reflection of the translating skills of each author. Other species of *Mysidiella*, including the type, *M. orientalis* (Bittner), do not show the prominent anterior tooth and shelf so clearly, and there is a reduced dental swelling in *M. newtonae* Waller (2005, Fig. 4.11-13; Newton 1987, Fig. 21). Yet the possibility must be considered that the similarities between *Eurydesma* and *Mysidiella* are due to convergence. Waller (2005, p. 8) stressed the presence of antimarginal fibrous micro-structure as characteristic of the family Mysidiellidae, and observed that such fibres in the shell of *Mysidiella newtonae* indicated mytilid affinities, whereas the outer shell of *Eurydesma* was recorded as homogeneous to lamellar in the left valve, and homogeneous, lamellar, to complex lamellar in the right valve (Dickins 1957). It is true that Hautmann (2001, Fig. 16) interpreted the shell structure quite differently for his Iranian species of *Mysidiella*, reporting and illustrating what he stated to be, and indeed looks like foliated calcite, rather than fibrous structure. Waller (2005) sharply disagreed, and argued for a mytiliform relationship, whereas Hautmann (2001) considered that an ambonychioid alliance was possible. It is scarcely necessary to point out that the dispute may have arisen from misidentification – of shell structure – or genus – or true family position. M. Hautmann (pers. comm.) has subsequently found considerable supporting evidence for an ambonychioid relationship in hinge and shell structure, and his evidence enables Waller's view of shell structure to be rejected, as far as *Mysidiella imago* is concerned. Hautmann also agrees on the close similarity of the hinge in *Eurydesma* and *Mysidiella*. But on the other hand, he has found rare examples of thin outer prismatic shell in *Mysidiella*, and this is absent from *Eurydesma,* as far as I am aware, though some may wish to note that if it is rare in *Mysidiella*, its absence from *Eurydesma* need not be of great consequence. Many Aviculopectinoidea have an outer prismatic shell layer, and ambonychioids and inoceramoids have a thick outer prismatic layer. If *Eurydesma* did develop from within Aviculopectinidina, it became modified in shell structure, habitat, shape and hinge. Even so, younger monotoid allies reverted to a more pectiniform shape and habit, with well developed byssal notch and right anterior ear, resilifer, weak radial ornament, and prismatic shell. Carter (1990) discussed the proposal that *Eurydesma* had been sourced from *Posidoniella* as suggested by Dickins (1983), and noted that the homogeneous mosaic and foliated structure of *Eurydesma* had replaced the ancestral calcitic simple prismatic structure, and the aragonitic CL structure of the inner shell of *Manticula* and possibly *Eurydesma* replaced an ancestral aragonitic nacreous structure. Both the foliated and aragonitic CL structure of *Eurydesma* and *Pergamidia*, he considered, evolved independently of the foliate and aragonitic CL structure of other Pteriomorphia.

Although Etheridge & Dun (1910) argued in some respects for a pterioid relationship of *Eurydesma*, through offering comparisons with *Pinctada,* the lack of well developed anterior wing and lack of prismatic shell do not favour such an alliance. Even in monomyarian pterioid genera and species, the posterior muscle complex is more posteriorly placed than the adductor complex of *Eurydesma*, and differently shaped. The pallial line is more broadly open dorsally in shells that are shaped rather like *Eurydesma*, such as *Limoptera macroptera* (Conrad), as illustrated by Pojeta (1986, pl. 46, fig. 1-5).

Waterhouse (1980b, 2001) proposed that the Mesozoic family Buchiidae Cox, 1953 was closely related to Eurydesmidae, pointing out various similarities in shape and hinge. Buchiids are small highly inequivalve shells with resilifer and anterior auricle developed below the ligament (Waterhouse 2001, pp. 136, 137). Such a view was also put forward by Waagen (1891) and Reed (1932, p. 18) with additional caveats by Etheridge & Dun (1910, p. 66), noting the closeness between *Eurydesma* and *Aucella* Keyserling, now synonymized with *Buchia* Rouillier. Both families are further discussed by Waller (2005) and Waterhouse (2001, p. 137).

Members of the family

Apart from *Glendella* Runnegar, which has been merged with *Eurydesma* by Newell & Boyd (1995), the family Eurydesmidae has been treated as monogeneric. It is here believed that *Frigidusia* n. gen., *Mysidiella* or at least *M. imago*, and other species subject to shell composition and structure, and ?*Krumbeckiella* are close enough to *Eurydesma* to imply persistence well into the Mesozoic Era. A genus that externally approaches *Eurydesma* and has a canalivincular ligament is *Oretia* Marwick, 1953 from the Late Triassic of New Zealand, but this genus has been shown to have a small anterior ear in each valve, and has isomyarian adductor scars, suggestive of Pteriida (see p. 38).

Speculations have been raised over the position of *Manticula* Waterhouse, 1960 (see p. 16), a genus found in the Triassic of New Zealand and reported from Cretaceous rocks of Antarctica (Crame 1995). *Manticula* has a very inflated right rather than left valve. The ligament is opisthodetic, high and short, unusual for any major bivalve group, but presumably contingent in shape and function on the unusually high shell. The apparently anisomyarian muscle scars and shape suggest a position within Ambonychioidea. For *Manticula,* Waterhouse (1960, Fig. 26-30) reported an outer zone of oblique fibrous and crystalline calcite, grading into more homogenous calcite, with a layer of inner lamellar calcite. Concentric sections suggest complex foliate structure over the outer shell. *Manticula* was classed with Pergamiidae Cox, 1969 by Cox (1969b), but Waller (2005, p. 8) disagreed with the placement, and suggested that *Eurydesma* and *Manticula* had similar calcitic microstructures, including those that are calcitic cross-foliated and innermost aragonitic microstructure, as described by Carter (1990, p. 203). Reports of a small skewed anterior auricle and a very broad shallow ligament pit do not accord with type *Manticula*, and the genus appears to lie outside of any eurydesmoid ambit, as underlined by the different muscle scars and lack of internal anterior shelf in each valve (see p. 18).

Genus ***Eurydesma*** Morris, 1845

Text-fig. 59 - 61

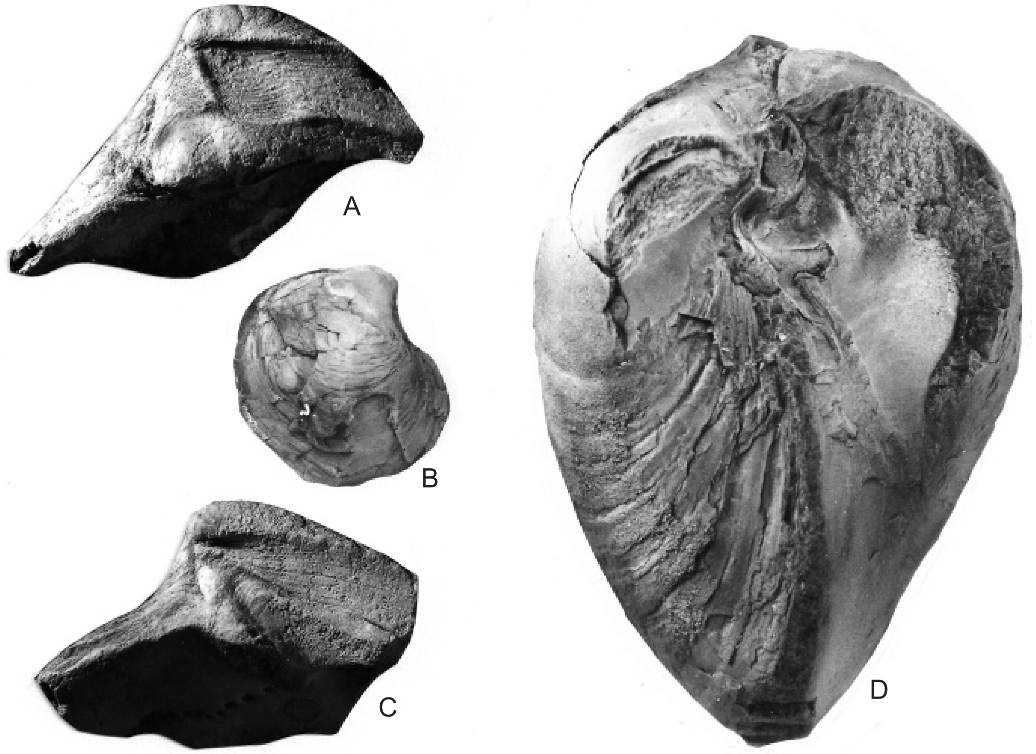
Type species: *Eurydesma cordatum* Morris, 1845, p. 276 from Early Permian (late Asselian) Allandale Formation, New South Wales.

Diagnosis: Large equivalve or subequivalve shells with anteriorly placed umbones, byssal notch and channel below small right anterior ear ledge which may jut into left valve hinge, left valve anterior ear ledge, may lie parallel to hinge or jut across commissure, adjoins channel like that of right valve, platyvincular opisthodetic ligament, hinge somewhat variable, right valve may have broad shallow socket or one or two low dental bosses, left valve may have one large or less commonly two dental bosses and may have intervening socket, posterior adductor muscle scar large, faintly impressed, subcentrally placed, pallial line continuous ventrally, pitted dorsally, pedal byssal scars present below umbones near dorsal ends of pallial line.

Discussion: *Leiomyalina* Frech, 1891 is a synonym of *Eurydesma*, being based on *L. antarctica* Frech, which is a close ally of *Eurydesma hobartensis* Johnston and especially close to *E. cordatum ovale* Etheridge & Dun.

Morphology of the hinge

Any assessment of species now assigned to *Eurydesma* is constrained by inadequate knowledge of the hinge for a number of species, and the degree to which it varies within and between presently recognised species. There have been varied interpretations of the hinge, concerning the presence and number of teeth, and the presence or absence of a right anterior ear. Newell & Boyd (1995) provided a very incomplete interpretation of the hinge for *Eurydesma*, ignoring the

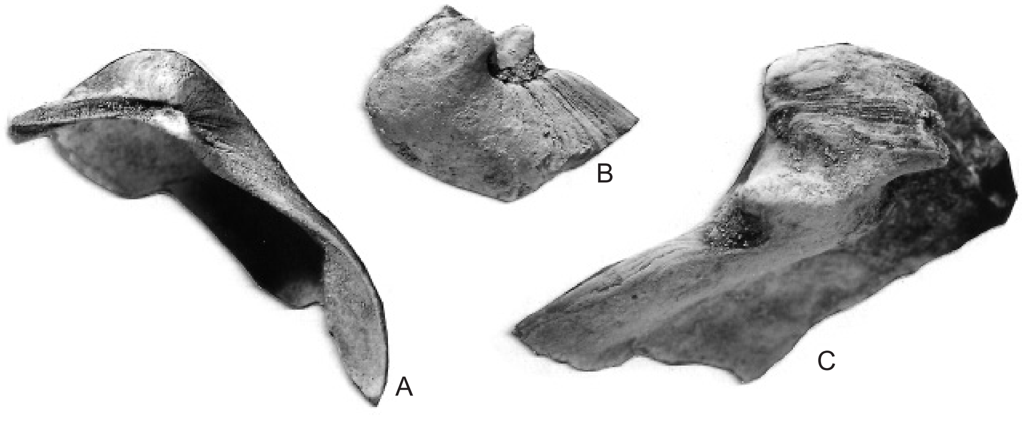


Text-fig. 59. A, *Eurydesma* cf. *protrudus* n. sp. Right valve UQF 51934 showing anterior pit in truncavincular ligament area, from Early Permian Darlington Limestone, Tasmania. B, C, D, *E. cordatum* Morris from Early Permian Allandale Formation, New South Wales. B, right valve aspect USNM 188134. C, unregistered right valve kept at Queensland Museum, Brisbane. D, anterior-dorsal aspect of USNM 3664 with valves conjoined. See Runnegar (1970) and Waterhouse (1987, 1988). Specimens x 0.75 approx.

variance of their analysis from other analyses of the dentition and hinge. Basing their presentation on a handful of specimens of *E. playfordi* Dickins (which is not the type species), they emphasized the presence of a large tooth in the left valve, fitting loosely into a broad socket just behind the byssal notch in the right valve, as though this were typical of all *Eurydesma*. That is not so: there is a range of morphologies, and their description applies to many, but far from all specimens. Dickins (1957) provided a more accurate summary of the hinge in *playfordi*, and contrary to Newell & Boyd (1995), reported “a right valve dental process” that projected into the body cavity of the left valve, and also recorded a smaller left valve dental process, well shown in Dickins (1957, pl. 5, fig. 4, 6, 8, 10). Although Newell & Boyd (1995) recorded a right valve socket, Stolizcka (1871) and Runnegar (1970, 1979, p. 261) stressed the importance of a right valve tooth.

The fact is that the hinge structures vary in specimens allocated to *Eurydesma,* and there is a degree of transposition. Individuals of *E. burnettensis* Waterhouse, 1987 (see Maxwell 1964, pl. 11, fig. 8, 10; Webb 1977, pl. 2, fig. 1-3) from the Yarrol Basin, Queensland, have a very prominent right anterior process, with minute if any right valve socket for a left valve tooth, and no left valve tooth in some valves. As Webb (1977, p. 56) noted, the relative size of the right valve tooth diminishes with increased size of the *burnettensis* shell, but Newell & Boyd (1995) paid no attention to the ontogeny. A bulbous right valve tooth is present in “*Eurydesma* sp. ind.” figured by Runnegar (1970, pl. 16, fig. 1) from “the Glacial Stage, Kuttung Series, Seaham Beds, Stanhope district, Hunter Valley, New South Wales", somewhat suggestive of *E. burnettensis*, although some detail is obscure. The Seaham beds are Carboniferous (Claoué-Long & Korsch 2003), and it is not clear whether Runnegar's *Eurydesma* is Carboniferous, or whether Runnegar's stratigraphy was at fault. Some individuals of *E. cordatum* Morris from the Allandale Formation, New South Wales, such as that figured by Runnegar (1970, pl. 14, fig. 4), are like the arrangement pictured in *playfordi* by Newell & Boyd (1995), and most of the Allandale specimens figured by Etheridge & Dun (1910) agree. Other specimens differ. For example right valves figured by Runnegar (1970, pl. 13, fig. 5, which is the lectotype of *E. cordatum* and type species of the genus, and pl. 14, fig. 4) show a very strong boss behind the dental socket. A left valve (Runnegar 1970, pl. 14, fig. 3) has a strong boss, with socket in front, and weaker anterior boss; another has an ear ledge covered by growth-lines, and no boss or socket. Specimens from Maria Island, Tasmania, include a right valve (Runnegar 1970, pl. 13, fig. 1) with boss continuing ventrally from the ear ledge in front of a small shallow socket, and in the specimen figured by Runnegar (1970, pl. 13, fig. 8) a large right valve boss continues inward from the truncated ear ledge, in front of a shallow narrow socket and a low ridge behind. These fragments were identified by Runnegar (1970) with *E. cordatum*, but appear to have umbones like those of the new species *Eurydesma protrudus* (see p. 121), and perhaps these features are characteristic of the new species. A somewhat worn left valve of what seems to be the new species from the Bundella Mudstone of Tasmania (Runnegar 1970, pl. 15, fig. 7) has a prominent internal boss with projection at the hinge. The left valve neotype of *E. hobartensis konincki* Johnston as figured by Runnegar (1970, pl. 16, fig. 2, 3) from the Darlington Limestone, Tasmania, has a posterior boss, a socket, and weak anterior ear ledge. The lectotype of *hobartense* has a small left valve socket. Two right valves figured as *konincki* from the "Spirifer Zone" of Maria Island, Tasmania, by Clarke (1992, Fig. 20F, G) are largely like the Newell-Boyd model, but a left valve figured as *Eurydesma* sp. from the same beds has a more complex arrangement, with a large posterior boss, separated by a hollow from a second anterior and more slender boss, passing into a broad ear ledge marked by growth-lines.

Both the figured type of *antarctica* Frech from the south Sydney Basin, New South Wales, and definitely a specimen from the Sirius Shale in the Bowen Basin, Queensland, lack a massive

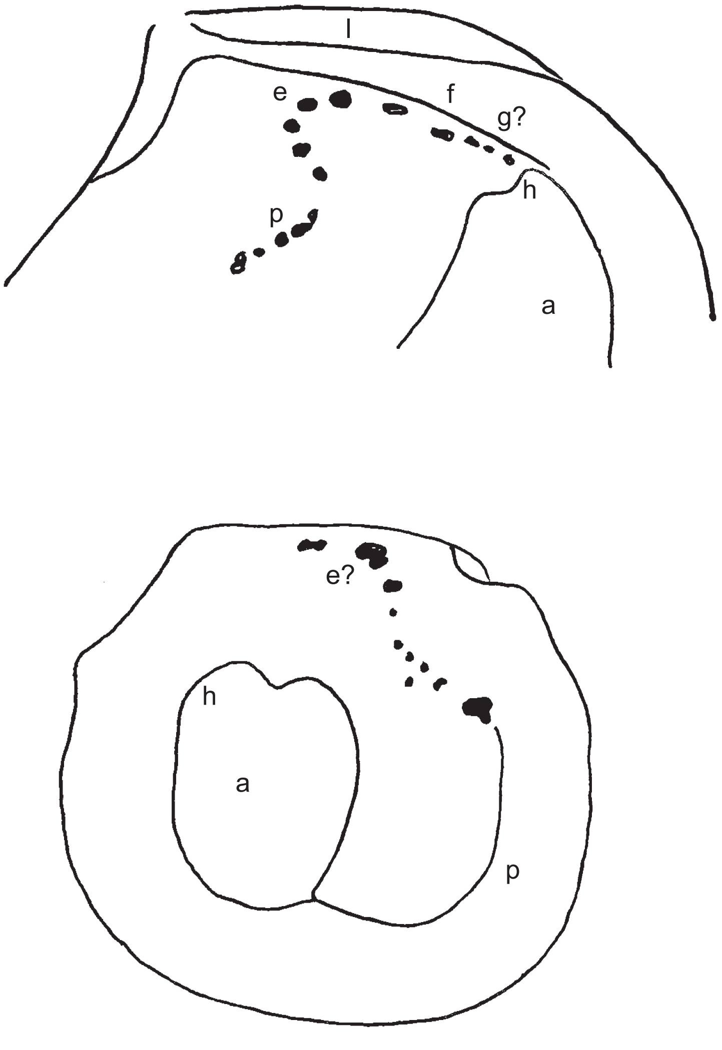


Text-fig. 60. *Eurydesma rotundatum* Reed. A, left valve OGC F 17 with projecting ear ledge. B, right valve with projecting anterior ear ledge, OGC F 20. C, right valve OGC F 18. From Early Permian (Asselian) Bap Formation, India, x1. See Waterhouse & Ranga Rao (1989).

internal left valve dental boss, but have a slender ridge-like ear in front of the ligament area, marked by growth lines in the Sirius specimen (Runnegar 1970, pl. 17, fig. 5, 9).

There is thus considerable variation displayed by individuals of *Eurydesma* from Australia. The variation is not the same as displayed by *Mysidiella imago* (Hautmann 2001), but there is some similarity. In many specimens the right anterior ear ledge, or the shelf that also bears the tooth, butts across the commissure into the left valve hinge, and in some specimens, the left ear ledge or commissural edge below the byssal channel butts into the right valve. This differs considerably from the commissure in aviculopectiniform shells. *Mysidiella* was classed as Mysidiellidae Cox, 1964, and treated as a member of Mytiloidea by Cox (1969a), but clearly in need of revision, though regarded as mytiloid by Waller (2005).

As shown by Etheridge & Dun (1910), the relative development of the right and left anterior



Text-fig. 61. *Eurydesma* pallial line and muscle scar x1. A, *E. cordatum* Morris left valve internal mould UQF 21075. B, *Eurydesma* n. sp. or n. subsp. aff. *cordatum*, right valve internal mould, unregistered UQ specimen from lower Tiverton Formation, Queensland. This is a less mature specimen and the shell between 'e' and 'h' appears smooth. a – adductor complex, e – anterior pedal byssal scar, f – posterior pedal byssal scar, g – gill suspensory scars, h – pedal retractor scar, l – ligament area, p – pallial line.

ear ledges differed in different specimens, and for some specimens a gap in the opposing valve accommodated the extended anterior ear ledge from the other valve, recalling the dorsal anterior gape in *Aucellina* and *Malayomaorica* (p. 170). There is a degree of consistency within some species, but further enquiry is needed for confirmation, and certainly for some species, the hinge varies. It remains an open question whether material presently ascribed to *Eurydesma* should be separated generically because of a right valve dental boss and left valve socket, and a further question concerning the nature of a left valve anterior boss or ear, but present usage favours recognition of one genus with varied and transposable dentition, and considerable variation in the size, shape and expression of anterior ear ledges.

Beyond Australia, hinge detail also differs. Of the internal fragments figured as *globosum* Dana and *ellipticum* Dana from the Salt Range, Pakistan, by Waagen (1891, pl. 6, fig. 5, 6), two right valves are somewhat like the Newell-Boyd arrangement, but the right valve socket is bordered by a slender ridge in front of the anterior ligament area. Three left valves figured as *globosum* Dana by Waagen (1891, pl. 6, fig. 2c, 3, 4) show a comparable socket, rather than a large dental boss, and in two specimens there is a slender ridge behind the middle of the socket. Any interlocking would have been feeble, and quite possibly the feeble ear ledge at the anterior left valve hinge fitted into the anterior right valve byssal channel. Further figures are provided by Waagen (1891, pl. 8, fig. 1b, 2 - "*ellipticum*", and 3a-c - "*cordatum*"), the latter suggestive of a right anterior ear ledge. Koken (1904) refigured and interpreted the Salt Range material, to provide very clear illustrations especially for the right anterior ear ledge, with a large left valve socket rather than tooth as observed in *playfordi* by Newell & Boyd (1995), into which the right anterior ear ledge may have protruded. Reed (1932) changed the identifications of Waagen (1891) and allocated the specimens to new species. South African specimens identified as *E. mytiloides* Reed by Dickins (1961, p. 142, pl. 18, fig. 1-6) show a very thin and linear right valve socket and tiny left valve tooth, which overlaps the byssal notch, covering the byssal opening, just as shown by Etheridge & Dun (1910, pl. 18, fig. 3, pl. 19, fig. 3; Dickins 1957, pl. 5, fig. 11) for Australian specimens, according to Dickins (1961). Right valves assigned to *Eurydesma hobartense rotundatum* Reed by Waterhouse & Ranga Rao (1989, Fig. 7.3, 6) from the Bap Formation of Peninsular India have a relatively prominent right anterior ear ledge projecting well beyond the commissure towards the left valve, and a large socket. The left valve hinge (Waterhouse & Ranga Rao 1989, Fig. 7.1) has a broad ear ledge which carries growth-lines on the anterior face (Text-fig. 60).

Muscle impressions, pallial line (Text-fig. 61)

As shown by Runnegar (1970, Fig. 1), the adductor scar is large, posteriorly placed, and apparently undivided, although it should be noted that the impression is as a rule very faint, and scarcely perceptible. Runnegar (1970, pp. 90, 91) compared the muscle impressions to those of Aviculopectinoida and Pectinoida, to show that the pedal-byssal musculature is weakly developed as in *Pernopecten* and *Pseudomonotis*, suggestive of an inactive life-habit. The scar approaches that of some Pectinoidea (Entoliidae, *Pernopecten*), and in both genera is much larger than that of Ambonychiidae. The pallial line is continuous ventrally, is as a rule not visible from above the adductor scar as far as below the beak, and then proceeds as a discontinuous line of pits parallel to the anterior dorsal margin, and curves parallel to the ventral margin into the lower adductor scar. The dorsal interval is occupied by one to three pits in some specimens (UQF 21075) and in a specimen from UQF 4514 forms a shallow groove almost as far as the adductor scar, although possibly the groove may be an artifact or in some way not related to a pallial line. Etheridge & Dun (1910) regarded the dorsal pits as pedal scars, and Dickins (1961, p. 139) allowed both options, stating that the impressions "probably represent the pedal muscles and the pits of the pallial attachment". Much as in *Etheriplica* for example (Waterhouse & Jell 1983, pl. 4, fig. 4, 6), or

“*Aviculopecten*” (= *Heteropecten*) *exemplarius* Newell (1938, Fig. 2.1, 5), the pallial line was not broadly open dorsally as in ambonychiids. Just below the ligament lies a small obliquely elongate depression, suggestive of a pedal retractor scar, and pallial-line pits continue up from the anterior and across to finish a little behind the scar. There is also a row or rows of fine pits closer to the posterior hinge.

Paleoecology

Eurydesma was semi-infaunal, and it evidently nestled in sandstones, but also in mudstone or shelly limestone (Waterhouse & Gupta 1982, p. 3), attached by byssus passing through a channel in both valves, being in that sense closer to ambonychiids, and regarded as reversionary: late Mesozoic pectinidians also showed a similar development (p. 165). Waterhouse & Gupta (1982) rejected the allegation by Runnegar (1979) that *Eurydesma*, at least under optimal conditions, lived “effectively floating on the substrate”, and that the shell was calcitic, because aragonitic shell with its greater specific gravity would have caused the shells “to sink slowly into the substrate as they were washed back and forth” (Runnegar 1979, p. 261), presumably under action of tides and waves. It is difficult to do other than dismiss Runnegar’s model as nonsensical. I am aware of no such modern analogue, and have found no evidence to suggest that *Eurydesma* lived in a moving slurry of sediment. In other respects, the habitat of *Eurydesma* would seem obvious, heavy shell and byssal opening pointing to stable attachment in a sublittoral situation subject to strong current or wave movement. A different claim, that *Eurydesma* was like the giant clam *Tridacna* (Etheridge 1892, Runnegar 1970) with one valve attached and the other clamping like a lid also seems highly questionable, as noted by Clarke (1992, p. 38). *Tridacna* was epifaunal; *Eurydesma* may have been semi-infaunal.

Eurydesma protrudus n. sp.

Text-fig. 62, cf. 59A

1845 *Eurydesma cordatum* [not Morris] – Morris, p. 276, pl. 12, fig. 2, 3 (part, not fig. 1 = *cordatum*).

1910 *E. hobartense* [not Johnston] – Etheridge & Dun, p. 75, pl. 20, fig. 6, pl. 22, fig. 1, 2, pl. 23, fig. 5, pl. 24, fig. 3, pl. 25, fig. 4, 5 (part, not pl. 18, fig. 2, 3, pl. 23, fig. 1, 2? = *konincki* Johnston).

1910 *E. cordatum* [not Morris] – Etheridge & Dun, p. 71, pl. 18, fig. 1, 2 (part, not pl. 17, fig. 1, 2, pl. 18, fig. 1, pl. 19, fig. 3-5, pl. 20, fig. 2-5, pl. 21. fig. 1?, pl. 22, fig. 3-5, pl. 23, fig. 3, 4, pl. 25, fig. 3 = *cordatum*, pl. 23, fig. 1 = *konincki*?).

1970 *E. hobartense konincki* [not Johnston] – Runnegar, p. 97.

1970 *E. cordatum* [not Morris] – Runnegar, pl. 13, fig. 1.

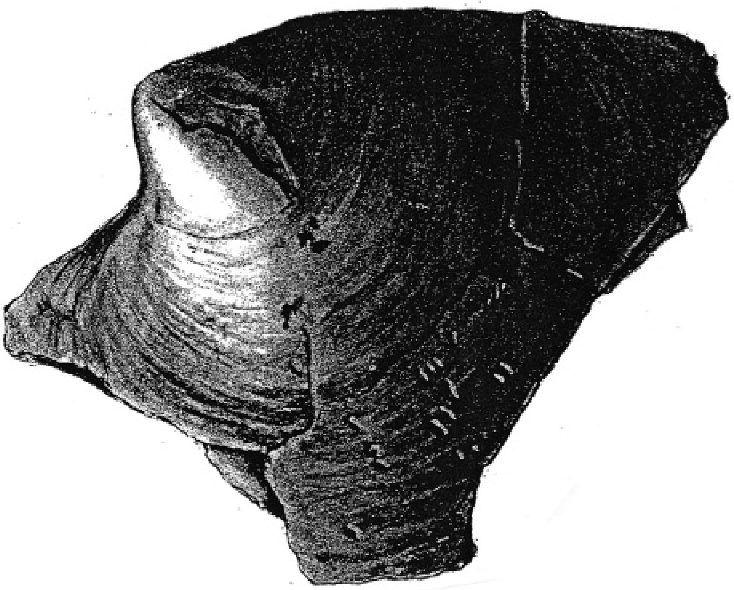
1970 *E. hobartense hobartense* [not Johnston] – Runnegar, pl. 15, fig. 7.

Derivation: protrudo - thrust forward, Lat.

Holotype: AMF 14656 from Early Permian (Asselian) Darlington Limestone, Maria Island, figured by Etheridge & Dun (1910, pl. 23, fig. 5) as *Eurydesma hobartense* [not Johnston], here designated.

Diagnosis: Characterized by low inflation, long hinge, strongly curved anterior dorsal margin, extended anterior, generally subcentral umbones, and often no lateral sulcus. Left valve has prominent anterior ear ledge, may have slender ridge behind ear ledge and in front of ligament, or boss below the ligament.

Description: The species is represented by a number of described and well figured specimens in the Australian Museum, Sydney. The shell is thin, the inflation low and the anterior variably extended, usually well forward, the hinge long, the flanks without a sulcus. The right valve (Etheridge & Dun



Text-fig. 62. *Eurydesma protrudus* n. sp. holotype AMF 14656 figured as *E. hobartensis* not Johnston by Etheridge & Dun (1910, pl. 23, fig. 5) from Early Permian (Asselian) of Maria Island, Tasmania, x1.

1910, pl. 20, fig. 6) has a large shallow socket. Left valve AMF 14778 of Etheridge & Dun (1910, pl. 25, fig. 4, 5) shows a swelling marked by growth-lines, in place of a distinct ear, behind a channel, and in front of the ligament. There is no tooth-like boss in this specimen.

Discussion: This species is readily distinguished by its extended anterior and subcentrally placed umbones, with slender shell and lack of sulcus, and thin posterior dorsal shell. It looks moderately like *Eurydesma hobartense* Johnston from the Middle Permian Deep Bay Formation of Tasmania (Clarke 1992), and this species is only a little more inflated and often lacks a lateral sulcus, but has more anteriorly placed umbones and short anterior and steep anterior dorsal margin. Some Tasmanian specimens of the new species were identified with *E. hobartense konincki* Johnston by Runnegar (1970, p. 97), but are much less inflated and shaped very differently from this species and have extended anterior and other differences. The species *protrudus* gave rise to *E. alisulcatum* Waterhouse, 1987, found in the late Early Permian Ulladulla Formation, and distinguished by a weakly defined posterior wing and a lateral sulcus.

Eurydesma cordatum var. *compressa* Reed (1932, pl. 10, fig. 7, 8, pl. 11, fig. 5) from the Agglomeratic Slate of Kashmir is very like *E. protrudus* in shape, and *E. cordatum quadrata* Reed (1932, p. 52, pl. 10, fig. 6) from the same beds is similar. It also compares with so-called *E. ellipticum* Dana of Waagen (1891, p. 141, pl. 6, fig. 5, 6, pl. 7, fig. 1, pl. 8, fig. 1, 2) from the Salt Range, Pakistan. Thus the form characterized by extended anterior and slender shell was apparently more common in the Indian subcontinent than in east Australia.

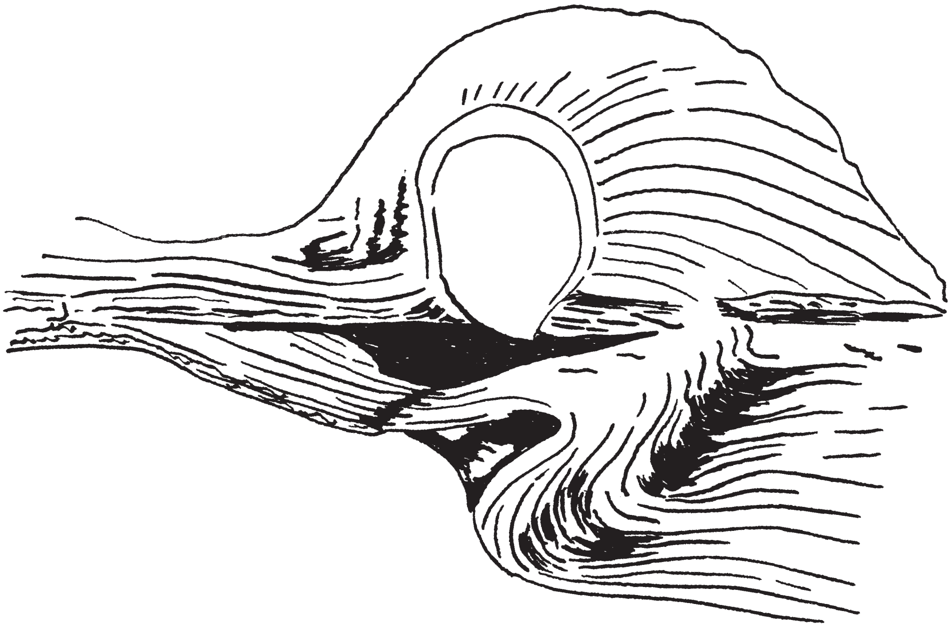
Genus ***Frigidusia*** new genus

Text-fig. 63

Derivation: frigidus – cold, Lat.

Type species: *Manticula complanata* Crame, 1995, p. 301 from the President Beaches Formation of Early Cretaceous (Berriasian) age, Byers Peninsula, South Shetland Islands, here designated.

Diagnosis: Medium-sized almost equivalve high suboval smooth shells with small and short anterior ear ledge, behind shallow channel in each valve; short high largely opisthodetic external ligament bearing broad resilifer, which commences just in front of the umbo, and lies above small internal anterior shelf, not bearing a tooth. Shell structure calcitic and cross-foliated as far as preserved, but incompletely known, above inner homogeneous zone.

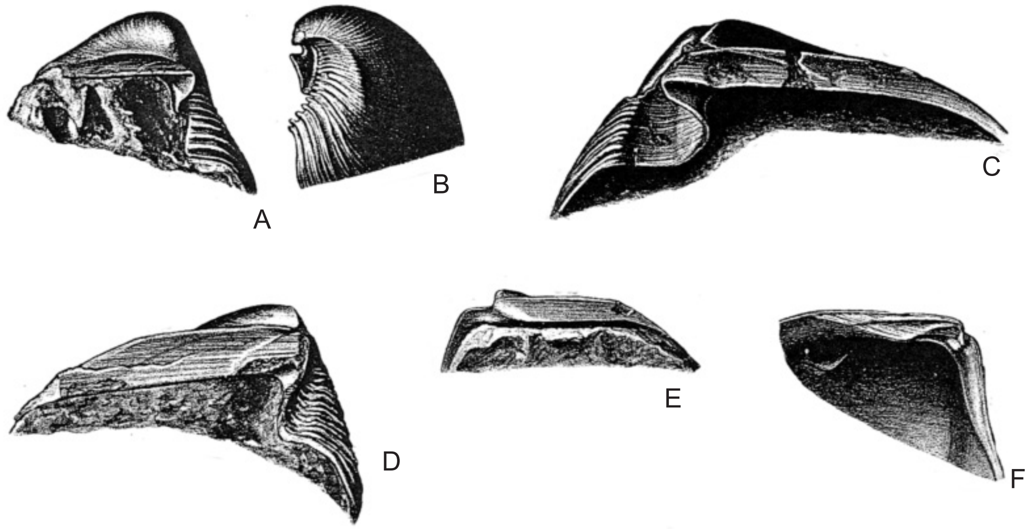


Text-fig. 63. *Frigidusia complanata* (Crame), hinge region of small left valve P 2201, x60, drawn from Crame (1995, pl. 2, fig. 1), from Berriasian Byers Group, west Antarctica.

Discussion: This genus is very close to *Eurydesma* Morris, 1845, largely smooth externally, subequivalve or equivalve, with shorter higher largely opisthodetic ligament, and shell structure close to that of *Eurydesma*, and small internal anterior shelf, without dental bosses, unlike that of *Eurydesma*. What is most striking is the nature of the hinge (Crame 1995, pl. 2, fig. 1, 2), which on the left valve at the anterior end of the ligament bears a small ear ledge, covered by growth-lines on the anterior side, behind a channel. This is very like the ear ledge and trench in left valves of *Eurydesma*, and shows the same relationship to the anterior shell, umbo, and ligament. The hinge of the right valve of *complanata*, not figured by Crame (1995), also has a structure very close to that of the right valve of *Eurydesma*, according to his text (p. 302). The two valves are like those of *Eurydesma* at an early growth stage – there is no development of the left valve tooth or right valve ridges that are found in mature *Eurydesma*. There are further differences between the two genera. The shape differs considerably, there are narrow radial ridges on the umbonal part of at least immature specimens of *Frigidusia*, and a shallow groove lies close to the posterior dorsal margin, unlike the broad depression found posteriorly in many *Eurydesma*. A resilifer pit is developed that is large and deep, with raised narrow areas each side considered to be part of the ligament, and growth-wrinkles are very much more in evidence. The shell is calcitic crossed-foliate in the hinge region of the “right valve”, passing into a fine-grained homogeneous zone that may represent an inner aragonitic layer. A prismatic layer in the central region of one specimen might be myostracal (Crame 1995).

Crame (1995) referred his species to *Manticula* Waterhouse, 1960 from Late Triassic faunas of New Zealand and New Caledonia. The type species *Mytilus problematicus* Zittel, 1864 lacks the posterior groove seen in *complanata*, and lacks the fine and close-set growth-wrinkles or early radial ribs of *complanata*. Further differences are provided in the discussion of Manticulidae (p. 18): *Manticula* does not have anterior ear ledge or internal shelf, and has inflated right rather than left valve. It is to be noted that Crame (1995, p. 306) confused the orientation of some of his own specimens – for example that figured by Crame (1995, pl. 1, fig. 6) is a left valve, not a right valve as he stated, and his holotype (Crame 1995, pl. 1, fig. 5) is probably a right valve, not a left valve. Another difficulty: Crame (1995) claimed a number of *complanata* specimens were equilateral or almost so, but this is because the shells were orientated from beak to anterior margin: here it is preferred to orient shells with dorsal commissure horizontal, and when that is done, the shells are not equilateral. No *Manticula* have been found that show the hinge structure revealed for the Antarctic shells illustrated by Crame. Extensive collections kept at the Institute of Nuclear and Geological Sciences (now GNS Science), Lower Hutt, and Department of Geology, University of Otago, Dunedin, show no approach to the hinge of small *complanata*, and the shell structure within the umbo shows nothing that might be interpreted as juvenile structures buried by later shell. That leaves open the possibility that the structure were resorbed in type *Manticula*, or that the small Antarctic specimens are not fact related to mature *complanata*, and the latter option has presumably been carefully explored and dismissed. The muscle field has not been ascertained for *complanata*. It certainly has hinge structure, and to some degree, crossed-foliate calcitic shell structure approaching that of *Eurydesma*.

Krumbeckiella Ichikawa, 1958, renamed for *Timoria* Krumbeck, 1924, p. 218 (not Kaye 1919), with type species *Timoria timorensis* Krumbeck from Triassic of Timor, has a largely opisthodetic ligament as in *Eurydesma* (Text-fig. 64). The genus has been fully figured by Krumbeck (1924, pl. 17, 18). The ligament is external, elongate, subplanar and striate, and usually bears an oblique resilifer sloping back from under the umbo, much smaller relatively than in *Frigidusia*. Whereas the ligament in *Eurydesma* becomes constricted under the umbo, it retains its height in *Krumbeckiella*. Below the anterior ligament lies, as a rule, a small internal shelf in each valve, somewhat like the socket of right valves and often left valves of *Eurydesma*, but there are no teeth or dental bosses. In front of the ligament area, a byssal channel is well developed in the right valve, as in *Eurydesma*, and not so well defined but present in the left valve. According to figures, the anterior end of the ligament projects forward as a tiny auricle, and may include the internal shelf. In the left valve, the ligament ends in a small ledge, varying to a modest ear ledge. In these details, *Krumbeckiella* is not identical with *Eurydesma*, but is very close in essential detail, and it would be useful to confirm the details as figured by Krumbeck (1924). Crame (1995, text-fig. 3c) figured a left valve of *Krumbeckiella* that shows an ear ledge below the umbo, projecting slightly forward between the commissure and a byssal-like recession, and broad ligament pit. The left valve ligament and anterior ledge of Crame’s *Krumbeckiella* is very like that of *Eurydesma* and his species *complanata*, and differs somewhat from the figures of *Krumbeckiella* presented by Krumbeck (1924). Efforts to confirm the nature of the hinge of type *Krumbeckiella* have not so far succeeded, with some difficulty over repository and accessibility, so that the nature of the hinge



Text-fig. 64. *Krumbeckiella* . A, B, view of left valve figured as *Timoria subtimorensis* n. sp. by Krumbeck (1924, pl. 17, fig. 12a, b), x1.5. C, right valve identified as *Timoria timorensis* var. *major* Krumbeck (1924, pl. 17, fig. 3b), x1.5. D, left valve figured as *T. subtimorensis* Krumbeck (1924, pl. 17, fig. 9b) x1. E, F, "*Pergamidia*" *timorensis* of Krumbeck. E, right valve figured by Krumbeck (1924, pl. 16, fig. 8b) x1. F, left valve figured by Krumbeck (1924, pl. 16, fig. 12d), x3. From Triassic of Timor. Material now kept at now kept at Nationaal Natuurhistorisch Museum Naturalis, Leiden.

requires further study. Nor does published description of the right valve hinge for *complanata* suffice to indicate whether it was close to that of *Krumbeckiella* or *Eurydesma,* although the indications are that it was identical to that of the left valve, implying similarity with *Eurydesma* rather than *Krumbeckiella*. *Krumbeckiella* has a large ligament pit, to help discriminate the genus from *Eurydesma*. Musculature remains not known. From available evidence, *Krumbeckiella* appears to be a member of Eurydesmidae, and close to *Frigidusia*, apart from its more elongate shape with more extended anterior and dorsally extended umbones, much longer hinge and greater inflation.

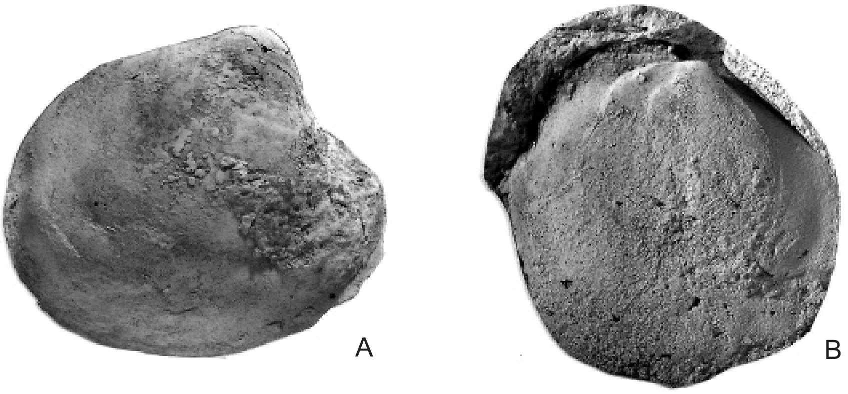
Mysidiella Cox, as discussed on p. 115, also appears to fall within this group, especially *M. imago* Hautmann, 2001, pl. 4. Yet a figure of the type species *Mysidia orientalis* Bittner, 1901 suggest fibrous material in the shell (see also Cox 1969a, Fig. 22.1a), and the figures in Bittner suggest that the valves have an anterior ear ledge rather than tooth as he described, unlike *Mysidiella imago* which has both tooth and ledge. Thus clarification is required.

Crame (1995) noted that *Eurydesma*, a genus characteristic of high Permian southerly paleolatitudes, was to be reasonably viewed as ancestral to Triassic bivalves that also were found in such latitudes as well as further afield. Although *Manticula* may not have been a good example, it is to be agreed that *Frigidusia* and its allies such as *Krumbeckiella* fall into such a category. The view adds support for the thesis that during the end-Permian life crisis, Permian high-latitude biota survived better than paleotropical and northerly life, and restocked the globe (Waterhouse 1976, 1994).

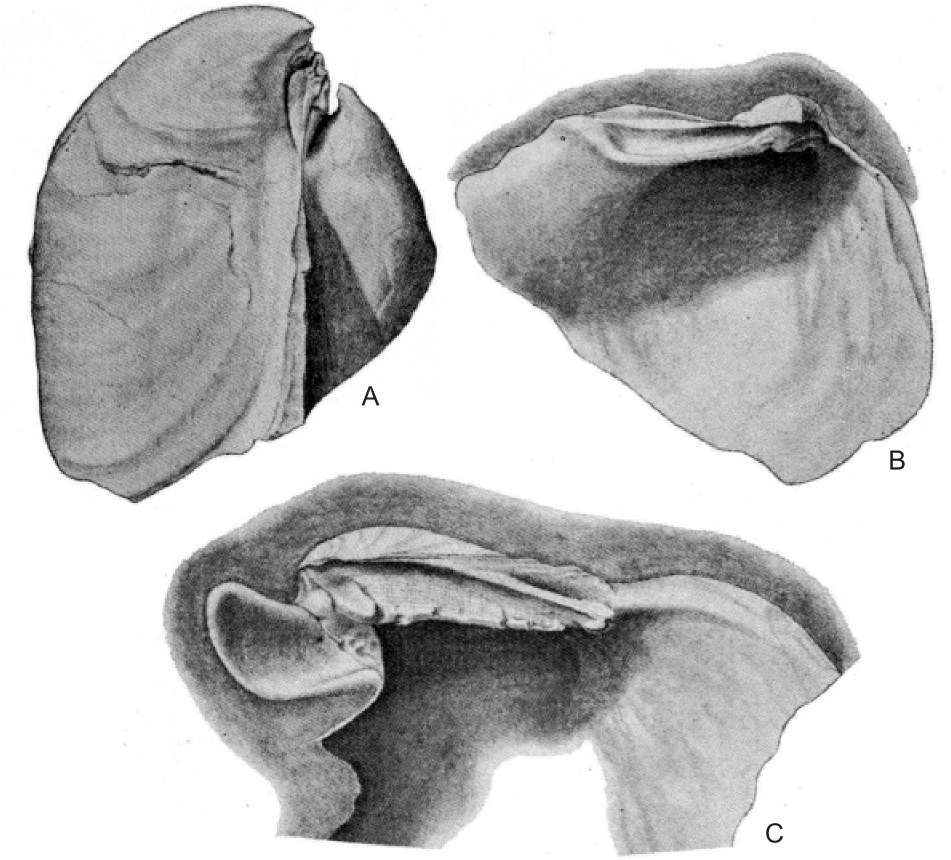
Family **BUCHIIDAE** Cox, 1953

Text-fig. 65 - 67

Diagnosis: Small to moderate in size, without developed wings as a rule, small right anterior ear as a rule, ligament opisthodetic, may be truncavincular.

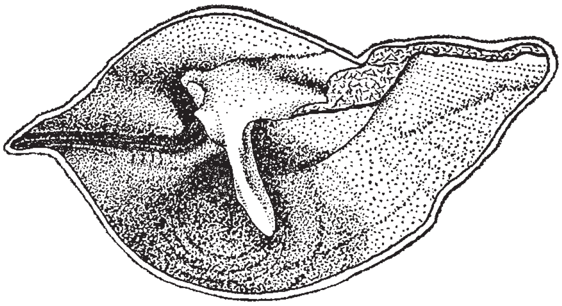


Text-fig. 65. *Glendella dickinsi* Runnegar. A, left valve UQF 73264. B, internal mould of right valve UQF 73265. From Kungurian (late Early Permian) Glendoo Sandstone Member, Blenheim Formation, Queensland, x1. See Waterhouse & Jell (1983).



Text-fig. 66. *Hokonuia limaeformis* Trechmann. A, lateral view of TM 2179 with valves conjoined, right valve to right. B, interior of left valve TM 2184. C, interior of right valve, showing right anterior ear projecting into the interior, TM 2183. Specimens x 1.5, from Late Triassic of Nelson, New Zealand. See Waterhouse (1960).

Discussion: Buchiidae show prismatic or homogeneous outer layer in one or both valves, a prominent foliate layer, and some CF structure and possibly inner aragonitic layer (Carter 1990, p. 248).



Text-fig. 67. *Hokonuia limaeformis* Trechmann, interior of specimen with valve conjoined, showing right anterior ear projecting into the interior, TM 2183 x1, from Late Triassic of Nelson, New Zealand. See Waterhouse (1960).

The oldest member of the family is provisionally judged to be *Glendella* Runnegar, 1970, which offers an example of a critical step in evolution and start of a new family, although it should be noted that *Glendella* lacks the small anterior right valve ear found in *Buchia*. The genus differs from *Eurydesma* in having an almost flat right valve, whereas the left valve is swollen and like *Eurydesma* in appearance (Text-fig. 65). A low ridge borders the anterior end of the left valve ligament, and the right valve ligament projects along the plane of the commissure over the byssal channel, and there are no teeth and no shelf. A large adductor scar is divided into posterior and anterior halves, suggesting that muscles were “quick” and “catch”. The shell structure shows an inner layer of crossed foliae and outer homogeneous layer (Runnegar 1970, p. 100, pl. 18, fig. 12, 16, 17). Carter (1990) pointed out that the particular valve was not stated, but the structure appears to be the same in both valves, as figured in Runnegar (1970, pl. 18, fig. 12). A somewhat similar ridge at the anterior end of the ligament is found in the late Mesozoic *Praebuchia* Zakharov, 1981 (see also Surlyk & Zakharov 1982).

Sichuana Chen in Chen & Liu, 1976 from Late Triassic beds of China is smooth-surfaced and subglobular with left valve much more inflated than the right, a triangular ligament area without resilifer, and no ears. It thus falls very close to *Glendella*, but muscle field and shell structure remain to be ascertained. It is assumed that there are no anterior wings and no teeth. The species *Sichunana*? *marwicki* Waterhouse, 1980b is even more buchiid in shape, and according to Begg & Campbell (1985) has been found to have a tiny right anterior auricle, suggesting placement with or close approximation to *Hokonuia* Trechmann (Text-fig. 66, 67). However no material to verify the claim has yet been viewed by the writer, despite efforts to see the critical specimens. The type material, based on a moderately extensive collection, does not clearly show a right valve ear, possibly because of inadequate preservation. Begg & Campbell (1985) suggested that the age was no younger than late Anisian, which requires further clarification, because they had regarded as Bithynian faunas which from ammonoid evidence are Illyrian or even younger (see p. 61).

Genus *Hokonuia* Trechmann, 1918, based on the Late Triassic New Zealand species *H. limaeformis* Trechmann, is close in many respects to *Eurydesma* in shell structure and smooth exterior. The right anterior ear ledge of *Eurydesma* is transformed into a long ear that projects into the interior of the left valve of *Hokonuia*, as shown by Waterhouse (1960). Like *Glendella*, the right valve of *Hokonuia* is small and much less inflated than the left valve. *Hokonuia* has a long shallow resilifer pit bordered by ridges in the truncavincular ligament, whereas *Eurydesma* rarely shows any pit. It was classed in Buchiidae by Cox (1969e, p. 374). The outer shell layer has a prismatic layer, and there is a middle layer with branching CF structure. The inner left valve shows a clear and homogeneous layer, possibly of altered aragonite; the inner right valve is similar, and the outer right valve is finely lamellar, and there is no simple prismatic layer. The presence or absence of a thin aragonitic CL layer is not confirmed (Carter 1990, p. 248).

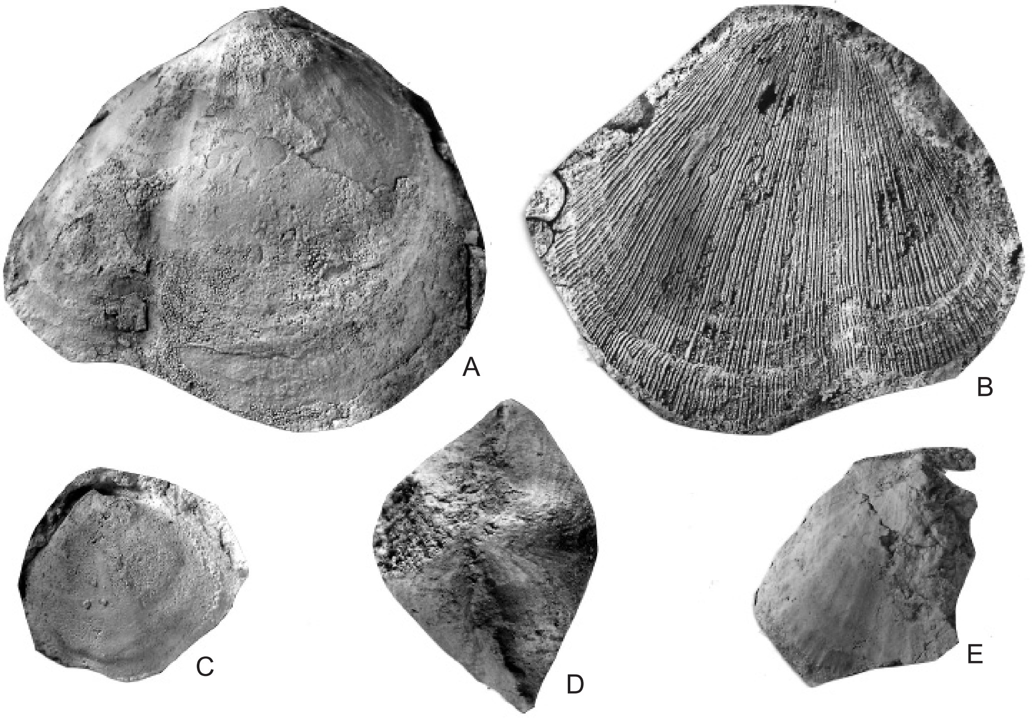
Superfamily **MONOTOIDEA** Fischer, 1887

Diagnosis: Right anterior ear small to large, ornament usually of radial ribs but not in all genera. Hinge edentulous, muscle field where known compact.

Family **DOLPONELLIDAE** Waterhouse, 2001

Text-fig. 68, 69

Family Dolponellidae Waterhouse, 2001, p. 135, is represented by *Dolponella* Waterhouse in Late Permian rocks of Nepal and the Salt Range, Pakistan (Waterhouse & Chen, 2006, p. 86). *Dolponella* is ornamented by fine radial costae, has a platyvincular ligament, and a prominent right anterior ear that is inclined forward slightly across the commissural plane. There is no



Text-fig. 68. *Dolponella sulcata* Waterhouse. A, left valve internal mould UQF 69008 x 0.8. B. external mould of same specimen x 0.8. C, interior of left valve holotype UQF 69009, x 0.8. D, dorsal view of specimen with valves conjoined, right valve to right, UQF 69007 x 1.5. E, right valve UQF 69006, x 0.8. Specimens from Changhsingian (Late Permian) Nisal Member, Dolpo, west Nepal. See Waterhouse (1978).

left valve anterior wing and no posterior wings. A left valve shows a comparatively thick outer prismatic layer, above a slightly thicker massive layer, with a comparatively thick ?inner prismatic layer. Superficially the genus approaches *Pseudomonotis* Beyrich in shape because it carries a prominent posterior-lateral sulcus, but the ligament is different, and *Eurydesma* also may exhibit a comparable sulcus: moreover both valves are considerably inflated, whereas species in Pseudomonotoidea have an alivincular ligament and small and little inflated right valve, except for members of Pegmavalvulinae, which bear strong spines and attachment scar and are of very different appearance. Because of the presence of a well-formed right anterior ear and radial ornament, it appears that members of Dolponellidae rather than Eurydesmidae gave rise to Triassic Monotidae. Monotidae are also edentulous and lack a left anterior wing or posterior wings, and generally have stronger ribbing and no posterior sulcus, and bear a resilifer.

Text-fig. 69. *Dolponella sulcata* Waterhouse, right valve UQF 69075 from Late Permian (Changhsingian) Luri Member, Dolpo, x2. See Waterhouse (1978).

Suborder Limidina Waller, 1978

Superfamily **LIMOIDEA** Rafinesque, 1815

Diagnosis: This remains to be fully circumscribed, given uncertainty over the position of Limatulinidae, and the need to clarify shell structure and muscle scars of Late Paleozoic members.

Family **LIMIDAE** Rafinesque, 1815

Diagnosis: Usually equivalve inequilateral, commonly higher than long, often retrocrescent, anterior and posterior wings usually small, rarely large or may be lacking, shell smooth or ornamented by ribs, rarely more ornate, mostly similar on each valve, umbones well separated, anterior gape and sometimes posterior gape. Commonly alivincular, rarely platyvincular, hinge edentulous or with simple taxodont teeth. Muscle field monomyarian.

Discussion: Some of the attributes of modern Limidae differ from Upper Paleozoic members. In the latter forms the muscle field, as far as it is preserved, may be compact and posteriorly placed, and the shell structure differs, approaching that of especially Upper Paleozoic Aviculopectinidina – it like them lacks a well developed layer of regular prisms.

Subfamily **LIMINAE** Rafinesque, 1815

Diagnosis: Small to medium in size, typically with anterior and posterior wings and radial ribs, taxodont teeth.

Discussion: Recent and Cenozoic limids belong to this group, which is moderately diverse, and includes a number of subgenera (Cox & Hertlein 1969, Fleming 1978). Genera that conform with the general diagnosis include *Lima* Bruguière and *Ctenoides* Mörch. *Limea* Bronn is characteristic, and first entered faunas during the Triassic Period, and *Plagiostoma* Sowerby and *Pseudolimea* Arkell, also of Triassic and younger Mesozoic age, are close. The Jurassic genus *Antiquilima* Cox of Jurassic age lacks teeth, but appears close in shape and ornament. The Mesozoic to Recent genus *Acesta* Adams & Adams has reduced anterior wings, and these are missing from *Costellacesta* Kauffman, treated as a subgenus by Cox & Hertlein (1969).

Subfamily **ECHINORBINAE** new subfamily

Name genus: *Echinorbis* Waterhouse, 1987, p. 160 from the late Early Permian (Kungurian) Brae Formation, Bowen Basin, Queensland, here designated.

Diagnosis: Small as a rule, anterior and posterior wings, ornament variable, from smooth to papillate to ribbed, hinge edentulous.

Text-fig. 70. *Echinorbis papillosa* Waterhouse, left valve UQF 70265, latex cast, x7, from upper Cisuralian (Kungurian) Brae Formation of Bowen Basin, Queensland. See Waterhouse (1987).

Discussion: This subfamily includes a number of chiefly Upper Paleozoic genera, moderately close to Liminae but without hinge teeth. The name bearer is selected because most detail is known, and further material is available for more study, such as shell structure, but the ornament is highly unusual.

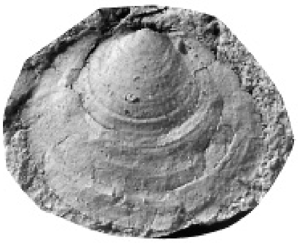
Tribe **ECHINORBINI** new tribe

Text-fig. 70, 71

Diagnosis: As for subfamily. Ligament alivincular.

Discussion: The most widely reported genus is *Palaeolima* Hind, 1903, first described from Early Carboniferous faunas of north Europe. Knowledge of the hinge is restricted, although Gonzalez (1972a) has shown that *P. antinaoensis* from mid-Carboniferous of Chubut, Argentina, has a resilifer, and the species *antecostata* Waterhouse, misidentified as *Calcicanicularia* by Waterhouse (1987) from the Flat Top Formation, Bowen Basin, Queensland, has a deep and broad resilifer. The ornament differs in different species. The latter form has simple ribs, the Argentinian species has branching twinned ribs, as also figured by Pagani (2005) and shown for the Early Carboniferous species of England described as *P. obliquiradiata* Hind (1903, pl. 19, fig. 17-19). The type species

Text-fig. 71. *Elimata symmetrica* Waterhouse. Right valve UQF 74375, x8, from Brae Formation, younger Cisuralian of Bowen Basin, Queensland. See Waterhouse (1987).



of *Palaeolima*, *P. simplex* (Phillips, 1836, pl. 6, fig. 27) of Early Carboniferous age in England is small with ribs that are possibly paired, but obscure, and specimens figured from the Isle of Man and Ireland by Hind (1903, pl. 19, fig. 24-27) have broad ribs, of which some split and stay paired on the left valve and simple ribs on the right valve. Although Hind (1903) did not describe a resilifer in recording a narrow groove along the *Palaeolima* hinge, he sometimes did not observe a resilifer, and he also noted that none of the three species from the Early Carboniferous of Ireland and United Kingdom that he described showed the hinge.

The Permian genus *Elimata* Dickins, 1963 is unusual in having a virtually smooth shell and subcentrally placed umbones, with one species *E. symmetrica* Waterhouse, 1987 having large anterior wings. Newell (1999, p. 5) claimed that the hinge of *Elimata* was unknown: not so: it has a small well developed resilifer (Waterhouse 1987). *Palaeolima laevis* Hind (1903, pl. 19, fig. 13-16) from the Early Carboniferous of England is close to this genus, which is widespread in Permian faunas. The Triassic to Recent genus *Limatula* Wood and Cenozoic *Limaria* Link lack teeth, and given the time range of *Limatula* in particular, would appear to have descended from edentulous stock, rather than have secondarily lost teeth. The Triassic genus *Tirolidia* Bittner is poorly known internally, but externally is like Echinorbinae and Liminae, with elaborate concentric ornament reminiscent in exceptionality to that of *Echinorbis*.

Tribe **CALCICANICULARIINI** new tribe

Text-fig. 72

Name genus: *Calcicanicularia* Waterhouse, 1983a, p. 164 from late Cisuralian (Kungurian) Brae fauna of Bowen Basin, Queensland, here designated.

Diagnosis: Hinge platyvincular.

Discussion: The genus *Calcicanicularia* Waterhouse is outstanding, in that the ligament is platyvincular, with no resilifer. In shape the genus is not exceptional, having small moderately delimited anterior and posterior wings and retrocrescent outline, with no teeth, as in Echinorbini.

The evidence from *Calcicanicularia* clearly shows that some Paleozoic limoids lacked a resilifer, because *Calcicanicularia* is limoid, not streblochondroid, judged from the lack of a right valve anterior auricle and byssal notch.

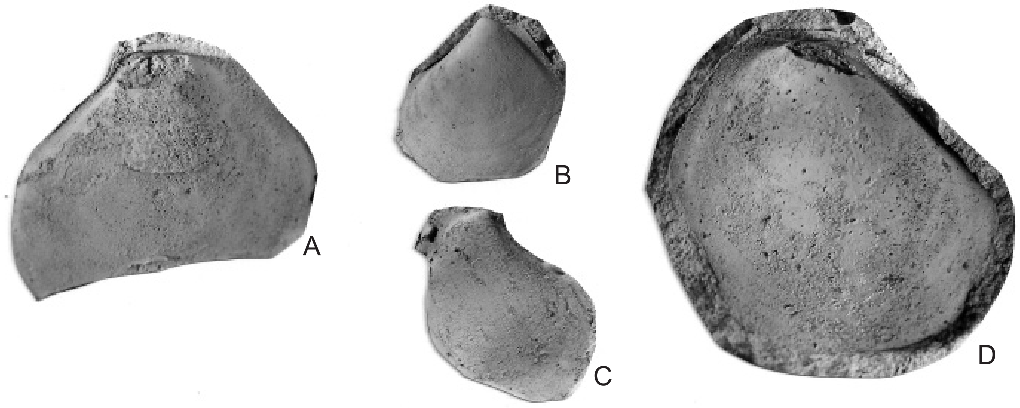
Subfamily **MYSIDIOPTERINAE** new subfamily

Text-fig. 73

Name genus: *Mysidioptera* Salomon, 1895, p. 117 from Upper Triassic Marmolatakalk of Austria, here designated.

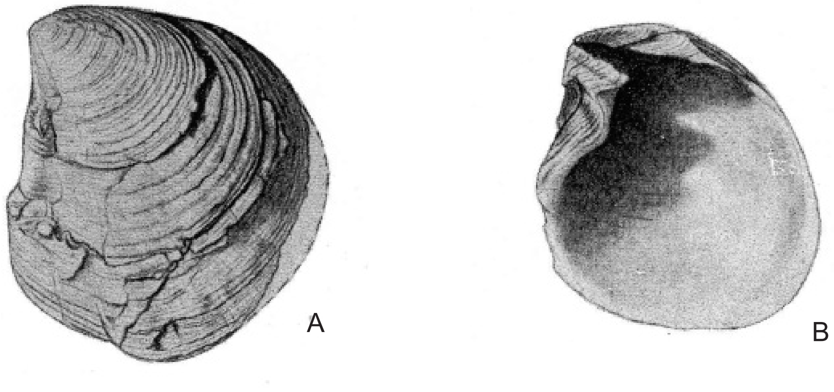
Diagnosis: Moderately large for the family, no posterior wings and feeble or generally no anterior wings, edentulous.

Discussion: *Mysidioptera* is a common and widespread Triassic genus, clearly limid in construct,



Text-fig. 72. *Calcicanicularia glabra* Waterhouse, x 1.5. A, left valve internal mould UQF 70075. B, left valve UQF 70071. C, right valve UQF 70072. D, right valve internal mould, holotype UQF 70073. From Early Permian (Artinksian) upper Tiverton Formation, Queensland. See Waterhouse (1983a).

but with reduced, or in my experience, no anterior wings, and no posterior wings, the posterior shell sloping back gradually to the posterior and dorsal margins. Many species are smooth, others are ribbed. A Jurassic genus *Regalilima* Cox is similar, and the strongly retrocrescent *Serania* Krumbeck of Late Triassic age in Indonesia is an extreme development from smooth *Mysidioptera*, but has developed the suggestion of a posterior wing. A more strongly ribbed genus *Badiotella* Bittner is also of Triassic age. The age and the nature of the hinge indicate derivation from Echinorbinae.



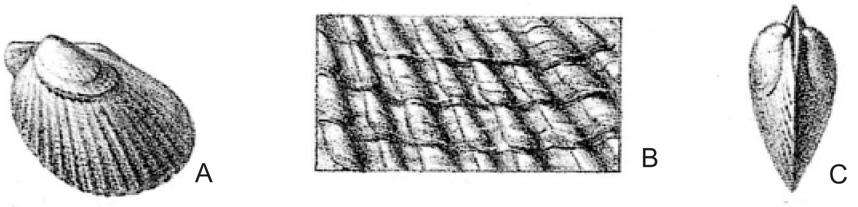
Text-fig. 73. *Mysidioptera riceae* Waterhouse. A, left valve holotype TM 2101 (PVC cast), from Waiwera River, Southland, New Zealand. B, internal view of right valve TM 2099 (PVC cast) from Wairoa Gorge, Nelson, New Zealand. Specimens of Late Triassic age, x2. See Waterhouse (1960).

?Family **LIMATULINIDAE** Waterhouse, 2001

Text-fig. 74

[nom. transl. hic ex Limatulininae Waterhouse 2001, p. 128].

Diagnosis: Medium-sized for family, normally procrescent, smooth or lightly ribbed, with



Text-fig. 74. *Limatulina radula* (Koninck), left valve, ornament detail and posterior view of original specimen IRSNB 4964 figured by Koninck (1885, pl. 36, fig. 15, 16, 17) from Visean (Early Carboniferous) of Belgium, x1.

comparatively prominent anterior wings or auricles above an unusually distinct sinus. Hinge edentulous.

Discussion: The position of *Limatula* Koninck, 1885 is not certain. It was considered to be aviculopectinid by Newell & Boyd (1981), as accepted by Waterhouse (2001), with good reason, it appeared, because a right anterior auricle is developed above a small but distinct byssal notch, and left anterior wing sinus. Yet otherwise the genus has been judged to be limid (Koninck 1885, Hind 1903). The valves are subequivalve, an anterior gape is developed, the shell is thick, and overall specimens convey an admittedly elusive impression of limiform affinities, that need to be tested further by examination of the shell structure and composition, which will at the same time strengthen the case for deeming how significant shell structure is to be regarded for classification. Unlike Aviculopectinoidea, the ornament does not involve plicae, and yet the shape is more upright with longer umbonal walls than found in Chaenocardioidea. If the genus is limid, it is unusual because of the procrescent rather than retrocrescent outline and depth of byssal notch and nature of the anterior wings. Some other limid genera show considerable similarities, but lack a byssal notch. Mature *Aviculolima* Phillipi of Triassic age is bicrescent, procrescent at first, then curving into a retrocrescent outline, and the anterior wings are large above a deep sinus, and the posterior wings large. A Permian genus *Gloverilima* Newell, 1999 also has small but clearly set-off posterior and anterior wings, and general appearance close to that of *Limatulina*, apart from a much higher cardinal area and signs of denticulate hinge. Newell synonymized his genus *Gryphellina* with this genus, considering he had misinterpreted the nominated type species. Koninck (1885) and Hind (1903) ascribed a number of species to *Limatulina*, and several appear limid and are shown as lacking any byssal recession. It is considered that these should be assessed before any decision is possible.

Order Ostreida Ferussac, 1822

Waller (1978, p. 352) showed Ostreiida as developing from Pterineidae separately from Limida, very different from what the fossils record. Originally it was assumed that the absence of nacre and presence of foliated calcite shell micro-structure characterized the clade, involving Ostreoidea, Pectinoidea, Anomioidea, and other groups, but Carter (1990) showed that nacre was replaced by aragonitic structures, and regular prismatic calcite by other structures, as part of ongoing evolution. Hautmann (2004) has outlined the characteristic and unusual development of what he called the alivincular-arcuate ligament in Ostreidae, involving arching of the attachment surface of the ligament. Waller (1998, p. 29) linked Monotoidea and Ostreioidea, but relied on the morphological interpretation for Monotoidea by Begg & Campbell (1985).

Classification and relationships

Waller (1998) treated oysters as belonging to a stand-alone order, expressed by Amler (1999, p. 240) as involving four superfamilies, all closely allied, with three of the superfamilies containing only one family each. Here it proposed to greatly expand the content of the order, by incorporating various Paleozoic forebears and even Mesozoic contemporaries. These groups were assigned to Pectinida by Waller (1978) and Amler (1999), but are much closer to oysters. The oysters in the strict sense are relegated to Suborder Ostreidina Waller, 1878, and are linked with Etheripectinidina new suborder.

Diagnosis: Inequivalve, ornament usually different on the two valves, hinge long or secondarily reduced, amphidetic and alivincular as a rule, usually byssally attached, may be cemented.

Suborder **ETHERIPECTINIDINA** new suborder

Diagnosis: Inequivalve, right valve less convex and as a rule differently ornamented, right anterior auricle usually well developed, rarely may be lost, posterior wings as a rule well developed, rarely may be lost, hinge normally amphidetic and ligament alivincular, monomyarian. Shell structure somewhat variable in structure but consistent in groups, and composition varies through time and in response to paleolatitude.

Discussion: In its diversity and evolutionary vigor, this suborder occupied a significant part of the panoply of Late Paleozoic and Mesozoic Pectinidia. Members differ from Pterinopectinida in the nature of the ligament, and from Aviculopectinidina in the less convex right valve with ornament different from that of the left valve. Monotidina are distinguished by the reduced anterior shell, and loss of amphidetic ligament. Some etheripectens approach this in the later Mesozoic, but retained for the most part a tiny anterior auricle and asymmetrically amphidetic ligament; a few lost the anterior auricle and the ligament became largely opisthodetic. These changes may be traced through the geological record, and caution against over-restrictive definitions: they also demand a sophisticated form of cladistics.

Classification: The following superfamilies are recognised:

Superfamily Etheripectinoidea Waterhouse, 1982
Superfamily Oxytomoidea Ichikawa, 1958
Superfamily Aulacomyelloidea Ichikawa, 1958
Superfamily Pseudomonotoidea Newell, 1938

Superfamily **ETHERIPECTINOIDEA** Waterhouse, 1982

[nom. transl. hic ex Etheripectininae Waterhouse, 1982, p. 15].

Diagnosis: Left valve convex, right valve small and gently convex to concave, left valve ornament usually different from that of right valve, left valve wings variably developed but long and well defined, right posterior wing long and well defined, right anterior auricle long with generally well developed byssal notch. Hinge alivincular, usually without teeth. Shell varies in composition.

Discussion: To simplify and rationalise the multiplicity of pectiniform families regarded as distinct from each other by various authorities lasting from Newell (1938) to Newell & Boyd (1995), groups hitherto regarded as disparate are linked by the nature of their left-valve – right-valve inflation, size, shape and ornament.

Classification: The superfamily is arranged in these divisions.

Family Etheripectinidae Waterhouse, 1982
    Subfamily Etheripectininae Waterhouse, 1982
    Subfamily Cassianoidinae Newell & Boyd, 1995
    Subfamily Heteropectininae new

Subfamily Girtypectininae new
Family Limipectinae Newell & Boyd, 1990
Family Annuliconchidae Newell & Boyd, 1995
Family Acanthopectinidae Newell & Boyd, 1995
Subfamily Acanthopectininae Newell & Boyd, 1995
Subfamily Lamnipectininae new
Subfamily Costatiplicatininae new

The superfamily is characterized by two major attributes – the right valve is almost flat, and the right valve ornament differs from that of the left valve, so that the group is readily distinguished from the mostly Late Paleozoic members of Aviculopectinidina. According to Fleming (1957a), living pectinids with flat valve opposed to convex valve are sessile, whereas biconvex shells are mobile. In other attributes, the alivincular long hinge, strongly defined left valve umbonal ridges and prominent right anterior auricle with deep byssal notch, are characteristic and shared with Aviculopectinoidea and to lesser degree with Chaenocardioidea. Etheripectinidae Waterhouse, 1982, p. 15 is the least outstanding, with alivincular ligament, and regular growth development. Shell structure includes species with calcite cross-foliae. The family is known in Early Carboniferous deposits. It seems likely that Etheripectininae provided the root-stock for the other subfamilies, but the source of Acanthopectinidae remains more conjectural. In addition, Etheripectininae were the source of Oxytomoidea and Aulacomyelloidea, mostly Mesozoic groups, and probably the source for Pseudomonotoidea.

The origins of the group appear to point in one direction. It is true that members of Undopectininae (Family Aviculopectinidae) show the costation, though less differentiated, of Etheripectinoidea, as well as the alivincular hinge and long posterior wings, but they have ornament similar on both valves, with convex right valve. The pterinopectiniform source stock Natalissiminae has a less convex right valve and ornament differing that of the left valve, and the left valve ornament of *Natalissima* is differentiated and close to that of *Etheripecten* itself. Its ligament is chevron duplivincular, not alivincular. That strongly suggests that Etheripectinoidea arose from Pterinopectinidina, independently of Aviculopectinoidea.

Family **ETHERIPECTINIDAE** Waterhouse, 1982

[nom. transl. Newell & Boyd 1995, p. 33 ex Etheripectininae Waterhouse, 1982, p. 15].

Diagnosis: Shells inequivalve, right valve comparatively flat, posterior wings large, umbonal slopes well defined, ornament primarily costate, not plicate, increase mostly by intercalation rather than branching on left or both valves, ornament more varied and elaborate on left valve, simpler and more closely spaced on right valve, growth-lines swing hingewards in interspaces. Hinge alivincular, hinge teeth rarely present.

Discussion: This is a large group (Newell & Boyd 1995) of Late Paleozoic age, readily distinguished from Aviculopectinidae by the less inflated right valve with usually different ornament: the differences are sharpened by the demonstration in Newell & Boyd (1995) and Fang & Morris (1999) of the nature of *Aviculopecten*, as confirmed herein, so that the positions of some family group units need to be readjusted from Waterhouse (2001).

Subfamily **ETHERIPECTININAE** Waterhouse, 1982

Diagnosis: Ornament of intercalate costae on left and right valve, branching exceptional, costae variably spinose.

Discussion: The genera that belong to the subfamily include *Etheripecten, Etheriplica* n. gen., *Primaspina* n. gen., *Vnigripecten* Muromseva, 1984 and *Glabripecten* Waterhouse, 1982. Of the new genera described herein from the Early Carboniferous of Ireland, Scotland and England, *Costellinaria* has very fine costae, of uncertain origin but appearing to increase both by branching and intercalation, so it is provisionally retained in Etheripectinae. It is not possible at present to confidently allocate all genera to either Etheripectininae and Heteropectininae, and in the present construct, Heteropectininae is interpreted as a group that began no later than Early Carboniferous and became clearly differentiated only in the Late Carboniferous and Permian.

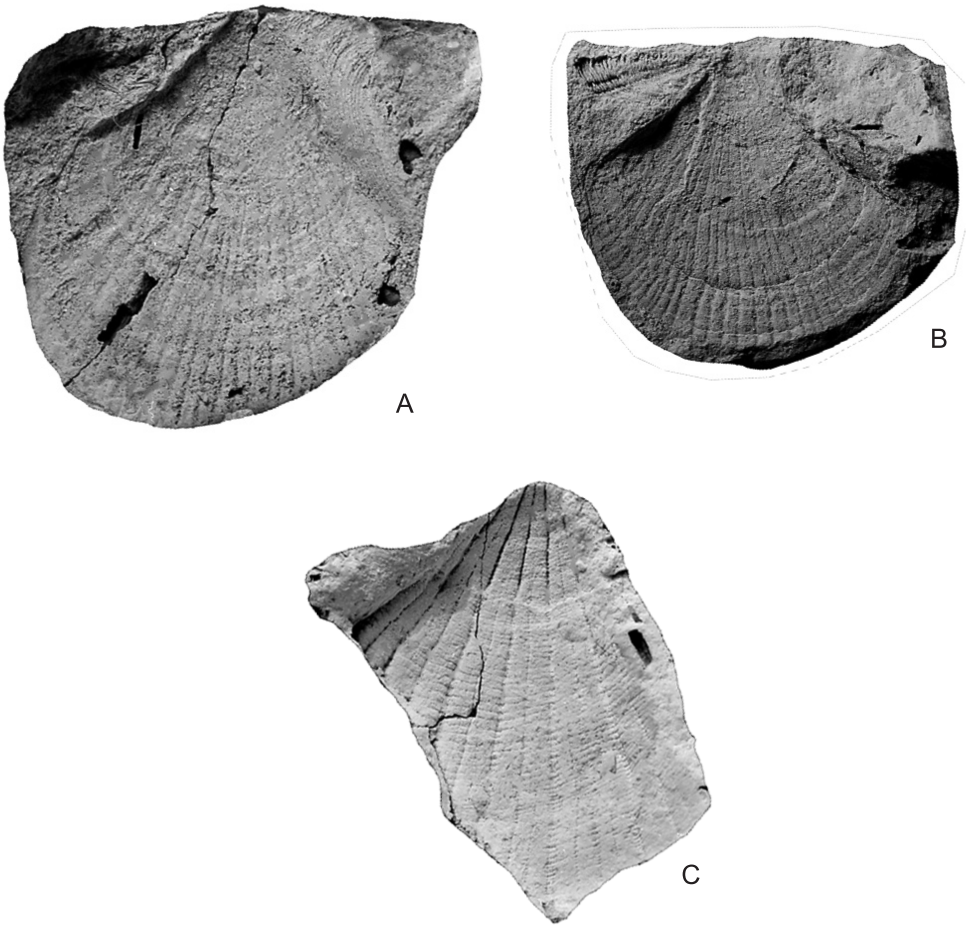
Genus ***Etheripecten*** Waterhouse, 1963

Text-fig. 75 - 77

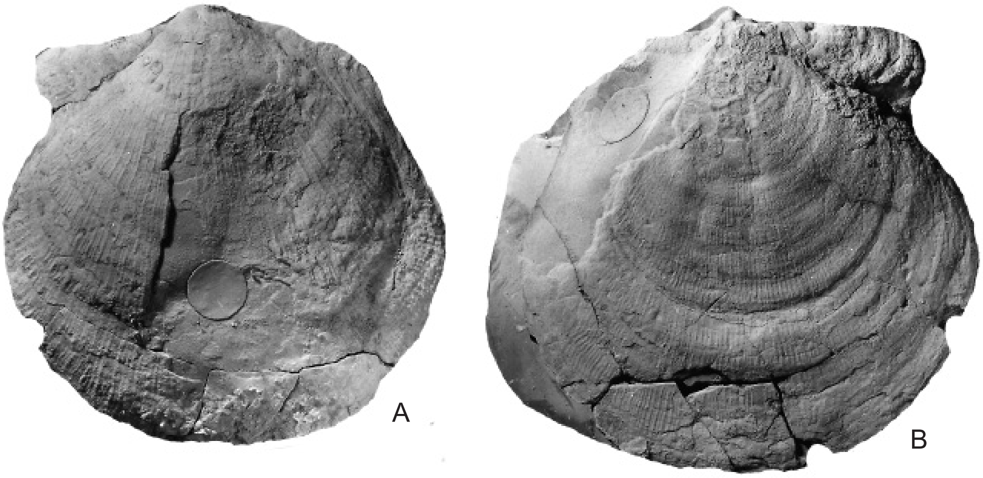
Type species: *Etheripecten striatura* Waterhouse, 1963, p. 195 from Late Permian (Changhsingian) Kildonan Member, New Zealand.

Diagnosis: Left valve bears costae in several orders as a rule, arising by intercalation, primary costae generally remaining prominent. Right valve costae simpler and more uniform. Growth lines arch dorsally in interspaces. Shell aragonitic or calcitic.

Discussion: The genus is amongst the most widespread of Late Paleozoic bivalves, and is

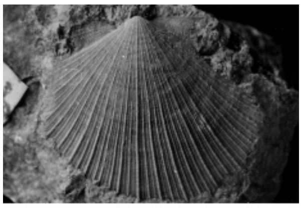


Text-fig. 75. *Etheripecten striatura* Waterhouse. A, external mould of left valve TM 3632, x3. B, right valve of same species, external mould TM 3631, x1.5. C, detail on external mould of left valve TM 3633, x4. From early Changhsingian (Late Permian) Kildonan Member, Bagrie Formation, New Zealand. See Waterhouse (1982, 2002a).



Text-fig. 76. *Etheripecten leniusculus* (Dana), left valve and right valve, unregistered specimen at Australian Museum, from Middle Permian (Wordian) of south Sydney Basin, New South Wales, x 0.66.

particular common in the Permian of east Australia, with many of the species described by Dana (1847, 1849), M'Coy (1847), Etheridge & Dun (1906) and Fletcher (1929), later revised and some refigured by Waterhouse (1982). Despite having been widely recognised, for example by Newell, Cox & Hertlein (1969), Nakazawa (1996) and Dickins (1981), *Etheripecten* was synonymized with *Heteropecten* Kegel & Costa, 1951 by Newell & Boyd (1995), with the claim that variation within *Heteropecten* encompassed *Etheripecten*-type shells. No specific examples were cited and no substantive evidence has been offered. The type species of *Heteropecten* (see Text-fig. 84 - 87), originally cited as of upper Carboniferous age, has been extensively figured by Reed (1930), Kegel & Costa (1951), Rocha-Campos (1967, pl. 29, fig. 1-3; 1970, pl. 1, fig. 1-11, pl. 2, fig. 1-10) and Waterhouse (1969, text-fig. 5; 1982, pl. 1, fig. a-c), and other species have received attention. The primary ribs in the left valve of *Heteropecten* are broad like narrow plicae, whereas the primary ribs in *Etheripecten* are solid costae, and the shell is undulose in *Heteropecten*, unlike that of the *Etheripecten* left valve. The left valve ornament varies considerably in the type and other species of both genera. The range is well illustrated by Rocha-Campos (1970) for the type species of *Heteropecten*. In all specimens, the primary ribs are coarser than in type or other *Etheripecten*. In some they are very broad, and bear several fine costae. Interspaces in *Heteropecten* remain narrow: it is the primary ribs that occupy much of the width of left valves. The interspaces may bear one or two orders of finer, close-set ribs, but are not as broad as in *Etheripecten*. A species described by Pagani (2005, Fig. 4C-F) shows strong left valve subplicae. In short, ribs are wider in



Text-fig. 77. *Etheripecten clathratus* (M'Coy), left valve NHM 45607 from Early Carboniferous of England, x1. Photograph courtesy of Natural History Museum, London.

Heteropecten, and interspaces are much wider in *Etheripecten.* In the right valve, as stressed by Nakazawa (1999), the ribs are broad and bifurcated in *Heteropecten*, and narrow and intercalated in *Etheripecten*, a difference also underlined by Fang & Morris (1999), although it appears that some right valves of *Heteropecten* have narrow ribs (see Rocha-Campos 1970, pl. 1, fig. 8, 11). There are further differences, some enumerated in Waterhouse (2001, p. 120). The two genera look very different, and there appears to be no gradation between the two suites, so that during an extensive survey of Late Paleozoic Aviculopectinidina, not a single species has been found that seems to span the two genera – ie. fall between the characteristics displayed by the two type species. The differences are well displayed in figures in Waterhouse (1969).

Newell & Boyd (1995) even extended the range of *Heteropecten* to include deltopectinid genera *Squamuliferipecten* Waterhouse and *Corrugopecten* Waterhouse, genera that not only have swollen right valves – unlike *Heteropecten* with its almost flat right valve, but lack a resilifer. Their misrepresentation of *Heteropecten* was so broad that they incorporated genera of different families under one generic name.

Earlier Newell in Newell et al. (1969, pp. 336, 337) had synonymized *Heteropecten* with *Aviculopecten*, and recognised *Etheripecten*. This may have been influenced by the very experienced L. R. Cox, who contributed to the same section, but also reflected the fact that Newell (1938) had identified North American species of *Heteropecten* as *Aviculopecten* (see p. 146). He had also interpreted *Aviculopecten* in such a way that it incorporated *Etheripecten*-like species as well as *Vanvleetia* Waterhouse, so that the 1969 Treatise conceded a partial revision of Newell (1938), and this was consolidated by revision of *Aviculopecten* and *Heteropecten* by Waterhouse (1969).

Genus ***Costellinaria*** new genus

Text-fig. 78

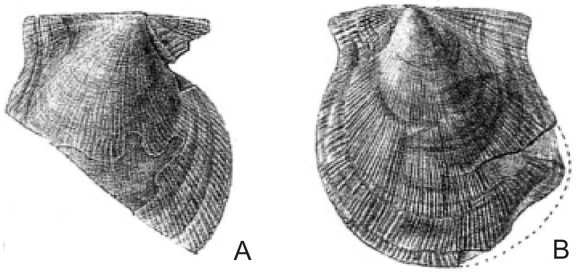
Derivation: costa – rib, Lat.

Type species: *Aviculopecten subconoideus* Etheridge, 1876, p. 96 from Early Carboniferous of Scotland, here designated.

Diagnosis: Pectiniform shells with numerous fine ribs on each valve, increase by branching and by intercalation. Byssal notch well developed and right anterior auricle distinct.

Discussion: This genus is distinguished by its fine ribbing and by its well-formed byssal notch and distinct right anterior auricle. The genus is widespread, and well represented in Carboniferous faunas of northern Europe, including the type species *Aviculopecten subconoideus* Etheridge (1876, p. 96, pl. 4, fig. 1, 2) from Knockhill, Fyfe, Scotland, also figured by Hind (1903, p. 76, pl. 17, fig. 1-5) and Wilson (1962, p. 56, pl. 4, fig. 8-10). The lectotype GSE 11852 was designated by Wilson (1962, p. 57). Newell (1938) had raised the possibility of denticles along the hinge, but this was dismissed by Wilson. A resilifer is present in NHM L47652 figured by Hind (1903, pl. 17, fig. 4), though not recorded in his text. An allied species is *Pecten plicatus* Sowerby, 1829, pl. 574, fig. 3, also figured by Hind (1903, p. 73, pl. 12, fig. 5, 6, 8, 9). The species has large posterior wings and includes, according to Hind (1903), *Pecten hians* M'Coy (1844, p. 94, pl. 16, fig. 6) and *P. micropterus* M'Coy (1844, p. 96, pl. 15, fig. 12), though the latter appears to have simpler ribbing.

The genus possibly includes *Aviculopecten* sp. A and *A. gravidus* Gordon & Pojeta (1975, pl. 3, fig. 5-7) from the Pennsylvanian Horseshoe Shale Member, Amsden Formation, Wyoming, but the valves appear very inflated, suggesting the need for further study. *Limipecten* sp. (Feng 1988, pl. 2, fig. 9a, b) from the Shiqiantan Formation, Junggar Basin, China, of Middle to Late Carboniferous age, may be allied to *Costellinaria*.



Text-fig. 78. *Costellinaria subconoideus* (Etheridge). A, B, right and left valve aspects of NHM specimens figured by Hind (1903, pl. 17, fig. 4, 5) from Carboniferous at Knockhill, Fyfe, Scotland, x1.

Limipecten multistriatus Maxwell (1964, p. 15, pl. 2, fig. 1-3, pl. 3, fig. 18-22) from Upper Carboniferous Branch Creek Formation, Yarrol Basin, Queensland is moderately well preserved, and is represented by a large collection kept at the Queensland Museum. The fine costae increase by branching and intercalation of the left valve; the right anterior auricle is large, and the posterior wing large on both valves. The resilifer shown by UQF 42957 (Maxwell 1964, pl. 3, fig. 20) is shallow and broad. *Aviculopecten flexicostatus* Mitchell, 1924 from the *Levipustula levis* Zone in New South Wales is related or congeneric. The ribs are fine, narrow, round-crested and intercalated on both valves, judged from inspection at the Australian Museum (eg. right valve AMF 26460). The mature left valve shows 6-8 fine growth increments between stronger laminae, which total about 68 (AMF 26461). That implies a life span close to three years, assuming that the growth increments were diurnal, and allowing for full size.

In many respects, the new genus looks like *Spyridopecten* Campbell & McKelvey, 1972 from the Buckets Gap Formation, of “Namurian” (Serpukhovian, Bashkirian) age in the Manning River valley of northern New South Wales, based on type species *S. monstrosus* Campbell & McKelvey, 1972. It has branching fine ribs on the gently convex right valve and some intercalated fine ribs in the left valve, which is more but not strongly inflated. *Spyridopecten* has a resilifer but unlike the new genus, has a very shallow byssal sinus, to the extent that it is scarcely visible in the various figures provided by Campbell & McKelvey. In addition right valve costae are feeble over much of the valve, and fine commarginal filae are well developed (see p. 76). A specimen ascribed to *Spyridopecten* by Newell & Boyd (1995) from the Upper Carboniferous Graham Shale or Jacksboro Formation of Texas is closer because the anterior right sinus is deeper than in *Spyridopecten*, and close to that of some specimens of *Costellinaria*, but usually a little shallower, and concentric laminae are more prominent and the ribs form a more regular pattern, intercalated, and ventrally branching to form narrow bundles in the left valve.

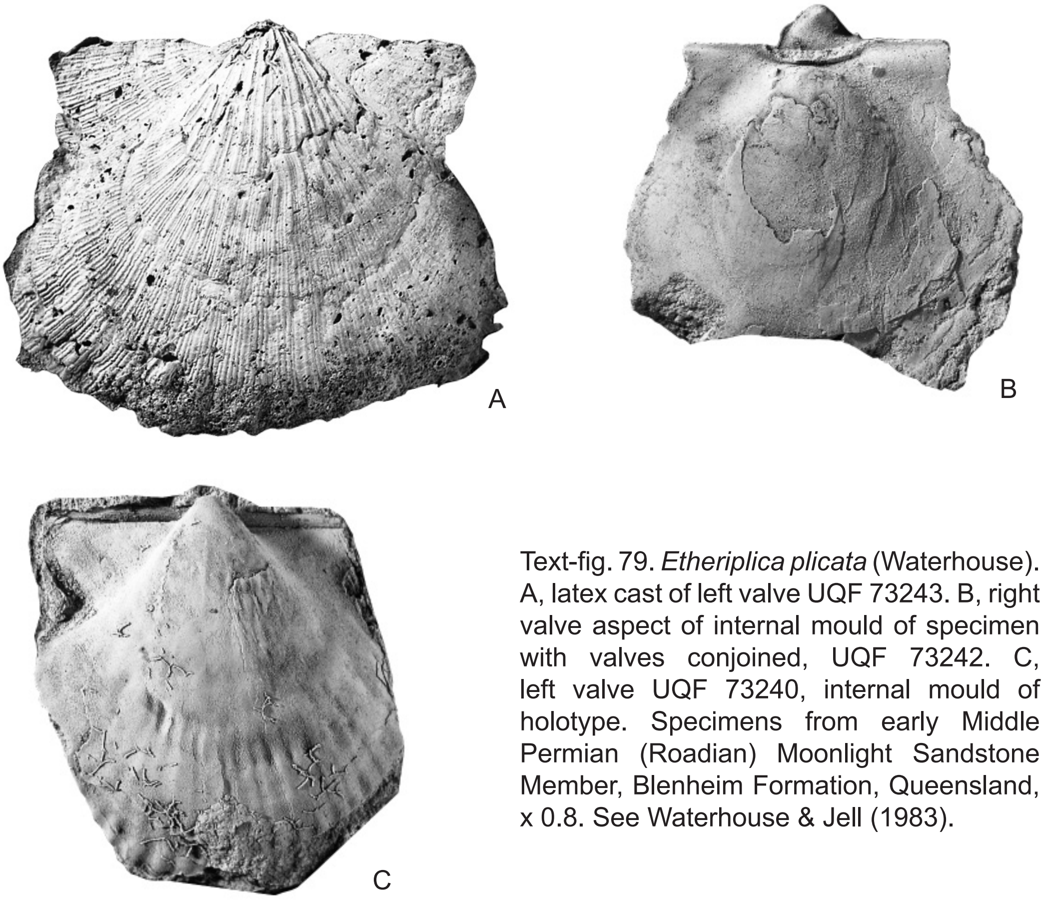
Genus ***Etheriplica*** new genus

Text-fig. 79, 80

Derivation: Named from R. Etheridge Jnr; plica – fold, Lat.

Type species: *Etheripecten plicatus* Waterhouse in Waterhouse & Jell (1983, p. 248) from the Roadian (Middle Permian) Moonlight Sandstone Member, north Bowen Basin, Queensland, here designated.

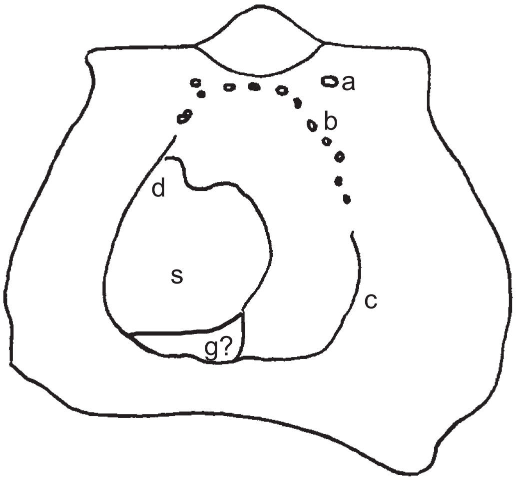
Diagnosis: Large shells, left valve convex with costae in several orders, increasing by intercalation, plicae develop below primary costae over lower two thirds of shell, without affecting costae. Right valve almost flat, covered by close-set costae, without plicae.



Text-fig. 79. *Etheriplica plicata* (Waterhouse). A, latex cast of left valve UQF 73243. B, right valve aspect of internal mould of specimen with valves conjoined, UQF 73242. C, left valve UQF 73240, internal mould of holotype. Specimens from early Middle Permian (Roadian) Moonlight Sandstone Member, Blenheim Formation, Queensland, x 0.8. See Waterhouse & Jell (1983).

Description: The species has been described in Waterhouse & Jell (1983). A new species yet to be described comes from the underlying Tiverton Formation in Queensland, and was figured under various names by Etheridge (1892, pl. 43, fig. 2), Dickins (1963, pl. 11, fig. 1?, 2, 3), Hill & Woods (1964b, pl. P11, fig. 13a, b, 14, 15) and Waterhouse (1982, pl. 3, fig. i). Both species show internal detail that differs slightly from the interior described for "*Aviculopecten*" by Newell (1938), and quoted widely – and without substantiation - as typifying the interior of *Aviculopecten* (see p. 146). Two figured mature left valves of *plicatus* (Waterhouse & Jell 1983, pl. 4, fig. 1, 3) show a compact muscle complex placed high and near the anterior edge of the valve with pallial line breaking into pits dorsally. A Tiverton specimen shows a pallial line almost at mid-height, an anterior row of pits and well formed pedal levator muscle. The posterior pallial line is faint (Text-fig. 80). The right valve (Waterhouse & Jell 1983, pl. 4, fig. 4, 6) confirms that the area enclosed by the pallial line is small and the pits are well defined. Unlike the arrangement figured for "*Aviculopecten*" *exemplarius* by Newell (1938), the gap between the anterior and posterior ends of the pallial line is occupied under the hinge by two and sometimes three well defined pits. This is reinforced by a right valve of the new *Etheriplica* species from the nearby Tiverton Formation, of slightly greater Permian age. It seems possible that the difference from Newell's "*Aviculopecten*" [which is now placed in *Heteropecten*] involved a different degree of mobility for *Etheriplica*, given the large size and thin shell, large muscle scar and deep resilifer. The right anterior auricle in particular of *Etheriplica* is very large, projecting beyond the body of the shell, which seems conducive neither to rapid movement, at least in a forward direction, nor to attachment by byssus.

Discussion: This genus is very close to *Etheripecten* Waterhouse, 1963, with similar costation, convex left valve, little inflated right valve, large right anterior auricle, alivincular hinge, and



Text-fig. 80. *Etheriplica plicata* (Waterhouse), x1 right valve internal mould UQF 72242, location as in Text-fig. 61. a, b – pedal levator scars, c – pallial line, d – pedal retractor muscle scar, g – gill scars, s – adductor muscle complex.

well preserved muscle complex and pallial line. It is distinguished from *Etheripecten* by the development of well spaced plicae over the lower ventral valve, and signifies a minor lineage within the *Etheripecten* complex: designation as subgenus would be appropriate. The material was described in Waterhouse & Jell (1983, p. 248, pl. 4, fig. 1-4, 6, 11, 14), with holotype UQF 73240 (pl. 4, fig. 3), and the specimens are kept at the Queensland Museum as part of the University of Queensland collections. It is difficult to determine the mode of increase of the right valve ribbing: but most, especially medianly, are intercalated, others especially on the flanks and anteriorly increase by branching.

Shells described as *Aviculopecten trichotomus* by Kegel & Costa (1951) from faunas assigned a Westphalian B age in Brazil are possibly related, with narrow ribs over the left valve umbo expanding into low costate plicae (Text-fig. 85H herein), but interspaces are narrow. The right valve is little inflated with branching simple costae.

Genus **Fletcheripecten** Waterhouse, 1982

Text-fig. 81

Type species: *Fletcheripecten heterosus* Waterhouse, 1982, p. 24 from Middle Permian (Wordian) Mangarewa Formation, Wairaki Downs, New Zealand.

Diagnosis: Left valve close to *Etheripecten* but with unusually high and broad primary costae, right valve with numerous fine costae increasing by intercalation.

Discussion: *Fletcheripecten* Waterhouse, 1982 was established for New Zealand and Australian species of Permian age that were characterized by having narrow primary plicae with narrow to wide interspaces that either lack costae, or bear narrow costae. The left valve is close to that of *Heteropecten*, as pointed out by Newell & Boyd (1995), but in the right valve, the slender ribs arise by intercalation, not branching, a critical difference. *Fletcheripecten* provides either a good example of convergent evolution from etheripectinid stock – or an example of divergent evolution from heteropectinin stock, and the first option seems to be favoured by available evidence,

Text-fig. 81. *Fletcheripecten*. A, *F. heterosus* Waterhouse, right valve TM 5205 from Middle Permian (Wordian) Mangarewa Formation, New Zealand, x 0.6. B, *F. laticostatus* Waterhouse, left valve USNM 3652, from Early Permian (Asselian) Allandale Formation, New South Wales, x 0.6. See Waterhouse (1982).

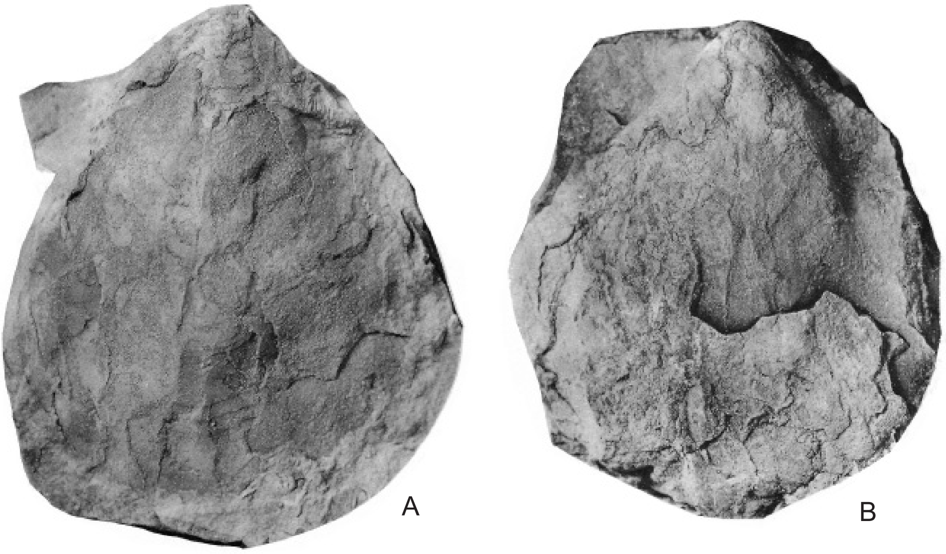
because the right valve costae are intercalated and slender, and the left valve interspaces broad, both characteristic features of *Etheripecten* and rare or absent in *Heteropecten*.

Species are common throughout the Permian sequences of east Australia and New Zealand.

Genus ***Glabripecten*** Waterhouse, 1982

Text-fig. 82

Type species: *Glabripecten glaber* Waterhouse, 1982, p. 27, from middle Guadalupian (Wordian) Mangarewa Formation, New Zealand.



Text-fig. 82. *Glabripecten glaber* Waterhouse from Middle Permian (Wordian) Mangarewa Formation, New Zealand, x 0.6. Left valves TM 3513 and holotype TM 3512. See Waterhouse (1982).

Diagnosis: Devoid of radial ornament and marked only by weak commarginal growth-lines, left valve convex, right valve weakly convex, wings large, right anterior auricle slightly shorter. Shell of both valves made up of thin lathes of alternating translucent and opaque calcite.

Discussion: Etheripectinid genera vary substantially in ornament, and this genus is outstanding in that radial ornament is completely lacking. It is etheripectinid, with inflated left valve, weakly convex right valve, wide hinge and well developed resilifer. The right anterior auricle is not as large as in a number of the species allocated to *Etheripecten*. The type species of *Glabripecten* shows a distinctive shell structure of fine lathes (6-10 in 1mm) of alternating translucent and opaque shell material, suggestive of cross-foliae. The genus is so far known only from New Zealand. It appears likely to have evolved from *Etheripecten leniusculus* (Dana, 1847), figured by Waterhouse (1982, pl. 5, fig. a-f, pl. 6, fig. a, b, e, pl. 9, fig. e; 1988, pl. 2, fig. 6, pl. 3, fig. 1, 2) from Guadalupian faunas of east Australia and Text-fig. 76 herein. This species has moderately convex right valve, swollen left valve, thick shell, fine costae in several orders on the left valve, and fine costae on the right valve.

The large size and comparatively smooth shell recall the Taimyr Permian species described as *Pecten* (*Pseudamusium*) *levis* Lutkevich & Lobanova (1960, pl. 21, fig. 7, 8, pl. 22, fig. 1-7, pl. 23, fig. 1, 2, pl. 25, fig. 1, 2) but the Siberian species has short posterior wings and low regular concentric laminae. Concentrics are stronger in another large Taimyr species *P*. (*P*). *rotundus* Lutkevich & Lobanova (1960, pl. 24, fig. 1, 2). These Siberian forms belong to *Concentiolineatus*.

Genus ***Primaspina*** new genus

Text-fig. 83

Derivation: primo – at first; spina – spine, Lat.

Type species: *Aviculopecten dawsonensis* Runnegar & Ferguson, 1969, p. 262, from mid-Permian (Wordian) Flat Top Formation, Bowen Basin, Queensland, here designated.

Diagnosis: Left valve convex with several orders of costae arising by intercalation, primary ribs spinose at regular intervals, right valve less inflated, with undifferentiated apparently intercalated ribs. Hinge alivincular.

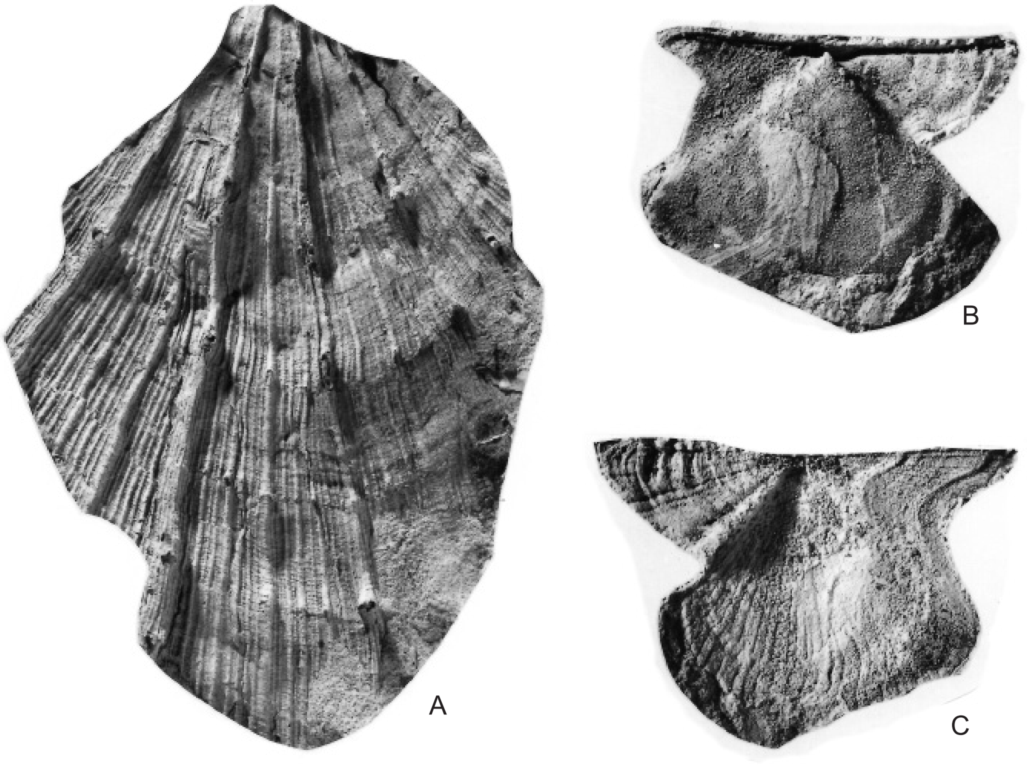
Discussion: In most respects this genus is very close to *Etheripecten*, and is distinguished by the development of lamellar spines at regular intervals on primary ribs of the left valve. The type species has been described and figured by Hill & Woods (1964b, pl. P11, fig. 16, 17), Hill et al. (1972, pl. P11, fig. 16, 17), Runnegar & Ferguson (1969, pl. 5, fig. 14, 15, 16?, 17-19) and Waterhouse (1987, pl. 5, fig. 4, 5, 7-10, 13). *Aviculopecten sprenti* Johnston, 1887, 1888 from Tasmania, and a new species from the Tiverton Formation of Queensland are congeneric. *Pecten intercostatus* M'Coy (1844, pl. 18, fig. 4) from the Carboniferous of Ireland has prominent spines shown as hooking dorsally on the left valve primary, secondary and even tertiary ribs.

Subfamily **HETEROPECTININAE** new subfamily

Name genus: *Heteropecten* Kegel & Costa, 1951, p. 18, from Early Permian of Brazil, here designated.

Diagnosis: Moderate to large, left valve more inflated than right valve, wings and right anterior auricle long, hinge amphidetic alivincular. Characterized by ribs branching on right valve and often strong and paired, or finer and bundled. Pallial line open dorsally, no pits between dorsal ends.

Discussion: This group is distinguished from Etheripectininae by the mode of increase of right valve costae. The ribs branch, and may remain associated in pairs, or form low more complex bundles. In addition, the pallial line opens dorsally to the hinge, whereas in *Etheripecten* and



Text-fig. 83. *Primaspina dawsonensis* (Runnegar & Ferguson). A, latex cast of left valve UQF 74341. B, C, right valve internal and external mould, UQF 74338. From Flat Top Formation (Wordian, Middle Permian), Bowen Basin, Queensland, x 0.8. See Waterhouse (1987).

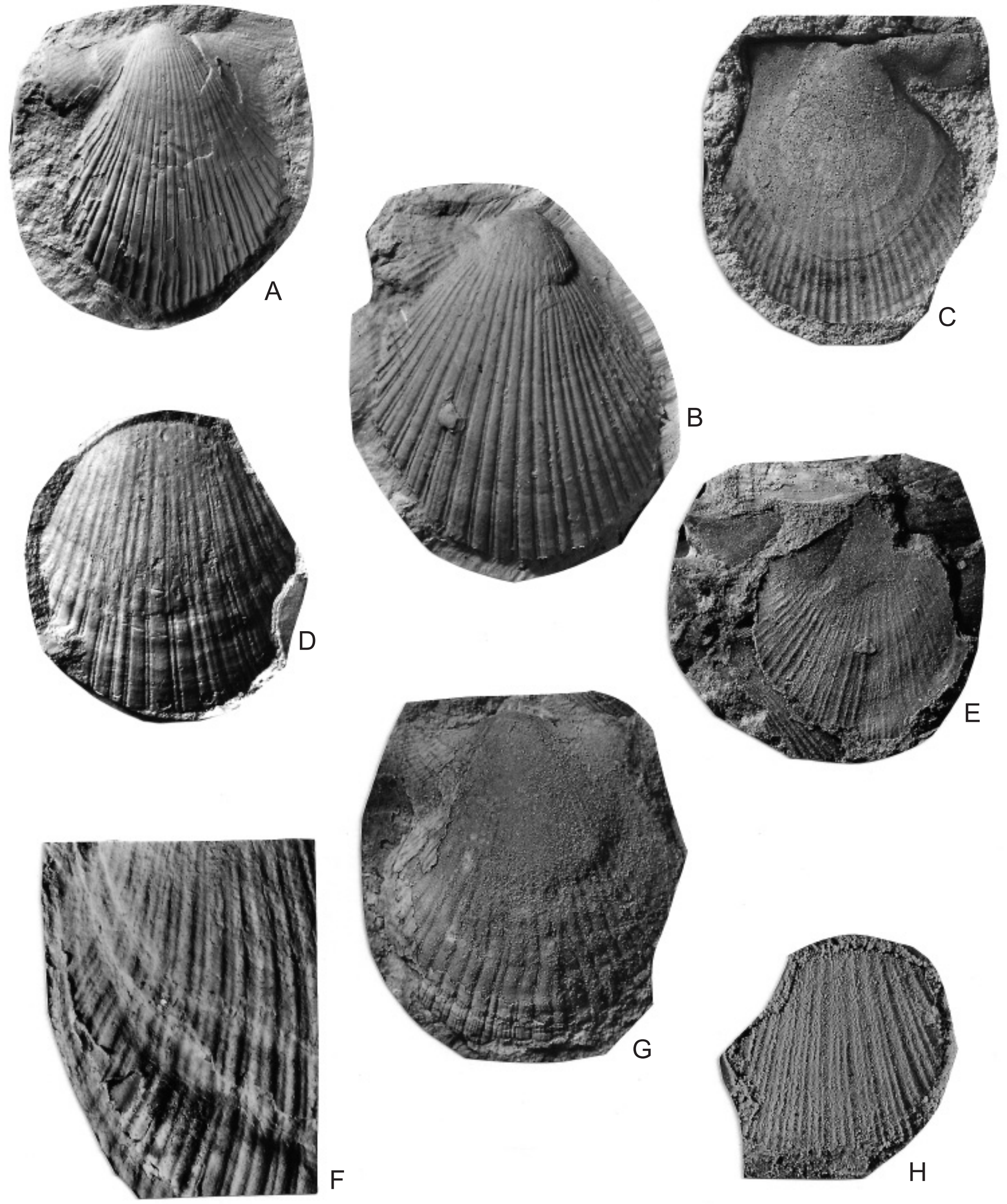
Etheriplica, the gap between the two ends is occupied by two or three small pits. *Heteropecten* and *Neptunella* Astafieva belong to the subfamily, and *Inaequalitaria* n. gen. is placed in the subfamily because right valve ribs branch. Species referred to *Fletcheripecten* Waterhouse, 1982, found in Australia and New Zealand, differ in that the right valve costae are fine and not bundled, and increase by intercalation, not branching. There is considerable approach to members of Acanthopectinidae Newell & Boyd, 1995, in the way that ribs may be weakly bundled on the right valve, but the bundles are flat, whereas those of Acanthopectinidae are elevated and arched. In addition it is possible that the narrow and often tapered left valve plicae of this family were close to the arched plicae of some Heteropectininae. On the other hand the left valve ornament and insignificant nature of commarginal laminae in the latter group suggest etheripectinid affinities.

Genus ***Heteropecten*** Kegel & Costa, 1951

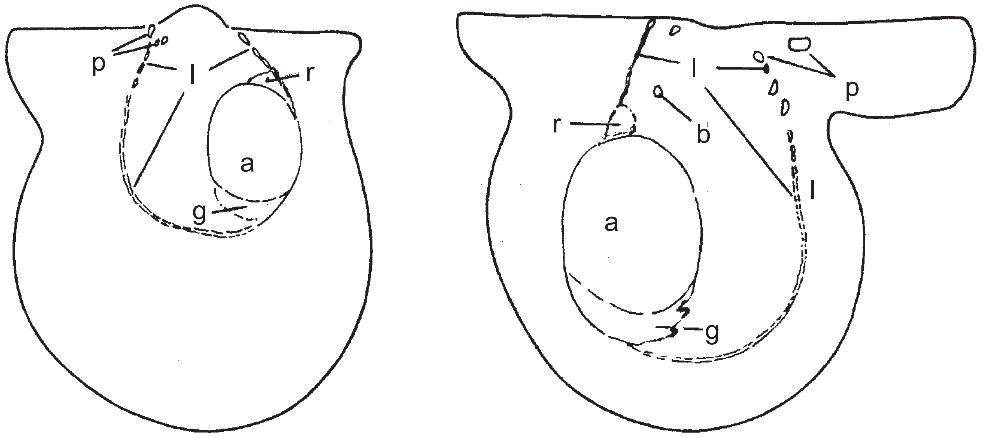
Text-fig. 84 - 87

Type species: *Aviculopecten (Deltopecten) catharinae* Reed, 1930, p. 10 from Early Permian of Brazil.

Diagnosis: Moderately large, left valve convex, right valve weakly inflated to flat, posterior wings moderately large, left anterior wing large, right anterior auricle long. Left valve ornamented by narrow plicae with flat to rounded crests, interspaces narrow to moderate in width with one or two orders of costae, concentric laminae not strong, right valve ornament of branching costae that are generally broad. Pallial line open dorsally.

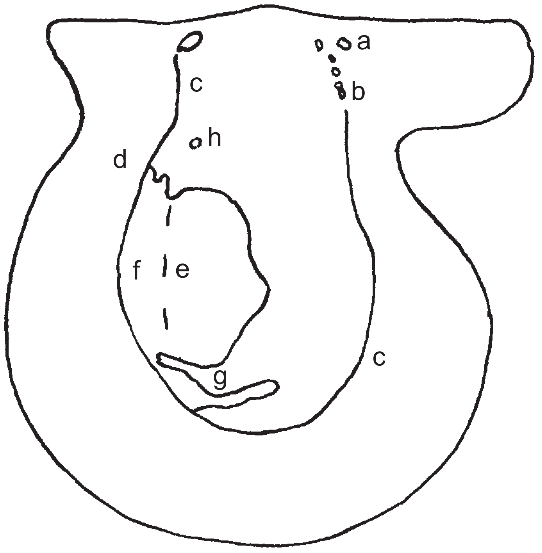


Text-fig. 84. A, *Heteropecten catharinae* (Reed), wax cast of left valve as figured by Reed (1928) and Kegel & Costa (1951, pl. 2, fig. 4). B, *H. catharinae* Reed var. *diglypha* Kegel No. 4061, figured by Kegel & Costa (1951, pl. 6, fig. 4). C, D, *H. bastosi* Kegel. C, right valve No. 4229 figured by Kegel & Costa (1951, pl. 6, fig. 3). D, left valve No. 4226a figured by Kegel & Costa (1951, pl. 2, fig. 2). E, G, *H. platicosta* Kegel & Costa. E, right valve No. 4324, figured by Kegel & Costa (1951, pl. 2, fig. 5). G, left valve holotype No 4232, figured by Kegel & Costa (1951, pl. 3, fig. 2). F, *H.* cf. *unicus* (Reed), No. 4226b, figured by Kegel & Costa (1951, pl. 5, fig. 1c). H, "*Aviculopecten*" *trichotomus* Kegel, left valve ornament No. 4149 Figured by Kegel & Costa (1951, pl. 1, fig. 2). From ?Westphalian B beds of Piaui State, Brazil. Photographs supplied by A. Rocha-Campos, Buenos Aires, at natural size. *Heteropecten* material comes from Taio Sandstone, State of Santa Catarina, Brazil, and is now regarded as making up the species *catharinae*, kept at DGM and DGP.

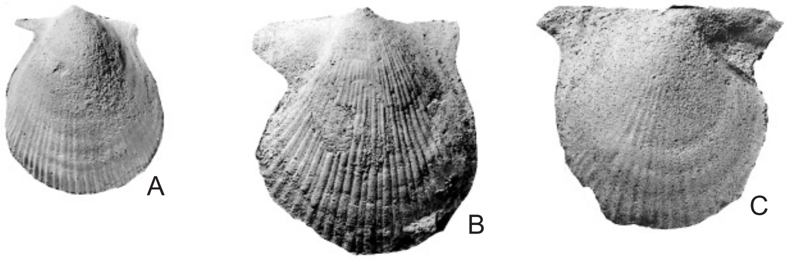


Text-fig. 85. *Heteropecten catharinae* (Reed). A, left valve interior. B, right valve interior. Located as for text-fig. 84, re-presented from Rocha-Campos (1970, Fig. 8, 9). A – adductor scar, b – brachial scar, g – brachial (or gill) scar, p – pedial scars, l – pallial line.

Discussion: The figures of the interior of *Heteropecten catharinae* by Kegel & Costa (1951, Fig. 1a, b) show a pallial line opening dorsally, with no pits under the hinge, unlike the arrangement in the genus *Etheriplica*. This agrees largely with the depiction of the interior for *Aviculopecten exemplarius* Newell by Newell (1938, Fig. 2.1, 2). Newell (1938) ascribed a number of species, some new, to *Aviculopecten*, and although several were poorly preserved with only the left valve



Text-fig. 86. *Heteropecten exemplarius* (Newell), right valve interior redrawn from Newell (1938, Fig. 2.2), x1. Registration and locality not stated, but probably from Missourian Bonner Springs Shale, Kansas, and kept at University of Kansas Paleontology collection. c – pallial line, d – pedal retractor scars, g – gill suspensory, e – “quick” muscle scar, f – “catch” muscle scar, h – superior suspensory for gills, a, b - pedal levator muscle scars.



Text-fig. 87. *Heteropecten catharinae* (Reed). A, left valve x 0.5. B, juvenile left valve x1. C, right valve, x1. Specimens each registered as USNM23686, from Early Permian "Aviculopecten Bed", Bina do Sul, Brazil.

extant, and generally with no shell structure and no hinge detail provided, some may be assessed as belonging to *Heteropecten*, including the following species assigned by Newell (1938) to *Aviculopecten*: *exemplarius* Newell, *arctisulcatus* Newell, *occidentalis* (Shumard), *mazonensis* Worthen, *basilicus* Newell and *sumnerensis* Newell. Few have primary ribs quite as wide or interspaces as narrow as those of some *Heteropecten catharinae*, but they come close. The right valve, where preserved, has broad branching ribs, as a rule splitting and staying close together, somewhat similar to the arrangement in the right valves of the type species *Heteropecten catharinae.* The left valves of these species do not show the strong primary costae and wide interspaces with thin intercalated secondary and further costae of *Etheripecten*, other than *A. halensis* Mather and *A. eaglensis* (Price), which may be assigned to that genus pending fuller knowledge of the right valve.

Heteropecten exemplarius shows incipient foliate shell structure in the largely simple prismatic outer layer of the right valve, and oblique laminae (Carter 1990, p. 241).

Genus ***Inaequalitaria*** new genus

Text-fig. 88

Derivation: in – not; aequalitas – equality, similarity, Lat.

Type species: *Aviculopecten subquadratus* Bell, 1929, p. 166, from Carboniferous Horton-Windsor Group, Nova Scotia, here designated.

Text-fig. 88. *Inaequalitaria subquadratus* (Bell). A, left valve no. 7593a. B, left valves 7555 for which the right side specimen is cited as lectotype. C, right valve no. 7555. Specimens from Horton Windsor Group, Nova Scotia, figured by Bell (1929, pl. 28, fig. 4, 6, 11) x 0.9. Now kept at Geological Survey of Canada, Ottawa.

Diagnosis: Left valve convex, right valve less inflated, posterior wings high, large and well formed, although shorter than maximum length of shell, anterior left valve wing and right valve anterior auricle moderately large, left valve ornament of prominent primary ribs and additional intercalated ribs becoming as strong as the primaries, right valve ribs branch and have broad flat crests. Ligament alivincular, byssal notch deep.

Discussion: The type species was described by Bell (1929, pl. 28, fig. 5-11), and is characterized by sturdy left valve ribs without the clearly defined additional orders arising by intercalation that are seen in *Neptunella, Nodulipecten* or *Heteropecten*. A further characteristic is the unusually high posterior wing in each valve. *Aviculopecten lyelli* Dawson from the lower Windsor Group of Nova Scotia has finer left valve costae of two or three poorly differentiated orders, and *A. lyelliformis* Bell, 1929 from the same group is also probably congeneric. *Aviculopecten xibeiensis* Feng (1988, p. 631, pl. 1, fig. 13, 14, 22) from China was considered to be closely allied by Feng, and has somewhat similar sturdy left valve ribbing: that of the right valve is not so clear in the figure (Feng 1988, pl. 1, fig. 13), but appears close. It is distinguished by its very long right anterior auricle, and the left posterior wings are comparatively large. The species comes from the Middle to Late Carboniferous Shiqiantan Formation of the Yunggar Basin.

Genus ***Neptunella*** Astafieva, 1997

Type species: *Neptunella sulciconcentrica* Astafieva, 1997, p. 23 from Upper Permian of Mongolia.

Diagnosis: Characterized by bundled and branching costae on right valve. Left valve ornamented by several orders of costae, primary ribs spinose, posterior wings large, anterior left valve wing large.

Discussion: The genus *Neptunella* Astafieva, 1997 has complex right valve ornament of branching and bundled ribs. According to Astafieva the genus ranged from Late Carboniferous to Late Permian in age. The genus appears to be the same as or very close to Russian species assigned to *Vorkutopecten* Guskov in Muromseva, 1984, p. 73. Muromseva (1984) included *Aviculopecten subclathratus* Keyserling and *A. netschajewi* Licharew in *Vorkutopecten*, and Astafieva (1997) referred *Aviculopecten subclathratus* Keyserling to *Neptunella*. The cited type species for *Vorkutopecten* is meagrely figured as two broken right valves, which show moderately complex ribbing, that approach the ribbing in right valves of *Corrugopecten* Waterhouse, 1982. The left valve is not known. Thus the genus is poorly based, and *Neptunella* is more readily interpreted. Nakazawa (1999, p. 13) described a species of *Vorkutopecten* from the Hovtinden Member and other units of the Kapp Starotsin Formation in Svalbard, judged to be of Ufimian (ie. Roadian) or early Middle Permian age. The right valve ornament is of complex branching and weakly bundled ribs, and the left valve ornament is obscure in the figure but apparently of three orders with increase by intercalation. It is difficult to accept the analysis of *Vorkutopecten* offered by Nakazawa (1999, p. 14). He stated that the ribs on both valves increase by intercalation, as in *Etheripecten* and *Limipecten,* but in figured right valves (Nakazawa 1999, pl. 1, fig. 6, 8, 9; aff. pl. 2, fig. 1) some of the ribs clearly increase by branching. Nakazawa (1999) even rejected the inclusion of *Aviculopecten netschajewi* Licharew in the genus by Guskov (in Muromseva 1984) on the basis that its right valve ribs branched. Like Guskov in Muromseva (1984), he included *Vorkutopecten* as a member of Deltopectinidae, without giving clear reasons.

The Permian genus *Vanvleetia* Waterhouse, 2001, p. 121, type species *Aviculopecten vanvleeti* Beede, 1902, p. 6 from Late Permian of United States, appears to be allied. The left valve is moderately convex, with strong primary ribs bearing spines at regular intervals. Further orders of ribs increase by intercalation. This and allied species are widespread in Permian of

United States, including *Aviculopecten mccoyi* Meek & Hayden (Kansas), *A. bellatulus* Newell (Arizona), *A. nodocosta* Newell (Nebraska) of Permian age and Late Carboniferous species *A. gradicosta* Newell (Kansas) and *A. moorei* Newell (Nebraska), described by Newell (1938) from left valves. Ciriacks (1963, p. 47, pl. 6, fig. 9) recorded a right valve of "*Aviculopecten*" *girtyi* Newell from the Grandeur Member of Utah that shows costae, split in pairs and associated in bundles of up to eight, as well as the large spines on the primary left valve costae, with prolonged bases. Bundling is not so clear on the small right valve figured in Ciriacks (1963, pl. 6, fig. 7). There are differences from *Neptunella*, but they are not great, and much of the difficulty in being certain arises from the poor preservation of the Russian type species. Thus it is still not clear that the type species *N. sulciconcentrica* Astafieva has comparable tubular and high spines placed on high and broad primary left valve costae, or that the right anterior auricle is as long as in species of *Vanvleetia*.

Genus ***Nodulipecten*** new genus

Derivation: nodosus – full of knots; pecten – bivalve, Lat.

Type species: *Nodulipecten hoskingi* n. sp. from Early Permian (Artinskian) Madeline Formation of Western Australia, here designated.

Diagnosis: Left valve convex with costae in several orders, arising by intercalation and by semicalation, primary costae moderately prominent and without spines. Right valve with strong nodose costae splitting into persistent pairs near hinge, interspaces wide with very fine costae.

Discussion: Unlike *Neptunella* or *Vanvleetia*, the primary costae of the left valve lack spines at regular intervals, and the right valve costae consist of prominent branching nodose pairs and very fine additional costae, without bundling. The left valve ornament lacks the narrow plicae-like costae and narrow interspaces of *Heteropecten*, and the right valve ornament differs considerably.

Nodulipecten hoskingi n. sp.

1995 *Heteropecten* cf. *laticostatus* [not Waterhouse] – Newell & Boyd, p. 34, Fig. 23, 24, 25.

Derivation: Named for L. V. Hosking.

Holotype: UWA 121050, figured by Newell & Boyd (1995, Fig. 24A, B) from Early Permian (Artinskian) Madeline Formation, Carnarvon Basin, Western Australia, here designated.

Diagnosis: Left valve ornament of three orders of intercalate ribs, primary ribs strong; right valve ornament of sets of two ribs, wide interspaces and fine filae.

Description: This species has been described and well illustrated. On the left valve the wings are large, and the primary ornament dominated by broad primary costae, and the right valve has a large posterior wing, and nodose primary ribs that branch near the hinge and traverse the valve in sets of two. The resilifer is well illustrated for the left valve by Newell & Boyd (1995, Fig. 23B). The shell has outer calcite prisms above foliated calcite, not aragonite as is more normal for aviculopectiniform and etheripectiniform species.

Discussion: Newell & Boyd (1995) provided valuable information and fine illustrations of the species. But their interpretation of the species and data presented on its occurrence were flawed. They wrongly ascribed the rocks from which the material came to the "Lyon" [sic – Lyons] Group, which is much older than the Madeline Formation, and they interpreted the generic position as *Heteropecten*, even though no other species referred to this genus, including large populations of the type species, ever display such unusual right valve ornament. They further claimed that the species belonged to *Fletcheripecten laticostatus* Waterhouse (1982), a name proposed for *Pecten comptus* Dana, 1847, p. 160, 1849 (not M'Coy, 1844, p. 90) from the Allandale Formation of New South Wales. Dana's type was refigured in Waterhouse (1988, pl. 2, fig. 4), showing the very broad primary costae and moderately narrow interspaces (Text-fig. 81B). This species is of early Cisuralian age, and has simple ribs spread evenly over the right valve, very different from the ornament in *Nodulipecten hoskingi*. A species *Fletcheripecten lyonsi* Waterhouse, 1986, p. 5 was overlooked by Newell & Boyd (1995), and was named for material from the upper 5m of the Lyons Group of the Carnarvon Basin. Figured by Dickins (1957, pl. 6, fig. 9), it is narrower with fewer primary costae than in the present species.

Deltopecten subquinquelineatus M'Coy var. *comptus* [not Dana] of Hosking (1931, p. 32, pl. 12, fig. 1-3, pl. 13, fig. 1-6) from the upper Lower Permian Wooramel Formation of the Carnarvon Basin, Western Australia, was considered to be the same as *hoskingi* n. sp. by Newell & Boyd (1995), but her left valves have much broader primary ribs with up to 8 finer costae in the interspaces, in two to four orders. The right valve figured in Hosking (1931, pl. 12, fig. 3) shows fine even non-branching ribs – see Plate 1, fig. 3 herein. Another right valve figured in Hosking (1931, pl. 13, fig. 1) has strong ribs, and the right valve of Hosking (1931, pl. 13, fig. 6) has simple ribbing according to the text. The description records a second series of ribs arising near half-length, and the interspaces are wide. The species appears to belong to *Fletcheripecten*.

The present species is comparatively large, and with prominent primary left valve ribs, and right valve ribs in pairs, whereas the various species assigned to *Neptunella* by Astafieva (1997) are smaller, with broader bundles bearing more ribs on the right valve. The type species of *Neptunella* is not very well preserved, but the left valve ornament appears moderately close. It is more inflated than the Australian form, with stronger and spinose ribbing in up to four orders on the left valve, less well developed concentric laminae and growth wrinkles, shorter hinge and deep high byssal notch. A second species *N. bellula* Astafieva, 1997 from Mongolia has broad simple and branching ribs, not very close. Astafieva (1997) assigned several Carboniferous and Permian species of Russia to the same genus, but she included *Aviculopecten keyserlingiformis* Licharew, 1927 and *A. wilczeckiformis* Licharew, 1927, which are biconvex forms with costate plicae crossed by regular concentric rugae, here assigned to *Undorugosa* n. gen. (see p. 76).

Subfamily **GIRTYPECTININAE** new subfamily

Plate 1, fig. 4, 5

Name genus: *Girtypecten* Newell, 1938, p. 77, from Middle Permian (Guadalupian Series) of United States, here designated.

Diagnosis: Hinge wide, wings large, left valve ornament of strong and anteriorly spinose primary costae crossed by strong well spaced concentric ribs, interspaces may bear finer ribs. Right valves poorly known, with subeven ribs, suggestive of strong primaries but much less conspicuous than ribs of left valve and no prominent concentric ribs or spines. Hinge alivincular.

Discussion: The ornament of the left valve is highly distinctive. The right valve was not known to Newell when proposing the genus, and is still seldom encountered, but thanks to the dissolving of numerous limestone blocks by G. A. Cooper & R. E. Grant, Smithsonian Institution, Washington D. C., two right valves have been found with some 350 left valves, as described by Newell & Boyd (1995, Fig. 30) for the type species *Girtypecten sublaqueatus* (Girty). The right valve costae are slender: primary costae occur in shallow grooves, and the broad interspaces contain a number of fine costae.

Sinopecten Fang, Sun & Balinski, 2006, p. 601, type species *S. newelli* Fang et al. from the Early Carboniferous Muhua Formation of Guizhou, China, was treated as a subgenus of *Girtypecten* by its authors, but is herein regarded as a full genus, characterized by pyramidal costal spines arising from ridge intersections, and anterior resilifer extending in front of the beak, with further differences. Several Permian species were assigned to the taxon.

Girtypecten ovalis Dickins (1963, p. 85, pl. 13, fig. 1-4) from the Fossil Cliff and Callytharra Formations of Western Australia, includes a right valve, but it is poorly preserved, and was not described in detail. The ribs appear to be simple and some are broad, pointing to a new genus, but preservation is marginal, and it is preferred to await further material.

Subfamily **CASSIANOIDINAE** Newell & Boyd, 1995

[nom. transl. hic ex Cassianoididae Newell & Boyd 1995, p. 32].

Cassianoides Newell & Boyd (1995), the sole member of Family Cassianoididae Newell & Boyd, 1995, is a small retrocrescent shell with convex left valve and very strong and spinose radial ribs, and flat right valve with fine and low radial ribs. A pair of lamellar teeth are developed each side of the resilifer. With alivincular hinge and large right anterior auricle and high byssal notch, it is here regarded as an extreme variant within Etheripectinidae, and is represented by just the one genus.

Family **LIMIPECTINIDAE** Newell & Boyd, 1990

Diagnosis: Shell structure distinguished by presence of nacre each side of cross-lamellar layer, left valve ornament of low broad ribs plicating the shell in two orders, crossed by low distinct somewhat ragged lamellae pointing ventrally in interspaces, right valve ribs finer and tend to be bunched over low plicae.

Discussion: In terms of ornament, the Late Carboniferous genus *Limipecten* Girty, 1903 is moderately distinctive, with close-set round-crested ribs in one or two orders on the left valve, and finer ribs in one or more orders on the right valve. Growth laminae are moderately prominent and well spaced on the left valve, as ragged rather than linear, and are finer and less noticeable on the right valve, which is somewhat less convex. The ornament may be readily distinguished from that of *Etheripecten*, through the way that growth-lamellae point ventrally in interspaces and by the somewhat bunched right valve ribbing, the close-set costation and spaced but distinctive lamination. The genus comes closer to *Heteropecten* because the primary left valve ribs are like very narrow plicae, and the weak bundling of costae on the right valve is reminiscent of a more marked bundling found in *Neptunella* Astafieva. The type species comes from the Upper Carboniferous Wayland Shale of Texas. Other North American species like type *Limipecten* include *L. konincki* (Meek & Worthen) from Demoinesian beds of Iowa, and *L. morsei* Newell from the Kendrick Shale of Kentucky. Newell (1938, p. 7, pl. 11, fig. 5) described an additional species *Limipecten wewokanus* from the Lower Pennsylvanian Wewoka Shale of Oklahoma, based solely on left valves. These show simpler ribbing with very close-set and regular concentric laminae, which, with the greater density of ribbing, suggest that the species belongs to *Lamnipecten* (see p. 157).

Limipectinidae was distinguished by Newell & Boyd (1990) as a family substantially on the basis of its unusual inner shell, which consists of nacre in two layers, separated by a crossed lamellar layer. The genus appears to be widely distributed, and it would be interesting to discover if species reported from Asia and Europe have the same nacre as that found in the type species from Texas.

Family **ANNULICONCHIDAE** Newell & Boyd, 1995

Diagnosis: Subequally biconvex shells with wide hinge and predominantly concentric ornament on both valves, that of right valve simpler than that of left valve.

Discussion: The family was named for an exceptional genus *Annuliconcha* Newell, 1938, p. 76. The two valves are unevenly convex, but Newell (1938) and Newell & Boyd (1995) did not provide measurements or comparative data for the right valve. However the right valve is distinctly smaller than the left, approaching the situation in Etheripectinoidea. The right valve ornament is of the same concentric pattern as that of the left valve, but less ornate and somewhat weaker. The superfamilial allegiance is not entirely clear, but is judged to lie with Etheripectinoidea. The approach to *Girtypecten* Newell, 1938, which also has prominent concentrics, restricted to the left valve, suggests an etheripectiniform relationship, as adopted by Waterhouse (2001, p. 122). Several genera in Chaenocardioidea have concentric ornament, and subequally inflated valves, but they also have shorter posterior wings and short umbonal slopes, and are often procrescent. The ornament on most chaenocardioids is of overall similar appearance on the two valves. *Undorugosa* n. gen. as a member of Undopectininae, a member of Aviculopectinidae, is subequally biconvex, and is broadly plicate with costae. But it does display regular concentric rugations, to imply that a somewhat similar and older form may have developed the concentric ornament and lost the radial ornament. Given the unusual aspects of the family, it appears to be a "deviant" development, with origins uncertain: it marked a short-lived group that failed to survive.

Genus ***Lineaspina*** new genus

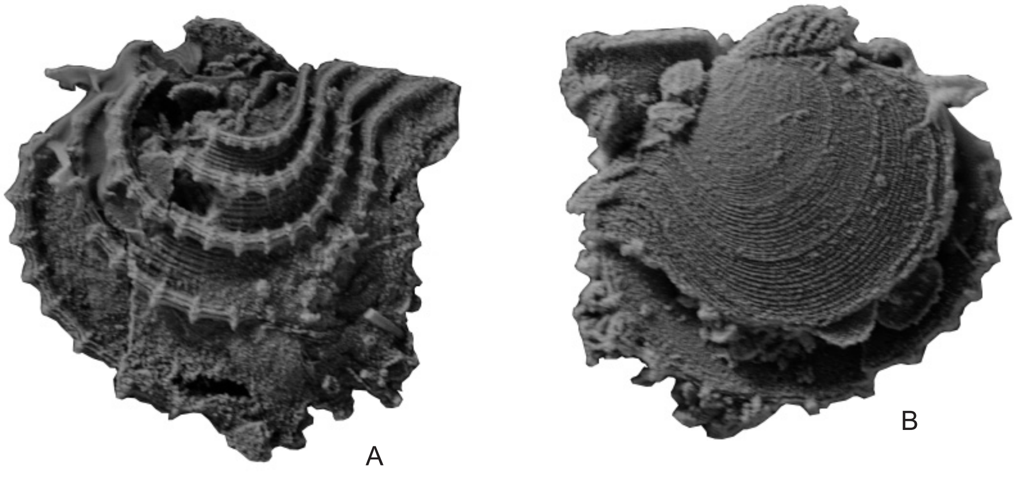
Text-fig. 89

Derivation: linea – line, string; spinosus – thorny, Lat.

Type species: *Annuliconcha dentata* Newell & Boyd, 1995, p. 59, from Lower and Middle Permian of United States, here designated.

Diagnosis: Left valve below the wings ornamented with prominent spines projecting from the prominent commarginal ribs.

Discussion: This genus is readily distinguished from *Annuliconcha* Newell, type species *Aviculopecten interlineatus* Meek & Worthen, 1860 from the Pennsylvanian faunas of the mid-continental United States, by the presence of evenly spaced blunt spines projecting forward from strong concentric ridges. The type species *dentata* comes from the Skinner Ranch Formation and other specimens from the Willis Ranch Formation (late Cisuralian, Guadalupian). *Annuliconcha*



Text-fig. 89. *Lineaspina dentata* (Newell & Boyd). A, B, holotype, left valve and right valve AMNH 43390 from Middle Permian Lower Getaway Limestone, Texas, x8. Photographs supplied courtesy of B. M. Hussaini, American Museum of Natural History, New York. See Newell & Boyd (1995).

interlineata is mostly Pennsylvanian, and said to extend into the Permian Neal Ranch, Road Canyon and lower Getaway Formations of west Texas. Newell & Boyd (1995, p. 60) noted that Wolfcampian (older Permian) specimens differed from *dentata* in having thicker and higher spines, and in lacking radial ornament, suggesting the presence of another species of *Lineaspina*. Both genera are represented in Asia, especially in Cisuralian faunas. For example, *Astarte volgensis* Stuckenberg belongs to the new genus, together with *Aviculopecten kitakamiensis* Murata (1964, pl. 34, fig. 11, 12) from the Middle Permian of Japan, and *A. spinosa* Astafieva-Urbaiitis & Ramovs (1978) from Late Carboniferous faunas of Karavanke Alps of Slovenia. *Annuliconcha placunensis* Nelzina & Koschman belongs to *Annuliconcha*, as does *Aviculopecten magnini* Mansuy from southeast Asia and China.

Family **ACANTHOPECTINIDAE** Newell & Boyd, 1995

Diagnosis: Distinguished by numerous narrow often acute-crested plicae on left valve, varying number of secondary costae, crossed by prominent lamellae which may arch towards hinge and may point ventrally in interspaces. Right valve much less inflated, with different ornament, concentrics close-set, not pointing ventrally in interspaces.

Discussion: This was proposed as a full family, with only one genus, *Acanthopecten* Girty, 1903. The genus is indeed outstanding in its ornament, although otherwise conforming with *Etheripecten* in overall shape and internal detail, and in having little inflated right valve with ornament differing from that of the left valve. The posterior wings are long, and resilifer wide.

Subfamily **ACANTHOPECTININAE** Newell & Boyd, 1995

[nom. transl. hic ex Acanthopectinidae Newell & Boyd, 1995, p. 45].

Diagnosis: Left valve plicae moderate in number and tend to be narrow-crested with angular interspaces, laminae point ventrally in interspaces.

Genus ***Acerplica*** new genus

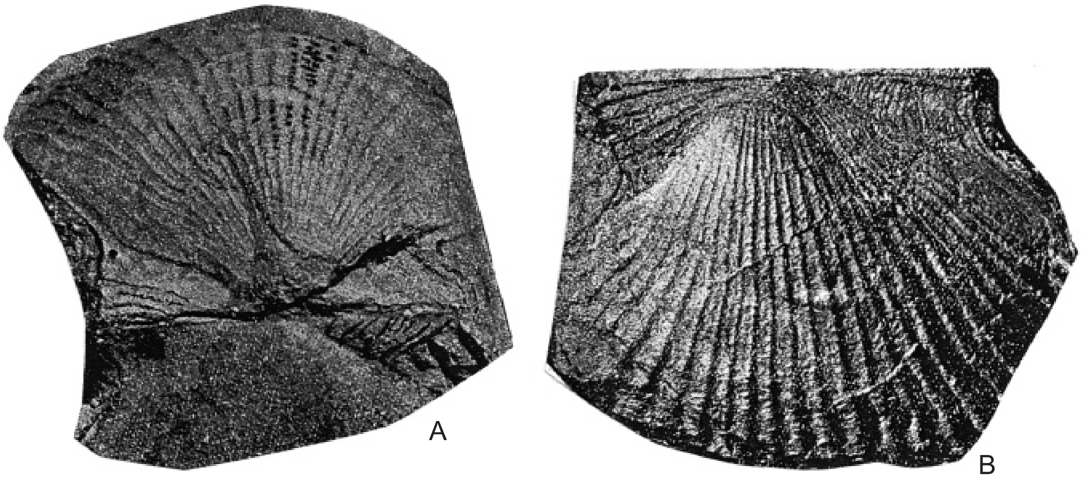
Text-fig. 90

Derivation: acer – sharp; plica – fold, Lat.

Type species: *Aviculopecten pincombei* Mitchell, 1924, p. 471 from upper Carboniferous of northern New South Wales, here designated.

Diagnosis: Left valve characterized by numerous narrow plicae with sharply pointed crests, crossed by narrow close-set laminae which point weakly ventrally in the interspaces. Right valve ornamented by fine weakly bundled costae.

Discussion: The type species was described by Mitchell (1924) from Bombah Point, Lake Boolambayt, northern New South Wales, and clearly falls within the Acanthopectininae. Type material is kept at the Australian Museum, and further unfigured and moderately well preserved material is kept and registered at the Australian Museum off-site storage. The hinge is long, with large and long posterior and anterior wings and deep sinuses in the left valve (Mitchell 1924, pl. 49, fig. 5, 6), involving specimens such as AMF 26457. The left valve plicae are narrower and more numerous than in species ascribed to *Acanthopecten* Girty and *Ciriacksia* n. gen., numbering some 13-15 primary ribs with a second series quickly becoming just as strong. The crests are not rounded, but taper to a narrow ridge, and are evenly spaced, with concave interspaces, and growth laminae do not project as far forward as in *Acanthopecten* or *Ciriacksia*. AMF 26442 has fine tertiary costae, and AMF 26887 is particular well preserved. The right valve is half as high as the left valve, and ornamented by narrow numerous weakly bundled costae, with mode of increase obscure, but possibly branching over the ventral fourth of the height. Right valve AMF



Text-fig. 90. *Acerplica pincombei* (Mitchell). A, left valve above right valve. B, left valve. Specimens figured as *Aviculopecten andrewsi* by Mitchell (1924, pl. 49, fig. 4, 5) from *Levipustula levis* Zone (early Late Carboniferous) near Macleay Lakes, New South Wales, both partly cropped, x1, kept at Australian Museum, Sydney.

25576 shows weak bundling, with costae in several orders and showing more splitting than on the left valve. Campbell (1961, p. 468) cited as lectotype AMF 26457 figured by Mitchell (1924, pl. 52, fig. 19), and refigured (in reverse?) by Campbell (1961, pl. 61, fig. 3). Internally the pitted pallial line is open dorsally. Campbell (1961) referred the species to *Limipecten*, but the ornament differs substantially from that typical of that genus. *Aviculopecten andrewsi* Mitchell (1924, p. 470, pl. 49, fig. 4-6, type specimen AMF 26463, fig. 5) was placed in synonymy by Campbell (1961). Mitchell's figures are actually better for this species rather than *pincombei*, and show well the left valve and the right valve with high byssal notch and weakly bundled right valve costae that seem to be intercalate (AMF 26463). Part of the ligament is visible, and several specimens show the resilifer well.

Superficially the ornament approaches that of *Acanthopecten carboniferus* (Stevens, 1858), with further material described by Newell (1938, p. 72, pl. 12, fig. 8-10) from the Willard Shale of Nebraska, but the plicae of this form are round-crested and carry a slender rib along the crest. The growth laminae pout ventrally in the interspaces of this species. The right valve of Mitchell's species has fine costae approaching those of *Ciriacksia* (see below) and the resilifer is broad and comparatively shallow. The left valve of the Mitchell species has narrower more sharp-crested plicae with wider interspaces and less conspicuous laminae, compared with *Ciriacksia*.

Genus ***Ciriacksia*** new genus

Derivation: Named for K. W. Ciriacks.

Type species: *Ciriacksia ciriacksi* n. sp. from Early Permian Bone Spring Formation, Texas, United States, here designated.

Diagnosis: Left valve gently convex with close-set plicae crossed by lamellae arching dorsally over the crests and pointing ventrally in interspaces; right valve with distinctive low costate plicae. Posterior wings comparatively long.

Discussion: This new genus is very close in its left valve to that of *Acanthopecten* Girty, 1903, type species *Pecten carboniferus* Stevens, 1858 from Pennsylvanian faunas of the mid-United

States, but the right valve of the new form is ornamented by bundled costae over low plicae. In *Acanthopecten*, the right valve ornament is made up of simple well spaced costae, as illustrated by Newell (1938, pl. 12, fig. 9), with very fine radial filae over the very broad interspaces. Newell (1938) also noted that the concentric filae were clumped in the umbonal region in *carboniferus*, whereas they are simple in the Permian type species of the new genus. In both genera the posterior wings are long, and the resilifer is comparatively broad, with cardinal scrolls and bourrelets.

Ciriacksia ciriacksi n. sp.

Text-fig. 91

1938 *Acanthopecten coloradoensis* [not Newberry] – Newell, p. 74, pl. 12, fig. 7a, b (part, not fig. 13-15 = *coloradoensis*).

1995 *Acanthopecten coloradoensis* [not Newberry] – Newell & Boyd, p. 45, Fig. 32. 1-3, 5-7, ?33A, B (part, not 32.4a, b = *Newellipectinia*?).

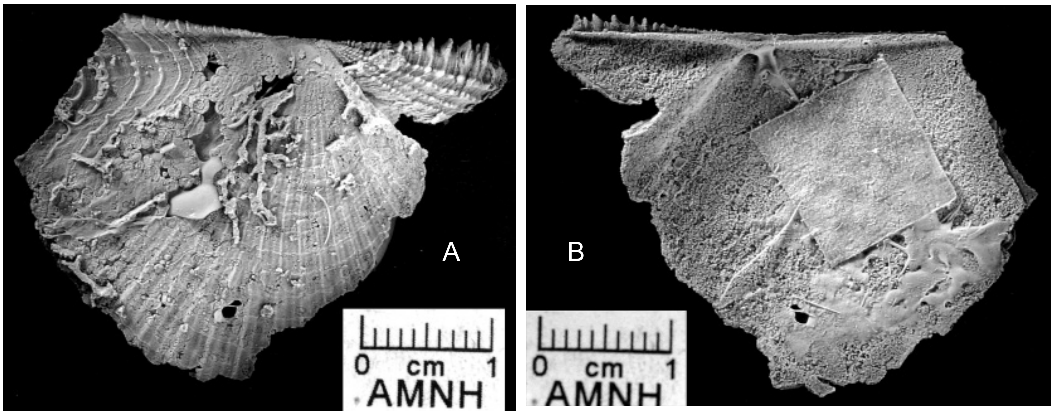
Derivation: Named for K. W. Ciriacks.

Holotype: ANHM 43399 from Cisuralian Bone Spring Formation, west Texas, figured by Newell & Boyd (1995, Fig. 32.1a,b), here designated.

Diagnosis: Moderately large shells with gently convex left valve and less inflated right valve, posterior wings large in both valves. Left valve bearing 16-20 ribs as a rule, angular or usually rounded crests, interspaces narrow, growth laminae point ventrally in interspaces and arch dorsally over the plicae. Right valve with costate plicae.

Description: The right anterior auricle is large and costate, and carries a strong scroll along the dorsal edge, above a comparatively short byssal notch that is largely infilled with growth laminae. The right valve posterior wing has fine costae, and has growth laminae parallel to the concave posterior margin, with acute cardinal extremity. The anterior wing of the left valve is convex forward in outline, with growth laminae and no ribs, and the left posterior wing has a concave posterior margin and acute cardinal extremity, with growth laminae that on some specimens form small forward pointing crenulations, even though there are no costae. The resilifer is broad, with well defined lateral bourrelets.

A right valve USNM 258971 figured by Newell & Boyd (1995, Fig. 32.4a, b) from the Willis Ranch Formation of the mid-Permian Glass Mountains sequence in west Texas lacks



Text-fig. 91. *Ciriackisa ciriacksi* n. gen., n. sp. A, B, external and internal views of right valve holotype AMNH 43399 from late Early Permian Bone Spring Formation, Texas. See Newell & Boyd (1995). Photographs courtesy of Bushra M. Hussaini, American Museum of Natural History, New York.

costae, but has rounded plicae crossed by well spaced prominent laminae, looking like those of the left valve. Perhaps there has been transposition, but it seems possible that the specimen belongs to *Newellipectinia* Waterhouse, 2001, although growth laminae point more ventrally in the interspaces, like left valves of *Ciriacksia*. It is excluded from synonymy. Right valves from the Road Canyon Formation and Bone Spring Formation have costate low plicae. A right valve from the lower Getaway Limestone figured by Newell & Boyd (1995, Fig. 33A, B) as *Acanthopecten coloradoensis* has simple faintly costate plicae without conspicuous growth laminae. The difference in ornament shows that there are several acanthopectinid species yet to be described in the Permian of the United States. What is clearly a problem is the sparsity of material, which has hindered adequate systematic description and made it difficult, unless great care is taken, to avoid lumping of different species into one taxon.

Discussion: The species *ciriacksi* was identified by Newell (1938) and Newell & Boyd (1995) with *Pecten* (*Monotis*?) *coloradoensis* Newberry, 1861, p. 129, from the Kaibab Limestone of the Little Colorado River, Arizona or New Mexico. Further specimens of *coloradoensis* were figured from the Kaibab Limestone by Newell (1938) and from the Franson Member of Wyoming by Ciriacks (1963, p. 52, pl. 7, fig. 8-11). These are all left valves, and they are close to the new species, but have more plicae, generally more than 20 and up to 27, compared with 17 to 20 in *ciriacksi*. The wings are preserved only in one Kaibab specimen figured by Newell (1938, pl. 12, fig. 15b) and are similar to those of the new species in so far as they lack ribs, but those of the Franson specimens figured by Ciriacks (1963) appear to have fine ribs or aligned crenulations on the posterior wing and on one of the anterior wings. The right valve ornament cannot be compared, as it is not preserved. It is therefore not certain whether *coloradoensis* belongs to *Ciriacksia*, but it seems likely. Quite possibly *Acanthopecten* was of Carboniferous age, and *Ciriacksia* of Permian age.

Aviculopecten laqueatus Girty (1908) from the Capitan Limestone of the Guadalupe Mountains, of upper middle Permian age, was referred to *Acanthopecten* by Newell (1938, p. 76) but seems likely to be related to *Girtypecten* Newell, 1938, type species *A. sublaqueatus* Girty, 1908. This genus has robust left valve ribs crossed by well spaced strong concentrics, and the only right valve ascribed to the species (Newell & Boyd 1995, Fig. 30.4b, 5) has much finer radial ribs, suggesting an etheripectinid relationship. No right valves of *laqueatus* are known.

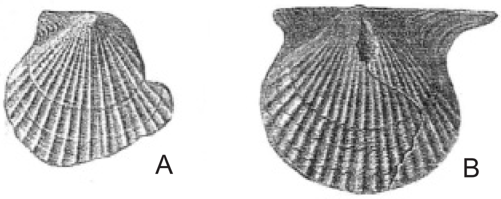
Genus ***Stellaripecten*** new genus

Text-fig. 92

Derivation: stellaris – species name; pecten – scallop, Lat.

Type species: *Pecten stellaris* Phillips, 1836, p. 212 from Early Carboniferous of England, here designated.

Diagnosis: Small shells with comparatively sturdy well-spaced radial ribs of mostly or entirely one



Text-fig. 92. *Stellaripecten stellaris* (Phillips). A, holotype, also figured by Hind (1903, pl. 16, fig. 7) from Settle. B, left valve figured by Hind (1903, pl. 16, fig. 8) from Castleton. NHM specimens x1, from Early Carboniferous of England.

order on left valve, finer ribs on less inflated right valve. Posterior wings long, right anterior auricle and byssal notch well developed.

Discussion: This genus is distinguished by the simplicity of ornament on each valve, and lack of bundling, and inconspicuous growth laminae. It is based on an Early Carboniferous species from England and Ireland, described by Phillips (1836, pl. 6, fig. 18 – holotype by monotypy) and Hind (1903, p. 88, pl. 16, fig. 7-11, the holotype refigured in fig. 7 – BMNH L47652). The interspaces between left valve ribs have low concentric striae, and the ribs on the right valve are very low (eg. NHM 97114) and more closely spaced than in the left valve. Growth lines arch dorsally over the left ribs costae, and the posterior wing is comparatively long. *Pecten incrassatus* M'Coy (1844, p. 94, pl. 16, fig. 1; Hind 1903, p. 89, pl. 16, fig. 12-15) is allied, if not conspecific, with less strong ribbing on the left valve and weakly ribbed right valves, not bundled, and no prominent concentric laminae.

Subfamily **LAMNIPECTININAE** new subfamily

Name genus: *Lamnipecten* n. gen. from Early Carboniferous of England, here designated.

Diagnosis: Concentric growth laminae well developed, left valve plicae slender and numerous, may have numerous secondary costae. Right valve laminate with finer costae, simple or differentiated.

Discussion: Members of this subfamily are distinguished from genera in Acanthopectininae by having more numerous and narrower left valve plicae with growth laminae that do not point so strongly in the interspaces.

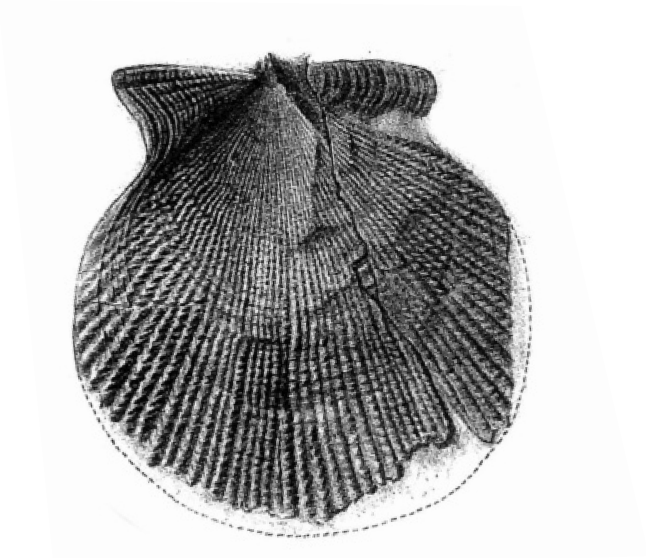
Genus ***Lamnipecten*** new genus

Text-fig. 93

Derivation: lamna – layer; pecten - bivalve, Lat.

Type species: *Pecten dissimilis* Fleming, 1828, p. 387 from Early Carboniferous of England, here designated.

Diagnosis: Medium-size shells with gently convex left valve and less inflated right valve, hinge



Text-fig. 93. *Lamnipecten dissimilis* (Fleming), left valve figured by Hind (1903, pl. 13, fig. 1) from Carboniferous at Corrieburn, Scotland, x1.

moderately wide and wings well formed. Left valve plicae narrow and numerous, with narrowly rounded crests, crossed by close-set well developed growth laminae, weakly arched ventrally or dorsally over plicae, not spinose or prolonged, right valve ornament of strong costae crossed by closely spaced low laminae, parallel to ventral margin.

Discussion: This genus is one of the oldest members of the family, and its plicae are narrow and the laminae, although well developed, are low and close-set compared with those of *Acanthopecten*, and do not point strongly towards the ventral margin in the interspaces. The right valve costae are simple. *Ciriacksia* and *Acerplica* also have stronger fewer ventral plicae, and the right valve ribs tend to be weakly bundled.

Pecten dissimilis Fleming, 1828 as revised by Hind (1903, p. 70, pl. 13, fig. 1-8) is a distinctive species with gently convex right valve and with long hinge, well developed right anterior auricle, and distinctive close-set narrow plicae with narrow or angular crests and strong close-set growth laminae. The species differs from *Aviculopecten* in having more numerous fine plicae and stronger laminae and finer right valve ornament. In synonymy Hind (1903) included *dissimilis* as figured by Phillips (1836, p. 212, pl. 6, fig. 17) and M'Coy (1855, p. 483t, pl. 3, fig. 5), with other specimens figured as *P. coelatus* M'Coy (1844, p. 90, pl. 18, fig. 2; Koninck 1885, p. 225, pl. 38, fig. 5-8), *P. rugulosus* M'Coy (1844, p. 98, pl. 17, fig. 7) and ?*P. undulatus* M'Coy (1844, p. 101, pl. 17, fig. 12). Right valves *P. concentricostriatus* M'Coy (1844, p. 91, pl. 14, fig. 5) and *A. textilis* Koninck (1885, p. 225, pl. 34, fig. 30) referred to the species by Hind (1903) show mostly concentric ornament and lack of radial ribbing, whereas the right valves figured as *dissimilis* by Hind (1903) are strongly ribbed. Other species are found in the Carboniferous of northern Europe, including *Pecten semicostatus* Portlock, 1843 (see Hind (1903, pl. 13, fig. 9-13), whilst *Limipecten wewokanus* Newell, 1938, pl. 11, fig. 5 from the lower Pennsylvanian middle Wewoka Shale of Oklahoma is congeneric. Various species have been referred to *Limipecten*, but *Limipecten* has different ribbing spaced further apart, and prominent and well spaced more irrregular laminae, scarcely perceptible on the right valve.

Genus ***Sinopectininia*** new genus

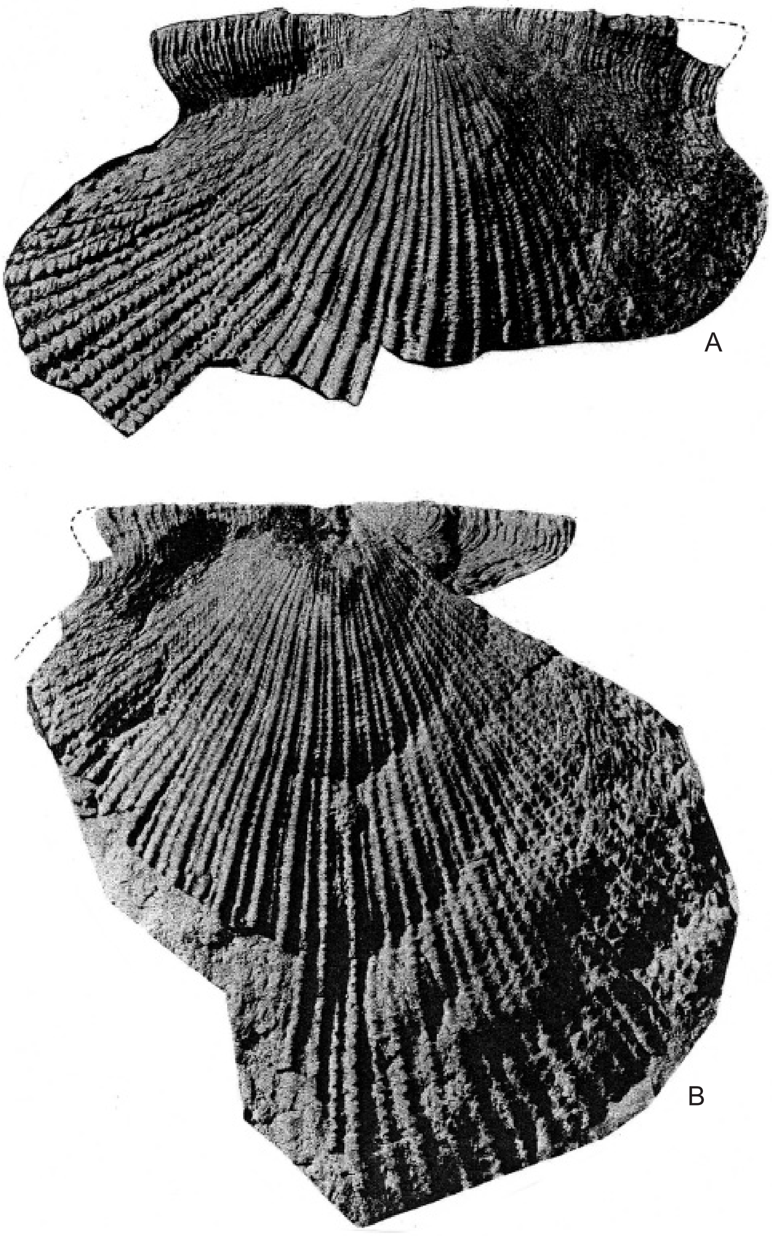
Text-fig. 94

Derivation: sinae – oriental people; pecten – scallop, Lat.

Type species: *Limipecten giganteus* Chao, 1927, p. 36 from Upper Carboniferous Houkou Limestone of China, here designated.

Diagnosis: Large, both valves gently convex, left valve wings of moderate length, with shallow sinuses, right anterior auricle short, high byssal notch, right posterior wing short with deep sinus. Ribs close-set, increase by semifurcation on left valve, ribs also close-set on right valve, increase by intercalation and semifurcation, both valves crossed by prominent close-set growth laminae, forming scales over costae that arch weakly towards hinge. Well formed resilifer.

Discussion: The type species was described from beds of the Taiyuan Group of south China by Chao (1927, p. 36, pl. 3, fig. 1-3, pl. 4, fig. 1-4) and Chen & Liu (1976, p. 177, pl. 6, fig. 17-20). The species described as *Deltopecten multistriatus* Chao (1927, p. 37, pl. 3, fig. 4-6, pl. 4, fig. 4) is similar except in having fewer secondary costae, and therefore comes very close to *Lamnipecten*. *Sinopectininia* does not conform in its ornament with that typical of Etheripectininae or the other subfamilies recognised. In general appearance the type species is very close to *Corrugopecten* Waterhouse, 1982 (see p. 85) from east Australia and New Zealand, though ornament on species of this form is slightly more elaborate with stronger primary plicae. There are a number of differences: most importantly, the right anterior auricle is much shorter and the hinge is alivincular with well developed resilifer and no pseudotrabeculae in the new genus, and posterior wings



Text-fig. 94. *Sinopectininia giganteus* (Chao). A, left valve cat. No. 1113. B, right valve lectotype cat. No. 1114. Figured by Chao (1927, pl. 3, fig. 1, 2) from Upper Carboniferous Houkou Limestone, Linching coal field, China, x1. Kept at Nanking Institute of Geology & Palaeontology, Academy of Science, Nanjing.

longer than in *Corrugopecten*. Left valve secondary ribs increase more by intercalation, with many branching, and in the right valve secondary costae split from the primary costae: on both valves the ornament is elaborate. Another genus *Squamuliferipecten* Waterhouse, 1986 (see p. 85) has very strong well spaced concentric laminae, stronger primary plicae and fewer secondary ribs. The right anterior auricle is long and the hinge platyvincular. In view of the similarity in some aspects of ornament and appearance to these two deltopectinid genera, it remains possible that the new genus is related, despite the differences in hinge and auriculation, and is not etheripectinoid. That would broaden the range of ligament and wings in Deltopectinidae. But given the considerable variation in ornament displayed by Pectinidia, the similarities are judged as due to convergence between aviculopectinoid and etheripectinoid stock.

Lamnipecten, based on *Pecten dissimilis* Fleming as figured by Hind (1903, p. 71, pl. 13, fig. 1-6) from Early Carboniferous faunas of England and Scotland, has similar subeven primary ribs crossed by close-set prominent growth laminae, with few secondary ribs (see p. 157) on the left valve, and simpler right valve ribs and less conspicuous laminae.

A more immediate question concerns the relationship to *Vorkutopecten* Guskov in Muromseva (1984, p. 73). The type species for this genus was cited as *Aviculopecten* (*Deltopecten*?) *giganteus* Chao var*. talis* Lutkevich & Lobanova (1960, pl. 16, fig. 10, pl. 17, fig. 1) from west Verchoyan and east Taimyr in Arctic Siberia. Only two right valves were figured, showing a very large anterior auricle on the holotype (pl. 17, fig. 1) and complex weakly bundled costae that increase by splitting off the primary ribs. There are differences from Chao's species. The right anterior auricle of Chao' species is much smaller in proportion to the valve, and the ribs include a number that appear to be intercalate, although at least some do branch from primary ribs, and concentric laminae are more prominent. Given that the left valve of *talis* is not known, and given that *talis* comes from comparatively high paleolatitudes, compared with the low-latitude source for the Chinese species, it is doubtful that *talis* can be established as a subspecies of *giganteus*, and questionable whether the two were congeneric or conspecific, and this uncertainty is reinforced by the differences in auriculation and ornament. Certainly the interpretation of *Vorkutopecten* by Guskov in Muromseva (1984) and Nakazawa (1999) has been that the left valve ornament in *Vorkutopecten* consists of intercalate *Etheripecten*-like costation and wide interspaces, quite different from the branching and close-set costae in only two orders in *giganteus*, and further distinguished by the presence of close-set laminae in *giganteus*. That said, evidence that Guskov and Nakazawa were correct in their interpretation remains uncertain, because of ignorance about so many aspects of type *Vorkutopecten*. I am inclined to regard most of the species assigned by Guskov and Nakazawa as similar to *Neptunella* Astafieva, and consider *Vorkutopecten* unrecognisable. Otherwise, in accepting Guskov and Nakazawa, *Vorkutopecten* may be either senior synonym of *Neptunella*, or include species with more costation than *Neptunella*.

Subfamily **COSTATOPLICATININAE** new subfamily

Name genus: *Costatoplicatina* n. gen. from uppermost Devonian of England, here designated.

Diagnosis: Left valve ornamented by costate plicae, right valve ornamented by costate plicae or costae, laminae comparatively subdued and closely spaced.

Discussion: Placement of this group is based on the nature of the ornament, with numerous narrow plicae on the left valve and plicae or no plicae on the right valve, and the concentric lamination is dense and fine. The widely known genus *Fasciculiconcha* Newell, 1938 is regarded as a member and is the best known genus, but is preserved largely as left valves. This genus also approaches costate members of *Heteropecten* Kegel & Costa in having narrow plicae and costae and narrow interspaces, but wings tend to be shorter in *Fasciculiconcha*, and right valve ribbing is not bundled or so bifurcate as in *Heteropecten*.

Genus ***Costatoplicatina*** new genus

Derivation: costa – rib; plica – fold, Lat.

Type species: *Pecten transversus* Sowerby, 1840, pl. 53, fig. 3 from Devonian of England, here designated.

Diagnosis: Plicae low and numerous on both valves, covered by costae, anterior gape slight or absent. Posterior wings long, right valve auricle with deep slender notch.

Discussion: The type species from southwest England has been further described by Phillips (1841, p. 46, pl. 21, fig. 77) and Whidborne (1897, p. 127, pl. 16, fig. 1-4) with synonymy provided by Paul (1941, p. 211) and was recorded from Late Devonian at Velbert of Bergisches Land, western Germany, by Amler et al. (1990, pl. 3, fig. 1, 2) and Amler (1992, p. 415, pl. 2, fig. 1, 2, 15) as *Fasciculiconcha transversa*. The genus is close in its left valve to that of *Fasciculiconcha* Newell, 1938, type species *F. knighti* Newell, 1938 from the Missourian of United States, in the ornament of costate plicae, but has many more and narrower plicae, and lacks the substantial anterior gape characteristic of this and other species in the Pennsylvanian of United States, as described by Newell (1938). No right valves were described for *F. knighti* by Newell (1938), and a species that is much more informative is *Pecten providencensis* Cox (1857, pl. 8, fig. 1; Newell 1938, pl. 7, fig. 7, 8, pl. 8, fig. 1a, b) from Desmoinesian of United States – unfortunately the type material is lost. The right valve of this species (Newell 1938, pl. 8, fig. 1b) shows fine primary costae and suggests that secondary costae arise by intercalation in the interspaces and immediately bifurcate, but are not bundled. Thus the genus differs from Undopectininae, in which the right valve is convex and is plicate.

Genus ***Fallaxopecten*** new genus

Derivation: fallax – species name; pecten – bivalve.

Type species: *Fallaxopecten mccoyi* n. sp. from Early Carboniferous of Ireland, here designated.

Diagnosis: Of moderate size, as long as high, with gently convex left valve and less inflated right valve, posterior wings long, byssal notch developed. Left valve costae fine, branching in bundles, right valve costae fine, branching.

Discussion: For *Pecten fallax*, M'Coy (1844, pl. 14, fig. 2, 2a) described and illustrated nodulose ribs alternating with fine non-nodose secondary ribs for the left valve, the ribs separated by broad interspaces, and not bundled. Many fine ribs were shown on the right valve. But the material illustrated by Hind (1903, p. 76, pl. 17, fig. 28-30) from Ireland does not show nodose primary left valve ribs, and ribs are of subequal strength and appear to be weakly bundled. They agree in this respect with a left valve figured by Phillips (1836, pl. 6, fig. 19) as *dissimilis*, and reallocated to *fallax* by M'Coy (1844). Both M'Coy's and Hind's material look similar in overall round shape and long posterior wings. Thus there is uncertainty, as to whether M'Coy had misdescribed or misfigured his species, or whether Hind had misidentified his material. Hind (1903, p. 76) pointed out that the two specimens then kept at the Geological Survey of Ireland in Dublin did not agree well with the illustrations in M'Coy (1844), although labelled as *fallax*, and it is clear that he was not completely sure that the two specimens were really the same as the original material on which M'Coy based his description. Matthew Parkes, of the Natural History Division in the National Museum of Ireland has kindly examined the material in the Griffith Collection, and agrees with Hind that the illustration of M'Coy (1844, pl. 14, fig. 2) may well be a composite. No specimen matches it, but each varies somewhat, probably due to differences in preservation style and lithology. One or two specimens look quite like *Bifurcatatia meleagrinoides* in ornament (see p. 45), and one or two give a hint of the nodose appearance, but it seems much exaggerated in the illustration. Hind (1903) decided to retain the species name, and redraft the scope of the species, as having bundled ribs that lack the nodes reported and figured by M'Coy (1844). There are thus two ways of approaching the question – either accepting the Hind revision as correctly presenting the scope of the species, remembering this is reinforced, partly at least, by the material in Dublin, or proposing a new species for Hind's described material, to remove uncertainty on the species, but leave a measure of conjecture about whether the new name should be synonymized with M'Coy's *fallax*. It would not affect the validity of the proposed new genus if it were to be discovered that the new name should be synonymized. On the other hand, discovery that *fallax* was really in accord with M'Coy's rather than Hind's interpretation would demolish or severely alter the genus. It appears that stability of nomenclature is best ensured by allowing integrity to the description and figures of *fallax* by M'Coy, and allow that the left valve of *fallax* was ornamented by nodose primary ribs with slender secondary ribs, just as M'Coy (1844) had described and illustrated. M'Coy's interpretation suggests an unusual genus allied to *Etheripecten*. Hind's form with weakly bundled nature of the left valve ornament appears to have been allied to *Costatoplicatina* n. gen., type species *Pecten transversus* Sowerby, 1840 of Devonian age, with narrow costate very weak plicae. The two genera are similar in shape, and the left valve plicae are fewer than in *Costatoplicatina*, and the right valve costae not clearly bundled, but dense and often bifurcate. Another ally is *Fasciculiconcha* Newell, 1938, p. 65 from Pennsylvanian rocks of United States. The type species *F. knighti* Newell, 1938 and other species figured by Newell (1938) are larger, higher shells, with much stronger bundling on the left valve, consistently shorter posterior left valve wing, and substantial anterior gape. The one figured right valve (Newell 1938, pl. 8, fig. 1b) assigned to *F. providencensis* (Cox) shows slender single and branching costae, close to those of *Fallaxopecten* rather than *Costatoplicatina*.

Fallaxopecten mccoyi n. sp.

Text-fig. 95

1836 *Pecten dissimilis* [not Fleming] – Phillips, p. 212, pl. 6, fig. 19.

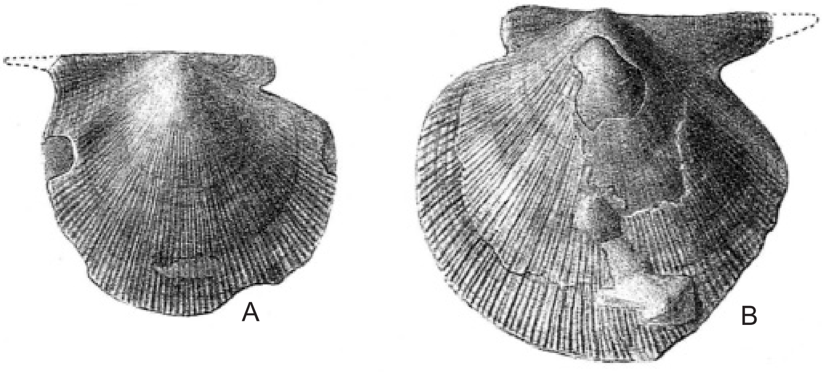
1903 *Aviculopecten fallax* [not M'Coy] – Hind, p. 76, pl. 17, fig. 28-30.

Derivation: Named for F. M'Coy.

Holotype: Specimen figured by Hind (1903, pl. 17, fig. 29), kept at Sedgwick Museum, Cambridge, from Early Carboniferous at Millicent, County Kildare, here designated.

Diagnosis: Small elongate shells with long posterior wings, long anterior left valve wing, long anterior right valve auricle, byssal notch, sinuses deep, ornament of weakly bundled fine ribs on both valves.

Discussion: The species has been described by Hind (1903) and contrasted with *Pecten fallax* M'Coy, notably in the lack of nodes on left valve primary ribs, and the presence of weak bundling. The overall subrounded shape, deep wing sinuses, and weak bundling distinguish the species.



Text-fig. 95. *Fallaxopecten mccoyi* n. sp. x1, right valve holotype CASM E 1317 figured by Hind (1903, pl. 17, fig. 29) from Millicent, Kildare, and left valve (pl. 17, fig. 30) from County Limerick, kept at National Museum of Ireland, from Early Carboniferous of Ireland.
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For *Pecten fallax*, M'Coy (1844, p. 92) described "numerous rounded nodulous ribs alternating with very thin smooth ones" and "intervening spaces striated transversely", which agrees with his figure (M'Coy 1844, pl. 15, fig. 11). Another specimen, not figured, was described as displaying "numerous radiating smooth equal ribs, the spaces between which are also smooth", and this appears to be the right valve. The ornament may differ for *fallax* M'Coy, but the shape comes close.

Superfamily **OXYTOMOIDEA** Ichikawa, 1958

[nom. transl. hic ex Oxytominae Ichikawa, 1958, p. 158].

Diagnosis: Pectiniform or suboval shells with gentle umbonal slopes, large to small or no posterior wings, anterior wing reduced and may be irregular or lost, byssal notch present and in many genera a gape between anterior right and left valves, right valve may be severely reduced in size. Ligament alivincular, may be irregular anteriorly, simple teeth in some genera, monomyarian.

Discussion: Oxytomoid genera are mostly Mesozoic in age and underwent a substantial reduction in the anterior shell, reverting from the expansion of the anterior seen in most Etheripectinidina. An early member, recorded from basal Triassic by Nakazawa (1981) in Kashmir, is *Eumorphotis* Bittner, a chiefly Triassic genus that displays the gentle umbonal slopes typical of Oxytomoidea, and was derived to judge from ornament and right valve from Etheripectinidae. Classification of Cretaceous members has been difficult. Whereas Triassic (or older) members such as *Oxytoma* and *Otapiria* have an ordinary alivincular ligament, a number of younger Mesozoic genera display a reduced anterior ligament often wrapped around a non-linear hinge structure and byssal notch, approaching the arrangement in some buchiid genera. The Cretaceous genus *Maccoyella* shows attributes of Oxytomidae, Eurydesmidae and Aucellininae, and such genera require further scrutiny, to be helped by examination of shell structure. Various components of this superfamily have been associated with Monotidae (Ichikawa 1958, Waller 1978, Carter 1990), but they are much closer to aviculopectiniform groups, especially Etheripectinidae.

The classification is as follows:

- Family Oxytomidae Ichikawa, 1958
  - Subfamily Oxytominae Ichikawa, 1958
  - Subfamily Maccoyellinae new
- Family Otapiriidae Waterhouse, 1982
  - Subfamily Otapiriinae Waterhouse, 1982
  - Subfamily Aucellininae Waterhouse, 2001
  - Subfamily Asoellinae Begg & Campbell, 1985

Family **OXYTOMIDAE** Ichikawa, 1958

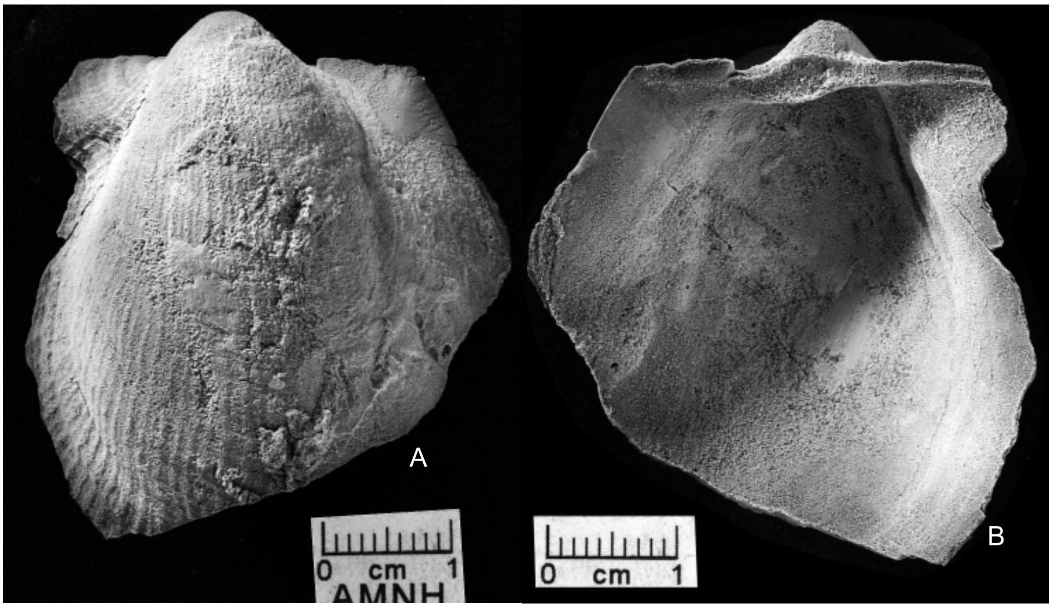
Diagnosis: Left valve more inflated than right valve, which varies from gently concave to moderately convex, ornament of costae and/or rugae, no plicae, posterior wing usually large on both valves, anterior reduced in size, byssal gape, ligament amphidetic and alivincular. Right valve ribs finer and more closely spaced than on left valve.

Subfamily **OXYTOMINAE** Ichikawa, 1958

Text-fig. 96, 97

Diagnosis: Right anterior auricle and left anterior wing small but unexceptional, ligament amphidetic, no teeth as a rule.

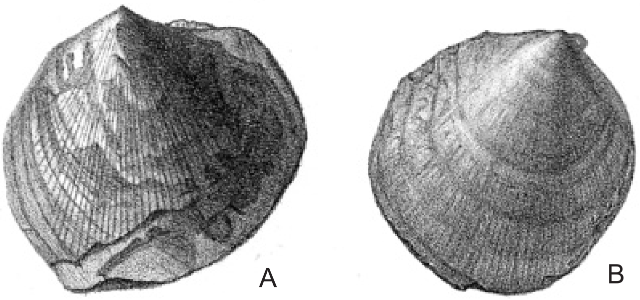
Discussion: Oxytomidae are Triassic to Cretaceous in age with smaller right valve bearing an anterior auricle and byssal notch. The pallial line is discontinuous, and the ligament is largely



Text-fig. 96. *Eumorphotis multiformis* (Bittner). A, B, left valve exterior and interior, AMNH 42892, as identified by Newell & Kummel, 1942 and Newell & Boyd, 1995. From upper Thaynes Formation, Utah. Photographs supplied by B. M. Hussaini, American Museum of Natural History, New York. See Newell & Boyd (1995).

external to semi-internal, generally with ligament pit. The greater inflation of the left valve and often moderately discordant ornament on right and left valves contrasts with Aviculopectinoidea or Chaenocardioidea which have subequally convex valves bearing much the same ornament, and Pseudomonotoidea have more irregular shape and shell structure differences. Rather the family approaches Etheripectinidae, but the shape is more rounded or oval, with less clearly defined posterior wings and gently rounded umbonal slopes, and smaller anterior left valve wing and right valve anterior auricle, and in general appearance members approach a pteriiform outline.

One of the early members is the genus *Eumorphotis* Bittner, 1901, p. 566, type species *Pseudomonotis telleri* Bittner, 1898, p. 170 (see Text-fig. 96). It has a moderately convex left



Text-fig. 97. *Pseudavicula australis* Moore, right valve and left valve from Cretaceous of Peak District and Coottanoonna, South Australia, partly altered in accord with Dickins (1960) from Etheridge (1892, pl. 24, fig. 13, 9) by adding right anterior auricle, x1. Originals at NHM, London.

valve, almost flat right valve, very large posterior wing in each valve not separated from the body of the shell, and well developed but not large anterior auricle and left valve anterior wing. A link between *Eumorphotis* and *Oxytoma* was also pointed out by Ichikawa (1958), and *Eumorphotis* was probably derived from *Etheripecten*-like species, judged from ornament and the low inflation of the right valve. Many authors have placed *Oxytoma* in Buchiidae, which is to completely misunderstand the two genera and families.

Oxytoma itself, of Upper Triassic to Upper Cretaceous age, is clearly close to etheripectinid stock, with little inflated right valve, well defined costae and comparatively large anterior left valve wing, and small but well formed anterior right auricle. *Hypoxytoma* Ichikawa and *Palmoxytoma* Cox were proposed as subgenera, but differ sufficiently in ornament to be regarded as full genera. The species described as *O. decemcostata* Whitehouse (1924, pl. 1, fig. 3) at the Australian Museum, Sydney, has a typical alivincular ligament and wide anterior gape, with anterior ribs curving round the gape.

Pseudavicula Hudleston, 1890 (Text-fig. 97) from the Lower Cretaceous beds of Australia retains its large but poorly delimited posterior wings, and has a very reduced right anterior auricle and no left valve anterior wing, and the degree of convexity of the two valves varies considerably (Dickins 1960). Some figures are provided from Etheridge (1892), with right anterior auricle added, to correct the impression of the genus provided by Cox (1969d, p. 346, Fig. C70.3), which illustrated a left valve and called it a right valve.

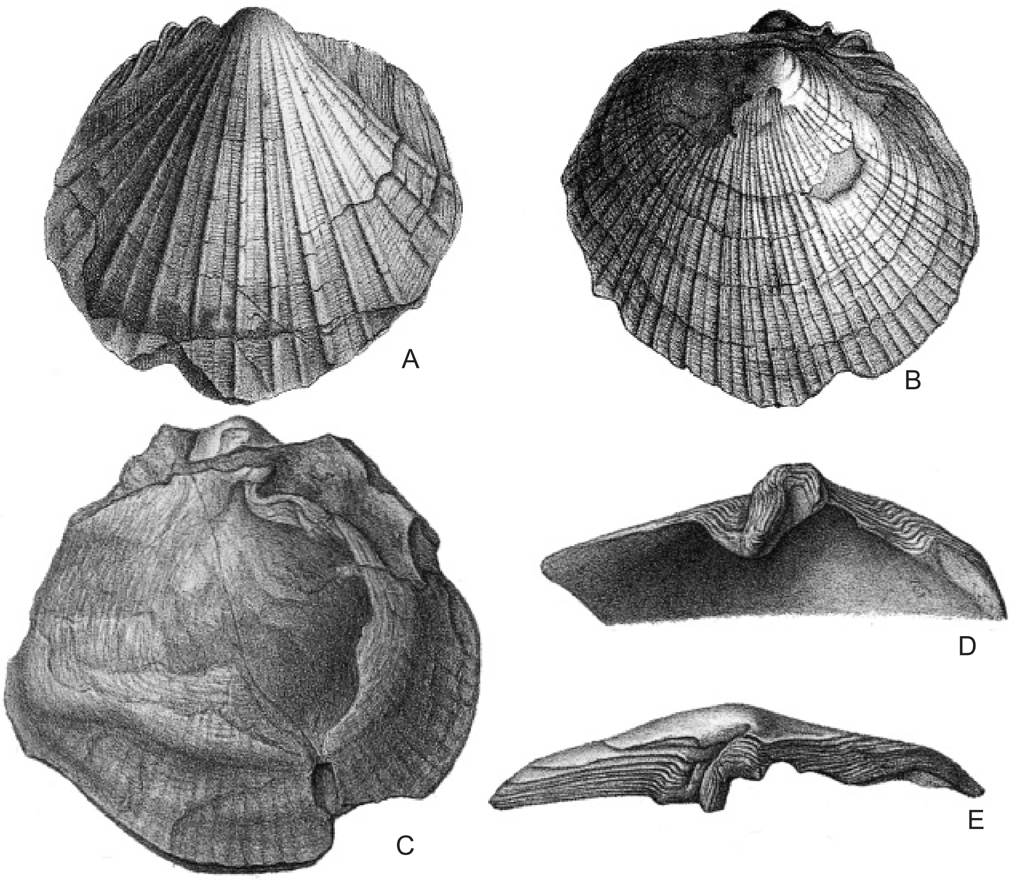
Subfamily **MACCOYELLINAE** new subfamily

Text-fig. 98 - 100

Name genus: *Maccoyella* Etheridge, 1892, p. 451 from Lower Cretaceous (chiefly Aptian) of Queensland, here designated

Diagnosis: Reduced anterior shell with small or no anterior wing, anterior ligament irregular, large left valve anterior tooth and right valve socket.

Discussion: *Maccoyella* Etheridge, 1892 is found in deposits of mostly Early Cretaceous age, especially in Australia, extending to New Zealand and South America. *Mimetostreon* Bonarelli, 1921 is a junior synonym (Waterhouse 2001, p. 122). *Maccoyella* has a small anterior wing and poorly defined posterior wing in the left valve, and scarcely defined if any posterior wing and a sturdy short anterior auricle that projects towards or over the commissure in the right valve. The ligament is irregular in outline. In the left valve, a large resilifer extends below the beak, in front of a slender posterior ligament sited along the posterior hinge, and the upper resilifer lies behind a slender ill-defined anterior ligament. The lower resilifer lies behind a long tooth, with a concave inner shelf in front, behind a shallow pseudolunular channel. The right valve hinge lies at the dorsal end of the shell, with a smaller resilifer, and posterior ligament extends along a more or less defined posterior wing. The anterior ligament in the right valve is narrow and scarcely defined, and curves above the resilifer, in front of the ill-defined umbo. In front lies a deep byssal channel heavily marked by growth-lines, and the byssal channel and anterior ligament enclose a hollow shelf, which receives the left valve tooth, and fits into the left valve area between the byssal channel and resilifer. Both valves may gape substantially in front of and below the byssal channel. These modifications recall those of *Eurydesma* (see p. 116) and the hinge in *Pinctada*, and it is believed that the similarity has been achieved independently from different stock, that ultimately shared ancestry, with employment of similar inherited morphological constructs to respond to shortening of the anterior shell. Conceivably, *Maccoyella* evolved from such genera as *Krumbeckiella* (Triassic) and *Frigidusia* (Cretaceous), but *Maccoyella* shares basic ornament, posterior wings and alivincular hinge with *Oxytoma*.



Text-fig. 98. *Maccoyella barklyi* (Moore). A, B, left valve and right valve figured by Etheridge (1892, pl. 22, fig. 1, 2), refigured from Moore (1870, pl. 63, fig. 2). C, *M. reflecta* (Moore), right valve aspect of GSQ F 1294 figured by Etheridge (1892, pl. 23, fig. 2). D, E. right valve hinge, from Etheridge (1892, pl. 23, fig. 6, 7). Specimens from Wollumbilla (A, B), Walsh River (C) and Mt Abundance (D, E), Cretaceous of Queensland, x1, kept at NHM, London except Text-fig. 98C.

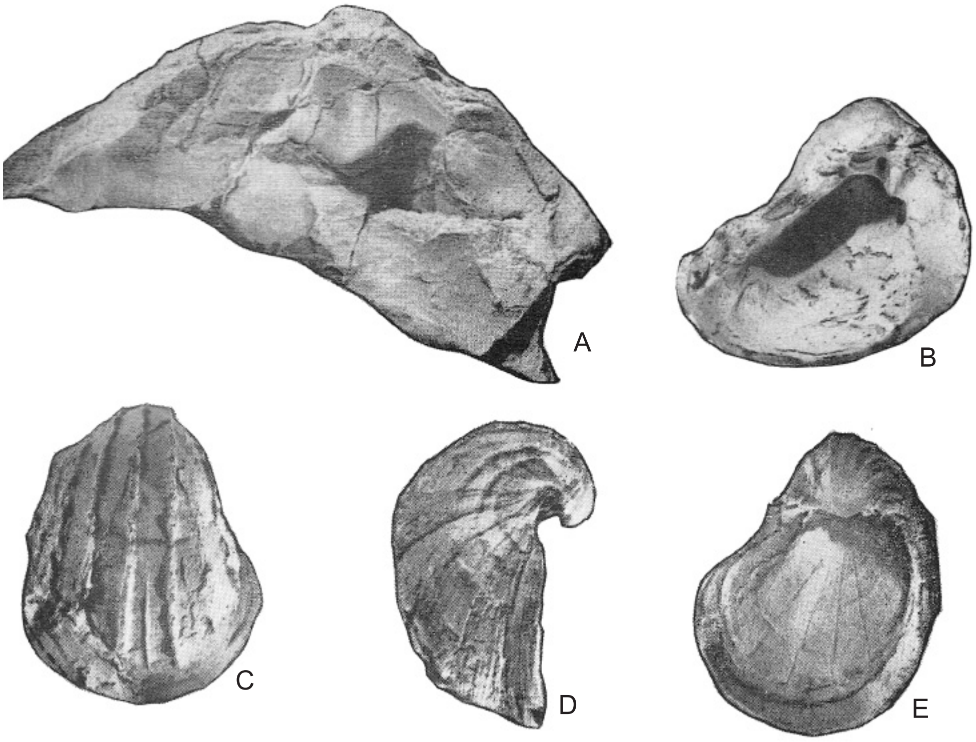
A companion genus *Zelotypia* Waterhouse, 2001, p. 122 based on *Maccoyella incurvata* Waterhouse, 1959b from Early Cretaceous of New Zealand, has a similar hinge and no posterior wing, so that it has assumed a buchiid shape, with highly convex left valve and almost flat right valve (Text-fig. 99). Waterhouse & Riccardi (1970) pointed to an allied species *Mimetostreon bonarelli* Leanza, 1963 in the southern Argentina. These two species provide rare examples of grypheation amongst the Etheripectinidina, and, given the distribution and time ranges and number of species, it is assumed that *Zelotypia* arose from *Maccoyella*.

The genera in Oxytomidae thus show considerable differences between genera, and this is believed to be real: evolution and change accelerated, but none of the stock survived into the Cenozoic.

Family **OTAPIRIIDAE** Waterhouse, 1982

[nom. transl. hic ex Otapiriinae Waterhouse, 1982, p. 41].

Diagnosis: Small prosogyrous inequivalve shells, right valve convex, smaller than left valve, right anterior auricle small or large, posterior wings small to absent, ornament of commarginal rugae,



Text-fig. 99. A, *Maccoyella reflecta* (Moore) = *M. magnata* Marwick left valve hinge, TM 2121, x1. B - E, *Zelotypia incurvata* (Waterhouse) x2. B, interior of left valve TM 2065. C, D, E, left, lateral and right valve views of holotype TM 2070, PVC cast. Specimens from Early Cretaceous (Aptian) of New Zealand. See Waterhouse (1970).

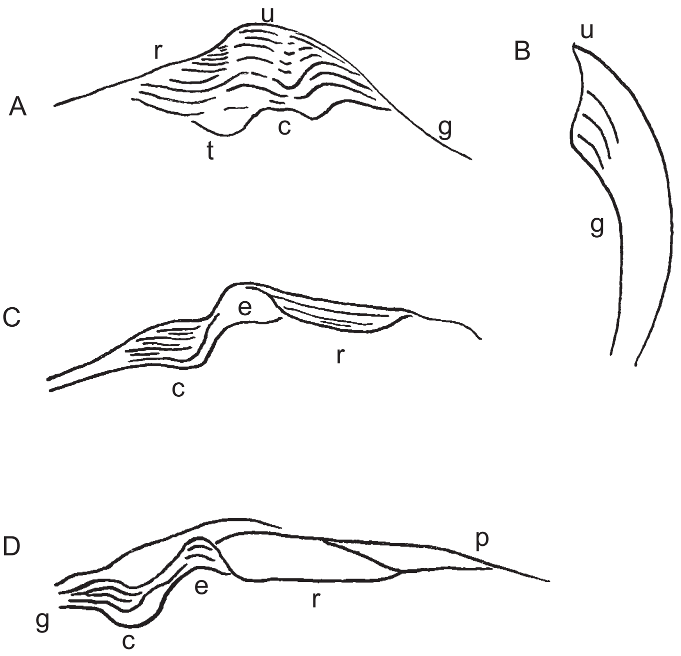
and/or fine radial ribs. Ligament amphidetic, external, alivincular, resilifer may be broad.
Discussion: Oxytomidae have better defined posterior wings.

Subfamily **OTAPIRIINAE** Waterhouse, 1982

Text-fig. 101

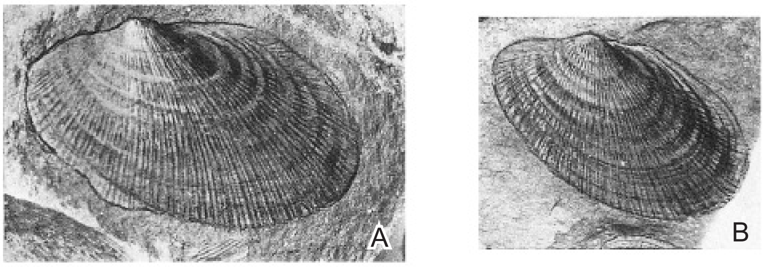
Diagnosis: Small prosogyrous inequivalve shells, umbones low and broad, right valve convex but less inflated than left valve, right anterior auricle small and simple, posterior wings moderately small to absent, ornament of commarginal rugae, and/or fine radial ribs.
Discussion: *Otapiria* Marwick, 1935 from the Late Triassic and Early Jurassic faunas of New Zealand and widely reported from elsewhere, is a small shell somewhat rounded in outline, with gently rounded umbonal slopes, small anterior right auricle and inconspicuous if any wings. Ribs are fine and crowded, intercalated on the left valve, branching on the right valve of the type species, whereas the right valve has commarginal rugae opposed to left valve ribs in another New Zealand species. The alivincular hinge is illustrated in Marwick (1935).

Many authors have ignored the nature of the alivincular amphidetic ligament and right anterior auricle, and compared the genus to Monotidae, including Marwick (1935), Zakharov (1962), Imlay (1967), Grant-Mackie (1978a, p. 100), Covacevich & Escobar (1979), Begg & Campbell 1985) and Damborenea (1987). Ichikawa (1958) rejected that relationship, as did Newell et al. (1969) and Yin et al. (2004), who referred the genus to Aviculopectinidae. This position



Text-fig. 100. Hinge in *Maccoyella reflecta* (Moore). A, left valve (posterior ligament lost) inner view and B, anterior view, AMF 51002, Lower Cretaceous of Queensland, x1 approx. C, D, right valve dorsal and inner lateral views of AMF 5149 from Lower Cretaceous of Bungeworgorai Creek near Mt Abundance, Queensland, x1 approx. a – anterior ligament, c – byssal channel, e – auricle, g – anterior gape, p – posterior ligament, r – resilifer, s – socket, t – tooth, u – umbo.

is certainly supported by the hinge and ligament, but the smaller size of the right valve, fine ribbing or only concentric rugae, tiny right anterior auricle and lack of posterior wings or anterior left wing led Waterhouse (2001, p. 124) to suggest that *Otapiria* belonged to a distinct Triassic group. Possibly, it was conjectured, *Otapiria* had descended from chaenocardioid stock, because *Chaenocardia* also has reduced posterior wings. Even so there would have been considerable change to much smaller wing, inequivalve state from subequivalve, and appearance of fine ribs on some forms, and commarginal rugae on others. These differences suggest that the genus is



Text-fig. 101. *Otapiria marshalli* (Trechmann). A, left valve, B left valve. From Lower Jurassic of Hokonui Hills, New Zealand, reproduced from the original figures by Trechmann (1923, pl. 15, fig. 7, 9), x1, kept NHM, London.

better regarded as a Triassic offshoot from Oxytomidae, displaying the same gentling of umbonal slopes and reduction of wings. An alternative source mentioned by Waterhouse (1982) lies in Claraiidae (Pterinopectinoidea), which may lack wings, and vary from ribbed to rugose, and have right valve smaller than left, with byssal notch, and small to large right anterior auricle. The hinge in well preserved Claraiidae is either duplivincular or replivincular (Gavrilova, 1996) or canaliform (Waterhouse 2000), constituting a strong difference, but on the other hand Waller (2005) and others have found no difficulty in postulating that genera with duplivincular hinge (*Caneyella, Posidonia*) gave rise to shells with alivincular hinge (*Bositra*). Conceivably a resilifer arose in an canaliform ligament, but this at present remains unproven.

Several genera of Triassic and Jurassic age share family characters with *Otapiria*. *Peribositra* Chen, 1981, p. 81 from Early Triassic of China, has commarginal rugae as in the right valve of *Otapiria masoni* Marwick, 1953. It is inequivalve, with commarginal flanges, alivincular hinge, and small right anterior auricle. Waller (2005) referred *Peribositra* to Claraiidae, but the nature of the hinge tells against such a position. *Lupherella* Imlay, 1967, p. 2 is close to *Otapiria*, and indeed Chen (1987) argued that the genus was indistinguishable from *Otapiria*, though this seems disputable. *Lupherella huidongensis* (Chen, 1987) as described by Yin et al. (2004, p. 323) differs from the type species of that genus in having a long right anterior auricle and extended byssal notch as in Asoellinae.

Genus ***Pteropiria*** new genus

Derivation: ptera – wing, Greek; piria - suffix of genus.

Type species: *Otapiria tailleuri* Imlay, 1967, p. 3 from Jurassic of California, here designated.

Diagnosis: Characterized by presence of well developed posterior wing on left and right valve.

Discussion: The type species has been described by Imlay (1967, p. B3, pl. 1, fig. 1-23). It is very close in most respects to *Otapiria marshalli* (Trechmann), the type species of *Otapiria* Marwick, with well developed radial costae over both valves and small anterior ear, but a well formed posterior wing is developed on each valve.

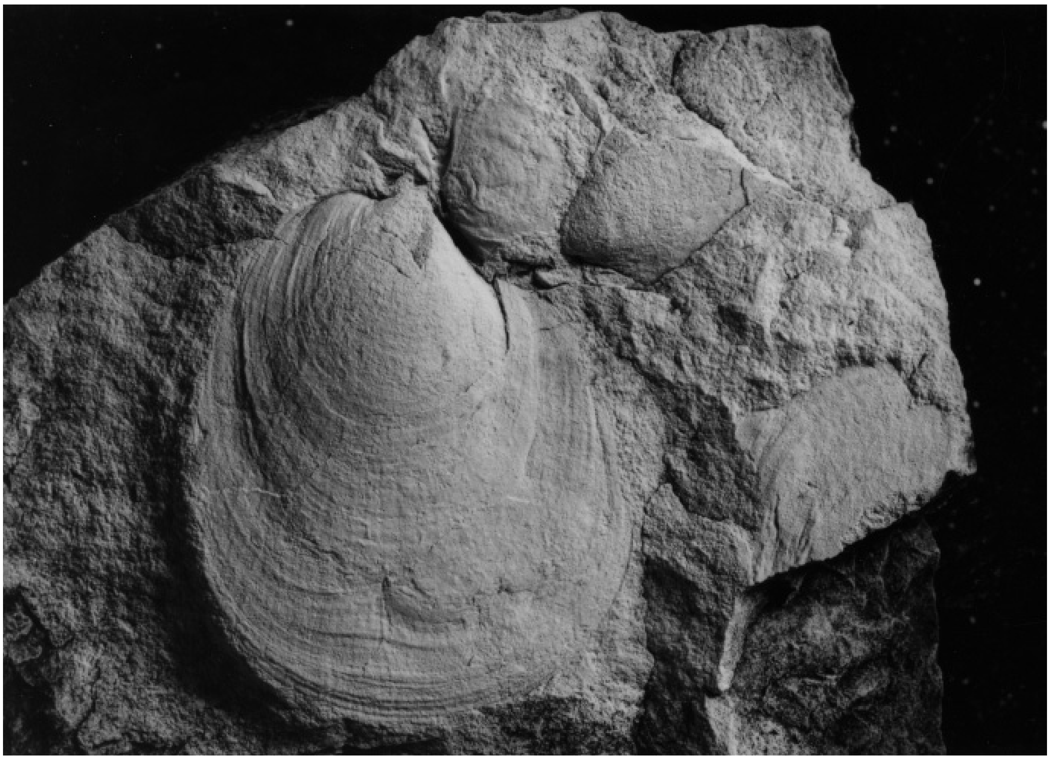
Subfamily **ASOELLINAE** Begg & Campbell, 1985

Text-fig. 102

[nom. transl. Waterhouse 2001, p. 124, ex Asoellidae Begg & Campbell 1985, p. 727].

Diagnosis: Small inequivalve shells with flat or gently convex to concave right valve, moderately inflated left valve, right anterior auricle moderately long and slender, ligament amphidetic and alivincular.

Discussion: Members of this subfamily are very close to *Otapiria* and allies, with similar subdued umbonal slopes and small to no wings. *Asoella* Tokuyama, 1959 approaches *Otapiria* in the variable presence or absence of radial costae, gentle umbonal slopes and poorly defined and reduced posterior wings. The presence of a long right anterior auricle provides a difference. The proposal of Family Asoellidae Begg & Campbell was not adequately buttressed by adequate analysis of the hinge, ornament, or shape, because the authors focused on differences from Monotidae, with its very different hinge. In that sense the proposal of the family-group name was inadequate, because the definition did not allow recognition or distinction of the group. But standing as a subfamily within Otapiriidae is provisionally justified through its long right anterior auricle, as proposed by Waterhouse (2001, p. 124), and the group may be resuscitated through redefinition and reallocation. *Etalia* Begg & Campbell (1985) is close in its left valve to *Otapiria*, and helps link the two subfamilies to the extent that the left valve wings may be lacking from



Text-fig. 102. *Etalia johnstoni* Begg & Campbell, left valve TM 5846, x3. From Anisian (Middle Triassic) Tearowhenua Formation, Nelson, New Zealand. Photograph courtesy of H. J. Campbell, GNS Science, Lower Hutt. See Begg & Campbell (1985).

procrescent specimens, and weakly developed in orthocrescent specimens (cf. Begg & Campbell 1985, Fig. 2b, c as compared with Fig. 2e). Both valves are made of calcite, the right valve with polygonal prismatic outer ostracum. Like *Asoella*, *Etalia* has a long right anterior auricle. The right valve is much less convex than the left valve, and even may be flat. Begg & Campbell (1985), followed by Waller (2005, p. 34), referred *Etalia* to Monotoidea Fischer, 1887, a position ruled out by the differences in morphology. *Monotis* has an opisthodetic ligament with small right anterior ear in front of the ligament (Text- fig. 57; Ando 1987, Fig. 27). In *Asoella*, the ligament is amphidetic, and passes along the inside of the right anterior auricle.

Subfamily **AUCELLININAE** Waterhouse, 2001, p. 125

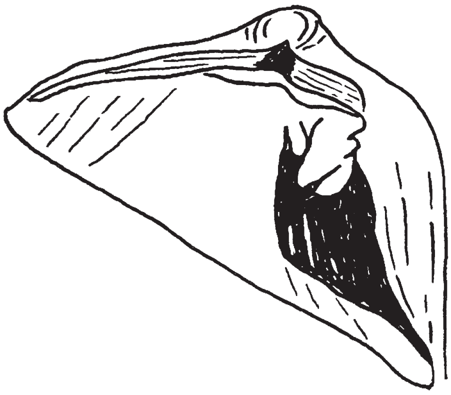
Text-fig. 103

[nom. transl. hic ex Aucellinini Waterhouse 2001, p. 125].

Diagnosis: Upright inequivalve pleurothetic shells with almost flat right valve, extended left umbo, faint commarginal ornament only, very small right anterior auricle which may be bent and lies above deep byssal notch, pseudoctenolium, no left anterior wing and very reduced if any left anterior wing, ligament amphidetic alivincular, dorsal anterior gape between right and left valves. No teeth.

Discussion: This subfamily is based on *Aucellina* Pompeckj, 1901 of Cretaceous age. The hinge is alivincular as in *Oxytoma*, but the anterior ligament is reduced, and there may be a substantial gape between right and left valve. There are no or very reduced posterior wings, small or no anterior left valve wing, and small often twisted right anterior auricle. Compared with *Otapiria*, *Aucellina* is more upright with prominent left valve umbo and lacks radial ornament, and is more

Text-fig. 103. *Malayomaorica malayomaorica* (Krumbeck), drawn from figure in Jeletsky (1963, pl. 21, fig. 2F), GSC 17007, from Upper Jurassic at Kawhia Harbour, New Zealand, x3. Showing right valve anterior auricle and anterior gape, left valve with alivincular ligament.



complex at the anterior hinge, and the left valve ligament may develop an anterior swelling, fitting into the interior of the right valve auricle. The right valve auricle is small, and left valve much more inflated than the right valve. Several upper Jurassic and Cretaceous genera belong to this subfamily, including *Malayomaorica* Jeletsky. Jeletsky (1963) also treated *Arctotis* Bodylevsky and *Meleagrinella* Whitfield (see Wandel 1936) to the same group, but this requires further study. *Aucellina* and *Malayomaorica* lack posterior and anterior wings, thus resembling Buchiidae, but differ from this family through their amphidetic ligament. They thus mark the culmination in the trend in anterior reduction shown by Otapiriinae.

Superfamily **AULACOMYELLOIDEA** Ichikawa, 1958

[nom. transl. hic ex Aulacomyellinae Ichikawa, 1958, p. 188].

Diagnosis: Small oval or anteriorly truncate shells ornamented by commarginal rugae and partly or entirely by radial round-crested firm costae, posterior wings feeble or usually absent, no anterior auricle, ligament largely or entirely opisthodetic or amphidetic alivincular.

Discussion: Members of this superfamily are close to Oxytomoidea, but lack as a rule posterior wings, and have no right anterior auricle. The genera are close to Otapiriidae in shape but have as a rule better defined ornament. The rules of priority and a marginal adherence to the rules for zoological nomenclature ensure that *Aulacomyella* is regarded as iconic for the group. Much better standards are offered by *Silberlingia* Imlay, and by *Bositra* Gregorio.

The superfamily is regarded as etheripectinidin, arising as an offshoot from etheripectinoid stock close to the commencement of Oxytomoidea, commencing probably with Bositridae, as is indeed confirmed, though to no great validity, by the fossil record. Early in its history, Bositridae followed the same trend exhibited by Oxytomoidea, shortening the anterior shell, with the ligament becoming much more opisthodetic. No members are known to have survived the Cretaceous Period.

Family **AULACOMYELLIDAE** Ichikawa, 1958

[nom. transl. hic ex Aulacomyellinae Ichikawa, 1958, p. 188]

Diagnosis: Small equivalve oval or anteriorly truncated genera with commarginal rugae, may be crossed by firm round crested costae over most or part of shell, no wings as a rule, no auricle, ligament opisthodetic or largely opisthodetic.

Discussion: This family is believed to be close to Bositridae, which is distinguished by its amphidetic alivincular ligament, but is close in size, shape and ornament. The two are close in time range, with the oldest genus *Ellesmerella* n. gen. being known from Late Scythian deposits, and *Didymotis* found in Upper Cretaceous faunas. The family includes *Aulacomyella* Furlani, with a truncate anterior shell and opisthodetic ligament, and distinctively patterned ornament allied to that of *Didymotis*.

Taxonomy: *Aulacomyella* Furlani, 1910, type species "*Posidoniella*" *problematica* Furlani (1910) from the Upper Jurassic of Dalmatia, was made name-giver of Aulacomyellinae n. subfam. by Ichikawa (1958, pp. 188, 198 ff.), supposedly as a group that also included *Posidonotis, "Diotis", Didymotis* and *Pseudodidymotis*, and was treated as a subfamily of Posidoniidae. They were distinguished from Halobiinae by the stronger radial ribbing ("Bie diesen Gattungen vermehren sich den Radialrippen hauptsächlich durch Einschaltung, wahrend die Rippen bei den Triasgattungen *Halobia* und *Daonella* sich ausschliesslich durch Gabelung, nicht aber durch Einschaltung vermehren" – p. 189). Such a definition verges on the extreme for inadequacy, but technically may be deemed acceptable under the loosely worded regulations for zoological nomenclature in ICZN (2000) Article 13.1 and 13.2. Article 13.2.1 states a family-group name first published after 1930 and before 1961 is available if it was used as valid before 2000. But it is not clear if "as valid" means it was validated with a description or definition that differentiated the taxon by that subsequent authority, or if simply by use, without definition, the name became validated. Several family-group names have been proposed "according to the rules", by promulgating a spurious definition that failed to make any real means of distinction and cases are not nearly as rare as they should be.

As a result, Aulacomyellinae has been ignored by a number of authors, including Cox & Newell (1969) and Freneix & Quesne (1985). The subfamily was recognised in Kelly & Doyle (1991, p. 100), but no diagnosis was offered, only a comparison, far from adequate, with other genera. Not surprisingly, a range of genera that vary in ornament and hinge have been incorporated by authors in the subfamily, commencing with Ichikawa (1958), and species have been referred to *Aulacomyella* itself that vary significantly from each other. Ideally, the proposal for Aulacomyellinae would be set aside, and a genus such as *Silberlingia* used to replace it, but since the requirements appear to have been met, not matter how marginally, this does not seem feasible.

Genus ***Ellesmerella*** new genus

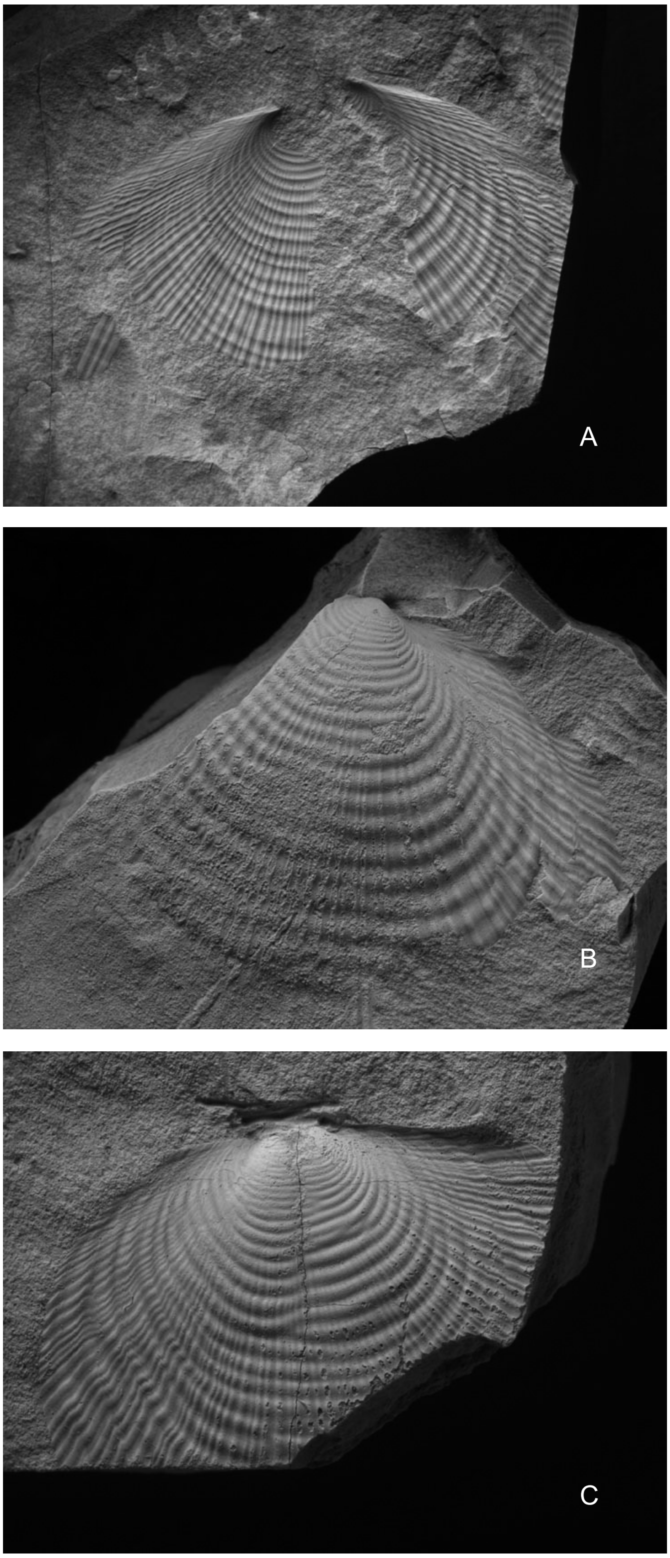
Text-fig. 104

Derivation: Named from Ellesmere Island, Canadian Arctic Archipelago.

Type species: *Posidonia aranea* Tozer, 1961, p. 102, from late Early Triassic (Mesokantoan, Smithian) Blind Fiord Formation, Ellesmere Island, Canada, here designated.

Diagnosis: Small, hinge much shorter than maximum length, umbones inconspicuous, no differentiated wings, nor byssal notch or right anterior auricle. Ornament of commarginal close-set rugae and firm ribbing.

Discussion: The type species was figured from the *Olenikites* beds in the Blind Fiord Formation on Ellesmere Island, of late Scythian (Early Triassic) age, and was described and figured by Tozer (1961, p. 102, pl. 28, fig. 13-15). The ornament is characteristic, and the ribs are crenulated by the concentric rugae, and appear to increase by branching. They become very fine anteriorly and posteriorly below the hinge, the ornament forming slightly differentiated areas to suggest a potential segregation of wings, though they are not differentiated by change in slope. The ligament is slender and starts under the umbones, and is short. The genus is readily distinguished from *Posidonia*, even externally, by the lack of anterior and posterior wings and presence of firm radial ribbing, and is much closer to *Bositra* and *Enteropleura*, but is marked by the distinctive radial ornament, and distinguished by the opisthodetic ligament. Like *Bositra*, the umbones are medianly placed and the valves moderately inflated.



Text-fig. 104. *Ellesmerella aranea* (Tozer). A, broken left valve GSC 14203. B, right valve holotype GSC 14202 with posterior hinge lost. C, left valve GSC 14203. From late Scythian (Early Triassic) Olenikites beds of Blind Fiord Formation, Ellesmere Island, Canada, x2. Photographs courtesy of E. W. Bamber, Institute of Sedimentary & Petroleum Geology, Calgary.

Tozer (1961) compared the species to *Daonella sanctae-anae* Smith (1914, p. 145, pl. 50, fig. 12-14) from Fossil Hill, Humboldt Range, western United States, but Smith's species has a longer hinge with angular cardinal extremities. Imlay (1963) made this taxon the type species of *Silberlingia* Imlay (1963, p. 101, pl. 14, fig. 1-9), characterized by strong commarginal rugae and disrupted marginals, procrescent outline and angular cardinal extremities. *Silberlingia* has a thick outer shell layer with large prisms on both valves, and the hinge was judged to be opisthodetic by Waller (2005, p. 19). It is now known to come from the Late Jurassic Bedford Canyon Formation of Santa Ana Mountains, California.

Aulacomyella Furlani (1910) , another Jurassic genus, is distinguished by its more truncate anterior, and comparatively strong and distinctive ornament, with ribbing limited largely to the subcentral shell, and the posterior shell especially ornamented by firm commarginal rugae, and less well rounded posterior dorsal margin. The genus is certainly close in known attributes to the Canadian form. The Upper Cretaceous genus *Didymotis* Gerhardt has weaker but essentially similar ornament, with a more extended anterior.

Ellesmerella aranea (Tozer, 1961)

Text-fig. 104

1961 *Posidonia aranea* Tozer, p. 102, pl. 28, fig. 13-15.

Holotype: GSC 14202 figured by Tozer (1961, pl. 28, fig. 13) from Late Scythian Blind Fiord Formation, Ellesmere Island, Canada.

Diagnosis: Weakly inflated with anterior and posterior shell defined by ornamental differences, ornament of radial ribs over most of shell, crenulated by low commarginal rugae.

Material: The collections from GSC 32363 and 28450 (see Table 5) were examined. Better material comes from the first locality, but none is as good as the figured types.

Dimensions in mm:

GSC	Valve	Length	Height	Width
32363	left	17.5	17	4.5
32363	left	23.5	?20	4

Description: The material includes large fragments, crowded like shells of *Daonella* or *Halobia*, or *Claraia* and *Pterinopecten* and such genera. One specimen is at least 34mm high, the others smaller. Three right valves show the posterior dorsal shell, not illustrated in the original study, and this is almost smooth, with very faint growth lines and traces of ribbing. The first formed shell is ornamented only by low commarginals, 5-6mm high in specimens from GSC 32363, and 8mm high on material from GSC 28450. Although wings are not delimited by a flattened area of shell, the dorsal shell does change in slope posteriorly. Radial ribs cover much or all of the remainder of the valves, about 9 in 5mm ventrally on many specimens and as few as 3 in 5mm on large specimens ventrally. The ribs on specimens from the type locality often commence as a pair in an interspace or on the flank of a commarginal rugation, as duocalated, and continue to the ventral margin without further increase in number. But on specimens from GSC 28540 the ribs are singles and increase by intercalation. As the ribs cross the commarginal rugae, they may arch forward to form small crenules, especially over the anterior shell below the umbo. The hinge is opisthodetic, and the anterior shell may incline steeply forward, or bulge more forward: a left valve shows the anterior hinge extending slightly past the umbo.

Family **BOSITRIDAE** new family

Name genus: *Bositra* Gregorio, 1886, p. 11 from Jurassic of southern Europe and widespread, here designated.

Diagnosis: Small and little inflated, equivalve or subequivalve, short hinge and no development of auricle or byssal notch in the right valve, wings may be present or absent, ornament as a rule of commarginal rugae, may be radially costellate. Alivincular, edentulous, monomyarian. Shell where known of calcite, forming a homogeneous mosaic not prisms in the left valve.

Discussion: *Bositra* was described from Jurassic deposits, and has been treated as senior synonym of the Early Triassic Russian genus *Peribositria* Kurushin & Trushchelev (1989) by Waller (2005). The mid-Triassic genus *Enteropleura* Kittl, 1912 from central Europe is similar in shape and has coarser and less regular rugae. These genera are united by commarginal ornament, alivincular hinge and monomyarian musculature, and lack of wings: the species with radial ornament and posterior wing that have been placed in *Enteropleura* by authors belong to *Wallerobia* n. gen. (p. 176) or await closer examination. Constituent genera range from Early Triassic (*Bositra*) to at least Upper Jurassic (*Kotickia*).

Text-fig. 105. Bositridae n. gen., n. sp. crowded mostly left valves from early Anisian Thorong Member, north central Nepal, x1.

A suite of poorly known genera may well fall within the family, as they appear to have a moderately long and amphidetic hinge, with simple radial round-crested ribs and varying degree of fine commarginal rugae. These include *Amonotis* Kittl, 1904, p. 736 from the Upper Triassic of Bosnia, distinguished by the presence of radial ribs, which increase by branching with some intercalated. The radially ribbed Jurassic genus *Diotis* Simonelli is possibly related, although the cardinal extremities are more angular, and indeed the left valve approaches that of *Asoella* Tokuyama. *Posidonotis* Losacco from mid-Jurassic of Europe has comparable ornament, with wings described as small but clearly delimited. Such genera have been referred to Aulacomyellinae by Ichikawa, 1958, though *Aulacomyella* has very anteriorly placed umbones and much more opisthodetic ligament.

In studies such as Cox & Newell (1969) and Waller (2005), *Bositra* has been regarded as a member of Posidoniidae. *Posidonia* is a Carboniferous genus with duplivincular hinge, dimyarian musculature and posterior and anterior wings. If *Bositra* evolved from *Posidonia* it involved substantial morphological change, of more than familial grade. The differences from Otapiriidae are much less. *Otapiria* may show commarginal ornament, and as it lacks developed wings as a rule, it was evidently a close relative, being, like *Bositra,* both alivincular and monomyarian. Carter (1990) pointed to similarities in shell structure to Pterineiidae and Myalinidae, but it is difficult to overlook the pectiniform ties in shape, musculature and hinge.

A new genus is represented by oval high shells, in which both valves are inflated, left more than right (Text-fig. 105). The umbones are moderately prominent, the anterior slopes steep and high, hinge short, cardinal extremities well rounded, with virtually no wings. Ornament consists of low rugae and growth-lines, and/or fine low radial costae, the ligament alivincular with shallow resilifer, and muscle scar posteriorly placed The outer shell in both valves is prismatic, covering a thin inner homogeneous layer: the inner layer appears nacreous. Some 100 specimens are found at localities in Nepal, including L 1514, Dolpo (west Nepal) and L 208 and L 218 (Manang). The species comes from the Thorong Member of the Gungdang Formation in the Manang district of Nepal, found in the *Epiczekanowskites plexus* Zone, with very large ammonoid faunules, including *Frechites, Gangadharites, Norites, Stenopopanoceras kukrii* Waterhouse, and *Grambergites annapurnaensis* Waterhouse (Waterhouse 1999, 2002c, p. 106), of early Anisian (Middle Triassic) age, and the faunas underlie the faunas and rocks of the Aegean *Paracrochordiceras anodosum* Zone in the Phukung Member and base of the Mukut Group. The bivalve is also found in the uppermost Sangjar Formation of west Dolpo in west Nepal.

Genus ***Kotickia*** new genus

Derivation: Named from name of formation which encloses the slide-block containing the fossil species.

Type species: *Aulacomyella willeyi* Kelly in Kelly & Doyle, 1991, p. 101 from Ameghino Member, Nodrenskjold Formation (Tithonian), in glide block contained within Kotick Point Formation, Gustav Group, Sharp Valley, northern James Ross Island, west Antarctica.

Diagnosis: Upright high subequilateral equivalve shells with moderately long hinge, obtuse cardinal extremities and fine radial costae covering the valves, in two or three orders, increase by bifurcation, crossed by low commarginal threads that form weak tubercles and crenulations with the ribs, especially anteriorly and posteriorly. Shell very thin.

Discussion: The type species was identified with *Aulacomyella* Furlani, 1910, but this genus, as discussed on p. 172 , has opisthodetic ligament and high steep anterior margin, and strong radial and concentric ribbing in a distinctive pattern. The present form clearly has an amphidetic ligament, as shown in several of the illustrations, and its hinge was compared with that of *Bositra*, as figured by Jeffries and Minto (1965, text-fig. 1). *Wallerobia*, as described below, is more elongate with slightly more prominent umbones, well defined slender posterior wings, and similar fine ribbing, more restricted to the median shell, and fine commarginals.

The type species was carefully described by Kelly in Kelly & Doyle (1991, Fig. 3-5), with holotype D.8757.31c, kept at the British Antarctic Survey Palaeontological Collections at Cambridge, also registed as BAS L.2548 in NHM curation system. On the basis of ammonoid evidence, Kelly & Doyle (1991, p. 99) suggested that the age was Late Tithonian.

Genus ***Wallerobia*** new genus

Text-fig. 106

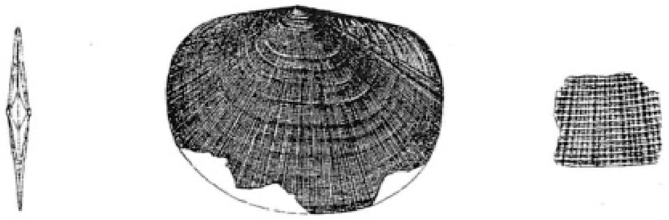
Derivation: Named for T. R. Waller.

Type species: *Enteropleura jenksi* Hopkin & McRoberts, 2005, p. 797, from Middle Triassic (Pelsonian) of Nevada, here designated.

Diagnosis: Thin equivalve or almost equivalve weakly inequilateral shells with submedian low umbones, moderately long hinge, slender posterior wing in each valve, and slight depression along its ventral margin, no anterior wing or auricle, ornament of fine radial threads and commarginal lirae. Ligament long and slender, poorly known but likely to be alivincular as judged from a species in Europe, adductor scar posteriorly placed between two low ridges tracking from the umbones to the posterior ventral margin. Outer shell prismatic, inner shell possibly calcitic.

Discussion: The type species was described by Silberling & Nichols (1982, p. 49) as *Enteropleura* cf. *bittneri* Kittl, and as *Enteropleura* sp. A by Waller (2005, p. 23, Fig. 6.4-6, 7. 8.1-3) and as *E. jenksi* by Hopkin & McRoberts (2005, p. 797, Fig. 3.1-3-12). It is found in the Fossil Hill Member of the Favret Formation, United States, occurring with *Balatonites* cf. *shoshonensis* Hyatt & Smith and *Favreticeras ransomei* (Smith) and other ammonoids of the *Shoshonensis* Zone (Bucher 1992), immediately below ammonoids of Illyrian age.

There is some discrepancy between the descriptions by Waller (2005) and Hopkin & McRoberts (2005). Waller (2005, p. 23) stated that one or two ridge-tracks were left by the posterior adductor scar, following Krumbeck (1924) and Campbell (1994, p. 44). The ridges slant from close to the posterior umbo to, it has been stated, the lower edges of the posterior adductor scar. Waller further stated that the adductor scar migrates ventrally and anteriorly, although the figures show no curvation in the tracking of the ridges – they are roughly straight. In fact, the ridges persist very close to, or right to the commissural margin, far beyond where the posterior adductor scar could have been placed. That suggests a degree of independence from the adductors on the part of the ridges, or rather, the adductor followed the ridge(s), not vice versa. It is deemed likely that the ridges, as slender and as inconstant as they may be, provided a low-grade strengthening for the posterior shell. The material figured as *Enteropleura jenksi* by Hopkin & McRoberts (2005) confirms the persistence of the internal ridge beyond any adductor scar, and they even reported a slight indentation at the shell margin where the ridge met the commissure. They reported the ridge as being anterior, not posteriorly placed. It seems likely, in view of the position of the muscle field, that the ridge was posterior. There is a further discrepancy in the two accounts. Waller (2005) reported and figured a slender convex posterior "auricle", ie. wing with obtuse cardinal extremity, faintly marked by growth striae in the specimen of Waller (2005, Fig. 6.6), separated from the body of the shell by a weak sulcus or channel, and bordered dorsally by a groove perhaps indicative of a slender linear ligament groove. Given the differences over whether the ridge was anterior or posterior, one might expect that Hopkin & McRoberts (2005) would have reported an anterior wing. But they also stated that "the posterior hinge margin is somewhat flattened to produce a small posterior auricle". That means, because of the dispute over whether valves were right or left, that the species apparently has anterior and posterior wings – if both authors were correct, and assuming that each overlooked one of two wings. I agree that some of the figures in Hopkin & McRoberts (2005, Fig. 3.1, 2, suggest an anterior flattening – not convexity, and that a similar flattening appears in some of the valves figured by Waller (2005). But the flattened part is not separated from the rest of the exterior, and it seems doubtful that it can be considered a wing



Text-fig. 106. *Wallerobia lamellosa* (Kittl) figured as *Posidonomya* nov. spec. by Arthaber (1896, text-fig. 12, p. 194) from Balatonitan of Austrian Alps, x1.

– with the proviso that the interpretation relies on figures, not specimens. If there is an anterior as well as posterior wing, the genus is close to the Bithynian specimen recorded from Nepal (Text-fig. 30), and shows some external approach to *Aparimella*, even though the wing size differs.

The ligament is clearly elongate and very slender, as shown by Waller (2005). The type species *jenksi* was identified by Waller (2005, p. 23, Fig. 6.4-6.6, 7, 8.1-8.3) with *Enteropleura* Kittl, 1912 from "Lower Muschelkalk" *Shoshonensis* Zone or equivalents of Germany and Hungary, but the type species of *Enteropleura*, *Daonella guembeli* Mojsisovics, 1874 (SD Diener 1923, p. 52), is more inflated with no posterior wing and with irregular commarginal ornament and no radial ribs. The muscle field in type *Enteropleura* was reported as being like that of *Posidonomya* by Ichikawa (1958). *Enteropleura bittneri* Kittl comes from the same general stratigraphic level as *guembeli* and is closer to *jenksi* in its radial ornament with posterior ridge reaching the posterior margin, though it appears to show no posterior wing. But the figures of *bittneri* are not satisfactory, and the presence of the posterior slender ridges and similar ornament in both type *Wallerobia* and in *bittneri* strongly suggest that the two are congeneric. The species *bittneri* has a resilifer, according to Arthaber (1896, p. 194, fig. 12).

Further information about *Enteropleura* was provided in the description of *E. walleri* Chen & Stiller (2007) from a Pelsonian (late Middle Anisian) fauna of the Banna Formation, northwest Guangxi, China. They described a distinctive species characterized by close-set commarginal wrinkles and very faint radial ribs, occasionally with a posterior internal ridge, and said to have a slender posterior wing though this is not clearly shown in illustrations, and is not as clearly defined as in *Wallerobia jenksi*. Chen & Stiller (2007) realised that shells referred to *Enteropleura* fall into two assemblages. The type species *guembeli* is small and subcircular to suboval in shape with irregular commarginal rugae and very weak if any radial striae. The same species has been identified from the lower Xinyuan Formation of Ziyun, China by Chen et al. (1974, pl. 175, fig. 22; Chen & Stiller 2007, Fig. 6), though it is clearly not the same species, having closer-set concentric wrinkles and stronger though still weak radials. The other species group proposed by Chen & Stiller (2007) included *bittneri* Kittl, *jenksi* Hopkin & McRoberts, *walleri* Chen & Stiller, and they suggested, *lamellosa* Kittl (1912, pl. 10, 23, 24), hitherto classed as *Daonella*. They did not note that the presence of a posterior wing in *jenksi* and *walleri* constituted a prime difference from *guembeli*.

Wallerobia cannot be placed in any simple evolutionary progression that leads from *Peribositria* = *Bositra* through *Enteropleura* to *Daonella* and then *Halobia* (or with the intervention of *Aparimella*). It has a slender but well developed posterior wing, whereas *Daonella* lacks any such wing, and it has a resilifer according to Arthaber (1896).

Superfamily **PSEUDOMONOTOIDEA** Newell, 1938

Diagnosis: Generally upright pectiniform shells with external alivincular ligament, often distorted through attachment. Right anterior auricle and byssal sinus well developed. Posterior sinuses weak, usually absent.

Discussion: A dorsally open pallial line and pedal levator muscle scar near the anterior end was illustrated for *Pseudomonotis* by Newell (1938, Fig. 2.5, 6). Newell & Boyd (1970) treated the group as closely related to Aviculopectinidae and Pectinidae, and Nevesskaya et al. (1971) also stressed an aviculopectinid relationship. Three families are recognised: Pseudomonotidae and Terquemiidae Cox, both superbly described by Newell & Boyd (1970), and more exceptionally, Hunanopectinidae Yin. The classification is as follows:

Family Pseudomonotidae Newell, 1938

Subfamily Pseudomonotinae Newell, 1938

Subfamily Pegmavalvulinae new

Family Terquemiidae Cox, 1964

Family Hunanopectinidae Yin, 1985

Subfamily Hunanopectininae Yin, 1985

Subfamily Leptochondriinae Newell & Boyd, 1995

Text-fig. 107. *Eumicrotis* [= *hemisphaericus* (Phillips)?], x1, from Early Carboniferous of England. Photograph courtesy of NHM, London.

Evolution: One of the oldest member of the superfamily so far known commenced in Lower Carboniferous deposits as *Pachypteria* Koninck, 1885, regarded as highly specialized by Newell & Boyd (1970, p. 230). It is an outstanding genus with no obvious links to contemporaneous and earlier genera. *Eumicrotis* Meek, 1864 was synonymized, incorrectly, with *Pseudomonotis* by Newell (1969c, pp. 341-342) and the upper Carboniferous type species *E. hawni* was illustrated by Newell (1938, pl. 18, fig. 8-16). *Eumicrotis* is close in several respects to Etheripectinidae, notably *Primaspina* n. gen. and *Vanvleetia* Waterhouse, with spinose primary ribs, intercalate further orders of ribs, thin right valve, byssal notch and anterior right auricle, and alivincular hinge. The genus is reported in the Early Carboniferous of England (Text-fig. 107), and is pseudomonotiform with apparent etheripectinin links. The fossil record does not establish whether pseudomonotids arose from etheripectinids, but it seems likely.

Pseudomonotoidea provided the source for Ostreidina Ferussac, through precocious development of a larval shell with a tendency to lie on one side, and become cemented to the substrate (Waller 1998, p. 30). They agree in shell shape, including highly lamellate and spinose shell and presence of resilifer. The calcite content of the ostreiid shell suggests derivation from a pseudomonotid survivor of the Permian/Triassic extinction shock in high southerly latitudes (cf. Waterhouse 1999, pp. 76, 77). There are some similarities to Monotidina, but shell structure as well as shape and ligament and auriculation are convincingly different in the two stocks.

Family **PSEUDOMONOTIDAE** Newell, 1938

Diagnosis: Distinctive shells, attached for at least part of their life cycle, with often misshapen valve, byssal notch often proximally rounded. The left valve sinus is weakly developed and generally absent. Hinge edentulous.

Subfamily **PSEUDOMONOTINAE** Newell, 1938

Diagnosis: Right valve small and gently concave or flat as a rule.

Subfamily **PEGMAVALVULINAE** new subfamily

Name genus: *Pegmavalvula* Newell & Boyd, 1970, p. 263, from late Cisuralian and early Guadalupian of Texas, here designated.

Diagnosis: Shells almost equivalved.

Discussion: Unlike members of Pseudomonotinae, the right valve is well inflated. Ornament in the name genus consists of comparatively uniform ribs, and the byssal notch is lost during early growth. As in other genera in the family, the posterior wings are small, spines are developed, and the left valve was cemented. The gills were filibranchiate.

Genus ***Sedeoconcha*** new genus

Text-fig. 108

Derivation: sedeo – sit; concha – shell, Lat.

Type species: *Pegmavalvula delicata* Newell & Boyd, 1970, p. 266, from Kungurian to Wordian (Early and Middle Permian) formations of Texas, here designated.

Diagnosis: Pseudomonotid shells with attached valve, both valves moderately convex, wings and auricle moderately defined, hinge long, ornament of fine scaly ribs, shell ventrally plicate. Protoconch and dissoconch small.

Discussion: The type species is a distinctive form from the Cathedral Mountain, Road Canyon and Willis Ranch Formations of the Glass Mountains and Lower Getaway beds of west Texas, of late Early and early Middle Permian age. The genus is readily distinguished by its ornament of fine scaly ribs on both valves, and the large cicatrix on the right valve umbo. The type species is like *Pegmavalvula* in having both valves inflated, but is ornamented by fine ribs, whereas *Pegmavalvula* has low irregular moderately well spaced plicae bearing large cylindrical spines, better defined right anterior auricle, and smaller better defined muscle scar that is complex irregularly rounded rather than ovally extended dorsal-ventrally. The early growth-stage for *Pegmavalvulina* when the spat was pectiniform and then became byssally attached was about twice as large as that of the new genus. Newell & Boyd (1995, p. 65) described a Lower Triassic species from Nevada and Utah as *P. triassica*, now referred to *Sedeoconcha*.

Family **HUNANOPECTINIDAE** Yin, 1985

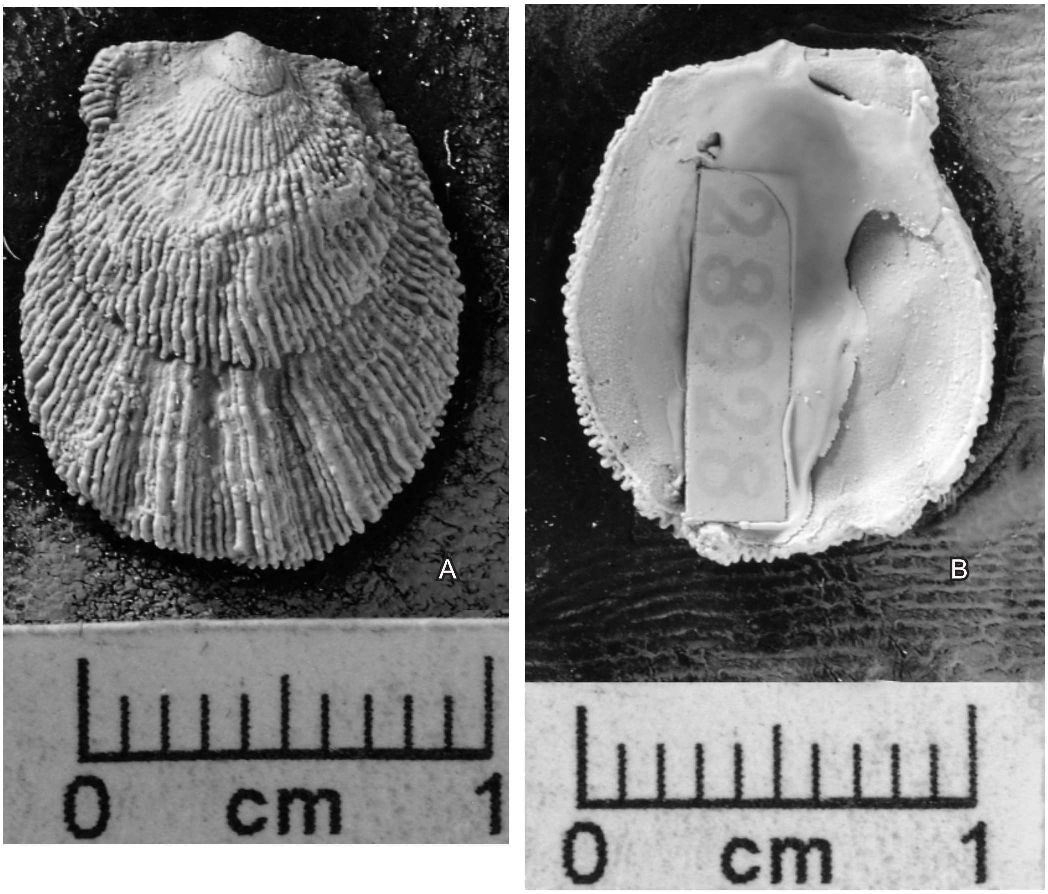
Diagnosis: Distinguished by simple teeth, posterior sinus weakly developed.

Discussion: Yin (1985a) claimed that *Hunanopecten* belonged to Pectinidae, and was corrected by Fang (1989), who treated *Hunanopecten* as a member of Aviculopectinidae, but noted the epibyssate nature of the genus. Newell & Boyd (1995) transferred the genus to Pseudomonotoidea, although the left wing does display a shallow sinus.

Subfamily **HUNANOPECTININAE** Yin, 1985

Diagnosis: Medium-small orbicular or weakly retrocrescent inequivalve shells, left valve more inflated, posterior wings small, left anterior wing weakly defined but relatively large with sinus, right anterior auricle large with deep narrow byssal notch. Right valve smooth, left valve smooth or costellate or subplicate. Ligament alivincular, lamellar tooth in each valve.

Discussion: The shells are orbicular, procrescent to very slightly retrocrescent, with small posterior wings, large right anterior auricle and large left posterior wing. The right valve is moderately



Text-fig. 108. *Sedeoconcha delicata* (Newell & Boyd). A, B, holotype AMNH 28928, external and internal aspects. Specimen from Lower Getaway Formation, west Texas. Photographs supplied by B. M. Hussaini, American Museum of Natural History, New York. See Newell & Boyd (1970).

convex. Pseudomonotidae generally have a flatter right valve, apart from *Pegmavalvula* Newell & Boyd, 1970 and *Sedeoconcha* n. gen. in Pegmavalvulinae n. subfam. Hunanopectininae are characterized by gentle umbonal slopes not unlike those of some Mesozoic Oxytomoidea, and are further distinguished by hinge supports. The overall symmetry and features of Hunanopectininae are unusual, but the Newell-Boyd interpretation is accepted, and although Hunanopectinidae shares with Chaenocardiidae Miller characters such as biconvexity, small posterior wings, ovoid retrocrescent to procrescent outline, and development of simple (though different) hinge teeth, the family differs considerably in symmetry, having a more upright shell and wide hinge.

Furcatia Waterhouse, 2001, p. p. 133, type species *Etheripecten petulantis* Waterhouse, 1987 from the Elvinia Formation of the southeast Bowen Basin has ribs that are bifurcate and intercalate on both valves, especially the right valve. This was deemed to signify a distinct tribe placed in Hunanopectininae Yin, 1985b by Waterhouse (2001) because of its large left valve anterior wing and other features, but the interior lacks the opposing bourrelets above hinge teeth, and appears to be chaenocardioid, as a member of Streblochondriidae Newell.

Subfamily **LEPTOCHONDRIINAE** Newell & Boyd, 1995

[nom. transl. Waterhouse 2001, p. 116 ex Leptochondriidae Newell & Boyd 1995, p. 69].

Diagnosis: Left valve convex with ribs, right valve less inflated, almost smooth, right anterior auricle large with deep byssal notch, left anterior wing large, posterior wings small. Ligament external alivincular with lativincular ligament, bourrelets narrow or absent, auricular buttress.

Discussion: Leptochondriinae is close to *Hunanopecten*, with bourrelets present or absent, and of Permian to Triassic age.

Family **TERQUEMIIDAE** Cox, 1964

Carter (1990) referred this group to Monotoidea, because of morphology, ligament structure and life habit, but the construct of these features suggests a pseudomonotid alliance. The name genus and other Triassic representatives are not well known, and Newell & Boyd (1970, p. 269) acceptably relied on a new Permian genus *Paleowaagia* Newell & Boyd for their interpretation of the family. They diagnosed the group as small subovate shells with convex right valve and poorly developed if any wings, with or without primitive isodont dentition.

Suborder **OSTREIDINA** Waller, 1978

Diagnosis: Shells that lose foot immediately after settlement, cemented by left valve, eulamellibranch gill structure as a rule, and posterior palliobranchial fusion, ostracum of lathed or foliated calcite, without nacre and crossed aragonitic structures. Ligament alivincular with resilifer.

Discussion: Waller (1998) has provided a summary of some of the more significant attributes of the suborder. He was inclined to dismiss the proposal that oysters may have arisen from Pteriida, suggested by Carter (1990), and so far most evidence favours a pectinidian alliance.

Anomioidea Rafinesque, 1815 differs considerably from other major groups classed within the pectiniform bivalves, and was treated as a superfamily within Ostreida by Waller (1998), whereas Starobogatov (1992) recognised Suborder Anomiiidina, Dall, 1883 within Order Pectinida. Constituent genera are of irregular outline rather than pectiniform, sessile as a rule, and usually inequivalve. The byssus during development becomes a horny plug passing through an embayment or foramen in the lower (usually right) valve, and the muscle scars are most strongly developed opposite the plug, as a subcentral adductor with byssal retractor scars on the left valve. Only two families are well established as belonging to the group according to Amler (1999), but Starobogatov (1992) recognised two infraorders, Dimyoinei Pelseneer, 1906 with reduced ascendant parts of the gills, in families Dimyidae and Heteranomiidae, and infraorder Anomionei Dall, in families Anomiidae Rafinesque, 1815 and Placunidae Gray, 1840 with normal filibranchous gills. The peculiar Permian family Permanomiidae Carter, 1990 shows general similarities, but Fürsich & Palmer (1977) described *Eonomia* as being a genuine ancestor of Jurassic age, and Yonge (1977) pointed to muscle scar differences from genuine Anomioidea, so that Waller (1998) rejected the alliance, whereas Carter (1990) rejected the Fürsich & Palmer conclusion. Waller (1998) treated the group as a superfamily, within Ostreida, whereas Amler (1999) classed it with Pectinida.

Order Pectinida Nevesskaya, Scarlato & Starobogatov, 1971

Pectinida was used as an order by Nevesskaya et al. (1971) and attributed to Adams & Adams, 1857: Carter (1990, p. 234) independently recognised the same order. The content differed in the two instances, Nevesskaya et al. (1971) excluding aviculopectens, euchondriids and other groups as Pteriida, whereas Carter (1990) included several of the groups in his interpretation of the order. Newell & Boyd (1995, p. 25) largely followed Carter (1990), but chose to claim the order for themselves, even though they referred to Carter's study. There may well be sound reasons for attributing Pectinida to Nevesskaya et al. only if their interpretation is adopted, and to Carter

(1990) if his version is accepted, by and large, but there appears to be little merit in attributing the order to Newell & Boyd. The present study does not follow the Carter interpretation, and it has not been found it possible to set aside the Russian view completely, in view of the implications from Euchondriidae and Crenipectininae, as discussed shortly.

Pectinida are distinguished by internal ligament, with different stomach type from Ostreida (Purchon 1987). In Pectinoidea, Amler (1999) recognised Proeamussiidae Abbott, Pectinidae Wilkes, Entoliidae Teppner, Spondylidae Gray and Pernopectinidae Nevesskaya, Scarlato & Starobogatov, possibly with Saharopteriidae Pareyn, Termier & Termier. These groups radiated in the early Mesozoic, Hautmann (2004) pointing to the ways in which the ligament became adapted to counter predation. He analysed the way in which the lateral ligament became replaced by hinge teeth, to limit the primary ligament to a central groove, or what he called alivincular-fossate ligament, as in Dimyidae Fischer, Plicatulidae Watson and Spondylidae Gray. Different growth directions of the resilium and lateral ligament led to an internal position for the resilium to enable fast and powerful opening of the valves, as in Entoliidae and Pectinidae, with their "alivincular-alate" ligament. This of course started in the Paleozoic times, which were not without predators of their own!

Pectinidae, Waller (1991) considered, may have arisen from Entoliidae Teppner, a limited group of small almost biconvex shells with high left valve ears, no byssal notch in adult specimens as a rule, deep resilifer pit, well developed auricular crura, and calcitic shell. One member *Pernopecten* Winchell, 1865 commenced in the Early Carboniferous, but it seems probable that root-stock was of greater age. Here it is suggested that Euchondriidae are close to Entoliidae, and although equipped with a modified form of alivincular-areate ligament, may have been ancestral or sibling stock for Entoliidae.

Family **EUCHONDRIIDAE** Newell, 1938

Diagnosis: Series of interlocking denticles along the hinge. Right valve less inflated than left valve, marked by subdued concentric or stronger radial ornament, left valve more inflated with fine ribbing increasing by intercalation.

Subfamily **EUCHONDRIINAE** Newell, 1938

Diagnosis: Shells with resilifer.

Discussion: *Euchondria* is usually placed as a member or ally of Aviculopectinidae, understandably, because it has wide hinge, amphidetic modified alivincular ligament, convex left valve and less inflated right valve, just as in members of Etheripectinoidea. On the other hand, the adductor complex is small and posteriorly placed (Newell 1938, pl. 19, fig. 18), and the shell structure involves quadrate or less commonly hexagonal prisms in the outer right valve. The long denticulate hinge involved a substantial modification to the alivincular ligament, and conjecturally, a step close to the replacement of the lateral ligament by a thin periostracum which joins the valves dorsally and internalisation of the resilifer in pectens. The resilifer of *Euchondria* is deep sunken compared with etheripectens and aviculopectens, but is not truly internal compared with the resilifer of *Pecten*. On the other hand there are aspects of the morphology that come close to those of *Pernopecten*, as pointed out by Waller (1998, p. 31). *Pernopecten* has comparable prisms in the shell, and a truely internal resilifer, and some plesiomorphic development of interlocking hinge structures, Waller highlighting the Lower Mississippian species *P. limaformis* (White & Whitfield). *Pernopecten* has mostly weak concentric ornament, and its most striking external feature lies in the dorsally projecting wings, with weak or no byssal sinus for the anterior of the right valve. In some species of *Euchondria*, the right anterior auricle is feebly developed, as in *E. menardi* (Worthen) figured by Newell (1938, pl. 19, fig. 14b), and usually the byssal notch is high and shallow. *Pernopecten* ranged from Upper Devonian to Permian and is classed in Entoliidae Teppner, 1922. *Euchondria* ranges from Devonian to Permian. Such time ranges do not offer reassuring evidence for euchondriids evolving into *Pernopecten*, but the fossil record is too meagre to be reliable. There may be a case to suggest that if Euchondriidae provided source material for Pectinida, it could be regarded as pectinid, and come to be associated with Entoliidae as a superfamily Entolioidea. But the suggestion for a link between Euchondriidae and Pectinida is no more than a hypothesis. At first sight, it would seem to imply that Pectinida shared common ancestry with Etheripectinidina, and that Euchondriidae acted as a bridge between the two. However that suggestion is challenged by the nature of the hinge in Crenipectininae, a subfamily of Euchondriidae, which was known in Early Devonian time, and lacks a resilifer (see p. 186).

Genus ***Euchondria*** Meek, 1874

Type species: *Pecten neglectus* Geinitz, 1866, p. 33 from Pennsylvanian Table Creek Shale, Nebraska.

Diagnosis: Left valve convex with acute posterior cardinal extremity and large wing and well spaced slender and firm costae increasing by intercalation, crossed by fine low growth laminae, may be weakly noded. Right valve smooth or marked by fine concentric striae.

Discussion: *Euchondria* has been widely reported from faunas of upper Devonian to Permian age. The type species *E. neglecta* (Geinitz, 1866, pl. 2, fig. 17), Meek (1872, pl. 9, fig. 1, a, b) and Newell (1938, pl. 19, fig. 1, 4) with *coxanus* Meek (1872, pl. 9, fig. 2) regarded as a synonym, comes from the Upper Carboniferous of Nebraska, and has a characteristic left valve, with long umbonal slopes, deep wing sinuses and well spaced ribs in two or three orders arising by intercalation on the left valve. Newell (1938) has discussed the nature of the type species of *Euchondria*, and pointed to some of the difficulties in circumscribing the species (and therefore the genus). Geinitz (1866, pl. 2, fig. 17) figured a right valve, which he considered to be a left valve (Newell 1938, p. 104), that Newell recorded as having a smooth surface. Meek (1872, p. 193) in describing further material stated that the "body part of both valves apparently marked by fine concentric striae", but presumably he had only right valves. The left valve of a species ascribed to *Aviculopecten coxanus*, believed by Newell to be the left valve of *neglectus*, has radial costae. It is thus difficult to be sure of the nature of the ornament, and it is reasonable to follow Newell (1938) in building up a picture of the genus from the nature of other North American species that as far as can be assessed, come close to *Euchondria neglecta*, and also in relying to considerable degree on well preserved specimens from the Jones Point Shale in Nebraska, which were believed by Newell to belong to *neglecta*. The left valve ribs are well formed, narrow, and separated by wide interspaces, with slightly differentiated second order ribs arising by intercalation, and crossed by fine growth laminae. The left anterior wing is moderately large, and the left posterior wing is large with acute extremity and deep sinus. Right valves of various species may show subdued radial undulations. *E. subcancellata* Newell is almost smooth, and there are signs of faint and very closely spaced growth laminae. Studies up to now have focused on the hinge as a means for determining whether or not the species should be placed in *Euchondria*. Here it is proposed to segregate species that differ in ornament from type and allied species of *Euchondria*.

Genus ***Aprathipecten*** new genus

Derivation: Named from Aprath, Germany.

Type species: *Euchondria aprathensis* Rathman & Amler, 1992, p. 50 from Early Carboniferous of Aprath, west Germany, here designated.

Diagnosis: High shells with moderately long umbonal slopes, short to moderately long hinge, right valve anterior auricle well defined, lightly ribbed, left valve posterior wing with rounded extremity. Left valve ornament of fine even and intercalated costae, right valve crossed by distinct evenly and well spaced concentric laminae.

Discussion: This species was described by Rathman & Amler (1992, pl. 5, fig. 1-9, pl. 6, fig. 1-10) from Early Carboniferous at Aprath, levels cd 111 α-β, with holotype Mbg. 3996 figured in pl. 5, fig. 1. Material is very well preserved, enabling the genus to be readily circumscribed. It differs in shape from *Euchondria neglecta*, being high, with hinge of variable length, and the posterior left wing has a less acute cardinal extremity than in *neglecta*, and the right anterior byssal notch is narrower. Left valve ornament is close to that of *Euchondria neglecta*, comprised of slender ribs increasing by intercalation in two or three orders, separated by wide interspaces, and crossed by fine concentric laminae, which unlike those of *neglecta*, do not form nodes or beads across the costae. The right valve is ornamented by even moderately spaced concentric lirae, much more regular and prominent than on *E. neglecta* or the other species ascribed to *Euchondria* by Newell (1938). In *E. subcancellata* Newell there are only faint and irregularly spaced threads, and the right valve of *E. neglecta* was figured as smooth.

Pecten aurilevis Roemer (1852, p. 91), also described in Paul (1941, p. 220) and Rathman & Amler (1992, p. 48, pl. 4, fig. 1-9) from the same region as the type species, at level cd 111 α, is congeneric.

Genus ***Callytharrachondria*** new genus

Derivation: Callytharra – name of sedimentary basin in Western Australia; chondria – bivalve ending.

Type species: *Euchondria callytharraensis* Dickins, 1963, p. 89 from top of the Early Permian (late Sakmarian or Artinskian) Callytharra Formation, Western Australia, here designated.

Diagnosis: Shells orthocrescent with umbonal slopes straight and of moderate length, left valve ornament of close-set ribs, increase by intercalation, semicalation and rarely branching, not strongly differentiated, growth increments inconspicuous. Right valve ornament of firm commarginal ribs. Posterior sinus virtually absent, better defined for anterior left valve wing and anterior byssal notch high but short.

Discussion: The strongest characteristic of this genus is the difference in wings, all, especially posteriorly, showing shallow or usually no sinus and in being relatively short, in contrast to *Euchondria, Velbertia* and *Pellucipecten*. As well the byssal notch is shorter and higher. The overall shape and nature of left valve ornament show strong similarities to features of *Velbertia* (see below). The type species comes from the upper Callytharra Formation, Fossil Cliff Formation and Nura Nura Member of middle Early Permian age in Western Australia, as has been described and illustrated by Dickins (1963, pl. 14, fig. 2-8). A less elongate species that has similar short wings but deeper sinuses was described as *E. weiensis* Wanner (1940, p. 378, pl. 1, fig. 2) from Tai Wei, Permian of Timor.

Genus ***Pellucipecten*** new genus

Derivation: pelluci – from species name; pecten – bivalve scallop, Lat.

Type species: *Aviculopecten pellucidus* Meek & Worthen, 1860, p. 435, Meek & Worthen 1866, p. 327, from Pennsylvanian Desmoines beds of Illinois, here designated.

Diagnosis: Left valve umbonal slopes well defined, ornament of subeven ribs closely spaced and crossed by well defined though low commarginal growth threads. Right valve covered largely by dense fine commarginal growth-threads.

Discussion: The type species is a distinctive form with umbonal slopes convex in section and the posterior margin less concave in outline than in *Euchondria* or *Velbertia*. The ornament of the left valve is characteristic, with fine ribs increasing by intercalation, and by semicalation laterally, the second and tertiary orders becoming as strong as primaries, and commarginal ornament better defined than in other genera. The ornament is dense compared with species of other genera. Right valve ornament consists of very closely and evenly spaced fine commarginals, much more compressed than in *Aprathipecten*. Sinuses are moderately deep, as in other genera.

The type species has been described and figured by Meek & Worthen (1866, p. 327, pl. 26, fig. 5a, b) and Newell (1938, pl. 19, fig. 16, 17, 19), with lectotype no. 10,932 kept at Illinois University.

Genus ***Velbertia*** new genus

Derivation: Named from Velbert, Rhine Schiefergebirge.

Type species: *Euchondria vera* Drevermann, 1902, p. 504, from uppermost Devonian of Bergisches Land, Germany, here designated.

Diagnosis: Small and generally acline, left valve with closely spaced moderately strong ribs, right valve crossed by low growth rugae and faint growth laminae, crossed by very fine radial threads, left valve wings and right valve posterior wings with fine costae, sinuses well developed, right posterior wing and anterior auricle ribbed, moderately developed short and high notch and anterior margin convex forward.

Discussion: By comparison with *Euchondria*, *Velbertia* has more closely spaced and slightly higher left valve ribs, and almost smooth right valve that is ornamented by low moderately close-spaced rugae and fine growth laminae, and, according to a well preserved specimen ascribed to *E. beushauseni* in Amler et al. (1990, pl. 4, fig. 2), very fine radial threads forming tiny beads at intersections. The wing sinus and byssal notch are not identical in the two suites, but are much the same, and wings and auricle carry ribs. Posterior umbonal slopes diverge more broadly than in *Euchondria* and are slightly shorter.

Velbertia vera was described by Drevermann (1902, pl. 14, fig. 18, 19) from the Etroeungt beds, and further described by Amler et al. (1990, p. 51, pl. 4, fig. 3) and Amler (1992, p. 2, fig. 8-10). Amler et al. (1990) indicated that *Aviculopecten schulzi* Frech (1891, p. 21, pl. 1, fig. 10) might be involved, and as noted by Amler (1992), it is difficult to separate *E. vera* from *E. beushauseni* Drevermann, 1902, p. 507, pl. 14, fig. 20 (see also Amler et al. 1990, pl. 4, fig. 2). The differences from *Euchondria* are not substantial, but appear to be justified by the consistency in ornament in a number of Carboniferous to Permian species that indicate a pool of closely related species, differing palpably from the Devonian form from Germany. One exception at least amongst American species is *E. smithwickensis* Newell (1938, pl. 19, fig. 12, 13b) from the Smithwick Shale of north-central Texas. This has close-set left valve ribbing approaching that of *Velbertia*, and as well the shell has shorter and more widely diverging umbonal slopes approaching those of *Velbertia*. The right valve of this species has a high byssal notch and is essentially smooth, with only traces of very fine commarginal laminae, low irregular rugae and fine faint radials. Provisionally it may be referred to *Velbertia*.

Subfamily **CRENIPECTININAE** Astafieva, 1991

Diagnosis: Radial ribs on right valve. No resilifer.

Discussion: *Crenipecten* Hall, 1883, p. 3 and *Crenipectinella* Astafieva, 1991a, p. 19 range from Lower Devonian in Rudny Altai as high as Middle Carboniferous in Asia, with North American occurrences as well. Euchondriinae was said to range from Upper Devonian to Permian by

Astafieva (1991a). *Crenipectinella* was stated by Astafieva to lack a resilifer, yet one appears to be developed in the figures (Astafieva 1991a, Fig. 4, 5) for the type species *Crenipecten altaicus* Muromseva and Turbanov in Muromseva (1974), of early Tournaisian age. On the other hand, the ornament of *altaicus* is like that of *Crenipecten* in being similar on both valves, and consisting of intercalated with some bifurcate ribs.

Conceivably the lack of a resilifer in *Crenipecten* provides evidence for a link to Leiopectinidae Krasilova, an Ordovician to Devonian family that lacks a well-defined byssal notch, and has auricular crura. If the fossil evidence is to be accepted, it appears that Crenipectininae were forebears of Euchondriinae and possibly provided root stock for Pectinida, independently from Aviculopectinidina with its alivincular hinge.

CONCLUSIONS AND QUESTIONS

Text-fig. 109 presents a sequomorph of monotidin, aviculopectinidin and etheripectinidin groups, pictured as having evolved close to each other, arguably overconstrained by the evidence from the fossil record. Time subdivisions are shown only crudely. The evolution as pictured very much rests on the major contributions from such authorities as K. A. Astafieva-Urbaiitis, M. M. Astafieva, D. W. Boyd, J. G. Carter, L. R. Cox, N. D. Newell and T. R. Waller, and many authors who have provided information on various genera. Even so, within the compilation as summarized, there are interpretations which are not fully in accord with the morphological evidence, and these are now outlined. The present proposals are more complex than presented by Waller (1978, 1998), Carter (1990) and Newell & Boyd (1995), yet even so, may prove to have been oversimplistic and too conservative. The following offers a commentary on Text-fig. 109, proceeding from left to right.

Monotidina

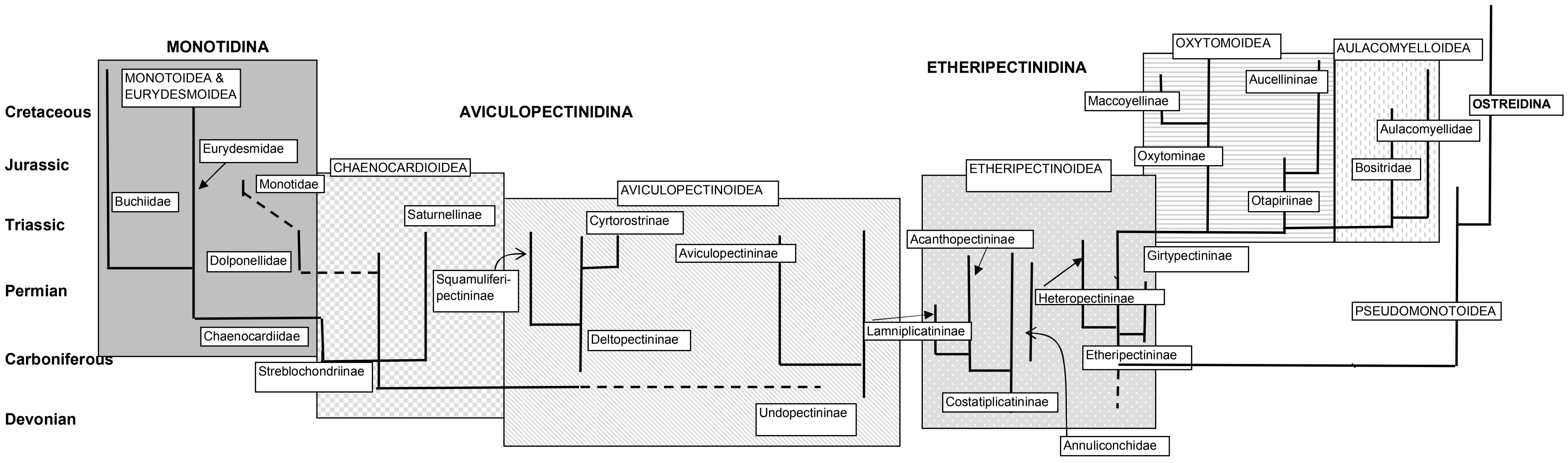
This group arose from biconvex shells with short posterior wings and well developed anterior wing and auricle, apparently during early Permian time, if not slightly sooner: the major change involved shortening of the anterior hinge and loss or reduction of posterior wings and anterior wing and in some cases right anterior auricle. A matter for further enquiry concerns the relationship between *Monotis* and *Eurydesma*. Although both are classed herein in Monotidina, there are differences to suggest co-development almost contemporaneously from different families within Chaenocardioidea. But so few early monotoid forms are known that the evolution is not yet fully clear. One of the intriguing facets brought out in the present study is the similarity of *Eurydesma* in its hinge to Cretaceous genera of Oxytomoidea – in particular, Maccoyellinae: the present classification suggests convergence, but this may be too conservative.

Chaenocardioidea

Regarded as root stock for Monotidina, this group is obscure in its origins, but shares short posterior wings and biconvexity with deltopectens, though these are not known before the Carboniferous, whereas there are a few Devonian genera of Streblochondriidae. Biconvexity and similar ornament (as a rule) on the two valves are shared with Pterinopectinida and with Aviculopectinoidea, but although the latter group would seem more likely to be root stock through sharing the long posterior hinge with pterinopectens, this is not supported so far by the fossil record. Furthermore, aviculopectens are normally plicate, whereas chaenocardioids generally share subdued ornament with most pterinopectens, which leads to the implication of ancestral stock changing in one direction towards a plicate form with retained long posterior wings, and a second group with retained ornament and abbreviated posterior wings.

Aviculopectinoidea

Characterized by biconvexity and strong radial ornament that is similar on the two valves, this



Text-fig. 109. Principal family groups within Monotidina and Aviculopectinidina. Some subfamilies are omitted. The text fig. is further discussed in the text under “Conclusions and Questions”. Time and ranges are very generalized.

group failed to survive the Permian extinction shock. Yet it has until now featured always as the main Paleozoic group of pectiniform bivalves, and its failure to survive the Paleozoic may reflect a conservative morphology, with unchangingly long hinge, and arguably, a concentrated distribution during Permian times in high southerly latitudes which changed drastically in climate after the Permian. (But the same strategy enabled the survival of Monotidina and possibly Etheripectinoidea and Pseudomonotoidea). The most significant of the subgroups appears to involved Undopectininae, entirely ignored by most studies. This subfamily includes genera that appear to link with Natalissimidae of the Pterinopectinidina, and provide strongly suggestive root-stock for Aviculopectininae, and doubtfully Costatiplicatininae and Etheripectininae of the Etheripectinoidea. It may seem too bold a suggestion that pterinopectens like the plicate pterinopecten *Pterinoplica* provided the source for aviculopectens, by losing its spines, for such is far from being confirmed by the fossil record. But the present essay does strongly suggest the need for much more fundamental analysis of individual faunas and systematic studies of species and genera, to reinforce and justify the necessarily sweeping proposals of higher level classification.

Etheripectinoidea

Etheripectinoidea are characterized by having a little inflated right valve ornamented differently from the left valve. They retained the long hinge, uncemented habit, and symmetry and generally hinge of the Aviculopectinoidea and Chaenocardioidea, and their descendents successfully survived the Permian life crisis. Early in their history they gave rise to more attached forms, Pseudomonotoidea, and in the Mesozoic developed also into Oxytomoidea and Aulacomyelloidea. A point source origin would suggest evolution from Undopectinae, sharing the alivincular hinge and fine costae. But a question is raised by the possibility that several stocks of Pterinopectinidina independently lost their duplivincular ligament. Thus *Natalissima* may have given rise to Etheripectinoidea, and *Pseudaviculopecten* to *Undopecten*, of the Aviculopectinidae.

There is also considerable similarity between Aviculopectinidae – especially Aviculopectininae, and the etheripectinoid group segregated as Lamnipectininae. Both have plicate left valves, as well as alivincular hinge and moderately developed posterior wings and byssal notch and right anterior auricle. The right valves differ somewhat, to the extent that those of Lamnipectininae are slightly less convex, and ornamented by finer plicae, as well as stronger concentric laminae, and fall closer in the present assessment to Acanthopectinidae, with flatter right valve and finer finer valve ornament. However family groups are arranged, there are convergences in auriculation, hinge, and especially ornament, and the text endeavours to point out such similarities.

Oxytomoidea

This Mesozoic group saw a reduction in anterior shell, so that *Oxytoma* came to mimic pteriids rather than pectens, and allies even lost the posterior wings and reduced the anterior shell so as to resemble *Buchia*. The two are kept separate because Oxytomoidea retained an alivincular as opppposed to opisthodetic ligament, but clearly converged in life style and shell architecture. The Cretaceous members especially deserve to be more closely analysed, and as well a number of Mesozoic genera are poorly known so that the overall picture is very incomplete.

Aulacomyelloidea

This group followed the trends of other groups to change from an amphidetic to and towards an opisthodetic ligament, and lost the right anterior auricle, thus approaching Halobiidae, and being similarly equivalved with similar ornament on each valve.

Pseudomonotoidea, Ostreida

Arising no later than Early Carboniferous (Visean), the pseudomonotoids adapted a specialized attachment mode and were replaced by Ostreida.

Pectinida

Common ancestry between Etheripectinidina and Pectinida is at first sight supported by the possibility that Euchondriidae preceeded pectens in their evolution. But early Euchondriidae, classed as Crenipectininae, suggest a possibly non-etheripectiniform origin, and that would agree with Starobogatov (1992), who separated pectens from aviculopectens, which included etheripectens.

CONCLUSIONS

THE PAST HISTORY OF LIVING PECTINIDIANS

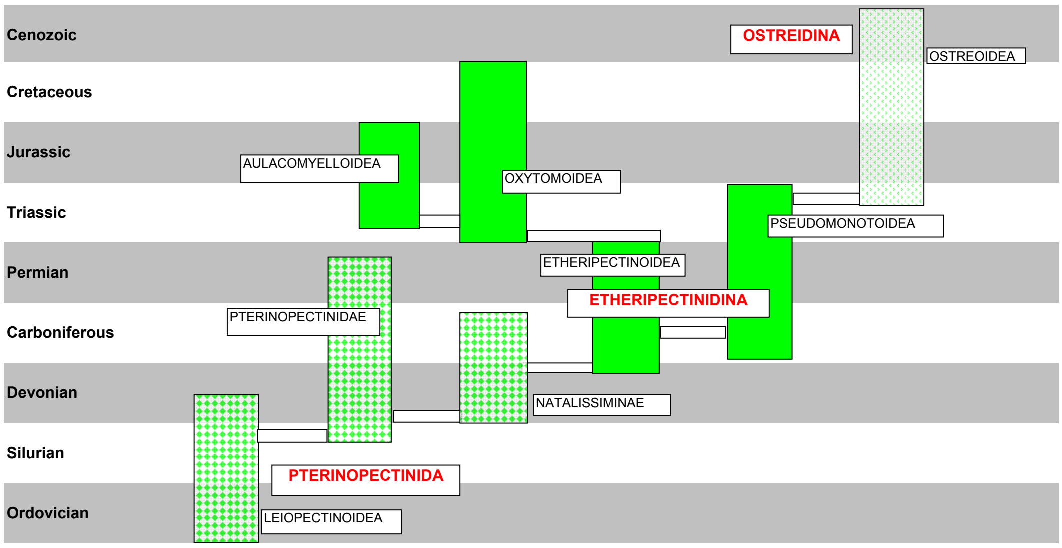
Tracing the fossil record of pteriomorphs within the pectinidian assemblage of genera and family-group members confirms the prime conclusions of Waller (1978) that there were three major groupings – his interpretation has proven to be pleasingly prescient. Limids, oysters and pectens each stand apart. Error arose from the association with other pectiniform groups, which were not assessed in the cladistic study. Thus the aviculopectens and etheripectens do not belong with the pectens, as Waller (1978) had supposed, but with the limids and oysters. Three diagrams summarise what is known of the development through time of each major living group.

Ostreida and their kin (Text-fig. 110)

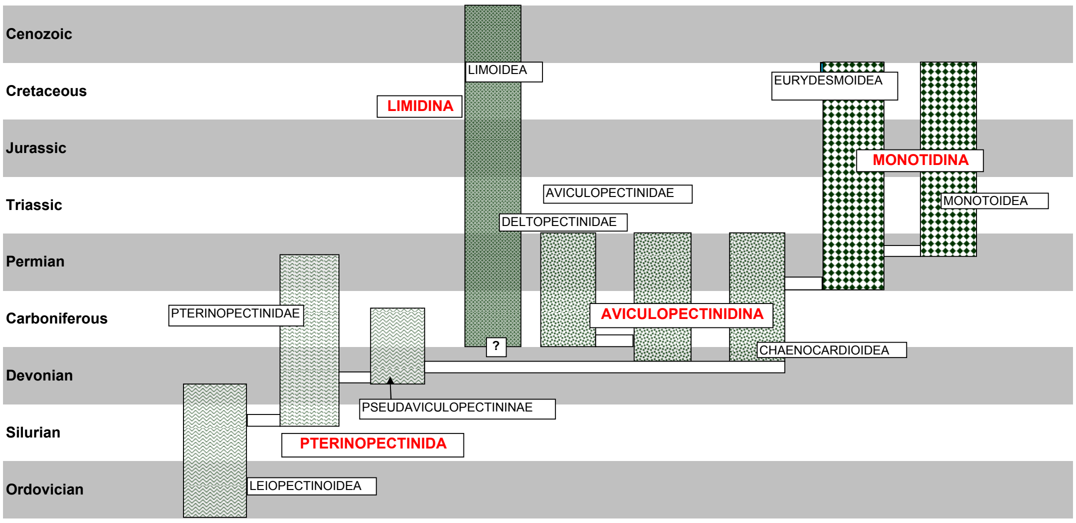
For Ostreida, the fossil record offers a reasonably full assembly of evolutionary steps, from Leiopectinoidea through Pterinopectinidae to Natalissiminae, a Lower Devonian group that developed inequivalve shape, with comparatively short hinge and well defined wings, transitional even in ornament to Etheripectinidae of the Etheripectinidina. *Etheripecten* itself with close allies occupied a central role in the diversification of the overall association, bridging the change from Pterinopectinida to Ostreidina, and spawning several significant superfamilies. Of these, Pseudomonotoidea gave rise to the Ostreidina, with eulamellibranch gills, shell chiefly of foliate calcite, and attached by the left valve, so that foot and byssus were lost. Not all of the superfamilies trended in that direction. Early Etheripectinidae resembled root stock Natalissiminae in shape and ornament, but gave rise to various and often highly ornamented descendents, whilst retaining the basic alivincular hinge that distinguished the superfamily from the duplivincular ligament of *Natalissima* and allies, and retaining also the long hinge and well developed anterior auricle and anterior wing. Descendent Oxytomoidea began to short the anterior shell, until the ligament became barely amphidetic, and the anterior auricle became a tiny sometimes twisted remnant, and members of Aulacomyelloidea largely lost the anterior ligament, and lost the anterior auricle and wing. But these did not survive into the Cenozoic.

Limida and other biconvex pectinidians (Text-fig. 111)

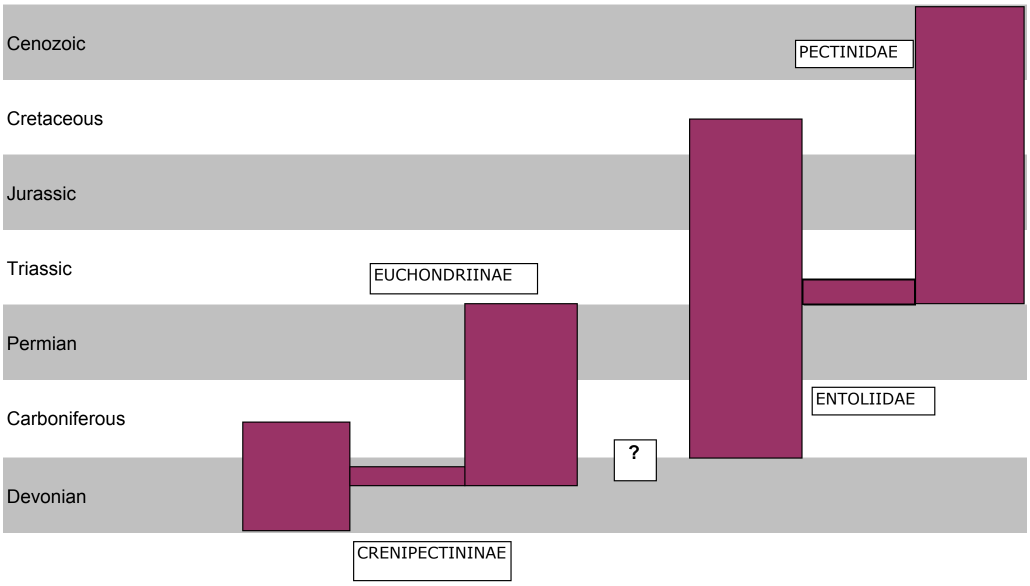
The ultimate beginnings of Limoidea are not under control. Although considered by some to stand well apart from other pectinidians, their basic construct is not so radically different, and Text-fig. 111 offers a summary of members that are largely biconvex, and thus differ substantially in left valve - right valve construct and ornament from Natalissiminae, Etheripectinoidea and descendent groups. The difficulty lies in tracking the evolutionary events of perhaps Late Devonian time. Whilst it may be feasible to propose that Pseudaviculopectininae gave rise to Aviculopectinidae, with *Pseudaviculopecten* and *Intercalatia* providing root stock for Undopectininae, there is no obvious source for Chaenocardioidea. Perhaps the Lower Devonian *Anulipecten*: perhaps a genus yet undiscovered within Pterinopectinidina. Or did the group share ancestry with Aviculopectinidae and even Deltopectinidae? Shared ligament, hinge and biconvexity and similar right valve – left valve ornament suggest the possibility of common ancestry for Aviculopectinoidea, Chaenocardioidea and even Limoidea, as indicated in Text-fig. 21. What is equally uncertain is the extent to which members of Pterinopectinida gave rise independently to somewhat similar, but separate strands now classed in Aviculopectinidina and Limidina. One of the problems with the “bottom – up” analysis of faunas is that stress tends to placed on the horizontal – associating groups because by common morphologies – groups that in fact gave rise to genera and subfamilies that diverged through the record into separated higher categories. The “vertical” dimension through time becomes lost or obscured, and may be brought out by cladistics.



Text-fig. 110. Order Pterinopectinida and constituent suborders and family groups of Order Ostreida.



Text-fig. 111. Major constituent family groups and suborders of Order Limida and Order Pterinopectinida. Whether Limidina and Aviculopectinidina came from a common source or from allied Pterinopectinida remains unclear: similar uncertainty surrounds the origins of Aviculopectinoidea and Chaenocardioidea, and Eurydesmidae and Monotoidea.



Text-fig. 112. Order Pectinida, showing two of the constituent families Entoliidae and Pectinidae, and putative allies Euchondriinae and Crenipectininae.

Pectinida (Text-fig. 112)
As shown in Text-fig. 112, the fossil record is thin, yet enduring, from Devonian to the present day. Even so, the figure has added what can at this stage be only a suggestion, by associating Pectinida with Euchondriidae: on its own, Euchondriidae could as in the past be regarded as a family – even a superfamily according to some authorities – somewhere amongst the cluster of etheripectiniform groups of Late Devonian and Early Carboniferous age. At present, there may be some possibility that the Euchondriidae arose from within Leiopectinoidea – which may lack a resilifer – and develop into Entoliidae and Pectinidae with their distinctive ligament, perhaps directly from Crenipectininae. Alternatively, Entoliidae commenced within that record gap of Devonian time, sibling even of the aviculopectens.

Why is the Devonian record for pectinidians so incomplete? There have been many fine studies over the years, not least by James Hall, and to this day, Devonian times are regarded as and proven to be a time of great flourishing of fossil faunas (Brunton 2006). Whether the bivalve components have to some extent been set aside, or whether pectinidian evolution proceeded in small or marginal populations, perhaps rapidly, that have been poorly preserved, I cannot say. Perhaps it is becoming clear now what we have to look for.

Table 5

Description of fossil localities in the Tiverton Formation, Homevale, Queensland.

UQL	Description.
1626	Tiverton Formation Homevale bed no. 9 above basal *Eurydesma* band. MACKAY 1:250 000 sheet. Coll. F. W. Whitehouse.
3127	Collected throughout middle Tiverton Formation. Coll. J. Armstrong & B. Runnegar.
4512	2m stratigraphic thickness up hillside NE of storage tank and gully, Homevale, *Costatumulus tumida* Zone, just below *Svalbardia* band. Coll. J. B. Waterhouse. Grid reference MACKAY amg 584 281.
4514	*Svalbardia* band 2-3m stratigraphically and 20m upslope to northeast from gulch northeast

	of storage tank. Coll. D. J. C. Briggs & J. B. Waterhouse. Grid ref. as above.
4519	Conspicuous band NE of gully beyond storage tank of Homevale fossil hill. *Taeniothaerus subquadratus* Zone. Coll. J. B. Waterhouse. Grid ref. as above.
4523	Richly fossiliferous band on NE side of road to Mt Britton in upper middle Tiverton Formation. *T. subquadratus* Zone. Coll. J. B. Waterhouse. Grid ref. as above.

Fossil localities with bositrid from Nepal.

1514	Uppermost Sungjar Formation, section 49, minor tributary on north side of Sebu Khola, downstream by 2km from Shey Gompa. Dolpo, west Nepal. Coll. J. B. Waterhouse.
208	Chulu ridge A, northern crest and upper beds of Thorong Member. Coll. J. B. Waterhouse.
218	Thorong Member, Mesokanto, western end of east ridge ridge x of Waterhouse (1999, text-fig. 3). Coll. J. B. Waterhouse.

Fossil localities with *Manticula problematica*, New Zealand.

4554	N28/f7517, boulder on west side of ridge separating branch B and main creek. Coll. J. Grant-Mackie.
7615	R17/f8557 immediately southeast and northeast of junction with Mangonui River and Turipoto Stream. Coll. H. W. Wellman, P. Vella, D. Hamilton.

Fossil localities with *Ellesmerella aranea,* Canada.

GSC 28450	West coast of Ellesmere Island between Hare and Otto Fiords, 15 miles northwest of mouth of Hare Fiord. Coll. E. T. Tozer.
GSC 32363	About 235 feet below the top of the Blind Fiord Formation, south side of Otto Fiord, near mouth, Ellesmere Island. Coll. R. Thorsteinsson.

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Index for genera and species

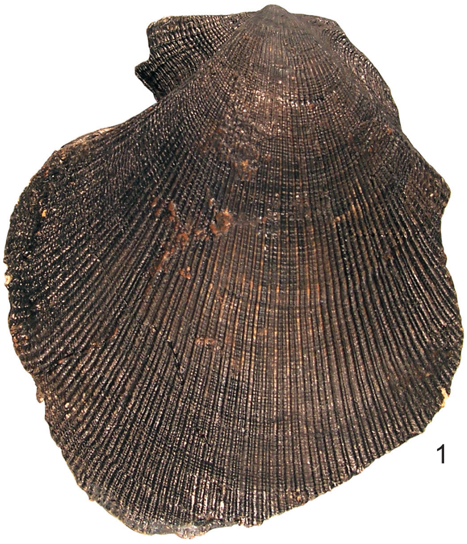
Plate 1

Fig. 1, 2. Left and right aspects of USNM 388890, Pennsylvanian of Texas, x1, identified as *Spyridopecten* by Newell & Boyd (1995). Photographs courtesy of Mark Florence, Smithsonian Institution, Washington D. C. See p. 77.

Fig. 3. *Deltopecten subquinquelineatus comptus* [not Dana] of Hosking (1931). Right valve UWA 8482b, x1. From Artinskian (upper Early Permian) Wooramel Formation, Carnarvon Basin, Western Australia. Photograph courtesy of David Haig, University of Western Australia, Perth. See p. 150.

Fig. 4, 5. *Girtypecten sublaqueatus* (Girty). A, left valve USNM 382768. B, exterior of right valve USNM 388874. Specimens silicified, from Guadalupian of Texas, x1. See Newell & Boyd (1995). Photographs courtesy of Mark Florence, Smithsonian Institution, Washington D. C. See p. 150.

PLATE 1.



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