MORPHOLOGY, RELATIONSHIPS AND PALAEOECOLOGY OF
LOWER DEVONIAN BIVALVES FROM SOUTHEASTERN AUSTRALIA

by

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Thesis submitted for the degree of Doctor of
Philosophy in the Australian National University

This thesis is my own work except where specifically acknowledged.

[Signature]

Paul A Johnston
ABSTRACT

Diverse and well preserved fossil bivalves representing twenty-seven genera (two newly named) and forty species (eighteen newly named) are described from Lower Devonian rocks (chiefly limestones) of New South Wales and Victoria, Australia. Taxonomic affinities of these species are closest with bivalves of the Old World Faunal Realm, although two genera are of Appalachian aspect. A new genus and species of Rhombopteridae of Middle Silurian age is also described.

New morphologic information for the Rhombopteridae indicates that this family arose from the Cyrtodontidae and gave rise at separate times to the Pterineidae, Pseudomonotidae and possibly the Pectinacea. Functional analysis reveals that the Rhombopteridae lived pleurothetically on the left valve, with advanced members converging on productid brachiopods in form and habit and showing posteroventral mantle fusion, as in oysters. Ontogenetic data for the Rhombopteridae and Pterineidae provide new information concerning tooth homologies in primitive pteriomorphs and the evolution of the duplivincular ligament, and support origin of the Pteriomorpha from the Cycloconchidae, as hypothesized by other workers. The Pterineidae were probably primitively inequivalved, epifaunal and pleurothetic on the right valve; reconstructions portraying either a productid-like or endobyssate habit for various pterineids are rejected. By analogy with Recent
pteriids, most Lower Devonian pterineids in the present study are interpreted as having attached to flexible organisms above the substrate. A new function is proposed for the wing-like posterior auricle and the associated auricular sulcus in pteriiform bivalves.

At least two lineages are recognized in the Modiomorphidae, one having growth lines covering a significant area of the hinge plate and a second without: the former lineage appears closely related to the Permorphororidae, the Anthracosiidae and possibly the Unionidae, whereas the Mecynodontidae are derivable from the second lineage and are therefore transferred to the Modiomorphoida.

The "split" hinge plate of trigoniaceans appears to be a morphological consequence imposed by the extreme dorsal insertion points of the pedal elevator muscles and the need for the valves to be able to gape widely. Newly described species of crassatellids show various lucinid features and support previous hypotheses of a phylogenetic relationship between the Crassatellacea and Lucinacea. A furrow is shown to be present on the hinge plate of several anomalodesmatans previously classified in the Grammysiidae; this character had been thought to differentiate the Edmondiidae and Grammysiidae. The two families are therefore combined, with the name Edmondiidae having priority. A close phylogenetic connection between the Orthonotidae and the heterodont superfamily Solenacea is considered unlikely, and the former is tentatively retained in the Anomalodesmata.
Differences in taxonomic composition and proportions of ecological groups represented in bivalves obtained from three stratigraphic intervals in the Murrumbidgee Group near Yass, New South Wales, are correlated with differences in water depth and associated environmental parameters.
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INTRODUCTION

The evolutionary history of the Bivalvia is characterized by two major adaptive radiations. The first of these occurred during Ordovician time and produced endobyssate and epibyssate forms, free-living shallow burrowers, and at least one borer in hard substrate (Pojeta 1971; Pojeta & Palmer 1976). Before the close of that period, all of the major lineages of bivalves had been established (Pojeta 1978). The second radiation began at the onset of the Mesozoic and accounted for the evolution of the major siphonate groups that dominate most infaunal macroinvertebrate communities in modern oceans (Stanley 1968).

Both of these adaptive radiations saw a major increase in the number of bivalve higher taxa, especially superfamilies. In the interval between, however, bivalves continued to evolve, but primarily at family and lower levels, thereby maintaining a substantial and continuous increase in diversity through the Palaeozoic (Newell & Boyd 1978), during times that were, but only by comparison, times of stasis. During the Devonian, for example, the focus of the present study, at least 31 families (representing 19 superfamilies) were present; of these, 11 families (and three superfamilies) are first recorded from that period (data emended from Moore [1969], on basis of Newell & Boyd [1975], Pojeta [1978], Morris [1978], and the present study), a not
insignificant number evolutionarily.

Nonetheless, taxonomic studies of Devonian bivalves have contributed only modestly to broader questions of bivalve phylogeny. Probable reasons seem mostly artifactual, and include: 1) known genera and species of Devonian bivalves require comprehensive taxonomic revision, as emphasized by McAlester (1962b) (studies by McAlester [1962b], and especially by Bailey [1983], have done much to alleviate this problem, but much additional work is needed); 2) characters of the hinge, which often provide the most important clues to genealogical relationships, are unknown or poorly known for most Devonian species, owing to inadequate preservation (remarkably preserved calcitic shells recently described by Bailey [1983] from the Middle Devonian of New York State provide a notable exception); 3) many of the bivalves for which hinge features are preserved have been found only as natural molds in clastic rocks (e.g., the Kahlebergsandstein, Germany) and were studied before the advent of modern casting techniques; consequently, descriptions and illustrations of hinge characters in these species are often based directly on internal molds and are difficult to interpret (e.g., Beushausen 1884); 4) the ontogeny of the hinge has not been described for any Devonian bivalves (and only rarely for Palaeozoic bivalves generally, e.g., Morris & Fortey [1976]); hence, a potentially major source of phylogenetic data has been unavailable to students of Devonian bivalve evolution.
Whenever specimens having well preserved, easily prepared internal shell characters (as with silicified assemblages in limestones) have been available for study, significant contributions to the understanding of bivalve evolution have followed (Pojeta 1971). Notable examples of such preservation are: 1) the silicified Ordovician bivalve assemblages of the Cincinnati Arch on which Pojeta (1971, 1978) based a review of Ordovician bivalves; and, 2) the silicified Permian bivalve assemblages of Texas and Wyoming, which have provided a core of information for the revision of several higher taxa (Boyd & Newell 1968 [Crassatellacea]; Newell & Boyd 1970 and 1975 [oyster-like forms and Trigoniacea, respectively]; and Runnegar & Newell 1974 [Edmondiacea]). But except for occasional research involving only one or two species (e.g., Saul [1976]), silicified assemblages of Devonian bivalves have not received the attention of systematists.

The present study is concerned primarily with the description of large and taxonomically diverse collections of silicified bivalves obtained from limestones of Early Devonian age in southeastern Australia. In addition, some taxa known from specimens preserved as natural molds in clastic rocks are described. The largest collections were made at localities in the Taemas Formation in the Taemas area, southwest of Yass, New South Wales (Text-fig. 1). These localities yielded approximately 1600 identifiable, although mostly incomplete, silicified specimens. A collection of approximately 100 identifiable shells (all silicified) was
Text-figs. 1 & 1A. Locality maps for Taemas and Wee Jasper areas. Text-fig. 1A shows enlargements of areas 1 & 2 in Text-fig. 1 (in vicinity of Taemas Bridge). White boxes at localities R1 and R3 in Text-fig. 1A,2 mark approximate stratigraphic and lateral extent of collecting areas. Fossils were collected at three horizons (a, b, & g) at Locality R1, and two horizons (a & b) at Locality R3. Collections at other localities in Text-fig. 1A were more restricted stratigraphically and laterally; each is indicated by an "X". Only major synclinal axes are shown in Text-fig. 1A. Geology in Text-fig. 1 based on Yass 1: 100 000 Geological Map, Geological Survey of New South Wales, Department of Mines, Geological Series Sheet 9628 (Edition 1) 1975, and Brindabella 1: 100 000 Geological Map, in Owen and Wyborn (1979). Geology in Text-fig. 1A based on geological sketch map of Taemas-Cavan area given in Browne (1969), with emendations based on field observations (note in Text-fig. 1A,2, previously unrecorded occurrence of Warroo Limestone in southern part of Taemas synclinorium).
taken from the same formation at localities near Wee Jasper, New South Wales (Text-fig. 1). A single locality (Locality CB1) in the southern part of the Taemas area (Text-fig. 1) yielded approximately 100 identifiable specimens from a sandy unit within the Cavan Formation. These fossils are preserved as natural molds and were studied by using latex casts, and by a new method of preparation (Zapasnik & Johnston 1984) (see Methods). A taxonomically similar assemblage, from an outlier of the Buchan Caves Limestone in an area known as "the Basin", near Buchan, Victoria (Text-fig. 2A), yielded approximately 200 identifiable shells, all silicified.

In addition to the species represented in the above collections, two other species, one from the Garra Formation near Wellington, New South Wales, and another (the only non-Devonian species described in the present work), from the Walker Volcanics (Middle Silurian) near Canberra, Australian Capital Territory, are described because of their phylogenetic and functional morphologic significance. Approximately 40 silicified specimens of the former species were obtained from Macquarie University, Sydney. These were collected by B. D. Johnson as part of a comprehensive palaeoecological study of the Garra Formation (Johnson 1975; 1981). The Silurian species is known from approximately 150 specimens preserved as natural molds in mudstone. These specimens were studied using the preparation and casting techniques mentioned above for the Cavan collection (see Methods).
Text-fig. 2. A) Geology of Buchan and Basin areas (slightly modified from Mawson 1984, fig. 7); B) enlargement of part of Basin area showing localities (areal extent shown for Taravale Formation is approximate).
In total, 41 species referrable to 28 genera are included in the present study (five of these species, all palaeotaxodonts, are figured but not described). A list of these species and their occurrences is given in Table 1.

Twenty species and three genera are newly named herein. Probably several other new species and possibly two new genera are also represented, but these have not been named, from either a lack of adequate material or the necessity for first-hand comparisons with bivalves elsewhere, described by other workers. In addition to the morphological data provided by these species, ontogenetic, phylogenetic and functional morphologic data have also been included wherever possible in the sections following. A general palaeoecological discussion of bivalve assemblages occurring at the Taemas localities is also presented, but except for a few comments, the palaeoecology of assemblages at other localities has not been considered.

STRATIGRAPHY, AGE AND DEPOSITIONAL ENVIRONMENTS

Uplift in southeastern Australia during the Bowning Orogeny (Late Silurian) produced an elongate, north-south trending structure known as the Condobolin High (Brown, et al. 1968; see Webby [1972] for alternative terminology). During transgression onto the southeastern flank of this structure in the Early Devonian, the Buchan and Taemas-Molong platforms were formed and thick sequences of carbonates deposited (op cit.). Remnants of these carbonates are
Table 1. List of bivalve species included in the present study and their known stratigraphic distribution in southeastern Australia.
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preserved in New South Wales near Wellington (the Garra Formation) and Yass (the Murrumbidgee Group), in Victoria at Buchan (the Buchan Group), and at various places between.

The Murrumbidgee Group is exposed 20-40 km southwest of Yass in the Taemas and Wee Jasper synclinoria (Text-fig. 1) and consists of limestones of the Cavan and Taemas formations and intervening shales and sandstones of the Majurgong Formation (Pedder, et al. 1970). This sequence conformably overlies Lower Devonian volcanics of the Black Range Group, and in the Wee Jasper area, is succeeded (apparently conformably) by the Hatchery Creek Conglomerate, a non-marine unit of probable Middle Devonian age (as determined from fossil fish [G. Young, 1983, pers. comm.]). Rock strata are not preserved above the Murrumbidgee Group in the Taemas area.

The sequence in the Wee Jasper area is preserved in a simple synclinal structure, but in the Taemas area, it is strongly folded and faulted. Browne (1959) subdivided the Taemas Formation in the Taemas area into seven subordinate units on the basis of palaeontological and lithological differences. These units are, in ascending order, the Spirifer yassensis, Currajong, Bloomfield, Receptaculites, Warroo and Crinoidal limestones, followed by a thin unit of tuffs and shales (Text-fig. 3). In the Wee Jasper area, only the three lowermost of these units can be differentiated (see Reynolds 1978, text-fig. 1a).
Text-fig. 3. Generalized stratigraphic column of Murrumbidgee Group showing stratigraphic position of localities and known stratigraphic distribution of bivalves (Taemas area only). Solid vertical lines denote occurrences of taxa based on samples for which detailed stratigraphic information is available. Broken vertical lines denote occurrences of taxa based on samples made by previous workers for which only the broad stratigraphic interval is recorded.
Rich assemblages of marine invertebrates occur at many horizons within the Murrumbidgee Group and have provided a basis for numerous palaeontological investigations, of which the major taxonomic works include: Pickett (1969), sponges; Pedder, et al. (1970), conodonts and corals; Chatterton (1971, 1973), trilobites and brachiopods, respectively; Reynolds (1978), ostracods; and Tassell (1982), gastropods. Bivalves have not previously been described from the Murrumbidgee Group, except for brief descriptions of a few species by Koninck (1876).

The occurrence of the conodont Polygnathus linguiformis dehiscens Philip & Jackson in the Cavan Formation in the Taemas and Wee Jasper areas indicates an early Emsian age for at least that part of the Murrumbidgee Group (Chatterton 1973). Polygnathus linguiformis foveolatus Philip & Jackson first appears in the Receptaculites Limestone and indicates a late Emsian age (Strusz 1972; but see Chatterton 1973: 9-10). Chatterton (1973: 15) concluded that "....the top [of the Murrumbidgee Group] is probably Upper Emsian, but may be as young as Eifelian: if the last is so, the boundary between the Emsian and the Eifelian in the Cavan-Taemas area is probably near the top of the Receptaculites Limestone." For simplicity, and in the absence of clear evidence to the contrary, a late Emsian age is assumed in the present study for all bivalve localities occurring in the Bloomfield, Receptaculites and Warroo limestones. Both palaeontological evidence and palaeogeographic reconstructions indicate a tropical to subtropical environment for southeastern

General discussions of the lithologies and palaeoenvironments represented in the Murrumbidgee Group in the Taemas area were given by Browne (1959), Chatterton (1969; 1973), Kolusz (1972), Campbell (1976), Shields (1976), Reynolds (1978) and Wu (1983). The Cavan Formation consists of supratidal to shallow subtidal sediments (chiefly limestones with some sandy beds) that were deposited in a series of minor transgressions and regressions across a broad, planar area (Wu 1983). Fossils are abundant at many horizons, but are not silicified. The overlying beds of the Majurgong Formation consist mostly of red shales and sandstones (showing ripple marks, mud cracks and current bedding), and are mostly unfossiliferous, except for thin horizons yielding Lingula sp. and gastropods (Browne 1959). The Majurgong Formation is thought to represent predominantly intertidal deposition during a regressive interval (Campbell 1976; Wu 1983). A transgressive interval initiated deposition of the overlying limestones of the Taemas Formation. The lithology and palaeontology of the lower units, including the Spinella yassensis, Currajong and Bloomfield limestones, have not been studied in detail (see Browne 1959, for brief discussion), and consequently the depositional history and palaeoenvironments represented are not well understood. However, available evidence indicates that these units were deposited at depths within the photic zone, in low to moderate energy regimes, on a shallow marine shelf
(Chatterton 1969, 1973; Campbell 1976). By contrast, the Crinoidal Limestone was probably deposited under high energy conditions in shallow water, as indicated by the occurrence (especially at the base of that unit) of massive, well sorted calcarenites consisting almost entirely of pelmatozoan ossicles (Browne 1959; Chatterton 1969, 1973).

Silicification is well developed at many localities in the upper Bloomfield, Receptaculites, and Warroo limestones, and preservation of fossils excellent. In other units of the Taemas Formation, silicification is poor or absent and fossils poorly preserved. As a consequence, the units in which silicification has occurred are the best studied palaeontologically (except for the Bloomfield).

Important discussions of the palaeoecology of the Receptaculites and Warroo limestones were given by Chatterton (1969; 1971; 1973) and, more recently, by Shields (1976) and Reynolds (1978). Both units consist primarily of fossiliferous micrite with generally little or no terrigenous content (Chatterton 1969, 1973; Shields 1976; Reynolds 1978). Reynolds (1978) concluded from the ostracod fauna that the Receptaculites Limestone represents an off-shore, shelf environment. She further suggested that the top of that unit was deposited in deeper water (possibly sub-photic) than was the base, and cited as evidence the abundance of siliceous sponges and erect fennestellid bryozoans, and the lack of calcareous sponges and seaweeds in the upper beds (for inferences about the latter, see Bivalve Associations in the
Taemas Area. As later discussed, the present study supports these conclusions, except that the upper *Receptaculites* and Warroo limestones, although representing a relatively deep environment, seem nonetheless to have been deposited within the photic zone, as indicated by the occurrence of receptaculitid algae at these horizons (Chatterton 1973).

The Buchan Group in Victoria is similar to the Murrumbidgee Group both faunally and in its depositional history, and it is likely that a marine connection linked the two areas (Brown, *et al.* 1968). The Buchan Group consists of three formations, the Buchan Caves Limestone and the overlying Taravale, the middle part of which grades laterally into the third formation, the Murrindal Limestone. The sequence is bounded below by the Snowy River Volcanics. Important discussions of the geology and palaeontology of these units are given in Talent (1956) and Teichert and Talent (1958). The Buchan Group is probably Emsian in age, although the Taravale Formation may extend into the Eifelian (Strusz 1972). R. Mawson (1984, pers. comm.) has informed me that conodonts which she collected from the same beds in the Buchan Caves Limestone in the Basin area (p. 15-16) as those which yielded bivalves described herein are characteristic of the *P. l. dehiscens* Zone and indicate an early Emsian age. Talent (1956) described a small collection of bivalves from the Buchan Caves Limestone which he referred to 11 species and nine genera. These fossils are very poorly preserved and none show the dentition. Talent collected only one specimen from the Basin area and referred it to *Actinopterella* sp.
indet. (this specimen is here referred to a new species of Actinopteria Hall; see under Systematics).

As noted earlier, the present study includes the description of a new genus and species of bivalve from the Garra Formation near Wellington, New South Wales. According to Johnson (1981, and 1984, pers. comm.), this bivalve occurs in a 20 m interval within "Unit 11" of the Garra Formation at "Section B" (see Johnson 1975, and Chatterton, et al. 1979 for explanation). Other bivalve species occur at this site and elsewhere in the Garra Formation; specimens of these were figured, but not described, by Johnson (1981). Bivalves in Unit 11 are probably of early Pragian (=Siegenian) age, as indicated by associated conodonts (G. C. O. Bischoff in fide Johnson 1975), and, hence, are older than the bivalves occurring in the Murrumbidgee and Buchan groups.

The single Silurian species (Coppinsia spodophila n. gen. & sp.) described herein occurs in volcaniclastic mudstones less than ten metres below the top of the Walker Volcanics at Locality F1, near Fairlight Station (Text-fig. 1). The Walker Volcanics are of late Wenlockian age and consist principally of dacitic ignimbrites and bedded tuffs, with some volcaniclastic sediments and limestones (Owen & Wyborne 1979). The sequence represents non-marine deposition with shallow marine incursions (ibid.). The fauna at Locality F1 is dominated by C. spodophila n. gen. & sp., ostracods, rostroconchs, gastropods and parablastooids (isolated plates only). A few specimens of other bivalves, including
nuculoids, a pterineid and a species of *Goniophora* Phillips were collected, but are too poorly preserved to warrant description.

**LOCALITIES**

Most of the specimens described in the present study were collected by the author. Additionally, a significant number were obtained from collections made in the Taemas-Wee Jasper areas by Dr. B. D. E. Chatterton, and by L. Reynolds (nee Shields) (Chatterton 1969, 1971, 1973; Shields 1976; Reynolds 1978). Many other important specimens were obtained from undescribed collections made in the Taemas-Wee Jasper areas by field parties from Macquarie University, Sydney, under the supervision of Dr. John Talent and Dr. Ruth Mawson. As noted earlier, the specimens described from the Garra Formation, near Wellington, were collected by Dr. B. D. Johnson for his dissertation research (see Johnson 1981).

In all, twenty localities yielded bivalves for the present study. The names of these localities and their descriptions are summarized in Table 2. The largest collections were obtained from localities in the Taemas Formation in the Taemas area. The stratigraphic position of these localities, and of Locality CB1 in the Cavan Formation below, is shown in Text-fig. 3. At Locality R1, collections were made from three horizons, one at the top of the Bloomfield Limestone, one at the base of the *Receptaculites* Limestone and another somewhat higher in that unit (these are
Table 2. Summary of bivalve localities.
<table>
<thead>
<tr>
<th>ANU Localities:</th>
<th>Area</th>
<th>Stratigraphic Unit</th>
<th>Universal Grid Reference</th>
<th>Map Sheet</th>
</tr>
</thead>
<tbody>
<tr>
<td>R1</td>
<td>Taemas</td>
<td>Taemas Formation</td>
<td>FB 680 242</td>
<td>Brindabella 1:100 000 Sheet</td>
</tr>
<tr>
<td>R2</td>
<td>Taemas</td>
<td>Taemas Formation</td>
<td>FB 671 267</td>
<td>Yass 1:100 000 Sheet</td>
</tr>
<tr>
<td>R3</td>
<td>Taemas</td>
<td>Taemas Formation</td>
<td>FB 688 235</td>
<td>Brindabella 1:100 000 Sheet</td>
</tr>
<tr>
<td>R4</td>
<td>Taemas</td>
<td>Taemas Formation</td>
<td>FB 686 236</td>
<td>Brindabella 1:100 000 Sheet</td>
</tr>
<tr>
<td>R5</td>
<td>Taemas</td>
<td>Taemas Formation</td>
<td>FB 667 292</td>
<td>Yass 1:100 000 Sheet</td>
</tr>
<tr>
<td>R6 ( Loc. A, Chatterton 1973, &amp; Loc. 3, Reynolds 1978)</td>
<td>Taemas</td>
<td>Taemas Formation</td>
<td>FB 655 307</td>
<td>Yass 1:100 000 Sheet</td>
</tr>
<tr>
<td>R7 ( Loc. B, Chatterton 1973)</td>
<td>Taemas</td>
<td>Taemas Formation</td>
<td>FB 673 265</td>
<td>Yass 1:100 000 Sheet</td>
</tr>
<tr>
<td>R8 ( Loc. C, Chatterton 1973)</td>
<td>Taemas</td>
<td>Taemas Formation</td>
<td>FB 674 264</td>
<td>Yass 1:100 000 Sheet</td>
</tr>
<tr>
<td>CB1</td>
<td>Taemas</td>
<td>Cavan Formation</td>
<td>FB 656 215</td>
<td>Brindabella 1:100 000 Sheet</td>
</tr>
<tr>
<td>WJx</td>
<td>Wee Jasper</td>
<td>Taemas Formation</td>
<td>FB 509 211</td>
<td>Brindabella 1:100 000 Sheet</td>
</tr>
<tr>
<td>WJy</td>
<td>Wee Jasper</td>
<td>Taemas Formation</td>
<td>FB 507 209</td>
<td>Brindabella 1:100 000 Sheet</td>
</tr>
<tr>
<td>Loc. 1</td>
<td>Wee Jasper</td>
<td>Taemas Formation</td>
<td>FB 507 209</td>
<td>Brindabella 1:100 000 Sheet</td>
</tr>
<tr>
<td>(Reynolds 1978)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>B2</td>
<td>The Basin</td>
<td>Buchan Caves Limestone</td>
<td>FB 754 023</td>
<td>Brindabella 1:100 000 Sheet</td>
</tr>
<tr>
<td>B3</td>
<td>The Basin</td>
<td>Buchan Caves Limestone</td>
<td>/</td>
<td>Bairnsdale 1:250 000 Sheet</td>
</tr>
<tr>
<td>B5</td>
<td>The Basin</td>
<td>Buchan Caves Limestone</td>
<td>/</td>
<td>Bairnsdale 1:250 000 Sheet</td>
</tr>
<tr>
<td>F1</td>
<td>Fairlight</td>
<td>Walker Volcanics</td>
<td>FB 654 321</td>
<td>Yass 1:100 000 Sheet</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>FB 507 211</td>
<td>Brindabella 1:100 000 Sheet</td>
</tr>
<tr>
<td>MQU Localities:</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>FB</td>
<td>Taemas</td>
<td>Taemas Formation</td>
<td>FB 654 321</td>
<td>Yass 1:100 000 Sheet</td>
</tr>
<tr>
<td>Barbers 17 &amp; 20</td>
<td>Wee Jasper</td>
<td>Taemas Formation</td>
<td>FB 507 211</td>
<td>Brindabella 1:100 000 Sheet</td>
</tr>
<tr>
<td>Slocombe's</td>
<td>The Basin</td>
<td>Buchan Caves Limestone</td>
<td>/</td>
<td>Bairnsdale 1:250 000 Sheet</td>
</tr>
<tr>
<td>Mountain View</td>
<td>Wellington</td>
<td>Garra Formation</td>
<td>/</td>
<td>(see Johnson 1975, fig. 1)</td>
</tr>
</tbody>
</table>
designated "a", "b" and "g" in Text-figs. 1A, 2 & 3).

Collections at Locality R3 were made at two horizons (designated "a" and "b", Text-figs. 1A, 2 & 3). As explained in Table 2, localities R6, R7 and R8 are the same as Chatterton's (1973) $\alpha$, $\beta$ and $\Gamma$, respectively. Reynolds made collections at Locality R6 (which she called "Loc. R3"), but these were taken from an imprecisely defined interval in the upper part of the Receptaculites Limestone (ibid., text-fig. 1b).

Collections yielding bivalves have also been made by palaeontologists at Macquarie University from various sites at or very close (less than 100 m) to Locality R6 (R. Mawson 1982, pers. comm.). The most important of these occur within a stratigraphic interval which is approximately that shown in Text-fig. 3 (designated "MqU Warroo sites"). Whenever locality information is given in the Systematics section and plate descriptions below, these sites are not differentiated from Locality R6. In addition, several Macquarie University sites (precise stratigraphic information unavailable) in the lower third of the Receptaculites Limestone at Locality R6 yielded a few bivalve remains. These sites are not shown in Text-fig. 3, and are designated in the plate descriptions as follows: "Locality R6, Receptaculites Limestone (lower third)." All other references to Locality R6 in the present work refer to the interval (or some part of it, where stated) shown in Text-fig. 3.
Locality R5 (Text-figs. 1A, 1 & 3) occurs in an intensely folded part of the *Receptaculites* Limestone, and consequently, its exact stratigraphic position could not be determined in the field. The fauna, however, is clearly like that from the lower third of the *Receptaculites* Limestone elsewhere (especially at Locality R2). Localities CB1, F1 and Mountain View have already been discussed in previous sections (see Introduction; Stratigraphy, Age and Depositional Environments).

The geographic locations of localities R1-R5, CB1, Pb and F1 are shown in Text-figs. 1 & 1A. Chatterton (1973, fig. 1) provides maps showing localities R6, R7 and R8 (= A, B and P, respectively).

The known stratigraphic occurrence of bivalves within the Murrumbidgee Group in the Taemas area is given in Text-fig. 3. Heavy black lines represent occurrences based on samples for which detailed stratigraphic information is available. Dotted lines show occurrences based on samples collected by previous workers for which only the broad stratigraphic interval was recorded (e.g., "Basal 200' of *Receptaculites* Limestone at Locality B").

Bivalves were recovered from four localities in the Wee Jasper area, all in close proximity (although I personally made collections from only two of these, WJx and WJy [see Text-fig. 1]). Locality WJx occurs within a two-metre interval in the Bloomfield Limestone, 30 m above the top of the Currajong Limestone. It yielded a meagre sample of six
bivalve specimens, referrable to *Atremapella misticia* n. gen. & sp., *Paracyclus proavia* (Goldfuss) and *Lucinacea* n. gen.? & sp. (in addition, a few specimens of *Goniophora duplisulca* n. sp. were observed at WJx but not collected). The specimens from WJx are nonetheless significant in that they represent the lowest known occurrences of these species in the Murrumbidgee Group. Locality WJy occurs within undifferentiated limestones 39 m above the top of the Bloomfield Limestone. This horizon falls within a stratigraphic equivalent of the lower part of the *Receptaculites* Limestone in the Taemas area (see Reynolds 1978, text-fig. 1b).

Locality 1 of Reynolds (1978) yielded bivalves, but Reynolds did not specify the exact stratigraphic position of this locality within the sequence of undifferentiated limestones in which it occurs; it evidently is below the level of WJy, however. The "Barbers" locality, worked by the Macquarie palaeontologists, occurs at the top of "section 3" of Pedder, et al. (1970, text-fig. 1) (R. Mawson 1982, pers. comm.), and is at about the same level as Reynolds' Locality 1. Collections yielding bivalves were made at two horizons, "Barbers 20" and (six metres below) "Barbers 17" (R. Mawson 1982, pers. comm.).

Dr. J. A. Talent first drew my attention to the occurrence of silicified bivalves in the Buchan Caves Limestone in the Basin area, Victoria. He kindly allowed me to describe a small collection that he had made from a single
locality known as "Slocombe's", and suggested that I make additional collections from there. Precise locality information was not available for the Slocombe's locality, and I was unable to relocate it. However, I made collections at new localities (B2, B3, B5; Text-fig. 2B) apparently slightly south of "Slocombe's" and at about the same stratigraphic level. Locality B2 occurs 2-3 m below Locality B5, but yielded essentially the same suite of bivalves and other organisms. Locality B3 occurs at an estimated 3-5 m below the level of B2. Collections from this locality yielded hundreds of specimens of the brachiopod Buchanathyris sp., but no bivalves, except for a single specimen of Mytilarca Hall & Whitfield, the first record of this genus from the Buchan Group (see under Systematics). Argillaceous, thinly bedded limestones were observed capping the section in the Basin area. R. Mawson has informed me (1984, pers. comm.) that these are, in fact, an outlier of the Taravale Formation (Text-fig. 2A & B). The precise level of the Basin localities above the Snowy River Volcanics has not been measured, but these localities clearly occur within the upper quarter of the Buchan Caves Limestone.

BIVALVE ASSOCIATIONS IN THE TAEMAS AREA

In the Taemas area, bivalves were collected from three broad stratigraphic intervals within the Murrumbidgee Group (Text-fig. 3). The lowest interval is near the middle of the Cavan Formation, the second includes the uppermost beds of
the Bloomfield Limestone and the lower part of the Receptaculites Limestone, and the third, the uppermost part of the Receptaculites Limestone and lower half of the Warroo Limestone. The inferred life habits of the bivalves from these intervals are shown in Text-fig. 4.

The bivalves from the Taemas area comprise taxonomically distinct associations at each interval, although some species occur in more than one interval. Additionally, each interval is characterized by bivalves of particular feeding groups (in the sense of Stanley 1968). This information is summarized in Text-fig. 5. Furthermore, from available collections, and from observations in the field at unsampled localities, it also is evident that the Taemas bivalves vary significantly taxonomically, ecologically and in relative abundance at different stratigraphic horizons within each of the three intervals. Detailed description and analysis of these more minor variations, requiring dense stratigraphic sampling and extensive statistical treatment, are outside the scope of the present study. Consequently, only the most evident patterns within the intervals are noted in the following discussion.

Bivalves at Locality CB1 (Text-fig. 5, I), the lowest in the sequence, occur in a sandy unit of the Cavan Formation, one of seven subdivisions described by Wu (1983). Although this unit is conventionally characterized as a limestone (ibid.), samples from it that yielded bivalves contained only a minor carbonate component and are better described as fine-grained sandstones and siltstones. According to Wu
20. *Goniophora duplisulca* n. sp.
21. *Cypricardinia sinuosa* n. sp.
22. *Cypricardinia minima* n. sp.
23. *Eoschizodus taemasensis* n. sp.
24. *Schizodus oweni* n. sp.
25. *Schizodus truemani* n. sp.
26. *Paracyclas proavia* (Goldfuss)
27. *Paracyclas cf. P. rugosa* (Goldfuss)
28. *Paracyclas* n. sp.
29. *Crassatellopsis yonqei* n. sp.
30. *Crassatellopsis lenticularis* n. sp.
31. *Sanquinolites concentrirugosa* (Talent)
32. *Sanquinolites phlyctaenatus* n. sp.
33. *Cimitaria?* sp.
(1971, figs. 7-9) has inferred for the morphologically similar palaeotaxodont *Ctenodonta* Salter. However, it may be that *Solemyacea* n. gen. & sp. lived in a Y-shaped burrow as do living solemyaceans (Stanley 1970), although the Devonian species lacks the cylindrical shell shape characteristic of modern forms.

**KEY:**

2. *Nuculites* sp.
3. *Deceptrix? clarkei* (Koninck)
4. *Nuculoidea* sp.
5. *Solemyacea* n. gen. & sp.
7. *Atremapella misticia* n. gen. & sp.
8. *Ptychopterisa* catellus n. sp.
9. *Ptychopterisa* sp. A
10. *Ptychopterisa* sp. B
11. *Limoptera murrumbidgeensis* n. sp. (a - juvenile; b - adult)
12. *Tolmaia erugisulca* n. sp.
   
   A. *murrindalensis* n. sp.
14. *Glyptodesma buchanensis* (Talent) (a - juvenile; b - adult)
15. *Pseudaviculoplecten etheridgei* (Koninck)
17. *Nargunella comptorae* n. sp.
18. *Guerangeria* sp.
19. *Goniophora pravinasuta* n. sp.
Text-fig. 4. Life habit reconstruction for bivalves occurring in the three collecting intervals of the Murrumbidgee Group in the Taemas area (see Text-fig. 3). (Locality R3 [horizon b] has been excluded from interval II, see p. 22-23.)

Shell outlines are drawn to scale for bivalves (except for Cypricardinia minima n. sp., which is shown at twice its relative size) within each interval. For any one species, the relative shell size indicated does not necessarily represent the maximum relative shell size attained for that species.

All species are shown in lateral view except: Cypricardinia sinuosa n. sp. (anterior view), Atremapella misticia n. gen. & sp. (anterior and posterior views), Pseudaviculopecten etheridgei (Koninck) (anterior view), Limoptera murrumbidgeensis n. sp. (dorsal view - one specimen), and Glyptodesma buchanensis (Talent) (dorsal view - one specimen).

More than one specimen is shown for certain species in some intervals, but this is not intended to indicate relative abundance.

Broken lines show either anterior mucus tubes (Paracyclas) or incompletely known shell outlines.

Reconstructions of palaeotaxodonts (not discussed in text) are based on comparisons with similar species discussed by Pojeta 1971, Stanley 1970 and Bailey 1983. Solemyacea n. gen. & sp. is reconstructed in a habit like that which Pojeta
II. Upper Bloomfield/Lower Receptaculites Interval
III. Upper *Receptaculites*/Lower Warroo Interval –
Text-fig. 5. Percentages of bivalve specimens (including both articulated shells and isolated valves that are more than two-thirds complete or that preserve at least part of hinge) representing various ecological groups in collections made from intervals I, II and III in Taemas area. Numbers below taxa indicate numbers of specimens. Specimens from Locality R3 (horizon b) have been excluded from calculations for Interval II (see p. 22-23).
I. CBI Interval

- Schizodus oweni n.sp. 22
- Polidevicia cf. Polidevicia insolita (Talent) 17
- Nuculoidea sp. 39
- Sanguinolites concentrirugosa (Talent) 8
- Guerangeria sp. 3
- Goniophora pravinasuta? n. sp. 1
- Mytilarca sp.? 1
- Glyptodesma buchanensis (Talent)* 4

Total Specimens: 95

II. Upper Bloomfield/Lower Receptaculites Interval

- Pseudaviculopxen etheridgei (Koninck) 11
- Palaeotaxodonta 29
- Lucinacea 16
- Atremapella misticia n.gen. & sp. 138
- Anomalodesmata 22
- Other Modiomorphoida 66
- Other Pterineidae 186
- Trigoniacea 77
- Limoptera murrumbidgeensis n.sp.* 222
- Goniophora dupliculosa n.sp. 190

Total Specimens: 1003
III. Upper *Receptaculites*/Lower Warroo Interval

Total Specimens: 250

Key:

- Deposit feeders
- Epibyssate
- Endobyssate
- Suspension feeders
- Shallow infaunal reclining
- Free burrowing

* Large individuals probably non-byssate
(1983), this unit was deposited in low to moderate energy conditions in a shallow subtidal to intertidal environment. Small-scale, low-angle cross-bedding, which occurs throughout the unit, may have resulted from tidal flow (ibid.). Reworking and transport of fossils appears to have been minimal, as indicated by: 1) the quality of preservation of the fossils (see Zapasnik & Johnston 1984, fig. 2C); 2) the occasional occurrence of articulated specimens (all of which are nuculoids and Schizodus oweni n. sp.); and, 3) the occurrence of dendritic horizontal burrows at several horizons.

Bivalves and brachiopods (especially Buchanathyris sp.) are the most common megafossils at Locality CB1. Also present are gastropod shells, spirorbid tubes, pelmatozoan ossicles, occasional tabulate corals (small colonies only), small fish vertebrae and conical shells of uncertain affinities (ibid.).

At CB1, Polidevcia cf. P. insolita (Talent), and especially Nuculoidea sp., are the most abundant bivalves and account for nearly 60% of the bivalve specimens collected. Schizodus oweni n. sp. is also common (about 20% of specimens collected), while Glyptodesma buchanensis (Talent) and Sanguinolites concentrirugosa (Talent) are infrequent; Guerangeria sp., Goniophora sp. and Mytilarca sp. are rare.

Nuculoidea sp. and Polidevcia cf. P. insolita are especially similar in size and shape to the Recent nuculoids Nucula proxima (Say) and Yoldia perprotracta Dall, and were probably similar in life habits (Text-fig. 4). According to
Stanley (1970), both *N. proxima* and *Y. perprotracta* are locally abundant in muddy, sheltered, shallow, subtidal conditions, environments similar to those that Wu (1983) inferred for deposition of the beds which contain *N. sp.* and *P. cf. P. insolita* at CB1.

The aberrant pterineid *Glyptodesma buchanensis* is particularly useful in characterizing the environment represented at Locality CB1. This species appears to have been an epifaunal suspension feeder that lived with the commissure aligned vertically, the anterior auricle submerged in the substrate, and the broad anterior surface of the shell body appressed against the substrate surface; a byssus was present in young individuals and apparently lost in the adult (see p. 254-255). The loss of a byssus in adult *G. buchanensis* makes it unlikely that the shell could have maintained stability in a high energy environment; it is an adaptation, however, that is consistent with the beds at CB1 having been the products of deposition under low to moderate energy conditions.

A significantly different association of bivalves occurs in the upper Bloomfield and lower *Receptaculites* limestones, the second stratigraphic interval at which collections were made (Text-fig. 3). Deposit-feeding palaeotaxodonts are taxonomically more diverse than in the sandy unit of the Cavan Formation, but numerically, they are much rarer, making up only about 3% of the bivalves collected. Epibyssate suspension feeders are the most abundant bivalves and, among
these, pterineids predominate, comprising about 40% of bivalves collected.

Lateral and vertical variations in the relative proportions of bivalve taxa and ecological groups are more evident in the upper Bloomfield and lower *Receptaculites* beds than at the intervals above and below. In the Bloomfield beds, bivalves generally occur in localized lens-like concentrations that are up to two or three metres thick and up to 100 metres or so in lateral extent. These lenses also contain brachiopods (mostly *Protochonetes culleni* [Dun]) and occasional gastropods, along with small tabulate corals, pelmatozoan ossicles, isolated columnals of *Receptaculites* and generally rare, fragmentary remains of fenestellid bryozoans. Pterineids are the most abundant animals preserved in the upper Bloomfield, but different pterineids predominate at different localities. For example, *Limoptera murrumbidgeensis* n. sp. predominates at Locality R1 (horizon a), whereas *Ptychopteria catellus* n. sp. predominates at Locality R4 and *Tolmaia erugisulca* n. sp. at Locality R7. Other bivalves show similar differences in frequency of occurrence between localities: *Goniophora duplisulca* n. sp., for example, is common at localities R1 (horizon a) and R7, but is absent at R4.

Articulated bivalve shells are rare in the upper Bloomfield, and most isolated valves are incomplete, indicating some degree of transport and reworking after death. Nonetheless, each of the species found within the
upper Bloomfield is represented by at least some well preserved shells, implying that individuals belonging to these species actually lived in the particular area of deposition.

In the Taemas area, the lower *Receptaculites* Limestone is more thickly bedded than the Bloomfield Limestone. Bivalves are generally less numerous in these beds than in the upper Bloomfield, but are nonetheless relatively abundant at some localities. *Atremapella misticia* n. sp. and *Goniophora dupliculca* n. sp. are the most abundant species (at Locality R1 [horizon b], for example, they comprise 23% and 56%, respectively, of the bivalves collected), and while pterineids are common generally, they are less so than in the upper Bloomfield (comprising only 14% of bivalves collected at Locality R1 [horizon b], for example, compared to 64% at Locality R1 [horizon a]). Several species show large differences in frequency of occurrence between localities within the lower *Receptaculites* Limestone (for example, *Eoschizodus taemasensis* n. sp. is a common element at some localities [especially R7], but is rare at others [R1, horizon b]), while various other species (e.g., *Pseudaviculoplecten etheridgei* [Koninck], lucinaceans and anomalodesmatans) at this level are nowhere abundant. In the Taemas area, 11 species first appear in the lower *Receptaculites* Limestone (Text-fig. 3), although at least two of these are known to occur earlier elsewhere: *Atremapella misticia* n. gen. & sp. has been found well down in the Bloomfield Limestone at Locality WJx at Wee Jasper, whereas
it is apparently absent from the Bloomfield beds at Taemas; and Solemyacea n. gen. & sp. occurs in the Buchan Caves Limestone (Table 1).

Brachiopods (especially Atrypa penelopeae Chatterton, Anatrypa erectirostris [Mitchell and Dun] and Howittia howitti [Chapman]) are the most abundant fossils occurring with the bivalves in the lower Receptaculites Limestone in the Taemas area, although gastropods are common here, as well. Massive favositid corals, solitary rugose corals, auloporid corals, spirorbid worm tubes, hyoliths, rostroconchs, pelmatozoan ossicles, fenestellid bryozoans (generally less fragmentary than in the upper Bloomfield Limestone), and receptaculitids (occasionally articulated) occur in fewer numbers.

Within the lower Receptaculites Limestone, bivalves tend to diminish in number of individuals up-section. At Locality 3 (horizon b), the stratigraphically highest locality within this interval, bivalves are few but well preserved (valves are often articulated). Faunally, the bivalves at this locality are transitional between those in the lower Receptaculites Limestone and in the upper Receptaculites/lower Warroo beds (and hence, are excluded from Text-fig. 511). Most of the species found at stratigraphically lower horizons in the Receptaculites Limestone occur here, but the most abundant bivalves at Locality 3 (horizon b) are Cypricardinia sinuosa n. sp. and Crassatellopsis lenticularis n. sp. These species are also
among the most common bivalves in the upper Receptaculites and lower Warroo limestones, while they are rare (C. sinuosa n. sp.) or absent (C. lenticularis n. sp.) at horizons below Locality 3 (horizon b).

The lower Receptaculites Limestone was probably deposited in lower energy conditions than the upper Bloomfield Limestone, as evidenced by the greater frequency of articulated bivalves and by the occasional occurrence of well preserved fennestellid bryozoans and articulated receptaculitids.

All of the samples processed from the upper Bloomfield/lower Receptaculites interval yielded a substantial residue of particulate carbon. Reynolds (1978) also observed carbon in her samples from the lower Receptaculites Limestone. She argued convincingly (ibid.: 149) that the carbon most likely originated from the decomposition of extensive banks of seaweed or other algae. Seaweed seems the more likely of these alternatives, as algal laminations (which would suggest mat-like accumulations of microscopic algae) do not occur in the upper Bloomfield/lower Receptaculites interval, and receptaculitids (dasycladacean-like algae) are too uncommon to be the source of such a large volume of carbon. Reynolds concluded (p. 149) that the lower Receptaculites Limestone was deposited near the limit of the photic zone (she suggests 90-130 m), but the environment was probably much shallower. Living species of attached algae inhabit inner subtidal (i.e., less than 50 m:
Hedgpeth, in Hedgpeth 1957, fig. 1) and intertidal environments (Holmes, in Hedgpeth 1957: 120). The outer limit of modern kelp beds is commonly 25-30 m in clear water (North, in North 1971: 14), and isolated kelp plants are rarely observed at depths greater than 40 m (ibid.: 14). The nature of seaweed-like algae inferred to have been present during deposition of the upper Bloomfield and lower Receptaculites limestones is unknown, but these algae were probably similar to modern attached algae in their requirements for light. Evidently, the upper Bloomfield and lower Receptaculites limestones were deposited in a subtidal environment at depths less than 50 m and probably less than 30 m.

Carbon was absent in samples processed from Locality CB1 (see Methods) and the upper Receptaculites/lower Warroo interval, indicating that seaweed was rare or absent at these horizons (see similar observations and conclusions in Reynolds [1978]). It is of interest that pterineid bivalves are taxonomically and numerically most abundant in the carbon-bearing interval. In modern oceans, morphologically similar bivalves of the family Pteriidae frequently attach to flexible objects, such as seaweed and, especially, alcyonarians (Allan 1959; Stanley 1972) (the term "epiphytic" is here suggested for the habit of attaching to flexible plants and "plant-like" animals). By analogy, many fossil pterineids probably lived in a similar way (see under general discussion of Pterineidae): pterineids in the upper Bloomfield and lower Receptaculites limestones probably
attached primarily to seaweeds, these apparently being the only large, flexible organisms available, except for pelmatozoans, which are generally uncommon in this interval (alcyonarians are unknown in pre-Jurassic rocks [Stanley 1972]).

In the lower Receptaculites Limestone, bivalves are widespread in the southern part of the Taemas synclinorium, but tend to be rare or absent in the northern part (also observed by Chatterton 1969). On the Y-shaped peninsula across the Murrumbidgee River from the hamlet of Good Hope (Text-fig. 1), I observed extensive biostromal deposits of corals and stromatoporoids at the base of the Receptaculites Limestone. Bivalves were rare. Comparable developments of coral and stromatoporoids do not occur elsewhere in the lower Receptaculites Limestone. These observations suggest an approximate north-south facies gradient in the Taemas synclinorium during lower Receptaculites time.

In the middle part of the Receptaculites Limestone, corals tend to be widespread throughout the Taemas area (Chatterton 1969, and pers. obs.). Small coral/stromatoporoid bioherms were observed in this interval above Locality R7 and about 150 m north of Locality R5. Bivalves are correspondingly rare or absent, although this may be owing in part to the generally poor silicification associated with this interval and, hence, the decreased likelihood of discovery.
In the uppermost collecting interval (the upper Receptaculites and lower Warroo limestones), compound rugose corals and tabular and massive tabulate corals are absent (Chatterton 1969). Nearly complete fenestellid bryozoan colonies are abundant at some horizons, and articulated pelmatozoan stem segments are relatively common. These observations indicate lower energy conditions than in the upper Bloomfield and lower Receptaculites limestones.

In the upper Receptaculites/lower Warroo interval, bivalves are less diverse than in the second collecting interval (the upper Bloomfield/lower Receptaculites interval) and comprise a relatively smaller fraction of the preserved biota. Only one species of pterineid, Ptychopteria catellus n. sp., is present, as compared to six species in the second interval. P. catellus n. sp. is, nonetheless, one of the most common bivalves at this horizon, making up about 25% of collected specimens. Endobyssate taxa are less diverse (three species instead of seven) and total only about 15% of collected specimens, compared with nearly 28% in the second interval. Free-living suspension-feeding burrowers are equally diverse taxonomically, but are relatively more abundant numerically (nearly 23% of collected specimens, as compared with 9% in the second interval). Cypricardinia minima n. sp. is the most abundant bivalve (nearly 28% of collected specimens), and was probably an epifaunal nestler (p. 331), a habit unrepresented among bivalves from the other collecting intervals (except possibly in some individuals of Mytilarca sp. [p. 47]).
A striking feature of the bivalve fauna from the uppermost collecting interval is the predominance of species of small body size (maximum shell length less than 20 mm). These include *Cypricardinia minima* n. sp., *Cypricardinia sinuosa* n. sp., *Crassatellopsis yongei* n. sp., *Crassatellopsis lenticularis* n. sp., *Polidevicea* cf. *P. insolita*, *Nuculites* sp. and *Deceptrix? clarkei* (Koninck), which together comprise 64% of bivalve specimens collected. By contrast, species in the second interval with a maximum shell length not exceeding 20 mm (these include the nuculoids and *C. sinuosa* n. sp.) comprise less than 4% of collected specimens. None of the other bivalve species in the uppermost collecting interval achieve body sizes as large as the largest bivalves in the other two intervals.

Brachiopods show a similar trend - large species are generally common in the lower two intervals but are comparatively rare in the uppermost collecting interval (pers. obs.). In general, lower relative frequencies of large-bodied shelly benthic taxa are associated with deeper shelf environments (Boucot 1975). These observations support Reynolds' (1978) conclusions that this interval represents a deeper environment.

**FAUNAL RELATIONSHIPS**

Devonian bivalves of Australia have been the subject of few systematic studies. Principal published works include: Chapman (1908, various units in the Melbourne Trough,
Victoria, mostly Siegenian-early Emsian, 58 species, 28 genera); Talent (1956, Buchan Caves Limestone, Victoria, early Emsian, 10 species, eight genera [two of the species are probably synonyms, p. 400]); Talent & Philip (1956, Marble Creek limestone, Victoria, late Siegenian, three species, three genera [two of these species are probably synonyms, p. 53]): Talent (1963, Tabberabbera Formation, Victoria, late Siegenian-early Emsian, 33 species, 19 genera); Philip (1962, Boola and Yering beds, Victoria, Siegenian, six species, four genera); McKellar (1966a & b, Etonvale Formation [subsurface], Queensland, five species, three genera); Fletcher (1975, Barrow Range Beds, New South Wales, Early Devonian, two species, two genera). Benson (1922) summarized the literature on Australian Devonian fossils, including bivalves, published up to that time. With few exceptions, specimens described in these studies are poorly preserved and do not show characters of the hinge or musculature. A large number of the generic identifications, especially in the pre-1960 studies, are probably incorrect.

The bivalve fauna occurring in the Taemas Formation is the best preserved and generically most diverse of any yet described from Australia. As evident from the number of new species represented (Table 1), the fauna bears little resemblance to bivalve faunas described from elsewhere in the Devonian of Australia. A few species occurring in the Taemas Formation also occur in the Buchan Caves Limestone and/or the Cavan Formation, including Nuculoidea sp., Polidevicia cf. P. insolita, Solemyacea n. gen. & sp., Ptychopteria
(Cornellites) sp. B, Paracyclus proavia, and, questionably, Mytilarca sp. and Goniophora pravinasuta n. sp. Although not conspecific, several species from the Taemas Formation are apparently closely related to species in the Cavan Formation and Buchan Caves Limestone (compare Actinopteria cf. A. murrindalensis and Actinopteria murrindalensis n. sp.; Phorinoplax striata n. gen. & sp. and Phorinoplax sp.; Schizodus truemani n. sp. and Schizodus oweni n. sp.; Sanguinolites phlyctaenatus n. sp. and Sanguinolites concentrirugosa). Only two genera represented in the Cavan Formation and Buchan Caves Limestone are absent in the Taemas Formation, these being Glyptodesma Hall and Guerangeria Oehlert. By contrast, several genera occurring in the Taemas Formation are absent in the Cavan Formation and Buchan Caves Limestone (see Table 1). None of the species known from the Buchan Caves Limestone, Cavan Formation and Taemas Formation can be positively identified as occurring in other described Devonian bivalve faunas from Australia (comparisons of the material described herein with specimens described by Talent [1956], Talent & Philip [1956] and Talent [1963] were made first-hand; comparisons with specimens described by other authors were based on published descriptions and illustrations). In addition, several genera, including Glyptodesma, Phorinoplax n. gen., Guerangeria, Atremapella n. gen., Crassatellopsis Beushausen, Cimitaria? and Solenomorpha Cockerell are unrepresented in these faunas. Australian Devonian bivalves are too poorly known, however, to determine to what extent these are age or facies related differences.
As noted by Kříž (1979), the relationships of Devonian bivalves to faunal provinces based on brachiopods (Boucot, et al. 1969) can be discussed in only the most general terms owing to the need for comprehensive revision of Devonian bivalves, especially at the generic level. With these limitations in mind, the following observations are made:

Of the 40 species of Lower Devonian bivalves recognized in collections made for the present study (Table 1), all are new and/or unnamed except five. Of these, only Paracyclus proavia is known outside of Australia, occurring in the Middle Devonian of Europe (Beushausen 1895) and eastern North America (LaRocque 1950; Bailey 1983). Of the 27 genera represented, at least 13 occur in the lower and/or Middle Devonian of both the Old World and the Appalachian faunal realms (see Bailey 1983 for relevant publications). These include: Nuculoidea Williams & Breger, Nuculites Conrad, Mytilarca, Ptychopteria Hall, Actinopteria, Limoptera Hall & Whitfield, Pseudaviculoopecten Newell (probably a number of species referred to Aviculopecten M'Coy by Hall [1884] belong here [Newell 1937: 38]; this appears true for all or most species of Aviculopecten figured by Frech [1891, pls. 1 & 2], as well), Goniophora Phillips, Cypricardinia Hall, Schizodus Verneuil & Murchison, Paracyclus Hall, Sanguinolites M'Coy (=Sphenotus Hall, p. 394-396) and Grammysioidea Williams & Breger. Some of these have also been reported in the Malvinokaffric Realm, including Nuculoidea (but see Bailey 1978: 126), Nuculites, Mytilarca, Actinopteria, Goniophora, Sanguinolites and Grammysioidea (DuToit 1954, Clarke 1913,
McAlester & Doumani 1966, Boucot 1971, *in fide* Kríž 1979). Of the remaining genera listed in Table 1 (excluding the Silurian genus *Coppinsia* n. gen.), five are recorded elsewhere only in Old World faunas. These include *Deceptrix* Fuchs, *Tolmaia* Williams, *Guerangeria*, *Crassatellopsis* and *Solenomorpha*. *Phorinoplax* n. gen. is questionably represented in the Lower Devonian of Germany (see p. 271-272), but is unknown elsewhere. Two of the genera listed in Table 1 are known elsewhere only in the Middle or Middle-Upper Devonian of the Appalachian Realm, these being *Glyptodesma* and *Cimitaria* Hall & Whitfield (the Australian species, *C.?* sp., is only questionably included in the latter genus; if not congeneric with species of *Cimitaria*, it is closely related; see p. 409). Except for the Australian occurrences, *Narquenella* Talent is represented elsewhere only in the Lower Devonian of New Zealand (Bradshaw 1979). *Polidevcia* Chernyshev has not previously been recorded from the Devonian; however, a species figured by Beushausen (1895, pl. 4, figs. 26-28) from the Lower Devonian of Germany, and several species figured by Hall (pl. 47, figs. 37-47, 49-50) are similar in shell outline to the Australian species of *Polidevcia* and may be congeneric.

Of the remaining genera, *Atremapella* n. gen., a new but unnamed genus of Solemyacea, and a questionably new but unnamed genus of Lucinacea are apparently restricted to southeastern Australia. *Atremapella* n. gen., however, is a member of the Rhombopteriidae, which, except for other Australian occurrences, is recorded elsewhere in the Devonian
only in central Europe (p. 55-56), and, hence, is of Old
World aspect.

From the above comparisons, it appears that although a
significant number of genera included in this study are
cosmopolitan (i.e., occurring in two or more faunal realms),
bivalve faunas of the Buchan Caves Limestone, Cavan Formation
and particularly the Taemas Formation, show strongest
affinities with Lower-Middle Devonian faunas of the Old World
Realm, particularly those of central Europe, with only a
slight Appalachian influence indicated by two genera,
Glyptodesma and Cimitaria. These observations agree with
biogeographic analyses of Lower Devonian brachipods and
trilobites of southeastern Australia, which also exhibit Old
1979). Especially striking, however, is the close agreement
with conclusions reached by Tassell (1982) in his discussion
of the biogeography of gastropods from the Lower Devonian of
Australia (including the Receptaculites Limestone). These he
showed to be of Old World aspect, but with a few genera
(including one from the Receptaculites Limestone) known
elsewhere only from the Upper Devonian of North America.

METHODS

Preparation: Silicified fossils recovered from the
Taemas Formation and Buchan Caves Limestone were freed from
their enclosing rock matrix using dilute hydrochloric acid,
as described by Cooper and Whittington (in Kummel & Raup
1965). At localities CB1 and F1, fossils occur primarily as natural molds, which were cast with latex in the laboratory. Recrystallized shell material still present in some specimens was dissolved with hydrochloric acid before casting. In addition, four rock samples from CB1 and five from F1 (and weighing about 1.5 kg each) were processed using a new casting technique described by Zapasnik and Johnston (1984). Briefly, this technique involves: 1) the leaching of carbonate (including shell material, if present) from clastic rocks, using hydrochloric acid; 2) impregnation of the resulting voids with liquid plastic; 3) dissolution of the rock matrix with hydrofluoric acid, leaving a residue of plastic-replaced fossils. Fossils recovered in this way are referred to in the text and plate descriptions as plastic replicas (e.g., Pl. 2, fig. 17).

All silicified specimens, plastic replicas and latex casts were whitened with ammonium chloride for photography.

**Measurements and terminology:** Specimens less than 10 mm in length were measured to the nearest 0.1 mm under a binocular microscope fitted with an ocular micrometre. Specimens preserved as natural molds and exceeding 10 mm were measured to the nearest 0.5 mm with a metric dial caliper. Silicified specimens and plastic replicas exceeding 10 mm were oriented on 1 mm square graph paper and measured to the nearest 0.5 mm. For some damaged specimens, length and height were estimated to the nearest millimetre. For all measurements, height was measured perpendicular to length.
Shell length for pteriomorphs (except *Mytilarca*) was taken as the maximum distance parallel with the hinge axis (Text-fig. 6A).

Non-pteriomorphs are in general more difficult to orient consistently for measurement than are pteriomorphs. Some authors (e.g., Newell & Boyd 1975; Bailey 1983) have used points at the edge of or within the adductor scars to determine a datum for orientation. The posterior adductor scar is too faint in most taxa described in the present study to provide a datum point. Consequently, specimens were oriented for measurement relative to a datum line determined from two or more points on the shell outline.

For *Mytilarca* and modioliform species, including *Phorinoplax* spp., *Margunella comptorae* n. sp., *Guerangeria* sp., *Goniophora* spp., and *Sanguinolites* spp., length was taken as the maximum distance parallel to a line intersecting the ventralmost points on opposite sides of the byssal sinus (Text-fig. 6C), or, if the ventral margin was relatively straight, a line approximately parallel with this edge. For *Goniophora* spp. and *Phorinoplax* sp., the ventrally protruding posteroventral "corner" of the shell outline was ignored in the determination of this datum (Text-fig. 6B).

For *Eoschizodus taemasensis* n. sp. and *Schizodus* spp., a datum was determined by a line passing through the apogee of the umbo and the most distal point at the posteroventral edge of the shell. Length was taken as the maximum distance parallel to a line forming a 55 degree angle with the datum
Text-fig. 6. Orientations of specimens for measurement (see p. 33-35): A) Ptychopteria (Cornellites) catellus n. sp.; B) Goniophora pravinasuta n. sp.; C) Nargunella comptorae n. sp.; D) Crassatellopsis lenticularis n. sp.; E) Eoschizodus taemasensis n. sp.; F) Schizodus truemani n. sp.

Abbreviations: D - datum; H - height; L - length.
for *E. taemasensis* n. sp. and a 25 degree angle for *Schizodus* spp. (Text-fig. 6E & F).

For *Crassatellopsis* spp. and *Paracyclas* spp., length was taken as the maximum distance between the anterior and posterior margins (Text-fig. 6D).

Most morphological terminology follows Cox (in Moore 1969: N4-N109). Some terms normally applied to oysters (Stenzel, in Moore 1971: N1028-1034) are used for certain features of the Rhombopteridae as explained in the section dealing with that family. Other terms, including some that are new, are as follows:

**Pallial punctae**: As used in Bailey (1983).

**Posterior angle**: Angle formed by the dorsal and posterior shell margins in pterioids that lack a posterior embayment.

**Posterior embayment**: Broad emargination of the posterior shell margin that offsets the posterior auricle in various pterioids (notably in pterineids).

**Posterior internal ridge**: Radially directed ridge on the inner surface of the posterior slope of the shell that extends toward the posterior adductor scar (and beyond in some Crassatellacea, *e.g.*, Pl. 36, fig. 11). This feature does not, however, represent the ontogenetic trace of the posterior adductor scar. In pterioids, this feature can occur on the inner expression of the posterior auricular sulcus.
(but see Pl. 13, fig. 8), but is nonetheless distinct. "Posterior internal ridge" is a descriptive term, as are terms such as "posterolateral tooth", and is not meant to imply that features so named among separate taxa are necessarily homologous.

Additional new terms are defined in the text, as appropriate.

Collections: Most of the specimens described in this work are deposited in the palaeontological collections of the Australian National University (ANU numbers), Canberra. All type and referred specimens obtained from collections at Macquarie University, Sydney, have been deposited in the Commonwealth Palaeontological Collection, Bureau of Mineral Resources, Geology and Geophysics (CPC numbers), Canberra, at the request of Dr. J. A. Talent (Macquarie University). It is the policy of the Bureau of Mineral Resources, Geology and Geophysics to provide only informal catalogue numbers for unpublished specimens. These numbers are used in the present work, but will be changed to permanent Commonwealth Palaeontological Collection numbers in ensuing publications (Johnston, in preparation).

Abbreviations for other institutions from which material was borrowed include: AM, Australian Museum, Sydney; GSV, Geological Survey of Victoria; HU, Museum für Naturkunde, Humboldt-Universität, Berlin; MUGD, Melbourne Univerity, Geology Department; NMV, National Museum of Victoria,
Classification: At present, there seems to be no consensus among taxonomists as to higher classification within the Bivalvia. Pojeta (1978), for example, subdivided the class into seven subclasses, an arrangement that Bailey (1983) criticized. Purchon (1978: 433) advocated a division of the Bivalvia into only two subclasses, "...one for [deposit-feeding] Protobranchia and the other for filter-feeding Lamellibranchia." Palaeontological evidence presented by Runnegar and Bentley (1983: 89) also suggests a two-fold division of the Bivalvia, but one different from that of Purchon (1978). It is outside of the scope of the present study to evaluate these and other proposals (e.g., Scarlato & Starobogatov 1978) for the higher classification of bivalves. Consequently, a conservative approach has been assumed, and the subclasses in Newell's (1965, and Newell, in Moore 1969) longstanding and widely accepted classification have been used without prejudice (although the taxonomic composition of these subclasses in the present work differs in some respects; see Systematics).
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SYSTEMATICS

Class Bivalvia Linné 1758

Subclass Palaeotaxodonta Korobkov 1954

Discussion: At least five palaeotaxodont species are represented in collections made for the present study. These include:

Deceptrix? clarkei (Koninck) 1898 (Pl. 1, figs. 1-3, this paper)

Nuculoidea sp. (Pl. 1, figs. 4 & 5)

Nuculites sp. (Pl. 1, figs. 9 & 10)

Polidevcia cf. P. insolita (Talent) 1956 (Pl. 1, figs. 11 & 12, this paper)

Solemyacea n. gen. & sp. (Pl. 1, figs. 6-8)

These species are being described elsewhere (P. A. Johnston, in preparation). Their known stratigraphic distribution in the Taemas area is shown in Text-fig. 3. The soleymyacean resembles, and is probably congeneric with, a soleymyiform species occurring in the Ordovician of Estonia (Pojeta 1978: 231 & fig. 4). The Solemyacea are here listed under the Palaeotaxodonta in response to Pojeta's (1978)
evidence that these groups are related, the former representing a probable derivative of the latter.
Subclass Pteriomorpha Beurlen 1944
Order Pterioida Newell 1965
Suborder Pteriina Newell 1965
Superfamily Ambonychiacea Miller 1877
Family Ambonychiidae Miller 1877
Genus Mytilarca Hall & Whitfield 1869

Type species: Inoceramus chemungensis Conrad 1842, by original designation.

Discussion: Pojeta (1966) provided the most recent review of Mytilarca. References to earlier discussions are listed by McAlester (1962b: 38). The musculature of Mytilarca has not been described before, although a few sketchy details are known from Mytilarca sp., as recorded below. The posterior internal ridge of that species (Pl. 2, fig. 13) has not been reported in other ambonychiids.

In his generic description of Mytilarca, Pojeta (1966: 186) noted that "...as far as [is] known the posterior lateral teeth [are] mounted on what is either a posterior shell thickening or a posterior vertical lamella." In Mytilarca sp., the shell is only slightly thickened, or not at all, at the site of the lateral teeth. In a single specimen questionably referred to Mytilarca sp. from the Buchan Caves Limestone at the Basin, the shell is more noticeably thickened at this position, but a vertical lamella is not developed (Pl. 2, figs. 18 & 20).
Pojeta (1978: 238) believed that the ligament grooves in the Ambonychiidae were shortest in the first formed part of the hinge plate and longest in the parts formed last, and were parallel with, instead of inclined to, the dorsal commissure. He concluded that the ligament of ambonychiids was not, therefore, truly duplivincular. In Mytilarca sp., the ligament grooves clearly are inclined to the dorsal commissure and longest in the first formed part of the shell (Pl. 2, figs. 12, 17, & 20), indicating that a fully duplivincular grade of ligament was present in at least some ambonychiids.

### Mytilarca sp.

*(Pl. 2; Text-figs. 4 & 7)*

**Referred specimens:** ANU 48480-48493, 48494(?), 48549(?); CPC F24944-F24946 (total, 19).

**Known stratigraphic and geographic distribution:**

(?)early Emsian, Buchan Caves Limestone, the Basin, near Murrindal, Victoria, and Cavan Formation, Taemas area, New South Wales; late Emsian, Bloomfield, *Receptaculites* and Warroo limestones, Taemas Formation, Taemas area, New South Wales, and *Receptaculites* Limestone equivalent in the Taemas Formation, Wee Jasper area, New South Wales.

**Description:**
Text-fig. 7. *Mytilarca* sp.: length/height scatter diagram; length/height estimates for incomplete specimens indicated with flags (length estimated - flag to side of point; height estimated - flag above point; both length and height estimated - flag to side and above point).
**External features** - Gross shell morphology in this species is highly variable. Most specimens are inflated, with a strongly developed but blunt diagonal ridge, a subrectangular posterior shell outline, and a trigonal cross-sectional profile with greatest inflation occurring in the ventral half of the shell (Pl. 2, figs. 1-7). By contrast, some specimens are only weakly inflated, with a weak diagonal ridge, a rounded posterior shell margin, and a lenticular cross-sectional profile, with greatest inflation occurring midlaterally (Pl. 2, figs. 10 & 11). Other specimens are more or less morphologically intermediate between these extremes (Pl. 2, figs. 8 & 9).

External ornament consists of weak growth lines and irregularly spaced growth rugae that tend to be obscure on and above the diagonal ridge at early and intermediate growth stages.

**Internal features** - The ligament area is channel-like and usually marked by from four to six shallowly inclined grooves (fewer grooves are present at early growth stages; up to ten grooves are present in exceptionally large individuals). The dentition is variable. Normally, two or three cardinal teeth are present, mounted on a septum at the anterior end of the hinge (but one left valve has five weak cardinal teeth). Cardinal teeth vary considerably in their shape, size and orientation. In some specimens, they are moderately elongate (Pl. 2, fig. 12), in others, tuberculiform (Pl. 2, fig. 5), although both types can be
found in the same individual. Adjacent teeth can be joined at their dorsal and/or ventral edges (Pl. 2, figs. 2, 5 & 17).

Usually two or three lateral teeth are present posteriorly below the end of the ligament area in each valve. Possibly four are present in some specimens (Pl. 2, fig. 12). Lateral teeth can become relatively robust in adult shells (Pl. 2, figs. 2 & 18), or remain small and thin (Pl. 2, fig. 12). A few specimens apparently lack lateral teeth altogether (Pl. 2, fig. 5), but the possibility of their having been abraded away after death cannot be ruled out in these instances.

Muscle insertions are rarely visible. The posterior adductor scar is evident in only one specimen, and is circular in outline, faintly impressed, and situated well posterior to the lateral dentition (Pl. 2, fig. 2). The pallial line is sometimes visible ventrally, and, in one specimen, can be traced onto the underside of the umbal septum and posteriorly below the hinge before being truncated by shell breakage (Pl. 2, figs. 14 & 15). A posterior internal ridge is consistently developed below the posterolateral dentition, and extends anteriorly into the umbal cavity (Pl. 2, fig. 13). The functional significance of the ridge is uncertain, but possibly it represents the insertion area of gill suspensor muscles (see discussion of the posterior ridge in various pterineids, p. 204).
Discussion: From the great variation in shell form among the bivalves referred here to *Mytilarca* sp., it might be supposed that they represent more than one species. However, inasmuch as the collection includes a range of morphologic intermediates between the extremes of variation, it is treated as representing a single variable species. Furthermore, differences in shell form do not seem to be correlated with differences in dentition, nor do the few measurements available (Text-fig. 7) suggest any obvious way to assign parts of the sample to more than one species at present. Particular shell variants show no distribution among localities that might imply taxonomic differences, albeit the size of the available sample could well be too small to reveal such differences if they were present. Among the bivalves referred to *Mytilarca* sp., the single specimen from the Buchan Caves Limestone, Victoria, stands most apart from the others: it is larger and more inflated than most specimens from the Taemas area, and has a more heavily constructed shell and a more strongly concave ventral margin. (The single specimen [a juvenile, Pl. 2, fig. 17] from the Cavan Formation is too incomplete to clearly establish conspecificity with specimens from the Taemas Formation.)

Recent species of *Mytilus*, a homeomorph of *Mytilarca* (Seed 1968, 1972), show even greater variation in shell form than that encountered in *Mytilarca* sp. Seed (1968) observed that populations of *Mytilus edulis* Linné inhabiting different environments exhibited substantial differences in growth rates, maximal attainable shell size and life expectancy. In
M. edulis, both growth rates and density of individuals per unit of inhabited area influence shell form significantly (ibid.: 574). Seed also observed (p. 566-571) that in any one population, shell morphology changes significantly with age, old individuals having proportionally heavier and wider shells, with a strongly concave ventral margin. All of these variables interact in M. edulis to produce a highly polymorphic species; the interaction of comparable factors may have produced the range in shell morphology encountered in Mytilarca sp.

**Autecology:** The mytiliform shell outline of Mytilarca sp. indicates that this species adopted an epibysate life mode similar to that of the Recent mytilid Mytilis edulis (Stanley 1972) (Text-fig. 4). One specimen of M. sp. (Pl. 2, fig. 16) occurs in the aperture of a large gastropod, which suggests that at least some individuals may have undertaken a nestling habit. However, without additional examples of this kind, the alternative that this specimen was fortuitously washed into the aperture by currents seems equally probable.
Superfamily Pteriacea Gray 1847
Family Rhombopteriidae Korobkov 1960

Type genus: Rhombopteria Jackson 1890.

Included genera: Atremapella n. gen.; Coppinsia n. gen.; Prantliella Růžička 1950; Rhombopteria Jackson 1890.

Known chronostratigraphic distribution: (?Middle Ordovician) Middle Silurian [Wenlockian] - Lower Devonian [Emsian].

Revised diagnosis: Shell moderately prosocline to orthocline, and suborbicular to subrhombic; moderately to markedly inequivalved; shell height greater than hinge length; posterior angle generally obtuse; posterior embayment lacking (generally) or weakly developed (rarely); anterior auricle generally confluent with anterior margin and not well differentiated from shell body; byssal notch absent; dorsal margin strophic; ligament duplivincular; dentition generally well developed, although possibly lacking in some forms; adductor musculature heteromyarian, with pedal protractor scar on posterior margin of anterior adductor scar; Quenstedt muscle present; advanced forms with posterior radial fold and sulcus.

Discussion: Both the morphologic concept and the taxonomic composition of the Rhombopteriidae, as given by Korobkov (1960), are quite different from those used here.
Korobkov believed that *Rhombopteria* was equivalved, but Růžička (1950) had already shown that the type species, *Rhombopteria mira* (Barrande) (hitherto known only from left valves), was in fact markedly inequivalved, and that *Rhombopteria scala* (Barrande) represented the right-valve counterpart. Korobkov included *Palaeopecten* Williams and *Posidonia* Bronn in the Rhombopteriidae, but these forms are quite different from the family as defined here and are excluded (the relationships of the Posidoniidae and the Pectinacea with the Rhombopteriidae are discussed later). *Rhombopteria* has been traditionally regarded as a pectinacean (Korobokov, in Orlov 1960; Newell 1937, and Newell, in Moore 1969); however, new information concerning *Rhombopteria* (unpublished - discussed on p. 57), together with evidence from newly discovered rhombopteriids described below, reveals greater morphologic similarities with the Cyrtodontidae and Pterineidae. In fact, *Coppinsia spodophila* (a new genus and species described below), the oldest and most primitive rhombopteriid for which internal characters of the shell are known, is, in a broad sense, morphologically intermediate between those families.

The shell outline of *C. spodophila* n. gen. & sp. is more cyrtodontid-like than pterineid-like (Pl. 4, fig. 1). As in cyrtodontids, and unlike the earliest known pterineids (Pojeta 1971, pls. 10 & 11; 1978, pl. 11 [Ahtioconcha Öpik is thought by some workers to represent the earliest known pterineid, but this genus is not accepted here as a pterineid nor as a pteriomorph for reasons given on p. 188-189]), a
posterior embayment is lacking, the auricles are neither extended nor well differentiated from the shell body, and there is no evidence of a byssal notch at any stage of growth (except possibly in Rhombopteria mira [Barrande 1881, pl. 226, figs. III & IV; pl. 227, fig. I], but see p. 105 below). A small accessory scar (probably for a pedal protractor muscle [see p. 139]), occurs adjacent to the posterior edge of the anterior adductor scar in certain cyrtodontids (Pojeta 1971: 36). A small scar is present at this position in C. spodophila n. gen. & sp., and in species of Atremapella n. gen. (Pl. 4, fig. 10; Pl. 7, figs. 3 & 7; Pl. 10, fig. 8), but has not been reported in the Pterineidae or in any other pteriomorphs.

Pterineid-like characteristics of C. spodophila n. gen. & sp. include: 1) relatively greater reduction of the anterior adductor scar than in cyrtodontids; 2) an inequivalved shell; 3) the presence of numerous hinge teeth at mature growth stages, with a tendency for these to be developed more or less continuously across the hinge plate, as in the dentally primitive pterineids Ptychopteria (Cornellites) catellus n. sp. and Pteronitella retroflexa (Wahlenberg) (see Text-figs. 10 & 23) - cyrtodontids, by contrast, show relatively fewer teeth and invariably show a large edentulous gap between anterior and posterior teeth.

The inequivalved shell of the Rhombopteriidae is of particular interest, the right valve being flatter than the left valve, as in the Pterineidae. The Cyrtodontidae, in
comparison, are consistently equivalved and must have lived with the comissure oriented perpendicular to the substrate (Pojeta 1971; Stanley 1972). Valve inequality in rhombopteriids and pterineids reflects the adoption of a non-vertical life orientation, but in wholly different ways. Early pterineids and most later pterineids were pleurothetic on the right valve (Pojeta 1971; Stanley 1972). (Some pterineids became secondarily vertical in their orientation; see discussion under Pterineidae.) By contrast, available morphological and autecological evidence suggests that rhombopteriids were pleurothetic on the left valve. The life mode was probably similar to that of gryphaeid oysters and productid brachiopods, with the shell partly buried in the substrate and the convex valve (left valve) undermost (Text-figs. 4 & 13D); see discussion beginning on p. 84).

The intermediate morphological grade of rhombopteriids, together with their apparently fundamentally different life mode, indicates sufficient morphologic and adaptive divergence from the Cyrtodontidae, Pterineidae and other known pteriomorphs to warrant placement in a separate family. Four genera are included in the family: Atremapella n. gen., Coppinsia n. gen., Prantliella and Rhombopteria.

I have encountered in the literature fourteen species that have been referred to Rhombopteria. These are: 1) R. mira (Barrande) 1881; 2) R. pseudomira (Barrande) 1881; 3) R. cognata (Barrande) 1881; 4) R. scala (Barrande) 1881; 5) R. patricia (Barrande) 1881; 6) R. glabra (Goldfuss) 1837; 7) R.
palliata (Barrande) 1881; 8) R. implexa Northrop 1939; 9) R. revoluta (Winchell & Marcy) 1865; 10) R. ulrichi Foerste 1909; 11) R. clathrata (originally clathratus) Weller 1903; 12) R. anfractaviara Talent & Philip 1956; 13) R. laminosum (Koninck) 1898; and, 14) R. obliqua Sherrard 1959. Characters of the hinge have not been described for any of these species.

Jackson (1890) first proposed Rhombopteria and included species 1-6 above, with R. mira the type species. These species are all figured by Barrande (1881, pls. 226-228). The left valve of R. mira exhibits unusual ornament that consists of widely spaced, commarginal lamellae (as in Atremapella n. gen.), and two sets of subradial costellae that criss-cross to produce a fine net-like pattern (ibid., pl. 226, fig. III). Although Jackson (1890) made no mention of this distinctive ornament, subsequent authors (e.g., Northrop 1939; Termier & Termier 1950; Růžička 1950; Talent & Philip 1956) have emphasized it. Talent and Philip suggested that forms such as R. patricia and R. glabra that lack the ornament pattern of the type species be excluded from the genus and that another of Barrande's species, Avicula palliata (Barrande 1881, pl. 220), be included. A. palliata, however, has a divaricate, rather than net-like, ornament, and for that reason was placed as the type species of its own genus, Prantliella (Růžička 1950).

From the species list above, only R. pseudomira, R. clathrata, R. cognata, R. ulrichi, and R. revoluta show the
net-like ornament of the type species, *R. mira*. *R. scala* represents right valves of *R. mira*, as Barrande (1881, note accompanying pl. 226) suspected (Růžička 1950). *R. implexa* and *R. anfractaviara* have divaricate costellae on the left valve and should be included with *A. palliata* in *Prantliella*. It should be noted that *Pterinea concentrilamellata* Talent & Philip, known only from right valves that closely resemble right valves of *Atremapella* n. gen., occurs in the same beds and at the same locality as *R. anfractaviara*, and very likely represents the right valve of that species (see Pl. 3, figs. 3-6). Also, *Avicula oblongata* Trenkner and *Avicula quadrata* Trenkner (both figured in Frech 1891, pl. 7, figs. 3 & 8) can be referred to *Prantliella* and appear to represent the right and left valves, respectively, of the same species. The Ordovician species *R. patricia* should be excluded from *Rhombopteria*, as Talent and Philip suggested, although it may represent a rhombopteriid close to *Coppinsia* n. gen., as discussed below. Kegel (1925) presented convincing evidence that *R. glabra* does not belong in *Rhombopteria*. Pojeta and Kříž (*in fide* Pojeta, et al. 1976) placed *R. glabra* as the type species in a new genus, *Cheiopteria*. *Cheiopteria* is equivalved and does not appear to be a rhombopteriid, but may be related. *R. laminosa* and *R. obliqua* (both figured in Sherrard 1959, pl. 29) do not resemble *R. mira* or other rhombopteriids, and are more likely pterineids.

Foerste (1909) erected the subgenus *Rhombopteria* (*Newsomella*) to include *R. ulrichi* and *R. revoluta*. *R. revoluta* was originally described on the basis of a single
external mold of an incomplete right valve from the Niagara Limestone at Bridgeport, Illinois (Winchell & Marcy 1865). The specimen is too fragmentary, and its description and illustration insufficiently clear, to be sure of its characters. Consequently, for the present study, this species is interpreted primarily on the basis of material from the Silurian of Tennessee referred to this species by Foerste (1909). However, judging from the illustration in Winchell and Marcy (1865, pl. 2, fig. 12), the type specimen appears to be more rhombopteriid-like in the shell outline than are Foerste's specimens. It may be that the Bridgeport species will eventually be shown to be a rhombopteriid, whereas the Tennessee species probably is not.

Foerste noted that, unlike R. *mira*, it is the right valve in *R.* (*Newsomella*) that is the more convex and that bears the cross-striated ornament. In my view, this indicates a fundamental morphologic and adaptive departure from *R. mira* and other rhombopteriids. Newell and LaRocque (in Moore 1969) apparently reached similar conclusions and removed *R.* (*Newsomella*) from Rhombopteria and elevated it to generic rank within the Pterineidae. *Newsomella*, however, shows little in common with pterineids. There are no undoubted pterineids known in which the right valve is more convex than the left valve. It is more likely that *Newsomella* is closely related to, if not congeneric with, the primitive heterodont *Cypricardinia*. Both genera have strong commarginal ribs and an inequivalved shell, with the right valve the more convex. The presence of net-like ornament on the right valve but not
the left, seen in *Newsomella*, also occurs in some species of *Cypricardinia*, such as *C. indenta* (see Hall 1885, pl. 79, figs. 6-16 & 23) and *C. crenistria* (see Talent 1963, pl. 68, fig. 8).

It is likely that *R. cognata* and *R. pseudomira* are also close to or congeneric with species of *Cypricardinia*. Both species are known only from right valves (Barrande 1881, pl. 226) that are closely similar in shell outline and ornamentation to species of *Cypricardinia* of the same age (e2) figured in Barrande (1881, pl. 225, fig. IX & pl. 285, fig. I, 15), and slightly younger species figured in Hall (1885, pl. 79). Like *Cypricardinia*, both species are more strongly prosocline and relatively more elongate than are undoubted rhombopteriids. *R. cognata* appears to be almost indistinguishable from *Cypricardinia consobrina* Barrande (*op. cit.*, pl. 225, fig. IX), except that in the former a remnant of net-like ornament is preserved at the posteroventral edge of the otherwise decorticated shell.

In summary, of the fourteen species of *Rhombopteria* listed above, only the type species, *R. mira* (=*R. scala*) and *R. clathrata* can be confidently referred to that genus. *R. mira* is known from the Kopanina Formation (Ludlovian) of Bohemia (J. Kříž 1982, pers. comm.), and *R. clathrata* occurs in the uppermost beds of the Coeymans Limestone (Lochkovian) near Hainesville, New Jersey (Weller 1903: 291). Two unidentified specimens (F31468 and F31453) in the collections of the Australian Museum are worth noting here (Pl. 3, figs.
1 & 2). Both are upright left valves that show ornament very similar to that of *R. mira*. The valves are clearly referrable to *Rhombopteria*, but they are too imperfect for species identification. The specimens were collected from the Wenlockian of Wren's Nest, Dudley, in the south of England.

*A. palliata*, *R. implexa*, *R. anfractaviara* and *A. oblonga* (=*A. quadrata*) are here included in *Prantliella*. *A. palliata*, the type species, occurs in the Lower Devonian Koneprusy Limestones (Prag Formation, Pragian) of Bohemia (J. Kříž 1982, pers. comm.). *R. implexa* occurs in the Middle Silurian (West Point and Indian Point formations, late Niagaran) of eastern Canada (Northrop 1939), and *R. anfractaviara* is known from the Lower Devonian (Marble Creek Limestone, Siegenian [Tassell 1982]) of Victoria (Talent & Philip 1956).

*Atremapella* n. gen. includes two known species, *A. newelli* n. sp. and *A. misticia* n. sp. (described below) from the Lower Devonian (Garra Limestone, Pragian, and Taemas Formation, Emsian, respectively) of New South Wales. *Coppinsia* n. gen. is known only from the type species (described below), which has been found at a single locality in the Walker Volcanics (Middle Silurian, Wenlockian), near Canberra, in southeastern Australia.

External ornament of the left valve appears to be a useful character for distinguishing rhombopteriid genera as presently defined. *Atremapella* n. gen., *Prantliella* and *Rhombopteria* all have widely spaced, imbricated, commarginal lamellae (Pls. 3, 6 & 10) (these shall henceforth be referred
to as "squamae", a term normally applied to similar imbrications on oysters [Stenzel, in Moore 1971]), and in this way differ from Coppinsia n. gen. (Pl. 4, fig. 1), which bears only weakly defined, closely spaced, growth rugae and growth lines. In Rhombopteria, two sets of costellae criss-cross to form a fine net-like pattern (Pl. 3, figs. 1 & 2). Prantliella exhibits divaricate costellae (Pl. 3, fig. 3), and Atremapella n. gen. (Pls. 6 & 10) has radial costae.

Internal features of the shell have not been described for either Rhombopteria or Prantliella. Kegel (1925: 297) mentions the presence of a posterolateral tooth preserved in a single specimen of Rhombopteria in the Denckmann Collection, but does not specify whether this specimen pertains to R. mira. J. Kříž (1982, pers. comm.) informs me that several well preserved specimens of R. mira in his possession show a well developed duplivincular ligament area, together with a large, relatively deep posterior adductor scar, and a small pedal retractor scar located posterodorsally of the anterior adductor scar, but no traces of the dentition can be seen. From this it appears that R. mira is edentulous despite the presence of well developed dentition in other members of the family. Kříž also informs me of a single right valve of P. palliata in his possession that shows internal features, including a distinct duplivincular ligament area, a short lateral tooth posteriorly, and a subtrigonal tooth anteriorly. More detailed discussion of Rhombopteria and Prantliella await Kříž's description of these specimens; however, it appears
that the generic distinction of *Atremapella* n. gen., *Rhombopteria*, and *Prantliella*, based primarily on shell ornament, is consistent with differences in the dentition of these taxa.

Undoubted rhombopteriids are known from rocks no older than Middle Silurian (Wenlockian). However, considering the probability that the Pterineidae were derived from a *Coppinsia*-like ancestor (see discussion below) and are themselves known from rocks as old as Middle Ordovician (Pojeta 1978), a Middle or Early Ordovician age for the origin of the Rhombopteriidae seems likely (Text-fig. 8). Certain Ordovician bivalves figured by Barrande (1881, pl. 227), including *Avicula patricia* Barrande, *Aviculopecten quadrarius* Barrande and *Avicula? improvisa* Barrande, are reminiscent of the Rhombopteriidae and may represent early species of that family. Hinge features of these species are unknown. Barrande's Ordovician species show a relatively longer and straighter hinge line than is typical for cyrtodontids, and in this way are more like rhombopteriids. *A. patricia* is very similar to *C. spodophila* n. gen. & sp. in shell proportions. Although known only from internal molds, some of Barrande's Ordovician species show aspects of the external ornament that have apparently been superimposed on the molds during diagenesis. The ornament of *A. patricia* is apparently similar to that of *C. spodophila* n. gen. & sp. and, as in that species, the anterior adductor scar appears to be more reduced than in cyrtodontids. *A. novella* shows traces of radial ornament, a feature characteristic of some
rhombopteriids, but unknown in the Cyrtodontidae (as defined by LaRocque [in Moore 1969]). A.? improvisa is apparently inequivalved, as are rhombopteriids. The type specimens of A. patricia, however, seem to be equivalved (J. Kříž 1982, pers. comm.).

It is evident that the Ordovician species in question are much in need of restudy and consequently, comparisons with rhombopteriids are limited. Although suggestive of the Rhombopteriidae, they are too incompletely known to warrant placement in that family at present, but they are significant to the extent that they document the presence of forms at least externally like rhombopteriids in the Ordovician, a time inferred from other criteria to represent the time of origin and early evolution of the family. Jackson (1890) included A. patricia in his genus Rhombopteria, but apart from the rhombic shell outline, there is little to suggest a close relationship between the two. Furthermore, A. patricia lacks the net-like ornament characteristic of Rhombopteria, as Talent and Philip (1956) noted. A. patricia is much more like Coppinsia n. gen., and may be related.

Relationships of the Rhombopteriidae - (see Text-fig. 8 for summary).

Origin. Cyrtodontid-like features of Coppinsia n. gen. strongly suggest that the Rhombopteriidae were derived from cyrtodontid ancestors. In fact, were it not for moderate valve inequality and continuity of dentition between anterior
Text-fig. 8. Hypothesized phylogenetic relationships of most groups of Pteriomorpha (based largely on Cox, et al., in Moore 1969; Newell and Boyd 1970; Pojeta 1971, 1975; and Stanley 1972, with emendations from present study): solid vertical lines show known stratigraphic distributions, broken vertical lines show inferred stratigraphic distributions, and broken oblique or horizontal lines indicate relationships between groups.
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- **Pseudomonotidae**
- **Pinnidae**
- **Posidoniidae**
- **Arcacea**
- **Rhombopteridae**
- **Cyrtodontidae**
- **Pterineidae**
- **Ambonychiidae**
- **Cycloconchidae**
- **Pteriomorphia**
and posterior teeth, Coppinsia n. gen. could easily be classified in the Cyrtodontidae. Some cyrtodontids, such as Cyrtodonta saffordi (Hall), Cyrtodonta grandis (Ulrich), Cyrtodonta huronensis Billings and Cyrtodonta bechneri Conkin (all figured in Pojeta 1971, pl. 7 and/or 1978, pl. 8) are not far removed from Coppinsia n. gen. in shell outline, and are dentally reminiscent of various growth stages of Coppinsia n. gen. However, without ontogenetic data for cyrtodontids, it is difficult to specify dental homologies (comparisons of rhombopteriid and cyrtodontid dentitions are given following description of Coppinsia spodophila n. gen. & sp. below), and it presently cannot be determined from dental or other criteria whether any one of the Ordovician genera cited is closer to rhombopteriid ancestry than any other. These genera are nonetheless significant in that they document in the Ordovician bivalves at least broadly appropriate in shell form and dental grade for derivation of the Rhombopteridae.

Origin of the Pterineidae and the Pectinacea. The Pterineidae are generally regarded as probable derivatives of the Cyrtodontidae (Newell 1954; Vogel 1962; Cox, in Moore 1969; Pojeta 1971) or less widely, the Ambonychiidae (Stanley 1972). Some authors (e.g., Newell 1954) visualize a cyrtodontid ancestry for the Pectinacea as well, while others (e.g., Stanley 1972) have suggested that the Pterineidae are their most likely progenitors. Discussions of the morphologic and adaptive changes associated with these hypothesized
transitions, if given at all, are invariably cast in the broadest terms, no doubt because of the general paucity of data for early pterineids and pectinaceans. Consequently, in spite of the attempts of bivalve systematists to outline the origin of these important bivalve groups, their derivation has remained cryptic, with few clues as to even their most general ancestry.

**Pterineidae - New morphologic and ontogenetic information for the Rhombopteriidae sheds considerable light on the origin of the Pterineidae.** As noted earlier, the primitive rhombopteriid, *Coppinsia spodophila* n. gen. & sp., exhibits features of both the Cyrtodontidae and the Pterineidae, and in this sense, is broadly intermediate between those families. On this basis, it is here suggested that the Pterineidae were derived from a *Coppinsia*-like rhombopteriid, probably during Middle, or perhaps Early, Ordovician time.

The phylogenetic significance of the dentition of *C. spodophila* n. gen. & sp. warrants particular attention. As shown in Text-figs. 15 & 23, ontogenetic changes in the dentition of *C. spodophila* n. gen. & sp. are strikingly similar to those of the Lower Devonian pterineid Ptychopteria (*Cornellites*) *catellus* (new species described below). Inasmuch as *C. spodophila* n. gen. & sp. is here hypothesized to be structurally and probably phylogenetically close to the ancestors of the Pterineidae, it is important that the ontogeny of the dentition can, in fact, be demonstrated to be
closely similar to that of *P. catellus* n. sp., an apparently primitive pterineid. However, these similarities alone do not imply a rhombopteriid ancestry for the Pterineidae. As discussed later (p. 143-148 & Text-fig. 18), the adult dentition of some cyrtodontids resembles the dentitions of intermediate growth stages of *C. spodophila* n. gen. & sp. and *P. catellus* n. sp. Although the ontogenies of these cyrtodontids are unknown, it would not be surprising if they were eventually shown to be similar to those of *P. catellus* n. sp. and *C. spodophila* n. gen. & sp. It could be argued, therefore, that dental configurations of at least the early and middle growth stages of *C. spodophila* n. gen. & sp. and *P. catellus* n. sp. may be primitive for the Cyrtodontidae, Rhombopteriidae and Pterineidae as a whole. Consequently, these resemblances by themselves cannot be used in support of a special relationship between the Rhombopteriidae and Pterineidae. However, the adult dentitions of pterineids such as *P. catellus* n. sp., and especially *Pteronitella retroflexa*, are clearly more like that of *C. spodophila* n. gen. & sp. than like any known cyrtodontid. This is taken as strong evidence for a phylogenetic connection between the Rhombopteriidae and the Pterineidae.

*P. retroflexa* occurs in the Upper Silurian of Gotland and the Welsh Borderland, and has been redescribed by Walmsley (1962). Two of Walmsley's figures are reproduced here in Text-fig. 9B-C, for comparison with *C. spodophila* n. gen. & sp. Similarities are mostly self-evident and require little elaboration. Interestingly, the left valve of *P.*
Text-fig. 9. Hinge structure in *Coppinsia spodophila* n. gen. & sp. and *Pteronitella retroflexa* (Wahlenberg): A) *C. spodophila* n. gen. & sp., ANU 48512 (holotype), left valve, stereo pair, X2.6; B-D) *P. retroflexa*; B-C) left and right valves, respectively, X1.5, from Walmsley 1962, pl.1, figs. 3 & 4; D) enlargement of anterior region of hinge in "C" above, showing inferred dental homologies with *C. spodophila* n. gen. & sp. (see Text-fig. 16).

White arrow in A & B indicates partly subdivided tooth.

Abbreviations as in Text-fig. 15.
P. retroflexa shown in Text-fig. 9B exhibits a few very short, thin teeth between longer teeth in the anterior part of the hinge. Also, at least one tooth in the central part of the hinge (see arrow) appears to be incompletely subdivided by a socket (see arrow in Text-fig. 9A for a similar tooth in C. spodophila n. gen. & sp.). These observations indicate that teeth and sockets increase in number at advanced growth stages by the bifurcation of pre-existing teeth and by the insertion of teeth in pre-existing sockets, as described later for C. spodophila n. gen. & sp. (p. 130-139).

P. retroflexa differs in its dentition from C. spodophila n. gen. & sp. in that the anteriormost teeth of mature specimens are orthocline (Text-fig. 9B) or moderately prosocline (Walmsley 1962, pl. 1, fig. 5), whereas in C. spodophila n. gen. & sp., the anteriormost tooth or teeth are moderately opisthocline (except in gerontic specimens, where the anterior teeth can become highly irregular in their shape and orientation, (e.g., Text-fig. 15, G). However, the hinge of the apparently dentally immature right valve figured by Walmsley (Text-fig. 9C, this paper) shows that the anteriormost tooth of this valve (and by inference the opposing valve) was opisthocline at an earlier ontogenetic stage. This tooth is joined dorsally with a prosocline tooth, forming an arch. A small tuberculiform tooth occurs below the arch. This configuration is closely similar to that of intermediate growth stages of the right valve of C. spodophila n. gen. & sp. (Text-fig. 16, V). Text-fig. 9D shows an enlargement of the anterior part of Walmsley's
specimen. Teeth and sockets inferred to be homologous with those of *C. spodophila* n. gen. & sp. are numbered accordingly (see p. 130-139 for description of numbering system for *C. spodophila* n. gen. & sp.).

A second difference between the dentitons of *P. retroflexa* and *C. spodophila* n. gen. & sp. is seen in the orientation of the posterolateral teeth. In mature specimens of *C. spodophila* n. gen. & sp., these teeth are strongly divergent from the hinge axis, whereas in *P. retroflexa*, they are weakly divergent. Both character states occur among other pterineids. *P. catellus* n. sp. and *Tolmaia erugisulca* n. sp. (described below), for example, show strongly divergent posterolaterals (Pl. 13, fig. 1; Pl. 15, fig. 10), whereas they are weakly divergent in *Actinopteria murrindalensis* n. sp. (described below; see Pl. 17, figs. 11-15). By outgroup comparison with *C. spodophila* n. gen. & sp. and cyrtodontids, strongly divergent posterolaterals appear to be the primitive state, and weakly divergent posterolaterals the derived state. Consequently, *P. retroflexa* is more derived than *P. catellus* n. sp. in this character, but *P. catellus* n. sp. is apparently more derived in other features of the dentition, in that fewer hinge teeth are present and these do not become subdivided at advanced growth stages (see p. 208-211 for description of ontogeny of *P. catellus* n. sp.).

From the discussion above, one would predict that the dentition of the Pterineidae was primitively *Coppinsia*-like or *Pteronitella*-like (but with divergent posterolaterals).
However, present stratigraphic evidence offers no support for this hypothesis. Pojeta (1971, pl. 11; 1978, pl. 11) figured several Ordovician pterineids in which features of the hinge are preserved. The geologically oldest of these, a new and undescribed species of *Palaeopteria* Whiteaves (late Middle Ordovician) has simple, laterally divergent, elongate teeth that are closely similar to, and probably homologous with, the primary teeth of early growth stages of *C. spodophila* n. gen. & sp. (Text-fig. 17) (primary and secondary teeth are defined on p. 132-134). Although geologically archaic, it is unlikely that the dental configuration of *Palaeopteria* represents the primitive state for the Pterineidae. Otherwise, the closely similar and relatively complex ontogenetic development of secondary teeth in the Silurian rhombopteriid *C. spodophila* n. gen. & sp. and the Devonian pterineid *P. catellus* n. sp. would have to be interpreted as the result of convergence, as would resemblances between adult stages of *C. spodophila* n. gen. & sp. and *P. retroflexa*. It is more likely that *Palaeopteria* is a paedomorphic form, and that dentally more primitive pterineids, resembling *P. retroflexa* and *C. spodophila* n. gen. & sp., will yet be found in Middle Ordovician, and perhaps older, horizons. A slightly younger pterineid, *Carotidens demissa* (Conrad) (middle Upper Ordovician), shows what appear to be secondary teeth developed anteriorly below the anterior primary tooth (Pojeta 1971, pl. 11, fig. 11; 1978, pl. 11, fig. 12 [same specimen]). These are not as extensive nor as strongly developed as the secondary teeth in
C. spodophila n. gen. & sp., P. retroflexa and P. catellus n. sp., and consequently, this species is probably paedomorphic (although not to the extent of Palaeopteria) relative to hypothesized, although as yet unknown, dentally more primitive Ordovician pterineids.

Pectinacea - Early Pectinacea are not well understood morphologically (Newell 1937). The internal surface of the shell is known for very few taxa, and even where known, provides few characters on which to base inferences of descent.

The oldest undoubted pectinaceans are Late Silurian in age and include representatives of two families, the Leiopectinidae and the Pterinopectinidae (Newell, in Moore 1969). The Pterinopectinidae are edentulous. The Leiopectinidae show simple elongate teeth diverging from the umbo; apparently one anterior tooth and at least one or two posterior teeth occur in each valve, judging from internal molds figured in Krasilova (1959; 1963). This dental configuration is reminiscent of that in early growth stages of rhombopteriids (Text-fig. 17A-D), but dental resemblances alone are insufficient to verify a close relationship of these taxa. Among the Pterineidae, juvenile stages, as well as adult stages of some species, resemble leiopectinids dentally (Text-fig. 17I), and it may be that this family is broadly ancestral to the Pectinacea, as suggested by Stanley (1972). However, a rhombopteriid, rather than a pterineid, origin for the Pectinacea seems more probable on the basis of
other criteria, including:

1) leiopectinids lack a well defined byssal notch and sinus (Newell, in Moore 1969), a condition characteristic of rhombopteriids but atypical of pterineids;

2) in both rhombopteriids and pectinaceans, the umbo is more centrally placed, the anterior lobe less reduced, and the shell less strongly prosocline than in typical pterineids;

3) in primitive rhombopteriids and certain early pectinaceans, such as Dunbarella Newell and Pterinopecten Hall, and unlike the earliest Pterineidae, the posterior auricle is not extended as a wing, and the posterior angle is obtuse.

If the Pectinacea arose from a rhombopteriid ancestor, it was probably by paedomorphosis, with the juvenile dentition, ligament and epibyssate habit being retained into adult growth stages (see discussion beginning on p. 119).

Rhombopteriids have long been suspected to include the ancestors of the Pterineidae and the Pectinacea. Jackson (1890) compared the shell outline of early growth stages of various Recent pectinaceans and pteriaceans with the adult shell outline of Rhombopteria, and from this concluded that Rhombopteria more closely approached the ancestral morphotype for the Pteriacea and Pectinacea than any other fossil species known at the time. Newell (1937) supported this view.
in regard to the Pectinacea, as did Stanley (1972). Stanley (ibid.: 191), however, questioned the role of Rhombopterida in the ancestry of the Pteriacea on the grounds that the Pterineidae preceded Rhombopterida geologically. Instead, he suggested that the Pectinacea were derived from the Pterineidae and that Rhombopterida provided a morphologic intermediate between these groups. New information about the Rhombopteriidae indicates that Jackson's view is more nearly the correct one, but with some modifications required. Rhombopterida and other rhombopteriids clearly do not represent derived pterineids; outgroup comparison of the Rhombopteriidae, the Pectinacea and the Pterineidae with the Cyrtodontidae leaves little doubt that the Rhombopteriidae (including Rhombopterida) are more primitive morphologically than either the Pectinacea or the Pterineidae. As Stanley (1972) pointed out, it is unlikely that Rhombopterida, especially in light of its emended stratigraphic distribution (discussed earlier), was itself involved in the ancestry of the geologically older Pterineidae, and if Rhombopterida was completely edentulous, as evidence from J. Kříž (1982, pers. comm.) suggests, it may not have been directly involved in pectinacean ancestry either. Nevertheless, Jackson was correct in recognizing, primarily from neontological evidence, that Rhombopterida more closely approached a proto-pectinacean and proto-pteriacan condition than any other fossil taxon known at that time. Known stratigraphic distributions of the Pectinacea and Pteriacea suggest that they originated individually, from separate rhombopteriid
ancestors, and at different times, the Pteriacea in the Early or Middle Ordovician, and the Pectinacea in the Middle or Late Silurian (Text-fig. 8).

Pojeta (1978) has noted the presence of equivalved pectiniform or limiform shells in the Ordovician of New York State. If these prove to be true pectinaceans, then they would imply a somewhat different history for that superfamily from that suggested above.

Origin of the Posidoniidae: Weigelt (1922) regarded the Silurian genus *Rhombopteria* as the probable ancestor of the Lower Carboniferous to Upper Jurassic genus *Posidonia*, and was so convinced of their similarity that he placed the two genera in synonymy. Newell (1937) regarded these forms as generically distinct, but supported Weigelt's view of their phyletic relationship in spite of a substantial stratigraphic gap between the two. Weigelt's comparisons of *Posidonia* were primarily with *Rhombopteria glabra*, a species which Kegel (1925) subsequently showed did not belong in *Rhombopteria*, nor does it appear to be a rhombopteriid. Furthermore, any resemblances of *Posidonia* with undoubted species of *Rhombopteria* are with the moderately convex right valves, which, at Weigelt's time, were not realized to belong with the highly convex left valves. Consequently, neither *Rhombopteria* nor other rhombopteriids appear to have been involved in the origin of the Posidoniidae. Stanley (1972) suggested that the Posidoniidae may have evolved from a genus like *Caneyella* Girty, which, being of Lower Carboniferous
age, is more suitable stratigraphically than Rhombopteria, and furthermore, is morphologically transitional between the Pterineidae and the Posidoniidae.

**Origin of the Pseudomonotidae** - The Pseudomonotidae comprise a relatively poorly known group of predominantly late Palaeozoic epifaunal pteriomorphs that are thought to represent the ancestral stock from which gryphaeid oysters and certain other oyster-like forms were derived (Newell & Boyd 1970). Newell and Boyd (1970) included four genera in the family: *Pachypteria* Koninck; *Prospodylus* Zimmerman; *Pegmavalyvula* Newell & Boyd; and the type genus *Pseudomonotis* Beyrich. *Limanomia* Gray probably belongs here as well (N. D. Newell 1981, pers. comm.).

The origin of the family is unclear. The stratigraphic record of the Pseudomonotidae is insufficiently dense to allow documentation of clear evolutionary trends within the family, thereby precluding projection of trends backward in the attempt to recognize ancestral morphotypes. The Upper Devonian genus *Limanomia*, probably the earliest known member of the family, is too incompletely known to be of help; internal features, of prime importance in discussions of ancestry, have not been described. The monotypic genus *Pachypteria*, of Lower Carboniferous age, is known only from five undoubted specimens and shows specialized features, such as cemented attachment early in ontogeny and the absence of radial ornament (Newell & Boyd 1970). These features are atypical of younger pseudomonotids (as exemplified by
Pseudomonotis) and suggest that Pachypteria is morphologically distant from the ancestors of the family. Pecmavalvula and Prospandylus, both of Permian age, show similar specializations and appear relatively late in the history of the family and, consequently, contribute little to our understanding of the origin of the Pseudomonotidae. Pseudomonotis is relatively well known morphologically and, among pseudomonotid genera, includes the most species, has the longest geological duration (Pennsylvanian-Permian), and appears to be the most primitive (except possibly Limanomia) in the family. Unlike other pseudomonotids, Pseudomonotis lacks cemented attachment and retains a functional byssal notch through all or most of ontogeny - probably primitive traits, from comparisons with early pectinaceans. Pseudomonotis, then, provides a useful starting point in assessing hypotheses about the origin of the family.

Newell (1937) suggested Pseudomonotis was a derivative of some unknown, primitive, Limipecten-like aviculopectinine, and erected the then monogeneric subfamily Pseudomonotinae within the Aviculopectinidae to include that genus. The Pseudomonotidae were subsequently elevated to familial rank within the Pectinacea (Newell, in Moore 1969), and are still regarded as closely allied to the Aviculopectinidae (Newell & Boyd 1970); the two families are thought to have diverged from some common (presumably pectinacean) ancestor during the Devonian or Early Mississippian (ibid.).
An alternative hypothesis of origin is suggested here on
the basis of comparisons of *Atremapella* n. gen. and
*Pseudomonotis*. These genera show certain similarities that
indicate that the *Pseudomonotidae* may have been derived
paedomorphically from an *Atremapella*-like ancestor.
Similarities between the *Pseudomonotidae* and the
*Aviculopectinidae* possibly result from convergence induced by
paedomorphic derivation of these families from different but
related ancestors, as explained later.

Aspects of *Atremapella* n. gen. and *Pseudomonotis*
important in assessing their mutual relationship are
discussed individually below.

1) **Ontogeny** - In both genera, the juvenile shell is
subrhombic in outline, with an elongate strophic hinge and an
obtuse posterior auricle that is neither extended nor
differentiated from the shell body (compare figs. 33-38 of
Newell [1937] with Pl. 6, figs. 2 & 8 [umbonal area] & Pl.
10, figs. 11 & 12, 14 & 15, this paper). A posterior
embayment is lacking but shows slight expression in later
stages in most specimens of *Atremapella misticia* n. gen. &
sp. and some species of *Pseudomonotis*, such as *P._
wandageensis* Newell & Boyd (ibid., fig. 14) and *P._
precursor* Mather (Newell 1937, pl. 17, fig. 8c). In these examples, the
posterior auricle when present is always small and bluntly
rounded. In both *Pseudomonotis* and *Atremapella* n. gen.
development of radial ornament in the left valve is delayed
in juvenile stages, leaving a smooth umbo (except for
commarginal ornament) in the adult shell (see Newell 1937, figs. 33-38 for Pseudomonotis).

Newell (1937) and Newell and Boyd (1970) noted that Pseudomonotis exhibits an unusual series of changes in shell form during ontogeny. Generally, earliest growth stages exhibit retrocrescent growth, followed by a stage of infracrescent growth (and then procrescent growth in some species) and finally by secondary reversion to retrocrescent growth at full maturity. (The terms "retrocrescent", "infracrescent" and "procrescent" are explained in Newell & Boyd 1970: 229.) Species of Atremapella n. gen. show a similar pattern. Nepionic stages show retrocrescent growth (note earliest preserved growth stages on umbo of right valve in Pl. 6, figs. 2 & 3), followed by infracrescent growth (Pl. 6, figs. 2 & 8) and then secondary retrocrescent growth at advanced stages (Pl. 6, fig. 11) (compare also Pl. 10, figs. 11 & 12 [nepionic stages], Pl. 10, fig. 4 [intermediate stages indicated by growth lines] & Pl. 10, fig. 7 [advanced stages]).

2) Shell Form - In both Pseudomonotis and Atremapella n. gen., the left valve is highly convex, almost hemispherical, in profile (compare anterior, posterior and dorsal views in Newell 1937, pls. 16-18, Logan 1967, pls. 2-3 & Pls. 6, 10). Pseudomonotis exhibits a flatter right valve than Atremapella n. gen., and a pedal embayment and pedal glide are lacking in the left valve (see p. 90-92 for description of these characters in Atremapella n. gen.), features presumably
reflecting the right-sided pleurothetic, fixed habit of that genus.

3) Ornamentation - Costae increase by intercalation in *Pseudomonotis* (Newell & Boyd 1970), by bifurcation in *Atremapella newelli* n. gen. & sp., and by bifurcation and intercalation in *A. misticia* n. gen. & sp. Divaricate ornament occurs on the right valve of *A. misticia* n. gen. & sp., but is unknown in *Pseudomonotis*. Ornament on the left valve of *Atremapella* n. gen. is especially similar to that in the Pennsylvanian pseudomonotid *P. equistriata* Beede (Newell & Boyd 1970, fig. 11E). Both show widely spaced squamae, usually with two or three orders of costae. An obvious trail (p. 87) is lacking in *Pseudomonotis*, and squamae on the right valve are never as prominently upturned.

4) Musculature - Interpretations of musculature for various pseudomonotids are given in Newell (1937) and Newell and Boyd (1970). It is evident from figures provided by these authors (*ibid.*, fig. 6; *op. cit.*, figs. 2 & 5) that nothing in the known musculature of the Pseudomonotidae precludes derivation of that family from an *Atremapella*-like ancestor. The only major difference is that the anterior adductor, which is reduced in *Atremapella* n. gen., is apparently lost in the Pseudomonotidae, a common condition in forms that adopt a sessile, attached epifaunal life mode (Yonge 1953a). The small scar terminating the pallial line in *Pseudomonotis* is conventionally interpreted as a pedal levator scar (=pedal
retractor scar), as in the living *Pinctada* Röding, rather than as a reduced anterior adductor scar (Newell 1937; Newell & Boyd 1970). It should be noted, however, that it would be difficult to distinguish a pedal levator scar that terminates the pallial line anteriorly from the scar of a vestigial anterior adductor which would lie in about the same anatomical position and which must have existed at some stage in the descent of the monomyarian Pseudomonotidae from a presumed anisomyarian ancestor, such as *Atremapella* n. gen. As shown for the pterineid *Glyptodesma buchanensis*, described below, the possibility that a scar in this position is in fact a reduced adductor scar can be eliminated only if continuity of the pallial line past the scar can be demonstrated, or if it can be shown that a muscle originating at the scar could not extend in an uninterrupted path to the opposing scar of the opposite valve (p. 201-202). I have not examined, first hand, specimens of *Pseudomonotis* with muscle scars preserved; however, judging from fig. 2 in Newell (1937), the extreme dorsal placement of the scar in *P. equistriata* seems to preclude a direct path to the opposite valve because of the hinge plate. If so, the scar must be the insertion of a pedal levator as Newell (1937) suggested. The same interpretation cannot be made confidently for *Pachypteria* (Newell & Boyd 1970, fig. 7C), in which the anterior terminal scar on the pallial line is more ventrally placed.

According to Newell (1937), a gill suspensor scar occurs below the posterior adductor in *P. equistriata* as in living
Pecten Müller, but pseudomonotids figured subsequently by Newell and Boyd (1970) did not show this feature and seemingly are inadequately preserved or actually lacked it. Atremapella n. gen. lacks any clear evidence of this scar. It may be that silicification is too coarse to preserve so subtle an impression. Some specimens show a slight widening of the pallial line near the posterior adductor, but it is not known if this is associated with the presence of a gill suspensor.

In Atremapella n. gen., a small circular muscle pit occurs roughly midway between the posterior adductor scar and the umbonal cavity (Pl. 7, figs. 3 & 4). By analogy with oysters, Newell and Boyd (1970) interpreted a similarly positioned muscle scar in pseudomonotids as the insertion of the Quenstedt muscle. Newell (1937) identified a muscle scar at this position in aviculopectinids as the superior gill suspensory scar by analogy with Recent pectinids. On the basis of Newell's (1937: 24) description of the superior gill suspensory muscle in a living pectinid, and Stenzel's (in Moore 1971: N965) description of the Quenstedt muscle in modern oysters, it appears that these muscles are probably homologous: both lie in an anatomically similar position, and both attach to the dorsal end of the gills. The Quenstedt muscles of oysters are thought to be homologous with anterior pedal muscles of dimyarian bivalves, which have become modified in oysters for a different function owing to the loss of the foot (Stenzel, in Moore 1971: N966, N1013). It is difficult, however, to visualize how anterior pedal muscles
could have become attached to the dorsal end of the gills following loss of the foot, as Stenzel's interpretation implies. Stenzel's hypothesis could, in principle, be tested by careful observation of the atrophy of the foot and pedal muscles in larval oysters to see if anterior or other pedal muscles remain and attach to the gills, but Stenzel (in Moore 1971) provides no direct evidence of this, nor does he cite embryological research in its support.

Palaeontological data at present appear to mitigate against Stenzel's view. Newell (1960) and Newell and Boyd (1970) have presented substantial morphologic, stratigraphic and palaeoecological evidence in support of the hypothesis suggested by Termier and Termier (1949) that oysters were derived from some member of the Pseudomonotidae. The Pseudomonotidae show a small muscle scar in the position of the Quenstedt muscle, but also have a full complement of anterior and other pedal scars (Newell 1937; Newell & Boyd 1970) that are far removed from the muscle scar inferred to be the Quenstedt. It is impossible, then, that any of these pedal scars could themselves be homologous with the Quenstedt muscle scar. Various Recent forms, such as Anomia Linné, the Solenidae and some Pectinidae, have a gill suspensor (=retractor) as well as anterior pedal muscle scars. I am not aware of any evidence that the gill suspensor in these forms is homologous with anterior or other pedal muscles. Consequently, it seems that the Quenstedt muscles of oysters are probably not homologous with anterior or other pedal muscles.
5) **Posteroventral mantle fusion** - Many species of both the Pseudomonotidae and the Gryphaeidae exhibit a posteroventral embayment (=branchitellum of Stenzel, in Moore 1971: N1019) of the shell margin, and a corresponding radial sulcus (left valve) and fold (right valve) on the shell surface (Newell & Boyd 1970, fig. 1). By analogy with Recent oysters, these features are thought to mark a point of mantle fusion and retraction at the posterior extremity of the gills, and are taken as evidence of close phylogenetic relationship between these families (Newell & Boyd 1970). In gryphaeid oysters, the posterior radial fold and sulcus offset a small ear-like lobe (=posterior flange), which is the site of the exhalent current (Stenzel, in Moore 1971: N1019 & fig. J74, 2a-b; Stenzel used the term "posterior flange" for the posterior lobe of the left valve only, but in the present work this term is also used for the corresponding posterior lobe of the right valve). Posteroventral mantle fusion in oysters facilitates efficient separation of inhalent and exhalent water currents and aids elimination of pseudofeces (Newell & Boyd 1970; Stenzel, in Moore 1971). The presence of a branchitellum, fold and sulcus at anatomically comparable positions in *Atremapella* n. gen. (see Pl. 8, figs. 12-14) invite an equivalent functional interpretation. Posteroventral mantle fusion, with its characteristic influence on shell morphology, has not been observed or inferred in any pteriomorphs other than *Atremapella* n. gen., the Pseudomonotidae and the Ostreina.
In spite of numerous similarities and apparent phylogenetic propinquity, *Pseudomonotis* and *Atremapella* n. gen. exhibit certain notable differences that include: 1) a well developed dentition is present in *Atremapella* n. gen., but is lacking completely in *Pseudomonotis*; 2) the ligament is duplivincular in *Atremapella* n. gen., but is marked by an obliquely triangular, shallowly depressed central resilifer in *Pseudomonotis*; 3) the well developed byssal notch characteristic of *Pseudomonotis* is not present at any stage of growth of *Atremapella* n. gen.; 4) the anterior adductor muscle, apparently lacking in *Pseudomonotis*, is present in *Atremapella* n. gen., though reduced; 5) the pedal embayment, pedal glide and conspicuous trail (p. 87) of *Atremapella* n. gen. are unknown in *Pseudomonotis*; 6) *Pseudomonotis* was pleurothetic on the right valve, whereas *Atremapella* n. gen. was pleurothetic on the left valve.

These differences in no way negate the proposed hypothesis that the Pseudomonototidae were derived from an *Atremapella*-like ancestor; in fact, all of the differences listed can be directly or indirectly accounted for by a single phenomenon – paedomorphosis. Looking first at the dentition, one sees in Pl. 8, figs. 4 and 9 that the earliest known growth stages of *Atremapella* n. gen. bear only a few teeth in each valve. The hinge plate of the early dissoconch is unknown, but given the tendency in known parts of the ontogeny for fewer and less prominent teeth to be present at progressively younger growth stages, the earliest post-larval stages may well have been edentulous. Whether edentulous, or
with a few weak teeth, such a hinge plate, if retained into adult stages, would require little modification to produce a pseudomonotid condition.

The ligament of the early dissoconch of Atremapella n. gen. is likewise unknown. However, the ontogeny of certain arcaceans (the only living pteriomorphs with a duplivincular ligament) has been well documented (Bernard 1896), and shows that the ligament of the prodissoconch and early dissoconch stages is confined to a small triangular fossette (ibid., in fide Thomas 1975, text-fig. 8). Assuming similar ontogenetic development of the ligament in Atremapella n. gen., neotenous retention of the pit-like resilifer into adult stages might explain the origin of the pit-like resilifer of the Pseudomonotidae. Pteriomorphs with this type of ligament insertion have evolved independently from duplivincular, ligament-bearing ancestors several times (e.g., Pteriidae from Pterineidae [Newell 1954]; Aviculopectinidae from Pterinopectinidae [Dickens 1963]; Limopsidae from duplivincular ligament-bearing arcoids [Thomas 1978]).

Similarly, adult byssus retention, with its characteristic influence on shell morphology (i.e., development of a byssal notch and/or byssal sinus), is a recurrent theme in bivalve evolution (Yonge 1962; Stanley 1972). There is no evidence of a byssal notch or byssal sinus at any stage of growth in Atremapella n. gen.; however, as in most living bivalves, the early post-larval stage was probably equipped with a byssus for initial attachment to the...
substrate after spatfall. The retention of the byssus into adult stages would account for the development of the byssal notch in *Pseudomonotis*. Indirect consequences of the retention of the byssus include: 1) the acquisition of a sessile, epifaunal, right-sided pleurothetic habit (see p. 119-124 for more detailed discussion of the evolution of this habit from left-sided pleurothetic ancestors); 2) the development of monomyarianism (a common result of byssal fixation and one acquired independently in several bivalve lineages [Yonge 1962]); 3) the loss of the pedal glide, pedal embayment, trail and frills (i.e., strongly upturned squamae on the right valve) (the first two structures would be functionally useless, and the second two virtually impossible to secrete, in the context of a right-sided pleurothetic habit, as later discussed]).

Even though the Pseudomonotidae seem derivable from an *Atremapella*-like ancestor, the fact remains that the former exhibit significant overall similarity with the Aviculopectinidae, as Newell (1937) noted, and the possibility of their mutual relationship must be examined. In a purely phenetic sense, *Aviculopecten* is more like *Pseudomonotis* than is *Atremapella* n. gen., as indicated in Table 3. Several major features of *Pseudomonotis*, including the central resilifer, byssal notch and right-sided pleurothetic habit, are clearly developed in *Aviculopecten* but are lacking in *Atremapella* n. gen. On the other hand, there is no development in *Aviculopecten*, or other aviculopectinids, of posteroventral mantle fusion, a highly
Table 3. Presence (+) or absence (-) of characters in Atremapella n. gen., Pseudomonotis Beyrich, Aviculopecten M'Coy and Pinctada Röding: summary.
<table>
<thead>
<tr>
<th>Character</th>
<th>Atrempella</th>
<th>Pseudomonotis</th>
<th>Aviculopecten</th>
<th>Pinctada</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allivincular ligament with central resilifer</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Right-sided pleurothetic habit</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Epifaunal</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Inner ostracum crossed-lamellar muscle</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Anterior adductor muscle</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pedal glide</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Pedal embayment</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Well developed trail dentition</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Posteroventral mantle fusion</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Highly convex left valve</td>
<td>+</td>
<td>+</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

* Some species of Pseudomonotis also undergo a procrecent stage (Newell 1937).
convex left valve, and the noted changes in principal growth gradients during ontogeny that are characteristic of *Pseudomonotis* and *Atremapella* n. gen. It seems, then, that conclusions about the relative degrees of relationship between *Aviculopecten*, *Pseudomonotis* and *Atremapella* n. gen. (and their respective families) rest largely on the weighting of these various characters.

In an analysis of proteid salamanders, Hecht and Edwards (1976) encountered a similar problem. The genera *Necturus* and *Proteus* had been regarded by many workers as closely related on the basis of numerous shared derived characters; however, nine of these are attributable to a single morphological phenomenon - paedomorphosis (Hecht & Edwards 1976; Gould 1977). Hecht and Edwards (1977: 8) argued that contrary to the views of previous workers, these were not nine independent characters, but in a sense were only a single character, the state of paedogenesis. However, Gould (1977) considers paedogenesis to be a process (rather than a character) that results in paedomorphosis; nevertheless, Hecht and Edwards' point is well taken, that in phylogenetic inference, characters attributable to a single growth process are not derived independently, and consequently should be given relatively less weight than more independently derived characters.

Applying similar logic here, those characters common to *Pseudomonotis* and *Aviculopecten* and lacking in *Atremapella* n. gen. are directly or indirectly attributable to
paedomorphosis, and consequently relatively little weight should be given them. Paedomorphosis is a recurrent theme among the Bivalvia (Stanley 1972), and it is not improbable that most similarities between *Aviculopecten* and *Pseudomonotis* arose convergently due to paedomorphic derivation from separate ancestors.

To emphasize this possibility, the Recent pteriid *Pinctada* has been included in Table 3, and it is of interest that except for shell microstructure, all features listed in common between *Pseudomonotis* and *Aviculopecten* also occur in that genus. The Pteriidae, however, are phylogenetically remote from *Pseudomonotis* and *Aviculopecten*, and probably arose from duplivincular ligament-bearing pterineid ancestors (Newell 1937, fig. 13, and 1954, fig. 1). Similarities of *Pinctada* with *Aviculopecten* and *Pseudomonotis*, especially in regard to ligament structure, are best explained as paedomorphic features that arose convergently.

There is no compelling evidence that these same similarities between *Pseudomonotis* and *Aviculopecten* are not also due to convergence. Features unique (i.e., synapomorph) to the Aviculopectinidae and the Pseudomonotidae among the Pteriomorpha have not been described.

By contrast, the development of posteroventral mantle fusion and the highly convex left shell of *Pseudomonotis* and *Atremapella* n. gen., as well as the noted changes in principal growth gradients through ontogeny, are not
explicable as paedomorphic features inherited from separate ancestors. Furthermore, as earlier stated, posteroventral mantle fusion is restricted among the Pteriomorpha to *Atremapella* n. gen., the Pseudomonotidae, and the probable derivatives of the Pseudomonotidae, the oysters. Consequently, in the present analysis, greater weight is placed on these characters than on those common to *Aviculopecten* and *Pseudomonotis*, with the result that the Pseudomonotidae are considered to be more closely related to the Rhombopteriidae than to the Aviculopectinidae. The Aviculopectinidae probably arose paedomorphically from pterinopectinid-like ancestors, which in turn may have originated from the Rhombopteriidae, perhaps by way of the Leiopectinidae, in the Late Ordovician or Early Silurian (see earlier discussion of the origin of the Pectinacea).

**Life mode of the Rhombopteriidae** - Given the apparent phylogenetic significance of the Rhombopteriidae, it is important to interpret their life mode correctly if the adaptive changes involved in the origin of their probable descendents, the Pterineidae, Pectinacea and Pseudomonotidae, are to be understood. At present, morphological, autecological, synecological and geological evidence pertinent to this question is more complete for *Atremapella* n. gen. than for other rhombopteriid genera; consequently, this genus will be considered first and in greater detail in the ensuing functional analysis. Then, with *Atremapella* n. gen. serving as a model, other rhombopteriids will be
considered, in the attempt to understand the adaptive history of the family as a whole.

Atremapella n. gen. By analogy with Recent inequivalved pteriomorphs, the inequivalved shell of Atremapella n. gen. suggests a pleurothetic habit. However, the possibility of a vertical orientation, like that of Mytilus Linne or Modiolus Lamarck must be considered, as Nicol (1958) has shown that many vertically living forms, such as Corbula Bruguière and Arca Linne are inequivalved. Furthermore, Stanley (1972) has interpreted Rhombopteria as a vertically oriented, endobyssate form like Modiolus. A vertical orientation for Atremapella n. gen. is here considered highly improbable for several reasons: 1) Atremapella n. gen. is more strongly inequivalved than any of the examples of vertically-living, inequivalved taxa cited by Nicol (1958), and, in addition, these examples pertain primarily to valve discordance, rather than to significant differences in valve convexity; 2) the orientation of articulated specimens of Atremapella n. gen. on bedding planes indicates a pleurothetic life mode (discussed below); 3) special morphological modifications required for extrusion of the foot in a pleurothetic habit (discussed below), would make little sense in a vertical orientation.

Given the likelihood of a pleurothetic habit for Atremapella n. gen., several questions arise, including: 1) Was Atremapella n. gen. oriented with the convex left valve undermost, or with the flatter, right valve undermost? 2) Was
Atremapella n. gen. epifaunal, semi-infaunal or infaunal? 3) Was Atremapella n. gen. byssate? These questions are addressed seriatim in the three sections (headed by Roman numerals) that follow.

I) Orientation of the shell. The near ubiquity of a right-sided pleurothetetic habit among the Pterineidae, Pectinacea and Pseudomonotidae, groups inferred to have been derived from rhombopteriid ancestors (see discussion above), invites a similar interpretation for the life orientation of Atremapella n. gen., and the Rhombopteriidae as a whole. If rhombopteriids were oriented in this way, derivation of these groups would have required little or no modification of orientation. On the other hand, if rhombopteriids were oriented with the left valve undermost, derivation of the aforementioned groups would have required a fundamental change in orientation, involving up to a 180 degree rotation of the shell relative to the substrate. Consequently, if there were no other evidence bearing on this question, one might be inclined, for the sake of parsimony, to orient rhombopteriids with the flatter right valve undermost. Surprisingly enough, evidence from several independent sources strongly suggests that Atremapella n. gen. (and by inference, other rhombopteriids) was in fact oriented with the convex left valve undermost, in a manner analogous to productid brachiopods (Text-figs. 4 & 13D). Sources of evidence relevant to this interpretation are considered separately below:
A) Morphological evidence. The cross-sectional profile of the shell of *Atremapella* n. gen. is strikingly similar to that of various productid and related brachiopods (Text-figs. 12F & 13D; Coleman 1957, fig. 3, 1 & 2; Rudwick 1970, fig. 25), and, consequently, some of the terminology normally used for these brachiopods has been applied to analogous features in *Atremapella* n. gen. discussed below. The right valve is geniculate ventrally. On the left valve, a ridge (=submarginal ridge, Pl. 7, fig. 2; Pl. 10, fig. 5) is developed internally a short way in from the valve margin. When the valves articulated, the distal surface of this ridge received the geniculation of the right valve. Those parts of the shell distal to the geniculation and internal ridge of the right and left valves, respectively, were closely appressed and parallel, forming the slit-like margin (or "trail"), as in productids. The frills of the right valve, and the distal ends of the squamae on the left valve, represent former positions of the trail at earlier growth stages (p. 116).

Shell profile alone does not necessarily imply a productid-like orientation for *Atremapella* n. gen. The Pseudomonotidae, for example, are basically similar to productid brachiopods in cross-sectional shape (e.g., *Pseudomonotis speluncaria* [Schlotheim], Logan 1967, pl. 2, figs. 1c, 6c & 9c), but undoubtedly lived with the flattened right valve undermost (Newell & Boyd 1970). However, the presence of a well developed trail is more powerful evidence for a left-sided pleurothetic habit. I am unaware of any
inequivalved bivalve that is oriented with the flatter valve undermost and in which a trail comparable to that in *Atremapella* n. gen. is produced. By contrast, certain inequivalved bivalves, such as the fossil oyster *Exogyra* Say, that lived with the convex left valve undermost and the growing edge of the shell directed away from the substrate (LaBarbera 1981), develop *Atremapella*-like features, including a slit-like commissure and vertical geniculation and erect frills (some species) on the right valve (Pl. 3, fig. 7).

The trail of some rhombopteriids was enormous (Pl. 3, figs. 5 & 6). A right valve (NMV PL1703) of *Praniellia anfractaviara* (Talent & Philip) (=Pterinea concentrilamellata) that I examined has a trail that stands 7.5 mm above the shell surface, a distance more than three-quarters of the total shell height (height=9.0 mm). It seems impossible that a trail of this magnitude could have developed if the growing edge of the shell was appressed against the substrate in a right-sided pleurothetic habit. Indeed, in many right-sided pleurothetic bivalves, the propinquity of the substrate apparently precludes the development of pronounced ornament on the right valve, whereas the left valve can be ornate (e.g., *Pseudomonotis*, Newell & Boyd 1970, figs. 11-16). The development of pronounced erect frills on the right valve of *Atremapella* n. gen. does not suggest inhibition by the substrate. Finally, even if a downwardly directed trail could be secreted, it is difficult to imagine how the trail would function in such an
orientation. There are no functional analogues among the Bivalvia (or Brachiopoda) with a trail oriented in this way, on which a functional interpretation could be based. By contrast, if *Atremapella* n. gen. was oriented on the left valve, a function of the trail analogous to that in *Exogyra* and productid brachiopods seems quite plausible.

Additional evidence for a left-sided pleurothetetic habit in *Atremapella* n. gen. comes from consideration of the functional complex of the foot and shell. The anterior lobe of rhombopteriids is no more reduced than in many cyrtodontids, such as *Cyrtodonta grandis* and *Cyrtodonta scofieldi* (Pojeta 1971, pl. 6, figs. 21-23; pl. 7, fig. 6), and, as inferred for these forms (ibid.: p. 37), it is probable that a fully functional foot was present in rhombopteriids, as well. It is apparent, however, that unlike the vertical posture of cyrtodontids, the left-sided pleurothetetic habit hypothesized for *Atremapella* n. gen., poses special problems for extrusion of the foot. Foremost of these is that the foot must bend sharply over the margin of the left valve to probe the substrate if the shell margin is at or near to the substrate surface. This is facilitated by two unusual modifications of the anterodorsal margin of the shell:

a) The pedal embayment - Left valves viewed anteriorly reveal that the trail is markedly reduced at the anterodorsal segment of the valve margin and as a result, a broad embayment (=pedal embayment) is developed approximately
normal to the commissural plane (Pl. 6, fig. 4; Pl. 7, fig. 6). This segment of the shell edge in the right valve shows corresponding development of a broad, shallow lobe, and the trail there is much reduced and not as steeply inclined to the valve surface as at the ventral edge of the valve (Pl. 6, fig. 13). Consequently, as evident in articulated specimens, the form of the commissure along the pedal embayment is not substantially different from that in typical burrowing bivalves.

Development of the pedal embayment of *Atremapella* n. gen. was essential for two reasons. Firstly, if the trail of the left valve continued unmodified from the ventral margin to the anterodorsal corner of the shell, an enormous gape would be required to produce an aperture anteriorly of sufficient size for extrusion of the foot. Reduction of the trail and concomitant development of the pedal embayment would allow extrusion of the foot at much lower angles of gape. In fact, judging from the height of the trail in adult shells, a sufficient aperture for the foot could probably be achieved without the geniculation at the ventral margin of the right valve clearing the edge of the trail of the left valve. Secondly, if no pedal embayment was present, the foot would have first to extend upward against the inner surface of the trail of the left valve, and then bend sharply over the lip of the trail to probe the substrate. This arrangement is clearly unworkable.
b) The pedal glide - Well preserved left valves reveal that the valve edge is strongly recurved where it forms the margin of the pedal embayment (Pl. 7, fig. 1; Pl. 10, figs. 6 & 10), but not elsewhere on the perimeter of the valve. It is likely that this provided a gliding surface over which the foot slid during downward probing motions, thereby avoiding the abrupt bending of the foot required by an unmodified valve edge. The term "pedal glide" has been chosen for the recurved segment of the valve edge. A few specimens show a series of pedal glides (or remnants of them) that mark former positions of the pedal embayment during ontogeny (Pl. 7, fig. 1). Pedal glides are thin and, consequently, are broken off in most specimens. On the right valve, the shell margin adjacent to the pedal embayment is moderately upturned and forms a small trail (this forming a series of small frills during ontogeny [Pl. 6, fig. 13; Pl. 10, fig. 10]), but it is not nearly as strongly recurved and an equivalent of a pedal glide is not formed. The resulting asymmetry of the anterodorsal shell margin (Pl. 10, fig. 10) is wholly consistent with a left-sided pleurothetic habit, but is wholly unexpected for a right-sided pleurothetic habit. In fact, the precise opposite would be predicted if Atremapella n. gen. lay on the right valve - that is, a pedal glide would be expected in the right valve but not the left valve. Neither is the pattern in Atremapella n. gen. anticipated for a vertical orientation. In such an orientation, pedal glides would presumably be lacking in both valves or, if present, would be developed symmetrically in both valves, as are the
moderately reflected margins forming the pedal/byssal gape in the limid genus *Ctenoides* Mörch (Cox & Hertlein, in Moore 1969, fig. C105, 5c).

Modification of the shell margin in a way broadly analogous to that in *Atremapella* n. gen. has been discussed by Stanley (1970: 79-80) for various pleurothethic species of the Tellinidae. The posterior end of the shell in these species is deflected to allow the inhalent siphon to extend past the shell edge without becoming sharply bent.

B) *Evidence from articulated specimens.* Articulated specimens of both *Atremapella misticia* n. gen. & sp. and *A. newelli* n. gen. & sp. are relatively rare. A total of 16 specimens of *A. misticia* n. gen. & sp. were encountered, exposed on bedding surfaces in the field, 11 at Locality R1 (horizon b) and five at Locality R2. Using a protractor, it was possible to determine the approximate inclination of the commissural plane relative to the bedding plane. (Cox [in Moore 1969: N103] defined the commissure as the "Line of junction of 2 valves"; this junction normally approximates a plane in bivalves, but in *Atremapella* n. gen., it is complicated by the development of the trail and pedal embayment. For the present discussion, the "commissural plane" of *Atremapella* n. gen. refers to the plane defined by the hinge axis and the junction ventrally of the submarginal ridge of the left valve and the geniculation of the right valve.) The position of the umbones and the valves relative to the bedding plane was recorded for each specimen. Of these
16 specimens, seven were oriented with the left valve undermost and the commissural plane roughly parallel with bedding (i.e., commissural plane not inclined to the bedding plane by more than 10 degrees). Two specimens were oriented with the right valve undermost and the commissural plane roughly parallel with bedding. The remaining seven specimens occurred in a variety of orientations, with the commissural plane inclined more than 10 degrees to bedding (for five of these, the commissural plane was inclined 30 or more degrees). In addition, oriented limestone blocks yielded two articulated specimens during etching (Pl. 9, figs. 1-3). Both specimens are oriented with the commissural plane inclined about 30 degrees relative to bedding planes, with the left valve undermost and the ventral edge of the shell raised above the level of the umbones. One of these specimens (Pl. 9, figs. 2 & 3) is intersected by a sheet of silica that represents the silicified infilling of a small, nearly vertical fracture through the rock matrix. Consequently, this specimen and several other fossils nearby were still preserved in their original attitudes relative to the bedding by the intersecting sheet of silica after the encompassing limestone was dissolved away.

Examination of collections made by other workers yielded several articulated specimens of *Atremapella* n. gen. For a few of these, it was possible to infer the approximate orientation of the shell at burial, using preserved geopetal structures. Three specimens were analyzed in this way, one specimen (CPC F24904) of *A. misticia* n. gen. & sp., from the
Receptaculites Limestone at Locality R7, and two specimens (CPC F24996-7) of *A. newelli* n. gen. & sp. from the Garra Formation. The specimen from the Receptaculites Limestone is shown in Pl. 9, fig. 4. The left valve of this specimen is mostly broken away, thereby revealing the contents of the shell. A layer of cryptocrystalline, partly silicified black material (labelled "X") occurs at the bottom of the left valve and probably represents the accumulation of mud and organic material that only partly filled the shell after burial. The attitude of the upper surface of this layer indicates that the shell was oriented with the commissural plane approximately parallel with bedding at the time of burial. The rest of the shell is filled with coarsely crystalline silica (labelled "Y") that apparently represents secondarily silicified sparry calcite that filled the shell cavity during diagenesis. Geopetal structures preserved in the two specimens (not figured) from the Garra Formation indicate that one of the specimens (CPC F24996) was oriented with the left valve undermost and the commissural plane approximately parallel with bedding, while the other specimen (CPC F24997) was oriented in the same way, but with the right valve undermost.

Text-fig. 10A shows the 21 specimens discussed above grouped into three classes. Class I includes those specimens oriented at burial with the left valve undermost and the commissural plane approximately parallel with bedding (i.e., not inclined to bedding more than 10 degrees). Class III is composed of specimens oriented in the same way, but with the
Text-fig. 10. A) Histogram showing numbers of articulated specimens of *Atremapella* n. gen. in collections or observed in field and oriented with: I) left valve undermost and commissural plane not inclined more than 10 degrees relative to bedding planes; II) commissural plane inclined more than 10 degrees relative to bedding planes; and, III) right valves undermost and commissural plane not inclined more than 10 degrees relative to bedding planes.

B) Histogram showing numbers of isolated left valves of *Atremapella* n. gen. observed in field and oriented with: I) convex surface undermost and commissural plane not inclined more than 10 degrees relative to bedding planes; II) commissural plane inclined more than 10 degrees relative to bedding planes; and III) convex surface uppermost and commissural plane not inclined more than 10 degrees relative to bedding planes.
right valve undermost. Specimens in Class II are oriented in various attitudes, with the commissural plane inclined more than 10 degrees relative to bedding.

Current-deposited, disarticulated shells of bivalves and brachiopods are typically oriented with the convex surface of the valves upward, a position of maximum hydrodynamic stability (Shrock 1948). From the profile of the articulated shell of *Atremapella* n. gen., one would predict that the shell would be hydrodynamically unstable if oriented on the highly convex left valve on the substrate surface, and that it would tend to be overturned on to the flatter right valve by water movements, thus approximating the orientation of disarticulated shells. It is noteworthy, therefore, that more than 40% of the articulated specimens (Class I, Text-fig. 10A) were oriented at burial with the left valve undermost and the commissural plane approximately parallel with bedding, a hydrodynamically stable position if these specimens were mostly submerged in the substrate, as in the hypothesized life position (Text-figs. 4 & 13D), but hydrodynamically unstable if they were resting on the substrate surface. By contrast, only 14% of the specimens were oriented in what would have been a hydrodynamically stable position on the substrate surface, that is, with the commissure approximately parallel with bedding and the right valve undermost (Class III, Text-fig. 10A).

With orientation data available for so few articulated specimens, it could be argued that the seemingly large number
of specimens in Class I of Text-fig. 10A is the result of sampling error, and that additional observations would reveal that most articulated specimens occur on bedding planes with the right valve undermost. In an attempt to test this possibility, the orientations were recorded for 133 isolated left valves exposed on bedding surfaces. These data are summarized diagrammatically in Text-fig. 10B. The specimens were grouped into three classes, as in Text-fig. 10A: I) those with the external valve surface undermost on the bedding plane and the commissural plane approximately parallel with bedding (i.e., not inclined more than 10 degrees); III) those in this orientation, but with the external valve surface uppermost; and, II) those oriented with the commissural plane inclined more than 10 degrees.

One would predict from the shape of the left valve that, as for articulated specimens, the most stable hydrodynamic position on the substrate would be with the convex surface uppermost. And, as might be expected, the majority of isolated left valves occur in this position (i.e., Class III, Text-fig. 10B). Assuming then, that the real distribution of the total population of articulated valves is like that of isolated left valves, what is the probability that, in a sample of 21 specimens, nine would fall into Class I? Or, in other words, is the observed difference in the relative number of specimens in Class I of Text-fig. 11A & B statistically significant? If not, one could assume that the distribution of the articulated valves, like that of the isolated valves, results primarily from orientation by
currents, and need not tell us anything about the original life position.

In order to test this possibility, the two samples were reduced to binomial samples. Two classes were recognized in each sample. These are: 1) specimens oriented with the convex surface undermost and the commissural plane inclined no more than 10 degrees to bedding (Class I in Text-fig. 10A & B); and, 2) specimens not in this orientation (Classes II & III in Text-fig. 10A & B). Assuming the null hypothesis that there is no significant difference between the samples, a zI test (Langley 1968) was used to calculate the probability that the sample of articulated shells did, in fact, come from a parent distribution like that of the isolated left valves. Calculating for "z", it was found that the probability that the null hypothesis is true is only slightly greater than 1%. The null hypothesis can therefore be rejected, and another explanation must be sought for the distribution of the articulated shells.

It seems that a satisfactory explanation is possible only if one assumes that during life the shell was partially buried in the substrate with the left valve undermost and the commissural plane approximately parallel with or perhaps moderately inclined to (see below), the substrate surface (Text-figs. 4 & 13D). From this position, most specimens would presumably be exhumed, spring open, and become disarticulated upon death (the vast majority of specimens of Atremapella n. gen. from the Receptaculites Limestone and
Garra Formation are, in fact, isolated valves). A few specimens would probably be exhumed and overturned onto the right valves after death, but would remain articulated (hence the relatively low number of specimens in Class III in Text-fig. 10A). Specimens comprising Class I in Text-fig. 10A presumably represent individuals that were not exhumed after death and that remained articulated. Specimens at unusual angles (i.e., Class II, Text-fig. 10A) may have been reoriented from their position at burial by bioturbation (perhaps by large shallow burrowers, such as Marginella comptorae n. sp. and Sanguinolites phlyctaenatus n. sp., both of which occur in beds with A. misticia n. gen. & sp.). However, the relative number of specimens occurring in Class II of Text-fig. 10A is anomalously high and would not be expected in a sample drawn from a parent distribution like that of Text-fig. 10B. There is no satisfactory explanation for this distribution at present. As later discussed (p. 101-102), the maximum range of feeding orientations for Atremapella n. gen. probably exceeded the range characterizing Class I of Text-fig. 10A and would include two of the specimens (i.e., those shown in Pl. 9, figs. 1-3) assigned to Class II of Text-fig. 10A. Even accounting for these two specimens, the remaining seven specimens represent 33% of the total sample, a disproportionally large fraction of the sample compared to 15% represented by Class II of Text-fig. 10B.

Two articulated specimens of A. newelli n. gen. & sp., not mentioned above, are worth noting here. These specimens
are of interest in that they represent the only available articulated specimens of *Atremapella* n. gen. that show significant encrustation of the shell exterior by epibionts. The distribution of the epibionts is consistent with the life orientation already hypothesized for *Atremapella* n. gen. In one of these specimens (CPC F24991) the valves are somewhat displaced (Pl. 10, fig. 10). The right valve shows an encrusting auloporid coral externally, and the floor of the left valve is filled with shelly debris presumably washed in after death. Epibionts are absent on the left valve. These two pieces of evidence suggest that the left valve was undermost during life and at the time of burial, although the attitude of the shell at burial cannot be determined as precisely as for the specimens discussed earlier.

The other specimen (CPC F24985) is more difficult to interpret. A large heliolitid coral has encrusted most of the anteroventral surface of the right valve (Pl. 9, fig. 6). On the left valve, encrusting auloporid corals are present anterodorsally, umbonally, and on much of the posterior flank of the shell body (Pl. 9, fig. 5). The shell cavity, as viewed through the broken ventral edge of the shell, is nearly empty, although there appears to be some shell debris that has been silicified into place on the floor of the right valve. There are at least two explanations for the pattern of epibionts on the exterior of the shell. Whatever the history of this specimen, it seems evident that the right valve must have been exposed above the substrate surface during the life of the heliolitid coral. Assuming that the left valve was
undermost during life, it is conceivable that the auloporid polyps were alive at the exposed valve edge, and later were smothered by the substrate as the shell grew larger. Expansion of the auloporid colony could presumably have kept pace with the growing edge of the valve. This explanation is rejected, however, because some branches of the auloporid colony show growth directions towards the umbo, the opposite direction of the growing valve margin (Pl. 9, fig. 7). It is more likely that the auloporid coral encrusted the left valve while it was uppermost and exposed above the substrate. Consequently, it appears that CPC F24985 was overturned during its predepositional history - the right valve being uppermost when the heliolitid grew, and the left valve uppermost when the auloporids grew. An hypothesized series of events that can account for all of the observations made on CPC F24985 is as follows: 1) the specimen lived in its life position as shown in Text-fig. 13D, with the heliolitid coral having encrusted the exposed right valve; 2) the bivalve died, was scoured out from its semi-infaunal position, and was overturned by water currents; 3) the shell gaped and detritus was washed in; 4) the valves eventually collapsed shut as the ligament rotted; 5) the auloporid coral colonized the newly exposed surface of the left valve; 6) ultimately, the specimen was buried, and the debris that washed into the shell was cemented on to the floor of the right valve during silicification.

The distribution of epibionts in CPC F24985 could be explained in terms of a right-sided pleurothetic habit, but
this would require that the auloporids colonize the left valve first; then the shell would have been flipped over to allow the heliolitid to colonize the right valve, and then flipped back again for the shell debris to accumulate on the floor of the right valve. This scenario is considered less probable, firstly, because it requires that the dead shell maintain a hydrodynamically unstable position throughout the life of the heliolitid, and secondly, because it requires that the valves remain articulated when the shell was flipped back on to the right valve, even though by that time it is likely that the ligament would have disintegrated.

II) Relationship of the respiratory margin and the sediment/water interface. Text-figs. 4 & 13D show Atremapella n. gen. oriented in a semi-infaunal position in a manner analogous to that inferred for structurally similar productid brachiopods. The left valve is shown mostly submerged in the substrate, with the horizontally oriented hinge line at or slightly below the substrate surface and the trail projecting upward above the muddy bottom like a snorkel. This orientation meets the requirements of both stability and ventilation, and seems most consistent with the evidence from shell morphology, oriented specimens and epibionts discussed earlier. Although this was perhaps the common or preferred orientation for feeding, the animal could probably have survived within a range of orientations. For example, greater pitching of the shell with the umbones lowermost (as in Pl. 9, figs. 1-3) seems compatible with the shell morphology.
Probably a limited amount of roll could be tolerated as well.

The range of feeding orientations was probably restricted primarily by the need to maintain the respiratory margin above the sediment/water interface. By analogy with gryphaeid oysters and other bivalves, it is possible to estimate the maximum extent of the respiratory margin (Pl. 8, fig. 13). The inhalent area was probably concentrated primarily along the ventral margin, as in living pleurothetic pteriomorphs (Cox, in Moore 1969, fig. 35), and may have extended anteriorly as far as the ventral edge of the pedal embayment. It is unlikely that the inhalent area extended anterodorsally beyond this point, as the area of the shell margin associated with the extension of the foot in bivalves is not normally involved in respiration (ibid.). The exhalent area was probably confined to the flange on the posterior side of the branchitellum, as in gryphaeid oysters (Stenzel, in Moore 1971: N1019), The inferred maximum extent of the respiratory margin, then, extended from the ventral end of the pedal embayment to a point adjacent to the posteroventral edge of the posterior adductor scar (Pl. 8, fig. 13). As might be expected, the respiratory margin coincides with the maximum development of the trail. At points dorsal to either end of the respiratory margin, the trail is markedly diminished, as indicated in right valves by the less prominent development of frills in those areas (Pl. 6, figs. 12 & 13).
III) Stability and reorientation. Although the external form and life orientation of *Atremapella* n. gen. is close to that of *Exogyra* and productid brachiopods, *Atremapella* n. gen. differed importantly from these organisms in that mobility provided by the foot facilitated reorientation of the shell if disturbed. Consequently, *Atremapella* n. gen. lacks stabilizing features analogous to the spines of productids or the umbonal thickening of *Exogyra*. It is possible that *Atremapella* n. gen. employed a byssus for anchorage, but there is no clear evidence for this, and it seems unlikely for several reasons. Firstly, features typically associated with a byssus in Recent bivalves, especially a byssal notch and/or byssal sinus, have not been observed in *Atremapella* n. gen. at any stage of growth. It could be argued that the pedal embayment corresponds to a byssal sinus and facilitates extrusion of a byssus. However, if a byssus was present, it presumably would have been extruded through the pedal embayment horizontally or else downward over the pedal glide. If horizontally disposed, it is questionable whether the byssus would have had a significant anchoring effect under so thin a veneer of sediment. Furthermore, a byssus in this orientation would block downward probing motions of the foot, and would need have been severed each time the foot was used to adjust the shell. Additionally, the resolution of forces on such a byssus by the retractor muscles would act parallel to the substrate surface and hence at a mechanically inefficient angle to forces (whether predators or water movement)
operating to exhume the shell. If byssal threads were draped over the pedal glide and downward in the sediment, the pedal glide would have acted as a fulcrum when the pedal retractor contracted, and the posterior end of the shell would have been raised and exposed to exhuming agents - clearly an improbable arrangement.

**Other rhombopteriids.** Having integrated a variety of data pertinent to the interpretation of the life orientation of *Atremapella* n. gen., it is now possible to discuss the orientation of other rhombopteriids for which few data are available, using *Atremapella* n. gen., as a model.

**Prantliella.** This genus is morphologically very similar to *Atremapella* n. gen. and probably lived in the same way. As noted earlier, the trail in *P. anfractaviara* is enormous, as indicated by isolated right valves (Pl. 3, figs. 5 & 6). Right valves of the type species, *P. palliata*, are similarly constructed (J. Kříž 1982, pers. comm.). Both *P. anfractaviara* (Pl. 3, fig. 4) and *P. palliata* (Barrande 1881, pl. 220, figs. 4, 7, 12, 15, 26 & 29) exhibit a well developed pedal embayment. There is no indication of pedal glides in Barrande's illustrations of *P. palliata*, nor in specimens of *P. anfractaviara* at hand. However, these species are known only from non-silicified specimens collected from indurated rocks split by hammer, and it is unlikely that the matrix would split around such delicate structures. I suspect that pedal glides will be found to be present in *Prantliella*
when silicified specimens or well preserved external molds are discovered. Unlike Atremapella n. gen., there is no clear evidence of a posteroradial sulcus and fold, and it may be that palliobranchial fusion was lacking in the genus.

**Rhombopteria.** This genus is very poorly known and its life orientation is unclear. Stanley (1972), thinking that the shell was subequivalved, reconstructed Rhombopteria in a vertically endobyssate position, and cited as evidence the modioliform shape of *R. pseudomira*. As noted earlier, *R. pseudomira* is probably a species of Cypricardinia and can be excluded from the present discussion. The type species, *R. mira*, is not modioliform, and the shell is in fact markedly inequivalved, as shown by Růžička (1950). Consequently, a vertical posture for *R. mira* seems very unlikely. Both right and left valves of *R. mira* (right valves = *A. scala* as shown by Růžička [1950]) illustrated by Barrande (1881, pls. 226 & 227) show a broad emargination of the anterior margin that resembles a byssal sinus. Unfortunately, Barrande did not provide anterior views of *R. mira*, and the possibility that the anterior emargination is the expression of a pedal embayment cannot be ruled out. *R. mira* is smaller and less inflated than species of Prantliella and Atremapella n. gen., and judging from Barrande's figures, a posterior radial fold and sulcus are not developed. It cannot be determined from Barrande's illustrations whether a trail was present. Frills on the right valve do not appear to be markedly upturned, but these may have been broken off during collecting, as
invariably occurs with right valves of _P. anfractaviara_.
Without clear information concerning the presence or absence of a trail, pedal embayment and glides, the life mode of Rhombopteria cannot be determined, although I suspect, on the basis of overall similarity, that it will be shown to be like that of _Atremapella_ n. gen. and _Prantliella_.

_Coppinsia_ n. gen. This genus is less like _Atremapella_ n. gen. than are other rhombopteriids. As discussed earlier, the overall shell form is essentially cyrtodontid-like, except that the right valve is moderately less convex than the left valve. Also, the shell is more elongate dorsoventrally than in typical cyrtodontids. Unlike _Atremapella_ n. gen., _Coppinsia_ n. gen. lacks structural analogues among other bivalves (and among brachiopods); consequently, its life mode is difficult to determine.

In view of the broadly intermediate morphology and phylogenetic position of _Coppinsia_ n. gen. relative to _Atremapella_ n. gen. and the Cyrtodontidae, it may be that the life mode of _Coppinsia_ n. gen. was also broadly intermediate between those taxa. Cyrtodontids are quite diverse in shell form and probably lived in a considerable range of habitats (Pojeta 1971). All are equivalved, and most (including those most similar to _Coppinsia_ n. gen., such as _Cyrtodonta_ Billings), were probably shallow burrowers that were oriented in life in a manner similar to that of most burrowing arcoids, with the commissure vertical and the posterior margin at or slightly above the sediment/water interface.
Coppinsia n. gen. does not show development of the special modifications of Atremapella n. gen., including the strongly inequivalved shell, trail, pedal embayment and pedal glide, that enable a productid-like life mode, with the commissure oriented parallel with, or at a low angle to, the substrate. Consequently, an Atremapella-like habit for Coppinsia n. gen. seems unlikely. A byssal notch is not developed in Coppinsia n. gen. at any stage of growth. The anterior margin is normally straight or slightly convex in adult specimens (Pl. 4, figs. 1 & 9), but in some specimens, a broad, weak byssal sinus is developed (Pl. 4, fig. 6), indicating a byssate habit. The anterior adductor scar is relatively reduced, as is common in byssate bivalves (Yonge 1953a), but unlike such forms, the anterior lobe of the shell is not significantly reduced, suggesting the presence of a fully functional foot. The inferred extent of the respiratory margin shown in Pl. 4, fig. 6 is based on analogy with Atremapella n. gen., discussed above.

Although the shell outline of Coppinsia n. gen. is essentially cyrtodontid-like, moderate valve inequality suggests a departure from a vertical orientation. Coppinsia n. gen. probably lived semi-infaunally, with the hinge axis inclined to the substrate surface (approximately as shown in Text-fig. 11, or perhaps somewhat more strongly inclined), and with the respiratory margin exposed. The adaptive
significance of this departure from the vertical habit of presumed cyrtodontid ancestors is uncertain; however, it is evident that inclining the commissure has several effects on the relationship of the shell edge and the substrate. If these are described, then the adaptive significance of an inclined habit may become more clear.

The most profound effect of inclination is that a relatively greater proportion of the shell edge can be exposed at and above the sediment/water interface, without increasing the profile of the shell above the substrate (see Text-fig. 11). Text-fig. 11,1a shows a shell of the cyrtodontid Cyrtodonta grandis oriented in probable life position with the commissure vertical, and the posterior margin of the shell protruding above the substrate surface. In this position, the maximum height of the shell margin above the substrate ("a") coincides with the maximum height of the shell above the substrate ("z"). The length of the shell margin exposed above the substrate is given by the distance along the perimeter of the shell between points "x" and "y". The same individual is shown in Text-fig. 11,1b in posterior view. The angle between the commissure and the substrate is given by $\theta$ (in this case, 90 degrees). The inflation of the right valve is indicated by "b". It is clear that if $\theta$ remains at 90 degrees, distance "x-y" cannot be increased unless the shell is less deeply buried in the substrate, or in other words, unless "a" (and "z") are increased. Part 1c shows the same individual with an increased "a". The former position of "x" and "y" are
Text-fig. 11. Relationships of shell margin and shell profile relative to substrate surface in vertically oriented shells and shells inclined on left valve (see text): 1a) shell vertically oriented, oblique lateral view (shell outline based on that of *Cyrtodonta grandis* [Ulrich] as figured in Pojeta 1971, pl. 6, fig. 23); 1b) same individual, dorsal view; 1c) same individual, shell not so deeply buried as in 1a, oblique lateral view; 2a) same individual, commissure inclined relative to substrate, oblique lateral view; 2b) same individual, dorsal view; 3) same individual, commissure less steeply inclined than in 2b, dorsal view; 4) *Coppinsia*-like shell with right valve less inflated than left and commissure inclined relative to substrate.

Symbols: a - maximum height of shell margin above substrate; b - maximum inflation of right valve; x-y - length of shell margin exposed above substrate; z - maximum height of shell above substrate; 0 - angle defined by commissure and substrate surface.
indicated by "x'" and "y'". With this amount of increase in "a", the distance "x-y" has increased by "xy minus x'y'". An increase in "a", however, has the effect of increasing the profile of the shell above the substrate. This, in turn, has the possible negative effect of exposing greater proportions of the shell surface to turbulence, as well as making the shell more conspicuous and accessible to predators.

Text-fig. 11,2a & b shows that if "a" is held constant, the distance "x-y" can be increased by inclining the commissure, or in other words, by decreasing $\theta$. If, however, $\theta$ continues to decrease, the lateral flank of the right valve will become exposed and eventually will become the highest point above the substrate (Text-fig. 11,3). In this orientation, "z" > "a" and similar, possibly negative, effects to those outlined earlier are incurred, namely increased exposure of the shell surface and increased profile of the shell above the substrate. Furthermore, with decreasing $\theta$, the centre of gravity is raised relative to the substrate and the shell becomes potentially less stable. If the value of $\theta$ shown in Text-fig. 11,3 is held constant, two ways remain by which "z" can be reduced and the centre of gravity lowered, namely by decreasing "a" and decreasing "b" (Text-fig. 11,4). Decreasing "b", of course, results in an inequivalved shell, as in Coppinsia n. gen.

The effect, then, of an inclined habit and a decrease in the inflation of the uppermost valve is that the length of the shell margin exposed above the substrate is increased
without increasing the exposed profile of the shell: in fact, the value of "z" is less in this orientation than in the vertical orientations shown in Part 1. Exposure of the right valve can be minimized and the exposed length of the shell margin maximized with the development of a trail and a horizontal attitude, as in Atremapella n. gen.

The adaptive value of exposing a greater proportion of the shell margin at the sediment/water interface is probably involved with increasing the length of the inhalent margin. This would presumably facilitate more efficient ventilation. Obviously, however, many bivalves, such as Arca Linné, Limopsis Sassi, Pandora Bruguière, Mytilus and Modiolus, have a relatively narrow inhalent margin (Cox, in Moore 1969, figs. 35 & 65; Stanley 1972, fig. 3), and yet are undoubtedly efficient feeders and respirers. Atkins (in fide Owen 1978) found that the Pteriomorphia (except the Ostreidae and possibly the Pinnidae) differ fundamentally from other bivalves in that the latero-frontal ciliary tracts of the gills consist of a single row of cilia. By contrast, other bivalves show more complex latero-frontal tracts. To reflect these differences, Atkins placed the pteriomorphs (with exceptions as noted) within a group termed the Microciliobranchia, and other bivalves within the Macrociliobranchia. Owen (1976, 1978) provided a functional interpretation of these differing ciliary patterns and suggested (1978: 380, 383) that in the Microciliobranchia, the collection of particles by the gills for possible ingestion is dependent on the flow of water currents produced
by the frontal ciliated tracts and channelled by the principal filaments, rather than on direct filtration and transport of particles by cilia. Consequently, particles for ingestion are transported dorsally in suspension, rather than by direct manipulation by cilia. Owen (1978: 384) later showed that this type of particle transport was not ubiquitous among the Microciliobranchia, and that, in fact, three subgroups were recognizable: 1) in the first, represented by the Arcidae and Glycimeridae, water currents do not appear to be important in collecting and transporting particles; 2) in the second, represented by the Anomidae, Pectinidae and Limidae, the flow of water currents plays a major role; 3) in the third, consisting of the Pinnidae, water currents are important, but the latero-frontal tracts show some differences from the other two groups.

It is of interest that Subgroup 2- and Subgroup 3-type bivalves exhibit a relatively longer inhalent margin than Subgroup 1 and macrociliobranchiate bivalves (see Cox, in Moore 1969, figs. 35 & 65; Yonge 1953a, fig. 7; 1953b, fig. 9). Although these are apparently correlated, I cannot demonstrate a functional relationship between Subgroup 2- and 3-type feeding with an enlarged inhalent margin. This requires analysis of numerous Recent pteriomorphs, which is beyond the scope of the present work. If, however, such a functional relationship can be demonstrated, then the development of an inequivalved shell and inclined habit in primitive rhombopteriids such as Coppinsia n. gen., together with the concomitant increase in the length of the
Growth and function of the trail (in *Atremapella n. gen.*). The distribution of growth lines in *Atremapella n. gen.* suggests an unusual mode of growth. On the right valve, the underside of the frills reveals distinct growth lines that are closely spaced adjacent to the shell surface and more widely spaced distally (Pl. 6, figs. 12 & 13; Pl. 7, fig. 3 & Pl. 10, fig. 9). Externally, growth lines are usually obscure (more so in *A. misticia n. gen. & sp.* than in *A. newelli n. gen. & sp.*) and if present, are usually weak, often widely spaced, and show no correspondence to growth lines on the underside of the squamae (Pl. 6, figs. 2, 8 & 10; Pl. 10, figs. 4 & 7). The left valve shows a similar pattern. Externally, growth lines are weak and widely spaced, often lacking. Squamae are appressed against the shell surface in the left valve, and their undersurfaces are not visible except distally. Here growth lines are often visible on the trail of the last formed squamae and on the pedal glide (Pl. 10, fig. 5), and are arranged in the same pattern as on the trail and frills of the right valve. As noted earlier, frills on the right valve and the distal segment of squamae on the left valve represent former positions of the trail at earlier growth stages. Consequently, any explanation of the growth of the trail also applies to previously formed squamae. Therefore, attention will be focussed primarily on the trail as the key to understanding the growth of the shell.
generally (except the hinge).

The broken surfaces of frills in some right valves show vestiges of gross internal shell structure, and reveal that growth lines on the inner surface of the trail and frills represent the distal edges of laminations that are parallel with the external surface of the trail.

It is evident that at a given growth stage, the shell-secreting part of the mantle edge could not have extended distally beyond the most proximal growth line on inner surface of the trail. Hence, the most proximal growth line must represent the distal edge of the last formed lamination. It follows that the distal edge of the trail represents the distal extent of the first formed lamination.

Development of a pronounced trail is rare among the Bivalvia, and I have not encountered examples comparable to Atremapella n. gen. except among the oysters, particularly the Gryphaeidae. Some species of Exogyra, such as Exogyra costata Say, for example, are strikingly similar to Atremapella n. gen. in overall shell form and exhibit geniculation of the right valve, frills, and a well developed trail (Pl. 3, fig. 7). Growth of the trail is rather different in E. costata, as revealed by the distribution of growth lines. The internal surface of the trail (and frills) is smooth and lacks growth lines (Pl. 3, fig. 7), whereas externally, growth lines are distinct and closely spaced. As in Atremapella n. gen., the trail is composed of laminations that are parallel with the external surface of the trail, but
Unlike *Atremapella* n. gen., the distal edge of the trail is constructed from the last formed lamination rather than the first. The smooth inner surface of the trail indicates that the shell-secreting part of the mantle extended over this area.

Growth of the trail in productid brachiopods appears to have been more like that in *E. costata* than in *Atremapella* n. gen. Numerous illustrations of the trail in productids are provided by Muir-Wood and Cooper (1960). None show growth lines on the inner surface of the trail, and it is generally agreed that this area was covered by mantle tissue in life (Coleman 1957; Grant 1968).

In biconvex brachiopods and bivalves that lack a trail, the shell cavity expands with shell secretion at the margins (Carter 1967, fig. 6). However, it is clear that in forms with trails, simple addition of shell material at the margin of the trail results in extension of the trail and hence of the linear dimensions of the shell, but with little or no increase in the volume of the shell cavity (Text-fig. 12A-B). This indeed occurs in some brachiopods that develop a trail early in ontogeny, as Coleman (1957, fig. 3; and Text-fig. 12C, this paper) noted. Consequently, there is something of a biological paradox here: how is a bivalved organism to increase the volume of the shell cavity, and at the same time maintain the benefits of the slit-like commissure produced by the trail at the shell edge? Observations of productacean brachiopods and various bivalves, including *Atremapella* n.
Text-fig. 12. A-D) Longitudinal profile of various productid brachiopods (from Coleman 1957, figs. 3 & 5, with some modification): A-B) *Taeniothaerus*, showing that, A) addition of shell material to distal edge of trail results in, B) increased linear dimensions but little or no increase in shell volume; C) *Linoproductus*; D) "Median longitudinal profile of a trailed shell, showing successive growth stages following on, or near upon, maturity (1-5). By internal thickening of the geniculated region both trail and visceral cavity can be enlarged" (Coleman 1957: 20, fig. 5); E) hypothetical productid showing effect of development of trail early in ontogeny, with shell material added continuously to geniculation and trail of right valve; F) *Atremapella* n. gen.: cross-sectional profiles through successive growth stages (i-viii) showing corresponding sequence of trails (1-8); profile shown for stage viii based on camera lucida outline of ANU 36684.
gen. and gryphaeid oysters, reveal at least three different responses to this paradox.

Many productaceans simply forego development of a trail until a shell cavity of sufficient volume is attained (Text-fig. 12A-D). I have not encountered equivalent examples among the Bivalvia. Coleman (1957: 20) showed that even with the development of a trail, expansion of the shell cavity will occur if shell layers are secreted along the inner surface of the trail and geniculation of the upper (brachial) valve (Text-fig. 12D). It is evident, however, that if a trail developed early in ontogeny and was maintained in this way, the upper valve would be enormously thick at maturity (Text-fig. 12E). The shell would therefore be top heavy and unstable, unless equivalent shell thickening occurred in the lower valve. This appears to be the strategy adopted by many species of Gryphaea Lamarck. The upper (right) valve has become massively thickened (especially in the latter half of ontogeny) by the continual secretion of shell layers over the inner shell surface, including the trail and geniculation. This is compensated for by even more massive thickening of the lower (left) valve (Stenzel, in Moore 1969, fig. J73, 2a). In this way, various species of Gryphaea were able to maintain a slit-like commissure through much or all of ontogeny and at the same time increase the volume of the shell cavity, as well as maintain stability of the shell on the substrate.
Atremapella n. gen. shows a different strategy. Shell volume was increased by abandoning the trail at a given growth stage and secreting another trail more distally (Text-fig. 12F). Consequently, the series of frills on right valves of Atremapella n. gen. (and Exogyra) represents the succession of discarded trails through ontogeny. While it is possible that the frills functioned secondarily in the trapping of sediment on the exterior of the right valve for the enhancement of crypsis, it is doubtful that they had any primary function (except at their respective ontogenetic stages when they formed the trail). Instead, they represent the inevitable consequence of increasing the shell volume through ontogeny and, at the same time, maintaining a slit-like commissure without massively thickening the upper valve. Frills that occur on the brachial valve of various productacean brachiopods, such as Overtonia (Rudwick 1970, fig. 25) and Marginifera (Grant 1968, pl. 7, fig. 1d) can be explained in the same way. E. costata combines features of both A. misticia n. gen. & sp. and Gryphaea, showing excessive shell thickening (Stenzel, in Moore 1971, fig. 75), as well as the development of a series of frills on the right valve (Pl. 3, fig. 7).

Various functions have been hypothesized for the trail in productacean brachiopods, including: 1) the trail acts as a snorkel, allowing the shell to become almost completely buried, but with the commissure protruding above and directed away from the substrate (Muir-Wood & Cooper 1960; Grant 1966); 2) the trail forms a slit-like filter device,
excluding coarse particles, as well as isolating the shell cavity from the muddy environment (Coleman 1957; Grant 1968); 3) the trail inhibits the entrance of predators (Coleman 1957); 4) the trail functions in rhythmic feeding by maintaining a slit-like aperture during diduction, thereby causing water to be sucked into the mantle cavity (Rudwick 1970).

The last of the functions mentioned has been heavily criticized for the Productina by Grant (1972), and it clearly has no applicability to Atremapella n. gen. or gryphaeid oysters. Many of Grant's criticisms hold for these forms as well, especially those concerning the inefficient energy expenditure associated with flapping the upper valve (although muscle energy is expended only during adduction in bivalves). Furthermore, it is very improbable that the ligament could maintain the rapid and successive pulses of diduction required for this type of feeding. Functions (1) and (2) seem the most probable for Atremapella n. gen. and gryphaeids. Clearly, however, any filtering action of the trail in Atremapella n. gen. was purely passive, because as already shown, mantle tissue probably did not extend over the inner surface of the trail. By contrast, tubercules are present on the inner surface of the trail of some productids "...suggesting former presence of papillae or setae to strain large or potentially harmful particles out of the water" (Grant 1968: 12). The mantle edge of Exogyra was probably equipped with short tentacles, as in modern oysters (Stenzel, in Moore 1971). These were presumably positioned at
or near the distal end of the trail during feeding, where, among other things, they may have been involved in sensing, and perhaps inhibiting, the entrance of coarse and harmful particles. If comparable tentacles were present at the mantle edge in *Atremapella* n. gen., they probably would not have extended distally much beyond the proximal end of the trail.

Stenzel (in Moore 1971: N1025), in his discussion of the trail in various gryphaeids, emphasized its role as a deterrent to predators that either break away the shell margin or dart in through the open commissure to gain entry to the shell cavity. While this may have been a secondary function of the trail in *Atremapella* n. gen., it was probably not the primary function. If it were, one might expect the development of trails to be widespread among the Bivalvia, many Recent species of which undergo attack at the shell margin (Carter 1968). To my knowledge, the distribution of prominent upturned trails is, in fact, quite restricted among bivalves; they are best developed in forms that employed a productid-like life mode, including various gryphaeids and rhombopteriids. This in turn reflects a functional relationship between this kind of life mode and an upturned trail. As argued earlier, the trail in rhombopteriids, together with valve inequality and a shallowly inclined habit, allowed an increase in the length of the respiratory margin, and at the same time minimized the area and profile of the shell exposed above the substrate. This is not to say that shell and mantle edge were not attacked by predators. Indeed, many specimens of *Atremapella* n. gen. show pre-mortem
attrition of the shell edge, probably by predators (p. 152-153). However, it seems implausible that the development of the trail in this genus was fundamentally associated with this phenomenon.

Derivation of the right-sided pleurothetic habit in the Pterineidae, Pseudomonotidae and Pectinacea - The oldest and most primitive pectinaceans, including the Leiopectinidae, Pterinopectinidae and Aviculopectinidae, show adaptations for a pleurothetic (=shallowly inclined or flat-lying) epibyssate habit with the right valve undermost (Stanley 1972). This life mode was probably primitive for the Pterineidae and Pseudomonotidae, as well (p. 178, 187). Morphological evidence presented earlier indicates that these groups were derived from the Rhombopteriidae, which apparently lived a shallow, infaunal existence and were pleurothetic on the left valve. The origin of right-sided pleurothetic descendants from left-sided pleurothetic ancestors poses evolutionary problems that are not easily resolved. Newell (1960) and Newell and Boyd (1970) encountered similar problems in attempting to explain the origin of left-sided pleurothetic oysters from right-sided pleurothetic pseudomonotids. They suggested that a reversal in orientation may have been accomplished by a single mutation, and cited for analogy, occurrences of reversed symmetry in living populations of flounders and gastropods. An alternative explanation is suggested below to account for the reversal in life position in derivatives of the Rhombopteriidae, but it does not seem
applicable to the oyster problem.

The origin of the Pseudomonotidae from an Atremapella-like ancestor (as I have hypothesized above) will be examined first. Those conclusions will then be drawn upon in investigating the origin of the right-sided habit in the Pterineidae and Pectinacea.

In view of the apparent fundamental role of paedomorphosis in the origin of at least some of the salient features of the Pseudomonotidae (viz. the retention of the byssus and central resilifer), it may be that this process was also of major importance in the origin of the right-sided pleurothetetic habit in that family. However, an understanding of the ontogeny of Atremapella n. gen. is necessary to show how paedomorphosis may have been involved in the evolution of the pseudomonotid habit. The ontogenies of the species of Atremapella n. gen., namely A. misticia n. sp. and A. newelli n. sp., were apparently closely similar, and consequently, information from both species has been pooled to produce the generalized ontogeny shown in Text-fig. 13.

The earliest post-larval stages of Atremapella n. gen. (Text-fig. 13B) probably attached to the substrate surface by a byssus, as do comparable stages in the majority of living bivalves (Yonge 1962). According to Yonge (1962: 114), the function of the post-larval byssus "....is to secure the post-larva while it is undergoing metamorphosis into the adult form which will enable it to exploit the adult habit". Some forms (e.g., pholads and certain solenaceans) lose the
Text-fig. 13. A-D) Generalized ontogeny of *Atremapella* n. gen. based on morphologic data obtained from *Atremapella misticia* n. sp. and *Atremapella newelli* n. sp.: A) larval stage; B) early post-larva; C) juvenile; D) adult - sectional view (schematic) showing productid-like features including "boat-like" shell profile, geniculation (g) on right valve, submarginal ridge (smr) on left valve and trail (t); E) hypothetical adult retaining various characters (see text) of early growth stages including vertical epibyssate habit inferred for early post-larva; F) same individual in a more hydrodynamically stable position.

Growth stages not necessarily to scale.
byssus very quickly, while in others, the adoption of the adult life mode is somewhat forestalled, and the young animal remains byssally attached on the surface for a considerable time (e.g., Mya arenaria Linné [ibid.]). A variety of bivalves retain the byssus into adult life and in this respect are paedomorphic (ibid.: 123).

In the ontogeny of Atremapella n. gen., it is not clear at what stage the byssus was lost, nor when an adult life orientation was assumed. The smallest available specimens of Atremapella n. gen. are subequivalved and Cyrtodonta-like in outline (Pl. 10, figs. 11-16). These specimens lack important adult features, including a strongly inequivalved shell, a pedal embayment, a pedal glide, and a well developed trail. It is therefore unlikely that they lived in an adult life orientation, and instead were probably byssally attached on the substrate surface as hypothesized for the early post-larva (Text-fig. 13B). Except for valve inequality, the adult features enumerated above were not normally developed until hinge lengths exceeding 10 mm were achieved. Consequently, an ontogenetic interval existed during which the shell was inequivalved but lacked other adaptations suited to the adult habit. Nonetheless, the inequivalved shell during this interval suggests a departure from the vertical habit hypothesized for early post-larval stages and, hence, is tentatively reconstructed in an adult orientation (Text-fig. 13C). Alternatively, the shell may have remained byssally attached at the surface, even at this relatively late stage in ontogeny, until features of the adult suited to
Uncertainties of this kind about the life mode of intermediate growth stages in Atremapella n. gen. are not, however, directly relevant to the problem of the origin of the right-sided pleurothetic habit in pseudomonotids.

Known aspects of the ontogeny of Atremapella n. gen. that are relevant to this problem include the following: 1) the early post-larval shell was subequivalved (and probably attached at the substrate surface by a byssus as in most Recent bivalves); 2) the right valve became significantly flatter than the left valve relatively early in ontogeny; and, 3) special modifications towards a productid-like habit (namely, the pedal embayment, pedal glide and pronounced trail) did not appear until relatively advanced ontogenetic stages. Pseudomonotids lack the special modifications in (3) above, and in at least this way, resemble juvenile stages of Atremapella n. gen. The paedomorphic retention of a juvenile (but not earliest post-larval) Atremapella-like shell form could therefore account for both the loss of these structures (in [3] above) and the origin of an inequivalved shell. If the byssus was also retained, as well as the epifaunal vertical habit of the early post-larva, the result would be an inequivalved shell, vertically oriented and byssally attached at the substrate surface (Text-fig. 13E).

The orientation of the shell in epibyssate bivalves must be such as to allow hydrodynamic stability to be maintained. A more hydrodynamically stable position for an inequivalved,
vertically-oriented, byssally-attached shell would be with
the right valve undermost, as shown in Text-fig. 13F.
Probably byssally attached shells having this shape would
tend to be automatically oriented in this way by the action
of water currents. Accordingly, the right-sided pleurothetic
habit in pseudomonotids can be regarded as the inevitable
consequence of the interaction of: 1) the paedomorphic
retention of the epibyssate habit in the early post-larva;
and, 2) positive selection for a life orientation ensuring
hydrodynamic stability of the already evolved inequivalved
shell.

Although some aspects of the ontogeny shown in Text-fig.
13 are uncertain, essential features, specifically the
vertical epibyssate habit of the early post-larva, the
development of an inequivalved shell at relatively early
stages, and the eventual assumption of a left-sided
pleurothetic habit, probably characterized the ontogeny of
rhomboceratids in general. Consequently, the origin of the
epibyssate, right-sided pleurothetic habit in the Pectinacea
and the Pterineidae can be explained in the same way as for
the Pseudomonotidae - that is, the epibyssate habit of the
early post-larval stage was retained paedomorphically, and
the right-sided habit developed to provide hydrodynamic
stability on the substrate surface for the marginally
attached, inequivalved shell. The subsequent development of
the anterior auricle/byssal notch complex and increased
flattening of the right valve enhanced stability, as Stanley
(1972) has already explained.
Genus *Coppinsia* n. gen.

**Etymology:** After Coppins Crossing, near the type locality. Gender is feminine.

**Type and only known species:** *Coppinsia spodophila* n. sp.

**Known chronostratigraphic distribution:** Middle Silurian [late Wenlockian].

**Diagnosis:** As for type and only species.

**Discussion:** Important features of *Coppinsia* that distinguish it from all other rhombopteriid genera include the lack of radial, divaricate or net-like ornament, the lack of widely spaced squamae, and the less strongly inequivalved shell. The dentition is closely similar to that of *Atremapella misticia* n. gen. & sp., leaving little doubt that these forms are closely related and belong in the same family (see p. 157-161 for comparisons). Implications of *Coppinsia* for the higher taxonomic relationships of the Rhombopteriidae were considered earlier in the general discussion of that family.

*Coppinsia spodophila* n. sp.

(Pls. 4 & 5; Text-figs. 9A, 14-16, 17A & B)

**Etymology:** From spodos, Gr., ashes, and philia, Gr., fondness: meaning "lover of ashes", with reference to the
occurrence of this species in volcaniclastic sediments at the type locality.

**Holotype:** ANU 48512.

**Referred specimens:** ANU 48513-48525 (paratypes); ANU 48526-46548 (total, 36).

**Type locality:** Upper 5 m of Walker Volcanics at Locality F1, Fairlight Station, 20 km west-northwest of Canberra, Australian Capital Territory.

**Known stratigraphic and geographic distribution:** late Wenlockian, Walker Volcanics, near Canberra, Australian Capital Territory.

**Diagnosis:** Shell inequivalved, subovoid, moderately prosocline and ventrally elongate; posterior angle obtuse, posterior embayment lacking; anterior shell margin in adult weakly convex, straight, or with weak byssal sinus; external ornament consisting of closely spaced, commarginal growth rugae and growth lines; hinge plate arcuate; dentition usually continuous across length of hinge plate in adult shell; posterior teeth elongate and extending posteroventrally well below level of anterior teeth.

**Description:**

**External features** - The shell is subovoid to subrhombic in outline, moderately prosocline, moderately inequivalved, and strophic. External ornament consists of fine, closely
Text-fig. 14. *Coppinsia spodophila* n. gen. & sp.: length/height scatter diagram; accessory symbols as in Text-fig. 7.
spaced, commarginal growth lines and growth rugae (Pl. 4, fig. 1). A few specimens show apparent widely spaced commarginal ribs, but these seem to be remnants of accentuated growth rugae in worn shells (Pl. 5, fig. 10). Adult shells are ventrally elongate, usually with a more or less straight or weakly convex anterior margin, but occasionally with a weak byssal sinus (Pl. 4, figs. 1, 6 & 9). Early and intermediate growth stages, however, are usually more Atremapella-like in outline, with a convex anterior margin and a more nearly equidimensional shell (Pl. 4, figs. 2 & 5). A posterior embayment is invariably lacking, and the posterior angle is always obtuse. There is no evidence of a byssal notch at any stage of growth. Auricular sulci are lacking; both anterior and posterior auricles merge into the body of the shell without interruption. Some specimens show a small embayment anteriorly, close to the hinge (Pl. 5, figs. 2, 4, 6, & 9). The function of this feature is uncertain, as it occurs above the byssal sinus (if present, e.g., Pl. 4, fig. 6), and is positioned too far dorsally to have been associated with the extrusion of the foot.

**Internal features**

**Musculature.** The adductor musculature is heteromyarian, with the anterior adductor scar small, circular and deeply inset on the valve floor just below the anterior end of the dentition, and the posterior adductor scar much larger, more ventrally placed and less deeply
impressed. A small accessory scar, probably the insertion of a pedal protractor muscle (see discussion), is usually visible at the posterior edge of the anterior adductor scar, as in certain cyrtodontids (Pojeta 1971: 36). A small, elliptical, ventrally facing, deeply inset scar occurs immediately posterodorsal to the anterior scar and marks the insertion of an anterior pedal retractor muscle. A much smaller circular scar, perhaps for a branch of that muscle, occurs between the anterior pedal retractor scar and the anterior adductor scar in some specimens (e.g., holotype, Pl. 4, fig. 10). An additional pedal retractor scar, often subdivided into a number of closely spaced pits, occurs on the anterior wall of the umbonal cavity. A few specimens show numerous small pits of uncertain significance on the dorsal wall of the anterior adductor scar (faintly visible in Pl. 4, fig. 10). Given their proximity to the pedal protractor, they perhaps represent multiple insertions of that muscle or of the anterior pedal retractor muscle.

The apparent dorsal extension of the posterior adductor scar visible in some specimens is probably the insertion of the posterior pedal retractor muscle. A small circular scar invariably occurs on the posterior flank of the valve floor, not far below the hinge plate. It probably marks the insertion of the Quenstedt muscle, by analogy with Atremapella n. gen. and the Pseudomonotidae, although it is more dorsally placed than in those taxa. The pallial line extends continuously from the posteroventral edge of the posterior adductor scar close to the ventral edge of the
anterior adductor scar. Here it is usually broken into several pits, often with a gap separating the last pit and the edge of the adductor scar (e.g., Pl. 4, fig. 7). Well preserved specimens exhibit pallial punctae scattered over the general surface of the valve floor (Pl. 4, fig. 10).

Ligament. In adult stages, the ligament area is broad and longitudinally traversed by numerous fine grooves. The inclination of the grooves is usually altered during ontogeny, and varies to some extent between individuals at the same stage of ontogeny. Generally, the ligament grooves are clearly inclined to the hinge axis early in ontogeny (Text-fig. 15B-C), becoming less obviously so at later growth stages. This is especially evident in several well preserved, mature specimens figured in Pl. 5, figs. 7 & 9 and Text-fig. 9A, which show chevrons formed immediately below the umbo and gently arcuate or essentially straight lines thereafter. Often the earliest formed grooves are coarser than those formed later. Such ontogenetic changes are not always present - several specimens show no obvious change in inclination or thickness of grooves, the grooves being relatively fine and very gently arcuate or nearly straight throughout the ligament area (e.g., Pl. 5, fig. 2). In one specimen, the first formed ligament grooves are finer than those formed subsequently (Pl. 5, fig. 8).

Because of the exceedingly low, nearly horizontal attitude of ligament grooves at advanced growth stages, only a small number of grooves (usually only one or two; rarely
more than four) intersect the hinge axis. In some specimens it is questionable whether the ventralmost grooves actually intersect the hinge axis, it being impossible to demonstrate any inclination of these grooves. They are better described simply as horizontal grooves that have not completely grown out from the chevron axis to the anterior and posterior edges of the ligament area. The evolutionary implications of the ligament insertion in *C. spodophila* are discussed later.

**Dentition.** The dentition of adult shells is well developed and usually consists of a more or less continuous series of teeth and sockets across the hinge plate. Anteriorly, teeth are relatively short and moderately opisthocline (often becoming complexly subdivided in large individuals); posteriorly, they are elongate and prosocline. Teeth in the interval between vary somewhat in length and inclination. Anterior teeth grade posteriorly into shorter, usually orthocline teeth in the middle part of the hinge plate. These in turn either grade posteriorly into increasingly prosocline teeth, imparting an actinodont aspect to the hinge (Pl. 5, fig. 2), or they continue posteriorly, changing little prior to the posterolateral teeth and imparting a taxodont appearance to the hinge (Pl. 5, fig. 4).

**Ontogeny of the dentition, and a new system of dental notation.** A reasonably complete ontogenetic series has been recovered for *C. spodophila*, important stages of which are shown in Text-figs. 15 & 16. Stages of the left valve are indicated with capital letters and stages of the right valve
Text-fig. 15. Ontogeny of hinge of left valve of *Coppinsia spodophila* n. gen. & sp.: A) ANU 48527, latex cast, centre of hinge slightly deformed; B) ANU 48534, plastic replica; C) ANU 48528, latex cast; D) ANU 48531, latex cast; E) ANU 48532, latex cast; F) ANU 48523, latex cast; G) ANU 48526, latex cast. See text for dental notation.

Abbreviations: Aa - anterior accessory tooth; Ap - anterior primary tooth; Pa - posterior accessory tooth; Pp - posterior primary tooth; s - secondary tooth.

All scale bars = 5 mm.
Text-fig. 16. Ontogeny of hinge of right valve of *Coppinsia* spodophila n. gen. & sp.: I) ANU 48535, plastic replica; II) ANU 48536, plastic replica; III) ANU 48537, plastic replica; IV) ANU 48538, plastic replica; V) ANU 48539, latex cast; VI) ANU 48540, latex cast; VII) ANU 48519, latex cast. See text for dental notation.

Abbreviations: O - socket; other abbreviations as for Text-fig. 15.

All scale bars = 5 mm.
with Roman numerals. Well preserved opposing valves, at or near the same stage of development, were rarely available. Consequently, the stages shown for the left and right valves often do not correspond. Stage C of the left valve, for example, is much more advanced ontogenetically than is stage III of the right valve.

Comparisons of the ontogeny of _C. spodophila_ with that of _Atremapella_ n. gen. (Pl. 8, figs. 4-13) and the pterineid _Ptychopteria catellus_ n. sp. (Text-fig. 23) reveal substantial similarities in dental pattern and development that in turn imply dental homologies between these taxa. It is difficult, however, to describe dental ontogeny in _C. spodophila_ and to convey inferred homologies using existing conventions of description and comparison. A system of dental notation suitable for these purposes is not presently available for pteriomorphs as a whole, nor for any one group of pteriomorphs. Boyd and Newell (in Moore 1969: N909) proposed a modified Steinmann notation for recording hinge morphologies of heterodonts, and recommended the notation for non-heterodonts, as well. However, this system was designed specifically to avoid implying dental homologies, and consequently, it is of little use in the present study. Even for purely descriptive purposes, the modified Steinmann notation has significant limitations. As Boyd and Newell (in Moore 1969: N910) point out, the notation is designed primarily for direct comparison with hinge illustrations; it has no utility for referring to specific teeth during description or discussion of dentitions, and in such
instances these authors must themselves resort to relatively unwieldy expressions as, "the outer anterior lateral of the left valve", and "the large central tooth on the right valve" (ibid.: N911), to refer to specific teeth in heterodonts. Reference to individual teeth in *C. spodophila* is even more awkward, there being far more teeth on the hinge plate than in heterodonts.

In response to these difficulties, a new system of dental notation has been employed for *C. spodophila*. The notation facilitates reference to specific teeth and sockets, and provides a means for conveying inferred homologies.

Four categories of teeth and sockets are recognized in *C. spodophila*. These are:

1. primary (abbreviated "p")
2. secondary (abbreviated "s")
3. tertiary (abbreviated "t")
4. accessory (abbreviated "a")

The first three categories correspond with three phases of dental development. The first phase is characterized by the development of eight teeth, two anterior and two posterior in each valve. These teeth are termed "primary" teeth. At their first appearance, primary teeth are relatively elongate and inclined at a low angle to the hinge axis. Some of the primary teeth undergo significant changes in shape and orientation during ontogeny, as discussed later. For purposes of description, primary teeth are divided into two groups, anterior (abbreviated "A") and posterior
(abbreviated "P"), and are numbered sequentially with Arabic numerals from ventral to dorsal, according to their relative positions when the valves are articulated (logic borrowed from the Bernard/Munier-Chalmas system of notation for heterodonts; see Boyd & Newell, in Moore 1969). Thus, the ventralmost anterior primary tooth occurs in the left valve and is designated "anterior primary one", that is, "Ap1" (stage B, Text-fig. 15). The next primary tooth dorsally occurs in the right valve and is designated "Ap2", and the one above that, in the left valve, "Ap3". Similarly, the ventralmost posterior primary tooth occurs in the left valve and is designated "posterior primary one" - that is, "Pp1". The one above that in the right valve is "Pp2", and so on, as shown in Text-figs. 15 & 16.

After the development of the primary teeth, the second phase of the ontogeny begins with the appearance of secondary teeth. Secondary teeth occur between Ap3 and Pp1 when the valves are articulated. They are numbered successively from anterior to posterior depending on their relative position on the hinge plate when the valves are articulated. The posteriormost secondary teeth tend to be variable and ill-defined, and consequently no attempt has been made to number them. By contrast, the anteriormost secondary teeth are quite consistent in their development, and, together with primary teeth, provide the most important clues concerning relationships. Consequently, particular attention is given them in the discussion below. The anteriormost secondary tooth occurs in the left valve, and is designated "s1" (stage
C, Text-fig. 15). It articulates immediately behind Ap2 of
the right valve. The secondmost anterior secondary, "s2",
occurs in the right valve, the next, "s3", in the left valve,
and so on. The tooth "s5" is easily recognized in the left
valve at early and intermediate growth stages, as it is
invariably joined dorsally to the posterodorsal end of Ap3,
forming an arch-like structure (stage D, Text-fig. 15). The
same is true of s4 and Ap2 in the right valve (stage V,
Text-fig. 16).

The third and final phase of dental ontogeny is
categorized by the development of tertiary teeth. These are
highly variable and form primarily by subdivision of
pre-existing teeth, or they may appear as small, often
nodular or vermiform teeth on and between pre-existing teeth.
Tertiary teeth do not lend themselves to numbering.

Accessory teeth occur both anteriorly and posteriorly,
immediately dorsal to Ap4 and Pp4 when the valves are
articulated. They resemble primary teeth in their form and
orientation, but unlike primary teeth, accessory teeth are
only variably developed, and when present, can differ in
strength between specimens. Normally, only two accessory
teeth are developed, one anteriorly and one posteriorly, both
in the left valve (stages C-D, Text-fig. 15). Accessory teeth
may be present at any growth stage, and are numbered from
ventral to dorsal, as are primary teeth.

Variably developed teeth are indicated with parentheses,
as, for example, "(Aa1)", the ventralmost of the anterior
accessory teeth (stage D, Text-fig. 15). Incipiently but consistently developed teeth are indicated by placing only their respective number in parentheses, as for example, "Pp(4)" in stage I, Text-fig. 16. Sockets are designated by placing an "O" prior to the notational term of the tooth they receive. For example, the socket below Pp2 shown in stage V, Text-fig. 16, received Pp1 from the left valve and is designated "OPp1". Incipiently developed sockets are indicated by placing the number of the tooth they receive in parentheses, as for example, "Os(3)" in stage III, Text-fig. 16. Variably developed sockets, if need be, can be indicated by placing the entire notational term in parentheses, as for example "(OAA1)". The dental configuration in C. spodophila is such that teeth and sockets in the right valve are numbered with even and odd numbers, respectively, and vice versa for the left valve.

The ontogenetic progression shown in Text-figs. 15 & 16 correlates generally, but not strictly, with increasing shell size. Consequently, a given shell may be more advanced in terms of dental development than another shell the same size or larger. For example, in ANU 48528 (stage C, Text-fig. 15), secondary teeth are well developed, whereas in some other shells about the same size and moderately larger, secondary teeth are weak or only incipiently developed (e.g., stage IV, Text-fig. 16). Nevertheless, the polarity of change in the ontogeny of the dentition is clear from the general correlation of increasing shell size with more advanced dental stages. The relative order of appearance of various
teeth can be resolved with reasonable certainty on the basis of the combinations of teeth present at various growth stages. For example, from the fact that some specimens exhibit Ap3 but not s3 (e.g., stage B, Text-fig. 15), and other, usually larger specimens, show both as Ap3 and s3 (e.g., stage D, same fig.), one can reasonably infer that Ap3 develops before s3 in ontogeny.

The smallest available right valve (hinge length=3.50 mm) of C. spodophila exhibits a well developed Ap2 and Pp2 (stage I, Text-fig. 16). Pp4 is only incipiently developed and was probably lacking at earlier growth stages. By stage II, Pp4 has enlarged, and Ap(4) has appeared, providing the full complement of primary teeth in the right valve. Earliest available growth stages of the left valve have a well developed Ap3, and Pp3 (stage A, Text-fig. 15). Ap1 is short and weak and was probably lacking at earlier growth stages. An anterior accessory tooth (Aa1) is variably present at this stage. Posteriorly, an accessory tooth, (Pa1), may develop at later growth stages (e.g., stage D, Text-fig. 15). Accessory teeth are normally lacking in the right valve, but one left valve (Pl. 5, fig. 7) exhibits two posterior accessories, (Pa1) and (Pa3), and presumably at least one accessory, (Pa2), was present in the right valve counterpart of this specimen.

Anterior secondary teeth are tuberculiform at their first appearance, and become increasingly elongate and more typically tooth-like during subsequent growth stages. In the
left valve, the first secondary teeth to appear are s5 and s1. Evidently, either of these may appear first (s5 in stage B, Text-fig. 15; and s1 in Pl. 5, fig. 3). In the right valve, sockets for these teeth first appear as shallow depressions on the proximal end of Ap2 (stage III, Text-fig. 16). The tooth s1 first appears as a local thickening of Ap1 (Pl. 5, fig. 3) and later becomes enlarged and extended, while Ap1 disappears (stages C & D, Text-fig. 15). s3 and s2 are the last of the six anteriormost teeth to appear. In the right valve, the developing socket for s3 bifurcates s4, the anterior limb of which becomes s2 (stage IV, Text-fig. 16). OPP1 appears fairly early in the ontogeny of the right valve (stage IV, Text-fig. 16) along the posteroventral slope of Pp2. It is usually weak throughout ontogeny, but in a few specimens, it becomes sufficiently developed for a small secondary tooth to be formed by its ventral wall (e.g., stage V, Text-fig. 16). Anterior primary teeth (other than Ap1, which normally disappears early in ontogeny) and to a lesser extent, posterior primary teeth, become increasingly more steeply inclined to the hinge axis through ontogeny.

In the right valve, Pp2 is the more robust of the posterior primary teeth and is continuous anteriorly with the ventral edge of the hinge plate, which tends to become thick and ridge-like, much more so than in the left valve. In the left valve, Pp3 is the more robust. Pp1 is quite variable in its expression. It may be relatively strong (Pl. 5, figs. 7 & 8, not labelled) or quite weak (stage F, Text-fig. 16), and is usually, but not always, continuous anteriorly with the
ventral edge of the hinge plate.

Most individuals develop a more or less continuous series of teeth between anterior and posterior primary teeth (e.g., stages F, VI; Text-figs. 15 & 16, respectively), but occasional individuals apparently retained an edentulous gap into advanced ontogenetic stages (e.g., stage G, Text-fig. 15). However, such individuals are invariably gerontic (i.e., tertiary teeth are excessively developed), and I suspect, therefore, that the edentulous gap in these specimens may be a secondary feature resulting from resorption of teeth and sockets in the middle part of the hinge, perhaps in association with an advancing ligament. In some gerontic specimens, the dentition is almost completely overrun by the advancing ligament. In a few specimens, teeth are incompletely resorbed, and leave a trace on the ligament area (Pl. 5, fig. 2). Advanced growth stages normally show the development of tertiary teeth, which form by the subdivision of pre-existing teeth and by the implantation of teeth in pre-existing sockets. Tertiary teeth are often excessively developed in gerontic individuals, to the extent that most previously formed teeth become unrecognizable (stages G & VII, Text-figs. 15 & 16, respectively). In the middle of the hinge plate, secondary teeth and sockets usually bifurcate longitudinally (note incipient bifurcations of s7 and s9 in stage E, Text-fig. 15) to produce thin, vertical tertiary teeth, whereas anteriorly, both secondary and primary teeth can become subdivided in a more complex way, producing small tuberculate and vermiform structures (stages G & VII,
Accessory teeth and posterior primary teeth usually are not substantially affected by tertiary tooth development. A socket sometimes develops obliquely across the proximal end of Pp3 (Text-fig. 9A; Pl. 5, fig. 7), and a few specimens show minor tuberculation of the proximal half of that tooth and Pp1 (stage G, Text-fig. 15). Occasionally, anterior secondary teeth are not subdivided at advanced growth stages. In these instances, they are relatively elongate and are morphologically very similar to Ap2 and Ap3 (e.g., Pl. 5, fig. 1).

**Discussion:** The phylogenetic implications of *C. spodophila* were considered earlier under the general discussion of the Rhombopteriidae.

**The pedal protractor** - The accessory scar on or adjacent to the posterior margin of the anterior adductor scar in *Coppinsia*, *Atremapella* n. gen. and some cyrtodontids (Pojeta 1971, pl. 7, fig. 2; pl. 8, figs. 6-9) probably marks the insertion of a pedal protractor muscle. Various dimyarian bivalves figured by Cox (in Moore 1969, fig. 31) show a pedal protractor scar at or near this position. To my knowledge, a pedal protractor scar has not been observed or inferred in other pteriomorphs except arcaceans, in which it inserts below the anterior adductor scar (*ibid.*, fig. 31F). Its insertion on the posterior margin in at least some cyrtodontids and rhombopteriids appears to be a feature unique
to these families among the Pteriomorphia.

Significance of C. spodophila in regard to the evolution of the duplivincular ligament - Pojeta (1978) observed that the ligament in cyrtodontids and ambonychiids differs from the duplivincular ligament of arcaceans and myalinids in that the ligament grooves are essentially parallel to the hinge axis, rather than inclined to it, and are shorter in the oldest, rather than the youngest, part of the shell. He suggested, therefore (p. 238), that this type of ligament is preduplivincular in evolutionary grade, and that the duplivincular ligament in presumed descendant taxa of the cyrtodontids and ambonychiids must have arisen polyphyletically.

C. spodophila is of interest in that it indicates that a chevroned arrangement of ligament grooves arose, in at least the Rhombopteriidae, as an adaptation in the juvenile. Consequently, rhombopteriids such as Atremapella n. gen. may have acquired their chevroned ligament structure by paedomorphic retention of the juvenile ligament into adult stages. The ligament area of some pterineids, such as Glyptodesma buchanensis, Tolmaia erugisulca n. sp. and Limoptera murrumbidgeensis n. sp., is similar to that in C. spodophila in that chevroned ligament grooves are formed early in ontogeny and essentially horizontal grooves thereafter (see descriptions of ligament area in these species on p. 246-247, 224, 238, respectively). This suggests that, as in the Rhombopteriidae, the ligament grade of these
species is primitive for the Pterineidae, and that forms with chevrons added throughout ontogeny may have arisen paedomorphically from such a grade. Stratigraphic evidence does not, however, support this conclusion. The earliest known pterineids show a fully duplivincular ligament, with chevrons developed throughout ontogeny (Pojeta 1978, pl. 11, fig. 2).

Pojeta's (1978) observations require further comment. First, new information concerning the cyrtodontid Ptychodesma Hall & Whitfield (Bailey 1983) and the ambonychiid Mytilarca (p. 43, this paper) reveals that a fully duplivincular ligament was developed in at least some members of those families. Secondly, it seems that Pojeta's observation of the relative length of the ligament grooves in various parts of the ligament area in cyrtodontids is critical if we are to understand the evolution of the duplivincular ligament. If, as he indicates, the last formed (i.e., ventralmost) ligament grooves are the longest grooves on the ligament area (therefore extending the full length of the ligament area), this would imply that the ligament-secreting epithelium laid down, alternately, a whole layer of fibrous, and then of lamellar, ligament (Thomas 1978: 185). Consequently, the whole length of a given ridge or groove on the ligament area would have developed simultaneously. This is in marked contrast to the formation of a duplivincular ligament, in which a given layer of fibrous or lamellar ligament is not formed all at once, but instead, is added to at the ends of the layer where it meets the mantle isthmus (Newell 1937).
The ligament insertions in adult specimens of *C. spodophila* and the aforementioned pterineids are significant in that they show essentially horizontal ligament grooves that grew by addition at their anterior and posterior ends. Consequently, the growth of the ligament in these forms does not appear to be qualitatively different from that in bivalves with an undoubted duplivincular ligament. The only real difference would seem to be in the relative rate at which new material was added to the ends of the ligament layers. The inclination of the ligament layers in a duplivincular ligament is presumably a vector determined by the rate of addition of material to the ends of the layers, and the rate of expansion ventrally of the ligament area (the latter is probably a function of the ventral growth of the entire hinge plate). If material is added to the ends of the ligament layers at a relatively slow rate compared to the ventral expansion of the ligament area, then the ligament layers (and hence, the ligament grooves and ridges) will be inclined to the hinge axis. By contrast, if material is added to the ends of the ligament layers at a very rapid rate compared to the ventral expansion of the ligament area, then the ligament layers will be parallel (or nearly so) to the hinge axis.

While there is no question that the ligament grooves in the cyrtodontids figured by Pojeta (1971; 1978) are essentially parallel with the hinge axis, it is difficult to verify from his figures that the ventralmost ligament grooves extend the full length of the ligament area. It is essential,
however, that this be demonstrated in numerous well preserved specimens if we are to accept that the secretion of the ligament in early cyrtodontids (and ambonychiids) was significantly different from that in pteriomorphs with a typical duplivincular ligament. Demonstration of such grooves in only a few specimens would not be sufficient evidence, as some specimens of *G. buchanensis*, for example, show ligament grooves at the ventral edge of the ligament area that appear to extend the length of the area (Pl. 21, fig. 6; see description of that species). These specimens presumably represent individuals that expired after the last formed groove had grown out to the ends of the area, but before a new groove was started. It appears that in at least one species of cyrtodontid figured by Pojeta (1971, pl. 7, fig. 10; see Text-fig. 18H, this paper), the ventralmost grooves (although quite faint) do not extend the full length of the ligament area, implying that the ligament of this species grew as in mature stages of *C. spodophila* and *G. buchanensis*.

Finally, from the recognition that duplivincular ligaments characterized by chevroned grooves and those characterized by horizontal grooves (as qualified above) differ fundamentally only in the rate at which material is added onto the ends of the ligament layers, one can visualize more easily the apparent polyphyletic development of chevroned duplivincular ligaments.

Comparisons of the dentition of *C. spodophila* with other pteriomorphs and the Cycloconchidae — Various dental patterns
expressed during the ontogeny of *C. spodophila* show striking similarities, not only with patterns in the rhombopteriid *Atremapella* n. gen. (as might be expected), but with those in a variety of primitive pteriomorphs, including the Cyrtodontidae, Pterineidae and early pectinaceans. Also of interest are similarities with the non-pteriomorphs *Cycloconcha* Miller and *Copidens* Pojeta & Gilbert-Tomlinson, representatives of a group (the Cycloconchidae) thought to have been involved in the ancestry of the Pteriomorpha (Vogel 1962; Pojeta 1975). Examples of dentitions of these taxa are shown in Text-figs. 17 & 18. A preliminary attempt has been made to indicate homologies with *C. spodophila*, but except for *Ptychopteria catellus* (new species described below) and *Atremapella* n. gen., growth series are unknown for these forms and, consequently, the homologies are tentative. It should be stressed that the hinge teeth in these bivalves are labelled on the basis of topographic similarity with comparable teeth in *C. spodophila*, not on the basis of the criteria used originally to establish the notation for *C. spodophila*. For example, the tooth labelled "s4" in *Cyrtodonta saffordi* (Text-fig. 18) is identified as such on the basis of its connection dorsally with another tooth, resulting in an arch-like structure like that formed by s4 and Ap2 in *C. spodophila* (see stage V, Text-fig. 16). This tooth is not numbered on the basis of the number of secondary teeth preceding it anteriorly, of which there were apparently five when the valves were articulated (this specimen is discussed further below).
Text-fig. 17. Comparison of hinge structure among early pteryaceans and pectinaceans: A-B) *Coppinsia spodophila* n. gen. & sp., Middle Silurian, family Rhombopteriidae; A) ANU 48513, juvenile, left valve, latex cast, X7.6; B) ANU 48514, juvenile, right valve, latex cast, centre of hinge and umbo deformed, X11.7. C-D) *Atremapella newelli* n. gen. & sp., Lower Devonian, family Rhombopteriidae: C) CPC F24981, relatively mature specimen, left valve, X5.9; D) CPC F24989, juvenile, right valve, X7.2.

E-F) *Palaeopteria* sp., Middle Ordovician, family Pterineidae, from Pojeta 1978, pl. 11, figs. 1 & 3: E) left valve, X6.3; F) right valve, X9. G-H) *Ptychopteria* (*Cornellites*) *catellus* n. sp., Lower Devonian, family Pterineidae: G) ANU 36568, left valve, X8; H) ANU 36564, right valve, X7.4. I) *Leiopecten rectangularis* Khalfin, Lower Devonian, family Leiopectinidae, left valve, internal mold, X4.6, from Krasilova 1959, pl. 4, fig. 1b.

Abbreviations as for Text-fig. 15.
Text-fig. 18. Comparison of hinge structure among cyrtodontids and cycloconchids: A-B) Ptychodesma knappianum Hall & Whitfield, Middle Devonian, family Cyrtodontidae, from Bailey 1983, fig. 20A & B: A) right valve, X4.5; B) left valve, X4.5. C) Cyrtodonta grandis (Ulrich), Middle Ordovician, family Cyrtodontidae, left valve, internal mold, X3.2, from Pojeta 1978, pl. 8, fig. 7. D) Cyrtodonta saffordi (Hall), Middle Ordovician, family Cyrtodontidae, right valve, X2.8, from Pojeta 1071, pl. 7, fig. 1. E) Copidens browni Pojeta & Gilbert-Tomlinson, Lower or Middle Ordovician, family Cycloconchidae, left valve, X8.4, from Pojeta & Gilbert-Tomlinson 1977, pl. 28, fig. 4. F-G) Cycloconcha ovata Ulrich, Middle or Upper Ordovician, family Cycloconchidae, from Pojeta 1978, pl. 5, figs. 5 & 8: F) right valve, X6.5; G) left valve, X14.5. H) Vanuxemia gibbosa Ulrich, Ordovician, family Cyrtodontidae, left valve, X3.9, from Pojeta 1971, pl. 7, fig. 10, arrows show apparent termination of ligament grooves at ventral edge of ligament area (see text).

Abbreviations as for Text-fig. 15.
Comparisons of dental development in *C. spodophila* and *Atremapella misticia* n. gen. & sp. are given under the description of the latter species below. Earliest available growth stages in these forms and *A. newelli* n. gen. & sp. show elongate diverging primary teeth with teeth lacking in the middle part of the hinge plate (Text-fig. 17A & D; Pl. 8, figs. 4, 5 & 9). Essentially the same configuration occurs in the Ordovician pterineid *Palaeopteria* (Text-fig. 17E & F) and in early growth stages of *P. catellus* n. sp. (Text-fig. 17G & H). *Palaeopteria* apparently lacks Ap1 and Pp1, although it is possible that these teeth were present at very early growth stages and were later lost, as in *A. misticia* n. gen. & sp. and many specimens of *A. newelli* n. gen. & sp.. Another Ordovician species, *Carotidens demissa*, shows evidence of secondary teeth anteriorly, but these are weakly developed (Pojeta 1971, pl. 11, fig. 11). Similarities between *C. spodophila* and the Silurian pterineid *Pteronitella retroflexa* were discussed earlier (p. 62-65; Text-fig. 9).

The ontogeny of the dentition of the Devonian pterineid *P. catellus* n. sp. is described in detail beginning on p. 208, and figured in Text-fig. 23 (left valve only). Except for relatively minor differences, dental homologies between early growth stages of *C. spodophila* and *P. catellus* n. sp. seem self-evident. Similarities are less evident between adult stages of these species (see p. 211 for comparison).

Early pectinaceans are edentulous, except for the *Leiopectinidae*, which, as noted earlier, show simple,
elongate, diverging dental elements that are reminiscent of primary teeth in *C. spodophila* and pterineids (Text-fig. 17I). Dentitions of cyrtodontids are normally more complex (an undescribed species of *Sphenolithium* Miller figured by Pojeta [1978, pl. 7, figs. 8 & 9] is an interesting exception, showing simple elongate teeth that resemble primary teeth in early growth stages of *C. spodophila*). Often arch-like structures are present anteriorly (Text-fig. 18A-D) that are similar to those formed in *C. spodophila* by the union of the proximal ends of Ap3 and s5 in the left valve, and Ap2 and s4 in the right valve (stages D & V of Text-figs. 15 & 16, respectively). Some cyrtodontids show more than one arch per valve. These presumably represent proximal fusion of teeth that are separated in *C. spodophila*. For example, teeth interpreted to be s1 and s3 in *Ptychodesma knappianum* Hall & Whitfield and in *Cyrtodonta grandis* are joined dorsally, and *C. grandis* shows possible union of s7 and what appears to be Aa(1) (Text-fig. 18C). *Cyrtodonta saffordi* is more difficult to interpret (Text-fig. 18D). A large arch-like element is present in the right valve that presumably represents the fusion of Ap2 and s4, as in *C. spodophila*. Interestingly, this specimen shows two teeth (joined dorsally in some specimens of *C. saffordi* [Pojeta 1978, pl. 8, figs. 8 & 9]) below the Ap2/s4 arch, whereas only one is normally present in *C. spodophila* (although teeth below the arch can be complexly subdivided at advanced stages to form tertiary teeth, as earlier discussed). These teeth may represent a bifurcation of s2 and are tentatively designated s2a and s2c.
in Text-fig. 18D. Presumably a tooth, s2b, was present in the right valve and articulated between these teeth. *Cyrtodonta beckneri* (Pojeta 1971, pl. 7, fig. 7) shows small, irregular teeth anteriorly that resemble tertiary teeth of *C. spodophila*.

*Cycloconcha* exhibits elongate lateral teeth on either side of the umbo that are reminiscent of the primary teeth at early growth stages of *C. spodophila*. Judging from photographs in Pojeta (1978, pl. 5), the ventralmost of the anterior and posterior lateral teeth are in the left valve. These teeth are, therefore, at anatomically comparable positions to Ap1 and Pp1 in early growth stages of the left valve in *C. spodophila*, and have been labelled as such in Text-fig. 18F & G. The short, vertically oriented teeth below the umbo in *Cycloconcha* may represent the equivalent of secondary teeth in *C. spodophila*. The monotypic genus *Copidens* is of particular interest in that the dentition is more like that of intermediate and advanced growth stages of *C. spodophila* than is the dentition of *Cycloconcha* (Text-fig. 18E; see also Pojeta & Gilbert-Tomlinson 1977, pl. 28). There is even a suggestion anteriorly in the left valve of an arch-like structure with two smaller teeth below.

Dental similarities of *C. spodophila* with *Cycloconcha* and especially *Copidens*, raise the question as to whether the presence of an edentulous gap between anterior and posterior teeth in the *Cyrtodontidae* is primitive or derived for that family and for the *Pteriomorphia* as a whole. It may be that
cyrtodontids will yet be found with a dentition more like that of Copidens and Coppinsia, in which event it could be argued that the continuity of the dentition across the hinge plate in Coppinsia and in various other pteriomorphs, such as Pteronitella Billings, is a primitive character traceable to cycloconchid ancestors. Alternatively, the continuous dentition in Coppinsia may have been secondarily acquired following descent from a cyrtodontid with an edentulous gap in the dentition. Regardless of these uncertainties, similarities between the cycloconchids and pteriomorphs shown in Text-figs. 17 & 18 strongly support a genealogical relationship between the two, as advocated by other workers.

**Autecology:** See under general discussion of Rhombopteriidae.
Genus *Atremapella* n. gen.

**Etymology:** *Atremapella*, literally, "holeless cup", from a-, Gr., prefix denoting "without"; *trema*, Gr., hole; and *pella*, Gr., cup. Reference is to the lack of a byssal notch. Gender is feminine.

**Type species:** *Atremapella misticia* n. sp.

**Included species:** *Atremapella newelli* n. sp.

**Known chronostratigraphic distribution:** Lower Devonian [late Emsian].

**Diagnosis:** Shell moderately prosocline to suborthocline and moderately inequivalved; shell outline subrhombic, right valve with widely spaced, imbricate squamae projecting above shell surface; squamae of left valve appressed against shell surface; left valve with pedal glide, pedal embayment and radial costae; anterior auricle confluent with anterior margin and not offset from body of shell; byssal notch and byssal sinus lacking; Quenstedt muscle and posterior radial sulcus (left valve) and fold (right valve) present.

*Atremapella misticia* n. sp.

(Pls. 6-9; Text-figs. 4, 12F)

**Etymology:** From *misticius*, L., of mixed race, with reference to the highly differing ornament of the right and left valves.
Holotype: ANU 36659.

Referred specimens: ANU 36660-36667 and ANU 36734-36735 (paratypes); ANU 36668-36685; CPC F24903-F24911 (total, 37).

Type locality: Locality R1 (horizon b), Receptaculites Limestone, Parish of Taemas, Taemas area, about 25 km southwest of Yass, New South Wales.

Known stratigraphic and geographic distribution: late Emsian, Receptaculites Limestone, Taemas Formation, Taemas area, New South Wales, and Bloomfield Limestone, Taemas Formation, Wee Jasper area, New South Wales.

Diagnosis: Left valve with well developed costae, right valve with divaricate costellae and weak plications; adult growth stages with small posterior embayment and continuous dentition below ligament area.

Description:

External features - The shell is suborthocline, prosogyrous, inequilateral, markedly inequivalved and strophic. Shell outline varies from subrhombic to suborbicular (Pl. 6, figs. 1, 6, 8, 10 & 11). The left valve is strongly convex. The right valve is moderately convex umbonally, becoming flatter distally in mature individuals (Pl. 6, figs. 3-5). The largest individual so far collected has a hinge length of 26 mm (CPC F24904).
The umbo of the left valve is more protruding and incurved than that on the right valve (Pl. 6, fig. 4). The anterior auricle is confluent with the anterior margin, is not well delineated from the shell body, and does not extend as far anteriorly as the extremity of the shell margin immediately below it. There is no evidence that a byssal notch or byssal sinus existed at any stage of growth. In adult stages, the posterior auricle is offset from the shell body by a shallow auricular sulcus on the left valve and by a corresponding shallow fold on the right valve (Pl. 6, fig. 5). These features are sometimes only incipiently developed (Pl. 6, fig. 7). In young individuals (hinge length less than 10 mm), a posterior embayment is normally absent and the posterior angle is about 90 degrees. With continued growth, a slight embayment develops immediately below the posterior end of the hinge and generally becomes moderately enhanced with increased shell size (Pl. 6, fig. 2; note successive growth stages shown by squamae). In some young individuals, the tip of the posterior auricle is the most posterior point of the shell (Pl. 6, fig. 8, note penultimate squama), but at adult stages the posteroventral edge of the shell margin marks the posterior extremity.

A shallow radial sulcus (best seen on large individuals) occurs on the posteroventral flank of the shell body on the left valve, and weakens umbonally. The right valve bears a corresponding shallow radial fold. The fold and sulcus are expressed on the posteroventral shell margin as a shallow sinus (=branchitellum; Pl. 6, fig. 10 and Pl. 8, figs. 12 &
13). The branchitellum and the posterior flange above it may be strong (rarely), moderate (occasionally) or weak (generally) in their development (Pl. 8, figs. 12-14, respectively).

In anterior view, the dorsal one-half to two-thirds of the anterior margin of the left valve is deflected to form the pedal embayment, and the margin of the right valve is correspondingly deflected to articulate against that surface (Pl. 6, figs. 4 & 13; Pl. 7, fig. 6). On the right valve, the distal edges of the squamae are upturned at intermediate and advanced growth stages to produce a series of concentric frills that project well above the shell surface (Pl. 6, figs. 12 & 13). On the left valve, squamae are appressed against the shell surface, except anteriorly. Here, their distal edges are upturned and recurved to form the pedal glides (Pl. 7, fig. 1). These occur only on that segment of individual squamae defined by the pedal embayment. The pedal glides are delicate structures and are broken off in most specimens.

In the right valve, the distal edges of the frills are very thin, almost invariably damaged, and, hence, ragged in appearance (Pl. 6, figs. 2 & 11). Similarly, the distal edges of squamae in the left valve are often irregular and ragged (e.g., Pl. 6, fig. 1) The ragged appearance of squamae, in at least the left valve, is probably the result of attrition caused primarily by pre-mortem processes, such as predators that might attack the exposed shell edge, rather than
post-mortem processes, such as shell transport or reworking: squamae in the left valve are closely appressed to the shell surface, and hence, could not be easily damaged on their distal edges, except when forming the trail.

It cannot be clearly established from the present material whether the valves were discordant. At least one articulated specimen appears strongly discordant ventrally, the left valve overlapping the right (Pl. 6, fig. 2); however, the edge of the last formed squama of the right valve in this specimen is damaged (note posteroventral edge of the right valve in Pl. 6, fig. 2), and, hence, the apparent overlap by the left valve may be an artifact. In a few other articulated specimens (e.g., ANU 36667, Pl. 9, figs. 2 & 3), the trail, although damaged, does not indicate valve discordance.

The fact that the trail is at least partially broken away ventrally in almost all specimens does not allow shell height and length to be measured accurately. Consequently, bivariate analysis of these parameters is not possible. The largest specimen collected so far has a hinge length of 26 mm.

Costae are well developed on the left valve. Costae formed at the shell edge between the posterior radial sulcus and the ventral edge of the pedal embayment are generally coarser and more widely spaced than costae formed dorsal to those points. Costae are disrupted where they intersect the distal edge of squamae; they usually resume again on the
successive squama, but often several costae appear in their place, or conversely, several costae may be replaced by one or two costae. One or more small costae occur variably on some, but not most, intervals between larger costae. They generally appear at the onset of a new squama, but may disappear again at the junction with the next squama, or they may continue, eventually becoming enlarged to the same size as neighboring larger costae. Costae seem to increase in number by both intercalation and bifurcation. Examples of both occur in the specimens shown in Pl. 6, figs. 1 & 9.

Two types of radial elements occur on the right valve, including weak divaricate costellae and weak, variably developed plications. Divaricate costellae developed after a hinge length of 10-15 mm was attained, and sometimes occur only in the posterior half of the shell. They are usually better developed in the interspaces between frills than on the frills, and are not obviously divaricate, except in well preserved specimens (Pl. 6, fig. 8). Plications are restricted to frills, and they are feebly developed (Pl. 6, fig. 2, see arrows).

**Internal features**

**Musculature.** Muscle insertions in *A. misticia* are illustrated in Pl. 7, figs. 3-6. The posterior adductor scar is relatively large (dorsoventral length about one-quarter to one-third of shell height), and elliptical to subcircular in outline. A thin line, presumably the pallial
line, extends dorsally from the scar, and curls anteriorly for a short distance below the posterior dentition. It forms the posterior and posterodorsal borders of a shallow depression that may represent a posterior pedal retractor scar (Pl. 7, figs. 3 & 4). The outline of the scar is sufficiently vague (especially in left valves) that it cannot be established with certainty.

The anterior adductor scar is small (dorsoventral length one-third to one-quarter that of the posterior adductor scar), circular, and deeply impressed on the valve floor. A differentiated area for insertion of the pedal retractor muscle is usually visible on the posterior edge of the anterior adductor scar, as in cyrtodontids (Pl. 7, fig. 3; see p. 139 for discussion). Some specimens, however, show no evidence of this, even though the anterior adductor scar is well preserved (e.g., Pl. 8, fig. 8).

A small, ovate, deeply impressed anterior pedal retractor scar lies directly posterodorsal to the anterior adductor scar on the ventral surface of the hinge plate. An additional retractor scar (sometimes subdivided into closely spaced pits) occurs further posteriorly or posterodorsally on the anterior slope of the umbonal cavity (Pl. 7, fig. 4). In some specimens this scar is elongate, and can extend as far anterodorsally as the posterior edge of the anterior adductor scar (Pl. 7, fig. 6, unlabelled). The Quenstedt muscle scar is consistently present about one-third to one-half of the distance from the anterodorsal edge of the posterior adductor
scar to the top of the umbonal cavity. One or more small scars of uncertain significance (possibly visceral or gill suspensor scars) are usually present in the depth of the umbonal cavity (Pl. 7, fig. 4, see arrows). Pallial punctae are normally obvious only in large, well silicified specimens (e.g., Pl. 7, fig. 8).

The pallial line is set well back from the valve margin and is continuous except near the anterior adductor scar, where it is usually marked by one to several small pits. In the left valve, two or three widely spaced, shallow, commarginal depressions are often present between the pallial line and the valve edge (Pl. 7, fig. 2). These represent former sites of the submarginal ridge in ontogeny, and should not be confused with the pallial line, which they can superficially resemble, especially in worn specimens.

Ligament. The insertion of the ligament is marked by a series of grooves arranged in shallow chevrons below the beak. The arms of the chevrons are often more steeply inclined near the chevron axis than laterally from it (Pl. 8, fig. 3). Although chevrons increase in number during ontogeny, there is no strict correlation between chevron number and shell size. CPC F24907 (Pl. 8, fig. 3), for example, has a hinge length of 24.0 mm and has 15 chevrons below the beak, whereas ANU 36683 is nearly the same size and has only about eight (Pl. 8, fig. 8); ANU 36669, although much smaller (hinge length=17.5 mm) than either of these, has 12 chevrons (Pl. 8, fig. 1). Ventral expansion of the
ligament area resulted in only slight to moderate divergence of the umbones during ontogeny (Pl. 6, fig. 3; Pl. 9, fig. 2).

Dentition. The dentition of the adult shell is closely similar to that of the primitive rhombopteriid *Coppinsia spodophila*, although the way in which the dentition forms during ontogeny differs somewhat from that species, as described later. Teeth and sockets are numerous, and form a continuous series below the ligament area. Anterior teeth (if not complexly subdivided; see below) are opisthocline to orthocline, posterior teeth are prosocline, and teeth between are normally gradational in their orientation. Consequently, the overall appearance of the dentition is more or less actinodont (Pl. 8, figs. 7 & 8), although the teeth and sockets do not radiate from the beaks as required by a strict definition of that term (Cox, in Moore 1960: N102). The number of teeth in the adult shell varies. It is impossible to characterize this variation statistically, owing to the tendency in many specimens for some teeth to be subdivided in a complex way or to be only partly subdivided, and because of the frequent occurrence of crenulations and nodular or vermiform teeth between larger teeth. Generally, however, in valves with a hinge length greater than 18.0 mm, there are usually about 16 to 20 conspicuous teeth developed, as well as a variable number of crenulations and/or small nodular or vermiform teeth.
Ontogeny of the dentition. The general pattern of the ontogeny of the dentition in *A. misticia* is shown in Pl. 8, figs. 4-13. The new system of dental notation (described fully on p. 130-139) developed for the primitive rhombopteriid *Coppinsia spodophila* is used here for teeth inferred to be homologous with teeth in that species.

Earliest available growth stages (Pl. 8, figs. 4 & 5, 9 & 10) show an arrangement of primary teeth closely similar to that in *C. spodophila*. Ap1 is very weak at early growth stages (Pl. 8, fig. 5) and becomes obscure at subsequent stages (e.g., Pl. 8, fig. 6). Apart from primary teeth, it is not generally possible to recognize teeth homologous with those in *C. spodophila*. Teeth that develop between the anterior and posterior primary teeth are variable in form and number, and generally resemble tertiary rather than secondary teeth of *C. spodophila*. It appears that the development of discrete secondary teeth has been largely suppressed, secondary teeth at their first appearance being already mostly subdivided to form tertiary teeth. A few left valves show somewhat more robust teeth posterior to the proximal end of Ap3 (Pl. 8, fig. 6). These teeth are reminiscent of secondary teeth at this position in early growth stages of *C. spodophila*, but it is not possible to specify homologies. None are clearly connected dorsally to Ap3 that might enable identification of As5. Since it is impossible to determine which, if any, of the teeth between the anterior and posterior primary teeth are equivalent to secondary teeth in *C. spodophila*, they are here referred to simply as
"secondary/tertiary" teeth.

Secondary/tertiary teeth usually appear first on that segment of the hinge plate immediately posterior to the proximal end of Ap3 (Pl. 8, fig. 6). A second set of secondary/tertiary teeth develops just posterior to the chevron axis of the ligament (Pl. 7, fig. 5; Pl. 8, fig. 2); these are separated from the anterior set by an edentulous gap. At about the same time, crenulations develop in the primary sockets. Secondary/tertiary teeth increase in number and become more elongate, and crenulations in the anterior primary sockets become enlarged and tooth-like (Pl. 8, figs. 7 & 11). The edentulous gap separating anterior and posterior teeth becomes progressively smaller, and by advanced growth stages, a continuous series of teeth and sockets has developed across the hinge plate (Pl. 8, figs. 8, 12-14). A single accessory tooth is often present anteriorly in the left valve (and rarely in the right valve), and several accessory teeth may develop posteriorly in both valves (Pl. 7, fig. 5; Pl. 8, figs. 8 & 13) (some of these apparent accessory teeth may in fact represent subdivisions of pre-existing accessory teeth and should therefore be classed as tertiary teeth).

Ap3 becomes progressively more steeply inclined throughout ontogeny. This tooth (and OAp3 in the right valves) can usually be identified even at advanced growth stages, as it is generally more robust and more markedly opisthoclone than adjacent teeth (Pl. 8, figs. 7 & 8). In the
right valve, Ap2 becomes thickened and continuous with the ventral edge of the hinge plate (Pl. 8, figs. 10-13). Ap4 can usually be distinguished throughout ontogeny, except at very early stages. Pp1 is only weakly developed at early stages (Pl. 8, figs. 4-6) and normally becomes obscured by crenulations and subdivision during subsequent stages (Pl. 8, figs. 7 & 8). The other posterior primary teeth are usually not substantially modified during ontogeny, although in a few specimens they become split along their long axes (Pl. 8, fig. 14). At advanced growth stages, all or most teeth are wrinkled, and small tuberculiform teeth can occur randomly in sockets between larger teeth. Teeth and sockets below and behind the anterior primaries can become complexly subdivided (Pl. 8, fig. 13). Secondary/tertiary teeth located posterior to the umbones occasionally form chevrons (Pl. 8, fig. 14). In large individuals, the dorsal ends of teeth and sockets are usually truncated by the ventral advance of the ligament (Pl. 7, fig. 8).

This pattern of development of the dentition correlates generally, but not precisely, with increasing shell size. Consequently, a given shell may appear somewhat more advanced or less advanced than another shell of the same size, in terms of the ontogenetic series shown in Pl. 8, figs. 4-13. For example, CPC F24911, a small right valve (Pl. 8, fig. 2), shows clear development of secondary/tertiary teeth, whereas in ANU 36661, a specimen of similar size, these are lacking (Pl. 8, fig. 9). Nevertheless, as in C. spodophila, described earlier, the polarity of change in the ontogeny of the
dentition is evident from the general correlation of increasing shell size with more advanced dental stages. Consequently, it can be inferred that any one mature individual underwent a series of changes in the dentition like that, or close to that discussed above, even though the timing of these changes relative to shell size varies to some extent among individuals.

**Autecology:** See under general discussion of Rhombopteriidae.

**Atremapella newelli** n. sp.

(Pl. 9, figs. 5-7; Pl. 10; Pl. 11, figs. 1-7; Text-fig. 17C & D)

**Etymology:** After Norman D. Newell, of the American Museum of Natural History, in recognition of his contributions to the study of bivalve evolution.

**Holotype:** CPC F24974.

**Referred specimens:** CPC 24975-24984 (paratypes); CPC 24985-24997 (total, 23).

**Type locality:** 50-70 m above base of outcrop in Unit 11 of Section B (see Johnson 1975), Garra Formation, near Mountain View, approximately 9 km south of Wellington, New South Wales.
Known stratigraphic and geographic distribution: early Pragian, unit 11 of Johnson (1975) and Chatterton, et al. (1979), near Wellington, New South Wales.

Diagnosis: Shell rhombic; posterior embayment lacking in left valves, incipiently present in some right valves; weak radial ornament on left valve; right valve with commarginal ornament only; dentition widely separated into anterior and posterior elements by edentulous gap below and behind umbones.

Description:

External features - Externally, _A. newelli_ agrees with _A. misticia_ in all particulars, except as follows:

1) The shell is relatively deeper dorsoventrally and is slightly more prosocline. 2) The anterodorsal and posterodorsal corners of the shell are more rounded. 3) The anterior margin of the shell is generally straighter and is usually more inclined anterodorsally (broadly convex and essentially orthocline in _A. misticia_); consequently, the anterior extremity of the shell usually occurs at a relatively more dorsal point on the anterior margin than in _A. misticia_. 4) A posterior embayment is lacking on the left valve, although in posterior view, the shell margin is slightly flexed at this point, producing an incipient posterior auricular sulcus (Pl. 10, fig. 3); a corresponding incipient fold is present in right valves and, in some specimens, this is expressed marginally as a slight posterior
embayment (Pl. 10, figs. 4 & 9) (in *A. misticia*, flexure of the posterior margin is usually more pronounced, and both valves generally display a stronger posterior embayment). 5) A posterior radial fold (right valve), sulcus (left valve) and branchitellum are present, but are less pronounced than in *A. misticia*. 6) The erect commarginal frills produced by upturned squamae in the right valve are generally less well developed than in *A. misticia*, although this is probably somewhat accentuated in *A. newelli* by pre- and postmortem wear. 7) The right valve exhibits commarginal ornament only (Pl. 10, fig. 4) (divaricate ornament characterizes *A. misticia*). 8) On the left valve, radial ribs are weaker and finer than in *A. misticia*, and often are clearly developed only on the distal segment of individual squamae (Pl. 10, fig. 1); costae increase by bifurcation in *A. newelli*, and by bifurcation and intercalation in *A. misticia*.

Features of the juvenile shell were described in the general discussion of the Rhombopteriidae. The largest specimen of *A. newelli* collected has a hinge length of 20 mm.

**Internal features** -

**Musculature.** Except for the adductor scars, features of the musculature are generally faint or obscure. The muscle pattern is essentially like that in *A. misticia*. As in that species, some specimens show a pedal protractor scar joined to the anterior adductor scar (Pl. 10, fig. 8). That segment of the pallial line extending dorsally above the
posterior adductor scar is generally clearer than in *A. misticia*. In some specimens, it is enlarged at its dorsal extent to form a small pit (Pl. 11, fig. 2). As in *A. misticia*, the posterior pedal retractor muscle presumably inserted in the shallow depression (weak or obscure in left valves) immediately anterior to this part of the pallial line. One specimen shows an apparent dorsal extension of the posterior adductor scar, which may also represent an insertion area for that muscle (Pl. 10, fig. 8). The anteriormost pedal retractor scar is usually not as large nor as deep as in *A. misticia*. The Quenstedt scar (only rarely preserved) is positioned farther umbonally than in *A. misticia* and consequently is less distinctly set off from the small, variably developed scars (gill or visceral suspensor scars?) occurring in the umbonal cavity (Pl. 11, fig. 1).

**Ligament and dentition.** The insertion of the ligament is similar to that in *A. misticia*. Five to eight chevrons are usually present below the umbo in adult growth stages.

Dentally, adult stages of *A. newelli* resemble early and intermediate growth stages of *A. misticia*. Ap2 and Pp2, and Ap3 and Pp3 are well developed in right and left valves, respectively. In the right valve, Ap4 and Pp4 are weakly but consistently developed, although they may appear to be lacking on worn or poorly silicified material. Other teeth are more variable in their development. Pp1 in the left valve and Ap4 and Pp4 in the right valve are usually weakly developed and are sometimes lacking. Ap1 is especially
variable, being conspicuously developed in some specimens (e.g., Pl. 10, fig. 2) and absent in others (e.g., Pl. 10, fig. 5 & Text-fig. 17C [same specimen]). Accessory teeth are lacking anteriorly; posteriorly, a single weak accessory tooth (Pal) is present in some left valves (not figured). In most specimens, secondary/tertiary teeth are weakly developed and are expressed simply as vertical crenulations anteriorly, and as oblique crenulations posteriorly. These occur in left valves primarily in the sockets OAp2 and OPP2, and in right valves, primarily in the sockets OAp3 and OPP3. In only a few specimens are crenulations sufficiently enhanced to form discrete teeth (Pl. 11, figs. 4 & 6). Secondary/tertiary teeth are sometimes lacking posteriorly (Pl. 11, figs. 4 & 7) and are occasionally lacking altogether (Pl. 10, fig. 5). Unlike adult stages in A. misticia, anterior and posterior teeth are invariably separated by a broad edentulous gap below and posterior to the umbo.

Earliest available growth stages are dentally similar to comparable stages in A. misticia and C. spodophila (Pl. 11, fig. 3; Text-fig. 17D). Available material is inadequate to allow a detailed account of the ontogeny of the dentition.

Discussion: Comparisons with the primitive rhombopteriid C. spodophila clearly indicate that A. newelli is more primitive than is A. misticia in shell outline. However, the dentition of A. newelli resembles that of early and intermediate growth stages of A. misticia, indicating that the former is dentally paedomorphic. Consequently, A. newelli
cannot be in the direct ancestry of *A. misticia*, but from their overall similarity, it is clear that the two forms are closely related.

*A. newelli* shows considerable plasticity in the development of the dentition. Some specimens develop secondary/tertiary teeth anteriorly but not posteriorly (Pl. 11, fig. 6); others, at relatively advanced growth stages in terms of shell size, lack secondary/tertiary teeth altogether, and retain a fully juvenile configuration (Text-fig. 17C). *A. newelli* is of particular interest in this respect because it indicates that at least some rhombopteriids were capable of retaining juvenile characters into advanced growth stages, and in this way, were ontogenetically predisposed as progenitors of groups that were inferred to have arisen paedomorphically from the Rhombopteriidae (although not necessarily from *A. newelli*), including the Pterineidae, Pectinacea and the Pseudomonotidae (see discussion above).

**Autecology:** See under general discussion of the Rhombopteriidae.
Discussion: The longstanding need for a comprehensive revision of pterineid genera is well known to students of Palaeozoic bivalves. McAlester (1962) discussed problems associated with distinguishing pterineid genera represented in Devonian rocks. He found that of the minimum of 35 generic names proposed to that date, most were defined on the basis of external ornament and minor differences in shape (features that he regarded to be of no more than specific value), the dentition of almost all the type species being too poorly known to serve as a generic character (ibid.: 26). Consequently, McAlester was able to provide only tentative generic assignments for his Chemung Stage pterioids. Essentially the same problem remains for the present study. Very little new morphological information concerning pterineid-type species (or pterineid species in general) has become available since McAlester's study, with one notable exception, that being Bailey's (1983) clarification of the internal shell features of *Cornellites fasciculata* (Goldfuss), the type species of *Cornellites* Williams. In accordance with Newell and LaRocque (in Moore 1969), Bailey retained *Cornellites* as a subgenus of *Ptychopteria*. That usage is tentatively followed here; however, it should be noted that *P. fasciculata* differs from *Ptychopteria eugenia* (Hall), the type species of *Ptychopteria*, in the presence of coarse radial ornament on the left valve, a flattened to resupinate right valve, and a well developed byssal notch,
byssal sinus, and corresponding auricular sulcus. In *P. eugenia* by contrast, radial ornament is comparatively fine on the left valve, the shell is biconvex with the right valve only moderately less inflated than the left, the byssal sinus and sulcus are weak, and a byssal notch is apparently lacking (Hall 1884: 131-132 & pl. XXIII). It may be that *Cornellites* warrants generic distinction, but investigation of this possibility is here deferred pending restudy of *P. eugenia*.

Newell and LaRocque (in Moore 1969) recognized only seven pterineid genera with Devonian representatives. These include: *Pterinea* Goldfuss, *Actinodesma* Sandberger, *Dolichopteron* Maurer, *Leptodesma* Hall, *Limoptera*, *?Palaeopinna* Hall, and *Ptychopteria*. Babin (1966: 166) considered *Dolichopteron* to be a synonym of *Actinodesma*. Of the eight pterineid species known from the Taemas and Buchan Caves limestones, seven are radially ornamented. The species lacking radial ornament is referred to *Glyptodesma*. This genus is not considered a synonym of *Actinodesma* (contra Newell & LaRocque, in Moore 1969) for reasons given on p. 240-241. Only four of Newell and LaRocque's genera are radially ornamented (or include at least some radially ornamented species); these are: *Actinodesma*, *Palaeopinna*, *Limoptera* and *Ptychopteria*.

Type species of the first two genera are utterly different in shell outline from the Australian species and need not be considered further. One of the Australian species is assigned to *Limoptera* on the basis of similarities with
the type species, *L. macroptera* Hall (see p. 238-239 for comparisons). The remaining six species fall within Newell and LaRocque's definition of *Ptychopteria*. While the Australian species are broadly similar to one another in shell form (i.e., pteriiform), some differ significantly in dentition, musculature and/or ornament, indicating that more than one generic level taxon is represented. Consequently, these species are tentatively assigned to three genera, *Actinopteria*, *Ptychopteria* and *Tolmaia*. Newell and LaRocque (in Moore 1969) considered *Actinopteria* a subgenus, and *Tolmaia* a junior synonym, of *Ptychopteria*, but these forms are here removed from *Ptychopteria* because, among other differences, neither shows the strongly opisthocl ine cardinal tooth characteristic of that genus (Hall 1884: xii, 130 & pl. 85, fig. 8). Instead, cardinal teeth in these forms are moderately to markedly prosocline, although the anteriormost tooth may be orthocline, or nearly so, early in ontogeny.

Pending comprehensive generic revision of the Pterineidae, generic (or subgeneric) names for radially ornamented species described herein are used as follows:

*Limoptera* Hall & Whitfield 1869 – Shell inequivalved; left valve markedly to moderately inflated, right valve weakly inflated at early growth stages, becoming flattened to moderately resupinate at intermediate and advanced stages; radial ribs on left valve prominent and usually widely spaced with few ribs intercalating during growth; radial ribs weak to obsolescent on body of right valve; anterior auricle and
byssal sinus weak to well developed; byssal notch well
developed in at least some species; posterior embayment
moderately developed at early and intermediate growth stages,
becoming obsolescent at advanced stages; anterior adductor
scar absent; auricular buttress short, thick, and somewhat
variably developed at early and intermediate growth stages,
becoming obsolescent at advanced stages; hinge plate narrow
except at junction with auricular buttress, where it is
thickened and sometimes bears a few highly variable, usually
poorly formed, teeth; one or two posterolateral teeth
present, weakly to moderately divergent from hinge axis;
edentulous gap present between cardinal and posterior teeth.

_Actinopteria_ Hall 1884 - Shell biconvex, moderately to
slightly inequivalved, weakly inflated; right valve less
inflated than left valve, and becoming flattened distally at
advanced growth stages in some species; radial ribs thin,
closely spaced, weaker on right valve; anterior auricle small
with rounded to somewhat flattened anterior edge; byssal
sinus broad and shallow, byssal notch absent; posterior
embayment moderately to well developed; anterior adductor
scar absent; auricular buttress prominent, thin and well
differentiated from hinge plate; hinge plate narrow below
ligament area; one to three cardinal teeth present in both
valves; cardinal teeth moderately to strongly prosocline
through most of ontogeny (anteriormost tooth may be
suborthocline at early to intermediate growth stages); one or
two posterolateral teeth present and weakly divergent from
hinge axis; edentulous gap present between cardinal and posterolateral teeth.

**Ptychopteria (Cornellites) Williams 1908** - Markedly inequivalved; left valve strongly inflated; right valve weakly inflated at early growth stages, becoming flattened to resupinate at advanced stages; coarse radial ribs present on left valve (with finer ribs interspersed in some species); ribs weak to obscure on body of right valve; anterior auricle relatively large and in most species well differentiated from shell body; byssal sinus and byssal notch generally well developed; posterior embayment moderately to well developed (possibly obsolescent at advanced growth stages in one species); anterior adductor scar present; auricular buttress feebly developed or absent, when present consisting of a short, thick ridge bordering anterodorsal edge of anterior adductor scar and continuous with anterior end of hinge plate; hinge plate narrow to broad below ligament area; dentition moderately to well developed; strongly opisthocline teeth present anteriorly at least during early growth stages, becoming orthocline to prosocline at intermediate and advanced stages in some species; posterolateral teeth weakly to strongly divergent from hinge axis; with or without edentulous gap between cardinal and posterolateral teeth.

**Tolmaia Williams 1908** - Shell weakly inflated; valves nearly equally convex at early growth stages; right valve becoming flattened to moderately resupinate at intermediate
and advanced stages; radial ribs thin, closely spaced, weaker on right valve; anterior auricle small, inconspicuous, poorly differentiated, if at all, from shell body; byssal sinus weak or absent in left valve, weak in right valve; distinct byssal notch lacking, but left valve overlapping right along byssal sinus; posterior embayment moderately to well developed; anterior adductor scar present(?); auricular buttress short, thick, poorly differentiated, continuous with anteroventral end of hinge plate and bordering anterodorsal edge of anterior adductor scar; hinge plate broad below ligament area; dentition well developed; cardinal teeth prosocline throughout ontogeny except anteriormost tooth, which may be orthocline at early growth stages; posterolateral teeth moderately to strongly divergent from hinge axis.

Autecology - Important discussions of the life mode of pterineids have been given by Kauffman (in Moore 1969: N144-146), Pojeta (1971: 34), Stanley (1972: 182-185) and Bailey (1983: 222-224). Both Kauffman and Pojeta relied primarily on analogy with Recent pteriids for their interpretation of fossil pterineids. Kauffman suggested that Leiopteria Hall, Pterinea and Cornellites lived like Recent pteriids, which preferentially attach by byssal threads to raised objects (often flexible), such as alcyonarians, algae, grasses and corals. (Kauffman [in Moore 1969] used the term "byssate free-swinging" for such bivalves, but see Stanley [1972: 191] for criticism of this usage.) Pojeta (1971) interpreted the Ordovician pterineids Pterinea and
Palaeopteria in a similar way, suggesting that both were entirely epifaunal, the former living in a manner like living Pinctada, with the flattened right valve against, or inclined to, the substrate. Pojeta noted that the attachment of edrioasteroids on left valves but not right valves of Pterinea supported this interpretation. Palaeopteria, he suggested, may also have lived like Pinctada, or alternatively, "...may have attached to trepostome bryozoans the way Pteria attaches to alcyonarians, although there is no direct evidence for this" (ibid.).

By contrast, Stanley (1972: 184) emphasized what he perceived as differences between many Palaeozoic pterineids and Recent pteriids. He believed that equivalved or near equivalved pterineids with a broadly rounded or lobate anterior and shallow byssal sinus, were endobyssate and lived vertically or obliquely in soft sediment. Difficulties with this view will be discussed later. Stanley interpreted inequivalved forms, such as "Cornellites" chemungensis, which have a well developed anterior auricle/byssal notch complex, as byssally attached on the substrate surface (ibid., text-fig. 17F). He did not discuss whether some of these forms may have attached to raised objects as does Pteria Scopoli.

Were some pterineids productid-like in habit? Bailey's (1983) hypothesis concerning the life mode of the Devonian pterineid Ptychopteria (Cornellites) fasciculata departs radically from the more conventional interpretations just
outlined. Bailey (p. 223) regarded Kauffman's (in Moore 1969) hypothesis of a Pteria-like habit to be improbable for this species, and proposed instead that *P. fasciculata* lived in a manner analogous to that of productid brachiopods — that is, with the convex left valve undermost and largely buried in the substrate, and the respiratory margin protruding above the sediment/water interface (Bailey 1983, fig. 11). This hypothesis is not accepted here for *P. fasciculata* nor for any other known pterineid, for reasons discussed below. First, however, it is necessary to review Bailey's reasons for rejecting Kauffman's hypothesis, as well as the evidence he presents in support of a productid-like habit.

These are summarized as follows:

1) Bailey states (p. 223): "Most free-swinging pterioids are equivalved for streamlining and, as Kauffman noted, thin-shelled due to the limitations imposed by weight in an elevated, attached position, their ability to swing to and fro with current changes being their primary protective device to prevent shell damage. In *P. fasciculata*, however, the shells are strongly equivalved and very thick."

2) Although acknowledging similarities between *P. fasciculata* and free-swinging pterioids, Bailey (p. 223) maintains that this species exhibits "unique modifications" that "suggest a more benthic life style." These include: "(1) pronounced inequity in valve development with swollen left and resupinate right shells; (2) deeply etched radial ribbing
and nodose reticulations confined mostly to the left valve;
(3) a strongly inflated left auricle with accentuated byssal sinus, permanent byssal gape, and a deep byssal groove or notch on the right valve; and (4) no internal evidence for attached byssal musculature."

3) Presumed productid-like features of P. fasciculata cited by Bailey (p. 224) include: a "boat-like" profile in anterior view (ibid., fig. 11B); strong radial ribs and nodose reticulations on the left valve which, "aided by the broad wing and swollen auricle", functioned in a way analogous to the anchoring spines of productids; weakly ornamented right valve analogous to the weakly ornamented upper valve of productids, with the resupinate shape forming a "snorkel-like" respiratory margin as in productids.

These three points are considered seriatum below:

1) While it is true that some pteriids are equivalved or nearly so (Pl. 12, figs. 25, 27 & 35), there are so many exceptions (Pl. 12, figs. 30, 32 & 41), all of which are epibysate, that the inequivalved condition of P. fasciculata need not imply a productid-like life mode. Similarly, some pteriids are indeed thin-shelled (e.g., Pterelectroma Iredale and Electroma Stoliczka), but many are not (e.g., various species of Pinctada and Pteria), or at least they show no obvious differences in relative shell thickness from the pterineids described herein (except Glyptodesma buchanensis,
which is massively thickened umbonally, and which shows a correspondingly unusual life mode, as discussed on p. 251-256). Judging from Bailey's figures, the shell of *P. fasciculata* seems thicker than usual for pterineids and pteriids (although I have no quantitative data for this), but it does not seem exceptionally thick and, in the absence of other special modifications (see below), need not imply a mode of life significantly different from that of living pteriids.

2) Are the so-called "unique modifications" of *P. fasciculata* really unique, as Bailey suggests? As already noted, some free-swinging pteriids are rather strongly inequivalved, almost to the same degree as *P. fasciculata* (compare Pl. 12, figs. 9 & 30). The anterior auricle of *P. fasciculata* (see Bailey 1983, fig. 7C, D) is no more inflated than in *Pteria penguin* Röding (Pl. 12, figs. 28-32). The byssal sinus is, in fact, less pronounced than in the type species of *Pteria*, *Pteria hirundo* Linné (Pl. 12, figs. 33-35; also, Hertlein & Cox, in Moore 1969, fig. C38, 4b), and a permanent byssal gape and deep byssal "groove" occur in many pteriids, such as *Pteria*, *Pinctada* and *Electroma* (Pl. 12, figs. 27, 29, 30, 32, 35, 40 & 41). The relevance of the ornament pattern in *P. fasciculata* is discussed later.

According to Bailey (1983: 216), "Neither anterior nor posterior byssal/pedal retractor scars are in evidence" in *P. fasciculata*, and from this he concluded (p. 223) that the byssal musculature was weakly attached to the shell. However,
judging from his figures, both posterior and anterior retractor scars appear to be present, as in the Australian species Ptychopteria (Cornellites) catellus n. sp. (Text-fig. 22). Bailey's fig. 8B is reproduced here in Pl. 11, fig. 13, and shows a prominent anterodorsal evagination of the posterior adductor scar that is here interpreted as a posterior pedal retractor scar. The groove extending above this scar in the left valve, interpreted by Bailey as the pallial line, is the inner edge of the posterior internal ridge. The posterior part of the pallial line does not appear to be preserved in specimens of P. fasciculata figured by Bailey (1983), nor is it visible in P. catellus n. sp., but in both species, it probably extended from the dorsal edge of the posterior adductor scar toward the posterior dentition, as in Ptychopteria sp. A (Pl. 14, fig. 8), Tolmaia erugisulca n. sp. (Pl. 15, fig. 10), Limoptera murrumbidgeensis n. sp. (Pl. 19, figs. 1 & 3), and the pteriid Pinctada (Newell 1937, figs. 1 & 2). Two internal molds of left valves figured by Bailey (1983, fig. 9C, E; the latter is reproduced here in Pl. 11, fig. 14) show a small projection anterodorsal to the anterior adductor scar that probably represents an anterior pedal retractor scar, as in P. catellus n. sp.

3) It is true that P. fasciculata is "boat-like" in anterior profile, but so are epibyssate pteriids, such as Pteria penguin and at least some specimens of Pteria columbus Röding (Pl. 12, fig. 30, and Stanley 1972, text-fig. 24B, respectively). Likewise, various pseudomonotids have a flat
to concave right valve and a highly inflated, almost hemispherical, left valve, and in fact, are more "productid-like" than is *P. fasciculata* (see Newell 1937, pl. 17, and Logan 1967, pl. 3). Yet there is strong evidence that the Pseudomonotidae were entirely epifaunal in habit, and attached by the right valve by a byssus or by a byssus early in ontogeny and by cementation later (Newell & Boyd 1970). Consequently, the "boat-like" profile of *P. fasciculata* need not imply a productid-like habit.

The productid shown by Bailey in his fig. 11, which he based on Grant (1966, 1968), is inaccurately illustrated, and portrays a greater degree of similarity with *P. fasciculata* than really exists. In the productids described by Grant, the margin of the upper valve is much more strongly upturned, and the main part of that valve more deeply sunken below the edge of the lower valve than in *P. fasciculata* (see Grant 1966, pl. 131, figs. 1 & 4; 1968, figs. 2c & 5). Contrary to Bailey's illustration, it is doubtful that a gape between upper and lower valves would be visible in these productids when viewed end on, unless the valves gaped very widely.

The shell edge of *P. fasciculata* is really no more "snorkel-like" than in *Electroma* and *Pterelectroma* and various species of *Pteria* (Pl. 11, figs. 8 & 9; Pl. 12, figs. 30 & 32), all of which are epibyssate. In none of these, nor in any known pteriid or pterineid, is a pronounced trail produced, comparable to that in *Atremapella* n. gen. and various species of *Exogyra*, bivalves for which a
productid-like habit can be reasonably argued (see p. 87-101 for discussion). Interestingly, in Recent pteriid species, including species of *Pteria* and *Pinctada*, and especially species of *Electroma* and *Pterelectroma*, the shell margin is remarkably flexible and the right valve bends distally to conform to the inner surface of the left valve when the valves close. Correspondingly, in most pteriid species, the nacreous layer in the right valve does not extend as far distally as in the left valve (pers. obs., e.g., Pl.12, fig. 16). In *Electroma* (Pl. 12, fig. 25) and *Pterelectroma*, the shell appears biconvex and more or less equivalved when the valves gape, but when tightly adducted, the edge of the right valve is flexed and a "pseudotrail" is formed (Pl. 11, figs. 8 & 9; the "pseudotrail" is unnaturally accentuated in these specimens [especially fig. 8] owing apparently to drying and shrinkage of the adductor muscle in museum specimens, which causes the right valve to be excessively "pulled into" the left valve), but this is obviously totally unrelated to a productid-like habit, as these forms live suspended from marine plants and alcyonarians, respectively.

The shell edge in *P. fasciculata* and the species of *Ptychopteria* (*Cornellites*) described herein (except *P. sp. B*) is somewhat different. The right valve is more strongly concave than in the gaping shell of *Electroma* and *Pterelectroma* (though only moderately more so than in some specimens of *Pteria penguin*), and the left valve shows greater overlap of the right valve [Pl. 13, figs. 3 & 9; Pl. 14, fig. 2]). The "exposed" internal border of the left valve
may have been covered by periostracum of the right valve when the shell was closed, as in other pteriomorphs such as Trisidos yongei Iredale (pers. obs.) and various oysters (Stenzel, in Moore 1971: N977-N978). The periostracum, being pliable, conforms closely to the inner surface of the left valve when the valves close, producing a tight seal (ibid.: N977). Also, the actual calcareous edge of the right valve of P. fasciculata (and by inference other P. (Cornellites) spp.) was probably flexible as indicated by microstructural evidence provided by Carter and Tevesz (1978a). These authors (1978b) discussed the functional significance of this type of valve closure, and it does not appear to be necessarily related to a "snorkel-like" function, nor does it necessarily imply a productid-like habit. Neither does it imply ipso facto an epibyssate free-swinging habit, since various Gryphaea-like oysters, all of which live with the convex left valve undermost, show a microstructurally and functionally similar pattern to that in P. fasciculata (Carter & Tevesz 1978a: 875-877). The point is that the form and function of the shell edge in P. fasciculata is equivocal in the determination of a left-sided productid-like habit or a right-sided epibyssate habit.

Similarly, the distribution of ornament in P. fasciculata is equivocal relative to this discussion. Certainly, the convex valve is more strongly ornamented as in productid brachiopods. Most Recent pteriids lack conspicuous radial ribs (although radially distributed periostracal structures are not uncommon); however, many pectinaceans and
pseudomonotids show the same distribution of ornament as *P. fasciculata*, yet lived (or live) epifaunally with the flatter right valve undermost (e.g., *Pseudomonotis equistriata* and *Pseudomonotis speluncaria*; see Newell & Boyd 1970, figs. 11D & E, and Logan 1967, pl. 3, respectively; also, *Acanthopecten* Newell and *Cyclopecten* Verrill; see Moore 1969, figs. C60, 1a & b, and C75, 2a & b, respectively).

At least one other objection to Bailey's hypothesis should be noted - that is, the extrusion of the byssus through the byssal notch in the right valve seems utterly ill-suited for the left-sided orientation of the three *P. fasciculata* individuals shown in his fig. 6 and the lowermost of the two shown in his fig. 5. The loosely tethered habit depicted for these shells violates Stanley's (1972: 191) "tight-clinging rule" for byssate bivalves (rare exceptions to this rule noted by Stanley, including *Musculus* Röding and *Lima scabra* (Born), are morphologically and ecologically inappropriate as analogues of *P. fasciculata*). Shells of *P. fasciculata* in this orientation would seemingly be very unstable and easily overturned. The auricle/byssal notch complex described by Stanley (1970: 31-32 & 1972: 184) would probably have little stabilizing effect, as this complex "...is only useful for attachment to hard substrate, which the auricle cannot penetrate" (ibid.: 184). According to Bailey (1983), some specimens of *P. fasciculata* occur in dark argillites, which he interpreted as originally representing a muddy substrate that was probably too soft to support
relatively heavily shelled bivalves, such as *Gosseletia* Barrois (ibid.: 234). Other specimens occur in rocks representing an originally sandier and presumably firmer substrate (ibid.). Even if this substrate were sufficiently cohesive to oppose at least partially penetration by the auricle, difficulties remain. Byssal threads draped over the margin of the left valve (note especially lowermost individual of *P. fasciculata* in Bailey's fig. 6), when acted upon by the contraction of the byssal retractor muscles, would have the presumably negative effect of raising the posterior part of the shell, and thus presenting it to whatever factors, whether predators or turbulence, might be acting to dislodge the shell. If the shell was lightly buried, as in Bailey's fig. 11, and the byssus extruded more or less parallel to the commissural plane, the above objection would not apply. It is questionable, however, whether a byssus in this orientation could provide adequate anchorage under such a thin covering of sediment. Also, the byssal threads are oriented at a mechanically inefficient angle (i.e., horizontal) relative to potential forces acting to exhume the shell (these and other problems associated with extrusion of a byssus by left-convex, left-sided pleurothetic pterioids have already been discussed for *Atremapella* (p. 103-104), and the objections raised there apply here, as well).

Were some pterineids endobyssate? Stanley (1972: 184) argued that the anterior auricle/byssal notch complex and
flattened lower (right) valve which characterize many living pteriids and pectinids, function to stabilize the shell in an epibyssate habit with the commissural plane at a low angle. He noted, however, that "In many pterineids these adaptations are poorly developed or absent", and instead, the shell tends to be nearly equivalved, with "...a broadly rounded or lobate anterior and shallow byssal sinus..." (ibid.: 184). He further observed, "...whereas nearly all modern adult pteriids are monomyarian, a substantial portion of pterineids were dimyarian..." (ibid.: 184). By analogy with groups known to be endobyssate (such as the Modiolinae), Stanley concluded (p. 184), "...the anterior adductor, rounded or lobate anterior, and approximate bilateral symmetry are pterineid characters associated with upright or oblique attachment in soft sediment." On this basis, Stanley (1972, text-figs. 17 & 18) reconstructed the pterineids Actinopteria, Leptodesma and Pteronites Hall in an endobyssate life mode. Although these conclusions have received some acceptance elsewhere (e.g., Bowen, et al. 1974; Thayer 1974; McGhee 1976; Bailey 1983), they are here considered improbable, or at best, poorly supported.

Stanley misappropriates the significance of the anterior adductor muscle. While the lack of an anterior adductor implies a probable attached epifaunal habit (Yonge 1953a), its presence is equivocal, since it occurs in both endobyssate and epibyssate mytilids, arcids (Stanley 1972), and myalinids (Newell 1942, fig. 6). Furthermore, whereas an anterior adductor scar is clearly present in various
pterineids showing epibyssate adaptations (such as
*Ptychopteria (Cornellites) fasciculata*, Bailey 1983, fig. 8;  
*Ptychopteria (Cornellites) catellus* n. sp., Pl. 13, fig. 1,  
this paper; *Pterinea laevis* Goldfuss, Frech 1891, pl. 2, fig.  
11), it has not, to my knowledge, been reported in any of the  
taxa regarded by Stanley as endobyssate. Indeed, *Actinopteria  
murrindalensis* n. sp. and *Actinopteria cf. A. murrindalensis*  
(described herein), the only species of *Actinopteria* for  
which muscle scars are clearly known, lack an anterior  
adductor scar. As for the two remaining alleged endobyssate  
features (a nearly equivalved shell and a rounded or lobate  
anterior), both features are widely represented among living  
pteriiids, all of which are epibyssate (e.g., Pl. 12, figs.  

Plate 12 emphasizes the basic similarity in overall  
shell form between alleged endobyssate pterineids (Pl. 12,  
figs. 1-6, 10 & 11) and various epibyssate pteriids (Pl. 12,  
figs. 14-41). While there are obviously some differences in  
detail between the pterineids shown and their closest living  
counterparts, particularly in ornamentation and the outline  
of the anterior auricle, these differences seem minor, and it  
would be a hazardous exercise to argue a fundamentally  
different life mode for the two groups on the basis of such  
differences. The only major difference cited by Stanley,  
which would at first seem to be of ecological significance,  
is in the modification of the shell associated with the  
extrusion of the byssus.
In the majority of the pteriids that I have observed, a strong byssal notch and often a permanent byssal gape are developed in the right valve (as in pectinids) through which the byssus is extruded (e.g., Pl. 12, figs. 29, 30, 35, 37, 38 40 & 41). In some species the left valve may be involved in the formation of the gape (e.g., Pl. 12, figs. 30 & 35), but usually to a lesser degree. While many pterineids show a pteriid-like byssal notch and gape (e.g., Pl. 12, fig. 8; Pl. 18, fig. 15), those thought by Stanley to be endobyssate apparently do not, and presumably the byssus was extruded as in mytilids, which lack a byssal notch and gape or else exhibit a very narrow slit-like gape that affects both valves equally.

Again, Stanley misappropriates the significance of these differences. While the presence of a byssal notch and markedly asymmetrical byssal gape would imply an epibyssate pleurothethic habit (Yonge 1953a), their absence need not imply an endobyssate habit, since both endobyssate and epibyssate mytilids lack a byssal notch and a comparable byssal gape. As for the byssal sinus of the left valve, a full spectrum in its relative development is present among living epibyssate pteriids, ranging from prominent (Pl. 12, fig. 14) to shallow (Pl. 12, fig. 21) to nearly absent (Pl. 12, fig. 26), as in fossil pterineids. The adaptive significance of these variations is unclear, since various species of Pteria that differ in the relative development of the sinus (compare, e.g., Pl. 12, figs. 14 & 36) live in apparently the same manner (i.e., attached to alcyonarians).
Clearly, careful anatomical and field studies of such living pteriids are required to provide a basis for interpretation of variations in the shape of the auricle (and other shell features) of fossil pterineids.

Living species of *Pteria* characteristically attach to alcyonarian branches in such a way that the byssal notch and gape of the right valve is closely appressed to the branch which in turn passes over the body of the right valve (Pl. 11, figs. 10-12). The lack of a byssal notch and gape in the right valve of pterineids such as *Actinopteria* and *Leptodesma* would presumably have allowed the object of attachment, if branch-like, to pass over either valve. Alternatively, the lack of a pteriid-like notch and gape, coupled with the presence of only a very shallow byssal sinus, may have enabled such shells to orient with the anterior margin directly adjacent to the object of attachment and with the commissural plane vertical to the surface of that object, as in *Mytilus*.

On the basis of the above discussion, Stanley's hypothesis of an endobyssate habit for the aforementioned pterineids seems unconvincing. By analogy with Recent pteriids, such pterineids are better interpreted as epibyssate. This conclusion, coupled with the recognition of the Rhombopteriidae as the most probable ancestral group of the Pterineidae, carries important implications concerning the early adaptive history of the Pterineidae. Stanley (1972) suggested that the Pterineidae arose at a vertically
endobyssate grade of evolution, and stated (p. 184), "The diversity of post-Ordovician endobyssate pterineids suggests that epifaunal pterineids arose polyphyletically." The fact that no known pterineids can be satisfactorily shown to have been endobyssate casts serious doubt on these views. More importantly, an inequivalved shell is apparently primitive rather than derived for the Pterineidae, having been inherited from rhombopteriid ancestors. An inequivalved shell is normally associated with a pleurothetic habit (Yonge 1953a); consequently, a pleurothetic habit is probably primitive for the Pterineidae, and a vertical habit (such as that exhibited by *Glyptodesma buchanensis*, p. 251-256), derived.

The alleged *Actinopteria decussata* - *A. taberi* - "Cornellites" *chemungensis* lineage (McAlester 1962a; see Pl. 12, figs. 11-13, this paper) cited by Stanley is unacceptable as evidence for a transition from endobyssate to epibyssate habits for several reasons:

1) The presumed intermediate Alaskan species, *Actinopteria taberi* McAlester, is known from very poorly preserved specimens, is far removed geographically from the other two species, which occur in New York State, and apparently occurs in a separate faunal province that was isolated from the eastern North American faunal provinces by the Transcontinental Arch (Bailey 1978; see also Carter & Tevesz 1978a, text-fig. 1). That such a lineage can be recognized under these circumstances and on the basis of
external features alone seems, at best, doubtful. The present investigation reveals that some pterineids placed by various authors in the same genus on the basis of broad similarities of shell outline and ornament differ considerably in musculature and dentition, and are only distantly related (see discussion on p. 169 concerning the assignment of species to Actinopteria, Tolmaia and Ptychopteria (Cornellites)).

2) Actinopteria was probably not endobyssate, as already discussed.

3) Alleged morphological changes involved in the transition are listed by Stanley (1972: 184). Most of the important differences separating end members of the proposed lineage occur between various living pteriids, all of which are epibyssate in habit (note, for example, differences in the relative convexity of the valves and the obliquity of the shell body in Pteria hirundo and Pinctada sp., or Pteria penguin, Pl. 12, figs. 28, 30, 33, 35, 39 & 41). Such differences, therefore, need not imply endobyssate versus epibyssate life modes for A. decussata and "C." chemungensis, respectively.

Stanley (1975) believed that the aberrant Ordovician bivalve, Ahtioconcha, possibly the earliest known pteriacean (Pojeta 1971), was transitional both morphologically and in life mode, between inequivalved epifaunal pterineids and infaunal equivalved ancestors. But on what basis is
Ahtioconcha referred to the Pteriacea? As Stanley himself noted, the shell outline is modioliform, not pteriiform. According to Eberzin (in Orlov 1960: 75), the hinge is edentulous. As discussed earlier (p. 65), present evidence indicates that the Pterineidae were primitively strongly dentigerous, as are Pteronitella and Coppinsia. The earliest known undoubted pteriaceans, though probably not the most primitive dentally (see p. 65), have relatively well developed dentitions (Pojeta 1971, pl. 11, figs. 9-11). The only pteriacean-like character of Ahtioconcha is the inequivalved shell. Even in this character, Ahtioconcha is not really pteriacean-like. Unlike the Pterineidae, the inequivalved shell is apparently produced simply by a lateral bend in the shell and not by any real decrease in the convexity of the right valve (Stanley 1975: 370). Is this sufficient evidence to warrant placement of Ahtioconcha in the Pteriacea? Inequivalved shells have arisen among many non-pteriomorph groups that are normally equivalved, such as the Modiolinae (e.g., Stavelia Gray and Fluviolanatus Iredale; Nichols 1958) and the Unionidae (e.g., Arconaia Conrad; Haas, in Moore 1969, fig. D18, 5). The possibility that Ahtioconcha represents an early example of this kind can not be ruled out. Without information concerning the ligament structure, Ahtioconcha cannot be confidently assigned to the Pteriomorphia, let alone the Pteriacea, and therefore, it is presently of little or no value in elucidating the early adaptive history of that superfamily.
Function of the posterior auricle-embayment-sulcus complex. A wing-like posterior auricle is a common feature in the Pteriidae and Pterineidae, and also occurs in other groups, such as the Bakevellidae and Myalinidae, though less frequently. The auricle is typically undercut by an embayment, which is expressed ontogenetically as a sulcus. Although widespread both taxonomically and stratigraphically (Ordovician-Recent), and hence, of obvious adaptive importance, this character complex has been the subject of surprisingly few functional investigations. Stanley (1972) provided the most recent treatment of the problem, and briefly discussed the views of other workers, including Yonge (1953a) and Kauffman (in Moore 1969). Yonge (1953a) noted that the occurrence of the exhalent current at the site of the posterior embayment effectively separates it from the inhalent area. Kauffman's views were summarized by Stanley (1972: 190) as follows: "....the pteriid auricle serves to aid the animal in swinging to an orientation parallel to environmental water flow, which allegedly aids in feeding and waste removal." Stanley (1972) provided the first experimental evidence relative to the problem. He observed that the extended posterior wing of the Recent pteriid Pteria colymbus, when oriented with the dorsal margin facing into a current, acts as a baffle that deflects the current around the exhalent discharge of the animal. This allows the exhalent discharge to proceed relatively farther from the shell, thereby providing more efficient separation of inhalent and exhalent currents. Stanley (p. 191) suggested
that this functional interpretation could be applied to all bivalve taxa with wing-like posterior auricles.

Major difficulties with Stanley's hypothesis are as follows:

1) The postulated function can occur only if the shell is oriented with the commissural plane essentially parallel to the current and the dorsal shell margin facing upstream (Stanley 1972: 191). However, pteriids attached to alcyonarians show random azimuth orientations even where other organisms are current oriented (ibid.: 191). Consequently, very few individuals in such settings are oriented in the appropriate manner for the auricle to function as Stanley suggests. Stanley apparently anticipated such objections, and argued (p. 191) as follows: "Considering the variety of water currents encountered in most habitats, the device should be of value to nearly every individual during at least part of its feeding time." It should be remembered, however, that the alcyonarian colonies to which species of *Pteria* typically attach, are flexible and bend in currents (Stanley 1970: 32). Consequently, even if water currents strike the shell in the manner required for Stanley's hypothesis, it seems doubtful that the shell could maintain such an obviously unstable hydrodynamic position for any significant length of time. More likely, the branch to which the shell was attached would simply rotate or bend until the shell was in a more hydrodynamically stable position. This seems especially likely for species of
Electroma (Pl. 12, figs. 23-27), which attach to flimsy marine plants.

2) Unlike the specimens of *P. columbus* figured by Stanley (1972, text-fig. 24), the posterior auricle in many pterineids and some pteriids is not markedly extended from the shell body, and the posterior embayment is weak (e.g., Pl. 12, figs. 1, 2, 5, 11, 17, 18, 22-24, 26, 36 & 37); see also bakevellids in Stanley 1972, text-fig. 19A & B). It is difficult to imagine that the posterior auricle in these forms could function in any significant capacity as a baffle to enhance exhalent flow.

An alternative hypothesis for the posterior auricle-sulcus-embayment complex is suggested here on the basis of preliminary observations of current flow over the shell of the Recent pteriid *Pinctada sugillata* Reeve. As shown in Text-fig. 19A-D, current flow is deflected and channeled across the exhalent area by the posterior auricular sulcus, when the shell is oriented with the dorsal margin and commissural plane essentially parallel to the current, and the anterior margin facing upstream. Experiments were not conducted for other orientations.

Kauffman (in Moore 1969) predicted such a channelling effect on pteriiform shells oriented more or less as in Text-fig. 19A-D. The significance of this channelling, he suggested (p. 146), would be to "...further insure rapid removal of waste and prevent deleterious concentration of
Text-fig. 19. A-B) Living specimen of *Pinctada sugillata* Reeve, X1.3, in flume tank; commissure parallel with current flow; current flowing left to right at 8 cm/sec; A) ink released on shell body immediately behind anterior auricle; B) ink released just above and slightly anterior to umbones; C-D) drawings of A & B above; E) same specimen as above (in still water), posteroventral view, stereo pair; arrows show exhalent and inhalent currents; note mantle edges in apposition between exhalent and inhalent apertures (dark patches).
these products in the water surrounding the shell" (see also Bailey 1983: 223). While channelling of water flow by the posterior auricular sulcus appears to be a real phenomenon, it is doubtful that waste removal represents its primary function. Stanley (1970 & 1972) showed that the exhalent current in *Pteria* and *Pinctada* is quite powerful and is apparently adequate to eject expended water well away from the shell. Consequently, the channelling of water over the exhalent area for this purpose seems redundant. It is suggested here that channelling is instead related to the generation of passive water flow into the shell.

An important feature of pteriiform shells that are oriented approximately as in Text-fig. 19A-D relative to environmental currents, is that water flowing over the exhalent area must first pass over the greatest convexity (or camber) of the shell (Text-fig. 20A). This, coupled with the channelling effect of the posterior sulcus, would presumably cause more rapid water flow over the exhalent margin than over the inhalent margin. Consequently, one would predict that an area of low pressure would occur at the exhalent margin (see also Bailey 1983: 223), with relatively higher pressure present along the inhalent margin (Text-fig. 20B). This in turn would presumably create differential hydrostatic pressure within the mantle cavity, thereby causing passive water flow into the shell along the inhalent area. Such a system would clearly be of major adaptive importance in that metabolic energy expended by cilia to ventilate the mantle cavity would be greatly supplemented.
Text-fig. 20. A) Anteroposterior cross-sectional profiles of *Pinctada sugillata* Reeve, uncatalogued specimen, personal collection (PAJ): i) section across dorsal part of shell, through posterior embayment and parallel with hinge axis; ii) section through ventral part of shell and parallel with hinge axis; arrows show relative effect of camber on current flow. B) Idealized pteriiform bivalve showing inferred water flow (solid arrows) over left valve, inhalent and exhalent currents (broken arrows), and inferred distribution of high (H) and low (L) pressure areas adjacent to respiratory margin. C) Approximate range of orientations (stippled) suitable for passive ventilation in idealized pteriiform bivalve with commissure parallel to current flow; rings joining pairs of shells indicate that for any one of orientations shown, shell can be rotated through 360 degrees about an axis parallel with current flow, without altering relationship between current flow and shell surface. D) Left - idealized pteriiform bivalves attached to alcyonarian (compare with Kauffman, in Moore 1969, fig. 87,6); right - same bivalves in current showing hypothesized tendency for shells to become oriented in positions suitable for passive ventilation.
This hypothesis of passive ventilation could in principle be tested by filling empty articulated pteriid shells with artificial material in such a way as to leave a space equivalent to the original mantle cavity. The shells could then be subjected to currents in a flume tank as in Text-fig. 19A & B, to see whether shell form alone is sufficient to generate ventilation of the mantle cavity. If the shape of the mantle cavity could not be adequately simulated, live animals subjected to a cilia-inhibitor could be used instead. If passive ventilation was shown to occur, the relative contribution of the posterior sulcus could be tested by artificially filling in the sulcus and then observing the effect on the rate of inhalent flow.

One would expect that passive ventilation for an idealized pteriid, aligned with the commissure parallel to current flow, would occur through a limited range of shell orientations, approximately as shown in Text-fig. 20C. Essential aspects of these orientations are: 1) the exhalent margin faces broadly downstream; and, 2) the exhalent area is preceded by relatively greater camber of the shell surface than the inhalent area. I am uncertain how much lateral deviation of the commissural plane from the current direction would be admissible. No doubt the range of effective orientations for passive ventilation in living pteriids would vary to some extent with differences in shell shape and convexity. But, I would expect that in every instance the essential aspects of orientation noted above would apply.
Differences in hydrostatic pressure along the shell margin would presumably be diffused if the mantle margin was open along its entire length. It is important to note, therefore, that in *P. sugillata* restricted inhalent and exhalent appertures are created by apposition (not fusion) of the mantle edges along much of the shell margin (Text-fig. 19E). I am uncertain how widespread this ability is among the Pteriidae (Yonge [1957: 154] mentioned its occurrence in the Arcidae).

The passive ventilation hypothesis, as an explanation of the function of the posterior auricle-embayment-sulcus complex, would at first seem to suffer from some of the same difficulties as Stanley's (1972) hypothesis. As noted earlier, pteriids attached to alcyonarians show random azimuth distributions, and consequently, seemingly few individuals would be oriented in the appropriate manner for the postulated passive ventilation system to take effect. It may be, however, that the habit of attaching to flexible objects is in fact fundamentally related to passive ventilation. Stanley (1970: 136; 1972: 189) observed that species of *Pteria* typically attach on alcyonarians with the posterior wing pointing upward (see also Reeve 1857, pl. 9; O'dhner 1917, pl. 1, figs. 6-8; Stanley 1972, text-fig. 24; Powell 1979, pl. 72A; Coleman 1981: 163; and Pl. 11, figs. 10-12). As shown in Text-fig. 20D, pteriids positioned in this way would tend to become oriented with the posterior auricle pointing more or less downstream (and hence, in an appropriate position for passive ventilation) as the
alcyonarian bends in the current. Where the auricle is strongly extended, it probably acts as a rudder (Kauffman, in Moore 1969) and aids in swinging the shell into a position suitable for passive ventilation.

Passive ventilation is probably more important in some pteriids than in others. It may be that species in which the posterior auricle-embayment-sinus complex is poorly developed or absent do not utilize passive ventilation to any significant degree (e.g., *Pinctada margaritifera* [Linne], Hertlein & Cox, in Moore 1969, fig. C38, 5 & *Electroma punctulata* Reeve, Pl. 12, figs. 26-27, this paper). The passive ventilation hypothesis seems applicable to all pteriomorphs having a well developed posterior auricle-embayment-sinus complex. Many of these (e.g., various isognomonids and myalinids [Stanley 1972, fig. 14]) probably lived on the substrate surface as do most species of *Pinctada*, instead of attaching above the substrate, as do species of *Pteria*. In some pteriomorphs, such as *Atremapella* (Pl. 6, figs. 2 & 11) and the arcoid *Cucullaea forbesi* Pictet & Campiche (Eberzin, in Orlov 1960, pl. 2, fig. 13b), the posterior auricle-embayment-sinus complex is extremely weak and seems inappropriately positioned to have functioned in passive ventilation (in *Atremapella*, for example, the posterior embayment occurs well above the exhalent area [Pl. 8, fig. 13]). Furthermore, some of these forms are inappropriate in their life mode for passive ventilation, being wholly or partly buried in the substrate (e.g., *Atremapella* and probably *C. forbesi*). Consequently, other
explanations must be sought for the function of the posterior auricle-embayment-sinus complex in these instances. In C. forbesi, the posterior embayment seems to be associated with the junction of the hinge plate and the posterior shell margin (Eberzin, in Orlov 1960, pl. 2, fig. 13b). In Atremapella, the posterior embayment appears to represent a flexure of the mantle associated with the termination of the trail posteriorly (Pl. 6, fig. 2), but this requires further study.

Clearly, many field and experimental observations are required to verify that passive ventilation actually occurs in Recent pteriids and to determine its relationship to various aspects of the structure, behaviour and ecology of these animals. The passive ventilation hypothesis seems to be of greater heuristic value than Stanley's "current baffle" hypothesis for several reasons: 1) passive ventilation is likely to occur over a greater range of shell orientations than is the baffle effect; 2) these orientations are more stable hydrodynamically and hence, are more likely to be realized in nature; 3) passive ventilation seems directly correlatable with the tendency for attachment on flexible objects with the posterior auricle facing upwards - Stanley's hypothesis bears no obvious relationship to this habit.

Life habits of some fossil pterineids. Some pterineids have been interpreted as endobyssate (Stanley 1972), and at least one species is thought to have been productid-like in habit (Bailey 1983). In the previous discussions, I have
attempted to show that the evidence presented in support of these hypotheses is either misappropriated or equivocal. Comparisons of these pterineids with modern pteriids (all of which are epifaunal and almost all, byssate) substantial similarities (Pl. 12) that are here interpreted as indicating a similar life mode. Potential sources of evidence, apart from morphological evidence, that might be used to support alternative hypotheses include: the distribution of pre-mortem wear and epibionts on the shell surface, geopetal structures, and observations of articulated specimens preserved in situ. (Examples of the use of these types of evidence in the interpretation of the life mode of various pteriomorphs can be found in Pojeta [1971: 34], Tanabe [1983], and p. 92-101, 251-256 of the present study.) Neither Stanley (1972) nor Bailey (1983) presented such evidence, and I am unaware of any evidence of this nature for pterineids that would suggest anything other than a right-sided pleurothethic or vertical epibyyssate habit. (Glyptodesma buchanensis appears to be a partial exception in that the byssus was apparently lost at advanced growth stages; this species was nonetheless epifaunal [see p. 253]).

As earlier discussed and as shown in Pl. 12, many of the variations in shell characters that occur in the Pterineidae also occur in living pteriids (although not always in the same combinations). In both groups the shell may be inequivalved to nearly equivalved and strongly prosocline to suborthocline. The posterior auricle-embayment-sulcus complex may be well developed or subdued, and much of the variation
in the shape and prominence of the anterior auricle and byssal sinus in the Pterineidae also occurs in the Pteriidae.

As noted earlier, the adaptive significance of such variations in the Pteriidae is unclear, since species apparently having a very similar life mode (e.g., attached to alcyonarians) may differ considerably in shell characters. It is difficult or impossible, therefore, to determine the functional significance of comparable variations in fossil pterineids. Among Recent pteriids, a moderately to strongly prosocline shell and a well developed posterior auricle-embayment-sulcus complex seems to correlate with attachment to flexible organisms above the substrate (i.e., an epiphytic habit, p. 24). However, the absence of, or weak expression of, one or more of these characters need not imply a non-epiphytic habit, since Electroma (Pl. 12, figs. 23-27) and at least one small species of Pinctada (Allan 1959, pl. 320) attach to marine plants.

Excluding G. buchanensis for the moment, the seven other species of pterineids described below are here interpreted as epibyssate, on the basis of analogy with Recent pteriids. Of these species, Ptychopteria catellus n. sp., Ptychopteria sp. A, Ptychopteria sp. B, Actinopteria murrindalensis n. sp., Actinopteria cf. A. murrindalensis, and Tolmaia erugisulca n. sp. show a generally well developed posterior auricle-embayment-sulcus complex and are moderately to strongly prosocline. It is tentatively suggested, therefore, that these species were epiphytic on flexible organisms,
probably algae or crinoids (p. 24-25). As in Recent pteriids, some individuals probably occasionally attached to inanimate objects.

At early growth stages, the shell of *Limoptera murrumbidgeensis* n. sp. is conspicuously prosocline, with a prominent anterior auricle, byssal sinus, and byssal notch, and a well developed posterior auricle-embayment-sulcus complex (Pl. 18, fig. 15; Pl. 19, fig. 10), as in the adult shells of the aforementioned pterineids. However, at advanced growth stages, the shell of *L. murrumbidgeensis* n. sp. is more orthocline, the posterior auricle-embayment-sulcus complex is obsolescent, the anterior auricle is proportionally smaller, and the byssal sinus and notch tend to become reduced (Pl. 19, figs. 2, 4 & 12). Consequently, the adult shell outline of *L. murrumbidgeensis* n. sp. resembles those of *Pinctada* spp. more than do the outlines of the other species of pterineids listed above. These observations suggest that *L. murrumbidgeensis* n. sp. may have undergone a change in life habit during ontogeny. At least one species of *Pinctada*, *P. maxima* Jameson, breaks free of its byssus and lies freely on the substrate, after reaching a shell diameter of about 20 mm (Allan 1959: 266; I am uncertain to what extent this change in habit is reflected in shell morphology). *L. murrumbidgeensis* n. sp. may have undergone a comparable change in habit, perhaps having been byssally attached and epiphytic at early growth stages and free-living on the substrate surface at later stages (Text-fig. 4).
It must be stressed that apart from being epifaunal and byssate, the life habits hypothesized for the pterineids described herein are tentative, as criteria for distinguishing epiphytic and non-epiphytic forms are poorly established. *G. buchanensis* is without analogues among Recent pteriids. The life mode of this species is discussed separately, beginning on p. 251.

Anterior and umbonal musculature in pterineids - All of the pterineids described in the present study show a small, usually deeply impressed muscle scar at the anterodorsal extent of the pallial line, immediately below the hinge plate, or within the umbonal cavity (Pl. 13, fig. 1; Pl. 14, fig. 3; Pl. 15, fig. 5; Pl. 16, fig. 6; Pl. 17, fig. 8; Pl. 18, fig. 2; Pl. 21, fig. 2). This scar is similar in size and position to the reduced anterior adductor scar of the Mytilacea (Newell 1942: fig. 6A, D) and certain myalinids (ibid., fig. 6E-G) and ambonychiids (Pojeta 1966: pl. 36, figs. 1 & 2). However, in some of the pterineids described herein, including *Glyptodesma buchanensis*, *Limoptera murrumbidgeensis* n. sp., and some specimens of *Actinopteria cf. A. murrindalensis*, the anterodorsal scar occurs on the underside of the auricular buttress (Pl. 18, figs. 2, 4 & 12; Pl. 21, figs. 1-4), and consequently, any muscle originating from that scar could not have extended unobstructed to the corresponding scar of the opposite valve. It is more probable, therefore, that the scar in these species represents the insertion of a pedal retractor muscle
(Runnegar [1970] used the same logic in identifying the anterodorsal scar of *Eurydesma* Morris as the insertion of a pedal retractor, rather than of an adductor muscle).

Additional information available for *G. buchanensis* supports this interpretation for at least that species. Close examination of well preserved specimens reveals that the pallial line is not obliterated where it meets the anterodorsal scar. Instead, it dips downward onto the anterodorsal wall of the depression that is formed in the valve floor by the scar, but not onto the scar itself, and then emerges from the depression and continues dorsally (this is faintly visible in Pl. 21, figs. 2 & 3). The adductor muscles of bivalves are thought to have evolved by local enlargement and cross-fusion of pallial muscles in the depth of the anterior and posterior embayment of the mantle (Owen 1958; Yonge 1953a). By this analysis, the adductor scars are essentially pronounced enlargements of the pallial line. The fact that the pallial line of *G. buchanensis* is not modified where it passes near the anterodorsal scar indicates that the muscle that inserted in that scar was not a homologue of the pallial musculature (and hence, not an adductor); more likely, it was a pedal retractor muscle.

The anterodorsal scar of *A. murrindalensis* n. sp. is presumably homologous with that of *A. cf. A. murrindalensis*, although it is not so completely obstructed by the auricular buttress (Pl. 17, figs. 8-15). The identification of the anterodorsal scar of *Tolmaia erugisulca* n. sp. is uncertain.
The scar occurs in an anatomically comparable position to that in *Actinopteria*, that is, on the lower, inner edge of the auricular buttress (compare Pl. 15, fig. 10 with Pl. 17, figs. 8 & 12). However, it is somewhat larger than in *Actinopteria*, is significantly larger than other pedal retractor scars in the umbonal cavity, and is never completely obstructed by the auricular buttress. It is therefore tentatively interpreted as a markedly reduced anterior adductor scar.

The anterodorsal scar in *Ptychopteria* (*Cornellites*) spp. is relatively larger than in the aforementioned pterineids (although still strongly reduced by comparison with isomyarian bivalves) and is here interpreted as an anterior adductor scar. The hinge plate in some specimens shows a slight embayment where it is in close proximity with the scar (e.g., Pl. 13, fig. 11; Pl. 14, fig. 12; see also *Ptychopteria* (*Cornellites*) *fasciculata* in Bailey 1983, fig. 8, B-D and Pl. 11, fig. 13, this paper). The presence of an embayment at this position suggests that the ventral growth of the hinge plate was here restricted by the need for the muscle originating from the anterodorsal scar to pass directly to the scar of the opposing valve, an observation consistent with the interpretation of this scar as the insertion of the anterior adductor muscle.

There is no consensus among palaeontologists as to the terminology for anterior and umbonal pedal scars in pterioids (compare, for example, Newell 1937, figs. 1 & 2; Newell 1942,
fig. 6C, E-G; Cox, in Moore 1969, fig. 34B; Runnegar 1970, fig. 1; Dickens 1981, fig. 1). In the present study, these scars have all been designated anterior pedal retractor scars.

Some specimens of *Tolmaia erugisulca* n. sp. (Pl. 16, fig. 6; Text-fig. 25) and at least one specimen of *Actinopteria cf. A. murrindalensis* (Pl. 18, fig. 2) show a few weak scars along the edge of the posterior internal ridge. This indicates that the posterior internal ridge in pterineids was associated with muscle attachment, possibly gill suspensors, by analogy with myalinids (Newell 1942, fig. 6, E & G). In the Rhombopteriidae, the inferred sister group of the Pterineidae, a posterior internal ridge is not developed, although at least one gill suspensor muscle scar (the Quenstedt scar) is present at an equivalent position anatomically (Pl. 4, fig. 10; Pl. 7, fig. 3; Pl. 11, fig. 1).
Genus Ptychopteria Hall 1883
Subgenus Cornellites Williams 1908

Type species: Ptychopteria - Ptychopteria eugenia Hall 1883, by subsequent designation of Miller 1889.
Cornellites - Pterinea fasciculata Goldfuss 1836, by original designation.

Ptychopteria (Cornellites) catellus n. sp.
(Pl. 13; Text-figs. 4, 17G & H, 21, 22 & 23)

Etymology: From catellus, L., young of an animal, alluding to the predominance of juveniles in samples of this species from the uppermost beds of the Receptaculites Limestone.

Holotype: ANU 36562.

Referred specimens: ANU 36563-36572 (paratypes); ANU 36573-36593; CPC F24900-F24902, F24998 (total, 35).

Type locality: Uppermost beds of Bloomfield Limestone at Locality R4, Parish of Cavan, Taemas area, about 25 km southwest of Yass, New South Wales.

Known stratigraphic and geographic distribution: late Emsian, Bloomfield, Receptaculites and Warroo limestones, Taemas Formation, Taemas area, New South Wales, and Receptaculites Limestone equivalent in the Taemas Formation, Wee Jasper area, New South Wales.
Diagnosis: Auricles separated from shell body by prominent sulci; radial ribs on right valve present on posterior auricle, anterodorsal half of anterior auricle, anterior half of shell body and variably on posterior half; orientation of anteriormost tooth changing through ontogeny from strongly opisthocline to moderately prosocline; seven to ten teeth present in the left valve at advanced growth stages, without edentulous gap between anterior and posterior teeth.

Description:

External features - The shell is inequilateral, prosocline and markedly inequivalved. The left valve is strongly convex. The right valve is slightly convex or nearly flat at early growth stages, becoming moderately to strongly resupinate at later stages. The left valve overlaps the right valve at all points on the shell margin except the hinge and the dorsal half of the auricles (Pl. 13, fig. 9).

The auricles are well developed and are sharply offset from the shell body by prominent auricular sulci (weaker in right valve). The anterior border of the anterior auricle is normally vertically or obliquely truncate but can be somewhat rounded. The ventral border of the auricle is broadly concave and inclined in the left valve, straight or concave and roughly parallel with the hinge axis in the right valve. The byssal notch is well developed.
Text-fig. 21. * Ptychopteria (Cornellites) catellus * n. sp.: length/height scatter diagram; accessory symbols as in Text-fig. 7.
On the left valve coarse radial ribs are developed early in ontogeny. Up to three ranks of finer costae are added during successive growth stages. Radial ribs are generally weak to obsolescent on the byssal sulcus. At early and intermediate growth stages, costae intersecting the posteroventral corner of the anterior auricle are more strongly developed than those more dorsally on the auricle (Pl. 13, fig. 2), but are not significantly different at advanced stages (Pl. 13, fig. 6). Growth lines and growth rugae are generally weak except on the byssal sulcus. Early and intermediate growth stages exhibit nodes or small scales at relatively regular intervals on the radial ribs where they are crossed by growth rugae and prominent growth lines. The nodes and scales become weak or obsolescent distally at advanced stages.

On the right valve, radial ribs are conspicuous on the posterior auricle, weak on the posterior half of the shell body and weak to obsolescent on the anterior half. Radial ribs occur on the anterodorsal half of the anterior auricle, but never on the other half (i.e., ribs are generated at the anterior but not on the ventral margin of the auricle). Some right valves show irregularly spaced commarginal undulations on the shell body (Pl. 13, fig. 3).

Internal features -

Musculature and ligament. The anterior adductor scar is small, circular, weakly impressed at early
growth stages, moderately to strongly impressed at advanced stages. The posterior adductor scar (usually vague) is comparatively large and is joined anterodorsally to a relatively large posterior pedal retractor scar (Text-fig. 22A). A single scar (often obscure), probably for the insertion of a pedal retractor muscle, occurs at or near the anterodorsal extremity of the umbonal cavity (Text-fig. 22B & Pl. 13, fig. 7). A few pallial punctae occur in the posterior part of the umbonal cavity of mature specimens, but preservation is rarely adequate to show these. Juveniles do not exhibit pallial punctae even when preservation is good. The pallial line is usually obscure, although it is reasonably clear in one specimen (Text-fig. 22A).

In the left valve, the posterior internal ridge is weakly to strongly developed and occurs on the internal expression of the posterior auricular sulcus (Text-fig. 22A). In the right valve, the posterior internal ridge is weak and only variably present (often obscured by poor preservation). When present, it is clearly differentiated from the internal expression of the posterior auricular sulcus, being inclined at a lower angle to the hinge axis (Pl. 13, fig. 8).

The ligament area is narrow. Mature shells normally show three to six ligament grooves. The grooves are usually gently arched below the umbo to form shallow chevrons. Posteriorly, the grooves are essentially parallel to the hinge axis.

Morphology and ontogeny of the dentition. Important stages in the ontogeny of the dentition of the left valve are
Text-fig. 22. Muscle insertions in Ptychopteria (Cornellites) catellus n. sp.: A) CPC F24902, left valve; B) same specimen oriented to show anterior pedal retractor scar; posterior edge of posterior adductor scar restored on basis of CPC F24901; pallial punctae restored on basis of ANU 36590.

Abbreviations: aa - anterior adductor scar; ar - anterior pedal retractor scar; m - pallial punctae; pa - posterior adductor scar; pir - posterior internal ridge; pl - pallial line; pr - posterior pedal retractor scar.
shown in Text-fig. 23. Description of the ontogeny of the right valve is here deferred until a more nearly complete growth series for that valve is obtained. For purposes of description, the five growth stages shown for the left valve are labelled with capital letters. These stages are not necessarily intended to correspond to those stages of Coppinsia spodophila shown in Text-fig. 15, which are also labeled with capital letters. As in C. spodophila, the ontogenetic stages figured for P. catellus correspond generally, but not precisely, with increasing shell size. In other words, a given shell may be more advanced ontogenetically than another shell the same size or somewhat larger. Determination of the relative order of appearance of teeth and sockets was made using the same approach used for C. spodophila (p. 135-136), and need not be repeated here. It is not possible, however, to be as precise in describing the relative order of appearance of teeth and sockets as for C. spodophila, because silicification is generally too coarse to recognize incipient secondary teeth and sockets with certainty.

As comparisons of Text-figs. 15 and 23 reveal, the ontogeny of the dentition of P. catellus shows significant similarities with that of C. spodophila, and teeth inferred to be homologous are numbered accordingly. Earliest available growth stages of the left valve show two primary teeth, Ap3 and Pp3 (stage A). Ap1, s3 and s5 are present by stage B. Their order of appearance is uncertain. One assumes that Ap1 develops before s3, since s3 seems to be an outgrowth of that
Text-fig. 23. Ontogeny of hinge of left valve of Ptychopteria (Cornellites) catellus n. sp.: A) ANU 36568; B) ANU 36581; C) ANU 36588; D) CPC F24998; E) ANU 36562 (holotype).

Abbreviations as for Text-fig. 15.

All scale bars = 5 mm.
tooth; however, there is no specimen available that clearly shows this. Ap1 is only weakly developed and disappears by stage C. Pp1 quite plainly does not appear until after at least s5 and s3 are developed (see stages B & C). Ap3 and s5 are connected dorsally by only a very narrow isthmus at stage B. This connection thickens at later stages (C & D) and is eventually broken by the ventral advance of the ligament (stage E). Teeth s1 and s7 develop after s5 and s3. At advanced stages, s3 and s1 vary considerably in their relative prominence: s3 is usually moderately larger than s1, but may be somewhat smaller or about the same size.

The development of tertiary teeth is almost completely suppressed in *P. catellus*. This phase of development is evidenced in the left valve only by the partial or complete bifurcation of s7 (stage E, not labelled) or occasionally of s5 (Pl. 13, fig. 11, not labelled). A single posterior accessory tooth is developed in some large left valves (Pl. 13, fig. 12). Anterior accessory teeth are invariably lacking. Teeth between s5 and the posterior primary teeth are quite variable. Tooth s7 can be well developed (see stages C & D) or poorly differentiated (stage E). Secondary teeth posterior to s7 are usually ill-defined or lacking (e.g., stage E). One large individual shows three well developed teeth posterior to s5 and anterior to the primary teeth (Pl. 13, fig. 12, not labelled). The two anteriormost of these are quite thin, and possibly represent tertiary teeth that developed from the bifurcation of s7.
A total of seven to ten teeth are present at the adult growth stages. The posterior primary teeth extend well forward and consequently, no real edentulous gap is formed between anterior and posterior teeth, although the secondary teeth immediately preceding the posterior primary teeth may be quite weak, as in the holotype (stage E).

Ap3 changes dramatically in its orientation during ontogeny, from strongly opisthocline at early stages (stages A & B) to essentially upright (stage D), to moderately prosocline (stage E), and is often recurved from intermediate stages onward. Posterior primary teeth also change in orientation, though less dramatically, becoming increasingly inclined to the hinge axis.

_P. catellus_ differs in the ontogeny of its dentition from that of _C. spodophila_ as follows: 1) fewer teeth are developed in the central part of the hinge; 2) the development of tertiary teeth is markedly suppressed; 3) accessory teeth are invariably lacking anteriorly; 4) Ap4 is very weak or absent in the right valve (Text-fig. 17H; figs. 7 & 8, unlabelled); 5) Ap3 is moderately prosocline at advanced stages, whereas in _C. spodophila_ it is moderately opisthocline; 6) s3 develops before s1 and is usually larger, whereas in _C. spodophila_, s1 develops first and is normally the larger.

**Discussion:** Bailey (1983) redescribed _Ptychopteria fasciculata_, the type species of the subgenus _Cornellites_, on
the basis of well preserved material from the Middle Devonian of New York State. This species is closely similar to *P. catellus*, leaving little doubt that these species are congeneric. Externally, *P. catellus* differs from *P. fasciculata* most notably in the presence of radial ribs on the body of the right valve. Similarities in the musculature of these species were considered earlier under the general discussion of the family (compare Pl. 11, figs. 13 & 14 and Text-fig. 22). Comparisons with primitive pterineid *Pteronitella retroflexa* and the rhombopteriid *C. spodophila*, reveal that *P. fasciculata* is more derived in its hinge structure than is *P. catellus*, there being fewer secondary teeth developed at mature growth stages.

**Autecology:** See under general discussion of Pterineidae.

*Ptychopteria (Cornellites) sp. A*

(Pl. 14; Text-fig. 4; Table 4)

**Referred specimens:** ANU 36540-36554 (total, 15).

**Known stratigraphic and geographic distribution:** late Emsian, uppermost beds of Bloomfield Limestone and basal beds of *Receptaculites* Limestone, Taemas Formation, Taemas area, New South Wales, and *Receptaculites* Limestone equivalent in the Taemas Formation, Wee Jasper area, New South Wales.

**Description:**
Table 4. Measurements for Ptychopteria (Cornellites) sp. A, Ptychopteria (Cornellites) sp. B, Actinopteria murrindalensis n. sp., Limoptera murrumbidgeensis n. sp. and Glyptodesma buchanensis (Talent).
| Specimen Name                      | ANU 36540 (LV) | ANU 36541 (LV) | ANU 36543 (LV) | ANU 36555 (LV) | ANU 36556 (LV) | ANU 36559 (RV) | ANU 36560 (LV) | CPC F24899 (RV) | ANU 36620 (LV) | ANU 36623 (LV) | ANU 36624 (LV) | ANU 36630 (LV) | ANU 36644 (RV) | ANU 36645 (RV) | ANU 36655 (RV) | ANU 36656 (RV) | ANU 36836 (LV) | ANU 48431 (LV) | ANU 48448 (LV) | ANU 48451 (LV) | Length | Height |
|-----------------------------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|----------------|--------|--------|
| Ptychopteria (Cornellites) sp. A  |                | 24*            | 65*            |                | 29*            | 50*            | 30*            | 7.5            | 43*            | 26*            | 20*            |                |                |                | 60*            | 48.0           | 86                | 102.0          | 65*            | 45.5            | 47.0            | 60*            | 54*            |
External features - The shell is moderately to strongly prosocline, and markedly inequivalved, the left valve being strongly convex, the right valve moderately to strongly resupinate. The left valve overlaps the right, anteriorly, ventrally, and apparently posteriorly, although the posterior margin is not well preserved in available articulated specimens (Pl. 14, fig. 2). The anterior auricle is strongly developed and protrudes well beyond the anterior extent of the shell body. The auricle of the right valve is particularly distinctive, being more or less triangular in outline and usually quite narrow dorsoventrally (Pl. 14, fig. 10). The posterior auricle of the left valve is well delineated from the shell body by a narrow, distinct auricular sulcus that is formed by an abrupt change in slope on the shell surface. In the right valve the auricular sulcus is weak or absent, the shell body being delineated from the posterior auricle by an abrupt weakening or loss of radial ribs. The posterior embayment is well developed at early and intermediate growth stages (Pl. 14, figs. 1 & 2), although in the only adult specimen preserving this part of the shell, it appears obsolete (Pl. 14, figs. 6 & 7). However, this may be owing to the extensive trauma and repair of the posterior region of the shell in this specimen, which evidently disrupted the growth of the posterior auricle (especially evident on the right valve, Pl. 14, fig. 7).

Ornament on the left valve consists mostly of coarse radial ribs, relatively regularly spaced growth rugae (with occasional irregularities), generally weak to obscure fine
growth lines, and projecting scales. The radial ribs are fine and closely spaced at early growth stages, becoming divergent and individually coarser with increasing shell size. A few additional ribs are added sporadically by intercalation at later growth stages. Ribs are weaker and more closely spaced on the posterior auricle than on the shell body. Ribs occur on both the anterior auricle and byssal sulcus, but become obscured on the latter by coarse growth rugae developed there at advanced growth stages. The most striking feature on the left valve is the presence of large projecting scales on the shell body where growth rugae cross radial ribs (Pl. 14, figs. 1, 6 & 14). The scales are much weaker on the auricles (especially the posterior auricle). On most specimens the scales have been mostly or wholly worn away. Scales are weak or absent at early growth stages.

On the right valve, radial ribs are conspicuous on the posterior auricle, absent or faintly developed on the shell body, and absent on the anterior auricle. Scales are lacking except at the distal extremity of some large individuals (Pl. 14, fig. 7).

Internal features -

Musculature. The musculature appears to be essentially like that in *P. catellus* (Text-fig. 22), except that: 1) pallial punctae are more numerous and more prominent; 2) the anterior adductor scar is more deeply impressed, especially along the posterior edge of the scar;
3) in the left valve the anterior adductor scar faces the commissural plane more or less squarely, whereas in *P. catellus* the anterior adductor is moderately inclined toward the posterior shell margin; 4) two small pedal(?) scars (often obscure), instead of a single scar, are present in the umbonal cavity; these are often clustered about by pallial punctae (Pl. 14, figs. 8 & 13). The posterodorsal segment of the pallial line is clearly visible in several specimens extending from the dorsal edge of the posterior adductor scar to the posterior end of the dentition (e.g., Pl. 14, fig. 8) (this part of the pallial line was not observed in *P. catellus*). The posterior internal ridge is weak to obscure in right valves, and weak to strong in left valves (not obviously differentiated from the internal expression of the posterior auricular sulcus in most of the left valves, but enhanced in some specimens, e.g., Pl. 14, fig. 12).

**Ligament and dentition.** The ligament grooves are nearly horizontal or form a gentle arch below the beak (Pl. 14, figs. 15 & 16).

In the left valve, the dentition at intermediate growth stages (early growth stages unavailable) shows two anterior and two posterior teeth, which closely resemble the primary teeth of early growth stages of *Ptychopteria catellus* and *Coppinsia spodophila* (Pl. 13, figs. 3 & 12). At more advanced growth stages, the anterior teeth usually become obscure, and that part of the hinge plate that supported the teeth becomes thickened to form an oblique buttress above the anterior
adductor scar (e.g., Pl. 14, figs. 9, 13, & 16). One atypical specimen shows a few weak prosocline teeth anteriorly (Pl. 14, fig. 11).

Discussion: Ptychopteria sp. A is readily distinguished from P. catellus by the narrower, more elongate and moderately attenuated anterior auricle (especially in the right valve), strong projecting scales, reduced dentition anteriorly, and larger shell size at mature growth stages. Minor differences in musculature were noted earlier. In spite of these differences, P. sp. A conforms to the concept of the subgenus Cornellites as defined earlier and is included therein. P. sp. A probably represents a new species, but has not been named owing to the fragmentary nature of most specimens, especially adult shells, and the limited sample size.

As noted above, the hinge of P. sp. A is essentially like that of early growth stages of P. catellus, except that the hinge plate supporting the anterior primary teeth becomes thickened and buttress-like, and the anterior teeth tend to be obscure at advanced growth stages. By outgroup comparison with the primitive pterineid Pteronitella and the rhombopteryiid Coppinsia, P. catellus is clearly more primitive dentally than is P. sp. A. The latter may have been derived paedomorphically from a P. catellus-like ancestor.

Worn specimens of P. sp. A may appear externally similar to specimens of Limoptera murrumbidgeensis n. sp. (described
below), but can be distinguished by the presence of an anterior adductor scar (absent in Limoptera). The hinge of these specimens is rather similar, as comparisons of Pls. 14 & 19 reveal, suggesting a possible relationship between Limoptera and Ptychopteria (Cornellites).

Ptychopteria sp. A shows broad similarities with Actinopteria mackayi Fleming from the Lower Devonian of New Zealand (Fleming 1957), but can be distinguished by its more elongate and narrower anterior auricle, and by the presence of erect lamellae (=scales) on, rather than between, costae. Internal shell features of A. mackayi are unknown. A. mackayi resembles Ptychopteria (Cornellites) fasciculata (the type species of Cornellites) and differs from Actinopteria decussata (the type species of Actinopteria) in the presence of a prominent anterior auricle and byssal sinus, and coarse radial ribs. A. mackayi is, therefore, transferred to Ptychopteria (Cornellites).

Autecology: See under general discussion of Pterineidae.

Ptychopteria (Cornellites) sp. B
(Pl. 15, figs. 1-8; Text-fig. 4; Table 4)

Referred specimens: ANU 36555-36561; CPC F24895-F24899 (total, 12).

Known stratigraphic and geographic distribution: early Emsian, Buchan Caves Limestone, the Basin, near Murrindal,
Victoria; late Emsian, *Receptaculites* Limestone, Taemas Formation, Taemas area, New South Wales, and *Receptaculites* Limestone equivalent in the Taemas Formation, Wee Jasper area, New South Wales.

**Description:**

**External features** - The shell is strongly prosocline, and biconvex; the left valve is more inflated than the right. The anterior auricle is bluntly rounded. The byssal sinus tends to be weakly defined. The posterior auricle is moderately to markedly extended, and well delineated from the shell body. Either the posterior tip of the auricle or the posteroventral edge of the shell body can form the posteriormost point on the shell. External ornament on the left valve consists of coarse, intercalating radial ribs and commarginal growth rugae and growth lines. Nodes or projecting scales occur on the ribs where crossed by growth rugae or prominent growth lines. Scales are most pronounced on the anterior part of the shell, especially the anterior auricle and the byssal sulcus (Pl. 15, fig. 1).

In the right valve, radial ribs are weak, and restricted to the posterior auricle. Growth rugae are well developed on the shell body (though often worn) and relatively regularly spaced (Pl. 15, figs. 2 & 3). Projecting scales are not developed.
**Internal features** - The anterior adductor scar is circular, variable in size although usually relatively large, and occurs on the anterior auricle below the cardinal dentition. Other features of the musculature were not observed. The ligament area is narrow, with a few, essentially horizontal, ligament grooves. The dentition resembles that of early growth stages of *P. catellus* and *Coppinsia spodophila*. Some of the teeth and sockets considered to be homologous are labelled in Pl. 15, figs. 5 & 8 using the notation system described earlier for *C. spodophila*.

**Discussion**: The single specimen recovered from the *Receptaculites* Limestone in the Taemas area (Pl. 15, figs. 3 & 4), and several specimens from the equivalent of that unit in the Taemas Formation in the Wee Jasper area (Pl. 15, fig. 6), resemble specimens of *P.* sp. B from the Buchan Caves Limestone in the Basin (Pl. 15, figs. 1, 2, 5, 7 & 8), and are tentatively included in that species. The radial ribs are finer than in the Basin specimens, but this may be preservational, the Wee Jasper and Taemas area specimens being quite worn externally. Also, the anterior auricle is generally less well differentiated from the shell body than in the Basin specimens. Larger and better preserved samples from the Wee Jasper and Taemas area localities are required to determine if these differences are taxonomically significant.

As noted above, the dentition is similar to that of early and intermediate growth stages of *P. catellus*. Unlike
P. catellus, secondary teeth remain relatively rudimentary after their first appearance in ontogeny, s1 and s3 are apparently only rarely developed, and Ap2 and Ap3 remain strongly opisthoclinc throughout ontogeny. The juvenile aspect of the hinge suggests paedomorphic derivation of this species, probably from a P. catellus-like ancestor.

**Autecology:** See under general discussion of Pterineidae.
Genus *Tolmaia* Williams 1908

**Type species:** *Pterinea lineata* Goldfuss 1863, by original designation.

*Tolmaia eruqisulca* n. sp.

(P1. 15, figs. 9 & 10; Pl. 16; Text-figs. 4, 24 & 25)

**Etymology:** From *erugo*, L., smooth, and *sulcus*, L., groove, with reference to the reduction of radial ornament on the posterior auricular sulcus.

**Holotype:** ANU 36594.

**Referred specimens:** ANU 36595-36604 (paratypes); ANU 36605-36619 (total, 25).

**Type locality:** Basal beds of *Receptaculites* Limestone at Locality R7, Bloomfield Station, Parish of Warroo, Taemas area, about 25 km southwest of Yass, New South Wales.

**Known stratigraphic and geographic distribution:** late Emsian, *Receptaculites* Limestone and uppermost beds of Bloomfield Limestone, Taemas Formation, Taemas area, New South Wales, and *Receptaculites* Limestone equivalent in the Taemas Formation, Wee Jasper area, New South Wales.

**Diagnosis:** Anterior auricle poorly differentiated from shell body; byssal sinus weak or absent in left valve, weak in right valve; posteriormost point on shell at posteroventral edge of shell body; numerous hinge teeth
present at advanced growth stages.

**Description:**

**External features** - The shell is inequilateral, prosocline and moderately compressed laterally. The left and right valves are nearly equally convex at early growth stages (Pl. 16, fig. 5), the latter becoming flatter or moderately resupinate with growth. The left valve overlaps the right anteriorly and ventrally (Pl. 16, fig. 4).

The posterior auricle and posterior embayment are moderately to well developed; the former never protrudes as far posteriorly as the posteroventral edge of the shell. The anterior auricle is inconspicuous and in the left valve blends smoothly with the shell body, but in the right valve, is usually slightly offset by a weak byssal sulcus. The anterior margin (including the auricle) of the left valve is normally straight or slightly convex in outline, although a weak byssal sinus is sometimes developed. The byssal sinus is slightly stronger and more consistently developed in right valves. The left valve overlaps the right valve where the byssus was extruded, but an obvious byssal notch is not developed. The shell outline becomes increasingly retrocrescent with growth.

External ornament consists of fine, closely spaced, intercalating radial ribs, irregularly spaced commarginal growth rugae and weak to obscure growth lines. Radial ribs are fine to obsolescent in the posterior auricular sulcus
Text-fig. 24. *Tolmaia erugisulca* n. sp.: length/height scatter diagram; accessory symbols as in Text-fig. 7.
Ornament on the right valve is like that of the left valve, except that the radial ornament is much weaker and is usually absent on the anterior auricle and along the anterior shell margin. Radial ribs are weak to obscure at very early growth stages.

**Internal features**

**Musculature.** The anterior adductor scar is small and deeply impressed, the posterior adductor scar much larger and faintly impressed (often obscure). Quick and catch regions are occasionally discernable on the posterior scar (Pl. 15, fig. 10). The posterior adductor scar is normally circular in outline, but can be evaginated slightly at its anterodorsal extent. The evaginated region clearly does not represent the insertion of the posterior pedal retractor, as the line separating quick and catch regions of the main part of the posterior adductor scar extends into this area as well (Pl. 15, fig. 10). Instead, the pedal retractor probably inserted in the larger, less clearly defined, elongate depression that is anterodorsally contiguous with the adductor scar (Pl. 15, fig. 10). A number of small muscle scars occur in the umbonal cavity (Text-fig. 25). These vary in number and position. Usually one to three of the scars are larger than the rest, and probably represent pedal retractor scars. The smaller scars are most numerous and are probably pallial punctae. Intermediate sized scars, when present, presumably represent either large pallial punctae or small pedal retractor scars, but there is no means available to
Text-fig. 25. Umbonal muscle scars in *Tolmaia erugisulca* n. sp.: ANU 36603, left valve, specimen oriented to show umbonal cavity.

Abbreviations: aa - anterior adductor scar; ar - anterior pedal retractor scars; gs - gill suspensor scars; m - pallial punctae; pir - posterior internal ridge; pl - pallial line.
distinguish them. Additional pallial punctae occur sporadically in the dorsal half of the shell within the perimeter of the pallial line. The posterior internal ridge is short, but usually well defined. A few small, weak gill suspensor(?) scars are sometimes visible along its length (Text-fig. 25; Pl. 16, fig. 6, see arrows). The pallial line is usually clearly visible anteriorly, where it is composed of closely spaced pits, or else is more or less continuous. Elsewhere, it is normally obscure, but is faintly visible in one specimen (Pl. 16, fig. 6, unlabelled). This same specimen shows a swelling of the line below the posterior adductor scar that may represent the insertion of a gill suspensor, as in aviculopectinids and pseudomonotids (Newell 1937, fig. 2). Also visible are faint radiating lines at the posteroventral extent of the pallial line that perhaps represent the impression of mantle retractor muscles.

**Ligament and dentition.** At early and intermediate growth stages, ligament grooves are usually slightly to moderately arcuate, but can be essentially parallel with the hinge axis, as are those formed at advanced growth stages (Pl. 16, figs. 8-12). Some specimens show an abrupt change from arcuate to horizontal grooves during ontogeny such that the last formed arcuate grooves are truncated by the first formed horizontal grooves (Pl. 16, figs. 10 & 12). One specimen shows a pit in the center of the ligament, but this is not a resilifer; rather, it represents simply a remnant of the unusually strong depression on the dentition below, which has been overgrown by the ventrally migrating ligament (Pl. 16, fig.
The dentition is well developed and (except at early growth stages) consists of numerous prosocline teeth and sockets. Anterior and posterior dental elements may or may not be separated by an edentulous gap. Teeth and sockets become increasingly more strongly prosocline posteriorly along the hinge plate. The dentition and hinge plate do not extend anteriorly onto the anterior auricle. The hinge plate descends anteroventrally at its anterior extent, forming a short, thick buttress over the anterior adductor scar.

Early growth stages are too poorly represented to allow a detailed account of the ontogeny of the dentition. It is clear that the number of teeth increases significantly through ontogeny (compare Pl. 16, figs. 12 & 13), but there is by no means an exact correlation of tooth number with shell size. Some large specimens, for example, show fewer teeth than some smaller specimens (compare Pl. 16, figs. 7 & 10). Likewise, the edentulous gap separating anterior and posterior elements occurs in the smallest available specimens, and is usually diminished or absent in large specimens, but here again, some large specimens show a gap and somewhat smaller specimens little or no gap (compare Pl. 16, figs. 10 & 14). Anterior and posterior teeth tend to be more robust than those formed at the site of the edentulous gap, as in the primitive pteriacean Coppinsia spodophila, described earlier. As in that species, some teeth are partly divided longitudinally, and thin weak teeth sometimes occur
in the sockets between more strongly formed teeth (Pl. 15, fig. 10; Pl. 16, fig. 12). This suggests that, as in *C. spodophila*, teeth increase in number not only by forming in the gap between anterior and posterior elements but also by bifurcation of pre-existing teeth and by insertion between pre-existing teeth. Unlike *C. spodophila* and *Ptychopteria* (*Cornellites*) spp., the anteriormost tooth is orthocline to moderately prosocline at early growth stages rather than opisthocline (Pl. 16, figs. 13-15). Tooth homologies with *C. spodophila* and *P. catellus* are uncertain.

**Discussion:** *T. eruquisulca* is referred to the genus *Tolmaia* on the basis of close similarities of shell outline, ornament and hinge structure with the type species, *Tolmaia lineata* (Goldfuss). Excellent examples of *T. lineata* have been figured by Maillieux (1937, pi. 2, figs. 1, 3-6). *T. eruquisulca* differs from that species primarily in the development of a greater number of teeth and sockets on the hinge plate.

The right valves figured in Maillieux (1937, pl. 2, figs. 2 & 2a) are not accepted here as belonging to *T. lineata* nor to any other species of that genus. The ornament is coarser, the shell body is relatively broader and more upright, and the byssal sinus is more prominent than in any of the other specimens of *T. lineata* figured by Maillieux. I suspect instead that the right valves in question represent a species of *Ptychopteria* (*Cornellites*). Except for the apparently reduced anterior auricle (which may be worn or
partly broken), these specimens are quite similar in shell outline, ornament, dentition and musculature to the Australian species *Ptychopteria* sp. A.

**Autecology:** See under general discussion of Pterineidae.
Genus *Actinopteria* Hall 1884

**Type species:** *Avicula decussata* Hall 1843, by subsequent designation of Bassler 1915.

*Actinopteria murrindalensis* n. sp.

(Pl. 17; Table 4)

1956. *Actinopteria* sp. indet., Talent, p. 46, pl. 3, fig. 13.

**Etymology:** After the village of Murrindal, near the type locality.

**Holotype:** ANU 36620.

**Referred specimens:** ANU 36621-36632, 36743 (all paratypes) (total, 13).

**Type locality:** Locality B5, Buchan Caves Limestone, approximately 7 km east of Murrindal, Victoria.

**Known stratigraphic and geographic distribution:** early Emsian, Buchan Caves Limestone, the Basin, near Murrindal, Victoria.

**Diagnosis:** Moderately inequivalved, two or three cardinal teeth present in each valve; one or two posterolateral teeth present in right valve and one in left valve.
Description:

External features - The shell is inequilateral, moderately inequivalved, and prosocline. The right valve is inflated umbonally, becoming flattened distally. The anterior auricle is relatively small, its height invariably exceeding its length. At early growth stages, the posterior auricle is relatively short and blunt, and the posterior embayment weakly developed; at later growth stages, the posterior auricle becomes extended and acuminate, and the posterior embayment pronounced. The posterior auricular sulcus is broad and weak. A single articulated specimen has been recovered (Pl. 17, figs. 3-5). Although the right valve has been slightly displaced and has been pushed partly into the left valve, it is clear that a byssal notch or byssal gape was not developed (see also articulated specimen of A. cf. A. murrindalensis, Pl. 18, fig. 8). Only a few specimens are sufficiently complete to allow measurements or close estimates of shell dimensions; these are given in Table 4.

External ornament consists of thin, closely spaced intercalating radial ribs, irregularly spaced growth rugae, and weak to obscure fine growth lines. Ornament tends to be more strongly developed on the left valve than on the right. Growth rugae are most pronounced on the anterior auricle and byssal sulcus. Radial ribs are lacking on the anterior auricle, and, at intermediate and advanced growth stages, on the byssal sulcus, as well.
Internal features -

Musculature. Silicification is generally too coarse to preserve details of the musculature. One or more anterior pedal retractor scars are preserved in a few specimens. These vary in number and position. Normally, a single prominent scar is present at the base of the auricular buttress, and one to three additional smaller scars occur more dorsally in the umbonal cavity (Pl. 17, figs. 8-10). One specimen shows three small scars near the base of the buttress and lacks scars more dorsally (Pl. 17, fig. 13). An anterior adductor scar is lacking. The posterior internal ridge is generally weak in adults, weak or obscure in juveniles. The pallial line is usually faintly visible anteriorly. The posterior adductor scar and posterior pedal retractor scar could not be recognized.

Ligament and dentition. The ligament area is narrow, elongate and occurs almost entirely posterior to the umbo. The widest part of the area occurs slightly posterior to the cardinal teeth (Pl. 17, fig. 12). The ligament grooves are inclined at a low angle to the ventral edge of the ligament area.

Two or three cardinal teeth occur in each valve. These are almost invariably prosocline, except that in one specimen, a juvenile, the anteriormost tooth is more or less orthocline and curved, with the concave surface of the tooth facing posteriorly (Pl. 17, fig. 15). One or more of the cardinal teeth can be continuous dorsally with the dorsal
edge of the auricle. The posterolateral teeth are thin and diverge little from the ventral edge of the ligament area; two occur in the right valve, one in the left valve. The anterior auricular buttress is well developed and septum-like. Dental homologies with C. spodophila and P. catellus are uncertain.

Discussion: A. murrindalensis is referred to Actinopteria on the basis of similarities in shell outline and external ornament with the type species Actinopteria decussata (see Hall 1884, especially pl. 17, figs. 24 & 28 and pl. 18; also, Pl. 12, figs. 10 & 11, this paper). A. murrindalensis differs from that species primarily in that the comm marginal ornament is less pronounced and more irregularly spaced, and the shell is less strongly prosocline (internal features are unknown for A. decussata).

Autecology: See under general discussion of Pterineidae.

Actinopteria cf. A. murrindalensis

(Pl. 18, figs. 1–8; Text-fig. 4)

Referred specimens: ANU 36633–36637 (total, 5).

Known stratigraphic and geographic distribution: late Emsian, Receptaculites Limestone and uppermost beds of Bloomfield Limestone, Taemas Formation, Taemas area, New South Wales, and Receptaculites Limestone equivalent in the Taemas Formation, Wee Jasper area, New South Wales.
Description and discussion: This species is a relatively rare element in the limestones in which it occurs. Only one specimen is known from the equivalent of the Receptaculites Limestone in the Wee Jasper area. Complete valves were not recovered. None are sufficiently complete to allow measurements. Shell size appears to have been close to that of *A. murrindalensis*. Most specimens are represented by only the anterodorsal part of the shell, including the anterior auricle, auricular buttress and cardinal dentition. One articulated specimen (Pl. 18, figs. 7 & 8) consists of most of the shell outline, except that the posterior auricle is broken off. Externally this species is like *A. murrindalensis*, although the anterior auricle tends to be smaller, less protruding anteriorly, and more flattened anterodorsally in outline. Additionally, radial ornament is lacking from the byssal sulcus throughout ontogeny, rather than only at intermediate and advanced stages.

The hinge is similar to that in *A. murrindalensis* except that 1) the cardinal teeth tend to be more strongly prosocline and relatively more elongate; 2) specimens with three cardinal teeth are rare (known in only one specimen, a left valve, Pl. 18, fig. 6); 3) a few right and left valves show only one cardinal tooth (at least two are present in specimens of *A. murrindalensis*); and, 4) the posterolateral dentition of the right valve (preserved in only one specimen, Pl. 18, fig. 5) consists of only one tooth (two are present in *A. murrindalensis*). Muscle insertions, as far as can be determined, are essentially like those known for *A.*
murrindalensis. Small scars are faintly visible on the ventral surface of the posterior internal ridge in one specimen (Pl. 18, fig. 2; see arrows) indicating that the posterior internal ridge was associated with muscle attachment, probably gill suspensors.

**Autecology:** See under general discussion of Pterineidae.
Genus Limoptera Hall & Whitfield 1869

Type species: Lima macroptera Conrad 1838, by original designation.

Limoptera murrumbidgeensis n. sp.
(Pl. 18, figs. 9-16; Pl. 19; Text-fig. 4; Table 4)

Etymology: After the Murrumbidgee River, which flows through the Taemas synclinorium.

Holotype: ANU 36644.

Referred specimens: ANU 36645-36658 (all paratypes) (total, 14).

Type locality: Locality R3 (horizon b), Receptaculites Limestone, Parish of Cavan, Taemas area, about 25 km southwest of Yass, New South Wales.

Known stratigraphic and geographic distribution: late Emsian, Receptaculites Limestone and uppermost beds of Bloomfield Limestone, Taemas Formation, Taemas area, New South Wales, and Receptaculites Limestone equivalent in the Taemas Formation, Wee Jasper area, New South Wales.

Diagnosis: Adult shell large, markedly inequivalved, suborbicular, and suborthocline; radial ribs simple, subequidistant and relatively widely spaced; posterior embayment present in juvenile shell, weak to obsolescent in adult shell; dentition weak and variable; cardinal teeth and
posterolateral teeth separated by edentulous gap; cardinal teeth often obsolescent in adult shell; normally three pedal retractor scars present in umbonal cavity.

**Description:** Although *Limoptera murrumbidgeensis* is one of the most abundant bivalves in the *Receptaculites* Limestone (but not at Wee Jasper), most specimens are very fragmentary. Of the more than 200 specimens collected to date, only six (all right valves) are sufficiently complete to allow measurements, or close estimates, of shell dimensions. These are given in Table 4.

**External features** - The shell is moderately prosocline and inequivalved. The left valve is strongly convex, the right valve flat or slightly resupinate, becoming moderately convex umbonally. As shown in Pl. 18, fig. 15, the left valve strongly overlaps the right valve posteroventrally and to a lesser extent along the anterior margin. The posterior margin is not preserved in available articulated specimens, so that the degree of valve overlap there, if any, is unknown. The anterior auricle normally extends well beyond the anterior edge of the shell body at early and intermediate growth stages (Pl. 18, figs. 9, 13 & 15), whereas in very large individuals, the shell body extends farther anteriorly (Pl. 19, figs. 2 & 4). Both the shape and relative prominence of the anterior auricle are variable. Generally at early and intermediate growth stages, the anterior auricle is conspicuously developed (Pl. 19, figs. 10, 11 & 13), but in
some specimens, it is comparatively subdued (Pl. 19, fig. 5). The outline of the auricle can be rounded, subrectangular or triangular (Pl. 18, fig. 9; Pl. 19, figs. 5, 9 & 13). The anterior auricle of large individuals is proportionally smaller than in most juvenile and intermediate sized shells. The byssal notch and sinus are generally well developed at early stages, but tend to become reduced at intermediate and advanced growth stages (Pl. 19, figs. 2 & 12). The posterior embayment is moderately developed at early growth stages, becoming weak to obsolescent at advanced stages. In the left valve, the posterior auricular sulcus is broad and weak at early growth stages and obsolescent at advanced growth stages. In the right valve, this sulcus is obsolescent throughout ontogeny.

External ornament in the left valve consists of simple, relatively widely spaced radial ribs, irregularly spaced growth rugae, and weak to obscure growth lines. Radial ribs are usually lacking on the byssal sulcus and anterior auricle. Radial ribs become individually larger and divergent with increasing shell growth. Few new ribs are added except early in ontogeny, and these by intercalation. Ribs may be moderately nodose where crossed by growth rugae and prominent growth lines. Growth rugae are most pronounced on the anterior auricle and byssal sulcus. On the right valve, radial ribs are present on the posterior auricle, are weak to obscure on the shell body, and are invariably lacking on the anterior auricle.
Internal features -

Musculature. The posterior adductor scar is large, circular, and usually weakly impressed, and is positioned centrally in the dorsal half of the shell. In some specimens, only a few millimetres separate the dorsal edge of the scar and the ligament area (Pl. 19, fig. 9). A large posterior pedal retractor scar (often faint or obscure) is continuous with the anterodorsal edge of the adductor scar. An anterior adductor scar is lacking. A prominent anterior pedal retractor scar occurs at the dorsal end of the pallial line in the anterodorsal extremity of the umbonal cavity, immediately posterior to the short, weak auricular buttress. Most specimens show two additional retractor scars in the umbonal cavity, one posterior and one posteroventral to the principal retractor scar (Pl. 18, fig. 12; Pl. 19, fig. 8). The scars are variable in their expression; one or the other, or both, can be faint or pronounced. The more dorsal of the two is usually elongate. Both can be subdivided into smaller, closely spaced scars. A weak groove, often subdivided, occurs more posteriorly on the underside of the ligament area in some left valves (Pl. 18, fig. 12). The posterior internal ridge is weakly developed or lacking. The pallial line is usually obscure except anteriorly. Here it usually becomes discontinuous before joining the anteriormost retractor scar. The entire length of the pallial line is clearly visible in the two large right valves from Locality R5 (Pl. 19, figs. 1 & 3). The better preserved of the two shows a lenticular expansion of the pallial line below the posterior adductor
scar. Newell (1937) noted the presence of somewhat larger impressions at comparable positions in *Aviculopecten* and *Pseudomonotis*, which he ascribed to the insertion of gill suspensors by analogy with Recent pectinids (*ibid.*, figs. 1 & 2). The pallial line extends vertically from the dorsal edge of the posterior adductor scar to the posterolateral tooth, where it terminates in a slight swelling.

**Ligament and dentition.** At early and intermediate growth stages, ligament grooves are coarse and arranged in chevrons (Pl. 19, figs. 5, 6, & 11); at later growth stages, they are generally finer and more or less parallel with the ventral edge of the ligament area (Pl. 18, fig. 10). The dentition is highly variable: two or three weak cardinal teeth are usually present at early and intermediate growth stages (Pl. 19, figs. 9, 11 & 14), although some individuals show only a single tuberculiform tooth at this position (Pl. 19, figs. 5 & 6). At advanced growth stages, the hinge plate usually grows over the cardinal teeth and obliterates them (Pl. 19, figs. 1 & 3). One or (rarely) two posterolateral teeth are present posteriorly in both valves throughout ontogeny; they are separated from the cardinal teeth by an edentulous interval. Dental homologies with *C. spodophila* and *P. catellus* are uncertain.

**Discussion:** *L. murrumbidgeensis* is referred to the genus *Limoptera* on the basis of similarities in shell outline, convexity and ornament in the type species, *Limoptera macroptera* (see figures in Hall 1884). In both species, the
adult shell is larger than in most pterineids, broad, suborthocline, markedly inequivalved, and monomyarian, with prominent, relatively widely spaced radial ribs externally (few new ribs are added during ontogeny), and an obsolescent posterior embayment and posterior auricular sulcus. *L. murrumbidgeensis* differs primarily in that the anterior auricle is generally more conspicuously developed throughout ontogeny, and three anterior pedal retractor scars, rather than one, are present in the umbonal cavity.

**Autecology:** See under general discussion of Pterineidae.
Glyptodesma Hall 1883

Type species: Glyptodesma erectum (Conrad), by subsequent designation of Miller 1889.

Discussion: Glyptodesma erectum (Middle Devonian, New York State), as figured in Hall 1884, exhibits an enormous range of variation in the expression of the anterior and posterior auricles. At one extreme, the auricles are relatively subdued (e.g., Hall 1884, pl. 25, figs. 16 & 17; pl. 87, fig. 3), and are not far removed morphologically from those of Glyptodesma buchanensis, described below. At the other extreme, the auricles are greatly extended (ibid., pl. 11, figs. 4 & 10) and resemble those of Actinodesma. The latter condition no doubt prompted Newell and LaRocque (in Moore 1969) to regard Glyptodesma as a junior synonym of Actinodesma; however, the dentition of the type species of Actinodesma, A. malleiforme (Sandberger & Sandberger 1850, pl. 29, fig. 17), is quite different from that of G. erectum, as Hall (1884, p. xiii) pointed out. Differences include: 1) the teeth of G. erectum are relatively smaller, weaker and more numerous; 2) the anterior teeth of G. erectum are orthocline (Hall 1884, pl. 86, fig. 3; pl. 87, fig. 1), suborthocline (ibid., pl. 13, figs. 9 & 10) or prosocline (ibid., pl. 13, fig. 13), whereas in A. malleiforme they are strongly opisthocl ine; 3) the hinge plate is dentigerous for a greater proportion of its length in A. malleiforme than in G. erectum; 4) the cardinal teeth are the longest dental
elements in *A. malleiforme*, whereas the posterolateral teeth are the longest in *G. erectum*; 5) the teeth are disposed symmetrically about the umbo in *A. malleiforme*, but in *G. erectum*, most teeth occur posterior to the umbo.

*G. erectum* and *A. malleiforme* may be related, as the overlap of their shell outlines suggests and as Newell and LaRocque (in Moore 1969) implied. However, I agree with Hall's (1884: xiii) original proposal that the differences in the dentition are best reflected by separation of these forms at the generic level. Furthermore, this arrangement permits the conclusion that *G. erectum* and *G. buchanensis* are congeneric (as discussed below) to be expressed, without necessarily implying a close relationship of the latter with *A. malleiforme*, from which it differs considerably.

**Glyptodesma buchanensis** (Talent) 1956
(Pls. 20 & 21; Text-fig. 4; Table 4)

1956. *Leiopteria buchanensis* Talent, p. 47, pl. 3, fig. 14; pl. 4, fig. 8.

**Holotype**: MUGD 2191; pl. 4, fig. 8 of Talent 1956.

**Type locality**: Locality R. C. R. 29 (Talent 1956: 53), 150 m up Rocky Camp Ridge from base of Buchan Caves Limestone exposed on the Murrindal River, Victoria.

**Referred specimens**: ANU 36836-36839, 48431-48451; CPC F24940-F24943 (total, 29).
Known stratigraphic and geographic distribution: early Emsian, Buchan Caves Limestone, Buchan area, Victoria, and Cavan Formation, Taemas area, New South Wales.

Diagnosis [Talent (1956) did not provide a diagnosis for this species]: Shell suborthocline, biconvex, inflated and moderately inequivalved; posterior auricle not extended; posterior embayment small in juvenile, usually lacking in adult; shell exterior with commarginal erect laminae; adductor musculature monomyarian; dentition variable, usually consisting in each valve of a single weak lateral tooth posteriorly, and a few taxodont teeth anteriorly.

Description:

External features - The shell is inequilateral, suborthocline, inflated, biconvex and inequivalved. The relative convexity of the right and left valves is shown in Pl. 20, figs. 2 & 3. Except for one specimen (Pl. 20, fig. 1), no individual yet collected is sufficiently complete to allow measurement of both the height and length of the shell. However, it has been possible to estimate height and/or length for a few specimens on the basis of curvature of preserved parts of the shell margin (Table 4).

The anterior auricle is small but distinct, and through most of ontogeny, is well offset from the shell body by a distinct byssal sinus and sulcus. With the onset of massive shell thickening at advanced growth stages (described below), the byssal sinus in many specimens becomes significantly
reduced (Pl. 20, fig. 7). The posterior auricle is not well differentiated from the body of the shell. A small posterior embayment is present in young shells (Pl. 20, fig. 9; note growth lines), but is almost invariably lacking at mature growth stages, ANU 48451 being the only known exception (Pl. 20, fig. 8).

The external ornament consists of more or less regularly spaced commarginal erect laminae, usually with faint growth rugae and growth lines between (Pl. 20, fig. 11). Radial ornament is lacking. Ornament on the right valve appears to have been somewhat more weakly developed than on the left valve, but available right valves are not well enough preserved to establish this clearly. Most specimens from the Basin localities (including both right and left valves) are worn nearly smooth over most of the external shell surface - except on the anterior parts of the shell, including the anterior auricle, byssal sulcus and posteroventral shell margin. Here the erect edges of the laminae are often well preserved. A few specimens show remnants of the erect laminae near the posterior and ventral shell margins (Pl. 20, fig. 1). Three specimens, including a juvenile from the Basin (Pl. 20, fig. 4) and two mature individuals (ANU 36836-7) from the Cavan Formation (only one of these is shown in Pl. 20, fig. 11), have erect laminae preserved over the entire shell surface. These specimens are important because they reveal that: 1) erect laminae were secreted around the entire growing edge of the shell and not just anteriorly; and, 2) laminae were secondarily eroded from
all but the anterior part of the shell in most individuals from the Basin localities. The relevance of this wear pattern concerning the life orientation of *G. buchanensis* is discussed later.

**Internal features -**

**Musculature.** An anterior adductor scar is absent. The posterior adductor scar is almost invariably obscure; in only one fragmentary specimen is it clearly defined (Pl. 20, fig. 5). A scar for the posterior pedal retractor muscle cannot be seen in any of the specimens at hand, although from comparisons with other pterineids, the muscle was almost certainly present, and probably inserted alongside the anterodorsal or anterior margin of the posterior adductor scar.

Normally, three pedal retractor scars (sometimes subdivided) are present in the anterodorsal region of the umbonal cavity (Pl. 21, figs. 1-4). The anteriormost of these occurs on the pallial line. The other two scars are often merged to various degrees (Pl. 21, figs. 2 & 4).

In CPC F24940, a fragmentary pair of articulated valves, and the only pair of articulated valves of this species yet recovered, the umbonal musculature is not symmetrically disposed between the two valves (Pl. 21, fig. 1). The anteriormost pedal retractor muscle of the left valve inserted into a single scar, although depressions on the floor of the scar indicate that this muscle was at least
incipiently subdivided (not visible in Pl. 21, fig. 1). In the right valve, insertion of the anteriormost pedal retractor is represented by several small, closely spaced, discrete pits. In most right valves, however, there is only a single scar at this position, although depressions on the floor of the scar in some specimens indicate incipient subdivision. These specimens, then, are essentially like the left valve of CPC F24940 in the form of the anterior pedal retractor scar (and other umbonal scars), and consequently, the asymmetry of the umbonal musculature in CPC F24940 is not necessarily typical of the species.

In addition to the pedal retractor scars, well preserved specimens usually show a variable number of small pits or depressions in the umbonal cavity, and sometimes further ventrally on the valve floor (Pl. 21, fig. 1). These pits are usually sporadically distributed and often vary in size and strength. Most are probably pallial punctae, although some of the dorsal ones may be visceral or gill suspensor scars, or small pedal retractor scars, but no means of distinguishing these is available.

The pallial line is not visible posteriorly or ventrally. Anteriorly, it is usually pitted below the anterior retractor scar and more uniform farther ventrally. In many specimens it cannot be distinguished at all, but this is probably an artifact of preservation. As noted earlier, the pallial line maintains its integrity where it passes the anterior retractor scar. From here it continues toward the
hinge as a thin line (sometimes slightly pitted), and is then deflected posteriorly and becomes progressively fainter (Pl. 21, figs. 1-4).

An interesting feature of *G. buchanensis* is that the adult shell is massively thickened in the anterior two-thirds of the umbonal cavity and along the anterodorsal region of the shell, including the anterior auricle and the byssal sinus. ANU 48438, for example (Pl. 20, fig. 10), has a maximum shell thickness of 5.4 mm in the umbonal cavity, a thickness nearly eleven times that on the posterior auricle (0.5 mm). Young shells show no appreciable thickening in the umbonal region, but thickening appears to have proceeded rapidly after a hinge length of 35.0-40.0 mm was attained, although this is variable. ANU 48431, for example, has a length of 41.0 mm and does not show appreciable thickening of the shell, while CPC F24940, a smaller individual (hinge length, 37.0 mm), is massively thickened. The junction of the thickened and non-thickened regions of the shell forms a break in slope or a shallow trough (Pl. 21, fig. 1).

**Ligament.** The ligament area is broad and is traversed by numerous, closely spaced ligament grooves. The orientation of the grooves varies somewhat between growth stages and between individuals at the same growth stage. In most individuals, the grooves are inclined to the hinge axis at early growth stages, and become essentially parallel with the hinge axis at successive growth stages, a pattern also observed in the primitive rhombopteriid *C. spodophila* and in various
pterineids discussed earlier. Ligament grooves are clearly inclined to the hinge axis (at about 6 degrees) in two relatively young shells shown in Pl. 21, figs. 5 & 9. Well preserved, mature specimens often exhibit chevrons in the first formed part of the ligament area, and essentially horizontal lines thereafter (Pl. 21, figs. 6, 8 & 11). This ontogenetic pattern is not always present, as several specimens (including one juvenile) show no evidence of chevrons at any stage of growth (Pl. 21, figs. 7 & 10).

In some individuals, ligament grooves formed at early stages are coarser than those formed later (Pl. 21, figs. 11 & 13). The transition from coarse to fine grooves may be abrupt (Pl. 21, fig. 11), indicating that in these instances, there was some kind of rapid change in ligament secretion. Although the ligament grooves formed at advanced stages (and in some specimens, at early stages) are horizontally disposed, close examination of well preserved specimens reveals that the last few grooves formed are usually abbreviated, extending only partway anteriorly and posteriorly from the chevron axis. The ends of these grooves are indicated by arrows in Pl. 21, fig. 7. In a few specimens, however, the ventralmost grooves seem to extend the full length of the ligament area (or at least that part of the ligament area that is preserved), but the possibility of wear in in these instances cannot be ruled out (Pl. 21, figs. 6, 8 & 10).
Dentition and hinge plate. A series of relatively weak and variable teeth occurs immediately below the insertion of the ligament. This region is often worn or poorly silicified so that it is sometimes difficult to determine whether differences observed between specimens reflect intraspecific variation or preservational differences. A single posterolateral tooth is usually present in each valve, but in some specimens it is very weak; occasionally, it is absent. The cardinal teeth are strongest below the umbones and become progressively weaker posteriorly, and finally disappearing altogether, leaving an edentulous gap before the posterolateral tooth. Sockets are open ventrally. Teeth protrude ventrally below the edge of the hinge plate. Beneath the umbo, teeth are prosocline (generally) or orthocline (occasionally), and become increasingly prosocline posteriorly. Cardinal teeth usually vary in number from less than five (Pl. 21, figs. 7, 10 & 11) to about twelve (Pl. 21, fig. 12), but are lacking in some specimens (Pl. 21, fig. 6). Small specimens consistently show few or no cardinal teeth (Pl. 21, figs. 5, 9 & 10). Apart from a general increase in the number of cardinal teeth with increasing shell size, there do not appear to be any major changes in the dentition during ontogeny. Dental homologies with *C. spodophila* are uncertain.

Below the ligament area, the hinge plate is deepest beneath and behind the beak, where it forms an arcuate ventral protrusion. Posteriorly, it thins markedly, and is deflected ventrally at its posterior extremity to form the
posterolateral tooth. The anterior auricular buttress is well developed in young individuals and rises to meet the hinge plate at its deepest point, behind the umbo (Pl. 21, fig. 9). It tends to be obscured by extensive shell thickening in mature individuals (Pl. 20, figs. 7 & 10; Pl. 21, fig. 1).

Discussion: G. buchanensis was originally described as Leiopteria buchanensis Talent on the basis of a few poorly preserved specimens from localities in the Buchan Caves Limestone, near Buchan, Victoria (Talent 1956). The material provides so few characters for comparison that it is difficult to demonstrate conspecificity of that material with the new material from the Basin localities described herein. The two samples are, nonetheless, regarded here as representing a single species. Features preserved in Talent's specimens are indistinguishable from those of the Basin specimens, and include: 1) an inflated, suborthocline and biconvex shell; 2) a similar shell size (the holotype and MUGD 2193 [Talent 1956, pl. IV, fig. 8; pl. III] indicate a shell size about equal to that of most specimens in the Basin sample); and, 3) ornament consisting of commarginal laminae.

Other data are consistent with the conspecificity of the samples as inferred from morphological data; these include: 1) specimens from the Basin were collected from calcilutite that contained abundant remains of the brachiopod Spinella buchanensis Talent, a lithological and faunal association characteristic of G. buchanensis in the Buchan Caves Limestone elsewhere (Talent 1956: 53); and, 2) occurrences of
G. buchanensis at Talent's localities and at the Basin are in the upper half of the Buchan Caves Limestone and are separated geographically by only a few kilometres.

Talent (1956: 46-47) described another species of Leiopteria, L. jacksonensis, on the basis of a single specimen from the Jackson's Crossing Limestone, an outlier of the Buchan Caves Limestone, about 5 km northwest of the Basin (Text-fig. 2A). The specimen is much smaller than most specimens of G. buchanensis, and it may be a juvenile of that species. Talent (1956) noted that, unlike specimens of G. buchanensis available to him, the posterior wing is well developed and relatively well differentiated from the body of the shell, but as shown earlier, these features can be found in juveniles of G. buchanensis in the Basin sample. Furthermore, L. jacksonensis occurs in a similar lithology and faunal association to that known for G. buchanensis from the Buchan Caves and Basin limestones, that is, calcilutite with abundant Spinella, and at about the same relative stratigraphic position. I hesitate, however, to place G. buchanensis in synonymy with L. jacksonensis because the latter appears to differ in that the ornamentation consists of smooth, relatively broad commarginal ribs rather than erect commarginal laminae. Additional specimens of L. jacksonensis are needed to confirm whether this is a consistent difference or simply an artifact of preservation unique to the holotype. If the holotype of L. jacksonensis is ultimately shown to be a juvenile of G. buchanensis, the former name will have priority.
G. buchanensis is most similar to G. erectum among known pterineids, especially in regard to the ligament, musculature and dentition. The latter differs primarily in that the anterior auricle is generally, and the posterior auricle invariably, more extended, and the right valve is flatter. Although the shell of G. erectum is reported to be thick (Hall 1884: 153), there is no evidence of the marked disproportionate thickening of the anterodorsal region of the shell that characterizes G. buchanensis.

**Autecology:** Morphological evidence indicates that Glyptodesma buchanensis was an epifaunal suspension feeder that lived with the commissure aligned vertically, the anterior auricle submerged in the substrate, and the broad anterior surface of the shell body appressed against the substrate surface (Text-fig. 4). Evidence for this life orientation includes the following:

1. Anterodorsal thickening of the shell is distributed evenly between right and left valves, as anticipated in bivalves that hold themselves in a vertical orientation (Pl. 21, fig. 1). By contrast, if G. buchanensis was pleurothetetic, one would expect the lowermost valve to be disproportionately thickened, as, for example, in the pleurothetetic oyster Gryphaea.

2. As discussed earlier, unworn specimens of G. buchanensis reveal that erect laminae were secreted around the entire growing edge of the shell (Pl. 20, figs. 4 & 11).
In most specimens from the Buchan Caves Limestone outcropping in the Basin, the laminae are excessively worn, often obliterated, over the entire shell surface, except near the anterior margins, where they are generally intact. The particular areas of the shell that usually avoid wear include the anterior auricle, byssal sulcus and anterior margin of the shell body, on both valves. This unusual wear pattern cannot be explained by post-mortem attrition from shell transport, grazing organisms or other extrinsic agents: why should post-mortem wear differentially affect the anterior part of the shell, for example? If, however, the abrasion of the laminae took place before death, the wear pattern is clearly inconsistent with a pleurothethetic epifaunal, or vertical semi-infaunal or infaunal life mode. One would predict that in the former mode, the underlying valve would be relatively free from pre-mortem wear; for the latter two modes, the same would be expected, but for all or most of the external surface of both valves. The wear pattern is consistent, however, with the vertical epifaunal life mode depicted in Text-fig. 4. In this orientation, laminae on the anterior surface of the shell are shielded from abrasion by the substrate.

3) Stanley (1970, 1972) has shown that among Recent mytilids, endobyssate and epibyssate species can be distinguished on the basis of cross-sectional shape. In endobyssate species, maximum shell width occurs midlaterally or above a midlateral line. In epibyssate species, maximum shell width is displaced ventrally, providing a broad contact
surface with the substrate. As shown in Pl. 20, fig. 3, *G. buchanensis* exhibits a cross-sectional shape more like that of epibyssate mytilids (especially if the anterior auricle is excluded).

In summary, aspects of *G. buchanensis*, including cross-sectional shape, distribution of shell thickening and postmortem wear, strongly support the hypothesis of a vertical, epifaunal orientation, as depicted in Text-fig. 4. This orientation is similar to that inferred for the aberrant, but morphologically similar, Permian pteriomorph *Eurydesma* (Runnegar 1979) and the Devonian megalodontid *Megalodon* Sowerby (Skelton 1978), but differs in two important ways: 1) the anterior auricle presumably had an anchoring effect that was enhanced by massive shell thickening in that region of the shell (*Eurydesma* and *Megalodon* lacked an anchoring anterior auricle, although the umbones may have penetrated the substrate and thus functioned in an analogous way [Runnegar 1979, fig. 5A; Skelton 1978, fig. 11e]); 2) the umbones were not rotated as far under the shell body, and, consequently, the angle formed by the hinge axis and the substrate is about 100 degrees (Text-fig. 4), a figure substantially less than that for *Eurydesma* (about 160 degrees according to Runnegar 1979: 264, and figs. 1B and 4K). Runnegar (1979) suggested that the dorsally weighted shells of *Eurydesma* would tend to right themselves even if washed about by water movement, thereby compensating for the apparent lack of mobility in *Eurydesma*. It is doubtful that
the weighted shell of *G. buchanensis* functioned in quite the same way. If shells of *G. buchanensis* were dislodged from life position, this position could not have been resumed by passive factors alone, owing to the presence of the anterior auricle. Life position could only be re-established by penetration of the substrate by the anterior auricle. Presumably, a small foot was retained for this purpose. It appears, then, that umbonal weighting in *G. buchanensis* functioned primarily to prevent initial dislodgement of the shell, rather than to right the shell afterward, whereas in *Eurydesma*, umbonal weighting probably functioned in both capacities.

Massive shell thickening in *G. buchanensis* was not achieved until relatively advanced growth stages. ANU 48431, for example, is a large individual, yet shows no appreciable shell thickening umbonally (Pl. 20, fig. 1), while other specimens this large and larger are massively thickened (Pl. 20, figs. 7 & 10; Pl. 21, fig. 1). The byssal sinus shows negative correlation with umbonal thickening (Pl. 20, figs. 5-7): thin shells, characteristic of early and intermediate growth stages, exhibit a well developed byssal sinus (Pl. 20, fig. 5), whereas massively thickened shells, representing older individuals, often show infilling of the byssal sinus such that a relatively straighter anterodorsal shell margin is produced (Pl. 20, fig. 7).

Progressive infilling of the byssal sinus at advanced growth stages in *G. buchanensis* suggests atrophy or loss of
the byssus. It appears, then, that the byssus was responsible for maintaining the orientation of the shell through most of ontogeny, but at advanced growth stages, this role was assumed by massive shell deposits anterodorsally. Essentially the same ontogenetic pattern occurs in *Eurydesma* and *Megalodon*, except that in at least *Eurydesma* umbonal thickening and loss of the byssus occurred at relatively earlier growth stages (Runnegar 1979; Skelton 1978).

Although the life orientation of *G. buchanensis* was broadly similar to that of *Eurydesma*, the shell is not nearly as large nor as massively thickened. These features, coupled with the loss of the byssus in the adult shell, make it improbable that *G. buchanensis* could have maintained positional stability in the high energy environments exploited by *Eurydesma* (Runnegar 1979). Instead, *G. buchanensis* probably inhabited quiet water environments, an inference consistent with the faunal and lithological associations characteristic of this species at Locality CB1 in the Cavan Formation (p. 17-19). In this way, *G. buchanensis* was more like *Megalodon* (the shell of which is also much smaller than in *Eurydesma*, but relatively thicker than in *G. buchanensis*), which "...tended to cluster together in calm 'ultra back reef' environments" (Müller-Jungbluth, *in fide* Skelton 1978: 308).

The source of pre-mortem wear on shells of *G. buchanensis* from the Basin localities is uncertain. The shells occur in beds with abundant, well preserved, and
occasionally articulated, shells of the brachiopod *Spirifer yassensis*, suggesting a low energy environment comparable to that at Locality CB1. Consequently, water movement seems an improbable source of pre-mortem abrasion. An alternative possibility is that grazing organisms (perhaps the large loxonemid and planispiral gastropods occurring with *G. buchanensis* at the Basin localities) fed on algae growing on the shells of living *G. buchanensis* and, in the process, abraded the exposed lamellae. This hypothesis is supported by the fact that large gastropods are absent at Locality CB1, and the lamellae of adult *G. buchanensis* are correspondingly well preserved.
Superfamily Pectinacea Rafinesque 1815
Family Pterinopectinidae Newell 1937
Genus Pseudaviculopecten Newell 1937

Type species: Monotis princeps Conrad 1838, by original designation.

Pseudaviculopecten etheridgei (Koninck)
(Pl. 22; Text-fig. 4)

1876. Aviculopecten Etheridgei Koninck, p. 89, pl. 3, fig. 9.

Neotype: ANU 36639 (Locality R7, Receptaculites Limestone).

Referred specimens: ANU 36638, 36640-36643 (total, 5).

Known stratigraphic and geographic distribution: late Emsian, Receptaculites and Bloomfield limestones, Taemas Formation, Taemas area, New South Wales.

Description:

External features - This species is represented by only a few fragmentary and mostly worn shells. Judging from ANU 36638 (Pl. 22, fig. 5), the most complete specimen available (length=70 mm [est.]; height=59 mm), the shell is nearly equilateral, but with the posterodorsal region moderately distended. In both valves, the auricles are subequal and well
differentiated from the shell body by auricular sulci and subauricular embayments. The posterior embayment is somewhat broader than the anterior. Ornament in the left valve consists of relatively coarse radial ribs and occasionally intercalating finer ribs, crossed by fine, closely spaced, commarginal growth lines (usually worn), and more widely and irregularly spaced growth rugae (Pl. 22, figs. 1 & 8). Commarginal ornament is more pronounced on the auricles than on the shell body. Ribs tend to be nodose where crossed by rugae and prominent growth lines.

In the right valve, auricular sulci are well developed. The anterior embayment is deeper and more acute in the right valve than in the left, owing to the development of a strong byssal notch. Radial ribs are finer and more closely spaced than in the left valve (Pl. 22, fig. 3). Commarginal ornament is conspicuous on the auricles, but faint or obscure on the shell body. On both valves, radial ribs tend to be weaker on the auricles (especially on the anterior auricle) than on the shell body, and sometimes occur only on the central part of the auricle (Pl. 22, figs. 1 & 3).

Internal features - The posterior adductor scar is circular and occurs relatively high in the shell, posterior to the umbo (Pl. 22, figs. 2, 4 & 6). A small, but prominent and consistently developed, anterior pedal retractor scar occurs near the dorsal end of the internal expression of the anterior auricular sulcus (Pl. 22, figs. 2 & 6). This scar is accompanied posteroventrally by a much smaller, fainter
retractor scar (often not preserved). A faint scar (or scars?) is visible in one specimen between the posterior adductor scar and the umbonal cavity, and may represent the insertion of the Quenstedt muscle (Pl. 22, fig. 6). The same specimen shows the pallial line faintly preserved anterodorsally. The ligament area is crossed by coarse, obtuse chevrons. Neither a resilifer nor dentition are developed.

Discussion: Koninck (1876) described *Aviculopecten etheridgei* on the basis of a silicified left valve. Locality information that Koninck provided is vague, reading simply, "the black argillaceous limestone of the Yass District" (1898: 90, translation of Koninck 1876). According to Benson (1922: 86), Koninck was referring to the Devonian limestone of the Murrumbidgee Valley. It is very likely, therefore, that Koninck's specimen was collected from the upper Bloomfield, *Receptaculites* or Warroo limestones, these being the only beds in the Murrumbidgee Valley of the Yass area that show significant development of silicification. The material described in the present study agrees closely with the figure and description of *A. etheridgei* given by Koninck (1876), and is regarded as conspecific. Koninck's specimen of *A. etheridgei* (and all other fossils described with it) was destroyed by fire (Benson 1922: 86), and, therefore, a neotype has been designated herein.

*A. etheridgei* lacks the central resilifer characteristic of *Aviculopecten* and should be removed from that genus. It is
here assigned to *Pseudaviculopecten* on the basis of its well
differentiated auricles and the general similarity of the
shell outline with that of the type species,
*Pseudaviculopecten princeps* (Conrad) (see Newell 1937: 38,
and Newell, in Moore 1969: N334, for generic diagnoses). *P.
etheridgei* represents the oldest known member of the genus.
Known features of the musculature agree closely with
comparable features described for the Aviculopectinidae
(Newell 1937, fig. 2, 1 & 2).