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BULLETIN 96

# Desmodont Bivalves from the Permian of Eastern Australia

BY

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## FOREWORD

The detailed survey of the Bowen and Surat Basins undertaken by the Bureau of Mineral Resources and the Geological Survey of Queensland has given a considerable stimulus to the study of the palaeontology of the Basins.

In particular, large collections of Permian fossils have opened the way to new and fundamental studies, which are the basis, among other things, for an understanding of the stratigraphy of the region.

Dr. Runnegar's monographic treatment of the primitive desmodonts of the eastern Australian Permian is largely based on the collections made during the survey, and is one of a number of studies undertaken on these collections; some by palaeontologists of the Bureau, and some by other research workers with particular knowledge of certain faunas, to whom our gratitude is due.

J. M. RAYNER,  
*Director.*

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## SUMMARY

Bivalves of the genera *Megadesmus* Sowerby, *Pyramus*, *Myonia*, and *Astartila* Dana, *Vacunella* Waterhouse, and *Pleurikodonta* Runnegar are common in the Permian strata of eastern Australia and are useful for both local and regional correlation. Some of these genera occur in New Zealand, Western Australia, India, and South America, but are uncommon in the northern hemisphere and appear to have been more or less endemic to the Gondwana province. Because of their common morphological features they can be grouped into a single family — the family Pholadomyidae.

*Notomya* McCoy, *Clarkia* de Koninck, and *Pyramia* Dana are considered to be synonyms of *Pyramus*, and *Maeonia* Dana and *Pachymyonia* Dun to be synonyms of *Myonia*. *Globicarina* Waterhouse is probably a junior synonym of *Megadesmus* (*Cleobis*) and it is doubtful whether it is worthwhile retaining *Cleobis* even at the subgeneric level. All the eastern Australian species which have previously been referred to *Chaenomya*, *Allorisma*, or 'Sanguinolites' can now be placed in *Vacunella*, a genus which may have been derived from *Myonia* in the Lower Permian.

*Megadesmus*, *Pyramus*, *Myonia*, and probably *Vacunella* have four pedal muscle scars (protractor, anterior retractor, umbonal retractor, and posterior retractor) and two accessory muscle scars of uncertain function, here termed muscle scars *a* and *b*. *Megadesmus*, *Astartila*, and *Pleurikodonta* lack a pallial sinus, but all species of *Pyramus* have a small pallial sinus. The type species of *Vacunella*, *V. curvata*, has a very large pallial sinus and probably an accessory (third) adductor scar at the base of the sinus, but other species of *Vacunella* appear to be less modified and have shallower pallial sinuses. *Megadesmus*, *Pyramus*, and *Astartila* have a blunt tooth in the right valve and a well defined socket in the left, and in *Megadesmus* and *Pyramus* the anterior margin of the right valve slightly overlaps that of the left. This valve overlap is absent in *Myonia* and *Vacunella* and neither genus has well defined teeth. *Megadesmus* has a prismatic outer shell layer and a nacreous inner layer, and it may be assumed that the other genera also had prismato-nacreous shells.

In all, 27 species of *Megadesmus*, *Astartila*, *Pleurikodonta*, *Pyramus*, *Myonia*, and *Vacunella* have been recognized in eastern Australia and 18 of these (the species of *Pyramus*, *Myonia*, and *Vacunella*) are described in the following paper. Three species—*Myonia carinella*, *Myonia? sulcata* and *Vacunella? dawsoneensis*—are new, but it has been possible to reduce the number of useful specific names from more than 38 to 15. No new generic names have been proposed at this stage, although it is possible that some of the species referred to *Vacunella*, for example *V? dawsoneensis*, will eventually require new generic names.

Most of the species are useful stratigraphically; but the genera are long-ranging and most occur throughout the Permian of eastern Australia. The oldest faunas containing these shells (of probable Sakmarian age) are from the Allandale Formation in the Hunter Valley and from the base of the Permian sequence on the south coast of New South Wales at Durras. Both localities contain *Megadesmus globosus* and *Pyramus laevis*, and these species are not known from younger formations in either area. *Myonia? sulcata* and *Myonia morrissi* also occur in the Allandale Formation, but they range into younger (lower Artinskian) strata in Queensland, where they are associated with *Megadesmus gryphoides*, *M. nobilissimus*, and *Pyramus concentricus?* The latter species range into the upper Artinskian in the Bowen Basin, where they are associated with *Vacunella etheridgei*. The lower Permian (Kazanian) fauna is perhaps the most distinct and is easily recognizable in Queensland, New South Wales, and Tasmania. The most characteristic species in all three areas are *Megadesmus grandis*, *Astartila intrepida*, *Myonia carinata*, *Pyramus myiformis*, and *Vacunella curvata*, although *Pleurikodonta elegans* and *Vacunella? dawsoneensis* also occur at this level in Queensland. Other species are of limited use at present, but with larger collections, particularly from the Sydney Basin and Tasmania, they may well be of greater use in the future.

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## INTRODUCTION

One of the characteristic elements of the Australian Permian invertebrate fauna is a large and relatively homogeneous group of bivalves, which Newell (1956) has called 'primitive desmodonts'. Although widely distributed in southern continents, these shells are poorly represented in or absent from most Permian deposits of the northern hemisphere, and they have been considered to be more or less endemic to the Gondwana province. Their association, at least in the Lower Permian, with glacial erratics, tillites, and occasional varves, suggests that they were limited to a cooler environment than the ammonoids and fusulinids of the Tethyan province. The following generic names have been proposed for Australian shells:

<i>Megadesmus</i> Sowerby, 1838	<i>Clarkia</i> de Koninck, 1876
<i>Pachydomus</i> Morris, 1845	<i>Pachymyonia</i> Dun, 1932
<i>Pyramus</i> Dana, July 1847	<i>Undulomya</i> Fletcher, 1946
<i>Cleobis</i> Dana, 1847	<i>Palaeocosmomya</i> Fletcher, 1946
<i>Astartila</i> Dana, 1847	(= <i>Cosmomya</i> Holdhaus, 1913)
<i>Myonia</i> Dana, 1847	<i>Praeundulomya</i> Dickins, 1957
<i>Notomya</i> McCoy, November 1847	<i>Globicarina</i> Waterhouse, 1965a
<i>Maeonia</i> Dana, 1848	<i>Vacunella</i> Waterhouse, 1965a
<i>Pyramia</i> Dana, 1849	<i>Pleurikodonta</i> Runnegar, 1965

In addition, some Australian species can be satisfactorily referred to the European and North American genera: *Edmondia* de Koninck, 1844, *Chaenomya* Meek, 1865, and *Wilkingia* Wilson, 1959 (= *Allorisma* of authors).

Recent papers by Newell (1955), Popov (1957), Lobanova (1959), Ciriacks (1963), and Dickins & Shah (1965) have provided evidence that some of the Australian genera are more widely distributed than had previously been thought, and occur in north-eastern Siberia (*Myonia*), and Greenland, Madagascar, Wyoming, and Russia (*Cosmomya* and *Undulomya*).

Many of the generic names that have been introduced for this group of shells are synonymous, and most authors have used a substantially reduced number of genera. The status of these genera has recently been discussed by Newell (1956), Dickins (1956, 1957, 1963), Dickins & Shah (1965), Waterhouse (1965a), and Runnegar (1965, 1966), but it has not been possible to reach conclusions acceptable to all authors. Waterhouse, for example, would prefer to use a greater number of generic names than Newell or I, whereas Dickins adopts an intermediate view. The following table summarizes the differences between the groupings used here and those used by Waterhouse (1965a).

Waterhouse, 1965a	Runnegar
1. <i>Megadesmus</i> (= <i>Pachydomus</i> , <i>Cleobis</i> )	1. <i>Megadesmus</i>
2. <i>Astartila</i>	1a. <i>Megadesmus</i> (= <i>Pachydomus</i> )
3. <i>Myonia</i> (= <i>Maeonia</i> )	?1b. <i>Cleobis</i> (= <i>Globicarina</i> )
	2. <i>Astartila</i>

- |   |   |
|---|---|
| 4. <i>Pachymyonia</i>                                   | 3. <i>Pleurikodonta</i> *   |
| 5. <i>Notomya</i>                                       | 4. <i>Pyramus</i> (= <i>Notomya</i> , <i>Pyramia</i> , <i>Clarkia</i> ) |
| 5a. <i>Notomya</i>                                      | 5. <i>Myonia</i> (= <i>Maeonia</i> , <i>Pachymyonia</i> )               |
| 5b. <i>Pyramus</i> (= <i>Pyramia</i> , <i>Clarkia</i> ) | 6. <i>Vacunella</i>   |
| 6. <i>Globicarina</i>                                   | 7. <i>Chaenomya</i>   |
| 7. <i>Vacunella</i>                                     |   |
| 8. <i>Chaenomya</i>                                     |   |

Although the initial purpose of this study was a revision of the eastern Australian species of *Pyramus*, *Myonia*, and *Vacunella*, it has been possible to show that all these genera have many features in common and are probably best grouped either in a single family, or in two closely related families (Runnegar, 1966). They appear to have been ancestral to living genera such as *Pholadomya* and *Laternula*, and are not closely related to *Panope* or *Panomya* as has been suggested by Newell (1956) and other authors. An understanding of their morphology has been made possible by a few excellently preserved specimens, kindly lent by the Australian Museum, Sydney, the Bureau of Mineral Resources, Canberra, and the Geological Survey of Queensland, Brisbane.

Most of the type specimens are housed in the British Museum, London, the Sedgwick Museum, Cambridge, or the Smithsonian Institution, Washington, but plaster casts of many of them are held by the Australian Museum, the University of Queensland, or the Bureau of Mineral Resources, Canberra.

Specimens which have been figured or mentioned in the text are prefixed by the initials of the institution in which they are housed, as follows:

- |        |   |
|--------|---|
| AM     | Australian Museum, Sydney.  |
| MM     | New South Wales Geological and Mining Museum, Sydney.                                 |
| BMR    | Bureau of Mineral Resources, Canberra.  |
| CPC    | Commonwealth Palaeontological Type Collection, Bureau of Mineral Resources, Canberra. |
| QM     | Queensland Museum, Brisbane.  |
| GSQ    | Geological Survey of Queensland, Brisbane.  |
| UQ     | Department of Geology and Mineralogy, University of Queensland, Brisbane.             |
| UT     | Department of Geology, University of Tasmania, Hobart.                                |
| TM     | Tasmanian Museum, Hobart.   |
| BM(NH) | British Museum (Natural History), London.   |
| SM     | Sedgwick Museum, Cambridge.   |
| USNM   | Smithsonian Institution, Washington, D.C.   |

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\* Although originally described as a subgenus of *Astartila*, *Pleurikodonta* is probably best treated as a separate genus, differing from *Astartila* in possessing well developed radial ornament.

## FOSSIL LOCALITIES

The Bureau of Mineral Resources and the Geological Survey of Queensland have recently carried out jointly an extensive regional mapping programme in the Bowen Basin, Queensland. A large number of the Permian bivalves collected in the course of this investigation have been kindly lent to me for this and future studies. All the specimens have been given BMR field numbers (for example B 686), which have been or will be used in the publications on the Bowen Basin. The prefixed letter of each locality number is an abbreviation of the name of the 1:250,000 map Sheet on which the locality occurs, as follows: B, Bowen; MC, Mount Coolon; M, Mackay; C1, Clermont; SL, St Lawrence; Em, Emerald; Du, Duaringa; Sp or Z, Springsure; Ba, Baralaba; T, Taroom. The location of these map areas is shown by Malone (1964, fig. 1, p. 264). In the following text, the BMR locality numbers are used to supplement the information on the distribution of Queensland species. All other localities referred to are described geographically.

## ACKNOWLEDGMENTS

This study has been carried out in the Department of Geology, University of Queensland, under the supervision of Professor Dorothy Hill, F.R.S., in partial fulfilment of the requirements of a Ph.D. degree in Geology, and was financed by a Commonwealth Postgraduate Award. Professor Hill and Dr J. M. Dickins of the Bureau of Mineral Resources have read, discussed, and criticized the manuscript at various stages of the study, and their assistance and encouragement in this and many other ways is gratefully acknowledged.

Specimens for the study were lent or given by the British Museum (Natural History), London, the Australian Museum and the Geological & Mining Museum, Sydney, and the Geological Survey and the Queensland Museum, Brisbane. The Bureau of Mineral Resources very kindly made available all the relevant bivalves from its Bowen Basin collections. I am grateful to the following people, who freely provided information, photographs, or curatorial assistance: Messrs J. Armstrong and F. S. Colliver, University of Queensland; Dr R. Both, Tasmanian Museum; Mr T. A. Darragh, National Museum of Victoria; Dr J. Dear and Messrs G. Fleming and R. G. McKellar, Geological Survey of Queensland; Dr J. W. Evans, Mr H. O. Fletcher, and Dr D. F. McMichael, Australian Museum, Sydney; Dr K. S. W. Campbell, Australian National University, Canberra; Dr E. G. Kauffman, Smithsonian Institution; Dr N. D. Newell, American Museum of Natural History; Dr A. C. Rocha-Campos, University of Sao Paulo; Dr J. B. Waterhouse, New Zealand Geological Survey; Mr S. Ware, British Museum (Natural History); and Dr R. E. Wass, University of Sydney. Mr J. S. Jell, University of Queensland, collected from several of the south coast localities of the New South Wales Permian, and Mr V. Gostin, Australian National University, has kindly permitted me to include some of the results of his unpublished work in this area. The generosity of Mr M. R. Banks, University of Tasmania, and the Department of Geology, University of Queensland,

enabled me to spend four weeks collecting in the Tasmanian Permian, and I am most grateful to Mr & Mrs Banks for the hospitality extended to me during this visit.

Through the courtesy of the Chief Geologist, Dr N. H. Fisher, I was able to spend eight weeks at the Bureau of Mineral Resources, Canberra, early in 1964.

All photographs not otherwise annotated were taken by Mr John Coker, Photography Department, University of Queensland.

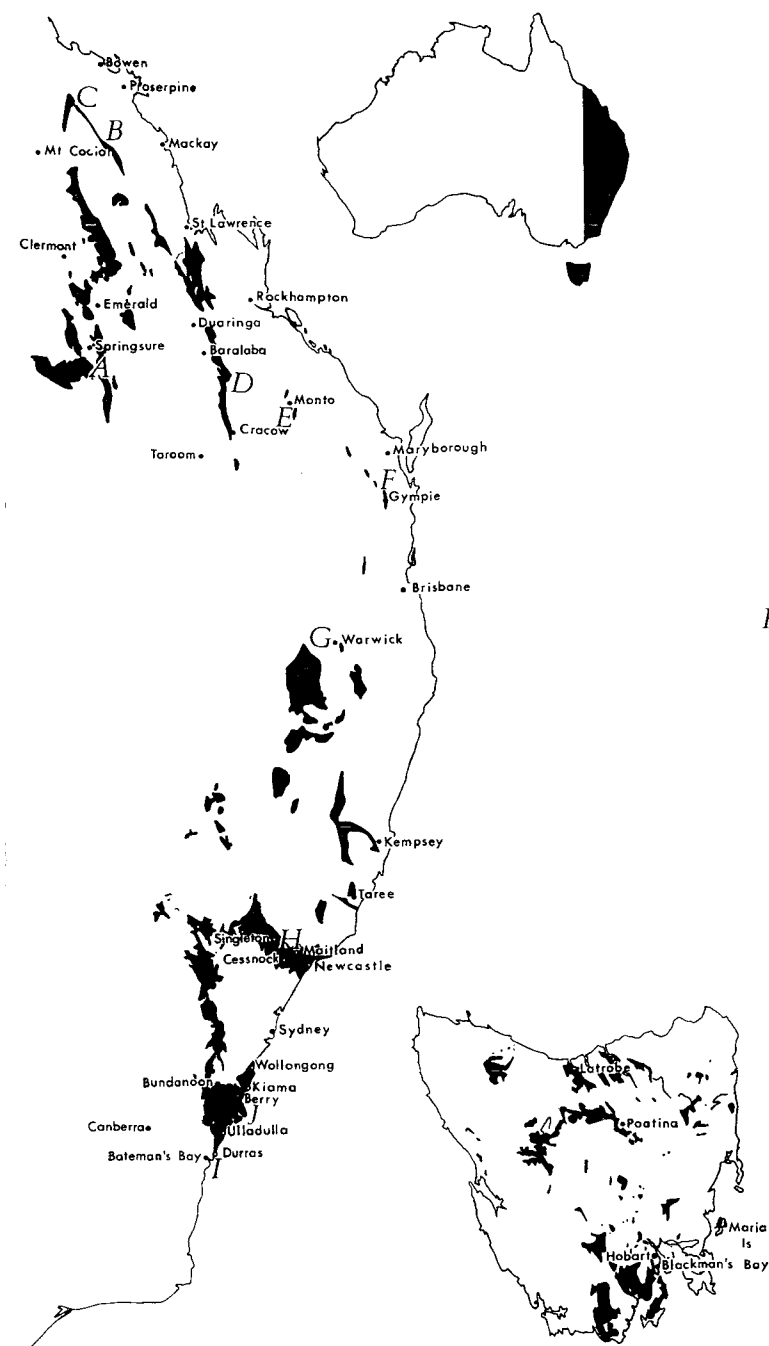
## STRATIGRAPHY

The Bowen Basin, Queensland, is probably the most completely mapped major Permian sedimentary basin in eastern Australia, and thus provides reference sections for correlations with the Permian of Western Australia and overseas. Much of the information on the geology of the Bowen Basin has been produced by a recent regional survey carried out jointly by the Bureau of Mineral Resources and the Geological Survey of Queensland (see Dickins, Malone, & Jensen, 1964), and has been or will be published by the Bureau of Mineral Resources.

During the course of this survey, Dickins found he was able to recognize three very distinct and one less distinct macrofossil assemblages (Faunas II to IV and Fauna I), which he considered to be confined to rock units of regional extent and usually of group rank. In the now accepted nomenclature, these are the Lizzie Creek Volcanics (Lower Bowen Volcanics), and Tiverton Subgroup ('Unit A'), Gebbie Subgroup ('Unit B'), and Blenheim Subgroup ('Unit C') of the Back Creek Group ('Middle Bowen Beds'). Previously, Dickins (1963) had recognized six main 'stages' in the development of the faunas in the Permian basins of Western Australia, and he was subsequently (1967) able to provide correlations of the Western Australian sequences with those of the Bowen Basin and the Hunter Valley of New South Wales.

Glenister & Furnish (1961) have correlated the ammonoid-bearing strata of the Western Australian Permian with those of the type sequences of the USSR and the United States, and these ammonoid faunas provide the strongest link for correlations with the faunas outside the Gondwana province. Very few ammonoids were known from the eastern Australian Permian in 1961 (Glenister & Furnish, p. 675), although recent discoveries of additional specimens of *Neocrinites* (Dickins in Dickins et al., 1964, p. 60; Armstrong, Dear, & Runnegar, 1967) and *Uraloceras* (Dear, 1966; Armstrong et al., 1967) support and supplement earlier correlations based primarily on the brachiopods (Hill, 1950; Maxwell, 1954; Campbell, 1959, 1960, 1961) and polyzoa (Phillips Ross, 1963).

The major areas of Permian marine sedimentation in eastern Australia (Text-fig. 1) are the Bowen, Yarrol, and Maryborough Basins of Queensland, the Sydney Basin and the Kempsey-Taree area of New South Wales, and the Tasmanian



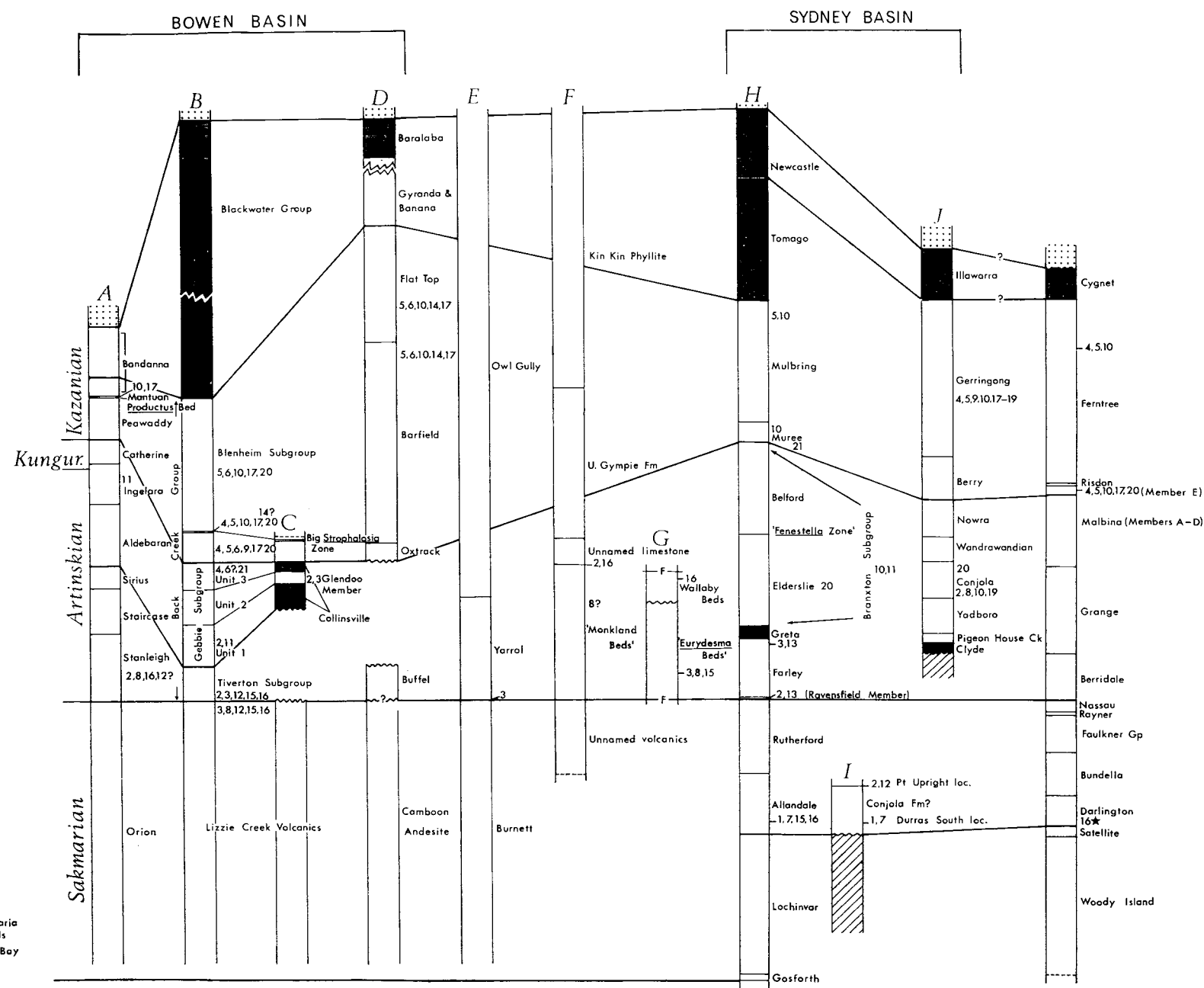
TEXT-FIG. 1

Fig. 1. Locality map and correlation table of major Permian sequences in eastern Australia (areas of Permian outcrop shown in black). The stratigraphic sections show approximate thicknesses and the lines connecting different sections are intended to indicate approximate time equivalence.

Sections A-J are from the areas labelled A-J on the map of eastern Australia (vertical scale of section 2000 feet = 1 inch) and the eleventh section is from the Hobart area in Tasmania (vertical scale 400 feet = 1 inch).

Species occurrences are shown by the numbers beside the columns, as follows:

- |                                   |   |
|-----------------------------------|---|
| 1. <i>Megadesmus globosus</i>     | 11. <i>Vacunella etheridgei</i>             |
| 2. <i>Megadesmus nobilissimus</i> | 12. <i>Vacunella</i> sp. nov. A             |
| 3. <i>Megadesmus gryphoides</i>   | 13. <i>Vacunella</i> cf. <i>waterhousei</i> |
| 4. <i>Megadesmus grandis</i>      | 14. <i>Vacunella?</i> <i>dawsonensis</i>    |
| 5. <i>Astartila intrepida</i>     | 15. <i>Myonia?</i> <i>sulcata</i>           |
| 6. <i>Pleurikodonta elegans</i>   | 16. <i>Myonia morrissi</i>                  |
| 7. <i>Pyramus laevis</i>          | 17. <i>Myonia carinata</i>                  |
| 8. <i>Pyramus concentricus?</i>   | 18. <i>Myonia elongata</i>                  |
| 9. <i>Pyramus myiformis</i>       | 19. <i>Myonia valida</i>                    |
| 10. <i>Vacunella curvata</i>      | 20. <i>Myonia corrugata</i>                 |
|                                   | 21. <i>Vacunella</i> sp. nov. B             |



The stratigraphic sections were compiled from data from the following sources:

- Section A (Springsure area, Bowen Basin)—Mollan et al. (1968).  
 Section B (Blenheim area, Bowen Basin)—Dickins et al. (1964).  
 Section C (Scottville, northern Bowen Basin)—Dickins et al. (1964).  
 Section D (south-eastern part of Bowen Basin)—Dear & Jensen (1965) and Wass (1965).  
 Section E (Yarrol Basin, Monto district)—Maxwell, 1964.  
 Section F (Maryborough Basin, Gympie district)—Runnegar (1963) (unpublished).  
 Section G (Stanthorpe Road fault block)—Armstrong (1965) (unpublished).  
 Section H (Hunter Valley, Sydney Basin)—Booker, 1960.  
 Section I (Durras-Point Upright area, Sydney Basin)—personal communication by V. Gostin, Australian National University.  
 Section J (South Coast, Sydney Basin)—Booker (1960) and McElroy & Rose (1962).  
 Hobart area, Tasmania—Banks & Hale (1957) and Sutherland (1964).

Basin of Tasmania. The stratigraphy of the Queensland basins has been summarized in Hill & Denmead (1960), of New South Wales in Packham (in press), and of Tasmania by Banks (in Spry & Banks, 1962), all of whom give references to earlier works. The stratigraphy of the Bowen Basin is exhaustively discussed in Dickins & Malone (in press), which culminates the work in that area, already discussed in several reports of the Bureau of Mineral Resources (see Bibliography).

#### *Russian stages in eastern Australia.*

The 9 foot Gosforth shale member of the Lochinvar Formation is considered to be the oldest Permian unit in the Hunter Valley of New South Wales, since it contains the Lower Permian marine bivalve *Eurydesma*, and since it is underlain (apparently conformably) by the 'Kuttung Series' of fluvioglacial sediments which contain a *Rhacopteris* rather than a *Glossopteris* flora (Browne, in Osborne, 1949, p. 207). In Queensland, Maxwell (1964) has mapped an apparently conformable and reasonably fossiliferous Carboniferous Lower Permian succession in the Yarrol Basin, but elsewhere in eastern Australia the base of the Permian is difficult to locate because of large thicknesses of unfossiliferous volcanic, freshwater, or occasionally tillitic 'Permo-Carboniferous' sediments.

Recent correlations of the eastern and Western Australian sequences by Dickins (1967), together with recent studies of the Western Australian ammonoid faunas (Glenister & Furnish, 1961), suggest that the Sakmarian-Artinskian boundary occurs at or near the base of the Farley Formation in New South Wales and at the base of the Middle Bowen Beds and Stanleigh Formation of the Bowen Basin, Queensland. This correlation is supported by a specimen of *Uraloceras cancellatum* Dear from the base of the Yarrol Formation, which has affinities with lower Artinskian species of *Uraloceras* from the Ural mountains and with *U. pokolbinense* from the Farley Formation of New South Wales (Dear, 1966). The semi-endemic lower Artinskian mollusc-brachiopod fauna (Fauna II of Dickens et al., 1964) is easily recognized throughout eastern Australia, so that the Sakmarian-Artinskian boundary can be reasonably accurately located in most areas. In Tasmania, for example, it probably occurs at or near the base of the Berriedale Limestone or Nassau Siltstone (Cascades Group), as shown by the presence of *Eurydesma hobartense*, *Deltopecten limaeformis*, *Ambikella* cf. *ovata*, *Ambikella* cf. *denmeadi*, *Cancrinella farleyensis*, *Anidanthus springsurensis*, *Taeniothaerus subquadratus*, *Strophalosia jukesi*, and *S. typica* in the Berriedale Limestone.

The position of the Artinskian-Kungurian boundary is less well known. Nassichuk, Furnish, & Glenister (1965) consider the Coolkilya Greywacke of the Carnarvon Basin, Western Australia, to be younger than the upper (Baigendzhinian) substage of the Artinskian as recognized by Glenister & Furnish (1961), but suggest that another stage could probably be recognized between the Artinskian and the Upper Permian (Guadalupian). For the purposes of this paper this interval



has been termed the Kungurian, and its position in eastern Australia as shown on Text-figure 1 and Table 1 is taken directly from Dickins' (1967) correlations of the faunas of eastern and Western Australia.

Waterhouse (1963), on the basis of correlations of the Permian faunas of Australia and New Zealand, considers that fossiliferous marine Upper Permian is unrepresented in eastern Australia, and places the base of the Kungurian at the base of the Peawaddy Formation and its equivalents. However, for the present it is proposed to follow Dickins in placing the boundary between the

TABLE 1. RANGES OF DESMODONT BIVALVES IN EASTERN AUSTRALIA

	Sakmarian	L. Artinskian	U. Artinskian	Kungurian	Kazanian
1. <i>Megadesmus globosus</i> ....	x				
7. <i>Pyramus laevis</i> ....	x				
15. <i>Myonia? sulcata</i> ....	x	x			
16. <i>Myonia morrisi</i> ....	x	x			
12. <i>Vacunella</i> sp. nov. A ....		x			
8. <i>Pyramus concentricus?</i> ....		x	?		
13. <i>Vacunella</i> cf. <i>waterhousei</i> ....		x			
3. <i>Megadesmus gryphoides</i> ....		x	x		
2. <i>Megadesmus nobilissimus</i> ....		x	x		
11. <i>Vacunella etheridgei</i> ....			x		
21. <i>Myonia carinella</i> ....				x	
4. <i>Megadesmus grandis</i> ....				x	x
6. <i>Pleurikodonta elegans</i> ....				x	x
20. <i>Myonia corrugata</i> ....			?	x	x
5. <i>Astartila intrepida</i> ....					x
17. <i>Myonia carinata</i> ....	?	?	?	?	x
18. <i>Myonia elongata</i> ....					x
19. <i>Myonia valida</i> ....			?		x
10. <i>Vacunella curvata</i> ....			?		x
14. <i>Vacunella? dawsonensis</i> ....					x
9. <i>Pyramus myiformis</i> ....				?	x

\*Locality in Conjola Formation.

Lower and Upper Permian at the base of the Peawaddy Formation in Queensland and at the base of the Muree Formation in the Hunter Valley. Since both of these units contain the first representatives of a widespread and distinct fauna (Fauna IV of Dickins et al., 1964), this horizon is easily located elsewhere in eastern Australia.

The youngest Permian units in eastern Australia containing marine fossils are probably the '*Chaenomya*' bed of the Mulbring Formation in the Hunter Valley (David, 1907, p. 77), the Flat Top Formation in the Bowen Basin, and the Ferntree Formation in Tasmania. All three units contain an apparently similar fauna which does not appear to differ markedly from that of the slightly older Peawaddy Formation and equivalents. Consequently the youngest faunas of the eastern Australian Permian are probably no younger than the Kazanian stage of the Upper Permian.

### Correlations

The distribution and occurrences of the species of *Megadesmus*, *Astartila*, *Pleurikodonta*, *Pyramus*, *Myonia*, and *Vacunella* are shown in Text-figure 1 and Table 1. Most species have restricted ranges, and when used in conjunction with the Polyzoa, Brachiopoda, and other Mollusca are useful stratigraphically in eastern Australia and New Zealand (Waterhouse, 1965a). Correlations with Western Australia, Timor, India, Madagascar, and South America are more difficult, but further study of the faunas should resolve some of these difficulties. Some of the Indian Permian bivalves are currently being studied by Mr S. C. Shah, Geological Survey of India, Calcutta, and Dr A. C. Rocha-Campos, Universidade do São Paulo, is undertaking a revision of the Permian bivalves from Taio described originally by Reed (1930). Dr J. B. Waterhouse (in press) has recently completed a monograph of the pholadomyid bivalves from the Permian of New Zealand.

The pholadomyid bivalves are most useful at localities where they occur in large numbers, often to the exclusion of virtually all other invertebrates. Most commonly these localities are in coarse pebbly sandstone, and it seems probable these shells lived in shallow nearshore banks.

The oldest stratigraphically useful species in eastern Australia are *Megadesmus globosus* and *Pyramus laevis*, which are known only from the Allandale Formation in the Hunter Valley, and from several thin but richly fossiliferous limonitic beds which occur some 200 feet above the base of the Permian sequence at Durras South, 6 miles north of Bateman's Bay on the south coast of New South Wales (Text-fig. 1). The two species dominate the fauna at Durras, and the only other stratigraphically useful fossil I have seen from the locality is a single specimen of *Eurydesma cordatum* (UQ F49663). In the Hunter Valley *E. cordatum* is also restricted to the Allandale Formation, so that the base of the Permian sequence on the south coast of New South Wales is probably best

correlated with the Allandale or Rutherford Formations of the Hunter Valley, rather than with the base of the Braxton Subgroup or Greta Coal Measures (Hill, 1955; McElroy & Rose, 1962).

*Myonia? sulcata* and *Myonia morrisi* occur in the Allandale Formation of the Hunter Valley, the Lizzie Creek Volcanics of the Bowen Basin, and the 'Eurydesma' and Wallaby Beds of the Warwick District. However, since the Queensland strata also contain *Megadesmus gryphoides* and *Eurydesma hobartense*, they are probably somewhat younger than the Allandale Formation, as suggested by Dickens (1967). *M. morrisi* is also common in the lower Artinskian faunas of Queensland (Text-fig. 1), where it is associated with *Megadesmus gryphoides*, *M. nobilissimus*, *Pyramus concentricus?*, *Eurydesma hobartense*, *Anidanthus springsurensis*, *Taeniothaerus subquadratus*, *Cancrinella farleyensis*, *Strophalosia preovalis*, *Ambikella ovata*, *A. profunda*, and *Fletcherithyrus homevalensis* (Faunas I or II of Dickens et al., 1964).

'*Pachymyonia* cf. *etheridgei*' and '*Notomya* cf. *antiquata*', two of the species which Dickens (in Malone et al., 1964, p. 54 & in Malone et al., 1967) has used to distinguish Fauna I from Fauna II, can now be referred to *Myonia morrisi* and *Pyramus concentricus?* respectively, and as such have relatively longer ranges which would probably make them unsuitable for distinguishing between the two faunas.

In Queensland, *Vacunella etheridgei* appears to be a useful index fossil for the upper Artinskian (Fauna III of Dickens et al., 1964), but the paucity of specimens of the other genera from this level makes adequate identification of what are possibly new species extremely difficult. For example, Hill & Woods (1964, pl. P 10, figs 6a, b) have figured a specimen of *Megadesmus* from the middle part (Unit B) of the Middle Bowen Beds which could well be either an aberrant specimen of *M. gryphoides* or an average individual of a new species. In the absence of several specimens, preferably from the same locality, the positive recognition of another species is extremely difficult.

The eastern Australian lower Upper Permian fauna is, however, quite characteristic, and the pholadomyid bivalves form an important and quite useful part of the fauna.

The lower Upper Permian fauna of Queensland, New South Wales, and Tasmania is characterized by *Megadesmus* (*Cleobis*) *grandis*, *Astartila intrepida*, *Myonia carinata*, *Myonia corrugata*, and *Vacunella curvata*, with the addition of *Pyramus myiformis* in Queensland and New South Wales and *Pleurikodonta elegans* and *Vacunella? dawsonensis* in Queensland. All these species range into some of the youngest Permian marine sediments in eastern Australia (the Blenheim Subgroup and the Flat Top Formation of the Bowen Basin, the Mulbring Formation and Gerringong Volcanics of the Sydney Basin, and the Ferntree

Formation of Tasmania), and are part of Dickins' Fauna IV in the Bowen Basin. Together with characteristic brachiopods such as *Strophalosia clarkei*, *S. ovalis*, *Terrakea solida*, *Ambikella magna*, *A. mantuanensis*, *Streptorhynchus pelicanensis*, *Marinurnula mantuanensis*, *Maorielasma globosum*, and *Gilledia ulladullensis*, they form a distinct and easily recognizable fauna.

The pholadomyid bivalves of this fauna have provided the first reasonably conclusive palaeontological evidence of the age of the poorly fossiliferous Ferntree Formation in the Hobart area, since a locality at Blackmans Bay, 12 miles south of Hobart (Banks, in ANZAAS Guidebook, 1965, p. 62, fig. 26), within 200 feet of the top of the formation has yielded *Megadesmus grandis*, *Astartila intrepida*, and *Vacunella curvata*. Thus the Ferntree Formation does not appear to be significantly younger than the upper part (Member E) of the underlying Malbina Formation, which contains *Megadesmus grandis*\*, *Astartila intrepida*, *Myonia carinata*, *M. corrugata*, *Vacunella curvata*, *Strophalosia ovalis*, and *Terrakea* cf. *solida*, and which is best correlated with the Peawaddy Formation and equivalents.

The oldest specimens of *Myonia corrugata* from Queensland and Tasmania are from the lower part of the Blenheim Subgroup and from Member E of the Malbina Formation, whereas in the Sydney Basin specimens of *M. corrugata* are known from the Branxton Subgroup in the Hunter Valley and from the Conjola Formation at Ulladulla on the south coast. Since *Eurydesma hobartense* has been recorded from the Branxton Subgroup (Woolnough, 1910) and from Ulladulla, where it is associated with *Deltopecten* (Raggatt & Fletcher, 1937, pp. 154-5), it is possible that the range of *M. corrugata* is longer in New South Wales than in Queensland or Tasmania.

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\* An examination of the lectotype of *Notomya trigonalis* (TM Z239, Johnston, 1887, p. 14; 1888, pl. 19, fig. 2, probably from Member E equivalent (Weston Formation) of the Malbina Formation in the Western Tiers near Deloraine) has shown that it is a specimen of *Megadesmus grandis* rather than a specimen of *M. nobilissimus* as was suggested previously (Runnegar, 1965, p. 237). Similarly *Astartila robertsi* (Johnston, 1887, p. 8) from Member E of the Malbina Formation at 'New Town Falls', Hobart, can now be confidently identified as *A. intrepida*, which is common in Member E elsewhere in the Hobart area.



## COMPARATIVE MORPHOLOGY

### *Musculature*

Yonge (1953, pp. 444-5) and Morton & Yonge (*in* Wilbur & Yonge, 1964, pp. 32-4) make a rather fundamental distinction between the *shell muscles* which occur in most molluscs and the *pallial muscles* found only in bivalves. The shell muscles pass from the shell into the foot and serve to attach the body to the shell, whereas pallial muscles connect the edge (and probably other parts) of the mantle to the shell. It seems likely (Yonge, 1953, p. 444) that primitive molluscs had a symmetrically arranged series of shell muscles such as those found in the primitive Ordovician monoplacophoran *Archaeophiala* (Knight, 1952). Yonge (1953), Vokes (1954), and McAlester (1965) feel that the numerous dorsal muscle scars of Ordovician nuculoid bivalves such as '*Nucula*' *amica* Barrande and *Ctenodonta bilunulata* Barrande (Vokes, 1954, p. 235, figs 2-5; Cox, 1959, fig. 1), and the eight pairs of pedal muscle scars found in the Lower Ordovician lucinoid *Babinka* (McAlester, 1965) are shell muscles whose position and number is similar to that of primitive univalves such as *Archaeophiala*, and presumably to the ancestral molluscs. Most living bivalves have only two pairs of shell muscles (now called pedal muscles), although three or four pairs may occur in the Solenacea and Tellinacea (Graham, 1934b).

The pallial muscles probably developed before the emergence of the bivalvia as a distinct class, and Yonge (1953, fig. 1B) suggests that the class was derived from a univalve that had an inner ring of shell muscles and a marginal ring of mantle muscles forming the pallial line. The two halves of the originally single valve were compressed about an uncalcified ligament; and the pallial muscles were probably cross-fused at either end of the ligament to give rise to the adductor muscles. Other modified pallial muscles are the siphonal retractor muscles, accessory ventral adductors, and the cruciform muscles of the Tellinacea, the latter two being formed by cross-fusion of the ventral edges of the mantle (Hunter, 1949; Graham, 1934a, b).

### *Pedal muscles*

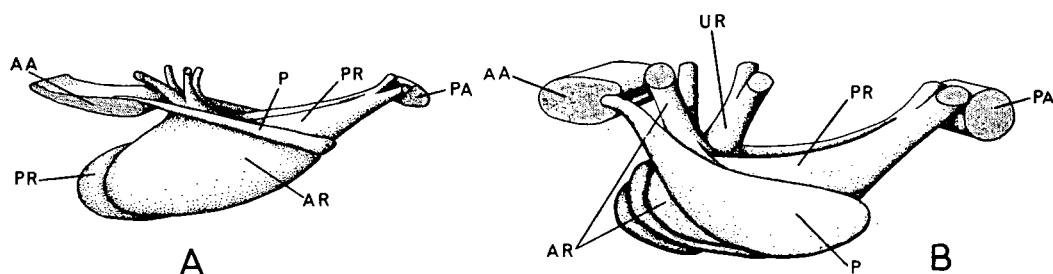
Two factors may complicate the study of pedal muscles from the scars on fossil bivalves. Firstly, a single muscle within the foot may have two or more quite distinct points of insertion on each valve (Text-fig. 2A, after Graham, 1934b, p. 177, fig. 10), and secondly, the anterior protractor muscle may be attached to the anterior adductor and not to the shell, as shown in Text-figure 2B (after Graham, 1934b, p. 174, fig. 8).

*Vacunella*, *Myonia*, *Pyramus*, and *Megadesmus* have two pedal scars above the front adductor: a larger scar attached to the upper edge of the rear adductor, and a small scar at or near the top of the umbonal cavity. The usual arrangement of these scars is shown by *Myonia valida* (Runnegar, 1966, fig. 1g). The most

anterior scar is the least distinct as it is often partly merged with the anterior adductor, and it is perhaps significant that it is this scar which is missing in *Astartila* (Waterhouse, 1965a, p. 372) and *Pleurikodonta* (Runnegar, 1965, p. 248). Text-figure 2A shows the arrangement of the muscles within the foot of *Donax vittatus*. The points of insertion of the pedal muscles are in much the same position as those of *Vacunella*, *Myonia*, or *Megadesmus*, except that the anterior pair of muscles is attached to the adductor muscle and not to the shell. In view of the partial merging of the most anterior pedal scar and the anterior adductor in genera such as *Megadesmus*, it is possible that two anterior pairs of pedal muscles were present in *Astartila* and *Pleurikodonta*, and that, as in *Donax*, one pair was attached to the anterior adductor.

I have previously followed Driscoll (1964) and termed the most anterior pair of scars *protractors* and the other three pairs *retractors* (anterior, umbonal, and posterior), whereas Waterhouse (1965a) has used the name protractor for both anterior pairs of scars. Graham's sketches of the foot of *Donax vittatus* (Text-fig. 2B) and *Cultellus pellucidus* (Text-fig. 2A) show that although the insertions of the protractor and anterior retractor muscles are close to one another, the protractor muscles are attached to the heel of the foot, whereas the retractors run directly into its anterior end. Consequently, while contraction of the latter results in a retraction of the foot into the shell, contraction of the former has the effect of protruding the foot beyond the margins of the shell (Driscoll, 1964, p. 63). It seems likely that the pedal muscles of *Vacunella* and the Pachydominae functioned in the same way as those of *Donax*; so it is proposed to continue to use the names protractor and anterior retractor.

Two, or possibly three, separate points of insertion of the protractor muscle can be seen in the protractor scar of one specimen of *Pyramus laevis* (Pl. 12, fig. 5), and other specimens of the same species sometimes have a bifid insertion of the umbonal retractor muscle. Otherwise there is little variation in the number



TEXT-FIG. 2

Fig. 2. Sketches of the arrangement of the pedal muscles in *Cultellus pellucidus* (A) and *Donax vittatus* (B), after Graham (1934b, figs 10 and 8).

AA, anterior adductor; PA, posterior adductor; P, pedal protractor; AR, anterior retractor; UR, umbonal retractor; PR, posterior retractor.

or position of the pedal muscle scars in different genera, except that in *Pyramus* the umbonal retractor is at the apex of the umbonal cavity instead of being on the anterior side.

Both protractor and anterior retractor scars are usually attached to the adductor scars, and the growth lines of the adductor scars continue directly into the growth lines of the pedal muscle scars. Consequently, even in species which have well differentiated muscle scars such as *Megadesmus gryphoides*, *Myonia carinata*, or *Pyramus laevis*, at least one third of the specimens will not show the protractor scar clearly, and often the protractor scar will be completely merged with that of the adductor. For this reason it is often necessary to have several well preserved internal moulds before the number and arrangement of the pedal muscle scars can be adequately described.

The presence of a large number of pedal muscle scars is often considered to be one of the primitive features of nuculoid bivalves, and there are usually only two pairs of pedal muscles in 'normal eulamellibranchs'. Although as many as four pairs may occur in members of the Tellinacea (Graham, 1934b), they control rather specialized movements of the foot (Morton, *in* Wilbur & Yonge, 1964, p. 411), and may therefore have developed independently. Consequently, it is difficult to say whether the presence of four pairs of pedal muscle scars in *Vacunella*, *Megadesmus*, *Myonia*, and *Pyramus* implies the retention of a somewhat primitive character or is a secondary adaptation for vigorous burrowing.

#### *Pallial muscles*

In all the genera studied, the pallial line is continuous, quite wide, and radially striated because of the insertions of the radially arranged pallial muscles. It does not extend above the adductors. *Vacunella* has a large pallial sinus, and a small sinus is usually present in species of *Pyramus*, and possibly in some specimens of *Myonia* (Pl. 5, fig. 19).

The pallial line of *Vacunella curvata* (Pl. 8, fig. 7; Runnegar, 1966, figs 1a, 3a) is relatively thin opposite the pedal gape and quite thick behind it. The development of the pallial muscles (as shown by the width of the pallial line) is, therefore, almost certainly related to the position of the ventral gape of the valves, which in turn reflects the position of the pedal gape of the mantle lobes. Consequently, it is most likely that cross-fusion of the radial pallial muscles, involving at least the inner fold of the mantle margin, has occurred below the pallial sinus. (If ventral fusion had not occurred in *Vacunella curvata*, or if it had involved only ciliary junctions or cuticular attachment of the lower edges of the mantle rather than tissue fusion, it is unlikely that the insertions of the pallial muscles would reflect the position of the pedal gape.)

Tissue is fused in living members of the Pholadomyacea (*Asthenothaerus* and *Periploma*) to form an accessory ventral adductor beneath the base of the siphons



(Pelseneer, 1911, *vide* Yonge, 1948, p. 595). The scars of similarly derived accessory adductors of the shells of the pholadid genera *Zirphaea* and *Pholadidea* (Purchon, 1955, pp. 868-869, figs 4, 5) resemble the thickened end of the pallial line in *Vacunella curvata*, so that it is quite likely that an accessory ventral adductor was present in *Vacunella*.

In *Pholadomya* the situation appears to be similar. Pelseneer (1890, 1906) has noted that the edges of the mantle lobes of living *Pholadomya* are fused along most of the ventral margin so that only a small anterior opening is retained for the protrusion of the foot. Most fossil species of *Pholadomya* have a pedal gape to the valves which extends backwards as far as either the first radial rib on the shell or the first strong radial rib (see Agassiz, 1842-5, pl. 4c, figs 5, 6; pl. 6a, figs 2, 3, 5-8; pl. 6c, figs 4, 5; pl. 6e, figs 1-3; pl. 6i, fig. 1-7; pl. 7b; figs 11, 12; pl. 7d, figs 9, 10; pl. 7e, fig. 1w; and pl. 7f, fig. 18). I have examined a plaster cast (AM L757) of a specimen of *Pholadomya gigantea* (Sowerby) figured by Moesch (1875, pl. 31, fig. 2a) which shows the pallial line exceptionally well. The line is thickened from the base of the pallial sinus to the first coarse rib, which by analogy with other species of *Pholadomya*, represents the posterior end of the pedal gape. Thus it seems likely that this represents the accessory adductor of *Vacunella* (*ava*, Runnegar, 1966, fig. 1a), which has been transformed into an elongate scar (*ava*?, Runnegar, 1966, fig. 1b) by the reduction of the pedal gape and the anterior migration of its posterior end.

The pallial line of *Vacunella* cf. *waterhousei* slightly thickens posteriorly, and the anterior end of the thickened part coincides with a marked change in the slope of the line, and probably with the rear end of the pedal shell gape. Consequently it is possible that the lower edges of the mantle lobes were fused behind the pedal gape, although a discrete and obvious muscle scar is not developed.

There is no evidence of tissue fusion of the ventral edges of the mantle in *Megadesmus*, *Pyramus*, or *Myonia*, but since none of these shells gapes ventrally, it is unlikely that the positions of the ventral apertures in the mantle would be reflected in the width of the pallial line.

Pits of the internal surface of the valves are common in a number of species of *Megadesmus*, *Myonia*, *Pyramus*, and *Vacunella*, but have not been observed either on *Astartila* or *Pleurikodonta*. They occur within the pallial line, and are formed by the insertions of muscles which attach the surface of the mantle to the shell. Similar though far more superficial pits have been observed in living species of *Laternula*.

In addition to having obvious pits, *Pyramus*, *Myonia*, and *Megadesmus* commonly have either a larger muscle scar or a short row of pits near the anterior adductor

(muscle scar *a*, Runnegar, 1966), and a narrow linear scar below and parallel to the lower edge of the posterior adductor (muscle scar *b*). The function of these muscles is unknown; from their position they are apparently related to the pallial muscles rather than to those associated with movements of the foot (shell muscles).

Muscle scar *b* also occurs in *Vacunella* cf. *waterhousei* (Pl. 10, fig. 13) and thus may well occur in other species of *Vacunella*. Unfortunately both scars *a* and *b* are rarely preserved in most species of *Myonia*, *Megadesmus*, and *Pyramus* (a notable exception being *Myonia carinata*), and since all species of *Vacunella* have very shallow muscle scars, only exceptionally preserved specimens show traces of these scars.

### *Dentition*

Most species of *Megadesmus*, *Astartila*, and *Pyramus* have a well developed blunt tooth in the centre of the hinge of the right valve, which fits a more or less well defined socket in the left valve (Runnegar, 1965, p. 232, pl. 14, figs 6-10). Exceptional specimens of *Megadesmus* (*Cleobis*) (Newell, 1956, fig. 5), *Vacunella* (Pl. 9, fig. 16), and *Myonia* (Newell, 1956, p. 7) have small thickenings of the hinge beneath the beak of either or both valves, but most other specimens appear to be more or less edentulous. However, because of the other similarities between *Megadesmus*, *Pyramus*, and *Myonia* (such as the possession of muscle scars *a* and *b*), the differences in the development of teeth are probably significant only at the generic or specific level (Runnegar, 1965, p. 232).

Similar 'cardinal teeth' occur in the Carboniferous genus *Scaldia* de Ryckholt, 1852. Whether the poorly developed teeth of living shells of *Pholadomya candida* are similar in structure or origin is not known.

In addition to the 'cardinal tooth' and socket found in *Megadesmus*, *Astartila*, and *Pyramus*, three other methods of interlocking of the anterior dorsal edges of the valves occur in the Permian genera considered in this paper. In both *Megadesmus* and *Pyramus* the anterior part of the cardinal margin of the right valve overlaps that of the left valve. This overlap is normally difficult to see, but is well shown in *Megadesmus gryphoides* by GSQ F9583 (Pl. 3, fig. 14) and is well developed in *Pyramus concentricus* (Pl. 3, fig. 9). It appears to be related to the overlap associated with the tooth and socket, and is probably homologous with the valve overlap in Mesozoic genera such as *Ceratomya* Sandberger (Runnegar, 1965, p. 230).

Secondly, the anterior dorsal margin of the right valve of *Myonia* and *Vacunella* may have a small narrow groove parallel to the edge of the valve, which receives either the edge of the left valve or an obscure thickening parallel to the edge of the valve (Pl. 9, fig. 17). Although normally difficult to see, this anterior

groove is probably homologous with the valve overlap in *Pyramus* and *Megadesmus*, and its comparatively small size may reflect a parallel reduction in the cardinal teeth.

Thirdly, the well developed radial costae of *Pleurikodonta* (Runnegar, 1965, p. 247, pl. 15, figs 22-26) interlock in front of the beaks and function as cardinal teeth.

### *Ligament*

All the genera discussed in this Bulletin appear to have had an external opisthodetic ligament of the type found in *Pyramus laevis* and described in detail in Runnegar (in press).

### *Shell Structure*

The shells of *Megadesmus*, *Pyramus*, *Myonia*, and probably *Vacunella* consisted of two thick calcareous layers, which are presumably covered by a thin periostracum. Unfortunately, except for three incomplete specimens of *Megadesmus nobilissimus*, all the shells examined had been replaced by coarse crystalline calcite, and only the boundaries between successive growth lamellae were retained. In *M. nobilissimus* the outer calcareous layer is prismatic, and the inner layer appears to have been nacreous; for reasons that have been given (Runnegar, 1966) it seems likely that all the Permian genera discussed in this Bulletin had prismato-nacreous shells.

The shell of a bivalve mollusc is composed of three layers of different origins—a superficial periostracum and underlying outer and inner calcareous layers. ‘The periostracum is secreted as a thin sheet within a groove between the outer and middle lobes of the mantle edge, while the outer calcareous layers are produced by the outer lobe of the mantle margin and the inner calcareous layers by the general surface of the mantle’ (Owen, Trueman, & Yonge, 1963). Students of shell microstructure have been able to show that a third calcareous layer is often present beneath the outer calcareous layers (Bøggild, 1930; Trueman, 1942; Oberling, 1964), and that it is produced by ‘the less active part of the mantle edge between the extreme edge where the growth is most active and the inner calcareous layer of the valves’ (Owen, Trueman, & Yonge, 1953, p. 75). In addition, a thin layer of aragonite is secreted at the insertions of the adductor, pallial, and pedal muscles.

The terminology that has been applied to the shell layers is somewhat confusing, since many authors, including Newell (1938) and Dickins (1957), have followed Thiele in his misuse of his own term ‘hypostracum’ (Oberling, 1964, pp. 6-7). Originally Thiele (1893) termed the outer shell layers the ostracum and the inner shell layers the hypostracum; but he apparently misidentified the layer secreted at the adductor muscle insertion of *Unio* as hypostracum. Unfortunately,

many authors have adopted the latter usage (Newell, 1938, p. 25). In order to avoid confusion Oberling has introduced the terms *ectostracum*, *mesostracum*, and *endostracum* for the three calcareous layers of the shell, which, together with the periostracum, form the *palliostracum*. He had termed the aragonitic layers secreted at the muscle insertions *myostracum*, and thus there may be adductor myostraca, pallial myostraca, etc. Oberling's terms are compared with those of Thiele and Newell below.

Thiele (1893)	Newell (1938)	Oberling (1964)	Owen, Trueman, & Yonge (1953)
periostracum	periostracum	periostracum	periostracum
ostracum	outer ostracum	ectostracum	} palliostracum outer shell layers
		mesostracum	
hypostracum	inner ostracum	endostracum	} inner shell layers
———	hypostracum	myostracum	

#### *Composition of the shell*

Newell (1942, p. 32) has noted that 'owing to the relative instability of aragonite, this mineral tends to be dissolved or altered to the more stable calcite, with the common result that fossil pelecypod shells that originally contained some aragonite exhibit unequal preservation of the aragonite structures as compared with the calcite structures. Quite commonly the inner aragonite part of the shell bearing muscle impressions, hinge, and ligament characters, is lacking in fossil shells; whereas, the outer film of calcite remains, with external ornamentation, perfectly preserved'. The transformation of aragonite to calcite would account for the almost universal destruction of the microstructure found in the shells studied, and it is likely that the shells were originally composed entirely of aragonite. This is confirmed by examination of shells of associated bivalves. A thin shell bed at Allandale in the Hunter Valley of New South Wales contains excellently preserved specimens of *Pyramus laevis*, *Megadesmus globosus*, *Eurydesma cordatum*, and *Merismopteria* sp. Sections were cut from all four species and it was found that both of the shell layers of *Pyramus laevis* and *Megadesmus globosus* were composed of coarsely crystalline calcite, whereas in *Eurydesma cordatum* and *Merismopteria* the outer prismatic layer was perfectly preserved. The outer shell layer of virtually all members of the 'Anisomyaria' is calcitic (Bøggild, 1930, p. 258), and it is likely that the preservation of the shell microstructure in *Eurydesma* and *Merismopteria* reflects the presence of calcite in the outer shell layers. In contrast, the inner layer of anisomyarian shells is usually aragonitic and is often replaced soon after burial. Since only the inner layer of *Eurydesma* and *Merismopteria*, but both the inner and outer layers of

*Megadesmus* and *Pyramus*, have been replaced, it is reasonably certain that the shells of the latter were composed entirely of aragonite.

#### *Outer shell layer*

Although I have (1965, p. 233) reported the presence of periostracum in *Megadesmus nobilissimus* it now seems likely that the thin outer layer observed represents no more than iron or manganese staining of the outer part of the shell.

The outermost calcareous layer consists of overlapping growth lamellae which are tangential to the inner layer and curve outwards to produce the imbricate ornament. Only two specimens of *Megadesmus nobilissimus* have been found in which the original microstructure has been preserved; both are very young shells that were trapped beneath a larger shell which probably protected them during fossilization. In both shells the outer layer is composed of polygonal prisms up to  $100\mu$  wide. The prisms divide and thin towards the outer edge of the shell, where they may be as narrow as  $20\mu$  (Pl. 6, fig. 12). The prisms remain perpendicular to the growth lamellae and are not continuous between adjacent lamellae.

#### *Inner shell layer*

The inner layer consists of thin laminae which are parallel to the inner surface of the shell. Each lamina overlaps the previously formed one towards the growing edges of the shell, and the youngest stops at the pallial line (Runnegar, 1965, p. 234, fig. 2a). Unfortunately, even in the well preserved specimens described above, the inner layer has been converted to coarse crystalline calcite. However, a single specimen has been found in which a very small part of the inner shell layer has been replaced by silica rather than calcite, and in this part the microstructure is preserved (Pl. 6, figs 13, 15).

The layer is composed of thin lamellae,  $2-4\mu$  wide, oriented strictly parallel to the inner surface of the shell. Nacre is composed of similarly arranged lamellae, commonly about  $1\mu$  wide ( $0.5-1.2\mu$ , Watabe, 1965, p. 356). In the nacreous layer of living shells, each lamella is a layer of tabular aragonite crystals oriented with the C-axis vertical to the shell surface. An organic matrix is interposed between the lamellae as thin horizontal sheets, and between the crystals as vertical walls, giving a brick-wall type of structure (Watabe, 1965, p. 351). In contrast, the equivalent calcitic structure, calcitostracum, is composed of long tabular crystals which run nearly parallel to the inner shell surface, but which overlap like shingles of a roof.

Unfortunately it has not been possible to prove the presence of lamellae as narrow as  $1\mu$ , but the recognition of lamellar boundaries  $2-4\mu$  apart is probably sufficient to differentiate the inner shell layer from all other shell microstructures except calcitostracum.

As mentioned before, the latter is calcitic and often has somewhat irregular lamellae, in contrast to the strictly parallel lamellae of the inner layer of *M. nobilissimus*.

### Granules

For a long time it has been realized that closely spaced granules cover the valves of *Goniomya* (Agassiz, 1842-5), *Ceratomya* (Morris & Lycett, 1853, pl. 10, fig. 5c), *Chaenomya* (Meek & Hayden, 1865, pl. 2, fig. 1c), *Grammysia* (Hall, 1885, pl. 59, fig. 20), *Edmondia* (Hind, 1896-1900, pl. 25, fig. 11a), *Homomya* (Dall, 1900, fig. 599, p. 358), *Laternula*, *Periploma*, and related genera. More recently they have been shown to occur in *Pholadomya* (Stenzel et al., 1957, pl. 18, figs 13-15), *Wilkingia* (Hoare, 1961, pl. 15, fig. 18), *Myonia* (Dickins, 1963, pl. 5, fig. 20), *Megadesmus* (Runnegar, 1965, pl. 2, fig. 9), and *Vacunella* (Waterhouse, 1965a, p. 377). In some genera (for example *Megadesmus*, *Myonia*, and *Grammysia*) the granules are arranged in radial rows, whereas in others (*Edmondia*, *Laternula*) they are more or less evenly distributed. Unfortunately the granules are so rarely preserved that it is not known whether they were present in *Pyramus* or *Astartila*, nor has it been possible to obtain a specimen suitable for sectioning. It has, however, been possible to section the shell of *Laternula*, and the following description is based on radial, transverse, and tangential sections of the anterior part of a left valve of *Laternula creccina* (Reeve) from Port Phillip Bay, Victoria.

The sheet of *Laternula* consists of an outer prismatic layer about  $70\mu$  thick and an inner nacreous layer about  $200\mu$  wide, composed of sublayers  $10\text{--}20\mu$  in width. The granules (or papillae) project  $60\text{--}80\mu$  from the surface of the shell and are up to  $130\mu$  wide at the base. They incorporate only the outer (prismatic) shell layer, which thins appreciably beneath the base of the granules.

## EVOLUTION

### *Myonia* - *Vacunella* lineage

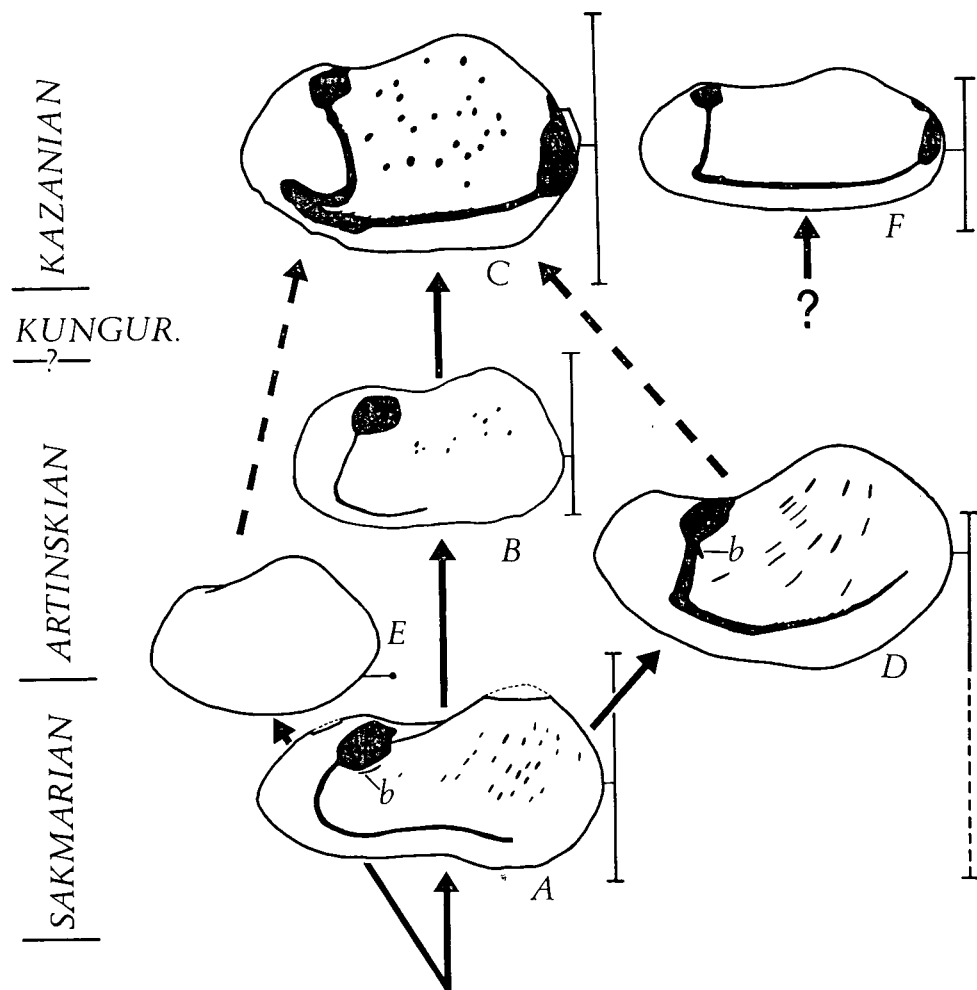
*Vacunella curvata* is a common and widely distributed species in the eastern Australian Upper Permian, occurring in large numbers at ten to twenty localities and in smaller numbers at many others. By contrast, shells which can be included in *Vacunella* are rare in the Lower Permian, and the number of individual specimens of *Vacunella* appears to have increased spectacularly between the Lower and Upper Permian. The obvious success of *V. curvata* may be due to the presence of a deep pallial sinus and thus substantially retractible siphons which allowed it to burrow deeply into the substratum. The most obvious ancestral species for *V. curvata* is *V. etheridgei*, which resembles *V. curvata* in general shape, but differs in having a deeper lateral sulcus. Significantly, *V. etheridgei* has a very much reduced pallial sinus and probably could not have burrowed as deeply as *V. curvata*.

If the increase in depth of the pallial sinus and the reduction in depth of the lateral sulcus between *V. etheridgei* and *V. curvata* are part of an evolutionary 'trend', then the series can possibly be extended backwards from *V. etheridgei* to the earlier Lower Permian species *Myonia? sulcata*, which on both stratigraphical and morphological grounds is the most suitable ancestor for *V. etheridgei* (Text-fig. 3). As the name implies, *M.? sulcata* is deeply sulcate (considerably more so than *V. etheridgei*) and has been tentatively included in *Myonia* as it lacks a pallial sinus, has little or no siphonal gape, and has muscle scar *b* well developed. It differs from the type and associated species of *Myonia* in lacking a distinct and angular carina, but in this respect resembles specimens of *Myonia valida*, which can unquestionably be referred to *Myonia*.

In New South Wales *M.? sulcata* appears to be restricted to the Allandale Formation and to be replaced by *Vacunella* cf. *waterhousei* in the Farley Formation. *V. cf. waterhousei* is considerably less sulcate and has a small but consistently developed pallial sinus and a small siphonal gape. It resembles *M.? sulcata* in shape, particularly in having a produced and somewhat upturned posterior end to the shell, and it can be reasonably assumed that the two species are closely related. (*V. cf. waterhousei* also appears to have developed a small pedal shell gape which was not present in *M.? sulcata*, and the ventral edges of the mantle lobes may have been cross-fused behind the pedal gape.) Consequently, it is possible that *M.? sulcata* gave rise to *V.? cf. waterhousei* as well as *V. etheridgei*. In Queensland *M.? sulcata* occurs in, and just above, the upper part of the Lizzie Creek Volcanics ('Lower Bowen Volcanics'), and is succeeded by *V. etheridgei* in the middle part of the Back Creek Group (*V. cf. waterhousei* is not known from Queensland). The stratigraphic position of *V. etheridgei* in New South Wales is not adequately known, but it certainly occurs in beds younger than those containing *M.? sulcata*.

### Other possibilities

Although *V. curvata* is thought to have been derived from *V. etheridgei*, an alternative explanation is that it evolved from *V. cf. waterhousei*, which in turn was derived from *M.?* *sulcata*. The picture is further complicated by the occurrence of *Vacunella* sp. nov. A with *M.?* *sulcata* in the Lizzie Creek Volcanics, and it is also possible that these forms gave rise to *V. etheridgei* or *V. curvata* or both.



TEXT-FIG. 3

Fig. 3. Possible evolutionary changes in species of *Vacunella*. The ranges of the species are shown by narrow vertical lines and the probable directions of evolution by solid arrows. Broken arrows indicate less likely possibilities.

A, *Myonia? sulcata* after the holotype, CPC 7509; B, *Vacunella etheridgei* after CPC 7517; C, *Vacunella curvata* after AM F8136; D, *Vacunella cf. waterhousei* after AM F51057 and AM F51056; E, *Vacunella* sp. nov. A after CPC 7521; F, *Vacunella? dawsonensis* after QM F1814. b, muscle scar b.



At the present time it is virtually impossible to prove that *Vacunella* (as used here) is not a diphyletic genus comprising species derived separately from *M.?* *sulcata* (or *M.?* *sulcata*-like forms) and a basal Permian or Upper Carboniferous stock of burrowing shells resembling or closely related to genera such as *Chaenomya*. The problem is difficult to solve, since even distantly related deep-burrowing shells tend to be more or less homeomorphic in general shape, size of siphonal gape, and depth of pallial sinus, and there are consequently few definite morphological features which can be used to trace evolutionary lineages. However, because of the differences in the shape and pedal musculature between *Chaenomya leavenworthensis* and *Vacunella curvata*, and the similarities in the pedal and pallial musculature of the Australian Permian Pholadomyidae (Runnegar, 1966), it is more likely that *V. curvata* (i.e. *Vacunella*) has evolved separately from *Chaenomya* and that the two are homeomorphs of slightly different origins.

## RANGES OF GENERA

The oldest specimens of *Myonia* in Australia are *Myonia pollocki* Maxwell (Pl. 4, fig. 14) from the Rands Formation of the Yarrol Basin, Queensland, which Maxwell (1964) considers to be of Upper Carboniferous age. *Pleurophorella papillosa* Girty, 1904, from the Pennsylvanian of Kansas may also be a species of *Myonia*. The oldest specimens from New South Wales are from 800 feet above the base of the Lochinvar Formation, and *Myonia* is common in the overlying Allandale Formation; in Tasmania *M. morrisoni* occurs in the upper part of the Quamby Mudstone or basal part of the Golden Valley Group, and in Western Australia the oldest specimens of *Myonia* are from the Carrandibby Formation of probable upper Sakmarian age.

*Megadesmus* appears almost simultaneously in the Allandale Formation of New South Wales, the Lyons Group of the Carnarvon Basin, Western Australia (Dickins, 1957, p. 26), and immediately above the *Tasmanites* bed of the Quamby Mudstone near Latrobe in northern Tasmania (Johnston, 1888, pl. 15; Dun, 1913). In Queensland it first occurs with *Pyramus* in the upper part of the Lizzie Creek Volcanics and also in the basal beds of the Yarrol Formation. The oldest specimens of *Pyramus* in New South Wales are from the Allandale Formation in the Hunter Valley, and *Pyramus* is associated with *Megadesmus* in the basal beds of the south coast Permian at Durras South near Bateman's Bay. The oldest specimen of *Pyramus* I have seen from Tasmania is from the Brumby Mudstone of the Golden Valley Group below Poatina in northern Tasmania, but Banks (*in* Spry & Banks, 1962, p. 196) records *Pyramus* (as *Notomya*) from the underlying Quamby Group. In addition, a single shell (UQ F48895) from the conglomerate overlying the basal tillite at Maydena (Spry & Banks, 1962, fig. 26, p. 191) may also be referable to *Pyramus*. *Pyramus* has not been recorded from Western Australia.

Shells which can possibly be referred to *Vacunella* have been recorded from the Lochinvar Formation (Browne & Dun, 1924) and from the Carrandibby Formation (Dickins, 1957, p. 29, pl. 4, figs 10-12), but in eastern Australia the first definite occurrences of the genus are from the Farley Formation of the Hunter Valley (*V. cf. waterhousei*) and the upper part of the Lizzie Creek Volcanics in Queensland (*V. sp. nov. A*).

The lower limit of the range of *Astartila* is less clear, as specimens of *Astartila* and *Schizodus* are often confused and it is often difficult to separate juveniles of *Megadesmus* from adults of *Astartila* (Runnegar, 1965, p. 239). In Queensland *Astartila* is not known from beneath the upper part of the Blenheim Subgroup and its equivalents, but species such as *Astartila compressa* (Fletcher, 1929, p. 58, pl. 28, figs 6-11) and *Astartila* sp. nov? (Dickins, 1967) appear to occur in somewhat older rocks in New South Wales. The oldest specimens of *Astartila* from Tasmania known to me are from Member E of the Malbina Formation;

in Western Australia *Astartila fletcheri* occurs in the Wandagee Formation of the Byro Group (Dickins, 1956, p. 17) but is preceded by *Astartila? condoni* in the uppermost part of the Lyons Group (Dickins, 1957, p. 23). In view of more recent studies, the other Western Australian species Dickins has referred to *Astartila?* would appear to be more correctly referred to *Megadesmus*.

*Pleurikodonta* is restricted to the Blenheim Subgroup and the top of the Gebbie Subgroup and has not been recorded outside the Bowen Basin.

The upper limits of the ranges of these genera are more difficult to determine, because late Upper Permian marine sediments are not known from eastern Australia, and the Tatarian faunas of Western Australia (Thomas & Dickins, 1954), New Zealand (Waterhouse, 1963), and India (Reed, 1944) are poorly known or contain relatively few bivalves. The youngest faunas of eastern Australia contain representatives of all genera, and it is to be expected that they would have continued to exist after marine conditions disappeared from eastern Australia. In Western Australia, *Megadesmus* and possibly *Myonia* and *Astartila* (Dickins, 1963, p. 17; personal observation) occur in the upper marine part of the Liveringa Formation (of probable Tatarian age), but the upper limits of all genera are still poorly known.

# SYSTEMATIC PALAEONTOLOGY

## Class BIVALVIA

### Subclass ANOMALODESMATA Dall, 1889

### Order PHOLADOMYOIDA Newell, 1965

### Superfamily PHOLADOMYACEA (= Anatinacea Gray, 1840, *fide* Newell, 1965)

### Family PHOLADOMYIDAE Fleming, 1828 (*fide* Newell, 1965)

*Diagnosis.* Small to large, equivalve and asymmetric isomyarian shells, having a short external ligament behind the beaks. Outer shell layer prismatic; inner layer nacreous; outer surface of shell covered with closely spaced granules. Pallial line with or without sinus; not extended above adductor scars. Hinge edentulous or with a blunt tooth in either or both valves.

*Discussion.* The following family names are the most applicable of those which have been proposed or used for Middle and Upper Palaeozoic bivalves more or less closely related to *Megadesmus*, *Astartila*, *Pleurikodonta*, *Pyramus*, *Myonia*, and *Vacunella*:

Pholadomyidae Fleming, 1828

Anatinidae Gray, 1840 (*fide* Newell, 1965)

Edmondiidae King, 1850

\*Caelonotidae McCoy, 1855 (*in* Sedgwick & McCoy, 1855)

Cardiomorphidae Miller, 1877

Grammysiidae Miller, 1877

Pholadellidae Miller, 1877

Palaeoanatinidae Miller, 1877

Sanguinolitidae Miller, 1877

Pachydomidae Fischer, 1887

\*Palaeosaxicavidae Popov, 1957

Allorismidae Astaf'yeva-Urbaitis, 1963 (= Edmondiidae)

*Vacunella* appears to have been a deep burrowing shell in contrast to *Megadesmus*, *Astartila*, *Pleurikodonta*, *Pyramus*, and *Myonia*, which were probably shallow burrowers, so that the characters resulting directly from its mode of life are probably unsuitable for separating it from the other genera at the family

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\* Both the Caelonotidae and the Palaeosaxicavidae lack a type genus bearing a generic name with the stem of the family name and are therefore invalid (Arts 29, 35b, 63, International Code of Zoological Nomenclature, Stoll et al., 1961).

level. The other similarities between these genera (Runnegar, 1966) enable them to be included in the same family—a conclusion which is supported by the possibility that *Myonia* may have given rise to *Vacunella*. *Vacunella*, and the apparently closely related Carboniferous genera *Chaenomya* (Meek, 1865) and *Wilkingia* (Wilson, 1959 = *Allorisma* of authors), are normally referred to the primarily Mesozoic and Cainozoic family Pholadomyidae (see Dickins, 1963, p. 51; Ciriacks, 1963, p. 71) or to the essentially Palaeozoic family Pholadellidae (see Yanishevskiy, 1960, p. 46). The present work emphasizes the close relationship of *Vacunella* to *Pholadomya*, and *Vacunella* can be conveniently included in the family Pholadomyidae, which has priority over the other families cited above. Unfortunately the morphology of the type genera of most of the remaining families is so poorly known that their status is difficult to assess at the present time, but further study will probably result in a considerable reduction in the number of useful family names.

#### Subfamily PACHYDOMINAE Fischer, 1887

*Nominate genus: Megadesmus* Sowerby, 1838

*Diagnosis.* Small to very large shells lacking a pedal shell gape and a well developed siphonal gape; pallial sinus very shallow or absent. Hinge either edentulous or more commonly with a blunt tooth in the right valve and a socket in the left; anterior dorsal margin of right valve may slightly overlap that of left valve. Anterior umbonal, and posterior pedal retractor scars always present but protractor scar may be absent. Mantle muscle pits and muscle scars *a* and *b* well developed in some genera (*Pyramus*, *Myonia*, *Megadesmus*), but absent in others (*Astartila*, *Pleurikodonta*).

*Discussion.* *Megadesmus*, *Astartila*, *Pyramus*, and *Myonia* have previously been referred to either the Pachydomidae (Fischer, 1887; Newell, 1956) or to the Edmondiidae (Dickins, 1956, 1957, 1961a, 1963; ?Waterhouse, 1965a, 1966; Runnegar, 1965). However, they lack the characteristic inner hinge plates of *Edmondia* and at present seem to be closer to *Vacunella* (and hence the Pholadomyidae) than to *Edmondia*.

The anterior valve overlap of *Megadesmus* and *Pyramus* is reminiscent of the valve overlap in the Jurassic genus *Ceratomya* Sandberger (Runnegar, 1965), but since the ligament of *Megadesmus* and *Pyramus* is wholly external in contrast to the partly internal ligament of *Ceratomya* (Cox, 1963, fig. 2b), the Pachydominae can easily be separated from the Ceratomyidae.

It is less easy to single out characters which will distinguish the Pachydominae from the Pholadomyidae s.s., since most of the characters are variably developed in even closely related genera (see Runnegar, 1966, fig. 1). As defined here,

the subfamily Pachydominae is restricted to the genera that are relatively short and robust, and which lack a well developed pallial sinus and siphonal gape (that is, those apparently less well adapted for burrowing).

In a recent article Waterhouse (1966) put forward the view that the Subfamily Pachydominae (as used here) is polyphyletic, composed of at least two generic lineages that can be traced back to early Carboniferous members of the family Edmondiidae. He has suggested that because of similarities in their anterior pedal musculature, hinge, and ligament structure it is likely that *Astartila* and *Pleurikodonta* were derived from the Carboniferous genus *Scaldia* de Ryckholdt, whereas *Myonia*, *Pachymyonia*, and possibly *Megadesmus* are more closely related to *Edmondia*. *Pyramus*, *Notomya*, and *Globicarina* Waterhouse, 1965a, are placed in a third group (Table 2) while *Chaenomya* (and presumably *Vacunella*) are considered to be more closely related to *Edmondia* and *Megadesmus*.

The most serious difficulty with Waterhouse's view is the artificial separation of *Megadesmus*, *Myonia* (= *Pachymyonia*), and *Pyramus* (= *Notomya*) (Table 2), and the placing of *Megadesmus* and *Pyramus* in two different subfamilies or families. Waterhouse argues that while *Pyramus* and *Megadesmus* both have a single tooth in the right valve, the anterior retractor muscle scar is joined to the anterior adductor muscle scar by a 'protractor isthmus' in *Megadesmus* but is discrete and isolated from the adductor scar in *Pyramus* (and *Notomya*). *Globicarina*, which the writer considers to be a junior synonym of *Megadesmus* (*Cleobis*), also lacks this protractor isthmus and is grouped with *Pyramus* and *Notomya* rather than *Megadesmus* and *Cleobis* (Table 2). However, because the anterior retractor is joined to the adductor in *Megadesmus* and *Cleobis*, they are placed closer to *Myonia* and *Pachymyonia* than to *Pyramus*, *Notomya*, and *Globicarina*, in spite of the fact that of the seven genera only *Myonia* and *Pachymyonia* are edentulous.

Although Waterhouse (1965a, 1966) argues otherwise, the *arrangement* of the anterior pedal muscle scars seems to be of very little use for distinguishing different genera of this group, even though the *number* of anterior scars clearly distinguishes *Astartila* from *Megadesmus*.

As mentioned previously, even in species such as *Megadesmus gryphoides*, *Myonia carinata*, or *Pyramus laevis* that normally have well defined muscle scars, at least one third of the specimens will not show the protractor scar clearly, and often the anterior retractor will be completely merged with the scar of the anterior adductor. In a few specimens both anterior and posterior retractor scars will be completely discrete (Pl. 3, fig. 14) and in very rare specimens (Pl. 12, fig. 7) the protractor scar will also be isolated from the adductor scar. For this reason it is normally necessary to have at least several well preserved internal moulds before the number of pedal muscle scars can be accurately determined.

The variation in the arrangement of the anterior pedal scars seems to be less within a single species than between different species of the same genus and may therefore be more useful for distinguishing between species rather than genera. *Myonia corrugata*, for example, always has the anterior retractor scar merged with the protractor scar and the edge of the adductor, whereas the

TABLE 2. GROUPINGS OF THE 'PACHYDOMID' GENERA PROPOSED BY RECENT AUTHORS

Newell, 1956	Dickins, 1963	Runnegar, 1966	Waterhouse, 1966
		EDMONDIA	Scaldia
Pachydomus	Astartila	Astartila Pleurikodonta	Astartila Pleurikodonta
Pachydomus* Pyramus	Pyramus Notomya	Pyramus	Pyramus Notomya Globicarina
Cleobis	Megadesmus	Megadesmus Cleobis	Megadesmus Cleobis
Myonia	Myonia Pachymyonia ?EDMONDIA	Myonia	Myonia Pachymyonia EDMONDIA
	Chaenomya Pholadomya	Chaenomya Vacunella Pholadomya	Chaenomya Vacunella

Solid horizontal lines indicate differences approximately equivalent to those between different families and broken lines to those between different subfamilies or tribes. *Cleobis* is treated as a subgenus by both Waterhouse and Runnegar.

\*Because Newell accepted Stoliczka's invalid designation of *Megadesmus cuneatus* Sowerby (= *Pyramus laevis*) as the type species of *Pachydomus* (= *Megadesmus*), some of the species he referred to *Pachydomus* are now referred to *Pyramus* or *Notomya*.

three scars are often distinct in *M. carinata* (particularly in Australian Museum specimens of *M. carinata* from Bundanoon, N.S.W.). Similarly Waterhouse (1965a, p. 372, fig. 2a) reports that normally in *Megadesmus nobilissimus* a large anterior retractor—protractor scar is attached to the adductor scar, whereas in *M. gryphoides* (Runnegar, 1965, pl. 13, fig. 8; herein Pl. 3, fig. 14) the retractor scar is usually isolated.

Because of similarities in shape, ornament, ligament structure, and the number of pedal muscle scars, as well as the presence of muscle scars *a* and *b* (Runnegar, 1966, fig. 1), I have argued that *Megadesmus*, *Myonia*, and *Pyramus* are more closely related to one another and to *Vacunella* than they are to *Edmondia*. Waterhouse, on the other hand, maintains that the lack of teeth in *Myonia* and *Pachymyonia* relates these genera to *Edmondia* rather than to *Megadesmus*, *Pyramus*, *Notomya*, or *Globicarina*, and that the presence of a tooth in each valve of *Astartila* relates it more closely to *Scaldia* than to *Megadesmus*, as has previously been thought (Newell, 1956; Dickins, 1963). The virtually edentulous genus *Pleurikodonta* is referred to the latter lineage, presumably because of its other similarities to *Astartila*. *Chaenomya* is edentulous and is therefore grouped with *Myonia* and *Edmondia* (Table 2) but in a different subfamily or tribe (Waterhouse, 1966, p. 556).

The most apparent significant difference between *Edmondia* and the 'pachydomids' (as well as *Chaenomya* and *Vacunella*) is the development in *Edmondia* of a posterior internal lamellar plate or 'ossicle', well illustrated by King (1850, pl. 20, figs 2-4), Hind (1896-1900, pl. 35, fig. 5), and Wilson (1960, pl. 8, fig. 4a). Some specimens of *Megadesmus*, *Myonia*, *Pyramus*, and *Vacunella* are reasonably thickened beneath the external ligament groove, but they lack this strong internal plate, usually considered to have supported an internal ligament or to have served for the attachment of special muscles controlling the movements of the valves (de Koninck, 1842-4, p. 66; King, 1850, p. 164; Hind, 1896-1900, p. 290; Wilson, 1960, p. 113; Waterhouse, 1966, p. 547). As Waterhouse's excellent illustrations clearly show (1966, pl. 15, figs 4-5; pl. 16, fig. 1), *Edmondia* has a well defined external ligament groove, so that if an internal ligament was present, it must have assisted the more normal external ligament in much the same way as does the internal 'cardinal' ligament of living representatives of the Tellinacean family Semelidae (Trueman, 1953, 1966). There is no trace of a comparable structure in the Pachydominae, and the structure which Waterhouse (1966, pp. 551-2) refers to in *Megadesmus*, *Astartila*, and *Pyramus* as an 'inner ligament pit' is probably caused by the small area of anterior outer layer (Runnegar, in press, fig. 3) of the normal opisthodetic ligament, and would therefore differ from a true inner ligament pit.

The significance of the 'ossicle' in *Edmondia* is difficult to assess. From an examination of latex casts of two internal moulds of *Edmondia* in the University of Queensland collections, as well as the specimen figured by Dickins (1963,



pl. 3, figs 16-18), the plate seems to have been more or less perpendicular to the plane of junction of the valves and thus may have been merely a supporting device for the umbonal region of the valves. However, from King's description of *Edmondia sulcata* (King, 1850, p. 164, pl. 20, figs 2-4; see also Wilson, 1960, p. 112, pl. 8, figs 2, 4a), the plates seem to have been curved and spoon-shaped and therefore much more like the resilifer of *Mya* or *Corbula*.

If the latter interpretation is correct and the plates in *Edmondia* supported a massive internal ligament, *Myonia* and the remainder of the Pachydominae could be easily removed from the Edmondiidae, since the structure of the ligament is probably of fundamental importance in the classification of most groups of the Bivalvia. However, if, as seems more likely, the plates merely functioned as strengthening devices, it is less easy to separate *Edmondia* and the Pachydominae.

Waterhouse's use of the hinge teeth as the primary differentiating feature is artificial in that *Megadesmus* (*Cleobis*) *grandis* has extremely feeble teeth (Newell, 1956, figs 5a-b), and a small tooth of the *Megadesmus* type is well shown by a latex cast of a specimen of *Myonia tayoensis* (Reed) sent to me by Dr A. C. Rocha-Campos, University of São Paulo (Pl. 13, fig. 14). Similarly the tooth development varies considerably in different species of *Pyramus*, and *P. laevis* is almost edentulous (Pl. 2, fig. 7). It therefore seems preferable to consider the presence of an 'ossicle' in *Edmondia* more significant than the absence of the tooth in *Myonia* and to separate *Edmondia* from *Myonia* and the Pachydominae, at least at the subfamily level. Similarly *Astartila* seems to be closer to *Megadesmus* than to *Scaldia* since, as Dickins (1963, p. 45) remarks, 'whether or not a tooth is present in the left valve of *Astartila* seems to be a matter of descriptive terminology rather than fact'.

It is unlikely that the Pachydominae are as directly descended from the early Carboniferous Edmondiidae as Waterhouse (1966, fig. 2) suggests, and in view of their morphological homogeneity it is probable that they radiated rapidly from one or two ancestral forms in the late Carboniferous or early Permian.

#### Genus PYRAMUS Dana, 1847

*Type species.* *Pyramus myiformis* Dana, 1847, p. 157; 1849, p. 697, pl. 6, figs 4a-c, by subsequent designation of Newell (1956, p. 7).

*Synonyms.* Objective synonyms: *Maeonia* (*Pyramia*) Dana, 1849, and *Clarkia* de Koninck, 1876.

Subjective Synonyms: *Notomya* M'Coy, November 1847 (*not Notomya* Cotton, 1931).

*Generic diagnosis.* Medium sized oval shells with low rounded umbones, and inwardly directed beaks; posterior umbonal slope separated from remainder of valve by a rounded ridge or gentle change in slope. Hinge with a single blunt tooth in right valve and anterior dorsal margin of right valve slightly overlaps left. Adductor, pedal, and pallial muscle scars usually well developed. Umbonal retractor scar at apex of umbonal cavity so that beaks of internal moulds are narrow and pointed, and a distinct wedge-shaped sulcus extends from the anterior side of the beaks to the ventral edges of the moulds. Siphonal gape and pallial sinus variably developed but always small.

*Discussion.* Dana (1847) erected the genus *Pyramus* to include two species, *P. ellipticus* and *P. myiformis*, which he described but did not figure. In 1849 he redescribed and figured both species but changed the spelling of the generic name to *Pyramia*, and used it as a subgenus of *Maeonia* (variant spelling of *Myonia* Dana, 1847). Four months after Dana's 1847 paper, M'Coy (1847) proposed the genus *Notomya* for three new species—*N. securiformis*, *N. clavata*, and *N. ovalis*—all of which are probably conspecific with *P. myiformis*. However, because of the confusion that resulted from Dana's (1849) grouping of *Myonia*, *Cleobis*, and *Pyramus*, Stoliczka (1871, p. 83) suggested that *Notomya* should be used in preference to *Pyramus*, and nominated *Notomya securiformis* M'Coy as the type species. De Koninck (1876) apparently overlooked Dana's earlier use of *Pyramus*, for he placed *Maeonia* (*Pyramia*) *myiformis* Dana in a new genus, *Clarkia*, to separate it from the strongly carinated species of *Maeonia* (= *Myonia* Dana, 1847). Newell's subsequent designation of *Pyramus myiformis* as the type species of *Pyramus* makes *Clarkia* an objective synonym of *Pyramus*.

Dana has been severely and somewhat unjustly criticized by Stoliczka (1871, p. 83) and Etheridge junior (1878, p. 72), both of whom adopted *Notomya* in preference to *Pyramus* 'because his [M'Coy's] description was far more intelligible than Dana's and also because he correctly indicated the affinities of the genus' (Etheridge, quoted by Fletcher, 1932, p. 393). Fletcher (1932, p. 395) accepted *Notomya* rather than *Pyramus* as, 'according to the published dates, both papers appeared in print in November, 1847, but *Notomya* was selected to stand as it was better described and figured'. However, although the title page of volume 54 of the *American Journal of Science and Arts* bears the date 'November, 1847', page 153 of Dana's paper is dated 'July, 1847'. M'Coy's paper (Part 3, p. 289) is equally definitely dated 'November, 1847', so that Dana's names clearly have priority.

Newell (1956, p. 7) considered *Pyramus myiformis* and *Notomya securiformis* to be conspecific, thus making *Notomya* a junior synonym of *Pyramus*. Dickins (1961a, p. 128) and Waterhouse (1965a, p. 374) have had reservations about accepting this. Dickins preferred the retention of *Notomya* as a genus for robust shells with prominent umbos and deep muscle scars; Waterhouse tentatively

considered *Notomya* to be a subgenus of *Pyramus* but pointed out that the two are closely allied. The differences he noted were in the posterior pedal musculature and possibly in the thickening of the lower edge of the ligament nymph. The present study supports Newell in uniting *Notomya securiformis* and *Pyramus myiformis*, so that *Notomya* is regarded as a junior synonym of *Pyramus*.

PYRAMUS LAEVIS (Sowerby, 1838)

(Pl. 1, figs 1-12; Pl. 2, figs 1-10)

- Megadesmus laevis* Sowerby, 1838, p. 15, pl. 3, fig. 1.  
*Megadesmus antiquatus* Sowerby, 1838, p. 15, pl. 3, fig. 2.  
*Megadesmus cuneatus* Sowerby, 1838, p. 15, pl. 3, fig. 3.  
*?Pyramus ellipticus* Dana, 1847, p. 157; 1849, p. 697, pl. 6, figs 5a-c.  
*Pachydomus cuneatus* (Sowerby); Dana, 1849, p. 693, pl. 5, figs 1a-b.  
*Pachydomus antiquatus* (Sowerby); Dana, 1849, p. 693, pl. 5, fig. 2.  
*Pachydomus laevis* (Sowerby); de Koninck, 1876-7, p. 214, pl. 20, fig. 1.  
*Pachydomus cuneatus* (Sowerby); Newell, 1956, fig. 2A, B.  
*Pachydomus cuneatus* (Sowerby); Müller, 1958, p. 523, fig. 639.  
*Pyramus laevis* (Sowerby); Runnegar, 1966, p. 375, fig. 1.

*Type material.* The lectotypes of *Megadesmus laevis*, *M. antiquatus*, and *M. cuneatus* (here designated) are respectively L 61050, PL 683, and PL 682 of the British Museum collections. The lectotype of *Pyramus ellipticus* is U.S. National Museum 3583 (Dana, 1849, pl. 6, figs 5a-c), chosen subsequently by Waterhouse (1965a, p. 373). All four specimens are from the Allandale Formation at Harper's Hill, 1 mile south-west of Lochinvar hamlet, Hunter Valley, New South Wales. Plaster casts of Sowerby's specimens are in the collection of the Australian Museum (L 942, L 945, and L 944), and are figured here (Pl. 1, figs 1, 3, 7).

*Remarks on the type material.* Under article 24 of the International Code of Zoological Nomenclature (Stoll et al., 1961), the first reviser is entitled to determine the relative priority of synonymous species which have been published simultaneously. I have used *Megadesmus laevis* as the senior synonym as it precedes *M. antiquatus* and *M. cuneatus* in the text of Sowerby's paper, and also because the lectotype is intermediate in shape and well preserved. In the text, Sowerby named the species *laevis*, whereas in the explanation to plate 3 it is spelt *loevis*. Because of the difference in ornament between this and the other two specimens figured, it is obvious Sowerby intended to use *laevis*, smooth.

In July 1847 Dana described *Pyramus ellipticus*, based on two specimens which he indicated were from Harpers Hill. He figured both specimens in 1849 (pl. 6, figs 5a-c, 6, 6a), but in the text gave the localities as 'Harper's Hill, valley of the Hunter?' and 'Wollongong, New South Wales'. Waterhouse (1965a, p. 373) assumed that the specimen he designated as the lectotype of

*P. ellipticus* (Dana, pl. 6, figs 5a-c) was from Wollongong and suggested that *Pyramus ellipticus* and *Notomya securiformis* M'Coy (November 1847) are conspecific. The lectotype of *P. ellipticus* is labelled 'Harper's Hill, Valley of the Hunter, Wollongong Illawarra, New South Wales' (letter from E. G. Kauffman, Smithsonian Institution), and the shape and preservation suggest that it is a young *P. laevis*. Most bivalves from Harpers Hill are articulated and have the shell preserved (Pl. 1, figs 3, 6) in the way illustrated by Dana's drawing. Furthermore, in 1847 Dana stated definitely that the locality of the specimen he described was Harpers Hill, so that this seems to be the most likely locality for the lectotype. In shape the specimen resembles *P. laevis*.

*Diagnosis.* Large, thick shelled, and globose species of *Pyramus* ornamented with fine to very coarse imbricate growth lamellae. Valves either round or oval when viewed from the side; rounder individuals tend to be symmetrical. Ligament short, lodged in large arcuate depression behind the beaks. A single weakly developed tooth in the right valve and a shallow socket in the left. The muscle scars are usually deeply depressed and pitting of the internal surface of the valves is relatively common.

*Description.* The shells are oval and inflated and have low inwardly pointing umbos. When viewed from the side, the anterior umbonal slope is separated from the remainder of the valve by a slight to marked change in shape which may produce an angular bend in the rear margin of the shell (Pl. 1, fig. 10). An extremely shallow sulcus is usually present near the middle of the valve and is reflected by a slight concavity of the ventral valve margin. In front of the beak the valve is flattened to form a narrow lunular depression which extends to near the front of the valve, but there does not appear to be much overlap of the left valve by the right, as in *P. concentricus*? Behind the beaks a similar but larger depression surrounds the ligament.

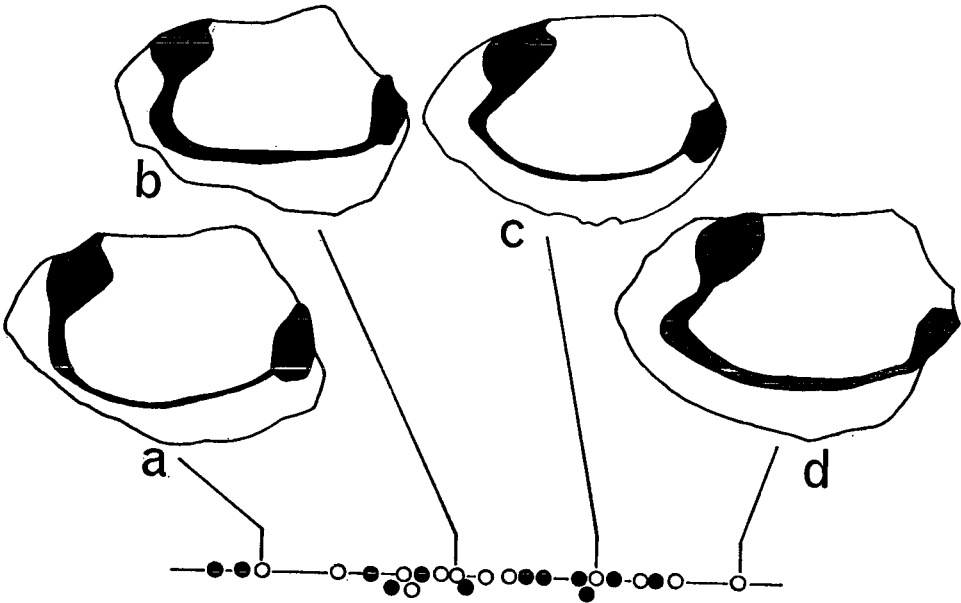
The hinge of the right valve has a blunt rounded tooth which fits an equally weakly developed concavity in the left valve. Growth-lines which cross the tooth (Pl. 2, fig. 7) show that it is derived from a fold in the hinge-line in much the same way as the tooth of *Megadesmus* (Runnegar, 1965, p. 232). Behind the tooth the growth-lines follow a J-shaped path to converge beneath the beak. The ligament is large and is situated in a well developed escutcheon; its detailed structure has been described previously.

The pedal muscles are well shown by UQ F47931 (Pl. 2, figs 1-3; Pl. 12, figs 5, 11). The posterior retractor scar is large and is joined to the upper edge of the adductor. The protractor scar is smaller but usually obvious, although always connected to the anterior adductor. Behind the protractor scar is a larger deep oval anterior retractor scar, and a fourth scar occurs at the apex of the umbonal cavity. Well preserved specimens such as UQ F47938 (Pl. 2, fig. 8)

have a small muscle pit (muscle scar *a*) near the base of the anterior adductor, and a small hook-shaped muscle scar (*b*) below the posterior adductor scar. Most specimens show a slight siphonal gape (Pl. 1, figs 11-12), but some do not (Pl. 1, fig. 8), and there is no evidence of a pedal gape to the valves. A small pallial sinus is developed in some specimens, and Text-figure 4 shows the variation in the size of the pallial sinus in 28 specimens.

*Dimensions of shells (in cm)*

	Height	Length	Width
Lectotype of <i>P. laevis</i> ....	7.8	9.3	5.8
Lectotype of <i>M. cuneatus</i> ....	5.5	6.7	—
MM F7893 ....	4.6	6.5	—



TEXT-FIG. 4

Fig. 4. Camera lucida drawings of four topotypes of *Pyramus laevis* to show the variation in the pallial sinus,  $\times \frac{1}{2}$ . Line at base of drawing represents the limits of variation shown by topotypes (open circles) and specimens from Durras (solid circles). *a*, AM F25768; *b*, AM F50456; *c*, AM F50452; *d*, AM F51558.

*Material.* More than 50 excellently preserved specimens from the collections of the Australian Museum, NSW Geological and Mining Museum, and University of Queensland.

*Distribution.* *Pyramus laevis* is known definitely from only three localities of two horizons—Harpers Hill and Allandale, Hunter Valley, New South Wales, in the Allandale Formation, and from a pebbly sandstone 200 feet stratigraphically

above the unconformity with the pre-Permian strata at Turisse Point and Wasp Head, Durras South, north of Batemans Bay, South Coast, NSW.

A single fragmentary internal mould (UQ F48911, Pl. 2, fig. 10) from the Brumby Mudstone (Quamby Group) in a road cutting below Poatina township, northern Tasmania, resembles *P. laevis* in having a low blunt umbo and a well developed lateral sulcus, but additional specimens will be necessary to confirm the identification.

*Range.* Sakmarian.

*Discussion.* The lectotypes of *Megadesmus laevis* (Pl. 1, fig. 1), *M. cuneatus* (Pl. 1, fig. 3), and *M. antiquatus* (Pl. 1, fig. 7) differ in shape, ornament, and size. The last is not significant and an examination of a large series of specimens in the Australian Museum suggests that both shape and ornament are highly variable. Differences in shape are well shown by figures 2, 3 and 10 of Plate 1, and figures 1, 4, 5 and 6 show the variation in the ornament. All these specimens are from either the type locality (Harper's Hill) or from nearby in the same horizon (Allandale), so that they would appear to belong to one highly variable species. Specimens from Durras South show a comparable variation in shape, but tend to have smooth shells like the lectotype of *P. laevis*. The lectotype of *P. ellipticus* is a little more elongate than the average specimen of *P. laevis*, but resembles it in having a thick shell and almost centrally placed umbos. The shells of *P. laevis* are rounder than those of *P. myiformis* or *P. concentricus*? and have more centrally placed umbos. The dentition of the three species is quite different; *P. laevis* has a very weakly developed rounded tooth (and socket) in contrast to the sharp triangular tooth of *P. concentricus*? and the inclined ledge-like tooth of *P. myiformis*. The muscle scars are usually well developed and the pedal protractor scar is nearly always distinct.

PYRAMUS MYIFORMIS Dana, July 1847

(Type species of *Pyramus* Dana, 1847, and *Clarkia* de Koninck, 1876)

(Pl. 2, figs 11-18; Pl. 3, fig. 1)

*Pyramus myiformis* Dana, 1847, p. 157; 1849, pl. 6, figs 4a-c.

*Cypricardia sinuosa* Dana, 1847, p. 157; 1849, p. 696.

*Notomya securiformis* M'Coy, November 1847, p. 304, pl. 15, figs 5, 5a.

*Notomya clavata* M'Coy, 1847, p. 304, pl. 15, fig. 4.

?*Notomya ovalis* M'Coy, 1847, p. 305.

*Maeonia (Maeonia) axina* Dana, 1849, p. 696, pl. 5, figs 5, 5a-c, c', d.

*Pachydomus carinatus* Morris, 1845, in part, pl. 5, fig. 4.

*Maeonia (Pyramia) elliptica*? Dana, 1849, p. 697, pl. 6, figs 6, 6a.

*Clarkia myiformis* (Dana); de Koninck, 1876-7, p. 267, pl. 18, figs 1, 1a-b.

?*Pleurophorus carinatus* (Morris); de Koninck, 1876-7, p. 285, pl. 19, fig. 8.  
*Pyramus myiformis* Dana; Newell, 1956, fig. 4.  
*Pyramus myiformis* Dana; Termier & Termier, 1960, p. 181, figs 1190-1.  
? *Pyramus* (*Notomya*) *ovalis* M'Coy; Waterhouse, 1965b, p. 851.

*Type material.* The lectotype of *Pyramus myiformis* is U.S. National Museum 3587 (Dana, 1849, pl. 6, figs 4a-c) from the Gerringong Volcanics at Wollongong Point, Wollongong, New South Wales, chosen subsequently by Newell (1956, p. 9). The lectotype of *Notomya securiformis* is Sedgwick Museum E 10776 (M'Coy, 1847, pl. 15, figs 5, 5a) from the same locality as the lectotype of *P. myiformis* and designated subsequently by Waterhouse (1965a, p. 373). Also from the same locality are the lectotype of *Notomya clavata* (Sedgwick Museum E 10778, M'Coy, 1847, pl. 15, fig. 4) and the type specimen of *Cypricardia sinuosa* (USNM 3585?, Dana, 1849, pl. 5, fig. 5d) by subsequent designation of Dana (1849, p. 696). The lectotypes of *Notomya ovalis* (M'Coy, 1847, not figured; Waterhouse, 196....., pl. 11, fig. 2) and *Maeonia axina* (Dana, 1849, pl. 5, figs 5a-c, c') are respectively Sedgwick Museum E 10780 (by subsequent designation of Waterhouse, 1965b, p. 851) and USNM 3585 (here designated). The former is from the Muree or Mulbring Formation in Loders Creek, south of Singleton, Hunter Valley, and the latter from the Gerringong Volcanics of the 'Illawarra District', New South Wales.

Plaster casts of M'Coy's type specimens are in the University of Queensland type collection, and the Australian Museum has casts of the lectotypes of Dana's species. Newell (1956, fig. 4e, f) has figured the lectotype of *Pyramus myiformis*, and Waterhouse (196....., pl. 11, fig. 2) has figured the lectotype of *Notomya ovalis*.

*Diagnosis.* Relatively elongate and narrowly inflated shells with rounded anterior and posterior margins. Tooth and socket ledge-like and subparallel to the valve margin. Muscle scars often shallow and inconspicuous.

*Description.* The shells are oval, only moderately inflated, and have low inconspicuous umbos which are usually placed towards the anterior end of the valve. In side view, the front of the valve is semicircular and most specimens taper posteriorly. Behind the beaks the upper edge of the valve is either flat or very slightly concave, and the ligament is lodged in a shallow and rather poorly defined escutcheon (Newell, 1956, fig. 4a). Some specimens have a weakly developed umbonal carina which may produce an angular bend in the posterior margin (Newell, loc. cit.). An extremely shallow sulcus occurs beneath the beaks and the valves are ornamented with relatively coarse imbricate growth lamellae which increase in frequency towards the margins of the valves. Most specimens appear to have a small siphonal gape, but the preservation usually makes it difficult to observe. A small but well developed pallial sinus was present in all specimens with the pallial line preserved.

The adductor scars are rather shallow and there is a wedge-shaped low buttress behind the anterior scar. Four pairs of pedal muscle scars can be seen in some specimens (AM F17773, Pl. 2, fig. 11; Pl. 12, fig. 12), but often only three pairs have been preserved (MM F12996, Pl. 2, fig. 17). The anterior retractor scar is large, deep, and only rarely joined to the anterior adductor; the posterior retractor is less obvious and is always merged with the dorsal edge of the adductor. As in other species of *Pyramus*, the umbonal retractor occurs at the apex of the umbonal cavity and appears to be related to a wedge-shaped thickening of the internal surface of the valve which runs backwards to the ventral margin of the valves. The protractor scar, when present, is small and is attached to the upper edge of the anterior adductor (Newell, 1956, fig. 4d; herein, Pl. 2, fig. 11). The ligament is relatively short, robust, and is lodged in deep grooves behind the beaks. A curved pointed tooth in the right valve fits a corresponding socket in the left valve; both tooth and socket are prominent beneath the beaks but posteriorly from the beaks they rapidly merge with the lower edge of the nymphs. They are well shown by the paralectotype figured by Newell (1956, fig. 4d).

*Dimensions of internal moulds (in cm)*

	Height	Length	Width
Lectotype of <i>P. myiformis</i> .....	2.8	4.9	—
Lectotype of <i>N. securiformis</i> .....	3.3+	5.5	2.4
MM F2439 .....	4.5	7.3	—
AM F17773 .....	3.5+	5.3	2.3
MM F12996 .....	3.9	6.2	2.4

*Material.* More than 20 well preserved specimens from the collections of the Australian Museum, NSW Geological and Mining Museum, Bureau of Mineral Resources, and University of Queensland.

*Distribution.* New South Wales: Sydney Basin — Gerringong Volcanics at Wollongong Point, Gerroa, and Gerringong; Muree? or Mulbring? Formation in Loders Creek, south of Singleton (*Notomya ovalis*). Queensland: Bowen Basin — Blenheim Subgroup (Dickins and Malone, in prep.), in the Clermont and Collinsville areas (BMR locs C1 12/1, Collinsville 5); Mantuan *Productus* Bed of Peawaddy Formation, Springsure area (Sp 649).

*Range.* Lower Upper Permian.

*Discussion.* It is unfortunate that Dana's description of the fossils he collected in New South Wales in 1840, and M'Coy's descriptions of part of another collection sent by W. B. Clarke to Cambridge in 1844, were both published in the latter half of 1847. Understandably, both Dana and M'Coy introduced new generic and specific names for the shells, which bore little or no resemblance to those of the Palaeozoic of Europe and North America, with the result that several of the names were needlessly duplicated, including probably *Pyramus*



*myiformis* and *Notomya securiformis*. The lectotypes of *P. myiformis* and *N. securiformis* (as well as those of *Notomya clavata*, *Pholadomya undata*, and *Cypricardia sinuosa*) are from the same locality—Wollongong Point—and it is not surprising that intermediates linking the type specimens can be found. The degree of inflation and the depth of the muscle scars (characters Dickins suggested might differentiate *Pyramus* and *Notomya*), seem to be quite variable, and it is relatively easy to select a series of topotypes (Pl. 2, figs 12, 15-18; Pl. 3, fig. 1) which will unite the lectotypes of the two species.

The number, depth, and arrangement of the pedal muscle scars and the depth of the adductor scars are different in different specimens, and sometimes in different valves of the same specimen. Commonly, the protractor scar is missing (or merged with that of the adductor), and in some specimens it occurs only in the left valve. The valves are relatively narrow and the anterior umbonal ridge is often absent in the right valve because of a slight overlap of the left valve by the right. This overlap results in shallower anterior muscle scars in the right valve and may be responsible for the frequent absence of the protractor scar as in the specimen figured by Waterhouse (1965a, fig. 2c).

Because the lectotype of *N. securiformis* is an internal mould of articulated valves, the edges of the mould have been broken and the specimen appears to have been a short robust shell. In contrast, the lectotype of *P. myiformis* is an internal mould of a disarticulated valve and the edges of the mould have been preserved as in MM F2439 (Pl. 2, fig. 15), so that the shell appears to have been elongate and narrowly inflated. The effect of the two types of preservation can be seen in Plate 2, figures 12, 15-16. In figure 16 the outer edges of MM F2439 have been removed and the specimen now resembles the lectotype of *N. securiformis* rather than the lectotype of *P. myiformis* (Newell, 1956, fig. 4e).

*P. myiformis* appears to be limited to the lower Upper Permian in both Queensland and New South Wales, although isolated specimens from the Gebbie Subgroup, which are difficult to identify, could belong to this species.

#### PYRAMUS CONCENTRICUS (Etheridge Snr, 1872)

(Pl. 3, figs 2-6)

*Edmondia concentrica* Etheridge Snr, 1872, p. 328, pl. 13, fig. 2.

*Edmondia obovata* Etheridge Snr, 1872, p. 328, pl. 13, fig. 3.

*Sanguinolites concentricus* (Etheridge Snr); Etheridge Jnr, 1892, p. 281, pl. 43, fig. 7.

*Edmondia? obovata* (Etheridge Snr); Etheridge Jnr, 1892, p. 281.

*Pyramus? concentricus* (Etheridge Snr); Dickins, 1961a, p. 128, pl. 16, figs 1, 2.

*Pyramus? concentricus* (Etheridge Snr); Dickins in Hill & Woods, 1964, pl. P 10, fig. 12.

*Type material.* The holotypes (by monotypy) of *Edmondia concentrica* and *Edmondia obovata* were from 'Gympie' and the 'fossiliferous greenstone of

Beehive Reef', midway between Musgrave and Queen Streets, Gympie, Queensland. Both specimens have apparently been lost. The neotype (here designated) of *Edmondia concentrica* is GSQ F9285, Geological Survey of Queensland, Brisbane (the specimen figured by Etheridge Jnr, 1892, pl. 43, fig. 7; Dickins, 1961a, pl. 16, fig. 1, 2; and Hill & Woods, 1964, pl. P 10, fig. 12), from the 'fossiliferous greenstone' of the 'First Volcanic Group, Middle Gympie Formation' (Hill & Denmead, 1960, p. 226) at the old gasworks, Mellor Street, Gympie, Queensland.

*Remarks on the type material.* The holotypes of *Edmondia concentrica* and *E. obovata* were collected by Richard Daintree (as part of a large collection of fossils from the Upper Palaeozoic and Mesozoic of Queensland), and were sent to Robert Etheridge senior at the Geological Survey, London. Etheridge subsequently (1872) described and figured the specimens and presumably returned them to Australia. In 1892 Etheridge junior mentioned (p. xvii) that the Daintree collection had become scattered, but that he had received some of the mollusca from the Queensland Museum. Neither of Etheridge senior's specimens could be located recently in the collections of the Queensland Museum or the Geological Survey of Queensland. Some of the specimens collected by Daintree are housed in the National Museum of Victoria, Melbourne, but it has not been possible to locate the types of *E. concentrica* and *E. obovata*, and it is most likely that both specimens are permanently lost.

Unfortunately the locality of the holotype of *E. concentrica* is not known, but the neotype which has been chosen closely resembles Etheridge's figure of his specimen (Pl. 3, fig. 3). The holotype of *E. obovata* and the neotype of *P. concentricus* are both from a thin 'greenish fossiliferous sandstone', several hundred metres to the west and southwest of Gympie Railway Station. Other specimens from the same unit to the north of Gympie Station (Horse Shoe Bend Road), now in the collections of the Geological Survey of Queensland (GSQ F9283-9), are virtually the only other specimens available, since the localities are now inaccessible because of growth of the township of Gympie. Nevertheless, the variation shown by these nine specimens suggests that *E. obovata* is probably conspecific with *E. concentrica*, and a neotype for *E. obovata* has therefore not been designated.

*Description.* The neotype has been described and figured by Dickins (1961a, p. 128, pl. 16, figs 1, 2). Specimens from Horse Shoe Bend Road such as GSQ F9288 (Pl. 3, fig. 4) and GSQ F9287 (Pl. 3, fig. 5) resemble the neotype in shape, but the shape varies considerably and other specimens are much less elongate. Although all specimens are to some extent crushed, there appears to have been a rounded posterior carina and a shallow lateral sulcus. Most specimens show a relatively deep rounded anterior adductor scar situated in front of an obvious wedge-shaped thickening of the valve which served as a buttress. Several specimens also show the umbonal pedal retractor scar at the apex of the umbonal cavity. Ornament is of relatively regular growth lamellae.

*Discussion.* The extremely poor preservation of these specimens prevents a confident identification of *P. concentricus* in beds other than those near the type locality. They are similar in shape to the species described herein as *Pyramus concentricus*?, and the associated fauna would suggest that they belong to it. However, as some doubt remains, it was felt that it would be preferable to separate the two groups for the time being.

Although Etheridge senior's figure of *E. obovata* is reminiscent of some species of *Vacunella* or *Chaenomya*, the presence of a strong anterior adductor scar on the left valve and the relatively sharp umbo of the right valve suggest that it was a specimen of *Pyramus*. Furthermore, although *Chaenomya* (now *Vacunella*) has been reported from the same horizon at Gympie (Reid, 1930) an examination of the Rands and Dunstan collections of the Geological Survey of Queensland has not yielded a single specimen of *Vacunella*. The left valve of one of the specimens from Horse Shoe Bend Road (GSQ F9285) is similar in shape to the right valve of Etheridge's figure (compare figs 2 and 6 of Pl. 3). The right valve of GSQ F9285 is, however, quite different in shape from the left valve because of deformation during metamorphism of the enclosing sediment (now a pelitic? rock of greenschist facies of metamorphism). Consequently, care must be taken if any emphasis is to be placed on the shape of either of Etheridge's figured specimens, and the extraordinary elongation of the holotype of *E. obovata* is probably due to post mortem deformation.

PYRAMUS CONCENTRICUS? Etheridge Snr, 1872)

(Pl. 3, figs 7-11, 13)

*Notomya cf. antiquata* (Sowerby); Dickins in Malone et al., 1967.

*Typical specimen.* CPC7495, Bureau of Mineral Resources, Canberra, from the upper part of the Lower Bowen Volcanics, 2½ miles west of Collaroy homestead, about ¼ mile west of the Connors River, central eastern Queensland (BMR locality SL199).

*Diagnosis.* Moderately inflated oval shells with a gently concave posterior dorsal margin. Hinge with a large triangular tooth and socket; beaks of internal mould narrow and relatively high.

*Description.* The shells are subtriangular to elongately oval and have a strongly to gently concave posterior dorsal margin and a flat to convex anterior dorsal margin. The umbonal ridge is not carinate, but there is a pronounced change in slope between the flanks and the posterior dorsal edges of the valves. A shallow sulcus occurs on the lateral flanks. Ornament is of regular imbricate growth lamellae bounded by low rounded ridges.

The ligament is external and lodged in deep arcuate grooves set in an obscure escutcheon. The siphonal gape appears to have been slight, but the pallial sinus is usually well developed, and is often associated with a slight concavity of the posterior ends of the external mould. Both adductor scars are usually deeply depressed and the depth of the posterior scar is partly responsible for the concave posterior dorsal margin of internal moulds. The four pairs of pedal muscle scars are well developed and are distributed as in other species of *Pyramus*. The right valve has a large triangular tooth beneath the beak which fits a deep socket in the left valve (Pl. 3, fig. 9). In front of the tooth the upper part of the anterior valve margin projects and partially overlaps the corresponding edge of the left valve.

*Dimensions of internal moulds (in cm)*

	Height	Length
CPC 7495	4.9	7+
UQ F13299	4.8	7.0
UQ F47941	4.0	5.5
CPC 7497	6.0	7.8

*Material.* More than 20 specimens from the collections of the University of Queensland and Bureau of Mineral Resources.

*Distribution.* New South Wales: Sydney Basin—Conjola Formation at Bawley Point, near Termeil, south coast. Queensland: Bowen Basin—upper part of Lizzie Creek Volcanics, west of Connors River, St Lawrence area (BMR loc. SL 199); Stanleigh Formation, Springsure area (Sp 408/2). Maryborough Basin—? 'greenish fossiliferous sandstone', Middle Gympie Formation (*P. concentricus*). Warwick area—'*Eurydesma* beds', Rokeby station, near Warwick.

*Range.* Lower Artinskian and perhaps upper Sakmarian.

*Discussion.* Although they resemble the poorly preserved topotypes of *P. concentricus*, the specimens described above may belong to a different species, and so they have been described separately. Internal moulds of these specimens differ from *P. laevis* in having high and more sharply pointed beaks, as well as markedly concave posterior dorsal margins. *P. myiformis* is more elongate and less inflated, and has lower umbos.

In contrast to *P. laevis* and *P. myiformis*, *P. concentricus*? has a large triangular tooth in the right valve and a deep socket in the left valve. The tooth and socket have been observed in specimens from the Lower Bowen Volcanics (SL199), the '*Eurydesma* beds' near Warwick, and the Conjola Formation? at Bawley Point, New South Wales. At each of these localities several specimens were available, so that one can be reasonably sure that the valve shape and the type of teeth are associated. However, the stratigraphic range of *P. concentricus*? is difficult to determine, as species of *Pyramus* are difficult to identify, and can only

be determined confidently if several well preserved specimens are available at each locality. Since only isolated specimens of *Pyramus* were available from sections equivalent of the Gebbie Subgroup and most of the Tiverton Subgroup, it is not clear whether *P. concentricus*? occurs in beds younger than those equivalent to the lower part of the Cattle Creek Group. The specimens of *Pyramus* available from beds equivalent to the Blenheim Subgroup, however, do not resemble *P. concentricus*?, and it is probable that at this level at least *P. concentricus*? is replaced by *P. myiformis*.

PYRAMUS? UNDATUS (Dana, 1847)

(Pl. 4, fig. 2)

*Pholadomya undata* Dana, 1847; 1849, p. 687, pl. 2, figs 11a-b.  
*Myonia undata* (Dana); Fletcher, 1932, p. 407, pl. 50, figs 1-2.

*Type material.* The lectotype (here designated) is USNM 3639 (Dana, 1849, pl. 2, figs 11a-b; Fletcher, 1932, pl. 50, fig. 2) from the Gerringong Volcanics at Wollongong, New South Wales.

*Discussion.* Fletcher (1932, p. 407) described and figured shells from the Gerringong Volcanics at Wollongong and Gerringong which he referred to *Myonia undata* (Dana). An examination of a plaster cast of the lectotype of *M. undata* and several poorly preserved internal moulds suggests that they might be better referred to *Pyramus*, since they lack a well developed carina and have relatively pointed beaks on the internal moulds.

As Fletcher has suggested, the shells are similar to a specimen from the Permian of Brazil named *Maeonia* cf. *cuneata* by Reed (1930, p. 37, pl. 6, fig. 7).

Genus MEGADESMUS Sowerby, 1838

*Synonyms.* Objective synonym: *Pachydomus* Morris, 1845. Subjective synonyms: *Cleobis* Dana, 1847, and *Globicarina* Waterhouse, 1965a.

*Type species.* *Megadesmus globosus* Sowerby (1838, p. 15, pl. 1, figs 1-2) by subsequent designation of Woodward (1854, p. 262).

*Discussion.* Apart from possible differences in the dentition, the type species of *Globicarina* (*G. grossula* Waterhouse, 1965a, p. 374, figs 4-5) is not very different from the type species of *Megadesmus* (*M. globosus*). Although Waterhouse considered that *Megadesmus* lacked a posterior umbonal ridge, topotypes of *M. globosus* such as AM F50468 and UQ F7960 (Runnegar, 1965, pl. 12, figs 6, 4) have a well developed and relatively angular posterior umbonal carina.

The holotype of *G. grossula* (AM F21570, Waterhouse, 1965a, figs 4, 5) is almost certainly conspecific with AM F7888, figured as *Megadesmus* (*Cleobis*) *grandis* by Runnegar (1965, pl. 15, figs 3, 4; herein Pl. 12, fig. 3). The latter specimen is probably from the type locality of *M. (C.) grandis*, and it resembles the lectotype in shape. As in the holotype of *G. grossula*, much of the anterior part of the ventral edge of the shell has been broken away, so that the umbones appear to have been close to the front of the shell. Other differences in shape between these specimens and the lectotype of *M. (C.) grandis* are small, and it seems likely that *G. grossula* is a junior synonym of *M. (C.) grandis*, and that *Globicarina* is a junior synonym of *Megadesmus* and *Cleobis*. Although I have previously used *Cleobis* as a subgenus of *Megadesmus* (Runnegar, 1965), the differences between *Megadesmus* and *Cleobis* are slight, and may not warrant separation even at the subgeneric level.

#### Subgenus MEGADESMUS (MEGADESMUS) Sowerby, 1838

##### MEGADESMUS (MEGADESMUS) OVALIS Sowerby in Jukes, 1847

(Pl. 6, figs 10-11)

*Pachydomus globosus* (Sowerby); Morris, 1845, p. 272, pl. 10, fig. 3, not figs 2, 4?  
*Pachydomus ovalis* Sowerby in Jukes, February 1847, p. 242; not *Pachydomus ovalis* M'Coy  
 November 1847, p. 302, pl. 14, fig. 4.

*Type material.* The lectotype of *Pachydomus ovalis* (here designated) is BM(NH) PL 3689 (Morris, 1845, pl. 10, fig. 3) from Permian beds at 'Spring Hill, Van Diemen's Land' [Tasmania]. A cast of this specimen, kindly provided by Mr S. Ware of the British Museum, is figured (Pl. 6, figs 10-11).

*Discussion.* Sowerby (in Jukes, 1847, p. 242) used the name *Pachydomus ovalis* for shells from Wollongong and for the specimens which Morris (1845) figured as *Pachydomus globosus* (Sowerby), which appeared to differ from the original specimens of *M. globosus* from Harpers Hill. Since Sowerby did not figure any of the shells from Wollongong, the name *ovalis* can only be referred to one of the specimens figured by Morris (1845, pl. 10, figs 2-4). Of these three, BM(NH) PL 3680 (Morris, pl. 10, fig. 4) was only doubtfully placed in *globosus* by Morris (see Morris, explanation to pl. 10), so that it is not available for selection as the lectotype. Unfortunately BM(NH) PL 3689 (Morris, pl. 10, fig. 3) is unsatisfactorily located as 'Spring Hill, Van Diemen's Land', and the third specimen appears to be lost (letter from S. Ware, British Museum, 10 May 1965). It has been possible to relocate Permian fossils at Spring Hill (Dickins, 1960, p. 387), so that the lectotype of *P. ovalis* is the only specimen known to come from the type locality. The specimen resembles *M. globosus* in shape, particularly in having a slightly concave area near the anterior ventral margin, and can be tentatively included in that species.

It is, however, difficult to be confident of an identification based on a single specimen, and it may eventually be possible to show that *P. ovalis* is either a distinct species or a junior synonym of another species such as *M. nobilissimus* de Koninck. In the former case it will again be possible to suppress the name *ovalis*, since *P. ovalis* would become a *nomen oblitum* under Article 23b of the International Code of Zoological Nomenclature (Stoll et al., 1961, p. 23).

It is also unnecessary to introduce a new name for *Pachydomus ovalis* M'Coy (1847), since Fletcher (1929, p. 68) has shown that M'Coy's species is a junior synonym of *Astartila intrepida* Dana, July 1847.

#### Genus MYONIA Dana, 1847

*Homonyms.* *Myonia* Walker, 1854 (Lepidoptera) and *Myonia* Adams, 1860 (Gastropoda).

*Synonyms.* Objective synonym: *Maeonia* Dana, 1848 (variant spelling of *Myonia*). Subjective synonym: *Pachymyonia* Dun, 1932.

*Type species.* *Myonia elongata* Dana (1847, p. 158) by subsequent designation of Fletcher (1932, p. 398).

*Generic diagnosis.* Medium to large inflated shells with a pronounced angular umbonal carina and a shallow to relatively deep lateral sulcus. Pedal muscle scars, mantle pits, and muscle scars *a* and *b* usually well developed and obvious. Teeth, pallial sinus, and pedal and siphonal gapes absent.

*Discussion.* The history of the genus has been carefully reviewed by Fletcher (1932). Dana initially included two species (*elongata* and *valida*) in *Myonia*, which he erected for inequilateral and gaping shells, with unequal valves, and a rounded posterior carina. He subsequently (1848, 1849) expanded *Myonia* to incorporate his 1847 genera *Pyramus* and *Cleobis*, and unnecessarily changed the spelling of the generic name to *Maeonia*. Very few authors have accepted Dana's 1849 groupings and there has been a good deal of confusion over the status of *Myonia*, *Pyramus*, and *Cleobis*.

*Myonia* can now be referred to the strongly carinated species *Myonia elongata*, which Fletcher has selected as the type species, in preference to *M. valida*, which lacks an angular carina. Dun (1932) proposed *Pachymyonia* for short, inflated species of *Myonia* which have a very prominent carina and a thick shell. Newell (1956, p. 7) thought that these differences would serve to distinguish species or even ecologically different populations rather than genera, and suggested that the two are synonymous. Dickins (1963, p. 48), however, preferred to retain *Pachymyonia* as a subgenus of *Myonia*, for shells that are wide across the valves

and strongly carinated; and Waterhouse (1965a, p. 376) advocated keeping *Pachymyonia* as a separate genus, because of differences in the pedal musculature, as well as the differences in shape.

Uncrushed specimens of the type species of *Myonia* are relatively uncommon and UQ F5629 (Pl. 5, figs 12-14) is the best preserved specimen that was seen. [Unfortunately the specimen is inadequately labelled 'Permo-Carboniferous, New South Wales', but the type of matrix and preservation leaves little doubt that it is from the Gerringong Volcanics at or near Black Head, south of Gerringong—the type locality of *M. elongata*.] The differences in shape between this specimen and specimens of *Pachymyonia morrissi* (Pl. 5, figs 3, 6, 16) are quantitative rather than qualitative, and are the kind of differences one would expect to find in different species of the same genus.

Waterhouse (1965a, p. 376) suggested that *Pachymyonia* lacks a second pedal muscle scar above the anterior adductor, and has the umbonal retractor on, instead of beside, the anterior umbonal ridge. Although it has not been possible to find a topotype of *P. morrissi* which shows the anterior musculature clearly, specimens from Queensland have two obvious pedal scars above the anterior adductor (Pl. 5, fig. 4; Pl. 12, fig. 4) in the same way as *Myonia elongata*. The umbonal retractor is closer to the hinge in *P. morrissi*, but this feature alone would hardly warrant a separation even at the subgeneric level, and *Pachymyonia* is probably best treated as a junior synonym of *Myonia*.

Fletcher (1932, p. 395) has noted that the type species of *Pleurophorella*, *P. papillosa* Girty (1904, p. 729, pl. 45, figs 4-6; pl. 46, fig. 5) from the Upper Carboniferous of Texas is strongly carinated and could well be a species of *Myonia*. Additional support for this conclusion is given by the fact that *Pleurophorella* is covered with radial rows of closely spaced granules as in *Myonia* (Dickins, 1963, pl. 5, fig. 20), but *Pleurophorella* may differ in having a deep lunule and a few radial costae. It is interesting to note that Girty reported an apparent 'single dental socket under the beak of the left valve', which suggests that the dentition could be like that of *Megadesmus* and *Pyramus*. Unfortunately the internals of *Pleurophorella* are unknown, so that it is difficult to reach a conclusion on its affinities.

#### MYONIA ELONGATA Dana, 1847

(Type species of *Myonia* Dana, 1847)

(Pl. 5, figs 12-15, 18)

*Myonia elongata* Dana, 1847, p. 158; 1849, p. 695, pl. 5, figs 3a-c.

*Myonia accentuata* Fletcher, 1932, p. 400, pl. 47, figs 4-5.

?*Myonia depressa* Fletcher, 1932, p. 405, pl. 48, fig. 4, not fig. 5.



?*Maeonia elongata* (Dana); de Koninck, 1876-7, p. 280, pl. 20, fig. 6.  
*Myonia elongata* Dana; Fletcher, 1932, p. 398, pl. 47, figs 1-3.  
*Myonia elongata* Dana; Newell, 1956, p. 7, fig. 3a.  
*Myonia elongata* Dana; Waterhouse, 1965a, p. 375 in part.

*Type material.* The lectotype of *Myonia elongata* is USNM 3584 (Dana, 1849, pl. 5, figs 3a-c), as indicated by Fletcher (1932, p. 409) from the Gerringong Volcanics at Black Head, Gerroa, south of Gerringong, south coast, New South Wales. The holotypes of *Myonia accentuata* and *M. depressa* (by original designation of Fletcher, 1932, pp. 401, 405) are AM F35613 (ex MM F2472) and MM F2466 (now housed at the Australian Museum), from the same horizon at Gerringong.

*Diagnosis.* Elongate and strongly inflated species of *Myonia* having a pronounced angular umbonal carina. Ventral margin concave over much of its length.

*Description.* *M. elongata* has been described in detail by Fletcher (1932, pp. 398-9) and Waterhouse (1965a) has given a diagnosis of *Myonia* based partly on the lectotype.

The shell is very elongate and has a strong angular carina which is curved in uncrushed specimens. A shallow sulcus on the flanks of the valves produces a gentle concavity in the ventral margin. Viewed from the side, the upper edge of the shell is slightly concave on both sides of the umbo, and the anterior margin is rounded. Because of the strong carina, the posterior margin is slightly to quite markedly angular, and the most posterior part of the shell is at the end of the carina.

The hinge is well shown by UQ F47946a (Pl. 5, fig. 15); there are no obvious teeth, and there appears to be no overlap of the anterior part of the valves. The ligament is external, opisthodetic, and relatively short, and is set in a narrow elongate escutcheon.

The adductor scars are large, circular, and relatively deep. Two deep and moderately well defined pedal scars (protractor and anterior retractor) occur above the anterior adductor, and a third large scar (posterior retractor) is attached to the upper edge of the posterior adductor (Pl. 5, fig. 19). A fourth pedal scar (umbonal retractor) is situated on the anterior side of the umbonal cavity. Muscle scars *a* and *b* are well developed, and pallial muscle pits occur on most specimens. Most specimens have a simple pallial line, but a small sinus may be developed in AM F8232 (Pl. 5, fig. 19).

Ornament is of relatively fine, regularly spaced concentric growth lamellae.

*Dimensions of UQ F5629 (in cm)*

Height	Length	Width (both valves)
6.5	15.2	5.2
	48	

*Material.* Several topotypes and other specimens from the collections of the Australian Museum and University of Queensland.

*Distribution.* *M. elongata* appears to be limited to the Sydney Basin, although occasional specimens of *M. carinata* from Queensland approach *M. elongata* in shape. Fletcher (1932) recorded *M. elongata* from Bundanoon, Wollongong, Gerringong, Kiama, Kioloa, Jamberoo, and Black Head, and *M. accentuata* from Gerringong and Conjola. The species seems to be characteristic of the Gerringong Volcanics, but may occur lower in the sequence.

*Discussion.* The holotype of *M. accentuata* has been crushed dorsoventrally, but otherwise resembles the lectotype of *M. elongata* (Fletcher, 1932, pl. 47, fig. 2), and since the two specimens are from the same beds at closely spaced localities, they are probably conspecific. The posterior end of the lectotype of *M. elongata* is broken off, but the apparently long shell, the position of the carina, and the presence of a well developed sulcus on the flanks of the valve are features shown by both the lectotype of *M. elongata* and UQ F5629 (Pl. 5, figs 12-14). Both of these shells differ somewhat from the specimen figured by Dana (1849, pl. 5, fig. 4; Fletcher, 1932, pl. 48, fig. 3) as *Maeonia valida*, but an examination of a series of specimens from the Illawarra District of New South Wales indicates that the lectotypes of *M. elongata* and *M. valida* may be conspecific, as suggested by Waterhouse (1965a, p. 375). The holotype of *M. depressa* Fletcher (1932, pl. 48, fig. 5) is also from Gerringong, and is intermediate in shape between *M. elongata* and *M. valida*. However, some of the specimens figured by Fletcher (e.g. AM F8206, Fletcher, 1932, pl. 48, fig. 1) lack a carina, and are much shorter than UQ F5629 and the type specimens of *M. accentuata* and probably *M. elongata*. Shells of this shape are plentiful at Kioloa and Bawley Point (Termeil), north of Batemans Bay, and Fletcher (p. 405) has included them in *Myonia depressa*. At present, these shells cannot be easily separated from specimens such as AM F8206 which can probably be referred to *M. valida*. Thus for the present time there seems to be some advantage in retaining *M. valida* for shorter, less carinate specimens such as AM F8206 and AM F30314 (Fletcher, 1932, pl. 48, fig. 4). If it can eventually be shown that the specimens from the Conjola Formation at Kioloa and Bawley Point are not conspecific with those from the Gerringong Volcanics, a new name will probably have to be introduced for these forms, since the holotype of *M. depressa* is from the Gerringong Volcanics and is probably a junior synonym of either *M. elongata* or *M. valida*.

*M. elongata* is longer and more inflated than *M. carinata* and has a deeper lateral sulcus. Most specimens of *M. carinata* have exceptionally deeply impressed muscle scars and pallial line, and well preserved internal moulds are usually covered with deep pallial muscle pits.

## MYONIA VALIDA Dana, 1847

- Myonia valida* Dana, 1847, p. 158; 1849, p. 695, pl. 5, figs 4, 4a-b.  
? *Pleurophorus carinatus*? (Morris); de Koninck, 1876-7, p. 283, pl. 19, fig. 8.  
*Myonia valida* Dana; Fletcher, 1932, p. 399, pl. 48, figs 1-3.  
? *Myonia depressa* Fletcher, 1932, p. 405, pl. 48, figs. 4, 5.  
*Myonia elongata* Dana; Waterhouse, 1965a *in part*, p. 375, figs. 2g, 3f.  
*Myonia valida* Dana; Runnegar, 1966, fig. 1g.

*Lectotype*. USNM 3665 (Dana, 1849, pl. 5, figs 4a-b; Fletcher, 1932, pl. 48, fig. 2) as indicated by Fletcher (1932, pp. 409, 410), from the Gerringong Volcanics at Black Head, Gerroa, south of Gerringong, south coast, New South Wales.

*Discussion*. *M. valida* has been carefully described by Fletcher (1932, p. 399), and Waterhouse (1965a) has described and drawn some of the features of the lectotype. AM F8206 (Runnegar, *in press*) shows most of the morphology of the species, and the ligament is described in the same paper.

As mentioned in the preceding discussion of *M. elongata*, the lectotype of *M. valida* is possibly conspecific with the lectotype of *M. elongata*, but the name has been retained for shorter shells lacking an angular carina.

*Distribution*. Fletcher (1932, p. 400) reported *M. valida* from the Gerringong Volcanics at Black Head, Gerroa; Flagstaff Hill, Wollongong; and Kiama; and the specimens he included in *M. depressa* from the Conjola Formation at Kioloa and Termeil (Bawley Point) can possibly be included in *M. valida*.

## MYONIA CARINATA (Morris, 1845)

(Pl. 4, figs 8-9; Pl. 5, fig. 20; Pl. 12, figs 7, 14)

- Pachydomus carinatus* Morris, 1845, p. 273, pl. 11, fig. 3, *not* fig. 4.  
*Cypricardia rugulosa* Dana, 1847, p. 157.  
? *Maeonia fragilis* Dana, 1849, p. 696, pl. 6, figs 2, 3.  
*Maeonia carinata* var. *minor* Etheridge Jnr, 1919, p. 187, pl. 29, figs 5-8.  
*Myonia minor* var. *etheridgei* Fletcher, 1932, p. 407.  
*Pachydomus carinatus* Morris; Jukes, 1847, p. 248.  
*Pachydomus carinatus* Morris; McCoy, 1847, p. 301.  
*Maeonia?* *carinata* (Morris); Dana, 1849, p. 696, pl. 6, figs 1a-b.  
*Pachydomus?* *carinatus* Morris; Etheridge Jnr, 1880, p. 300, pl. 16, fig. 53.  
*Notomya* (*Maeonia*) *elongata* (Dana); Ratte, 1887, p. 139, pl. 3.  
*Maeonia carinata* (Morris); Etheridge Jnr, 1892, p. 283.  
*Maeonia carinata* var. *minor* Etheridge Jnr; Reid, 1929, pl. 37, fig. 9.  
? *Chaenomya* sp. nov. Reid, 1929, pl. 37, fig. 7.  
*Myonia carinata* (Morris); Fletcher, 1932, p. 401, pl. 49, figs 1-3.  
*Myonia minor* Etheridge Jnr; Fletcher, 1932, p. 405, pl. 49, figs 4-6; pl. 48, figs 6-7.  
*Myonia fragilis* Dana; Fletcher, 1932, p. 409.  
*Myonia carinata* (Morris); Dickins in Hill & Woods, 1964, pl. P 10, figs 9-10.  
*Myonia carinata* (Morris); Dickins in Dickins et al., 1964, table 1.  
? *Myonia carinata* (Morris); Waterhouse in Waterhouse & Vella, 1965, p. 77, pl. 5, fig. 11.

*Type material.* The lectotype of *Myonia carinata* is BM(NH) L61055, figured by Morris (1845, pl. 11, fig. 3), and probably from the Gerringong Volcanics of the Illawarra District, New South Wales, as indicated by Fletcher (1932, p. 401) and formally designated by Waterhouse (in Waterhouse and Vella, 1965, p. 77). The lectotype (here designated) of *Cypricardia rugulosa* is USNM 25640 (figured by Dana, 1849, pl. 6, figs 1a-b as *Maeonia? carinata*), from the upper part of the Gerringong Volcanics by Wollongong Point, Wollongong, New South Wales. The lectotype of *Maeonia fragilis* is the specimen figured by Dana (1849, pl. 6, fig. 2) as indicated by Fletcher (1932, pp. 406, 409) from the Maitland Group? at Glendon, Hunter Valley, New South Wales. The lectotype of *Maeonia carinata* var. *minor* (by subsequent designation of Fletcher, 1932, p. 410) and the holotype (by monotypy) of *Myonia minor* var. *etheridgei*, are respectively AM F13939 and AM F13929, both from Bundanoon Gully, near Bundanoon, 90 miles southwest of Sydney.

*Diagnosis.* Medium to large sized strongly carinated shells lacking a deep sulcus beneath the umbos. Beaks usually more than one third of shell length from anterior end; muscle scars and pallial line large and very deep; internal surface of valve often covered with large, closely spaced pits.

*Description.* The shells are of medium size and have a prominent angular umbonal carina which extends to the posterior margin of the valve. The umbos are situated at least one third of the shell length from the anterior margin. Viewed from the side, the anterior margin is rounded and the anterior umbonal slope gently concave. The posterior umbonal slope is more markedly concave and the posterior margin of the shell is slightly to distinctly pointed. A very shallow sulcus may extend from the umbo to the ventral surface of the shell, but it is usually not deep enough to produce a marked concavity in the ventral margin.

The ligament is external, opisthodontic, and set in a moderately well defined escutcheon as in most other species of *Myonia*. The hinge appears to have lacked teeth. All well preserved internal moulds show the musculature clearly, and, as in other members of the Pachydominae such as *Megadesmus gryphoides* (de Koninck), there is a correlation between the depth of the muscle scars and the frequency of occurrence of mantle muscle pits. The adductors are unequal, quadrate, and connected by a deep, wide, and heavily fringed non-sinuate pallial line. A large discrete pedal scar (anterior retractor) occurs above the anterior adductor, and a second scar (protractor) is more or less completely merged with the lobed posteriodorsal edge of the anterior adductor. In exceptional specimens such as AM F17752 (Pl. 5, fig. 20; Pl. 12, figs 7, 14), the two anterior scars are isolated from each other and from the adductor scar. The umbonal retractor scar is relatively large and occurs on the outer side of the umbonal cavity (Pl. 12, figs 7, 14), and a large posterior retractor scar is attached to the upper edge of the posterior adductor (Pl. 12, fig. 14). Muscle

scars *a* and *b* are extremely well developed, and deep mantle muscle pits cover the valve inside the pallial line. Ornament is of relatively coarse imbricate growth lamellae and finer growth lines.

*Material.* Numerous specimens from the collections of the Australian Museum, Bureau of Mineral Resources, Geological Survey of Queensland, and University of Queensland.

<i>Dimensions of internal mould (in cm)</i>					Height	Length	Width
UQ F15781	.....	.....	.....	.....	7.2	11.5	6.0

*Discussion.* *Myonia carinata* occurs in large numbers at several lower Upper Permian localities in Queensland, New South Wales, and Tasmania, where it can be distinguished by its relatively large size (commonly over 10 cm in length), its relatively straight carina, and its deeply impressed pallial line, adductor and pedal muscle scars, and mantle pits. In the development of the latter features it resembles *Megadesmus gryphoides* and *Pyramus laevis*, and the depth of the pedal and pallial muscle scars appear to be useful characters for separating species of *Megadesmus*, *Myonia*, and *Pyramus*.

Specimens of *Myonia* resembling *M. carinata* are relatively common throughout the marine Permian of eastern Australia, but unfortunately it has not been possible to find consistently useful ways of separating these shells into different species. The ranges of most other species of the Australian pholadomyid bivalves are considerably less than the apparent range of *M. carinata*, and it is probable that shells from the upper Sakmarian/lower Artinskian such as those shown in Plate 4, figures 11-13 will eventually be placed in a different species. However, at present the variation in shape due to (1) original phenotypic variation, (2) differences in the method of preservation, and (3) differences in post mortem crushing, make the recognition of different species very difficult.

Nevertheless, very few of the Lower Permian specimens have well developed muscle scars, and there are no Lower Permian localities such as at Gerringong or Bundanoon where virtually all of the specimens have deeply impressed muscles like the specimen shown in Plate 4, figure 8. Consequently, *M. carinata* can to some extent be used as an indicator of a lower Upper Permian age, provided a relatively large number of well preserved specimens are available. In this restricted sense *M. carinata* occurs at the following localities:

New South Wales: Sydney Basin—Gerringong Volcanics at Wollongong, Gerringong, Gerroa; ?Gerringong Volcanics at Bundanoon.

Queensland: Bowen Basin (northern part)—Blenheim Subgroup, Big *Strophalosia* Zone of the Bowen River area; (south-eastern part)—Flat Top Formation and

upper part of Barfield Formation, Dawson Valley (including BMR locs T 274 and 0.13); (Springsure area)—Mantuan *Productus* Bed, Peawaddy Formation.

Tasmania: Member E, Malbina Formation, Hobart and Claremont.

The lectotypes of *M. minor* and *M. minor* var. *etheridgei* are both from Bundanoon Gully, Bundanoon, and the simplest explanation is that they are juvenile specimens of *M. carinata*, which occurs at the same locality. The collections of the Australian Museum, Sydney, contain a number of larger specimens from Bundanoon (e.g. AM F17752, pl. 5, fig. 20) and it is relatively easy to find specimens which form intermediates between the three species.

#### MYONIA MORRISI (Etheridge Jnr), 1919

(Type species of *Pachymyonia* Dun, 1932)

(Pl. 4, figs 3-5; Pl. 5, figs 1-11, 16-17; Pl. 12, fig. 4)

*Maeonia morrisii* Etheridge Jnr, 1919, p. 186, pl. 28, figs 7-8.

*Pachymyonia etheridgei* Dun, 1932 (*in part*), p. 412, pl. 51, figs 2, 3, *not* pl. 52, fig. 6?

?*Myonia farleyensis* Dun, 1932, p. 413, pl. 51, figs 5, 6; pl. 52, fig. 5.

?*Myonia davidis* Dun, 1932, p. 413, pl. 51, fig. 4; pl. 52, fig. 4.

*Maeonia morrisii* var? Etheridge Jnr, 1919, p. 187, pl. 30, figs 1, 2.

*Pachymyonia morrisii* Etheridge; Dun, 1932, p. 412, pl. 51, fig. 1.

*Myonia* cf. *davidis* Dun; Dickins in Hill & Woods, 1964, pl. P 10, fig. 8.

*Pachymyonia* cf. *etheridgei* Dun; Dickins in Malone et al., 1964, p. 54.

*Myonia* cf. *davidis* Dun; Dickins in Dickins et al., 1964, Table 1.

*Pachymyonia morrisii* Etheridge; Waterhouse, 1965a, p. 376, fig. 3g.

*Pachymyonia etheridgei* Dun; Waterhouse, 1965b, p. 850.

*Type material.* The holotype of *M. morrisi* (by monotypy) is AM F16978 (Etheridge Jnr, 1919, pl. 28, figs 7, 8; figured herein (Pl. 5, figs 15, 16) from the Allandale Formation at Harpers Hill, 1 mile south-west of Lochinvar hamlet, Hunter Valley, New South Wales. The lectotype of *Pachymyonia etheridgei* (by subsequent designation of Waterhouse, 1965b, p. 850) is AM F31083 (Dun, 1932, pl. 51, figs 2, 3) from the same locality. The lectotypes of *M. farleyensis* and *M. davidis* (chosen subsequently by Waterhouse, 1965b, p. 850) are respectively AM F51786 ex MM F1748 from the Farley Formation? at Farley, New South Wales (Dun, 1932, pl. 51, fig. 6), and AM F30600, from the Ravensfield Sandstone Member of the Farley Formation, Ravensfield Quarry, near Farley (Dun, 1932, pl. 52, fig. 4).

*Diagnosis.* Short, strongly inflated shells with a prominent cord-like umbonal carina and a deep precardinal sulcus.

*Description.* Uncrushed shells are short and strongly inflated so that the width of both valves may almost equal the length of the shell. An obvious cord-like carina extends from the beak to the rear end of the ventral margin of the shell, where it may project ventrally as a short blunt spine (Pl. 5, fig. 1). In front of the carina, the valves are slightly to markedly concave, and, correspondingly, the ventral margin is slightly to deeply indented. Viewed from the side, the anterior margin of the shell is rounded and the anterior umbonal slope flat to slightly concave. Behind the carina the shells are either flattened as in the holotype (Pl. 5, figs 8, 10) or extended as in CPC 7504 (Pl. 5, figs 1-2). Similar extension of the posterior margin occurs in topotypes such as the lectotype of *P. etheridgei* (Dun, 1932, pl. 51, fig. 2) and AM F50560 (Pl. 5, fig. 16).

External features of the valves are well shown by UQ F21224b (Pl. 5, figs 6-7). Ornament is of relatively coarse but regular imbricate growth lamellae, which are coarser in front of the carina than behind it. The ligament is external and opisthodontic, and is set in grooves which are relatively short and lodged in a shallow but well defined escutcheon (Pl. 5, fig. 7). In front of the beaks is a well defined flattened area which can be termed a lunule. The beak of the left valve is perforated as a result of contact with the beak of the right valve, so that the beak of the internal mould is flattened, and often slightly bifid. The hinge appears to have lacked teeth, and Waterhouse (1965a, p. 376) was unable to see teeth in a specimen (AM.F26275) from the type locality.

Although the internal features of most topotypes are not well preserved, specimens from Queensland such as UQ F21224a (Pl. 5, figs 4-5; Pl. 12, fig. 4) show the musculature clearly. The adductor scars are unequal, the anterior being much smaller and deeper, and they are connected by a relatively thin non-sinuate pallial line. Muscle scars *a* and *b* are faint and pitting of the internal surface of the valves is uncommon. A deep C-shaped pedal scar is attached to the upper edge of the anterior adductor in most specimens, but since upper and lower parts of this scar are reasonably separated in most specimens (e.g. UQ F20917), it is fairly certain that both protractor and anterior retractor scars are present. The posterior retractor scar is relatively obscure and is attached to the dorsal edge of the adductor. The umbonal retractor scar is small and occurs on the anterior side of the umbonal cavity, and in UQ F20917 (Pl. 5, fig. 9) the muscle was supported by a tiny buttress on the anterior side of the scar.

*Dimensions of internal moulds (in cm)*

	Height	Length	Width
Holotype .....	4.4	7.2	—
UQ F21224a .....	5.3	8.6	5.3+
CPC 7504 .....	5.0	6.8	3.0 (single valve)

*Material.* Several topotypes as well as other specimens from the collections of the Australian Museum, Bureau of Mineral Resources, and University of Queensland.

*Distribution.* New South Wales: Sydney Basin—Allandale Formation, Harpers Hill and in railway cutting 400 yards east of Allandale railway station. ?Farley Formation, Farley Road immediately east of Farley railway station.

Queensland: Bowen Basin (northern part)—Lizzie Creek Volcanics,  $\frac{3}{4}$  mile north-west of Lizzie Creek road crossing of Hazelwood Creek (BMR loc. MC 479);  $2\frac{1}{2}$  miles west of Collaroy homestead,  $\frac{1}{4}$  mile west of the Connors River (BMR loc. SL 199). Tiverton Subgroup (Homevale Beds), Homevale homestead, north-west of Nebo;  $1\frac{1}{2}$  miles south-west of Lizzie Creek crossing of Hazelwood Creek (loc. MC 485). (Springsure area)—Dilly Beds, 3 miles east of Crystal Hill (KOE 3). Maryborough Basin—unnamed limestone, Chatsworth, 5 miles north of Gympie; gully on creek flowing north into Teebah Creek, Gigoongan. Warwick area—'Wallaby Beds', Rokeby station, 10 miles south of Warwick.

Tasmania: Kansas Creek Beds (upper Quamby Group or lower Golden Valley Group), Western Creek, Quamby 1 mile map sheet 872N; 446.5E.

*Range.* Sakmarian and lower Artinskian.

*Discussion.* The type specimens of *M. morrisi* and *P. etheridgei* are from the same locality and are almost certainly conspecific, as suggested by Waterhouse (1965b, p. 850). Shells from the Farley Formation (Dun, 1932, pl. 51, figs 4, 5, 6?, pl. 52, figs 4, 5) described by Dun as either *Myonia farleyensis* or *M. davidis* are not very different from the topotypes of *M. morrisi* and at present with the limited material available are difficult to separate specifically.

Specimens which can be confidently referred to *M. morrisi* are relatively common in the Bowen Basin, Queensland, at localities such as Homevale homestead, and in Queensland the species seems to be characteristic of Dickins's Faunas I and II.

Dickins (*in* Dickins et al., 1964, Table 1) has tentatively referred several incomplete internal moulds from the lower part of the Gebbie Subgroup (BMR loc. M 415) to *Pachymyonia* sp. nov. These specimens (e.g. Pl. 4, figs 6-7) resemble *M. morrisi* in many respects, but appear to lack a well developed sulcus in front of the carina. However, since only a few specimens are available it is difficult to know whether they should be referred to another species.

*M. morrisi* appears to be closely related to *Pachymyonia occidentalis* Dickins, 1957, from the Lyons Group of the Carnarvon Basin, Western Australia, and to *P. cf. occidentalis* Dickins, 1963, from the Fossil Cliff Formation of the Irwin River area, Western Australia. *Pachymyonia elata* Popov, 1957, from the Kazanian (or Ufimian) of Verkhoyan'ya, Siberia, has a much less angular carina and lower less prominent umbos.



MYONIA CORRUGATA Fletcher, 1932

(Pl. 6, figs 1-9)

*Notomya (Maeonia) recta* (Dana); Etheridge Jnr, 1880, p. 37.

*Myonia corrugata* Fletcher, 1932, p. 404, pl. 50, figs 3, 4.

*Myonia* cf. *corrugata* Fletcher; Dickins in Dickins et al., 1964, table 1.

*Holotype* (by original designation). AM F30014 (Fletcher, 1932, pl. 50, fig. 3) from the Braxton Subgroup? at Millfield, south-west of Cessnock, Hunter Valley, New South Wales.

*Diagnosis.* Very large (commonly over 15 cm in length) and enormously thickened shells covered with coarse, ledge-like, concentric ribs.

*Description.* Adult shells are extremely large, often reaching lengths of over 16 cm. Large uncrushed specimens such as GSQ F9584 (Pl. 6, figs 6-8) have strongly inflated valves with little or no trace of a carina, but younger specimens, and particularly those crushed laterally, are usually strongly carinated (Pl. 6, fig. 1; Fletcher, 1932, pl. 50, figs 3-4).

Although not readily visible on the specimens described by Fletcher, the anterior part of the valve is strongly flattened to produce an extremely large lunular area, below and in front of the beaks (Pl. 6, figs 3-4). The shell in this region is enormously thickened (reaching a maximum thickness of 5.5 cm), and the anterior adductor scars may be up to 1.5 cm deep at their anterior end. The remainder of the shell is relatively thin, so that only severely abraded parts of the anterior regions of the valves (Pl. 6, fig. 9) are common at some localities.

The anterior adductor scar is deep and quadrate and situated low on the valve near the anterior margin. By contrast the posterior adductor is large and obscure, and occurs high on the shell near the posterior end of the hinge. None of the specimens available showed a convincing differentiation of the anterior pedal muscle scar into protractor and anterior retractor scars, so that it is not known whether a protractor muscle was present. Because of the normally inferior preservation of the rear parts of the shells, the shape and position of the posterior pedal retractor scar is not known. The pallial line is well marked on the front of the shell, but is obscured on all specimens behind the carina, so that it is not known whether or not a pallial sinus was present. Muscle scar *a* is obvious on several specimens such as CPC 7507 (Pl. 6, fig. 5); it is extremely long and in CPC 7507 may be connected with a line of pits scattered towards the umbonal region of the shell. The same specimen has a larger cluster of pits beneath the beak which probably represent the point of attachment of the umbonal retractor muscle. As in large specimens of

*Megadesmus grandis* (Runnegar, 1965, p. 243) this scar is absent from very well preserved large specimens such as GSQ F9584 (Pl. 6, figs 6-8), and the muscle may well become atrophied in larger shells.

Several specimens, including GSQ F9584, show the hinge clearly, but none shows any trace of teeth.

<i>Dimensions</i> (in cm)			
	Length	Height	Width
Holotype .....	13.2	7.7	2.6
MM F2478 .....	13.3	7.6	—
MM F2469 .....	16.0	11.1	4.3
GSQ F9524 .....	17.4	9.5	13.7 (internal
			mould,
CPC 7506 .....	16.5	9.4	— valves
			slightly
			gaping)

*Material.* Numerous specimens from the collections of the Bureau of Mineral Resources, University and Geological Survey of Queensland, Australian Museum, and University of Tasmania.

*Distribution.* New South Wales: Sydney Basin—Branxton Subgroup, Millfield near Cessnock; Conjola Formation at Wyro?, Conjola, and Ulladulla; Nowra Sandstone, Pointer Gap Road, west of Milton.

Queensland: Bowen Basin (northern part)—Blenheim Subgroup, below the *Strophalosia clarkei* Bed, at the unconformity with pre-Permian strata at Grassy Tank, Clermont; in the *S. clarkei* Bed and equivalent 'Pelecypod Bed' in the Clermont area (BMR locs C1 225/1, C1 40/2, C1 132 B, and C1 12/1); and in and above the Big *Strophalosia* Zone of the Collinsville area (BMR locs M 85c, B 1570, and Collinsville 1).

Tasmania: Member E, Malbina Formation, at Eaglehawk Neck, Tasman Peninsula, and Kangaroo Bay, Cygnet Peninsula.

*Range.* Lower upper Permian and perhaps upper Lower Permian.

*Discussion.* *M. corrugata* is a large and easily recognized species characterized by its coarse imbricate ornament and the enormous thickening of the anterior end of the shell. Its range may be longer in the Sydney Basin than in the Bowen Basin or Tasmania since it is associated with *Eurydesma hobartense* in both the Ulladulla mudstone (Conjola Formation) and the Branxton Subgroup. In both Queensland and Tasmania a significant interval of strata separates the youngest *Eurydesma* and the oldest *M. corrugata*.

MYONIA CARINELLA sp. nov.

(Pl. 4, fig. 10; Pl. 13, figs 5-13)

?*Sanguinolites undatus* (Dana); de Koninck, 1876-7, p. 260, pl. 17, fig. 1.

?*Notomya* ?sp. nov. Dickins in Dickins et al., 1964, table 1.

*Holotype*. UQ F50996 from immediately below the Big *Strophalosia* Zone, Blenheim Subgroup, on track about 1 mile west of Mulgrave Yards, west of Parrot Creek, west of Havilah homestead, Bowen 1:250,000 Sheet area, lat. 20° 50'S., long. 147° 42'E., north Queensland.

*Diagnosis*. Medium-sized ovate shells with subcentral umbos and evenly tapering but not recurved posterior margin. Umbonal carina weakly developed or absent.

*Description*. The valves are medium-sized, relatively elongate and have low rounded umbos situated at least one third of the shell length from the anterior margin. Viewed from the side, the anterior margin is evenly rounded and the posterior margin slightly pointed because of the inconspicuous umbonal ridge.

The adductor scars are subequal—the anterior scar being slightly smaller—and they are connected by a relatively wide, radially striated pallial line. There is no pallial sinus. The pedal protractor scar is visible on several specimens and is attached to the dorsal edge of the anterior adductor (Pl. 13, fig. 8). It is separated from a deep and normally very distinct anterior retractor scar, and a small but obvious umbonal retractor scar occurs on the anterior side of the umbonal cavity. The posterior retractor scar is larger and is merged with the dorsal edge of the posterior adductor. One specimen (Pl. 13, fig. 13) shows muscle scar *b* beneath the posterior adductor, and pitting of the internal surface of the valves occurs in several specimens.

The ligament is short, external, and opisthodetic (Pl. 13, fig. 6) and the hinge has a feeble tooth in the right valve. Several specimens show evidence of perforation of one of the beaks during growth but the umbos are not greatly incurved. Ornament is of scattered, relatively fine growth lines (Pl. 3, fig. 10).

*Dimensions of internal moulds* (in cm)

	Height	Length	Width
Holotype . . . . .	4.4	7.6	1.6
			(right valve)
UQ F50997 . . . . .	4.3	7.2+	—
UQ F29574 . . . . .	4.2	7.2	—
CPC 7501 . . . . .	4.1	—	3.6
			(both valves)

*Material*. Ten specimens from the collections of the University of Queensland and Bureau of Mineral Resources.

*Range.* Kungurian? and lowermost Upper Permian.

*Distribution.* Eight specimens from the type locality as well as one specimen from the Gebbie Subgroup in the Mackay 1:250,000 Sheet area, Queensland (BMR loc. M 416), and one specimen from either the Muree Formation or the upper part of the Branxton Subgroup,  $\frac{3}{4}$  mile west-south-west of Mulbring Post Office, Hunter Valley, New South Wales.

*Discussion.* Although *M. carinella* lacks a distinct and well developed carina it resembles other species of *Myonia* in general form and has the distinct and well developed accessory muscle scars normally found in species of *Myonia*.

The specimen figured by de Koninck (1876-7, pl. 17, fig. 1) as *Sanguinolites undatus* Dana is not conspecific with the lectotype of *Pholadomya undata* Dana (see Fletcher, 1932, pl. 50, fig. 2), but is closely similar to the specimens from Queensland and in particular to the specimen not from the type locality (Pl. 3, fig. 10; Pl. 13, figs 5-6). De Koninck's specimen is now lost, but it is said to have come from either 'Mt Vincent' or 'Burrageood on the Paterson', Hunter Valley district of New South Wales. One of the specimens described above is from Mulbring, which is quite close to Mount Vincent, and is possibly from the same locality as de Koninck's specimen (Pl. 13, fig. 12).

Johnston (1888, pl. 11, fig. 14) figured a shell from 'Porter's Hill', Hobart, which resembles *M. carinella*. Unfortunately the specimen appears to have been lost, so that a positive identification cannot be made. The 'Porter's Hill beds' of Johnston (1888 et seq.) are now considered to be part of the Bundella Mudstone of probable upper Sakmarian age (Banks & Hale, 1957), but the specimen may have come from younger beds which crop out in the same general area.

*M. carinella* differs from most other species of *Myonia* in lacking a well defined carina, and from the weakly carinated species *M. valida* in being more elongate and in lacking an obvious lateral sulcus. The lack of a pallial sinus and its deep pedal muscle scars differentiates it from *V. curvata*, with which it may be associated.

#### MYONIA? SULCATA sp. nov.

(Pl. 7, figs 1-6, 10-14)

*Myonia waterhousei* Dun, 1932 in part, p. 412, pl. 52, fig. 2, not pl. 52, fig. 3.  
? *Myonia etheridgei* Dun, 1932, p. 412, pl. 52, fig. 6, not pl. 51, figs 2-3.

*Holotype.* CPC 7509 from the upper part of the Lizzie Creek Volcanics,  $\frac{3}{4}$  mile north-west of Turrawalla-Eungella road crossing of Hazelwood Creek, Mount Coolon 1:250,000 Sheet area, Qld (BMR loc. MC 479).

*Diagnosis.* Strongly inflated, non-carinated, and deeply sulcate shells lacking a pallial sinus and with little or no siphonal gape.

*Description.* Well preserved internal moulds are reasonably elongate and have a deep sulcus extending from the umbos to the midventral margin. In front of the sulcus the shell margin is evenly rounded and the sulcus causes a pronounced concavity in the outline of the ventral margin. The posterior margin is somewhat pointed and the posterior dorsal margin distinctly concave giving an upswept look to the rear end of the shell. The umbos are relatively high, strongly incurved, often perforated, and point slightly towards the rear of the shell. An elongate lunule extends from the beaks to the anterior margin and the external ligament is set in a wide and relatively deep escutcheon. A small siphonal gape is present on two specimens, but a third appears to lack a gape; none of the specimens showed any evidence of a pedal gape.

The adductor scars are rounded, of medium size, and are connected by an even but obscure pallial line which lacks any trace of a sinus (Pl. 7, figs 12-13). Muscle scar *a* was not observed, but muscle scar *b* can be seen in two specimens (Text-fig. 3). Most moulds are covered with obscure radial muscle tracks resulting from the radial movement of the mantle muscle pits, but the pits are not obvious. A large pedal retractor scar is attached to the upper edge of the rear adductor and a smaller umbonal retractor scar, with an associated muscle track, occurs on the anterior umbonal slope. The anterior pedal musculature was not observed. The hinge lacked teeth and ornament is of concentric growth lines and occasional rugae.

*Dimensions of internal moulds (in cm)*

	Height	Length	Width
UQ F21155a	5.1	—	4.1
CPC 7510	5.2	—	4.1
CPC 7511	5.7	—	5.1
Holotype	—	8.3	3.4

*Material.* Holotype and sixteen other specimens from the collections of the Bureau of Mineral Resources, Australian Museum, and University of Queensland.

*Distribution.* New South Wales: Sydney Basin—Allandale Formation at Harpers Hill, Lochinvar, and east of Allandale railway station.

Queensland: Bowen Basin (northern part)—upper part of Lizzie Creek Volcanics,  $\frac{3}{4}$  mile west of Lizzie Creek road crossing of Hazelwood Creek (BMR loc. MC 479); Tiverton Subgroup, Homevale Beds, Homevale homestead, north-west of Nebo, and Lat.  $21^{\circ}29'30''$ S.; Long.  $148^{\circ}32'45''$ E. (loc. M 412b). Warwick area—'Eurydesma Beds' in gully 1700' at  $150^{\circ}$  from Rokeby homestead, 10 miles south of Warwick.

*Range.* Upper Sakmarian and lower Artinskian.

*Discussion.* *M.?* *sulcata* lacks an angular carina and has a small siphonal gape, so at present it is only tentatively referred to *Myonia*. It seems likely that *M.?* *sulcata* or a closely related species gave rise to species such as *Vacunella* cf. *waterhousei* and *V. etheridgei*, so that generic position of *M.?* *sulcata* is still somewhat doubtful. Shells from the Allandale Formation at Harpers Hill such as AM F31084 (Pl. 7, fig. 6) have a deep lateral sulcus and thus differ from specimens of *V. cf. waterhousei* which occur in the younger Farley Formation. However, apparent intermediates such as AM F49860 (Pl. 7, fig. 10) occur at Harpers Hill and it may be difficult to identify either species confidently using one or two specimens. Nevertheless, as none of the specimens of *V. cf. waterhousei* from the Farley Formation is as deeply sulcate as AM F31084, it seems likely that *M.?* *sulcata* is present at Harpers Hill. Whether *V. cf. waterhousei* is present as well is difficult to say at this stage.

The lectotype of *Myonia parallela* Dun, 1932 (by subsequent designation of Maxwell, 1964, p. 49) is a relatively nondescript internal mould from the Allandale Formation at Harpers Hill. Its left valve resembles the crushed left valve of AM F44044 (Pl. 7, figs 7-8) from the same locality, but the right valve of AM F44044 is like another specimen (AM F31084, Pl. 7, fig. 6) here referred to *M.?* *sulcata*. Because of the relatively small number of specimens available from the Allandale Formation it is not easy to decisively identify somewhat crushed individual specimens, and it is possible that *M.?* *sulcata* may eventually be shown to be a junior synonym of *M. parallela*.

A single specimen (UQ F48558, Pl. 7, fig. 11) from the 'Eurydesma beds', at Rokeby, near Warwick, southern Queensland, can be reasonably confidently included in *M.?* *sulcata*, but additional specimens will be required to confirm the identification. *M.?* *sulcata* resembles a specimen of *Pachymyonia elata* Popov (1957) held by the Bureau of Mineral Resources, Canberra (BMR F21979), but differs in having a recurved posterior margin.

#### MYONIA OR VACUNELLA? sp.

(Pl. 4, figs 15-16)

*Discussion.* Mr J. D. Armstrong, University of Queensland, recently collected a number of highly crushed but extremely elongate internal moulds of *Myonia?* or *Vacunella?* from the Artinskian 'Eurydesma Beds' at Rokeby station, 10 miles south of Warwick, south-east Queensland. In their extreme elongation they resemble shells from the Permian of Argentina described as *Stutchburia?* *argentinensis* by Harrington (1955) and referred to *Praeundulomya* by Dickins (1963, p. 23), but the similarity in shape may well be purely coincidental.

Subfamily PHOLADOMYINAE Fleming, 1828 (*vide* Newell, 1965)

*Diagnosis.* Relatively elongate thin shells, with a large siphonal gape and a smaller pedal gape. Pallial sinus moderately to well developed; hinge teeth obsolete or absent; valve overlap negligible.

Living members of the subfamily have the ventral edges of the mantle lobes fused to produce pedal and fourth apertures in addition to paired siphonal openings. The siphons are long, completely united, naked (i.e. lacking an outer sheath of periostracum), and incompletely retractile (Pelseneer, 1906, p. 275).

Australian Permian members have a shallow to deep pallial sinus, a large siphonal gape and a smaller but relatively elongate pedal gape, and sometimes a more or less discrete ventral adductor scar. Muscle scar *b* is well developed in at least one member of the subfamily (*Vacunella?* cf. *waterhousei*), and the foot is controlled by four pairs of pedal muscles (protractor, anterior, umbonal, and posterior retractors).

Other fossil members appear to have fewer pedal muscle scars (e.g. Agassiz, 1842, pl. 6b) and a shorter pedal shell gape. Radial ornament is well developed in *Pholadomya* and V-shaped ribbing occurs in several Upper Palaeozoic and Mesozoic genera (Dickins & Shah, 1965); other shells are ornamented with simple concentric rugae.

*Discussion.* See previous remarks on the subfamily Pachydominae.

Genus VACUNELLA Waterhouse, 1965

*Type species.* *Allorisma curvatum* Morris (1845, p. 270, pl. 10, fig. 1) by original designation of Waterhouse (1965a, p. 377).

*Generic diagnosis.* Inflated shells with anterior umbos, and a shallow to moderately deep sulcus on the flanks of the valves. Posterior dorsal shell margin more or less strongly concave in profile; umbonal carina absent. Siphonal gape relatively large, situated at the posteriodorsal part of the shell; pedal gape long and narrow. Pallial line of the type species with a large deep sinus, and a thickening beneath the base of the sinus probably due to the scar of an accessory adductor muscle; other species have shallow pallial sinuses. Hinge either edentulous or with a feeble tooth in each valve; foot controlled by four pairs of muscles.

*Discussion.* Waterhouse proposed *Vacunella* for inflated shells resembling *Chaenomya* (Meek, 1865) but having a much reduced siphonal gape, a more rounded ventral margin, and finer and more closely spaced granules on the external surfaces of the valves. Although these characters would not seem to

warrant the recognition of a new genus, it is now known that the type species of *Vacunella* has a much larger pallial sinus than the type species of *Chaenomya*, *C. leavenworthensis* Meek & Hayden (1858; see also Meek & Hayden, 1865, pl. 2, figs 1a-c; herein Pl. 11, figs 12, 13), and that there may be a different number of anterior pedal muscle scars in the two species. Also, *Vacunella curvata* has a long ventral gape for the protrusion of the foot (Pl. 8, figs 8-9), and probably an accessory adductor muscle at the base of the pallial sinus. Teeth are not well developed, but the hinge of AM F8136 (Pl. 9, fig. 16) is thickened beneath the umbos to form two alternate rounded projections reminiscent of the poorly developed teeth of *Pyramus laevis* and *Megadesmus grandis*. It seems likely that the 'isthmus', which Waterhouse (1965a, p. 377) observed connecting the anterior adductor to a nearby deeply depressed pedal retractor scar, is formed by the insertion of a second anterior pedal muscle corresponding to the pedal protractor muscle in the other Australian genera. *Vacunella* cf. *waterhousei* shows this protractor scar clearly (Pl. 10, fig. 9) but it is less distinct in even the best preserved specimen of *V. curvata* (Pl. 7, fig. 15). In contrast, the type specimen of *Chaenomya leavenworthensis* (USNM 1019a) shows no trace of a second anterior scar (Waterhouse, 1965a, p. 377; herein Pl. 11, fig. 12), and the anterior retractor scar is joined directly to the adductor muscle.

The differences between *Chaenomya* and *Vacunella* appear to be minimized if other Australian species (here referred to *Vacunella*) are examined, since both *V. etheridgei* and *V. cf. waterhousei* have a shallow pallial sinus like that of *C. leavenworthensis*. But the two genera are kept separate at present, firstly because the Australian species appear to be more closely related to one another than they are to *C. leavenworthensis* (this can be seen in their similarity in shape, size of the siphonal gape, and arrangement and number of pedal muscle scars), and secondly because of the possibility that *Vacunella* has been derived from *Myonia* during the Permian as suggested in a previous section (see also Text-fig. 3).

The generic position of *Vacunella? dawsonensis* sp. nov. remains uncertain since it differs considerably in shape from the other species here referred to *Vacunella*, and it is possible that it will eventually require a new generic name.

*Wilkingia* (Wilson, 1959) appears to differ from *Vacunella* in having the ligament supported by very narrow, slender nymphs (Wilson, 1959, pl. 71, fig. 1b) set in a narrow, elongate escutcheon, in contrast to the strong, thick nymphs and short ligament of *Vacunella*.

#### VACUNELLA CURVATA (Morris), 1845

(Pl. 7, figs 15-16; Pl. 8, figs 1-9; Pl. 9, figs 15-16, 17?; Pl. 11, fig. 14?; Pl. 12, figs 9-10)

(Type species of *Vacunella* Waterhouse, 1965)



*Allorisma curvatum* Morris, 1845, p. 270, pl. 10, fig. 1.  
*Allorisma audax* Dana, 1847, p. 153; 1849, p. 678, pl. 3, figs 1a-c.  
*Pholadomya* (*Homomya*) *glendonensis* Dana, 1849, p. 687, pl. 2, fig. 12.  
*?Sanguinolites mitchellii* de Koninck, 1876-7, p. 261, pl. 16, figs 3, 3a.  
*Chaenomya? bowenensis* Etheridge Jnr, 1892, p. 280 (= *Sanguinolites* sp. ind., Etheridge Jnr, 1880, p. 40, pl. 16, fig. 54).  
*Chaenomya? carinata* Etheridge Jnr, 1892, p. 279, pl. 43, figs 5, 6.  
*Pholadomya* (*Homomya*) *curvatus* (Morris); Dana, 1849, p. 686, pl. 3, figs 2a-b.  
*Panopaea* (*Mya*) *splicata* Sowerby var. *acuta* Etheridge Snr, 1872 in part, p. 347, pl. 21, fig. 3 not fig. 3a.  
*Sanguinolites etheridgei* de Koninck; Johnston, 1888, pl. 11, figs 13a-c.  
*Chaenomya? acuta* Etheridge Snr; Etheridge Jnr, 1892, p. 280.  
*Chaenomya etheridgei* (de Koninck); Reid, 1929, pl. 36, fig. 3.  
*Chaenomya bowensis* Etheridge Jnr; Dickins in Hill and Woods, 1964, pl. P 10, fig. 11.  
*Vacunella curvata* (Morris); Waterhouse, 1965a, p. 377.  
*Vacunella curvata* (Morris); Runnegar, 1966, fig. 1a.

*Type material.* The lectotype of *Allorisma curvatum* is British Museum No. PL 3692 (Morris, 1845, pl. 10, fig. 1), said to have come from 'Illawara', New South Wales, and probably from the Gerringong Volcanics, designated subsequently by Waterhouse (1965a, p. 377). The lectotypes (herein designated) of *Allorisma audax* and *Pholadomya glendonensis* are USNM 3643\* (Dana, 1849, pl. 3, figs 1a-c) from the upper part of the Gerringong Volcanics at Wollongong Point, and USNM 25643 (Dana, 1849, pl. 2, fig. 12) from the Maitland Group at Glendon, Hunter Valley, NSW. The holotypes (by monotypy) of *Chaenomya? carinata* and *Chaenomya? bowenensis* are QM F1218 and GSQ F1502 from the Blenheim Subgroup—the former from Banana Creek, near Banana, and the latter from Coral Creek, below Sonoma Road, south-west of Collinsville. The only specimen of *Sanguinolites mitchellii* figured by de Koninck (1877, pl. 16, figs 3, 3a) was destroyed by fire at the Garden Palace, Sydney, in 1882. A neotype has not been designated, and the specific name is related to the specimen de Koninck illustrated (Pl. 16, fig. 3), said to have come from either Aellalong or Wollongong, N.S.W.

*Remarks on the type material.* As Dickins (1961b, p. 143) has pointed out, it is now reasonably certain that Morris' specimens of *Deltopecten illawarensis* and *Eurydesma cordatum*, said to have come from 'Illawara N.S.W.', were from Harpers Hill in the Hunter Valley. The lectotype of *Allorisma curvatum* is also said to have come from 'Illawara', but in this case there is little doubt that the specimen is from the Illawarra district. Similar, well preserved specimens used to be relatively common at Wollongong Point, and this is probably the type locality.

*Diagnosis.* Strongly inflated shells lacking a deep and obvious sulcus in the lateral flanks of the valves. Posterior margin recurved and not markedly tapered.

\* Could not be located recently at the Smithsonian Institution (letter from F. J. Collier, 7.7.1966).

*Description.* Almost all the characters of this species are shown by an excellently preserved specimen (AM F8136, Pl. 7, figs 15-16; Pl. 8, figs 6-8; Pl. 9, fig. 16; Pl. 12, figs 9-10) from Wollongong Point, the probable type locality. Although the specimen is much larger than usual, the shape is characteristic, and there does not appear to have been any distortion of the shell. The valves are strongly convex and gape both posteriorly (Pl. 8, fig. 6) and ventrally (Pl. 8, fig. 8), and an extremely shallow sulcus is present on the flanks of the valves, beneath the umbos. The valves are joined by a short strong ligament (Pl. 8, fig. 5) set on nymphs, the lower edges of which can be seen in Plate 9, figure 16. In front of the nymphs the hinge-line is slightly thickened to form two obscure projections, which presumably represent obsolete teeth.

The anterior adductor muscle is large, square, and placed low on the valve, in contrast to the relatively small posterior adductor, which occurs on the posterior dorsal slope. The pallial line is wide, and there is a large sinus below the posterior adductor. As was pointed out previously, the pallial line thins opposite the pedal gape, and thickens behind it, to produce a scar which probably represents the area of attachment of an accessory ventral adductor (*ava*, Runnegar 1966, fig. 1A). A large pedal retractor scar is attached to the dorsal edge of the posterior adductor and another large retractor scar is situated above the anterior adductor, and connected to it by a smaller protractor scar. A small third retractor scar occurs on the anterior umbonal ridge (Pl. 12, fig. 9). The internal surface of the valves is pitted in this specimen, but in other specimens pitting is rare.

Other specimens often have a narrower siphonal gape (Pl. 8, fig. 2), but this may be due to post-mortem lateral compression, which seems to have affected the specimens at some localities. For this reason the pedal gape is difficult to observe and can only be seen on exceptional specimens (Pl. 8, figs 8, 9). The shell was apparently quite thin and ornament consists of regularly spaced rugae.

*Dimensions of internal moulds (in cm)*

	Height	Length	Width
AM F8136	9.0	14.3	7.1
AM F51560	5.3	8.5	4.2
CPC 7514	3.8	6.1	3.8
AM F51561	4.3	10.7	5.2
CPC 7513	3.5	6.1	3.5

*Material.* Numerous well preserved specimens from Queensland and New South Wales, in the collections of the Australian Museum, N.S.W. Geological and Mining Museum, Bureau of Mineral Resources, University of Queensland, and University of Tasmania.

*Distribution.* New South Wales: Sydney Basin—Mulbring Formation beneath railway bridge, north bank of Hunter River, Singleton; Muree Formation in quarry immediately west of school, Newcastle 4 mile 465955 (BMR loc. HV 15);

Branxton Subgroup (undifferentiated) at Lelaw Main, 8 miles due south of Farley railway station (UQ F252) and 'between Greta and Branxton' (AM F51560); Gerringong Volcanics at Flagstaff Hill and Wollongong Point, Wollongong; Dead Mans Gulch, 8 miles south of Kiama; Mount Brown; Berry; Gerringong cliffs; and Black Head, Gerroa. The species also occurs at Bundanoon and possibly in the Conjola Formation at Schnapper Point, Kioloa, and between Willingia and Bawley Points, Termeil.

Queensland: Bowen Basin (northern part)—Blenheim Subgroup, above Big *Strophalosia* Zone and *clarkei* bed about 15 feet stratigraphically below 'Streptorhynchus bed' (BMR loc. Collinsville 1a) and close to 'Streptorhynchus bed' in Bowen South area (B 270a); in Big *Strophalosia* Zone and *clarkei* bed of Clermont and Collinsville areas (locs C1 12/1, C1 14, C1 25/1, C1 30/1; C1 42/6, C1 225/1, C1 318/1, Collinsville 5; B 594). Bowen Basin (Springsure area)—in Mantuan *Productus* bed, Peawaddy Formation, Reids Dome road, 1 $\frac{3}{4}$  miles from Rewan-Rolleston Road, and in the Peawaddy Formation below Mantuan *Productus* bed (loc. Sp. 169). Bowen Basin (south-eastern part)—upper part of Barfield and lower part of Flat Top Formations (locs Ba814, Ba813, Ba321, T111, T274).

Tasmania: Hobart area—Member E, Malbina Formation, Claremont, Eaglehawk Neck, Bellerive, Maria Island; Ferntree Formation, Flowerpot Point, Blackmans Bay.

*Range.* Lower Upper Permian.

*Discussion.* The lectotypes of *Allorisma curvatum* Morris (Morris 1845, pl. 10, fig. 1), *Allorisma audax* Dana (Dana, 1849, pl. 3, figs 1a-c), and *Chaenomya? bowenensis* (Etheridge; Hill & Woods, 1964, pl. P 10, fig. 11) are similar in shape and do not appear to represent consistently recognizable morphological groups. The lectotype of *Chaenomya? carinata*, although badly crushed, appears to have had similar proportions to other Queensland specimens of *V. curvata*. (Particularly significant is the upturning of the posterior end of the shell, which usually occurs in both squashed and unsquashed specimens of *V. curvata*.) Unfortunately, the locality of the lectotype of *Chaenomya? carinata* is known only in a general way as 'Banana Creek'. The marine Permian formations exposed in or near Banana Creek are the Flat Top, Barfield, Oxtrack, and Buffel Formations, but the latter is very thin and absent in Banana Creek. Badly crushed specimens of *V. curvata*(?) and *Myonia carinata* occur in the Flat Top Formation (BMR locs T274, T31b), and this seems to be the most likely source for the lectotype of *C.? carinata*.

The lectotype of *Pholadomya glendonensis* (Dana, 1849, pl. 2, fig. 12) is fragmentary and badly crushed, and could be only tentatively referred to *V. curvata*, if it were not that *V. curvata* is very common in the Mulbring Formation,

which outcrops at or near the type locality of *P. glendonensis*. De Koninck (1876-7) failed to indicate whether the specimen he figured as *Sanguinolites mitchellii* was from Aellalong (Hunter Valley) or Wollongong Point, and without knowing the accuracy of his drawing, it is difficult to identify the species he illustrated. De Koninck's illustration is closest to *V. curvata*, but *S. mitchellii* may best be regarded as an unrecognizable species.

Etheridge senior (1872, p. 342) described *Panopaea plicata* var. *acuta* as a Cretaceous species, but Etheridge junior (1892, p. 289) suggested that the specimens were from the Bowen River Coal Field, and were therefore of Permian age. However, the specimen which Waterhouse (1965b, p. 851) has chosen as lectotype for *Panope acuta* (QM F1251, Etheridge Snr, 1872, pl. 21, fig. 3a) is probably of Cretaceous age (J. T. Woods in Waterhouse, 1965b). The other specimen is from Upper Permian beds in Pelican Creek, Queensland, and appears to belong to *V. curvata*. *V. curvata* is the commonest and most widely distributed species of *Vacunella* in eastern Australia, occurring at numerous localities in the Upper Permian of Queensland, New South Wales, and Tasmania, and is a useful index fossil for the upper part of the sequences in these areas.

#### VACUNELLA ETHERIDGEI (de Koninck), 1876

(Pl. 9, figs 1-12, 13?, 14)

*Sanguinolites etheridgei* de Koninck, 1876-7, p. 262, pl. 17, fig. 2, not pl. 16, fig. 2.

*Chaenomya? etheridgei* (de Koninck); Etheridge Jnr, 1892, p. 279.

*Chaenomya etheridgei* de Koninck; Etheridge Jnr, 1894, p. 532, pl. 40, fig. 5.

*Chaenomya* sp. nov. B Dickins in Dickins et al., 1964, Table 1.

*Type material.* Both syntypes appear to have been destroyed, and the species has been compared with the specimen figured by Etheridge junior (1894, pl. 40, fig. 5, GSQ F1558) apparently from the Gebbie Subgroup in Stoodleigh Creek, 1½ miles above 'Beak's Farm', (probably near Lat. 22°35'42"S; Long. 149°41'15"E), about 12 miles north-west of Marlborough, central eastern Queensland. However, because this specimen is not from the type locality in the Hunter Valley, it has not been formally designated as a neotype. Two specimens from New South Wales labelled 'Permian, New South Wales' (UQ F5631, pl. 9, fig. 12) and 'Maitland, N.S.W.' (AM F197) are probably conspecific with the specimen figured by Etheridge, but are inadequately located and are therefore not suitable for selection as a neotype.

*Remarks on the type material.* De Koninck (1876-7, pl. 16, fig. 2, pl. 17, fig. 2) figured two specimens, both of which appear to have been destroyed while on exhibition at the Garden Palace, Sydney, in 1882. The localities given by de Koninck for the two specimens are 'Muree sandstone' (pl. 17, fig. 2) and 'Mount Vincent' (pl. 16, fig. 2), in the Hunter Valley of New South Wales.

The two specimens are not conspecific and Etheridge (1894) has based his understanding of the species on the former (pl. 17, fig. 2). It is, however, not certain whether this specimen was in fact from the Muree Formation, and if so whether, as Clarke (1878, p. 140) implies, it was from between Muree and Morpeth (Raymond Terrace and East Maitland).

Although Etheridge (1894, p. 533) gave 'Bent's Farm, Woodleigh Creek' as the locality of the specimen he figured, the specimen is correctly labelled 'Stoodleigh Creek' and 'Beak's Farm'. Stoodleigh Creek is a tributary of the Styx River, between Rockhampton and Mackay, and an examination of the records of the Queensland Lands Department has shown that Por. 1583, Parish of Clayton (County Murchison) was leased to Henry Beak in 1884, whereas other portions also held by the Beak family were taken up after the publications of Etheridge's paper (1894). It is therefore reasonably certain that Etheridge's specimen is from one and three quarter miles above Por. 1583, Par. Clayton.

According to recent mapping carried out by the Bureau of Mineral Resources and Geological Survey of Queensland, the locality is in undifferentiated Back Creek Group. However, because of the apparently restricted range of *V. etheridgei* elsewhere in Queensland, it is probable that the beds at this locality are from the Gebbie Subgroup, and they are probably part of a small area of Gebbie Subgroup which has been identified north-west of Rockhampton (Malone, 1964, fig. 6).

*Diagnosis.* Short, globose species of *Vacunella* with an obvious sulcus on the lateral flanks.

*Description.* The specimen figured by Etheridge (Pl. 9, figs 2-5) is well preserved and apparently undistorted. As in *V. curvata* the valves of *V. etheridgei* are strongly convex, but they differ in having a well marked sulcus on the lateral flanks. The siphonal gape appears to have been quite narrow and it is not known whether a pedal gape was present. The anterior adductor muscle scar is relatively small; it is prolonged dorsally towards a large and relatively deep pedal scar, presumably that of the anterior retractor. No separate protractor scar could be recognized, and the umbonal scar and posterior musculature were not visible. The posterior part of the pallial line (visible on two specimens) has a very shallow sinus (Pl. 9, figs 9-10) apparently much like that of *V. dawsonensis*. The ligament is external and opisthodontic, and presumably supported by strong nymphs as in other species of the genus.

The shell appears to have been rather thin and is ornamented with low rugae covered with fine growth-lines.

*Dimensions of internal moulds (in cm)*

		Height	Length	Width
GSQ F1558	.....	4.6+	8.4	4.9
CPC 7516	.....	3.6	—	3.8
CPC 7517	.....	4.3+	7.1	4.5
CPC 7515	.....	4.6	9.1	4.1+

*Material.* 22 specimens from the collections of the Bureau of Mineral Resources and Geological Survey of Queensland.

*Distribution.* The only reasonably located specimens from New South Wales I have seen which can be tentatively referred to *V. etheridgei* are AM F197 from 'Maitland, N.S.W.' and AM F44024 from Branxton. It is unlikely that these specimens are from a formation stratigraphically lower than the Branxton Subgroup, and they are most probably from the Branxton Subgroup. In Queensland the species is known from below the Glendoo Member of the Collinsville Coal Measures (BMR locs M 413, M 415) and from Gebbie Subgroup (Dickins et al., 1964) in the Mount Coolon and Saint Lawrence areas (BMR loc. MC 420 and in Stoodleigh Creek, Par. Clayton). A single well preserved specimen has been recovered from the Ingelara Formation in Dry Creek, 5 miles at 263° from 'Ingelara' homestead, Springsure area (loc. Z66).

*Range.* Upper Artinskian.

*Discussion.* *V. etheridgei* is easily distinguished from other species of *Vacunella*, which lack a deep sulcus on the lateral flanks.

VACUNELLA? WATERHOUSEI (Dun, 1932)

(Pl. 10, fig. 1)

*Myonia waterhousei* Dun, 1932, p. 412, pl. 52, fig. 3 *not* fig. 2.

*Myonia waterhousei* Dun; Waterhouse, 1965b, p. 850.

*Type material.* The lectotype (by subsequent designation of Waterhouse, 1965b, p. 850) is AM F6589 (Dun, 1932, pl. 52, fig. 3) from the Farley Formation at Farley, Hunter Valley, New South Wales.

*Discussion.* The lectotype of *Myonia waterhousei* (Pl. 10, fig. 1) is a badly crushed internal mould in which only the left valve is carinated, and the carina may have been produced by crushing. Many of the specimens figured by Dun (1932) from the 'Lower Marine' of the Hunter Valley are crushed in this way and it is often quite difficult to relate these specimens to the species recognizable in larger collections. Although a series of topotypes is available at the Australian Museum, these problems are not easily solved at the present time, and it will probably be necessary to have larger collections of specimens from the type localities.

The lectotype of *M. waterhousei* resembles a species of *Vacunella* which occurs near the top of the Farley Formation at Farley (e.g. AM F26265, pl. 10, figs 4-5), and which is common in the Ravensfield Sandstone member of the Farley Formation in the Ravensfield Quarry. The pallial line is known from a number of specimens from the latter locality and all have a shallow posterior sinus. The lectotype of *M. waterhousei* lacks a definite sinus, but the shape and position of the line are comparable in so far as comparisons can be made between this and the uncrushed specimens. The outline of the lectotype is similar to that of the uncrushed specimens (here referred to *Vacunella* cf. *waterhousei*), but only the depth of the pallial sinus and the presence or absence of an angular umbonal carina can be used to distinguish some species of *Myonia* and *Vacunella*. Unfortunately post-mortem compaction may either produce or obliterate a carina on either or both valves (see Pl. 7, figs 7-8), so that at this stage it is difficult to prove that the lectotype and the specimens here referred to *V. cf. waterhousei* are conspecific.

VACUNELLA cf. WATERHOUSEI (Dun), 1932

(Pl. 10, figs 2-13)

*Vacunella?* cf. *waterhousei* (Dun); Runnegar, 1966, fig. 1c.

*Diagnosis.* Large, elongate, and narrowly inflated shells lacking a deep lateral sulcus and having gently tapering posterior dorsal and ventral margins. Pallial sinus very shallow; umbos directed posteriorly.

*Description.* Well preserved internal moulds are elongate and narrowly inflated, and have a shallow sulcus extending from the umbos to the mid-ventral margin. Viewed from the side, most specimens show a pronounced change in outline just in front of the sulcus, so that the posterior part of the ventral margin forms an angle of about  $150^\circ$  with the anterior part. Both anterior and posterior margins have rounded outlines and the umbonal slope in front of the umbos is evenly convex. The umbos are relatively low, incurved, and point slightly rearwards. A narrow elongate lunule extends from the beaks to the anterior shell margin and the external ligament is set in a narrow escutcheon.

The adductor scars are subequal and rounded—the anterior scar is at mid-valve height and the posterior scar near the posterior dorsal margin. The pallial line (well shown by five specimens) lacks a deep sinus (Text-fig. 3; Pl. 10, fig. 13) and is somewhat thickened in, below, and just behind the sinus. At the rear edge of the lateral sulcus it changes direction relatively abruptly and instead of paralleling the ventral margin, it ascends diagonally across the shell towards the lower edge of the anterior adductor. Associated with this bend in AM F50157 there is a perceptible thinning of the line, so that in front of the bend the line

is thinner and markedly striated. Muscle scar *a* has not been observed, but AM F50157 shows a small scar below the rear adductor (Pl. 10, fig. 13) which is unquestionably muscle scar *b*. Small pallial muscle pits are preserved on some specimens such as AM F51056 (Pl. 10, fig. 10), where they are followed by long, slightly arcuate muscle tracks.

A large pedal retractor scar is attached to the upper edge of the rear adductor and a smaller umbonal retractor is situated on the anterior umbonal slope some distance from the hinge (Pl. 10, fig. 11). A relatively large, discrete, and rounded anterior retractor scar is located on the outer edge of the lunule, and on most specimens its position is emphasized by a long muscle track which reinforces the edge of the lunule. Only one specimen (AM F30021, Pl. 10, figs 8-9; Pl. 12, fig. 1) shows the pedal protractor scar clearly—in other specimens it is more or less completely merged with the anterior adductor scar. All specimens have a well developed but relatively small siphonal gape, and AM F30021 at least appears to have a small pedal gape which extends to the posterior edge of the lateral sulcus.

The hinge lacks teeth and ornament is of growth-lines and scattered rugae.

*Dimensions of internal moulds (in cm)*

	Height	Length	Width
AM F51056 ....	6.9	11.6	4.8
AM F51057 ....	5.1	—	3.9
AM F51058 ....	5.8	8.7	—
AM F51048 ....	5.7	9.8	4.3
AM F26265 ....	4.3	8.0	3.3
AM F30021 ....	4.5	7.4	3.3

*Material.* Ten well preserved internal moulds from the collections of the Australian Museum and University of Queensland. Other specimens are available at the Geological and Mining Museum, Sydney.

*Distribution.* New South Wales (Sydney Basin): Farley Formation at Farley and Ravensfield Sandstone Member of Farley Formation at Ravensfield Quarry, south-west of Farley, Hunter Valley. Doubtfully recorded from Allandale Formation at Harpers Hill and Allandale, and from the base of the Conjola Formation at Wasp Head, Durras South.

*Range.* Lower Artinskian and perhaps upper Sakmarian.

*Discussion.* *V. cf. waterhousei* has only been definitely identified in the Farley Formation, and although specimens such as AM F49860 (Pl. 7, fig. 10) from the Allandale Formation at Harper's Hill may belong to this species, they also resemble other specimens from the Allandale Formation which have been referred to *Myonia? sulcata* sp. nov. The two species appear to be closely related,



and it has been suggested that *M.?* *sulcata* may have given rise to *V. cf. waterhousei*, so that some difficulty would be expected in identifying crushed specimens of either species.

*V. cf. waterhousei* is similar in shape to three shells from the Lower Permian of Western Australia described by Dickins (1963, p. 51, pl. 8, figs 12-16) as *Chaenomya* sp., but appears to differ in being somewhat more elongate and in having a slightly less pointed posterior margin. The Western Australian specimens are from the Fossil Cliff and Callytharra Formations and the Nura Nura Member of the Poole Sandstone, which can be correlated approximately with the Farley Formation of New South Wales (Dickins 1967), and the similarity of these shells with those from the Farley Formation tends to support that correlation.

VACUNELLA sp. nov. A

(Pl. 11, figs 9-11)

*Chaenomya* sp. nov. A Dickins in Dickins et al., 1964, table 1.

*Tentative diagnosis.* Short, narrowly inflated shells with a strongly curved ventral margin.

*Description.* Rather short and rounded shells having a shallow lateral sulcus. The posterior margin is strongly recurved so that the ventral margin is quite convex. The siphonal gape is relatively narrow and it is not known whether there was a pedal gape. Other details of the musculature, ligament, and hinge are unknown. Ornament is of low concentric rugae.

*Dimensions* of CPC 7521 (in cm)

Height	Length	Width
2.3	3.9	0.8

*Material.* Seven specimens from the collections of the Bureau of Mineral Resources and University of Queensland.

*Distribution.* Queensland (Bowen Basin): upper part of Lizzie Creek Volcanics,  $\frac{3}{4}$  mile north-west of Lizzie Creek Road crossing of Hazelwood Creek, Mount Coolon area (BMR loc. MC 479), and Tiverton Subgroup, Lat.  $20^{\circ}55'45''$ S., Long.  $148^{\circ}08'30''$ E. (BMR loc. B 686). Shells from the Stanleigh Formation and 'Dilly beds' of the Springsure area, Queensland (locs KOE 6 and KOE 3), can probably be included in this species. A single internal mould (UQ F47950) from the Conjola Formation at Point Upright, south coast, N.S.W., resembles the specimen shown in Plate 11, figure 11, but it is impossible to make a confident identification at this stage.

*Range.* Upper Sakmarian and lower Artinskian.

*Discussion.* The three specimens from the northern part of the Bowen Basin (CPC 7521-7523, pl. 11, figs 9-11) are shorter than most specimens of *V. curvata* and lack a deep sulcus like *V. etheridgei*. Since *V. curvata* has not been recorded below the Blenheim Subgroup, these specimens almost certainly belong to a different species. It is possible that the shape and size of the pallial sinus of *V. sp. nov.* A will prove useful in separating the two species.

VACUNELLA? DAWSONENSIS sp. nov.

(Pl. 11, figs 1-8; Pl. 13, figs 1-4)

?*Sanguinolites* sp. nov. Dickins in Veevers et al., 1964.

*Chaenomya*? n. sp. Runnegar, 1966, fig. 1d.

*Holotype.* UQ F51000 from the Flat Top Formation in a small quarry about 8 miles from Theodore on the Theodore-Banana Road, Dawson Valley, central Queensland (Monto 1:250,000 Sheet 304907; lat. 24°52'S., long. 150°08'E.).

*Diagnosis.* Elongate shell with subparallel dorsal and ventral margins and low, inconspicuous umbos.

*Description.* The shell is elongate and has rounded ends. The umbos are about one third of the length from the anterior end, and are low and inconspicuous. In front of the umbos the upper margin is convex, but behind them it is gently concave so far as the upper end of the large posterior gape. Although the anterior edge of most specimens is broken, there appears to have been a small anterior gape, which may have extended some distance along the ventral margin. The adductor scars are relatively small; the anterior scar is kidney-shaped and placed low on the shell, in contrast to the rounded posterior scar, which is situated at the dorsal margin. A single deep pedal retractor scar is attached to the posterior adductor, and there are two well defined pedal scars (protractor and anterior retractor) above the anterior adductor. The retractor is relatively large, deep and circular, and is merged with the smaller protractor, which is joined to the upper edge of the anterior adductor. The posterior retractor is attached to the upper edge of the posterior adductor (Pl. 11, fig. 2) and a third (umbonal) retractor occurs on the anterior umbonal ridge (Pl. 11, fig. 7).

The pallial line has a wide and extremely shallow sinus (Pl. 11, fig. 2), but pits on the internal surface of the valve have not been observed. The ligament is rather long, but is of the C-spring type (Pl. 11, fig. 5), and is supported by relatively slender nymphs which are set in a narrow elongate escutcheon.

The hinge appears to lack teeth and a slight thickening of the lower edges of the nymphs of GSQ F9439 (Pl. 11, fig. 6) is perhaps reminiscent of the inner

plates of *Edmondia*. The shell is ornamented with fine concentric growth-lines and occasional coarse rugae.

*Dimensions of internal moulds (in cm)*

	Height	Length	Width
Holotype	3.1	9.5	2.8
QM F1814	4.1	8.0	2.9
GSQ F9439	3.9	—	3.0

*Material.* Twenty-five specimens from the collections of the Bureau of Mineral Resources, University of Queensland, Queensland Museum and Geological Survey of Queensland.

*Distribution.* All but one of the specimens are from the Dawson River Valley, south-east Queensland. Well located specimens are from the upper part of the Barfield Formation in the Baralaba area (Ba 814, Ba 321) and the Flat Top Formation on the Theodore-Banana Road, 7.6 miles from Theodore Post Office. Other specimens are labelled 'Cracow Station' and 'Castle Creek, Dawson Valley'. A single reasonably well preserved specimen from the *Stophalosia clarkei* bed of the Blenheim Subgroup in the Clermont area (BMR loc. C1. 14) can be tentatively included in the species.

*Range.* Lower Upper Permian.

*Discussion.* The shape of the species is quite characteristic and it does not closely resemble other shells from the east Australian Permian.

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# PLATE 1

Figs 1-10 are from the Allandale Formation at Harpers Hill, Hunter Valley, N.S.W.  
Figs 11-12 are from Turisse Point, Durras South, near Batemans Bay, N.S.W., 200 feet stratigraphically above the unconformity with the pre-Permian strata.

Figs 1-12. *Pyramus laevis* (Sowerby), 1838 ..... Page 34

Fig. 1—Right valve of plaster cast of lectotype of *Megadesmus laevis*,  $\times\frac{1}{2}$ .

Fig. 2—Right valve, AM F14757,  $\times\frac{1}{2}$ .

Fig. 3—Plaster cast of lectotype of *Megadesmus cuneatus*,  $\times\frac{1}{2}$ .

Fig. 4—Right valve, AM F29328,  $\times\frac{1}{2}$ .

Fig. 5—Ornament of left valve, intermediate between that of figs 4 & 6, AM F18959,  $\times\frac{1}{2}$ .

Fig. 6—Right valve, AM F18988,  $\times\frac{1}{2}$ .

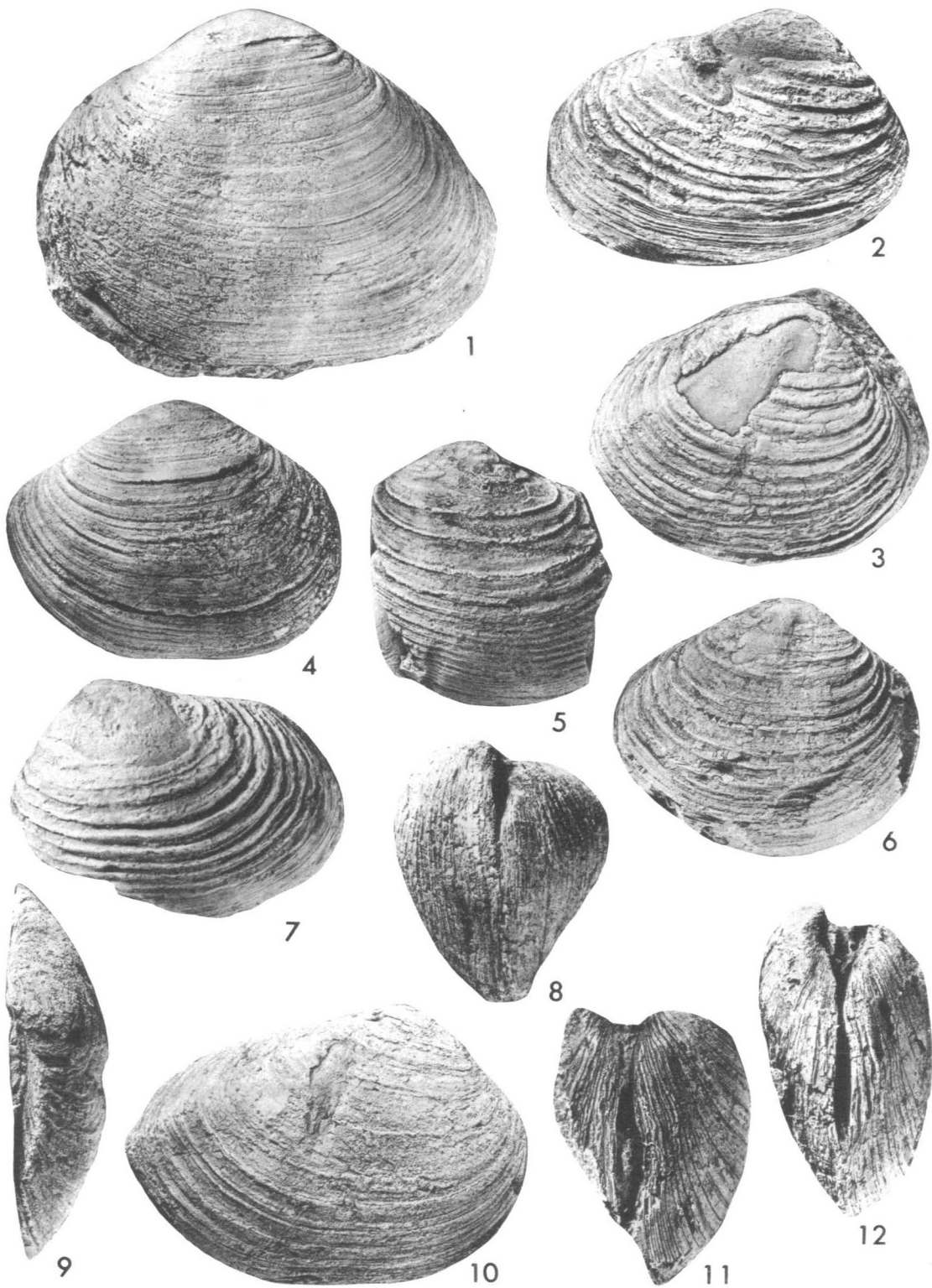
Fig. 7—Plaster cast of lectotype of *Megadesmus antiquatus*,  $\times\frac{1}{2}$ .

Fig. 8—Posterior view of MM F2440 showing the complete absence of a siphonal gape,  $\times\frac{1}{2}$ .

Figs 9-10—Dorsal and lateral views of MM F7893,  $\times 1$ . Note the escutcheon and well defined carina.

Fig. 11—Posterior view of latex cast of UQ F47935 to show the siphonal gape,  $\times 1$ .

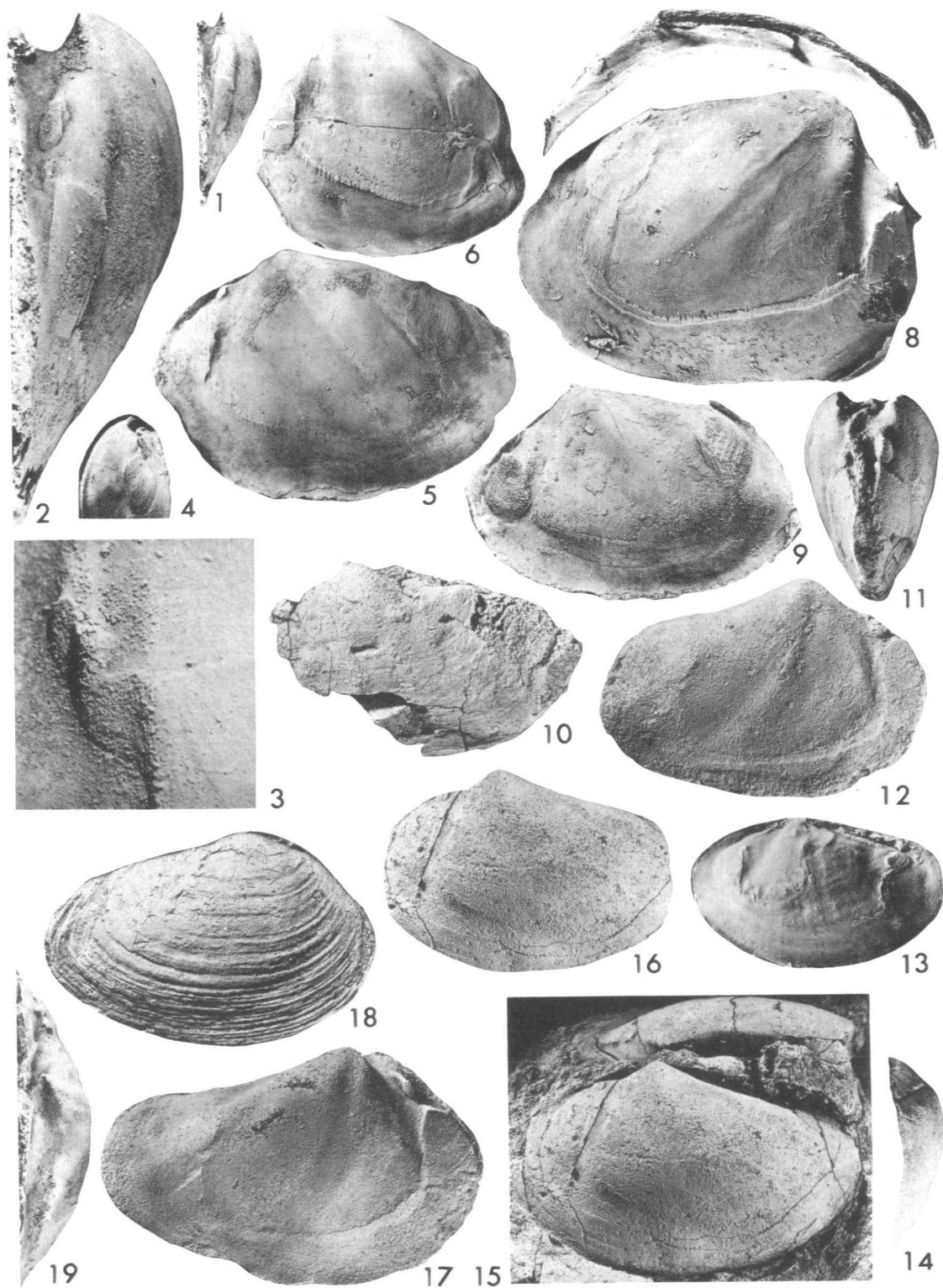
Fig. 12—Latex cast of UQ F47933 showing the siphonal gape,  $\times 1$ .



## PLATE 2

Figs 1-9, 19 are from Turisse Point, Durras South, near Batemans Bay, 200 feet stratigraphically above the unconformity with the pre-Permian strata. Fig. 10 is from the Brumby Marl (Golden Valley Group) below Poatina, northern Tasmania. Figs 11-12, 14-18 are from the Gerringong Volcanics at Wollongong, N.S.W., and Fig. 13 is from the Mantuan *Productus* Bed, Peawaddy Formation, 2.0 miles at 188° from Tanderella homestead (previously Nardoo homestead), Springsure area, central Qld (BMR loc. Sp 649).

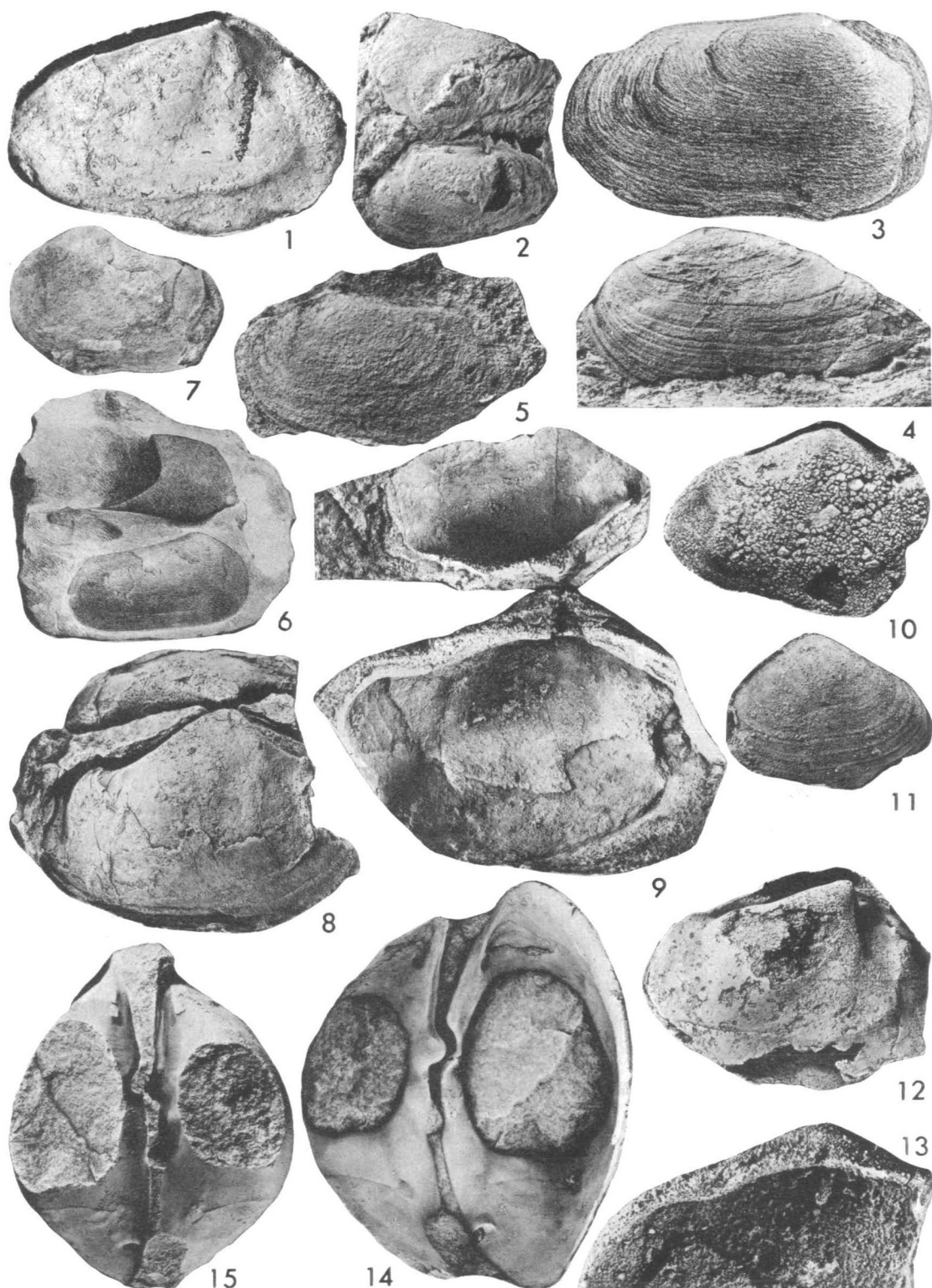
- Figs 1-10, 19. *Pyramus laevis* (Sowerby), 1838 ..... Page 34
- Figs 1-3—UQ F47939.
- 1—Anterior view of internal mould,  $\times\frac{1}{2}$ .
  - 2—Same view enlarged to show pedal musculature,  $\times 2$ .  
(See also Pl. 12, fig. 11).
  - 3—Enlargement of pedal protractor scar showing two or three points of insertion,  $\times 10$ .
- Figs 4, 19—UQ F47931,  $\times\frac{1}{2}$ .
- 4—Anterior view of internal mould showing umbonal retractor scar.
  - 19—Dorsal view of same.
- Fig. 5—Internal mould of left valve, UQ F47932,  $\times\frac{1}{2}$ .
- Fig. 6—Internal mould of left valve with well developed pallial sinus, UQ F47930,  $\times\frac{1}{2}$ .
- Figs 7-8—UQ F47938,  $\times 1$ .
- 7—Latex cast of hinge to show blunt tooth and ligament groove.
  - 8—Internal mould of right valve showing muscle scars *a* and *b*.
- Fig. 9—Internal mould of left valve showing bifid insertion of umbonal retractor scar, UQ F47937,  $\times\frac{1}{2}$ .
- Fig. 10—Fragmentary internal mould of left valve, UQ F48911,  $\times\frac{1}{2}$ .
- Figs 11-18—*Pyramus myiformis* Dana, 1847 ..... Page 37
- Figs 11-12—AM F17773,  $\times 1$ .
- 11—Anterior view of internal mould showing protractor and anterior retractor scars (See also Pl. 12, fig. 12).
  - 12—Lateral view of internal mould resembling lectotype of *Notomya securiformis*.
- Fig. 13—Lateral view of juvenile showing well developed pallial sinus, CPC 7494,  $\times 2$ .
- Fig. 14—Posterior view of internal mould to show siphonal gape, MM F12997,  $\times 1$ .
- Figs 15-16—MM F2439,  $\times\frac{1}{2}$ .
- 15—Internal mould of both valves.
  - 16—The same specimen trimmed at the edges to show resemblance to Fig. 12.
- Fig. 17—Internal mould of right valve intermediate in shape between lectotypes of *P. myiformis* and *N. securiformis*, MM F12996,  $\times 1$ .
- Fig. 18—Latex cast of external mould of right valve, AM F51562,  $\times\frac{1}{2}$ .





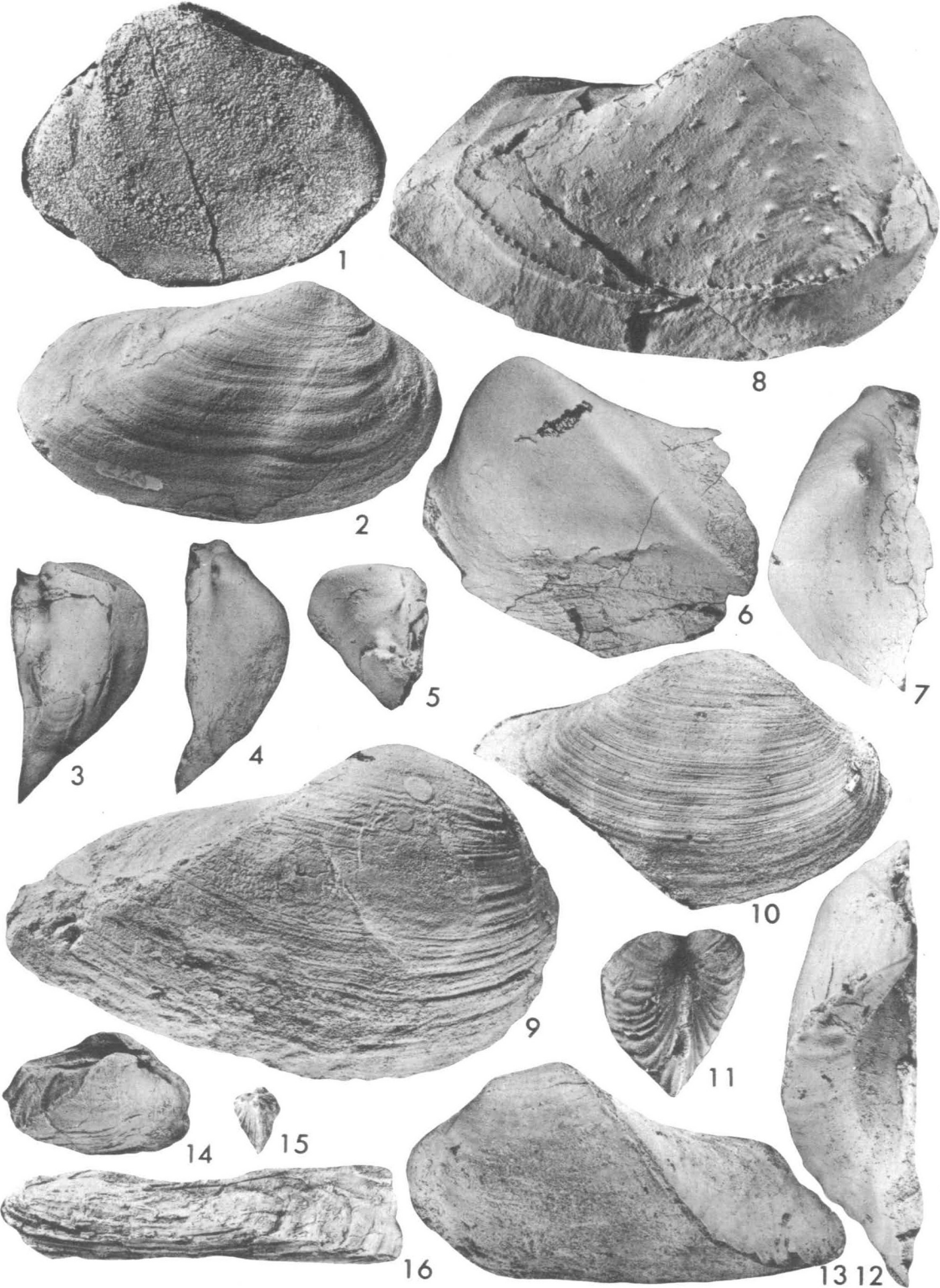
# PLATE 3

- Fig. 1—*Pyramus myiformis* Dana, 1847 .... Page 37  
Internal mould of right valve, AM F51285,  $x\frac{3}{4}$ .
- Figs 2-6—*Pyramus concentricus* (Etheridge Snr), 1872 .... Page 40
- Fig. 2—Internal mould of both valves showing the differences in shape caused by post-mortem distortion: GSQ F9285,  $x\frac{1}{2}$ , 'Monkland beds', Horse Shoe Bend Road, Gympie.
- Fig. 3—Etheridge's figure of *Edmondia concentrica*,  $x1$ .
- Fig. 4—Internal composite mould of left valve, GSQ F9288,  $x1$ ; same loc. as Fig. 2.
- Fig. 5—Internal mould of left valve, GSQ F9287;  $x1$ ; same loc. as Fig. 2.
- Fig. 6—Etheridge's figure of *Edmondia obovata* from 'fossiliferous greenstone, Beehive Reef, Gympie',  $x\frac{1}{2}$ .
- Figs 7-11, 13—*Pyramus concentricus?* (Etheridge Snr), 1872 .... Page 42
- Fig. 7—Left valve. UQ F13299,  $x\frac{1}{2}$ ; 'Eurydesma beds', Rokeby station, south of Warwick, Queensland.
- Figs 8-9—CPC 7495, upper part of Lower Bowen Volcanics,  $2\frac{1}{2}$  miles west of Collaroy homestead, about  $\frac{1}{4}$  mile west of the Connors River, central Qld (BMR loc. SL 199).
- 8—Internal mould of both valves,  $x\frac{3}{4}$ .
- 9—Latex cast showing strong triangular tooth and socket,  $x1$ .
- Fig. 10—Internal mould of right valve, UQ F47941,  $x\frac{1}{2}$ ; Conjola Formation?, Bawley Point, Termeil, south coast, N.S.W.
- Fig. 11—Latex cast of external mould of left valve, UQ F47942,  $x\frac{1}{2}$ ; same loc. as Fig. 10.
- Fig. 13—Latex cast of hinge of left valve, UQ F47944,  $x1$ ; same loc. as Fig. 10.
- Fig. 12—*Pyramus* sp.  
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- Figs 14-15—*Megadesmus (Megadesmus) gryphoides* (de Koninck), 1876 .... Page 31  
GSQ F9583,  $x\frac{1}{2}$ ; Homevale Beds, Homevale homestead, north-west of Nebo, Qld
- 14—Latex cast to show slight overlap of anterior part of left valve by right valve.
- 15—Dorsal view of internal mould.



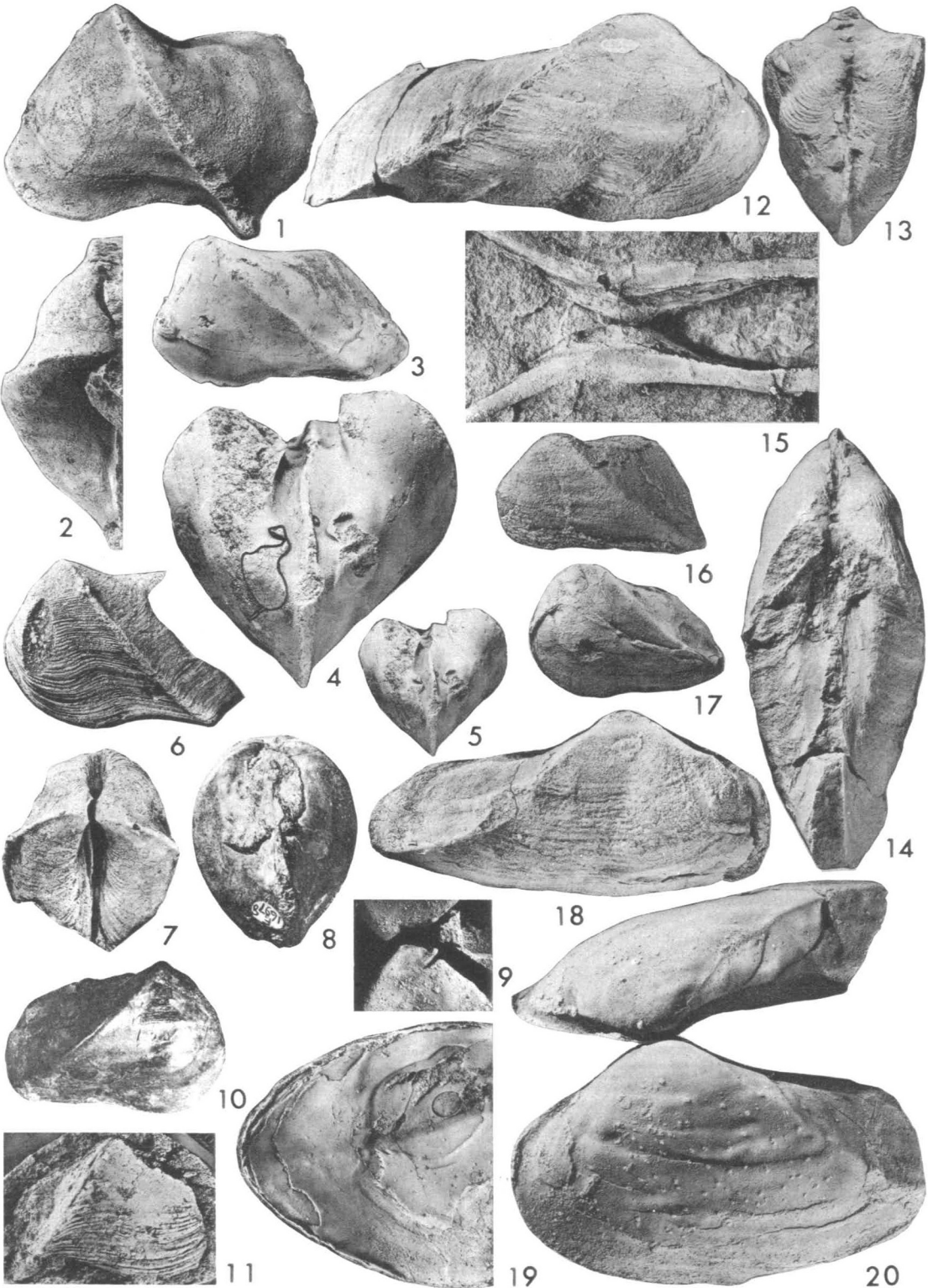
# PLATE 4

- Fig. 1—*Pyramus concentricus*? (Etheridge Snr), 1872 ..... Page 42  
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- Fig. 2—*Pyramus*? *undata* (Dana), 1847 ..... Page 44  
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- Figs 3-5—*Myonia morrisi* Etheridge Jnr, 1919 ..... Page 53  
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- Figs 4-5—CPC 7499, Homevale Bed D, Homevale, north-west of Nebo, Qld, x $\frac{1}{2}$ .  
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5—Anterior view of same specimen.
- Figs 6-7—*Myonia* sp. nov? ..... Page 55  
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- Figs 8-9—*Myonia carinata* (Morris), 1845 ..... Page 50  
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- Fig. 9—Left valve; GSQ F1495, Peawaddy Formation,  $\frac{1}{2}$  mile north-west of Consuelo homestead, Springsure area, Qld, x $\frac{1}{2}$ .
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- Figs 11-13—*Myonia carinata*? ..... Page 52  
11—Anterior view of internal mould; CPC 7502; lower part of Middle Bowen Beds (Unit A), 1 $\frac{1}{2}$  miles south-east of Lizzie Creek road crossing of Hazelwood Creek (BMR loc. MC 485), x1.  
12-13—Lateral and dorsal views of internal mould; CPC 7503, same loc. as Fig. 3, x1.
- Fig. 14—*Myonia pollocki* Maxwell, 1964 ..... Page 25  
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16—Lateral view of crushed internal mould; UQ F48556, same loc. as Fig. 15, x $\frac{1}{2}$ .
- Figs 3-7 from negatives kindly supplied by Dr J. M. Dickins, Bureau of Mineral Resources, Canberra.



## PLATE 5

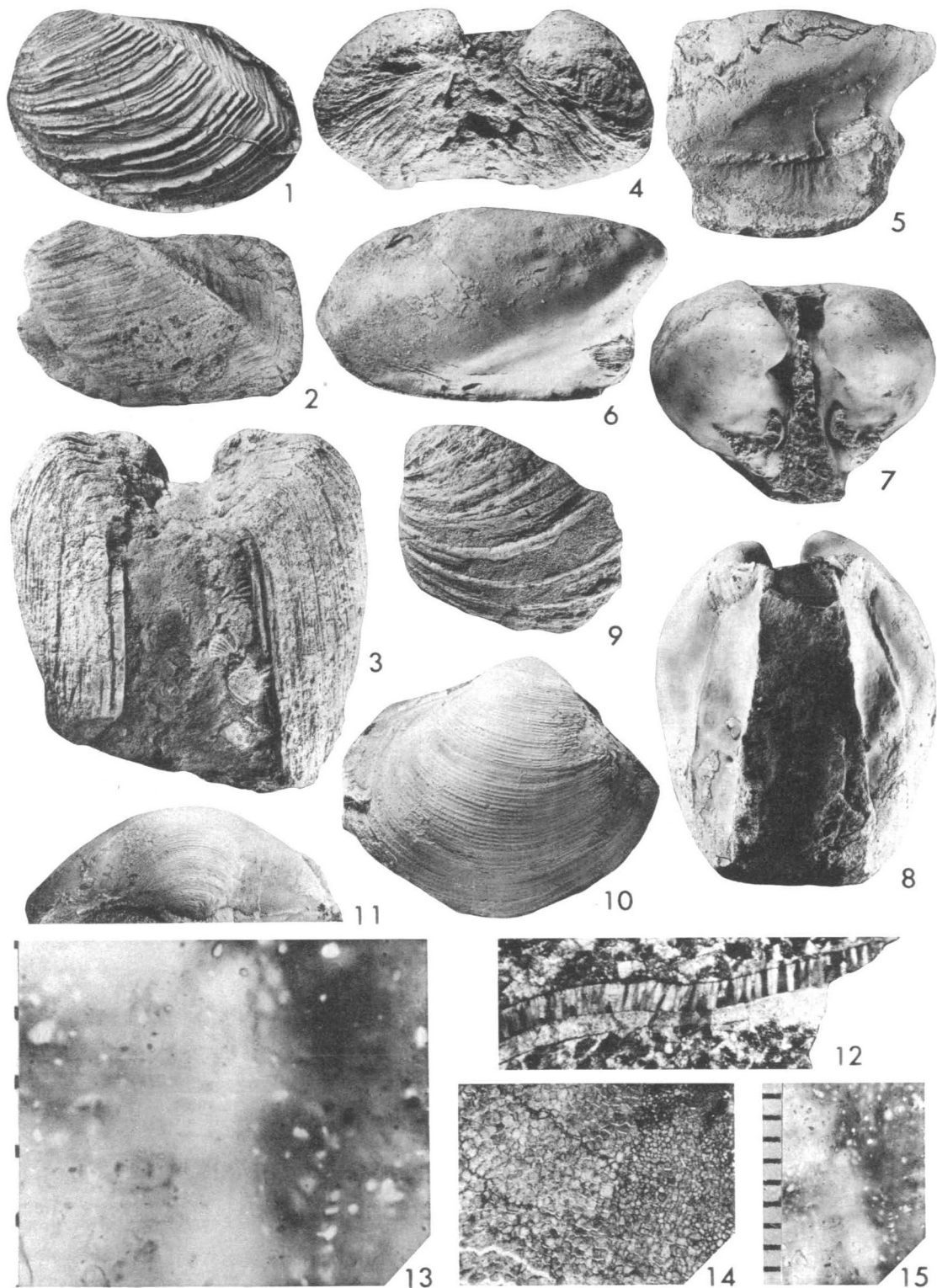
- Figs 1-11—*Myonia morrisoni* Etheridge Jnr, 1919 ..... Page 53
- Figs 1-2—CPC 7504, upper part of Lower Bowen Volcanics, 2½ miles west of Collaroy homestead, about ¼ mile west of the Connors River (BMR loc. SL 199), x½.
- 1—Internal mould of left valve showing strong carina and ventral spine.
- 2—Dorsal view of same specimen.
- Figs 3-7—UQ F21224, Homevale beds, Homevale homestead, north-west of Nebo, central Qld.
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- 4—Anterior view of internal mould to show pedal musculature (see also Pl. 12, fig. 4), x½.
- 5—Same view, x½.
- 6—Latex cast of external mould, x½.
- 7—Dorsal view of latex cast showing ligament grooves, lunule and escutcheon, and perforated beak of left valve, x½.
- Figs 8, 10—Holotype of *M. morrisoni*, AM F16978, Allandale Formation, Harper's Hill, Hunter Valley, N.S.W., x½. (Photographs by courtesy of the Australian Museum, Sydney).
- 8—Posterior-lateral view of internal mould.
- 10—Internal mould of right valve.
- Fig. 9—Internal mould of beak of right valve showing mould of small septum in front of umbonal retractor scar, UQ F20917, same loc. as Fig. 3, x1.
- Fig. 11—Latex cast of external mould of right valve; UQ F49080, Kansas Creek Beds, Western Creek, Quamby 1 mile series 872N; 446.5E., northern Tasmania, x1.
- Figs 12-15, 18-19—*Myonia elongata* Dana, 1847 ..... Page 48
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- 12—Lateral view of right valve.
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- 15—Latex cast of hinge to show absence of teeth, x1.
- 18—Internal mould of right valve, x½.
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- Figs 16-17—*Myonia morrisoni* Etheridge Jnr, 1919 ..... Page 53
- Fig. 16—Internal mould of young topotype showing pronounced prolongation of posterior dorsal margin; AM F50560, x1.
- Fig. 17—Internal mould of slightly crushed left valve; UQ F47948, Allandale Formation east of Allandale railway station, Hunter Valley, N.S.W., x½.
- Fig. 20—*Myonia carinata* (Morris), 1845 ..... Page 50
- Internal mould of both valves showing pedal musculature, mantle muscle pits, and muscle scar *a*; AM F17752, Bundanoon, N.S.W., x½. (See also Pl. 12, figs 7, 14).





## PLATE 6

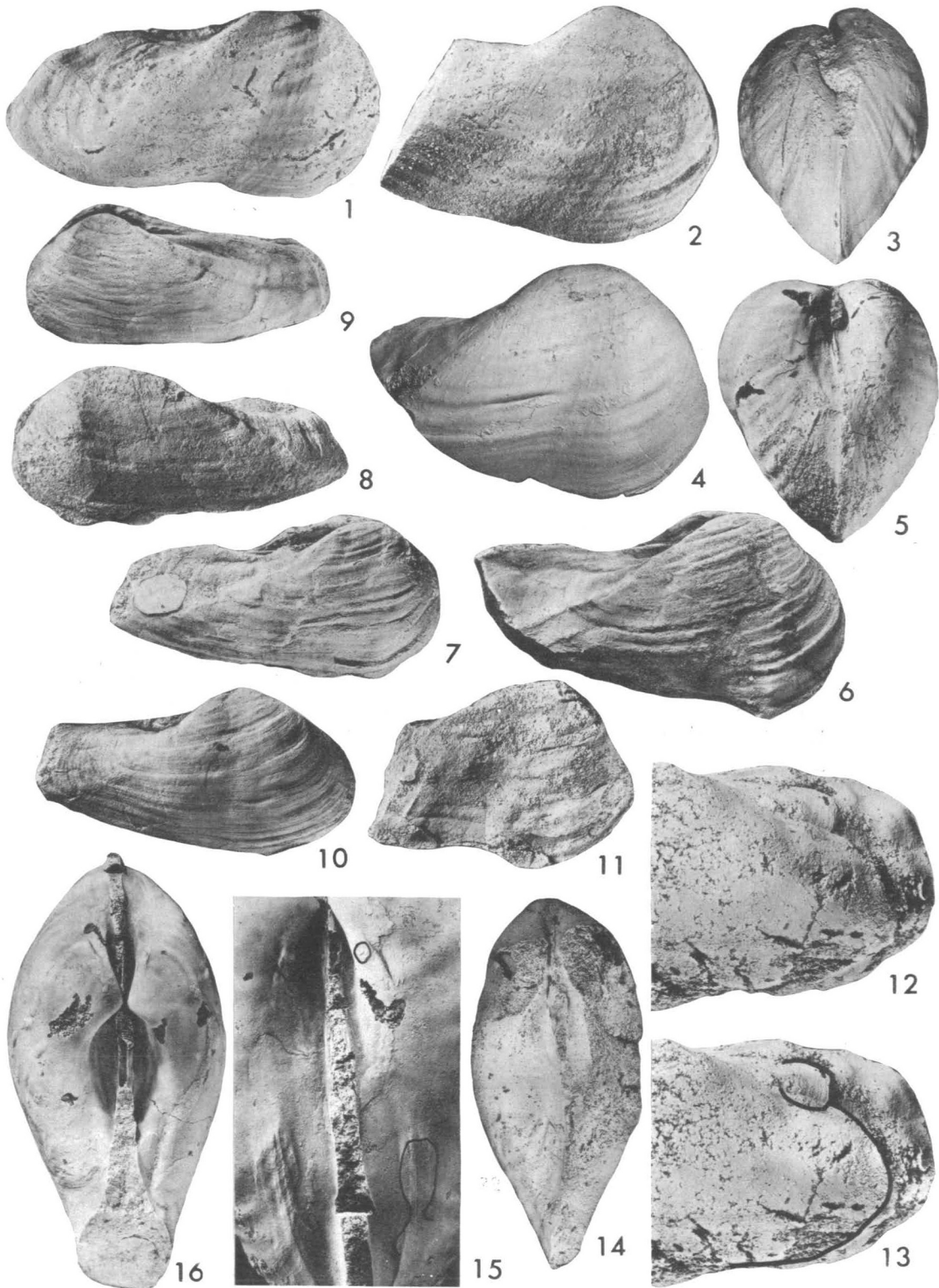
- Figs 1-9—*Myonia corrugata* Fletcher, 1932 ..... Page 56
- Fig. 1—Latex cast of external mould showing coarse imbricate ornament; CPC 7505, upper part of Middle Bowen Beds (Unit C), Clermont district, Qld (BMR loc. C1 42/6),  $\times\frac{1}{2}$ .
- Fig. 2—Plaster replica of internal mould of left valve (UT 86693a); UQ F49582, Member E, Malbina Formation, Kangaroo Bay, Cygnet Peninsula, southern Tasmania,  $\times\frac{1}{2}$ .
- Figs 3-4—CPC 7506, upper part of Middle Bowen Beds (Unit C), Clermont area, Qld (BMR loc. C1 255/1),  $\times\frac{1}{3}$ .
- 3—Ventral view of shell showing thickened anterior margin and large lunule. Compare with Fig. 8.
- 4—Anterior view of same specimen. Compare with Fig. 7.
- Fig. 5—Internal mould of anterior part of right valve. Note deep adductor scar and well developed muscle scar *a*; CPC 7507, upper part of Middle Bowen Beds (Unit C), Clermont area, Qld (BMR loc. C1 12/1),  $\times\frac{1}{2}$ .
- Figs 6-8—GSQ F9584, upper part of Middle Bowen Beds (Unit C)?, 'Bowen River Coalfield', Qld,  $\times\frac{1}{3}$ .
- 6—Lateral view of internal mould showing deep anterior adductor scar.
- 7—Anterior view to show pedal musculature.
- 8—Ventral view.
- Fig. 9—Abraded fragment of thickened anterior part of valve as commonly found in the field. CPC 7508, upper part of Middle Bowen Beds (Unit C), Clermont district, Qld (BMR loc. C1 132/B),  $\times\frac{1}{2}$ .
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- Lateral and dorsal views of plastic replica of the lectotype, BM(NH) PL3689, located as 'Spring Hill west', Tasmania;  $\times 1$ .
- Figs 12-15—*Megadesmus (Megadesmus) nobilissimus* (de Koninck), 1876 Page 20
- Figs 12-14—UQ F50277, base of unnamed limestone, 'Middle Gympie Formation', Chatsworth, 5 miles north of Gympie, Qld;  $\times 10$ .
- 12—Thin section photographed in polarized light of shell showing prismatic outer layer and nacreous inner layer.
- 14—Tangential section of prismatic layer of same specimen.
- Figs 13, 15—Two views at different magnifications ( $\times 250$  and  $\times 1000$ ) of inner shell layer. Black lines at left hand side of photographs are  $10\ \mu$  apart. Note layers 2-4  $\mu$  apart in lower parts of photographs: UQ F45395, same loc. as Fig. 12. (Photographs by courtesy of Mr T. R. Haskell, University of Queensland).





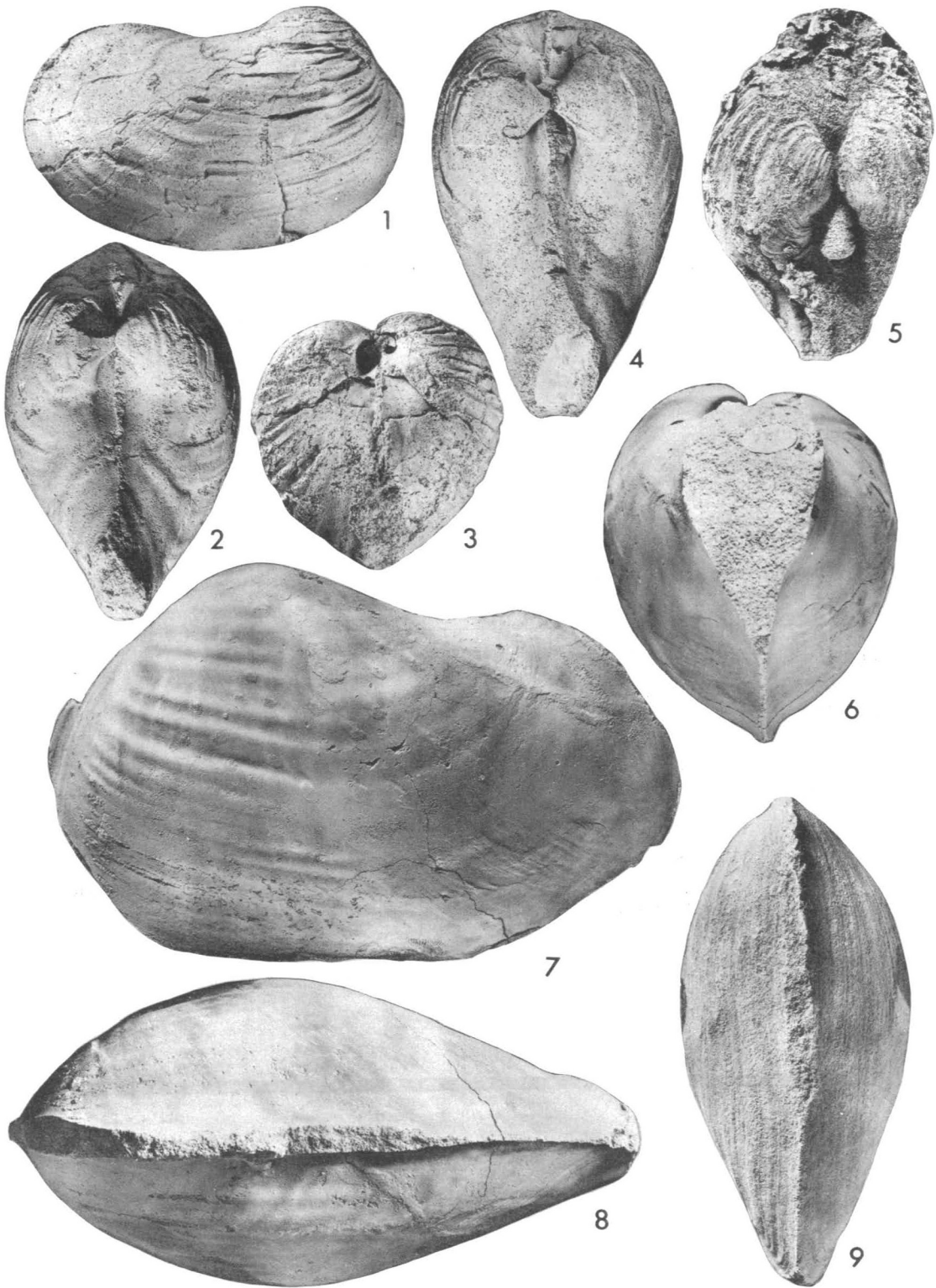
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- Figs 1-6, 10-14—*Myonia? sulcata* sp. nov. .... Page 59
- Figs 1, 14—Holotype; lateral and dorsal views of internal mould; CPC 7509, upper part of Lower Bowen Volcanics,  $\frac{3}{4}$  mile north-west of Turrawalla-Eungella road crossing of Hazelwood Creek, Mt Coolon area, Qld (BMR loc. MC 479),  $\times\frac{1}{2}$ .
- Fig. 2—Lateral view of internal mould; UQ F21155a, Homevale Beds, Homevale homestead, north-west of Nebo, Qld,  $\times\frac{1}{2}$ .
- Figs 3-4—Anterior and lateral views of internal mould; CPC 7510, same loc. as Fig. 1,  $\times\frac{1}{2}$ .
- Fig. 5—Anterior view of internal mould showing umbonal retractor scar; CPC 7511, same loc. as Fig. 1,  $\times\frac{1}{2}$ .
- Fig. 6—Plaster cast of right valve (see also Dun, 1932, pl. 52, fig. 2); AM F31084, Allandale Formation, Harper's Hill, Hunter Valley, N.S.W.,  $\times 1$ .
- Fig. 10—Internal mould of right valve; AM F49860, same loc. as Fig. 6,  $\times\frac{1}{2}$ .
- Fig. 11—Internal mould of right valve; UQ F48558, 'Eurydesma beds', 1700' at 150° from Rokeby homestead, 10 miles south of Warwick, Qld,  $\times 1$ .
- Figs 12-13—Identical views of posterior part of left valve of internal mould to show rear part of pallial line; CPC 7512, same loc. as Fig. 1,  $\times 1$ .
- Figs 7-9—*Myonia parallela* Dun, 1932 .... Page 61
- Figs 7-8—AM F44044, same loc. as Fig. 6,  $\times\frac{1}{2}$ .
- 7—Internal mould of right valve for comparison with Fig. 6.  
Note the absence of a well developed carina.
- 8—Left valve of same specimen showing well developed carina.  
Compare with Fig. 9 from same loc.
- Fig. 9—Plaster cast of left valve of lectotype of *M. parallela* (see also Dun, 1932, pl. 52, fig. 1), same loc. as Fig. 6,  $\times\frac{1}{2}$ .
- Figs 15-16—*Vacunella curvata* (Morris), 1845 .... Page 63
- AM F8136; Gerrington Volcanics, Wollongong, N.S.W.
- 15—Anterior part of internal mould to show pedal musculature (see also Pl. 12, fig. 9),  $\times 1$ .
- 16—Dorsal view of internal mould,  $\times\frac{1}{2}$ .
- Figs 3, 4, 14 from negatives kindly supplied by Dr J. M. Dickins, Bureau of Mineral Resources.



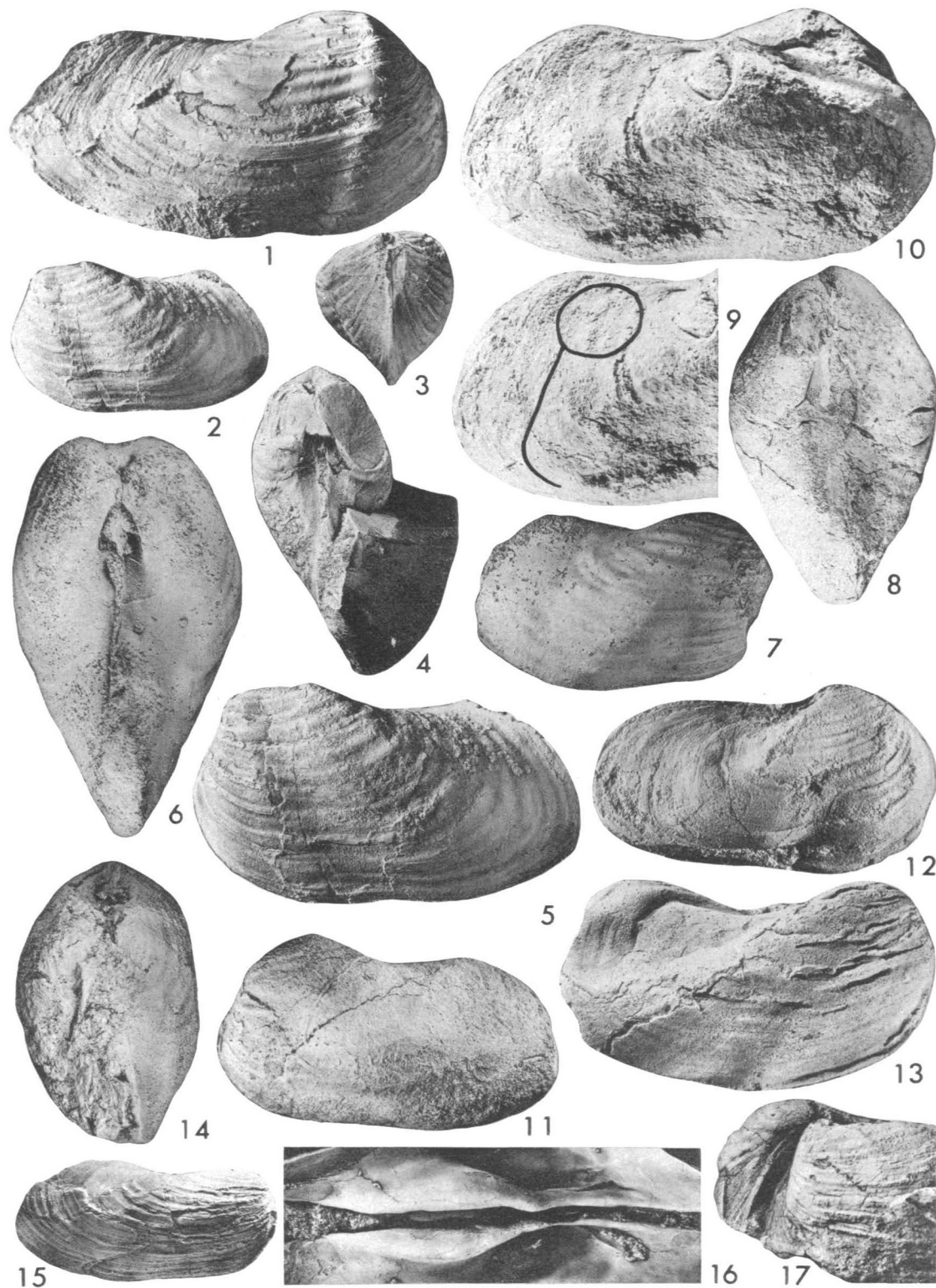
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- Figs 1-9—*Vacunella curvata* (Morris), 1845 .... Page 63
- Figs 1-2—CPC 7513, upper part of Middle Bowen Beds, Clermont area, Qld (BMR loc. C1 12/1), x1.  
 1—Lateral view of internal mould.  
 2—Dorsal view showing small siphonal gape.
- Figs 3-4—CPC 7514, same loc. as Fig. 1, x1.  
 3—Anterior view of internal mould.  
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- Fig. 5—Latex cast of external mould showing short external ligament; CPC 7357, upper part of Middle Bowen Beds (Unit C), Clermont area, Qld (BMR loc. C1 25/1), x1.
- Figs 6-8—AM F8136, Gerringong Volcanics, Wollongong, N.S.W., x $\frac{1}{2}$ .  
 (See also Pl. 7, figs 15-16, Pl. 9, fig. 16, and Pl. 12, figs 9-10).  
 6—Posterior view of internal mould showing well developed siphonal gape.  
 7—Left valve showing deep pallial sinus, accessory ventral adductor scar, and mantle muscle pits.  
 8—Ventral view showing long pedal gape.
- Fig. 9—Ventral view of internal mould to show long pedal gape; AM F51561, Gerringong Volcanics, near Berry, N.S.W., x $\frac{1}{2}$ .
- Figs 1-4 from negatives kindly supplied by Dr J. M. Dickins, Bureau of Mineral Resources, Canberra.



# PLATE 9

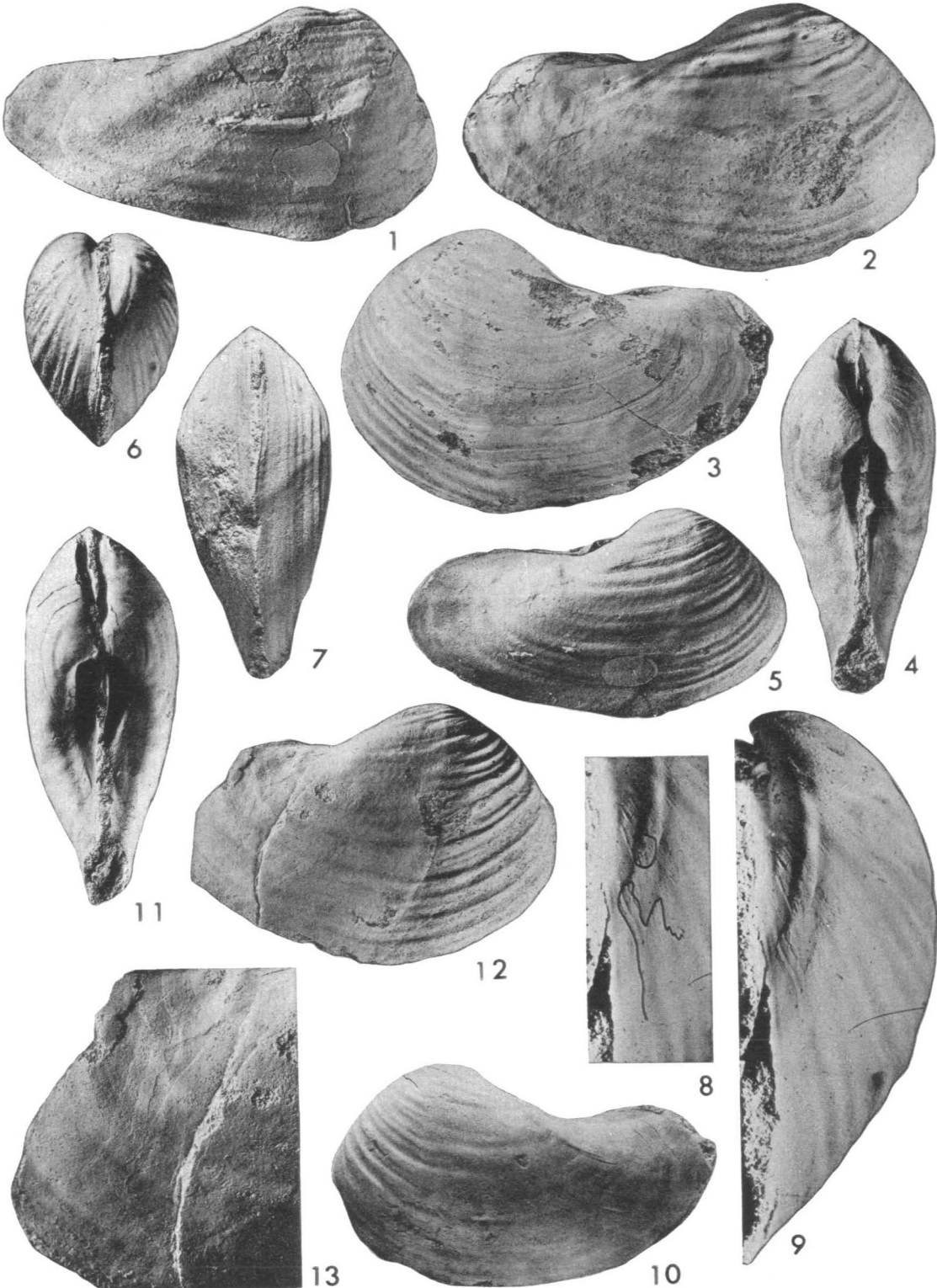
- Figs 1-12, 14—*Vacunella etheridgei* (de Koninck), 1876 .... Page 67
- Fig. 1—Partly decorticated right valve showing mantle muscle pits; CPC 7515, Ingelara Formation, Eddystone 1:250,000 Sheet area in Dry Creek, 5 miles at 263° from Ingelara homestead (BMR loc. Z 66),  $\times\frac{1}{2}$ .
- Figs 2-5—GSQ F1558, middle part of Middle Bowen Beds (Unit B), Stoodleigh Creek, 12 miles north-west of Marlborough, Qld.
- 2-4—Lateral, anterior, and dorsal views of internal mould,  $\times\frac{1}{2}$ .
- 5—Lateral view of internal mould,  $\times\frac{1}{2}$ .
- Figs 6-7—CPC 7516, middle part of Middle Bowen Beds (Unit B1), Lat. 21° 28'00"S.; Long. 148°31'15"E. (BMR loc. M 415).
- 6—Dorsal view of internal mould,  $\times 1$ .
- 7—Lateral view of same specimen,  $\times\frac{1}{2}$ .
- Figs 8-11—CPC 7517, same loc. as Fig. 6.
- 8—Dorsal view of internal mould,  $\times\frac{1}{2}$ .
- 9-10—Identical prints of right valve to show extremely shallow pallial sinus,  $\times 1$ .
- 11—Lateral view of left valve,  $\times\frac{1}{2}$ .
- Fig. 12—Internal mould of right valve, UQ F5631, located as 'Permo-Carboniferous, N.S.W.',  $\times\frac{1}{2}$ .
- Fig. 14—Dorsal view of internal mould; CPC 7518, same loc. as Fig. 6,  $\times\frac{1}{2}$ .
- Fig. 13—*Vacunella etheridgei*? (de Koninck), 1876  
Internal mould of right valve; UQ F924, Branxton Subgroup?, Cessnock, Hunter Valley, N.S.W.,  $\times\frac{1}{2}$ .
- Figs 15-17—*Vacunella curvata* (Morris), 1845 .... Page 63
- Fig. 15—Internal mould to show shape of dorsoventrally crushed specimen; UQ F47945, Mulbring Formation, beneath railway bridge over Hunter River, Singleton, N.S.W.,  $\times\frac{1}{2}$ .
- Fig. 16—Latex cast of hinge of AM F8136 (see also Pl. 7, figs 15-16; Pl. 8, figs 6-8) showing weakly developed teeth,  $\times\frac{1}{2}$ .
- Fig. 17—Oblique view of front of shell to show narrow groove in front of right valve which may receive edge of left valve; AM F21916, Conjola Formation, Schnapper Point, Kioloa, N.S.W.,  $\times 1$ .
- Figs 6-8, 11, 14 from negatives kindly supplied by Dr J. M. Dickins, Bureau of Mineral Resources, Canberra.



# PLATE 10

- Fig. 1—*Vacunella? waterhousei* (Dun), 1932 ..... Page 69  
Lectotype; internal mould of right valve showing pallial line and adductor muscle scars; AM F6589, Farley Formation, Farley, Hunter Valley, N.S.W., x1.
- Figs 2-13—*Vacunella cf. waterhousei* (Dun), 1932 ..... Page 70
- Fig. 2—Internal mould of right valve; AM F51048, Ravensfield Sandstone Member, Farley Formation, Brown's Quarry, Ravensfield, Hunter Valley, N.S.W., x $\frac{1}{2}$ .
- Fig. 3—Internal mould of left valve; AM F51058, same loc. as Fig. 2, x $\frac{1}{2}$ .
- Figs 4-5—AM F26265, same loc. as Fig. 1, x $\frac{1}{2}$ .
- 4—Dorsal view of internal mould showing siphonal gape.
- 5—Lateral view showing elongated mantle muscle pits.
- Figs 6-9—AM F30021; Farley Formation?, Maitland, N.S.W.
- 6—Anterior view of internal mould, x $\frac{1}{2}$ .
- 7—Ventral view showing probable pedal gape, x $\frac{1}{2}$ .
- 8-9—Identical photographs of the anterior part of the left valve to show the protractor and anterior retractor scars (see also Pl. 12, fig. 1), x2.
- Figs 10-11—AM F51056, same loc. as Fig. 2, x $\frac{1}{2}$ .
- 10—Lateral view of internal mould showing elongated mantle muscle scars.
- 11—Dorsal view showing escutcheon and lunule.
- Figs 12-13—AM F51057, same loc. as Fig. 2.
- 12—Internal mould of right valve, x $\frac{1}{2}$ .
- 13—Enlargement of posterior part of mould to show small pallial sinus and muscle scar *b* below the posterior adductor scar, x1 $\frac{1}{2}$ .

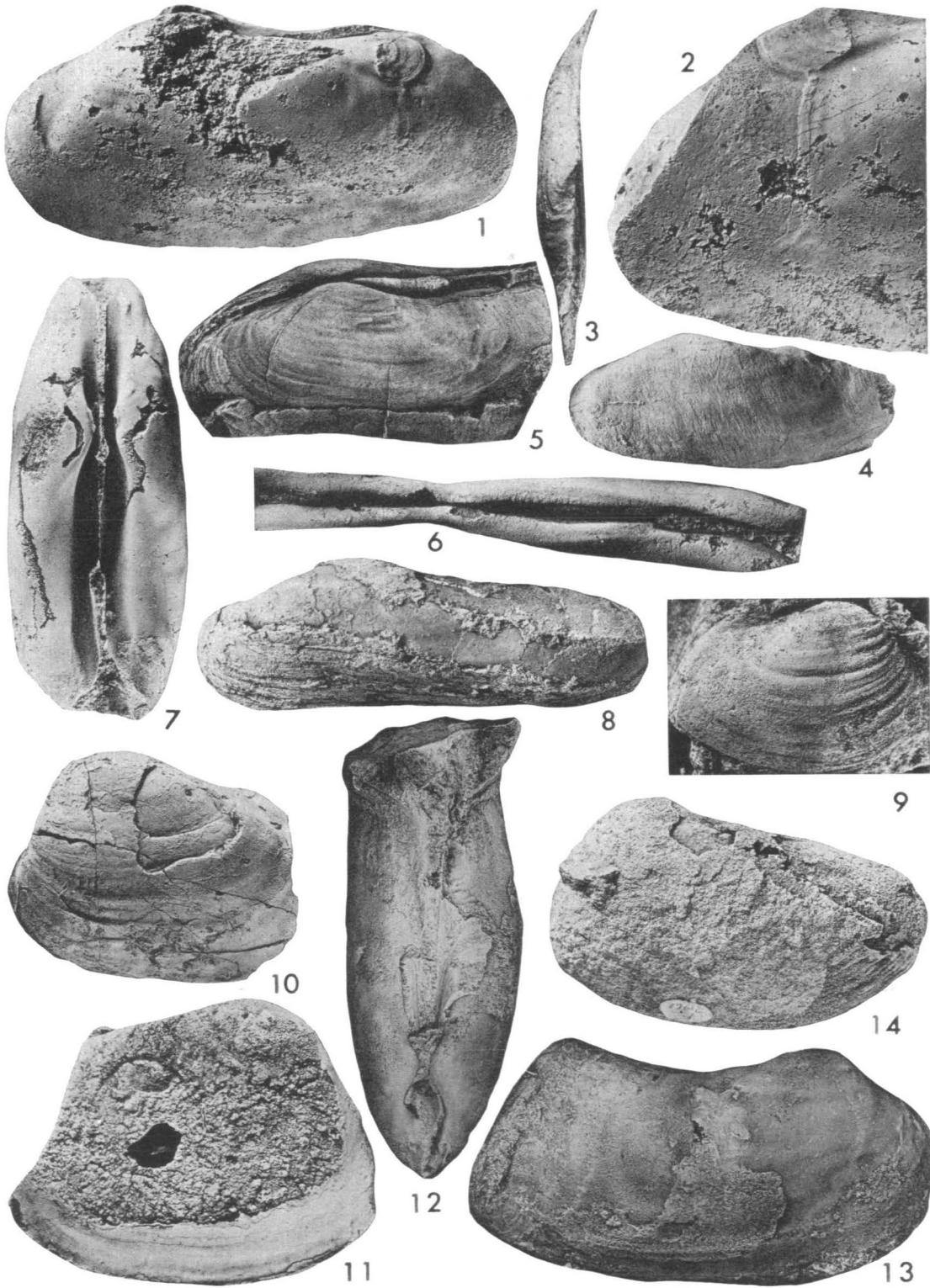






# PLATE 11

- Figs 1-8—*Vacunella? dawsone* sp. nov. .... Page 73
- Figs 1-2—QM F1814, Barfield or Flat Top Formations, Castle Creek, Dawson Valley, Qld.
- 1—Internal mould of left valve, x1.
- 2—Posterior part of right valve to show shallow pallial sinus, x1½.
- Figs 3-4—CPC 7519, upper Barfield or lower Flat Top Formation, 5 miles east of Baralaba, Dawson Valley (BMR loc. Ba 321), x½.
- 3—Internal mould of left valve.
- 4—Dorsal view of latex cast of hinge showing ligament groove and well developed escutcheon.
- Fig. 5—Holotype; latex cast of external mould to show external shape and ligament; CPC 7358, upper part of Barfield Formation, 5 miles east of Baralaba (BMR loc. Ba 814), x1.
- Figs 6-7—GSQ F9439, Barfield or Flat Top Formation, Cracow station, Dawson Valley.
- 6—Latex cast of hinge viewed from interior of shell showing absence of teeth. Note ligament nymphs and slight thickening of inner edge of nymph reminiscent of inner hinge plate of *Edmondia*, x1½.
- 7—Internal mould showing anterior and umbonal pedal musculature, x1.
- Fig. 8—Partly decorticated left valve, CPC 7520, Flat Top Formation, Lonesome Creek Road, 7.6 miles from Theodore Post Office, Dawson Valley, x½.
- Figs 9-11—*Vacunella* sp. nov. A .... Page 72
- Fig. 9—Internal mould of right valve, CPC 7521, upper part of Lower Bowen Volcanics, ¾ mile north of Lizzie Creek Road crossing of Hazelwood Creek, Mt Coolon area (BMR loc. MC 479), x1.
- Fig. 10—Internal mould of left valve, CPC 7522, lower part of Middle Bowen Beds (Unit A), Lat. 20°55'45"S.; Long. 148°08'30"E. (BMR loc. B 686), x½.
- Fig. 11—Internal mould of right valve, CPC 7523, same loc. as Fig. 10, x½.
- Figs 12-13—*Chaenomya leavenworthensis* Meek & Hayden, 1858 .... Page 63
- Dorsal and lateral views of USNM 1019a, showing large siphonal gape, shallow pallial sinus, and anterior pedal musculature, x1. (Photographs by courtesy of Dr J. B. Waterhouse, New Zealand Geological Survey).
- Fig. 14—*Vacunella curvata?* (Morris), 1845 .... Page 63
- Lateral view of left valve; AM F21961, Conjola Formation, Schnapper Point, Kioloa, N.S.W., x½.



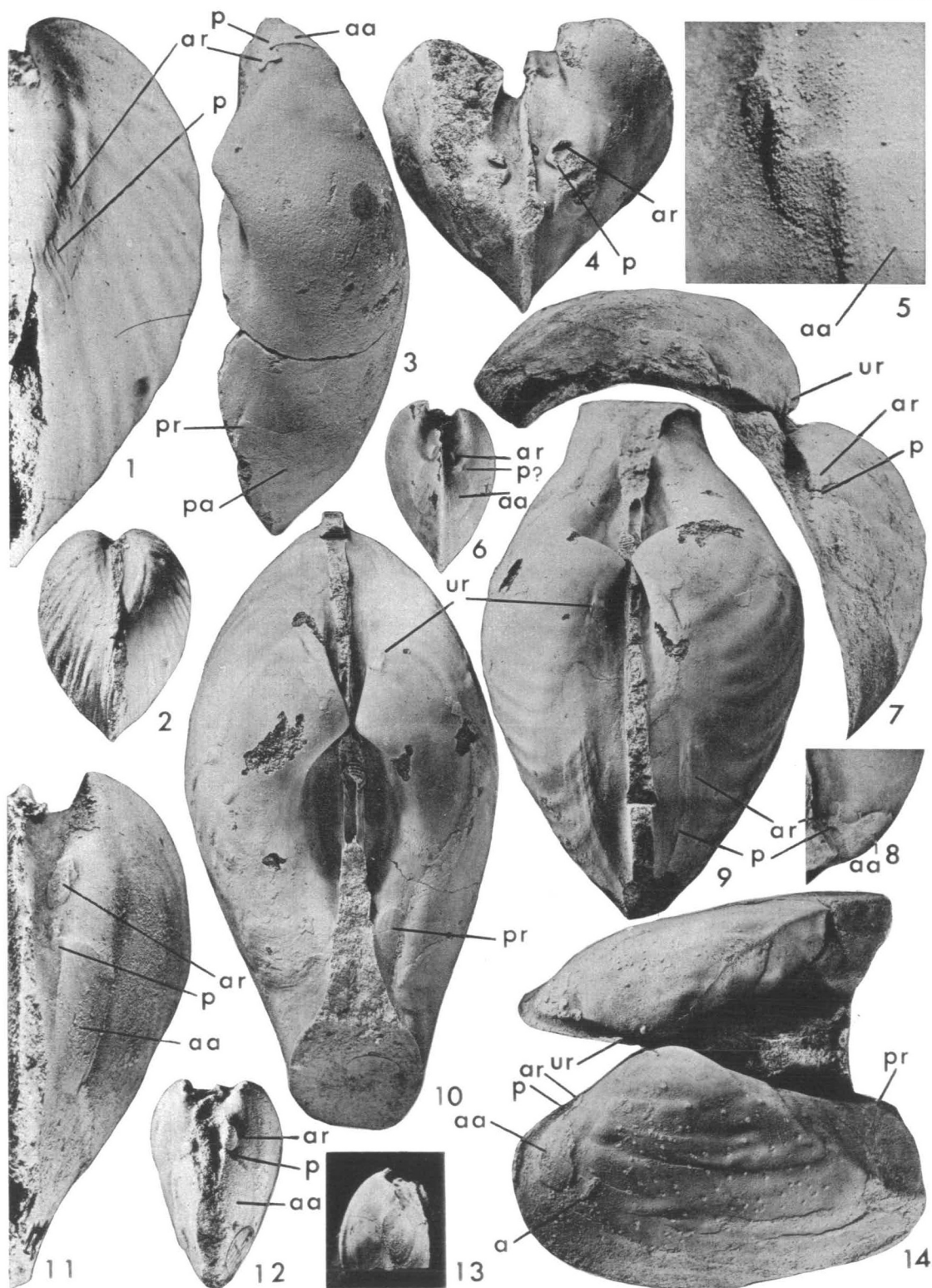
# PLATE 12

Well preserved specimens labelled to show the pedal and other musculature of the Australian Permian pholadomyid bivalves.

*aa*, anterior adductor  
*a*, Muscle scar a  
*ar*, anterior retractor

*p*, protractor  
*pa*, posterior adductor  
*pr*, posterior retractor  
*ur*, umbonal retractor

- Figs 1-2—*Vacunella* cf. *waterhousei* (Dun), 1932.  
 1—Anterior part of left valve, x2.  
 2—Anterior view of same specimen, x $\frac{3}{4}$ .  
 Fig. 3—*Megadesmus* (*Cleobis*) *grandis* Dana, 1847, x $\frac{3}{4}$ .  
 Fig. 4—*Myonia morrisoni* Etheridge Jnr, 1919, x $\frac{3}{4}$ .  
 Figs 5, 11—*Pyramus laevis* (Sowerby), 1838.  
 5—Enlargement of protractor scar, x10.  
 11—Anterior view of internal mould of same specimen, x2.  
 Fig. 6—*Astartila intrepida* Dana, 1847, x1.  
 Figs 7, 14—*Myonia carinata* (Morris), 1845. 7, x1; 14, x $\frac{3}{4}$ .  
 Fig. 8—*Megadesmus* (*Megadesmus*) *gryphoides* (de Koninck), 1876, x1.  
 Figs 9-10—*Vacunella curvata* (Morris), 1845, x $\frac{3}{4}$ .  
 Fig. 12—*Pyramus myiformis* Dana, 1847, x1.  
 Fig. 13—*Pyramus laevis* (Sowerby), 1838.  
 Anterior view of umbonal region of internal mould showing prominent umbonal retractor scar, x $\frac{3}{4}$ .



# PLATE 13

- Figs 1-4—*Vacunella? dawsonensis* sp. nov. .... Page 73  
 Figs 1-3—Holotype; anterior, lateral, and dorsal views of internal mould, UQ F51000, Flat Top Formation, Theodore-Banana Road, Dawson Valley, Qld, x1.  
 Fig. 4—Dorsal view of anterior part of internal mould showing protractor and anterior retractor scars; UQ F51001, same loc. as Fig. 1, x1.
- Figs 5-13—*Myonia carinella* sp. nov. .... Page 58  
 Figs 5-6—Dorsal views of internal mould (5) and latex cast of external mould (6), x $\frac{1}{2}$ ; CPC 7501, middle part of Middle Bowen Beds (Unit B<sub>3</sub>), Lat. 21°27'45"S., Long. 148°30'00"E., BMR loc. M 416).  
 Fig. 7—Lateral view of internal mould, x $\frac{1}{2}$ ; UQ F50997, immediately below Big *Strophalosia* Zone, west of Parrot Creek, west of Havilah homestead, Bowen 1:250,000 sheet area.  
 Figs 8-10—Holotype; anterior, lateral, and dorsal views, x $\frac{1}{2}$ ; same loc. as Fig. 7.  
 Fig. 11—Dorsal view of internal mould showing pedal musculature, x1; UQ F50998, same loc. as fig. 7.  
 Fig. 12—Internal mould of left valve, x $\frac{1}{2}$ ; UQ F29574, Muree Formation or Branxton Subgroup, Mulbring, Hunter Valley, N.S.W.  
 Fig. 13—Internal mould of posterior part of left valve showing posterior adductor and muscle scar *b*, x $\frac{1}{2}$ ; UQ F50999, same loc. as fig. 7.
- Fig. 14—*Myonia tayoensis* (Reed), 1930 .... Page 32  
 Latex cast of right valve showing muscle scars *a* and *b*, x1 $\frac{1}{2}$ ; University of São Paulo, D.G.M. 246A, Rio Bonito Formation, Taió, Santa Catarina, Brazil. (Cast by courtesy of Dr A. C. Rocha-Campos, University of São Paulo).

