

Primitive Desmodont Pelecypods of the Australian Permian

BY NORMAN D. NEWELL

Many generic names have been introduced for a homogeneous group of "Carboniferous" marine pelecypods of New South Wales, Australia, which generally are considered endemic to the Gondwana province. The associated fossil faunas indicate that they belong to the Artinskian stage of the Permian (Teichert and Fletcher, 1943; Teichert, 1954). Association of beds of tillite with the marine faunas and the character of the faunas themselves have led to a rather general conclusion that they inhabited cool or cold waters (Teichert, 1950).

Many of the pelecypods belong to a group that are now burrowers in near-shore sandy bottoms. These fossils most commonly are preserved either as calcareous shells in sandy limestones or as hollow molds in sandstone concretions. In almost every case the valves are closed, having been undisturbed by current action after death. Although field data are not available, it may be assumed that many of the fossils in the rocks occupy the normal attitude of the animals as they lived a few inches below the sand bottom.

Suitable casting substances, such as liquid latex, were unavailable to the early workers, so that critical characters of the hinge hardly ever were made clearly known. Also, it seems that variations in size and form due to growth were not evaluated. In spite of the fact that the majority of species described in the early days came from a very few localities, notably Harper's Hill (Lower Marine horizon), Wollongong, and Black Head (Upper Marine horizon) in New South Wales, there has been a steady multiplication of closely similar "species" based on unique specimens. Small lots in which variations possibly are attributable to growth and preservation, or to normal population variability, are not readily assessed. Modern taxonomists are prone to stress similarities among associated specimens rather than to concentrate on their differences, because mutual association in the rocks of closely similar fossils is important *a priori* indication of possible relationship. Indiscriminate multiplication of names for unevaluated specimens is, of course, equally disadvantageous to the student of ancient life and to the stratigrapher.

Evaluation of the very many specific names that have been used for these Australian fossils is quite beyond the scope of the present study and can be undertaken only by someone who has an opportunity to collect his own specimens. The purpose of this contribution is to attempt evaluation of poorly understood pelecypod genera of desmodont affinities and to undertake a practical resolution of some of the confusion that surrounds their nomenclature. In this task I have found aid in the important studies of Fletcher (1929, 1932) who has summarized the long history of work on this subject.

The shells under consideration are somewhat unlike living pelecypods, and for this reason a new family is proposed here for their reception. They are probably related to *Panope* and *Panomya*, referred by malacologists to Myacea or Saxicavacea, and this general relationship long has been recognized (Dana, 1849; Stoliczka, 1871; and Fletcher, 1932).

Generic names that have been proposed for the Australian fossils in question are as follows:

Megadesmus Sowerby, 1838 Pachydomus Morris, 1845 Myonia Dana, 1847 Pyramus Dana, 1847 Cleobis Dana, 1847 Astartila Dana, 1847 Notomya M'Coy, 1847 Maeonia Dana, 1849 Pyramia Dana, 1849 Clarkia DeKoninck, 1877 Pachyonyonia Dun, 1932

The following taxonomic summary indicates the general conclusions of this study:

Pachydomidae Newell, new family Pachydomus Morris (syn., Astartila Dana) Myonia Dana (syn., Maeonia Dana, Pachymyonia Dun) Pyramus Dana (syn., Notomya M'Coy, Pyramia Dana, Clarkia DeKoninck) Cleobis Dana The collections available to me included many of Dana's types at the United States National Museum, M'Coy's types at the Sedgwick Museum, Cambridge University, and supplementary specimens at the British Museum (Natural History), Yale Peabody Museum, and the Australian Museum. To the curators at these institutions I express my appreciation and thanks for the opportunity to study these fossils.

ORDER DESMODONTIDA NEUMAYR, 1883 PACHYDOMIDAE NEWELL, NEW FAMILY

Lenticular to gibbous pelecypods, concentrically ornamented, nearly smooth or rugose, without lunule or escutcheon, beaks orthogyrous, margin with or without slight posterior gape, ligament opisthodetic and parivincular, supported by very heavy nymphs; adductors nearly equal, two pedal retractors between anterior adductor and center of umbonal cavity; dentition feeble, becoming obsolescent in large individuals, consisting of a single cardinal tooth on each valve below the beaks, that of the left valve lying ahead of that of the right, lateral teeth lacking; pallial line commonly radially striate, entire, or with very shallow sinus. From the Permian of India, Australia, and Tasmania.

DISCUSSION: From living hiatellids and panopeids these forms differ in being less specialized for the burrowing habit. The Permian shells lack the pedal gape, and in some genera (*Pachydomus* and *Myonia*) the syphonal gape characteristic of the nearest modern forms appears to be completely lacking. Furthermore, with the exception of a very shallow pallial sinus in *Pyramus*, the Permian shells are integripalliate.

Throughout the early work on bivalve mollusks it was believed that the possession or lack of a pallial sinus was sufficient to distinguish higher categories such as superfamilies and orders. It has become clear, however, that desmodonts with very short siphons (e.g., *Cryptomya*) may lack the sinus, and it is to be expected that primitive desmodonts may be variable in this respect. In such forms as these Permian genera, the presence or absence of the sinus is of lower taxonomic significance than among more specialized burrowers with long siphons.

Important points of resemblance between the Permian genera and certain living forms such as *Panope* and *Panomya* are found in the general form and ornamentation, and, particularly, in the nature of the hinge. The cardinal teeth tend to become separated and non-functional late in ontogeny in some of the genera because of the rapid expansion of the ligament nymphs. The latter serve as rollers around which the two valves slide and twist during burrowing, and hinge motion is no

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longer limited to a fixed axis. This dentition cannot be confused with dentitions of other groups of pelecypods. Its occurrence as far back as the late Paleozoic suggests that these forms are in fact quite unrelated to the heterodonts, with which they are sometimes classed.

GENUS PACHYDOMUS MORRIS, 1845

Figures 1, 2A–C, 3B–H

GENOTYPE: Megadesmus cuneatus Sowerby, 1839, designated subsequently by Stoliczka (1871).

Pachydomus was introduced as a replacement for the preoccupied Megadesmus Sowerby, 1939 (not Megadesma Bowdich, 1822). Subjective synonym: Astartila Dana, 1847 (genotype A. intrepida Dana, designated by Stoliczka, 1871).

DIAGNOSIS: Ovid, strongly gibbous, rugose shells, with prominent umbones, without gape, without umbonal carina, height about three-fourths of the length; adductors approximately equal, subquadrate, pallial line entire, posterior pedal retractor situated in deepest part of umbonal pit, teeth prominent, functional in mature shells. Permian (Lower and Upper Marine), New South Wales, Tasmania, India.

DISCUSSION: Morris (1845) called attention to the fact that *Mega*desmus Sowerby, which was introduced in 1839 at the very beginning of paleontological exploration in Australia, was preoccupied by *Megadesma* Bowdich, 1822, and he proposed *Pachydomus* as a replacement, the genotype, of course, remaining the same as for *Megadesmus* Sowerby. Thus *Pachydomus* Morris, 1845, becomes the oldest of the names available for the shells here under consideration. Stoliczka (1871, p. 274) subsequently selected as the type *Megadesmus cuneatus* Sowerby, 1839, from among the original species. Sowerby's illustration indicates a specimen (this paper, fig 1B) having a shallow sulcus behind the pedal area, but in other respects it is like the associated gibbous and rugose valves so characteristic of this genus.

Dana figured a well-preserved internal mold of this species (unfortunately now lost) showing the unmodified pallial line and the dentition characteristic of the Pachydomidae (this paper, fig. 2A, B; Dana, 1849, pl. 5, fig. 1A, B). Shells and internal molds of *Pachydomus cuneatus* are superficially similar to those of *Pyramus myiformis*, but the pallial sinus and the less inflated, thinner, and smoother shell of the latter readily distinguish it from *Pachydomus*.

Pachydomus usually has been regarded as distinct from Astartila by

most authors, excepting DeKoninck (1877), the supposed differences being smaller size and lack of hinge teeth in *Astartila* (see Fletcher, 1929). The two genera are virtually identical in form. However, carefully prepared latex casts from well-preserved internal molds invariably show hinge characters of *Astartila* exactly like those of *Pachydomus* and *Myonia*. Small size alone cannot be taken as a criterion of generic dif-

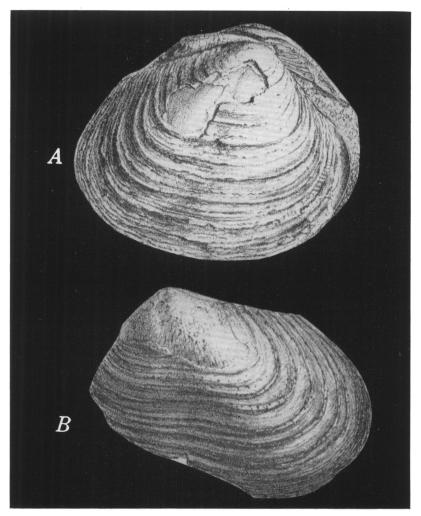


FIG. 1. Pachydomus cuneatus (Sowerby), Lower Marine horizon, probably at Harper's Hill. After Sowerby (1839). A. Holotype of P. antiquatus (=P. cuneatus). B. Holotype of P. cuneatus. \times 1.

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ference. *Pachydomus cuneatus* is a Lower Marine species collected originally at Harper's Hill. *Astartila intrepida*, on the other hand, from the Upper Marine horizon at Wollongong, is considerably younger.

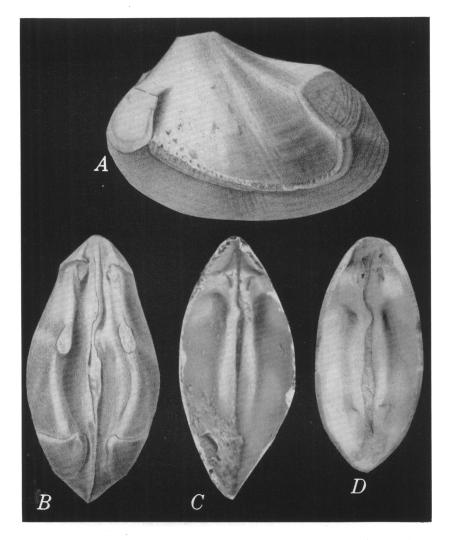


FIG. 2. Morphology of Pachydomidae. A, B. Internal mold of *Pachydomus* cuneatus, Lower Marine horizon, Harper's Hill. After Dana (1849). \times 1. C. Internal view of latex cast of syntype of *Astartila cyclas* Dana (=*Pachydomus intrepida*), U.S.N.M. No. 3592, Upper Marine at Wollongong. \times 2. D. Internal view of latex cast, holotype of *Notomya securiformis* M'Coy (=*Pachydomus cuneatus*), Sedgwick Mus. No. E10776, Upper Marine at Wollongong. \times 1.

GENUS MYONIA DANA, 1847

Figure 3A

GENOTYPE: Myonia elongata Dana, 1847 (=M. valida Dana, 1847) designated subsequently by Fletcher, 1932. Objective synonym: Maeonia Dana, 1849 (variant spelling of Myonia). Subjective synonym: Pachymyonia Dun, 1932 (genotype Maeonia morrisii Etheridge, 1919).

DIAGNOSIS: Shell lenticular, with small umbones, tapering backward as viewed from above and from the side, posterior extremity straight, forming obtuse angle with hinge line, obscure sulcus extending from beaks to middle of ventral margin, usually bounded behind by an umbonal. carina, margins not gaping; integripalliate, pallial line radially striate, posterior pedal retractor well forward of umbonal pit. Permian (Lower and Upper Marine), New South Wales.

DISCUSSION: In July, 1847, Dana published Myonia without designating a genotype from among the list of described species. His paper was not illustrated and his genera were unrecognizable until appearance of a second, illustrated, report two years later. In the latter publication the treatment was somewhat different. The spelling of Myonia was changed without comment to Maeonia. The listing of species shows that Dana was dealing with the same group covered in the earlier paper. Maeonia was not a substitution for a preoccupied homonym, and the revised spelling is invalid. The first unequivocal designation of a genolectotype for Myonia that I can find is that of Fletcher (1932) who cites M. elongata Dana.

Dun's Pachymyonia was based on Maeonia morrisii Etheridge (Dun, 1932). This genus was supposed to differ from Myonia in having somewhat thicker shells and it was thought to characterize a lower horizon (Lower Marine) than Myonia, which is especially characteristic of the higher part of the Permian sequence (Upper Marine series). It appears to me that these differences, if they can be documented, would distinguish species, or even ecotype populations, rather than genera. Examination of Dana's specimens of Myonia elongata, especially the originals of his plate 5, figure 4 (1849), shows that this species has a hinge like that of Pachydomus and Pyramus.

GENUS PYRAMUS DANA, JULY, 1847 Figures 2D, 4

GENOTYPE: Pyramus myiformis Dana, July, 1847 (=Notomya securiformis M'Coy, November, 1847, and Notomya clavata M'Coy, November, 1847; Maeonia axinia Dana, 1849), designated subsequently by

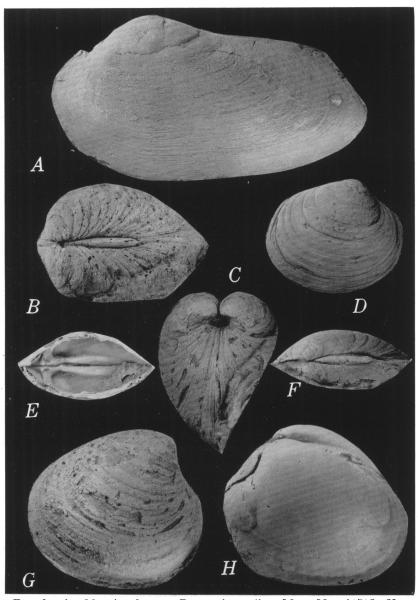


FIG. 3. A. Myonia elongata Dana, Australian Mus. No. 21715, Upper Marine, Gerringong. $\times \frac{1}{2}$. B-H. Pachydomus intrepidus (Dana), Upper Marine, Wollongong. $\times 1$. B, C, G. Latex cast of syntype of Astartila cytherea Dana, U.S.N.M. No. 3856. D, E, F. Latex cast of syntype of Astartila cyclas Dana, U.S.N.M. No. 3592. H. Syntype of A. cyprina Dana, U.S.N.M. No. 3588.

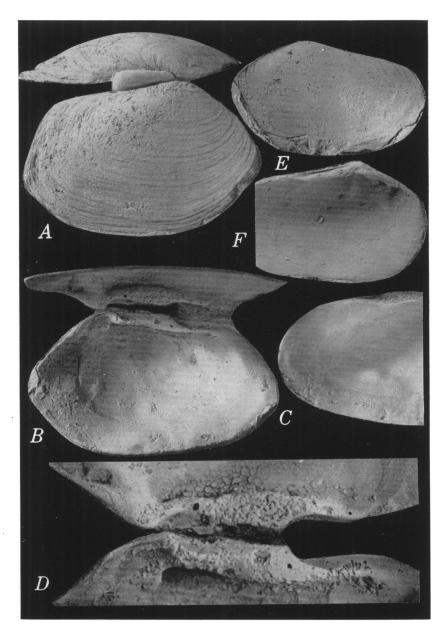


FIG. 4. Pyramus myiformis Dana, latex casts. A-D. U.S.N.M. No. 3585, Upper Marine, Blackhead. A-C. \times 1. D. \times 2. E, F. Lectotype, U.S.N.M. No. 3587, Upper Marine, Wollongong. \times 1.

Newell, herein. Objective synonyms: *Notomya* M'Coy, November, 1847; *Pyramia* Dana, 1849 (variant spelling of *Pyramus*); *Clarkia* DeKoninck, 1877.

DIAGNOSIS: Shell lenticular, with small umbones, elongate, tapering backward as viewed from above and from the side, posterior extremity straight, forming obtuse angle with hinge line, with slight siphonal gape; weakly sinu-palliate, pallial line not striate, posterior pedal retractor in pit of umbonal cavity, without well-defined umbonal carina. Permian (Upper Marine series), New South Wales.

DISCUSSION: Dana's revision of the spelling of *Pyramus* to *Pyramia* two years after the original publication was whimsical and without authority. In November, 1847, four months after the publication of *Pyramus*, M'Coy published *Notomya*. Stoliczka later (1871, p. xvi) designated *N. securiformis* M'Coy as lectotype of *Notomya*. This species is, in my view, the same as *P. myiformis* established earlier by Dana. A genotype has never been designated for *Pyramus*; consequently, I here designate *Pyramus myiformis* Dana as the genotype of *Pyramus*. The monotypical genus *Clarkia* DeKoninck, 1877, was also based on this species. Consequently, both *Notomya* and *Clarkia* are junior synonyms of *Pyramus*.

GENUS CLEOBIS DANA, 1847

Figure 5

GENOTYPE: Cleobis grandis Dana, July, 1847 (=Pachydomus gigas M'Coy, November, 1847), designated subsequently by Newell, herein.

DIAGNOSIS: Ovoid, strongly gibbous shells with prominent umbones, smooth, thin-shelled, attaining gigantic proportions for Paleozoic pelecypods (15–20 cm. long at maturity), gaping slightly behind; hinge teeth becoming obsolete in large shells, possibly integripalliate. Permian (Upper Marine), New South Wales.

DISCUSSION: The described examples of *Cleobis* and the specimens that I have seen are internal molds; consequently there is at least some uncertainty about the external surface of the shell. Strong surface ornamentation might have been impressed on the internal molds, depending on the amount of compaction of matrix after leaching of the shell material. Muscle impressions are hardly reflected on the molds, which suggests unusual thinness of the valves for shells so large. At size comparable to that of *Pachydomus* or *Astartila*, the shells of *Cleobis* might be indistinguishable from those genera in general form. This strongly suggests

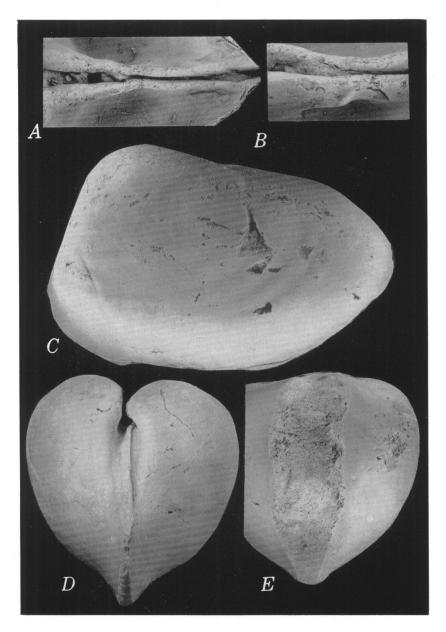


FIG. 5. Cleobis grandis Dana, U.S.N.M. No. 25639, Upper Marine, Illawara. A, B. Latex cast of interior of hinge, showing obsolete teeth, left valve below. A. $\times \frac{1}{2}$. B. $\times 1$. C-E. Internal mold. $\times \frac{1}{2}$.

the possibility that the characteristically small shells of Astartila may be immature representatives of Cleobis with which they are associated in the rocks. The museum specimens at hand do not shed much light on this possibility. Nevertheless, I am not at all sure that I could distinguish a juvenile of Cleobis from Pachydomus or Astartila. The hinge teeth of large examples of Cleobis become disarticulated as the hinge margins become enrolled during growth. The general expression of Cleobis suggests close relationship to Pachydomus rather than to Myonia or Pyramus.

The development of a slight siphonal gape suggests the burrowing habit. However, the marked ventricosity of the shell does not indicate marked specialization for this mode of life.

REFERENCES

BOWDICH, T. EDWARD

- 1822. Elements of conchology including the fossil genera and the animals, part 1. Univalves. Paris, J. Smith, vi + 74 pp., 19 pls.
- DANA, J. D.
 - 1847. Descriptions of fossil shells of the collections of the exploring expedition under the command of Charles Wilkes, U.S.N., obtained in Australia. Amer. Jour. Sci., ser. 2, vol. 4, pp. 151–160.
 - 1849. Geology. In United States exploring expedition during the years 1838–1842, under the command of C. Wilkes. New York, vol. 10, pp. 681–713.
- DEKONINCK, L. G.
 - 1877. Recherches sur les fossiles paléozoiques de la Nouvelle-Galles du Sud (Australie). Mém. Soc. Roy. Sci. Liége, ser. 2, vol. 6, 140 pp.
- DUN, W. S.
- 1932. The Lower Marine forms of *Myonia*, with notes on a proposed new genus, *Pachymyonia*. Rec. Australian Mus., vol. 18, pp. 411–414.
- Etheridge, Robert, Jr.
 - Occasional descriptions of New South Wales fossils. Rec. Australian Mus., vol. 12, pp. 183–192.
- FLETCHER, H. O.
 - 1929. Revision of genus Astartila. Rec. Australian Mus., vol. 17, pp. 53-75.
 - 1932. A revision of the genus *Myonia* with notes on allied genera from the Permo-Carboniferous of New South Wales. *Ibid.*, vol. 18, pp. 389-410.
- M'Cov, Frederick
 - 1847. On the fossil botany and zoology of the rocks associated with the coal of Australia. Ann. Mag. Nat. Hist., ser. 1, vol. 20, pp. 145–157, 226–236, 298–312.
- Morris, John
 - 1845. Descriptions of fossils. In de Strzelecki, P. E., Physical description of New South Wales and Van Dieman's Land. London, Longman, Brown and Co., pp. 270–291.

1839. Fossils. In Mitchell, T. L., Three expeditions into the interior of eastern Australia. London, T. and W. Boone, vol. 1, p. 15.

STOLICZKA, FERDINAND

1871. Cretaceous fauna of southern India. The Pelecypoda. Palaeont. Indica, ser. 6, vol. 3, 537 pp.

TEICHERT, CURT

- 1950. Climates of Australia during the Carboniferous, Permian, and Triassic. Internatl. Geol. Congr., Rept. 18th Session, Great Britain, 1948, pt. 1, pp. 206-208.
- 1954. A new ammonoid from the eastern Australian Permian province. Jour. Proc. Roy. Soc. New South Wales, vol. 87, pp. 46–50.

TEICHERT, CURT, AND H. O. FLETCHER

1943. A Permian ammonoid from New South Wales and the correlation of the Upper Marine series. Rec. Australian Mus., vol. 21, pp. 156–163.

SOWERBY, JAMES