

A NEW TRANSITIONAL MYALINID BIVALVE FROM THE LOWER PERMIAN OF WEST TEXAS

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ABSTRACT. *Novaculapermia boydi* gen. et sp. nov. is a remarkable Lower Permian vertically elongate bivalve that superficially resembles 'razor' clams of the superfamily Solenoidea. Our 'razor' clam possessed a duplivincular ligament and early ontogeny of the Myalinidae. The flattened, equiconvex form suggests that *Novaculapermia* was a shallow vertical burrower in soft sediments possibly anchored by byssal attachment; evidently it was not a reef dweller, but lived in near-reef environments.

THE silicified fauna of the Permian Glass Mountains of west Texas has provided one of the world's most spectacular palaeontological windows into Late Palaeozoic reef and associated environments. Although well known for its rich brachiopod fauna (e.g. Grant 1971; Cooper and Grant 1972), other groups, such as the sponges (e.g. Finks 1960) and bivalves (e.g. Newell and Boyd 1970, 1995), are numerically less diverse, but an equally important constituent of the west Texas Lower Permian fauna. Together with the Permian reefs of China and Tunisia, the Texas reefs testify to the morphological and ecological complexity achieved in Late Palaeozoic tropical marine biotas.

Among tropical Permian Bivalvia, the Myalinidae and Alatoconchidae perhaps best illustrate morphological specialization and adaptation to a variety of reef and level-bottom habitats. The myalinids are a diverse group of marine and non-marine bivalves extending back at least to the early Carboniferous and reaching their developmental zenith during the mid Permian. They are an especially noteworthy group because several independent lineages within the family provide numerous classic examples of 'progressive' evolutionary trends related to their transition from an endobyssate to epibyssate life-habit (Newell 1942; Stanley 1972). Equally striking are the Alatoconchidae, the giant clams of the Permian, whose extreme size and large wing-like medial projections enabled these bivalves to recline on soft substrates without the aid of a strong byssus. The close affinities between the Alatoconchidae and Myalinidae were known soon after their first description and in fact they were grouped in a single family by Runnegar and Gobbett (1975). Differences in the ligament and valve symmetry have subsequently required assignment of these giant clams into the Alatoconchidae, a family based on poorly preserved material from Afghanistan (Termier *et al.* 1973), which are presumably derived from the myalinids (Yancey and Boyd 1983).

We describe here a collection of bivalves whose form is unlike that of any other known to us and which show characteristics of both the Myalinidae and Alatoconchidae. The specimens were collected from near-reef sedimentary rocks of the Lower Permian Road Canyon and Cathedral Mountain formations of the Glass Mountains of west Texas. A more complete account of the Permian stratigraphy and geology of the Glass Mountains and neighbouring Guadalupe Mountains can be found in Cooper and Grant (1972) and Newell *et al.* (1972). The specimens are preserved as silicified pseudomorphs in which fine skeletal detail can be discerned, although the original shell ultrastructure has been obscured during diagenesis. The significance of the shells is that they exhibit morphological features which, although known independently from unrelated bivalve clades, have never been described in combination. They represent yet another example of extraordinary morphological development among the fauna of the Permian Glass Mountains and provide clues to the evolutionary relationships among Late Palaeozoic bivalves.

SYSTEMATIC PALAEOLOGY

Institutional abbreviations: AMNH, American Museum of Natural History (New York); USNM, Museum of Natural History Smithsonian Institution (Washington). Following the recommendation by the International Code of Zoological Nomenclature (Ride *et al.* 1985), the suffix '-oidea' is used in superfamily names.

Order PTERIOIDA Newell, 1965
 Superfamily AMBONYCHIOIDEA Miller, 1877
 Family MYALINIDAE Frech, 1891

Genus NOVACULAPERMA gen. nov.

Type species. *Novaculapermia boydi* sp. nov., by monotypy.

Derivation of name. From a combination of Latin *novacula*, in reference to its razor-like shape, and *perma*, in reference to its only known occurrence from Permian strata.

Diagnosis. Equivalved Myalinidae; shell large, showing change from retrocrescent to infracrescent during growth, adults adapically elongated; possessing simple opisthodontic duplivincular ligament, ligamental grooves slightly curved, intersecting hinge margin; valve width narrow; pallial line deeply bilobed; probably anisomyarian, posterior adductor scar large, sub-circular, positioned in dorsal lobe of pallial impression; surface sculptured with commarginal growth squamae, lacking radial sculpture.

Remarks. This genus is placed tentatively within the Myalinidae because of its possession of an opisthodontic duplivincular ligament. It differs from other myalinids in possessing an umbonal groove, in its narrow valve width and equivalved condition. New material, documenting the shell structure, however, may warrant erection of a new family to accommodate the unusual morphology.

Novaculapermia boydi sp. nov.

Plate 1; Text-figure 1

Derivation of name. After Donald C. Boyd, significant contributor to our understanding of Permian Bivalvia.

Holotype. USNM 487771; from USNM loc. 702.

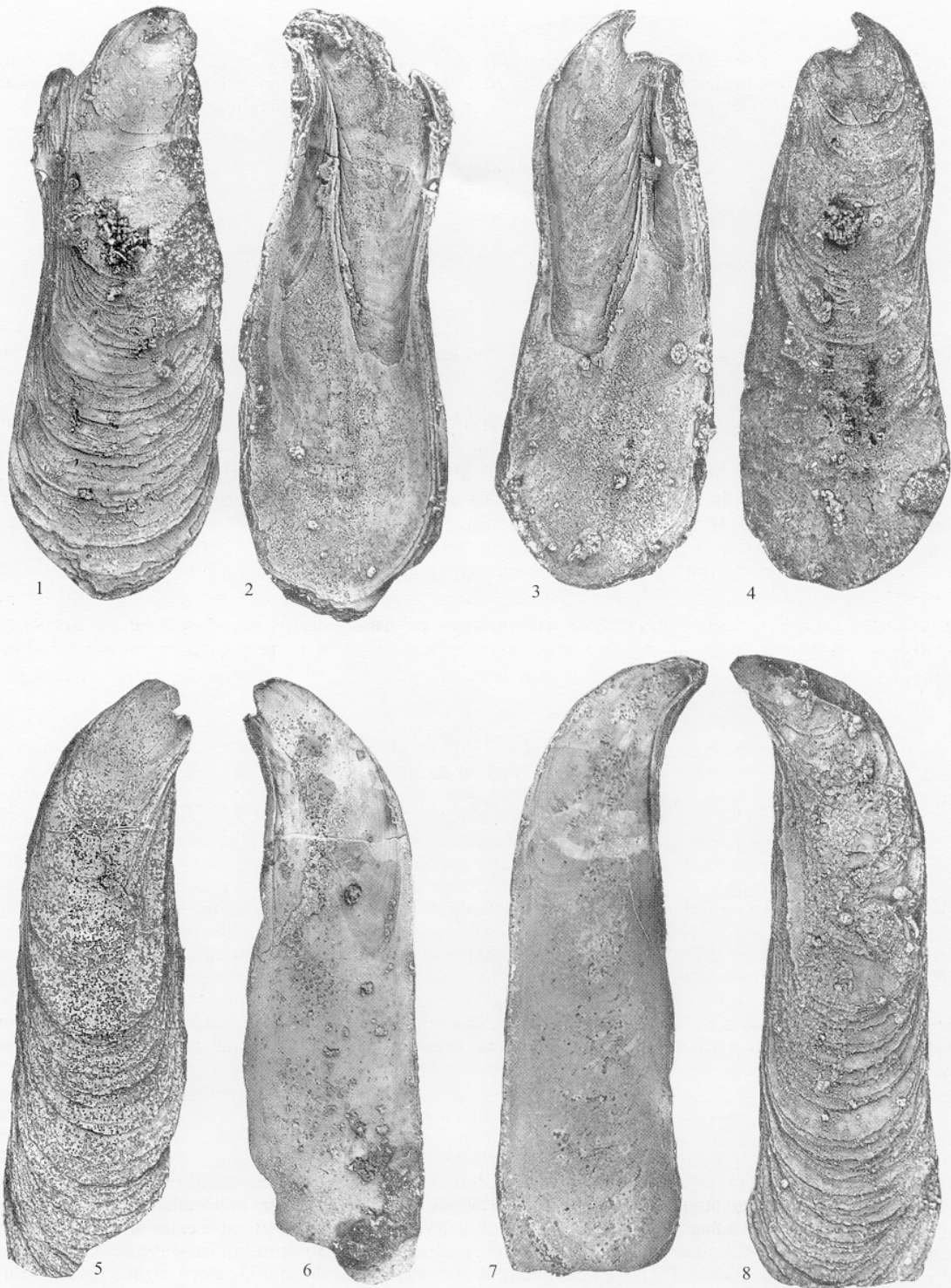
Paratypes. USNM 487772–487773; from AMNH loc. 500 × and USNM loc. 702-un respectively.

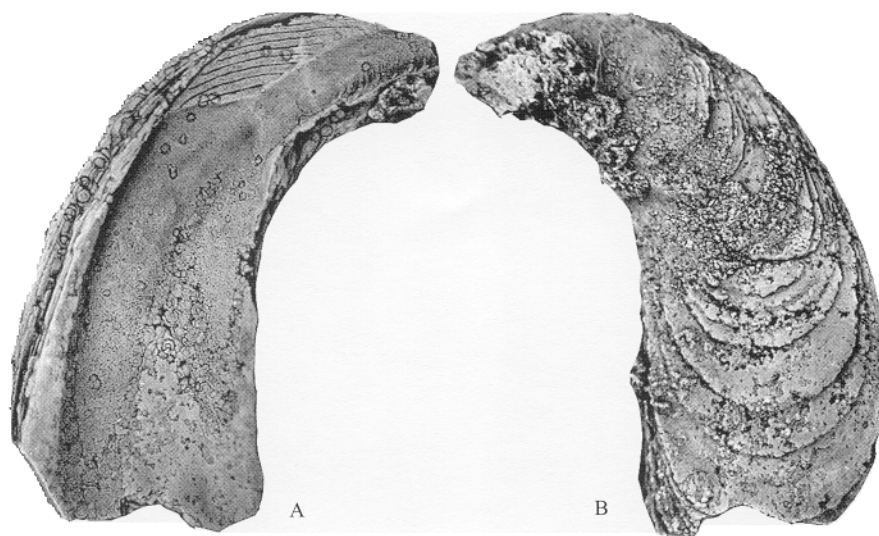
Material. The new species is based on six nearly complete valves representing four individuals, in addition to abundant fragmentary material.

Localities and age. The specimens come from the Road Canyon and Cathedral Mountain formations, west Texas, which are considered to be Middle Permian (Leonardian) in age (Newell *et al.* 1953). Complete

EXPLANATION OF PLATE 1

Figs 1–8. *Novaculapermia boydi* gen. et sp. nov.; Cathedral Mountain Formation, Glass Mountains, Texas. 1–4, USNM 487772, paratype; adult individual; AMNH loc. 500 ×. 1, right valve exterior. 2, right valve interior showing well defined bilobate pallial line. 3, left valve interior. 4, left valve exterior. Note that the exterior surface of both valves is encrusted indicating probable excavation and exposure above the sediment-water interface. 5–8, USNM 487773, paratype; adult individual; USNM loc. 702-un. 5, right valve exterior. 6, right valve interior. 7, left valve interior. 8, left valve exterior showing epibiont encrustation. All × 0.75.





TEXT-FIG. 1. *Novaculapermia boydi* gen. et sp. nov.; holotype, USNM 487771; Cathedral Mountain Formation, Glass Mountains Texas (USNM loc. 702). A, left valve interior showing broad flattened opisthodetic duplivincular ligamental area with eight acute ligamental grooves and shallow excavated umbonal groove. B, exterior of same specimen showing commarginal growth lamellae. Both $\times 1.5$.

descriptions of localities (AMNH loc. 500 \times , USNM locs. 702, 702-un, 703-c, 706-c) can be found in Cooper and Grant (1972).

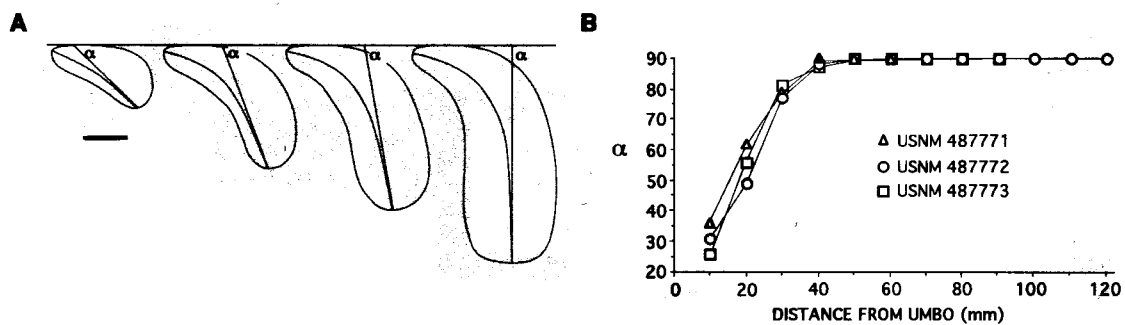
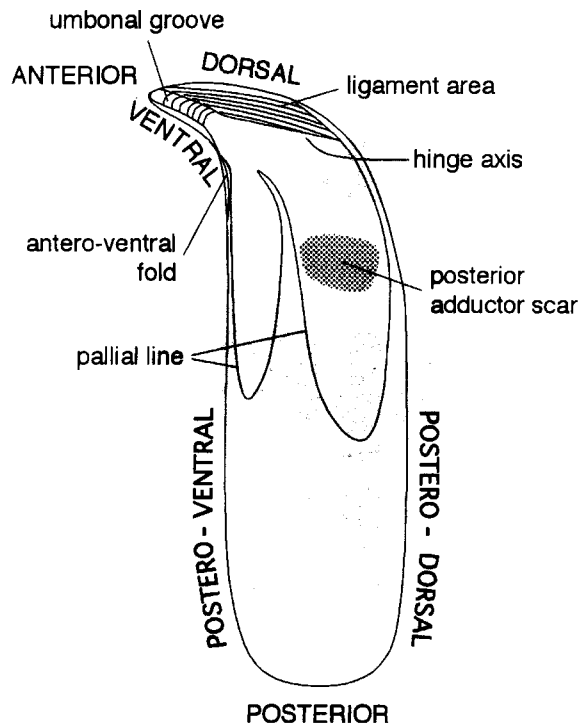
Diagnosis. As for genus.

Description. A schematic diagram of the internal morphological features and shell measurements is provided in Text-figure 2. An orientation similar to that proposed for the myalinids and alatoconchids, with the apical end anterior and adapical end posterior (Newell 1942; Runnegar and Gobbett 1975), is favoured, even though the inferred living position does not reflect this orientation.

The shells of *Novaculapermia* are fairly large, often exceeding 130 mm in their greatest curvilinear dimension measured along the vector of maximum growth. The rounded umbones occupy the anteriormost extremity of the shell which, during early growth stages, is retrocrescent and later becomes infracrescent. The exterior surface of both valves is sculptured with fairly coarse and unevenly spaced commarginal growth lamellae. Both the strength of, and spacing between individual lamellae is apparently equal for the two valves of the same individual. The valves are relatively flat, lacking an umbonal ridge or keel. The maximum width of two valves when placed in opposition is very narrow (< 10 mm). There is a slight gape (1–2 mm wide) at the posterior adapical end in one specimen with complete margins (Pl. 1, figs 1–2). Although there is no evidence of a byssal collar or byssal gape along the antero-ventral margin in adult specimens, there appears to be a slight infolding of the shell margin in this position which might indicate passage of a byssus. A more pronounced byssal gape may have existed during early life stages, yet the accretion of new shell during growth has obscured the relationship between the two valves along the juvenile commissure margin precluding any such observation.

Muscle scars can be observed on the valve interior of a few well preserved specimens. The most pronounced features observed on the shell interior are the bilobate pallial muscle insertion scars. These scars, observed in both right and left valves (Pl. 1, figs 2–3, 6–7), are bilobate; the dorsal lobe is the larger, extending beyond half the length of the shell. The ventral lobe is narrow and abuts against the antero-ventral shell margin. A sharp medial constriction of the pallial line separates the two lobes and is presumably formed by the fixation of the pallial muscle. The pallial scar may have been diagenetically enhanced by the subsequent removal of nacreous shell enclosed by the pallial line prior to silicification. Situated within the dorsal pallial lobe at about half its distance is a faint impression of a large (c. 9 mm in diameter) sub-circular muscle insertion scar, presumably indicating the position of the posterior adductor muscle. Evidence for additional musculature has not been

TEXT-FIG. 2. Morphological features and orientation for a right valve interior of *Novaculapermia*. Note: orientation is similar to that used by Runnegar and Gobbett (1975) and Yancey and Boyd (1983) for the Alatoconchidae.



TEXT-FIG. 3. Post-larval growth sequence of *Novaculapermia* showing the retrorescent to infracrescent trend in ontogeny. α = the angle between the tangent to the vector of maximum growth at the valve margin and the hinge axis. A, graphical illustration of growth series in the holotype (Text-fig. 1) where the horizontal line approximates the hinge axis. Scale bar represents 10 mm. B, plot showing change in α at a given distance from the umbo in three specimens.

recognized. Both the shape and position of the pallial line and posterior adductor scar are strikingly similar to those found in certain pinnaceans, such as *Pinna* and *Exitopinna*, where the inner shell layer of the area enclosed by the pallial muscles is nacreous (see Cox and Hertlein 1969, fig. C23.3). These similarities in the shape of musculature among elongated semi-infaunal bivalves are believed to reflect a constructional constraint in the position and size of mantle cavity due to shell growth.

Extending from the umbone along an arc parallel to shell growth and extending into the body cavity is a shallow U-shaped groove which is difficult to interpret. The groove has only been observed in a single well preserved left valve (Text-fig. 1). The groove is about 4 mm wide and exhibits convex (towards the beak) growth lines. On one hand, this structure may serve as an umbonal deck with a function similar to that of the umbonal septum described from other myalinids (Newell 1942) and some alatoconchids (e.g. Boyd and Newell

1979, fig. 9). If this were the case the groove might reflect the migration tract of the anterior adductor muscles during growth. On the other hand, the groove may have had a function similar to that of the byssal groove of some other alatoconchids (e.g. Yancey and Boyd 1983) and represent the passage for a byssus. The first interpretation is favoured here because it is unlikely that a byssus would be channelled in an orientation unknown among other byssate bivalves.

The ligamental characters of *Novaculapermia* can be deduced from the valve interior of one well preserved left valve (Text-fig. 1). Right valves showing an equivalent ligamental area are not preserved, but presumably would show a similar form. In this specimen, the broad flat ligamental area lies entirely behind the beak and is bounded antero-ventrally by the shallow umbonal groove. At least eight thin grooves, in which lamellar bands of an external ligament were inserted, transverse across the ligamental area. The spacing between the grooves (c. 1 mm) is several times greater than the width of the grooves. The ligament insertion grooves are only slightly curved and are inclined towards the hinge axis. Two of the grooves intersect the hinge axis at an angle of about 10°. Unfortunately, articulated valves with an intact ligament are unknown, but, provided our assessment of ancestry is correct, *Novaculapermia* probably had a ligament similar to that of *Septimyalina*, described by Carter (1990), in which the fibrous sublayers extended continuously from one valve to the other.

Growth sequences of *Novaculapermia* illustrate a post-larval ontogenetic trend in shell shape from retrorescent to infracrescent (Text-fig. 3). During the retrorescent juvenile stage (up to about 30 mm long), the growth vector is curved anteriorly. After about 30 mm the growth vector ceases to be curved and the adult shape becomes infracrescent and continues accreting new shell along a straight vector nearly normal to the hinge axis. Similar ontogenetic trends have been identified in several myalinid species, and are thought to have arisen independently in several different lineages (Newell 1942). Such radical changes in growth have traditionally been interpreted as reflecting a change in living habits, and among several myalinid lineages similar trends probably reflect the transition from a semi-infaunal to an epifaunal habit (Stanley 1972). A new problem arises in that *Novaculapermia* was probably not an epifaunal bivalve (see below) and such an interpretation for the trend is not warranted in this case.

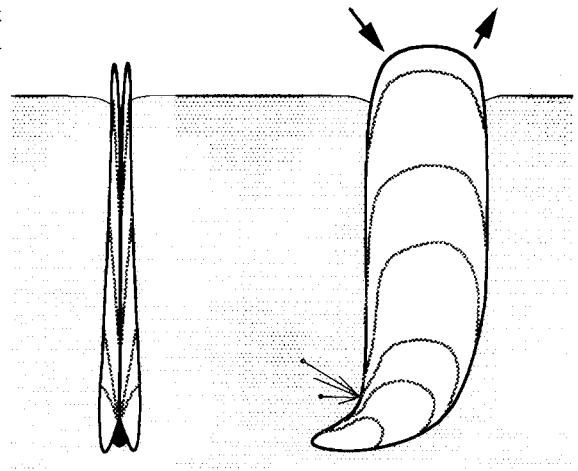
Remarks and comparisons. This species is unlike any known to us and it is unlikely that it would be confused with other Permian Bivalvia. Given the few samples available to us, it is impossible to know the limits of variation within the species. Some variation does exist in shell shape and observable features (e.g. ligamental area and musculature) which may be due to preservational factors, genetic differences or ecophenotypic variation. The discovery and description of additional material of a sufficient sample size may require the separation of two or more distinct species.

PALAEOECOLOGY

Like other pteriomorphs, we assume that *Novaculapermia* was a filter feeder utilizing a suspended food source. Because the specimens were not recovered *in situ*, the life orientation for *Novaculapermia boydi* remains questionable and can only be inferred using a functional morphological approach. Such dependence on purely functional morphology in reconstructing life-habits does have its pitfalls (see discussion in Fürsich 1980), yet remains a powerful, and sometimes the only, tool in the absence of unequivocal field evidence or modern analogues. The following discussion is considered only preliminary; we await further evidence from an *in situ* association.

Several clues indicate that *Novaculapermia boydi* was sessile, semi-infaunal and oriented with its sagittal plane normal to the sediment-water interface. A hypothesized reconstruction is provided in Text-figure 4 and shows a habit similar to that proposed for other 'mud sticking' bivalves such as *Cochlearites* and *Lithiotis* (e.g. Seilacher 1984). The equivalved condition is an ubiquitous feature in bivalves which have their sagittal plane oriented vertically (e.g. Stanley 1970, 1972), a condition which can also be inferred for *Novaculapermia*. If the interpretation of the anterior marginal fold as a passage for a byssus is correct, then *Novaculapermia* may have employed a byssus during its entire life, which would have aided in fixation, especially in more agitated water where sediments would be more likely to shift. We interpret *Novaculapermia* to be only weakly byssate given the absence of a distinct byssal gape. Byssal attachment is not a prerequisite for a semi-infaunal habit because *Novaculapermia* could also have been supported by enclosing sediment, which would also have aided in stabilization, especially in less agitated water. Although the question of how deeply

TEXT-FIG. 4. Reconstruction of hypothesized life habit for *Novaculapermia*. Arrows indicate relative position of inhalant and exhalant currents.



Novaculapermia was buried in the sediment is difficult to assess, a clue can be found on the two valves of one specimen (Pl. 1, figs 5–8) where the posterior margins are broken 10–20 mm from their former posterior shell margin. Such breakage, frequently induced by predators, is common amongst semi-infaunal pinnids such as *Pinna carnea* which are typically buried to a depth of about half their greatest dimension (Stanley 1970). Although such a shallow burial depth may be possible, we favour a slightly deeper burial depth on the grounds that it would be more stable for a weakly byssate *Novaculapermia*.

MYALINID AFFINITIES

The specimens referred to herein exhibit many morphological features which suggest affinities with several different bivalve groups depending on which morphological characters are emphasized.

Although a duplivincular ligament is believed to have been derived independently among several bivalve clades (Newell and Boyd 1987) it is a consistent feature shared among all Myalinidae. The ligament system observed in *Novaculapermia* is perhaps most similar to that found in the myalinids *Liebea* and *Septimyalina*, in which the ligament grooves are fewer in number and intersect the hinge line at a steep angle. This is in contrast to the ligament of *Selenimyalina* and some *Myalina sensu stricto* where the numerous fine ligament grooves incise a narrow ligament area and run nearly parallel to the hinge axis. It is also possible to argue for homology in the umbonal features (umbonal deck and groove) between myalinids and *Novaculapermia* depending upon their interpretation. We favour an interpretation of the umbonal groove and deck as homologous to the umbonal deck of some myalinids. An additional similarity of *Novaculapermia* to the Myalinidae is that of general shell shape, especially early in ontogeny. In both *Novaculapermia* and many Upper Carboniferous and Permian myalinids, shell shape changes from markedly retrocrescent mytiliform to an upright infracrescent position.

The genus *Novaculapermia* also exhibits some obvious similarities to members of the Alatoconchidae which are thought to have been derived from the Myalinidae (Runnegar and Gobbett 1975; Yancey and Boyd 1983; Yancey and Ozaki 1986). Like the myalinids, alatoconchids also have a duplivincular ligament and a broad ligament area. Unlike the myalinids and *Novaculapermia*, the ligamental grooves of alatoconchids are somewhat sinuous and not straight or slightly arched. Like *Novaculapermia*, alatoconchids are equivalved; a condition unknown in other myalinids. However, *Novaculapermia* lacks the pronounced alate wing-like flanges, byssal collar, and extreme large size characteristic of the alatoconchids.

We concluded that *Novaculapermia* shares more common features with the Myalinidae than the Alatoconchidae and prefer to place it in the former. We believe that the similarities in the two

groups stem from their recent common ancestry. A more complete treatment of phylogenetic affinities among the myalinids and their ancestors is underway (McRoberts and Newell 1995).

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