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Marine Myalinidae (Bivalvia: Pterioida) from the Permian of West Texas

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ABSTRACT

Marine bivalves of the family Myalinidae are an important benthic constituent of the Permian Reef Complex of West Texas and New Mexico. We describe and summarize the myalinids from Lower and Middle Permian reef and near-reef settings and infer living habits as either epifaunal or semi-infaunal byssally attached suspension feeders. The six myalinid species described are exceptionally preserved as silica pseudomorphs. Included in the fauna are two new taxa: *Myalina lamellosa*, a species with distinctive commarginal lamellae, and *Myalina plicata*, the only known myalinid with prominent radial plicae. The family Myalinidae is placed in the Ambonychioidea (Order Pterioida) and an emended diagnosis incorporates ligament characters and details of shell ultrastructure.

INTRODUCTION

In terms of taxonomic richness and morphologic innovation, the marine Myalinidae is one of the most successful of Late Paleozoic–Early Mesozoic bivalve families. Although myalinids are known from as far back as the early Carboniferous, and perhaps even to the Devonian if *Myalina squamosa* Sowerby is considered a true myalinid, they did not reach their glory until the Permian, where richness exceeds 10 genera and 25

species. Following the end-Permian mass extinction, the marine Myalinidae were greatly diminished in taxonomic and ecological diversity but persisted until possibly the Middle Triassic, when the group became extinct. Their resilience, however, is underscored by the fact that several myalinid species comprise a significant component of the Early Triassic recovery fauna (e.g., Schubert and Bottjer, 1995).

Marine myalinids are an abundant and conspicuous component in near-reef and lev-

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	CONODONT ZONE	STRATIGRAPHY	
DZH.	<i>M. shannoni</i>	Tessey Formation	
GUADALUPIAN	<i>M. postserrata</i>	Altuda Fm.	Capitan Limestone Gilliam Ls.
	<i>M. aserrata</i>	Vidrio Formation	
	<i>M. nankingensis</i>	Word Formation	Appel Ranch Member Willis Ranch Member China Tank Member
		Road Canyon Formation	
LEONARDIAN	<i>N. sulcopicatus</i>	Cathedral Mountain Formation	
	<i>N. prayi</i>		
	<i>N. foliatus</i>	Skinner Ranch Formation	Hess Formation
	<i>M. gujioensis</i>		
WOLF.		Lenox Hills Formation	
			Neal Ranch Formation

Fig. 1. Generalized Wolfcampian to Dzhulfian Permian stratigraphy of Glass Mountains region West Texas. Modified from Rohr and others (2000).

el-bottom paleocommunities associated with the spectacular Permian reef complex of West Texas and southern New Mexico. Although several myalinid taxa have been described from the Permian reef complex in recent years (McRoberts and Newell, 1997, 2001), this contribution represents a more complete account of the taxonomic and morphological richness of the family from the Permian of West Texas. Furthermore, we provide a revised account of the morphology of the family, with a revised diagnosis which will complement Newell's monograph on the Myalinidae published more than a half century ago (Newell, 1942).

MATERIAL AND COLLECTIONS

Most of the material described herein comes from the Glass Mountains of West Texas situated on the south margin of the Permian Delaware Basin. The bulk of the specimens come from the Leonardian-Guadalupian Cathedral Mountain, Road Canyon and Word Formations (fig. 1). They were collected and processed by G.A. Cooper as a byproduct of his work on Permian brachiopods (e.g., Cooper and Grant, 1972). More complete geographic and stratigraphic details of the listed U.S. Geological Survey locality numbers can be found in Cooper and Grant (1972).

The bivalve specimens are preserved as silica pseudomorphs which preserve the fine details of the outer calcite shell layers and external surface ornamentation. Unfortunately, the inner shell layers of the bivalves, which were presumably composed of aragonite and would exhibit muscle scars, were most often not silicified and are typically not preserved. A few of the better preserved specimens, however, exhibit coarse silicification of the inner aragontic shell layers, and therefore preserve interior adductor muscle scars. A more complete description of the unique mode of preservation can be found in Cooper and Grant (1972) and Newell et al. (1953).

Institutional repository abbreviations for type and figured specimens and localities are: AMNH, American Museum of Natural History; USNM, Museum of Natural History, Smithsonian Institution; KU, University of Kansas Paleontological Collections; UWM, Geological Museum of the University of Wisconsin, Madison.

MORPHOLOGY

The shell morphology of myalinid bivalves has been the subject of much discussion which has led to greatly different views on the structure and significance of many morphologic features. Because descriptive terms for myalinid morphology are mostly available elsewhere, the reader is referred to Newell (1942) for a summary.

Although many morphologic features, including shell outlines, have proven useful in discriminating myalinid genera and species, it is noteworthy that shape is often controlled by environmental factors such as the grain size and stability of substrate, water chemistry, and water temperature (e.g., Hickey, 1987) and should not in itself be a single criterion for species definition. While recognizing the value of shell shapes and sizes in discriminating between different populations, our approach is to maximize the use of discrete character traits in defining new taxa. A summary of internal features used in the descriptions is provided in figure 2 and general conventions of measurement axes and orientation are shown in figure 3.

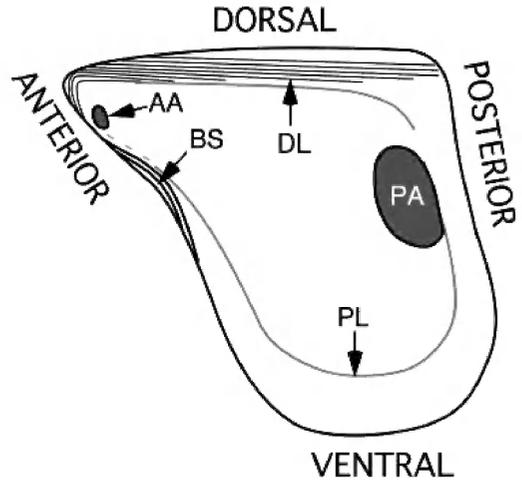


Fig. 2. Generalized internal morphologic features. DL, duplivincular ligament grooves; BS, byssal sinus; PL, pallial line; PA, posterior adductor insertion scar; AA, anterior adductor insertion scar.

SYSTEMATIC PALEONTOLOGY

ORDER PTERIOIDA NEWELL, 1965

SUPERFAMILY AMBONYCHIOIDEA MILLER, 1877

FAMILY MYALINIDAE FRECH, 1891

emended McRoberts and Newell

REVISED DIAGNOSIS: Mostly inequivalved Ambonychiacea with right valve slightly less convex than left valve; inequilateral; edentulous or with cardinal tooth or boss beneath beak of right valve and corresponding furrow in left valve; pallial line entire, generally pitted; anisomyarian; ligament duplivincular continuous, not extending to calcitic shell layer; inner shell layer in both valves nacreous aragonite; outer shell layers either prismatic calcite in both valves or prismatic calcite in right valve and homogeneous calcite or homogeneous calcite with mosaic structure in outer shell layer in left valve.

REMARKS: Newell (1942: 44) revised the family as: "Shell inequivalve, the right valve slightly less convex and slightly smaller at the margin than the left; beaks at or near the small and projecting anterior end; posterior margin sub-ovate, quadrate, or extended in a posterodorsal auricle; ligament external, duplivincular, mainly opisthodontic, but with amphidetic remnant before the beaks in some

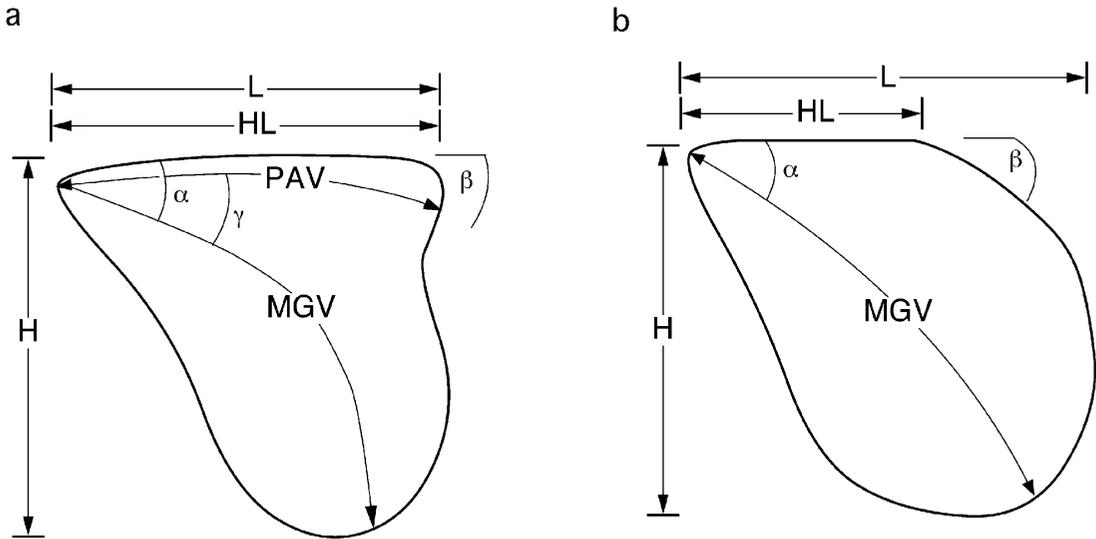


Fig. 3. Measurement axis conventions and orientations for extreme forms **a** and **b**. H, height; L, length; HL, hinge length; LG, number of ligament grooves; MGV, maximum growth vector (umbonal ridge); PAV, posterior auricle vector; α , angle subtended by the postero-ventral terminus of maximum growth vector and hinge line; β , angle subtended by hinge line and posterior margin; γ , angle subtended by PAV and MGV.

genera; hinge edentulous or with weak cardinal teeth 1/2a, 2b at the front end of hinge; inner shell layer lamellar, probably aragonite; outer layer composed of calcite, either homogeneous or finely prismatic, the prisms and optic axes nearly normal to the shell surface; musculature characteristically anisomyarian, but monomyarian in a few species. The genera that unquestionably belong here do not possess well-defined radial ornamentation, and all pass through a form stage in the early ontogeny similar to adult *Modiolopsis*."

Later, Newell (1969: N289) defined the family as: "Inequivalved, with RV slightly less convex than LV; edentulous, or with cardinal tooth or boss beneath beak of RV and corresponding furrow in LV; pallial line entire, generally pitted."

To this discussion, Carter (1990: 201) added that myalinids have a simple prismatic calcite or both simple prismatic and homogeneous calcite outer shell layer with the homogeneous structure commonly restricted to the left valve; the middle and inner shell layers are nacreous and aragonitic prismatic. Carter (1990) also noted that the ligament in Myalinidae is duplivincular with one fibrous

sublayer per ligament ridge, and with each fibrous sublayer initially spanning the two valves.

There has been much discussion concerning the taxonomic content and systematic placement of the Myalinidae within higher categories of the Bivalvia. Contrary to earlier workers who have aligned them with the Pterioidea, Newell (1942) was impressed with the similarities, especially in musculature, with the Mytiloidea. However, it was later determined that similarities in ligament indicate placement into the superfamily Ambonychoidea (Newell, 1965; Pojeta, 1966). Furthermore, it is likely that based on similarities in ligament, the Alatoconchidae, a group of aberrant giant clams, are closely related to, or descended from, the Myalinidae (Yancey and Boyd, 1983).

Currently, the following genera and their ranges are here considered to be marine Myalinidae: *Myalina* (?Devonian, Carboniferous–L. Triassic, ? M. Triassic), *Septimyalina* (Carboniferous–L. Permian), *Orthomyalina* (U. Carboniferous–L. Permian), *Myalinella* (U. Carboniferous–L. Triassic), *Arctomyalina* (U. Carboniferous), *Elversella* (M. Permian), *Pseudomyalina* (L. Permian), *Seleni-*

TABLE 1
Myalina lamellosa McRoberts and Newell, new species
 (Measurements in millimeters; see fig. 3 caption for abbreviations.)

Specimen	Valve	H	L	HL	MGV	α	β	LG
USNM 431335 ^a	LV	17.3	22.1	18.3	23.7	42	69	4
USNM 431336	LV	21.3	26.3	19.9	28.1	41	63	5
USNM 431337 ^a	RV	16.8	19.7	17.2	23.1	36	80	4
USNM 431338 ^a	LV	13.7	16.5	17.2	18.8	38	85	5
USNM 431339	LV	10.5	11.5	11.6	13.6	42	92	—
USNM 431340	LV	19.2	16.9	22.4	28.4	36	67	—
USNM 431341 ^a	LV	14.1	17.8	16.3	21.5	38	79	4
USNM 431342 ^a	LV	12.3	15	14.7	17.1	37	71	—
USNM 431343 ^a	LV	17.2	23.3	19.1	25.2	35	52	—
USNM 431344 ^a	LV	28.6	30.5	28.9	35.2	41	97	7
USNM 431345 ^a	LV	13.5	16.2	14.3	17.1	43	80	12
USNM 431346 ^a	LV	8.8	10.1	9.3	10.9	49	89	—
USNM 431347	RV	15.6	23.2	20.7	23.8	38	102	—
USNM 431348 ^a	LV	12.1	16.7	15.8	16.5	41	89	—
USNM 431348 ^a	RV	16.8	19.2	18.5	23.2	44	69	—
USNM 431349 ^a	LV	37.4	41.3	36.2	45.2	37	96	—
USNM 431349 ^a	RV	35.3	37.6	33.3	43.4	36	92	—
USNM 431350 ^a	LV	17.5	21.6	17.9	23.4	34	97	—
USNM 431350 ^a	RV	17.6	20.3	17.8	23.9	42	103	na

^a Measurements taken on commarginal growth lamellae.

myalina (U. Carboniferous), *Novaculapermia* (L. Permian), *Promyalina* (L. Triassic), and less certainly, *Liebea* (U. Permian) and *Aviculomyalina* (M. Triassic).

Genus *Myalina* De Koninck 1842

TYPE SPECIES: *Myalina goldfussiana* DeKoninck, 1842, subsequently designated by Stoliczka, 1871.

Myalina lamellosa McRoberts and Newell, new species Figure 4

TYPE SPECIMENS: Holotype: USNM-431335; Paratypes: USNM-431336, USNM-431344, USNM-431348.

DIAGNOSIS: Thin-shelled and triangular-shaped *Myalina* possessing distinct irregular commarginal overlapping growth lamellae, a broad anteroventral fold in left valve and corresponding sulcus in right valve, and lacking a distinct anterior auricle.

DESCRIPTION: Shell medium sized (max. height = 3.7 cm), triangular in outline; hinge-line straight, less than total length of shell; small posterior auricle present in most

specimens, especially in later growth stages; anterior margin slightly concave, indicating small byssal sinus; posterior margin broadly convex, nearly parallel to anterior margin; broad fold in left valve along anteroventral margin corresponds to broad sulcus in right valve; beaks terminal, arcuate, and projecting inwards, shell retrocrescent, with maximum growth vector α moderately steep ($\sim 65^\circ$) at early growth stages, becoming steeper ($\sim 75^\circ$) at later growth stages (see fig. 5) but never infracrescent; left valve slightly larger than right. Surface of both valves ornamented by numerous commarginal overlapping growth lamellae which do not terminate in hemispherical spines. Lamellae becoming more pronounced and at wider spaced intervals by curling up and outwards in later growth stages. Body cavity extending far into the umbones, umbonal septum or deck absent. Ligament opisthodontic, duplivincular; between 4 and 12 parallel grooves, slightly acute, intersecting hinge-line at less than 10° . Musculature characterized by moderate-sized ovate posterior adductor. Anterior adductor or other musculature unknown. Thin-shelled,

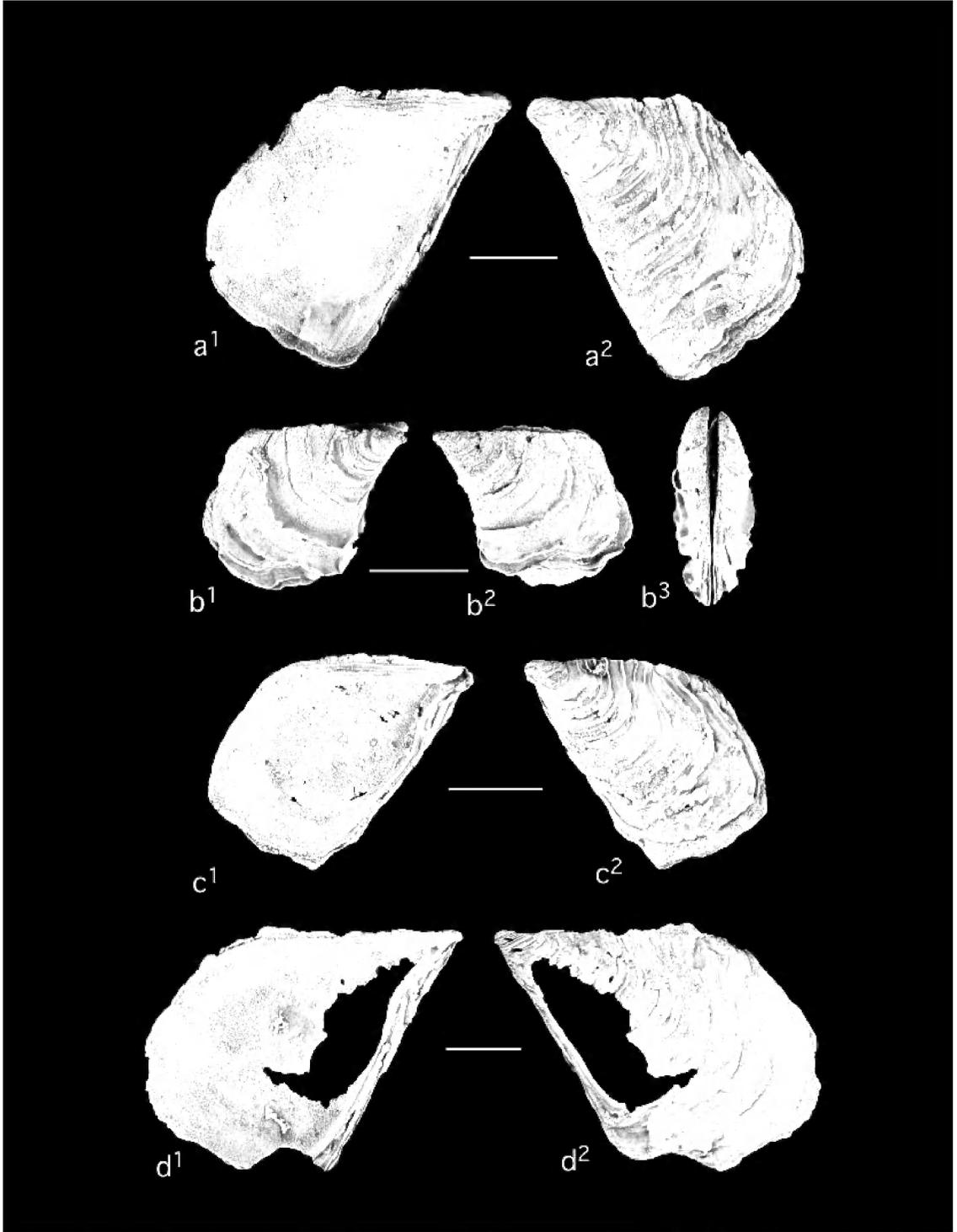


Fig. 4. *Myalina lamellosa* McRoberts and Newell, new species. Scale bar is 1 cm. **a**, holotype, USNM 431335 (USNM loc. 702), left valve interior (**a**¹), exterior (**a**²); **b**, paratype, articulated valve pair, USNM 431348 (USNM loc. 702), right valve (**b**¹), left valve (**b**²), dorsal view (**b**³); **c**, paratype, left valve interior USNM 431336 (USNM loc. 702), (**c**¹), exterior (**c**²); **d**, paratype, USNM 431344 (USNM loc. 702), left valve interior (**d**¹), exterior (**d**²).

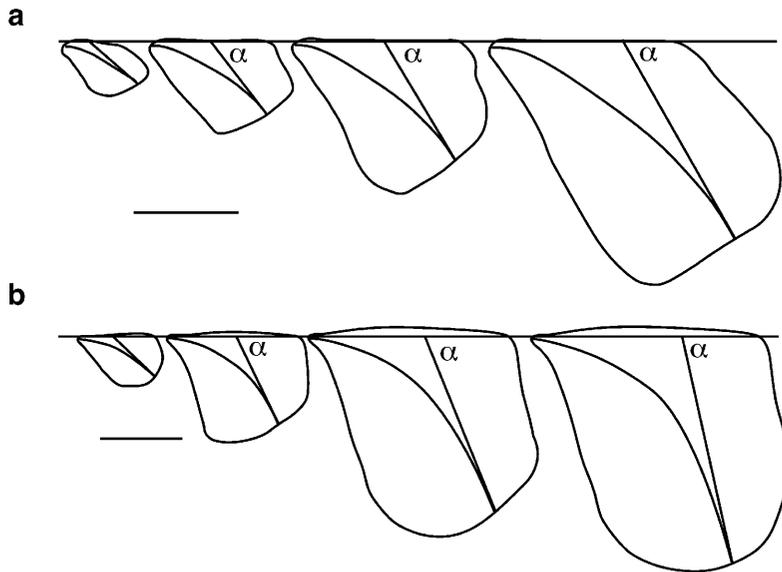


Fig. 5. Ontogenetic series showing increasing α angle in *Myalina lamellosa* (a) and *M. plicata* (b).

ultrastructure unknown. See table 1 for measurements.

REMARKS AND COMPARISONS: This species shows similarities to forms regarded by Newell (1942) as *Septimyalina burmai* Newell 1942, yet differs from that species in the absence of spinelike projections of growth lamellae and thickness of shell. Additionally, *Myalina lamellosa* lacks a prominent umbonal septum or deck which presumably occurs in *S. burmai* although none is illustrated. Differs from *Myalina plicata*, n.sp., in the presence of weak posteroventral fold and sulcus and absence of radial plicae.

PALEOAUTECOLOGY: Several features lead to the conclusion that *Myalina lamellosa* was byssally attached in an edgewise position resting on the anterior end (fig. 6a). Although the two valves differ in their size, the equality in the inflation of both valves and of commarginal lamellae suggests the animal was oriented with its commissure plane nearly vertical and slightly resting on its left valve.

AGE AND OCCURRENCE: Cathedral Mountain Formation (Leonardian), localities: USNM-702, USNM-721-u; Road Canyon Formation (Guadalupean), localities: ?USNM-721-j, USNM-721-t, USNM-721-z, USNM-724-b, USNM-726-d, USNM-726-z; Word Formation (Guadalupean), localities:

USNM-706-e. To these from the USNM, add Girty's (1908, pl. 29, fig. 15) specimen from Delaware Mountain Formation, southern Delaware Mountains (station 2935).

MATERIAL: The collection consists of 10 articulated valves, 23 left valves, and 8 right valves.

ETYMOLOGY: Specific name refers to prominent growth lamellae.

Myalina plicata McRoberts and Newell,
new species
Figure 7

TYPE SPECIMENS: Holotype: KU-310505; Paratypes: USNM-431351, USNM-431353.

DIAGNOSIS: Medium to thin-shelled *Myalina* possessing distinct commarginal growth squamae, broad radial plicae, and distinct byssal sinus.

DESCRIPTION: Shell moderately large (max. height = 5.2 cm); triangular in outline; hinge-line straight, less than total length of shell; small posterior auricle present in most specimens, especially in later growth stages; anterior margin slightly concave indicating small byssal sinus; posterior margin broadly convex, nearly parallel to anterior margin; beaks terminal, arcuate, and projecting inwards; shell retrocrescent with angle α about

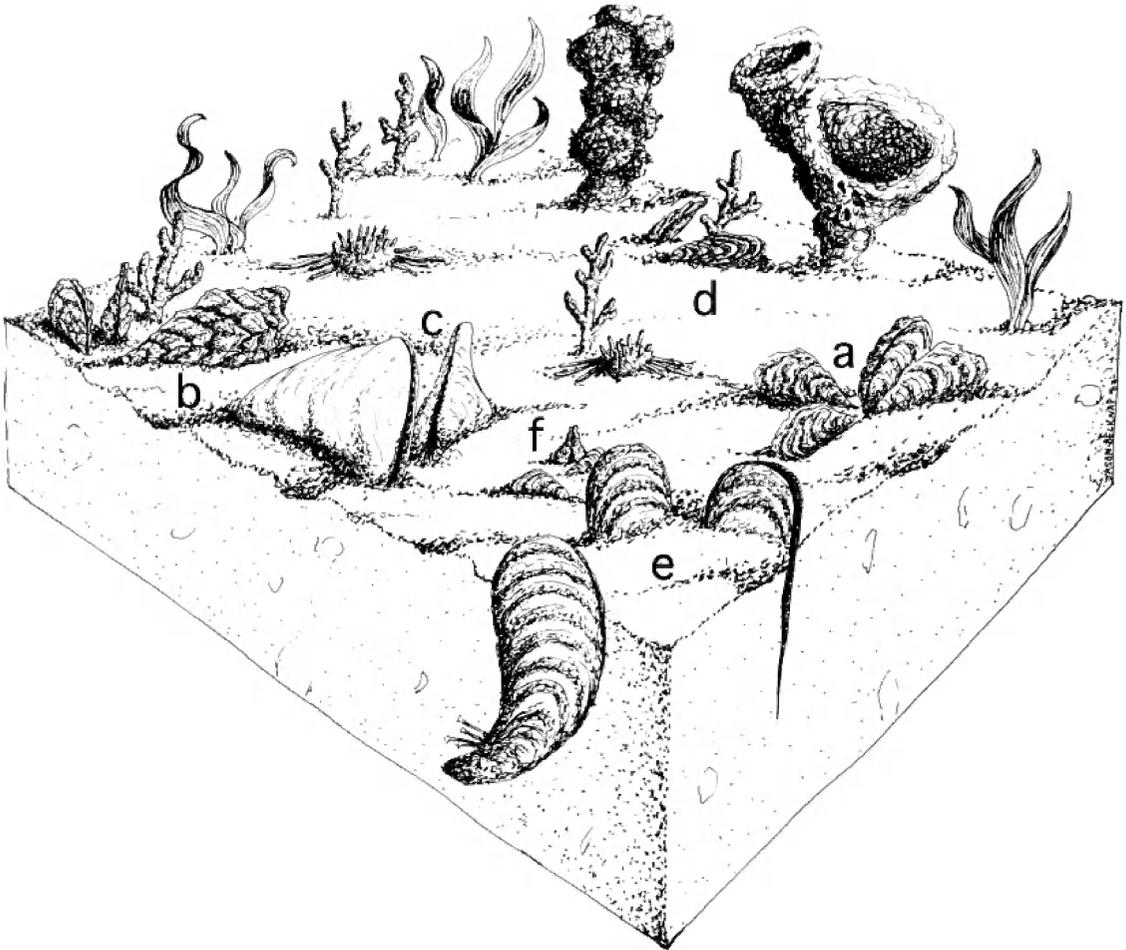


Fig. 6. Hypothesized living habits of Permian Myalinidae. **a**, *Myalina lamellosa* McRoberts and Newell, n.sp.; **b**, *Myalina plicata* McRoberts and Newell, n.sp.; **c**, *Myalina copei*; **d**, *Elversella rugosa*; **e**, *Novaculapermia boydi*; **f**, *Myalinella acutirostris*.

40° in earlier growth stages, becoming nearly infracrescent in adult stages. Surface of both valves ornamented by numerous commarginal growth lamellae. Lamellae becoming more pronounced and at wider spaced intervals by curling up and outwards in late growth stages; strong radial plications in both valves, more pronounced on valve exterior, becoming fainter on posterodorsal margin. Body cavity extending far into umbones; dentition consists of single linear tooth on right valve formed by sharp fold in cardinal area, fitting into a narrow furrow in left valve. Ligament opisthodontic, duplivincular; between 5 and 10 grooves slightly acute to nearly parallel,

intersecting hinge-line at less than 10°, grooves becoming fainter posteriorly along a broadening hinge plate. Pallial line faint but continuous, with a single large ovate raised posterior adductor scar nearly 1 cm in diameter. Shell moderately thin; ultrastructure unknown. See table 2 for measurements.

REMARKS AND COMPARISONS: This being the only known *Myalina* with radial plicae, it is unlike any other species known to us. In other characteristics, however, this species resembles, especially in early growth stages, *Myalina lamellosa* in its position of raised growth squamae. However, *M. plicata* differs from *M. lamellosa* in having greater α angles

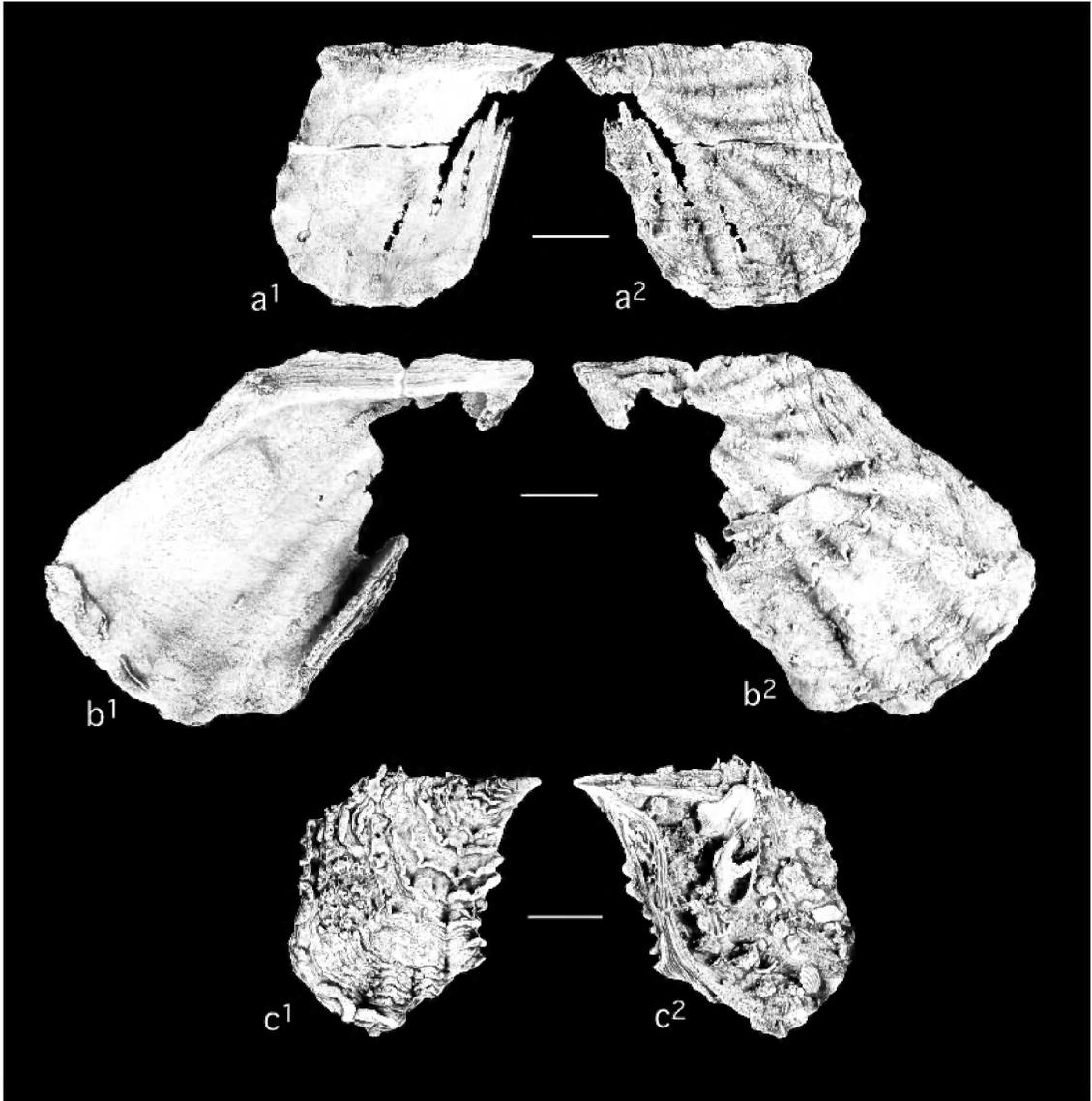


Fig. 7. *Myalina plicata* McRoberts and Newell, n.sp. Scale bar is 1 cm. **a**, holotype KU 310505 (KU loc. 27), left valve interior (**a**¹), exterior (**a**²); **b**, paratype, USNM 431351 (USNM loc. 706c), left valve interior (**b**¹), exterior (**b**²); **c**, paratype, USNM 431353 (USNM loc. 706c), right valve exterior (**c**¹), interior (**c**²).

and tending to become more infracrescent in later growth stages.

MATERIAL: The collection consists of 10 left valves and 5 right valves.

AGE AND OCCURRENCE: Word Formation (Guadalupian), localities: USNM-706c, USNM-721j, ?USNM-706e, University of Kansas Loc. 27.

ETYMOLOGY: Specific name refers to prominent and radial plications.

Myalina copei Whitfield, 1902
Figure 8

Myalina copei Whitfield, 1902: 63–66, text fig. 2 (not fig. 1).

TABLE 2
Myalina plicata McRoberts and Newell, new species
 (Measurements in millimeters; see fig. 3 caption for abbreviations.)

Specimen	Valve	H	L	HL	MGV	α	β	LG
KU 310505	LV	37.6	38.9	32.9	48.7	72	74	6
USNM 431351	LV	52.8	67.9	41	75.7	58	42	10
USNM 431352	LV	26.1	28.5 ^a	23.7 ^a	32.5 ^a	68	92	5
USNM 431353	RV	43	42.1	38.6 ^a	53.2	82	81 ^a	8
USNM 431354 ^b	RV	18.3	25.6	25.6	26.9	65	90	6
USNM 431355 ^b	LV	27.1	33	30.1	39.1	59	86	na
USNM 431356 ^b	LV	28.1	34.1	29.7	38.9	61	92	na

^a Estimated from broken shell.

^b Measurements taken on commarginal growth lamellae.

Myalina copei Whitfield, Newell, 1942: 55, pl. 4, figs. 1a–c, pl.

TYPE SPECIMEN: Lectotype AMNH-8364/2 designated by Newell (1942).

DESCRIPTION: Shell large (max. height nearly 7 cm), retrocrescent becoming infracrescent later in ontogeny. Posterior alation moderately to strongly developed and relatively flattened; anterior lobe small developed in both valves; byssal sinus formed by broad invagination on anterior-ventral margin. Shell surface relatively smooth except for faint, evenly spaced commarginal growth lines in some specimens. Body cavity broad, extending deeply to anterior margin; ligament duplivincular, ligament area broad, possessing numerous deeply incised grooves essentially parallel to the hinge margin or intersecting at a very low angle ($< 5^\circ$); musculature unknown. Shell ultrastructure unknown. See table 3 for measurements.

REMARKS AND COMPARISONS: The outline, angular dimensions, hinge features, and especially the extended posterior auricle seem to agree with previously illustrated specimens of *M. copei*. Although Newell (1942) described *Myalina copei* as inequivalved as the right valve was somewhat smaller and fitting within the left valve, we have no conjoined or disarticulated valve pairs from the same individual to confirm this observation. Newell (1942) commented on the similarity in shape of *Myalina copei* and *Myalina pliopectina* Newell. *Myalina copei* can be distinguished from *M. pliopectina* Newell in possessing a somewhat thicker shell and having a more upright form (greater angle α in adult

specimens. This difference in angle α may be difficult to discern in immature or fragmented specimens.

MATERIAL: The collection consists of five left valves and two right valves.

AGE AND OCCURRENCE: Lower Hueco Formation (Wolfcampian), locality AMNH 48. Although this Formation is not listed in figure 1 as it is known from the Hueco Mountains near El Paso, Texas, according to Cooper and Grant (1972), it is likely age-equivalent to either the lower part of the Neal Ranch Formation or the underlying "Udenites-bearing shale member" of the Gaptank Formation. According to Newell (1942), *M. copei* is known from the Hueco Mountains and other localities in Texas (including the type specimens from Shackelford County) as well as Kansas and Nebraska.

Genus *Myalinella* Newell, 1942
 [nom. transl. Newell, 1969]

TYPE SPECIES: *Myalina meeki* Dunbar, 1924, by original designation

Myalinella acutirostris
 (Newell and Burma, in Roth et al., 1941)
 Figure 9d

Myalina squamosa Girty, 1908: 429, pl. 16, fig. 22, non pl. 29, fig. 15 (= *Myalina lamellosa*).
Myalina sp. Newell, 1940: 286, pl. 2, fig. 1.
Myalina acutirostris Newell and Burma in Roth et al., 1941: 315, pl. 45, figs. 11–15.
Myalina acutirostris Newell et al., 1953, pl. 22, fig. 14.

TYPE SPECIMEN: Holotype UWM 20846.

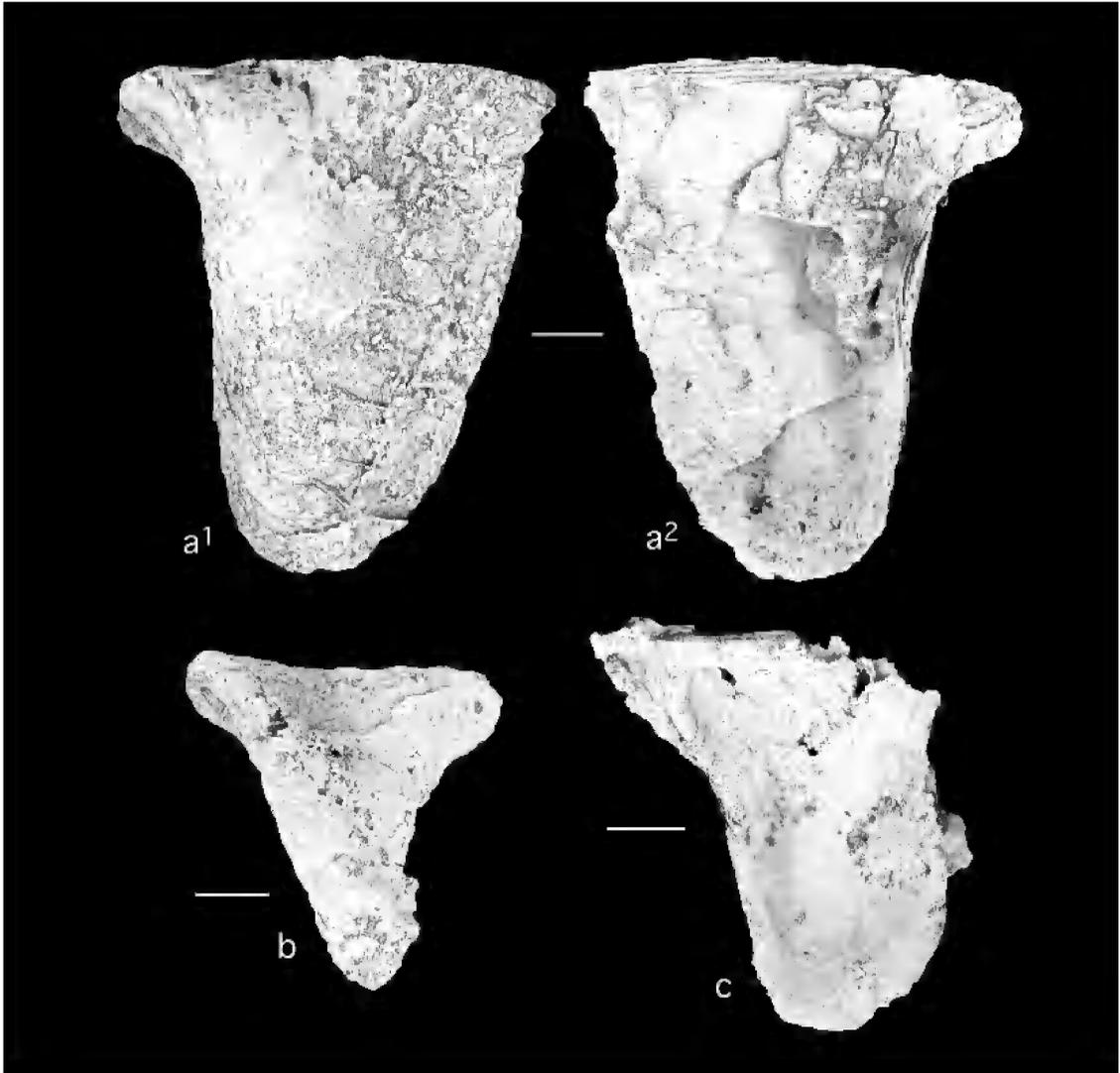


Fig. 8. *Myalina copei*. Scale bar is 1 cm. Specimens from AMNH locality 48. **a**, AMNH 43310, left valve exterior (**a**¹), left valve interior (**a**²); **b**, AMNH 43320, left valve interior; **c**, AMNH 433214, right valve interior.

TABLE 3
Myalina copei Whitfield
(Measurements in millimeters; see fig. 3 caption for abbreviations.)

Specimen	Valve	H	L	HL	MGV	PAV	α	β	γ	LG
AMNH 43310	LV	69.7	62.1 ^a	62.1 ^a	78.9	64.0 ^a	89	107	83	5
AMNH 43312 ^b	LV	27.6	27.8	29.5	43.3	28.9	84	98	65	1
AMNH 43313	LV	47.6 ^a	42.5	48.6	59.0 ^a	59.1	87	119	51	3
AMNH 43314	RV	51.4	49 ^a	49.0 ^a	62.9	46 ^a	82	99 ^a	32	5

^a Estimated from broken shell.

^b Measurements taken on commarginal growth lines.

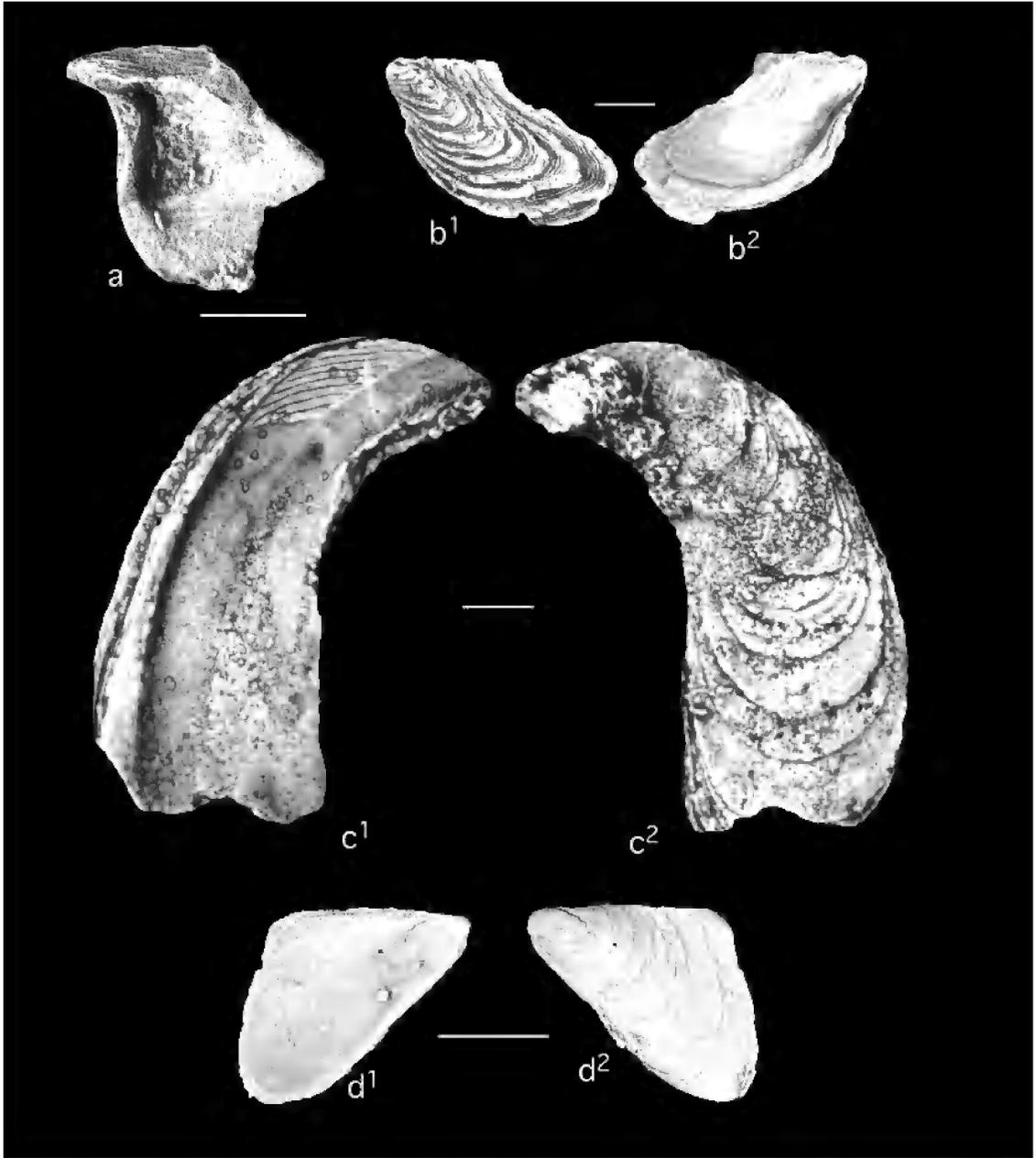


Fig. 9. **a,b.** *Elversella rugosa*. **a**, right valve interior USNM 431322; **b**, articulated valve pair USNM 431323, left valve (**b**¹), right valve (**b**²); **c.** *Novaculapermia boydi*, holotype USNM 487771, left valve interior (**c**¹), exterior (**c**²); **d.** *Myalinella acutirostris*, USNM 431357 (USNM loc. 721-u), left valve interior (**d**¹), exterior (**d**²).

DESCRIPTION: Shell moderately small (height = 1.8 cm), triangular; hinge margin dorsal, slightly arched, 0.8 times as long as the greatest shell length and about equal to the shell height; umbo slightly behind ante-

rior-most margin, umbonal ridge rounded in early stages, becoming broad and poorly defined at later growth stages; retrocrescent with α slightly increasing from 42° to 60° during growth; β angle increasing from 35°

to 72° during growth; shallow indentation or byssal sinus along anteroventral margin; anterior lobe small, poorly demarcated from main part of shell. Surface of left valve ornamented by six primary commarginal growth squamae, interspaced with numerous finer commarginal growth lines. Body cavity broad, extending deeply to anterior margin; ligament duplivincular, ligament area narrow, possessing two or three posterior deeply incised grooves essentially parallel to the hinge margin; musculature unknown. Shell thin, ultrastructure unknown.

REMARKS AND COMPARISONS: Appears to differ from other Myalinidae in its small size, triangular form, rather smooth surface, small anterior lobe demarcated by shallow sulcus, and straight anteroventral margin.

MATERIAL: Our only specimens from the Glass Mountains are two left valves.

AGE AND OCCURRENCE: Lower Cathedral Mountain Formation (Leonardian), locality USNM 721u; Getaway Member, Cherry Canyon Formation (Guadalupian), locality AMNH 512 (= USNM 728). Additional Guadalupian specimens assigned to this species are known from Quartermaster Formation of Texas (Newell and Burma *in* Roth et al., 1941) and the Whitehorse Sandstone of Oklahoma (Newell, 1940).

Genus *Novaculapermia* McRoberts and Newell, 1997

TYPE SPECIES: *Novaculapermia boydi* by original designation (McRoberts and Newell, 1997).

Novaculapermia boydi McRoberts and Newell, 1997
Figure 9c

Novaculapermia boydi McRoberts and Newell, 1997: 488, pl. 1, figs. 1–8, text-fig. 1.

TYPE SPECIMEN: Holotype USNM 487771.

DESCRIPTION: Shells large (max. dimension about 12 cm), relatively flat, lacking umbonal ridge or keel; juvenile specimens retro-crescent becoming infracrescent at about 4 cm from umbo, with an elongated posterior margin and nearly parallel anteroventral and posterodorsal margins; slight anteroventral fold which likely served as a byssal sinus. Surface of both valves equally ornamented

by numerous commarginal growth squamae that are somewhat unevenly spaced; lacking radial ornament. Body cavity narrow; umbonal septum absent. Ligament duplivincular, ligament area of left valve broad and flat, incised by eight parallel ligament grooves that are at a steep angle to lower margin of the hinge area, the anterior ends of the ligament grooves abruptly terminate along a steep diagonal groove radiating from the beak to the body cavity. In well-preserved specimens, clear bilobate pallial line extending along internal valve margin to a length of 7 cm in adult specimens, posterodorsal lobe the larger of the two; posterior adductor scar large (9 mm in diameter) and ovate, situated within posterodorsal pallial lobe. Shell moderately thick; ultrastructure unknown.

REMARKS AND COMPARISONS: This species is unlike any known to us, and it is unlikely that that it would be confused with other Permian Bivalvia.

PALEOAUTECOLOGY: Because none of the specimens were recovered *in situ*, the life orientation for *Novaculapermia boydi* remains in question. A hypothesized reconstruction in which the bivalves were semi-infaunal with their sagittal plane oriented vertically was illustrated by McRoberts and Newell (1997). This interpretation is further corroborated by the discovery of additional specimens exhibiting encrusting serpulid(?) tubes beginning about 4 cm from the beak and extending to the posterior shell terminus.

MATERIAL: The collection consists of more than 30 valves including several articulated valve pairs.

AGE AND OCCURRENCE: Cathedral Mountain Formation (Leonardian), localities USNM 702, 702un, AMNH 500; Road Canyon Formation (Guadalupian) locality USNM 703c; Word Formation (Guadalupian), locality 706c.

Genus *Elversella* McRoberts and Newell, 2001

TYPE SPECIES: *Elversella rugosa* by original designation (McRoberts and Newell, 2001).

Elversella rugosa McRoberts and Newell,
2001

Figure 9a,b

Myalina squamosa?, Girty, 1908: 429, pl. 29, fig. 15, not *Myalina squamosa* Sowerby, which is a Devonian form.

Elversella rugosa McRoberts and Newell, 2001: 2, fig. 2.

TYPE SPECIMEN: Holotype USNM 431325.

DESCRIPTION: The valves are moderately small (maximum dimension generally less than 5 cm). In profile, the beaks are conspicuous and extended forward above a broad and shallow anterior sinus. The umbonal ridge, which is poorly defined in later growth stages, curves down and backward at the margins, forming an angle of less than 45° with the hinge at the rounded posteroventral extremity. The specimens bear five or six duplivincular ligament grooves that are slightly curved and intersect the hinge margin at an angle slightly less than 30°. The left valve bears as many as 15 coarse commarginal rugae, whereas the right valve is less convex and nearly smooth. Between the coarse rugae of the left valve are numerous fine commarginal growth lines. The right valve margin below the hinge lies well within the edge of left valve; both valves bear a small anterodorsal auricle above a rounded sinus and byssal gape. The specimens contain a poorly preserved but simple and continuous pallial line roughly parallel to the posteroventral margin. Further details of the musculature and shell microstructure are unknown due to poor preservation.

REMARKS AND COMPARISONS: *Elversella rugosa* appears similar in outline and ornamentation to one of the several specimens Girty (1908: 29, fig. 15) attributed to *Myalina squamosa* Sowerby from the Permian of the Glass Mountains and may therefore be conspecific. However, other Permian specimens attributed by Girty to *M. squamosa* (e.g., Girty, 1908: 16, fig. 22) bear distinctively different ornamentation and lack an anterior auricle and therefore clearly represent a different species.

MATERIAL: More than 40 specimens, including many articulated valve pairs and nearly equal numbers of left and right valves.

AGE AND OCCURRENCE: *Uddenites*-bearing

Shale Member, Gaptank Formation (Wolfcampian), locality USNM 701e; Neal Ranch Formation (Wolfcampian) localities USNM 701, USNM 701a, USNM 701c, USNM 701d, USNM 701k; Taylor Ranch Member, Hess Formation (Leonardian), localities USNM 702d, USNM 702e; Cathedral Mountain Formation (Leonardian), localities USNM 702, USNM 702a; Road Canyon Formation (Guadalupian) locality USNM 702c.

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