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## Silicified *Leptodesma* (Bivalvia; Pteriomorphia) from the Texas Permian

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### ABSTRACT

The description here of *Leptodesma falcata*, new species, continues our ongoing study of bivalve mollusks of the Permian-Triassic faunal crisis. Our collection of silicified valves is from a single locality in the intensively sampled Permian strata of West Texas, which suggests that *L. falcata* appeared and became extinct rapidly. Such easily missed endemic populations may explain the disjunct records of some Permo-Triassic Lazarus taxa. Unusual features of the new species include its simple dentition, in contrast to the complex array of teeth of middle Paleozoic pterineids, and its evidence of fibrous prismatic microstructure, an addition to the known microstructural variability of the family.

### INTRODUCTION

*Leptodesma falcata*, the new species described here, is of interest from several standpoints. Unlike most fossils of the family Pterineidae, our study collection is a particularly fine sample of excellent specimens. The quality of the silicified valves, freed in the laboratory by dissolution of the host limestone, has allowed detailed observation of important shell characters such as denti-

tion and microstructure. This view of pterineid morphology is especially noteworthy because the species in question lived during the final chapter of the family's long history, and the last third of that history is very poorly known. The first representative appeared in the Ordovician bivalve radiation and the family disappeared in the sweeping faunal extinction of the Permian. Although pterineids are common in many lower and middle Paleozoic bivalve assemblages, their post-

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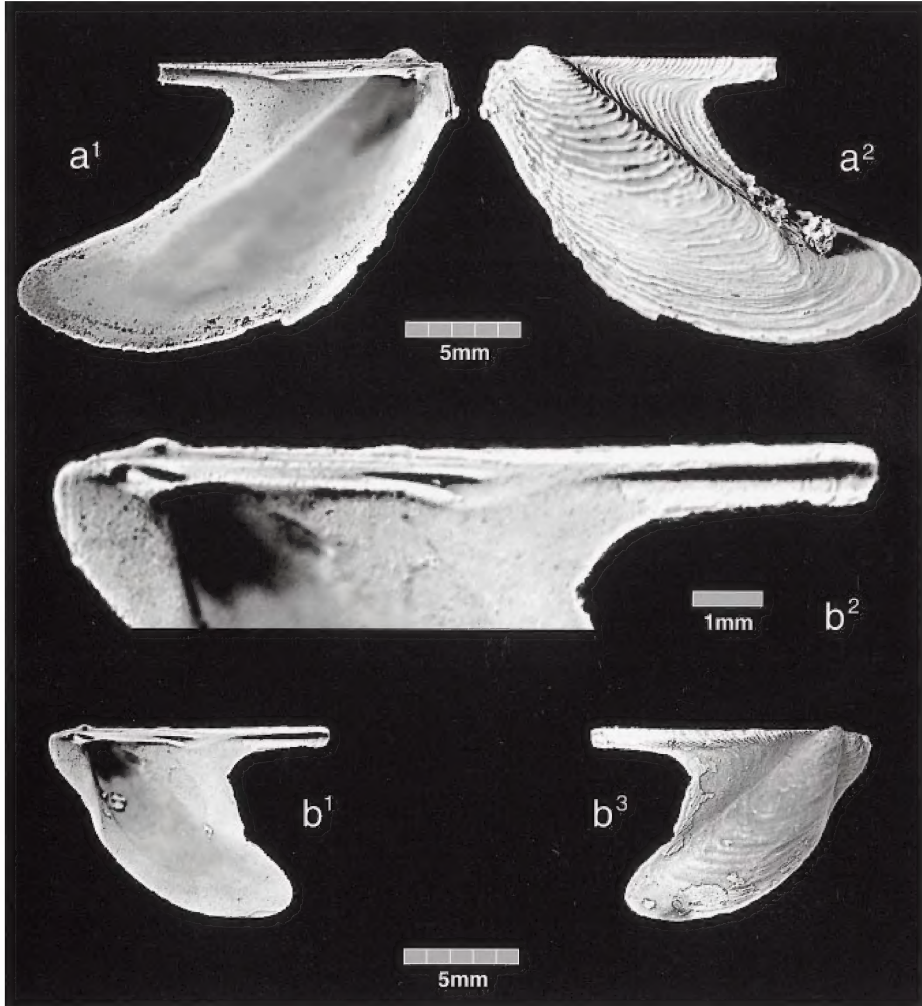


Fig. 1. *Leptodesma falcata* Boyd and Newell, new species, silicified valves, Middle Permian, Road Canyon Fm., West Texas, USNM loc. 703c. **a.** Holotype, LV, interior (a<sup>1</sup>) and exterior (a<sup>2</sup>) views, USNM 431327; **b.** RV, interior (b<sup>1</sup>, b<sup>2</sup>) and exterior (b<sup>3</sup>) views, USNM 431328.

Devonian record is poor in both quantity and quality.

Another point of interest is the apparently localized occurrence of the new species in time and space. We have found it in only one of the many West Texas Permian collections at our disposal, suggesting that it appeared and became extinct rapidly. It could easily have been missed in a less intensively sampled geographic and stratigraphic venue. If gaps in the known ranges of Lazarus taxa were originally filled by a succession of endemic and short-lived species, the unlikeli-

hood of discovering such evidence may explain some of the disjunct records.

#### THE FAMILY PTERINEIDAE

For students of Paleozoic bivalves, the pteriomorphian family Pterineidae poses more than its share of problems. It is composed of numerous Paleozoic genera with or without surface ornament. They are characterized by retrocrescent shape, forward-positioned beak, small anterior auricle, large posterior wing, and a dentate hinge plate

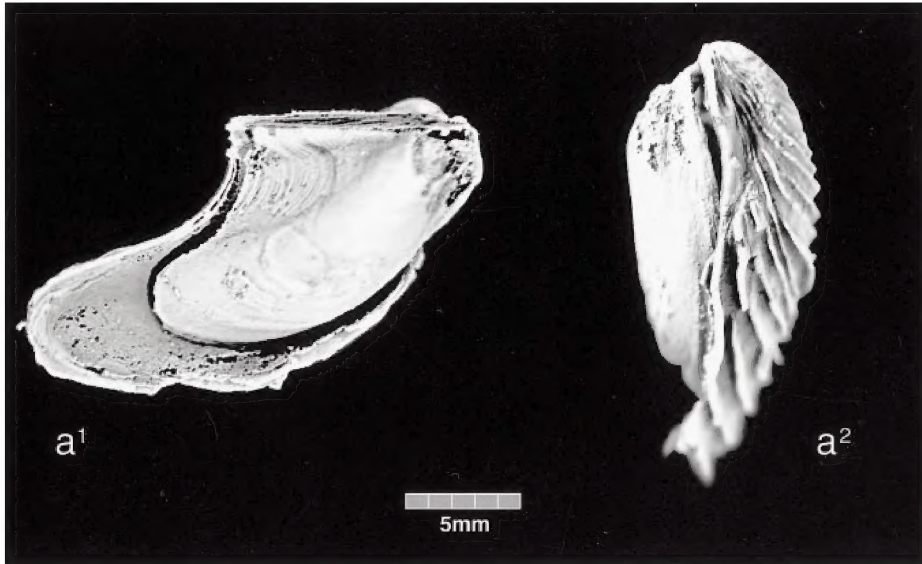


Fig. 2. *Leptodesma falcata* Boyd and Newell, new species, silicified articulated shell, USNM loc. 703c, USNM 431329. **a1**. RV toward viewer; note strongly discordant valve margins; **a2**. anterior end toward viewer; slitlike byssal gape visible in upper part of commissure.

with a duplivincular ligament insertion (Newell and LaRocque, 1969: 299). The poor preservation typical of pterineid fossils has resulted in a proliferation of poorly characterized taxa with little morphological information other than general shape and ornamentation.

The unsatisfactory status of pterineid generic-level taxonomy was recognized decades ago by McAlester (1962: 12, 26) who eloquently expressed his frustration in assigning generic names to Devonian pterineid species. The uncertainty concerning taxonomic significance of particular morphological features has been echoed by others (e.g., Pojeta et al., 1986: 92). Given this state of affairs, it is not surprising that phylogenetic relationships of the Pterineidae are matters for speculation. In a recent paper dealing with bivalve phylogeny, Waller (1998: 26) interpreted the Pterineidae as a paraphyletic stem group that gave rise to several other pteriomorphian clades. In his analysis, pterineid plesiomorphic characters include the duplivincular ligament and the shell structure consisting of inner nacreous layers and outer prismatic calcitic layers.

Another controversial subject involves pterineid mode of life. Theories and evidence

concerning life habits were reviewed by Johnston (1993). That paper, based on unusually well-preserved Devonian material, provides a perceptive analysis of the possible functional significance of various morphological features of pterineid shells.

The classification below follows that of the Treatise on Invertebrate Paleontology (Newell, 1969).

#### SYSTEMATICS

SUBCLASS PTERIOMORPHIA BEURLIN, 1944

ORDER PTERIOIDA NEWELL, 1965

SUPERFAMILY PTERIOIDEA GRAY, 1847

FAMILY PTERINEIDAE MILLER, 1877

Genus *Leptodesma* Hall, 1883

TYPE SPECIES: *Leptodesma potens* Hall, 1883. SD S.A. Miller, 1889.

DIAGNOSIS: Shells lacking costae; left valve umbo more prominent than right; large posterior auricle with deeply embayed margin; cardinal teeth few and variable in number.

DISTRIBUTION: Middle Silurian-Permian, cosmopolitan.

DISCUSSION: Hall (1883) differentiated his new genera *Leptodesma* and *Leiopteria* by

TABLE 1  
Measurements (mm) of *Leptodesma falcata* Boyd and Newell, new species, USNM loc. 703-c

L	H	L/H	MD	AT-PT	MD angle	C
Left valves						
28.9	18.2	1.6	29.7	—	30°	5.5
19.4	13.4	1.4	20.5	6.7	31	3.8
16.4	11.0	1.5	17.5	6.9	30	3.6
16.3	9.5	1.7	16.4	6.5	25	3.1
13.8	9.9	1.4	14.9	5.3	31	3.1
12.5	8.5	1.5	12.8	5.5	27	2.9
10.8	8.4	1.3	11.3	4.2	32	2.7
9.2	6.5	1.4	9.7	4.0	29	2.1
7.0	6.2	1.1	8.0	2.8	37	1.6
6.1	5.1	1.2	6.9	2.9	41	1.7
Right valves						
18.2	11.7	1.6	19.3	7.7	32°	3.1
17.6	9.4	1.9	18.6	7.2	24	3.1
11.8	9.8	1.2	14.0	5.3	40	2.0
10.7	8.5	1.3	11.8	4.9	40	2.0
10.3	7.3	1.4	11.1	5.2	35	1.8
8.5	6.6	1.3	9.7	4.3	36	1.6
7.9	6.4	1.2	8.9	4.2	39	1.7
7.7	5.7	1.4	8.4	3.9	36	1.5
5.2	4.8	1.1	6.1	3.1	46	1.5
4.5	3.9	1.2	4.9	2.9	45	1+

**L** = distance, parallel to hinge line, between anterodorsal corner and vertical projection of posteroventral extremity. **H** = distance, perpendicular to hinge line, between high point on dorsal margin and horizontal projection of ventral extremity. **MD** = length of straight line between high point of dorsal margin and posteroventral extremity. **AT-PT** = on LVs, distance from anterior end of anterior tooth to posterior end of posterior tooth (on RVs, use the equivalent sockets). **MD angle** = angle between dorsal margin and MD line. **C** = convexity.

the form of the anterior auricle, angular in the former versus rounded in the latter. In the Treatise on Invertebrate Paleontology, Newell and LaRocque (1969: 300–301) accepted this distinction at the subgeneric level, recognizing *Leptodesma* (*Leptodesma*) and *L. (Leiopteria)*. This practice was followed by Pojeta et al. (1986: 94), who refigured the original drawings of the type specimens and discussed their dissimilarities. We concur with the subgeneric usage and assign our new species to *L. (Leptodesma)*. It is worth noting, however, that our study collection exhibits significant variation in topography and outline of the anterior auricle.

*Leptodesma (Leptodesma) falcata* Boyd  
and Newell, new species

Figures 1–4

**DIAGNOSIS:** Small, posteriorly elongated shell with sharply pointed posterior wings;

valves strongly discordant; right valve (RV) less convex than left valve (LV); anterior auricle truncate; LV bears strong commarginal<sup>3</sup> ridges, RV unornamented; two cardinal teeth on LV, one on mature RVs; one prominent posterior lateral tooth on each valve.

**ETYMOLOGY:** Latin *falcata* (sickle-shaped) refers to the distinctive form of mature valves.

**DISTRIBUTION:** Road Canyon Formation; Middle Permian (Roadian Stage); Glass Mountains, West Texas, USA. *Leptodesma falcata* is known from a single locality, USNM 703c, described in detail by Cooper and Grant (1972: 142).

**MATERIAL:** Our study collection consists of 270 disarticulated valves (165 L; 105 R) and three articulated shells. All specimens are si-

<sup>3</sup> Cox (1969: N103) introduced this term “for direction usually described as concentric”. We accept the spelling established by Cox.

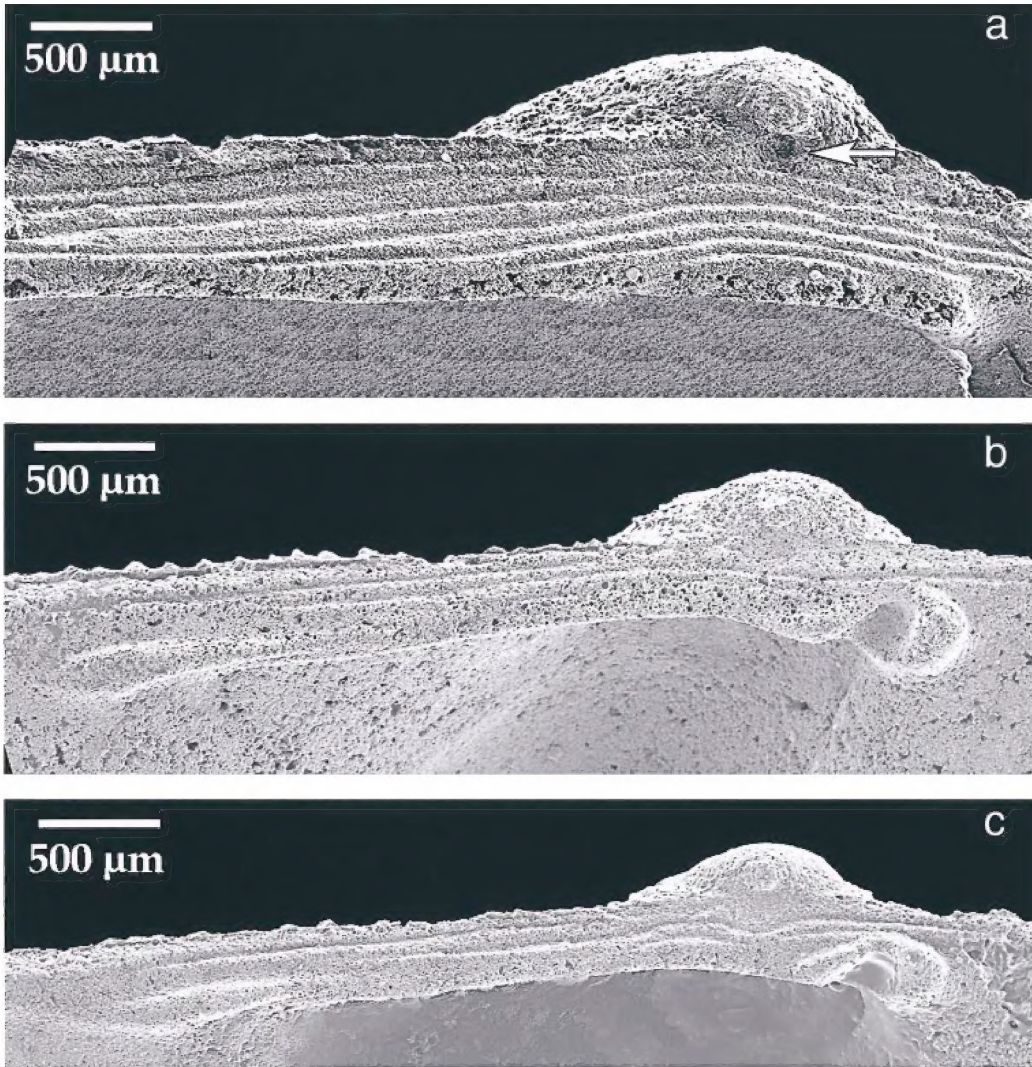


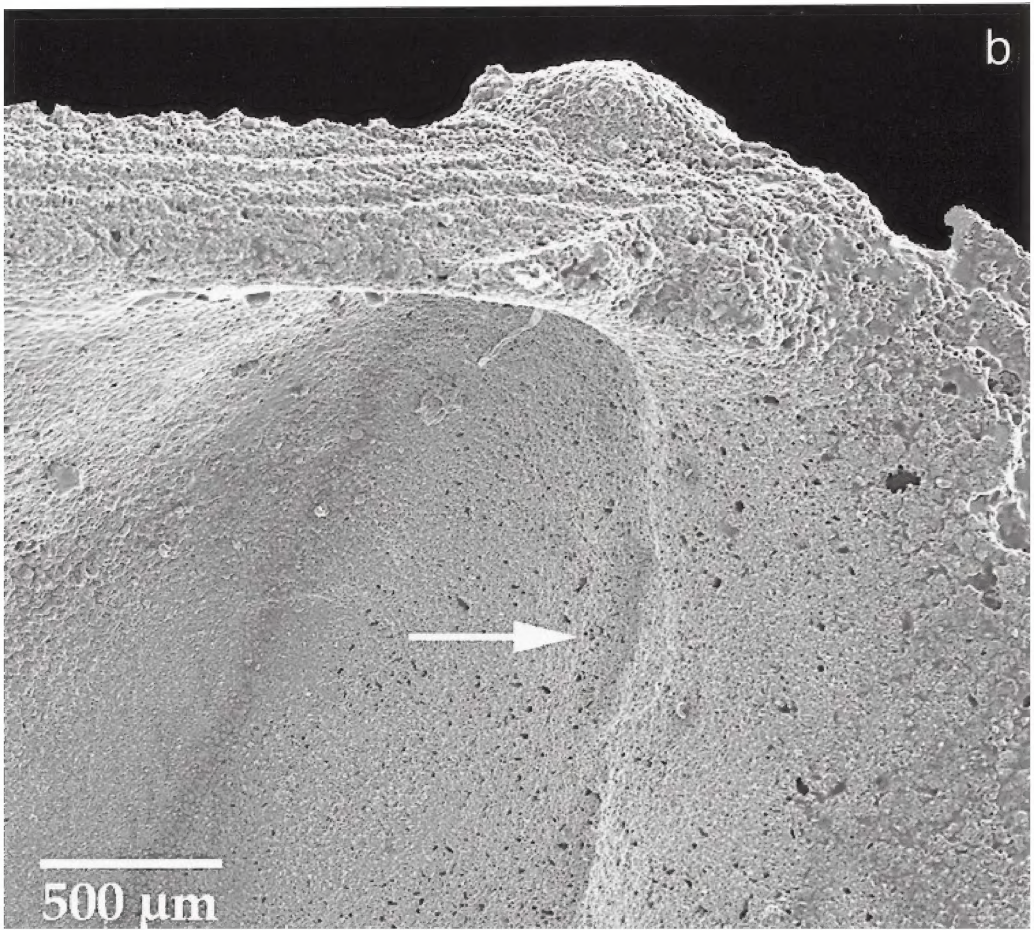
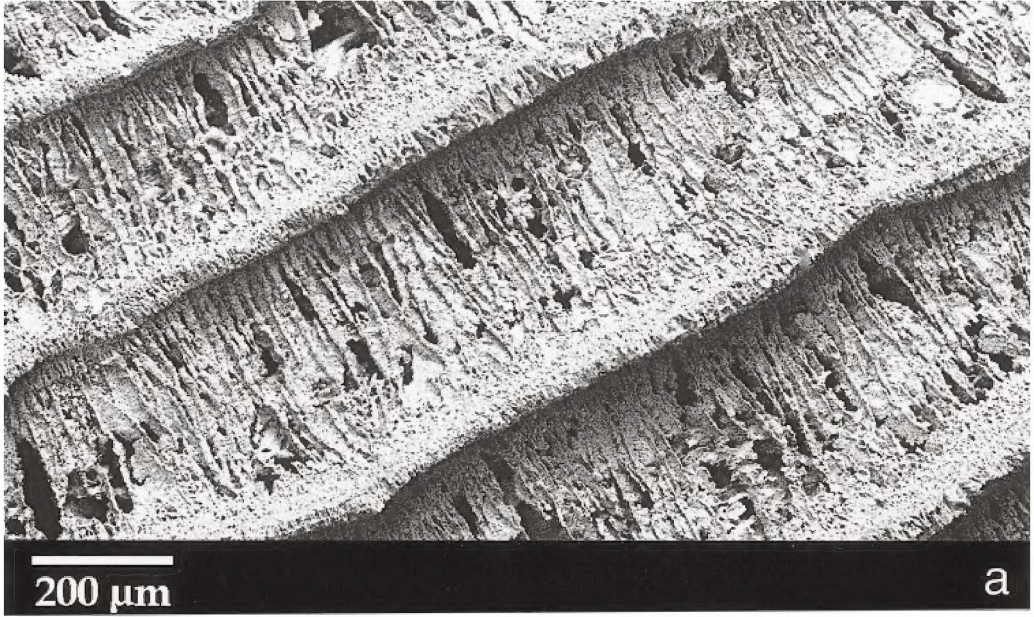
Fig. 3. *Leptodesma falcata* Boyd and Newell, new species, SEM views of three silicified LVs, USNM loc. 703c. Secondary electron images acquired from carbon-coated specimens. **a.** Duplivincular ligament area; note tiny resiliferlike pit (arrow) beneath beak; cardinal teeth broken; USNM 431330; **b.** Hinge area, tilted slightly to emphasize two cardinal teeth and posterior lateral tooth; USNM 431331; **c.** Cardinal area with few ligament grooves but full complement of teeth; USNM 431332.

licified. Forty-seven LVs and 25 RVs are essentially undamaged except for common breakage of the distal part of the posterior wing.

**DESCRIPTION:** The following observations are arranged in this sequence: 1. valve shape; 2. ornamentation; 3. muscle scars; 4. ligament; 5. dentition; and 6. microstructure.

1. During ontogeny, progressive accentuation of the posterior growth component produced the distinctive retrocrescentic shape

and arcuate umbonal ridge, both especially pronounced in LVs (table 1). The truncation of the anterior auricle margin, commonly cited as a criterion for the subgenus *L.* (*Leptodesma*) (e.g., Newell and LaRocque, 1969), is obvious on typical LVs but is less angular on many RVs. A change in slope, rather than a distinct sulcus, separates the anterior auricle from the main body of each valve. LVs lack a byssal sinus although the anterior margin below the auricle is slightly concave on



large specimens. By contrast, a concavity in this part of the margin typifies small RVs but is lost with increase in valve size. Our one well-preserved articulated shell (fig. 2) exhibits a slitlike byssal gape in anterior view. The deep posterior sinus, a distinctive feature of undamaged valves, is commonly diminished due to breakage of the mucronate posterior wing.

2. The flangelike commarginal ridges of LVs are prominent on umbo and anterior flank, but are weakly developed or absent beyond valve heights greater than 7 or 8 mm. On some valves, the change is abrupt. Where most prominent, the ridges rise sharply above the intervening troughs. They vary in spacing and in lateral continuity; mergers, offsets, and terminations are common. Ridge continuations on the posterior flank are subdued but they become closely spaced and uniform where meeting the long dorsal margin behind the beak, giving a serrate profile to that area.

3. Muscle attachment sites are poorly represented in our collection. Of the numerous valves with well-preserved inner surfaces, many show no indication of either muscle scars or pallial line. Where such evidence is present, it is commonly vague, as for the posterior adductor, or difficult to interpret because of inconsistent size and location, as for small anterodorsal pits. Johnston (1993: 33) discussed similar interpretive problems regarding umbonal scars in Devonian pterineids.

The part of the interior surface where a pallial line might be expected is featureless in most valves. Rare exceptions exhibit a well-defined line in the anterodorsal region, but it fades out ventrally and is not present on the posterior side of the valve. The posterior adductor scar, never sharply outlined, is commonly represented by a flattened or slightly indented area on the slope between the shelllike posterior auricle and the strong-

ly concave interior. In the anterodorsal part of each valve, we recognize a small scar on the shoulder separating the anterior auricle from the umbonal cavity (fig. 4b). In our interpretation, this scar is the imprint of a small anterior adductor.

4. The ligament area is dominated by as many as seven strongly asymmetric chevron grooves. The long and slightly sinuous posterior limbs of the chevrons meet the ventral margin of the cardinal area at very low angles (e.g., 6°). Well-preserved valves have a tiny (e.g., 0.2 mm base) resiliferlike pit directly beneath the beak, separating it from the apex of the first chevron (fig. 3a). This situation suggests the ontogenetic discontinuity described by Waller (1998: 21) who noted that in some Pteriomorphia a primary resilium is replaced by a duplivincular ligament system.

5. The simple dentition of this species (fig. 3b, c) contrasts sharply with the complex array of major and minor teeth in mature shells of some Silurian and Devonian pterineids (e.g., Johnston, 1991: fig. 9B; 1993: fig. 26). However, the growth series of the Devonian *Cornellites catellus*, elegantly diagrammed by Johnston (1993: fig. 26), begins with a simple hinge that invites comparison with that of our Permian material. One can speculate that the anterior cardinal and prominent posterior lateral of the LV of *Leptodesma falcata* are homologous with, respectively, teeth Ap3 and Pp3 of Johnston's figure 26. However, the equivalent to the posterior cardinal of *L. falcata* has to be sought among the secondary teeth that are introduced early in the ontogeny of *C. catellus*. In that series, tooth s5 bears the desired relationship to Ap3 (Johnston, 1993: fig. 26C), but the absence of s1 and s3 in *L. falcata* suggests that the relationship of its posterior cardinal to s5 of *C. catellus* represents analogous topog-

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Fig. 4. *Leptodesma falcata* Boyd and Newell, new species, SEM views of parts of two silicified LVs, USNM loc. 703c. **a.** Fibrous prismatic microstructure of outer ostracum revealed in incompletely silicified portion of posterior auricle; prominent ridges are commarginal ornament; backscattered electron image acquired from uncoated surface; USNM 431333; **b.** Anterodorsal area of LV interior; arrow indicates pit interpreted as anterior adductor muscle scar; cardinal teeth damaged; secondary electron image acquired from carbon-coated specimen; USNM 431334.

raphy rather than homology. In contrast, Johnston (personal commun., 2000) thinks there is reason to believe that s5 teeth in *Leptodesma*, *Umburra*, and *Cornellites* are homologs. He notes that s5 appears before s1 and s3 in *Umburra*. Assuming a similar ontogeny for *Leptodesma*, the loss of s1 and s3 could have occurred through pae-domorphosis.

As with the LV, the RV hinge of *L. falcata* is reminiscent of that of juvenile *Cornellites* (Johnston, 1993: figs. 23G, H; 29G). This is especially true of the posterior area with its prominent splinterlike tooth (Pp2 of Johnston) below the distinctive wedge-shaped socket. The slightly thickened dorsal rim of that socket is the equivalent of tooth Pp4 of Johnston's (1993) figure 29G. By contrast, tooth Ap2, the apparent equivalent of the knoblike cardinal tooth of *L. falcata*, is a ridge that slopes downward from the ligament area toward the anterior margin. At the anterior end of the hinge, *L. falcata* RVs lack an equivalent of the arcuate tooth Ap4 although a tiny protuberance in front of the anterior socket is present in small (<10 mm maximum dimension) valves. The absence of that minor tooth in mature RVs is the only change we can document involving addition or subtraction of teeth in the ontogeny of *L. falcata*. It is noteworthy that another Permian pterineid for which we have information on dentition resembles our hinges in simplicity although not in detail. Nakazawa and Newell (1968) described poorly preserved *Leptodesma* valves from Japan with one (LV) or two (RV) cardinal teeth and one (LV) or two (RV) posterior lateral teeth.

6. External surfaces of many LVs include areas that show evidence of the original microstructure of the outer ostracum (fig. 4a). In these places, closely spaced fibers and laths of silica are arrayed roughly perpendicular to growth lines. Dr. Joseph Carter (personal commun., 2000) interprets this pattern as fibrous prismatic to irregular spherulitic prismatic. This structure was not described in Carter's (1990: 205) review of pterineid microstructure, which summarized the sparse information on Devonian and Carboniferous species. As a

matter of historical interest, we note that Hall (1884: 184) may have observed this structure in a Devonian *Leptodesma*. His description of *L. protextum* stated that the surface of an exfoliated shell shows "obsolescent radii which appear to belong to the intimate shell-structure, and which are not shown on well-preserved specimens".

In Carter's (1990) report, the structure of the calcitic outer layer of *Leptodesma* LVs was said to be regular simple prismatic although in some other pterineids it varies from irregular simple prismatic to homogeneous mosaic. The same report mentioned only regular simple prismatic structure for the outer layer of pterineid RVs. In our collection, we have no unequivocal evidence of RV microstructure. Most external surfaces are unbroken expanses of cryptocrystalline silica. In rare valves, such surfaces are interrupted by granular patches with texture suggestive of very small simple prisms. The strongly discordant margins of closed valves (fig. 2) provide circumstantial evidence for a RV prismatic layer that originally extended posteroventrally beyond the inner layer. The resulting flexible margin of the RV should have produced a wide margin of contact between the two valves, with the adaptive aspects discussed by Carter and Tevesz (1978). Presumably, the flexible marginal area decayed soon after death. Carter (1990: 205) noted that middle and inner layers of pterineid shells are nacreous. Our specimens offer no evidence in this regard; the inner layer is represented either by cryptocrystalline silica or by a fine honeycomb of silica that we suspect represents partial replacement of recrystallized carbonate.

Comparisons: *Leptodesma gouldii* (Beebe), a common fossil in the Permian Whitehorse Sandstone of Oklahoma and Texas, was described in detail by Newell (1940). The new genus he erected for it, *Dozierella*, was later placed in the synonymy of *Leptodesma* (Newell and LaRocque, 1969). The Whitehorse species differs from *L. falcata* in having a more complex dentition and in lacking commarginal ridges and alate wing.

Girty (1908) illustrated a LV from the West Texas Permian that resembles ours in



general form and ornamentation. He based a new species, *Pteria guadalupensis*, on the specimen and provided a single illustration in which the entire anterior margin is restored. Hinge characters are unknown. Although his description is based on one specimen, he cited two occurrences of the species in the Capitan Formation of the Guadalupe Mountains. More material from that formation would be necessary to determine the validity of Girty's species. Furthermore, as Girty (1908: 426) recognized, an unequivocal generic assignment would require knowledge of hinge characters. The problem of homeomorphy in the families of pteroid bivalves is exemplified by the striking resemblance of our duplivincular species to the multivincular *Bakevella ceratophaga* from the Permian of England (Logan, 1967: pl. 4, figs. 13–16).

Another Permian species similar in general form to *L. falcata* is *Leiopteria carandibbiensis* Dickins, 1957, from Australia. It lacks the arcuate umbonal ridge and prominent beak of our species, and the ligament grooves are parallel longitudinal lines rather than chevrons. Its dentition is unknown.

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