A Unique Pterioid Bivalve from the Early Triassic of Utah

Authors: BOYD, DONALD W., and NEWELL, NORMAN D.

Source: American Museum Novitates, 2002(3375) : 1-9

Published By: American Museum of Natural History

URL: https://doi.org/10.1206/0003-0082(2002)375<0001:AUPBFT>2.0.CO;2

AMERICAN MUSEUM
Novitates

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, NY 10024
Number 3375, 9 pp., 2 figures, 1 table July 25, 2002

A Unique Pterioid Bivalve from the Early Triassic of Utah

DONALD W. BOYD[1] AND NORMAN D. NEWELL[2]

ABSTRACT

The new species *Bakevellia*? *silberlingi* is described from a single locality in the upper Thaynes Formation (mid-Spathian) near Salt Lake City. The 133 specimens studied are natural casts of siltstone freed from limestone in the laboratory by acid dissolution. In external form, *B.*? *silberlingi* resembles inequivalved and auriculate taxa of several pterioid families. However, its peculiar combination of hinge characters precludes unqualified assignment to either an established genus or family. The shallow, troughlike ligament scar extending backward from the beak resembles that of some pteriids, whereas the numerous teeth form a pattern typical of multivincular bakevelliids and their putative duplivincular ancestors. The new form is provisionally assigned to *Bakevellia* in recognition of the numerous characters it has in common with that familiar genus. The single-locality occurrence and unlikely mode of fossilization of this unusual taxon suggest that a significant amount of the diversity of early Triassic marine faunas may consist of short-lived, geographically isolated taxa awaiting discovery.

INTRODUCTION

Our purpose here is to call attention to a unique pterioid bivalve that adds to the sparse record of morphological grades and modes of life that characterized marine life following the end-Permian extinctions. The unusual hinge of the new form combines characters not found together in a currently recognized family. Its dentition is like that of many bakevelliids, but its pteriid-like ligament scar differs markedly from the bakevelliid multivincular condition. Otherwise, the

---

[1] Research Associate, American Museum of Natural History, Division of Paleontology (Invertebrates); Professor Emeritus, Department of Geology and Geophysics, University of Wyoming, Laramie, WY 82071.

[2] Curator Emeritus, American Museum of Natural History, Division of Paleontology (Invertebrates); Professor Emeritus, Columbia University, New York.

ISSN 0003-0082

morphology of the new species is generally compatible with that of *Bakevellia* in the family Bakevelliidae. The tentative assignment of our specimens to genus reflects their anomalous ligament condition. We should note that the second author finds the bakevelliid resemblance less than compelling, in that the special form of ligament pits is highly distinctive of the genus *Bakevellia*. He would tend to give greater importance to the fact that there are no multivincular ligaments in our specimens, and thus would place them in *Pteria*. However, he is willing to defer to the lead author's preference in this matter.

We have decided against creating a new taxon for several reasons. First, the new form is known from a single locality. Second, the specimens are imperfect siltstone casts; some have lost detail due to exfoliation of surface grains and others reflect imperfections of the preexisting mold. Third, existing literature on Paleozoic and early Mesozoic pteriaform bivalves indicates the need for major reassessment of their diagnostic characters and phylogenetic relationships. We are not prepared to undertake that task, but we believe the fossils described here should be on record for those who eventually will do so.

Our collection consists of 133 siltstone casts; all but two represent disarticulated valves. They were obtained by acid leaching of limestone blocks from a few ledges in the upper Thaynes Formation (Lower Triassic) at Salt Lake City, Utah. The peculiar mode of fossilization at this locality, injection of fluidized silt into open molds, is described elsewhere (Boyd et al., 1999). It resulted in highly variable preservation of morphological detail and none of the casts is a perfect replica of the original shell. Nevertheless, a credible morphological characterization has emerged from study of the entire collection.

The strata in question are in lithologic unit F, and within the Spathian conodont range zone 12 as reported in a study of Thaynes conodonts by Solien et al. (1979). Subsequent work on Spathian conodonts by Orchard (1995) resulted in taxonomic revision and reevaluation of the stratigraphic significance of some of the species reported by Solien (1979). The conodont assemblage listed for zone 12 by Solien et al. (1979) is probably mid-Spathian in age (M. J. Orchard, 2001, personal commun.).

SIGNIFICANCE

The new species reported here is of special interest from two standpoints. First, it enhances our perspective concerning the low-density recovery fauna that followed the end-Permian extinctions. Second, its peculiar hinge morphology includes features not found together in a currently recognized family of pterioid bivalves.

The new species is an addition to the sparse fauna that records the slow recovery of life in Early Triassic seas. The limited and unvaried nature of Early Triassic marine faunas has intrigued several generations of paleontologists (e.g., Newell, 1952; Twitchett, 1999). For this initial epoch of the Mesozoic, discovery of a new species has a greater influence on our sense of diversity than would the addition of yet another item to a lengthy faunal list. Furthermore, the single-locality occurrence and small size of the new form encourage the suspicion that a significant amount of the original diversity of Early Triassic faunas may reside in inconspicuous species that existed for a short time and in a limited area. In the present case, the habitat was an inner-shelf environment of a low latitude (circa 15°N paleolatitude) sea whose eastern shoreline was in western Wyoming (Carr and Paull, 1983; Dubiel, 1994).

Our discovery also calls attention to the role of preservation in determining faunal diversity (Erwin and Pan, 1996). The morphological details that distinguish our Thaynes species probably would not have been recognized were it not for the study of insoluble casts freed from limestone host rock. Typical Lower Triassic bivalves are either imprints on bedding surfaces of siliciclastic strata or recrystallized valves locked in carbonate matrix. The casts we studied for this report are the product of a complex, no doubt rare, taphonomic scenario (Boyd et al., 1999).

The unusual hinge morphology of the new species calls attention to the need for reappraisal of the taxonomy and phylogenetic relationships of pterioid bivalves. Suspicions that the family Bakevelliidae is not monophyletic have been expressed by several workers (e.g. Tokuyama, 1959; Nakazawa and Newell, 1968; Cox, 1969). Pteriid versus pterineid ancestry for bakevelliid genera has been a matter of speculation by these and other authors (e.g., Carter, 1990: 207; Waller, 1998: 26). The great variability of bakevelliids in shape, dentition, and ligament is impressively documented by the 34 species of 13 genera illustrated in Muster's (1995) monograph on the family.

The ligament system naturally plays a role in discussions of ancestry (e.g., Waller, 1998: 6–27), and the bakevelliid multivincular condition achieved unusual potential for interpretation with discovery of ontogenetic series that begin with a one-pit stage (Nakazawa, 1959; Tokuyama, 1959; Farsan, 1972). This condition was termed the *Pteria* stage of bakevelliid ontogeny by Nakazawa (1959) and Tokuyama (1959) who considered it evidence for pteriid origin of some bakevelliid genera. Later, Nakazawa and Newell (1968) noted that the opposite line of descent could be possible if multiple pits had been reduced to one, a phenomenon documented by Stephenson (1952) in a growth series of the Cretaceous bakevelliid *Phelopteria dalli*.

The anomalous troughlike ligament scar of our new species represents an additional complexity that will have to be taken into account in any future reappraisal of relationships of bakevelliform genera. The unusual ligament scar might be an apomorphic character associated with a plesiomorphic dental pattern. The dentition is reminiscent of the hinge teeth of some Silurian duplivincular pterineids (e.g., Johnston, 1991: fig. 2A, B). The anterior series of irregular, transverse teeth is especially similar in Silurian and Triassic shells.

RELATIONSHIPS

For present purposes, we accept the diagnosis of the family Bakevelliidae and diagnoses of its included genera given by Cox (1969), with Carter's (1990: 206) addition concerning shell microstructure. As such, the family consists of elongate, inequilateral, variably inequivalved shells with or without a small anterior auricle and lacking a byssal notch. The ligament area is marked by multiple pits and dentition typically consisting of an anterior series of short, transverse teeth together with a few elongate posterolateral teeth. The calcitic outer layer of the shell commonly has regular simple prismatic structure; inner layers are nacreous. Valve surfaces are with or without radial sculpture.

Within that context, the type genus is set apart by its small to medium-size rhomboidal shape, anterior auricle, obtuse to pointed posterior wing, narrow anterior gape, and ‘‘never strongly inequivalved’’ condition (Cox, 1969).

Given the above criteria, our new species is deficient at the family level for lack of a multivincular ligament. An additional discrepancy at the generic level is the stronger valve inequality resulting from the negligible convexity of its RV.

As previously noted, a single ligament pit characterizes the early ontogeny of several bakevelliid species (e.g., Nakazawa, 1959: 202; Tokuyama, 1959: 150; Farsan, 1972: 147). These are tiny juveniles, typically $<$ 6 mm in hinge length, and later growth stages exhibit two or more pits. Our valves are in the size range where more than one pit would be expected, but the only noted ontogenetic change in ligament condition is progressive increase in height and length of the single ligament pit. The possibility that the Thaynes species is a paedomorphic representation of the one-pit stage seems unlikely because its broad troughlike ligament scar extending behind the beak is unlike the symmetrical resilifer beneath the beak in the one-pit stage of *Bakevellia* (e.g., Nakazawa, 1959: text fig. 5).

The form of the ligament pit in the new species is more like the posteriorly elongated resilifer of some pteriids (e.g. Hertlein and Cox, 1969: fig. C39, 4a) and we recognize other morphological similarities between our shells and members of that family. In two important characters, however, the Thaynes shells resemble bakevelliids more than pteriids. First, they lack the RV byssal notch characteristic of the family Pteriidae (Hertlein and Cox, 1969: N302). Second, their dentition includes an anterior series of irregular transverse teeth and one or two elongate posterior teeth, a combination typical of bakevelliids (e.g., Tokuyama, 1959: text fig., p. 150) and of some Silurian duplivincular pteriomorphians (e.g., Newell and LaRocque, 1969: fig. C35, 7b; Johnston, 1991: fig. 2B) that include likely ancestors of the Bakevelliidae (Waller, 1998: 26).

In summary, except for its anomalous ligament condition and strongly inequivalved shell, the new species qualifies for inclusion in *Bakevellia* sensu lato. Those atypical characters account for our qualified assignments to both genus and family.

SYSTEMATICS

SUBCLASS PTERIOMORPHIA BEURLEN, 1944

ORDER PTERIOIDA NEWELL, 1965

SUPERFAMILY PTERIOIDEA GRAY, 1847

DIAGNOSIS: Right valve commonly less convex than left; retrocrescent[3] with beaks far forward; ligament varied, external, and commonly opisthodetic; dentition absent to strong, with variable number of small transverse anterior teeth and elongate posterior laterals; microstructure typically calcitic simple prismatic outer layer and nacreous inner layers; byssate.

RANGE: Ordovician to Recent, cosmopolitan.

? FAMILY BAKEVELLIIDAE KING, 1850

DISCUSSION: As described above, we utilize the diagnosis of Cox (1969: N306) with the addition by Carter (1990: 206). In lacking multiple ligament pits, our new species fails to meet a basic condition of that diagnosis. Our decision to make a provisional assignment to the Bakevelliidae rather than to omit a family designation was prompted by two considerations. First, the assignment is consistent with our decision at the generic level. Second, as currently utilized (e.g. Muster, 1995), the family includes taxa representing a broad spectrum of hinge details.

? Genus *Bakevellia* King, 1848

DISCUSSION: In accepting Cox's (1969: N306) diagnosis of *Bakevellia*, we assign our new species to this genus with a query. In addition to its atypical single ligament pit, the new form is significantly inequivalved.

Bakevellia*? *silberlingi Boyd and Newell, new species

Figures 1, 2

DIAGNOSIS: Inequivalved, retrocrescent shells with protruding anterior auricle and prosogyrate umbones; beaks far forward on long but nonacuminate dorsal margin. Left valve (LV) with inflated umbonal ridge and broad posterior wing; right valve (RV) nearly flat. Unornamented except for sparse commarginal ridges. Cardinal area dominated by posteriorly elongated resilifer. Anterior array of irregular, short transverse teeth well separated from two or three inclined posterior teeth.

ETYMOLOGY: *silberlingi*, for Dr. Norman J. Silberling, expert on Triassic biostratigraphy of western North America.

DISTRIBUTION: Thaynes Formation; Lower Triassic (mid-Spathian); Wasatch Mountains, Utah, USA. *Bakevellia*? *silberlingi* is known from a single locality near Salt Lake City (SW¼, SE¼, SW¼ sec. 34, T1N, R1E, Fort Douglas 7½′ quadrangle, Utah). Here, several limestone ledges in the upper Thaynes contain siltstone casts of pelecypods which can be freed by acid dissolution of the enclosing rock. We have described this unusual mode of fossilization elsewhere (Boyd et al., 1999).

MATERIAL: Our study collection consists of 131 disarticulated valves (88L; 43R) and two articulated shells. The material is housed in the collection of fossil invertebrates, Department of Geology and Geophysics, University of Wyoming, Laramie. All specimens are siltstone casts. Eighteen LVs and seven RVs are essentially complete, but few of them retain sharply defined hinge features. The typically blurred aspect of dentition and ligament scar reflects imperfection of the original mold and/or loss of surface grains after the siltstone casts were freed from the matrix. Some specimens have been deformed by compaction. Although no obviously de-

---

[3] The term retrocrescent (Newell and Boyd, 1970: 229) replaces prosocline for an inequilateral valve outline produced by preferential posteroventral growth. Similarly, the terms infracrescent and procrescent replace orthocline and opisthocline. The replaced terms are misleading in that they describe valve outlines in directional terms contradictory to growth dynamics.

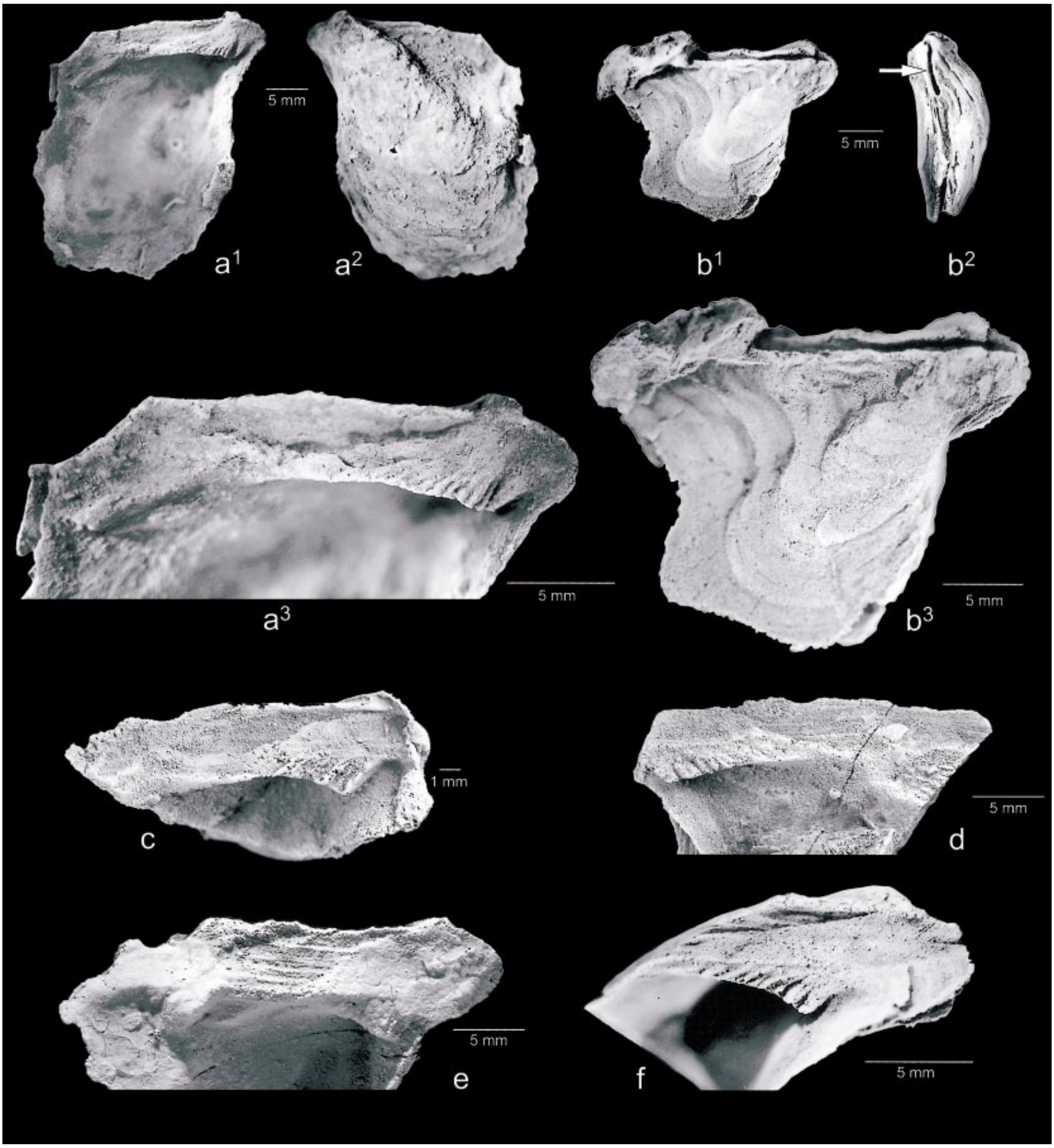

Fig. 1. *Bakevellia*? *silberlingi* Boyd and Newell, new species, natural casts (siltstone), Lower Triassic, upper Thaynes Fm., Salt Lake City, Utah, UW locality B7861. **a.** Holotype (UW A3979), LV, interior (a^1, a^3) and exterior (a^2); on enlargement (a^3), note elongate ligament scar with apex near beak, anterior row of transverse teeth, and poorly preserved inclined posterior teeth at left. **b.** Articulated specimen (UW A3982), right side (b^1, b^3) and anterior (b^2); posterodorsal corner concealed by pod of siltstone; note narrow byssal gape (arrow) at top-center of anterior view (b^2) and commarginal ridges formed by margins of successive growth stages (b^3). **c.** LV cardinal area (UW A3987) showing typical posteriorly expanded ligament scar; posterior teeth not preserved; irregular area at right is remnant of siltstone dike. **d.** RV cardinal area (UW A3988); note posteriorly expanded ligament scar; anterior and posterior valve margins incomplete. **e.** LV cardinal area (UW A3985) showing growth lines crossing ligament scar; dentition poorly preserved. **f.** Anterodorsal part of LV (UW A3981) showing relationship of narrow proximal part of ligament scar to beak and dentition.

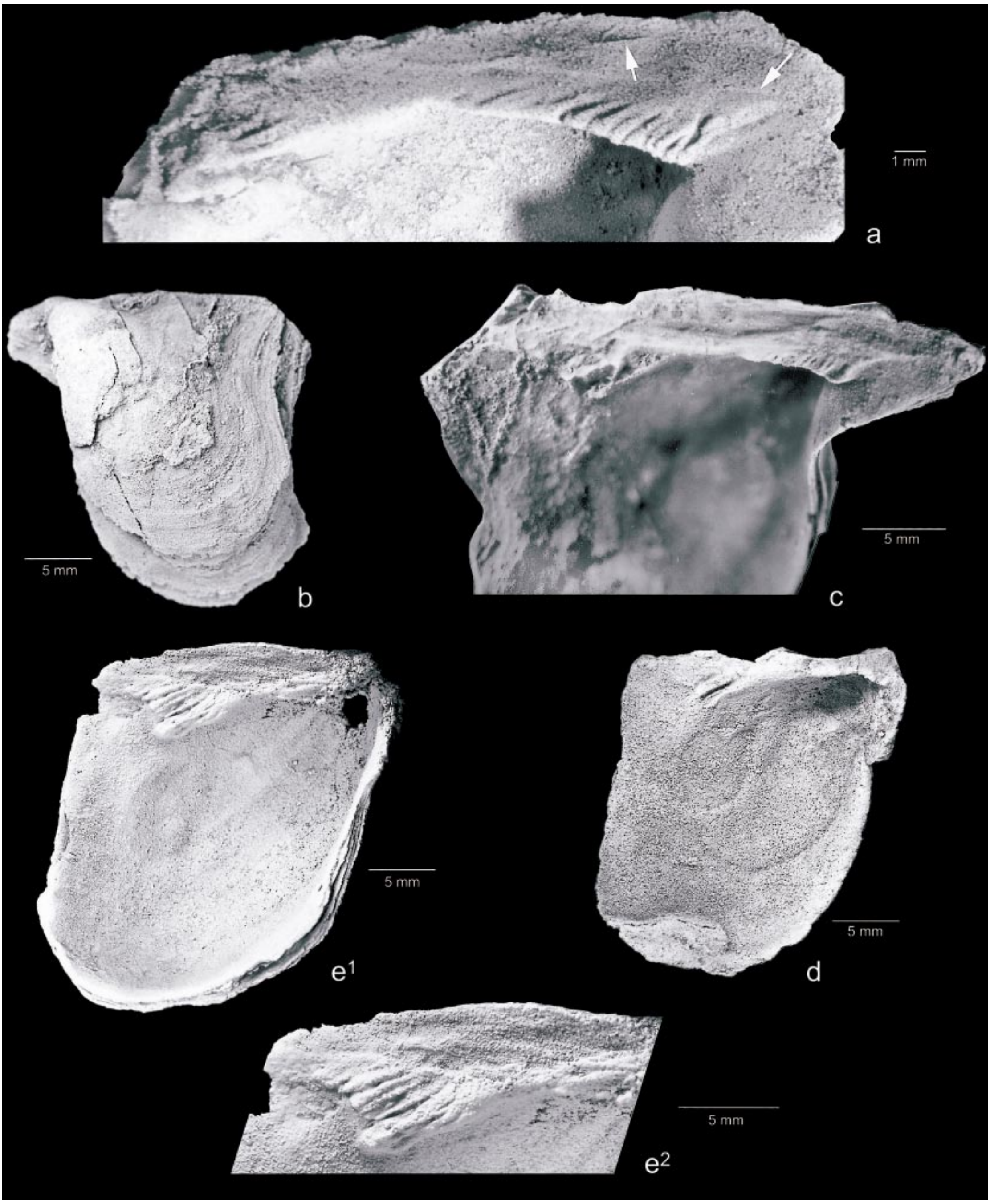

Fig. 2. *Bakevellia*? *silberlingi* Boyd and Newell, new species, natural casts (siltstone), Lower Triassic, upper Thaynes Fm., Salt Lake City, Utah, UW locality B7861. **a.** LV cardinal area with typical dentition (UW A3983); note irregularity of anterior teeth, more ventral location of inclined posterior teeth (at left), straight edge of hinge plate (right arrow), and ventral margin of ligament scar (left arrow); valve margins incomplete; dorsal part of ligament scar missing. **b.** LV exterior (UW A3986); note rounded anterior auricle. **c.** LV interior (UW A 3980); note angular anterior auricle; posterodorsal part of cast is deformed. **d.** LV interior with well-preserved pallial line and posterior adductor scar (UW

TABLE 1

***Bakevellia? silberlingi* Boyd and Newell, new species**[a]

L= length, H = height, MD angle = angle between dorsal margin and line connecting beak and ventral extremity, C = convexity.

max L of dorsal margin	max H ⊥ dorsal margin	H of card. area	MD angle	C
Left valves				
35	29+	5	46	10
33+	34+	8	—	10
31+	33	4	50	8
27+	34	6	64	10
27+	26	2	57	7
27	30	5	45	10
23	20	3	52	—
22+[b]	32	4	55	7
22+	26	4	55	10
20+	24	4	60	6
Right valves				
28[c]	28[c]	—	50	negligible
28	21	2	40	3
20	21	—	60	4
14+	17	2	50	3

[a] Measurements in millimeters; MD angle in degrees.

[b] Holotype.

[c] Restored margin.

formed valves were chosen for measurement, some of the variation shown in table 1 may be of secondary origin.

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

1. Typical valves are slightly higher than long (fig. 1a). The ventral margin joins anterior and posterior margins in a smooth curve; the slightly concave posterior margin forms a high angle (e.g. 70°) with the dorsal margin. In outline, the protruding anterior auricle varies from truncate (fig. 2b) to angular (fig. 2c). Its straight ventral margin slopes 30° to 40° relative to the dorsal margin of the valve. In typical LVs, the anterior auricle and posterior wing are set apart from the valve body by abrupt change in slope rather than by furrows. In the single well-preserved articulated shell (fig. 1b), the convex LV and flat RV have concordant margins. A very narrow gape high on the anterior commissure of this specimen (fig. 1b^{2}) presumably accommodated a byssus. None of the RVs exhibits a byssal notch.

Two of our rare complete specimens (figs. 1a, b) provide evidence of ontogenetic change in growth gradients reminiscent of the retrocrescent to infracrescent progression documented by Newell (1942) for *Myalina subquadrata*. The inequivalved, infracrescent adult of that species was interpreted by Stanley (1972) to have been epifaunal, attached by byssal threads, and recumbent on the flattened right valve. We envision a similar life style for *Bakevellia*? *Silberlingi*.

2. Sparse, irregularly spaced commarginal ridges represent times when mantle retreat was followed by renewed accretion leaving the edge of the previous valve surface topographically above the newer surface that ex-

---

←

A3989); dorsal and anterior areas incomplete. **e.** LV interior (UW A3984); note posterior adductor scar (e^{1}) and unusually large array of posterior teeth (e^{2}); anterodorsal area incomplete.

tends beyond it (fig. 1b^3). Such events were common in late growth stages of this species.

3. Although most of our specimens lack muscle scars, several show an oval posterior adductor scar about one-third of the way between the posterior teeth and the ventral extremity of the valve (fig. 2d). A few valves have a small, indistinct depression on the steep slope below the anterior end of the row of transverse teeth; we suspect that it represents the attachment site of a small anterior adductor muscle. Most of our specimens show no evidence of a pallial line. However, one LV (fig. 2d) exhibits a well-defined continuous line through the anterior half of the valve.

4. The distinctive ligament scar expands posteriorly from an apex just behind the beak (figs. 1a^3, c–e; 2c). The proximal part is a sharply defined depression (fig. 1f) whose ventral margin diverges from the upper edge of the cardinal area at a low angle (e.g., 15°). Posterior to the transverse teeth, the depression continues as a broad, shallow trough extending beyond valve mid-length (fig. 1a^3). On a few valves, parallel growth lines cross the ligament scar (fig. 1e).

5. A row of uneven transverse teeth occupies a narrow, posteriorly tapering shelf below the smooth anterior part of the cardinal area (fig. 1f). The teeth, typically eight or nine, decrease in length and relief from front to rear in the array. Likewise, the angle at which they meet the straight dorsal margin of the shelf (fig. 2a) decreases progressively along the row (e.g, from 60° to 30°). Posterior teeth are fewer, longer, and more ventrally located than the anterior teeth. Typical valves exhibit two prominent inclined ridges on the interior of the posterior wing (fig. 2c, d); they form an acute angle (e.g., 30°) with the lower margin of the cardinal area. Rare valves have a more complex posterior dentition apparently resulting from subdivision of the major teeth and sockets (fig. 2e). The lack of such complexity in many valves could be due to incomplete preservation of topographic detail. Poorly preserved hinges (e.g,. fig. 2c) invite this explanation but it seems unlikely to apply in other cases (e.g., fig. 2d).

COMPARISONS: We know of no other species with the unique combination of pteriid ligament scar and bakevelliid dentition found in *Bakevellia*? *silberlingi*. Its asymmetrical resilifer resembles that of the Jurassic pteriid *Pteroperna costatula* (Hertlein and Cox, 1969: fig. C39, 4a) whereas anterior and posterior teeth resemble those of the Triassic bakevelliid *Bakevelloides hekiensis* (Cox, 1969: fig. C40, 3).

Phelopteria dalli and *P. timberensis* from Cretaceous strata of Texas (Stephenson, 1952) are very similar in overall form to our new species, and *P. dalli* possesses a single shallow ligament groove extending backward from the beak. However, this feature characterizes the final growth stage in a growth series that begins with multivincular juveniles and demonstrates lateral expansion and merging of separate pits during ontogeny (Stephenson, 1952: 69). We see no evidence of such a transition in our collection. In dentition, *Phelopteria* differs markedly from *Bakevellia*? *silberlingi*.

ACKNOWLEDGMENTS

Most of the specimens described here are from limestone blocks processed in facilities at the University of Wyoming. The assistance of Dr. Xunhong Chen, then a graduate student at that institution, was especially helpful in both field and laboratory work. Additional specimens from the same locality were kindly provided by Dr. Christopher A. McRoberts, and we benefited from communications with Dr. Thomas Yancey concerning his work with Pennsylvanian bakevelliids. Photographic equipment and film were supplied by Dr. J.A. Lillegraven at the University of Wyoming, where Kelli Trujillo assisted with specimen photography. Additional photographs were taken at the American Museum of Natural History by Steve Thurston who also produced the final images for publication. We thank Walter Elvers for help in locating literature, and Margaret Boyd and Gillian Newell for the manuscript processing. Dr. M.J. Orchard advised us on the age significance of certain conodonts, and our final revision benefited from the work of reviewers Dr. Thomas R. Waller and Dr. Thomas E. Yancey.

REFERENCES

Boyd, D.W., D.E. Nice, and N.D. Newell. 1999. Silt injection as a mode of fossilization: a Triassic example. Palaios 14: 545–554.

Carr, T.R., and R.K. Paull. 1983. Early Triassic stratigraphy and paleogeography of the Cordilleran miogeocline. *In* M W. Reynolds and E D. Dolly (editors), Mesozoic paleogeography of the west-central United States: 39–55. Denver, CO: Rocky Mountain Section, Society of Economic Paleontologists and Mineralogists.

Carter, J.G. 1990. Evolutionary significance of shell microstructure in the Palaeotaxodonta, Pteriomorphia and Isofilibranchia (Bivalvia: Mollusca). *In* J.G. Carter (editor), Skeletal biomineralization: patterns, processes and evolutionary trends: 1: 135–296. New York: Van Nostrand, Reinhold.

Cox, L.R. 1969. Family Bakevelliidae King, 1850. *In* R. C. Moore (editor), Treatise on invertebrate paleontology N(1), Mollusca 6: 306–310. Lawrence: University of Kansas.

Dubiel, R.F. 1994. Triassic deposystems, paleogeography, and paleoclimate of the Western Interior. *In* M.V. Caputo, J.A. Peterson and K.J. Franczyk (editors), Mesozoic systems of the Rocky Mountain region, U.S.A.: 133–168. Denver, CO: Rocky Mountain Section., SEPM (Society for Sedimentary Geology).

Erwin, D.H., and H.Z. Pan. 1996. Recoveries and radiations: gastropods after the Permo-Triassic mass extinction. *In* M.B. Hart (editor), Biotic recovery from mass extinction events. Geological Society London Special Publication 102: 223–229.

Farsan, N.M. 1972. Stratigraphische und Paläogeographische Stellung der Khenjan-serie und deren Pelecypoden (Trias, Afghanistan). Palaeontographica Abteilung A(140): 131–191.

Hertlein, L.G., and L.R. Cox. 1969. Family Pteriidae Gray, 1847 (1820). *In* R.C. Moore (editor), Treatise on invertebrate paleontology N(1), Mollusca 6: 302–306. Lawrence: University of Kansas.

Johnston, P.A. 1991. Systematics and ontogeny of a new bivalve, *Umburra cinefacta*, from the Silurian of Australia: implications for pteriomorphian evolution. Alcheringa 15: 293–319.

Johnston, P.A. 1993. Lower Devonian Pelecypoda from southeastern Australia. Association of Australasian Palaeontologists Memoir 14: 1–134.

Muster, H. 1995. Taxonomie und Paläobiogeographie der Bakevelliidae (Bivalvia). Beringeria 14: 3–161.

Nakazawa, K. 1959. Permian and Eo-Triassic *Bakevellias* from the Maizuru Zone, southwest Japan. Memoirs of the College of Science, University of Kyoto, Series B, Geology and Mineralogy, 26(2) 8: 193–213.

Nakazawa, K. and N.D. Newell. 1968. Permian bivalves of Japan. Kyoto University, Memoirs of the Faculty of Science, Series of Geology and Mineralogy 35(1): 1–108.

Newell, N.D. 1942. Late Paleozoic pelecypods: Mytilacea. State Geological Survey of Kansas 10(2): 1–80.

Newell, N.D. 1952. Periodicity in invertebrate evolution. Journal of Paleontology 26: 371–385.

Newell, N.D., and A. LaRocque. 1969. Family Pterineidae Miller, 1877. *In* R.C. Moore (editor), Treatise on invertebrate paleontology N(1), Mollusca 6: 298–302. Lawrence: University of Kansas.

Newell, N.D., and D.W. Boyd. 1970. Oyster-like Permian Bivalvia. Bulletin of the American Museum of Natural History 143: 221–281.

Orchard, M.J. 1995. Taxonomy and correlation of Lower Triassic (Spathian) segminate conodonts from Oman and revision of some species of *Neospathodus*. Journal of Paleontology 69: 110–122.

Solien, M.A. 1979. Conodont biostratigraphy of the Lower Triassic Thaynes Formation, Utah. Journal of Paleontology 53: 276–306.

Solien, M.A., W.A. Morgan, and D.L. Clark. 1979. Structure and stratigraphy of a Lower Triassic conodont locality, Salt Lake City, Utah. Brigham Young University Geology Studies 26: 165–177.

Stanley, S.M. 1972. Functional morphology and evolution of byssally attached bivalve mollusks. Journal of Paleontology 46: 165–212.

Stephenson, L.W. 1952. Larger invertebrate fossils of the Woodbine Formation (Cenomanian) of Texas. U.S. Geological Survey Professional Paper 242: 1–226.

Tokuyama, A. 1959. ''*Bakevellia*'' and ''*Edentula*'' from the Late Triassic Mine Series in West Japan. Transactions, Proceedings, Palaeontological Society of Japan, new series 35: 147–155.

Twitchett, R.J. 1999. Palaeoenvironments and faunal recovery after the end-Permian mass extinction. Palaeogeography Palaeoclimatology Palaeoecology 154: 27–37.

Waller, T.R. 1998. Origin of the molluscan class Bivalvia and a phylogeny of major groups. *In* P.A. Johnston and J.W. Haggart (editors), Bivalves: an eon of evolution—paleobiological studies honoring Norman D. Newell: 1–45. Calgary: University Press.

Recent issues of the *Novitates* may be purchased from the Museum. Lists of back issues of the *Novitates* and *Bulletin* published during the last five years are available at World Wide Web site http://library.amnh.org. Or address mail orders to: American Museum of Natural History Library, Central Park West at 79th St., New York, NY 10024. TEL: (212) 769-5545. FAX: (212) 769-5009. E-MAIL: scipubs@amnh.org