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Permian Pelecypods from Tunisia

DONALD W. BOYD¹ AND NORMAN D. NEWELL²

ABSTRACT

Fifteen Late Permian pelecypod species belonging to 15 genera and 13 families are described from Tunisia. *Shikamaia ? ogulineci*, a remarkable ambonychiacean, *Gigantocyclus zidensis*, a lucinid of surprisingly modern aspect, and a new species, *Lyroschizodus djemelensis* are morphologically unusual elements of the fauna. A new non-byssate

pteropectinid, *Denguiria azzouzi*, new genus and new species, is described. A minor element of an extraordinarily rich assemblage of marine invertebrates dominated by reef-building calcareous sponges, the pelecypods show surprisingly little resemblance to contemporaneous assemblages of other areas.

INTRODUCTION

This contribution is devoted to bivalve molluscs of Late Permian age (Guadalupian, as indicated by associated fusulinaceans and ammonoids) from southern Tunisia (fig. 1). They were collected as part of a large biostratigraphic survey involving several scientists in excursions from 1967 through 1976. The investigations were undertaken in collaboration with the Service Géologique de Tunisie, the Smithsonian Institution, and the American Museum of Natural History and were aided by National Science Foundation grants administered by Dr. William H. Kanes, Director of the International Geologic Studies Program, University of South Carolina. The fieldwork and stratigraphic conclusions are described in a preliminary publication by Newell et al. (1976) to which the reader is referred for general in-

formation. Biologic groups other than the pelecypods are being studied and published elsewhere by taxonomic experts and results of additional fieldwork are being published separately by J. Keith Rigby.

The fossiliferous rocks, somewhat more than 800 meters thick, contain a diverse, well-preserved fauna dominated by sclerosponges, fusulinaceans, and algae found primarily in small limestone bioherms and their marginal debris (fig. 2). The pelecypods occur mainly in interreef shales and thin limestone beds. They belong mainly to endemic species that show little resemblance to contemporaneous fossils of Sosio in Sicily, or the Salt Range in Pakistan. The differences are probably attributable to unlike physical environments at time of deposition.

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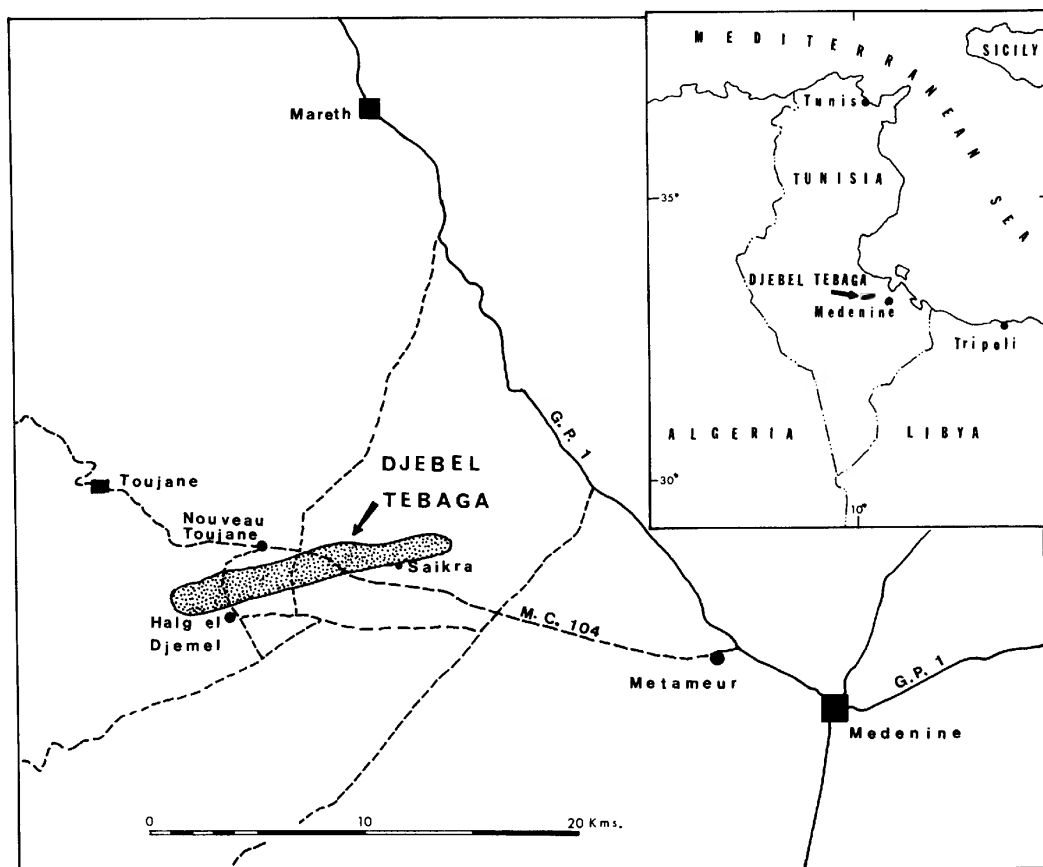


FIG. 1. Index map showing location of Djebel Tebaga outcrops of Permian strata near Medenine in southern Tunisia. (From Newell et al., 1976.)

A comprehensive work on Tunisian Permian fossils was completed recently by Termier et al. (1977). Our work, together with that of the other collaborators responsible for the bulk of our collections, will provide new information on stratigraphic distribution, morphology and taxonomy of the fossils. Since the Tunisian outcrops are readily accessible and contain the most complete sequence of Permian rocks in western Tethys they may well serve as a regional stratotype for the Mediterranean region.

Invertebrate paleontology is still plagued by the introduction and use of specific names for imperfect, poorly preserved, and isolated specimens. Some of the bivalves described herein belong to groups with generalized, simple morphologies. Characterization of real populations by such forms requires good samples that reveal diverse characters, preferably including in-

ternal features of musculature and hinge. Furthermore, most pteriomorphians are substantially different on the two sides—the valves are unequal in form and ornamentation. Both valves are needed for secure characterization and identification. Consequently, we have not ventured definite assignments for a number of apparently distinctive shells presented here. We believe that their inclusion is needed for future analysis of the entire fauna in which they occur.

The specimens figured herein are deposited in the collections of the Paleobiology Department of the National Museum of Natural History, Washington, D. C. Duplicates, where available, are deposited with the Service Géologique de Tunisie and the American Museum of Natural History. Most of the morphological terms used here are defined in

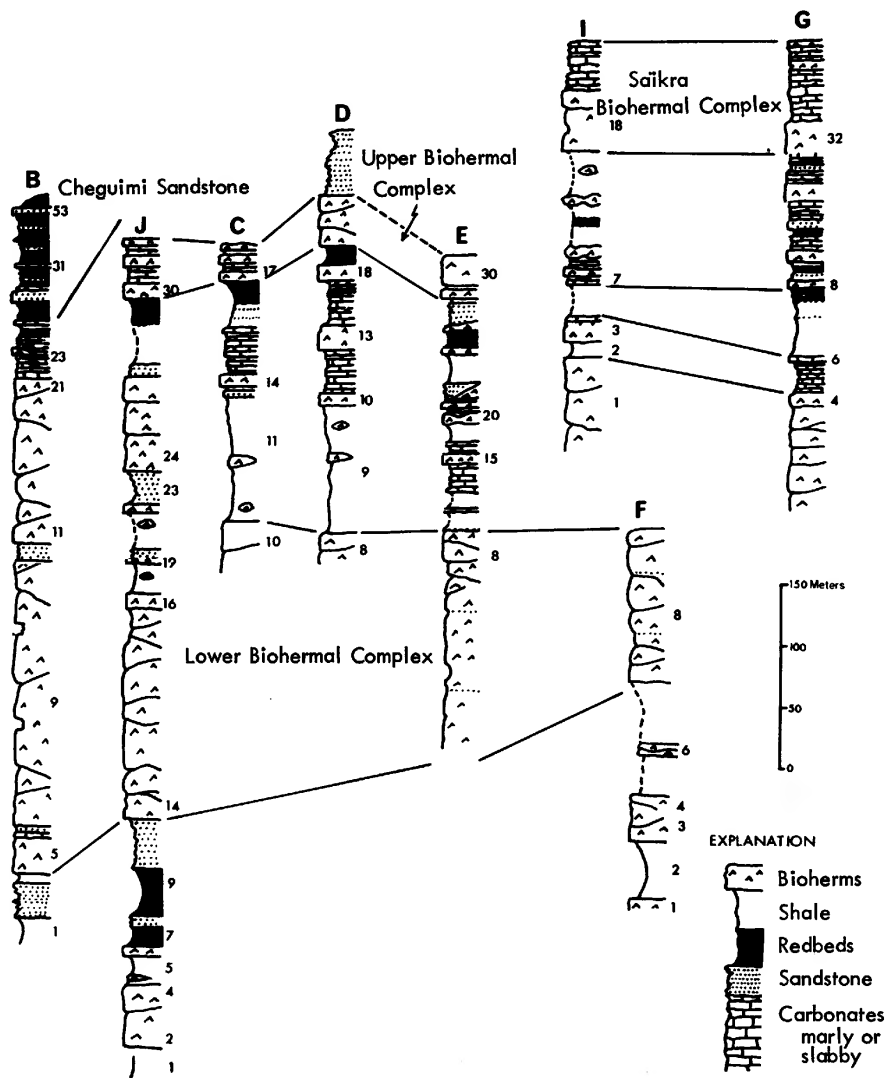


FIG. 2. West-East correlation of stratigraphic sections of Permian rocks in the Djebel Tebaga. Djebel Tebaga Biohermal Complex on the west (e.g., units 5 through 23 of section B) gives way eastward to two tongues separated by Middle Shaly Facies (e.g., units 9 through 19, section D. From Newell et al., 1976).

Moore (1969, p. 102) and Newell and Boyd (1975). The terms prorescent and retrorescent replace opisthocline and prosocline for reasons explained elsewhere (Newell and Boyd, 1970, p. 229).

ACKNOWLEDGMENTS

Our understanding of Permian pelecypods has been substantially aided by grants from the National Science Foundation. Mr. G. Robert Adlington photographed our fossils and Mr.

Frank Lombardi helped us with laboratory preparation of specimens. Both men are in the Department of Invertebrates at the American Museum of Natural History.

We appreciate the courtesy of Doctors Niichi Nishiwaki, Bruce Runnegar, and Adolph Seilacher in bringing to our attention papers relative to the genus *Shikamaia*. We have also benefited from discussions of this fossil with Runnegar and Dr. Thomas Yancey. Dr. Sara Bretsky helped us to evaluate *Gigantocyclus zidensis*. A review of the manuscript by Dr.

John Pojeta, Jr., resulted in numerous improvements in the final version.

SYSTEMATIC DESCRIPTIONS

SUPERFAMILY NUCULACEA GRAY, 1824

FAMILY NUCULIDAE GRAY, 1824

GENUS *NUCULOPSIS* GIRTY, 1911

Nuculopsis alta (Termier and Termier, 1959)
Figure 3

Nucula alta Termier and Termier, 1959, p. 277, text-pl. 1, figs. 1-5.

Nucula alta Termier and Termier, 1977, p. 79, pl. 17, fig. 3.

DIAGNOSIS: Umbo prominent and very strongly opisthogyrate; beak at truncated posterior margin of valve.

DESCRIPTION: Shell very elongate because of marked prolongation of pre-umbonal portion, the greatest linear dimension being arbitrarily taken as basis for measuring length (table 1). Umbonal flanks steep and slightly concave. Resilifer unusually small, separating anterior and posterior dental series. One left valve 9.4 mm. long has five teeth behind and 12 in front of resilifer.

DISTRIBUTION: Long-ranging: Saikra Biohermal Complex (I 12); Djebel Tebaga Biohermal Complex (J 16-18); Middle Shaly Facies (C 11; E12, 13).

REMARKS: Our best sample consists of 32 specimens from a single locality, unit 11 of

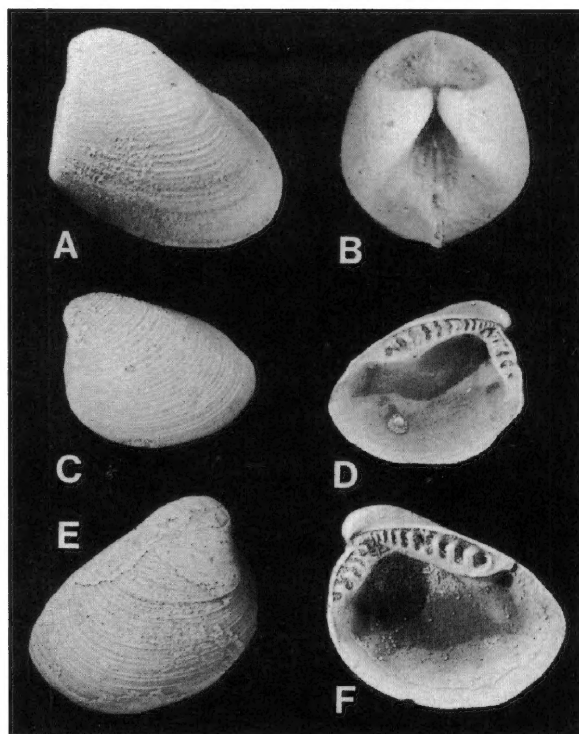


FIG. 3. *Nuculopsis alta* (Termier and Termier). A. Right valve of articulated specimen from Middle Shaly Facies (C11), USNM 258949. $\times 3$. B. Dorsal view of same, posterior at top. $\times 3$. C. Right valve from Djebel Tebaga Biohermal Complex (J17), USNM 258950. $\times 3$. D. Interior of same. $\times 3$. E. Left valve from Middle Shaly Facies (C11), USNM 258951. $\times 3$. F. Interior of same. $\times 3$.

Section C. There are also isolated specimens from other localities and horizons. All possess

TABLE 1
Dimensions (in Millimeters) of 20 Articulated Shells of *Nuculopsis alta* from One Bed (C11) of the Middle Shaly Facies
(Length is greatest dimension of valve; height measured perpendicular to length.)

Length	Height	Biconvexity	Length	Height	Biconvexity
12.2	8.8	8.0	9.9	7.2	6.5
12.0	8.5	8.2	9.8	6.9	6.4
11.1	8.1	7.4	9.7	6.1	5.5
10.9	7.4	7.7	9.4	6.9	5.9
10.9	7.8	7.1	9.2	6.6	5.6
10.9	7.6	6.9	9.0	6.8	5.6
10.7	7.8	6.9	8.8	6.5	5.2
10.6	7.7	7.0	8.8	5.9	5.4
10.5	7.8	6.8	8.3	6.1	4.6
10.0	7.4	6.2	7.8	5.6	4.3

a smooth inner ventral margin, so we have referred the species to the Upper Paleozoic *Nuculopsis*. The shape of this species is closely similar to that of the Jurassic genus *Nuculoma* and it probably would have been so classed by us if it had been found in rocks known to be Jurassic. However, we are not now prepared to undertake a critical comparison of our species with that genus. It is worthwhile, however, to consider *Nuculopsis alta* as a putative ancestor of *Nuculoma*.

SUPERFAMILY NUCULANACEA ADAMS AND ADAMS, 1858

FAMILY MALLETIIDAE ADAMS AND ADAMS, 1858

GENUS *PALAEONEILO* HALL AND WHITFIELD, 1869

Palaeoneilo tebagaensis (Termier and Termier, 1959)
Figure 4

Nucula tebagaensis Termier and Termier, 1959, p. 277; text-pl. 1, figs. 6, 7

Palaeoneilo tebagaensis Termier and Termier, 1977, p. 79-80; text-fig. 37; pl. 17, figs. 1, 2.

DIAGNOSIS: Elongate shells with length/height ratio between about 1.62 and 1.83, averaging about 1.7 (table 2). Only external ornament a faint ridge extending backward from the beak nearly parallel to dorsal margin with inter-

vening area very narrow (0.7 mm. on a valve 13.2 mm. long) and slightly concave.

DESCRIPTION: Prosogyrate beaks well forward of midlength. Ventral margin smoothly curved, with most ventral point near midlength. Taxodont dental series extends full length of dorsal margin, with largest teeth at anterior end. A right valve 13.2 mm. long has 10 teeth in front of beak and 40 behind. Inconspicuous posterior ligament groove extends from beak about half length of posterior row of teeth. Adductor scars directly below ends of dental series. Pallial line not visible.

DISTRIBUTION: Long-ranging: Saikra Biohermal Complex (G 6); Oum El Afia Shale (?) (J1); Djebel Tebaga Biohermal Complex (B24; J5, 17); Middle Shaly Facies (C11; E13, 18, 21-23, 25-28).

REMARKS: A collection of 50 specimens from E27, in the Middle Shaly Facies, is our largest sample of this species.

FAMILY NUCULANIDAE ADAMS AND ADAMS, 1858

GENUS *PHESTIA* CHERNYSHEV, 1951

?*Phestia* sp.

Figure 5

DESCRIPTION: Small, inflated, slightly opisthogyrate, taxodont with anterior and ven-

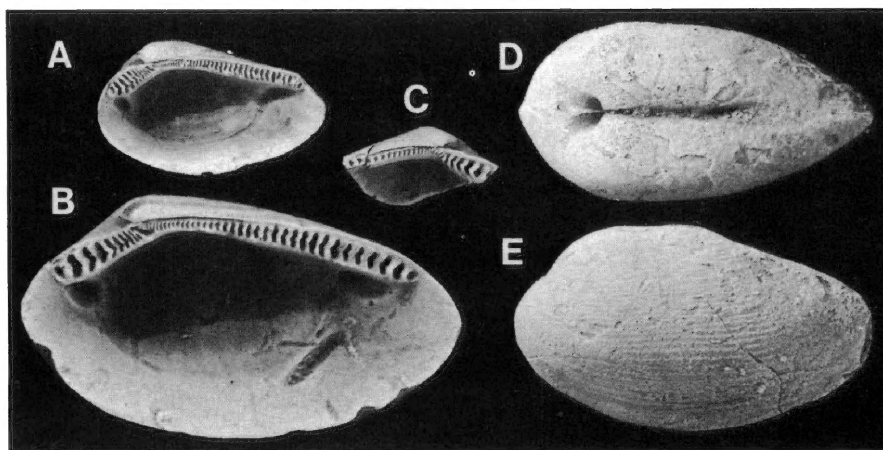


FIG. 4. *Palaeoneilo tebagaensis* Termier and Termier from Middle Shaly Facies. A. Right valve (E27), USNM 258981. $\times 2$. B. Right valve (E18) with pit resembling resiliifer below beak, USNM 258983. $\times 3$. C. Left valve (C11), lacks median pit, USNM 258982, $\times 2$. D. Bivalved specimen, dorsal view, USNM 258952. $\times 2$. E. Same specimen, left side view. $\times 2$.

TABLE 2
Dimensions (in Millimeters) of 20 Articulated Shells of *Palaeoneilo tebagaensis* from One Bed (E27) of the Middle Shaly Facies

Length	Height	Biconvexity	Length	Height	Biconvexity
7.5	4.3	3.6	13.0	8.0	6.8
10.0	5.7	4.7	13.2	8.4	7.4
10.2	5.7	4.8	13.5	7.5	6.3
10.2	5.6	5.0	13.6	7.6	6.9
10.6	6.5	5.5	13.8	8.1	6.7
10.8	6.6	5.8	14.0	8.6	7.7
11.7	6.7	5.6	14.3	8.7	7.0
12.2	7.4	6.4	14.8	8.8	7.4
12.6	7.5	6.9	15.2	9.2	7.6
12.6	6.9	5.9	15.7	9.5	8.0

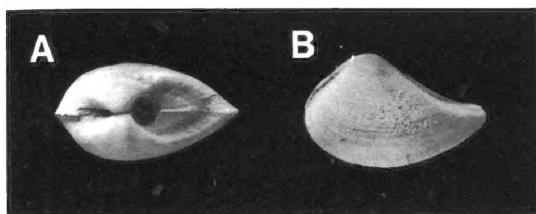


FIG. 5. *?Phestia* sp. from Djebel Tebaga Biohermal Complex (B24). Bivalved specimen, USNM 258953. A. Dorsal view. $\times 2$. B. Left side view. $\times 2$.

tral margins forming continuous curve connecting anterior end of hinge with posterior extremity; long dorsal profile behind beak concave. Fine, concentric sculpture except on broad, steep, flank between posterior ridge and hinge line. Largest specimen 11.1 mm. long, 7.1 mm. high, 5.9 mm. in biconvexity.

DISTRIBUTION: Djebel Tebaga Biohermal Complex (J16, 17); Middle Shaly Facies (C11; E13).

REMARKS: Although it is conventional to refer Permian nuculaniform shells to *Phestia* on external resemblance alone, the distinction between this genus and the Mesozoic *Nuculana* is based on internal features. Our qualification of the assignment of this species to *Phestia* reflects the absence of exposed valve interiors in our collections.

Our 30, mainly imperfect, specimens resemble juveniles of some of the larger Pennsylvanian species of *Phestia* (e.g., the Russian *P. ninae* Chernyshev). This group is so conserva-

tive that specific assignment cannot be confidently made solely on external characters.

It is interesting that *Phestia* is rare in Permian faunas of Tethys. *?Phestia subacuta*, a less inflated form from the Salt Range of India, was described by Waagen (1881) on the basis of two specimens. Reed (1932) had the same number at hand when he described the larger and more acuminate *?P. thompsoni* from Kashmir.

SUPERFAMILY ARCACEA LAMARCK, 1809

FAMILY PARALLELODONTIDAE DALL, 1898

GENUS *PARALLELONDON* MEEK AND WORTHEN, 1866

Parallelodon sp.

Figure 6

DESCRIPTION: Shell somewhat reduced anteriorly. Beak toward anterior end of hinge; maximum convexity behind beak. Maximum height near posterior end of shell. Narrow, closely spaced ligament grooves form obtuse (168°) chevrons. Transverse teeth beneath beak bounded by anterior and posterior lateral teeth; hinge plate broadened posteriorly. Surface sculpture limited to growth interruptions of two or three ranks. Largest specimen 21.7 mm. long, 13.9 mm. high, and 6.2 mm. in convexity.

DISTRIBUTION: Djebel Tebaga Biohermal Complex (B24); Middle Shaly Facies (C11; E25, 27).

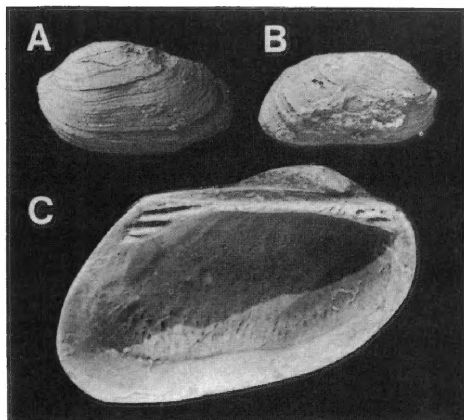


FIG. 6. *Parallelodon* sp. A, B. From Djebel Tebaga Biohermal Complex (B24). A. Left valve, USNM 258954. $\times 1$. B. Right valve, USNM 258955. $\times 1$. C. Left valve interior, from the Middle Shaly Facies (C11). USNM 258984 $\times 2$.

REMARKS: The late Paleozoic arcaceans need to be revised. The family resemblances are so strong that there is much uncertainty about criteria for discrimination of genera and species, and good population samples are scarce.

Several of our six specimens are fragmental or crushed, and only one exhibits hinge characters. Unlike the *Parallelodon* specimen figured by the Termiers (1977, text fig. 38), the several transverse teeth beneath the beak are bordered anteriorly by lateral teeth, recalling *Grammatodon*. Although shorter and less prominent than their posterior counterparts, the anterior laterals resemble them in being subparallel to the dorsal margin.

SUPERFAMILY AMBONYCHIACEA MILLER, 1877

FAMILY ALATOCONCHIDAE TERMIER, TERMIER,
AND DE LAPPARENT, 1973

GENUS *SHIKAMAIA* OZAKI, 1968

Alatoconcha Termier, Termier and de Lapparent,
1973

Tanchintongia Runnegar and Gobbett, 1975

?*Shikamaia ogulineci* (Kochansky-Devidé,
1978)

Figures 7-14

DIAGNOSIS: Apical part of keel periphery forms 90 degree angle with plane of com-

missure. Incurved beaks of articulated valves nearly in contact. Extensive platform beneath beak shields apical end of body cavity and is bordered on anterior edge by prominent collar around byssal orifice. Duplivincular ligament area with lightly incised, closely spaced, retilinear grooves.

DESCRIPTION: Very large, massive shell; valve folded outward at an acute angle, with arcuate, flangelike keel separating flattened anterior area from reflexed, concave posterior area. Hinge edentulous. Outer shell layer coarsely prismatic. Maximum dimension for full-grown shell estimated at 30 cm.

DISTRIBUTION: Saikra Biohermal Complex (G16).

REMARKS: This large, aberrant bivalve is represented by 34 fragments from a thin layer of shell rubble at the base of unit 16 in section G. Our specimens, all incomplete and many extensively abraded, include two articulated shells, eight left valves, and eight right valves. The remaining specimens are too fragmentary to be identified as to valve. We have given the collection more attention than its quality would seem to justify because a similar bizarre form has been independently described and interpreted differently by investigators dealing with Permian *Alatoconcha* from Afghanistan (Termier, Termier and de Lapparent, 1973) and the similar *Tanchintongia* from Malaysia (Runnegar and Gobbett, 1975) and Yugoslavia (Kochansky-Devidé, 1978). These workers were also handicapped by inadequate, fragmentary material with the result that their descriptions are incomplete and their interpretations speculative. We, too, are uncertain as to overall form and body-shell relationships, but the shell seems most analogous to that of a myalinid in which abnormally angular umbonal ridges are extremely bowed outward from the plane of commissure.

The most distinctive aspect of the form is the flangelike character of the arcuate umbonal keel (fig. 7). This sharp flexure separates two major parts of the valve. The area in front of the flange is flat to undulatory, whereas the part behind is broadly concave. The flanks of the keel are essentially parallel near its periphery, with the result that isolated fragments of the keel as seen in cross section have the aspect of

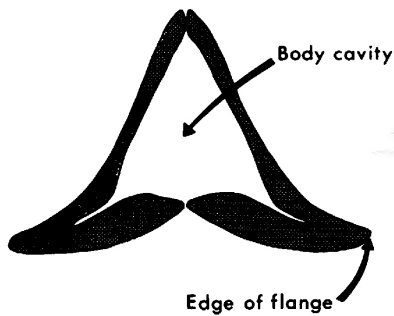


FIG. 7. *Shikamaia perakensis* (Runnegar and Gobbett). Cross section after Runnegar and Gobbett (1975). One-third natural size. (Permission of the publisher).

an isoclinal fold in sedimentary rocks (fig. 8). The minimal internal space relative to external surface area in such a situation is illustrated by measurements of one fragment in which opposing surfaces of the valve interior are only 6 mm. apart at a point 50 mm. inward from the flange margin.

A duplivincular ligament area borders the dorsal margin (fig. 9b). This part of the valve, in a plane roughly perpendicular to that defined by the proximal half of the curved umbonal ridge, is incomplete in all our specimens. Beneath the incurved beak, a massive platform bridges the space between the diverging valve margins (fig. 9c), thereby shielding the apical end of the body cavity. This umbonal septum typically is concave in longitudinal profile whereas its central part varies from concave to slightly convex in transverse profile. The resemblance of this area to a resilifer is enhanced by concave (toward beak) growth irregularities (fig. 10A).

The anterior edge of the plate is bordered by an offset, slightly arcuate collar (figs. 9d, 10A, 11). It combines with its counterpart on the opposite valve to form a spoutlike neck (fig. 11). Collars vary in relief from very prominent to negligible. Much of this variation may reflect vagaries of preservation since the collar forms a topographic prominence on the relatively flat surface of the valve. The collar has as much as 2.5 cm. relief in a few specimens (fig. 12A). It is sheathed by a prismatic layer which thickens on the inner (toward opposite

valve) side of the collar, where transverse striations represent discontinuities between 0.5 mm.-thick growth increments. The rugose growth pattern exhibited by the inner surface of the collar together with the presence, on some specimens, of a shallow groove along the inner margin of the collar, suggests that the collar developed in association with a byssus.

The part of the shell best represented in our collection is the apical one-third. By contrast, our interpretation of the abapical region is based mainly on one incomplete valve (fig. 13). In this specimen, the two major surfaces on either side of the umbonal ridge converge ventrally. This is accomplished by posteroventral warping of the surface that is predominantly flat in the anterior half of the valve. As a result, cross-sections of the valve become progressively constricted abapically. Articulation of two such valves would produce an abapical configuration similar to that of the anterior region of brachiopods with angular fold and sulcus, even though the commissure in the pelecypod coincides with the plane of symmetry.

Body space was much more restricted than suggested by external dimensions. As noted above, space in the hollow keel is very confined. Moreover, umbonal thickening is very prominent in large valves.

The surface of most of our specimens is worn. However, an outer gray prismatic layer is present in places on a few fragments of both left and right valves (fig. 14). Where the prisms are 1 or 2 millimeters long and perpendicular to the surface, the prismatic layer represents about one-fifth the wall thickness. Rarely, the prisms are notably longer and inclined at a low angle to the valve surface. The remainder of the wall thickness, as much as several centimeters in our thickest fragments, does not adequately retain details of its original microstructure. Some layering is apparent, commonly involving shades of gray and brown.

In their interpretation of life orientation of fossils similar to ours, Runnegar and Gobbett (1975) envisioned the shell resting on its broad anterior surface (fig. 7). We think this applies equally well to the Tunisian species. In this position, in contrast to the reconstruction of

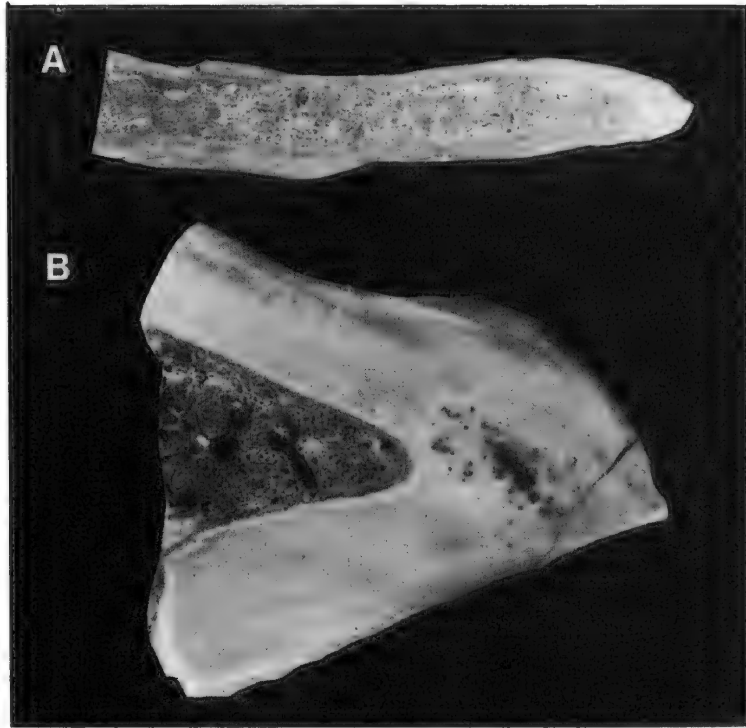


FIG. 8. *Shikamaia ?ogulineci* (Kochansky-Devidé). From Saikra Biohermal Complex (G16). A. Polished surface, cut through umbonal ridge and flange showing hairpin outfolding of shell, USNM 258961. $\times 1$. B. Polished section through thick part of reflexed wall. USNM 258962. $\times 1$.

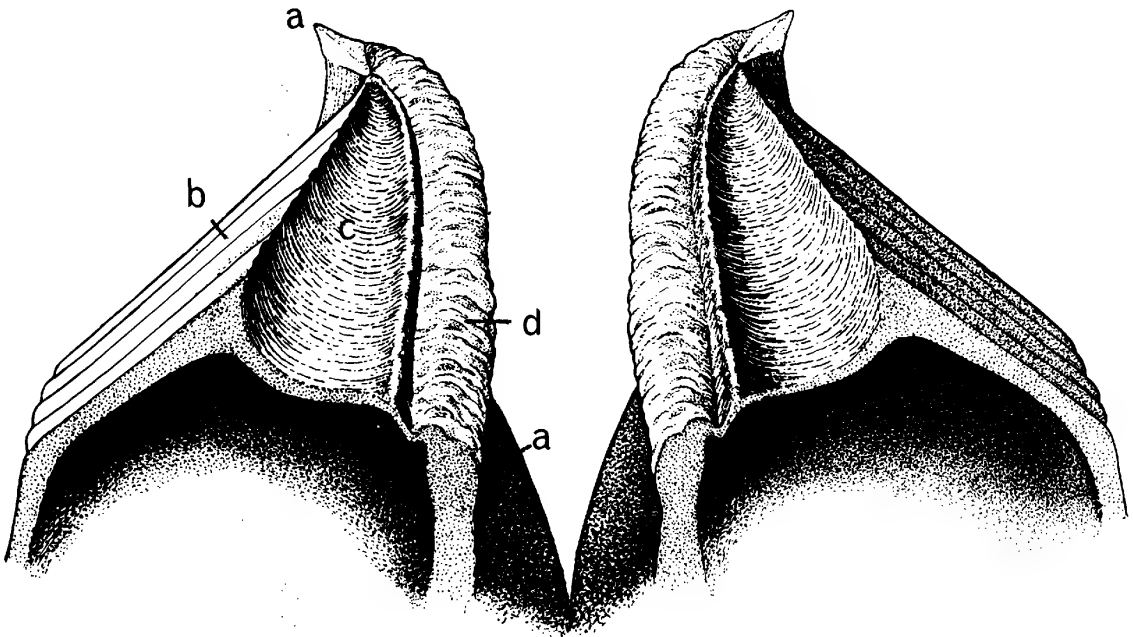


FIG. 9. *Shikamaia ?ogulineci* (Kochansky-Devidé). Interpretation of hinge and adapical part of shell. The plane of commissure is parallel to the page. Symbols (on left valve): a, umbonal ridge; b, duplivincular ligament area; c, umbonal septum below beak; d, anterior collar. $\times 2/3$.

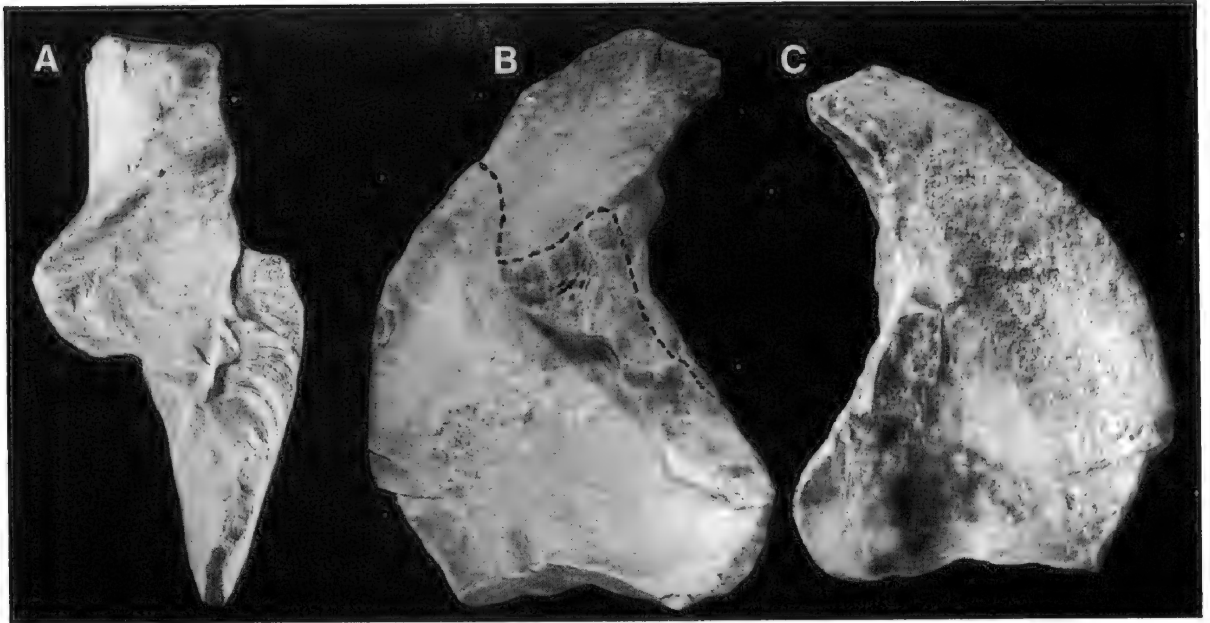


FIG. 10. *Shikamaia ?ogulineci* (Kochansky-Devidé). From Saikra Biohermal Complex (G16). A-C. Fragment of left valve, USNM 258956. $\times \frac{1}{2}$. A. Internal view, commissure parallel with page, beak at upper right; umbonal septum below beak and marked by lunulate growth lines, bounded at right by byssal trough and rugose collar. B. Same, rotated 90° to the right; commissure perpendicular to page. Dashed line follows fracture between exterior (above) and interior (below). Beak at upper right. C. Anterior view of same.

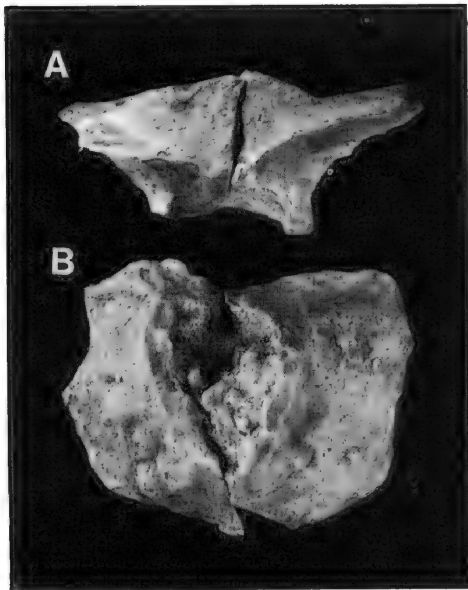


FIG. 11. *Shikamaia ?ogulineci* (Kochansky-Devidé). From Saikra Biohermal Complex (G 16). $\times \frac{1}{2}$. A. Apical view of broken fragment of bivalved specimen. Beaks at lower center terminating nearly horizontal umbonal ridges. B. Same specimen, view of byssal collar. Commissure vertical, beaks at center of upper margin. USNM 258957.

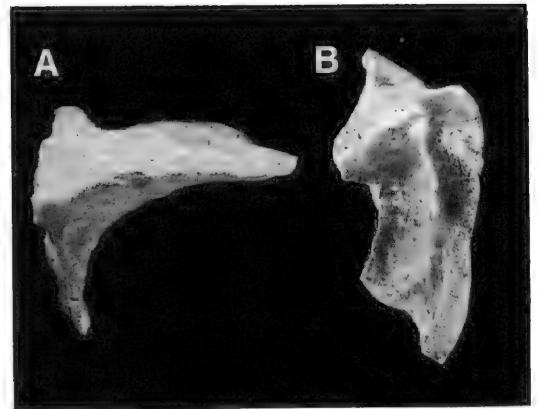


FIG. 12. *Shikamaia ?ogulineci* (Kochansky-Devidé). From Saikra Biohermal Complex (G 16). A. Fragment of beak portion of left valve with beak at left center. Plane of commissure vertical with edge view of prominent collar below. Extension to the right is reflexed umbonal ridge and its continuation in the flange, USNM 258958. $\times \frac{1}{2}$. B. Another specimen from the same locality. Inner view of apex, commissure parallel to page. Right (anterior) margin is edge of collar. Central concavity is umbonal septum with beak at apex, USNM 258959. $\times \frac{1}{2}$.

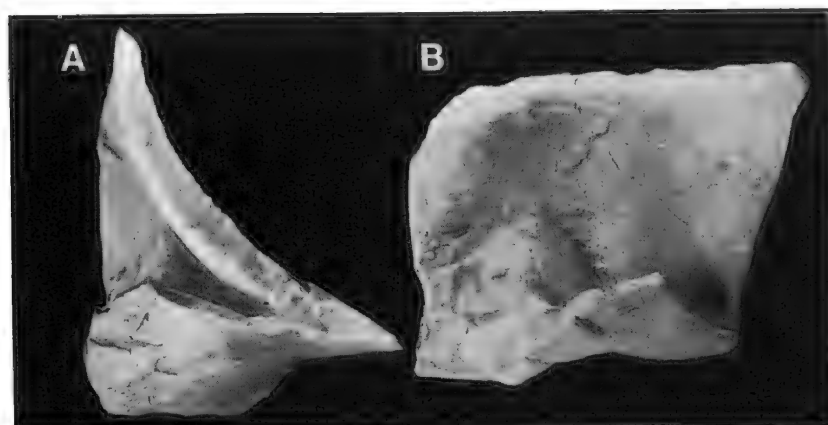


FIG. 13. *Shikamaia ? ogulineci* (Kochansky-Devidé). From Saikra Biohermal Complex (G 16). A. Abapical part of right valve broken through flange. anterior surface below. B. Same specimen showing body cavity. USNM 258960. $\times \frac{1}{2}$.

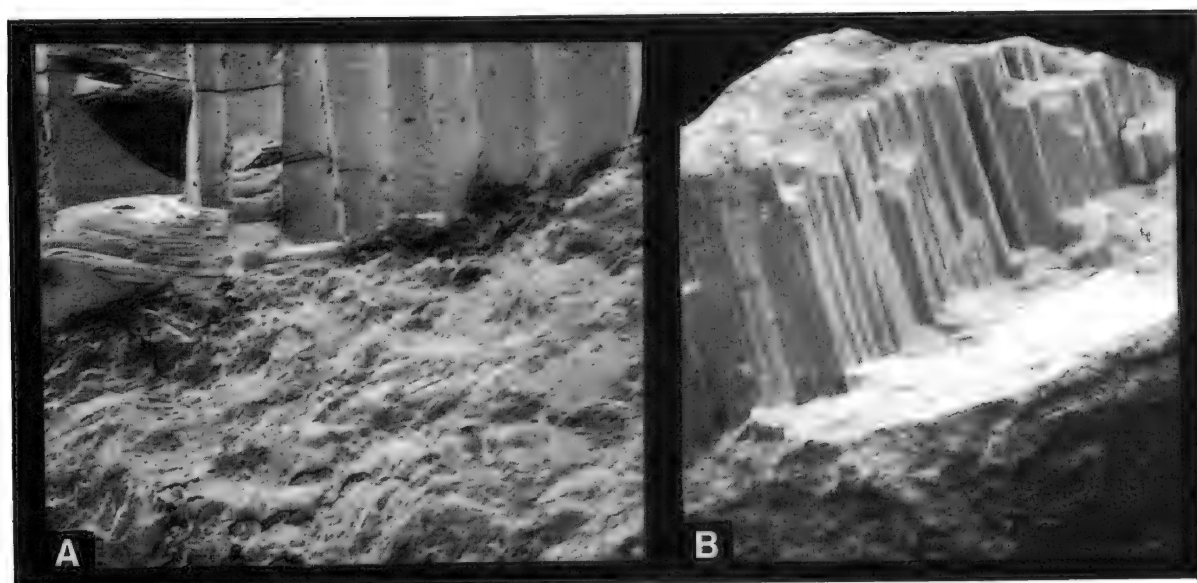


FIG. 14. *Shikamaia ? ogulineci* (Kochansky-Devidé). From Saikra Biohermal Complex (G 16). A. Prismatic and foliated (?) layers of the shell. SEM photograph, $\times 120$. B. SEM photograph, $\times 22$.

Kochansky-Devidé (1978), the collars of articulated valves would be directed toward the substrate.

The reflexed winglike form of our specimens also characterizes four species recently described from Permian strata of other countries. They are *Shikamaia akasakaensis* from Japan (Ozaki, 1968), *Alatoconcha vampyra* from Afghanistan (Termier, Termier and de Lapparent,

1973), *Tanchintongia perakensis* from Malaysia (Runnegar and Gobbett, 1975), and *T. ogulineci* from Yugoslavia (Kochansky-Devidé, 1978). In each of the first three papers, a new genus was created to receive a new species. At the respective times of writing, Termier and coauthors did not know of Ozaki's paper, and Runnegar and Gobbett had encountered neither that reference nor the description of the Afghan form. *Alato-*

concha was said by its authors to be allied to the Megalodontacea, whereas *Tanchintongia* was assigned by its authors to the Ambonychiacea. Each of the two groups of investigators was without knowledge of the other's work. Considering the aberrant morphology involved and the poor quality of specimens at both localities, it is not surprising that the two investigations resulted in different opinions concerning taxonomic affinities. Although it is possible that the Afghan and Malaysian specimens are unrelated, their common geologic age, biogeographic province, and distinctive characteristics lead us to believe that they are congeneric. Some of the differences in the original diagnoses probably are artificial. Thomas Yancey has called our attention to the probable homology of the distinctive furrow which the authors of *Alatoconcha* interpreted as a ligament groove and the authors of *Tanchintongia* described as a byssal notch.

Ozaki's diagnosis of *Shikamaia* is based on three fragmental specimens embedded in massive limestone (*Parafusulina* zone) from Akasaka, Japan. He was unable to determine the phylum represented by his material, but his illustrations leave no doubt that the shells in question are closely similar to those described subsequently from Afghanistan, Malaysia, and Yugoslavia. The Japanese fossils are bivalved, large (more than 16 cm. in maximum dimension and as much as 2 cm. in thickness of shell wall), and distinguished by a reflexed wall resulting in a broad flange perpendicular to the commissure. We conclude that *Alatoconcha* and *Tanchintongia* are junior synonyms of *Shikamaia*.

The Tunisian species differs from both Afghanistan and Malaysian forms in character and position of the duplivincular ligament area, possession of apical platform and bordering collar, proximity of opposed beaks, and abrupt lateral expansion of the umbonal ridge away from the beak. These differences may later prove to be significant at the generic level, but the present state of knowledge does not justify creation of another genus. Pending results of further study, the Tunisian species is assigned to *Shikamaia*.

Our Tunisian material is very similar to the recently described Yugoslavian species *Tanchin-*

tongia ogulineci. Shells from the two areas share, in addition to generic characters, a prominent byssal collar, notable flange width at the apical end, and a very thick prismatic outer layer. Furthermore, Kochansky-Devidé's (1978) illustrations suggest incurved, nearly touching beaks (her fig. 2), and a probable umbonal septum (her fig. 3, part 5).

Several differences between the Tunisian and Yugoslavian specimens give rise to our hesitancy in declaring them conspecific. The Yugoslavian byssal furrow appears to be a more deeply inset trough than its Tunisian counterpart. Moreover, the furrow's position on the byssal collar and its termination at a well-defined aperture are not duplicated on our specimens. The umbonal septum in our largest specimens is notably concave toward the opposing valve. This seems to be different from the form shown in Kochansky-Devidé's figure 2c. We see evidence in our specimens of a duplivincular ligament area with rectilinear grooves. This should be located along the lower right margin of Kochansky-Devidé's figure 3, part 5, assuming that the striated area below the byssal furrow in that illustration is an umbonal septum. Finally, we attribute greater relief to the abapical half of our shells than that indicated by Kochansky-Devidé in her figure 3, part 2. These differences, if real, would justify recognition of the Tunisian fossils as a separate species. However, we suspect that a number of the contrasts simply reflect inadequacies of the samples and their interpretation.

SUPERFAMILY PTERIACEA GRAY, 1847

FAMILY PTERINEIDAE MILLER, 1877

GENUS *LEPTODESMA* HALL, 1883

?*Leptodesma* sp.

Figure 15

Monopteria sp. Termier and Termier, 1977, p. 81, fig. 39; pl. 17, fig. 4.

DESCRIPTION: Elongated pterioid with dorsal and ventral margins of posterior half of shell subparallel to hinge. Beak subterminal. Ligament area broad and flat, with fine striations parallel to hinge. One or two posterior lateral teeth.

DISTRIBUTION: Middle Shaly Facies (E25, 27).

REMARKS: Our sample consists of 15 separated valves from a single locality. They are tightly cemented in skeletal debris, and most have the interiors exposed. All but one are left valves, and all have been damaged by abrasion, compaction, and recrystallization. Consequently, the specimens cannot be accurately measured and are not a good representation of a population.

The shell is unusually elongate by horizontal extension of the posterior part after passing through the usual oblique growth stage characteristic of many pteroids. The beak is well forward, but not terminal as with *Monopteria*. The rather blunt posterior wings probably reflect systematic breakage. This conclusion seems to be confirmed by two associated, apparently juvenile shells, with elongate, strongly acuminate wings intact.

The striations on the ligament area resemble growth lines; there is some uncertainty whether or not they are duplivincular ligament grooves. In any case, no unequivocal evidence of a resilifer has been found. Two specimens display

short, posterior lateral teeth joining the ligament area at a low angle. Unlike *Monopteria*, no anterior teeth are present.

Two small valves with the exterior exposed display papillate ornamentation most conspicuous in front of the posterior ridge. Each papilla is elongate parallel to the growth lines.

FAMILY BAKEVELLIIDAE KING, 1850

GENUS *GERVILLIA* DEFRANCE, 1820

SUBGENUS *CULTRIOPSIS* COSSMAN, 1904

Gervillia ?(*Cultriopsis*) sp.

Figure 16

DESCRIPTION: Small, long-bodied valves with posteroventral part produced far behind posterior auricle. Angular posterior ridge arcuate on umbo but rectilinear and parallel to hinge on main shell body. Two serrate ribs on front end of left valve extend from beak to anteroventral margin. Triangular ligament area exhibits resilifer beneath beak and one or more additional pits posterior of it. Small peglike teeth at anterior end of hinge; elongate posterior teeth subparallel to hinge line.

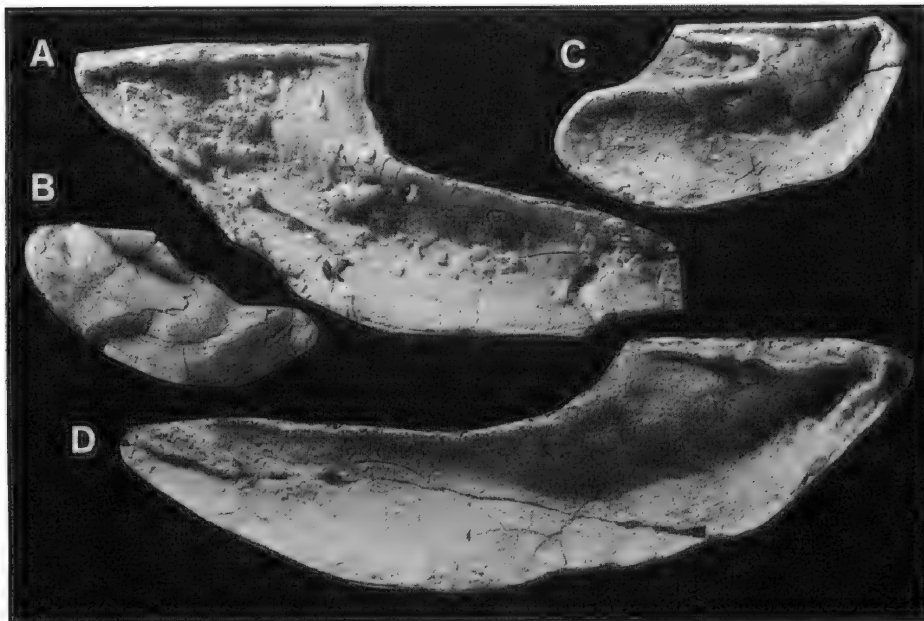


FIG. 15. ?*Leptodesma* sp. from Middle Shaly Facies (E25). A. Interior of right valve retaining posterior hinge teeth, USNM 258964. $\times 1$. B. Left valve with fine papillate ornamentation, USNM 258986. $\times 2$. C. Left valve interior showing entire posterior auricle, USNM 258987. $\times 2$. D. Large, imperfect left valve, USNM 258963. $\times 1$.

DISTRIBUTION: Middle Shaly Facies (C16; E25, 27).

REMARKS: The angular posterior ridge is at mid-height on the long posterior extension of the valve, resulting in a triangular transverse section for that part of a valve. Our largest specimen is 27.5 mm. long and may be incomplete at the posterior end. The height is only 6.8 mm., yielding a distinctive length/height ratio of 4. A narrow but well-differentiated posterior auricle extends between the posterodorsal margin of the ligament area and the adjacent steep umbonal flank.

The ligament area is asymmetrically triangular and warped as a result of more rapid shell addition along the posterior part of the hinge. The beak is on the anterior side of the triangle rather than at its apex.

Small anterior teeth, three on the right valve and two on the left, project perpendicular to the hinge. The posterior part of the hinge is characterized by slender, rectilinear teeth and sockets with their long axes slightly inclined anteriorly.

Two ribs at the anterior end of the left valve are unequal. The anterior one is unobtrusive, whereas its neighbor rises prominently above the surrounding surface like a cockscomb. These ribs are absent on the few right valves available for study. On a few specimens, the beak and anterior flank exhibit remnants of a

fine reticulate pattern formed by radial and concentric threads (fig. 16A, B).

In overall form, our specimens resemble *Ensipteria* from the Permian of Japan (Nakazawa and Newell, 1968). However, that monotypic genus is characterized by a narrow ligament area bearing a single pit. By contrast, the Tunisian specimens possess triangular ligament areas. Although convincing ligament scars cannot be discerned on most of these, one specimen exhibits two or more pits (fig. 16D). On the basis of this evidence, we interpret the specimens as bakevelliids, and refer them with question to *Gervillia* (*Cultriopsis*). This subgenus of ensiform shells has heretofore been recognized only in Mesozoic strata.

FAMILY ISOGNOMONIDAE WOODRING, 1925

GENUS *TAMBANELLA* NAKAZAWA AND NEWELL, 1968

?*Tambanella* sp.

Figure 17

DESCRIPTION: Outline rhomboidal without wings. Beak terminal. Posterior and dorsal margins form wide (e.g., 140°) angle; dorsal part of anterior margin reflexed, producing troughlike area subjacent to beak. Small, concave septum covers apical end of umbonal cavity. Ligament area opisthodetic and

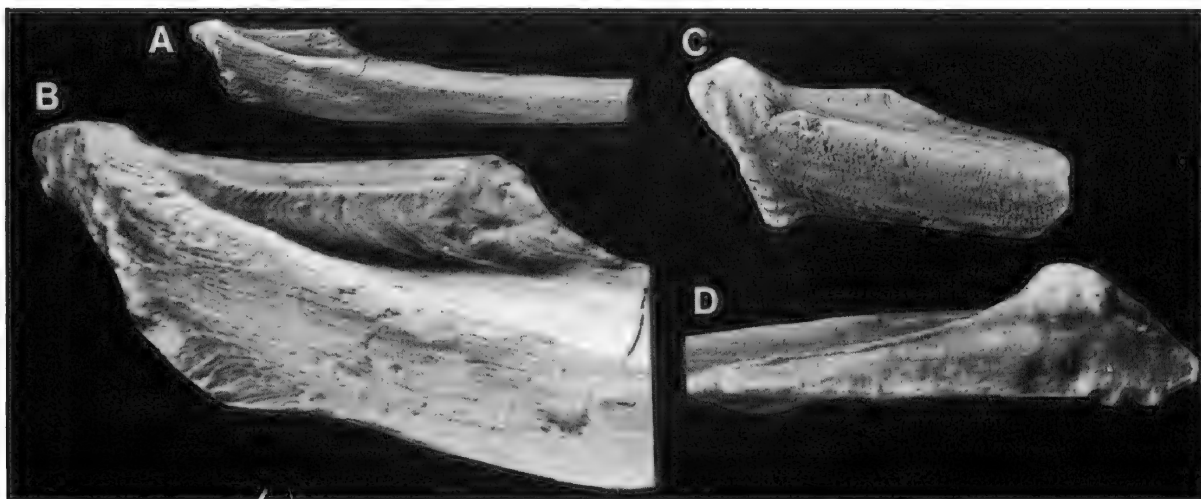


FIG. 16. *Gervillia* ? (*Cultriopsis*) sp. A, B from the Middle Shaly Facies (E 27). Left valve USNM 258988. A. $\times 2$. B. Same, enlarged to show ornament. $\times 7$. C, D from Middle Shaly Facies (C 16). C. Note the two ribs and intervening trough at front of shell, USNM 258965. $\times 4$. D. Ligament area of same specimen as C, showing posterior tooth (lower left), two peglike anterior teeth, and two ligament pits. $\times 9$.

multivincular, with pits separated by distances equal to, or greater than, pit width. One or two lamellar teeth parallel to valve margin at posterior end of ligament area.

DISTRIBUTION: Djebel Tebaga Biohermal Complex (B25; J16, 17); Middle Shaly Facies (C11, 16; E25, 26).

REMARKS: Of the dozen specimens in our collection, all but the illustrated one are less than 16 mm. in maximum dimension. Irregularly spaced growth lines provide the only surface sculpture.

A similar form was illustrated by Termier and Termier (1959, text-pl. 1, figs. 23, 24) as a *bakevelliid*. They subsequently (1977, p. 82) reassigned it to *Waagenoperna* of the *Isognomonidae*. Our specimens have more widely spaced ligament pits than does the valve illustrated by the Termiers. Furthermore, they did not report dentition, whereas our material exhibits posterior teeth. We are referring our specimens with hesitation to *Tambanella*, a genus currently represented by a single species from the Permian of Japan. The uncertainty arises from lack of unequivocal evidence for a cardinal tooth in our specimens, and from ap-

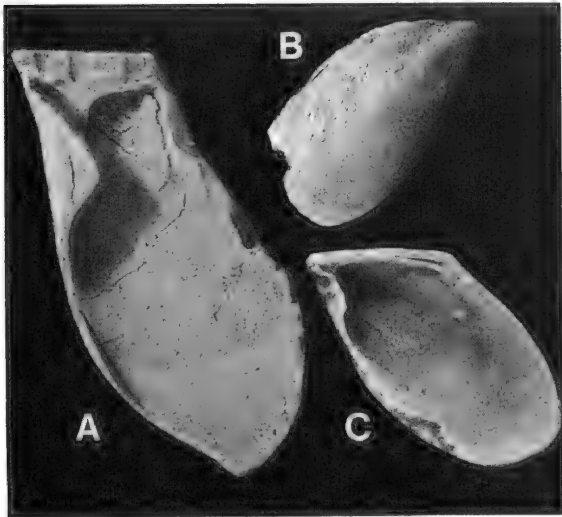


FIG. 17. *Tambanella* sp. A. Interior of large right valve from Djebel Tebaga Biohermal Complex (B 25). Posterior part of the hinge is missing, USNM 258966. $\times 2$. B. Right valve from Djebel Tebaga Biohermal Complex (J 16), USNM 258967. $\times 2$. C. Interior of a small right valve from Middle Shaly Facies (C 16) showing posterior lateral teeth, USNM 264362. $\times 3$.

parent absence of an apical septum in the Japanese material.

SUPERFAMILY PECTINACEA RAFINESQUE, 1815

FAMILY PTERINOPECTINIDAE NEWELL, 1938

GENUS *DENGUIRIA*, NEW GENUS

ETYMOLOGY: Denguir, a prominent hill in the southern Djebel Tebaga, southern Tunisia.

TYPE SPECIES: Monotypic.

DIAGNOSIS: Adult right valve lacks byssal notch. Otherwise like *Dunbarella*.

Denguiria azzouzorum, new species

Figure 18

HOLOTYPE: USNM 264364.

ETYMOLOGY: Named in honor of Ahmed and Azzedine Azzouz, of Tunis, who greatly facilitated work leading to discovery of this species.

DIAGNOSIS: Orbicular, retrocrescent shells with weakly differentiated anterior auricles and flattened posterior auricles; beaks well forward. Very low ligament area extends full length of hinge; sharply incised duplivincular grooves diverge at very obtuse angles below beak. Hinge edentulous. Radial ribs crossed by closely spaced growth threads on both valves.

DISTRIBUTION: Middle Shaly Facies (E27).

REMARKS: This thin-shelled pectinacean is systematically flattened by compaction and our 10 fragmental specimens have been crushed against the irregular surface of a thin layer of skeletal debris. Nevertheless, the umbonal cavity is not crushed and the original convexity was probably quite low in both valves. Costae of left valves are narrower and more regular than those of right valves. Costae increase during growth by intercalation on left valves. Increase in right valves is probably by bifurcation, as in *Dunbarella*, but preservation is too poor to allow a definite conclusion.

FAMILY AVICULOPECTINIDAE MEEK AND HAYDEN, 1864

GENUS *ANNULICONCHA* NEWELL, 1938

Annuliconcha sp.

Figure 19B

REMARKS: We have a single specimen, an imperfect left valve, representing this distinc-

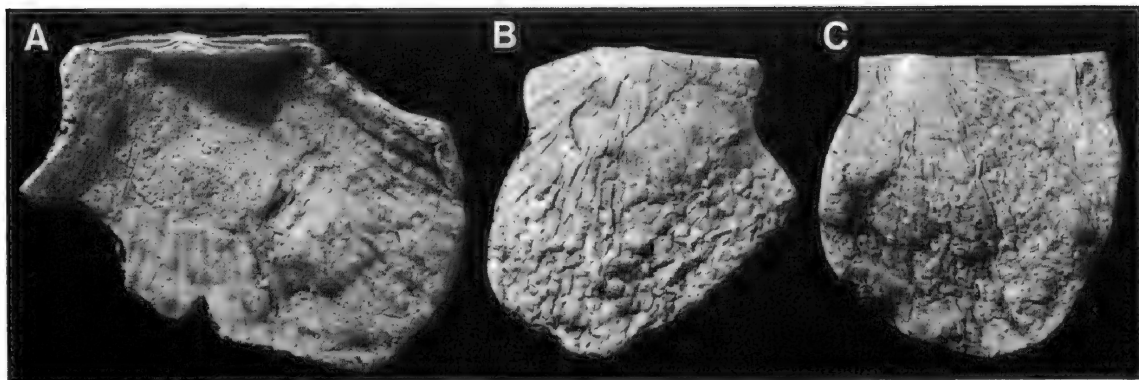


FIG. 18. *Denguiria azzouzorom*, new genus and new species from Middle Shaly Facies (E27). A. Right valve, the holotype, interior showing duplivincular ligament area and lack of a byssal notch, USNM 264363. $\times 3$. B. Right valve exterior showing lack of a byssal notch, USNM 264364. $\times 3$. C. Left valve, USNM 264365. $\times 2$.

tive genus. The surface ornament includes radial and concentric threads as well as a prominent series of beaded concentric ridges.

DISTRIBUTION: Middle Shaly Facies (C11).

GENUS *STREBLOPTERIA* M'COY, 1851

?*Streblopteria* sp.

Figure 19A

REMARKS: The single specimen representing this taxon is a right valve 26.4 mm. high. It is slightly prorescent and has a small posterior auricle, a prominent anterior auricle, and a narrow and deep byssal notch. The evenly convex valve surface lacks radial ornament but is marked by innumerable, somewhat irregular growth threads. This aspect is unlike the smooth surface typical of *Streblopteria* valves.

DISTRIBUTION: Djebel Tebaga Biohermal Complex (J17).

GENUS *CLARAIA* BITTNER, 1901

?*Claraia posidoniformis* Termier and Termier, 1977

Figure 20

Claraia ? *posidoniformis* Termier and Termier, 1977, p. 82; pl. 16, fig. 10.

DESCRIPTION: Suborbicular, retrorescent valves with long, straight hinge line and slight convexity. Anterior (small) and posterior (large) auricles of left valve weakly differentiated. Subjacent anterior and posterior marginal

sinuses very shallow. Radial ribs and fine concentric growth threads as in *Claraia stachei*.

DISTRIBUTION: Saikra Biohermal Complex (I12); Middle Shaly Facies (E27).

REMARKS: Our collection includes two-dozen fragments of this enigmatic form. Most are left valves, all but one from the same collecting site (I12), and all are exposed on the surfaces of seams of fibrous calcite, varying from 2 mm. to 2 cm. in thickness. The unusual development of the fibrous calcite, resulting in duplicate images on opposite surfaces of a crust, is similar to an occurrence involving Lower Triassic *Claraia* in Idaho (Boyd and Newell, 1976).

The genus *Claraia* has long been considered to be a good indicator of Early Triassic age for enclosing deposits. However, *Claraia* is now known in association with a Permian fauna in Kashmir (Nakazawa, 1977) so that we agree with the Termiers that it may be reasonably considered in the present situation.

One good left valve demonstrates rib increase by intercalation. Left valve auricles stand out not because of topographic differentiation, but because they lack the prominent radial ribs that cover the rest of the valve. The posterior auricle of the right valve appears similar to its left valve counterpart. One right valve exhibits a narrow, anterior, subauricular notch parallel to the hingeline. Poor preservation of the specimen and absence of other right valves with the critical area preserved make it impossible to be sure that the notch is an origi-

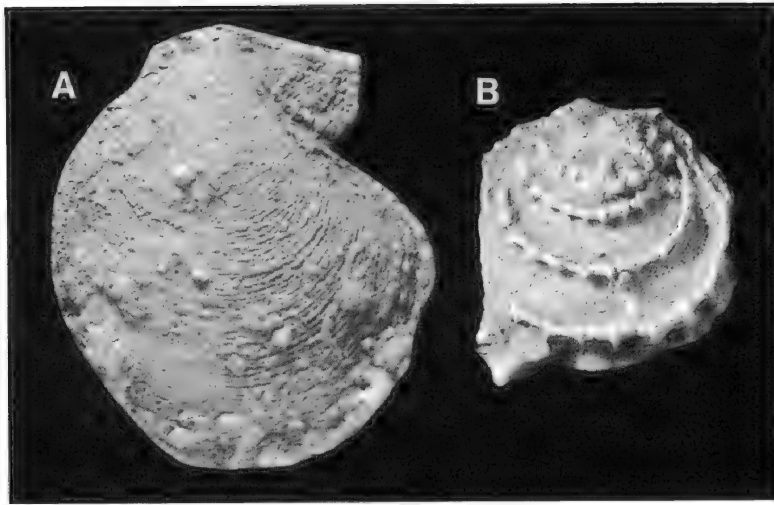


FIG. 19. ?*Streblopteria* sp. and *Annuliconcha* sp. A. Right valve of ?*Streblopteria* sp. from Djebel Tebaga Biohermal Complex (J 17), USNM 258968. $\times 2$. B. *Annuliconcha* sp. Left valve. From Middle Shaly Facies (C 11), USNM 258969. $\times 2$.

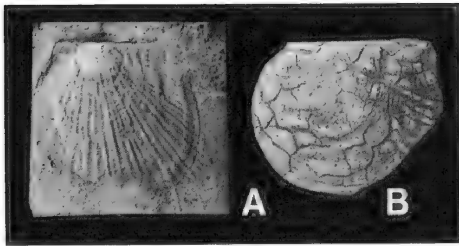


FIG. 20. ?*Claraia posidoniformis* Termier and Termier from Saikra Biohermal Complex (I 12). A. Latex replica of exterior of left valve, USNM 258985. $\times 1$. B. Right valve, inner surface of outer layer showing byssal notch. USNM 264366. $\times 1$.

nal feature of the specimen. Other reasons for uncertainty in the generic assignment include the strong ornamentation, the poorly developed anterior auricle of the left valve, and a weak posterodorsal, subauricular sinus.

SUPERFAMILY TRIGONIACEA LAMARCK, 1819

FAMILY SCHIZODIDAE NEWELL AND BOYD, 1975

GENUS *SCHIZODUS* DE VERNEUIL AND MURCHISON, 1884

Schizodus cf. *S. pinguis* Waagen, 1881
Figure 21

DESCRIPTION: Large (e.g., 48 mm. high) shell with hinge of schizodian grade (Newell

and Boyd, 1975, p. 77). Slightly carinate posterior ridge bounds concave corselet.

DISTRIBUTION: Saikra Biohermal Complex (G17).

REMARKS: This form is represented by a dozen fragmental specimens from one collecting site. They are too incomplete and abraded to allow an adequate species characterization. Overall form and lack of surface relief other than the slightly raised crest of the posterior ridge suggest that the Tunisian specimens are conspecific with *S. pinguis* from the upper Productus Limestone of the Salt Range. The posterior ridge is less strongly carinate, and the outline less trigonal, than is the case with *S. canalis* from the western United States.

FAMILY TRIGONIIDAE LAMARCK, 1819

GENUS *LYROSCHIZODUS* NEWELL AND BOYD,
1975

Lyroschizodus djemelensis, new species
Figure 22

Myophoria sp. Termier and Termier, 1959, p. 278; text-pl. I, fig. 25.

Cardinia sp. Termier and Termier, 1959, p. 278; text-pl. II, figs. 1-4.

Astartella gemmifera Termier and Termier, 1977 [partim], p. 85, text-figs. 43b, c; pl. 17, figs. 8-10.

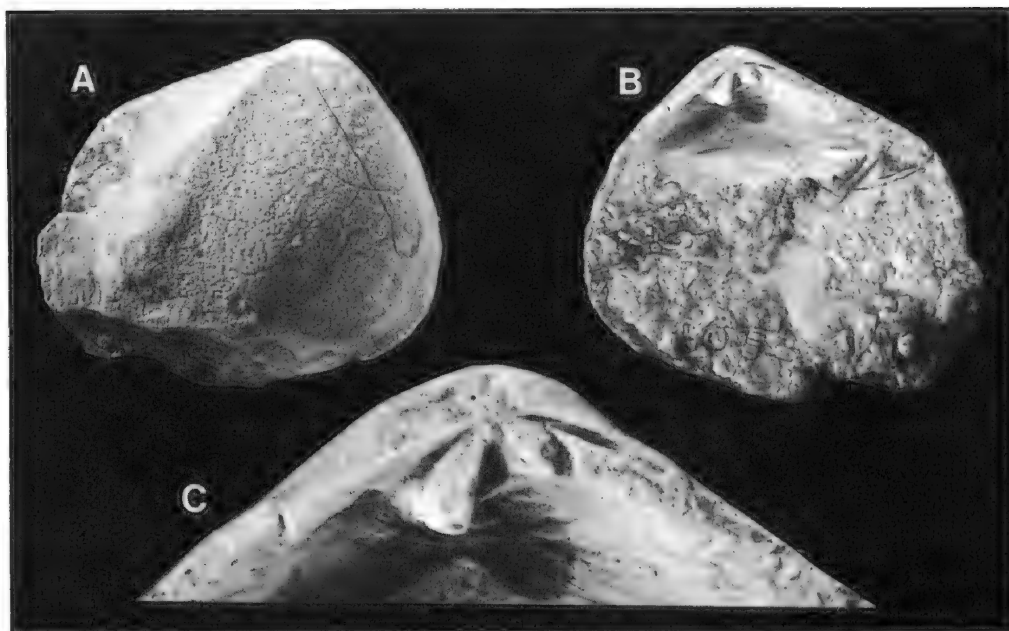


FIG. 21. A right valve of *Schizodus* cf. *S. pinguis* Waagen from the Saikra Biohermal Complex (G 17), USNM 258970. A. Exterior. Note carinate posterior ridge. $\times 1$. B. Interior. $\times 1$. C. Enlargement of hinge. Schizodian hinge grade, with ligament groove and nymph on right. Posterior tooth damaged. $\times 3$.

HOLOTYPE: USNM 258972.

ETYMOLOGY: The trivial name is from the village of Halg el Djemel.

DIAGNOSIS: Posterior ridge indistinct; ligament groove broad, troughlike; imbricating, conspicuous rugae formed by growth interruptions.

DESCRIPTION: Small, oval shells with prosogyrate beaks located slightly anterior to mid-length. Maximum convexity behind beak, on broadly rounded posterior ridge. Dorsal margin slopes gently downward behind beak, but more steeply in front of beak, resulting in relatively sharply curved anterior margin and a higher, somewhat truncate posterior margin. Corselet slightly flatter than the adjacent surface, but not sharply defined. Two ranks of concentric surface relief produced by fine concentric ridges superimposed on shinglelike growth increments. Ligament groove broad (as much as 0.6 mm.), troughlike, with length about equal to distance from beak to distal end of major tooth. Dentition schizodian, major teeth bulbous; major sockets three-fourths floored. In three specimens the average length/height ratio is 1.10; height/convexity ratio, 3.10; ratio length/partial

length (distance from beak to anterior extremity), 2.54. Largest specimen: length, 18 mm, height, 16 mm, biconvexity, 10 mm, partial length, 7 mm.

DISTRIBUTION: Saikra Biohermal Complex (G6, 16; I12); Oum El Afia Shale (?) (B1; F4); Middle Shaly Facies (C11; E13, 25, 27); Djebel Tebaga Biohermal Complex (B23, 24; C18; J18).

REMARKS: Following a smooth juvenile stage at the umbones, the first growth interruption forms a rugosity at a height ranging between 3.5 mm. and 6.0 mm. in different shells. In some valves, minor concentric ridges appear before the first growth interruption; in others, the first minor ridge appears just ventral to the first ruga. The rugae, or growth imbrications, are spaced from 0.5 mm. to 2.5 mm. Valves 15 mm. high possess from eight to 11 rugae. Although much less conspicuous, the minor concentric ornament is more consistent in form and spacing. The minor ridges are from 0.1 mm. to 0.2 mm. wide, with intervening troughs of comparable width.

The posterior cardinal tooth and ligament nymph of the right valve are parts of the same

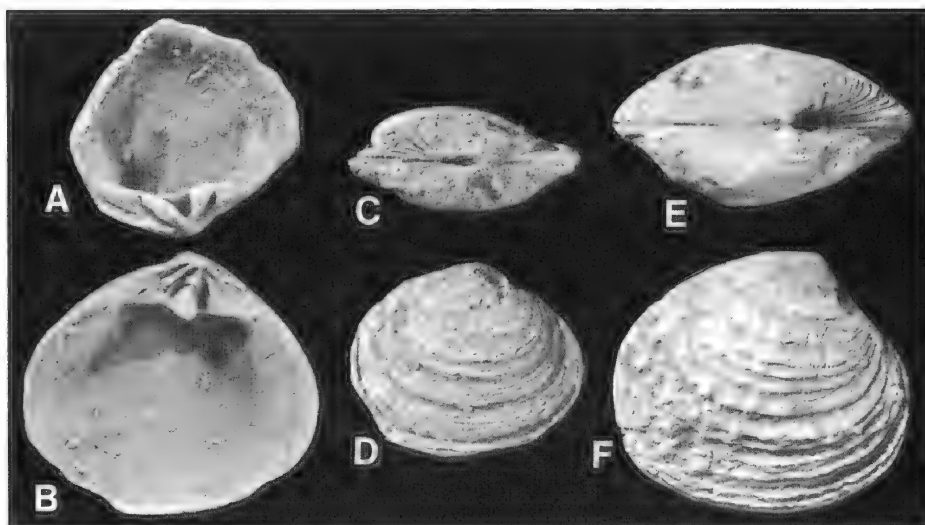


FIG. 22. *Lyroschizodus djemelensis*, new species. A. Right valve from Middle Shaly Facies (E 27). Posterior tooth forms thickened anterior edge of nymph. Major socket floored, paratype USNM 258971. $\times 2$. B. Holotype, a left valve from Middle Shaly Facies (E 27). Narrow ligament nymph lacks associated tooth, USNM 258972. $\times 2$. C. Dorsal view of articulated valves, anterior on right, from Middle Shaly Facies (E 13). Elongate cavity behind beaks is ligament area, paratype USNM 258973. $\times 2$. D. Right valve of shell shown in fig. C, illustrating both major and minor concentric ridges. $\times 2$. E. Dorsal view of articulated shell, anterior on right, from Saikra Biohermal Complex (G 6). Abraded area behind beaks. Absence of well-defined posterior ridge is typical of species, paratype USNM 258974. $\times 2$. F. Right valve of shell shown in figure E. Subcircular outline is typical of this species. Minor concentric ornament not well preserved. $\times 2$.

ridge but the narrower nymph of the left valve lacks an associated tooth. Muscle scars are poorly defined in the specimens at hand but the two adductors appear to be subequal. There is a suggestion of an anterior retractor imprinted at the anteroventral end of the hinge plate, next to, but partly separated from, the subjacent adductor scar.

Several specimens illustrated by Termier and Termier (1959, 1977) appear to be representatives of *Lyroschizodus djemelensis*. In their 1959 paper, these include a left valve illustrated as *Myophoria* sp. (their text-pl. 1, fig. 25) and several specimens assigned to *Cardinia* sp. (their text-pl. 11, figs. 1-4). In 1977, the Termiers reassigned all these specimens to *Astartella gemmifera*, a species first described in the 1959 contribution. As illustrated in that paper (text-pl. II, figs. 10-13), *A. gemmifera* differs from *Lyroschizodus djemelensis* in possessing more ornate, beaded ornamentation and in exhibiting a series of interlocking denticles along the inner ventral margin. Lateral teeth, lacking in *L. djemelensis*, are said to be present in *A. gem-*

mifera (Termier and Termier, 1977, p. 85). However, several of the specimens illustrating *A. gemmifera* in the 1977 paper appear to us to represent *L. djemelensis*. The likely candidates include their text-figures 43b and c, and figures 8 to 10 on plate 17.

Our collection consists of 28 calcareous specimens, most of them articulated and deformed by compaction. Hinge features are illustrated by three left valves and four right valves. The species is assigned to *Lyroschizodus* because of its ornamentation and hinge characters.

SUPERFAMILY LUCINACEA FLEMING, 1828

FAMILY LUCINIDAE FLEMING, 1828

GENUS *GIGANTOCYCLUS* TERMIER AND TERMIER, 1977

The original description of this monotypic genus did not include observations on the hinge and muscles needed to characterize it. Consequently, we are revising it here from our more ample collection.

DIAGNOSIS: Shell subcircular and large for a lucinoid. Hinge edentulous; nymph long and narrow. Surface sculpture limited to concentric growth imbrications. Closely similar only to the Cenozoic *Anodontia* Link from which it differs in having a much broader anterior than posterior adductor.

Gigantocyclus zidensis Termier and Termier, 1977

Figure 23

Incertae sedis Termier and Termier, 1959, p. 280; text-pl. II, fig. 8.

Gigantocyclus zidensis Termier and Termier, 1977, p. 84-85; text-fig. 42.

DIAGNOSIS: Compressed shell with maximum convexity centrally located. Anterior adductor scar strongly divergent from pallial line, with maximum dimension twice that of posterior scar.

DESCRIPTION: Shell prosogyrate; narrow, slightly concave escutcheon behind beak. External surface relief formed by growth irregularities of two ranks, with the coarser imbrications from 2 to 4 mm. apart.

DISTRIBUTION: Djebel Tebaga Biohermal Complex (B 25a).

REMARKS: Our collection includes a dozen valves with interiors exposed although ones with sharply defined muscle scars are rare.

Only one valve in our collection demonstrates unequivocally the distinctive configuration of the anterior adductor scar. The only accessory scar we have identified is that of the posterior pedal retractor, located at the anterodorsal margin of the posterior adductor scar.

Sharply delineated anterior and posterior dorsal areas typical of many modern lucinids (Bretsky, 1976, p. 227) are not present on the Tunisian shells.

The long, narrow nymph is accentuated ventrally by a bordering shallow groove. The hinge plate of the left valve exhibits a broad, low mound expanding posteroventrally from the beak, and separated from the proximal part of the nymph by a furrow. Although these features suggest weak dentition, appropriate counterparts are absent across the plane of commissure. The posterior furrow is opposed on the right valve by a comparable furrow, and the ill-defined mound is opposite a featureless platform beneath the beak of the right valve. The concave dorsal margin in front of the beak bears a faint inward-projecting ridge, equally prominent in both valves. Considering the variability of each of these features and the lack of opposed positive and negative relief, the shell is best described as edentulous. In this respect, and in its form, it resembles Cenozoic lucinids of the genus *Anodontia* (table 3).

TABLE 3
Dimensions (in Millimeters) of 11 Valves of *Gigantocyclus zidensis* from One Unit (B25a) in the Djebel Tebaga Biohermal Complex

(Partial length = length from beak to anterior extremity; beak-nymph = distance from beak to distal end of nymph.)

Length	Height	Convexity	Partial Length	Beak-Nymph
		(Left Valves)		
75	66	11	23	33
72	61	—	26	27
71	57	9	27	28
71	56	9	—	—
69	56	9	23	33
61	50	—	—	—
		(Right Valves)		
78	60	10	—	—
74	59	7	19	31
71	56	8	17	30
61	47	7	23	26
56	47	—	—	—

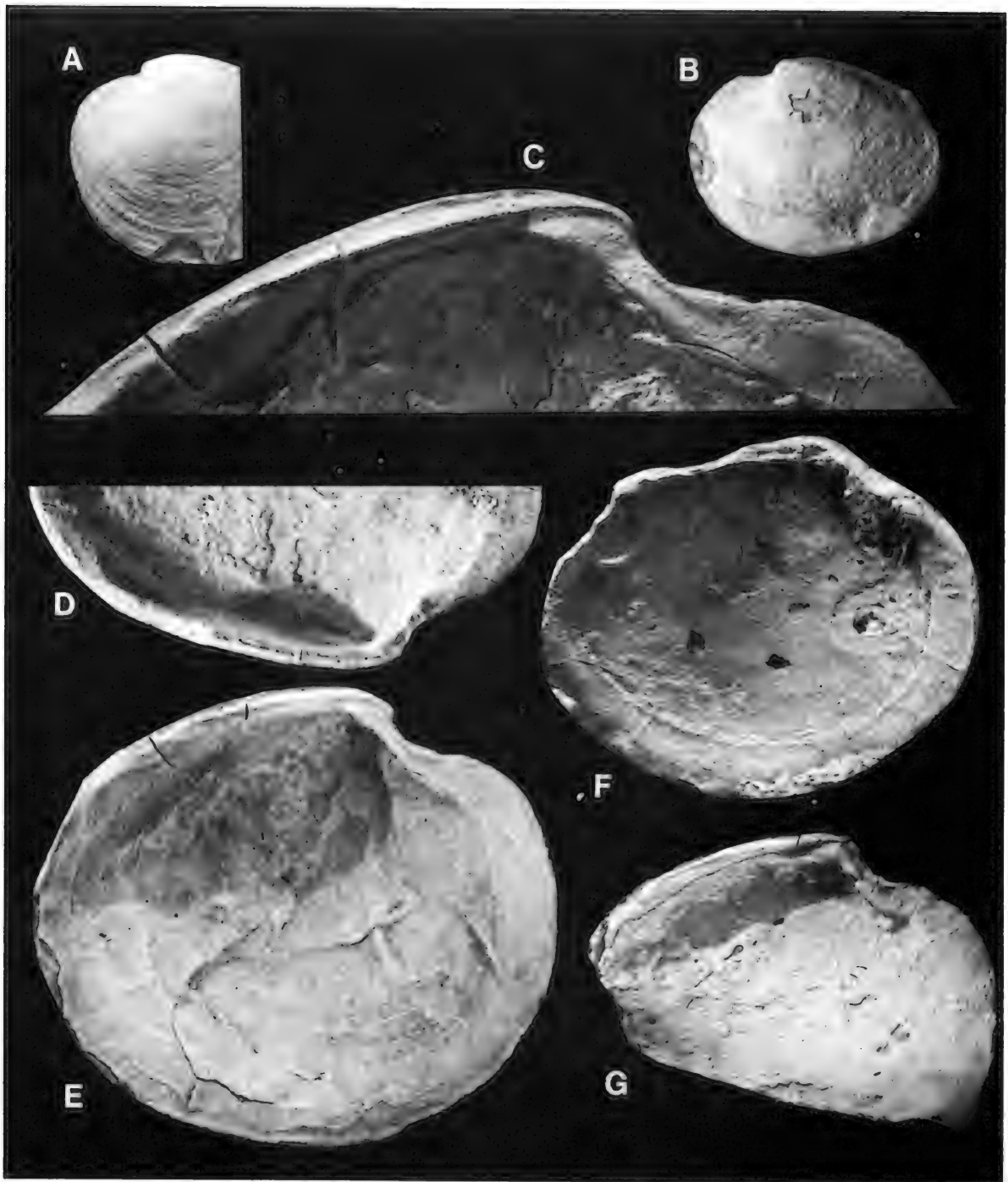


FIG. 23. *Gigantocyclus zidensis* Termier and Termier from Djebel Tebaga Biohermal Complex (B 25). A. Anterior half of left valve, exhibiting irregularly spaced concentric growth ridges, USNM 258975. $\times \frac{1}{2}$. B. Weathered exterior of left valve. Note very faint umbonal ridge, USNM 258976. $\times \frac{1}{2}$. C. Enlarged hinge of left valve shown in fig. E. $\times 2$. D. Interior of right valve, USNM 258978. $\times 1$. E. Interior of a complete left valve, USNM 258977. $\times 1$. F. Interior of left valve with unusually well-defined pallial line and muscle scars. Anterior adductor scar diverges posteroventrally from pallial line, USNM 258979. $\times 1$. G. Interior of dorsal part of left valve, USNM 258980. $\times 1$.

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