Relationships of the Devonian *Strobilepis* and related Pennsylvanian problematica

RICHARD D. HOARE and ROYAL H. MAPES

Hoare, R.D. & Mapes, R.H. 1995. Relationships of the Devonian *Strobilepis* and related Pennsylvanian problematica. *Acta Palaeontologica Polonica* **40**, 2, 111–128.

Reinterpretation of the North American *Strobilepis spinigera* Clarke 1888 from the Devonian and the find of *Diadeloplax paragrapsima* gen. et sp. n. from the Pennsylvanian provide the basis for the recognition of a new class of uncertain affinity, Multiplacophora. The range of the class is Middle Devonian (Erian) to Pennsylvanian (Morrowan). Multiplacophora differ from the order Hercolepadida and the classes Thambetolepida and Polyplacophora in the number, shape, and arrangement of plates; the presence of large spines; and the complexity of internal canal systems in the plates and spines.

Key words: Multiplacophora, Devonian, Pennsylvanian, problematica.

Richard D. Hoare, Department of Geology, Bowling Green State University, Bowling Green, OH 43403 USA Royal H. Mapes, Department of Geological Sciences, Ohio University, Athens, OH 45701 USA.

Introduction

This proposed new class is based on discoveries of new materials and reinterpretation of fossils previously assigned by various authors to such diverse groups as barnacles, gastropods, and the polyplacophorans. Specimens previously assigned to the Paleozoic barnacles have been described and illustrated by Whitfield (in Hall & Clarke 1888) as *Protobalanus hamiltonensis* and by Aurivillius (1892) as *Hercolepas signata*. These taxa were assigned to the class Machaeridia Withers 1926 by Dzik (1986). Later, Adrain (1992) restricted the Machaeridia to the orders Turrilepadomorpha Pilsbry 1916 and Lepidocoleomorpha Schallreuter 1985, deleting such taxa as *Protobalanus* and *Hercolepas*.

Clarke (in Hall & Clarke 1888) described a partially articulated specimen from the Hamilton Group of New York (Moscow Formation; C.E.

Brett, personal communication) and named it *Strobilepis spinigera*. He believed the specimen to be a barnacle which he assigned to the family Lepadidae, and illustrated its restoration in an unnumbered figure on page lxiii. His lithographic figures (Hall & Clarke 1888: pl. 36: 20–22) do not do justice to the complexity of the specimen (see Figs 1–2).

Rowley (1908) described and illustrated two small plates from the Late Devonian (Chautauquan) Louisiana Limestone of Missouri as a platyceratid gastropod, *Platyceras? anomalum*. Williams (1943) questionably assigned the larger of the two plates, the other being lost, to the polyplacophoran genus *Cymatochiton*. Hoare (1976) erroneously erected a new genus, *Lobarochiton*, for this specimen. Comparison of the plate (Fig. 3) with the posterior plate of the type specimen of *Strobilepis spinigera* leaves no doubt that it is *S. spinigera*.

Disarticulated spines and plates of a related form, *Diadeloplax paragrapsima* gen. et sp. n. (Figs 4–7), have been recently found in the Early Pennsylvanian Gene Autry Formation (Morrowan) of Oklahoma. The disjunct specimens are rare and found in a dominantly molluscan fauna. The spines and plates are similar to those of *Strobilepis spinigera* Clarke 1888 but the plates are significantly different in shape, size, and location of apices. There is little question that the Devonian *Strobilepis* is a precursor of *Diadeloplax*, extending the range of this new class from Middle Devonian (Erian) to Early Pennsylvanian (Morrowan). It is considered likely that multiplacophorans originated in the pre-Devonian and that earlier related taxa remain to be discovered. The class probably represents an extinct Paleozoic taxon and may be found to contain the order Hercolepadida Dzik 1986.

Biological affinity

The presence in our specimens of large marginal spines and plates, many of which are left- and right-handed, compares favorably with such taxa as *Protobalanus* and *Hercolepas*. The structure of the marginal spines of the latter genera is unknown and the size of the spines in relation to plate and strobilus size is much smaller than in *Strobilepis* and *Diadeloplax*. The plates in the strobilus of *Protobalanus* and *Hercolepas* are basically arranged in three rows and marginal insertion plates appear to be lacking. The strongly developed insertion plates present in *Strobilepis* and *Diadeloplax* are distinctive and, together with the shape of the plates, show the close relationship of the two genera and readily distinguish them from *Protobalanus* and *Hercolepas*. However, the plates in *Strobilepis* and *Diadeloplax* are believed to have been arranged in a single row (Fig. 8) because of their shape rather than in multiple rows as in the order Hercolepadida Dzik 1986. Pores and canal systems have been reported in *Thambetolepis* by Jell (1981) but they do not reach the complexity exhibited in *Strobilepis* and *Diadeloplax* and the shape, arrangement, attachment areas, and

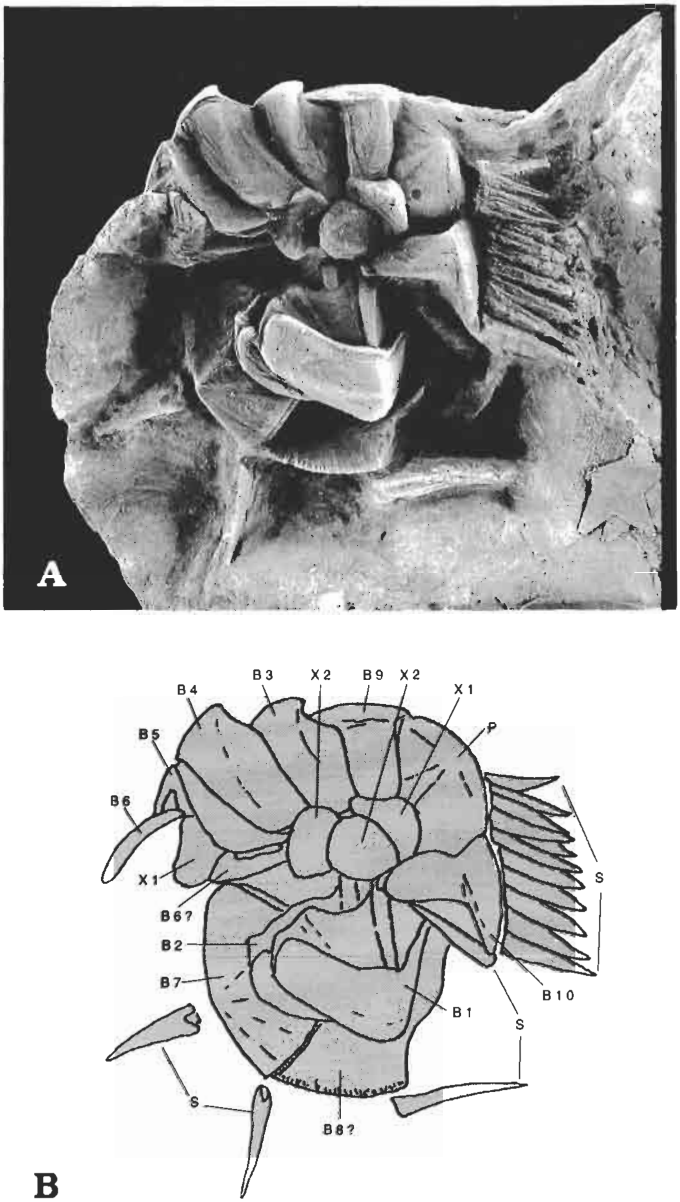


Fig. 1. *Strobilepis spinigera* Clarke 1888 from the Moscow Formation of New York. A. Partially articulated and partially incomplete holotype NYSM 4815; × 2. B. Diagrammatical representation of specimen shown in Fig. 1A identifying plates and spines. Abbreviations: P — posterior plate, B — intermediate plates, X — auxiliary plates, S — spines.

internal structure of the sclerites of the former are much different than in the latter. Van Name (1926) did not find pores or tubes in the plates of *Protobalanus*. Withers (1915) described the plates of *Hercolepas* as having punctae, but whether they possess an internal canal system is unknown. The insertion plates of *Strobilepis* and *Diadeloplax* are distinctly different from any taxon in that they are formed from the under shell layer with a distinct demarcation from the upper shell layer.

The plates of *Strobilepis* and *Diadeloplax* are most similar to those of polyplacophorans but differ in that: (1) the canal system penetrates into the lower shell layer whereas in the polyplacophorans canals are limited to the outer tegmentum layer, (2) there are only two shell layers instead of the three or four present in polyplacophorans, (3) they lack bilateral symmetry since several types of plates show left- and right-handiness, (4) they lack strong sutural laminae found in most Paleozoic polyplacophorans, and (5) there are small auxiliary plates associated with some intermediate plates. Not all intermediate plates in *Strobilepis* have a duplicature and a posterior apex but all in *Diadeloplax* do, as in most Paleozoic polyplacophorans. Some early Paleozoic polyplacophorans also do not show a duplicature or posterior apex (e.g., *Matthevia*, *Hemithecella*, *Chelodes*).

Many polyplacophorans have numerous small spines embedded in the girdle. Some have larger spines, as in modern species of *Acanthopleura* which have some spines over 10.0 mm in length (Hyman 1967; illustrated by Van Belle 1983: pl. 11: 4). None are known to approach the arrangement, complexity, and canal systems of the spines in *Strobilepis* and *Diadeloplax*.

The function of the pores and canal systems in the plates and spines is open to question. In the plates the canal systems run through the insertion plates to the plate margins (Fig. 6E–F). In the spines the middorsal and midventral canals lead into the central cavity, while the lateral pores lead into canals paralleling the septa and emerge at the proximal end (Fig. 7J–S). It is believed that these structures, and the central cavity of the spines, were filled with tissue. The systems may have provided either respiratory or sensory functions, or both.

The function of left- and right-handiness of elements in organisms with multiple rows of elytra or plates is readily seen in the structure of their body plan (e.g. *Protobalanus*, *Hercolepas*). Attempts were made to reconstruct *Strobilepis* and *Diadeloplax* with a multiple row body plan. However, the plate shapes, apices, duplicatures, and insertion plate configurations would not realistically conform to a multiple row pattern so a single row body plan was adopted. In specimens with a single row of plates the function of left- and right-handiness is less clear. Possibly, having developed from a form with multiple rows, this is a vestige of that structural characteristic. The function of the strongly notched plates and the associated small auxiliary plates is unknown.

The basic body plan of *Strobilepis* and *Diadeloplax*, as interpreted, appears significantly different from that of any other taxonomic group. Whether the clade including *Strobilepis* and *Diadeloplax* originated from a procoelomate organism (Bergström 1989) or from a flatworm-like organism (Pojeta 1980) is open to conjecture.

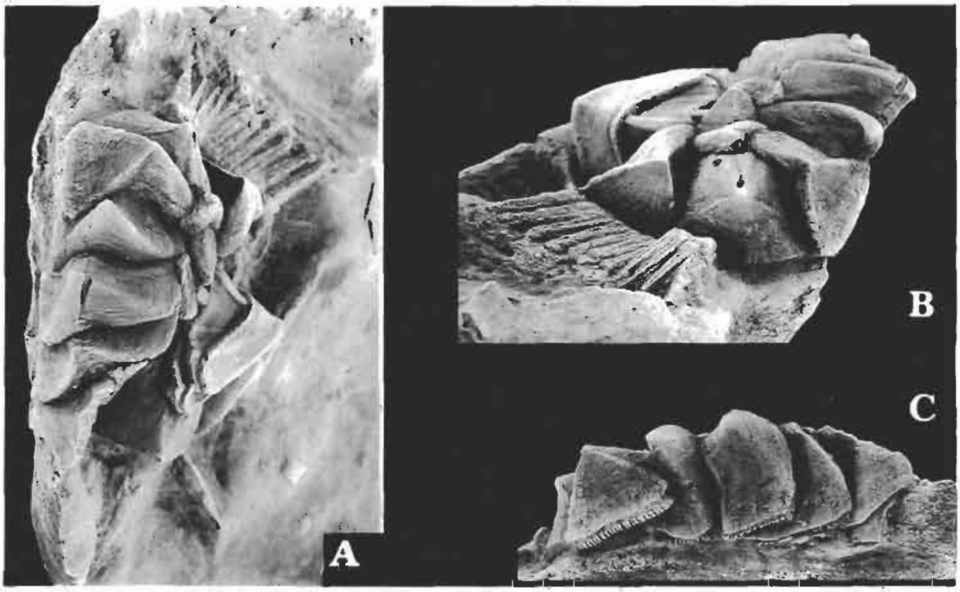


Fig. 2. *Strobilepis spinigera* Clarke 1888 from the Moscow Formation of New York; holotype NYSM 4815; × 2. A. Nearly dorsal view of row of intermediate and posterior plates showing terminal apex and duplicature on B5 and anteriorly directed apices on B4 and B3. B. Posterior plate and intermediate plates B9 and B10, the latter plates have a terminal apex and duplicature. C. A lateral view of the row of intermediate plates showing inclination of apices and distinct insertion plates.

There is an emerging concensus that biologic diversity is much greater than has been reported from the fossil record (Pojeta 1980; Strathmann 1991). The discovery of *Diadeloplax*, machaeridians, and other multiplated and spinose taxa of uncertain affinity from the Pennsylvanian, presently under study, are representative examples. Although many new taxa fall into established taxonomic groups, others do not. Such is the case with *Strobilepis* and *Diadeloplax*. The authors find it necessary to propose a new class for these genera.

Reconstructions

Reconstructions of unfamiliar, completely disarticulated skeletons are very difficult in terms of number of elements and their organization. When a related, partially articulated specimen is present, part of the problem is alleviated. In the case of the holotype of *Strobilepis spinigera* (Figs 1–2), although numerous plates and spines are preserved, they have been moved about, compressed together, displaced, and broken. Additionally, one plate and numerous spines are apparently missing or are buried in matrix. Apices and duplicatures are located posteriorly on certain plates. This indicates that intermediate plates B3–B6 have been turned 180

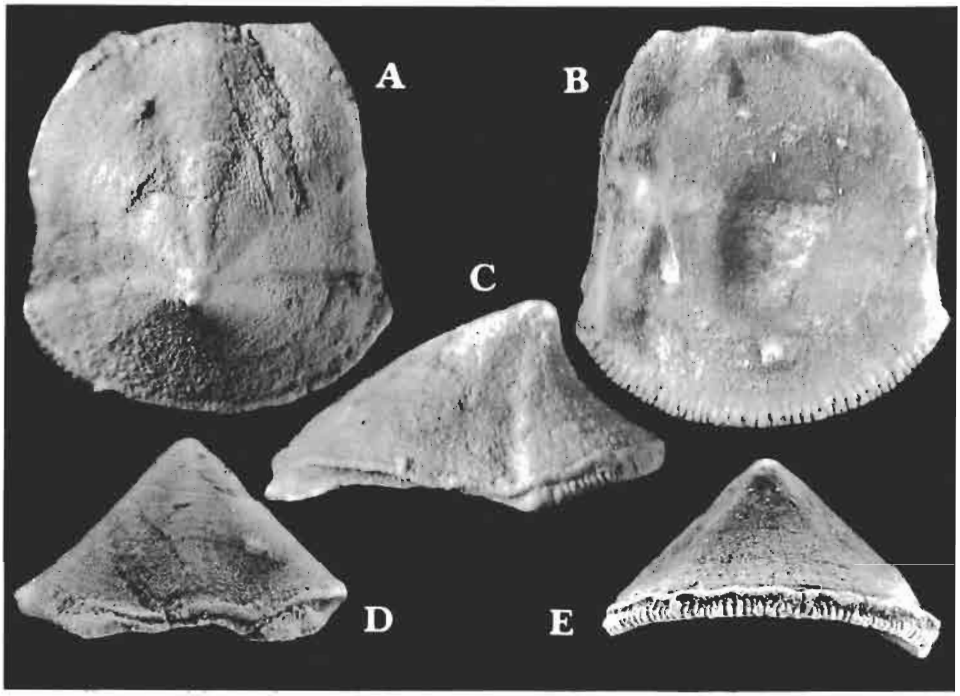


Fig. 3. *Strobilepis spinigera* Clarke 1888 from the Louisiana Limestone of Missouri; posterior valve, hypotype UI RX-75; × 10. A. Dorsal view showing uniform lobation. B. Ventral view. C. Left lateral view. D. Anterior view. E. Posterior view. (Figs A–C are reproduced from Hoare 1976 with the permission of The Ohio Journal of Science).

degrees in relation to intermediate plates B9 and B10 and the posterior plate (P) (Fig. 1). Plate B6 is broken and one part of it is partially buried below other plates. Intermediate plate B7, a right-handed plate, does not have a counterpart unless it is the overturned partial plate labeled B8?, a left-handed plate. The anterior plate is missing. The four auxiliary plates X1 and X2, which are believed to fit into the notches of intermediate plates B9 and B10 are displaced. The row of spines indicates their spacing but they presumably do not represent the entire population of spines. Whether the spines formed a complete marginal halo around the plates or were restricted to the lateral margins of the organism is unknown.

The reconstruction of *Strobilepis spinigera* (Fig. 8A–B) shows 12 major plates, including the B8? plate, and assumes that the anterior plate is missing or buried in matrix. The designations given beside the plates correspond to the designations given in Fig. 1B. The reconstruction of the shape of the anterior plate is based upon the head plate of *Diadeloplax paragrapsima* which may be close to that of *S. spinigera*. A pair of the auxiliary plates X1 and X2 are placed in the notches of B9 and B10. The shape of the posterior plate is based, in part, on the isolated plate from the Louisiana Limestone of Missouri (Fig. 3). Spines are shown only as a

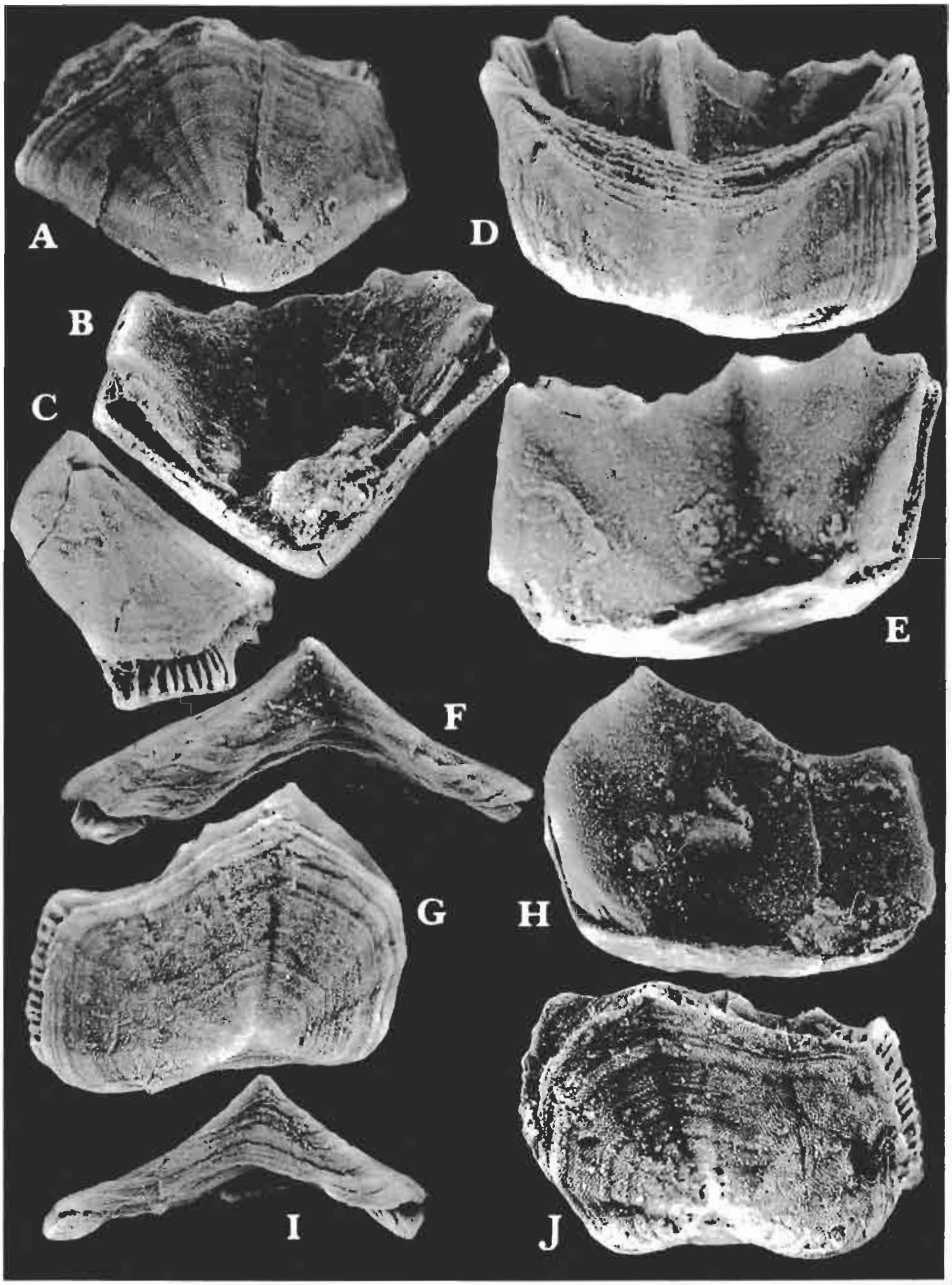


Fig. 4. *Diadeloplax paragrapsima* gen. et sp. n. from the Gene Autry Formation of Oklahoma; × 10. A–C, Dorsal, ventral, and right lateral views of anterior plate, holotype OUZC 1200. D–F. Dorsal, ventral, and posterior views of right-handed intermediate valve B1, paratype OUZC 1201. G–I. Dorsal, ventral, and posterior views of right-handed intermediate valve B8, paratype OUZC 1202. J. Dorsal view of left-handed intermediate valve B7, paratype OUZC 1203.

grouping on one side, the actual extent of their distribution is left open to conjecture.

The reconstruction of *Diadeloplax paragrapsima* (Fig. 8C–D) was based on completely disarticulated elements, and was supported by comparison with the holotype of *S. spinigera* and its reconstruction. Most likely the number of major plates in the two genera were the same. However, the diversity of plates in *Strobilepis* is greater than in *Diadeloplax*; there are five different types of major intermediate plates in the former and only three types in the latter. Although both genera have anterior and posterior terminal plates and intermediate plates B1, B2, B7, B8, B9, and B10, *D. paragrapsima* does not have homologous B3, B4, B5, and B6 intermediate plates. Therefore, the latter four plates in *D. paragrapsima* must be represented by other plate types. The number of plates of *D. paragrapsima* present in the collections are: 3 anterior, 6 posterior, 12 left- and right-handed intermediate plates homologous to B7 and B8 in *S. spinigera*, and 14 left- and right-handed intermediate plates comparable to B9 and B10 in *S. spinigera*. The larger numbers of the two types of intermediate plates would indicate that they were more numerous in individual specimens of the organism and two of each type of plate, both left- and right-handed, have been incorporated into the reconstruction of *D. paragrapsima* in place of the intermediate plates B3, B4, B5, and B6 in *S. spinigera* (see Figs 1 and 8).

Another difference between the two genera lies in the small auxiliary plates. In *Strobilepis* the X1 and X2 plates fitting into the notches of intermediate plates B9 and B10, although different in shape, are of about the same size. In *Diadeloplax* the X1 plates are much larger than the X2 plates that fit into the notches of B7–B10.

The number and disposition of spines in *D. paragrapsima* is unknown. Probably they were arranged as in *S. spinigera*. As in the reconstruction of the latter, only a few are shown along a lateral margin.

Systematics

Specimens are deposited at the New York State Museum (NYSM), University of Illinois (UI), and the Ohio University Zoological Collection (OUZC).

Phylum uncertain

Class Multiplacophora classis n.

Diagnosis. — Animals with a single row of thick, calcareous anterior, posterior, and 10 intermediate left- and right-handed plates; distinct insertion plates on borders of plates; narrow, elongate spines bordering plates; plates and spines with numerous surface pores leading to complex internal canal systems.

Order Strobilepida ord. n.

Diagnosis. — As for the class.

Family Strobilepidae fam. n.

Diagnosis. — As for the class.

Genus *Strobilepis* Clarke *in* Hall & Clarke 1888

Type species: *Strobilepis spinigera* Clarke *in* Hall & Clarke 1888.

Diagnosis. — Single row of 12 major plates with two types of small auxiliary plates; five types of intermediate plates; posterior plate uniformly lobed anteriorly, with insertion plate ridged posteriorly, smooth laterally and anteriorly; numerous narrowly elongate spines bordering plates; plates and spines with closely spaced pores leading to complex internal canal systems.

Remarks. — *Strobilepis spinigera* is the only known species. It is a precursor to the new Pennsylvanian species *Diadeloplax paragrapsiman*.

Stratigraphic range. — Devonian (Erian to Chautauquan).

Strobilepis spinigera Clarke *in* Hall & Clarke 1888

Figs 1–3, 8A–B.

Strobilepis spinigera Clarke; Hall & Clarke 1888: pp. lxiii, 213, pl. 36: 20–22; Clarke 1896: pl. 7: 11–12.

Platyceras? anomalum n. sp.; Rowley 1908: p. 90, Pl. 19: 15–19.

Gryphochiton? anomalus (Rowley); Williams 1943: p. 100, pl. 9: 19–20.

Lobarochiton anomalus (Rowley); Hoare 1976: p. 117, figs. 1–3.

Pterochiton? anomalus (Rowley); Hoare & Sturgeon 1979: p. 178, pl. 2: 1–3.

Lobarochiton anomalus (Rowley); Smith & Hoare 1987: p. 11.

Holotype: Specimen NYSM 4815 (Figs 1, 2).

Type horizon and locality: Moscow Formation (Erian) exposed near Menteth's Point, Canandaigua Lake, New York.

Diagnosis. — As for the genus.

Description. — Large (est. length 7–8 cm), narrow, elongated scleritome; plates thick with numerous closely spaced pores and comarginal growth lines. Anterior plate unknown. Posterior plate subquadrangular in outline; elevated mucro posterior to midlength; posterior area steeply concave, set-off from convex anterior area by shallow sulci extending from mucro to lateral margins; anterior area divided into three lobes by sulci radiating from mucro to anterolateral margins; insertion plate on posterior margin ridged, on lateral and anterior margins smooth; ventral surface smooth except for grooves extending from the posterior insertion plate; dimensions of posterior valve of holotype, 5.0 mm high, length and width unknown, of hypotype, length 5.2 mm, width 4.8 mm, height 2.7 mm.

Intermediate plates of five different forms: (1), B1–B2, left- and right-handed; strongly arched; apex pointed forward, located anterior to posterior margin; lateral margins with short, wide insertion plates ridged on one side; anterior process broad with prominent ridge near midline; posterior portion of plate separated from anterior area by angle in plate extending from apex to posterolateral corners; dorsal anterior area concave, dorsal posterior area convex; length (including large anterior process) 10.0 mm, width 12.0 mm, height 7.0 mm; (2), B3–B4, left- and right-handed; strongly arched; wider than long; forward directed apex near midlength; lateral margins with short, wide insertion plates, ridged on one side;

posterior portion of plate separated from anterior portion by angle in plate extending from apex to posterolateral corners; dorsal anterior area concave, dorsal posterior area convex; length 7.0 mm, width 9.5 mm, height 5.0 mm; (3), B5–B6, strongly arched; apex at posterior margin above distinct duplicature; lateral margins with short wide insertion plates, ridged on one side; length 6.0+ mm, width 10.0 mm, height 7.5 mm; (4), B7–B8, left- and right-handed; moderately arched; apex at posterior margin above distinct duplicature; lateral margins with short, very wide insertion plates, ridged on one side; surface marked by several ridges radiating from apex; length unknown, width 12.5 mm, height 3.0 mm; (5), B9–B10, left- and right-handed; moderately arched; apex at posterior margin above distinct duplicature; one side larger, subtriangular in shape with short, wide, ridged insertion plate; opposite side small, narrower with short, small, smooth insertion plate; differences in size of lateral areas forming a broad V-shaped anterolateral notch in valve; surface marked by several faint, radial ridges extending from apex; length 7.0 mm, width 9.5 mm, height 4.0 mm.

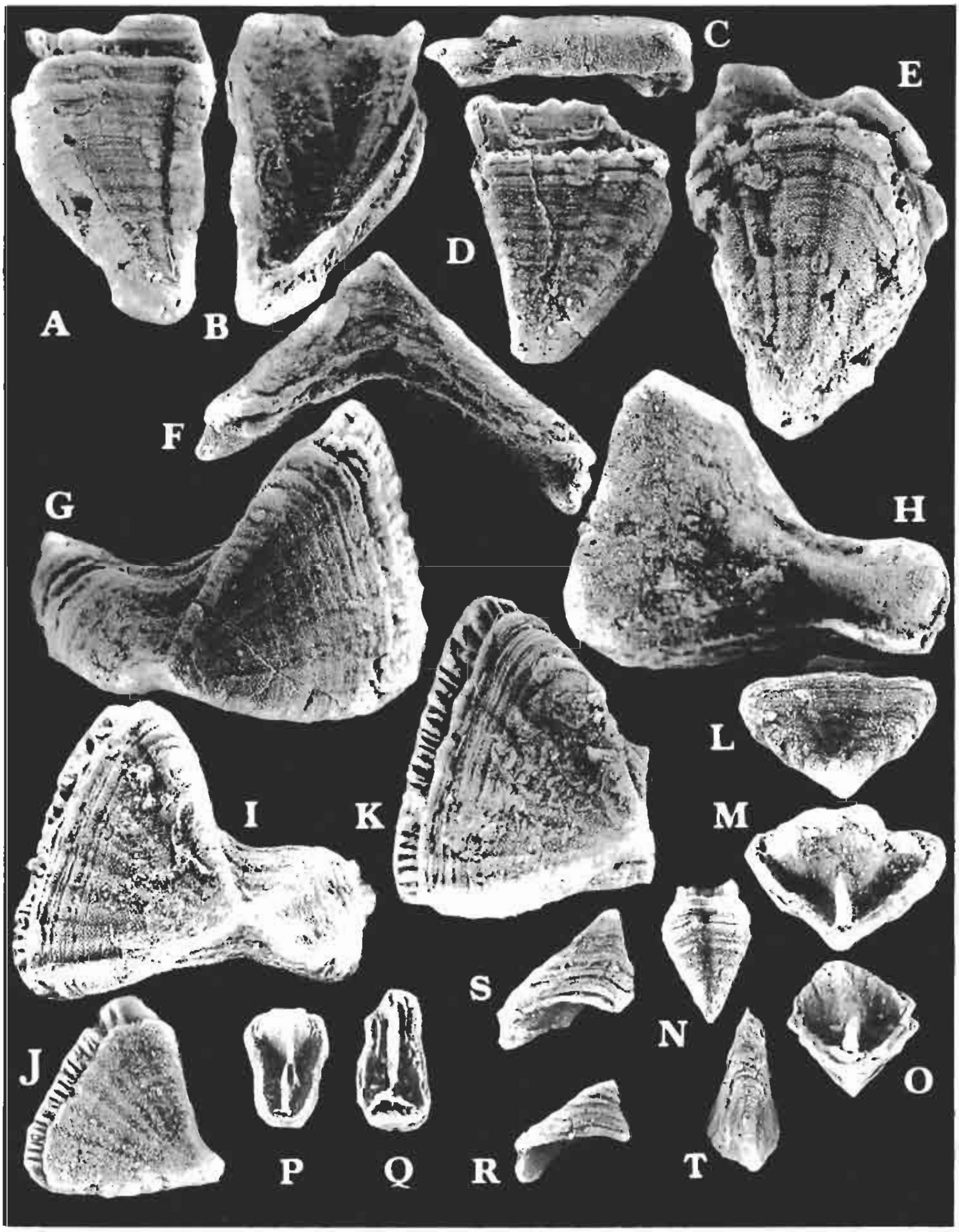
Auxiliary plate X1; small, fitting into notch of B9–B10 plates; subtriangular in shape; length 2.5 mm, width 4.0 mm; auxiliary plate X2, small, fitting into notch of B9–B10 plates; suboval in shape; length 4.0 mm, width 4.0 mm.

Spines narrowly elongate, concave on one side, subquadrangular in cross section; proximal end with insertion process showing where outer shell layer is notched; surface with numerous closely-spaced pores; length 5.0–10.0 mm, width at proximal end 1.0–2.0 mm.

Remarks. — The holotype of *S. spinigera* and the isolated posterior valve are the only specimens known. Although incomplete and disarranged, the holotype presents a relatively good idea of the body plan of the species.

The pores in the plates lead to an internal canal system which can be seen on the broken edge of plate B6 when it is wetted. Whether this system is as complex as that in *Diadeloplax paragrapsima* is unknown. Likewise, the pores in the spines lead to an internal canal system seen where the outer shell layer was partially removed on some of the spines during preparation. It appears to be similar to that in *D. paragrapsima*. Whether the concave surface on the spines is dorsal as appears in Figure 1 or is ventral and the row of spines was overturned is unknown. The spine in the lower left-center of the figure has the concave side to the right, and the notch at the insertion process in the proximal end is more open to the right side as in spines of *D. paragrapsima*. The life position of the marginal spines is unknown, whether forming a flat fringe lying on the substrate or were raised above the substrate. The spines were probably attached through a girdle-like structure.

Fig. 5. *Diadeloplax paragrapsima* gen. et sp. n. from the Gene Autry Formation of Oklahoma; × 10. A–B, Dorsal and ventral views of left-handed auxiliary plate X1, paratype OUZC 1204. C–D, left lateral and dorsal views of right-handed auxiliary plate X1, paratype OUZC 1205.



E. Dorsal view of right-handed auxiliary plate X1 showing more strongly developed radial ridges, paratype OUZC 1206. F–H. Posterior, dorsal, and ventral views of right-handed intermediate plate B8, paratype OUZC 1207. I. Dorsal view of left- handed intermediate plate B9, paratype OUZC 1208. J–K. Two dorsal views of partial left-handed intermediate plates B9, paratypes OUZC 1209 and 1210. L–M. Dorsal and ventral views of auxiliary plate X2, paratype OUZC 1234. N. Dorsal view of auxiliary plate X2, paratype OUZC 1235. O–Q. Three ventral views of auxiliary plates X2, paratypes OUZC 1236–1248. R. Lateral view of auxiliary plate X2, paratype OUZC 1239. S–T. Lateral and dorsal views of auxiliary plate X2, paratype OUZC 1240.

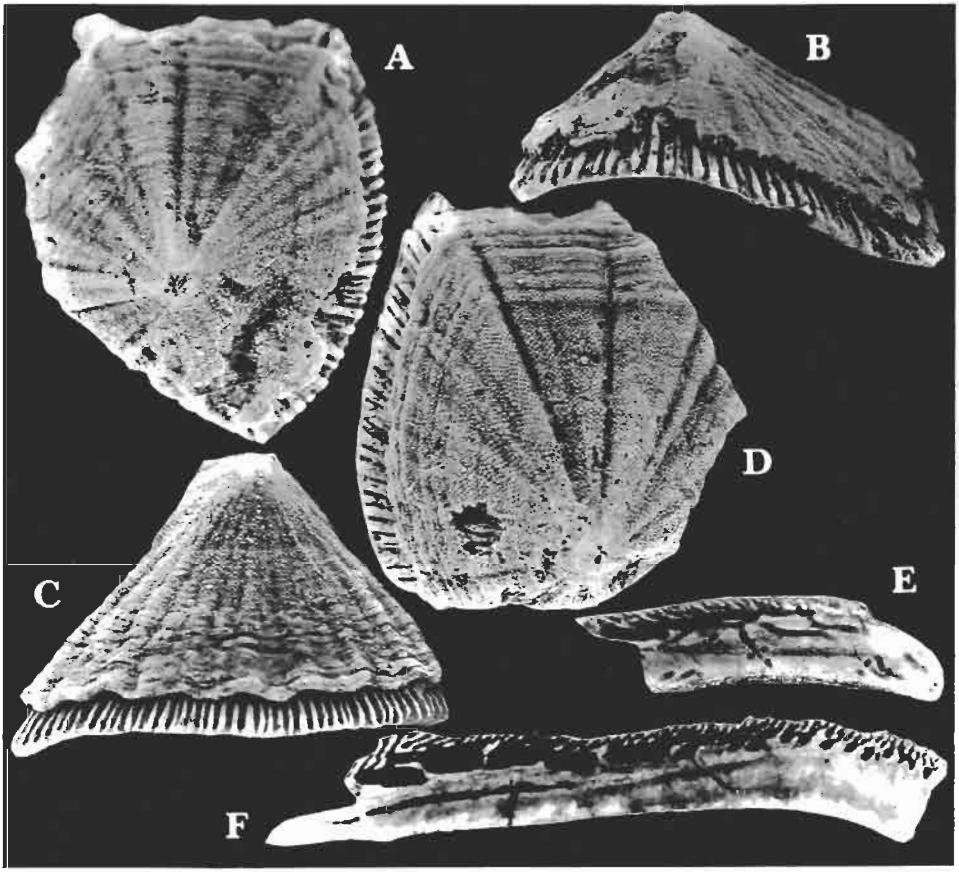
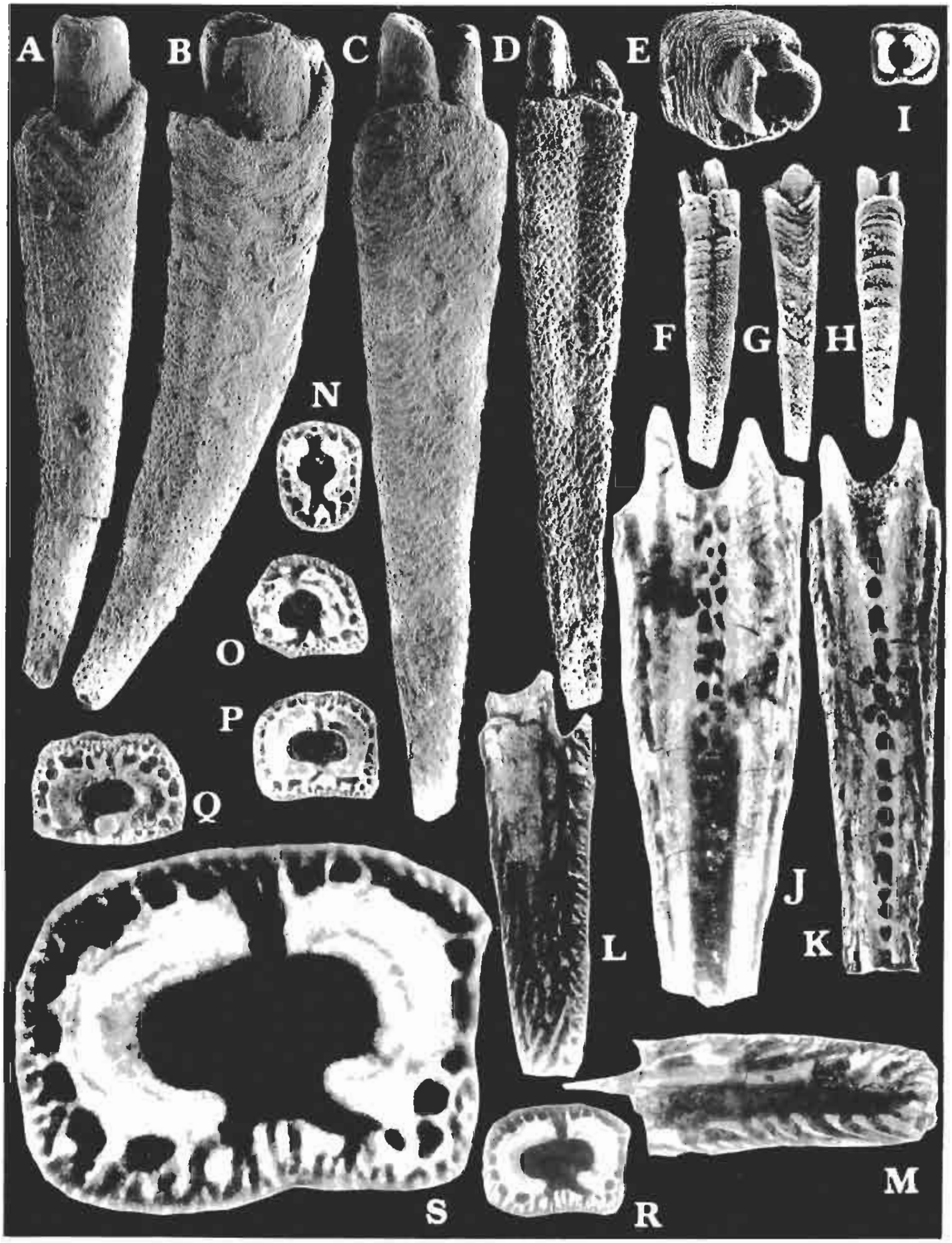


Fig. 6. *Diadeloplax paragrapsima* gen. et sp. n. from the Gene Autry Formation of Oklahoma. A–B. Dorsal and right lateral views of posterior plate, paratype OUZC 1211; × 10. C. Posterior view of posterior plate, paratype OUZC 1212; × 10. D. Dorsal view of posterior plate, paratype OUZC 1213; × 10. E–F. Thin sections of two intermediate plate fragments showing pores and internal canal systems (dark areas), paratypes OUZC 1214 and 1215; × 25.

The insertion plates were undoubtedly embedded in soft tissue. Whether a girdle-like structure into which the insertion plates extended existed, as in polyplacophorans, is unknown. The large, anterior process of plates B1–B2 is dissimilar to insertion plates on the rest of the valves and their function is open to question although they could have strengthened the anterior portion of the body.

Occurrence and stratigraphic range. — Type locality and Louisiana Limestone (Chautauquan) exposed in hillside above State Highway 79 just south of the bridge over Buffalo Creek, NW1/4 sec. 28, T54N, R1W, Pike County, Missouri.

Fig. 7. *Diadeloplax paragrapsima* gen. et sp. n. from the Gene Autry Formation of Oklahoma. A–E. Lateral, oblique lateral, dorsal?, ventral?, and oblique proximal views of spines, paratypes OUZC 1216–1220; ö 25. F–I. Ventral?, lateral, dorsal?, and proximal views of spines,



paratypes OUZC 1221–1224; × 10. J–K. Longitudinal thin sections of spines cut near center and above center showing central cavity, canals leading into central cavity, and pores and lateral canals (dark areas), paratypes OUZC 1225 and 1226; × 25. L–M. Lateral longitudinal sections of spines cut near right lateral side and near center showing pores and canal systems and central cavity (dark areas), paratypes OUZC 1227 and 1228; × 25. N–S. Transverse thin sections of spines cut near distal end, midlength, and near proximal end showing pores, canal systems, central cavity, and C-shaped septa, paratypes OUZC 1227–1233; N–Q × 25; S — an enlargement of R, approx. × 78.

Genus *Diadeloplax* gen. n.

Type species: *Diadeloplax paragrapsima* sp. n.

Etymology: *diadelos*, Greek, distinctive, plus *plax*, Greek, plate.

Diagnosis. — Single row of 12 major plates; three types of intermediate plates, all with posterior apex above duplicature; two types of small auxiliary plates; posterior plate unevenly ridged anteriorly and posteriorly with ridged insertion plate posteriorly and laterally, smooth anteriorly; numerous narrowly elongate spines bordering plates; plates and spines with closely spaced pores leading to complex internal canal systems.

Remarks. — *Diadeloplax* is monotypic. The genus differs from *Strobilepis* in having only three types of intermediate plates, all of which have a posterior apex and duplicature, by a less uniformly lobed posterior valve, and by the greater difference in size of the two types of auxiliary plates.

Stratigraphic range. — Pennsylvanian (Morrowan).

Diadeloplax paragrapsima sp. n.

Figs 4–7, 8C–D.

Holotype: Specimen OUZC 1200 (Fig. 4A–C).

Type horizon and locality: Exposure of the Gene Autry Formation in a series of east-west gullies, on the east side of an unnamed tributary of Sycamore Creek on the Daube Ranch, NW1/4,NW1/4,SW1/4 sec. 2, T4S, R4E, Johnson County, southern Oklahoma, Ravia 71/2' quadrangle.

Etymology: *paragrapsimos*, Greek, exceptional.

Diagnosis. — As for the genus.

Description. — Small (est. length 4–5 cm), narrow, elongated scleritome; all plates thick, marked with closely spaced pores and comarginal growth lines. Anterior plate semicircular, steep-sided, slightly asymmetrical; apex just anterior to posterior margin with steep convex slope posterior to it; insertion plates on anterior and lateral margins, ridged on right side, smooth elsewhere; surface marked by faint, broad, radiating ridges; ventral surface with grooves bordering lateral margins formed by lateral plate margins and inner ridges extending from area under apex to margin of insertion plate; length 1.00–3.80 mm, width 1.80–5.20 mm, height 1.00–3.50 mm (n=3).

Posterior plate semi-oval; mucro located posterior to midlength; posterior slope steeper than lateral and anterior slopes; insertion plate along entire margin, ridged posteriorly and laterally, smooth anteriorly; surface marked by irregularly spaced, pronounced, broad, radial ridges; ventral surface smooth; length 5.8 mm, width, 5.0 mm, height 3.0 mm (n=6).

Intermediate plates of three forms: (1), B1–B2, left- and right-handed; short with large, extended anterior process; strongly arched; terminal apex leading anteriorly to narrow median ridge; anterior margin a broad U-shape; posterior margin with duplicature below apex; short, wide insertion plates on lateral margins, ridged on one side, smooth on other side; anterior process thin, forming grooves where it meets lateral insertion

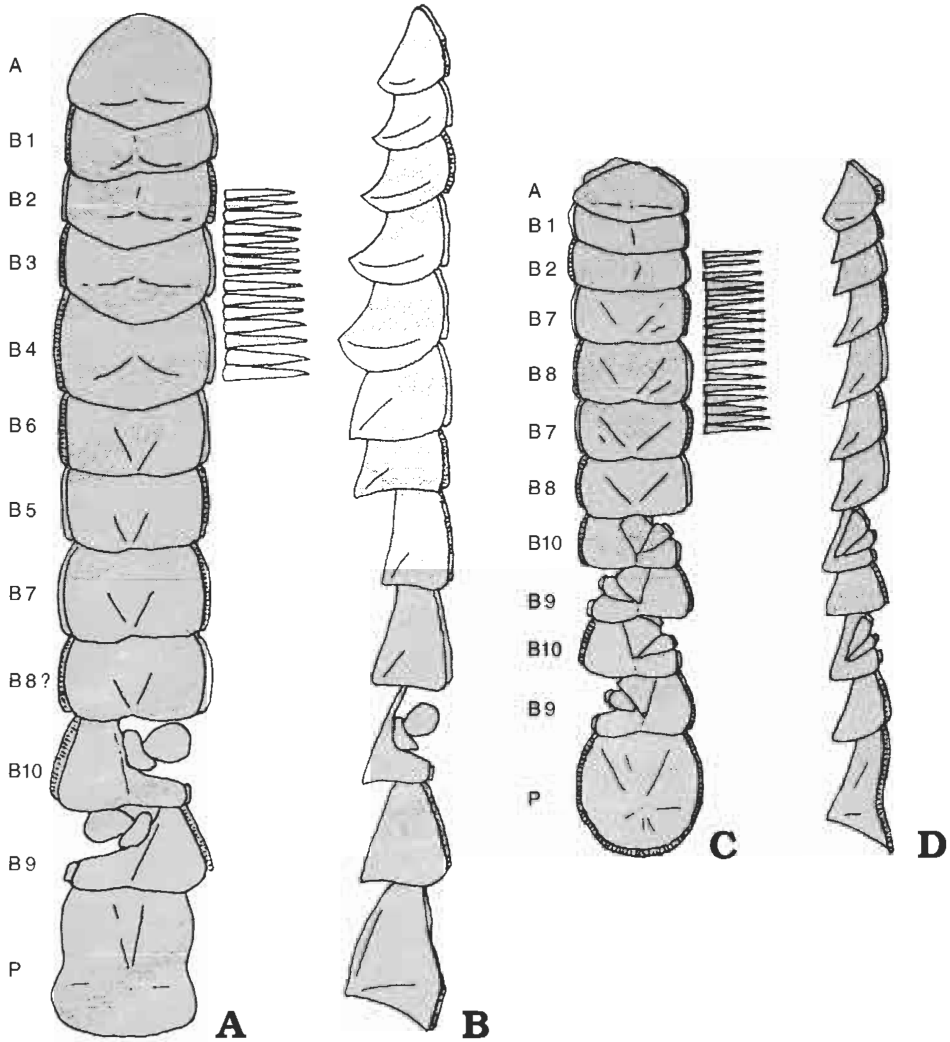


Fig. 8. Possible reconstructions. ❑A–B, *Strobilepis spinigera* Clarke 1888; dorsal and right lateral views; not all spines are included, designation of plates corresponds to lettering in Fig. 1B; approx. × 2.0. ❑C–D, *Diadeloplax paragrapsima* gen. et sp. n.; dorsal and right lateral views; not all spines are included, designation of plates is related to plate designations of similar form in Figs 1B and 8A; approx. × 2.0.

plates, with sharp ridge extending anteriorly out from under median ridge on plate surface; ventral surface with broad ridges under grooves where anterior process and lateral insertion plates meet; length (including anterior process) 2.40–3.90 mm, width 4.20–6.80 mm, height 1.90–2.6 mm (n=6); (2), B7–B8, left- and right-handed; moderately asymmetrical with shallow, anterolateral notch on one side; larger side more steeply sloped than notched side; surface slopes from terminal apex to lateral and anterior margins; duplicature located below apex; short, wide insertion plates on lateral and anterior margins, ridged on shorter lateral margin, smooth elsewhere; surface marked by broad radiating ridges; ventral surface smooth; length 3.70–4.30 mm, width 5.50–7.40 mm, height 2.00–2.20 mm (n=12); (3), B9–B10, left- and right-handed, strongly arched; strongly asymmetrical with deep notch anterolaterally making one side much larger; surface slopes from terminal apex to lateral margins; duplicature located below apex; insertion plates on lateral margins, short, wide, ridged on larger side, short, narrow, smooth on smaller side; surface marked by prominent ridge extending from apex along margin of notch on larger side and faint radial ridges on surface of larger side; ventral surface with ridges extending from corners of insertion plate on smaller side paralleling posterior and anterior margins, becoming obsolete on larger side; length 3.10–4.20 mm, width 4.20–5.40 mm, height 2.50–3.40 mm (n=14).

Auxiliary plate X1; large, left- and right-handed; subtriangular; flat to arched dorsal surface extending from nearly terminal apex; margins downturned posteriorly and laterally; short, wide, smooth insertation plate opposite from apex ending on one side in a heavy reflexed ridge on ventral surface extending towards apex of plate; ventral surface with narrow groove formed by plate margin and a parallel ridge closely paralleling reflexed ridge of insertion plate; dorsal surface may be marked by faint, low, broad, radial ridges; length 4.0–4.90 mm, width 3.30–3.50 mm, height 1.00–2.00 mm (n=7); auxiliary plate X2; small, bilaterally symmetrical; narrow to broadly subtriangular in shape; apex at posterior margin; subtriangular in lateral view; short, wide insertion plate on anterior margin; ventrally with narrow septum extending from under apex towards or to anterior margin; length 1.60–2.20 mm, width 1.00–2.60 mm, height 0.90–1.40 mm (n=8).

Spines narrowly elongate, subquadrangular in cross section; straight to curved; one surface slightly concave laterally; proximal end with attachment area exposed on all sides consisting of two laterally placed septa; septa extend to distal end, C-shaped in cross section with concave side towards center of spine bordering central cavity; outer wall layer with numerous, closely-spaced pores; pores near middorsal and midventral regions lead into canals running into central cavity; laterally, pores lead into small canals which periodically coalesce into larger canals running longitudinally along septa towards proximal end; length 2.0–5.1 mm, width at proximal end 0.4–0.7 mm (n=132).

Remarks. — *Diadeloplax paragrapsima* is about one-half the length of *Strobilepis spinigera*. The spines of the former are about one-half the length of those in the latter. *D. paragrapsima* also differs in having three types of intermediate plates instead of five types, a greater difference in size of the auxiliary plates, duplicatures and terminal apices present on all intermediate valves instead of only on part of the intermediate valves, and a more highly but less uniformly ornamented posterior valve.

Occurrence. — Known only from the type locality.

Acknowledgements

We thank E.L. Yochelson, and M.H. Nitecki for their thoughtful reviews which has led to significant improvement of the paper. We are gratefull to E. Landing, New York Geological Survey, and D.B. Blake, University of Illinois, for making specimens available for study; to C.E. Brett, University of Rochester, for providing helpful information on the Hamilton Group of New York and to T.L. Thompson, Missouri Geological Suvey, on the Louisiana Limestone of Missouri. This research was supported in part by a grant from the Ohio University Research Committee, the National Science Foundation(EAR 9117700) and the American Petroleum Research Fund, administered by the American Chemical Society (PRF No. 15821-AC2 and PRF No. 20742-B8C) to R. H. Mapes.

References

Adrain, J.M. 1992. Machaeridian classification. *Alcheringa* **16**, 15–32.

Aurvillius, C.W.S. 1892. Ueber einige Ober-Silurische Cirripeden aus Gotland. *Kongliga Svenska Vetenskapsakademiens Handlingar* **18**, 4(3), 1–24.

Bergström, J. 1989. The origin of animal phyla and the new phylum Procoelomata. *Lethaia* **22**, 259–269.

Clarke, J.M. 1896. The structure of certain Paleozoic barnacles. *American Geologist* **17**, 137–143.

Dzik, J. 1986. Turrilepedida and other Machaeridia. In: A. Hoffman & M.H. Nitecki (eds) *Problematic Fossil Taxa*, 116–134. Oxford University Press, New York.

Hall, J. & Clarke, J.M. 1888. Trilobites and other Crustacea of the Oriskany, Upper Helderberg, Hamilton, Portage, Chemung and Catskill Groups. *New York Geological Survey, Paleontology* **7**, 1–236.

Hoare, R.D. 1976. *Lobarochiton*, new generic designation for *Gryphochiton? anomolus* (Rowley) (Polyplacophora). *The Ohio Journal of Science* **76**, 116–118.

Hoare, R.D. & Sturgeon, M.T. 1979. Stratigraphic distribution of Polyplacophora in the Mississippian and Pennsylvanian of North America. *Compte Rendu Huitieme Congres International de Stratigraphie et de Geologie Carbonifere, Moscow, 1975* **3**, 176–183.

Hyman, L.H. 1967. *The Invertebrates. Volume VI, Mollusca I.* 792 pp. McGraw-Hill Book Company, New York.

Jell, P.A. 1981. *Thambetolepis delicata* gen. et sp. nov., an enigmatic fossil from the Early Cambrian of South Australia. *Alcheringa* **5**, 85–93.

Pojeta, J., jr. 1980. Mollusca phylogeny. *Tulane Studies in Geology and Paleontology* **16**, 55–80.

Rowley, R.R. 1908. *The Geology of Pike County*. 122 pp. Missouri Bureau of Geology and Mines.

Schallreuter, R. 1985. Mikrofossilien aus Geschieben IV. Machaeridier. *Der Geschiebesammler* **18**, 157–171.

Strathmann, R.R. 1991. Divergence and persistence of highly ranked taxa. In: A.M. Simonetta & S. Conway Morris (eds) *The Early Evolution of Metazoa and the Significance of Problematic Taxa*, 15–18. Cambridge University Press, Cambridge.

Smith, A.G. & Hoare, R.D. 1987. Paleozoic Polyplacophora: A Checklist and Bibliography. *Occasional Papers of the California Academy of Sciences* **146**, 1–71.

Van Belle, R.A. 1983. The Systematic Classification of the Chitons (Mollusca: Polyplacophora). *Informations de la Societe Belge de Malacologie* **11**, 1–179.

Van Name, W.G. 1926. A new specimen of *Protobalanus*, supposed Paleozoic barnacle. *American Museum Novitates* **227**, 1–6.

Williams, J.S. 1943. Stratigraphy and fauna of the Louisiana Limestone of Missouri. *U.S. Geological Survey Professional Paper* **203**, 1–133.

Withers, T.H. 1915. Some Palaeozoic fossils referred to the Cirripedia. *Geological Magazine* **2**, 112–123.
Withers, T.H. 1926. *Catalogue of the Machaeridia*. 99 pp. British Museum (Natural History), London.

Streszczenie

Środkowodewońska *Strobilepis* należy do najbardziej tajemniczych skamieniałych organizmów młodszego paleozoiku. Autor ilustruje i analizuje muzealne okazy *Strobilepis* (w tym również identyfikowane niegdyś jako ślimaki i chitony) dowodząc, że poszczególne skleryty ułożone były liniowo na grzbiecie zwierzęcia a więc odmiennie niż morfologicznie i strukturalnie podobne płytki sylurskiej *Hercolepas* i dewońskiego *Protobalanus*.

Z późnego karbonu stanu New York pochodzą podobne do *Strobilepis* zestawy sklerytów opisane jako *Diadeloplax paragrapsima* gen. et sp. n. Dla tych dwu form utworzona została nowa gromada Multiplacophora z rzędem Strobilepida.