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# A NEW GENUS AND TWO NEW SPECIES OF MULTIPLACOPHORANS (MOLLUSCA, POLYPLACOPHORA, NEOLORICATA), MISSISSIPPIAN (CHESTERIAN), INDIANA

STEPHANEY S. PUCHALSKI,[1] CLAUDIA C. JOHNSON,[1] ERLE G. KAUFFMAN,[1] AND DOUGLAS J. EERNISSE[2]

[1]Department of Geological Sciences, Indiana University, Bloomington 47405; and [2]Department of Biological Science, California State University, Fullerton 92831

ABSTRACT—*Deltaplax* new genus, *Deltaplax burdicki* new species, and *Deltaplax dellangeloi* new species (Mollusca, Polyplacophora, Neoloricata, Multiplacophora) from the Mississippian Lower Buffalo Wallow Group (Chesterian) of Indiana, USA are described. The new genus is established by one partially articulated and one associated specimen with marginal fringes of two types of large spines, bilaterally symmetrical head and tail valves, and fifteen medial valves arranged in three longitudinal columns similar to those described previously for other multiplacophorans. The two specimens represent separate species differentiated by morphologies of the auxiliary valves, one type of spine, and subtrapezoidal versus triangular tail valves. The tail valve of the articulated specimen also had sutural laminae that projected under the preceding intermediate valve. The presence of sutural laminae allows for placement of multiplacophorans in Subclass Neoloricata of Class Polyplacophora. The head, intermediate, and tail valves are mucronate with comarginal growth lines and ridged insertion plates that probably inserted into soft tissue comparable to the girdle of modern polyplacophorans. The new specimens also indicate one left-handed, one auxiliary, and one right-handed valve in multiplacophorans was equivalent to a single bilaterally-symmetrical intermediate valve of extant polyplacophorans. However, multiplacophoran head valves have plates that project from the lower layer at the lateral margins and articulate with the first intermediate valves that overlap the head and second intermediate valves. These features have not been observed in more typical neoloricates, fossil or modern. Pending systematic revision of the class, Multiplacophora thus is retained as a separate order distinguished by the unique shared characters.

## INTRODUCTION

TWO NEARLY complete multiplacophoran (Mollusca, Polyplacophora) specimens were discovered in separate limestone lenses in a shale unit of the Lower Buffalo Wallow Group (Chesterian) near Eckerty, Indiana, USA. Both specimens have large marginal spines with internal canal systems, bilaterally symmetrical head and tail valves, columns of left- and right-handed intermediate valves, and a central column of bilaterally symmetrical auxiliary valves (Fig. 1.1–1.6), similar to those described previously for other multiplacophorans. One specimen was preserved with at least fifteen valves and about one-third of the spines partially articulated (Fig. 1.1–1.3). A second specimen has all seventeen valves and about half the spines from the same individual preserved in close association (Fig. 1.4–1.6). The head and tail valves of the two specimens differ from other multiplacophorans in valve morphology and preservation details, which provide further information on the multiplacophoran body plan. Reconstructions (Fig. 1.3, 1.6) suggest that a transverse row of one left-handed valve, one auxiliary valve, and one right-handed valve was equivalent to one bilaterally-symmetrical intermediate valve of extant polyplacophorans (more commonly called chitons). The morphologically-based reconstructions also highlight similarities and differences between the two specimens.

Rare fossil taxa afford unique challenges to systematists when new material consisting of few specimens must be evaluated to determine species affiliation. In these cases, morphological differences among specimens must be assessed as attributable to taphonomic processes, ontogenic stages, and/or intraspecific variation. Taphonomy cannot account for the differences observed in the exceptionally well preserved Eckerty multiplacophorans. Both specimens exhibit effects due to transport/deposition and decay processes, but neither indicate that abrasion or dissolution significantly affected the skeletal material prior to burial. The partially articulated specimen apparently was ''folded'' in half (Fig. 1.1–1.3) during transport and/or deposition. ''Folding'' fractured the tail valve through the mucro (Fig. 1.7) and exposed the sutural lamina (Fig. 1.8) as the tail was pulled away from the preceding intermediate valve. The tail originally was subtrapezoidal and slightly wider than long (~4.4 × 4.1 mm) with an elevated mucro located centrally or just anterior to the center of the valve at about 2.3 mm from the posterior margin. The morphology of this tail valve cannot be compared directly to the associated specimen's tail valve because the anterior of the latter valve is obscured by overlying intermediate valves (Fig. 2.1). However, the mucro of the associated specimen's tail valve is 1.7 mm from the posterior margin, and the total posterior width of the valve is about 4.7 mm. Assuming the valve is roughly equidimensional similar to the partially articulated specimen's positions the mucro at about one-third of the length from the posterior margin. Assuming the mucro is approximately centrally-located like the partially articulated specimen results in a tail valve that is triangular and wider than long. Either assumption suggests distinct morphology compared to the partially articulated specimen's tail valve. A triangular valve fits better with the preceding valves as shown in the final reconstruction (Fig. 1.6). Although not visible anterior to the mucro, the growth lines support triangular morphology for the associated specimen's tail valve. Ontogeny does not explain a triangular versus subtrapezoidal tail, because the valves of both specimens are similar in size with comarginal growth lines indicating isometric expansion due to holoperipheral growth styles (i.e., accretion along all valve margins equally).

Intraspecific variation cannot account for the morphological differences in the tail valves of the two specimens. Features of tail valves including the mucro, ornamentation, and/or morphology have been used previously to distinguish between fossil species of the same age and locality. For example, Kues (1978) described a second species in the Mississippian Salem Limestone at Cleveland Quarry, Indiana, USA based on two tail valves. Van Belle (1981) accepted both species as valid. Smith and Hoare (1987) also accepted the designation but noted that the species may be a variant of the more common species because head and intermediate valves were unknown. Ashby and Cotton (1939) described five species based on one tail valve each in Pliocene exposures at Muddy Creek (3 species) and Hamilton (2 species), Australia. All five specific designations were accepted as valid by Van Belle (1981). Morphological characters of the tail valves also

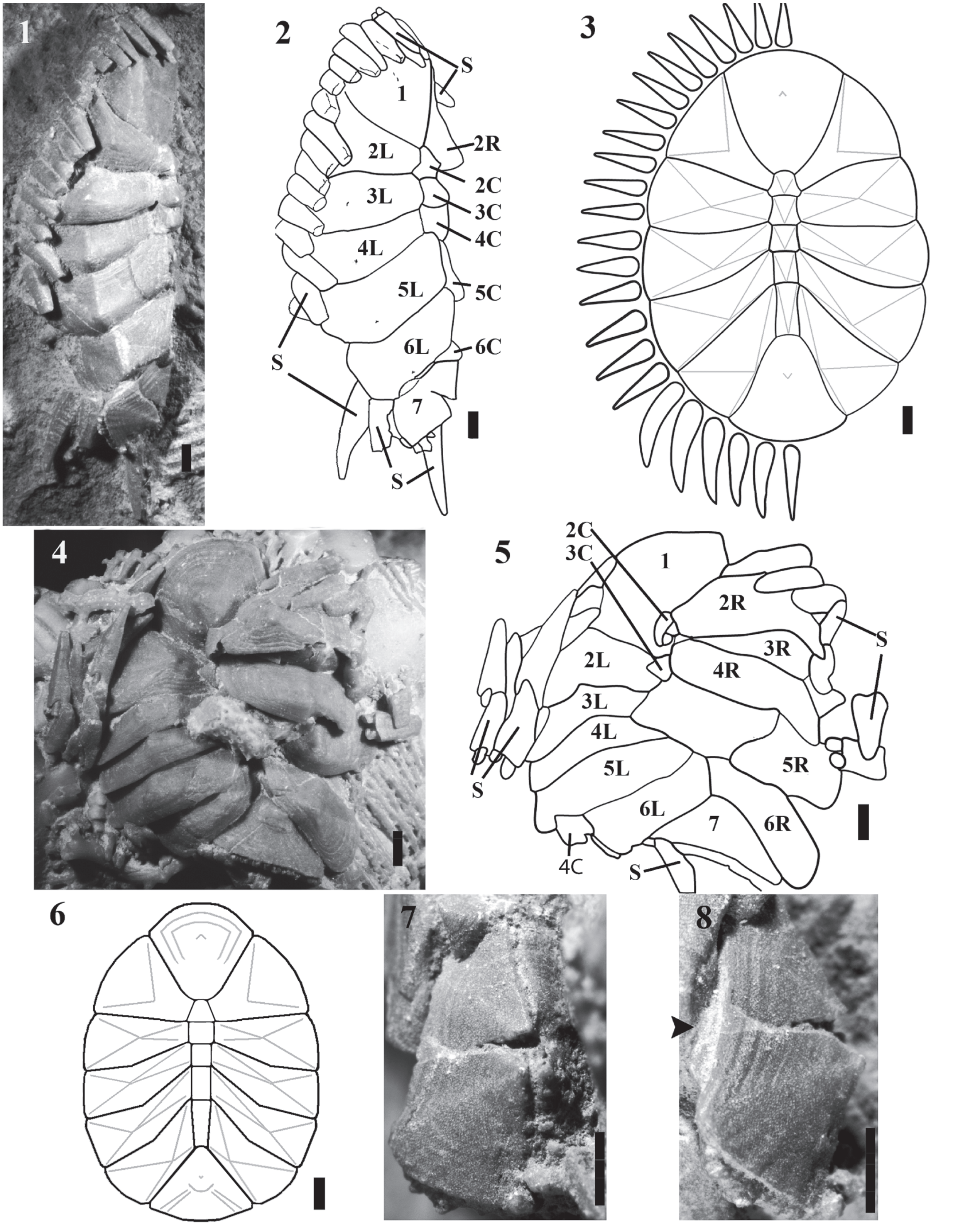


FIGURE *1*— Photomicrographs of *Deltaplax burdicki* new species, INSM71.1.9648, holotype: *1,* entire partially-articulated specimen; *2,* labeled camera lucida drawing of Fig. 1.1 to show features discussed in text, numbers indicate valve order from anterior to posterior, L = left, R = right, and C = central auxiliary valves, S = spine; *3,* reconstruction. *Deltaplax dellangeloi* new species, INSM71.1.9649, holotype: *4,* entire specimen; *5,* labeled camera lucida drawing as in figure 1.2; *6,* reconstruction, spines not shown. *Deltaplax burdicki* new species, INSM71.1.9648, holotype: *7,* tail valve in dorsal view; *8,* sutural lamina of the tail valve (arrow). Anterior is to top and scale bars = 1.0 mm in all figures.

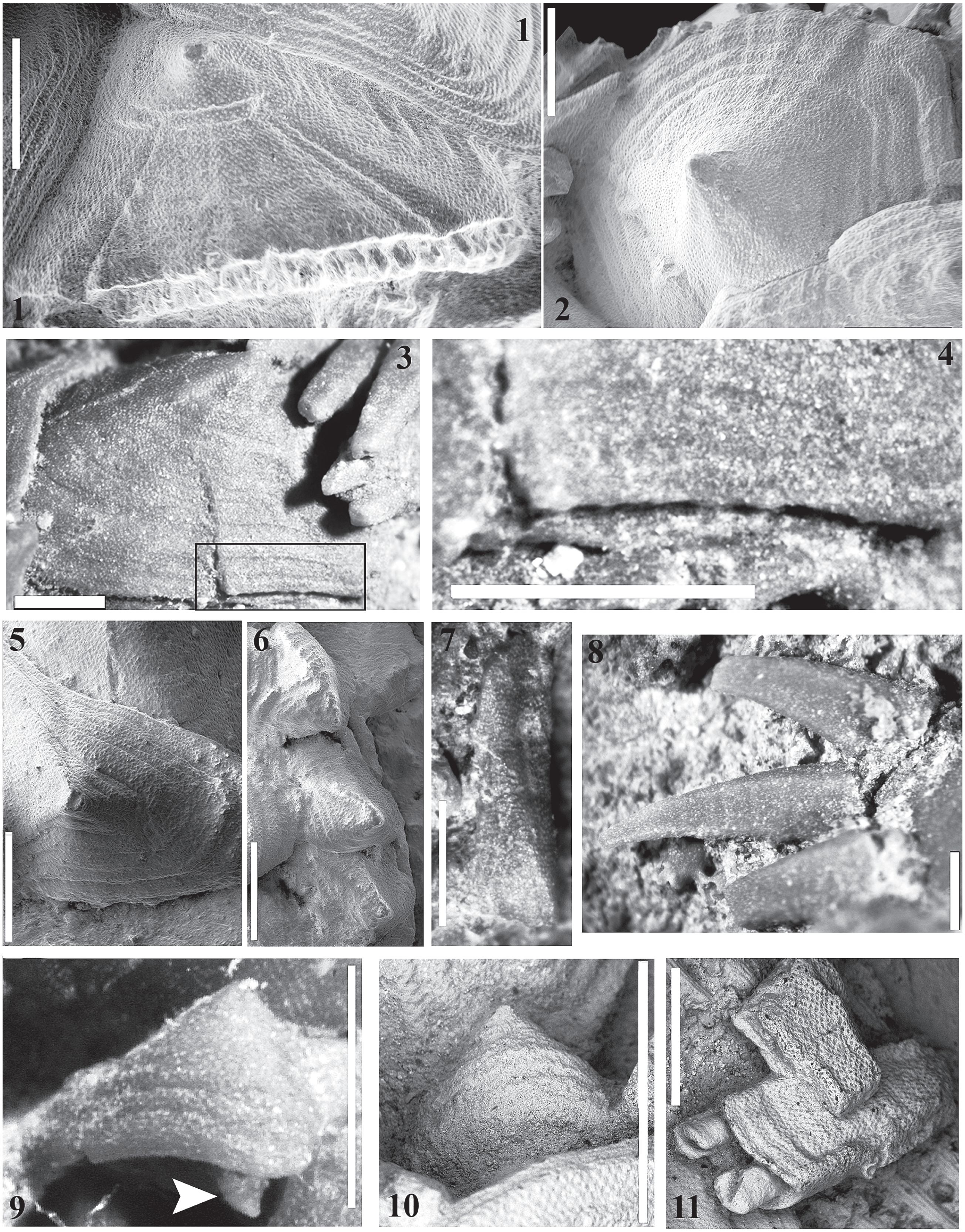


FIGURE 2—*Deltaplax dellangeloi* n. sp., INSM71.1.9649, holotype: *1,* tail valve with distinctively ridged insertion plates (SEM); *2,* head valve (SEM). *Deltaplax burdicki* n. sp., INSM71.1.9648, holotype: *3,* profile of head valve, box shows location of enlargement in 2.4; *4,* detail of plate projecting from lower layer of valve at lateral margins of head valve for articulating with first intermediate valve; *5,* detail of first intermediate valve (2L in figure 1.2) showing medial part with apex and comarginal growth lines, top of triangular lateral area on left, anomalous overlap of head and second intermediate valve also shown (SEM); *6,* detail of first through third auxiliary valves (2C, 3C, and 4C in figure 1.2, top to bottom; SEM); *7,* detail of fourth auxiliary valve (5C in figure 1.2); *8,* detail of larger posterior spines, showing curvature and convex upper surface (Note: anterior-most spine not shown in figures 1.1 or 1.2).

are used, at least in part, to distinguish between closely related extant species (e.g., see keys in Eernisse, 1986). Although the tail valve of some extant species (e.g., *Callistochiton* spp.) undergo an allometric shape change from a normal to increasingly inflated profile, the fact that the two multiplacophoran tail valves are similar in size implies that allometry cannot explain the differences. Therefore, assuming that characteristics of multiplacophoran tail valves are diagnostic similar to more typical chiton species, the Eckerty specimens are described herein as two morphologically distinct species. The first and second auxiliary valves and one type of spine are additionally diagnostic.

## TAPHONOMY

The rarity of articulated or associated specimens of fossil chitons despite a Cambrian to Recent record suggests that uncommon conditions were required for the preservation of articulation. The new Mississippian specimens are recrystallized calcite but do not indicate a unique depositional environment or unusual fossilization conditions other than rapid burial. The environment has been interpreted as a protected open lagoon where currents or wave base agitation due to storms periodically disturbed muddy bottom sediments and the diverse fauna living at or near normal wave base (D. Burdick, 2006, personal communication). These disturbances briefly transported entire communities, forming grainstone lenses that were buried rapidly as the mud settled out of suspension. Most of the grainstone comprises exceptionally well-preserved to slightly abraded fragments of crinoids, *Archimedes* sp., and other fenestrate bryozoans in a muddy matrix, but the assemblages also include bryozoans (both encrusting and ramose), brachiopods, blastoids, ostracods, and the rare multiplacophorans (D. Burdick, 2006, personal communication). The multiplacophorans and many echinoderms were preserved as partially to completely articulated skeletons, which suggest episodic and rapid burial (Speyer and Brett, 1988 and references therein).

Two grainstone lenses yielded multiplacophoran specimens with preservation states indicating slightly different effects of taphonomic processes. The arrangement of the partially articulated specimen's skeletal elements suggests the skeleton was "folded" in half longitudinally during transport and/or deposition (Fig. 1.1–1.3). The edges of at least three right-handed intermediate valves can be seen under the central and left-handed valves, which are displaced from the normal position. The head valve has been compressed laterally, and the tail valve has been rotated and fractured into quadrants (Fig. 1.1, 1.7). The arrangement of the larger, more posteriorly-located spines implies near life position, but the anterior left-side spines are turned over the dorsal surface (Fig. 1.1, 1.2). A few right-side spines under the head valve point in the same direction as the left-side spines. Gaps between the bases of the left-side spines and the valves imply that the soft tissue in which the elements were embedded (i.e., "girdle") was pulled away from the valve margins. The separation and orientation of the spines could have occurred during transport and deposition, assuming a slightly decayed carcass or a living animal with flexible spines and tender soft tissues that held the skeletal elements together. Alternatively, the separation and orientation of the left-side spines could be attributed to a short post-depositional period of decay and brief exposure to weak currents followed by the rapid burial that preserved the disturbed arrangement of skeletal elements.

The positions of the associated specimen's skeletal elements indicate that burial was delayed for a short time after deposition. A small cache of spines implies currents or waves strong enough to detach and orient the elements but not strong enough to transport them elsewhere (Fig. 1.3–1.6). Assuming effects similar to modern chiton carcasses that disarticulate when slightly disturbed after only two weeks of post-mortem decay (Puchalski, 2002), currents strong enough to transport the entire animal would have resulted in disarticulation during the original depositional event. Burial thus must have been delayed long enough for the connective tissues to decay and weak currents to reposition the spines. Decay of the "girdle" and other soft tissues also likely caused the carcass to collapse around underlying fragments and displace the valves slightly (Fig. 1.3, 1.4). Rapid burial then preserved association of the skeletal elements.

## SYSTEMATIC PALEONTOLOGY

Phylum MOLLUSCA Cuvier, 1797
Class POLYPLACOPHORA de Blainville, 1816
Subclass NEOLORICATA Bergenhayn, 1955

*Diagnosis*.—Polyplacophorans with valves composed of multiple calcareous layers, including an articulamentum layer that extends out from under the tegmentum to form insertion plates and/or sutural laminae on one or more valves.

*Occurrence*.—Silurian to Recent.

*Discussion*.—Multiplacophorans had ridged insertion plates that probably inserted into soft tissue similar to the girdle of extant chitons. The partially articulated specimen demonstrates that at least some multiplacophorans also had sutural laminae that projected under the preceding intermediate valve as a lower layer of the tail valve (Fig. 1.8), comparable to the articulamentum layer in extant chiton valves. In current systematics, the presence of articulamentum classifies multiplacophorans as neoloricates based on Bergenhayn (1955), who proposed dividing Polyplacophora by the presence or absence of this lower layer. Placement within the Neoloricata is supported by independently published cladistic analyses that included multiplacophorans in addition to Paleozoic and Recent chiton species (Vendrasco, 1999; Cherns, 2004).

Order MULTIPLACOPHORA Hoare and Mapes, 1995

*Diagnosis*.—Dorsal exoskeleton consisting of seven-fold iteration with seventeen calcareous valves in overlapping series; bilaterally symmetrical anterior, posterior and central auxiliary valves; left- and right-handed intermediate valves with mirror symmetry in transverse rows; marginal fringe of elongate calcareous spines.

*Occurrence*.—Silurian to Permian.

*Discussion*.—Multiplacophora originally was proposed as a class in an uncertain phylum, based on characters atypical for extant chitons (Hoare and Mapes, 1995). Multiplacophorans later were placed as an order within Class Polyplacophora because cladistic analysis showed the group shares more character states with chitons than any other known extant or fossil taxon (Vendrasco et al., 2004). Despite the similarities, placement of Multiplacophora at the order level within existing systematics for Polyplacophora is problematic because some characteristics unique to multiplacophorans are uncommon in more typical chitons. Pending systematic revision of the subclass, multiplacophorans thus are retained within Neoloricata as a separate order distinguished by shared characters. Separation of the two groups is supported by a recently published cladistic analysis that resolves a monophyletic clade of neoloricates with multiplacophorans as a stem-group (Sigwart and Sutton, 2007).

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*Deltaplax dellangeloi* n. sp., INSM71.1.9649, holotype: *9,* first auxiliary valve with keel-like process shown by arrow (2C in figure 1.5); *10,* spinose second auxiliary valve (3C in figure 1.5; SEM); *11,* larger spine type showing two c-shaped processes, accretionary growth lines, surface pores, and doubly grooved, slightly convex upper surface (SEM). Anterior is to top in all views except for head valve in Figs. 2.3 and 2.4 where anterior is to right. SEM = photomicrographs with scanning electron microscope. Scale bars = 1.0 mm.

Genera included in the order are *Diadeloplax* Hoare and Mapes, 1995; *Polysacos* Vendrasco, Wood and Runnegar, 2004; *Hercolepas* Withers, 1915; *Protobalanus* Whitfield *in* Hall and Clarke, 1888; *Aenigmatectus* Hoare and Mapes, 1996; and *Deltaplax* n. gen. *Beloplaxus* Oehlert, 1850 is questionably included based on a bilaterally symmetrical tail valve and non-bilaterally symmetrical intermediate valves (Hoare, 2002). The intermediate valves of *Beloplaxus* appear to be similar to the multiplacophorans in shape, terminal apex, and canal systems, but articulated specimens, large marginal spines, heads and auxiliary valves have not been reported in the literature. The valves also lack the distinctive ridged insertion plates of other multiplacophorans, although the absence may be taphonomic.

### Suborder STROBILEPINA Hoare and Mapes, 1995

*Type genus*.—*Strobilepis* Clarke *in* Hall and Clarke, 1888.

*Diagnosis*.—As for the order, but with thick and mucronate calcareous valves having ridged insertion plates on outer margins; articulated specimens with first intermediate valves overlapping both head and second intermediate valves; auxiliary valves with keel-like central processes; spines narrow and elongate, straight or curved with concave or grooved upper surface, subquadrangular in cross section with two c-shaped peg-like projections of underlying layer; spines and valves having numerous surface pores in an outer layer, pores lead down into a complex internal canal system.

*Description*.—Head valve with curved apex, ridged insertion plate along anterior margin, articulated specimens with first intermediate valves overlapping both head and second intermediate valves; intermediate valves thick with apex, duplicatures and ridged insertion plates on lateral margins; tail valve mucronate with ridged insertion plate along posterior margin. Auxiliary valves morphologically variable, consisting of several different forms per individual. Spines narrow and elongate, straight or curved with concave or grooved upper surface; proximal end subquadrangular in cross-section with two c-shaped peg-like projections of underlying layer. Comarginal growth lines showing accretion at the margins of valves; growth lines indicating accretion at the base of spines. Numerous surface pores leading to complex internal canal system in both valves and spines.

*Occurrence*.—Devonian to Pennsylvanian.

*Discussion*.—Genera included in the suborder are *Strobilepis* Clarke *in* Hall and Clarke, 1888; *Polysacos* Vendrasco, Wood and Runnegar, 2004; *Deltaplax* n. gen.; and, possibly *Beloplaxus* Oehlert, 1850 and *Diadeloplax* Hoare and Mapes, 1995. Articulated specimens of *Strobilepis, Polysacos,* and *Deltaplax* all show the anomalous overlap of the first intermediate valves. Other diagnostic characters include structurally similar spines and valves, two or three types of auxiliary valves in the same individual, and mucronate intermediate, anterior, and posterior valves. *Diadeloplax* and *Beloplaxus* show the other characteristics of the suborder, but have not been found as articulated specimens necessary to show the anomalous overlap.

The genera *Hercolepas, Aenigmatectus.* and *Protobalanus* are not included in the suborder despite some similarities in surface pores and possibly the canal system. The three genera are placed in ?Hercolepadina Dzik, 1986 because valve morphologies and structures differ markedly from other multiplacophorans. The unique valve morphology and ornamentation of *Hercolepas* and *Protobalanus* have not been reported in any other multiplacophorans. Illustrations of the articulated specimens do not show the anomalous overlap of the first intermediate valves. The valves also are much thinner and apparently lacked insertion plates. Surface pores were noted, but the inner canal systems were not described in valves of either genus. *Aenigmatectus* has canal systems and surface pores similar to other multiplacophorans but differs in having distinctly offset and thinner insertion plates, greater variation in valve morphology, and the presence of spinose dorsal ''sclerites'' (Hoare and Mapes, 1996). Insertion processes at the margins of these ''sclerites'' differ from the keel-like central processes seen in the auxiliary valves of other multiplacophorans. The multiple insertion processes of *Aenigmatectus* spines also differ greatly from the two c-shaped processes of other multiplacophoran spines.

### Family STROBILEPIDAE Hoare and Mapes 1995

*Type species*.—*Strobilepis spinigera* Clarke *in* Hall and Clarke, 1888.

*Diagnosis*.—As for the class, with smooth articulating surfaces on lateral margins of head valve.

*Occurrence*.—Devonian to Pennsylvanian.

*Discussion*.—*Strobilepis*, *Diadeloplax*, and *Deltaplax* n. gen. are included in the family. The head valves of all three genera have smooth-surfaced plates on the lateral margins. The plates are unlike any feature of extant chiton head valves that have teeth (plates) for insertion into soft tissue and are more similar to the ridged insertion plates on the anterior margin of multiplacophoran valves. The smooth lateral plates provide articulation of the head with the first intermediate valves, which overlap both the succeeding intermediate valve and the head valve in multiplacophorans. Articulation in extant chitons is achieved through sutural laminae that project anteriorly from the first intermediate valve and under the head valve. The anomalous overlap in multiplacophoran valves was observed in *Polysacos vickersianum* and *Strobilepis spinigera* (Vendrasco et al., 2004), although the lateral articulating plates on the head valves were only noted in the latter species (Hoare and Mapes, 1995). *Polysacos* thus is not included in the family at this time pending further research. *Beloplaxus* also is not included because articulated specimens have not been reported, and head valves are unknown (Hoare, 2002).

### Genus DELTAPLAX new genus

*Type species*.—*Deltaplax burdicki* n. sp.

*Other species*.—*Deltaplax dellangeloi* n. sp.

*Diagnosis*.—As for the family, but with triangular to subtriangular head valve with anteriorly curved apex near or just anterior to midpoint; triangular to subtrapezoidal tail valve with mucro anterior to or in center of valve, post-mucronal area defined by furrows or grooves radiating from mucro to valve margins; first auxiliary valve triangular to subtriangular with anteriorly-curved apex and straight to concave posterior margin, remaining auxiliary valves square to rectangular with central to terminal apices; spines of two distinct types, elongate anterior spines narrow and rounded with concave upper and convex lower surfaces; posterior spines broader and larger than anterior spines, straight or curved and somewhat flattened with convex lower surfaces.

*Description*.—Valves with apices and ridged insertion plates; head valve subtriangular with curved margins, rounded points and anteriorly-curved apex just anterior to or in valve center, ridged insertion plates on anterior margin, smooth articulating surfaces on lateral margins that project from lower layer and under first intermediate valves; faint to strong comarginal growth lines indicative of holoperipheral style of growth.

Left- and right-handed intermediate valves; first intermediate valve subtriangular in outline with flat and nearly smooth lateral area, other intermediate valves trapezoidal, wider than long; slightly elevated and upright apices slightly off-center to valve width, central to valve length on first intermediate valve and shifted progressively more toward posterior margin to terminal on last intermediate valve; duplicatures from apex to anterior margin and to posterior corners, lateral areas defined by shallow furrow from apex to anterior corners; ridged insertion plates on lateral margins for insertion into soft tissue; ornamentation consisting of surface pores, strong comarginal growth lines at anterior and lateral margins with growth lines more closely spaced along posterior margin, indicating mixoperipheral growth style with accretion of more material along anterior and lateral margins and less material at the posterior margin.

Arched tail valve with radial grooves extending from elevated mucro and defining post-mucronal area, short and rounded sutural laminae on anterolateral margin, posterior margin with ridged insertion plate; ornamentation consisting of surface pores and comarginal growth lines indicating holoperipheral accretion. Auxiliary valves variable in shape, first triangular, second and third squarish, fourth and fifth rectangular, all with central to terminal apices, and comarginal growth lines. Spines morphologically variable, larger posteriorly, growth lines indicating accretion at proximal base of spine.

*Etymology*.—From Greek, referring to the shape of the head, tail and first auxiliary valves.

*Occurrence*.—Mississippian (Chesterian).

*Discussion*.—*Deltaplax* n. gen. differs from *Strobilepis, Diadeloplax,* and *Polysacos* in general valve morphology. The head valves of *Deltaplax* are subtriangular with an anteriorly-directed apex located just anterior to midline (Fig. 2.2, 2.3). In comparison, *Polysacos* and *Strobilepis* head valves are suboval with terminal apices (Vendrasco et al., 2004). *Diadeloplax* head valves are described as semicircular with an apex located just anterior to the posterior margin (Hoare and Mapes, 1995).

The intermediate valves of *Deltaplax* are morphologically distinct compared to other multiplacophoran genera. The triangular-shaped lateral area of the first intermediate valve is flat and nearly smooth with faint radial ridges. These ridges are not apparent on the medial side of the valve, which has strong comarginal growth lines that outline the centrally-located apex and suggest a holoperipheral style of growth (Fig. 2.5). The corresponding valve in *Polysacos* has faint growth lines, an apex located nearly at the anterior margin, and a lateral area with distinct ridges that radiate from the apex in approximately all directions. The slightly elevated apices on the other intermediate valves of *Deltaplax* are straight (Fig. 1.1, 1.4) and not markedly or slightly curved as seen in *Strobilepis* and *Polysacos*, respectively. *Deltaplax* intermediate valves are subrectangular or trapezoidal, about twice as wide as long, rather than suboval and nearly equidimensional as in *Polysacos. Deltaplax* intermediate valves also seem to lack the "large, extended anterior processes" of *Diadeloplax* (Hoare and Mapes, 1995, p. 124).

*Deltaplax* tails have slight to deeply incised radial grooves extending from an elevated mucro to define the post-mucronal area (Fig. 1.7, 2.1) but otherwise lack distinct ridges radiating across the lateral and anterior areas of the valves as seen for the tail valves of the other genera. *Deltaplax* tail valves are similar in outline to *Polysacos*' subtriangular and *Strobilepis*' subtrapezoidal tails. However, the mucros are located anterior to or in center of valve rather than near the posterior margin for *Polysacos* or *Strobilepis.* The mucro is located posterior to midlength of semi-oval *Diadeloplax* tails.

The second through fifth auxiliary valves differ morphologically among the genera. However, the first auxiliary valves of *Deltaplax* are grossly similar to one type of *Diadeloplax* auxiliary valve and to the first auxiliary valve of *Strobilepis.*

The approximately 22 mm long (including spines) partially articulated *Deltaplax* specimen has about 45 spines of two types. Although the specimen is roughly the same size as *Polysacos,* the number of spines is reduced in *Deltaplax* in comparison to *Polysacos* and *Strobilepis* that have smaller and more numerous spines (~60) with uniform morphology among spines including a concave upper surface and a central groove. Both types of *Deltaplax* spines have concave upper surfaces but do not have central grooves. The two types of *Deltaplax* spines are similar to *Diadeloplax* spines, but the arrangement and number of spines per individual is unknown for *Diadeloplax.* The anterior *Deltaplax* spines are narrower with four or five spines attached to the intermediate valve margins compared to the more posterior valves, which has only three larger spines that curve toward the posterior (Fig. 1.3). The tail has similar larger and posteriorly-curved spines, except for a straight terminal one.

### DELTAPLAX BURDICKI new species
Figures 1.1–1.3, 1.7, 1.8, 2.3–2.8

*Diagnosis*.—As for the genus, but with subtriangular head valve wider than long; subtrapezoidal tail valve with mucro just anterior to center, shallow post-mucronal area defined by shallow grooves extending radially from mucro to lateral margins near posterior corners, convex anterior and posterior margins; first auxiliary valve triangular with concave lateral margins, remaining auxiliary valves rectangular to square with pyramidal and upright apices terminal and posteriorly directed.

*Description*.—Head valve subtriangular in outline with slightly convex margins and rounded points, wider than long; anteriorly curved apex located approximately centrally or slightly anterior of center, not terminal, concave slope anterior to apex, slightly convex on sides and posterior; lateral margins with narrow and smooth surfaces that articulate with first intermediate valves; ornamentation comprised of surface pores and weak comarginal growth lines suggesting holoperipheral growth style.

Tail valve subtrapezoidal, slightly wider at posterior than long, elevated mucro located just anterior of center, slope shallow and flat from mucro to posterior margin; post-mucronal area defined by faint, shallow grooves that extend diagonally from mucro to lateral margin near corners; convex anterior margin; anterolateral margins slightly concave near posterior corners forming 'notch' that preceding valve fits into, giving valve a bell-shaped outline; thin, short, and rounded sutural laminae on anterolateral margin for articulation with preceding intermediate valve; convex posterior margin with ridged insertion plates; surface pores; distinct comarginal growth lines.

First auxiliary valve triangular with sinuous posterior margin, rounded 'points' and concave sides, terminal apex, elevated duplicature forming central triangular ridge from apex to anterior; remaining auxiliary valves subtriangular or longitudinally elongated rectangle in outline with pyramidal apices located on and directed toward posterior; flat, raised triangular areas anterior to terminal apices of second, third, and fifth auxiliary valves; fourth auxiliary valve has duplicatures extending from the terminal apex to the anterior corners and forming central longitudinal groove; ornamentation consisting of surface pores, strong comarginal growth lines indicative of holoperipheral growth for first auxiliary and slightly to strongly mixoperipheral growth for other auxiliary valves.

Spines narrow, elongate, straight and rounded at anterior, concave upper surface; straight and elongate terminal spine, other posterior spines broader than anterior spines and curved toward posterior, somewhat flattened with concave upper surface; proximal end subquadrangular with two peg-like projections of underlying shell layer; pores on all surfaces except processes, pores lead down into internal canal system; growth lines indicating accretion at proximal ends.

*Etymology*.—Named for Dennis Burdick, who discovered both specimens during a detailed study of the Eckerty fauna.

*Types*.—Holotype, INSM71.1.9648, Indiana State Museum, Indianapolis, Indiana, USA. Mississippian (Chesterian), shale unit of the Lower Buffalo Wallow Group, 9.1 m above the Glen Dean Limestone, abandoned Mulzer Brothers Quarry (38.358N, 86.616W), approximately 4 km north of Eckerty, Crawford County, Indiana, USA.

*Measurements*.—The reconstruction suggests the specimen was about 16.2 mm long and 11.5 mm wide, excluding the spines; head valve 5 mm long; tail valve about 4.4 mm long, maximum width 4.1 mm at posterior, about 1.8 mm wide at anterior, mucro just anterior to center at about 2.1 mm from anterior margin; anterior spines 2.0–2.5 mm in length, posterior curved spines about 3.5 mm length, and terminal spine approximately 4.0 mm long.

*Occurrence*.—Known only from the type locality.

*Discussion*.—Reconstruction of the nearly complete, articulated specimen suggests that the species had one head valve, ten intermediate valves, five auxiliary valves, and one tail valve per individual with a marginal fringe comprised of at least two different types of large spines (Fig. 1.3). Growth lines indicate holoperipheral growth of the head valve (Fig. 2.3) similar to head valves of modern chitons and the other Eckerty specimen (Fig. 2.2). Holoperipheral growth is suggested for the first intermediate valves of the two multiplacophoran species. This valve in *D. burdicki* is subtriangular with very strong comarginal growth lines on the medial side and a nearly smooth, triangular lateral area that has faint grooves radiating from the apex (Fig. 2.5). The intermediate valves of most modern chitons typically have mixoperipheral growth styles (Vendrasco, 1999), similar to the second through fifth intermediate valves of multiplacophorans. These valves have slight morphological variations but are more or less rectangular and wider than long, in *D. burdicki*. similar to *S. spinigera.*

The sutural laminae are not diagnostic of only *D. burdicki.* Sutural laminae have not been reported for any other (partly) articulated multiplacophoran, but recognition of the sutural laminae for *D. burdicki* was possible only because slight rotation of the tail valve exposed part of the sutural lamina yet partially preserved articulation with the preceding valve. The laminae ordinarily would not be observable in a fully articulated specimen or preserved in disarticulated valves due to rapid fracturing of the thin structures. Nonetheless, the illustration of an isolated tail valve of *S. spinigera* shows remnants of sutural laminae (Hoare and Mapes, 1995, fig. 3), and possible remains of similarly broken off sutural laminae are also discernible in figured *Diadeloplax* tails (Kirkby, 1859; Hoare and Mapes, 1995; Hoare and Mapes, 2000).

*Deltaplax burdicki* auxiliary valves comprise three types (Fig. 2.6, 2.7). All three types have posteriorly-directed terminal apices, flat triangular areas anterior to apices, and comarginal growth lines indicating holoperipheral to mixoperipheral accretion. The triangular anterior-most valve is similar to one type of auxiliary valve figured for *Diadeloplax paragrapsima* (Hoare and Mapes, 1995, fig. 5T) including a posteriorly located and directed apex, but all three margins of the triangular *Diadeloplax* valve are straight. The *D. burdicki* valve differs from the 'squarish' first auxiliary valve of *Polysacos vickersianum* (Vendrasco et al., 2004), which is more similar morphologically to the second and third *D. burdicki* auxiliary valves. The two rectangular posterior-most auxiliary valves differ from *P. vickersianum*'s two posterior-most auxiliary valves. The two duplicatures that extend from the apex to the anterior corners and form a central groove, in particular, are distinct in the fourth auxiliary of *D. burdicki.*

The curved spines of *D. burdicki* have a convex lower surface and concave upper surface (Fig. 2.8), similar to *D. paragrapsima* spines (Hoare and Mapes, 1995, fig. 7). The straight anterior spines (Fig. 1.1) are similar to the second type of *D. paragrapsima* spines as well as the single type of *P. vickersianum* and *S. spinigera* spines. However, both types of *D. burdicki* spines lack the conspicuous central grooves on the upper surface of the spines described for the other three species.

### DELTAPLAX DELLANGELOI new species
Figures 1.4–1.6, 2.1, 2.2, 2.9–2.11

*Diagnosis*.—As for the genus, but with subtriangular head valve, similar in length and width; triangular tail valve, wider than long, mucro just anterior to or in center, trapezoidal post-mucronal area well-defined by two pairs of deep radial grooves extending from base of mucro to posterior margin; first auxiliary valve triangular with straight lateral margins, slightly convex posterior margin, anterior apex, distinct duplicature lacking; remaining auxiliary valves spinose, squarish at base with central apex; two types of spines, smaller type straight with concave upper surface, larger type broad, flat with two longitudinal marginal grooves and slightly convex upper surface.

*Description*.—Head valve subtriangular in outline, as long as wide with apex located just anterior of center, apex highly elevated and anteriorly curved, concave slopes anterior and lateral to apex; anterior margin convex; lateral margins straight with rounded points; ridged insertion plates along anterior margin; lateral margins with projections of lower layer for articulation with first intermediate valves, projections short and narrow with smooth surfaces; ornamentation consisting of surface pores and deeply incised comarginal growth lines.

Tail valve triangular with mucro in valve center or just anterior to midlength; two pairs of deep radial grooves that extend diagonally from base of bulbous mucro to posterior margin and define the trapezoidal post-mucronal area; ridged insertion plates on convex posterior margin; ornamentation consisting of surface pores and strong comarginal growth lines.

First auxiliary valve triangular in dorsal view, straight-sided with anterior apex, arched and without distinct duplicature. Second through fourth auxiliary valves squarish at base, spinose with central apex. Fifth auxiliary valve also spinose but probably rectangular at the base. All auxiliary valves with surface pores and strong comarginal growth lines.

Hollow marginal spines of two types; narrow, elongate, straight and rounded distally with concave upper and convex bottom surfaces or broader and straight at posterior, flattened with two longitudinal marginal grooves and slightly convex upper surface, distally subrectangular; proximal end of both spine types subquadrangular with two peg-like projections of underlying shell layer; growth lines indicating proximal accretion; surface pores leading down into complex internal canal system.

*Etymology*.—Named for Bruno Dell'Angelo of Prato, Italy, who has contributed much to the study of fossil and living chitons.

*Types*.—Holotype, INSM71.1.9649, Indiana State Museum, Indianapolis, Indiana, USA. Mississippian (Chesterian), Lower Buffalo Wallow Group, 9.1 m above the Glen Dean Limestone at the abandoned Mulzer Brothers Quarry (38.358N, 86.616W), approximately 4 km north of Eckerty, Crawford County, Indiana.

*Measurements*.—The specimen is about 10.1 mm long and 7.6 mm wide, excluding the approximately 2.0 mm long spines.

*Occurrence*.—Known only from the type locality.

*Discussion*.—*Deltaplax dellangeloi* n. sp. shares some characters with *Deltaplax burdicki* n. sp. Both have valves with distinct comarginal growth lines, shallow furrows that separate the lateral and central areas of intermediate valves, broad radial furrows on head and tail valves, and morphologically differentiated spines with two c-shaped insertion processes. Both head valves have articulating surfaces on the lateral margins (Fig. 2.4), and differ only slightly in morphology. The head valve of *D. dellangeloi* is subtriangular in outline with an anteriorly curved apex located anterior to the midpoint of the valve, strong comarginal growth lines, and shallow radial furrows (Fig. 2.2). The head valve of *D. burdicki,* in comparison, is triangular in outline and lacks strong growth lines or radial furrows. The intermediate valves of both species are grossly similar in size and shape with similarly located apices. The tails of both species have similar comarginal growth lines and ridged insertion plates on the posterior margin. Despite these similarities, intraspecific variation cannot explain satisfactorily morphological differences observed in the two Eckerty specimens. The auxiliary valves, tails valves, and one type of spines are distinct for *D. dellangeloi* versus *D. burdicki.*

*Deltaplax dellangeloi*'s anterior-most auxiliary valve (Fig. 2.9) differs from *D. burdicki* in having three straight margins similar to one type of auxiliary valve figured for *Diadeloplax paragrapsima* Hoare and Mapes, 1995 (fig. 5L). Both have central keels, probably for muscle attachment and insertion into soft tissue. However, the more anteriorly located and directed apex of the *D. dellangeloi* valve is more like that of *Strobilepis spinigera* Hoare and Mapes, 1995 (fig. 2A, B). The same valve in *D. burdicki* has markedly curved lateral margins, a sinuous posterior margin, anterior duplicature, and a terminal apex directed toward the posterior (Fig. 2.6). Reconstruction suggests that the bases of the second through fourth auxiliaries probably are square (Fig. 1.6), similar to the 'squarish' first auxiliary valve of *Polysacos vickersianum.* The second auxiliary valve is spinose with a central apex (Fig. 2.10). Although partially buried in matrix, the top of the third auxiliary valve appears to be similarly spinose. In comparison, the second and third auxiliaries of *D. burdicki* have terminal apices (Fig. 2.6). The *D. dellangeloi* auxiliary valves also apparently lack the anterior raised triangular area. The fourth auxiliary has been displaced and overturned, which hides the upper surface but reveals keel-like structures similar to the first auxiliary valve. The fifth auxiliary valve is mostly buried in matrix, but the apex, which is just visible under the fifth intermediate valve by rotating the specimen, suggests the valve is spinose similar to the second and third auxiliaries. Reconstruction indicates the base of the fourth and fifth valves may be more rectangular than square similar to *D. burdicki*'s fourth and fifth auxiliary valves.

The dual radial grooves that define the sides of the trapezoidal post-mucronal area are distinctive to *D. dellangeloi* (Fig. 2.1). The deeply incised grooves extend from the base of the mucro to the posterior margin (Fig. 2.1) compared to a single faint furrow that extends to the lateral margins of *D. burdicki*'s tail (Fig. 1.8), which has a less well-defined post-mucronal area. The morphology of *D. dellangeloi*'s tail valve cannot be compared directly to *D. burdicki*'s tail because the anterior portion of the former is hidden by the overlying intermediate valves (Fig. 2.1). However, comarginal growth lines suggest similar holoperipheral accretion and isometric growth of the valve. The mucro in *D. dellangeloi* is posterior to the valve center, if similar morphologies for the two tails are assumed. Assuming the mucro is centrally located or slightly anterior to the center like *D. burdicki,* the tail valve is triangular and about as long as wide. Either assumption infers morphology different from *D. burdicki*'s trapezoidal tail valve. The triangular morphology fits better with the growth lines and shapes of the preceding valves as shown in the reconstruction (Fig. 1.6).

The spines of *D. dellangeloi* are broader and less elongated than *D. burdicki* spines. The approximately 10 mm long animal had 40–50 spines of which about 20 complete and 3–4 fragments are preserved in association with the valves (Fig. 1.4). One type of spine is relatively broader and 'flatter' compared to the other type (Fig. 2.11). Several of these spines are present, suggesting that the shape is morphological and not taphonomic due to compression and collapse of the internal canals. These larger spines probably were posterior and the narrower spines were anterior, similar to the arrangement seen in the partially articulated *D. burdicki* specimen (Fig. 1.3). The presumed posterior spines differ from *D. burdicki* spines in lacking evidence of curvature and having dual longitudinal grooves with slightly convex upper surface. The concave upper surface of the presumed anterior spines is similar to *D. burdicki*'s anterior spines, one type of *Diadeloplax* spine, and the single type of spine reported for *Strobilepis spinigera* and *Polysacos vickersianum.*

## IMPLICATIONS FOR THE FOSSIL RECORD

Because relatively poorly-preserved and disarticulated valves comprise most of the chiton fossil record (Puchalski et al., 2008), rare partially-articulated or associated fossil specimens are particularly important to the study of systematics, evolution, and taphonomy of the group. Placement of Multiplacophora outside Class Polyplacophora or as stem polyplacophorans (e.g., Sigwart and Sutton, 2007) is not supported. Multiplacophora shares more character states with chitons than any other known extant or fossil taxon (Vendrasco et al., 2004). Based on current systematics for the class, the presence of sutural laminae (articulamentum) seen in *Deltaplax burdicki* indicates the placement of multiplacophorans in Neoloricata, the subclass to which all extant chitons belong. The placement extends the range of neoloricates, previously reported as Carboniferous to Recent (Sirenko, 2006), to the Silurian. The close relationship of Neoloricata and multiplacophorans is supported by several independently published cladistic analyses (Vendrasco, 1999; Cherns, 2004; Vendrasco et al., 2004; Sigwart and Sutton, 2007). The systematic placement and corresponding range extension suggest that the origin of the neoloricates may be earlier than noted in previous literature, but the multiplacophorans still are problematic. The evolutionary relationship of multiplacophorans and crown group chitons remains to be elucidated. Sutural laminae may have evolved independently in the two lineages because multiplacophorans are distinguished by unique characters that have not been observed in more typical neoloricates, fossil or modern. One challenge to resolving the issue is that the evolutionary history of Polyplacophora is poorly known compared to other molluscan classes. This is partly due to the paucity of a fossil record comprised of only 430 extinct chiton species, including multiplacophorans, and 123 extant species also known as fossils, not including indeterminate taxa (Puchalski et al., 2008). More typical chitons have been reported as fossils on every continent except Greenland (Puchalski et al., 2008) whereas multiplacophorans have been described only from North America and Europe. The sporadic distribution can be attributed at least in part to taphonomic or sampling biases. Bias is implied by the relatively high proportion of multiplacophoran species described from articulated specimens (six out of fourteen or ~43%) compared to more typical chitons (~4% articulated, excluding indeterminate taxa). Disarticulated valves and/or spines may have been more fragile than more typical chiton valves, and thus less likely to have become fossils, or more difficult to identify unless the researcher is familiar with the morphology of the skeletal elements. In either case, resolution of the systematic, evolutionary, and taphonomic issues must be deferred until gaps in the fossil record can be filled by the collection and description of more fossil material.

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