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MACURDABLASTUS, A MIDDLE ORDOVICIAN BLASTOID
FROM THE SOUTHERN APPALACHIANS¹

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Abstract.—*Macurdablastus uniplicatus*, n. gen. and n. sp., is the oldest reported blastoid and occurs in thinly interbedded shale and argillaceous packstone and wackestone of the Benbolt Formation (Middle Ordovician, Caradoc) in eastern Tennessee. It is distinguished by a single hydrospire fold in each hydrospiralium, a unique feature among early blastoid species. Poorly preserved ambulacral structures suggest at least a two-part lancet plate entirely underlain by part of the radial plate. Lack of preservation of the distal lancet and ambulacral side plates precludes definite ordinal assignment within the Blastoidea. Biotic associates of *M. uniplicatus* include abundant and diverse other echinoderms, sponges, bryozoans, brachiopods and a low-diversity skeletonized algal flora.

THE ECHINODERM subphylum Blastozoa contains at least six extinct classes; most are characterized by distinctive biserial food-gathering brachioles and by a variety of specialized respiratory structures developed within principal thecal plates (Broadhead, 1980). Until now, all blastozoan classes except the Blastoidea were known with certainty in rocks of Ordovician age. Blastoids comprise the most diverse and familiar group of blastozoans and previously have been reported only from rocks ranging in

age from Silurian to Permian (Breimer and Macurda, 1972). Most Ordovician taxa previously assigned to the blastoids have been reinterpreted subsequently as belonging to other echinoderm classes (Regnéll, 1945; Fay, 1962, 1968a, 1978; Kesling, 1968). Possible blastoid affinity of isolated plates from the Middle Ordovician of Nevada (Sprinkle, 1973) has subsequently been rejected (Sprinkle, personal communication, 1979).

Recent discovery of unquestionable blastoid remains assigned to the new genus and species *Macurdablastus uniplicatus* represents the earliest

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certain occurrence of the class. The resulting disjunct stratigraphic distribution extends from this occurrence in the Middle Ordovician (Caradoc) to the next highest in the Upper Silurian (Wenlock), at which level both orders, *Fissiculata* and *Spiraculata*, are well differentiated.

Repository.—All figured specimens are at the U. S. National Museum of Natural History (NMNH 359645-359651).

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ORDOVICIAN BLASTOID HOMEOMORPHS

Several genera of Ordovician echinoderms have a strong superficial resemblance to blastoids; seven of these were included in the Protoblastoidea of Bassler (1938) and were listed as such under the Blastoidea by Bassler and Moody (1943). Four genera (*Asteroblastus*, *Asterocystis*, *Metasterocystis*, and *Mesocystis*) have thecal pores characteristic of diploporan cystoids, to which they were assigned by Kesling (1968). In addition to the nonblastoid respiratory structures (diplopores), these genera further diverge from the Blastoidea by the characteristically large number of thecal plates (apparently several hundred in *Mesocystis*).

A perhaps more closely related group of homeomorphs are the Parablastoidea comprising three genera (*Blastocystis*, *Blastoidocrinus*, and *Meristoschisma*). Like the diploporites, parablastoids show a tendency, although much less pronounced, toward a larger number of plates in the dorsal theca. Respiratory structures of parablastoids include thin folds of stereom similar to blastoid hydrospires, but appear to have developed largely within the deltoid plates; blastoid respiratory structures involve both radials and deltoids. In addition, ambulacral plating in parablastoids is not so complex as in true blastoids (Sprinkle, 1973).

The remaining Ordovician blastoid home-

omorphs include genera of the recently described class Coronioidea (Brett and others, 1983: e.g., *Paracystis*, *Tormoblastus*) and *Asterocystites*, the single reported genus of the class Edrioblastoidea. *Asterocystites* does not figure in blastoid ancestry because it lacked brachioles and belongs in the subphylum Echinozoa (Sprinkle, 1973; Bell, 1980). Coronoids, although previously regarded as crinoids (Fay, 1978), are now considered to be blastozoans (Sprinkle, 1979; Brett and others, 1983) and are increasingly believed to be closely related to blastoids (Brett and others, 1983:646-648; C. R. C. Paul, personal communication, 1982).

EVOLUTIONARY SIGNIFICANCE

The origins of the Blastoidea long have been unclear. Fay (1968b:S300) suggested a descent from edrioblastoids (now regarded as a class of echinozoans), whereas Sprinkle (1973:172) believed that they were derived from the Eocrinioidea independently from other blastozoan classes (e.g., Parablastoidea). Sprinkle's (1973) belief in an eocrinoid ancestry for blastoids was predicated upon the inclusion of the coronate "crinoids" (*sensu* Fay, 1978) in the Eocrinioidea. Reexamination of eocrinoid morphology (Broadhead, 1980, 1982) excludes the coronates, which Brett and others (1983) now regard as a separate blastozoan class possibly ancestral to blastoids. Breimer and Macurda (1972:309-311) refrained from suggesting a blastoid ancestor but did comment upon probable trends leading to the development of several blastoid features (e.g., ambulacral system, hydrospires).

The discovery of Middle Ordovician blastoids provides few clues to blastoid ancestry. Articulated specimens of *Macurdablastus uniplicatus* exhibit several features, such as narrow, moderate-length ambulacra and few hydrosphere folds, that may be considered primitive (Breimer and Macurda, 1972). These specimens, however, are typical blastoids in all observable principal aspects; they lack extra thecal plates or other structures that might ally them with other blastozoans.

If blastoids originated rapidly, as many other echinoderm classes apparently did (see Eldredge and Gould, 1972), ancestral forms should be at least superficially blastoidlike. Breimer and Macurda (1972:311) suggested

that they may have originated "from a relatively slender form with a relatively small number of plates." Two groups likely to contain the ancestor of the blastoids are the coronoids (Sprinkle, 1980) and the Parablastoidea. Both tend to be characterized by small numbers of thecal plates, although only the coronoids exhibit a tendency to slender thecal form. Coronoids also possess principal thecal plating homologous to that of blastoids, but their feeding appendages (Fay, 1978; Brett and others, 1983) are unlike any known in other blastozoans. Coronoid respiratory structures are canals or tubes developed within the interradianal prongs or crests characteristic of most species (Brett and others, 1983), and are unlike the hydrospires of blastoids.

Parablastoids bear a strong superficial similarity to blastoids, but have been discounted as possible ancestors. They predate (Lower Ordovician, Arenig) known first occurrences of both blastoids and coronoids (Middle Ordovician). Besides their strongly developed pentamerous symmetry, parablastoids have a relatively small number of thecal plates and respiratory structures (cataspires) that are similar in gross morphology to the hydrospires of blastoids. Such complex parablastoids as *Blastoidocrinus carchariaedens* are unlikely to be the blastoid ancestor; however, the much simpler *Meristoschisma hudsoni*, which occurs together with *Macurdablastus uniplicatus*, has many more blastoidlike characters. Basic thecal plating in *Meristoschisma hudsoni* includes five large radials and deltoids; its basals are unknown. Association of the respiratory structures with three types of thecal plates in parablastoids (Sprinkle, 1973:143) does not mitigate against a relationship with blastoids because respiratory structures are also intimately associated with radial, deltoid, and ambulacral plates in spiraculate blastoids. The subdivided posterior oral plate in *Meristoschisma hudsoni* (Sprinkle, 1973:164) may be homologous to the compound deltoid plates characteristic of most blastoids (e.g., see Beaver, 1968:S316). Nevertheless, the single type of ambulacral plate and apparent absence of a lancet plate in *Meristoschisma* and other parablastoids separate them from the Blastoidea. In addition, *Meristoschisma* is characterized by wide ambulacra, whereas the poorly known Lower Ordovician *Blastocystis rossica* has

much narrower, linear ambulacra, as do species of *Blastoidocrinus* (Paul and Cope, 1982). Such narrow ambulacra are more like those of *Macurdablastus uniplicatus* or the Silurian spiraculate *Troosticrinus reinwardti*. Detailed study of specimens of *B. rossica* is needed to clarify possible blastoid-parablastoid affinities. Certainly paeomorphous reduction of aboral plates in a parablastoid ancestor could have been a logical step in development of the conservatively plated blastoids.

The relationship of *Macurdablastus* to subsequent blastoid genera is obscured both by their stratigraphic separation (Caradoc to Wenlock) and by our incomplete knowledge of such morphologic features as ambulacra, deltoid plating, and the basal circle. The lack of preserved entire lancet and ambulacral plates precludes assignment of *Macurdablastus* to either the Fissiculata or Spiraculata. The large triangular anal area (Fig. 1, I) is bounded adorally by one of what originally were at least two deltoid plates surrounding the small anal opening. Much of the aboral part of the anal area was probably occupied by a large hypodeltoid comparable to that of the Silurian fissiculate *Decaschisma pulchellum* (Fay and Wanner, 1968, fig. 234:3f) or of the spiraculate *Troosticrinus*. Poor preservation of basals precludes recognition of the azygous basal, which predominantly occurs in the AB interray of other blastoids (Beaver, 1968:S309). Its abnormal occurrence in other positions has been reported in a study of extremely large numbers of specimens of a single species of *Pentremites* (Macurda, 1980) but not in large samples of *Orophocrinus stelliformis* (Macurda, 1968). Consistent occurrences of the azygous basal in other positions, such as the DE interray of *Crioblastus* (Macurda, 1978), are notably rare. Nonetheless, specimens of *M. uniplicatus* exhibit characteristics that afford a general comparison with Silurian fissiculates and spiraculates.

The high conical pelvis of *M. uniplicatus* is comparable to that characterizing both early fissiculates (e.g., *Decaschisma*, *Polydeltoideus*) and early spiraculates (e.g., *Troosticrinus*). Ambulacra are also linear, but ambulacral sinuses appear to be shallower and perhaps narrower in *M. uniplicatus* than in early fissiculates. Hydrosphere distribution is uniform in *M. uniplicatus*, contrasting with a trend to suppression or

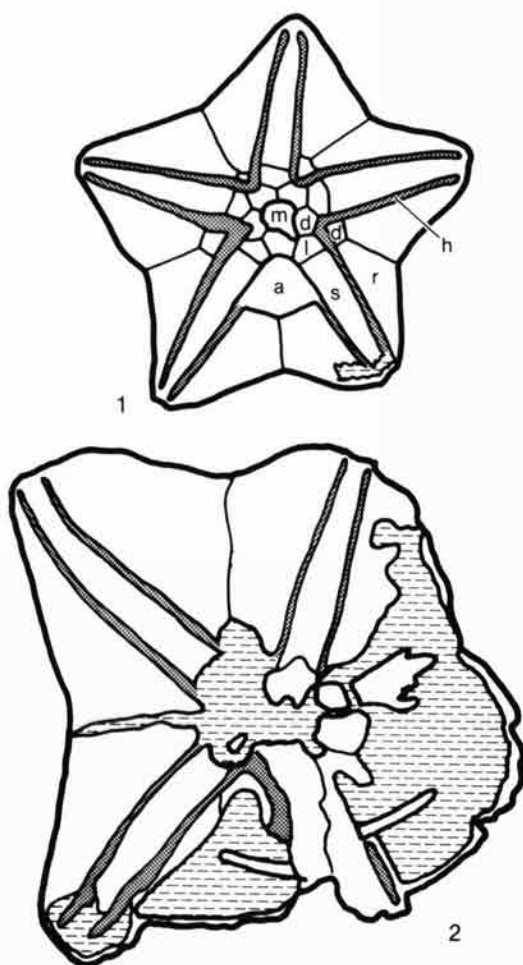


Fig. 1. Summit views of specimens of *Macurdablastus uniplicatus*, n. gen., n. sp.; areas of erosion through thecal plates and patches of indurated sediment adhering to theca lightly shaded. 1. Holotype (see Fig. 3,1) with representative plates and areas on the theca labeled: a, anal area (deltoid plates missing); d, main body (right) and lip (left) of deltoid plate; h, hydrospire cleft (heavily shaded); l, lancet plate; m, mouth; r, radial plate; s, part of radial plate forming a platform under the ambulacral (including lancet) plates; $\times 8.2$. 2. Best preserved paratype (see Fig. 3,3); $\times 8.2$.

modification of hydrospires in the anal inter-radius of a large number of later forms. The small number of hydrospire folds (one per side of an ambulacrum) in *M. uniplicatus* contrasts markedly with the numbers found in Silurian forms: 3 to 5 in *Troosticrinus* (Fay and Wanner, 1968:S416), 3 to 6 in *Decaschisma* (Breimer and Macurda, 1972:56), and 4 to 7 in *Polydeltoideus*

(Breimer and Macurda, 1972:61) (smaller numbers characterize anal hydrospires). The lack of differentiation of hydrospires into lamellae and enlarged ducts, regarded by Breimer and Macurda (1972:59) as a primitive feature, characterizes both *Macurdablastus* and *Decaschisma*, but not *Polydeltoideus*. The lack of preserved ambulacral structures precludes ordinal assignment of *Macurdablastus*, although Breimer and Macurda (1972:359-360) proposed a polyphyletic origin for the spiraculates from various genera of the fissiculate family Phaenoschismatidae.

OCCURRENCE

All specimens of *Macurdablastus uniplicatus* have been collected from a 30-cm unit of argillaceous packstone and wackestone of the Benbolt Formation. The unit is about 182 m above the post-Knox unconformity and 7.5 m above the contact of the Benbolt with the underlying, more massively bedded Rockdell Formation. The locality (36°11'30" N., 83°55'30" W.) is in the Hunter Valley allochthon that includes, father to the northeast, well-known localities in Hogskin Valley and at Evans Ferry.

Associated with *M. uniplicatus* are a variety of cryptostomate and trepostomate bryozoans, sponges (*Allosaccus* sp., *Hudsonospongia* sp., *Hindia* sp.), brachiopods (lingulides, *Mimella* sp., *Macrocoelia* sp., *Hesperorthis* sp., *Sowerbyites* sp., *Camerella* sp.), gastropods (*Raphistoma* sp.), and trilobites (*Isotelus* sp., *Calyptaulax* sp., *Bumastus* sp., *Dolichoharpes* sp., *Nanillaneus* sp.). Other echinoderms include the Crinoidea *Archaeocrinus peculiaris* (Miller and Gurley), *Diabolocrinus vespertalis* (White), *Acolocrinus hydraulicus* Kesling and Paul, *Apodasmocrinus punctatus* (Brower and Veinus), *Hybocrinus punctatus* (Miller and Gurley), *Palaeocrinus avondalensis* Brower and Veinus, *P. planobasalis* Brower and Veinus, *Triboloporus cryptoplicatus* Kesling and Paul, and *Carabocrinus micropunctatus* Brower and Veinus; the Paracrinoidea *Canadocystis tennesseensis* Parsley, *Batherocystis appressa* Bassler, and a species of *Globulocystites*; the Rhombifera *Coronocystis angulatus* (Wood), a new genus and species of the Cheirocrinidae, *Regulaecystis pyriformis* (Parsley), and a species of *Amecystis*; the Eocrinoidea *Ulrichocystis eximia* Bassler; and the Parablastoidea *Meristoschisma hudsoni* Sprinkle.

Biotic and lithic associations of *M. uniplicatus* suggest a predominantly suspension-feeding community characterized by several tiers of filtration (see Ausich and Bottjer, 1982). The lowest levels of suspension feeders probably included many sponges, brachiopods, such "bottom sitting" echinoderms as *Canadocystis* and *Hybocrinus*, and perhaps all of the rhombiferans. Somewhat higher levels (up to a few tens of centimeters) included other sponges and bryozoans, the majority of small crinoids, and perhaps *Macurdablastus*. The highest level likely was dominated by such large camerate crinoids as *Archaeocrinus* and *Diabolocrinus*. Low-level browsers and detritivores were mostly gastropods and trilobites, respectively. Thin-section examination for algae (Ashworth, 1982) in thin carbonate beds at this level revealed a low-diversity association of *Girvanella* sp. and *Ka-*

zakhstanelia sp. Receptaculitids are common higher in the Benbolt at this and other localities along strike.

Middle Ordovician rocks in eastern Tennessee record a marine transgression from southeast to northwest (Harris and others, 1983) followed by a regression caused by rapid influx of terrigenous clastics from the southeast (Walker and others, 1980). The Benbolt represents a smaller scale deepening to shoaling carbonate shelf regime within this broader environmental context. Biotic diversity is highest in the lower third (deepening part), which contains the blastoid-bearing beds. Diversity drops off sharply toward the top, with only about 20 percent of the echinoderm species represented. Mudcracks occur locally near the Benbolt-Wardell contact, but have not been observed at this locality.

SYSTEMATIC DESCRIPTION

Class BLASTOIDEA Say, 1825

Order Indeterminate

Family Indeterminate

Genus MACURDABLASTUS, new

Type species.—*M. uniplicatus*, n. sp.

Etymology.—The genus is named for D. B. Macurda, Jr., whose research has contributed immeasurably to knowledge of the Blastoidea.

Diagnosis.—Theca broadly subconical, pentagonal to asteriform in transverse section, vault low; ambulacral sinuses narrow, shallow; interambulacral pyramids poorly developed; deltoids small with small DD sectors; ambulacra linear, lancet compound; 10 hydrospires with one slit per side of ambulacrum, extending nearly full length of ambulacrum.

MACURDABLASTUS UNIPLICATUS, new species

Figures 1-3

Material.—Four partial thecae, a single zygous basal, and 35 radial plates.

Description.—Thecal form broadly pentamerous in oral view with interambulacral areas only slightly indented. Thecal width greatest at top of pelvis. Crushing of thecae and consequent poor preservation of basal circlet precludes precise determination of lateral profile, which was likely vase- or pear shaped (see Beaver, 1968:S302-S303). Vault extremely low (25 percent of height or less), and gently arched.

Basal plates poorly preserved in articulated specimens (Fig. 3,2,10); only single zygous basal (Fig. 3,6) being recognized among disarticulated plates. Number of basals probably 3 (2 zygous, 1 azygous), location of azygous basal uncertain.

Basals forming relatively narrow cone broadening and flaring slightly outward at top. Height of basal circlet probably approaching 40 percent of thecal height (e.g., Fig. 3,10), and BR growth direction apparently dominating (Fig. 3,6). Plate margins of zygous basals concave where abutting entire lower radial margins (Fig. 3,6), other BR sutures (Fig. 3,10) and BB

sutures linear. Isolated basal evenly rounded in transverse section, evenly tapering aborally in lateral view, but with medial ridge of questionably secondary calcite extending adorally from base for approximately one-third of basal height. Medial height of zygous basal 6.9 mm, maximum width 5.2 mm. Stem facet and stem not preserved.

Radial circlet containing 5 radial plates. Each radial probably subquadrate in plan view (Fig. 3,9) and triangular in lateral view with slightly convex vault side and slightly concave pelvic side (Fig. 3,8). RB margins of radials convex, RR margins linear to slightly convex (Fig. 3,10). Pair of short ridges (Fig. 3,2,7,10) extending aborally from tip of ambulacrum approximately one-third length of radial body, then becoming less distinct aborally and marking boundaries between RR and RB sectors. Radial height in holotype ranging from 2.3 to 3.3 mm, but not indicative of true dimension because of crushing. Width ranging from 2.8 to 3.3 mm. Single radial lacking most of adoral part (Fig. 3,9) 9.2 mm high.

Radial sinuses shallow and extending approximately half radial length (Fig. 3,1,4,5,7,11). Interambulacral pyramids virtually absent as are ambulacral sinuses.

Growth lines relatively well preserved on only single radial plate (Fig. 3,9), showing RB growth at slightly higher rate than RR growth (approximately 5:3). RD sectors extremely small and apparently not demarcated from adoral parts of RR sectors.

Four regular deltoids small, with deltoid body commonly smaller than lip (Fig. 1,1). Anal deltoids not preserved except for adoral plate, which is either epideltoid or superdeltoid. Lip of adoral plate and remaining 4 deltoid lips forming peristomial ring. Deltoids directly abutting radials aborally with no apparent overlap, not extending out of shallow ambulacral sinuses.

Anal area relatively well preserved only in holotype, broadly subtriangular (Fig. 1,1). Per-

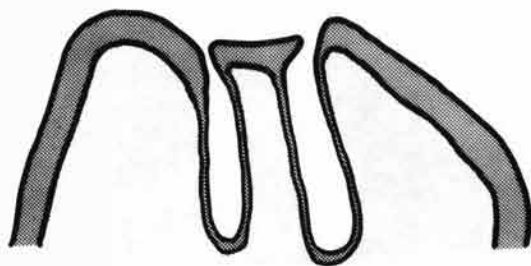


Fig. 2. Cross section through hydrospires of *Macurdablastus uniplicatus*, n. gen., n. sp. (drawn from specimen in Fig. 3, 9). Ducts only slightly inflated; skeletal material dark and thecal interior lightly shaded; $\times 23$

istome generally subpentagonal, 0.5 mm in holotype.

Five ambulacra narrow, straight, and tapering slightly aborally. All radials with ambulacral platform (Fig. 1;2,3,1,4,5,7,11) (secondary calcite of Breimer and Macurda, 1972:51) extending entire ambulacral length to peristomial ring. Platform aborally continuous with radial plate, apparently not formed from fused pair of hydrospire plates. Floor of platform gently concave for attachment of lancet plate or plates. Underside of platform flat to gently arched (Fig. 2).

Ambulacral structures mostly unknown, only holotype with plating preserved above ambulacral platform of radials. Small subpentagonal plate, here regarded as part of lancet, abutting peristomial ring in each ambulacrum. Additional part of lancet apparently abutting aboral edge of each of these plates, possibly resulting in series of lancet plates rather than usual single plate. Main ambulacral groove shallow, passing along each DD suture and aborally onto small "lancet" plate. Side plates and brachioles unknown.

Hydrospiralium a single fold on each side of each ambulacrum, apparently not modified in anal interray. Each fold extending entire length of ambulacrum, composed of 2 thin lamellae united by slightly inflated hydrospire duct (Fig. 2).

Fig. 3. *Macurdablastus uniplicatus*, n. gen. and n. sp., Benbolt Formation, eastern Tennessee. 1, 2, 4. Summit, basal and lateral (A-E-D ray with A at left) views of holotype (NMNH 359645), $\times 6$. 3. Summit view, orientation uncertain, paratype (NMNH 359646), $\times 5$. 5. Summit view of laterally crushed theca preserving parts of only 4 radial plates, orientation uncertain, paratype (NMNH 359647), $\times 5$. 6. Lateral view of isolated zygous basal plate, paratype (NMNH 359648), $\times 5$. 7, 8. Lateral views of aboral tip of isolated radial plate fragment, paratype (NMNH 359649), $\times 5$. 9. Lateral view of large radial plate with aboral tip broken to expose cross section of hydrospires (see Fig. 2), paratype (NMNH 359650), $\times 5$. 10, 11. Lateral, summit views of large thecal fragment, paratype (NMNH 359651), $\times 5$.



Fig. 3. (Explanation on facing page.)

Discussion.—The most unusual features of *M. uniplicatus* are the simplicity of its hydrospires and apparent complexity of the lancet plate. Blastoids characterized by only a single hydrospire fold along each ambulacrum include, in addition to *Macurdablastus*, 5 genera of fissiculates (all Permian) and 8 genera of spiraculates (all Lower Carboniferous). Among the fissiculates, only *Timoroblastus* is known to have uniform hydrospire development in all 10 positions. *Angioblastus* (not all species), *Pterotoblastus*, and *Indoblastus* have only 8 folds, with those in the CD interray absent. *Nannoblastus* has only 6, lacking any folds on C or D radials (Breimer and Macurda, 1972). In contrast, all spiraculate genera (*Orbitremites*, *Ellipticoblastus*, *Nodoblastus*, *Granatocrinus*, *Monoschizoblastus*, *Poroblastus*, *Ptychoblastus*, *Monadoblastus*) have uniform hydrospire development (Fay and Wanner, 1968). This simplicity seen in *Macurdablastus* and several groups of Late Paleozoic blastoids contrasts with the tendency toward a large number of hydrospire folds alongside each ambulacrum in Silurian species (e.g., up to 6 in *Decaschisma pulchellum*, 6 or 7 in *Polydeltoideus enodatus*, 3 to 5 in *Troosticrinus reinwardti*; Breimer and Macurda, 1972; Fay and Wanner, 1968). Thus, hydrospires seem first to have evolved into more complex forms, then, in many groups, become more simple due to paedomorphosis.

The lancet plate of blastoids is characteristically a single narrow ossicle that extends from the oral frame of the deltoids aborally to or very nearly to the tip of the ambulacrum. Accessory ambulacral plates lie on top of or laterally adjacent to the lancet and support the brachioles. Although ambulacral structures of *Macurdablastus uniplicatus* are poorly preserved, a small pentagonal plate is present in each ambulacrum immediately distal to the oral frame

of deltoids. Aborally, a pronounced step down to the subjacent platform of radial-plate material is flanked on either side by a hydrospire fold. The consistent form of the small pentagonal plates and presence of a medial shallow groove extending toward the mouth on each suggest that they are parts of a lancet complex of plates and are not broken parts of simple lancets.

The skeletonized radial platform beneath the lancet complex is an additional unusual feature in *M. uniplicatus*. In cross section (Fig. 2), this structure appears as a thickened (approximately normal plate thickness) biconcave mass between the hydrospire folds. It doubtless underlay other plates and does not actually represent the ambulacrum. It is at least partly comparable to the "underlancet," "sublancet," and "fused hydrospire plate" discussed by Beaver (1968:S235) and the "secondary calcite under the lancet" of Breimer and Macurda (1972:52). The structure preserved in radial plates of *M. uniplicatus* lacks evidence of medial fusion and appears to be a simple solid extension of the radial plate (see Macurda, 1966, pl. 12, fig. 15). A secondary origin as suggested by Breimer and Macurda (1972) for this structure seems unlikely. Rather, it probably represents a closure of the thecal cavity and an integral part of the RD growth sector. The adoral end was probably in continuous contact with the lateral-aboral parts of a pair of deltoids in each ray. Although the presence of this additional subambulacral thecal closure might seem superfluous in comparison to later blastoids, the fact that later forms are commonly found with lancets in place suggests its necessity in *Macurdablastus*, where ambulacral structures were not so firmly united with the theca proper.

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