Pyritized tube feet in a protasterid ophiuroid from the Upper Ordovician of Kentucky, U.S.A.

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A single specimen of the protasterid ophiuroid *Protasterina flexuosa* from the Kope Formation (Cincinnatian, Upper Ordovician) of Kentucky exhibits three-dimensionally pyritized tube feet. This represents the first report of soft-tissue preservation in an echinoderm from the type-Cincinnatian series. The tube feet are solid and lack all internal structure. They consist of aggregated masses of small euhedral to subhedral pyrite crystals suggesting that pyritization, although decay-induced and mediated, did not necessarily replicate soft-tissues but might instead have formed inside the void-spaces left behind during the decay process. The discovery of pyritized soft-tissue as delicate as ophiuroid tube feet suggests that similar forms of soft-tissue preservation might be found in other taxa in the Kope Formation. Perhaps much more importantly, this unexpected occurrence demonstrates the incompleteness of our knowledge of permissible conditions for the preservation of soft-tissues and it thereby indicates promise for discovery of other such occurrences in diverse organisms in unexpected settings. Systematics of Paleozoic ophiuroids remains problematic in spite of many years of study by capable paleontologists. The incomplete but well-preserved specimens treated here include the types of *Protasterina flexuosa* and *Protasterina fimbriata* as well as previously undescribed specimens. Together they permit a revised diagnosis and detailed description of the genus *Protasterina*. *Protasterina fimbriata* is the type species of the genus but is a subjective junior synonym of *Protaster flexuosus* (= *Protasterina flexuosa*). The genus is clearly differentiated from the only other known protasterid ophiuroid from the Cincinnatian series, *Taeniaster spinosus*, and from all other protasterid genera.

Key words: Ophiuroidea, Protasteridae, soft-tissue preservation, pyritization, Cincinnatian, Edenian, Ordovician, Kentucky.

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Introduction

Ophiuroids (Echinodermata) are important invertebrates in many modern marine environments, and their fossil diversity indicates an enduring significant presence since their Ordovician diversification. Nevertheless, ophiuroid systematics and paleobiology are poorly understood because of a limited fossil record and commonly poor preservation, both limitations almost certainly imposed by taphonomic constraints. Among Paleozoic ophiuroids, one of the most diverse families is the Protasteridae, yet almost all protasterid species are poorly known and consensus over morphological features and phylogenetic relationships are lacking; further, we are nearly devoid of sound data on the functional morphology and ecological roles of protasterids. The writer is seeking to clarify the paleobiology of protasterids through evaluation of member genera (Glass and Blake 2004; Glass in press). In the process of reviewing significant collections including protasterids, the well-preserved lectotype (Fig. 1) of the very incompletely understood protasterid *Protasterina fimbriata* (Ulrich, 1878) was discovered in the collections of the Cincinnati Museum Center; this and other specimens from the same collection and found in other museums allow synonymizing of *Protaster flexuosus* (senior name) with *Protasterina fimbriata* (junior

name, but type species of the genus) and redescription of the genus. Further, the lectotype is particularly interesting and important because of the presence of fossilized tube feet (Fig. 2). The discovery of tube feet is important in part because it provides some data on the nature of these structures in ancient ophiuroids, but probably more important is that the presence of tube feet represents an unusual mode of preservation of soft-tissues and this occurrence further draws attention to the potential for discovery of potentially highly informative volatile soft-tissues at other localities and for other animal groups.

The tube feet occur in a single specimen of *Protasterina flexuosa* (Miller and Dyer, 1878) from the Kope Formation (Edenian, Cincinnatian, Upper Ordovician) of Northern Kentucky. The specimen is extensively pyritized and exhibits remnants of numerous three-dimensionally preserved tube feet. Similar soft-tissue preservation is known only from the Lower Devonian Hunsrück Slate of Germany (Glass and Blake 2004).

Five species of protasterid ophiuroids were originally described from the Cincinnatian Series of Indiana, Kentucky, and Ohio. Of these, *Protaster miamiensis* Miller, 1882, *Taeniaster elegans* Miller, 1882, and *Protaster granuliferus* Meek, 1872 were synonymized with *Taeniaster spinosus* (Billings, 1858) by Hotchkiss (1970). *Protaster flexuosus* Miller and

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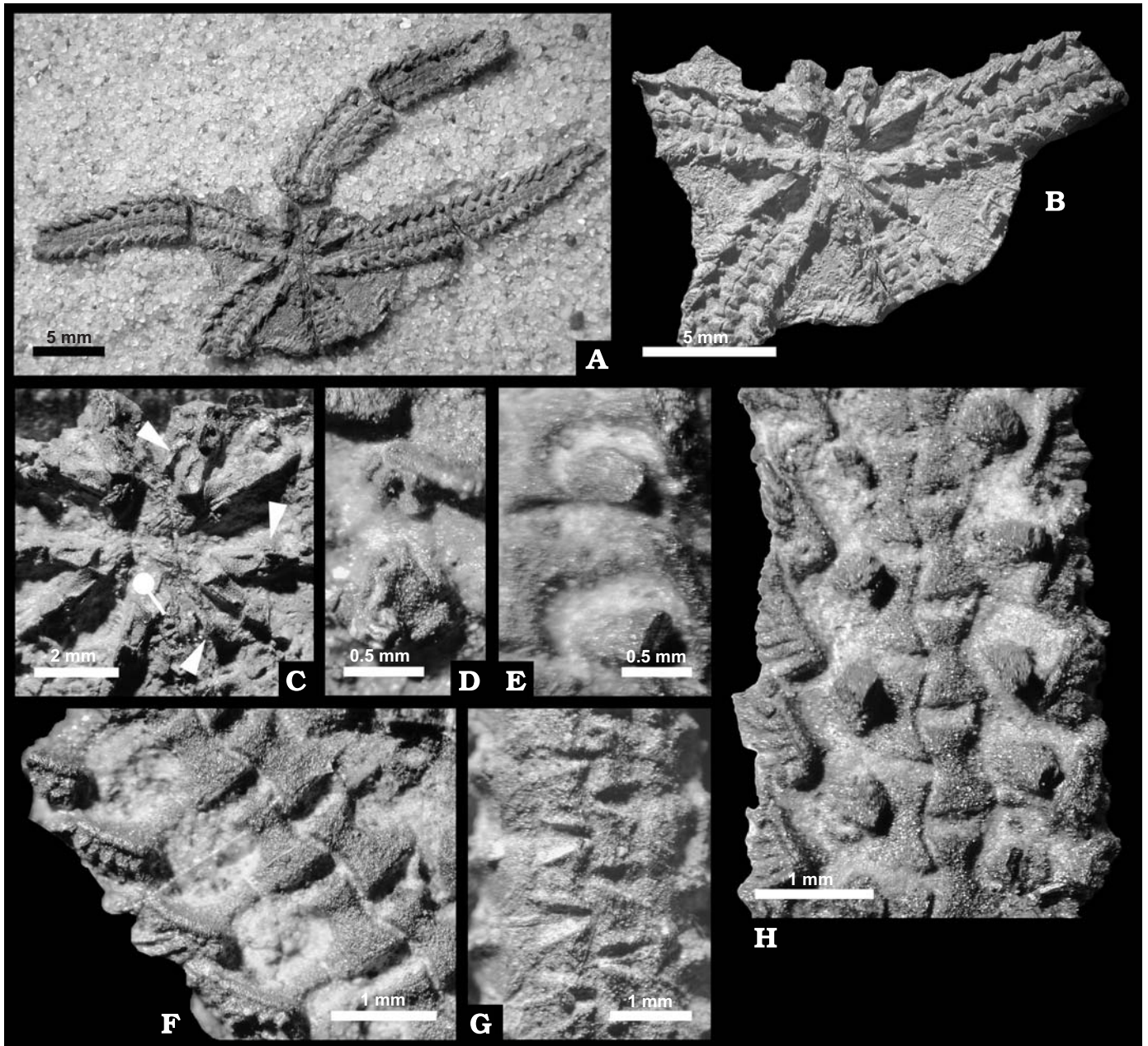
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Fig. 1. *Protasterina flexuosa* (Miller and Dyer, 1878), Edenian (Upper Ordovician) near Covington, Kentucky. Specimen with pyritized tube feet, CMC 25001. **A**. Fragmented specimen originally figured by Ulrich (1878), ventral, photographed on sand for support. **B**. Disk, and proximal portions of arms, small disk spines are visible along edges. **C**. Mouth frame, note depressions on mouth angle plates, and preserved buccal tentacles (arrows); possible remains of small spines visible on abradial edge of one of the mouth angle plates (circle). **D**. Madreporite. **E**. Two podial basins with remnants of pyritized tube feet. **F**. Ventral surface of ambulacrals and podial basins without pyritized tube feet; proximal ends of groove spines preserved, laterals attach to ambulacrals via an elongated process. **G**. Dorsal surface of ambulacrals with large interambulacral muscle gaps. **H**. Section of arm bearing numerous remnants of tube feet; note groove spines on laterals.

Dyer, 1878 was first described in the same journal and year as *Protasterina fimbriata* Ulrich, 1878 but in an earlier issue. Hotchkiss (1970) recognized *Protasterina fimbriata* as a junior synonym of *Protaster flexuosus* but gave no detailed justification or new description of the type material.

This study provides the first detailed description and discussion of *Protasterina flexuosa* since it was reported by Miller and Dyer (1878). Materials discussed here include the original type fossils (Fig. 3) of Miller and Dyer (1878) as well as the originals of *Protasterina fimbriata* described by Ulrich (1878). Several previously unreported specimens of *Protasterina flexuosa* discovered in museum collections are also encompassed by the description.

Institutional abbreviations.—CMC, Cincinnati Museum Collection, Cincinnati, Ohio; MCZ, Museum of Compara-
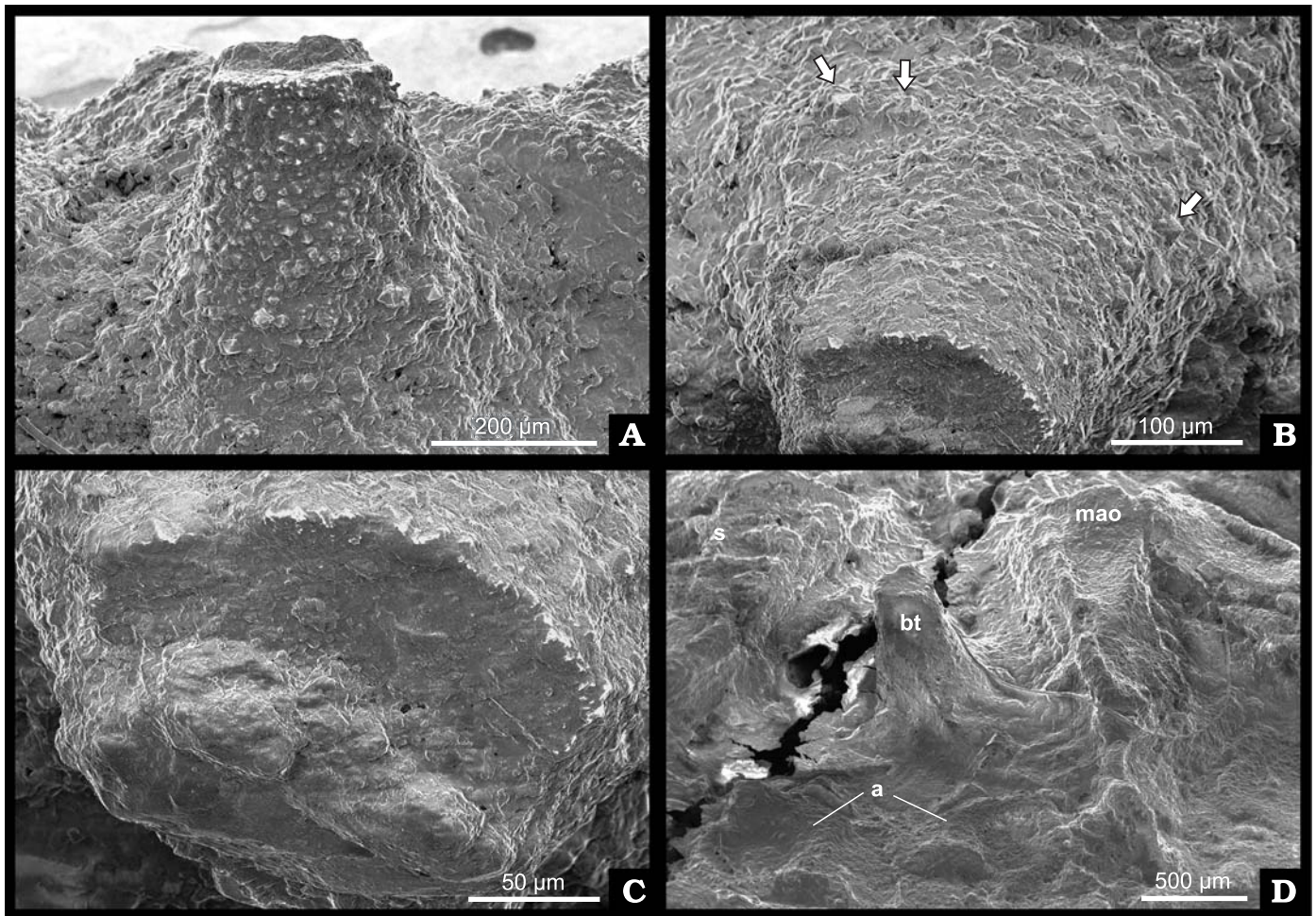
Fig. 2. *Protasterina flexuosa* (Miller and Dyer, 1878), Edenian (Upper Ordovician) near Covington, Kentucky. ESEM photographs of pyritized tube feet, CMC 25001. **A**. Broken tube foot preserved in arm outside the disk. **B**. Close-up of outside surface of tube foot showing subhedral and euhedral crystals; note euhedral octahedra (arrows). **C**. Close-up of broken cross-section of same tube foot. **D**. Buccal tentacle inside mouth frame (bt); view is from the axis of the arm into the mouth area; proximal ambulacrals visible at bottom (a); concave mouth angle ossicles (mao) at upper right; mouth angle ossicles with possible spine bearing ridge in upper left (s).

tive Zoology, Harvard University, Cambridge, Massachusetts; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C. All in U.S.A.

Geological setting

The rocks of the type-Cincinnatian (Upper Ordovician) Series have long been known for their abundance and rich diversity of invertebrate fossils. Echinoderms, although diverse, are comparatively rare and localized; soft-tissue preservation has never been reported.

The lower Upper Ordovician Kope Formation (Edenian) marks the base of the type-Cincinnatian Series in the area where Indiana, Kentucky, and Ohio come together along the Ohio River. It is bound below by the Point Pleasant Formation (Shermanian, Middle Ordovician) and above by the Fairview Formation (Edenian–Maysvillian, Upper Ordovician). Stratigraphy is complex in the Cincinnatian and corre-

lations and applied nomenclature have varied among states and authors and throughout the long history of study in this area (see Cuffey 1998; Davis 1998; Hay 1998). Terminology and stratigraphy applied follow the most recent comprehensive revision and discussion of the Kope Formation by Brett and Algeo (1999b).

The Kope Formation primarily consists of thick packages of largely unfossiliferous mudstones and shales with only local occurrences of fossils, including brachiopods, bryozoans, graptolites, echinoderms, and trilobites. Interbedded within the fine-grained clastics are calcisiltites and skeletal limestone beds of centimeter to decimeter thicknesses (Brett and Algeo 1999b; St. Louis Diekmeyer 1998).

The Kope Formation was deposited at the distal part of a northward dipping carbonate ramp of the Cincinnati Arch. Sedimentary features and faunal analysis suggest that the Kope Formation was deposited below fairweather wave base and that genesis of both shales and limestone intervals was heavily influenced by storm events. Estimates of water depths

range from several tens of meters but nevertheless might not have exceeded 50 meters (Anstey and Fowler 1969; Brett and Algeo 1999b; Holland 1998; Holland et al. 1997; Jennette and Pryor 1993; Schumacher 1998). Jennette and Pryor (1993) and Brett and Algeo (1999a) provided evidence of and argued for storm-related, rapid deposition of many of the mudstones and shales in the Kope Formation. Such events facilitated the rapid burial (e.g., obrution events) of epifaunal communities (e.g., Hughes and Cooper 1999).

Extensively pyritized fossil communities have not been reported from the Kope Formation but evidence of pyrite formation occurs locally in the form of "rusty" horizons, pyritic burrow linings, pyritic surface crusts, and pyrite-containing carbonate concretions (Brett and Algeo 1999a, b). Hughes and Cooper (1999) described a partially pyritized trilobite cluster from the Kope Formation with pyritic linings on surfaces and filled void spaces within the skeletons. Specific forms of soft-tissue preservation have not been recognized to date in these occurrences but the tube feet described here suggest the value of revisiting the collections. Possible additional candidates are annelid body fossils described by Ulrich (1878) from the Kope Formation. These fossils might represent another form of soft-tissue preservation although Ulrich (1878) provided no information on whether they were pyritized. Significantly, these worms appear to have been found at the same level in the Kope Formation as the pyritized specimens of *Protasterina* described here. Alternatively, the worms might also simply be trace fossils and they need to be reassessed carefully to establish their identity and mode of preservation.

Material and methods

Detailed locality information for specimens described in this paper is provided in the Appendix 1. A single specimen exhibited tube feet preservation (CMC 25001). Environmental Scanning Electron microscope work on the pyritized tube feet was undertaken on a Philips XL30 ESEM-FEG at the Beckmann Institute at the University of Illinois at Urbana-Champaign. Because of the fragile nature of the specimen, the presence of very fine cracks, and the presence of pyrite, the specimen was not cleaned prior to ESEM analysis other than by light brushing with a fine, soft brush. Hence, numerous foreign particles as well as remnants of glue and varnish remained on the specimen, locally obscuring the surface. Analysis was limited to the exposed surfaces of the ossicles and tube feet; freshly fractured surfaces were not available. Because of its fragility, the specimen was examined uncoated at low kV (1–2 kV) in "wet mode" only, which limited resolution.

Taphonomic discussion

In his original description of *Protasterina fimbriata*, Ulrich (1878: 95) noted that the podial basins of the type specimen (CMC 25001) were "occupied by loosely-fitting, sub-pyrami-

dal plates, some of which have a deep depression in the top, as though they were perforated." In his detailed description he also referred to these ossicles as being "obtusely conical" (Ulrich 1878: 96). Ulrich (1878) did not speculate as to the nature or function of these ossicles. In a short synopsis of the genus, James (1896: 140) appeared to paraphrase Ulrich (1878) when he wrote that the podial basins are "closed by obtusely conical or pyramidal plates." Whereas Ulrich (1878) merely stated that the ossicles occupied the podial basins, James (1896) appears to have interpreted them as covering plates. This might explain why Spencer (1934: 491) sought to provide an alternative explanation for the so-called "pore coverings" in *Protasterina*. He believed that the ossicles were merely the outer edges of the podial basins exposed through slight rotation towards the arm axis. However, neither his schematic figure (Spencer 1934: fig. 315) nor his description of the crescentic outer edges of the podial basins match the morphologies accurately observed by Ulrich (1878). Comments by Spencer (1934: 491) suggest that he did not have access to the actual material but based his interpretations on photographs provided in Schuchert (1915). Schuchert (1915: 230) suggested that if the ossicles within the pores existed, they would clearly differentiate *Protasterina* from such protasterid genera as *Alepidaster* Meek, 1872 and *Protaster* Forbes, 1849. The "plates" described by Ulrich (1878: 95) are here interpreted as the pyritized remains of tube feet reaching out of the podial basins. These structures are not mineralized ossicles but a form of soft-tissue preservation. Edward O. Ulrich, Joseph F. James, Charles Schuchert, and William K. Spencer were acute observers of fossils and might have suspected tube feet but perhaps the tenor of their time did not allow them to suggest such an interpretation.

The only known specimen of *Protasterina flexuosa* (Miller and Dyer, 1878) with preserved tube feet is the originally figured type specimen of *Protasterina fimbriata* Ulrich, 1878 (CMC 25001). CMC 25002, CMC 25003, CMC P3874, and MCZ 108086 are similarly thoroughly pyritized but no tube feet are present. CMC 25001 (Fig. 1A) preserves approximately 115 complete podial basins in the arms and disk. Fifty of these preserve three-dimensional tube feet that extend at various angles out of the podial basins (Fig. 1A, B, E, H). The remaining basins are either completely filled with pyrite or show various short, fractured bumps interpreted here as the bases of broken tube feet. Additionally, remains of at least three buccal tentacles are preserved in the mouthframe area (Figs. 1C, 2D). The tube feet are as wide as the podial basins (Fig. 1H), supporting previous suggestions that podial basins size is reflective of tube foot dimensions (Byrne and Hendler 1988; Glass and Blake 2004). The average width of a proximal podial basin is approximately 0.6 mm. Tube feet in life are capable of retraction and this is likely to have taken place under the stress of the burial event. Retraction coupled with the crude preservation renders interpretation problematic. Nevertheless, the vast majority and perhaps all of the tube feet appear broken toward their tips. Some of them are long enough, however, to extend out of the furrow created by the raised
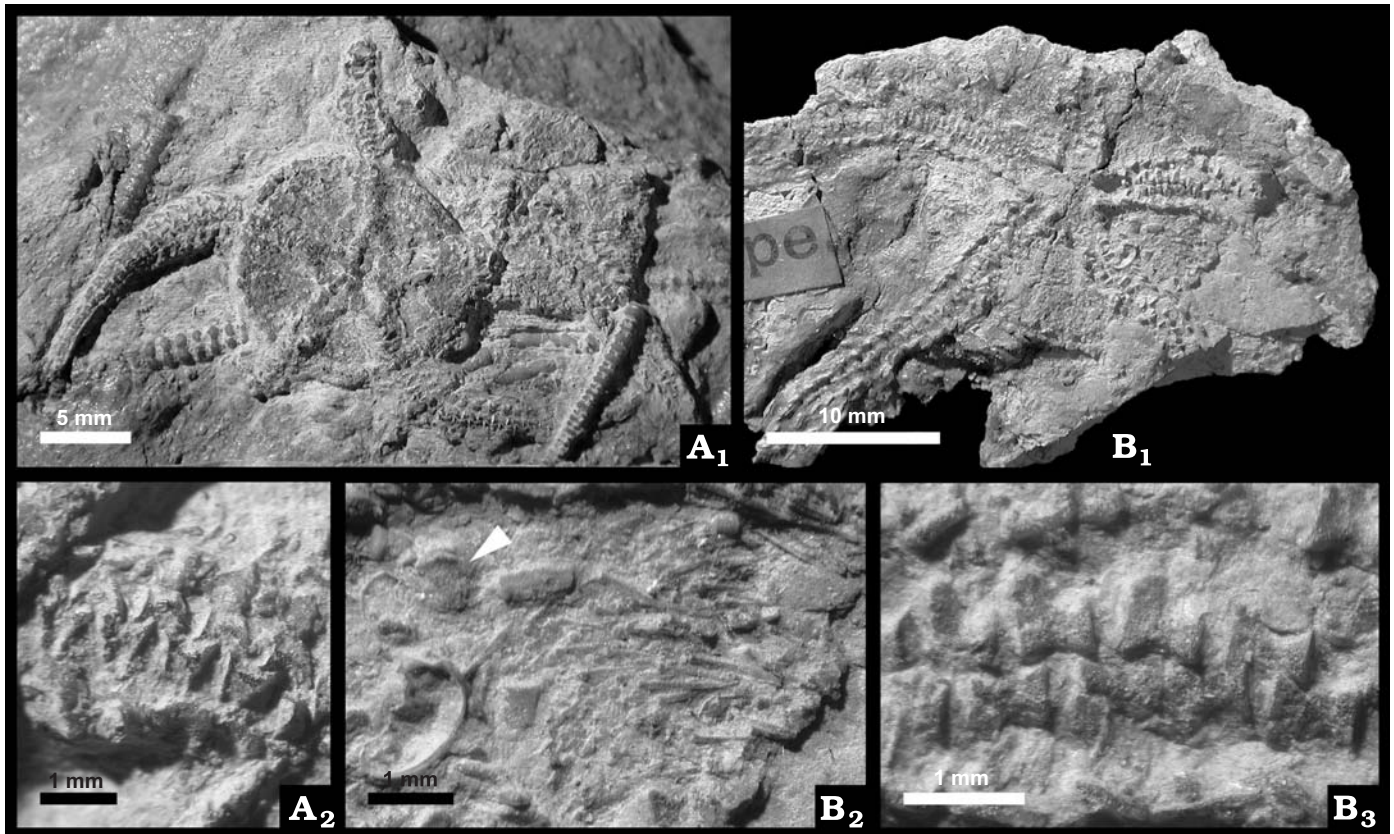
Fig. 3. *Protasterina flexuosa* (Miller and Dyer, 1878), Edenian (Upper Ordovician), Cincinnati region. Lectotype, MCZ 108078 (**A**), and paralectotype, MCZ 108079 (**B**). A_1. Lectotype (dorsal, at left) and additional specimen (ventral, at right). B_1. Paralectotype, ventral. A_2. Lectotype, dorsal surface of ambulacrals with large interambulacral muscle gaps. B_2. Paralectotype, disk spines, and small madreporite (arrow). B_3. Section of arm inside disk showing shape of proximalmost ventral ambulacrals.

edges of the laterals on each side of the arm. The longest tube foot remnant, one of the buccal tentacles, is 1.4 mm long (Fig. 2D). For comparison, a typical proximal ambulacral tube foot in the free arm is 0.6 mm long. The tube feet are generally round to oval in cross-section (Fig. 1E). Some have fractured resulting in an angular termination [the "pyramidal" shape of Ulrich (1878: 95)]. Some of the tube feet appear to have sharp folds running along their sides. What this means in terms of soft-tissue morphology and the taphonomic overlay is not known. There is no evidence of surface papillae.

The term "soft-tissue" is applied here to all non-mineralized tissues. Soft-tissue is divisible into two types. Refractory soft-tissues are made up of relatively decay-resistant compounds like lignin and chitin. Examples of refractory soft-tissue preservation in the fossil record include arthropod cuticle and some plant membranes (Allison and Briggs 1991). In contrast, volatile soft-tissues, like muscle, skin, and tube feet described here, almost always degrade rapidly following death, and preservation is rare. Volatiles potentially can be preserved as molds but mineralization soon after death is usually required (Allison 1988). Common compounds involved in the mineralization of volatile soft-tissues include phosphate, calcite, silica, clay minerals, siderite, and pyrite (Briggs 1999). Extensive pyritization of soft-tissue is known only from the Lower Devonian Hunsrück Slate of Germany, the Upper Or-

dovician Beecher's Trilobite Bed of New York, and the Middle Jurassic lower Callovian beds at La Voulte-sur-Rhône, France (Bartels and Blind 1995; Bartels et al. 1998; Bartels and Wuttke 1994a, b; Briggs et al. 1991; Briggs and Edgecombe 1993; Etter 2002a, b; Wilby et al. 1996). The Middle Devonian Silica Formation of Ohio is also well-known for the occurrence of pyritized fossils (Kesling and Chilman 1975; Nussmann 1975); however, soft-tissue preservation has not been reported from this locality.

Refractory tissue usually pyritizes through permineralization (Grimes et al. 2001; Tibbs et al. 2003), whereas volatile soft-tissue is more likely preserved in the form of pyrite coatings, casts, or molds (Allison 1988; Canfield and Raiswell 1991). Authigenic pyrite formation is a bacterially mediated product of anaerobic decay. Hydrogen sulfide, produced by microbial sulfate reduction, combines with dissolved pore-water iron to form various iron monosulfides. These initial mineral phases react with elemental sulfur to form pyrite (Berner 1970, 1984; Morse and Wang 1997; Raiswell and Canfield 1998; Wang 1996). Canfield and Raiswell (1991), Raiswell et al. (1993), Bartels and Wuttke (1994a), and Raiswell (1997) developed a theoretical model and discussed the necessary geochemical conditions for the pyritization of non-mineralized tissues. The model suggests that pyritization of soft-tissues occurs only if microbially

produced hydrogen sulfide is trapped immediately at the decay site. For this to take place, dissolved pore water iron concentrations surrounding the carcass must be at least an order of magnitude greater than sulfide concentrations. Briggs et al. (1991; 1996) discussed the pyritization of non-mineralized tissue in Beecher's Trilobite Bed and discussed the applicability of the theoretical model to the Hunsrück Slate.

The preservation of the delicate, volatile tissues that make up ophiuroid tube feet presents special problems. The typical ophiuroid tube foot consists of a very thin outer cuticle covering an epithelium, a neurofibrillar plexus (podial nerve, sensu Pentreath 1970), a connective tissue layer, longitudinal muscles, and an epithelial layer that lines the water vascular cavity. Some ophiuroids have connective tissue on both sides of the nerve layer (Hajduk 1992; Hyman 1955; Pentreath 1970; Smith 1938; Woodley 1967). Glass and Blake (2004) reported the first fossilized ophiuroid tube feet in the fossil record in the protasterid *Bundenbachia beneckei* Stürtz, 1886 from the Hunsrück Slate. Tube feet in the Hunsrück are preserved as flattened, thin films of pyrite. These films are often extremely delicate and are consistent with the view that pyritization in the Hunsrück was limited to a thin coating on the outside of the tube foot. There is no clear evidence of crushing or distortion due to compaction suggesting that the tube feet of *Bundenbachia beneckei* were flattened by sediment load before pyritization occurred. In contrast, the specimen of *Protasterina flexuosa* described here shows no significant evidence of flattening, and tube feet are preserved as solid three-dimensional shapes. Such preservation requires that the tissue layers, or at least gross overall form, were replicated by pyrite and the water vascular cavity filled before collapse of the tissues could occur. Alternatively, preservation was very different: perhaps molds left by the decaying tube feet filled with pyrite as decay proceeded. Such preservation still calls for special conditions.

Analysis of the tube feet under an Environmental Scanning Electron Microscope (ESEM) showed no visible evidence of high-fidelity tissue replication (e.g., primary surface textures, tissue layers, cellular details; see Fig. 2A–D) as might be expected through permineralization or surface coats. Where broken off, several tube feet are exposed in both horizontal and diagonal cross-sections. Tube feet are solid (Figs. 1H, 2A–C), without hollow interiors (e.g., water vascular cavity). Fine-grained crystalline cores as in pyrite stalactites (Hudson 1982) have not been observed (Fig. 2C) although the tube feet bear some superficial resemblance to these structures. Internal layering or differences in pyrite crystal texture that might give clues to the timing and mechanism of pyritization (e.g., Grimes et al. 2002) are absent. Instead, the tube feet consist of an aggregated mass of different-sized subhedral to euhedral pyrite crystals (Fig. 2A, B). Euhedral pyrite octahedrons are exposed at the surface (Fig. 2B). Framboids, clusters, or bladed pyrite (Canfield and Raiswell 1991; Hudson 1982) were not observed. Generally, euhedral pyrite is viewed as forming within void spaces (Hudson 1982). Pyritization might have begun as mineral
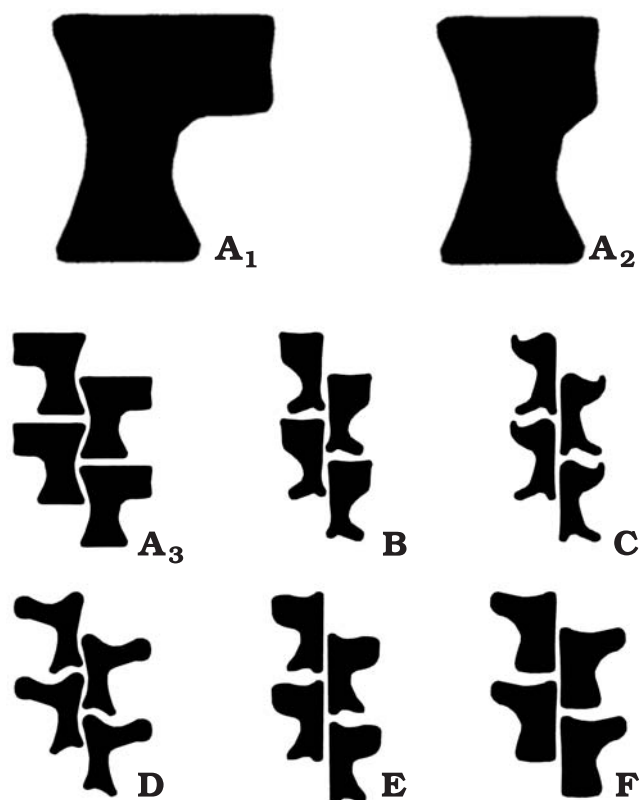

Fig. 4. Shape of the ventral surface of ambulacrals. The leg is parallel to the median suture; the foot articulates via the toes to the lateral. Proximal is top. **A**. *Protasterina flexuosa* (Miller and Dyer, 1878); A$_1$, ambulacrals inside disk and proximal portions of free arms; A$_2$, typical hour-glass shape of ambulacrals beyond the proximal portion of the disk; A$_3$, four proximal ambulacrals for comparison with other taxa, median suture clearly sinuous*. **B**. *Strataster ohioensis* Kesling and LeVasseur, 1971 and *Eugasterella logani* (Hall, 1867), median suture straight to slightly sinuous. **C**. *Bundenbachia beneckei** Stürtz, 1886; median suture straight to slightly sinuous. **D**. *Palaeophiomyxa grandis**(Stürtz, 1886); median suture sinuous. **E**. *Taeniaster spinosus* (Billings, 1858); median suture straight to slightly sinuous. **F**. *Bohemura jahni* (Jaekel, 1903), *Mastigophiura grandis** Lehmann, 1957, and *Protaster sedgwickii** Forbes, 1849; median suture straight to slightly sinuous. Taxa marked "*" were reconstructed based on a study of the type material. All other reconstructions are based on published photographs.

coats on the surface of the tube feet and then continued through the tissue layers and into the water vascular cavity. However, the aggregated pyrite texture is uniform throughout the tube feet. If pyritization initially followed tissue layers and went through similar stages of mineralization as is known from plants (Grimes et al. 2002), then the lack of expected differences in crystal textures must be explained through an "overprinting" during the formation of coarser grained pyrite crystals. Alternatively, pyritization might not have taken place directly on or inside the tissues but proceeded to fill the small voids in the sediment created as a result of the slow decay of the tube feet. Hydrogen sulfide trapped in these small voids might have created small micro-environments for pyrite crystals to form. This could ex-
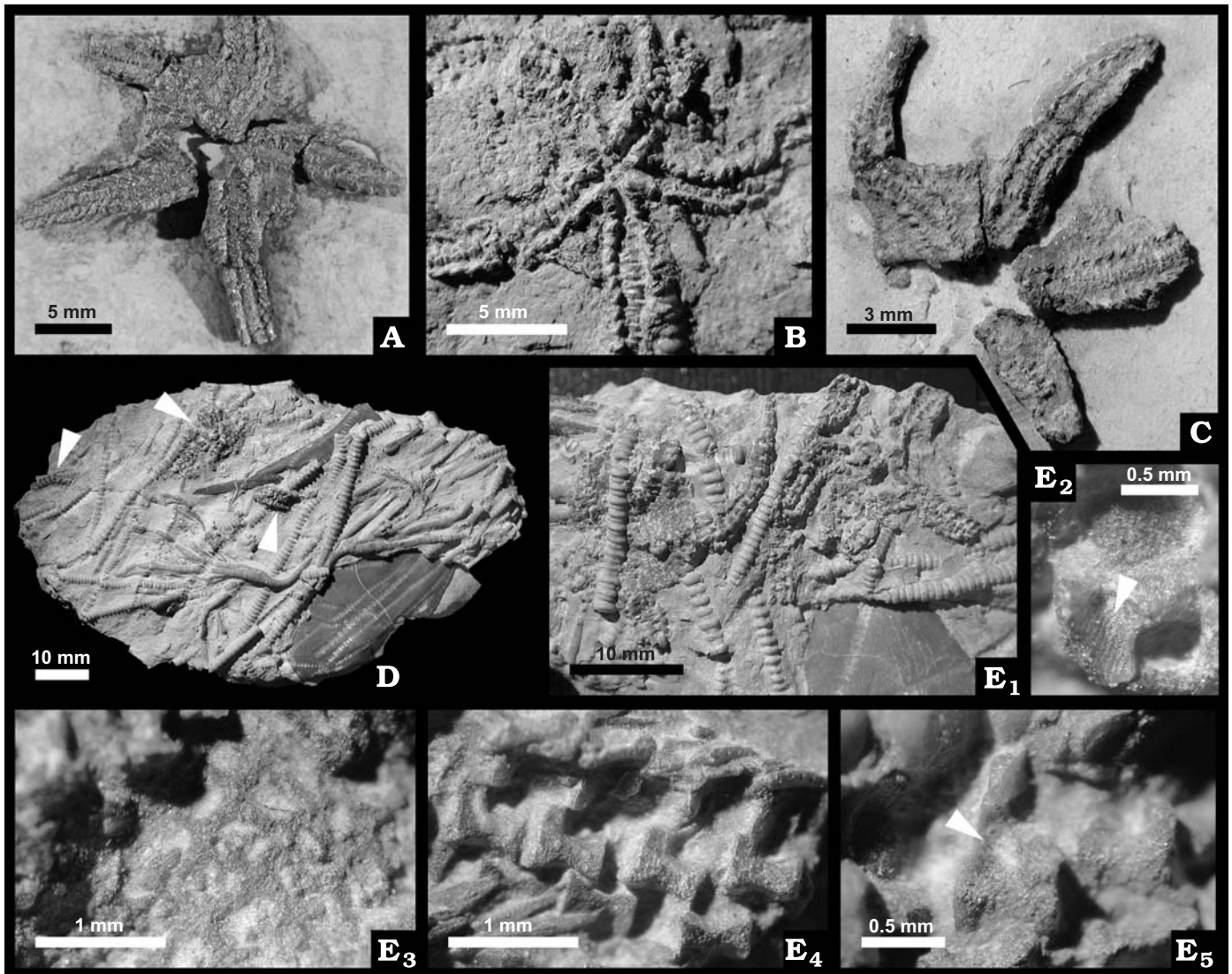
Fig. 5. *Protasterina flexuosa* (Miller and Dyer, 1878), Upper Ordovician of the Cincinnati region (see Appendix 1 for details). **A**. Previously unfigured specimen of the original suite of specimens described by Ulrich (1878); CMC 25002, ventral. **B**. Previously unfigured specimen of the original suite of specimens described by Ulrich (1878); CMC 25003, ventral. **C**. Another specimen that was possibly part of the original suite described by Ulrich (1878); MCZ 108086, ventral. **D**. Several fragments (arrows) of *Protasterina flexuosa* preserved among crinoid stems and trilobite fragments, articulated crown of *Ectenocrinus simplex* (Hall, 1847) near center of slab, CMC P506354. **E**. CMC P50635; E_1, two additional specimens, one dorsal (left), one ventral (right), trilobite fragment in lower right; E_2, fine ribbing (arrow) preserved on distal articulation surface of ventral interambulacral muscle field; E_3, stellate scales on dorsal surface of disk; E_4, ventral surface of ambulacrals immediately outside the disk; E_5, partial disarticulation exposed the triangular podial basin floor (arrow) and large interambulacral muscle gaps.

plain the euhedral size and uniform texture of the preserved tube feet. Hence, the tube feet might better be classified as pyrite casts rather than a combination of pyrite coats and permineralization.

Systematic paleontology

Class Ophiuroidea Gray, 1840
Order Oegophiurida Matsumoto, 1915
Suborder Lysophiurina Gregory, 1897
Family Protasteridae S.A. Miller, 1889

Genus *Protasterina* Ulrich, 1878

not 1849 *Protaster* gen. nov.; Forbes 1849: 1–2, pl. 4: 1–4.
not 1858 *Taeniaster* gen. nov.; Billings 1858: 81, pl. 10: 3a–d.
not 1872 *Alepidaster* gen. nov.; Meek 1872: 275.
1878 *Protasterina* gen. nov.; Ulrich 1878: 95–96, pl. 9: 9, 9a–c.

Type species: *Protasterina fimbriata* Ulrich, 1878; by monotypy; Edenian (Upper Ordovician), Cincinnati region.

Age and geographic distribution: Kope Formation, Edenian, Cincinnatian, Upper Ordovician, near Covington, Kentucky and Cincinnati, Ohio, central United States; also possibly Maysvillian aged rocks (for details see Appendix 1).

Note.—Terminology for the ventral outlines of the ambulacrals follows Glass and Blake (2004).

Revised diagnosis.— Protasterid ophiuroid with wide dorsal interambulacral muscle gaps. The dorsal surface of the ambulacral is trapezoidal with raised proximal and distal ridges. The dorsal surface of the disk is covered by ossicles of uncertain shape although some of these are distinctly star-shaped in outline. The ventral surface of the disk is covered by ossicles of uncertain shape. Both the dorsal and ventral surfaces of these ossicles are overlain by small irregularly distributed granules. Thin, pointed, articulated spines are present on both sides of the disk. A small, round, flattened madreporite with a wavy channel running around its circumference is situated near the second ambulacral. Dorsal arm covering not preserved. Arms taper evenly but distal arm tips are not preserved. The ventral surface of the ambulacrals is boot-shaped with flattened distal and proximal edges. The abradial edge of the toe is straight. The foot is nearly twice as wide as the distal fitting. In the first two ambulacrals the foot is as wide as the leg is long, and this ratio is retained well into the proximal portions of the arms, although foot width decreases distally. The width of the central leg is narrower than the width of the distal fitting giving the leg of the boot a distinctive hour-glass appearance, especially distally where the width of the foot decreases. The median suture is strongly sinuous, almost sharply angular. Ventrally, laterals are straight to slightly crescent-shaped. The proximal, free laterals bear at least five slightly petaloid groove spines and at least four evenly tapering vertical spines.

Comparison.—Because protasterid ophiuroids are in need of revision, modern phylogenetic treatment and consensus on generic diagnoses are unavailable (but see Hammann and Schmincke 1986). Ventral outline of ambulacral plates traditionally has been found to be useful in differentiating among Paleozoic ophiuroids (e.g., Ulrich 1887; Gregory 1897; Spencer 1934), although there has been no effort to develop comprehensive comparative analysis. As a first step toward such analysis, Glass and Blake (2004) provided six different ambulacral ventral outlines suggested to be representative of nine protasterid ophiuroids. Ambulacral outline varies among and within specimens; the reconstructions are based primarily on those ambulacrals immediately distal to the disk of specimens of average size. The six shapes of Glass and Blake (2004) are slightly modified here and reproduced in sets of four to aid orientation (Fig. 4A$_3$–F). The shape of *Protaster* ambulacrals is re-assigned. Based on drawings by Spencer (1934: text-fig. 297) and notes by Hammann and Schmincke (1986), Glass and Blake (2004) suggested that the ambulacrals of *Protaster* are similar to those of *Bundenbachia*. Study of the type material of *Protaster sedgwickii* (BMNH E6374b) could detect no indication of the prominently hooked toe and concave proximal fittings depicted by Spencer (1934: text-fig. 297). *Protaster* is now aligned with *Bohemura* although phylogenetic implications of all suggested shape groupings must be left to future work. Glass and Blake (2004) developed a terminology for different parts of the ambulacral; this terminology is retained unaltered. Comparison will focus on characters found here to differentiate *Protasterina* Ulrich, 1878 from other protasterids.

The wide dorsal interambulacral muscle gaps in *Protasterina* are shared by only five other protasterid genera. These are *Palaeophiomyxa* Stürtz, 1899, *Strataster* Kesling and Le Vasseur, 1971, *Drepanaster* Whidborne, 1896, and perhaps *Eugasterella* Schuchert, 1914. The dorsal ambulacrals of *Chattaster* Hahn and Brauckmann, 1981 have been described as trapezoidal but their rod-like shape with an almost undifferentiated ventral toe are unlike those of any other protasterid genus. Haude (1982) and Haude and Thomas (1994) discussed the atypical nature of the morphology of *Chattaster*.

The ventral shape of the ambulacrals of *Protasterina*, with their flattened distal and proximal articulations, the distally hour glass shaped leg, and the great length and width of the toe proximally is different from those of all other protasterid ophiuroids with large dorsal muscle gaps.

Eugasterella logani (Hall, 1867), the type species of *Eugasterella*, is known only from the ventral surface. However, additional material assigned to this species by Harper (1985) exhibits wide interambulacral muscle gaps. *Eugasterella* and *Strataster* are very similar, especially in the ventral shape of their ambulacrals. Indeed, Harper (1985) saw *Strataster* as a junior synonym of *Eugasterella*, but Hotchkiss (1993) continued to recognize *Strataster*. In both genera, the foot is not significantly wider than the width of the distal fitting and the central width of the ambulacral is only slightly less than the total width of the leg. The abradial edge of the ambulacral is nearly straight and distal and proximal fittings are usually slightly to distinctly concave. The overall ventral shape of the ambulacrals of both *Strataster* and *Eugasterella* (Fig. 4A, B) easily distinguish them from *Protasterina*. In addition, *Strataster* has a well-developed carinal row of spines on the arms, and *Eugasterella* lacks spines on the disk.

Palaeophiomyxa is known from a single specimen from the Lower Devonian Hunsrück Slate of Germany (Glass and Blake 2004). *Palaeophioymxa* differs from *Protasterina* in the lack of spines on the disk, the ventral shape of its ambulacrals (Fig. 4D), which have distinctly concave distal and proximal fitting, a wider, much more rounded toe, and possibly a greater number of groove spines.

Little is known about *Drepanaster*. The specimens figured by Whidborne (1898: pl. 29: 1, 2) show little detail and are highly stylized. Hammann and Schmincke (1986) pointed out that Spencer (1934, 1940) discussed the genus but based much of his interpretations on *Drepanaster grayae* Spencer, 1943 rather than the type species *Drepanaster scabrosus* (Whidborne, 1896). His reconstruction of the dorsal surface of *D. scabrosus* (Spencer 1940: text-fig. 326C) is based on an additional specimen that was not part of the original type series. This specimen is figured with large interambulacral muscle gaps. Much of the discussion of *Drepanaster* in Spencer (1940) is based on the species *Drepanaster grayae* Spencer, 1934. Until the type material of *Drepanaster* is redescribed, full comparison to other protasterids must be deferred.

Hammann and Schmincke (1986) placed *Mastigophiura* Lehmann, 1957 alongside protasterids with wide muscle gaps. Re-examination of all of the *Mastigophiura* type material listed

in Lehmann (1957: 51) and an additional specimen figured by Opitz (1931: fig. 57, Forschungsinstitut und Naturmuseum Senckenberg, SNF 5a) demonstrated that the ambulacrals are better described as quadrate (Glass in press). Because the ambulacrals are wider than long the muscle gaps can appear relatively large, especially where ossicles have shifted during preservation. *Mastigophiura* further differs from *Protasterina* in its highly variable groove and vertical spines and the presence of a well-developed carinal row of spines on the arms.

Taeniaster Billings, 1858, *Bundenbachia* Stürtz, 1886 (see Glass and Blake 2004), *Protaster* Forbes, 1849, *Bohemura* Jaekel, 1903, and *Klarasterina* Petr, 1989, all have narrow dorsal interambulacral muscle gaps.

The protasterid genera *Astutuaster* Boczarowski, 2001 and *Weigeltura* Boczarowski, 2001 are only known from suites of disarticulated ossicles. Unfortunately, it is not clear how Boczarowski (2001) grouped different disarticulated ossicle types into genera and species. It is possible that his suites of ossicles represent a mixture of different taxa. The holotypes of the type species of both *Astutuaster* and *Weigeltura* consist of a single ambulacral (Boczarowski 2001: figs. 5A and 7A respectively) both of which are quadrate in dorsal outline and can therefore be distinguished from *Protasterina*.

Too little is known about the protasterid genera *Palaeophiura* Stürtz, 1890 (Lower Devonian, Hunsrück Slate, Germany), and *Inyoaster* Phleger, 1936 (Middle Ordovician, Inyo Mountains, California) for effective comparison. However, *Inyoaster* is likely a member of the Palaeuridae instead of the Protasteridae (Frederick H.C. Hotchkiss, personal communication, 2005). Glass (in press) argued that *Palaeophiura* is a juvenile specimen of *Bundenbachia*. The figured specimens of *Inyoaster bradleyi* (Phleger 1936: pl. 20: 1, 2) are too poorly preserved to allow comparison. Indeed, although Spencer and Wright (1966) listed this genus under the family Protasteridae, they described the specimens as unrecognizable.

Discussion.—Hotchkiss (1970) tentatively placed one of the paralectotypes of *Palaeocoma spinosa* Billings, 1857 (GSC 1404a), as well as *Protaster whiteavesianus* Parks, 1908, *Taeniaster maximus* Willard, 1937, *Drepanaster grayae* Spencer, 1934, and the fossils described as *Taeniaster spinosus* (Billings, 1858) by Cramer (1957) into the genus *Protasterina* Ulrich, 1878 because all of these specimens exhibit wide dorsal interambulacral muscle gaps. However, this character is not restricted to *Protasterina* and is therefore not diagnostic by itself. Revision of these taxa is beyond the scope of the present study, and because the dorsal gap is not a unifying apomorphy, they are all allowed to stand pending reevaluation. Cramer (1957) found that the type and only known specimen of *Taeniaster maximus* had been lost but F. Hotchkiss located the specimen (USNM 111699) at the Smithsonian National Museum of Natural History (Frederick H.C. Hotchkiss, personal communication, 2005).

Hotchkiss (1970) also noted that a specimen described by Schuchert (1915) as *Alepidaster* sp. from the Trenton Limestone (Middle Ordovician; MCZ 108076) of New York has a mouthframe and ambulacrals that resemble those of *Prota-*

sterina. This specimen is only partially exposed but restudy of the material revealed that the shape of the ambulacrals is quite different from that of *Protasterina* and it is not included in *Protasterina* here.

Protasterina flexuosa (Miller and Dyer, 1878)
Figs. 1–3, 4A$_1$–A$_3$, 5.

1878 *Protaster flexuosus* sp. nov.; Miller and Dyer 1878: 31, pl. 2: 1, 1a.
1878 *Protasterina* ("*Protaster*" lapsus) *fimbriata* gen. nov., sp. nov.; Ulrich 1878: 95–96, pl. 4: 9, 9a–c.
1878 *Protaster flexuosus* Miller and Dyer; Ulrich 1878: 96.
1880 *Protasterina fimbriata* Ulrich; Ulrich 1880: 10.
1880 *Protasterina flexuosa* (Miller and Dyer); Ulrich 1880: 10.
1883 *Protaster flexuosus* Miller and Dyer; Miller 1883: 287.
1888 *Taeniaster fimbriata* (Ulrich); Ulrich 1888: 184, 313.
1888 *Taeniaster flexuosa* (Miller and Dyer); Ulrich 1888: 184, 313.
1889 *Protaster flexuosus* Miller and Dyer; Miller 1889: 276, fig. 409.
1896 *Protasterina fimbriata* Ulrich; James 1896: 139–140.
1896 *Protasterina flexuosa* (Miller and Dyer); James 1896: 140.
1902 *Taeniaster fimbriatus* (Ulrich); Nickles 1902: 70.
1902 *Taeniaster flexuosus* (Miller and Dyer); Nickles 1902: 70.
1908 *Protaster flexuosus* Miller and Dyer; Parks 1908: 364.
1908 *Protasterina fimbriata* Ulrich; Parks 1908: 368.
1914 *Alepidaster flexuosus* (Miller and Dyer); Schuchert 1914: 11.
1915 *Alepidaster flexuosus* (Miller and Dyer); Schuchert 1915: 231–233, pl. 36: 4.
1915 *Alepidaster flexuosus* (Miller and Dyer); Bassler 1915: 25.
1915 *Alepidaster fimbriatus* (Ulrich); Bassler 1915: 25.
1934 ?*Taeniaster spinosus* (Billings); Spencer 1934: 491, pl. 31: 10.
1934 ?*Drepanaster flexuosus* (Miller and Dyer); Spencer 1934: 491.
1940 "*Protaster*" *flexuosus* (Miller and Dyer); Spencer 1940: 497.
1962 *Protasterina fimbriata* Ulrich; Hansman et al. 1962: 102.
1965 *Taeniaster fimbriatus* (Ulrich); Owen 1965: 550.
1970 ?*Protasterina flexuosa* (Miller and Dyer); Hotchkiss 1970: 73.
1986 *Protasterina fimbriata* Ulrich; Hammann and Schmincke 1986: 61, text-fig. 3.
1995 *Protasterina fimbriata* Ulrich; Hotchkiss 1995: 433, table 6.
1999 *Protasterina fimbriata* Ulrich; Hotchkiss et al. 1999: 192.
2002 *Protasterina fimbriata* Ulrich; Glass and Blake 2002: 36.

Diagnosis.—Same as genus by monotypy.

Material.—Fifteen specimens housed at CMC and MCZ: MCZ 108078a (lectotype by designation herein), MCZ 108078b, MCZ 108079 (paralectotype), MCZ 108086, CMC 25001, CMC 25002, CMC 25003 (three specimens), CMC P3874 (two specimens), CMC P50635 (four specimens). Details on preservation and condition of specimens are given in the Appendix 1.

Description.—The interradial margin of the disk is rounded to straight and lacks marginal ossicles (Figs. 1B, 3A$_1$). The ventral and dorsal surface of the disk is covered by closely abutting ossicles and in at least one specimen these are well-enough exposed to show that they are shaped like four-pointed stars (Fig. 5E$_3$). Fine granules are irregularly distributed across both the ventral and dorsal disk surfaces (Figs. 1B, 3B$_2$). Very fine evenly tapering spines are present on each side of the disk though they appear to have been denser on the ventral surface. Some spines are as long as the lengths of the laterals (Fig. 3B$_2$). A madreporite is present. It is a small, rounded, slightly raised plate-like ossicles with a wavy circumferential channel. The channel has five loops that are

raised toward the upper surface of the ossicle. It is situated next to the second lateral (Figs. 1D, $3B_2$).

None of the available material adequately exposes the dorsal surface of the mouth frame so description is limited to its ventral aspects (Figs. 1C, 5B). The mouth-angle ossicles (first ambulacrals) are not significantly longer than the length of the proximal ambulacrals. Their ventral surfaces are broad with a centralized depression that is surrounded by a distinctly raised margin. Adradially, this margin varies from flat to exhibiting raised bumps. In at least one place the remains of what might have been spines are associated with these bumps (Figs. 1C, 2D). The proximal ends of the mouth angle ossicles abut to form scoop-shaped depressions facing towards the center of the mouth. The proximalmost edges of the mouth angle ossicles are slightly raised, increasing the size of these elongated depressions inside the mouth. Several small spines extend from the mouth-angle ossicles into the mouth area. A torus could not be clearly identified; however, in at least one place the spines appear to come together and attach to a small base or possible torus that does not completely fill the scoop-shaped depression. The laterals of the second ambulacral, some affiliated with preserved buccal tube feet (Fig. 1C), are clearly differentiated from the mouth-angle ossicles by a skeletal gap. They are small, subquadrate, and slightly concave abradially. They are distinctly raised above the level of both the arm surface and the mouth-angle ossicles. The ventralmost edge carries at least three petaloid spines.

Arms are widest at the disk margin and taper evenly beyond the disk (Figs. 1A, $3B_1$). All arm tips are missing in available specimens. The dorsal surface of the arms is exposed in all specimens showing the ambulacrals below. The dorsal surface of the ambulacrals is finely granulated. Whether this represents the granulated surface texture of the ossicles or remnants of granulated skin cannot be determined. Evidence for a carinal row of spines or ossicles is absent. The dorsal interambulacral muscle gaps are wide, giving the ambulacrals a trapezoidal to nearly triangular dorsal outline (Fig. 1G). This shape is most pronounced in the free arms just outside the disk (Fig. $3A_2$). The ambulacrals are fringed distally and proximally by raised ridges, which decrease in height along the arm.

The number of ambulacrals in the disk varies between three and five but can appear to be greater when the disk is distorted or folded underneath the arms. The ventral surface of the ambulacrals is typically boot-shaped with a shallow saddle in the middle of the leg (Figs. 1F, H, $3B_3$, $5E_4$). Small, rounded depressions at the ankle of the boot are clearly absent. In the proximal ambulacrals (up to the fifth), the foot is as wide (W_F, abbreviations follow Glass and Blake 2004: fig. 6B) as the leg is long (L_L) (Figs. $3B_3$, $4A_1$–A_3). This also applies to the first two to three ambulacrals immediately outside of the disk (Fig. $5E_4$) but distally along the arm, the width of the foot becomes shorter than the lengths of the leg creating a distinctive hourglass appearance (Figs. 1H, $4A_1$–A_3). Description here focuses on the ambulacrals immediately outside of the disk (Figs. $4A_1$, $5E_4$). The length of the toe (L_T) is slightly less than half the length of the leg (L_L). The length of the foot (L_T) is

nearly equal to the width of the distal fitting (W_{DF}). All of the articulation sites—distal, proximal, and toe—are straight. The surface of the ventral interambulacral muscle articulation bears small ridges (Fig. $5E_2$). The width of the distal fitting (W_{DF}) is larger than the width of the central leg (W_{CL}). The width of the foot (W_F) is greater than the width of the distal fitting (W_{DF}). The width of the toe (W_T) is nearly half the width of the foot (W_F). The lace area of the boot is nearly circular from toe to distal fitting (Figs. 1F, $3B_3$). The podial basin is triangular in shape due to the large dorsal interambulacral muscle gaps (Fig. $5E_5$). Because the width of the central leg (W_{CL}) is distinctly less than the distal fitting, the ventral median suture is distinctly sinuous and almost angular (Figs. 1H, $3B_3$).

The laterals are slightly curved abradially but appear nearly straight in ventral view (Fig. 1H). They articulate to the ambulacrals by a prominent, thin, straight neck (Fig. 1F). The lateral edge bearing the groove spines is sharply raised above the articulating neck. Consecutive laterals imbricate along the arm. Laterals bear both groove and vertical spines (Figs. 1F, H, $5E_4$).

The exact number of groove and vertical spines per lateral is difficult to ascertain because of the small size of the specimens as well as vagaries of preservation. A maximum of five groove spines can be seen on laterals of arms inside the disk. In places, there is also evidence for a sixth spine on the distalmost corner of the spine-bearing ridge, but this could also be the ventralmost lateral spine. Most of the tips of the groove spines are broken off but partial preservation in places suggests that they are of variable length. Their small size makes it difficult to judge their shape. Many of them appear to taper evenly to blunt tips, others seem slightly petaloid. Whenever preserved, a lateral's groove spines generally point in the same direction.

Disk laterals bear one, or perhaps two vertical spines that articulate along the distal, slightly abradial edge of the lateral. None of the vertical spines are preserved in their full length but the maximum preserved size reaches the length of a lateral. Some vertical spines bear a distinct axial groove. Along the proximal free arms, at least four vertical spines are present on each lateral. The ventralmost vertical spine is the longest and spine size decreases along the lateral's proximal edge. The vertical spines on the free arms are preserved parallel to the arm axis. Where vertical spines are lost, distinct articulation sites are visible along the lateral's edge.

Occurrence.—Same as genus. For details on available stratigraphical and geographical information see Appendix 1.

Conclusions

The pyritized tube feet described herein in a single specimen of the protasterid ophiuroid *Protasterina flexuosa* represent the second report of tube foot preservation in a fossil ophiuroid. However, unlike the only other known occurrence from the Hunsrück Slate (Glass and Blake 2004), the tube feet from the Kope Formation are preserved in three-dimensions. The presence of these delicate structures in pyrite and other

reports of pyrite associated with fossils (e.g., Hughes and Cooper 1999) suggest that similar conditions, necessary for the pyritization of volatile soft-tissues, might have existed elsewhere in the Kope Formation. Perhaps a targeted search for pyrite-containing fossiliferous horizons in the Kope Formation will yield other examples of rare and potentially important occurrences of soft-tissue preservation.

Acknowledgments

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Appendix 1

Details on specimens examined.—By designation herein, the lectotype is MCZ 108078a (Fig. 3A$_1$, dorsal), and para-lectotype is MCZ 108079a (Fig. 3B$_1$, ventral/dorsal). Miller and Dyer (1878) do not give the number of specimens that were available to them. At least two specimens are figured and there is mention of "small pieces ... from other specimens" (Miller and Dyer 1878: 31–32). A second specimen (Fig. 3A$_1$, MCZ 108078b) is preserved immediately next to and partially covered by the lectotype. It consists of a single arm attached to a cracked but nearly complete disk. This specimen is preserved in ventral view and it is of nearly identical size as the lectotype. This specimen carried no collection number and it was not explicitly mentioned by Miller and Dyer (1878). It is figured here for the first time. All three specimens are preserved in calcite.

Both the lectotype and the adjacent specimen were covered in a thick, heavily cracked, plastic-like material. The irregular surface and fine internal cracks of this coating obscured all detail of the specimens when examined under a microscope. Using a soft, water-moistened paintbrush this material was removed from both specimens for the purpose of this study. It was during the removal of this layer that the additional specimen adjacent to the lectotype was discovered. It is not known when the surface coating was added but it is possible that it might have been applied immediately after discovery in the field in order to protect the soft shaly rock surface. Perhaps the second specimen was obscured when Miller and Dyer (1878) studied the block.

The exact number of specimens used for the original description of *Protasterina fimbriata* by Ulrich (1878) is unclear. CMC 25001 (Fig. 1A–H) is labeled as the holotype and was the only specimen figured by Ulrich (1878: pl. 4: 9, 9a–c) but the descriptions mentioned the existence of more specimens. CMC 25001 is to be regarded a lectotype selected by Schuchert (1915:300). CMC 25001 has a previous registration history as USNM 60615 at the Smithsonian National Museum of Natural History (see Schuchert 1915; Spencer 1934; Owen 1965) and No. 25001 in the University of Cincinnati Museum (see Hansman et al. 1962). A second specimen (Fig. 5A, CMC 25002) is labeled as a "topotype" but the label gives "Skinner Collection" as the source. Three additional specimens on two slabs carry the number CMC 25003 (one specimen figured here in Fig. 5B). Whether CMC 25002 and CMC 25003 are part of the original suite available to Ulrich (1878) cannot be known for certain; however, the fact that they are consecutively numbered and kept in green boxes with red labels (designation for type material) suggests that this is very likely. A sixth specimen was found in the collections at the Harvard Museum of

Comparative Zoology (Fig. 5C, MCZ 108086) with a label describing it as "one of Ulrich's specimens."

CMC 25001, CMC 25002 and MCZ 108086 are completely free from the surrounding matrix and glued to pieces of cardboard. When this was done or by whom is unknown. All three specimens were mounted ventral side up and are preserved in pyrite, which gives them a light brown to black color. Details of preservation for CMC 25003 are provided below.

Prior to this publication, the only figured specimen was the lectotype CMC 25001. Ulrich (1878) provided only drawings whereas Schuchert (1915: pl. 36: 4) was the first and Spencer (1934: pl. 31: 10) the last to provide a photograph of CMC 25001. At the time of Spencer (1934) the specimen appeared in good conditions with only two arms missing and a largely intact disk. The picture of Spencer (1934), however, shows evidence of having been drawn upon with white and black pen. This is especially true for the mouthframe and disk. As oriented in the photograph, the lower part of the disk appears to have been drawn in and the lower arm does not appear to be actually attached to the specimen. As mentioned above, there is also evidence that Spencer (1934) merely reproduced the picture published by Schuchert (1915). The specimen today consists of six major fragments and some smaller pieces. At some point all of the arms had broken off, and been glued back with an apparently thick, now reddish resin. At the time of this study, only the disk and one arm remained loosely attached to the cardboard. For the present study, the remaining disk and arm were carefully separated from the cardboard, which allowed examination of their dorsal surfaces. The pieces are now kept separately.

CMC 25002 (Fig. 5A) consists of seven fragments. It is covered by a glossy varnish or glue, which obscures much detail. No attempt was made to remove the specimen from its backing.

CMC 25003.1 (Fig. 5B) is a single ventrally exposed specimen limited to the disk, the proximal portions of the arms, and a single distal arm fragment. It is preserved in a gray shale containing thin horizons of black organic material. Fragments of crinoid stems are exposed at the edges of the rock specimen. CMC 25003.2 consists of the remains of at least two specimens preserved in a gray shale. The ventrally exposed specimen is nearly complete with the exception of three distal arm portions. It is covered by a thick coating of yellow, heavily cracked varnish, that obscures most of the specimen. The dorsal specimen consists of the disk and three arm fragments. Most of it is heavily covered in varnish. A single crinoid stem is exposed on the same surface as the ophiuroids, and on the reverse side of the small slab an exquisitely preserved specimen of *Ectenocrinus simplex* (Hall, 1847) is exposed.

MCZ 108086 (Fig. 5C) is incomplete and consists of six fragments of parts of the disk and four proximal arm fragments.

Six additional, previously unpublished specimens of *Protasterina flexuosa* were identified in the Cincinnati Museum Center collection. CMC P3874 (not figured due to poor conditions) is a small piece of hardened resin to which are affixed two fragmentary, ventrally exposed specimens that are in extremely poor condition. Both specimens appear to be pyritized. CMC P50635 consists of two small slabs of gray shale with the remains of at least two specimens of *Protasterina flexuosa* on each slab. These specimens are entangled in a dense "log-jam" (*sensu* Brett and Algeo 1999a: 69) of crinoid stems and large brown trilobite fragments (see Fig. 5D–E₁). At least two complete crowns of *Ectenocrinus simplex* (Hall, 1847) are also present (CMC P50635a, Fig. 5D). CMC P50635a has a ventral arm fragment and the disk and proximal arm portions of another specimen (Fig. 5D). CMC P50635b exhibits complete disks and fragmented proximal arm portions of one ventral and one dorsal specimen (Fig. 5E₁). All of the specimens of CMC P50635 are preserved in calcite, however a thin veneer and some euhedral crystals of pyrite cover some parts of their skeleton. A small pyritized unidentified bivalve lies immediately next to the specimens on CMC P50635b. Neither the crinoids nor the trilobite fragments are pyritized.

Notes on stratigraphical and locality data.—Existing locality and stratigraphic data on both the type material of *Protaster flexuosa* (Miller

and Dyer, 1878) and the additional specimens is limited or vague. Miller and Dyer (1878: 32) said their specimens (MCZ 108078 and MCZ 108079) were from "different elevations from near low-water mark in the Ohio river to the top of the hills at Cincinnati." The most recent museum label gives the Maysville Formation (Upper Ordovician), Cincinnati, Hamilton County, Ohio for locality data but it is not known on what authority this assignment is based and it should be treated as unverified. A photocopy of what appears to be the oldest label of specimen MCZ 108079 merely lists the Hudson River Group, a traditional term for the Cincinnatian series. A third but newer label adds the additional information "Eden, Cincinnati, Ohio," which likely refers to the "Eden Shales," an older name for parts of the Kope Formation (Anstey and Fowler 1969).

All of the fossil material described by (Ulrich 1878) came from the "Cincinnati Group" and his specimens of *P. fimbriata* were collected at "100 ft. above low water mark in the Ohio river, at Covington, KY" (Ulrich 1878: 96). In a detailed stratigraphic paper, Ulrich (1888) listed "*Taeniaster*" *fimbriata* and "*Taeniaster*" *flexuosa* from bed XIb and possibly from XIa. The museum labels of the specimens list the Economy Formation as the stratigraphic unit from which both CMC 25001 and CMC 25002 were collected. The Economy Formation is now recognized as the Economy Member, the basal member of the Kope Formation.

MCZ 108086 merely gives "Hudson River Group, Covington, Kentucky" for locality data.

CMC P3874 (two specimens) is from the "Eden-Economy, Covington, KY" and CMC 25003 (two specimens) provides "Maysville gr., Ordovician, Covington, KY" as locality data.

All four specimens of CMC P50635 are from the "Lower Rapid Run, Kope Formation." The lower Rapid Run probably refers to a locality of the same name rather than a stratigraphic horizon.

Additional specimens in the Smithsonian NationalMuseum of Natural History provide limited locality information (F. Hotchkiss, personal communication, 2005). USNM 92621 is from the Maysville Formation probably near Cincinnati, Ohio, whereas labels on the remaining specimens all cite Covington, Kentucky as the source. USNM 60626 is from the Cincinnatian, USNM 93331 from the "Cincinnati Group," USNM 92620 is from the "Eden," and USNM "uncatalogued" provides no locality data.

Brett and Algeo (1999b) constructed a composite reference section of the Kope Formation. However, it remains unclear how to translate the elevations in terms of feet above low-water mark given by Ulrich (1878) or the beds listed in Ulrich (1888) onto the reference section [see also comments about the stratigraphy of Ulrich (1888) in Nickles (1902)]. Furthermore, since sections vary in thickness at different outcrops and it is not known which of these outcrops was collected by Miller and Dyer (1878) or Ulrich (1878), measurements on the reference section must be viewed as highly tentative. At best, 30.5 meters (the "100 feet" of Ulrich 1878) measured from the base of the section would place the site into the Southgate Member, about 8.5 meters above the Economy Member. This interval is known as the Pioneer Valley Submember and interestingly, Brett and Algeo (1999b) mentioned the existence of a "starfish bed" consisting of the protasterid ophiuroid *Taeniaster* at this stratigraphic level (about 7.7 meters above the base of the Southgate Member). The writer has not seen specimens from this horizon but it is possible that these are or include *Protasterina*. Furthermore, the pyritized trilobites of Hughes and Cooper (1999) are also from the Pioneer Valley Submember about 13 meters above its base, though this bed might only occur locally at this level (Brett and Algeo 1999b). In this part of the Kope Formation the crinoid *Ectenocrinus simplex* (Hall), 1847 also becomes abundant (Brett and Algeo 1999b). At least one complete crown of this crinoid occurs on the same slab as the type (MCZ 108078) and on one of the hypotypes (CMC 25003.2).

It is impossible to say with certainty at which horizons in the Kope Formation the material studied here was collected. At best, the evidence suggests that *Protasterina* could have been found but is not necessary limited to the lower 30 meters of the Kope Formation, which includes the Economy member and parts of the Southgate member. A range extending into rocks of Maysvillian age cannot be ruled out (see CMC 25003).