EARLY ASTEROZOAN (ECHINODERMATA) DIVERSIFICATION: A PALEONTOLOGIC QUANDARY

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ABSTRACT—The Asterozoa as traditionally recognized is monophyletic, although ancestry within the Echinodermata is unknown. The asterozoan class Somasteroidea is most readily recognized by presence of series of simple ossicles termed virgals that extend laterally from each ambulacral ossicle. Virgal series reduction to two or three together with ossicular specializations provide apomorphies of the class Stenuroidea (new ranking). Both asteroid-like and ophiuroid-like configurations as well as expressions less suggestive of those of the surviving classes emerged within stenuroids during an early period of diversification. The classes Ophiuroidea and Asteroidea are separate lineages marked by virgal series reduction to a single ossicle and other ambulacral column specializations. It is uncertain whether one or both surviving classes were derived directly from somasteroids or originated through stenuroids. All three of the derived asterozoan classes can be argued to be either monophyletic and thereby justifying class status, or alternatively either paraphyletic or polyphyletic and thereby indicative of multiple plesions; here, monophyletic class-level status is favored for all three.

INTRODUCTION

THE PALEONTOLOGIC literature documents varied early echinoderms. The Cambrian fauna includes helicoplacoids, diverse edrioasteroids, and many blastozoan and carpoid classes, all with no fully accepted phylogenetic connections among them nor to the Ordovician diversification of the surviving groups, including the Asterozoa. Students of fossil asterozoans traditionally assigned new specimens to the inferred most appropriate extant class and ordinal taxa, a workable approach for Jurassic and younger species but less satisfactory for earlier occurrences. In searching for phylogenetic linkage between asteroids and ophiuriods, Spencer (1914–1940) repeatedly returned to a notion of an ancestral "root stock," neither truly asteroid nor ophiuroid (1914, p. 1, 19; 1918, p. 125). Discoveries of very early asterozoans in the south of France (Thoral, 1935) and Bohemia (Jaekel, 1923) led to two new taxon concepts (Spencer, 1951), the (sub)class Somasteroidea for a small suite of Ordovician asterozoans and an ophiuran order Stenurida for a heterogeneous assemblage of genera, these summarized by Spencer (1940). Both taxa were retained by Spencer and Wright (1966).

More important than the recognition of the new taxa, however, are their implications. It is indicative of the uncertainties surrounding the early history of the Asterozoa that after decades of effort and many hundreds of pages of text by acute researchers (Spencer, 1914–1940; see also Spencer, 1951, p. 88), the study of a comparatively few new specimens led to fundamental revision of early phylogenetic interpretations, the Somasteroidea assigned place at the base of asterozoan diversification (Spencer, 1951). Regardless of differing opinions on the positioning of somasteroids (e.g., Spencer, 1951; Shackleton, 2005), their discovery argues how much of significance might remain unknown, a view reinforced by the unique but incompletely understood Devonian asterozoan fauna of the Hunsrück Slate (Lehmann, 1957; Bartels et al., 1998; Blake, 2009).

The work of Spencer (1914–1940, 1951) remains essential to evaluation of early asterozoan history, and viewpoints of this author are widely cited here. The text of Spencer and Wright (1966), however, was brought together after the 1954 death of

Spencer (Spencer and Wright, 1966, p. U5), and therefore it cannot fully reflect Spencer's final perspectives.

Other more comprehensive studies of asterozoan history include Gregory (1900) and Schuchert (1915). For ordinal-level taxa, Spencer (1951) provided the current terminological starting point, and Ubaghs (1953) and Müller (1963) largely followed this lead. A comprehensive listing of then-known fossil and extant genera is found in Spencer and Wright (1966), and Owen (1965) provided a guide to Spencer (1914–1940). A summary history of classification of early asterozoans with emphasis on asteroids was provided by Mah and Blake (2012).

To facilitate comparisons, figures cluster the class groupings recognized here: somasteroids (Fig. 1), those stenuroids that are unlike either asteroids or ophiuroids (Figs. 2–4), largely asteroids and asteroid-like stenuroids (Figs. 5, 6), and a mixed grouping (Fig. 7). Institutional abbreviations are as follows: AMNH, American Museum of Natural History, New York; BMNH, British Museum of Natural History, London; CMC, Cincinnati Museum Center; FMNH, Field Museum of Natural History, Chicago; FSL, VOMN, Université Claude Bernard, Lyon, France; GSI, Geological Survey of Ireland; IPM, Rheinische Friedrich-Wilhelms-Universität Institut für Paläontologie, Bonn; LS PWL, Naturhistorisches Museum, Landessammlung für Naturkunde Rheinland Pfalz, Mainz; MB.E., Museum fur Naturkunde Institut für Paläontologie, Berlin; MCZ, Museum of Comparative Zoology, Harvard University; MNHN, Museum National d'Histoire Naturelle, Paris; SM, Sedgwick Museum of Geology, University of Cambridge; UI, University of Illinois, Urbana; USNM, United States National Museum, Washington.

TAXONOMIC APPROACH

A computer-based hypothesis of Ordovician asterozoan phylogeny was provided by Shackleton (2005), and selected genera from the span of asteroid history were treated in Blake et al. (2000) and Blake and Hagdorn (2003). Although published before computer-based techniques were available, important interpretations of early asterozoan history also were provided by Ubaghs (1953), Kesling (e.g., 1969, 1971a, 1971b), and McKnight (1977).
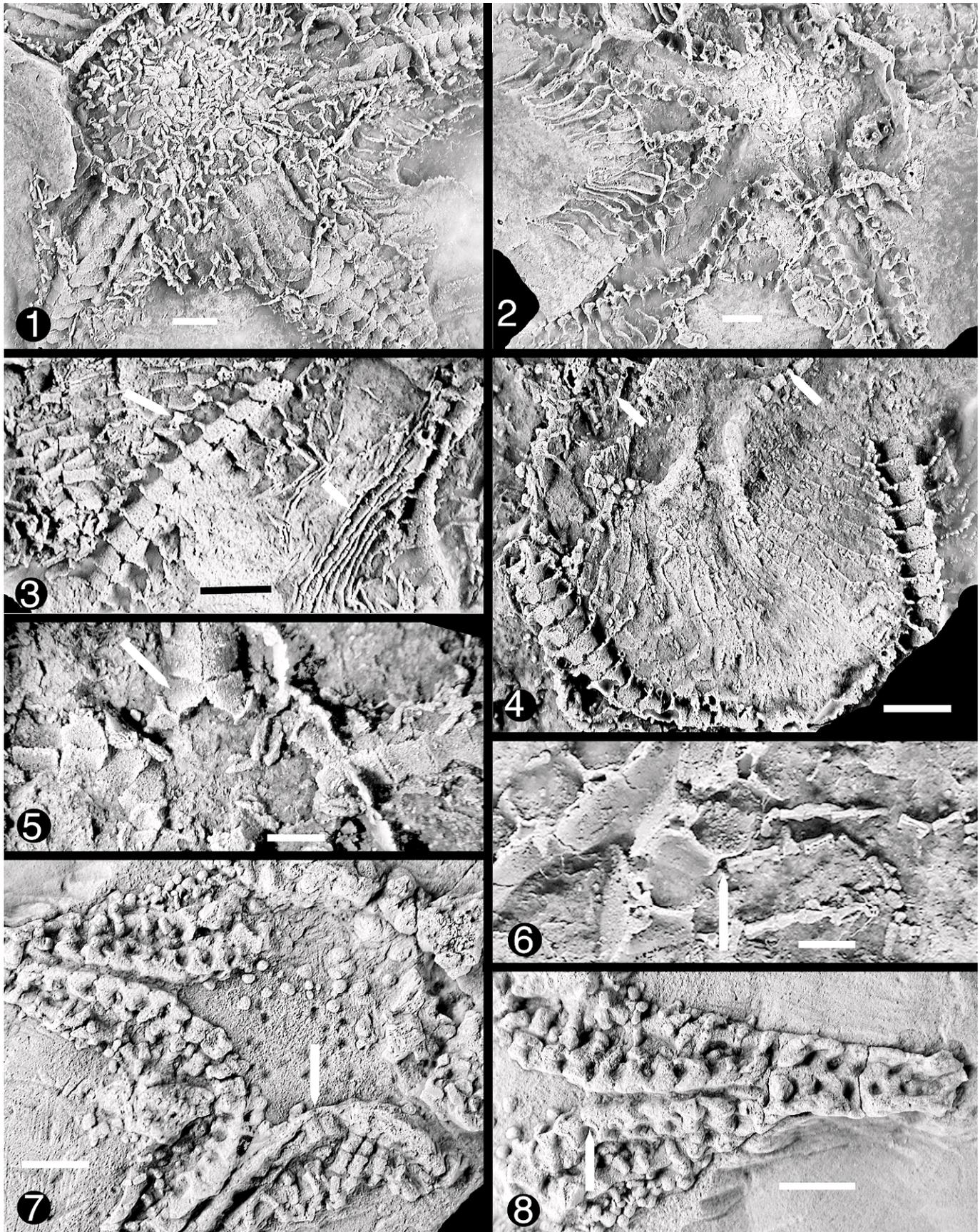
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FIGURE *1—1, 2, Chinianaster levyi* Thoral, lectotype FSL 168691, dorsal and ventral views, skeletons in approximate life position, but in the ventral view the large radial channel is flattened and ambulacrals are pulled apart approaching the mouth frame; mouth frame ossicles, which would have been closely situated in

In light of the divergent views expressed in the literature, a large data matrix (176 binary characters, 72 taxa) was developed and analyzed in the course of preparation of the present paper. The emerging configurations echoed inconsistencies among the earlier studies, positioning proving somewhat unstable with limited changes in character treatment and taxon inclusion. Inconsistent results reflect a "bad" fossil record (sensu Jefferies, 1986, p. 10) in that fossils are few and complex in construction. Species vary in subtle but important ways (e.g., positioning of ambulacrals across arm midlines), and many evolutionary changes were gradual (e.g., positioning of ambulacrals and adjacent ossicles; emergence of podial pores, Haude, 1995; Blake, 2000a). Taphonomic events disrupted the imbricate, articulated elements that form the flexible asterozoan body. Widely scattered distribution of specimens among museums limits access and ongoing review of interpretations. Finally, varied asterozoans are first recorded from within a limited Ordovician stratigraphic interval, implying a rapid period of diversification of skeletonized lineages and narrowing the ideal interval for sampling.

In studies directed toward the development of reliable phylogenetic results, Heath et al. (2008, p. 239) argued "extensive taxon sampling is one of the most important determinants of accurate phylogenetic estimation." Reliable phylogenetic results for the interpretation of early asterozoan diversification calls for a much larger, well-preserved representation from within the seemingly narrow Ordovician diversification interval. Given what is known of global geology, attaining this goal lies well into the future, if it can be attained at all.

In a contribution developing approaches to taxon selection for phylogenetic analyses, Brusatte (2010) noted that paleontologic studies commonly address relationships among accepted clades of higher taxa. Discussions in this paper focused on exemplar sampling approaches for the ingroup clades; unfortunately, reliable in-groups are not readily available for Paleozoic asterozoans, and phylogenetic interpretations for those that have been recognized are sketchy because of the limitations of the fossil record. Further, although the Asterozoa are deemed monophyletic, no reliable outgroup taxon is available for the interpretation of character polarities.

Evaluations of phylogenetic history of Spencer (1914–1940) were impaired by the limited understanding of stenuroids and the then-unavailability of somasteroids, these difficulties partially corrected in Spencer (1951). Emphasizing ambulacrals, virgals, and virgal-derivatives, four class-level taxa are recognized, consisting of a basal Somasteroidea and derived Asteroidea, Ophiuroidea, and Stenuroidea. Character distributions are complex enough to allow arguments of paraphyly or polyphyly for all three derived clusters; consistency, however, calls for uniform treatment, and therefore all three derived classes should be accepted as monophyletic at the class level, as is followed here, or multiple plesions of uncertain affinities should be recognized for all. Taxon

recognition and phylogenetic reconstruction within the four classes are left for the future.

CONCEPT OF THE ASTEROZOA

The concept of the Asterozoa of Spencer and Wright (1966) is essentially unaltered here. Asterozoan body form is more or less flattened and stellate, the near-oral ambulacra of uniform morphology and radiating from a central, ventral mouth; the ambulacral ossicles and the associated tube feet are directed ventrally. The skeleton is of comparatively small (relative to body size) unfused skeletal elements. The three (sub)classes, Somasteroidea, Asteroidea, and Ophiuroidea of Spencer and Wright (1966) are augmented by the class Stenuroidea, based on the order Stenurida Spencer, 1951.

TERMINOLOGY AND HOMOLOGIES OF THE ASTEROZOA

Morphologic terminology is from Spencer and Wright (1966) and Blake and Hagdorn (2003). Skeletal homologies were reviewed by Shackleton (2005), and select concerns are revisited. "Ossicle" rather than the more typical echinoderm "plate" was used by Spencer and Wright (1966) and this usage is followed here, restricting plate-like to more or less flat ossicles. Primary ossicles are the more or less enlarged foundation ossicles of the body wall, and accessory ossicles are the spines, spinelets, granules, and pedicellariae seated on primaries.

In asteroids, paired ambulacral ossicles are positioned above adambulacrals and are partially obscured in ventral view (Fig. 6.1, 6.4). In ophiuroids, laterals articulate with the abradial (or "lateral") sides of the ambulacrals (Fig. 7.1, 7.2). In somasteroids, a series of rather simple, rod-like virgals extends laterally from each ambulacral (Fig. 1.1–1.4, 1.6–1.8). In stenuroids, one or two ossicles are emplaced between the ambulacral and an abradial, terminal member of the series (Figs. 2–4, 5.4, 5.8, 6.6, 7.3, 7.6). Terminology and interpretation of these ossicles differ in the literature. The term "outer lateral" has been used for the adambulacral/lateral-like ossicle and "inner lateral" for the emplaced ossicle (Spencer, 1940; Spencer and Wright, 1966, e.g., fig. 68.1c). Based on the hypothesis of derivation of somasteroids from crinoids (Fell, 1963), the term metapinnule is available for the virgal series, and this terminology was employed by Spencer and Wright (1966, p. U14, U29, U78). The interpretation is important because it allows derivation of the ossicle series of stenuroids from somasteroid virgals, but the inferred homology is founded on an interpretation of phylogenetic history through crinoids, which has not been widely accepted, e. g., Shackleton (2005), who used the term podial plate. The lateral series of stenuroids are considered virgal derivatives (Blake, 2008) and therefore the term virgal series is preferred. Picking up on usage of Spencer (1940), the abradial virgal is the outer virgal and adradial ossicles are embedded virgals, identified as first embedded virgal and second embedded virgal as needed. Ambulacral, adambulacral/lateral, and first virgal series ossicles extend to the tip of the arm, either reaching or essentially reaching the proximal side of an almost
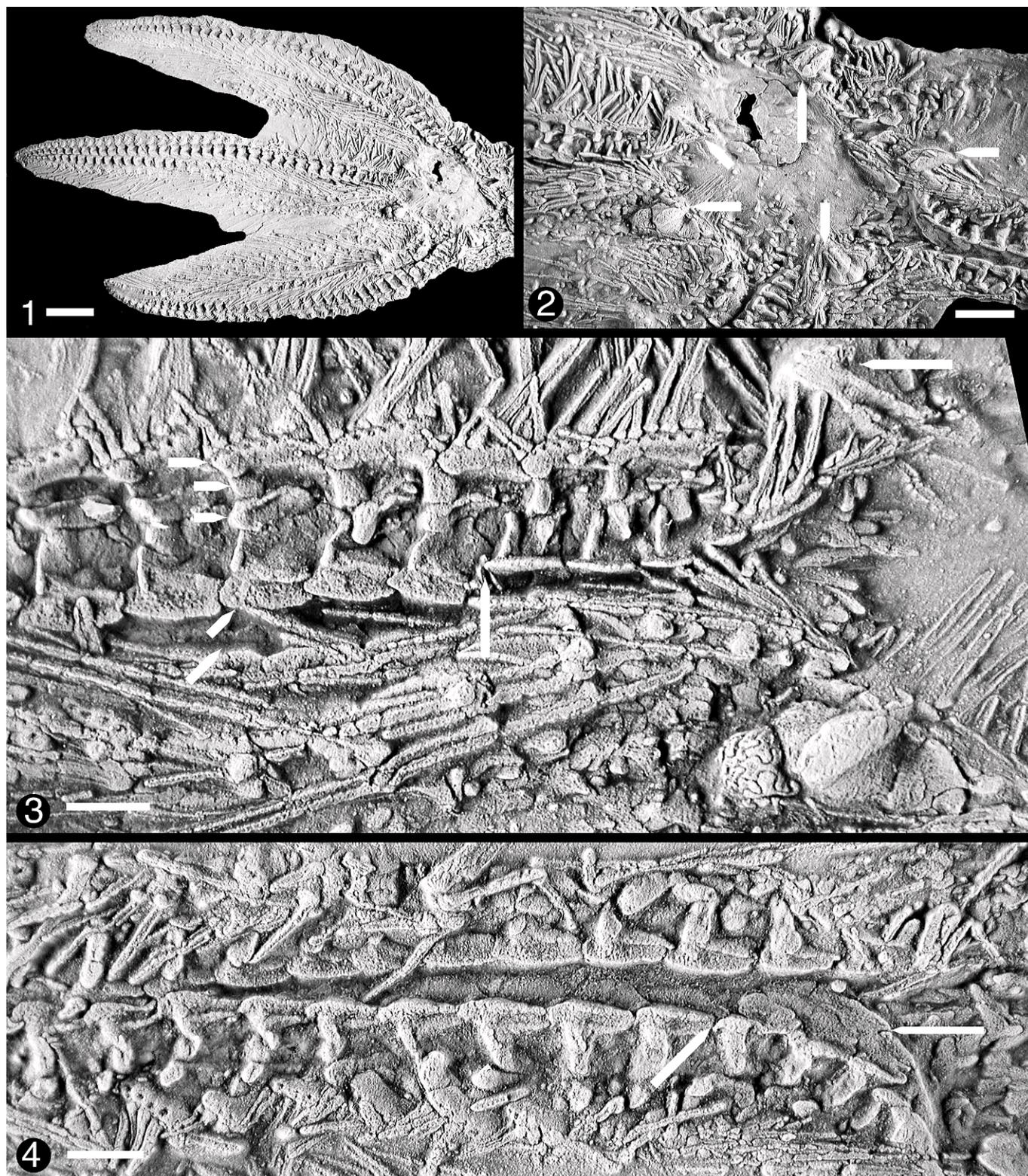

FIGURE 2—*Eriniceaster tenuispinosus* Lehmann, IPM Mt. 8; *1*, ventral view, two arms to right are not illustrated; *2*, disk area, arrows mark positions of MAO pairs, madreporite beyond lower left arrow, compare with Fig. *2.3*; *3*, five arrows to left, top to bottom, outer virgal, 2nd embedded virgal, 1st embedded virgal, cross-furrow muscle scar at the edge of the water-vascular channel, and the opposite side of the channel, the roof of the channel visible between arrows. Only the edges of the ossicular series below are exposed; most are collapsed into the sediment with only outer-virgal spines and small portions of outer virgals exposed. The vertical arrow at middle marks the transition from arm ambulacrals to those of the disk. MAO pair at upper right arrow, madreporite with MAO pair to lower right, spines extended into mouth area; *4*, arm to right of *2.1*, the radial channel opened proximally revealing the dorsal surfaces of the ambulacrals abutted to form the roof of the radial channel (arrow to right), the ventral edges of the radial channel closing distally, approximating the life expression. All three virgal series locally exposed but embedded virgals are disrupted and partially obscured by burial events and outer virgals and spines. Left arrow marks the distal edge of differentiated near-oral ambulacrals and probable position of transverse canal of water vascular system. Abactinals exposed within mouth frame to far right. Scale=10 mm for *1*; 5 mm for *2*; 5 mm for *3, 4*.

always unpaired so-called terminal ossicle. Distal portions of arms are not always preserved, and terminals cannot be recognized in many essentially intact arms, although recognition can be difficult because of the typically small sizes of arm tip ossicles. Ambulacrals are assumed to be homologous and plesiomorphic throughout the Asterozoa, and they provide reference for interpretation of the remainder of the skeleton. The radial water vascular canal lay along the ventral midline of the paired ambulacrals, and it is supported by a skeletal channel. The madreporite is taken as homologous throughout the Asterozoa.

The asterozoan mouth frame consists of the ten proximal-most ambulacral ossicles, which are differentiated as mouth-angle ossicles (MAO). An unpaired torus occurs at the proximal tip of the MAO pair of some asterozoans, and an unpaired odontophore braces the dorsal distal MAO contact area of many asteroids. Still not satisfactorily resolved issues surrounding the derivation of the odontophore were treated in Fell (1963, p. 401), Spencer and Wright (1966), Blake et al. (2006), and Blake (2008). The first ossicle of the ambulacral series beyond the MAO is the circumoral.

One or two differentiated framework ossicles, traditionally termed marginals, form the lateral edges of many asterozoans, but apparent series number and ossicular size, form, and even presence vary enough to have led to differing interpretations of series genesis (Spencer, 1918, p. 126; Spencer, 1940, p. 508; Spencer and Wright, 1966, p. U23; Shackleton, 2005, p. 39). The term marginal and an assumption of homology are retained within asteroids. Based on overall form and position, asteroid marginal series arguably are homologous with those of the somasteroids in which they occur. The ambital frame found in a few ophiuroids was judged not to be homologous with those of somasteroids because in ophiuroids ossicles arise along the arm (Shackleton, 2005). Disk collapse during ophiuran preservation can superimpose disk edge ossicles in a potentially misleading manner reminiscent of an ambital framework (Spencer, 1925, p. 277; Fig. 7.5 in a stenuroid). Because of these difficulties, the term "ambital frame" is used descriptively without implication of homology.

In some asterozoans, ambital framework ossicles separate dorsal (abactinal) and ventral (actinal) ossicles, and the two ossicular groups usually are distinctive. Virgals of somasteroids have been considered homologous with actinal surface ossicles of asteroids (Shackleton, 2005) whereas virgal ontogeny, including positioning of series genesis and addition as well as morphologic expression, are judged sufficiently different from corresponding expressions of asteroid actinals as to favor a hypothesis of independent origins. There is no apparent reason not to treat abactinals of asteroids as derived through those of somasteroids and therefore asteroid abactinals and actinals must have had separate origins. A usually unpaired dorsal midarm carinal series and a dorsal disk primary circlet are found in some asteroids.

Most ophiuroids and stenuroids lack ambital framework ossicles to separate abactinal and actinal series, and body wall ossicles are uniform. Although body form of most stenuroids lacking a marginal frame appears to have been thickened, the disks of many ophiuroids are more or less flattened and therefore presumably subject to functional specialization, yet morphologic differentiation is not strong. Lack of differentiation is consistent with views of Spencer (1914, p. 37; Spencer, 1919, p. 180), cited from MacBride (1906, 1907), arguing that ophiuran dorsal disk interradii "grow round" onto the oral surface. Based largely on these considerations, body wall

ossicles in taxa without an ambital frame have a single phylogenetic origin.

UNCERTAIN ANCESTRY OF THE ASTEROZOA

Among most paleontologists, acceptance of a monophyletic pairing of asteroids and ophiuroids has not been an issue (e.g., Ubaghs, 1967); indeed, the two have been considered similar enough to warrant recognition at the "subclass" rather than the "class" level (Spencer and Wright, 1966). Evolving perspectives on the ancestry of the Asterozoa are seen in the work of Spencer (1914, 1951). In 1914, he agreed with the then-current view of a likely edrioasteroid ancestry, but he was skeptical in the later paper because somasteroids, which he considered basal within the Asterozoa at the latter date, lack the ambulacral groove of edrioasteroids. Subsequently, the notion of an edrioasteroid ancestry has been both rejected (e.g., Mooi and David, 2000) and accepted (e.g., Shackleton, 2005). The concept of a crinoid ancestry was noted and rejected by Spencer (1925, p. 243) but later developed from a different perspective by Fell (e.g., 1963), a viewpoint accepted by Spencer and Wright (1966) but widely regarded with skepticism (e.g., Philip, 1965).

Edrioasteroids and crinoids, like asterozoans, are constructed of a large number of small, radially directed ossicles, and these similarities provide fertile ground for phylogenetic speculation; however, known fossils do not bridge the morphological gaps between the closely abutted skeletal elements of edrioasteroids and crinoids and the flexible skeletons of asterozoans. Mouth frame constructions differ markedly. Further, the transition from a sessile or attached edrioasteroid or crinoid living with its mouth directed into the water column to a free-living descendent living with the mouth directed to the substrate is not bridged. In reviewing the uncertainties, Ubaghs (1953) found asterozoans to be of unknown derivation, and his viewpoint is retained here.

Presence of many Cambrian echinoderm types lacking morphologic intermediates, as well as existence of asteroid-like trace fossils significantly pre-dating the earliest-known body fossils (Mikuláš, 1992), argue that clear skeletal linkages between asterozoans and a more basal echinoderm group might never be found. A posited increase in calcification of the body wall through time (e.g., Spencer, 1914, p. 8; Schuchert, 1915, p. 31) would be consistent with an asterozoan record beginning with trace fossils, although weakly calcified extant species (e.g., Fig. 6.7) allow the possibility of secondary reduction.

Posited ancestral or outgroup taxa are seen as at least as likely to mislead as to enlighten.

AN ALTERNATIVE: ASTEROZOAN POLYPHYLY

Based on data from extant exemplars, some researchers over the years have argued that asteroids and ophiuroids are not sister taxa (Pisani et al., 2012), and even that somasteroids might have had an origin independent of those of other asterozoans (Paul and Smith, 1984, p. 469), the latter interpretation implicitly challenging any phylogenetic reconstruction beginning with a monophyletic Asterozoa. Only the fossil record is considered here, and a traditional paleontologic approach is followed; resolution is not attempted. Nevertheless, a number of arguments based on the fossil record support monophyly: Moving back in time, early asterozoans strongly converge morphologically, encompassing taxa considered not readily assigned to either surviving class (Spencer, 1914, p. 1, 19). Fossil Asterozoa sensu Spencer and Wright (1966) form a grouping readily separable from other known early Paleozoic echinoderms whereas no known fossil suggests intermediacy with any non-asterozoan. Reduction of the virgal series provides an objective marker for sequencing within the Asterozoa.
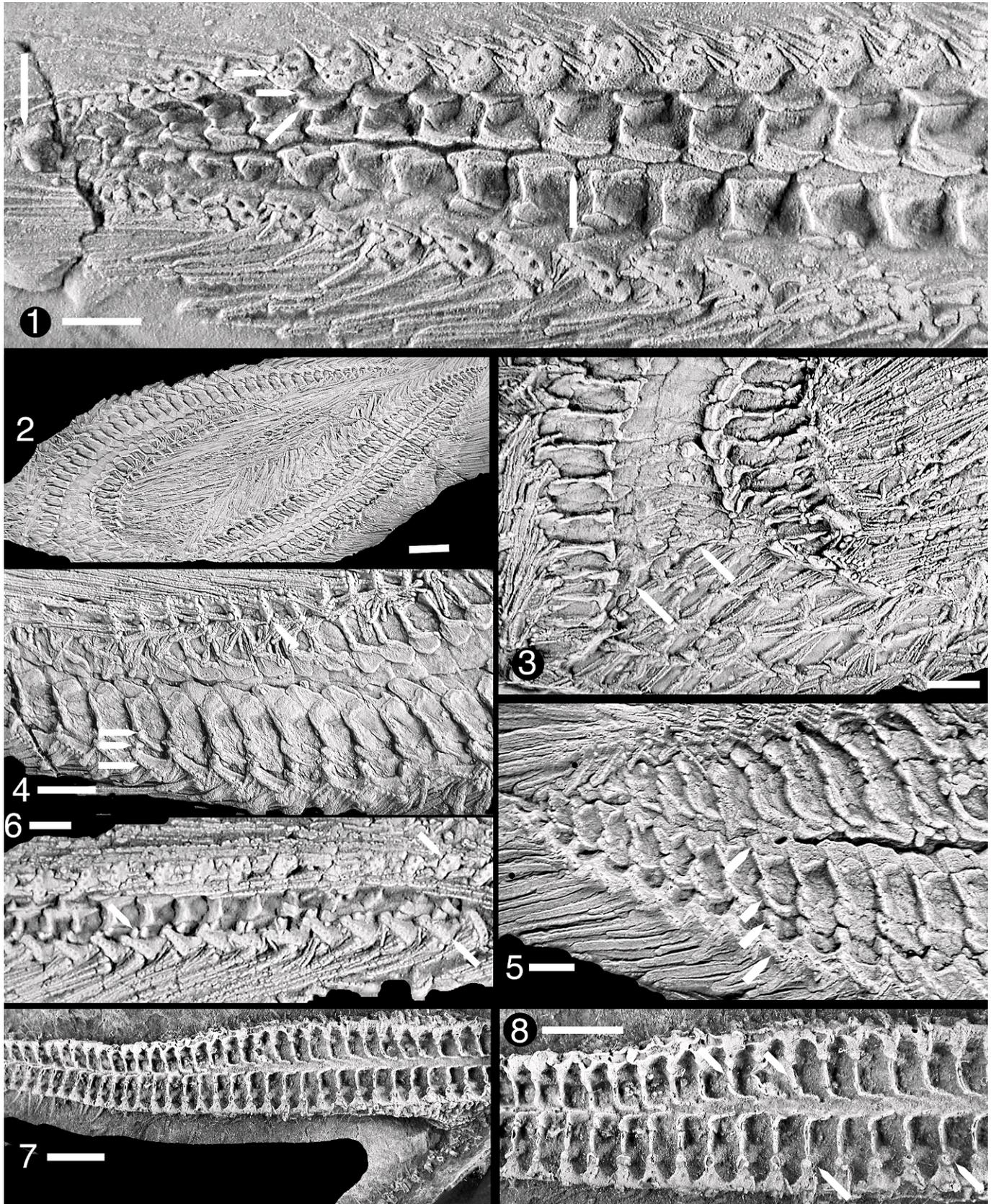
FIGURE *3—Erineaster tenuispinosus* Lehmann, *1*, IPM Mt. 8; ventral view of distal portion of medial arm of Fig. *2.1*; cresentic terminal at arm tip (left arrow); sequence of three arrows identify outer, 2nd, and 1st virgals; the 2nd embedded virgal is visible on series distal to the arrow but only on the first more proximal series; 2nd virgals are also visible on three successive midarm series on the opposite side of the arm at base of right arrow, which marks the overlap of successive ambulacrals as well as edges of cross-furrow muscle scars; the radial channel is slightly pulled apart for an interval distal to the arrow; *2–5*, IPM Esch

Finally, homeomorphy between genera with and those lacking what are here termed embedded virgals favors an integrated phylogenetic reconstruction. Nevertheless, because of ambiguity and in recognition of common usage, major divisions are treated as "classes" rather than "subclasses" and the concept of a comprehensive "class Stelleroidea" (Spencer and Wright, 1966) is not used.

<center>SIGNIFICANCE OF THE SOMASTEROIDEA</center>

If a satisfactory non-asterozoan outgroup is unavailable then phylogenetic polarization must be sought from within the Asterozoa. The parsimonious explanation for origin of ossicles intervening between the ambulacrals and putative adambulacral/laterals of a few early asterozoans is through reduction of the virgal series of somasteroids (Fig. 1) to one or two adradial embedded virgals and a differentiated and enlarged abradial outermost virgal (Figs. 2–4). Virgal reduction was the key innovation that in turn was followed by a period of rapid early diversification and parallel experimentation (i.e., homoplasy) among closely related lineages. Three separate class-level lineages ultimately were derived directly or indirectly from the somasteroid ancestry.

Somasteroids and the significance of virgal ossicles have been subject to differing interpretations since their recognition and assignment to a basal position within the Asterozoa (Spencer, 1951). When a two-branched asterozoan divergence pattern has been chosen, somasteroids have been assigned to the ophiuran branch (e.g., Blake, 2000a; Shackleton, 2005) whereas Mooi and David (2000) favored a more complex history in which a broadly Y-shaped somasteroid diversification encompassed the base of the Asterozoa together with those of both asteroids and ophiuroids. With the addition of the Stenuroidea, the view of Mooi and David (2000) anticipated interpretation here.

<center>CONSTRUCTION OF THE ASTEROZOA</center>

For evaluation, the asterozoan body is divided into four sections, the arms, mouth frame, disk, and madreporite (Spencer, 1914, p. 9; Spencer, 1925, p. 246). Arm arrangements provide the clearest apomorphies, an interpretation largely implicit in the diagnoses of Spencer (1951, p. 91, 106, 121), although less so for the Stenurida (p. 110). Mouth frame and body wall development augment arm characters, but expressions are complex. Madreporite expression is varied among somasteroids thereby allowing different phylogenetic interpretations, which is consistent with complexities recognized by Spencer (1914–1940).

Construction of the ambulacral column.—Prior to the recognition of the somasteroid genera and their potential phylogenetic significance, reconstruction of asterozoan diversification focused on the surviving classes, the asteroids and the ophiuriods. A notion of a basal "root-stock" was favored (Spencer, 1914, p. 1, 19, 20) because if "we trace the history of the forms (i.e.,

asteroids and ophiuroids) backwards we find that the difference between them tends to disappear" (p. 9). Important was that extant asterozoans can be separated into two groups, first the "graspers" (i.e., asteroids), in which tube feet are used in locomotion and for opening bivalve shells, a behavior enabled by the arching of the furrow, and secondly the "wrigglers" (i.e., ophiuroids), in which locomotion is accomplished by means of arm movements, the tube feet much reduced (MacBride, 1906; Spencer, 1914, p. 9; Spencer, 1919, p. 178). Elsewhere in his texts, MacBride did recognize more diverse feeding habits among asteroids, but these remain within his basic functional concept.

Permanent vaulting of the ambulacral furrow identifies asteroid affinities, the arched ambulacral ossicles supported by the adambulacrals, which border the furrow. The significance of vaulting to asteroid organization was developed by O'Neil (1989, 1990), her argumentation later extended to the full history of asteroid diversification (Blake and Rozhnov, 2007). Like the asteroid pattern, the complex, closely articulated arm construction of modern ophiuroids also emerged during the Ordovician (e.g., Spencer, 1925, p. 246–262), it consisting of either paired or offset ambulacrals enclosed by shield-like laterals. Arm ambulacrals and laterals are largely restricted to a single plane, although laterals of early ophiuroids were thought to have considerable mobility (e. g., Spencer, 1925, p. 256).

Morphology of the ambulacral ossicles of asteroids and ophiuroids was found to differ, the ambulacrals of early asteroids are similar to the floor plates of edrioasteroids (Spencer, 1914, p. 21; Spencer, 1919, 185, 186). Ambulacral positioning across the arm midline among early asteroids is "irregularly alternating" (p. 19), an arrangement found in somasteroids and stenuroids and therefore plesiomorphic among asteroids. Ophiuran ambulacrals are more complexly differentiated, abandoning the floor plate appearance. Ophiuran configurations were thought to relate to life mode in which tube feet were less used for locomotion (Spencer, 1914, p. 9, 15), although Paleozoic species retained larger podial sizes than those of recent species (Spencer, 1925, p. 262).

Stenuoids are recognized based primarily on presence of an extra ossicle (rarely two) between the ambulacrals and an outer, somewhat variably differentiated ossicle. In contrast with the flexible but robustly interconnected ambulacral systems of asteroids and ophiuroids, articular faceting of stenuroids is delicate, providing a different and more plesiomorphic approach to asterozoan movement. Arm constructional differences among classes imply habit differences, but differences that seemingly lie within the context of generalist feeding among extant asterozoans (Jangoux, 1982; Warner, 1982). The embedded virgals of stenuroids provide ample space for podia and ampullae, configurations more like those of asteroids than of the later ophiuroids.

Construction of the mouth frame.—Construction, function, and inferred evolutionary differentiation of the mouth frames of the comparatively robust early asteroids and ophiuroids were

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599: *2*, complete specimen, ventral surface; *3*, ventral view of base of an arm with the dorsal surface of the disk exposed within the mouth frame; the dorsal surface is reticulated, arrows mark proximal edge of roof of radial water channel; *4*, conical bases of abactinal ossicles at top with spines largely obscuring the body wall, 1st and 2nd embedded virgals and outer virgal marked by left arrow sequence, the edges of the boot-shaped spinose outer virgals imbricating proximally; laterally directed outer virgal (single arrow, medial above) differs from outer virgal orientations on opposite side of furrow; although orientation might in part reflect the death event, correlated, consistent alignments argue mobility in life; the radial channel gradually closes distally; *5*, arm tip, spines are mostly those of the outer virgals; sequence of arrows top to bottom show the ambulacral cross-furrow muscle scar, 1st and 2nd embedded virgals, boot-shaped spine-bearing outer virgal overlapping proximally. The radial channel is slightly opened toward right beyond the arrow sequence; *6*, IPM Hubo 159, ventral view of a portion of an arm, arrows to right identify the outer virgal series, the series above partially obscured by ossicular debris; arrow to left marks the two embedded virgals, here partially displaced; *7*, *8*, *Ptilonaster princeps* Hall, AMNH 5945; radial channel was closed in life as in ophiuroids but taphonomically opened more proximally; J-shaped transverse ridge with transverse canal is like ambulacrals of asteroids, the transverse ridge abutting the apparent embedded virgals (Fig. *1.8*, upper arrows) although expression is difficult to determine on other ossicles. The linear series of uniform nodes were though to be skeletal by Rudemann (1916), but consistency of shape and texture might indicate blunt-tipped podia (lower arrows). Scale=2 mm for *1*, *5*, *6*; 10 mm for *2*; 5 mm for *3*, *4*, *7*, *8*.
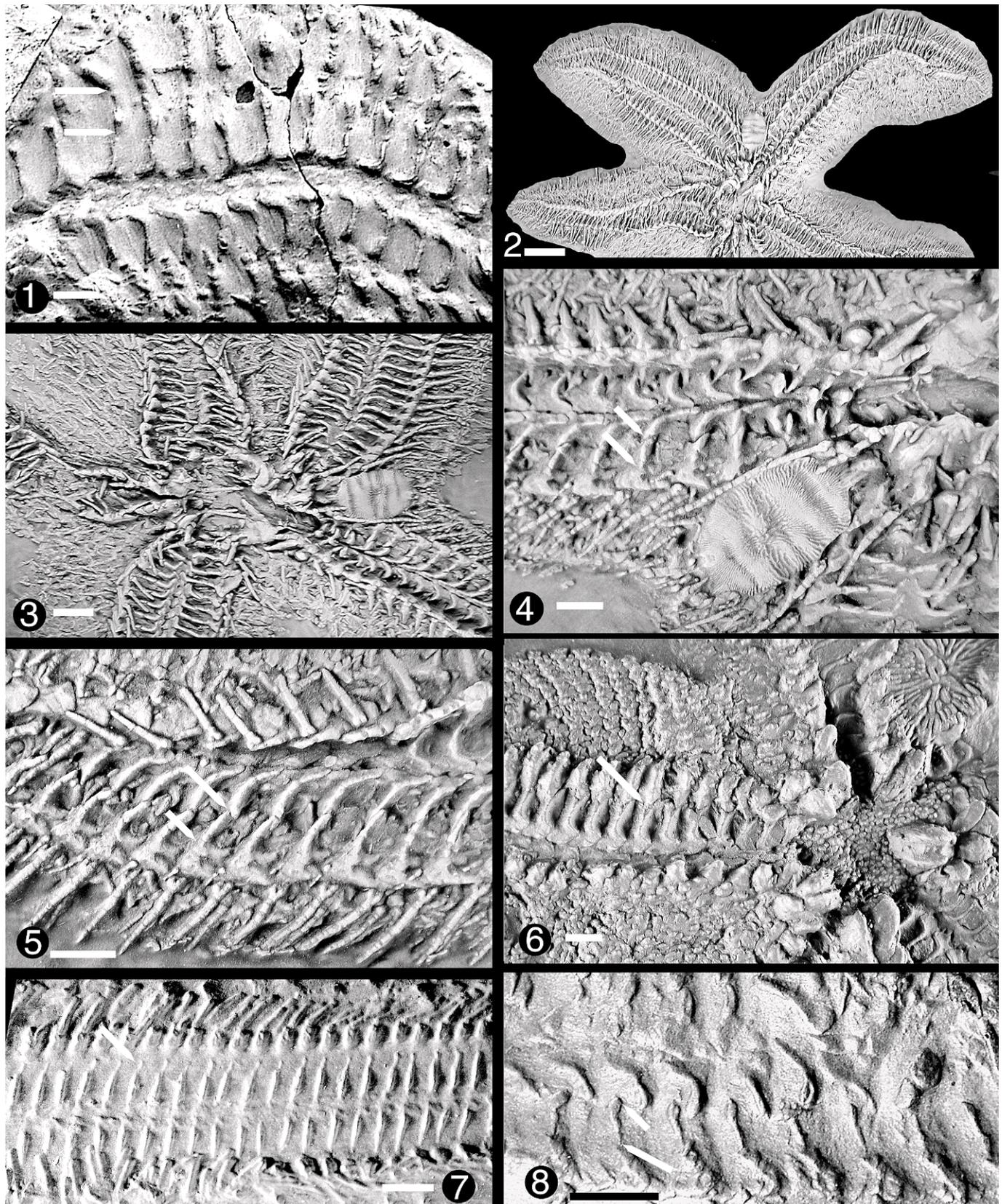
FIGURE 4—1–6, *Palasteriscus devonicus* Stuertz: *1*, holotype MB.E. 889, ventral view of arm interval, arrows indicating adradial and abradial ends of inferred embedded virgal; *2–5,* IPN Hubo 157: *2*, arms thickened in life, now flattened, madreporite in upper interbrachium; *3*, central portion of disk; the mouth frame is differentially distorted, the near-proximal interval of the left ambulacrum is still near to the inferred life orientation whereas the medial ambulacrum (above) is distorted; the radial channel is in the closed inferred life orientation of the lower right ambulacrum but spread by compaction in the lower left; *4*, the madreporite dominates the central disk, arrows mark adradial and abradial sides of an embedded virgal; the rectangular outer virgals have large muscle scars; the radial water

extensively reviewed by Spencer (1914, 1919, 1925), and the more delicately arranged stenuroid and somasteroid genera were treated in later studies (Spencer, 1940, 1951). Interpretation is difficult because arrangements are transitional among taxa and expressions are commonly obscured either by sediment or remnants of the dorsal skeleton, with the delicate mouth frames of somasteroids and stenuroids being particularly vulnerable.

Mouth frames are differentiated proximal ambulacral column ossicles. An enduring issue has been the precise source of the mouth angle ossicles, now effectively demonstrated to have been derived from the ambulacral series (Mooi and David, 2000). As a part of extended treatment of mouth frame construction, Spencer (1925, p. 268, 270) interpreted the dorsal aspect of the Ordovician ophiuroid *Lapworthura* Gregory, 1897, as asteroid-like whereas the ventral configuration was found to be distinctive. The ventral proximal ambulacra and mouth frame arrangement of the Ordovician asteroid *Phyrtosaster* Blake, 2007 (Fig. 7.8) is similar to that of the ophiuroid *Stenaster* Billings, 1858, (Fig. 7.7), and the Y-shaped internal configuration of the mouth frame of *Jugiaster*, Blake, 2007 (Fig. 5.5) is similar to those of many early ophiurans (Fig. 7.2), with enlarged mouth frame regions associated with buccal podia. In external aspect, the appearance of the mouth frame of this genus is closely arranged and bud-like in appearance, as is typical of asteroids.

Like the arms, the mouth frames of stenuroids are less robustly articulated than those of the surviving classes. Arrangement might indicate that feeding among early asterozoans took advantage of a more readily distended mouth frame (Spencer, 1934, p. 443, 456), although echinoids ingested intact by a modern asteroid with a closely articulated jaw frame (Blake, 1982) demonstrates delicate articulation is not necessary for feeding on larger particles.

Mouth frame construction offers considerable taxonomic potential, but diversity of expression is not yet well understood.

Construction of the body wall.—Early in his monograph, Spencer (1914, p. 7; Spencer, 1919, 180) argued that the stellate shape of asteroids predated the disk and cylindrical arms of ophiuriods, a conclusion thought supported by embryology. Basing interpretations in part on the arguments of MacBride (1906), the disk of asteroids was envisioned as having been built through the adhesion of the arms, as evidenced by the presence in extant species of soft interradial septa, these calcified in some taxa (Spencer, 1919, p. 180). Presence of such a septum in the Hudsonasteridae, with its small, comparatively heavily calcified disk, was questioned by Spencer (1919, p. 180), but any process of arm merger must have had some beginning.

Ophiuran arms did not merge in such a manner, rather dorsal interradii were envisioned as growing toward the oral surface (Spencer, 1919, p. 180–182), conveying the madreporite from a lateral to a ventral position, an interpretation judged further supported by ontogeny. Evolutionary history of madreporite positioning nonetheless is difficult to determine (Spencer, 1919, p. 170). True marginal ossicles are not possible with the ophiuran growth habit, which would dictate separation of the two surviving classes prior to the origin of marginal series. As apparent marginals are found in some somasteroids, separation might predate stenuroid organization. Differentiation of growth mode was thought to relate to feeding, the earliest asterozoans having combined ciliary and podial feeding whereas the enlarged disk of

ophiurans was related to a mud-eating habit (Spencer, 1919, p. 170, 195). Nonetheless, although skeletonized interbrachial webs seem typical among ophiurans, well-defined disks cannot always be recognized (e.g., specimens of *Furcaster* Stuertz, 1886, *Lapworthura*, *Pectenura* Haude, 1982, *Stenaster, Taeniaster* Billings, 1858), these constructions implying that differentiation of well-defined disks described by MacBride (1906) had not yet emerged. Potentially misleading are portions of disk-like collapsed dorsal surfaces extended into interbrachia (e.g., Fig. 7.5); different expressions among interbrachia and specimens of a single species provide guides to interpretation.

Somasteroids, with clearly differentiated virgal ossicles, cannot have had the ophiuran growth habit, whereas growth form, especially in occurrences with inferred deep interbrachial reentrants (Spencer and Wright, 1966, fig. 39.4), would allow the early emergence of asteroid interbrachial partitions.

Stenuroid genera differ; *Bdellacoma* Salter, 1857, *Embolaster* Blake, 2008, and *Rhopalocoma* Salter, 1857, are asteroid-like in growth, whereas *Pradesura* Spencer, 1951, has a well-defined disk and that of *Eophiura* Jaekel, 1903, is more web-like. Interbrachia of *Eriniceaster tenuispinosus* Lehmann, 1957, *Klasmura* Ruedemann, 1916, *Pectenura*, and *Stuertzaster* Etheridge, 1899, are either web-like or essentially lacking; the latter genera also lack an ambital frame.

Asterozoan body wall skeletal elements are highly varied and similar expressions occur in different classes. Nevertheless, dorsal surfaces of *Archegonaster* (and other somasteroids) and certain early ophiuroids (and asteroids) led Mooi and David (2000) to interpret disorganized arrangements (commonly reticulate in somasteroids) of many small ossicles as plesiomorphic and potentialy related to such basal echinoderms as edrioasteroids. Differentiated carinals found in both asteroids and ophiuroids might have been derived from a common ancestor (Hotchkiss, 1993), but alternatively, they might reflect a constructional response to shingling dorsal abactinal ossicles against a vaulted midline (Blake and Rozhnov, 2007). Broadly similar primary ossicles of the body wall and superficially similar spinelets, scales, and platelets are widely distributed among asterozoans. Pedicellariae have been recognized in only a very Paleozoic few asteroids and stenuroids; nevertheless, MacBride (1906, p. 492) wondered if small hooks of certain extant ophiuroids might represent pedicellarial "vestiges."

Madreporite occurrences.—Although a hydropore seems fundamental in echinoderms, expression among asterozoans is varied. Madreporite presence cannot be established for all species, which led to the idea that the passageway could have been limited to small, unrecognized openings (Spencer, 1914, p. 35). Madreporic positioning in those asterozoans in which it has been recognized ranges from near to the mouth frame, as is typical of ophiuroids and some stenuroids (Figs. 2.3, 4.2, 7.5) to near the dorsal center of the disk, as is typical of asteroids. Disk growth in ophiuriods was thought to have forced the madreporite from a lateral to a ventral position (Spencer, 1914, p. 37) whereas a primitive lateral position was preferred by Fell (1963, p. 407). Among somasteroids, the madreporite is dorsal in *Archegonaster* and bears asteroid-like radiating ridges and grooves; it is ventral in *Chinianaster* Thoral, 1935, although possible taphonomic displacement was proposed by Spencer (1951, p. 99). The

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vascular canal is closed at this interval; prominent spines are unusual in this specimen; *5*, midarm interval, arrows marking sides of embedded virgals, radial water vascular channel closing distally to left; well-exposed outer virgals are rectangular with well-developed muscle scars; *6*, LS PWL 1995/267, outer virgals are upright and closely abut ambulacrals; any embedded virgals are collapsed into disk, or a separate taxon might be represented with the essential *Palasteriscus* morphology; converging ambulacra at mouth frame are close to life positions; *7*, *Jaekelaster* Stuertz, IPN Esch 462, ventral view of arm interval with apparent embedded virgal (arrow); *8*, *Echinasterella* Stuertz, BMNH E3489, ventral view of arm interval, midarm above, with apparent embedded virgal (arrows). Scale=3 mm for *1*, *4–8*; 10 mm for *2*; 5 mm for *3*.
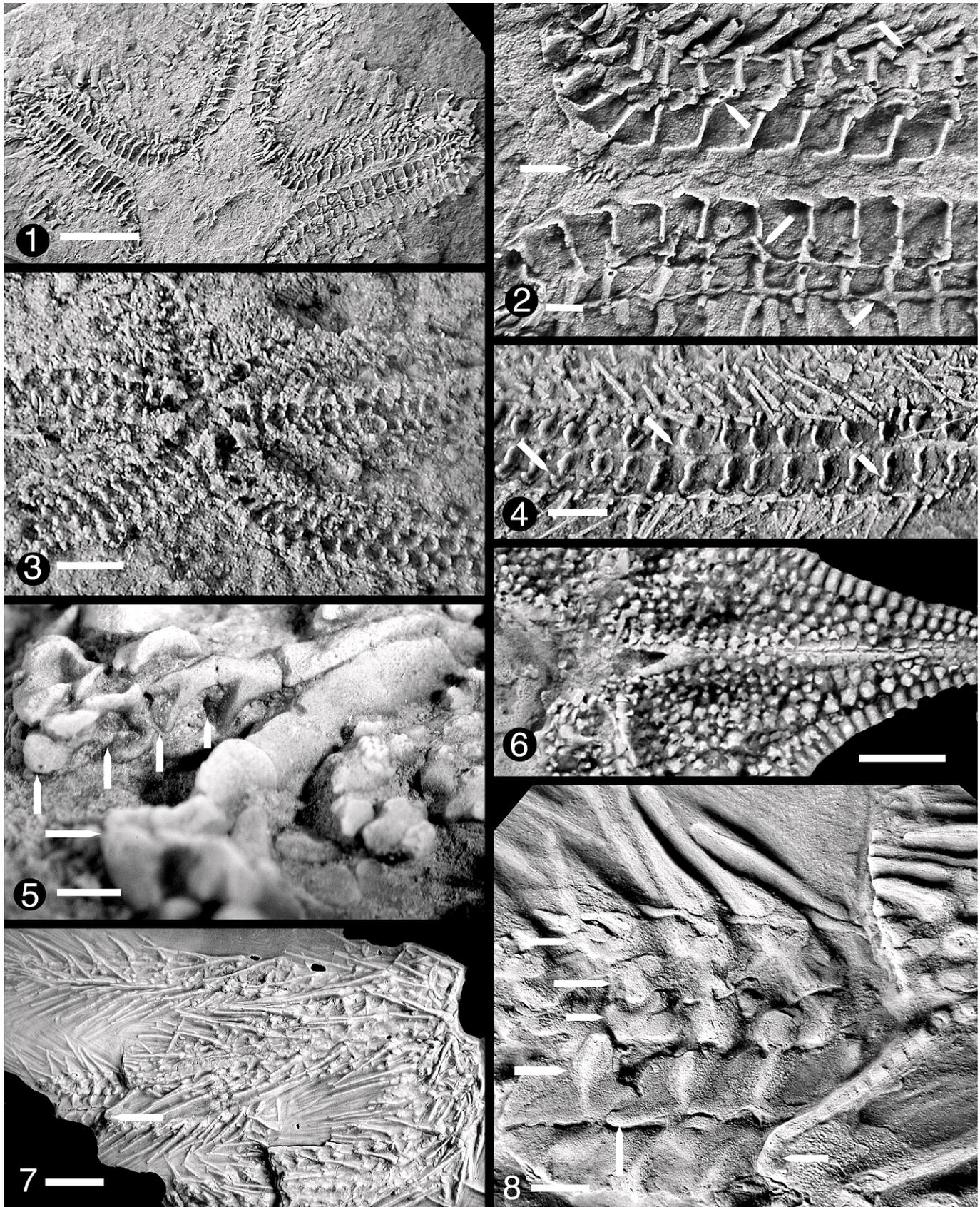
FIGURE 5—*1, 2, Rhopalocoma pyrotechnica* Salter, BMNH 40293: *1,* ventral view, specimen flattened, the mouth frame widely dilated; *2,* articulation facets mark distal edge of vaulted mouth frame region (left arrow); embedded virgals (medial arrows); T-shaped outer virgals (right arrows), outer virgals articulated at Y-shaped joints with embedded virgals; *3, 4, Bdellocoma vermiformis* Salter: *3,* BMNH E1480, central disk region and proximal arm intervals; *4,* BMNH 40297, embedded virgals (lower arrows); radial channel (upper arrow); *5, 6, Jugiaster speciosus* (Miller and Dyer): *5,* CMC P56030, inclined dorsal view of mouth

surfaces in two specimens of *Chinianaster* appear granular, although appearance might result from taphonomic alteration. The madreporite has not been recognized in *Villebrunaster*, which is known from comparatively numerous specimens. Contrasting madreporic expressions among somasteroids allows different interpretations of basal positioning within the derived classes.

TAXONOMIC OVERVIEW 1: THE CLASS SOMASTEROIDEA

Somasteroid morphology.—The Somasteroidea is most readily recognized by the presence of series of rod-like virgal ossicles extending laterally from each ambulacral ossicle; other ventral primary ossicular types are lacking. Fewer virgals are found on the more distal ambulacrals and therefore series addition continued through life. Alignment of ambulacrals and virgals indicates that no permanent ambulacral furrow was present, although skeletal configurations imply flexibility, including the potential ability to form a facultative furrow. Podial basins are large, and the radial canal is usually large and closed ventrally. The dorsal surface is constructed of small, similar ossicles. An ambital frame (i.e., "marginals") is present or absent. Mouth frame ossicles appear relatively little differentiated. Recognized somasteroid genera are comparatively few and of generally uniform morphology, although in *Archegonaster*, the virgal adjacent to the ambulacral is enlarged and broadly similar to adambulacrals and laterals of asteroids and ophiuroids. Accessories are few, although granules occur in *Archegonaster*. Somasteroid skeletal elements generally were small and lightly constructed with relatively delicate articular faceting as compared to expressions of asteroids and ophiurids. Most fossils are partially disarticulated and disrupted in part because of construction, likely contributing to the sparse fossil record.

Discussion.—As viewed in ventral aspect, the radial channel of many somasteroids is more or less dilated, leading Spencer (1951, p. 98) to conclude that the channel of *Chinianaster* was "almost closed." Here, the markedly differing degrees of closure among specimens is accepted as evidence of displacement during sediment compaction from a closed condition. Closure in taxa with ventral radial canals provided protection, see below.

Generic summary.—Five genera, *Archegonaster* Jaekel, 1923, *Chinianaster* Thoral, 1935, *Ophioxenikos* Blake and Guensburg, 1993, *Thoralaster* Shackleton, 2005, and *Villebrunaster* Spencer, 1951, are known from fairly well preserved material whereas *Catervaparmaster* Blake, 2000b, was proposed for poorly preserved material that exhibits morphologies not known elsewhere. The family Archophiactinidae was included in the Somasteroidea by Spencer and Wright (1966), although the three included genera lack virgals. The Ordovican archophiactinid was transferred to the Ophiuroidea (Shackleton, 2005), and inclusion of the Silurian and Devonian genera is also rejected here.

THE KEY INNOVATION: REDUCTION OF THE VIRGAL SERIES

Criteria for interpretation of the embedded ossicles as virgal derivatives were reviewed in Blake (2008); the interpretation was not original although it traditionally received mixed support. Interpretation is parsimonious; derivation of the diversity of stenuroid genera through reduction from the virgal series of somasteroids does not require repeated parallel emergence of a new ossicular type. The classifications of Spencer and Wright (1966), Hotchkiss (1976), and Shackleton (2005) document a number of pairs of genera that differ most distinctly from one another based on presence or absence of

embedded ossicles, yet the pairs distinctly differ from one another in other expressions (e.g., *Pradesura* and *Paleura* Spencer, 1951, vs. *Klasmura* and *Stenaster*). A hypothesis of origins other than through reduction from virgal series demands natural selection to have selected both for and against embedded ossicles in otherwise similar lineages (and therefore presumably in aspects of adaptive advantage) among otherwise dissimilar morphologic pairs. Presence of two embedded ossicles in two dissimilar Devonian Hünsruck Slate taxa further supports derivation from virgal-series ossicles (Figs. 2.3, 2.4, 3.1–3.6, 5.7, 5.8). Finally, because embedded ossicles are not known from rocks younger than Carboniferous, hypotheses other than reduction require the selective advantages among disparate taxa to have disappeared through time.

Adambulacrals of asteroids and laterals of ophiuroids have been considered virgal derivatives (Spencer and Wright, 1966, p. U28, U29), although their specific homologue within the virgal series of somasteroids is problematic. If the two surviving classes do not represent a single monophyletic branch, then presence of a single ossicle is the only reason to favor derivation from the same ossicle of the somasteroid series; this argument is deemed weak and retention of both terms is preferred.

The posited derivation of embedded ossicles places somasteroids in the basal position in asterozoan diversification. Presence of two or rarely three ossicles lateral to the ambulacral is interpreted as the monophyletically derived key innovation of the Stenuroidea. The more familiar asteroids and ophiuriods are considered first.

TAXONOMIC OVERVIEW 2: THE CLASS ASTEROIDEA

Apomorphies of the Asteroidea.—Adambulacrals are the only remnants of the virgal series, these robust, typically wider than long, and forming more or less coin-like overlapping series edging the ambulacral furrows. Ambulacrals are irregularly alternating in early Paleozoic species and permanently vaulted throughout the arm length, thereby forming the ambulacral furrow. Podial pores are absent from early Paleozoic species but begin to emerge in mid-Paleozoic (Blake, 2000a). Ambulacrals are either recessed and articulating only near the dorsal adradial corner of the adambulacral, or they are fully dorsal and articulated more or less across the dorsal surface of the adambulacrals, the two paired rather than alternating in early species. The radial water channel is small and not skeletally closed. Articular construction of the ambulacral column is robust and therefore relics of furrow arching is retained in almost all fossils. Citing edrioasteroids, Spencer (1914, p. 21; Spencer, 1919, p. 183, 186; Spencer, 1940, p. 508. 515) viewed early asteroid and stenuroid ambulacrals as "mere flooring-plates," and as such they differ from more complex ophiuroid ambulacrals. The mouth frame is vaulted, and circumorals are more or less clearly differentiated, but many are similar to those of somasteroids. One or two ambital frame (=marginal) series are present in all know stem-group taxa.

Other morphology.—Body forms are varied and arms are not sharply set off from the central disk region. Abactinal ossicles are varied, and carinals and primary abactinal circlet series commonly are differentiated. The madreporite usually is dorsal where recognized (Spencer, 1914, p. 20, although ventral occurrences have been posited, Spencer, 1922, p. 216, 225, 236). Actinals can be numerous, few, or lacking. An axillary is

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frame, proximal ambulacrals diverge, providing space for enlarged buccal podia (three arrows to right); MAO, arrows to left; *7, 8, Hystrigaster horridus* Lehmann, BMNH E13633: *7*, entire specimen; arrow identifies tip of spine identified at lower right of Fig. 5.8; *8*, ambulacral series lies to left of lower right arrow; body wall spines and spine bases lie above and to right of arrow, probable outer virgal spines above ambulacral series; left arrows from top to bottom are the outer virgal, 2nd and 1st embedded virgals, ambulacral; vertical arrow at overlapping, articular flange; also at crack at arm midline. Scale=5 mm for *1–5, 7, 8*; 3 mm for *6*.
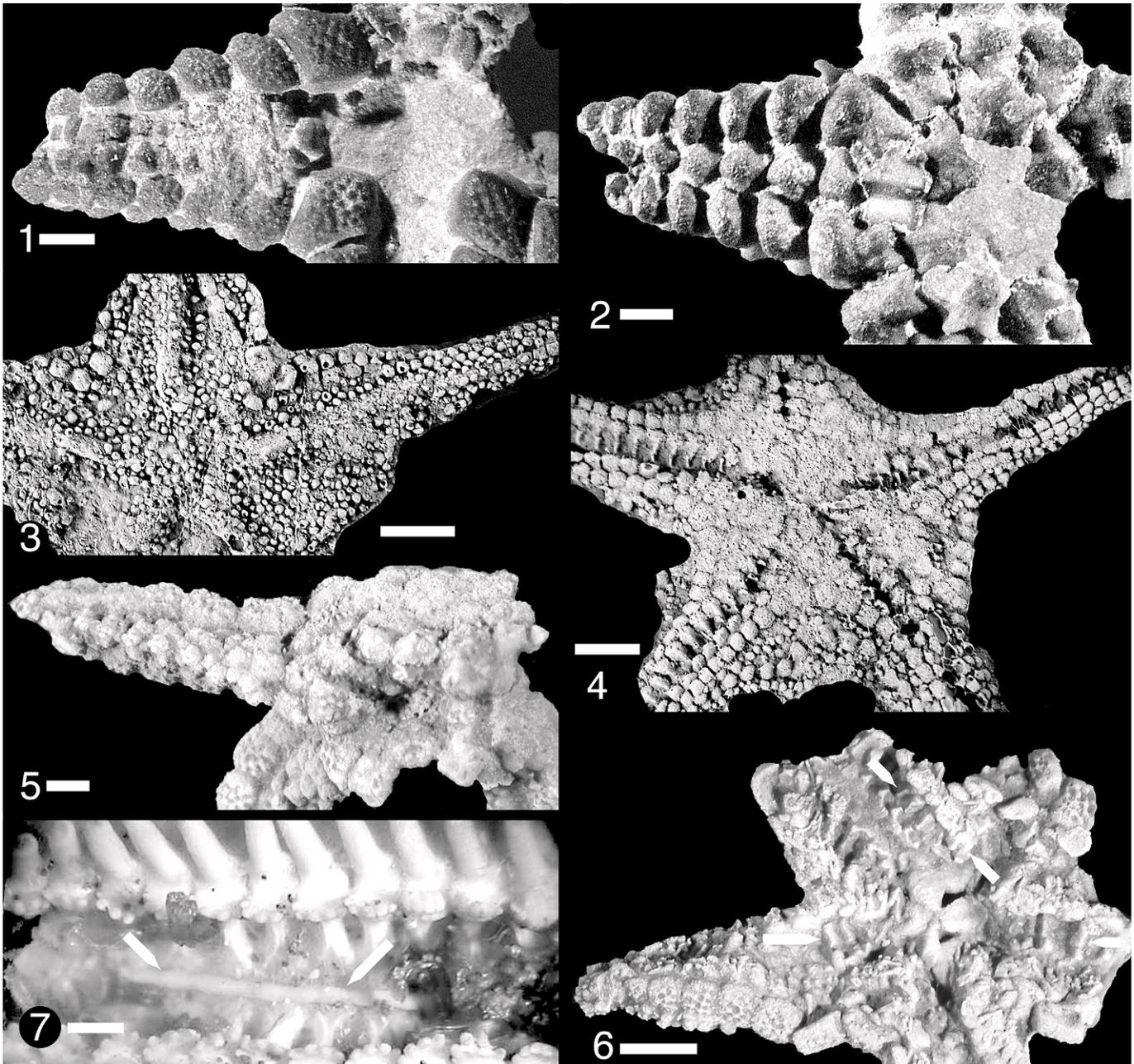
FIGURE 6—*1, 2, Hudsonaster incomptus* (Meek), USNM 40882b; *3*, GSI/F 00073; *4,* GSI/F 00066, *Petraster kinihani* (Baily); relatively early occurrence of contrasting configurations offer two basal asteroid hypotheses; *5, 6, Embolaster* Blake: *5*, paratype FMNH 60757, inclined dorsal view, triangular arms are asteroid-like; *6*, FMNH holotype PE 60756, ventral view of flattened arms and disk region; outer three arrows mark embedded virgals, the inner near-central arrow marks position of poorly preserved MAO pair with proximal ambulacrals narrowing toward MAO; *7*, the modern asteroid *Asteropsis carinifera*, USNM 33060, ventral view of ambulacral furrow, arrows identify plating over radial water canal, providing a protective mechanism in this relatively lightly calcified genus. Scale=1 mm for *1, 2, 5, 6*; 5 mm for *3,* 4; 2 mm for *7*.

well defined in those Paleozoic genera with fewer actinals, but the ossicle is at least difficult to recognize in genera with many. The mouth angle pair is upright, abutted, and more or less keel-like, the five pair (in five-armed asteroids) forming a budlike pattern as viewed ventrally. As viewed dorsally, the circumorals almost always form a closely articulated, inverted-V-shaped arch over the MAO, but arrangement can be ophiuroid-like, enclosing enlarged buccal podia (Fig. 5.5, 5.6). An apparent odontophore apart from the axillary has been recognized in some genera, although preservation of most specimens does not allow their evaluation.

TAXONOMIC OVERVIEW 3: THE CLASS OPHIUROIDEA

Apomorphies of the Ophiuroidea.—Articulation of the ambulacral column, including the mouth frame, is robust, with the MAO and adjacent ambulacrals forming an upright, more or less Y-shaped structure. Arm ambulacrals are not vaulted, the ossicles either vertebra-like and paired across the arm midline or more or less boot-like and offset. Water vascular canals are narrow and skeletally protected (Spencer, 1914, p. 24). Arms are largely filled with skeletal material and articular tissues, the arm coelomic space limited but larger in earlier representatives. The virgal series is reduced to a single ossicle (the lateral) that abuts the

abradial edge of each ambulacral, forming a shield-like distally directed closure to the podial basin. Laterals and ambulacrals become more closely articulated through time (Spencer, 1925, p. 250).

Other morphology.—In most genera, the adult body is differentiated into a sharply defined disk and elongate, narrow, cylindrical arms, although the disk of many earlier taxa appears more web-like, as are those of many asteroids. Dorsal and ventral disk ossicles are scalar or granular, although larger plates are known. The madreporite is ventral where recognized. Ambital frame ossicles arise at midarm in some genera.

TAXONOMIC OVERVIEW 4: THE CLASS STENUROIDEA

Apomorphies of the Stenuroidea.—Two or rarely three virgal derivatives extend laterally from each ambulacral. Internal (embedded) virgal derivatives are differentiated from the delicate somasteroid expression, these ossicles in stenuroids either fairly robust and rectangular or forming a rim-like abradial closure for the podial basin. The outer virgals of most genera are plate-like (but see *Pectenura* Haude, 1982) and more varied. Arm ambulacral series and mouth frame ossicles are not strongly faceted and articulated but variously differentiated to form a vaulted mouth region.

Other morphology.—Body wall ossicles of most genera are small and closely spaced; carinals and a primary circlet occur in a few taxa. Madreporite expression is varied. Ambital framework ossicles are absent from most taxa and similar body-wall ossicles extend from the dorsal surface to the ambulacral furrow.

Ambulacral ossicles not permanently vaulted; within specimens, ambulacrals can be nearly paired in some intervals and irregularly offset elsewhere. Ambulacral ossicles are about as wide as long and podial basins are large and deep; the radial water channel usually is large and enclosed or nearly so. At rest, ambulacrals and embedded virgals lie at least near to the ventral plane but faceting indicates facultative folding. Mouth frame ossicles are varied but generally quite small. Accessory ossicles are common.

Compilation of stenuroid names.—At the end of his monograph, Spencer (1940, p. 506) treated five diverse genera thought to share presence of an embedded ossicle between the ambulacral and an abradial, lateral-like or adambulacral-like ossicle; these were *Phragmactis* Spencer, 1940; *Stuertzaster*, Etheridge, 1899; *Bdellacoma*, Salter, 1857; *Rhopalcoma*, Salter, 1857; and *Ptilonaster* Hall, 1868. In recognizing the order Stenurida, Spencer (1951) formalized the combination of genera, and he included *Stenaster* Billings, 1858, *Eophiura* Jaekel, 1903, and *Palaeura* Spencer, 1951; Spencer and Wright (1966) added *Medusaster* Stüertz, 1890. *Antiquaster* Kesling, 1971a, followed, and Hotchkiss (1976) combined *Antiquaster*, *Klasmura* Ruedemann, 1916, and *Stenaster* into a new suborder Scalarina of the Stenurida; *Protasteracanthion* Stuertz, 1886, a Hünsruck Slate genus, was compared with *Klasmura* and *Antiquaster* but it was not considered sufficiently well understood to receive formal assignment. Three further stenuroid additions were *Acinetaster* Kesling, 1982, *Pectenura*, and the asteroid-like *Embolaster* Blake, 2008. Newly recognized stenuroids from the Lower Devonian Hünsruck Slate of Germany are discussed after review of earlier assignments.

Review of stenuroid assignments.—Although equivocating on presence of embedded virgals in *Phragmactis*, Shackleton (2005) coded absence in her data matrix, and following review of specimens, this interpretation is followed here. *Ptilonaster* was diagnosed in part by presence of a "well exposed" embedded virgal (Spencer and Wright, 1966, p. U81). The holotype is a mold preserved in a medium-grained subangular to angular quartz sandstone (B. Hussaini, personal commun., 2012), and details are difficult to establish. Based on a new preparation of the type, presence of an embedded virgal is considered equivocal (Fig. 3.7,

3.8) but it is tentatively accepted; it is particularly important because it would represent occurrence of a multi-armed configuration within the Stenuroidea. Although appearing only infrequently in the literature, the concept of *Ptilonaster* has had a complex history. Many or most ambulacral ossicles appear to have an ossicular boundary at the transverse ridge of the ambulacrals, but this possible boundary is close to the radial channel and if present would require a highly elongate embedded virgal. Taphonomic alteration cannot be ruled out, nor can the possibility of fusion or loss of only some of the ossicles to form single ambulacral elements. The position of the ossicular boundary between the ambularal/embedded virgal and the adambulacral/outer virgal is obscured in most podial basins of the holotype by a putative, blunt tube foot. Subsequently, a new external mold was assigned to *Ptilonaster* (Wells, 1952) but no cast has been prepared. No embedded virgals could be recognized in this specimen; however, casting is necessary both for final determination of presence and taxonomic assessment.

Palaeura, *Medusaster,* and *Stenaster* lack embedded virgals. The first two were assigned to the Palaeuridae Spencer, 1951, diagnosed in part on characters typical of ophiuroids but also "Like Eophiuridae but arm extremities tapering and no sublaterals (=embedded virgals) visible" (Spencer and Wright, 1966, p. U82). Well-preserved material of neither was available, but descriptions indicate ophiuroids. Earlier, *Stenaster* affinities at the class level were debated, but more recent researchers agree on ophiuran affinities (Spencer, 1914, p. 22; Spencer, 1951, p. 110–111; Hotchkiss, 1976; Dean, 1999).

The youngest-known stenuroid occurrence is that of *Pectenura* from the Namurian (Carboniferous) of Germany (Haude, 1982). *Pectenura* is similar to *Klasmura* in overall form and presence of paired ambulacral ossicles. The slender embedded virgals with expanded termini are similar to the virgals of somasteroids whereas the delicate, Y-shaped outer virgals are unique. The holotype and only-known specimen of *Acinetaster* is morphologically unusual, not well preserved, and difficult to interpret, but presence of embedded virgals is tentatively accepted based on the original photographs.

New Hünsruck Slate occurrences.—A number of taxa with embedded virgals are recognized from the Early Devonian Hunsrück Slate of Germany. *Eriniceaster tenuispinosus* Lehmann, 1957 (Figs. 2, 3.1–3.6) is a large species with small body wall ossicles, long spines, lacking an ambital frame, and most important, presence of two embedded virgals between each ambulacral and outer virgal. The first embedded virgal forms an abradial rim or closure about the podial basin whereas the second is thickened, rodlike, and thereby more reminiscent of a somasteroid virgal; *E. tenuispinosus* thus exhibits both typical embedded virgal stenuroid configurations of Spencer (1940, fig. 331). Presence of two embedded virgals in three specimens confirms the expression, although appearance and exposure of the embedded virgal pairs differ locally on individual specimens because of distortion and flattening under the complex conditions of Hunsrück preservation (Fig. 3.2–3.5). Although *Eriniceaster* was judged to be a synonym of *Stuertzaster* (Spencer and Wright, 1966), a second embedded virgal has not been recognized in the literature nor among available specimens, and therefore *Eriniceaster* is retained pending further study of *Stuertzaster* material.

A second Hunsrück Slate species, *Hystragaster horridus* Lehmann, 1957, is difficult to evaluate because body form was thickened and primary ossicles of the reticulated skeleton are relatively delicate; "horrid" elongate spines dominate appearance of typical fossils (Fig. 5.7). Nevertheless, two embedded virgals are exposed in a single small arm interval of one specimen (Fig. 5.8). Although preservation is poor, the adradial embedded virgal does not appear to have formed a closing rim for the podial basin,
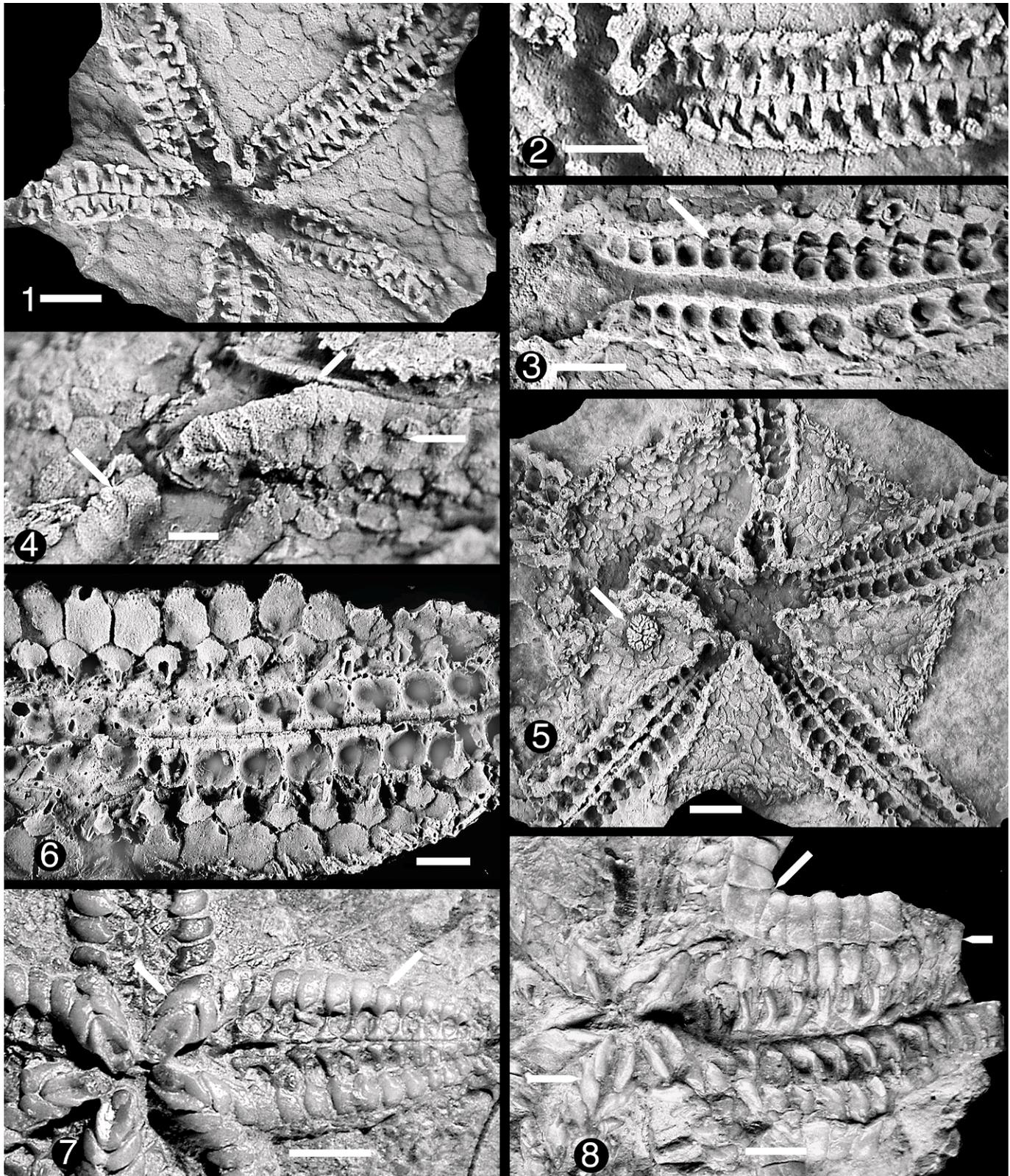
FIGURE 7—*1, 2*, the ophiuroid *Protaster sedgwickii* Forbes, paratype SM A6374b, ventral views; ambulacrals are hammer-shaped and offset, the laterals robust, extended distally and closing the podial basins; *3–5*, the stenuroid *Pradesura jacobi* (Thoral), FSL 168 688: *3*, ventral view, ambulacrals cup-shaped, irregularly alternate, rimmed by an embedded virgal (arrow); *4*, inclined dorsal view of mouth frame area; little-differentiated ambulacral series converging distally; proximal ambulacrals (upper arrows) not differentiated as in ophiuroids; a depressed longitudinal groove of ambulacrals (lower right arrow) is similar to expression in *Chinianaster* (Fig. 1.1); *5*, collapsed disk margins do not represent a differentiated ambital frame; madreporite (arrow); *6*, the stenuroid *Eophiura bohemica* Schuchert, MCZ 140218; both embedded virgals and outer virgals are plate-like and unlike those of other stenuroids and ophiuroids; ambulacrals square, cup-shaped similar to those of *Pradesura* (Fig. 7.3), abradial edge Y-shaped indicating flexibility; *7*, the ophiuroid *Stenaster salteri* Billings, UI-X-8888, Bobcaygeon Fm., and *8*, the asteroid *Phyrtosaster casteri* Blake, CMC TT5305, Fairview Fm.?, the similar mouth frame construction

as in *E. tenuispinosus*. Ambital frame ossicles have not been recognized, ambulacral column ossicles are broadly similar to those of *E. tenuispinosus*, and an enlarged, near-oral madreporite is present. Presence of two embedded virgal ossicles of different configuration in different genera is argued to support a hypothesis of derivation of embedded virgals through reduction from an extended virgal series. Embedded virgals also occur in British Silurian *Bdellacoma vermiformis* Salter, 1857 (Fig. 5.3, 5.4), the genus now including the Hunsrück Slate species *Urasterella verruculosa* Lehmann, 1957 (Hotchkiss and Glass, 2010).

Although problematic for different reasons, a single embedded virgal apparently occurs in *Palasteriscus* Stuertz, 1886 (Fig. 5.1–5.5, but see 5.6) and probably both *Jaekelaster* Stuertz, 1899 (Fig. 5.7) and *Echinasterella* Stuertz, 1890 (Fig. 5.8). Additional specimens need to be prepared to test for presence. Similarities of expression between the slate genus *Protasteracanthion* and the stenuroids *Klasmura* and *Antiquaster* were noted by Hotchkiss (1976), although presence of embedded virgals has not been tested in this genus.

Taxonomic summary.—The following ten genera here are included in the Stenuroidea: *Antiquaster Bdellacoma, Embolaster, Eriniceaster* (*E. tenuispinosus* only), *Eophiura, Hystragaster, Klasmura, Pectenura, Rhopalcoma*, and *Stuertzaster*; inclusion of five genera, *Acinetaster, Echinasterella Jaekelaster Palasteriscus, and Ptilonaster* is tentative, and *Protasteracanthion* is in need of further study. Four genera from the listing of Spencer and Wright (1966) are excluded: *Medusaster, Palaeura, Phragmactis*, and *Stenaster*. No attempt is made to group taxa between the generic and class levels. Two suborders and seven families were recognized for ten genera in the Stenurida of Spencer and Wright (1966); elimination of taxa lacking embedded virgals leaves both suborders (Proturina, Parophiurina) and four families (Pradesuridae, Rhopalocomidae, Bdellacomidae, Eophiuridae). The Klasmuridae and Embolasteridae have been added, and the treatment of Lehmann (1957) might indicate additional as yet unrecognized genera. The Stenuroidea ranges from Ordovician to Carboniferous.

MORPHOLOGIC COMPLEXITIES OF THE SOMASTEROIDEA AND STENUROIDEA

Ambulacral column construction.—The ambulacral series of somasteroids and their associated virgal series lay in the ventral plane (Spencer, 1951), the ambulacral channel in most species large and closed (Fig. 1.1–1.4, a smaller example in Fig. 1.7, 1.8). Accepting a planar orientation, Fell (1963) went on to argue that somasteroids had the ability to contract to form a facultative furrow. A V-shaped rim correctly positioned to be ventral cross-furrow muscle depressions are preserved in two or three ambulacral ossicles of the holotype of *Ophioxenikos* (Fig. 1.7, 1.8), and similar muscle pads occur in the stenuroid *Eriniceaster* (Figs. 2.3, 2.4, 3.1–3.5) (interpretation in *Eriniceaster* rests on positioning and form of the scars; offset of successive ambulacrals weakens the argument). Ventral cross-furrow muscles, together with the body wall musculature posited by Spencer (1951, who noted similar body wall musculature in modern asteroids), would allow contraction and a facultative furrow. Somasteroid and stenuroid virgal-to-virgal and virgal-to-ambulacral contact surfaces are relatively small and overlapping and therefore consistent with considerable flexibility, yet any temporary contraction in life appears readily lost with death-related relaxation and sediment compaction.

In spite of commonly small contact surfaces, linkage of ambulacral series of somasteroids and stenuroids appears to have been quite strong in that many virgal series ossicles remain closely articulated (Figs. 2.3, 3.1, 3.4, 3.5; Spencer, 1940, fig. 331A–331C). Flooring ossicles in stenuroids were seen as "forming a stiff bony axis which keeps the arm in shape during pulls of the musculature of the body walls" (Spencer, 1940, p. 508). In some specimens in which ambulacral series are pulled apart along the arm midline, longitudinal articulation can be retained, the flange-like and overlapping adradial tips of ambulacrals presumably supporting some connective tissue (Fig. 5.8, vertical arrow), an expression seemingly retained from somasteroids (Fig. 1.1).

Closure of the ambulacral channel.—Ventral closure of the radial water channel, variously expressed in early asterozoans, would protect the water vascular canal. The ventral radial canal of early ophiuroids was partially enclosed (Spencer, 1914, p. 24; Spencer, 1925, fig. 184B; Spencer, 1927,fig. 224), although the plating of modern ophiuroids was lacking. Among modern asteroids, the radial water canal is external but partially enclosed and protected by the vaulting of the ambulacral furrow; consistent with a protective interpretation are the skeletal platelets that lie below the radial water canal and at the peak of the furrow of the lightly skeletonized living asteroid *Asteropsis* Müller and Troschel, 1840 (Fig. 7.7).

Regardless of phylogenetic sequencing (i.e., whether expressions are homoplastic or apomorphic), stenuroid ambulacral channel evolution experimented with expressions found in the surviving classes, the radial channels of the more asteroid-like species appearing less tightly closed (Figs. 5.1, 5.2, 6.6) than those of the more ophiuroid-like species (Fig. 7.3, 7.5, 7.6). Taking preserved expression at face value, Spencer (1940, p. 515) noted the enclosed radial channel in the stenuroid *Stuertzaster colvini* (Salter, 1857), but he thought it open in *S. marstoni* (Salter, 1857) and *S. spinosissimus* (Roemer, 1863). The ambulacrals of *Rhopalocoma* were thought to resemble those of *S. marstoni* (Spencer 1940, p. 536), the *Rhopalocoma* ambulacrals thought to have "fallen away" from the arm midline to expose "the deep tubular hollow of the ambulacral channel" (1940, p. 538). Although the radial channel was large and therefore plesiomorphic, it does not appear tightly closed in *Stuertzaster marstoni*, *Embolaster*, *Rhopalocoma*, and *Eriniceaster*, the channel being prone to distension and spreading with death and sediment compaction (Figs. 3.2–3.4, 5.1, 5.2). In more distal intervals of the arm of most specimens, the radial channel commonly is closed (Figs. 2.4, 3.1, 3.2, 3.4, 3.5, 3.7, 3.8), the small distal intervals likely more resistant to sediment compaction, although MacBride (1906, p. 502) thought it became closed phylogenetically, the process seen as beginning toward the arm tip in *Bohemura* Jaekel, 1903. Closure provides protection equivalent to the recessed furrow of asteroids.

Mouth frame construction of somasteroids and stenuroids.—The mouth frame is important to the interpretation of asterozoan phylogeny, but it is difficult to study because its complex construction usually is incompletely exposed. The so-called "buccal slit," a divergent positioning of the proximal-most ambulacral series, was considered to be a life occurrence in many of the earliest asterozoans (Spencer, 1940, 1951) (for different expressions, see Figs. 1.2, 1.5–1.8, 2, 3.3, 4.3–4.6, 7.1–7.5). Near-oral ambulacral series ossicles are preserved abutted across the furrow in a few somasteroids (Fig. 1.5), and in these specimens, mouth frame ossicles do not appear distorted nor displaced but instead are similar to arrangements of later asteroids. In disrupted

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← marks early homeomorphy among asterozoans, arrows to left marking ossicles immediately distal to inclined, grooved, mouth angle ossicles; arrows to right mark lateral/adambulacral series (*7, 8*) and axillary (medial arrow, *8*) at interbrachial convergence of marginal sequence. Scale=1 mm for *1–4, 6;* 3 mm for *5, 8;* 2 mm for *7.*

specimens, displacement is not the same in all specimens of a single species nor all arms of a single specimen, rather ossicular series are pulled apart for different intervals along arms, in extreme but not infrequent occurrences extending to the arm tip (Spencer, 1951, pl. 2.32), all seemingly demanding "buccal slits" of different sizes. Vaulted somasteroid (Fig. 1.5) mouth frames would have been prone to taphonomic flattening and spreading, yet successive ossicles held together, yielding the appearance of a buccal slit. Such similarities apparently led Fell (1963, p. 403) to conclude that the so-called slit of *Chinianaster* is taphonomic, as did Smith and Jell (1990, p. 757) for *Archegonaster*, and these interpretations are extended here to all available somasteroids and stenuroids.

The adradial walls of near-oral ambulacral ossicles (i.e., within the "buccal slit" interval) of at least some stenuroid genera are semi-circular (Figs. 2.2–2.4, 4.3–4.6, 5.3). If the so-called slit in these genera were real in life, then unprotected surfaces of the radial vessels would have been directed toward the mouth region in this vulnerable (e.g., during feeding) interval of the radial canal. Abutted ambulacral ossicles closed the radial channel and protected the water vascular canal. Many early ophiurans and even asteroids (Fig. 5.5), however, have enlarged buccal podia, and basins for these tube feet are associated with the divergent, near oral ambulacral column ossicles; these expressions in appearance can be "buccal slits," but the arrangement differs from oral frame vaulting and linkages of somasterids and stenuroids (e.g., Figs. 2.3, 2.4, 5.2).

Little morphologic differentiation of near-oral ambulacrals has been recognized among somasteroids, whereas stenuroids are more varied. The vaulting of somasteroids (Fig. 1.5) was retained in stenuroids (Fig. 7.4), although usually with ossicular differentiation unlike that of asteroids and ophiuroids. In the stenuroids *Stuertzaster marstoni* and *Eriniceaster*, the cross-section of the radial channel of the proximal-most ambulacral ossicles was semicircular whereas more distal ossicles are less tightly curved and almost spoon-shaped (Figs. 2.3, 2.4, 3.1, 3.3, 3.4). Distinct ventral cross-furrow muscle pads occur on *Eriniceaster* arm ambulacrals but any muscle pads are only weakly developed on ambulacrals near the mouth frame; muscles would have served to close and vault the furrow but apparently were not needed on the proximal ambulacrals, which, based on a somasteroid ancestry, were already deflected (Fig. 1.5). Providing another indication of vaulting and closure of the proximal ambulacrals, in *Rhopalocoma*, the fourth and fifth ambulacrals, and only these, bear cross-furrow articular grooves and facets (Fig. 5.1, 5.2). These ossicles are positioned as to provide a hinge-like linkage between the near-oral ossicles and ambulacrals found more distally on the arm. In describing the mouth frame of the stenuroid *Stuertzaster marstoni*, Spencer (1940, p. 520, 521) remarked that in the proximal direction the ambulacrals are "hidden well below the oral surface," an occurrence consistent with vaulting.

PHYLOGENETIC COMPLEXITIES

The transition to the Stenuroidea.—About taxa later incorporated into the Stenurida, Spencer (1940, p. 506) argued that "The genera are united by a number of common primitive characters. It is probable that these characters indicate the survival of a number of isolated genera from a primitive stock rather than that all the genera are nearly related." Although this sentence can be read in different ways, the monograph of Spencer (1914–1940) includes many phylogenetic interpretations, and in recognizing an order Stenurida, Spencer (1951) and Spencer and Wright (1966) imply a phylogenetically cohesive entity. Taxonomic and morphologic diversity described and compiled since Spencer (1951) and

Spencer and Wright (1966) favors recognition at the class level, a step perhaps earlier deemed premature.

Review of diagnoses (Spencer, 1951, p. 110; Spencer and Wright, 1966, p. U78) reveals uncertainty as to unifying ordinal characters of the Stenurida, although shared basins for tube feet are cited, along with inferred presence of buccal slits in some genera. Important, if somewhat unclear, is the argument that arm joints and musculature allowed only simple movement; this is taken as serving to contrast stenuroids with the complex articular patterns seen in both asteroids and ophiuroids. Other expressions cited by Spencer (1951) appear plesiomorphic, although there are concerns based on the concept of the Stenurida as there formulated. In addition to virgal reduction, arm construction of the Stenuroidea, as formulated here, is unlike those of asteroids and ophiurods, and therefore stenuroid origin is judged likely to have been apart those of asteroids and ophiuroids.

Transitions to the Asteroidea.—Three stenuroid genera are superficially asteroid-like, but in different ways. *Bdellacoma* (Salter, 1857) (Fig. 5.3, 5.4) was transferred to the Asteroidea based on unusual specimens with preserved soft parts (Sutton et al., 2005). Pedicellariae occur in *Bdellacoma*, although they are unknown among ophiuroids (but see MacBride, 1906, p. 492), and spines were judged to be similar between *Bdellacoma* and modern asteroids. Presence of offset ambulacral ossicles, an ophiuran expression, was challenged by Sutton et al. (2005). Presence of a dorsal madreporite in a Devonian Hünsruck Slate species provided partial evidence in support of its transfer to *Bdellacoma* and the Asteroidea (Hotchkiss and Glass, 2010).

Although specimens of *Bellacoma* are fairly numerous, their interpretation is difficult because body wall ossicles are small and typically obscured by spines and pedicellariae. The slender arms typically are preserved tightly closed, revealing little of the interior. The radial water channel was judged to be external by Sutton et al. (2005), and Hotchkiss and Glass (2010) supported this interpretation. In his discussion, Spencer (1940, p. 527) appears to have equivocated, noting that some specimens show the ambulacral channel to be unroofed whereas elsewhere ambulacra were thought to enclose and hide the water vascular canel; specimen appearance remains equivocal (Fig. 5.4). Because of relatively uniform ossicular sizes, Hotchkiss and Glass (2010) argued against presence of differentiated carinal and primary circlet series in *Bdellacoma*, although occurrences are difficult to determine with certainty; carinal series, a primary circlet, and a madreportite might all be represented in BMNH E.1254. Ambulacral ossicle arrangement across the arm midline is neither strictly paired nor alternate, which is consistent with the view of Spencer (1914, p. 19) and earlier workers that ambulacral arrangement in the most primitive asterozoans was "irregularly alternating."

Embolaster Blake, 2008, (Fig. 6.5, 6.6) was assigned to the Asteroidea based on presence of an overall form and ossicular configuration typical of many early asteroids, including presence of a single marginal series, robust carinal and primary circlet series, lateral dorsal series, and two axillary ossicles. Ambulacrals and virgals are similar to those of other stenuroids, although positioning of faceting and a closed furrow in one specimen (Fig. 6.5) indicates vaulting, favoring the facultative ability found in somasteroids (Fell, 1963).

Rhopalocoma (Salter, 1857) (Fig. 5.1, 5.2) has not been assigned to the Asteroidea. The enlarged disk bordered by a well-defined marginal series that separates large fields of distinctive abactinal and actinal ossicles is paralleled in the expressions of many asteroids, although ambulacral column construction remains stenuroid. The flattened mouth frame in a specimen of

Rhopalocoma appears more stenuroid-like or asteroid-like than the ophiuroid-like reconstruction of Spencer (1940, fig. 347).

Each of these three genera would provide a different pathway to asteroid configuration, but reconstruction of early asteroid history is difficult even without the stenuroids. In his initial work, Spencer (1914, p. 19, 20) favored a "primitive Asterozoa" that was neither asteroid nor ophiuroid, but the inference of Schuchert (1915, p. 34) that "*Hudsonaster* is ... near the radicle that gave rise ... to all subsequent Stelleroidea" was immediately contested by Spencer (1916, p. 57), the term Stelleroidea includdng ophiuroids as well as asteroids. Although a basal position within asteroids for hudsonasterids seems favored (Spencer, 1916, p. 61; 1919, p. 179), a phylogenetic reconstruction (1916, p. 65) is equivocal, deriving the Uranasteridae (Petrasteridae of Spencer and Wright, 1966) from a "common stock" before the Hudsonasteridae, an inference based on the absence of supero-marginals (1919, p. 180; also 1918, p. 126). Ontogenetic events were frequently revisited as guides to phylogeny in the Spencer monograph, and because early post-metamorphic stages of asteroid development includes comparatively few ossicles, the relatively simple construction of hudsonasterids might find favor as indicating a basal positioning. The Uranasteridae included *Uranaster kinihani* (later *Petraster*), a species with an enlarged disk and many small body wall ossicles (Fig. 6.3, 6.4). The stenuroid *Rhopalocoma* is at least superficially similar to *Petraster kinihani* (Fig. 6.3, 6.4) whereas *Embolaster* (Fig. 5.5, 5.6) might be closer to *Hudsonaster*; *Hudsonaster* and *Petraster* differ enough to allow hypotheses of at least paraphyletic origins for the Asteroidea. Issues were further complicated by recognition of the Eoactinidae Spencer, 1919, which included *Schuchertia* Gregory, 1899, judged "to lie at the base of the Ophiuroidea" (Spencer, 1919, p. 178), although *Eoactis* itself appears to have been included among asteroids (Spencer, 1914, p. 30), and the eoactinid genera subsequently were included with asteroids (Spencer and Wright, 1966). Finally, the robust, asteroid-like marginal frame and differentiated first virgals of the somasteroid *Archegonaster* Jaekel, 1923, must at least raise a hypothesis of direct derivation of asteroids from somasteroids. A paraphyletic or polyphyletic Asteroidea as currently generally recognized can be argued.

Transition to the Ophiuroidea.—Even with exclusion of stenuroids, ophiurans remain varied. Early ophiurans can have either more or less boot-like ambulacral ossicles offset across the arm midline, or paired, vertebra-like ossicles, these fused later in ophiuran history. Past viewpoints on phylogenetic interpretation of the two arrangements verge on recognition of two class-level taxa (Sollas and Sollas, 1912; Spencer, 1914, p. 52; Hotchkiss, 1976) whereas Shackleton (2005) recognized an ophiuran complex including genera with both alternate and paired ambulacrals. Diversity of ophiuran expressions earlier led to the proposed class Auluroidea Schöndorf, 1910, a concept rejected by Spencer (1914), although Kesling (1964) revisited the notion. As with asteroids, issues of polyphyly and paraphyly are not clearly resolved within the Ophiuroidea.

Probably the most appealing candidate for title of "proto-ophiuroid" among stenuroids is *Pradesura* Spencer, 1951 (Fig. 7.3–7.5), which has a well-defined disk built of uniform, overlapping scales, a ventral madreporite, cylindrical arms, and a mouth frame that is broadly Y-shaped and ophiuroid-like. Disk and arm expressions have not been consistently treated as basal apomorphies of the Ophiuroidea. The disks of many early ophiurans, including *Stenaster* and *Taeniaster* Billings, 1858 (as well as those of many stenuroids) are webs of small ossicles, these typically associated with broad, strap-like rather than cylindrical arms. An asteroid-like body shape was seen as typical of both

immature and stratigraphically earlier ophiuroids (Spencer, 1919, p. 180), further arguing that presence of a disk was not basal among ophiuroids. The argument of MacBride (1906, 1907), that among modern ophiurans, dorsal disks "grow over" to the ventral, is treated as likely homoplastic in *Pradesura*, and correlated with differentiation of overall arm form. Ambulacral ossicles of *Pradesura* are arranged in the irregularly alternating pattern of other stenuroids, and ambulacrals in dorsal aspect are simple, shield-like, and distally overlapping in a manner similar to those of the somasteroid *Chinianaster;* a depressed groove similar to that found in the somasteroid (Fig. 1.1) indents the dorsal surfaces of at least proximal ambulacrals (Fig. 7.4). Ambulacral ventral expression is also plesiomorphic (Figs. 1, 7.3). The ambulacral ossicles approaching the mouth frame, are numerous (about five), small, similar, and unlike the more robust mouth frame ossicles typical of ophiuroids (Fig. 7.1.–7.4). External form is striking but homoplastic.

ASPECTS OF LIFE MODE

Construction and life mode.—Different interpretations of the life habits of early asterozoans are available. Disks of somasteroids, deemed better-preserved than the distal arm intervals, were interpreted as occurring in the deeper portions of burrows by Spencer (1951), whereas the arms were seen as extending upward "into the top layers of the mud, to feed from the layers richest in organic remains" (p. 90, fig. 3). Alternative possibilities of burial resulting from such abrupt disturbances as storm events were not treated. Burrowing was thought to have employed a body wall with opposing muscles similar to those found in earthworms (Spencer, 1951, p. 93), although interpretation focused on shallow burial rather than directed motion within the substrate. Both the later somasteroid *Archegonaster* and "primitive" ophiuroids were thought to have been burrowers (Spencer, 1951, p. 107). A suspension-feeding life mode linked to a ciliary-feeding pelmatozoan ancestor (Spencer, 1951, p. 91, 93, 97) was favored for *Villebrunaster*, Spencer arguing (p. 96) that the ventral surface was ciliated, allowing collection of food particles in a mode similar to that described in a living asteroid (Gemmill, 1915). A ciliary feeding habit closely matching the mechanism found in crinoids was preferred for the earliest asterozoans by Fell (1963), who found absence from most modern asteroids and many ophiuroids to be "clearly secondary" (p. 429).

Without commenting on Spencer or Fell, Shackleton (2005, p. 60) opined that "the amuscular, pentagonal somasteroids and eopentaroids appear to be adapted to a relatively sedentary, dominantly epifaunal life position, with deposit feeding as their primary trophic strategy. They were much more asteroid-like in biology ... . With the possible exception of *Stenaster* there is no evidence of ciliary or suspension feeding in Ordovician ophiuroids." The phylogenetic analysis of Shackleton (2005) assigned somasteroids and her eopentaroids (including the stenuroids *Rhopalocoma* and *Stuertzaster*) to basal positions in the ophiuroid branch.

There is no simple resolution for the differing interpretations, although somasteroid and stenuroid construction here is taken as favoring a viewpoint closer to those of Spencer (1951) and Fell (1963). Skeletal arrangement of all asterozoans is basically similar (hence an "Asterozoa"), and presence of muscles equivalent to those found in the body wall and ambulacra of modern asteroids would allow emergence of an integrated asterozoan configuration without the need to argue first the evolution of a skeleton followed by muscles to set all in motion, as is implicit if the early representatives were amuscular. Free-living animals, even in apparently quiet environments such as the Montaine Noir setting of *Chinianaster*, *Villebrunaster*, and *Pradesura*, are subject to disruption from current motion and

activities of other organisms, thereby demanding the ability to return to living orientations. Nevertheless, the earthworm-like hypothesis of Spencer (1951) seems exaggerated in light of the apparently somewhat thickened radial (rather than bilateral) external form, together with the overall skeletal delicacy typical of the extinct classes. Distinct articular facets (such as cross-furrow facets, Fig. 1.8) are infrequently found; however, ambulacrals can be flanged and overlapping (Figs. 1.1; in a stenuroid, 5.8), implying articular linkages. Members of the surviving classes, while retaining the asterozoan body plan, are capable of complex movement making use of comparatively closely fitted and complexly articulated ambulacrals and adambulacral/laterals, the continuity of structure indicating likely derivation from corresponding stuctures already in place in early asterozoans.

Virgal series motion.—As preserved, virgal series differ significantly in orientation, ranging from extended laterally to extended more or less distally, with sides of adjacent series abutted (Fig. 1.2–1.4). Although the broad surfaces of flatter virgals typically are preserved lying in the ventral plane, in some specimens they are nearly upright. Varied orientations favor the ability to move through an arc arising at the point of linkage of the virgal series to the abradial margin of the ambulacral, which commonly is recurved or broadly Y-shaped (e.g., Fig. 1.6, arrow; 1.7), thereby providing a rotational socket; a folding hand fan is analogous. Mobility of the outer virgal was stressed by Spencer (1951) for *Rhopalocoma* (Fig. 5.2) and *Eophiura* (Fig. 7.6), and imbricating outer virgals with complex muscular facets (Fig. 4.4, 4.5) as well as differing orientations of outer virgal series within species of stenuroids (Figs. 2, 3) also indicate retention of mobility within this group.

SUMMARY

The order Stenurida Spencer, 1951, is recognized at the class level as the Stenuroidea. Four classes therefore comprise the subphylum Asterozoa (phylum Echinodermata) sensu Spencer and Wright (1966), the extinct Somasteroidea and Stenuroidea and the extant Ophiuroidea and Asteroidea; the Asterozoa as so formulated is monophyletic. Ancestry of the Asterozoa is unknown and therefore subphylum-level apomorphies cannot be recognized.

The clearest diagnostic character of the Somasteroidea is presence of virgal ossicular series extending laterally from each ambulacral ossicle.Distribution of virgals and their ossicular derivatives among early Paleozoic asterozoans indicate that somasteroids are basal within the Asterozoa. The Stenuroidea was derived from the Somasteroidea through reduction of the virgal series to one or two ossicles (=embedded virgals) between the ambulacral and an outer virgal. Both plesiomorphies and other apomorphies accompany virgal series reduction. All genera with one or two embedded virgals, and only these genera, are assigned to the Stenuroidea, including those earlier assigned to ophiuroids (e.g., *Antiquaster*, *Eophiura*, *Pradesura*) as well as to asteroids (*Bdellacoma*, *Embolaster*).

Two evolutionary end-member scenarios for the origin of the stenuroids are available. According to the first, stenuroid diversity indicates that virgal reduction from the somasteroid condition was paraphyletic or polyphyletic, documenting evolutionary tinkering and widespread homoplasy. Recognition of many classes, clades, or plesions would be appropriate for this scenario.

In a second scenario, reduction of the virgal series was the key innovation that enabled morphologic and functional diversification; evolutionary tinkering and homoplasy followed loss. Recognition of a monophyletic class Stenuroidea is the

appropriate interpretation in this scenario, and it is followed here.

Asteroids and Ophiuroids lack embedded virgals, and their robustly articulated arm construction identifies separate lineages apart from that of the Stenuroidea. It is uncertain if one or both were derived through stenuroids or directly from somasteroids but direct derivation is consistent with the nearly coeval first occurrences of all three derived classes.

Phylogenetic interpretation parallel to that for origin of stenuroids is appropriate for the origins of both asteroids and ophiuroids; the surviving classes arguably also are either monophyletic or polyphyletic. Consistent interpretation requires all three groups, stenuroids, ophiuroids, and asteroids, to be treated in the same manner, and here all are treated as monophyletic and retained at the class level.

Functional significance of somasteroid and stenuroid morphology has been subject to differing interpretations. Here, members of both extinct groups are argued to have been flexible and active in benthic marine settings. Mouth frame arrangements in the extinct groups presage those of the extant classes, favoring parallel habits.

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