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A new Devonian asteroid-like ophiuroid from Spain

D.B. BLAKE[1] S. ZAMORA[2,3,*] J.L. GARCÍA-ALCALDE[4]

[1]Department of Geology, University of Illinois
506 W Springfield, Champaign, 61820, USA. E-mail: dblake@illinois.edu

[2]Instituto Geológico y Minero de España
C/ Manuel Lasala, 44, 9ºB, 50006, Zaragoza, Spain. E-mail: s.zamora@igme.es

[3]Department of Paleobiology, National Museum of Natural History, Smithsonian Institution
Washington DC, 20013-7012, USA

[4]Departamento de Geología (Área Paleontología), Universidad de Oviedo
C/ Jesús Arias de Velasco s/n, 33005. Oviedo (Asturias), Spain. E-mail: jalcalde@geol.uniovi.es

* Corresponding author

ABSTRACT

A Lochkovian (Early Devonian) ophiuroid (Echinodermata), *Ophiocantabria elegans* n. gen. and sp., is based on a single small, well-preserved specimen collected from a shale-rich horizon of the Furada Formation, Asturias, Spain. Sedimentologic and palaeontologic data suggest its occurrence was in a near-shore setting subjected to frequent storms. *Ophiocantabria* is assigned to the Encrinasteridae based on the morphology of individual skeletal elements, although overall form of the new species is similar to that of approximately coeval members of the asteroid family Xenasteridae. Such homoplasy, especially among earlier members of asterozoan class-level clades, is an important but not well understood aspect of subphylum evolution.

KEYWORDS Ophiuroidea Echinodermata. Devonian. Spain. Phylogeny.

INTRODUCTION

Fossil asterozoans are rare at almost all localities, and few occurrences have been recorded from the Palaeozoic of Spain. A single specimen of the ophiuroid ?*Urosoma* sp. from the Darriwilian (Middle Ordovician) of Ventas con Peña Aguilera (Toledo) (Chauvel and Meléndez, 1978) was the first Palaeozoic asterozoan recorded from Spain, subsequently reassigned to *Palaeura neglecta* Schuchert, 1915 var. *hispanica* (Smith, 1984). In addition, a possible juvenile of *P. neglecta* was recorded by Smith, along with a number of small and poorly preserved ophiuroids of the Encrinasteridae. Six specimens of the ophiuroid *Taeniaster ibericus* were reported from the Darriwilian (Middle Ordovician) so-called "Tristani beds" at a locality near Almadén (Ciudad Real) (Hamman and Schmincke, 1986).

Ophiocantabria elegans n. gen. and sp., the first Devonian ophiuroid recorded from Spain, is based on a complete specimen exposed in dorsal aspect together with a ventral arm counterpart. Because of overall similarities between *O. elegans* and Devonian xenasterid asteroids, positioning of the new genus within the subphylum Asterozoa is outlined in a phylogenetic analysis.

GEOLOGICAL SETTING AND STRATIGRAPHY

The Devonian of the Cantabrian Mountains includes some of the best preserved and well-exposed rocks of this age known from Spain. In the Cantabrian Mountain area, two well-differentiated facies are represented in the so-called Asturo-Leonian and Palentian domains (Brouwer, 1964; García-Alcalde *et al.*, 1990) (Fig. 1). The former consists primarily of rocks deposited in nearshore settings whereas the latter were deposited in more off-shore environments. The new ophiuroid specimen was collected from the Furada Formation (Fig. 2) at the small village of El Fresno, west of the city of Oviedo, and belongs to the Asturo-Leonian facies. The Furada Formation consists of a 200-250 meters-thick succession of red, ferruginous sandstones, with thin shaly beds and sandy limestones, and dolostone lenses higher in the section (García-Alcalde *et al.*, 2002). In the studied area, the Furada Formation is poorly exposed and partially covered by vegetation (García-Alcalde, 2011). The ophiuroid was collected from the top of the formation where it was associated with many specimens of the brachiopod *Mutationella fresnoensis* García-Alcalde, 2013, as well as ostracods, tentaculitids, bivalves, bryozoans and, homalonotid and *Acastella* trilobites. Based on faunal content, the rocks are assigned to the lower Lochkovian (Lower Devonian) conodont Postwoschmidti Biozone (García-Alcalde, 2011).

TERMINOLOGY

Terminology is based largely on Spencer and Wright (1966) and Blake (2013). The ambulacral ossicles form a double series along the axis of the arm and enclose the radial water vessel. In ophiuroids, a lateral ossicle articulates at the abradial, or lateral margin of each ambulacral whereas the ambulacral ossicles of asteroids are dorsal to the adambulacrals, the two series together forming an ambulacral furrow. The Mouth Angle Ossicles (MAO) are the proximal-most ossicles of the ambulacral series, and the circumorals are the first, typically differentiated ambulacral-series ossicles immediately distal to the MAO. The term "marginals" has been widely used in descriptions of asterozoans, cyclocystoids and edrioasteroids for the differentiated and commonly enlarged ossicles that brace the ambitus of many species. Because of inevitable uncertainties surrounding descriptive vs. genetic usages of terminology (Shackleton, 2005; Blake, 2013), the term "ambital framework" is used instead of "marginals" and "marginal frame" without implication of homology (Blake and Guensburg, 2015). "Pustules" were defined as a "minute boss on ossicle with central depression in which spine articulates" (Spencer and Wright, 1966, p. U30), whereas common dictionary definitions refer to any pimple-like or blister-like swelling; the word "pustule" is retained in its traditional usage here. Spine attachment sites are not recognized in *Ophiocantabria*; however, granules dictate some mode of accessory attachment. "Primary ossicles" are the foundation ossicles of the asterozoan skeleton, including ossicles of the ambulacral, lateral and ambital framework series, whereas "accessory ossicles" are spines, granules and pedicellariae seated on ossicles of the different primary series.

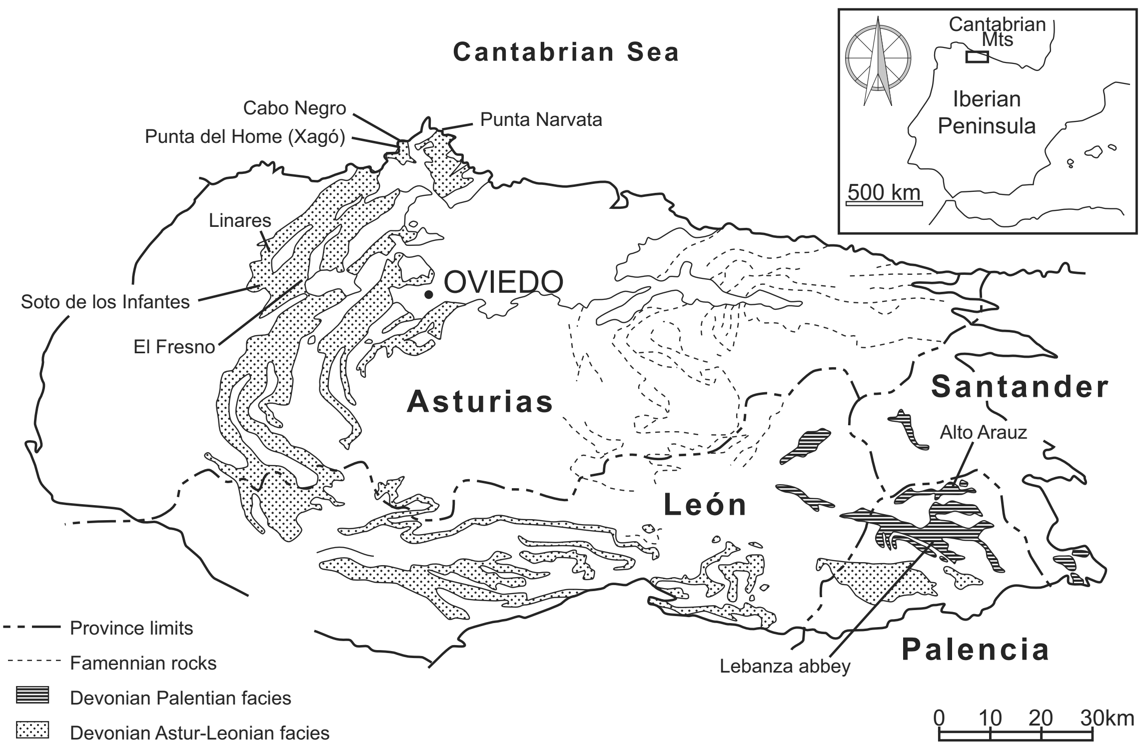

FIGURE 1. Geological map of the Cantabrian Mountains with the distribution of the different Devonian facies and the position of El Fresno fossil site. Modified from García-Alcalde (2011).

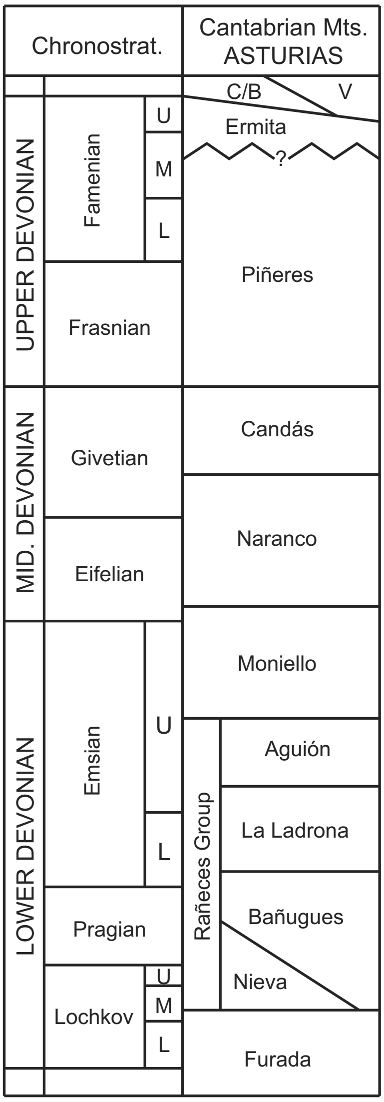

FIGURE 2. Chronostratigraphic position of Devonian formations cropping out in Asturias. Specimen of *Ophiocantabria elegans* was collected from the upper part of the Furada Fm. C/B: Candamo and Baleas fms. V: Vegamian Fm. L,M,U: Lower, Middle, Upper. MID: Middle. After García-Alcalde (2013).

HOMOPLASY AND LIFE MODES

The ancestry of both the Asteroidea and Ophiuroidea is judged to have been in the Somasteroidea (Spencer, 1951; Spencer and Wright, 1966; Blake, 2013) at a time no later than during the Early Ordovician (Tremadocian) (Blake and Guensburg, 2015). Because of common ancestry and diversification in comparable marine environments, parallel plesiomorphic and homoplastic morphologic expressions are widespread, and similarities and differences are important to the interpretation of *Ophiocantabria* n. gen. (Fig. 3).

Protaster Forbes, 1849 (Fig. 4E, F) is a more typical ophiuroid as expressed by a clearly differentiated, flattened central disc and narrow, serpentine arms. Body wall ossicles are small, scalar and uniform. Ambulacrals are offset and boot-shaped, and laterals are shield-like and directed distally. The mouth frame is of the characteristic open, Y-shaped ophiuran configuration, with prominent MAO extended toward the mouth area. In contrast, genera of the Encrinasteridae are suggestive of asteroids, and although now generally accepted as ophiuran (*e.g.*, Spencer and Wright, 1966), their departure from more typical expressions led to recognition of a class-level Auluroidea as well as debate surrounding this interpretation (Schöndorf, 1910a, b; Sollas and Sollas, 1912; Spencer, 1914, p. 47 et seq.; Schuchert, 1915; Kesling, 1964). In contrast with *Protaster* and in common with *Ophiocantabria*, the disc of *Encrinaster* (Fig. 4C, D) is bordered by robust ossicles, and arms are broad and proportionately flat. Ambulacrals of *Ophiocantabria* are similar to those of *Encrinaster* in that ossicles are offset across the midline, and they are robust and spool-like; laterals are similar. *Ophiocantabria* exhibits the essential ambulacral, lateral, and insofar as can be determined, mouth frame ossicular configurations of ophiurans.

Ophiocantabria, nevertheless, is also striking in its outward similarity to the approximately coeval asteroid *Xenaster* Simonvitsch, 1871, in presence of broad, flattened, triangular arms that are very different from the cylindrical, serpentine arms typical of ophiuroids. The concave disc profile of *Ophiocantabria* is braced by a robust ambital framework, which is similar to that of the *Xenaster*, and unlike the commonly convex margins typical of ophiuroids. Although focus here is on Palaeozoic ophiuroids, both Triassic *Aspidura* Agassiz, 1835, and extant *Ophiambix epicopus* Paterson and Baker, 1988 (see photographs, Museum of New Zealand Te Papa) are ophiuroids also of overall form similar to that more typical of asteroids. Among asteroids, ophiuroid-like morphologic expressions occur among ancient asteroids (Blake, 2007) as well as in the extant Brisingida, whose members have highly elongate, subcylindrical arms and a small, subcircular disc similar to those more typical of ophiuroids. Although major lineages separated early in the Palaeozoic, convergence in form has been an enduring and relatively little-studied phenomenon.

Interpretation of the behaviour of ancient organisms is almost always difficult, but *Ophiocantabria* and *Xenaster* are both close enough to each other and different enough from such ophiuroids as *Protaster* as to suggest some generalization. The slender, cylindrical arms of most ophiuroids, the so-called "serpent stars", typically are highly flexible, capable of manipulating prey but also of extension into the water column for suspension-feeding, whereas the large disc and short, triangular arms of *Xenaster* as well as those of *Ophiocantabria* are suggestive, for example, of those of the extant asteroid Goniasteridae. Goniasterids

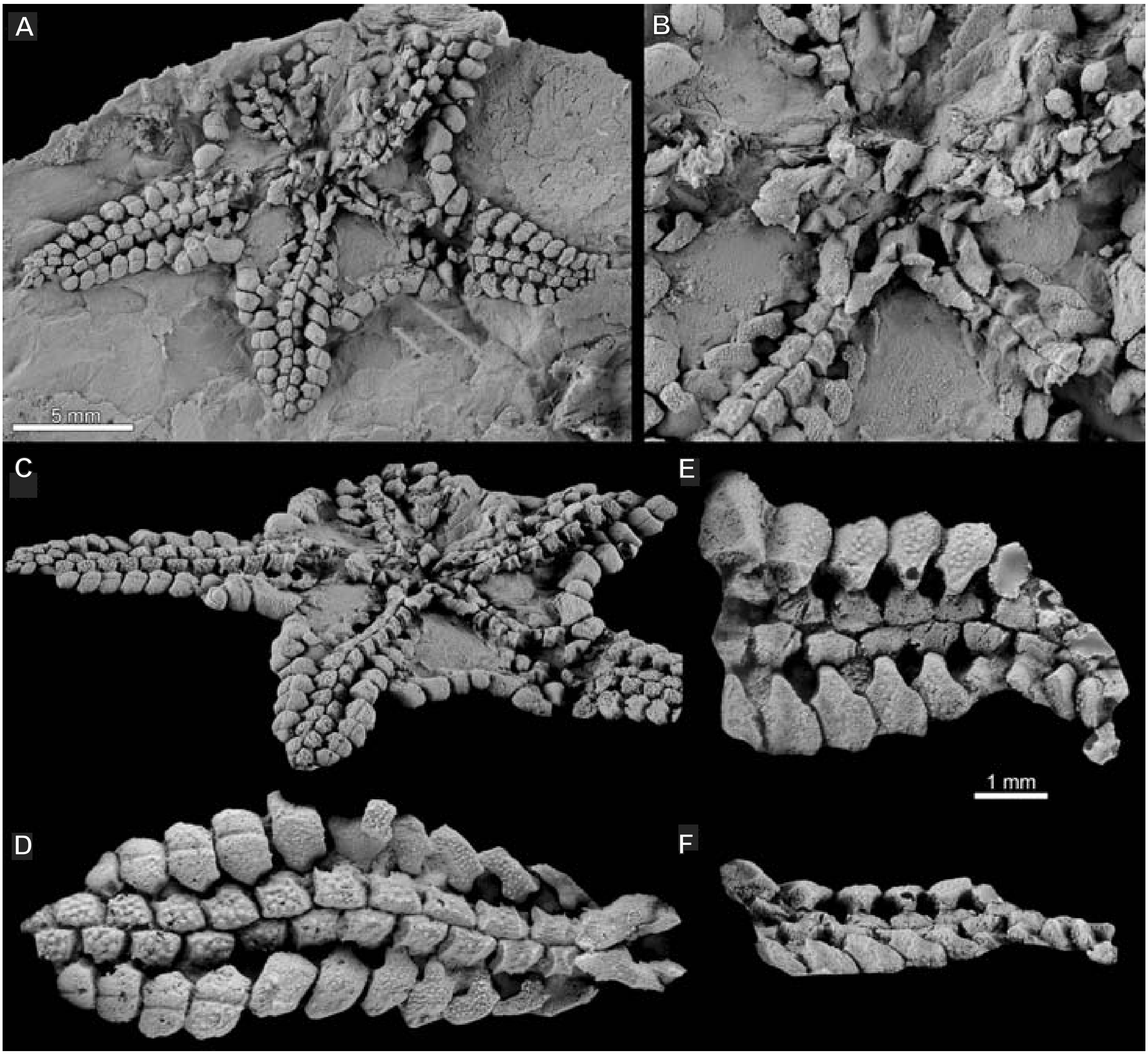

FIGURE 3. *Ophiocantabria elegans* n. gen. and sp. from the Lochkovian (Lower Devonian) Furada Formation. A-F) Holotype number DPO 33484. A) General view of a nearly complete specimen in dorsal view. B) Detail of central disc; the paired mouth angle ossicles (MAO) with possible spinelets are visible in the lower interbrachium, these followed distally by robust circumorals and offset ambulacral and lateral series, both series pustulate. Apparent granules visible especially in the lower interbrachium.C) Oblique view; the proximal laterals are L-shaped and extend distally whereas the more distal laterals extend radially. Scale: 1mm. D) Arm in dorsal view showing MAO to the right followed by circumorals, ambulacrals, and laterals. The distal laterals bear a longitudinal groove of unknown significance. The ambulacrals, covered by the dorsal dermal layer in life, are more coarsely pustulate than the exposed laterals. The radial channel of the water vascular system is skeletally enclosed both in dorsal and ventral (E, F) aspects, as is typical of ophiuroids but unlike asteroids. E) Ventral arm counterpart, differs from dorsal aspect in ambulacral shape, presence of podial gaps, lack of pustules, and absence of a longitudinal lateral groove. F) Oblique-lateral view of specimen in E. All specimens are photographs from latex casts whitened with ammonium chloride sublimate.

are feeding generalists (Jangoux, 1982) exploiting varied benthic food items, including encrusting algae and biofilms, sponges, cnidarians and detrital materials. Diverse food sources potentially were available to both *Ophiocantabria* and *Xenaster*, and like many extant goniasterids, a generalist feeding habit appears likely for *O. elegans*, but one apart from those ophiuroids with serpentine arms.

PUSTULE OCCURRENCE AND FUNCTION

Many ossicles of both *O. elegans* and *Xenaster* are pustulate, although pustules of *Xenaster* do not appear to occur on ambulacrals whereas the largest of those of *O. elegans* are on the ambulacrals. Broadly similar pustules have been described from certain Campanian (Late Cretaceous)

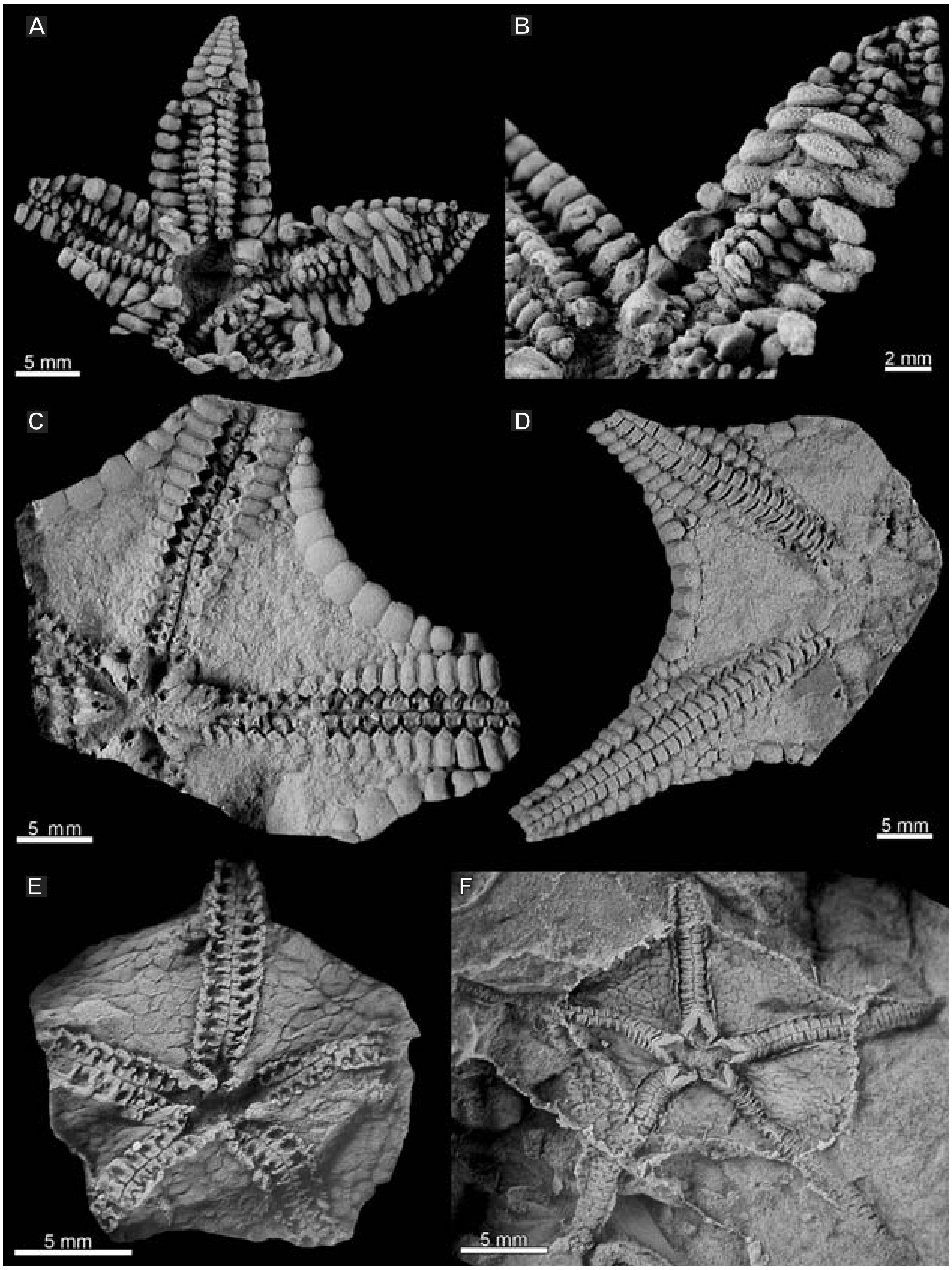

FIGURE 4. Comparative morphology of select Palaeozoic Asterozoans. A-B) *Xenaster* sp. (BMNH EE13471) in dorsal aspect. Heiligenberg bei Oberstadtfeld, Eifel (Germany), Emsian (Lower Devonian). Although overall aspect is suggestive of *Ophiocantabria*, the ambulacral ossicles are vaulted and abut comparatively small adambulacral ossicles below, these best visible in B, to center right. The robust, rectangular ossicles suggestive of the laterals of *Ophiocantabria* are abactinals and marginals. C-D) *Encrinaster goldfussi* (Schöndorf, 1910a), Univ. Marburg Mbg 3388, Lower Emsian, Oberstadtfeld, Germany. Ventral and dorsal views; as in *Ophiocantabria*, the disc is bordered by an ambital framework series of robust ossicles that terminate at a midarm position against the lateral series. Ambulacrals and laterals are robust, the latter, poorly exposed, are inclined distally nearer the mouth frame but directed laterally more distally. The arm intervals beyond the disc are robust and triangular, as in *Ophiocantabria*, and *Xenaster*, but unlike those of *Protaster*. E-F) .*Protaster* sedgwickii Forbes, Sedgwick Museum, Cambridge, paratype A.6374, lower Ludlowian, near Kendal, Westmorland, U.K. Ventral and dorsal views of a more typical ophiuran, with a well-defined disc and cylindrical arms, boot-shaped ambulacral ossicles, and an open mouth frame. The disc edging (F) appears to result from disc collapse rather than presence of an ambital framework series. All specimens are photographs from latex casts whitened with ammonium chloride sublimate.

asterozoans, these judged to be similar to structures found on some extant echinoderms that function as photosensitive microlenses (Gorzelak *et al.*, 2014), thereby suggesting a parallel interpretation for the Paleozoic pustules. If pustules of *O. elegans* were to have functioned as microlenses, however, then ambulacral covering tissues must have been thin enough as to have allowed light passage, and ventral pustules (Fig. 3E) would be less clear in function. The Cretaceous occurrences were a suggested response to increased predation pressure during the time of the Mesozoic Marine Revolution, and the Devonian examples might represent a similar mid-Paleozoic response. Microstructural analysis would allow some testing of a microlens hypothesis.

SYSTEMATIC PALEONTOLOGY

Class: Ophiuroidea GRAY, 1840
Order: Oegophiurida MATSUMOTO, 1915
Suborder: Lysophiurina GREGORY, 1897
Family: Encrinasteridae SCHUCHERT, 1914
Subfamily: Encrinasterinae SCHUCHERT, 1914

Diagnosis. "Small- to large-sized ophiuroids; ambulacral ossicles alternating, commonly with boot-shaped oral surfaces; adambulacral ossicles subventral, composed of heavy plates continuous in a radial direction, with broad oral surfaces, often bearing rows of pustules, and commonly with curved sutures producing rope-like twists; disc large, with well-developed interrays, commonly bounded by stout frame of marginal ossicles; podial basins supported by ambulacrals and adambulacrals, tending toward size reduction laterally" (Harper and Morris, 1978, p. 156).

Remarks. Taxonomic arrangements and rankings of genera of the Palaeozoic Ophiuroidea still is evolving. Perspectives on the encrinasterids are provided by Schöndorf (1910a, b), Schuchert (1914, 1915), Spencer (1930), Spencer and Wright (1966), Harper and Morris (1978), Haude (1995), Jell and Theron (1999), and Shackleton (2005). Concepts of Harper and Morris (1978) were developed from Spencer (1930) and Spencer and Wright (1966). Harper and Morris (1978) recognized two subfamilies, a new Armathyrasterinae in addition to the Encrinasterinae; additionally, these authors were of the view that *Cheiropteraster* STÜRTZ, 1890, and *Loriolaster* STÜRTZ, 1886, probably should be separated as well, based on the form of the disc and ambulacral ossicles. *Mastigactis* SPENCER, 1930, was listed, although Harper and Morris (1978) noted that a personal communication from F.H.C. Hotchkiss suggested that *Mastigactis* should be assigned to the Protasteridae. These considerations left *Encrinaster* HAECKEL, 1866, *Euzonosoma* SPENCER, 1930, *Crepidosoma* SPENCER, 1930, and *Urosoma* in the family. Jell and Theron (1999) favored synonymizing *Euzonosoma* with *Encrinaster* based on preservational expression of the lateral ossicles. *Marginura* HAUDE, 1999, has been added to the listing of Encrinasterinae.

Ophiocantabria n. gen. departs from the diagnosis of Harper and Morris (1978) quoted above in that the ventral outline of the ambulacrals is more nearly rectangular than boot-like, and the lateral (=adambulacral) ossicles are more nearly lateral than subventral. Survey of encrinasterid studies (*e.g.*, Spencer, 1930; Spencer and Wright, 1966; Harper and Morris, 1978), however, documents considerable variation among assigned fossils for these and other characters.

GENUS *Ophiocantabria* n. gen.

Type species. *Ophiocantabria elegans* n. sp. by monotypy.

Etymology. *Ophiocantabria* for the Cantabrian Mountains, source of the only-known specimen.

Species *Ophiocantabria elegans* n. sp.
Figure 3

Diagnosis. Encrinasterid in which the arms beyond the disc margin are elongate and triangular rather than more or less petaloid, as is typical of encrinasterids. Disc margins concave, bordered by comparatively few, perhaps four to eight, ambital framework ossicles, these partially inset into the laterals. Dorsal disc surface granulate; no primary ossicles in evidence on the dorsal surface. Ambital framework, ambulacral and lateral ossicles robust, differing from those of other encrinasterids in specific details (see below).

Description. Presence of comparatively few dorsal disc granules together with the expression of the ambital framework ossicles suggest the cross-section of living *Ophiocantabria* was low. Ambulacral column and ambital framework ossicles robust and block-like. Ambulacral ossicles approximately spool-like or square in outline in dorsal aspect; distal ambulacrals approximately rectangular in at least ventral aspect. Lateral surfaces of ambulacral ossicles concave and edged by a low ridge, indicating robust inter-ossicular articular tissues. Podial gap large and shared by successive ambulacrals and laterals. Ambulacrals grooved for articulation with laterals, this grooving lateral on the ossicle (thereby indicating the lateral was approximately upright in life orientation). Proximal-most laterals boot-shaped and articulating with the ambulacrals at the position of the ankle of the boot, the ossicles arched or deflected distally. Lateral shape becoming progressively more nearly rectangular distally, the morphologic transition most marked at the position of the ambital ossicles. Ambulacral articulation facet of distal laterals forming a triangular adradial ossicular margin. Dorsal surfaces of lateral ossicles distal to the ambital framework margin bearing a continuous, linear groove. Ambital framework, ambulacral and lateral ossicles pustulate, the ambulacrals more coarsely so than the laterals. Circumoral ossicles robust, forming a V-shaped wedge above the MAO. The first ambulacrals distal to the circumorals probably shorter than the subsequent ossicles but not clearly overlapped or deflected distally by the circumoral positioning. MAO only poorly exposed in dorsal aspect, appearing stout, accessory ossicles possibly present (Fig. 3B). Accessory granules occur on the disc but no enlarged primary disc ossicles in evidence. Spinelets not recognized with the pustules of the primary ossicles.

Etymology. The name *elegans* refers to the overall morphologic expression of the new species.

Type. The single specimen is housed in the Museo del Departamento de Geología-Paleontología de Oviedo (Asturias, Spain) under repository number DPO 33484. The ventral arm interval is a partial counterpart.

Occurrence. See "Geologic Setting and Stratigraphy".

Remarks. Skeletal surfaces of the moldic original are well preserved, and the specimen is not seriously distorted. The specimen is small; all arms are incomplete, the longest existing arm radius is 16.5mm, the disc radii as preserved approximately 7mm. The specimen might represent an early ontogenetic stage of a species that would have changed significantly during life, a possibility that cannot be evaluated without the discovery of added material. Lacking appropriate data, interpretation of *Ophiocantabria* must treat the fossil as representative of the genus throughout its ontogeny. Many extant ophiuroid species, however, are small when fully grown, and xenasterids are not known to attain large size; if *Ophiocantabria* was similar in behavior as well as external form to *Xenaster*, then the available specimen likely at least approached full size for its species.

Disc configuration provides differences among encrinasterid genera. Of the seven genera assigned to the family by Spencer and Wright (1966, p. 86), *Cheiropteraster*, *Loriolaster*, and *Mastigactis* lack ambital framework ossicles, whereas specimens of *Urosoma* from only one horizon show ossicles that "might be" so interpreted (Spencer, 1930, p. 433); ambital framework ossicles are well-developed in *Ophiocantabria*. The disc margins of typical *Encrinaster*, *Euzonasoma* and *Crepidosoma* are convex, the ossicular series approximately perpendicular to the arm margin whereas the margin of *Ophiocantabria* is concave, the ambital framework series inclined to the arm and partially inset into lateral ossicular margins. The edge of *Marginura* is also concave, but the ambital framework ossicles are comparatively small, numerous and irregular in shape and arrangement. Disc ossicles occur in *Encrinaster*, *Euzonasoma*, *Crepidosoma*, *Marginura* and *Mastigactis*, and "irregular calcifications" occur "here and there" in *Cheiropteraster* and *Loriolaster* (Spencer, 1930, p. 439), but none appear to occur in *Urosoma* and none have been recognized in *Ophiocantabria*, although granules do occur. Changes in ambulacral and particularly in lateral configuration along the length of the arm are typical of encrinasterids, but proportions of *Ophiocantabria* are distinctive and best evaluated in direct comparison with published illustrations, although the drawings of Spencer (1930) appear somewhat generalized. Authors have argued that the laterals of encrinasterids are at least sublateral in position and capable of at least some rotation toward the ventral portion of the arm axis. The narrow articular grooving between ambulacrals and laterals of *Ophiocantabria* argues against sublateral positioning and flexibility in this genus, and lack of such flexibility would be another expression convergent with expressions of *Xenaster*. Many earlier illustrations of encrinasterids, however, suggest positions similar to those of *Ophiocantabria*.

PHYLOGENETIC ANALYSIS

The phylogenetic analysis of Blake and Guensburg (2015) delineated major clades of Palaeozoic asterozoans as based on taxa selected to illustrate early subphylum diversity; the present analysis positions similar *Ophiocantabria* and *Xenaster* within that earlier listing. The sampling of Blake and Guensburg (2015) was too limited to allow evaluation of phylogenetic sequencing within recognized clades, and similarly, evaluation of encrinasterid phylogeny must await comprehensive familial revision.

Twenty-eight binary and multistate characters were developed (Blake and Guensburg, 2015); the revised data matrix is included here whereas character listing is in that paper. Parsimony Analysis employed PAUP 4.0b8 (Swofford, 1998). Characters were unordered and they were weighted equally regardless of number of states. In analyses using the branch and bound algorithm, six trees of minimum length of 85 were retained; all characters are parsimony-informative. Statistical results are as follows: consistency index CI=0.4824; homoplasy index HI=0.5176, retention index RI=0.7197.

The four ophiuroids occurred in a single clade in all six trees, and the two encrinasterids, *Encrinaster* and *Ophiocantabria*, emerged as sister taxa in all six. Three arrangements of the other two ophiuroids were associated with the encrinasterid pairing: in separate trees, both *Protaster* and *Stenaster* occurred in the basal position, and the two occurred together as a sister group to the encrinasterids in the third configuration. All three arrangements of the ophiuroids occurred with two arrangements of the somasteroids, one with the somasteroids arranged in sequence, and in the other, *Thoralaster* and *Villebrunaster* emerging as sister taxa. Selection of the illustrated cladogram (Fig. 5) was arbitrary and not argued to represent a preferred interpretation. Bremer and bootstrap values, included in the diagram,

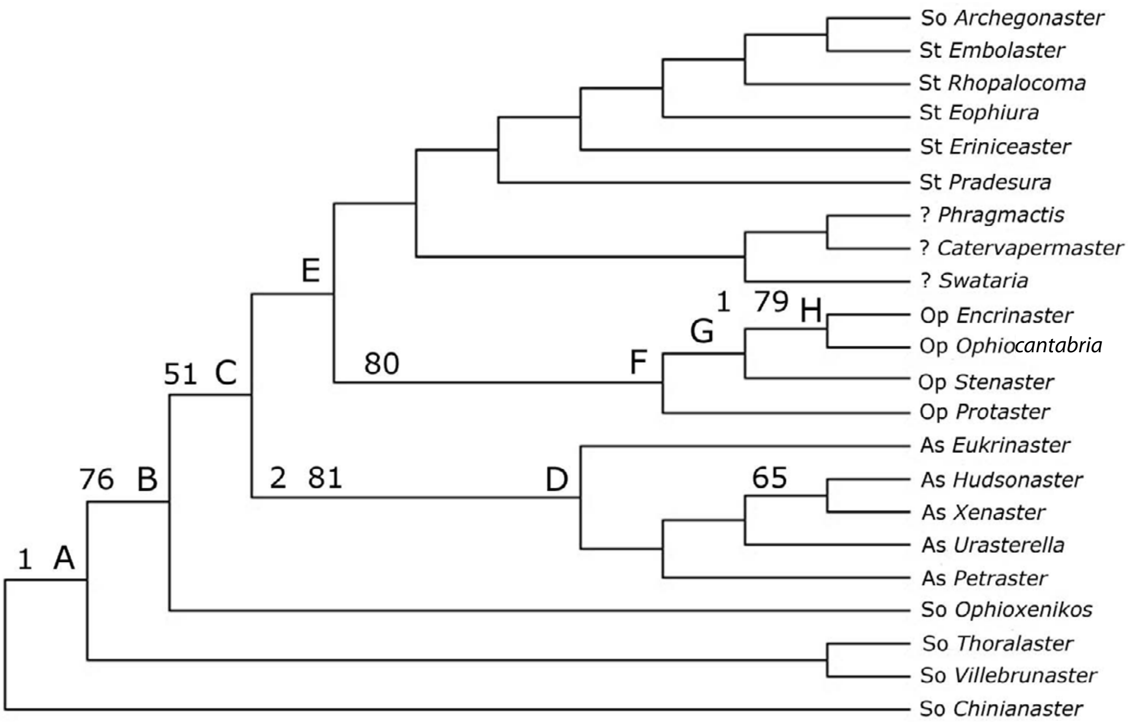

Figure 5. One of six equally parsimonious cladograms obtained after cladistic analysis. So: Somasteroidea; St: Stenuroidea; A: Asteroidea; Op: Ophiuroidea; ?: of uncertain affinities. Bootstrap values above 50% are identified by two-digit numerals, single digit is Bremer support. Select apomorphy listing, nodes are capital letters. A to B: no character transformations. B to C: 1, 3, 4, 27, 0>1; 7, 1>2. C to D: 6, 9, 12, 14, 16, 18, 0>1; 19, 21, 23, 0>2. C to E: 14, 15, 0>1; 19, 21, 0>2. E to F: 3, 1>2; 7, 2>0; 10, 0>2; 11, 13, 23, 24, 25, 0>1. F to Protaster, 1, 1>2; 20, 0>2; 21, 2<1; 28, 0>1. F to G, no character transformations. G to Stenaster, 10, 2>1. H to Ophiocantabria, 2, 28, 0>1. G to Encrinaster, no character transformations.

are comparatively weak, at least in part because the rapid appearance of diverse clades in the fossil record favors rapid phylogenetic diversification and therefore a narrow ideal sampling interval (Blake, 2013; Blake and Guensburg, 2015). Although *Ophiocantabria* in overall arrangement is suggestive of *Xenaster*, specific aspects of the two clearly reflect separate affinities.

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ELECTRONIC APPENDIX I

Character listing for parsimony analysis.—Many character expressions are intergrading, including those of overall body form, abactinal and ambulacral shape, and ambulacral-column articulation arrangements. Coding defines usage.

Overall body form.—

1. 0=Pentagonal; 1=stellate; 2=disk subcircular, arms cylindrical.

Abactinals.—The many abactinal ossicular morphologies among early asterozoans suggest rapid diversification from an uncertain basal condition. Primary ossicles, including abactinals, are separated from accessory spines and granules.

2. 0=Primary abactinal ossicles present; 1=Primary abactinal ossicles not developed.
3. 0=Abactinals delicate, branching, rod- or strap-like; 1=abactinals granular to robust paxilliform; 2=abactinals are small platelets; 3= abactials are large plates.
4. 0=Abactinal arrangement reticulated; 1=abactinal arrangement not reticulated.
5. 0=Abactinals not aligned in series; 1=abactinals aligned in series.

Madreporite.—In Rhopalocoma, the madreporite is at the ambital frame; in B. M. Palaeont. 46601, the madreporite is preserved rotated onto the dorsal surface, and it is so coded here.

6. 0=Madreporite on ventral surface; 1=madreporite on dorsal surface.

Ambital framework.—Ambital framework expressions are varied at lower taxonomic levels providing few characters for recognition of major clades. True "marginals" are separated from necklace and ophiuroid disk frame ossicles, the latter expression (char. 8), although uninformative, is retained here because of the ambiguities surrounding framework ossicles.

7. 0=Marginal framework absent; 1=marginal necklace present; 2=marginal framework present.
8. 0=Disk frame absent; 1=disk frame present.
9. 0=Axillary ossicle absent; 1=axillary present.

Ambulacral series.—

10. 0=Positioning of the ambulacrals across the arm midline irregular, i. e., locally paired, locally offset; 1= ambulacrals clearly paired across arm midline; 2=ambulacrals clearly offset.
11. 0=In dorsal view, successive ambulacrals overlap; 1=in dorsal view, successive ambulacrals abutted.
12. 0=Ambulacrals broad and shield-like, width and length similar; 1=ambulacrals rectangular, wider than long.
13. 0=In dorsal view, ambulacrals not spool-like; 1=in dorsal view, ambulacrals spool-like.
14. 0=Ambulacral-first virgal facets small, abutted or overlapping; 1=ambulcral-first virgal facets large, ossicles closely fitted.
15. 0=Radial water channel large; 1=radial water channel small.
16. 0=Radial water channel closed; 1=radial water channel at least weakly opened.
17. 0=Podia supported by solid basins; 1=podial openings at least suggestive of podial pores present.
18. 0=Arm ambulacrals not vaulted to form furrow; 1=arm ambulacrals vaulted to form furrow.

Virgal series.—

19. 0=Virgal-series ossicles multiple, number diminishing distally; 1=two or three virgal-series ossicles; 2=one virgal-series ossicle; 3=no virgal-series ossicle.
20. 0=First virgal ossicle directed radially; 1=first virgal ossicle directed proximally; 2=first virgal ossicle directed distally.

Radially directed first virgals are oriented approximately perpendicular to the arm midline on a specimen in the inferred resting position. Among many somasteroids as preserved, sequential series are deflected away from this orientation.

21. 0=First virgal-series ossicle delicate, rod-like; 1=first virgal-series ossicle cup- or shield-like; 2=first virgal-series ossicle robust, more or less blocky.

Cup-shaped first virgals form a partial abradial rim to the podial position in a manner similar to the proportionately much shorter adambulacrals of asteroids.

22. 0=Neither second nor third virgal paddle- or shoe-shaped; 1=either second or third virgal paddle- or shoe-shaped.
23. 0=Successive first virgal ossicles not in contact; 1=subsequent first virgals in limited contact; 2=successive first virgals in contact over broad surfaces.

Mouth frame.—

24. 0=Mouth angle ossicles upright, closely appressed; 1=mouth angle ossicles narrowed and extended toward mouth area; 2=mouth angle ossicles flairing.

25. 0=Circumorals in dorsal aspect similar to next-distal ambulacrals, forming an A-frame; 1=circumorals in dorsal aspect forming a Y-frame, the juncture distally inclined; 2=circumoral ossicles cylindrical.
26. 0=Ossicles of ambulacral series not narrowing as the mouth frame is approached; 1=ossicles of ambulacral series narrowing as the mouth frame is approached.

Accessories.—
27. 0=Few or no short spinelets beyond furrow series; 1=shorter spinelets on body wall beyond those of virgal series.
28. 0=Accessory granules few or lacking; 1=accessory granules abundant.

TABLE I. Data matrix for parsimony analysis. "9" is unknown

Archegonaster	0 1999 1 200 009900110 02101 009 01
Catervaparmaster	0 1999 9 209 090011900 39999 999 99
Chinianaster	0 0009 0 100 000000000 00000 000 00
Embolaster	1 0211 9 201 090000100 10111 001 01
Encrinaster	1 0310 9 010 219111000 20292 110 00
Eophiura	0 0210 0 000 000001000 10110 991 90
Eriniceaster	1 0210 0 000 099900000 11111 091 20
Eukrinaster	1 0110 9 201 001010101 20292 000 11
Hudsonaster	1 0311 1 201 101011101 20292 000 01
Ophiohispania	1 1999 9 010 210111990 20202 110 01
Ophioxenikos	1 0110 9 200 090901000 00000 000 99
Petraster	0 0110 1 201 101011101 20292 000 10
Phragmactis	1 1999 0 201 000011000 21191 220 01
Pradesura	2 0210 0 000 000001000 11111 011 10
Protaster	2 0210 0 000 219111000 22191 110 11
Rhopalocoma	0 0310 1 200 099900000 10111 001 20
Stenaster	1 0210 9 000 119111000 20291 110 10
Swataria	1 0210 0 001 090010010 21191 220 00
Thoralaster	0 0009 9 100 010000000 00000 000 10
Urasterella	1 0111 1 201 101011101 20292 000 10
Villebrunaster	0 0009 9 200 010000000 00000 000 10
Xenaster	1 0311 1 201 111011111 20202 000 01