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Degeneraster spenceri n. gen., n. sp. (Asteroidea; Ordovician) and interpretating the early history of the Asterozoa

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Degeneraster spenceri n. gen., n. sp. (Asteroidea; Ordovician) and interpretating the early history of the Asterozoa

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ABSTRACT
Degeneraster spenceri n. gen., n. sp., a new genus and species of Asteroidea de Blainville, 1830 (Echinodermata) from the Late Ordovician (middle Katian) of Morocco, is described. Similarities and differences between basal Somasteroidea Spencer, 1951 and *D. spenceri* n. gen., n. sp. are reviewed. Based on ambulacral (i.e., axial and adaxial) morphology, *D. spenceri* n. gen., n. sp. is assigned to the basal asteroid order Euaxosida Blake, 2018; extraxial morphology in contrast includes expressions that are widely found among more derived Paleozoic asterozoans. *Degeneraster spenceri* n. gen., n. sp. is anomalous among euaxosidan Asteroidea in lacking an ambital framework. In addition, the aboral skeleton is distinctive, and podial pores, otherwise undocumented among euaxosidans, might occur. Atypical expressions provide basis for the recognition of the new family Degenerasteridae n. fam. Differences among *D. spenceri* n. gen., n. sp., other Euaxosida, and the derived asteroid Paleozoic orders Hadrosida and Kermasida are surveyed. To exemplify early asterozoan diversity, the ophiuroid *Componaster* Glass, Blake & Lefebvre, 2024 and unassigned *Falloaster* Blake, Gahn & Guensburg, 2020a, are cited and illustrated for comparison with *D. spenceri* n. gen., n. sp. and other early Asterozoa.

KEY WORDS
Asteroidea,
anomalous morphology,
Late Ordovician,
Morocco,
new family,
new genus,
new species.

RÉSUMÉ

Degeneraster spenceri *n. gen., n. sp. (Asteroidea; Ordovicien) et l'interprétation de la diversification initiale des astérozoaires.*

Degeneraster spenceri n. gen., n. sp., nouveau genre et nouvelle espèce d'Asteroidea de Blainville, 1830 (Echinodermata) de l'Ordovicien supérieur (Katien moyen) du Maroc, est décrit. Sa morphologie ambulacraire (i.e., axiale et adaxiale) permet d'attribuer *D. spenceri* n. gen., n. sp. à l'ordre Euaxosida Blake, 2018 ; néanmoins, sa morphologie extraxiale atypique suggère que des caractères plésiomorphes à l'échelle du sous-phylum ont pu persister chez les premières étoiles de mer, au moins jusqu'à l'Ordovicien supérieur. La morphologie de *Degeneraster spenceri* n. gen., n. sp. se distingue de celle des autres Asteroidea primitifs par l'absence de structure ambitale, la présence possible de pores podiaux, ainsi que par la texture superficielle et la position du madréporite. Ces caractéristiques inhabituelles justifient la création de la nouvelle famille Degenerasteridae n. fam. Les différences entre *D. spenceri* n. gen., n. sp., d'autres Euaxosida et les ordres paléozoïques dérivés Hadrosida et Kermasida sont discutées. Deux autres astérozoaires ordoviciens, *Componaster* Glass, Blake & Lefebvre, 2024 (Ophiuroidea) et *Falloaster* Blake, Gahn & Guensburg, 2020a (classe non assignée), qui présentent également des morphologies atypiques, sont cités et illustrés à des fins de comparaison avec *D. spenceri* n. gen., n. sp. et d'autres astérozoaires primitifs.

MOTS CLÉS
Asteroidea,
morphologie atypique,
Ordovicien supérieur,
Maroc,
famille nouvelle,
genre nouveau,
espèce nouvelle.

INTRODUCTION

The subphylum Asterozoa has been interpreted as derived from an echinoderm suspension-feeding ancestor that lived with the mouth frame directed into the water column, the habit of the ancestor giving way to mobile descendants living with the mouth frame directed toward the substrate (e.g., Spencer 1951; Fell 1963). The Asterozoa attained broad diversity early in its recognized skeletal history, as is argued by recognition of four Early Ordovician class-level taxa, the Asteroidea de Blainville, 1830, Ophiuroidea Gray, 1840, Stenuroidea Spencer, 1951, and the basal Somasteroidea Spencer, 1951 (Blake 2013; Blake & Lefebvre 2025).

From the time of taxon recognition, the Somasteroidea has been treated as basal among asterozoans by some authors (Spencer 1951: 87, as "first stages") but not by all (e.g., Dean Shackleton 2005). Because asterozoan ancestry is not identified and a robust sister group for phylogenetic analysis has been argued to be unknown (e.g., Blake & Lefebvre 2025), phylogenetic analysis of the Asterozoa is not undertaken here; to do so would require the speculative designation of a sister group as well as the necessarily idiosyncratic development of a data matrix that would compromise interpretation of the very ambiguities that *Degeneraster* n. gen. and other cited genera serve to exemplify.

Because of the uncertainties, the Somasteroidea was treated as a working outgroup in some phylogenetic studies (Blake & Guensburg 2015; Blake *et al.* 2015a; Blake 2024). Evolutionary skeletal sequencing within the Somasteroidea has been argued (e.g., Blake & Lefebvre 2025; below) but seeking to minimize influence of these hypotheses on analyses, development of data matrices sought to allow designation of either individual or all somasteroid genera as the "ingroup outgroup".

In a seminal treatment (Spencer & Wright 1966: 9), the asterozoan skeleton was subdivided into "axial", "adaxial", and "extraxial" components. The axial and adaxial series embrace the water-vascular system and, in that respect, are crucial to asterozoan life habits. Axial and adaxial evolutionary changes were coordinated, integrated, and progressive from the basal somasteroids to the derived asterozoan lineages; axial and adaxial series therefore are emphasized in the recognition of higher taxa. The remainder of the skeleton, the extraxial, was much varied both within and among asterozoan lineages, therein reflecting evolutionary flexibility under localized environmental constraints. The extraxial, although important, is secondary in the recognition of higher taxa (e.g., Blake 2013, 2018, 2024; Blake & Lefebvre 2024, 2025; Glass *et al.* 2024).

Adaxial expression provides the fundamental guide to the designation of class-level taxa of Asterozoa (Blake 2013; Blake & Lefebvre 2025: 459). Presence of multiple virgalial series is necessary and sufficient for assignment to the basal Somasteroidea, although the series was lost at the mouth frame of the somasteroid *Archegonaster* Jaekel, 1923, and virgals and virgalia potentially were retained on the disk but not the arms of unassigned *Catervaparmaster* Blake, 2000. Virgalia were reduced to two to four ossicles in the Stenuroidea, a single ossicle in the Asteroidea and Ophiuroidea, and fully lost in problematic *Falloaster* Blake, Gahn & Guensburg, 2020a.

Although readily assigned to the asteroid Euaxosida, aspects of *Degeneraster spenceri* n. gen., n. sp. morphology are plesiomorphic derivatives of the basal Somasteroidea and are discussed in the concluding section "Survey of Asterozoan Configuration and Construction". Axials and adaxials indicate assignment of *D. spenceri* n. gen., n. sp. to the basal asteroid order Euaxosida Blake (Figs 1-3E-H; 4A, B; 5B-F) rather than the derived Paleozoic orders Hadrosida Blake (Figs 4C-E; 5A, G, H) and Kermasida Blake (Fig. 4F-H). *Degeneraster spenceri* n. gen., n. sp. and the unusual ophiuroid *Componaster spurius* Glass, Blake & Lefebvre, 2024 (Fig. 5I, J) illustrate some atypical morphologies of early asteroids and ophiuroids, whereas unassigned *Falloaster* (Fig. 5K) exemplifies unsuccessful adaptations, "unsuccessful" because of morphologies not recognized elsewhere among asterozoans.

The skeleton of early asterozoans was reviewed by a number of studies including Spencer (1914-1940, 1951), Spencer & Wright (1966), Smith & Jell (1990), Mooi & David (2000), Dean Shackleton (2005), Blake (2018, 2024), and Villier *et al.* (2018). The Somasteroidea was emphasized in several titles (Spencer 1951; Fell 1963; Blake 2013; Blake & Guensburg 2015; Blake & Lefebvre 2025). *Degeneraster* n. gen. (Figs 1; 2) exemplifies differences between basal somasteroids (e.g., Fig. 3A-D), select basal asteroids (e.g., Figs 1-3E-H; 4A, B; 5B-F), and select derived Paleozoic asteroids (e.g., Figs 4C-H; 5G, H). *Componaster* Glass, Blake & Lefebvre, 2024 (Fig. 5I, J) and *Falloaster* (Fig. 5K) exemplify differences between somasteroids, asteroids, and other early lineages.

GEOLOGY AND STRATIGRAPHY

All specimens of *Degeneraster spenceri* n. gen., n. sp. come from Isthlou (ECR-F6), in the Tafilalt region, eastern Anti-Atlas, Morocco (for locality details and map, see Nohejlová & Lefebvre 2022). They were collected in October 2010, during a field campaign co-organized by the Cadi-Ayyad University (Marrakesh, Morocco) and Claude Bernard Lyon 1 University (Villeurbanne, France). The study material is registered in the paleontological collections of Cadi-Ayyad University in Marrakesh (AA).

The Isthlou section exposes the transition between the uppermost beds of the Lower Ktaoua Formation and the overlying Upper Tiouririne Formation (*Acanthochitina barbata* Zone, middle Katian, Upper Ordovician; Colmenar *et al.* 2022). At Isthlou, several small excavations explored during the 2010 field campaign and excavated by local fossil traders in the sandstones of the Upper Tiouririne Formation have yielded abundant and diverse echinoderm remains, including at least two asteroid taxa (*Degeneraster spenceri* n. gen., n. sp. and *Petraster caidramiensis* Blake & Lefebvre, 2024), as well as caryocystitid rhombiferans, crinoids, diploporites, mitrocystitid mitrates, ophiuroids, and pyrgocystid edrioasteroids (Lebrun 2018; Botting 2022; Sumrall & Zamora 2022; Van Iten *et al.* 2022). Edrioasteroids are attached to various objects, including large specimens of the conulariid *Pseudoconularia* cf. *grandissima* (Sumrall & Zamora 2022; Van Iten *et al.* 2022). Other faunal elements include brachiopods, bryozoans, machaeridian annelids and, mostly, trilobites (e.g., illaenids, trinucleids; Lebrun 2018; Colmenar *et al.* 2022; Van Iten *et al.* 2022).

At Isthlou, the remarkable preservation of most echinoderms, including the three nearly complete and fully articulated specimens of *Degeneraster spenceri* n. gen., n. sp., suggests that they were buried alive (or shortly after death) by storm-generated obrution deposits. However, the lithology in which they are preserved (fine micaceous sandstones) hinders the observation of fine morphological details of many specimens.

TERMINOLOGY OF THE ASTEROIDEA

Terminology with minor edits is from Blake (2024) and Blake & Lefebvre (2024, 2025). The aboral surface is directed toward the water column, the oral surface toward the substrate. The primary skeleton forms the body wall. Axial (or ambulacral) ossicles form a double series along the axis of the arm. Axial ossicles are divided into two components: the adradial ridge lies at the arm midline and forms the radial water-vascular channel, and the transverse ridge extends abradially from the adradial ridge to abut the adaxial. Because of variation among taxa, narrow component definition is not possible, the terms a convenience for description. The unpaired axial terminal is the distal-most axial, at the arm tip. Mouth-angle ossicles (MAO) are the proximal-most ossicles of the axial series. The mouth frame ring is the actinostome, in many asteroids vaulted toward the disk interior and conveying the MAO away from the substrate. Somasteroid virgal ossicles that are aligned to form virgalia and asteroid adambulacrals are adaxial ossicles. Ossicles other than axials and adaxials are extraxial. The somasteroid and asteroid body is edged by a single or double series of more or less clearly differentiated marginal ossicles. Because the term "marginals" has been broadly applied within echinoderms with unclear implications of homology, the genetically neutral term ambital framework was proposed (Blake 2013; Blake & Guensburg 2015). A single inferomarginal ambital framework series is treated as homologous throughout Paleozoic asteroids. A second ambital framework series, the superomarginal, occurs in many asteroids; the superomarginal series might have been emergent among somasteroids (Blake & Lefebvre 2025). The axillary (or odontophore) is a more or less clearly differentiated unpaired ossicle typically aligned with the inferomarginal series at the interbrachial midline. Abactinals are all the ossicles aboral to the ambital framework except the water-vascular madreporite. Among many asterozoans, a medial disk abactinal, the centrale, is differentiated. The centrale can be enclosed by a so-called primary circlet of more or less differentiated ossicles. Midarm ossicles can be enlarged and/or otherwise differentiated to form a carinal series. Actinal ossicles are extraxials found between the marginals and adaxials. Spines, spinelets, and granules are extraxial and termed accessories. Accessories are common to abundant on all asteroid and somasteroid ossicles except arm axials. Differentiation of accessories among Paleozoic asteroids appears generally limited as compared to corresponding ossicles of post-Paleozoic asteroids, but differentiation among Paleozoic exemplars is generally incompletely understood because of the limitations of preservation.

Abbreviations

Institutional abbreviations

AA	Université Cadi Ayyad, Marrakesh;
CMC	Cincinnati Museum Center, Cincinnati;
FMNH	Field Museum of Natural History, Chicago;
GSI/I	Geological Survey of Ireland, Dublin;
IMNH	Idaho Museum of Natural History, Pocatello;
MHNM	Muséum d'Histoire naturelle, Marseille;
MUGM	Karl E. Limper Geology Museum, Miami University, Miami, Ohio;
PIN	Paleontological Institute RAS, Moscow;
TMM	University of Texas Museum of Paleontology, Austin;
UCBL-FSL	collections de paléontologie, Université Claude Bernard Lyon I, Villeurbanne;
UI-X	Prairie Research Institute, University of Illinois Urbana-Champaign;
UMMP	University of Michigan, Museum of Paleontology, Ann Arbor;
USNM	National Museum of Natural History, Washington.

Other abbreviation

MAO	mouth-angle ossicle.

SYSTEMATIC PALEONTOLOGY

Class ASTEROIDEA de Blainville, 1830
Order EUAXOSIDA Blake, 2018

Family Degenerasteridae n. fam.

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Type and only known genus. — *Degeneraster* n. gen.

Diagnosis. — Same as for type species, by monotypy.

Genus *Degeneraster* n. gen.

urn:lsid:zoobank.org:act:E94EE171-B0A1-4C5F-BB4E-315E8C23D5C0

Type species. — *Degeneraster spenceri* n. sp.

Diagnosis. — Same as for type species, by monotypy.

Etymology. — Latin, *degener*, departing from its kind; referring to absence and inferred phylogenetically significant loss of the marginal series; also, atypical abactinal expression; atypical development of the madreporite; potential axial enclosure of the water-vascular tissues; potential presence of podial pores; and the ambiguities these unusual expressions bring to interpretation of the early history of Asterozoa; and Greek, *ἀστήρ*, star.

Degeneraster spenceri n. gen., n. sp.
(Figs 1; 2)

urn:lsid:zoobank.org:act:3339267A-0574-4547-80C2-669F34FB9D33

Material examined. — **Holotype. Kingdom of Morocco** • AA.IST.OS.62; Eastern Anti-Atlas, Isthlou; Upper Tiouririne Formation; Late Ordovician (middle Katian). Of the three available specimens, the holotype was designated because it is the only one of the three available specimens known from both the aboral and oral surfaces. The ossicular detail of the oral surface of paratype AA.IST.OS.34 is the best preserved of the three.
Paratypes. Kingdom of Morocco • 2 specimens: AA.IST.OS.34; AA.IST.OS.59; Eastern Anti-Atlas, Isthlou; Upper Tiouririne Formation; Late Ordovician (middle Katian).

Derivation of name. — Named in honor of W.K. Spencer, who recognized the complex diversity of early Asterozoa (Spencer 1914-1940, 1951), *D. spenceri* n. gen., n. sp. providing a new example.

Type locality and stratum. — Kingdom of Morocco, eastern Anti-Atlas, Isthlou; Upper Tiouririne Formation; Late Ordovician (middle Katian).

Diagnosis. — Abactinals sub-granular to plate-like, closely abutted, broadly uniform in total but individually somewhat varied in outline. Aboral ossicular differentiation (e.g., carinals, aboral circlet) not definitively recognized; scattered papular pores might be developed. Madreporite oral, offset from mouth frame, surface texture granular. Marginals not developed. Interbrachial oral surface actinals irregular in form and arrangement, those adjacent to mouth frame more plate-like, those of arm nearly granular. Axials robust; adradial ridge might enclose radial water-vascular tissues; abradial terminus of transverse ridge not flared but rather abutting a prominent facet of the adaxial. Podial receptacles large, podial pores might be present.

Description

Overall form five-armed, stellate, disk moderately large, low-vaulted; interbrachial angles weakly rounded, arms triangular, taper quite abrupt, arm tips rounded. R/r 2.5:1 of paratype AA.IST.OS.34. Abactinal ossicles plate-like to granular, irregular in outline, size variation limited; abactinals closely abutted, edges perhaps overlapping; respiratory papular pores possibly developed. Abactinal alignment in defined rows, either parallel to the arm axis or transverse to the axis, not recognized; primary circlet and centrale if present at most only weakly differentiated. Madreporite subcircular, located on oral interbrachial surface near to but not abutting MAO, axials, or adaxials. Ambital framework series not recognized. Axillary/odontophore if occurring not clearly differentiated. Disk oral surface actinals plate-like, irregular, those of arm adjacent to adaxials smaller, more nearly equidimensional than those of disk interbrachia, both unlike abactinals.

Axials nearly paired across arm midline. Axials approximately equidimensional and approximately bilateral. Adradial ridge thickened, potentially enclosing water-vascular tissues; successive adradial ridges abutted, not appearing overlapping. Transverse ridge comparatively short, thickened; not flared abradially, rather directly abutting prominent facet on adaxial. Podial receptacle large, potentially opening as a podial pore rather than closed as a podial basin. Podial receptacle approximately equally shared by successive axials. Axials weakly offset aborally onto adaxials. Axials not appearing to narrow significantly approaching MAO suggesting only limited vaulting of the actinostome. MAO pair quite large, narrowly keel-shaped. Torus not recognized. Linear series of small spinelet attachment sites

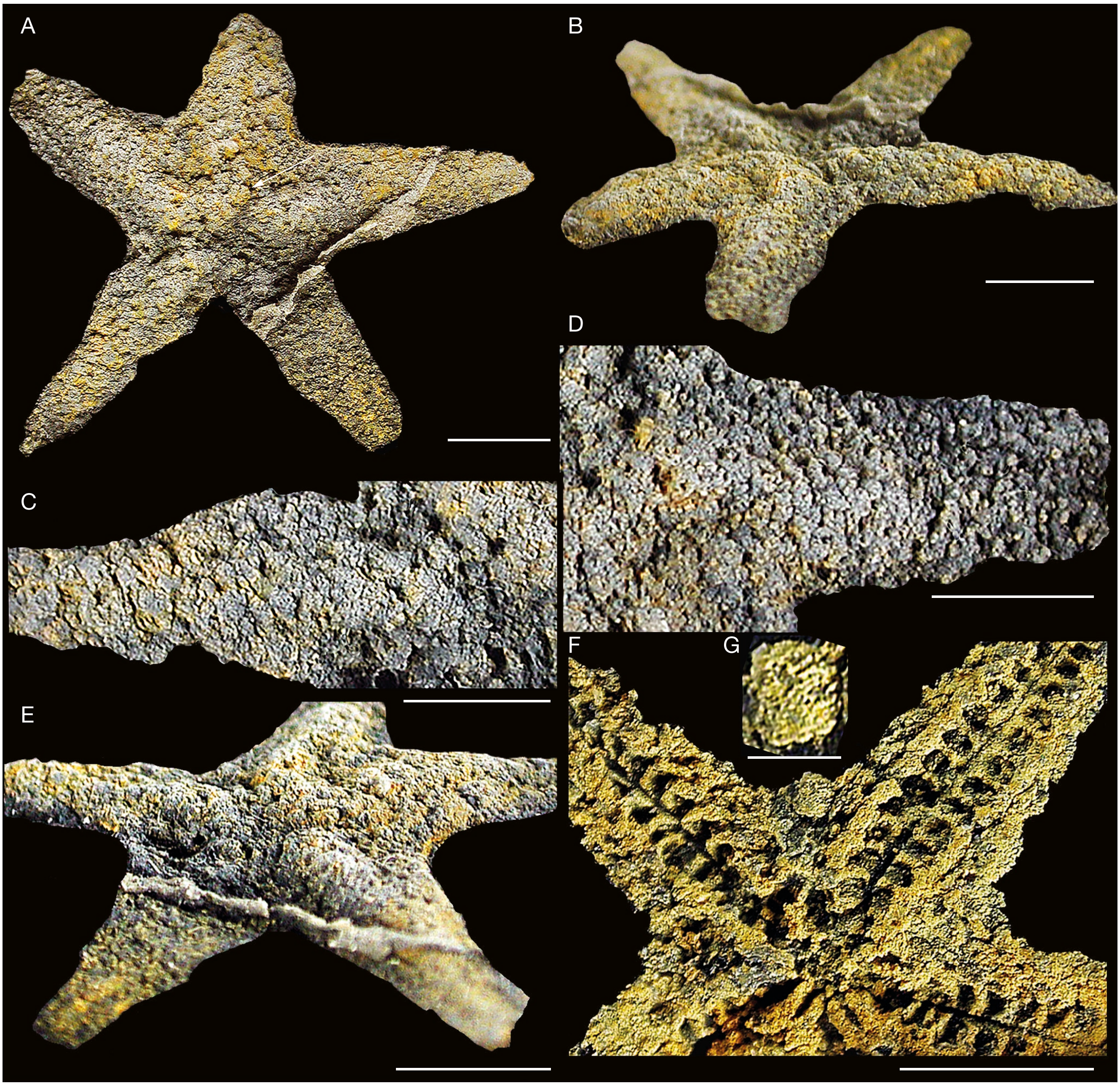

Fig. 1. — *Degenerasterspenceri* n. gen., n. sp., holotype AA.IST.OS.62, artificial casts; Euaxosida: **A**-**E**, aboral views: **A**, **B**, **E** entire remnant, the breakage surface serving to orient images, **B**, **E**, oblique views; **C**, arm to SW of A; **D**, arm to NW of A. Distal arm intervals pass out of plane of focus in inclined views. The central disk collapsed into the interior, specimen distortion from original life shape appearing limited. Abactinals are uniform if somewhat irregular and appear to have overlapped slightly, overlap perhaps enhanced with preservation. Configuration of the disk might suggest some minor differentiation of centrale and an aboral circlet (A, **arrow at possible ring margin**). Any alignment of abactinals in rows is minor, and no views suggest presence of an ambital framework. Scattered dark spots might represent papular pores, alternatively these might be preservational irregularities; **F**, oral aspect, closely appressed mouth-angle ossicles (MAO) and axials indicate specimen is little distorted and flattened from life configuration; extraxials irregular, small, inferomarginals not differentiated; madreporite in upper interbrachium; **G**, granular madreporite surface similar to that of *Chinianaster* (Blake & Lefebvre 2025: fig. 3A, B) and differing from those typical of most asteroids (e.g., Fig. 5E). Scale bars: A, B, E, F, 5 mm; C, D, 3 mm; G, 1 mm.

possibly developed on MAO edge but no enlarged accessory faceting recognized. A weakly differentiated terminal ossicle might occur. Adaxials approximately equidimensional; a prominent facet abuts the axial, lateral faceting linking adjacent adaxials thought to be present; enlarged accessory boss located centrally. Other accessories at most only weakly developed.

Remarks

Ordinal assignment for *D. spenceri* n. gen., n. sp. to the Euaxosida is largely based on presence of a shallow, low-vaulted ambulacral furrow; approximately equidimensional axials with weakly defined cross-furrow articulation faceting with large podial receptacles; and robust adaxials with limited linkages to the axials (Figs 1-3E-H; Blake 2018).

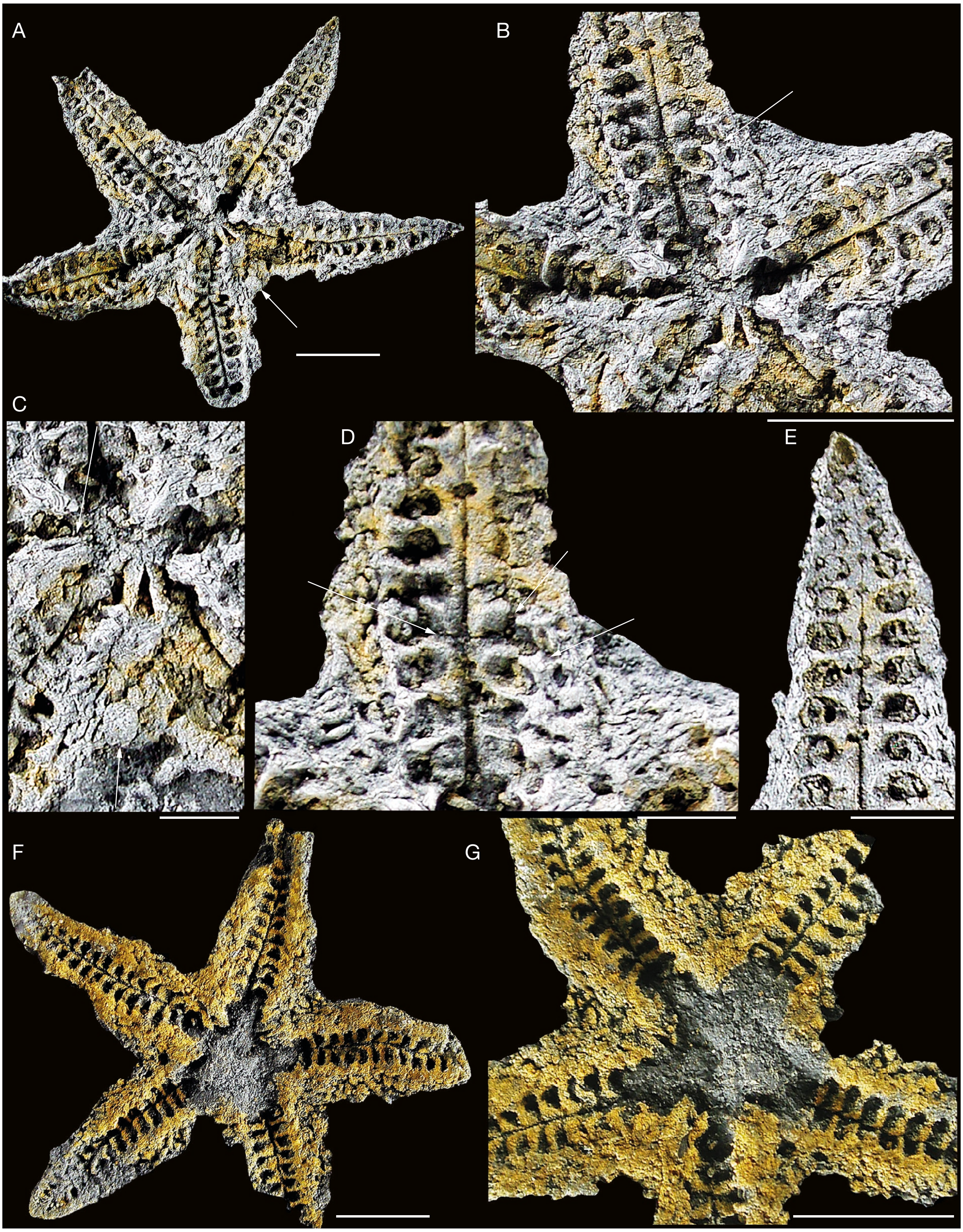

Fig. 2. — *Degeneraster spenceri* n. gen., n. sp., artificial casts, Euaxosidea Blake, 2018: **A**-**E**, paratype AA.IST.OS.34: **A**, entire remnant, madreporite (**arrow**); **B**, disk area; closely abutted mouth-angle ossicles (MAO) indicate only minor burial distortion; ossicles unlike abactinals (Fig. 1) arguing actinal differentiation; adaxial of D (**arrow**); **C**, MAO configuration, torus lacking, linear series of spots (**upper arrow**) might identify MAO spinelet bases; madreporite (**lower arrow**); **D**, NW arm of A, no differentiated marginal series in evidence; interbrachial ossicles plate-like, arm ossicles granular, neither series similar to abactinals; axials equidimensional, podial basins large, shared by successive axials; axials longitudinally abutted, not overlapping (**left arrow**); axials and adaxials slightly displaced, not overlapping significantly (**lower right arrow**); adaxials T-shaped with a stem extended toward the axial; spine base medial (lower right arrow); adradial adaxial margins rounded for podia; **E**, NE arm tip of A, terminal not recognized; podial depressions suggest podial pores, see Discussion; **F**, **G**, paratype AA.IST.OS.59, oral view; **F**, entire remnant; **G**, mouth frame partially distended, axial exposure and shadows indicate arms retain asteroid ambulacral furrow; madreporite not recognized but likely obscured. Scale bars: A, B, F, G, 5 mm; C-E, 2 mm.

Because an ambital framework inferomarginal series is recognized in all known somasteroid genera, and because asteroids are considered derivatives of somasteroids, inferomarginal presence in the (unknown) first asteroid is assumed. A recent study of a large Early Devonian fauna from Central Victoria, Australia, treats many taxonomically diverse and morphologically complex asterozoans (Jell 2026). Because of availability of only a limited number of complex specimens that suffered varying degrees of diagenetic disruption, interpretation was difficult, the new genus and species *Quarreriaster madelynae* particularly so because of the small size and uniform morphology of the extraxial ossicles. In "Remarks" under the generic diagnosis (Jell 2026: 81), the inferomarginal column is noted to have been "… reduced to a single plate…" although it is also noted that the inferomarginal column might have been "indiscernible" (Jell 2026: 82). Recognition of marginal series even among some crown-group asteroids can be problematic, a definitive identification of marginals calling for tracing of the marginal series to the terminal ossicle at the arm tip, that not practical for *Q. madelynae* specimens. Phrasing in the description of *Q. madelynae* argues extraxial ossicular series alignment beyond that recognized for *D. spenceri* n. gen., n. sp. Unlike *D. spenceri* n. gen., n. sp., differentiation of abactinals and actinals is not recognized in *Q. madelynae*. Again, perhaps only because of preservation, marginal series were not found in Carboniferous *Illusioluidia* Blake & Guensburg, 1989, it too assigned familial status (Blake 2018). All three species differ significantly in many aspects of morphology with similarities limited to class and ordinal-level manifestations, the loss, or potential loss of marginal series convergent.

Among most asteroids, the skeletal ambital framework provides a line of demarcation between typically distinctive aboral abactinals and oral actinals; although a skeletal framework is not recognized in *D. spenceri* n. gen., n. sp., abactinals and actinals are differentiated. Recognition of the family Degenerasteridae n. fam. also emphasizes differences between abactinals and actinals; the positioning and surface texture of the madreporite; and the potential presence of podial pores.

Closest affinities of the Degenerasteridae n. fam. are thought to lie with the Palasterinidae Gregory, 1899, the family revised in some detail in Blake (2018: 23). The Palasterinidae is a large and diverse compilation of genera, perhaps itself of complex ancestry.

Definitive evaluation of radial water-vascular tissue positioning among Paleozoic asteroids can require transverse views of arms, unfortunately unavailable for *Degeneraster* n. gen. Although preservation is difficult, an external skeletally defined water-vascular pathway is not recognized. Axial shape and arrangement suggest radial water-vascular tissues were skeletally enclosed, if so a potential holdover from somasteroids.

Form and positioning of the madreporite of *Degeneraster* n. gen. is like that of the somasteroid *Chinianaster* Thoral, 1935, again suggesting plesiomorphy.

Specifics of abactinals of *Degeneraster* n. gen. are unlike those known among somasteroids, but uniformity and small size are analogous, therein potentially derivative with limited change.

The ratio of arm radius to disk radius, R:r, is commonly included in taxonomic descriptions of asterozoans, and is included here; there are reservations (Tablado & Calcagno 1994). Decay accompanied by compaction under a sediment load affect fossil proportions and thereby potential interpretation of life R:r, see discussions on the "buccal slit".

A series of small openings are developed along the adradial boundary distally on one arm of a single specimen (Fig. 2E). Viewed from the arm tip and depending on how preservation is interpreted, the first several axial pairs lack a pore; the next two pairs exhibit a pore at the proximal edge of each pair; the next three pairs share a pore approximately medially, the more proximal two pores irregular; a pore of each axial of the next pair appears slightly inset from the midline; no further pore pairs are recognized on this arm. An enlarged opening occurs on an adjacent arm with a very small elliptical opening on the next-proximal axial pair (distally, Fig. 2D). Given disparities of occurrences, the openings are tentatively interpreted as diagenetic artifacts that nevertheless potentially reflect some aspect of ossicular construction.

SURVEY OF ASTEROZOAN CONFIGURATION AND CONSTRUCTION

Background

Interpretations of skeletal homologies among early asterozoans have differed significantly among authors leading to significantly differing phylogenetic and taxonomic conclusions (e.g., Spencer 1914-1940, 1951; Fell 1963; Spencer & Wright 1966; Smith 1984, 2005; Smith & Jell 1990; Mooi & David 2000, 2008; Dean Shackleton 2005; Blake 2013, 2018; Telford *et al.* 2014; Blake *et al.* 2015b; Villier *et al.* 2018; Hunter & Ortega-Hernández 2021; Blake & Hotchkiss 2022; Blake & Lefebvre 2025: 482). Supplementing this rich literature, ongoing new discoveries and reevaluations of Ordovician Somasteroidea, Asteroidea (e.g., Blake & Lefebvre 2024), Ophiuroidea (e.g., Glass *et al.* 2024), and unassigned Asterozoa (e.g., *Falloaster*) have continued to provide significant new data addressing early asterozoan diversity and evolution. With emphasis on atypical *Degeneraster* n. gen., the following discussions follow the leads of earlier workers (e.g., Ubaghs 1953; Spencer & Wright 1966; Dean Shackleton 2005) in developing overview of the early history of the Asterozoa.

Body form

Overall body configuration provides guidance to class-level affinities among Paleozoic asterozoans, but many, including some ophiuroids (e.g., *Componaster*, Fig. 5I, J), are at least broadly similar and therefore form is not a definitive indicator of affinities of *D. spenceri* n. gen., n. sp.

The axial skeleton: arm axials

Arm axials of *D. spenceri* n. gen., n. sp., like those of somasteroids, are approximately equidimensional and bilateral with the adradial ridges potentially enclosing the radial

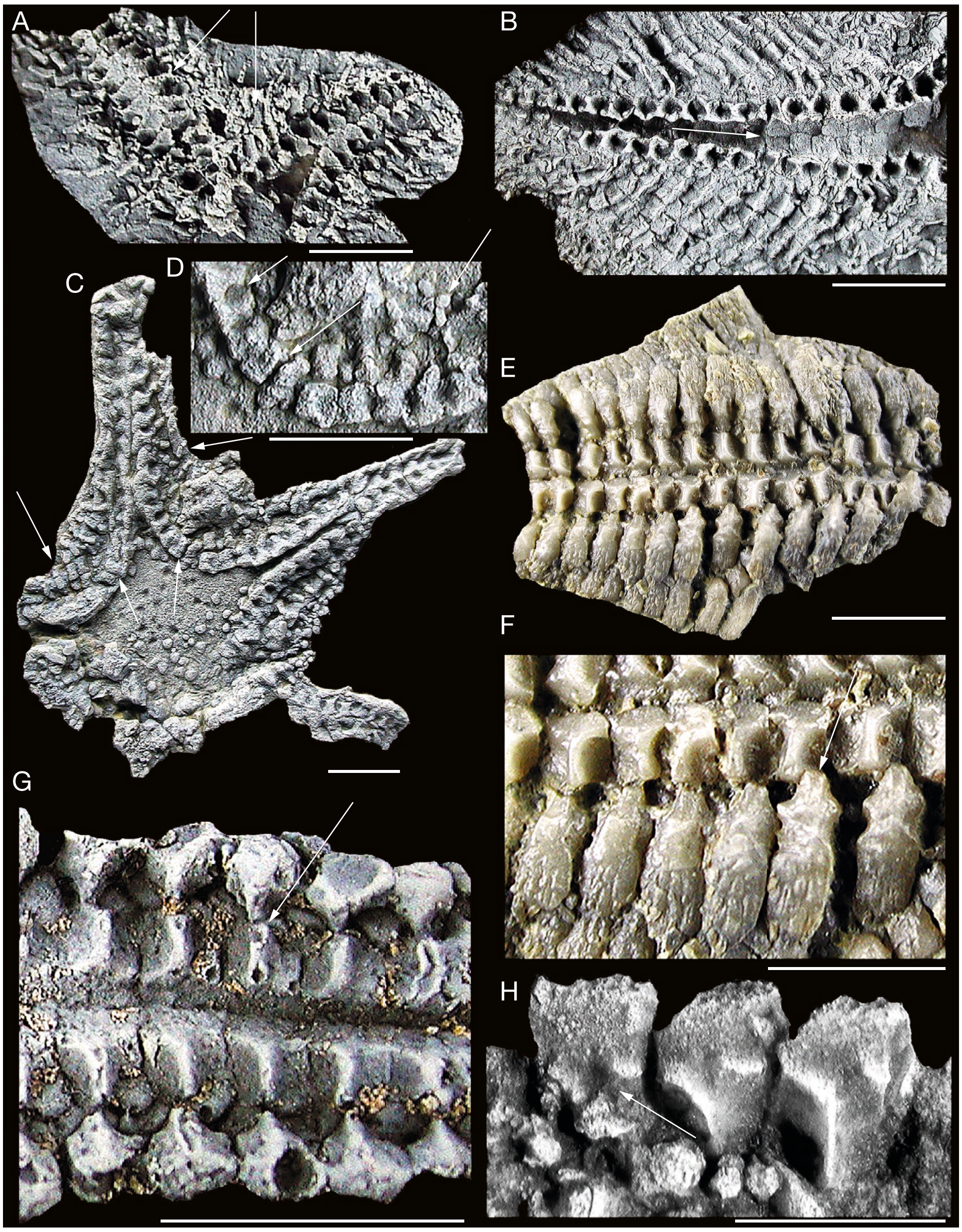

Fig. 3. — Diverse Somasteroidea Spencer, 1951 (**A**-**D**) and Euaxosida (**E**-**H**); **A**, **B**, and **G** are artificial casts, others are original specimens: **A**, *Chinianaster levyi* Thoral, 1935, Saint-Chinian Formation, Early Ordovician (late Tremadocian); Montagne Noire; UCBL-FSL 712003, oral view, axials of left ambulacrum abut at mouth frame as in life, dilated in ambulacrum to right to yield an artifactual "buccal slit"; radial channel closed orally by a shield-like skeletal arch, the transverse ridge flaring abradially to abut virgal series (**left arrow**); disrupted virgalia arise at oral frame (**right arrow**) thereby perhaps contributing to the view that the first axial series was deflected to form the inferomarginal series (Spencer 1951; Spencer & Wright 1966). **B**, *Cantabrigiaster fezouataensis* Hunter & Ortega-Hernández, Fezouata Formation, Early Ordovician (late Tremadocian); Zagora area, Central Anti-Atlas, Morocco; holotype UCBL-FSL 424961, oral view, enlarged and flattened radial water-vascular channel exposes large aboral surface, axials both paired and offset along arm midline (**arrow**); axial intervals beyond radial channel boundary equidimensional and approximately bilateral; adaxials robust, abutted to form platform; **C**, **D**, *Ophioxenikos langenheimi* Blake & Guensburg, Lower Pogonip Group, Early Ordovician (late early to middle Floian); Ely Springs Mountain Range, south-central Nevada, United States; holotype UI–X–4751, oral views: **C**, entire specimen, disk dilated, granular abactinals and darkened circular abactinal "footprints" exposed within mouth frame, axial series dilated proximally, remaining closed distally; mouth-angle ossicles (MAO) pair (**abutted arrow pair**), MAO little differentiated from and aligned with subsequent axials; adaxial series deflected to form platform like configuration at disk (**left arrow**), virgalia appearing less robust, perhaps separated in life (**upper right arrow**); **D**, mouth frame and adjacent axial series; MAO pair (**medial arrow**), abactinals and abactinal "footprint" beyond; shared skeletally closed podial basin (**left arrow**); adaxial series near mouth frame not suggesting a platform (**right arrow**); **E**, **F**, *Jugiaster specious* (Miller & Dyer, 1878), CMC P50629, specimen locality data lost, oral views: **E**, most of remnant, axial form similar to that of somasteroids but radial water-vascular channel proportionately smaller, adaxials and inferomarginals extend laterally in a convergent configuration suggestive of virgalia; **F**, axials weakly displaced but articulate at a small point (**arrow**) suggesting plesiomorphic flexibility; podial basins closed but adaxial curvature suggests podial tissues extended laterally, an apparent skeletal discontinuity at least suggesting a podial pore; **G**, *Petraster kinihani* (Baily, 1879), Ballymoney Group (Sandbian; see Donovan *et al.* 1996), near Bannow, County Wexford, Ireland; GSI/F 00084, oral view, distal right, flattened arm interval, small water vascular channel dilated, axial interval beyond radial channel bilateral, approximately equidimensional, in that similar to **A**-**F**; water channel ridge distal to right of transverse ridge depressed relative to that to left marking transverse water-vascular channel; transverse ridge abutment with adaxial small point (**arrow**) marking weak euaxosidan vaulting and suggesting retention of potential lateral flexure as in somasteroids; adaxial curvature suggests ossicles bordered soft tissues as **F**; **H**, *Estoniaster maennili* Blake & Rozhnov, Late Ordovician (late Sandbian, upper part of the *Didymograptus multidens* Zone), Vasalemma Quarry, near Tallinn, northern Estonia; PIN 4125/766, oral view of adradial termini of axials, cross-furrow articular faceting clear but weak, transverse channel to podial basin (**arrow**) on ossicular surface, not obscured between successive axials as in derived orders (Fig. 4D). Scale bars: A, C, D, F-H, 3 mm; B, E, 5 mm.

water-vascular tissues. Podial receptacles are large and approximately shared between successive ossicles; podial receptacles of *D. spenceri* n. gen., n. sp. potentially open as podial pores, and in that similar in appearance to the somasteroids *Archegonaster*, *Chinianaster*, and *Thoralaster* Dean Shackleton, 2005 (Blake & Lefebvre 2025: figs 1A, F; 8F, G). Adaxial configuration and furrow presence of *D. spenceri* n. gen., n. sp. in contrast are typically euaxosidan.

Critical in the transition from ancestral somasteroids to basal euaxosidan asteroids was onset of axial displacement onto the adaxial as a part of the vaulting process to form the ambulacral furrow. An axial oral skeletal shield has been recognized among the unvaulted somasteroids (e.g., Fig. 3A; Blake & Lefebvre 2025) that served to enclose and protect the oral surfaces of the radial water vascular tissues (skeletal shields, however, commonly were destroyed taphonomically as to expose the aboral surface of the water-vascular channel, especially so toward the thickened disk; Fig. 3B). Oral shield loss accompanied the evolution of asteroid ambulacral furrow vaulting.

The nature of podial tissue seating is important to the evaluation of asteroid history. Podial receptacles of most Paleozoic somasteroids and asteroids are skeletally closed as to yield so-called "podial basins" ("podial roof" is descriptively better), the solid "podial basin" surfaces restricting podial tissues to the exposed furrow exterior. Podial openings, "podial pores", allowed retreat of some podial tissues into the protected disk and arm interiors. Presence of podial pores among Ordovician asteroids has been argued (e.g., Branstrator 1975), discussed, and challenged (Blake & Guensburg 1988; Blake 2018: 11), challenged in part because true podial pores are clearly and uniformly sculptured whereas putative "podial pores" tend to be small and irregular in form and occurrence, and in part because putative "podial pores" typically are found near the axial-adaxial juncture where articulation is particularly weak and subject to minor displacement with sediment compaction. Although interpretation is problematic, podial pores potentially were developed in *D. spenceri* n. gen., n. sp. Curvature of the adradial margins of adaxials of both *D. spenceri* n. gen., n. sp. (Fig. 2D) and *Jugiaster speciosus* (Miller & Dyer, 1878) (Fig. 3F) served to constrain podia; however, because of preservational limitations, possible presence of an aperture is obscure in these genera. Podial pores, however, are recognized in some later Paleozoic asteroids including the kermasidan *Delicaster* Blake & Elliott, 2003 (Kesling 1967; Fig. 4F). A clearly illustrated Devonian occurrence was documented by Haude (1995) and reported Paleozoic occurrences were summarized (Blake 2018). Podial pores are universal among crown group Asteroidea and are developed in unassigned *Falloaster* (Fig. 5K). Given breadth of occurrences, podial pores are homoplastic.

In some somasteroids, the transverse ridge flares abradially to seat the virgal series, the virgalia capable of coordinated lateral flexure in the oral plane (Fig. 3B; Blake & Lefebvre 2025). Some lateral flexure appears to have been retained in some euaxosidans (Fig. 3E-G) but abandoned in the *Degeneraster* n. gen. lineage (Fig. 2), and flexure was entirely lost among derived asteroids, loss suggesting evolving behavioral differences perhaps including shifting from suspension to emphases on substrate-feeding (e.g., Spencer 1951: 91, 121).

Derivation of the Hadrosida from the Euaxosida continued phylogenetic displacement of axials toward the aboral surface of the adaxial (Fig. 4D, E), that of the Kermasida to a fully aboral positioning (Fig. 4F). The breadth of the axial series of relatively weakly constructed euaxosidans commonly was exposed with specimen compaction (e.g., Fig. 3E, G), whereas those of the more compaction-resistant derived Hadrosida and Kermasida are progressively more likely to approximate life configurations (Fig. 4D, E, G). The comparatively intact *D. spenceri* n. gen., n. sp. (Figs 1; 2) specimens are unusual among euaxosidans, perhaps reflecting unusual burial conditions or potentially unrecognized aspects of skeletal construction.

Among more derived Paleozoic asteroids, axials were foreshortened, the nearly equidimensional outline typical of euaxosidan axials (e.g., Figs 2A-E; 3E-G) giving way to rectangular shapes (e.g., Fig. 4D). The transverse water-vascular channel of the broad euaxosidan axial commonly was exposed on the oral surface (e.g., Fig. 3E-H) whereas the transverse channel typically is obscured in the proportionately narrow axials of derived genera (e.g., Fig. 4D). Narrowing of axials has the potential advantage of increasing podial number per unit arm length.

Axial and adaxial configurations of *Componaster* (Fig. 5K) are characteristic of Ophiuroidea and unlike corresponding expressions of the Asteroidea. The transverse axial ribbing and large, rimmed podial pores of *Falloaster* (Fig. 5K) are unique, and adaxials are lacking, placing that genus well apart from currently recognized asterozoan classes.

The axial skeleton: mouth frame

The enlarged potentially weakly vaulted keel-like MAO of *D. spenceri* n. gen., n. sp. is asteroid-like and in that, unlike the mouth frames of somasteroids. As preserved, ambulacra of many somasteroids and early asteroids are dilated at the mouth frame in V-shaped configurations (e.g., Fig. 3A, C), the occurrences historically judged as reflecting life positioning and termed "buccal slits" (e.g., Spencer 1951). Presence of true "buccal slits" in life would carry significant implications for the interpretation of life mode and subphylum phylogeny; however, comparison of specimens among individuals of individual taxa, including *D. spenceri* n. gen., n. sp. (e.g., Figs 1F; 2A, F), among ambulacra of single individuals (Fig. 3A), of specimens among taxa (Figs 1F; 2B, G; 3A, C; 4A), and the general "buccal slit" absence from occurrences of the more robustly constructed derived asteroids (e.g., Fig. 4D, G) demonstrates that "buccal slits" are preservational artifacts produced by differential disk flattening. Based on occurrence, the Y-shaped mouth frames typical of ophiuroids (Fig. 5J) are an apomorphic derivative of somasteroids and apart from asteroid evolution.

Considerable debate has surrounded the interpretation of the homologies of the ossicles of the jaw frame, reviewed with emphasis on the Asteroidea (Mooi & David 2000) and for all Asterozoa (Dean Shackleton 2005: 44). In a summation,

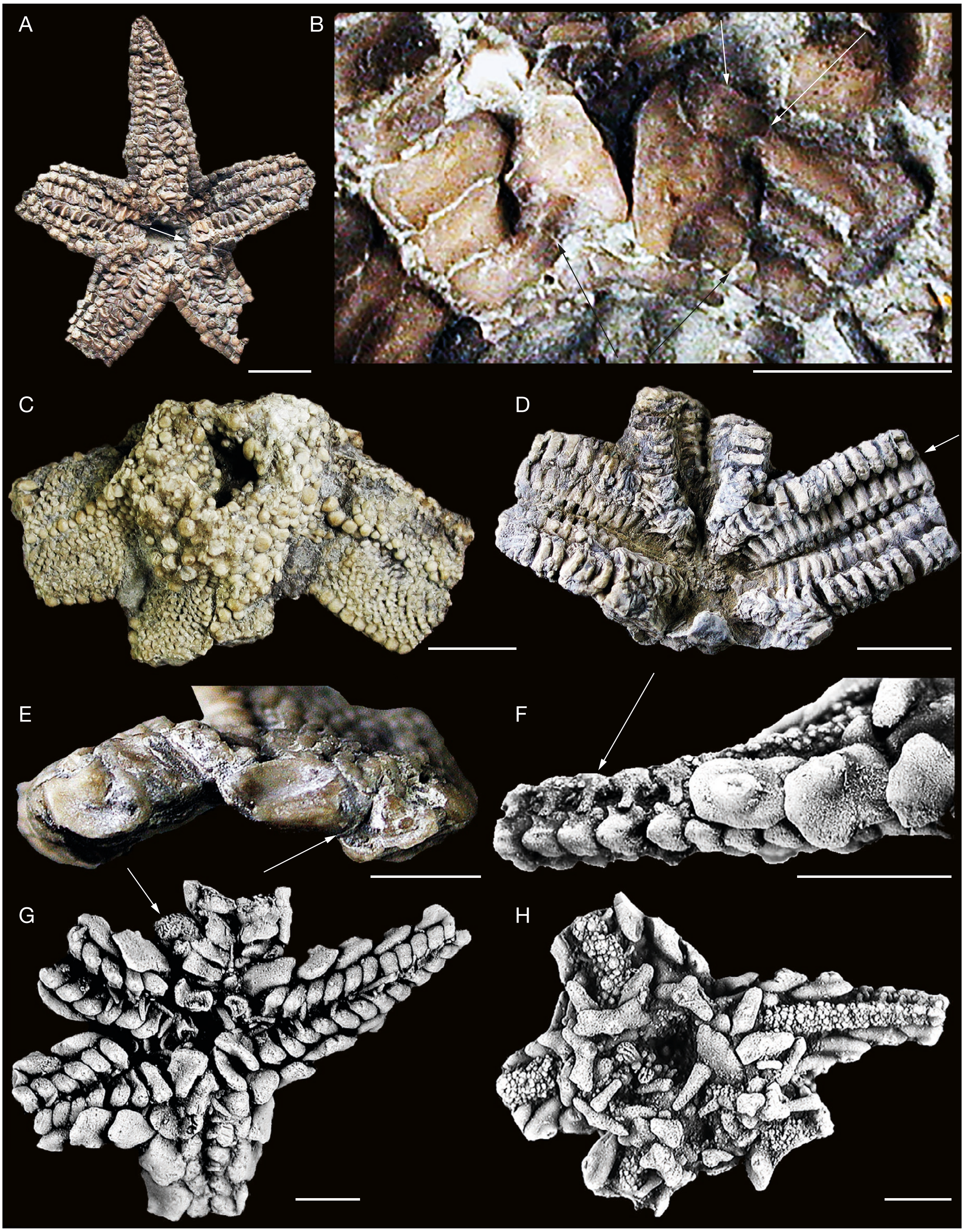

FIG. 4. — Differentiation of ambulacral construction among Euaxosida Blake, 2018 (**A**, **B**), Hadrosida Blake, 2018 (**C**-**E**), and Kermasida Blake, 2018 (**F**-**H**); all original specimens: **A**, **B**, "*Palaeaster*" *exculptus* (Miller, 1881), Richmond Formation, Late Ordovician (Richmondian, Katian), near Waynesville, Ohio, United States, USNM 60608: **A**, specimen remnant, relatively weakly articulated axial/adaxial series and low-arched ambulacra flattened to expose full axial breadth, as is typical of Euaxosida; **arrow** identifies site of (B); **B**, mouth-angle ossicles (MAO) pair flattened, each bearing multiple axials, see text; **C**-**E**, *Anthroosasterias stibareus* Blake, Gilmore City Formation, Early Carboniferous (Kinderhookian, Tournaisian), Gilmore City, Iowa, United States, USNM 611002: **C**, aboral view, disk vaulted, differentiated ossicles likly indicate an aboral circlet; carinal series, marginals on arms; lateral abactinals aligned; **D**, oral view of remnant, actinostome vaulted; **E**, transverse view of arm; position of axial/adaxial contact (D, **arrow**), axials displaced more aborally onto adaxials than in a euaxosidan (Figs 1-3E-G) to form a stronger, deeper furrow; **F**-**H**, *Delicaster enigmaticus* (Kesling), Paint Creek Formation, late early Carboniferous (Chesterian), St. Clair County, Illinois, United States, UMMP 54262: **F**, lateral view of arm, large marginals to right; proportionately small axials (**arrow**) fully vaulted onto adaxials, axials abutted laterally, podial pores present; **G**, ambulacral groove closed as is typical of kermasidan preservation, MAO closely arranged around mouth opening; madreporite (**arrow**) appears lateral but might be displaced from life position; **H**, aboral view, disk ossicles robust and enlarged relative to arm granular abutted abactinals; carinals not developed. Scale bars: A, C, D, 10 mm; B, E, F-H, 3 mm.

Mooi & David (2000: 336) argued "… the available evidence from both ontogeny and adult morphology suggest that the first ambulacral is at least involved in the construction of the MAO. It is possible that the first adambulacral is also part of the MAO, but there is some good evidence against this idea".

In accord with thinking of Mooi & David (2000), the MAO and immediately adjacent axials of the somasteroid *Ophioxenikos* Blake & Guensburg, 1993, are similar in form and size (Fig. 3C), and no other ossicles appear to be incorporated into the jaw frame. Supernumerary ossicles, however, have been recognized associated with the mouth frames of the somasteroids *Thoralaster* and *Villebrunaster* Spencer, 1951 (Blake & Lefebvre 2025: 458). The mouth frame of *Cantabrigiaster* Hunter & Ortega-Hernández, 2021, incorporates both compound axials and apparent reduction of adradial adaxial number (Blake & Lefebvre 2025: 469, fig. 4). Variation among basal somasteroids might indicate more than a single evolutionary sequence leading toward derived asterozoan lineages.

Although not reminiscent of any somasteroid, supernumerary ossicles also are incorporated into the mouth frame of the only known specimen of the euaxosidan "*Palaeaster*" *exculptus* Miller, 1881, the generic assignment tentative (Blake 2018). MAO of this specimen were flattened and dilated distally but nearly abutted toward the mouth opening (Fig. 4A, B). Two axials fully abut the MAO, the more proximal sharing a podial basin with the MAO, the basin directed toward the mouth. On the right side of the mouth frame as viewed here, a third more distal axial contacts both the MAO and a small adaxial that abuts the distal side of the MAO; configuration on the left is similar but the adaxial was lost. The "*P.*" *exculptus* configuration has at least two explanations, the first, that near-MAO adaxials fused with the MAO and their accompanying axials were evolutionarily displaced onto the fused MAO; and secondly, complete adaxial loss accompanied axial displacement onto a still-simple MAO. Ossicular fusion has been favored for some taxa: "The oral plate (= MAO) is seemingly a fused plate which is composed of oral plate proper and the 1st adambulacral plate" (Hayashi & Komatsu 1971: 77). Because there is no evidence of partial ossicular fusing for "*P.*" *exculptus*, adaxial loss accompanying axial displacement appears to provide the readier interpretation. Either process would increase podial density at the mouth frame, an outcome attained in derived lineages (Hadrosida, Fig. 4D; Kermasida) through proportional shortening of axials, and in some lineages, vaulting of the actinostome (Fig. 4D), vaulting later strongly developed for example in the crown-group Asteriidae.

The axial skeleton: terminals

The terminal ossicle occurs at the distal tip of the arm, with axial, adaxial, marginal, and any carinal series arising at its proximal side. The terminal ossicle, although not specifically assigned to category, was implicitly treated as axial (Spencer & Wright 1966: 11) and specifically so by many later authors (e.g., Mooi & David 2000: 330).

Although a terminal can be recognized in some fossil asterozoans (e.g., Blake 2008: fig. 2.2, 2.3, 2.5), recognition usually is difficult because many terminals are similar in size and form to adjacent ossicles and also because arm tips are readily disrupted during preservation, thereby obscuring ossicular identification.

Terminals have not been recognized among somasteroids (e.g., Blake & Lefebvre 2025). Although the best-preserved tips of *D. spenceri* n. gen., n. sp. appear largely intact, a terminal is possible but not definitively recognized (Fig. 2E). Although the terminal arises early during the skeletal ontogeny of extant asteroids (e.g., Kano *et al.* 1974; Komatsu 1975, 1982; Oguro *et al.* 1976; Siddall 1979), the possibility that the terminal arose phylogenetically late perhaps as a derivative of the extraxial inferomarginal series cannot be dismissed based on expressions among fossils. If the terminal is to be treated as axial or adaxial (Spencer & Wright 1966) then the aligned inferomarginal series might also be argued as adaxial.

The adaxial skeleton

The adaxial skeletal cohort consists of somasteroid virgalia; stenuroid embedded and outer virgals; asteroid adambulacrals; and ophiuroid laterals. Although earlier favored (Spencer 1951; Spencer & Wright 1966), the ambital framework is not adaxial (Blake 2024; Blake & Lefebvre 2025). Euaxosidan adaxials and axials are comparatively weakly articulated, the adaxials commonly (e.g., Figs 2D; 3G; 4A) but not always (e.g., Fig. 3E, F) approximately equidimensional; among derived hadrosidans and kermasidans, axials and adaxials are more strongly and closely articulated (e.g., Fig. 4D-G) and adaxials generally are approximately equidimensional. Adaxial expression of the superficially asteroid-like *Componaster* (Fig. 5J) is typical of ophiuroids, whereas superficially asteroid-like *Falloaster* (Fig. 5K) lacks adaxials. The literature on adaxials was reviewed in Blake (2018: 7).

The extraxial skeleton: abactinals

Abactinals of somasteroids and many early asteroids are intraspecifically uniform, the ossicles small, closely spaced, and not differentiated into carinal series, an aboral circlet, or centrale (e.g., Fig. 5D, F). Abactinal differentiation arose promptly during asteroid evolution (e.g., Fig. 5G), the broad taxonomic distribution of occurrences indicating homoplasy, with carinals argued under a specified constructional constraint (Blake & Rozhnov 2007: 526).

Abactinals of *D. spenceri* n. gen., n. sp., like those of somasteroids, are small and uniform, but with specifics of shape and arrangement diagnostic for this species. The only available aboral disk surface of *D. spenceri* n. gen., n. sp. suggests limited and perhaps phylogenetically emergent differentiation of a primary circlet and centrale (Fig. 1A), and in this, a step beyond somasteroids; aspects of the appearance of the *D. spenceri* n. gen., n. sp. abactinal skeleton, however, might reflect preservation.

The enlarged, abutted plate-like abactinals of the ophiuroid *Componaster* (Fig. 5I) are comparable to those of some derived asteroids indicating homoplasy among diverse asterozoan lineages.

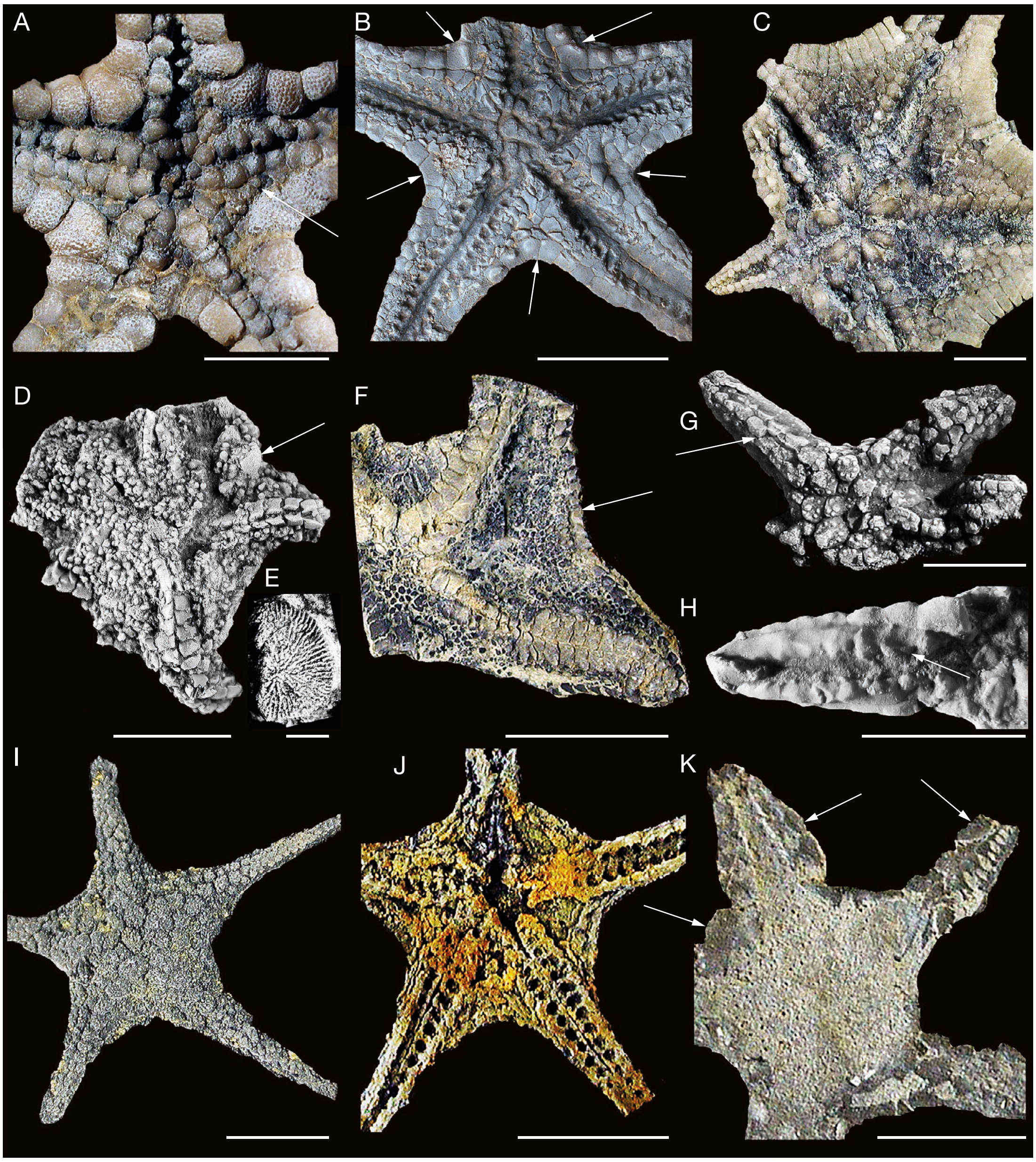

Fig. 5. — Diverse early Asterozoa, all but **I** and **J** are original specimens: **A**, *Hudsonaster*? sp., Hadrosida, Decorah Shale, Trenton Group, Middle Ordovician, Minneapolis, Minnesota, United States; CMC IP36520, oral view. Geologic data from a label identify it originally as a Ward's Natural Science Establishment assigning the specimen to *Hudsonaster narrawayi* (Hudson, 1912), the overall shape and presence of actinals would be atypical of *Hudsonaster*. The irregular development of actinals (**arrow**) suggests a secondary, space-filling genesis; **B**, *Aerliceaster nexosus* Blake *et al.*, 2020b, Euaxosida, Garden City Formation, Early to Middle Ordovician, Bear River Range, Franklin County, Idaho; holotype IMNH IP-276/850, oral view, the mouth frame is weakly distended and the ambulacra variously flattened to expose the aboral surfaces of the axials. Axillaries are varied in shape and positioning (**arrows**), in one interbrachium (**lower arrow**) two ossicles "competing" as the axillary. Within the marginal frame, actinals variously developed suggesting an early stage of differentiation; **C**, *Jugiaster speciosus* (Miller & Dyer, 1878), Euaxosida, MUGM T-565, Waynesville Formation, Late Ordovician, Indiana, oral view, abundant somewhat irregularly arranged actinals lie within the marginal framework; lower left arm regenerating at time of death; **D**, **E**, *Estoniaster maennili* Blake & Rozhnov, 2007, Euaxosida, Late Ordovician (late Sandbian, upper part of the *Didymograptus multidens* Zone), Vasalemma Quarry, near Tallinn, northern Estonia; PIN 4125/766: **D**, aboral view, abactinals are closely fitted and granular, not appearing differentiated into series and in that similar to those of *Ophioxenikos* (Fig. 3C); shield-like laterally abutted axials that are common among early Asterozoa; **E**, madreporite (at **arrow**, D), radiating ridge-and-groove configuration is common among younger asteroids and unlike the granular texture of *D. spenceri* n. gen., n. sp. (Figs 1G; 2A). **F**, *Eukrinaster ibexensis* Blake, Guensburg, Sprinkle & Sumrall, 2007, Euaxosida, upper Fillmore Formation, Ibex area, west-central Utah, zone J, early middle Arenig (Floian), Early Ordovician; paratype TMM 1965TX11, aboral view, disk is large and bordered by well-defined marginal series (**arrow**); both abactinals and axials are similar to those of basal *Ophioxenikos* and *E. maennili* (D); **G**, **H**, *Eriaster ibexensis* Blake & Guensburg, 2005, Hadrosida, Fillmore Limestone, G-2 trilobite zone, equivalent to the very top of the Tremadocian, Early Ordovician; Ibex area, western Utah; FMNH PE 52741: **G**, extraxial abactinal morphology clearly differentiated in a very early asteroid, unlike those of both Somasteroidea and *D. spenceri* n. gen., n. sp.; carinal series remains only distal to the arrow; **H**, poorly preserved adaxial shape identifies ordinal assignment; **I**, **J**, *Componaster spurius* Glass *et al.*, Ophiuroidea, Tizi n'Mourghi (Cricket's Pass), eastern Anti-Atlas, Morocco; Lower Ktaoua Formation, Upper Ordovician (lower Katian): **I**, paratype AA.TNMb. OS.28, aboral view, see Discussion; **J**, holotype MHNM.15690.113, oral view, see Discussion; **K**, *Falloaster anquiroisitus* Blake, Gahn & Guensburg, 2020a; IMNH IP-276/849, class unassigned, Garden City Formation, Early Ordovician, (Floian/Blackhillsian), Bear River Range, Bear Lake County, Idaho; the only known specimen of an aberrant asterozoan not assigned at the class level, outcrop weathering differentially exposing arms, the disk obscured. An arm is deeply weathered as to exposed large podial pores (**middle arrow**). Only the aboral surface has been largely lost on a second arm to expose a large, plate-like abactinal (**right arrow**) and vaulted axials with unique transverse ribbing. Madreporite is lateral (**left arrow**). Scale bars: A-C, 5 mm; D, F, 10 mm; E, 1 mm; G-K, 3mm.

THE EXTRAXIAL SKELETON: MADREPORITE

Madreporite variation among both somasteroids and derived asterozoans was significant, arguing homoplastic emergence of a robust calcified condition from an at most weakly calcified ancestral hydropore. Whether because of homoplasy, limitations of preservation, or absence, a madreporite has not been recorded from many early asterozoans, but where recognized, madreporites are varied in position and surface textures (e.g., Figs 1F, G; 4G; 5D, E, K).

The granular surface texture and a positioning offset from the MAO of the *D. spenceri* n. gen., n. sp. madreporite correspond with expressions of the somasteroid *Chinianaster*. In contrast, aboral positioning and the ridge-and-groove texture of the somasteroid *Archegonaster* (Smith & Jell 1990) are similar to those of *Estoniaster* (Fig. 5E). Lateral madreporite positioning among Paleozoic asterozoans (e.g., Figs 4G; 5D, K) is of uncertain significance.

THE EXTRAXIAL SKELETON: AMBITAL FRAMEWORK

Because many ambiguities surround use of the term "marginal" among echinoderms (e.g., Mooi & David 2000, 2008; Dean Shackleton 2005; Hotchkiss 2012; Blake 2013, 2018), the descriptive term "ambital framework" was proposed as a non-genetic supplement for use if homology is unclear (Blake 2013: 357; 2018: 7; 2024: 4; Blake & Guensburg 2015: 479).

An ambital framework inferomarginal series is recognized in all somasteroid genera (Blake & Hotchkiss 2022, contra Hunter & Ortega-Hernández 2021), and except for *D. spenceri* n. gen., n. sp., all genera of the basal Euaxosida. Series expression among somasteroids has been argued as illustrating a general evolutionary sequencing toward greater clarity of definition (Blake 2013; Blake & Lefebvre 2025). Given presence in ancestral somasteroids, absence of a marginal series from derivative *Degeneraster* n. gen. is considered a phylogenetic loss supporting familial recognition.

The much-varied robusticities of marginal ossicles found among asteroids (e.g., Figs 4A, C, F-H; 5A-H) correlate at least in part with arm shape rather than phylogenetic positioning, more robust in taxa with flat arms, more weakly differentiated in taxa with cylindrical arms (Spencer 1922: 202; Blake & Rozhnov 2007: 526).

THE EXTRAXIAL SKELETON: AXILLARY/ODONTOPHORE

The term "axillary", typical of Paleozoic usage, and "odontophore", typical of post-Paleozoic crown group usage, are synonyms (Spencer 1916: 62). An axillary has not been recognized among somasteroids (Blake & Lefebvre 2025). The axillary has been widely considered a derivative of the inferomarginal series (e.g., Schuchert 1915: 14, under "interbrachial"; Spencer & Wright 1966: 14). The varied interbrachial expressions of a single specimen of *Aerliceaster* Blake, Gahn & Guensburg, 2020b, suggest that the axillary is a part of the ambital framework and that axillary differentiation was emergent among early Asteroidea (Fig. 5B).

Although some ossicular debris is developed distal to the MAO of *D. spenceri* n. gen., n. sp. (e.g., Fig. 2B-D), potential axillary presence cannot be established or rejected based on available specimens.

THE EXTRAXIAL SKELETON: ACTINALS

Because of morphological differences, and because no intermediate state has been recognized, "actinals" of asteroids are considered phylogenetically independent of somasteroid virgalia, the adaxial virgals lost before actinals emerged (Blake 2013, 2018, 2024; Blake & Lefebvre 2025). Actinals of most euaxosidans are irregular in form and arrangement (e.g., Figs 1F; 2B; 5B, C) arguing derivation as a space-filling device with distribution among taxa favoring homoplasy. Unlike somasteroid virgals, actinals are extraxial. Actinals are abundant in some early asteroids (e.g., Fig. 5C), in time and among lineages becoming more uniform in appearance and arrangement, including alignment into one or two clearly defined series (e.g., Hotchkiss & Clark 1976; Blake & Hotchkiss 2004; Blake *et al.* 2015b: 1049).

Among most asteroids, the ambital framework/marginal series separates abactinals from actinals, thereby providing an interpretive device unavailable for *D. spenceri* n. gen., n. sp. An ambital framework also is lacking from most ophiuroids, the aboral disk ossicles commonly extending without interruption around the disk edge to the oral surface. The ophiuran configuration has been interpreted as representing "downgrowths of the apical interradii" (Spencer 1919: 178, also 181; 1927: 367), a disposition endorsed by Dean Shackleton (2005: 42) and Gladwell (2018: 6). Arm ossicles adjacent to the adaxials of *D. spenceri* n. gen., n. sp. appear granular and those near the mouth frame are wide, flat, and plate-like (Figs 1; 2, esp. 2B, D), both unlike aboral abactinals (Fig. 1A-E). Although a marginal series is lacking, the ossicular differentiation of *D. spenceri* n. gen., n. sp. suggests actinal differentiation rather than ophiuran "downgrowth". Abactinal and actinal series differentiation in *D. spenceri* n. gen., n. sp. is consistent with evolutionary skeletal ambital framework loss, and yet a loss with retention of the boundary between ossicular series.

THE EXTRAXIAL SKELETON: ACCESSORIES

Accessories of somasteroids and more basal asteroids are predominantly small and little differentiated. Few accessories can be recognized on any of the three *D. spenceri* n. gen., n. sp. specimens, probably largely because of taphonomic loss. A prominent adaxial spine base, however, is recognized (e.g., Fig. 2D), and a possible row of attachment sites for small spinelets along MAO edges (Fig. 2C).

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