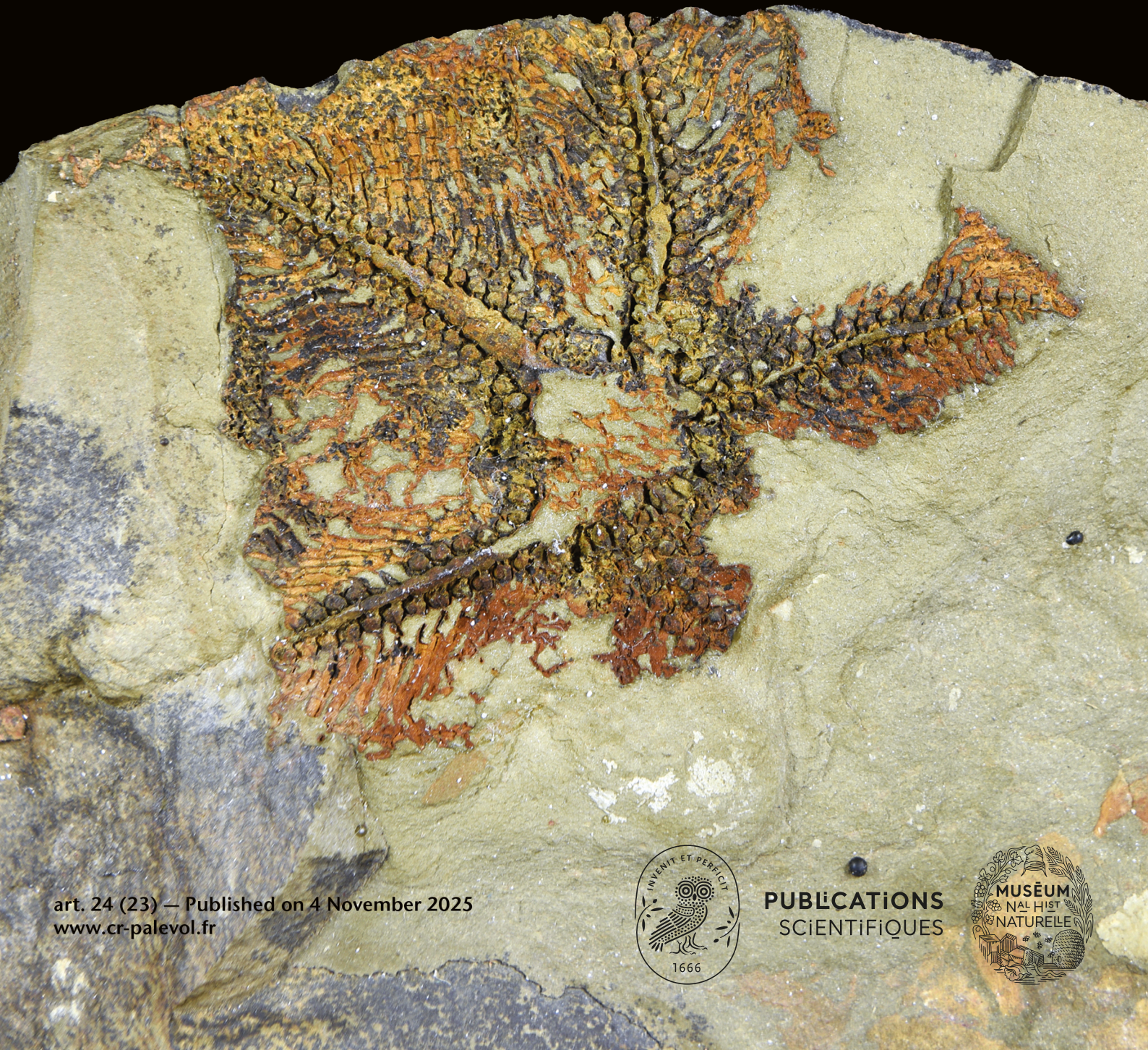


The class Somasteroidea and its significance among early Asterozoa (Echinodermata)

Daniel B. BLAKE & Bertrand LEFEBVRE



DIRECTEURS DE LA PUBLICATION / PUBLICATION DIRECTORS :

Gilles Bloch, Président du Muséum national d'Histoire naturelle
Étienne Ghys, Secrétaire perpétuel de l'Académie des sciences

RÉDACTEURS EN CHEF / EDITORS-IN-CHIEF: Michel Laurin (CNRS), Philippe Taquet (Académie des sciences)

ASSISTANTE DE RÉDACTION / ASSISTANT EDITOR: Adenise Lopes (Académie des sciences; cr-palevol@academie-sciences.fr)

MISE EN PAGE / PAGE LAYOUT: Audrina Neveu (Muséum national d'Histoire naturelle; audrina.neveu@mnhn.fr)

RÉVISIONS LINGUISTIQUES DES TEXTES ANGLAIS / ENGLISH LANGUAGE REVISIONS: Kevin Padian (University of California at Berkeley)

RÉDACTEURS ASSOCIÉS / ASSOCIATE EDITORS (*, took charge of the editorial process of the article/a pris en charge le suivi éditorial de l'article):

Micropaléontologie/Micropalaeontology

Lorenzo Consorti (Institute of Marine Sciences, Italian National Research Council, Trieste)

Paléobotanique/Palaeobotany

Cyrille Prestianni (Royal Belgian Institute of Natural Sciences, Brussels)

Anaïs Boura (Sorbonne Université, Paris)

Métazoaires/Metazoa

Annalisa Ferretti* (Università di Modena e Reggio Emilia, Modena)

Paléoichthyologie/Palaeoichthyology

Philippe Janvier (Muséum national d'Histoire naturelle, Académie des sciences, Paris)

Amniotes du Mésozoïque/Mesozoic amniotes

Hans-Dieter Sues (Smithsonian National Museum of Natural History, Washington)

Tortues/Turtles

Walter Joyce (Universität Freiburg, Switzerland)

Lépidosauromorphes/Lepidosauromorphs

Hussam Zaher (Universidade de São Paulo)

Oiseaux/Birds

Jingmai O'Connor (Field Museum, Chicago)

Paléomammalogie (mammifères de moyenne et grande taille)/Palaeomammalogy (large and mid-sized mammals)

Grégoire Métais (CNRS, Muséum national d'Histoire naturelle, Sorbonne Université, Paris)

Paléomammalogie (petits mammifères sauf Euarchontoglires)/Palaeomammalogy (small mammals except for Euarchontoglires)

Robert Asher (Cambridge University, Cambridge)

Paléomammalogie (Euarchontoglires)/Palaeomammalogy (Euarchontoglires)

K. Christopher Beard (University of Kansas, Lawrence)

Paléoanthropologie/Palaeoanthropology

Aurélien Mounier (CNRS/Muséum national d'Histoire naturelle, Paris)

Archéologie préhistorique (Paléolithique et Mésolithique)/Prehistoric archaeology (Palaeolithic and Mesolithic)

Nicolas Teyssandier (CNRS/Université de Toulouse, Toulouse)

Archéologie préhistorique (Néolithique et âge du bronze)/Prehistoric archaeology (Neolithic and Bronze Age)

Marc Vander Linden (Bournemouth University, Bournemouth)

RÉFÉRÉS / REVIEWERS: <https://sciencepress.mnhn.fr/periodiques/comptes-rendus-palevol/referes-du-journal>

COUVERTURE / COVER:

Holotype of *Cantabrigiaster fezuataensis*, UCBL-FSL 424 961. Credits: photo by Emmanuel Robert.

Comptes Rendus Palevol est indexé dans / *Comptes Rendus Palevol* is indexed by:

- Cambridge Scientific Abstracts
- Current Contents® Physical
- Chemical, and Earth Sciences®
- ISI Alerting Services®
- Geoabstracts, Geobase, Georef, Inspec, Pascal
- Science Citation Index®, Science Citation Index Expanded®
- Scopus®.

Les articles ainsi que les nouveautés nomenclaturales publiés dans *Comptes Rendus Palevol* sont référencés par /
Articles and nomenclatural novelties published in Comptes Rendus Palevol are registered on:

- ZooBank® (<http://zoobank.org>)

Comptes Rendus Palevol est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris et l'Académie des sciences, Paris
Comptes Rendus Palevol is a fast track journal published by the Museum Science Press, Paris and the Académie des sciences, Paris

Les Publications scientifiques du Muséum publient aussi / The Museum Science Press also publish:

Adansonia, *Geodiversitas*, *Zoosystema*, *Anthropozoologica*, *European Journal of Taxonomy*, *Naturae*, *Cryptogamie* sous-sections *Algologie*, *Bryologie*, *Mycologie*.

L'Académie des sciences publie aussi / The Académie des sciences also publishes:

Comptes Rendus Mathématique, *Comptes Rendus Physique*, *Comptes Rendus Mécanique*, *Comptes Rendus Chimie*, *Comptes Rendus Géoscience*, *Comptes Rendus Biologies*.

Diffusion – Publications scientifiques Muséum national d'Histoire naturelle

CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)

Tél.: 33 (0)1 40 79 48 05 / Fax: 33 (0)1 40 79 38 40

diff.pub@mnhn.fr / <https://sciencepress.mnhn.fr>

Académie des sciences, Institut de France, 23 quai de Conti, 75006 Paris.

© This article is licensed under the Creative Commons Attribution 4.0 International License (<https://creativecommons.org/licenses/by/4.0/>)
ISSN (imprimé / print): 1631-0683/ ISSN (électronique / electronic): 1777-571X

The class Somasteroidea and its significance among early Asterozoa (Echinodermata)

Daniel B. BLAKE

Department of Earth Sciences and Environmental Change, University of Illinois,
3081 NHB, 1301 West Green Street, 61801 Urbana, IL (United States)
dblake@illinois.edu

Bertrand LEFEBVRE

Université Claude Bernard Lyon 1, CNRS, LGL-TPE,
2 rue Raphaël Dubois, F-69622 Villeurbanne cedex (France)
bertrand.lefebvre@univ-lyon1.fr (corresponding author)

Submitted on 23 March 2025 | Accepted on 31 May 2025 | Published on 4 November 2025

[urn:lsid:zoobank.org:pub:C15073D3-DE34-4FB0-97BE-C261F05C0342](https://zoobank.org/pub:C15073D3-DE34-4FB0-97BE-C261F05C0342)

Blake D. B. & Lefebvre B. 2025. — The class Somasteroidea and its significance among early Asterozoa (Echinodermata). *Comptes Rendus Palevol* 24 (23): 449–487. <https://doi.org/10.5852/cr-palevol2025v24a23>

ABSTRACT

Many specimens of the echinoderm subphylum Asterozoa from the Mediterranean Gondwanan Ordovician of France and Morocco have been compiled from many collections, the composite including representation of all four asterozoan classes. While providing a basis for survey of early asterozoan history, the large fauna remains geographically and environmentally localized, and therefore it does not depict Ordovician Asterozoa globally. Overall uniformity of expression has led to widespread agreement on the composition of the subphylum Asterozoa; however, consensus has not been reached on recognition of a precursor (or sister-group) that can clearly advance interpretation of early asterozoan history, a vacancy contributing to differing evaluations in the literature. Based on survey of early skeletal asterozoans, the class Somasteroidea Spencer, 1951 is considered stemward at the subphylum level. Presence of adaxial virgalia (an ontogenetically lengthening series of ossicles, i.e., of discrete virgals) extending laterally from each axial is considered necessary and sufficient for exemplar assignment to the Somasteroidea. Varied adaxial evolutionary histories provide the first steps toward interpretation, recognition, and classification of derived asterozoan lineages. The Somasteroidea is known from seven genera, all reviewed with emphasis on the Mediterranean representatives. The Chinianasteridae Spencer and Villebrunasteridae Fell are recognized at the subfamilial level, and the new subfamily Ophioxenikosinae n. subfam. is described. Recognition of ordinal-level taxonomic subdivisions of the class Somasteroidea is not deemed justified. The two genera *Ampullaster* Fell, 1963b and *Cantabrigiaster* Hunter & Ortega-Hernández, 2021 here are considered valid.

KEY WORDS

Somasteroidea,
Asterozoa,
Ordovician,
morphological evolution,
new subfamily.

RÉSUMÉ

La classe Somasteroidea et son importance au sein des premiers astérozoaires (Echinodermata).

L'Ordovicien de France et du Maroc (Province méditerranéenne) a livré des assemblages particulièrement abondants et diversifiés d'échinodermes comprenant notamment des représentants des quatre classes d'astérozoaires. Ce matériel permet d'analyser comment se sont déroulées les premières étapes de la diversification de ce sous-phylum dans les mers australes du domaine péri-gondwanien. Dès leur apparition dans le registre fossile, les astérozoaires partagent un certain nombre d'apomorphies qui permettent de les identifier sans hésitation. Cette grande uniformité pose par contre le problème de leur origine et de l'identification d'un groupe-frère au sein des échinodermes. L'examen des plus anciens restes connus d'astérozoaires suggère que la classe Somasteroidea Spencer, 1951 occupe une position basale à l'échelle du sous-phylum. Les somastéroïdes sont caractérisés par la possession de plaques virgales adaxiales qui s'étendent latéralement depuis chaque axiale. L'analyse de l'expression très variable de ces adaxiales chez les somastéroïdes permet de décrypter une histoire évolutive complexe conduisant aux patterns plus dérivés observés dans les trois autres classes. Les somastéroïdes ne sont connus que par sept genres, dont six proviennent de l'Ordovicien inférieur à moyen de la Province méditerranéenne. Différentes sous-familles sont identifiées au sein des Chinianasteridae et des Villebrunasteridae, dont une est nouvelle (Ophioxenikosinae n. subfam.). Les genres *Ampullaster* Fell, 1963b et *Cantabrigiaster* Hunter & Ortega-Hernández, 2021 sont ici reconnus comme valides.

MOTS CLÉS
Somasteroidea,
Asterozoa,
Ordovicien,
évolution
morphologique,
sous-famille nouvelle.

INTRODUCTION

A large and diverse specimen array of Asterozoa recovered from the Ordovician of France and Morocco has enabled reevaluation of aspects of early subphylum diversification (Blake & Lefebvre 2024; Glass *et al.* 2024). Reevaluation continues here with survey of the class Somasteroidea Spencer, 1951, the survey beginning with the following perspectives, some tendentious.

The subphylum Asterozoa as compiled by Ubaghs (1953) and Spencer & Wright (1966) is accepted as monophyletic.

Interpretations are based on the fossil record; enduring debates surrounding significance of early development of extant taxa (e.g. Fell 1948; Smith 1984) are not treated.

The earliest-known skeletal asterozoans are earliest Ordovician (Tremadocian). Ambiguous trace fossils suggest Cambrian occurrence of at most only lightly calcified representatives (Alpert 1976; Mikuláš 1992). The abrupt diversity of the earliest asterozoans is consistent with an interpretation of clade diversifications prior to first appearances in the fossil record (e.g. Erwin *et al.* 2011).

Asterozoan derivation is controversial in the literature. Two potential ancestral or sister-group candidates, the Edrioasteroidea Billings, 1858 (e.g. Dean Shackleton 2005) and the Crinoidea Miller, 1821 (e.g. Fell 1963a; Hunter & Ortega-Hernández 2021) have been favored. Additionally, problematic *Camptostrotra* Ruedemann, 1933, has been selected (Smith & Jell 1990). Alternatively, no known Cambrian or other Early Ordovician echinoderm is similar enough to any asterozoan as to provide a well-supported sister-group (e.g. Blake 2013), “acceptable” meaning that the requisite changes between the sister-group designate and known early asterozoans are great enough as to be considered at least as likely to mislead as to usefully guide. Fundamental differences among *Camptostrotra*,

early Edrioasteroidea, and early Crinoidea serve to exemplify uncertainties. Evaluations do not reject the nominates, rather they argue that supporting data are inadequate.

The Somasteroidea is accepted as stemward in the subphylum. Known somasteroids are few, at least in part because of epifaunal habits and delicate construction, the limitations hindering interpretations.

Guidelines for specimen assignment are needed. Presence of proximally-lengthening virgalia is necessary and sufficient for specimen assignment to the Somasteroidea. Presence of two to four virgal derivatives extending laterally from each axial is necessary and sufficient for specimen assignment to the Stenuroidea. Potential for phylogenetic complexities within these designated limitations are recognized; however, use is considered justified by the present state of knowledge while providing objective points of departure for future evaluations. Representatives of both the Asteroidea de Blainville, 1830 and Ophiuroidea Gray, 1840 have a single adaxial virgal derivative, the so-called adambulacral of asteroids and lateral of ophiuroids. As emphasized by Spencer (1914-1940, 1951; also Glass *et al.* 2024), assignment of many early exemplars at the class level is difficult thereby requiring use of additional criteria. Most important but not categorical, ophiuroid axials and commonly upright plate-like adaxials are laterally aligned, and an ambulacral furrow is absent, whereas an ambulacral furrow is developed among asteroids, the axials partially to fully displaced onto the aboral surface of approximately equidimensional adaxials. Partial displacement with broad furrows is characteristic of more stemward asteroids with full displacement onto the aboral adaxial surface and relatively narrow furrows characterizing the more derived (Blake 2018). Adaxial expressions of a number of problematic genera are variously uncertain and ambiguous (e.g. Blake 2000, 2007, 2014, 2024).

Skeletal development, taxonomy, and history of the subphylum Asterozoa have been treated by a number of authors (Agassiz 1877; Viguier 1879; Spencer 1951; Ubaghs 1953; Fell 1963a; Spencer & Wright 1966; Dean Shackleton 2005; Blake 2013, 2018; Blake & Guensburg 2015; Gladwell 2018; Villier *et al.* 2018; Blake & Hotchkiss 2022). Figures 1 through 14 illustrate somasteroid morphology based on earlier reconstructions (Figs 1; 12A, C, E) and photographic documentation (Figs 2-11; 12B, D, F-14). Problematic specimens (Fig. 14) exemplify diversity while illustrating complexities of incomplete preservation.

TERMINOLOGY

The aboral surface is directed toward the water column, the oral surface, toward the substrate. The primary skeleton forms the body wall. The accessory skeleton includes the spines, spinelets, granules, and pedicellariae seated on all primary ossicles except axials. Accessories are not a part of the primary skeleton. Axial (ambulacral a synonym) ossicles form a double series along the axis of the arm. Podial basins of most asterozoans, although commonly more or less obscured in preservation, are either approximately shared between successive axials (Figs 2B, C; 3C; 4A, B; 7E; 8D, F), or the basin lies almost entirely on one side of the transverse ridge (Figs 10-12). Interpretation of axial shape can be ambiguous in part because of incomplete preservation and in part because of integrated series deflection accompanying preservation. A few axials are enlarged, asymmetrical, and contain portions of multiple basins rather than only a shared basin on each side of the transverse ridge (Figs 1B; 6B, C); no suggestion of fusion of discrete ossicles has been recognized, and therefore interpretation is that the configuration represents a single ossicle, termed compound, rather than the product of ontogenetic fusion of more than one ossicle. The unpaired terminal is at the arm tip, presence generally difficult to verify among fossils, especially so among somasteroids. Mouth-angle ossicles are the proximal-most paired ossicles of the axial series; an unpaired ossicle, the torus (dental plate of Dean Shackleton (2005: char. 148, a synonym) is found on the oral side of the pair of some stem-group asterozoans. The adaxial skeleton as treated herein consists of the full linear series abutting each axial and directed abradially. In the Somasteroidea, each ossicle of the series is termed a “virgal”, a single series a “virgalium”, and multiple series “virgalia”. In the Stenuroidea, virgalia were phylogenetically reduced to one or three “embedded virgals” and an “outer virgal” and reduced to the “adambulacral” of the Asteroidea and the “lateral” of Ophiuroidea. The remainder of the skeleton is extraxial. The body can be edged by a single or double series of more or less clearly differentiated marginal ossicles. Because the term “marginal” has been broadly applied within echinoderms with unclear implications of homology, the genetically neutral term ambital framework was proposed (Blake 2013). A single marginal series has been judged to be homologous throughout stem-group asteroids, it recognized as inferomarginal. All skeletal components

“above” or seaward of the inferomarginals for convenience are referred to as aboral, including any superomarginal and intermarginal series, and in some taxa, the madreporite. The axillary (odontophore) typically is a more or less clearly differentiated unpaired ossicle, among Paleozoic asteroids typically external and aligned with the inferomarginal series at the interbrachial midline. Abactinal ossicles are aboral to the marginal series; see discussion below under Abactinals. A medial disk centrale can be recognized in some exemplars, it enclosed by a ring of more or less differentiated ossicles, a primary circlet or aboral ring. Midarm ossicles can be enlarged and/or otherwise differentiated to form a carinal series, and in many asteroids, lateral differentiated abactinal series or adradialia are aligned with midarm carinals. A hydropore or madreporite provides opening to the water-vascular system (edited from Blake & Lefebvre 2024).

ABBREVIATIONS

Institutional abbreviations

AA	Université Cadi Ayyad, Marrakesh;
MBB	Musée du Biterrois, Béziers;
MHNN	Muséum d'Histoire naturelle, Nantes;
MNHN	Muséum national d'Histoire naturelle, Paris;
NMP	Národní Muzeum, Prague;
PRI	Prairie Research Institute, University of Illinois, Urbana-Champaign;
UCBL-FSL	Collections de paléontologie, Université Claude Bernard Lyon 1, Villeurbanne;
YPM	Yale Peabody Museum, Yale University.

Other abbreviation

MAO	mouth-angle ossicles.
-----	-----------------------

TAPHONOMY AND OCCURRENCES

For the most of geologic history, authors have recognized two classes (or subclasses) of the subphylum Asterozoa, the Asteroidea and Ophiuroidea, but reasoning and outcomes surrounding class subdivisions have differed (for Paleozoic occurrences, see Spencer 1914-1940, 1951; Ubaghs 1953; Fell 1963a, b; Spencer & Wright 1966; McKnight 1975; Smith & Jell 1990; Dean 1999; Mooi & David 2000; Dean Shackleton 2005; Blake 2013, 2018, 2024; Blake & Guensburg 2015; Villier *et al.* 2018). Usage here of a four-fold subphylum partitioning (Blake 2013, 2024) does not argue finality but rather serves in part to emphasize the diversity and complexity of the earliest asterozoans, an interpretation indirectly exemplified by usage of “plesion” categories (Dean Shackleton 2005) and recognition of genera left unassigned at the class level (Blake 2000, 2014; Blake *et al.* 2020).

The many proportionately small skeletal elements of asterozoans are seated in soft tissues, and therefore individuals are readily disrupted and destroyed with death and decay (e.g. Brett *et al.* 1997; Gorzelak & Salamon 2013; Fraga & Vega 2024). Specimen remains are all but inevitably incomplete in various ways. Essentially planar, only one surface of many or most specimens is available, and even if both part and coun-

terpart remain, the margins of curved and partially collapsed disks and arms typically are variably obscured. If the specimen is essentially intact, accessories hide primary skeletal elements, and morphological and positional details of abutted ossicles and internal ossicular surfaces are incompletely available. Ossicular detail is readily lost with outcrop weathering. The relatively abundant and diverse Mediterranean Gondwanan fauna partially inverts the more usual difficulties, the fossils including many very fragmentary specimens demanding ongoing reevaluation of taxon limits.

Although initially not recognized at a higher taxonomic level, somasteroid fossils were first described from Early Ordovician Montagne Noire localities of the south of France (Thoral 1935) and the Middle Ordovician of Czech Republic (Spencer 1951). This limited distribution was broadened with description of *Ophioxenikos* Blake & Guensburg, 1993, from the Floian of Nevada, United States, and reports of somasteroids in the Lower Ordovician Fezouata Shale of the Anti-Atlas, Morocco (Lefebvre *et al.* 2016). Markedly different environmental settings are represented. The Czech, French, and Moroccan specimens were all collected from high latitude Mediterranean Gondwanan siliciclastic sequences interpreted as deposited in relatively distal, cool, and presumably relatively quiet waters, below storm wave-base (Vizcaïno & Lefebvre 1999; Lefebvre 2007; Lefebvre *et al.* 2016, 2022). The equatorial Laurentian source outcrop of the only specimen of *Ophioxenikos* consists of interbedded calcisiltites alternating with calcarenites, some of the latter preserved as megaripples extending into mounds, the outcrop interpreted as deposited in shallow, warm waters. No other fossils were recovered from the small outcrop of the *Ophioxenikos* specimen. No definitive data are available to determine which geography and morphological expressions more closely reflect the stemward somasteroid condition, although *Ophioxenikos* is younger.

Archegonaster Jaekel, 1923 and *Ophioxenikos* have been reviewed in some detail (Spencer 1951; Smith & Jell 1990; Dean Shackleton 2005; Blake & Guensburg 2015) and treatment here is limited. Geological context and paleoenvironmental conditions associated with occurrences of Early Ordovician somasteroids from the Montagne Noire (southern France) and the Anti-Atlas (Morocco) are summarized below. In part seeking to more broadly document somasteroid diversity, *Ampullaster* Fell, 1963b, and *Cantabrigiaster* Hunter & Ortega-Hernández, 2021, are recognized here, although previously challenged.

MONTAGNE NOIRE

In southern France, the Montagne Noire yielded the most abundant and diverse assemblage of somasteroids in the world (over 30 specimens belonging to four taxa). The available material is the result of over 150 years of sampling mostly in the surroundings of Caunes-Minervois (Aude), Félines-Minervois (Hérault) and Saint-Chinian (Hérault). This material is deposited in the paleontological collections of the Musée du Biterrois, Béziers (Griffe collection), the Muséum national d'Histoire naturelle, Paris (Courtessole-Griffe, and Vizcaïno collections), and the Université Claude Bernard

Lyon 1, Villeurbanne (Lignières, Marty, Monceret, Thoral, Villebrun, and Vizcaïno collections). In the Montagne Noire, the Lower Ordovician corresponds to an almost continuous sedimentary succession comprising the uppermost part of the Val d'Homs/La Gardie Formation, as well as the overlying La Dentelle, Saint-Chinian, La Maurerie, Cluse de l'Orb, Foulon and Landeyran formations (Courtessole *et al.* 1981, 1983, 1985, 1988; Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003; Lefebvre *et al.* 2023). This succession records two large scale regressive-transgressive cycles, with the alternation of proximal, sandstone-dominated units (La Dentelle and Cluse de l'Orb formations) and distal, shale and siltstone-dominated units (Saint-Chinian and Landeyran formations), separated by transitional facies and lithologies (Val d'Homs/La Gardie, La Maurerie, and Foulon formations) (Vizcaïno *et al.* 2001; Tortello *et al.* 2006).

Biostratigraphy of the Lower Ordovician of the Montagne Noire relies primarily on trilobites (Vizcaïno & Álvaro 2003), with rare additional data based on agnostids (Tortello *et al.* 2006) and conodonts (Serpagli *et al.* 2007). The Val d'Homs/La Gardie Formation is a 60 to 300 m thick unit consisting mainly of shales and intercalated limestones. This formation has yielded both typical Furongian (late Cambrian) brachiopods, echinoderms and trilobites (Feist & Courtessole 1984; Ubaghs 1998) and, in its uppermost levels, a typical early Tremadocian trilobite assemblage (*Proteuloma geinitzi* trilobite Zone; Vizcaïno & Álvaro 2003). This suggests that the Cambrian-Ordovician boundary occurs within the upper part of the Val d'Homs/La Gardie Formation. The overlying sandstones of the La Dentelle Formation are azoic (Vizcaïno *et al.* 2001). The next unit, the Saint-Chinian Formation, is over 500 m thick and consists primarily of shales and fine siltstones, with numerous levels of fossiliferous siliceous concretions. The age of the lower part of the Saint-Chinian Formation is particularly well-constrained based on its diverse trilobite (*Shumardia pusilla* trilobite Zone; Vizcaïno & Álvaro 2003), agnostid (Tortello *et al.* 2006) and conodont faunas (Serpagli *et al.* 2007), all indicating a middle Tremadocian age (*Paltodus deltiifer* conodont Zone; for global correlation, see e.g. Bergström *et al.* 2009; Goldman *et al.* 2020). The long suspected late Tremadocian age of the middle (*Euloma filacovi* trilobite Zone) and upper parts (base of the *Taihungshania miqueli* trilobite Zone) of the Saint-Chinian Formation was confirmed by their particularly diverse agnostid assemblages (Tortello *et al.* 2006). The occurrence of typical early Floian agnostid taxa in the overlying, particularly thick (900 m) La Maurerie Formation suggests that the Tremadocian-Floian boundary more or less coincides with the transition between the Saint-Chinian and La Maurerie formations (Tortello *et al.* 2006; Van Iten & Lefebvre 2020; Lefebvre *et al.* 2023). The age of the three overlying units is less constrained, and relies solely on trilobite assemblages suggesting a mid Floian age for the Cluse de l'Orb (*Colpocoryphe maynardensis* Zone) and Foulon (*Neseuretus* (*N.*) *arenosus* Zone) formations, and a late Floian age for the Landeyran Formation (*Apatokephalus incisus* and *Hangchungolithus primitivus* zones) (Van Iten & Lefebvre 2020; Lefebvre *et al.* 2023).

The four somasteroid taxa *Ampullaster ubaghsi* Fell, 1963b, *Chinianaster levyi* Thorall, 1935, *Thorallaster spiculiformis* Dean Shackleton, 2005 and *Villebrunaster thoralis* Spencer, 1951 were found in siliceous concretions of the middle part of the Saint-Chinian Formation (*Euloma filacovi* Zone; Vizcaïno & Lefebvre 1999; Vizcaïno *et al.* 2001). In the Montagne Noire, these levels have yielded the most abundant and diverse assemblage of the whole Lower Ordovician succession (Vizcaïno *et al.* 2001). Faunas are dominated by trilobites, but they also comprise numerous annelids (machæridians), brachiopods, conulariids, graptolites, hyolithids, and molluscs (bivalves, cephalopods, gastropods, rostroconchs, tergomyans) (Thorall 1935; Capéra *et al.* 1978; Babin *et al.* 1982; Courtessole *et al.* 1983; Vidal 1996a; Vizcaïno *et al.* 2001; Vizcaïno & Álvaro 2003; Kröger & Evans 2011; Van Iten & Lefebvre 2020). The middle part of the Saint-Chinian Formation has also yielded one of the most diverse late Tremadocian echinoderm assemblages in the world (Vizcaïno & Lefebvre 1999; Sprinkle & Guensburg 2004; Lefebvre *et al.* 2013). This assemblage is dominated by unattached epibenthic taxa, well-adapted to the life on soft siliciclastic substrates: primarily cornute and mitrate stylophorans, but also asterozoans (somasteroids, stenuroids), glyptocystitid rhombiferans and solutans (Vizcaïno & Lefebvre 1999; Lefebvre & Fatka 2003). Crinoids, edrioasteroids and eocrinoids are also present, but they represent minor components of benthic communities (Vizcaïno & Lefebvre 1999; Lefebvre & Fatka 2003). The preservation of nearly complete, articulated to slightly disarticulated echinoderm skeletal remains is suggestive of quiet, relatively distal (shelf) environmental conditions, below storm wave base (Vizcaïno & Lefebvre 1999; Lefebvre 2007).

Chinianaster levyi also occurs in siliceous concretions of the uppermost part of the Saint-Chinian Formation (base of the *Taihungshania miqueli* Zone; Vizcaïno & Lefebvre 1999; Vizcaïno *et al.* 2001). These late Tremadocian levels have also yielded particularly diverse marine assemblages, dominated by trilobites, associated with brachiopods, conulariids, graptolites, hyolithids, machæridians and molluscs (Vizcaïno *et al.* 2001). Although less diverse than in the underlying *Euloma filacovi* Zone (e.g. glyptocystitids and stenuroids are absent), echinoderms still represent a major component of epibenthic assemblages (Vizcaïno & Lefebvre 1999; Vizcaïno *et al.* 2001). In these levels, cornutes and kirkocystid mitrates are the most abundant echinoderm taxa. Taphonomic and environmental conditions are similar to those of the *E. filacovi* Zone (Vizcaïno & Lefebvre 1999; Vizcaïno *et al.* 2001).

ANTI-ATLAS

In the Anti-Atlas (Morocco), the first specimens of Early Ordovician somasteroids were collected in the early 2000s (Van Roy *et al.* 2010; Lefebvre *et al.* 2016). In the last 20 years, intensive scientific and commercial sampling in this region yielded several dozens of specimens, with *c.* 50 of them deposited in the paleontological collections of the Museum of Comparative Zoology, Cambridge, Massachusetts (United States), the Prairie Research Institute, Champaign, Illinois (United States), the Université Claude Bernard Lyon 1,

Villeurbanne (France), the Université Cadi Ayyad, Marrakesh (Morocco), and the Yale Peabody Museum, New Haven, Connecticut (United States). However, in spite of a high number of available specimens, taxonomic diversity remains lower than in the Montagne Noire, with a single somasteroid described so far (*Cantabrigiaster fezouataensis* Hunter & Ortega-Hernández, 2021 [Hunter & Ortega-Hernández 2021; Blake & Hotchkiss 2022]). Most specimens deposited in public collections were collected in the Ternata plain, *c.* 15 to 30 km N of Zagora, although their precise locality and stratigraphic position are often approximative. Somasteroids belonging to the Prairie Research Institute come from Jbel Kissane (Agdz area), about 68 km NW of Zagora.

In the Agdz and Zagora areas, the *c.* 900 m thick Lower Ordovician deposits are unconformably overlying the Guzhangian (middle Cambrian) sandstones of the Tabanite Group (Destombes *et al.* 1985; Martin *et al.* 2016a). In the Anti-Atlas, the Lower Ordovician succession is traditionally subdivided into the Lower Fezouata, Upper Fezouata, and Zini formations (Destombes *et al.* 1985; Álvaro *et al.* 2022). All together, these three units record a single long-term eustatic cycle, with the maximum flooding surface coinciding more or less with the boundary between the Lower and Upper Fezouata formations (Destombes *et al.* 1985; Vidal 1996b; Lefebvre *et al.* 2016; Vaucher *et al.* 2016). In the Agdz and Zagora areas, in the absence of the iron-rich glauconitic bed which marks the limit between the Lower and Upper Fezouata formations, these two units are generally considered as forming together the Fezouata Formation, consisting of *c.* 850 m of fine siltstones (Lefebvre *et al.* 2016, 2018; Martin *et al.* 2016a; Vaucher *et al.* 2016, 2017). The overlying black sandstones of the Zini Formation represent the proximal-most deposits of the Lower Ordovician succession (Vaucher *et al.* 2016, 2017). They are unconformably overlain by the Darriwilian shales of the Tachilla Formation (Dapingian gap; Destombes *et al.* 1985). Biostratigraphy of the Lower Ordovician succession in the Central Anti-Atlas is well-constrained, and based on conodonts (Lehnert *et al.* 2016), graptolites (Destombes 1960; Gutiérrez-Marco & Martin 2016; Martin *et al.* 2016a), and palynomorphs (acritarchs and chitinozoans; Elaouad-Debbaj 1984, 1988; Nowak *et al.* 2016). Ages obtained from these different taxonomic groups can be readily compared with other regions, therefore allowing correlation of the Moroccan deposits with the international time scale (Lefebvre *et al.* 2018).

The lowermost 250 m of the Fezouata Formation (early-middle Tremadocian, *Anisograptus matanensis* to *Aorograptus victoriae* graptolite zones; Gutiérrez-Marco & Martin 2016) have yielded depauperate, low-diversity assemblages (Destombes *et al.* 1985; Lefebvre *et al.* 2016). In marked contrast, the overlying 150 m are extremely fossiliferous and comprise the *c.* 70 m thick interval, where most taxa of the late Tremadocian Fezouata Biota were collected (*Sagenograptus murrayi* graptolite Zone; Van Roy *et al.* 2010; Lefebvre *et al.* 2016, 2018; Martin *et al.* 2016a; Saleh *et al.* 2020a, 2021, 2024). This interval yielded extremely abundant and diverse fossil remains, comprising not only taxa with a recalcitrant

organic skeleton (graptolites) or mineralized hard parts (bivalves, brachiopods, cephalopods, conulariids, echinoderms, gastropods, hyolithids, machaeridians, ostracods, rostroconchs, tergomyans, and trilobites), but also a wealth of more lightly skeletonized organisms seldom preserved in the fossil record (e.g. aglaspidids, demosponges, eurypterids, lobopodians, marrellomorphs, paleoscolecids, radiodonts, xyphosurans) (Destombes *et al.* 1985; Botting 2007, 2016; Vinther *et al.* 2008, 2017; Van Roy *et al.* 2010, 2015; Van Roy & Briggs 2011; Kröger & Lefebvre 2012; Ebbestad 2016; Gutiérrez-Marco & Martin 2016; Lefebvre *et al.* 2016; Martí Mus 2016; Martin *et al.* 2016b; Polechová 2016; Van Iten *et al.* 2016; Drage *et al.* 2023; Laibl *et al.* 2023; Potin *et al.* 2023; Candela *et al.* 2024; Lustri *et al.* 2024). Echinoderms are one of the major components of the late Tremadocian Fezouata Biota (Lefebvre *et al.* 2016). All specimens of the somasteroid *Cantabrigiaster fezouataensis* were apparently collected in this c. 70 m thick interval (with the limitation of approximative locality information, when the material was acquired from local fossil traders). Echinoderm assemblages are dominated by epibenthic, vagrant taxa, primarily cornute stylophorans, along with glyptocystitid rhombiferans, mitrates, somasteroids, and solutans (Lefebvre & Botting 2007; Lefebvre *et al.* 2016; Hunter & Ortega-Hernández 2021; Dupichaud *et al.* 2023). Eocrinoids can be also locally abundant (Allaire *et al.* 2017), while permanently attached taxa (crinoids, diploporitans, edriasteroids) are extremely rare (Sumrall & Zamora 2011; Lefebvre *et al.* 2016). The preservation of echinoderms illustrating various stages of decay, some of them with exceptionally preserved soft parts (Lefebvre *et al.* 2019; Saleh *et al.* 2023), implies their burial by occasional distal storm deposits in an otherwise quiet, distal (shelf) environment. No soft parts have been observed so far in *C. fezouataensis*; putative carbonaceous films observed in podial basins of some specimens are the result of latex casting (Saleh *et al.* 2020b).

In the Agdz-Zagora area, the upper part of the Fezouata Formation (early-late Floian, *Cymatograptus? protobalticus* Zone to “*Azygograptus* interval”; Gutiérrez-Marco & Martin 2016; Lefebvre *et al.* 2018) consists of micaceous siltstones, with some siliceous concretion-bearing levels, and towards the top of this unit, more and more frequent and thicker intercalated sandstone beds (Vaucher *et al.* 2016, 2017). Within this 400 m thick succession, exceptional preservation has been recorded in a narrow, c. 50 m thick interval (*Baltograptus? jacksoni* Zone, mid Floian; Lefebvre *et al.* 2018). However, lightly sclerotized taxa are far less numerous and diverse than in the late Tremadocian Fezouata Biota (Lefebvre *et al.* 2018; Saleh *et al.* 2024). In the Central Anti-Atlas, Floian assemblages are dominated by brachiopods, molluscs and trilobites, along with conulariids, echinoderms, graptolites, hyolithids, and ostracods (Destombes *et al.* 1985; Kröger & Lefebvre 2012; Ebbestad 2016; Gutiérrez-Marco & Martin 2016; Lefebvre *et al.* 2016; Martin *et al.* 2016b; Polechová 2016; Van Iten *et al.* 2016; Candela *et al.* 2024). In the upper part of the Fezouata Formation, echinoderm assemblages are dominated by various epibenthic taxa adapted to life on soft, siliciclastic

substrates; primarily eocrinoids (e.g. *Balantiocystis*), as well as glyptocystitid rhombiferans, solutans, and stylophorans (Chauvel 1966, 1971; Lefebvre *et al.* 2016; Saleh *et al.* 2022; Dupichaud *et al.* 2023). Crinoids and edriasteroids are rare (Donovan & Savill 1988; Sumrall & Zamora 2011; Lefebvre *et al.* 2016). Somasteroid remains are also present, in both siltstones and siliceous concretions; however, their preservation hinders so far any more precise taxonomic identification (Lefebvre *et al.* 2016).

INTERPRETING THE SOMASTEROIDEA: REVIEW OF THE LITERATURE

To emphasize the evolution of interpretation, citations are chronological and authors recur. Titles not specifically addressing the Somasteroidea but nevertheless germane are included.

Spencer 1914-1940. — Nearly all named Paleozoic asterozoan genera were surveyed, the author finding exemplar morphology converged back in time such that many genera could not be assigned at the (sub)class level. Rather than strict usage of Linnaean terminology, eight subdivisions termed “Sections” were recognized. The somasteroids *Archegonaster* and *Chinianaster* Thoral, 1935 were not included.

Spencer 1919. — The new genus *Platanaster* Spencer, 1919 was described from the Late Ordovician and assigned with *Palasteriscus* Stürtz, 1886 from the Early Devonian to the new family Platanasteridae Spencer, 1919. Familial recognition emphasized a shared flattened form in which the adambulacral ossicles are broad, their alignment with the ambulacral ossicles yielding a shallow ambulacral groove, these expressions emphasized in an interpretation of asterozoan origins (Fell 1963a). The Platanasteridae was not assigned at the class level.

Jaekel 1923. — *Archegonaster* was recognized in a brief study encompassing the morphological diversity of Asterozoa. *Archegonaster* was found to combine a primitive internal construction with an external form comparable to that of the living asteroid *Goniaster* Agassiz, 1836.

Spencer 1927. — The family Archophiactinidae was recognized for three genera, these poorly known and not assigned to subclass but judged “nearly related to primitive Asterozoa” and “lying near root genera which gave rise to some of the Palaeozoic Ophiuroidea” (p. 360).

Thoral 1935. — *Chinianaster* was recognized, its unique nature among asterozoans not clearly identified.

Spencer 1951. — The author’s last sole-authorship title. Interpretations summarized in the abstract included recognition of the Somasteroidea, it interpreted as “the first stages in the differentiation of a starfish” (p. 87), the term “starfish” used as a collective for all Asterozoa. Three subclasses were recognized, the Ophiuroidea, Asteroidea, and the exclusively Early and Middle Ordovician Somasteroidea. Use of “subclass” rather than “class” was not discussed; however, in Spencer (1914-1940), affinities of many genera, whether asteroid or ophiuroid, were found to be indeterminate thereby seemingly implying differences between groups were not of a level that warranted class-level recognition.

All somasteroids were assigned to a single new order “Goniactinida”. Two new familial concepts were recognized, the Chinianasteridae Spencer, 1951 for *Chinianaster* and then-new *Villebrunaster* Spencer, 1951, and the Archegonasteridae limited to *Archegonaster*. Linnaean terms below the subclass level were cited, the earlier “Section” usage abandoned. Function was stressed (p. 87): “grouping of the starfish adopted here is based on the activities of the arms, especially during feeding”, the asteroid arm “from the beginning is adapted for a carnivorous diet of large food” whereas for ophiuroids, feeding depended on “small food in or near the sea bottom”, the “primitive” representatives with a “burrowing habit”. The Somasteroidea was thought to include the earliest asterozoan occurrences (Tremadocian, the others Arenig [Floian]) representing the “first stages in the differentiation of a starfish”. Comparisons with extant crinoids were provided. Although many photographs were included, details are obscure, the reader referred to diagrammatic reconstructions, some calling for reevaluation (e.g. below on Spencer 1951: fig. 7).

The diagnostic characters of the Somasteroidea (p. 91) stressed presence of only two oral-surface ossicular types, the “ambulacralia” and rows of “interambulacralia” (or “virgalia”). The latter were found “especially characteristic”, although nevertheless “entirely wanting” among “later genera”, the “later” not clearly identified. The “ambulacralia” also were found to be “characteristic”. The aboral skeleton, “when present”, was described as a reticulate meshwork of multiradiate ossicles.

For the Asteroidea, the order Platysterida was recognized for the Platanasteridae. Two new orders of Ophiuroidea were recognized and distinguished based on presence of “vertebrae”, the Stenurida in which “vertebrae” were lacking, and the Ophiurida, in which they are present. “Vertebrae” was not clearly defined for the Stenurida; however, the laterals “usually” occur as a double series, these termed “laterals” and “sublaterals”.

Historically, it was noted that starfish had “arrived in a series of transgressions which began in the Tremadocian”, the use of “arrive” seemingly implying earlier occurrences elsewhere, although a broader reading might argue a phylogenetic “arrival”. *Villebrunaster* was judged a suspension feeder, a habit that served to connect it with a “probably ciliary pelmatozoan ancestor” (p. 91). The potential for ciliary feeding was discussed (p. 96).

Ubaghs 1953. — In a comprehensive survey of early asterozoans, morphology was reviewed and the taxonomic subdivisions of Spencer (1951) retained (p. 813). Three families (Archegonasteridae, Archophiactinidae, Chinianasteridae) were assigned to the Somasteroidea. In a diagrammatic reconstruction (fig. 64, p. 837), Paleozoic and post-Paleozoic asterozoans were separated and somasteroids were assigned a stemward positioning. Many subdivisions were recognized; however, no direct linkages between those of the Paleozoic and the post-Paleozoic were proposed.

Fell 1963a. — In a detailed series of contributions including 1963a, Fell hypothesized a phylogenetic sequencing in which the Crinoidea were seen as ancestral to the Asterozoa.

Interpretation focused on inferred “growth gradients” in which so-called lateral gradients represented by the pinnules of the crinoid arm evolved into the laterally radiating virgalia of somasteroids, the latter in Fell’s terminology, “metapinnules”. The living asteroid genus *Platasterias* Gray, 1871 was reassigned to the Somasteroidea and envisioned as transitional to derived asterozoans. Virgalia in turn transitioned to the longitudinal growth gradients of the Asteroidea, first the fossil Platanasteridae, next the extant Luidiidae, finally to more derived asteroids (Fell 1963a: 391, 395, table 1, fig. 7). A parallel sequencing was envisioned for the Ophiuroidea. In an extended and detailed discussion, the “sublateral” of stenuroids represent a first phase as the ancestral virgalia progressed to the single lateral of derived ophiuroids (Fell 1963a: 403, 410, table 2).

Fell 1963b. — A new Ordovician somasteroid *Ampullaster* was proposed (Fell 1963b), and it and *Villebrunaster* Spencer were assigned to the new Villebrunasteridae.

Philip 1965. — The broader conclusion of Fell (1963a), the proposed derivation of the Asterozoa from the Crinoidea, was rejected. Relationships between extant asterozoans and Ordovician somasteroids were not discussed.

Spencer & Wright 1966. — In a summary discussion, Wright noted that a classification of asterozoans of all ages had been outlined but not completed prior to the 1954 passing of Spencer. The chapter was completed by Wright emphasizing the thinking of Fell, including interpretation of extant *Platasterias* as a surviving somasteroid. In a cautionary phrasing, however, Fell’s derivation of somasteroids from crinoids only “seems to be true” (p. 31).

Expanding on the earlier two-fold subdivision of the somasteroid oral skeleton (“ambulacralia” and “interambulacralia” Spencer 1951), a seminal three-fold subdivision – “axial”, “adaxial”, and “extraxial” – was proposed, it providing a descriptive classification while also drawing attention to issues surrounding the interpretation of homologies among skeletal series.

Somasteroids, asteroids, and ophiuroids were recognized as subclasses of the class Stellerioidea Lamarck, 1816 somasteroids ancestral to the other two (e.g. fig. 38). The Villebrunasteridae (for *Villebrunaster*, *Ampullaster*), the monogeneric Platasteriidae, and Archophiactinidae were retained as families of Somasteroidea. Among asteroids, the Palasteriscidae (for *Platanaster*, *Palasteriscus*) Gregory replaced the junior name Platysterida Spencer, and it and the extant Luidiidae were assigned to the Platysterida. The term Ophiurida was abandoned.

Madsen 1966. — In a brief treatment, the interpretation of *Platasterias* as a somasteroid (Fell 1963a) was rejected.

Ubaghs 1967. — Somasteroids were treated as ancestral to both asteroids and ophiuroids, the three recognized at the subclass level. Neither the crinoid nor edrioasteroid ancestry was found convincing (p. 56).

Blake 1972, 1982. — Based on comparison among discrete ossicle types, *Platasterias* was removed from the Somasteroidea, recognized as a subgenus of extant *Luidia* Forbes, 1839, and returned to the Asteroidea. Döderlein (1920) subdivided

speciose *Luidia* into four groups, three skeletally similar to *Platasterias*, the fourth distinctive; Fell's (1963a) *Luidia* exemplar, a member of the disparate fourth, likely misled his interpretations of *Platasterias*.

McKnight 1975. — The classification of Spencer & Wright (1966) was largely retained. Absence of an odontophore (synonym of axillary, Spencer [1916]) was recognized as a defining characteristic of the Somasteroidea. The Helianthasteridae was added to Somasteroidea, an interpretation later rejected (Blake 2009).

Paul & Smith 1984. — Somasteroids were found to be “poorly understood” (p. 468). In a diagram of the radiation of echinoderm classes (fig. 19), *Archegonaster* was illustrated as a derivative of *Stromatocystites* and stemward of one branch leading to asteroids and a second to a primitive “ophiuroid.” Discussions (p. 469) interpreted virgals, adambulacrals, and laterals as transformed cover plates from stromatocystitids. Significance of the marginal framework was emphasized.

Smith & Jell 1990. — Select edrioasteroids and an asterozoan representing each of the three subclasses were included in a phylogenetic reconstruction of asterozoan early history. *Archegonaster* was the somasteroid exemplar, it described, illustrated, and interpreted in detail. Problematic Cambrian *Camptostroma* Ruedemann, 1933, provided the outgroup. Asterozoan branching sequence was not resolved (fig. 52).

Blake & Guensburg 1993. — The new somasteroid genus *Ophioxenikos* was based on a previously unassigned “starfish” specimen (Byrd 1970). Earlier designation of an edrioasteroid outgroup was rejected.

Mooi & David 2000. — In an analysis applying their Extraxial-Axial Theory (EAT) model to asterozoan evolution, the authors proposed complex differentiation. Interpretation of somasteroid virgals as derivatives of stem echinoderm cover plates (Paul & Smith 1984: 469) was rejected. Spencer & Wright's (1966) “adaxial” was not found to be useful beyond the Asterozoa.

Dean Shackleton 2005. — Comprehensive evaluations of early asterozoans included phylogenetic analysis. Descriptions were extended and detailed, and careful reconstructions were provided; photographic documentation was limited. Two branches of Asterozoa above an edrioasteroid outgroup were recognized, one branch dominated by the Asteroidea began with two stemward “plesions” (*Petraster* Billings, 1858, and *Promopalaeaster* Schuchert, 1914), the second branch consisting of a terminal Ophiuroidea and a number of more stemward plesions, including the Somasteroidea. “Plesion 1 (Order) Somasteroidea” was restricted to two families, the monogeneric Archegonasteridae and the Chinianasteridae, the latter including *Chinianaster*, *Villebrunaster*, then-new *Thoralaster* Dean Shackleton, 2005, and *Ophioxenikos*, the last in the phylogenetic analysis emerging as the sister of *Thoralaster* (fig. 13, p. 52) and referred to as a metataxon of *Chinianaster* (p. 68). Included archophiactinid genera were assigned to plesions between somasteroids and ophiuroids. *Ampullaster* Fell, 1963b was synonymized with *Villebrunaster*.

In discussion of the aboral skeleton of *Villebrunaster*, Dean Shackleton (2005: 67R) described “elongate rod-like ossicles (that) are often coincident with the adradial groove of underlying ambulacrals”. “Coincident” to the extent suggesting exact correspondence of position would favor differentiation of carinal arm series that are otherwise unknown among somasteroids; a carinal series has not been recognized here, nor was presence postulated in the author's figure 6B p. 41 (here Fig. 12E; then “FSL 1879 591”, now UCBL-FSL 711092). Carinals in a somasteroid suggest a step toward the Asteroidea, although differentiation likely was homoplastic even within the latter and associated with vaulting to cylindrical arm configurations (Blake & Rozhnov 2007). Cylindrical arms have not been recognized among somasteroids.

Blake 2013. — Emphasizing usages for the extant, major asterozoan subdivisions were recognized at the class rather than subclass level. Presence of adaxial virgalia was recognized as the unifying expression of the Somasteroidea. As the three genera of Archophiactinidae lack virgalia, earlier assignment to the Somasteroidea was not accepted and generic assignments were left in abeyance.

Blake & Guensburg 2015. — Status of knowledge of the class Somasteroidea was surveyed. The Blake & Guensburg (1993) rejection of edrioasteroids as an outgroup was further developed, and a phylogenetic analysis of select comparatively well-known early asterozoan genera beginning with the Somasteroidea as an “ingroup outgroup” was developed. In accord with Spencer (1951) and Dean Shackleton (2005), two somasteroid families were recognized, the Chinianasteridae and Archegonasteridae.

Villier *et al.* 2018. — The somasteroid *Archegonaster* provided the outgroup in a phylogenetic analysis of select Paleozoic Asteroidea directed toward taxonomic positioning of a new Triassic asteroid.

Blake 2018. — Following redescription of the superficially somewhat somasteroid-like *Platanaster* (Blake 1994), the Platanasteridae Spencer was reconstituted to include *Platanaster*, *Lanthanaster* Branstrator, 1972, *Phyrtosaster* Blake, 2007, and “*Palaeaster*” *exculptus* Miller, 1881 the family assigned to the new asteroid order Euaxosida Blake.

Hunter & Ortega-Hernández 2021. — A new genus and species of Somasteroidea, *Cantabrigiaster fezhouataensis*, was proposed, it interpreted as lacking an ambital framework. Phylogenetic analysis was undertaken incorporating diverse asterozoans and early non-asterozoan echinoderm genera. The Crinoidea emerged as the sister to the Asterozoa with *C. fezhouataensis* basal within somasteroids.

Blake & Hotchkiss 2022. — An ambital framework series was recognized in the type suite of *C. fezhouataensis* Hunter & Ortega-Hernández, including the holotype. The genus was redescribed and synonymized with *Villebrunaster*. Character delineation for the data matrix of Hunter & Ortega-Hernández was found flawed, and the phylogenetic hypothesis proposing a crinoid ancestry for the subphylum Asterozoa rejected. Reevaluation of the data matrix was not undertaken.

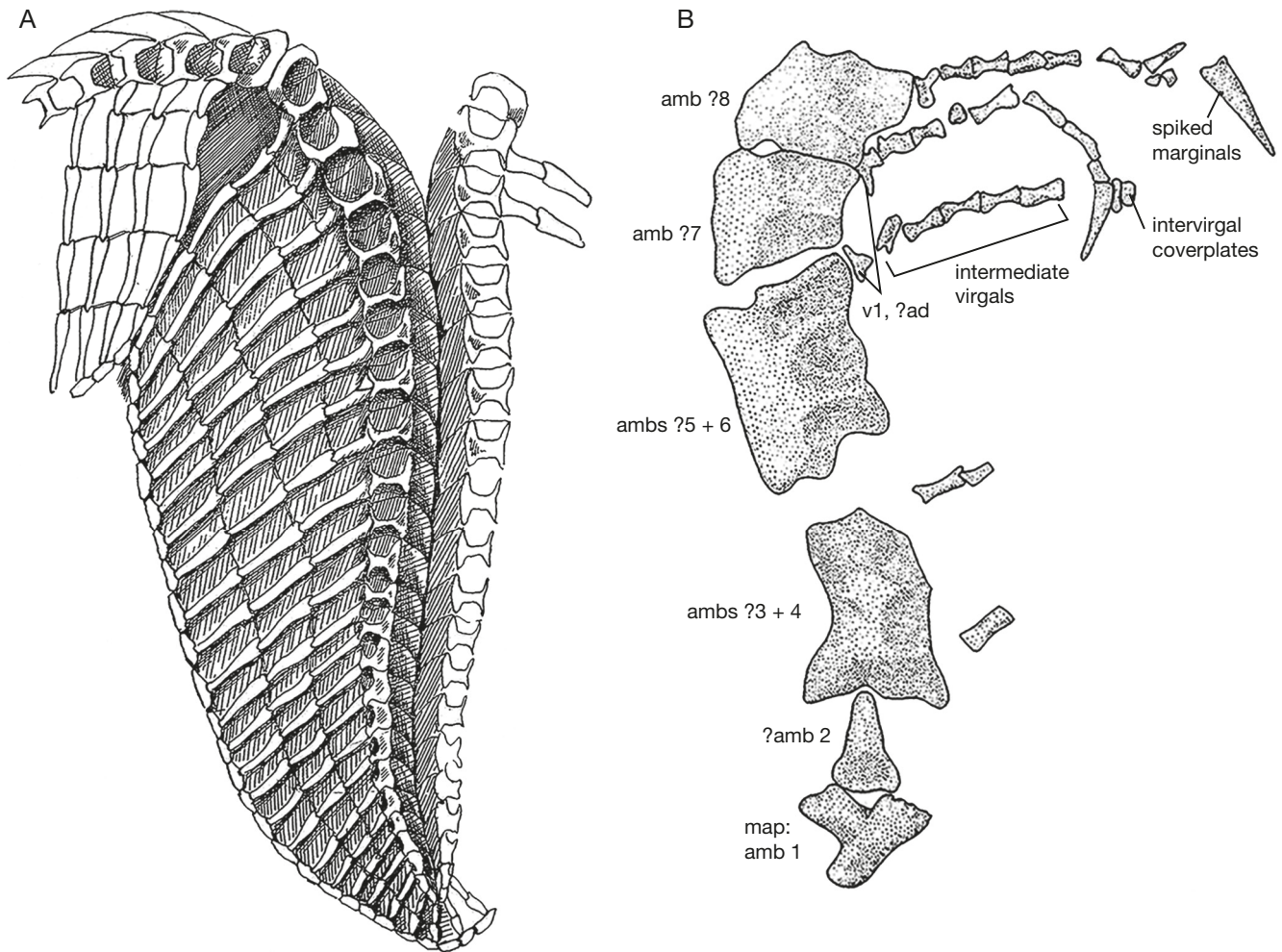


FIG. 1. — **A**, Reconstruction of part of the oral surface of *Chinianaster* Thoral, 1935, Spencer (1951: fig. 7; Spencer & Wright 1966: fig. 39.4). The **darkened area** abradial to the MAO is the posited “gap” or “cleft” of Spencer and of Fell, it bordered by the first virgalium shown extended to the arm tip; see text. Specimens available to Spencer, including the lectotype, attained arm radii of 25 to 30 mm; **B**, axials and adaxials of *Thoraster spiculiformis* Dean Shackleton, 2005 (Dean Shackleton 2005: fig. 7; see Fig. 6B); “intervirgal cover plates” are accessories and not the same as “intervirgal struts” *sensu* Dean Shackleton (2005). Abbreviations: ?ad, adambulacral; amb, ambulacral, an axial; v1, virgal 1, also questionably an adambulacral, see text. The two ossicles marked “ambs ?3 + 4” and “ambs ?5 + 6” are about 4 mm in length.

INTERPRETING SOMASTEROID MORPHOLOGY

BACKGROUND

The seminal three-fold skeletal classification of Spencer & Wright (1966) together with the skeletal reconstruction of Spencer (1951: fig. 7; see also Spencer & Wright 1966: fig. 39.4; here Fig. 1A) serve as background for the following discussions. Absence of an outgroup or stemgroup for the subphylum imposes logical ambiguities on interpretations of homologies; the Spencer & Wright skeletal classification herein is modified to emphasize objectivity of ossicular series recognition rather than inferences on homology. The axial skeleton consists of the mouth frame and the water-vascular ossicular progression extending to the arm tip and including any terminal. The adaxial series consists of ossicular series aligned with and immediately lateral to the axial. The remainder of the skeleton is extraxial. The Spencer figure is important because it diagrams core interpretations of this author, later endorsed by Fell

(e.g. Fell 1963a, b, c) that are crucial to the interpretation of skeletal homology and aspects of life mode. Aspects of the reconstruction are contested.

Although much of the discussion of Spencer focused on *Villebrunaster*, figure 7 (here Fig. 1A) is of *Chinianaster*; generic differences are significant. Overall form as reconstructed in the Spencer diagram was flattened and distended; flattening is documented by variation in appearance both among specimens and among ambulacra within specimens (Figs 2-13). The most direct evidence for a flattened reconstruction is the portrayal of the adaxial series (Fig. 1A). In life, the virgalia away from the central disk lay essentially in the oral plane, and as reconstructed, virgalia are flattened against the substrate, the life configuration of these series accurate. The medial portion of the somasteroid disk and proximal arm intervals were arched in life and subject to distension with burial; as reconstructed, the more proximal interval of the large cylindrical water vascular channel was flattened against the substrate as to show the full breadth of the channel interior, the arm tip of com-

paratively low relief less distorted. The central disk and arms as reconstructed are distended, an interpretation with major implications for interpretation of morphology and phylogeny. Spencer (1951: fig. 7; here Fig. 1A) illustrates irregularity of axial positioning at the arm midline. Where not eroded, a shield-like skeletal axial flange closed over the water-vascular channel of *Chinianaster* (Figs 2E; 3B, E). Flanges were not illustrated; however, the bilateral appearance of virgals after loss of skeletal closure is portrayed. Neither podial pores nor transverse water vascular channels were proposed. Adaxials are associated with distal-most axials, and no differentiated terminal is shown. In contrast with the reconstruction of Spencer (1951: fig. 7; here Fig. 1A), the best-preserved arm tips do not suggest virgalia extended distally beyond the axial series (Figs 2F; 9E; 12B, F; 13).

Spencer (1951) and Fell (1963a) argued that the ambital framework is a reoriented first virgalium extended distally as to embrace subsequent virgalia to become transformed into the inferomarginal series, the interpretation calling for transformation of an adaxial series into an extraxial series. Additionally, the mouth area was interpreted as extending along the axis of the arm as to separate the proximal axial series on each side of the midline to form a so-called “buccal slit” (Spencer & Wright 1966: 29). Positing presence of such a configuration argues that a distended mouth likely was plesiomorphic among early asterozoans and might thereby also have been plesiomorphic among all pentaradial echinoderms. Both interpretations are rejected.

BODY FORM AND PRESERVATION

For the most part, somasteroids were subpentagonal in outline, although disk sizes and arm breadths were exaggerated with burial and compaction. The nature of distortion of many specimens indicates that somasteroids were low arched in life, the central disk thickened and particularly susceptible to disruption. With flattening, all ossicles of a series were potentially subject to coordinated partial rotation in a manner that can obscure life shapes, including placement of the podial basin line of abutment; many axial series as viewed in oral aspect provide examples. In comparison with living asterozoans, somasteroids are known to have reached only comparatively small sizes, the lectotype of *Chinianaster* with an arm radius of approximately 25 mm.

AXIAL SKELETON: MOUTH FRAME

In contrast with the 2-1-2 mouth frames of radiate stemmed echinoderms, the five ambulacra of asterozoans are uniform and closely fitted throughout their length (see below on so-called “buccal slits”). The 2-1-2 mouth frame appears comparatively rigid whereas the delicate construction of somasteroids was flexible, flexibility essential to mobility. Derivation of the somasteroid configuration and life modes provide enduring challenges to the selection of an outgroup for phylogenetic analyses (Blake & Guensburg 1993, 2015).

Interpretation of the configuration of the somasteroid jaw frame as exemplified by *Villebrunaster* accompanied recognition of the subclass (Spencer 1951: 94): “The ambulacralia

near the mouth form a frame around the central opening. The frame is not circular but is prolonged into V's along each radius. The broadened end of the V's open into the cavity of the frame. The interradian angles are joined together by a pair of mouth-angle plates; short, broad ossicles, almost spade-like in outline”. The interpretation, encompassing both mouth angle ossicles and proximal axials, was diagrammed and labeled in all three somasteroid genera then recognized (Spencer 1951: figs 1, 7 [herein Fig. 1A], 9, 13). The “prolonged [...] Vs” were referred to as “buccal slits” and were important to the author's interpretations in that the configuration was envisioned as providing space for food particle reception (Spencer 1951). Significant variation in mouth frame configurations both within and among specimens – as documented by widely available published illustrations – demonstrates that so-called “buccal slits” are artifacts of preservation, the closely fitted life configurations having been distorted and dilated with burial and sediment compaction (e.g. Blake 2013, 2018, 2024; Blake & Guensburg 2015; herein). Potential minor divergence of proximal axials of asteroids in life, however, was recognized (Blake & Etnensohn 2009) whereas the “Y”-shaped configurations common among ophiuroids were independently derived.

The *Chinianaster* MAO as illustrated by Spencer (1951: fig. 7; Fig. 1A) are proportionately small, rounded and aligned with subsequent axials (e.g. Figs 2B, E; 3E, F; also *Thoralaster* Fig. 8D, the transverse ridges of the latter remaining in a simple A-frame-like configuration as to enclose an apparent phylogenetically largely occluded podial basin). In contrast, a specimen of *Villebrunaster* (Fig. 11B) exhibits upright spinelet-bearing MAO, the apparent circumorals differentiated with podia directed toward the mouth, the overall MAO configuration suggestive of the mouth frame of asteroids.

The distended mouth frame of the *Cantabrigiaster* holotype (Fig. 4A, D) argues that the differences between *Chinianaster*/*Thoralaster* and *Villebrunaster* as preserved are in ossicular orientation that are fortuitous artifacts of preservation rather than reflective of taxonomic differences. The MAO pair to the right of the *Cantabrigiaster* holotype are similar to those of the *Villebrunaster* example, the ossicles upright, slab-like, and bearing apparent spinelet bases whereas the pair to the left suggests the small, rounded expressions of the selected *Chinianaster* and *Thoralaster*. The one MAO pair of the *Cantabrigiaster* holotype that is suggestive of the *Villebrunaster* pair is directed toward the mouth with accessory positioning exposed at essentially an inferred at rest or passive position, whereas those suggestive of the *Chinianaster* and *Thoralaster* examples are rotated into the mouth area and likely oriented as to thrust food material into the interior. Therefore somasteroid configurations insofar as is known were broadly uniform and comparatively simple, indicating mouth frame flexibility that accompanied free-living epifaunal life modes: the varied expressions of the fossils are products of the serendipity of preservation.

Departure from the otherwise straightforward somasteroid jaw frame construction is the potential presence of supernumerary mouth frame ossicles in *Thoralaster* and perhaps

Villebrunaster. Enlarged flanges are developed in *Thoralaster* (Figs 7A, C; 8A), the flanges aligned with the remainder of the axial series. Flange status is uncertain, potentially an extension of the MAO whereas discontinuities as preserved suggest a separate ossicle favoring treatment either as a circumoral, or alternatively, as an intercalated extraxial. An apparent small ossicle in *Villebrunaster* (Fig. 11B) might represent a homologue of the supernumerary mouth frame ossicle in *Thoralaster*. A compound axial is developed in the *Cantabrigiaster* holotype (Fig. 4C), its accompanying first virgal bearing a “Y”-shaped ridge that also abuts the adjacent axial. These departures from typical mouth frame construction are known from limited occurrences and therefore of unknown general significance.

AXIAL SKELETON: ARM AXIALS

The aboral surfaces of axials beyond the mouth frame among somasteroids are separable into three configurations: the shield-like axials of *Chinianaster*, *Thoralaster*, *Cantabrigiaster*, and probably *Ophioxenikos*; the asymmetrical axials of *Villebrunaster* and *Ampullaster*, and the “T”-shaped axials of *Archegonaster*. Water-vascular tissues of planar somasteroids were protected by skeletal closure (except probably *Archegonaster*, it with apparent podial pores), closure variably developed among genera. The delicate oral flange-like skeletal arches of *Chinianaster* (Figs 2C, E; 3B, E) were readily eroded, especially more proximally, whereas the abutted axials of *Villebrunaster* were comparatively resistant (Fig. 9). The water vascular channel of most genera was relatively large and commonly flattened and dilated in preservation as to expose aboral surfaces, the resulting broad appearance potentially misleading. Axials of most genera were approximately equidimensional and podial basins large and shared equally by sequential axials. Axial intervals abradial to the water vascular channel are bilateral at the midpoint of the transverse ridge, the ridge flaring abradially to seat the virgulum. Axial series can be deflected in preservation as to suggest placement of the podial basin on one side of the transverse ridge (e.g. distally Figs 3C; 4C).

Axial positioning across the arm midline among asterozoans has been interpreted as either alternate or opposite. For *Villebrunaster*, Dean Shackleton (2005: 66L) thought axials are only rarely in “chance opposition [...] in rare circumstances” and this a result of *post-mortem* disturbance of only weakly linked ossicles. Asteroids were coded as opposite by this author. Ophiuroid suborders based on midline positioning have been recognized (e.g. Spencer & Wright 1966), whereas genera exhibiting both conditions have been assigned to single families (e.g. Dean Shackleton 2005; Jell & Cook 2020). In earlier studies, reliance on positioning in taxonomy was found unreliable (Gregory 1899: 342), Spencer (1914: 19) finding that “the most primitive forms had ambulacralia which are irregularly alternating” with both opposite and alternating configurations emergent from the primitive condition. The view here is in accord with those of Gregory and Spencer, that axial positioning across the midline in stemward asterozoans was irregular, subsequently becoming differentiated with both ontogeny and phylogeny (also Blake 2009, 2018).

Water vascular passageways between the radial canal and the podial basins were recognized by Dean Shackleton (2005), and although presumably requisite, exemplification has been found all but impossible, although irregularities along oral margins of axials can be suggestive.

All crown-group asteroids have “podial pores” between successive axials that serve to isolate and protect internal ampullae, and some later Paleozoic have openings that appear equivalent to those of the crown group. The “T”-shape of *Archegonaster* axials suggests podial openings to the arm interior, as do a few “C”-shaped axials of *Chinianaster* (Fig. 2A). Regularly shaped and positioned apparent arm openings in an arm of a specimen of *Thoralaster* suggest podial pores (Fig. 8G, H), yet the openings cannot be recognized elsewhere in the specimen (e.g. Fig. 8I, J), their actual status unknown but perhaps reflecting an emergent condition.

AXIAL SKELETON: TERMINAL

The so-called “terminal” is an unpaired ossicle at the arm tip, the proximal edge of the terminal the site of genesis of a number of ossicular series. Terminal ossicles among many asterozoans are little differentiated in size and form from immediately adjacent ossicles and therefore terminal recognition is generally problematic, a difficulty exacerbated by taphonomic disruption. Terminal ossicles, however, have not been definitively recognized even among better-preserved somasteroids (Figs 2F; 9E; 12B, F; 13).

ADAXIAL SKELETON

The adaxial skeleton is considered critical to the interpretation of the Asterozoa, an evaluation seen as complimenting interpretations focused on the laterals (adaxials of ophiuroids; Thuy & Stöhr 2011). The adaxial skeleton consists of the virgals of somasteroids and their phylogenetic derivatives, the adambulacrals of asteroids, laterals of ophiuroids, and embedded and outer virgals of stenuroids. Initially, ambital framework marginals were interpreted as virgal-series derivatives and assigned to the adaxial category (Spencer 1951; Spencer & Wright 1966), see below.

The first adaxial, the ossicle immediately abradial to the axial, ranges in form from nearly identical to the more abradial virgals (e.g. *Chinianaster* and *Thoralaster*) to much differentiated (e.g. *Archegonaster*), the variants suggesting evolutionally progressive differentiation, and thereby favoring treatment of the first ossicle as a part of a single integrated virgal series. The nature of stenuroid differentiation also is interpreted as favoring a single series (Blake 2024). In contrast, the first lateral ossicle has been treated essentially as representing a different ossicular series (Smith & Jell 1990).

A differentiated adradial ossicle associated with each virgulum was recognized in *Villebrunaster*, it termed an “intervirgal strut” (Dean Shackleton 2005: 66R). A corresponding ossicle was recognized in the *Ampullaster* holotype, and based largely on inferred homology, Dean Shackleton (2005) synonymized *Ampullaster* with *Villebrunaster*. Ossicular differentiation varies both within and among specimens of *Villebrunaster* ranging from presence of well-defined, arched, “C”-shaped

ossicles to local absence of obvious differentiation (Figs 9; 10; 11C, D; 12B), whereas corresponding ossicles of *Ampullaster* (Fig. 13), albeit known from a single specimen, are uniform in morphology and positioning, and based largely on these differences, generic status is retained for *Ampullaster*. See further Remarks under *Ampullaster*.

Complexly differentiated adradial virgals were diagrammed in a reconstruction of *Villebrunaster* (Dean Shackleton 2005: 36, 41; here Fig. 12A, C). Photographic documentation of the specific interval was not provided but the careful reconstruction enabled precise site identifications (Fig. 12B, D, the reconstructions and photo images reversed). Ossicles on one side approach life configuration, that on the other side providing the largely disrupted complex reconstruction. Although the series immediately distal to that of Figure 12C appears broadly similar, equivalent occurrences have not been recognized elsewhere on this specimen or others. Specifics of the reconstruction at the single site portray current status but reflect diagenetic alteration rather than differentiation of virgal series.

Rarely, the axial transverse ridge appears either broken, or alternatively, a small intervening ossicle might be present (Fig. 12B; perhaps Fig. 10C), it suggestive of the embedded adaxial of the Stenuroidea; even if a separate ossicle, no direct evolutionary linkage is proposed.

Near-oral (proximal) virgalia were judged as lacking from *Archegonaster* (Spencer 1951; Smith & Jell 1990), and virgalia immediately adjacent to mouth frame ossicles were not recognized in either *Chinianaster* or *Villebrunaster* (Dean Shackleton 2005: 66R, 68L). Interpretation of near-oral absence of virgalia from *Chinianaster* and *Villebrunaster* is not accepted based on presence of disrupted virgals and virgal debris in the interbrachia of these genera (Figs 2E; 3B) as well as in *Cantabrigiaster* (Fig. 4E). Interpretation of *Archegonaster* is retained.

A so-called “superambulacral” ossicle spanning the interval between the axial and more lateral ossicles was recognized both in the recognition of *Platanaster* and in extant *Astropecten* (Spencer 1919: 176, fig. 115). Subsequently, the superambulacral was interpreted as an occluded somasteroid virgal (Fell 1963a). The ossicle in *Platanaster* was reinterpreted as a taphonomic artifact, as offset edges of adambulacrals (Blake 1994). A superambulacral has not been recognized in other stem-group asteroids and no linkage to somasteroids is recognized. Superambulacral sourcing is unknown.

ABACTINALS

Three abactinal configurations are recognized among somasteroids. Abactinals of most genera consist of a little-thickened central area bearing multiple radiating bar-like “flanges” or “rays”. Discrete simple rods also might occur, although potential significance of breakage of radiating flanges can be difficult to determine. The central area of somasteroid abactinals appears at most weakly thickened, and their greatest dimension lay in the aboral plane. Spinelets are not readily recognized in the commonly associated fine debris. The “paxilla” of asterozoans consists of a “shaft surmounted by a tuft of spinelets” (Spencer & Wright 1966: 30), “shaft surmounted” implying an upright

column; the term “paxilla” is not considered appropriate for the somasteroid abactinals. *Archegonaster* abactinals are small, closely packed granules, *Ophioxenikos* abactinals are closely fitted irregular platelets. Differentiated midarm series (e.g. “carinals”) and specialized disk ossicles (e.g. “aboral circlets”) have not been recognized among somasteroids, but see above under Literature Review, Dean Shackleton (2005).

MADREPORITE

A madreporite is positioned on the oral surface of *Chinianaster* (Figs 2C; 3A, B), on the aboral surface of *Archegonaster*, and offset from the central disk in a specimen of *Cantabrigiaster* (Fig. 5A, B), the present positioning in this specimen disrupted during preservation. The granular madreporite surfaces in *Chinianaster* and *Cantabrigiaster*, although potentially reflecting diagenetic change, are unlike the radiating ridge-and-groove configuration of *Archegonaster* (Smith & Jell 1990: fig. 39C) and typical of asteroids. Differences together with absence of a recognized madreporite among other somasteroids suggests homoplastic emergence of a calcified madreporite within somasteroids.

THE AMBITAL FRAMEWORK

A body-framing so-called “marginal” series has been widely recognized among early echinoderms, but how broadly occurrences reflect homology is problematic. Presence of a “marginal” series in edrioasteroids homologous with inferomarginals of asteroids has been both accepted (e.g. Dean Shackleton 2005) and challenged (Blake & Guensburg 2015). Because of uncertainty, the term “ambital framework” was proposed as a descriptive substitute for any differentiated series found at or near the ambital margin of an early echinoderm (Blake 2013). Presence of a distinct ambital framework in all known somasteroids is taken as indicating framework presence is stemward in the subphylum (Blake & Hotchkiss 2022) and therefore asteroid inferomarginals are plesiomorphic, marginal absence from ophiuroids is a class-level apomorphy, and ambital framework-like expressions among stenuroids are problematic (Blake 2024).

A second marginal series, “superomarginal”, is found in many asteroid genera, its origin apart from the inferomarginal (Spencer 1916: 67; 1918: 126; 1951: 123) and perhaps derived from the aboral skeleton (Spencer & Wright 1966: 23). Complex ambital framework configurations of *Villebrunaster* and *Cantabrigiaster* suggest a potential for the onset of differentiation of a double series (i.e., inferomarginal and superomarginal) within Somasteroidea, the derivative class Asteroidea then potentially paraphyletic or polyphyletic.

Ambital framework differentiation among somasteroids argues evolutionary progression (but not one lineage) beginning with the stemward complex ambital necklaces of *Chinianaster* (Fig. 2B-D) and *Thoraster* (Fig. 6E, F), the more robust complexes of *Cantabrigiaster* (Figs 4E; 5A, D, E) and *Villebrunaster* (Figs 10A; 11A, D; 12E, F) next, and the more uniform inferomarginals first of *Ophioxenikos* and then *Archegonaster* marking further transformation at least analogous with the generally well-defined series typical of Asteroidea.

Although the ambital outline of somasteroids is broadly subpentagonal, the outline in *Villebrunaster* and *Chinianaster* (Spencer 1951: 93-10; figs 1, 3, 4, 7; Spencer & Wright 1966: figs 5, 30, 39.4) was reconstructed with deep interrarial reentrants extending to the axial immediately distal to the MAO, the configuration yielding petaloid arm outlines. In evaluating the three then-recognized genera of Somasteroidea, no mention was made of marginal ossicles in either *Chinianaster* or *Villebrunaster* (Spencer 1951). Reconstruction of *Chinianaster* (Spencer 1951: fig. 7; reproduced Spencer & Wright 1966: fig. 39.4; Fig. 1A) shows the first virgal series arising at the circumoral, then arching distally along the arm margin, and with reduction of ossicular lengths, transforming into an ambital framework series with each ossicle of the circumoral series abutting the abradial terminus of each more distal virgalium, thereby becoming positional “inferomarginal”. The interpretation was later elaborated (Spencer & Wright 1966): “(T)he outermost row of virgals may become continuous and form a row of inferomarginals” (p. 15), and from the glossary definition of inferomarginals (p. 29) “[...] in origin part of the adaxial skeleton, i.e., a virgal”. In contrast, the marginal series at the body margin of *Archegonaster*, the third genus then recognized by Spencer (1951: pls 3.37, 3.38; 4.39, 4.40), was seen as forming a continuous, sub-pentagonal series across the interbrachial arc, the “marginalia and adambulacralia [...] differentiated as end-members of [...] interambulacral rows” (p. 91), the “interambulacral rows” the virgalia. Phrasing implies the stemward gap condition among somasteroids was abandoned in the derivation of *Archegonaster*, the marginal series closed across the interbrachium.

Fell (1963a: 396, entry 1[6], diagram fig. 11D) concurred with both aspects of Spencer’s reconstruction, recognizing a “deep interrarial cleft” in *Chinianaster* and envisioning the “terminal virgalium (as) forming a hinged, free, acuminate radiole”. In the generic diagnosis of *Chinianaster*, Spencer & Wright (1966: 39) followed Fell in terming virgalia as “metapinnules”, those of *Chinianaster* ending in a “free marginal radiole”. The *Villebrunasteridae* was described and reconstructed with “marginal elements” but no “marginal radioles” (Fell 1963a: 397, fig. 6A, as *Ampullaster* fig. 6B, and *Villebrunaster*).

Proposed presence of an interrarial “gap” or “cleft” delineated by deeply reentrant ambital framework series as to yield petaloid arms in *Chinianaster* and *Villebrunaster* is not accepted, rather broadly arched interbrachia defined by the ambital framework is interpreted as developed in these genera, as in *Archegonaster* (e.g. Spencer 1951: figs 37-40). The ambital framework of the lectotype of stemward *Chinianaster* extends around the interbrachium, the medial disk ossicles displaced with burial (Fig. 2C, D).

The problematic nature of marginal series further emerged in the treatment of Dean Shackleton (2005). Inferomarginals were recognized in all somasteroids (char. 65: 109, 113), and were judged “[...] probably derived from abactinal plating...” (p. 42L), a perspective differing from the virgal derivation of Spencer (1951) and Fell (1963a). Marginal allocation, whether axial or extraxial, was termed “equivocal” in that

in some taxa extraxials separate marginals from the adaxial adambulacral (p. 39L, under “Development”); however, both inferomarginals and superomarginals subsequently were interpreted as axial because both arise behind the terminal (p. 43L, under “Development”).

The “radiole”-bearing specimens of the type suite of *Chinianaster* were assigned to a new genus, *Thoralaster* (Dean Shackleton 2005). In the *Thoralaster* generic diagnosis (p. 68R, 70R), one marginal was recognized for “each” ambulacral (axial) for the “entire arm”, marginals including the “radiole” of Fell (1963a). Radioles were described as tapering ossicles, their diameter greater than those of more adradial ossicles of the virgalium, and skeletal stereom was found to differ. Positioning of radioles is at the abradial tips of virgalia, and where clearly differentiated, “radioles” lie at the abutted termini of two virgalia (Figs 1B; 6A, B, D), although potential examples occur at tips of some simple virgalia (Figs 1B, “spiked marginal”; 6F). Abutted virgalia have not been recognized among other somasteroids.

In treating radioles as a marginal series, the delicate ambital necklace of *Thoralaster* (Fig. 6E, F), comparable to that of *Chinianaster* (Fig. 2B-D), was not recognized (Dean Shackleton 2005); recognition of both the delicate ambital framework and radioles as “marginal” would be redundant. Because of delicacy and preservational limitations, interpretation of arm margins of most arm intervals of delicate *Thoralaster* specimens is problematic: partial burial commonly obscures the terminal ossicle of the virgal series, the ossicle potentially descending beneath the sediment surface as to suggest taper (Fig. 6E, F). The elongate, abradially projecting form of radioles is unlike that typical of marginals, and unlike marginals, radioles do not form a continuous abutted series. Locally at least, radioles and adjacent intervals of virgalia now extend abradially beyond the ambital necklace (Figs 6E, F; 7E, F). Interpretation of the radiole as “hinged” and “free” (Fell 1963a: 396, 2[3]) argued atypical virgal construction.

The preferred interpretation here is to treat “radioles” both descriptively and genetically as a part of virgalia based on their positioning at series termini and elongate, rod-like virgal form. Interpretation of “radioles” as ambital framework/marginal ossicles is not accepted. No unequivocal articulation surfaces have been recognized that might clearly support the “hinged” interpretation of Fell, the deflected, “articulated”, appearances (Figs 1B; 6B, E) potential artifacts of preservation.

Yet evaluation of “radioles” remains problematic. Multiple derivation hypotheses are available. If virgalia continued to be lengthened during ontogeny and acuminate radioles are restricted to termini, then an acuminate radiole at the terminus (Dean Shackleton 2005: 70) would call for a two-step growth sequence, the radiole initially attenuated, then thickening before or with development of a new “radiole” abradial to the precursor. Alternatively, a new virgal might be inserted within a virgalium thereby allowing a true “radiole” formed early in ontogeny to remain at the terminus, an interpretation challenging virgal addition only at the virgalium terminus. No evidence of either sequence has been recognized. Radioles might be accessory spines rather than

virgals, and therefore insertion of a new ossicle would not demand interruption of the continuing virgalium growth sequence; however, treatment as a terminal accessory would call for insertion of new virgals within the growth sequence. Further, as few accessories have been recognized among somasteroids, radioles as true accessories would be striking because of both presence and form.

Because radioles are recognized only at body margins, they are tentatively interpreted as aberrancies accompanying slowing of growth later in life, perhaps associated with body flexure, and therein, teratological.

ACCESSORIES

Accessories are extraxial ossicles seated on the primary ossicles of the skeletal wall. Only smaller platelets and spinelets are known among somasteroids, although generally poor preservation limits knowledge.

INTERPRETING THE SOMASTEROIDEA: ASPECTS OF LIFE MODE

Somasteroid configurations are similar to those of extant asterozoans thereby favoring similar life habits, although apomorphies of the derived clades might favor major changes.

Configuration of virgalia led Spencer (1951) to interpret the virgal field as indicating suspension-feeding habits using water currents with ciliary and tube foot activity to transfer particles toward the mouth; exhaust currents and rejected particles found “[...] outlet at the interradial angles (that were) devoid of skeleton” (p. 97). Posited interradial skeletal discontinuity, a “gap” or “cleft”, resulted in deeply petaloid arms (Spencer 1951; Spencer & Wright 1966). The arched type specimens of *Villebrunaster* (Fig. 9A; 10D) further led Spencer to envision arms upraised in life in accordance with a ciliary feeding mode while also living “partially under the bottom mud”. Seemingly challenging the interpretation of *Villebrunaster*, *Chinianaster* “specimens give little information as to mode of life” (p. 100). Living with food-collecting surfaces against the substrate was viewed with disfavor because the habit would “tend to choke” ciliary channels (Spencer 1951: 97). The “slightly built” somasteroid skeleton was envisioned as capable of considerable changes of form in a manner exemplified by earthworms. Abilities of other living organisms to construct reinforced supporting burrow walls also was noted (p. 93), somasteroid habits apparently seen in parallel. The skeletal flanges (Figs 7A, C; 8A, C, E) on the aboral mouth frame of *Thoralaster* are suggestive of exhaust passageways envisioned by Spencer (1951); the flanges, however, appear to be internal calling for any water exhaust passageways to be developed through the aboral body wall. More simply, the *Thoralaster* flanges might have served for gut confinement and support.

Considerations of somasteroids in titles of Fell (e.g. Fell 1963a) were directed primarily toward that author’s phylogenetic interpretations, suspension-feeding crinoids treated as ancestral to somasteroids. Although retaining interpreta-

tions of ciliary feeding, Fell (1963a) accepted selective detrital feeding in extant *Platasterias* Gray, 1871, based on presence of small inferred prey at the mouth. *Platasterias* was assigned to the Somasteroidea but later recognized as a subgenus of the extant asteroid *Luidia* (Blake 1982).

Interpretations of Spencer (1951) were later modified (Spencer & Wright 1966: 24). Ciliary activity was seen as serving to collect particles that fell “on or near” the somasteroid, and although no mention was made of somasteroid burrowing in Spencer & Wright (1966), reconstruction of an Ordovician ophiuroid with upraised arms was interpreted as having withdrawn into its burrow prior to its death (fig. 4). In contrast, somasteroids were envisioned as “amuscular [...] relatively sedentary, dominantly epifaunal [...] with deposit feeding [...] primary” (Dean Shackleton 2005: 60), challenging ciliary feeding among somasteroids.

The broadly stellate overall form of somasteroids similar to those of many asteroids suggests epifaunal habits with the oral surface directed toward the substrate. Although Spencer (1951) suggested at least semi-infaunal “burrows”, most fossil occurrences appear more or less restricted to single planes (e.g. Fig. 5C). The challenge of Spencer (1951) that virgalia directed toward the substrate would foul ciliary feeding can be answered either by an emphasis on selective detrital feeding or epifaunal lifting of the arms for ciliary feeding, as in bryozoan asteroids and many extant ophiuroids.

The number of specimens of *Cantabrigiaster* that have been offered for sale on the marketplace together with occurrence of as many as six closely adjacent specimens on a single block (Fig. 5C) favor local concentrations rather than only scattered occurrences.

SYSTEMATIC PALEONTOLOGY

RECOGNITION OF ASTEROZOA

Phylum-level expressions treated as plesiomorphic among asterozoans are presence of a water vascular system, approximate pentaradial symmetry, and at least a precursor to a readily preserved stereom skeleton. Expressions either plesiomorphic at the subphylum level or subphylum apomorphies are essentially uniform pentamery of closely fitted mouth frames and proximal axials (i.e., absence of a so-called “buccal slit”), the actual presence of a readily preserved skeleton, ambulacra directed toward the substrate, and free-living epifaunal life modes. “Essentially” is uniformity of ambulacra around the mouth frame but not necessarily biologically important differentia that do not markedly alter overall uniformity, including but perhaps not limited to expression of Lovén’s Law, hydropore differentiation, and anal presence. As noted earlier, marked variability among so-called buccal slits identifies these as aberrancies of preservation.

REMARK

For reading convenience and clarity, diagnoses and the key to somasteroid taxa are comparative rather than compilations of inferred apomorphies.

KEY TO THE SOMASTEROIDEA SPENCER, 1951

1. Axial ossicles “T”-shaped, forming enlarged gaps (podial pores?) between sequential transverse ridges. First virgals enlarged, strongly differentiated. Virgal series not recognized proximally. Ambital framework ossicles proportionately large, abutted, aligned in linear series. Abactinals are tiny granules monogeneric Archegonasteridae
- Axial ossicles square to weakly rectangular, few possible small podial pores recognized in two genera. First virgals at most weakly differentiated. Virgal series recognized proximally. Ambital framework ossicles small, otherwise varied. Abactinals are weakly enlarged spicules or platelets Chinianasteridae Spencer, 1951, 2
2. Overall form more nearly stellate, arms comparatively narrow. Ambital framework ossicles more robust, rod-like, elongate, overlapping but not irregular. Abactinals granular to plate-like, closely abutted, arrangement not reticulate monogeneric, Ophioxenikosinae n. subfam.
- Overall form more nearly polygonal, arms comparatively broad. Ambital framework ossicles less robust, granular to weakly elongate, arrangement more or less irregular. Abactinals rod-like, spicular, arrangement reticulate, not closely abutted 3
3. In oral view, axials “L”-shaped, podial basin proximal of transverse ridge 2 genera, Villebrunasterinae Fell, 1963b, 4
- In oral view, axial interval abradial to radial channel bilateral; podial basins approximately shared by successive podial basins 3 genera, Chinianasterinae Spencer, 1951, 5
4. Abradial adaxials variously differentiated, arrangement varied *Villebrunaster* Spencer, 1951
- Abradial adaxials uniform, arrangement uniform *Ampullaster* Fell, 1963b
5. Axials in aboral aspect shield-like and clearly overlapping distally, compound axials unknown. Abactinals comparatively less delicate. Madreporite where recognized on oral surface near but not abutting mouth frame. Ambital framework of many tiny platelets forming a complex apparently somewhat ill-defined series. Virgals moderately robust, rectangular; medial ridge lacking. Adjacent virgalia potentially forming a robust platform when deflected distally. “Radioles” not developed *Chinianaster* Thoräl, 1935
- Axials in aboral aspect approximately square in outline and weakly overlapping distally, compound axial known only at mouth frame. Abactinals comparatively more delicate. Madreporite where recognized on aboral surface away from central disk. Ambital framework ossicles numerous, small but not tiny, forming a complex well-defined series. Virgals stout, rectangular, with a medial ridge. Adjacent virgalia forming a platform with well-defined grooving shared by adjacent virgalia. “Radioles” not developed *Cantabrigiaster* Hunter & Ortega-Hernández, 2021
- Axials in aboral aspect approximately square in outline, at most weakly overlapping distally, compound axials can be developed at least near mouth frame. Abactinals comparatively more delicate. Madreporite not recognized. Ambital framework ossicles of many tiny platelets forming a complex apparently somewhat ill-defined series. Virgals very delicate, grooved, rodlike. Adjacent virgalia too slender to form a platform. An enlarged attenuated “radiole” can occur at the abradial termini of abutted virgalia *Thoraster* Dean Shackleton, 2005

Class SOMASTEROIDEA Spencer, 1951

DIAGNOSIS. — Overall form low arched; outline ranging from subpentagonal with arms broad, more abruptly tapering, to outline substellate, arms triangular, elongate, more gradually tapering. Abactinals small, individually irregular but aboral surface in total uniform. Abactinals divisible into three types: abactinals delicate, multiradiate, arrangement reticulate; abactinals closely fitted small platelets; enlarged primary abactinals absent, ossicles limited to granules. Abactinals not aligned in rows, carinal, centrale, and aboral ring differentiation unknown. Madreporite recognized in three genera. Ambital frameworks varied, ranging from complexly arranged tiny platelets to single well-defined abutted series. Axial positioning across arm midline irregular, locally clearly offset to nearly opposite. Axials not permanently vaulted to form a furrow, but arm and disk capable of facultative flexure as to yield temporary furrow-like configurations. Axials nearly equidimensional, form differing among genera. Axial radial water vascular channel large, closed or nearly closed over water-vascular tissues in most genera. Transverse water-vascular channel ill-defined. Transverse ridge generally narrow, podial basins large, deep in most genera.

Mouth frame ossicles relatively small, differentiation from more distal axials comparatively limited. Mouth-angle ossicles upright; small spinelets can occur; podial basin of adjacent axial aligned with those of more distal axials. Axillary (odontophore) not recognized. Terminal ossicle problematic, not definitively recognized. Linear, transverse series of proportionately small rod-like ossicles (“virgals”, the single series a “virgalium”, plural “virgalia”) radiate abradially from each axial, the first of the series more (e.g. *Archegonaster*) or less (e.g. *Chinianaster*) clearly differentiated from the remainder of the series. Virgalia occupy the interspace between ambital framework and axials thereby occupying the oral disk plane: actinal ossicles not recognized. Virgalium in life capable of some rotation about the longitudinal axis, virgalia capable of coordinated series deflection in the body plane. Virgalia thought to be lacking proximally from one genus. Accessories limited to relatively small spinelets and granules.

Family CHINIANASTERIDAE Spencer, 1951

Chinianasteridae Spencer, 1951: 93.

Chinianasteridae restricted to *Chinianaster* Fell, 1963b: 144; Spencer & Wright 1966: 39.

Chinianasteridae included *Villebrunaster*, *Chinianaster*, *Thoralaster*, *Ophioxenikos*: Dean Shackleton 2005: 30.

TYPE GENUS. — *Chinianaster* Thoral, 1935.

TYPE SPECIES. — *Chinianaster levyi* Thoral, 1935.

DIAGNOSIS. — Abactinal skeleton well-developed, consisting of many small, irregular but uniform ossicles. Ambital framework varied among genera, ossicles proportionately small, series well defined but ossicular arrangement irregular, varying among genera. Axials approximately equidimensional to rectangular; localized podial pores possibly occurring in two genera. Water-vascular channel skeletally closed orally. Virgalia reaching mouth frame. First virgal at most weakly differentiated.

Subfamily CHINIANASTERINAE Spencer, 1951

Chinianasteridae Spencer, 1951, here recognized at the subfamily level for *Chinianaster*, *Cantabrigiaster*, and *Thoralaster*.

TYPE GENUS. — *Chinianaster* Thoral, 1935.

TYPE SPECIES. — *Chinianaster levyi* Thoral, 1935.

DIAGNOSIS. — Subpentagonal Chinianasteridae. Abactinals spiculate, arrangement reticulate. Ambital framework ossicles tiny, granular or plate-like; overall arrangement thought irregular. Radial water vascular canal large, skeletally delicate, closed orally, where closure was diagenetically lost abradial portion of ossicle doubly bilateral at midpoint of transverse ridge. Podial basin boundary approximately medial, basin shared equally by successive axials. Adradial adaxials weakly differentiated, virgalia relatively elongate.

Genus *Chinianaster* Thoral, 1935

Chinianaster Thoral, 1935: 127.

DIAGNOSIS. — As for *Chinianaster levyi*, the type and only recognized species.

Chinianaster levyi Thoral, 1935 (Figs 1A; 2; 3)

Chinianaster levyi Thoral, 1935: 127, pl. 9, fig. 1a, 1b; *non* pl. 8, fig. 1; *non* pl. 10, fig. 4. — Spencer 1951: 98, pl. 3, figs 35, 36, text figs 7, 8, *non* pl. 2, figs 32, 33. — Ubaghs 1953: 814, text fig. 17. — Fell 1963a: *pars* 393–403, fig. 8B, *non* 6E. — Spencer & Wright 1966: U39, figs 8.2, 13, 19.1, 39.4. — Blake 1982: fig. 1E, *non* fig. 1C. — Dean Shackleton 2005: 68, pl. 3, figs 3, 4, text figs 5, 12B. — Blake 2013: 363, figs 1.1, 1.2. — Blake & Guensburg 2015: 467, figs 1.1–1.6, 2.1–2.7, 3.1–3.4. — Blake 2018: 2, 21; pl. 1.1, 1.2, fig. 2.1. — Blake 2024: 2 *et seq.*, pl. 2.1–2.3.

TYPE MATERIAL. — **Lectotype.** France • 1 specimen (specimen distorted, arm radii approximately 25 to 30 mm); Hérault, Saint-Chinian; Saint-Chinian Formation; *Euloma filacovi* Zone, late Tremadocian (Early Ordovician); Villebrun leg.; UCBL-FSL 168691 (Figs 2A1–4; 3A).

REFERRED SPECIMENS. — Eight specimens (UCBL-FSL 711093 [FSL 1879 553 of Dean Shackleton 2005], UCBL-FSL 711094 [FSL 1879 558 of Dean Shackleton 2005], UCBL-FSL 711095

[FSL 1879 563 of Dean Shackleton 2005], UCBL-FSL 712002–712004, UCBL-FSL 712090, UCBL-FSL 713577. Questionable, four more specimens (MBB-GG20, MBB-GG23, UCBL-FSL 712017, UCBL-FSL 713576). Assignment of two more specimens is problematic (MBB-GG2, MBB-GG18).

TYPE LOCALITY AND HORIZON. — Saint-Chinian Formation, Early Ordovician (late Tremadocian); Saint-Chinian (Hérault), Montagne Noire, France.

DIAGNOSIS. — Abactinals moderately robust, arrangement quite closely reticular (Fig. 2A). Ambital framework ossicles tiny, plate-like; arrangement complex, series as preserved ill-defined, irregular (Fig. 2B–D). Axials in aboral view shield-like, successive axials overlapping (Fig. 2A). In oral view, compound axials not recognized. MAO not bearing an enlarged flange-like aboral process. Where not eroded, radial-water vascular channel enclosed at arm axis by an enclosing skeletal arch (Figs 2C, E; 3B, E). Adaxials moderately large, thin, broad surface longitudinally grooved, groove broad (Figs 2E; 3C).

DESCRIPTION

Overall form in life low-arched, outline subpentagonal; arms broad, triangular, taper gradual. Abactinals spiculate, multiradial, rod-like abactinals likely developed; abactinal arrangement open hexagonal reticular. Madreporite on oral surface offset from MAO, surface texture granular (Figs 2C; 3A, B). Ambital framework a continuous well-defined but irregular necklace of tiny platelets; ambital framework not deflected toward mouth frame to form a gap or cleft (Fig. 2B–D). In aboral aspect, axials shield-like, surface curved, sequential axials overlapping, axial series longitudinally grooved approximately at position of abradial margin of podial basins; proximal axials with possible podial pore (Fig. 2A, F). In oral aspect, where preserved (generally distally), radial water-vascular channel oral surface closed by shield-like skeletal arch (Figs 2C, E; 3B); where shield eroded (generally proximally) and axial series dilated, axials appearing approximately double-bilateral along and normal to transverse ridge; podial basin boundary medial; abradial margin concave. MAO proportionately small, appearing plate-like where directed toward mouth, rounded where deflected toward interior; lateral margins concave for tube foot; differentiation of circumoral appearing limited (Fig. 3E). Virgalia abutting abradial terminus of axial transverse ridge, virgalia reaching mouth frame (Figs 2B; 3B, C, E). Virgals relatively thin, rectangular, planar, grooved, termini expanded; virgals when rotated to exposed broad surface potentially robust enough as to have formed a continuous platform at least where deflected distally. First virgals less elongate than more lateral virgals, otherwise similar. Virgal accessories, if any, small, granular.

REMARKS

The concept of *Thoralaster* Dean Shackleton 2005, was based on a part of the *Chinianaster* type suite, see under that genus.

Shield-like overlapping axials and flat, rectangular adaxials provide guides to the recognition of *Chinianaster*. Although uncommonly clearly preserved, an ambital framework of fine platelets is shared only with *Thoralaster*. Dean Shackleton (2005: 68R), however, posited presence of robust marginals in *Chinianaster*, some a “large spike”. The interpretation

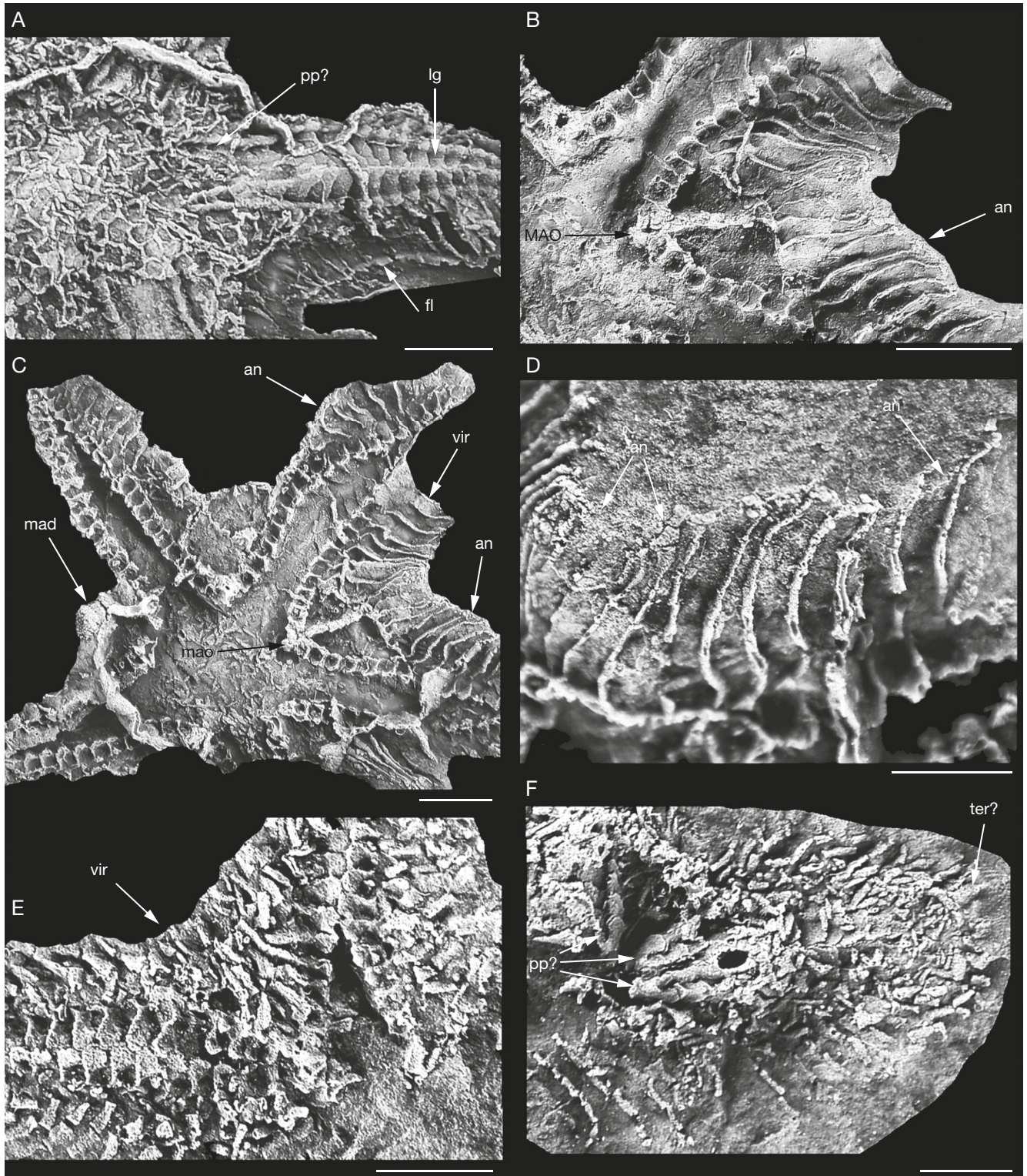


FIG. 2. — *Chinianaster levyi* Thor, 1935 Saint-Chinian Formation, Early Ordovician (late Tremadocian); Montagne Noire, France; latex casts: **A–D**, lectotype UCBL-FSL 168691 (Villebrun collection), Saint-Chinian (Hérault): **A**, aboral view; abactinal configuration to left is hexagonal reticulate; some axials “C”-shaped with possible podial pores that are aligned with longitudinal grooving of axial series; flange-like series of unknown origin but suggestive of deflected adaxials, the “intervirgal struts” (Dean Shackleton 2005) postulated for *Villebrunaster* Spencer, 1951; **B**, area to right of **C**, ambital necklace (**an**) of fine ossicles, homologous with robust marginals of many more derived asterozoans; **C**, oral view, the proximal intervals of the ambulacra and mouth angle ossicles (**MAO**) were widely distended by sediment compaction, the virgalia to right pulled away from the axials; axials where not deflected are approximately bilateral at transverse ridge; madreporite; **D**, area to right of **B**, virgalia rotated to expose edges, details of the ambital necklace; **E**, oral view, axials remain closed by oral shields more distally but in ambulacrum to right, proximal axial series distended and eroded; virgalia disrupted but reaching oral frame; **F**, aboral view, photograph of distal arm, see reconstruction of Dean Shackleton (2005: fig. 5B); inflections suggesting gaps or possible podial pores; small ossicles fringing the arm suggest adaxials and remnant ambital framework platelets; large spinelet, a possible terminal (**ter?**). Abbreviations: **fl**, flange-like series; **lg**, longitudinal grooving; **mad**, madreporite; **pp?**, possible podial pores; **vir**, virgalia. Scale bars: A–C, 5 mm; D–F, 3 mm.

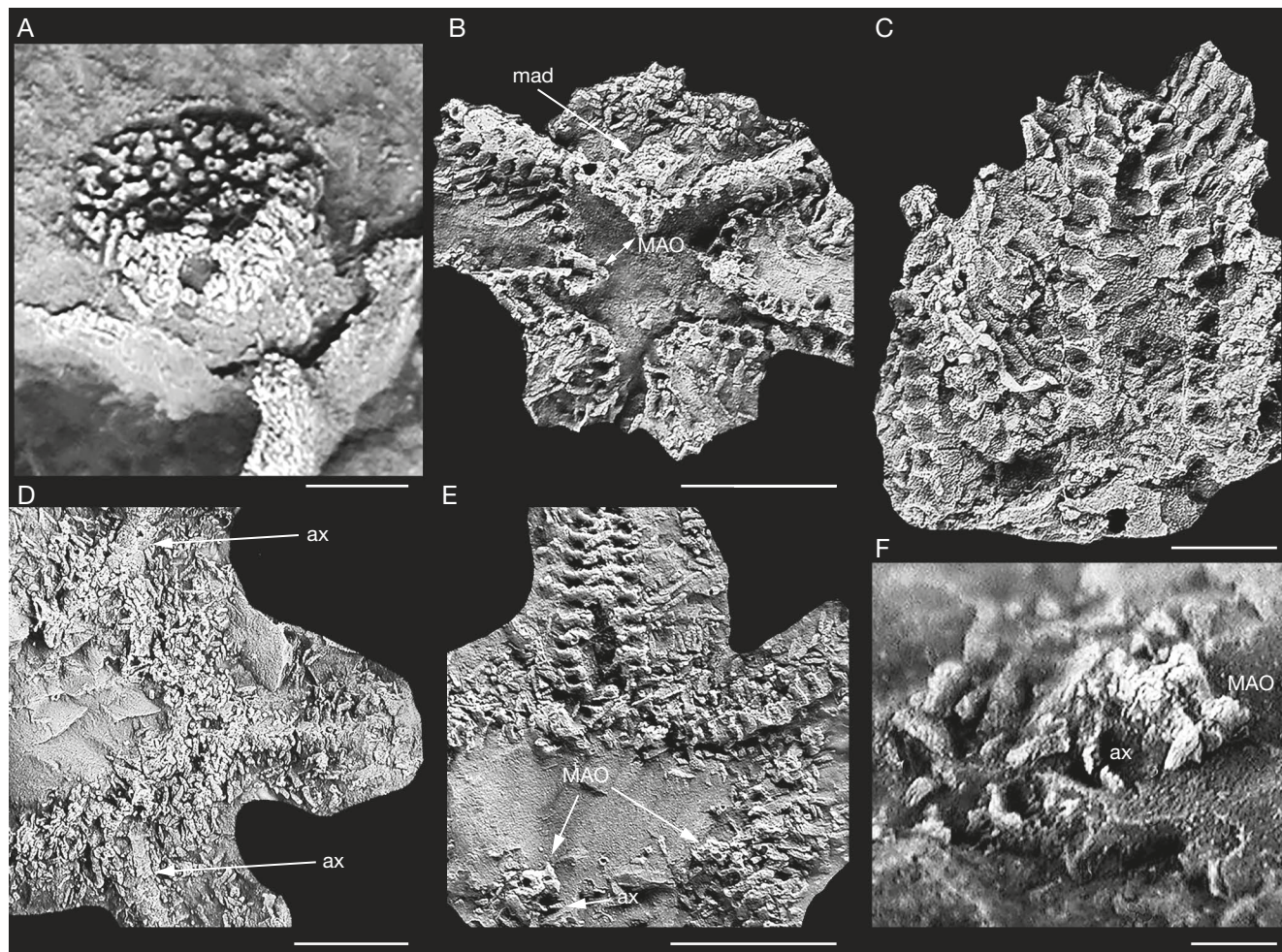


FIG. 3. — *Chinianaster levyi* Thoral, 1935 Thoral, Saint-Chinian Formation, Early Ordovician (late Tremadocian); Montagne Noire, France; latex casts: **A**, lectotype UCBL-FSL 168691 (Villebrun collection), Saint-Chinian (Hérault); madreporite, the granular surface and ridged margin unlike madreporites of most asterozoans; **B**, UCBL-FSL 712002 (Vizcaíno collection), Félines-Minervois (Hérault); oral view, mouth angle ossicles pair, proximal axials distended, more distal approximate life positioning; madreporite with disrupted near-oral virgalia and abactinals; **C**, UCBL-FSL 713577 (Vizcaíno collection), Félines-Minervois (Hérault); oral view, specimen in bud-like posture; axials distended; podial basins equally shared by successive axials; unlike those of Figure 2, virgalia largely show broad surfaces, those to right largely in place, those to left disrupted but reaching mouth frame area; **D-F**, UCBL-FSL 712004 (Vizcaíno collection), Félines-Minervois (Hérault); **D**, aboral view, axial surfaces arched; spike-like ossicles of uncertain origin at arm tip; **E**, **F**, oral views, **F**, mouth frame ossicles to left of **E**, mouth angle ossicles retain well-defined curvature for podium; for orientation analogy, see Figure 4; axial remnant. Abbreviations: **ax**, axial; **mad**, madreporite; **MAO**, mouth angle ossicles. Scale bars: A, F, 1 mm; B, D, E, 5 mm; C, 3 mm.

appears to have been based on her figure 5B (p. 40), the apparent interval illustrated here (Fig. 2F) in which ossicles are displaced and enlarged “spikes” are found at the arm tip. Spike identity is uncertain but more proximal ossicles argue terminal ossicles of virgalia, the ambital necklace all but lost from this specimen (Fig. 2F). A single ossicle at the arm tip of a *Chinianaster* or near-*Chinianaster* specimen (Fig. 14H) suggests a spike-like terminal. Dean Shackleton (2005) interpreted virgalia as lacking at the mouth frame of *Chinianaster*; although largely disrupted, remnants of virgalia are common, including in the lectotype (Fig. 2C, D).

Genus *Cantabrigiaster*
Hunter & Ortega-Hernández, 2021

Cantabrigiaster Hunter & Ortega-Hernández, 2021: 2.

Villebrunaster Blake & Hotchkiss, 2022: 30.

TYPE SPECIES. — *Cantabrigiaster fezouataensis* Hunter & Ortega-Hernández, 2021.

DIAGNOSIS. — As for *Cantabrigiaster fezouataensis*, the type and only recognized species.

Cantabrigiaster fezouataensis
Hunter & Ortega-Hernández, 2021
(Figs 4; 5)

Cantabrigiaster fezouataensis Hunter & Ortega-Hernández, 2021: 2, fig. 1; electronic supplemental material.

Villebrunaster fezouataensis — Blake & Hotchkiss 2022: 29, figs 2-5.

TYPE MATERIAL. — **Holotype**. Morocco • 1 specimen (only oral surface, good preservation of ossicular detail; arm radius R 27 mm; disk radius r 18 mm; both measurements and especially that of the latter extended by sediment compaction); Central Anti-Atlas,

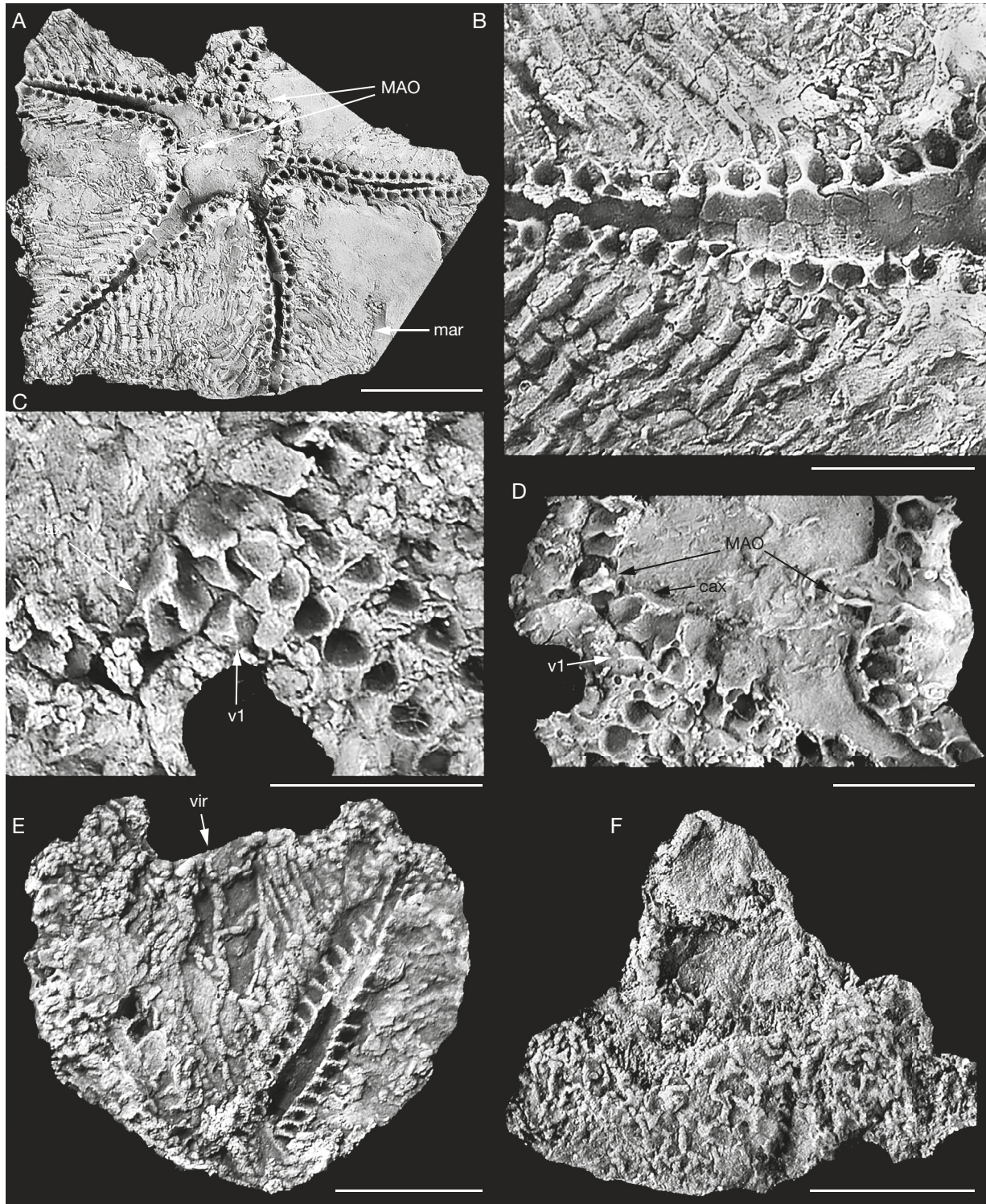


FIG. 4. — *Cantabrigiaster fezouataensis* Hunter & Ortega-Hernández, 2021 Fezouata Formation, Early Ordovician (late Tremadocian); Central Anti-Atlas, Morocco; latex casts: **A–D**, holotype UCBL-FSL 424961 (Van Roy collection), Ternata plain, N of Zagora: **A**, oral view of specimen remainder; adaxials approximately in life configuration near arm tips, largely lost diagenetically in interbrachia; mouth angle ossicles, arrows correspond with **D**; marginals; **B**, arm to lower left of **A**, axials with adaxial virgals abutted to form a platform, axial positioning across midline irregular, both paired and offset; **C**, **A** rotated clockwise, a single adaxial first virgal abuts the two proximal axials; compound axial; podial basins of proximal axials to right appear inclined toward mouth angle ossicles although this might reflect preservation rather than life configuration; **B**, **C** and **D** are separate latex casts differing in expression of details of mouth angle ossicles; first virgal and compound axial of **C** and **D** correspond; mouth angle ossicles pair fortuitously differ in orientation, pair to right in inferred at life rest position, with faint accessory bases; pair to left with mouth angle ossicles rotated in inferred feeding position as to direct particulates into disk; **E**, paratype UCBL-FSL 711938 (Lefebvre collection), Jbel Tizagzaouine, c. 21 km N of Zagora; specimen in bud-like posture, mouth frame obscure, two dilated ambulacra, tips obscured by marginals; virgalia forming a platform distally; a single virgalium (**vir**) extends from mouth frame thereby demonstrating absence of an interrarial “gap” or “cleft”; **F**, paratype UCBL-FSL 711939 (Lefebvre collection); Jbel Tizagzaouine, c. 21 km N of Zagora; aboral view, abactinal form and arrangement, aboral surface of arm largely lost, part of ambital framework remains. Abbreviations: **cax**, compound axial; **mar**, marginals; **MAO**, mouth angle ossicles; **v1**, first virgal. Scale bars: **A**, 10 mm; **B–F**, 5 mm.

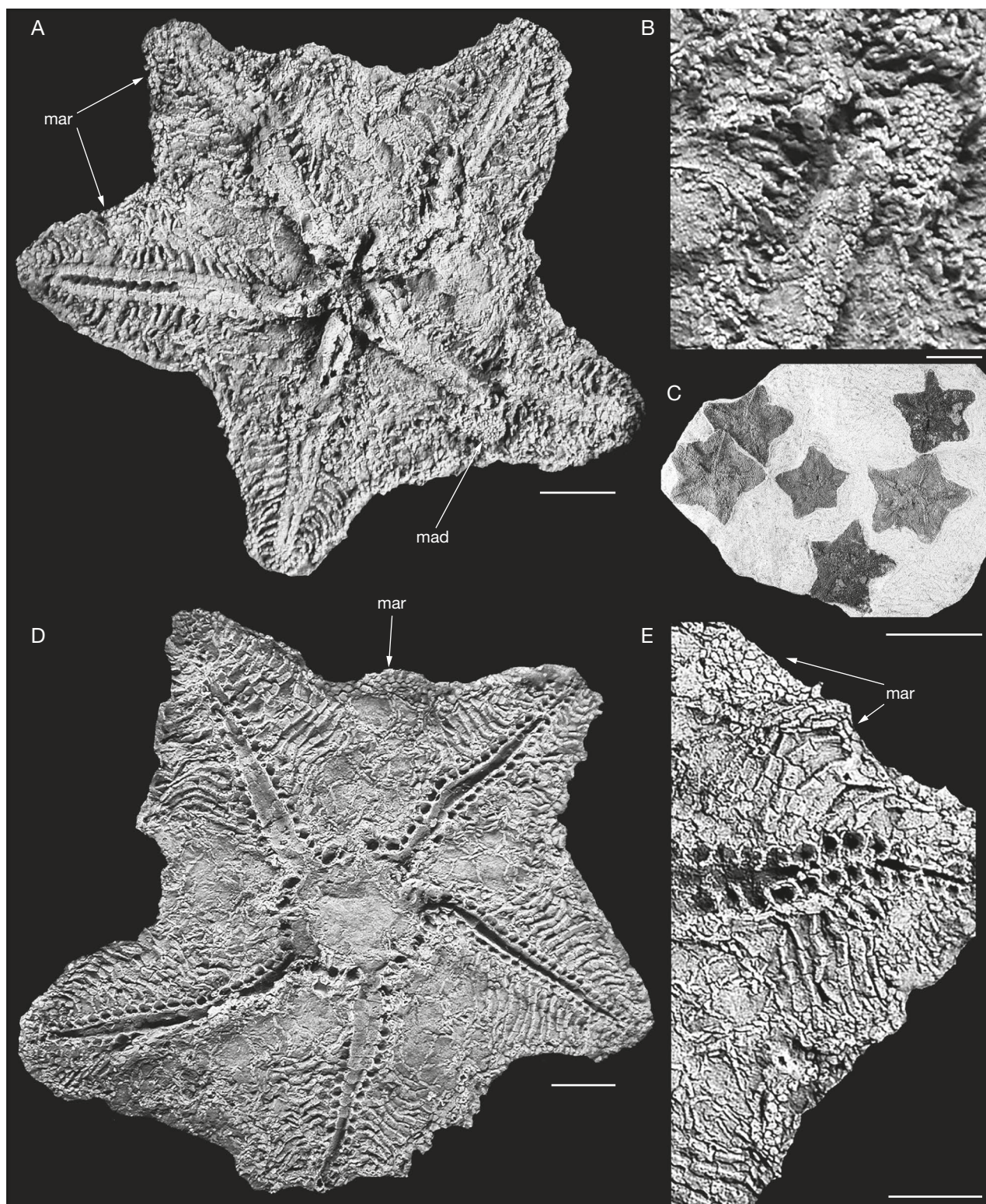


FIG. 5. — *Cantabrigiaster fezouataensis* Hunter & Ortega-Hernández, 2021 Fezouata Formation, Early Ordovician (late Tremadocian); Jbel Kissane, c. 5 km E of Agdz, Central Anti-Atlas, Morocco; **C** is the original specimen, the remainder are latex casts: **A**, **B**, PRIP 20029-1 (Blake collection), aboral view; **A**, overall aboral view; distal left axials slightly pulled apart; radiating virgalia dominate distally on arms; some abactinals remain at interbrachia; madreporite and some marginals remain; **B**, madreporite granular surface (upper right) suggestive of that of *Chinianaster* Thoral, 1935, see Figure 3; offset of axial series suggests madreporite displacement from life position; **C**, PRIP 20028-1 – 20028-6 (Blake collection), six individuals on a single slab, medial and lower right specimens in aboral view, remainder in oral view. The slab is 10 mm to 15 mm in thickness and shows no clear indication of depositional discontinuity. The surface of the block was reworked in preparation but appears homogeneous. The specimen to far left is separated from the adjacent by a 1-2 mm sediment band, that to upper right by about 5 mm; **D**, PRIP 20029-2 (Blake collection), oral view; disk, proximal arms distended to show axial aboral surfaces; marginals remain locally; abactinals exposed in interbrachia; radiating virgalia form a platform distally; **E**, PRIP 20030-1 (Blake collection), oral view, axial form, series closing distally, adaxials toward tip disrupted, many marginals remain, abactinals at interbrachium. Abbreviations: **mad**, madreporite; **mar**, marginals. Scale bars: A, D, E, 5 mm; B, 2 mm; C, 50 mm.

Ternata plain (north of Zagora); *Sagenograptus murrayi* Zone, late Tremadocian (Early Ordovician); 2003, Van Roy leg.; UCBL-FSL 424961 (Fig. 4A-D).

REFERRED SPECIMENS. — 34 specimens (MHNN.P045596, PRIP 20026-20027, PRIP 20028.1-6; PRIP 20029.1-2, PRIP 20030.1-2, UCBL-FSL 424962, UCBL-FSL 711937-711939, UCBL-FSL 711945-711946, YPM IP 535545-535559).

TYPE LOCALITY AND HORIZON. — Fezouata Formation, Early Ordovician (late Tremadocian); Ternata plain, Zagora area, Anti-Atlas, Morocco.

DIAGNOSIS. — Abactinal arrangement open reticular (Figs 4F; 5A, C, D). Ambital framework ossicles small, granular, complexly overlapping but closely abutted as to form a clearly defined series (Figs 4E; 5A, D, E). Axials in aboral view rectangular, successive axials abutted, not notably overlapping (Fig. 5A). In oral view, compound axials can occur at mouth frame (Fig. 4C). Radial water-vascular channel narrowly enclosed at arm axis (Figs 4A, C; 5A). Adaxials strongly robust, rectangular, longitudinal ridges well-defined, adjacent abutted virgalia forming a transverse well-defined groove, abutted virgalia forming a distinct platform (Figs 4A, B; 5D, E).

DESCRIPTION

Overall form in life low-arched, outline subpentagonal; arms broad, short, triangular. Abactinals rod-like; multiradiate abactinals not identified. Only identified madreporite (Fig. 5A, B) aboral, surface texture granular, madreporite offset from central area of disk. Ambital framework well-defined, marginal series forming a continuous pentagonal outline extending around the arm tip, series not deflected toward mouth frame to form gap or cleft. Ambital framework ossicles small, numerous, equidimensional, granular to weakly elongate; ossicles overlapping, not differentiated as to suggest inferomarginals and superomarginals.

In aboral aspect, axials nearly paired or slightly offset across arm midline, axial outline nearly square, sequential axials abutted; axial series (only where better preserved?) appearing longitudinally grooved. In oral aspect, axial outline approximately rectangular, water vascular channel large, enclosed. Axial transverse ridge narrow, axial approximately doubly bilateral at midpoint of transverse ridge, podial basin large, equally shared by subsequent axials, transverse ridge flared abradially to form concave seat for virgallium. Compound axial can occur at mouth frame. Terminal not recognized. First virgals smaller than but similar to more abradial; all virgals robust, rectangular, bearing a medial ridge and lateral groove shared by adjacent virgalia, ossicular boundaries approximately medial in groove. As typically preserved, adjacent virgalia deflected distally as to form a pavement. Accessories not clearly identified, some circular pustules and circular depressions might favor accessories.

REMARKS

A posited absence of an ambital framework was foundational to the recognition of *Cantabrigiaster fezouataensis*, and putative absence essential to *Cantabrigiaster* assignment to a

basal position within Somasteroidea. Presence of an ambital framework similar to that of *Villebrunaster* was documented in the holotype and other specimens of the type suite, and with emphasis on the framework, *Cantabrigiaster* was synonymized with *Villebrunaster* (Blake & Hotchkiss 2022). Herein, axial and adaxial expressions are argued as providing essential guides to asterozoan affinities (e.g. Blake 2013, 2018, 2024; Blake & Guensburg 2015; Glass *et al.* 2024), the differences between *Cantabrigiaster* and other somasteroids calling for generic recognition.

Most distinctive, the robust adaxials of *Cantabrigiaster* differ from those of other somasteroid genera in both form and arrangement, with adjacent virgalia abutted laterally to form a robust platform. The ambital framework of *Cantabrigiaster* differs from those of *Chinianaster*, *Villebrunaster*, and *Ampulaster* in ossicular shape but not in overall series configuration. Surface texture of the madreporite (Fig. 5A, B) is similar to that of *Chinianaster* (Fig. 3A, B) although the two differ in madreporite positioning. Axial series offset and disruption of more proximal abactinals of the only *Cantabrigiaster* example exhibiting a madreporite indicate some displacement accompanied preservation, the present positioning therefore of unknown general significance.

Genus *Thoralaster* Dean Shackleton, 2005

Thoralaster Dean Shackleton 2005: 68.

TYPE SPECIES. — *Thoralaster spiculiformis* Dean Shackleton, 2005.

DIAGNOSIS. — As for *Thoralaster spiculiformis*, the type and only recognized species.

Thoralaster spiculiformis Dean Shackleton, 2005 (Figs 1B; 6-8)

Chinianaster levyi Thoral, 1935, pl. 8, fig. 1. — Spencer 1951: pl. 2.32, 2.33. — Fell 1963a: fig. 6E. — Blake 1982: fig. 4C.

Thoralaster spiculiformis Dean Shackleton, 2005: 68, pl. 4.1-4.6, fig. 7. — Blake 2013: fig. 1.6. — Blake & Guensburg 2015: 472, figs 5.1-5.5, 6.1-6.8.

TYPE MATERIAL. — **Holotype.** France • 1 specimen (part and counterpart); Hérault, Saint-Chinian, La Croix-Rouge; *Euloma filacovi* Zone, late Tremadocian (Early Ordovician); 1953, Thoral leg.; UCBL-FSL 168697 (“ES1” of Dean Shackleton 2005); (Fig. 6A1-6).

Paratype. France • 1 specimen; Hérault, Saint-Chinian; *Euloma filacovi* Zone, late Tremadocian (Early Ordovician); 1879, Lignières leg.; UCBL-FSL 711096 (“FSL 1879 564” of Dean Shackleton 2005) (Fig. 7B).

REFERRED SPECIMENS. — Five specimens (UCBL-FSL 168690, UCBL-FSL 424943, UCBL-FSL 712005, [MNHN.F.A90271](#), [MNHN.F.A97739](#)).

TYPE LOCALITY AND HORIZON. — Saint-Chinian Formation, Early Ordovician (late Tremadocian); La Croix-Rouge, E of Saint-Chinian (Hérault), Montagne Noire, France.

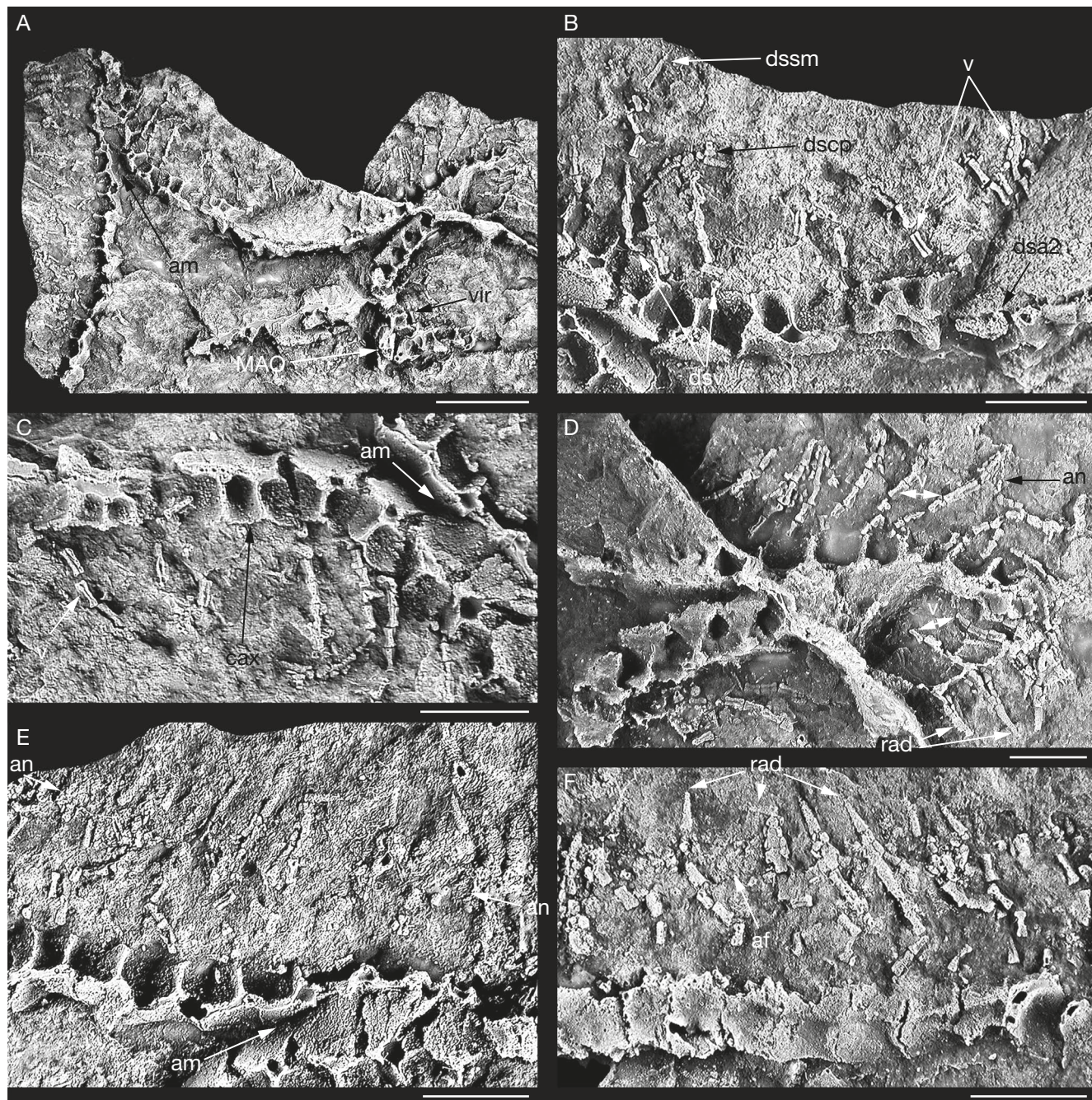


Fig. 6. — *Thoraster spiculiformis* Dean Shackleton, 2005 Saint-Chinian Formation, Early Ordovician (late Tremadocian); Saint-Chinian (Hérault), Montagne Noire, France; latex casts, holotype UCBL-FSL 168697 (Thoral collection): **A-E**, oral views: **A**, most of remnant; mouth frame distended, closure in life likely yielded a sub-stellate overall shape; arm midline corresponds with **C**, **E**; remnants of virgulum at mouth frame, mouth angle ossicles appearing blunt, rounded; **B**, upper left area of **A**, corresponds with Dean Shackleton (2005: fig. 7, here Figure 1B and rotated counter-clockwise); **C**, arm midline, dilated aboral surface of water vascular channel, corresponds with **A** and **E**; delicate, grooved virgals; compound axials; **D**, area to upper right of **A**; virgals delicate as is typical of *Thoraster* Dean Shackleton, 2005; ambital necklace remnants; virgals bear longitudinal grooves; virgals extend to enlarged attenuated terminal radioles; ambital framework locally largely lost; **E**, arm midline corresponds with **A** and **C**; possible tube foot remnants to upper right; disrupted ambital framework (facing ambital necklace) extending transversely between virgals and appearing adradial to terminal virgals; **F**, aboral view; axial series below, virgals ambital framework disrupted; abutted virgals with terminal attenuated? virgal, which is the “radiole” in terminology of Fell (1963a) radioles; positioning of medial radiole might suggest articulation *sensu* H.B. Fell; virgal accessories remain with medial virgulum. Abbreviations: **am**, arm midline; **an**, ambital necklace; **cax**, compound axials; **DS**, refer to identifications of Dean Shackleton (2005) of Figure 1B; **dssm**, DS “spiked marginals”, here “radiole”; **dscp**, DS “intervirgal cover plates”; **dsv**, DS “v1, ?ad”; some axials to lower left are compound; **dsa2**, DS ?amb2; **MAO**, mouth angle ossicles; **rad**, radioles; **v**, virgals; **vir**, virgulum. Scale bars: A, 10 mm; B-F, 5 mm.

DIAGNOSIS. — Abactinals delicate, arrangement open reticular (Fig. 7A-C). Ambital framework ossicles tiny, plate-like, arrangement complex, series as preserved ill-defined, irregular (Figs 6D-F; 7A, C, E, F). Radial-water vascular channel narrowly enclosed at

arm axis (Fig. 8D, distal). In oral view, compound axials recognized near mouth frame (Figs 1B; 6A-C; 8D). MAO bearing an enlarged flange-like aboral process (Figs 7A, C; 8A, C, E). Adaxials very delicate, rodlike, longitudinal groove narrow (Figs 1B; 6B, F; 7A, C; 8B).

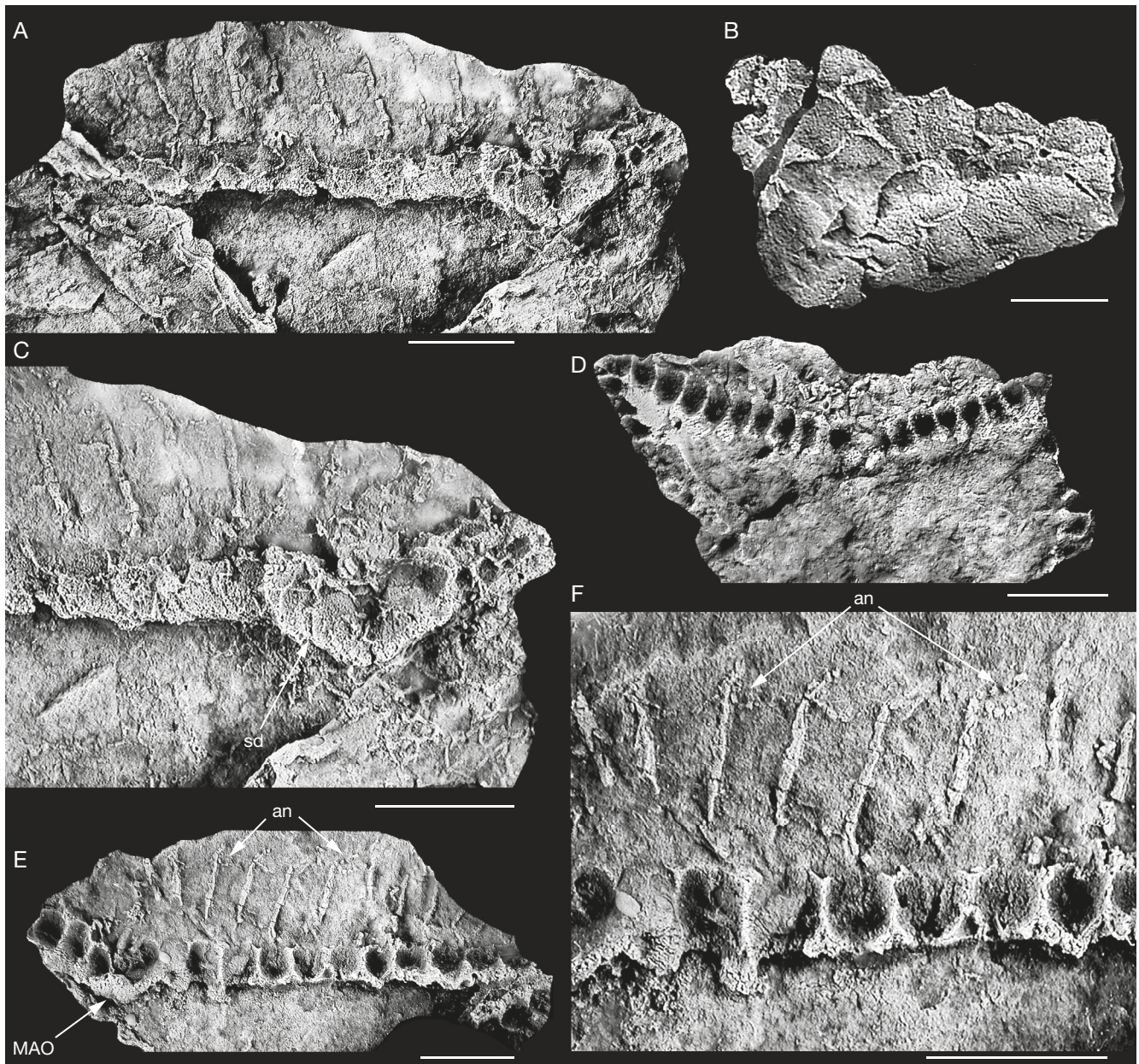


FIG. 7. — *Thoraster spiculiformis* Dean Shackleton, 2005, Saint-Chinian Formation, Early Ordovician (late Tremadocian); Montagne Noire, France; latex casts: **A–C, E, F**, UCBL-FSL 712005 (Vizcaino collection), Caunes-Minervois (Aude): **A–C**, aboral views: **A**, most of specimen fragment, axials converging toward arm tip to left, virgalia above, jaw frame to right with reticulated abactinal remnants; **B**, distal arm interval, very delicate abactinals retain reticulate life arrangement; **C**, right side of **A**, flared mouth frame suggestive of an open bivalve, skeletal discontinuity might indicate presence of both the mouth angle ossicle and a circumoral; **D**, paratype UCBL-FSL 711096 (Lignières collection), Saint-Chinian (Hérault); oral view, disk dilated; mouth angle ossicles pair at middle rounded bluntly toward mouth area; proximal-most axials little differentiated; virgalia remnants adjacent to mouth frame document absence of interrarial “gap” or “cleft”; **E, F**, oral views, aboral surfaces of water-vascular channels lost, axials bilateral at transverse ridge, podial basins large; virgalia appearing locally to extend beyond ambital necklace; mouth angle ossicles and first podial basin aligned with subsequent basin, proximal axials not appearing differentiated. Abbreviations: **an**, ambital necklace; **MAO**, mouth angle ossicles; **sd**, skeletal discontinuity. Scale bars: A, C, E, F, 5 mm; B, D, 3 mm.

DESCRIPTION

Overall form low-arched, outline substellate, arm outline in life thought to be triangular, moderately abruptly tapering. Abactinals delicate, spiculate, configuration open hexagonal reticular. Madreporite unknown. Ambital framework forming a continuous, well-defined, irregular necklace of tiny platelets, series not deflected toward mouth frame to form a gap or cleft.

In aboral aspect, axial ossicles shield-like, sequential ossicles weakly overlapping (Figs 6F; 7A–C; 8A, C, E), axial series

longitudinally weakly grooved (Fig. 8A). In oral aspect, radial water vascular channel closed (near arm tips, Figs 6A; 7A; 8D, F). Some axials compound, i.e., bearing more than a portion of a podial basin on each side of the transverse ridge (Figs 1B; 6A, C; 8D); non-compound axials appearing approximately double-bilateral along and normal to the transverse ridge; podial basin boundary medial, abradial axial margin concave. Mouth-angle ossicle transverse ridges converge abradially in an “A”-frame-like pattern (Fig. 8D). Ossicle immediately

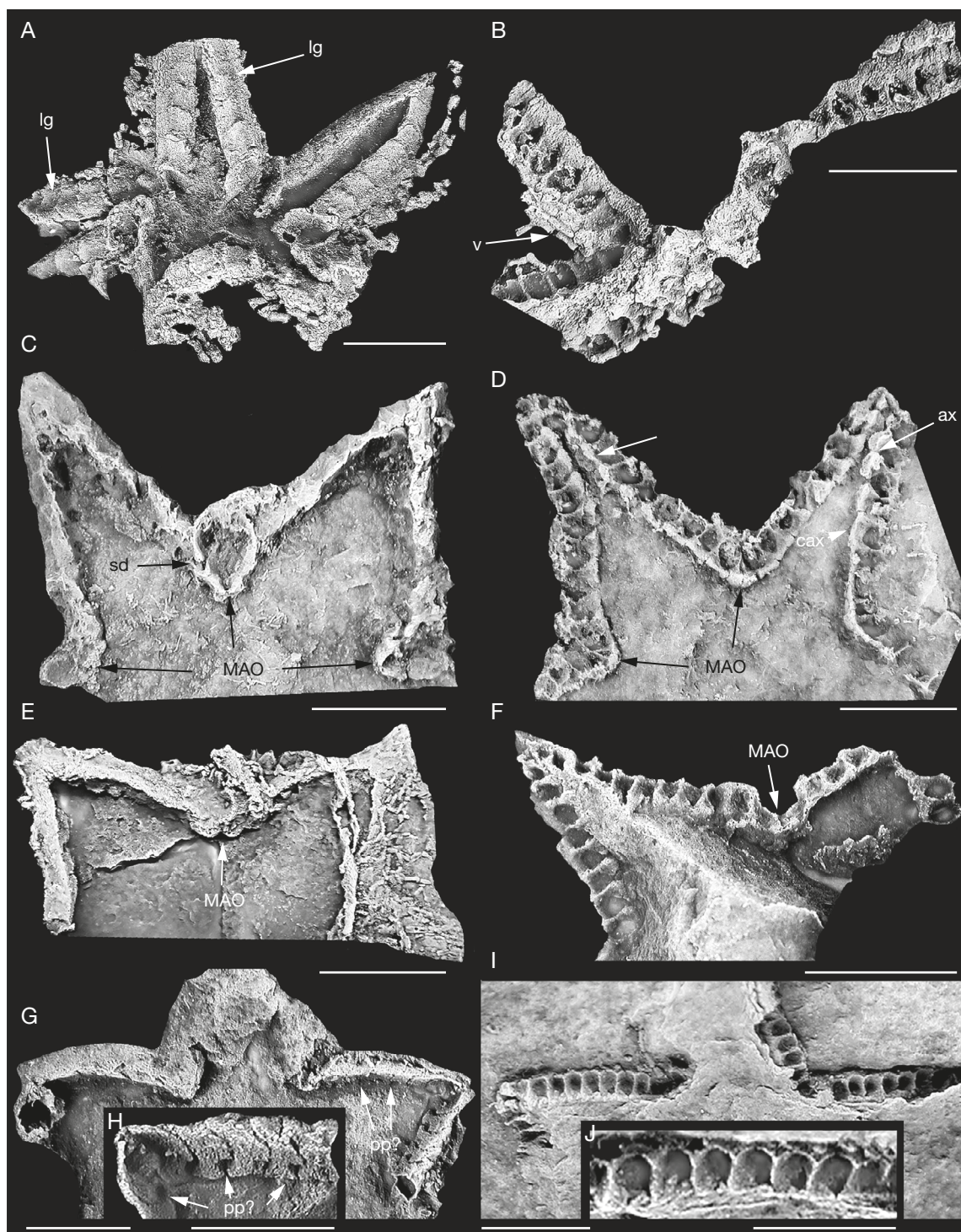


FIG. 8. — *Thorolaster spiculiformis* Dean Shackleton, 2005, Saint-Chinian Formation, Early Ordovician (late Tremadocian); Montagne Noire, France; latex casts; **A, B**, MNHN.F.A90271 (Courtessole-Griffe collection), Félines-Minervois (Hérault): **A**, aboral view, flared mouth frame suggestive of an open bivalve, alignment and positioning favoring an integrated axial series; axials weakly overlap distally and weakly grooved longitudinally, radial water channel appearing large, traces of virgalia extend distally to upper right; **B**, oral view, surface incomplete; axials converging on mouth frame, with virgal remnants at mouth frame; **C, D**, MNHN.F.A97739 (Courtessole-Griffe collection), Babeau-Bouldoux (Hérault): **C**, aboral view, skeletal discontinuity suggests more than a single ossicle; proximal margins of mouth angle ossicles bluntly rounded; **D**, oral view, mouth angle ossicles margins rounded, transverse ridges of mouth angle ossicles converge distally yielding an A-frame-like configuration; axials immediately adjacent to mouth angle ossicles little differentiated from the more distal, perhaps favoring the “bivalves” as circumorals; compound axials; two distal axials retain channel closure flanges; remnants of virgalia and the ambital necklace are to right; **E, F**, UCBL-FSL 168690 (Marty collection), Saint-Chinian area (Hérault): **E**, oral view, specimen highly distended; proximal margins of mouth angle ossicles rounded, abactinal and virgal debris to upper right; **F**, oral view, truncation of MAO framework suggests bivalve-like flanges were separate ossicles, thereby a circumoral; first podial basin aligned with more distal basins and directed toward arm midline; **G–J**, UCBL-FSL 424943 (Lignières collection), Saint-Chinian (Hérault): **G, H**, aboral view, most of aboral surfaces of axials lost; **H**, right side of right arm of **G** rotated, axials suggest podial pores; **I, J**, oral view: **J**, left arm of **I**, arm midline below, no indication of podial pores in this interval suggesting emergent pore status in **G** and **H**. Abbreviations: **ax**, axials; **cax**, compound axials; **lg**, grooved longitudinally; **MAO**, mouth angle ossicles; **pp?**, possible podial pores; **sd**, skeletal discontinuity; **v**, virgal. Scale bars: A–G, I, 5 mm; H, J, 3 mm.

adjacent to MAO (i.e., circumoral?) strongly flared as to yield an appearance suggestive of an open bivalve (Figs 7A, C; 8A, C, E). First subsequent axial similar to those of remainder of series, podial basin aligned with those of subsequent axials (Figs 7D, E; 8D, F). Virgalia abutting abradial terminus of axial transverse ridge, concentration of debris arguing virgalia reached mouth frame (Figs 6A; 7D; 8A, B). Virgals proportionately very small, delicate, rod-like, grooved longitudinally, termini weakly expanded; first virgals short, otherwise similar to more lateral virgals. Virgalia too delicate to have formed an abutted platform. Some adjacent virgalia termini abutted abradially to support an enlarged, attenuated, distal “radiole” (Fig. 6B, D, F). Virgal accessories small, plate-like to granular (Figs 1B; 6B, D, F).

REMARKS

The concept of *Thoralaster* was based on a few specimens taken from the type suite of *Chinianaster* (Dean Shackleton 2005); additional specimens are included here.

The clearest criterion for specimen inclusion is presence of an enlarged, flanged surface suggestive of an open bivalve in the mouth frame, it most readily viewed in aboral aspect. Because variously preserved among specimens, it is unclear whether the flange is a part of the MAO or a separate ossicle, as is suggested by discontinuities (Figs 7C; 8C), the flange then either the circumoral or a supernumerary

Additional generic criteria include presence of proportionately large, delicate axials, some compound in that the ossicle bears more than a partial podial basin on each side of the transverse ridge. Adaxials are very slender and rod-like. Perhaps suggesting structural integrity, most arm tips of *Thoralaster* held together during diagenesis, the axial series on the sides of the arm as preserved more (Figs 6A; 7A) or less (Fig. 8A) strongly diverging toward the disk. Although recognized only in a single arm interval and thereby potentially indicative of a transitional state, positioning and regularity of expression of apparent openings suggest podial pores (Fig. 8H). As compared to other somasteroid genera, overall construction of *Thoralaster* was somewhat delicate.

Subfamily VILLEBRUNASTERINAE Fell, 1963b

Villebrunasterinae Fell, 1963b: 143.

TYPE GENUS. — *Villebrunaster* Spencer, 1951.

DIAGNOSIS. — Subpentagonal Chinianasteridae. Abactinals spiculate, arrangement reticulate. Ambital framework ossicles granular to somewhat elongate, overall arrangement somewhat irregular, ossicles overlapping. Radial water-vascular channel large, cylindrical, robust; axials asymmetrical. Podial basin on proximal side of transverse ridge. Adradial adaxials complexly differentiated, virgalia relatively elongate.

REMARKS

The Villebrunasterinae is separated from both the Chinianasterinae and the Ophioxenikosinae n. subfam. based on axial and adradial virgal differentiation, the Ophioxenikosinae

n. subfam. further differing in form, abactinal, and ambital framework expressions. The Villebrunasterinae and Chinianasterinae earlier were recognized at the familial level (Fell 1963b; Spencer & Wright 1966).

Genus *Villebrunaster* Spencer, 1951

Villebrunaster Spencer, 1951: 93.

TYPE SPECIES. — *Villebrunaster thoralis* Spencer, 1951.

DIAGNOSIS. — As for *Villebrunaster thoralis*, the type and only known species.

Villebrunaster thoralis Spencer, 1951 (Figs 9-12)

Chinianaster levyi Thoral, 1935: *pars* 127, pl. 10.4, UCBL-FSL 168698.

Villebrunaster thoralis Spencer, 1951: 93, pl. 2, figs 29-31, text-figs 1, 3, 4. — Fell 1963a: 393 *et seq.*, figs 6B, 6C, 8C. — Spencer & Wright 1966: 41, figs 8.1a, 8.1b, 39.1. — Blake 2013: 363, fig. 1.3-1.5. — Blake & Guensburg 2015: 472, fig. 5.1-5.6, 6.1-6.8.

Villebrunaster Spencer, 1951 — Blake 2018: 7, pl. 1.3. — Blake 2024: 4 *et seq.*, fig. 1.1; pl. 2.9-2.12, *non* 1.1.

TYPE MATERIAL. — **Holotype.** France • 1 specimen (individual with five arms preserved; in the same concretion as paratype UCBL-FSL 168692a.2, see below); Hérault, Saint-Chinian, La Croix-Rouge; *Euloma filacovi* Zone, late Tremadocian (Early Ordovician); 1953, Thoral leg.; UCBL-FSL 168692a.1 (Fig. 9A, C-E).

Paratype. France • 1 specimen (only two arms preserved; part and counterpart with different registration numbers, see below); Hérault, Saint-Chinian, La Croix-Rouge; *Euloma filacovi* Zone, late Tremadocian (Early Ordovician); 1953, Thoral leg.; UCBL-FSL 168692a.2 (part) and UCBL-FSL168693c (counterpart).

REFERRED SPECIMENS. — Six specimens (UCBL-FSL 168693, UCBL-FSL 168698, UCBL-FSL 424948, UCBL-FSL 711092 [FSL 1879 561 of Dean Shackleton 2005], MNHN.FA47188, MNHN.FA97740).

DIAGNOSIS. — Abactinal arrangement open reticular (Figs 10B; 11A; 12F). Ambital framework ossicles equidimensional to somewhat rodlike and elongate, abutted to weakly overlapping (Figs 9A; 10A; 11A, D; 12E, F). Axials in aboral view only exposing square surface over water-vascular channel, the transverse ridge obscured; series grooved longitudinally (Figs 10B; 11A; 12F). In oral view, compound axials not recognized; radial-water vascular channel cylindrical, transverse ridge narrow, podial basin proximal (Figs 9; 10A, C; 12B, D). Adaxials moderately large, thin, broad surface longitudinally broadly grooved (Figs 9C; 10B, C; 11C, D; 12B). Adradial-most adaxial configurations not uniform but complexly varied both within and among specimens (Figs 9; 10; 11C; 12B, D).

DESCRIPTION

Overall form in life low-arched, outline subpentagonal; arms broad, triangular, taper gradual. Abactinals delicate, spiculate, rod-like and multiradiate; abactinal arrangement open hexagonal reticular. Madreporite, if any, unknown. Ambital framework well-defined and forming a continuous pentagonal

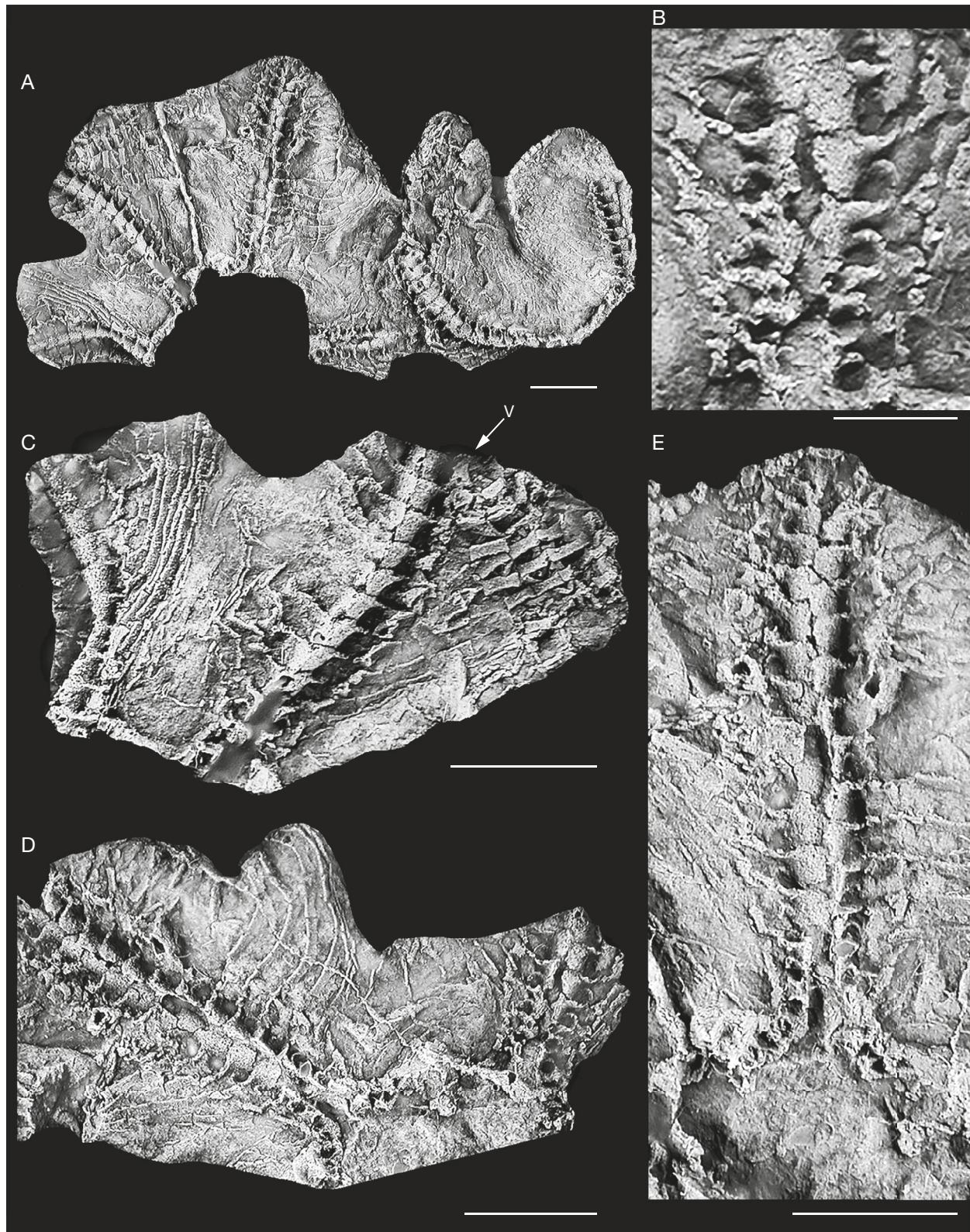


FIG. 9. — *Villebrunaster thoralis* Spencer, 1951, Saint-Chinian Formation, Early Ordovician (late Tremadocian); Saint-Chinian (Hérault), Montagne Noire, France: **A**, two specimens on a single block, oral views; holotype UCBL-FSL 168692a.1 to left (Thoral collection); paratype UCBL-FSL 168692a.2 (Thoral collection) to right; although now largely lost, virgalia are interpreted as having reached the mouth frame in both specimens; **B**, ambulacrum, lower right of holotype **A**; axials irregular, transverse ridges variably curved and closing about podial basins; noted by Spencer (1951: fig. 4, b); **C-E**, arms of holotype, axials irregularly positioned across arm midline; axials more or less hammer shaped, podial basins proximal of transverse ridge; **C**, adaxial virgals immediately adjacent to axials are not well preserved but differentiation appears limited; more abradial virgals exposed in both edge and lateral aspect; **D**, mouth frame distended, virgalia exposed in lateral aspect, virgals near axials disrupted; **E**, axials little disrupted; marginal traces remain at arm tip but a terminal is not recognized; fine debris perhaps includes accessories. Abbreviation: v, virgals. Scale bars: A, C-E, 5 mm; B, 2 mm.

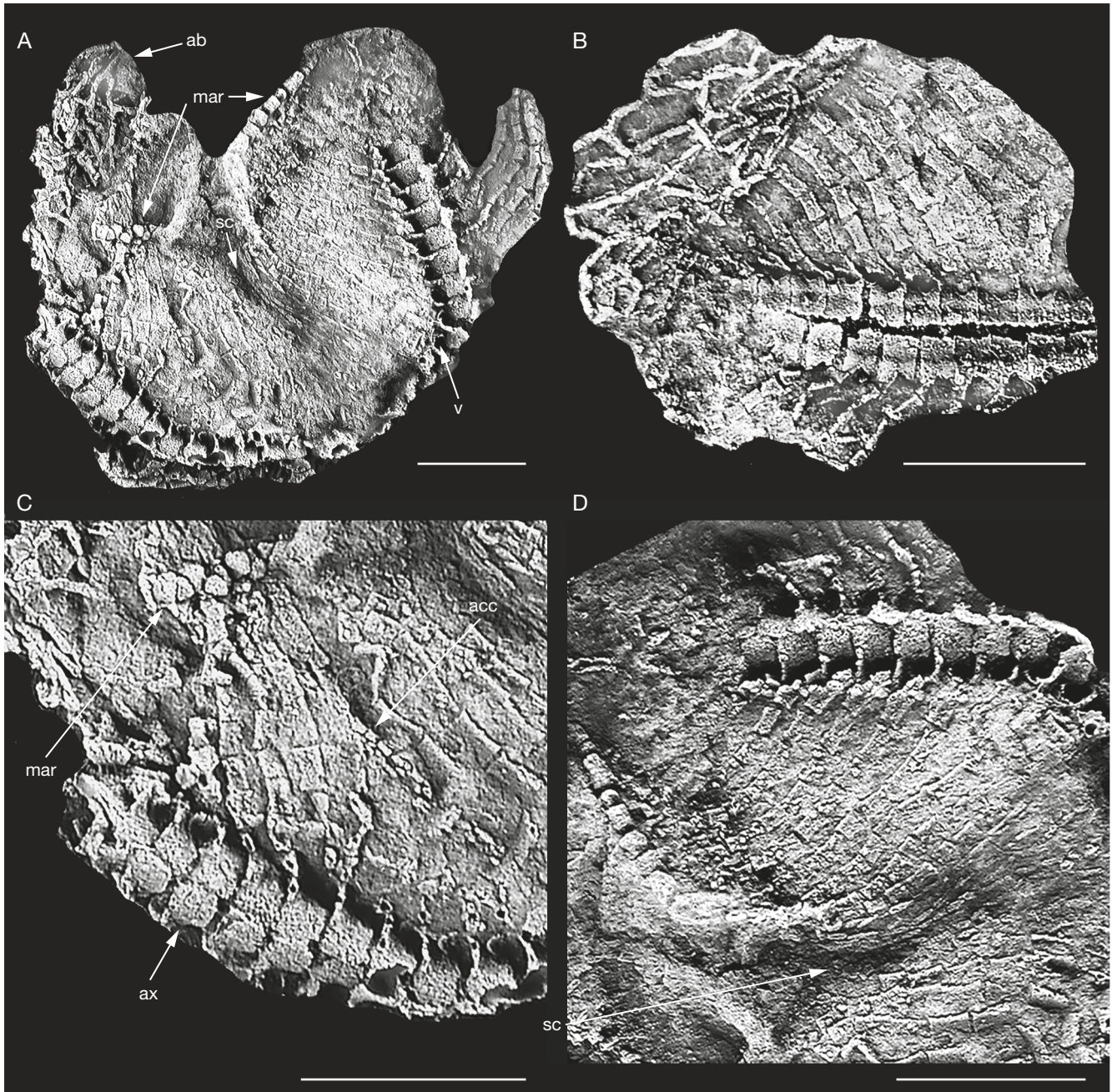


FIG. 10. — *Villebrunaster thoralis* Spencer, 1951, Saint-Chinian Formation, Early Ordovician (late Tremadocian); Saint-Chinian (Hérault), Montagne Noire, France: **A, C, D**, paratype UCBL-FSL 168692a.2 (Thoral collection): **A**, abactinals; marginals; adaxial virgals to right more clearly defined than those to left, see also **C**; specimen curvature was argued as indicating uplifted arms and an infaunal habit (Spencer 1951); **C**, lower left of **A**, displaced marginal series abuts lateral virgalia; axial some transverse ridges recurved to enclose next-distal podial basin, others are linear; virgals adjacent to the axials disrupted; aligned series of small ossicles appear to be virgal accessories; **D**, upper right area of **A** rotated counter-clockwise; transverse ridges straight and recurved; adradial adaxial series partially obscured by ossicular debris but those to left appear similar to those as exposed aborally; **B**, to medial left, granular skeletal debris associated with adaxials suggesting adaxial accessories; specimen curvature suggested infaunal life mode with arms extended (Spencer 1951); **B**, paratype UCBL-FSL 168693 (Thoral collection), reverse (aboral) surface of 168692a.2, distorted abactinal configuration is open reticulate; adradial portion of axial outlines approximately square, transverse ridges not exposed, axial series longitudinally grooved; broad surfaces of virgals exposed; first virgals aligned with more lateral virgals, no indication of offset as “struts”. Abbreviations: **ab**, abactinals; **acc**, virgal accessories; **ax**, axial; **mar**, marginals; **sc**, specimen curvature; **v**, virgals. Scale bars: 5 mm.

series extending around the arm tip, the series not deflected toward the mouth frame to form a gap or cleft. Marginal ossicles granular to rod-like, abutted to overlapping.

Axials in aboral aspect appearing approximately square, sequential axials abutted, longitudinal grooving weakly expressed, transverse ridge in aboral aspect generally obscured

as preserved. Axials in oral aspect of an “L”-shape, form dominated by cylindrical water-vascular skeletal closure; transverse ridge generally appearing short, linear to recurved (Fig. 9A, B; 10C, D); podial basin on proximal side of transverse ridge. Mouth-angle ossicles when extended toward mouth area appearing relatively narrow, abutted, upright,

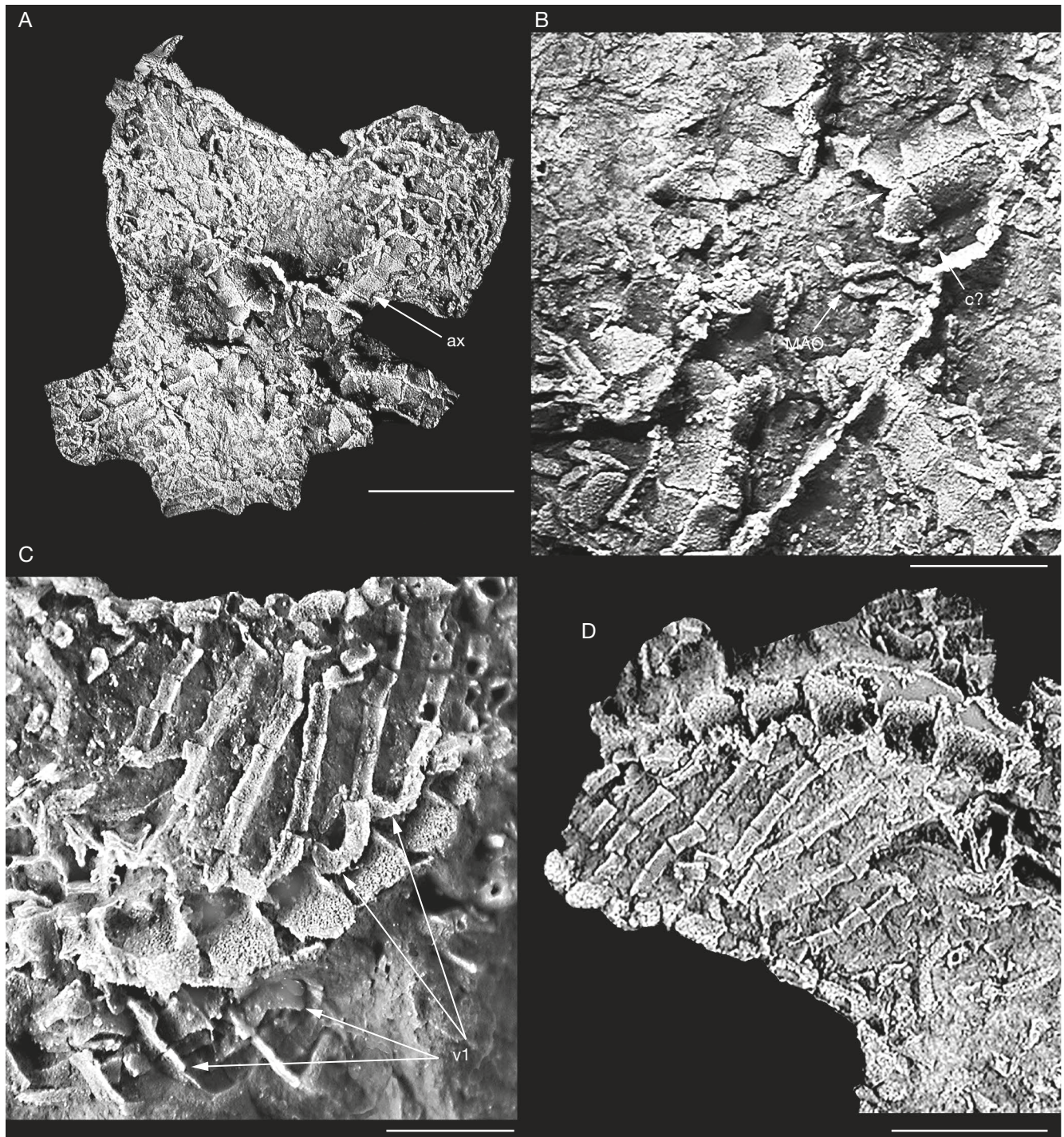


FIG. 11. — *Villebrunaster thoralis* Spencer, Saint-Chinian Formation, Early Ordovician (late Tremadocian); Montagne Noire, France: **A, B**, MNHN.F.A47188 (Vizcaïno collection), les Rocs de Sayrols, Félines-Minervois (Hérault); aboral view: **A**, most of remnant, mouth frame and arms only weakly distended to largely retain life configuration, no “buccal slit” is developed; abactinals form reticulate network, marginals irregular, rod-like; axial series (**ax**) abutted at midline, circumoral? with proximal margin curved; **B**, rotated clockwise from **A**, either larger ossicles or intercalated smaller ossicle is the circumoral? and the possible homologue of the bivalve-like oral flange of *Thoralaster*; upright mouth angle ossicles with spinelets; **C, D**, UCBL-FSL 711092 (Lignières collection), Saint-Chinian; oral views: **C**, to right, axial series below abutting “C”-shape first virgals (“intervirgal struts” of Dean Shackleton) rotated as to show full breadth; lower middle, first virgals rotated as to show edge; **D**, axial series above, marginals below, first virgals disrupted but not appearing much differentiate. Abbreviations: **ax**, axial; **mar**, marginals; **c?**, circumoral?; **v1**, first virgals. Scale bars: A, 5 mm; B, 2 mm; C, D, 3 mm.

bearing simple accessory spinelets (Fig. 11B). Next ossicular pair (circumoral?) upright, abutted at arm midline, proximal margins curved (Fig. 11A, B); possible small ossicle (Fig. 11B) might represent circumoral. Terminal, if dif-

ferentiated, obscure (Figs 11A; 12F). Adradial-most virgals judged variably differentiated and variably linked to axials, possibly locally with an embedded virgal equivalent between the axial and a more strongly differentiated second ossicle

(Fig. 12B). Abradial virgals elongate, grooved, sub-planar, termini expanded, rectangular in outline, edges narrow in ossicles rotated laterally; adjacent virgalia not closely spaced, perhaps not close enough to have formed a continuous platform when deflected distally. Localized alignment of granular debris suggests presence of virgal accessories. Other possible accessories not recognized.

REMARKS

Interpretation of *Villebrunaster* and *Ampullaster* is entangled in a number of morphological complexities as well as the uncertainties of preservation. *Villebrunaster* is most clearly differentiated by axial shape and complexities of the immediately adjacent adaxials. The axial transverse ridge can be recurved as to partially enclose podial basins (Figs 9A, B; 10C, D). The apparent circumoral is enlarged, the adoral edge curved, thereby potentially reflecting presence of a podium directed toward the mouth. An apparent small ossicle is developed between the MAO and the “circumoral” (Fig. 11B), it potentially the homologue of the enlarged flange or circumoral of *Thoraster* (Fig. 7A, C). Madreporite presence in *Villebrunaster* was noted but not illustrated (Dean Shackleton 2005, char. 77), and no example was recognized here. The ambital framework of *Villebrunaster* is well-defined but somewhat irregular, locally appearing to form a linear series, locally appearing slightly overlapping. Small virgal accessories occur (Fig. 10C, D). Marginal and abactinal accessories are not recognized although widely occurrent fine debris might indicate presence.

Genus *Ampullaster* Fell, 1963b

Villebrunaster — Dean Shackleton 2005: 64.

TYPE SPECIES. — *Ampullaster ubaghsi* Fell, 1963b.

DIAGNOSIS. — As for *Ampullaster ubaghsi*, the type and only recognized species.

Ampullaster ubaghsi Fell, 1963b (Fig. 13)

Ampullaster ubaghsi Fell, 1963b: 145, pl. 1; fig. 1. — Fell 1963a: fig. 6A,D. — Spencer & Wright 1966: 41, fig. 48. — Blake 1982: fig. 1D.

Villebrunaster thoralis Spencer, 1951 — Dean Shackleton 2005: 64, pl. 3, fig. 6; *non* pl. 3, fig. 7, text-figs 2B, 6. — Blake & Guensburg 2015: 472.

TYPE MATERIAL. — **Holotype.** France • 1 specimen (oral surface exposed; much ossicular surface detail lost); Hérault, Saint-Chinian; *Euloma filacovi* Zone, late Tremadocian (Early Ordovician); Villebrun leg.; UCBL-FSL 168673 (Fig. 13A-D).

DIAGNOSIS. — First virgals aligned in well-defined series between successive virgalia; first virgals uniform, longitudinally elongate and shelf-like, possibly exhibiting an outer rim edging an inner, inclined surface. Marginals appearing small, irregular, perhaps weakly elongate; overall, marginal series uniform. Abradial virgals possibly relatively slender, otherwise similar to *Villebrunaster*.

DESCRIPTION

Overall form in life low-arched, outline subpentagonal; arms broad, triangular, taper gradual. Abactinals spiculate, rod-like, arrangement reticulate. Ambital framework of relatively small, irregular, granular to rod-like ossicles forming a well-defined marginal series continuous across the interbrachia, not deflected toward mouth frame to form a gap or cleft. In oral aspect, axials “L”-shaped, form dominated by enlarged, skeletally closed, cylindrical water-vascular channel. Transverse ridge narrow, linear. Lateral edges of first virgals narrow, bar-like. Abradial virgals potentially extremely slender, elongate, rod-like. Accessories not clearly recognized, some debris suggests possible presence.

REMARKS

Ampullaster is known only from the holotype, it nearly complete and exposed in oral aspect. At the time of recognition, both *Ampullaster* and *Villebrunaster* were assigned to a new Villebrunasteridae (Fell, 1963b). Dean Shackleton (2005: 68), however, synonymized *Ampullaster* with *Villebrunaster* based primarily on equating differentiated adradial ossicles found in both as so-called “intervirgal struts”. The interpretation of Dean Shackleton earlier was accepted (Blake & Guensburg 2015) but it is rejected here, the interviral struts reinterpreted as adradial adaxials rather than calling for a new ossicular category.

The adradial adaxials of the two generic designates are argued as differing enough in morphology and positioning as to be treated as independently derived from a more stemward state (e.g. such as that of *Chinianaster*), thereby justifying retention of the generic status of *Ampullaster*. The so-called “intervirgal struts” of *Villebrunaster* are much varied in shape and orientation both among and within individuals (Figs 9A; 10; 11C; 12B), whereas corresponding ossicles of *Ampullaster* (Fig. 13) are regular in form and arrangement, each forming a shelf that partially confines the podial basin in a manner suggestive of expressions found in stenuroids (Spencer 1940: fig. 331; Blake 2024). No direct linkage between somasteroids and stenuroids is suggested. Other apparent adaxial variants are found in *Chinianaster* (Fig. 2A), in a *Chinianaster*-like unassigned specimen (Fig. 14G), and different adaxial specializations have been recognized in a number of problematic early asterozoans (e.g. Blake *et al.* 2020; Blake 2024). Adaxial differentiation thus was widespread not only within the Somasteroidea but also among early asterozoans in general, the varied specializations affording apomorphies serving to differentiate among both class-level asterozoan entities as well as a few genera not assigned at the class level (Blake 2013, 2018, 2024).

Further potentially contributing to generic separation, marginals of *Ampullaster* appear smaller and more irregular than those of *Villebrunaster*. Abradial virgals of the *Ampullaster* appear slender and rod-like; if, however, these are similar to virgals of *Villebrunaster* and *Chinianaster* and were rotated into plan view, they might prove comparable, as is suggested by a small area of the holotype (Fig. 13B, lower right). Added comments are included above under “Adaxial skeleton.”

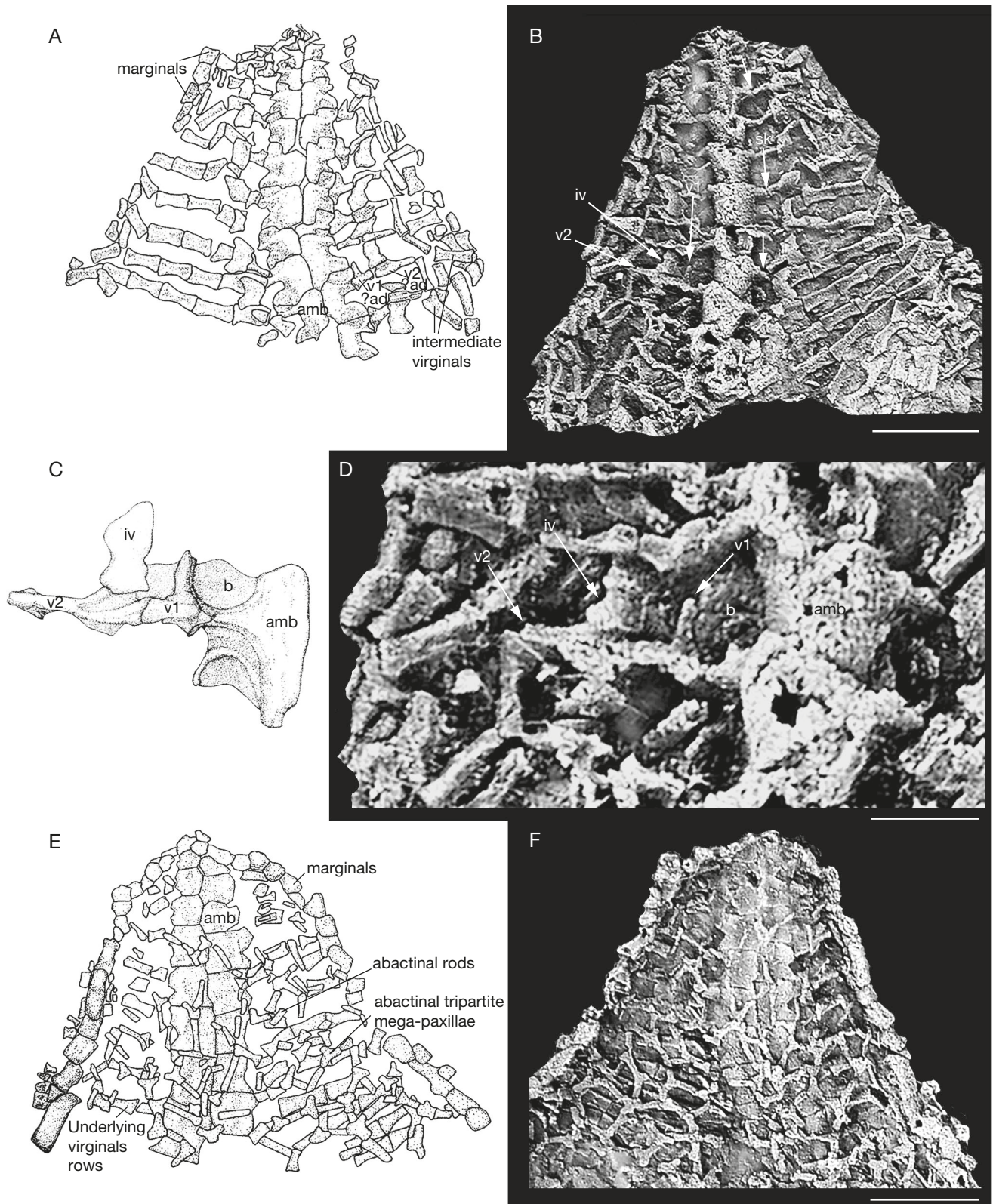


FIG. 12. — *Villebrunaster thoralis* Spencer, 1951, Saint-Chinian Formation, Early Ordovician (late Tremadocian); Saint-Chinian (Hérault), Montagne Noire, France, UCBL-FSL 711092 (Lignières collection). The drawings, figures **A**, **C**, and **E** are reconstructions of Dean Shackleton (2005), these accurate enough as to allow corresponding photo documentation, **B**, **D**, and **F**. **A** is reversed in the reconstruction from the photograph of **B** but **C** is not reversed, see **D**. In the Dean Shackleton reconstruction, ambulacral, here axial is used. **B**, skeletal discontinuities to right of axials are suggestive of the embedded virgal configuration of stenuroids, their significance here uncertain but part of the complexities of the adradial virgalia of *Villebrunaster*; **E**, **F**, aboral views; axials, abactinals, and marginals are clearly exposed; neither a carinal series nor a terminal is recognized. Remaining abbreviations of Dean Shackleton (2005). Abbreviations: **amb**, ambulacral; **ax**, axial; **b**, podial basin; **iv**, interviral struts; **sk**, skeletal discontinuities; **v1**, first virgals; **v2**, interviral struts. Scale bars: **B**, **F**, 3 mm; **D**, 1 mm.

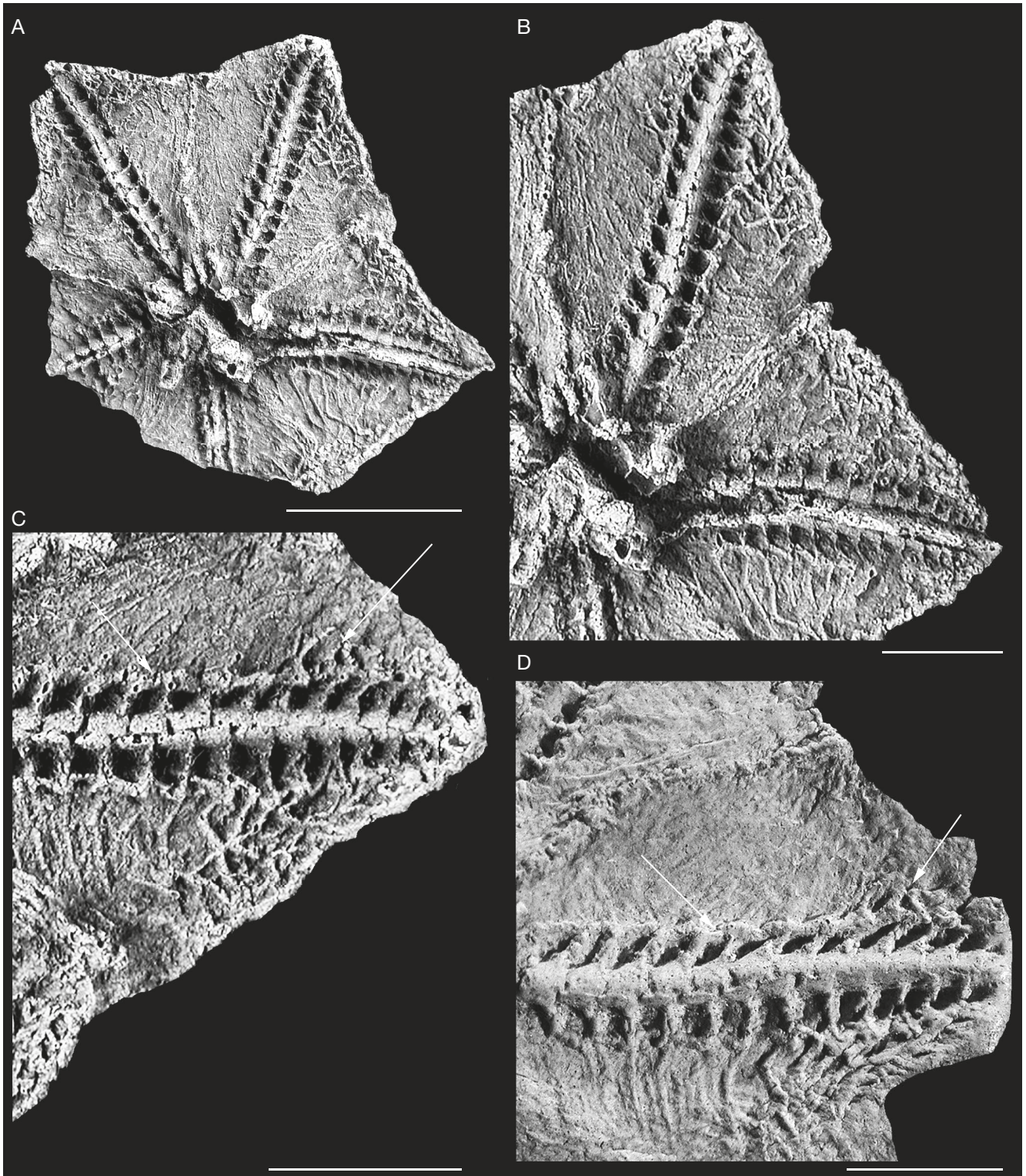


FIG. 13. — *Ampullaster ubaghsi* Fell, 1963b, UCBL-FSL-168673 (Villebrun collection), holotype and only recognized specimen, oral view, Saint-Chinian Formation, Early Ordovician (late Tremadocian); Saint-Chinian (Hérault), Montagne Noire, France: **A**, specimen remnant; **B**, enlargement of upper right; the proximal interval of the ambulacrum to right was slightly distended, other ambulacra lifelike. Axials across the arm midline are offset distally, but more nearly paired proximally, here considered an ontogenetic realignment retained phylogenetically within Asterozoa. Sediment compaction pushed some abactinals to the oral surface. Virgalia reach the mouth frame. Virgals toward the top of the image appear slender whereas those to the lower right suggest broader surfaces, these perhaps differentially rotated. A terminal is not recognized. Marginal form is not clearly expressed but appears more irregular than typical of *Villebrunaster* Spencer, 1951; **C**, **D**, two copies using different casting materials, **D** an unnumbered NHM cast of W.K. Spencer. **Arrows** correspond. First virgals ossicles are uniform, rectangular, possibly with lip-like shelves bordering the podial basins, these the “intervirgal struts” of Dean Shackleton (2005) and fundamental to the proposed synonymizing of *Ampullaster* Fell, 1963b with *Villebrunaster*. The interpretation here is that expressions differ enough to retain the generic concept of *Ampullaster*. Scale bars: A, 10 mm; B-D, 5 mm.

In the original diagnosis of Fell (1963b), marginal series were interpreted as edging deep interrarial “V”-shaped “clefs” that produced petaloid arm outlines. It is argued here that the ambital framework was continuous across the interbrachium, as in all somasteroids. Fell (1963b) envisioned presence of gradational changes of axial expression along the length of the arm of *Ampullaster*, the most important the presence of skeletal discontinuities interpreted as podial pores. The interpretation is not accepted here.

Subfamily OPHIOXENIKOSINAE n. subfam.

[urn:lsid:zoobank.org:act:FDF53B0D-66B0-46B5-A22A-B60C7C4BB7CD](https://zoobank.org/act:FDF53B0D-66B0-46B5-A22A-B60C7C4BB7CD)

TYPE GENUS. — *Ophioxenikos* Blake & Guensburg, 1993.

DIAGNOSIS. — Substellate Chinianasteridae. Abactinals granular to plate-like, closely appressed. Ambital framework ossicles moderately elongate, aligned, weakly overlapping. Radial water-vascular channel small; skeletally closed. Podial basin boundary approximately medial, basin shared equally by successive axials. Adradial adaxials weakly differentiated, virgalia relatively short.

REMARKS

For purposes of comparison, the diagnosis is written in parallel with those for the Chinianasterinae and Villebrunasterinae. The Ophioxenikosinae n. subfam. is known only from *O. langenheimi*; the diagnosis applies at the species level.

Genus *Ophioxenikos* Blake & Guensburg, 1993

Ophioxenikos langenheimi Blake & Guensburg, 1993

starfish Byrd, 1970: 29, fig. 5.

Ophioxenikos langenheimi Blake & Guensburg, 1993: 109, figs 2.1-2.3, 2.5, 3. — Dean Shackleton 2005: 71, pl. 3.5. — Blake & Guensburg 2015: 470, fig. 4.1.

TYPE MATERIAL. — **Holotype. United States** • 1 specimen; south-central Nevada, Ely Springs Mountain Range; Lower Pogonip Group, late early to middle Floian (Early Ordovician); PRIP UI X-4751.

TYPE LOCALITY AND HORIZON. — Lower Pogonip Group, Early Ordovician (late early to middle Floian); Ely Springs Mountain Range, south-central Nevada, United States.

DESCRIPTION

Overall form in life low-arched, outline substellate; arm outline in life triangular, quite abruptly tapering. Abactinals irregular, abutted, small, granular to plate-like. Madreporite unknown. Ambital framework well-defined, series forming a continuous outline extending around the arm tip, not deflected toward the mouth frame; marginals rod-like, robust, overlapping, alignment irregular to regular; accessory faceting not recognized. Axials approximately equidimensional, aboral appearance unknown; in oral aspect, radial water-vascular channel enclosed, small, tubular. Axials

approximately bilateral both along and perpendicular to transverse ridge; podial basin shared by sequential axials; compound axials not recognized. Mouth frame ossicles small, appearing little differentiated from more distal ossicles; mouth-angle ossicles rectangular. First virgal short, otherwise similar to more lateral virgals. Abradial virgals somewhat enlarged irregular to cylindrical, rod shaped. Any accessories unknown.

REMARKS

The differing preservational styles of *Ophioxenikos* and the French-Moroccan genera render comparisons difficult. Floian *Ophioxenikos* is younger than Tremadocian *Cantabrigiaster* and the Saint Chinian genera but older than Middle Ordovician *Archegonaster*.

Family ARCHEGONASTERIDAE Spencer, 1951

Archegonasteridae Spencer, 1951: 101.

TYPE GENUS. — *Archegonaster* Jaekel, 1923.

DIAGNOSIS. — Abactinal skeleton limited to tiny granules. Ambital framework ossicles proportionately large, angular, forming a linear sequence. Axials “T”-shaped, gaps between successive axials suggesting podial pores. Water-vascular channel not skeletally closed orally. Virgalia not known to reach mouth frame. First virgal strongly differentiated.

REMARKS

For purposes of comparison, the diagnosis is written in parallel with that for the Chinianasteridae. The Archegonasteridae is known only from *A. pentagonus*; the diagnosis applies at the species level.

Genus *Archegonaster* Jaekel, 1923

Archegonaster pentagonus Spencer, 1951

Archegonaster pentagonus Spencer, 1951: 101, pl. 2, fig. 34; pl. 3, figs 37, 38; pl. 4, figs 39, 40; text-figs 9, 10, 12-15. — Ubaghs 1953: fig. 18. — Fell 1963c: 463, fig. 5I. — Spencer & Wright 1966: 41, fig. 39.3. — Smith & Jell 1990: 753, fig. 37-51. — Dean Shackleton 2005: 64, pl. 3.2, fig. 12a. — Blake & Guensburg 2015: 477, fig. 4.2. — Villier *et al.* 2018: 404.

TYPE MATERIAL. — **Holotype. Czech Republic** • 1 specimen; Prague Basin, Osek; Šárka Formation, Darriwilian (Middle Ordovician); NMP L10143 (part) and NMP L10144 (counterpart).

REFERRED SPECIMENS. — Reviewed from the literature (see Smith & Jell 1990; Dean Shackleton 2005).

TYPE LOCALITY AND HORIZON. — Šárka Formation (Llanvirn), close to Ošek, Prague Basin, Czech Republic.

DESCRIPTION

Somasteroid in life low-arched, outline pentagonal. Aboral skeleton limited to granules. Madreporite aboral, surface

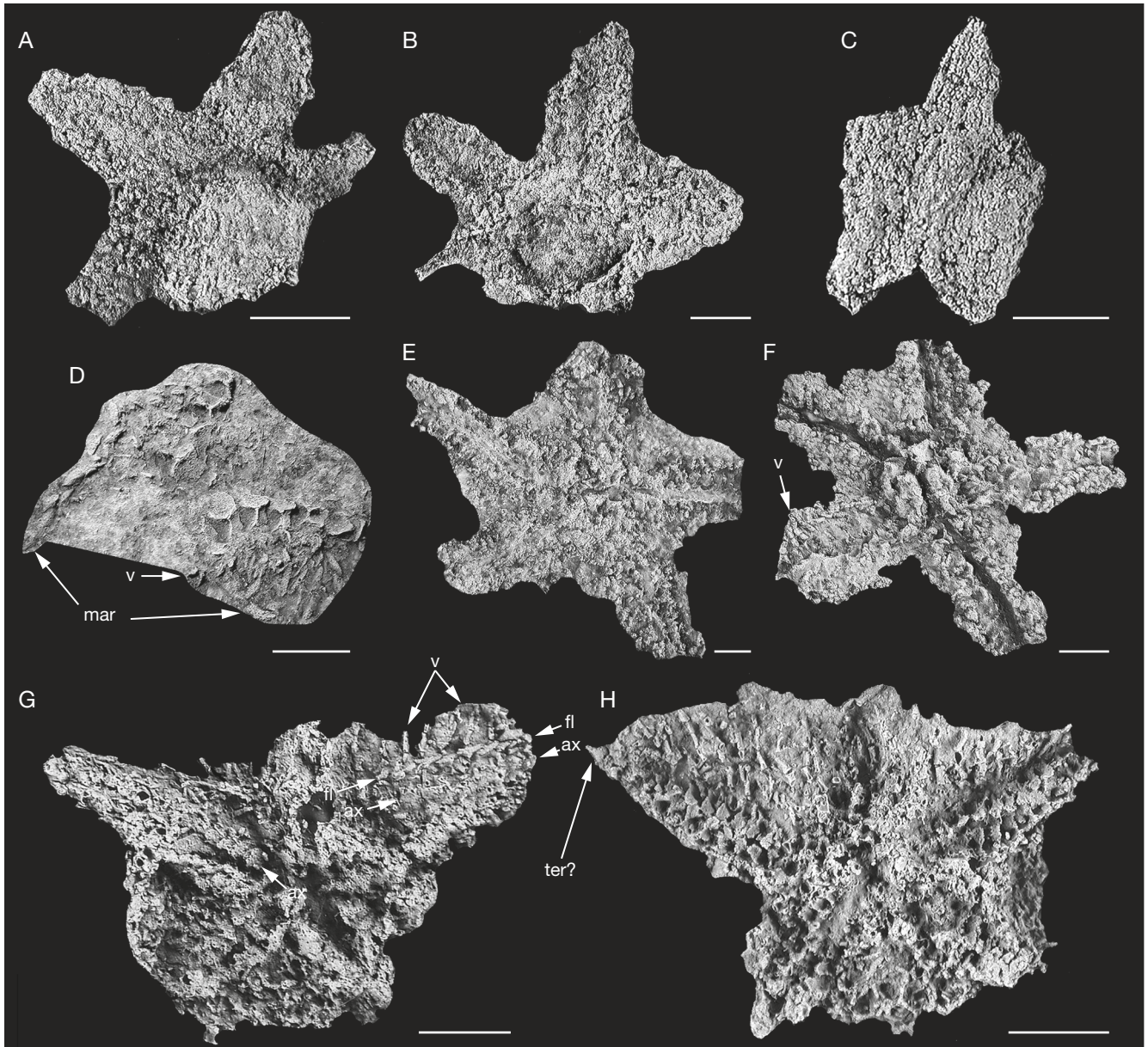


FIG. 14. — Many specimens of the French/Moroccan asterozoan specimen suite are not complete enough to assign at lower taxonomic levels: select examples are illustrated: **A, B, C**, asterozoans too poorly preserved to be assigned at the class level; UCBL-FSL 712046 (Reboul collection); Fezouata Formation, Early Ordovician (early Floian); Toumiat, c. 17 km NE of Zagora, Central Anti-Atlas, Morocco. Two of three individuals together on a small slab, the early Floian age making them among the oldest-known asterozoans: **A, B**, both surfaces of one specimen, aboral vs oral difficult to determine; arm midlines suggest axials; smaller ossicles are suggestive of somasteroid abactinals and virgals. The central disk appears filled with sediment suggesting substrate feeding rather than suspension feeding; **C**, disk distortion suggests compaction around sediment and substrate feeding rather than differentiation of disk ossicles; **D**, Somasteroidea Spencer, 1951 indeterminate, AA.BCBb.OI.36 (Lefebvre collection); Fezouata Formation, Early Ordovician (middle Floian), Bou Chrebeb, c. 27 km NE of Zagora, Central Anti-Atlas, Morocco. Oral view, dilated ambulacral column converges distally to left; axial form suggestive of those of *Chinianaster* Thoral, 1935, small, rodlike virgals and irregular elongate overlapping marginals are not readily equated with those of a recognized somasteroid genus; **E, F**, Somasteroidea indeterminate, UCBL-FSL 424964 (Reboul collection); Fezouata Formation, Early Ordovician (middle Floian), Zagora area, Central Anti-Atlas, Morocco. Aligned adaxial virgalia indicate a somasteroid; however, although representatives of other ossicular series can be identified, generic assignment is not justified; **G, H**, *Chinianaster?* sp., Saint-Chinian Formation, Early Ordovician (late Tremadocian); MBB-GG18 (Griffe collection); **G**, aboral view, virgalia are not readily equated with *Chinianaster*; enlarged, differentiated flange-like ossicles appear offset from axial series, as in *Chinianaster* (Fig. 2A); **H**, oral view; the small ossicles edging the upper margin suggest the ambital necklace of *Chinianaster*, as does the possible terminal (Fig. 2F); oral surface of axials retain an oral shield as Figure 2E. Abbreviations: **fl**, flange-like; **mar**, marginals; **ter?**, possible terminal; **v**, virgals; **vir**, virgalia. Scale bars: A–F, 3 mm; G, H, 5 mm.

of radiating ridges and grooves. Ambital framework well-defined, marginals robust. Axials “T”-shaped, overlapping, with a large opening, an apparent podial pore. First adaxials strongly differentiated, more lateral adaxials proportionately small, rod-like. Proximal virgalia not recognized.

REMARKS

The Jaekel (1923) treatment of *Archegonaster* was cursory, the specific name later designated from a Jaekel manuscript (Spencer 1951: 101). Morphology was reviewed in detail by Spencer (1951), Smith & Jell (1990), and Dean Shackleton (2005).

PROBLEMATIC SPECIMENS

Specimens too incomplete to fully assign at lower taxonomic levels are selected to illustrate the difficult nature of both the French/Moroccan suite (Fig. 14) and interpretation of early asterozoans in general. Crown-group asterozoans are difficult as well: Extensive sophisticated techniques enabled reevaluation of the large and well-known family Asteroiidae (Fau *et al.* 2024), thereby obliquely addressing concerns surrounding evaluation of early asterozoans.

SUMMARY AND INTERPRETATIONS

The subphylum Asterozoa *sensu* Spencer (1951), Ubaghs (1953), and Spencer & Wright (1966) is accepted as monophyletic, “accepted” meaning in accord with current information while acknowledging potential paraphyly or polyphyly.

Because morphologically diverse asterozoans are known from a comparatively narrow Early Ordovician stratigraphic interval and also because no tenable outgroup for phylogenetic analysis is recognized, divergence of the Asterozoa potentially preceded the emergence of a robust skeleton.

Construction of the ambulacral column, consisting of the axials and adjacent adaxials, is fundamental to interpretation of the early phylogeny and taxonomy of Asterozoa whereas the extraxial skeleton, under more immediate environmental evolutionary pressures, is secondary.

The Somasteroidea is interpreted as stemward among robustly skeletonized asterozoans.

Specialization of the adradial-most virgals was emergent among somasteroids, with reduction to a single or few differentiated adaxials providing apomorphies that chart both the recognized classes as well as a number of genera not assigned at the class level.

The complexity of somasteroid construction with only delicate linkages among ossicles is interpreted as reflecting body flexibility and mobile life modes with the oral surface directed toward the substrate. At least in part a reflection of this skeletal construction, the fossil record of the Somasteroidea is scanty.

Yet ambiguities surround interpretation (and therefore any coding for phylogenetic analysis) of many aspects of axial and adaxial somasteroid development. Was the stemward positioning of axials at the arm midline offset or irregular (Figs 2A, E; 4A, B; 9-11; 13)? Presumably there was linkage between the radial water vascular channel and the podium, yet as survey of specimens shows, recognition is problematic. Are podial pores emergent within somasteroids (Figs 2A, F; 8G, H)? Are compound axials the product of axial fusion or are they a stemward aberrancy occurring before axial uniformity fully emerged (see Terminology; Figs 4C; 6C; 8D)? Should ossicles immediately lateral to axials be treated as “adaxials” or as representing a potentially independent series (see “Adaxial Skeleton”, Smith & Jell [1990])? Is there a separate “intervirgal strut” series (see “Adaxial Skeleton”, Dean Shackleton [2005])? What was the genesis of the so-called “radiole” (see discussions, figure citations under “The Ambital Framework”)? What is

a “buccal slit” (see discussions under “Axial skeleton: Mouth frame”, many figures)? Do supernumerary ossicles occur in the mouth frame of some taxa (see discussions under “Axial skeleton: Mouth frame”, cited figures)? What is the nature and genesis of “marginal” series, and should ambital framework “marginals” be treated as adaxial or extraxial (see discussions under “The ambital framework”)?

Somasteroid mouth frame ossicles are proportionately small and relatively little differentiated; however, understanding of asterozoan mouth frame construction is incomplete because of ossicular delicacy, overall body three-dimensionality, and animal flexibility in life, all leading to mouth frame disruption with death.

In spite of the typical overall simplicity of the somasteroid mouth frame, possible supernumerary ossicles might occur (*Thoralaster*, *Villebrunaster*). Near-oral compound axials and complex first adaxial configurations occur (*Thoralaster*, *Cantabrigiaster*). Arm axials vary among genera, although ossicles of most are approximately bilateral and podial basins are proportionately large and equally shared by successive axials. Terminal ossicles known from derived lineages have not been recognized among somasteroids.

Specialization of adradial-most virgals was emergent among somasteroids, with reduction to a single or few much differentiated ossicles providing the key apomorphies in the derivation and recognition of both class-level and unassigned lineages (e.g. Blake 2013, 2024).

Abactinals vary among somasteroids but all are proportionately small and uniform within each genus. No phylogenetic sequencing of abactinal form within Somasteroidea is suggested.

A madreporite has been recognized in only three somasteroid genera suggesting calcification of the presumed stemward hydropore might have been homoplastic within the class.

An ambital framework series is recognized in all somasteroids arguing presence is plesiomorphic in the subphylum. Varied marginal expressions within the class suggest an evolutionary sequencing extending from many tiny platelets to a robust configuration similar to those of many Asteroidea. Absence of true marginals from the Ophiuroidea suggests loss was a class-level apomorphy whereas status of differentiated arm margin ossicles in some Stenuroidea is problematic (Blake 2024).

Because of constraints of preservation, accessories are generally difficult to recognize but appear to have been limited to proportionately small sizes and simple shapes.

Somasteroids have been reported only from normal marine settings. Overall configuration and sedimentary occurrences argue mobile epifaunal habits with the mouth frame directed toward the substrate. Virgals are varied among somasteroids, expressions suggesting behavioral variation of an unknown nature. Disk configurations reflect substrate grazing or possible suspension-feeding with extension of the arms into the water column.

That somasteroids exhibit essential asterozoan configuration has been recognized since the description of the first exemplar (Thoral 1935), yet the nature of the oral surface has allowed a multiplicity of interpretations important to the interpretation of asterozoan phylogeny and life mode: uncertainties persist.

Acknowledgments

Figure 1A is from “Early Palaeozoic Starfish”, W.K. Spencer, Philosophical Transactions of the Royal Society, Series B, reprinted by permission of The Royal Society (United Kingdom). Figures 1B, 12A, C, and E are from “Skeletal homologies, phylogeny and classification of the earliest asterozoan echinoderm”, J. Dean Shackleton Journal of Systematic Paleontology, copyright © 2005 The Trustees of the Natural History Museum, London, reprinted by permission of Taylor & Francis. Authors are grateful for the positive and helpful reviews of anonymous reviewers, and also for the editorial work provided by the associated editor, Annalisa Ferretti, and the editor-in-chief, Michel Laurin. This paper is a contribution to IGCP 735 “Rocks and the Rise of Ordovician Life” (Rocks n’ROL), and to the ANR project “Evolution of the Cambrian-Ordovician Biodiversification Onset Over Space and Time” (ECO-BOOST). Denis Audo and Jean-Michel Pacaud (MNHN, Paris), Emmanuel Robert (Université Lyon 1, Villeurbanne) and Roxelane Cicekli (Musée du Biterrois, Béziers) are thanked for having provided access to important specimens deposited in the collections they are curating.

REFERENCES

- AGASSIZ L. 1836. — Prodrôme d’une monographie des radiaires ou échinodermes. *Mémoires de la Société des Sciences naturelles de Neuchâtel* 1: 168-199.
- AGASSIZ A. 1877. — North American starfishes. *Memoirs of the Museum of Comparative Zoology, Harvard College* 5 (1): 1-136. <https://www.biodiversitylibrary.org/page/4304838>
- ALLAIRE N., LEFEBVRE B., NARDIN E., MARTIN E. L. O., VAUCHER R. & ESCARGUEL G. 2017. — Morphological disparity analysis and systematic revision of the eocrinoid genus *Rhopalocystis* (Echinodermata, Blastozoa) from the Lower Ordovician of the central Anti-Atlas (Morocco). *Journal of Paleontology* 91 (4): 685-714. <https://doi.org/10.1017/jpa.2017.6>
- ALPERT S. P. 1976. — Trilobite and star-like trace fossils from the White-Inyo Mountains, California. *Journal of Paleontology* 50 (2): 226-239. <http://www.jstor.org/stable/1303490>
- ÁLVARO J. J., BENHARREF M., DESTOMBES J., GUTIÉRREZ-MARCO J. C., HUNTER A. W., LEFEBVRE B., VAN ROY P. & ZAMORA S. 2022. — Ordovician stratigraphy and benthic community replacements in the eastern Anti-Atlas, Morocco, in HUNTER A. W., ÁLVARO J. J., LEFEBVRE B., VAN ROY P. & ZAMORA S. (eds), The Great Ordovician Biodiversification Event: Insights from the Tafilalt Biota, Morocco. *Geological Society, London, Special Publications* 485: 37-67. <https://doi.org/10.1144/SP485.20>
- BABIN C., COURTESOLE R., MÉLOU M., PILLET J., VIZCAÍNO D. & YOCHELSON E. 1982. — *Brachiopodes (articulés) et mollusques (bivalves, rostroconches, monoplacophores, gastéropodes) de l’Ordovicien inférieur de la Montagne Noire (France méridionale)*. Société d’Études Scientifiques de l’Aude, Carcassonne: 1-62.
- BERGSTRÖM S. M., XU C., GUTIÉRREZ-MARCO J. C. & DRONOV A. 2009. — The new chronostratigraphic classification of the Ordovician System and its relations to major regional series and stages and to $\delta^{13}\text{C}$ chemostratigraphy. *Lethaia* 42 (1): 97-107. <https://doi.org/10.1111/j.1502-3931.2008.00136.x>
- BILLINGS E. 1858. — On the Asteriadae of the Lower Silurian rocks of Canada. *Geological Survey of Canada, Separate Report* 425: 75-85. <https://doi.org/10.4095/222579>
- BLAKE D. B. 1972. — Sea star *Platasterias*: Ossicle morphology and taxonomic position. *Science* 176 (4032): 306-307. <https://doi.org/10.1126/science.176.4032.306>
- BLAKE D. B. 1982. — Somasteroidea, Asteroidea, and the affinities of *Luidia* (*Platasterias*) *latiradiata*. *Palaeontology* 25: 167-191.
- BLAKE D. B. 1994. — Re-evaluation of the Palasteriscidae Gregory, 1900, and the early phylogeny of the Asteroidea (Echinodermata). *Journal of Paleontology* 68 (1): 123-134. <http://www.jstor.org/stable/1306091>
- BLAKE D. B. 2000. — An *Archegonaster*-like somasteroid (Echinodermata) from Pomeroy, Co. Tyrone, Northern Ireland. *Irish Journal of Earth Sciences* 18: 89-99.
- BLAKE D. B. 2007. — Two Late Ordovician asteroids (Echinodermata) with characters suggestive of early ophiuroids. *Journal of Paleontology* 81 (6): 1476-1485. <https://doi.org/10.1666/05-130.1>
- BLAKE D. B. 2009. — Re-evaluation of the Devonian family Helianthasteridae Gregory, 1899 (Asteroidea: Echinodermata). *Paläontologische Zeitschrift* 83: 293-308. <https://doi.org/10.1007/s12542-009-0020-x>
- BLAKE D. B. 2013. — Asterozoan (Echinodermata) diversification: a paleontologic quandary. *Journal of Paleontology* 87 (3): 353-372. <https://doi.org/10.1666/12-042.1>
- BLAKE D. B. 2014. — Two Ordovician asterozoans (Echinodermata) of problematic affinities. *Journal of Paleontology* 88 (6): 1163-1173. <https://doi.org/10.1666/13-114>
- BLAKE D. B. 2018. — A history of the Paleozoic Asteroidea (Echinodermata). *Bulletins of American Paleontology* 394: 1-96.
- BLAKE D. B. 2024. — A Review of the Class Stenuroidea (Asterozoa, Echinodermata). *Bulletins of American Paleontology* 409: 1-110.
- BLAKE D. B. & ETTENSOHN F. R. 2009. — The complex morphology of a new Lower Silurian asteroid (Echinodermata). *Journal of Paleontology* 83 (1): 63-69. <https://www.jstor.org/stable/29739066>
- BLAKE D. B. & GUENSBURG T. E. 1993. — New Lower and Middle Ordovician stelleroids (Echinodermata) and their bearing on the origins and early history of the stelleroid echinoderms. *Journal of Paleontology* 67 (1): 103-113. <https://doi.org/10.1017/S0022336000021211>
- BLAKE D. B. & GUENSBURG T. E. 2015. — The class Somasteroidea (Echinodermata, Asterozoa): morphology and occurrence. *Journal of Paleontology* 89 (3): 465-486. <https://doi.org/10.1017/jpa.2015.22>
- BLAKE D. B. & HOTCHKISS F. H. C. 2022. — Origin of the subphylum Asterozoa and redescription of a Moroccan Ordovician somasteroid. *Geobios* 72-73: 22-36. <https://doi.org/10.1016/j.geobios.2022.07.002>
- BLAKE D. B. & LEFEBVRE B. 2024. — Ordovician *Petraster* Billings (Asteroidea; Echinodermata) and early asteroid skeletal differentiation. *Comptes Rendus Palevol* 23 (17): 217-239. <https://doi.org/10.5852/cr-palevol2024v23A17>
- BLAKE D. B. & ROZHNOV S. 2007. — Aspects of life mode among Ordovician asteroids: implications of new specimens from Baltica. *Acta Palaeontologica Polonica* 52 (3): 519-533.
- BLAKE D. B., GAHN F. J. & GUENSBURG T. E. 2020. — An Early Ordovician (Floian) asterozoan (Echinodermata) of problematic class-level affinities. *Journal of Paleontology* 94 (2): 358-365. <https://doi.org/10.1017/jpa.2019.82>
- BOTTING J. P. 2007. — “Cambrian” demosponges in the Ordovician of Morocco: insights into the early evolutionary history of sponges. *Geobios* 40 (6): 737-748. <https://doi.org/10.1016/j.geobios.2007.02.006>
- BOTTING J. P. 2016. — Diversity and ecology of sponges in the Early Ordovician Fezouata Biota, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 75-86. <https://doi.org/10.1016/j.palaeo.2016.05.018>
- BRANSTRATOR J. W. 1972. — *Lanthanaster cruciformis*, a new Upper Ordovician sea star from Cincinnati, Ohio. *Journal of Paleontology* 46 (1): 66-69. <https://www.jstor.org/stable/1302912>

- BRETT C. E., MOFFAT H. A. & TAYLOR W. 1997. — Echinoderm taphonomy, taphofacies, and Lagerstätten, in WATERS J. A. & MAPLES C. G. (eds), *Geobiology of Echinoderms. Paleontological Society Papers* 3: 147-190. <https://doi.org/10.1017/S1089332600000243>
- BYRD W. J. 1970. — Geology of the Ely Springs Range, Lincoln County, Nevada. *Wyoming Geological Association Earth Science Bulletin* 3 (2): 23-32.
- CANDELA Y., HARPER D. A. T. & MERGL M. 2024. — The brachiopod faunas from the Fezouata Shale (Lower Ordovician; Tremadocian–Floian) of the Zagora area, Anti-Atlas, Morocco: evidence for a biodiversity hub in Gondwana. *Papers in Palaeontology* 10 (5): e1592. <https://doi.org/10.1002/spp2.1592>
- CAPÉRA J. C., COURTESOLE R. & PILLET J. 1978. — Contribution à l'étude de l'Ordovicien inférieur de la Montagne Noire. Biostratigraphie et révision des Agnostida. *Annales de la Société Géologique du Nord* 98: 67-88.
- CHAUVEL J. 1966. — *Échinodermes de l'Ordovicien du Maroc*. Éditions du CNRS, Paris: 1-120.
- CHAUVEL J. 1971. — Les échinodermes carpoïdes du Paléozoïque inférieur marocain. *Notes du Service géologique du Maroc* 31: 49-60.
- COURTESOLE R., PILLET J. & VIZCAÏNO D. 1981. — *Nouvelles données sur la biostratigraphie de l'Ordovicien inférieur de la Montagne Noire. Révision des Taihungshaniidae, et de Megistaspis (Ekeraspis) et d'Asaphopsoïdes (Trilobites)*. Société d'Études Scientifiques de l'Aude, Carcassonne: 1-32.
- COURTESOLE R., MAREK L., PILLET J., UBAGHS G. & VIZCAÏNO D. 1983. — *Calymenina, Echinodermata et Hyolitha de l'Ordovicien inférieur de la Montagne Noire*. Société d'Études Scientifiques de l'Aude, Carcassonne: 1-62.
- COURTESOLE R., PILLET J., VIZCAÏNO D. & ESCHARD R. 1985. — *Étude biostratigraphique et sédimentologique des formations arénacées de l'Arenigien du Saint-Chinianais oriental (Hérault) versant Sud de la Montagne Noire (France méridionale)*. Société d'Études Scientifiques de l'Aude, Carcassonne: 1-99.
- COURTESOLE R., PILLET J. & VIZCAÏNO D. 1988. — *Stratigraphie et paléontologie du Cambrien moyen gréseux de la Montagne Noire (versant méridional)*. Société d'Études Scientifiques de l'Aude, Carcassonne: 1-55.
- BLAINVILLE H. M. DE 1830. — *Zoophytes. Dictionnaire des Sciences Naturelles, tome soixantième*. Zooph-Zyt. Levrault, Strasbourg; Le Normant, Paris: 1-546.
- DEAN J. 1999. — What makes an ophiuroid? A morphological study of the problematic Ordovician stelleroid *Stenaster* and the palaeobiology of the earliest asteroids and ophiuroids. *Zoological Journal of the Linnean Society* 126 (2): 225-250. <https://doi.org/10.1111/j.1096-3642.1999.tb00154.x>
- DEAN SHACKLETON J. D. 2005. — Skeletal homologies, phylogeny and classification of the earliest asterozoan echinoderms. *Journal of Systematic Palaeontology* 3 (1): 29-114. <https://doi.org/10.1017/S1477201905001525>
- DESTOMBES J. 1960. — Sur l'extension du Trémadoc dans le Sud marocain. *Comptes Rendus de la Société des Sciences naturelles et physiques du Maroc* 3: 45-47.
- DESTOMBES J., HOLLARD H. & WILLEFERT S. 1985. — Lower Palaeozoic Rocks of Morocco, in HOLLAND C. H. (ed.), *Lower Palaeozoic Rocks of the World. 4. Lower Palaeozoic of North Western - Central Africa*. Wiley, Chichester & New York: 91-336.
- DÖDERLEIN L. 1920. — Die Asteriden der Siboga-Expedition 2: Die Gattung *Luidia* und ihre Stammesgeschichte. *Siboga-Expedition Monograph* 46b: 193-293.
- DONOVAN S. K. & SAVILL J. J. 1988. — *Ramseyocrinus* (Crinoidea) from the Arenig of Morocco. *Journal of Paleontology* 62 (2): 283-285. <https://doi.org/10.1017/S0022336000029929>
- DRAGE H. B., LEGG D. A. & DALEY A. C. 2023. — Novel marrellomorph moulting behaviour preserved in the Lower Ordovician Fezouata Shale, Morocco. *Frontiers in Ecology and Evolution* 11: 1226924. <https://doi.org/10.3389/fevo.2023.1226924>
- DUPICHAUD C., LEFEBVRE B., MILNE C. H., MOOI R., NOHEJLOVÁ M., ROCH R., SALEH F. & ZAMORA S. 2023. — Solutan echinoderms from the Fezouata Shale Lagerstätte (Lower Ordovician, Morocco): diversity, exceptional preservation, and palaeoecological implications. *Frontiers in Ecology and Evolution* 11: 1290063. <https://doi.org/10.3389/fevo.2023.1290063>
- EBBESTAD J. O. R. 2016. — Gastropoda, Tergomya and Paragastropoda (Mollusca) from the Lower Ordovician Fezouata Formation, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 87-96. <https://doi.org/10.1016/j.palaeo.2016.01.003>
- ELAOUAD-DEBBAJ Z. 1984. — Acritarches et chitinozoaires de l'Arenig-Llanvirn de l'Anti-Atlas (Maroc). *Review of Palaeobotany and Palynology* 43 (1-3): 67-88. [https://doi.org/10.1016/0034-6667\(84\)90027-7](https://doi.org/10.1016/0034-6667(84)90027-7)
- ELAOUAD-DEBBAJ Z. 1988. — Acritarches et chitinozoaires du Tremadoc de l'Anti-Atlas central (Maroc). *Revue de Micropaléontologie* 31: 85-128.
- ERWIN D. H., LAFLAMME M., TWEEDT S. M., SPERLING E. A., PISANI D. & PETERSON K. J. 2011. — The Cambrian conundrum: Early divergence and later ecological success in the early history of animals. *Science* 334 (6059): 1091-1097. <https://doi.org/10.1126/science.1206375>
- FAU M., WRIGHT D. F., EWING T. A. M., GALE A. S. & VILLIER L. 2024. — Phylogenetic and taxonomic revisions of Jurassic sea stars support a delayed evolutionary origin of the Asteroidea. *PeerJ* 12: e18169. <https://doi.org/10.7717/peerj.18169>
- FEIST R. & COURTESOLE R. 1984. — Découverte du Cambrien supérieur à trilobites de type est-asiatique dans la Montagne Noire (France méridionale). *Comptes-rendus hebdomadaires des séances de l'Académie des Sciences de Paris* 298: 177-182.
- FELL H. B. 1948. — Echinoderm embryology and the origin of chordates. *Biological Reviews* 23: 81-107. <https://doi.org/10.1111/j.1469-185X.1948.tb00458.x>
- FELL H. B. 1963a. — The phylogeny of sea-stars. *Philosophical Transactions of the Royal Society B* 246 (735): 381-435. <https://doi.org/10.1098/rstb.1963.0010>
- FELL H. B. 1963b. — A new family and genus of Somasteroidea. *Transactions of the Royal Society of New Zealand, Zoology* 3 (13): 143-146.
- FELL H. B. 1963c. — The evolution of the echinoderms. *The Smithsonian Report for 1962* (4559): 457-490.
- FORBES E. 1839. — On the Asteroidea of the Irish Sea. *Memoirs Wernerian Natural History Society of Edinburgh* 8: 113-129.
- FRAGA M. C. & VEGA C. S. 2024. — How does rapid burial work? New insights from experiments with echinoderms. *Palaeontology* 67 (2): e12698, 1-10. <https://doi.org/10.1111/pala.12698>
- GLADWELL D. J. 2018. — Asterozoans from the Ludlow Series (Upper Silurian) of Leintwardine, Herefordshire, UK. *Papers in Paleontology* 4 (1): 101-160. <https://doi.org/10.1002/spp2.1101>
- GLASS A., BLAKE D. B. & LEFEBVRE B. 2024. — An unusual new ophiuroid (Echinodermata) from the Late Ordovician (early Katian) of Morocco. *Comptes Rendus Palevol* 23 (25): 401-415. <https://doi.org/10.5852/cr-palevol2024v23a25>
- GOLDMAN D., SADLER P. M. & LESLIE S. A. 2020. — The Ordovician Period, in GRADSTEIN F. M., OGG J. G., SCHMITZ M. D. & OGG G. M. (eds), *Geologic Time Scale 2020*. Vol. 2. Elsevier, Amsterdam: 631-694. <https://doi.org/10.1016/B978-0-12-824360-2.00020-6>
- GORZELAK P. & SALAMON M. A. 2013. — Experimental tumbling of echinoderms – Taphonomic patterns and implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 386: 569-574. <https://doi.org/10.1016/j.palaeo.2013.06.023>
- GRAY J. E. 1840. — A synopsis of the genera and species of the class Hypostoma (*Asterias* Linnaeus). *The Annals and Magazine of Natural History* 6: 175-184, 275-290.

- GRAY J. E. 1871. — Description of *Platasterias*, a new genus of Astropectinidae from Mexico. *Proceedings of the Zoological Society of London* 1871 (1): 136-137. <https://www.biodiversitylibrary.org/page/28553937>
- GREGORY J. W. 1899. — On *Lindstromaster* and the classification of the palaeasteroids. *Geological Magazine* 6 (8): 341-354. <https://doi.org/10.1017/S0016756800142384>
- GUTIÉRREZ-MARCO J. C. & MARTIN E. L. O. 2016. — Biostratigraphy and palaeoecology of Lower Ordovician graptolites from the Fezouata Shale (Moroccan Anti-Atlas). *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 35-49. <https://doi.org/10.1016/j.palaeo.2016.07.026>
- HUNTER A. W. & ORTEGA-HERNÁNDEZ J. 2021. — A new somasteroid from the Fezouata Lagerstätte in Morocco and the Early Ordovician origin of Asterozoa. *Biology Letters* 17 (1): 20200809. <https://doi.org/10.1098/rsbl.2020.0809>
- JAÉKEL O. 1923. — Zur Morphogenie der Asterozoa. *Paläontologische Zeitschrift* 5: 344-350. <https://doi.org/10.1007/BF03160383>
- JELL P. A. & COOK A. G. 2020. — New Carboniferous ophiuroid from central coastal New South Wales. *Alcheringa* 44 (4): 520-527. <https://doi.org/10.1080/03115518.2020.1837240>
- KRÖGER B. & EVANS D. H. 2011. — Review and palaeoecological analysis of the late Tremadocian-early Floian (Early Ordovician) cephalopod fauna of the Montagne Noire, France. *Fossil Record* 14: 5-34. <https://doi.org/10.1002/mmng.201000013>
- KRÖGER B. & LEFEBVRE B. 2012. — Palaeogeography and palaeoecology of early Floian (Lower Ordovician) cephalopods from the Upper Fezouata Formation, Anti-Atlas, Morocco. *Fossil Record* 15 (2): 61-75. <https://doi.org/10.1002/mmng.201200004>
- LAIBL L., GUÉRIAU P., SALEH F., PÉREZ-PERIS F., LUSTRI L., DRAGE H. B., BATH ENRIGHT O. G., POTIN G. J. M. & DALEY A. C. 2023. — Early developmental stages of a Lower Ordovician marrellid from Morocco suggests simple ontogenetic niche differentiation in early euarthropods. *Frontiers in Ecology and Evolution* 11: 1232612. <https://doi.org/10.3389/fevo.2023.1232612>
- LAMARCK J. B. P. A. DE 1816. — *Stellerides. Histoire naturelle des animaux sans vertèbres*. Ed. 1.2. Imprimerie Abel Lanoë, Paris: 522-568.
- LEFEBVRE B. 2007. — Early Palaeozoic palaeobiogeography and palaeoecology of stylophoran echinoderms. *Palaeogeography, Palaeoclimatology, Palaeoecology* 245 (1-2): 156-199. <https://doi.org/10.1016/j.palaeo.2006.02.021>
- LEFEBVRE B. & BOTTING J. P. 2007. — First report of the mitrate *Peltocystis cornuta* Thorall (Echinodermata, Stylophora) in the Lower Ordovician of central Anti-Atlas (Morocco). *Annales de Paléontologie* 93 (3): 183-198. <https://doi.org/10.1016/j.annpal.2007.06.003>
- LEFEBVRE B. & FATKA O. 2003. — Palaeogeographical and palaeoecological aspects of the Cambro-Ordovician radiation of echinoderms in Gondwanan Africa and peri-Gondwanan Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology* 195 (1-2): 73-97. [https://doi.org/10.1016/S0031-0182\(03\)00303-1](https://doi.org/10.1016/S0031-0182(03)00303-1)
- LEFEBVRE B., SUMRALL C. D., SHROAT-LEWIS R. A., REICH M., WEBSTER G. D., HUNTER A. W., NARDIN E., ROZHNOV S. V., GUENSBURG T. E., TOUZEAU A., NOAILLES F. & SPRINKLE J. 2013. — Palaeobiogeography of Ordovician echinoderms, in HARPER D. A. T. & SERVAIS T. (eds), *Early Palaeozoic Biogeography and Palaeogeography. Geological Society, London, Memoirs* 38: 173-198. <https://doi.org/10.1144/M38.14>
- LEFEBVRE B., ALLAIRE N., GUENSBURG T. E., HUNTER A. W., KOURAÏSS K., MARTIN E. L. O., NARDIN E., NOAILLES F., PITTET B., SUMRALL C. D. & ZAMORA S. 2016. — Palaeoecological aspects of the diversification of echinoderms in the Lower Ordovician of central Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 97-121. <https://doi.org/10.1016/j.palaeo.2016.02.039>
- LEFEBVRE B., GUTIÉRREZ-MARCO J. C., LEHNERT O., MARTIN E. L. O., NOWAK H., AKODAD M., EL HARIRI K. & SERVAIS T. 2018. — Age calibration of the Lower Ordovician Fezouata Lagerstätte, Morocco. *Lethaia* 51 (2): 296-311. <https://doi.org/10.1111/let.12240>
- LEFEBVRE B., GUENSBURG T. E., MARTIN E. L. O., MOOI R., NARDIN E., NOHEJLOVÁ M., SALEH F., KOURAÏSS K., EL HARIRI K. & DAVID B. 2019. — Exceptionally preserved soft parts in fossils from the Lower Ordovician of Morocco clarify stylophoran affinities within basal deuterostomes. *Geobios* 52: 27-36. <https://doi.org/10.1016/j.geobios.2018.11.001>
- LEFEBVRE B., NOHEJLOVÁ M., MARTIN E. L. O., KAŠIČKA L., ZICHA O. & GUTIÉRREZ-MARCO J. C. 2022. — New Middle and Late Ordovician cornute stylophorans (Echinodermata) from Morocco and other peri-Gondwanan areas, in HUNTER A. W., ÁLVARO J. J., LEFEBVRE B., VAN ROY P. & ZAMORA S. (eds), *The Great Ordovician Biodiversification Event: insights from the Tafilalt Biota, Morocco. Geological Society, London, Special Publications* 485: 345-522. <https://doi.org/10.1144/SP485>
- LEFEBVRE B., ÁLVARO J. J., GHIENNE J. F., HERBOSCH A., KOCH L., LOI A., MONCERET E., VERNIERS J., VIDAL M., VIZCAÍNO D. & SERVAIS T. 2023. — The Ordovician of France and neighbouring areas from Belgium and Germany, in HARPER D. A. T., LEFEBVRE B., PERCIVAL I. G. & SERVAIS T. (eds), *A Global Synthesis of the Ordovician System Part 1. Geological Society, London, Special Publications* 532: 375-408. <https://doi.org/10.1144/SP532-2022-268>
- LEHNERT O., NOWAK H., SARMIENTO G. N., GUTIÉRREZ-MARCO J. C., AKODAD M. & SERVAIS T. 2016. — Conodonts from the Lower Ordovician of Morocco - Contributions to age and faunal diversity of the Fezouata Lagerstätte and peri-Gondwana biogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 50-61. <https://doi.org/10.1016/j.palaeo.2016.03.023>
- LUSTRI L., GUÉRIAU P. & DALEY A. C. 2024. — Lower Ordovician synziphosurine reveals early euechelic diversity and evolution. *Nature Communications* 15: 3808. <https://doi.org/10.1038/s41467-024-48013-w>
- MADSEN F. J. 1966. — The Recent sea-star *Platasterias* and the fossil Somasteroidea. *Nature* 209: 1367. <https://doi.org/10.1038/2091367a0>
- MARTÍ MUS M. 2016. — A hyolithid with preserved soft parts from the Ordovician Fezouata Konservat-Lagerstätte of Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 122-129. <https://doi.org/10.1016/j.palaeo.2016.04.048>
- MARTIN E. L. O., PITTET B., GUTIÉRREZ-MARCO J. C., VANNIER J., EL HARIRI K., LEROSSEY-AUBRIL R., MASROUR M., NOWAK H., SERVAIS T., VANDENBROUCKE T., VAN ROY P., VAUCHER R. & LEFEBVRE B. 2016a. — The Lower Ordovician Fezouata Konservat-Lagerstätte from Morocco: age, environment and evolutionary perspectives. *Gondwana Research* 34: 274-283. <https://doi.org/10.1016/j.gr.2015.03.009>
- MARTIN E. L. O., VIDAL M., VIZCAÍNO D., VAUCHER R., SANSJOFRE P., LEFEBVRE B. & DESTOMBES J. 2016b. — Biostratigraphic and palaeoenvironmental controls on the trilobite associations from the Lower Ordovician Fezouata Shale of the central Anti-Atlas, Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 142-154. <https://doi.org/10.1016/j.palaeo.2016.06.003>
- MCKNIGHT D. G. 1975. — Classification of somasteroids and asteroids (Asterozoa: Echinodermata). *Journal of the Royal Society of New Zealand* 5 (1): 13-19. <https://doi.org/10.1080/03036758.1975.10419376>
- MIKULÁS R. 1992. — The ichnogenus *Asteriacites*: paleoenvironmental trends. *Vestník Českého geologického ústavu* 67: 423-433.
- MILLER J. S. 1821. — *A Natural History of the Crinoidea or Lily-Shaped Animals, with Observations on the Genera Asteria, Euryale, Comatula and Marsupites*. Bryan, Bristol: 1-150.

- MILLER S. A. 1881. — Description of some new and remarkable crinoids and other fossils of the Hudson River Group. *Journal of the Cincinnati Society of Natural History* 4: 69-77.
- MOOI R. & DAVID B. 2000. — What a new model of skeletal homologies tells us about asteroid evolution. *American Zoologist* 40 (3): 326-339. [https://doi.org/10.1668/0003-1569\(2000\)040\[0326:WANMOS\]2.0.CO;2](https://doi.org/10.1668/0003-1569(2000)040[0326:WANMOS]2.0.CO;2)
- NOWAK H., SERVAIS T., PITTET B., VAUCHER R., AKODAD M., GAINES R. R. & VANDENBROUCKE T. R. A. 2016. — Palynomorphs of the Fezouata Shale (Lower Ordovician, Morocco): age and environmental constraints of the Fezouata Biota. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 62-74. <https://doi.org/10.1016/j.palaeo.2016.03.007>
- PAUL C. R. C. & SMITH A. B. 1984. — The early radiation and phylogeny of echinoderms. *Biological Reviews* 59: 443-481.
- PHILIP G. M. 1965. — Ancestry of sea-stars. *Nature* 208: 766-768. <https://doi.org/10.1038/208766a0>
- POLECHOVÁ M. 2016. — The bivalve fauna from the Fezouata Formation (Lower Ordovician) of Morocco and its significance for palaeobiogeography, palaeoecology and early diversification of bivalves. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 155-169. <https://doi.org/10.1016/j.palaeo.2015.12.016>
- POTIN G. J. M., GUÉRIAU P. & DALEY A. C. 2023. — Radiodont frontal appendages from the Fezouata Biota (Morocco) reveal high diversity and ecological adaptations to suspension-feeding during the Early Ordovician. *Frontiers in Ecology and Evolution* 11: 1214109. <https://doi.org/10.3389/fevo.2023.1214109>
- RUEDEMANN R. 1933. — *Camptostroma*, a Lower Cambrian floating hydrozoan: *Proceedings U.S. National Museum* 82 (13): 1-8.
- SALEH F., PITTET B., SANSJOFFRE P., GUÉRIAU P., LALONDE S., PERRILLAT J. P., VIDAL M., LUCAS V., EL HARIRI K., KOURAÏSS K. & LEFEBVRE B. 2020a. — Taphonomic pathway of exceptionally preserved fossils in the Lower Ordovician of Morocco. *Geobios* 60: 99-115. <https://doi.org/10.1016/j.geobios.2020.04.001>
- SALEH F., LEFEBVRE B., HUNTER A. W. & NOHEJLOVÁ M. 2020b. — Fossil weathering and preparation mimic soft tissues in eocrinoid and somasteroid echinoderms from the Lower Ordovician of Morocco. *Microscopy Today* 28 (1): 24-28. <https://doi.org/10.1017/S1551929519001238>
- SALEH F., VAUCHER R., ANTCLIFFE J. B., DALEY A. C., EL HARIRI K., KOURAÏSS K., LEFEBVRE B., MARTIN E. L. O., PERRILLAT J. P., SANSJOFFRE P., VIDAL M. & PITTET B. 2021. — Insights into soft-part preservation from the Early Ordovician Fezouata Biota. *Earth Science Reviews* 213: 103464. <https://doi.org/10.1016/j.earscirev.2020.103464>
- SALEH F., VAUCHER R., VIDAL M., EL HARIRI K., LAIBL L., DALEY A. C., GUTIÉRREZ-MARCO J. C., CANDELA Y., HARPER D. A. T., ORTEGA-HERNÁNDEZ J., MA X., RIDA A., VIZCAÍNO D. & LEFEBVRE B. 2022. — New fossil assemblages from the Early Ordovician Fezouata Biota. *Scientific Reports* 12: 20773. <https://doi.org/10.1038/s41598-022-25000-z>
- SALEH F., LEFEBVRE B., DUPICHAUD C., MARTIN E. L. O., NOHEJLOVÁ M. & SPACCESI L. 2023. — Skeletal elements controlled soft-tissue preservation in echinoderms from the Early Ordovician Fezouata Biota. *Geobios* 81: 51-66. <https://doi.org/10.1016/j.geobios.2023.08.001>
- SALEH F., ANTCLIFFE J. B., BIROLINI E., CANDELA Y., CORTHÉSY N., DALEY A. C., DUPICHAUD C., GIBERT C., GUENSER P., LAIBL L., LEFEBVRE L., MICHEL S. & POTIN G. J. M. 2024. — Highly resolved taphonomic variations within the Early Ordovician Fezouata Biota. *Scientific Reports* 14: 20807. <https://doi.org/10.1038/s41598-024-71622-w>
- SCHUCHERT C. 1914. — *Fossilium Catalogus 1: Animalia, pars 3: Stellerioidea Palaeozoica*. Junk, Berlin: 1-53.
- SERPAGLI E., FERRETTI A., VIZCAÍNO D. & ÁLVARO J. J. 2007. — A new early Ordovician conodont genus from the Southern Montagne Noire, France. *Palaeontology* 50 (6): 1447-1457. <https://doi.org/10.1111/j.1475-4983.2007.00714.x>
- SMITH A. B. 1984. — Classification of the Echinodermata. *Palaeontology* 27: 431-459.
- SMITH A. B. & JELL P. A. 1990. — Cambrian edrioasteroids from Australia and the origin of starfishes. *Memoirs of the Queensland Museum* 28: 715-778.
- SPENCER W. K. 1914. — The British Palaeozoic Asterozoa. *Palaeontographical Society of London, Monograph, Part 1* (for 1913) 67: 1-56. <https://doi.org/10.1080/02693445.1914.12035566>
- SPENCER W. K. 1914-1940. — The British Palaeozoic Asterozoa. *Palaeontographical Society of London, Monograph, Parts 1-10* (for 1913-1940): 1-540.
- SPENCER W. K. 1916. — The British Palaeozoic Asterozoa. *Palaeontographical Society of London, Monograph, Part 2* (for 1915) 69 (335): 57-108. <https://doi.org/10.1080/02693445.1916.12035573>
- SPENCER W. K. 1918. — The British Palaeozoic Asterozoa. *Palaeontographical Society of London, Monograph, Part 3* (for 1916) 70 (338): 109-168. <https://doi.org/10.1080/02693445.1918.12088367>
- SPENCER W. K. 1919. — The British Palaeozoic Asterozoa. *Palaeontographical Society of London, Monograph, Part 4* (for 1917) 71 (342): 169-196. <https://doi.org/10.1080/02693445.1919.12035577>
- SPENCER W. K. 1927. — The British Palaeozoic Asterozoa. *Palaeontographical Society of London, Monograph, Part 7* (for 1925) 79 (366): 325-388. <https://doi.org/10.1080/02693445.1927.12035601>
- SPENCER W. K. 1951. — Early Palaeozoic starfish. *Philosophical Transactions of the Royal Society B* 235 (623): 87-129. <https://doi.org/10.1098/rstb.1951.0001>
- SPENCER W. K. & WRIGHT C. W. 1966. — Asterozoans, in MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology, Pt. U, Echinodermata* 3. Vol. 1. The Geological Society of America and The University of Kansas, Lawrence: U4-U107.
- SPRINKLE J. & GUENSBURG T. E. 2004. — Crinozoan, blastozoan, echinozoan, asterozoan, and homalozoan echinoderms, in WEBBY B. D., PARIS F., DROSER M. L. & PERCIVAL I. G. (eds), *The Great Ordovician Biodiversification Event*. Columbia University Press, New York: 266-280. <https://doi.org/10.7312/webb12678-027>
- SUMRALL C. D. & ZAMORA S. 2011. — Ordovician edrioasteroids from Morocco: faunal exchanges across the Rheic Ocean. *Journal of Systematic Palaeontology* 9 (3): 425-454. <https://doi.org/10.1080/14772019.2010.499137>
- THORAL M. 1935. — *Contribution à l'étude paléontologique de l'Ordovicien inférieur de la Montagne Noire et révision sommaire de la faune cambrienne de la Montagne Noire*. Imprimerie de la Charité, Montpellier: 1-362.
- THUY B. & STÖHR S. 2011. — Lateral arm plate morphology in brittle stars (Echinodermata: Ophiuroidea): new perspectives for ophiuroid micropaleontology and classification. *Zootaxa* 3013: 1-47. <https://doi.org/10.11646/zootaxa.3013.1.1>
- TORTELLO M. F., VIZCAÍNO D. & ÁLVARO J. J. 2006. — Early Ordovician agnostoid trilobites from the southern Montagne Noire, France. *Journal of Paleontology* 80 (3): 477-495. [https://doi.org/10.1666/0022-3360\(2006\)80\[477:EOATFT\]2.0.CO;2](https://doi.org/10.1666/0022-3360(2006)80[477:EOATFT]2.0.CO;2)
- UBAGHS G. 1953. — Classe des Stelléroïdes, in PIVETEAU J. (ed.), *Traité de Paléontologie* Tome 3. Masson et Cie, Paris: 774-842.
- UBAGHS G. 1967. — General characters of Echinodermata, in MOORE R. C. (ed.), *Treatise on Invertebrate Paleontology*. Part 5, Echinodermata 1. Vol. 1. The Geological Society of America and The University of Kansas, Lawrence: S3-S60.
- UBAGHS G. 1998. — Échinodermes nouveaux du Cambrien supérieur de la Montagne Noire (France méridionale). *Geobios* 31 (6): 809-829. [https://doi.org/10.1016/S0016-6995\(98\)80111-3](https://doi.org/10.1016/S0016-6995(98)80111-3)
- VAN ITEN H. & LEFEBVRE B. 2020. — Conulariids from the Lower Ordovician of the southern Montagne Noire, France. *Acta Palaeontologica Polonica* 65 (3): 629-639. <https://doi.org/10.4202/app.00728.2020>

- VAN ITEN H., MUIR L., SIMÕES M. G., LEME J. M., MARQUES A. C. & YODER N. 2016. — Palaeobiogeography, palaeoecology and evolution of Lower Ordovician conulariids and *Sphenothallus* (Medusozoa, Cnidaria), with emphasis on the Fezouata Shale of southern Morocco. *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 170-178. <https://doi.org/10.1016/j.palaeo.2016.03.008>
- VAN ROY P. & BRIGGS D. E. G. 2011. — A giant Ordovician anomalocaridid. *Nature* 473: 510-513. <https://doi.org/10.1038/nature09920>
- VAN ROY P., ORR P. J., BOTTING J. P., MUIR L. A., VINSTER J., LEFEBVRE B., EL HARIRI K. & BRIGGS D. E. G. 2010. — Ordovician faunas of Burgess Shale type. *Nature* 465: 215-218. <https://doi.org/10.1038/nature09038>
- VAN ROY P., BRIGGS D. E. G. & GAINES R. R. 2015. — The Fezouata fossils of Morocco; an extraordinary record of marine life in the Early Ordovician. *Journal of the Geological Society, London* 172: 541-549. <https://doi.org/10.1144/jgs2015-017>
- VAUCHER R., MARTIN E. L. O., HORMIÈRE H. & PITTET B. 2016. — A genetic link between Konzentrat- and Konservat-Lagerstätten in the Fezouata Shale (Lower Ordovician, Morocco). *Palaeogeography, Palaeoclimatology, Palaeoecology* 460: 24-34. <https://doi.org/10.1016/j.palaeo.2016.05.020>
- VAUCHER R., PITTET B., MARTIN E. L. O., LEFEBVRE B. & HORMIÈRE H. 2017. — A wave-dominated tide-modulated model for the Lower Ordovician of the Anti-Atlas. *Sedimentology* 64 (3): 777-807. <https://doi.org/10.1111/sed.12327>
- VIDAL M. 1996a. — Quelques Asaphidae (Trilobita) de la Formation de Saint-Chinian, Ordovicien inférieur, Montagne Noire (France) : systématique et paléoenvironnements. *Geobios* 29 (6): 725-744. [https://doi.org/10.1016/S0016-6995\(96\)80018-0](https://doi.org/10.1016/S0016-6995(96)80018-0)
- VIDAL M. 1996b. — Le modèle des biofaciès à trilobites : un test dans l'Ordovicien inférieur de l'Anti-Atlas, Maroc. *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Terre et des planètes* 327 (5): 327-333. [https://doi.org/10.1016/S1251-8050\(98\)80051-7](https://doi.org/10.1016/S1251-8050(98)80051-7)
- VIGUIER C. 1879. — *Anatomie comparée du squelette des stellérides. Thèse présentée à la Faculté des Sciences de Paris pour obtenir le grade de Docteur ès Sciences Naturelles*. A. Hennuyer, Paris: 1-250.
- VILLIER L., BRAYARD A., BYLUND K. G., JENKS J. F., ESCARGUEL G., OLIVIER N., STEPHEN D. A., VENNIN E. & FARA E. 2018. — *Superstesaster promissor* gen. et sp. nov., a new starfish (Echinodermata, Asteroidea) from the Early Triassic of Utah, USA, filling a major gap in the phylogeny of asteroids. *Journal of Systematic Palaeontology* 16 (5): 395-415. <https://doi.org/10.1080/14772019.2017.1308972>
- VINSTER J., VAN ROY P. & BRIGGS D. E. G. 2008. — Machaeridians are Palaeozoic armoured annelids. *Nature* 451: 185-188. <https://doi.org/10.1038/nature06474>
- VINSTER J., PARRY L., BRIGGS D. E. G. & VAN ROY P. 2017. — Ancestral morphology of crown-group molluscs revealed by a new Ordovician stem aculiferan. *Nature* 542: 471-474. <https://doi.org/10.1038/nature21055>
- VIZCAÍNO D. & ÁLVARO J. J. 2003. — Adequacy of the Early Ordovician trilobite record in the southern Montagne Noire (France): biases for biodiversity documentation. *Transactions of the Royal Society of Edinburgh, Earth Sciences* 93 (4): 393-401. <https://doi.org/10.1017/S0263593300000493>
- VIZCAÍNO D. & LEFEBVRE B. 1999. — Les échinodermes du Paléozoïque inférieur de Montagne Noire : biostratigraphie et paléodiversité. *Geobios* 32 (2): 353-364. [https://doi.org/10.1016/S0016-6995\(99\)80049-7](https://doi.org/10.1016/S0016-6995(99)80049-7)
- VIZCAÍNO D., ÁLVARO J. J. & LEFEBVRE B. 2001. — The Lower Ordovician of the southern Montagne Noire. *Annales de la Société Géologique du Nord* 8: 213-220.

Submitted on 23 March 2025;
accepted on 31 May 2025;
published on 4 November 2025.