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Daniel B. BLAKE & Bertrand LEFEBVRE

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Ordovician *Petraster* Billings, 1858 (Asteroidea: Echinodermata) and early asteroid skeletal differentiation

Daniel B. BLAKE
Departement 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, ENSL, CNRS, LGL-TPE,
43 boulevard du 11 Novembre, F-69622 Villeurbanne (France)
bertrand.lefebvre@univ-lyon1.fr (corresponding author)

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ABSTRACT

A large and taxonomically diverse collection of Ordovician Asterozoa from France and Morocco enables new insights into the early evolution of the subphylum. Available specimens of both Asteroidea and Stenuroidea are comparatively few, the collection dominated by Ophiuroidea and to a lesser extent, Somasteroidea. Nearly all the asteroid specimens are assigned to *Petraster* Billings, 1858; *P. caidramiensis* n. sp. is differentiated based on the complexity of the extraxial skeleton. The genus *Petraster* is reviewed. Another asteroid fragment, Euaxosida sp. A, is too incomplete to assign below the ordinal level. Among species of *Petraster*, the extraxial skeleton suggests homoplastic emergence of ossicular series definition whereas evolution of ambulacral axial-adaxial series expressions was conservative. The stemward asteroid axial/adaxial configuration is considered largely a plesiomorphic derivative of the somasteroid condition. Ossicular details of all series, however, differ among *Petraster* species. Euaxosida sp. A also offers oral-surface expressions suggestive of a transitional status. Differences among ossicular series expressions exemplify concerns surrounding interpretation of early asterozoan phylogeny and taxonomy.

KEY WORDS
Asteroidea,
Euaxosida,
Ordovician,
morphological evolution,
new species.

RÉSUMÉ

Le genre ordovicien Petraster *Billings, 1858 (Asteroidea: Echinodermation) et la différenciation du squelette chez les premiers astéroïdes.*

Les faunes particulièrement abondantes et diversifiées d'astérozoaires ordoviciens de France et du Maroc apportent des connaissances nouvelles sur les premiers stades de la diversification au sein de ce sous-phylum. Ces assemblages sont dominés par les Ophiuroidea et, dans une moindre mesure, les Somasteroidea, tandis qu'Asteroidea et Stenuroidea y sont très peu représentés. Parmi les astéroïdes, la quasi-totalité des échantillons sont attribués au genre *Petraster* Billings, 1858 ; ce genre est révisé et *P. caidramiensis* n. sp. est décrit. Un autre fragment d'astéroïde, Euaxosida sp. A, est trop incomplet pour être identifié en deçà du niveau ordinal. L'expression du squelette extraxial au sein des différentes espèces du genre *Petraster* permet de mettre en évidence plusieurs paliers évolutifs durant l'évolution des premiers astéroïdes, ainsi que de potentielles homoplasies. Malgré de petites différences interspécifiques, l'expression des séries ambulacraires axiales et adaxiales semble, au contraire, très conservative et leur configuration étroitement liée à l'origine des Asteroidea. La morphologie de la face orale d'Euaxosida sp. A suggère qu'il s'agit probablement d'une forme de transition. L'histoire de la différenciation du squelette des astéroïdes est particulièrement difficile à interpréter en raison des variations observées dans l'expression des séries ossiculaires.

MOTS CLÉS
Asteroidea,
Euaxosida,
Ordovicien,
évolution
morphologique,
espèce nouvelle.

INTRODUCTION

Water-vascular tissues and their skeletal enclosure –the axial or ambulacral ossicles together with the adaxial or adambulacral ossicles– are fundamental to asterozoan organization and function, and once the basic ambulacral column configuration was established at the onset of subphylum history, evolutionary changes were limited. The remainder of the skeleton, the extraxial, is under the more immediate influence of local environmental conditions, and through time, homoplastic extraxial morphologies emerged among lineages. Axial and adaxial ambulacral construction of species of *Petraster* Billings, 1858, are comparatively uniform whereas the more varied extraxial expressions offer insights into complexity of early asteroid evolution. Extraxial variation cannot be simply linked to environmental specifics. Known *Petraster* occurrences, however, are too late in time to represent more than then-surviving indicators of earlier events. Euaxosida sp. A configuration also suggests early steps in asteroid evolution. Specificities of ossicular form –e.g. "paxilliform", "platelike"– are issues apart from skeletal series definition.

Following sections treating geologic setting and terminology, the taxonomy of *Petraster* is summarized, and succeeded by a discussion section interpreting morphological complexity. Species of *Petraster* are illustrated in figures one to six, specimens illustrating inferred phylogenetically significant variation in skeletal construction are illustrated in figures seven to ten.

GEOLOGY AND STRATIGRAPHIC DISTRIBUTION OF NEW SPECIMENS FROM FRANCE AND MOROCCO

In spite of numerous recent discoveries, the fossil record of the early diversification of all main asterozoan clades (asteroids, ophiuroids, somasteroids, and stenuroids) remains extremely scarce and limited to the Lower Ordovician of two distinct paleobiogeographic areas (Lefebvre *et al.* 2013). The equatorial shelves of Laurentia (modern western United States: Idaho, Nevada, and Utah) have yielded remarkably diverse Early Ordovician asterozoan remains comprising asteroids (*Aerliceaster nexosus* Blake, Gahn & Guensburg, 2020b, *Eukrinaster ibexensis* Blake, Guensburg, Sprinkle & Sumrall, 2007, and *Eriaster ibexensis* Blake & Guensburg, 2005), somasteroids (*Ophioxenikos langenheimi* Blake & Guensburg, 1993), and problematic taxa, unassigned to any particular asterozoan class (*Falloaster anquiroisitus* Blake, Gahn & Guensburg, 2020a).

The high-latitude regions of the Mediterranean Province (France and Morocco) and nearby areas from Avalonia (United Kingdom) represent the second diversity hotspot for Early Ordovician asterozoans. In the Montagne Noire (southern France), the Saint-Chinian Formation (late Tremadocian) has yielded the most diverse assemblage of early asterozoans including somasteroids (*Chinianaster levyi* Thoral, 1935, *Villebrunaster thorali* Spencer, 1951, and *Thoralaster spiculiformis* Dean Shackleton, 2005), and stenuroids (*Pradesura jacobi* (Thoral, 1935)) (see Thoral 1935; Spencer 1951; Fell 1963; Vizcaïno & Lefebvre 1999; Dean Shackleton 2005; Blake 2013; Blake & Guensburg 2015). In this region, yet undescribed ophiuroids and stenuroids (cf. MHNT.PAL.2014.0.010, UCBL-FSL 170968-972, 424938-439, 712008, 712010, 712021, 712093-095, 712101) are also present in the Landeyran Formation (late Floian); much material, however, is fragmentary and not readily identified. In the Anti-Atlas (southern Morocco), the Fezouata Shale (Tremadocian–Floian) has also yielded relatively abundant asterozoan remains, but belonging exclusively to somasteroids, e.g. *Villebrunaster fezouataensis* (Hunter & Ortega-Hernández, 2021) (see also Lefebvre *et al.* 2016; Blake & Hotchkiss 2022). In the Early Ordovician, the micro-continent Avalonia had just begun to rift away from Gondwana (Cocks & Fortey 2009). Consequently, on both sides of the opening Rheic Ocean, faunal affinities remain strong between Avalonian and Mediterranean echinoderm assemblages (Lefebvre *et al.* 2013). A single asteroid, *Petraster*? *ramseyensis* (Hicks, 1873) (see below), has been described so far in the Lower Ordovician of Avalonia (Wales).

In marked contrast with their Early Ordovician counterparts, later asterozoan faunas from the Middle and Upper Ordovician of France and Morocco have been little studied. The aim of this paper focusing on the asteroid genus *Petraster* is thus to contribute to a wider project devoted to the still poorly known diversification of asterozoans in high-latitude regions of the Mediterranean Province during the Ordovician. In recent years, several new occurrences of asterozoans were described in the Darriwilian and the Katian of the Armorican Massif (western France; Hunter *et al.* 2007; Blake *et al.* 2016). One of them, *Petraster crozonensis* Blake, Guensburg & Lefebvre, 2016, is redescribed here (see below), and its stratigraphic position reevaluated. The two known specimens of *P. crozonensis* (holotype LPB 15174 and paratype LPB 15175) were collected by E. Clarkson in 1971 during the field trip organized during the 1st International Conference on the Ordovician and Silurian systems (Babin 1971). Both specimens were sampled in beige micaceous siltstones exposed behind the shower cabins of Morgat harbor, in Crozon (Finistère, France). This outcrop is no longer existing today, and the two specimens were tentatively assigned to the base of the Kermeur Formation (*Euconochitina tanvillensis* chitinozoan Zone, early Katian), based on their lithology (Blake *et al.* 2016). However, Y. Plusquellec (pers. comm., Sept. 2016) and P. Morzadec (pers. comm., Jan. 2022), who were both attending the 1971 field excursion, confirmed independently that the two specimens were originally collected in the same level as the mitrate *Aspidocarpus* Ubaghs, 1979 ("*Mitrocystites* sp." in Chauvel 1981; see Renaud *et al.* 2023), i.e., in the Morgat Member of the Postolonnec Formation (late Darriwilian). Consequently, the asteroid *Petraster crozonensis* occurs in the same stratigraphic interval (*Linochitina pissotensis* chitinozoan Zone, *Hustedograptus teretiusculus* graptolite Zone), where abundant remains of ophiuroids and stenuroids have been reported in the Andouillé, Mont de Besneville, Postolonnec, and Traveusot formations in the Armorican Massif (Tromelin & Lebesconte 1876; Tromelin 1877; Hunter *et al.* 2007; Blake *et al.* 2016).

Contrary to the situation in the Armorican Massif, no asterozoan remains have been documented so far in the Middle Ordovician of Morocco. In contrast, the occurrence of diverse and locally abundant asterozoan assemblages in the Upper Ordovician of the Tafilalt (eastern Anti-Atlas) has been regularly mentioned (Gutiérrez-Marco *et al.* 2003; Lefebvre *et al.* 2007, 2008, 2010, 2022; Hunter *et al.* 2010). Although most of these assemblages are dominated by yet undescribed ophiuroids, some of them have also yielded well-preserved remains of asteroids, including the material of *Petraster caidramiensis* n. sp., which is described below. Assessing the precise stratigraphic position of each asteroid-bearing level in the Tafilalt area is challenging, because of the absence of key index taxa (e.g. conodonts, graptolites, palynomorphs) in most fossiliferous localities. Moreover, contrary to the situation in the Central Anti-Atlas, where the Upper Ordovician succession consists of lithologically well-contrasted units (with the sandstones of the Upper Tiouririne Formation intercalated between the shale-dominated Lower and Upper Ktaoua formations), the Ktaoua Group is predominantly composed of coarse siltstones and sandstones in the Tafilalt (Destombes *et al.* 1985; Destombes 2006a, b, c; Álvaro *et al.* 2022). In the eastern Anti-Atlas, the identification of the stratigraphic position of asteroid levels thus relies both on direct field observations made with J. Destombes in Oct. 2010, and on indirect estimations obtained by reporting the precise GPS coordinates of the sites on the two corresponding 1:200.000 geological maps (Service géologique du Maroc 1986, 1988).

All available specimens of *P. caidramiensis* n. sp. and Euaxosida sp. A were originally collected in the field by R. and V. Reboul, D. Vizcaïno, and F. Auvray, and subsequently donated to the paleontological collections of Lyon 1 University (Villeurbanne, France), where they are now deposited (UCBL-FSL). Asteroid specimens belonging to the Auvray and Reboul collections are from three distinct localities, all situated in a small geographic area, in the eastern Maïder, south of the N12 road between Msissi and Rissani: ECR-F12 (Tarafin Signit), ECR-F19 (El Kraouia), and Isthlou (ECR-F6) (for locality details and map, see Nohejlová & Lefebvre 2022).

Five specimens of *P. caidramiensis* n. sp. and the single individual assigned to Euaxosida sp. A are from the stratigraphically oldest site (ECR-F12; early Katian, middle part of the Lower Ktaoua Formation). This locality yielded abundant, remarkably preserved remains of a taxonomically diverse benthic assemblage comprising brachiopods, bryozoans, crinoids, fully articulated machaeridians (*Plumulites* Barrande, 1872), rhombiferans (*Homocystites* Barrande, 1887), mitrate stylophorans, solutans (*Dendrocystites* Barrande, 1887), and trilobites (Nohejlová & Lefebvre 2022). A single specimen of *P. caidramiensis* n. sp. was found at ECR-F19. This site yielded a relatively diverse fauna, comparable to, but slightly younger (early Katian, upper part of the Lower Ktaoua Formation) than that occurring in ECR-F12 (Nohejlová & Lefebvre 2022). The stratigraphically youngest specimens of *P. caidramiensis* n. sp. were collected in two distinct levels at Isthlou (ECR-F6). One of them (UCBL-FSL 711739) was sampled in the uppermost beds of the Lower Ktaoua Formation (early Katian). It is associated with the solutan *Dendrocystites sedgwicki* (Barrande, 1867) (see Nohejlová & Lefebvre 2022). The second specimen (UCBL-FSL 711757) comes from the base of the overlying Upper Tiouririne Formation (middle Katian), which yielded a particularly rich and diverse benthic assemblage, including brachiopods, bryozoans, conulariids (*Pseudoconularia* Bouček, 1939), crinoids (*Euptychocrinus*? Brower, 1994, *Isthloucrinus* Botting, 2022, monobathrids indet., *Trichinocrinus*? Moore & Laudon, 1943), diploporitans, edrioasteroids (*Spinadiscus* Sumrall & Zamora, 2022), machaeridian annelids (*Plumulites*), ophiuroids, rhombiferans, mitrate stylophorans, and trilobites (e.g. illaenids, trinucleids) (Lebrun 2018; Botting 2022; Lefebvre *et al.* 2022; Sumrall & Zamora 2022; Van Iten *et al.* 2022).

Locality details and stratigraphic position of specimens of *P. caidramiensis* n. sp. belonging to the Vizcaïno collection (including the holotype, UCBL-FSL 712025) are not known precisely. Labels indicate they are from the El Caïd Rami area, which is named after a dried river (Oued El Caïd Rami) located a few kilometers away from the three above mentioned sites, north of the N12 road between Msissi and Rissani. The Lower Ktaoua and Upper Tiouririne formations are largely exposed in the classical El Caïd Rami area, where numerous fossiliferous sites (e.g. ECR-F2, ECR-F5) have been exploited in the early 2000s (see e.g. Lefebvre *et al.* 2007, 2010, 2022; Hunter *et al.* 2010). By comparison with the other occurrences of *P. caidramiensis* n. sp., it can be reasonably postulated that the stratigraphic position of specimens from the El Caïd Rami is probably comprised between the middle part of the Lower Ktaoua Formation and the base of the overlying Upper Tiouririne Formation (early-middle Katian).

Specimens from France and Morocco were compiled and latex casts prepared by BL, the casts forwarded to DBB, the latter author adding documentation available from other sources.

TERMINOLOGY OF THE ASTEROIDEA

Terminology begins with Spencer & Wright (1966) as reviewed by Dean Shackleton (2005) and Blake *et al.* (2020b). 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 generally abundant spines, granules, and pedicellariae seated on all primary ossicles except axials. Axial (or "ambulacral") ossicles form a double series along the axis of the arm. The unpaired terminal is at the arm tip. Mouth-angle ossicles are the proximal-most ossicles of the axial series. Axial ossicles articulate with the adaxial ossicles (adambulacrals are adaxials). The remainder of the skeleton is extraxial. The body is edged by a single or double series of more or less clearly differentiated marginal ossicles. Because the term "marginals" has been broadly applied within echinoderms with unclear implications of homology, the genetically neutral term ambital framework has been proposed (Blake 2013). A single marginal series has been judged to be homologous throughout stem-group asteroids, it recognized as inferomarginal. Because focus herein is on the implications of the aboral surface of *Petraster*, all skeletal components "above" the inferomarginals for convenience are referred to as "aboral", including a second superomarginal series. The axillary (or "odontophore") typically is a more or less clearly differentiated unpaired ossicle aligned with the inferomarginal series at the interbrachial midline of asteroids. Abactinal ossicles are above the marginal series. Among many asterozoans, a medial disk centrale can be recognized, it enclosed by rings 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. In many asteroids, lateral abactinal series or adradialia are aligned with midarm carinals. A hydropore or madreporite provides opening to the water-vascular system.

Abbreviations

Institutional abbreviations

GSC	Geological Survey of Canada, Ottawa;
GSI/I	Geological Survey of Ireland, Dublin;
IMNH	Idaho Museum of Natural History, Pocatello;
L	Manchester Museum, Manchester;
LPB	Université de Bretagne occidentale, Brest;
MHNT	Muséum d'histoire naturelle, Toulouse;
NHM	Natural History Museum, London;
TMM	University of Texas Museum of Paleontology, Austin;
UCBL-FSL	collections de paléontologie, Université Lyon 1, Villeurbanne;
UI-X	Prairie Research Institute, University of Illinois, Urbana-Champaign;
UMMP	University of Michigan, Museum of Paleontology, Ann Arbor;
USNM	National Museum of Natural History, Washington.

Other abbreviation

MAO	mouth-angle ossciles.

SYSTEMATIC PALEONTOLOGY

Remark

Ordinal and familial classification of Asteroidea follows Blake (2018).

Class ASTEROIDEA de Blainville, 1830
Order EUAXOSIDA Blake, 2018
Family Palasterinidae Gregory, 1899, revised Blake (2018: 23)

Genus *Petraster* Billings, 1858

Petraster Billings, 1858: 79.

Uranaster Gregory, 1899: 348. — Spencer & Wright 1966: 43.

Diagnosis. — Euaxosidans attaining moderate size, arm radius R reaching at least *c.* 35 mm; disk arched, arms subcylindrical, elongate. Abactinal ossicles small proportional to overall body size, irregular equidimensional to subspherical, bases commonly faceted; aboral ring, superomarginals, intermarginals, carinal series variably and not clearly differentiated, especially not on disk. Inferomarginal series well-defined. Superomarginals dorsal-lateral in position. Intermarginals thought to be limited to disk, in a single or irregular series.

Description

Palasterinid, disk size moderate, interbrachia narrowly rounded; arms elongate, outline triangular and gradually tapering to narrowly rounded tips; disk and arms probably moderately arched in life. Configuration of extraxial ossicles aboral to inferomarginals varied among species. Abactinals small relative to overall body size, somewhat varied in size and form, plate-like, granular, irregular spicular, or rod-like. Aboral ring, centrale not definitively recognized. Carinal series obscure to moderately well-defined. Superomarginals enlarged relative to ossicles of adjacent series, approximately equidimensional, domal; disk superomarginals obscure in some species. Adradialia granular or spicular, variably developed. Intermarginals granular, variably developed. Madreporite where known circular, aboral; on larger specimens, can be partially enclosed by pair of enlarged, crescentic ossicles. Inferomarginals, adaxials well-developed, adaxials rectangular to equidimensional, domal, pustulate; enlarged accessory bases lacking. Inferomarginals on oral surface proximally, becoming marginal distally, abutting adaxials for at least most of arm length.

Axials nearly equidimensional to weakly rectangular, wider than long; radial water-vascular channel relatively broad; transverse ridge well-developed, podial basins approximately equally shared by subsequent axials. Adaxials approximately equidimensional, external surface texture similar to that of inferomarginals; adaxials more numerous than inferomarginals at least on disk, more nearly paired on arms. Oral disk

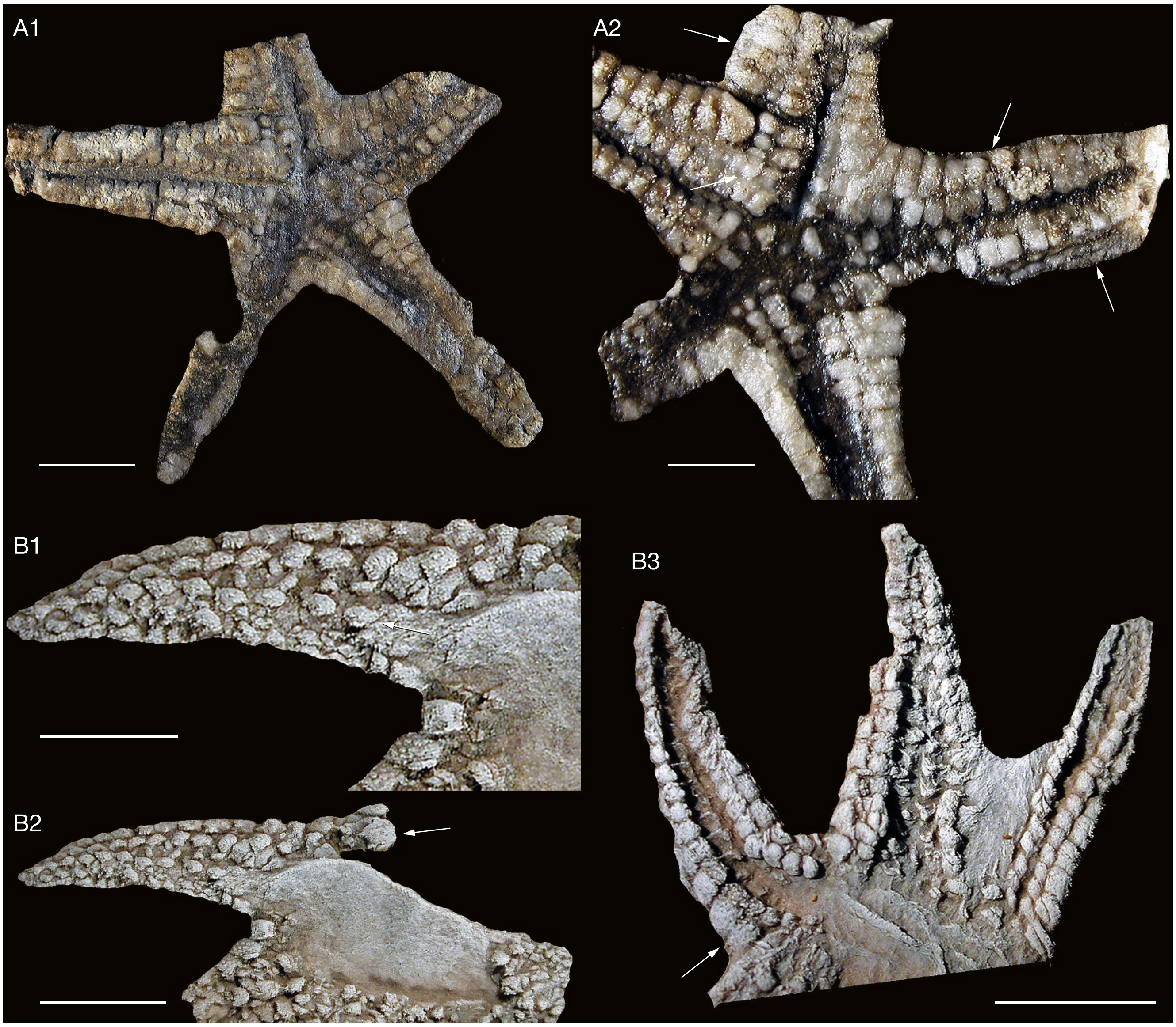

FIG. 1. — Problematic species of *Petraster* Billings, 1858: **A1**, **A2**, *Petraster rigidus* (Billings, 1858), generic type species; Trenton Limestone, Late Ordovician (Sandbian-early Katian), 45°026'37"N, 75°026'9"W, Ottawa, Canada; original specimen, holotype GSC 1401; **A1**, specimen remnant, surfaces of disk ossicles to left appearing largely unaltered, those to right more abraded thereby obscuring original surface appearances; **A2**, specimen wetted, axillary of interbrachium to left is triangular, possible second axillary (**lower left arrow**) immediately distal of MAO pair at base of single actinal series. Ossicles to right interbrachium altered but appearance unlike those to left interbrachium, significance of diagenetic alteration uncertain; upper two arrows mark position of inferomarginal near apparent termini of actinal series. Ossicles edging adaxial at one arm margin (**arrow to lower right**) appearing somewhat enlarged as compared to traces at other arm margins, the nature of the skeleton aboral to inferomarginals obscure; **B1**-**B3**, *Petraster*? *ramseyensis* (Hicks, 1873); Early Ordovician (early Arenig); Ramsey Island, Wales; latex casts; **B1**, **B2**, NHM E13707 = Manchester L10038, abactinals are differentiated, carinals (**B1**, **arrow**) bordered by small rectangular adradials, two marginal series; aboral disk largely lost, madreporite? (**B2**, **arrow**) remains; **B3**, NHM E13703 = Manchester L10036a distended specimen in oral aspect, ambulacra variously flattened, inferomarginals, adaxials, and axials dominate; possible axillary (**arrow**). Scale bars: A1, A2, B2, B3, 5 mm; B1, 3 mm.

ossicles variably developed. Axillary number where known one or two, actinal series present or absent, variably developed. Accessories where known including relatively small spinelets and granules; large spines not recognized.

REMARKS

Uranaster was synonymized with *Petraster* (Spencer & Wright 1966). The type species of *Petraster*, *P. rigidus* Billings (Fig. 1A1, A2), is incompletely known leading to the use of *P. kinahani* (Baily, 1879) as the generic standard of comparison (Dean Shackleton 2005). These interpretations are followed here.

Species inclusion in *Petraster* emphasizes irregularity of the skeleton aboral to the inferomarginals together with a fundamental uniformity of oral configuration. Five species are included, *P. ramseyensis* tentatively. *Petraster caidramiensis* n. sp., *P. crozonensis*, and *P. kinahani* are known from fairly complete specimens, in all three, aboral series (i.e., "above" the inferomarginals) of the arms are more clearly defined than those of the disk, in part because of limitations of preservation but also because disk ossicles appear less clearly differentiated. The subcylindrical proximal arm intervals of *Petraster* specimens were subject to compaction under sediment load exaggerating water-vascular channel breadth, the proportionately more robust distal arm intervals retaining a more natural water-vascular channel appearance.

Petraster rigidus (Billings, 1857) (Fig. 1A)

Palasterina rigidus Billings, 1857: 291.

Petraster rigidus – Billings 1858: 80, pl. 10, fig. 3. — Spencer 1914: 40. — Schuchert 1915: 141, pl. 27, fig. 5. — Spencer 1927: 359. — Spencer & Wright 1966: 43. — Blake 2018: 28, pl. 4, fig. 5.

Palaeaster matutina – Hall 1868: 294.

Type material. — **Holotype. Canada** • GSC 1401a, *Palasterina rigidus* Billings, 1857; an incomplete, weathered specimen, only the oral surface exposed.

Diagnosis. — *Petraster* species thought to exhibit two axillaries, one triangular and reaching the lateral margin, the second embedded; a single series of robust actinals well developed, it limited to disk.

Type locality and horizon. — Cobourg beds, Ottawa, 45°026’37”N, 75°026’9”W; Trenton Limestone, Sandbian-early Katian.

Description

Petraster in which arms are moderately elongate, R reaching at least *c.* 20 mm. Inferomarginals robust, rectangular, relatively wide on disk, more nearly equidimensional on arm; some ossicles appear to bear accessory pustules. Two available interbrachia of the holotype differ, one with a well-defined triangular axillary and a possible second small axillary enclosed on disk adjacent to MAO. Actinals on disk in well-defined single series. Second interbrachium, ossicular arrangement poorly preserved and ill-defined. Axillary, actinals not clearly defined. Adaxials rectangular, transversely elongate.

Remarks

The poorly known type species is similar to other species assigned to the genus based on overall form and the limited data available on oral-surface expression, including inferomarginal shape, disk configuration, axillary, and actinal expressions. The diagnosis focuses on expression of the better-preserved interbrachium. The skeleton aboral to inferomarginals is almost unknown, the madreporite, axials, and MAO unknown.

Posited presence of two axillaries serves to separate *P. rigidus* from other *Petraster* species except from *P. kinahani*, with specificities of expression differing between these two. The more lateral axillary is similar to the single axillary of *P. crozonensis*, the adjacent inferomarginals differ in outline. A few small elongate ossicles lateral to the inferomarginals of one arm appear unlike expressions among other species, although these ossicles as preserved appear dissimilar from traces exposed on other arms.

Petraster caidramiensis n. sp. (Figs 2; 3)

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Derivation of name. — The species name is based on the El Caid Rami area source of the holotype.

Type material. — **Holotype. Morocco** • UCBL-FSL 712025 [ao] (Vizcaïno coll.). Arm radius approximately 35 mm, disk radius approximately 11-13 mm; only limited distortion accompanied sediment compaction.

Paratypes. Morocco • Specimens are variously preserved, all incomplete. Specimens known from both surfaces marked “[ao]”, only aboral marked “[a]”, only oral marked “[o]”; assignment of some to species is tentative, these also marked “[?]” UCBL-FSL 711739 [o?], UCBL-FSL 711757 [ao], UCBL-FSL 712077 [o?], and UCBL-FSL 712820 [ao?] (Reboul coll.); UCBL-FSL 712024 [o], UCBL-FSL 712027 [o], and UCBL-FSL 712028 [a] (Vizcaïno coll.); UCBL-FSL 712910 [a?], UCBL-FSL 712914 [o?], UCBL-FSL 713032 [o], and UCBL-FSL 713034 [a] (Auvray coll.).

Diagnosis. — Aboral series of arms proportionately delicate, not tightly and closely abutted; many small accessories intercalated among the larger ossicles. Carinals, adradiallia recognized. Axillary similar in size to adjacent inferomarginals; polygonal, enclosed by marginals. Actinal ossicles few, enlarged. Axials bilateral at transverse ridge.

Material examined. — Three arms and the disk of the holotype, in aboral view, and one arm and a portion of the disk of the oral surface of the counterpart. Abactinals of the medial portion of the disk are collapsed into the disk. Paratypes are variously preserved, all incomplete.

Type locality and horizon. — El Caid Rami area, eastern Anti-Atlas, Morocco; Lower Ktaoua-Upper Tiouririne formations, early-middle Katian, Late Ordovician.

Description

Petraster in which arms are moderately elongate, R reaching at least *c.* 37 mm. Aboral series (i.e., all series aboral of inferomarginals) of arms proportionately delicate, not tightly and closely abutted; many small accessories intercalated among larger. Carinal series in part identified by positioning and alignment, series not demonstrably reaching central disk; carinals approximately equidimensional, ossicular central area enlarged, possibly flanged laterally. Arm adradialia appearing weakly aligned in single series, ossicles similar to, approximately aligned with carinals; carinal and adradial series possibly separated by granulate interareas. Madreporite on aboral disk, bordered laterally by enlarged, crescentic ossicles. Superomarginal series on arms clearly defined, differentiation weakening on disk. Arm superomarginals approximately equidimensional, central area of ossicle enlarged, successive ossicles appearing flanged; superomarginals approximately aligned in transverse series with both adjacent carinal and inferomarginal, the latter weakly exposed in aboral aspect. In oral aspect, inferomarginals of disk rectangular, aligned with and abutting adaxial series; appearing to become more nearly equidimensional, less clearly differentiated from adjacent ossicles on arms; surfaces of disk inferomarginals pustulate, possibly with thin, delicate spinelets, no enlarged spines. Intermarginals perhaps

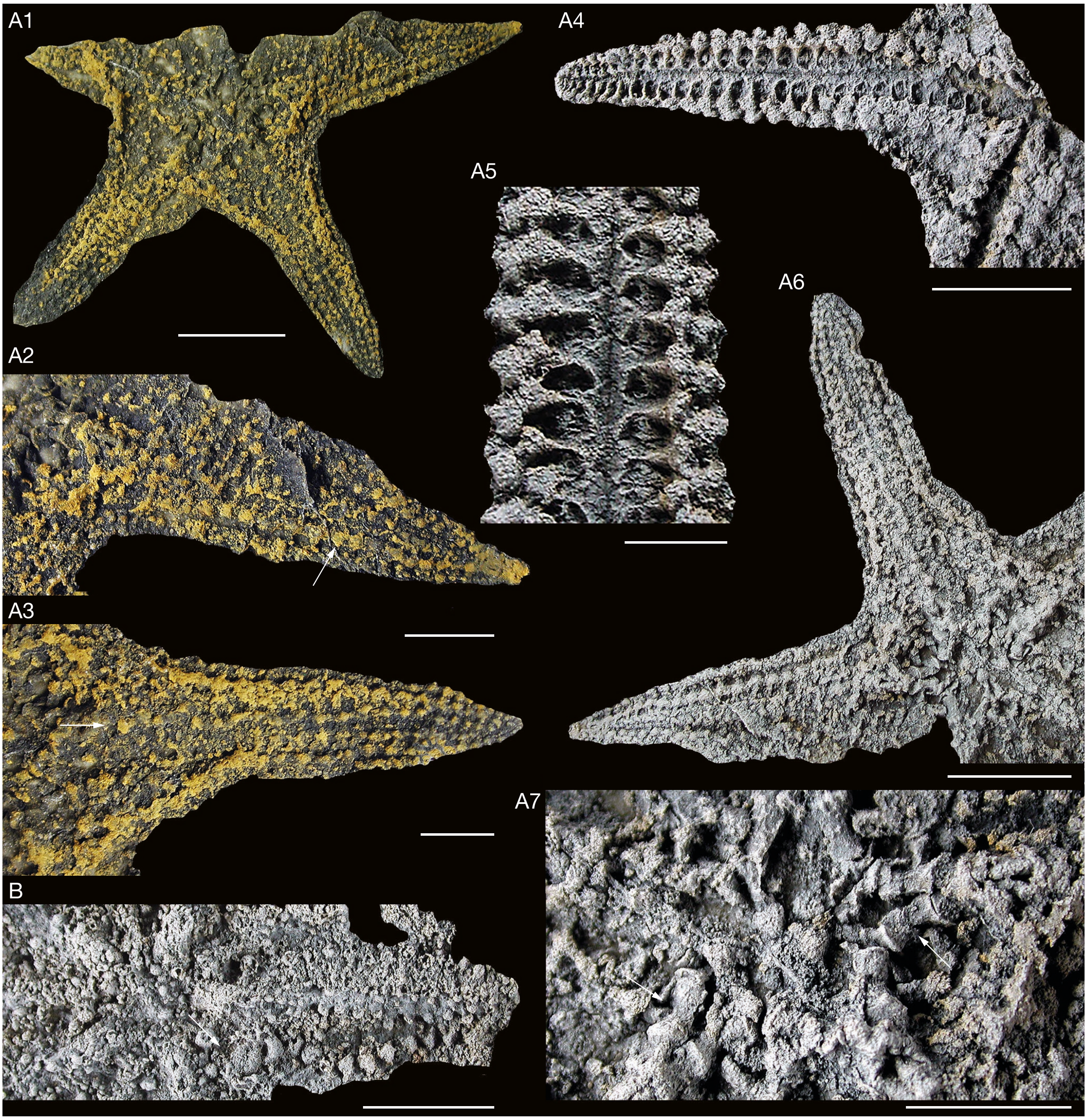

Fig. 2. — **A1**-**A7**, *Petraster caidramiensis* n. sp.; Lower Ktaoua/Upper Tiouririne formations, Late Ordovician (early–middle Katian); El Caid Rami area, Morocco; latex casts; holotype UCBL-FSL 712025: **A1**, aboral view of remnant; **A2**, **A3**, inclined, aboral views of "NE" and "SE" arms of (**A1**), **arrows** identify superomarginals (**A2**) and carinals (**A3**), adradialia weakly defined; **A4**, oral view; axillary abuts MAO, actinals obscure; **A5**, midarm axials, adaxials, inferomarginals; **A6**, **A7**, aboral views, extraxials small, irregular; circumorals dumbbell-shaped (**A7**, **arrows**); **B**, *Petraster caidramiensis*?; Lower Ktaoua Formation, Late Ordovician (early Katian); Tarafin Signit, Morocco; latex cast, UCBL-FSL 712910; madreporite (**arrow**) texture granular, bordered to right by crescentic ossicle; disk ossicles not differentiated. Scale bars: A1, A4, A6, B, 10 mm; A2, A3, A5, A7, 5 mm.

numerous on disk but recognition obscured by weakening of superomarginal definition; intermarginals appearing to reach or nearly reach arm tip. Axillary little enlarged relative to adjacent inferomarginals, polygonal, distal end truncated, proximal margin rounded. Actinal ossicles relatively few, quite large, similar in form to adjacent inferomarginals and axillary.

Axials approximately equidimensional, sequential axials abutted laterally, not overlapping, approximately bilateral at transverse ridge; transverse channel not well-defined. MAO robust; circumorals enlarged, dumbbell shaped. Adaxial preservation varied among specimens, appearing approximately equidimensional, thought to lack a prominent nose.

Remark

Petraster caidrami is separated from *P. crozonensis* and *P. kinahani* by presence of only moderately differentiated enlarged aboral arm ossicles with numerous small intercalated granular accessary ossicles; presence of a single pentameral axillary similar in size to adjacent inferomarginals; presence of abutted, bilateral axials, the transverse ridge "T"-shaped.

Petraster crozonensis Blake, Guensburg & Lefebvre, 2016 (Fig. 4)

Petraster crozonensis Blake, Guensburg & Lefebvre, 2016: 169, figs 6.1-6.9, 7.1, 7.2. — Blake 2018: pl. 2, fig. 16; pl. 5, figs 3, 4.

Diagnosis. — Aboral ossicles proportionately robust, uniform, closely fitted, smaller accessories not recognized. Carinals, adradialia recognized. Axillary enlarged, triangular, reaching disk margin. Actinal ossicles few if developed. Axial transverse ridge "J"-shaped.

Material examined. — Two incomplete specimens, LPB 15174, LPB 15175, E.N.K. Clarkson collection, Université de Bretagne occidentale, Brest, France.

Type locality and horizon. — Morgat harbor, Crozon, Finistère, France; Postolonnec Formation, Morgat Member, *Linochitina pissotensis* chitinozoan Zone, late Darriwilian, Middle Ordovician.

Description

Petraster in which arms are moderately elongate, R reaching at least *c.* 22 mm. Aboral series (i.e., all series aboral of inferomarginals) of arms appearing proportionately moderately robust and quite closely abutted; smaller accessories intercalated among larger not recognized. Carinals with bordering adradialia, superomarginals clearly developed, ossicles similar, ovate, thickened; inferomarginals as exposed in aboral aspect appearing enlarged relative to superomarginals; inferomarginals slightly offset from superomarginals. Disk superomarginals thought to be only weakly differentiated, recognition based on differentiation of three ossicle series, including intermarginals (Fig. 4B1). In oral aspect, inferomarginals robust, closely abutted, approximately equidimensional, ossicular sizes appearing to diminish in size abruptly on arms; form elliptical, bulbous. Axillary triangular, narrowing distally, barely reaching lateral edge of inferomarginals series. Actinal ossicles few and small if present.

Axials relatively wide, adradial ridge elongate, termini overlapping; transverse ridge broadly "J"-shaped, transverse water-vascular channel well-defined. Adaxials possibly elliptical and transversely elongate; weak nose possibly developed.

Remark

Petraster crozonensis is separated from *P. caidramiensis* n. sp. and *P. kinahani* by presence of clearly differentiated, aligned, and similar distal carinal, adradial, and superomarginal ossicles; arm intercalated granules absent; axial single, enlarged, triangular, reaching the disk margin; axials rectangular, overlapping, transverse ridge "J"-shaped.

Petraster kinahani (Baily, 1879) (Figs 5; 6)

Palasterina kinahani Baily, 1879: 56, fig. 6.

Uranaster kinahani – Gregory 1899: 348. — Schöndorf 1910: 225. — Schuchert 1915: 155. — Spencer 1916: 105. — Owen 1965: 567.

Petraster kinahani – Spencer & Wright 1966: 43, fig. 43.4. — Dean Shackleton 2005: 91, pl. 6, figs 5, 6; fig. 12C. — Blake 2018: pl. 2, fig. 16; pl. 5, figs 1, 2.

Diagnosis. — Arms proportionately elongate, tapering evenly. Aboral ossicles uniform, equidimensional, closely fitted; carinal, adradialia not definitively recognized; intercalated accessories not recognized. Two enclosed axillaries present, disk actinal field large. Axials rectangular, transverse ridge "L" shaped.

Material examined. — Latex casts of approximately 20 specimens, many fragmentary, poorly preserved; Geological Survey of Ireland, Natural History Museum, London.

Type locality and horizon. — Ballymoney Group (Sandbian; see Donovan *et al.* 1996), near Bannow, County Wexford, Ireland.

Description

Petraster in which arms are relatively elongate, R reaching at least *c.* 35 mm. Aboral ossicular series of arms approximately equidimensional and closely fitted; smaller accessories not recognized. Carinal series differentiation suggested by some weak alignment; adradialia not recognized. Madreporite on aboral disk of larger specimens bordered laterally by enlarged, crescentic ossicles. Enlarged, subcircular, aligned ossicles lateral to arm midline recognized as superomarginal, series differentiation weakening on disk. Inferomarginals robust, approximately equidimensional, weakly increasing in size on disk. Intermarginals present but irregularity of size and alignment obscures delineation. Axillaries represented by two approximately elliptical ossicles, the more distal small, abutting inferomarginal series. Actinal definition poorly known, actinals restricted to disk, proximal arms appearing small, equidimensional, irregular.

Axials approximately equidimensional, sequential axials abutted, not overlapping; transverse ridge broadly J-shaped, transverse channel well-defined. MAO pair narrow, circumorals not thought to be dumbbell shaped. Adaxials with prominent "nose" articulating with axial. Adaxials possibly elliptical, longitudinally elongate prominent nose developed.

Remarks

Petraster kinahani is separated from *P. caidramiensis* n. sp. and *P. crozonensis* by presence of distal abactinal arm ossicles that lack clear differentiation in form or into series; the absence of aboral intercalated granular accessories; the irregular arrangement of proximal superomarginals and intermarginals; the complex, multiossicular oral disk ossicular configuration with two axillaries; and equidimensional abutted axials with a "J"-shaped transverse ridge.

A small ambulacral area (Fig. 6A1) is problematic. One area (horizontal arrow to upper left) shows a series of five axial transverse ridges offset from prominent noses of adaxials, the displacement accompanying sediment compaction, whereas

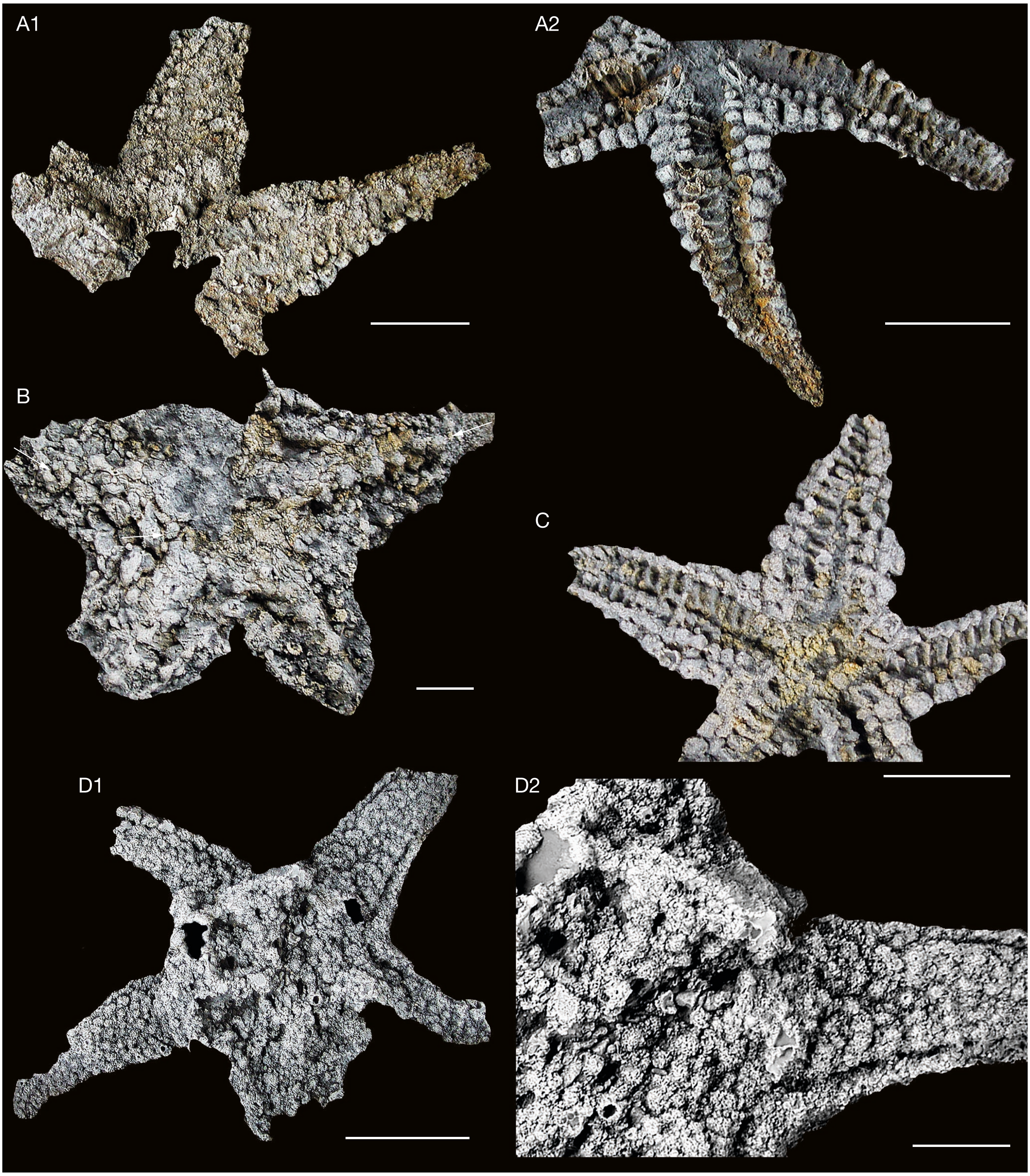

Fig. 3. — **A**-**C**, *Petraster caidramiensis* n. sp.; Upper Tiouririne Formation, Late Ordovician (middle Katian); Isthlou, Morocco; latex casts: **A1**, **A2**, paratype UCBL–FSL 711757; **A1**, aboral view, both marginal series remain, remainder of aboral ossicles obscured; **A2**, oral view, diamond-shaped axillary is enclosed by MAO and inferomarginals; MAO robust, mouth frame dilated; **B**, **C**, Lower Ktaoua Formation, Late Ordovician (early Katian); Tarafin Signit, Morocco; **B**, UCBL-FSL 713034; small individual, aboral view; superomarginal series (**upper left arrow**); madreporite? (**middle arrow**), carinal series (**right arrow**); **C**, paratype UCBL-FSL 713032; small individual, oral view, inferomarginal series, axillary well-defined, actinals not developed; **D1**, **D2**, *Petraster caidramiensis*?; Lower Ktaoua Formation, Late Ordovician (early Katian); El Caid Rami area, Morocco; UCBL-FSL 712028; only aboral surface available, carinals, part of ambital framework exposed. Scale bars: A1, A2, D2, 5 mm; B, C, 3 mm; D1, 10 mm.

another area (inclined arrow to lower left) suggests a series of five separate small ossicles between the axials and adaxials. Presence of an "extra" ossicle emplaced between the axial and adaxial is diagnostic of the Stenuroidea (Blake 2013). A similar expression was found in none of the other specimens of *P. kinahani*, the interval to lower left interpreted as preservational aberrancy while recognizing the occurrence might reflect paraphyly or polyphyly of the stenuroid condition.

Petraster*? *ramseyensis (Hicks, 1873)
(Fig. 1B)

Palasterina ramseyensis Hicks, 1873: 51, pl. 4, figs 21-23.

Palasterina? *ramseyensis* – Schuchert 1915: 154.

Uranaster ramseyensis – Spencer 1918: 109, pl. 4, figs 1-4; text figs 64-66. — Owen 1965: 567.

Petraster ramseyensis – Blake 2018: 24.

"*Petraster*" *ramseyensis* – Blake 2018: pl. 4, figs 3, 4.

DIAGNOSIS. — *Petraster*? with clearly differentiated carinal and adradial series, the latter rectangular and variously oriented, oblique to carinals.

MATERIAL EXAMINED. — Two specimens in the collections of the Manchester Museum; London NHM casts reviewed. Spencer (1918: 109) proposed the syntype Manchester L. 11037 = NHM E.13705 as "holotype".

TYPE LOCALITY AND HORIZON. — Ramsey Island, Wales; early Arenig (early Floian).

DESCRIPTION
Petraster? size uncertain, interpretation based on distorted available specimens, R *c.* 15 mm. Aboral disk unknown; arm abactinals robust, clearly differentiated into series. Carinals elliptical, subconical, appear to have a small accessory pustule. Adradialia appearing to be in a single series on each side of carinals series; adradials irregular, rectangular, oriented both nearly parallel as well as oblique to arm axis; series possibly not reaching arm tips. Madreporite? on aboral disk. Superomarginals of arms similar in overall appearance to carinals but larger, arrangement and orientation appearing somewhat irregular. Intermarginals unknown. Inferomarginals incompletely known, robust, in aboral aspect appearing rectangular in outline on arms, more nearly equidimensional in oral aspect; any enlargement of inferomarginals on disk unclear. One incomplete interbrachium suggests presence of axillary nearly reaching disk margin; actinal field small. Axials appearing approximately bilateral at transverse ridge, abutted, not overlapping. Mouth frame unknown. Adaxials equidimensional.

REMARKS
At the time of description, *ramseyensis* was assigned to *Palasterina*, the species subsequently transferred to *Uranaster* based on perceived strong similarities with '*Uranaster*' *kinahani* (Spencer 1918). *Uranaster* was synonymized with *Petraster* (Spencer & Wright 1966), but *ramseyensis* later was left unassigned at the generic level (Blake 2018). The Spencer (1918) generic interpretation is tentatively followed here, in part based on some aboral similarities with *P. caidramiensis* n. sp. and of the distal arm interval of *P. crozonensis*.

OTHER NAMES ASSOCIATED WITH *PETRASTER*

Branstrator (1982) based '*Petraster*' *wigleyi* from the Ordovician Bromide Formation of Oklahoma on a fragment free of enclosing matrix and consisting of most of one arm as judged by arm taper, and the proximal interval of a second, the two linked by a small portion of the disk margin. The sharply angular, evenly tapered arms are marked by a clearly demarcated carinal series, the carinals differing little from ossicles of the well-defined longitudinally and transversely aligned adjacent abactinal series. The transverse series ossicles are aligned with those of the carinal series as to yield a uniform overall arm appearance. Abactinals are proportionately small, uniform, and in aboral aspect appear approximately diamond-shaped and separated by small and uniform apparent papular pores. Of the disk, only the marginal sequence and a few associated ossicles remain. The ambulacral furrow is closed, the outer surfaces of the adaxials weakly transversely elongate and nearly equidimensional. The remainder of the adaxials are obscured and axials are not exposed. Only a single marginal series is developed, the ossicles robust, rectangular, larger than the adaxials, and fewer in number. A somewhat weakly differentiated axillary appears to be present.

As reconstructed by Branstrator (1982: fig. 76), a linear actinal series is developed on the disk, it as reconstructed similar to that of the type species *P. rigidus*. Small spinelets were reported (Branstrator 1982: 317). The concept of *Petraster* as developed here stresses irregularity of ossicular expression of the aboral skeleton, presence of two marginal series, and to a lesser extent, presence of cylindrical arms; '*P.*' *wigleyi* Branstator, 1982 is not in accord with these delineations and it is not assigned to *Petraster* herein.

Withers & Keble (1934) assigned three new species from the Silurian of Australia to *Petraster*, two from the Yarravian Series. An aboral arm surface and its ossicular configuration of *Petraster richi* are essentially in accord with the present concept of *Petraster*; however, data adequate for interpretation are not available and therefore species assignment is left in abeyance. Little data are available for the other two species names, these not further considered.

Palaeasterina speciosa Miller & Dyer, 1878, was assigned to *Petraster* (Schuchert 1915) and later recognized as the type species of *Jugiaster* Blake, 2007.

Family, genus, and species unknown

Euaxosida sp. A
(Fig. 7A1, A2)

MATERIAL EXAMINED. — UCBL-FSL 712909 (coll. Auvray), the oral surface of about one-half of a single specimen consisting of

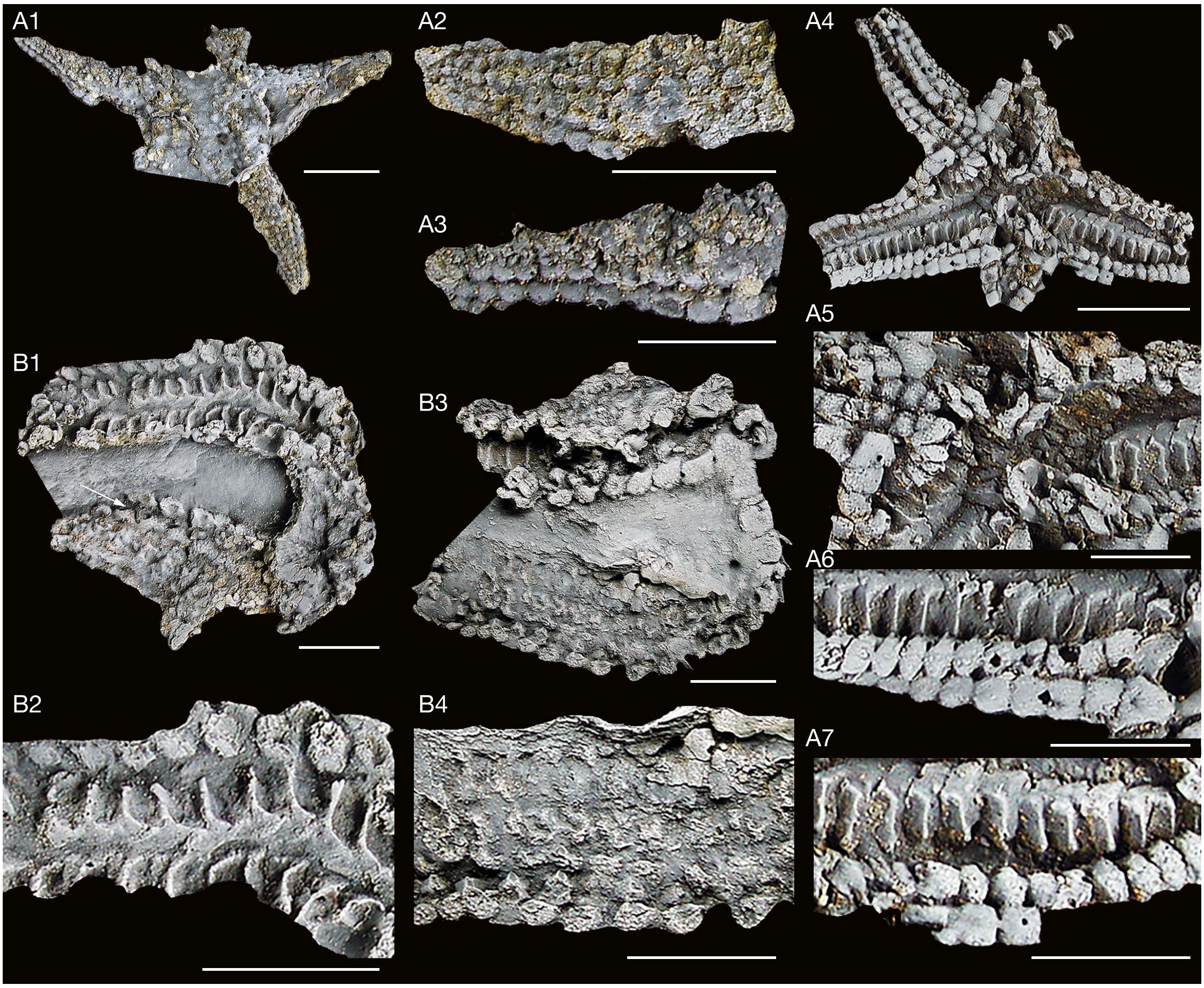

Fig. 4. — *Petraster crozonensis* Blake, Guensburg & Lefebvre, 2016; upper part of Postolonnec Formation (Morgat Member), Middle Ordovician (late Darriwilian); Morgat harbor, Crozon Peninsula (Finistère), France; latex casts: **A1**-**A7**, holotype LPB 15174: **A1**-**A3**, aboral view of remnant, distal intervals of two arms show carinal and marginal series; weakly differentiated series might represent adradialia; **A4**-**A7**, oral views, incomplete arm tips not shown, disk disrupted but mouth frame not significantly dilated; MAO, axillaries triangular, no actinals are in evidence in disrupted disk; arms differentially dilated to expose axial, adaxial, and inferomarginal series; **B1**-**B4**, paratype LPB 15175; specimen twisted and partially inverted, the proximal aboral surface obscured but the more medial ossicles appear irregular in form and aligned in irregular series; identification of superomarginals is uncertain but potentially are small and separated from inferomarginals by intermarginals (**B1**, **arrow**). The adradial surfaces of the distended axials document an elongate, overlapping shape. Scale bars: A1, A4, B3, 10 mm; A2, A3, A5-B2, B4, 5 mm.

two interbrachia, two arms, and a portion of the disk. Only overall ossicular form survives, the surface texture of remaining ossicles altered and pitted after removal of the secondary rust-colored deposits. Radii of two remaining arms approximately 19 mm and 23 mm; two remaining interradii 11 mm and 13 mm, the distended mouth frame indicating flattening with concomitant increases in radii values.

Locality. — Tarafin Signit, Morocco; middle part of the Lower Ktaoua Formation, early Katian.

Description

Disk large, arms triangular, abruptly tapering; interbrachium thought abruptly rounded. Vaulting probably low. Aboral skeleton might consist of small, spicular ossicles. Any madreporite unknown. Specimen margin appearing marked by an ambital framework series of approximately equidimensional, triangular? ossicles. Actinals rectangular, elongate transverse to ambulacral ossicles. Axials known only from incomplete transverse ridges, axials appearing rectangular, podial basins relatively small. Adaxials appearing proportionately small, rectangular, and transversely elongate.

Remarks

Ossicular preservation is poor. Arm taper and ossicular arrangement suggest arms are complete. The two remaining arm tips as preserved appear to have been somewhat rounded suggesting some specimen arching in life. Mouth angle ossicles are represented by incomplete ossicular swellings, these dilated as to indicate some specimen flattening with burial.

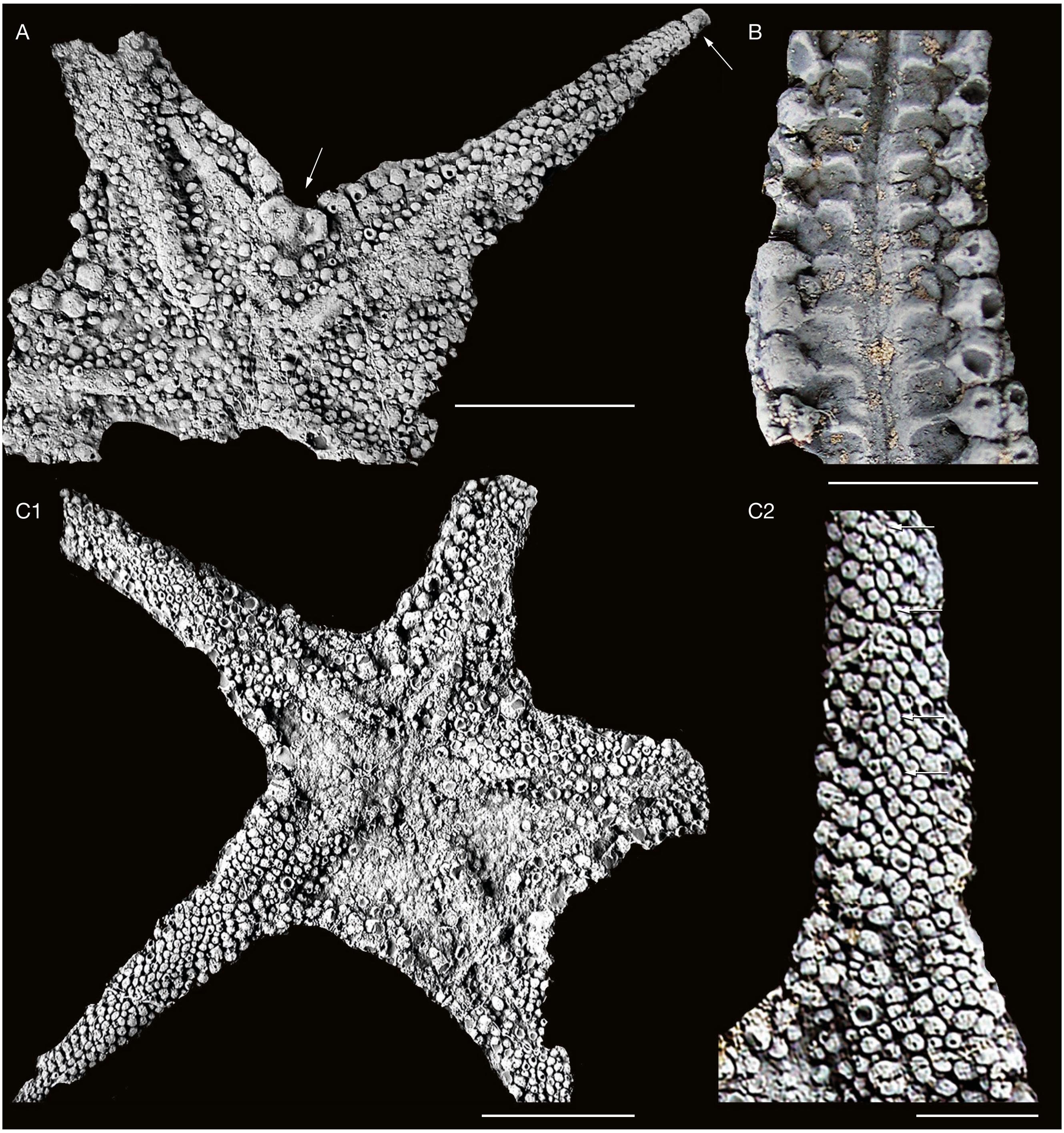

Fig. 5. — *Petraster kinahani* (Bailey, 1878); Ballymoney Group, Late Ordovician (Sandbian); Wexford County Ireland; latex casts; **A**, GSI/I 00073, aboral view, ossicular differences from those of **C1** in part reflect preservation. Madreporite (**left arrow**, compare Fig. 2B) bordered laterally by enlarged crescentic ossicles. Identities of arm series lateral to madreporite obscure, midarm arching indicates these are not carinals. Terminal (**A**, **right arrow**); **B**, GSI/I 00084; axials across arm midline at radial channel, it dilated by compaction; groove for transverse water vessel on distal side of transverse ridge; podial basin shared by successive axials; the adaxial "nose" or prominence abuts the axial in the weakly vaulted euaxosidan configuration; **C1**, **C2**, GSI/I 00069; aboral views; suggestion of carinal series limited to weak alignment of midarm series (**C2**, **arrows**). Scale bars: A, C1, 10 mm; B, C2, 3 mm.

Both surviving interbrachia exhibit now-disrupted irregular elongate ossicles, at least some directed away from the axials, these suggestive of somasteroid virgals; however, the ossicles do not correspond in number with the axial-adaxials, they are not uniform, and orientation of distal ossicles appears irregular (Fig. 7A1). Although uncommon among asteroids, homoplastic ossicular alignment suggestive of virgal series is developed in crown-group *Tremaster* Verrill, 1879 (Fig. 7B1, B2), and Jurassic occurrences similar to that of extant *Tremaster* have been described

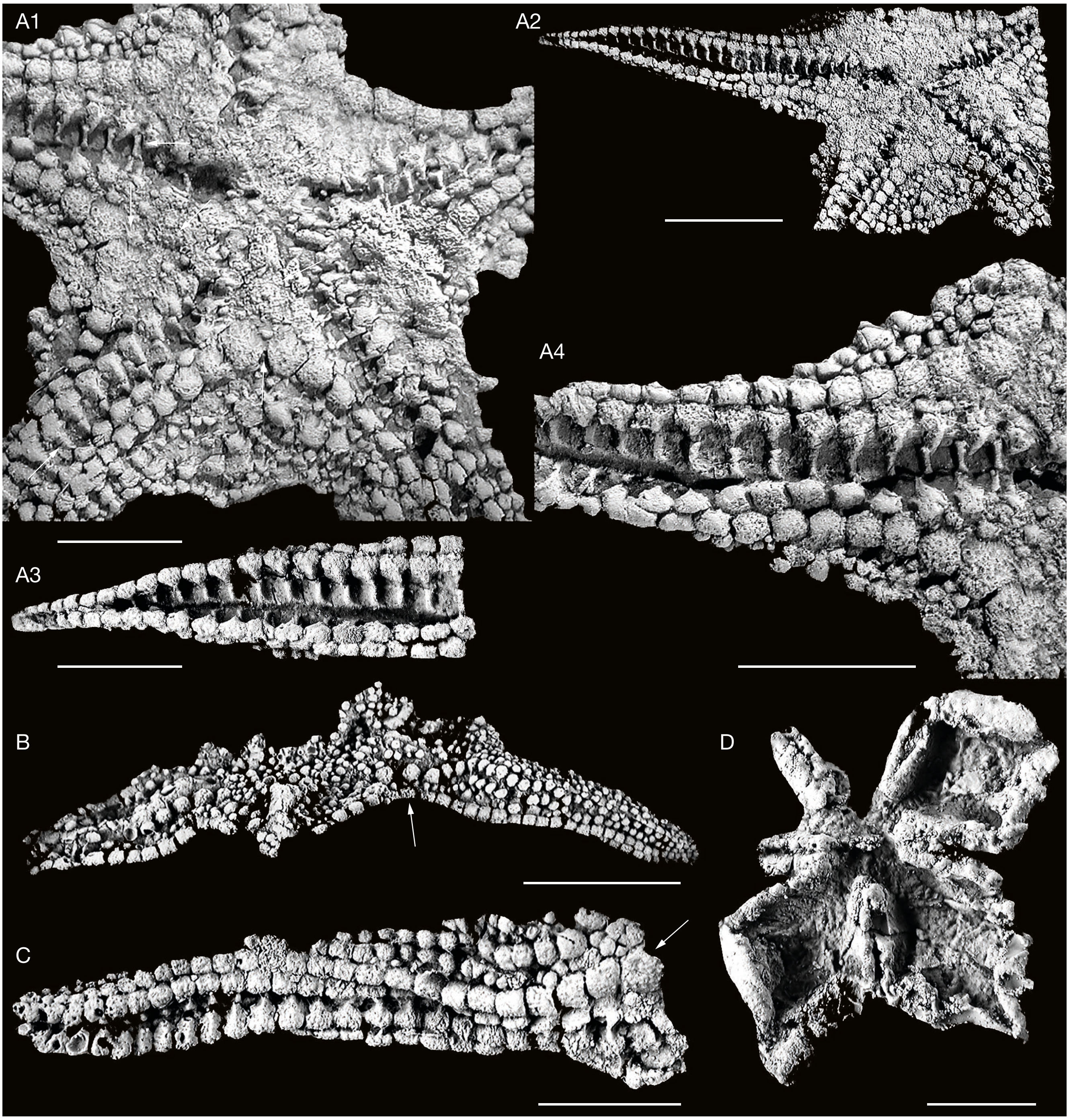

Fig. 6. — *Petraster kinahani* (Bailey, 1878); Ballymoney Group, Late Ordovician (Sandbian); Wexford County, Ireland; latex casts: **A1**-**A4**, GSI/I 00066, oral views; **A1**, orientation as **A2**; small axillaries? (**short vertical arrows**) are immediately adjacent to enlarged IM series, larger more proximal swellings suggest larger axillaries (**long inclined arrows**). Axials appear to directly abut adaxials (**horizontal arrow to upper left**) whereas smaller ossicles appear to be intercalated between axials and adaxials (**inclined arrow to lower left**), see text; **A2**, IM series extends around interbrachium, like *Aerliceaster* Blake, Gahn & Guensburg, 2020 without a clearly differentiated axillary marking the series (Fig. 9A2); **A3**, arm tip, lower axials obscured; **A4**, disk and proximal arm; **B**, GSI/I 00074; lateral view, inferomarginal series at edge is well-defined, sides of adaxials exposed distally to right; inset enlarged ossicles on disk (**arrow**); aboral series of enlarged aligned ossicles and interwoven smaller ossicular series are of problematic identity; series of smaller aligned ossicles on arm to right are thought likely carinals; **C**, GSI/I 00071; inferomarginal series (**arrow**) overlies adaxials and weakly exposed axials; identity of series of ossicles of variable sizes aboral to inferomarginals is problematic; **D**, GSI/I 00088, mouth frame ossicles in dorsal view, ossicles abutting MAO, although weathered, do not appear to be of the dumbbell shape of those of *P. caidrami* n. sp. (Fig. 2A7). Scale bars: A1, A3, A4, C, 5 mm; A2, B, 10 mm; D, 3 mm.

(Hess 1981; Smith & Tranter 1985). Axial shape, including transverse ridge expression, is asteroid-like. Inferred euaxosidan affinities are based on the apparently weak linkage between the axial and adaxial based on ossicular positioning and presence of a pulled-apart and therefore weakly linked axial/adaxial series. A large disk with peripheral marginal series is unusual but occurs elsewhere (Fig. 9D) among Paleozoic asteroids.

DISCUSSION

Interpreting the asterozoan skeleton

Given the evidence provided by a sketchy fossil record, the taxonomic composition of the Asteroidea as generally recognized (e.g. Ubaghs 1953; Spencer & Wright 1966; Dean Shackleton 2005; Blake 2018) is readily treated as monophyletic while also recognizing potential for paraphyly or polyphyly. Beginning with designation of the Somasteroidea as stemward among asterozoans (Spencer 1951; Blake 2013), the history of the class Asteroidea was marked by relatively few fundamental changes in skeletal configuration, "fundamental" descriptively defined as differences likely to receive emphases at higher taxonomic levels.

Class-level asteroid apomorphies assuming a somasteroid ancestry consist of reduction of adaxial virgalia from the somasteroid series to a single ("adambulacral") ossicle; displacement of the axials toward the aboral surfaces of the adaxial; axial vaulting to form an ambulacral furrow; and loss of radial water vascular channel skeletal closure, closure among somasteroids likely serving to protect water-vascular tissues, protection in asteroids afforded by vaulting and furrow narrowing. Radial water vascular channel size was reduced among Asteroidea, although sediment load can produce potentially misleading channel spreading and flattening. Plesiomorphic expressions retained from the somasteroid evolutionary grade include lateral pairing of axials and adaxials, somewhat irregular alignment ("pairing") of axials across the ambulacral midline, and at least in some lineages, the capacity for coordinated lateral flexure of adaxials in the horizontal or body plane as reflected in configuration of the abradial margin of the axials (e.g. *Eukrinaster* Blake, Guensburg, Sprinkle & Sumrall, 2007; *Cnemidiactis* Spencer, 1918; *Jugiaster* Blake 2018: pl. 2). Somasteroid-like abactinal expressions are thought to have been retained in the earliest Asteroidea.

The skeletal morphology of the Asterozoa, here focusing on the classes Somasteroidea and Asteroidea, is subdivided into a comparatively small number of skeletal categories or series, but interpretation of some series is difficult, here exemplified with reference to *Petraster* and Euaxosida sp. A. For evaluation, series are partitioned into categories in accord with two overlapping schemes. First, the three-fold subdivision of Spencer & Wright (1966: 9, as modified herein) consists of an "axial" series, including the ambulacral (or "axial") ossicles, the mouth angle ossicles, and the unpaired terminal ossicle at the distal tip of the arm, it here treated as axial. The terminal ossicle is difficult to recognize among fossil asterozoans because in many species it is little differentiated in size and form from immediately adjacent ossicles, and preservational events commonly further obscure its recognition. The terminal ossicle is important in that ossicular series (e.g. axials, adaxials, marginals) arise on the proximal side of the ossicle. However, it is the unknown evolutionary biology of the position on the proximal side of the terminal that is important. The terminal ossicle itself does not generate ossicular series. The problematic nature of somasteroid terminal ossicle recognition has been treated elsewhere (Blake & Guensburg 2015: 478, fig. 9). "Adaxial" series include virgals of somasteroids, the adambulacrals of asteroids, the laterals of ophiuroids, and the embedded virgals and outer virgals of stenuroids. The remainder of the skeleton is extraxial, including abactinals, the ambital framework, actinals, madreporite, and accessories. Because the extraxial skeleton partially encloses and obscures the axial and adaxial, it is the extraxial that is immediately obvious in most specimens and most readily provides characters for taxonomic evaluation, but it is the expression of the adaxial and axial that is crucial to interpretation at higher taxonomic levels, in part because the extraxial skeleton is under the more immediate influence of the local environment, and therefore more readily susceptible to evolutionary change. The axial/adaxial series of asteroids, although crucial to interpretation, are incompletely understood because of typically limited exposure among fossils.

In a second scheme for partitioning, the extraxial ambital framework series of somasteroids and its asteroid homologous inferomarginal series serve to separate the extraxial aboral skeleton from the axial, adaxial, and extraxial oral skeleton.

Discussions here seek dissociation of expressions of relatively widespread uniformity that in a phylogenetic analysis would best provide apomorphies unifying clades assigned higher taxonomic rankings from the varied expressions more useful at lower taxonomic levels, the former largely made up of axial and adaxial characters whereas all three ossicular categories contribute usefully to the latter. Because more complete specimens are rare but discrete ossicles comparatively common at least in some European Jurassic and Cretaceous localities, specificities of ossicular variation have received much attention among paleontologists. Review and limitations of usage of ossicular morphology, and the need for comparative complete specimens, ancient and modern, has been reviewed (Villier *et al.* 2004: 811). Reviews of asteroid skeletal construction include Spencer & Wright (1966), Dean Shackleton (2005), and Blake (2018).

Evolution of the asteroid ambital framework and *Petraster*

An ambital framework series is recognized in all known somasteroids (but see Hunter & Ortega-Hernández 2021; Blake & Hotchkiss 2022) and all or nearly all (but see Blake & Guensburg 1989) stem-group asteroids. Three ambital framework series are recognized, the "inferomarginal", which includes the "ambital necklace" subdivision (Blake & Guensburg 2015: 466), "superomarginals", and any "intermarginals" intercalated between the superomarginals and inferomarginals.

Descriptively, an ambital framework progression within Somasteroidea begins with the diffuse, delicate ambital network of *Chinianaster* Thoral, 1935 (Fig. 8A2), continues with the better defined but locally irregular series of *Villebrunaster* Spencer, 1951 (Fig. 8B) and the more clearly defined series of *Ophioxenikos* Blake & Guensburg, 1993 (Fig. 8C), and concludes with *Archegonaster* Jaekel, 1923. If only a single series is present it is considered "inferomarginal" presumably based on position and widespread occurrence of a so-called

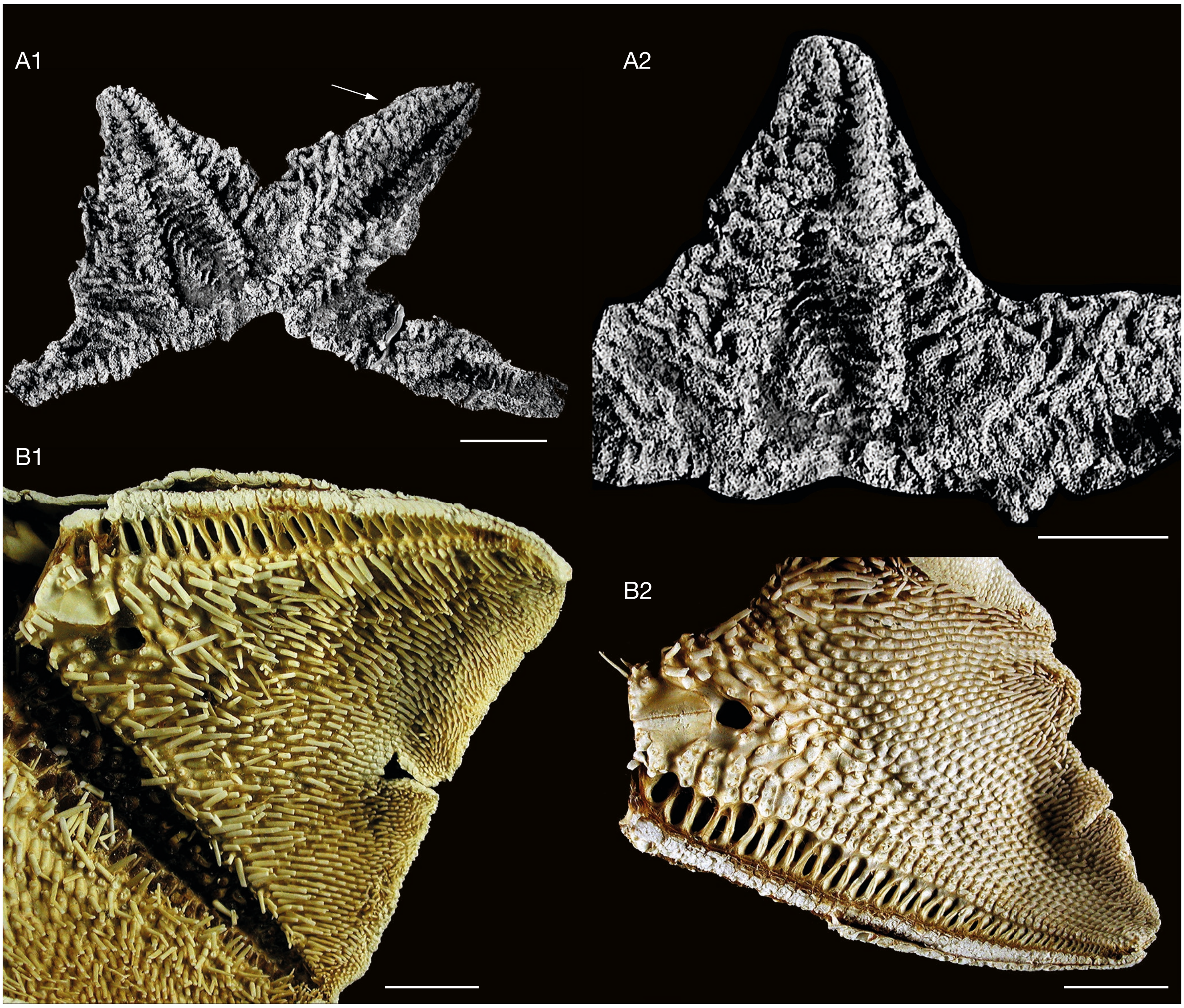

Fig. 7. — **A1**, **A2**, *Euaxosida* sp. A; Lower Ktaoua Formation, Late Ordovician (early Katian); Tarafin Signit, Morocco; UCBL-FSL 712909; latex cast, oral views; **A1**, entire remnant and central area. The radiating rod-like actinals in interbrachia are reminiscent of somasteroid virgals, although appearing less well defined distally (**A1**, **arrow**); **A2**, inferred ambital framework and abactinal remnants edge arms; **B1**, **B2**, *Tremaster mirabilis* Verrill, 1879; east of Newfoundland, Canada; USNM E37444, extant; mouth-angle ossicles to upper left; alignment of actinal ossicles is suggestive of Euaxosida sp. A and the virgalia of Somasteroidea; **B2**, podial recepticles in double series is uncommon but taxonomically widespread among Asteroidea. Scale bars: A1, 3 mm; A2, B1, B2, 5 mm.

"axillary", see below. Surveying the history of interpretations of "marginals" is beyond the scope of the present study. Of significance here, however, is that the extraxial inferomarginal series of *Petraster*, like the axial and adaxial series, are clearly recognized among species, their presence and definition providing the marker for separation and interpretation of the axial, adaxial, and extraxial oral skeleton from the entirely extraxial aboral skeleton.

In *Petraster*, the inferomarginal series is well-defined and the superomarginal series difficult to interpret, the weak differentiation leading Spencer (1916: 106) to express uncertainty as to whether superomarginals of *Uranaster kinahani* (now *Petraster kinahani*) were as yet incompletely differentiated (i.e., emergent), or alternatively, in the process of being lost. Later, Spencer (1918: 126) suggested superomarginals were "secondary" but he did not nominate a derivation whereas Dean Shackleton, (2005: 39) thought superomarginals of *Hudsonaster* "and similar taxa" were modified abactinals, and inferomarginals probaby so (Dean Shackleton 2005: 42).

In an alternative hypothesis for superomarginal origin, the irregular ambital framework series of *Villebrunaster* (Fig. 8B) and *Ophioxenikos* (Fig. 8C) suggest independent lineages might have led to both the single and double marginal series of asteroids. Additionally, the irregular marginal series of the early asteroid *Eukrinaster* (Fig. 9D) is suggestive of appearance of *Villebrunaster* thereby indicating that well-defined marginal series, either single or both single and double, could have originated after the origin of the asteroid condition, that is, after the origin of the defining asteroid ambulacral furrow.

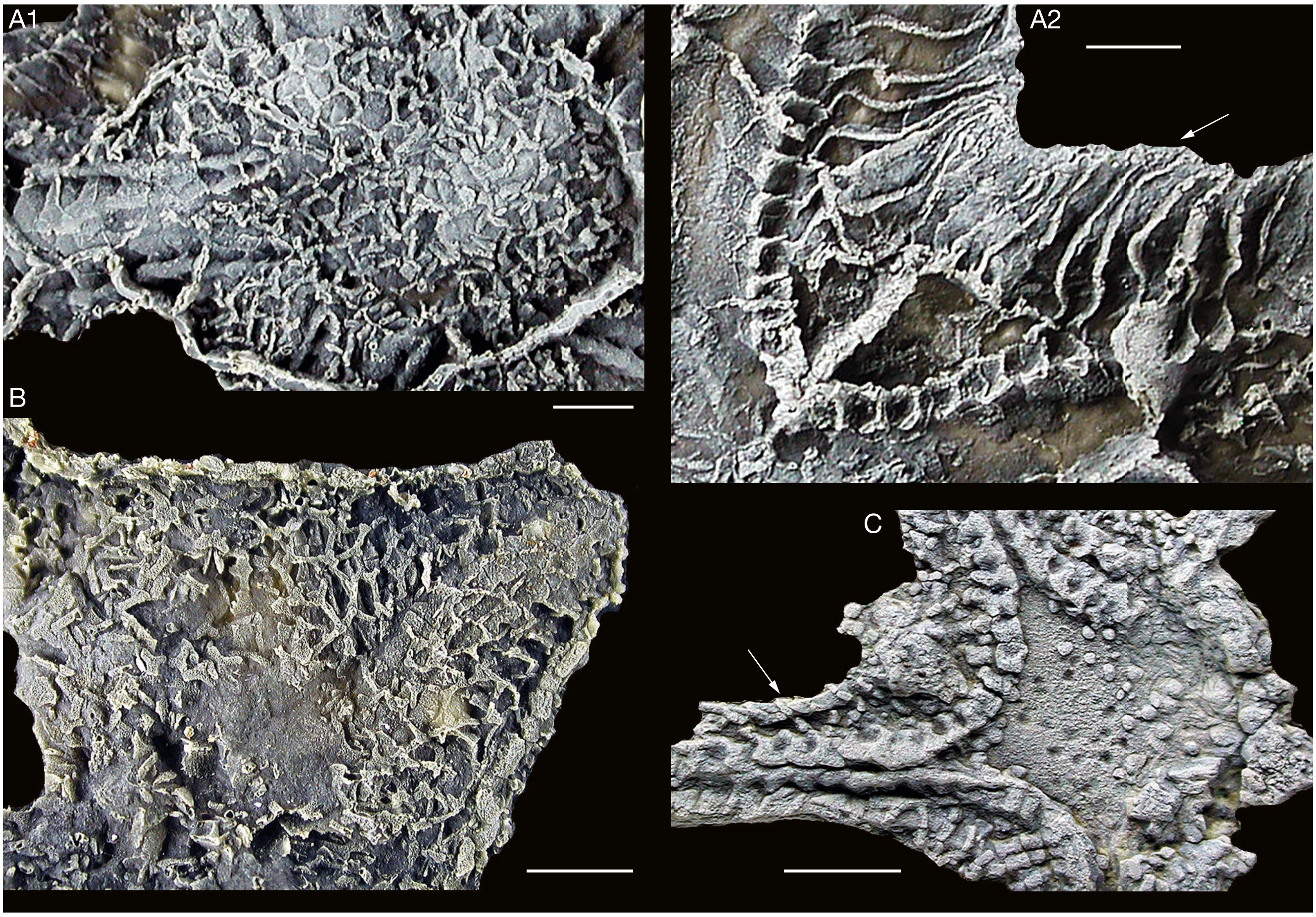

Fig. 8. — **A**, **B**, Saint-Chinian Formation, Early Ordovician (late Tremadocian); Saint-Chinian (Hérault), Montagne Noire, France; latex casts: **A1**, **A2**, *Chinianaster levyi* Thoral, 1935; lectotype UCBL-FSL 168691: **A1**, aboral view of central disk, abactinals delicate, spicular; **A2**, oral view of disk, axials to left, adaxial series extending to ambital necklace (**arrow**); **B**, *Villebrunaster thorali* Spencer, 1951 paratype UCBL-FSL 711092. Aboral view, complex ambital framework edges specimen, abactinal network of fine spicules, axial series visible distally but obscured; **C** *Ophioxenikos langenheimi* Blake & Guensburg, 1993; Pogonip Group, early to middle Floian, early Ordovician; Ely Springs Range, Nevada; holotype UI-X-4751; original specimen; oral view, the disk distended in preservation, ossicles weathered; ambital framework (**arrow**), comparatively few abactinals remain toward the right with "footprints" of lost abactinals in the matrix within mouth frame. Scale bars: 3 mm.

The more clearly developed series of enlarged ossicles aboral to the inferomarginal series of *Petraster* are recognized herein as superomarginal, and although superomarginal origin(s) appears apart from that of the inferomarginals, sourcing is considered uncertain.

Regardless of series origin, specificities of asteroid marginal form are highly varied, in part correlated with overall arm shape. Ossicles commonly are enlarged relative to adjacent ossicles in species with flatter arms (e.g. *Delicaster* Blake & Elliott, 2003; Fig. 10A) whereas they are similar in size in more nearly cylindrical arms (e.g. Figs 1-6) (Spencer 1922: 202).

Inferomarginal series of Paleozoic asteroids with proportionately small disks and few actinal ossicles typically radiate from a so-called "axillary", it centered on the interbrachial midline and abutting or nearly abutting the mouth-angle ossicles. Spencer (1916: 62; details, 1919: 180) argued that the "odontophore" of the crown group is the stem-group axillary. Axillary recognition can be problematic in taxa such as *Eukrinaster* with an enlarged disk (Fig. 9D; Blake *et al.* 2007). The absence of a clearly defined axillary in *P. kinahani* (Fig. 6A) is reminiscent of expression of the early asteroid *Aerliceaster* Blake, Gahn & Guensburg, 2020b (Fig. 9A2) arguing potential emergence of the axillary within Asteroidea, and therefore the potential for homoplasy among axillary occurrences.

"Intermarginals" are by definition body wall ossicles bounded by the "inferomarginal" and "superomarginal" series. Occurrences in widely divergent stem-group (e.g. *Xenaster* Simonovitsch, 1871) and crown-group (e.g. Echinasteridae) asteroids demonstrate homoplasy. Given uncertainties of genesis of superomarginals, "intermarginals" in the first asteroids might be derivatives of either the complex ambital framework of a *Villebrunaster* -like ancestry or of abactinal origin and homoplastic. Present interpretation of the aboral skeleton differs from that of Dean Shackleton (2005: 93), who argued "true superomarginals are in direct abutting contact with inferomarginals over the entire arm length", in this interpretation apparently not recognizing intermarginal series.

Evolution of the asteroid abactinal series and *Petraster*

"Abactinals" are those ossicles other than the madreporite above all marginal series, a working usage independent of the

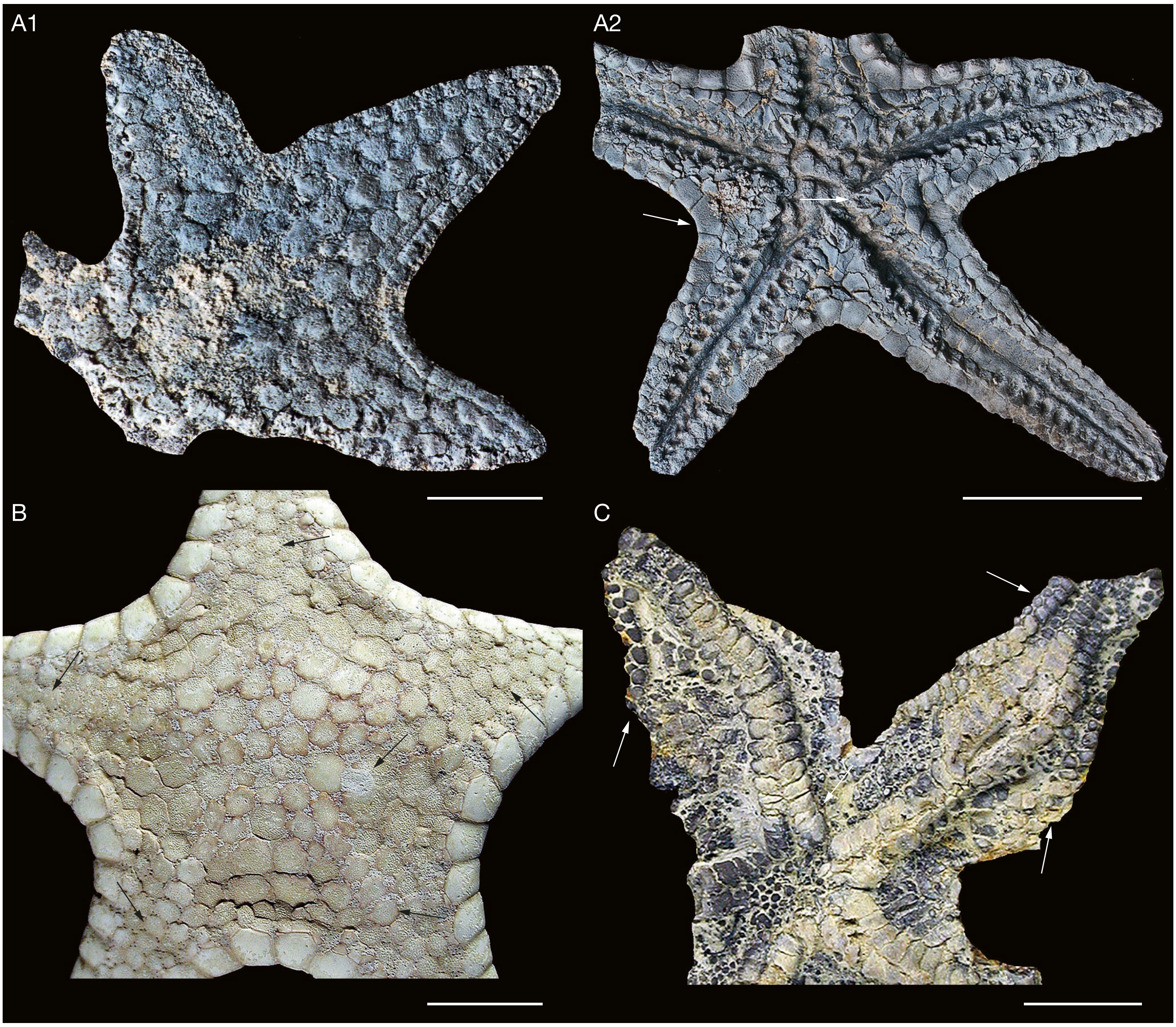

Fig. 9. — **A1**, **A2**, *Aerliceaster nexosus* Blake, Gahn & Guensburg, 2020; Garden City Formation, *Strigigenalis plicolabeona* Zone (Adrain *et al.* 2009), Early Ordovician (Floian); Bear River Range, Idaho; original specimens: **A1**, IMNH IP-276/855 paratype, aboral view, rectangular inferomarginals are exposed along the ambital margin; plate-like abactinals are uniform and aligned in series on arm but series identities are uncertain, unlike those of *Anthenoides* Perrier, 1881 (**B**); **A2**, IMNH IP-276/850 holotype, oral view, specimen weathered at the outcrop, axial transverse ridges of middle of arm to lower right were destroyed, those of the remaining axials exposed by preparation. The inferomarginal series is well-defined but weathered; axillaries (**left arrow**) vary among interbrachia, as in *Petraster rigidus* (Billings, 1858) (Fig. 1A1, A2); MAO pair (**right arrow**); **B**, *Anthenoides* ; extant; low-latitude Atlantic Ocean; unnumbered specimen; aboral view, plate-like abactinals similar to those of *Aerliceaster* Blake, Gahn & Guensburg, 2020, carinal series well-defined on arms (**five arrows on arms**) but losing clarity of definition on disk; anus not recognized, madreporite (**medial arrow**) appearing little differentiated, as is also true of many fossils; **C**, *Eukrinaster ibexensis* Blake, Guensburg, Sprinkle & Sumrall, 2007; Fillmore and Wah Wah formations; TMM paratype 196TX11, original specimen; Early Ordovician (Whitlandian Stage, early middle Arenig); Ibex area, Utah; dorsal view, axials robust and rounded (**arrow at disk**), abactinals insofar as can be seen uniform, small, and closely spaced as in *Ophioxenikos* Blake & Guensburg, 1993 (Fig. 8C), marginal series (**arrows on arms**) irregular as in *Villebrunaster* Spencer, 1951 (Fig. 8B). Scale bars: A1, A2, 3 mm; B, 10 mm; C, 5 mm.

hypothesis that so-called superomarginals and intermarginals might have had an "abactinal" source, and occurrences among taxa might be homoplastic.

Three abactinal configurations are recognized within Somasteroidea: spicular and reticulated (e.g. *Chinianaster*, Fig. 8A1); plate-like and abutted (*Ophioxenikos*, Fig. 8C); and limited to an apparent granular layer lacking enlarged ossicles (*Archegonaster*). Skeletal reduction is a seemingly recurrent theme among Asteroidea and most readily visualized among the extant, including the Poraniidae and Acanthasteridae, the latter a derivative of the typically skeletally robust Oreasteridae (Blake 1979; Yasuda *et al.* 2006; Mah & Foltz 2011). Among somasteroids, differentiation into series (e.g. aboral ring, centrale, superomarginals, carinals, adradialia) has not been recognized.

Two divergent emergent configurations from a posited somasteroid ancestry are recognized among early asteroids, one retaining proportionately small aboral ossicles (e.g. *Eukrinaster*; Fig. 9D) that are at least broadly suggestive of those of *Ophioxenikos* (Fig. 8C), and the second of enlarged plate-like abactinals exemplified by *Aerliceaster* (Fig. 9A1). In the latter, some linear alignment is recognized but not series readily correlated with those typical among more derived asteroids (Fig. 9C). The complexly varied abactinal series expressions among species of *Petraster* suggest variously emergent differentiation of aboral ossicular series.

Unlike the stemward Somasteroidea, an unpaired aboral arm midline "carinal" series occurs widely among asteroids, in some genera bordered by generally less clearly differentiated "adradialia" (Figs 2A3, A6; 4A2, A3). Carinal series in taxa with rounded arms might arise as the support equivalent of a ridgepole of a gable roof (Blake & Rozhnov 2007: 526), and therefore carinal and any accompanying adradialia potentially are widely homoplastic. *Petraster* species exemplify varied carinal and adradial differentiation, and with that, potential homoplasy.

An "aboral ring" (synonym of "primary circlet") and variably developed "centrale" have been recognized among asteroids of all ages. Differentiation from the uniformity of the Somasteroidea could have been gradational, initially limited, and homoplastic. Because of poor preservation, recognition can be difficult, as potentially true of *Petraster*. The five ossicles of an "aboral ring" might represent the proximal ossicles of the carinal series and therefore a single ossicular group, but alternatively, in Carboniferous *Delicaster* (Fig. 10A1), the ring is well-defined and no carinal series is apparent, seemingly favoring independent series origins. Sediment compaction around the pentameral mouth frame can perhaps incorrectly argue "aboral ring" presence.

The axial and adaxial series

Three fundamental changes can be recognized in the history of the axial/adaxial skeletal configuration of Asteroidea. The first the emergence of the ambulacral furrow. In somasteroids, axials and adaxial virgalia at rest lie in the oral plane, although delicately articulated ossicles suggest presence of a capacity that could yield temporary furrow-like flexure. Three ordinal-level lineages, the Euaxosida, Hadrosida, and Kermasida, are recognized based on extent of displacement of the axial series onto the aboral surfaces of the adaxials (Blake 2018). Axial displacement was accompanied by progressive deepening of the furrow, the latter expressed in the lessening of the at-rest angle between the axial pair across the arm midline. Although extent of these changes appears susceptible to convergence among lineages, a phylogenetic sequencing in an independent and unrelated study (Villier *et al.* 2018) emphasizing alternative evaluation criteria and directed toward other concerns reached many phylogenetic interpretations in common with the taxonomy of Blake (2018).

Next, among stemward asteroids, the water-vascular system is entirely external, the podia and any associated tissues (e.g. perhaps ampullae) roofed by solid skeletal surfaces, so-called "podial basins". In contrast, so-called "podial pores", passageways for podial tissues between sequential axials, emerged during the middle Paleozoic (Blake & Guensburg 1988) (Fig. 10A2), the generic diversity of occurrences favoring homoplasy. Podial pores are universal within the crown-group (e.g. Fig. 10B1, B2), the enclosure of podial tissues potentially favored for providing protection and freeing space in the furrow. Earlier studies argued presence of podial openings near the lateral margins of the ambulacral furrow, these interpreted as resulting from diagenetic displacement (Blake & Guensburg 1988).

Finally, is positioning of axials and adaxials. In all known stem-group Asteroidea –these as now known exclusively Paleozoic–, each axial directly abuts and is associated with a single adaxial, whereas among all known crown-group asteroids Asteroidea –these as now known exclusively post-Paleozoic– axials and adaxials are offset in a zipper-like arrangement (reviewed, Blake & Guensburg 1988). The configuration is the critical element in separation of stem and crown-group asteroids, a separation not recognized by earlier authors (e.g. Spencer & Wright 1966) but stressed more recently (e.g. Blake 1987; Gale 1987).

The Carboniferous derived (order Kermasida) stem-group species *Delicaster enigmaticus* (Kesling, 1967) (Fig. 10A2, A3) in comparison with the earlier asterozoans usefully exemplifies important evolutionary changes. *Delicaster* does not represent an aberrant potentially misleading lineage because it is similar to Permian asteroids from Australia (Kesling 1969) and dissimilar from other later Paleozoic asteroids (e.g. Kesling & Strimple 1966; Blake *et al.* 2014). Axial ossicles of *Delicaster* are fully aboral to the adaxials, and, as in crown-group species, well-developed medial podial pores are present, but the ossicles are "T"-shaped, lacking the wing-like tissue flanges found for example in the crown group *Anthenoides* Perrier, 1881 (Fig. 10B1, B2), these correlated with the zipper-like axial-adaxial arrangement. Marginal ossicles of most crown-group asteroids are developed in a double series (although only a single series occurs in the Zoroasteridae; Blake 1987; Blake & Elliott 2003), but in a single series in *Delicaster* (Fig. 10A1-A3). The triangular, fully external axillary (Fig. 10A3) is unlike the nearly universal internal occurrence of the homologous crown group "odontophore". Also unlike the typical crown group expression, no actinals are apparent in *Delicaster*, the axillary closely fitted against the adjacent MAO, proximal inferomarginals, and adaxials (Fig. 10A3). Arm abactinals are uniform, small and granular, the ridgepole carinal configuration arguably not useful to the flat, strap-like arms of *Delicaster*. Ossicles of the robust aboral ring (Fig. 10A1) are wholly and clearly differentiated from the small arm abactinals suggesting series differentiation, unlike the ambiguous differentiation between any aboral ring and adjacent abactinals of *Petraster*.

Interpreting Euaxosida sp. A

Known only from the incomplete fragment of a single specimen exposed in oral aspect, Euaxosida sp. A (Fig. 7A1, A2) is problematic, but like *Petraster*, it suggests intermediacy in the emergence of morphology typifying derived Asteroidea. Euaxosida sp. A is assigned to the Asteroidea at the ordinal level based on what can be seen of axial form and relationship of the axials to the adaxials. Overall form and abactinal and ambital framework series, insofar as they are known, are broadly somasteroid-like and tentatively interpreted as plesiomorphic.

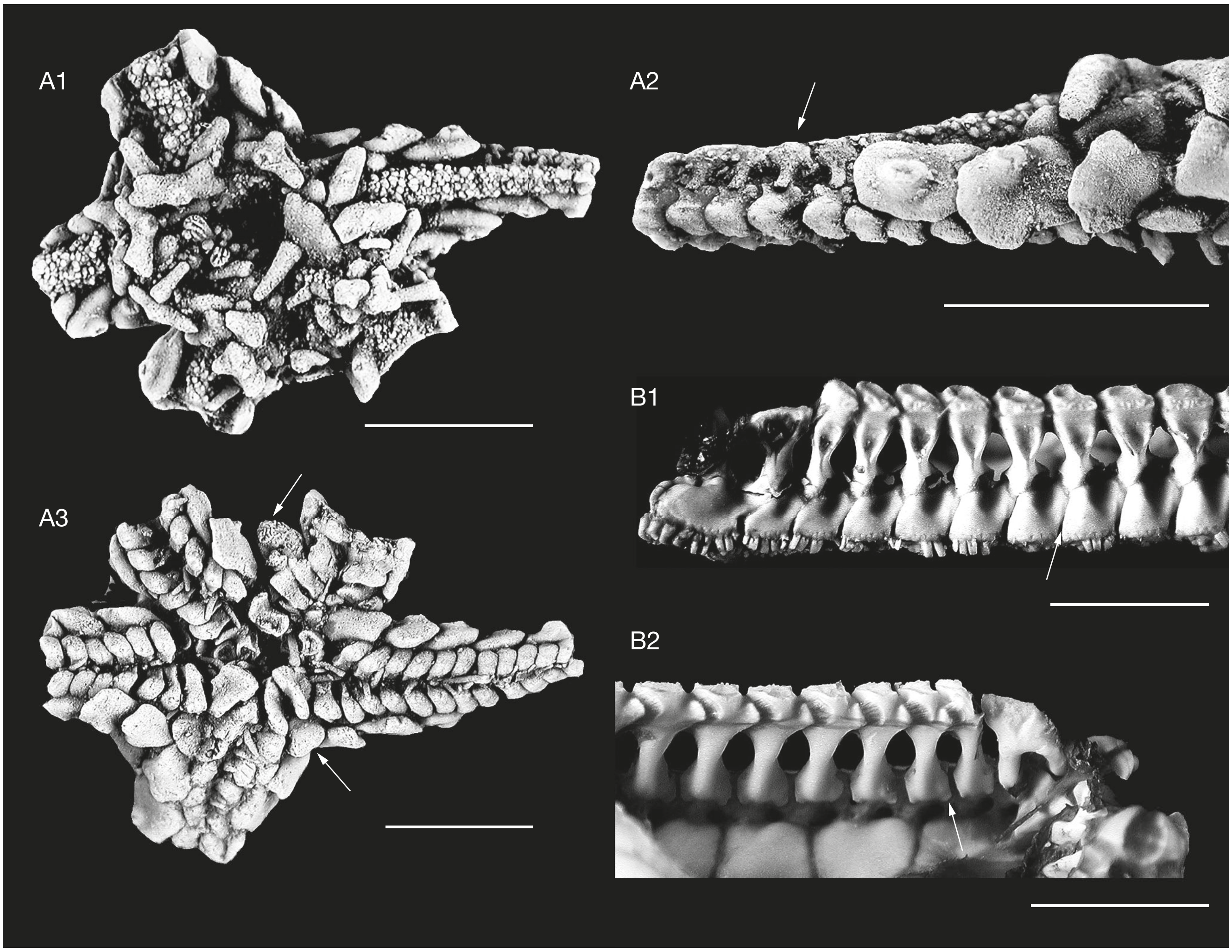

Fig. 10. — **A1**-**A3**, *Delicaster enigmaticus* (Kesling, 1967); Paint Creek Formation, Mississippian (Visean); Saint Clair County, Illinois; UMMP 54262 holotype, original specimen: **A1**, aboral view, arm abactinals tiny, not differentiated; inferomarginals large, plate-like; aboral ring ossicles large, triangular, both latter series with a large medial spine base; **A2**, lateral view of arm, axials (**arrow**) "T"-shaped, the indented sides are podial pores, axials abut the aboral surfaces of adaxials, not zipper-like as in the crown group (**B**); inferomarginals to right; **A3**, oral view, adaxials closed over ambulacral furrow, madreporite (**upper arrow**) is lateral, axillary (**lower arrow**) abuts large MAO, these dilated medially; **B1**, **B2**, *Anthenoides* Perrier, 1881; extant; low-latitude Atlantic Ocean; unnumbered specimen; podial pores well-developed although (**B1**) partially obscured by background ossicles; **B1**, axial series, lateral furrow view, each axial abuts two successive adaxials, cross-furrow muscles depressions are large; **B2**, axial series, inclined dorsal view, flanged axials (**arrow**) for tissues extended to successive adaxials are not found in *Delicaster* Blake & Elliott, 2003, the inter-axial and adaxial articulation structures more complexly differentiated in crown-group species. Scale bars: 3 mm.

More problematic is interpretation of the ossicles between the marginals and the adaxials, these of an elongate form and positioning suggestive of somasteroid virgals, but interpreted as asteroid actinals because they are not aligned with the axials, size differences, and irregularity of shape. Crown-group asteroid actinal series alignment among a few species, including *Tremaster mirabilis* Verrill, 1879 (Fig. 7B1, B2; also see Hess 1981; Smith & Tranter 1985), are reminiscent of somasteroid virgalia, but no other evidence is available that might argue in favor of a more direct linkage between somasteroids and later asteroids.

SUMMARY STATEMENT

Fundamental axial and adaxial skeletal expressions of the Asterozoa originated within the Somasteroidea, and following reduction of adaxial virgal series among the derived lineages, were largely retained through time. This stability is argued as reflecting intimate linkages with the inferred functionally and evolutionarily comparatively stable soft tissues of the water vascular system. Early configurations of extraxial series in contrast are varied and interpreted as emergent and widely homoplastic among later derived asterozoans, the relative plasticity reflecting evolutionary effects of more localized environmental conditions. These interpretations are argued as supported by extraxial complexities of *Petraster* and Euaxosida sp. A.; available specimens of both, however, are Late Ordovician in age and therefore can only provide inferred guidelines to earlier events.

Because of relative accessibility among both ancient and extant representatives, the extraxial skeleton has received emphasis in phylogenetic reconstruction and taxonomy, although it is the axial and adaxial series that are critical to the evaluation of basal asterozoan events and relationships.

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