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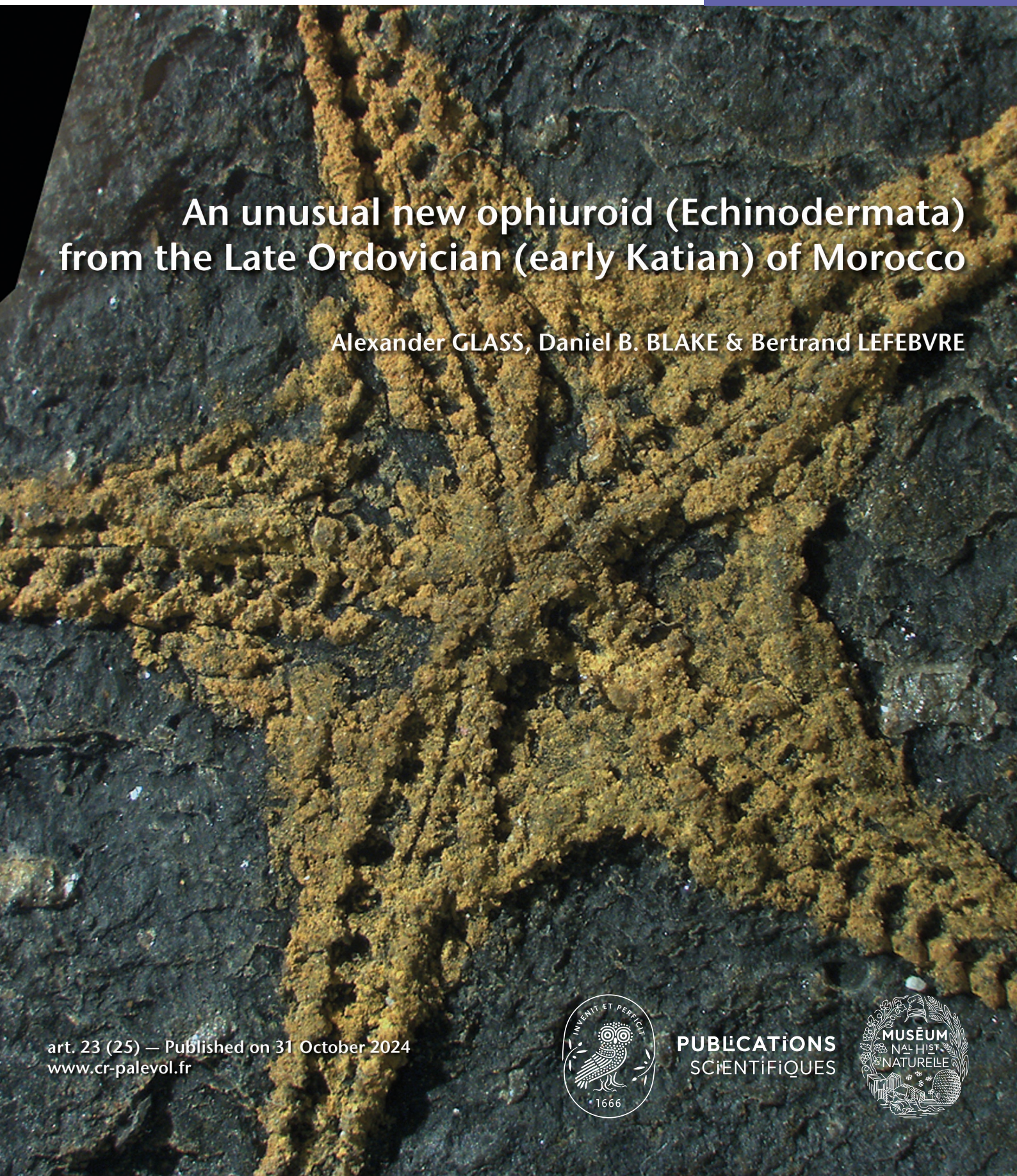

An unusual new ophiuroid (Echinodermata) from the Late Ordovician (early Katian) of Morocco

Alexander GLASS, Daniel B. BLAKE & Bertrand LEFEBVRE

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An unusual new ophiuroid (Echinodermata) from the Late Ordovician (early Katian) of Morocco

Alexander GLASS
Division of Earth and Climate Sciences
Duke University, 9 Circuit Drive, Durham, North Carolina, 27708 (United States)
alex.glass@duke.edu (corresponding author)

Daniel B. BLAKE
Department of Geology, University of Illinois,
1301 W Green Street, Urbana, 61801 (United States)
dblake@illinois.edu

Bertrand LEFEBVRE
Laboratoire de Géologie de Lyon : Terre, Planète, Environnement, Université Claude-Bernard,
Lyon 1, 2, rue Raphaël-Dubois, F-69622 Villeurbanne Cedex (France)
bertrand.lefebvre@univ-lyon1.fr

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ABSTRACT
A distinctive new genus and species of the subphylum Asterozoa, *Componaster spurius* n. gen., n. sp., is described from the Late Ordovician (early Katian) of Morocco. Construction of the ambulacral column is considered key to delineation of classes of the subphylum Asterozoa: morphology and configuration of the mouth frame, axial (ambulacral series), and adaxial (lateral series) enable class-level assignment of *C. spurius* n. gen., n. sp. to the Ophiuroidea Gray, 1840. However, overall form and aspects of extraxial skeletal expression from beyond the ambulacral column are strongly reminiscent of expressions of the Asteroidea de Blainville, 1830. The character complex of *C. spurius* n. gen., n. sp. precludes its alignment with any available ophiuran ordinal concept, and available data do not justify proposal of new ordinal terminology: the species is left *incertae sedis* at the ordinal level but a new familial taxon, Componasteridae n. fam., is recognized. Although Late Ordovician, the complex morphology of *Componaster spurius* n. gen., n. sp. suggests either plesiomorphic expressions from asterozoan diversification surviving until the Katian or significant homoplasy during early asterozoan history.

KEY WORDS
Ophiuroidea,
Echinodermata,
Asterozoa,
Late Ordovician,
Lower Ktaoua
Formation,
Morocco,
new family,
new genus,
new species.

RÉSUMÉ
Un nouvel ophiuroïde (Echinodermata) inhabituel de l'Ordovicien supérieur (début du Katien) du Maroc.
Un nouvel astérozoaire, *Componaster spurius* n. gen., n. sp. est décrit dans l'Ordovicien supérieur (Katien inférieur) du Maroc. L'attribution d'un taxon à l'une des classes du sous-phylum Asterozoa repose principalement sur l'architecture de ses structures ambulacraires. Chez *C. spurius* n. gen., n. sp., la morphologie et la configuration du péristome (axiale [série ambulacraire] et adaxiale [série latérale]) permettent de le placer au sein de la classe Ophiuroidea Gray, 1840. Néanmoins, sa morphologie générale et l'extension du squelette extraxial au-delà de la colonne ambulacraire sont des caractéristiques qui évoquent davantage la classe Asteroidea de Blainville, 1830. Cette combinaison inédite de caractères ne permet pas d'attribuer *C. spurius* n. gen., n. sp. à l'un des ordres connus à ce jour chez les ophiures. Toutefois, comme les données disponibles ne justifient pas de proposer la création d'un nouvel ordre, l'espèce est donc placée au sein d'une nouvelle famille, Componasteridae n. fam., mais laissée en nomenclature ouverte au niveau ordinal. La morphologie très particulière de *Componaster spurius* n. gen., n. sp. pourrait refléter la survivance tardive (Katien) de morphologies plésiomorphes héritées de la diversification des astérozoaires à l'Ordovicien inférieur ou alors, témoigner de l'existence de fortes homoplasies au début de l'histoire évolutive de ce sous-phylum.

MOTS CLÉS
Ophiuroidea,
Echinodermata,
Asterozoa,
Ordovicien supérieur,
Formation inférieure du Ktaoua,
Maroc,
famille nouvelle,
genre nouveau,
espèce nouvelle.

INTRODUCTION

The echinoderm subphylum Asterozoa includes four class-level taxa. Of these, the Asteroidea de Blainville, 1830 and Ophiuroidea Gray, 1840 are extant, whereas the Somasteroidea Spencer, 1951 is restricted to the Ordovician and the Stenuroidea Blake, 2013, from Ordovician to Permian. Although generally treated at the class-level, earlier studies (e.g. Spencer 1951; Spencer & Wright 1966) cited asteroids, ophiuroids, and somasteroids at the subclass level, the lower ranking likely based on inferred propinquity of descent. Stenuroids were described at the ordinal level (Spencer 1951) and raised to the class level (Blake 2013). Fossils asterozoans are almost always rare, their preservation hampered by delicate, multi-part skeletons prone to rapid post-mortem disarticulation, scattering, and destruction. All four classes are first recorded from a relatively brief interval of the Early Ordovician (Tremadocian-Floian), their nearly common first occurrences limiting efforts to evaluate relationships based on stratigraphic positioning.

The Somasteroidea, treated as stemward among asterozoans (Spencer 1951; Blake 2013), is most clearly delineated by presence of series of rod-like so-called virgal ossicles that extend laterally from each ambulacral ossicle. In the derived Asteroidea and Ophiuroidea, the virgal series was reduced to a single ossicle, the so-called "adambulacral" of asteroids and the "lateral" of ophiuroids, and in stenuroids, the series reduced to two to four ossicles.

The entirety of the asterozoan skeleton was subdivided into three sections (Spencer & Wright 1966: 9), and a slightly modified version of this classification is employed here, it valuable in part because it serves to outline crucial differences that are stressed below: the ambulacral series, including the mouth-angle ossicles and the terminal, are "axial"; the virgal series and its phylogenetic derivatives are "adaxial"; and the remainder of the skeleton, including a madreporite where recognized as well as any accessories, are "extraxial". The axial and adaxial skeletons are argued as providing crucial guidance to class-level affinities, the extraxial skeleton more susceptible to localized evolutionary changes (e.g. Blake 2013, 2018, 2024; Blake & Guensburg 2015). The terminology of Spencer & Wright (1966) is emphasized here.

Class-level relationships remain elusive because an outgroup for phylogenetic analysis has not been clearly identified (Blake 2013, 2024; Blake & Hotchkiss 2022; but also see Jell 2014). The presence of stellate trace fossils (Mikulaš 1992) together with absence of known asterozoan body fossils from Cambrian strata allow the hypothesis that initial diversification of the Asterozoa took place prior to the emergence of a significantly calcified skeleton (Blake 2013), an interpretation in accord with thinking of Erwin *et al.* (2011), and in that, challenging efforts to recognize a viable outgroup.

The new asterozoan genus and species *Componaster spurius* n. gen., n. sp. from the Late Ordovician (Katian) of Morocco is described. The ambulacral column, including the mouth frame, axials, and adaxials, identify *Componaster* n. gen. as an ophiuroid, whereas overall shape and the extraxial abactinal ossicles are suggestive of those of asteroids. Presence of only a single adaxial in *Componaster* n. gen. eliminates somasteroids and stenuroids from further comparisons.

Because of the mixture of characters, *Componaster* n. gen. is significant to interpretation of early asterozoan skeletal history. The Katian age of *Componaster* n. gen. is well beyond the Tremadocian and Floian first recorded occurrences of the subphylum; known *Componaster* n. gen. is not stemward in subphylum diversification. The preferred interpretation at the current level of knowledge is that skeletal complexities favor *Componaster* n. gen. as representing a doomed lineage; any similarities with later asterozoans are either remnant plesiomorphies or homoplasies, and beyond these, *Componaster* n. gen. cannot inform on post-Ordovician subphylum evolutionary events and relationship.

GEOLOGY AND STRATIGRAPHY

All specimens of *Componaster* n. gen. were sampled at Tizi n'Mourghi ("cricket's pass", ECR-F1) in the western Tafilalt area, eastern Anti-Atlas, Morocco. This locality is situated about 25 km NW of Rissani and about 30 km SW of Erfoud (see maps in e.g. Lefebvre *et al.* 2007, 2010; Nohejlová & Lefebvre 2022). Although two "starfish beds" were relatively intensely exploited at Tizi n'Mourghi by local fossil dealers in the last 20 years (Lebrun 2018), the precise geological context and stratigraphy of this section remain poorly known. The Tizi n'Mourghi assemblages are generally assigned to the upper part of the Lower Ktaoua Formation (lower Katian, Upper Ordovician) based on the composition of faunal assemblages and geological maps (Service géologique du Maroc 1986, 1988). This stratigraphic position was also confirmed by the late J. Destombes, during a visit of the locality in 2010 (Nohejlová & Lefebvre 2022).

The Tizi n'Mourghi section is about 6 m high, and is located along the steep flanks of the eponymous hill. Three main fossiliferous sandstone beds yielded a low-diversity assemblage composed exclusively of echinoderms: mainly ophiuroids (*Componaster* n. gen. and at least two other yet undescribed taxa), and solutans (*Dendrocystites* aff. *sedgwicki* (Barrande, 1867)), as well as occasional glyptocystitid rhombiferans (*Homocystites adidiensis* Zamora, Nardin, Esteve & Gutiérrez-Marco, 2022), diploporitans (*Asterocystis* Haeckel, 1896) and stylophorans (mitrocystitid mitrates), and extremely rare crinoids (Lefebvre *et al.* 2007, 2010; Hunter *et al.* 2010; Nohejlová & Lefebvre 2022). *Componaster* n. gen. was found in all three distinct fossiliferous beds.

The lower starfish bed consists of a *c.* 20 cm-thick bed of grey, massive sandstone, located at the base of the hill, and yielding mostly ophiuroids (including the holotype of *C. spurius* n. gen., n. sp.), and rare solutans. The uppermost starfish bed is located about 3 m above, where it forms a *c.* 20 cm thick sandstone bed, well-exposed all around the hill. Although ophiuroids are diverse and common in this level, the assemblage is numerically dominated by the solutan *Dendrocystites* aff. *sedgwicki* (Nohejlová & Lefebvre 2022). The intermediate level is thinner (*c.* 15 cm thick) and situated *c.* 1 m below the upper bed. This level is less accessible (along the slope) and has been less exploited than the two other ones. It yielded both ophiuroids and solutans.

At Tizi n'Mourghi, the exceptional preservation of echinoderm specimens (e.g. complete, fully articulated ophiuroids, diploporitans with intact brachioles) is suggestive of the sudden burial (or transport) of living or freshly killed organisms by obrution deposits (Lefebvre *et al.* 2007, 2010; Hunter *et al.* 2010; Nohejlová & Lefebvre 2022). In particular, most specimens of stemmed echinoderms (*Asterocystis* Haeckel, 1896, *Dendrocystites* Barrande, 1887, *Homocystites* Barrande, 1887) are clearly current-aligned in the uppermost bed. Pending a detailed sedimentological investigation, it is not yet possible to conclude if the Tizi n'Mourghi echinoderm Lagerstätte (*sensu* Smith 1988) was generated by storm deposits, or if it results from the *en-masse* downslope transportation of shallower assemblages.

MATERIAL AND METHODS

Twenty-one moldic specimens of *C. spurius* n. gen., n. sp., were available. Of these, ten specimens provide both oral and aboral surfaces, eight of the aboral, and three of the oral surface only.

For the purpose of study and photography, all specimens were cast in latex and some whitened with ammonium chloride. Specimens range 5 mm to 14 mm in arm radii, and 1.5 mm to 4 mm in disk radii. However, none of the arms appear to be preserved fully to the arm tips.

Some specimens were photographed using a Leica MC190HD camera attached to a Leica S8APO microscope, and figured using a series of vertically stacked images at different focal depths, merged with the Leica Application Suite 10 Z-stack Live Image Builder software.

TERMINOLOGY

Terminology begins with Spencer (1914-1940) and is rooted in Spencer & Wright (1966), with developments by Dean (1999), Blake & Hagdorn (2003), and Dean Shackleton (2005). Axial (ambulacral) or axial ossicles form a double series along the axis of the arm, or ambulacral column. Expression of the axial and adaxial elements are fundamental to the class-level assignment of asterozoans, including that of *Componaster* n. gen., whereas the extraxial skeleton is under the more immediate influence of local environmental conditions. The extraxial skeleton of *Componaster* n. gen. is superficially suggestive of the Asteroidea. The axial/adaxial emphasis continues the emphases of earlier publications (Blake 2013, 2018; Blake *et al.* 2020a, b). The oral surface of axials consists of an adradial ridge (perradial ridge or bar) that extends longitudinally along the arm midline, and a transverse ridge, which separates consecutive podial basins. Mouth-angle ossicles are the proximal-most ossicles of the axial series, followed by the more or less differentiated circumorals. Axial ossicles articulate with the adaxial ossicles (adambulacrals of asteroids, laterals of ophiuroids). The remainder of the skeleton is extraxial. The body of many asteroids is edged by a single or double series of more or less clearly differentiated ossicles traditionally termed marginals, which arise behind the terminal. Because the term "marginals" has been broadly applied within echinoderms with unclear implications of homology, the genetically neutral term ambital framework was proposed (Blake 2013). When present, the ambital framework of ophiuroids is limited to the interbrachial disk margin between the arms, and does not extend to the arm tips. In asteroids, a single or double series of marginals separates aboral abactinal disk ossicles from oral actinals, whereas lacking an ambital framework, the term "abactinal" has been used for both aboral and oral disk ossicles, among ophiuroids. Among many earlier asteroids, and in some Paleozoic ophiuroids, a central apical ossicle can be recognized in the middle, or apex of the disk, it enclosed by a ring of more or less differentiated ossicles. A similar but not necessarily homologous feature is also common in crown-

group ophiuroids, where it is referred to as a "centrale" with "primary circlet", "rosette", or aboral ring. Aboral midarm ossicles can be enlarged and/or otherwise differentiated to form a carinal series. A hydropore or madreporite provides opening to the water-vascular system, although a madreporite is difficult to locate in many Paleozoic fossils.

ABBREVIATIONS

Intitutions

AA	Université Cadi Ayyad in Marrakesh;
MDC	Musée des Confluences, Lyon;
MHNM	Muséum d'Histoire naturelle de Marseille;
MHNT	Muséum d'Histoire naturelle de Toulouse.

Other

ad	adaxial;
ax	axial;
co	circumoral;
mao	mouth angle ossicle;
pb	podial basin;
pbr	podial basin rim;
t	torus.

TAXONOMIC ASSESSMENT

Higher level taxonomy of Paleozoic ophiuroids is still evolving. With the elevation of the ophiuroid (see Spencer & Wright 1966) order Stenurida to the class level (Blake 2013), asterozoans with more than a single adaxial ossicle adjacent to the axial are removed from further consideration. All Paleozoic members of the order Phrynophiurida Matsumoto, 1915 have been reassigned to other orders (see Hotchkiss *et al.* 2007; Hotchkiss & Glass 2012; Thuy & Stöhr 2018). The order Oegophiurida Matsumoto, 1915, with its suborders Lysophiurina Gregory, 1897 and Zeugophiurina Matsumoto, 1929, divide Paleozoic ophiuroids based on axial arrangement that is either alternating or paired/fused across the midline of the arm. The most comprehensive available phylogenetic analysis of Paleozoic ophiuroid taxa (Dean Shackleton 2005) did not recover this dichotomy (also see Glass 2005, 2006a). *Componaster* n. gen. exhibits more or less clearly paired as well as offset axials within single arms suggesting an early stage before positioning was fully established within lineages, and therefore *Componaster* n. gen. must remain unassigned at the ordinal and subordinal levels.

SYSTEMATIC PALEONTOLOGY

Class OPHIUROIDEA Gray, 1840

Order *incertae sedis*

REMARK

Apomorphies and additional morphological characteristics used to assign *Componaster* n. gen. to the Ophiuroidea are summarized in Blake (2013, 2014), and amended and/or discussed in Blake & Guensburg (2015), Blake *et al.* (2017) and Blake & Nestell (2019).

Family COMPONASTERIDAE n. fam.

urn:lsid:zoobank.org:act:41895DB8-90EE-4449-B483-8598742EBED4

TYPE AND ONLY-KNOWN GENUS. — *Componaster* n. gen.

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

Genus *Componaster* n. gen.

urn:lsid:zoobank.org:act:26BBD941-4010-451B-8F52-94F2D3A9C1D2

TYPE SPECIES. — *Componaster spurius* n. sp., by monotypy.

ETYMOLOGY. — Latin, *compono*, put together, mix, unite, in reference to the combining of expressions typical of both asteroids and ophiuroids; and Latin, *aster*, star (Brown 1956: 528).

Componaster spurius n. gen., n. sp.
(Figs 1-4)

urn:lsid:zoobank.org:act:D6E0704E-575A-4EA6-9AD3-30C9A1CC450D

MATERIAL EXAMINED. — **Holotype. Kingdom of Morocco** • 1 specimen; Tizi n'Mourghi (Cricket's Pass); Lower Ktaoua Formation, Upper Ordovician (lower Katian); MHNM.15690.113.3.1-2, oral (MHNM.15690.113.3.1) and aboral (MHNM.15690.113.3.2) on separate slabs.
Paratypes. Kingdom of Morocco • 17 specimens; same as for the holotype; AA.TNMa.OS.4, AA.TNMa.OS.5, AA.TNMb.OS.13, AA.TNMb.OS.23, AA.TNMb.OS.28, AA.TNMb.OS.29, MHNM.15690.113.1.1-2, MHNT.PAL.2005.0.138.1.1, MHNT.PAL.2005.0.138.2.1, MHNT.PAL.2005.0.146.1.1-8, MHNT.PAL.2005.0.146.2.1-8, MHNT.PAL.2005.0.155.

TAXON ASSIGNMENTS UNCERTAIN. — Several specimens that co-occur with *C. spurius* n. gen., n. sp. are too poorly preserved to allow unequivocal assignment. Some exhibit sufficient morphology to be suggestive of *C. spurius* n. gen., n. sp. and are listed for completeness. These are AA.TNMb.OS.14, AA.TNMb.OS.18.1, AA.TNMb.OS.18.2, AA.TNMb.OS.20, AA.TNMb.OS.26, AA.TNMb.OS.27, AA.TNMb.OS.30, AA.TNMc.OS.2, ML.20.269412, MHNM.15690.113.2.1-2, and MHNT.PAL.2005.0.163.

ETYMOLOGY. — Latin, *spurius*, false, spurious, illegitimate, in reference to an ophiuroid with form and an aboral skeleton that are suggestive of those of asteroids.

TYPE LOCALITY AND STRATUM. — Lower Ktaoua Formation, Upper Ordovician (lower Katian), Tizi n'Mourghi (Cricket's Pass), Kingdom of Morocco.

DIAGNOSIS. — Ophiuroid with proximally paired, otherwise ontogenetically offset axials distally. Proximal axials with transverse ridge located proximally along adradial ridge (i.e., "boot-shaped"), but positioned medially in offset axials (i.e., "T-shaped"). Abactinals closely abutted, polygonal, aligned in more or less regular series across the arms and aboral interbrachial areas of the disk. An irregular aboral circlet encloses a central apical ossicle.

DESCRIPTION (HOLOTYPE MHNM.15690.113.3.1-2)

Overall form stellate with concave interbrachial margins that smoothly merge with the arms (Figs 1A, B; 3A, E). Aboral disk covered by closely abutting or partially overlapping

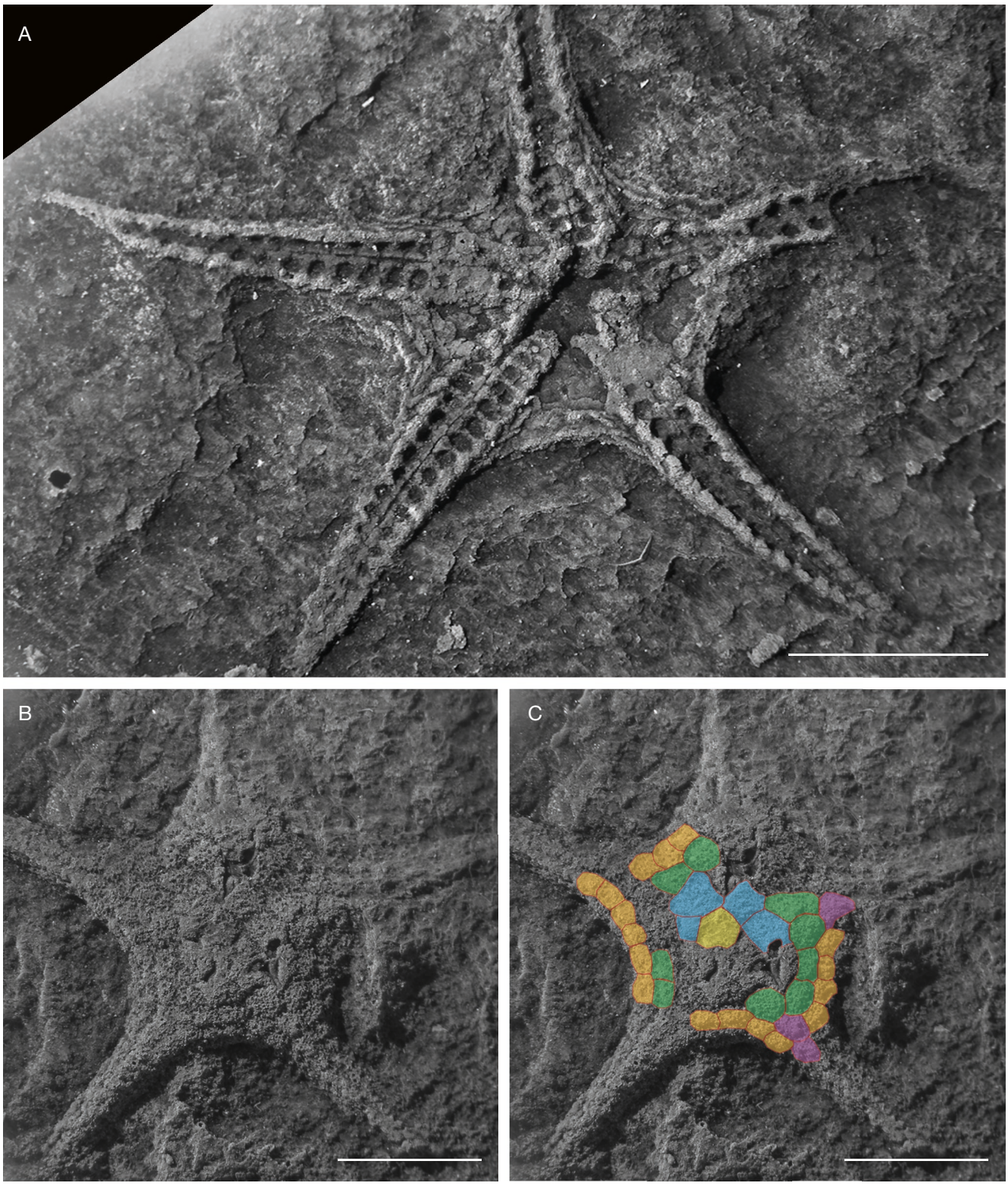

FIG. 1. — *Componaster spurius* n. gen., n. sp., holotype, part and counterpart (MHNM.15690.113.3.1-2): **A**, oral surface; **B**, aboral surface; **C**, aboral surface with interpretation of ossicular arrangement; **yellow**, circlet at apex; **blue**, "primary" circlet; **pink**, mid-arm ossicles; **green**, inner series of ossicles; **orange**, outer series of ossicles framing mid-arm ossicles and extending into interbrachial areas. Scale bars: 4 mm.

ovate to polygonal ossicles, surfaces bearing densely arranged shallow pits (Figs 1B; 2A, C, E, F). Apex of disk bearing single polygonal ossicle (yellow in Figures 1C; 2B, D, F), it surrounded by circlet of ossicles of which at least four are distinguishable (Figs 1C; 2B, D, F). A single row of smaller irregular to polygonal, slightly longer than wide ossicles extend across axis of the proximal arm portions (pink in Figures 1C; 2). Where each of these rows enters the disk area it joins a series of similar ossicles (green in Figures 1C; 2B, D, F) that extend parallel to interbrachial margin curvature to join central ossicular rows of neighboring arms. The latter (green in Figure 1C) series of ossicles abut directly to the circlet of ossicles that surround the apex (Figs 1C; 2D, F). Adjacent, on each side of the mid-arm ossicles extends an additional row of often smaller and slightly longer than wide ossicles (orange in Figures 1C; 2B, D, F, H) that follow the gradual curvature of the interbrachial disk area to the adjacent arm. Evidence of a potential additional outer series of aboral adradial ossicles, as marked by the remnants of multiple individual ossicles of uncertain size and shape along the outermost edges of the disk (see adradial to the orange circlet in Figures 1C). Accessory disk ossicles (spines, granules, articulation sites) not observed. The oral interbrachial disk areas covered by irregular rows of closely abutting, tightly packed, elongated scalar ossicles (Fig. 3B, C, E). Madreporite not observed.

Arms taper evenly. At least ten axial-adaxial pairs inside disk, free arm length about as or slightly longer than maximum disk diameter (Figs 1; 2; 3A). Axial arrangement across arm midline inconsistent along and among arms: proximally axials (first 3-4 axials) paired or slightly offset, gradually becoming significantly offset (fully alternating) for remainder of arm (Figs 1A; 3A, B, E; 4A-C). Axial midline straight to slightly sinusoidal (Figs 4A, B). Oral axial adradial ridge surfaces closely abutting proximally and distally, lacking orally visible interaxial muscle gaps (Figs 3A, E; 4A). Transverse ridge located proximally along the adradial ridge in proximal (first 3-4) axials, thereafter location changes gradually more distally to medially along each axial's adradial ridge (Figs 1A; 3A, D, E; 4A). Podial basins round to slightly wider than long (Figs 1A; 3A, E). Where visible at proximal arm region, podial basin floors formed by the proximal axials, with slightly raised, rounded abradial edges forming rims (Figs 3D; 4A), some with possible skeletal gaps between basin floor edge and adradial adaxial wall (Fig. 4A). Aboral surface of axials smooth with proximal and distal boundaries slightly curved abradially and distally, resulting in skewed axial shape (Fig. 4B, C). Adaxials stout, oral abradial surface slightly below axials. Consecutive adaxials closely abutting proximally and distally. Proximal adaxials with single, distal flange, bordering podial basins. More distally, the abradial podial basin margin is partially shared with a proximal flange on distal adaxial. Abradial edge of adaxials slightly curved (Figs 3E; 4A). Lateral or groove spines, or associated articulation sites, not recognized. Orally, single adradial podial basin on each mouth angle ossicle, and a proximal-most, scoop-shaped depression between adjacent (Fig. 3E). Aboral surface of mouth frame ossicles hidden by aboral skeleton.

Morphological variation in the paratypes

Some of the paratypes exhibit some minor morphological variation from the holotype. Paratype MHNM.15690.113.1.2 exhibits an additional irregular circlet of ossicles between the centermost (blue in Figure 2B) and the outermost aboral circlet (orange in Figure 2B). This paratype is the largest specimen and presence of additional ossicles could be reflective of increased size. Paratype AA.TNMb.OS.2 (Fig. 2F) exhibits an unequivocal central apical ossicle surrounded by an aboral circlet of six equally-sized ossicles. In paratype AA.TNMb.OS.28, one of these circlet ossicles appears compound, constructed of three closely fitted ossicles (Fig. 2D). Paratype AA.TNMb.OS.23 (Fig. 2H) lacks an unequivocal central apical ossicle and associated circlet but the specimen's overall poor preservation makes identifying ossicular boundaries particularly difficult.

Paratypes MHNM.15690.113.1.2 (Fig. 2B) and AA.TNMb.OS.28 (Fig. 2D) support the interpretation of a possible additional series of aboral ossicles along the margin of the disk, as described in the holotype. Alternatively, these features might be the aborally exposed abradial edges of the scalar ossicles that cover the oral interbrachia.

In contrast to the tightly fitted and stout polygonal ossicles on the aboral surface, the interradii of the oral surface consist of oval-shaped scalar ossicles. In places they appear to imbricate slightly towards the mouth as in the holotype (Fig. 3E). This is also visible in at least one interbrachial of the paratype MHNT.PAL.2005.0.138.2.1 (Fig. 3B) where they form shingle-like rows, however, they are more irregularly distributed in others (Fig. 3C), perhaps due to disruption.

The number of proximally paired axials appears to vary within and among specimens. Whereas the holotype exhibits 3-4 paired axials before the first offset, at least one arm in each paratype MHNT.PAL.2005.0.146.1.3 and MHNT.PAL.2005.0.138.2.1 has up to five paired axials. In contrast, paratype MHNT.PAL.2005.0.146.2.3 shows a slight offset of the aboral axial distal surface of the axial immediately beyond the paired circumorals (Fig. 4C, D), whereas this shift doesn't occur in some of the arms of paratype MHNT.PAL.2005.0.146.2.8 until the second or third axial after the circumoral (Fig 4B).

The floors of the podial basins and associated abradial cup-like rims adradial to the abutting adaxial are visible on proximal axials of the holotype and paratype MHNT.PAL.2005.0.146.1.3 (Fig. 3D). Here, consistent with a proximal abradial ridge, podial basin floors consist of a single axial. Ossicular boundaries of the podial basins shared by consecutive axials due to centrally located adradial ridges are poorly preserved in all available specimens. It cannot be determined unequivocally that shared podial basins consist of a partial distal floor and the proximal floor of the distal axial, as is the case in some other asterozoans, or whether they consist of distally extended floors of the proximal axial.

The aboral surface of the mouth frame is covered by the disk skeleton in the holotype. Paratypes MHNT.PAL.2005.0.146.2.3 and MHNT.PAL.2005.0.146.28 have exposed oral mouth frames that exhibit mouth angle ossicles that are long and slen-

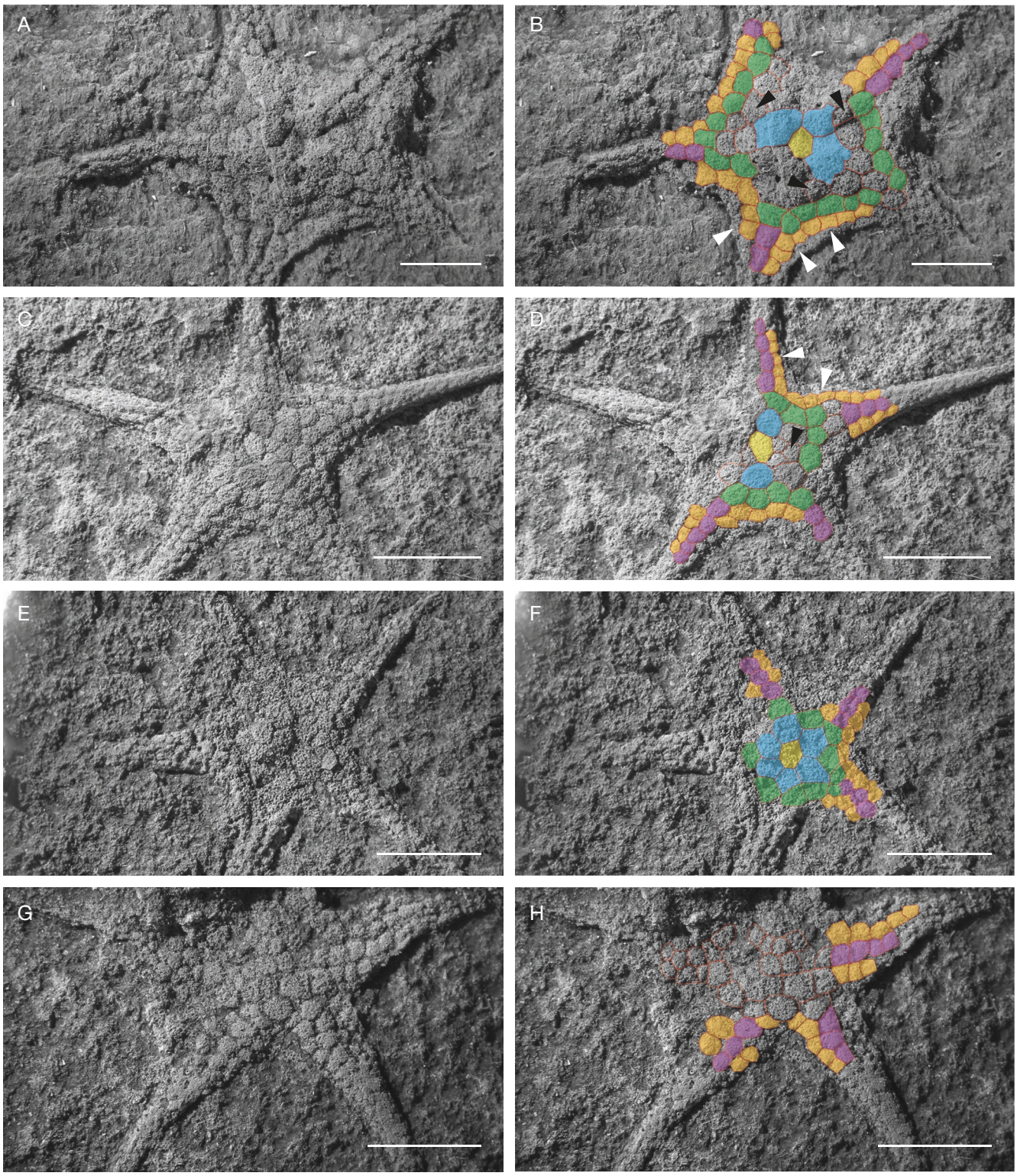

FIG. 2. — *Componaster spurius* n. gen., n. sp., aboral surfaces, interpretations of ossicular arrangement: **A**, **B**, only specimen exhibiting ossicles (**black arrow**) between the primary circlet (**blue**) and the series of aboral ossicles (**green**) onto which the mid-arm ossicles (**pink**) abut. Note presence of undifferentiable ossicles (**white arrows**) along the edge of disk (MHNM.15690.113.1.2); **C**, **D**, irregular primary circlet (**blue**) includes a composite of smaller ossicles (**black arrow**). Note presence of undifferentiable ossicles (**white arrows**) along the edge of disk (AA.TNMb.OS.28); **E**, **F**, specimen exhibiting well formed "primary circlet" (**blue**) consisting of six ossicles (AA.TNMb.OS.29); **G**, **H**, specimen without discernable primary circlet, central disk ossicles irregularly arranged (AA.TNMb.OS.23). Scale bars: 4 mm.

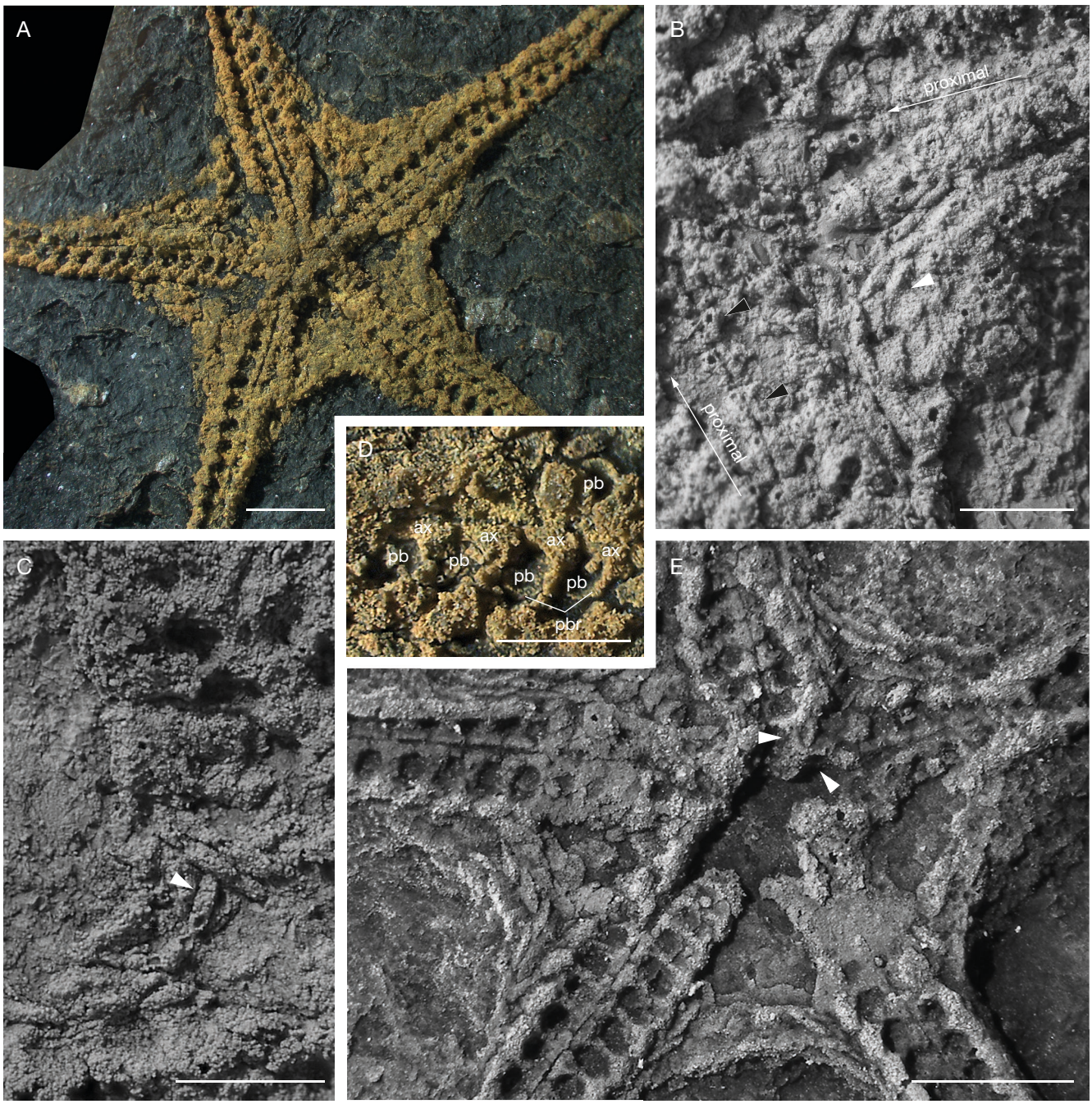

Fig. 3. — *Componaster spurius* n. gen., n. sp.: **A**, oral surface, color due to iron oxide staining of mold; evenly tapering arms; proximal-most axials paired or slightly offset, then changing to offset and fully alternating axials distally (MHNT.PAL.2005.0.146.1.3); **B**, oral view, proximal arms and interbrachial area; axials paired to slightly offset (**black arrows**); rows (**white arrows**) of elongated scalar disk ossicles (MHNT.PAL.2005.0.138.2.1); **C**, oral view, possibly disrupted irregular distribution of scalar disk ossicles (**white arrow**) in interbrachial area (MHNT.PAL.2005.0.138.2.1); **D**, oral view, proximal region of left-most arm (**A**), axial (**ax**) transverse ridge transitions from proximal to medial; large podial basins (**pb**) with floors on single axial; abradial rims (**pbr**) of basin rounded (MHNT.PAL.2005.0.146.1.3); **E**, holotype, oral view, disk with imbricated scalar interbrachial ossicles; podial basins prominent (**white arrows**) on pair of mouth angle ossicles; axials transition from irregularly paired to more offset (MHNM.15690.113.3.1). Scale bars: A, E, 2 mm; B-D, 1 mm.

der aborally, together with circumorals creating characteristic ophiuran Y-shaped configuration with small, proximal-most torus in MHNT.PAL.2005.0.146.2.3 (Fig. 4D).

Remarks on preservational ambiguities

Even though *Componaster spurius* n. gen., n. sp. is known from multiple specimens in both oral and aboral aspect, ambiguities and poor preservation among and within specimens leave room for alternative interpretations. Some molds are partially filled with a powdery to very-fine, grainy crystalline residue of iron oxide (see Figs 3A, D; 4B-D). The effects on the latex casts include partial or complete loss of boundaries between ossicles, and a granular surface "veneer" obscuring true ossicular surface textures. Missing or partially preserved

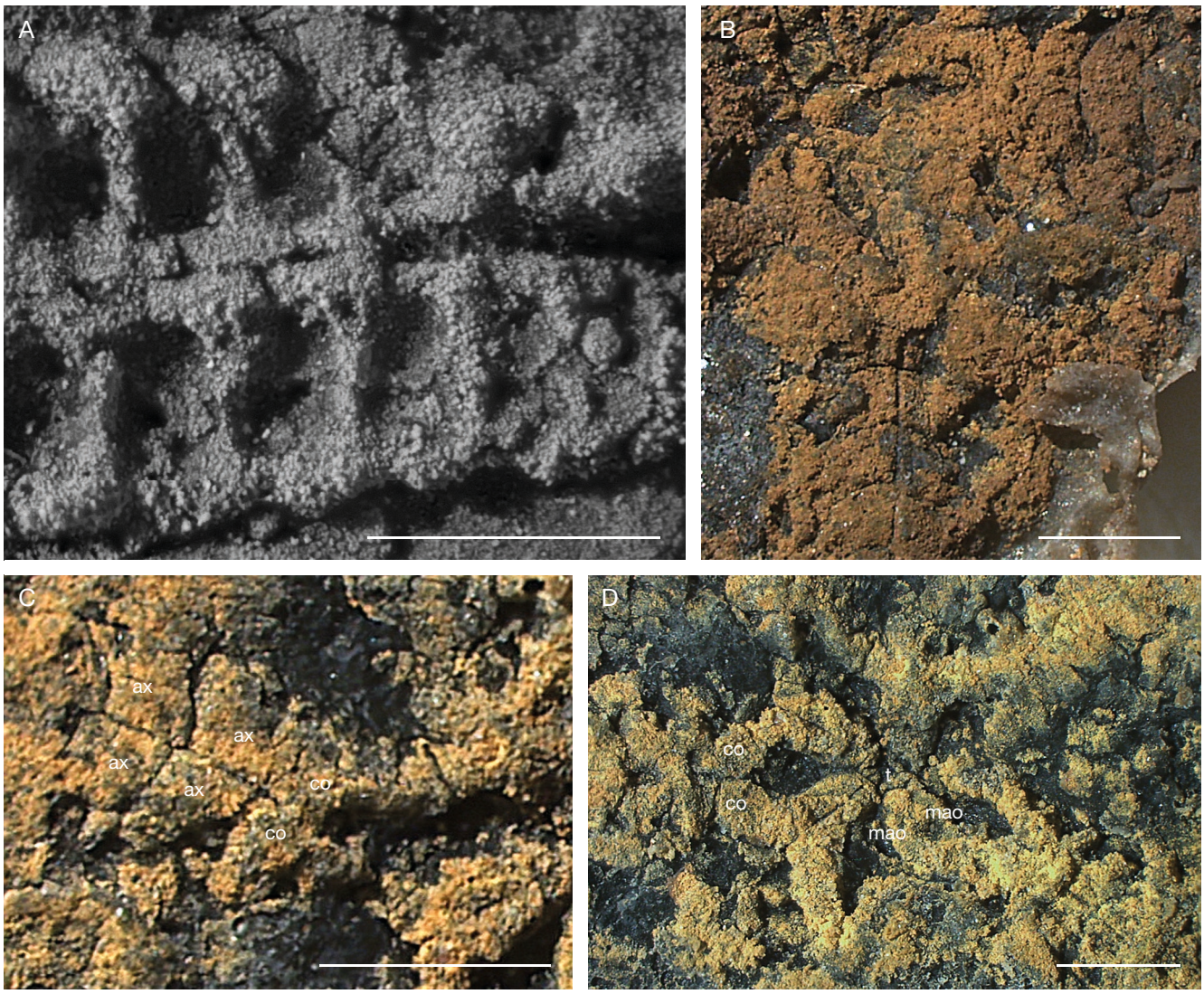

Fig. 4. — *Componaster spurius* n. gen., n. sp.: **A**, holotype, proximal oral arm region, transition between irregularly paired to increasingly offset axials; position of transverse ridge changes from proximal to more medial; podial basin rims (**pbr**), possible skeletal gaps (**gp**) visible between rims of podial basins and adradial surfaces of cupping adaxials (MHNM.15690.113.3.1); **B**, aboral view of portion of mouth frame and proximally paired axials; axials rectangular and skewed abradially (MHNT.PAL.2005.0.146.2.8); **C**, aboral view of circumoral (**co**) and paired to slightly offset proximal axials (**ax**) (MHNT.PAL.2005.0.146.2.3); **D**, aboral view of mouth frame; circumoral (**co**), mouth angle ossicles (**mao**), and possible torus (**t**), (MHNT.PAL.2005.0.146.2.3). Scale bars: 1 mm.

ossicles, including variations in ossicular depth, might not necessarily be due to taphonomic or diagenetic factors, but a result of variable infilling of the molds with the iron oxides – affecting the fidelity of the final latex cast. These vagaries challenge observation and interpretation of morphology. In particular, it severely limits the application of the detailed "lateral arm plate" (LAP) morphologies proposed by Thuy & Stöhr (2011) and used for post-Paleozoic ophiuroids and Paleozoic crown-group members. Adaxial surfaces in available specimens exhibit too few unambiguous details to allow such a comprehensive analysis.

Among available specimens of *C. spurius* n. gen., n. sp., the distal-most arm tips have been lost, and ossicular boundaries are equivocal. Whether the mid-arm ossicles, and adjacent aboral series of adradial ossicles extend to the distalmost arm tips cannot be determined.

Coding for Lovén's law was not possible due to poor preservation and lack of consistent exposure of relevant arm regions.

DISCUSSION OF MORPHOLOGY

Componaster n. gen. exhibits well-articulated axials, adaxials, and mouth frame ossicles. Offset and paired axials are closely articulated across the arm midline, skeletally encapsulating the central radial channel. Midline axial articulation is planar (not vaulted as in asteroids), and the position of the single adaxial, paired with each axial, is lateral. Adaxials are shield-like, with slightly raised oral abradial ridges. Mouth angle ossicles are narrow, and elongate, and together with the circumorals, project into the mouth in a characteristic Y-shape. These ophiuran characteristics justify assignment to the class

Ophiuroidea (Blake 2013, 2014). Assessment and discussion of *Componaster* n. gen. morphologies unusual for stem-group ophiuroids follows.

Central and aboral circlet

Most stem-group Paleozoic ophiuroids lack regular rows or circlets of stout, plate-like, aboral disk ossicles. Instead, granulated or pustulated skin, and/or irregularly arranged overlapping or abutting scalar ossicles make up the disk skeleton. In contrast, many crown-group ophiuroids exhibit a "centrale" with a "primary circlet" or "rosette" either in ontogeny or as adults (Stöhr & Martynov 2016). Hotchkiss (1980: 93) reported "a centrale and five primary radials" in a juvenile protasterid from the Devonian, and hypothesized therefore that this condition is plesiomorphic among ophiuroids, albeit phenotypically unexpressed, until it first (re)appears in the fossil record in the stem-group juvenile protasterid in question, as well as the Late Devonian *Ophiaulax decheni* (Dewalque, 1881), and the Mississippian *Aganaster gregarious* Meek & Worthen, 1869. The latter are both ophiuroids of the crown-group (Hotchkiss & Haude 2004; Thuy *et al.* 2022). Such a feature is also present in some early asteroids in the Paleozoic (Blake 2018). Although a central apical ossicle is readily identified in most specimens of *Componaster* n. gen., the only completely identifiable circlet consists of six ossicles, rather than five, and the remaining specimens exhibit variability in both shape, size, and number of candidate circlet ossicles. This argues against it being homologous to a possible plesiomorphic centrale and aboral circlet in ophiuroids, or asteroids. Nevertheless, it represents a unique example of an early experiment in stout aboral ophiuroid disk skeletonization, but an innovation that failed to establish itself further. Subsequent evolution seems to have favored lightly constructed aboral disk skeletons in Paleozoic stem-group ophiuroids.

Midarm ossicles

Midarm ossicles are lacking among somasteroids but are present in some asteroids. A single row of aboral arm ossicles matched to each arm vertebra first appears in the Devonian and is limited to ophiuroids of "modern aspect" (Hotchkiss & Haude 2004). The Devonian occurrences have been treated as homologous with the aboral arm ossicles or dorsal arm plates (DAPs) common among extant forms (Thuy *et al.* 2022), and DAPs are such a fundamental part of the crown group that some early workers were led to arguments favoring presence in Paleozoic representatives, mistaking the exposed aboral surface of the vertebrae for DAPs (e.g. Stürtz 1886a, b; also see discussion in Hotchkiss 1993). In contrast, the arms of Paleozoic ophiuroids are typically covered by either multiple small irregularly arranged granules, or scale-like ossicles, or were entirely void of skeletal cover. Hotchkiss (1980, 1993) identified spine-bearing aboral arm ossicles in a juvenile protasterid, and the protasterid *Strataster* Kesling & Le Vasseur, 1971. However, unlike the DAPs of extant members, ossicles are not in a one-to-one correlation with the underlying axials, and do not extend to the arm tips. Glass & Poschmann (2006) reported four more or less regular rows of elongated, plate-like aboral arm ossicles not correlated with the axials in the Devonian ophiuroid *Lapworthura lehmanni* Glass & Poschmann, 2006. Smith *et al.* (1995) judged the morphology of *Strataster* to be similar enough to be used as an outgroup taxon to anchor their molecular phylogeny of extant ophiuroids to those in the Paleozoic, yet a recent phylogenetic analysis (Thuy *et al.* 2022) suggests that protasterids such as *Strataster* and *Lapworthura* Gregory, 1897 are members of clades that are neither closely related to each other nor to the lineage leading to the extant crown-group, in contrast with the posited phylogenetic positioning of Dean Shackleton (2005: fig. 15). As with *Strataster*, and the unidentified juvenile protasterid of Hotchkiss (1980), the single series of midarm ossicles of *Componaster* n. gen. are not correlated with the axials. Their proximal-most extent on the disk and their distal expression towards the arm tips equivocal or unknown. Aboral arm configuration of *C. spurius* n. gen., n. sp., like that of the disk, is suggestive of those of many asteroids (e.g. *Aerliceaster* Blake, Gahn & Guensburg, 2020a [Blake & Hotchkiss 2022]) rather than either the lighter aboral arm skeletons common in Paleozoic stem-group ophiuroids or the regular, single DAPs common in crown-group ophiuroids.

Following ontogenetic and developmental review of extant ophiuroids, midarm ossicles were argued to have been plesiomorphic in both asteroids and ophiuroids but lost to resorption among most Paleozoic lineages, then re-established in the crown-group lineage (Hotchkiss 1993). The aboral arm expression of *C. spurius* n. gen., n. sp. is consistent with this viewpoint; however, no such differentiation has been recognized among stem-group somasteroids, raising doubts about their plesiomorphic status. For those asteroids with cylindrical arms, differentiation of the midline carinal series was a suggested constructional adaptation (Blake & Rozhnov 2007), and arguably widespread homoplasy. Similar homoplasy might be present in several early ophiuroid lineages.

Ambital series

Traditionally the term "marginals" has been applied across echinoderm clades, including edrioasteroids, to describe differentiated ossicles that frame body margins. The robust ambital framework of encrinasterids/euzonosomatids and Paleozoic crown-group ophiuroids such as *Ophiurina lymani* Stürtz, 1890 (Glass 2006a) are not homologous with the ambital frameworks of somasteroids and asteroids, because they are restricted to the disk (Dean Shackleton 2005) and therefore the term "ambital framework" was introduced for descriptive purposes (Blake & Guensburg 2015). Because of preservational limitations, presence of a marginal series extending to the arm tips cannot be unequivocally dismissed, but none has been recognized among the many available specimens, and although a negative argument, it is concluded that such a series was absent from *C. spurius* n. gen., n. sp. The better preserved more regular aboral disk ossicles that frame the interbrachial areas and appear to extend onto the arm margins in *Componaster* n. gen. are not noticeably differentiated in size or shape from other disk ossicles. True marginals and ambital frameworks usually stand out, not just in their regular

continuity, but due to their shape being differentiated from other disk ossicles (see discussion in Dean Shackleton 2005: 39-41). Hence, at minimum, if any aboral disk ossicles along the margins of *Componaster* n. gen. form an ambital framework, their lack of differentiation is consistent with the generally uniform nature of stem-group ophiuroid disk skeletonization.

Notably, aboral ossicles of *C. spurius* n. gen., n. sp. consistently form an asteroid-like concave disk margin in plan view that smoothly grades into the length of the arms. Light skeletonization and absence of an ambital framework allows great flexibility in many extant ophiuroids, where interbrachial disk margins can vary from concave to convex, even in the same individual [A.G. personal observation on *Ophioarachna incrassata* (Lamarck, 1816)], a phenomenon that is also preserved in many Paleozoic forms, especially those with lightly scaled or granular disks. The consistent shape of the interbrachial disk margins of *Componaster* n. gen. suggests that the stouter aboral disk ossicles along the margins could provide stiffness to the disk, hence providing functional benefits equivalent to the more differentiated ambitals found in asteroids.

Aboral and oral disk skeleton

In general, there is little to no differentiation of aboral and oral interbrachial disk skeletons in stem-group ophiuroids. In contrast, in *C. spurius* n. gen., n. sp., even with absence of unequivocal ambital series, the stout, tightly fitted, and more or less regular arrangement of circlets and series on the aboral disk surface is in significant contrast with the imbricated, irregularly arranged scalar and plate-like ossicles of the oral interbrachials, the former "asteroid-like," the latter more ophiuran. Such a level of differentiation of aboral from oral disk ossicles is unusual for stem-group ophiuroids. Suggestion of a circlet and irregular continuity of potential midarm ossicles and ambital framework is reminiscent of the irregular order of the aboral disk ossicles described in the early asteroid *Aerliceaster nexosus* Blake, Gahn & Guensburg, 2020a; the latter can be described as an emergent condition in asteroids, whereas that of *C. spurius* n. gen., n. sp. did not endure in stem-group ophiuroids.

Mouth frame

Where exposed, the mouth frame of *Componaster* n. gen. consists of the typically elongated and slender proximal-most axials, the mouth angle ossicles, and circumorals (second axials) forming a characteristic Y-shaped mouth skeleton that is typical of those found throughout stem-group and some Paleozoic crown-group ophiuroids.

Axial arrangement

The presence of both variably paired to alternating axials makes *Componaster* n. gen. unusual among ophiuroids. Traditional classifications of Paleozoic ophiuroids (e.g. Spencer & Wright 1966) have emphasized differences in the arrangement of the axials across the arm axis: double rows of alternating, or double rows of opposing axials. A third configuration, opposed and fused axials (i.e., vertebra), represents the typical axial ossicle expression in crown-group ophiuroids since at least the Silurian (Thuy *et al.* 2022, but also see discussion in Stöhr & Martynov 2016). Vertebrae develop in the extant ophiuroids by fusion of two separate, but opposing, incipient axial ossicles during ontogeny (see Ludwig 1878), which led Sollas & Sollas (1912) to argue that Paleozoic stem-group ophiuroids with opposing but unfused axials represent the ancestral evolutionary state (see also Spencer 1951). In turn, ophiuroids with alternating axials were posited to be plesiomorphic to those with paired axials (Spencer 1914; Fell 1963; Hotchkiss 1995). Current phylogenetic hypotheses suggest opposing axials in ophiuroids to be either homologous across the group (Thuy *et al.* 2022: fig. 2) or due to homoplasy (Dean Shackleton 2005: 55, 58, fig. 14; Glass 2005, 2006a: fig. 7.2; Hunter & Ortega-Hernández 2021: fig. 2; also see Blake & Hotchkiss 2022). Dean Shackleton (2005: 58, fig. 14) furthermore suggested reversal from opposing back to alternating axials in the protasterid ophiuroids (*sensu* Dean Shackleton 2005; also see Hunter *et al.* 2016: 4). Although consensus on potential homoplasy is lacking, opposite, unfused axials were found to have been derived from alternating axials in all phylogenetic hypotheses. Since taxa with opposite, unfused axials (*Stenaster* Billings, 1858; *Lapworthura* , *Hypophiura* Jaekel, 1923, and *Hallaster* Stürtz, 1886a) are first known from the Late Ordovician (Sandbian-Katian), derivation must have occurred early in ophiuroid evolution. Indeed, Blake *et al.* (2016) reported an upper Floian (Lower Ordovician) occurrence of a possible *Stenaster* sp. with affinities to *Stenaster obtusus* (Forbes, 1848). Notably, its axials are paired proximally, as is typical for *Stenaster*, but offset distally towards the arm tips, suggesting a gradational emergence of the paired-offset dichotomy of later ophiuroids (Blake *et al.* 2016). The presence of proximally fully or irregularly paired, and distally, irregularly offset axials in the Katian *C. spurius* n. gen., n. sp., implies plasticity of this character continued even after the dichotomy had been well established in other lineages. The presence of both paired and irregularly offset axials in a single taxon calls for re-evaluation of this character in future character coding for cladistic analysis.

During growth, extant ophiuroids add arm segments at the tip of arms (Clark 1914), and growth habits of Paleozoic forms might have been the same (see discussion in Hotchkiss 1980, 1993; Hotchkiss & Haude 2004). Hence, the change from paired to offset axials in *C. spurius* n. gen., n. sp., and *Stenaster* aff. *obtosus*, distally along the arm, might intimate a possible derivation of offset axials in ophiuroids through allometric repatterning in ontogeny (Webster & Zelditch 2005) of an ancestor with paired axials. Dean Shackleton (2005: 58) recovered at least one example of such a "reversal" in her protasterid clade, however, the alternative of deriving paired axials independently is only a single step from parsimony. In contrast, expression of juvenile features in extant ophiuroids is found in the distal arm elements (Stöhr & Martynov 2016), and paedomorphic expression might reflect plesiomorphic conditions. If this phenomenon applies to the relative positioning of axial elements, then both the examples of *Stenaster* aff. *obtusus* and *Componaster* n. gen. are consistent with an offset to paired axial trajectory. However, whether offset or paired axials are plesiomorphic in stem-group ophiuroids

remains equivocal, furthermore, the variable nature of the axials in *C. spurius* n. gen., n. sp. creates a third possibility, that paired and/or alternating axials as discrete character states emerged from an irregular arrangement, rather than one from the other.

Position of axial oral transverse ridge

The offset axials of *Componaster* n. gen. exhibit medial to slightly proximal oral transverse ridges. Paleozoic stem-group ophiuroids with unfused axials typically exhibit proximal transverse ridges, creating a proverbial "boot-shaped" oral axial surface (see Spencer & Wright 1966: U83; see also Glass & Blake 2004: fig. 6B; Glass 2006b, c and discussion therein). Podial basins are distal of the ridge and floored within a single axial. Notable exceptions are *Stenaster* and *Palaeura* Jaekel, 1903, and perhaps *Medusaster* Stürtz, 1890, in which the transverse ridge is more medially-placed (Spencer 1951; Spencer & Wright 1966; Glass 2006a), creating "T-shaped" oral axial surfaces (e.g. Smith *in* Gutiérrez-Marco *et al.* 1984). *Medusaster* remains poorly understood (see Lehmann 1957), precluding comparison with *Componaster* n. gen., whereas the unusual and unique morphology of *Stenaster* (see Dean 1999) readily differentiates it from *Componaster* n. gen. and all other Paleozoic ophiuroids.

This leaves *Palaeura* as a taxon with potential similarities to the oral axial expression of *Componaster* n. gen. Spencer (1951: fig. 24) has heretofore provided the only close-up interpretative drawing of the axials of *Palaeura neglecta* Schuchert, 1914, showing transverse ridges placed slightly more proximally compared to other early Ordovician asterozoans with clearly medially placed ridges. Spencer (1951) argued that the resultant oral surface shape presented a step towards the emerging "boot-shaped" axials of later ophiuroids with proximally placed ridges. Spencer & Wright (1966) alluded to this intermediate morphology when defining the family Palaeuridae as having "ambulacrals with incipient boot-shaped median ridge" (Spencer & Wright 1966: U82). A similar slightly more proximal than medial transverse ridge is figured by Smith in Gutiérrez-Marco *et al.* (1984: fig. 12A) in the subspecies *Palaeura neglecta hispanica*, and although Dean Shackleton (2005: 78) describes the oral axial surface as being "T-shaped, she also notes that the distal podial basin flange was larger than the proximal flange, suggesting a transverse ridge slightly offset proximally from a medial position.

The position of the transverse ridge in *Componaster* n. gen. varies from proximal in axials near the mouth frame, to fully medial in distal axials outside of the disk. Hence, some of the proximal oral axial surfaces inside the disk of *Componaster* n. gen. bear similarity to those of *Palaeura.* A careful study of the type material of *Palaeura neglecta*, particularly an assessment of whether and how the position of the transverse ridge changes along its arms, will be necessary to fully assess any similarities to *Componaster* n. gen. Such assessment is beyond the scope of this study.

Other than the taxa mentioned above, Blake *et al.* (2017) described variable placement, including more medially placed transverse ridges in a Silurian encrinasterid ophiuroid, and Hunter & McNamara (2018) described a Permian protasterid with significantly more medially placed transverse ridges than had been previously recorded for the family. Better documentation and careful analysis of existing taxa is necessary to assess variability in the placement of the transverse ridge in stem-group ophiuroids with unfused axials.

CONCLUSIONS

In accord with the skeletal classification of Spencer & Wright (1966), the new genus and species *Componaster spurius* n. gen., n. sp. is assigned to the Ophiuroidea based on the clear development of the axial and adaxial skeletons. In contrast, the extraxial skeleton shares commonalities with many representatives of the Asteroidea. Because of its Katian age, *C. spurius* n. gen., n. sp. cannot readily be treated as a stem genus marking the ophiuroid – asteroid separation.

Explanation for the extraxial configuration of *C. spurius* n. gen., n. sp. is uncertain because no stemward taxon can be identified. Extraxial expressions might be plesiomorphic or alternatively they might at least in part reflect more immediate environmental evolutionary pressures. Although certain aspects of morphology, such as presence of a distinct middorsal disk ossicle, are found among later ophiuroids, it is the unique combination of expressions of *C. spurius* n. gen., n. sp. that is crucial. Because of character combination, *C. spurius* n. gen., n. sp. is interpreted as representing an extinct, stem-group lineage. It cannot be determined which expressions of *C. spurius* n. gen., n. sp. that are shared with younger ophiuroids might be plesiomorphic and which might be homoplastic among the latter, and therefore extended comparison with later ophiuroids is not justified.

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