

Research



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Palaeontology

A new somasteroid from the Fezouata Lagerstätte in Morocco and the Early Ordovician origin of Asterozoa

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The somasteroids are Lower Palaeozoic star-shaped animals widely regarded as ancestors of Asterozoa, the group of echinoderms that includes brittle stars and starfish. However, the origin of asterozoans, the assembly of their distinctive body organization, and their relationships with other Cambrian and Ordovician echinoderms remain problematic owing to the difficulties of comparing the endoskeleton between disparate groups. Here, we describe the new somasteroid *Cantabrigiaster fezouataensis*, a primitive asterozoan from the Early Ordovician Fezouata Lagerstätte in Morocco. *Cantabrigiaster* shares with other somasteroids a unique endoskeletal arm organization and the presence of rod-like virgal ossicles that articulate with the ambulacrals, but differs from all other known asterozoans in the absence of adambulacral ossicles defining the arm margins, evoking parallels with non-asterozoan echinoderms. Developmentally informed Bayesian and parsimony phylogenetic analyses, which reflect the homology of the biserial ambulacral ossicles in Palaeozoic echinoderms according to the extraxial–axial theory, recover *Cantabrigiaster* as the earliest divergent stem-group asterozoan. Our results illuminate the ancestral morphology of Asterozoa, and clarify the affinities of problematic Ordovician Asterozoa. Bayesian inference and parsimony demonstrate that somasteroids represent a paraphyletic grade within stem- and crown-group Asterozoa, whereas stenuroids are paraphyletic within stem-group Ophiuroidea. Our results also offer potential insights on the evolutionary relationships between asterozoans, crinoids and potential Cambrian stem-group representatives.

1. Introduction

Asterozoans—whose most familiar members include starfish and brittle stars—are the dominant group of extant echinoderms based on their diversity, abundance and biogeographic distribution [1]. Despite their ecological success and a fossil record spanning more than 480 Myr [2–4], the origin and early evolution of asterozoans, and those of crown-group echinoderms more generally, remain uncertain given the difficulty of comparing the organization of the calcified endoskeleton in diverse Lower Palaeozoic groups, such as the edrioasteroids and blastozoans [5–13]. The extraxial–axial theory (EAT), which supports the homology of the biserial ambulacral ossicles of pentaradial and non-pentaradial echinoderms based on embryonic and ontogenetic data [14–16], has been proposed as a developmentally informed model that facilitates comparisons among groups with disparate morphologies. Although the EAT can potentially clarify the early evolution of crown-group Echinodermata, the broad implications of this hypothesis

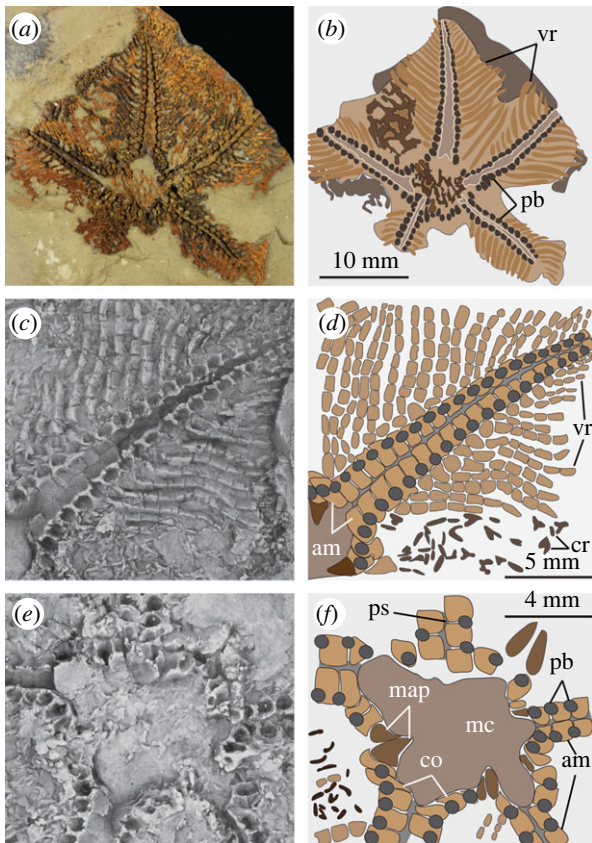


Figure 1. *Cantabrigiaster fezouataensis* from the Lower Ordovician (Tremadocian) of Morocco. Holotype UCBL-FSL 424961 (Van Roy coll.). (a) Oral view (body fossil). (b) Interpretative diagram of (a). (c) Close-up of extended arm (latex mould). (d) Interpretative diagram of (c). (e) Close-up of oral region (latex mould). (f) Interpretative diagram of (e). am, ambulacral ossides; co, circumoral ossides; cr, carinal region ossides (preserved on the aboral surface); map, mouth angle plates; mc, mouth cavity; pb, podial basins; ps, podial suture; vr, virgal ossides.

have never been examined under a comprehensive quantitative phylogenetic framework. Consequently, the main phylogenetic predictions of the EAT pertaining to the evolutionary relationships of Cambrian and Ordovician echinoderms, such as the origin of the crown group from edrioasteroid-like ancestors [14–17], although analysed with other homology schemes [9,11,18], have yet to be critically tested using EAT.

Here, we describe the new somasteroid *Cantabrigiaster fezouataensis* gen. et sp. nov. (figure 1) from the Early Ordovician (Tremadocian) Fezouata Shale in Zagora, central Anti-Atlas, Morocco [4] (electronic supplementary material, figure S1 and SI Text). The exceptionally preserved morphology of *Cantabrigiaster* reveals a unique plate organization among somasteroids, and allows us to test the phylogenetic implications of this taxon for the origin of total-group Asterozoa. Central to our phylogenetic hypothesis is the presence of an imperforate extraxial body capsule on the aboral surface of the somasteroids which is then lost in derived asterozoans so that the aboral surface is entirely composed of perforate extraxial body wall, for example, carinals in asteroids, and ventral, dorsal and lateral arm plates in ophiuroids [15].

2. Material and methods

(a) Specimen analysis

The studied material is deposited in the palaeontological collections of the University of Lyon 1 (UCBL-FSL), Natural History

Museum of Nantes (MHNN), National Museum, Prague (NM-P) and Yale Peabody Museum, Yale University (YPM). Latex moulds were made of all the material with the exception of that from the YPM. The material was photographed with a Nikon D5500 SLR fitted with Micro Nikkor 40 mm.

(b) Phylogenetic analysis

The character matrix for the phylogenetic analyses includes 38 taxa and 74 characters (see electronic supplementary material, datasets S1 and S2); detailed discussion of character scoring and applicability are provided in electronic supplementary material, SI Text. The Bayesian analysis was run in MrBayes 3.2 using the Monte Carlo Markov chain model for discrete morphological characters [19,20] for 10 million generations (four chains), with every 1000th sample stored (resulting in 10 000 samples), and 25% burn-in (resulting in 7500 retained samples). The parsimony analyses were run in TNT [21] under New Technology Search, using Driven Search with Sectorial Search, Ratchet, Drift and Tree fusing options activated with standard settings [22,23]. The analysis (figure 2) was set to find the minimum tree length 100 times and to collapse trees after each search. All characters were treated as unordered. For comparative purposes, analyses were performed under equal and implied weights ($k=3$) to test the effect of homoplasy penalization on the position of *Cantabrigiaster* and the robustness of the dataset [25]. Comparisons between results of the phylogenetic analyses are presented in the electronic supplementary material. Parsimony-based analysis under Traditional Search with 10 000 replicates produced results identical to those obtained under New Technology Search.

3. Systematic palaeontology

(Crown group) Echinodermata [26]

(Stem group) Asterozoa [27]

Family Somasteroidea [28]

Genus *Cantabrigiaster* gen. nov.

Type species *fezouataensis* sp. nov.

(a) Diagnosis of new genus and species

Somasteroid typified by biserial and offset ambulacrals with thin transverse bar, wide perradial groove, multiple interconnected virgal ossicles and aboral carinal region with network of spicule-like ossicles. Adambulacral ossicle series lacking along abaxial body margins (perpendiculars (virgals), structures 90° to the axial ambulacrals).

(b) Age and horizon

Primarily stylophoran-dominated beds in the upper part of the *Araneograptus murrayi* Zone, late Tremadocian, Z-F2 (Jbel Tizagzaouine), Z-F4 (Bou Izargane) and Z-F9 (Bou Glef), in the lower part of the Fezouata Shale Formation, Lower Ordovician, Zagora area (central Anti-Atlas), Morocco. The 70 m thick interval yields assemblages typical of the Fezouata Biota at about 260–330 m above the base of the Ordovician.

(c) Holotype material

UCBL-FSL 424961 (figure 1). Articulated specimen and latex moulds deposited at the University of Lyon 1 (UCBL-FSL) (Van Roy coll.).

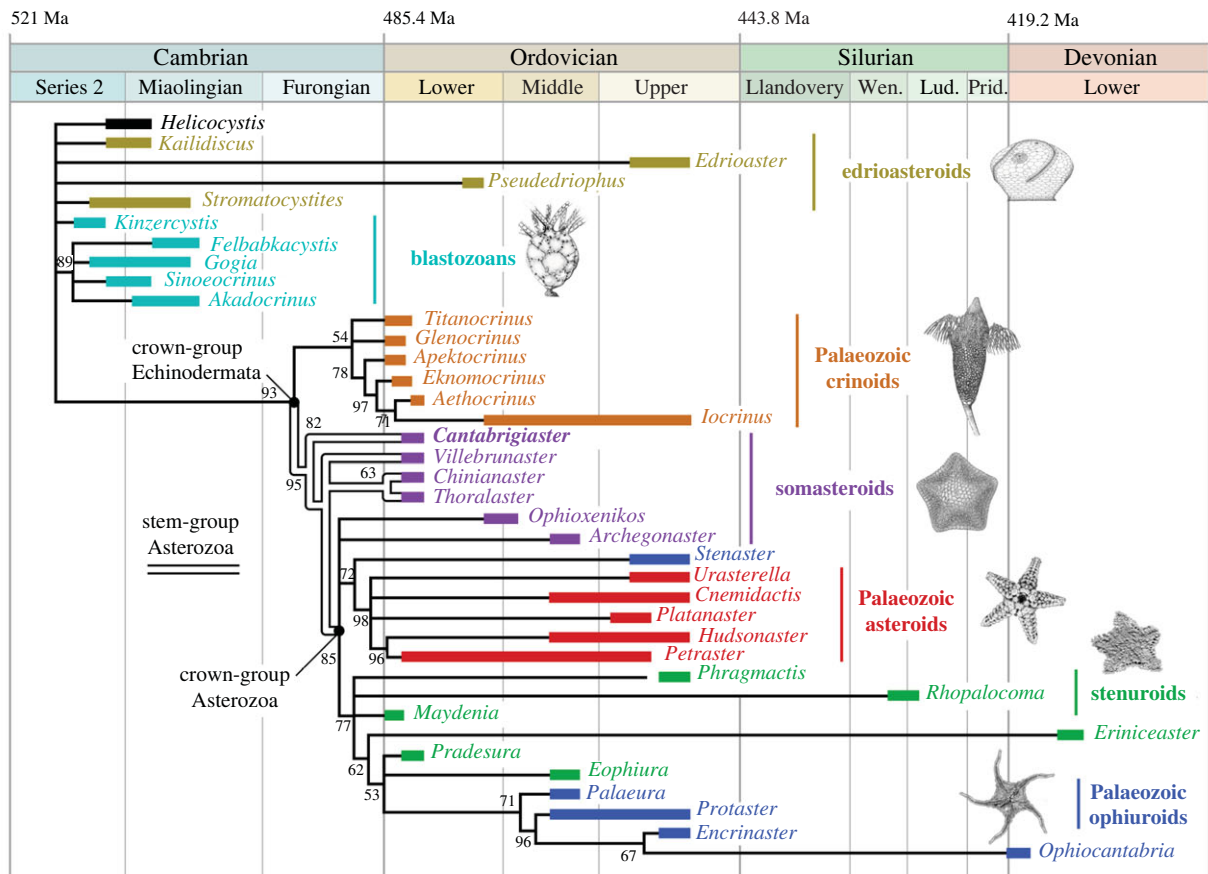


Figure 2. Phylogeny of total-group Echinodermata. Strict consensus topology based on the Bayesian-inference analysis of 38 taxa and 74 morphological characters informed by the EAT [14,15] (electronic supplementary material, SI Text). See electronic supplementary material, figure S6 for support values and comparison with the results of the parsimony-based phylogenetic analyses. Stratigraphic ranges of taxa based on [3,6,12,24]. The asterozoan/crinoid clade represented does not imply a sister group relationship; echinozoan/asterozoan monophyly has been established using molecular data (see electronic supplementary material, SI Text). Wen., Wenlock; Lud., Ludlow; Prid., Pridoli.

(d) Referred material

Thirty-one specimens in total (see electronic supplementary material, table S1), including: specimens housed at the Yale Peabody Museum, Yale University, Hotchkiss collection (YPM IP 535545–535559, electronic supplementary material, figure S2); the collections of Vizcaino (UCBL-FSL 424962, electronic supplementary material, figure S3f,g) and Lefebvre (UCBL-FSL 711938 and 711939, electronic supplementary material, figure S3b,d, respectively) housed at the University of Lyon 1 (reconstruction, electronic supplementary material, figure S4 based on material figured in electronic supplementary material, figures S2 and S3); and the Catto collection deposited in the Natural History Museum of Nantes (MHNN.P.045596, electronic supplementary material, figure S5e).

(e) Etymology

Genus name derived from ‘*Cantabrigia*’, after the cities of Cambridge in the UK and USA, which were home to the influential asterozoan workers John William Salter (University of Cambridge), Juliet Shackleton (née Dean) (University of Cambridge) and Howard Barraclough ‘Barry’ Fell (Harvard University).

(f) Description

The arms are broad, petaloid and arranged in a pentagonal outline (figure 1a,b and electronic supplementary material, figure S2a,c,d). The aboral skeleton (carinal region) is

composed of randomly scattered spicule-like ossicles arranged into an irregular network (figure 1a,b; electronic supplementary material, figures S2e,g and S3d). On the oral side, the ambulacrals consist of flattened ossicles with a subquadrate outline. These ossicles abut each other following the orientation of the perradial axis (figure 1c,d; electronic supplementary material, figure S3a,c,f,g). The perradial suture is straight, and the ambulacrals at either side are stepped out of phase by approximately half an ossicle. The abaxial organization of the ambulacrals consists of an elevated perradial ridge, less than a quarter in width relative to the ambulacral, and bears a thin transverse bar that occupies a central position, conferring a T-shape in oral view (figure 1c,d; electronic supplementary material, figure S3a,e,g). The perradial ridges of the ambulacral ossicles at either side of the perradial suture are substantially separated from each other, forming a wide oral groove (figure 1c–e; electronic supplementary material, figure S3a–c,g). The podial basins are shared equally between adjacent ambulacrals. Abaxially, the following ossicle series consist of the perpendiculars, also known as virgals in somasteroids [2,5,6]. The perpendicular series is composed of interconnected and robust rod-like virgal ossicles without spines. These ossicles follow a perpendicular orientation relative to the perradial suture (figure 1a–d; electronic supplementary material, figure S3). The virgal ossicles close to the ambulacrals are the largest, becoming smaller in length and width towards the abaxial body margins. Likewise, adjacent perpendicular series are in direct contact with each other adaxially relative to the perradial suture, whereas it is

possible to observe open gaps between them towards the abaxial body margins. Proximal (relative to the mouth) perpendicular series consist of up to nine virgal ossicles, which gradually decrease in number towards the tips of the arms (figure 1*a–d*; electronic supplementary material, figure S4). The circumoral ossicles are enlarged relative to ambulacral ossicles, and the first podial pore is shared equally with the small and sub-triangular mouth angle plates (figure 1*e,f*). The madreporite is not preserved.

4. Discussion

The presence of virgal ossicles in *Cantabrigiaster* strongly supports its affinities with somasteroids [2,5–9]. *Cantabrigiaster* bears the greatest similarity to the Tremadocian taxa *Chinianaster*, *Thoralaster* and *Villebrunaster* (electronic supplementary material, figure S5), but is unique among somasteroids in lacking ossicles along the abaxial lateral margins of the arms (figure 1*a,d*). The arm construction of *Cantabrigiaster* consists of flattened and offset biserial ambulacra, each of which articulates with an abaxially oriented perpendicular series composed of simple virgal ossicles (electronic supplementary material, figure S4). In addition to these features, the arms of all other somasteroids also possess a series of axially oriented ossicles along the lateral margins that vary from small and bead-like—albeit with occasional spikes—in Tremadocian taxa [2,5,6] (electronic supplementary material, figure S5*a,b*), to robust and block-like in the stratigraphically younger (Floian) *Ophioxenikos* [10] and (Darriwilian) *Archegonaster* [9] (electronic supplementary material, figure S5*e*). The absence of this key character and the results of our phylogeny (figure 2) demonstrate that *Cantabrigiaster* embodies the ancestral condition by virtue of lacking ossicles defining the lateral arm margins (figure 1; electronic supplementary material, figure S4), whereas other somasteroids record the first appearance of these structures along the edges of the arms, and their subsequent changes in size and shape. Based on this sequence, we propose that the origin of new axially oriented ossicle series in early asterozoans required their formation on the abaxial edges of the arms. Our hypothesis implies that the proximity of axially oriented ossicle series relative to the perradial axis reflects the order of their evolutionary appearance (figure 2; electronic supplementary material, figures S6 and S7, and SI Text); since virgals are abaxially oriented, they are not directly comparable with any of the axially oriented ossicle series observed in Palaeozoic asterozoans. In this context, *Cantabrigiaster* specifically lacks the adambulacral ossicle series present in more derived somasteroids, ophiuroids, asteroids and stenuroids (a group considered intermediate between somasteroids and ophiuroids/asteroids), highlighting its profound significance for understanding the evolution of the asterozoan body plan.

The EAT supports the homology of the ambulacra across pentaradial total-group echinoderms based on their developmental origin and postembryonic ontogeny [14–17], and allows comparison of the skeletal organization of *Cantabrigiaster* on a broader phylogenetic scale. Outside Asterozoa, the absence of adambulacra in *Cantabrigiaster* draws parallels with Tremadocian crinoids (e.g. protocrinoids, *Apektocrinus*, *Eknomocrinus*), whose arm construction incorporates flattened and offset biserial ambulacra articulated to an abaxially oriented (perpendicular) series of simple ossicles, here expressed as the cover plates [13,16,17,24] (electronic supplementary material, figure S7 and SI Text). A similar axial skeletal organization is also

observed among Cambrian forms, most notably edrioasteroids—which also possess flattened and offset biserial ambulacra but lack feeding appendages [9,11,29]—and to a lesser extent blastozoans, which have feeding appendages formed by modified ambulacra known as brachioles [12,30,31]. The widespread occurrence of these characters among non-asterozoan groups suggests that their presence in *Cantabrigiaster* is symplesiomorphic.

Our phylogenetic analysis of representative Lower Palaeozoic total-group echinoderms tests the significance of *Cantabrigiaster* for the origin of Asterozoa. The dataset reflects the ambulacral homology proposed by the EAT [14–17,24], the oral symmetry model proposed by Universal Element Homology [32–34] and our hypothesis for the correspondence of axially oriented ossicle series in early asterozoans (electronic supplementary material, figure S7 and SI Text). Bayesian and parsimony-based analyses recover practically identical topologies (figure 2; electronic supplementary material, figure S6), despite a loss in tree resolution in the earliest divergent representatives that can be expected from the former methodology, indicating a robust phylogenetic signal within Asterozoa [35]. *Cantabrigiaster* occupies the earliest diverging position within total-group Asterozoa, supporting our hypothesis that the absence of adambulacra is an ancestral condition, rather than a case of secondary reduction. Tremadocian somasteroids are resolved as a paraphyletic grade of stem-group asterozoans (*per* [2,36]; *contra* [5]), whereas the Floian *Ophioxenikos* [10] and Darriwilian *Archegonaster* [9] consistently occupy a more derived position as members of crown-group Asterozoa. The analyses argue against the monophyly of stenuroids [6], but corroborate their close phylogenetic relationship to ophiuroids, specifically as their earliest diverging stem-group representatives [2,5,7,36]. These findings indicate that the evolution of a well-developed adambulacral ossicle series constitutes a critical step in the origin of crown-group Asterozoa, and suggest that the abaxially oriented virgals of somasteroids became independently reduced—and ultimately lost—within the stem lineages of Ophiuroidea and Asteroidea (electronic supplementary material, figure S7).

Ethics. We received all the necessary permissions to use and figure the specimens from the Museum collections of the Claude Bernard University Lyon 1 and Yale University used in this study.

Data accessibility. All the dates are provided as electronic supplementary material.

Authors' contributions. A.W.H. and J.O.-H. contributed equally to the conception, design, acquisition of data, analysis and interpretation of data, discussion and drafting the article. A.W.H. photographed fossil material and prepared the specimen figures. J.O.-H. designed and ran the phylogenetic analyses, and prepared the corresponding diagrams. Both authors approved the final version of the manuscript and agree to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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