Journal of Paleontology

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Paleobiogeographic implications of the earliest echinoderms from western Gondwana

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Invited Article

Cite this article: Dupichaud C., Nardin E., Álvaro J.J., Lefebvre B., Nohejlová M., and Zamora S. 2026. Paleobiogeographic implications of the earliest echinoderms from western Gondwana. *Journal of Paleontology*, 1–11 https://doi.org/10.1017/jpa.2026.10268

Received: 15 January 2026 UTC
Revised: 18 June 2026 UTC
Accepted: 25 June 2026 UTC

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Handling Editor:
Rich Mooi

Abstract

Since their first appearance in the fossil record (Cambrian Stage 3, ~520 Ma), echinoderms were already relatively diverse (classes Edrioasteroidea, Eocrinoidea, Helicoplacoidea) and cosmopolitan. Herein, we describe the gogiid *Atlaseocrinus* new genus—the oldest echinoderm known so far from the African continent (Issafen Formation, Cambrian Series 2, Stage 3; Morocco). The discovery of the oldest articulated specimens from the Iberian Chains (northeastern Spain) clarifies the systematic position of '*Rhopalocystis*' *mesonesensis* (Clausen, 2004), which is assigned to the new genus *Atlaseocrinus*. *Atlaseocrinus issafenensis* new genus new species has a weakly differentiated stem composed of small, irregularly arranged circular plates. The theca is made of a mosaic of irregularly polygonal plates in five regular circlets, each ornamented with fine granulation and numerous respiratory structures (epispires). The aboral end consists of a single basal plate, which is a trait unique among gogiids. The brachioles comprise two series of alternating floor plates and two series of alternating cover plates. These long appendages branch as bundles of generally three from elevated spouts around the oral frame. *Atlaseocrinus mesonesensis* new combination from Spain, is included in the new genus based on a single cup-shaped basal plate. Its basal plate has a single through-going canal leading from theca to stem.

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Non-technical Summary

Living echinoderms (e.g., sea stars, brittle stars, sea urchins, sea cucumbers, sea lilies, and feather stars) are a major component of all marine environments on the planet. Their oldest fossils, dating from the Stage 3 of the Cambrian (more than half a billion years ago), are already very diverse, with three different major groupings with wide ranges across the paleocontinents. Here, we describe a new genus of oldest known African echinoderms (Issafen Formation, Cambrian Series 2, Stage 3; Morocco). The discovery of articulated specimens of the oldest echinoderms from northeastern Spain clarifies the systematic position of '*Rhopalocystis*' *mesonesensis* (Clausen, 2004), which is assigned to our new genus *Atlaseocrinus*, which belongs to the Gogiida, an order of echinoderms comprising a stem and erect feeding appendages called brachioles. *Atlaseocrinus* is unique among gogiids due to the presence of a single basal plate connecting the body to the stem. It currently comprises two species: *Atlaseocrinus issafenensis* new genus new species from Morocco, which has straight brachioles, and *Atlaseocrinus mesonesensis* new combination from Spain, with coiled brachioles.

Introduction

The earliest known fossil echinoderms appear in Cambrian Stage 3 strata and already include disparate forms belonging to three classes: Edrioasteroidea, Eocrinoidea, and Helicoplacoidea (Ubaghs, 1975; Zamora et al., 2013). These earliest echinoderm records have been documented from at least three different paleocontinents: Gondwana and peri-Gondwanan regions (e.g., Richter and Richter, 1940; Donovan and Paul, 1982; Ubaghs and Vizcaïno, 1990; Elicki and Schneider, 1992; Smith et al., 2013); Laurentia (e.g. Durham and Caster, 1963; Durham, 1967); and Siberia (e.g., Rozhnov et al., 1992; Kouchinsky et al., 2011, 2015). The combination of high initial taxonomic disparity with a global paleobiogeographic distribution, hints at an even earlier, but undocumented origin of the phylum (Mooi and David, 1998; Zamora and Rahman, 2014).

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Among those early occurrences, eocrinoids were the first to develop free (erect) feeding appendages: the brachioles (sensu Sprinkle, 1973). Historically, the oldest known eocrinoids were described in the Cambrian Series 2, Stage 3 of Laurentia (Sprinkle, 1973; Durham, 1978; Wilbur, 2005; Nardin et al., 2009). New occurrences have also been described from the Cambrian, Series 2, Stage 4 from China (Balang Biota) (Zhao et al., 2007; Yang et al., 2015; Wang et al., 2024). However, the oldest known eocrinoids date from Cambrian Series 2, Stage 3 (Zamora et al., 2013). These include isolated skeletal elements from Laurentia and Siberia (Sprinkle, 1973; Rozhnov et al., 1992; Kouchinsky et al., 2015) and well-preserved articulated material from two Gondwanan occurrences: the gogiid *Alanisicystis andalusiae* Ubaghs and Vizcaïno, 1990 from southern Spain, and as yet undescribed specimens from the Issafen Formation, Morocco (e.g., Ubaghs and Vizcaïno, 1990; Zamora et al., 2013).

The Moroccan eocrinoid material was formerly assigned to the genus *Alanisicystis* Ubaghs and Vizcaïno, 1990, suggesting probable affinities with coeval Spanish gogiids (see, e.g., Nardin, 2007; Smith et al., 2013). However, the Issafen eocrinoid has never been formally described. Consequently, the aims of this study are to (1) describe one of the oldest echinoderms ever found in Gondwana; (2) discuss its systematic position within gogiid eocrinoids; and (3) compare it with more recent echinoderm remains from the Valdemiedes Formation (Cambrian Stage 4) in the Iberian Chains, Spain.

Geological setting

New specimens of eocrinoids from Cambrian Series 2, Stage 3, here assigned to *Atlaseocrinus* new genus, have been discovered in the Issafen Formation of the central Anti-Atlas (Morocco) and the Valdemiedes Formation of the eastern Iberian Chains (Spain). The Issafen Formation (Siegert, 1986), 25–400 m thick, consists of variegated shales with subsidiary nodular ('calcaire scoriacé'), lenticular, and bedded carbonate intercalations, exhibiting nonreefal shelly and reefal microbial-archaeocyathan fabrics (Álvaro and Debrenne, 2010; Álvaro et al., 2014). The fauna also includes brachiopods, chancelloriids, hyoliths, trilobites (Geyer and Landing, 1995), skeletonized microfossils, and echinoderms (Smith et al., 2013). The geological section that yielded the new specimens of *Atlaseocrinus* was first mentioned by Hupé (1953, 1960), who reported fossiliferous shales rich in trilobites in the vicinity of Timkit (or Timguite). The trilobite assemblage allowed him to identify the *Antatlasia* (or IV) Biozone, although some of the trilobite species were also found in the overlying *Bondonella* and *Neltneria* (V), and *Longianda* and *Gigantopygus* (VI) biozones belonging to the Issafenian Stage. Geyer (1990b) and Geyer and Landing (1995, 2004) proposed a new chronostratigraphic framework and subdivided the same stratigraphic interval into the *Antatlasia hollardi* and *Antatlasia guttapluviae* biozones (Bani or Banian Stage), which correspond to the archaeocyath-based *Polystillicidocyathus-Halysicyatus* Biozone (Debrenne and Debrenne, 1995; Álvaro et al., 2014). The co-occurrence of sclerites of *Antatlasia* sp. indet. and *Atlaseocrinus*, at ~335 m above the Amouslek/Issafen contact, allows the assignation of the eocrinoid remains to the *Antatlasia hollardi-Antatlasia guttapluviae* biozones of the Banian Stage (Fig. 1.1, 1.2, 1.5).

On the other hand, silicified echinoderm holdfasts were etched from shelly limestone interbeds of the Valdemiedes Formation in the vicinity of Mesones de Isuela village, eastern Iberian Chains (Clausen, 2004). This formation, 20–150 m thick, is composed of shale/limestone alternations, the latter exhibiting shelly and stromatolitic fabrics (Álvaro and Vennin, 1997), and hydrothermally induced silicification processes in the Mesones sampling area (Martínez-Benítez et al., 2025). These partially silicified limestones have also yielded disarticulated hexactinellid spicules and the trilobite *Alueva undulata* Sdzuy, 1961, indicating the top of the regional Bilbilian Stage. The eocrinoid remains occur ~37 m below the first occurrence of *Acadoparadoxides mureroensis* (Sdzuy, 1958), which marks the regional Bilbilian–Leonian (formerly 'lower–middle Cambrian') boundary (Álvaro et al., 1993). Due to their disarticulated preservation, eocrinoid remains were initially tentatively assigned to previously described taxa, e.g., '*Rhopalocystis*' (Clausen, 2004) and *Alanisicystis*-like gogiids (Smith et al., 2013; Zamora et al., 2015). Additional articulated specimens and disarticulated ossicles of the same species were also found in the vicinity of Jarque, another classical section of the eastern Iberian Chains (Fig. 1.1, 1.3, 1.4). Due to their co-occurrence with *Protolenus jilocanus* (Liñán and Gozalo, 1986), these remains can be placed within the coeval biozone, which marks the top of the Bilbilian Stage.

The regional 'lower–middle Cambrian' boundary is different in Iberia and Morocco: in the former, it is placed at the First Appearance Datum (FAD) of *Acadoparadoxides mureroensis*; and in Morocco, at that of the genus *Hupeolenus* Sepkoski, 2002 (Álvaro et al., 1993; Geyer and Landing, 1995). However, the presence of common taxa allows the identification of chronostratigraphic links between the two regions, such as the FAD of the trilobite species *Hupeolenus termierelloides* (Geyer, 1990a), *Onaraspis altus* (Liñán and Gozalo, 1986), and *Acadoparadoxides mureroensis* (see Sundberg et al., 2016; Álvaro et al., 2018).

Material and methods

Material. Forty-three specimens from Morocco (Issafen Formation) and seven specimens from Spain (Valdemiedes Formation) were studied here. All specimens are fully to partially articulated and preserved as natural molds in mudstones.

Methods. Some specimens were carefully prepared using a Micro Jack 2 air scribe (Paleotools; Brigham, Utah, USA). Morphology was observed from latex casts, which were coated with ammonium chloride sublimate. Photographs were then taken with a Nikon D7100 camera (Nikon, Tokyo, Japan) equipped with a macro 60 mm lens. Some specimens were drawn using a camera lucida mounted on a Zeiss Discovery.V8 binocular microscope.

Repositories and institutional abbreviations. Natural History Museum, London, UK (BMNHUK); Museo Geominero IGME-CSIC, Madrid, Spain (MGM); Muséum d'Histoire Naturelle, Nantes, France (MHNN); Muséum d'Histoire Naturelle, Toulouse, France (MHNT); collections of the Museo de Ciencias Naturales, Universidad de Zaragoza, Spain (MPZ); and paleontological collections of the Université Claude Bernard Lyon 1, Villeurbanne, France (UCBL-FSL).

Systematic paleontology

Terminology and higher classification follow Sprinkle (1973), although the monophyly of the Eocrinoidea and Gogiida has been questioned (e. g., Smith, 1984; David et al., 2000; Zamora et al., 2009; Zamora and Smith, 2012).

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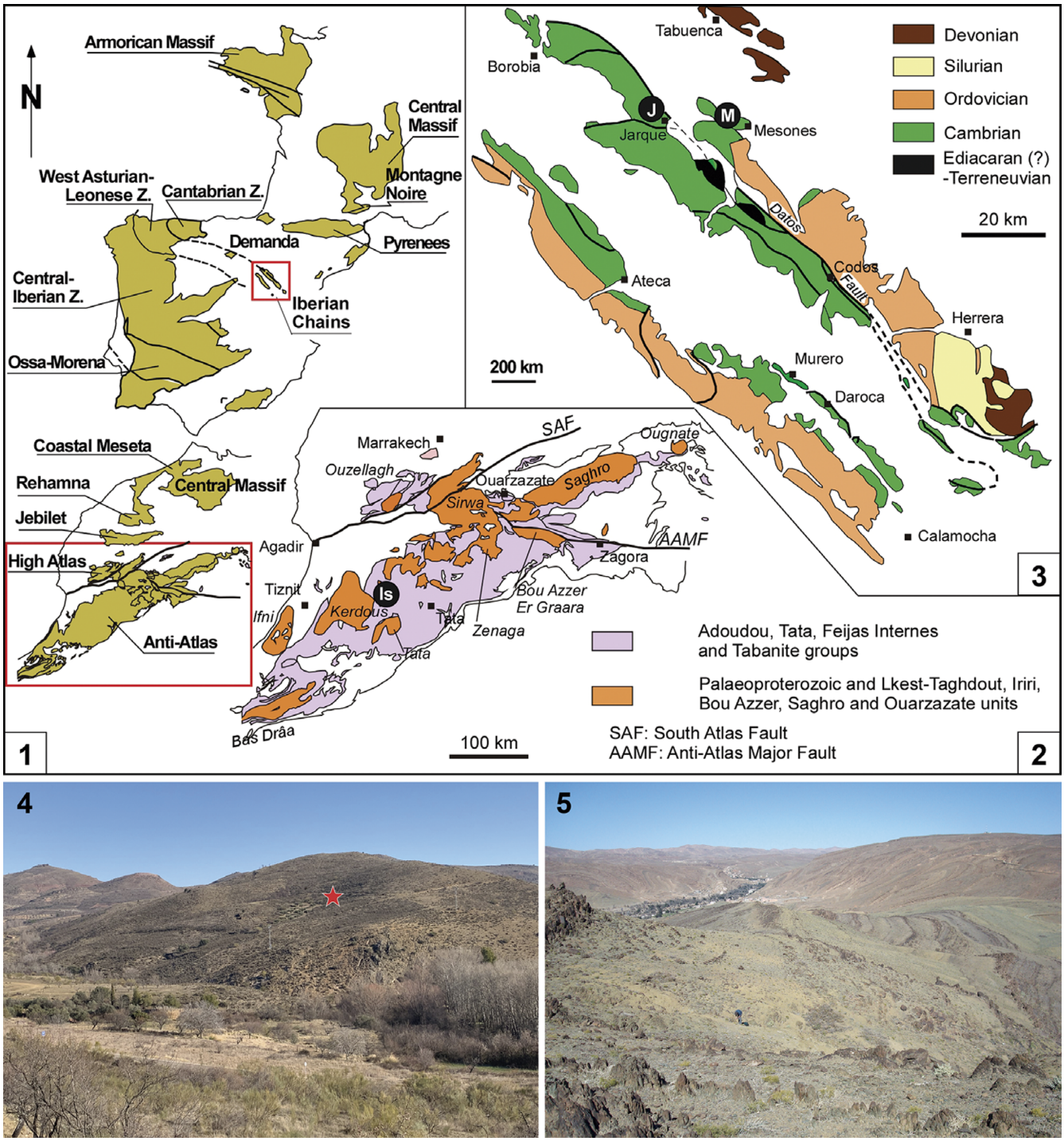


Figure 1. Simplified geological map reporting occurrences of *Atlaseocrinus*: (**1**) Cambrian outcrops of France, Morocco, Portugal, and Spain; (**2**) Cambrian outcrops in High Atlas and Anti-Atlas regions of Morocco; (**3**) Paleozoic outcrops of Iberian Chains in Spain; (**4**) Jarque locality (J), red star marks outcrop; (**5**) Issafen locality (Is). M = Mesones locality.

Phylum **Echinodermata** Klein, 1778
Subphylum **Blastozoa** Sprinkle, 1973
Class **Eocrinoidea** Jaekel, 1918
Order **Gogiida** Broadhead, 1982

Remarks. Gogiids are loosely divided into monogeneric families of derived forms (i.e., Lichenoidae Jaekel, 1918; Rhopalocystidae Ubaghs, 1967; Lyracystidae Sprinkle and Collins, 2006) and larger families grouping seemingly basal forms (Eocrinidae Jaekel, 1918). The latter is defined with broad characteristics to encompass blastozoans that cannot be attributed to other families, and as such are considered paraphyletic (Parsley and Zhao, 2006). Thus, family attribution is pending until further revision of the order Gogiida.

Family unassigned
Atlaseocrinus new genus

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Type species. *Atlaseocrinus issafenensis* new genus new species.

Other species. *Atlaseocrinus mesonesensis* (Clausen, 2004), see below.

Diagnosis. A genus of gogiids with a single basal plate and a theca partly organized in regular circlets of tesselate polygonal plates.

Occurrence. The genus *Atlaseocrinus* occurs in the Issafen Formation (Morocco) and the Valdemiedes Formation (Spain); Cambrian Series 2, Stages 3 and 4.

Etymology. The prefix *Atlas-* is given both because of the location of the type locality in the Moroccan Anti-Atlas, and because of the presence of a single basal plate bearing the rest of the theca, evoking the support provided by the god Atlas in the ancient Greek myth. The suffix *-eocrinus* is used to indicate an eocrinoid genus.

Remarks. Articulated eocrinoid remains from the Issafen Formation have been repeatedly assigned to *Alanisicystis* (e.g., Nardin, 2007; Smith et al., 2013; Zamora et al., 2013; Zhao et al., 2022; Rahman and Zamora, 2024). Initially described as a subgenus of *Gogia* Walcott, 1917 (Ubaghs and Vizcaïno, 1990), *Alanisicystis* was later considered a separate genus (see, e.g., Zamora et al., 2009, 2013). A major difference between *Alanisicystis* and the Issafen eocrinoid lies in their aboral region: *Alanisicystis* has a short, wide stem leading to a large polyplated anchor disc, whereas no fully preserved stem has yet been found for *Atlaseocrinus*. In the latter, the few remains of the stem suggest that it was extremely narrow. Moreover, the stem in *Atlaseocrinus* is attached to a single thecal basal plate, and the theca is organized in circlets. These two characters are unique to *Atlaseocrinus* among other gogiid echinoderms, thus justifying its assignment to a new genus. Finally, brachioles of *Atlaseocrinus* seem to be arranged in bundles of three and supported by spouts emerging from the oral face of the theca, unlike those observed in *Alanisicystis*. Although *Atlaseocrinus mesonesensis* was originally described by Clausen (2004), its description was exclusively based on disarticulated basal plates. The new material of *Atlaseocrinus mesonesensis* described here is partially articulated. Therefore, *Atlaseocrinus issafenensis*, represented by more numerous and better-preserved specimens exhibiting most of the morphological traits of the genus, has been designated as the type species of the new genus.

Atlaseocrinus issafenensis new genus new species
Figures 2–4

2007 *Alanisicystis*; Nardin, figs. III-14, III-48.
2013 *Alanisicystis*; Álvaro et al., p. 76.
2013 *Alanisicystis*; Smith et al., p. 3, figs. 3, 4d.
2013 *Alanisicystis* n. sp.; Zamora et al., p. 162.
2014 *Alanisicystis*; Clausen et al., p. 83.
2022 *Alanisicystis* sp.; Zhao et al., p. 6, fig. 4.
2024 *Alanisicystis* sp.; Rahman and Zamora, p. 301.

Holotype. BMNHUK EE 14823 (Figs. 2.2–3).

Materials. BMNHUK EE 14813, EE 14814, EE 14818, EE 14821, EE 14825, EE 14834, and EE 18364; MGM-7986X–7991X; MHNN.P.04521–04530; MHNT.PAL.2005.0.186–191; UCBL-FSL 711749–711751, UCBL-FSL 711969–711976.

Diagnosis. A species of *Atlaseocrinus* with at least eight straight brachioles. Theca rotund, with five rings of plate crowned by elevated spouts supporting the brachioles. Thecal plates bearing fine granulations and simple, moderately deep, circular sutural pores on their shared side. Sutural pores rarely covered by a circular platelet. Single basal plate likely connected to a polyplated stem.

Occurrence. *Atlaseocrinus issafenensis* occurs in the Issafen Formation (Morocco), at the type locality of Issafen, ~50 km northwest of Tata, central Anti-Atlas, Morocco. The type stratigraphic level is the Issafen Formation, *Antatlasia hollardi* and *Antatlasia guttapluviae* trilobite zones, Tasousekhtian regional substage, Banian regional stage, Cambrian Series 2, Stage 3.

Description. Subspherical theca aborally enclosed by single basal plate and five weakly differentiated circlets; a highly constricted, oral region forming a very short spout. Thecal plates with very fine sinuous ridges and pustules radiating from plate centers. Simple circular epispires shared equally across plate sutures. Sutural pores prominent and raised. Lateral edges of thecal plates bearing from none to three halves of sutural pores. Epispires never occurring at plate corners. Epispire number and distribution apparently correlated with ontogeny (see Ontogeny and morphological implications subsection in the Discussion). Sutural pores open, except on two specimens (EE 14813a, EE 14829) preserving covering platelets inside several sutural pores (Figs. 2.6, 3.3). Adorally, single thecal basal plate bearing epispires. Longitudinal central lumen ~1 mm in diameter, piercing basal plate. Basal plate connected in some specimens to thin, polyplated stem. Stem plates small, polygonal, and seemingly arranged randomly. Neither fully preserved stem nor anchor structures have been found. Oral face situated on top of theca, bearing at least eight straight brachioles. Brachioles arrayed in clusters of three; four clusters visible. Each cluster supported by spout rising from theca. Each spout encased by two series of smooth, rectangular plates bent in a U shape and bearing no epispires. Transition between aboralmost thecal circlet and spout poorly preserved. Oral area unknown, but rays connected to base of each spout apparently converging with it. Each ray covered by series of small plates. Periproct and non-epispire pores unknown. Up to eight brachioles observed on single specimen. Brachioles straight, long, comprising two series of alternating floor plates and two series of cover plates, folding closed to cross portion of next cover plate. Each cover plate aligned with floor plate supporting it. Disconnected floor plates showing two grooves: one on top of plate, at base of insertion of cover plate; another in middle of floor plates, forming a circular lumen inside each brachiole, in suture between floor plates.

Etymology. After the type locality.

Remarks. Some of this material was already reported and assigned to *Alanisicystis*. Nardin (2007) provided camera lucida drawings and latex casts of several specimens, and Smith et al. (2013) figured another specimen and proposed a first tentative reconstruction. However, none of these works provided a complete description of the gogiid material from the Issafen area. The main difference from the Spanish material (see below) lies in the morphology of the brachioles: they are straight in *Atlaseocrinus issafenensis* and coiled in the Spanish specimens. Ornamentation also differs between species, with *Atlaseocrinus issafenensis* harboring a minute granulation, compared to the coarser pustulation in *Atlaseocrinus mesonesensis*.

Atlaseocrinus mesonesensis (Clausen, 2004) new combination
Figure 5

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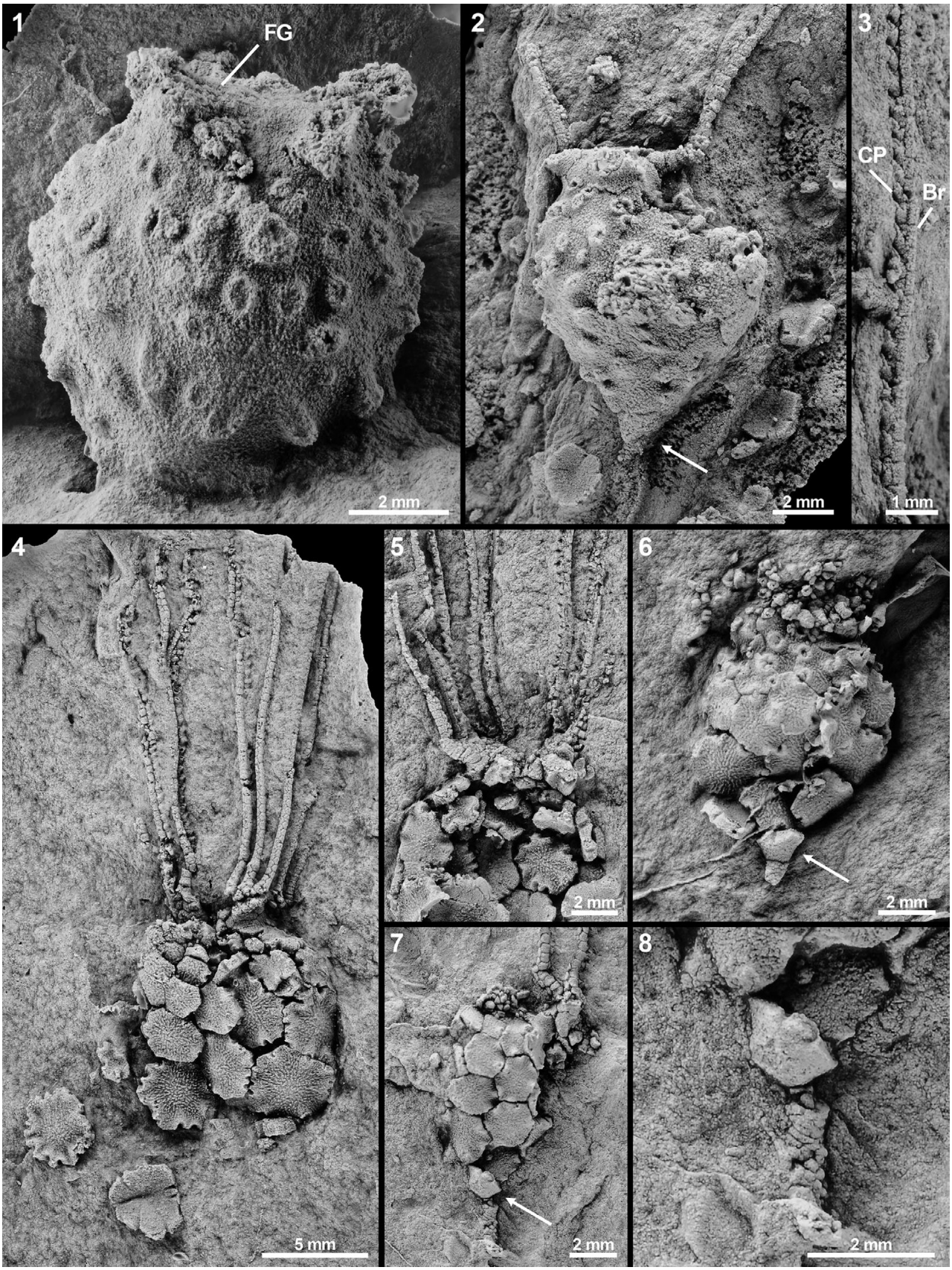


Figure 2. Latex casts of *Atlaseocrinus issafenensis*: (**1**) MGM-7987X preserved in three dimensions; (**2**) holotype, BMNHUK EE 14823, showing brachioles and part of stem; (**3**) magnified view of brachiole of holotype, BMNHUK EE 14823; (**4, 5**) part and counterpart of mostly complete specimen, MGM-7986X; (**6**) BMNHUK EE 14829 showing partly complete theca and part of stem; (**7**) BMNHUK EE 14814 showing brachioles and part of stem; (**8**) magnified view of basal plate and partial stem of BMNHUK EE 14814. Arrows indicate basal plate. Br = brachiole; CP = cover plate; FG = food groove.

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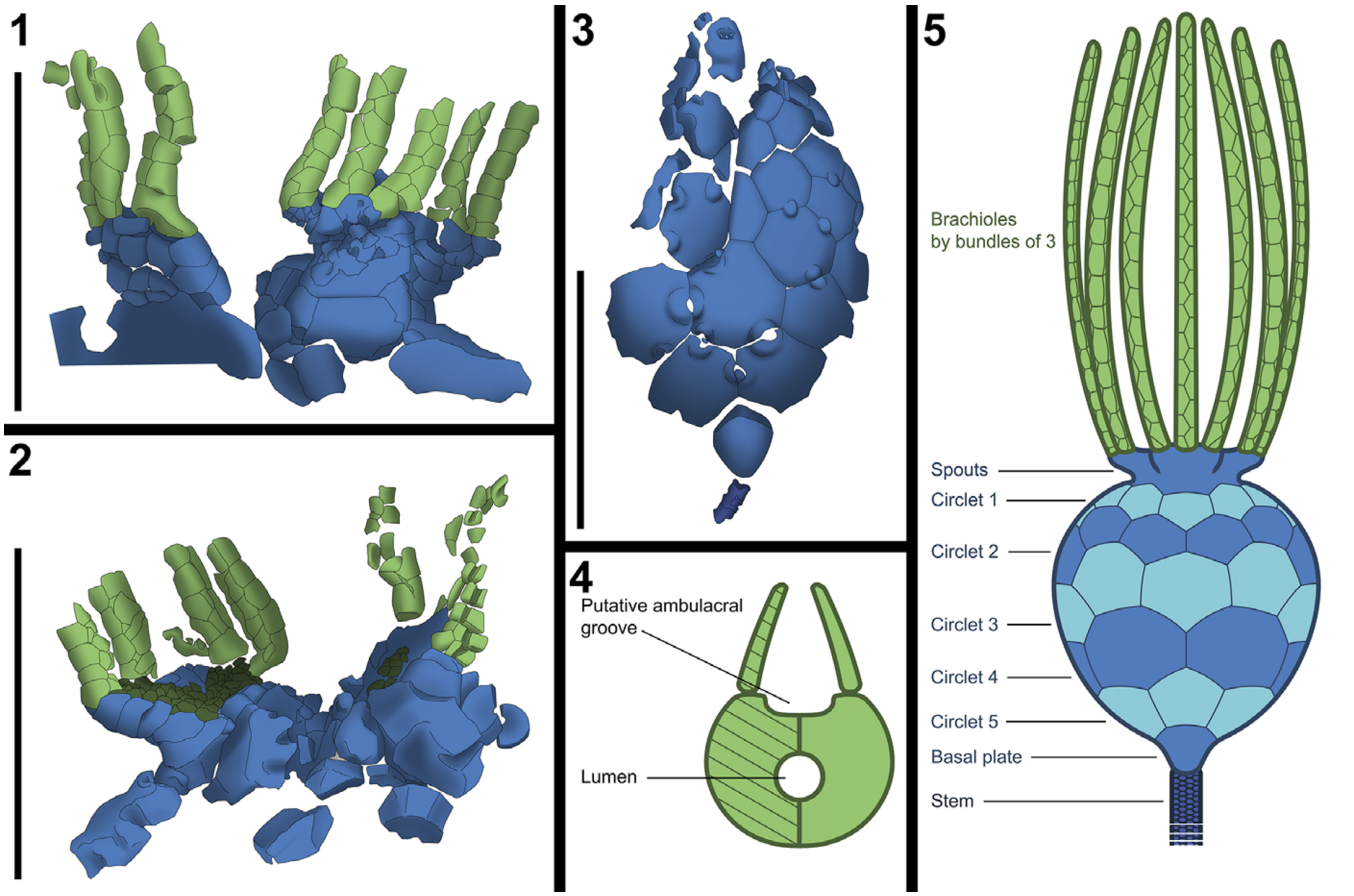


Figure 3. Interpretative drawings of *Atlaseocrinus issafenensis*: (**1, 2**) partial oral surface and brachiole insertion, respectively; (**3**) partial specimen BMNHUK EE 14813a showing development of epispires from lower half of theca; (**4**) transverse slice of brachiole; (**5**) simplified morphology of reconstructed specimen. green = axial region; light blue = perforate extraxial region; dark blue = imperforate extraxial region. Scale bars = 5 mm.

2004 *Rhopalocystis*? *mesonesensis* Clausen, p. 373, fig. 3A, pl. 1, figs. 1–13.
2004 *Rhopalocystis*? cf. *mesonesensis*; Clausen, p. 376, fig. 3B, pl. 1, figs. 14–16.
2004 gen. et sp. indet.; Clausen, p. 376, fig. 3C, pl. 1, figs. 17–19.
2007 *Rhopalocystis*?; Zamora et al., p. 253, fig. 3.
2008 *Rhopalocystis*? *mesonesensis*; Zamora and Rahman, p. 302.
2008 *Rhopalocystis*? cf. *mesonesensis*; Zamora and Rahman, p. 302.
2008 gen. et sp. indet.; Zamora and Rahman, p. 302.
2009 *Rhopalocystis*? *mesonesensis*; Zamora et al., p. 253.
2011 *Rhopalocystis*?; Zamora, p. 65.
2013 isolated gogiid plates; Zamora et al., p. 162.
2015 gogiid eocrinoid closely related to *Gogia*; Zamora et al., p. 215.
2016 *Rhopalocystis*? *mesonesensis*; Zamora, p. 11.
2017 undescribed gogiid eocrinoid; Zamora in Allaire et al., p. 685.
2021 *Rhopalocystis mesonesensis*; Jell and Sprinkle, p. 15.

Holotype. MPZ 17070 (Clausen, 2004), from the Valdemiedes Formation, near Mesones de Isuela village, Iberian Chains, northeastern Spain.

Emended diagnosis. A species of *Atlaseocrinus* with at least six left-hand coiled brachioles. Theca rotund and bearing numerous minute sutural pores. Thecal plates bearing relatively coarse granulations. Stem unknown.

Revised description. Seemingly rotund theca bearing at least six brachioles coiled in a left-handed arrangement. Disarticulated theca or isolated plates showing relatively coarse granulations and epispires located on both sides and corners. Single thecal basal plate bearing thin epispires adorally. Oral face, brachiole insertion, periproct, non-epispire pores, and stem unknown.

Remarks. Rhopalocystis? *mesonesensis* was originally described by Clausen (2004), based on silicified, isolated sketelal elements that were identified as large basal thecal plates, similar to those present in the genus *Rhopalocystis*, previously known from Lower Ordovician strata of Morocco. Within eocrinoids (and blastozoans), the genus *Rhopalocystis* is one of the very few taxa possessing a single basal plate (Ubaghs, 1963; Chauvel, 1971; Allaire et al., 2017). In recent years, additional material was collected from equivalent levels of the Valdemiedes Formation at a new locality close to Jarque de Moncayo village. The new specimens are preserved as dissolved skeletal elements, sometimes in partial anatomical connection. One specimen (MPZ 2026/58) shows the basal plate associated with other thecal plates, the morphology of which is closely similar to those found in *Atlaseocrinus issafenensis* or even *Gogia* (i.e., polygonal plates with sutural pores and a granular

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Figure 4. Paleoart reconstruction of *Atlaseocrinus issafenensis* by C. Dupichaud. Cover plates open at distal ends of each brachiole, revealing tube feet.

ornamentation; Figs. 5.6–7), hence the revised attribution to the genus *Atlaseocrinus*. One specimen, despite the lack of basal plate, comprises thecal plates associated with coiled brachioles, highlighting the difference with the straight brachioles of *Atlaseocrinus issafenensis*. Basal plates are also common both as dissolved residues from limestone or as disarticulated elements in

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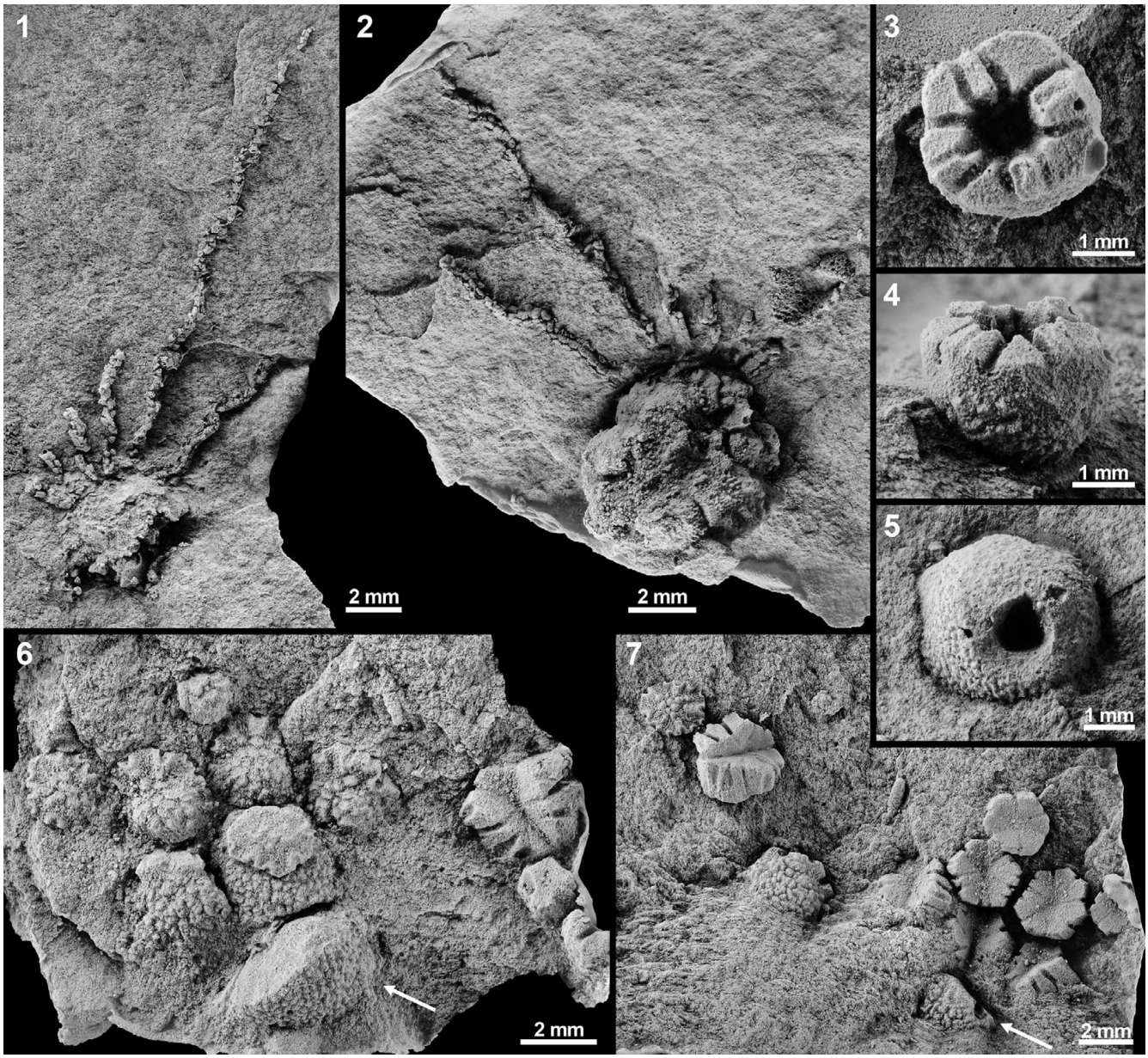


Figure 5. Latex casts of *Atlaseocrinus mesonesensis*: (**1, 2**) part and counterpart, respectively, of MPZ 2026/55 showing brachioles associated with partial theca; (**3, 4**) isolated basal plate of MPZ 2026/56; (**5**) isolated basal plate of MPZ 2026/57; (**6, 7**) part and counterpart, respectively, of isolated basal plate of MPZ 2026/58 showing several thecal plates associated with basal plate. Arrows indicate basal plate.

shale beds. Such occurrences suggest that the disarticulated specimens described by Clausen (2004) most likely belong to the same taxon.

Discussion

Ontogeny and morphological implications. The 43 studied specimens of *Atlaseocrinus issafenensis* exhibit large variation in the number and distribution of sutural pores on the theca. One specimen (BMNHUK EE 14813a; Fig. 3.3) bears only a few sutural pores around the two adoralmost circlets, where lie the largest thecal plates. Aborally, some plate junctions display pustules akin to closed sutural pores. Neither sutural pores nor pustules are present on the aboralmost circlet. This specimen is also one of the smallest (based on thecal dimensions). In some larger specimens (e.g., BMNHUK EE 14829; Fig. 2.6), the sutural pores are arranged around the theca, but with no more than one pore per plate side. The largest individuals (Figs. 2.4–5) display up to three sutural pores per plate side, with the number of pores being higher on the two adoralmost circlets. The presence of multiple sutural pores on a single plate edge seems to be more pronounced on the largest thecal plates, both in fully articulated specimens and in isolated plates. The variations observed in the distribution and density of epispires seem related to the thecal size, suggesting that this pattern could be controlled by ontogeny. It is difficult to establish a reliable correlation with size, because only a few specimens are preserved well enough to show the aboral and adoral ends of the theca, and even among these, taphonomic flattening biases length measurements.

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Despite variation in thecal size and individual thecal plates, no new thecal plates seem to have been added during ontogeny (holoperipheric growth). Therefore, the thecal organization remains unchanged throughout growth.

Based on the above observations, the following postmetamorphic ontogenetic sequence can be described for the theca of *Atlaseocrinus issafenensis*: (1) an initial stage in which the theca lacks sutural pores, and consists of a single basal plate, five circlets, and spout plates; (2) an early stage, with the first sutural pores restricted to the two aboralmost circlets, and with a maximum of one pore per plate edge, pustules can also appear on upper circlets, upon which forthcoming epispires will occur; (3) a medium stage with sutural pores distributed all over the theca, from the basal plate to the lowermost spout elements, but with only one pore per plate edge; and (4) a late stage with additional sutural pores appearing alongside those already existing, starting from the two aboralmost circlets, and extending to the basal plate and upper circlets.

Comparing the ontogeny of *Atlaseocrinus* with that of *Acanthocystites* Barrande, 1887 (Nohejlová and Fatka, 2016), it is remarkable that the theca of the former enlarges solely through the accretionary growth of individual plates, and not through the addition of new ones. Further material will be necessary to determine if the number of brachioles increases during ontogeny, as seen in *Acanthocystites.* Growth patterns for the brachioles and stem remain unknown. The former probably follows the Ocular Plate Rule (OPR), as is commonly the case for the axial region of echinoderm body wall (Mooi and David, 1998).

Atlaseocrinus is the oldest known example of an echinoderm with free feeding appendages, along with the co-occurring, undescribed lepidocystid from the Issafen Formation (Smith et al., 2013), and *Alanisicystis andalusiae* (see Ubaghs and Vizcaïno, 1990). Despite being one of the oldest known echinoderms, *Atlaseocrinus* exhibits a surprisingly organized thecal plate pattern, with one basal plate surmounted by five circlets of thecal plates. Furthermore, this thecal pattern appears to remain unchanged throughout ontogeny. Evolutionary trends in echinoderms usually tend toward a reduction in the number of plates and an increase in organisation, as in other blastozoans (Nardin, 2007), or more specifically, in solutans (Parsley, 1997) or stylophorans (Lefebvre, 2001). Compared to other gogiids, e.g., *Alanisicystis* or *Gogia*, which have unorganized thecal plating, the organised thecal pattern of *Atlaseocrinus* suggests a relatively derived morphology. This observation is further supported by the co-occurrence of an undescribed lepidocystid alongside *Atlaseocrinus issafenensis* (see Smith et al., 2013). Lepidocystids have been described as exhibiting a supposedly plesiomorphic body plan among blastozoan echinoderms, because they lack a theca (Lefebvre et al., 2015; Nardin et al., 2017; Wang et al., 2024). This suggests that diversification of body plans among the blastozoans could have occurred even before early Cambrian Stage 3.

Paleobiogeographic and paleoecologic implications. *Atlaseocrinus issafenensis* and *Atlaseocrinus mesonesensis* both occur in comparable settings, within two paleogeographically neighboring margins of West Gondwana (Álvaro et al., 2013; Clausen et al., 2014). Both the Valdemiedes and Issafen formations show meter-thick, shallowing-upward cycles, starting with offshore-dominant claystone substrata (remains from Issafen and Jarque del Moncayo localities), locally punctuated by shelly storm-induced carbonate interbeds (from Mesones de Isuela).

In these calm environments, *Atlaseocrinus* was very likely sessile, although the exact nature of its attachment to the substratum remains unknown. Its slender stem was probably fragile, which could explain why specimens with broken or missing stems have only been found so far. It is therefore possible that the appendage was more or less elongated and terminated by an anchoring structure, e.g., a disk, allowing attachment to hard substrata, e.g., trilobite sclerites or brachiopod valves (e.g., Lin, 2009; Zamora et al., 2017). *Atlaseocrinus* appears to have adopted a 'pelmatozoan' lifestyle, comparable to that of stemmed crinoids and most gogiids.

Taphonomy. The samples from Issafen and Jarque de Mesones are preserved as natural molds encased in shale. In contrast, the isolated basals of *Atlaseocrinus mesonensis* described by Clausen (2004) are preserved as three-dimensional calcite elements in packestone tempestites (Álvaro and Vennin, 1996). *Atlaseocrinus issafenensis* exhibits diverse states of preservation, ranging from isolated ossicles to nearly complete skeletal remains. Most specimens preserved in anatomical connection are laterally collapsed, rendering the oral face inaccessible. Brachioles are locally present, but rarely connected to the theca, and their tips are commonly disarticulated. In a few cases, part of the stem is preserved and connected to the basal plate. However, even in this case, the stem is invariably broken, and no distal end is preserved. Thus, the theca appears to represent the most taphonomically resistant part of the *Atlaseocrinus* skeleton, followed by the brachioles, and finally the stem.

A few rare specimens of *Atlaseocrinus issafenensis* (3 of 43) exhibit a theca preserved in three dimensions, mostly undeformed. In these specimens, the plate sutures are hardly discernible, giving the theca a smooth appearance, even though the epispires remain visible. This unusual preservation likely resulted from rapid burial in extremely fine clayey substrata that favored the three-dimensional preservation of the theca and leaving a smooth impression of the epidermis covering the skeleton. In one case (MHNN.P.045822), this type of preservation is also associated with the record of eight brachioles loosely disconnected from the theca.

Conclusions

Atlaseocrinus issafenensis is one of the oldest articulated echinoderm fossils known to date. Its theca displays unique traits among gogiid echinoderms (i.e., thecal plates organized in regular circlets and a single basal plate). These characteristics justify the erection of a new genus. The fossils can be interpreted as representing a constrained, 'derived' morphology relative to that of coeval and later Cambrian gogiids. This unique morphology is also present in gogiids from the Valdemiedes Formation, which led to the assignment of the material originally described there to *Atlaseocrinus mesonesensis.* The exceptionally well-preserved material from the Issafen Formation allows the proposal of an ontogenetic model for the growth of *Atlaseocrinus issafenensis.*

Acknowledgments. We would like to address our thanks to R. and V. Reboul and D. Vizcaïno for relating their rediscovery of Hupé's locality in the Issafène Valley. T. Ewin (BMNHUK), Y. Laurent (MHNT), and S. Régnault (MHNN) are acknowledged for access to material in collections. I. Pérrez-Urresti (Zaragoza) and V. Perrier (Lyon) took the photographs. Financial support for fossil sampling in Morocco was provided by a French CNRS project led by S. Clausen (Lille). This work was supported by the Spanish Ministry of Science, Innovation and Universities (PID2021-125585NB-I00), cofinanced by the European Regional Development Fund, project 'Aragosaurus: Recursos Geológicos y Paleoambientales' (E18_17R) funded by the Government of Aragon. The authors are also grateful to the two reviewers, T.E. Guensburg and J.-P. Lin, and the associate editor, R. Mooi, for their constructive comments, which greatly improved the manuscript.

Competing interests. The authors declare none.

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