Swiss Journal of Palaeontology

RESEARCH ARTICLE
Open Access

A relict Triassic brittle star (Echinodermata, Ophiuroidea) in Lower Jurassic strata of Asturias, north-west Spain

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Abstract

Ophiuroids, also known as brittle stars, are an important component of modern marine benthos, yet their fossil record is still poorly understood. Here, we describe new finds of ophiuroids from the upper Sinemurian (Lower Jurassic) of Asturias, north-west Spain. The material consists of several articulated specimens that show all relevant anatomical details to allow for an exhaustive description of a new species, *Arenorbis santameraensis* sp. nov., which adds a Jurassic member to the genus *Arenorbis* previously known exclusively from the Middle Triassic of central Europe. We demonstrate that *Arenorbis* has characters that are typically found in the suborder Ophiodermatina. The new Jurassic record of *Arenorbis* shows remarkable parallels with its Middle Triassic equivalents in terms of sedimentological and taphonomic context, suggesting niche conservatism in this genus. In contrast to its wide geographical distribution during the Middle Triassic, the new species is currently only known from a restricted area, which suggests that it represents a Jurassic relict of a formerly widespread Triassic lineage.

Keywords Ophiuroids, Sinemurian, Exceptional preservation, New species

Introduction

Ophiuroids, also called brittle stars, are the slender-armed cousins of starfish (Asteroidea) that represent a major component of present-day marine benthos (Stöhr et al., 2012). Their skeleton is composed of microscopic calcite plates that readily fossilise, either as dissociated ossicles or, more rarely, as (semi-)articulated skeletons (Ausich et al., 2001). The pioneering work by Hess (1960, 1962a, 1962b, 1964) demonstrated that ophiuroid fossils are much more abundant and taxonomically insightful than previously assumed. Systematic assessments of the fossil record of brittle stars have recently been geared up, following critical insights into the micromorphology of the ophiuroid skeleton (Martynov, 2010; Thuy & Stöhr, 2011, 2016), and alignment of morphological and molecular phylogenies. This has led to fleshing out a clade-based, higher-level classification of the Ophiuroidea (O'Hara et al., 2014).

However, with more than 2000 extant species, compared to some 310 extinct forms in the entire post-Palaeozoic (Stöhr et al., 2023), it is clear that the bulk of the ophiuroid fossil record remains dramatically understudied. In view of the high potential of the Ophiuroidea to serve as a model group for large-scale evolutionary studies (e.g. Bribiesca-Contreras et al., 2017; Thuy, 2013; Thuy et al., 2012, 2014), it is important to explore the fossil record of the group as exhaustively as possible.

Here, we describe a new species of ophiuroid from the Lower Jurassic (upper Sinemurian) of Asturias, north-west Spain, on the basis of a collection of exceptionally well-preserved, articulated skeletons. Not only are these

Handling editor: Daniel Marty.

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specimens the first brittle stars to be described formally from the Jurassic of Spain, they also belong to a genus that was previously thought to be restricted to the Middle Triassic.

Material and methods

For the purpose of the present study, we have examined a large collection of fossil ophiuroids from the Lower Jurassic of Asturias housed at the Museo del Jurásico de Asturias in Colunga, Asturias (collection acronym: MUJA). This lot consists of 41 complete individuals, most of them intact but some showing signs of incipient disarticulation, and all preserved as calcitic skeletons on limestone slabs. To document their micromorphological features, we have used a USB camera equipped with integrated LEDs, connected to a portable computer. For the sake of morphological comparison, we have also examined dissociated lateral arm plates of *Arenorbis squamosus* (Picard, 1858) from the Middle Triassic of Schillingstadt (Baden-Württemberg, Germany), hand-picked from sieving residues, cleaned using an ultrasonic bath, mounted on aluminium stubs and gold-coated for scanning electron microscopy using a JEOL NeoScope JCM-5000 at the Natural History Museum Luxembourg. The lateral arm plates of *A. squamosus* illustrated herein have been deposited in the collections of the Natural History Museum Luxembourg (acronym: MnhnL). We here adopt the terminology by Stöhr et al. (2012), Thuy and Stöhr (2011, 2016) and Hendler (2018) and use the classification proposed by O'Hara et al. (2018).

Geographical and geological setting

The spectacular Jurassic rock outcrops in Asturias extend, almost continuously, along a narrow section of coast between the Cabo Torres (Gijón) and Arra beach (Ribadesella), being limited in both cases by large vertical faults (Veriña fault in the west; Ribadesella fault in the east), which relate them to rocks from the Palaeozoic Era (Fig. 1a). Lower and Middle Jurassic strata in Asturias were grouped into a high-order lithological unit, the Villaviciosa Group (Valenzuela et al., 1986), which is predominantly made up of carbonate rocks of littoral (Gijón Formation) and open-marine origin (Rodiles Formation).

The Gijón Formation marks the onset of Jurassic sedimentation in Asturias with a succession of limestones, dolostones and marls that were laid down on a low and irregular coast, rich in carbonate muds and evaporites (sabkha) (Valenzuela et al., 1986; García-Ramos et al., 2011).

Later on, a gradual rise in sea level left a major part of the region submerged, with a depth that at times would have hit the 100-m mark. The carbonate muds accumulating on the bottom of that sea resulted in a thick succession of limestone–marl alternations (Rodiles Formation, Fig. 1b), the lower part of which (Buerres Member, Fig. 1c) comprises nodular limestones with some thin marly layers, representing the proximal inner part of a carbonate ramp. The middle and upper parts of the formation (Santa Mera Member) is characterised by tabular limestone and marl beds, which show a rhythmic character, representing the median and external parts of the ramp (Valenzuela et al., 1986; García-Ramos et al., 2011).

The fauna through the latter formation was rich and varied with a predominance of molluscs (mainly bivalves, ammonites and belemnites) as well as brachiopods (Dubar, 1925a, 1925b; Dubar & Mouterde, 1957; Dubar et al., 1971; Suárez Vega, 1974; Comas-Rengifo & Goy, 2010; Comas-Rengifo et al., 2010, 2023). Less abundant are echinoderms (crinoids, echinoids and ophiuroids), decapod crustaceans and worms. The two last-named groups are represented by abundant and diverse trace fossil suites (García-Ramos et al., 2011). In addition, there are remains of marine reptiles, such as plesiosaurs and ichthyosaurs (Bardet et al., 2008; Fernández et al., 2018).

The ophiuroids studied herein are from the Punta La Llastra W section in the sea cliffs at Santa Mera (Fig. 2) in the municipality of Villaviciosa, where they appear on the lower planar surface of a 4-cm-thick limestone bed with wave-ripple cross-lamination in the upper part. This limestone bed is included into a larger nodular and lenticular wavy-bedded limestone-dominated interval with thin and discontinuous marl interlayers belonging to the Buerres Member (Rodiles Formation). The age of this part of the succession is late Sinemurian (Comas-Rengifo et al., 2021), belonging to the Obtusum ammonite Zone and Subzone. The ophiuroid-bearing interval represents a small-scale regressive episode included in a generalised transgressive trend within a large wave- and storm-influenced shallow carbonate ramp.

This particular environment is very similar to other epicontinental shallow-marine carbonate ramps (e.g. Muschelkalk facies) covering most of central and western Europe during the Middle Triassic (Adams & Diamond, 2019; Ajdanlijsky et al., 2019; Borkhataria et al., 2005; Chatalov, 2018; Götz & Lenhardt, 2011; Matysick, 2019; Matysick & Szulc, 2019; Warnecke & Aigner, 2019). Some of these also comprise ophiuroid beds such as the ones documented from Poland by Radwański (2002), Salamon & Boczarowski (2003), Zatoń et al. (2008), Salamon et al. (2012) and Surmik et al. (2020).

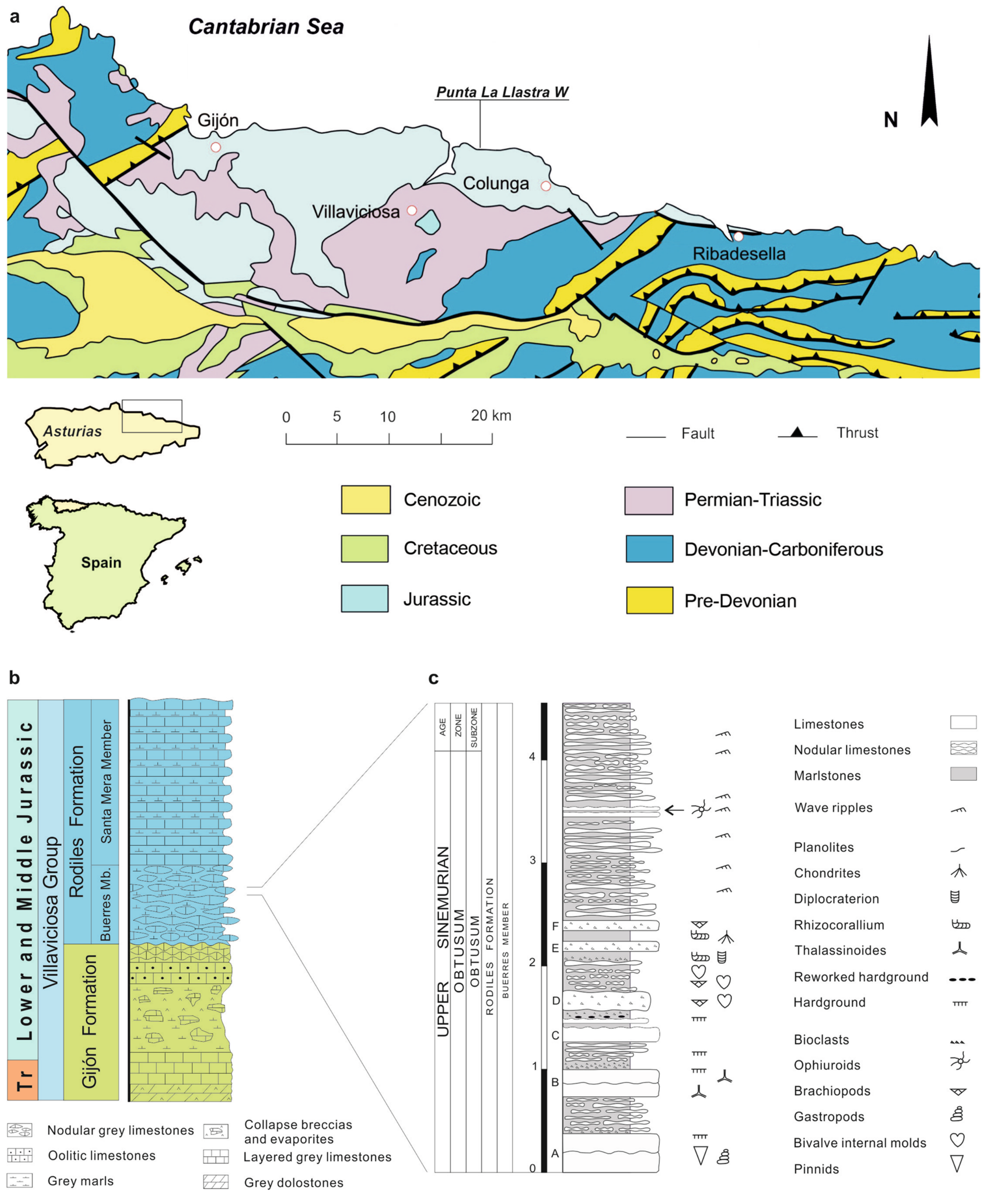

Fig. 1 **a** Location of the Punta La Llastra W section (Santa Mera, Villaviciosa) on the geological map of the east-central region of Asturias (north-west Spain; modified from García-Ramos & Gutiérrez Claverol, 1995); **b** general stratigraphical log (not to scale) of the Lower and Middle Jurassic of Asturias (modified from García-Ramos et al., 2011); **c** detailed stratigraphical log of the studied section with ophiuroids: the letters indicate several recognised levels (see Fig. 2B)

Fig. 2 **a** General view of the Santa Mera sea cliffs (Villaviciosa); the arrow indicates the section sampled; **b** partial view of the Punta La Llastra W section; the letters refer to beds indicated in Fig. 1C; **c** detail of the interval that yielded the ophiuroids; the arrow indicating their level of provenance

Systematic palaeontology

Class Ophiuroidea Gray, 1840

Subclass Myophiuroida Matsumoto, 1915

Infraclass Metophiurida Matsumoto, 1913

Superorder Ophintegrida O'Hara et al., 2017.

Order Ophiacanthida O'Hara et al., 2017.

Suborder Ophiodermatina Ljungman, 1867

Family unknown.

Genus *Arenorbis* Hess, 1970

Type species: *Aspidura squamosa* Picard, 1858, by original designation.

Emended diagnosis: Ophiodermatin genus with disc densely covered by tiny granules except for rounded triangular to pear-shaped radial shields; small, short adoral shields and large, arrow-shaped oral shields, both with proximal tips covered by granules; two tooth papillae per jaw apex, bordered on both sides by a single larger infradental papilla, two to three lateral oral papillae and two adoral shield spines; arms slender; lateral arm plates relatively stout, not constricted, with relatively large spine articulations integrated in outer surface stereom and separated from distal edge by a thin ledge; arm spines conical, pointed, as long as one arm segment or shorter; tentacle pores covered by two large tentacle scales and several much smaller scales.

Arenorbis santameraensis sp. nov.

Holotype: MUJA-1215.

Paratypes: MUJA-0511, MUJA-0811 (specimen exposing ventral side), MUJA-3785 (complete specimen exposing dorsal side, 5 mm disc diameter); MUJA-3785 (specimen exposing dorsal side, 4.2 mm disc diameter).

Type locality and stratum: Punta La Llastra W section along sea cliffs at Santa Mera in the municipality of Villaviciosa (Asturias, Spain); Buerres Member, Rodiles Formation, upper Sinemurian, Obtusum ammonite Zone and Subzone, Lower Jurassic.

Etymology: Species name refers to the village of Santa Mera (near Villaviciosa), closest to the Punta La Llastra W section cliffs.

Diagnosis: Species of *Arenorbis* with adoral shields meeting proximally, arm spines as long as one arm segment, and small spine articulations.

Description of holotype: MUJA-1215 (Fig. 3) is an articulated skeleton exposing the ventral side. Disc rounded pentagonal (Fig. 3a, b), 5.4 mm in diameter, interradii covered by small, rounded, imbricating scales

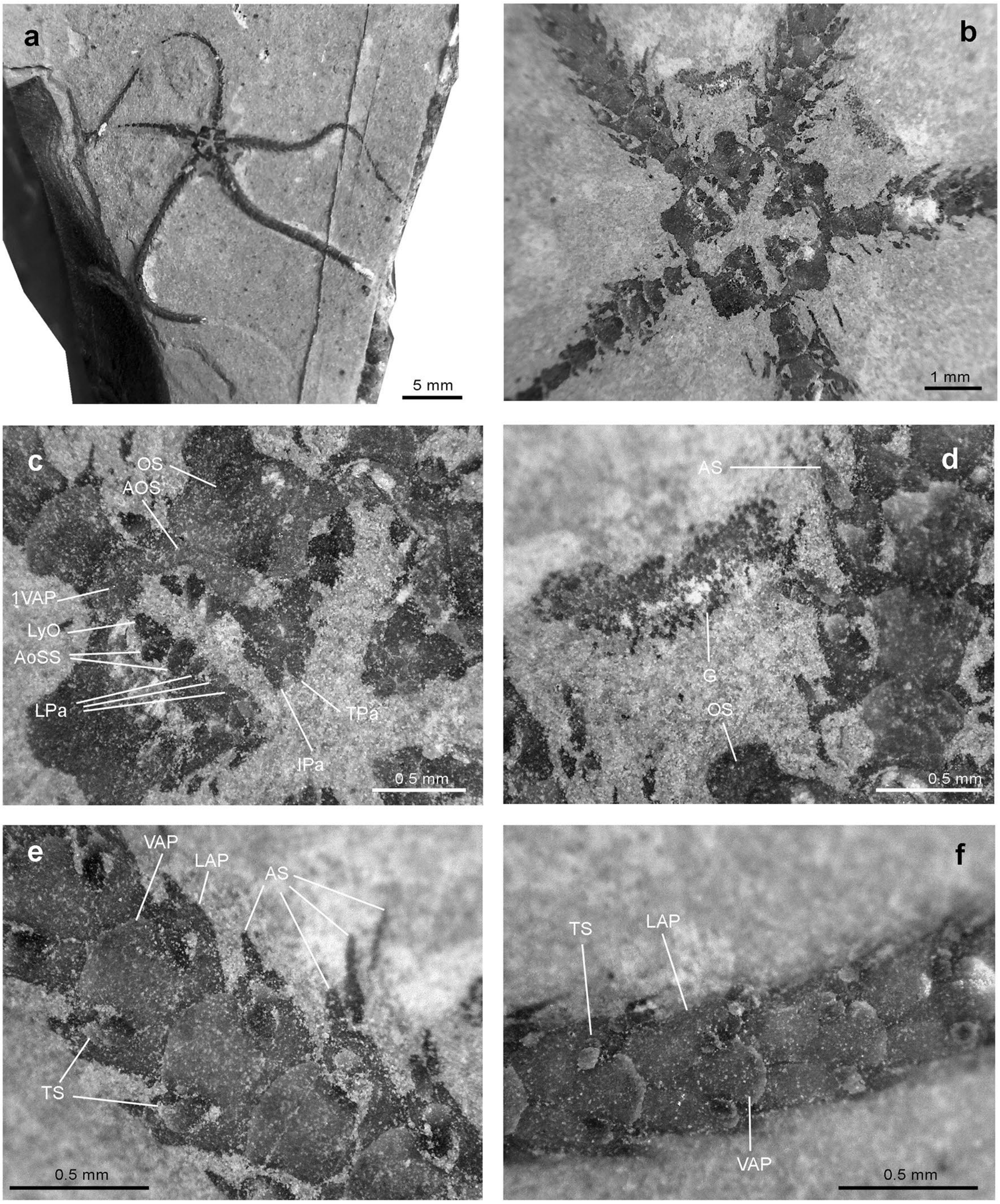

Fig. 3 *Arenorbis santameraensis* sp. nov. from the upper Sinemurian of the Punta La Llastra W section, Villaviciosa (Asturias, north-west Spain); holotype (MUJA-1215); **a** general view of specimen exposing the ventral side; **b** detail of disc; **c** detail of mouth skeleton; **d** detail of ventral interradius; **e** detail of proximal arm segments; **f** detail of distal arm fragments. *AOS* adoral shield *AoSS* adoral shield spine *AS* arm spines *G* disc granules *IPa* infradental papillae *LAP* lateral arm plate *LPa* lateral oral papillae *LyO* Lyman's ossicle *OS* oral shield *TPa* tooth papillae *TS* tentacle scales *VAP* ventral arm plate *1VAP* first ventral arm plate

bearing a dense cover of tiny, spherical granules (Fig. 3d); oral shield as long as wide, accounting for a quarter of the disc radius (Fig. 3b), proximal tip covered by granules, arrow shaped, with a right proximal angle composed of straight latero-proximal edges, incised latero-distal edges and a narrower, rounded distal tip; adoral shields (Fig. 3c) relatively wide and short, narrowly meeting proximally but not extending around the lateral corner of the oral shield, proximal tips covered by granules; oral plates relatively slender and short; buccal skeleton (Fig. 3c) composed of an assumed triangular Lyman's ossicle at the edge between first ventral arm plate and adoral shield, two relatively large, oval adoral shield spines on the edge of the adoral shield, followed by two to three smaller, leaf-shaped lateral oral papillae, a single slightly larger infradental papilla and a slightly larger, conical tooth papilla; ventralmost tooth slightly larger than tooth papillae, conical; genital slits covered by matrix; five arms preserved (Fig. 3a), relatively slender, longest arm 14.3 mm in length; three first arm segments incorporated into disc; first ventral arm plate (Fig. 3c) 1.5 times wider than long, drop shaped; following ventral arm plates in contact in proximalmost arm segments (Fig. 3d), approximately as long as wide, with a convex distal edge, incised lateral edges and a pointed proximal tip; tentacle pores large (Fig. 3e), encompassed by ventral and lateral arm plates, covered by two large, operculiform main scales and two to three much smaller additional scales; lateral arm plates (Fig. 3e) relatively thin, with large, ventral to ventro-distalwards pointing tentacle notch, ventro-proximalwards projecting ventral portion, outer surface smooth; at least two conical, pointed arm spines (Fig. 3e) on distal edge of lateral arm plates, half as long as an arm segment; lateral arm plates meeting ventrally and separating ventral arm plates into median to distal arm segments (Fig. 3f).

Paratype supplements and variation: MUJA-0511 (Fig. 4) is an articulated skeleton exposing the dorsal side, disc 5.4 mm in diameter, rounded pentagonal outline (Fig. 4a) as in holotype, covered by numerous small, rounded, imbricating scales, covered by tiny granules (Fig. 4b) originally forming a dense cover; central primary plate (Fig. 4a) slightly larger than surrounding scales; radial primary plates not discernible with certainty; radial shields (Fig. 4b) rounded triangular to pear-shaped, exposing most of their surface, not covered by granules, fully separated over entire length, accounting for one-third of disc radius; proximal dorsal arm plates (Fig. 4c) slightly longer than wide, fan shaped with convex distal edge and straight lateral edges, in contact; proximal

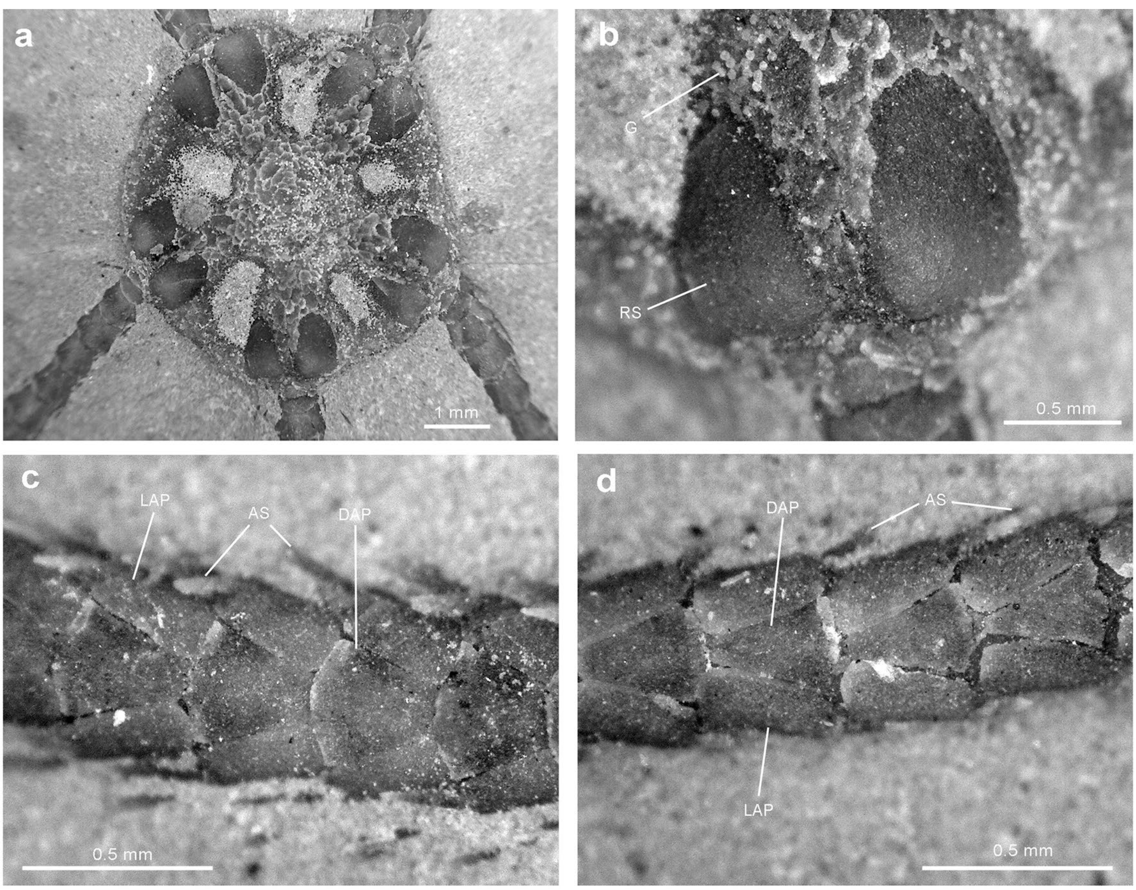

Fig. 4 *Arenorbis santameraensis* sp. nov. from the upper Sinemurian of the Punta La Llastra W section, Villaviciosa (Asturias, north-west Spain); paratype (MUJA-0511); **a** general view of specimen exposing dorsal side; **b** detail of radial shields; **c** detail of proximal arm segments; **d** detail of distal arm segments. *AS* arm spines *DAP* dorsal arm plates *G* disc granules *LAP* lateral arm plates *RS* radial shields

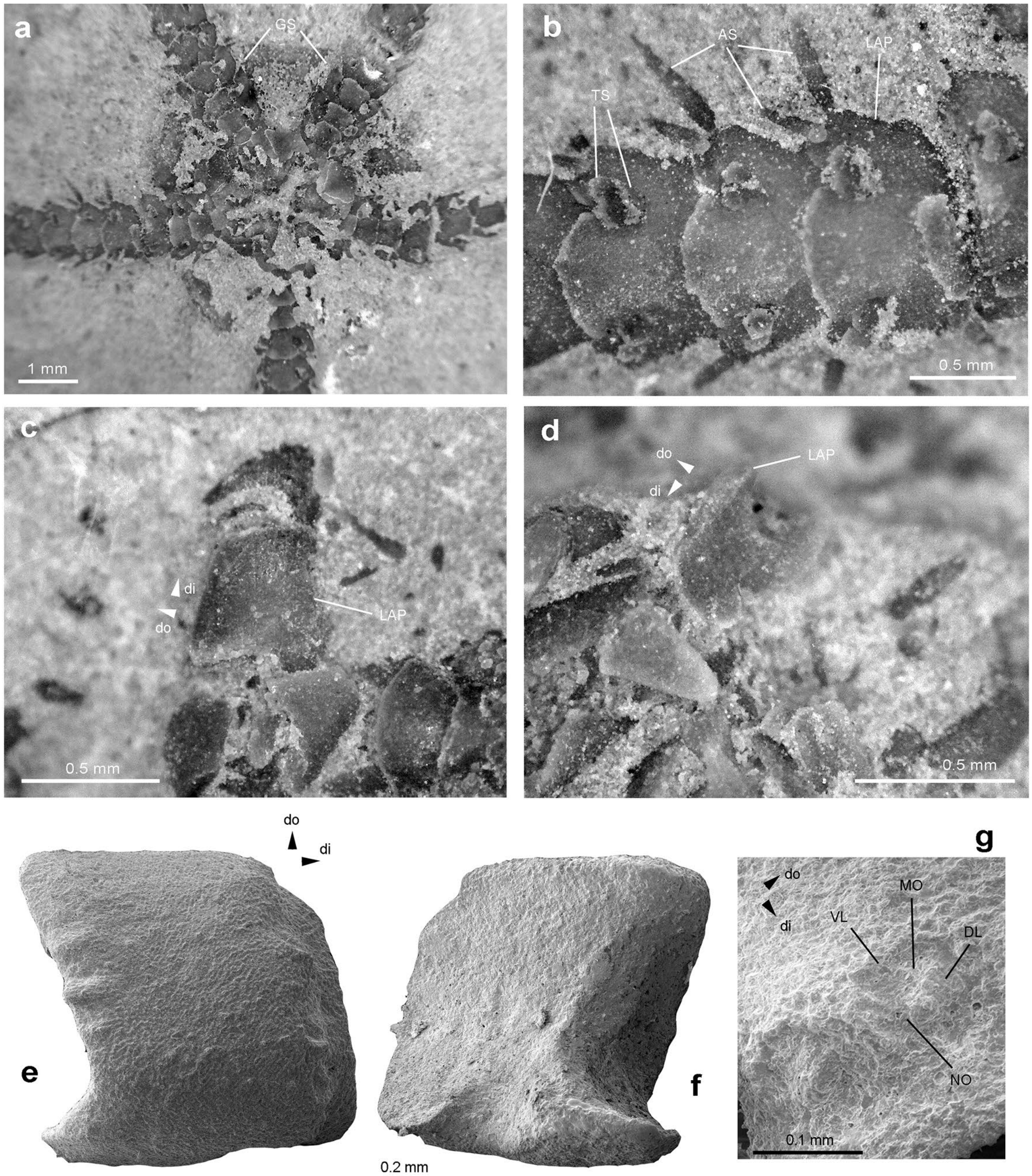

Fig. 5 **a**–**d** *Arenorbis santameraensis* sp. nov. from the upper Sinemurian of the Punta La Llastra W section, Villaviciosa (Asturias, north-west Spain); paratype (MUJA-3785); **a** general view of the specimen exposing ventral side; **b** detail of proximal arm segments; **c** dissociated lateral arm plate in external view; **d** dissociated lateral arm plate in internal view; **e**–**g** *Arenorbis squamosus* (Picard, 1858) from the Middle Triassic of Schillingstadt, Baden-Württemberg, Germany; dissociated lateral arm plate (MnhnL OPH198) in external (**e**) and internal (**f**) views and with detail of spine articulations (**g**). *AS* arm spines *di* distal *DL* dorsal lobe *do* dorsal *GS* genital slit *LAP* lateral arm plate *MO* muscle opening *NO* nerve opening *TS* tentacle scales *VL* ventral lobe

lateral arm plates carrying up to four arm spines similar to those in holotype, adpressed or at a low angle to the arm, second dorsal spine longest, as long as one arm segment; dorsal arm plates in median arm segments (Fig. 4d) in contact, clearly longer than wide.

MUJA-0811 is a slab with two specimens; the paratype specimen designated herein is an articulated skeleton exposing the ventral side (Fig. 5a, b), disc diameter of 5 mm; buccal skeleton (Fig. 5a) as in holotype; ventral interradii better preserved, showing relatively long

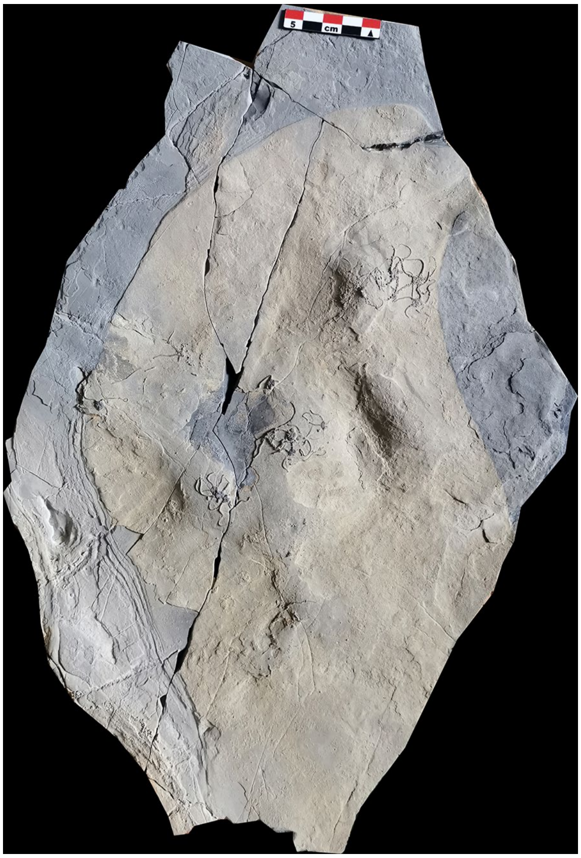

Fig. 6 *Arenorbis santameraensis* sp. nov. from the upper Sinemurian of the Punta La Llastra W section, Villaviciosa (Asturias, north-west Spain); slab (MUJA-0810) with several articulated specimens

genital slit (Fig. 5a) extending to the edge of the disc; arms as in holotype, longest arm 22 mm in length; details of ventral arm skeleton (Fig. 5b) better preserved, showing shallow groove lining tentacle notch in lateral arm plates.

MUJA-3785 is a slab with four specimens; one of the paratypes designated herein being a complete specimen exposing the dorsal side, with a disc diameter of 5 mm; one arm partly disintegrated, with arm plates scattered; proximal lateral arm plate exposing external side (Fig. 5c), with straight dorsal edge, ventro-proximalwards protruding ventral portion, rounded convex distal edge, and concave proximal edge with at least three small, poorly defined spurs; outer surface smooth; three moderately large spine articulations at the same level as outer surface stereom, separated from distal edge by a thin ledge; large but relatively shallow tentacle notch.

The second paratype on slab MUJA-3785 is a specimen exposing the dorsal side, with a disc diameter of 4.2 mm; disarticulated arm plates include a median lateral arm plate showing the internal side (Fig. 5d), with a single, large, well-defined, arched vertebral articular ridge devoid of conspicuous kinks, extensions of thickened parts; tentacle notch well defined and distally bordered by a slightly thickened ventro-distal tip of the lateral arm plate.

Discussion

The ophiuroids described herein show a striking similarity to those from the Middle Triassic Muschelkalk of Germany, originally described by Picard (1858) as *Aspidura squamosa*, and later redescribed by Hess (1970) on the basis of material from the Middle Triassic Muschelkalk of Silesia, south-west Poland. Hess (1970) introduced the new genus *Arenorbis* to account for morphological differences with species of the coeval (and often co-occurring) genera *Aplocoma* d'Orbigny, 1852 and *Aspiduriella* Bolette, 1998. The diagnostic features of *Arenorbis*, adapted to the latest terminological standards (Hendler, 2018; Stöhr et al., 2012; Thuy & Stöhr, 2016), include a dense cover of tiny disc granules, short adoral shields with their proximal tips covered by granules, a buccal skeleton with a pair of tooth papillae, slender arms with pointed arm spines equaling the length of an arm segment, and large tentacle pores covered by two large and several much smaller scales. All these features can be observed in the material described herein, which is why we assign them to the genus *Arenorbis*.

At the species level, the present show great similarities to *Arenorbis squamosus*, the type and previously only known species of the genus. They differ, however, in having adoral shields that meet proximally, as well as longer arm spines and smaller spine articulations. Therefore, we introduce the new species, *Arenorbis santameraensis* sp. nov., to accommodate the new form from north-west Spain.

With respect to the higher-level classification of *Arenorbis*, conclusive evidence is provided by the spine articulations observed on specimens described herein and on the dissociated lateral arm plates of *Arenorbis squamosus* from the Middle Triassic of Schillingstadt, Germany (Fig. 5e–g). In fact, the spine articulations of *Arenorbis* are composed of a slender, comma-shaped ventral lobe and a shorter, thicker dorsal lobe, merged proximally, lacking a sigmoidal fold, and forming an oblique, ear-shaped structure encompassing a muscle perforation and a slightly smaller nerve perforation (Fig. 5g). This type of spine articulation is typically found in members of the suborder Ophiodermatina (Martynov, 2010; Thuy & Stöhr, 2016). Within this suborder, however, *Arenorbis* cannot be accommodated in any of the extant families on the basis of the combination of its morphological features. We therefore refrain from assigning *Arenorbis* to a family within the Ophiodermatina. Pending a phylogenetic analysis, we hypothesise a basal position within the Ophiodermatina, close to *Aplocoma* (Thuy & Stöhr, 2016) and possibly as a member of a still unnamed extinct family at the stem of the extant ophiodermatin clades.

The species described herein represents the first Early Jurassic member of the originally Middle Triassic genus *Arenorbis* and thereby significantly expands its stratigraphical range. In Middle Triassic epicontinental, shallow-marine carbonate ramps of the Muschelkalk facies (Matysick, 2019; Matysick & Szulc, 2019; Warnecke & Aigner, 2019), *Arenorbis squamosus* is common and widespread and often occurs in so-called brittle star beds (Radwański, 2002; Surmik et al., 2020; Zatoń et al., 2008). Interestingly, the rocks that yielded the Early Jurassic congener *Arenorbis santameraensis* sp. nov. (Figs. 2, 6) bear striking similarities to those of the Triassic Muschelkalk facies in terms of lithology, sedimentology and depositional setting. This suggests consistent palaeoecological preferences and niche conservatism in *Arenorbis* between the Middle Triassic and Early Jurassic. While *Arenorbis* was common and geographically widespread in the Middle Triassic of Europe (e.g. Hess, 1970; Radwański, 2002), *Arenorbis santameraensis* sp. nov.is currently known only from a restricted area in north-west Spain, in spite of intense efforts to explore the Early Jurassic ophiuroid record during several decades (e.g. Hess, 1962a, 1962b, 1964; Thuy, 2013). This suggests that the new species represents a Jurassic relict of a once widespread Middle Triassic genus.

Acknowledgements
We thank the reviewers John W.M. Jagt (Maastricht, The Netherlands) and Tania Pineda (Los Angeles, USA) whose constructive comments improved the quality of this manuscript.

Author contributions
LPS and JCG-R collected the specimens and provided the geological background. BT carried out the morphological analyses. All authors contributed to writing the manuscript and compiling the figures, and all authors read and approved the final manuscript.

Funding
LPS and JCG-R are supported by Sociedad Pública de Gestión y Promoción Turística y Cultural del Principado de Asturias.

Availability of data and materials
All data generated or analysed during this study are included in this published article.

Declarations

Competing interests
The authors declare that they have no competing interests.

Received: 31 March 2023 Accepted: 13 May 2023
Published online: 09 June 2023

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