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EXCEPTIONALLY WELL-PRESERVED BRITTLE STARS FROM THE PLIENSBACHIAN (EARLY JURASSIC) OF THE FRENCH ARDENNES

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Abstract: Two new genera and species of ophiuroid, *Inexpectacantha acrobatica* new gen. et sp. and *Eirenura papillata* new gen et sp., are described on the basis of 39 articulated specimens and several hundreds of arm fragments and isolated skeletal parts. The material was extracted from a lumachellic bed in a late early Pliensbachian succession of argillites at Sedan, French Ardennes. The material is unusually well preserved with even finest structures of the skeleton discernible. Despite the exceptionally detailed morphological data extractable from the material, the higher taxonomic classification in the system of recent ophiuroids could only be tentatively attained. *Inexpectacantha acrobatica* seems best placed within the Ophioplinthacinae inside the Ophiacanthidae whereas *Eirenura papillata* shares greatest similarities with the Ophioleucinae. The occurrence of articulated specimens of different sizes, with some of the most delicate skeletal structures left intact, together with completely disarticulated skeletons of the same species suggests that the ophiuroids were preserved as autochthonous faunule among an *in situ* population of *Modiolus sp.* during a period of more favourable bottom water conditions in an otherwise largely hostile near-shore soft-bottom environment. Based on its small size, the highly flexible arms and the presence of well-developed hooks on distal arm segments, an epizoic way of life is inferred for *I. acrobatica* while *E. papillata*, with its rigid arm structure and the conspicuously large tentacle pores, is interpreted as mostly deposit-feeding bottom surface dweller.

Key words: France, ophiuroids, palaeoecology, Pliensbachian, Sedan, taxonomy.

THE fossil record of the ophiuroids, as of most multisclerite organisms, is dominated by isolated and mostly microscopic remains with articulated skeletons occurring only occasionally. Rapidly decaying after death, ophiuroid skeletons require quick and definite burial to be preserved intact (Kerr and Twitchett 2004). For most depositional settings, the conditions necessary for articulated preservation are only given under exceptional circumstances such as storms, gravity flows, submarine channels and migrating sand waves (Ausich 2001), thus explaining the scarcity of intact ophiuroid fossils. Although early Jurassic strata of Europe are among the more productive in terms of articulated brittle stars, with such renowned localities such as the British Dorset coast starfish beds (Goldring and Stephenson 1972), and although a comparatively large number of early Jurassic ophiuroid species have been described based on articulated specimens (Hess 1960*b*, 1964, 1991; Kutscher 1992), there are still new and puzzling discoveries of early Jurassic ophiuroids to be made. This study reports on such a new faunule of brittle stars based on extraordinarily well-preserved material from the Pliensbachian of the French Ardennes. The material is exceptional not only because most skeletons are intact but especially because even finest structures of the skeletal parts are preserved. Furthermore, both ventral and dorsal sides of the specimens are observable in many cases. Isolated ossicles assignable to the described species provide morphological data on internal skeletal structures. The material thus allows an unusually detailed insight into an ophiuroid assemblage from a period that is supposed to have witnessed at least part of the major postpalaeozoic radiation of the ophiuroids (Smith *et al.* 1995; Kutscher and Villier 2003).

GEOLOGICAL AND PALAEONTOLOGICAL CONTEXT

Construction works on the highway N43 south-west of Sedan (Text-fig. 1) led in 2002 to a temporarily well-accessible exposure of early Jurassic sediments in the slopes of the road cutting. A succession of dark grey argillites crop out over a total height of about four metres on the southern slope. The argillites appear monotonous and grossly laminated and are very poor in macrofossils. Every few decimetres of the succession, single layers of lumachellic

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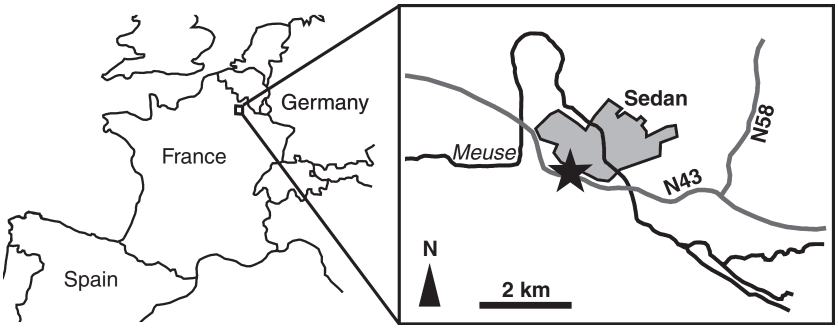

TEXT-FIG. 1. Location of the sampled site near the motorway N43 south-west from Sedan, France.

(here, lumachelle designates a high concentration of iridescent shell material) siderite concretions, generally less than five centimetres thick and conspicuous because of numerous white, glossy bivalve fragments, are intercalated. The lateral continuity of these beds could not be determined because of the limited accessibility of the outcrop.

The ophiuroid remains described herein originate from the basalmost of the outcropping lumachellic beds approximately situated at the level of the road. This bed has yielded rare remains of ammonites. Despite their small size (diameter of <1 cm), the ammonites are most probably assignable to the genus *Androgynoceras* Hyatt, 1867, and probably belong to more advanced forms with affinities to species of the genus *Amaltheus* De Montfort, 1808 (Maisch, pers. comm. 2007), and thus allow an age assignment to the lower Pliensbachian *Davoei* zone.

Mouterde *et al.* (1980) describe the upper part of the lower Pliensbachian as mainly marly to argillaceous, with high abundances of belemnites in the lower part of the *Davoei* zone for the region of Sedan and in general the south-western margin of the emerged landmass of the Ardennes. Lumachellic beds are not mentioned though.

Belemnites, also common in the limestones of the *Davoei* zone in the neighbouring parts of the Paris basin of Luxembourg and Lorraine-region (Mouterde *et al.* 1980, Lucius 1948), seem to be very rare in the studied outcrop. Bivalves of the genus *Modiolus* Lamarck, 1799, are by far the dominant faunal component in the lumachellic beds. Other macrofossils include the aforementioned ammonites, small ostreid and pectinid bivalves, crinoid columnals, echinoids with adhering spines and pedicellaria, and the ophiuroid remains described herein. The rich microfauna is dominated by remains of crinoids, ophiuroids, echinoids, asteroids and holothurians. Other groups represented are ostracods, foraminifers, gastropods and rare osteichthyan teeth and scales.

MATERIAL AND METHODS

The studied material was collected during a field trip in 2002 in the course of which the basalmost of the exposed lumachellic beds was sampled for microscopic echinoderm remains. A total of about 4 kg of sediment comprising the concretions and a few centimetres of the over- and underlying argillites were collected, dried, washed and sieved (mesh size of 250 μm), and sorted under a dissecting microscope. The concretions, rarely exceeding dimensions of a few centimetres, were isolated during the sieving process and washed with a soft brush. A total of 39 discs and disc fragments (26 of which isolated and mostly with both sides visible, and 13 on a slab) together with several hundreds of arm fragments and disarticulated plates were collected. The fractures across the arm joints are very often postdiagenetic; most isolated discs and arm fragments probably belong to complete specimens from less consolidated parts of the lumachellic layer and were dissociated during the sieving process. A solution of about 10 per cent of hydrogen peroxide was used to get rid of clayey encrustations in some of the isolated disc and arm fragments. The assignment of the isolated skeletal parts to either of the species described herein was based on comparisons with articulated and semi-articulated or distorted specimens exposing the relevant skeletal parts *in situ*.

Most specimens are excellently preserved, with the microstructures of the skeleton hardly blurred by recrystallization. A few specimens are affected by spots of pyritization and gypsum encrustations. The best preserved isolated disc and arm fragments were mounted on stubs and coated with gold or gold-palladium for SEM observation. Three slabs containing specimens were carbon coated. In the descriptions, the morphological terminology follows Stöhr (2005) and higher-level classification is adopted from Smith *et al.* (1995).

Apart from the two new species described herein, the ophiuroid faunule comprises rare isolated skeletal elements or at most articulated arm fragments of three more species (*Palaeocoma milleri* (Phillips, 1829), *Sinosura sp.* and *Ophiomusium sp.*), which are not treated any further in this study pending a general revision of all known early Jurassic ophiuroids (Thuy in prep.).

The material has been deposited at the Musée national d'histoire naturelle (MnhnL), Luxembourg, and the Muséum National d'Histoire Naturelle (MNHN), Paris.

SYSTEMATIC PALAEONTOLOGY

Order OPHIURIDA Müller and Troschel, 1840
Suborder OPHIURINA Müller and Troschel, 1840
Family OPHIACANTHIDAE Perrier, 1891
Subfamily OPHIOPLINTHACINAE Paterson, 1985

Genus INEXPECTACANTHA gen. nov.

Derivation of name. Genus name composed of 'inexpect(atus)', from the Latin for 'unexpected', and 'Acantha', a nymph in Greek mythology, literally translated 'thorny'. Name is chosen because of the unexpected and unusual combination of characters in the taxon (well-developed hooks, long spines and highly flexible arms together with overall heavy plating).

Type and only known species. Inexpectacantha acrobatica sp. nov.

Diagnosis. Small, five-armed ophiuroid; dorsal disc plating consisting of numerous stout, imbricating plates and similarly stout, small and round radial shields proximally covered by disc plates; scattered spherical granules and short conical spines on ventral and dorsal disc plates, probably including radial shields, and on parts of the mouth plating; five spine-like, blunt oral papillae, small apical papilla; up to three spine-like tentacle scales; lateral arm plates massive, coarsely granulated, bearing up to six erect spines with the dorsalmost spine exceeding the length of two arm segments; vertebrae with hour-glass-shaped articulation condyles; two ventralmost arm spines transformed into highly differentiated hooks in median to distal arm segments.

Inexpectacantha acrobatica sp. nov.
Plates 1–3; Plate 4, figures 1–6

Derivation of name. From the Latin for 'acrobatic', referring to the highly flexible arms of the new species.

Holotype. MnhnL PL227 (Pl. 1, figs 1–3).

Paratypes. MNHN A30315, MnhnL PL229, MnhnL PL221, MnhnL PL222 and MnhnL PL224.

Other material. MnhnL PL223, MnhnL PL226, MnhnL PL230, MnhnL PL231, MnhnL PL233, MnhnL PL236, MnhnL PL237, MnhnL PL238, MnhnL PL239-4 – PL239-6, MnhnL PL239-8, PL239-12 – PL239-17, MnhnL PL241-1 – PL241-11, MnhnL PL242-2 – PL242-3, MnhnL PL243, MnhnL PL245, MnhnL PL246, MnhnL PL247, MnhnL PL248, MnhnL PL249, MnhnL PL250, MnhnL PL251, MnhnL PL252, MnhnL PL253, MnhnL PL254, MnhnL PL255, MnhnL PL256.

Locality and horizon. Motorway cutting south-west from Sedan, Ardennes, France; lumachellic bed in a series of clays of early Pliensbachian age (*Davoei* zone).

Diagnosis. As for genus.

Description of holotype. Disc round to subpentagonal, disc diameter 2.84 mm. Dorsal side with finely granulated round imbricating plates of rather stout aspect. Centrodorsal plate well discernible, slightly larger than surrounding disc plates. Largest portion of radial shields covered by imbricating disc plates; only distal tips emerge close to arm base, indicating short round radial shields of stout and granulated aspect similar to other disc plates. Small spherical granules, 0.07 mm in diameter, scattered on disc plates, suggesting loose granulation covering whole dorsal disc, probably including radial shields (Pl. 1, fig. 2). Ventral side of disc with small round imbricating plates. Oral shield pentagonal to arrow-shaped, nearly as long as broad, with slightly obtuse proximal angle. Adoral shields large, broadly abutting in front of oral shield and extending around lateral angles of oral shield (Pl. 1, fig. 1). Second oral tentacle pore opens within mouth slit. Jaws not elongate. Oral papillae partly lost, no complete row of oral papillae discernible but the combination of the observations from more than one jaw edge suggests at least four spine-like elongate oral papillae in continuous row along jaw edge; two distalmost papillae slightly flattened and blunt, positioned on adoral shield and in the angle between the adoral shield and the oral plate respectively; two proximalmost papillae are on oral plate, smaller and pointed. Single conical slender apical papilla, much smaller than oral papillae (Pl. 1, fig. 3). At least part of the mouth plating seems to have been covered by a loosely scattered granulation, as documented by few spherical granules mainly on adoral shields, but probably also on oral plates and oral shields. Three arms broken at base, one arm with one free segment preserved, fifth arm curled on dorsal face, with several segments preserved (Pl. 1, fig. 2). First ventral arm plate pentagonal, wider than long, straight proximal edge and obtusely pointed distal edge. Subsequent ventral arm plates widest distally, with strongly convex distal edge, concave lateral edges encompassing the tentacle pore, and pointed proximal edge. First two to three ventral arm plates contiguous, subsequent ones separated by lateral arm plates. Tentacle pores of the first two arm segments conspicuously large, covered by at least two spine-like scales; following tentacle pores smaller, covered by two small scales. Dorsal arm plates visible on a very short portion of one arm only; fan-shaped, in proximalmost segments probably contiguous. Lateral arm plates of massive aspect, bearing five arm spines on large, free-standing, ear-shaped spine articulations. Spines tapering, blunt, coarsely striated, slightly longer than one arm segment; dorsalward increase in size of spines; dorsalmost spine not observable.

Paratype supplements and variation. Specimen MNHN A30315 (Pl. 1, figs 4–6 is a small individual exposing the ventral disc with a diameter of 1.9 mm, three arms broken, one arm dipping dorsalwards into matrix, and fifth arm partly visible ventrally and laterally. The specimen generally fits the description of the holotype very well, but the mouth plating is better preserved and allows some additional observations. Five spine-like elongate oral papillae in continuous row along jaw edge; three distalmost papillae slightly flattened and blunt, positioned on adoral shield, in the angle between the adoral shield and the oral plate, and on the oral plate, respectively; two proximalmost papillae on oral plate smaller and pointed (Pl. 1, fig. 5). Single conical slender apical papilla, smaller than oral papillae. The adoral shields as well as the oral plates bear very few scattered granules, suggesting, as in the holotype, a loose granulation covering at least part of the mouth plating.

Specimen MnhnL PL222 (Pl. 2, fig. 1) is a small disc with a diameter of 2.3 mm, and with all five arms broken at their base. Dorsal disc plating well exposed and largely denuded of granules. The few remaining granules are spherical to slightly elongate. Relatively large centrodorsal plate surrounded by a circle of five larger, round plates, possibly representing the primary rosette, which are accompanied by a few smaller plates. Remaining disc plates densely imbricating and almost completely covering the radial shields. In one radius, a larger part of the radial shields is exposed owing to partly lacking disc plates. Radial shields not conspicuously different from disc plates.

Specimen MnhnL PL229 (Pl. 2, figs 2 and 4–5) exposes the ventral side, disc diameter 2.2 mm, two arms broken but with several segments preserved, one arm concealed by matrix and two arms almost complete. The round and rather stout imbricating plates of one ventral interradial area bear a small conical spine, about 2.5 times as long as thick and smaller than the arm spines. This spine is likely to represent part of the disc granulation, which thus not only consists of spherical granules. Apart from that, the ventral disc plating generally fits the description of the holotype very well. However, the well-preserved arms provide supplementary morphological data. The most complete arm has a total length of 7.4 mm and is composed of 22 segments, the two proximalmost of which are incorporated in the disc. Ventral arm plates are observable on most arm segments but rapidly decrease in size towards the tip of the arm. Tentacle pores rapidly decrease in size after the first few arm segments, but are developed throughout the arm, and are covered by one or two scales on median arm segments and a single flat spine-like scale in distal arm segments (Pl. 2, fig. 5). Lateral arm plates rugose and of massive aspect; meeting on the mid-line after the first two to three arm segments, abutting on increasingly large portions towards the tip of the arm. Distal arm plates clearly elongate. On the 6th or 7th segment not incorporated in the disc, the two ventralmost spines develop into highly differentiated hooks, oriented ventralwards and attached to specialized enlarged and smooth articulations on the distal edge of the lateral arm plates (Pl. 2, figs 4,5). Additional to the two hooks, the distal lateral arm plates bear one or two undifferentiated conical arm spines, roughly striated and slightly shorter than one arm segment. The pairs of hooks are present on the distalmost preserved arm segments.

Specimen MnhnL PL224 (Pl. 2, fig. 6) is a loose disc with a diameter of 3.1 mm. Two arms have the first few segments preserved. The discernible skeletal structures of the specimen fit the description of the holotype very well. The specimen provides supplementary information on the tentacle scales of the first arm segments, in that the tentacle pore of the second segment of one arm is covered by three tightly packed, spine-like scales.

Specimen MnhnL PL221 (Pl. 3, fig. 7), on the same slab as the holotype of *Eirenura papillata*, exposes the dorsal side of a disc largely concealed by matrix. Several granules are preserved on the rugose imbricating disc plates, some of which are spherical and some elongate and blunt. Two arms are coiled on the dorsal side of the disc, exposing their ventral faces. The arm skeleton fits that of specimen MnhnL PL229 very well, but as a result of the coiling, some arm spines are better preserved than on the other type material. The dorsalmost arm spine of the proximal segments is by far the longest, exceeding the length of two arm segments.

Isolated ossicles and fragments. Lateral arm plates (Pl. 3, figs 1–5): proximal lateral arm plates higher than long, of massive and bulging aspect, with convex distal edge; outer surface rugose; sharp line of constriction close to proximal edge; small oval knob of dense stereom in the central part of the proximal edge; up to six free-standing spine articulations close to distal edge, in diffuse shallow depressions; spine articulations and gaps between them slightly increasing in size dorsalwards. Distal lateral arm plates longer than high, with four to five spine articulations. Inner side of lateral arm plates with single large central ridge, well defined and prominent, widest dorsally, confluent with dorsal edge of the plate in proximal lateral arm plates, clearly separated from the dorsal edge in distal plates; ventral tip of the ridge most prominent. Ventral edge of the plate swollen, thickest at margin of the tentacle notch.

Arm fragments (Pl. 2, fig. 3, Pl. 3, figs 6, 8): some arm fragments expose the fan-shaped dorsal arm plates (Pl. 3, fig. 6) and the distal hooks (Pl. 2, fig. 3) very clearly. One coiled distal arm fragment exemplifies the high degree of flexibility of the arms. One fragment comprises the first three vertebrae of a ray (including the mouth vertebra) and two pairs of oral plates exposing the denuded dorsal side. There is seemingly a pair of

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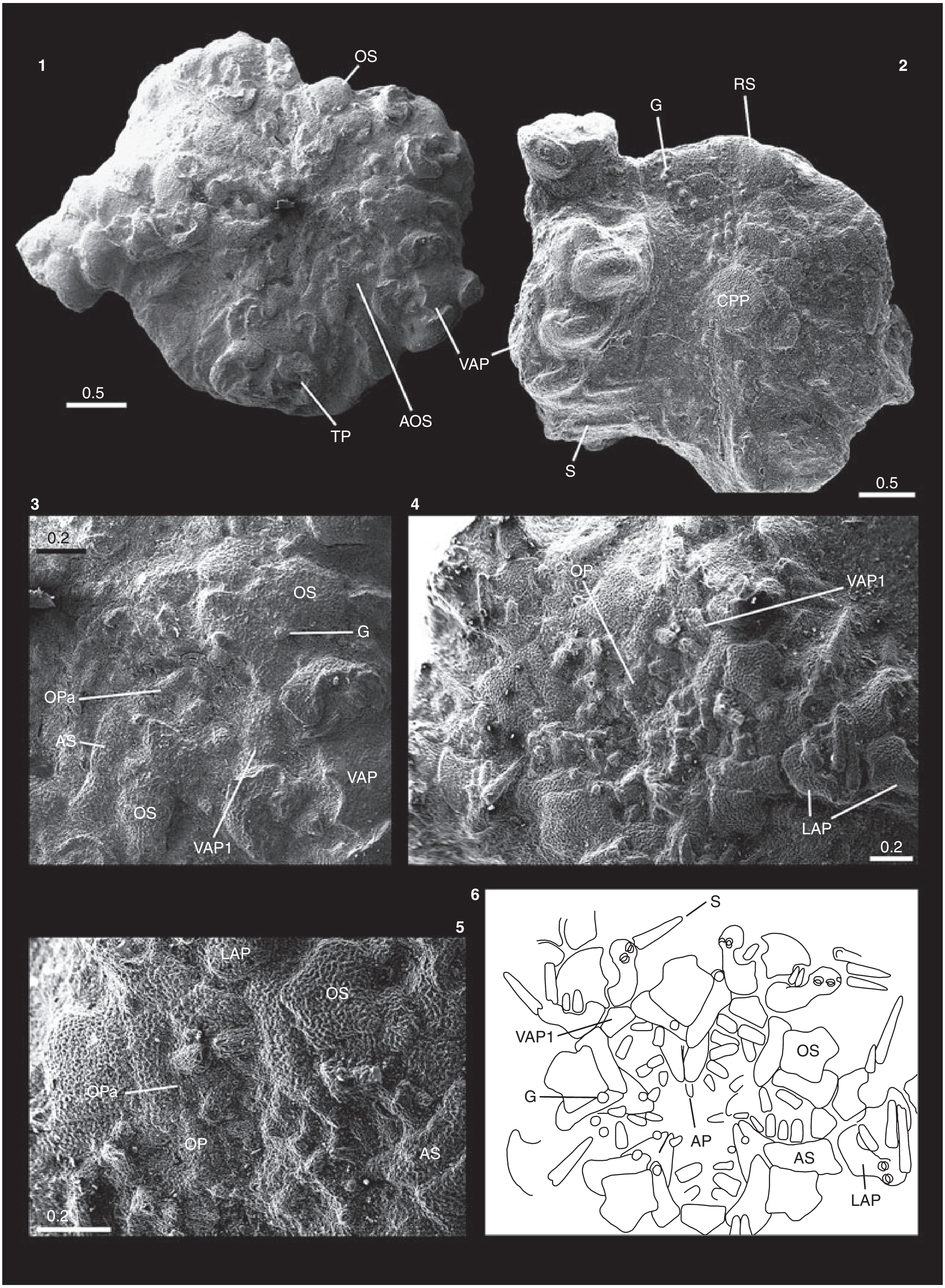
EXPLANATION OF PLATE 1

Figs 1–6. *Inexpectacantha acrobatica* gen. et sp. nov. from the early Pliensbachian of Sedan, France. 1, MnhnL PL227 (holotype, SEM) ventral surface. 2, MnhnL PL227 (holotype, SEM) dorsal surface with two arms curled upwards. 3, MnhnL PL227 (holotype, SEM) detail of fig. 1 showing mouth plating. 4, MNHN A30315 (paratype, SEM) mouth plating 5, MNHN A30315 (paratype, SEM) detail of mouth plating of fig. 4. 6, MNHN A30315 (paratype) drawing of mouth plating of fig. 4.

Abbreviations: AS, adoral shield; CPP, centrodorsal plate; G, disc granule; LAP, lateral arm plate; OPa, oral papilla; OS, oral shield; RS, radial shield; S, spine; TS, tentacle scale; VAP, ventral arm plate; VAP1, first ventral arm plate.

Scale bars are in mm.

PLATE 1



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peristomial plates, although it cannot be ruled out that the two plates are the result of one single plate fractioned as it was pressed against the edges of the oral plates.

Vertebrae (Pl. 4, figs 4–6): prominent hour-glass-shaped articulation condyles on distal and proximal faces; no accessory pegs. This type of vertebral articulation explains the high flexibility of the arms in the articulated specimens and arm fragments, allowing extreme degrees of horizontal and vertical curling. Vertebrae narrow; dorso-proximal fossae large and wing-like, constituting widest part of vertebra; dorso-distal fossae narrow and regressing, ventro-distal ones strongly protruding. Distal vertebrae elongate.

Radial shields (Pl. 4, fig. 3): rounded triangular shape, almost as wide as long, of stout aspect and with rugose outer surface, distal edge with very faint indentation.

Oral plates (Pl. 4, figs 1,2): nearly twice as long as high, not tapering distalwards; abradial muscle area rather small, adradial muscle area on ventro-distal edge of plate; notch for ring water canal deep.

Discussion. None of the early Jurassic ophiuroid species known from articulated specimens are comparable to *Inexpectacantha acrobatica*. However, there are some similarities with species based on isolated lateral arm plates. *Sigsbeia*? *lunaris* (Hess 1962) from the Pliensbachian of Switzerland and the Toarcian–Aalenian of Germany (Kutscher 1996) is characterized by stout and strongly arcuate lateral arm plates with up to 8 (Kutscher (1996) mentions up to 11) spine articulations resembling artiodactyls footprints. The associated vertebrae have hour-glass-shaped articulation condyles. The lateral arm plates of *Inexpectacantha acrobatica* differ from those of *Sigsbeia*? *lunaris* in their general aspect, the constriction, the rugose outer surface, the shape and number of the spine articulations and the better developed tentacle notches. A set of articulated arm fragments from the Pliensbachian of Great Britain was assigned to *Hemieuryale*? *lunaris* by Hess (1964) although the lateral arm plates slightly differ from the Swiss-type material. The British specimens have up to six ear-shaped spine articulations and thus are more similar to *Inexpectacantha acrobatica*. However, the spines preserved on some of the British fragments are considerably shorter than in *Inexpectacantha acrobatica*, the tentacle notches are less well developed and the shape of the dorsal arm plates differs. An undescribed articulated specimen in the BMNH collection from the Pliensbachian of Great Britain, mentioned by Smith *et al.* (1995) as '?*Hemieuryale*', new genus of Ophiochondrinae, presents an arm skeleton very similar to the aforementioned arm fragments. A preliminary examination of this specimen revealed a dorsal disc plating consisting of much smaller and thinner plates than in *Inexpectacantha acrobatica*. Despite the superficial similarities including strongly curled arms, the British specimen is not assignable to *Inexpectacantha acrobatica*. Isolated lateral arm plates from the Sinemurian of Luxembourg described as *Hemieuryale*? n. sp. by Kutscher and Hary (1991) show the greatest affinities with *Inexpectacantha acrobatica*, but a detailed comparison and possible attribution to *I. acrobatica* requires examination of the original material.

Hook-shaped distal arm spines are encountered in many different ophiuroid families and thus are not diagnostic in higher taxonomic classification. They rather represent the expression of a certain mode of life, being generally best developed in small epizoic forms. Fossil hooks ascribed to ophiuroids have been occasionally mentioned (Mostler and Krainer 1993; Kutscher 1996) but all occurrences known to date consist of isolated hooks. The material described herein comprises the first crown-group fossil ophiuroids with hook-shaped spines *in situ*.

The long erect spines, the loose granulation on the disc and the shape of mouth plating justify the attribution of *Inexpectacantha acrobatica* to the Ophiacanthidae. The oral plates are comparable to those of *Ophiopristis mitsuii* (Murakami 1942) figured *in* Murakami (1963) as *Ophiacantha mitsuii*, thus not contradicting an ophiacanthid attribution of *I. acrobatica*. Among the ophiacanthid subfamilies defined by Paterson (1985), strongest affinities are shared with the Ophioplinthacinae because of the thick disc plates, the well-developed and not bar-like radial shields and the relatively short jaws. In the Ophioplinthacinae, *Ophiocopa spatula* Lyman, 1883, presents a dorsal disc plating and scattered spherical granules very similar to those of *Inexpectacantha acrobatica*, and *Ophiurothamnus clausa* (Lyman 1878) has similarly hour-glass-shaped vertebral articulation condyles (O'Hara and Stöhr, 2006). There are some affinities with species of the

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EXPLANATION OF PLATE 2

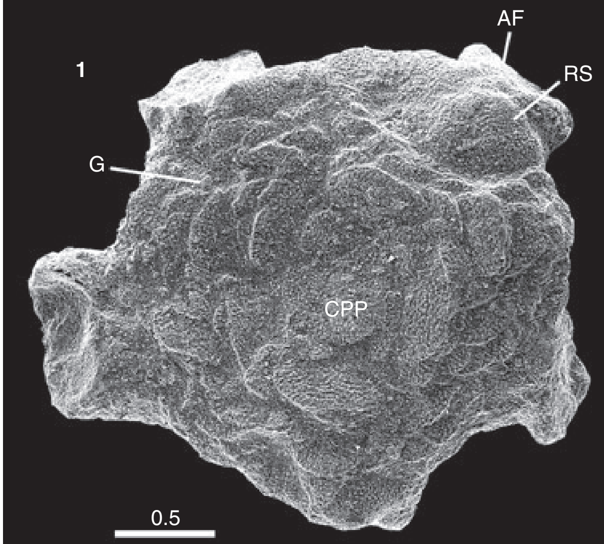
Figs 1–6. *Inexpectacantha acrobatica* gen. et sp. nov. from the early Pliensbachian of Sedan, France. 1, MnhnL PL222 (paratype, SEM) dorsal surface largely denuded of granules. 2, MnhnL PL229 (paratype) ventral surface. 3, MnhnL PL239-16 (SEM) hook adhering to distal lateral arm plate of isolated arm fragment. 4, MnhnL PL229 (paratype, SEM) ventral side of distal arm segments showing arm spines and hooks *in situ*. 5, MnhnL PL229 (paratype, SEM) ventral side of distal arm segments showing spines and hooks *in situ*. 6, MnhnL PL224 (paratype, SEM) detail of ventral surface showing interradial area and part of an arm base.

Abbreviations: AF, arm fragment; CPP, centrodorsal plate; G, disc granule; IRP, ventral interradial plate; LAP, lateral arm plate; RS, radial shield; S, spine; SSA, specialized spine articulation; TS, tentacle scale.

Scale bar values are in mm.

PLATE 2

1



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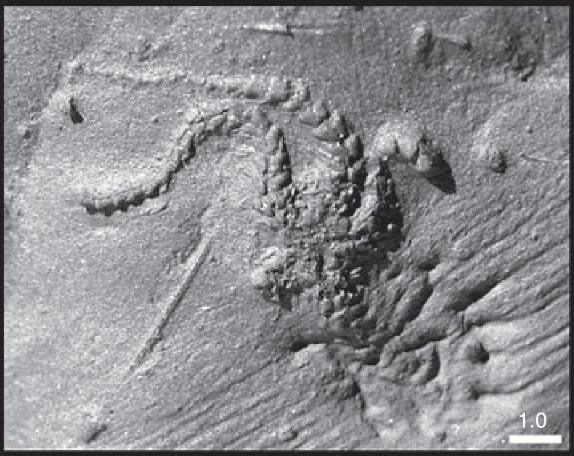

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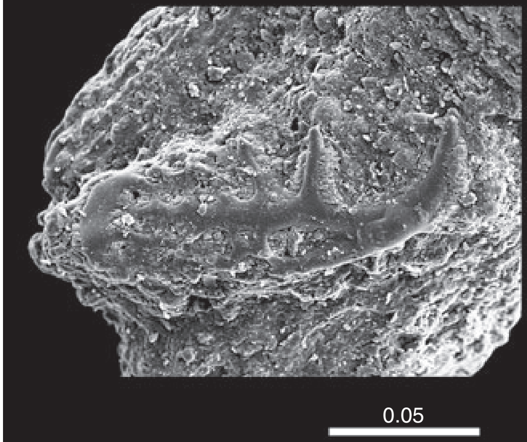

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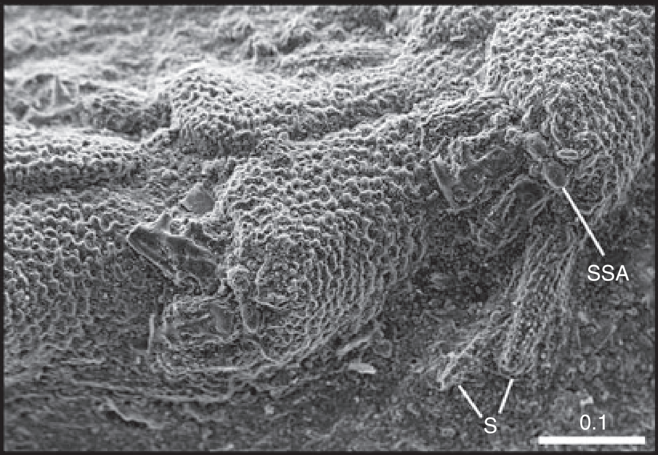

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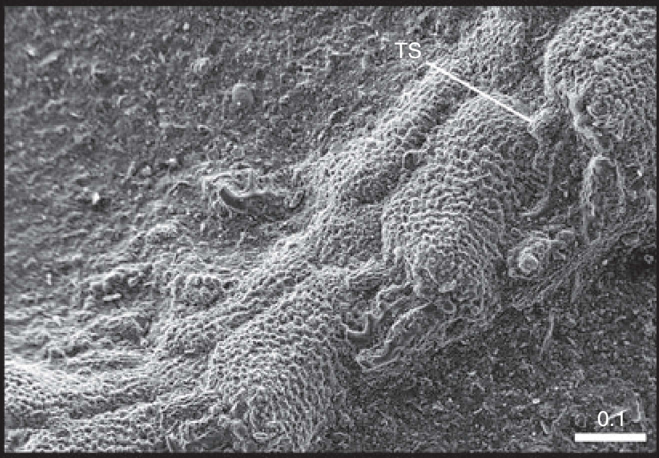

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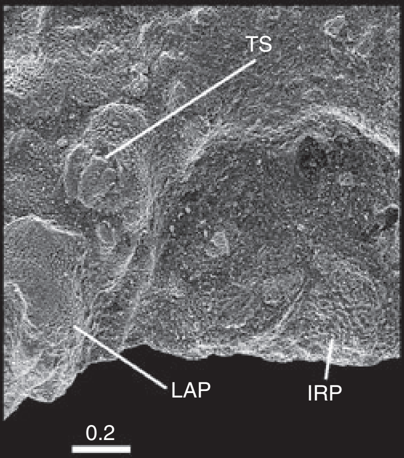

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hemieuryalid genus *Ophiomoeris* (O'Hara and Stöhr 2006) concerning the massive arm plating, but in *Inexpectacantha acrobatica* the radial shields are less conspicuous and the spines considerably longer. Hour-glass-shaped vertebral articulation is characteristic for the Hemieuryalidae, but is also found in many ophiacanthid species, especially the small epizoic ones, thus blurring the distinction between both families (O'Hara and Stöhr 2006). Based on similarities in the structure of arm spine articulations, Martynov (2010) suggests transferring at least the genera *Ophiomoeris* Koehler, 1904 and *Ophiochondrus* Lyman, 1869 into the Ophiacanthidae. The spine articulations of *Inexpectacantha acrobatica* show great similarity with those of *Ophiosemnotes sp.* (Martynov 2010) and of an unidentified species of *Ophiotrema* Koehler, 1896 (Martynov, pers. comm. 2007). Pending a revision of the Ophiacanthidae and the Hemieuryalidae, it seems best supported by morphological evidence to place *Inexpectacantha acrobatica* in the Ophioplinthacinae. The combination of characters unique for *Inexpectacantha* makes it incompatible with any known fossil or recent ophiuroid genus and requires the creation of a new genus.

Family OPHIURIDAE Lyman, 1865
Subfamily OPHIOLEUCINAE Matsumoto, 1915

Genus EIRENURA gen. nov.

Derivation of name. Genus name composed of 'Eirene', the personification of peace in Greek mythology, and 'ura' from Greek for 'tail'.

Type species. Eirenura papillata sp. nov.

Other species included. Eirenura kohli (Thuy, 2005).

Diagnosis. Small five-armed ophiuroid, dorsal disc and ventral interradial areas completely covered by dense granulation, developing into a fringe of short papillae between the arm bases at the edge of the disc; very large, elongate oral shields encompassed by narrow adoral shields; up to two supplementary plates proximal to oral shields on oral plates; second oral tentacle pore nearly superficial, partly enclosed by first ventral arm plate and adoral shield, covered by four scales; continuous row of seven oral papillae, including two of the scales of the second oral tentacle pore; small conical apical papilla; dorsal shields tiny; tentacle pores very large, covered by up to nine scales; up to nine short and adpressed arm spines.

Eirenura papillata sp. nov.
Plate 4, figures 7–15; Plates 5, 6

Derivation of name. From the Latin for 'bearing papillae', referring to the numerous papillae typical for this species.

Holotype. MnhnL PL220 (Pl. 5 fig. 1–4).

Paratypes. MNHN A30316, MNHN A30317 and MnhnL PL228.

Other material. MNHN A30318, MnhnL PL225, MnhnL PL234, MnhnL PL235, MnhnL PL239-1 – PL239-3, MnhnL PL240-1 – PL240-9, MnhnL PL242-1, MnhnL PL2424 – PL242-6, MnhnL PL244, MnhnL PL257, MnhnL PL258, MnhnL PL259, MnhnL PL260, MnhnL PL261.

Locality and horizon. Motorway cutting south-west from Sedan, Ardennes, France; lumachellic bed in a series of clays of early Pliensbachian age (*Davoei* zone).

Diagnosis. Proximal edge of lateral arm plates with fine, but conspicuous horizontal striation.

Description of holotype. Disc round, 4.09 mm in diameter. Dorsal side concealed by matrix. Dense granulation visible in one ventral interradial area, composed of small spherical to bluntly elongate granules (Pl. 5, fig. 1). Mouth plating, including oral shields, free of granules. Bursal slits well developed, extending at least to disc edge. Oral shields conspicuously large, longer than

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EXPLANATION OF PLATE 3

Figs 1–8. *Inexpectacantha acrobatica* gen. et sp. nov. from the early Pliensbachian of Sedan, France. 1, MnhnL PL242-2 (SEM) proximal isolated lateral arm plate, external face, dorsal side upwards, distal edge to the left. 2, MnhnL PL242-2 (SEM) detail of fig. 1 showing spine articulations. 3, MnhnL PL241-7 (SEM) proximal isolated lateral arm plate, internal face, dorsal side upwards, distal edge to the left. 4, MnhnL PL241-5 (SEM) median to distal isolated lateral arm plate, external face, dorsal side upwards, distal edge to the right. 5, MnhnL PL241-5 (SEM) median isolated lateral arm plate, internal face, dorsal side upwards, distal edge to the right. 6, MnhnL PL241-11 (SEM) dorsal face of isolated median arm fragment, distal end to the left. 7, MnhnL PL221 (paratype, SEM) detail of arm curling dorsalwards (thus exposing ventral face) on disc largely concealed by matrix. 8, MnhnL PL241-1 (SEM) isolated coiled distal arm fragment.

Abbreviations: G, disc granules; TP, tentacle pore.

Scale bar values are in mm.

PLATE 3

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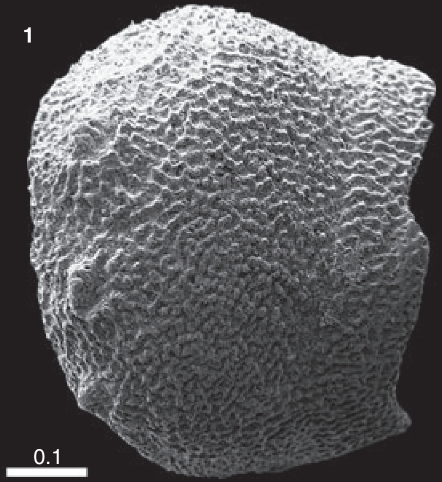

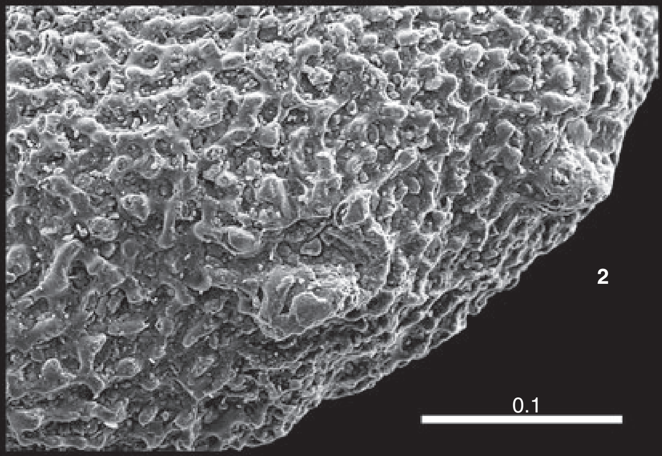

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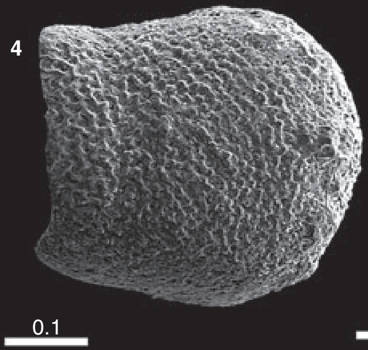

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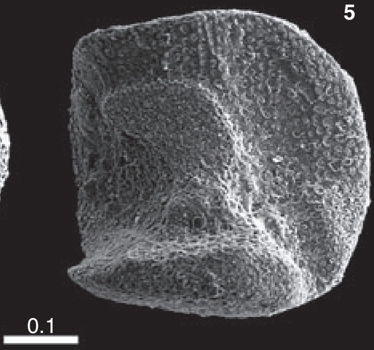

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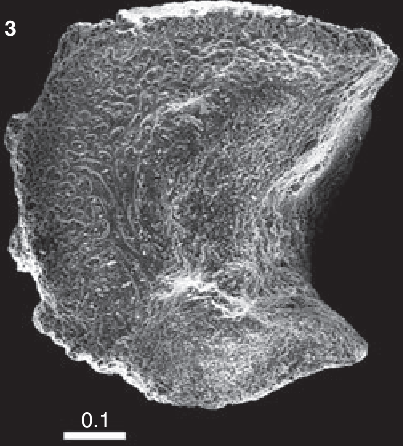

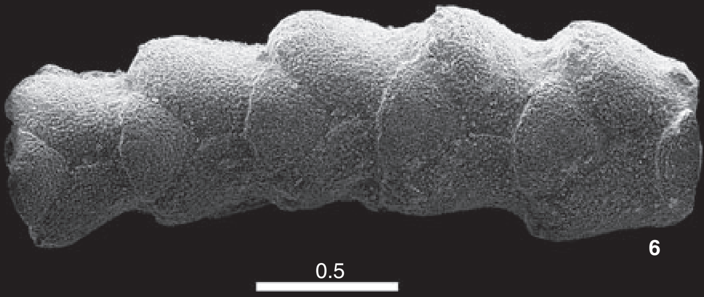

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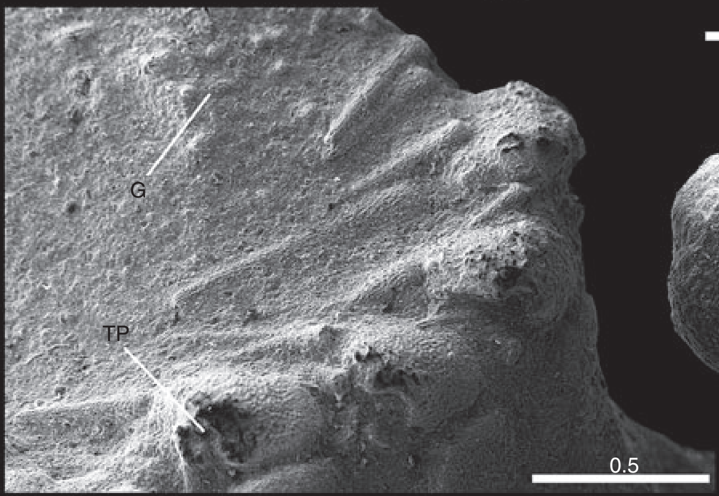

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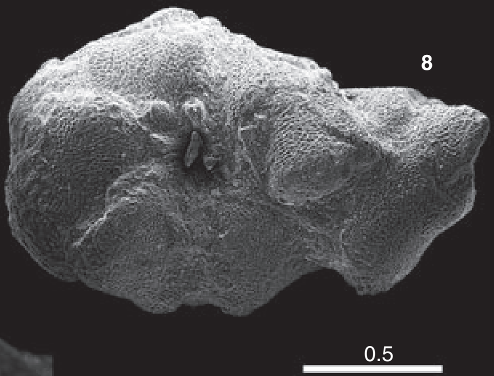


THUY, *Inexpectacantha acrobatica*

wide, with rounded rectangular distal edge and acute rounded proximal angle with slightly concave lateral edges. Adoral shields long and narrow, hardly abutting in front of oral shield, distal part strongly concave. Jaws not elongate, slender. Narrow ventral tip of dental plate visible. Continuous row of up to seven flat, round leaf-like oral papillae with fine longitudinal striation, almost equal in size, increasingly narrow proximalwards (Pl. 5, fig. 4). Single slender, roundly conical apical papilla, smaller than oral papillae. Second oral tentacle pore opening within mouth slit, but partly enclosed by lateral edge of first ventral arm plate protruding into the mouth slit, and concave distal part of adoral shield, covered by two distalmost oral papillae and two papillae sitting on first ventral arm plate, giving the aspect of a second oral tentacle pore opening outside the mouth slit (Pl. 5, fig. 4). Two arms broken at base, three arms with several arm segments preserved. Visible part of longest arm measures 7.4 mm in length and comprises 14 segments. Tip of the arm concealed by matrix. Arms wide and low. Ventral arm plates contiguous throughout the visible portions of the arms, proximal ones wider than long, widest distally, with roundly obtuse proximal angle, slightly concave distal edge and strongly concave and swollen lateral edges. Distal ventral arm plates longer than wide. Tentacle pores conspicuously large, in proximal segments covered by up to nine scales strongly resembling the oral papillae (Pl. 5, fig. 3), five of which sitting on the ventro-distal edge of the lateral arm plate and the remaining four on the lateral edge of the ventral arm plate, with the outermost scale twice as wide as the others. In median to distal segments, three to four tentacle scales on the lateral arm plate and a single wide scale on the ventral arm plate are observable. Lateral arm plates finely striated transversely (or vertically). Basalmost spine visible in some arm segments, pointed, tapering, adpressed against arm, slightly longer than half an arm segment (Pl. 5, fig. 3).

Paratype supplements and variation. Specimen MNHN A30316 (Pl. 6, figs 1–3) is a loose disc fragment comprising two complete pairs of jaws. The dorsal side of the disc is covered by a dense granulation consisting of small, roughly spherical granules about 0.055 mm in diameter. The radial shields are almost completely concealed by dense granulation, only the distal edges seem to be discernible. The ventral interradial areas are covered by a similarly dense granulation but here, the granules tend to be slightly elongate, as seen in the holotype, and both their size and length increase towards the disc margin where they seem to constitute a kind of fringe of blunt spine-like papillae. Most of the oral papillae and tentacle scales are lost or not discernible. One slender apical papilla is followed by conical pointed teeth, clearly larger than apical papilla. A small round plate, obviously displaced (Pl. 6, figs 1, 2), is visible on the lateral edges of both jaws. Both plates are slightly too large to be interpreted as oral papillae and furthermore lack the conspicuous striation of the papillae. Their microstructure rather resembles the stereom of the oral shields. They could thus represent dislocated additional plates of the external mouth skeleton. The dorsal arm plates are very small, triangular, widely separated by lateral arm plates, and lost in most of the preserved arm segments (Pl. 6, fig. 3). Lateral arm plates bear about up to seven or eight pointed tapering arm spines, which are slightly longer than half a segment and decreasing in size dorsalwards. A part of the ventral arm plates is covered by clusters of tiny spherical structures that superficially resemble granules, but are more likely representing pyrite framboids as artefacts of preservation.

Specimen MnhnL PL228 (Pl. 6, figs 4, 5) is a loose disc fragment corresponding to a radius of a small individual (estimated disc diameter 2.1 mm) with one free arm segment preserved. The dorsal side of the fragment is well preserved and exposes a densely granulated dorsal disc, with the small, rough and subspherical granules covering also the radial shields. The indented distal edge of the slightly distorted radial shields is visible, suggesting that the radial shields of the same radius were contiguous at least distally. A group of grossly striated spine-like papillae seemingly disposed in at least two rows arises between

EXPLANATION OF PLATE 4

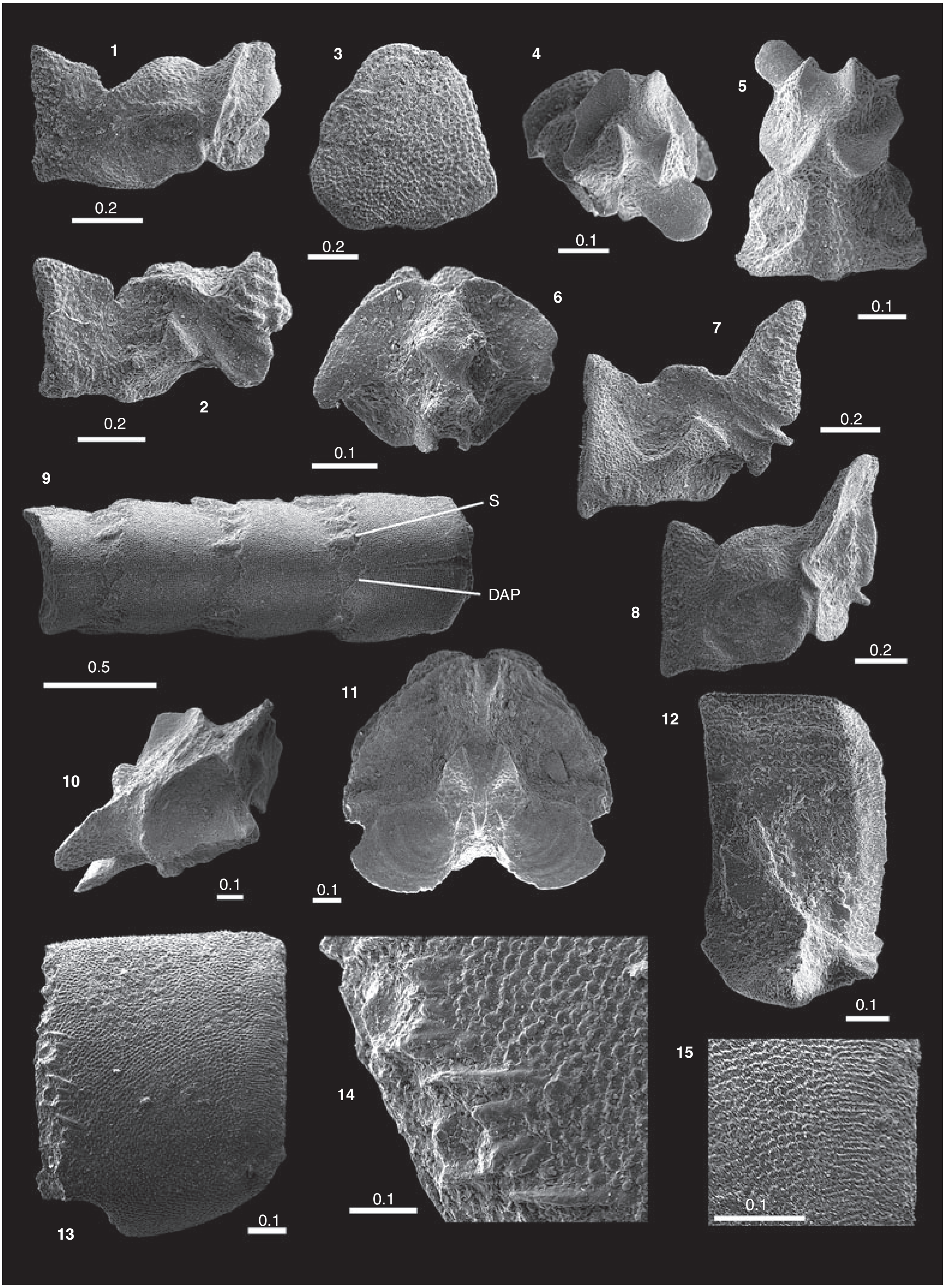
Figs 1–6. *Inexpectacantha acrobatica* gen. et sp. nov. from the early Pliensbachian of Sedan, France. 1, MnhnL PL239-5 (SEM) isolated oral plate, abradial face, dorsal side upwards, distal edge to the right. 2, MnhnL PL239-4 (SEM) isolated oral plate, adradial face, dorsal side upwards, distal edge to the right. 3, MnhnL PL239-8 (SEM) isolated radial shield with proximal tip pointing upwards. 4-5, MnhnL PL239-14 (SEM) isolated median vertebra, exposing distal articulation condyles, dorsal side upwards, (fig. 4) and dorsal face with distal articulation condyles pointing upwards (fig. 5). 6, MnhnL PL239-12 (SEM) isolated proximal vertebra exposing proximal articulation condyles, dorsal side upwards.

Figs 7–15. *Eirenura papillata* gen. et sp. nov. from the early Pliensbachian of Sedan, France. 7, MnhnL PL239-2 (SEM) isolated oral plate, adradial face, dorsal side upwards, distal edge to the right. 8, MnhnL239-1 (SEM) isolated oral plate, abradial face, dorsal side upwards, distal edge to the right. 9, MnhnL PL240-5 (SEM) dorsal face of isolated median arm fragment, distal end to the left. 10, MnhnL PL242-4 (SEM) isolated proximal vertebra in lateral view, distal side to the left. 11, MnhnL PL242-6 (SEM) isolated proximal vertebra in distal view exposing growth bands on ventro-distal fossae, dorsal side upwards. 12, MnhnL PL240-4 (SEM) isolated proximal lateral arm plate, internal face, dorsal side upwards, distal edge to the right. 13, MnhnL PL242-1 (SEM) isolated proximal to median lateral arm plate, external view, dorsal side upwards, distal edge to the left. 14, MnhnL PL242-1 (SEM) detail of fig. 13 showing arm spine articulations and ornamentation of outer surface. 15, MnhnL PL242-1 (SEM) detail of fig. 13 showing horizontal striation on the proximal edge of the lateral arm plate.

Abbreviations: DAP, dorsal arm plates; S, spine.

Scale bar values are in mm.

PLATE 4



THUY, *Inexpectacantha acrobatic, Eirenura papillata* the distal edge of the radial shield and the arm base. The papillae are clearly larger than the disc granules and elongate. A group of similar papillae is observable on the edge of the interradial disc, visible from the ventral side of the specimen. These papillae most probably formed a continuous fringe on the edge of the disc between the arm bases.

Specimen MNHN A30317 (Pl. 6, figs 6, 7) exposes the ventral disc and has one-third slightly compressed. It generally fits the description of the holotype well but provides supplementary morphological information on the mouth plating. In two pairs of jaws, a small round plate with two shallow indentations in their distal edge can be seen proximal to the large oral shield, covering the proximal tip of the adoral shields. A second round plate of similar size but without indentations is situated proximal to the first plate in one of the two pairs of jaws, covering the distal tips of the oral plates. In a third pair of jaws, a similar round plate without discernible indentations partly conceals the distal tip of the adoral shields. These plates are most probably additional elements of the interradial mouth plating. As mouth papillae of the specimen are largely lost, the second oral tentacle pores are well exposed. They clearly open within the mouth slit, but are largely encompassed by the lateral edges of the first ventral arm plate.

Isolated ossicles. Lateral arm plates (Pl. 4, figs 12–15): characteristic rectangular shape, with nearly straight dorsal, distal and proximal edges; no constriction; outer surface with small scale-like pustules mostly arranged in vertical rows, creating a diffuse striation; proximal edge with band of finely horizontally striated stereom (Pl. 4, fig. 15). Up to nine spine articulations inserted into distal edge of the plate and partly overlain by outer surface; median spine articulations sometimes slightly emerging and separated by sharp oblique ridges; proximal lateral arm plates higher than wide, distal ones elongate. Inner surface with thin and sharply defined oblique ridge.

Vertebrae (Pl. 4, figs 10, 11): general aspect strongly oblique, with receding ventro-proximal and protruding ventro-distal fossae. The latter ones large and wing-like, and sometimes with clearly defined concentric growth bands. Similar but less clear growth bands visible on the dorso-proximal fossae.

Arm fragments (Pl. 4, fig. 8; Pl. 5, fig. 5): in some of the arm fragments, adhering spines, adpressed, grossly striated and at most equalling the length of half an arm segment preserved. Dorsal arm plates, very small and nearly triangular, as in specimen MNHN A30316, visible in some arm fragments.

Radial shields (not figured): rounded triangular shape, longer than wide; distal edge with pronounced indentation; two-headed condyle bordering indentation on inner side of the radial shield.

Oral plates (Pl. 4, figs 7, 8): slightly elongate, with strongly dorsalwards extended and pointed dorso-proximal tip; adradial muscle area small; abradial muscle area large.

Discussion. Its peculiar combination of characters makes *Eirenura papillata* unique among the Jurassic and Triassic species known from articulated specimens. Among the forms with a densely granulated disc, species of the genera *Arenorbis* Hess, 1970*a* (middle Triassic of Europe), *Aplocoma* D'Orbigny, 1852 (middle Triassic to early Cretaceous of Europe, Hess 1965, 1970*a*, *b*, 1985, 1991; Hess and Meyer 2008), *Geocoma* D'Orbigny, 1850 (middle Jurassic to at least late Jurassic of Europe, Hess and Meyer 2008), *Sinosura* Hess, 1964 (early Jurassic to late Cretaceous of Europe, Guillaume 1926; Hess 1964, 1991; Kutscher and Jagt 2000), *Ophiohybris* Hess, 1964 (middle Jurassic of Great Britain) and *Ophiopetra* Enay & Hess, 1962 (middle to late Jurassic of Europe) all differ from *Eirenura papillata* in their lower number of tentacle scales and their mouth plating. A certain similarity is shared with species of *Palaeocoma* D'Orbigny, 1849 (mainly early Jurassic of Europe) in respect of the numerous tentacle scales and the short adpressed arm spines; there are, however, clear differences in the mouth plating as well as the shape of the dorsal and lateral arm plates. The mould of an articulated ophiuroid described as *Sinosura wolburgi* Hess, 1960*a* by Delsate and Jagt (1996) from the Pliensbachian of Belgium shows some superficial similarities in disc granulation and arm structure with *Eirenura papillata*. A possible attribution to *E. papillata* would require a detailed examination of the Belgian specimen, ideally including a silicon cast.

Among the species described on the basis of isolated lateral plates, greatest similarities are found in *Sinosura*? *kohli* Thuy, 2005 (Hettangian of Belgium and Luxembourg and possibly Sinemurian of Luxembourg, see Thuy (2005)). The lateral arm plates of *Eirenura papillata* differ from the Hettangian ones by the distinct horizontal striation at their proximal edge, and by their generally

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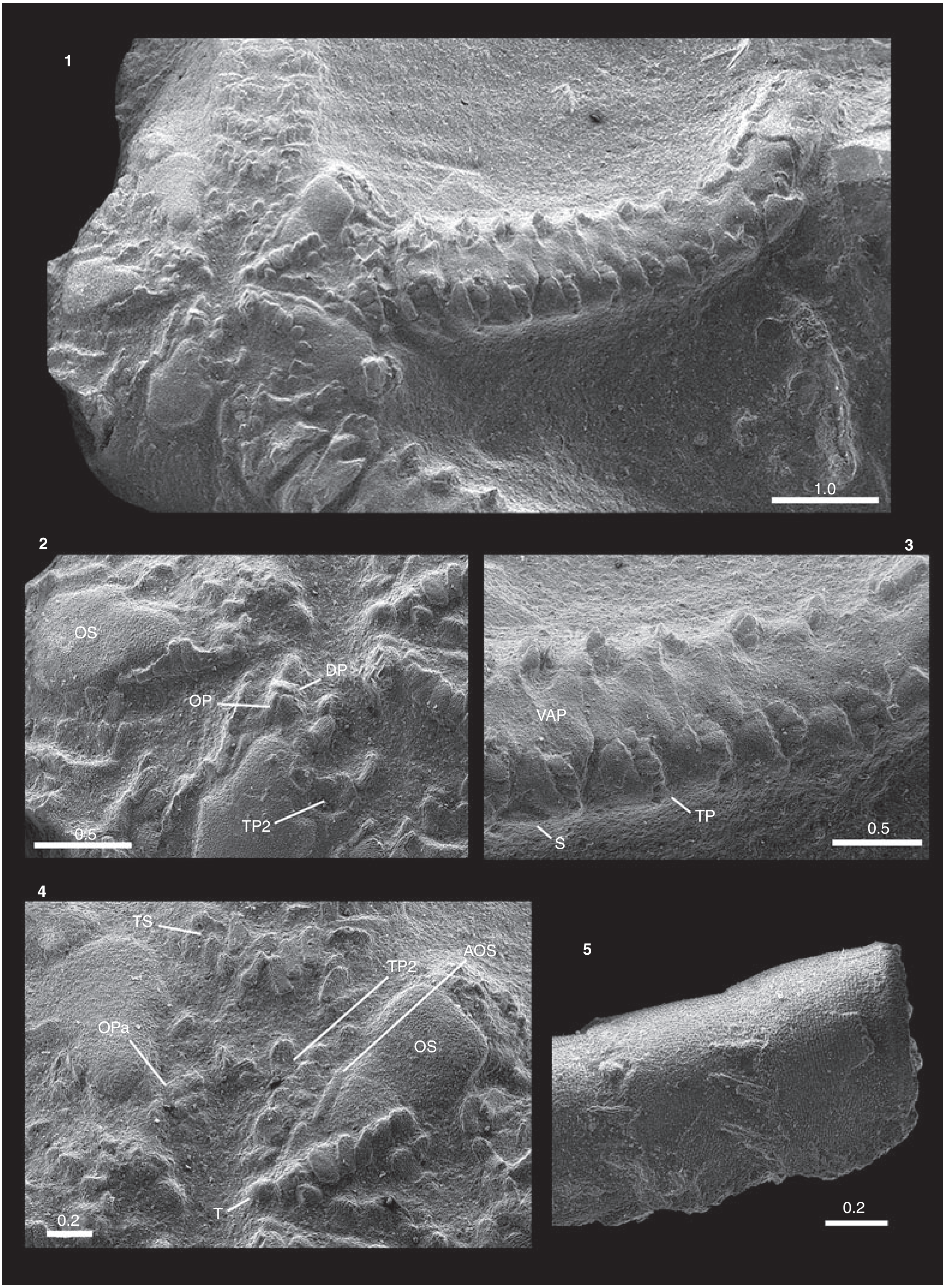
EXPLANATION OF PLATE 5

Figs 1–5. *Eirenura papillata* gen. et sp. nov. from the early Pliensbachian of Sedan, France. 1, MnhnL PL220 (holotype, SEM) ventral face. 2, MnhnL PL220 (holotype, SEM) detail of fig. 1 showing mouth plating. 3, MnhnL PL220 (holotype, SEM) detail of fig. 1 showing proximal to median arm segments with tentacle scales. 4, MnhnL PL220 (holotype, SEM) detail of fig. 1 showing mouth plating and proximalmost arm segments. 5, MnhnL PL240-9 (SEM) isolated proximal to median arm fragment in lateral view showing spines, distal end to the left.

Abbreviations: AS, adoral shield; DP, dental plate; OP, oral plate; OPa, oral papilla; OS, oral shield; S, spine; TP2, second oral tentacle pore; TS, tentacle scale.

Scale bar values are in mm.



THUY, *Eirenura papillata*

lower number of arm spines. The morphologically almost identical lateral arm plates of both species as well as the presence of very similar vertebrae, oral plates and ventral arm plates in the Hettangian material, however, allow transferring *Sinosura*? *kohli* into the new genus *Eirenura*.

The densely granulated disc, the continuous row of oral papillae along the jaws and the short, adpressed arm spines place *Eirenura papillata* close to the Ophiodermatidae, Ophioleucinae and the extinct subfamily Aplocominae (as defined by Hess and Meyer 2008). The unusually large number of tentacle scales, however, interferes with an uncompromising attribution to any of these taxa. Similarly, numerous tentacle scales are found in many species of *Ophiura* Lamarck, 1816, *Amphiophiura* Matsumoto, 1915 and *Stegophiura* Matsumoto, 1915 all belonging to the Ophiurinae. Although in this subfamily a densely granulated disc is not unknown, as exemplified by *Uriophaios* Paterson, 1980, an arm comb (set of papillae on the distal tip of the abradial genital plate) as main diagnostic feature of the subfamily could not be found in *Eirenura papillata*. Similarly, the truly superficial second oral tentacle pore is lacking. An attribution to the Ophiurinae as currently defined must therefore be excluded. The nearly superficial second oral tentacle pore partly enclosed by the adoral shield and the first ventral arm plate in *Eirenura papillata* strongly resembles that of *Ophioleuce oxycraspedon* Baranova, 1954, a species that furthermore exhibits a fringe of papillae at the edge of the disc strongly reminiscent of the structures seen in *Eirenura papillata*. The shape and size of the oral shield as well as the presence of supplementary plates at the proximal tip of the oral shield make the Pliensbachian species drastically differ from *O. oxycraspedon*. The arm spine articulation of *E. papillata* bears a certain similarity with the arm spine articulations of the ophioleucid ophiuroids figured in Martynov (2010), although a more detailed examination would be required to draw conclusion. The oral plates of *Eirenura papillata* are different from the oral plates described and figured in Murakami (1963) both of the Ophioleucidae and Ophiodermatidae and are instead closest to the oral plate of *Stegophiura sterea* (H. L. Clark 1908). The accessory plates at the proximal tip of the oral shield are an extremely rare phenomenon among modern ophiuroids. Only very few recent species display a comparable mouth plate pattern. One of these species is *Ophiocypris tuberculosus* Koehler, 1930, ascribed to the Ophiolepididae (Stöhr 2009).

Despite some morphological incompatibilities, especially the high number of tentacle scales, *Eirenura papillata* seems to be best placed in the subfamily Ophioleucinae as defined by Madsen (1983). Its highly peculiar combination of characters requires the creation of a new genus.

GENERAL COMMENTS ON MESOZOIC OPHIUROID SYSTEMATICS

The ophiuroid species described herein are prime examples of extinct brittle star taxa of modern aspect, which, in spite of their excellent state of preservation, are not uncompromisingly compatible with any of the groups of recent ophiuroids proposed by Smith *et al.* (1995). Especially *Eirenura papillata*, with its unusual set of characters, challenges crown-group classification as currently accepted. Most of the Triassic and Jurassic ophiuroid forms known from complete individuals, like the Middle Triassic *Arenorbis*, *Palaeocoma* from the Early Jurassic and *Dermocoma* Hess, 1964 from the Middle Jurassic, combine characters that are diagnostic of more than one modern ophiuroid family (Hess 1960*b*, 1964; Hess and Meyer 2008). Either most of the early Mesozoic forms belong to extinct and so far undefined families or the currently accepted concepts of the modern clades need reappraisal. Hess (1965) opted for the first possibility in the case of his Triassic and Jurassic genera *Aplocoma* and *Ophiopetra*, and erected the family Aplocomidae. Many mesozoic forms of until then uncertain higher taxonomic affinity like *Sinosura* were subsequently included in the Aplocomidae (Hess and Meyer 2008). However, combinations of characters defying the presently accepted higher

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EXPLANATION OF PLATE 6

Figs 1–7. *Eirenura papillata* gen. et sp. nov. from the early Pliensbachian of Sedan, France. 1, MNHN A30316 (paratype, SEM) ventral face. 2, drawing of fig. 1. 3, MNHN A30316 (paratype, SEM) dorsal face. 4, MnhnL PL228 (paratype, SEM) ventral face of disc fragment showing arm base and interradial area with papillae at its edge. 5, MnhnL PL228 (paratype, SEM) dorsal face of disc fragment showing arm base with papillae. 6, MNHN A30317 (paratype, SEM) ventral face showing mouth plating. 7, MNHN A30317 (paratype, SEM) detail of fig. 6 showing two jaws with supplementary plates proximal to oral shields.

Abbreviations: AS, adoral shield; AP, apical papilla; DAP, dorsal arm plate; DP, dental plate; In, interradial area; OP, oral plate; OS, oral shield; Pap, papillae at disc edge; RS, radial shield; S, spine; SOP, supplementary plates of oral skeleton; T, tooth; TP, tentacle pore; TP2, second oral tentacle pore; VAP1, first ventral arm plate.

Scale bar values are in mm.

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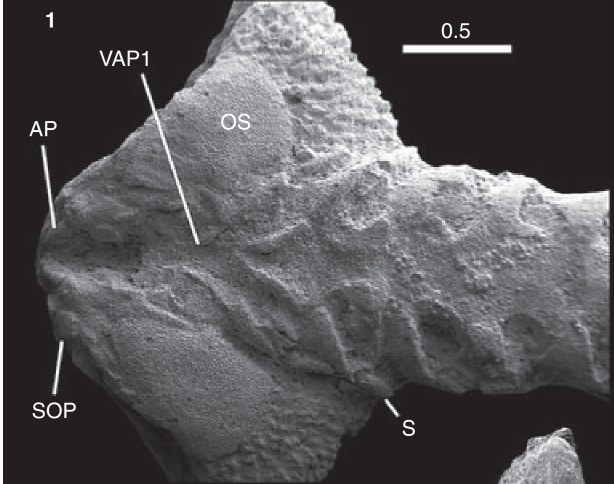

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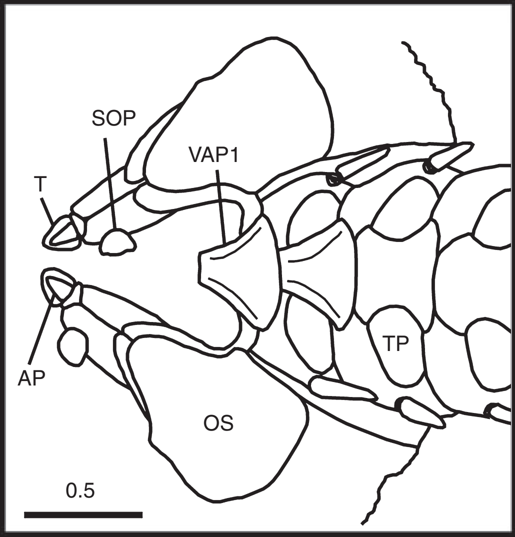

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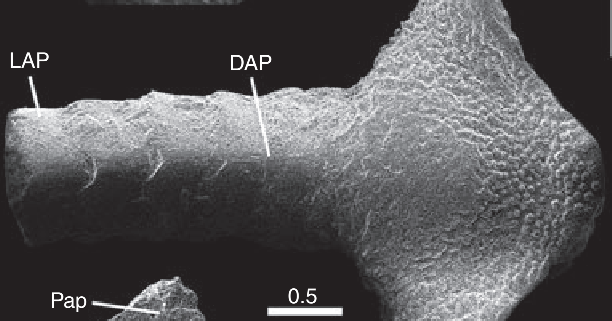

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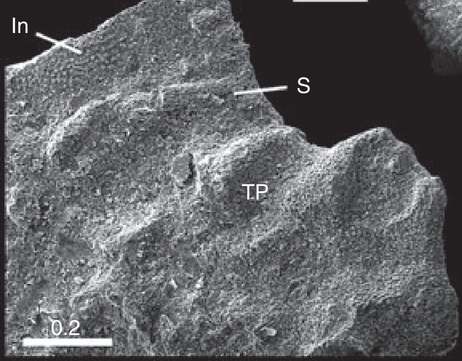

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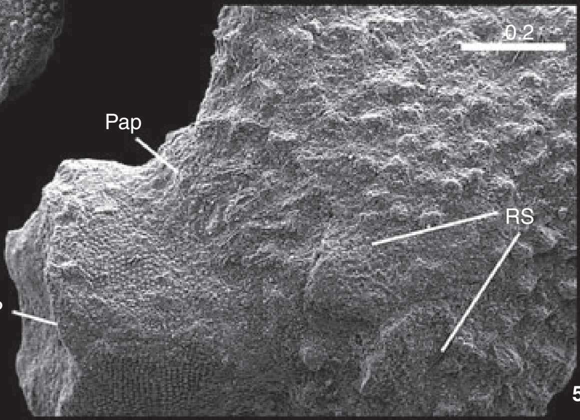

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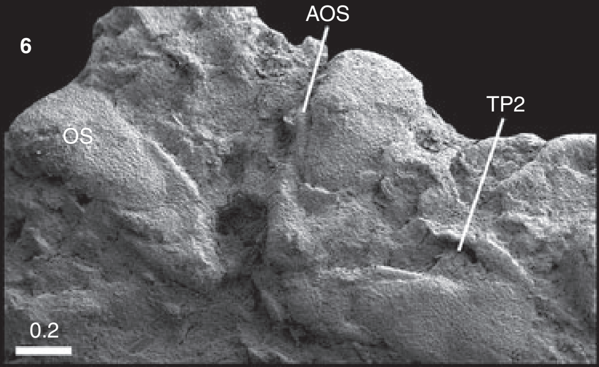

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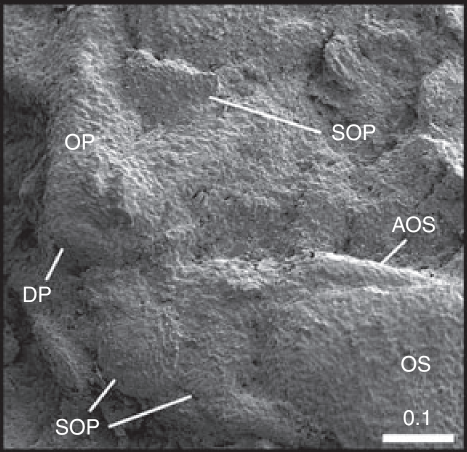

THUY, *Eirenura papillata*

taxonomic classification can also occur in modern ophiuroids, as exemplified by the recently described *Ophienigma spinilimbatum* Stöhr and Segonzac, 2005.

A revision of at least some of the modern groups of ophiuroids taking into consideration the early Mesozoic forms is likely to improve our concept of these groups and their origins. The early Mesozoic is considered to have witnessed a major part of the postpalaeozoic radiation of ophiuroids (Smith *et al.* 1995; Kutscher and Villier 2003). Our knowledge on Triassic and Jurassic ophiuroids is currently not sufficient to satisfyingly address the question of early crown-group diversification. More undescribed extinct forms need to be known in detail, and many of the Triassic and Jurassic ophiuroid species need reappraisal paying special attention to the characters relevant in recent ophiuroid classification.

PALAEOECOLOGY AND TAPHONOMY

The series of argillites near Sedan that yielded the faunule described herein has not been the focus of any detailed palaeoecological study so far. Field observations, the accompanying faunas as well as the brittle stars themselves however provide some valuable pieces of evidence for a palaeoecological model of the occurrence. The monotony of the series and the general scarcity of macrofossils and in particular of nektonic organisms like belemnites, so frequently encountered in other coeval localities of the north-eastern Paris Basin (Mouterde *et al.* 1980; Lucius 1948) and the Swabian Basin (pers. obs.), of the argillites is surprising. The scarcity of macrobenthos remains in most parts of the series suggests a high rate of sedimentation and/or unfavourable conditions for bottom dwellers. The latter aspect is corroborated by the presence of microscopic clusters of framboidal pyrite, indicative of dysoxic conditions at least in the upper few centimetres of the sediment (Brett and Baird 1986) discouraging most burrowing organisms. The unusual scarcity of nektonic organisms might be explained by the proximity of the emerged landmasses of the Ardennes; in fact, according to the palaeogeographical interpretations, the Sedan area can be considered as a near-shore setting (Mouterde *et al.* 1980). At first sight, this very proximal setting seems to conflict with the stagnant conditions suggested by the almost purely argillaceous rocks and the dysoxic conditions deduced from the framboidal pyrite. One possible explanation could be a nearby river discharging great amounts of clay and fresh water and thus contributing to a high sedimentation rate and to a strong stratification of the water column, leading to poorly aerated bottom waters. In the given proximal and thus supposedly shallow settings, the bottom water layer was most probably thin and rapidly depleted of oxygen during phases (probably seasons) of decreased vertical mixing of water layers (Tyson and Pearson, 1991).

How can the highly fossiliferous, lumachellic beds be explained under these conditions? It is striking that the shelly beds occur every few decimetres within the argillite series and hardly exceed a few centimetres in thickness. These sporadic accumulations of fossils in an otherwise nearly sterile series suggest episodically favourable conditions for benthic organisms. Although always dominated by large numbers of small, semi-endobyssate bivalves of the genus *Modiolus* (Amler *et al.* 2000), the diversity of benthic organisms within the lumachellic beds was rather high. The high content in both macro- and microfossils might be of primary origin, reflecting a densely populated sediment surface under improved bottom water conditions, or might be the product of a secondary accumulation related to a decreased sedimentation rate. It most likely represents a mixture of both. Either way, a probable factor could be an episodically reduced river discharge, decreasing water column stratification and sediment supply.

The lumachellic bed that yielded the ophiuroid faunule stands out because of its numerous articulated echinoderm remains. Furthermore, many *Modiolus*-specimens not only present articulated valves but are supposedly preserved in life position (nearly vertical to the bedding plane, see Amler *et al.* 2000). The brittle stars very often present hardly any sign of decomposition, with most easily lost appendages still adhering. Considering the extremely rapid postmortem decomposition rate of an ophiuroid skeleton, we must assume very quick and effective burial of the specimens (Kerr and Twitchett 2004; Ausich 2001) and thus exclude any significant transportation. The presence of completely and partly disarticulated skeletons among the perfectly articulated ones excludes transportation of the intact animals into the site of deposition. Many specimens of the highly flexible species *Inexpectacantha acrobatica* have their arms curled on the disc, often in a way suggesting overturning of the disc by external forces, such as strong currents. Furthermore, one articulated arm fragment of a large *Ophiomusium*-like species (MnhnL PL232) shows definite signs of predepositional fragmentation, corroborating strong mechanical stress accompanying burial. The most probable model is that of an autochtonous bivalve and ophiuroid community buried by a catastrophic, high-energy obrution event such as strong bottom currents during a storm (Aigner 1985). The autochtonous or at least parautochtonous nature of the ophiuroid faunule is further corroborated by the presence of individuals of different sizes. The fossiliferous siderite concretions associated with the lumachelle beds are most likely of early diagenetic origin, as suggested by the noncrushed echinoid tests inside the concretions, in contrast to the mostly crushed ones on their surface. The small gastropods encountered among the microfossils of the lumachelle beds suggest a soft-bottom environment (A. Warén, pers. comm. 2008), making a synsedimentary formation of the concretions less likely.

The detailed morphological analysis of the brittle stars provides some evidence for the interpretation of the autecology of the studied species. The small size of both species described herein is not related to any general trend of small body size in early Pliensbachian organisms, as suggested for early Triassic organisms in the aftermath of the Permian–Triassic extinction event (Twitchett *et al.* 2005), because the coeval *Palaeocoma milleri* is a very large ophiuroid species (Hess 1964, and pers. obs.). It is more likely related to unfavourable environmental conditions like the poorly oxygenated bottom waters documented by the clusters of framboidal pyrite encountered together with the ophiuroid specimens, less frequently than in the surrounding argillites though, and the benthic foraminifera (L. Numberger, pers. comm. 2006). At least in *Inexpectacantha acrobatica*, the small size might also be related to an epizoic lifestyle (Hendler *et al.* 1995). Highly flexible arms and well-developed hooks in distal arm segments, both enabling the animal to cling to a host, corroborate an epizoic way of life for this species. Possible hosts of *I. acrobatica* could have been stalked crinoids, whose remains are frequently encountered together with the brittle stars, or sponges and other organisms not yet documented by fossils, or the *Modiolus*-bivalves (see Stöhr and Segonzac 2005 for recent examples of bivalve-ophiuroid associations). *Eirenura papillata*, on the contrary, has short and highly rigid arms because of the nearly rectangular lateral arm plates. An infaunal way of life, typically bound to long and at least horizontally very flexible arms in recent brittle stars (Hendler *et al.* 1995), can thus be considered as improbable. More likely is a life on the sediment surface, with the conspicuously large tentacle pores providing an increased surface for gaseous exchange and/or enabling efficient collecting of organic particles in the bottom water or, in the light of the rigid arms, more likely from the sediment surface (Hendler *et al.* 1995). The analysis of further occurrences of the two ophiuroid species studied herein would possibly allow assessing the facies preferences of the species and test the relationship between body size and bottom water oxygenation.

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