The oldest representative of a modern deep-sea ophiacanthid brittle-star clade from Jurassic shallow-water coral reef sediments

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Ophiurites crinitus is a fossil brittle-star species which passed largely unnoticed since its original description. In this paper, we redescribe the type material of *O. crinitus* with the aim to put it into the context of modern ophiuroid systematics, and propose the new genus name *Ophiosternle* to replace the invalid *Ophiurites*. The re-assessed species is shown to be a member of the extant deep-sea family Ophiacanthidae, articulated fossils of which are extremely rare. It presents greatest affinities with members of the *Ophioplinthaca–Ophiocamax–Ophiomitra* clade, of which it most probably represents the oldest known fossil species. The depositional environment of the strata, which yielded the described specimens is interpreted as shallow, storm-influenced marine setting in the immediate vicinity of coral reefs. This contrasts with the distribution pattern of extant species of the *Ophioplinthaca–Ophiocamax–Ophiomitra* clade, which almost exclusively occur at depths exceeding the shelf break.

Key words: Echinodermata, Ophiuroidea, Ophiacanthidae, coral reef, deep-sea group, Late Jurassic, Mergelstetten Formation, Germany.

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Introduction

The brittle-star skeleton is subject to rapid post-mortem disintegration and thus requires burial conditions which are rarely met in a normal marine sedimentation regime (e.g., Ausich 2001). As a result, fully articulated brittle stars are extremely rare fossils. All the more surprising is that brittle-star palaeontology started as early as 1804 with the description of *Asterites scutellatus* Blumenbach, 1804 (currently placed in the genus *Aspiduriella* Bolette, 1998) from the Triassic of Germany, only a few decades after the first ever description of brittle stars in the Systema Naturae (Linnaeus 1758). Another few decades later, Quenstedt (1876) already included some 22 fossil brittle-star species in volume 4 of his pioneering "Petrefactenkunde Deutschlands". Many more species have been added since, and most of the brittle-star fossils described in the mid-nineteenth century were subsequently reassessed, critically discussing their position in modern ophiuroid systematics (e.g., Boehm 1889; Hess 1965b).

In contrast, though, a number of Quenstedt's (1876) ophiuroid species were hardly mentioned again following the original description. This is surprising, considering that Quenstedt's (1876) descriptions and illustrations were among the most accurate available at that time. Probably the most remarkable among Quenstedt's (1876) ophiuroid species that seem to have passed into oblivion is "*Ophiurites crinitus* Quenstedt, 1876" from the Late Jurassic of Steinenfeld, south Germany. This species is exceptional because it still remains one of the very few latest Jurassic finds of articulated ophiuroids not originating from the lithographic limestone of south Germany and France. In addition, its unusual morphology caused Quenstedt (1876) to hesitate upon the ophiuroid nature of his finds. He noted an apparent resemblance with some of the crinoids he described from the same strata, and hence named the species *O. crinitus*.

The status of *Ophiurites crinitus*, however, has not been investigated since its original description. While browsing the Quenstedt (1876) collection at GPIT, we came upon the two specimens of *O. crinitus* figured by Quenstedt (1876: pl. 96: 23, 24), one of which (GPIT/69/96-24) described as the

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most typical of his new species, thus constituting the holotype. In addition, another very similar specimen not figured in the "Petrefactenkunde Deutschlands" but from the same locality could be located in the Friedrich August Quenstedt collection at GPIT. Upon first examination of the specimens, we were struck by their ophiacanthid-like morphology. Considering how rare articulated brittle-star fossils assignable to the extant deep-sea family Ophiacanthidae are, we decided to inspect the exceptionally well preserved specimens more carefully. The present study therefore aims at (i) re-describing the type material of "*Ophiurites crinitus*" from the perspective of modern ophiuroid systematics (using the terminologies by Stöhr [2005] and Thuy and Stöhr [2011]), (ii) clarifying its position within the currently accepted ophiuroid classification and phylogeny (Smith et al. 1995; Thuy et al. 2012), and (iii) discussing its significance as a fossil species of an extant deep-sea ophiacanthid clade found in Jurassic shallow-water coral reef sediments.

Institutional abbreviations.—GPIT, Palaeontological Institute of the University of Tübingen, Germany.

Systematic palaeontology

Phylum Echinodermata Klein, 1734

Order Ophiurida Müller and Troschel, 1840

Family Ophiacanthidae Ljungman, 1867

Genus *Ophiosternle* nov.

Type species: *Ophiurites crinitus* (Quenstedt, 1876), monotypic; see below.

Etymology: Name derived from the Swabian diminutive of German *stern*, star, in reference to Swabia in south Germany, where the type material of the taxon was discovered, originally described and eventually housed (gender neutral).

Diagnosis.—Ophiacanthid with conspicuously large radial shields, as long as three quarters of the disc radius and separated interradially by numerous small plates; jaw tips with a cluster of three to four small, conical apical papillae; dorsal arm plates broad and smooth; arm spines circular in section, thick, smooth.

Ophiosternle crinitum (Quenstedt, 1876) comb. nov.

Figs. 1, 2.

1876 *Ophiurites crinitus* Quenstedt, 1876: 170.

Holotype: GPIT/69/96-24, partial articulated sceleton.

Type locality: Buchenbrunnen near Steinenfeld, S-Germany.

Type horizon: Reef debris beds within the Mergelstetten Formation (*Hybonoticeras beckeri* Zone, *Lithacoceras ulmense* Subzone), latest Kimmeridgian, Upper Jurassic.

Material.—GPIT/69/96-23, GPIT/AS/56.

Diagnosis.—As for genus.

Description.—The holotype (GPIT/69/96-24) is an articulated skeleton exposing both dorsal and ventral sides and preserving large portions of three arms; disc diameter 9.8 mm; disc interradii strongly incised; dorsal disc plating dominated by large, conspicuous radial shields, triangular in outline, contiguous on their entire length, longer than three quarters of the disc radius, distal edge with notch; remaining disc plates tiny, rounded, restricted to centre of the disc and narrow interradial areas; no enlarged plates distally lining radial shields; no disc granules or spines discernible, possibly worn away during preparation process; ventral interradial plates covered by matrix, thus not observable; oral shields relatively large, arrow-shaped to rhombic, with nearly right, rounded proximal angle; adoral shields broad and relatively short, not extending around lateral edges of oral shield, broadly abutting in front of oral shield; jaws not elongate; oral plates stout, beset with four to five spine-like lateral oral papillae, pointed, three to four times longer than broad; distalmost lateral papilla nearly two times wider than others, irregularly leaf-like and pointed, positioned in the corner formed by the oral plate and the adoral shield; ventral tip of dental plate beset with a cluster of three to four small, conical apical papillae; dorsally following teeth conical, in single row and slightly larger than apical papillae.

Arms broad, composed of numerous short segments and with "longitudinal furrow" on ventral side, formed by the ventrally protruding rows of arm spine articulations on the lateral arm plates (and probably causing Quenstedt [1876] to hesitate on the ophiuroid nature of the specimen, mistaking the "furrow" for an open ambulacral grove); proximal ventral arm plates nearly twice as wide as long, smooth, with gently convex proximal edge, obtuse distal angle and strongly incised lateral edges, separated by ventral protrusions of lateral arm plates on all observable arm segments; tentacle pores relatively small; at least one leaf-like tentacle scale; dorsal arm plates twice as wide as long, nearly rectangular to trapezoid in outline, with gently convex distal edge, broadly separating lateral arm plates on all observable arm segments; lateral arm plates very high and narrow, with conspicuous pointed ventral protrusion; ornamentation of outer surface not discernible; arm spine articulations large, ear-shaped with well-developed sigmoidal fold, positioned in continuous row on conspicuously elevated vertical ridge on distal portion of lateral arm plates, at least 10 spine articulations on each lateral arm plate; spines circular in section, very large, smooth to finely striated longitudinally, equalling at least the length of four arm segments; vertebrae and inner side of lateral arm plates unknown.

There are two additional specimens, one large, fully articulated arm fragment consisting of proximal and median arm segments (GPIT/69/96-23) and one articulated disc (10 mm in diameter) with five arms preserving proximal and median arm segments and exposing the dorsal side (GPIT/AS/56). The morphological details of both specimens are very well in agreement with those of the holotype.

Remarks.—The long, erect spines attached to large, ear-shaped spine articulations with a well-developed sigmoidal fold, in combination with the single row of teeth unquestionably place the specimens described above in the extant fam-

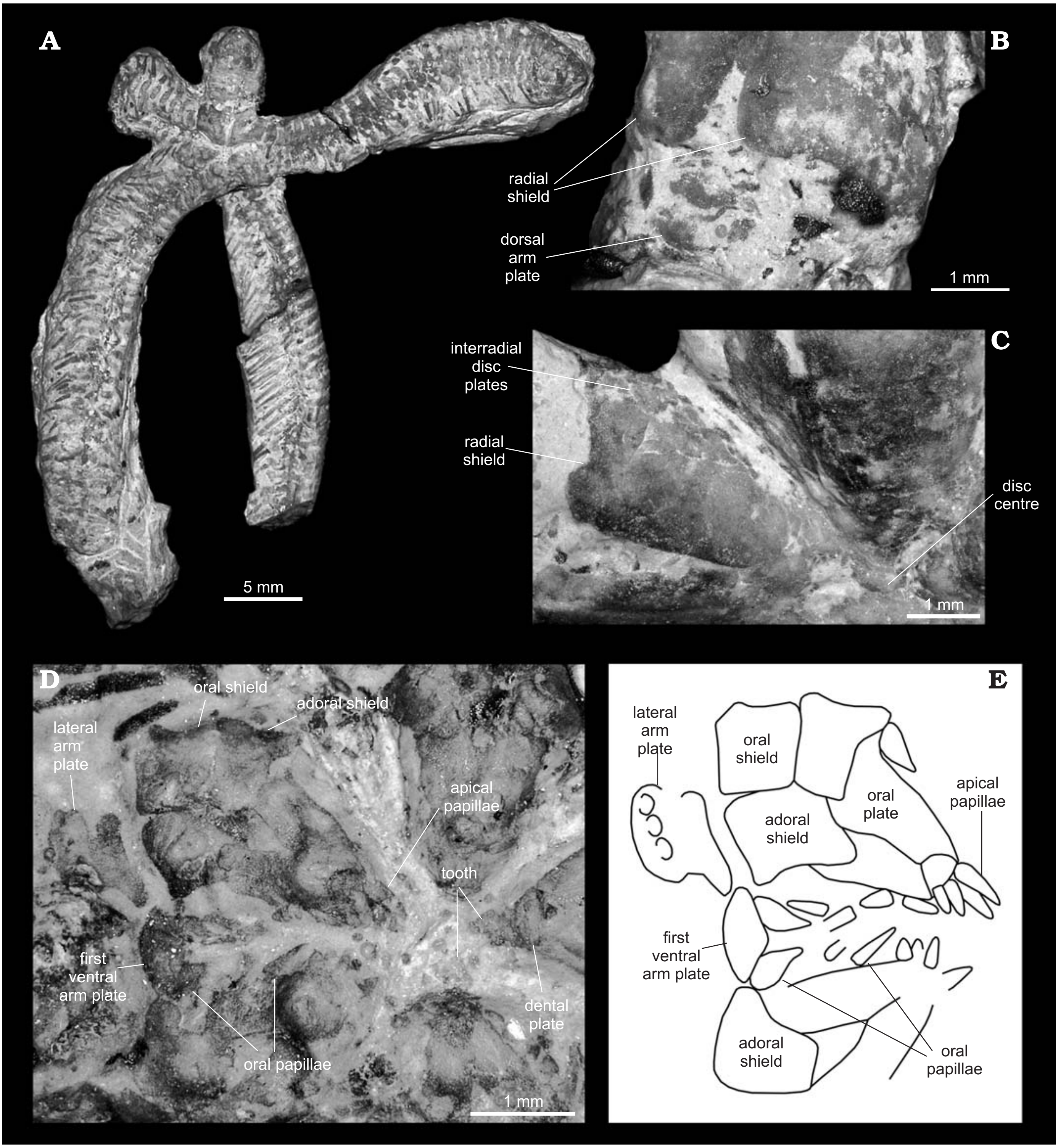

Fig. 1. Ophiacanthid brittle-star *Ophiosternle crinitum* (Quenstedt, 1876), GPIT/69/96-24 (holotype), from the Reef debris beds within the Mergelstetten Formation (*Hybonoticeras beckeri* Zone, *Lithacoceras ulmense* Subzone), latest Kimmeridgian, Late Jurassic of Buchenbrunnen near Steinenfeld, S-Germany. **A**. Complete specimen in ventral view. **B**. Detail of dorsal side showing arm base and distal tip of radial shields. **C**. Detail of disc in dorsal view. **D**, **E**. Detail of disc in ventral view; photograph (**D**) and explanatory drawing (**E**).

ily Ophiacanthidae. The specimens share superficial similarities with extant Ophiocomidae, assignment to which, however, is precluded by the presence of a single row of teeth rather than a cluster of tooth papillae. Within the Ophiacanthidae, greatest similarities are shared with species of the major, yet unnamed ophiacanthid clade uniting all genera of the former subfamily Ophioplinthacinae (Thuy et al. 2012), with respect to the well developed dorsal disc plates

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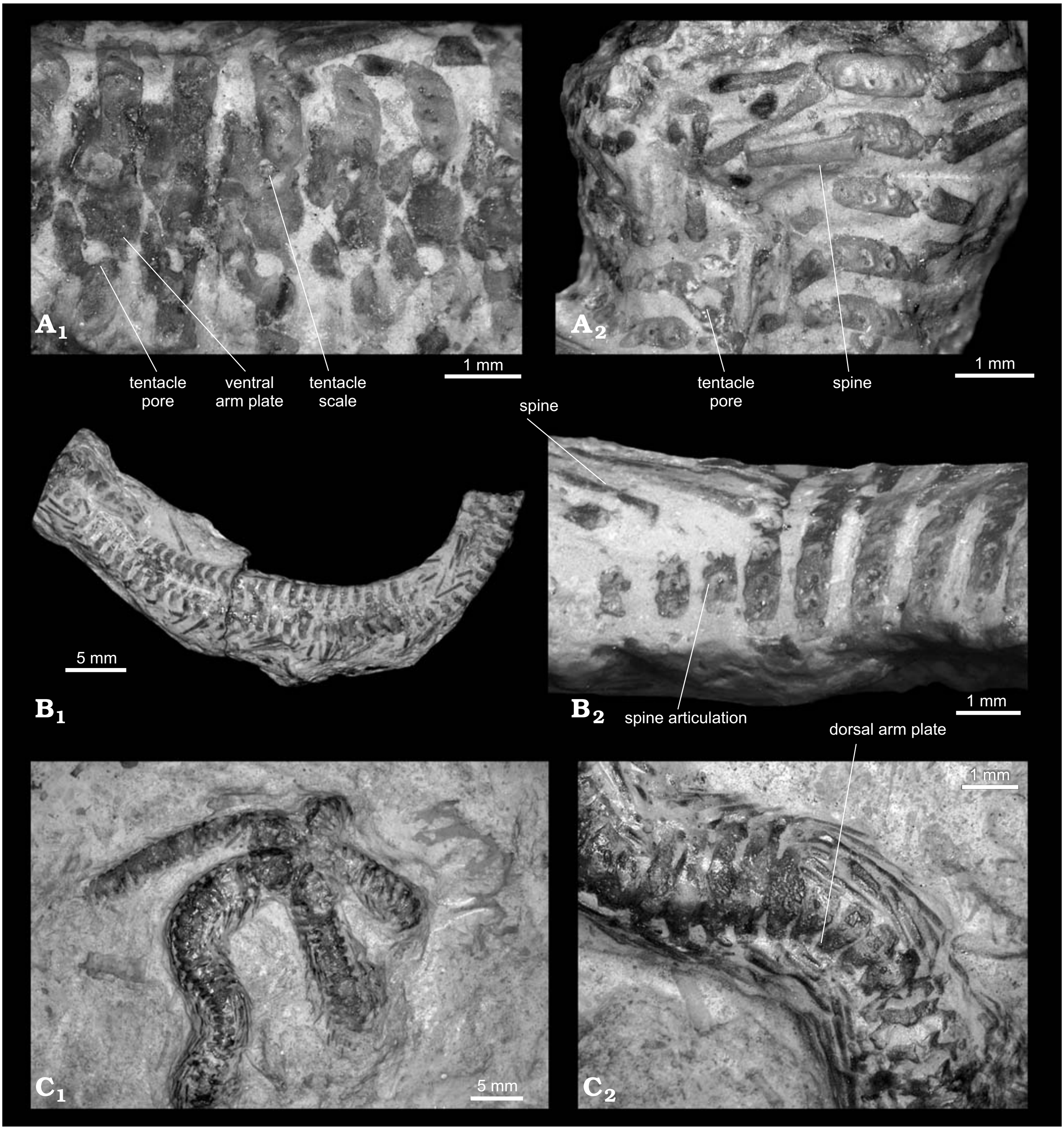

Fig. 2. Ophiacanthid brittle-star *Ophiosternle crinitum* (Quenstedt, 1876), from the Reef debris beds within the Mergelstetten Formation (*Hybonoticeras beckeri* Zone, *Lithacoceras ulmense* Subzone), latest Kimmeridgian, Late Jurassic of Buchenbrunnen near Steinenfeld, S-Germany. **A**. GPIT/69/96-24 (holotype). Detail of proximal arm segments in ventral view without arm spines (A_1) and with arm spines (A_2). **B**. 96/23 (paratype). Arm fragment in ventral view (B_1), proximal arm segments in lateral view (B_2). **C**. GPIT/AS/56 (paratype). Complete specimen (C_1) and detail of proximal to median arm segments (C_2) in dorsal view.

and the large, exposed radial shields. The combination of deeply incised interradii and very long arm spines, as observed in the above described specimens, is found in the extant former ophioplinthacinid genera *Ophioplinthaca* Verrill, 1899 and *Ophiocamax* Lyman, 1878. The closely related genus *Ophiomitra* Lyman, 1869 generally lacks the incised interradii. Nevertheless, a number of species, including the type species *Ophiomitra valida* Lyman, 1869 display more or less well developed incisions, suggesting that the genus is rather polymorphic. As already pointed out by O'Hara and Stöhr (2006), it is far from clear that *Ophiomitra* as well as many other former ophioplinthacinid genera represent monophyletic taxa.

The specimens described herein differ from *Ophiocamax* in lacking the multiple rows of spine-like oral papillae, as well as the highly characteristic ring of erect, spine-like tentacle scales surrounding the proximalmost pores. In addition, most extant species of *Ophiocamax* have strongly serrate arm spines and small thorns on the dorsal arm plates. In contrast to *Ophiosternle crinitum*, extant species of *Ophioplinthaca* are characterised by enlarged disc plates distally lining the interradial incisions. In addition, *Ophioplinthaca* generally has a single apical papilla rather than a cluster of papillae. Similarities are greatest with species of *Ophiomitra*, especially the species displaying deeply incised interradii. In these, however, dorsal arm plates are generally much narrower and separated by lateral arm plates at least from median arm segments onwards. Furthermore, *Ophiomitra* species tend to have smaller radial shields, thornier arm spines, shorter jaws and a larger disc in comparison to the width of the arms.

Evidently, the above described specimens are not satisfyingly compatible with any modern ophiacanthid genus. This is not surprising in the light of the considerable stratigraphic gap of some 155 Ma separating the specimens from their modern relatives. The genus name *Ophiurites* Schlotheim, 1820, which Quenstedt (1876) assigned his new species *O. crinitus* to, is invalid since it falls into the category of names ending with -ites, introduced only to differentiate fossils from extant taxa (in this case *Ophiura*), and explicitly banned by the ICZN (1999: article 20). Ironically, the first species included in *Ophiurites* (*O. filiformis octofilatus* Schlotheim, 1820, *O. decafilatus* Schlotheim, 1820, and *O. pennatus* Schlotheim, 1820) turned out to be crinoids (Boehm 1889), which is further reason not to use it for ophiuroids, had the name not been made invalid altogether. Other species originally assigned to *Ophiurites* include *O. trunensis* Böhm, 1891, probably a synonym of *Ophiomusium granulosum* (Roemer, 1840) (Jagt 2000), and *O. eocaenus* Leriche, 1931, re-assigned by Jagt (1990) to *Ophiozona* (now *Ophiolepis*).

Since the name *Ophiurites* is invalid, we thus introduce the new genus *Ophiosternle* to accommodate the specimens originally described as *Ophiurites crinitus*. The new genus is most probably a member of the clade formed by the extant *Ophioplinthaca*, *Ophiocamax*, and *Ophiomitra* (Thuy et al. 2012). The only known fossil record of this clade apart from *Ophiosternle* is the material from the Miocene of Japan described as *Ophiocamax* sp. by Ishida (2001). *O. crinitum* thus represents the oldest occurrence of the *Ophioplinthaca*– *Ophiocamax*– *Ophiomitra* clade. The assessment of its exact position within this group, however, requires further research.

Ophiosternle crinitum is the first ophiacanthid brittle star known from the Kimmeridgian. The fossil ophiacanthids which are stratigraphically nearest to *O. crinitum* are the species described by Hess (1965a, 1966, 1975a, b) from the Oxfordian of Switzerland and France on the basis of dislocated lateral arm plates. Among these, however, only *Ophiacantha*? *constricta* Hess, 1966 bears a certain resemblance with *O. crinitum*, especially in terms of number of arm spines and ventrally protruding ridge bearing the spine articulations. The lateral arm plates of *O.*? *constricta*, however, are considerably smaller and more fragile than those of *O. crinitum*, and furthermore lack the conspicuous pointed ventral extension, making a confusion unlikely.

Quenstedt (1876) described a specimen from the same locality as *O. crinitum* under the name *Ophiura annulata* Quenstedt, 1876. These share a superficial similarity with the above-described material as far as the large, short arm segments, the long arm spines and the large radial shields are concerned. Preservation of the type specimen, however, precludes any further comparison: the disc exposes only the dorsal side, and the arms are so heavily worn as a result of the preparation process that only a few spines and the vertebrae remain visible (hence the species adjective *annulata*). *Ophiura annulata* should therefore be considered a nomen dubium.

Stratigraphic and geographic range.—Type locality and horizon only.

Discussion

The specimens of *Ophiosternle crinitum* originate from beds of bioclastic limestone, which yield abundant ooids and skeletal debris derived from nearby coral reefs, and which crop out in quarries in the Blaubeuren area on the eastern Swabian Alb, south Germany (Geyer and Gwinner 1986; Günter Schweigert, personal communication 2011). Stratigraphically, these beds are part of the Mergelstetten Formation, dated to the latest Kimmerdigian *Lithacoceras ulmense* Subzone within the *Hybonoticeras beckeri* Zone, and uniting the former Liegende Bankkalk and Zementmergel formations (Schweigert and Franz 2004). The bioclastic limestone beds produced abundant specimens of articulated echinoderms, which, apart from *O. crinitum*, mostly consist of crinoids, echinoids, and other ophiuroids. As a consequence of the rapid post-mortem disintegration of most echinoderms, the preservation of articulated skeletons requires rapid and effective burial (e.g., Ausich 2001). In the case of the bioclastic limestone beds, the most likely scenario is obrution (sudden burial) through storm currents, as suggested by the high concentration and low degree of sorting of components like large bivalve shells, ooids, smaller reef-derived debris, and articulated but in part fragmented echinoderms. This interpretation implies a deposition depth above storm wave base, probably no deeper than 20 or 30 m, which is in line with the proximity of shallow-water coral reefs, and with the palaeoenvironmental reconstructions for the area in general (Pieńkowski et al. 2008).

According to the above made observations, *Ophiosternle crinitum* thus most likely lived in a shallow-water setting in the immediate vicinity of coral reefs. Modern representatives

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of the *Ophioplinthaca–Ophiocamax–Ophiomitra* clade, which *O. crinitum* most likely belongs to, predominantly occur at greater depths, mostly of several hundred to a few thousand metres (e.g. O'Hara and Stöhr 2006). Only a single species of *Ophiocamax*, *O. vitrea* Lyman, 1878, is known to occur at depths shallower than 130 metres, which corresponds to the worldwide average depth of the continental shelf break (Davis 1977). These occurrences, however, are very rare and generally represent single or very few specimens only (e.g., Koehler 1922). Within *Ophioplinthaca*, *O. pulchra* Koehler, 1904 is documented at a depth as shallow as 38 metres from Indonesia (Koehler, 1930). In this case again, the shallow occurrence is a single specimen, and separated from the other Indonesian occurrences by more than 200 metres (Koehler, 1930). *Ophioplinthaca sexradia* Mortensen, 1933, from a depth of 44 metres from off South Africa, is known from two specimens only, and bear a much greater resemblance with species of the genus *Ophiomoeris* Koehler, 1904 than with its congeners. All other *Ophioplinthaca* species occur at depths greater than 150 metres (e.g., Paterson 1985; O'Hara and Stöhr 2006). *Ophiomitra valida* is reported by Lyman (1882) from a depth as shallow as 18 metres from the Caribbean, without, however, specifying any locality details or specimen numbers. All other reports of the species are from depths no shallower than 130 metres (e.g., Lyman 1869, 1883; Verrill 1899), thus casting doubt on Lyman's (1882) claim.

As can be concluded from the above made observations, extant representatives of the *Ophioplinthaca–Ophiocamax–Ophiomitra* clade can, indeed, be found at relatively shallow depths, potentially within storm wave base and especially in tropical seas, but these occurrences are very uncommon and limited to two or three of all 52 currently accepted species of this clade (Stöhr and O'Hara 2007). The vast majority of the clade, however, is found at much greater depths, and it thus legitimately qualifies as a deep-sea group.

Our study provides the oldest unequivocal fossil record of the *Ophioplinthaca–Ophiocamax–Ophiomitra* clade. It furthermore clearly shows that species of the clade occurred in shallow-water coral reefs in the Late Jurassic. More research is necessary to test whether the find of *O. crinitum* is an exceptional reef occurrence of an otherwise deep-sea group or, instead, evidence for a considerably extended bathymetric distribution of this group during the late Mesozoic.

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