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A new bathyal ophiacanthid brittle star (Ophiuroidea: Ophiacanthidae) with Caribbean affinities from the Plio-Pleistocene of the Mediterranean

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Abstract

Identifiable remains of large deep-sea invertebrates are exceedingly rare in the fossil record. Thus, every new discovery adds to a better understanding of ancient deep-sea environments based on direct fossil evidence. Here we describe a collection of dissociated skeletal parts of ophiuroids (brittle stars) from the latest Pliocene to earliest Pleistocene of Sicily, Italy, preserved as microfossils in sediments deposited at shallow bathyal depths. The material belongs to a previously unknown species of ophiacanthid brittle star, *Ophiacantha oceani* **sp. nov.** On the basis of morphological comparison of skeletal microstructures, in particular spine articulations and vertebral articular structures of the lateral arm plates, we conclude that the new species shares closest ties with *Ophiacantha stellata*, a recent species living in the present-day Caribbean at bathyal depths. Since colonization of the deep Mediterranean following the Messinian crisis at the end of the Miocene was only possibly via the Gibraltar Sill, the presence of tropical western Atlantic clades in the Plio-Pleistocene of the Mediterranean suggests a major deep-sea faunal turnover yet to be explored.

Keywords: ophiuroids, microfossils, lateral arm plates, deep-sea fossils

Introduction

Brittle stars, or ophiuroids, are close relatives of the sea stars and live in almost every part of the present-day world oceans (Stöhr *et al.* 2012). They have always fascinated and puzzled marine researchers (e.g., Forbes 1852) and were even among the very first organisms to be brought up from the deep sea (a basket star recovered during deep-sea soundings in the Baffin Bay by John Ross in 1818) considered uninhabitable until then (Etter & Hess 2015). Recently, brittle stars have gained an increasing amount of attention in the scientific community because of their potential as a model organism for the study of biogeographic patterns and the evolution of marine benthos (e.g., Thuy 2013; O'Hara *et al.* 2014; Woolley *et al.* 2016; Bribiesca-Contreras *et al.* 2017).

The basis for these new perspectives is a robust phylogeny based on outstandingly extensive molecular data (O'Hara *et al.* 2014, 2017) in agreement with state-of-the-art morphological evidence (Thuy & Stöhr 2016, 2018), and combined with an unexpectedly rich fossil record (e.g., Thuy 2013). Although ophiuroids only rarely fossilize as intact skeletons due to rapid post-mortem decay, dissociated skeletal plates abundantly occur as microfossils in marine rocks from all kinds of depositional environments at least from the Silurian onwards (e.g., Reich & Kutscher 2001). Thanks to continuous efforts in deciphering ophiuroid micromorphology (e.g., Hess 1962; Martynov 2010), it is now well documented that ophiuroid microfossils, in particular the lateral arm plates, are potentially identifiable to species level (Hess 1962; Thuy & Stöhr 2011) and accessible for cladistics analyses (Thuy & Stöhr 2016, 2018).

Since ophiuroid microfossils are both abundant and taxonomically identifiable, they provide insights into otherwise virtually inaccessible palaeo-environments, in particular ancient deep-sea settings. Unaltered, fossiliferous deep-sea sediments from settings are generally rare or inaccessible, thus making the fossil record of bathyal or even abyssal communities notoriously difficult to study (e.g., Smith & Stockley 2005). Since even small volumes of bulk sediment samples recovered from deep-sea drill cores have been shown to yield identifiable ophiuroid microfossils

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(Thuy *et al.* 2012), however, ophiuroids are highly promising candidates to unlock the fossil record of deep-sea benthos.

Here, we describe a new ophiuroid from Plio-Pleistocene bathyal deposits of Sicily, Italy. The material consists of dissociated lateral arm plates retrieved as microfossils from bulk sample sieving residues. We disentangle the taxonomic affinities of the new species and discuss the palaeo-biogeographic implications of our discovery.

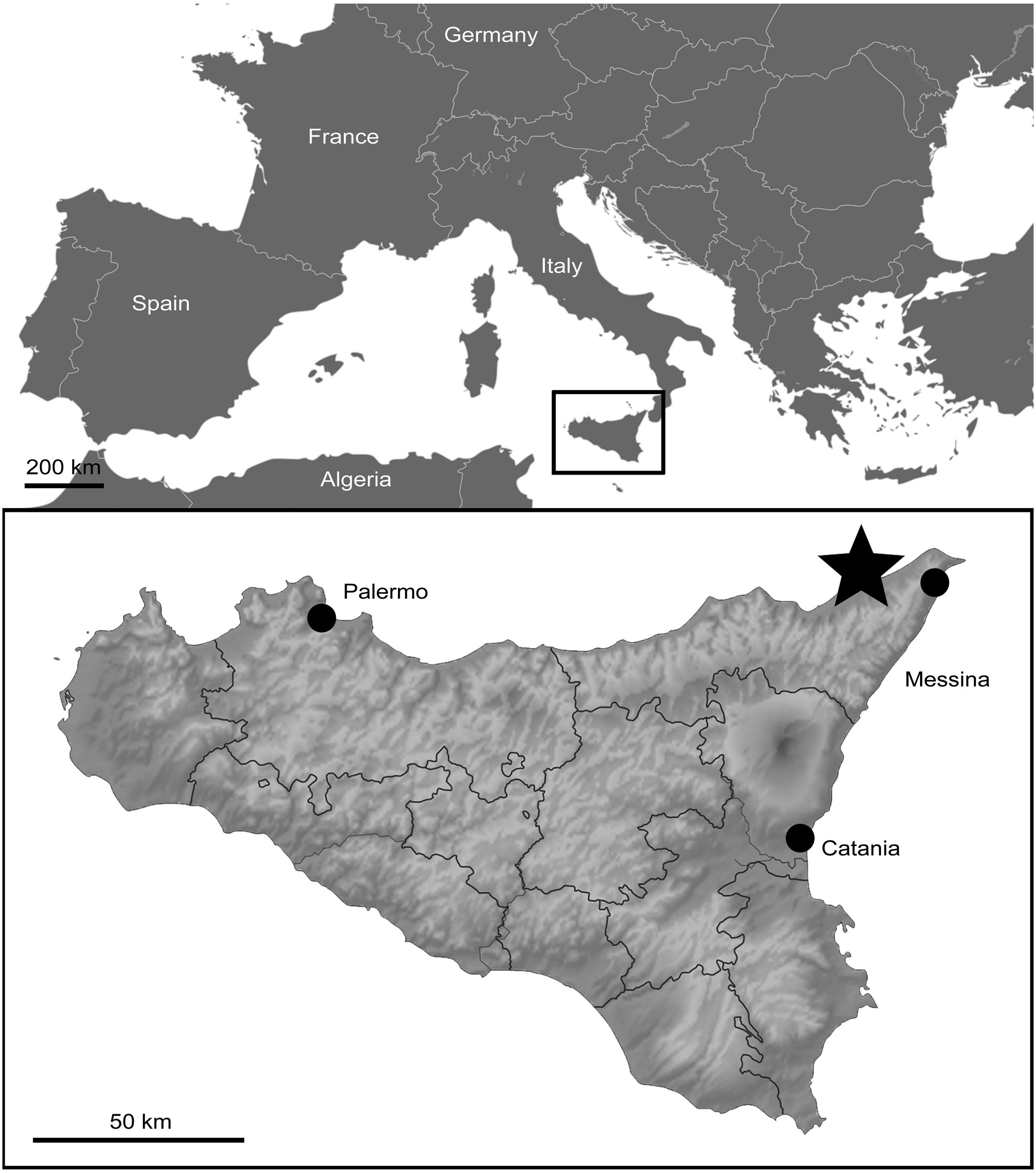

FIGURE 1. Map showing the position of the Punta Mazza section at Capo Milazzo, NE Sicily, Italy, marked by a star. Maps redrawn from publicly available material by Sémhur/Wikimedia Commons.

Material and methods

The material we studied consists of 13 dissociated lateral arm plates picked from dry residues of a screen-washed bulk sediment sample, using a dissecting microscope. Selected lateral arm plates were cleaned in an ultrasonic bath, mounted on stubs using spray adhesive and gold-coated for scanning electron microscopy (SEM). All figured specimens were deposited in the collections of the Natural History Museum Luxembourg (acronym MnhnL). Terminology follows Martynov (2010) and Thuy & Stöhr (2011, 2016). We here introduce the new term 'vertebral articular structures of the lateral arm plate' to provide a consistent and anatomically meaningful designation for the complex, highly diagnostic structures previously referred to as ridges or knobs on the inner side of the lateral arm plate. Details are provided below in the discussion section. We use the classification proposed by O'Hara *et al.* (2017, 2018).

Geological context

The bulk sediment sample that yielded the ophiuroid remains described herein was taken from a yellowish marl bed exposed along the coastline at the Punta Mazza section at Capo Milazzo, NE Sicily, Italy. The outcrop was described among others by Violanti (1988), Fois (1990) and Borghi *et al.* (2014). The yellowish marls are dated to the Piacenzian to Gelasian (latest Pliocene to earliest Pleistocene, approximately 2.6 million years) zones MPL5 to MPL6 (MPL: Mediterranean Pliocene) of Cita (1975). They yield abundant octocoral, echinoid and brachiopod fossils and are interpreted as shallow bathyal sediments originally deposited at several hundred metres palaeo-depth and subsequently brought to the surface by exceptionally intense tectonic uplift in the surroundings of the Messina Strait (Borghi *et al.* 2014).

Results

Systematic palaeontology

Class Ophiuroidea Gray, 1840

Subclass Myophiuroidea Matsumoto, 1915

Superorder Ophintegrida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Order Ophiacanthida O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Suborder Ophiacanthina O'Hara, Hugall, Thuy, Stöhr & Martynov, 2017

Family Ophiacanthidae Ljungman, 1867

Genus *Ophiacantha* Müller & Troschel, 1842

Remarks. *Ophiacantha* is one of the most species-rich (Stöhr *et al.* 2012) and heterogeneous genera among the living ophiuroids (O'Hara & Stöhr 2006; Thuy 2013). Latest molecular evidence confirmed earlier suspicions that the genus, as currently defined, represents a polyphyletic amalgam of species (O'Hara *et al.* 2017, 2018) that should be subdivided into several genus-level clades. Previous studies already hinted at morphologically coherent species groups within *Ophiacantha* potentially representing such genus-level clades (O'Hara & Stöhr 2006; Thuy 2013). A revision of *Ophiacantha* and allied genera combining molecular and morphological evidence by far exceeds the scope of the present paper. We therefore preliminarily assign the species described herein to *Ophiacantha*, emphasizing, however, that it belongs to a separate species group than the type species *O. bidentata*.

Ophiacantha oceani sp. nov.

Figure 2

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Etymology. Species named in honour of progressive metal band 'The Ocean'. Musicians who so skillfully combine arts and science, composing albums like 'Precambrian' (with songs named after the periods of the Precambrian), 'Pelagial' (with songs named after the bathymetric subdivisions of the water column) and 'Phanerozoic' as well as the song 'Turritopsis dohrnii' referring to the immortal jellyfish from the Mediterranean, are more than deserving of being immortalized in the fossil record.

Holotype. MnhnL (Musée national d'histoire naturelle, Luxembourg) OPH074, dissociated lateral arm plate.

Paratypes. MnhnL OPH075 and OPH076, two dissociated lateral arm plates.

Additional material. MnhnL OPH077, ten dissociated lateral arm plates.

Diagnosis. Species of *Ophiacantha* with lateral arm plates showing a very strong constriction; weak vertical striation close to the row of spine articulations; large, poorly defined, proximalwards protruding and slightly prominent spur on the outer proximal edge; up to seven dorso-ventrally compressed spine articulations composed of massive dorsal and ventral ridges fully separated at their proximal tips; inner side of lateral arm plates with vertebral articular structures composed of a well-defined prominent triangular central knob and a similarly well-defined oblique, slightly arched proximal ridge with a ventralward-pointing dorsal tip.

Locus typicus. Punta Mazza, Capo Milazzo, NE Sicily, Italy (38.270694° N, 15.239373° E).

Stratum typicum. Yellowish marls of the MPL5–MPL6, Piacenzian to Gelasian, latest Pliocene to earliest Pleistocene, approximately 2.6 mya.

Description of the holotype. MnhnL OPH074 (Fig. 2A–B) is a dissociated proximal to median lateral arm plate approximately 1.3 times longer than high with deeply concave dorsal edge as a result of an extreme constriction; ventral edge weakly convex; outer proximal edge convex, with a large, smooth, protruding, slightly prominent and poorly defined spur proximally fading into the crest of the outer surface curvature; outer surface with moderately coarsely meshed stereom with very weak vertical striation in a narrow line along the proximal edge of a well-defined, slightly wavy ridge bordering the row of spine articulations; outer surface stereom slightly more densely meshed on crest of curvature in distal continuation of the spur on the outer proximal edge; seven spine articulations on strongly bulging distal portion of lateral arm plate, forming a row from the ventral to the dorsal edge of the lateral arm plate and probably forming a continuous to near-continuous fan of arm spines in the intact individual; size of spine articulations and of gaps separating them increasing towards the dorsal edge of the lateral arm plate; spine articulations dorso-ventrally compressed, consisting of a large, comma-shaped, near-horizontal dorsal lobe composed of compact stereom and a much shorter, straight, horizontal ventral lobe composed of compact to weakly perforate stereom; dorsal and ventral lobes proximally and distally completely separate, with weak sigmoidal fold distally; spine articulations distally bordered by brink composed of slightly more finely meshed stereom than on outer surface, with brink starting at second ventralmost spine articulation, widest at second dorsalmost spine articulation.

Inner side of lateral arm plate (Fig. 2B) with thick ventral edge showing a large contact surface with opposite lateral arm plate suggesting small ventral arm plates widely separated by lateral arm plates; dorsal edge much thinner but also showing extensive contact surface with opposite lateral arm plate, suggesting small dorsal arm plates restricted to the distal quarter of the arm segment; vertebral articular structures consisting of a well-defined, prominent central knob composed of slightly more finely meshed stereom than remaining inner side of lateral arm plate, proximally bordered and seemingly merged with a much smaller but similarly prominent and well-defined knob; additional vertebral articular structure consisting of a similarly well-defined, boomerang-shaped proximal ridge; weakly developed, narrow vertical ridge in distal third of the lateral arm plate, distally bordered by a very weak vertical furrow without clearly discernible perforations; inner distal edge with a large but poorly defined area of compact to very dense stereom corresponding to spur on outer proximal edge; tentacle notch small and inconspicuous.

Paratype supplements. MnhnL OPH075 (Fig. 2C–D) is a dissociated proximal to proximalmost lateral arm plate slightly higher than long; dorso-proximal tip missing, otherwise well preserved, with respect to finer stereom structures even better preserved than holotype specimen; outer proximal edge and outer surface ornamentation as in holotype; seven spine articulations as in holotype except for enlarged and distalwards displaced dorsalmost spine articulation.

Inner side with vertebral articular structures as in holotype except for more clearly separated large and small central knobs.

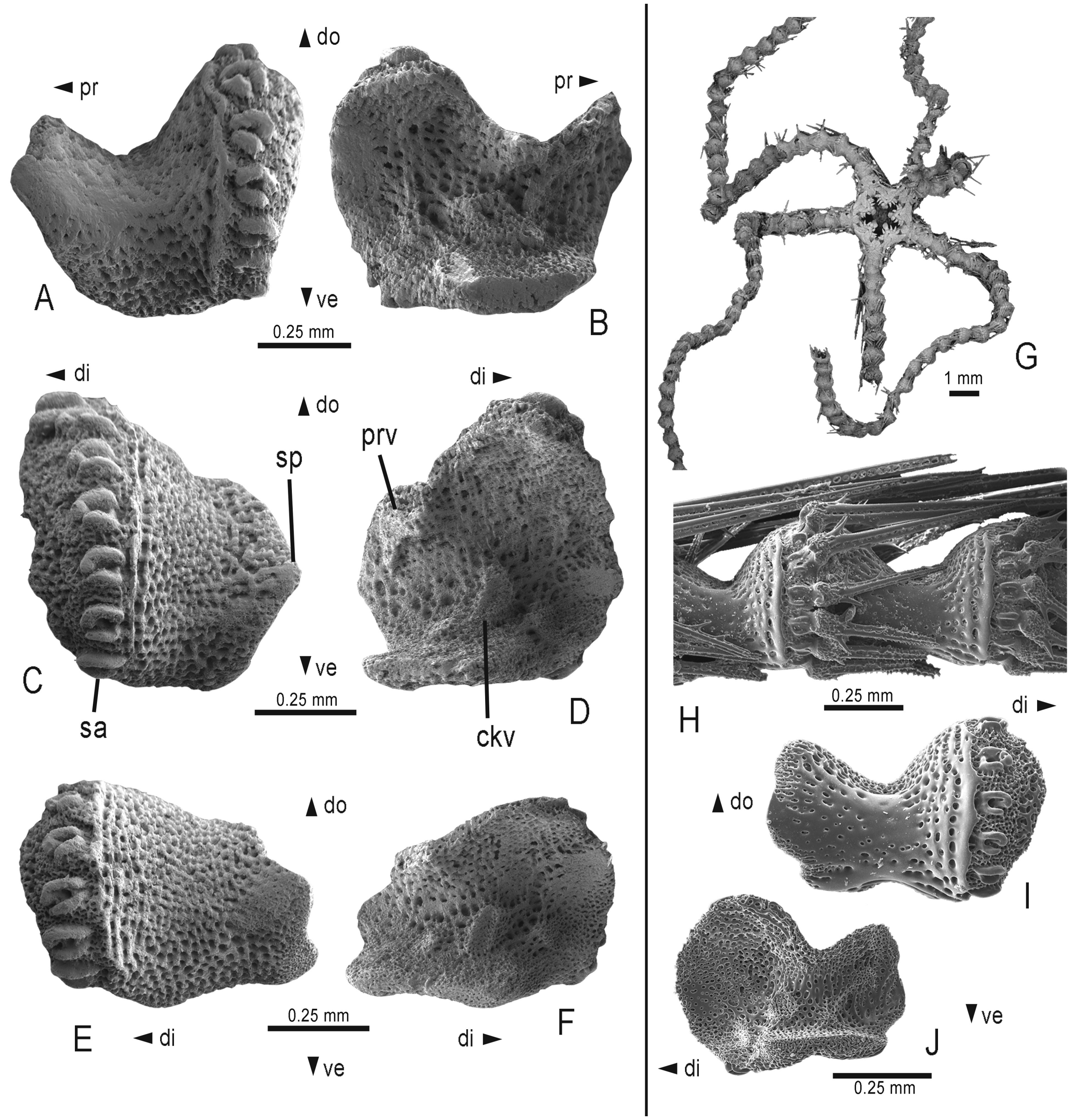

FIGURE 2. *Ophiacantha oceani* sp. nov. (A–F) from the Piacenzian to Gelasian, latest Pliocene to earliest Pleistocene (approximately 2.6 mya) of Punta Mazza, Capo Milazzo, NE Sicily, Italy, A–B: MnhnL OPH074, holotype, proximal lateral arm plate in external (A) and internal (B) views; C–D: MnhnL OPH075, paratype, proximal lateral arm plate in external (C) and internal (D) views; E–F: MnhnL OPH076, paratype, distal lateral arm plate in external (E) and internal (F) views. Recent *Ophiacantha stellata* (G–J) from the tropical NW-Atlantic as closest living relative of *Ophiacantha oceani* sp. nov., G: complete skeleton in ventral view; H: detail of arm in lateral view; I–J: lateral arm plate in external (I) and internal (J) views. Abbreviations: ckv: central knob of the vertebral articular structures; di: distal; do: dorsal; pr: proximal; prv: proximal ridge of the vertebral articular structures; sa: spine articulation; sp: spur; ve: ventral.

MnhnL OPH076 (Fig. 2E–F) is a dissociated distal lateral arm plate approximately 1.5 times longer than high; general plate outline, outer surface ornamentation and outer proximal edge as in holotype but with weaker constriction and thus less strongly concave dorsal edge; dorso-proximal tip of lateral arm plate missing; six spine articulations as in holotype; size of gaps separating spine articulations increasing dorsalwards but size of spine articulations unchanging.

Inner side as in holotype but with widely separated large and small central knobs; proximal vertebral articular structure roughly boomerang shaped but very poorly defined.

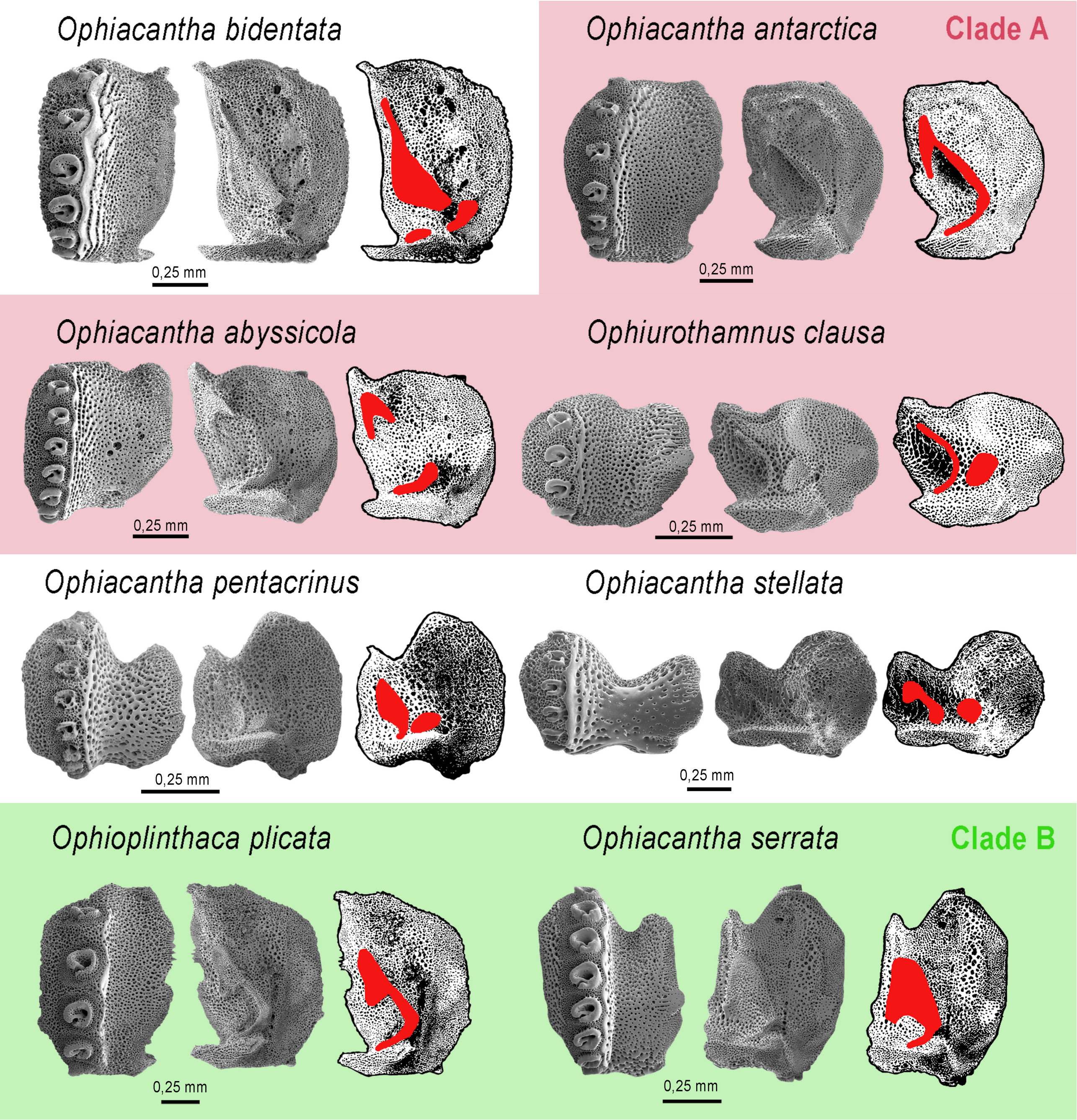

FIGURE 3. Lateral arm plates of various extant species of Ophiacanthidae, all shown with dorsal edges upwards, and with external view (left), internal view (middle) and the same internal view with the vertebral articular structures marked in red (right) for every species. Colours of background correspond to clade colours in Fig. 5. White background means the species are not included in the tree on Fig. 5. Scale bars equal 0.25 mm.

Discussion

Taxonomic position

The lateral arm plates from the Plio-Pleistocene of Sicily described herein unequivocally belong to the suborder Ophiacanthina because of their strong constriction and large spine articulations with a sigmoidal fold. The non-protruding ventral portion, the spine articulations proximally bordered by a dorso-ventrally striated ridge and the shape of the vertebral articular structures on the inner side place the lateral arm plates within the family Ophiacanthidae as defined by O'Hara *et al.* (2018).

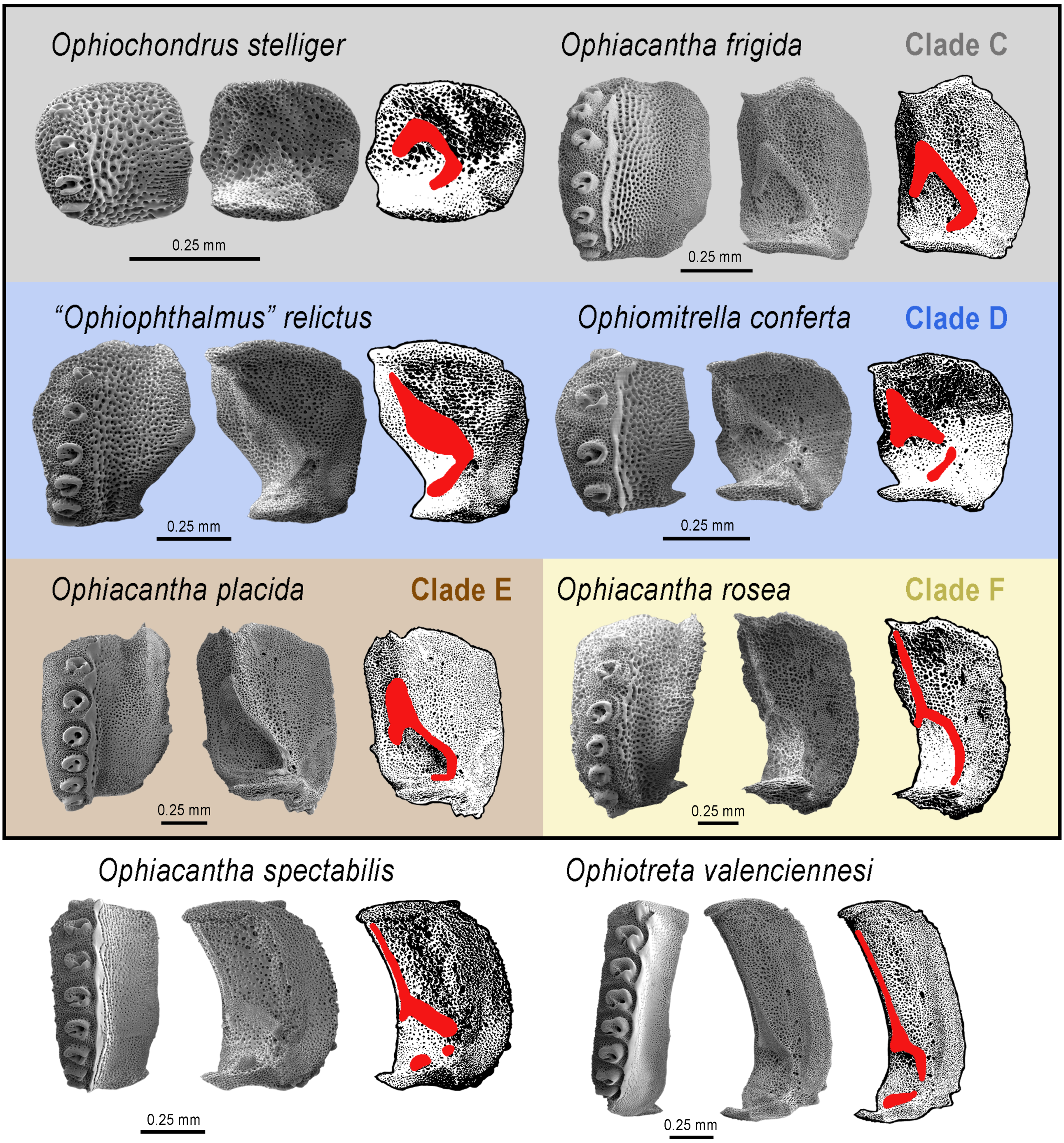

FIGURE 4. Lateral arm plates of various extant species of Ophiacanthidae (black-rimmed area) and Ophiotomidae, all shown with dorsal edges upwards, and with external view (left), internal view (middle) and the same internal view with the vertebral articular structures marked in red (right) for every species. Colours of background correspond to clade colours in Fig. 5. White background means the species are not included in the tree on Fig. 5. Scale bars equal 0.25 mm.

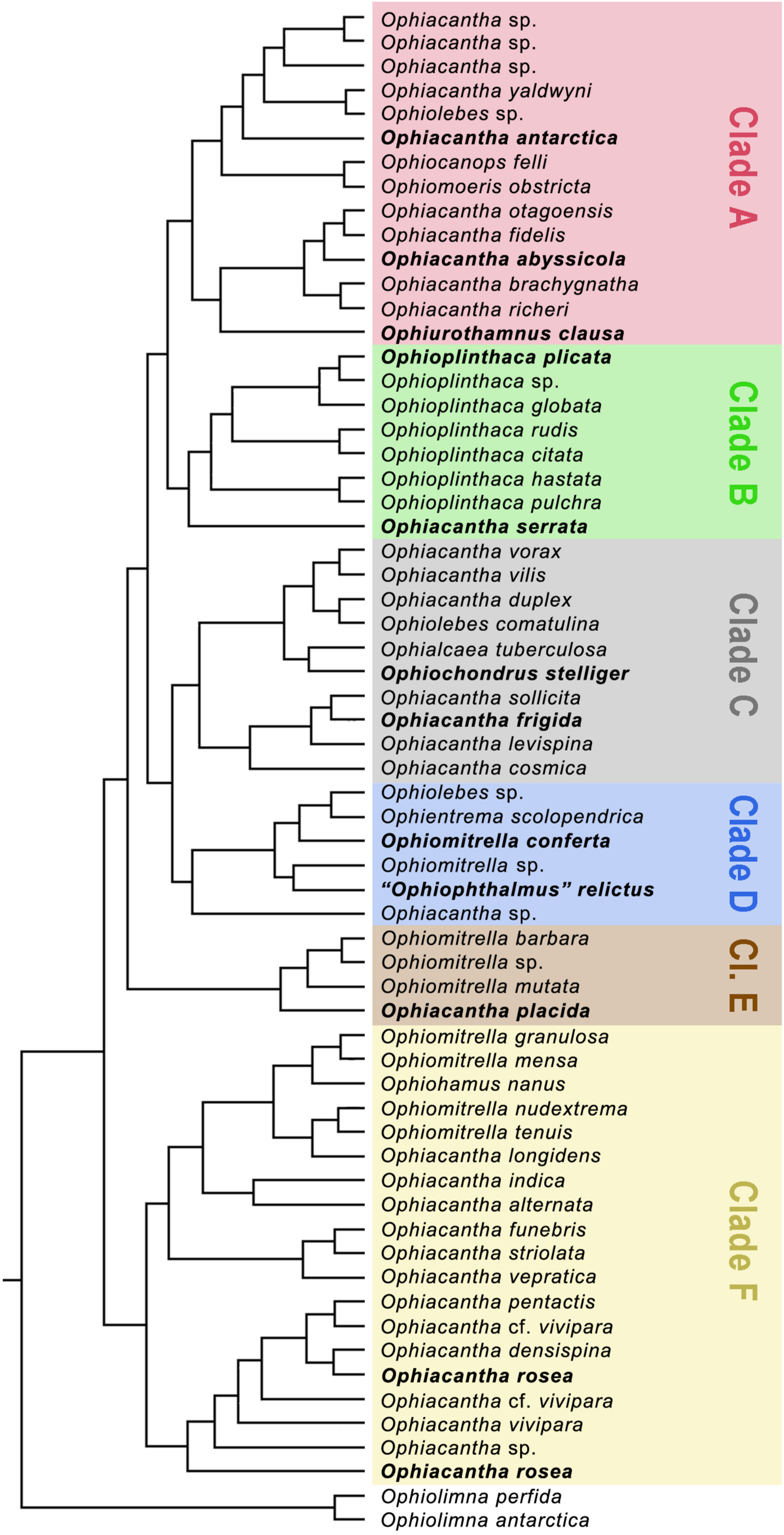

FIGURE 5. Phylogenetic tree of the Ophiacanthidae modified from O'Hara *et al.* (2017), with clades informally designated and colour-coded as in Figs. 3–4. Species represented in Figs. 3–4 in bold.

Latest molecular evidence resolves several clades within the Ophiacanthidae (O'Hara *et al.* 2017) but suggests that most genera assigned to the family require revision. Species currently placed in *Ophiacantha* are found in almost every clade, corroborating previous suspicions that the genus is polyphyletic (O'Hara & Stöhr 2006; Thuy 2013). As currently defined, the genus is one of the most species-rich among the living ophiuroids, comprising as many as 132 accepted extant species and an additional four extinct species (Stöhr *et al.* 2018). Previous morphological studies already identified several groups of *Ophiacantha* species that should be separated on genus level to reflect their monophyletic status (e.g., Paterson 1985; O'Hara & Stöhr 2006), in some cases corroborated by consistent lateral arm plate features (Thuy 2013).

An exhaustive revision of the genus *Ophiacantha* reconciling molecular evidence with patterns of general morphology and lateral arm plate microstructure exceeds the scope of this study. In order to taxonomically assess the fossil lateral arm plates described herein, however, we build on the previous observations and further explore the patterns in lateral arm plate morphology among the *Ophiacantha* species.

Key features characterizing *Ophiacantha* species groups essentially pertain to the spine articulations and structures on the inner side of the lateral arm plates called ridges and knobs. Spine articulations have been amply studied, described and illustrated in recent systematic studies (Martynov 2010; Thuy & Stöhr 2016). The ridges and knobs on the inner side of the lateral arm plates, in contrast, have not been systematically assessed so far, although they were recently confirmed to be diagnostic on various taxonomic levels (Thuy & Stöhr 2011, 2016; Stöhr *et al.* 2012; Thuy 2013). To enhance terminological accuracy, we here introduce 'vertebral articular structures of the lateral arm plate' as an anatomically consistent term to designate all ridges, knobs and other structures on the inner side of the lateral arm plate in contact with the lateral side of the corresponding vertebra.

The complexity of the vertebral articular structures in Ophiacanthidae is often difficult to describe in simple words (e.g., Thuy & Stöhr 2016). We therefore opted for a graphical compilation of lateral arm plates extracted from various living species (Figs. 3-4) following the techniques outlined by Thuy & Stöhr (2011), and arranged according to the position of the respective species in the phylogenetic tree by O'Hara *et al.* (2017) (Fig. 5), whenever possible. The family Ophiacanthidae is subdivided into several clades that have not yet been defined on genus or subfamily level. Here, we informally name these clades A-F, pending a revision of the family.

In almost all the sampled members of the Ophiacanthidae, the vertebral articular structures are reminiscent of a digit 1, rotated some 40° counterclockwise and missing the right foot serif, as fundamental shape. The only exception is *Ophiacantha rosea* Lyman, 1878 (Fig. 4), a member of clade F that is sister to all the other Ophiacanthidae clades. Rather than a rotated digit 1, *O. rosea* shows vertebral articular structures reminiscent of an inversed sickle, close to that of *Ophiotreta valenciennesi* (Lyman, 1879) and *Ophiacantha spectabilis* G.O. Sars, 1872 (Fig. 4), which are both members of the family Ophiotomidae according to O'Hara *et al.* (2017).

In all other sampled Ophiacanthidae clades, the vertebral articular structures evolve around variations of the rotated digit 1, e.g., an undivided digit one with a broad, nose-shaped beak in clade B (Fig. 3), an undivided digit one with a slender beak in clade C (Fig. 4), and a divided or undivided digit one with a large, drop-shaped beak in clade D (Fig. 4). Interestingly, the type species of the genus, *Ophiacantha bidentata*, was not included in the tree of O'Hara *et al.* (2017) but shares greatest similarities with clade D in terms of lateral arm plate morphology including the shape of the vertebral articular structures, a position confirmed by latest, unpublished molecular analyses (O'Hara, pers. comm.).

The lateral arm plates of *Ophiacantha oceani* sp. nov. show vertebral articular structures divided into a central knob and a proximal ridge similar to those of *Opiurothamnus clausa* (Lyman, 1878) and of *Ophiacantha stellata* Lyman, 1875 and *Ophiacantha pentacrinus* Lütken, 1869 (Fig. 3). The latter two were not included in the tree of O'Hara *et al.* (2017) but latest, unpublished molecular analyses confirm a close relationship with *O. clausa* for both species (O'Hara, pers. comm.).

With respect to similarities in outer surface ornamentation, spine articulation morphology and the shape of the vertebral articular structures, *Ophiacantha oceani* sp. nov. is closest to *O. stellata*. Pending a phylogenetic analysis using (or including) morphological evidence, we hypothesize that *O. stellata* is the closest living relative of the extinct *O. oceani* sp. nov.

Paleo-biogeographic implications

The present-day deep-sea fauna of the Mediterranean is impoverished in comparison with the neighbouring Atlantic areas, with low diversities and only few strictly bathyal species (Emig & Geistdoerfer 2004; Danovaro *et al.* 2010). A recent compilation of echinoderm species recorded in the deep Mediterranean found a total of nine ophiuroid species occurring at depths greater than 300 m (Mecho *et al.* 2014), which is only a small fraction of the total ophiuroid diversity recorded in the deep northeast Atlantic (Paterson 1985). Fossil evidence, however, suggests much more diverse ancient deep-sea communities in the Mediterranean during the Plio-Pleistocene (e.g., Roux *et al.* 1988; Gaetani & Saccà 1984; Di Geronimo & La Perna 1997; Marsili 2007; Borghi *et al.* 2014). Most of the species recorded in the Plio-Pleistocene of the Mediterranean deep sea have strong affinities with northeast Atlantic relatives, which is not surprising considering that the Gibraltar Sill was the only gate for faunal exchange following the Messinian crisis (Harzhauser *et al.* 2007) when the Mediterranean underwent a near-complete desiccation (Hsü *et al.* 1973).

The ophiuroid species described herein aligns with previous records of a diverse Plio-Pleistocene Mediterranean deep-sea fauna. It differs, however, in the present-day distribution of its closest living relative. While most Plio-Pleistocene Mediterranean deep-sea guests can be traced to a northeast Atlantic living relative, *Ophiacantha oceani* sp. nov. shares closest ties with *Ophiacantha stellata*, a species living in the Caribbean (mostly off Cuba and the lesser Antilles) (Pawson *et al.* 2009). Our record thus adds to the record of extra-Mediterranean Plio-Pleistocene deep-sea taxa with tropical western Atlantic, and more specifically Caribbean, affinities (e.g., Borghi *et al.* 2014). Since colonization of the Mediterranean deep-sea following the Messinian crisis was only possible via the Gibraltar Sill (Harzhauser *et al.* 2007), the presence of clades nowadays restricted to the tropical western part of the Atlantic cannot be explained by the mere expulsion of Atlantic guests due to deteriorating conditions in the Mediterranean deep waters. It rather suggests a deep-sea faunal turnover at a much greater scale yet to be explored using more extensive evidence.

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