On an unusual shallow occurrence of the deep-sea brittle star Ophiomyces delata *in the Duncan Passage, Andaman Islands (Northern Indian Ocean)*

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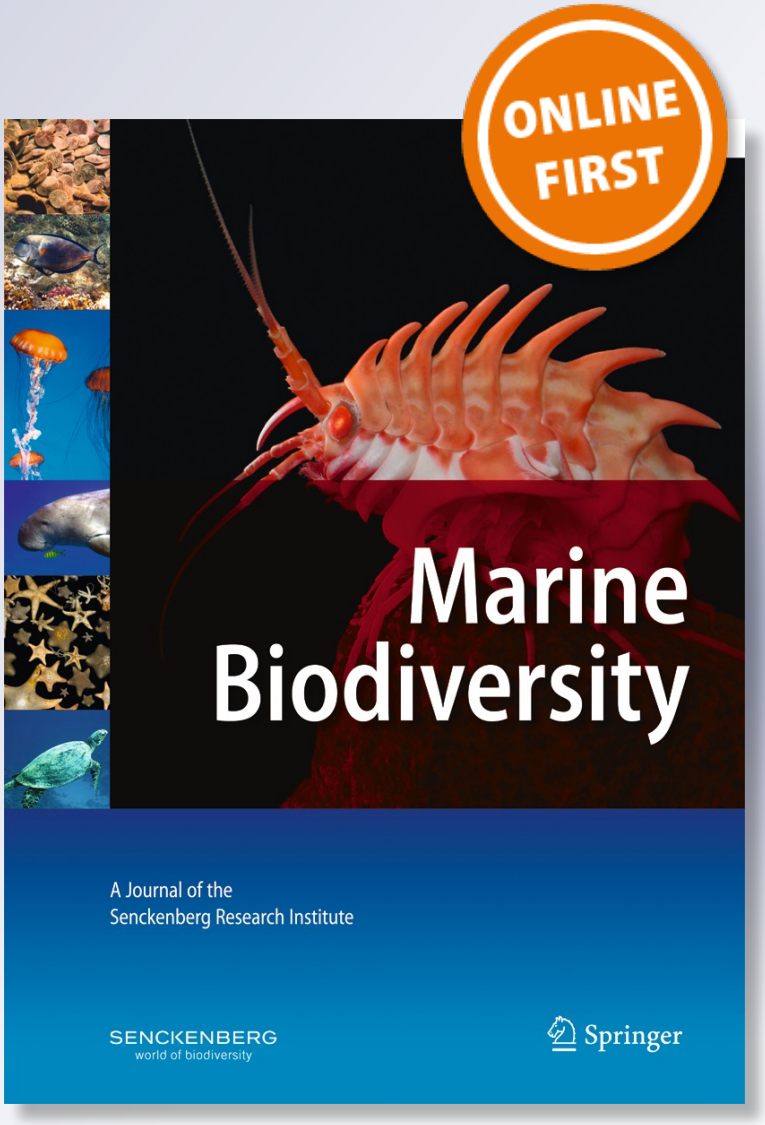

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On an unusual shallow occurrence of the deep-sea brittle star *Ophiomyces delata* in the Duncan Passage, Andaman Islands (Northern Indian Ocean)

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Abstract The deep-water brittle star *Ophiomyces delata* Koehler, 1904 is reported from the Duncan Passage, Andaman Islands, for the first time, at a relatively shallow depth of 56 m. A detailed description of the specimens is provided, as the genus *Ophiomyces* comprises nine nominal species that exhibit morphological plasticity and have considerable overlap in geographic range. The recently resurrected name for the family, Ophiomycetidae Verrill, 1899, is replaced with the senior synonym Ophiohelidae Perrier, 1893, and a key to genera is provided. This family represents a strongly conservative lineage among Ophiuroidea, having originated in the deep-sea and temporarily extended their range to shallow shelf settings around the middle Jurassic, before apparently retreating to bathyal and abyssal depths. The present discovery of *Ophiomyces delata* represents the first report of this lineage at shallow depths since the mid-Jurassic.

Keywords Ophiuroidea · *Ophiomyces delata* · Ophiohelidae · New record · Andaman Islands · Bathymetric range

Introduction

The ophiomycetids or ophiohelines are a group of peculiar ophiuroids, possessing an uncharacteristically flexible disc, which lacks radial shields, and is dorsoventrally elongate and sac-like in preserved specimens. The arms, which number 5–7, are flexed dorsally over the globose disc. The oral papillae are usually set in multiple rows along the margin as well as the ventral surface of the oral plate; at least some of these papillae are wide, flattened, or fan-shaped, and are all adpressed over the oral frame, thereby obscuring it. This group is represented by four genera: *Ophiomyces* Lyman, 1869, *Ophiohelus* Lyman, 1880, *Ophiotholia* Lyman, 1880, and *Ophiothauma* H. L. Clark, 1938, whose higher level taxonomy has undergone considerable upheaval since their original descriptions. These four genera have variously been referred to three different families, at various times: Ophiacanthidae Ljungman, 1867, Ophiohelidae Perrier, 1893, and Ophiomycetidae Verrill, 1899. Among the notable revisions, those of Paterson (1985) and Martynov (2010) recognised these genera collectively as subfamily Ophiohelinae under Ophiacanthidae, while also noting that they may represent a separate family. Thuy and Meyer (2013) conclusively proved that the four genera represent a separate lineage, distinct from the Ophiacanthidae; and resurrected the family name Ophiomycetidae Verrill, 1899. This, however, is a junior synonym of Ophiohelidae Perrier, 1893, and so an amendment to the family name is proposed in this paper. A key to the genera of Ophiohelidae is also provided based on literature.

Modern representatives of the Ophiohelidae are reported almost exclusively from bathyal depths of all tropical and temperate oceans: *Ophiomyces* (Atlantic, Indian & Pacific Oceans, ~160–5100 m), *Ophiotholia* (Atlantic & Pacific, ~175–3300 m), *Ophiohelus* (Atlantic & Pacific, ~150–1300 m), *Ophiothauma* Clark, 1938 (off northern Australia, bathyal). Interestingly, the few records of the family shallower than 200 m (i.e. 150–180 m) are based on isolated collections from seamount areas, while all records from continental and insular margins are from depths >250 m.

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While members of the genus *Ophiomyces* are considered typical 'deep-water forms', a unique shallow-water population of *Ophiomyces delata* Koehler, 1904 was collected from a sandy shelf (56 m) off the southwest of Rutland Island in the Andamans. This region represents the western side of the Duncan Passage, one of many channels traversing the Andaman and Nicobar Ridge, and connecting the Andaman Sea to the Bay of Bengal. It is a relatively shallow channel (maximum depth ~40 m in the central part), where submerged reef banks have been reported (at 25–70 m depths), separate from the nearshore fringing reefs found throughout the Andaman & Nicobar Archipelago (Nayak and Bahuguna 1998). The specimens of *Ophiomyces delata* collected here are described in detail, and the significance of their discovery from shallow shelf sediments, for the first time since the Jurassic, is discussed.

Materials & methods

During a benthic survey of the Fishery Oceanographic Research Vessel (FORV) *Sagar Sampada* (Cruise 292, November 2011), specimens of *Ophiomyces delata* were obtained from a single station in the Duncan Passage, Andaman Islands (Fig. 1), at a depth of 56 m (Stn. 7, Lat. 11°14.85'N, Long. 92°27.01'E). They were collected using a Smith-McIntyre grab and naturalist dredge. The substrate was coralline sand, and organic matter content was <0.5 %. Bottom water salinity was 33.46, temperature was 28.13 °C, and dissolved oxygen was 3.73 ml/l. The samples were preserved in 90 % ethanol. Identification was carried out using Leica EZ4 and MZ16 microscopes, measurements were made using Leica LAS Image Analyser Software, and photographs of specimen were taken using a CatCam 130 Microscope Camera.

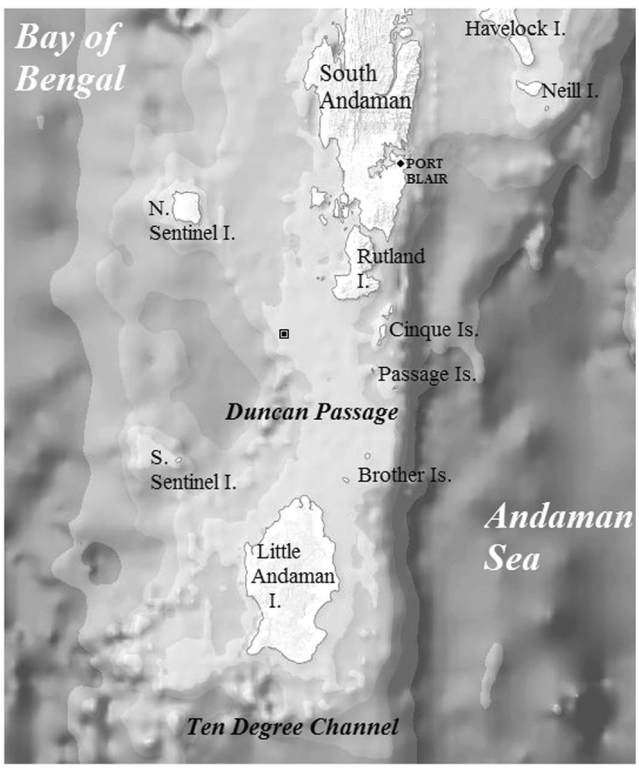

Fig. 1 Map of the southern part of the Andaman Islands showing the location of collection of *Ophiomyces delata*

Systematics

Class Ophiuroidea Gray, 1840
Order Ophiurida Müller & Troschel, 1840
Family Ophiohelidae Perrier, 1893
Type genus *Ophiohelus* Lyman, 1880 with type species *O. umbella* Lyman, 1880

Diagnosis Radial shields lacking; disc globose. Arms numbering 5-7, often flexed dorsally in preserved specimen. Arm spine often numerous and sometimes parasol-shaped in distal segments; spine articulations on lateral arm plates simple. Tentacle pores relatively prominent; tentacle scales numbering up to five. Oral papillae usually set in multiple rows along margin and ventral surface of oral plate; at least some papillae wide, flattened, or fan-shaped; and all papillae adpressed over oral frame, thereby obscuring it.

Genera *Ophiomyces* Lyman, 1869, *Ophiohelus* Lyman, 1880, *Ophiotholia* Lyman, 1880, and *Ophiothauma* H. L. Clark, 1938

Systematics The family Ophiohelidae was first proposed by Perrier (1893) to include five genera, all with discs covered in scales along with pointed or blunt spines; these were *Ophiomitra* Lyman, 1869, *Ophiothamnus* Lyman, 1869, *Ophiocamax* Lyman, 1878, *Ophiohelus* Lyman, 1880, and *Ophiotholia* Lyman, 1880. A separate family Ophiomycetidae was proposed by Verrill (1899) to include *Ophiomyces* Lyman, 1869 and *Ophiotholia* Lyman, 1880, which possessed a sac-like disc and raised arms. However, all the aforementioned genera were treated as members of Ophiacanthidae by Clark (1915). Fell (1960) suggested that the Ophiomycetidae, if valid, would also include *Ophiothauma* H. L. Clark, 1938, while *Ophiohelus* was placed in Ophiomyxidae Ljungman, 1867. In revising the Ophiacanthidae, Paterson (1985) noted the close similarity between *Ophiohelus*, *Ophiomyces*, *Ophiotholia*, and *Ophiothauma*, and also suspected that they represent a separate family. These four genera were, nevertheless, gathered by Paterson (1985) into a subfamily Ophiohelinae under Ophiacanthidae, giving priority to and amending the name proposed by Perrier (1893). This work also mentions the

'simple' shape of arm spine articulations on the lateral arm plates of *Ophiomyces*, in contrast to the characteristic 'coma shaped' articulations in other genera of Ophiacanthidae (Paterson 1985). Smith et al. (1995) also raised doubts regarding the affinities of these genera with the Ophiacanthidae, which was later substantiated by Martynov (2010), who confirmed Paterson's (1985) observations on the differences between Ophiacanthidae and Ophiohelinae in the shape of spine articulations on the lateral arm plates. Conclusive proof of paraphyly of ophiohelines was provided by the discovery of the fossil species of *Ophiotholia aurora* Thuy & Meyer, 2013 from a middle Jurassic shallow-water fossil bed. The fossil form displayed only small morphological differences from modern representatives, and was placed within the extant genus *Ophiotholia*. Taking into consideration the timescale of separation of the fossil and modern forms, Thuy and Meyer (2013) suggested that this group is a distinct lineage, which has been morphologically conservative for at least 160 million years. Thus, *Ophiohelus*, *Ophiomyces*, *Ophiotholia*, and *Ophiothauma* were separated from Ophiacanthidae and placed in Ophiomycetidae Verrill, 1899, which was resurrected by Thuy and Meyer (2013). However, it is evident that the name Ophiomycetidae is a junior synonym of Ophiohelidae Perrier, 1893, and therefore, a replacement of the family name is proposed.

Remarks In Paterson (1985), the authority for Ophiohelinae is erroneously given as Perrier, 1891 instead of 1893, and this has unfortunately been replicated by subsequent workers (e.g. Litvinova 1992; Smith et al. 1995; O'Hara and Stöhr 2006; Martynov 2010).

A type genus for family Ophiohelidae was not provided by Perrier (1893). Paterson (1985) assigned *Ophiomyces* Lyman, 1869 as the type for subfamily Ophiohelinae, possibly owing to its priority. However, as per the guidelines of the International Code of Zoological Nomenclature (ICZN), the names of higher level taxa must be derived only from the type. Thus, *Ophiohelus* Lyman, 1880 is suggested herein as the type genus for the family.

Key to Genera of Ophiohelidae Perrier, 1893

Radial shields absent; disc globose and covered by thin scales and spines; arm spines and tentacle scales usually numerous; oral papillae often scale-like, distally directed and covering the jaw in multiple rows. ..... Ophiohelidae Perrier, 1893

1. Parasol-shaped, hyaline spines present on distal arm segments..... 3

2. Parasol-shaped arm spines absent..... 5

3. Oral papillae spiniform and arranged in a single series along the edge of the jaw. ..... *Ophiohelus* Lyman, 1880

4. Oral papillae flattened, wide or spatulate, arranged in several series on the edge and ventral surface of the jaw. ..... *Ophiotholia* Lyman, 1880

5. Oral papillae short, blunt or truncated, in a cluster at the apex of the jaw, as well as five papillae in a single series along the edge of the jaw; seven arms. ..... *Ophiothauma* Clark, 1938

6. Most oral papillae flattened, spatulate, or comma-shaped, arranged in several series on the edge and ventral surface of the jaw; five arms. ..... *Ophiomyces* Lyman, 1869

Genus *Ophiomyces* Lyman, 1869

***Ophiomyces delata* Koehler, 1904**

(Fig. 2)

Ophiomyces delata – Koehler, 1904: 100–101, pl. 17 (9), pl. 18 (1–2).

Ophiomyces delata – Koehler 1922: 41–42, pl. 22 (11–12), pl. 96 (13); 1930: 57. – Clark, H. L. 1939: 55–56. – Baker 1979: 36, fig. 5 (d).

Ophiomyces delatus – Litvinova, 2001: 148–149, Fig. 1.

Ophiomyces delata – O'Hara & Stöhr, 2006: 117–118, fig. 15 (A–D).

Material examined Duncan Passage, Andaman Islands: 12 individuals; FORV *Sagar Sampada* Cruise 292, Stn. 7; 11°14.85'N 92°27.01'E, 56 m; coll. 22 November 2011, Smith-McIntyre grab & modified naturalist dredge.

Diagnosis Disc sac-like, finely scaled, lacking radial shields, and with needle-like spines. Arms bent upwards. Oral plate obscured by flat, scale-like oral papillae arranged in four imbricating rows on their lateral, as well as ventral surface. Proximal arm segments with three tentacle scales: two borne on the ventral arm plate and one on the lateral arm plate; 8-12 arm spines in basal segments varying with specimen size.

Description Disc tumescent, sac-like, lacking clear distinction between dorsal and ventral sides (Fig. 2a). Disc diameter (d.d.) 0.5–1 mm, disc height 0.4–1.7 mm; arms 3-4 times d.d. Disc without radial shields, covered with fine imbricating scales, which bear sharp pointed spines in central and interradial areas (Fig. 2b). Teeth are prominent, rounded, clearly distinguished within the mouth (Fig. 2d). Three elongate, bluntly conical oral papillae at apex of jaw (Fig. 2c and d). Each oral plate bearing six oral papillae in two rows: one at ventro-lateral margin and one on ventral face (Fig. 2c and d); each row with three, sometimes four papillae; innermost oblong with squared edges, progressively widening at tip, outermost markedly fan-shaped with a hyaline edge (Fig. 2d). The four rows of distal oral papillae on each jaw lie flattened over oral surface, oriented away from mouth, thereby

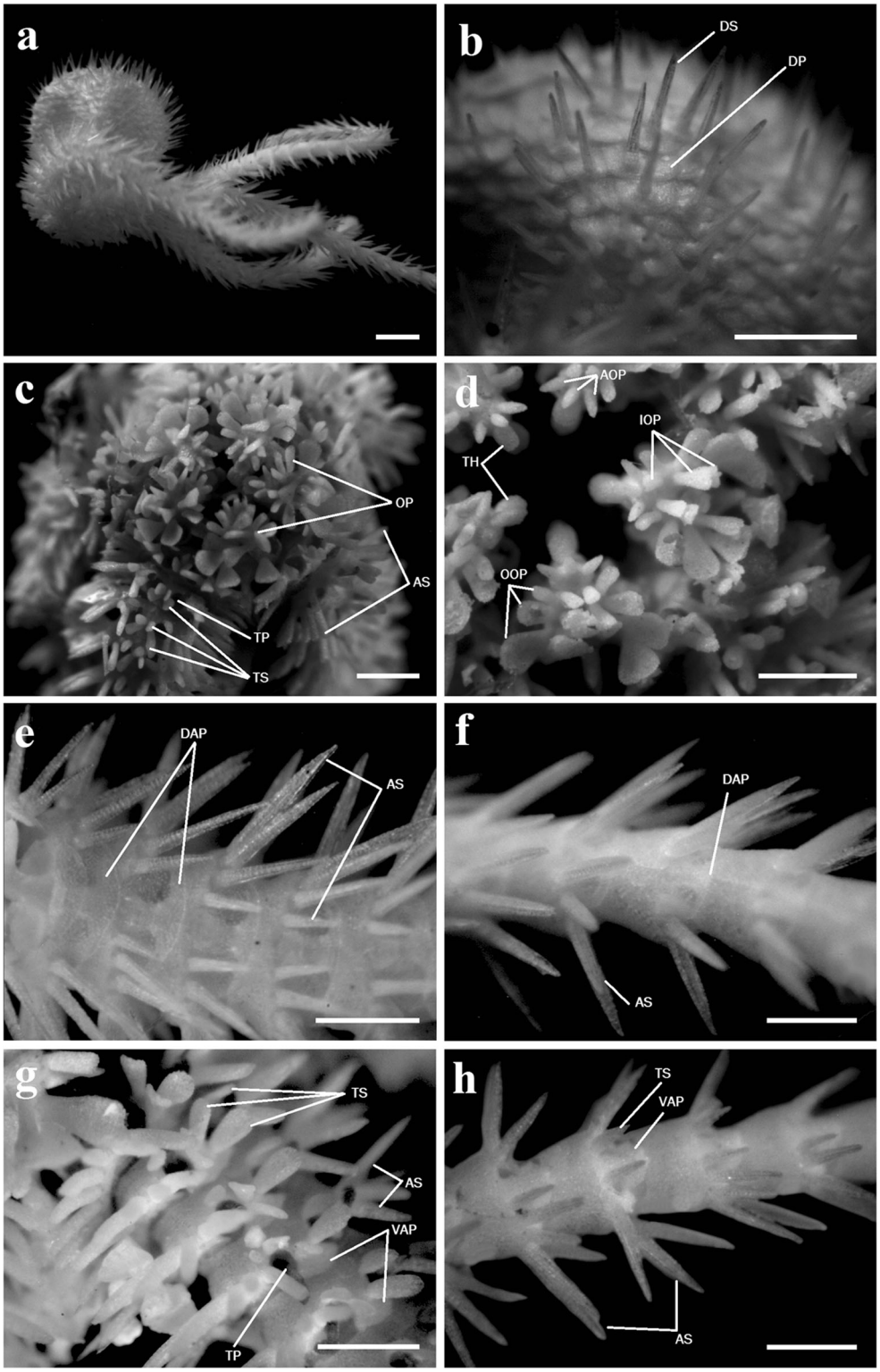

Fig. 2 *Ophiomyces delata*, **a**. Entire organism, lateral view, **b**. Dorsal disc surface, **c**. Ventral aspect of disc, **d**. Jaw structures, **e**. Dorsal aspect of arm, proximal portion, **f**. Dorsal aspect of arm, distal portion, **g**. Ventral aspect of arm, proximal portion, **h**. Ventral aspect of arm, distal portion. *AOP* apical oral papillae, *AS* arm spines, *DAP* dorsal arm plate, *DP* disc plates, *DS* disc spines, *IOP* inner row of distal oral papillae, *LAP* lateral arm plate, *OOP* outer row of distal oral papillae, *OP* oral papillae, *TH* teeth, *TP* tentacle pore, *TS* tentacle scales, *VAP* ventral arm plate. Scale bar 0.25 mm

obscuring oral frame entirely (Fig. 2c and d). Arms usually rising vertically and bent back towards dorsal side. Dorsal arm plates fan-shaped, often glassy; consecutive plates in contact proximally, distally separated by lateral arm plates (Fig. 2e and f). Ventral arm plates 'axe-head' shaped with rounded distal margins, opaque; consecutive plates separated throughout length of arm (Fig. 2g and h). Up to 12 slender arm spines at base of arm on each side (Fig. 2e and g); uppermost arm spines extremely short, less than a third of arm segment, with sharp tip (Fig. 2e); subsequent spines increasing in length;

longest spine up to 1.5 times segment length, slender, sharp tipped (Fig. 2e); four lowermost spines shorter and flattened with relatively blunt tips (Fig. 2g). Proximal arm joints with three elongate leaf-like tentacle scales (Fig. 2g); two arising on ventral arm plate, one on lateral arm plate, just below ventral-most arm spine (Fig. 2g). Tentacle scales of first 2–3 arm segments longer, more similar in shape to outer oral papillae, with flattened flared tips (Fig. 2g). Distal arm segments with up to five pointed arm spines (Fig. 2f and h) and single flattened spine-like tentacle scale arising from lateral arm plate (Fig. 2h).

Distribution Mozambique Channel (640 m), Eastern Arabian Sea (1300–3100 m), Carlsberg Ridge (2620 m), Duncan Passage, Andaman Islands (56 m), Java Sea (210–4240 m), Sulu Sea (350–535 m), Philippine Sea (1272–4239 m), East China Sea (818–824 m), Coral Sea (656–897 m), off northern New Caledonia (375–3690 m), Tasman Sea (500–922 m), Norfolk Ridge (510–1400 m), Southwestern Pacific (northeast of New Zealand, 1028–1600 m), Southeastern Pacific Ocean (Sala y Gomez-Nazca Ridge, 170–548 m).

Remarks The present specimens match well with Koehler's (1904) original description of the species from the Sulu Sea, with three elongate spiniform apical oral papillae, 8–12 arm spines and three tentacle scales on proximal arm joints. However, Koehler's specimens (350–4239 m) are described as having four distal oral papillae in each row, while the present specimens have predominantly three. A large number of specimens of *O. delata* from across the Indo-Pacific were described by Litvinova (2001), who noted a wide variability in several characters, including length and location of disc spines, numbers of distal oral papillae (16–18), and arm spines. O'Hara and Stöhr (2006) described specimens collected from New Caledonia (375–3790 m) having up to 15 arm spines and three tentacle scales, of which one was diminutive in comparison to the other two. The only stable identification character of *O. delata*, as noted by Litvinova (2001), is the presence of three tentacle scales on proximal arm segments, two of which are borne on the ventral arm plate and one on the lateral arm plate, these being 'oval' proximally and transforming into conical spine-like scales distally. This character is clearly observed in the Andaman specimens.

Discussion

Nine species are presently known in the genus *Ophiomyces*, and of these, five are recorded in the Indo-Pacific: *Ophiomyces delata* (distribution range: bathyal depths from Mozambique Channel to the Nazca Ridge, 170–3690 m; Duncan Passage, Andaman Islands, 56 m), *O. grandis* Lyman 1879 (Tasman Sea, 1630 m), *O. papillospinus* Litvinova 2001 (Tasman Sea, 510 m), *O. nadiae* Litvinova 2001 (New Caledonia, 470-3690 m), and *O. danielae* Litvinova 2001 (New Caledonia, 440–450 m). Perusal of literature reveals that differences between these species are determined by numbers and relative sizes of oral papillae, arm spines and tentacle scales; and also possibly, the point of articulation of the tentacle scales (Litvinova 2001; O'Hara and Stöhr 2006). Some of these characters, particularly numbers of arm spines, show considerable intra-specific variation with age and across geographic ranges among Ophiuroidea. Coupled with the fact that *Ophiomyces* is represented at bathyal and abyssal depths of the tropical and temperate oceans, this could result in character overlap and misidentification. As an example, the major difference between *O. delata* and *O. grandis* is that the former has maximally three tentacle scales while the latter possesses up to five. While *O. grandis* is predominantly an Atlantic species, it has also been recorded from off southeastern Australia (O'Hara 1990), a region which falls within the range of *O. delata*. Considering the wide distribution range of *O. delata* (Mozambique Channel to Nazca Ridge), it may even emerge that *O. grandis* is synonymous with it, or that together, these two species actually represent a multiple-species complex. Such ambiguity necessitates a comprehensive revision of this genus, with supporting molecular analyses.

While expanding the bathymetric and geographic range of the extant taxon *Ophiomyces delata*, the present discovery also marks the first record of an Ophiohelidae at shelf depths since the Jurassic. Diversification of this lineage is believed to have occurred before the early Jurassic, most likely in deep-sea settings, as the earliest known ophioheline fossil was collected from an Early Jurassic north Tethyan deep-sea bed (Thuy et al. 2014). The discovery of the fossil species *Ophiotholia aurora* in a shallow-water (5–10 m) fossil bed indicates that this lineage had temporarily expanded its bathymetric range to shallow shelves around the Middle Jurassic (Thuy and Meyer 2013) before retreating to the bathyal and abyssal depths where they are found today. Such a temporary invasion onto the shelf around the same time is believed to have occurred for stem-groups of other modern deep-sea echinoderms such as ophiacanthid ophiuroids and pterasterid asteroids (Thuy 2013; Thuy et al. 2014). The exact drivers for invasion of shelves by these groups and for their retreat to the deep-sea are not clearly understood. Prevailing hydrodynamic and ecological factors are likely to have played a key role, and such influences may be expected to affect morphological adaptations in connection with physiological shifts. The Ophiohelidae are of particular interest in this regard, since their unique morphological features appear to have been conserved for at least 160 million years. Indeed, it proved impossible for Thuy and Meyer (2013) to separate their Middle Jurassic fossil specimens from the modern *Ophiotholia* at the genus level. The close similarities between fossil and modern forms, and also between the deep-water

(modern) and shallow water (Middle Jurassic and Andaman specimens), demonstrate the fact that distribution patterns and depth preferences of groups may have shifted over geological time, without being reflected in their morphology and also possibly their physiology (Thuy and Meyer 2013).

Although systematic benthic surveys (using grab and dredge) have been carried out at 50–200 m all around the Andaman & Nicobar Islands (~150 sites) *O. delata* was collected only at a single site on the western side of the Duncan Passage. The previously known shallow shelf record of an ophiohelid (i.e., *Ophiotholia aurora* from Middle Jurassic) was associated with high-energy carbonate platforms with oolithic and detrital sands as well as patch reefs (Thuy and Meyer 2013), drawing similarities with the present report from coralline sandy sediments in a region with fringing coral reefs as well as submerged reefs further from the shore (Nayak and Bahuguna 1998). The occurrence of *Ophiomyces delata* in this region suggests that hydrographic or ecological factors which restrict its distribution to abyssal depths do not operate in the Duncan Passage, Andaman Islands. Interestingly, the polychaete communities in the Duncan Passage were also found to be unique and distinct from the surrounding areas (Gopal et al., unpublished). Further studies are warranted to determine the key factors that enable *Ophiomyces delata* to live at such a shallow depth in the Duncan Passage.

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