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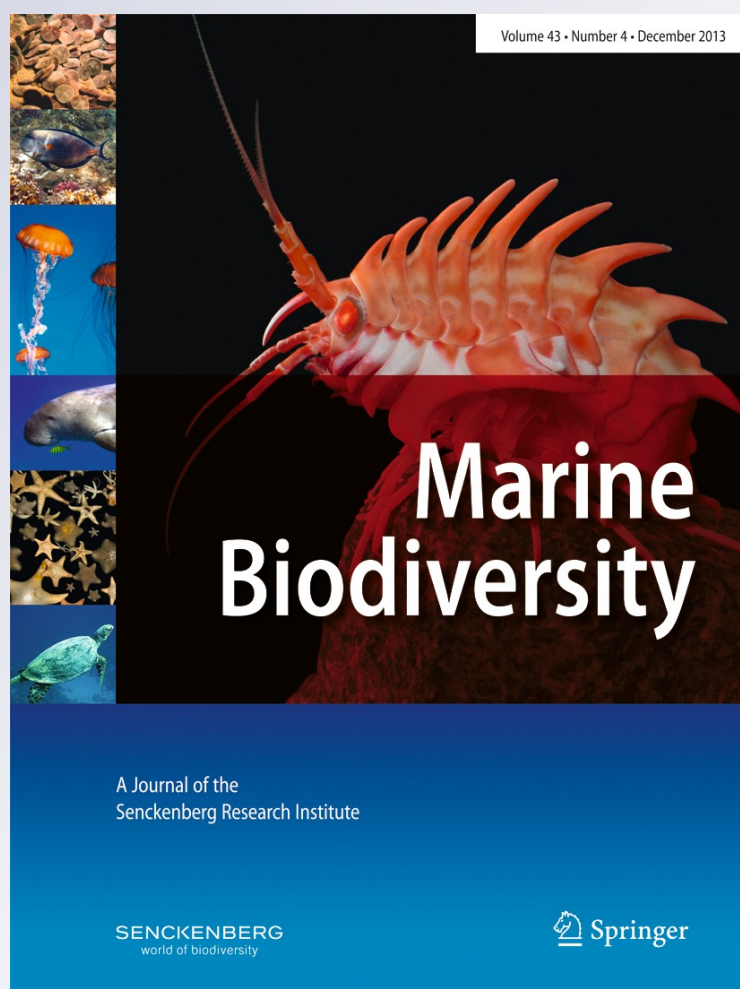
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Ophiodaphne scripta (Ophiuroidea: Amphiuridae), a brittle star exhibiting sexual dimorphism and epibiosis: first record from India, with notes on adaptations, systematics and distribution

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Abstract *Ophiodaphne scripta* (Koehler, 1904) is an amphiurid brittle star exhibiting an unusual form of conspicuous sexual dimorphism and epibiosis. The males are much smaller and exist as epibionts on the larger female. These male–female pairs, attached mouth-to-mouth, are in turn epibionts on cake urchins such as *Echinodiscus auritus* Leske, 1778, attaching themselves via the aboral side of the female. In this paper, *Ophiodaphne scripta* (Koehler, 1904) is reported from off the southern Indian peninsula for the first time, extending the range of this species eastwards. The distribution of this species is discussed in conjunction with that of the only other species in this genus, *Ophiodaphne formata* (Koehler, 1905), which also exhibits similar sexual dimorphism and epibiotic behavior. A detailed description of the specimens from India is provided, along with adaptations to their peculiar lifestyle. In addition, a brief historical review of the systematics of the genus *Ophiodaphne* Koehler, 1930 is presented, pointing out some discrepancies which persist, despite numerous revisions.

Keywords Ophiuroidea · Sexual dimorphism · Epibiosis · *Ophiodaphne scripta* · India · Morphology · Distribution · Systematics · *Ophiodaphne* · *Ophiodaphne formata*

Introduction

Sexual dimorphism is rare in echinoderms, and only four species among the Ophiuroidea are known to exhibit

conspicuous dimorphism, with respect to size and morphology: *Ophiodaphne scripta* (Koehler, 1904), *O. formata* (Koehler, 1905), *Ophiosphaera insignis* Brock, 1888 and *Astrochlamys bruneus* Koehler, 1912. In all four species, the male is smaller and found epibiotic on the female; it is attached to the aboral side of the disc of the female in *Astrochlamys bruneus*, and to the oral side in the other three species. Another species, *Amphiopholis linopneusti* Stöhr, 2001, exhibits morphological dimorphism, with no conspicuous difference in size.

The genus *Ophiodaphne* Koehler, 1930 is distributed in the Indo-west Pacific region and consists of only two species *Ophiodaphne scripta* (Koehler, 1904) and *O. formata* (Koehler, 1905). Both were initially placed in the genus *Amphiura* Forbes, 1843, but, following a series of taxonomic revisions (Clark 1967; Cherbonnier and Guille 1978 and Guille 1981), they are now placed in the genus *Ophiodaphne* Koehler, 1930, family Amphiuridae Ljungman, 1867. Possibly owing to the similar androphorous habit, the two species of *Ophiodaphne* have many superficial similarities, and it has been previously suggested but not proven that they are, in fact, conspecific (Clark 1967; Cherbonnier and Guille 1978). Apart from the male–female pairing in these species (Fig. 1), these pairs are epibionts, living on the surface of echinoids, most commonly *Echinodiscus auritus* Leske, 1778 (Fig. 2) and *E. bisperforatus* Leske, 1778 in the case of *Ophiodaphne scripta* (Mortensen 1933; Cherbonnier and Guille 1978; Guille 1981) and on *Clypeaster reticulatus* (Irimura 1981), and *Astrichypeus manni* Verill, 1867 (Tominaga et al. 2004) in the case of *Ophiodaphne formata*.

During benthic surveys of Fishery Oceanographic Research Vessel *Sagar Sampada* (Cruises 275, 282 and 289), specimens of *Ophiodaphne scripta* were collected using a naturalist dredge between depths of 30 and 100 m off the west and east coasts of India, in association with *Echinodiscus auritus* Leske, 1778 (Fig. 3). These specimens are described here, along with

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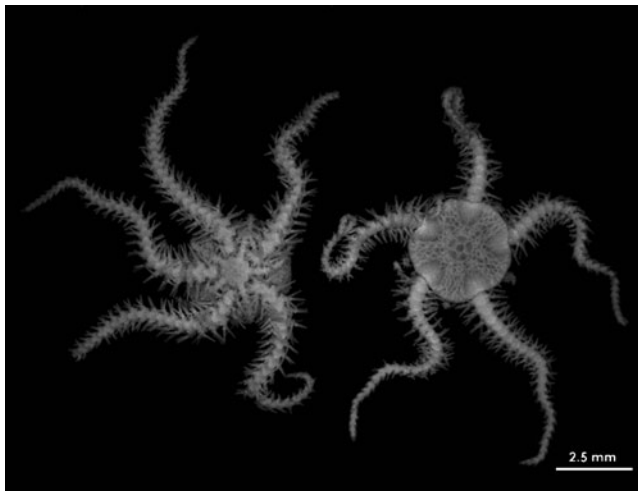


Fig. 1 *Ophiodaphne scripta*, female. Dorsal (right) and ventral (left) aspect of female, with dwarf male (arrow) visible on ventral side

adaptations in the males for attachment to females and in females for attachment to the host echinoid. A brief taxonomic review of the genus *Ophiodaphne* Koehler, 1930 is also presented, with a note on the distribution of the two species included therein.

Systematics and description

Order OPHIURIDA Müller & Troschel, 1840

Family AMPHIURIDAE Ljungman, 1867

Genus *Ophiodaphne* Koehler, 1930

Systematics

The two species currently placed in the genus *Ophiodaphne* were originally described by René Koehler, who placed them in the genus *Amphiura* Forbes, 1843, as *Amphiura scripta* Koehler, 1904 from the Red Sea and *Amphiura formata* Koehler, 1905 from the north and east of Sumbawa Island, Indonesia, respectively. The genus *Ophiodaphne* was erected by Koehler (1930) to describe a new species *Ophiodaphne materna* from the Kei Islands, Indonesia, which he considered as an adult incubating a juvenile on its oral side. In 1933, Mortensen described a new dimorphic species, *Amphilycus androphorus* from Inhaca Island, Mozambique.

Clark (1967) synonymized *Amphiura scripta* Koehler, 1904 with *Amphilycus androphorus* Mortensen, 1933 after comparing museum specimens of the former with Mortensen's description of the latter. Clark (1967), and later Cherbonnier and Guille (1978), suggested that *Ophiodaphne materna* and *Amphilycus scripta* were at least congeneric, if not conspecific. However, the comprehensive keys of Clark and Rowe (1971) recognized

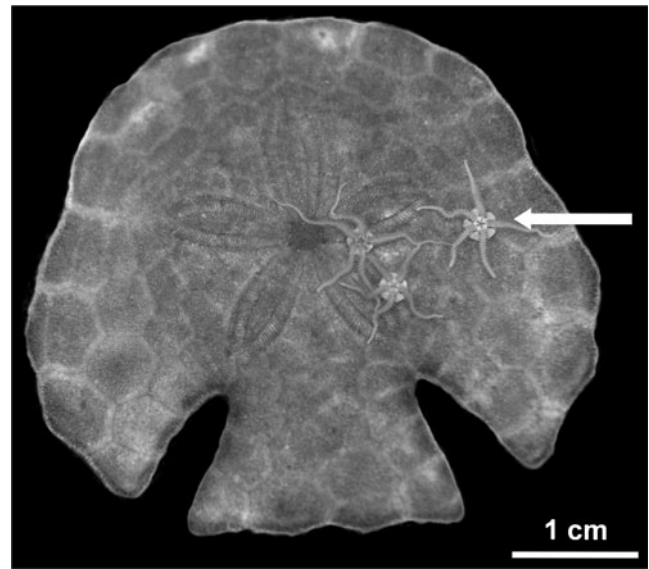


Fig. 2 *Ophiodaphne scripta*, females (arrow) on host echinoid *Echinodiscus auritus*

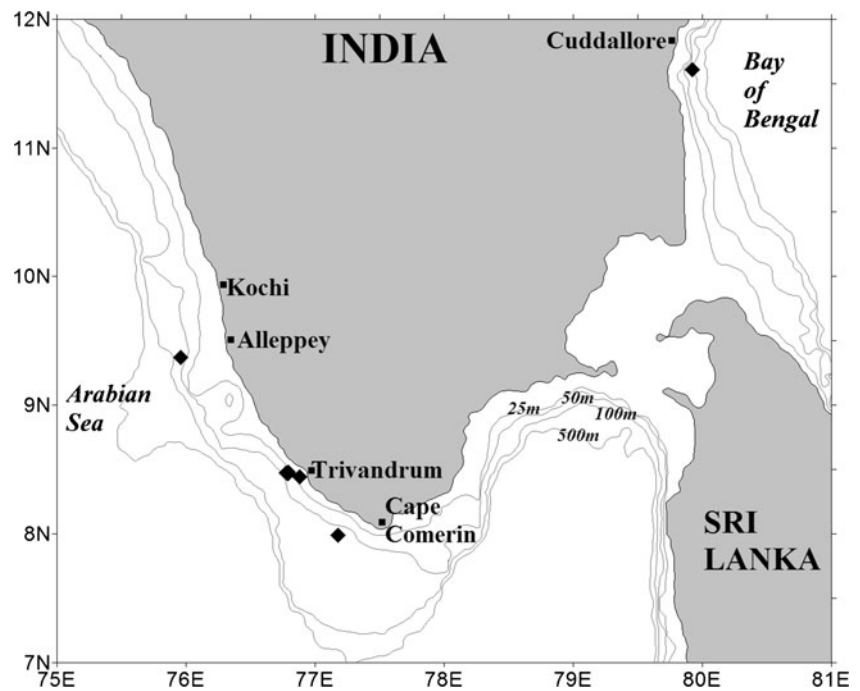
these species as *A. scripta* (Koehler, 1904) and *O. materna* (Koehler, 1905).

Upon comparing extensive collections of *Ophiodaphne materna* from the Philippines in the campaign of MUSORS TOM with Koehler's type specimen of *Amphiura formata* collected from the same region during the Siboga Expedition (1905), Guille (1981) demonstrated that both species were one and the same.

Fell (1960) and Clark and Rowe (1971) placed *Amphilycus* in the family Amphiuridae, while *Ophiodaphne* was placed in the family Ophiactidae. Cherbonnier and Guille (1978) argued that *Ophiodaphne* lies in the limit between Amphiuridae and Ophiactidae, and they were unable to place this genus in either family with certainty.

Guille (1981) was also of the opinion that *Amphilycus scripta* and *O. materna* were congeneric, and he proved they were distinct species by pointing out the following characters of the latter which distinguish it from the former: the pointed conical oral papillae, the much broader and longer tentacle scales, the growth lines on the dorsal disc scales, the contiguous radial shields with transverse striations, and the presence of arm spines which are transformed into hooks distally. The genus *Ophiodaphne* (Koehler, 1930) was recognized to have priority over *Amphilycus* (Mortensen, 1933) and *formata* (1905) had priority over *materna* (1930). The placement of *Ophiodaphne* in Amphiuridae was proposed by Guille (1981), which he explained by the presence of a continuous and contiguous row of oral papillae along the side of the jaw, along with paired infra-dental papillae. However, Guille also noted that the presence of spiniform oral papillae and hollow arm spines did not entirely validate this placement. Martynov (2010) unambiguously placed the genus in Amphiuridae,

Fig. 3 The south coast of India showing sites of collection of *Ophiodaphne scripta*



citing the presence of paired infradental papillae, which are clearly evident at least in the females.

Thus, the two species are now accepted as *Ophiodaphne scripta* (Koehler, 1904) and *O. formata* (Koehler, 1905), with the genus being placed in the family Amphiuridae.

Distribution

The genus *Ophiodaphne* Koehler, 1930 is known only from the Indo-west Pacific region, with a range from Mozambique to Japan and southern Polynesia and from intertidal depths to 245 m. *Ophiodaphne scripta* is reported from the western and northwestern Indian Ocean: from the Persian Gulf (Koehler 1904), the Red Sea (Tortonese 1936; Clark 1967), Madagascar (Cherbonnier and Guille 1978) and Mozambique (Mortensen 1933; Balinsky 1957), while the present report extends the distribution range of this species to the southwest and southeast coast of India. *Ophiodaphne formata* is reported from the South China Sea (OBIS China, <http://www.iobis.org.cn>), Philippines (Guille 1981), Sumbawa Islands, Indonesia (Koehler 1905), Kei Islands, Indonesia (Koehler 1930), north Australia (Clark 1938; OBIS Australia, <http://www.iobis.org.au/>; NMNH-SI, <http://www.nmnh.si.edu/iz/>; South western Pacific OBIS, <http://nzobis.niwa.co.nz/>), Japan (Irimura 1981; Tominaga et al. 2004) and southern Polynesia (NMNH-SI, <http://www.nmnh.si.edu/iz/>).

Ophiodaphne scripta (Koehler, 1904)

(Figs. 1, 4 and 5)

Amphiura scripta Koehler, 1904

Amphilycus androphorus Mortensen, 1933

Amphilycus scripta Clark, 1967; Clark & Rowe, 1971; Clark & Courtman-Stock, 1976

Ophiodaphne scripta Cherbonnier & Guille, 1978; Guille, 1981

Materials

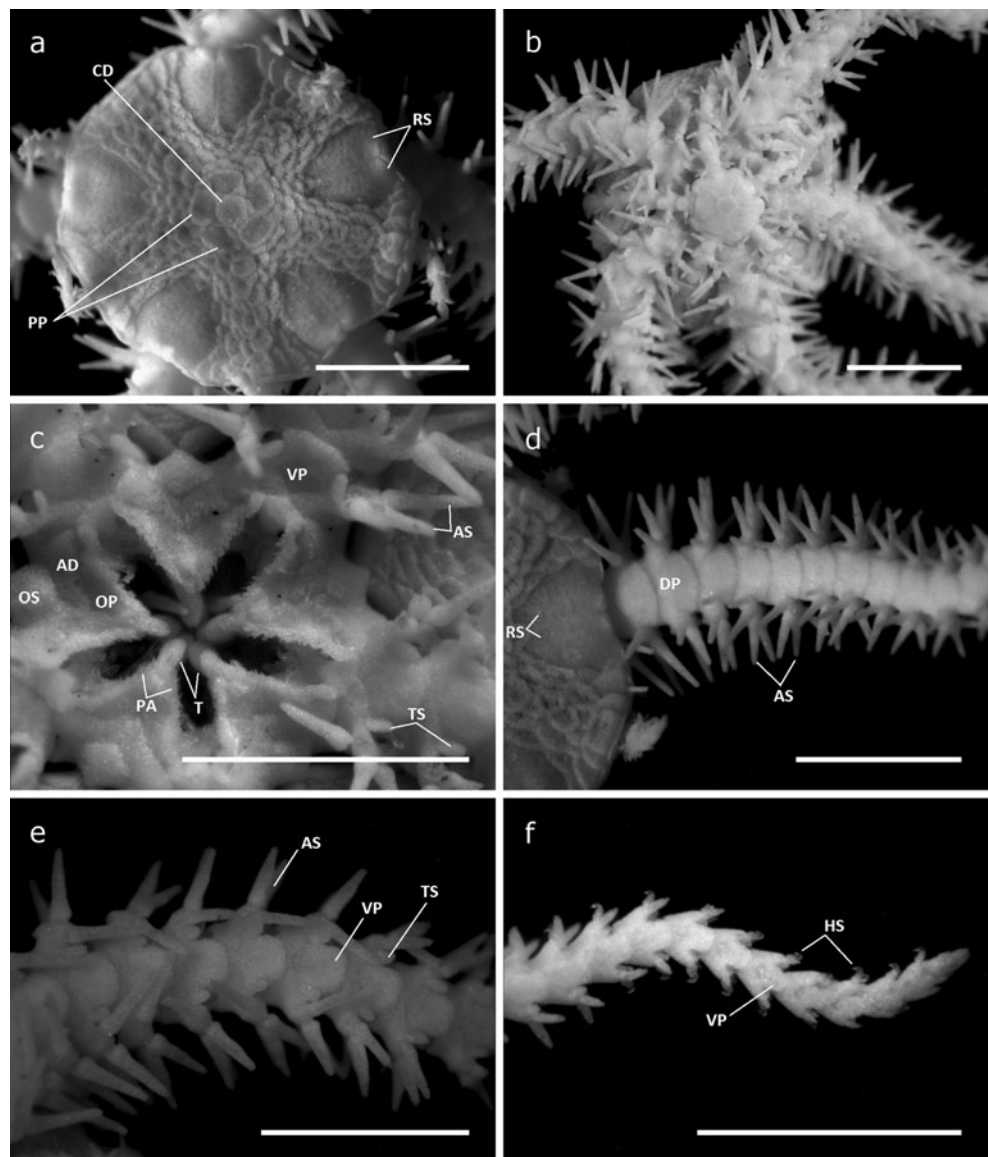
Southwest Coast of India (Southeast Arabian Sea) – Off Alleppey, 9°22.37'N, 75°57.61'E, 71 m, 14.05.10 (FORVSS 275, St. 7), 2 ♀+♂ pairs. Off Cape Comorin, 7°59.26'N, 77°10.76'E, 49 m, 15.11.10 (FORVSS 282, St. 8), 2 ♀+♂ pairs, 1 ♀. Off Trivandrum, 8°26.57'N, 76°52.83'E, 40 m, 30.08.11 (FORVSS 289, St. 18), 1 ♀+♂ pair, 2 ♀; 8°28.66'N, 76°47.62'E, 48 m, 02.09.11 (FORVSS 289, St. 29), 1 ♀+♂ pair; 8°28.03'N, 76°47.23'E, 49 m, 04.09.11 (FORVSS 289, St. 37), 1 ♀+♂ pair, 1 ♀; 8°28.36'N, 76°46.55'E, 50 m, 06.09.11 (FORVSS 289, St. 45), 1 ♀+♂ pair; 8°28.18'N, 76°47.66'E, 49 m, 07.09.11 (FORVSS 289, St. 49) 1 ♀+♂ pair.

Southeast Coast of India (Southwest Bay Of Bengal) – Off Cuddalore, 11°36.60'N, 79°55.33'E, 78 m, 22.05.10 (FORVSS 275, St. 30), 1 ♀+♂ pair.

Description

Female Disc diameter (d.d.) up to about 3.2 mm and arms about 1.5–2 times d.d. Dorsal face of disc paved by small imbricating scales, with primary rosette and radial shields clearly distinguished. Primaries rounded and separated from centrodorsal by a row or two of small scales. Radial shields about one-half of disc radius, contiguous along their whole length and separated by a few small disc plates except at the

Fig. 4 *Ophiodaphne scripta*, female; **a** dorsal aspect of disc; **b** ventral aspect of disc, with male covering over mouth; **c** jaw structures; **d** dorsal aspect of arm; **e** ventral aspect of arm, proximal segments; **f** ventral aspect of arm, distal segments. *CD* centrodorsal plate, *PP* primary plates, *RS* radial shields, *OS* oral shield, *AD* adoral shield, *OP* oral plate, *PA* oral papillae, *T* teeth, *VP* ventral arm plate, *AS* arm spines, *TS* tentacle scales, *DP* dorsal arm plates, *HS* hooked arm spines. Scale bar=1 mm



proximal end. Radial shields with transverse parallel grooves along inner edge or across entire surface. Small grooves also visible on remaining dorsal disc scales of most female specimens. One or two rows of scales distinct at the disc periphery (Fig. 4a).

Ventral inter-radii covered by small imbricating scales. Genital slits fairly narrow but clearly distinguished. Oral shields small and rhomboid with a rounded distal edge. Adoral shields large; oral plates distinct. Infradental papillae extremely small and poorly distinguished. Oral papillae more or less fused together, forming a continuous row along the sides of jaws; provided with numerous minute thorns on their edge. Oral and adoral shields along with oral plates distinctly sunken and bearing minute inwardly directed thorns all over their surface. Teeth are conspicuous, rounded and conical structures, 4–5 in a vertical row (Fig. 4c).

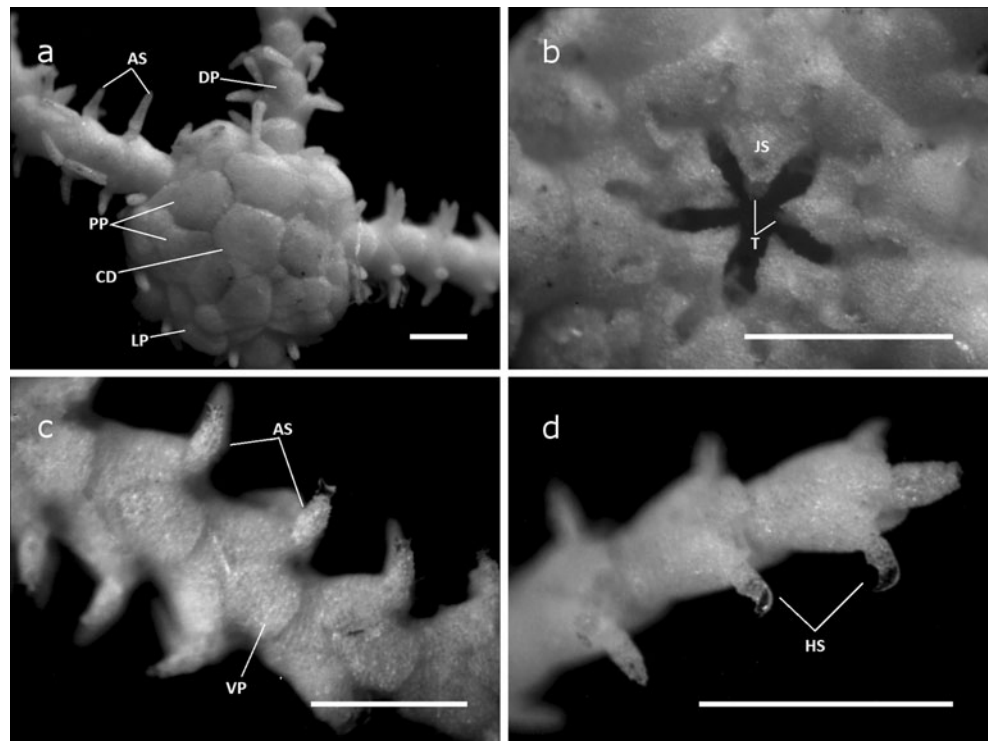
Dorsal arm plates pentagonal with rounded distal edges, just contiguous proximally; becoming fan-shaped and separated

distally (Fig. 4d). Ventral arm plates more or less square, contiguous proximally; reducing in size and becoming separated distally (Fig. 4e, f). Five rounded conical arm spines at the arm base (Fig. 4c–e). Usually, 4 arm spines towards distal end of arm, of which the two dorsal-most are transformed into hooks. Last few segments bearing only two hook-shaped arm spines (Fig. 4f). A single leaf-like tentacle scale present throughout the arm (Fig. 4e f).

Examination of the female specimen collected in FORVSS 275 St. 30 (off Cudallore) suggested that it was a juvenile. D.d. was 1.7 mm; dorsal face covered almost completely by primary rosette plates and radial shields, with very few intervening scales.

Male Disc slightly tumid at interradii, more or less pentagonal in outline. D.d. 0.3–0.4 mm; arms about 4–5 times d.d. (Figs. 4b, 5a). Dorsal face of disc completely covered by large rounded primary rosette plates. Disc periphery marked in some specimens by erect scales of the lateral faces

Fig. 5 *Ophiodaphne scripta*, male; **a** dorsal aspect; **b** jaw structures; **c** ventral aspect of arm, proximal segments; **d** ventral aspect of arm, distal segments. *CD* centrodorsal plate, *PP* primary plates, *LP* lateral disc plates, *AS* arm spines, *DP* dorsal arm plate, *JS* jaw structure, *T* teeth, *VP* ventral arm plate, *HS* hooked arm spines. Scale bar=0.1 mm



(Fig. 5a). No grooves or striations on disc scales (Fig. 5a). Ventral face of disc paved by small imbricating scales. Genital slits and jaw structures minute and poorly developed (Fig. 5b). As in females, a continuous row of fused, thorny oral papillae present, bearing minute thorns. Teeth rounded and conical (Fig. 5b). Dorsal arm plates fan-shaped and separated throughout arm (Fig. 5a); ventral arm plates pentagonal and separated throughout arm (Fig. 5c). Tentacle scales absent. Three short cylindrical arm spines at the arm base; two in number and sometimes ending in glassy thorns (Fig. 5c); transformed into curved hooks in distal segments (Fig. 5d).

Sexual dimorphism Apart from the obvious distinctions in size, the males and females differ significantly in skeletal elements, chiefly the number, disposition and ornamentation of dorsal disc scales; and numbers and shape of arm spines, which are described above. Apart from this, tentacles scales and genital slits are altogether absent in males but present in females.

Remarks

Clark (1967) describes the teeth of *A. scripta* as ‘wide and blunt’. In their detailed drawings of *O. scripta* from Madagascar, Cherbonnier and Guille (1978) have also depicted the teeth to be wide and blunt. The characters of the present specimens match the descriptions of *Ophiodaphne scripta*, except in the shape of the teeth of both males and females; in this character (Figs. 4c, 5b) they resemble *Ophiodaphne formata*. In fact, following the comprehensive key to the shallow water Indo-west Pacific Echinoderms (Clark and Rowe 1971) leads to misidentification of the present specimens as

Ophiodaphne formata, since the sole character used therein to differentiate *Amphilycus scripta* from *Ophiodaphne materna* is the shape of the teeth. However, the radial shields of *Ophiodaphne formata* are described as divergent and joined only at the distal ends, while they are contiguous throughout their length in *O. scripta*, with transverse grooves across them and often also on the other dorsal disc scales. Most characters of the present specimens, like the distal dorsal hooked arm spines of the females (Fig. 4f), the sunken jaw structures covered with spines (Fig. 4c) are reminiscent of Mortensen’s original description of *Amphilycus androphorus* (1933) which was synonymized with *Amphiura scripta* (Clark 1967). Taking this into account, the present specimens are treated as *Ophiodaphne scripta*, rather than *Ophiodaphne formata*.

Pairing and adaptations

The males are attached mouth-to-mouth, to the ventral side of the females with the arms of the male fitting into the interradii of the female, in such a way that they cover over the jaw structures of the latter (Figs. 1, 4b). The specialized structures which facilitate pairing in this species include (a) the distal hooked arm spines of the males (Fig. 5d) and (b) the sunken nature of the jaw structure of the female and the thorns present on it (Fig. 4c) (Mortensen 1933). Of the 14 females collected in 8 locations, 9 occurred with male epibionts attached to their oral side. Male–female pairs as well as unpaired females were found in the months of May 2009 (spring inter-monsoon), November 2009 (winter monsoon) and September 2011 (summer monsoon); suggesting that

pairing was not likely a seasonal phenomenon. No males were obtained without female ‘hosts’, and so the possibility that the male might be parasitic on the female cannot be ruled out (Mortensen 1933). The juvenile specimen collected off Cudallore also bore a small male on the oral side.

Biological association

O. scripta was always collected together with the Cake Urchin *Echinodiscus auritus* Leske, 1778 (Astriclypeidae) (Fig. 2) at the west coast (off Alleppey, Trivandrum and Cape Comorin). At the east coast (off Cudallore), it was not found associated with an echinoid, but the sand dollar *Clypeaster rarispinus* was also collected in the same haul. The distal, hooked arm spines of the female (Fig. 4f) enable its attachment to the host (Mortensen 1933), most likely by hooking on to the miliary spines of the latter. The females, with or without paired males, attached themselves with their aboral side adpressed to the oral side of *E. auritus* (Fig. 2). The attachment is not a fixed one, and the females can be observed actively moving across the host test. Other specimens of *O. scripta* and also *O. formata* (female) have also been reported to position themselves with their mouth turned away from the test of the host urchin (Mortensen 1933). *O. scripta* collected from Madagascar were epibionts on *E. auritus* (Cherbonnier and Guille 1978); it is also reported to be an epibiont on *E. bisperforatus* Leske, 1778 (Mortensen 1933) and the crinoid *Comanthus parvicirrus* (Müller, 1841) (Cherbonnier and Guille 1978). *Ophiodaphne scripta* is believed to feed on detritus that passes through the mouth (of both the male and female), due to ciliary currents of the host echinoid (Mortensen 1933).

Distribution

O. scripta was originally described from the Persian Gulf (Koehler 1904) and has consequently been reported from the Inhaca Island, East Africa (Mortensen 1933; Balinsky 1957), Madagascar (Cherbonnier and Guille 1978) and the Red Sea (Tortonese 1936; Clark 1967). The present report from the southwest coast of India (40–71 m off Alleppey, Trivandrum and Cape Comorin) is the first record in the eastern Arabian Sea (Fig. 3). A good population of *Echinodiscus auritus* occurs in the sandy near-shore sediments (about 30–75 m depth) of the southwest coast, particularly around Trivandrum and Cape Comorin; and *O. scripta* is also collected in good numbers along with *E. auritus* in this region. Clark and Rowe (1971) indicate a positive record of this species in the Bay of Bengal, based on specimen in the British Museum collections, but the exact location of collection is not known. In this present paper, *O. scripta* is recorded in the Bay of Bengal, off Cudallore (78 m) on the southeast coast of India (Fig. 3).

Discussion

Clark (1967) suggested that *Amphilycus scripta* and *Ophiodaphne materna* are congeneric, while also noting that ‘the two species are superficially very alike in the size and shape of the disc scales and radial shields, the very large and somewhat irregular (often fragmented) adoral shields slightly sunken to accommodate the male and fused oral papillae with fringed edges.’ At least some of these similarities were attributed to the similar ‘androphorous’ habit of both species. According to Clark (1967), the shape of the teeth, grooves on the dorsal disc scales and the large distal lobe of the oral shields are the characters distinguishing the two species. Apart from the first two characters mentioned above, Guille (1981) also pointed out that *O. scripta* could be distinguished from *O. materna* by the broader and longer tentacle scales, the contiguous radial shields with transverse grooves, and the presence of arm spines that are modified into hooks distally. In the key of Clark and Rowe (1971), the two species are distinguished solely based on the shape of the teeth.

The genus *Ophiodaphne* has a disjunct distribution; with *Ophiodaphne scripta* being recorded from the western Indian Ocean (Mozambique, Madagascar, Red Sea, Persian Gulf), while *O. formata* is described chiefly from the Eastern Indian Ocean (Malay Archipelago, South China Sea, Philippines) and Southwest Pacific (Australia, Japan, southern Polynesia). The present specimens from India possess contiguous radial shields that have distinct transverse grooves, as described for *Ophiodaphne scripta*, but the teeth in these specimens are clearly rounded and conical, as described for *Ophiodaphne formata*. It is interesting to note that the descriptions of *O. formata* from Japan (Irimura 1981; Tominaga et al. 2004) depict similar contiguous radial shields in these specimens, but the teeth in these are not distinctly pointed. While describing a specimen of *Ophiodaphne materna* from Broome in Western Australia, Clark (1938) made comparisons with the paratype collected from Kei Island. He noted that the specimen collected from Broome had a ‘smooth and flat’ disc covering, as compared to the ‘coarser and rough’ disc scales of the Kei Island paratype. The smooth and coarse nature of the disc possibly refers to the presence or absence of grooves on the disc scales. Clark (1938) also noted that the specimen was collected from very different depths (intertidal areas in Broome and 245 m off Kei Island), but could not justify the placement of his specimen into a new species.

It can be concluded that, despite the numerous taxonomic revisions, some confusion still exists in the classification of this genus, which have been made more evident from examination of the present specimens from southern India. The morphological characters used by Guille (1981) to distinguish the two species of *Ophiodaphne*, such as the degree of separation of the radial shields, the presence or absence of grooves on the disc scales and the shape of the teeth, seem to vary across the two species of *Ophiodaphne*,

without being directly indicative of either species. It is possible that *Ophiodaphne formata* and *O. scripta* are in fact conspecific, with a gradation or range of variation in certain characters. Examination of specimens of *Ophiodaphne* from across their geographic range, with supplementary molecular studies, is necessary to provide a much needed synthesis on the systematics of this genus.

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References

- Balinsky JB (1957) The Ophiuroidea of Inhaca Island. Ann Natal Mus 14:1–33
- Brock J (1888) Die ophiuriden fauna des indischen archipels. Z Wiss Zool 47:465–539
- Cherbonnier G, Guille A (1978) Echinodermes: ophiurides. Faune Madagascar no. 48
- Clark HL (1938) Echinoderms from Australia: an account of collections made in 1929 and 1932. Mem Mus Comp Zool Harvard 55:1–596
- Clark AM (1967) Echinoderms from the Red Sea. Part 2. Bull Sea Fish Res Stn Isr 41:26–58
- Clark AM, Courtman-Stock J (1976) The echinoderms of southern Africa. Publ. No. 766, British Museum (Natural History), London
- Clark AM, Rowe FWE (1971) Monograph of shallow-water indo-west pacific echinoderms. Trustees of the British Museum (Natural History), London
- Fell H (1960) Synoptic keys to the genera of Ophiuroidea. Zool Publ Vic Univ Wellingt 26:1–44
- Guille A (1981) Echinodermes: Ophiurides. Résultats des Campagnes MUSORSTOM. I - Philippines (18–28 March 1976). Mem ORSTOM 91:413–456
- Irimura S (1981) Ophiurans from Tanabe Bay and its vicinity, with the description of a new species of *Ophiocentrus*. Publ Seto Mar Biol Lab 26:15–49
- Koehler R (1904) Ophiures nouvelles ou peu connues. Mem Soc Zool Fr 17:54–119
- Koehler R (1905) Ophiures de l'expédition du Siboga. Part 2. Ophiures littorales. Siboga Expeditie 45b
- Koehler R (1912) Echinodermes (Asteries, Ophiures et Echinides). Deuxième Expédition Antarctique Française 1908–1910 J. Charcot. Masson et Cie, Paris
- Koehler R (1930) Ophiures recueillies par le Docteur Th. Mortensen dans les Mers d'Australie et dans l'Archipel Malais. Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. LIV. Vidensk Medd Dan Nat hist Foren 89:1–295
- Martynov A (2010) Reassessment of the classification of the Ophiuroidea (Echinodermata), based on morphological characters. I. General character evaluation and delineation of the families Ophiomyxidae and Ophiacanthidae. Zootaxa 2697:1–154
- Mortensen T (1933) Papers from Dr. Th. Mortensen's Pacific Expedition 1914–16. 63. Biological observations on ophiurids, with descriptions of two new genera and four new species. Vidensk Medd Dan Nat Hist Foren 93:171–195
- Stöhr S (2001) *Amphipholis linopneusti* n.sp., a sexually dimorphic amphipurid brittle star (Echinodermata:Ophiuroidea), epizoic on a spatangoid sea urchin. In: Barker M (ed) Echinoderms 2000. Proceedings of the 10th International Echinoderm Conference, Dunedin, New Zealand. Swets & Zeitlinger, Lisse, 317–322
- Tominaga H, Nakamura S, Komatsu M (2004) Reproduction and development of the conspicuously dimorphic brittle star *Ophiodaphne formata* (Ophiuroidea). Biol Bull 206(1):25–34
- Tortonese E (1936) Echinodermi del Mar Rosso. Ann Mus Civ Stor Nat "Giacomo Doria" 59:202–245