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Lophoura Kölliker in Gegenbaur, Kölliker & Müller, 1853 species (Copepoda: Siphonostomatoida: Sphyriidae) off South Africa with a key to all valid species

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Abstract *Lophoura* Kölliker in Gegenbaur, Kölliker & Müller, 1853 is one of the eight genera of Sphyriidae which currently consists of 19 accepted species. *Lophoura* species are mesoparasites of various teleosts occurring worldwide. Post metamorphic females are highly transformed with longitudinally elongated cephalothoraces and elongated necks bearing holdfast organs anteriorly. The shape and structure of the holdfast organ is mostly the main character used for the identification of species. Additionally, the structure of the posterior processes attached laterally to the perianal swelling on the posterior margin of the trunk is also used to distinguish different species. The posterior processes consist of a central porous peduncle with stalks of varying shapes and sizes. The morphology of *Lophoura* males bear resemblance to that of lernaeopodid males. Re-descriptions of the habitus of the post metamorphic females of *L. tetraloba* Ho & Kim I.H., 1989, *L.* cf. *edwardsi* Kölliker, 1853, *L. caparti* (Nuńes-Ruivo, 1962) and *L. cornuta* (Wilson C.B., 1919), including notes on the immature females of *L. tetraloba* and *L.* cf. *edwardsi*, are provided. Additionally, information regarding the structure and position of some of the appendages of *L. tetraloba*, *L.* cf. *edwardsi* and *L. caparti* is provided. Furthermore, the study provides the first illustrated descriptions of the male of *L. tetraloba*. A description is also done of an incomplete unidentied *Lophoura* species which differs from other accepted species. A morphological identification key to post metamorphic females of all accepted *Lophoura* species is provided, as well as new host and geographical records of *Lophoura* species.

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Introduction

Sphyriidae Wilson C.B., 1919 is a family consisting of eight genera with 44 accepted species (Walter & Boxshall, 2021). Four genera of Sphyriidae infect elasmobranchs while the other four infect teleosts (Gómez et al., 2010). To date, only two genera and four species [(*Sphyrion laevigatum* (Quoy & Gaimard, 1824) (Barnard, 1955; Payne, 1986; Dippenaar & Sebone, 2022); *S. lumpi* (Krøyer, 1845) (Barnard, 1955; Kensley & Grindley, 1973; Dippenaar & Sebone, 2022); *S. quadricornis* Gaevskaya & Kovaleva, 1984 (Dippenaar & Sebone, 2022) and *Lophoura elongata* Kensley & Grindley 1973 (Kensley & Grindley, 1973)] were reported from teleosts off South Africa while six species of *Tripaphylus* (i.e. *T. elongatus* (Wilson C.B., 1932); *T. vaissierei* (Delamare Deboutteville & Nuñes-Ruivo, 1954); *T. benzi* Dippenaar, 2018; *T. hoi* Dippenaar, 2018; *T. beatricae* Dippenaar, 2018 and *T. lewisi* Dippenaar, 2018) were reported from elasmobranchs from South African

waters (Dippenaar & Jordaan, 2007; Dippenaar, 2018).

Lophoura is the largest genus in the family Sphyriidae with 19 accepted species (Walter & Boxshall, 2021). Members of the genus are mesoparasites of teleosts, and have been reported from five teleost families worldwide, namely Epigonidae Poey; Macrouridae Bonaparte; Moridae Moreau; Sparidae Rafinesque and Synaphobranchidae Johnson (Ho & Kim, 1989). Macrouridae is apparently the preferred host family with 12 reported *Lophoura* species (Gómez et al., 2010).

Adult *Lophoura* females possess highly modified bodies, similar to other sphyriid females. The cephalothoraces are longitudinally elongated with the cephalic appendages on the anterior end, separated from the rest of the cephalothorax by a circular groove. The elongated part of the cephalothorax is sometimes smooth and sometimes transversely wrinkled (Kabata, 1979; Ho & Kim, 1989). The anterior end of the neck possesses a holdfast organ with varying structure and shape amongst species. The elongated neck is heavily sclerotized, sometimes smooth and sometimes with small knobs. The posterior part of the neck slightly expands into the dorsoventrally flattened trunk. The shape of the trunk also varies amongst species and has an abdomen at the posterior end (Wilson, 1919; Kabata, 1979; Ho & Kim, 1989). The posterior processes are lateral to the abdomen and consist of a porous peduncle bearing numerous stalks (Stadler, 1978). The egg sacs are long, with multi-seriate eggs.

Females of different species are mainly differentiated by the morphology of the holdfast organ on the neck, the neck length relative to the trunk length, the trunk shape while the shape and branching of the posterior processes are also considered as distinguishing features of each species (Wilson, 1919; Kabata, 1979; Ho & Kim, 1989). *Lophoura* males are dwarf males resembling those of the family Lernaeopodidae Milne Edwards, 1840 (Kabata, 1979; Ho & Kim, 1989).

Previous *Lophoura* descriptions rarely mentioned the morphology of appendages of the females, while males are rarely encountered which impedes full comparisons among *Lophoura* species. This study provides re-descriptions of some appendages of females of *L. tetraloba* Ho & Kim I.H., 1989; *L.* cf. *edwardsi* Kölliker, 1853, and *L. caparti* (Nuñes-Ruivo, 1962) and includes the first description of the male of *L. tetraloba*. It also provides a re-description of the general habitus of *L. cornuta* (Wilson C.B., 1919) which differs from the structure of the posterior processes previously described as well as a partial description of an unidentified species different from known species. Additionally, an identification key based on the morphology of *Lophoura* post metamorphic females is compiled.

Materials and methods

Specimens were collected between 1991 and 2016 from fish caught as by-catch during demersal cruises off the south, west and east coasts of South Africa and preserved in 70% ethanol. The collected specimens were stained in lactic acid with a small amount of dissolved lignin pink. The external morphology of collected specimens was studied using the wooden slide technique (Humes & Gooding, 1964) through stereo- and compound microscopes and drawings done with the aid of drawing tubes. Measurements were done using a 2 mm stage micrometer and presented as the mean (range). Additionally, selected specimens were prepared for scanning electron microscopy (SEM) by dissecting off the cephalic areas of the specimens which were dehydrated through ethanol series (70% – 80% – 90% – 100% – 100%) with each over 30 minutes intervals whereafter the samples were transferred into hexamethyldisilazane for at least 30 minutes and then transferred into a petri dish to dry completely. Samples were mounted onto stubs, sputter-coated with carbon and gold palladium and viewed with a scanning electron microscope (FEI Quanta 250 FEG SEM). Host names were verified using Fishbase (Froese & Pauly, 2022). Morphological terminology followed were mostly according to Kabata (1979), Ho & Kim (1989), Benz and Boxshall (2017) and Dippenaar (2018). Voucher material was deposited in the Iziko South African Museum, Cape Town.

Family Sphyriidae Wilson C.B., 1919
Genus Lophoura Kölliker in Gegenbaur, Kölliker & Müller, 1853

Lophoura tetraloba Ho & Kim I.H., 1989

Host: *Coelorinchus fasciatus* (Günther) (Gadiformes: Macrouridae).

Locality: Off the west coast (Atlantic Ocean), South Africa.
Material examined: 6♀♀ (2 immature and 4 post metamorphic) from three host specimens and 1♂ (immature attached to female posterior processes).
Material collected: 24♀♀ and 1♂ from *C. fasciatus*, 14♀♀ and 1♂ from *Lucigadus ori* (Smith) and 7♀♀ from unknown hosts; all specimens collected off the west coast (Atlantic Ocean), South Africa.
Voucher material: 2♀♀ (SAMC-A095124 and 1♂ (SAMC-A095125) deposited in the Iziko South African Museum, Cape Town, South Africa.

Re-description (Figs 1-3)

Immature female [Based on three specimens.] Body length from tip of cephalothorax to tip of abdomen 21.6 mm (20.4–22.7 mm), cephalothorax length 5.4 mm (4.8–5.7 mm), width 1.1 mm (1.0–1.3 mm); holdfast organ width 4.1 mm (3.8–4.5 mm); neck length 10.0 mm (9.1–11.2 mm), width 0.4 mm (0.3–0.4 mm); trunk length 6.1 mm (5.7–7 mm), width 4.5 mm (3.9–5.5 mm); posterior processes length 4.4 mm (3.4–5.6 mm), width 7.4 mm (5.9–8.4 mm).

Cephalothorax (Fig. 1a) longitudinally elongated, smooth. Neck (Fig. 1a) heavily sclerotized, elongated and cylindrical, with small knobs on surface; anteriorly bearing holdfast organ with four short processes extending outwards; each process with or without outgrowths. Trunk (Fig. 1a) longer than wide with small abdomen (Fig. 1a) posteriorly. Posterior processes (Fig. 1a) attached lateral to abdomen, consisting of a short peduncle, bearing numerous elongated, straight stalks extending mostly posteriorly.

Post metamorphic female [Based on four specimens.] Body length from tip of cephalothorax to tip of abdomen 26.7 mm (25.1–29.5 mm), cephalothorax length 7 mm (6.5–8.1 mm), width 1.7 mm (1.4–2.1 mm); holdfast organ width 5.5 mm (4.2–6.3 mm); neck length 12.3 mm (8.4–15.1 mm), width 0.7 mm (0.6–0.7 mm); trunk length 8 mm (7.6–8.7 mm), width 8.5 mm (8.3–8.7 mm); posterior processes length 7.1 mm (5.7–8.5 mm), width 10.6 mm (10.4–10.9 mm) egg-sac length 16.8 mm, width 2.1 mm (2–2.2 mm).

Cephalothorax (Fig. 1b) longitudinally elongated, smooth or sometimes transversely wrinkled, anterior surface (Fig. 2a) with two types of enlarged processes, i.e., antennary (ap) and maxillary processes (mp) (Benz & Boxshall, 2017; Dippenaar, 2018). Neck (Fig. 1b) heavily sclerotized, elongated and cylindrical, with small knobs on surface; anteriorly bearing holdfast organ (Fig. 1b) with four processes extending outwards; each process with or without short outgrowths. Trunk (Fig. 1b) sub-circular, dorsal and ventral side with 2 rows of 3–4 depressions; well-defined abdomen posteriorly (Fig. 1b). Posterior processes (Fig. 1b) attached lateral to perianal swelling, comprising of short peduncle, bearing numerous (more than 30) elongate, straight stalks extending posteriorly. Egg sacs (Fig. 1b) long, eggs multi-seriate.

Cephalic appendages situated on the anterior surface (Fig. 2a), with circular groove (cg) (Fig. 2a) separating cephalic region from rest of cephalothorax. Antennule (a_1) (Fig. 2b) anterodorsal to antenna (a_2) (Fig. 2a), digitiform with blunt tip. Antenna (a_2) (Fig. 2c) with three small apical tubercles of different sizes (one curved, large tubercle, with two smaller setae). Mandible not observed. Labrum (Fig. 2d, e) with very small blunt tubercle and two small openings distally (Fig. 2e). Maxilla represented by large, bulbous maxillary process (mp) (Fig. 2a) with maxillary gland pore (mgp) (Fig. 2a). Maxilliped (mxp) (Fig. 2f) posterolateral to maxillary processes (Fig. 2a), subchelate, corpus robust, myxa raised; small spine below base of subchela, subchela indistinctly subdivided into shaft and claw, sharply curved with elongated pointed tip.

Immature male [Based on one specimen.] Body length from tip of cephalothorax (including mouth tube) to tip of posterior end about 0.633 mm. Cephalothorax (Fig. 3a) more than half of total length, about half of total length in adult male (Fig. 3b). Trunk (Fig. 3a) segmented, with caudal rami (Fig. 3j) posteriorly.

Antennule (Fig. 3c) 3-segmented; first segment with distomedial whip; second with distal solus and last segment with 6 long setae on apex (nr 4 aesthetasc) (see lernaeopodid males in Kabata (1979)). Antenna (Fig. 3d) 4-segmented, exopod shorter than endopod, 1-segmented, bulbous, equipped with a long spine-like papilla apically, endopod 2-segmented, basal segment with few denticles anterolaterally, distal segment with strong hook 1, thin long spine 2, and seta 5 emerging from swelling 4 covered with denticles (according to Kabata (1979)). Mouth tube with labrum and labium fringed by denticles (Fig. 3e). Mandible (Fig. 3f) with

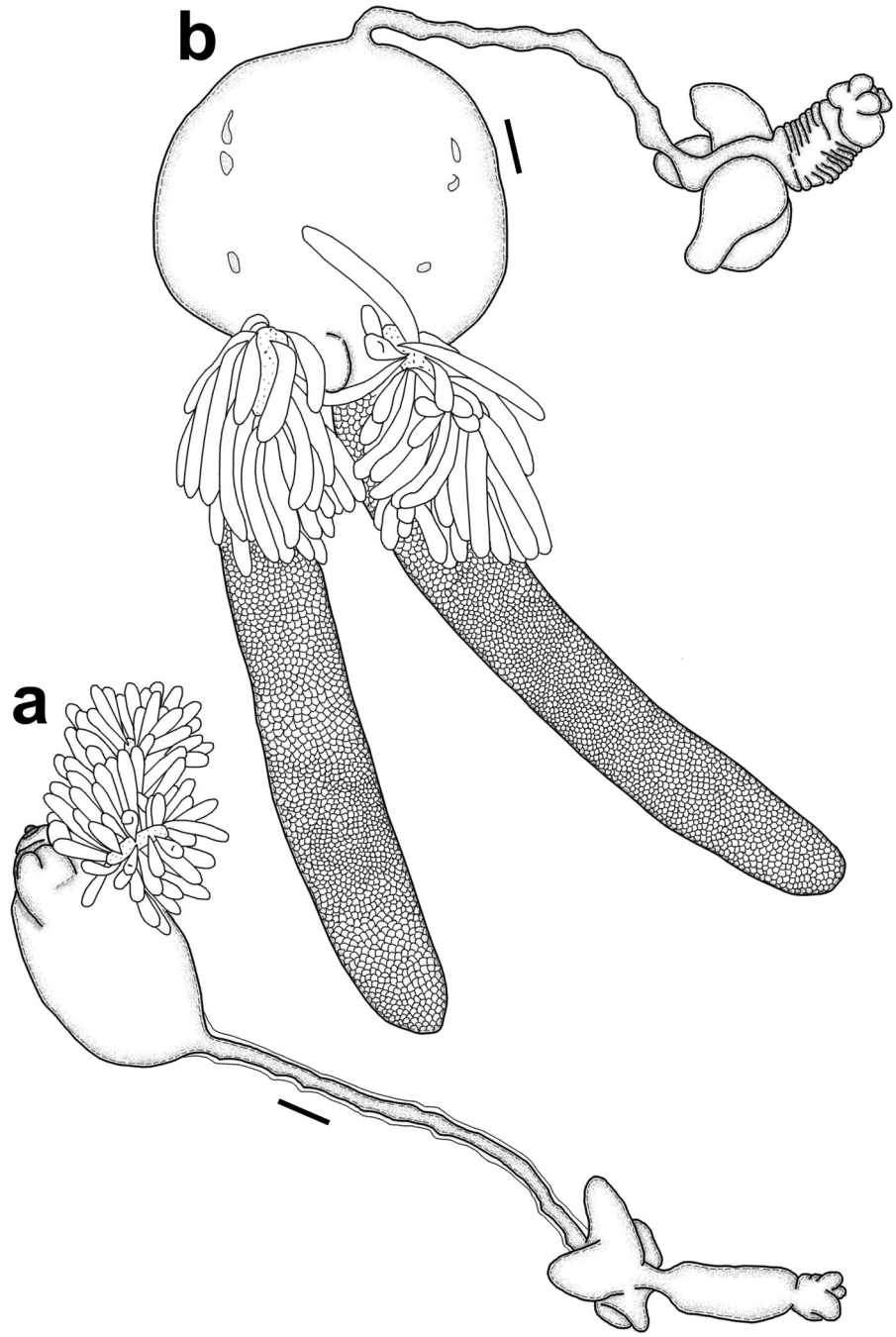

Fig. 1 *Lophoura tetraloba* Ho & Kim I.H., 1989, female. a. immature female, general habitus, trunk ventral view, cephalothorax lateral view; b. post metamorphic female, general habitus, trunk dorsal view, cephalothorax ventral view. Scale bars: a, b = 1 mm

5 equally sized teeth. Maxillule (Fig. 3i) endite armed with two long truncated apical setae; palp blunt bulbous process at base of endite. Maxilla (Fig. 3g) broad, subchelate, robust corpus with protuberance armed with two small spines medially; myxa raised, accommodating tip of claw; subchela indistinctly separated from claw, tip sharply curved. Maxilliped (Fig. 3h) subchelate, corpus with myxal area bearing 3 processes, middle process divided into three small variable projections; subchela short and broad with

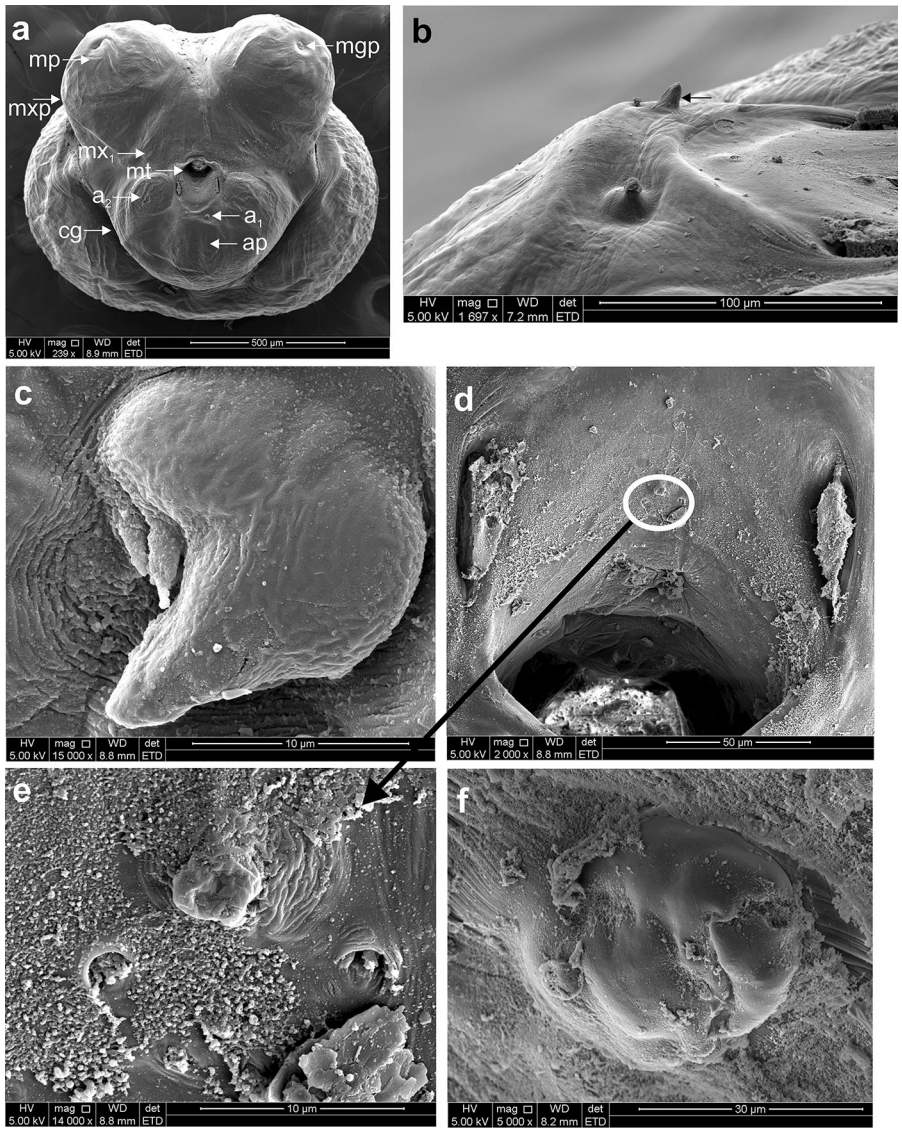

Fig. 2 *Lophoura tetraloba* Ho & Kim I.H., 1989, post metamorphic female. Scanning electron micrographs: a. cephalothorax, cephalic region, anterior view; b. antennules (arrowed); c. antenna; d. mouth tube. e. labium tubercle and pores; f. maxilliped. (ap – antennary process, a_1 – antennule, a_2 – antenna, mt – mouth tube, mx_1 – maxillule, mp – maxillary process, mgp – maxillary gland pore, mxp – maxilliped; cg – circular groove).

small seta and raised tubercle near base of claw; claw short, broad with short seta apically. Caudal rami (Fig. 3j) paired, each with a digitiform process with an enlarged tip and an elongated spiniform seta.

Remarks

The studied specimens belong to *Lophoura* species with four processes on the holdfast organ of the post metamorphic females. These include *L. tetraphylla* Ho, 1985; *L. brevicollum* Gomez, Deets, Kalman & Morales-Serna, 2010; *L. edwardsi*; *L. cornuta* and *L. tetraloba*. *Lophoura tetraloba* differs from *L. tetraphylla* [see Fig. 5 in Ho (1985)] by possession of a holdfast organ with four slender processes, with or without tubercles, a neck longer than trunk and posterior processes with straight stalks (see Fig. 1b) whereas *L. tetraphylla* possesses a holdfast organ with four, large, inflated processes with tubercles, a neck shorter or sometimes equal to the trunk length and

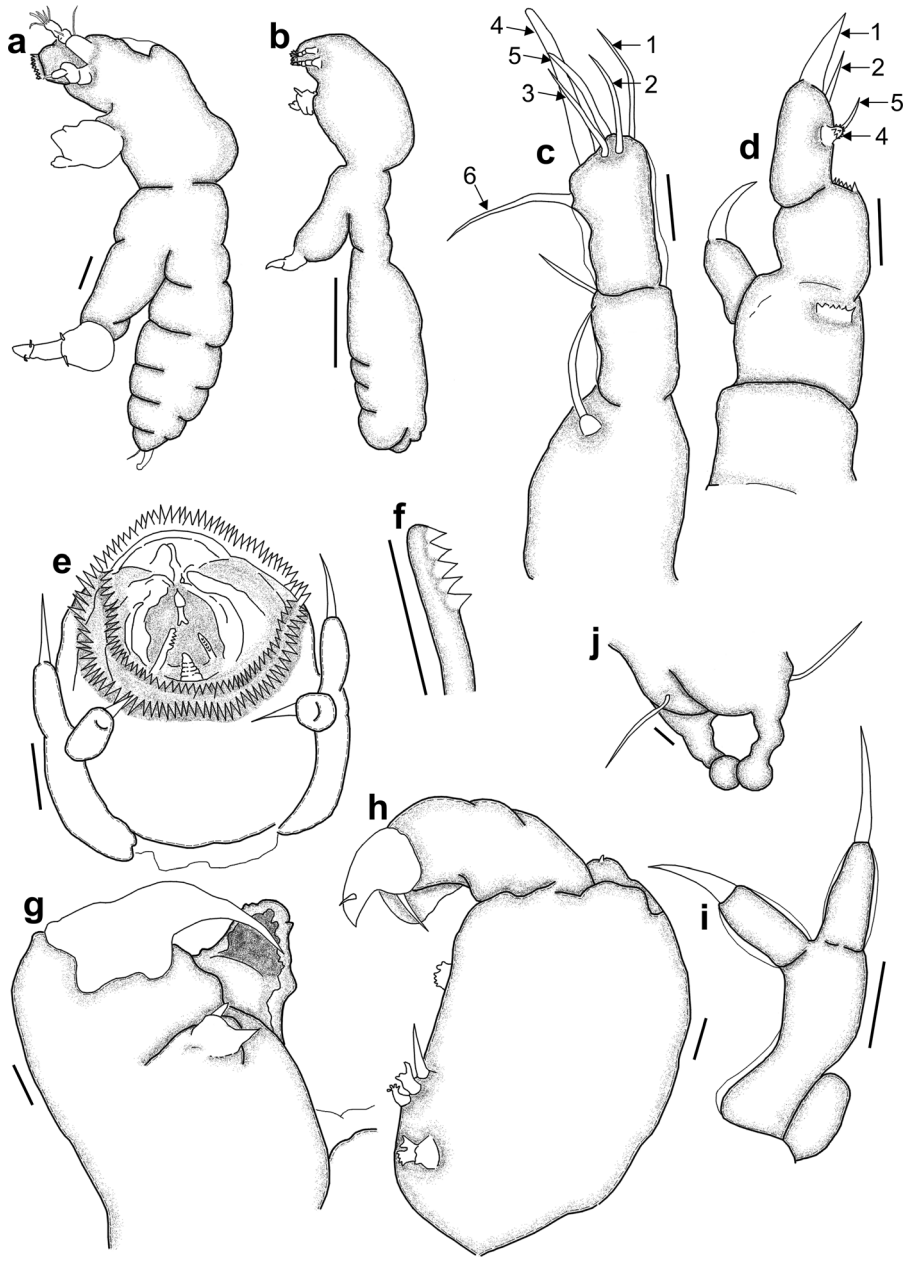

Fig. 3 *Lophoura tetraloba* Ho & Kim I.H., 1989, male. a. immature male, general habitus, lateral view; b. mature male, general habitus, lateral view. Immature male. c. antennule; d. antenna; e. mouth tube; f. mandible; g. maxilla; h. maxilliped; i. maxillule; j. caudal rami, ventrolateral view. Scale bars: a = 50 μm; b = 1 mm; c-e = 10 μm; f = 5 μm; g-j = 10 μm.

posterior processes with slightly curved stalks. Additionally, no similarities are found between the appendages of *L. tetraloba* (illustrated in this study) and those of *L. tetraphylla* described by Hogans (1986). *Lophoura tetraloba* differs from *L. brevicollum* [see Figs 1-6 in Gómez et al., (2010)] by possessing a regularly shaped holdfast organ and unbranched stalks of the posterior processes whereas *L. brevicollum* possesses an irregularly shaped holdfast organ, each process with multiple outgrowths, posterior processes with multiple stalks branched up to tertiary stalks. *Lophoura tetraloba* differs from

L. cornuta [see Fig. 46 in Wilson (1919)] by possession of a holdfast organ with four slender processes with or without tubercles, a neck longer than the trunk while *L. cornuta* [see Fig. 46 in Wilson (1919)] possesses a holdfast organ with the four processes each dividing immediately into variable, long, slender branches, irregularly shaped and a neck shorter than the trunk [see Fig. 9A in Boxshall (1989)]. The antennules of both *L. tetraloba* (see Fig. 2b) and *L. cornuta* [see Fig. 9C in Boxshall (1989)] are small tubercles but with no distal armature observed in *L. tetraloba*. The morphology of the antennae also seems similar but with *L. tetraloba* possessing two short setae (see Fig. 2c) rather than three as in *L. cornuta* [see Fig. 9C in Boxshall (1989)]. The maxillipeds of both species are very similar [see Fig. 2f and Fig. 9D in Boxshall (1989)]. *Lophoura tetraloba* differs from *L. edwardsi* [see Fig. 1451 in Kabata (1979)] by the possession of a neck which is clearly longer than the trunk while that of *L. edwardsi* is almost as long as the trunk, although the holdfast organ [see Figs 1451, 1452 in Kabata (1979)] resembles that of *L. tetraloba*. *Lophoura tetraloba* was reported from *Nezumia condylura* Jordan & Gilbert off Japan (Ho & Kim, 1989).

The morphology of the described mature *Lophoura* males of *L. bouvieri* (Quidor, 1912) [see fig. 41 in Wilson (1919)], *L. cornuta* [see figs 47, 48 in Wilson (1919)], *L. caparti* [see Fig. 6F in Nuñes-Ruivo (1962)], *L. tetraloba* (see Fig. 3b) and *L. ventricula* Ho & Kim I.H., 1989 [see Fig. 5A in Ho & Kim (1989)] is slightly different from theimmature *L. tetraloba* male studied (Fig. 3a). The observed differences include an enlarged, less segmented trunk, inflated posteriorly in the mature males [e.g. *L. bouvieri* (see fig. 41 in Wilson (1919)], *L. cornuta* [see figs 47, 48 in Wilson (1919)], *L. caparti* [see Fig. 6F in Nuñes-Ruivo (1962)], *L. tetraloba* (see Fig. 3b) and *L. ventricula* [see Fig. 5A in Ho & Kim (1989)] whereas the immature possesses a shorter trunk with distinct segmentation in *L. tetraloba* (see Fig. 3a). Mature males possess paired reduced caudal rami but the digitiform processes, seen in the immature *L. tetraloba* (see Fig. 3j), were not observed (e.g. *L. bouvieri* [see fig. 41 in Wilson (1919)], *L. cornuta* [see figs 47, 48 in Wilson (1919)], *L. caparti* [see Fig. 6F in Nuñes-Ruivo (1962)], *L. tetraloba* (see Fig. 3b) and *L. ventricula* [see Fig. 5A in Ho & Kim (1989)]. Maxillipeds in the mature males are less than half of the trunk length (e.g. *L. bouvieri* [see fig. 41 in Wilson (1919)], *L. cornuta* [see figs 47, 48 in Wilson (1919)], *L. caparti* [see Fig. 6F in Nuñes-Ruivo (1962)], *L. tetraloba* (see Fig. 3b) and *L. ventricula* [see Fig. 5A in Ho & Kim (1989)]), while in the immature (see Fig. 3a) they are almost the same length as the trunk. Thus, it seems there is a certain degree of body modification in maturing *Lophoura* males.

The distal segments of the antennules of *L. tetraloba* (Fig. 3c) and *L. cornuta* [see fig. 49 in Wilson (1919)] are armed with six setae, those of *L. bouvieri* [see fig 39 in Wilson (1919)] and *L. ventricula* [see Fig. 5F in Ho & Kim (1989)] with four setae while *L. caparti* [see Fig. 6g in Nuñes-Ruivo (1962)] has three. The mandible of *L. tetraloba* (Fig. 3f) has 5 teeth while that of *L. ventricula* [see Fig. 5H in Ho & Kim (1989)] has about 7–8 equally sized teeth. The maxillule endite is armed with 2 truncated setae in *L. tetraloba* (Fig. 3g), *L. caparti* [see Fig. 6g in Nuñes-Ruivo (1962)] and *L. ventricula* [see Fig. 5I in Ho & Kim (1989)] and has a bulbous palp at the base of the endite of *L. tetraloba* (Fig. 3g) which was not observed in the other species. The maxilla of *L. tetraloba* (Fig. 3h) has a raised tubercle on the corpus which is absent in *L. ventricula* [see Fig. 5J in Ho & Kim (1989)]. The maxillipeds of *L. tetraloba* (Fig. 3i), *L. bouvieri* [see fig. 40 in Wilson (1919)] and *L. cornuta* [see fig. 53 in Wilson (1919)] are mostly similar.

Lophoura cf. edwardsi Kölliker, 1853

Host: *Coelorinchus fasciatus* (Günther) (Gadiformes: Macrouridae).

Locality: Off the west coast (Atlantic Ocean), South Africa.

Material examined: 4♀♀ (2 post metamorphic and 2 immature).

Material collected: 6♀♀ from *C. fasciatus* and 2♀♀ from *Lucigadus ori*; all specimens collected off the west coast (Atlantic Ocean), South Africa.

Voucher material: 2♀♀ (SAMC-A095126) deposited in the Iziko South African Museum, Cape Town, South Africa.

Description (Figs 4, 5)

Immature female [Based on two specimens.] Body length from tip of cephalothorax to tip of abdomen 21.9 mm (21–22.8 mm), cephalothorax length 5.6 mm

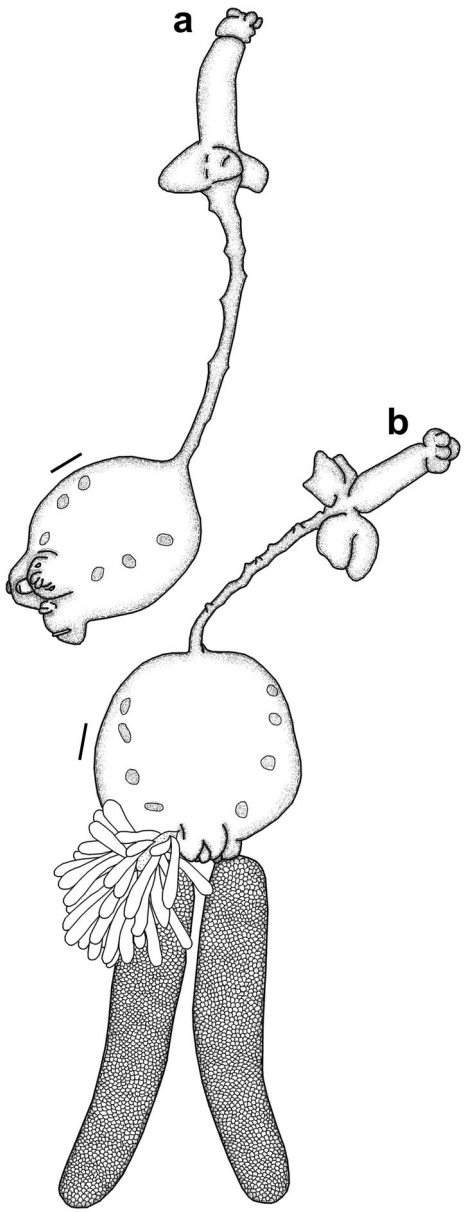

Fig. 4 *Lophoura* cf. *edwardsi* Kölliker, 1853. a. immature female. general habitus, trunk ventral view, cephalothorax lateral view; b. post metamorphic female, general habitus, trunk dorsal view, cephalothorax ventral view. Scale bars: a, b = 1 mm.

(5.2–5.9 mm), width 1.2 mm (1.1–1.3 mm); holdfast organ width 2.6 mm (1.8–3.4 mm); neck length 10.7 mm (8.8–12.5 mm), width 0.5 mm (0.4–0.6 mm); trunk length 5.8 mm (5.2–6.3 mm), width 3.9 mm (2.9–4.9 mm); posterior processes not observed.

Cephalothorax (Fig. 4a) smooth, longitudinally elongated. Neck (Fig. 4a) elongated and cylindrical, with short knobs on the surface; anterior part bearing holdfast organ with four short processes without outgrowths, extending laterally. Trunk (Fig. 4a), longer than wide, dorsal and ventral side with 2 rows of 3 depressions, posteriorly with abdomen. Posterior processes not observed.

Post metamorphic female [Based on two specimens.] Body length from tip of cephalothorax to tip of abdomen 25 mm (19.5–30.4 mm), cephalothorax length 6.3 mm (6.0–6.6 mm), width 1.1 mm (1.0–1.2 mm); holdfast organ width 4 mm (3.8–4.2 mm); neck length 8.1 mm (6.7–9.4 mm), width 0.4 mm; trunk length 6.9 mm (6.7–7 mm), width 7.1 mm (6.7–7.4 mm); posterior process length 4.9 mm (4.6–5.1 mm); egg-sac length 14 mm (11.2–16.8 mm), width 2.1 mm (2.0–2.2 mm).

Cephalothorax (Fig. 4b) smooth, longitudinally elongated; anterior surface (Figs 4b, 5a) with enlarged processes anteriorly, i.e., antennary (ap, Fig. 5a) and maxillary (mp, Fig. 5a) processes. Neck (Fig. 4b) elongated, cylindrical, with short knobs on surface; anterior part bearing holdfast organ with four short, blunt processes extending laterally. Trunk (Fig. 4b) sub-circular, dorsal and ventral side with 2 rows of 3–4 depressions; with well-defined abdomen (Fig. 4b) posteriorly. Posterior processes (Fig. 4b) attached to perianal swelling, with short porous peduncle, bearing numerous (more than 30) stalks. Egg sacs (Fig. 4b) long, eggs multi-seriate.

Cephalic appendages on anterior surface, with circular groove (cg) separating cephalic region from posterior part (Fig. 5a). Antennule (a_1) and antenna (a_2) mostly similar to *L. tetraloba*. Mandible not observed. Maxilla, represented by large bulbous maxillary processes (mp) (Fig. 5a) with maxillary gland pores (mgp) (Fig. 5a). Maxilliped (mxp) (Fig. 5b) posterolateral to maxillary processes (Fig. 5a), corpus broad, myxa curved, small spine at base of subchela; subchela not distinctly subdivided into shaft and claw, claw sharply curved with pointed tip.

Remarks

The studied specimens resemble both *L. edwardsi* and *L. tetraloba* but differ slightly from *L. tetraloba* (Ho & Kim, 1989) by possessing a relatively shorter neck

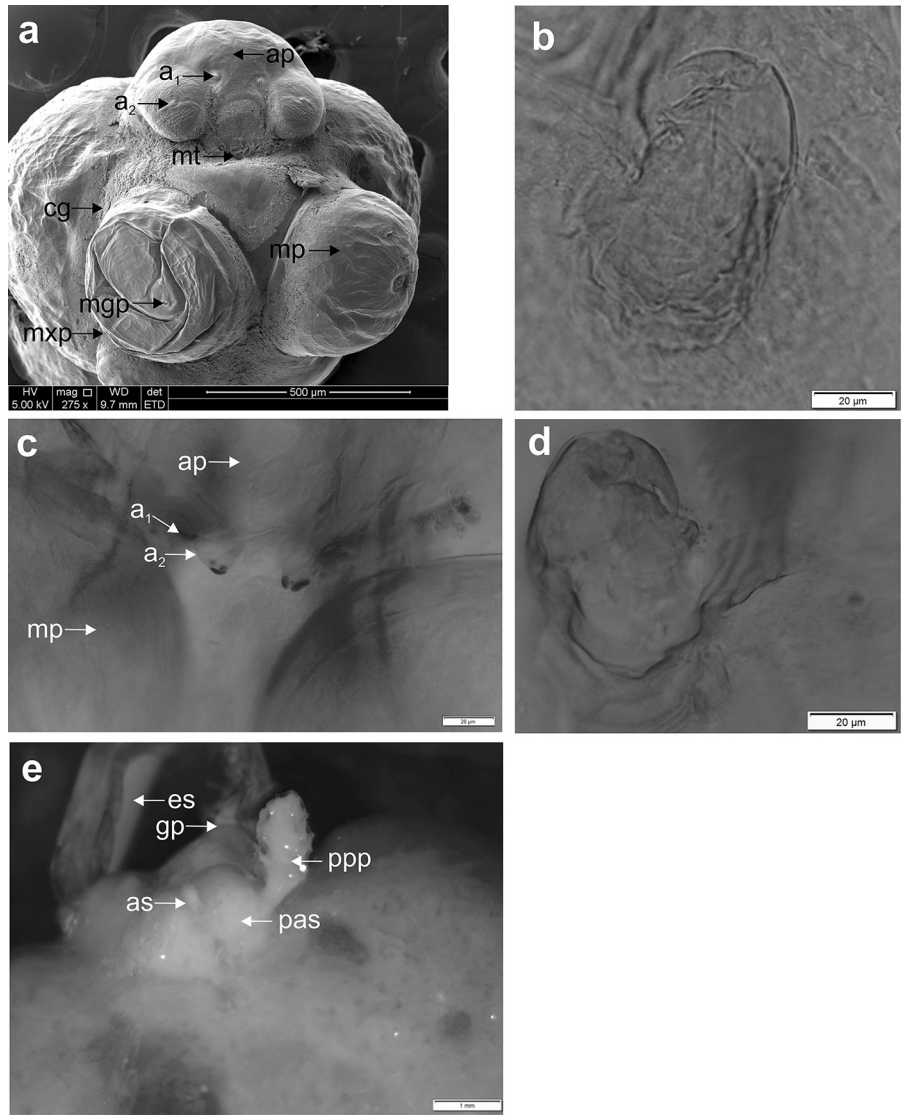

Fig. 5 *Lophoura* cf. *edwardsi* Kölliker, 1853. a. post metamorphic female, cephalothorax anterior view, scanning electron micrograph; b. maxilliped, photograph. *Lophoura caparti* (Nuñes-Ruivo, 1962), post metamorphic female, photographs. c. cephalic region, anterior view; d maxilliped. *Lophoura* sp., photograph. e. abdomen, dorsal view. (ap – antennary process, a_1 – antennule, a_2 – antenna, mt – mouth tube, mp – maxillary process, mgp – maxillary gland pore, mxp – maxilliped; cg – circular groove, es – egg sac, gp – genital pore, ppp – posterior process peduncle, as – anal slit, pas – perianal swelling).

(mean length 8.1 mm vs 12.3 mm in *L. tetraloba*) as well as short, blunt processes of the holdfast organ (with few or no outgrowths) (cf. Figs 1b and 4b) which is why it is referred to as *L.* cf. *edwardsi*. According to descriptions and illustrations of *L. edwardsi* [Candeias (1952) and Kabata (1979)] this species is characterised by a holdfast organ with four rounded or irregular processes, with or without outgrowths [see Fig. 2 in Candeias (1952) and Fig. 1451 in Kabata (1979)]; sub-circular to sub-quadrangular trunk, with 2 rows of 4–7 depressions on the dorsal side [see Figs 1451, 1456 in Kabata (1979)]; and posterior processes with 16–18 stalks [according to Fig. 1451 in Kabata (1979)] and 44 stalks [according to Fig. 1 in Candeias (1952)] on each peduncle. However, this is similar to the features of *L. tetraloba* e.g. a holdfast organ with four processes, with or without outgrowths [see Fig. 1b and Figs 6B, C in Ho & Kim (1989)], a sub-circular to

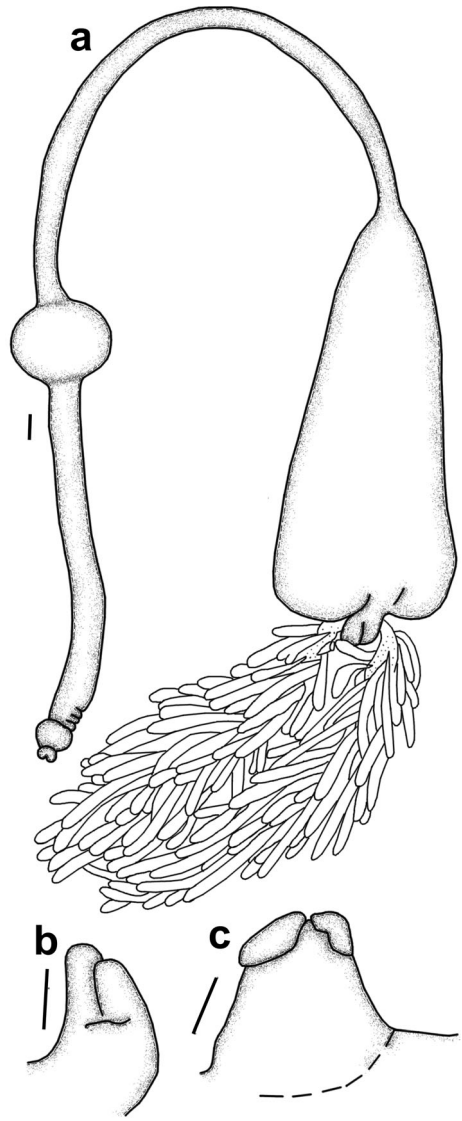

Fig. 6 *Lophoura caparti* (Nuñes-Ruivo, 1962), post metamorphic female. a. general habitus, trunk dorsal view, cephalothorax ventral view; b. antennule; c. antenna. Scale bars: a = 1 mm; b, c = 10 µm.

sub-quadrangular trunk, with 2 rows of 3–5 depressions on the dorsal and ventral side [see Fig. 1b and Figs 6A, D in Ho & Kim (1989)]; and posterior processes with stalks (more than 30) on each peduncle [see Fig. 1b and Figs 6A, D in Ho & Kim (1989)]. Currently the identity of the studied species could not be confirmed based on the descriptions of *L. edwardsi*.

The morphology of the post metamorphic females of *L. edwardsi* (see Kabata, 1979) and *L. tetraloba* (see Ho & Kim, 1989) are very similar according to the illustrations and descriptions as well as in the currently examined species identified as *L. tetraloba* (see Figs 1, 2) and *Lophoura* cf. *edwardsi* (Figs 4, 5a, b). Apparently, Ho & Kim (1989) described *L. tetraloba* as a new species without considering previous descriptions of *L. edwardsi* since no mention was made of *L. edwardsi* and thus no comparisons was done. Thus, it is possible that *L. edwardsi* and *L. tetraloba* are synonyms. This is supported by their reported characteristic features that are applicable to both *L. edwardsi* and *L. tetraloba*. *Lophoura edwardsi* and *L. tetraloba* are apparently distinguished based on the length of the neck with *L. edwardsi* having a shorter neck (Kabata, 1979), which is slightly longer or as long as the trunk and *L. tetraloba* with a neck which is clearly longer than the trunk (Ho & Kim, 1989). However, neck length varies considerably amongst the collected specimens examined. Additionally, the difference in neck lengths may be due to the attachment site of the specimen on its host, e.g., attachment to host musculature may require a shorter neck than attachment near the visceral cavity. According to Ho & Kim (1989), *L. tetraloba* is the only *Lophoura* species to penetrate the host's liver although Kabata (1979) mentioned that *L. edwardsi* attaches near the visceral cavity which is close to the liver. Furthermore, neck length may be related to the age of the specimen and whether the final attachment site has been reached. Thus, more specimens are needed in order to determine the validity of *L. edwardsi* and to highlight morphological differences (if any) between *L. edwardsi* and *L. tetraloba*.

Lophoura tetraloba has only been reported once, from *Nezumia condylura*, whereas *L. edwardsi* has been reported multiple times from *Coelorinchus caelorinchus* (Risso) and *Macrourus* sp. (only once). In this study both *Lophoura* cf. *edwardsi* and *L. tetraloba* were collected from *L. ori* and *C. fasciatus*. Regarding the preferred habitat and host species of *L. tetraloba* and *L. edwardsi*, the host species, *C. fasciatus* and *L. ori*, share a similar vertical distribution as *C. caelorinchus* while *N. condylura* inhabits shallower waters (Froese & Pauly, 2022).

Lophoura caparti (Nuñes-Ruivo, 1962)

Host: *Epigonus denticulatus* Dieuzeide (Acropomatiformes: Epigonidae).

Locality: Off the west coast (Atlantic Ocean), South Africa.

Material examined: 3♀♀ from three host specimens.
Material collected: 4♀♀ from *E. denticulatus* hosts collected off the west coast (Atlantic Ocean), South Africa; 1♀ from *Epigonus telescopus* (Risso) collected off the east coast (Indian Ocean), South Africa.
Voucher material: 1♀ (SAMC-A095127) deposited in the Iziko South African Museum, Cape Town, South Africa.

Re-description (Figs 5, 6)

Post metamorphic female [Based on three specimens.] Body length from tip of cephalothorax to tip of abdomen 58.7 mm (57.1–60.8 mm), cephalothorax length 14.3 mm (11.2–16.8 mm), width 1.6 mm (1.3–2.0 mm); holdfast organ length 2.6 mm (2.2–2.8 mm), width 4.1 mm (3.9–4.2 mm); neck length 28.3 mm (28.0–28.6 mm), width 0.9 mm (0.8–1.0 mm); trunk length 16.8 mm (15.4–17.9 mm), width 8.1 mm (6.3–9.2 mm); abdomen length 1.3 mm (1.3 mm), width 1.4 mm (1.3–1.4 mm); posterior process length 17.3 mm (15.8–18.5 mm), width 8.7 mm (7.0–9.8 mm); egg-sac width 2 mm.

Cephalothorax (Fig. 6a) smooth, longitudinally elongated; anterior surface with enlarged processes i.e. antennary processes (ap) and maxillary processes (mp) (Fig. 5c); circular groove separating the anterior part of cephalothorax from elongated posterior part. Neck (Fig. 6a) elongated, smooth; anterior part bearing bulbous, rounded holdfast organ (Fig. 6a). Trunk (Fig. 6a) elongated, pyriform, longer than wide with a well-defined abdomen (Fig. 6a). Posterior processes (Fig. 6a) lateral to perianal swelling, consisting of elongated porous peduncle, bearing numerous straight stalks (sometimes diverging into secondary stalks) extending posteriorly, resembling "bananas on a tree".

Cephalic appendages on anterior surface (Fig. 5c). Antennary processes raised, accommodating antennules and antennae. Antennule (Fig. 6b) bifid tubercle, dorsolateral to antennae. Antenna (Fig. 6c) anteromedial to maxillary processes (see Fig. 5c), with two apical tubercles. Maxillule not observed. Maxilla represented by large, bulbous maxillary processes (mp) (Fig. 5c). Maxilliped (Fig. 5d) posterior to maxillary processes, subchelate, corpus broad, myxa raised; subchela not distinctly subdivided into shaft and claw, claw sharply curved with pointed tip.

Remarks

The studied specimens belong to the *Lophoura* species with post metamorphic females that have simple holdfast organs, bearing bulbous processes including *L. caparti*, *L. unilobulata* Castro & Gonzalez, 2009 and *L. bouvieri*. *Lophoura caparti* (see Fig. 6a) possesses a holdfast organ consisting of one bulbous process, *L. unilobulata* [Figs 22-25 in Castro-Romero & Gonzalez (2009)] possesses a holdfast organ with two large, bulbous processes while *L. bouvieri* possesses three large, bulbous processes on the holdfast organ [see Figs 34, 35 in Wilson (1919)]. Posterior processes of *L. caparti* (Fig. 6a) and *L. unilobulata* [Fig. 22 in Castro-Romero & Gonzalez (2009)] bear elongated porous peduncles with multiple stalks while those of *L. bouvieri* [see Fig. 34 in Wilson (1919)] possess short porous peduncles with short stalks. *Lophoura caparti* (Fig. 6a) lacks longitudinal rows of depressions on the trunk while *L. unilobulata* [Fig. 22 in Castro-Romero & Gonzalez (2009)] and *L. bouvieri* [see Fig. 34 in Wilson (1919)] possess longitudinal rows of depressions on the trunk. The studied specimens (see Fig. 6a) have shorter stalks of the posterior processes than those illustrated by Nuñes-Ruivo (1962). Additionally, the antennules, antennae, maxillae and maxillipeds are described. *Lophoura caparti* was reported from *E. telescopus* off Angola (Nuñes-Ruivo, 1962).

Lophoura cornuta (Wilson C.B., 1919)
Host: *Bassanago albescens* (Barnard) (Anguilliformes: Congridae).
Locality: Off the south coast, South Africa.
Material examined: 1♀
Material collected: 1♀ from *B. albescens* collected off the south coast, South Africa.
Voucher material: 1♀ (SAMC-A095128) deposited in the Iziko South African Museum, Cape Town, South Africa.

Re-description (Fig. 7)

Post metamorphic female [Based on one specimen.] Body length from tip of cephalothorax to tip of abdomen 28.4 mm, cephalothorax length 8.4 mm, width 1.5 mm; holdfast organ length 5.6 mm, width 5.6 mm; neck length 9.8 mm, width 1.1 mm; trunk length 10.2 mm, width 7 mm; abdomen length 1.3 mm,

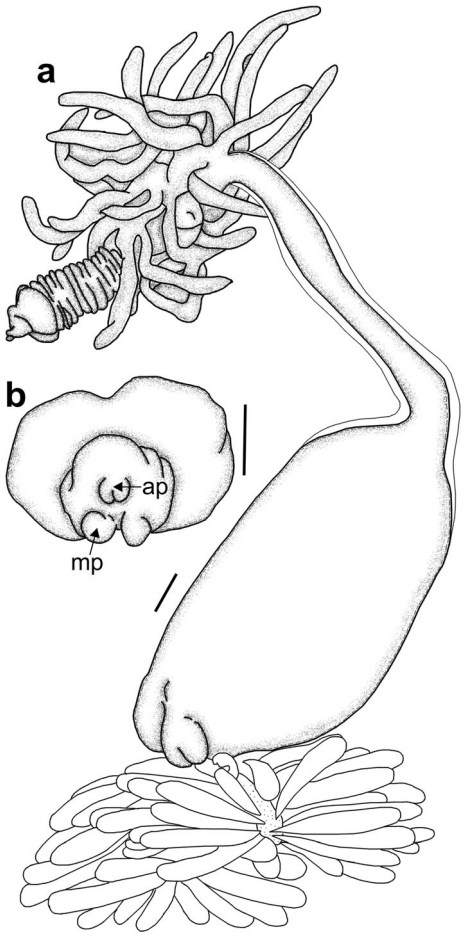

Fig. 7 *Lophoura cornuta* (Wilson C.B., 1919), post metamorphic female. a. general habitus, trunk ventrolateral view, cephalothorax lateral view; b. cephalothorax, anterior view. Scale bars: a = 1 mm; b = 500 µm. (ap – antennary process, mp – maxillary process).

width 1.4 mm; posterior processes length 5.6 mm, width 9.8 mm.

Cephalothorax (Fig. 7a) longitudinally elongated, transversely wrinkled, anterior surface (Fig. 7b) with two pairs of enlarged processes, i.e. antennary (ap) and maxillary (mp) processes. Neck (Fig. 7a) cylindrical; anteriorly with irregularly shaped holdfast organ with four main processes, immediately dividing into numerous elongated thin strips (Fig. 7a). Trunk (Fig. 7a) sub-quadrangular, longer than wide, dorsally and ventrally with 2 rows of 4 depressions; posterior with abdomen. Posterior processes (Fig. 7a) lateral to perianal swelling, each comprising a short peduncle bearing numerous straight stalks extending posteriorly. Appendages not examined.

Remarks

Lophoura cornuta bears a close resemblance to *L. cardusa* (Leigh-Sharpe, 1934). However, *L. cornuta* (Fig. 7a) differs from *L. cardusa* [see Fig. 1 in Ho & Kim (1989)] by possession of a holdfast that consists of four main processes dividing immediately into tentacle-like strips/outgrowths (Fig. 7a) while *L. cardusa* has an irregularly shaped holdfast organ, formed by tentacle-like structures which are not organized into main processes [see Fig. 1 in Ho & Kim (1989)]. The current re-description and illustration of *L. cornuta* differs from both Wilson (1919) and Boxshall (1989) regarding the structure and total size of the posterior processes which are less than the length of the trunk and with stalks extending laterally on peduncles (see Fig. 7a) while illustrations by Wilson (1919) and Boxshall (1989) have posterior processes longer or as long as the trunk with stalks extending mostly posteriorly on peduncles [see Fig. 46 in Wilson (1919) and Fig. 9A in Boxshall (1989)]. *Lophoura cornuta* was reported from *Synaphobranchus brevidorsalis* Günther off New Caledonia (Boxshall, 1989) and from *Synaphobranchus affinis* Günther off Japan (Wilson, 1919), both of which belong to Anguilliformes, whereas *L. cardusa* was reported from *Hymenocephalus striatissimus* Jordan & Gilbert (Gadiformes: Macrouridae) off Japan (Ho & Kim, 1989).

Lophoura sp.

Host: *Nezumia umbracincta* Iwamoto & Anderson (Gadiformes: Macrouridae).

Locality: Off the west coast (Atlantic Ocean), South Africa.

Material examined: 1♀ (broken) from one host specimen.

Material collected: 1♀ (broken) from *N. umbracincta* collected off the west coast (Atlantic Ocean), South Africa.

Description (Figs 5, 8)

Post metamorphic female [Based on one specimen.] Body length from tip of cephalothorax to tip of abdomen unknown, cephalothorax length 5.6 mm, width 1.4 mm; holdfast organ length 1.4 mm, width 6.3 mm; trunk length 11.5 mm, width 11.9 mm; abdomen length 1.7 mm, width 1.7 mm; posterior process length 16.8 mm.

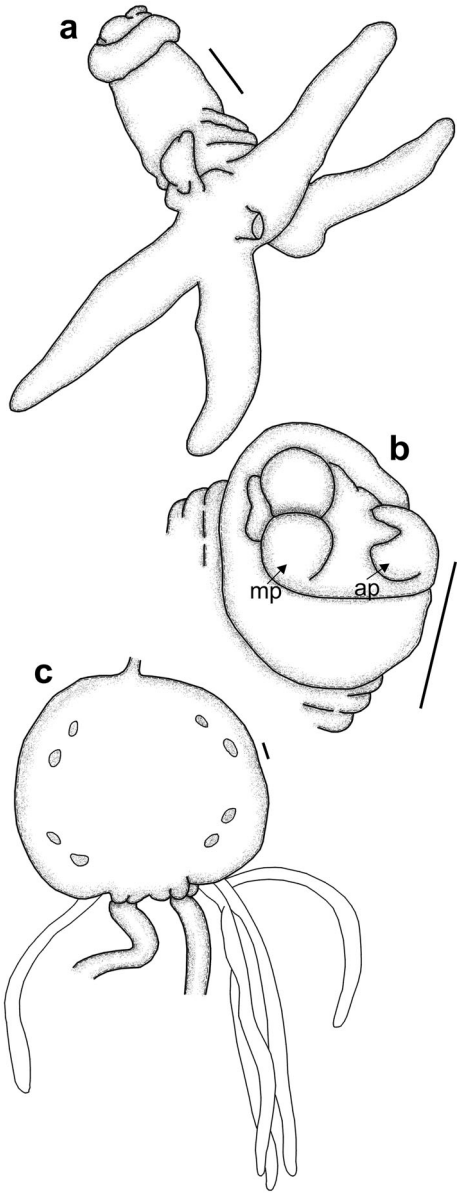

Fig. 8 *Lophoura* sp., post metamorphic female. a. cephalothorax and holdfast organ, posterolateral view; b. cephalothorax, anterolateral view; c. trunk, ventral view. Scale bars: a-c = 1 mm. (mp – maxillary process, ap – antennary process).

Cephalothorax (Fig. 8a) longitudinally elongated, anterior surface (Fig. 8b) with two pairs of enlarged processes i.e. antennary (ap) and maxillary (mp) processes; cephalic part separated from posterior part by circular groove. Neck heavily sclerotized, cylindrical, with small knobs; anterior part bearing holdfast organ with five elongated processes (Fig. 8a) extending laterally. Trunk (Fig. 8c) circular, slightly wider than long, dorsally with 2 rows of 5 depressions, ventrally with 2 rows of 4 depressions; abdomen (Figs 8c, 5e) terminal. Posterior processes (Fig. 8c) lateral to perianal swelling with anal slit medially, consisting of short porous peduncle (ppp) bearing long, elongated straight stalks, extending posteriorly, longer than trunk. Egg sacs (es) (Fig. 5e) extending from genital pore (gp). Appendages not examined.

Remarks

The studied specimen has five processes on the holdfast organ. There are only two known species with five processes, i.e., *L. pentaloba* Ho, 1985 and *L. ventricula* Ho & Kim I.H., 1989. The studied *Lophoura* sp. differs from *L. pentaloba* and *L. ventricula* by possession of a circular trunk with posterior processes extending posteriorly and a short peduncle bearing elongated, straight stalks whereas both *L. ventricula* [see Fig. 4 in Ho & Kim (1989)] and *L. pentaloba* [see Fig. 2 in Ho & Kim (1989)] possess pyriform trunks and posterior processes extending anteriorly, with well curved stalks which intertwine across the trunk's dorsal surface. Additionally, *Lophoura* sp. possesses a holdfast organ with five slender processes, without outgrowths while *L. ventricula* possesses a holdfast organ with five long tentacle-like processes [see Figs 4A-F in Ho & Kim (1989)] and *L. pentaloba* [see Fig. 2 in Ho & Kim (1989)] possesses a holdfast organ with five short processes with outgrowths. *Lophoura* sp., *L. pentaloba* and *L. ventricula* have only been reported from macrourid host species (i.e. *Lophoura* sp. was collected from *Nezumia umbracincta*, *L. pentaloba* was reported from *Coryphaenoides armatus* (Hector), *Coryphaenoides filifer* (Gilbert) and *Nezumia bairdii* (Goode & Bean) (Ho & Kim, 1989) while *L. ventricula* was reported from *Coryphaenoides nasutus* Günther (Ho & Kim, 1989)) with overlapping vertical distributions according to Froese & Pauly (2022).

Discussion

Although there are multiple variations in the habitus amongst post metamorphic females of *Lophoura* species, the shape, size and number of processes on the holdfast organ are the primary features used to

differentiate these species. Additionally, the shape and branching of the posterior processes also distinguish species. Other features such as the relative neck and trunk lengths and trunk shape seem to vary amongst individuals of the same species. The cephalothorax of *Lophoura* species is soft and not sclerotized, thus its shape may change due to increased pressure. From previous reports of *Lophoura* species, some were described with transversely wrinkled cephalothoraces, including *L. tetraloba* [see Fig. 7D in Ho & Kim (1989)]. However, some of the examined *L. tetraloba* specimens have smooth cephalothoraces [Fig. 1a and also Fig. 7C in Ho & Kim (1989)], while others have transversely wrinkled cephalothoraces (Fig. 1b). Maybe wrinkling occurs as the specimen ages with all cephalothoraces initially being smooth but then wrinkle and shrink once subjected to pressure (pressure from host musculature, since all species are mesoparasites) which may also depend on the attachment and feeding site of the species on the host. Additionally, the occurrence of these species on deep-water hosts (Ho & Kim, 1989) (depth ranges of host species according to Froese & Pauly (2022) are 73–1700 m) may also have an influence on their morphological and physiological adaptations (Gómez et al., 2010). However, more studies are needed to confirm these possible effects.

Of the 19 accepted *Lophoura* species, scanty illustrated descriptions of the female appendages exist only for *L. cornuta* (see Boxshall, 1989), *L. gracilis* (see Hogans & Dadswell, 1985) and *L. tetraphylla* (see Hogans, 1986). This is probably due to the difficulty to observe and dissect these small appendages which may be covered with host tissue. Thus, the existing descriptions are mostly incomplete and not useful in comparing species. In this regard an attempt has been made to contribute not only to the structure of the appendages but also to their location on the cephalothorax. Thus, more information regarding the morphology of the antennules, antennae, maxillae and maxillipeds is provided for the post metamorphic females of *L. tetraloba*, *L.* cf. *edwardsi* and *L. caparti*. Furthermore, similar to *Sphyrion* females (Moran & Piasecki, 1994; Dippenaar & Sebone, 2022) the maxillae of *Lophoura* females are represented by maxillary processes with maxillary gland pores (see Figs 2a, 5a).

To date, only four males of *Lophoura* species have been reported including *L. bouvieri* (see Wilson, 1919), *L. cornuta* (see Wilson, 1919), *L. caparti* (see Nuñes-Ruivo, 1962) and *L. ventricula* (see Ho & Kim, 1989). This is the first description of the male of *L. tetraloba*. Similar to other sphyriid males (see Dippenaar & Sebone, 2022), *Lophoura* males also resemble lernaeopodid males (Kabata, 1979). The habitus of *Lophoura* males are similar, but the armature of the appendages seem to differ slightly. However, complete comparisons could not be done for *L. tetraloba*, *L. bouvieri*, *L. cornuta* and *L. caparti* as previous descriptions and illustrations are incomplete.

The current report constitutes new host records (*C. fasciatus* and *L. ori*) for *L. tetraloba* and *L.* cf. *edwardsi* off South Africa [west coast (Atlantic Ocean)] which is also a new geographic record for both *L. tetraloba* and *L.* cf. *edwardsi*. *Lophoura caparti* has been reported from the family Epigonidae (Nuñes-Ruivo, 1962). In addition to the known host i.e., *E. telescopus* from a new geographical location [south coast (Indian Ocean), South Africa], it was also collected from *E. denticulatus* which constitutes a new host record as well as a new geographical record [west coast (Atlantic Ocean), South Africa]. *Lophoura cornuta* has previously been reported from members of Synaphobranchidae (Wilson, 1919; Boxshall, 1989). However, it has been collected from *B. albescens* in the current study, constituting a new host record and the first *Lophoura* species to be reported from Congridae which also constitutes a new geographical record [south coast (Indian Ocean), South Africa]. All the host species reported in this study are deep-water fish, hence, confirming that *Lophoura* species are mesoparasites of deep-water teleosts (Kabata, 1979; Ho & Kim, 1989).

Identification key for the post metamorphic females of Lophoura species

(Compiled from current study as well as Wilson, 1919, 1935; Nuñes Ruivo, 1962; Hewitt, 1964; Szidat, 1971; Kensley & Grindley, 1973; Stadler, 1978; Kabata, 1979; Ho, 1985; Hogans & Dadswell, 1985; Hogans, 1986; Ho & Kim, 1989; Boxshall, 1989, 2000; Castro-Romero & Gonzalez, 2009; Gómez et al., 2010).

1a. Without holdfast organ……...……*L. simplex*

1b. Irregularly shaped holdfast organ without main processes …..…..…..……..…….*L. cardusa*

1c. Regularly shaped holdfast organ with main processes…..……..…...……..............……….….….2
2a. Cephalothorax length longer or as long as trunk length……...…….………...….….………….…….3
2b. Cephalothorax shorter than neck…...………..……..…….……….………….…..…..5
3a. Cephalothorax 2 times longer than neck; holdfast organ with short, knob-like outgrowths; posterior processes with short straight stalks…......…..……….….……….……......*L. elongata*
3b. Cephalothorax less than 2 times length of the neck; holdfast organ without short, knob-like outgrowths.......……….……….……….……….…4
4a. Cephalothorax similar width throughout; holdfast organ with a single bulbous process; posterior processes bearing elongated porous peduncle with long stalks diverging into secondary stalks…….……..…….……….……….……..*L. caparti*
4b. Cephalothorax slightly decreasing in width posteriorly; small holdfast organ, width slightly wider than neck; straight stalks of posterior processes, shorter than half trunk length …..…………..*L. gracilis*
4c. Cephalothorax (baton/club shaped) increasing in width anteriorly; holdfast organ with short rounded outgrowths (bowtie-shaped); posterior process shorter than half of trunk length with slightly curved stalks.……..…..…...………….……….…….*L. szidati*
4d. Cephalothorax slightly increasing in width; holdfast organ with 2 main processes with finger-like outgrowths; stalks of posterior processes curved and heavily intertwined………….……….…......*L. bipartita*
5a. Holdfast organ simple, without complex outgrowths..…..……….……….……….……..…6
5b. Holdfast organ complex, with several outgrowths…...…..……….……….……….……9
6a. Holdfast organ bulbous, with 3 rounded processes; posterior processes length shorter than trunk length, with straight stalks.…….……..……..… …..…..……….……….……….……….…..*L. bouvieri*
6b. Holdfast organ with 4 – 5 main processes, barely wider than cephalothorax; posterior processes almost same length as trunk, with straight stalks …..............……….……….…….............*L. edwardsi*
6c. Holdfast organ consisting of 2 bulbous processes, wider than cephalothorax; length of posterior processes longer than trunk length, elongated porous peduncle, stalks diverge into secondary stalks…. ……….……….……….……….……….*L. unilobulata*
6d. Holdfast organ with 2 main processes, each with 3 short knob-like outgrowths; neck increasing in width anteriorly; posterior processes length shorter than trunk length, with straight stalks…..…..*L. laticervix*
6e. Holdfast organ with globular and diverging extended outgrowths; posterior processes length shorter than trunk length, with straight stalks……....……….……….……….……..*L. magna*
7a. Holdfast organ with 4 inflated main processes, with outgrowths; spherical trunk; stalks of posterior processes slightly curved…..…..…......*L. tetraphylla*
7b. Posterior processes heavily intertwined…..… ……….……….……….……….……….…….8
7c. Posterior processes with straight stalks…..…..…...……….……….……….…….9
8a. Holdfast organ with 5 main processes, with knob-like outgrowths ……….……….…..*L. pentaloba*
8b. Holdfast organ with 5 main processes, with finger-like outgrowths extending anteriorly…... ……….……….……….……….…..*L. ventricula*
9a. Holdfast organ with elongated outgrowths of varying lengths…..……….……….……….……10
9b. Holdfast organ with knob-like outgrowths of varying lengths.……….……….……….…...11
10a. Holdfast organ with 3 main processes, with irregular outgrowths; posterior processes with straight stalks that diverge into secondary stalks..……. ……….……….……….……….…*L. tripartita*
10b. Holdfast organ with 4 main processes, with elongated tentacle-like outgrowths; posterior processes longer than trunk …..…..……..…*L. cornuta*
11a. Holdfast organ with 4 main processes, with irregular knob-like outgrowths; cephalothorax wider at base; neck as long as trunk; stalks of posterior processes diverge into tertiary stalks………….………. ……….……….……….……….…*L. brevicollum*
11b. Holdfast organ with 4 main processes, with irregular knob-like outgrowths; cephalothorax of constant width; neck longer than trunk; posterior processes with single straight stalks..……*L. tetraloba*

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Author contributions SMD: Conceptualization, Funding acquisition, Field collection, Supervision, Writing—reviewing and editing. MMS: Performed research, Writing—original draft preparation reviewing and editing, Illustrations.

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Data availability Voucher specimens are deposited in the Iziko South African Museum, Cape Town, South Africa.

Declarations

Competing Interests The authors declare that they have no conflict of interest.

Ethical approval All applicable institutional, national and international guidelines for the care and use of animals were followed.

Consent to participate Not applicable.

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