LOPHOURA BREVICOLLUM N. SP. (COPEPODA: SIPHONOSTOMATOIDA: SPHYRIIDAE), A PARASITE OF THE SMOOTH GRENADIER *NEZUMIA LIOLEPIS* (GILBERT, 1890) (PISCES: MACROURIDAE) FROM THE EASTERN PACIFIC, AND A NEW RECORD AND NEW HOST OF *LOPHOURA UNILOBULATA* CASTRO R. AND GONZALEZ

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ABSTRACT

Specimens of the deep-water macrourid *Nezumia liolepis* were caught during a survey of the effects of the oxygen minimum layer on the vertical distribution of crustaceans, polychaetes, and fishes in the Gulf of California. Two specimens were each carrying one parasitic copepod each, initially judged to be identical to *Lophoura tetraloba* in almost all respects. An additional specimen of *N. liolepis* carrying one copepod was collected in the San Pedro Channel between San Pedro and Santa Catalina Island (southern California), and another specimen of *N. liolepis* carrying another copepod, collected between Cabo Corrientes (Jalisco) and Manzanillo (Colima), Mexico, was found in the collection of the California Academy of Sciences. Detailed inspection revealed several important differences between *L. tetraloba* from the South China Sea and Tosa Bay (Japan), and the new material, which along with the different depth and distribution, support the hypothesis of a new sphyriid species, described here as *L. brevicollum*. *Lophoura tetraloba* and *L. brevicollum* can be separated by the length of the neck, the number of dorsal and ventral depressions of the genito-abdomen, the length of the egg sacs, and by the general shape of the posterior processes. Finally, a new record and a new host for *L. unilobulata*, as well as some comments on the systematic position of *Driocephalus* are given.

KEY WORDS: Eastern Tropical Pacific, Gulf of California, Lophoura, *Nezumia*, parasitic Copepoda, Siphonostomatoida, southern California, Sphyriidae

INTRODUCTION

Sphyriidae are extremely modified siphonostomatoid copepods that parasitize both Osteichthyes and Elasmobranchii, and are characterized by partial or complete loss of thoracic appendages and by some degree of degeneration of head appendages (Dojiri and Deets, 1988). Boxshall and Halsey (2004) recognized the following genera within Sphyriidae Wilson, 1919: *Sphyrion* Cuvier, 1830, *Lophoura* Kölliker in Gegenbaur et al., 1853, *Tripaphylus* Richiardi, 1880, *Opimia* Wilson, 1908, *Paeon* Wilson, 1919, *Periplexis* Wilson, 1919, *Paeonocanthus* Kabata, 1965, *Norkus* Dojiri and Deets, 1988, and *Thamnocephalus* Diebakate, Raibaut & Kabata, 1997. Apparently Boxshall and Halsey (2004) were not aware that the name *Thamnocephalus* was a junior homonym of *Thamnocephalus* Packard, 1877 (Anostraca, Branchiopoda), and that Raibaut (1999) remedied this by replacing the name *Thamnocephalus* with *Driocephalus* Raibaut, 1999. Of these, the epipelagic branchial-cavity dwellers of the genera *Tripaphylus*, *Opimia*, *Paeon*, and *Norkus*, which parasitize Elasmobranchii, constitute the *Tripaphylus*-clade, whereas the mesopelagic to bathypelagic body-musculature burrowers of the genera *Sphyrion*, *Lophoura*, *Periplexis*, and *Paeonocanthus*, which parasitize Teleostei, constitute the *Sphyrion*-clade, with the *Sphyrion-Lophoura* complex as the

sister-group of the *Periplexis-Paeonocanthus* complex (Dojiri and Deets, 1988). Diebakate et al. (1997) omitted any comment on the phylogenetic position of *Driocephalus* [*Thamnocephalus* in Diebakate et al. (1997)] and only suggested some similarity in the general shape of the posterior processes of *Opimia*, *Paeon*, *Paeonocanthus*, *Tripaphylus*, and *Norkus*, and also a slight similarity in the holdfast with that of *Norkus*. Later, Benz et al. (2006) questioned the validity of the characters used by Dojiri and Deets' (1988) in their analyses, and presented a new cladistic analysis based on different and fewer characters using a different coding regime. Briefly, Benz et al. (2006) found that their results were not congruent with the cladogram presented by Dojiri and Deets (1988) in that Benz's et al. (2006) results do not support neither Dojiri and Deets' (1988) host nor ecological summary (Sphyriidae being composed of two clades, of which one infected only elasmobranchs and the other infected only teleosts). Also, Benz's et al. (2006) results showed *Driocephalus* as the sister taxon of *Lophoura* in 50% of all the shortest trees, and as the sister taxon to a clade composed of *Lophoura* and *Sphyrion*.

The genus *Lophoura* is by far the most species rich genus with 18 taxa: *L. edwardsi* (Kölliker in Gegenbaur et al., 1853), *L. bouvieri* (Quidor, 1912), *L. cornuta* (Wilson,

1919), *L. gracilis* Wilson, 1919, *L. cardusa* (Leigh-Sharpe, 1934), *L. tripartita* (Wilson, 1935), *L. caparti* (Nunes Ruivo, 1954), *L. laticervix* Hewitt, 1964, *L. magna* Szidat, 1971, *L. elongata* Kensley and Grindley, 1973, *L. pentaloba* Ho, 1985, *L. tetraphylla* Ho, 1985, *L. ventricula* Ho and Kim, 1989, *L. bipartita* Ho and Kim, 1989, *L. tetraloba* Ho and Kim, 1989, *Lophoura* sp. *sensu* Ho and Kim (1989) (likely to belong to a new species, but the only specimen was incomplete and Ho and Kim (1989) felt unjustified to give it a name), *L. simplex* Boxshall, 2000, and *L. unilobulata* Castro R. and Gonzalez, 2009.

At present, the genus *Lophoura* is known to parasitize the body musculature (Dojiri and Deets, 1988) of apogonids, synaphobranchids, morids, sparids, and macrourids (Boxshall and Halsey, 2004; Kensley and Grindley, 1973; Hogans and Dadswell, 1985; Dojiri and Deets, 1988; Ho and Kim, 1989; Castro R. and Gonzalez, 2009). The Macrouridae serves as host for the following ten species: *L. bipartita*, *L. bouvieri*, *L. cardusa*, *L. edwardsi*, *L. laticervix*, *L. pentaloba*, *L. tetraloba*, *L. kamoharai*, *Lophoura* sp. *sensu* Ho and Kim (1989), *L. ventricula*, and *L. unilobulata* (Hewitt, 1964; Dojiri and Deets, 1988; Ho and Kim, 1989; Boxshall and Halsey, 2004; Castro R. and Gonzalez, 2009). Eight species, *L. pentaloba*, *L. cornuta*, *L. cardusa*, *L. ventricula*, *L. tetraloba*, *L. bipartita*, *Lophoura* sp. *sensu* Ho and Kim (1989), and *L. unilobulata* are known to occur in the Pacific Ocean. Of these, *L. cardusa*, *L. ventricula*, *L. tetraloba*, *L. bipartita*, and *Lophoura* sp. *sensu* Ho and Kim (1989), are known from the Western Pacific, and only *L. pentaloba*, *L.* cornuta, and *L. unilobulata* are known from the Eastern Pacific. Also, *L. cornuta* is the only species of *Lophoura* from the Pacific known to parasitize a different host family (cutthroat eels, Synaphobranchidae).

Specimens of the deep-water macrourid, *Nezumia liolepis* (Gilbert, 1890), were caught during a survey of the effects of the oxygen minimum layer on the vertical distribution of crustaceans, polychaetes and fishes in the Gulf of California. Two specimens of *N. liolepis* were found carrying one parasitic copepod each (Fig. 2A-C). Another specimen of *N. liolepis*, carrying one parasitic copepod, was collected in the San Pedro Channel between San Pedro and Santa Catalina Island (southern California). Additional material of *N. liolepis* collected in 1968 in the Eastern Tropical Pacific, which was found carrying another copepod, was borrowed from the California Academy of Sciences. These four copepods turned out to belong to a new species closely related to *L. tetraloba*, the latter having been found attached to *Nezumia* sp. and *N. condylura* Jordan and Starks, 1904 from South China Sea and from Tosa Bay, Japan (Ho and Kim, 1989).

MATERIALS AND METHODS

Specimens of *N. liolepis* were caught with bottom trawls at depths of 1270 m and 1295 m off the coast of Sinaloa, Mexico, in March 2001, on board R/V El Puma of the Universidad Nacional Autónoma de México during the research campaign TALUD VI. The fishes were preserved in 10% formalin and inspected for attached copepods. Two specimens of *N. liolepis* were infected with one copepod each (Figs. 2B, C) posterior to the dorsal fin (Fig. 2A). An additional specimen of *N. liolepis* carrying one parasitic copepod was collected by otter trawl on the R/V "Yellowfin" in the San Pedro Channel between San Pedro and Santa Catalina Island

(southern California) on 21 September 2001. Another specimen of *N. liolepis*, carrying one parasitic copepod, and collected from the Eastern Tropical Pacific in 1968, was borrowed from the California Academy of Sciences. The fish were fixed in 10% formalin, then rinsed and stored in 70% ethanol. The copepods were carefully detached from their hosts and were preserved in 70% ethanol. The parasites were inspected at a magnification of 40× with a dissecting microscope equipped with a drawing tube. Additional observations were done with a Leica DMLB compound microscope at a magnification of 100×. The type material has been deposited in the Copepoda collection of the Institute of Marine Sciences and Limnology, Mazatlan Marine Station in Mazatlan, Mexico (EMUCOP), and in the collection of the Cabrillo Marine Aquarium (San Pedro, California) (CMA). The hosts have been deposited in the Copepoda collection of the Institute of Marine Sciences and Limnology, Mazatlan Marine Station in Mazatlan (Mexico), in the collection of the Natural History Museum of Los Angeles County, and in the collection of the California Academy of Sciences (see below).

A phylogenetic analysis to assess the position of *Driocephalus* was conducted using PAUP* Phylogenetic Analysis Using Parsimony (*and other methods) version 4.0b10 (Swofford, 2000). This analysis was based largely on the character matrix presented by Dojiri and Deets (1988) for Sphyriidae, which was updated and edited in Mesquite version 1.05 (build g24) (Maddison and Maddison, 2004). For out-group information see Dojiri and Deets (1988: 687, Appendix I and II).

SYSTEMATICS

Order Siphonostomatoida
Sphyriidae Wilson, 1919
Lophoura Kölliker in Gegenbaur et al., 1853
Lophoura brevicollum n. sp.
(Figs. 1-6)

Type material.—Female holotype (EMUCOP-160301-1) and one female paratype (EMUCOP-170301-1) preserved in alcohol (catalogues numbers for the hosts are the same as for the copepods); collected off Sinaloa state (24°56′N, 109°05′W, and 25°43′N, 109°54′W); 16 and 17 March 2001, at 1270 m depth and 1295 m depth, and 1.4 and 0.86 ml l^{-1} O_2, respectively; coll. S. Gómez and F. N. Morales-Serna; copepod removed by S. Gómez. One female paratype (CMA 2009.04.0015) preserved in alcohol (host voucher deposited in the collection of the Natural History Museum of Los Angeles County under catalogue number LACM 56761-1); collected in the San Pedro Channel between San Pedro and Santa Catalina Island (southern California) (33°34.5′N, 118°31′W); 29 September 2001, at 880 m depth; coll. J. E. Kalman; copepod removed by J. E. Kalman. One female paratype (CMA 2009.04.0016) preserved in alcohol (host voucher deposited in the collection of the California Academy of Sciences under catalogue number CAS 57877); collected midway between Cabo Corrientes (Jalisco) and Manzanillo (Colima), Mexico (19°43′30″N, 105°35′30″W); 10 July 1968, at 600-800 m depth; coll. Margaret G. Bradbury; copepod removed by J. E. Kalman.

Type locality.—Off Sinaloa state (24°56′N, 109°05′W).

Other localities.—Off Sinaloa state (25°43′N, 109°54′W), San Pedro Channel between San Pedro and Santa Catalina Island (southern California) (33°34.5′N, 118°31′W), and between Cabo Corrientes (Jalisco) and Manzanillo (Colima), Mexico (19°43′30″N, 105°35′30″W).

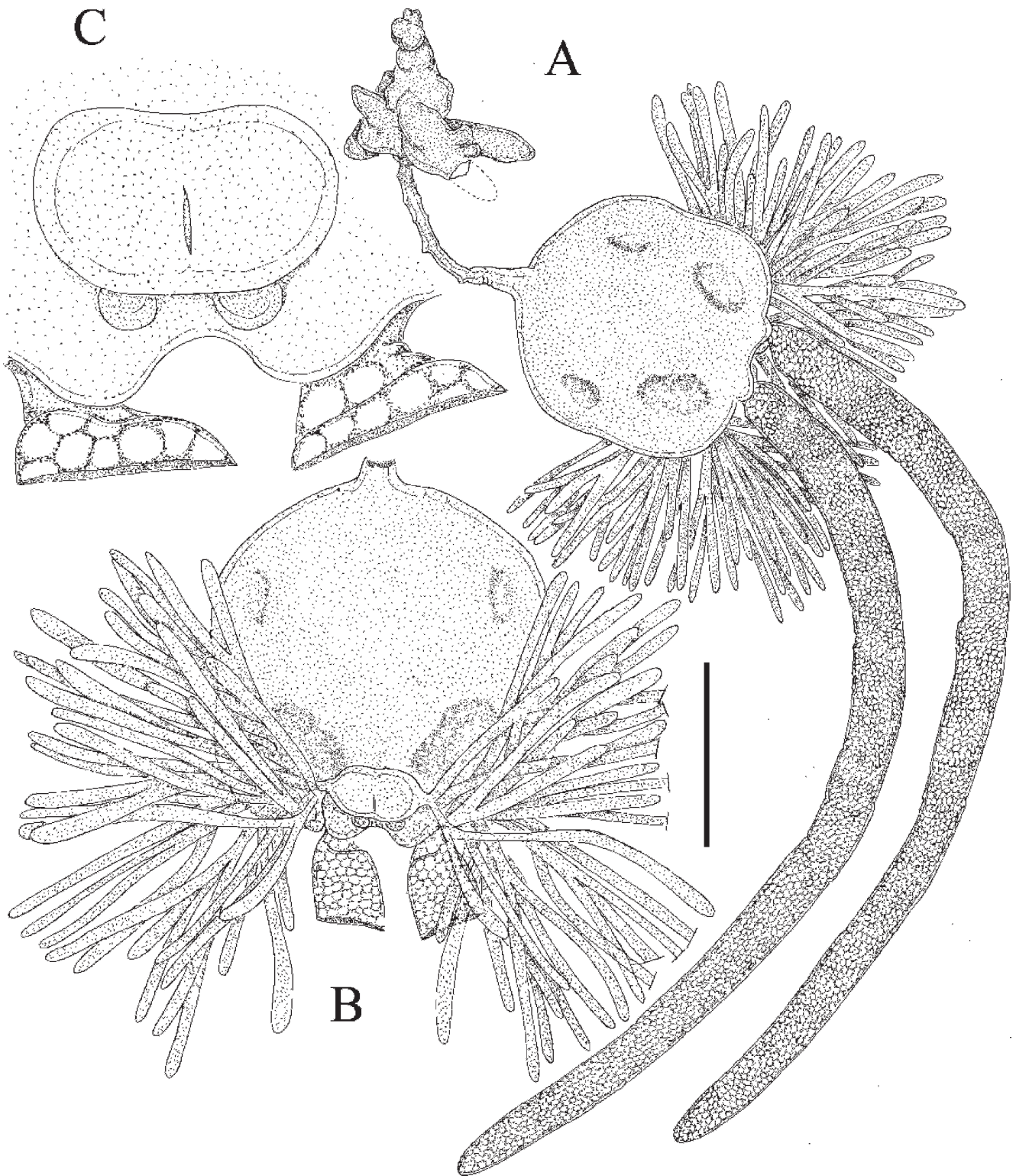Host.—*Nezumia liolepis* (Gilbert, 1890) (Pisces: Macrouridae).

Fig. 1. *Lophoura brevicollum* n. sp., female. A, habitus, dorsal; B, genito-abdomen, ventral; C, posterior region of genito-abdomen, ventral. Scale bar: A, B, 5 mm; C, 1 mm.

Site of infestation.—Posterior base of dorsal fin, mesoparasitic in body musculature.

Etymology.—The specific name (Latin *brevis*, short; *collum*, neck; a noun in apposition) alludes to its comparatively short neck when compared to its most closely related species, *L. tetraloba*.

Description.—Female: Total body length from tip of cephalothorax to posterior margin of genito-abdomen
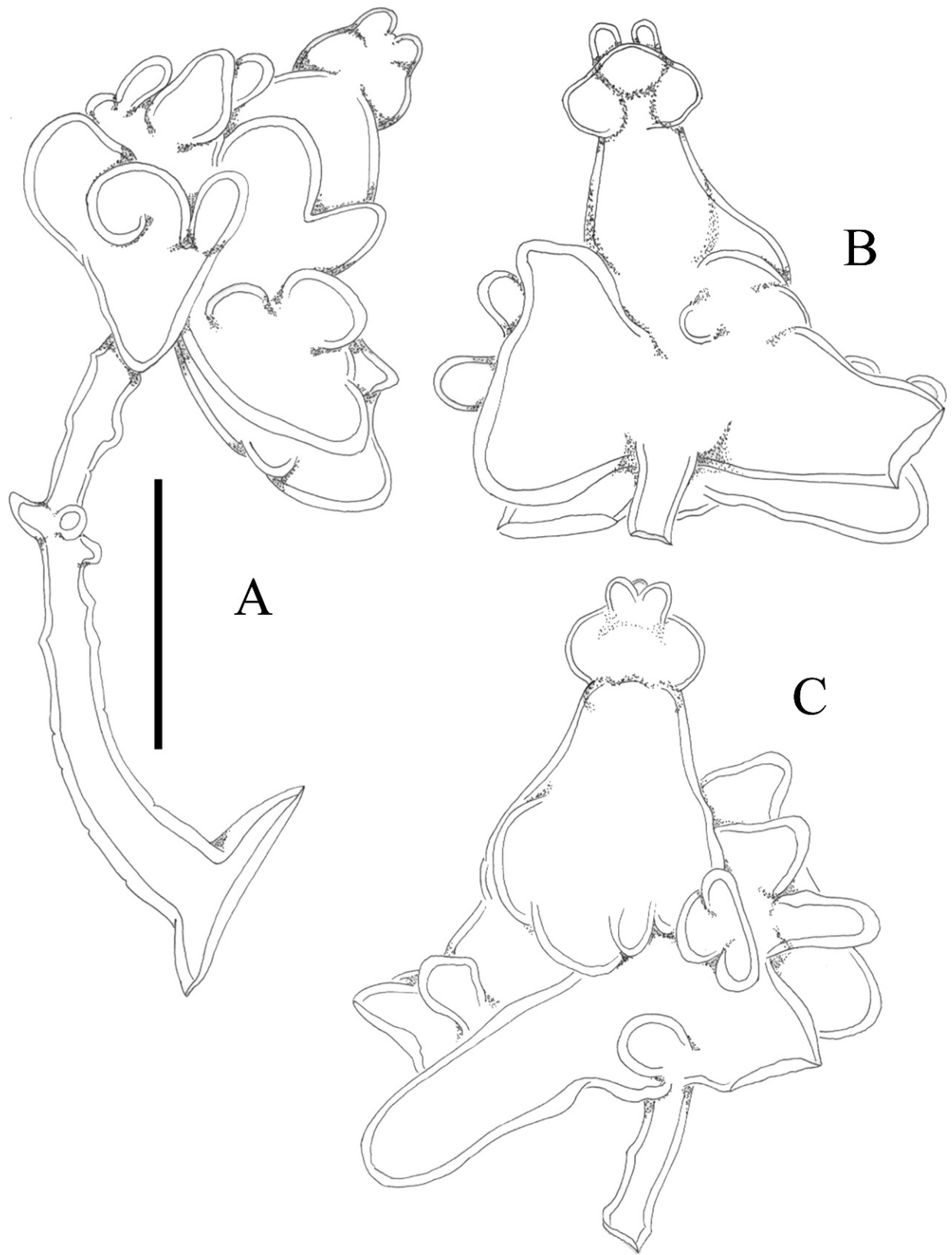
Fig. 2. *Lophoura brevicollum* n. sp., female. A, cephalothorax, holdfast organ, and neck, side view; B, cephalothorax and holdfast organ, ventral; C, cephalothorax and holdfast organ, dorsal. Scale bar: 2 mm.
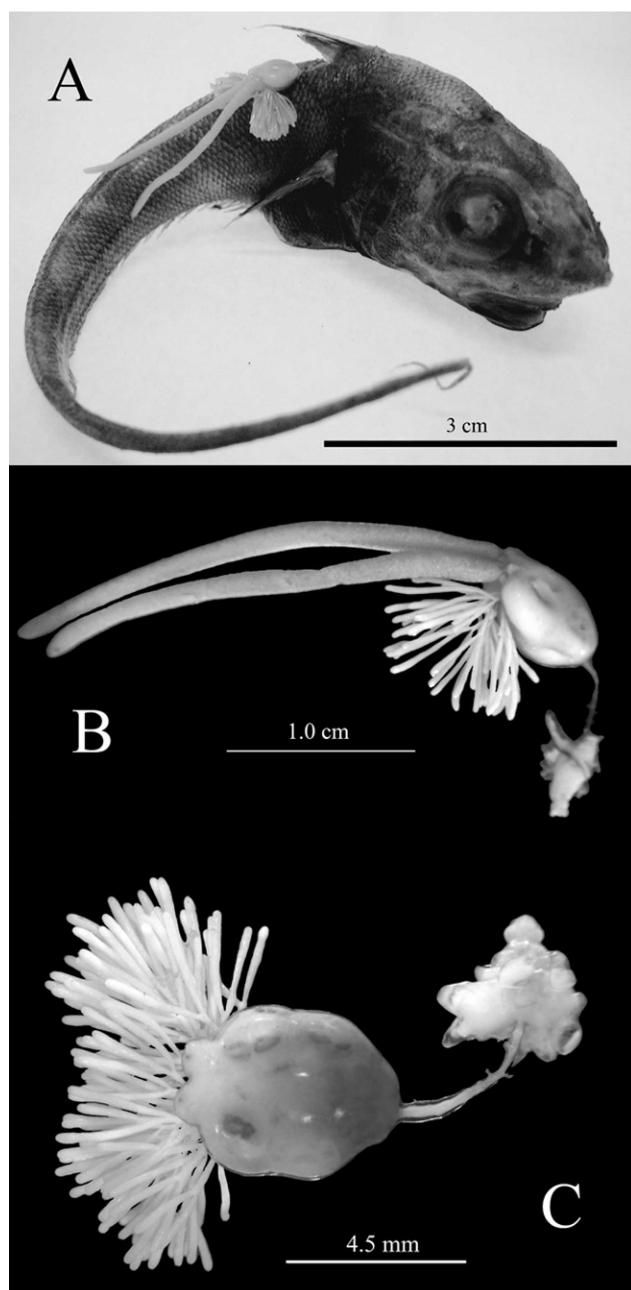
anterior depressions being smaller; with pair of posterior processes and egg sacs (Fig. 1A, B). Posterior processes consisting of several long, slender cylinders attached to tertiary, secondary and primary stalks through short, narrow necks; primary stalk attached to central stalk (Figs. 1B, 5A, B). Attachment area of egg sacs sharply demarcated from posterior surface of trunk, with concave posterior margin (Fig. 1B, C). Egg sacs attached to oviducal opening. Ventral elliptical perianal lobe present with longitudinal slit in center; with pair of genital tubercles behind perianal lobe (Fig. 1B, C). Egg sacs about six times as long as genito-abdomen (Figs. 1A, 3B).

Male: unknown.

Variability.—The posterior processes of the specimens from the San Pedro Channel (southern California) and from the Eastern Tropical Pacific (between Cabo Corrientes (Jalisco) and Manzanillo (Colima), Mexico) are almost twice as long as in the specimens from Sinaloa (see Fig. 6).

Lophoura unilobulata Castro R. and Gonzalez, 2009
(Fig. 7)

Remarks.—Castro R. and Gonzalez (2009) described *L. unilobulata* Castro R. and Gonzalez, 2009 from the macrourid *N. pulchella* (Pequeño, 1971) collected between Taltal and Coquimbo, Chile. The specimens of *L. unilobulata* collected by the above authors were found attached close to the pectoral or dorsal fins of the host (Castro R. and Gonzalez, 2009). One of us (JEK) found one specimen of a parasitic copepod (Fig. 7) attached dorso-laterally near the caudal fin of one specimen of the macrourid *N. stelgidolepis* (Gilbert, 1890) housed in the collection of the Natural History Museum of Los Angeles County under catalogue number LACM 33886-3, collected on 23 January 1974 by Coyer-Engle, 55 miles south of Lobos de Afuera, Peru (7°44′S, 80°30′W) at 750-760 m. The specimen parasitic on *N. stelgidolepis* from Peru is similar to *L. unilobulata* by the presence of simple lobes on the holdfast, the presence of an abdomen, total body length (26.4 mm compared to 30.8 mm), and the posterior processes consisting of a central stalk with more than 30 single slender cylinders attached. Therefore, this results in a range extention and a new host report for *L. unilobulata*. The copepod has been deposited in the collection of the Cabrillo Marine Aquarium (San Pedro, California) under catalogue number CMA 2009.04.0017.

Fig. 3. *Lophoura brevicollum* n. sp. A, female attached to *Nezumia liolepis* (Gilbert, 1890); B, ovigerous female, lateral; C, non-ovigerous female, dorsal.

15.7 mm. Cephalothorax and holdfast organ forming irregular, cylindrical anterior part (Figs. 1A, 2A-C, 3B, C, 4B). Cephalic region of cephalothorax with bilobed tip, with pair of relatively large posterior lobes ventrally (Figs. 1A, 2A-C, 4A, B). Holdfast made up of four main trunks with or without tubercles, the number and size of which varying among trunks in the same specimen and between specimens (Figs. 1A, 2A-C, 4B-D). Neck region posterior to the holdfast organ heavily sclerotized, slightly shorter than genito-abdomen (Figs. 1A, 3B, C). The latter rounded and flattened, with two sets of two depressions each arranged longitudinally on ventral and dorsal surface,

DISCUSSION

Three species are known to have a four-part holdfast organ: *L. tetraloba* from the South China Sea and Tosa Bay (Japan), *L. tetraphylla* from the New York Bight (western North Atlantic), and *L. cornuta* from off Ochiishi Saki (eastern Hokkaido, Japan). Of these, only *L. tetraloba* was found attached to species of the genus *Nezumia* (*Nezumia* sp. and *N. condylura* (Ho and Kim, 1989)). *Lophoura tetraphylla* was found parasitizing *Antimora rostrata* (Günther, 1878) (Pisces: Moridae) (Ho, 1985) and *L. cornuta* was found attached to *Synaphobranchus affinis*
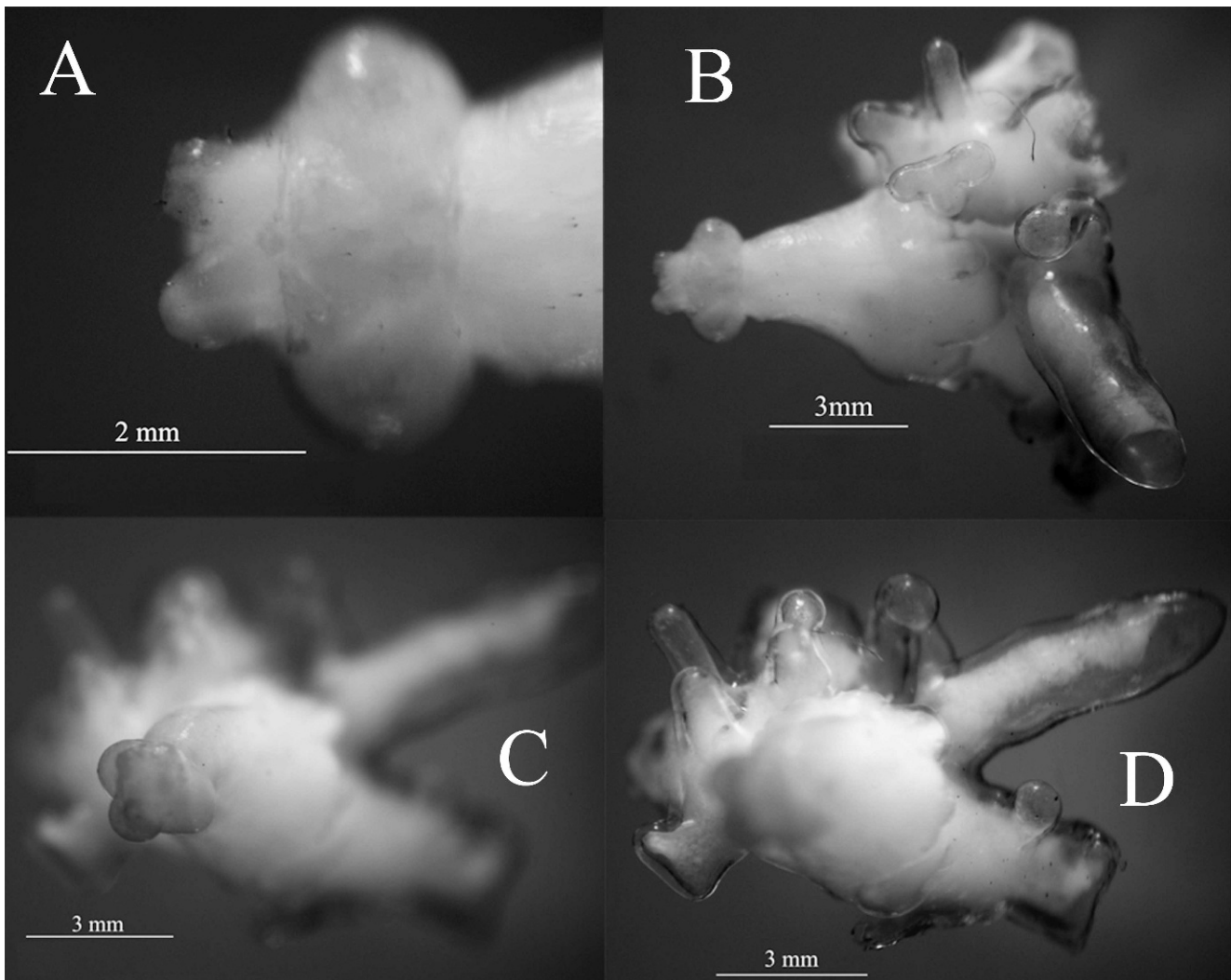
Fig. 4.   *Lophoura brevicollum* n. sp., female. A, cephalothorax, dorsal; B, cephalothorax and holdfast organ, dorsal; C, cephalothorax and holdfast organ seem from above (holdfast out of focus); D, cephalothorax and holdfast organ seem from above (cephalothorax out of focus).

Günther, 1877 (Pisces: Synaphobranchidae) (Wilson, 1919). *Lophoura cornuta* can be separated easily from the other two species by the more greatly enlarged genito-abdomen, size and disposition of the posterior processes, number of dorsal depressions of the genito-abdomen and, above all, by the shape of the holdfast organ with long, profusely branched, slender and twisted processes (Ho and Kim, 1989; see also Wilson, 1919). *Lophoura tetraphylla* can be separated from the other two species by the shape of the cephalic region (with a pair of lateral, wing-like spherical swellings (Ho, 1985)), relative size of the holdfast organ (as large as the genito-abdomen, and composed of four extremely enlarged subdivided lobes), subcircular genito-abdomen, and number of dorsal and ventral depressions of the genito-abdomen. *Lophoura tetraloba* can be separated by its subquadrate genito-abdomen and the shape and size of the holdfast organ. The number of dorsal and ventral depressions of the genito-abdomen is similar in both *L. tetraloba* and *L. tetraphylla*.

Ho and Kim (1989) described *L. tetraloba* from eight specimens of *Nezumia* sp. collected in the South China Sea

and three specimens of *N. condylura* from Tosa Bay (Japan). *Lophoura brevicollum*, which was found attached to specimens of *N. liolepis* from the Gulf of California, from southern California and from the Eastern Tropical Pacific, is identical to *L. tetraloba* in almost all respects. In fact, upon preliminary inspection, the specimens of *L. brevicollum* were identified with *L. tetraloba*, and the small differences between these two populations, i.e., the length of the neck (comparatively shorter in *L. brevicollum*), number of dorsal and ventral depressions of the genito-abdomen (16 in *L. tetraloba*, only eight in *L. brevicollum*), length of the egg sacs (more than twice as long as the genito-abdomen in *L. tetraloba* (see Ho and Kim, 1989), but up to six times as long as the genito-abdomen in *L. brevicollum*), were attributed to geographic variation within the species (Ju-shey Ho, California State University, Long Beach, personal communication). Even though some intraspecific geographic variation should be expected in the subdivisions of the processes in the holdfast organ (Ho, 1985), the shape and size of this structure is the most reliable character to recognize the different species of
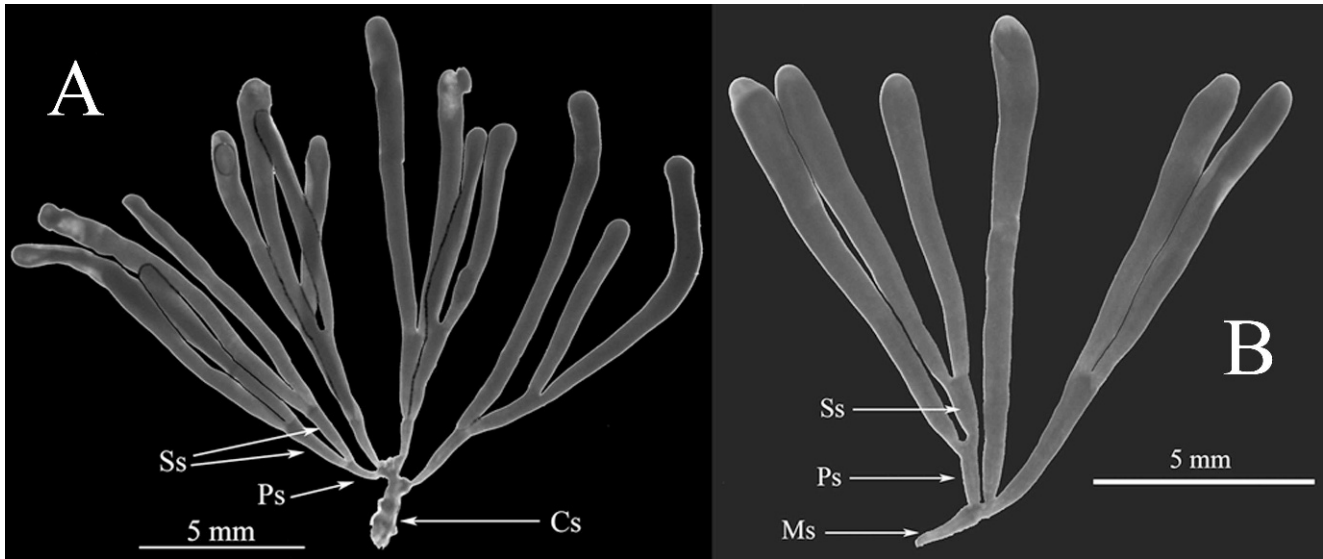
Fig. 5. *Lophoura brevicollum* n. sp., female. A, Distal part of posterior process; B, primary stalk detached from central stalk. Cs, central stalk; Ps, primary stalk; Ss, secondary stalk; Ts, tertiary stalk.

Lophoura (Ho, personal communication). Initially, based on the character state of this structure and on the possibility of geographic variation, the specimens of the Mexican populations and those from southern California were thought to belong to *L. tetraloba*. However, further detailed inspection of the new material revealed some subtle and important differences that supports the proposal of a new species, *L. brevicollum*. In addition to the differences noted above (length of neck, number of dorsal and ventral depressions of genito-abdomen, and length of egg sacs), *L. brevicollum* differs from *L. tetraloba* also in the general shape of the posterior processes (a central stalk with more than 30 single slender cylinders attached to the stalk through a short, narrow neck in *L. tetraloba* (Ho and Kim, 1989), in contrast to the long, slender cylinders attached to tertiary, secondary, and primary stalks through short, narrow necks, and the primary stalk attached to the central stalk in *L. brevicollum*) (Fig. 4A, B).

Nezumia liolepis is restricted to the eastern Pacific from California to mainland Mexico, including Baja California and the Sea of Cortez, whereas *N. condylura* is restricted to Japan, the East China Sea and Taiwan (Cohen et al., 1990; Neighbors and Wilson, 2006). The vertical distributions of these two species are also different and their habitats do not overlap. The depth range of *Nezumia liolepis* is 681-2,825 m, while that of *N. condylura* is 200-720 m (Cohen et al., 1990; Neighbors and Wilson, 2006). Both the vertical distribution of deep-sea fishes and their attached ectoparasites bears important consequences in speciation. Among the environmental factors that typify the deep-sea, hydraulic pressure plays the most important role in vertical distribution of species and speciation in the deep-sea. The differential ability of different species to tolerate extreme hydraulic pressures through specific biochemical and physiological attributes allow them to live in different depth regimes throughout their geographic distributions (Morita, 1999 and references cited therein; Sebert, 2002). Uyeno (1967, 1980) showed that deep-sea fishes in general

appeared sometime during the Miocene and Pliocene. More recently, Morita (1999) showed that the abyssal *Coryphaenoides armatus* (Hector, 1875) and *C. yaquinae* Iwamoto and Stein, 1974 (Pisces: Macrouridae) diverged from nonabyssal species approximately 3.2-7.6 million years ago. According to Morita (1999), the first speciation event of the genus took place into the upper continental slopes, before the radiation of nonabyssal species. Afterwards, nonabyssal species spread on the upper slopes and environmental factors other than hydraulic pressure would be involved in their subsequent speciation (Morita, 1999; see also Rogers, 2000). Morita (1999) also suggested that differences in the adaptation to hydraulic pressure resulted in the speciation between abyssal and nonabyssal species. To the best of our knowledge, there have been no studies on the evolution and radiation of the genus *Nezumia*. Nevertheless, a scenario similar to that of the genus *Coryphaenoides* as presented by Morita (1999) can be envisaged since these two genera are, at least, confamilial.

One factor limiting the vertical distribution of species is the presence of oxygen-minimum zones (OMZ's waters with $< 0.5 \text{ ml l}^{-1}$ O$_2$ (Levin et al., 1991; Levin, 2003; Schneider and Bush-Brown, 2003)). The expansion and contraction of OMZ's due to global warming and cooling, might have presented many opportunities for allopatric speciation through geographic restriction of populations or selection for tolerance to oxygen deficiency (Kennett, 1982; Armstrong, 1996; Rogers, 2000; Levin, 2003; Smith & Demopoulos, 2003). Such speciation events may have been favoured by adaptations such as an increased body surface among others, to cope with hypoxic conditions (Schneider and Bush-Brown, 2003; Rogers, 2000 and references cited therein). At present, the largest OMZ's are confined to bathyal depths (1000-4000 m) in the Arabian Sea, Bay of Bengal, the eastern Pacific, and off southwestern Africa (Rogers, 2000 and references cited therein; Levin, 2002, 2003; Kamykowski and Zentara, 1990). Hypoxic ($< 0.2 \text{ ml l}^{-1}$ O$_2$ (Kamykowski and
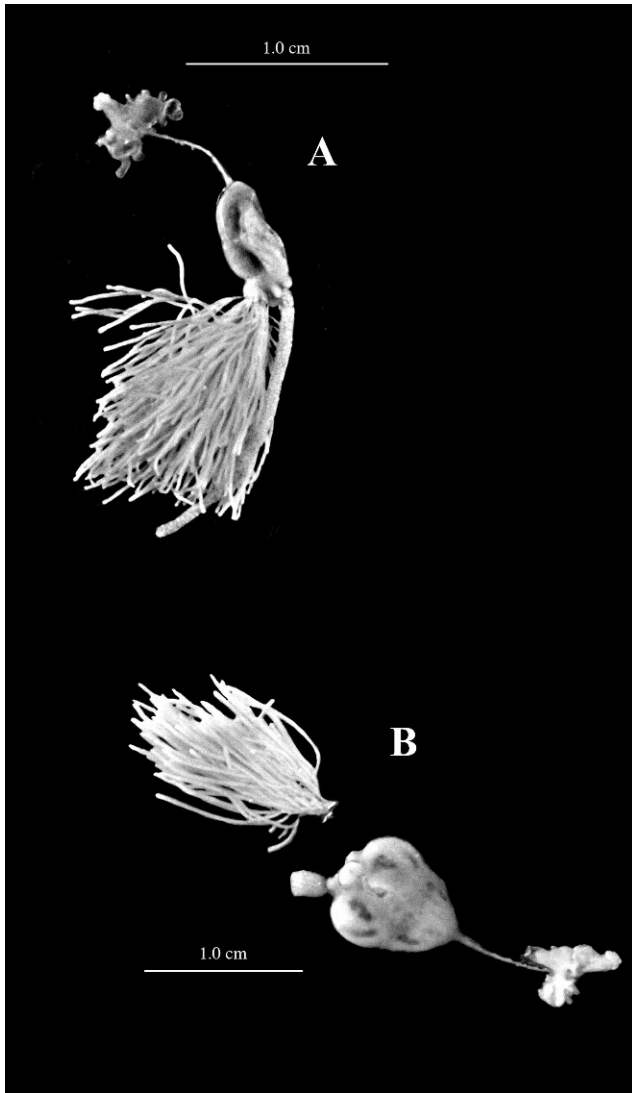
Fig. 6. *Lophoura brevicollum* n. sp., female. A, Paratype from California; B, Paratype from the Eastern Tropical Pacific.

Fig. 7. *Lophoura unilobulata* Castro R. and Gonzalez, 2009, female, from Peru.

Zentara, 1990)) or anoxic conditions (0.0 ml l⁻¹ O₂ (Levin, 2003)) also are found in shallow-sill basins and trenches such as the Black Sea, the Baltic Sea, Gulf of Aden, the Philippine region, the Red Sea, north-west Pacific margin, Norwegian fjords, basins of the California Continental Borderlands, the Cariaco Trench, and near the outflows of large rivers as well as in fjords, sea lochs, and shelf seas (Rogers, 2000 and references cited therein; Levin, 2003 and references cited therein).

Childress and Siebel (1998) emphasised that animals living in OMZ's must adapt to limited oxygen availability, not to a complete absence of oxygen. Even at very low oxygen concentrations, there is sufficient oxygen available in the water if organisms can access it; it is the reduced PO_2 gradient driving diffusion from the animal exterior to the mitochondria that poses the main problem. The effectiveness of oxygen uptake may be increased by raised ventilation rates, increased efficiency of O_2 removal from the bloodstream, elevated circulation capacity, increased g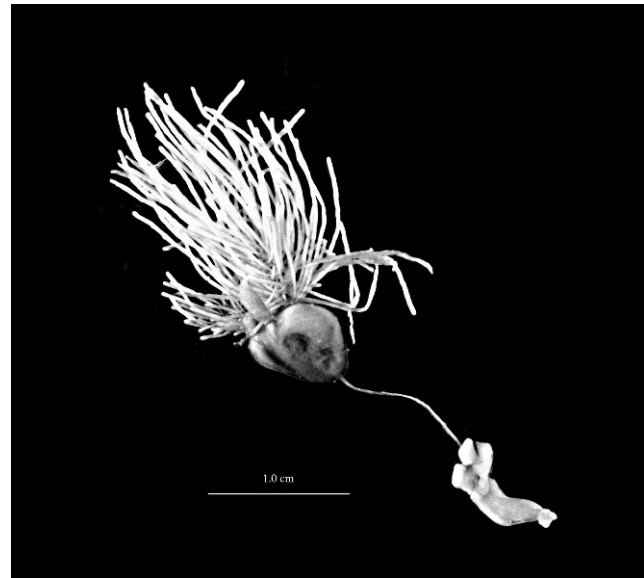ill surface area, reduced blood-to-water diffusion distanc-es, and increased blood pigment affinity for oxygen (Childress and Siebel, 1998; Schneider and Bush-Brown, 2003).

There is evidence that OMZ benthos maximize oxygen uptake through morphological and physiological adaptation (Schneider and Bush-Brown, 2003; Levin, 2003). As far as we know, the role of the posterior processes present in the sphyriids is still unknown, and Kabata (1979) suggested that these structures might represent modified caudal rami. A similar "pattern of repeatedly branching growth" (Ho and Kim, 1989) and structure of the posterior processes has been observed, at least, for *L. pentaloba*, which was found attached to *N. bairdii* and *C. armatus* collected in the New York Bight near the Grand Banks (south of Newfound-land), at depths of 828-914 m and 2931-2967 m, respec-tively (Ho and Kim, 1989). The depths at which *L. brevicollum* was found (880 m depth in the San Pedro Channel, from 600-800 m depth in the Eastern Tropical Pacific, and 1270 and 1295 m deep off Sinaloa) lie within the depth range of *L. pentaloba*. The similar posterior processes of *L. pentaloba* and *L. brevicollum* are hypoth-esized to be an adaptation to high hydraulic pressure and/or poorly oxygenated deep waters. For poorly oxygenated deep waters, the posterior processes of the above mentioned two species might enhance oxygen uptake through increasing their body surface. Similar adaptations have been observed in bottom-crawling crustaceans, mysids, fishes, cephalopods and polychaete worms (Levin, 2002). If a similar scenario as in the observed for the genus *Coryphaenoides* (Morita, 1999; see above) is assumed for the genus *Nezumia* from southern California, from the Gulf of California and from the Eastern Tropical Pacific, and also assuming a high degree of host specificity (*Nezumia liolepis*, and probably *L. brevicollum* as well, are endemic to the eastern Pacific) and a close relationship between *L. tetraloba* and *L. brevicollum*, it seems reasonable to envisage a scenario in which these two species diverged

from a common ancestor through allopatric speciation, with the oxygen minimum layer and hydrostatic pressure being the possible physical mechanisms responsible for the breakdown in genetic cohesion and subsequent speciation. An example of genetic differentiation can be found between populations of the myctophid *Triphoturus mexicanus* (Gilbert, 1890) (Pisces: Myctophidae), whose levels of genetic differentiation between the northern (from South Francisco to southern Mexico) and southern (from Guatemala to Chile) populations is sufficiently high that their taxonomic status is uncertain (Creasey and Rogers, 1999; Rogers, 2000), the oxygen minimum zone being, in such cases, an effective barrier for species distribution.

Diebakate et al. (1997) provided the diagnosis for the genus *Thamnocephalus* and described its only species, *T. cerebrinoxius* Diebakate, Raibaut and Kabata, 1997 but omitted any comment regarding its phylogenetic position. A few years later, Raibaut (1999) changed the name *Thamnocephalus* to *Driocephalus* and Benz et al. (2006) presented a new cladogram for Sphyriidae based on a new data set with fewer and different characters, and utilizing a different coding regime questioned Dojiri and Deets' (1988) analyses and conclusions. Following Dojiri and Deets (1988), *Periplexis* and *Paeonocanthus* are the sister taxa of the lineage *Lophoura-Sphyrion* and suggested that "the conspicuous distinction between *Norkus* and the remaining three genera of the *Tripaphylus*-clade is reflected in the host cladogram''. *Norkus* was collected from Rajiformes while *Tripaphylus*, *Paeon*, and *Opimia* were collected from Carcharhiniformes. *Periplexis* and *Paeonocanthus* were found in Salmoniformes, while *Lophoura* and *Sphyrion* share two host orders, the Gadiformes and Perciformes. Additionally, *Lophoura* has been found in Anguilliformes, and *Sphyrion* in Scorpaeniformes and Pleuronectiformes. Dojiri and Deets (1988) observed that their parasite-inferred host phylogeny largely corresponds to that suggested by ichthyologists (see Nelson, 1984, 2006) except for the "relatively apomorphic placement of the presumably plesiomorphic Anguilliformes" (Dojiri and Deets, 1988), and suggested a probable back-colonization of the eel-parasitizing species of *Lophoura* to that host order.

In their report of new locality records and a new host for *D. cerebrinoxius*, Benz et al. (2006) observed the need of a cladistic analysis to propose a hypothesis of the phylogenetic relationships of *Driocephalus* to other sphyriid genera, which were omitted by Diebakate et al. (1997). Benz et al. (2006) showed their concern regarding the use of body condition (character A in Dojiri and Deets (1988)), egg sac length (character B in Dojiri and Deets (1988)), shape and length of posterior processes (characters D-J in Dojiri and Deets (1988)), shape of the genital complex (characters K and L in Dojiri and Deets (1988)), shape of the cephalothorax (characters R and S in Dojiri and Deets (1988)), and shape of the gut diverticula, antennule and antenna (characters V, W and X in Dojiri and Deets (1988)). Conversely, Benz et al. (2006) accepted Dojiri and Deets' (1988) character N (neck holdfast: absent/multiple planes) in their character states a, b, c and d of character No. 5 (Cephalothorax) (Benz et al. (2006: 3, Table 1), and

Table 1. Characters and character states for Sphyriidae, modified from Dojiri and Deets (1997).

Character	Character state
A	Body condition: nonrotated/rotated
B	Egg sac length: moderate/elongate
C	Neck length: moderate/elongate
D	Posterior processes: diminutive/prominent
E	Posterior processes: tubercular/single, medium or long, cylindrical
F	Posterior processes: tubercular/single, short, cylindrical
G	Posterior processes: tubercular/single, short, transversely constricted
H	Posterior processes: tubercular/complex, branching
I	Posterior processes: tubercular/branching, grapelike
J	Posterior processes: tubercular/multiple cylinders
K	Genital complex: ovoid/discoid
L	Genital complex: ovoid/gradually expanding
M	Neck holdfast: absent/collar
N	Neck holdfast: absent/multiple planes
O	Neck holdfast: absent/single plane
P	Cephalothorax: cylindrical/branching (antlerlike or dendritic)
Q	Cephalothorax: cylindrical/lateral aliform expansions
R	Cephalothorax: cylindrical/bulbous
S	Cephalothorax: cylindrical/bulbous with protuberances
T	Cephalothorax: cylindrical/lateral hornlike projections
U	Cephalothorax: cylindrical/paired rounded protuberances
V	Gut diverticula: simple/anastomosing
W	First antenna: digitiform/reduced lobe
X	Second antenna: biramous/reduced lobe

combined this with the shape of the cephalothorax (compact/compact or not) in their character states a and b only. Benz's et al. (2006) trees were not congruent with that of Dojiri and Deets (1988) but observed that the genus *Paeon* could be represented by two distinct groups (*Paeon* group A, and *Paeon* group B) which are different in Benz's et al. (2006) character 3 (shape and length of the trunk). Also, they observed that *Driocephalus* (which infects elasmobranchs) appeared as the sister taxon of *Lophoura* (which infects teleosts) in 50% of all shortest trees, and of the clade *Lophoura-Sphyrion* (which infects only teleosts) in 50% of the remaining shortest trees, questioning the results of Dojiri and Deets (1988) regarding the presence of two clades, one infecting only elasmobranchs and the other infecting only teleosts. However, Benz et al. (2006) did not consider their trees robust enough to support any ecological association amongst sphyriids, and suggested that a robust phylogeny should be sought with molecular tools. Our analysis based on the character states of Table 1 and the character matrix in Table 2 (both slightly modified from Dojiri and Deets (1988)) resulted in a single tree with a length of 25 and a CI of 0.96 (Fig. 8), in which *Driocephalus* is placed as the sister taxon to *Norkus*, in the elasmobranch clade.

Briefly and as expected from the new character data set, the new cladogram is largely congruent with that of Dojiri and Deets (1988). Two clades were observed, one consisting of *Driocephalus*, *Norkus*, *Tripaphylus*, *Paeon* and *Opimia*, which parasitize elasmobranchs, and the other composed by *Paeonocanthus*, *Periplexis*, *Sphyrion* and *Lophoura*, which parasitizes teleostei. The first clade seems to be defined by character E (Table 1). Within this clade, *Driocephalus* and *Norkus* are defined by characters M and

Table 2. Character data matrix for Sphyriidae. Codes 0/1 indentify plesiomorphic/apomorphic character states (note that code 0 does not necessarily indicate absence). Modified from Dojiri and Deets (1988).

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X
Out-group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Norkus	1	1	1	1	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	0
Paeon	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	0	1	0	0	0
Tripaphylus	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	0
Opimia	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Periplexis	1	1	1	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
Paeonocanthus	1	1	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1
Lophoura	1	1	1	1	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1	1
Sphyrion	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1
Driocephalus	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1

P, whereas *Tripaphylus*, *Paeon* and *Opimia* share characters L and R. *Driocephalus* seems to be defined by characters W and X, and *Norkus* by character K. *Tripaphylus* and *Paeon* share character S, being the former defined by character T, and the latter by character U. The teleostei-parasitizing clade is defined by characters W and X, which as mentioned above, defines also *Driocephalus*, suggesting that the digitiform first antenna and the biramous second antenna might have evolved independently in *Driocephalus* and the teleostei-parasitizing clade. *Paeonocanthus* and *Periplexis* are defined by characters F and N (*Periplexis*

being defined by character G), while *Sphyrion* and *Lophoura* are defined by characters H and V (*Sphyrion* being defined by characters I and Q, and *Lophoura* by characters J and O). Thus our cladogram is consistent with the ecological summary cladogram proposed by Dojiri and Deets (1988).

Driocephalus was originally reported from the nasal capsule of *Leptocharias smithii* (Müller and Henle, 1839), *Carcharhinus plumbeus* (Nardo, 1827), and *Iago omanensis* (Norman, 1939) (Carcharhiniformes) (Diebakate et al., 1997). In fact, the attachment site for *Driocephalus* is the
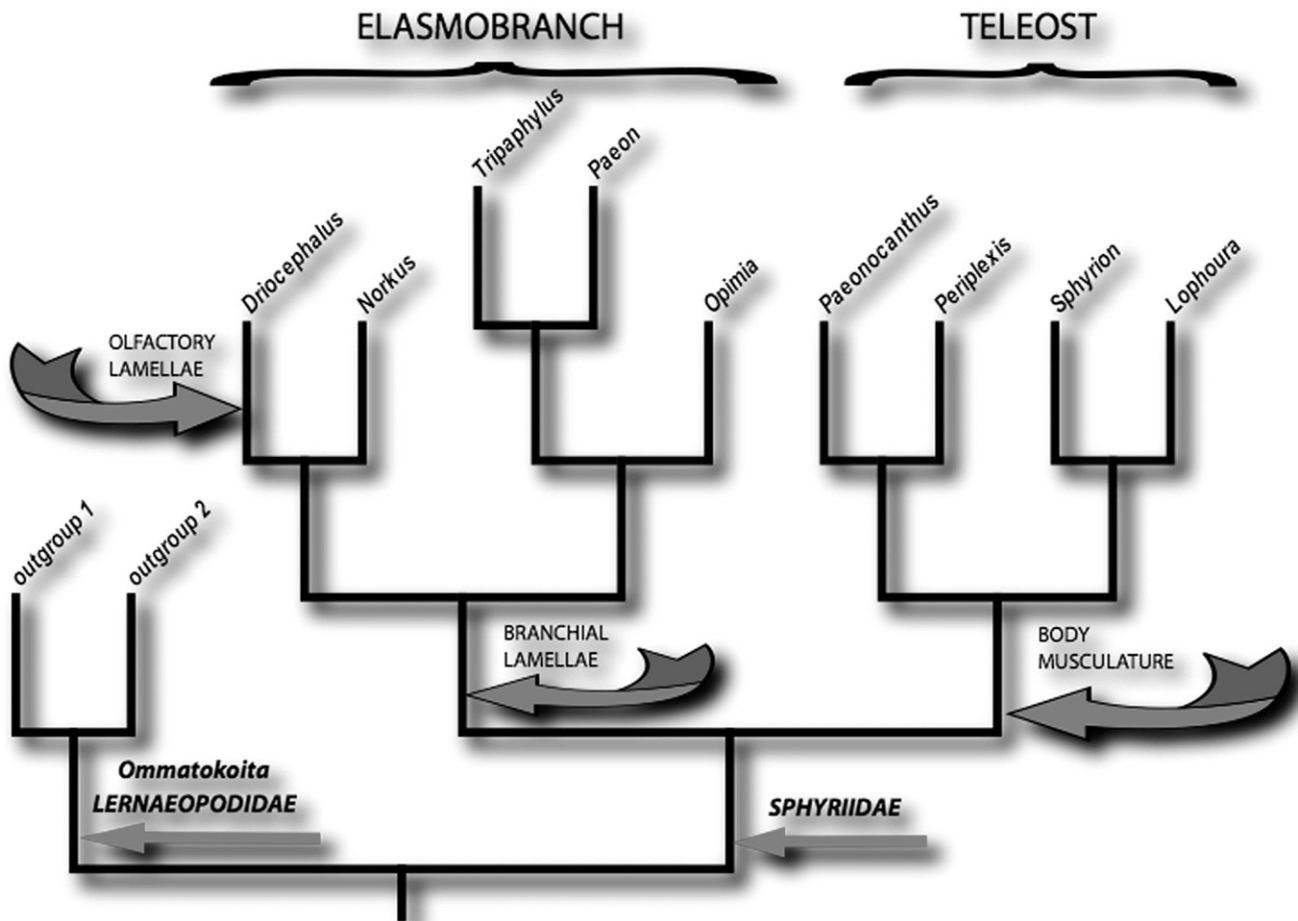

Fig. 8. Cladogram of Sphyriidae based on the character-state matrix of Table 1 and 2. Modified from Dojiri and Deets (1988).

olfactory lamellae of elasmobranchs (with the dendritic cephalothoracic holdfast penetrating the olfactory lobe), not the branchial lamellae as in the remaining cohorts of this clade. Although elasmobranch olfactory and branchial components include an infolding of ectoderm, they develop with completely different and unrelated ontogenetic trajectories (John Maisey, American Museum of Natural History, personal communication). Hence, the branchial and olfactory lamellae are actually analogous attachment sites (not serial homologs), creating an even more complex and interesting ecological summary cladogram than what was originally posited by Dojiri and Deets (1988).

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