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A Redescription of *Lepeophtheirus longipes* Wilson, 1905 (Copepoda; Caligidae) Parasitic on Giant Sea Bass, *Stereolepis gigas* Ayres, 1859 (Polyprionidae), off California

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Abstract.—The giant sea bass (GSB), *Stereolepis gigas* Ayres, 1859, is the largest teleost (exceeding 2 m in length and 200 kg in weight) and megacarnivore found in California kelp forest communities. Overfishing of GSB in the late 1920s crashed the population off California and in 1996 it was classified as an International Union for Conservation of Nature (IUCN) critically endangered species. Recently, three GSB were collected off San Onofre, California and held at the Southern California Marine Institute in San Pedro. Two of the three GSB were infected with *Lepeophtheirus longipes* Wilson, 1905 (Siphonostomatoida; Caligidae), a poorly described species of parasitic copepod previously recorded from the GSB and purportedly on other fish hosts. In this study, a detailed redescription of the female and the first description of the male of *L. longipes* are provided and all records of *Lepeophtheirus longipes* are reviewed. The latter revealed that *L. longipes* is host specific to GSB. *Lepeophtheirus longipes* is distinguished from its congeners by a combination of female characters that includes: (1) genital complex with prominent posterolateral lobes and is about half the length of the cephalothorax and just over two times longer than the cylindrical, indistinctly 2-segmented abdomen; (2) an antennule with a small conical process on the proximal segment; (3) maxillule with an outer conical process at the base of the dentiform process; (4) sternal furca with pointed and slightly splayed tines; (5) first exopodal segment of leg 3 with a terminal spine; and (6) third exopodal segment of leg 4 with three unequal apical spines.

The giant sea bass (GSB), *Stereolepis gigas* Ayres, 1859 (Polyprionidae Bleeker, 1874), is the largest teleost and megacarnivore found in California, U.S.A. kelp bed communities. It ranges from Humboldt Bay, northern California to Oaxaca, southern Mexico, including the Gulf of California (Love and Passarelli 2020), but is most common from southern California southward along Baja California and into the Gulf of California (Allen and Andrews 2012). It forms spawning aggregations during the summer months (July-September) (Shane et al. 1996) and is often found in kelp forests on rocky reefs as adults, while juveniles are found at sandy bottom areas (Domeier 2001).

These large, demersal teleosts reach lengths longer than 2 m, weights greater than 200 kg, ages of up to 76 yrs, and are apex predators (Horn and Ferry-Graham 2006; Allen

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and Andrews 2012; Hawk and Allen 2014; Chabot et al. 2015; House et al. 2016; Allen 2017). Like many apex predators, these fish grow slowly and were historically easily overfished. At the end of the 1920s, the commercial fishing fleet out of San Pedro, California was growing and began fishing (gill netting and hand lining) GSB in earnest, often targeting their spawning aggregations in the summer months. This practice led to the near complete demise of the GSB fishery off California by 1934 (Croker 1937). Since 1934, the only appreciable commercial landings of GSB were from off Baja California. Their commercial landings and populations decreased to almost nothing until, in 1982, the Mexican government prohibited the commercial take of this species from Mexican waters. In the same year, the California Department of Fish and Game (now the California Department of Fish and Wildlife - CDFW) placed a complete moratorium on the recreational catch, and the commercial catch was limited to two fish and later to one per trip. In fact, the population of GSB dwindled so rapidly during the 20th century that they are now on the International Union for Conservation of Nature (IUCN) Red List as a critically endangered species (Musick et al. 2000; Cornish 2004). Then, in 1990, the voters of California passed Proposition 132, which banned all gill netting from inshore waters and up to three miles offshore. Its implementation in 1994 has benefited some predatory fishes, including GSB (Pondella and Allen 2008), and the GSB population now appears to be in the early stages of recovery (Allen 2017).

Recently, three GSB were captured off southern California and then transported to the Southern California Marine Institute (SCMI) in San Pedro for morphological studies. Two of the three GSB were infected with at least 60 individuals of *Lepeophtheirus longipes* Wilson, 1905 (Siphonostomatoida Burmeister, 1835; Caligidae Burmeister, 1835), a species of parasitic copepod that was poorly described based on two females (host and locality unknown) and later recorded from GSB, kelp bass, *Paralabrax clathratus* (Girard, 1854) (Serranidae Swainson, 1839), and treefish, *Sebastes serriceps* (Jordan & Gilbert, 1880) (Scorpaenidae Risso, 1826), captured off the California coast and from other fish hosts caught in far-flung localities (Table 1). *Lepeophtheirus* von Nordmann, 1832 is the second most speciose genus of the family Caligidae, with 125 valid species and 2 recognized subspecies (Walter and Boxshall 2021). Although members of *Lepeophtheirus* (and other caligid genera) are predominantly external parasites of marine fishes (Dojiri and Ho 2013), the adult female of *Lepeophtheirus semicossyphi* Yamaguti, 1939 and *Lepeophtheirus alvaroi* Suárez-Morales and Gasca, 2012 are known to occur in the plankton (Venmathi Maran et al. 2016).

Due to the small population size and protection status of the GSB host, reports in the primary literature of *L. longipes* in California have been sparse (Wilson 1908, 1921a; Hobson 1971). We take this opportunity to provide a redescription by modern standards of *L. longipes* based on the new material and to review all records of *L. longipes*.

Materials and Methods

Three GSB, ranging from 1.15-1.39 m Total Length and 28.9-49.5 kg, were collected by hook and line (CDFW Scientific Collecting Permit #000032 issued to LGA) approximately 3 km offshore from an onshore point slightly southeast of the San Onofre Nuclear Generating Station (33º20.612'N, 117º34.132'W) in August and September 2017 (Table 2). All three fish were subsequently transported alive to the SCMI where they were held in captivity in tanks.

Table 1. Historical records of fish hosts and localities for *Lepeophtheirus longipes*.

Host family	Host species	Locality	Reference
Unknown	Unknown	Unknown	Wilson (1905)
Polyprionidae	*Stereolepis gigas* Ayres, 1859	La Jolla, California, U.S.A.	Wilson (1908)
Serranidae	*Paralabrax clathratus* (Girard, 1854)	Catalina Island, U.S.A.	Wilson (1921a)[a]
Sciaenidae	*Argyrosomus regius* (Asso, 1801) (as *Sciaena aquila*)	Mauritania; Mediterranean Sea from Gibraltar to Cape Bon, Tunisia	Brian (1924)[b]; Rose and Vaissière (1953)[c]
	Argyrosomus regius (Asso, 1801)	Mediterranean Sea	Raibaut et al. (1998)[d]
Echeneidae	*Echeneis naucrates* Linnaeus, 1758	Port Etienne, Mauritania	Brian (1924)[b]
Haemulidae	*Plectorhinchus mediterraneus* (Guichenot, 1850) (as *Diagramma mediterraneum*)	Mauritania	Brian (1924)[b]
Scorpaenidae	*Sebastes serriceps* (Jordan & Gilbert, 1880)	Southern California, U.S.A.	Hobson (1971)[e]
Scorpaenidae	*Sebastes maliger* (Jordan & Gilbert, 1880) (as *Sebastodes maliger*)	San Juan Islands, Washington, U.S.A.	Nichols (1975)[f]

[a] Copepod specimens were reported as *L. longipes*, but examination of voucher specimens revealed they are *Lepeophtheirus constrictus* Wilson, 1908.

[b] Copepod specimens were reported as *L. longipes*, but examination of digital photographs of these specimens revealed they are not conspecific with *L. longipes*.

[c] The locality for this record is provided in Rose and Vaissière (1952). Also, this record of *L. longipes* from *A. regius* is doubtful.

[d] This record of *L. longipes* from *A. regius* is doubtful.

[e] Copepod specimens were reported as *L. longipes*, but they were likely *Lepeophtheirus paulus* Cressey, 1969.

[f] Copepod specimens were reported as *L. longipes*, but examination of voucher specimens revealed they are *Lepeophtheirus oblitus* Kabata, 1973.

All three fish were treated with a freshwater dip and detached copepods were collected and then preserved in 70% ethanol. Two of the three fish were infected: fish designated SOK-1 had few copepods while SOK-2 harbored many copepods (LGA, personal observation). Microscopic examination, measurements, and illustrations of copepod

Table 2. Giant sea bass collection information.

Specimen	Date of Capture	Location	Vessel	Time of Day	Total Length (m)	Weight (kg)	Disposition
SOK-1	8/29/17	San Onofre Kelp	MV Reel Fun	10:45 AM	1.39	49.5	Tank at SCMI expired 9/11/17
SOK-2	8/29/17	San Onofre Kelp	MV Reel Fun	11:15 AM	1.15	28.9	Tank at SCMI
SOK-3	9/28/17	San Onofre Kelp	SCE Parker 2520	11:30 AM	1.24	36.1	Tank at SCMI

specimens follow Passarelli and Tang (2017). In the description, length measurements are provided first, followed by width measurements; all measurements given are expressed as the mean followed by the range in parentheses. Morphological terminology follows Huys and Boxshall (1991) and Dojiri and Ho (2013). Fish classifications and names conform to Froese and Pauly (2020) and Love and Passarelli (2020). Voucher specimens are deposited at the Crustacea Department of the Natural History Museum of Los Angeles County (LACM), Los Angeles, California, and at Cabrillo Marine Aquarium (CMA), San Pedro, California.

The following specimens of *L. longipes* deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, D.C., U.S.A., and the Muséum national d'Histoire naturelle (MNHN), Paris, France, were examined for comparative purposes:

1. Preserved material comprising 1 female syntype (USNM 12488), host, locality, and collection date unknown.
2. Preserved material comprising 27 females (USNM 38567), ex *Stereolepis gigas*, La Jolla, California, U.S.A., May 18, 1906, collected by J. F. McClendon, identified by C. B. Wilson.
3. Preserved material comprising 5 females (USNM 74301), ex outside of jewfish (=giant sea bass), La Jolla, California, U.S.A., July 1907, collected by J. F. McClendon, identified by C. B. Wilson.
4. Preserved material comprising 6 females and 3 males (USNM 49779), ex mouth of *Paralabrax clathratus*, Crescent Bay, Santa Catalina Island, U.S.A., June 19, 1913, collected by P. S. Barnhart, identified by C. B. Wilson.
5. Preserved material comprising 7 females and 1 male (USNM 180909), ex surface of *Sebastes maliger* (as *Sebastodes maliger*), San Juan Islands, Friday Harbor, Washington, U.S.A., collection date unknown, identified by R. F. Cressey.
6. Five digital photographs of 1 female (MNHN-IU-2007-2964 (=MNHN-Cp53)), ex mouth of *Echeneis naucrates*, Mauritania, 1923, collected by T. Monod, identified by A. Brian.
7. Five digital photographs of 1 female (MNHN-IU-2007-2975 (=MNHN-Cp54)), ex *Plectorhinchus mediterraneus* (as *Diagramma mediterraneum*), Mauritania, May 1923, collected by T. Monod, identified by A. Brian.
8. Three digital photographs of 1 male (MNHN-IU-2007-2986 (=MNHN-Cp55)), ex tail of *Argyrosomus regius* (as *Sciaena aquila*), Mauritania, May 1923, collected by T. Monod, identified by A. Brian.
9. Six digital photographs of 2 females (MNHN-IU-2007-3008 (=MNHN-Cp57)), ex gills of *Argyrosomus regius* (as *Sciaena aquila*), Mauritania, April 1923, collected by T. Monod, identified by A. Brian.

Digital photographs of the maxillulary dentiform process and the distal exopodal segment of leg 1 (both appendages mounted on the same slide) of the holotype female of *Lepeophtheirus interitus* Wilson, 1921, deposited in the Swedish Museum of Natural History (SMNH-98034), were also examined for comparative purposes.

Results

Lepeophtheirus longipes Wilson, 1905
(Figs. 1-6)

Material examined. 36 ovigerous females (3 dissected), 4 mature non-ovigerous females, 16 immature females, and 4 males (1 dissected), ex 1 *Stereolepis gigas*, off San Onofre, California, U.S.A., August 29, 2017, collected by L. G. Allen. Six females and 1 male (LACM:DISCO:19981) deposited at LACM; 6 females and 1 male (CMA 2020.04.0003) deposited at CMA.

Description of adult female. Body (Fig. 1A) 8.27 (8.10-8.53) mm long (excluding caudal setae) (n = 4). Cephalothoracic shield subcircular, slightly longer than wide [4.36 (4.30-4.43) mm × 4.03 (3.98-4.10) mm], with well-developed paired frontal plates; posterior margin of thoracic zone extending beyond posterior limit of lateral zone; hyaline membrane present along margin of frontal plates and lateral zones. Free fourth pedigerous somite about two times wider than long [0.72 (0.70-0.73) mm × 1.54 (1.50-1.60) mm] and indistinctly separated from genital complex. Genital complex slightly longer than wide [2.24 (2.18-2.40) mm × 1.92 (1.79-2.08) mm], about half the length of cephalothoracic shield and slightly over two times longer than abdomen, with prominent posterolateral processes and numerous spiniform sensilla (Fig. 4C). Abdomen indistinctly separated from genital complex, composed of 2 indistinct somites, 631 (610-650) μm × 480 (460-500) μm and 368 (340-400) × 455 (430-475) μm, respectively. Caudal ramus (Fig. 1B) longer than wide [310 (280-330) μm × 183 (170-195) μm], with 1 unipinnate and 5 plumose setae (seta I absent) plus short row of setules along inner distal margin; seta II situated on ventral surface near insertion of seta III. Egg sacs (not figured) uniseriate.

Antennule (Fig. 1C) 2-segmented. Proximal segment longer than distal segment, bearing 1 small bifid process on posterodistal corner and 1 small conical process plus 27 setae (25 hirsute and 2 variably ornamented—see Variability section below) along anterior margin. Distal segment cylindrical, bearing 12 naked setae and 2 aesthetascs (2 setae near posterodistal corner share a common base; 1 apical seta and 1 apical aesthetasc share a common base).

Antenna (Fig. 1D) 3-segmented, comprising coxa, basis and 1-segmented endopod incorporating distal claw; situated on pedestal. Coxa with acuminate, posteriorly-directed process. Basis stout, with corrugated surface on inner distal corner and 1 corrugated adhesion pad (Fig. 1E) on dorsolateral surface. Endopod long, uncinate, bearing 1 finely spinulate proximal seta and 1 naked seta at middle of claw.

Postantennal process (Fig. 1F) recurved, with pair of setulose papillae on base and 1 setulose papilla posterior to base.

Mandible (Fig. 2A) modified into elongate stylet bearing distolateral hyaline membrane and 12 distomedial teeth.

Maxillule (Fig. 2B) composed of trisetose papilla and bifid dentiform process; latter with small, proximolateral conical process and subequal tines (outer tine slightly more curved than inner tine).

Maxilla (Fig. 2C), brachiform, 2-segmented, composed of elongate, unarmed syncoxa and slender basis. Basis with flabellum at mid-length plus long apical calamus and shorter subapical canna; calamus with finely serrated membranes along anterior margin; canna with finely serrated posterior margin.

Maxilliped (Fig. 2D-E) large, subchelate, 3-segmented, comprising long protopod (corpus) and subchela consisting of free endopodal segment (shaft) and claw. Protopod with small, semispherical process in myxal area plus 3 patches of crescentic denticles and 1 tiny element on anterior surface. Shaft with tiny distal element on posterior surface. Claw with naked proximal seta on posterior surface.

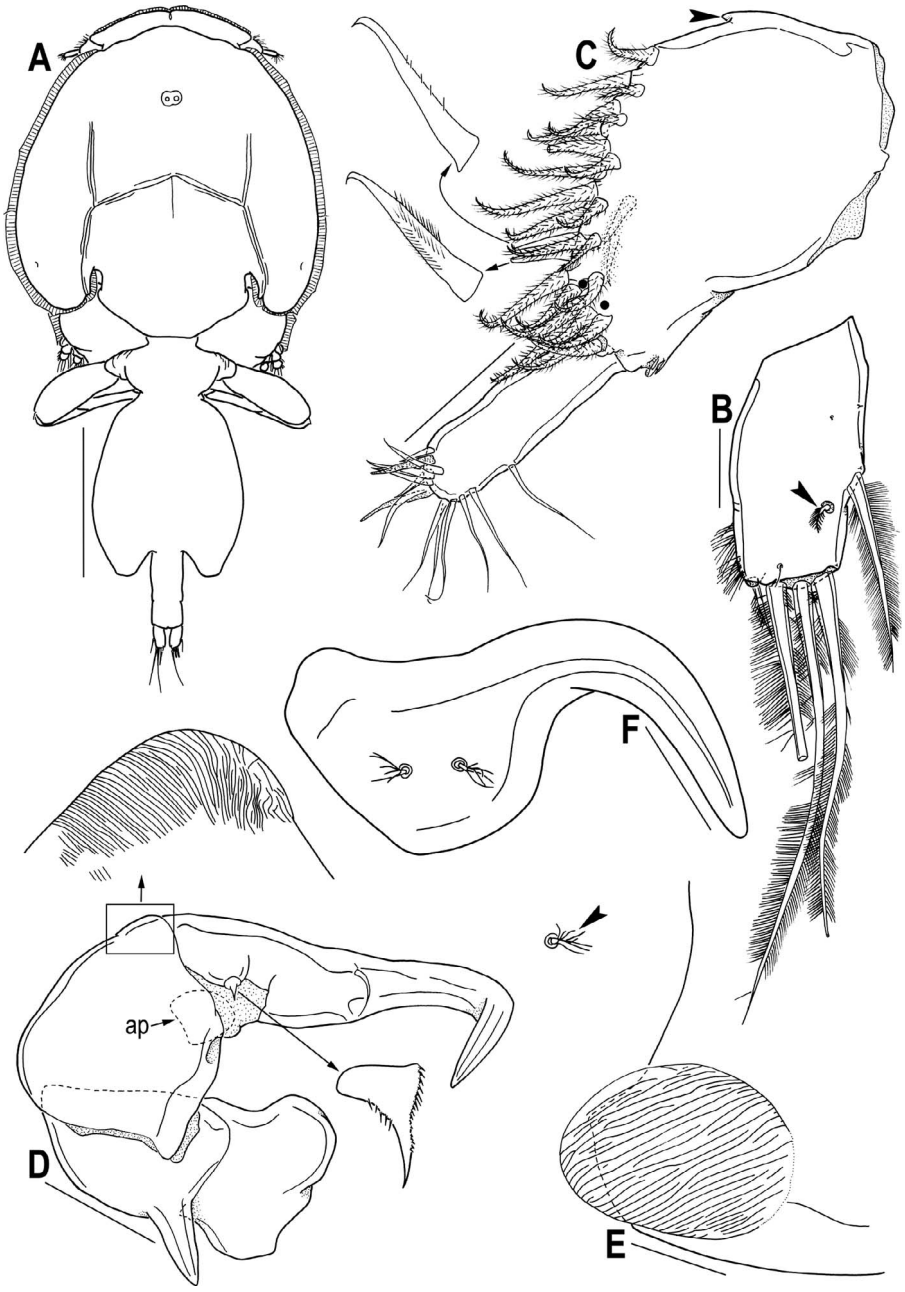

Fig. 1. *Lepeophtheirus longipes* Wilson, 1905, adult female. A) Habitus, dorsal; B) Left caudal ramus (arrowhead indicates seta II), ventral; C) Right antennule with detail of two subapical setae inserted on dorsal surface of anterior margin, black circles indicating position of additional setae on male antennule, and arrowhead indicating conical process on proximal segment, ventral; D) Left antenna with detail of anterodistal corner of second segment (ap = adhesion pad) and proximal seta on third segment, ventral; E) Adhesion pad on posterodistal corner of second segment of left antenna, dorsal; F) Postantennal process (arrowhead indicates multifurcate sensillum on ventral surface of cephalothorax), ventral. Scale bars: 2.00 mm for A; 100 μm for B, F; 150 μm for C; 200 μm for D; 50 μm for E.

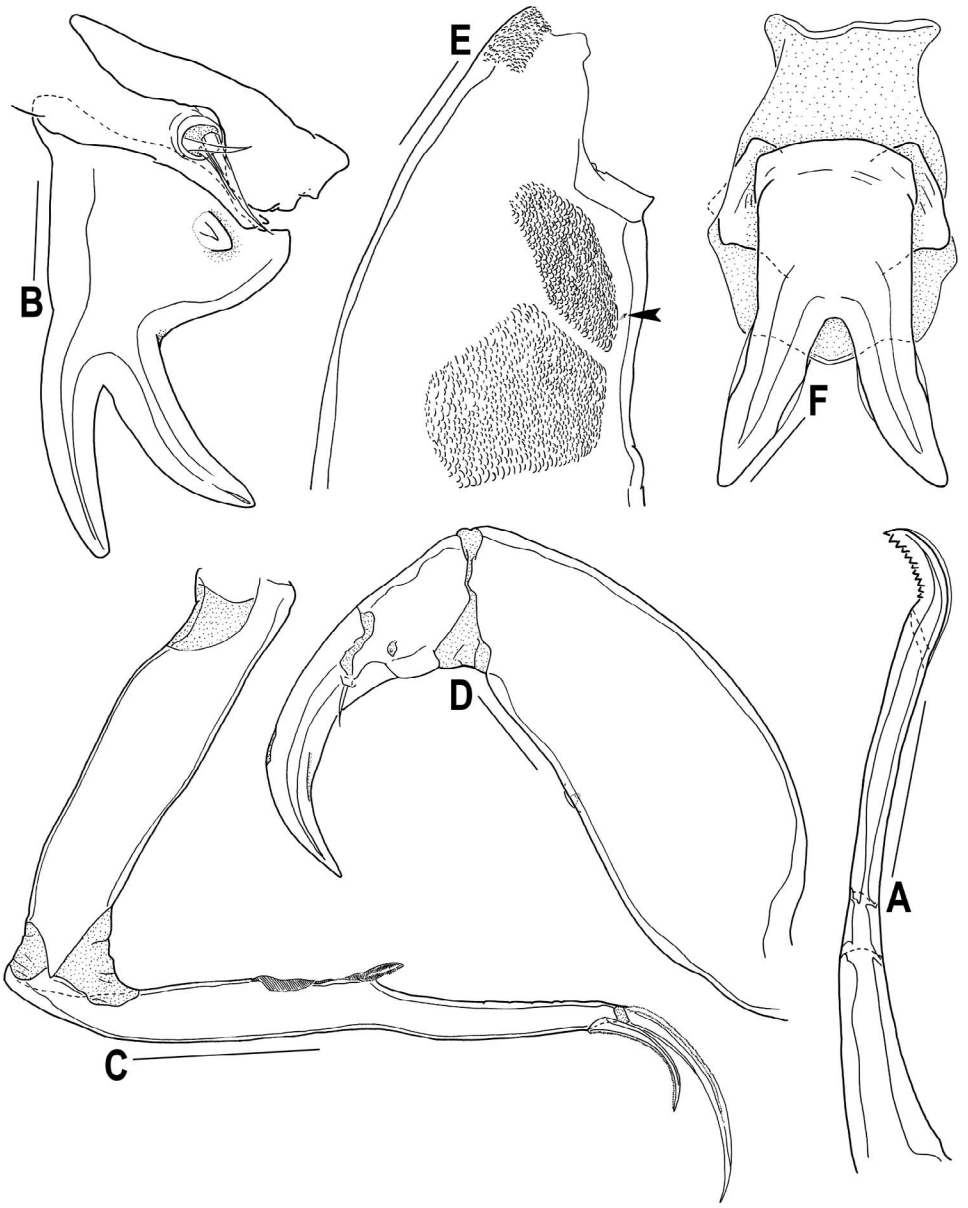

Fig. 2. *Lepeophtheirus longipes* Wilson, 1905, adult female. A) Right mandible, anterior; B) Left maxillule, ventral; C) Left maxilla, posterior; D) Left maxilliped, posterior; E) Distal half of protopod of left maxilliped (arrowhead indicates minute inner element), anterior; F) Sternal furca, anterior. Scale bars: 100 μm for A, B, E, F; 300 μm for C; 150 μm for D.

Tines of sternal furca (Fig. 2F) as long as box, splayed apart, furnished with short hyaline flange on outer and inner margins, and pointed at tip.

Legs 1 to 3 (Figs. 3A, E, G) biramous; leg 4 (Fig. 4A) uniramous. Armature formula of legs 1-4 is shown in Table 3.

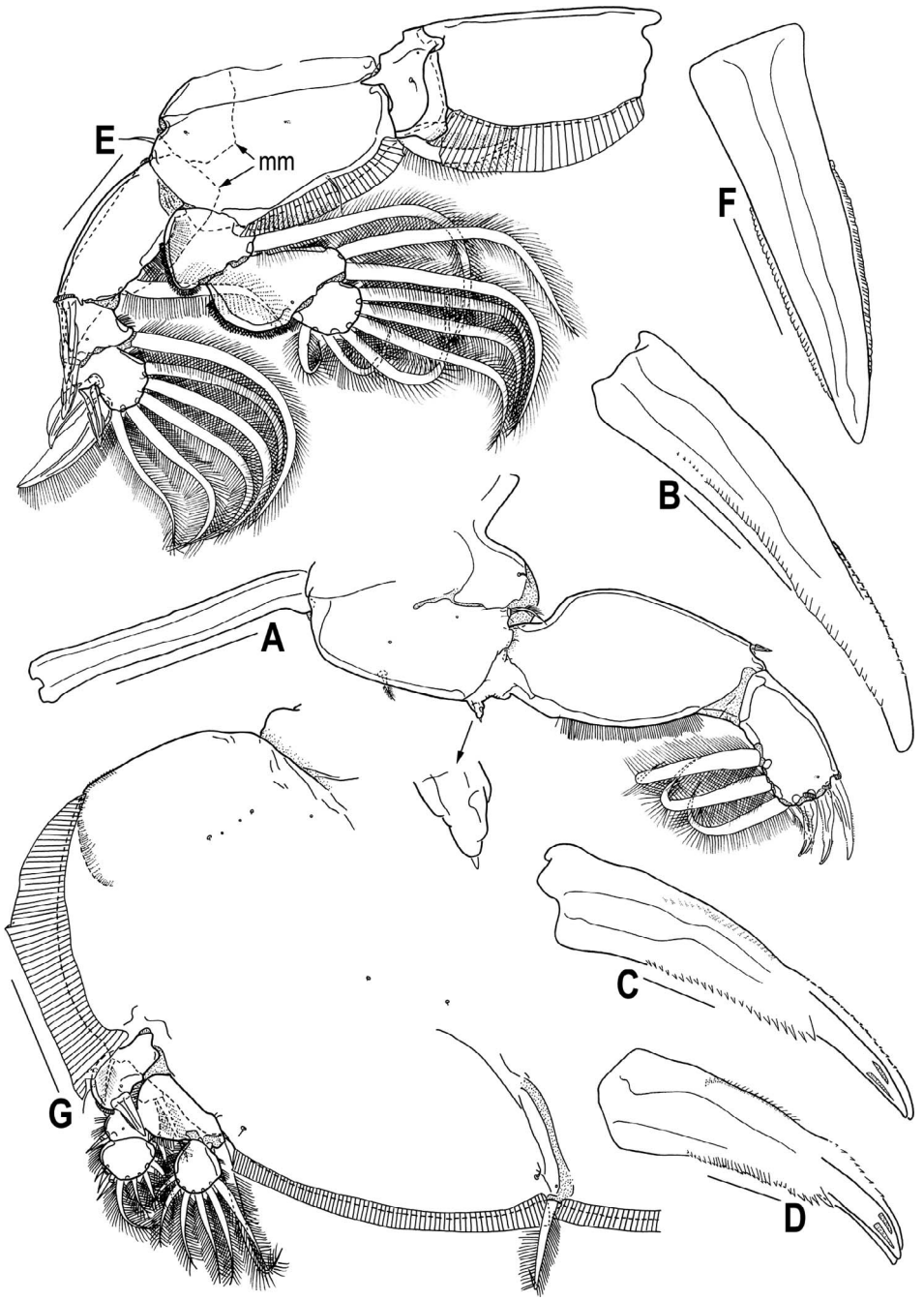

Fig. 3. *Lepeophtheirus longipes* Wilson, 1905, adult female. A) Left leg 1 with detail of endopod, anterior; B) Outer apical spine on second exopodal segment of left leg 1, anterior; C) Middle apical spine on second exopodal segment of left leg 1, anterior; D) Inner apical spine on second exopodal segment of left leg 1, anterior; E) Right leg 2 (mm = marginal membrane), anterior; F) Outer spine on middle exopodal segment of right leg 2, anterior; G) Right leg 3, ventral. Scale bars: 300 μm for A, G; 25 μm for B, C, D; 250 μm for E; 50 μm for F.

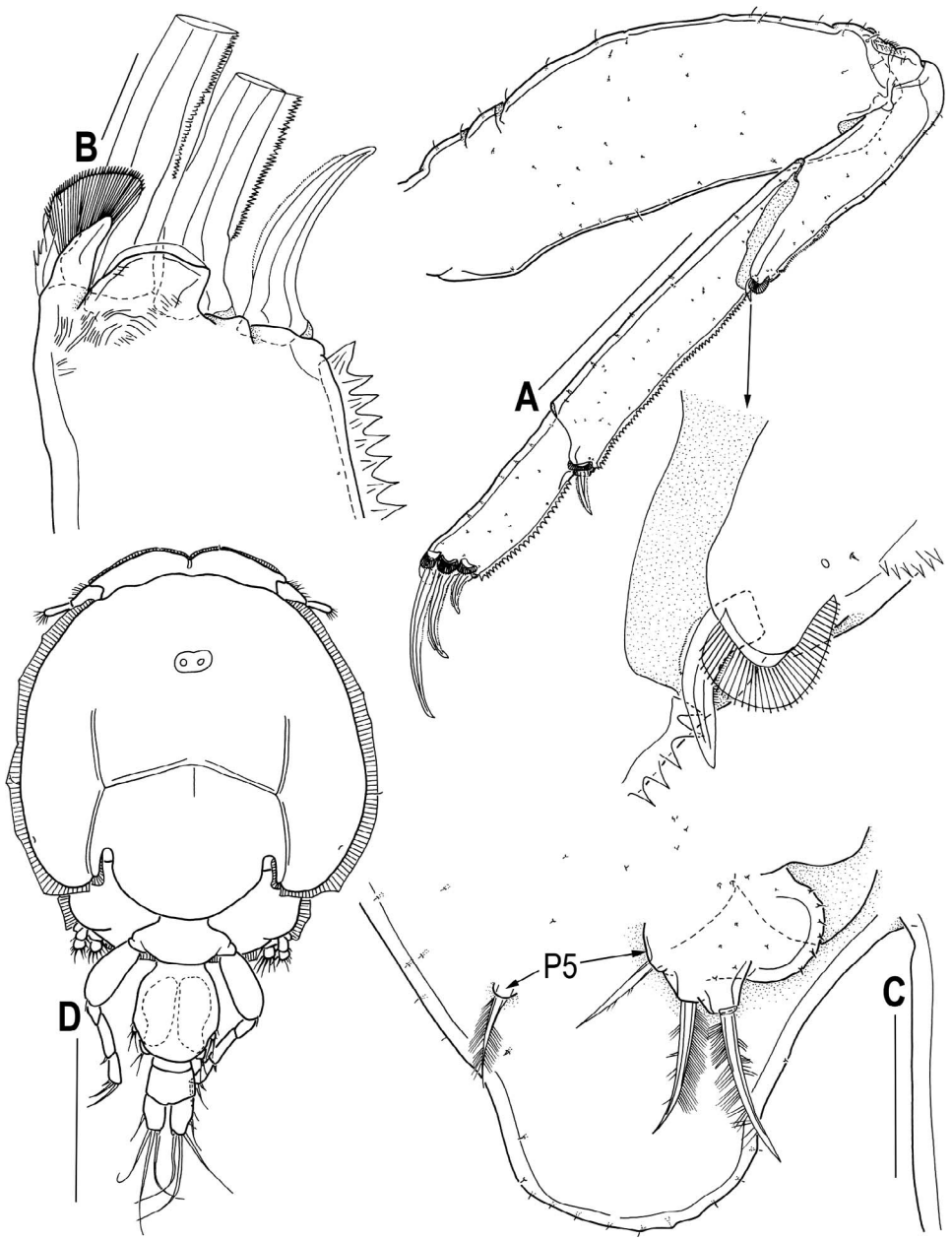

Fig. 4. *Lepeophtheirus longipes* Wilson, 1905, adult female (A-C) and adult male (D). A) Left leg 4 with detail of outer spine on first exopodal segment, ventral; B) Tip of third exopodal segment of left leg 4, dorsal; C) Posterolateral process of genital complex showing leg 5 (P5), ventral; D) Habitus, dorsal. Scale bars: 600 μm for A; 50 μm for B; 200 μm for C; 1.00 mm for D.

Table 3. Armature on legs 1-4 (Roman numerals = spines; Arabic numerals = setae).

	Coxa	Basis	Exopod	Endopod
Leg 1*	0-0	1-1	I-0; 0,III+1,3	vestigial
Leg 2	0-1	1-0	I-1; I-1; II,I,5	0-1; 0-2; 6
Leg 3*	0-1	1-0	I-1; I-1; II,I,4	0-1; 6
Leg 4*	0-0	1-0	I-0; I-0; 0,III,0	absent

*Although the coxa and basis are fused to form a protopod in this leg, these segments are treated separately in this Table.

Leg 1 (Fig. 3A) intercoxal sclerite naked and elongate. Protopod with 1 outer and 1 inner plumose setae, 1 proximolateral setulose papilla, and 2 surface pores. First exopodal segment with 1 small, naked outer spine and inner row of setules. Second exopodal segment with 3 apical spines (inner spine shortest), 1 apical seta, 3 inner plumose setae, surface pore near apical margin, and pectinate membrane at base of each apical spine; outer apical spine (Fig. 3B) with row of tiny denticles along distal half of anterior margin and row of small denticles along posterior margin; middle and inner apical spines (Fig. 3C-D) each with an accessory process and 2 rows of tiny denticles along anterior margin and row of larger denticles along posterior margin; apical seta plumose and as long as inner apical spine. Endopod vestigial, bearing 1 tiny apical element.

Leg 2 (Fig. 3E) intercoxal sclerite subquadrate, with hyaline membrane along distal margin. Coxa with 1 inner plumose seta plus 1 surface pore and 1 short sensillum on anterior surface. Basis with 1 outer naked seta, 2 surface pores, 1 large inner sensillum, large hyaline membrane along inner margin, and membrane on posterolateral surface. Exopod 3-segmented, with large hyaline membrane covering posterior surface of ramus. First segment with outer distal spine furnished with pectinate membrane at base, 1 inner plumose seta, and inner row of setules. Second segment with 1 outer distal spine, 1 surface pore, 1 inner plumose seta, and inner row of setules. Third segment with 3 outer spines, 5 inner plumose setae, and inner row of setules; middle outer spine with hyaline membrane along outer margin; outer distal spine with hyaline membrane along outer margin and row of setules along inner margin. Spine on first two exopodal segments and proximal outer spine on third exopodal segment each with finely serrated margins (Fig. 3F). Endopod 3-segmented. First segment with several rows of setules on outer margin and 1 inner plumose seta. Second segment with multiple rows of setules along outer margin, 1 surface pore, 2 inner plumose setae, and short row of setules along inner margin. Third segment with proximolateral row of setules, 6 plumose setae, and proximomedial row of setules.

Leg 3 (Fig. 3G) protopod large, modified to form apron, with 1 outer plumose seta situated near insertion of exopod, 1 inner plumose seta near large intercoxal sclerite, 1 proximolateral corrugated pad on dorsal surface, 3 marginal membranes, tiny sensilla scattered on ventral surface, and 2 widely separated sensilla along posterior margin. Exopod 3-segmented, ramus not extending beyond distal margin of second endopodal segment. First segment with 1 inner plumose seta, 1 apical spine reflexed over second segment and ornamented with sclerotized flange along outer margin, and 1 surface pore, several sensilla and sclerotized flange on outer basal swelling. Second segment with 1 outer naked spine, 1 inner plumose seta, 1 surface pore, and setules along outer and inner margins. Third segment with 3 naked spines, 4 plumose setae, and setules along outer and

inner margins. Endopod 2-segmented. First segment with 1 inner plumose seta and outer row of setules. Second segment with 6 plumose setae and setules along outer and inner margins.

Leg 4 (Fig. 4A) protopod with 1 distolateral plumose seta and numerous sensilla (combination of long and thin plus tiny and spiniform) scattered on the surface. Exopod 3-segmented, longer than protopod, with each segment ornamented with many tiny, spiniform sensilla. First exopodal segment with short row of serrations along outer distal third of segment and crescentic pectinate membrane at base of small, outer spine furnished with fine spinules along both margins. Second exopodal segment longer than other two segments (based on length of inner margin), with serrations along outer margin and crescentic pectinate membrane at base of outer distal spine furnished with fine spinules along both margins. Third exopodal segment with 3 unequal apical spines; outer spine about one-half length of middle spine, furnished with fine spinules along both margins and crescentic pectinate membrane at its base; middle spine about two-thirds length of inner spine, with fine spinules along both margins, crescentic pectinate membrane on ventral side of its base, and rhomboid process equipped with an apical hyaline flange on dorsal side of its base (Fig. 4B); inner spine with fine spinules along outer margin, crescentic pectinate membrane on ventral side of its base, and digitiform process furnished with apical pectinate membrane on dorsal side of its base (Fig. 4B).

Leg 5 (Fig. 4C) vestigial, situated proximally on ventral surface of posterolateral lobe of genital complex, and comprised of small setiferous papilla near outer margin and broad trisetose lobe near juncture of abdomen; broad lobe with spiniform sensilla and finely serrated flange at base of inner apical seta.

Leg 6 (not figured) rudimentary, represented by unarmed genital operculum at gonopore opening.

Description of adult male. Body (Fig. 4D) 3.49 (3.43-3.55) mm long (excluding caudal setae) (n = 4). Cephalothoracic shield orbicular, slightly longer than wide [2.23 (2.20-2.28) mm × 2.06 (1.96-2.13) mm], ornamented as in female. Free fourth pedigerous somite about twice as wide as long [265 (240-285) μm × 605 (580-630) μm]. Genital complex slightly longer than wide [575 (530-610) μm × 533 (520-545) μm]. Abdomen composed of 2 somites, 75 (60-80) μm × 243 (220-260) μm] and 190 (180-200) μm × 294 (270-305) μm], respectively. Caudal ramus (Fig. 5A) longer than wide [219 (210-225) μm × 138 (130-140) μm], with 6 plumose setae and inner row of setules; seta II situated on outer margin near insertion of seta III.

All appendages as in female, except for the following. Antennule with 2 additional setae on ventrodistal surface of proximal segment (position of each seta indicated by black circle in Fig. 1C). Antenna (Fig. 5B-C) 3-segmented, comprising coxa, basis, and 1-segmented endopod incorporating distal claw. Coxa with short row of fine striations plus large corrugated pad on posterior side and row of fine striations on anterior side. Basis with 4 corrugated pads on posterior side and 2 corrugated pads plus 1 long and 1 short rows of fine striations on anterior side. Endopod forming robust recurved claw bearing 2 proximal naked setae, 1 proximal accessory claw, sclerotized flange on each side of claw, and 1 small projection distal to sclerotized flange on anterior side. Maxillule (Fig. 5D) with rounded basal process, corrugated accessory process, and inner hyaline element on dentiform process. Postoral process (Fig. 5D) elongate and corrugated. Protopod of maxilliped (Fig. 5E) with conical process equipped with 1 spiniform element in myxal area and 1 medial surface pore. Tines of sternal furca (Fig. 5F) with rounded tip. Third exopodal segment of leg 4 (Fig. 6A) with smaller process and smaller pectinate membrane on dorsal side of base of

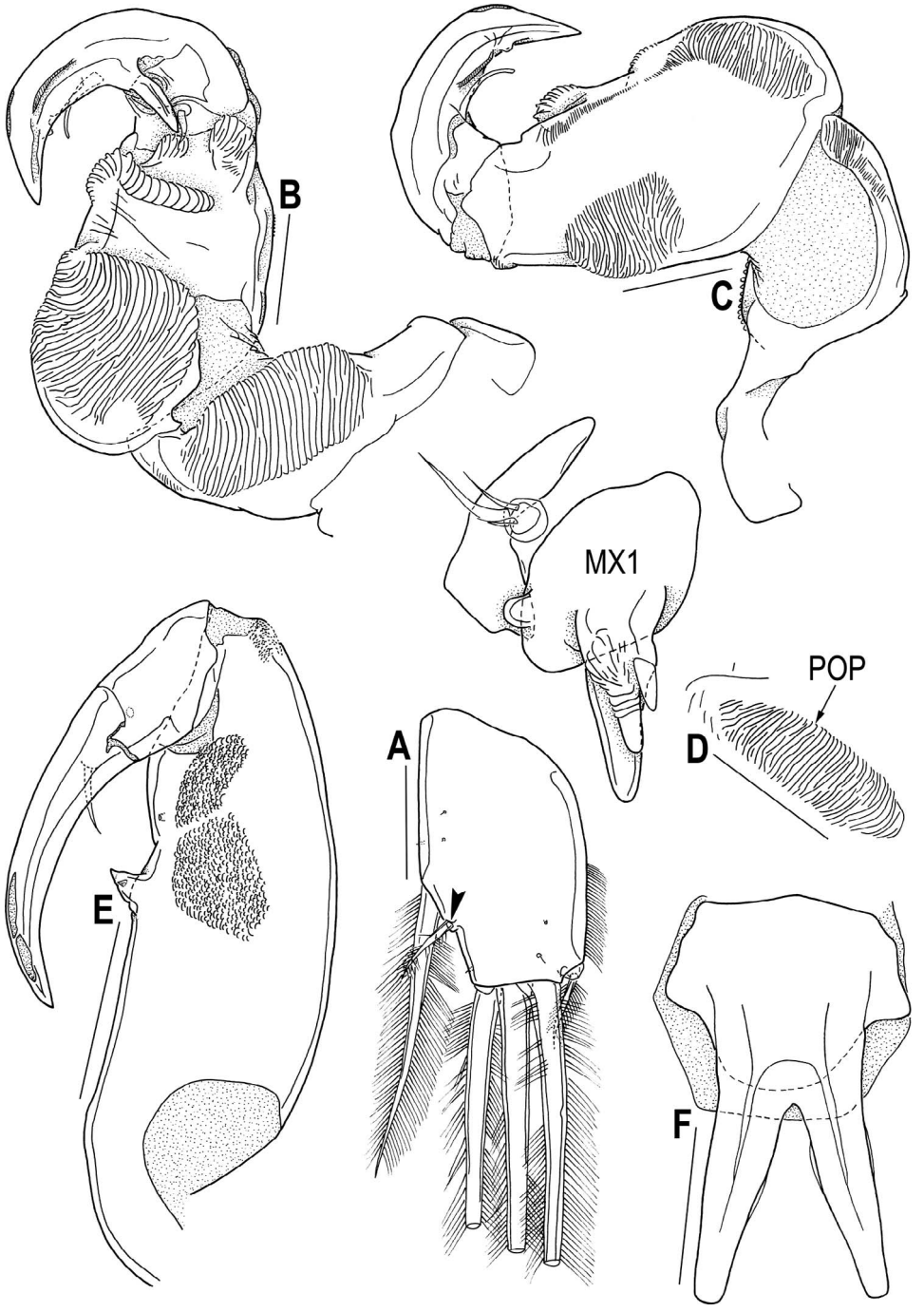

Fig. 5. *Lepeophtheirus longipes* Wilson, 1905, adult male. A) Right caudal ramus (arrowhead indicates seta II), ventral; B) Left antenna, posterior; C) Left antenna, anterior; D) Right maxillule (MX1) and postoral process (POP), ventral; E) Right maxilliped, anterior; F) Sternal furca, anterior. Scale bars: 100 μm for A, B, C, D, F; 150 μm for E.

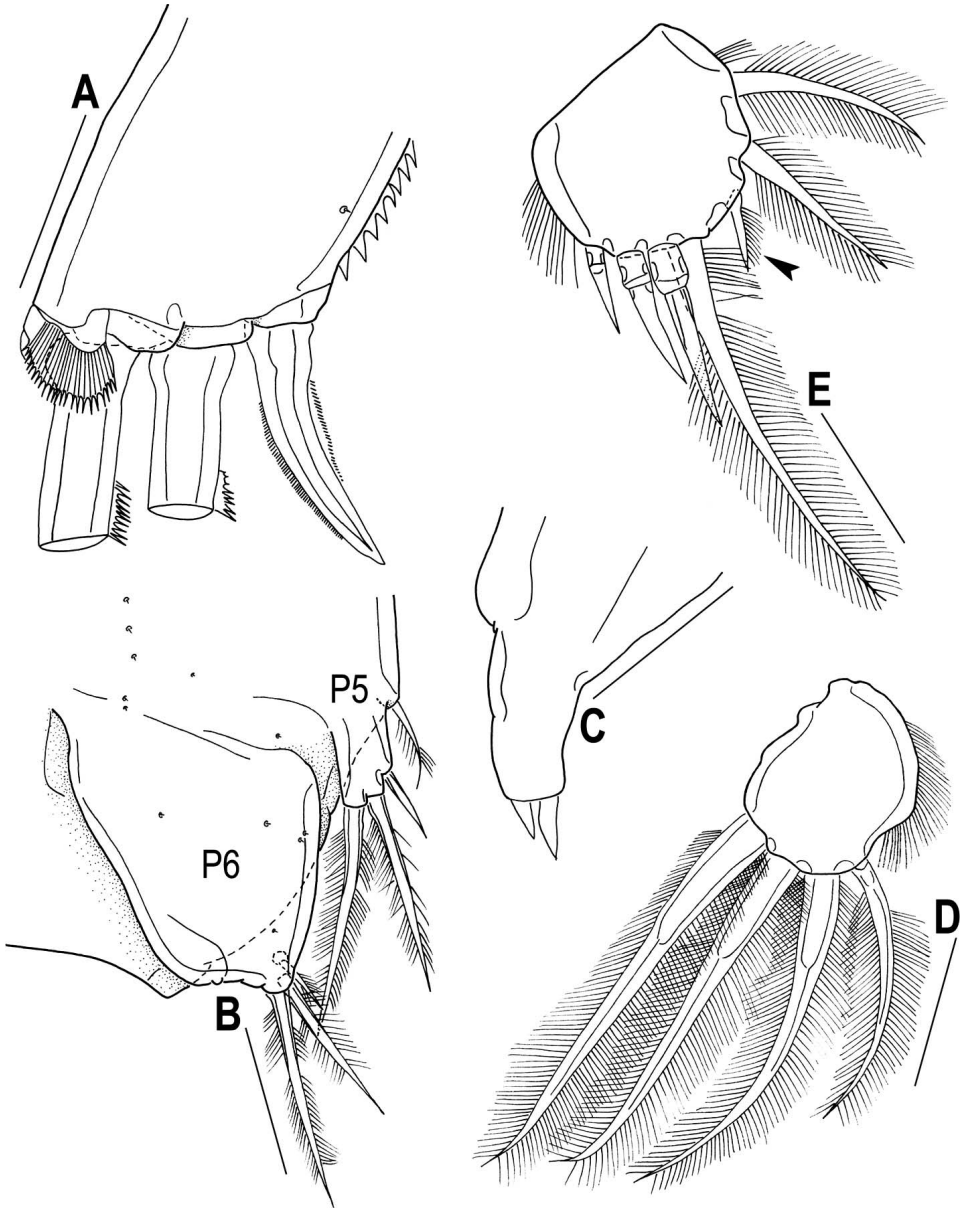

Fig. 6. *Lepeophtheirus longipes* Wilson, 1905, adult male (A, B, E) and adult female (C, D). A) Tip of third exopodal segment of right leg 4, dorsal; B) Left legs 5 (P5) and 6 (P6), ventral; C) Endopod on right leg 1, anterior; D) Second endopodal segment of left leg 3, ventral; E) Third exopodal segment of right leg 3 (arrowhead indicates abnormal seta), ventral. Scale bars: 50 μm for A; 100 μm for B, D; 25 μm for C; 50 μm for E.

middle and inner spines, respectively. Leg 5 (Fig. 6B) vestigial, comprising 1 plumose seta on surface of genital complex and 1 naked spiniform seta plus 2 plumose setae on rectangular segment. Leg 6 (Fig. 6B) forming genital operculum, armed with 3 plumose setae on outer distal corner.

Variability. Two subapical antennulary setae called out in Fig. 1C variably ornamented in 3 dissected females: 1 specimen with sparsely spinulated seta and hirsute seta on right antennule (Fig. 1C) and sparsely spinulated seta and naked seta on left antennule (not figured); another specimen with both setae sparsely spinulated on both antennules (not figured); another specimen with both setae naked on both antennules as is typical in other congeners (not figured). One female with 2 apical naked elements on endopod of leg 1 (Fig. 6C) and four plumose setae on second endopodal segment of left leg 3 (Fig. 6D). One male with 1 atrophied seta on third exopodal segment of right leg 3 (Fig. 6E).

Attachment site. Mainly on the head, few on the eyes and body.

Remarks. Examination of the female syntype of *L. longipes* (USNM 12488) from an unknown host and locality, including two specimen lots containing *L. longipes* from GSB captured off La Jolla, California (i.e., Wilson's (1908) 27 female voucher specimens (USNM 38567) and an additional lot (USNM 74301) of five female specimens identified by C. B. Wilson), revealed they are conspecific with our specimens of *Lepeophtheirus* recently collected from GSB off San Onofre, California. Wilson (1905) described and illustrated a 2-segmented abdomen, inwardly curved caudal rami, and a small, curved claw at the tip of a medially concave second endopodal segment of leg 2 in the female, but we did not observe those features in the material noted above. Features of the female of *L. longipes* documented for the first time include the armature of the antennule, the spiniform process on the coxa and ornamentation on the basis of the antenna, the structure of the mandible, the small conical process at the base of the dentiform process of the maxillule, the structure of the maxilla, the ornamentation on the protopod of the maxilliped, the outer spine on the first exopodal segment and accessory process on the middle and inner apical spines on the second exopodal segment of leg 1, the ornamentation on the rami and the proximal outer spine on the third exopodal segment of leg 2, the structure of leg 3, the ornamentation on leg 4, the structure of leg 5, and the armature of the caudal rami.

Examination of Wilson's (1921a) voucher specimens of both sexes of *L. longipes* (USNM 49779) from kelp bass, *Paralabrax clathratus*, captured off Santa Catalina Island revealed they are *Lepeophtheirus constrictus* Wilson, 1908 rather than *L. longipes*. *Lepeophtheirus constrictus* has been previously reported from kelp bass and other related serranids such as spotted sand bass, *Paralabrax maculatofasciatus* (Steindachner, 1868) (type host), and barred sand bass, *Paralabrax nebulifer* (Girard, 1854), captured in waters off southern California (Wilson 1908; Love and Moser 1983). Regardless, a redescription of *L. constrictus* by modern standards is needed.

Examination of specimens of both sexes of *L. longipes* (USNM 180909) from quillback rockfish, *Sebastes maliger*, caught off the San Juan Islands in northwest Washington revealed they are *Lepeophtheirus oblitus* Kabata, 1973 rather than *L. longipes*. Although the collector of those specimens was not provided on the vial label, we are certain they were collected by Nichols (1975), because the collection information provided on the vial label is nearly identical to that in her publication, i.e., "*Udonella caligorum* was found on the parasitic caligoid copepod, *Lepeoptheirus longipes* which infests the skin of the quillback rockfish, *Sebastodes maliger* taken by otter trawl in San Juan Channel (48°35'N, 123°03'W) near Friday Harbor, Washington." *Lepeophtheirus oblitus* also has been reported from quillback rockfish (type host), kelp greenling, *Hexagrammos decagrammus* (Pallas, 1810) (Hexagrammidae Gill, 1889), whitespotted greenling, *Hexagrammos stelleri* Tilesius, 1810, copper rockfish, *Sebastes caurinus* Richardson, 1844, and Pacific ocean perch, *Sebastes alutus* (Gilbert, 1890), captured in waters off western Canada (Kabata 1973, 1988).

Examination of digital photographs of Brian's (1924) voucher specimens of *L. longipes* from a sharksucker, *Echeneis naucrates*, rubberlip grunt, *Plectorhinchus mediterraneus*, and meagre, *Argyrosomus regius*, captured off Mauritania in northwestern Africa revealed they are not conspecific with *L. longipes*. Furthermore, the two females collected from a meagre and included in the same lot (MNHN-IU-2007-3008 (=MNHN-Cp57)) represent two different species of *Lepeophtheirus*. The female specimen from a sharksucker (Fig. 7A-C) and rubberlip grunt (Fig. 7D-F), as well as one of the two females from a meagre (Fig. 7G-I), differ from the female of *L. longipes* by two or more of the following characters: the genital complex lacks prominent posterolateral lobes; the abdomen is equal in length to the genital complex; the spine on the first exopodal segment of leg 3 is inserted subdistally on the basal swelling; and the inner apical spine on the third exopodal segment of leg 4 is relatively shorter. The other female from a meagre (Fig. 8A-B) differs from the female of *L. longipes* and the other female in the same lot (Fig. 7G-I) by having a genital complex that is about the same length as the cephalothorax, an abdomen that is about two-thirds the length of the cephalothorax, a larger, thinner, and strongly recurved postantennal process, and a sternal furca with widely divergent tines. The male from a meagre (Fig. 8C-D) differs from the male of *L. longipes* by having a shorter third exopodal segment on leg 4 and a shorter inner apical spine on the third exopodal segment of leg 4. We could not determine whether the male from a meagre is conspecific with one of the two females from the same host species based on the limited number of photographs available for this study. To the best of our knowledge, there are no reports of any other nominate species of *Lepeophtheirus* from the sharksucker, rubberlip grunt, and meagre. Since sharksuckers (and other remoras) are known to pick parasites off a wide range of fish taxa (Cressey and Lachner 1970), the female specimen of *Lepeophtheirus* found in the mouth of a sharksucker at the time of capture by T. Monod in 1923 may represent a prey item rather than a parasite association. Suffice it to say, direct observations of Brian's (1924) five specimens of *Lepeophtheirus* are needed to determine their species identity.

L. longipes shares a female genital complex that bears prominent posterolateral lobes and is about half the length of the cephalothorax and just over two times longer than the abdomen with *Lepeophtheirus argentus* Hewitt, 1963, *Lepeophtheirus crassus* (Wilson and Bere, 1936), *Lepeophtheirus formosanus* Ho and Lin, 2010, *Lepeophtheirus heegaardi* Hewitt, 1963, *Lepeophtheirus nordmanni* (Milne-Edwards, 1840), and *Lepeophtheirus polyprioni* Hewitt, 1963. *L. argentus*, *L. heegaardi*, and *L. polyprioni* were all reported from New Zealand waters, but on unrelated hosts: *L. argentus* on the bluenose warehou, *Hyperoglyphe antarctica* (Carmichael, 1819) (as *Hyperoglyphe porosa*) (Centrolophidae Bonaparte, 1846); *L. heegaardi* on the silver scabbardfish, *Lepidopus caudatus* (Euphrasen, 1788) (Trichiuirdae Rafinesque, 1810); and *L. polyprioni* on the hapuku wreckfish, *Polyprion oxygeneios* (Schneider and Forster, 1801), and wreckfish, *Polyprion americanus* (Bloch and Schneider, 1801) (as *Polyprion moeone*) (Polyprionidae) (Hewitt 1963). *Lepeophtheirus crassus* is a widely distributed species that is host specific to remoras (Echeneidae) (Lewis 1967; Ho et al. 2006). *Lepeophtheirus nordmanni* and *L. formosanus* are both host specific to the ocean sunfish, *Mola mola* (Linnaeus, 1758) (Molidae Bonaparte, 1832), but *L. nordmanni* has a cosmopolitan distribution whereas *L. formosanus* has been reported only off Taiwan (Kabata 1979; Ho and Lin 2010).

Lepeophtheirus argentus can be distinguished from *L. longipes* by the larger body size (9.55-11.00 mm vs. 8.10-8.53 mm) and having a suborbicular genital complex, a distinctly 2-segmented abdomen, an antennule without a small conical process on the first segment,

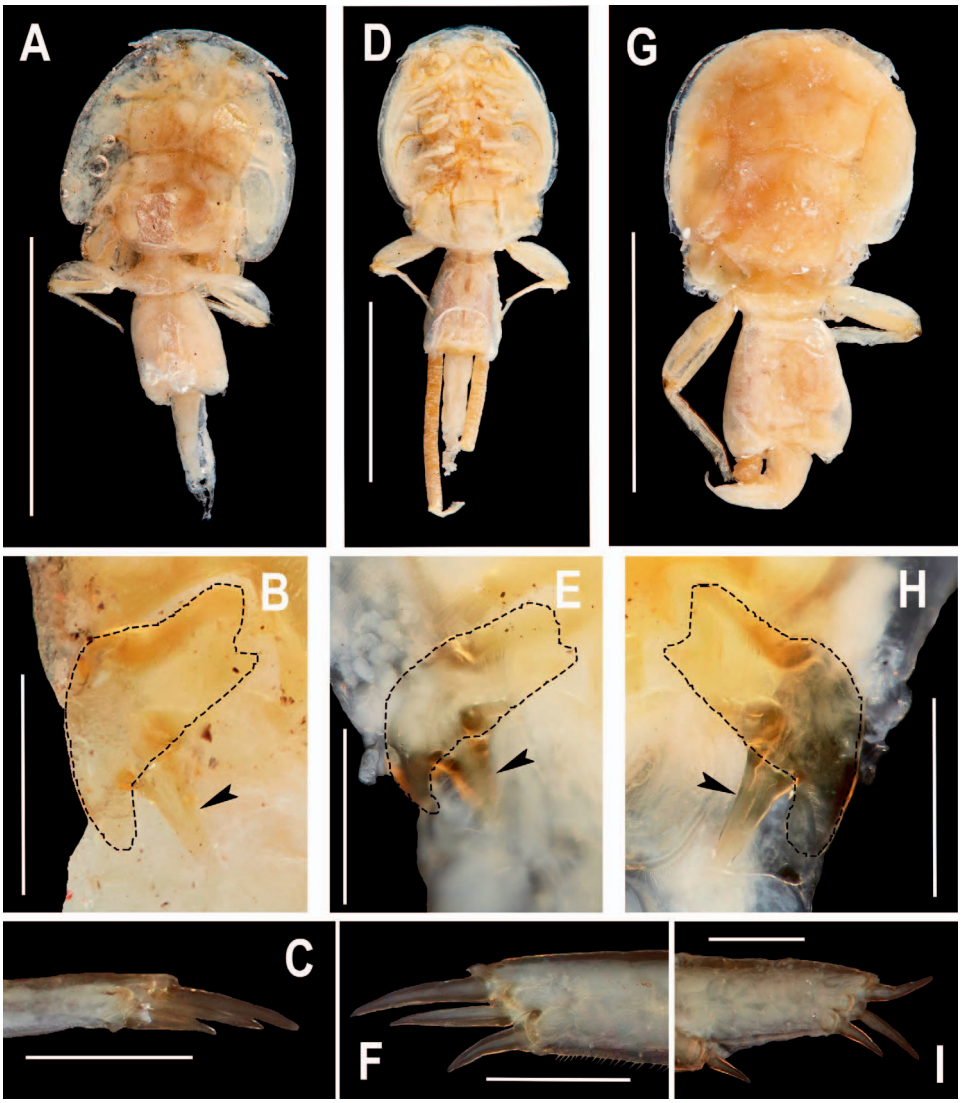

Fig. 7. *Lepeophtheirus* sp., adult female, specimen MNHN-IU-2007-2964 (=MNHN-Cp53) (A-C), specimen MNHN-IU-2007-2975 (=MNHN-Cp54) (D-F), and specimen MNHN-IU-2007-3008 (=MNHN-Cp57) (G-I). A) Habitus, dorsal; B) First exopodal segment of right leg 3, with dashed line indicating segment edge and arrowhead indicating subapical spine, ventral; C) Third exopodal segment of right leg 4, ventral; D) Habitus, ventral; E) First exopodal segment of right leg 3, with dashed line indicating segment edge and arrowhead indicating subapical spine, ventral; F) Third exopodal segment of left leg 4, ventral; G) Habitus, dorsal; H) First exopodal segment of left leg 3, with dashed line indicating segment edge and arrowhead indicating subapical spine, ventral; I) Third exopodal segment of right leg 4, ventral. Scale bars: 5 mm for A, D, G; 0.25 mm for B-C, E-F, H-I. Photos by Sébastien Soubzmaigne (Muséum national d'Histoire naturelle).

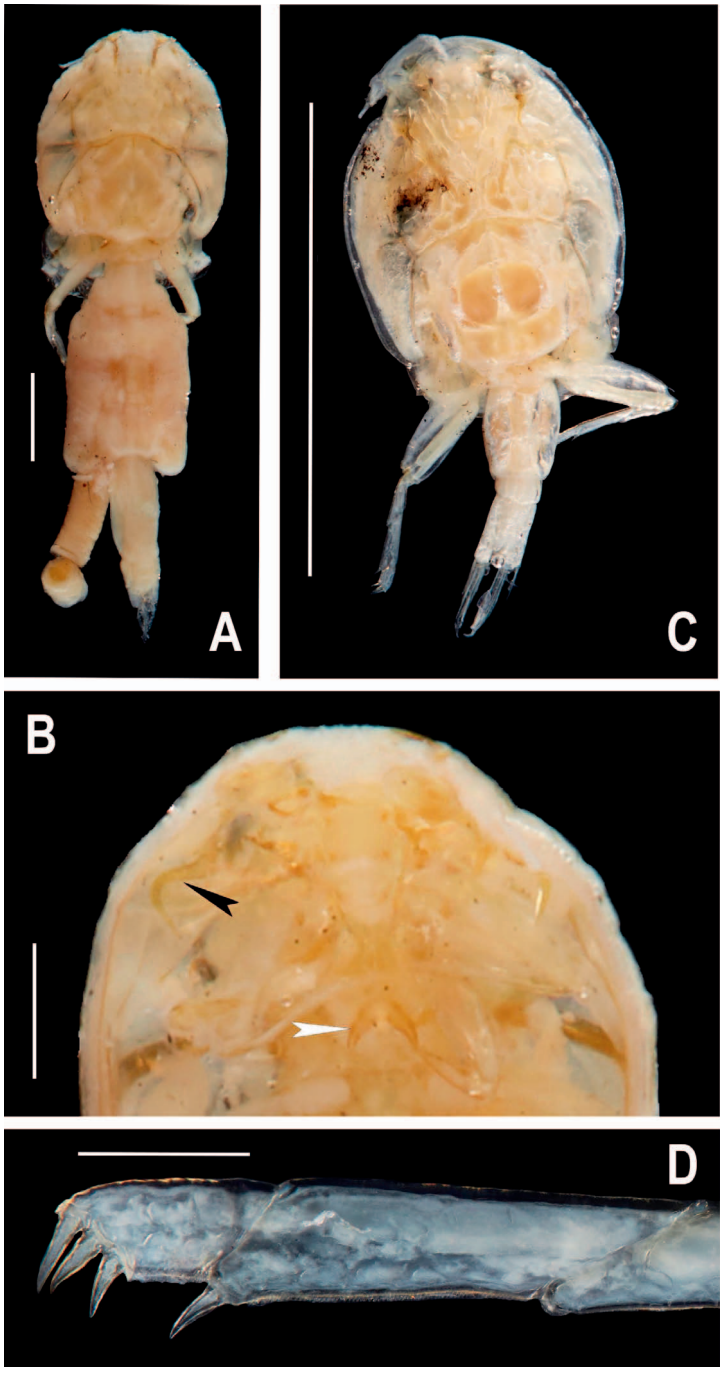

Fig. 8. *Lepeophtheirus* sp., adult female, specimen MNHN-IU-2007-3008 (=MNHN-Cp57) (A-B), and adult male, specimen (MNHN-IU-2007-2986 (=MNHN-Cp55) (C-D). A) Habitus, dorsal; B) Cephalothorax (right postantennal process indicated by black arrowhead; sternal furca indicated by white arrowhead), ventral; C) Habitus, dorsal; D) Exopodal segments of left leg 4, ventral. Scale bars: 1 mm for A-B; 5 mm for C; 0.25 mm for D. Photos by Sébastien Soubzmaigne (Muséum national d'Histoire naturelle).

a straighter postantennal process, a maxillule with unequal, straight tines and lacking an outer conical process on the dentiform process, an inwardly curved apex on each tine of the sternal furca, a subdistal spine on the first exopodal segment of leg 3, and subequal middle and inner apical spines on the third exopodal segment of leg 4 in the female (Hewitt 1963). In addition, the male of *L. argentus* is larger (6.60-7.00 mm vs. 3.43-3.55 mm) and has a longer first abdominal somite compared to the second abdominal somite, a maxillule that lacks a basal projection on the dentiform process, and apically pointed tines on the sternal furca (Hewitt 1963).

Lepeophtheirus crassus can be delineated from *L. longipes* by the smaller body size (4.56-7.05 mm vs. 8.10-8.53 mm) and having a suborbicular genital complex, a distinctly 2-segmented abdomen, an antennule without a small conical process on the first segment, a blunt process on the antennal coxa, a maxillule lacking an outer conical process on the dentiform process, a sharply pointed apex on each tine of the sternal furca, a shorter second exopodal segment of leg 4, an elongate leg 5 that protrudes beyond the posterolateral process of the genital complex, caudal seta II situated on the outer margin, and a tiny caudal seta VII in the female (Shiino 1960; Lewis 1967). Furthermore, the male of *L. crassus* is slightly larger (4.66-4.80 mm vs. 3.43-3.55 mm) and has a small proximal swelling on the antennal claw, a maxillule that lacks corrugations and a basal projection on the dentiform process, a papilliform protuberance armed with two tiny spinules on the protopod of the maxilliped, apically pointed tines on the sternal furca, and three plumose setae on the free segment of leg 5 (Shiino 1960; Lewis 1967).

Lepeophtheirus formosanus differs from *L. longipes* by having a barrel-shaped abdomen, an antennule lacking a bifid process on the proximal segment, an inner basal accessory process on the postantennal process, a maxillule ornamented with a hyaline membrane on both margins of each tine and lacking a proximal conical process on the dentiform process, an elongate third exopodal segment of leg 3, serrations on the subequal middle and inner apical spines on the third exopodal segment of leg 4, and a triangular leg 5 that is visible in dorsal view in the female (Ho and Lin 2010).

Lepeophtheirus heegaardi can be differentiated from *L. longipes* by having a rounded genital complex, an abdomen that is noticeably wider in the proximal half, an antennule without a small conical process on the first segment, a maxillule lacking an outer conical process on the dentiform process, apically rounded tines on the sternal furca, and subequal middle and inner apical spines on the third exopodal segment of leg 4 in the female (Hewitt 1963).

Lepeophtheirus nordmanni can be distinguished from *L. longipes* by the much larger body size (11.00-12.60 mm vs. 8.10-8.53 mm) and having a blunt process on the coxa and a long, slender claw on the antenna, a slender postantennal process, a maxillule with slender tines and lacking an outer conical process at the base of the dentiform process, slender and apically rounded tines on the sternal furca, a subtriangular process on each side of the sternal furca, a long endopod on leg 1, a long spine on the first exopodal segment of leg 3 that reaches to the second endopodal segment of the same leg, a longer exopod on leg 3, and serrations on the subequal middle and inner apical spines on the third exopodal segment of leg 4 in the female (Shiino 1957; Hewitt 1971; Kabata 1979). Moreover, the male of *L. nordmanni* is larger (6.00-6.90 mm vs. 3.43-3.55 mm) and has a small, subapical secondary process on the antennal claw, a maxillule that lacks corrugations and a basal protuberance on the dentiform process, short tines on the sternal furca, a subtriangular process on each side of the sternal furca, and legs 5 and 6 each represented by a prominent lobe (Hewitt 1971; Kabata 1979).

Lepeophtheirus polyprioni differs from *L. longipes* by having a rounded genital complex, a distinctly 2-segmented abdomen that is wider proximally, an antennule without a small conical process on the first segment, a maxillule lacking an outer process on the dentiform process, apically rounded tines on the sternal furca, no accessory process on the middle and inner apical spines of the distal exopodal segment of leg 1, and subequal middle and inner apical spines on the third exopodal segment of leg 4 in the female (Hewitt 1963). Additionally, the male is slightly larger (4.20-4.90 mm vs. 3.43-3.55 mm) and has a longer first abdominal somite, an antenna without an accessory process, a maxillule that lacks a basal projection and corrugations on the dentiform process, and a smooth protopod on the maxilliped (Hewitt 1963).

Wilson (1921b) briefly noted that *L. longipes* is closely related to *L. interitus*. *Lepeophtheirus interitus* was established based on a single ovigerous female collected in 1917 from a related polyprionid fish, namely the hapuku wreckfish, *P. oxygeneios* (as *Polyprion prognathus*), captured off the Juan Fernandez Islands, Chile (Wilson 1921b). The hapuku wreckfish was subsequently reported as a host of *L. polyprioni* in New Zealand waters (Hewitt 1963) as noted above. *Lepeophtheirus interitus* has not been reported in the primary literature since its discovery. Wilson (1921b) did not illustrate the inner apical seta, as well as an accessory process on the middle and inner apical spines, on the distal exopodal segment of leg 1 of *L. interitus*, but these features are present in the type material. *Lepeophtheirus interitus* can be distinguished from *L. longipes* by having a smaller body size (5.50 mm vs. 8.10-8.53 mm), a subcircular genital complex that is over three times longer than the abdomen, a maxillule lacking an outer conical process on the dentiform process, and a longer endopod on leg 1 (Wilson 1921b). *Lepeophtheirus interitus* differs from *L. polyprioni* by having a smaller body size (5.50 mm vs. 7.70-8.25 mm), a rectangular 1-segmented abdomen, longer and more widely divergent tines on the sternal furca, and an accessory process on the middle and inner apical spines of the distal exopodal segment of leg 1. Nevertheless, a redescription of *L. interitus* based on fresh specimens from the type host and type locality is needed, since the original description is inadequate by modern standards and the type material accessioned at the Swedish Museum of Natural History, Stockholm, consists of only the maxillule and leg 1 mounted on a slide (Rasmus Hovmöller, pers. comm.).

Discussion

A review of specimens of *Lepeophtheirus* collected from kelp bass captured off Santa Catalina Island (Wilson 1921a), from quillback rockfish caught off the San Juan Islands (Nichols 1975), and from sharksucker, rubberlip grunt, and meagre captured off Mauritania (Brian 1924) revealed they were misidentified as *L. longipes*. In addition, Brian's (1924) female copepod samples from a meagre contained two different species of *Lepeophtheirus*. Rose and Vaissière (1953) and Raibaut et al. (1998) also recorded *L. longipes* on meagre, but from the Mediterranean Sea. Neither record indicated the specific capture location of the host or deposition of voucher material. Both records are doubtful considering the species of *Lepeophtheirus* collected on the same host species from Mauritania are not *L. longipes* as noted above and, more importantly, it is unlikely *L. longipes* occurs in two geographically disparate locations (eastern Pacific and Mediterranean Sea). Hobson's (1971) record of *L. longipes* from treefish from southern California is also doubtful, because *Lepeophtheirus paulus* Cressey, 1969 has been reported from treefish (type host) collected off La Jolla (Cressey 1969), as well as from yellowtail rockfish, *Sebastes flavidus*

(Ayres, 1862), quillback rockfish, tiger rockfish, *Sebastes nigrocinctus* Ayres, 1859, yelloweye rockfish, *Sebastes ruberrimus* (Cramer, 1895), and walleye pollock, *Gadus chalcogrammus* Pallas, 1814 (as *Theragra chalcogramma*) (Gadidae Rafinesque, 1810) captured in waters off western Canada (Kabata 1973, 1988; Arthur 1984). Collectively, these multiple lines of evidence strongly suggest that *L. longipes* is host specific to GSB. As such, the recent collection of 60 specimens of *L. longipes* from a GSB captured off San Onofre and held at the SCMI represents the first authenticated record of this parasitic copepod in over 100 years. Moreover, this study provides the first description of the male of *L. longipes*.

The life cycle of species of *Lepeophtheirus* consists of eight stages: two naupliar, one copepodid, two chalimi, two pre-adults, and the adult. The naupliar stages are free-swimming, the copepodid is the infective stage, each chalimus stage is attached to a host by a frontal filament, and the pre-adults and adult are mobile over a host's body surface (Venmathi Maran et al. 2013). Semi-transparent caligid copepods of various sizes have been observed on juvenile GSB as small as 7.6 cm in southern California (Fig. 9). Those caligids are likely *L. longipes* based on the high fidelity of this species to GSB as noted above and are probably chalimus, pre-adults, or adult males based on their small size (approximately 1-3 mm) relative to the adult female of *L. longipes* (8.10-8.53 mm). Further research of caligid copepods on juvenile GSB are needed, however, to confirm our hypotheses.

The GSB is a large, charismatic fish, and is thus photographed often by divers. Photographs of adult GSB invariably show large numbers of *L. longipes* attached on the face and a few on the eyes of the host (Fig. 10). The darkly pigmented copepods with a pair of light-colored, cylindrical egg sacs trailing at the posterior end of their body in Fig. 10 are the ovigerous females of *L. longipes*. The thin, white strands hanging off the egg sacs of some females of *L. longipes* in Fig. 10B are individuals of an unidentified species of the hyperparasitic monogenean *Udonella* Johnston, 1835 (Udonellidae Taschenberg, 1879). Fifteen specimens of *L. longipes* in our collection were infected by this unidentified udonellid. Señorita, *Oxyjulis californica* (Günther, 1861) (Labridae Cuvier, 1816), island kelpfish, *Alloclinus holderi* (Lauderbach, 1907) (Labrisomidae Hubbs, 1952), giant kelpfish, *Heterostichus rostratus* Girard, 1854 (Clinidae Swainson, 1839), kelp bass, and bluebanded goby, *Lythrypnus dalli* (Gilbert, 1890) (Gobiidae Cuvier, 1816) have been observed cleaning GSB in California waters (Limbaugh 1955; De Wett-Oleson and Love 2001). The presence of numerous individuals of *L. longipes* often pictured on the head of GSB suggests the grazing success or grazing frequency in the head area of GSB by cleaner fishes is low. While cleaner fishes may be less vulnerable to predation because of the services they provide to predators, they are not entirely immune to being eaten (Hobson 1971).

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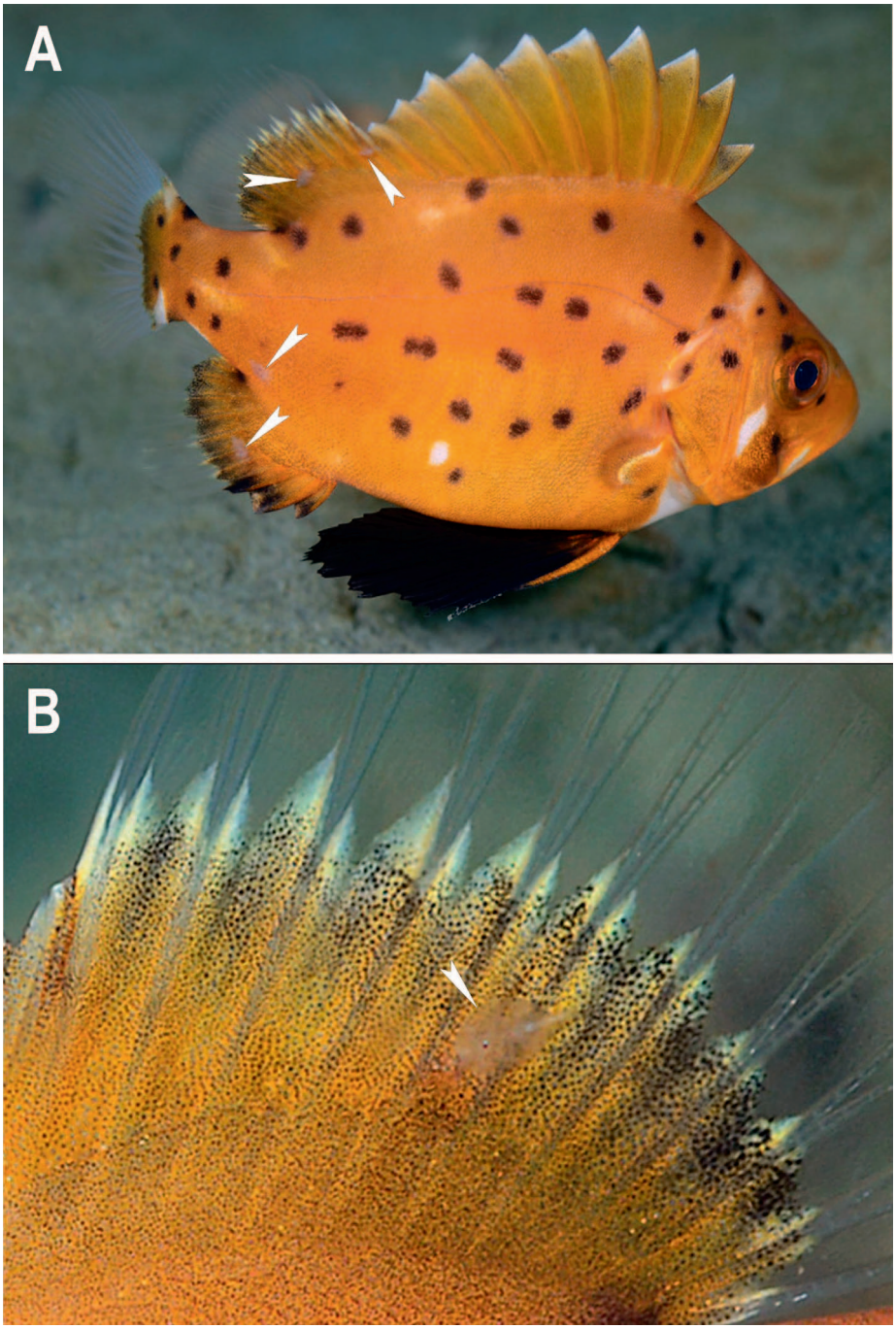

Fig. 9. (A) A juvenile giant sea bass (about 7.6 cm long) with four individuals (indicated by white arrowheads) of an unidentified species of caligid copepod on the right side of its body and fins (photo captured on November 28, 2014 at Newport Pier, California); (B) Close-up image of a caligid copepod (indicated by white arrowhead) on the left side of the soft-rayed portion of the dorsal fin of the same juvenile giant sea bass. Photos by Kevin Lee.

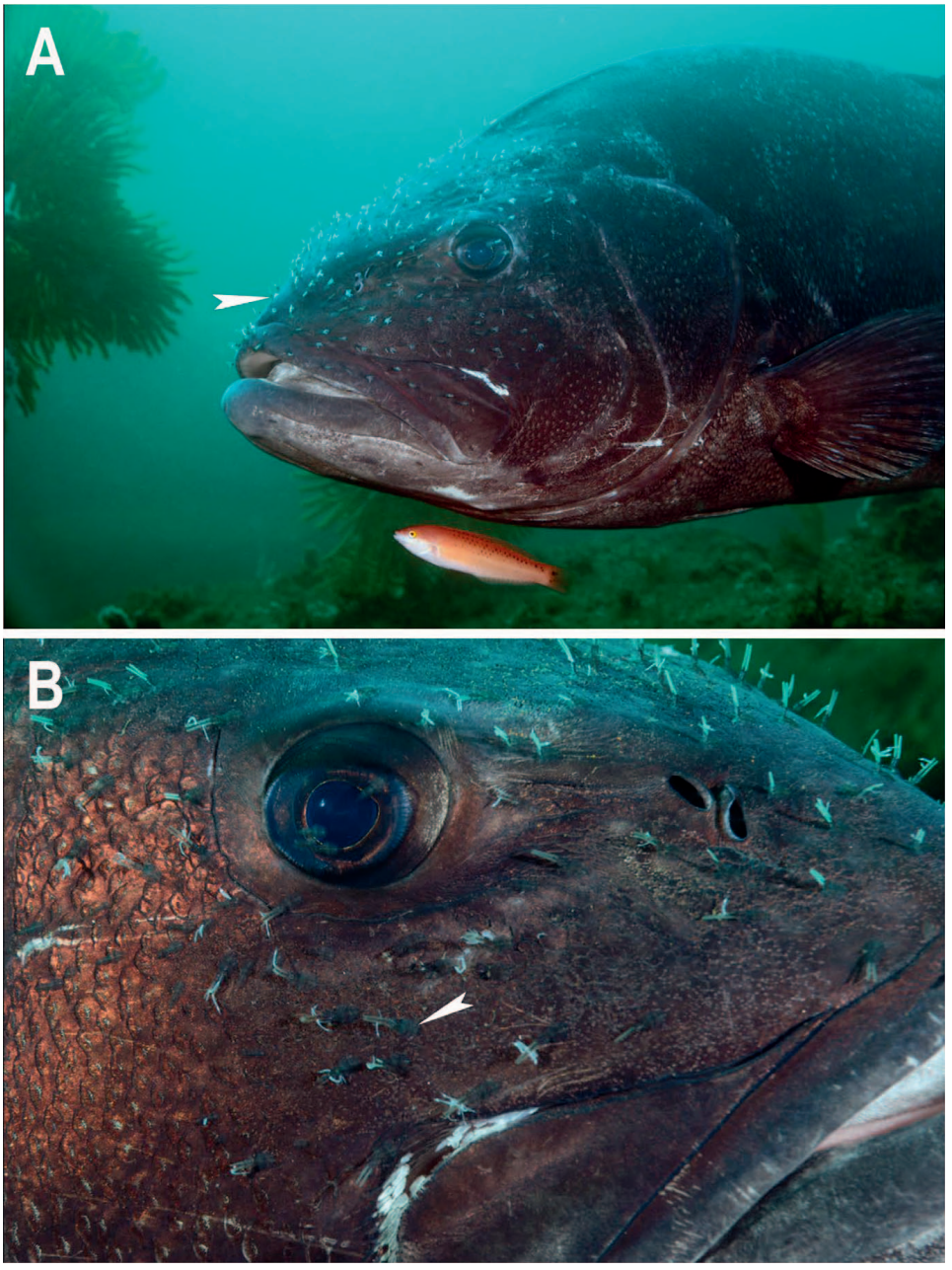

Fig. 10. (A) An adult giant sea bass—flanked below by a rock wrasse, *Halichoeres semicinctus* (Ayres, 1859) (Labridae Cuvier, 1816)—with numerous individuals of *Lepeophtheirus longipes* Wilson, 1905 (one individual indicated by white arrowhead) clustered on its head (photo captured on September 13, 2015 at the Hermosa Artificial Reef, California); (B) Close-up image of individuals of *L. longipes* (one individual indicated by white arrowhead) on the head of the same giant sea bass. Photos by Kevin Lee.

Museum of Natural History, Stockholm, for providing information on the type material of *Lepeophtheirus interitus*, Kevin Lee for allowing us to use his photos of infected giant sea bass in this study, and Julie O'Donnell for translating pertinent literature.

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