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The sea lice (Copepoda: Caligidae) of Moreton Bay (Queensland, Australia), with descriptions of thirteen new species

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Abstract

Fifty species of sea lice, members of the family Caligidae, were collected from the marine fishes of Moreton Bay, Queensland, during two workshops held in 2016. Only 21 of these species had previously been reported from Australian waters: of the remaining 29 species, 13 are new to science and another 16 are recorded from Australia for the first time. An illustrated differential diagnosis is presented for well known species; but for new or poorly known species a full description is provided. The 13 new species are: *Anuretes amplus* **sp. nov.** and *A. amymichaelae* **sp. nov.**, both from *Diagramma pictum* (Thunberg, 1792); *Caligus abigailae* **sp. nov.** from *Sphyraena obtusata* Cuvier, 1829; *C. elasmobranchi* **sp. nov.** from *Himantura uarnak* (Gmelin, 1789), *H. toshi* Whitley, 1939, *Dasyatis fluviorum* Ogilby, 1908, *Aetobatus ocellatus* (Kuhl, 1823) and *Pastinachus atrus* (Macleay, 1883); *C. hyporhamphi* **sp. nov.** from *Hyporhamphus quoyi* (Valenciennes, 1847); *C. nataliae* **sp. nov.** from *Herklotsichthys castelnaui* (Ogilby, 1897) and *Neoarius graeffei* (Kner & Steindachner, 1867); *C. neoaricolus* **sp. nov.** and *C. paranengai* **sp. nov.** both from *Neoarius graeffei*; *C. pseudorhombi* **sp. nov.** from *Pseudorhombus arsius* (Hamilton, 1822); *C. turbidus* **sp. nov.** from *Tripodichthys angustifrons* (Hollard, 1854); *C. upenei* **sp. nov.** from *Upeneus tragula* Richardson, 1846; *Lepeophtheirus robertae* **sp. nov.** from *Scarus ghobbhan* Forsskål, 1775 and *Pupulina keiri* **sp. nov.** from *Aetobatus ocellatus*. The rare species *Caligodes alatus* Heegaard, 1945 is redescribed and transferred to the genus *Caligus* Müller, 1785, but requires a replacement name due to secondary homonymy: *Caligus alepicolus* **nom. nov.** is proposed. Similarly, *Parapetalus spinosus* Byrnes, 1986 is redescribed and transferred to the genus *Caligus* where it becomes a secondary homonym: the replacement name *Caligus seriolicolus* **nom. nov.** is proposed. Five large species-groups within the genus *Caligus* are recognised here on the basis of suites of morphological character states. They are based around the following species: *C. bonito* Wilson, 1905, *C. confusus* Pillai, 1961, *C. diaphanus* von Nordmann, 1832, *C. macarovi* Gusev, 1951 and *C. productus* Dana, 1852. These species-groups can be used to navigate this relatively large genus, but their monophyletic status should not be assumed.

Key words: Parasites, copepods, sea lice, taxonomy

Introduction

Sea lice (members of the copepod family Caligidae) are a major health hazard for cultured marine finfish and the commercial losses for the salmon farming industry alone were estimated at US$480 million per annum (Costello, 2009). In the Northern Hemisphere *Lepeophtheirus salmonis* (Krøyer, 1837) is the major pest for salmonid aquaculture while in Chile it is *Caligus rogercresseyi* Boxshall & Bravo, 2000. Worldwide, over 30 different caligid species have now been reported as causing commercial losses in finfish aquaculture (Johnson *et al.*, 2004; Venmathi Maran *et al.*, 2012a). Outbreaks of sea lice in aquaculture facilities have already been reported in Australian waters, for example, on farmed southern Bluefin tuna, *Thunnus maccoyii* (Castelnau, 1872) in South Australia (Hayward *et al.*, 2008). Given the diversity of the Australian fish fauna, it appears that the caligid fauna of Australia is relatively poorly known.

The earliest published report of a caligid from Australia is that of Nicholls (1944) who described an unidentified *Caligus* male from dredgings made in Spencer Gulf, South Australia. However, the first major work on Australian Caligidae (used in the sense of Boxshall & Halsey (2004) to include the four genera formerly placed in the Euryphoridae) was Heegaard (1962) who recorded 12 species of *Caligus* Müller, 1785, ten of them new, two new species of *Lepeophtheirus* von Nordmann, 1832, a new species and genus, *Caligulus longispinosus* Heegaard, 1962, a new species of *Tuxophorus* Wilson, 1908 plus two other previously described species, *Gloiopotes longicaudatus* (Marukawa, 1925) and *Alebion carchariae* Krøyer, 1863. Unfortunately, Heegaard's (1962) taxonomy was not robust and a survey of the current status of the 14 new species of Caligidae established by Heegaard (1962) from Australian waters reveals that only five are still accepted as valid (Table 1), and his new genus *Caligulus* Heegaard, 1962 is now treated as junior subjective synonym of *Caligus*.

TABLE 1. Species of Caligidae recorded from Australian waters

Current valid name	Originally reported as:	Source of Australian record
Abasia platyrostris Pillai, 1963	*Abasia platyrostris*	Kazachenko, 1975a
Alebion carchariae Krøyer, 1863	*Alebion carchariae*	Heegaard, 1962; Newbound & Knott, 1999
Anuretes anomalus Pillai, 1967	*Lepeophtheirus anomalus* (Pillai, 1967)	Ho & Dojiri, 1977
Anuretes branchialis Rangnekar, 1953	*Henicophilus japonicus* Yamaguti & Yamasu, 1959	Kabata, 1965a
Arrama cordata Dojiri & Cressey, 1991	*Arrama cordata*	Dojiri & Cressey, 1991
Arrama tandani Dojiri & Cressey, 1991	*Arrama tandani*	Dojiri & Cressey, 1991
Caligodes laciniatus (Krøyer, 1863)	*Caligodes laciniatus*	Cressey & Collette, 1970
Caligus alaihi Lewis, 1968	*Caligus alaihi*	Kazachenko, 1975a
Caligus amblygenitalis Pillai, 1961	*Caligus amblygenitalis*	Hutson *et al*., 2007a
Caligus asymmetricus Kabata, 1965	*Caligus asymmetricus*	Kabata, 1965b
Caligus biseriodentatus Shen, 1957	*Caligus obovatus* Heegaard, 1962	Heegaard, 1962
	Caligus proboscidatus Heegaard, 1962	Heegaard, 1962
Caligus bonito Wilson, 1905	*Caligus kuroshio* Shiino, 1959	Kabata, 1965b
	Caligus bonito	Cressey & Cressey, 1980
Caligus chiastos Lin & Ho, 2003	*Caligus rapax* Milne Edwards, 1840	Heegaard, 1962
	Caligus rapax Baird, 1850	Kabata, 1965b
	Caligus elongatus von Nordmann, 1832	Hewitt, 1971
	Caligus sp. 1	Roubal *et al*., 1983
	Caligus chiastos	Hayward *et al.,* 2007, 2008
Caligus confusus Pillai, 1961	*Caligus confuses*	Hutson *et al*., 2011
Caligus cornutus Heegaard, 1962	*Caligus cornutus* [female only]	Heegaard, 1962
Caligus coryphaenae Steenstrup & Lütken, 1861	*Caligus coryphaenae*	Hutson *et al.,* 2011
Caligus cresseyorum Kabata, 1992	*Caligus cresseyorum*	Kabata, 1992

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TABLE 1. (Continued)

Current valid name	Originally reported as:	Source of Australian record
Caligus cybii Bassett-Smith, 1898	*Caligus quinqueabdominalis* Heegaard, 1962	Heegaard, 1962
	Caligus cybii	Cressey *et al.,* 1983
Caligus dampieri Byrnes, 1987	*Caligus dampieri*	Byrnes, 1987
Caligus dasyaticus Rangnekar, 1957	*Caligus dasyaticus*	Kabata, 1966
Caligus epidemicus Hewitt, 1971	*Caligus epidemicus*	Hewitt, 1971; Byrnes, 1987
Caligus fortis Kabata, 1965b	*Caligus fortis*	Kabata, 1965b
Caligus furcisetifer Redkar, Rangnekar & Murti, 1949	*Caligus furcisetifer*	Morgan *et al.,* 2010
Caligus infestans Heller, 1865	*Caligus maculatus* Heegaard, 1962	Heegaard, 1962
	Caligus infestans	Kabata, 1965b
Caligus kurochkini Kazachenko, 1975	*Caligus kurochkini*	Kazachenko, 1975b
Caligus lalandei Barnard, 1948	*Caligus lalandei*	Hutson *et al.,* 2007a, b
Caligus latus Byrnes, 1987	*Caligus latus*	Byrnes, 1987
**Caligus lobodes* (Wilson, 1911)	*Caligus cornutus* [male only]	Heegaard, 1962 (see Pillai, 1966)
Caligus longipedis Bassett-Smith, 1898	*Caligus lucidus* Heegaard, 1962	Heegaard, 1962
	Caligus longipedis Bassett-Smith, 1898	Catalano & Hutson, 2010
Caligus longirostris Heegaard, 1962	*Caligus longirostris*	Heegaard, 1962; Nowak *et al.,* 2011
Caligus longispinosus (Heegaard, 1962)	*Caligulus longispinosus* Heegaard, 1962	Heegaard, 1962
Caligus malabaricus Pillai, 1961	*Caligus malabaricus*	Cressey & Collette, 1970
Caligus nuennonae Andrews, Bott, Battagiene & Nowak, 2009	*Caligus nuennonae*	Andrews *et al.,* 2009
Caligus oculicola Tang & Newbound, 2004	*Caligus oculicola*	Tang & Newbound, 2004
Caligus oviceps Shiino, 1955	*Caligus truncatogenitalis* Roubal, 1981	Roubal, 1981
Caligus pelamydis Krøyer, 1863	*Caligus pelamydis* Hewitt, 1963	Catalano & Hutson, 2010

……continued on the next page

TABLE 1. (Continued)

Current valid name	Originally reported as:	Source of Australian record
Caligus platytarsus Bassett-Smith, 1898	*Caligus bombayensis* Rangnekar, 1955	Kabata, 1965b
Caligus productus Dana, 1852	*Caligus dentatus* Heegaard, 1962	Heegaard, 1962
	Caligus microdontus Heegaard, 1964	Heegaard, 1964
	Caligus productus	Cressey & Cressey, 1980
Caligus punctatus Shiino, 1955	*Caligus punctatus*	Catalano & Hutson, 2010
Caligus quadratus Shiino, 1957	*Caligus quadratus*	Hutson *et al.,* 2011
Caligus regalis Leigh-Sharpe, 1930	*Caligus alveolaris* Heegaard, 1962	Heegaard, 1962
	Caligus regalis	Cressey et al., 1983
Caligus schlegeli Ho & Lin, 2003	*Caligus epinepheli* Yamaguti, 1936	Kabata, 1965b
	Caligus pagrosomi Yamaguti, 1939	Roubal, 1981
	Caligus pagrosomi schelegeli Ho & Lin, 2003	Ho & Lin, 2003a
Caligus sclerotinosus Roubal, Armitage & Rohde, 1983	*Caligus sclerotinosus*	Roubal *et al.,* 1983
Caligus sensorius Heegaard, 1962	*Caligus sensorius*	Heegaard, 1962
Caligus spinosus Yamaguti, 1939	*Caligus spinosus*	Rohde, 1978; Byrnes, 1986
Caligus stokesi Byrnes, 1987	*Caligus stokesi*	Byrnes, 1987
Caligus tanago Yamaguti, 1939	*Caligus tanago*	Byrnes, 1987
Caligus triabdominalis Byrnes, 1987	*Caligus triabdominalis*	Byrnes, 1987
Caligus willungae Kabata, 1965	*Caligus willungae*	Kabata, 1965b
Gloiopotes huttoni (Thomson, 1889)	*Caligus longicaudatus* (Marukawa, 1925)	Heegaard, 1962
	Gloiopotes huttoni	Kabata, 1966
Hermilius youngi Kabata, 1964	*Hermilius youngi*	Kabata, 1964a
Lepeophtheirus epinepheli Ho & Dojiri, 1977	*Lepeophtheirus epinepheli*	Ho & Dojiri, 1977
Lepeophtheirus hastatus Shiino, 1960	*Lepeophtheirus molae* Heegaard, 1962	Heegaard, 1962

... ...continued on the next page

TABLE 1. (Continued)

Current valid name	Originally reported as:	Source of Australian record
Lepeophtheirus histioperidi Kazacheno, Korotaeva & Kurochkin, 1972	*Lepeophtheirus histioperidi*	Kazacheno et al., 1972
Lepeophtheirus kabatai Ho & Dojiri, 1977	*Lepeophtheirus kabatai*	Ho & Dojiri, 1977
Lepeophtheirus litus (Lewis, 1964)	*Dentigryps litus* Lewis, 1964	Kabata, 1965a; Ho & Dojiri, 1977
Lepeophtheirus plectropomi Nunes-Ruivo & Fourmanoir, 1956	*Lepeophtheirus plectropomi*	Kabata, 1966; Ho & Dojiri, 1977
Lepeophtheirus polyprioni Hewitt, 1963	*Lepeophtheirus polyprioni*	Hutson et al., 2011
Lepeophtheirus sekii Yamaguti, 1936	*Lepeophtheirus sekii*	Byrnes, 1987
Lepeophtheirus ulua (Lewis, 1964)	*Dentigryps ulua* Lewis, 1964	Ho & Dojiri, 1977
Mappates alter Kabata, 1964	*Mappates alter*	Kabata, 1964b
Paralebion elongatus (Wilson, 1911)	*Lepeophtheirus elongatus* Heegaard, 1962	Heegaard, 1962
Parapetalus occidentalis Steenstrup & Lütken, 1861	*Parapetalus gunteri* Pearse, 1952	Kabata, 1966
***Parapetalus spinosus* Byrnes, 1986	*Parapetalus spinosus*	Byrnes, 1986
Pseudanuretes chaetodontis Yamaguti, 1936	*Pseudanuretes chaetodontis*	Kabata, 1965a
Pseudanuretes fortipedis Kabata, 1965	*Pseudanuretes fortipedis*	Kabata, 1965a
Sinocaligus formicoides (Redkar, Rangnekar & Murti, 1949)	*Pseudopetalus formicoides* (Redkar, Rangnekar & Murti, 1949)	Collette, 1974
	Sinocaligus formicoides	Dojiri & Ho, 2013
Sinocaligus timorensis (Izawa, 1995)	*Pseudopetalus timorensis* Izawa, 1995	Izawa, 1995
Tuxophorus cervicornis Heegaard, 1962	*Tuxophorus cervicornis*	Heegaard, 1962

*The female and male of *Caligus cornutus* described by Heegaard (1962) are not conspecific. The female, as the designated holotype, remains the type of *C. cornutus*, a valid species. The male was recognised as the male of *Midias lobodes* Wilson, 1911 by Pillai (1966) but this genus was not regarded as valid by Kabata (1979) and Boxshall & Halsey (2004) (but see Dojiri & Ho, 2013 for conflicting view): its current valid name is *Caligus lobodes* (Wilson, 1911).

**Dojiri & Ho (2013) concluded that *Parapetalus spinosus* Byrnes, 1986 is not a species of *Parapetalus*. They considered it most likely a species of *Caligus*, bearing a close resemblance to *Caligus parapetalopsis* Hameed & Pillai, 1973. *Parapetalus spinosus* is here transferred to *Caligus* but becomes a secondary homonym: the replacement name *Caligus seriolicolus* nom. nov. is proposed.

In a series of papers, Kabata (1964a, b, 1965a, b, 1966) enhanced knowledge of Australian caligids by describing one new species each in the genera *Hermilius* Heller, 1865, *Mappates* Rangnekar, 1958, and *Pseudanuretes* Yamaguti, 1963, as well as four new species of *Caligus*. In addition, Kabata (1965a, b, 1966) reported the presence of another five species of *Caligus*, two species of *Lepeophtheirus* (one as a species of *Dentigryps* Wilson, 1913), plus one species each of *Anuretes* Heller, 1865 (as *Henicophilus* Yamaguti & Yamasu, 1959), *Gloiopotes* Steenstrup & Lütken, 1861, *Parapetalus* Steenstrup & Lütken, 1861 and *Pseudanuretes*.

In 1971 Hewitt described a new species, *Caligus epidemicus* Hewitt, 1971, from a sparid and four mugilid hosts caught in the lower Mitchell River in Victoria (Australia). This species has since been reported widely from across the Indo-West Pacific. Hewitt (1971) also reported *C. elongatus* von Nordmann, 1832 from a balistid fish caught at Port Hacking (NSW), and considered that the *C. rapax* Milne Edwards, 1840 reported by both Heegaard (1962) and Kabata (1965a) should be referred to *C. elongatus*, citing the revision of Parker (1969). Hayward *et al.* (2008) suspected that some records of *C. rapax* and *C. elongatus* from wild fishes off southern Australia and New Zealand might refer to *C. chiastos* Lin & Ho, 2003.

Kazachenko (1975a, b) reported *Abasia platyrostris* Pillai, 1963 and *Caligus alaihi* Lewis, 1968 from western Australian waters and described a new species, *C. kurochkini* Kazachenko, 1975, from the Great Australian Bight. Rohde (1978) noted the presence of *C. spinosus* Yamaguti, 1939 off Coff's Harbour, New South Wales. Ho & Dojiri (1977) described two new species of *Lepeophtheirus* from the Great Barrier Reef and recorded another four existing species (one currently placed in *Anuretes* and the other three in *Lepeophtheirus*). Uncertainty concerning the delimitation of genera such as *Anuretes* and *Lepeophtheirus*, as well as changes in status of other genera, such as *Dentigryps*, *Henicophilus* and *Caligulus*, and the recognition of numerous species level synonymies, have all contributed to the instability of the list of names of Caligidae reported from Australian fishes.

The next phase of studies of Australian Caligidae is exemplified by the work of Roubal and colleagues (Roubal, 1981; Roubal *et al.*, 1983), and later by Byrnes (1986, 1987). These works were more focused on host parasite relationships and typically involved the exploration of the metazoan parasite fauna of a particular host fish taxon. One taxonomic output of these studies was the reporting or description of numerous additional caligids from Australian waters. In his study of the metazoan parasites of *Acanthopagrus australis* (Günther, 1859), Roubal (1981) reported three known species of *Caligus*, and described two new ones, although he named only one of them (*C. truncatogenitalis* Roubal, 1981). In a subsequent work (Roubal *et al.*, 1983) the unnamed species was fully described, as *C. sclerotinosus* Roubal, Armitage & Rohde, 1983, and additional host-parasite records provided. This phase of work culminated in the survey by Byrnes (1987) of copepod parasites found on the *Acanthopagrus* Peters, 1855 species of Australia. In total, Byrnes (1987) recorded eleven species of caligids including four new species of *Caligus*.

Two other host focused studies were carried out on a more global scale: Cressey & Collette (1970) studied the parasitic copepods found on needlefish (Belonidae) worldwide, and Cressey & Cressey (1980) surveyed copepods found on the economically important Scombridae. Both of these important studies included records from Australian waters. All of these records, together with numerous more recent reports of individual species and the results of the large survey of metazoan parasites of inshore fishes in southeastern Australia (Hutson *et al.*, 2011), are summarised in Table 1, which provides a comprehensive list of the 69 species of sea lice currently reported from Australian waters, and incorporates any relevant changes in parasite nomenclature.

This paper reports on a large collection of sea lice collected from the fishes of Moreton Bay, Queensland. A total of 50 species of Caligidae is reported here: 13 of these are new to science and another 16 are recorded in Australian waters for the first time. The new species are described in detail and some poorly known species are redescribed: for the majority of other species only certain diagnostic features have been illustrated.

Materials and methods

The copepod material was largely collected during two parasitology workshops organised by Thomas Cribb and Scott Cutmore (University of Queensland) and held at the University of Queensland's Marine Laboratory on North Stradbrooke Island in Moreton Bay. The workshops both took place during 2016, one in the austral summer (January 9th to 22nd) and one in winter (June 24th to July 7th). Live fish were sourced each day, either from commercial fishermen using nets set in different parts of Moreton Bay, or by seine netting from the beach, spear-fishing or rod-and-line fishing, from around the shore of the island. Fish from the commercial fishermen were

transported live to the laboratory for examination; those that died during capture were usually placed on ice. Fish that were still alive on arrival at the laboratory were placed in holding tanks in the aquarium room. Fish caught by spear-fishing or rod-and-line were transported in coolboxes containing a mix of seawater and ice. During the second workshop these fish were bagged individually before transportation to prevent contamination.

The laboratory protocol for the parasitological examination of the fish is detailed in Cribb & Bray (2010), although this was designed primarily for helminths and it has been adapted to make it more suitable for copepods. In brief, the main steps of the modified protocol are as follows (for teleost fishes):

Live fish were removed from aquarium tanks and placed in kill buckets containing seawater with an excess of AQUI-S® as anaesthetic.
The water in the kill buckets was filtered periodically to collect any ectoparasites dislodged during anaesthesia.
The water in the coolboxes used to transport dead fish was filtered for parasites.
The inside of the vessel (coolbox or plastic bag) used for transporting the fish (either collectively, or individually) was rinsed with seawater; the rinse water was filtered and examined for parasites.
Fish were identified, measured and given a unique reference number.
The head including the branchial chamber was removed and placed in a petri dish.
Gills were dissected and laid out for examination.
The inside wall of the operculum, the oral and branchial cavities, and the external nares were examined for the presence of copepods.
The gut and associated organs were removed and prepared for extraction of endoparasites following Cribb & Bray (2010).
The gutted body and the detached head were immersed in an appropriately-sized vessel containing physiological saline for a minimum of 30 minutes.
After soaking for at least 30 minutes, the body of the fish was agitated and removed, then the saline solution was filtered and examined for copepods.

For elasmobranch hosts the protocol was similar:

The external body surface was examined by eye for any ectoparasites which were removed by hand, by lifting off the surface of the host using a scalpel.
Gills were dissected and placed in petri dishes for subsequent examination.
The nostril cavities and oral cavity were examined and, in the January workshop, a hot formalin-seawater flushing technique was used to extract ectoparasitic monogeneans and copepods from these cavities.

A small amount of additional material was collected from the Bay after the workshops and is also included in this paper. After removal from the host, the copepods were typically preserved in 70% ethanol. When multiple specimens of a species were available, a subsample was fixed in 95% ethanol for molecular characterization. Prior to morphological examination the specimens were cleared in lactic acid for 2 h and mounted on glass slides as temporary preparations in lactic acid or lactophenol. Limbs were dissected where necessary to observe fine details. Measurements were made using an ocular micrometer and drawings were made using a drawing tube on a Leitz Diaplan microscope equipped with differential interference contrast. Morphological terminology follows Boxshall (1990a) and Huys & Boxshall (1991); host fish names have been updated according to FishBase (Froese & Pauly, 2017). Synonyms are given when they have been used for previous records from Australian waters.

All holotypes are deposited in the collections of the Queensland Museum (QM); paratypes and voucher specimens of known species are deposited in QM and in the Natural History Museum, London (NHMUK), although in the event of a single specimen being collected, priority was given to the QM so that it received a complete set of the species found.

Systematics

Order Siphonostomatoida Thorell, 1859

Family Caligidae Burmeister, 1895

Genus *Abasia* C.B. Wilson, 1908

***Abasia platyrostris* Pillai, 1963**
(Fig. 1)

Material examined. 1♀ from *Saurida undosquamis* (Richardson, 1848) (TC17620) 26 June 2016; 1♀, 1♂ from (TC17625) 27 June 2016, NHMUK Reg. Nos 2017.173–175; 6♀♀ from (TC17850) 04 July 2016. QM Reg. No. W53040.

Site on host. all females were attached to the membrane running along the groove in the upper jaw, just the inside tooth row; the male was found on the gills.

Differential diagnosis. Body tripartite, comprising cephalothorax, genital complex and abdomen (Fig. 1A). Cephalothorax with ventrally-folded lateral margins. Frontal plates reduced, carried on anteriorly-projecting rostral region; lunules well developed (Fig. 1B). Fourth pedigerous somite free. Genital complex widest part of body and 1.2 times wider than long; dorsal surface ornamented with fingerprint-like rows of minute nodules (Fig. 1C). Abdomen 2-segmented; first free somite much broader than second and with posterolateral lobes overlapping small anal somite (Fig. 1A). Antennule with 23 setae on proximal segment, distalmost setae strongly spinulate (Fig. 1B). Antenna subchelate but reduced in size (Fig. 1D), lacking posterior process on proximal segment. Post-antennal process vestigial, represented by unisensillate papillae (Fig. 1D). Mandible stylet-like with 12 marginal teeth subapically. Maxillule with 3 well developed, hirsute setae on anterior papilla (Fig. 1D); posterior process absent. Maxilla with robust calamus and canna. Maxilliped subchelate, with smooth myxal margin. Sternal furca absent. Leg 1 lacking plumose setae on posterior margin of distal exopodal segment; spines on distal margin without accessory processes. Leg 2 with 3-segmented rami; outer spines on exopodal segments 1 and 2 directed obliquely across surface of ramus; endopodal segment 1 ornamented with crescent of spinules distally; segment 2 with row of stout spinules along outer margin. Leg 3 (Fig. 1E) with reduced apron ornamented with spinules laterally and rosette of larger denticles medially; exopod 2-segmented; first segment with small outer spine, lacking inner seta; compound distal segment armed with 3 outer spines and 3 inner plumose setae, all derived from incorporated third exopodal segment: endopod 2-segmented, first segment with reduced velum and armed with inner seta, second segment with 2 apical setae. Leg 4 uniramous, 3-segmented; first and second exopodal segments with I and III spines, respectively (Fig. 1F). Mean body length of adult female 2.95 mm, range 2.77 to 3.07 mm (based on 4 specimens).

Body length of adult male 1.54 mm.

Remarks. *Abasia platyrostris* was described by Pillai (1963) based on material collected from the buccal cavity of the lizardfish *Saurida tumbil* (Bloch, 1795) and *Synodus indicus* (Day, 1873) caught off Trivandrum, India. It was subsequently reported from Australia by Kazachenko (1975a) who found it on *Saurida tumbil* and *S. undosquamis* caught off the northwestern coast. Cressey & Cressey (1979) also reported *A. platyrostris* from the latter host in the Arabian Sea, as well as from *Synodus ulae* Schultz, 1953, taken off Honolulu, Hawaii. This record from Moreton Bay is the first from Queensland, and from the east coast of Australia.

Key features of both sexes were described by Pillai (1963, 1985) and Cressey & Cressey (1979) provided supplementary morphological details on the female as well as an identification key to females of the six species known in the genus at the time. No further species have been added since 1979. Within the genus, the 2-segmented state of both rami of leg 3 is a unique feature of *A. platyrostris*.

Genus *Alebion* Krøyer, 1863

***Alebion maculatus* Wilson, 1932**
(Fig. 2)

Material examined. 1♂ from *Carcharhinus* cf. *limbatus* (Müller & Henle, 1839) (TC17372), 21 January 2016, QM Reg. No. W53041.

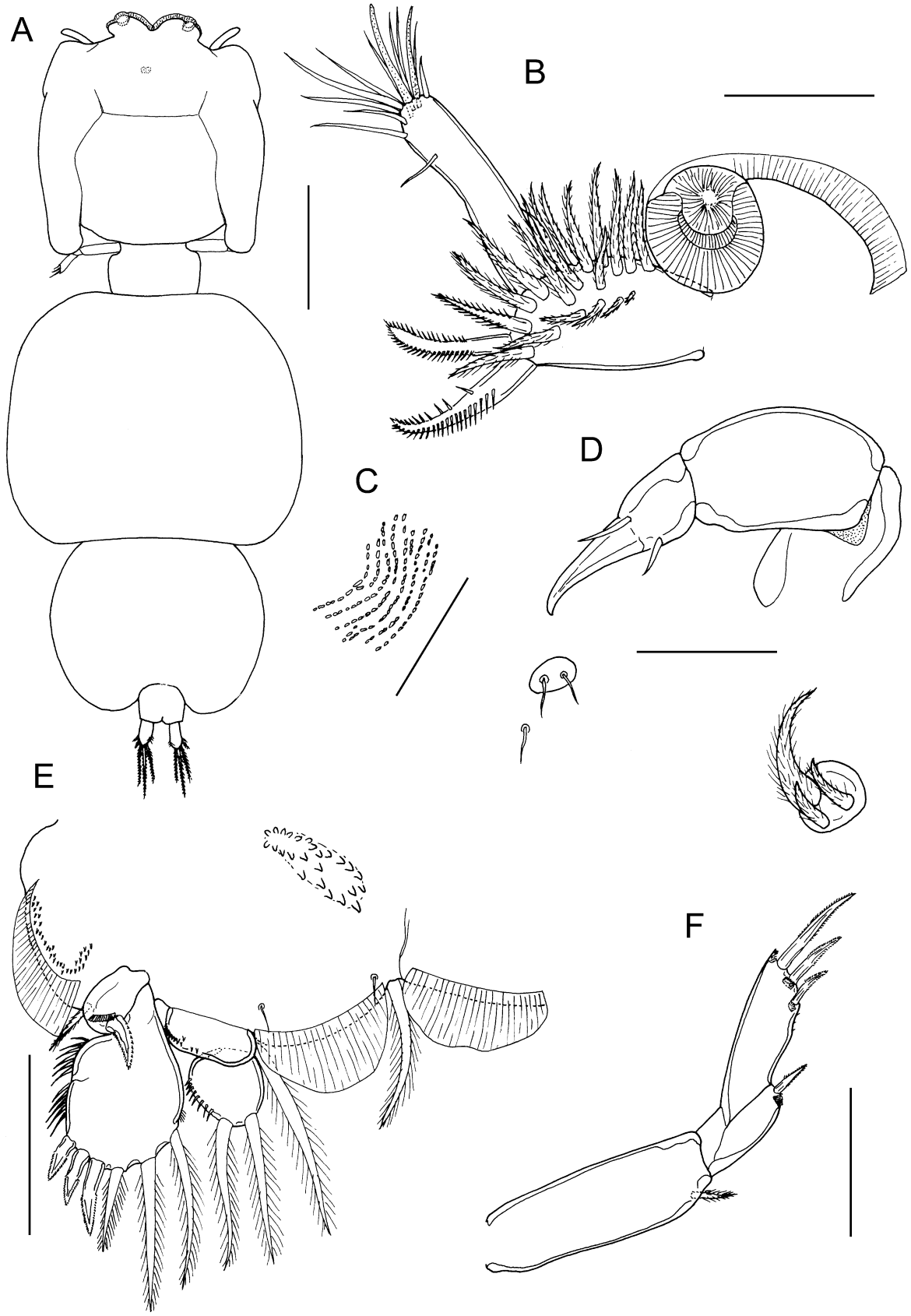

FIGURE 1. *Abasia platyrostris* Pillai, 1963, female. A, habitus, dorsal; B, right frontal plate with lunule, and antennule, ventral; C. detail of surface ornamentation of genital complex; D, antenna, vesitigial post-antennal process and anterior papilla of maxillule, drawn *in situ*; E, leg 3, ventral; F, leg 4. Scale bars: 0.5 mm on A, 100 µm on B, C, E, F, 50 µm on D.

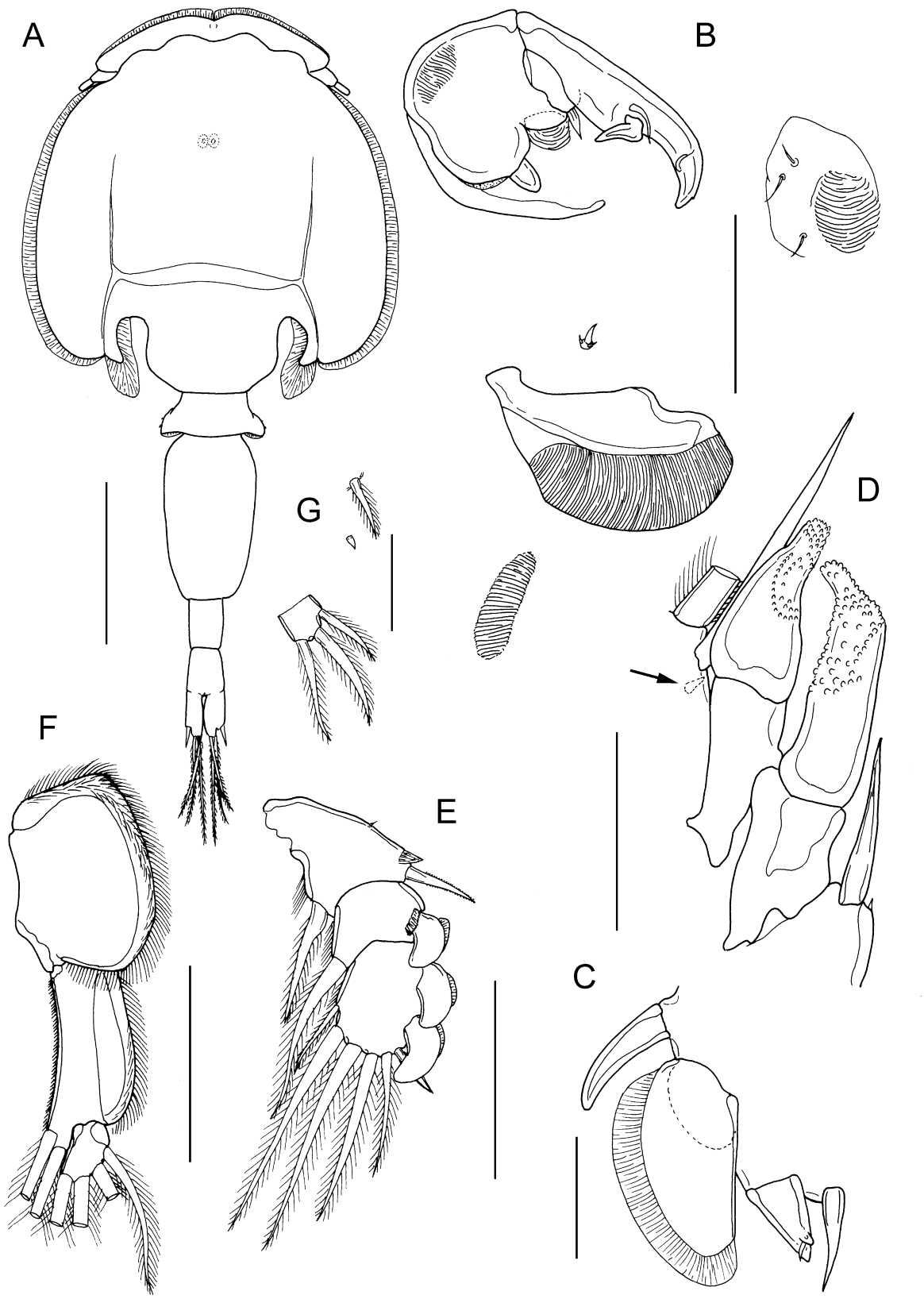

FIGURE 2. *Alebion maculatus* Wilson, 1932, male. A, habitus, dorsal; B, antenna, post-antennal process, maxillule and post-oral process, drawn *in situ*; C, setal elements on distal margin of exopod of leg 1, showing modified spatulate spine 2; D, outer margin of exopod of leg 2 showing sexually dimorphic modified spines on segments 2 and 3; E, exopod of leg 3, showing modified spatulate outer spines on segments 2 and 3; F, endopod of leg 3; G, leg 5, ventral. Scale bars: 1.0 mm on A, 200 µm on B, E, F, 100 µm on D, 50 µm on C, G.

Site on host. Body surface.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; frontal plates well developed, lacking lunules. Fourth pedigerous somite with bilobed dorsal plate in female; with small dorsal expansions in male (Fig. 2A). Female genital complex with lateral swellings and elongate fifth legs extending beyond tip of abdomen. Male genital complex about 1.5 times longer than wide; lateral margins linear, tapering slightly posteriorly (Fig. 2A). Abdomen 2-segmented in both sexes. Caudal rami incompletely fused to anal somite. Male antenna with blunt spinous process on proximal segment; subchela with accessory claw (Fig. 2B). Post-antennal process without tine, sclerite forming corrugated adhesion pad; associated papillae unisensillate (Fig. 2B). Posterior process of maxillule broad and flat, forming adhesion pad ornamented with fine surface striations (Fig. 2B). Post-oral process present; elongate with corrugated surface. Maxilliped with smooth myxal margin in female; with prominent myxal process in male. Sternal furca lacking. Leg 1 with 2-segmented endopod armed with 0-0; 3 setae: distal exopodal segment with 3 plumose setae on posterior margin: distal margin (Fig. 2C) armed as follows: spine 1 simple, spine 2 modified plate-like, spine 3 short and stout, with accessory process, seta 4 naked, longer than spine 3. Leg 2 sexually dimorphic: with modified plate-like spines on second and third exopodal segments of female; spines forming highly ornamented rods in male (Fig. 2D), spine on second segment about as thick as, and extending nearly to tip of, spine on third segment. Leg 3 with 3-segmented rami: spine on first exopodal segment linear and directed away from ramus (Fig. 2E); spine on second segment and 2 proximal spines on third segment modified, plate-like: endopod (Fig. 2F) with unarmed first segment expanded to form velum; second segment elongate, with outer velum-like expansion and 2 inner plumose setae; small third segment with 4 plumose setae. Leg 4 reduced to single segment bearing 4 short setal elements. Fifth leg of male located near mid-length of genital complex, comprising isolated outer seta plus exopodal lobe bearing 3 setae (Fig. 2G). Body length of adult male 4.50 mm.

Remarks. Cressey (1972) revised the genus *Alebion*, recognizing eight species as valid and providing a key to the adults of both sexes. Following Cressey's key, the single male from Moreton Bay is identified as *A. maculatus*, based on the size and form of the modified spines on the second exopodal segment of leg 2 (Fig. 2D).

Alebion maculatus was first figured by Bassett-Smith (1898a) who reported two mature females (under the name *Alebion carchariae* Krøyer, 1863) taken from an unidentified "small shark" caught off Aden. Wilson (1932) pointed to significant differences in the shape of the genital complex and abdomen between Bassett-Smith's description and the original description of *A. carchariae* by Krøyer (1863) and proposed *A. maculatus* as a new species to accommodate Bassett-Smith's specimens. This species has previously been recorded from Aden, India (Gnanamuthu, 1951; Rangnekar, 1959), Sri Lanka (Kirtisinghe, 1956) and Madagascar (Cressey, 1967). This is the first report of *A. maculatus* from Australian waters, and this represents a significant range extension.

The only identified host species known for *A. maculatus* is *Carcharhinus limbatus* caught at Nosy Bé, Madagascar (Cressey, 1967, 1972); most other reports have named hosts only as "carcharhinid shark" (e.g. Gnanamuthu, 1951 - as *Alebion alatus* Gnanamuthu, 1951, and Kirtisinghe, 1956 - as *Alebion megacephalus* Kirtisinghe, 1956), or "unidentified shark" (e.g. Rangnekar 1959 - as *Alebion spinosus* Rangnekar, 1959).

Genus *Anuretes* Heller, 1865

Anuretes amplus sp. nov.

(Figs. 3, 4)

Type material. Holotype ♀, 7 paratype ♀♀ from *Diagramma pictum* (Thunberg, 1792) (TC17266), 19 January 2016, QM Reg. Nos Holotype ♀ W53042, 3 paratype ♀♀ W53043; 4 paratype ♀♀ NHMUK Reg. Nos 2017.176–179.

Type Host. *Diagramma pictum* (Thunberg, 1792).

Site on host. Gills.

Etymology. The species name is derived from the Latin *amplus*, meaning large, ample, and alludes to the broad genital complex of the female.

Description. Adult female (Fig. 3A) mean body length including caudal rami 1.01 mm, range from 0.97 to 1.04 mm (based on 7 specimens). Cephalothorax subcircular with small posterior sinuses; cephalothorax

comprising about 56 % of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly about level with rear margins of lateral portions. Frontal plates without lunules. Free fourth pedigerous somite visible in dorsal view (Fig. 3A). Genital complex distinctly wider than cephalothorax, about 1.7 times wider than long, with strongly convex lateral margins (Fig. 3A). Abdomen reduced and incorporated into genital complex. Caudal rami directed posterolaterally on margin of abdomen, about 1.4 times longer than wide: each ramus (Fig. 4A) armed with long setae at inner and outer distal angles, 1 shorter plumose seta on lateral margin, and 3 long plumose setae on distal margin.

Antennule (Fig. 3B) 2-segmented; large proximal segment with 25 hirsute setae arrayed along anteroventral surface and 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 3C) comprising proximal segment bearing acutely-pointed, posteriorly-directed spinous process equipped with long medial flange extending onto inner margin of segment; middle segment subrectangular, tapering slightly distally, unarmed; terminal segment forming recurved claw bearing blunt element proximally and slender seta near anterior margin. Post-antennal process (Fig. 3C) weakly curved; ornamented with 2 unisensillate papillae on basal part and single similar unisensillate papilla on adjacent ventral cephalothoracic surface.

Mandible of typical caligid, stylet-like structure, with 12 marginal teeth (Fig. 3D). Maxillule (Fig. 3C) comprising anterior papilla bearing 3 unequal, naked setae and simple, tapering posterior process. Pair of rounded post-oral processes present (Fig. 3C). Maxilla 2-segmented, comprising elongate syncoxa and basis: syncoxa unarmed; basis (Fig. 3E) bearing spiniform flabellum on anterior margin and terminating in 2 claw-like elements (calamus and canna). Calamus much longer than canna, both ornamented with strips of finely serrated membrane. Maxillary whip with broad base and tapering distal whip (Fig. 3E). Maxilliped subchelate (Fig. 3F); robust proximal segment with ridge-like swelling on myxal surface; distal subchela short and strongly curved; with slender seta present proximally, surface of apical claw ornamented with striations.

Sternal furca with widely separated and slightly divergent tines, each ornamented with marginal flanges (Fig. 3G)

First swimming legs biramous (Fig. 4B); joined by intercoxal sclerite; sympod with inner and outer plumose setae derived from basis, ornamented with surface spinules: endopod represented by minute flaccid vestige. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment armed with small outer (anterior) spine and ornamented with interrupted row of spinules along posterior margin; second segment armed with 3 very short plumose setae along posterior margin and 4 distal elements along distal margin as follows: spine 1 (anterior-most) longest with minute serrations along both margins; spine 2 markedly longer than spine 3, each with accessory process and with bilateral strips of finely serrated membrane; seta 4 offset, originating on anterior surface of segment, about as long as spine 2 and shorter than segment.

Second leg (Fig. 4C) biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by intercoxal sclerite bearing extensive flap of marginal membrane posteriorly. Coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segments 1 and 2 each with bilaterally serrate outer spine, plus inner plumose seta; spines aligned close to longitudinal axis of ramus; flap of membrane originating on first segment reflexed back over dorsal surface of ramus; segment 3 with naked proximal spine and curved bilaterally-serrate distal spine; apical spine with marginal membrane laterally and pinnules medially, plus 5 inner plumose setae. Endopodal segments 1 and 2 armed with 1 and 2 inner plumose setae respectively, outer margins smooth; segment 3 with 6 plumose setae.

Third leg pair (Fig. 4D) forming flattened plate closing posterior part of cephalothoracic sucker. Protopodal part flattened, joined by plate-like intercoxal sclerite forming apron, ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod: bearing inner plumose seta at junction with intercoxal plate and outer plumose seta located dorsally near base of exopod; sensillae located adjacent to inner coxal seta and adjacent to origin of endopod; rami originating close together. Exopod 2-segmented; first segment armed with acutely-pointed claw directed over ventral surface of ramus, lacking inner seta; compound distal segment armed with 4 outer spines and 5 plumose setae. Endopod 2-segmented; first segment with slightly expanded lateral margin (forming small velum) ornamented with spinules and lacking inner plumose seta; compound distal segment with 5 plumose setae.

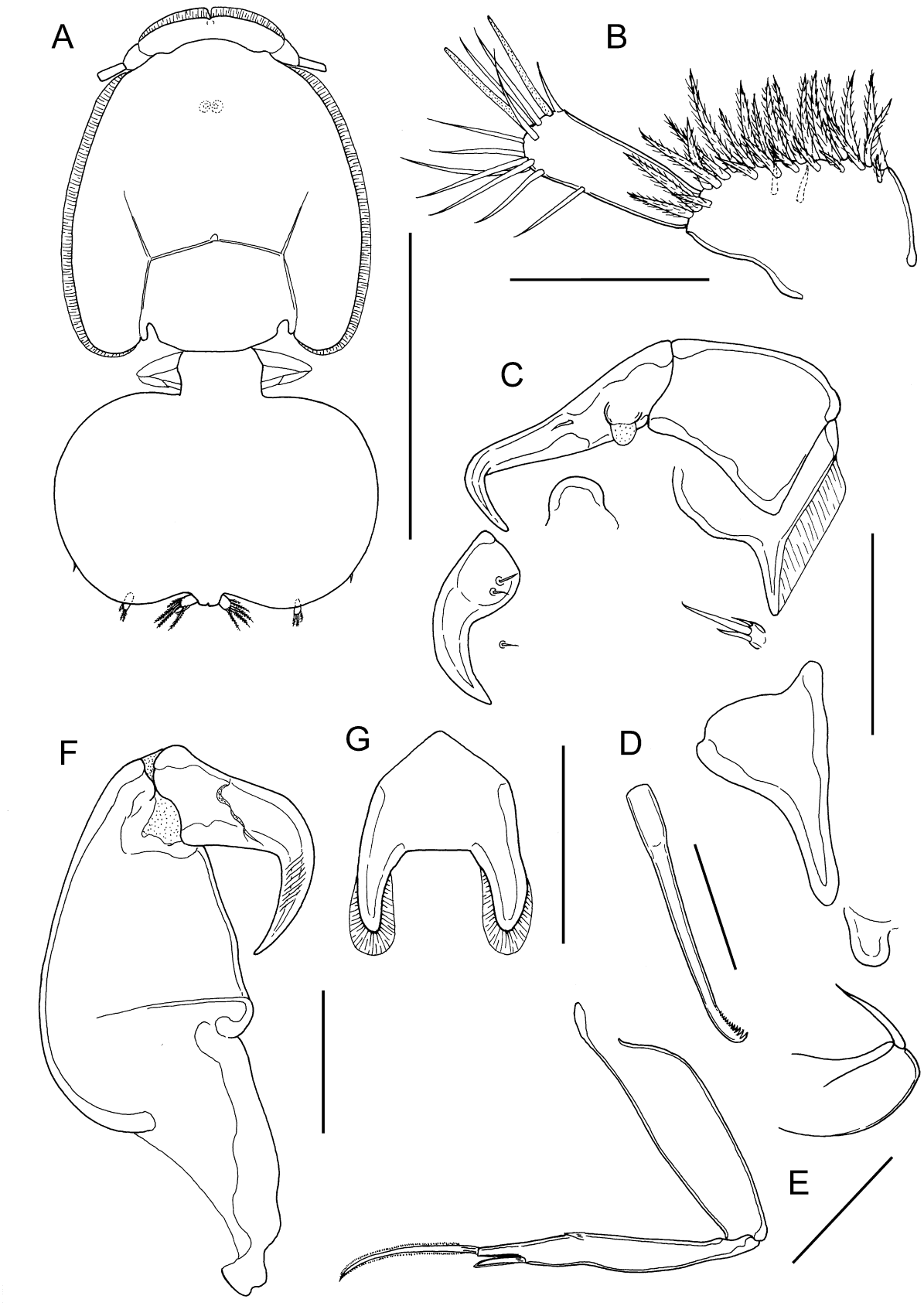

FIGURE 3. *Anuretes amplus* **sp. nov.**, paratype female. A. habitus, dorsal; B, antennule, ventral ; C, antenna, post-antennal process, maxillule and post-oral process, drawn *in situ*; D, mandible; E, left maxilla and maxillary whip, drawn *in situ*; F, maxilliped; G, sternal furca. Scale bars: 0.5 mm on A, 50 µm on B–C, E–G, 25 µm on D.

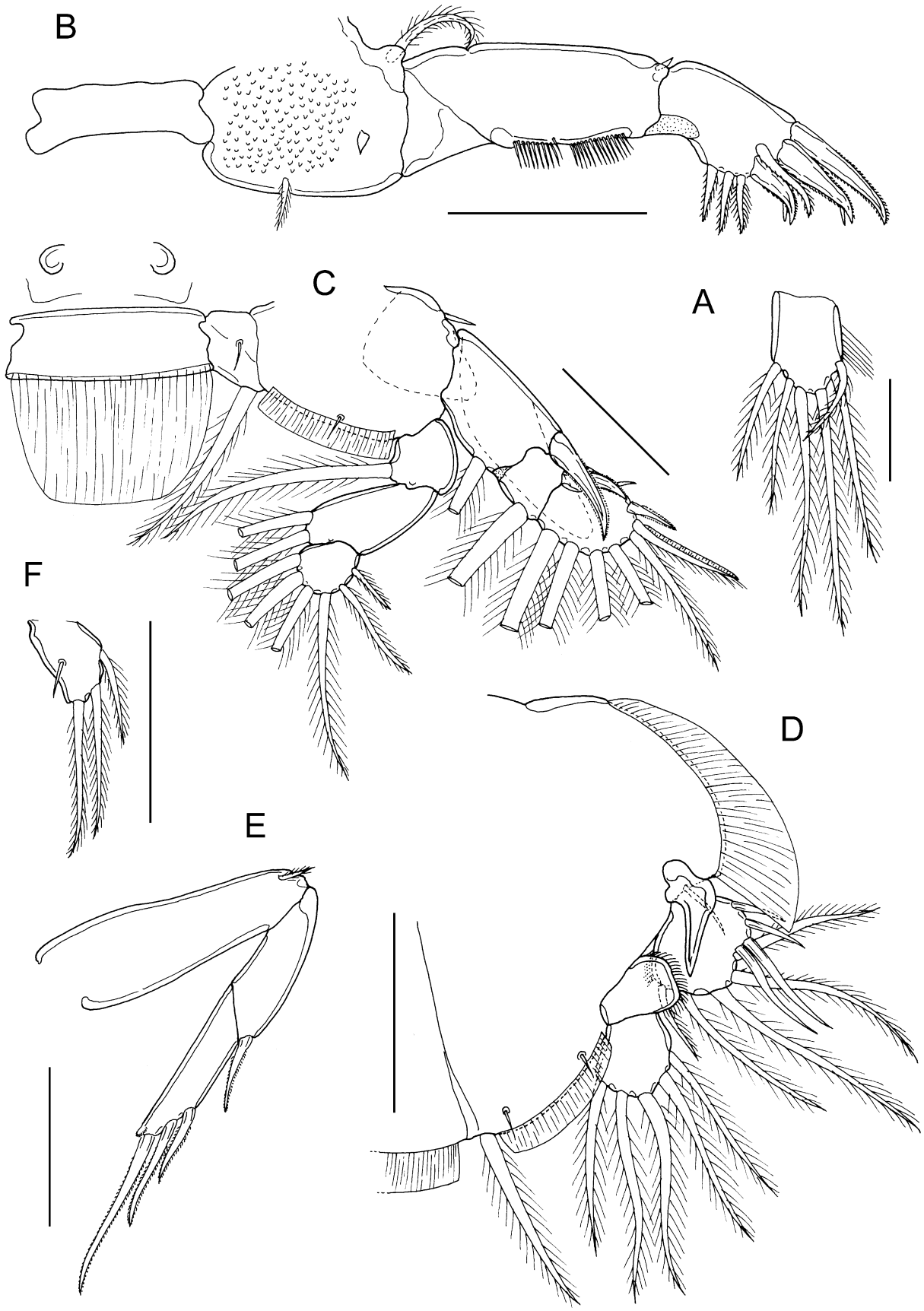

FIGURE 4. *Anuretes amplus* **sp. nov.**, paratype female. A. caudal ramus, ventral; B, leg 1; C, leg 2, D, leg 3; E, leg 4; F, leg 5. Scale bars 25 μm on A, 50 μm on D–F.

Fourth leg (Fig. 4E) 3-segmented, comprising slender protopodal segment and 2-segmented exopod: protopodal segment with plumose seta distally; first exopodal segment armed with slender bilaterally-serrate outer spine; second segment with 3 distal margin spines, each ornamented with bilateral strips of serrated membrane.

Fifth legs well defined comprising anterior protopodal seta located on surface of genital complex and process representing exopod (Fig. 4F) armed with 3 plumose setae and ornamented with conspicuous sensilla.

TABLE 2. Body lengths of both sexes of species of *Anuretes*.

Species	Female body length mean (range) mm	Male body length mean (range) mm	Source
A. amplus **sp. nov.**	1.01 (0.97–1.04)	unknown	present account
A. amymichaelae **sp. nov.**	0.93 (0.92–0.93)	0.74 (0.72–0.77)	present account
A. anomalus	3.0	unknown	Pillai, 1967
A. branchialis	1.61 (1.53–1.69)	unknown	Dojiri & Ho, 2013
A. brevis	unknown	1.55	Pearse, 1951
A. grandis	1.72 (1.50–1.98)	unknown	Ho & Lin, 2000
A. heckeli	2.27 (2.09–2.46)	1.16	Dojiri & Ho, 2013
A. hoi	2.1	unknown	Prabha & Pillai, 1986
A. indicus	2.1	1.4	Pillai, 1985; Prabha & Pillai, 1983
A. justinei	1.15 (1.06–1.22)	unknown	Venmathi Maran *et al.*, 2008
A. menehune	1.68 (up to 2.05)	1.31 (up to 1.39)	Lewis, 1964a
A. occultus	1.7	unknown	Prabha & Pillai, 1983
A. perplexus	3.0	unknown	Pillai, 1985
A. plataxi	3.0	unknown	Prabha & Pillai, 1986
A. plectorhynchi	(1.50–1.87)	unknown	Yamaguti, 1936
A. quadrilaterus	5.86	3.21	Shiino, 1954a
A. rotundigenitalis	1.6	unknown	Hameed, 1976
A. rotundus	2.5	1.2	Prabha & Pillai, 1983, 1986
A. serratus	2.48	1.64	Lewis, 1964a
A. shiinoi	2.8	unknown	Prabha & Pillai, 1983
A. similis	1.8	unknown	Prabha & Pillai, 1986

Remarks. The new species combines possession of a maxillary whip with a I; III spine formula for the 2-segmented exopod of leg 4. Seven other species exhibit this same combination: *A. anomalus* Pillai, 1967, *A. grandis* Ho & Lin, 2000, *A. hoi* Prabha & Pillai, 1986, *A. justinei* Venmathi Maran, Ohtsuka & Boxshall, 2008, *A. occultus* Ho & Lin, 2000, *A. rotundigenitalis* Hameed, 1976, and *A. similis* Ho & Lin, 2000. Three of these species possess a very large genital complex: in *A. grandis* the female genital complex is usually longer than wide and about two-thirds as long as the cephalothorax, in *A. rotundigenitalis* it is about as long as wide and about as long as the cephalothorax, and in *A. occultus* it is longer than wide and longer than the cephalothorax. The proportions of these three species are markedly different from those of the new species, with its enlarged genital complex that is distinctly wider than long and shorter than the cephalothorax. *Anuretes hoi* differs from the new species in possessing a large pointed myxal process on the maxilliped (Prabha & Pillai, 1986) and in the setation of both rami of leg 3 (exopod I-0; III,4 and endopod 0-0; 6 compared to I-0; IV,5 and 0-0; 5 in the new species). Both *A. justinei* and *A. similis* are similar to the new species in having a transverse fold in the myxal area of the female maxilliped. The tines of the sternal furca are strongly divergent in *A. justinei*, the posterior process of the maxillule is broad-based triangular in shape, and the endopod of leg 3 has setation of 0-0; 6 (Venmathi Maran *et al.*, 2008). In contrast, the new species has straight to weakly divergent tines on the sternal furca, the posterior process of the maxillule is long and narrow at the base, and the endopod of leg 3 has setation of 0-0; 5. The new species differs from *A. similis* in the setation of both rami of leg 3: the exopod has I-0; IV,5 and the endopod 0-0; 5 in the new species compared to I-0; III,5 and 0-0; 6, respectively, in *A. similis* (Prabha & Pillai, 1986).

Using the key to species of *Anuretes* provided by Ho & Lin (2000), the new species keys out as *A. anomalus* which, as *Lepeophtheirus anomalus*, has already been reported from Queensland, on the same host (as *Spilotichthys pictus*) caught at Heron Island (Ho & Dojiri, 1977). However, there are numerous differences between the Moreton Bay females and *A. anomalus*. The most obvious is the disproportionate width of the genital complex of the new species. It is markedly wider than the cephalothorax in the holotype and all 7 female paratypes whereas in *A. anomalus* it is narrower than the cephalothorax. In addition, there are differences in leg setation: *A. anomalus* has 6 setae on the distal endopodal segment of leg 3 whereas the new species has only 5 setae (Fig. 4D), and the first exopodal segment of leg 3 has an inner seta in *A. anomalus* (Ho & Dojiri, 1977) but none in the new species. Finally, the presence of the long medial flange on the proximal segment of the antenna is a unique feature of the new species. These differences are sufficient to justify the establishment of a new species.

Comparison with *A. brevis* Pearse, 1951 is problematic since this species is known only from a single male. The body lengths of known species (Table 2) provide relevant data. *Anuretes brevis* has a male body length of 1.55 mm (Pearse, 1951): the female of the new species has a mean body length of only 1.01 mm and it is the second smallest member of the genus discovered to date. In caligid species, the female is typically larger than the conspecific male, although exceptions are known (e.g. *Caligus curtus* Müller, 1785 and C. *dicentrarchi* Cabral & Raibaut, 1987) where the male is larger than the female. A sexual size disparity of such a magnitude (female of 1.01 mm versus male of 1.55 mm) is unknown and in all *Anuretes* species where both sexes are known, the female is larger than the male (Table 2). In addition, there are apparent differences between the new species and *A. brevis* in some of appendages that do not usually show sexual dimorphism, for example, the exopod of leg 4 of *A. brevis* carries 4 long spines, whereas in the new species the 3 more proximal spines are markedly shorter than the distal spine. Leg 3 also appears very different in the illustration of Pearse (1951: Fig. 67g) but the leg may have been damaged or misinterpreted since it does not resemble leg 3 in any of its congeners.

***Anuretes amymichaelae* sp. nov.**
(Figs. 5–7)

Type material. Holotype ♂, 2 paratype ♀♀, 4 paratype ♂♂, I immature ♀ from *Diagramma pictum* (TC17266) 19 January 2016, QM Reg. Nos Holotype ♀ W53044, 1 paratype ♀, 2 paratype ♂♂ W53045; 2 paratype ♀♀, 1 paratype ♂, NHMUK Reg. Nos 2017.180–182.

Type Host. *Diagramma pictum* (Thunberg, 1792).

Site on host. Unknown (in body soak).

Etymology. The species is named after my daughter Amy Michaela Boxshall who has helped to database and curate numerous collections of parasitic copepods over the years.

Description. Female (Fig. 5A) body length 0.92 and 0.93 mm. Cephalothorax subcircular (length 0.81 x width 0.69 mm), with small posterior sinuses; cephalothorax comprising about 86 % of total body length. Frontal plates without lunules. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly beyond rear margins of lateral portions and almost completely concealing free fourth pedigerous somite (Fig. 5A). Genital complex sub-rectangular, about 1.5 times wider than long (Fig. 5B) incorporating abdomen although vestiges of sutures defining limits of abdomen visible in ventral view (Fig. 6A). Genital complex with copulatory pores and genital apertures located dorsally. Fifth legs positioned on posterior margin and directed medially, overlaping dorsal surface of abdomen. Caudal rami about as long as wide (22 µm x 23 µm). Each ramus armed with 6 subequal plumose setae (Fig. 5B).

Antennule (Fig. 5C) 2-segmented; large proximal segment with 25 plumose setae arrayed along anteroventral surface and 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 5D) comprising proximal segment bearing tapering, posteriorly-directed spinous process; middle segment subrectangular, unarmed; terminal segment forming recurved claw with weak swelling proximally, bearing small blunt element, and slender distal seta near anterior margin. Post-antennal process weakly curved; ornamented with 2 unisensillate papillae on basal part and single similar unisensillate papilla on adjacent ventral cephalothoracic surface.

Mandible of typical stylet-like structure, with 12 marginal teeth (Fig. 5E). Maxillule (Fig. 5D) comprising anterior papilla bearing 3 unequal, naked setae and simple posterior process. Pair of pointed post-oral processes

present (Fig. 5D). Maxilla 2-segmented, comprising elongate syncoxa and basis: syncoxa unarmed; basis (Fig. 5F) bearing semicircular membranous flabellum on anterior margin, terminating in 2 claw-like elements (calamus and canna); calamus about 3 times longer than canna. Maxillary whip short, tapering process (Fig. 5F). Maxilliped subchelate (Fig. 5G); robust proximal segment with smooth myxal margin; distal subchela short with slender seta on concave margin.

Sternal furca (Fig. 6B) with widely separated, short, more-or-less parallel tines. Pair of hook-like processes present on ventral cephalothoracic surface posterior to intercoxal sclerite of leg 1 (Fig. 6B).

First swimming legs joined by slender intercoxal sclerite (Fig. 6C); sympod with inner and outer plumose setae derived from basis; endopod vestigial. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment armed with small outer (anterior) spine and ornamented with row of setules along middle section of posterior margin; second segment armed with 3 plumose setae along posterior margin and 4 distal elements along distal margin as follows: spine 1 (anterior-most) longest, ornamented with row of fine spinules along concave margin, longer than spine 2; spine 2 markedly longer than spine 3, each with accessory process; seta 4 plumose, almost as long as spine 2, shorter than segment.

Second leg (Fig. 6D) biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by intercoxal sclerite bearing expanded marginal membrane posteriorly; each coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segment 1 with slightly curved outer spine aligned almost with longitudinal axis of ramus, plus inner plumose seta, carrying flap of membrane anteriorly, reflexed back over dorsal surface of ramus; segment 2 with outer spine directed distally plus inner plumose seta; segment 3 with small naked proximal spine and broader distal spine; apical spine with marginal membrane laterally and pinnules medially, plus 5 inner plumose setae. Endopodal segments 1 and 2 armed with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; free outer margins of all endopodal segments ornamented with fine setules.

Third leg pair (Fig. 6E) forming flattened plate closing posterior part of cephalothoracic sucker. Protopodal part flattened, limb pair joined by broad, plate-like intercoxal sclerite forming apron, ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate and outer plumose seta dorsal to base of exopod; sensillae located adjacent to inner coxal seta and adjacent to origin of endopod; rami originating close together, no velum present. Exopod 2-segmented (Fig. 6F); first segment armed with short claw directed over ventral surface of ramus; compound distal segment armed with 3 outer spines and 5 plumose setae along margins. Endopod 2-segmented; first segment unarmed; compound distal segment with 6 plumose setae.

Fourth leg (Fig. 5B) comprising protopodal segment with plumose seta distally, plus 2-segmented exopod: first exopodal segment armed with long outer distal spine; distal segment with 3 long distal margin spines ornamented with finely serrated or smooth membrane.

Fifth legs forming setose lobe originating posterolaterally on genital complex (Fig. 5B) and extending medially over surface of abdomen beneath: each fifth leg comprising lateral seta located near corner of genital complex and process representing exopod armed with 3 reduced setae.

Male (Fig. 7A) mean body length 0.74 mm, range 0.72 to 0.77 mm (based on 5 specimens). Cephalothorax subcircular as in female (length 0.63 mm x width 0.56 mm). Paired areas of striated cuticle located either side of middle on ventral surface of frontal plates (Fig. 7B) forming weakly defined adhesion pads. Genital complex about 2.4 times wider than long, as measured along mid-line (Fig. 7C); with smoothly convex lateral margins and fifth and sixth legs together forming posterior margin of genital complex (Fig. 7C, D). Abdomen incorporated into genital complex but with traces of sutures ventrally helping to define original boundaries (Fig. 7D); carrying paired caudal rami distally. Caudal rami about as long as wide, armed with 6 plumose setae around distal margin.

Antennule, mandible and maxilla as in female. Antenna modified (Fig. 7E); first segment elongate; second segment reflexed with large digitiform process arising ventromedially, opposing tip of subchela; distal segment forming short powerful subchela, with accessory claw. Post-antennal process (Fig. 7F) more highly curved than in female; associated papillae unisensillate. Maxillule with minute tooth on surface of posterior process (Fig. 7G). Post-oral processes (Fig. 7G) longer in male than in female. Maxilliped (Fig. 7H) with smooth myxal margin; distal subchela as in female. Sternal furca with short, widely-separated but strongly incurved tines (Fig. 7I).

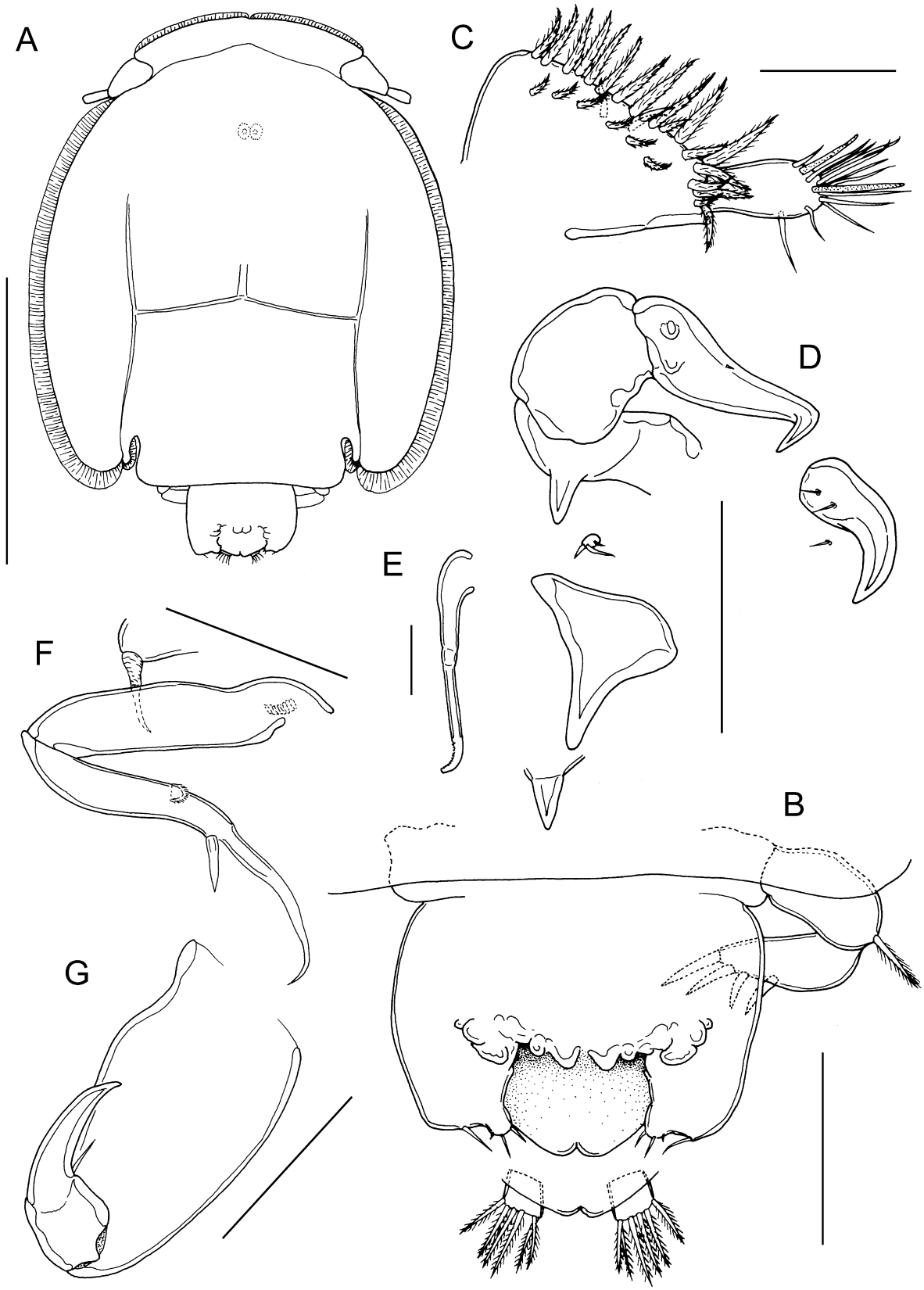

FIGURE 5. *Anuretes amymichaelae* **sp. nov.**, paratype female. A. habitus, dorsal; B, fourth pedigerous somite, genital complex and abdomen, dorsal view, with inset showing position of caudal rami on distal margin of abdomen; C, antennule; D, antenna, post-antennal process, maxillule and post-oral process, drawn *in situ*; E, mandible; F, right maxilla and maxillary whip, drawn *in situ*; G, maxilliped. Scale bars: 0.5 mm on A, 100 µm on B, D, F, G, 50 µm on C, 20 µm on E.

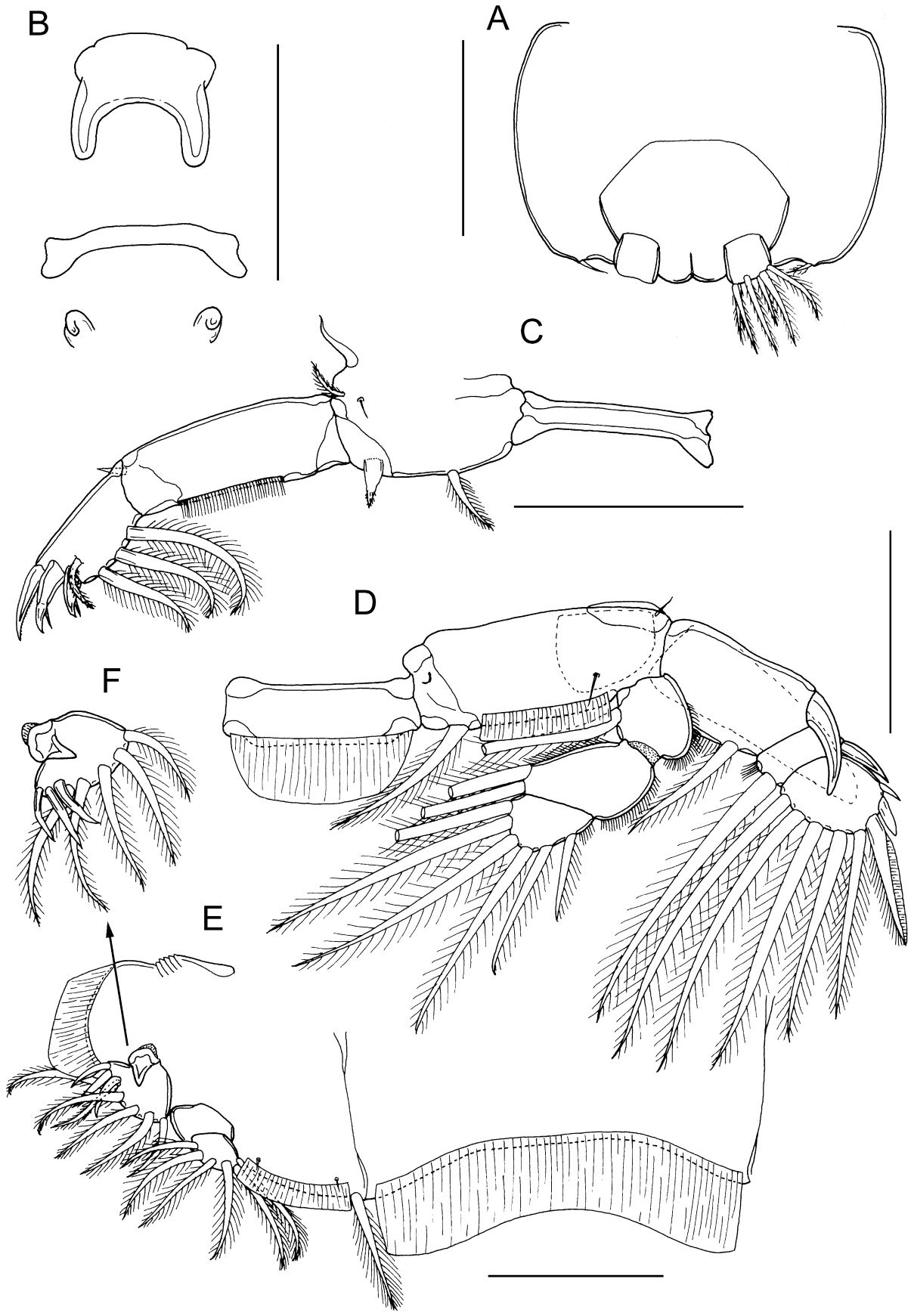

FIGURE 6. *Anuretes amymichaelae* **sp. nov.**, paratype female. A, genital complex and abdomen, ventral; B, sternal furca, drawn *in situ* relative to interpodal bar of leg 1; C, leg 1; D, leg 2; E, leg 3; F, detail of exopod of leg 3. All scale bars 100 µm.

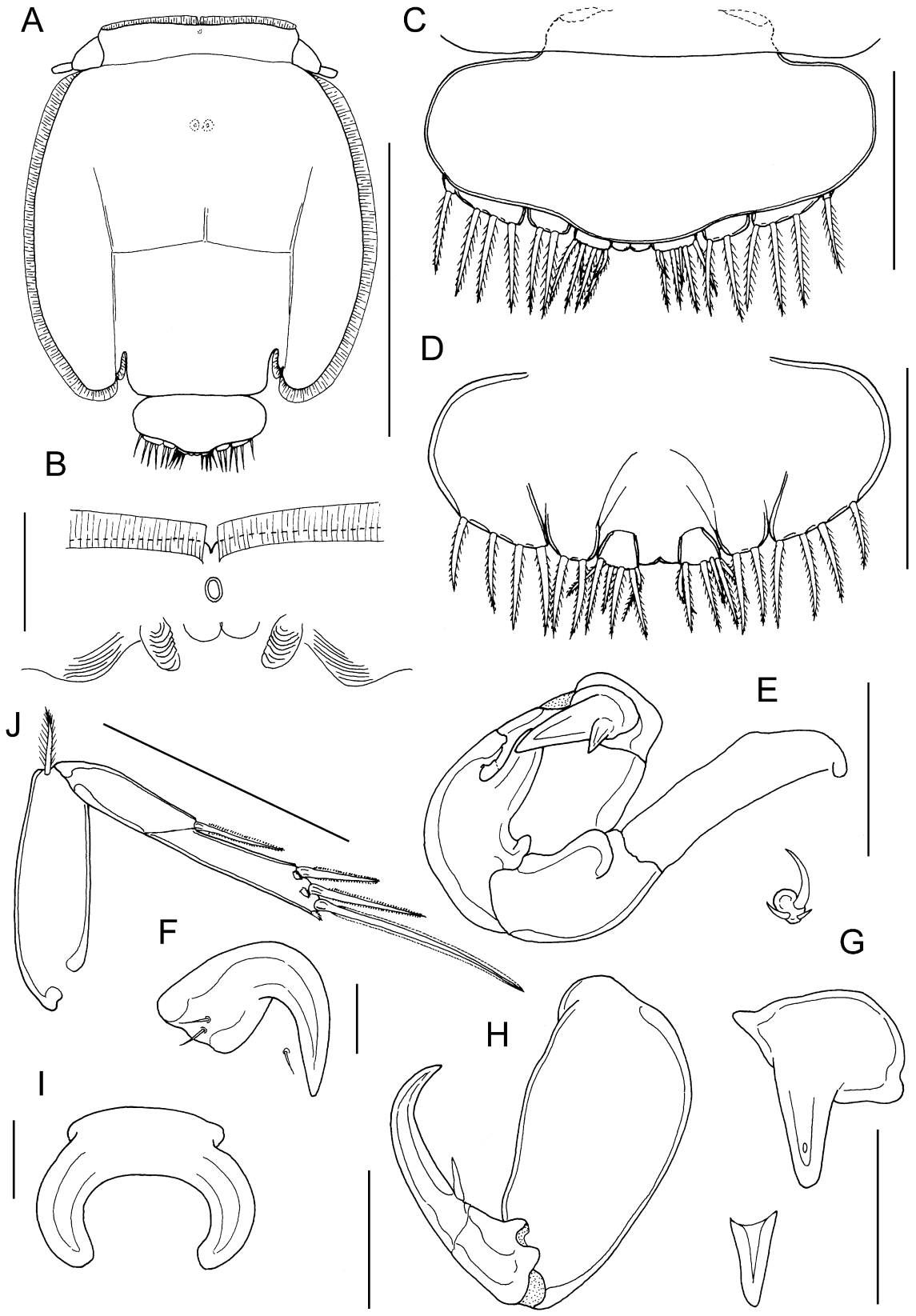

FIGURE 7. *Anuretes amymichaelae* **sp. nov.**, holotype male. A. habitus, dorsal; B, corrugated adhesion pads on ventral surface of cephalothorax, either side of midline near frontal plates; ventral; C, genital complex and abdomen, dorsal view; D, genital complex and abdomen, ventral view showing fifth and six legs; E, antenna; F, post-antennal process; G, maxillule and post-oral process, drawn *in situ*; H, maxilliped; I, sternal furca; J, leg 4. Scale bars: 0.5 mm on A, 100 µm on C, D, J, 50 µm on B, E, G, 20 µm F, I.

Leg 4 (Fig. 7J) more slender than in female. Legs 5 and 6 (Fig. 7D) together with caudal rami forming evenly convex, setose, posterior margin of body; consisting of paired fifth legs, each with 4 plumose setae, paired sixth legs, each with 2 plumose setae, and paired caudal rami, each with 6 plumose setae.

Remarks. This unusual copepod keys out to the *Pseudanuretes*/*Anuretes* couplet in the most recent key to genera of Caligidae (Dojiri & Ho, 2013). The genus *Pseudanuretes* was maintained as valid by Dojiri & Ho (2013) and was defined by the presence of an accessory claw on the female antenna, combined with the absence of the post-antennal process, the posterior process of the maxillule, and the sternal furca. The new species from Moreton Bay lacks an accessory claw on the antenna but possesses a post-antennal process, a posterior process on the maxillule, and a sternal furca. On this basis it is placed in *Anuretes*.

The new species has a total of 4 spines on the exopod of leg 4, a character state shared with 12 other species: *A. amplus* **sp. nov.**, *A. anomalus*, *A. branchialis*, *A. grandis*, *A. hoi*, *A. justinei*, *A. occultus*, *A. perplexus* Bassett-Smith, 1898, *A. plectorhynchi*, *A. quadrilaterus* Shiino, 1954, *A. rotundigenitalis* and *A. similis*. Three of these species, *A. branchialis*, *A. perplexus*, and *A. quadrilaterus*, differ from the new species in lacking a maxillary whip. Of the remaining species only two, *A. rotundigenitalis* and *A. similis*, exhibit a total of 8 setal elements on the distal exopodal segment of leg 3, as found in the new species (Fig. 6E, F). The other species either have 9 (*A. anomalus*, *A. grandis* and *A. justinei*) or 7 (*A. hoi* and *A. occultus*) setal elements on this segment (Ho & Lin, 2000; Venmathi Maran *et al.*, 2008).

The new species can be distinguished from *A. rotundigenitalis* by the size of the female genital complex: in the latter species it is almost as long as the cephalothorax and is about as long as wide, whereas in the new species it is wider than long and comprises only 15% of the length of the cephalothorax. The armature of the exopod of leg 3 also differs: all 8 setal elements on the compound distal segment are of similar length in *A. rotundigenitalis* (cf. Hameed, 1976) whereas in the new species they are clearly differentiated into 3 short outer spines and 5 longer inner setae. In addition, the outer spine on exopodal segment 1 is tiny in the new species but extends almost to the distal tip of the ramus in *A. rotundigenitalis*.

The new species is most similar to *A. similis*, the original description of which is published in Prabha & Pillai (1986) under the misapplied name of *A. plectorhynchi* (see Ho & Lin, 2000). These two species can be distinguished by: the maxillary whip is apparently bifid in *A. similis* but simple in the new species, the 3 outer spines on the compound distal exopodal segment of leg 3 differ in length (1 short, 1 medium and 1 long) in *A. similis*, but all are more or less equal in length in the new species, and the outer spine on the first exopodal segment of leg 3 is tiny in the new species but extends almost to the distal tip of the ramus in *A. similis*. These differences are sufficient to justify the establishment of a new species.

Comparisons have been restricted to limb structure despite an obvious difference between these two species in the size and shape of the genital complex (which is unusual in the new species in its small size, in the dorsal location of the genital apertures, and in the inward-facing orientation of the fifth legs), because of uncertainty over the state of maturity of the female specimen. The figured female is the best developed female collected and was found in amplexus with the figured male, which displays the typical secondary sexual characteristics of caligid males and is clearly adult. However, as caligids exhibit pre-copulatory mate guarding (Boxshall, 1990b) it is possible that this female is either adult and has yet to undergo a post-mating enlargement of the genital complex which is known to occur (e.g. Boxshall, 1974), or is the final moult stage prior to the adult. In either case the shape of the genital complex might be unreliable as a species discriminant.

The male exhibits sexual dimorphism in the configuration of the genital complex, and in the antenna, the post-antennal process, maxillule, post-oral process, maxilliped, and sternal furca, as well as in legs 5 and 6. The paired areas of striated cuticle either side of mid-line on the ventral surface of the frontal plates (Fig. 7B) are interpreted here as weakly defined adhesion pads. They appear to be involved in mating behaviour as they were held in contact with the dorsal surface of the female cephalothoracic shield in the pair observed in amplexus.

Anuretes branchialis Rangnekar, 1953
(Fig. 8)

Syn: *Henicophilus japonicus* Yamaguti & Yamasu, 1959

Material examined. 14♀♀ from *Platax teira* (Forsskål, 1775) (TC16981), 11 January 2016; 7♀♀ QM Reg. No. W53046; 7♀♀ NHMUK Reg. Nos. 2017.183–189.

Site on host. attached near distal tips of gill filaments.

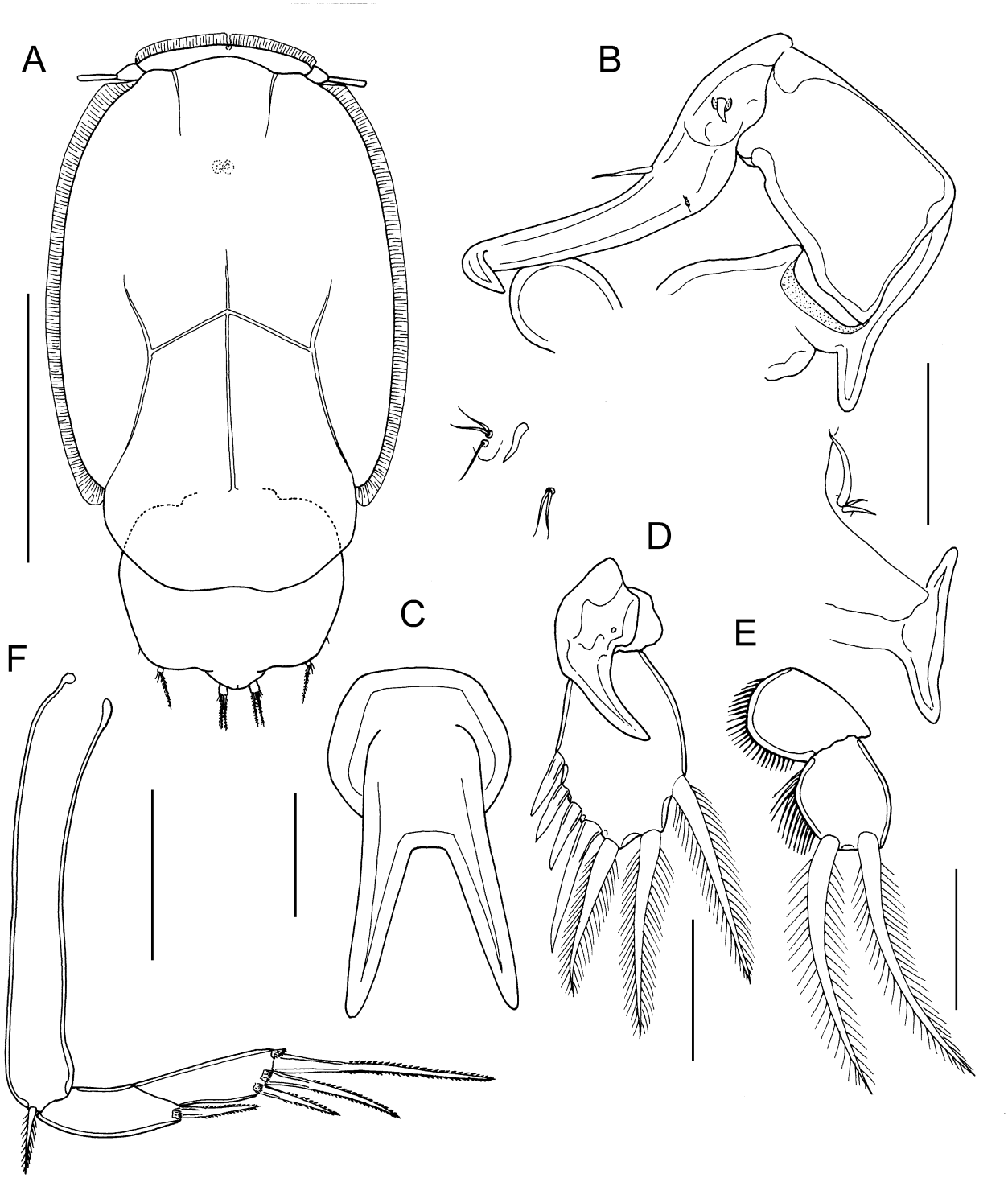

FIGURE 8. *Anuretes branchialis* Rangnekar, 1953, female. A, habitus, dorsal; B, antenna, vestigial post-antennal process, maxillule and post-oral process, drawn *in situ*; C, sternal furca; D, exopod of leg 3; E, endopod of leg 3; F, leg 4. Scale bars: 1.0 mm on A, 100 µm on B, C, F, 50 µm on D, E.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; elongate, about 1.6 times longer than wide, and somewhat rectangular in outline; thoracic zone extending posteriorly completely concealing fourth pedigerous somite and anterior part of genital complex in dorsal view (Fig. 8A). Frontal plates lacking lunules. Genital complex quadrangular, about 1.2 times wider than long; abdomen

reduced and fused to genital complex. Antenna with posteriorly-directed spinous process on proximal segment (Fig. 8B). Post-antennal process vestigial; associated papillae uni- or bisensillate. Maxillary whip lacking. Sternal furca with straight, slightly divergent, pointed tines (Fig. 8C). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; spine 1 short, distal spines 2 and 3 each with accessory process; seta 4 just longer than spine 1. Leg 3 with 2-segmented exopod (Fig. 8D); proximal segment bearing large curved spine and lacking inner seta, compound distal segment with 4 naked spines plus 3 plumose setae; endopod 2-segmented (Fig. 8E), first segment unarmed, distal segment with 2 terminal setae. Leg 4 uniramous, 3-segmented (Fig. 8F); exopodal segments 1 and 2 armed with I and III spines, respectively. Mean body length of adult female 2.47 mm, range 2.34 to 2.55 mm (based on 10 specimens).

Remarks. The complex taxonomic history of *A. branchialis* was summarised by Dojiri & Ho (2013) who provided an up-to-date synonymy and a detailed redescription of the female. The male is still unknown, more than half a century after discovery of the female. The distinctive features of *A. branchialis* include: the extensive thoracic zone of the dorsal cephalothoracic shield which completely conceals the fourth pedigerous somite and extends over the anterior half of the genital complex, combined with the presence of a sternal furca, lack of maxillary whip, and the 2-segmented endopod in leg 3, armed with 0-0; 2 setae.

This species has been reported from the gills of six host species representing five different families (Dojiri & Ho, 2013: Table VII). It has a wide geographical range in the Indo-Pacific, having been reported from the Arabian Sea, India, Sri Lanka, Indonesia, Taiwan, Japan, the Philippines and Australia (see Dojiri & Ho, 2013). It was previously reported from *Platax teira* captured in Moreton Bay by Kabata (1965a), under the name *Henicophilus japonicus*.

Anuretes plectorhynchi Yamaguti, 1936

(Fig. 9)

Material examined. 1♀, 3♂♂ from *Diagramma labiosum* MacLeay, 1883 (TC16955), 10 January 2016; 1♀, 1♂ QM Reg. No. W53047; 2♂♂ NHMUK Reg. Nos 2017.190–191.

Site on host. Unknown (in body wash).

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; about 1.17 times longer than wide; thoracic zone extending posteriorly to completely conceal short fourth pedigerous somite in dorsal view (Fig. 9A). Frontal plates lacking lunules. Genital complex broadest anteriorly, with convex lateral and posterior margins resulting in a semicircular outline in dorsal view; about 1.8 times wider than long; genital complex and abdomen less than 20% of length of cephalothorax; abdomen reduced, largely incorporated into genital complex; bearing paired caudal rami posteroventrally (Fig. 9B). Antenna (Fig. 9C) with acute posteriorly-directed process on proximal segment. Post-antennal process curved; associated papillae unisensillate. Tine of maxillule long and straight; post-oral process short, hook-like (Fig. 9C). Maxillary whip simple (not bifid). Sternal furca (Fig. 9D) with slightly-divergent tines. Pair of well-developed, hook-like processes present on ventral cephalothoracic surface posterior to intercoxal sclerite of leg 1 (Fig. 9D). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spines 2 and 3 each with accessory process; seta 4 offset, originating on ventral surface of segment, just longer than spine 1. Leg 2 with outer spine on first exopodal segment straight and elongate, lying obliquely across surface of ramus and extending almost to distal tip of ramus (Fig. 9E); outer spine on segment 2 similar in shape but smaller; proximal outer spine of segment 3 smaller than distal; distal outer spine with lateral membrane around tip. Leg 3 (Fig. 9F) with 2-segmented exopod; bearing large straight spine on proximal segment and 8 setal elements on compound distal segment: endopod 2-segmented; first segment unarmed, compound distal segment with 6 setae. Leg 4 uniramous, 3-segmented; exopodal segments with I; III spines. Leg 5 comprising outer protopodal seta isolated on surface of genital complex and well-defined exopodal lobe bearing 3 plumose setae and rudimentary spine (Fig. 9B). Body length of adult female 1.28 mm. Mean body length of adult male 0.82 mm, range 0.78 to 0.86 mm (based on 3 specimens).

Remarks. Yamaguti (1936) described *A. plectorhynchi* based on three females collected from *Diagramma pictum* (as *Plectorhynchus pictus*) caught in the "Pacific", presumably close to Japan (from the title of the paper). The species recorded as *A. plectorhynchi* by Prabha & Pillai (1986) from Indian waters was clearly not conspecific with Yamaguti's type material, and was recognized as a distinct species by Ho & Lin (2000) and renamed *A. similis* Ho & Lin, 2000. *Anuretes plectorhynchi* was recently reported from the Philippines on *Platax orbicularis* (Forsskål, 1775) (Venmathi Maran *et al.*, 2016). This is the first record from Australian waters.

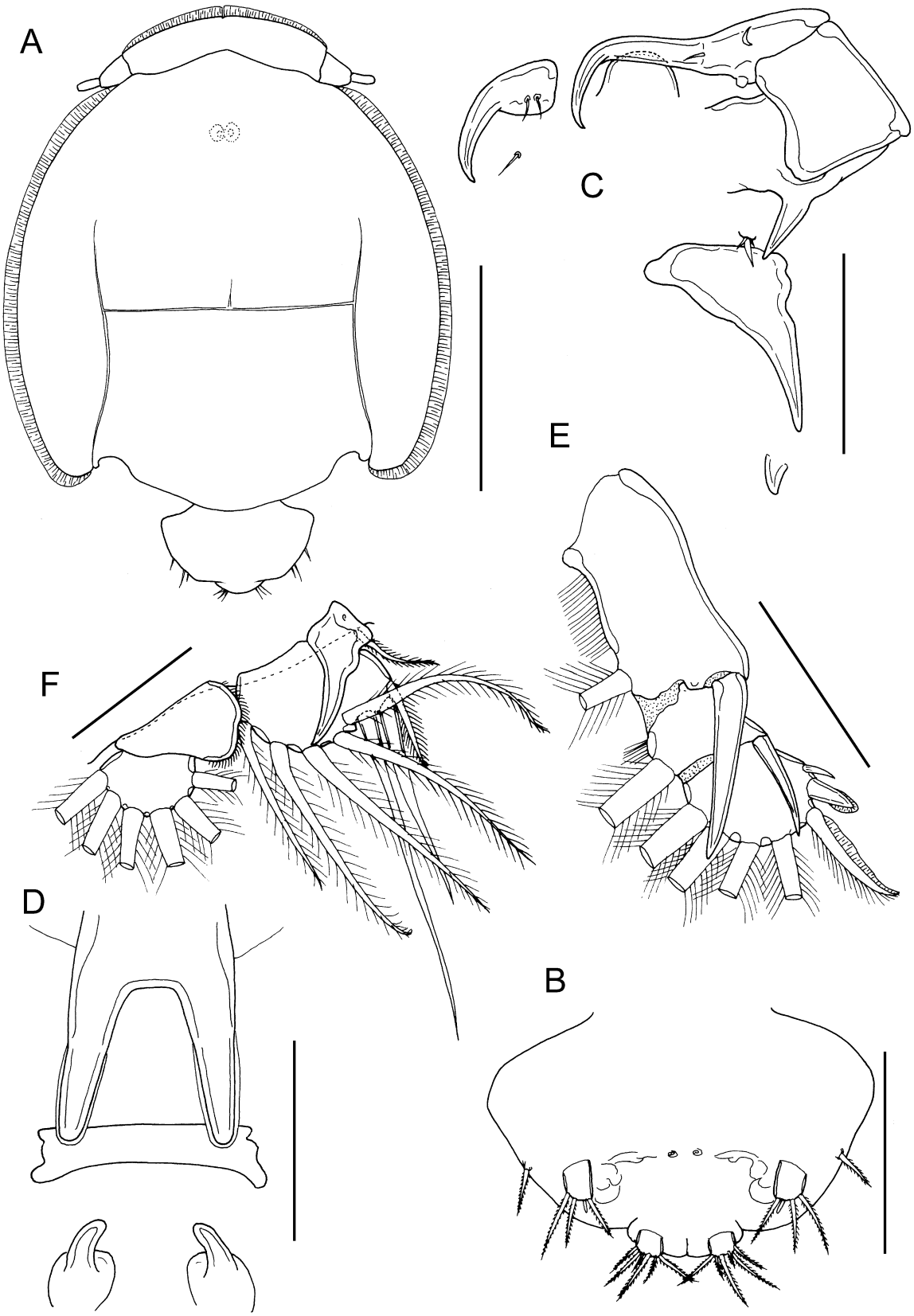

FIGURE 9. *Anuretes plectorhynchi* Yamaguti, 1936, female. A, habitus, dorsal; B, genital complex and abdomen, ventral; C, antenna, post-antennal process, maxillule and post-oral process, drawn *in situ*; D, sternal furca, interpodal bar of leg 1 and ventral processes; E, exopod of leg 2; F, exopod and endopod of leg 3, ventral view drawn *in situ*. Scale bars: 0.5 mm on A, 200 µm on B, 100 µm on C–E, 50 µm on F.

***Anuretes serratus* Shiino, 1954**
(Figs. 10, 11)

Material examined. 1♀ in washings of cool box used to transport *Prionurus microlepidotus* Lacepède, 1804 (TC17609) and other fishes on 26 June 2016, QM Reg. No. W53048.

Site on host. Unknown.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; about 1.07 times longer than wide; thoracic zone extending posteriorly about level with tips of lateral zones, not overlapping fourth pedigerous somite. Frontal plates lacking lunules. Fourth pedigerous somite visible in dorsal view (Fig. 10A). Genital complex with lateral margins evenly convex, posterior margin more-or-less transverse, with fifth legs visible at posterolateral corners in dorsal view; genital complex about 1.95 times wider than long and less than quarter length of cephalothorax; abdomen 1-segmented, not separated from genital complex by articulation. Caudal rami elongate, 2.9 times longer than maximum width, bearing only 5 caudal setae (Fig. 10B). Antennule (Fig. 10C) with 25 anteroventral setae and 2 dorsal setae on proximal segment; distal segment with 10 setae plus 2 aesthetascs plus posterior margin seta. Antenna with posteriorly-directed spinous process on proximal segment; middle segment unarmed; distal segment strongly curved, armed with proximal and distal setae (Fig. 10D). Post-antennal process with small tapering tine; associated papillae multisensillate. Maxillulary process bifid, inner lobe rounded, outer lobe pointed (Fig. 10D). Maxillary whip lacking. Maxilla (Fig. 10E) elongate. Maxilliped (Fig. 10F) slender, with bulbous lobe on concave margin of subchela. Sternal furca absent: ventral cephalothoracic surface with 2 pairs of rounded swellings anterior to intercoxal sclerite of leg 1 (Fig. 11A) and 1 pair anterior to intercoxal sclerite of leg 2 (Fig. 11B). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal margin spine 1 longest; spines 2 and 3 each hand-like, with multiple digitiform processes (Fig. 11A); seta 4 just shorter than spine 1. Leg 2 (Fig. 11B) with 2-segmented endopod, compound distal segment bearing 8 setae: exopod 3-segmented; with outer spine on first segment directed obliquely across ramus and ornamented with large serrations; outer spine on second segment aligned with longitudinal axis of ramus plus inner seta; third segment with 2 outer spines, apical spine and 5 plumose setae. Leg 3 (Fig. 11C) with 2-segmented exopod; bearing large tapering outer spine and inner plumose seta on proximal segment; compound distal segment bearing 4 spines and 5 short plumose inner setae: endopod 2-segmented; first segment expanded to form velum, but lacking inner seta; distal segment with 6 setae. Leg 4 (Fig. 11D) uniramous, 3-segmented; first exopodal segment with outer spine, compound distal segment with 1 long and 3 short spines, all on oblique distal margin. Body length of adult female 2.60 mm.

Remarks. This distinctive species was originally described on the basis of three females collected from the body surface of *Prionurus scalprum* Valenciennes, 1835 (as *Xesurus scalprum*) caught off Seto, Japan (Shiino, 1954a). It was reported subsequently from Hawaii by Lewis (1964a) who redescribed the female and described the male for the first time. The host of the Hawaiian material was *Naso hexacanthus* (Bleeker, 1855). The female from Moreton Bay was found in washings from a cool box used to transport freshly caught fish to the laboratory. This box had contained a mix of fish species caught by spear fishers (viz. one specimen each of *Apogon limenus* Randall & Hoese, 1988, *Canthigaster solandri* (Richardson, 1845), *C. valentini* (Bleeker, 1853), *Gerres* sp., *Girella tricuspidata* (Quoy & Gaimard, 1824), and *Microcanthus strigatus* (Cuvier, 1831) and two specimens of *Prionurus microlepidotus*). Given that this species of *Anuretes* has only been found on acanthurids and that its type host is *Prionurus scalprum*, it seems likely that this specimen had been dislodged from *P. microlepidotus* during transportation in the cool box.

Anuretes serratus displays an interesting array of unusual and unique features: it lacks a sternal furca but it has a bulbous lobe on the subchela of the maxilliped, spines 2 and 3 on the distal exopodal segment of leg 1 have multiple digitiform processes; leg 2 has a 2-segmented endopod due to the fusion of ancestral segments 2 and 3, and it carries a prominent serrated spine on the first exopodal segment of leg 2. In all of these characters and in other subtle details, the female from Moreton Bay conforms exactly to the original description (Shiino, 1954a). There are, however, some differences when compared with the Hawaiian material. Firstly, the Hawaiian female genital complex has convex rounded posterolateral margins which serve to conceal the fifth legs in dorsal view and it has a very short abdomen that is about 2.5 times wider than long. In contrast, typical *A. serratus* has a straighter posterior margin to the genital complex, the prominent fifth legs are visible in dorsal view, and the abdomen is only about 1.5 times wider than long. The caudal rami, which have only 5 setae, are elongate (about 2.9 times longer than

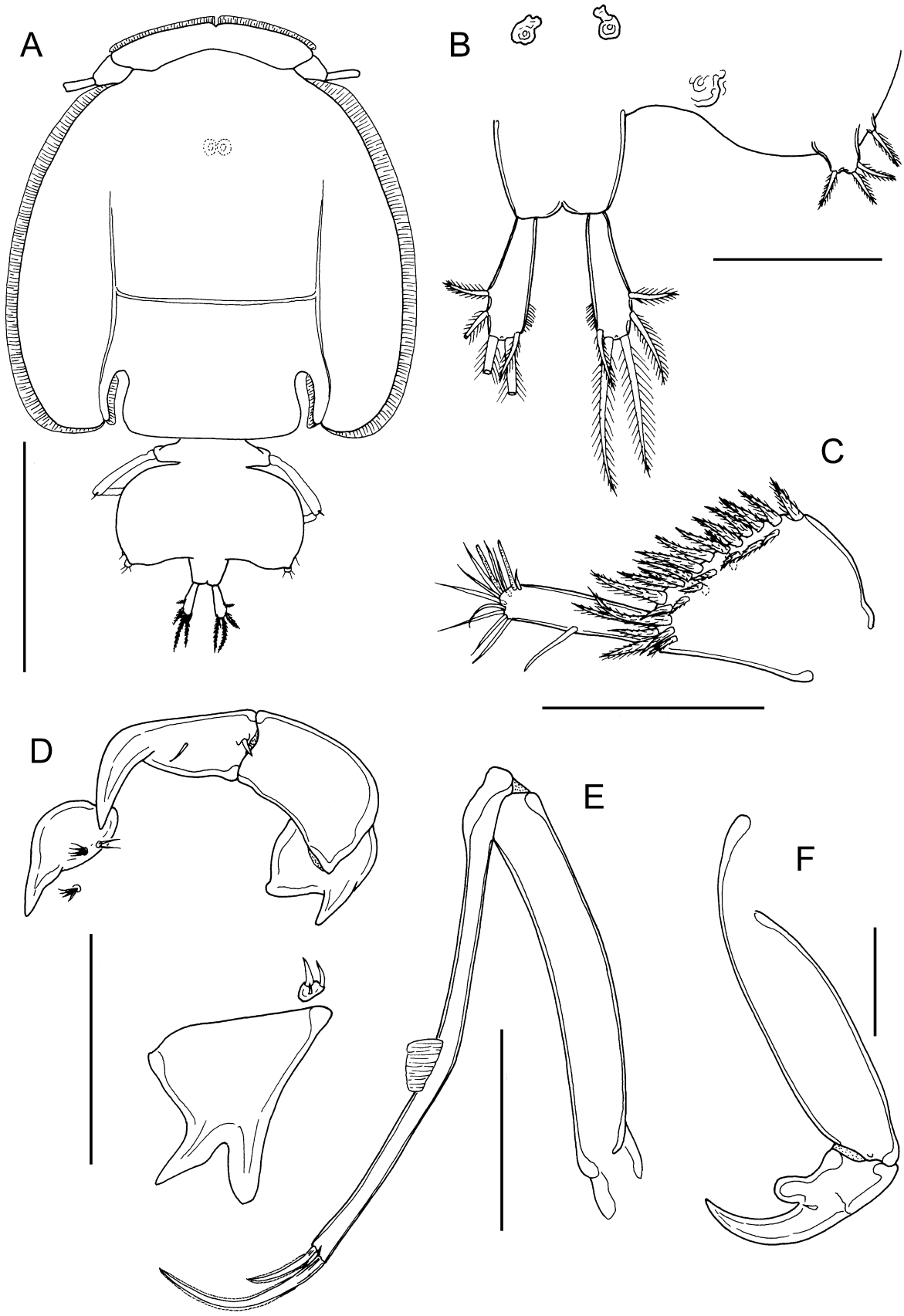

FIGURE 10. *Anuretes serratus* Shiino, 1954, female. A, habitus, dorsal; B, left corner of genital complex and abdomen, ventral view showing caudal rami and left fifth leg; C, antennule; D, antenna, post-antennal process, and bifid maxillule, drawn *in situ*; E, maxilla; F, maxilliped. Scale bars: 1.0 mm on A, 200 µm on B–E, 100 µm on F.

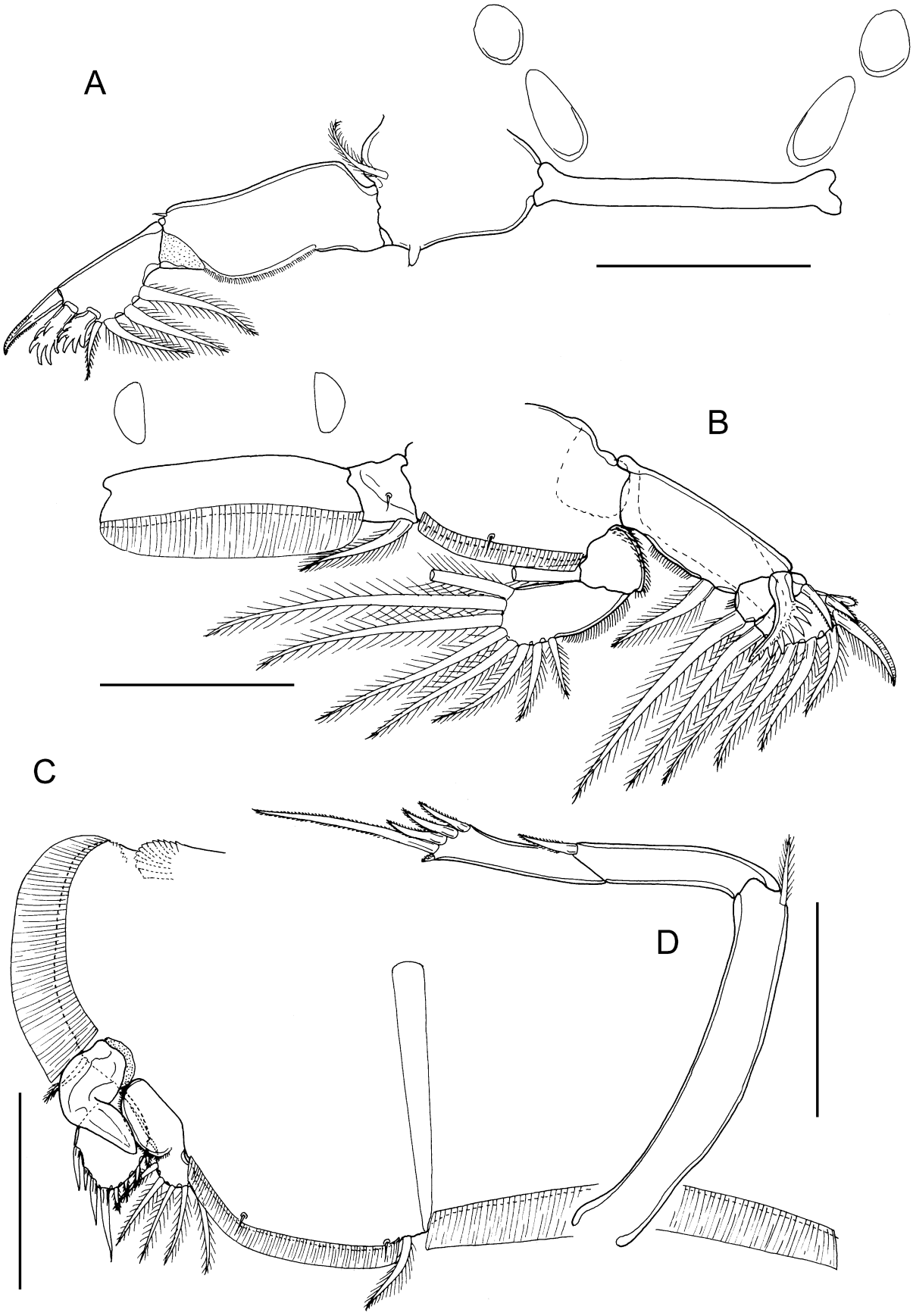

FIGURE 11. *Anuretes serratus* Shiino, 1954, female. A, leg 1, showing paired surface swellings anterior to interpodal bar; B, leg 2, showing surface swellings anterior to interpodal bar; C, leg 3, ventral; D, leg 4. All scale bars 200 μm.

maximum width) in typical *A. serratus* whereas they are only about 1.5 to 1.6 times longer than wide in Lewis's material. I consider the identity of the Hawaiian material to be in doubt, but the Moreton Bay female is in close agreement with *A. serratus*.

Genus *Caligodes* Heller, 1865

Caligodes laciniatus (Krøyer, 1863)

(Fig. 12)

Material examined. 8♀♀ from *Tylosurus gavialoides* (Castlenau, 1873) (TC17113) 13 January 2016, QM Reg. No. W53049; 13♀♀ (TC17297) 19 January 2016, QM Reg. No. W53050; 1♀ (TC17114) 13 January 2016, 1♀ (TC17270) 19 January 2016, 6♀♀ (TC17282) 19 January 2016, 3♀♀ (TC17671) 28 June 2016, 5♀♀ (TC17826) 3 July 2016, NHMUK Reg. Nos 2017.192–201.

Site on host. Gills arches and floor of branchial cavity.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; frontal plates with lunules. Fourth pedigerous somite fused to slender anterior part of genital complex, forming elongate "neck" region (Fig. 12A). Genital complex elongate, about 2.2 times longer than wide; narrow anteriorly, broadest posteriorly, bearing very large, diverging posterolateral lobes armed with apical setae, representing fifth legs at tip (Fig. 12B). Abdomen elongate about 5 times longer than wide; slightly shorter than posterolateral lobes of genital complex, giving a trifid appearance to habitus in dorsal view. Caudal rami each with 6 setae. Antennule 2-segmented: armed with 25 setae on proximal segment. Antenna (Fig. 12C) with short blunt posterior process on proximal segment. Post-antennal process without tine, represented by multisensillate papillae on weakly defined surface sclerite (Fig. 12C). Anterior process of maxillule with 3 setae, posterior process corrugated (Fig. 12D). Maxilliped of female with myxal margin inflated proximally. Sternal furca small with divergent tapering tines; paired lateral processes present on ventral surface posterolateral to furca (Fig. 12E). Leg 1 with vestigial endopod: distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spine 1 longer and more robust than other spines; spines 2 and 3 reduced, without accessory processes; seta 4 smaller than spine 3. Leg 2 with second and third endopodal segments mostly fused, surface of distal endopodal segments ornamented with patches of small denticles: exopodal segments 2 and 3 fused but with vestige of suture marking plane of fusion (Fig. 12F); outer spine on exopodal segment 1 small and proximal 2 spines on compound distal segment small and slender, directed disto-laterally away from ramus. Leg 3 apron ornamented with patch of fine denticles on ventral surface; exopod 2-segmented (Fig. 12G) with large recurved spine on first segment; compound distal segment with total of 4 naked outer spines and 4 short plumose setae; endopod 2-segmented, first segment bearing inner plumose seta not forming expanded velum; second segment with 4 setae. Leg 4 uniramous, indistinctly 3-segmented; exopodal segments with I; III spines. Leg 5 represented by elongate lobes bearing 3 reduced seta at apex (Fig. 12B). Mean body length of adult female 5.59 mm, range 5.20 to 6.0 mm (based on 10 specimens).

Male unknown.

Remarks. This species was common on *T. gavialoides* in Moreton Bay, with a prevalence of about 57%. In their monographic survey of the copepod parasites of needlefishes (Belonidae), Cressey & Collette (1970) reported *C. laciniatus* from *T. gavialoides* (as *Lhotskia gavialoides*) caught in Australian waters, but there is some confusion over the precise locality as in the main text of the taxonomic part (p. 378) they refer to "off northern Australia" while in the summary of host material examined they refer only to "New South Wales, Australia" (p. 398). However, in the addendum (p. 430) they provide additional records of *C. laciniatus* from *T. gavialoides* in New South Wales, from *Strongylura leirua* (Bleeker, 1850) in the Gulf of Carpentaria and from *Tylosurus crocodilus* (Péron & Lesueur, 1821) in Queensland, the Torres Strait and the Gulf of Carpentaria. *Caligodes laciniatus* has an almost cosmopolitan distribution in warm temperate to tropical waters, occurring in the North and South Atlantic, North and South Pacific and Indian Oceans, and Cressey & Collette (1970) recorded it on seven host species within the family Belonidae.

The mean body length exhibited by ovigerous females from Moreton Bay was 5.59 mm, which is larger than the mean of 4.66 mm given for ovigerous females parasitic on *T. gavialoides* in the Indo-West Pacific by Cressey & Collette (1970). Dojiri & Ho (2013) commented that the large posterolateral processes on the genital complex of

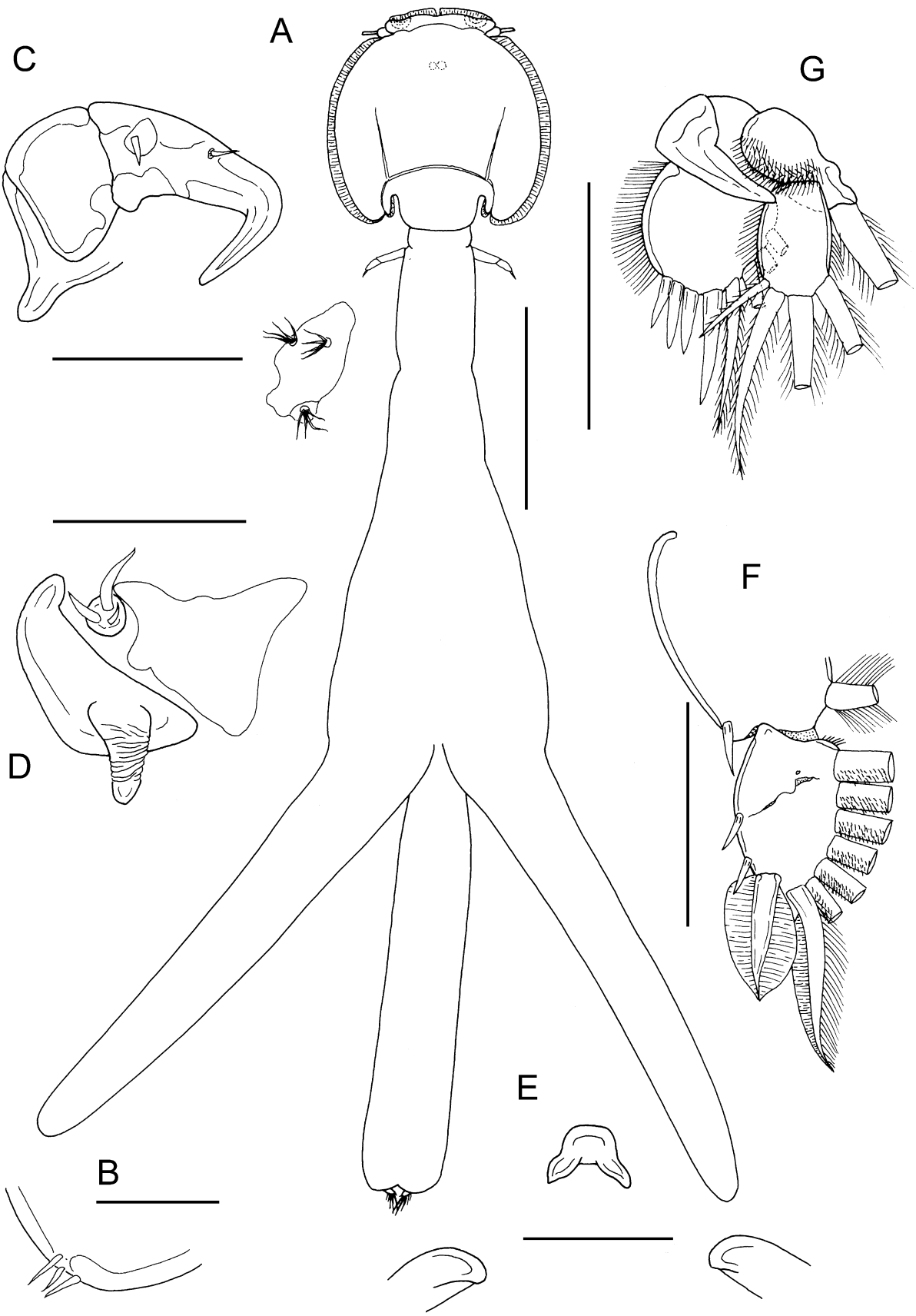

FIGURE 12. *Caligodes laciniatus* (Krøyer, 1863), female. A, habitus, dorsal; B, setal elements on tips of fifth leg processes; C, antenna and vestigial post-antennal process, drawn *in situ*; D, maxillule; E, sternal furca and adjacent paired ventral processes; F, exopod of leg 2; G, rami of leg 3, drawn *in situ*. Scale bars: 1.0 mm on A, 50 µm on B, 100 µm on C–G.

C. laciniatus may represent the fifth legs, citing Cressey & Collette (1970) who referred to these processes as the fifth legs. The presence of 3 setae on the tip of each process is strong evidence in support of the interpretation of Cressey & Collette (1970).

The validity of the genus *Caligodes* Heller, 1865 needs to be tested. According to Dojiri & Ho (2013) *Caligodes* can be differentiated from other members of the family by the combination of the long posterodorsal processes on the genital complex, the elongate abdomen, the enlarged spine 1 on the distal exopod segment of leg 1, the slender exopodal spines of leg 2, and the segmentation and armature of the rami of leg 4. Except for the long posterodorsal processes on the genital complex (here identified as fifth legs), none of these characters appears to be particularly robust as a generic level discriminant. Even the hyper-development of the fifth legs into long processes, taken alone, could be interpreted as a unique difference (i.e. an autapomorphy) that provides no information on relationships. There are major uncertainties concerning the validity of *Caligodes*, but it is treated as valid here pending a thorough revision of the caligid genera.

Genus *Caligus* O.F. Müller, 1785

Caligus abigailae sp. nov.

(Figs. 13, 14)

Type material. Holotype ♀ and 19 paratype ♀♀ from 6 heads of *Sphyraena obtusata* Cuvier, 1829 (TC16953) caught by anglers at Amity, North Stradbrooke Island, 10 January 2016; 2 paratype ♀♀ from *S. obtusata* (TC16970) 11 January 2016. QM Reg. Nos. Holotype ♀ W53051, 10 paratype ♀♀ W53052; 10 paratype ♀♀ NHMUK Reg. Nos 2017.202–211.

Type Host. *Sphyraena obtusata* Cuvier, 1829.

Site on host. Roof of pharynx, gill arches, wall of branchial cavity.

Etymology. This species is named after Abigail Whittaker, who has, over the years, provided me with considerable support and encouragement.

Description. Adult female (Fig. 13A) mean body length including caudal rami 3.35 mm, range 3.19 to 3.58 mm (based on 10 specimens). Cephalothorax subcircular; comprising about 36% of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly just beyond rear margins of lateral portions. Well developed lunules present ventrally on frontal plates. Genital complex bottle-shaped, i.e. with rounded convex lateral margins, widest towards posterior end and narrowing anteriorly, about 1.4 times longer than maximum width; fifth legs located ventrally close to posterolateral corners (Fig. 13B). Genital complex about 2.2 times longer than abdomen. Abdomen 1-segmented; about 2.0 times longer than wide in dorsal view; bearing paired caudal rami distally; anal slit terminal. Caudal rami with parallel sides, just longer than wide, measured at midpoints of margins. Each ramus armed with short hirsute seta at inner distal angle, slightly longer hirsute seta at outer distal angle, minute hirsute seta located just ventral to outer distal seta, and 3 long plumose setae on distal margin.

Antennule 2-segmented; large proximal segment with 25 plumose setae arrayed along anteroventral surface and 2 setae located dorsally; short distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 13C) comprising proximal segment bearing weakly defined posteriorly-directed spinous process; middle segment short, subrectangular, unarmed; terminal segment forming recurved claw bearing long proximal seta and slender distal seta. Post-antennal process (Fig. 13C) with weakly-developed, more-or-less straight tine ornamented with 2 multisensillate papillae on basal part and single multisensillate papilla on adjacent ventral cephalothoracic surface. Rounded swelling present between base of antenna and post-antennal process.

Mandible of typical stylet-like structure, with 12 marginal teeth (Fig. 14A). Maxillule (Fig. 13D) comprising anterior papilla bearing 3 unequal, naked setae and posterior, tapering process. Maxilla 2-segmented (Fig. 14B), comprising elongate unarmed syncoxa and basis: basis bearing membranous subapical flabellum on anterior margin, and terminating in 2 subequal claw-like elements (calamus and canna); calamus slightly longer than canna, ornamented with strips of serrated membrane arranged obliquely around surface; canna ornamented with bilateral strips of serrated membrane. Maxilliped subchelate (Fig. 14C); proximal segment robust, with transverse fold and swelling on myxal surface; distal subchela with apical claw; short, slender seta present on concave margin.

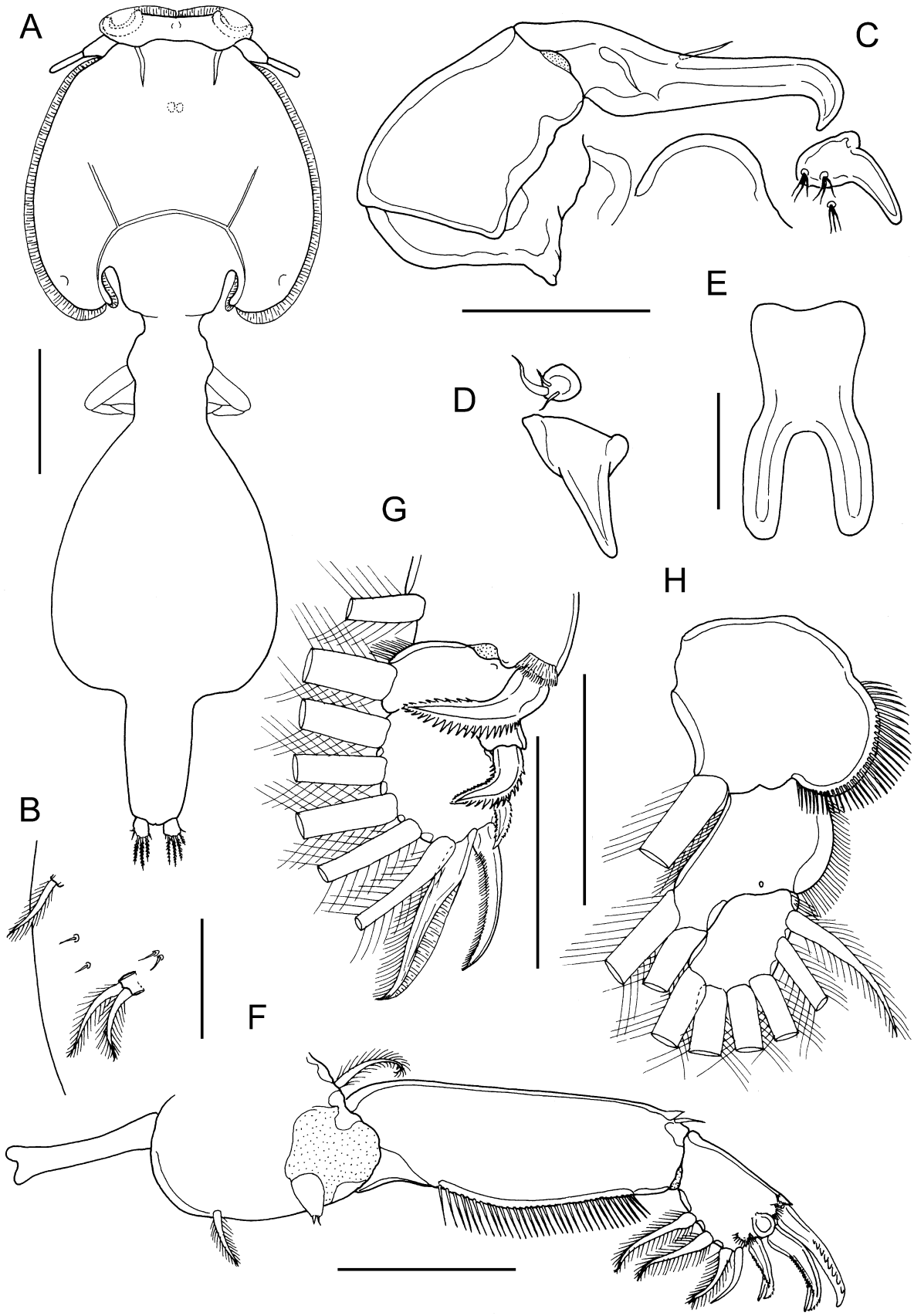

FIGURE 13. *Caligus abigailae* **sp. nov.**, paratype female. A, habitus, dorsal; B, right fifth leg at posterolateral corner of genital complex, ventral; C, antenna and post-antennal process, drawn *in situ*; D, maxillule; E, sternal furca; F, leg 1; G, exopod of leg 2; H, endopod of leg 2. Scale bars: 0.5 mm on A, 50 µm on B, E, 100 µm on C, D, F–H.

Sternal furca (Fig. 13E) with slightly divergent tines, with bluntly-rounded tips.

First swimming leg pair (Fig. 13F) joined by slender intercoxal sclerite; sympod with inner and outer plumose setae derived from basis. Endopod represented by process on posterior margin of basis, bearing 2 minute setal vestiges on apex. Exopod 2-segmented, directed laterally and forming main axis of leg; first segment robust, about 2.9 times longer than wide and armed with small outer (anterior) spine and ornamented with row of setules along posterior margin; second segment short, with bulbous swelling on posterior surface at base of spine 2, armed with 3 short plumose setae along posterior margin and 4 distal elements along oblique distal margin. Distal elements as follows: spine 1 (anterior-most) longest ornamented with row of robust denticles; spines 2 and 3 progressively smaller, each with rows of spinules and accessory process; seta 4 about as long as spine 3, shorter than segment.

Second leg biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by intercoxal sclerite bearing marginal membrane posteriorly; each coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopod 3-segmented (Fig. 13G); first exopodal segment with inner plumose seta and bilaterally serrate, curved outer spine extending obliquely across lateral side surface of ramus; segment 2 with smaller but similar outer spine extending across surface, plus inner plumose seta; segment 3 with 2 outer spines (proximal spine small and bilaterally serrate, distal spine with unilateral row of fine setules); apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. Endopodal segments 1 and 2 (Fig. 13H) armed with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; outer margin of first endopodal segment expanded distally and ornamented with stout setules around convex expansion.

Third leg pair (Fig. 14D) forming flattened plate closing posterior part of cephalothoracic sucker as typical for genus. Protopodal part flattened joined by plate-like, intercoxal sclerite to form apron, ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate and outer plumose seta dorsal to base of exopod; sensillae located adjacent to inner coxal seta and adjacent to origin of endopod; apron also ornamented with rosette-like array of spinules plus prominent bifid rib on ventral surface, and corrugated adhesion pad dorsally at anterior corner; space between rami covered by short, flap-like velum ornamented with fine setules along free margin. Exopod 3-segmented; first segment armed with large recurved spine (Fig. 14D) directed over ventral surface of ramus but lacking inner seta; second segment with 1 outer spine and inner plumose seta; third segment with 3 spines on outer margin plus 5 plumose setae on inner margin; free outer margins of segments 2 and 3 each ornamented with rows of slender setules. Endopod 2-segmented; first segment forming velum and bearing inner plumose seta; second with 6 setal elements increasing in length from outermost to innermost.

Fourth leg (Fig. 14E) uniramous, 4-segmented; comprising protopodal segment and 3-segmented exopod: protopodal segment armed with plumose seta distally; exopodal segments with I; I; III spines; each spine with associated pecten.

Fifth legs located posterolaterally on genital complex (Fig. 13B); represented by plumose seta on anterior papilla and 2 plumose setae on posterior papilla representing exopod.

Remarks. This long-bodied species belongs to a group of species, referred to as the *C. confusus* group (see remarks below under *C. confusus*), which is characterized by a suite of character states including: the presence of a raised bifid cuticular rib and a circular rosette-like array of denticles on the apron of leg 3, the possession of a large recurved hook (= the outer margin spine) on the first exopodal segment of leg 3, the possession of a 3-segmented exopod of leg 4 with a I, I, III setal formula, and, in some species only, the presence of an accessory tine on both the post-antennal process and the posterior maxillulary process. Within this grouping, the new species is most similar to *C. clavatus* Kirtisinghe, 1964, which was described from females found on *Sphyraena obtusata* caught off the coast of Sri Lanka (Kirtisinghe, 1964), and *C. inopinatus* Kabata, 1994 which is parasitic on *S. flavicauda* Rüppell, 1838 in the Red Sea (Kabata, 1994). As well as the bottle-shaped genital complex and long abdomen, these three species share numerous fine details of appendage armature, including the form and ornamentation of the setal elements on the exopod of leg 1, and the form of the outer margin spines on the exopods of legs 2 and 3.

Caligus clavatus occurs on a range of other barracuda species, including *Sphyraena jello* Cuvier, 1829 and *S. acutipinnis* Day, 1876 in Indian waters (Pillai, 1967, 1985), and *S. japonica* Bloch & Schneider, 1801 from Taiwan (Lin & Ho, 2002). A modern detailed description of the adult female of *C. clavatus* was presented by Ho & Lin (2004). It differs from the new species in its longer abdomen, which is about 2.9 times longer than wide and is

equal to about 75 to 80% of the length of the genital complex, compared to 2.0 times longer than wide and about 45% of the length of the genital complex in *C. abigailae* **sp. nov.**

Caligus inopinatus is only known from the original report in the Red Sea. It has a relatively short abdomen which is only about 1.5 times longer than wide and is equal to about 35% of the length of the genital complex. In contrast, in the new species the abdomen is 2.0 times longer than wide and about 45% of the length of the genital complex. Other minor differences are apparent including the shape of the posterior process of the proximal antenna segment (bluntly rounded in *C. inopinatus* but tapering in *C. abigailae* **sp. nov.**) and the outline shape of the sternal furca (V-shaped in *C. inopinatus* versus U-shaped in *C. abigailae* **sp. nov.**).

In Moreton Bay, this new copepod was found only on the type host, *Sphyraena obtusata.*

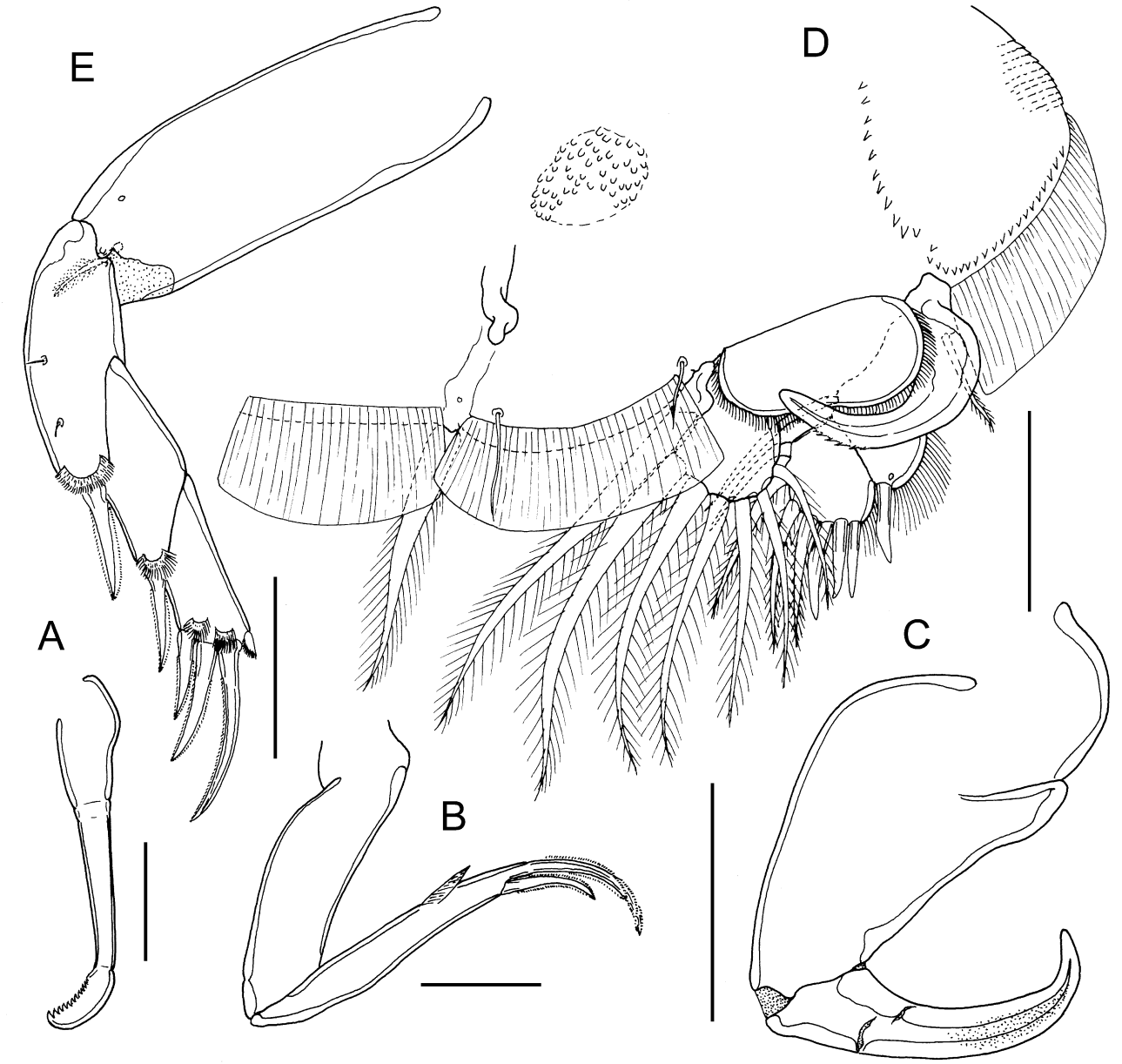

FIGURE 14. *Caligus abigailae* **sp. nov.**, paratype female. A, mandible; B, maxilla; C, maxilliped; D, leg 3; E, leg 4. Scale bars: 50 µm on A, 100 µm on B, D, E, 200 µm on C.

***Caligus aesopus* Wilson, 1921**
(Fig. 15)

Material examined. 2♀♀, 1♂ from *Seriola hippos* Günther, 1876 (TC18352) 28 March 2017, 1♀, 1♂ QM Reg.No. W53053; 1♀ NHMUK Reg. No. 2017.212.

Site on host. Unknown.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones; frontal plates with lunules; thoracic zone very small, extending posteriorly about level with posterior ends of lateral zones (Fig. 15A). Genital complex about 1.5 to 1.6 times longer than wide; abdomen indistinctly 2-segmented, with constriction at about posterior third; genital complex about 2 times longer than abdomen (Fig. 15A). Antenna with rounded posterior process on proximal segment (Fig. 15B). Post-antennal process bifid, main tine straight; associated papillae multisensillate. Posterior process of maxillule bifid; main (inner) tine much larger than outer. Maxilliped of female with rounded process proximally (Fig. 15C). Sternal furca with broad gape; tines incurved with rounded tips. Sympod of leg 1 ornamented with spinules and bearing rounded process anteriorly on ventral surface (arrowed in Fig. 15D); vestigial endopod elongate with 2 setal vestiges apically: distal exopodal segment with 3 plumose setae on posterior margin; distal spine 1 longer than other spines; spines 2 and 3 with accessory processes; seta 4 longer than spine 1 and about as long as segment. Leg 2 with marginal setules on endopodal segments 2 and 3; outer spine on exopodal segment 1 lying obliquely across segment 2, spine on segment 2 aligned close to longitudinal axis of ramus. Leg 3 (Fig. 15E) apron with raised rib, with bluntly rounded tip, plus circular array of large denticles on ventral surface and corrugated adhesion pad near outer margin on dorsal surface; exopod indistinctly 3-segmented, first segment with large recurved outer spine, lacking inner seta; second and third segments incompletely separated, outer margins hirsute, with multiple rows of long setules: endopod 2-segmented, first endopodal segment forming velum and bearing inner seta; distal segment with partial suture, armed with total of 6 plumose setae. Leg 4 uniramous, 4-segmented; exopodal segments (Fig. 15F) with I; I; III spines; innermost spine distinctly longer than middle spine. Body lengths of adult females 4.54 and 4.79 mm; length of adult male 3.46 mm.

Remarks. *Caligus aesopus* was first described from off the Juan Fernandez Islands in the East Pacific and the host was given as probably *Seriola peruana* Steindachner, 1881 (Wilson, 1921). Hewitt (1963) subsequently reported *C. aesopus* from *Seriola lalandi* Valenciennes, 1833 (as *Seriola grandis* Castelnau) caught off New Zealand. However, *C. aesopus* has been confused with a very similar species, *C. spinosus* Yamaguti (1939), which was originally described by Yamaguti (1939) based on material from *Seriola quinqueradiata* Temminck & Schlegel, 1845 caught off Japan. Unfortunately, Yamaguti did not compare his new species with *C. aesopus*. *Caligus spinosus* was recognised as a junior subjective synonym of *C. aesopus* by Fernandez & Villalba (1986) and this synonymy was followed by Lin & Ho (2007). However, Choe & Kim (2010) recently found two *Caligus* species on species of *Seriola* Cuvier, 1816 in Korean waters. They provided full descriptions of both sexes of both species, and they reinstated *C. spinosus* as a valid species, distinct from *C. aesopus*. *Caligus aesopus* can be distinguished by the presence of a constriction subdividing the female abdomen into a wider anterior part (two thirds) and a narrower posterior part (one third), by the large size and lower number (less than 15) denticles present in a rosette on the apron of leg 3, and by the apical spine on the distal exopodal segment of leg 4 being distinctly longer than the adjacent middle spine. Choe & Kim (2010) listed a few other minor character differences for the females, such as the presence of an anterior process on the surface of the sympod of leg1 (Fig. 15D), and documented a difference in the form of the myxal processes on the male maxilliped.

Caligus aesopus was found on *S. lalandi* in Korean waters (Choe & Kim, 2010) and it can be found on the same host from South Africa (Kensley & Grindley, 1973) to New Zealand (Hewitt, 1963). In addition, it occurs on *S. dumerili* (Risso, 1810) in Taiwan (Lin & Ho, 2007) and on "probably *S. peruana*" in the eastern Pacific (Wilson, 1921). Choe & Kim (2010) concluded that the material from *Sphyraena obtusata* caught off India and described by Pillai (1963) could be attributed to *C. aesopus*, but possible confusion with *C. abigailae* **sp. nov.** described above from this host should also be considered. Choe & Kim (2010) demonstrated that the material redescribed and illustrated by Shiino (1960) as "*C. spinosus*" should be attributed to *C. aesopus*. The host in Moreton Bay, *S. hippos*, is a new host record for *C. aesopus*.

Caligus spinosus has previously been reported from Australian waters (e.g. Rohde, 1978, Byrnes, 1986, Hutson *et al.*, 2007a, b) but there is uncertainty over these identifications since during at least some of the period covered by these reports, the two species were considered to be synonyms.

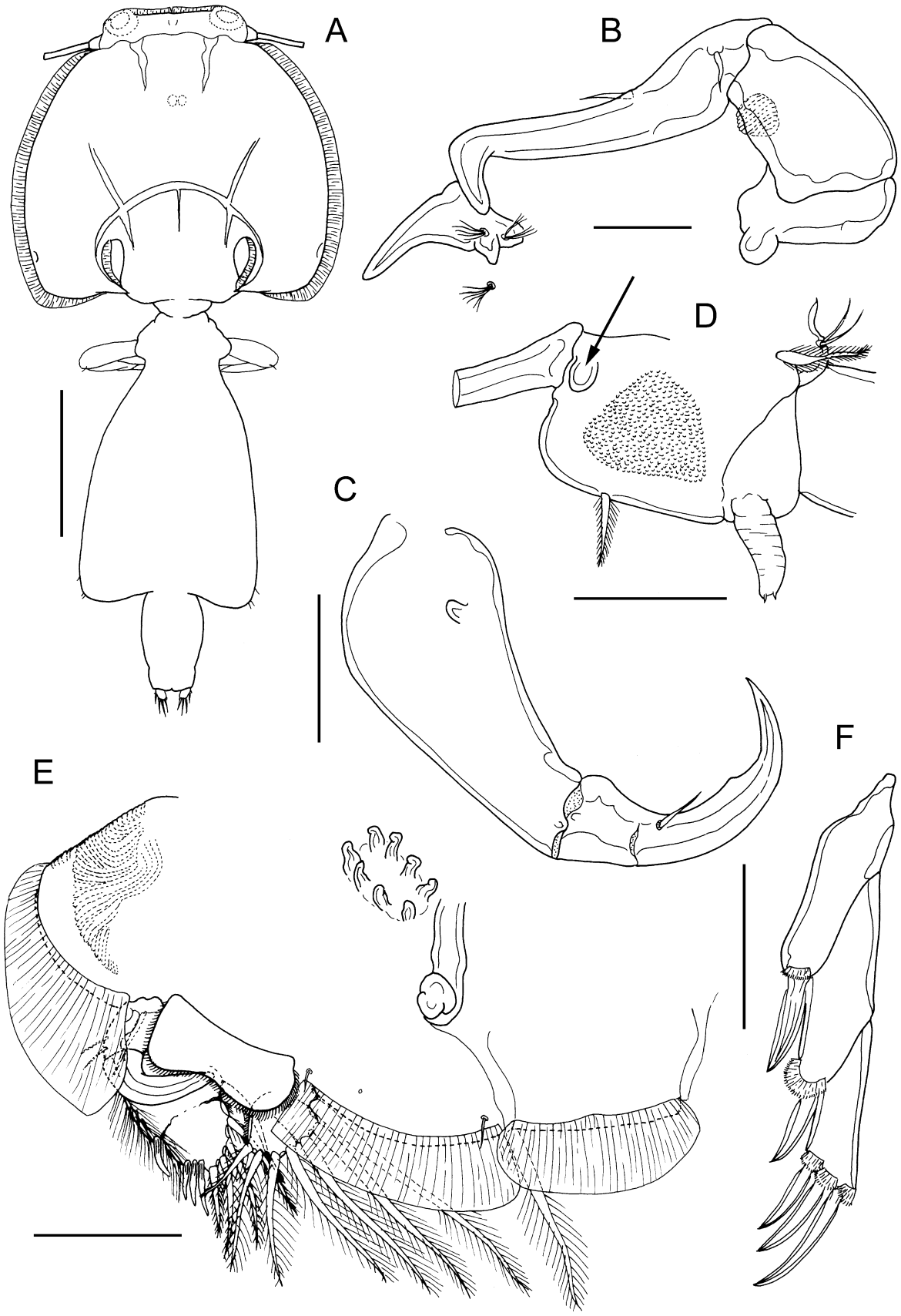

FIGURE 15. *Caligus aesopus* Wilson, 1921, female. A, habitus, dorsal; B, antenna and post-antennal process, drawn *in situ*; C, maxilliped; D, sympod of leg 1, showing anterior process on ventral surface; E, leg 3; F, exopod of leg 4. Scale bars: 1.0 mm on A, 100 µm on B, D, 200 µm on C, E, F.

***Caligus alepicolus* nom. nov.**
(Figs. 16, 17)

Syn: *Caligodes alatus* Heegaard, 1945

Material examined. 1♀ from *Alepes apercna* Grant, 1987 (TC17073), 13 January 2016, QM Reg. No W53054.

Site on host. Gills.

Redescription. Adult female (Fig. 16A) body length 6.03 mm, including caudal rami. Cephalothorax subcircular (1.94 mm long x 2.16 mm wide); comprising about 32% of total body length. Cephalic portion of dorsal cephalothoracic shield well developed, raised dorsally and with strongly defined and rigid posterior margin. Thoracic portion of dorsal cephalothoracic shield small, posterior margin not reaching as far as rear margins of lateral portions. Lunules present ventrally on frontal plates. Genital complex with paired, broad-based, sheath-like posterior expansions arisiring laterally and enclosing anterior part of abdomen from 3 sides: genital complex shorter than abdomen, measured along midline. Abdomen indistinctly 2-segmented (Fig. 16A, B); elongate, 1.68 times longer than wide and longer than genital complex; first segment expanded laterally: anal somite short, carrying paired caudal rami distally; anal slit terminal. Caudal rami with parallel sides, just longer than wide, measured at midpoints of margins. Each ramus armed with short hirsute seta at inner distal angle, slightly longer hirsute seta at outer distal angle, minute hirsute seta located just ventral to outer distal seta, and 3 long plumose setae on distal margin.

Antennule (Fig. 16C) 2-segmented; large proximal segment with 25 plumose setae arrayed along anteroventral surface and 2 setae located dorsally; short distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 16D) with proximal segment lacking posterior process; middle segment short, subrectangular, unarmed; terminal segment forming slender recurved claw armed with slender proximal and distal setae. Post-antennal process (Fig. 16D) small with short tine; ornamented with 2 bisensillate papillae on basal part and single bisensillate papilla on adjacent ventral cephalothoracic surface.

Mandible of typical stylet-like structure, with 12 marginal teeth. Maxillule (Fig. 16D) comprising anterior papilla bearing 3 unequal setae and posterior, tapering process with tiny area of thin integument. Maxilla 2-segmented, comprising elongate unarmed syncoxa and basis: basis bearing membranous but spiniform subapical flabellum on anterior margin, and terminating in 2 subequal claw-like elements (calamus and canna). Calamus longer than canna (Fig. 16E), ornamented with strips of serrated membrane arranged obliquely around surface near tip; canna ornamented with bilateral strips of serrated membrane. Maxilliped subchelate (Fig. 17A); robust proximal segment unarmed but with rounded swollen myxal margin; distal subchela with slender seta proximally, apical claw strongly curved, ornamented with surface striations.

Sternal furca (Fig. 16F) with short, more-or-less parallel tines, median space between tines square-sided.

First swimming leg pair joined by slender intercoxal sclerite; sympod with inner and outer plumose setae derived from basis, ornamented with patch of large surface denticles (Fig. 17B); endopod represented by unarmed process on posterior margin of basis. Exopod 2-segmented, directed laterally and forming main axis of leg; first segment robust, about 2.9 times longer than wide, armed with small outer (anterior) spine and ornamented with row of setules along posterior margin; second segment short, armed with 3 reduced plumose setae on posterior margin and 4 distal elements along oblique distal margin as follows: spine 1 (anterior-most) longest with marginal row of minute serrations; spines 2 and 3 progressively smaller, each with unilateral serrated membrane plus accessory process; seta 4 naked, longer than spine 3, shorter than segment.

Second leg (Fig. 17C) biramous, with flattened protopodal segments and both rami 3-segmented. Coxae of leg pair joined by intercoxal sclerite bearing marginal membrane posteriorly. Each coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segment 1 with inner plumose seta and large serrate outer spine aligned with longitudinal axis of ramus, bearing flap of membrane anteriorly, reflexed back over dorsal surface of segment; exopod segment 2 with outer spine directed distally plus inner plumose seta; segment 3 with 2 small outer spines, apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. Endopodal segments 1 and 2 armed with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; outer margins of all endopodal segments ornamented with fine setules.

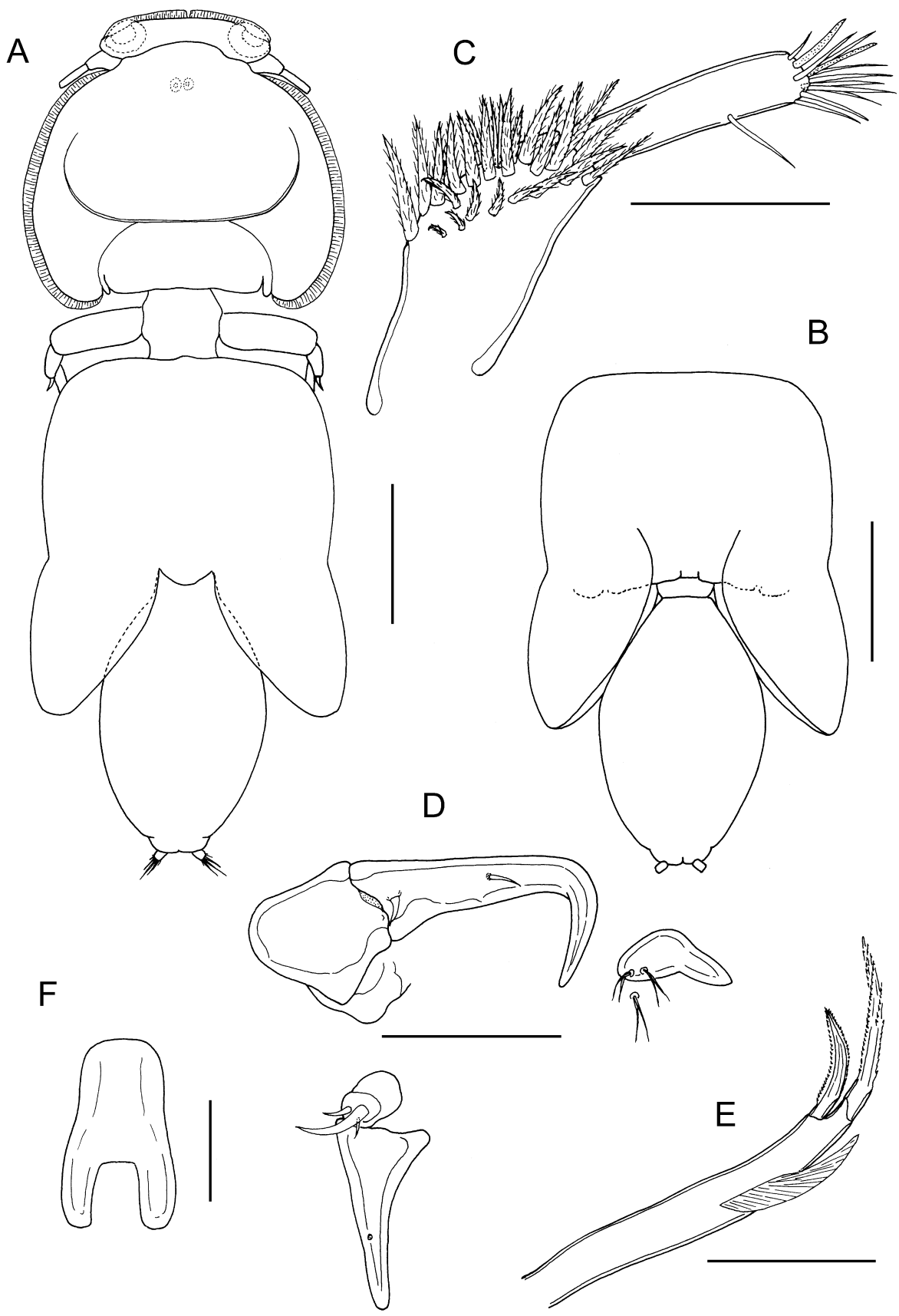

FIGURE 16. *Caligus alepicolus* **nom. nov.**, female. A, habitus, dorsal; B, genital complex and abdomen, ventral; C, antennule; D, antenna, post-antennal process and maxillule, drawn *in situ*; E, distal tip of maxilla; F, sternal furca. Scale bars: 1.0 mm on A, B, 100 µm on C–E, 50 µm on F.

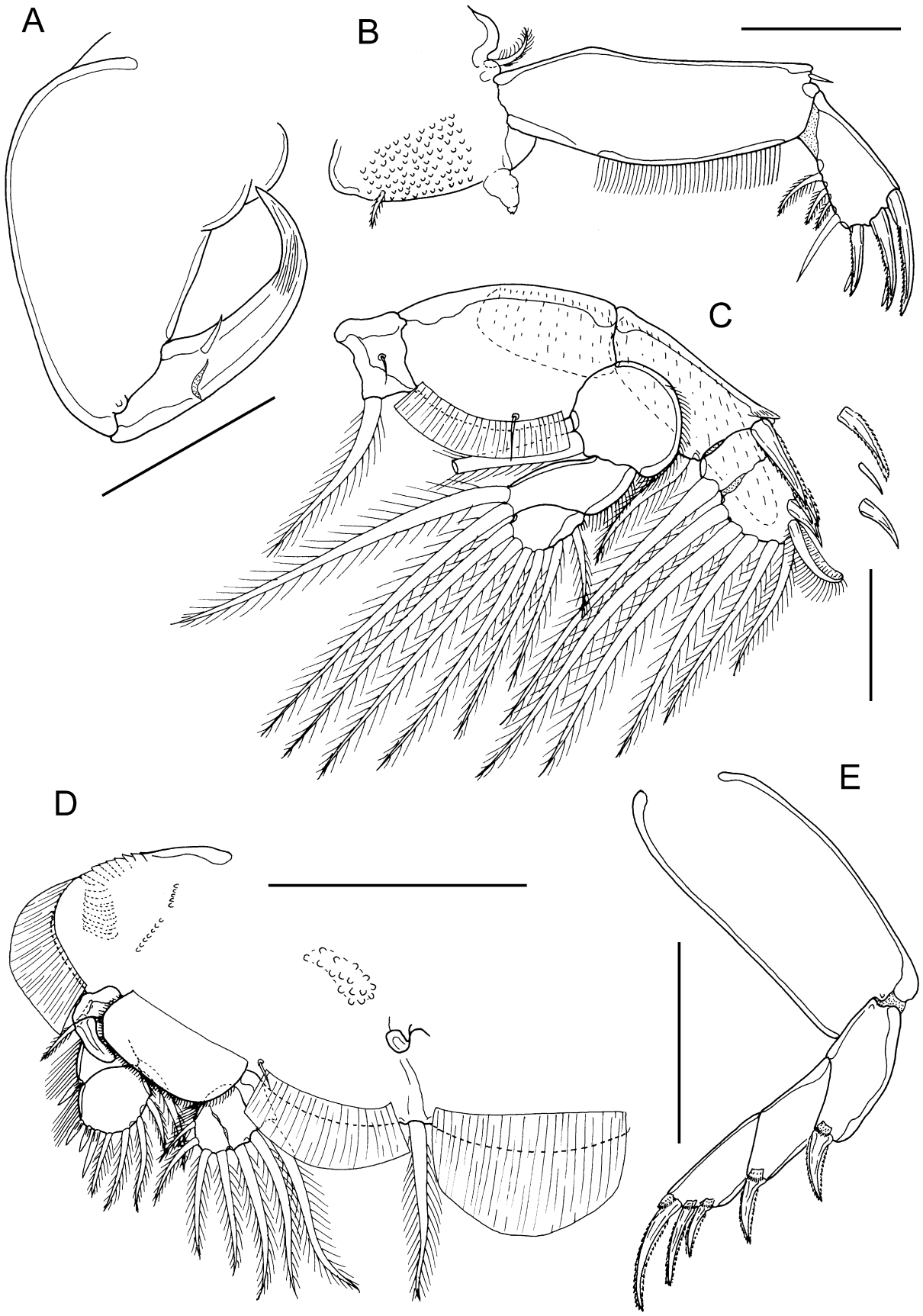

FIGURE 17. *Caligus alepicolus* **nom. nov.**, female. A, maxilliped; B, leg 1;, C, leg 2, with insets showing outer spine of exopodal segment 2, and proximal and distal outer spines on exopodal segment 3; D, leg 3; E, leg 4. Scale bars: 200 µm on A, D, E, 100 µm on B, C.

Third leg pair (Fig. 17D) forming flattened plate closing posterior section of cephalothoracic sucker. Protopodal part flattened joined by plate-like, intercoxal sclerite forming apron; ornamented with extensive flap of marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate, and outer plumose seta dorsal to base of exopod; sensillae located adjacent to origin of endopod; antero-lateral corner with corrugated surface, ventral surface with lateral line of denticles plus rosette-like array of denticles closer to mid-line and raised, bilobed rib-like process. Exopod 3-segmented; first segment armed with slightly curved outer claw directed over ventral surface of ramus, lacking inner seta; second segment with outer spine and inner seta; third segment with 3 spiniform elements on outer margin plus 4 plumose setae on inner margin; outer margins of segments 2 and 3 ornamented with rows of slender setules. Endopod 2-segmented; first segment expanded laterally to form flap-like velum closing off space between rami, free margin of velum ornamented with row of fine setules, armed with inner plumose seta; compound distal segment with 6 plumose setae increasing in length from outermost to innermost.

Fourth leg (Fig. 17E) 4-segmented, comprising slender protopodal segment and 3-segmented exopod: protopodal segment armed with plumose seta distally; exopodal segments armed with I, I, III spines, each spine bilaterally serrate and with well-developed pecten at base. Fifth legs not observed.

Remarks. Heegaard (1945) established *Caligodes alatus* Heegaard, 1945 on the basis of a single ovigerous female collected from "the mouth cavity of a *Cardus* sp. from Rambang, Java". The identity of the host is problematic since "*Cardus*" does not appear as a genus name in Eschmeyer's (1998) comprehensive *Catalog of Fishes*. The polychelid crustacean genus *Cardus* Galil, 2000 was established too recently (Galil, 2000) to be relevant. In his original account, Heegaard (1945) also described *Caligus bicycletus* Heegaard, 1945 as co-occurring on the same host fish ("*Cardus* sp."). Subsequent records of *C. bicycletus* have all been from *Alepes djebaba* (Forsskål, 1775) (as *Atule djedaba* and as *Selar kalla*) (see Pillai, 1985). It seems likely that the identity of "*Cardus*" as used by Heegaard (1945) is the carangid *Alepes djebaba*. This assumption gains some support from the second record of *C. alatus*, reported here, from the congeneric *Alepes apercna*.

The original description (Heegaard, 1945) was inadequate by modern standards, so Dojiri & Ho (2013) were unable to confirm the generic placement of this species in *Caligodes* in their major review. Examination of the second female of this taxon to be discovered allows the generic placement to be revisited. It does not belong in the ill-defined genus *Caligodes* because it does not share most of the features that serve to diagnose *Caligodes* according to Dojiri & Ho (2013), namely the long posterodorsal processes on the genital complex (derived from fifth legs), the enlarged spine 1 on the distal exopodal segment of leg 1, the slender exopodal spines of leg 2, and the segmentation and armature of leg 4. It does have a long abdomen, but this is found in species of several caligid genera. It also has broad-based posterior expansions at the posterolateral corners of the genital complex. Presumably Heegaard (1945) based his placement in *Caligodes* on the potential homology of these paired expansions with the long fifth legs of *C. laciniatus*. This homology cannot be confirmed, however, as setae representing the fifth legs were not observed in the Moreton Bay specimen. In the absence of any differentiating characters, Heegaard's species should be placed in *Caligus* Müller, 1785, but this creates a secondary homonym; as *Caligus alatus* already exists, established by Heegaard in 1943 for a parasite collected from the balistid *Canthidermis* Swainson, 1839 (probably *C. maculata* (Bloch, 1786)) in the West Indies. Although *Caligus alatus* Heegaard, 1943 is now recognized as a junior subjective synonym of *C. balistae* Steenstrup & Lütken, 1861 (Cressey, 1991), it remains unavailable. A replacement name is required and *Caligus alepicolus* **nom. nov.** is proposed here, in reference to the host genus, *Alepes* Swainson, 1839.

The affinities of *C. alepicolus* **nom. nov.** appear to lie with the *Caligus confusus* group of species discussed below. Members of this group are typically found on carangid hosts and share a suite of characters including the raised rib and rosette of large denticles on the apron of leg 3.

Caligus ariicolus Wilson, 1928

(Fig. 18)

Material examined. 6♀♀, 2♂♂, 5 immature specimens, from *Neoarius graeffei* (Kner & Steindachner, 1867) (TC17597) 26 June 2016, QM Reg. No. W53055; 2♂♂ (TC17624) 27 June 2016; 15♀♀, 4♂♂ from *N. graeffei* (TC17881) 4 July 2016, NHMUK Reg. Nos 2017.213–222. 11♀♀, 2♂♂ from *Netuma proxima* (Ogilby, 1898) (TC18830) 01 August 2017, NHMUK Reg. Nos 2017.223–232.

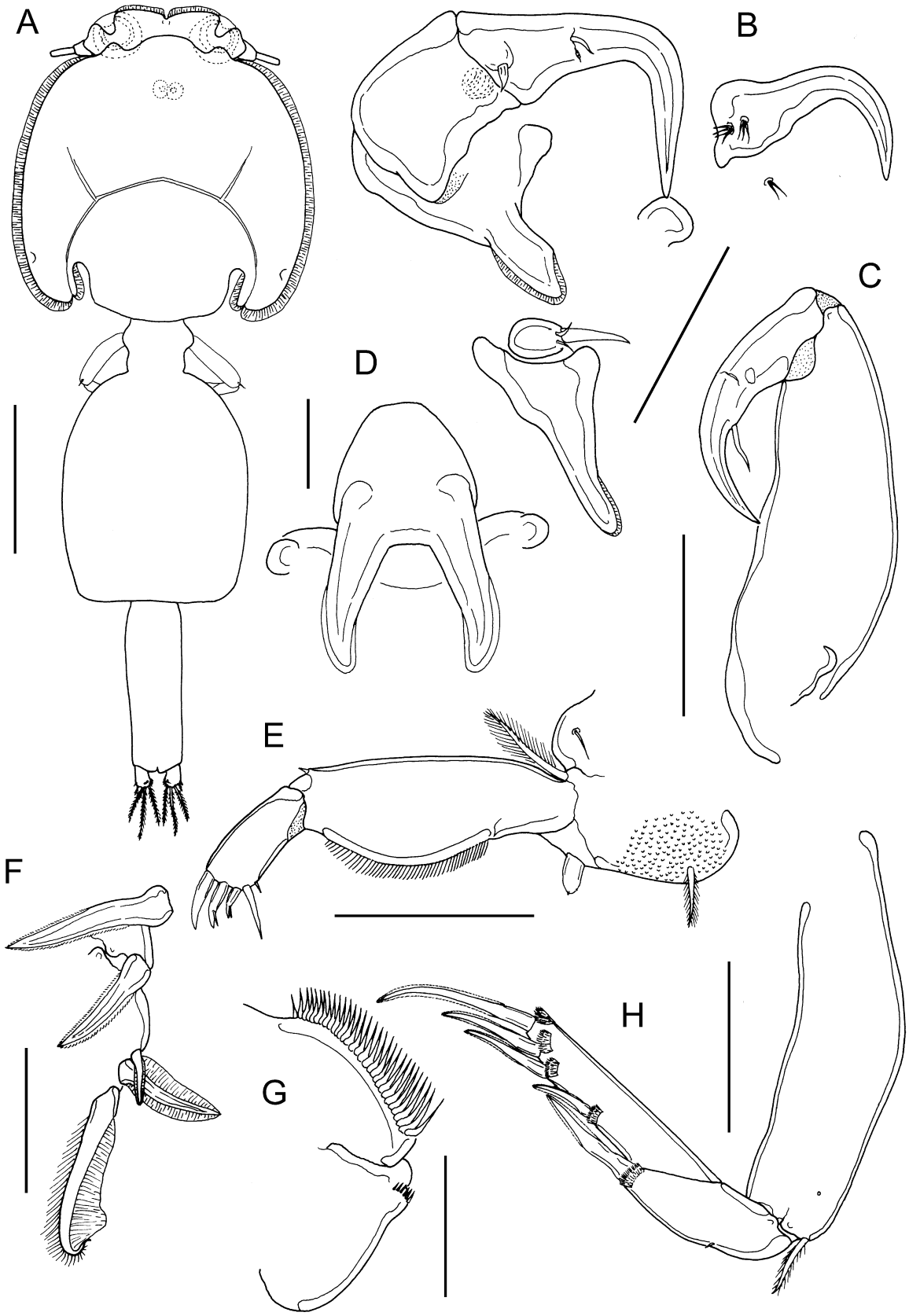

FIGURE 18. *Caligus ariicolus* Wilson, 1928, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, maxilliped; D, sternal furca, showing adjacent accessory processes; E, leg 1; F, outer margin spines on exopod of leg 2; G, ornamentation on lateral margin of endopodal segments 1 and 2 of leg 2; H, leg 4. Scale bars: 1.0 mm on A, 200 µm on B, C, E, H, 100 µm on D, 50 µm on F, G.

Site on host. Roof of mouth, oral cavity.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes. Frontal plates with large lunules. Genital complex with short neck section anteriorly, about 1.4 times longer than wide (Fig. 18A), with weakly convex lateral margins, without posterolateral lobes; abdomen about 2.9 times longer than wide, and about 70% as long as genital complex. Proximal segment of antenna with large posterior process provided with marginal flange (Fig. 18B). Post-antennal process strongly recurved, with multisensillate papillae. Maxillule with narrow flange distally on lateral margin of posterior process. Maxilliped with smooth myxal margin (Fig. 18C). Sternal furca with divergent, flanged tines (Fig. 18D), slightly incurved at tip; small rounded accessory processes present either side of furca. Distal exopodal segment of leg 1 (Fig. 18E) without plumose setae on posterior margin but retaining 1 minute, naked vestigial seta on posterior margin; distal spine 1 longest; spines 2 and 3 each with accessory process; seta 4 just longer than spine 1, shorter than segment. Leg 2 outer spines on first and second exopodal segments aligned obliquely across ramus (Fig. 18F); proximal outer spine on third segment short, distal spine with marginal membrane bilaterally; outer margin of endopodal segment 2 (Fig. 18G) ornamented with large, long-tailed denticles. Leg 3 with 3-segmented exopod; bearing weakly curved spine on first segment, outer spine and inner seta on second, 3 spines and 4 setae on third segment; endopod 2-segmented; first segment with well developed velum and inner seta; compound distal segment with 6 plumose setae. Leg 4 uniramous, 3-segmented (Fig. 18H); first and second exopodal segments with I and IV spines, respectively; outer spine on first exopodal segment blade-like, extending nearly to tip of lateral spine on second segment. Mean body length of female 2.41 mm, range 2.27 to 2.58 mm (based on 10 specimens): mean length of male 1.89 mm, range 1.69 to 2.08 mm (based on 4 specimens).

Remarks. This poorly known species was considered as a valid member of the *Caligus productus*-group by Boxshall & El-Rashidy (2009) even though the original description (Wilson, 1928) was inadequate by modern standards. The morphological description is supplemented here. The presence of a setal vestige on the posterior margin of the distal exopodal segment of leg 1 was overlooked by Wilson (1928) and, therefore, the key in Boxshall & El-Rashidy (2009) which uses this character, will need revision. Apart from the overall fit of the body tagmata proportions, the only distinctive character apparent in Wilson's description that can be used to positively identify this species is the unusual blade-like shape of the outer spine on the first exopodal segment of leg 4 (Fig. 17H). The tip of this spine reaches beyond two-thirds of the length the lateral spine on the second segment and is blade-like, as figured by Wlison (1928: Fig. 9).

This species was originally described from material of both sexes obtained from the floor of the mouth of a marine catfish, *Nemapteryx caelata* (Valenciennes, 1840) (as *Arius caelatus*) captured in the Menam Chao Phya at Paknam, Thailand (Wilson, 1928). It was subsequently listed as occuring on a second ariid host *Netuma thalassina* (Rüppell, 1837) (as *Arius thalassinus*) (Hirunraks *et al.*, 1977) in Thai waters. The discovery of this species in Moreton Bay represents a major extension of its known geographical range. The host in Australia, *Neoarius graeffei,* is a new host record.

Caligus asymmetricus Kabata, 1965

(Fig. 19)

Material examined. 3♀♀, 2♂♂ from *Euthynnus affinis* (Cantor, 1849) (TC18121), 21 November 2016, QM Reg. No. W53056; I ♀ from *Thunnus tonggol* (Bleeker, 1851) (TC17991), NHMUK Reg. No. 2017.233; I ♀ from *Auxis thazard* (Lacepède, 1800) (TC18122), 21 October 2016, NHMUK Reg. No 2017.234.

Site on host. Body surface.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; frontal plates with lunules. Genital complex about 1.2 times longer than wide, wider posteriorly, with rounded posterolateral corners (Fig. 19A); abdomen short, just wider than long; genital complex about 3.8 times longer than abdomen. Antenna with very small, narrow posterior process on proximal segment (Fig. 19B). Post-antennal process with small, acutely-pointed tine; associated papillae multi- or bisensillate. Maxilliped of female with slight expansion on myxal margin (Fig. 19C). Sternal furca (Fig. 19D) small, with slender, pointed tines (often asymmetrical). Distal exopodal segment of leg 1 with 3 short plumose setae on posterior margin; distal spine 1 simple, longer than spines 2 and 3, each armed with accessory process; seta 4 about as long as spine 1 and shorter

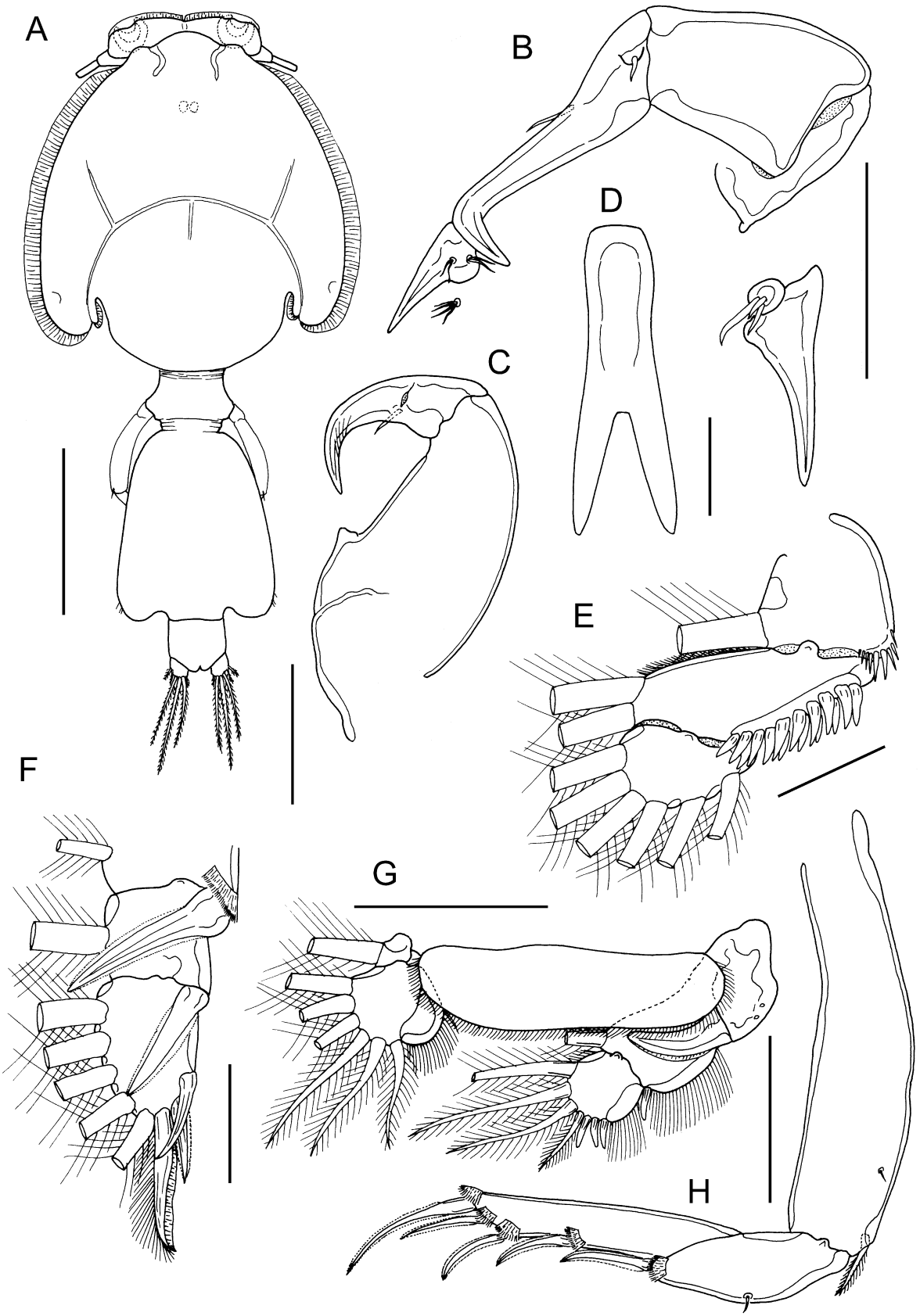

FIGURE 19. *Caligus asymmetricus* Kabata, 1965, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule, drawn *in situ*; C, maxilliped; D, sternal furca; E, endopod of leg 2, showing denticulate ornamentation on lateral margin of second segment; F, exopod of leg 2; G, rami of leg 3, drawn *in situ*; H, leg 4. Scale bars: 1.0 mm on A, 200 µm on B, C, G, H, 100 µm on E, F, 50 µm on D.

than segment. Leg 2 with double row of about 7 or 8 strong denticles along outer margin of endopodal segment 2 (Fig. 19E); outer spines on exopodal segments 1 and 2 lying obliquely across axis of ramus (Fig. 19F); proximal outer spine on segment 3 long and slender, longer than distal outer spine. Leg 3 with 3-segmented exopod (Fig. 19G); first exopodal segment bearing curved outer spine, lacking inner seta; second segment with outer spine and inner seta; third segment with 3 small spines, plus 4 plumose setae: endopod 2-segmented, first segment forming long velum, and armed with inner seta; compound distal segment with slightly swollen lateral margin, armed with 6 plumose setae. Leg 4 uniramous, 3-segmented; first and second exopodal segments with I and IV spines, respectively (Fig. 19H). Mean body length of female 3.78 mm, range 3.58 to 3.97 mm (based on 3 specimens): male lengths 3.73 and 3.81 mm.

Remarks. *Caligus asymmetricus* was originally described as a new species by Pillai (1963) but the name he proposed, *Caligus thynni*, was preoccupied by *Caligus thynni* Dana, 1852.

The replacement name, *C. asymmetricus*, is attributed to Kabata (1965b) and refers to the often asymmetrical form of the sternal furca. Kabata's (1965b) brief account was based on a single female from *Euthynnus alletteratus* caught off Queensland and Pillai's (1963) description was based on a single female from *E. affinis* taken off Trivandrum in the south of India. Lewis (1967) subsequently provided full descriptions of both sexes based on material collected off Hawaii on *E. affinis* (as *E. yaito*). Cressey & Cressey (1980) and Cressey *et al.* (1983) recorded *C. asymmetricus* on ten different scombrid host species across the Indo-West Pacific, including *E. affinis*, *Sarda australis* (MacLeay, 1881), *Scomberomorus commerson* (Lacepède, 1800) and *Auxis* sp. all from New South Wales, and *Cybiosarda elegans* (Whitley, 1935) from western Australia. The single female reported here from *Thunnus tonggol* caught in Moreton Bay constitutes a new host record.

There is a group of 12 species that share the possession of a 3-segmented leg 4 armed with four spines on the compound distal exopodal segment, in combination with the presence of the three plumose setae on the posterior margin of the distal exopodal segment of leg 1, and the possession of an ornamentation of large denticles along the outer margin of the second endopodal segment of leg 2. This group, referred to here as the *C. bonito*-group, comprises *C. asperimanus* Pearse, 1951, *C. asymmetricus*, *C. biseriodentatus*, *C. bonito*, *C. cossacki* Bassett-Smith, 1898, *C. grandiabdominalis* Yamaguti, 1954, *C. hoplognathi* Yamaguti & Yamasu, 1959, *C. malabaricus*, *C. mutabilis* Wilson, 1905, *C. omissus* Cressey & Cressey, 1980, *C. phipsoni* Bassett-Smith, 1898, and *C. triabdominalis*. Several other members of this group, i.e. *C. biseriodentatus*, *C. bonito*, *C. mutabilis*, and *C. omissus* primarily use scombrids as hosts, but the small size and slender pointed tines of the sternal furca of *C. asymmetricus*, in addition to the proportional lengths of the genital complex and abdomen, serve to distinguish this species from these others.

Caligus biseriodentatus Shen, 1957

(Fig. 20)

Syns: *Caligus obovatus* Heegaard, 1962
Caligus proboscidatus Heegaard, 1962

Material examined. 1♂, 2 chalimus from *Scomberomorus queenslandicus* Munro, 1943, (TC17388), 21 January 2016, NHMUK Reg. No. 2017.236; 2♀♀ from *Auxis thazard* (Lacepède, 1800) (TC 18122), 21 October 2016, 1♀ QM Reg. No. W53057; 1♀ NHMUK Reg. No. 2017.235.

Site on host. Body surface.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; frontal plates with lunules. Genital complex 1.14 times longer than wide (measured along dorsal midline) with small posterolateral lobes; abdomen elongate, about 3.2 times longer than maximum width; just shorter than genital complex (Fig. 20A). Antenna with small, blunt posterior process. Post-antennal process with slender, weakly-curved tine; associated papillae each bisensillate. Posterior process of maxillule slender. Maxilla with smooth distal margin on brachium. Maxilliped of female with slight expansion on myxal margin. Sternal furca with broad, truncate, slightly diverging tines, with lateral flanges (Fig. 20B). Leg 1 with ornamentation of large spinules on sympod; distal exopodal segment (Fig. 20C) with 3 short plumose setae on posterior margin, basal setules on margin of plumose setae nearest apex unusually stout; distal spine 1 simple, longer than spine 2, spine 2 longer than spine 3, each armed with accessory process and serrated membrane; seta 4 about twice as long as spine 1 and just

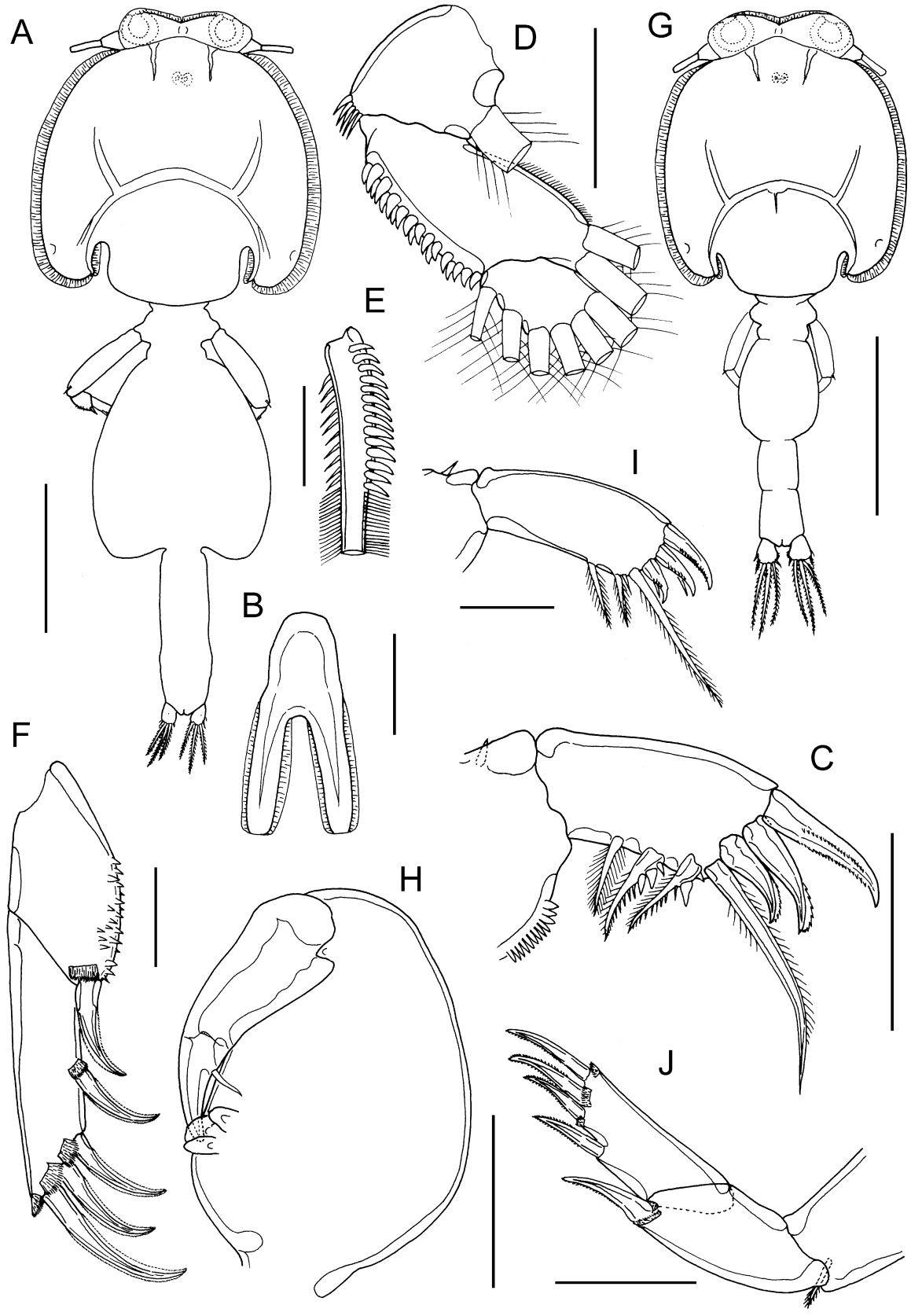

FIGURE 20. *Caligus biseriodentatus* Shen, 1957, female. A, habitus, dorsal; B, sternal furca; C, distal exopodal segment of leg 1; D, endopod of leg 2; E, modified plumose seta from third segment of exopod of leg 2; F, exopod of leg 4. Male, G, habitus, dorsal; H, maxilliped; I, distal exopodal segment of leg 1; J, exopod of leg 4. Scale bars: 1.0 mm on A, G, 200 µm on H, 100 µm on C, D, J, 50 µm on B, E, F, I.

longer than segment. Leg 2 with strong denticles along outer margins of endopodal segments 1 and 2 (Fig. 20D); plumose setae on distal segments of both rami modified, with enlarged spinules basally (Fig. 20E); outer spines on exopodal segments 1 and 2 lying obliquely across axis of ramus. Leg 3 with 3-segmented exopod; first exopodal segment bearing slightly curved outer spine, lacking inner seta; second segment with outer spine and inner seta; third segment with 3 naked spines, plus 4 plumose setae. Leg 4 uniramous, 3-segmented; first and second exopodal segments with I and IV spines, respectively (Fig. 20F); apical spine on distal margin distinctly longer than adjacent middle spine; first exopodal segment ornamented with conspicuous denticles along outer margin. Body lengths of adult females 4.58 and 5.04 mm.

Male (Fig. 20G) with cephalothorax just longer than wide. Genital complex slender with weakly convex margins, about 1.26 times longer than wide. Abdomen 2-segmented; first and second somites subequal; abdomen about 2.6 times longer than wide, and about as long as genital complex. Fifth legs located ventrolaterally near lateral margin at about two thirds length of genital complex. Post-antennal process very large and more strongly recurved than in female; associated papillae multisensillate. Maxilliped (Fig. 20H) with conspicuous trifid process on myxal margin opposing tip of subchela. Sternal furca with strongly divergent tapering tines. Distal exopodal segment of leg 1 with 2 small plumose setae on posterior margin plus very small distal seta (Fig. 20I). Leg 2 with setae on distal segments of both rami plumose (not modified as in female). Leg 4 with smooth unornamented outer margin on first exopodal segment; 3 distal margin spines on second exopodal segment similar in length (Fig. 20J). Body length of male 3.03 mm.

Remarks. *Caligus biseriodentatus* was first described from immature specimens of both sexes obtained from *Scomberomorus commerson* (as *Cybium commersoni*) in Chinese waters (Shen, 1957). It is a member of the *C. bonito*-group of species characterized by the shared possession of a 3-segmented leg 4 armed with four spines on the compound second exopodal segment, in combination with the presence of the three plumose setae on the posterior margin of the distal exopodal segment of leg 1, and the possession of an ornamentation of large denticles along the outer margin of the second endopodal segment of leg 2. Within this group, *C. biseriodentatus* can be readily distinguished by the small size of the three plumose setae on the posterior margin of the distal exopodal segment of leg 1: in the female these setae are only about as long as spine 2 and have modified ornamentation (Fig. 20E). The male maxilliped of *C. biseriodentatus* has a conspicuous trifid myxal process.

In their large survey of parasitic copepods of scombrid fishes, Cressey & Cressey (1980) redescribed *C. biseriodentatus* and reported it from four species of *Scomberomorus* Lacepède, 1800 as well as from *Auxis thazard*. Subsequently Cressey *et al.* (1983) added another three species of *Scomberomorus* to the list of known hosts. However, they considered that *Scomberomorus* species served as hosts only for immature stages. The life cycle of *C. biseriodentatus* is unusual: Cressey & Cressey (1980) noted that adults appear to be found on a different host from the immature stages and they recognized the species originally described as *C. auxisi* by Pillai (1963) as the adult of *C. biseriodentatus*. The only host known to harbour an adult was *Auxis thazard* but Cressey & Cressey (1980) speculated that the adult may prefer a non-scombrid host. The discovery here of two more adult females on *A. thazard* from Moreton Bay indicates that this scombrid may well be the preferred host of the adult.

This species is widely distributed from the Malagasy Republic, Zanzibar and Somalia in the western Indian Ocean, via the Arabian Sea, India and Sri Lanka, across to the Philippines, Thailand and China in the western Pacific, and as far south as Papua New Guinea and Australia (Cressey & Cressey, 1980). It was first reported from Australian waters (Queensland) by Heegaard (1962), as *C. obovatus* and *C. proboscidatus*, both from *Scomberomorus queenslandicus* and *S. commerson*. Subsequent records include material from *S. queenslandicus* caught off West Australia (Cressey & Cressey, 1980). This is the first report of *C. biseriodentatus* from Moreton Bay.

Caligus bonito **Wilson, 1905**
(Figs. 21, 22)

Syn: *Caligus kuroshio* Shiino, 1959

Material examined. 20♀, 9♂♂ from *Euthynnus affinis* (Cantor, 1849) (TC18121), 21 November 2016; 10♀♀, 4♂♂ QM Reg. No. W53058; 10♀♀, 5♂♂ NHMUK Reg. Nos 2017.237–246.

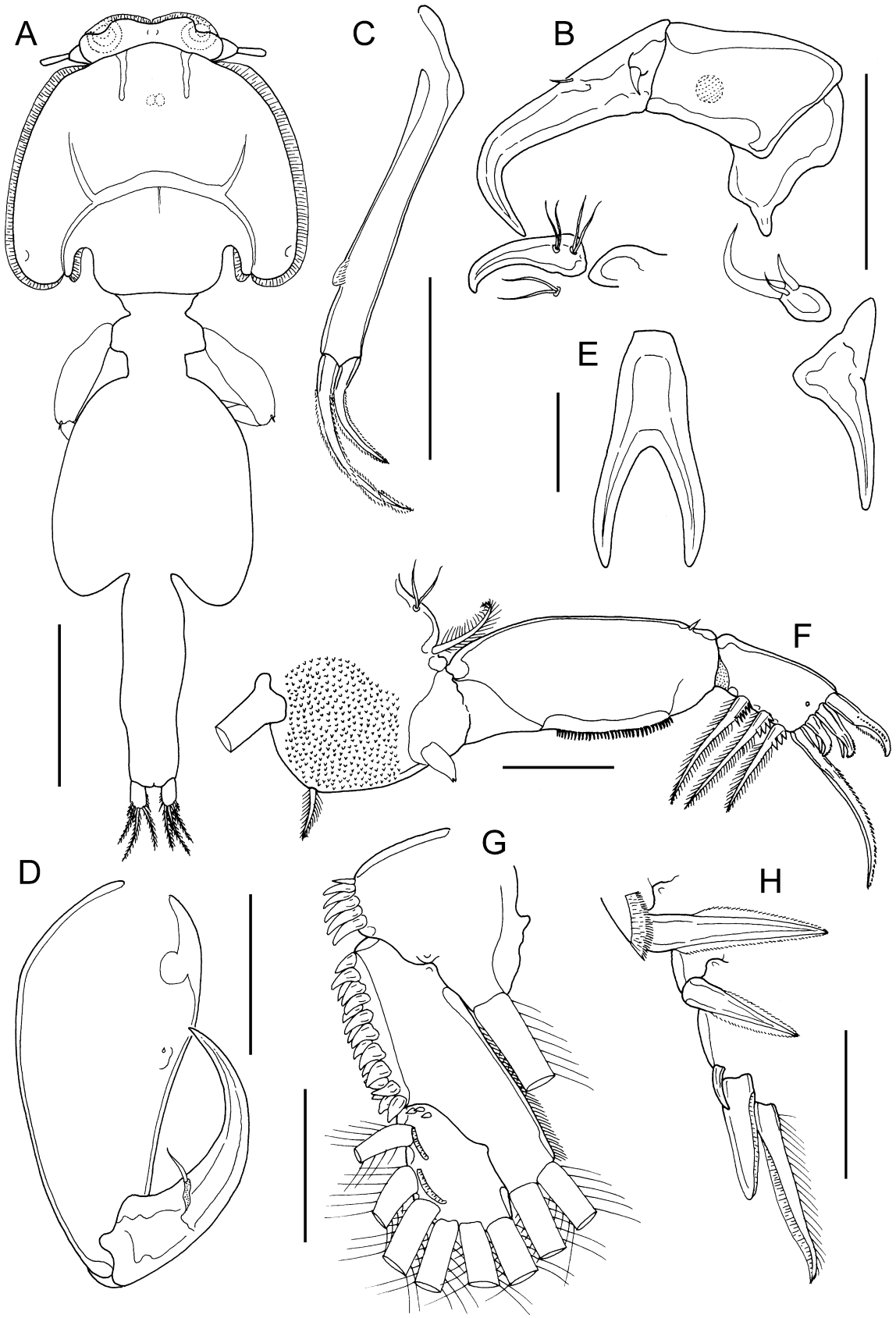

FIGURE 21. *Caligus bonito* Wilson, 1905, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, brachium of maxilla; D, maxilliped; E, sternal furca; F, leg 1; G, endopod of leg 2, showing denticulate ornamentation on lateral margin of first and second segments; H, outer spines on exopod of leg 2. Scale bars: 1.0 mm on A, 200 µm on B–D, 100 µm on E–H.

Site on host. Gill cavity.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; frontal plates with lunules. Genital complex 1.04 times longer than wide (measured along dorsal midline) with small posterolateral lobes (Fig. 21A); abdomen elongate, about 3.8 times longer than wide and longer than genital complex. Antenna with small, blunt posterior process (Fig. 21B). Post-antennal process with weakly-curved tine; associated papillae each bisensillate. Posterior process of maxillule slender (Fig. 21B). Maxilla with smooth distal margin on brachium (Fig. 21C). Maxilliped of female with slight expansion on myxal margin (Fig. 21D). Sternal furca with slender, diverging tines without lateral flanges (Fig. 21E). Distal exopodal segment of leg 1 (Fig. 21F) with 3 plumose setae on posterior margin, basal setules on margin of plumose setae nearest apex unusually stout; distal spine 1 simple, longer than spines 2 and 3, each armed with accessory process; seta 4 about twice as long as spines and about as long as segment, ornamented with setule row on one side and marginal membrane on other. Leg 2 with strong denticles along outer margins of endopodal segments 1 and 2 (Fig. 21G); endopodal segment 3 ornamented with 2 shallow membranous ridges on ventral surface; outer spines on exopodal segments 1 and 2 lying obliquely across axis of ramus (Fig. 21H); proximal outer spine on segment 3 tiny, much shorter than distal spine. Leg 3 with 3-segmented exopod; first exopodal segment (Fig. 22A) bearing small slightly curved outer spine, lacking inner seta; second segment with outer spine and inner seta; third segment with 3 naked spines, plus 4 plumose setae; distal endopodal segment with swollen lateral margin. Leg 4 uniramous, 3-segmented (Fig. 22B); first and second exopodal segments with I and IV spines, respectively. Mean body length of female 4.80 mm, range 4.46 to 5.31 mm (based on 10 specimens).

Male (Fig. 22C) with cephalothorax as in female. Genital complex slender with linear margins, about 1.7 times longer than wide. Abdomen 2-segmented; first segment just shorter than second; including caudal rami, about 3.4 times longer than wide and longer than genital complex. Fifth legs located ventrally near posterior corners of genital complex, not visible in dorsal view. Post-antennal process (Fig. 22D) more strongly recurved than in female; associated papillae bisensillate. Maxilliped (Fig. 22E) with 3 small processes along myxal margin, middle process largest with bifid apex. Mean body length of male 4.91 mm, range 4.31 to 5.27 mm (based on 5 specimens).

Remarks. The distinctive features of *C. bonito*, within the *C. bonito*-group, are its long genital complex and long abdomen combined with the presence of stout denticles along the outer margins of endopodal segments 1 and 2 of leg 2, plus the unusually stout basal setules on the margin nearest the limb apex of the 3 plumose setae on the posterior margin of the distal exopodal segment of leg 1. Interestingly, Ho & Lin (2004) noted the existence of two forms of *C. bonito* in Taiwanese waters. Lin & Ho (2001) initially reported *C. bonito* from *Katsuwonus pelamis* (Linnaeus, 1758) and *Euthynnus affinis*, and their redescription of the female showed an abdomen about 3.7 times longer than wide and shorter than the cephalothorax, a sternal furca with tapering, slightly curved tines that lacked marginal flanges, bisensillate papillae on the post-antennal process, and seta 4 on the distal exopodal segment of leg 1 is much longer than the segment. In their subsequent study of *C. bonito* from *Sarda orientalis* (Temminck & Schlegel, 1844) Ho & Lin (2004) illustrated another form characterized by an abdomen that is about 4.0 times longer than wide and markedly longer than the cephalothorax, a sternal furca with divergent linear tines that have marginal flanges, multi-sensillate papillae on the post-antennal process, and seta 4 on the distal exopodal segment of leg 1 is only just longer than the segment. There are other minor differences, for example, the posterior process on the female antenna is much larger in the latter form (from *S. orientalis*).

The Moreton Bay material can be attributed to typical *C. bonito* as described by Wilson (1905), Kabata (1979) and Pillai (1985), all of which show females with the abdomen shorter than the cephalothorax. The detail provided by Pillai (1985) confirms the presence of other relevant character states, such as the tapering tines without marginal flanges on the sternal furca, the bisensillate papillae on the post-antennal process, and a seta 4 on the distal exopodal segment of leg 1 that is much longer than the segment. The Moreton Bay sample shares these character states with the material described by Lin & Ho (2001). The status of the second, atypical, form (from *S. orientalis*) described by Ho & Lin (2004) needs to be re-assessed as it may represent a distinct species.

Although it has been reported from at least 24 different hosts (Ho & Lin, 2004), *C. bonito* is typically a parasite of scombrids of the tribes Sardini and Thunnini (Cressey & Cressey, 1980) and of dolphinfish (Coryphaenidae) (Burnett-Herkes, 1974; Carbonell *et al.*, 1999; Hutson *et al.*, 2011), and it has a broad distribution in low to middle latitudes in all oceans (Cressey *et al.*, 1983: Fig. 10). *Caligus bonito* has previously been reported from Queensland on *Euthynnus alletteratus* (Rafinesque, 1810) as *C. kuroshio* (Kabata, 1965b), from New South Wales on *Sarda*

australis (Cressey & Cressey, 1980) and from southeastern Australia on *Arripis truttacea* (Cuvier, 1829), *A. trutta* (Forster, 1801) and *Coryphaena hippurus* Linnaeus, 1758 (Catalano & Hutson, 2010; Hutson *et al.*, 2011). The material collected in Moreton Bay was found on *Euthynnus affinis*, a previously known host of *C. bonito* (Cressey & Cressey, 1980).

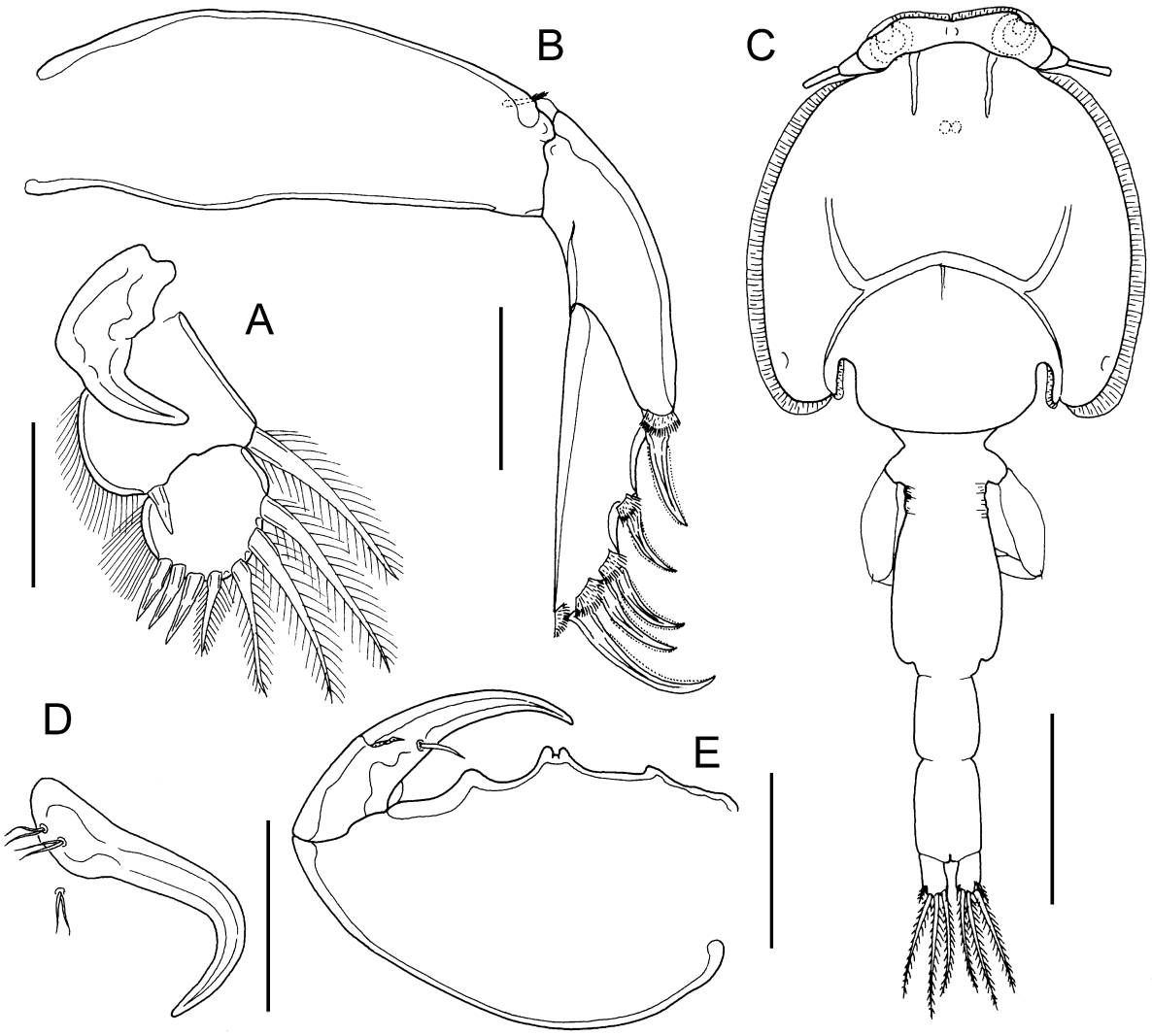

FIGURE 22. *Caligus bonito* Wilson, 1905, female. A, exopod of leg 3; B, leg 4. Male, C, habitus, dorsal; D, post-antennal process; E, maxilliped. Scale bars: 100 µm on A, 200 µm on B, 1.0 mm on C, 250 µm on D–E.

Caligus brevicaudus Pillai, 1963
(Fig. 23)

Material examined. 2♀♀, 1♂ from *Caranx ignobilis* (Forsskål, 1775) (TC17579) 25 June 2016; 1♀, 1♂ QM Reg. No. W53059; 1♀ NHMUK Reg. No. 2017.248.

Site on host. gill arches.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones; frontal plates with lunules (Fig. 23A); thoracic zone small, posterior margin about level with posterior margins of lateral zones. Genital complex about 1.1 to 1.2 times longer than wide; abdomen small, 1-segmented, wider than long; genital complex about 4.3 times longer than abdomen (including caudal rami). Antenna with well developed posterior process on proximal segment. Post-antennal process bifid (Fig. 23B), tine without marginal flange; associated papillae bisensillate, unisensillate papilla on adjacent cephalothoracic surface.

Posterior process of maxillule bifid (Fig. 23C); smaller outer tine arising near base of main (inner) tine. Maxilliped of female with bilobed swelling on surface and fold in myxal area; claw strongly recurved with striations along concave margin (Fig. 23D). Sternal furca with blunt tines bearing conspicuous flanges (Fig. 23E). Distal exopodal segment of leg 1 with 3 short plumose setae on posterior margin (Fig. 21F); distal spine 1 longer than other spines; spines 2 and 3 each with accessory process; seta 4 longer than spines 2 and 3, shorter than segment. Leg 2 with marginal setules on endopodal segments 2 and 3; outer spines on exopodal segments 1 and 2 aligned close to longitudinal axis of ramus. First exopodal segment of leg 3 with large recurved outer spine but lacking inner seta (Fig. 23G); apron with raised bifid rib-like process plus circular array of large denticles on ventral surface and corrugated adhesion pad on outer margin and adjacent dorsal surface. Leg 4 uniramous, 4-segmented; exopodal segments armed with I; I; III spines. Leg 5 comprising exopodal papilla bearing 2 setae, located adjacent to protopodal papilla bearing single seta (Fig. 23H). Body lengths of females 1.93 mm and 2.19 mm; length of male 1.66 mm.

Remarks. This is a distinctive but uncommon member of the *Caligus confusus*-group. It was originally described by Pillai (1963), based on material of both sexes collected from an unspecified species of *Caranx* Lacepède, 1801 caught off Trivandrum (India). However, there have been no new records since the original description although it was widely cited, e.g. in reviews by Pillai (1967b, 1968) and in his monograph (1985). It is also interesting to note that this species has not been recorded from Taiwan, despite intensive study of Taiwanese waters by Ho & Lin (see Ho & Lin, 2004, 2007; Lin & Ho, 2007).

In Moreton Bay *C. brevicaudus* was found only on *Caranx ignobilis*, where it attached to the gill arches, the same microhabitat as *C. confusus*. At 1.93 to 2.19 mm the females found in Australian waters were only half the length of the Indian specimens, reported as 4.3 mm by Pillai (1963). Despite this marked size difference, no morphological differences were apparent.

Caligus chiastos Lin & Ho, 2003
(Fig. 24)

Syn: *Caligus* sp. 1. Roubal, Armitage & Rohde, 1983

Material examined. 1♀ from *Lutjanus fulviflamma* (Forsskål, 1775) (TC17525) 23 June 2016, QM Reg. No. W53060; 1♀ from *Sillago ciliata* Cuvier, 1829 (TC17557-8) 24 June 2016, NHMUK Reg. No. 2017.251; 1♀ from *Abudefduf bengalensis* (Bloch, 1787) (TC17806) 2 July 2016, NHMUK Reg. No. 2017.248; 1♀ from *Acanthopagrus australis* (TC17816) 3 July 2016, QM Reg. No. W53061; 2♀♀ from *Lagocephalus lunaris* (Bloch & Schneider, 1801) (TC17899) 5 July 2016, NHMUK Reg. Nos 2017.252–253; 2♀♀ from *Aetobatus ocellatus* (Kuhl, 1823) (TC17933) 5 July 2016, NHMUK Reg. Nos 2017.249–250.

Site on host. Body surface.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; frontal plates with lunules. Genital complex just slightly wider than long (Fig. 24A); abdomen 1-segmented, 1.85 times longer than wide; genital complex about 1.4 times longer than abdomen. Antenna with small, pointed posterior process on proximal segment (Fig. 24B). Post-antennal process with weakly curved tine; associated papillae bisensillate with unusually long sensillae (Fig. 24B). Maxilliped of female with smooth myxal margin. Sternal furca with long, slender, slightly incurved tines (Fig. 24C). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spine 1 simple, about same length as spines 2 and 3 (Fig. 24D), each armed with accessory process; seta 4 about twice as long as spines and markedly longer than segment. Leg 2 with fine setules along margins of endopodal segments 1, 2 and 3; outer spines on exopodal segments 1 and 2 lying obliquely across axis of ramus; proximal outer spine on exopodal segment 3 curved and well developed, lying across blunt distal spine (Fig. 24E). Leg 3 with 3-segmented exopod; first exopodal segment bearing small straight outer spine but no inner seta; second segment with outer spine and inner plumose seta; third segment with 3 subequal outer spines, plus 4 plumose setae; endopod 2-segmented; first segment forming velum, and armed with inner seta; distal endopodal segment with swollen lateral margin and bearing 6 plumose setae. Leg 4 uniramous (Fig. 24F), 3-segmented; first and second exopodal segments with I and IV spines, respectively; each spine with pecten on surface of segment adjacent to base. Mean body length of female 3.34 mm, range 3.15 to 3.85 mm (based on 8 specimens).

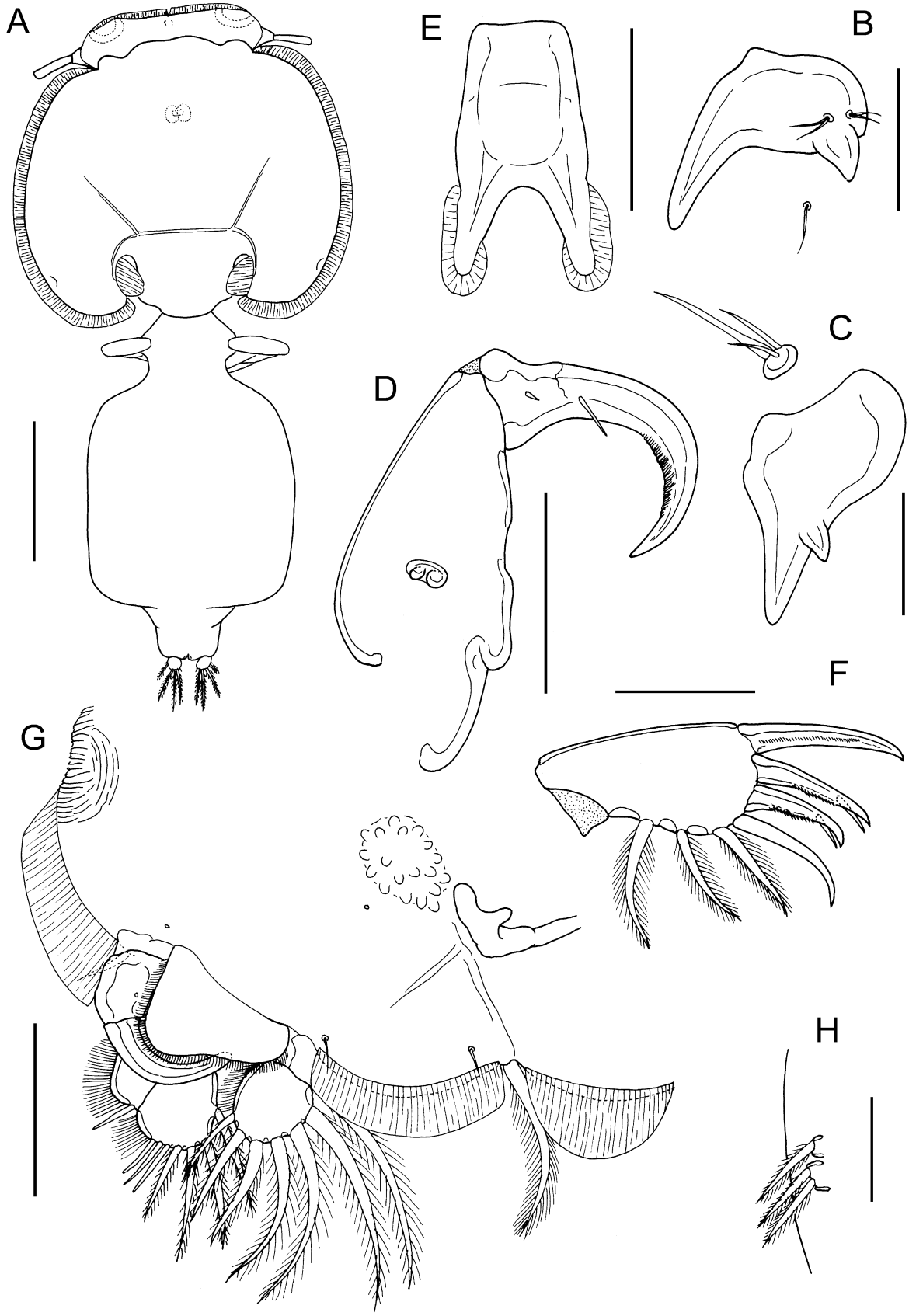

FIGURE 23. *Caligus brevicaudus* Pillai, 1963, female. A, habitus, dorsal; B, bifid post-antennal process; C, bifid maxillule; D, maxilliped; E, sternal furca; F, distal exopodal segment of leg 1; G, leg 3; H, leg 5. Scale bars: 1.0 mm on A, 200 µm on B, C, G, H, 100 µm on E, F, 50 µm on D.

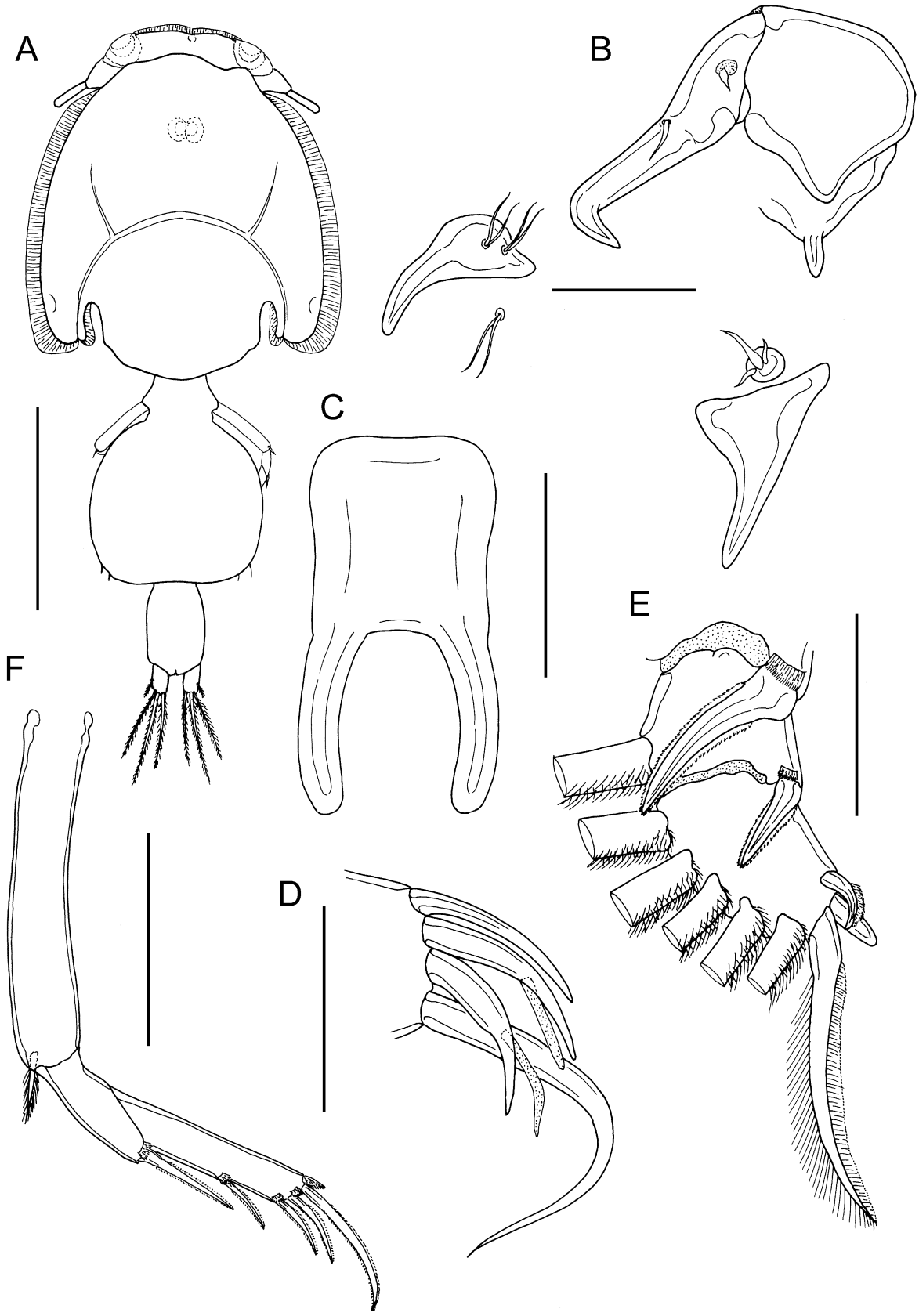

FIGURE 24. *Caligus chiastos* Lin & Ho, 2003, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, sternal furca; D, distal margin of exopod of leg 1; E, exopod of leg 2, showing well developed, curved proximal outer spine of third exopodal segment; F, leg 4. Scale bars: 1.0 mm on A, 200 μm on F, 100 μm on C, E, 50 μm on B, D.

Remarks. One of the most characteristic features of *C. chiastos* is the form of the outer margin spines on the third exopodal segment of leg 2. Unusually, the proximal spine on this segment is curved and slightly longer than the straight distal spine (Fig. 24E). The significance of this feature in distinguishing *C. chiastos* from the closely related *C. acanthopagri* Lin, Ho & Chen, 1994 was emphasized by Ho & Lin (2004).

Caligus chrysophrysi is very similar to *C. chiastos*. Indeed, the differences in body proportions are trivial. When *C. chiastos* was established, Lin & Ho (2003) presented detailed comparisons with *C. acanthopagri* Lin, Ho & Chen, 1994 but did not compare their material with *C. chrysophrysi*. Pillai (1985) only had a single female and presented an incomplete description of *C. chrysophrysi*, but it agrees with that of *C. chiastos* in every important respect, including the form of the proximal outer spine on the distal exopodal segment of leg 2, which is as long as the distal spine and curves across its surface, as highlighted by Lin & Ho (2003). It is possible that *C. chiastos* is a junior synonym of *C. chrysophrysi*, but the species are maintained as separate here on the basis of female body size: the females of *C. chiastos* range from 3.15 to 3.85 mm whereas female *C. chrysophrysi* is only 2.1 mm in length according to Pillai (1985). In addition, the lateral spine on the compound distal exopodal segment of leg 4 reaches well beyond the base of the outermost distal spine in *C. chiastos* (Fig. 24F) but barely reaches this spine in *C. chrysophrysi*.

Caligus chiastos is a pest of both farmed and cultured marine teleost fishes (Hayward *et al.* 2008; Venmathi Maran *et al.*, 2009). It was described by Lin & Ho (2003) to accommodate specimens of both sexes collected from the haemulid, *Plectorhinchus cinctus* (Temminck and Schlegel, 1843) in Taiwanese waters. Lin & Ho (2003) also noted that the female caligid reported as *Caligus* sp. 1 by Roubal *et al.* (1983) could also be attributed to this species. Roubal *et al.*'s (1983) material was collected from the sparid *Pagrus auratus* (as *Chrysophrys auratus*) caught off Coff's Harbour (NSW) in Australian waters. Ho & Lin (2004) listed three additional hosts, *Caranx sexfasciatus* Quoy & Gaimard, 1825 (Carangidae), *Otolithes ruber* (Bloch & Schneider, 1801) (Sciaenidae) and *Pelates quadrilineatus* (Bloch, 1790) (Terapontidae) from Taiwan, and it has since been reported from cultured *Lutjanus johnii* (Bloch, 1792) (Lutjanidae) in Malaysia (Venmathi Maran *et al.*, 2009). This species is a known pest of farmed fish in Australian waters, including *Argyrosomus japonicus* (Temminck & Schlegel, 1843) (Sciaenidae), *Seriola lalandi* (Carangidae), and *Thunnus maccoyii* (Scombridae) (Hayward *et al.* 2007, 2008). In addition, early records of *C. elongatus* and *C. rapax* from Australian waters (e.g. Heegaard, 1962; Munday *et al.*, 2003; Nowak, 2004) can also, in all probability, be considered as belonging to *C. chiastos* (Hayward *et al.* 2008). In Moreton Bay *C. chiastos* was found on *Abudefduf bengalensis* (Pomacentridae), *Acanthopagrus australis*, *Lutjanus fulviflamma*, *Lagocephalus lunaris* (Tetraodontidae), *Sillago ciliata* (Sillaginidae) and *Aetobatus ocellatus* (Myliobatidae). Having been reported from at least eleven families of actinopterygian fishes, and now from an elasmobranch, it appears that *C. chiastos* exhibits relatively low host specificity.

Caligus confusus Pillai, 1961

(Fig. 25)

Material examined. 2♀♀ from *Caranx ignobilis* (Forsskål, 1775) (TC17542) 24 June 2016, QM Reg. No. W53062; 1♀ from (TC17561) 24 June 2016, 2♀♀ from (TC17579) 25 June 2016, 1♀ from (TC17702) 28 June 2016: 3♀♀ NHMUK Reg. Nos 2017.254–256. 2♀♀ from *Caranx sexfasciatus* Quoy & Gaimard, 1825 (TC17655) 28 June 2016, 23♀♀, 9♂♂ (TC17668) 28 June 2016; 10♀♀, 5♂♂, QM Reg. No. W53063; 4♀♀, 1♂ (TC17690) 28 June 2016, 15♀, 4♂♂, NHMUK Reg. Nos 2017.257–266.

Site on host. Gill arches.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones; frontal plates with lunules; thoracic zone very small, extending posteriorly about level with posterior ends of lateral zones (Fig. 25A). Genital complex about 1.5 to 1.6 times longer than wide; abdomen small, 1-segmented, just longer than wide; genital complex about 5 times longer than abdomen (Fig. 25A). Antenna with flattened membranous flange located posteriorly on proximal segment (Fig. 25B) instead of posterior process. Post-antennal process bifid, primary tine straight with marginal flange; associated papillae multisensillate. Posterior process of maxillule trifid (Fig. 25B); main (inner) tine with marginal flanges. Maxilliped of female with conspicuous ridges in myxal area (Fig. 25C). Sternal furca with tapering pointed tines, each with distinctive dense central core (Fig. 25D). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spine 1

longer than other spines; spines 2 and 3 each with accessory process; seta 4 about as long as spines 2 and 3. Leg 2 with marginal setules on endopodal segments 2 and 3; outer spine on exopodal segment 1 lying obliquely across segment 2, spine on segment 2 aligned close to longitudinal axis of ramus. Leg 3 (Fig. 25E) apron with raised bifid rib plus circular array of large denticles on ventral surface and corrugated adhesion pad near outer margin on dorsal surface; exopod 3-segmented, first segment with large recurved outer spine, lacking inner seta: endopod 2-segmented, distal endopodal segment with partial suture, armed with total of 6 plumose setae. Leg 4 uniramous, 4-segmented (Fig. 25F); exopodal segments with I; I; III spines; first exopodal segment with conspicuous sensillar ornamentation. Mean body length of female 3.61 mm, range 3.38 to 4.04 mm (based on 10 specimens).

Male with genital complex and 1-segmented abdomen forming ovoid unit. Maxillule with simple posterior process ornamented with marginal flanges and proximal adhesion pad. Maxilliped with transverse ridge fringed with membrane on proximal segment. Mean body length of male 2.20 mm, range 2.15 to 2.29 mm (based on 8 specimens).

Remarks. This distinctive species is a widely distributed and common parasite of carangid hosts. It was originally established by Pillai (1961) to accommodate material from *Caranx ignobilis* (as *C. sansun* (Forsskål)) caught at Trivandrum, India. Pillai (1961) placed in the synonymy of his new species, material previously confused with *C. constrictus* Heller, 1865 by Shiino (1959) and Wilson (1937b), and material confused with *Caligus alalongae* Krøyer, 1863 by Kirtisinghe (1937).

About 50 species of *Caligus* retain a 3-segmented exopod on leg 4 armed with I, I, III spines. Within these, *C. confusus* can be placed in a species-group characterized by a suite of character states including: the presence of a raised bifid cuticular rib and a circular array of denticles on the apron of leg 3, the possession of a large recurved hook (= the outer margin spine) on the first exopodal segment of leg 3, and, commonly, the presence of an accessory tine on the post-antennal process and on the posterior maxillulary process. This group is referred to here as the *C. confusus*-group.

In addition to *C. confusus*, the core group of species sharing these character states comprises *C. aesopus* Wilson, 1920, *C. bicycletus* Heegaard, 1945, *C. brevicaudus*, *C. chorinemi* Krøyer, 1863, *C. cordyla* Pillai, 1963, *C. equulae* Ho & Lin, 2003, *C. kurochkini* Kazatchenko, 1975, *C. lichiae* Brian, 1906, *C. lunatus* Wilson, 1924, *C. platurus* Kirtisinghe, 1964, *C. randalli* Lewis, 1964, *C. regalis* Leigh-Sharpe, 1930, *C. spinosus* Yamaguti, 1939, *C. tenax* Heller, 1865 and *C. zylanica* Hameed & Pillai, 1986. Linked with the core *C. confusus*-group are a number of other *Caligus* species which share most but not all of the characteristics. Examples of such species include *C. fortis* Kabata, 1965, which has a slightly curved spine instead of the large recurved hook on the first exopodal segment of leg 3, *C. isonyx* Steenstrup & Lütken, 1861, and *C. inopinatus* Kabata, 1994, both of which have simple instead of bifid tines on the post-antennal process and the posterior maxillulary process. The trifid form of the maxillulary posterior process in *C. confusus* is unique within the genus, and the form of the sternal furca combined with the presence of a hyaline membrane on the proximal segment of the antenna, help to distinguish *C. confusus* from all other core members of the *C. confusus*-group.

Caligus confusus has been reported from a wide range of carangid fishes including: *Caranx hippos* (Linnaeus, 1766), *C. ignobilis* (and as *C. sansun*), *C. melampygus* Cuvier, 1833, *C. sexfasciatus*, *C. caballus* Günther, 1868, *C. caninus* Günther, 1867, *Alepes djedaba* (as *Caranx kalla* and *C. djedaba*), *Elagatis bipinnulata* (Quoy & Gaimard, 1825) and *Seriola dumerili* (Risso, 1810) (Pillai, 1961, Kirtisinghe, 1937 (as *C. alalongae*), Wilson, 1937a, Lewis, 1968, Ho & Lin, 2001, 2004; Morales-Serna *et al.*, 2014). There are also records from non-carangid fishes such as *Coryphaena hippurus* (Wilson, 1937, as *C. constrictus*), *Epinephelus tauvina* (Forsskål, 1775) (Ho & Sey, 1996), and *Rhabdosargus holubi* (Steindachner, 1881) (Grobler *et al.*, 2003). In Moreton Bay it was found on two previously reported hosts, *C. ignobilis* and *C. sexfasciatus*.

The geographical distribution of *C. confusus* includes the Indo-Pacific from the Arabian Gulf, Sri-Lanka and India, through the South China Sea to Taiwan, and across to Eniwetok Atoll, and the Pacific coast of Mexico, Columbia and Panama (Ho & Lin, 2004; Morales-Serna *et al.*, 2014). In the Southern Hemisphere it has been reported from South Africa (Kensley & Grindley, 1973; Grobler *et al.*, 2003) and New Caledonia (Kabata, 1968). It was first reported from Australian waters on *Elagatis bipinnulata* by Hutson *et al.* (2011) who recorded it off the southeastern coast. This is the first report from Queensland.

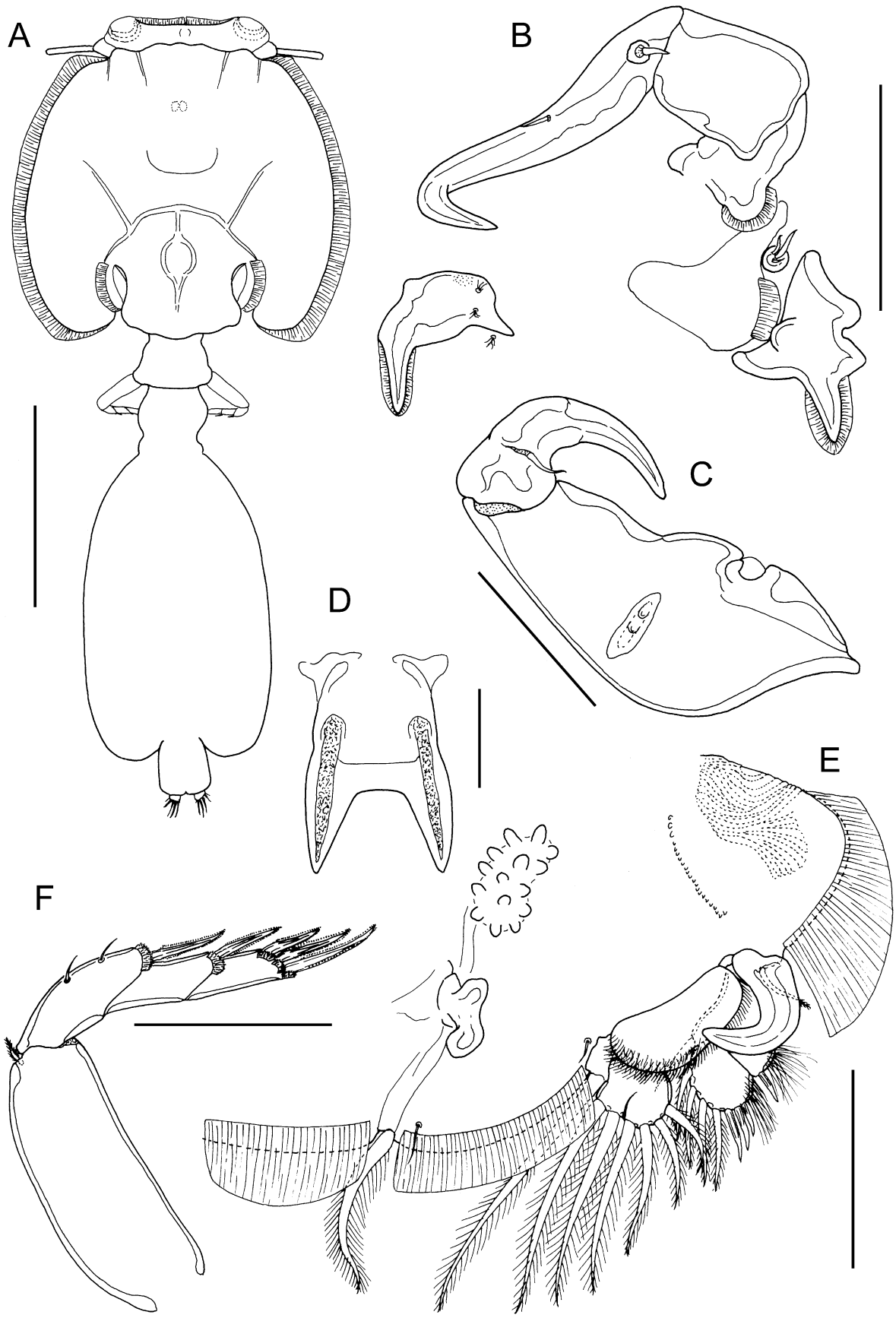

FIGURE 25. *Caligus confusus* Pillai, 1961, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, maxilliped; D, sternal furca; E, leg 3; F, leg 4. Scale bars: 1.0 mm on A, 200 µm on B, C, E, F, 100 µm on D.

***Caligus dasyaticus* Rangnekar, 1957**
(Fig. 26)

Material examined. 1♀ from *Neotrygon kuhlii* (Müller & Henle, 1841) (TC17336) 20 January 2016, QM Reg. No. W53064.

Site on host. Lower body surface.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones; frontal plates with very small lunules. Genital complex just longer than wide (1.02 to 1.10 times); abdomen indistinctly 2-segmented, about 1.8 times longer than wide (Fig. 26A); genital complex about 1.7 times longer than abdomen. Antenna without posterior process on proximal segment (Fig. 26B). Post-antennal process strongly recurved, tine without marginal flange; associated papillae multisensillate (Fig. 26B). Posterior process of maxillule long, slender and slightly curved outwards (Fig. 26B). Maxilliped of female slender with smooth myxal margin. Sternal furca with long, slender divergent tines (Fig. 26C). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spine 1 longer than other spines, ornamented with finely striated membrane bilaterally; spines 2 and 3 each with accessory process and striated marginal membrane around tip; seta 4 naked, less than half length of spines 2 and 3 (Fig. 26D). Leg 2 with marginal setules on endopodal segments 2 and 3; outer spines on exopodal segments 1 and 2 small (each shorter than next segment) and aligned parallel with longitudinal axis of ramus (Fig. 26E). Leg 3 apron lacking distinctive ornamentation; exopod 2-segmented (Fig. 26F) with second and third segments fused to form compound distal segment; first segment bearing straight outer spine with marginal flanges and inner plumose seta; compound distal segment with 4 outer spines and 5 plumose setae; proximal outer spine derived from third segment (arrowed in Fig. 26F) ornamented with marginal membrane distally. Leg 4 3-segmented (Fig. 26G); first exopodal segment with outer spine and large pecten; distal exopodal segment with 3 spines around apex, long spine more than twice as long as 2 short spines; segment ornamented with marginal membrane distally. Body length of adult female 4.23 mm.

Remarks. This species was originally described by Rangnekar (1957) based on two females from the body surface of a dasyatid sting ray named as "*Dasyaticus* [sic!] *uarnac*" by Rangnekar and caught off Bombay, India. The identity of the host should be considered as uncertain given the changes in understanding of species level taxonomy of chondrichthyan fishes in general and of the *Himantura uarnak* (Gmelin, 1789) species group in particular (see Naylor *et al.*, 2012). The body length of Rangnekar's single intact female was 3.80 mm (Rangnekar, 1957). Shiino (1960) subsequently reported this species from *Dasyatis akajei* (Müller & Henle, 1841) taken off Hamazima, Japan and provided the first description of the male. The body length of the largest female recorded by Shiino was 6.00 mm and that of the male was 2.89 mm (Shiino, 1960). Kabata (1966) was the first to report *C. dasyaticus* from Australian waters: based on two males collected from *Neotrygon kuhlii* (as *Amphotistius kuhlii*) caught in Moreton Bay. With a body length of 2.23 mm, Kabata's male was smaller than that of Shiino, but so is the female from Moreton Bay (at 4.23 mm).

As already highlighted by Ho *et al.* (2007), the taxonomy of *C. dasyaticus* became confused after Pillai (1968) published a detailed description of a different species of *Caligus* as "*C. dasyaticus* Rangnekar" from a specimen of the sawfish *Pristis* examined at Trivandrum, India. The female described by Pillai (1968) had a body length of 7.0 mm and the male was 3.3 mm in length. In his 1985 monograph, Pillai (1985) re-used the figures from his 1968 description. Ho *et al.* (2007) redescribed female *C. dasyaticus* from a single specimen with a body length of 5.62 mm, collected from the body surface of *Dasyatis navarrae* (Steindachner) landed in Taiwan. Ho *et al.* (2007) stated that "Pillai's (1968) "*C. dasyaticus*" very likely represents a different species". A new species, *Caligus elasmobranchi* **sp. nov.**, is established below, to accommodate the species described by Pillai (1968) from *Pristis* sp.

Both species are present in Moreton Bay: typical *C. dasyaticus* as described by Rangnekar (1957) was only found on *Neotrygon kuhlii* (Kabata, 1966; present account) while *C. elasmobranchi* **sp. nov.** was found on five different elasmobranch hosts. The best character for distinguishing between females of these two widely distributed species is leg 4: in *C. dasyaticus* leg 4 is shorter than the genital complex and bears 1 long and 2 short spines at its apex (cf. Fig. 26G), whereas in *C. elasmobranchi* **sp. nov.** the leg is much longer than the genital complex, extending beyond the middle of the abdomen, and bears 3 short to medium length apical spines (cf. Fig. 27G). Another significant difference is the size of the outer margin spine on exopodal segment 1 of leg 3: in *C. dasyaticus* it is short and does not reach the articulation between exopodal segments 2 and 3, whereas in *C. elasmobranchi* **sp. nov.** it is longer, extending well beyond this articulation.

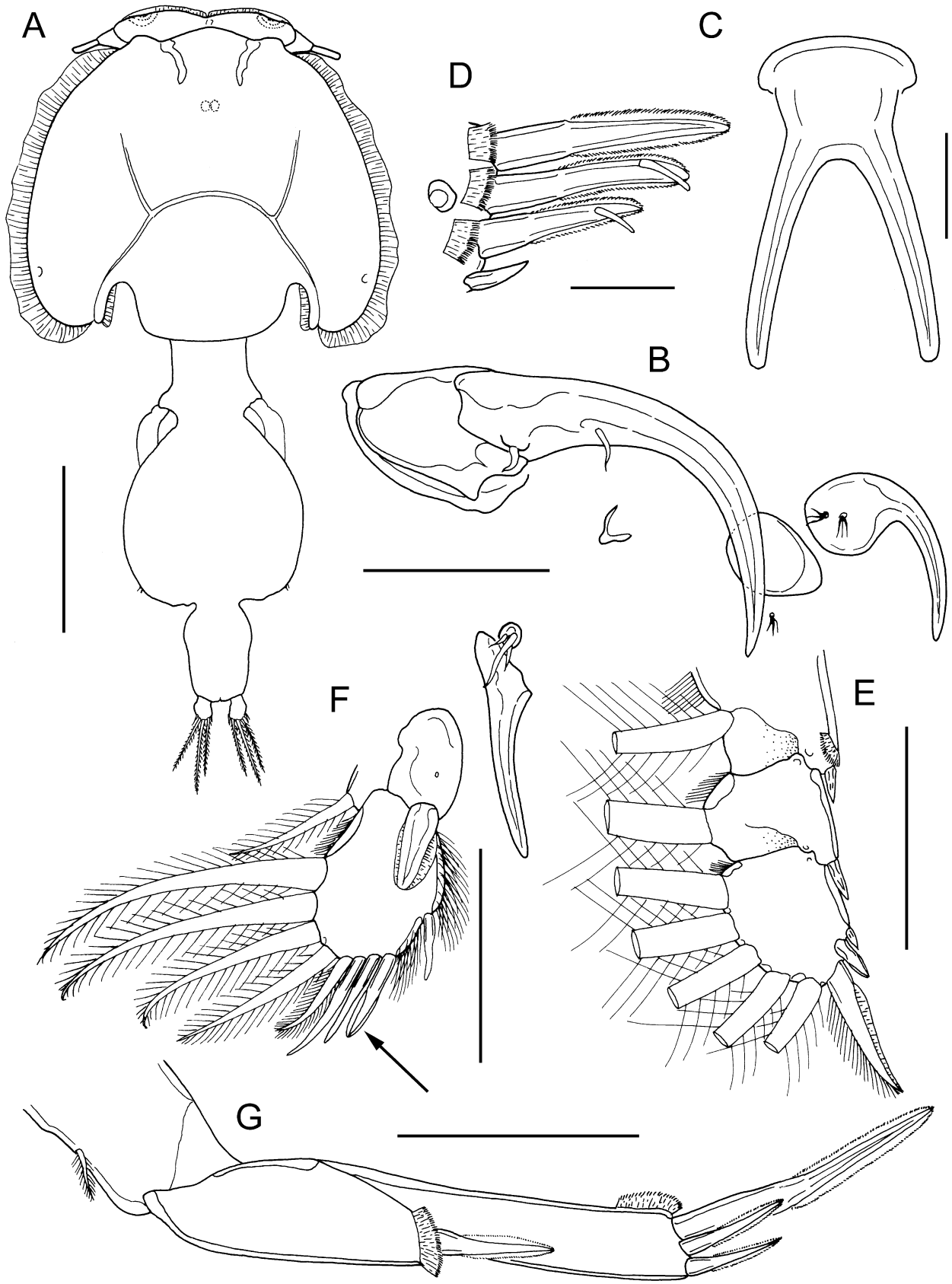

FIGURE 26. *Caligus dasyaticus* Rangnekar, 1957, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, sternal furca; D, distal margin of exopod of leg 1; E, exopod of leg 2; F, exopod of leg 3; G, exopodal segments of leg 4. Scale bars: 1.0 mm on A, 200 µm on B, E–G, 100 µm on C, 50 µm on D.

***Caligus elasmobranchi* sp. nov.**
(Fig. 27)

Syn. *Caligus dasyaticus*: Pillai, 1968, p. 9–11, figs. 1A–K. Pillai, 1985, p. 280–282, Figs. 88A–K.

Type material. 7♀♀, 3♂♂ from *Himantura uarnak* (Gmelin, 1789) (TC17112) 13 January 2016, Holotype ♀ QM Reg. No. W53065, 4 paratype ♀♀ and 2 paratype ♂♂ QM Reg. No. W53066; 2 paratype ♀♀ and 1 paratype ♂, NHMUK Reg. Nos 2017.267–268.

Additional non-type material. 2 late chalimus from *Aetobatus ocellatus* (Kuhl, 1823) (TC17287) 19 January 2016; 2♀♀, 1♂, 12 immatures from *Dasyatis fluviorum* Ogilby, 1908 (TC17360) 21 January 2016, NHMUK Reg. Nos 2017.269–271; 2 immature ♀♀, from *Himantura toshi* Whitley, 1939 (TC17189) 15 January 2016; 5♀♀, 3♂♂ and 22 immature stages from *Pastinachus atrus* (MacLeay, 1883) (TC17166) 15 January 2016, QM Reg. No. W53067.

Site on host. Upper and lower body surfaces.

Etymology. The species name refers to the wide range of elasmobranchs that have been recorded as hosts of this copepod.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; frontal plates with small lunules. Genital complex about 1.1 to 1.3 times longer than wide (Fig. 27A); abdomen 1-segmented, about 2.0 to 2.1 times longer than wide; genital complex dimensions variable (see Table 3), ranging from shorter than to 1.3 times longer than abdomen. Antenna without posterior process on proximal segment; middle segment short (Fig. 27B). Post-antennal process with slender, strongly curved tine without marginal flange; associated papillae multisensillate. Posterior process of maxillule slender and slightly curved outwards (Fig. 27B). Maxilliped of female slender, with smooth myxal margin. Sternal furca with long divergent tines (Fig. 27C). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spine 1 just longer than other spines (Fig. 27D), with blunt tip and marginal membrane on one side; spines 2 and 3 each with accessory process and rounded tip ornamented with membrane; seta 4 naked, markedly shorter than spines 2 and 3. Leg 2 ornamented with setules along lateral margins of endopodal segments 1 to 3; outer spines on exopodal segments 1 and 2 (Fig. 27E) small and aligned with long axis of ramus, not reflexed. Leg 3 apron without conspicuous ornamentation: exopod 3-segmented (Fig. 27F); with straight outer spine and plumose inner seta on first segment; second and third segments incompletely separated, armed with total of 4 spines and 5 setae. Leg 4 extremely long, reaching almost to base of caudal rami (Fig. 27A); exopod 2-segmented; first exopodal segment with slightly curved outer spine and large pecten; compound distal segment with 1 medium length and 2 short apical spines, distal segment ornamented with modified pecten on margin and numerous surface sensillae (Fig. 27G). Mean body length of female 5.46 mm, range 4.85 to 6.18 mm (based on 6 specimens). Mean body length of male 7.03 mm, range 6.60 to 7.30 mm (based on 7 specimens).

Remarks. Both sexes of this species were described in detail by Pillai (1968, 1985) under the name *C. dasyaticus*. Pillai's material, four females and 1 male, came from the gills of *Pristis* sp. caught near Trivandrum, India and is not conspecific with *C. dasyaticus* of Rangnekar (1957), as previously noted by Ho *et al.* (2007). These species are closely related and share numerous character states including the unusual marginal membrane near the apex of the distal segment of leg 4. However, as noted above, *C. elasmobranchi* **sp. nov.** can be distinguished from *C. dasyaticus* by the length of leg 4, which is shorter than the genital complex in the former, but extends almost to the base of the caudal rami in the latter.

The material of this species exhibited unusual size variation (Table 3). The measurements given in the diagnosis are based on a sample of 6 complete females, five of which were ovigerous, plus a detached genital complex plus abdomen which retained its egg sacs. These had a mean body length of 5.46 mm. However, the sample contained another ovigerous female which was 10.34 mm in length, almost twice as long as the others, and its abdomen more than twice as long as wide. Its dimensions are given in Table 3, but it was excluded from the calculations of the mean. In other respects, this large female displayed all the morphological characteristics of *C. elasmobranchi* **sp. nov.**, as described by Pillai (1968, 1985, under the name *C. dasyaticus*). At 7.0 mm, the body length of female given by Pillai (1968, 1985) is intermediate between the typical and the large females in the current sample (Table 3). Only a single female of this size was found, but this size disparity in a single locality and on the same host, deserves further study.

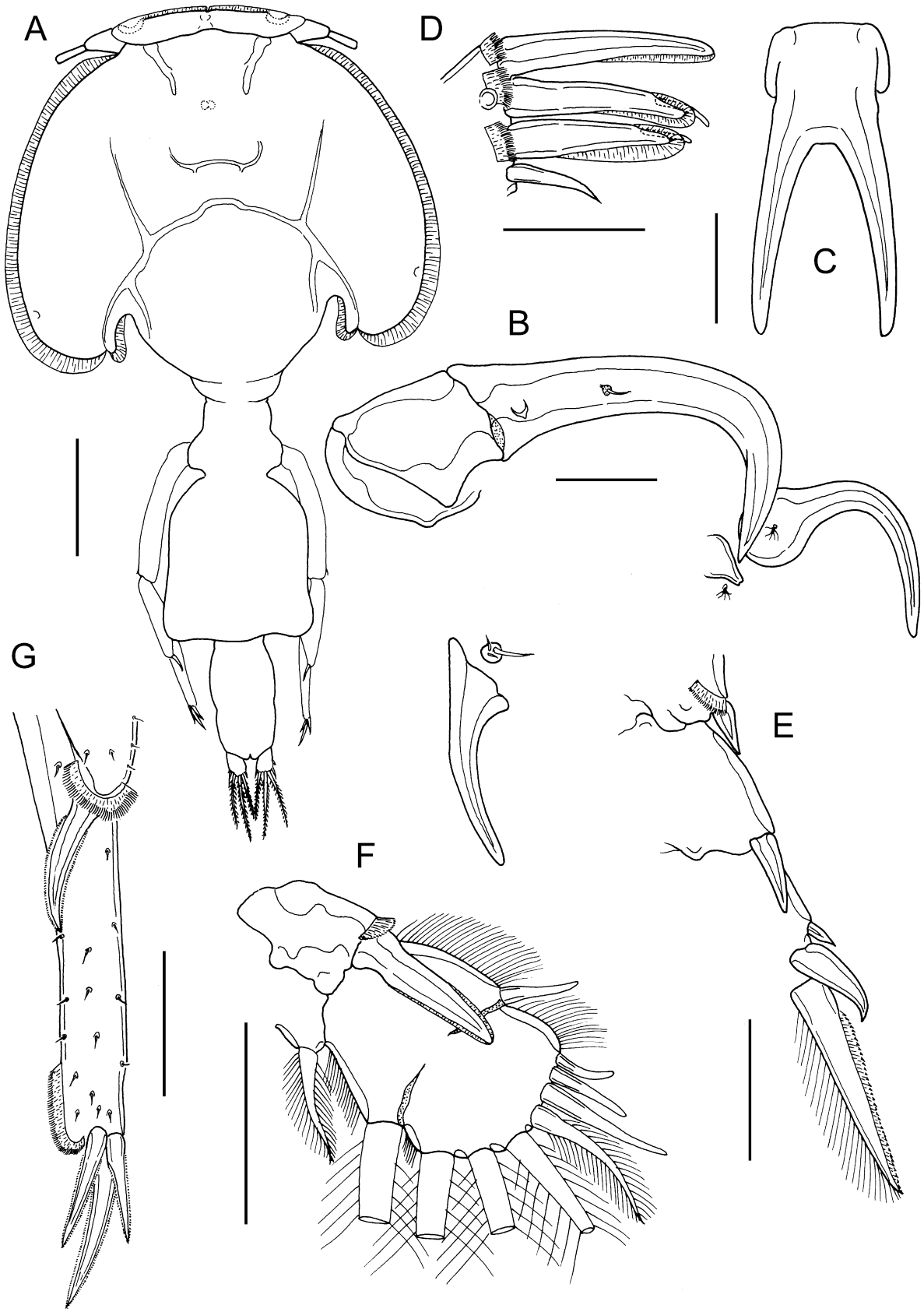

FIGURE 27. *Caligus elasmobranchi* **sp. nov.**, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, sternal furca; D, distal margin of exopod of leg 1; E, outer margin spines on exopod of leg 2; F, exopod of leg 3; G, distal part of exopodal segments of leg 4. Scale bars: 1.0 mm on A, 200 µm on B, F, G, 250 µm on C, 100 µm on D, E.

In Moreton Bay, four of the hosts, *Dasyatis fluviorum, Himantura toshi, H. uarnak* and *Pastinachus atrus* are members of the family Dasyatidae while *Aetobatus ocellatus* is in the Myliobatidae. The only previously known host of *C. elasmobranchi* **sp. nov.** is an unidentified species of *Pristis* (family Pristidae) from India (Pillai, 1968).

TABLE 3. Body dimensions (in mm) of adult females of *Caligus elasmobranchi* **sp. nov.** [Abbreviations: BL = body length, CL = dorsal cephalothoracic shield length, CW = dorsal cephalothoracic shield width, GCL = genital complex length, GCW = genital complex width, ABL = abdomen length, ABW = abdomen width, ESL = egg sac length]

Female	BL	CL	CW	GCL	GCW	ABL	ABW	ESL
1	6.18	3.14	3.24	1.02	0.79	1.10	0.58	none
2	5.98	2.84	3.14	1.18	1.02	1.18	0.51	2.55
3	5.0	2.35	2.65	1.08	0.90	0.87	0.39	2.16
4	4.85	2.45	2.89	1.02	0.86	0.88	0.39	1.57
5	5.59	2.75	3.19	1.23	1.12	1.02	0.49	3.24
incomplete	-	-	-	1.08	1.06	0.88	0.41	3.04
6	5.13	2.65	3.04	1.08	0.93	0.88	0.39	3.04
mean	5.46	2.70	3.03	1.10	0.95	0.97	0.45	2.60
outlier	10.34	4.02	4.12	2.06	1.37	2.58	0.75	8.43

***Caligus epidemicus* Hewitt, 1971**
(Fig. 28)

Material examined. 1♀ from *Acanthopagrus australis* (Günther, 1859) (TC17129) 14 January 2016, QM Reg. No. W53068; 2♀♀, 1♂ (TC 17862) 4 July 2016, QM Reg. No. W53069; 5♀♀, 2♂♂ (TC17855) 4 July 2016, QM Reg. No. W53070; 2♀♀ immatures (TC 17176) 15 January 2016, 1♀ (TC17489); 5♀♀ (TC17544) 24 June 2016, 1♀ (TC 17562) 24 June 2016, 2♂♂ (TC 17786) 1 July 2016, 2♀♀ (TC17814) 3 July 2016, 1♀, 1♀ immature (TC17816–17822) 3 July 2016, 3♀♀ (TC17822) 3 July 2016, 2♀♀ (TC17829) 3 July 2016, 3♀♀, 1♂ (TC17849) 4 July 2016, NHMUK Reg. Nos 2017. 418–427. 1♂ from *Abudefduf vaigiensis* (Quoy & Gaimard, 1825) (TC17091) 13 January 2016, NHMUK 2017.428; 1♀ immature, 1♂ from *Acanthurus* sp.; 5♀♀, 1♂ from *Gerres* sp. (juveniles), 26 June 2016, NHMUK 2017.429–434; 7♀♀ from *Girella tricuspidata* (Quoy & Gaimard, 1824) (TC17803) 2 July 2016, NHMUK 2017.435–441; 1♂ immature (TC17744) 29 June 2016; 1♂ from *Kyphosus bigibbus* Lacepède, 1801 (TC17792) 1 July 2016, 1♂ (TC17864) 4 July 2016, NHMUK 2017.442–443; 2♀♀ from *Kyphosus cinerascens* (Forsskål, 1775) (TC17922) 5 July 2016, NHMUK 2017.444–445; 4♀♀ from *Lagocephalus lunaris* (Bloch & Schneider, 1801) (TC 17899) 5 July 2016, QM Reg. No. W53071; 1♂, 1 chalimus from *Liza subviridis* (Valenciennes, 1836) (TC17797) 4 July 2016, NHMUK 2017.446; 1♀ from *Lutjanus fulviflamma* (Forsskål, 1775) (TC17567) 24 June 2016, NHMUK 2017.447; 1♀ from *Mugil cephalus* Linnaeus, 1758 (TC17734) 29 June 2016, 3♀♀ (TC17856) 4 July 2016, NHMUK 2017.448–451; 1♀, 1 chalimus from *Chrysophrys auratus* (Forster, 1801) (TC17575) 25 June 2016; 1 ♀ immature from *Pomatomus saltatrix* (Linnaeus, 1766) (TC 17549) 24 June 2016; 1♂ from *Saurida undosquamis* (Richardson, 1848) (TC17854) 4 July 2016; 1♂ from *Sillago analis* Whitely, 1943 (TC16816), NHMUK 2017.452.

Site on host. Body surface.

Differential diagnosis. Cephalothorax extremely dorso-ventrally flattened, giving translucent appearance, and with distinctive square-ish outline (Fig. 28A). Marginal membranes on lateral zones of dorsal cephalothoracic shield well-developed. Frontal plates with lunules. Genital complex short, about 1.6 to 1.7 times wider than long; abdomen small, 1-segmented, wider than long; genital complex about 3.5 times longer than abdomen. Antenna with broad posterior process on proximal segment (Fig. 28B). Post-antennal process short and blunt (Fig. 28B); associated papillae unisensillate. Posterior process of maxillule simple; post-oral process present (Fig. 28B). Maxilliped of female slender, with smooth myxal margin. Sternal furca short, with short parallel tines (Fig. 28C). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spine 1 about as long as spines 2 and 3; spines 2 and 3 each with accessory process; seta 4 shorter than spine 3. Leg 2 with marginal setules on

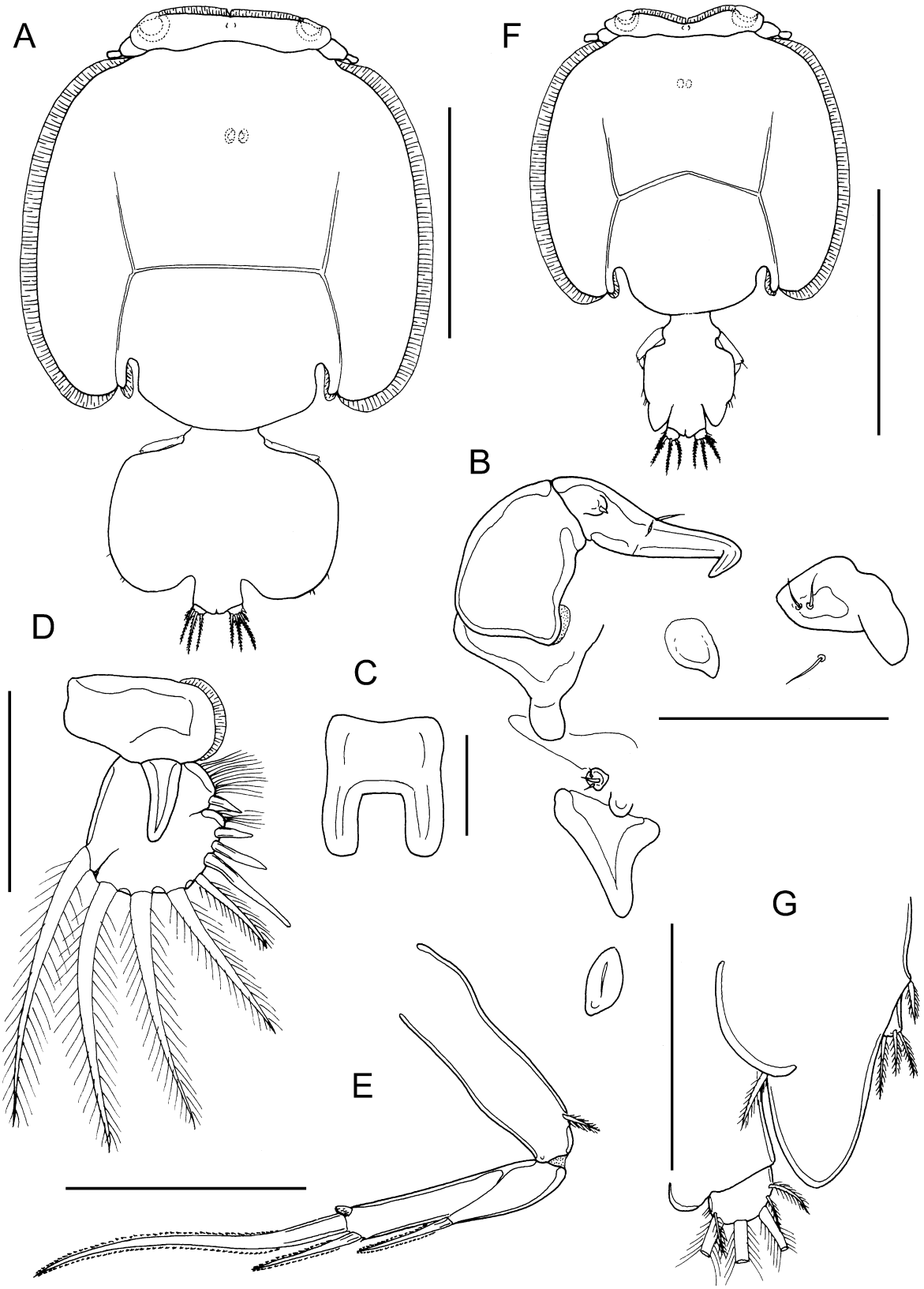

FIGURE 28. *Caligus epidemicus* Hewitt, 1971, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, sternal furca; D, exopod of leg 3; E, leg 4. Male, F, habitus, dorsal; G, left fifth and sixth legs, and caudal ramus, ventral view. Scale bars: 1.0 mm on A, F, 200 µm on B, E, G, 100 µm on D, 50 µm on C.

TABLE 4. Hosts reported for *Caligus epidemicus*

Fish Host species	Host Family	Locality	Source
Abudefduf vaigiensis (Quoy & Gaimard, 1825)	Pomacentridae	Australia	Present account
Acanthopagrus australis (Günther, 1859)	Sparidae	Australia	Byrnes (1987), present account
Acanthopagrus berda (Forsskål, 1775)	Sparidae	Australia	Byrnes (1987)
Acanthopagrus butcheri (Munro, 1949) (as *Mylio butcheri*)	Sparidae	Australia	Hewitt (1971), Byrnes (1987)
Acanthopagrus latus (Houttuyn, 1782)	Sparidae	Australia	Byrnes (1987)
Acanthopagrus schlegeli (Bleeker, 1854)	Sparidae	Taiwan	Ho & Lin (2004)
Acanthurus sp.	Acanthuridae	Australia	Present account
Acanthurus mata Cuvier, 1829	Acanthuridae	Philippines	Ho *et al.* (2004)
Aldrichetta forsteri (Valenciennes, 1836) (as *Alorichetta forsteri*),	Mugilidae	Australia	Hewitt (1971)
Chanos chanos (Forsskål, 1775)	Chanidae	Taiwan	Ho & Lin (2004)
		Philippines	Ho *et al.* (2004)
Chrysophrys auratus (Forster, 1801)	Sparidae	Australia	Present account
Epinephelus malabaricus (Bloch & Schneider, 1801)	Serranidae	Taiwan	Ho & Lin (2004)
Epinephelus coiodes (Hamilton, 1822)	Serranidae	Philippines	Ho *et al.* (2004)
		Malaysia	Venmathi Maran *et al.* (2009)
Gerres sp.	Gerreidae	Australia	Present account
Girella tricuspidata (Quoy & Gaimard, 1824)	Kyphosidae	Australia	Present account
Glossogobius celebius (Valenciennes, 1837)	Gobiidae	Philippines	Ho *et al.* (2004)
Kyphosus biggibus Lacepède, 1801	Kyphosidae	Australia	Present account
Kyphosus cinerascens (Forsskål, 1775)	Kyphosidae	Australia	Present account
Lagocephalus lunaris (Bloch & Schneider, 1801)	Tetraodontidae	Australia	Present account
Lates calcarifer (Bloch, 1790)	Latidae	Taiwan	Ho & Lin (2004)
		Malaysia	Venmathi Maran *et al.* (2009)
		Thailand	Johnson *et al.* (2004)

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TABLE 4. (Continued)

Fish Host species	Host Family	Locality	Source
Liza argentea (Quoy & Gaimard, 1825)	Mugilidae	Australia	Hewitt (1971)
Liza subviridis (Valenciennes, 1836)	Mugilidae	Australia	Present account
Lutjanus argentimaculatus (Forsskål, 1775)	Lutjanidae	Philippines	Ho *et al.* (2004)
Lutjanus fulviflamma (Forsskål, 1775)	Lutjanidae	Australia	Present account
Monodactylus argenteus (Linnaeus, 1758)	Monodactylidae	Philippines	Ho *et al.* (2004)
Mugil cephalus Linnaeus, 1758	Mugilidae	Australia	Hewitt (1971), present account
		Taiwan	Ho & Lin (2004)
Myxus elongatus Günther, 1861	Mugilidae	Australia	Hewitt (1971)
Oreochromis aureus (Steindachner, 1864)	Cichlidae	Taiwan	Ho & Lin (2004)
Oreochromis mossambicus (Peters, 1852)	Cichlidae	Taiwan	Lin (1996), Ho & Lin (2004)
		Philippines	Ho et al. (2004)
Oreochromis niloticus (Linnaeus, 1758)	Cichlidae	Philippines	
Oreochromis urolepis hornorum (Trewavas, 1966)	Cichlidae	Philippines	Ho *et al.* (2004)
Paramugil parmata (Cantor, 1849) (as *Liza parmata* (Cantor))	Mugilidae	Philippines	Ho *et al.* (2004)
Pomatomus saltatrix (Linnaeus, 1766)	Pomatomidae	Australia	Present account
Rachycentron canadum (Linnaeus, 1766)	Rachycentridae	Philippines	Ho *et al.* (2004)
Saurida undosquamis (Richardson, 1848)	Harpadontidae	Australia	Present account
Seriola lalandi Valenciennes, 1833	Carangidae	Australia	Hutson *et al*., 2011
Siganus guttatus (Bloch, 1787)	Siganidae	Philippines	Ho *et al.* (2004)
Sillago analis Whitely, 1943	Sillaginidae	Australia	Present account
Trachinotus blochii (Lacepède, 1801)	Carangidae	Taiwan	Ho & Lin (2004)
Crustacean Host species			
Penaeus monodon Fabricius, 1798	Decapoda	Thailand	Ruangpan & Kabata (1984)

endopodal segments 1, 2 and 3; outer spines on exopodal segments 1 and 2 aligned close to longitudinal axis of ramus. Leg 3 without distinctive ornamentation on apron: exopod indistinctly 2-segmented (Fig. 28D); first exopodal segment with outer marginal flange plus short, slightly curved outer spine, without inner seta; compound distal segment subdivided by partial suture, armed with total of 4 outer spines and 5 plumose setae. Leg 4 uniramous, 3-segmented (Fig. 28E); first exopodal segment with long outer spine, second with apical spine longer than ramus plus subapical spine about one-third length of apical spine. Mean body length of female 2.51 mm, range 2.39 to 2.67 mm (based on 10 specimens).

Male (Fig. 28F) with similarly shaped and extremely flattened cephalothorax, as in female. Genital complex produced into large, triangular posterior lobes either side of short, 1-segmented abdomen. Leg 5 located laterally anterior to lobe and leg 6 located medial to lobe (Fig. 28G). Maxilliped with small spinous process on myxal surface. Mean body length of male 1.63 mm, range 1.56 to 1.75 mm (based on 9 specimens).

Remarks. *Caligus epidemicus* was first described from the lower Mitchell River in Victoria (Australia) by Hewitt (1971) based on material from a sparid host, *Acanthopagrus butcheri* (Munro, 1949) (as *Mylio butcheri*), and four mugilids, *Mugil cephalus*, *Aldrichetta forsteri* (Valenciennes, 1836) (as *Alorichetta forsteri*), *Liza argentea* (Quoy & Gaimard, 1825) and *Myxus elongatus* Günther, 1861. Roubal (1981) reported *C. epidemicus* from *Acanthopagrus australis* caught at Coffs Harbour (NSW). Subsequent parasitological surveys of four species of the genus *Acanthopagrus* Peters by Byrnes (1987) revealed the presence of *C. epidemicus* along the coast of every state of mainland Australia (not in Tasmania). It was discovered in Thailand on cultured decapods (giant tiger prawns) in 1977 (Ruangpan & Kabata, 1984). This species has since been reported from numerous localities across the Indo-Pacific region including Taiwan (Lin, 1996) and the Philippines (Ho *et al.*, 2004b). Its life cycle was elucidated by Lin *et al.* (1996b).

Caligus epidemicus exhibits a low level of host specificity and has previously been reported from at least 13 different families of fishes (Table 4). As well as occurring on wild fishes, *C. epidemicus* occurs widely in finfish aquaculture systems: for example, Ho & Lin (2004) reported it from nine different host species cultured at three different localities around Taiwan (see Table 4), and it has even been recorded infesting the cultured decapod *Penaeus monodon* Fabricius, 1798 in Thailand (Ruangpan & Kabata, 1984). It occurred at high prevalence rates and at high intensity on this very unusual host. Ho *et al.* (2004b) reported it from ten different host fish species in the Philippines and Venmathi Maran *et al.* (2009) recorded it from marine fish cultured in floating cage systems (Table 4). Roubal (in Hallet & Roubal, 1995) reported high population levels on captive *Acanthopagrus australis* in Australia.

In the Moreton Bay survey, *C. epidemicus* was collected from 14 host species, of which 12 are new host records and this adds an additional seven host families to Table 4. It was never very common and often individuals were not adult, but the extreme flattening and the characteristic square shape of the cephalothorax are evident in the later developmental stages of this species, allowing them to be positively identified.

In its original description, *C. epidemicus* was reported as abundant in plankton samples taken in the brackish waters (salinity 4.5 to 28 ppt) of the lower reaches of the Mitchell River (Hewitt, 1971). Ho & Lin (2004) confirmed its tolerance to low salinities when they recorded *C. epidemicus* infestations that resulted in mortality among cultured host fishes in brackish water ponds in southern Taiwan. Similarly, *C. epidemicus* has been recorded on tilapia species (*Oreochromis* spp.) in brackish water culture facilities at multiple sites across the Philippines (Natividad *et al.*, 1986).

Caligus furcisetifer Redkar, Rangnekar & Murti, 1949
(Fig. 29)

Syn. *Caligus lepeophtheiropsis* Pillai, 1967

Material examined. 2♀♀ from *Glaucostegus typus* (Anonymous [Bennett], 1830) (TC17251) 18 January 2016; 1♀ QM Reg. No. W53072, 1♀ NHMUK 2017.272; 2♂♂ (TC17425) 22 January 2016; 1♂ QM Reg. No. W53073, 1♂ NHMUK 2017.273; 1♀ immature (TC 17360) 21 January 2016, 1♀ immature (TC 17416) 22 January 2016.

Site on host. Body surface.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes

along margins of lateral zones of dorsal cephalothoracic shield; frontal plates with minute, inconspicuous lunules located laterally (Fig. 29A). Genital complex about as long as wide; abdomen small, 1-segmented, about 1.3 times longer than wide; genital complex about 2.7 times longer than abdomen. Antenna with tapering posterior process on proximal segment (Fig. 29B). Post-antennal process with large tapering tine; associated papillae multisensillate. Posterior process of maxillule simple; process on anterior sclerite extending over base of posterior process (Fig. 29B). Maxilliped of female with smooth myxal margin on proximal segment. Sternal furca with widely spaced, slightly divergent tines (Fig. 29C). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spine 1 stout, about as long as spine 2 (Fig. 29D); spine 3 shorter than spine 2, both with accessory process; seta 4 shorter than spine 3. Leg 2 with margin of endopodal segments 1 and 2 ornamented with setules; outer spine on exopodal segment 1 (Fig. 29E) directed obliquely over surface of ramus, spine on second segment aligned closer to longitudinal axis of ramus; proximal and distal outer spines on third segment well developed (Fig. 29E), with fine serrations along both margins. Leg 3 with well developed apron lacking distinctive ornamentation: rami located close together (Fig. 29F): exopod indistinctly 3-segmented; first segment with large tapering spine and inner plumose seta, second segment with outer spine and inner seta and incompletely separated from third segment, armed with 3 outer spines and 4 plumose setae. Endopod 2-segmented: first segment forming short velum and bearing inner seta; compound distal segment with 6 plumose setae. Leg 4 uniramous, 3-segmented; first exopodal segment with outer spine; second with 1 long and 2 short apical spines (Fig 29G); long spine more than 3 times longer than short spines. Mean body length of female 8.07 mm, range 7.63 to 8.50 mm (based on 2 specimens). Mean body length of male 6.68 mm, range 6.60 to 6.75 mm (based on 2 specimens).

Remarks. *Caligus furcisetifer* was originally described from India by Redkar *et al.* (1949), based on 3 females and 2 males collected from *Eusphyra blochii* (Cuvier, 1816) (as *Sphyrna blochii*) caught off Bombay. However, it was poorly characterised so that Pillai (1967b, 1968) didn't recognize it when he established a new species, *C. lepeophtheiropsis* Pillai, 1967, to accommodate two females collected from an unidentified species of *Pristis* Linck, 1790 (Pristidae) caught at Trivandrum, India. Subsequently, in his monograph, Pillai (1985) placed *C. lepeophtheiropsis* in synonymy with *C. furcisetifer*.

The tiny size of the lunules on the frontal plates is a distinctive feature of this species. As Pillai (1968) commented, the lunules are inconspicuous and easily overlooked, and "the animal looks very much like a *Lepeophtheirus*". The species was discovered in Australian waters by Morgan *et al.* (2010) who found both sexes on the body surface and head of the critically endangered largetooth sawfish, *Pristis microdon* Latham, 1794, in the brackish reaches of the Fitzroy River (Western Australia) and the Leichhardt River opening into the Gulf of Carpentaria (Queensland). In Moreton Bay *C. furcisetifer* occurred only on *Glaucostegus typus* (Rhinobatidae). Although restricted to elasmobranch hosts, *C. furcisetifer* appears to exhibit relatively low host specificity having been recorded from three different orders, Carcharhiniformes, Pristiformes and Rajiformes.

***Caligus hyporhamphi* sp. nov.**

(Figs. 30, 31)

Type material. Holotype ♀ from *Hyporhamphus quoyi* (Valenciennes, 1847) (TC17880) 5 July 2016, QM Reg. No. W53074.

Type Host. *Hyporhamphus quoyi* (Valenciennes, 1847).

Site on host. Unknown (in body wash).

Etymology. The species name refers to the generic name of its type host.

Description. Holotype female (Fig. 30A) body length 5.26 mm, including caudal rami. Cephalothorax slightly longer than wide (2.90 x 2.48 mm). Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly beyond rear margins of lateral portions. Large lunules present ventrally on frontal plates. Genital complex just longer than wide (1.29 x 1.23 mm), with convex lateral margins and rounded corners (Fig. 30A); fifth legs (Fig. 30B) located ventrally close to posterolateral corners. Genital complex about 1.5 times longer than abdomen. Abdomen 1-segmented, about 1.6 times longer than wide (0.87 x 0.55 mm) in ventral view; carrying paired caudal rami distally; anal slit terminal. Caudal rami with parallel sides, about 1.4 times longer than wide, measured at midpoints of margins: each ramus armed with short hirsute seta at inner distal angle, slightly longer hirsute seta at outer distal angle, minute hirsute seta located just ventral to outer distal seta, and 3 long plumose setae on distal margin.

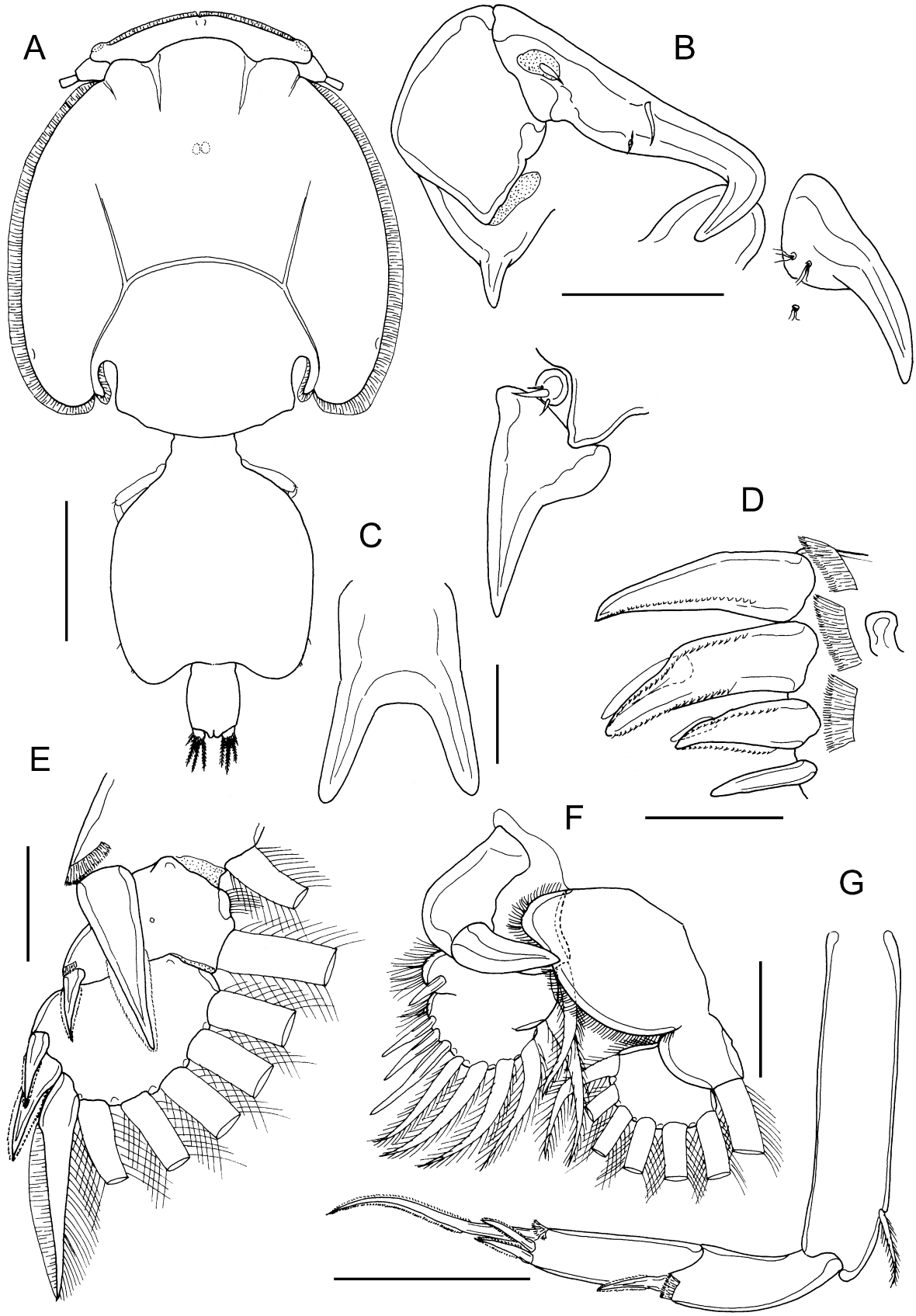

FIGURE 29. *Caligus furcisetifer* Redkar, Rangnekar & Murti, 1949, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, sternal furca; D, distal margin of exopod of leg 1; E, exopod of leg 2; F, rami of leg 3; G, leg 4. Scale bars: 1.0 mm on A, 200 µm on B, G, 100 µm on C, E, F, 50 µm on D.

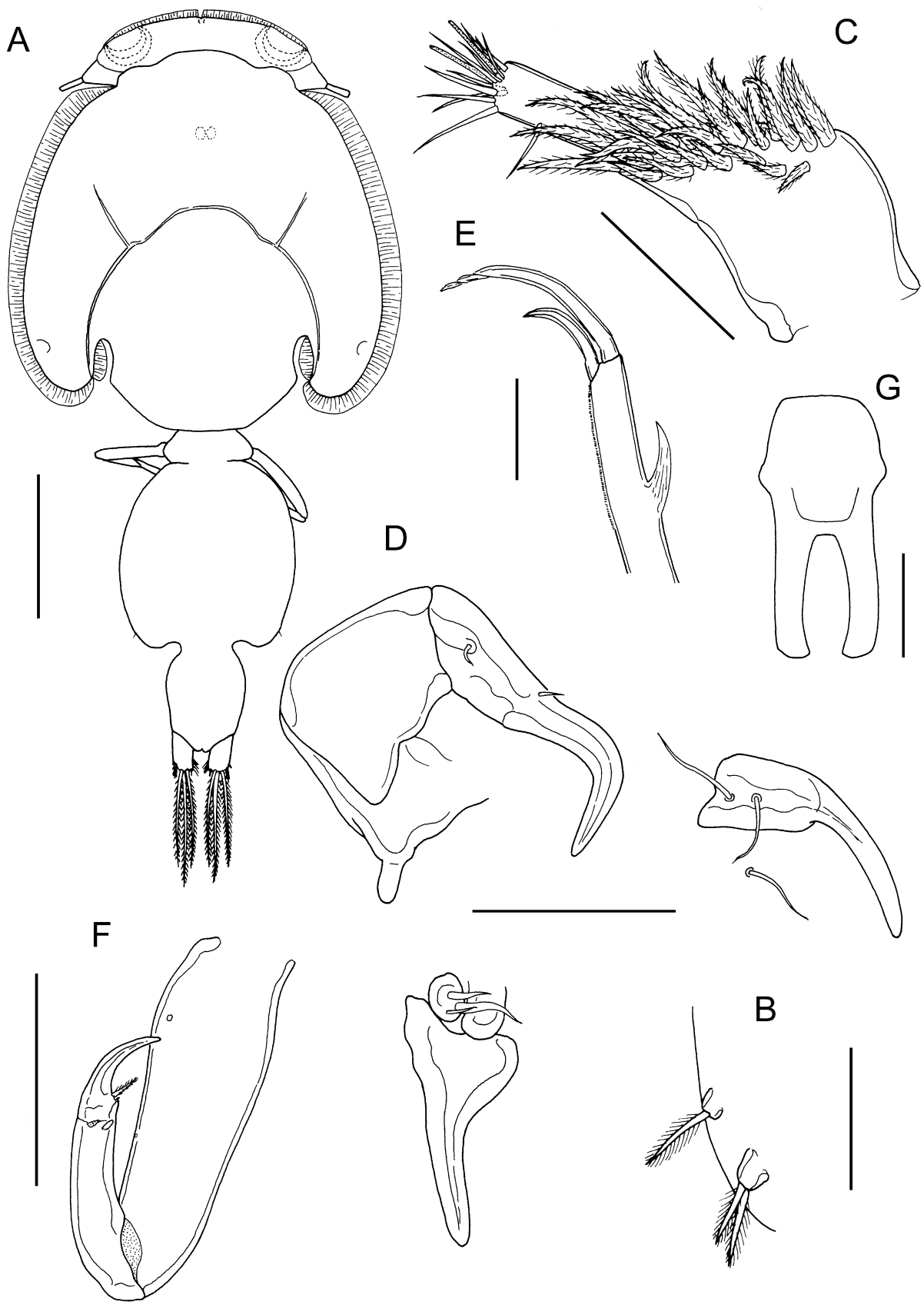

FIGURE 30. *Caligus hyporhamphi* **sp. nov.**, holotype female. A, habitus, dorsal; B, right posterolateral corner of genital complex with leg 5, ventral; C, antennule; D, antenna, post-antennal process and maxillule drawn *in situ*; E, tip of maxilla showing marginal corrugations; F, maxilliped; G, sternal furca. Scale bars: 1.0 mm on A, 200 µm on C, D, F, 100 µm on B, E, G.

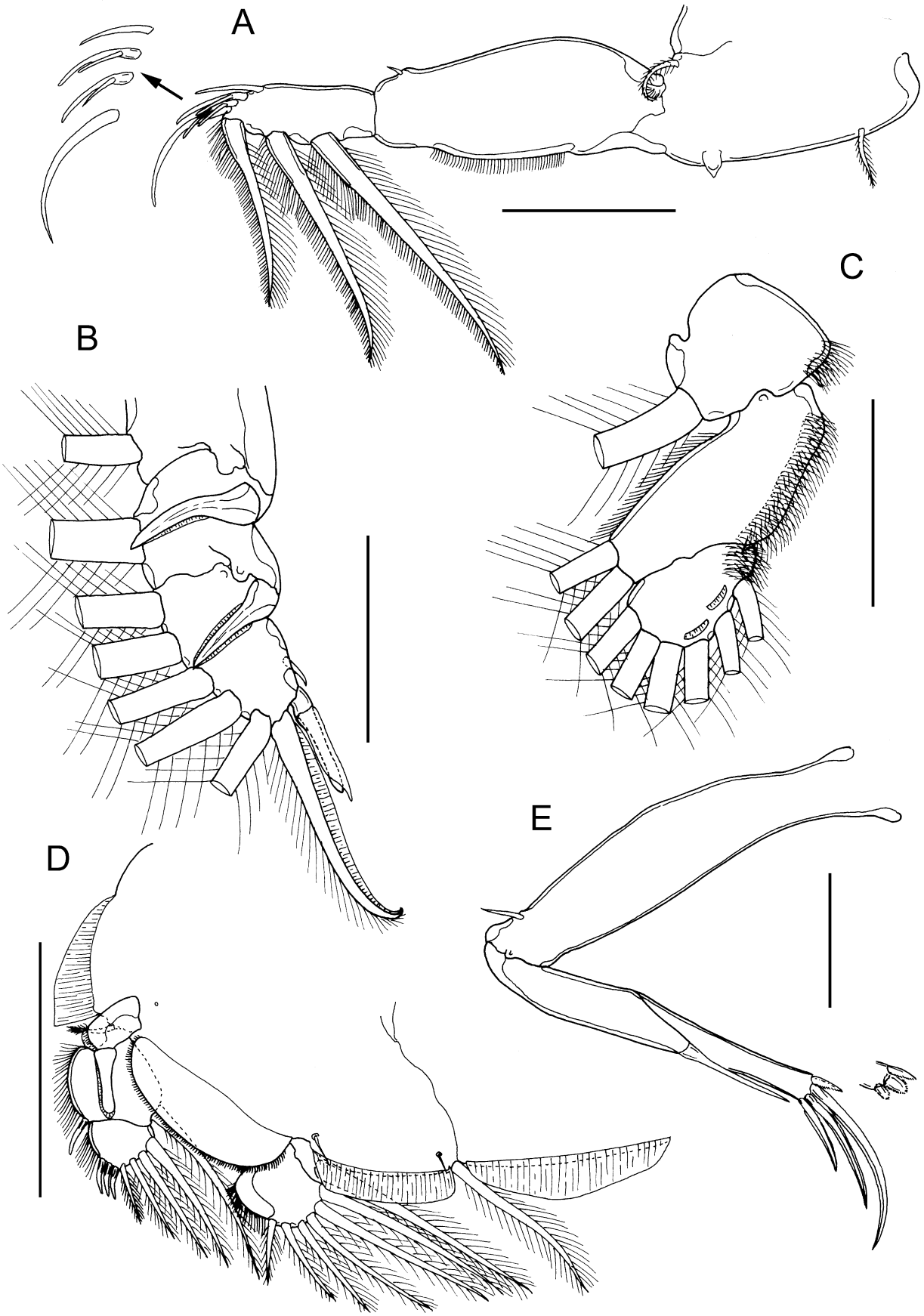

FIGURE 31. *Caligus hyporhamphi* **sp. nov.**, holotype female. A, leg 1, with inset showing details of distal margin spines 1 to 3 and seta 4; B, exopod of leg 2; C, endopod of leg 2; D, leg 3; E, leg 4. Scale bars: 200 µm on A–C, E, 0.5 mm on D.

Antennule (Fig. 30C) 2-segmented; large proximal segment with 25 plumose setae arrayed along anteroventral surface plus 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 30D) comprising proximal segment bearing narrow, posteriorly-directed spinous process; middle segment subrectangular, unarmed; terminal segment forming recurved claw bearing seta on small swelling proximally and distal seta near anterior margin. Post-antennal process well-developed, slender and slightly curved; ornamented with 2 unisensillate papillae on basal part and single similar unisensillate papilla on adjacent ventral cephalothoracic surface (Fig. 30D).

Mandible of typical stylet-like structure, with 12 marginal teeth. Maxillule (Fig. 30D) comprising anterior papilla bearing 3 unequal, naked setae and slender posterior, tine-like process; sclerite adjacent to anterior papilla with rounded posterior process overlapping base of posterior process. Maxilla 2-segmented (Fig. 30E), comprising elongate syncoxa and basis; basis bearing membranous but spiniform subapical flabellum on anterior margin, ornamented with minute corrugations distally along posterior margin, and terminating in 2 claw-like elements (calamus and canna): calamus longer than canna, ornamented with strips of serrated membrane arranged obliquely around surface; canna ornamented with bilateral strips of serrated membrane. Maxilliped subchelate (Fig. 30F); slender protopodal segment lacking any process on myxal surface; distal subchela with apical claw separated from proximal segmental part by incomplete suture; seta present on concave margin.

Sternal furca (Fig. 30G) with long parallel tines, slightly expanded and incurved at tip.

First swimming leg pair (Fig. 31A) joined by slender intercoxal sclerite; sympod with inner and outer plumose setae; endopod represented by unarmed tapering process on posterior margin of basis. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment robust, about 2.4 times longer than wide armed with small outer (anterior) spine, and ornamented with row of setules along posterior margin; second segment armed with 3 long plumose setae along posterior margin and 4 distal elements along oblique distal margin. Distal elements as follows: spine 1 (anterior-most) simple, about as long as spine 2; spines 2 and 3 subequal in length, each with accessory process; seta 4 about twice as long as spines and slightly longer than segment.

Second leg biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by intercoxal sclerite bearing marginal membrane posteriorly. Coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segments 1 and 2 (Fig. 31B) each with large outer spines reflexed and extending obliquely across ventral surface of ramus, plus inner plumose seta; first segment with flap of membrane anteriorly reflexed back across dorsal surface of ramus; segment 3 with 2 outer spines (proximal spine minute, distal spine armed with flap of membrane), apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. First and second endopodal segments (Fig. 31C) armed with 1 and 2 inner plumose setae, respectively; segment 3 armed with 6 plumose setae and ornamented with 2 shallow crescentic strips of membrane; outer margins of all endopodal segments ornamented with fine setules extending from margin onto surface of segment.

Third leg pair (Fig. 31D) forming flattened plate closing posterior part of cephalothoracic sucker as typical for genus. Protopodal part flattened and joined by plate-like intercoxal sclerite, forming apron ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod: bearing inner plumose seta at junction with intercoxal plate, and outer plumose seta dorsal to base of exopod; long sensillae located adjacent to inner coxal seta and adjacent to origin of endopod. Exopod 3-segmented; first segment armed with straight outer claw directed over ventral surface of ramus, claw and outer distal margin of segment ornamented with strip of membrane; second segment with slender outer spine and inner plumose seta; third with 3 outer spines and 4 inner plumose setae; outer margins of segments 2 and 3 ornamented with row of slender setules. Endopod 2-segmented; first segment forming flap-like velum ornamented with row of fine setules along free margin, closing space between rami, and armed with inner plumose seta; compound distal segment expanded laterally, armed with 6 setal elements increasing in length from outermost to innermost.

Fourth leg (Fig. 31E) 3-segmented, comprising slender protopodal segment and 2-segmented exopod: protopodal segment armed with plumose seta distally; first exopodal segment armed with long slender outer spine; compound distal segment with 3 distal margin spines increasing in size from outer to inner; innermost with elongate pecten at base.

Fifth legs located posterolaterally on genital complex (Fig. 30B); each fifth leg comprising anterior papilla bearing plumose seta (representing outer protopodal seta) and inner exopodal papilla armed with 2 plumose setae.

TABLE 5. Species of *Caligus macarovi*-group: characterised by a 3-segmented leg 4 bearing 3 distal spines only on the distal exopodal segment, in combination with the setal armature on the distal segment of leg 1 consisting of 3 plumose posterior setae, spines 1 to 3 of similar length (spines 2 and 3 only with accessory processes), and seta 4 about twice length of spines. [Abbreviations: ABL = abdomen length, ABW = abdomen width, GCL = genital complex length, GCW = genital complex width, Mx = spinules on distal margin of maxilla, PAP = papilla associated with post-antennal process unisensillate]

Species	GCL:GCW	GCL:ABL	ABL:ABW	PAP	Mx	Reference
C. praecinctorius Hayes, Justine & Boxshall, 2012	0.4:1	2.3:1	1.3:1	yes	no	Hayes *et al.*, 2012
C. quadrigenitalis Venmathi Maran, Ohtsuka & Shang, 2012	0.5:1	4.5:1	0.6:1	yes	no	Venmathi Maran *et al.*, 2012b
**C. eventilis* Leigh-Sharpe, 1934	0.6:1	2.6:1	0.5:1	?	?	Leigh-Sharpe, 1934
C. longipedis Bassett-Smith, 1898	0.6:1	2.0:1	1.3:1	yes	yes	present account
C. orientalis Gussev, 1951	0.6:1	2.4:1	0.6:1	no	no	Ho & Lin, 2004
C. sclerotinosus Roubal, Armitage & Rohde, 1983	0.6:1	4.1:1	0.7:1	yes	yes	present account
C. brevis Shiino, 1954	0.7:1	2.3:1	1.1:1	yes	no	Shiino, 1954b
**C. mordax* Leigh-Sharpe, 1934	0.7:1	1.1:1	1.2:1	?	?	Leigh-Sharpe, 1934
C. oculicola Tang & Newbound, 2004	0.7:1	2.8:1	1.0:1	yes	no	Tang & Newbound, 2004
C. polycanthi Gnanamuthu, 1950	0.7:1	1.7:1	1.0:1	yes	yes	Ho & Lin, 2004
C. punctatus Shiino, 1955	0.7:1	2.4:1	1.1:1	no	no	Ho & Lin, 2004
C. upenei **sp. nov.**	0.7:1	5.2:1	0.9:1	yes	yes	present account
C. flexispina Lewis, 1964	0.8:1	3.1:1	1.0:1	no	no	Lewis, 1964a
C. kalumai Lewis, 1964	0.8:1	2.3:1	1.0:1	no	no	Lewis, 1964a
**C. lolligunculae* Capart, 1941	0.8:1	2.4:1	0.9:1	?	?	Capart, 1941
C. oviceps Shiino, 1952	0.8:1	2.3:1	1.4:1	yes	yes	Ho & Lin, 2004
C. absens Ho, Lin & Chen, 2000	0.9:1	1.5:1	2.3:1	no	no	Ho & Lin, 2004
C. aduncus Shen & Li, 1959	0.9:1	2.4:1	0.9:1	?	?	Shen & Li, 1959
C. antennatus Boxshall & Gurney, 1980	0.9:1	4.1:1	0.8:1	yes	no	Boxshall & Gurney, 1980
C. hamruri Pillai, 1964	0.9:1	2.0:1	2.1:1	no	no	Pillai, 1985
C. pseudokalumai Lewis, 1968	0.9:1	3.3:1	0.7:1	yes	no	Lewis, 1968

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TABLE 5. (Continued)

Species	GCL:GCW	GCL:ABL	ABL:ABW	PAP	Mx	Reference
C. stokesi Byrnes, 1987	0.9:1	2.5:1	1.2:1	yes	yes	Byrnes, 1987
C. dampieri Byrnes, 1987	1.0:1	2.1:1	1.1:1	yes	yes	Byrnes, 1987
C. hyporhamphi **sp. nov.**	1.0:1	1.7:1	1.4:1	yes	yes	present account
C. *itacurussensis* Luque & Cezar, 2000	1.0:1	2.1:1	1.5:1	yes	no	Luque & Cezar, 2000
C. latus Byrnes, 1987	1.0:1	2.3:1	1.4:1	yes	?	Byrnes, 1987
C. macarovi Gussev, 1951	1.0:1	1.3:1	1.9:1	yes	yes	Shiino, 1959
C. thyrsitae Kazachenko, Korotaeva & Kurochkin, 1972	1.0:1	1.2:1	2.0:1	yes	yes	Kazachenko *et al.*, 1972
C. wilsoni Delamare Deboutteville & Nuñes-Ruivo, 1958	1.0:1	1.3:1	1.8	yes	?	Cressey, 1991
C. longiabdominis Shiino, 1965	1.1:1	1.0:1	2.5:1	yes	?	Shiino, 1965
C. rogercresseyi Boxshall & Bravo, 2000	1.1:1	3.4:1	1.4:1	yes	yes	Boxshall & Bravo, 2000
C. scribae Essafi, Cabral & Raibaut, 1984	1.1:1	3.3:1	1.0:1	yes	yes	Essafi et al., 1984
C. solea Demirkale, Özak, Yanar & Boxshall, 2014	1.1:1	1.6:1	1.5:1	yes	no	Demirkale *et al.*, 2014
C. tetrodontis Barnard, 1948	1.1:1	2.4:1	1.2:1			Unpublished data
C. triangularis Shiino, 1954	1.1:1	2.1:1	1.3:1	?	?	Shiino, 1954c
C. kahawai Jones, 1988	1.2:1	3.3:1	1.4:1	yes	yes	Jones, 1988
C. kuwaitensis Kabata & Tareen, 1984	1.2:1	7.9:1	0.6:1	yes	?	Kabata & Tareen, 1984
C. lalandei Barnard, 1948	1.2:1	1.6:1	2.3:1	yes	yes	Ho et al., 2001
C. fistulariae Yamaguti, 1936	1.3:1	3.5:1	1.0:1	yes	no	Shiino, 1964
C. klawei Shiino, 1959	1.3:1	4.4:1	0.9:1	yes	no	Shiino, 1959
C. nolani Longshaw, 1997	1.3:1	2.5:1	1.6:1	yes	no	Longshaw, 1997
C. sibogae Boxshall & Gurney, 1980	1.3:1	0.9:1	1.8:1	yes	yes	Boxshall & Gurney, 1980
C. longicaudatus Brady, 1899	1.4:1	1.4:1	3.0:1	yes	yes	Jones, 1988
C. amblygenitalis Pillai, 1961	1.6:1	2.6:1	2.1:1	yes	yes	Pillai, 1985

*These poorly described species are included but many morphological details are lacking.

Remarks. The female from *H. quoyi* has a 3-segmented leg 4 with the first and second exopodal segments bearing 1 and 3 distal spines, respectively. This configuration, where there is no lateral spine on the compound second segment, is exhibited by about 65 valid species of *Caligus*. In 1980, Boxshall & Gurney recognized a cluster of 28 species, which they referred to as the *C. macarovi*-group, which was characterized by this form of leg 4 exhibited in combination with a suite of other features including: the distal exopodal segment of leg 1 armed with 3 posterior margin plumose setae, spines 1, 2 and 3 all subequal in length and only spines 2 and 3 with accessory processes, and seta 4 markedly longer than the spines, plus a 1-segmented abdomen in the female. In addition, they noted that many core members of this group also possessed serrations distally on the margin of the brachium of the maxilla. Numerous additional species sharing most or all of these character states have been described since 1980, therefore all 42 current members of the *C. macarovi* group are listed in Table 5. Excluded are another 23 species which have a 3-segmented leg 4 with the first and second exopodal segments bearing 1 and 3 distal spines, but which display a different form of armature on the distal exopodal segment of leg 1, including: having spine 1 reduced (e.g. *C. cresseyorum*), seta 4 shorter than the spines (e.g. *C. pampi*), lacking plumose setae on posterior margin (e.g. *C. lethrinicola*), possessing an accessory process on spine 1 (e.g. *C. amblygenitalis*), or lacking an accessory process on spine 2 and/or spine 3 (e.g. *C. calotomi*).

The genital complex in female caligids can vary in shape somewhat according to the reproductive state of the individual female (Parker *et al.*, 1968; Boxshall, 1974) and it is necessary to allow for potential variability when making comparisons of body proportions between species. The new species has a genital complex that is about as long as wide: allowing for about variability of about 10% eliminates species with a genital complex that is markedly wider than long (length: width ratio $\leq$ 0.8:1) and species where it is markedly longer than wide (L: W ratio $\geq$ 1.2:1). Species exhibiting these shapes are delimited in Table 5, which lists species in order from a "broad" to an "elongate" genital complex.

Only 18 species share a genital complex with a L: W ratio between 0.9:1 and 1.1:1. Four of these, *C. absens*, *C. hamruri*, *C. thyrsitae* and *C. longiabdominis*, have an abdomen that is at least twice as long as wide, compared to 1.4 times in the new species. Another seven species, *C. aduncus*, *C. antennatus*, *C. pseudokalumai*, *C. rogercresseyi*, *C. scribae*, *C. stokesi* and *C. tetrodontis*, have a genital complex that is at least 2.4 times longer than the abdomen, compared to 1.7 times in the new species.

The remaining seven species can be compared in more detail. *Caligus dampieri* is an Australian species found on single host species, *Acanthopagrus latus*, caught at Port Samson in Western Australia (Byrnes, 1987). Both of these species share the presence of a pair of crescent-shaped membranes on the surface of the distal endopodal segment of leg 2.The most obvious difference between these two species is the wide gape between the divergent tines of the sternal furca in *C. dampieri* compared to the parallel to slightly convergent tines in the new species. The two segments of the exopod of leg 4 are subequal in the new species whereas in *C. dampieri* the second segment is markedly longer than the first. An additional minor difference is the size of the posterior process on the antenna.

Caligus itacurussensis was found on *Atherinella brasiliensis* (Quoy & Gaimard, 1825) (as *Xenomelaniris brasiliensis*) in Sepetiba Bay, Brazil (Luque & Cezar, 2000). It differs from the new species in having relatively shorter tines on the post-antennal process and the maxillule. The tines on the sternal furca are also shorter and are distinctly divergent rather than parallel, as in the new species. In addition the first exopodal segment of *C. itacurussensis* has a slightly curved outer spine and lacks marginal membrane, whereas the new species has a straight spine and the outer margin is ornamented with membrane.

Caligus latus was also found at Port Samson on *Acanthopagrus latus* (Byrnes, 1987). Comparison is handicapped by lack of information on some of the appendages but the female genital complex is 4.0 times wider than the abdomen in *C. latus* but only 2.2 times wider in the new species. The gape between the divergent tines of the sternal furca in *C. latus* is very wide compared to the parallel to slightly convergent tines in the new species.

Shiino's (1959) redescription of *C. macarovi* shows an elongate abdomen that is 1.9 times longer than wide, compared to only 1.4 times in the new species. The exopodal segments of leg 4 are stouter in *C. macarovi* and the outer spines are shorter relative to the apical spine in *C. macarovi* than in the new species. The posterior process on the proximal segment of the antenna and the tines on both the post-antennal process and the maxillule are all shorter and stouter in *C. macarovi* than in the new species.

Caligus wilsoni is a replacement name proposed by Delamare Debouteville & Nuñes-Ruivo (1958) to accommodate material misidentified as *C. belones* Krøyer, 1863 by C.B. Wilson (1905). Comparison with the redescription by Cressey (1991) reveals significant differences in the shape of the sternal furca and in the armature

of leg 2. The short tines of the sternal furca are broad at the base and taper towards the tip whereas in the new species the tines are elongate and do not taper distally. The outer spines on the first and second exopodal segments of leg 2 are directed nearly parallel with the long axis of the ramus in *C. wilsoni* but are reflexed obliquely across the surface of the ramus in the new species.

The recently established *C. solea* is known only from *Solea solea* (Linnaeus, 1758) in the Mediterranean Sea (Demirkale *et al.*, 2014). In *C. solea* the distal segment of the exopod of leg 4 is markedly longer than the proximal whereas the two segments are subequal in the new species. In addition, the spines on this leg in *C. solea* are much shorter and more blade-like than in the new species.

Shiino (1954c) established *C. triangularis* to accommodate material collected from *Halichoeres poecilopterus* (Temminck & Schlegel, 1845) in Japanese waters. It differs from the new species in having relatively short outer spines on the exopodal segments of leg 4: the spine on the proximal exopodal segment reaches only halfway to the tip of the ramus whereas in the new species it almost reaches the tip, and the middle spine on the distal segment is less than half the length of the apical spine compared to 75% in the new species. Spines 1 to 3 are stout in *C. triangularis* but slender in the new species. These detailed comparisons justify the establishment of a new species to accommodate the female from *Hyporhamphus quoyi*.

Caligus lagocephali Pillai, 1961

(Fig. 32)

Syn. *Caligus fugu* Yamaguti & Yamasu, 1959

Material examined. 1♀ from *Lagocephalus lunaris* (Bloch & Schneider, 1801) (TC17942) 6 July 2016, QM Reg. No. W53075; 1♂ (TC 17892) 5 July 2016, QM Reg. No. W53076; 1♂ (TC 17899) 5 July 2016, NHMUK 2017.274; 1♀ (TC17944) 6 July 2016, NHMUK 2017.275.

Site on host. Unknown (in body wash).

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones of dorsal cephalothoracic shield; frontal plates with prominent lunules. Genital complex about 1.3 to 1.4 times longer than wide (Fig. 32A), with narrow anterior neck region; abdomen elongate, about 2.9 times longer than wide; genital complex about 1.3 times longer than abdomen. Antenna with tapering posterior process (Fig. 32B). Post-antennal process simple, tine slender, short and strongly recurved; associated papillae bisensillate. Anterior papilla of maxillule well developed with 1 large and 2 small setae; posterior process simple, tapering, without marginal flange (Fig. 32B). Maxilliped of female with robust proximal segment swollen proximally with transverse ridge and marginal fold in myxal area (Fig. 32C). Sternal furca with divergent tapering tines (Fig. 30D). Distal exopodal segment of leg 1 (Fig. 32E) lacking 3 plumose setae on posterior margin, only single naked vestigial seta present; distal margin spine 1 longer than other spines; spines 2 and 3 each with accessory process; seta 4 as along as spine 1 and ornamented with short pinnules bilaterally. Leg 2 with strong, distally tapering marginal spinules on endopodal segments 2 and 3 (as in *C. ariicolous*, cf. Fig. 18G); outer spines on exopodal segments 1 and 2 very slender, aligned obliquely across surface of ramus (Fig. 32F). Leg 3 with patch of tiny spinules located laterally on apron: first exopodal segment with short straight spine but lacking inner seta; second and third segments armed with I-1; III,4. Leg 4 uniramous, 3-segmented; first and second exopodal segments with I and IV spines, respectively (Fig. 32G). Body length of female 4.16 mm; body length of 2 males 2.65 and 2.88 mm.

Remarks. The valid name of this species has recently changed. In their revision of the *Caligus productus* species group, Boxshall & El-Rashidy (2009) recognized the conspecific status of *C. fugu* Yamaguti & Yamasu, 1959 and *C. lagocephali* Pillai, 1961, and treated the latter as a subjective synonym of the former. However, the subsequent recognition of the generic level synonymy of *Pseudocaligus* A. Scott, 1901 and *Caligus* by Dojiri & Ho (2013), resulted in the recognition of *Caligus fugu* (Yamaguti, 1936) as a senior homonym. So, *Caligus fugu* Yamaguti & Yamasu, 1959 became a junior secondary homonym. According to Özak *et al.* (2013) the oldest available valid name for this taxon is *Caligus lagocephali* Pillai, 1961.

The original description of *Caligus fugu* of Yamaguti & Yamasu (1959) revealed several distinctive characteristics: the tine of the post-antennal process is slender and set at a right angle to the base; the maxilliped has

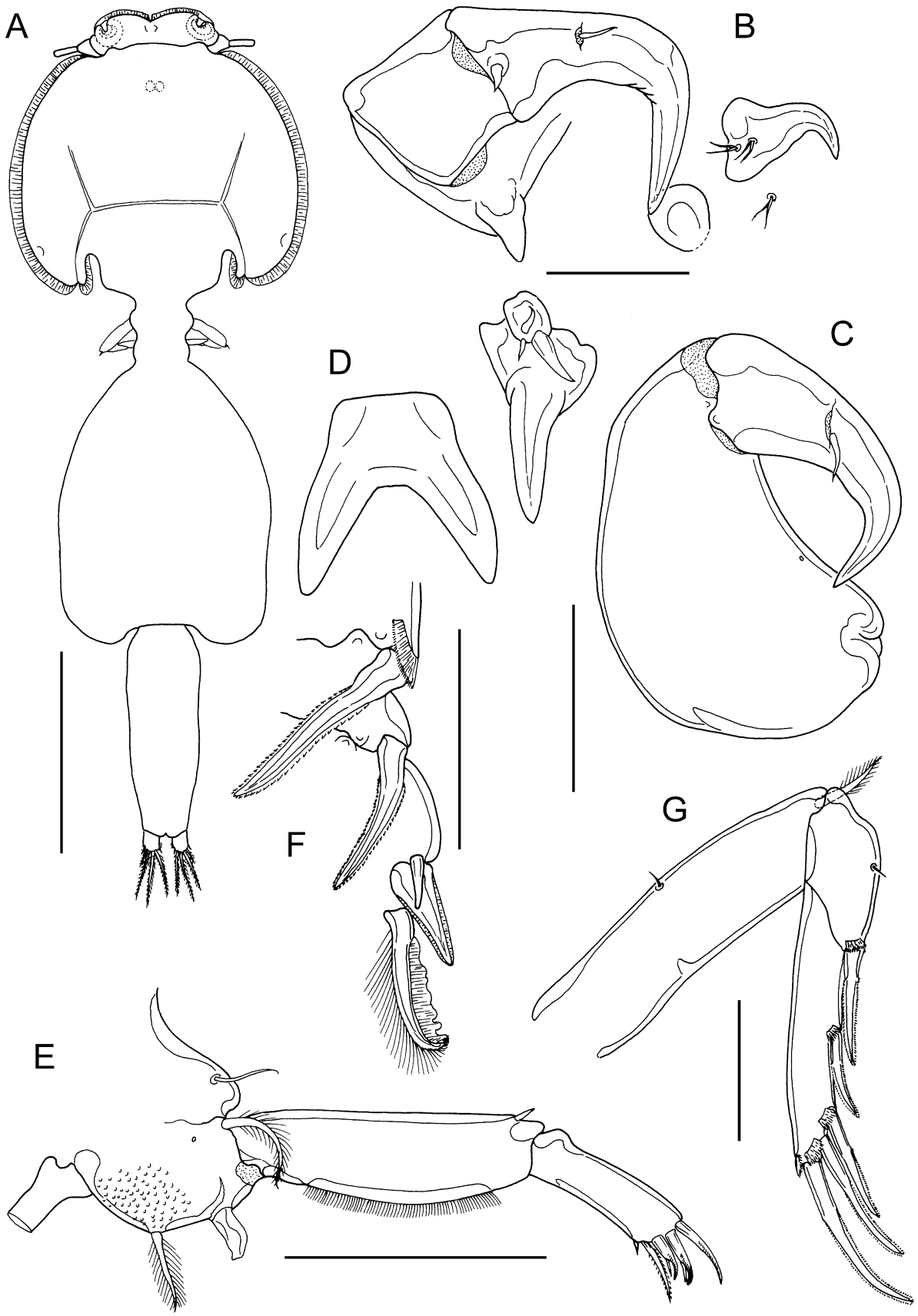

FIGURE 32. *Caligus lagocephali* Pillai, 1961, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, maxilliped; D, sternal furca; E, leg 1; F, outer margin spines on exopod of leg 2; G, leg 4. Scale bars: 1.0 mm on A, 100 μm on B–D, F, G, 200 μm on E.

a robust proximal segment; leg 1 has unusually slender exopodal segments and the outer spines on the exopod of leg 2 are also unusually slender. The Moreton Bay material from *Lagocephalus lunaris* shares these features. There are minor differences such as the structure of the myxal surface of the female maxilliped which is shown as having a pointed process by Yamaguti & Yamasu (1959: Fig. 141). However, this apparent process can be also interpreted as a ridge and marginal fold as figured for the Moreton Bay material (Fig. 32C). The minute vestige of a posterior margin seta on the distal exopodal segment of leg 1 was probably overlooked by Yamaguti & Yamasu (1959). The synonymy proposed by Boxshall & El-Rashidy (2009) of *C. fugu* Yamaguti & Yamasu, 1959 and *C. lagocephali* Pillai, 1961 is maintained here, although this should be verified since the female figured by Pillai (1961) was somewhat damaged, as suggested by Pillai (1985).

The type host of *C. lagocephali* in Indian waters is *Lagocephalus inermis* and the Japanese material described by Yamaguti & Yamasu (1959) was from *Takifugu rubripes* (Temminck & Schlegel, 1850), *T. alboplumbeus* (Richardson, 1845), *T. niphobles* (Jordan & Snyder, 1901) and *T. pardalis* (Temminck & Schlegel, 1850) (as *Spheroides rubripes, S. alboplumbeus, S. niphobles* and *S. pardalis*, respectively). This species (as *C. fugu* Yamaguti & Yamasu, 1959) has also recently been reported in Mediterranean waters, off the Turkish coast, on two Red Sea invasive hosts *Lagocephalus spadiceus* (Richardson, 1845) and *L. suezensis* Clark & Gohar, 1953 (Özak *et al.*, 2012). The new material from Moreton Bay is from *L. lunaris*. It appears that this copepod utilises a range of tetraodontid fishes as hosts.

Caligus laminatus (Rangnekar, 1955)

(Fig. 33)

Syn: *Pseudocaligus laminatus* Rangnekar, 1955

Material examined. 1♀ from *Lagocephalus lunaris* (Bloch & Schneider, 1801) (TC 17944) 06 July 2016, QM Reg. No. W53077.

Site on host. Unknown (in body wash).

Differential diagnosis. Cephalothorax trapezoidal in outline (Fig. 33A), dorsoventrally flattened with well-developed marginal membranes; frontal plates with small lunules. Genital complex rectangular, about 1.5 times longer than wide and about 7.2 times longer than abdomen; abdomen reduced, 1-segmented, wider than long and bearing caudal rami on oblique posterolateral margins. Antenna with broadly rounded posterior margin on proximal segment ornamented with flange (Fig. 33B), without defined process; second segment with striated outer margin; subchela strongly recurved. Post-antennal process with short tine ornamented with surface striations; associated papillae bi- or trisensillate; additional swelling present medial to post-antennal process, ornamented with membranous flange. Posterior process of maxillule simple, ornamented with surface striations (Fig. 33B). Maxilla with short basis (Fig. 33C) bearing inconspicuous membranous flabellum; canna short, not reaching tip of segment; calamus, stout, tapering and bilaterally serrate. Maxilliped of female (Fig. 33D) with 3 rounded ridges basally on proximal segment, surface around ridges wrinkled; myxal area lacking ornamentation; subchela with claw bearing large, blunt-tipped, accessory element, ornamented with short surface setules. Sternal furca with more or less parallel, blunt-tipped tines (Fig. 33E). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal margin spine 1 larger than other spines (Fig. 33F); spines 1, 2 and 3 each with accessory process and with marginal fringe; seta 4 absent. Leg 2 with marginal membrane on outer edge of endopodal segment 1 (Fig. 33G); segments 2 and 3 with short marginal setules; outer margin spines on exopodal segments 1 and 2 aligned closer to longitudinal axis of ramus. Leg 3 apron with medial and lateral patches of spinules; exopod 2-segmented (Fig. 33H); first segment with slightly curved outer spine and with inner plumose seta; compound distal segment with 4 outer spines and 5 plumose setae; first endopodal segment forming small velum, bearing inner seta; compound distal segment with 6 setae. Leg 4 vestigial, represented by small lobe with 2 setae (Fig. 33I). Body length of female 2.92 mm.

Remarks. On the basis of both morphological (Dojiri & Ho, 2013; Özak *et al.*, 2013) and molecular evidence (Freeman *et al.*, 2013), the genus *Pseudocaligus* is no longer considered valid; it is treated as a junior subjective synonym of *Caligus*. *Pseudocaligus laminatus* was formally transferred to *Caligus* by Özak *et al.* (2013).

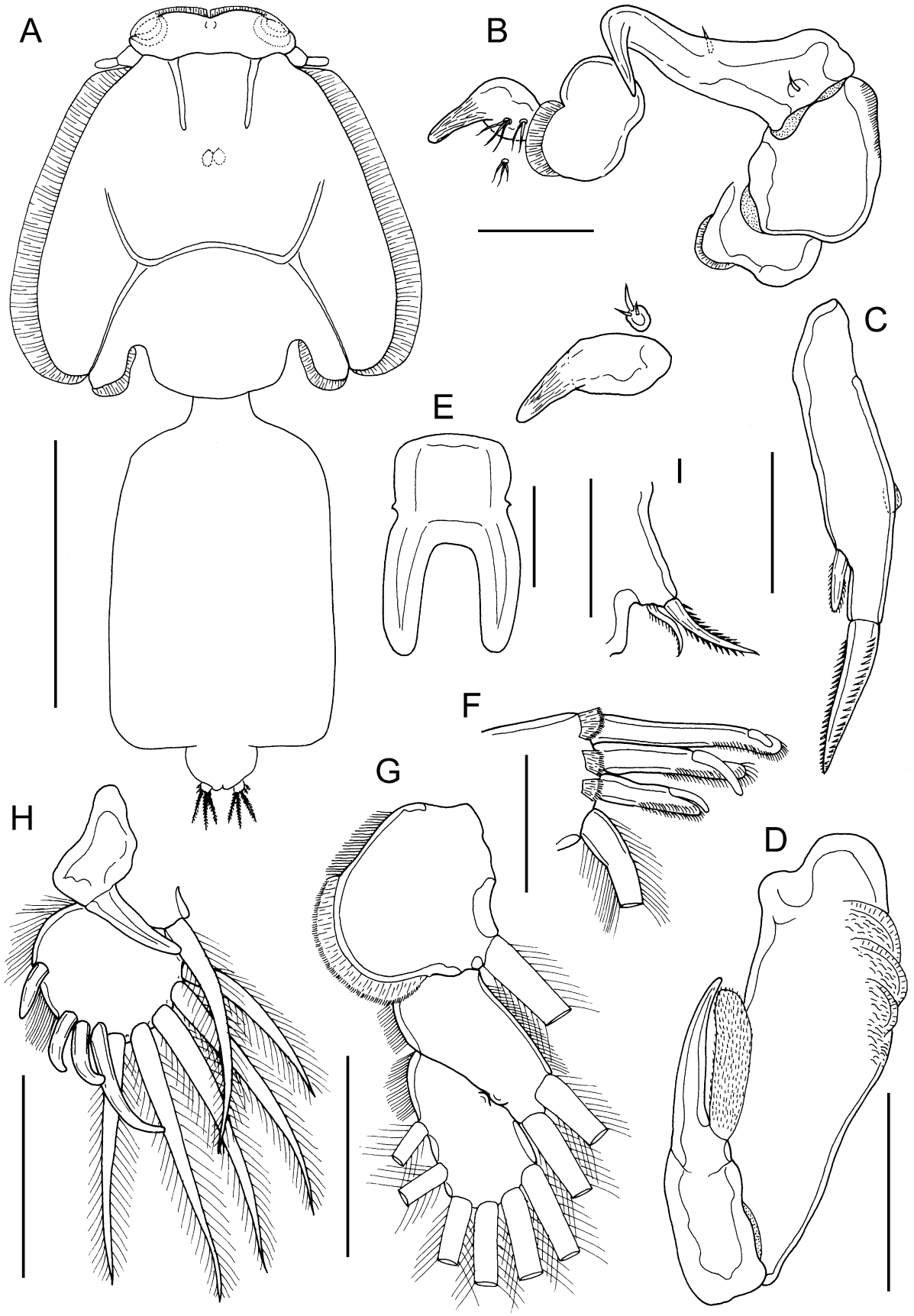

FIGURE 33. *Caligus laminatus* (Rangnekar, 1955), female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, brachium of maxilla; D, maxilliped; E, sternal furca; F, distal armature on exopod of leg 1; G, endopod of leg 2; H, exopod of leg 3; I, reduced leg 4. Scale bars: 1.0 mm on A, 100 µm on B, D, G, H, 50 µm on C, E, F, I.

The type host of *C. laminatus* is *Lagocephalus lunaris* (Rangnekar, 1955a). A single female was subsequently recorded from *Liza macrolepis* (Smith, 1846) caught off Taiwan (Lin & Ho, 2003), although Ho & Lin (2004) expressed some reservations about the conspecificity of their specimen with Rangnekar's species. The Moreton Bay female was also from *L. lunaris* and its features conform closely to the redescription given by Ho & Lin (2004). In particular, it possesses two very unusual shared character states, the absence of seta 4 from the distal exopodal segment of leg 1, and the presence of a large, hirsute, accessory process on the subchela of the maxilliped. I consider that these shared features, plus others such as the tridentate process at the posterolateral corner of the proximal segment of the antennule, serve to validate Ho & Lin's identification. Ho & Lin (2004) noted the presence of the usual 6 setae on the compound distal exopodal segment of leg 3. This was a difference between their Taiwanese specimen and the Indian type material described by Rangnekar (1955a), which was reported as having only 4 setae. The Australian specimen from *L. lunaris* agrees with Ho & Lin's (2004) account, and might indicate that this apparent difference is an inaccuracy in Rangnekar's original description.

There is, however, one minor difference between the previously described material of *C. laminatus* from India and Taiwan, and the Moreton Bay female. Leg 4 was described by Rangnekar (1955a) as bearing 3 apical setae whereas Ho & Lin (2004) showed only a single vestigial seta on the stub of this leg. The Moreton Bay specimen possessed 2 setae on the leg on one side, but the other side was damaged. This character relates to a vestigial limb which is hard to observe; there may be variability but its significance cannot be assessed yet since only single females were found by Ho & Lin (2004) and in the present study. Ho & Lin (2004) stated that the male was unknown, but Rangnekar (1955a) described the male and noted that the maxilliped of the male was similar to that of the female in possessing the large accessory element on the subchela.

The discovery of *C. laminatus* in Australian waters significantly extends its known geographical range, as it had previously been reported only from India and Taiwan. The typical host of this rare copepod is the tetraodontid *L. lunaris*: Rangnekar (1955a) reported "some 20 females and 8 males" from an unspecified number of hosts collected over a period of two months. The Australian record is from the same host, and it seems possible that the single female found on a *Liza macrolepis* landed at the fish market in Dong-shi, Taiwan (Ho & Lin, 2004) might be a contaminant, resulting from transfer after the death of the commercially-caught host.

Caligus laticaudus Shiino, 1960

(Fig. 34)

Material examined. 2♀♀ from *Gnathanodon speciosus* (Forsskål, 1775) (TC17577) 25 June 2016, QM Reg. No. W53078; 2♀♀ (TC17106) 13 January 2016, NHMUK 2017.276–277;1♀ from *Caranx sexfasciatus* Quoy & Gaimard, 1825 (TC17673) 28 June 2016, NHMUK 2017.278; 3♀♀ from *Kyphosus bigibbus* Lacepède, 1801 (TC17792) 1 July 2016, QM Reg. No. W53079; 1♀ (TC17864) 4 July 2016, NHMUK 2017.279;1♂, 1 chalimus from *Heniochus acuminatus* (Linnaeus, 1758) (TC17874) 4 July 2016, NHMUK 2017.280; 1♀ from *Pseudolabrus guentheri* Bleeker, 1862 (TC17662) (in body wash) 27 June 2016, NHMUK 2017.281; 1♀ from *Pagrus auratus* (Forster, 1801) (TC17060) 13 January 2016, NHMUK 2017.282.

Site on host. Roof of mouth.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones of dorsal cephalothoracic shield; frontal plates with small lunules (Fig. 34A). Genital complex about 1.2 to 1.3 times wider than long; abdomen 2-segmented; anterior somite typically distinctly wider and with more strongly convex lateral margins than posterior, but distinction less marked in some specimens; genital complex longer than abdomen, narrowing anteriorly; transverse posterior margin with paired swellings close to base of abdomen. Antenna without posterior process on proximal segment. Post-antennal process with nearly straight tine; associated papillae multisensillate. Maxilliped of female with large myxal process (Fig. 34B). Sternal furca with short, blunt, slightly incurved tines (Fig. 34C). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spine 1 markedly shorter than other spines (Fig. 34D); spines 2 and 3 without accessory processes; seta 4 slightly shorter than spines 2 and 3. Leg 2 with outer margin of first endopodal segment unornamented (Fig. 34E); endopodal segments 2 and 3 with patches of fine setules extending onto ventral surface; outer spines on exopodal segments 1 and 2 aligned close to longitudinal axis of ramus (Fig. 34F); proximal spine on third exopodal segment more than half length of next spine. Leg 3 with 3-segmented exopod (Fig. 34G); first

segment bearing small straight outer spine with cuticular flange at base of spine, lacking inner seta; second segment with small outer spine plus inner seta; third segment with 3 spines increasing in length distally, plus 4 plumose setae. Leg 4 uniramous, 4-segmented; exopodal segments with I; I; III spines; each spine with elongate strip of membrane (modified pecten) on surface of segment adjacent to base (Fig. 34H). Mean body length of female 3.36 mm, range 3.28 to 3.42 mm (based on 8 specimens). Length of adult male 2.51 mm.

Remarks. *Caligus laticaudus* was re-described in detail by Ho *et al.* (2000) based on material from Taiwan. Most of the Moreton Bay material conforms exactly to Ho *et al.*'s description in all aspects of limb structure and armature, and the basic habitus is the same with a conspicuously swollen anterior somite of the indistinctly 2-segmented abdomen. This configuration is the same as in the typical material described from Japan by Shiino (1960), as well as in material from India (Pillai, 1985) and Taiwan (Ho & Lin, 2004). However, the material caught in Moreton Bay on *Pagrus auratus* and *Pseudolabrus guntheri* has a more slender abdomen, with the anterior somite less markedly swollen (Fig. 34A). Material recently described from Korea also had this more slender abdomen (Moon & Kim, 2012), similar to that of the Moreton Bay material. However, in the absence of any other differences, the Moreton Bay material is identified as *C. laticaudus*.

Caligus laticaudus belongs to a group of species referred to here as the *Caligus diaphanus*-group. This group is characterized by numerous shared features including: the lack of a posterior process on the proximal segment of the antenna, a vestigial or weakly developed tine on post-antennal process, the lack of accessory processes on spines 2 and 3 on the distal exopodal segment of leg 1, the alignment of the outer spines of exopodal segments 1 and 2 of leg 2, the presence of patches of fine setules extending over the surface of endopodal segments 2 and 3 of leg 2, and the presence of strips of membrane (modified pectens) associated with each spine on exopodal segments 1 to 3 of leg 4. In addition to *C. diaphanus* von Nordmann, 1832 and *C. laticaudus*, this group also includes: *C. pelamydis* Krøyer, 1863, *C. stromatei* Krøyer, 1863, *C. cybii* Bassett-Smith, 1898, *C. robustus* Bassett-Smith, 1898, *Caligus platytarsis* Bassett-Smith, 1898, *C. rotundigenitalis* Yü, 1933, *C. seriolae* Yamaguti, 1936, *C. tanago* Yamaguti, 1939, *C. pagelli* Delamare Deboutteville & Nunes-Ruivo, 1958, and *C. kapuhili*, 1967. Özak *et al.* (2017) redescribed *Caligus macrurus* Heller, 1865 and reduced *Sciaenophilus* van Beneden, 1852 to synonymy with *Caligus*, thereby transferring the type species, as *C. tenuis* (van Beneden, 1852): both *C. macrurus* and *C. tenuis* share this suite of characters and belong in the *C. diaphanus*-group. The presence of very small accessory processes on spines 2 and 3 on the distal exopodal segment of leg 1 in *C. macrurus* was visualised by scanning electron microscopy (Özak *et al.*, 2017), and similar vestigial processes may be present on spines 2 and 3 in other members of the group even though they appear to be absent under the light microscope. *Caligus kanagurta* Pillai, 1961 has a somewhat atypical leg 4 with the pectens modified as arrays of long setules at bases of exopodal spines but it shares the lack of a posterior process on the antenna, a vestigial or weakly developed tine on post-antennal process, the lack of accessory processes on spines 2 and 3 on the distal exopodal segment of leg 1, the alignment of the outer spines of exopodal segments 1 and 2 of leg 2, and the presence of patches of fine setules extending over the surface of endopodal segments 2 and 3 of leg 2. *Caligus kanagurta* should also be included in the *C. diaphanus*-group.

The males of species in the *C. diaphanus*-group are characterised by the possession of an accessory tine on the sexually dimorphic antenna.

Caligus laticaudus was originally described from Japanese waters (Shiino, 1960) and has since been reported from India (Pillai, 1961), Einewetok Atoll (Lewis, 1968), Taiwan (Ho *et al.*, 2000), China (Ho & Lin, 2004), Korea (Moon & Kim, 2012), and Malaysia (Leong, 1984). This is the first report of *C. laticaudus* from Australian waters.

The type host was *Pagrus major* (Temminck & Schlegel, 1843) (as *Pagrosomus major*) (Shiino, 1960). Pillai (1961) subsequently recorded it from *Filimanus heptadactyla* (Cuvier, 1829) (as *Polynemus heptadactylus*) and *Rhabdosargus sarba* (Forsskål, 1775). According to Ho & Lin (2004), its hosts in Taiwan are *Caranx melampygus* Cuvier, 1833, *Lutjanus vitta* (Quoy & Gaimard, 1824), *L. russellii* (Bleeker, 1849), *Parapristipoma trilineatum* (Thunberg, 1793), *Polydactylus plebeius* (Broussonet, 1782) and *P. sextarius* (Bloch & Schneider, 1801). Other hosts include *Acanthurus olivaceus* Bloch & Schneider, 1801, *Evynnis japonica* Tanaka, 1931, *Parastromateus niger (*Bloch, 1795) (as *Formio niger*), and *Liza haematocheila* (Temminck & Schlegel, 1845). All six of the host species reported here are new host records.

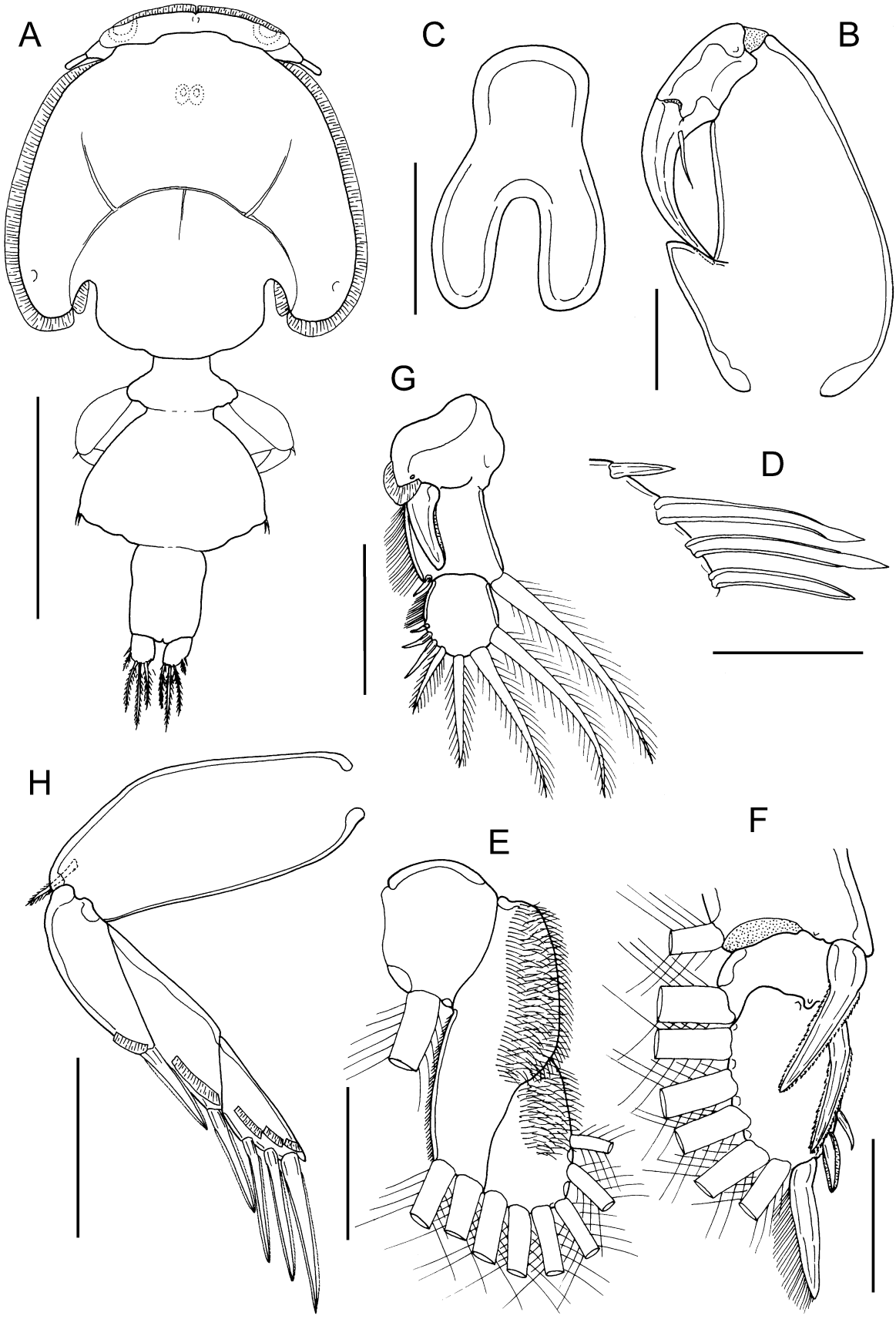

FIGURE 34. *Caligus laticaudus* Shiino, 1960, female. A, habitus, dorsal; B, maxilliped; C, sternal furca; D, distal margin armature on exopod of leg 1; E, endopod of leg 2; F, exopod of leg 2; G, exopod of leg 3; H, leg 4. Scale bars: 1.0 mm on A, 100 µm on B, C, E–G, 200 µm on H, 50 µm on D.

***Caligus longipedis* Bassett-Smith, 1898**
(Fig. 35)

Syn: *Caligus lucidus* Heegaard, 1962

Material examined. 1♀ from *Gerres* sp. juveniles (caught by seine net from shore at Adams Beach, North Stradbroke Island) on 26 June 2016, QM Reg. No. W53080.

Site on host. Body surface.

Differential diagnosis. Cephalothorax dorsoventrally flattened with slightly irregular lateral margins (Fig. 35A) bearing well-developed marginal membranes; frontal plates with well-developed lunules. Genital complex about 1.6 times wider than long, produced into slight postero-lateral lobes; abdomen 1-segmented, about 1.3 times longer than wide; genital complex about 2.0 times longer than abdomen. Caudal rami about 2 times longer than wide. Antenna with posterior process (Fig. 35B) on proximal segment; distal subchela with striations on surface. Post-antennal process weakly curved; associated papillae unisensillate, sensillae long (Fig. 35C). Posterior process of maxillule simple, ornamented with surface striations (Fig. 35D). Maxilla with distal margin of brachium spinulate (Fig. 35E). Maxilliped of female with smooth myxal margin and short claw on subchela. Sternal furca with short, spatulate tines (Fig. 35F). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spine 1 simple and slightly shorter than other spines; spines 2 and 3 each with accessory process; seta 4 about 1.4 times longer than spines 2 and 3. Leg 2 with patches of setules extending onto surface of endopodal segment 2; segment 3 with raised patch of setules and 2 striated crescentic membranes on surface (Fig. 35G); outer spines on exopodal segments 1 and 2 aligned obliquely across surface of ramus. Leg 3 exopod 3-segmented; first segment with short almost straight spine ornamented with lateral strip of membrane and ornamented with membranous flange along outer margin, lacking inner seta. Leg 4 uniramous, 3-segmented (Fig. 35H); exopodal segments 1 and 2 with I and III long spines, respectively, each ornamented with narrow strips of smooth membrane. Body length of female 5.36 mm.

Remarks. This is a large and distinctive species of *Caligus* readily characterized by the possession of posterolateral lobes on the female genital complex, in combination with the elongate spines on the exopod of leg 4, the spatulate tines of the sternal furca, the ornamentation of the distal margin of the maxilla and the presence of crescentic membranes on the third segment of the endopod of leg 2. The male described by Ho & Lin (2004) is not conspecific with the female; the true male of *C. longipedis* was redescribed by Venmathi Maran *et al.* (2009).

Caligus longipedis is widely distributed: having been reported from across the Atlantic and the Indo-Pacific, including from Aden (Bassett-Smith, 1898a), Belize (Cressey, 1991), Mexico (Shiino, 1959, as *C. amplifurcus* Pearse, 1953; Morales-Serna *et al.*, 2014), Florida (USA) (Pearse, 1953, as *C. amplifurcus*), Hawaii (Lewis, 1967), India (Gnanamuthu, 1950, as *C. scabiei*), Japan (Kubota & Takakuwa, 1963), Korea (Moon & Kim, 2012), Malaysia (Venmathi Maran *et al.*, 2009), and Taiwan (Ho & Lin, 2004). This species has also been reported from Australian waters by Heegaard (1962), under the name *Caligus lucidus* (Table 1), and by Catalano & Hutson (2010) from *Arripis truttaceus*.

This copepod is most commonly reported as a parasite of carangids including *Caranx melampygus*, *C. hippos*, *C. caninus*, *C. crysos* (Mitchill, 1815), *C. lugubris* Poey, 1860, *Carangoides chrysophrys* (Cuvier, 1833), *Megalaspis cordyla* (Linnaeus, 1758), *Pseudocaranx dentex* (Bloch & Schneider, 1801), *Selene vomer* (Linnaeus, 1758) and *Seriola* sp. However, it has been reported from a range of other fish families including: Acanthuridae, Haemulidae, Ostraciidae, Paralichthyidae, Pomacanthidae, Scaridae and Serranidae (Cressey, 1991). In Australian waters Heegaard (1962) recorded it from *Nelusetta ayraud* (Quoy & Gaimard, 1824) (as *Cantherhines ayraud*) (Monacanthidae) at Cape Hawke (New South Wales); Catalano & Hutson (2010) reported it from *Arripis truttaceus* off the southeastern coast, and the new record from Moreton Bay was from juvenile *Gerres* (Gerreidae). *Caligus longipedis* is known to be a pest of the carangid *Pseudocaranx dentex* cultured in Japanese waters (Ogawa, 1992).

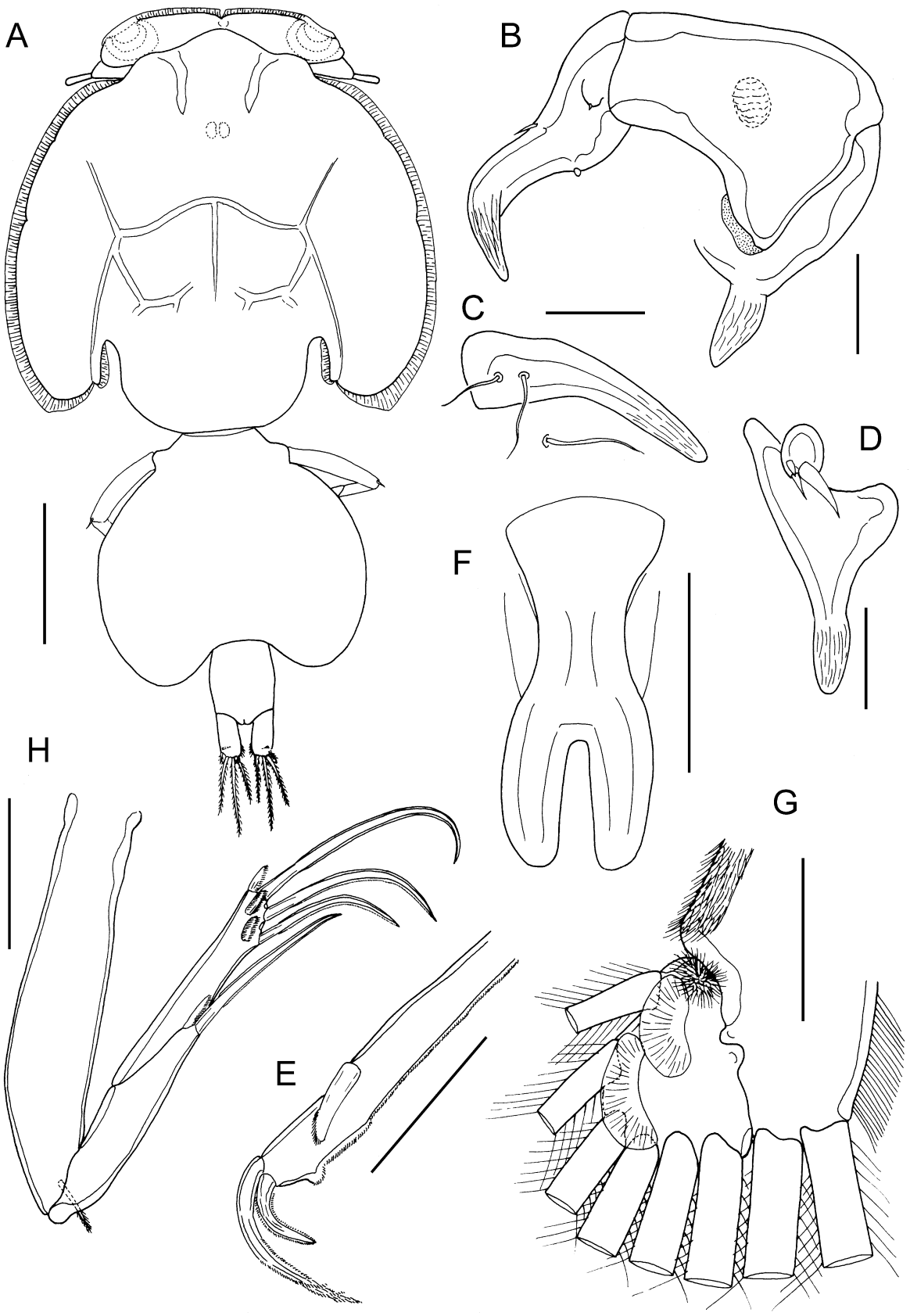

FIGURE 35. *Caligus longipedis* Bassett-Smith, 1898, female. A, habitus, dorsal; B, antenna; C, post-antennal process; D, maxillule; E, distal part of maxilla; F, sternal furca; G, distal part of endopod of leg 2; H, leg 4. Scale bars: 1.0 mm on A, 100 μm on B–D, G, 200 μm on E, F, 250 μm on H.

***Caligus malabaricus* Pillai, 1961**
(Fig. 36)

Material examined. 1♀ from *Hyporhamphus regularis ardelio* (Whitley, 1931) (TC 17757), 30 June 2016, QM Reg. No. W53081.

Site on host. Floor of mouth.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones of dorsal cephalothoracic shield; frontal plates with large lunules. Genital complex with constricted anterior region (Fig. 36A); about 1.1 times longer than wide, and about 1.4 times longer than abdomen. Abdomen about 2.7 times longer than wide, indistinctly 2-segmented, first segment about 3.5 times longer than second. Genital complex and abdomen together about 1.4 times longer than cephalothorax. Antenna with posterior process on proximal segment (Fig. 36B). Post-antennal process with curved tine; associated papillae bisensillate, papilla on ventral cephalothoracic surface trisensillate. Posterior process of maxillule simple (Fig. 36B). Maxilliped of female with 2 small processes on myxal surface. Sternal furca with divergent tines with truncated tips (Fig. 36C). Distal exopodal segment of leg 1 (Fig. 36D) with 3 plumose setae on posterior margin; distal spine 1 markedly longer than other spines; spines 2 and 3 each with accessory process; seta 4 unilaterally plumose, longer than spine 1 and longer than segment. Leg 2 ornamented with strong spinules along outer margins of endopodal segments 1 and 2 (Fig. 36E); outer spines on exopodal segments 1 and 2 aligned obliquely across surface of ramus (Fig. 36F); proximal outer spine on third segment small, bilaterally serrate, distal spine twice as long and with membranes bilaterally. Leg 3 apron with ornamentation of fine spinules laterally and area of spinules medially; exopod 3-segmented (Fig. 36G); first exopodal segment with slightly curved outer spine, without inner seta; second with outer spine and inner plumose seta; third with 3 outer spines and 4 plumose setae. Leg 4 uniramous, 3-segmented (Fig. 36H); first and second exopodal segments armed with I and IV spines, respectively. Body length of female 3.71 mm.

Remarks. This species was established by Pillai (1961) based on two females collected from the buccal cavity of *Tylosurus crocodilus* caught off Trivandrum, India. It was next reported from *Ablennes hians* (Valenciennes, 1846) caught in the Torres Strait, off Northern Australia, by Cressey & Collette (1970) who noted that the female was ornamented with paired patches of fine spinules posterolaterally on the anal somite. The Indian females were 4.4 mm in length (Pillai, 1961), whereas the Australian females were smaller, ranging in length from 3.60 mm to 4.13 mm. These are the only published records of *C. malabaricus* and both are from belonid hosts.

The Moreton Bay female from *Hyporhamphus regularis ardelio* was dark brown in colour and it retained this coloration even after preservation in ethanol. It was 3.71 mm in length and agreed with the description of Pillai (1961) in detailed features of the paired appendages, such as the configuration and ornamentation of the setal elements on the distal exopodal segment of leg 1, the size and alignment of the spines on the exopods of legs 2 and 4, and the shape and ornamentation of the antenna, post-antennal process and maxilla. The denticles along the margin of the second endopodal segment of leg 2 are shown by Pillai (1961: Fig. 13L) as stouter than in the Moreton Bay female, but this difference may be due to the style of illustration. The genital complex and abdomen illustrated by Pillai (1961) are both broader than in the Moreton Bay female, generating some uncertainty about this identification. The only supplementary illustration of *C. malabaricus*, provided by Cressey & Collete (1970: Fig. 118), confirms that the 2-segmented abdomen has a broad anterior somite, more than twice as wide as the small anal somite. In the Moreton Bay female the anterior somite is relatively narrower (Fig. 36A), only 1.4 times wider than the anal somite, however, close examination reveals that its surface is unusually wrinkled which I interpret as evidence that the abdomen in this species, as well as the genital complex, might vary according to the reproductive state of the female. Because of this, the identification of this female as *C. malabaricus* is tentative, and any future revision should take into consideration the additional, similar-looking material from belonids, reported by Cressey & Collette (1970) as *Caligus* species A, C and D.

***Caligus nataliae* sp. nov.**
(Figs. 37–38)

Type material. Holotype ♀, 1 immature ♂ paratype, from *Herklotsichthys castelnaui* (Ogilby, 1897) (TC17275—pooled data from 24 hosts) 19 January 2016, QM Reg. Nos Holotype ♀ W53082, 1 immature ♂ paratype

W53083;1 paratype ♀ from *Neoarius graeffei* (Kner & Steindachner, 1867) (TC17597) 26 June 2016, QM Reg. No. W53084.1 paratype ♀ (TC17881) 4 July 2016, NHMUK Reg. No. 2017.283.

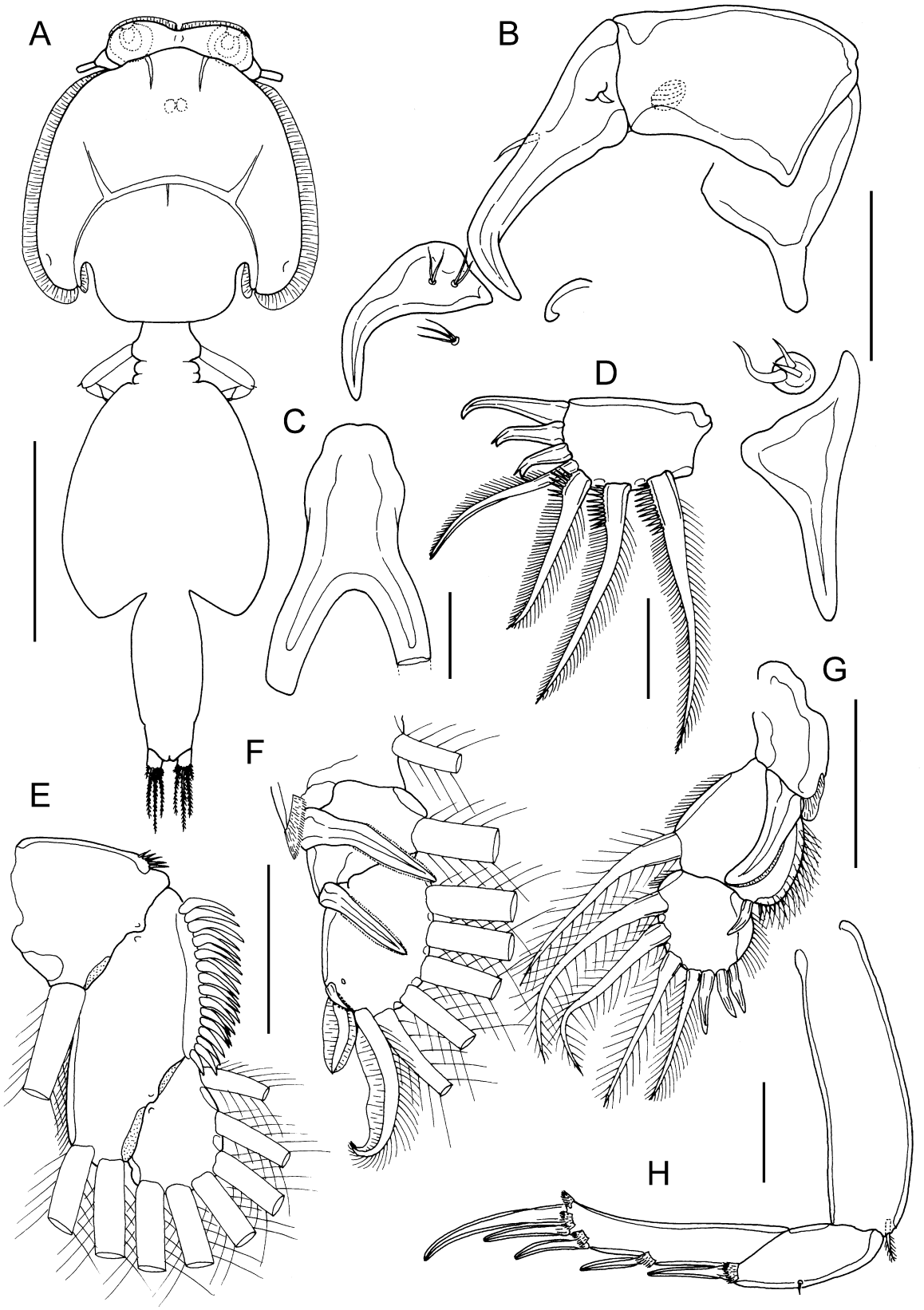

FIGURE 36. *Caligus malabaricus* Pillai, 1961, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, sternal furca; D, distal segment of exopod of leg 1; E, endopod of leg 2; F, exopod of leg 2; G, exopod of leg 3; H, leg 4. Scale bars: 1.0 mm on A, 100 µm on B, E–H, 50 µm on C, D.

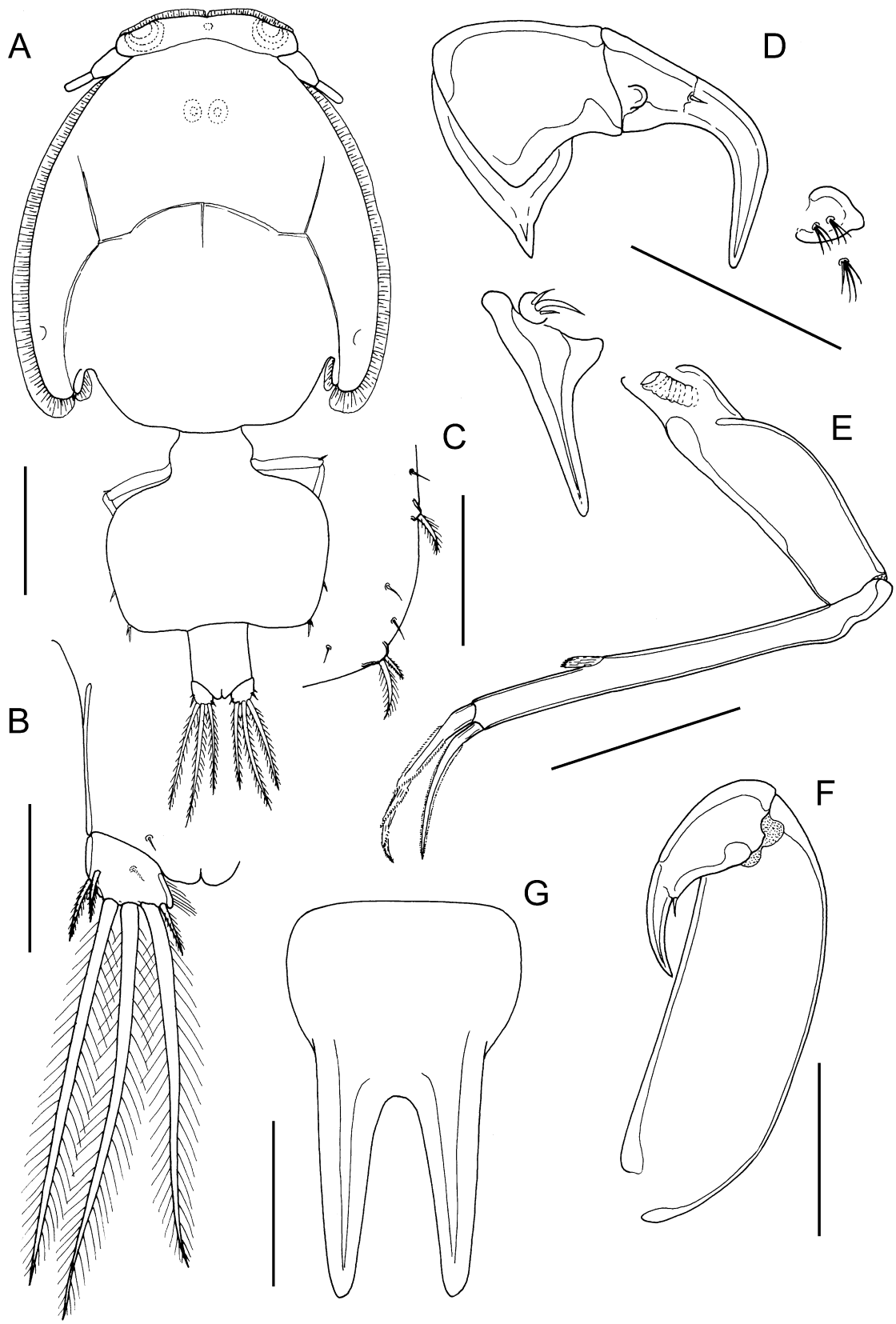

FIGURE 37. *Caligus nataliae* **sp. nov.** paratype female. A, habitus, dorsal; B, caudal ramus, ventral; C, left corner of genital complex showing fifth leg, ventral; D, antenna, post-antennal process and maxillule drawn *in situ*; E, maxilla; F, maxilliped; G, sternal furca. Scale bars: 250 µm on A, 200 µm on B–F, 100 µm on G.

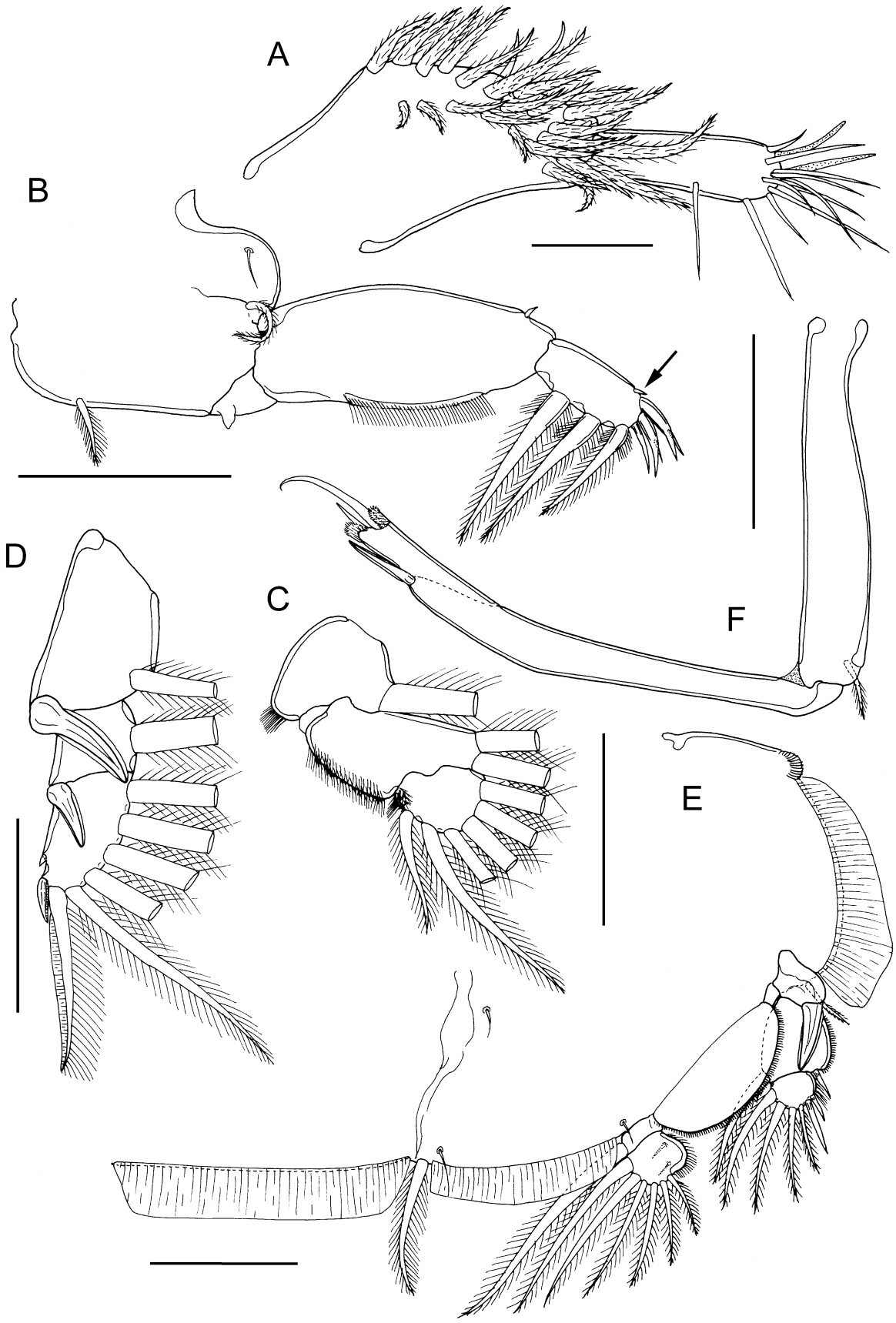

FIGURE 38. *Caligus nataliae* **sp. nov.** paratype female. A, antennule, ventral; B, leg 1, anterior view with reduced spine 1 arrowed; C, endopod of leg 2, anterior; D, exopod of leg 2, anterior; E, leg 3, ventral; F, leg 4. Scale bars: 100 µm on A, 200 µm on B–F.

Type Host. *Herklotsichthys castelnaui* (Ogilby, 1897).

Site on host. Body surface.

Etymology. The new species is named after Mrs Natalie Latham, in gratitude for all her help with curating and labeling copepods for accession into the NHM collections.

Description. Adult female (Fig. 37A) mean body length including caudal rami 5.97 mm (range 5.29 to 6.56 mm) (based on 3 specimens). Cephalothorax about 1.2 times longer than wide; comprising about 60% of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly just beyond rear margins of lateral portions. Lunules present ventrally on frontal plates. Genital complex about 1.5 times wider than long with linear lateral margins, narrowing slightly posteriorly (Fig. 37A). Genital complex about 2.0 times longer than abdomen. Abdomen 1-segmented, about 1.3 times longer than wide; carrying paired caudal rami distally; anal slit terminal. Surface of genital complex, abdomen and caudal rami ornamented with sparsely scattered sensillae (Figs. 37B, C). Caudal rami wider than long (Fig. 37B), measured at midpoints of margins: each ramus armed with short hirsute seta at inner distal angle, slightly longer hirsute seta at outer distal angle, short hirsute seta located just ventral to outer distal seta, and 3 plumose setae on distal margin.

Antennule (Fig. 38A) 2-segmented; proximal segment with 25 plumose setae along anteroventral margin and 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 37D) comprising proximal segment with short sharply-pointed, posteriorly-directed spinous process; middle segment subrectangular, tapering slightly distally, unarmed; terminal segment forming recurved claw bearing sclerotized swelling proximally, and armed with slender distal seta near anterior margin. Post-antennal process (Fig. 37D) vestigial, ornamented with 2 trisensillate papillae on basal part; plus single multisensillate papilla on adjacent ventral cephalothoracic surface.

Mandible of typical stylet-like structure, with 12 marginal teeth. Maxillule (Fig. 37D) comprising anterior papilla bearing 3 unequal, naked setae and elongate, slender posterior process. Maxilla 2-segmented (Fig. 37E), comprising elongate syncoxa and basis: syncoxa unarmed, bearing opening of maxillary gland; basis bearing subapical membranous flabellum on anterior margin and terminating in 2 subequal, claw-like elements (calamus and canna). Calamus just longer than canna, ornamented with strips of serrated membrane arranged obliquely around surface; canna with linear strips of serrated membrane. Maxilliped subchelate (Fig. 37F); slender proximal segment unarmed; distal subchela with small apical claw separated from proximal segmental part by incomplete suture; segmental part armed with 1 small seta.

Sternal furca (Fig. 37G) with tapering parallel tines.

First swimming leg pair (Fig. 38B) with sympods joined by slender intercoxal sclerite; sympod with inner and outer plumose setae; endopod represented by unarmed process on posterior margin of basis. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment robust, about 2.3 times longer than wide and armed with small outer (anterior) spine and ornamented with setule row along mid-section of posterior margin; compound distal segment armed with 3 long plumose setae along posterior margin and 4 distal elements: distal margin elements as follows: spine 1 (anterior-most) short and naked (arrowed in Fig. 38B); spines 2 and 3 equal in length, both with accessory process; seta 4 naked, slightly shorter than spine 3, and markedly shorter than segment.

Second leg biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by plate-like intercoxal sclerite bearing marginal membrane posteriorly. Coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Endopodal segments 1 and 2 (Fig. 38C) armed with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; outer margins of all endopodal segments ornamented with fine setules, extending onto surface of second and third segments. Exopodal segments 1 and 2 (Fig. 38D) each with inner plumose seta and large reflexed outer spine extending obliquely across ventral surface of ramus; outer spines ornamented with bilateral membranous strips; first exopodal segment bearing flap of membrane anteriorly, reflexed back over dorsal surface; segment 3 with 2 outer spines (proximal spine minute, distal spine curved with inner marginal membrane), apical spine with marginal membrane laterally and pinnules medially, plua 5 inner plumose setae.

Third leg pair (Fig. 38E) forming flattened plate closing posterior part of cephalothoracic sucker, as typical for genus. Protopodal part flattened joined by plate-like, intercoxal sclerite forming apron, ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate, and outer plumose seta dorsal to base of exopod; sensillae located adjacent to inner coxal seta and

adjacent to origin of endopod; with corrugated expansion anterior to lateral margin membrane. Exopod 3-segmented; first segment armed with almost straight outer claw directed over ventral surface of ramus, lacking inner seta; second segment with slender outer spine and inner plumose seta; third with 7 setal elements (3 outer spiniform elements and 4 inner plumose setae); outer margins of segments 2 and 3 ornamented with rows of slender setules. Endopod 2-segmented; first segment forming flap-like velum ornamented with row of fine setules along free margin, and with inner plumose seta; compound distal segment with expanded and setulate lateral margin, bearing 6 setal elements increasing in length from outermost to innermost, ornamented with 2 sensillae on dorsal surface.

Fourth leg (Fig. 38F) 3-segmented, comprising slender protopodal segment and indistinctly 2-segmented exopod; exopodal segments separated by oblique articulation visible on dorsal surface only: protopodal segment armed with outer seta; first exopodal segment longer than protopodal segment, armed with slender outer spine reaching to tip of ramus; distal segment short armed with 2 unequal naked spines on apex, each with pecten at base.

Fifth leg located posterolaterally on ventral surface near margin of genital complex, represented by anterior plumose seta on papilla and posterior papilla bearing 2 unequal plumose setae representing exopod (Fig. 37C).

Remarks. This unusual species displays a number of distinctive features. The form of the 3-segmented leg 4 is unique. The first exopodal segment of leg 4 is longer than the protopodal segment and the second exopodal segment is very short and armed with only 2 spines. Only five species of *Caligus* have a 3-segmented leg 4 bearing only 2 spines on the second exopodal segment: *C. centrodonti* Baird, 1850, *C. epidemicus*, *C. labracis* T. Scott, 1902, *C. mortis* Kensley, 1970, and *C. sensorius*. In *C. centrodonti, C. epidemicus* (Fig. 28E) and *C. sensorius* the first exopodal segment is shorter than the second, while in *C. labracis* and *C. mortis* the first and second segments (as measured along the inner margin) are about equal in length. Only the new species has a leg 4 exopod with the first segment more than twice as long as the second segment, and armed with I, II spines.

Other unusual features of *C. nataliae* **sp. nov.** include the vestigial post-antennal process, the long canna on the tip of the maxilla (almost as long as the calamus), the linear tapering tines of the sternal furca, plus the reduction of spine 1 on the distal margin of the exopod of leg 1. Each of these character states is found in other species of *Caligus*, but in no other species are they combined. When sorting these caligids freshly caught, they could be recognised by the distinctive exopod of leg 3: the second segment is relatively long (compared to the first and third segments) and the outer spine on the first segment is linear and extends the entire length of the second segment.

In Moreton Bay the new species was found on two unrelated hosts, a pelagic clupeid, *Herklotsichthys castelnaui,* and a bottom-living ariid, *Neoarius graeffei*.

Caligus neoaricolus sp. nov.

(Figs. 39–41)

Type material. Holotype ♀, 14 paratype ♀♀, 12 paratype ♂♂, 1 immature ♀ paratype from *Neoarius graeffei* (Kner & Steindachner, 1867) (TC17881) 4 July 2016, QM Reg. Nos Holotype ♀ W53085, 1 paratype ♀♀ and 1 immature ♀ paratype W53086, 6 paratype ♂♂ W53087; 7 paratype ♀♀ and 6 paratype ♂♂ NHMUK 2017.283–292; 1 paratype ♂ from (TC17597) 26 June 2016, 1 paratype ♂ from (TC17624) 27 June 2016.

Additional non-type material. 1♀ from *Netuma proxima* (Ogilby, 1898) (TC18830) 01 August 2017, NHMUK 2017.294. 1♀ (possible contaminant) from *Sillago maculata* Quoy & Gaimard, 1824 (TC17904) 5 July 2016;1♂ incomplete (possible contaminant) from *Gerres* sp, juveniles (collected 26 June 2016).

Type Host. *Neoarius graeffei* (Kner & Steindachner, 1867).

Site on host. Body surface.

Etymology. The name of this species alludes to the genus of the type host.

Description. Adult female (Fig. 39A) mean body length including caudal rami 5.91 mm (range 5.73 to 6.24 mm) (based on 10 specimens). Cephalothorax about 1.18 times longer than wide; comprising about 54% of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly just beyond rear margins of lateral portions. Lunules present ventrally on frontal plates. Genital complex 1.13 times longer than wide; narrowing slightly anteriorly and with linear lateral margins (Fig. 39A). Genital complex about 1.4 times longer than abdomen. Abdomen 1-segmented, about 2.0 times longer than wide; carrying paired caudal rami distally; anal slit terminal. Caudal rami longer than wide, measured at midpoints of margins. Each ramus armed with short hirsute seta at inner distal angle, slightly longer hirsute seta at outer distal angle, minute hirsute seta

located just ventral to outer distal seta, and 3 plumose setae on distal margin.

Antennule (Fig. 39B) 2-segmented; proximal segment with 25 plumose setae along anteroventral margin and 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 39C) comprising proximal segment with small sharply-pointed, posteriorly-directed spinous process; middle segment subrectangular, unarmed; terminal segment forming strongly curved claw with proximal sclerotized swelling bearing small seta, and armed with stout distal seta. Post-antennal process (Fig. 39C) weakly curved, ornamented with 2 multisensillate papillae on basal part; plus single multisensillate papilla on adjacent ventral cephalothoracic surface.

Mandible of typical stylet-like structure, with 12 marginal teeth (Fig. 39D). Maxillule (Fig. 39C) comprising anterior papilla bearing 3 small naked setae and slender, tapering posterior process. Maxilla comprising elongate syncoxa and basis: syncoxa unarmed but bearing opening of maxillary gland; basis bearing subapical membranous flabellum on anterior margin, and terminating in 2 subequal, claw-like elements (calamus and canna) (Fig. 39E): calamus just longer than canna, ornamented with strips of serrated membrane arranged obliquely around surface; canna with linear strips of serrated membrane. Maxilliped subchelate (Fig. 39F); slender proximal segment with fine transverse ridges on myxal surface; distal subchela with small inner seta.

Sternal furca (Fig. 39G) with weakly divergent, tapering tines.

First swimming leg pair (Fig. 40A) with sympods joined by slender intercoxal sclerite; sympod with inner and outer plumose setae; endopod represented by unarmed process on posterior margin of basis, bearing minute vestiges of 2 setae apically. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment robust, about 2.5 times longer than wide and armed with small outer (anterior) spine and ornamented with setule row along mid-section of posterior margin; second segment armed with 3 long plumose setae along posterior margin and 4 distal elements. Distal margin elements as follows: spine 1 (anterior-most) longest and naked; spine 2 longer than spine 3, each with accessory process; seta 4 twice as long as spine 1 and longer than segment.

Second leg biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by plate-like intercoxal sclerite bearing marginal membrane posteriorly; armed with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segments 1 and 2 each with inner plumose seta and large reflexed outer spines extending obliquely across ventral surface of ramus (Fig. 40B); outer spines ornamented with bilateral membranous strips; first exopodal segment bearing flap of membrane anteriorly, reflexed back over dorsal surface; segment 3 with 2 outer spines, proximal spine small, distal spine ornamented with membrane; apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. Endopodal segments 1 and 2 armed with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; outer margins of all endopodal segments ornamented with fine setules.

Third leg pair (Fig. 40C) forming flattened plate closing posterior part of cephalothoracic sucker, as typical for genus. Protopodal part flattened joined by plate-like, intercoxal sclerite forming apron, ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate, and outer plumose seta dorsal to base of exopod; sensillae located adjacent to inner coxal seta and adjacent to origin of endopod. Exopod indistinctly 3-segmented; first segment armed with straight outer claw directed parallel with long axis of ramus and overlying lateral margin, lacking inner seta; second and third segments incompletely separated by partial suture; armed with slender outer spine and inner plumose seta derived from second segment and 3 outer spiniform elements and 4 inner plumose setae (derived from third segment); outer margins of segments 2 and 3 ornamented with rows of slender setules. Endopod 2-segmented; first segment expanded to form flap-like velum closing off space between rami, velum ornamented with row of fine setules along free margin; segment armed with inner plumose seta; compound distal segment with expanded and setulate lateral margin; bearing with 6 setal elements increasing in length from outermost to innermost.

Fourth leg (Fig. 40D) 3-segmented, comprising slender protopodal segment and 2-segmented exopod; exopodal segments separated by oblique articulation: protopodal segment armed with outer plumose seta; first exopodal segment armed with short outer spine; second segment armed with short lateral spine and 3 unequal spines along distal margin; all spines with pecten at base.

Fifth leg located posterolaterally on margin of genital complex, represented by anterior plumose seta on papilla and posterior papilla bearing 2 unequal plumose setae representing exopod (Fig. 39H).

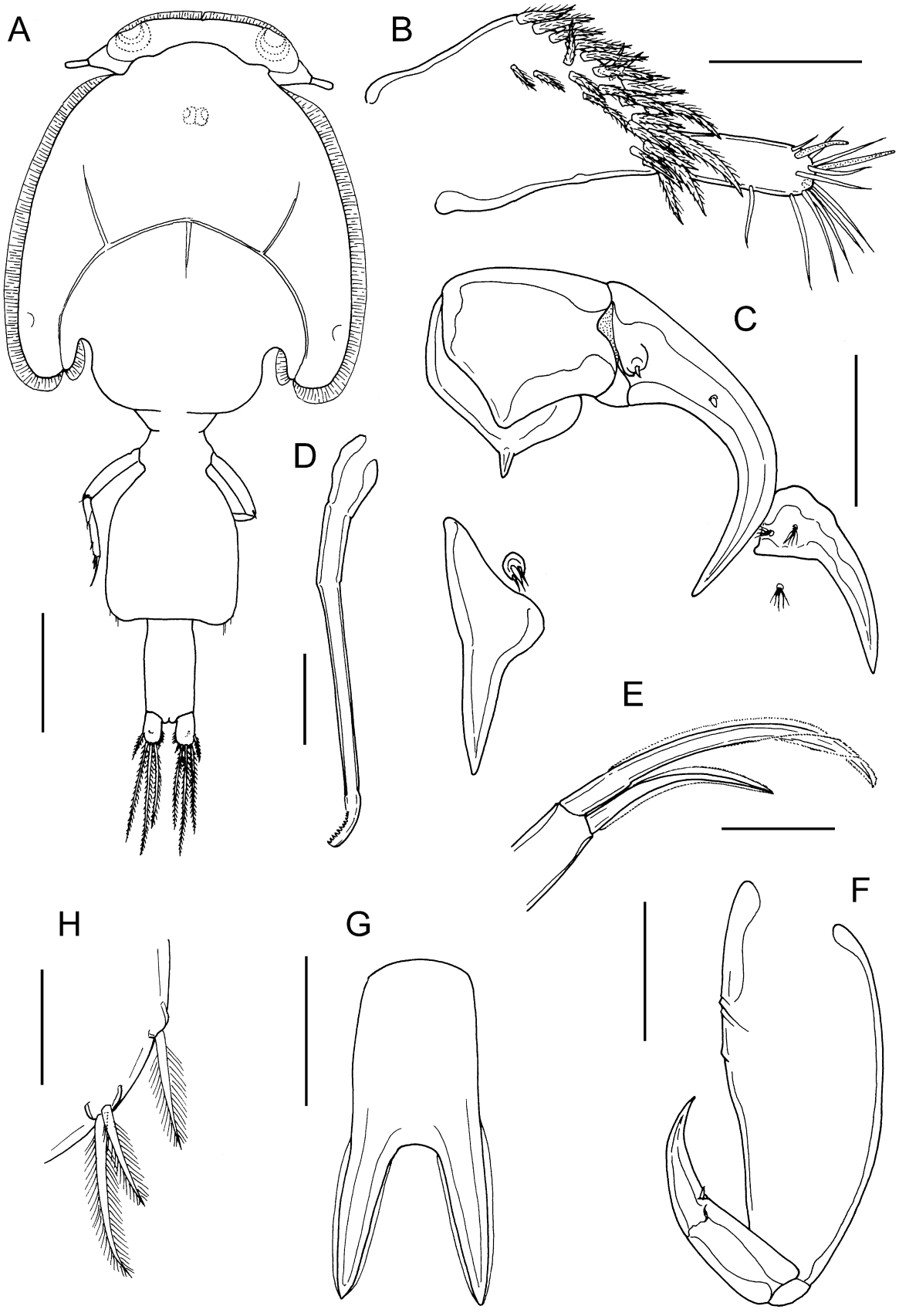

FIGURE 39. *Caligus neoaricolus* **sp. nov.** paratype female. A, habitus, dorsal; B, antennule, ventral; C, antenna, post-antennal process and maxillule drawn *in situ*; D, mandible; E, tip of maxilla; F, maxilliped; G, sternal furca; H, left corner of genital complex showing fifth leg, ventral. Scale bars: 1.0 mm on A, 200 µm on B, C, G, 250 µm on F, 100 µm on D, E, H.

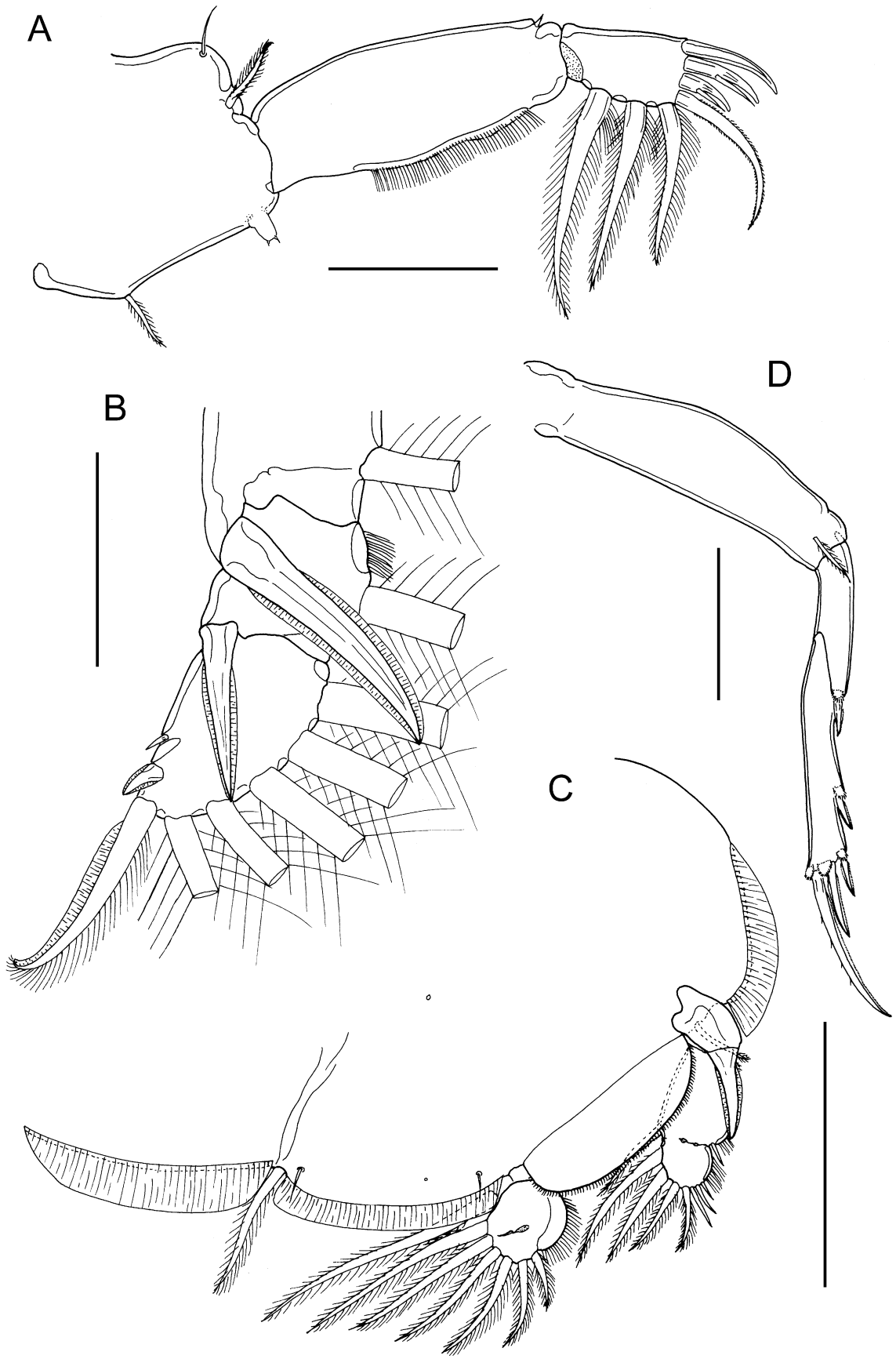

FIGURE 40. *Caligus neoaricolus* **sp. nov.** paratype female. A, leg 1, anterior; B, exopod of leg 2, anterior; C, leg 3, ventral; D, leg 4. Scale bars: 200 µm on A, B, 0.5 mm on C, 250 µm on D.

Male (Fig. 41A) mean body length including caudal rami 5.62 mm, range 5.41 to 5.99 mm (based on 10 specimens). Cephalothorax subcircular as in female. Fourth pedigerous somite incompletely fused to genital complex. Genital complex about 1.2 times longer than wide, measured along the mid-line; with weakly convex lateral margins. Abdomen 2-segmented, separated from genital complex dorsally but fused ventrally. Caudal rami longer than wide; armed with short plumose seta at inner distal angle, 2 short plumose setae at outer distal angle, and 3 longer plumose setae on distal margin.

Antennule, mandible, maxillule and maxilla as in female. Antenna modified (Fig. 41C); first segment elongate; second segment reflexed, swollen proximally with surface forming corrugated adhesion pads ventrally, plus corrugated distal swelling opposing tip of claw; distal segment forming short powerful apical claw armed with 2 setae proximally. Post-antennal process more robust than in female (Fig. 41D).

Maxilliped (Fig. 41E) with weakly inflated myxal margin on proximal segment; distal subchela longer relative to syncoxa, than in female.

Legs 5 and 6 (Fig. 41B) each forming paired flattened processes posterolaterally on genital complex. Leg 5 represented by 3 plumose setae, 1 outer seta and 2 short inner setae representing exopod. Leg 6 represented by paired opercula closing off genital apertures; each armed with 1 long and 1 short plumose seta on distal margin, plus a minute spine.

Remarks. This new species possesses a 3-segmented leg 4 bearing I and IV spines on the first and second exopodal segments, respectively. This is a common configuration shared with nearly 90 other *Caligus* species, including the 14 members of the *C. productus*-group which are characterized by loss or major reduction of the three plumose setae on the posterior margin of the distal exopodal segment of leg 1. These can be eliminated from further comparison since these posterior margin setae are normally developed in the new species. Another 12 species, members of the *C. bonito*-group, all of which share the presence of large denticles on the outer margin of the second endopodal segment of leg 2, can be excluded from detailed comparison as the new species has an ornamentation of fine setules along this margin. The remaining pool of similar species is reduced to 30 by restricting further comparisons to species that have a female genital complex that is as long as or longer than wide, and an abdomen that is longer than wide. Allowing for individual variation in genital complex shape in the order of 10%, generates a short list of 13 species that exhibit a genital complex with a L:W ratio in the range of 1.0 to 1.2:1 for comparison with the new species (Table 6).

Caligus gurnardi differs from the new species in having a genital complex that is 2.3 times longer than the abdomen (Parker, 1965), compared to only 1.5 times longer in the new species. Four species, *C. elongatus*, *C. tripedalis*, *C. ogawai* and *C. tenuifurcatus*, all have a very broad abdomen (i.e. abdomen at least 50% of width of genital complex), whereas in *C. neoaricolus* **sp. nov.** the abdomen is only 38% of the width of the genital complex. Three of the remaining species, *C. longirostris*, *C. rapax*, and *C. rufimaculatus*, have a relatively short abdomen, i.e., that is only 1.4 to 1.5 times longer than wide, compared to 2.0 times longer in the new species.

The leg 4 of *C. chiastos* (Fig. 24F) has a long outer spine on exopodal segment 1 that extends beyond the origin of the lateral spine on the distal segment. In contrast, the new species has a much shorter outer spine that does not reach halfway to the base of the lateral spine on the distal segment. Other differences include the smaller posterior process on the proximal segment of the antenna in the new species, the small size of the outer spines on the distal exopodal segment of leg 2, the shape of the sternal furca, and the relative lengths of spines 1 to 3 on the distal margin of the exopod of leg 1.

Caligus clemensi exhibits a similar arrangement of outer spines on the third exopodal segment of leg 2, to that of the new species: both have a minute pointed proximal spine and a longer blunt-tipped distal spine. The configuration of spines 1 to 3 on the distal margin of the exopod of leg 1 differs: in the new species spines 1 to 3 decrease in length in order from outer to inner, whereas in *C. clemensi* spines 2 and 3, with their very long accessory processes, are both longer than spine 1 (Parker & Margolis, 1964). Another noticeable difference is the outer spines on the exopodal segments of leg 4: they are much smaller in the new species, not reaching the origin of the next most distal spine, whereas in *C. clemensi* each of the outer spines reaches the origin of the next spine.

The redescription of *C. praetextus* by Cressey (1991) reveals that leg 1 has an unusually squat shape in this species: the first exopodal segment is only 1.7 times longer than wide compared to 2.5 times longer in the new species. Spines 2 and 3 on the distal margin of the exopod have marginal membrane extending apically from about the origin of the accessory process, producing a spatulate appearance (Cressey, 1991: Fig. 158). These spines lack marginal membrane in *C. neoaricolus* **sp. nov.** The proximal outer spine on the third exopodal segment of leg 2 is

longer than the distal spine and curves across its surface, just as highlighted for *C. chiast*os by Lin & Ho (2003), whereas in *C. neoaricolus* **sp. nov.** the proximal spine is only half as long as the distal (cf. Fig. 40B).

In terms of body proportions *C. lutjani* is the most similar to the new species (cf. Table 6). Both species also share a similar configuration of spines 1 to 3 on the distal margin of the exopod of leg 1, small outer spines on the distal exopodal segment of leg 2, multisensillate papillae associated with the post-antennal process, and tapering, pointed tines on the sternal furca. The outer spines on the exopodal segments of leg 4 are much smaller in the new species, not reaching the origin of the next most distal spine, whereas in *C. lutjani* each of the outer spines reaches at least to the origin of the next spine. Other differences include the more strongly recurved post-antennal process in *C. lutjani*, and its slender maxilliped with its smooth myxal margin, compared to the more robust and ridged myxal area in *C. neoaricolus* **sp. nov.** The males differ in the proportional lengths of the two free abdominal somites: in *C. lutjani* the first somite is 1.24 times longer than the second, whereas in *C. neoaricolus* **sp. nov.**, the first is only half the length of the second.

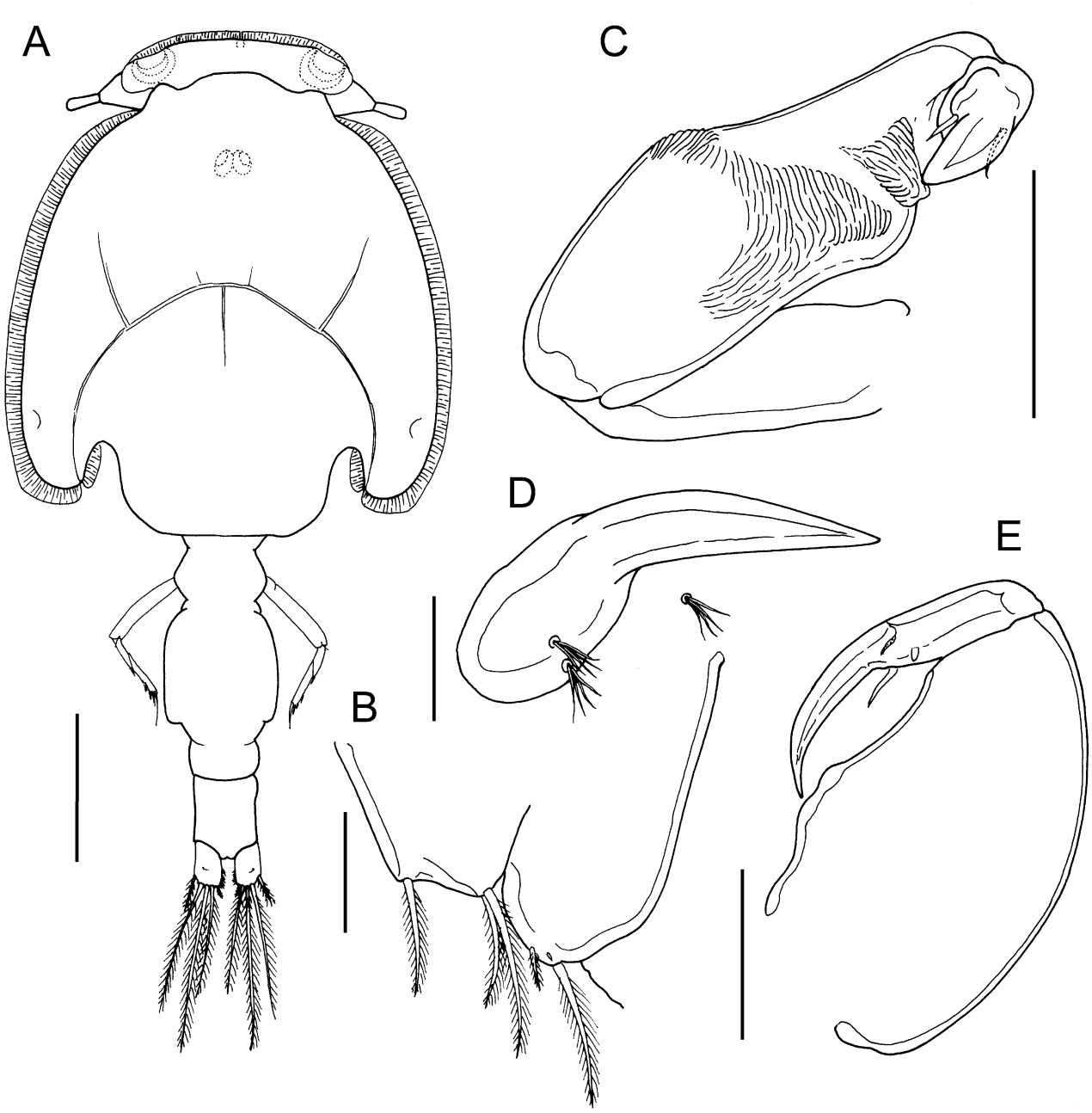

FIGURE 41. *Caligus neoaricolus* **sp. nov.** paratype male. A, habitus, dorsal; B, left corner of genital complex showing legs 5 and 6, ventral; C, antenna; D, post-antennal process, E, maxilliped. Scale bars: 1.0 mm on A, 250 μm on E, 200 μm on C, 100 μm on B, D.

TABLE 6. Selection of species of *Caligus* characterised by a 3-segmented leg 4 bearing 4 distal spines on the second exopodal segment, in combination with the setal armature on the distal segment of leg 1 consisting of 3 plumose posterior setae, and the presence of an ornamentation of fine setules on the outer margin of the second endopodal segment of leg 2. [Abbreviations: ABL = abdomen length, ABW = abdomen width, GCL = genital complex length, GCW = genital complex width].

Species	GCL:GCW	GCL:ABL	GCW:ABW	ABL:ABW	Reference
C. chiastos Lin & Ho, 2003	1.00:1	1.8:1	3.1:1	1.8:1	Ho & Lin, 2004
C. gurnardi Krøyer, 1863	1.02:1	2.3:1	3.4:1	1.6:1	Parker, 1965
C. longirostris Heegaard, 1962	1.02:1	1.7:1	2.3:1	1.4:1	Heegaard, 1962
C. rapax Milne Edwards, 1840	1.02:1	1.8:1	2.5:1	1.4:1	Parker & Margolis, 1967
C. chrysophrysi Pillai, 1985	1.04:1	1.9:1	3.1:1	1.7:1	Pillai, 1985
C. rufimaculatus Wilson, 1905	1.05:1	1.8:1	2.4:1	1.5:1	Cressey, 1991
C. elongatus von Nordmann, 1832	1.06:1	1.7:1	2.0:1	1.4:1	Parker, 1969
C. clemensi Parker & Margolis, 1964	1.07:1	1.8:1	3.0:1	1.8:1	Kabata, 1988
C. praetextus Bere, 1936	1.10:1	1.6:1	2.3:1	1.6:1	Cressey, 1991
C. neoaricolus **sp. nov.**	1.13:1	1.5:1	2.6:1	2.0:1	present account
C. tripedalis Heegaard, 1972	1.13:1	1.4:1	1.7:1	1.5:1	Heegaard, 1972
C. lutjani Ho, Lin & Chang, 2007	1.14:1	1.7:1	2.9:1	2.0:1	Ho *et al.*, 2007
C. ogawai Venmathi Maran, Ohtsuka & Shang, 2012	1.21:1	1.7:1	2.0:1	1.4:1	V. Maran *et al*., 2012b
C. tenuifurcatus Wilson, 1937	1.21:1	1.1:1	1.8:1	1.9:1	Wilson, 1937b

The material described here differs from similar congeners and these differences justify the establishment of a new species. In the type locality, Moreton Bay, its type host *was Neoarius graeffei*. A single female was recovered from a wash of *Sillago maculata* (TC17904) but this is thought to be a contaminant. Similarly an incomplete male was recovered from a container that had been used to hold a batch of juvenile *Gerres* sp. The partly decayed state of this male suggests that it may have been left in an inadequately rinsed dish from the previous sample.

Caligus oviceps Shiino, 1952
(Fig. 42)

Syn: *Caligus truncatogenitalis* Roubal, 1981

Material examined. 1♀, 4 chalimus stages from *Meuschenia trachylepis* (Günther, 1870) (TC17598) 26 June 2016, QM Reg. No. W53088;1♀ from *Kyphosus cinerascens* (Forsskål, 1775) (TC17922) 5 July 2016, NHMUK 2017.295.

Site on host. Chalimus attached to fins, adult unknown (in body wash).

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones of dorsal cephalothoracic shield; frontal plates with lunules. Genital complex not clearly demarcated from fourth pedigerous somite (Fig. 42A); about 1.06 times longer than wide; abdomen 1-segmented, about 1.30 times longer than wide; genital complex about 3 times longer than abdomen. Caudal rami about twice as long as wide. Antenna with blunt-tipped posterior process on proximal segment (Fig. 42B). Post-antennal process curved, associated papillae unisensillate. Posterior process of maxillule simple (Fig. 42B). Maxilla with ornamentation of denticles along distal margin (Fig. 42C). Maxilliped of female slender, with smooth myxal margin; claw on subchela short. Sternal furca with blunt-tipped, slightly incurved tines (Fig. 42D). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal margin spine 1 slender, about as long as spines 2 and 3; spines 2 and 3 each with long accessory process; seta 4 longer than spines but shorter than segment (Fig. 42E). Leg 2 with marginal setules on endopodal segments 1, 2 and 3; outer spines on exopodal segments 1 and 2 aligned obliquely across surface of ramus (Fig. 42F); proximal outer spine on third segment short, naked, distal outer spine ornamented with expanded membrane on apical side only. Leg 3 without distinctive ornamentation on apron; exopod 3-segmented (Fig. 42G) first segment with short curved spine, lacking inner seta; second segment with outer spine and inner seta plus sensilla on dorsal surface; third with 3 spines and 4 plumose setae: endopod 2-segmented, with 0–1; 6 setal formula. Leg 4 uniramous, 3-segmented; exopodal segments with I, III spines; each spine with well-developed pecten (Fig. 42H). Body length of female 3.95 mm.

Remarks. *Caligus oviceps* was established by Shiino (1952) based on material taken from *Siganus fuscescens* (Houttuyn, 1782) in Japanese waters. This inadequately characterized species was fully redescribed by Lin *et al.* (1996a) and again by Ho & Lin (2004). The Moreton Bay females conform closely to these redescriptions in overall body proportions, shape of genital complex, and relative size and shape of the abdomen. Other similarities include: the relative weakly curved subchela of the antenna, the unisensillate papillae ornamenting the curved post-antennal process, the ornamented distal margin of the maxilla, the shape of the sternal furca, the lengths and format of the distal setal elements on the exopod of leg 1, the relative length and position of the outer margin spines on the exopod of leg 2, and the curved outer spine of the first exopodal segment of leg 3 that does not reach the articulation with the second segment. In addition, the relative lengths of the 4 spines on leg 4 are the same. *Caligus oviceps* is a member of the *C. macarovi*-group.

Lin *et al.* (1996a) also confirmed that *C. truncatogenitalis* Roubal, 1981 was a junior subjective synonym of *C. oviceps*. *Caligus truncatogenitalis* was originally described based on a single female taken from *Acanthopagrus australis* caught off Coffs Harbour, only about 400 km south of Moreton Bay (Roubal, 1981). The body length of female *C. oviceps* given by Shiino (1955b) was 3.41 mm and Roubal's female (as *C. truncatogenitalis*) was 3.54 mm (Roubal, 1981). The female from *Kyphosus cinerascens* in Moreton Bay is slightly larger at 3.95 mm.

Detailed comparison between *C. oviceps* and *C. latus* Byrnes, 1987 reveals only relatively minor differences. They share numerous character states including: the configuration of the distal elements on the tip of the exopod of leg 1, the possession of unisensillate papillae associated with the post-antennal process, the shape of the flanged tines of the sternal furca, and the relative lengths of the spines on leg 4. There are minor differences in the shape of

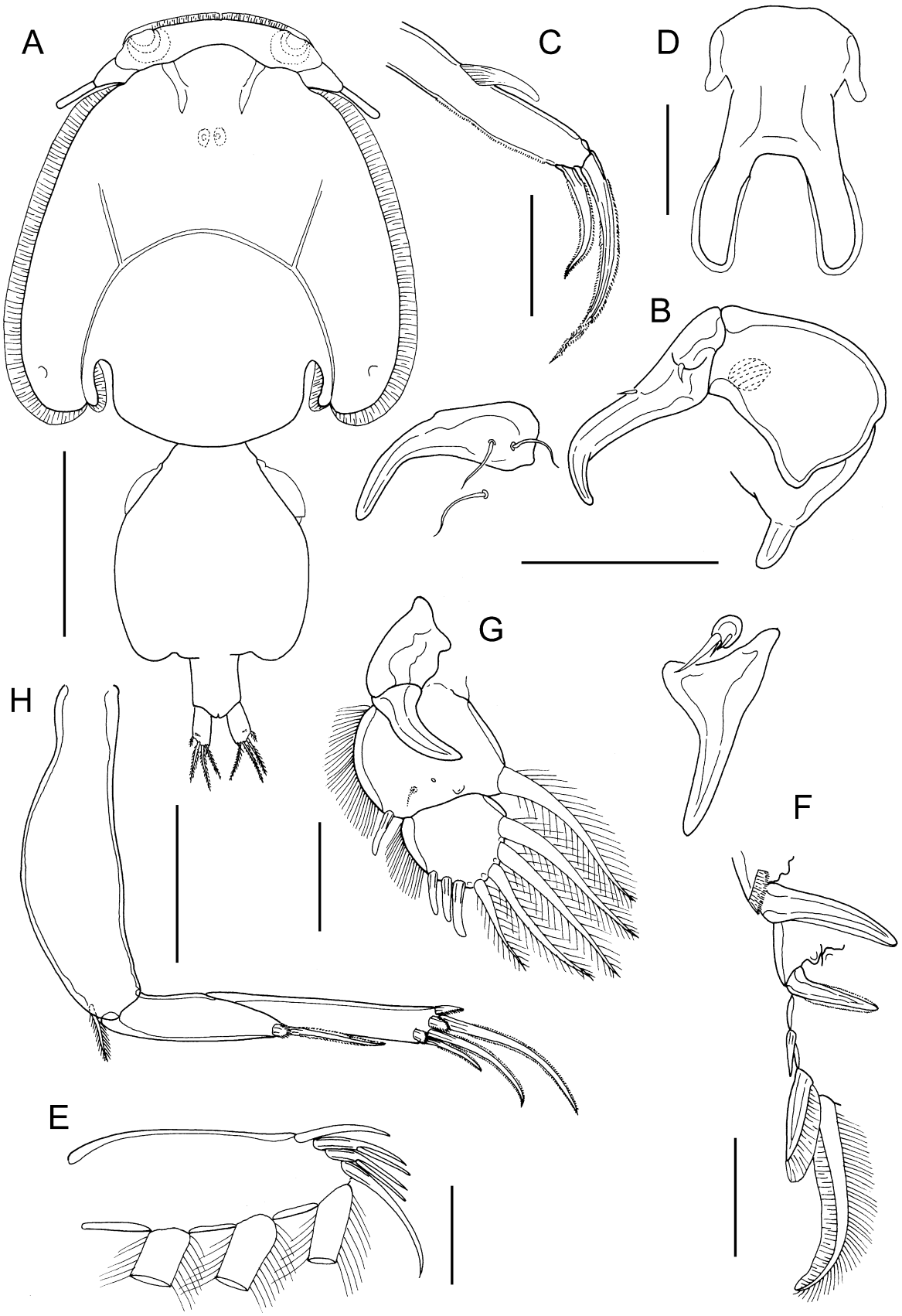

FIGURE 42. *Caligus oviceps* Shiino, 1952, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, tip of maxilla; D, sternal furca; E, distal segment of exopod of leg 1; F, outer margin spines of exopod of leg 2; G, exopod of leg 3; H, leg 4. Scale bars: 1.0 mm on A, 200 µm on B, H, 100 µm on C, D, F, G, 50 µm on E.

the female genital complex but these could possibly be attributed to the reproductive status of individual females. The distal margin of the brachium of the maxilla is ornamented with denticles in *C. oviceps* (Fig. 42C) but Byrnes (1987) did not figure this limb for *C. latus* and described it as "typical". In the same paper, Byrnes did note the denticulate margin of the maxilla in *C. dampieri* and *C. stokesi*, indicating that he was aware of the significance of this character. It seems possible that *C. latus* Byrnes, 1987 is as a synonym of *C. oviceps*, but confirming this requires examination of the type material of the former.

In addition to the type host *Siganus fuscescens*, this copepod has been reported from *Parupeneus chrysopleuron* (Temminck & Schlegel, 1843) (as *Pseudupeneus chrysopleuron*), *Cheilodactylus quadricornis* (Günther, 1860) (as *Goniistius quadricornis*), *Calotomus japonicus* (Valenciennes, 1840) (as *Leptoscarus japonicus*), *Stephanolepis setifer* Bennett, 1831 (as *Monacanthus setifer*), *Lethrinus haematopterus* Temminck & Schlegel, 1844, *Girella punctata* Gray, 1835, *Istiblennius edentulus* (Forster & Schneider, 1801) (as *Salarias enosimae*), and *Entomacrodus stellifer* Jordan & Snyder, 1902 (as *Salarias stellifer*) in Japanese waters (Shiino, 1959), and from *Acanthopagrus australis* and *A. latus* in Australia (Roubal, 1981; Byrnes, 1987). Both *Kyphosus cinerascens* and *Meuschenia trachylepis* are new host records for *C. oviceps* and this is the first report of this widely distributed copepod from Queensland, although it was previously known from New South Wales.

***Caligus paranengai* sp. nov.**
(Figs. 43–44)

Type material. Holotype ♀, 8 paratype ♀♀, 2 paratype ♂♂ from *Neoarius graeffei* (Kner & Steindachner, 1867) (TC17881) 4 July 2016, QM Reg. Nos Holotype ♀ W53089, 4 paratype ♀♀ W53090, 1 paratype ♂ W53091; NHMUK Reg. Nos 4 paratype ♀♀, 1 paratype ♂ NHMUK 2017.296–300.

Type Host. *Neoarius graeffei* (Kner & Steindachner, 1867).

Site on host. body surface.

Etymology. The name refers to the close affinity between the new species and *C. nengai* Rangnekar, Rangnekar & Murti, 1953.

Description. Adult female (Fig. 43A) mean body length including caudal rami 3.78 mm (range 3.50 to 3.96 mm), (based on 7 specimens). Cephalothorax about 1.07 times longer than wide; comprising about 50% of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly just beyond rear margins of lateral portions; additional posterior sutures present on surface of dorsal cephalothoracic shield. Lunules present ventrally on frontal plates. Genital complex about 1.04 times longer than wide; with linear, lateral margins and rounded corners (Fig. 43A). Genital complex about 4.0 times longer than abdomen. Abdomen indistinctly 2-segmented, about 1.1 times longer than wide; carrying paired caudal rami distally; anal slit terminal. Caudal rami wider than long, measured at midpoints of margins. Each ramus armed with short hirsute seta at inner distal angle, slightly longer hirsute seta at outer distal angle, minute hirsute seta located just ventral to outer distal seta, and 3 plumose setae on distal margin.

Antennule 2-segmented; proximal segment with 25 plumose setae along anteroventral margin and 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 43B) comprising proximal segment with short blunt posterior process ornamented with marginal flange; middle segment subrectangular, unarmed but with dorsal adhesion pad; terminal segment forming strongly curved claw with proximal swelling bearing stout seta, and armed with slender distal seta. Post-antennal process (Fig. 43B) with broad base and distal marginal membrane, tine not developed; ornamented with 2 multisensillate papillae on basal part; plus single multisensillate papilla and sclerotized irregular process on adjacent ventral cephalothoracic surface.

Mandible of typical stylet-like structure, with 12 marginal teeth. Maxillule (Fig. 43C) comprising anterior papilla bearing 3 small naked setae and slender, tapering posterior process. Postoral process present as surface ridge (Fig. 43C). Maxilla comprising elongate syncoxa and basis: syncoxa unarmed but bearing opening of maxillary gland; basis bearing subapical membranous flabellum on anterior margin, and terminating in 2 subequal, claw-like elements (calamus and canna); calamus just longer than canna, ornamented with strips of serrated membrane arranged obliquely around surface; canna with linear strips of serrated membrane. Maxilliped subchelate (Fig. 43D); slender proximal segment with 2 transverse ridges on surface near base; distal subchela with long inner seta.

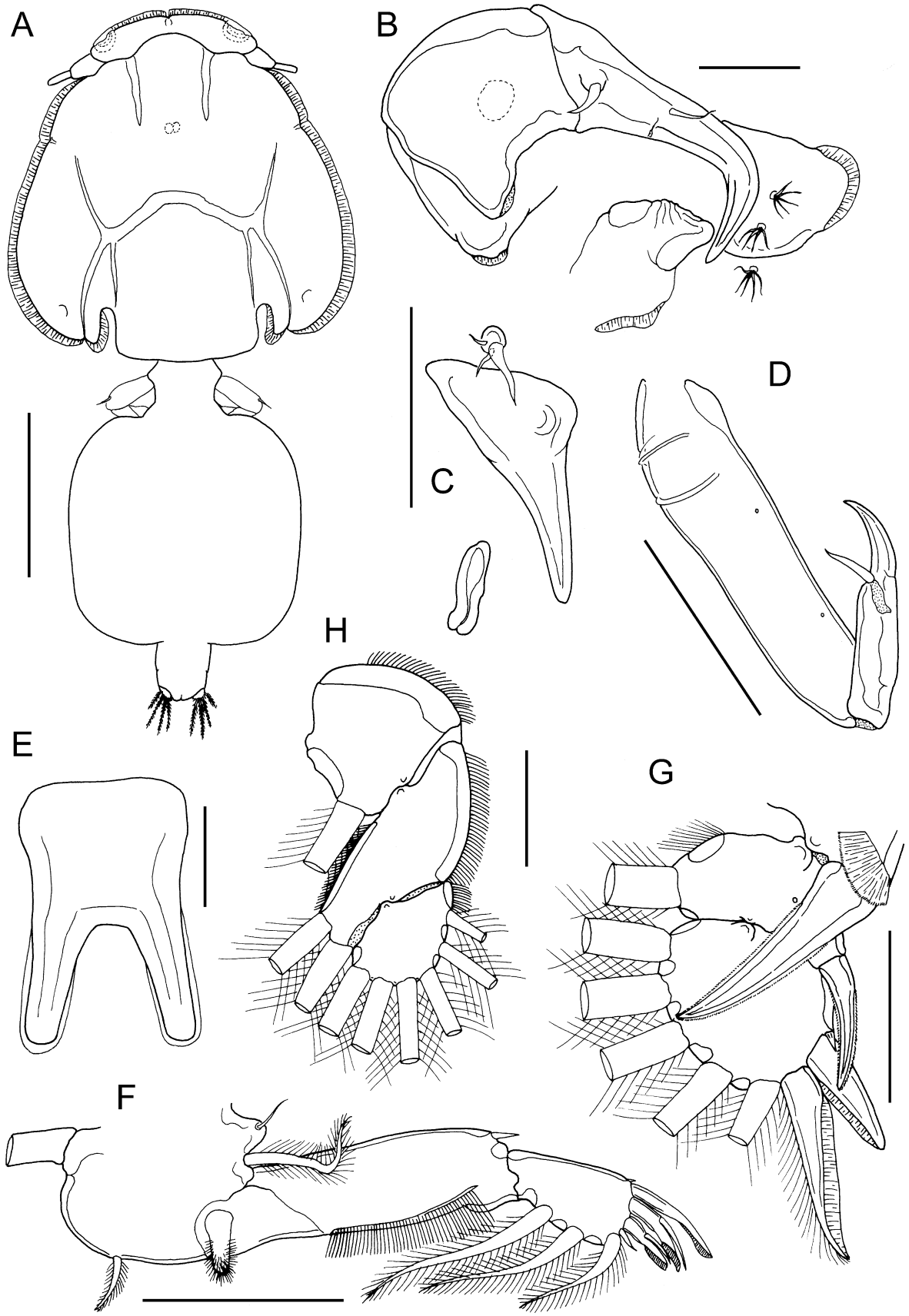

FIGURE 43. *Caligus paranengai* **sp. nov.** paratype female. A, habitus, dorsal; B, antenna and post-antennal process drawn *in situ*; C, maxillule and postoral process, drawn *in situ*; D, maxilliped; E, sternal furca; F, leg 1; G, exopod of leg 2; H, endopod of leg 2. Scale bars: 1.0 mm on A, 100 µm on B, C, E, G, H, 200 µm on D, F.

Sternal furca (Fig. 43E) with weakly divergent, flanged tines.

First swimming leg pair (Fig. 43F) with sympods joined by slender intercoxal sclerite; sympod with inner and outer plumose setae. Vestigial endopod large and densely ornamented with hair-like setules. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment robust, about 2.8 times longer than wide and armed with small outer (anterior) spine and ornamented with setule row along mid-section of posterior margin; second segment armed with 3 long plumose setae along posterior margin and 4 distal elements. Distal margin elements as follows: spine 1 (anterior-most) strongly developed, almost as long as segment and longer than other spines, ornamented with strip of striated membrane distally; spine 2 longer than spine 3, each with long accessory process and strip of striated membrane; seta 4 naked, markedly shorter than spine 3.

Second leg biramous: with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by plate-like intercoxal sclerite bearing marginal membrane posteriorly; armed with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segment 1 (Fig. 43G) with large outer spine lying obliquely across surface of ramus, with large pecten at base, plus inner plumose seta; also bearing flap of membrane anteriorly, reflexed back over dorsal surface; segment 2 with outer spine aligned close to longitudinal axis of ramus and inner plumose seta; segment 3 with 2 outer spines, proximal spine minute and naked, distal spine stout with marginal membrane on apical side; apical spine with marginal membrane laterally and pinnules medially, plus 5 inner plumose setae. Endopodal segments 1 and 2 (Fig. 43H) armed with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; outer margins of all endopodal segments ornamented with fine setules.

Third leg pair (Fig. 44A) forming flattened plate closing posterior part of cephalothoracic sucker, as typical for genus. Protopodal part flattened joined by plate-like intercoxal sclerite forming apron, ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate and outer plumose seta dorsal to base of exopod; sensillae located adjacent to inner coxal seta and adjacent to origin of endopod. Both rami flattened and swollen. Exopod indistinctly 3-segmented; first segment markedly expanded laterally so wider than velum; armed with short and slightly curved outer claw almost reaching inner margin of ramus and ornamented with single lateral setule plus strip of membrane along elongate margin; second and third segments incompletely separated by partial suture; armed with short outer spine and inner plumose seta derived from second segment and 3 outer spiniform elements and 4 inner plumose setae (derived from third segment); proximal spine derived from third exopodal segment minute, middle spine short, distal spine long; outer margins of segments 2 and 3 ornamented with rows of slender setules. Endopod 2-segmented; first segment forming flap-like velum ornamented with row of fine setules along free margin, armed with inner plumose seta; second segment with expanded and setulate lateral margin, armed with 6 setal elements distally, increasing in length from outermost to innermost.

Fourth leg (Fig. 44B) uniramous, 4-segmented, comprising slender protopodal segment and 3-segmented exopod; protopodal segment armed with outer plumose seta; first exopodal segment broader than distal segments, armed with long outer spine and ornamented with membranous pecten at base of spine; second segment armed with outer spine; third segment short, armed with 2 large spines and minute vestigial spine along oblique distal margin; pectens on exopodal segments 2 and 3 each forming tuft of long setules close to base of spine. Spines on exopodal segments 1 and 2, and 2 distal spines on segment 3 each ornamented bilaterally with membrane.

Fifth leg located posterolaterally on ventral surface of genital complex near margin, represented by anterior plumose seta on papilla and posterior papilla bearing 2 unequal plumose setae representing exopod.

Male. Body lengths 2.00 and 2.04 mm, including caudal rami. Cephalothorax subcircular as in female; additional posterior sutures present on surface of dorsal cephalothoracic shield (Fig. 44C) as in female. Fourth pedigerous somite incompletely fused to genital complex. Genital complex about as long as wide, measured along mid-line; with convex lateral margins in anterior part (to level of fifth legs). Abdomen 1-segmented. Caudal rami wider than long; armed with short plumose seta at inner distal angle, 2 short plumose setae at outer distal angle, and 3 longer plumose setae on distal margin.

Antennule, mandible and maxilla as in female. Antenna modified (Fig. 44D); first segment elongate with marginal adhesion pad; second segment reflexed, wider proximally, surface ornamented with adhesion pads plus corrugated distal swelling opposing tip of claw; distal segment forming short powerful apical claw armed with 2 setae proximally plus small tooth-like accessory process. Maxillule as in female but post-oral process corrugated in male (Fig. 44E).

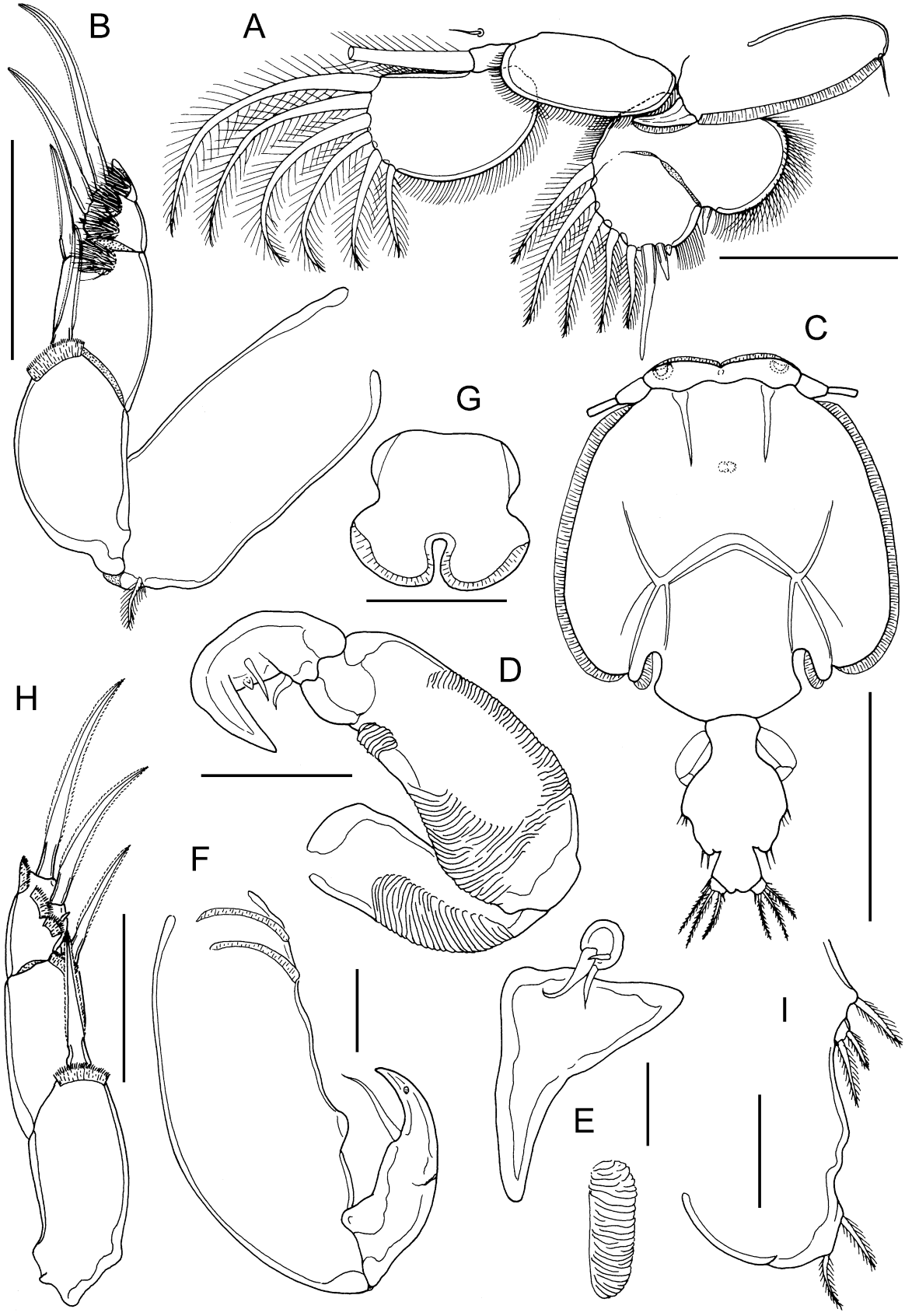

FIGURE 44. *Caligus paranengai* **sp. nov.** paratype female. A, rami of leg 3, ventral; B, leg 4. Paratype male, C, habitius, dorsal; D, antenna, E, maxillule and postoral process, drawn *in situ*; F, maxilliped, G, sternal furca; H, exopod of leg 4; I, left side of genital complex showing legs 5 and 6. Scale bars: 200 µm on A, B, 1.0 mm on C, 100 µm on D, G–I, 50 µm on E, F.

Maxilliped (Fig. 44F) with proximal segment more robust than in female; ornamented with transverse cuticular ridges proximally as in female, but with rounded distal process on myxal margin of proximal segment; distal subchela robust, armed with long seta and with small area of thin cuticle on claw.

Sternal furca (Fig. 44G) short with flattened spatulate tines, each with marginal flange.

Legs 1 to 3 as in female. Leg 4 as for female except exopodal segments 2 and 3 with normal membranous pectens (Fig. 44H) not tufts of spinules.

Leg 5 (Fig. 44I) forming paired processes located laterally on genital complex; each represented by exopodal process armed with 2 plumose setae, plus (protopodal) seta on adjacent surface. Leg 6 located posteriorly; represented by oblique operculum closing off genital aperture armed with 2 plumose setae around outer distal margin.

Remarks. This species is very closely related to *C. nengai* Rangnekar, Rangnekar & Murti, 1953 which was originally described on the basis of material from a marine catfish, *Nemapteryx nenga* (Hamilton, 1822) (as *Arius nenga*), caught off Bombay, India (Rangnekar *et al.*, 1953). Subsequently, a mutilated female from a specimen of *Tachysurus* sp. caught off Trivandrum, India was described as *Caligus distortus* Pillai & Natarajan, 1977 (Pillai & Natarajan, 1977). However, Ho *et al.* (2000) formally recognized *C. distortus* as a junior subjective synonym of *C. nengai* and provided a detailed redescription of the female based on Taiwanese material. The material from Moreton Bay is identical in many respects to the material redescribed by Ho & Lin (2004); both share a number of unusual characteristics, such as the pattern of sutures on the dorsal cephalothoracic shield, the flanged post-antennal process, the hirsute endopod of leg 1, the laterally expanded first exopodal segment on leg 3, and the presence of tufts of setules replacing the pectens on the second and third exopodal segments of leg 4. Despite these similarities, there are a few important differences: the abdomen of the female is wider than long and 1-segmented in *C. nengai*, but longer than wide and indistinctly 2-segmented in the Australian material; there is a long slender posterior process on the antenna of female *C. nengai*, whereas in the new species there is a bluntly rounded posterior process ornamented with a membranous flange (Fig. 43B); the maxilliped of female *C. nengai* has 4 medial tooth-like protuberances on the proximal segment whereas in the new species there are paired transverse ridges in this position (Fig. 43D). These differences are sufficient to justify the establishment of a new species, *C. paranengai* **sp. nov.**

Ho & Lin (2004) mentioned and figured only 2 large spines on the distal exopodal segment of leg 4 in the Taiwanese material of *C. nengai*, but in the Moreton Bay females a minute third spine is present proximally in both sexes. This might be an additional difference between the species but the vestigial spine is partly concealed by the setular tuft representing the pecten in the female and could easily be overlooked.

The new species and *C. nengai* appear related to *Caligus arii* Bassett-Smith, 1898 as redescribed by Pillai (1985) since both species share the unusual leg 3, with its large lamellate rami, as well as the hirsute ornamentation of the vestigial endopod of leg 1. However, this latter character state is also present in some other caligids parasitic on catfish hosts, including *Hermilius longicornis* Bassett-Smith, 1898 (cf. Ho & Kim, 2000: Fig. 3J) and *Lepeophtheirus longipalpus* Bassett-Smith, 1898 (cf. Pillai, 1985: Fig. 151D) and has been inferred as being due to convergence between parasites using closely related hosts.

Equally intriguing are the numerous derived character states shared with *Parapetalus hirsutus* (Bassett Smith, 1898c): these include the presence of setulose tufts (rather than pectens) associated with the spines on the second and third exopodal segments of leg 4, the hirsute vestigial endopod of leg 1, the unusual pattern of sutures on the dorsal cephalothoracic shield (Fig. 43A), and the reduced post-antennal process. In addition, the first exopodal segment of leg 3 is transversely expanded and is ornamented with a conspicuous marginal sensilla, as in the new species. The expansion of the segment is not as extreme as in the new species and *C. nengai*, but this is a very unusual configuration within the Caligidae. The affinities of *P. hirsutus* appear to lie with *C. nengai* and *C. paranengai* **sp. nov.**, rather than with other members of the poorly defined and heterogeneous genus *Parapetalus*. It is proposed here to return it to its original combination, *Caligus hirsutus*, as established by Bassett-Smith (1898c).

The extent of the sexual dimorphism exhibited by *C. paranengai* **sp. nov.** is unusual: the sternal furca and leg 4 both show marked sexual dimorphism, in addition to the more typically dimorphic limbs such as the antennae and maxillipeds.

***Caligus parvilatus* Kim, 1998**
(Figs. 45–47)

Syn: *Caligus latus* Kim, 1995
Non *Caligus latus* Byrnes, 1987

Material examined. 8♀♀, 3♂♂ from *Abudefduf bengalensis* (Bloch, 1787) (TC16957-61) 11 January 2016, QM Reg. No. W53092; 1 chalimus (TC17966), 4♀♀, 2♂♂ (TC 17806) 2 July 2016, NMHUK 2017.301–306; 1 immature ♀ from *Abudefduf whitleyi* Allen & Robertson, 1974 (TC16966) 11 January 2016;1♀ from *Kyphosus bigibbus* Lacepède, 1801 (TC17864) 4 July 2016, 1♀ (TC17792) 1 July 2016, NMHUK 2017.307–308.

Site on host. Body surface.

Description. Adult female (Fig. 45A) mean body length including caudal rami 2.18 mm (range 1.95 to 2.43 mm), (based on 11 specimens). Cephalothorax slightly longer than wide with shallow posterior sinuses; comprising about 60% of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly beyond rear margins of lateral portions. Lunules present ventrally on frontal plates. Genital complex subrectangular, 1.3 times wider than long; with rounded corners (Fig. 45B); fifth legs located close to posterolateral corners (Fig. 45C). Copulatory pores located near midline, oviduct openings marked by 2 swellings, 1 with finely ridged surface. Genital complex more than 4 times longer than abdomen. Abdomen 1-segmented; about 1.2 times wider than long in ventral view (Fig. 45B); carrying paired caudal rami distally; anal slit terminal. Caudal rami with parallel sides, longer than wide, measured at midpoints of margins. Each ramus armed with short hirsute seta at inner distal angle, slightly longer hirsute seta at outer distal angle, minute hirsute seta located just ventral to outer distal seta, and 3 long plumose setae on distal margin.

Antennule (Fig. 45D) 2-segmented; large proximal segment with 25 plumose setae arrayed along anteroventral surface and 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 45E) comprising proximal segment bearing spatulate posteriorly-directed spinous process; middle segment subrectangular, tapering distally, unarmed; terminal segment forming short, recurved claw bearing short spinous swelling proximally, and minute setal vestige near anterior margin. Post-antennal process (Fig. 45F) well-developed, curved; ornamented with 2 bisensillate papillae on basal part and single bisensillate papilla on adjacent ventral cephalothoracic surface.

Mandible of typical stylet-like structure, with 12 marginal teeth (Fig. 45G). Maxillule (Fig. 46A) comprising anterior papilla bearing 3 unequal, naked setae and blunt posterior, tine-like process. Maxilla 2-segmented (Fig. 46B), comprising elongate syncoxa and basis: syncoxa unarmed; basis bearing membranous subapical flabellum on anterior margin, and terminating in 2 subequal claw-like elements (calamus and canna). Calamus slightly longer than canna, ornamented with strips of serrated membrane arranged obliquely around surface; canna ornamented with strips of serrated membrane. Maxilliped subchelate (Fig. 46C); slender proximal segment unarmed and without process on myxal surface; distal subchela with apical claw separated from proximal segmental part by incomplete suture; slender seta present on concave margin.

Sternal furca (Fig. 46D) with slightly divergent tines, expanding distally and with bluntly truncated tip.

First swimming leg pair (Fig. 46E) with joined by slender intercoxal sclerite; sympod with inner and outer plumose setae derived from basis; endopod represented by unarmed process on posterior margin of basis. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment robust, about 2.8 times longer than wide and armed with small outer (anterior) spine and ornamented with row of setules along middle section of posterior margin; second segment armed with 3 long plumose setae along posterior margin and 4 distal elements along oblique distal margin. Distal elements as follows: spine 1 (anterior-most) simple, longer than spine 2; spine 2 markedly longer than spine 3, each with accessory process; seta 4 about 25% longer than spine 1, and shorter than segment.

Second leg (Fig. 46F) biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by intercoxal sclerite bearing marginal membrane posteriorly. Coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segments 1 and 2 each with large unilaterally-dentate, reflexed outer spines extending obliquely across ventral surface of ramus (Fig. 46G), plus inner plumose seta; first segment also with flap of membrane anteriorly, reflexed back over dorsal surface of segment: segment 3 with 2 outer spines (proximal spine minute; distal spine unilaterally pinnate), apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. Endopodal segments 1 and 2 armed

with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; outer margins of second and third endopodal segments ornamented with fine setules.

Third leg pair (Fig. 47A) forming flattened plate closing posterior part of cephalothoracic sucker as typical for genus. Protopodal part flattened, joined by plate-like, intercoxal sclerite forming apron ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate, and outer plumose seta dorsal to base of exopod; long sensillae located adjacent to inner coxal seta and adjacent to origin of endopod. Exopod 3-segmented; first segment armed with weakly curved outer spine directed over ventral surface of ramus, spine and outer distal margin of segment ornamented with strips of membrane, lacking inner seta; second segment with slender outer spine and inner plumose seta; third with 7 setal elements (3 outer spiniform elements and 4 inner plumose setae); outer margin of segment 2 ornamented with row of slender setules. Endopod 2-segmented; first segment expanded laterally to form flap-like velum closing off space between rami; velum ornamented with row of fine setules along free margin; segment bearing inner plumose seta; second segment with 6 setal elements increasing in length from outermost to innermost.

Fourth leg (Fig. 47B) 2-segmented, comprising slender protopodal segment and 1-segmented exopod: protopodal segment armed with plumose seta distally; exopodal segment armed with slender outer spine with pecten at base, and 1 long naked apical spine plus shorter naked subapical spine, each with pecten at base.

Fifth legs located posterolaterally on genital complex (Fig. 45B,C); each fifth leg comprising anterior spinous process bearing short plumose seta (representing outer protopodal seta) and long exopodal process with bifid tip armed with 2 plumose setae.

Mean body length of male including caudal rami 1.71 mm (range 1.61 to 1.75 mm) (based on 5 specimens).

Remarks. *Caligus parvilatus* was originally described by Kim (1995) under the name *C. latus*, which was preoccupied by *Caligus latus* Byrnes, 1987. Kim (1998) proposed *C. parvilatus* as a replacement name. The adult female body form of *C. parvilatus* resembles *C. tylosuri* (Rangnekar, 1956) and *C. cordiventris* Shiino, 1952, particularly in the shared possession of a short broad genital complex which bears a distinctive fifth leg in the form of two rigid marginal processes, the anterior bearing the outer protopodal seta and the posterior representing the exopod and bearing plumose setae at its tip. It seems likely that the inadequately described *C. eventilis* Leigh-Sharpe, 1934 is also closely related to these three species.

Rangnekar (1956) originally placed *C. tylosuri* in *Tuxophorus* Wilson, 1908 but Pillai (1961) re-assigned it to *Caligus*. Comparison with Lin & Ho's (2007) redescription of female *C. tylosuri* reveals many differences from *C. parvilatus*: the post-antennal process is bifid in the former but simple in *C. parvilatus*; the tines of the sternal furca are strongly divergent in *C. tylosuri* but weakly divergent with expanded truncate tips in *C. parvilatus*; the outer margin spines on the first and second exopodal segments of leg 2 are ornamented with finely serrate marginal membrane and are aligned close to the longitudinal axis of the ramus in *C. tylosuri* whereas in *C. parvilatus* they both lie obliquely across the surface of the ramus and are strongly serrated; leg 4 is slender in both species but carries 3 unequal apical spines in *C. tylosuri*, the longest of which is as long as the entire exopod, whereas in *C. parvilatus* there are only 2 relatively shorter, apical spines.

Shiino (1952) established *C. cordiventris* on the basis of five females collected from *Prionurus scalprum* (as *Xesurus scalprum*) in Japanese waters. Subsequently he described the male from the same host (Shiino, 1955a). This appears to be a rare species as it has not been reported since 1955, although it has been listed in syntheses such as the compendium of Yamaguti (1963). *Caligus cordiventris* is very similar to *C. parvilatus*: both species have serrated outer spines on the first and second exopodal segments of leg 2 and both have only 2 well developed spines on the distal margin of leg 4. These two species are best distinguished by the form of the exopod of leg 4: the spine marking the edge of the proximal exopodal segment is located about a third of the distance along the ramus in *C. cordiventris* and it extends less than half the distance to the apex of the limb, whereas in *C. parvilatus* the homologus outer margin spine is located about mid-margin along the unsegmented exopod, and it reaches nearly three quarters of the way to the tip. In addition, the sternal furca has slender tines with rounded tips in *C. cordiventris* whereas in *C. parvilatus* it has spatulate tines with broad, truncated tips.

Leigh-Sharpe (1934) described *C. eventilis* from a "black pomacentrid fish" caught north of Damar Island in the Banda Sea (= Siboga Station 144, Anchorage. Salomakië Island). The description lacks detail but the structure and armature of leg 4 and the possession of a broad genital complex with prominent anterior and posterior processes representing the fifth legs, suggest a close relationship with *C. tylosuri*, *C. cordiventris* and *C. parvilatus*. The shape of the short abdomen, with its unusually broad base, serves to separate *C. eventilis* from these other three species.

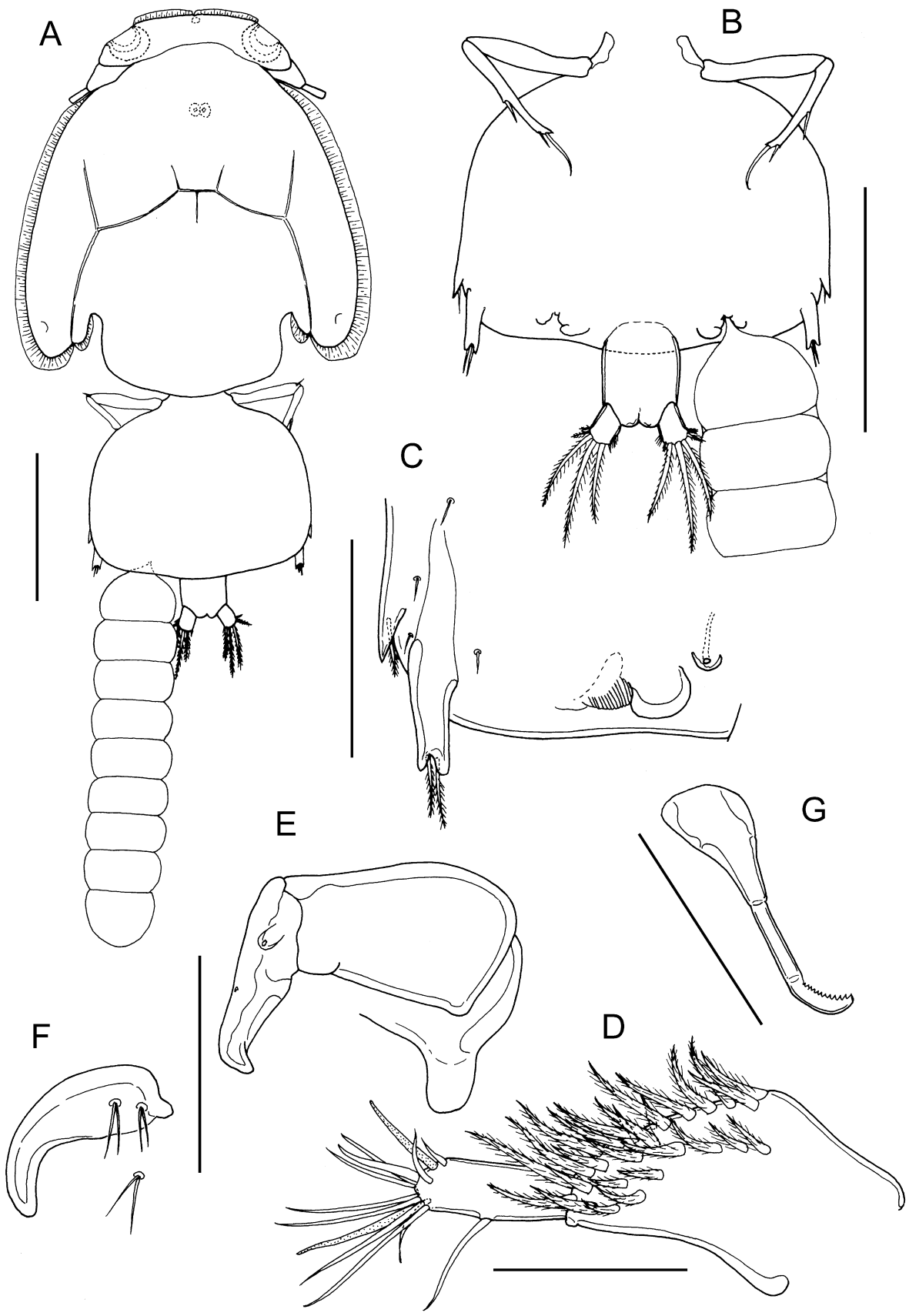

FIGURE 45. *Caligus parvilatus* Kim, 1998, female. A, habitus, dorsal; B, fourth pedigerous somite, genital complex and abdomen, ventral; C, right corner of genital complex showing fifth leg, ventral; D, antennule; E, antenna, ventral; F, post-antennal process, ventral; G, mandible. Scale bars: 0.5 mm on A, B, 200 µm on C, 100 µm D–G.

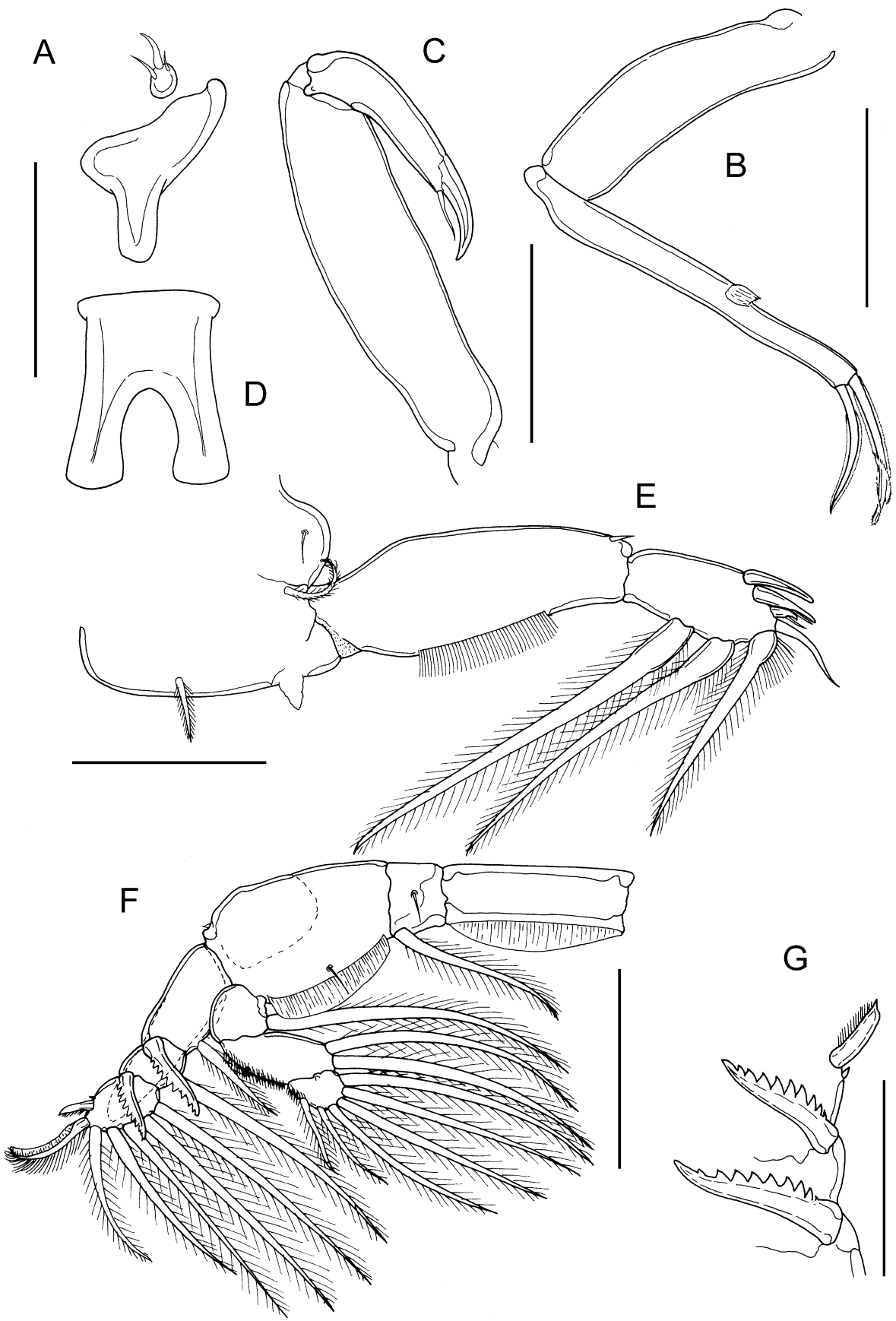

FIGURE 46. *Caligus parvilatus* Kim, 1998, female. A, maxillule; B, maxilla; C, maxilliped; D, sternal furca; E, leg 1, ventral; F, leg 2, ventral; G, detail of outer spines on exopod of leg 2. Scale bars: 100 µm on A–E, 200 µm on F.

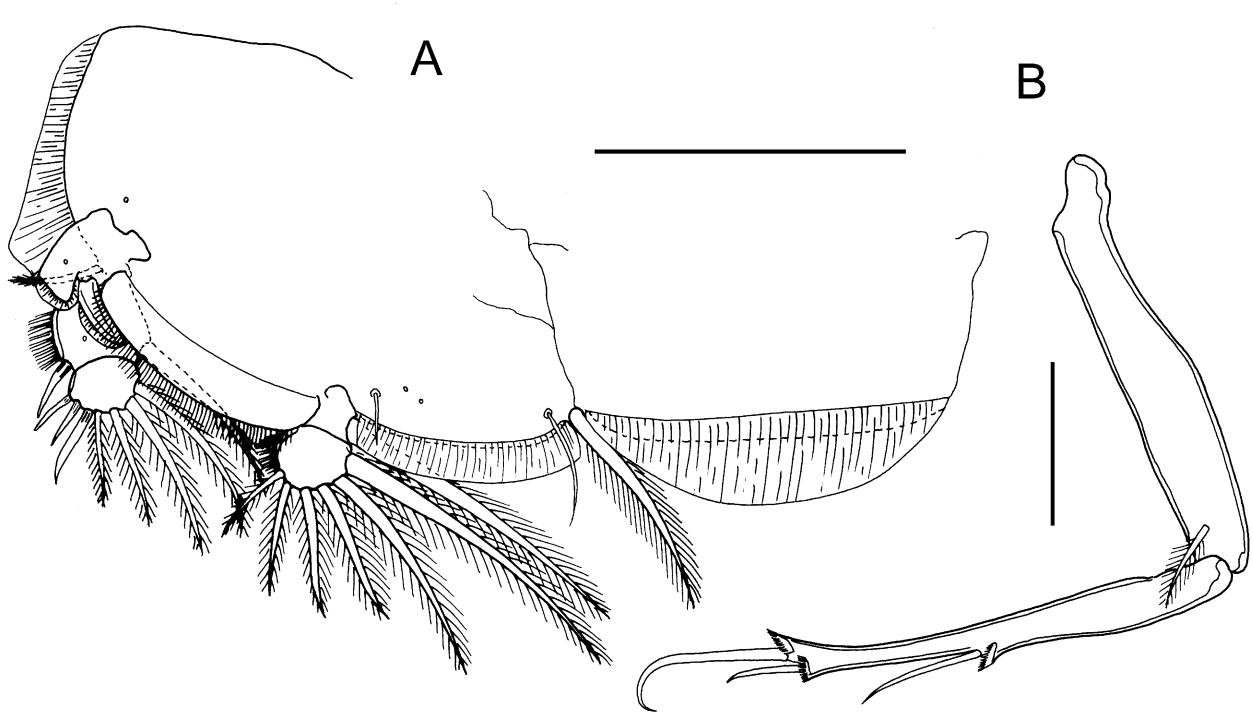

FIGURE 47. *Caligus parvilatus* Kim, 1998, female. A, leg 3, ventral; B, leg 4. Scale bars: 200 µm on A, 100 µm on B.

Caligus parvilatus was originally established on the basis of females found on the body surface of *Ditrema temmincki* Bleeker, 1853 (Embiotocidae) caught in the Korea Strait (Kim, 1995). Subsequently Kim (1998) reported both sexes of *C. parvilatus* from a parrotfish *Calotomus japonicus* (Scaridae) collected in Korean waters. In Moreton Bay, it was found on three different hosts, two species of the pomacentrid *Abudefduf*, *A. bengalensis* and *A. whitleyi*, and *Kyphosus bigibbus* (Kyphosidae).

***Caligus pelamydis* Krøyer, 1863**
(Fig. 48)

Material examined. 1♀ from *Pomatomus saltatrix* (Linnaeus, 1766) (TC17537) 24 June 2016, QM Reg. No. W53093.

Site on host. Unknown (in body wash).

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes; frontal plates with small lunules. Genital complex about 1.1 times longer than wide (Fig. 48A); abdomen elongate, about 3.0 times longer than wide, indistinctly 2-segmented, with anterior somite about 3.1 times longer than short anal somite; genital complex shorter than abdomen, with convex lateral margins narrowing anteriorly. Antenna without posterior process on proximal segment (Fig. 48B). Post-antennal process reduced, with vestigial tine; associated papillae multisensillate. Maxilliped of female with smooth myxal margin. Sternal furca with slightly incurved blunt-tipped tines. Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal margin spine 1 shorter than other spines; spines 2 and 3 with tapering tips without accessory processes (Fig. 48D); seta 4 shorter than spine 3. Leg 2 with patches of fine setules extending onto ventral surface of endopodal segments 2 and 3 (Fig. 48E); outer margin of first endopodal segment unornamented; outer spines on exopodal segments 1 and 2 aligned close to longitudinal axis of ramus (Fig. 48F); proximal spine on third exopodal segment naked, about 65% length of distal spine. Leg 3 with 3-segmented exopod; first segment bearing small straight spine with cuticular flange at base (Fig. 48G); second segment with small outer spine plus long inner seta; third segment with 3 spines increasing in length distally, plus 4 plumose setae. Leg 4 uniramous, 4-segmented (Fig. 48H); exopodal segments armed with I; I; III spines; each spine with elongate strip of membrane (modified pecten) on surface of segment adjacent to base. Body length of female 3.92 mm.

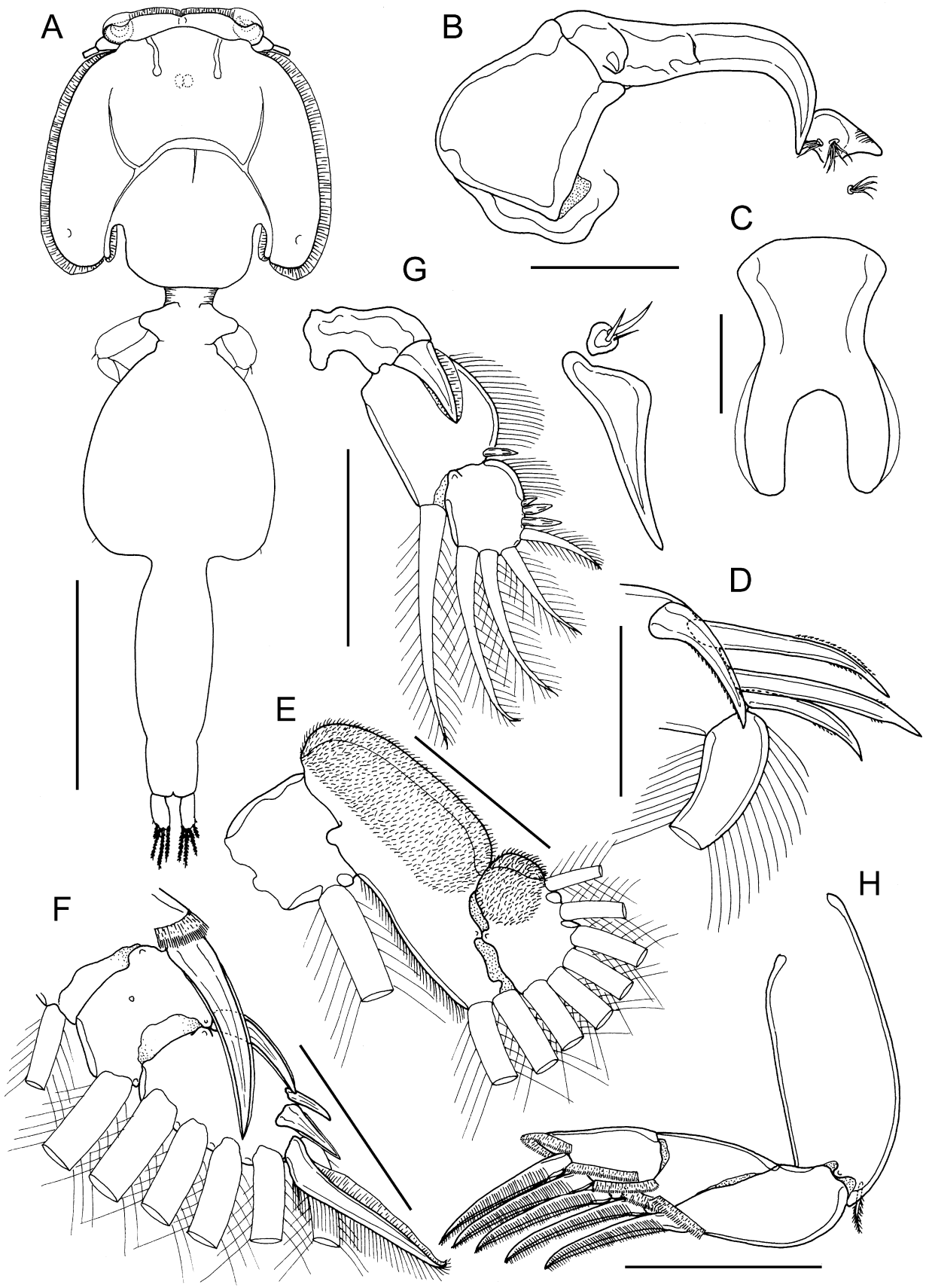

FIGURE 48. *Caligus pelamydis* Krøyer, 1863, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, sternal furca; D, distal armature on exopod of leg 1; E, endopod of leg 2; F, exopod of leg 2; G, exopod of leg 3; H, leg 4. Scale bars: 1.0 mm on A, 100 μm on B, E–G, 50 μm on C, D, 200 μm on H.

Remarks. This is a distinctive species characterized by its unusually long abdomen. It is a core member of the *C. diaphanus*-group. *Caligus pelamydis* is most frequently reported from scombrid hosts and has an almost cosmopolitan distribution (Cressey & Cressey, 1980) in the North and South Atlantic, Indian, and North and South Pacific Oceans. It has been recorded in Australian waters off New South Wales, on *Euthynnus affinis*, *Sarda australis* and *Auxis* sp. (Cressey & Cressey, 1980), and on *Arripis trutta* by Hutson *et al.* (2011). In Moreton Bay it was found on *P. saltatrix*; it has been reported previously from this host taken off the African coast in the South Atlantic (Capart, 1959).

Caligus platytarsis Bassett-Smith, 1898
(Fig. 49)

Syn: *Caligus bombayensis* Rangnekar, 1955

Material examined. 9♀♀, 4♂♂ from *Mugil cephalus* Linnaeus, 1758 (TC17257) 18 January 2016, QM Reg. No. 9♀♀, 1♂ W53094; 4♀♀ (TC17714) 29 June 2016, NHMUK Reg. Nos 2017.309–311.

Site on host. Gill arches.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones of dorsal cephalothoracic shield; frontal plates with lunules. Female genital complex about 1.2 times longer than wide, becoming wider posteriorly, with slightly convex lateral margins and nearly transverse posterior margin; fifth legs forming conspicuous process on posterolateral corner of genital complex (Fig. 49A): abdomen elongate, about 2.9 times longer than wide and just longer than genital complex. Antenna without posterior process on proximal segment (Fig. 49B). Post-antennal process vestigial; associated papillae unisensillate. Posterior process of maxillule with broad tine (Fig. 49B). Maxilliped of female with smooth myxal margin. Sternal furca with extremely broad (about as wide as long), spatulate tines (Fig. 49C). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal margin spine 1 distinctly shorter than spine 2 (Fig. 49D); spines 2 and 3 lacking accessory process but with minutely pointed apex; seta 4 longer than spine 3, naked. Leg 2 with patches of fine setules extending onto surface of endopodal segments 2 and 3; outer spine on exopodal segment 1 passing obliquely across surface of ramus; spine on segment 2 aligned closer to long axis of ramus. Leg 3 lacking distinctive ornamentation on apron; exopod 3-segmented (Fig. 49E); first segment with straight outer spine not reaching articulation with second segment, lacking inner seta; second segment with outer spine and inner plumose seta; third with 3 outer spines and 4 plumose setae: endopod 2-segmented (Fig. 49E); first segment forming well developed velum, armed with inner plumose seta; compound distal segment with lateral margin expanded proximal to partial suture marking plane of fusion, armed with 6 plumose setae. Leg 4 uniramous (Fig. 49F), 4-segmented; exopodal segments with I, I, III spines; all spines sub-equal in length, proximal 4 spines hirsute, apical spine with smooth membrane bilaterally; each spine with elongate pecten associated with base. Mean body length of female 5.09 mm, range 4.88 to 5.31 mm (based on 7 specimens): mean body length of male 3.15 mm, range 3.11 to 3.19 mm (based on 3 specimens).

Remarks. Originally described from *Mugil* sp. caught at Muscat, Oman (Bassett-Smith, 1898b), *C. platytarsis* has been reported infrequently but is known to occur widely across the Indo-Pacific, from the Arabian Gulf and India (Rangnekar, 1955b; Pillai, 1967b, 1985), and to Australia (Kabata, 1965b). Pillai (1967b) considered *C. bombayensis* Rangnekar, 1955, described from specimens collected from *M. cephalus* caught off Bombay, to be a junior subjective synonym of *C. platytarsis* and confirmed this after examining Bassett-Smith's types (Pillai, 1971). The first report of *C. platytarsis* from Australia (as *C. bombayensis*) was from *Mugil cephalus* caught off Heron Island (Kabata, 1965b).

The distinctive features of *C. platytarsis* are the body proportions, with its long abdomen, the prominent fifth legs on the posterolateral corners of the genital complex, the highly flattened, spatulate tines of the sternal furca, and the form of the spines on leg 4. *Caligus platytarsis* belongs in the newly identified *C. diaphanus*-group and it shares with another member of the group, *C. tanago*, the unusual form of the spines on the exopod of leg 4. However, these species differ in the form of the sternal furca, since *C. platytarsis* has extremely flattened spatulate tines that are wider than long, compared to longer than wide in *C. tanago*. The post-antennal process lacks a tine in *C. platytarsis* but has a small tapering tine in *C. tanago*.

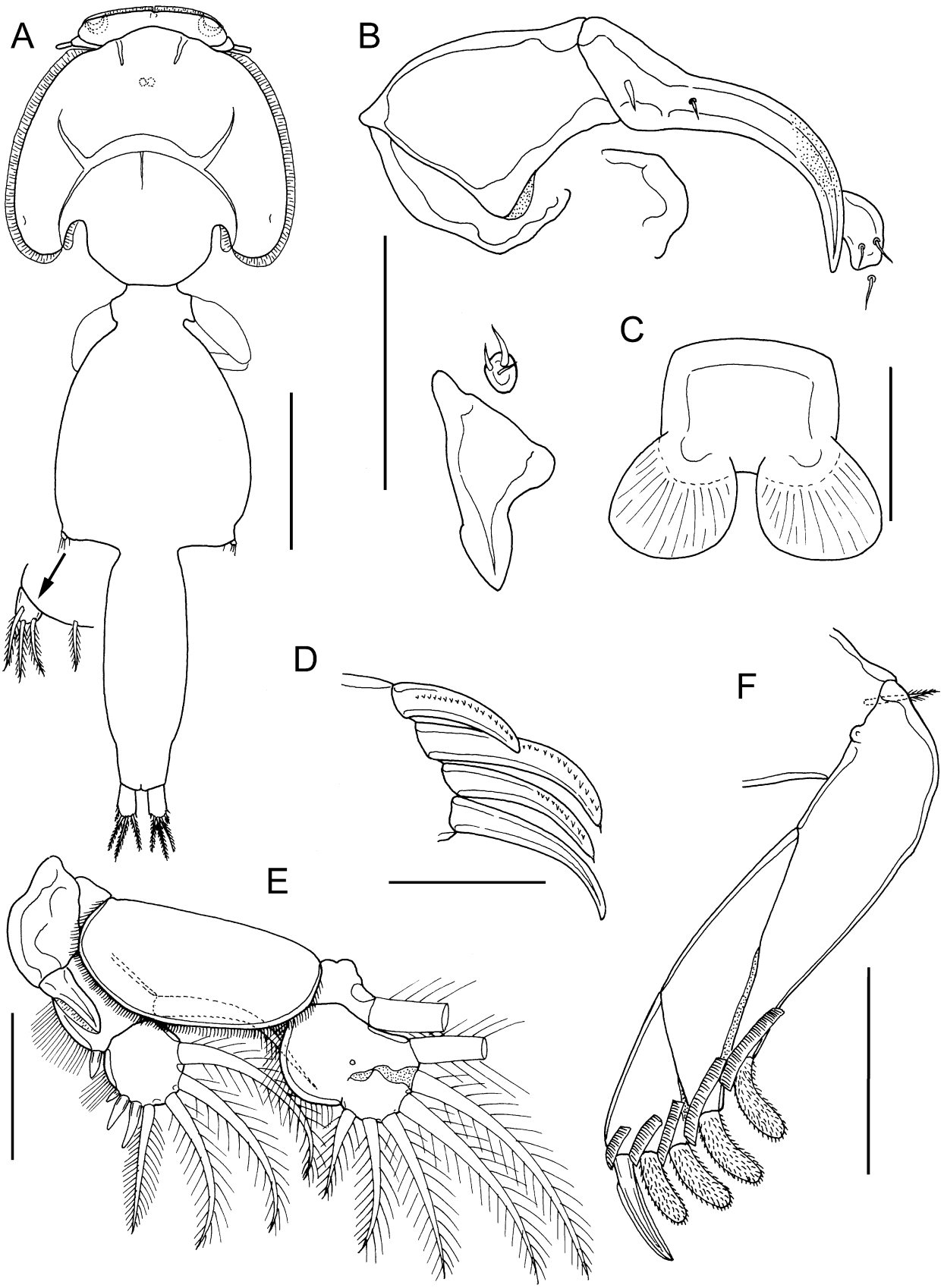

FIGURE 49. *Caligus platytarsis* Bassett-Smith, 1898, female. A, habitus, dorsal view with inset showing detail of leg 5; B, antenna, post-antennal process and maxillule drawn *in situ*; C, sternal furca; D, distal armature on exopod of leg 1; E, rami of leg 3; F, exopod of leg 4. Scale bars: A, 1.0 mm on A, 200 µm on B, F, 100 µm on C, E, 50 µm on D.

The reported body lengths for females vary: Kabata (1965b) gave a length for the female of 4.75 mm, and commented that it was larger than the Indian material from Bombay studied by Rangnekar (1955b) which had a length of 3.74 mm. In contrast, Pillai (1985) gave a length of 6.00 mm for the female. The Australian females from Moreton Bay have a mean body length of 5.09 mm (range 4.88 to 5.31 mm).

***Caligus pseudorhombi* sp. nov.**
(Figs. 50–52)

Type material. Holotype ♀, allotype ♂ from *Pseudorhombus arsius* (Hamilton, 1822) (TC17859) 04 July 2016, QM Reg. Nos Holotype ♀ W53095, allotype ♂ W53096.

Type Host. *Pseudorhombus arsius* (Hamilton, 1822).

Site on host. Body surface.

Etymology. The name of this species is derived from the host genus.

Description. Adult female (Fig. 50A) body length 4.42 mm including caudal rami. Cephalothorax slightly longer than wide; comprising about half (52%) of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly beyond rear margins of lateral portions. Lunules present ventrally on frontal plates. Genital complex about as long as wide, with angular posterolateral corners (Fig. 50A, B); complex about 2.1 times longer than abdomen. Abdomen 1-segmented; about as long as wide; carrying paired caudal rami distally; anal slit terminal. Caudal rami with parallel sides, just wider than long, measured at midpoints of margins: each ramus armed with long hirsute seta at inner distal angle, slightly longer hirsute seta sub-distally on outer margin, minute hirsute seta located just ventral to outer distal seta, and 3 long plumose setae on distal margin.

Antennule (Fig. 50C) 2-segmented; large proximal segment with 25 plumose setae arrayed along anteroventral surface and 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 50D) comprising proximal segment bearing acutely pointed, posteriorly-directed spinous process; middle segment subrectangular, tapering slightly distally, unarmed; terminal segment forming recurved claw bearing short spine on swelling proximally, and minute seta near anterior margin. Post-antennal process (Fig. 50D) well-developed, tine curved; ornamented with 2 multisensillate papillae on basal part and single multisensillate papilla on adjacent ventral cephalothoracic surface.

Mandible of typical stylet-like structure, with 12 marginal teeth. Maxillule (Fig. 50D) comprising anterior papilla bearing 3 unequal, naked setae and blunt posterior, tine-like process. Maxilla 2-segmented (Fig. 50E), comprising elongate syncoxa and basis: syncoxa unarmed; basis bearing membranous subapical flabellum on anterior margin, and terminating in 2 subequal claw-like elements (calamus and canna): calamus longer than canna, ornamented with strips of serrated membrane arranged obliquely around surface; canna ornamented with strips of serrated membrane. Maxilliped subchelate (Fig. 50F); proximal segment unarmed and with ridge-like process on myxal surface; distal subchela with apical claw separated from proximal segmental part by incomplete suture; small blunt knob present on proximal part, long seta present on concave margin.

Sternal furca (Fig. 50G) with short, tapering, pointed tines, separated widely at base.

First swimming leg pair (Fig. 51A) joined by slender intercoxal sclerite; sympod with inner and outer plumose setae derived from basis; endopod represented by unarmed process on posterior margin of basis. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment robust, about 3.4 times longer than wide and armed with small outer (anterior) spine and ornamented with row of setules along middle section of posterior margin; second segment armed with 3 long plumose setae along posterior margin and 4 distal elements along oblique distal margin. Distal elements as follows: spine 1 minute (arrowed in Fig. 51A); spine 2 longer than spine 3, each with accessory process; seta 4 longer than spines 1 and 2, and markedly longer than segment.

Second leg biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by intercoxal sclerite bearing marginal membrane posteriorly. Coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segments 1 and 2 (Fig. 51B) each with large reflexed outer spines (ornamented with strips of membrane), extending obliquely across ventral surface of ramus, plus inner plumose seta; first exopodal segment bearing flap of membrane anteriorly, reflexed back over dorsal surface; segment 3 with 2 outer spines (proximal spine minute; distal spine with membrane bilaterally); apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. Endopodal

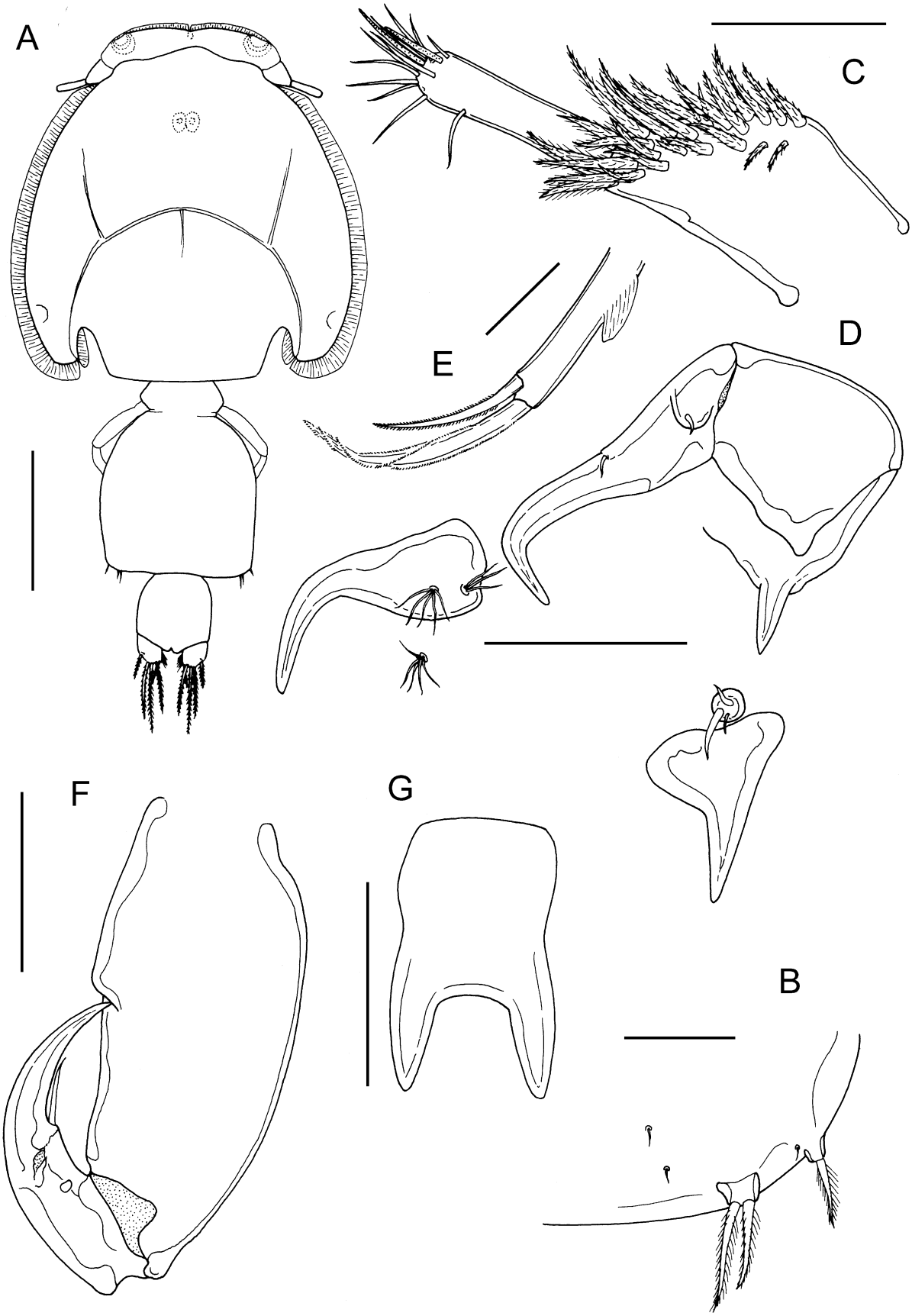

FIGURE 50. *Caligus pseudorhombi* **sp. nov.** holotype female. A, habitus, dorsal; B, left corner of genital complex showing fifth leg, ventral; C, antennule; D, antenna, post-antennal process and maxillule drawn *in situ*; E, tip of maxilla; F, maxilliped; G, sternal furca. Scale bars: 1.0 mm on A, 100 µm on B, E, 200 µm on C, D, F, G.

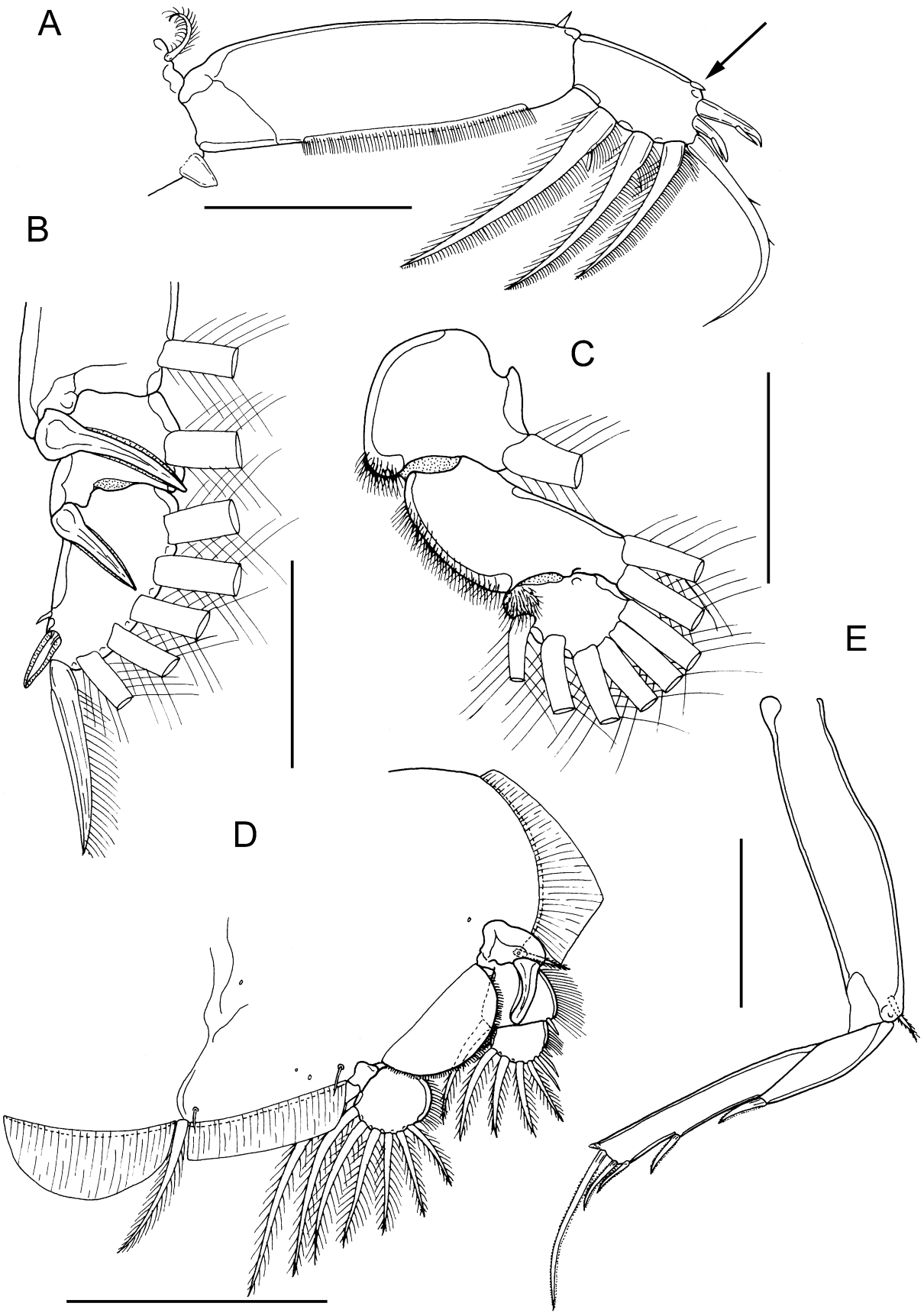

FIGURE 51. *Caligus pseudorhombi* **sp. nov.** holotype female. A, exopod of leg, ventral view with distal spine 1 arrowed; B, exopod of leg 2; C, endopod of leg 2; D, leg 3, ventral; E, leg 4. Scale bars: 200 µm on A–C, 500 µm on D, 250 µm on E.

segments 1 and 2 armed with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; outer margins of first, second and third endopodal segments ornamented with fine setules (Fig. 51C).

Third leg pair (Fig. 51D) forming flattened plate closing posterior part of cephalothoracic sucker as typical for genus. Protopodal part flattened joined by plate-like, intercoxal sclerite forming apron, ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate, and outer plumose seta dorsal to base of exopod; long sensillae located adjacent to inner coxal seta and adjacent to origin of endopod. Exopod 3-segmented; first segment lacking inner seta, armed with weakly curved outer spine directed over ventral surface of ramus, spine ornamented with inner strip of membrane; second segment with small outer spine and inner plumose seta; third with 3 unequal outer spines and 4 inner plumose setae; outer margins of segment 2 ornamented with row of slender setules. Endopod 2-segmented; first segment forming flap-like velum ornamented with row of fine setules along free margin, armed with inner plumose seta; second with 6 setal elements increasing in length from outermost to innermost.

Fourth leg (Fig. 51E) 3-segmented, comprising slender protopodal segment and 2-segmented exopod: protopodal segment armed with plumose seta distally; first exopodal segment armed with slender outer spine; second with 1 lateral spine plus 3 distal spines; apical spine more than twice length of middle spine; middle spine about 1.4 times longer than shortest spine; each spine with pecten at base.

Fifth legs located posterolaterally on genital complex (Fig. 50B); each fifth leg comprising anterior process bearing short plumose seta (representing outer protopodal seta) and broader exopodal process armed with 2 plumose setae.

Adult male (Fig. 52A) body length including caudal rami 3.96 mm. Cephalothorax as in female. Genital complex 1.42 times wider than long (0.85 x 0.66 mm), measured along mid-line; with evenly convex lateral margins. Abdomen 1-segmented; about as long as wide (0.36 x 0.36 mm); carrying paired caudal rami distally; anal slit terminal. Caudal rami as in female.

Antennule, mandible, maxillule and maxilla as in female. Antenna modified (Fig. 52C); first segment elongate; second segment reflexed, elongate, bearing corrugated adhesion pads proximally, in mid section of ventral surface, and distally; distal segment forming short powerful claw with shorter blade-like process and armed with 2 setae proximally. Post-antennal process (Fig. 52D) more strongly curved than in female; ornamented with multisensillate papillae as in female.

Maxilliped (Fig. 52E) with complex myxal margin on proximal segment produced into 2 spinous projections proximally, with tip of claw opposing base of longer process, plus rounded myxal process located distally on margin.

Legs 1 to 4 as in female.

Leg 5 (Fig. 52B) represented by process at posterolateral corner of genital complex; process weakly bifid at tip with outer point armed with plumose protopodal seta and inner papilla representing exopod bearing 2 plumose setae. Sixth leg represented by plate closing off genital opening armed with 1 seta and 2 minute spines on outer distal corner of genital operculum.

Remarks. This new species has a 2-segmented exopod on leg 4 and the distal exopodal segment carries 4 spines. It shares this form of leg 4 with about 90 congeneric species, although only 15 of them have similar body proportions in the adult female, with a genital complex (without posterolateral lobes) that is about as long as wide and about twice as long as the abdomen, which is itself about as long as wide. The species possessing this form of leg 4 and most closely matching these body proportions are: *C. acanthopagri* Ho, Lin & Chen, 1994, *C. asymmetricus, C. bifurcus* Shen, 1958, *C. buechlerae* Hewitt, 1964, *C. hobsoni* Cressey, 1969, *C. ligatus* Lewis, 1964, *C. longirostris, C. musaicus* Cavaleiro, Santos & Ho, 2010, *C. nuenonnae, C. olsoni* Pearse, 1953, *C. pectinatus* Shiino, 1965, *C. priacanthi* Pillai, 1961, *C. pterois* Kurian, 1949, *C. similis* Ho, Kim & Nagasawa, 2005 and *C. xystercus* Cressey, 1991.

The most similar species in overall body shape is *C. pterois*, a parasite of *Pterois* species described from Indian coastal waters (see Pillai, 1985, who redescribed this species under its synonym, *C. russellii* Kurian, 1950). However, the new species differs from *C. pterois* in having a reduced spine 1 on the distal exopodal segment of leg 1 which is offset subapically on the outer margin. *Caligus pterois*, like the majority of these 15 species, has a well developed spine 1 which is about equal in length to spine 2. Only in the case of *C. priacanthi* is a similarly reduced spine 1 specifically mentioned (Pillai, 1961), although spine 1 was not seen in *C. xystercus* according to Cressey (1991), Heegaard (1962) only observed a single distal spine in *C. longirostris*, and Cressey (1969) shows a spine

missing in *C. hobsoni*. These latter 3 species are easily to distinguish from the new species by other characters: *C. hobsoni* has a bifid post-antennal process and bifid posterior process on the maxillule whereas the new species has simple processes. The male of *C. longirostris* has a clearly 2-segmented abdomen which is equal in length to the genital complex, unlike the 1-segmented abdomen that is shorter than the genital complex in the male of the new species. In *C. xystercus* the female genital complex is more than 3 times longer than the abdomen, rather than exactly twice as long as in the new species.

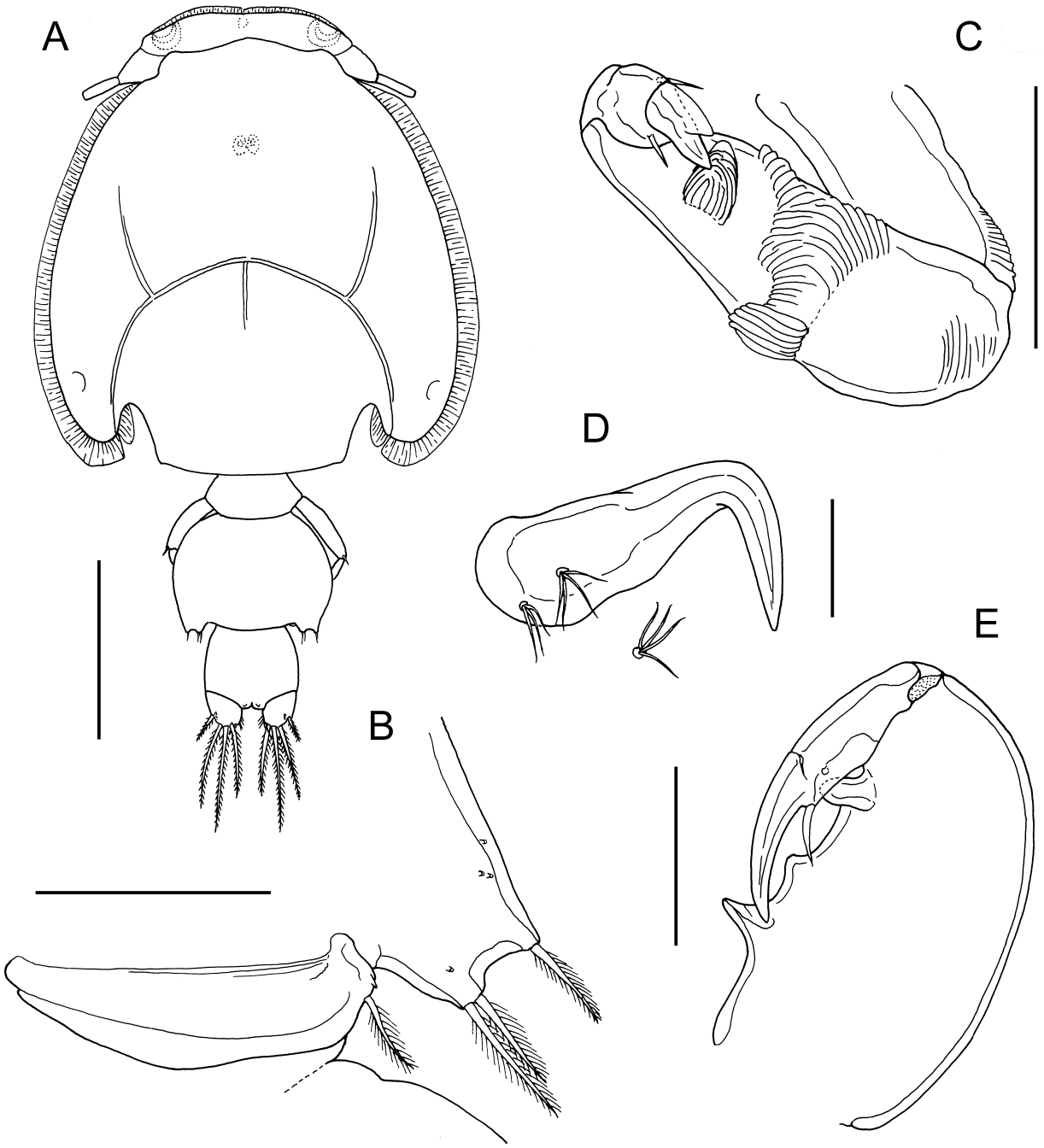

FIGURE 52. *Caligus pseudorhombi* **sp. nov.** allotype male. A, habitus, dorsal; B, left corner of genital complex, ventral view showing legs 5 and 6; C, antenna; D, post-antennal process, E, maxilliped. Scale bars: 1.0 mm on A, 200 µm on B, C, 100 µm on D, 250 µm on E.

Despite sharing a reduced spine 1 on the tip of the exopod of leg 1 with *C. priacanthi*, the new species differs in numerous features. Spines 2 and 3 both lack accessory processes in *C. priacanthi* and are similar in length to seta 4, whereas in the new species spines 2 and 3 both have accessory processes and seta 4 is about 3 times longer than spine 2. The most obvious difference is the form of leg 4: in *C. priacanthi* all 4 spines on the second exopodal

segment originate close together on the oblique distal margin of the segment whereas in *C. pseudorhombi* **sp. nov.**, this segment is elongate and the proximalmost spine originates on the lateral margin with its tip only just reaching the distal margin. In addition, the outer margin spines on exopodal segments 1 and 2 of leg 2 are strongly dentate in *C. priacanthi*.

Caligus schlegeli Ho & Lin, 2003
(Fig. 53)

Syns: *Caligus pagrosomi*: Roubal (1981)
Caligus epinepheli: Byrnes (1987)
Caligus pagrosomi schelegeli Ho & Lin, 2003
C. schelegeli: Boxshall & El-Rashidy, 2009

Material examined. 2♀♀, 1 chalimus from *Acanthopagrus australis* (Günther, 1859) (TC17123) 14 January 2016, QM Reg. No. W53097; 2♀♀, 3♂♂ (TC17126) 14 January 2016, QM Reg. No. W53098; 1♀ (TC17133) 14 January 2016, QM Reg. No. W53099; 2♀♀, 1 chalimus (TC17135) 14 January 2016, QM Reg. No. W53100; 5♀♀ (TC17145) 14 January 2016, QM Reg. No. W53101; 1♀ (TC17250) 18 January 2016, QM Reg. No. W53102; 3♀♀ (TC17310) 20 January 2016, QM Reg. No. W53103; 9♀♀, 2♂♂, 7 chalimus (TC17316) 20 January 2016, QM Reg. No. W53104; 1♀ (TC17544) 24 June 2016, QM Reg. No. W53105; 3♀♀ (TC17580) 25 June 2016, QM Reg. No. W53106; 1♀, 1 immature ♀, 2♂♂, 2 chalimus (TC17624) 27 June 2016, 7♀♀ (TC17855) 4 July 2016, 1♂, 4 chalimus (TC17583) 25 June 2016, 1♀, 2♂♂ (TC17629) 27 June 2016, 1♂, 4 chalimus (TC17716) 29 June 2016, 1♀ (TC17727) 29 June 2016, 7♀♀, 3 immature ♀, 5 ♂♂ (TC 17786) 1 July 2016, 1♀ (TC17814) 3 July 2016; NHMUK 2017.312–321. 1♂ from *Apogon doederleini* Jordan & Snyder, 1901 (TC17160) 14 January 2016, NHMUK 2017.359;1♀, 1♂, 1 chalimus from *Girella tricuspidata* (Quoy & Gaimard, 1824) (TC17604) 26 June 2016, 4♀♀, 2♂♂ (TC17146) 14 January 2016, 1 immature (TC17130) 14 January 2016, 1♂ (TC 17803) 2 July 2016, 2♀♀ (TC 17820) 3 July 2016; NHMUK 2017.403–407. 1 immature ♂ from *Pentapodus paradiseus* (Günther, 1859) (TC17600) 26 June 2016, NHMUK 2017.360;1♀ from *Rhabdosargus sarba* (Forsskål, 1775) (TC17318) 20 January 2016, 2♂♂ (TC17324) 20 January 2016;5♀♀ from *Selenotoca multifasciata* (Richardson, 1846) (TC17062) 13 January 2016, QM Reg. No. W53107; 7♀♀ (TC17099) 13 January 2016, 1♀ (TC17137) 14 January 2016, 10♀♀ (TC17153) 14 January 2016, 5♀♀, 6♂♂ (TC 17169) 15 January 2016, 2♂♂ (TC 17225) 18 January 2016, QM Reg. No. W53108; 1♀, 1♂ (TC17303) 20 January 2016; NHMUK 2017.408–417. 1♂ from *Sillago maculata* Quoy & Gaimard, 1824 (TC17546) 24 June 2016, NHMUK 2017.361.

Site on host. Roof of mouth, oral cavity, tongue.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes. Frontal plates with large lunules. Genital complex with waist-like anterior region, lateral margins tapering anteriorly more-or-less parallel posteriorly, about 1.2 times longer than wide, without posterolateral lobes (Fig. 53A); abdomen indistinctly 2-segmented; about 2.1 times longer than wide and shorter than genital complex. Proximal segment of antenna with short rounded posterior process provided with marginal flange (Fig. 53B). Post-antennal process strongly curved; associated papillae bisensillate. Maxillule with slight marginal flange on posterior process (Fig. 53B). Sternal furca with incurved tines; accessory processes present on ventral surface of cephalothorax either side of sternal furca. Distal exopodal segment of leg 1 with 1 minute, unarmed vestigial seta on posterior margin (Fig. 53C), lacking plumose setae; distal spines 2 and 3 each with accessory process; seta 4 about 40% longer than spine 1, shorter than segment. Leg 2 outer spines on first and second exopodal segments aligned obliquely across ramus; proximal outer spine on third segment short, distal outer spine with extensive bilateral membrane (Fig. 53D). Leg 3 with 3-segmented exopod; first segment bearing weakly curved outer spine, lacking inner seta; second with outer spine and inner seta; third with 3 spines and 4 setae: endopod 2-segmented; first segment forming well developed velum, bearing inner seta; compound distal segment with 6 plumose setae. Leg 4 uniramous, 3-segmented (Fig. 53E); exopodal segments with I; IV spines; outer spine on first segment reaching almost to middle of lateral spine; lateral spine just reaching base of outermost distal spine, apical spine longest, middle distal spine 0.8 times as long as apical, outermost distal spine 0.6 times as long as apical. Mean body length of female 3.14 mm, range 2.81 to 3.42 mm (based on 10 specimens); mean body length of male 2.41 mm, range 2.15 to 2.62 mm (based on 10 specimens).

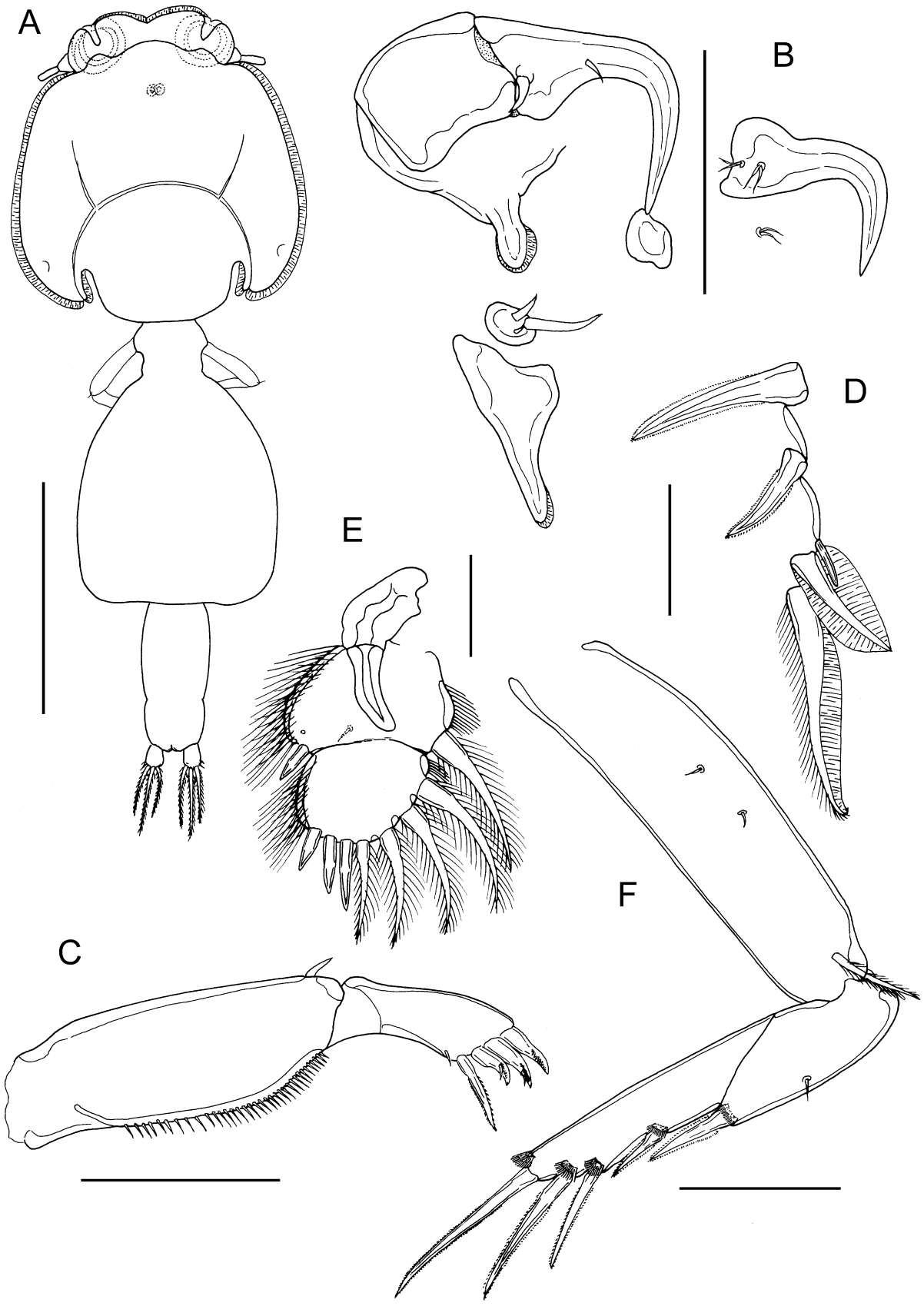

FIGURE 53. *Caligus schlegeli* Ho & Lin, 2003, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, exopod of leg 1, ventral; D, outer margin spines on exopod of leg 2; E, exopod of leg 3; F, leg 4. Scale bars: 1.0 mm on A, 100 µm on B, C, F, 50 µm on D, E.

Remarks. This species is a member of the *C. productus*-group of species characterized by the extreme reduction or loss of the three plumose setae on the posterior margin of the distal exopodal segment of leg 1 (Boxshall & El-Rashidy, 2009). It was originally recognised as a subspecies of *C. pagrosomi* by Ho & Lin (2004), but Boxshall & El-Rashidy (2009) subsequently raised this subspecies to species level, as C. *schelegeli* Ho & Lin. 2004. It is proposed here to amend the spelling of the name: Ho & Lin (2004) spelled the name *C. schelegeli* in the section heading, but in the legends of figures 121 to 123 in the same work, the name was given as *C. schlegeli*. Whilst not explicitly stated, the name choosen by Ho & Lin (2003) appears to refer to the name of its "major" host *Acanthopagrus schlegeli* (Bleeker, 1854) (Ho & Lin, 2004) which, in turn, honours the nineteenth Century German biologist Hermann Schlegel. The change to *C. schlegeli* can be considered a justified emendation. The Moreton Bay material from *A. australis* keys out to *C. schlegeli* (as *C. schelegeli*) using Boxshall & El-Rashidy (2009).

In Moreton Bay *C. schlegeli* is a common species occurring at high abundance on its preferred host *A. australis*. This species has previously been reported from localities off New South Wales and Queensland by Roubal (1981), as *C. pagrosomi*, and by Byrnes (1987), as *C. epinepheli*. Ho & Lin (2004) explicitly included *C. epinepheli* of Byrnes in the synonymy of their new subspecies, *Caligus pagrosomi schelegeli*. In Moreton Bay *C. schlegeli* was found on six different hosts in addition to *A. australis*: *Rhabdosargus sarba*, *Selenotoca multifasciata*, *Girella tricuspidata, Apogon doederleini*, *Pentapodus paradiseus* and *Sillago maculata,* although from the last three host species only single male specimens were recovered.

Caligus sclerotinosus Roubal, Armitage & Rohde, 1983
(Figs. 54, 55)

Syn: *Caligus* sp. Roubal 1981: 31–33pp., figs. 157–170.

Material examined. 1♀ from *Acanthopagrus australis* (Günther, 1859) (TC17580) 25 June 2016, QM Reg. No. W53109; 1♀ (TC17786), 01 July 2016, NHMUK Reg. No. 2017.322; 1♂ (TC17577) 25 June 2016, QM Reg. No. W53110.

Site on host. body surface.

Differential diagnosis. Cephalothorax extremely dorsoventrally flattened with well-developed marginal membranes along margins of lateral zones of dorsal cephalothoracic shield; frontal plates prominent, with large lunules. Genital complex broad, about 1.7 times wider than long, with conical fifth legs visible in dorsal view at posterolateral corners of complex (Fig. 54A); abdomen 1.4 times wider than long, only about 25% as long as genital complex. Antenna with broad spatulate posterior process on proximal segment (Fig. 54B). Post-antennal process with broad simple tine, associated papillae unisensillate. Maxillule with broad tine on posterior process, and smooth post-oral process (Fig. 54C). Maxilla with minute marginal ridges distally giving appearance of spinules in lateral view (Fig. 54D). Maxilliped slender, lacking myxal process. Sternal furca with short spatulate tines (Fig. 54E). Longitudinal ridges present on ventral cephalothoracic surface, either of sternal furca. Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal spine 1 shorter than spines 2 and 3, offset proximally; spines 2 and 3 each with accessory process; seta 4 naked, longer than spine but markedly shorter than segment. Leg 2 with endopodal segments 2 and 3 ornamented with marginal setules; outer spines on exopodal segments 1 and 2 lying obliquely across segment; proximal spine on third segment short, distal spine more than twice as long and unilaterally plumose (Fig. 54F). Leg 3 with 3-segmented exopod; first segment bearing short, blunt spine but lacking inner seta; second segment with outer spine and inner plumose seta; third with 3 outer spines and 4 plumose setae (Fig. 54G). Leg 4 uniramous, with long 2-segmented exopod armed with 1 lateral and 3 distal margin spines (Fig. 54H), each with elongate pecten near base. Leg 5 large, conical, projecting from posterolateral corner of genital complex: armed with single seta at base and 2 setae at tip. Mean body length of female 2.76 mm, range 2.73 to 2.78 mm (based on 2 specimens).

Male body length 2.31 mm, including caudal rami. Cephalothorax as in female, unusually flattened dorsoventrally and with prominent frontal plates (Fig. 55A). Genital complex with slightly convex lateral margins and with conspicuous paired fifth and sixth legs along posterior margin (Fig. 55B). Abdomen 1-segmented, about as long as wide, carrying paired caudal rami distally; anal slit terminal. Caudal rami with parallel sides, just longer than wide, measured at midpoints of margins. Each ramus armed with short plumose seta at inner distal angle,

slightly longer seta at outer distal angle, small seta located just ventral to outer distal seta, and 3 long, plumose setae on distal margin.

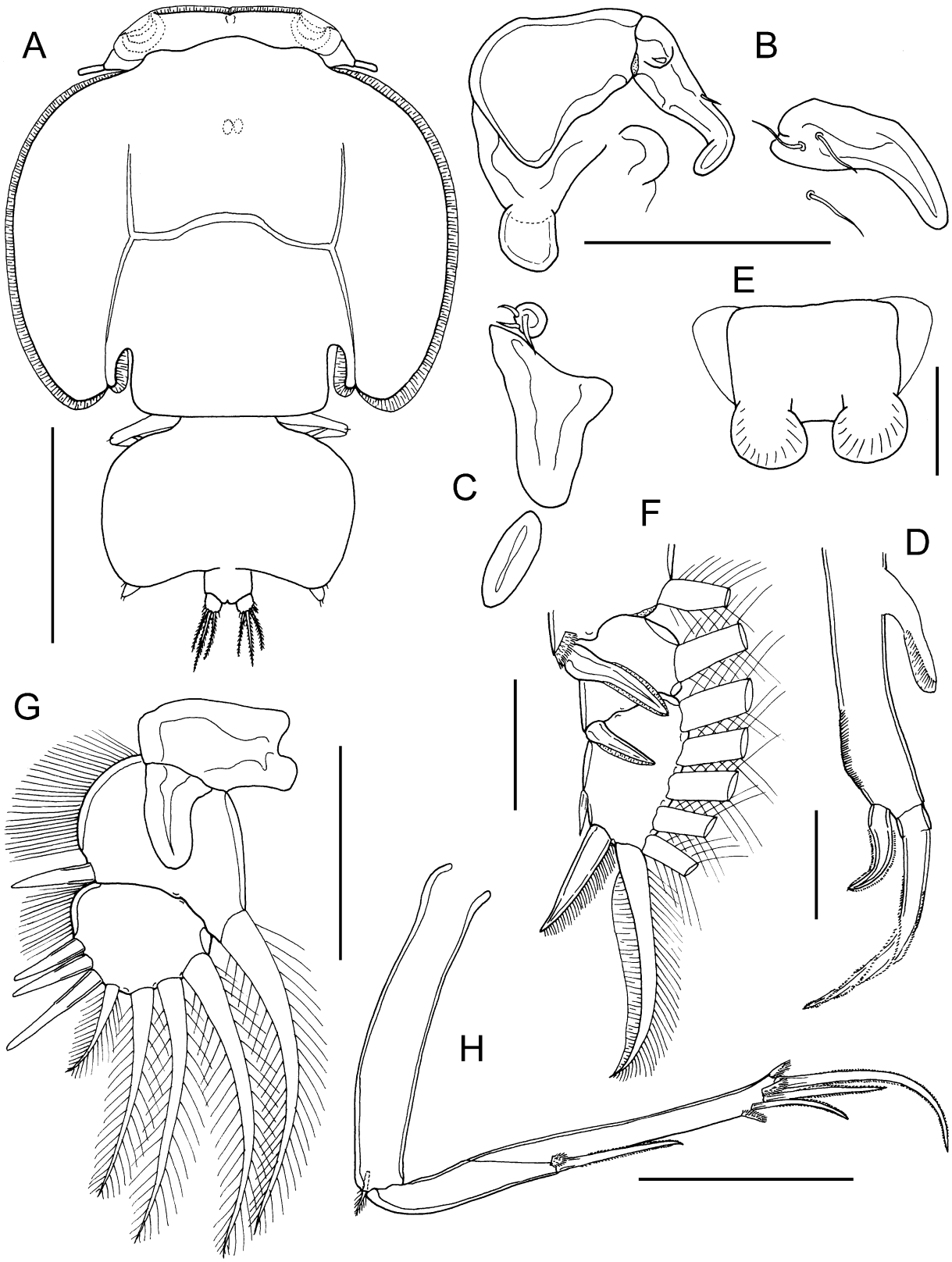

FIGURE 54. *Caligus sclerotinosus* Roubal, Armitage & Rohde, 1983, female. A, habitus, dorsal; B, antenna and post-antennal process drawn *in situ*; C, maxillule and postoral process drawn *in situ*; D, tip of maxilla; E, sternal furca; F, exopod of leg 2; G, exopod of leg 3; H, leg 4. Scale bars: 1.0 mm on A, 200 µm on B, C, H, 50 µm on D, E, 100 µm on F, G.

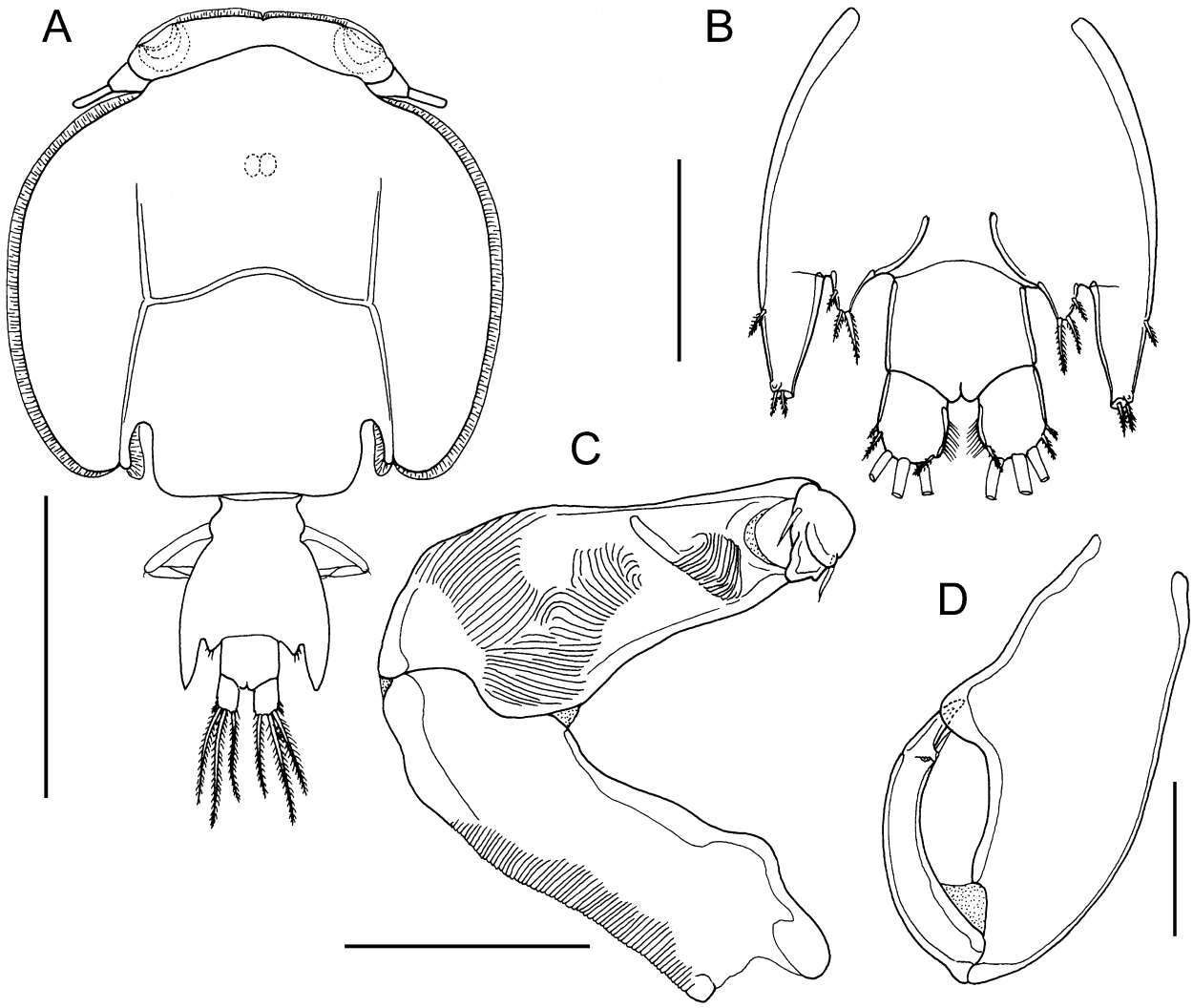

FIGURE 55. *Caligus sclerotinosus* Roubal, Armitage & Rohde, 1983, male. A, habitus, dorsal; B, genital complex and abdomen, ventral; C, antenna; D, maxilliped. Scale bars: 1.0 mm on A, 250 µm on B, 100 µm on C, D.

Antennule, mandible, maxillule and maxilla as in female. Antenna modified (Fig. 55C); first segment elongate with marginal corrugations forming adhesion pad; second segment reflexed, elongate, bearing corrugated adhesion pads proximally and distally; distal segment forming short powerful claw, armed with 2 setae proximally. Maxilliped (Fig. 55D) with rounded myxal process on proximal segment (syncoxa) directly opposing tip of claw.

Legs 1 to 4 as in female.

Leg 5 (Fig. 55B) forming large conical process at posterodistal corner of genital complex, armed with outer protopodal seta proximally plus 2 plumose setae derived from exopod and originating in apical concavity. Leg 6 (Fig. 55B) represented by small process armed with 3 setae along distal and outer margins contiguous with genital operculum, closing off genital opening.

Remarks. This species was first reported and partly described by Roubal (1981) as *Caligus* sp. from *Acanthopagrus australis* caught at an unspecified locality on the coast of New South Wales (NSW). It was subsequently named by Roubal *et al.* (1983) after the discovery of additional material on another sparid host, *Pagrus auratus* (as *Chrysophrys auratus*), taken off Coffs Harbour (NSW). *Caligus sclerotinosus* was redescribed by Ho *et al.* (2004) based on material from *Pagrus major* cultured in Japanese waters. The report and redescription by Ho *et al.* (2004) was the first record of this species from outside of Australian waters, but more recently it has also been reported as a serious pest of cultured *P. major* in Korea (Venmathi Maran *et al.*, 2012a) and a single female was found in a plankton tow taken near a fish farm in Japan (Venmathi Maran & Ohtsuka, 2008). In 2014, *C. sclerotinosus* was reported from three species of *Lutjanus* Bloch, 1790 in Chamela Bay on the Pacific coast of Mexico (Morales-Serna *et al.*, 2014).

The extremely broad shape of the female genital complex with its conspicuous fifth legs located at the posterolateral corners is distinctive. The only other species with a genital complex of similar shape with a conspicuous fifth leg is *C. praecinctorius* Hayes, Justine & Boxshall, 2012. This species was originally reported from New Caledonia on *Gymnocranius grandoculis* Valenciennes, 1830, *G. euanus* (Günther, 1879) and *Epinephelus fasciatus* (Forsskål, 1775) (Hayes *et al.*, 2012). Both species have the unusual longitudinal ridges on ventral cephalothoracic surface, either side of the sternal furca, and share many other detailed features. They can be distinguished by the broader genital complex which is 2.7 times wider than long in female *C. praecinctorius* compared to 1.7 times wider in *C. sclerotinosus*. The posterior border of the female genital complex is also much more strongly concave in the former species than in the latter. The specific epithet *sclerotinosus* refers to the "heavily sclerotized carapace" (Roubal *et al.*, 1983). Only the primary sutures on the dorsal surface of the cephalothoracic shield are shown in figures 54 and 55.

The male was described by Roubal *et al.* (1983): it has the same extremely flattened body form as the female and the fifth legs are conspicuously produced at the posterolateral corners of the genital complex. The Moreton Bay material of both sexes was collected from the original host reported by Roubal (1981), *Acanthopagrus australis*.

Caligus seriolicolus **nom. nov.**
(Fig. 56)

Syn: *Parapetalus spinosus* Byrnes, 1986

Material examined. 1♀, from *Seriola hippos* Günther, 1876 (TC18352) 28 March 2017, QM Reg. No. W53111.

Site on host. Unknown.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones; frontal plates with lunules (Fig. 56A); thoracic zone small, posterior margin about level with posterior margins of lateral zones. Genital complex about 1.1 times longer than wide measured along midline and with conspicuous posterolateral processes formed by fifth legs (Fig. 56B): genital complex about 1.7 times longer than abdomen. Abdomen 2-segmented, first free abdominal somite dorsoventrally flattened, wider than long and with rounded posterolateral processes; anal somite about one third width of preceding somite, bearing caudal rami. Antenna (Fig. 56C) with well developed posterior process on proximal segment. Post-antennal process bifid (Fig. 56C), main tine slightly curved; associated papillae multisensillate. Posterior process of maxillule bifid; smaller outer tine arising near base of main (inner) tine. Maxilliped of female with small process proximally on surface of myxal area; claw strongly recurved. Sternal furca with angular, incurved tines, bearing conspicuous flanges. Leg 1 with anterior process (arrowed in Fig. 56D) and extensive patch of small spinules on sympod; distal exopodal segment with 3 short plumose setae on posterior margin; distal spine 1 longer than other spines; spines 2 and 3 each with accessory process; seta 4 just longer than spine 1, about as long as segment. Leg 2 with expanded convex margin on endopodal segment 1 ornamented with spinules; with marginal setules on segments 2 and 3; outer spines on exopodal segments 1 and 2 aligned close to longitudinal axis of ramus. First exopodal segment of leg 3 with large recurved outer spine but lacking inner seta (Fig. 56E); apron with strongly-bifid, raised rib-like process plus circular array of large and conspicuous denticles on ventral surface and corrugated adhesion pad on outer margin and dorsal surface. Leg 4 uniramous, 4-segmented; exopodal segments armed with I; I; III spines. Leg 5 (Fig. 56B) comprising elongate posterolateral process on genital complex, with distinct papilla at apex bearing 3 plumose setae, protopodal seta located proximally on lateral margin of process. Body length of female 4.24 mm.

Remarks. This species was originally described as *Parapetalus spinosus* Byrnes, 1986, based on material of both sexes collected from *Seriola hippos* caught off Coffs Harbour, New South Wales (Byrnes, 1986). In their major review of the Caligidae, Dojiri & Ho (2013: 297) concluded that *P. spinosus* is not a species of *Parapetalus* and they considered it "most likely a species of *Caligus* bearing close resemblance to *Caligus parapetalopsis* Hameed & Pillai, 1973". However, in the same work Dojiri & Ho (2013: 299) stated that "the widely expanded genital complex and abdomen [of *Caligus parapetalopsis*] suggest a closer affinity to *Parapetalus* than to *Caligus*", and they pointed out that Ho & Lin (2010) had treated *C. parapetalopsis* as a valid species of *Parapetalus*. These contradictory remarks simply highlight the lack of any clear generic distinction between *Parapetalus* and *Caligus*.

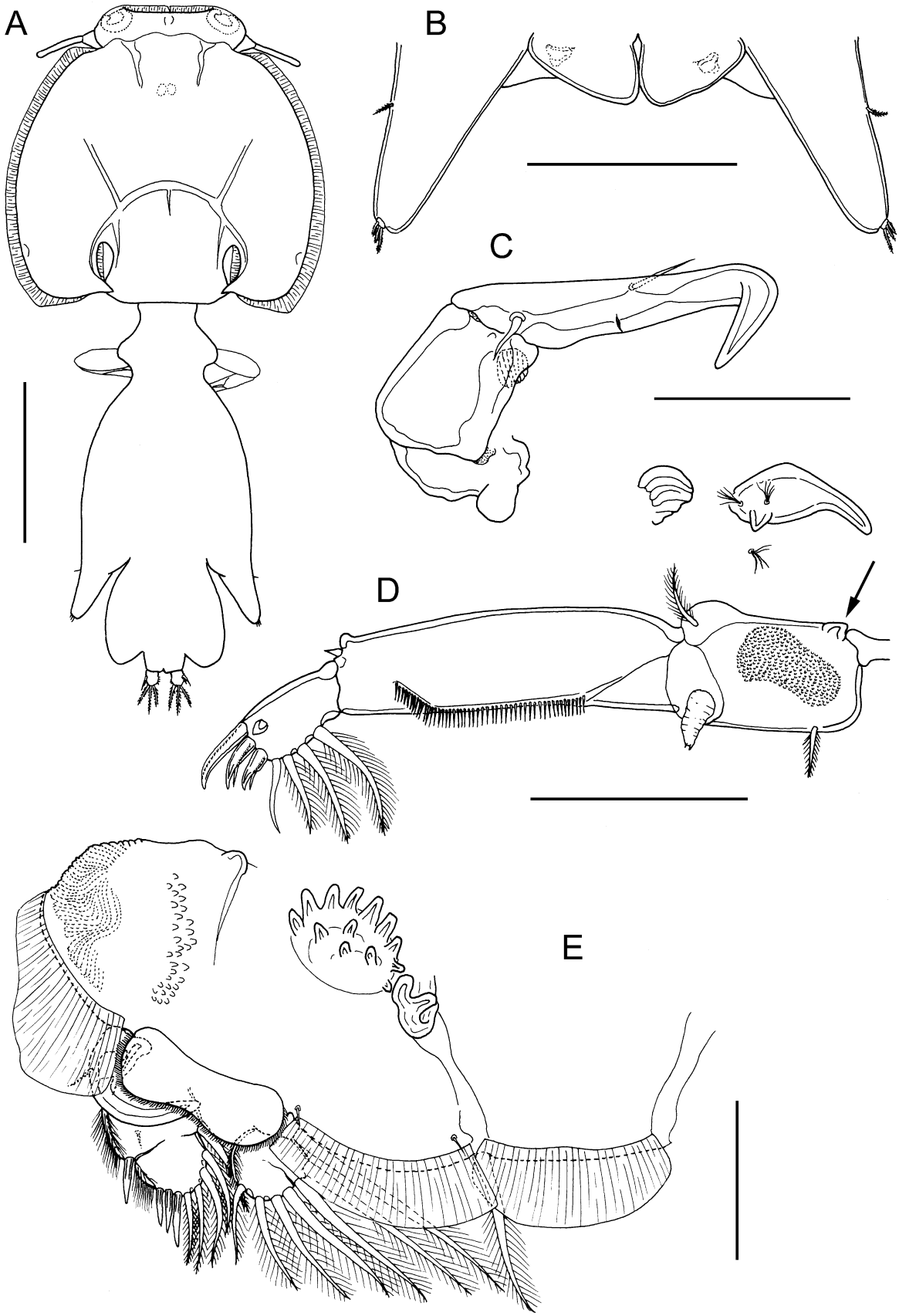

FIGURE 56. *Caligus seriolicolus* **nom. nov.** female. A. habitus, dorsal; B, posterior part of genital complex, ventral view showing fifth legs and flattened ventral lobes concealing oviduct openings; C, antenna and post-antennal process, drawn *in situ*; D, leg 1 with anterior process arrowed; E, leg 3. Scale bars: 1 mm on A, 0.5 mm on B, 200 µm on C–E.

The shared possession of the characteristic suite of features of the *C. confusus*-group by both *Parapetalus parapetalopsis* and *P. spinosus* provides robust evidence that they should be classified within that species group. Both possess an unusually broad genital complex with prominent lobate fifth legs and an unusually broad abdomen, but there seems to be no valid reason to treat these features as of generic level significance. It is proposed here to return *Parapetalus parapetalopsis* (Hameed & Pillai, 1973) to its original combination, as *Caligus parapetalopsis* Hameed & Pillai, 1973, and to transfer *Parapetalus spinosus* Byrnes, 1986 to *Caligus*. This latter action would create a secondary homonym, because the name is preoccupied by *Caligus spinosus* Yamaguti, 1936, so the replacement name *Caligus seriolicolus* **nom. nov.** is proposed. The name refers to the host genus.

Caligus seriolicolus **nom. nov.** exhibits the characteristic suite of features of the *C. confusus*-group: a 3-segmented exopod on leg 4 armed with I, I, III spines, the raised bifid cuticular rib and a circular rosette-like array of large denticles on the apron of leg 3, the large recurved hook on the first exopodal segment of leg 3, and the presence of an accessory tine on both the post-antennal and posterior maxillulary processes.

The body length of the Moreton Bay female, 4.24 mm, falls within the range of 3.47 to 4.90 mm given by Byrnes (1986) for his material from New South Wales. This is only the second report of this species and *Seriola hippos* is the only known host.

Caligus sicarius Kabata, 1984

(Figs. 57, 58)

Material examined. 1♀ from *Mugil cephalus* Linnaeus, 1758 (TC17307) 20 January 2016, QM Reg. No. W53112.

Site on host. Unknown (in body wash).

Description. Adult female (Fig. 57A) body length 2.42 mm including caudal rami. Dorsal cephalothoracic shield subcircular (1.66 mm long x 1.56 mm wide); comprising about 70% of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly beyond rear margins of lateral portions. Lunules present ventrally on frontal plates. Genital complex fused to fourth pedigerous somite; subrectangular, 1.6 times wider than long (0.89 x 0.53 mm); with convex lateral margins and rounded corners (Fig. 57B); fifth legs located ventrally close to posterolateral corners (Fig. 57C). Genital complex about 4.2 times longer than abdomen. Abdomen 1-segmented; about 1.4 times wider than long (0.30 x 0.21 mm) in ventral view (Fig. 57B); carrying paired caudal rami distally; anal slit terminal. Caudal rami with parallel sides, just longer than wide, measured at midpoints of margins. Each ramus armed with short hirsute seta at inner distal angle, slightly longer hirsute seta at outer distal angle, minute hirsute seta located just ventral to outer distal seta, and 3 long plumose setae on distal margin.

Antennule (Fig. 57D) 2-segmented; large proximal segment with 25 plumose setae arrayed along anteroventral surface and 2 setae located dorsally; short distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 57E) comprising proximal segment bearing spatulate posteriorly-directed spinous process; middle segment short, subrectangular, unarmed; terminal segment forming slender recurved claw bearing accessory spine proximally, and armed with slender distal seta. Post-antennal process (Fig. 57E) well-developed, weakly curved; ornamented with 2 unisensillate papillae on basal part and single unisensillate papilla on adjacent ventral cephalothoracic surface. Small process present between base of antenna and post-antennal process.

Mandible of typical stylet-like structure, with 12 marginal teeth. Maxillule (Fig. 57E) comprising anterior papilla bearing only 2 unequal, naked setae and posterior, tapering process; sclerite lying medial to papilla enlarged and forming spinous process overlapping base of maxillulary process. Maxilla 2-segmented, comprising elongate unarmed syncoxa and basis: basis bearing membranous subapical flabellum on anterior margin, and terminating in 2 subequal claw-like elements (calamus and canna). Calamus slightly longer than canna, ornamented with strips of serrated membrane arranged obliquely around surface; canna ornamented with strips of serrated membrane. Maxilliped subchelate (Fig. 57F); slender proximal segment unarmed and without process on myxal surface; distal subchela with apical claw; short, slender seta present on concave margin.

Sternal furca (Fig. 58A) with wedge-shaped tines, gape between tines square-sided. Tapering accessory processes present either side of furca.

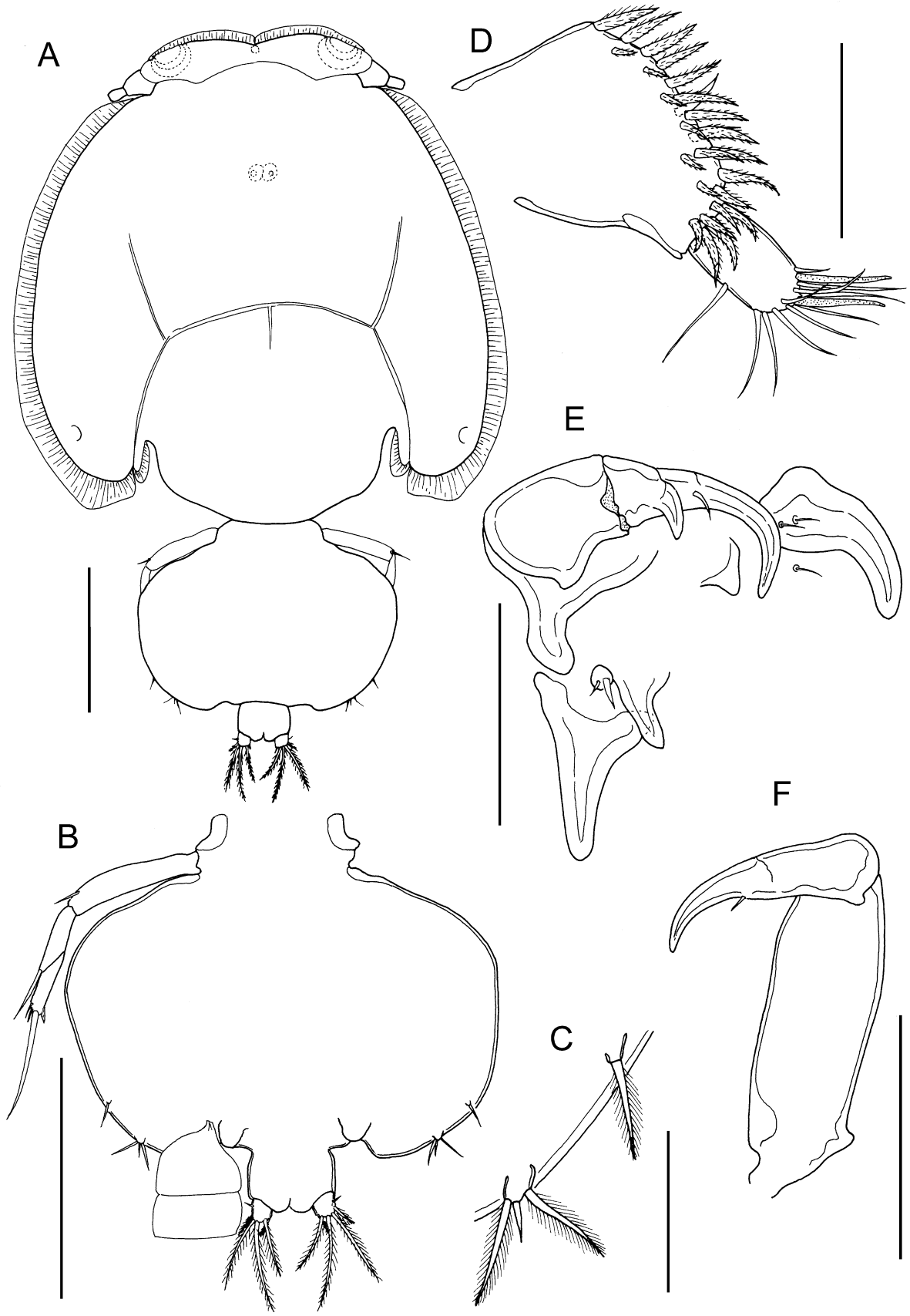

FIGURE 57. *Caligus sicarius* Kabata, 1984, female. A, habitus, dorsal; B, fourth pedigerous somite, genital complex and abdomen, ventral; C, left corner of genital complex showing leg 5, ventral; D, antennule; E, antenna, post-antennal process and maxillule drawn *in situ*; F, maxilliped. Scale bars: 500 µm on A, B, 100 µm on C–D, 200 µm on E–F.

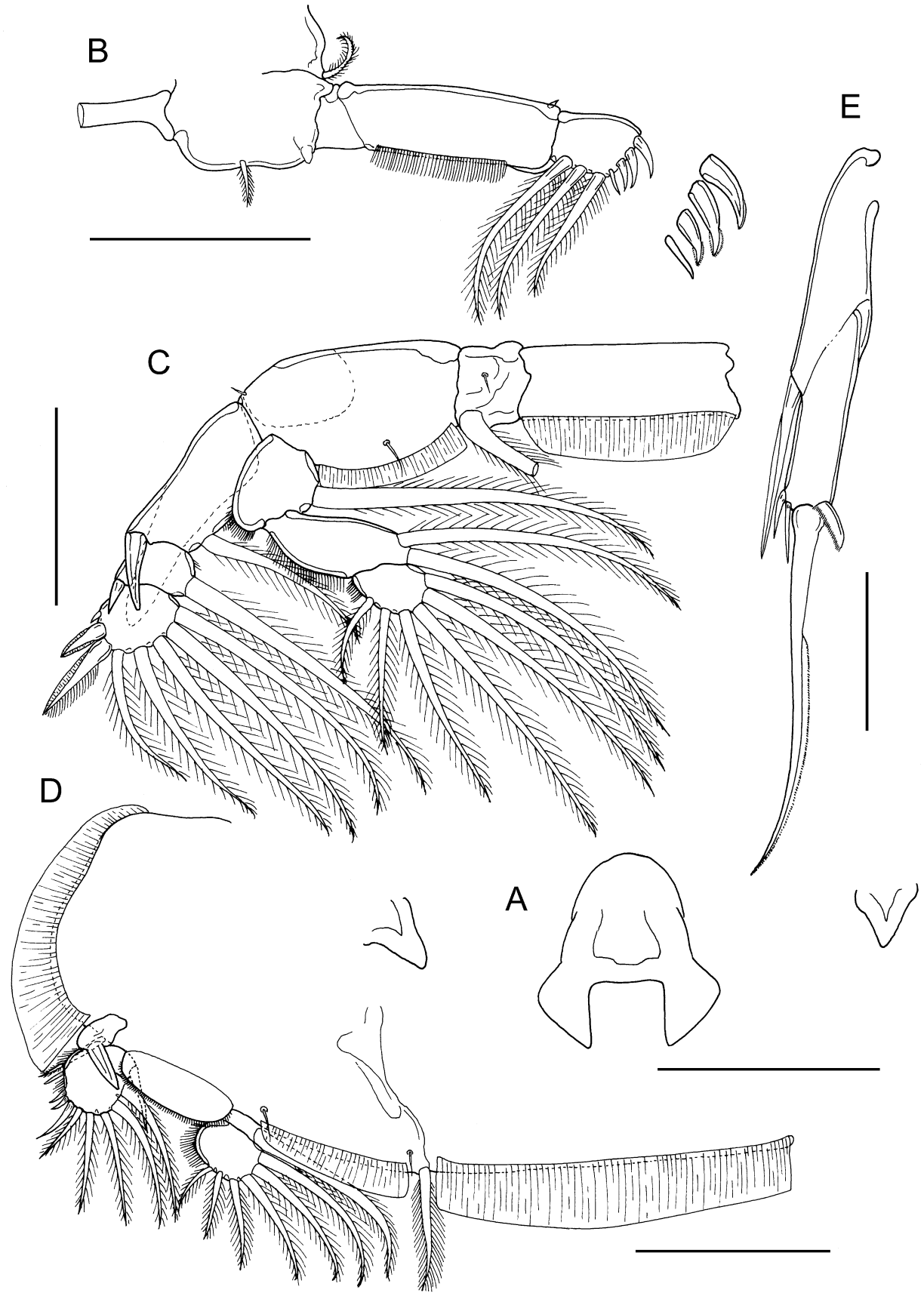

FIGURE 58. *Caligus sicarius* Kabata, 1984, female. A, sternal furca and accessory processes, ventral view *in situ*; B, leg 1, with inset showing setation elements of distal margin; C, leg 2; D, leg 3, ventral; E, exopod of leg 4. Scale bars: 200 µm on A–D, 100 µm on E.

First swimming leg pair (Fig. 58B) joined by slender intercoxal sclerite; sympod with inner and outer plumose setae derived from basis; endopod represented by unarmed process on posterior margin of basis. Exopod 2-segmented, directed laterally and forming main axis of leg; first segment robust, about 2.9 times longer than wide and armed with small outer (anterior) spine and ornamented with row of setules along posterior margin; second segment short, armed with 3 long plumose setae along posterior margin and 4 distal elements along oblique distal margin. Distal elements (Fig. 58B, inset) as follows: spine 1 (anterior-most) longest with margin membrane distally; spines 2 and 3 progressively smaller, each with bilateral serrated membrane distally; seta 4 naked, about as long as spine 3, shorter than segment.

Second leg (Fig. 58C) biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by intercoxal sclerite bearing marginal membrane posteriorly. Coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segment 1 with inner plumose seta and large naked outer spine extending obliquely across surface of ramus but closely aligned to lateral margin, ornamented with flap of membrane anteriorly, reflexed back over dorsal surface of segment; exopodal segment 2 with outer spine directed-distally plus inner plumose seta; segment 3 with 2 outer spines (proximal spine small and naked, distal spine with bilateral membrane); apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. Endopodal segments 1 and 2 armed with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; outer margins of all endopodal segments ornamented with fine setules.

Third leg pair (Fig. 58D) forming flattened plate closing posterior part of cephalothoracic sucker as typical for genus. Protopodal part flattened joined by plate-like, intercoxal sclerite (apron) ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate, and outer plumose seta dorsal to base of exopod; sensillae located adjacent to inner coxal seta and adjacent to origin of endopod. Exopod 2-segmented; first segment armed with straight outer claw directed over ventral surface of ramus and small inner plumose seta; distal segment compound, with 1 proximal and 3 distal spiniform elements on outer margin and 5 plumose setae on distal and inner margins; outer margin of distal segment ornamented with rows of slender setules either side of first outer spine. Endopod 2-segmented; first segment expanded laterally to form flap-like velum closing off space between rami; velum ornamented with row of fine setules along free margin and bearing inner plumose seta; compound distal segment with 6 setal elements increasing in length from outermost to innermost.

Fourth leg 2-segmented (Fig. 57B), comprising slender protopodal segment and 1-segmented exopod: protopodal segment armed with plumose seta distally; exopodal segment (Fig. 58E) with partial suture marking plane of fusion between former segments; armed with outer spine extending beyond distal margin of segment, long apical element with serrated membrane on along inner margin, plus 2 short naked spines located just lateral to base of apical spine, apical spine with well-developed pecten at base.

Fifth legs located posterolaterally on genital complex (Fig. 57B); represented by plumose seta on anterior papilla plus 1 short naked seta and 2 plumose setae on posterior papilla representing exopod (Fig. 57C).

Remarks. This small *Caligus* has not been reported since its original discovery in the Red Sea (Kabata, 1984) and is redescribed here because it exhibits several unusual character states. It has a secondary (accessory) tine located proximally on the distal segment of the female antenna. This is a common state for males in the genus, as in males of the *Caligus diaphanus*-group, but is relatively rare among females. The wedge-shaped tines of the sternal furca of *C. sicarius* are also unusual, especially when combined with the presence of paired accessory processes either side of the furca. Accessory processes are present in several other species, including *C. coryphaenae* Steenstrup & Lütken, 1861 and some members of the *Caligus productus*-group such as *C. haemulonis* Krøyer, 1863 and *C. turbidus* **sp. nov.** (Boxshall & El-Rashidy, 2009; present account).

Leg 3 was not fully figured by Kabata (1984). It has a 2-segmented exopod with a compound distal segment representing the second and third ancestral segments. This state is characteristic of other caligid genera such as *Anuretes* and *Mappates*, but is less common in *Caligus* species which most commonly retain a 3-segmented condition. The presence of an inner plumose seta on the first exopodal segment of leg 3 is also uncommon in *Caligus*.

The exopod of leg 4 is unique: no other *Caligus* has such a configuration. The exopodal segments are separated only by a trace of the suture marking the plane of the original articulation between the ancestral first and second exopodal segments. There is a long spine on the outer margin derived from the first exopodal segment and the

distal margin carries a long apical spine with a conspicuous pecten at its base, plus 2 reduced outer spines. It most closely resembles the leg 4 of *Caligus pageti* Russell, 1925, which has a 1-segmented exopod bearing one outer spine about at mid margin, and one long apical spine plus a short outer spine.

The type host was a mugilid, *Crenimugil crenilabis* (Forsskål, 1775) (as *Crenimugil crenilabris*), caught in the Gulf of Aqaba (Red Sea). The single female found in Moreton Bay is only the second record of this copepod and it was collected from another mugilid, *Mugil cephalus*. This rare but widely distributed species appears to be specific to mugilids. Interestingly, *Caligus pageti* is also a parasite of mugilids and has been found in the Mediterranean and adjacent Atlantic coastal waters.

Caligus triabdominalis Byrnes, 1987

(Fig. 59)

Material examined. 1♀ from *Pomatomus saltatrix* (Linnaeus, 1766) (TC17696) 28 June 2016, QM Reg. No. W63113.

Site on host. Roof of mouth.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones of dorsal cephalothoracic shield; frontal plates with lunules. Genital complex with constricted anterior neck region; complex 1.35 times longer than wide with rounded posterolateral corners; abdomen elongate, 2.5 times longer than wide; shorter than genital complex (Fig. 59A). Antenna with small, blunt posterior process on proximal segment (Fig. 59B). Post-antennal process with weakly curved tine; associated papillae bisensillate (Fig. 59B). Maxillule with simple tine on posterior process. Maxilliped of female with slight expansion on myxal margin. Sternal furca with slender, diverging tines (Fig. 59C). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin, basal setules on margin of plumose setae nearest apex unusually stout; distal spine 1 simple, longer than spines 2 and 3, each armed with accessory process; seta 4 about twice as long as spines and about as long as segment. Leg 2 with strong denticles along outer margin of endopodal segment 2 (Fig. 59D); outer spines on exopodal segments 1 and 2 lying obliquely across axis of ramus; proximal outer spine on segment 3 tiny, much shorter than distal spine (Fig. 59E). Leg 3 with 3-segmented exopod (Fig. 59F); first segment bearing small slightly curved spine, lacking inner seta; second segment with outer spine and inner seta; third segment with 3 long spines, plus 4 plumose setae; distal endopodal segment with swollen lateral margin. Leg 4 uniramous, 3-segmented; exopodal segments 1 and 2 with I and IV spines, respectively (Fig. 59G). Body length 3.81 mm.

Remarks. The original description of *C. triabdominalis* was based on material of both sexes collected from *Acanthopagrus latus* caught off Broome, Western Australia (Byrnes, 1987). When establishing it as a new species, Byrnes (1987) only made detailed comparisons with *C. omissus*, therefore some additional comparisons with other related species are included here. The distinctive features of *C. triabdominalis* are its long genital complex and long abdomen combined with the presence of stout denticles along the outer margins of endopodal segment 2 of leg 2 and the 2-segmented exopod of leg 4 bearing 4 spines on the distal segment. It shares these characteristics with a group of congeners including: *C. asperimanus*, *C. biseriodentatus*, *C. bonito*, *C. hoplognathi*, *C. malabaricus*, *C. mutabilis*, and *C. tenuifurcatus* Wilson, 1937. *Caligus bonito*, *C. mutabilis* and *C. omissus* all possess patches of fine spinules posteriorly on the ventral surface of the abdomen, which are absent in *C. triabdominalis*. In *C. biseriodentatus* the posterior margin setae on the distal exopodal segment of leg 1 are all very reduced in size, whereas they are well developed in *C. triabdominalis*. In *C. malabaricus* the female genital complex is wider than long and the first somite of the abdomen is twice as wide as the second, while in *C. triabdominalis* the genital complex is longer than wide and the two abdominal somites are similar in width. *Caligus triabdominalis* is similar to *C. asperimanus* as redescribed by Cressey (1991) in body proportions but differs in the size and shape of the tines of the sternal furca and in having a more slender distal exopodal segment on leg 4 with spines that differ in relative length. In female *C. hoplognathi* the abdomen is twice as long as wide, compared to 2.5 times longer in *C. triabdominalis* and the sternal furca is flanked by a pair of accessory processes (Yamaguti & Yamamsu, 1959). Finally, *C. tenuifurcatus*, as the name suggests, has long slender tines on the sternal furca that are longer than the box (Wilson, 1937b) whereas those of *C. triabdominalis* are shorter than the box of the furca.

The females in the type material had a body length ranging from 4.00 to 4.18 mm (Byrnes, 1987). The sole female collected in Moreton Bay was found in the mouth of a new host, *Pomatomus saltatrix*, and was a little smaller, with a body length of 3.81 mm. This is the first record of *C. triabdominalis* from Queensland.

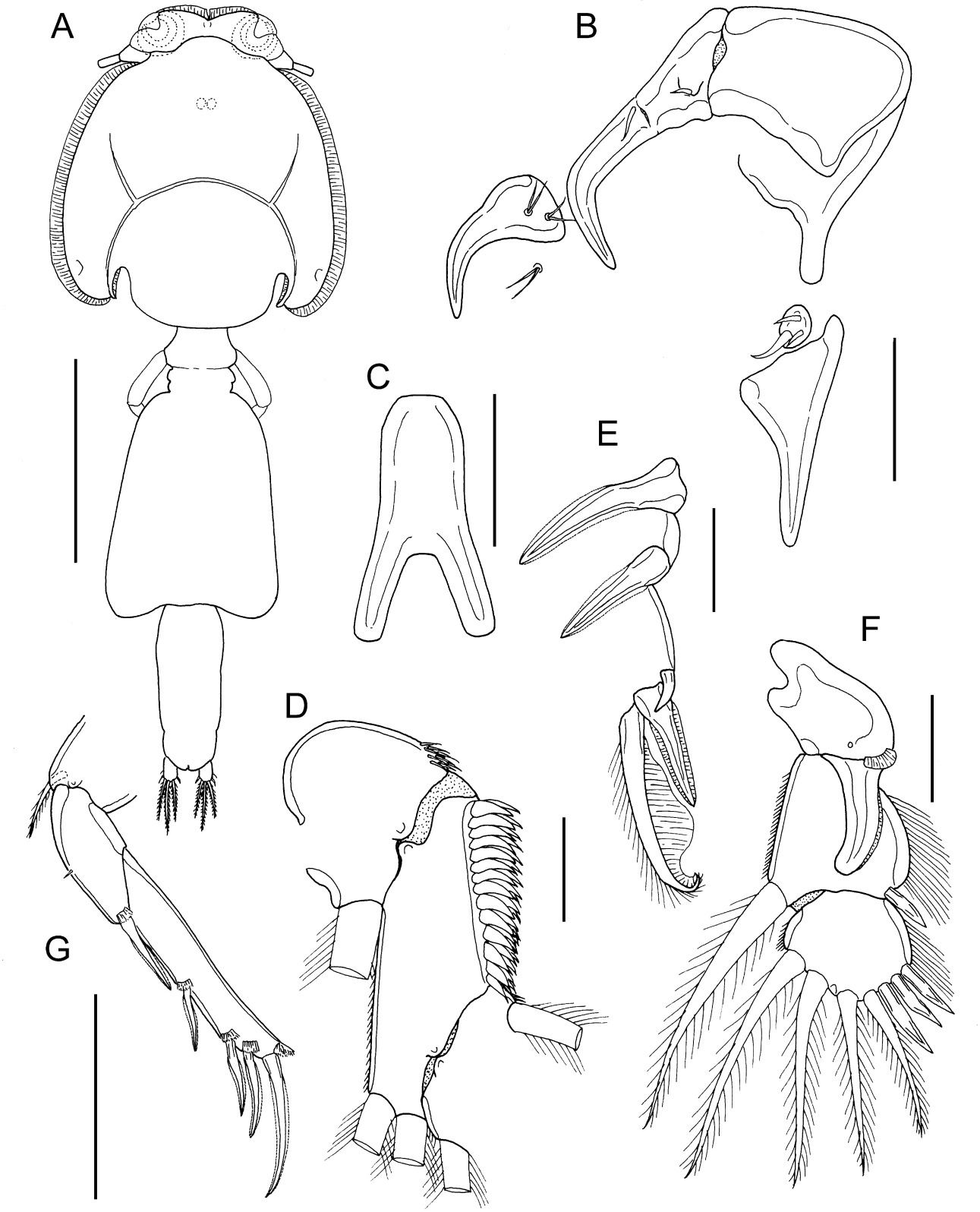

FIGURE 59. *Caligus triabdominalis* Byrnes, 1987, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, sternal furca; D, endopod of leg 2; E, outer margin spines on exopod of leg 2; F, exopod of leg 3; G, exopod of leg 4. Scale bars: 1.0 mm on A, 100 µm on B, C, 50 µm on D–F, 200 µm on G.

***Caligus turbidus* sp. nov.**
(Figs. 60–62)

Type material. Holotype ♀ and 3♀♀ paratypes from *Tripodichthys angustifrons* (Hollard, 1854) (TC17072) 13 January 2016, QM Reg. Nos Holotype ♀ W53114, 3 ♀♀ paratypes W53115; 1♀ paratype (TC17024) 12 January 2016, 1♂ paratype (TC17080) 13 January 2016, QM Reg. No. W53116, 3♀♀, 1 immature ♀ paratypes (TC 17335) 20 January 2016, QM Reg. No. W53117; 8♀♀ paratypes (TC17096) 13 January 2016, 3♀♀ paratypes (TC17927) 5 July 2016, NHMUK Reg. Nos 2017.323–333.

Type Host. *Tripodichthys angustifrons* (Hollard, 1854).

Site on host. Roof of mouth and surface of tongue.

Etymology. The name of the new species is derived from the Latin, *turbidus*, meaning unclear.

Description. Adult female (Fig. 60A) body length 2.76 mm, including caudal rami; range 2.54 to 2.92 mm (based on 11 specimens). Dorsal cephalothoracic shield subcircular; comprising about 35 % of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly beyond rear margins of lateral portions. Lunules present ventrally on frontal plates. Fourth pedigerous somite separated from genital complex by narrow constriction. Genital complex with anterior section defined by constriction, main part of complex narrow anteriorly, becoming wider posteriorly; about 1.5 times longer than wide; with linear lateral margins and rounded corners (Fig. 60A); fifth legs located ventrally close to posterolateral corners. Genital complex about 2.0 times longer than abdomen; genital complex and abdomen combined about 1.4 times longer than cephalothorax. Abdomen 2-segmented, about 1.3 times longer than wide. Anal somite (Fig. 61A) carrying paired caudal rami distally; anal slit terminal; ornamented with patches of minute spinules ventrally near origin of caudal rami. Caudal rami with parallel sides, just longer than wide, measured at midpoints of margins. Each ramus armed with short hirsute seta at inner distal angle, slightly longer hirsute seta at outer distal angle, minute hirsute seta located just ventral to outer distal seta, and 3 long plumose setae on distal margin.

Antennule (Fig. 60B) 2-segmented; large proximal segment with 25 plumose setae arrayed along anteroventral surface and 2 setae located dorsally; short distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 60C) comprising long proximal segment bearing broad, posteriorly-directed spinous process with marginal flanges; middle segment subrectangular, unarmed but with dorsal adhesion pad; terminal segment forming recurved claw bearing accessory spine proximally, and armed with slender distal seta. Post-antennal process (Fig. 60C) with well-developed curved tine; ornamented with 2 bisensillate papillae on basal part and single bisensillate papilla on adjacent ventral cephalothoracic surface. Small tapering process present between base of antenna and post-antennal process.

Mandible of typical stylet-like structure, with 12 marginal teeth. Maxillule (Fig. 60C) comprising large anterior papilla bearing 1 large and 2 small naked setae and posterior, tapering process with blunt tip. Maxilla 2-segmented (Fig. 60D), comprising unarmed syncoxa and basis: basis bearing rounded membranous subapical flabellum on anterior margin, and terminating in 2 subequal claw-like elements (calamus and canna). Calamus longer than canna, ornamented with strips of serrated membrane arranged obliquely around surface; canna ornamented with strips of serrated membrane. Maxilliped subchelate (Fig. 60E); proximal segment unarmed, with 4 ridges proximally on posterolateral surface; distal subchela with apical claw; short, slender seta present on concave margin.

Sternal furca (Fig. 60F) with incurved tines, with wide gape; small knob-like accessory processes present either side of furca.

First swimming leg pair (Fig. 60G) joined by slender intercoxal sclerite; sympod with inner and outer plumose setae derived from basis; sympod ornamented with extensive patch of spinules; endopod represented by rounded process on posterior margin of basis. Exopod 2-segmented, directed laterally and forming main axis of leg; first segment robust, about 2.6 times longer than wide and armed with small outer (anterior) spine and ornamented with row of setules along posterior margin; second segment short, lacking well developed plumose setae on posterior margin but with interruptions in thickness of cuticle and 1 minute setal vestige (arrowed in Fig. 60G), oblique distal margin with 4 elements as follows: spine 1 (anterior-most) longest with marginal membrane distally; spines 2 and 3 progressively smaller, each with accessory process; seta 4 plumose, about as long as spine 1, shorter than segment.

Second leg (Fig. 61B) biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by intercoxal sclerite bearing extensive marginal membrane posteriorly. Coxa with plumose seta and surface

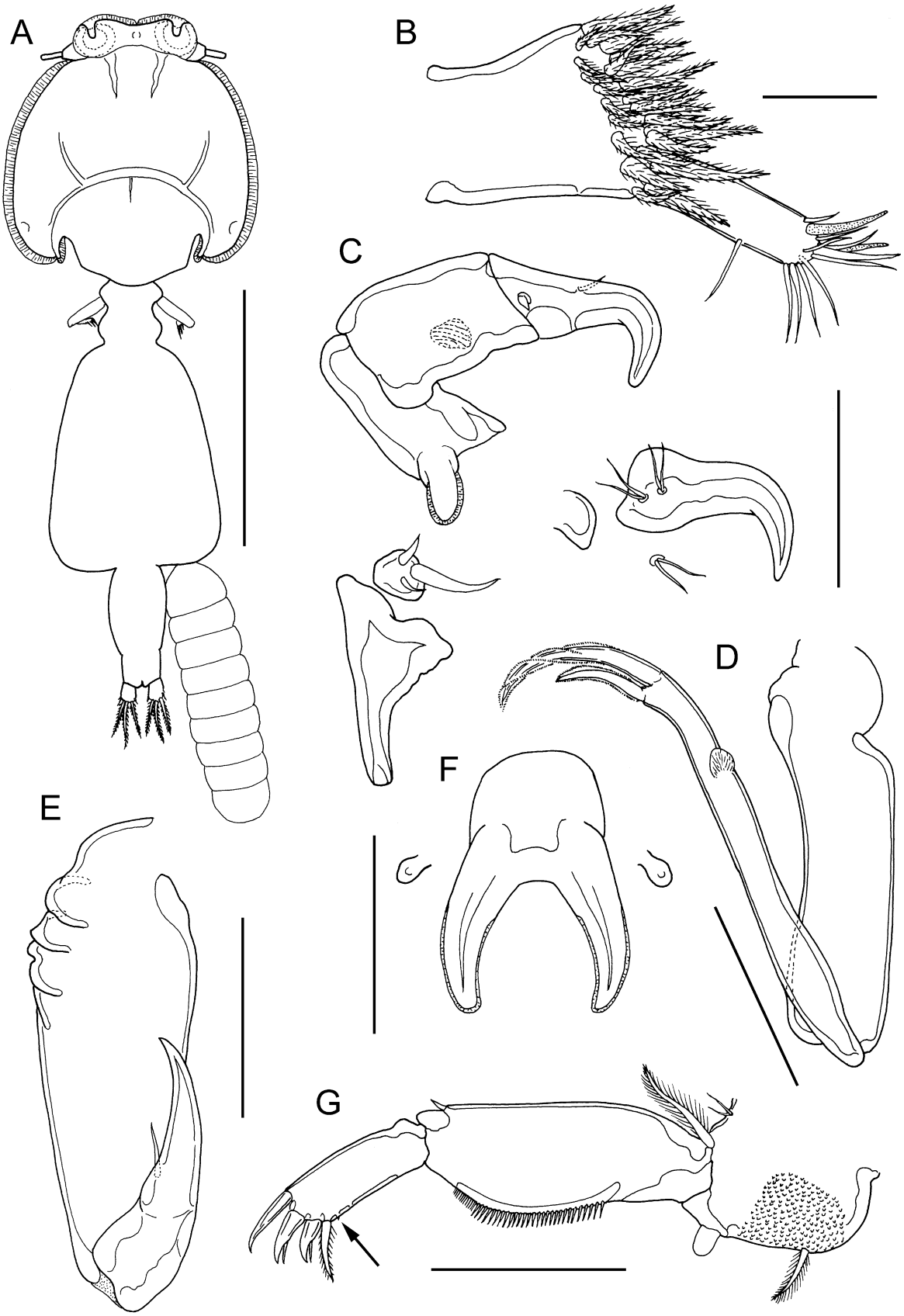

FIGURE 60. *Caligus turbidus* **sp. nov.**, paratype female. A, habitus, dorsal; B, antennule; C, antenna, post-antennal process and maxillule drawn *in situ*; D, maxilla; E, maxilliped; F, sternal furca; G, leg 1 with minute vestige of seta arrowed. Scale bars: 1.0 mm on A, 100 µm on C–G, 50 µm on B.

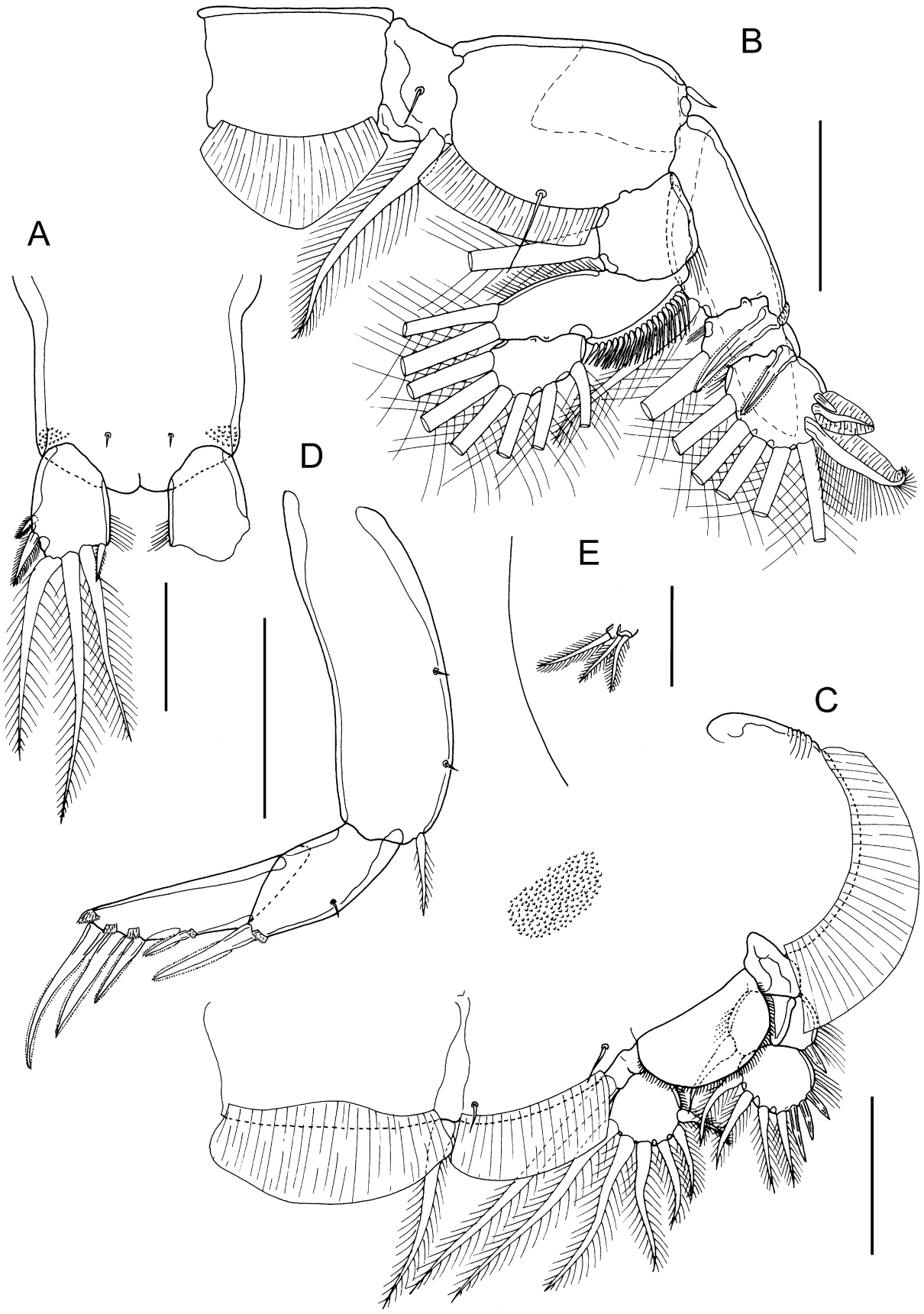

FIGURE 61. *Caligus turbidus* **sp. nov.**, paratype female. A, anal somite and caudal rami, ventral view showing spinule patches; B, leg 2; C, leg 3; D, leg 4; E, leg 5. Scale bars 100 µm on A–D, 50 µm on E.

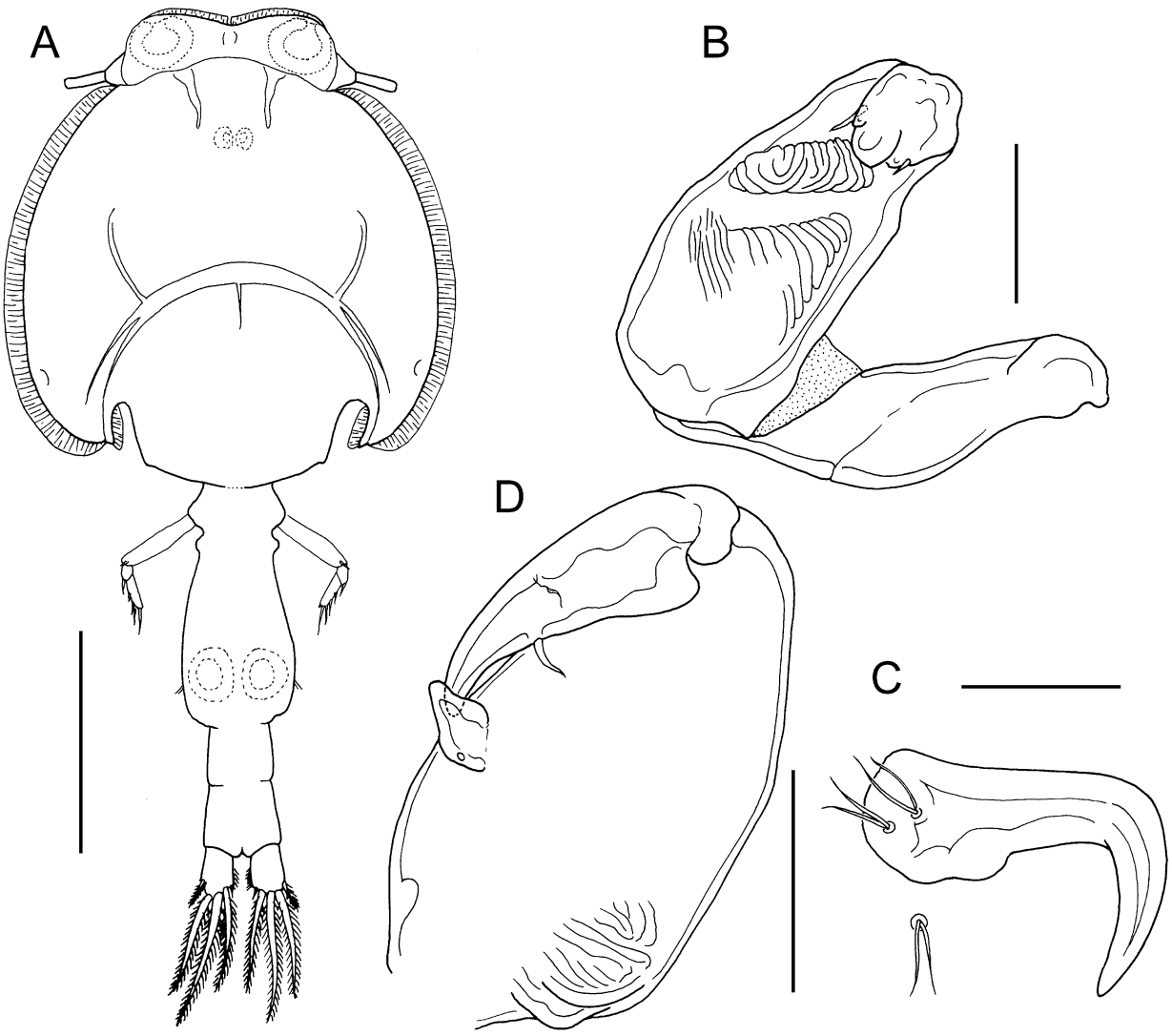

FIGURE 62. *Caligus turbidus* **sp. nov.**, paratype male. A, habitus, dorsal; B, antenna; C, post-antennal process; D, maxilliped. Scale bars 0.5 mm on A, 50 μm on B, C, 100 μm on D.

sensilla. Basis armed with outer naked seta; ornamented with long surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segment 1 with inner plumose seta and large outer spine extending obliquely across surface of ramus, ornamented with flap of membrane anteriorly, reflexed back over dorsal surface of segment; exopodal segment 2 with outer spine directed obliquely across surface of ramus plus inner plumose seta; segment 3 with 2 outer spines (proximal spine slender and naked, distal spine with extensive membrane bilaterally); apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. Endopodal segments 1 and 2 armed with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; outer margin of endopodal segment 1 ornamented with setules distally, segment 2 margin with stout tapering spinules.

Third leg pair (Fig. 61C) forming flattened plate closing posterior part of cephalothoracic sucker as typical for genus. Protopodal part flattened joined by plate-like, intercoxal sclerite (apron) ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal sclerite, and outer plumose seta dorsal to base of exopod; apron ornamented with circular patch of small spinules medially; sensillae located adjacent to inner coxal seta and adjacent to origin of endopod. Exopod 3-segmented; first segment armed with stout outer claw directed over ventral surface of ramus, without inner seta;

second segment with outer spine and inner plumose seta; distal segment with 3 spiniform elements on outer margin and 5 plumose setae on distal and inner margins; outer margins of segments 2 and 3 ornamented with slender setules. Endopod 2-segmented; first segment expanded laterally to form flap-like velum closing off space between rami; velum ornamented with row of fine setules along free margin; bearing inner plumose seta; compound distal segment with 6 setal elements increasing in length from outermost to innermost.

Fourth leg 3-segmented (Fig. 61D), comprising protopodal segment and 2-segmented exopod: protopodal segment armed with plumose seta distally and ornamented with 2 sensillae; first exopodal segment armed with outer spine extending beyond tip of lateral margin spine on distal segment; compound distal segment armed with short spine on lateral margin and 3 unequal spines on oblique distal margin; apical spine about 25% longer than middle spine, about 45% longer than outer spine; all spines with well-developed pecten at base.

Fifth legs located ventrally near posterolateral corner of genital complex (Fig. 61E); comprising plumose seta on anterior papilla and 2 plumose setae on posterior papilla representing exopod.

Male body length 1.95 mm, including caudal rami. Cephalothorax as in female, dorsoventrally flattened and with prominent frontal plates bearing large lunules (Fig. 62A). Genital complex with slightly convex lateral margins; about 1.5 times longer than abdomen. Abdomen 2-segmented, first somite just longer than wide; anal somite longer than preceeding somite, carrying paired caudal rami distally; anal slit terminal. Caudal rami with parallel sides, longer than wide. Each ramus armed with short plumose seta at inner distal angle, slightly longer seta at outer distal angle, small seta located just ventral to outer distal seta, and 3 long, plumose setae on distal margin.

Antennule, mandible, maxillule and maxilla as in female. Antenna modified (Fig. 62B); first segment elongate; second segment reflexed, elongate, bearing corrugated adhesion pads proximally and distally; distal segment forming short powerful claw, armed with 2 setae proximally. Post-antennal process (Fig. 62C) more highly curved than female. Maxilliped (Fig. 62D) with pointed myxal process on proximal segment (syncoxa) directly opposing tip of claw.

Legs 1 to 4 as in female.

Leg 5 located on ventral surface, just anterior to rounded posterodistal corner of genital complex; comprising protopodal seta and 2 plumose setae on papilla derived from exopod. Leg 6 forming operculum, closing off genital opening, armed with naked seta.

Remarks. This species belongs to the *Caligus productus*-group characterized by the loss of 2 of the 3 plumose setae, and strong reduction or loss of the third, from the posterior margin of the distal exopodal segment of leg 1. The key to species of the *C. productus*-group provided by Boxshall & El-Rashidy (2009) already requires amendment because of the presence of a setal vestige on the posterior margin of the distal exopodal segment of leg 1 of *C. ariicolus* that was overlooked by Wilson (1928) (see above). Given the difficulty in observing such minute setal vestiges using light microscopy, it is clear that the use of this character in an identification key is problematic.

The new species is most similar to *C. schlegeli* even in fine scale ornamentation such as the presence of sensillae on the protopodal and first exopodal segments of leg 4 (Fig. 53E), the bisensillate papillae associated with the post-antennal process, and the ornamentation of the exopodal spines of leg 2. However, these two species can be distinguished by the more robust spine of the first exopodal segment of leg 3 in the new species and by the armature of leg 4. Leg 4 is more robust in the new species (Fig. 61D) than in *C. schlegeli* (Fig. 53E) and the outer spine on the first exopodal segment extends beyong the tip of the small lateral spine on the distal segment, whereas in the latter species it barely reaches the mid-point of the lateral spine. In addition, the post-antennal process of the female is larger and more highly recurved in *C. schlegeli* than in *C. turbidus* **sp. nov.**

In Moreton Bay, the new species, with a mean female body length of 2.76 mm (range 2.54 to 2.92 mm), is smaller than *C. schlegeli*, mean body length 3.14 (range 2.82 to 3.42 mm).

***Caligus upenei* sp. nov.**
(Figs. 63, 64)

Type material. Holotype ♀ from *Upeneus tragula* Richardson, 1846 (TC17214) 18 January 2016, QM Reg. No. W53118.

Type Host. *Upeneus tragula* Richardson, 1846.

Site on host. Unknown (in head wash).

Etymology. The name of the new species refers to the generic name of the host.

Description. Adult female (Fig. 63A) mean body length including caudal rami 2.45 mm. Cephalothorax subcircular; maximum width about 1.44 mm, maximum length 1.51 mm; comprising about 62% of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly just beyond rear margins of lateral portions. Lunules present ventrally on frontal plates. Genital complex 1.4 times wider than long; with rounded convex lateral margins and rounded corners bearing fifth legs (Fig. 63B). Genital complex about 5.2 times longer than abdomen. Abdomen 1-segmented, wider than long; carrying paired caudal rami distally; anal slit terminal. Caudal rami about as long as wide, measured at midpoints of margins. Each ramus armed with short hirsute seta at inner distal angle, slightly longer hirsute seta at outer distal angle, minute hirsute seta located just ventral to outer distal seta, and 3 plumose setae on distal margin.

Antennule (Fig. 63C) 2-segmented; proximal segment with 25 plumose setae along anteroventral margin and 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 63D) comprising proximal segment with posteriorly-directed spinous process; middle segment subrectangular, tapering slightly distally, unarmed; terminal segment forming short recurved claw bearing short spinous element on swelling proximally, and armed with slender distal seta on anterior margin. Post-antennal process (Fig. 63E) well-developed, curved, ornamented with 2 unisensillate papillae on basal part; single unisensillate papilla on adjacent ventral cephalothoracic surface.

Mandible of typical stylet-like structure, with 12 marginal teeth. Maxillule (Fig. 63F) comprising anterior papilla bearing 3 unequal, naked setae and posterior tine-like process. Maxilla 2-segmented (Fig. 63G), comprising elongate syncoxa and basis: syncoxa unarmed; basis bearing subapical membranous flabellum on anterior margin, and terminating in 2 claw-like elements (calamus and canna). Calamus longer than canna, ornamented with strips of serrated membrane arranged obliquely around surface; canna with linear strips of serrated membrane. Maxilliped subchelate (Fig. 63H); slender proximal segment unarmed, with spinous process located proximally on posterior surface; tubular membranous structures (possibly filamentous epibionts) present, originating on posterior surface; distal subchela with small apical claw separated from proximal segmental part by incomplete suture; segmental part and claw each armed with 1 seta.

Sternal furca (Fig. 63I) with divergent tines, each with linear sides and blunt tip.

First swimming leg pair (Fig. 64A) with sympods joined by slender intercoxal sclerite; sympod with inner and outer plumose setae (derived from basis); endopod represented by unarmed process on posterior margin of basis. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment robust, about 2.05 times longer than maximum width (near base) and armed with small outer (anterior) spine and ornamented with setule row along mid-section of posterior margin; second segment armed with 3 long plumose setae along posterior margin and 4 distal elements. Distal elements as follows: spine 1 (anterior-most) simple, shortest; spines 2 and 3 equal in length, both lacking accessory process; seta 4 about twice length of spines 2 and 3, and shorter than segment.

Second leg (Fig. 64B) biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by plate-like intercoxal sclerite bearing marginal membrane posteriorly. Coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segment 1 with large reflexed outer spine extending obliquely across ventral surface of ramus and inner plumose seta, ornamented with flap of membrane anteriorly reflexed back over dosal surface of ramus; segment 2 with outer spine extending obliquely across ventral surface of ramus and inner plumose seta; segment 3 with 2 outer spines (proximal spine small), apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. Endopodal segments 1 and 2 armed with 1 and 2 inner plumose setae respectively; segment 3 with 6 plumose setae; outer margins of all endopodal segments ornamented with fine setules.

Third leg pair (Fig. 64C) forming flattened plate closing posterior part of cephalothoracic sucker, as typical for genus. Protopodal part flattened joined by plate-like, intercoxal sclerite forming apron, ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal sclerite, and outer plumose seta dorsal to base of exopod; sensillae located adjacent to inner coxal seta and adjacent to origin of endopod; space between rami covered by flap-like velum ornamented with row of fine setules along free margin. Exopod 3-segmented; first segment armed with short, weakly curved, outer claw directed over ventral surface of ramus; second segment with slender outer spine and inner plumose seta; third with 7 setal elements (3 outer spiniform elements and 4 inner plumose setae); outer margins of segments 2 and 3

ornamented with rows of slender setules. Endopod 2-segmented; first segment with inner plumose seta; second with 6 setal elements increasing in length from outermost to innermost.

Fourth leg (Fig. 64D) 3-segmented, comprising slender protopodal segment and 2-segmented exopod with exopodal segments separated by oblique articulation: protopodal segment armed with outer seta; first exopodal segment just shorter than second, armed with slender outer spine not reaching distal tip of ramus; second segment armed with 3 unequal spines along distal margin, each with pecten at base; spines increasing in length from outer to inner.

Fifth leg located posterolaterally on genital complex, represented by plumose, outer protopodal seta originating on anterior papilla and 2 unequal plumose setae on small inner papilla representing exopod (Fig. 63B).

Remarks. This species shares a 3-segmented leg 4 with a 2-segmented exopod bearing I, III spines with 65 other species of *Caligus*. However, it does not share all aspects of the armature of the distal exopodal segment of leg 1 characteristic for the *C. macarovi*-group (as discussed above in the remarks section for *Caligus hyporhamphi* **sp. nov.**): spine 1 is less than half as long as spines 2 and 3 whereas spines 1, 2 and 3 are subequal in members of the core *C. macarovi*-group. Comparisons are restricted here to those 19 species exhibiting a 3-segmented leg 4 with a 2-segmented exopod bearing I, III spines in combination with a broad genital complex in the female (Table 7). Broad is defined here as having a L: W ratio between 0.6:1 and 0.8:1. Included in this list are three species, *C. punctatus*, *C. orientalis* and *C. oviceps*, which are common and widely distributed in the Indo-Pacific, but all three have a genital complex that is about 2.3 to 2.4 times longer than the abdomen, compared to 5.2 times longer in the new species.

Few of the species listed in Table 7 have such a short abdomen relative to the genital complex. Only four of these species have a genital complex that is 3.0 or more times longer than the abdomen: *C. calotomi*, C. *sclerotinosus*, *C. flexispina* and *C. sicarius*. Comparisons with these species follow. *Caligus calotomi* was redescribed by Lin & Ho (2007) who showed that the distal exopodal segment of leg 1 carries only three setal elements rather than the typical four, and it seems probable that spine 1 is the missing element. Spines 2 and 3 both lack an accessory process. In *C. calotomi* the two exopodal segments of leg 4 are unequal, the proximal is markedly shorter than the distal, whereas, in the new species these segments are subequal.

Lewis (1964a) described *C. flexispina* from *Acanthurus triostegus* (Linnaeus, 1758) (as *Acanthurus triostegus sandvicensis* Streets) caught off Hawaii. The presence of accessory processes on spines 2 and 3 of the distal exopodal segment of leg 1 was not noted. There are numerous small differences: the papillae on the post-antennal process are bisensillate in *C. flexispina* but unisensillate in the new species, the distal margin of the maxilla is smooth in the former but spinulate in the latter, and the 2 setae on the exopodal papilla of leg 5 in the female are equal in *C. flexispina* but in the new species the inner seta is nearly 3.0 times longer than the outer. The outer spine on the first exopodal segment of leg 3 is pointed in *C. flexispina* but blunt in the new species, and the outer spines on segments 2 and 3 increase in length distally in the former but are all similar in length in the latter (Fig. 64C).

Caligus sclerotinosus is redescribed herein and can be distinguished from the new species by its prominent fifth legs, visible in dorsal views of the genital complex (Fig. 54A), and by the broad spatulate tines of the sternal furca (Fig. 54E).

Caligus sicarius was found in Moreton Bay and is redescribed in the present account. It can be readily distinguished from the new species by the extremely unusual leg 4 (see Figs. 57B, 58E) and by the possession of wedge-shaped tines on sternal furca plus accessory processes adjacent to the furca (Fig. 58A).

Caligus callyodoni Prabha & Pillai, 1986 was not included in Table 7 because it has a L: W ratio of 0.88:1 for the genital complex, however, in other respects its general habitus closely resembles that of the new species. It is known as a parasite of parrotfish of the genus *Scarus* Forsskål, 1775 from India (Prabha & Pillai, 1986) to Taiwan (Lin & Ho, 2007). These species share the possession of a small (about half as long as spine 2) spine 1 on the distal exopodal segment of leg 1 and both have unisensillate papillae on the post-antennal process, but there are numerous differences. The post-antennal process is short and straight in *C. callyodoni* but curved in the new species, the distal margin of the maxilla is smooth in the former but spinulate in the latter, and the tines of the sternal furca are parallel in *C. callyodoni* compared to strongly divergent in the new species. There are sufficient differences to justify the establishment of a new species to accommodate the material from *Upeneus tragula.*

The new species was found in Moreton Bay on a single occasion. The tubular membranous structures present on the syncoxa of the maxilliped (Fig. 63H) are possibly filamentous epibionts.

TABLE 7. Species of *Caligus* characterised by a 3-segmented leg 4 bearing 3 distal spines only on the second exopodal segment in combination with a broad genital complex in the female (defined as length with range of 0.6 to 0.8 times width). [Abbreviations: ABL = abdomen length, ABW = abdomen width, GCL = genital complex length, GCW = genital complex width, Mx = spinules on distal margin of maxilla, PAP = papilla associated with post-antennal process unisensillate]

Species	GCL:GCW	GCL:ABL	ABL:W	PAP	Mx	Reference
**C. eventilis* Leigh-Sharpe, 1934	0.6:1	2.6:1	0.5:1	?	?	Leigh-Sharpe, 1934
C. longipedis Bassett-Smith, 1898	0.6:1	2.0:1	1.3:1	yes	yes	present account
C. orientalis Gussev, 1951	0.6:1	2.4:1	0.6:1	no	no	Ho & Lin, 2004
C. sclerotinosus Roubal, Armitage & Rohde, 1983	0.6:1	4.1:1	0.7:1	yes	yes	present account
C. tylosuri (Rangnekar, 1956)	0.6:1	2.9:1	1.0:1	no	no	Lin & Ho, 2007
C. brevis Shiino, 1954	0.7:1	2.3:1	1.1:1	yes	no	Shiino, 1954b
C. calotomi Shiino, 1954	0.7:1	3.0:1	0.9:1	yes	no	Lin & Ho, 2007
**C. mordax* Leigh-Sharpe, 1934	0.7:1	1.1:1	1.2:1	?	?	Leigh-Sharpe, 1934
C. oculicola Tang & Newbound, 2004	0.7:1	2.8:1	1.0:1	yes	no	Tang & Newbound, 2004
C. polycanthi Gnanamuthu, 1950	0.7:1	1.7:1	1.0:1	yes	yes	Ho & Lin, 2004
C. punctatus Shiino, 1955	0.7:1	2.4:1	1.1:1	no	no	Ho & Lin, 2004
C. upenei **sp. nov.**	0.7:1	5.2:1	0.9:1	yes	yes	present account
C. willungae Kabata, 1965	0.7:1	2.0:1	0.9:1	no	?	Kabata, 1965b
C. flexispina Lewis, 1964	0.8:1	3.1:1	1.0:1	no	no	Lewis, 1964a
C. kalumai Lewis, 1964	0.8:1	2.3:1	1.0:1	no	no	Lewis, 1964a
**C. lolliguncula* Capart, 1941	0.8:1	2.4:1	0.9:1	?	?	Capart, 1941
C. oviceps Shiino, 1952	0.8:1	2.3:1	1.4:1	yes	yes	Ho & Lin, 2004
C. patulus Wilson, 1907	0.8:1	3.3:1	1.2:1	no	no	Ho & Lin, 2004
C. sicarius Kabata, 1984	0.8:1	3.9:1	0.8:1	yes	no	Kabata 1984; present account

*These poorly described species are included but many morphological details are lacking.

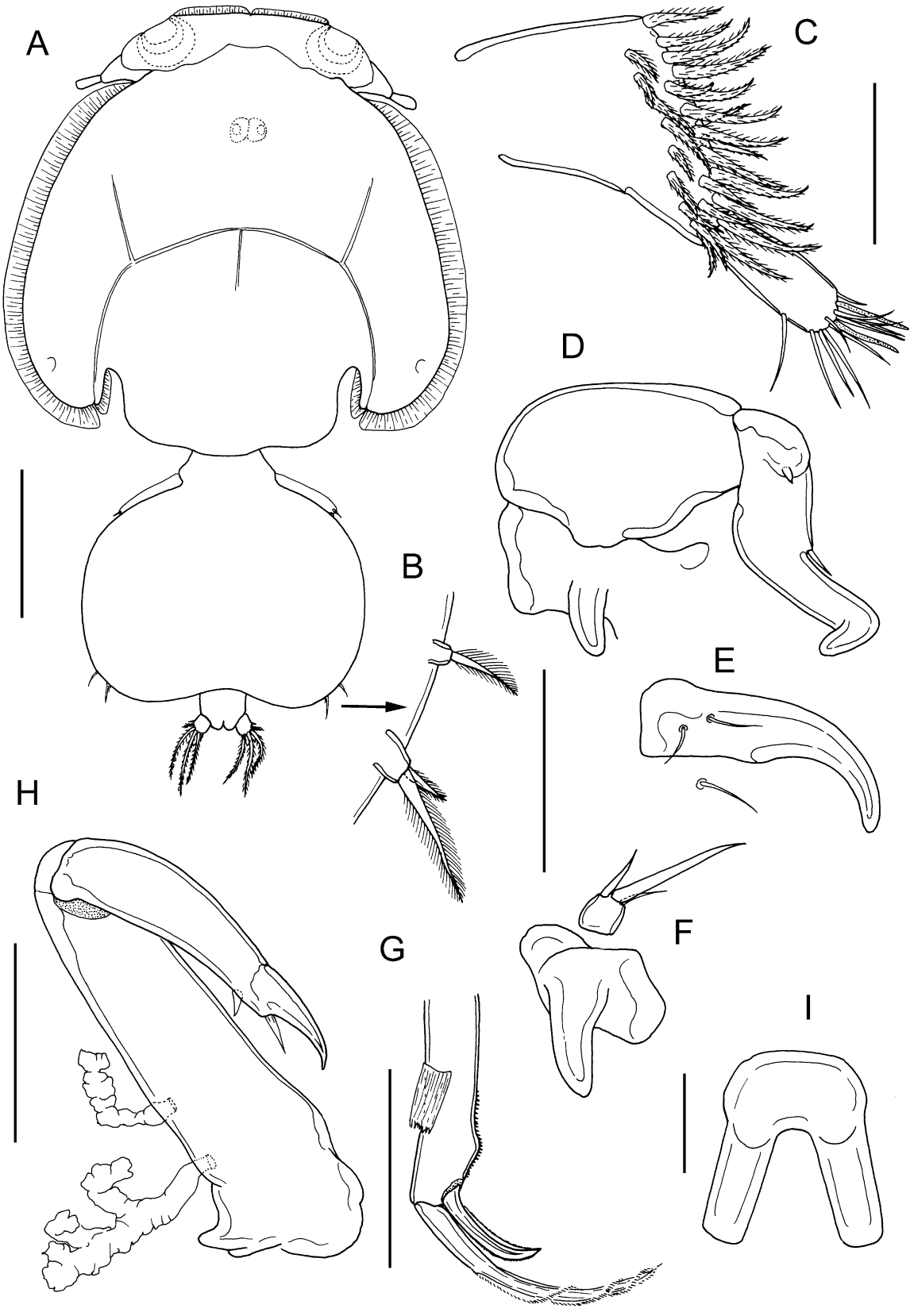

FIGURE 63. *Caligus upenei* **sp. nov.**, holotype female. A, habitus, dorsal; B, left corner of genital complex showing fifth leg, ventral; C, antennule; D, antenna; E, post-antennal process; F, maxillule; G, tip of maxilla; H, maxilliped; I, sternal furca. Scale bars: 0.5 mm on A, 100 µm on B–H, 50 µm on I.

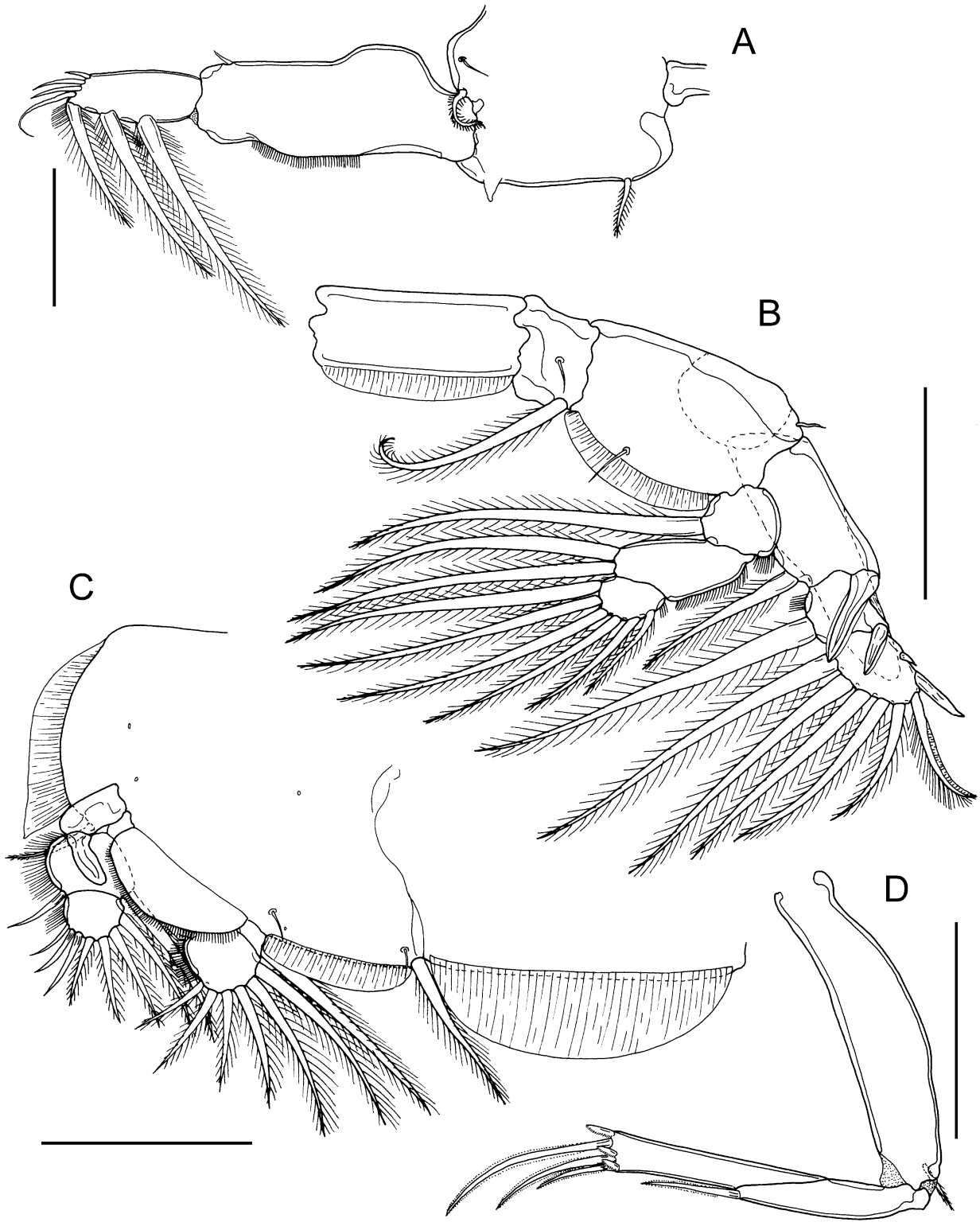

FIGURE 64. *Caligus upenei* **sp. nov.**, holotype female. A, leg 1, ventral; B, leg 2, ventral; C, leg 3, ventral; D, leg 4. Scale bars: 100 μm on A, 200 μm on B–D.

Genus *Hermilius* Heller, 1865

***Hermilius longicornis* Bassett-Smith, 1898**
(Fig. 65)

Material examined. 3♀♀ from *Netuma proxima* (Ogilby, 1898) (TC16993) 11 January 2016, QM Reg. No. W53119; 12♀♀ (TC16997) 11 January 2016, 6♀♀ QM Reg. No. W53120, 6♀♀ NHMUK Reg. Nos 2017.334–339.

Site on host. Gill filaments.

Differential diagnosis. Cephalothorax well developed with lateral zones folded ventrally (Fig. 65A, B) and supported by prominent ribs; outer margins of lateral zones provided with marginal membrane. Frontal plates with marginal membrane, lacking lunules. Fourth pedigerous somite forming narrow "waist" region; fourth legs concealed by genital complex. Genital complex large and dorsoventrally flattened, with wide wing-like lateral extensions reaching to base of free abdomen (Fig. 65A, C); genital complex about 1.76 times longer than wide, with rounded posterolateral corners. Abdomen indistinctly subdivided by constriction at mid-length (Fig. 65C); about 1.4 times longer than wide and shorter than genital complex. Caudal rami longer than wide, armed with short setae. Antenna comprising short unarmed first segment, lacking any process, slightly longer second segment and well developed subchela forming large apical hook with conspicuous accessory hook (Fig. 65D); subchela with single seta on proximal part and subapical seta on accessory hook. Tine of post-antennal process vestigial; papillae on vestigial process bisensillate; no papilla found on adjacent body surface. Maxillule with long slender posterior process. Maxilla with robust calamus and canna fused to basis. Maxilliped very slender. Sternal furca with short blunt tines, box of furca largely incorporated into ventral cephalothoracic surface. Leg 1 (Fig. 65E) with short sympod bearing enlarged outer basal seta and hirsute vestigial endopod; spines 1 to 3 on distal exopodal segment of leg 1 extremely developed, as long as (spine 3) or markedly longer than segment (spines 1 and 2); seta 4 short and naked: posterior margin with 3 short plumose setae. Leg 2 biramous, with 3-segmented rami: outer spines on exopodal segments aligned close to longitudinal axis of ramus; proximal outer spine on third segment similar in length to spine on second segment (Fig. 65F). Leg 3 with indistinctly 3-segmented exopod (Fig. 65G); first segment bearing weakly curved spine but lacking inner seta; second segment incompletely separated from third, armed with outer spine and inner seta; third segment with 3 spines and 4 setae; endopod 2-segmented; first segment forming small rounded velum and bearing inner seta; compound distal segment with 6 plumose setae. Leg 4 uniramous, indistinctly segmented (Fig. 65H); exopod with 1 lateral spine and 3 distal spines; outer and middle distal spines about equal in length. Body length of female 7.36 mm, range 7.0 to 7.36 mm (based on 10 specimens).

Remarks. This species can be characterized by the lack of any transverse suture line located distal to the accessory hook on the subchela of the antenna, combined with the setiform state of the caudal setae. According to the most recent key to species of the genus *Hermilius* produced by Ho & Kim (2000), these two character states are shared by *H. longicornis*, *H. alatus* Hameed, 1981, *H. ariodi* Prabha & Pillai, 1986 and *H. youngi* Kabata, 1964. Two of these species have markedly reduced setation on the exopod of leg 3: *H. ariodi* has a total of only 5 setal elements on the compound distal exopodal segment while *H. youngi* has 6 elements (cf. Fig. 66G). In *H. longicornis* the second and third exopodal segments of leg 3 are incompletely separated and have a setal formula of I-I; III,4 (Fig. 65G). In contrast, the second and third segments are clearly separated in *H. alatus* and exhibit reduced armature: the second segment has a long outer spine but lacks an inner seta, while the third carries 3 long naked spines plus a single plumose seta around its distal margin (Hameed, 1981: Fig 3a).

Hermilius longicornis was previously reported from Sri Lanka (Bassett-Smith, 1898b; Kirtisinghe, 1964), Trivandrum, India (Pillai, 1963), Malaysia (Leong, 1985) and Kuwait (Ho & Kim, 2000). This is the first report from Australian waters. Previously recorded hosts include the ariids *Arius acutirostris* Day, 1877, *Plicofollis dussumieri* (Valenciennes, 1840) (as *A. dussumieri*) and *A. thalassius* (Ho & Kim, 2000). The host in Moreton Bay, *Netuma proxima*, is a new host record.

***Hermilius youngi* Kabata, 1964**
(Fig. 66)

Material examined. 4♀♀ from *Neoarius graeffei* (Kner & Steindachner, 1867) (TC17597) 26 June 2016, 2♀♀

QM Reg. No. W53121, 2♀♀ NHMUK 2017.340–341; 1♀ from (TC17624) 27 June 2016, NHMUK Reg. No. 2017.342.

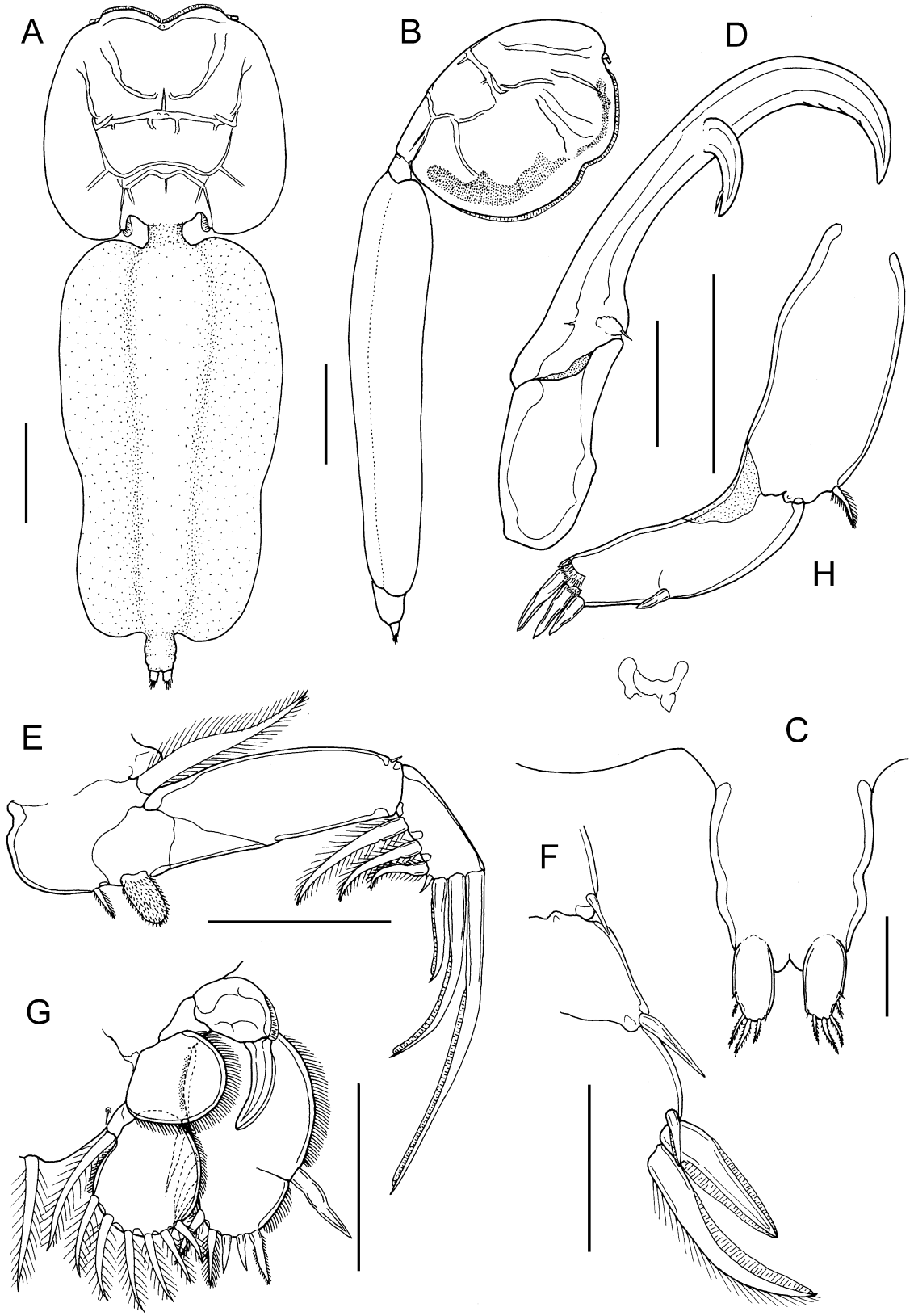

FIGURE 65. *Hermilius longicornis* Bassett-Smith, 1898, female. A, habitus, dorsal; B, habitus, lateral; C, abdomen, ventral; D, antenna; E, leg 1; F, outer margin spines on exopod of leg 2; G, rami of leg 3; H, leg 4. Scale bars: 1.0 mm on A, B, 200 µm on C, E, G, H, 100 µm on F, 250 µm on D.

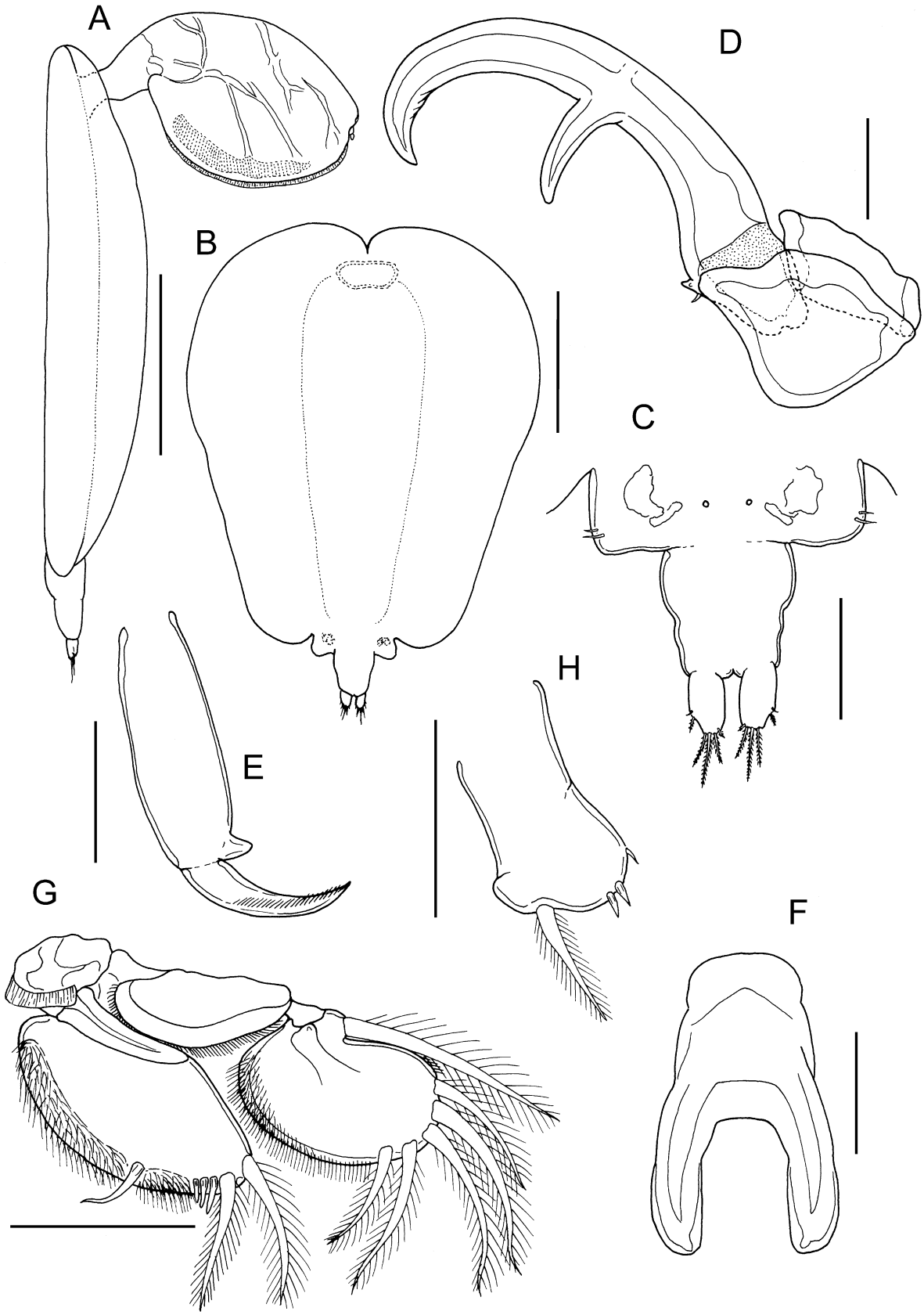

FIGURE 66. *Hermilius youngi* Kabata, 1964, A, habitus, lateral; B, genital complex and abdomen, ventral; C, posterior end of genital complex and abdomen, ventral; D, antenna; E, brachium of maxilla; F, sternal furca; G, rami of leg 3; H, leg 4. Scale bars: 1.0 mm on A, B, 250 µm on C, 100 µm on D, G, 50 µm on E, F, H.

Site on host. Gill filaments.

Differential diagnosis. Cephalothorax well developed with lateral zones folded ventrally (Fig. 66A) and supported by prominent ribs and with membrane along outer margins. Cephalothorax flexed ventrally in fixed specimens. Frontal plates with marginal membrane lacking lunules. Fourth pedigerous somite distinct but concealed by genital complex. Genital complex large and dorsoventrally flattened, with wide wing-like lateral extensions not reaching to base of abdomen (Fig. 66B,C); about 1.2 times longer than wide, with rounded posterolateral corners. Abdomen indistinctly subdivided by constriction at mid-length (Fig. 66C), about as long as wide. Caudal rami longer than wide, with setiform caudal setae. Antenna comprising short unarmed first segment, lacking any process, longer second segment (Fig. 66D) and well developed subchela forming large apical hook with conspicuous accessory hook; subchela with single seta and small process on proximal part. Tine of post-antennal process vestigial; papillae on vestigial process bisensillate; no papilla found on adjacent body surface. Maxillule with long slender posterior process. Maxilla with robust calamus and short stumpy canna fused to basis (Fig. 66E). Maxilliped very slender. Sternal furca with medium-length, more or less parallel tines (Fig. 66F). Leg 1 with hirsute vestigial endopod; spines 1 to 3 on distal exopodal segment well developed, as long as (spine 3) or markedly longer than segment (spines 1 and 2); seta 4 short and naked: posterior margin with 3 plumose setae. Leg 2 biramous, with 2-segmented rami: outer spines on exopodal segments aligned close to longitudinal axis of ramus; proximal outer spine on third segment similar in length to spine on second segment. Leg 3 with 2-segmented exopod (Fig. 66G); first segment bearing straight spine but lacking inner seta; compound distal segment armed with outer spine laterally, and with 3 spines and 2 plumose setae around distal margin (Fig. 66G); endopod 2-segmented; first segment with elongate velum and inner seta; compound distal segment with 5 plumose setae. Leg 4 lobate (Fig. 66H), broader near apex; armed with large plumose seta laterally, plus 3 vestigial spines around apex. Mean body length of female 3.95 mm, range 3.75 to 4.13 mm (based on 4 specimens).

Remarks. Kabata (1964a) distinguished this species from its congeners using a combination of features of the antenna, leg 4 and genital complex. The flattened genital complex of *H. youngi* has wing-like lateral expansions which terminate some distance anterior to the base of the abdomen, so the most posterior part of the genital complex is only a little wider than the abdomen itself. In *H. longicornis* the wing-like expansions extend right to the base of the abdomen. Leg 4 of *H. youngi* was not figured in Kabata's original description because he was unable to observe it clearly (Kabata, 1964a). Study of the new material reveals that it is an irregularly cylindrical lobe armed with 3 reduced setal elements distally plus a well developed seta laterally, which probably represents the outer protopodal seta. It is very different from leg 4 in other *Hermilius* species. The reduced setation of both rami of leg 3 also helps to distinguish *H. youngi* from its congeners; the compound distal exopodal segment carries a total of 4 spines and only 2 setae, while the compound distal endopodal segment carries only 5 plumose setae instead of the usual 6.

Kabata (1964a) found one ovigerous female on each of two catfish hosts; he gave *Neoarius australis* as the type host and *Netuma australis* as a second host. The species name *australis* within the Ariidae is from the original combination *Arius australis* Günther, 1867, and its current valid name is *Neoarius graeffei* according to Eschmeyer (1998) and Bailly (2015). It seems likely that both *Neoarius australis* and *Netuma australis*, which were collected on different occasions, could be referable to *Neoarius graeffei*. The new material from Moreton Bay, the type locality, was also collected from *Neoarius graeffei*, the type host.

Genus *Lepeophtheirus* von Nordmann, 1832

Lepeophtheirus acutus Heegaard, 1943

(Fig. 67)

Material examined. 28♀♀ from *Aetobatus ocellatus* (Kuhl, 1823) (TC17287) 19 January 2016, QM Reg. No. W53122; 7♀♀, 1♀ immature, 2♂♂ (TC17294) 19 January 2016, QM Reg. No. W53123; 2♀♀ (TC17115) 13 January 2016, 1♀ (TC 17360) 21 January 2016, 6♀♀, 1 incomplete, 1♂ (TC17940) 6 July 2016, 1♀, 2♂, 1 immature (TC17932) 5 July 2016, 1♀, 1 immature, 1♂ (TC 17933) 5 July 2016; NHMUK Reg. Nos 2017.453–462. 1♀ from *Himantura* cf. *astra* Last, Manjaji-Matsumoto & Pogonoski, 2008 (TC17750) 30 June 2016, NHMUK Reg. No. 2017.463.

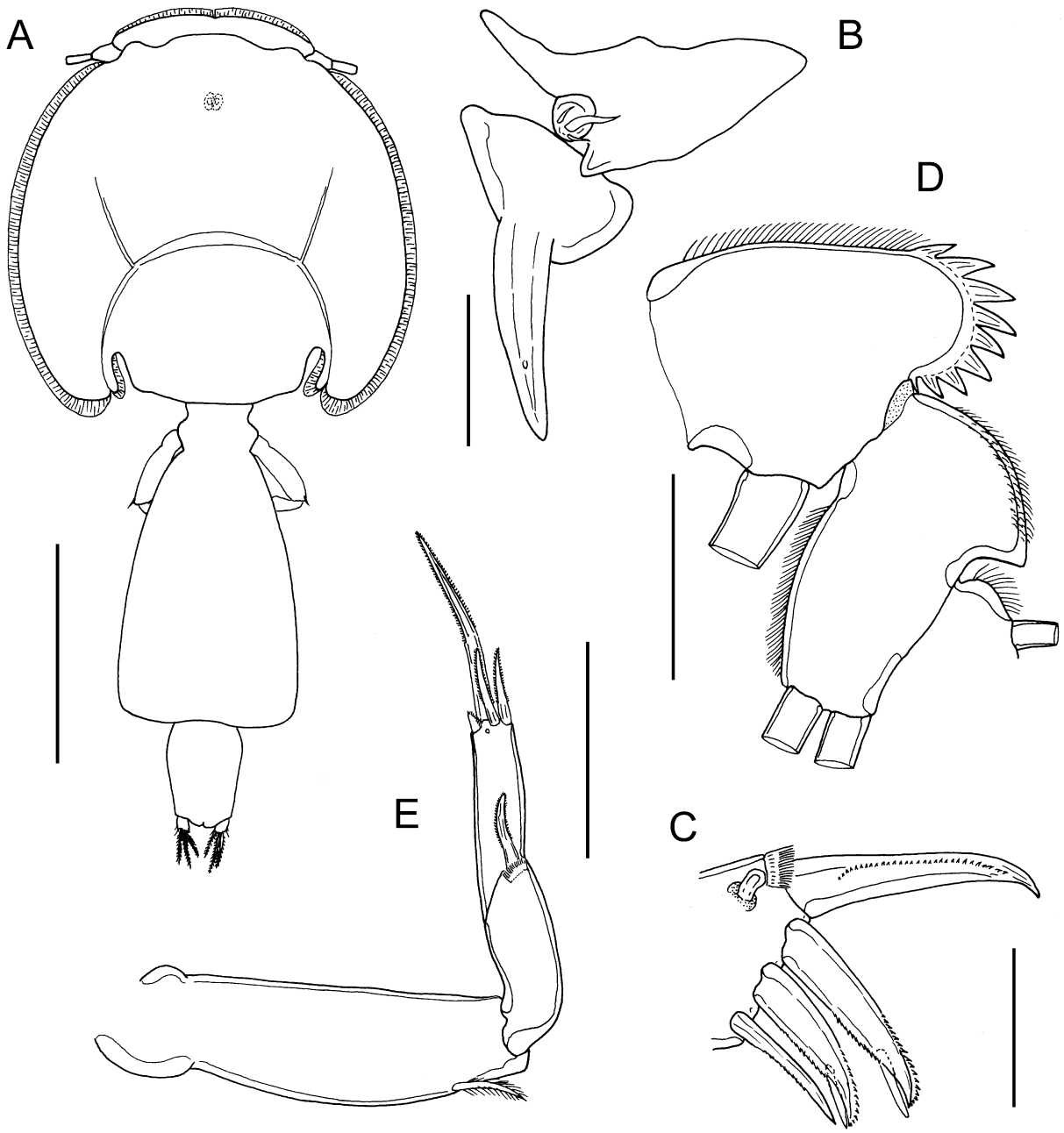

FIGURE 67. *Lepeophtheirus acutus* Heegaard, 1943, female. A, habitus, dorsal; B, maxillule; C, distal margin spines on exopod of leg 1; D, first and second endopodal segment of leg 2; E, leg 4. Scale bars: 1.0 mm on A, 100 µm on B, D, 200 µm on E, 50 µm on C.

Site on host. Body surface.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral zones of dorsal cephalothoracic shield; frontal plates lacking lunules. Genital complex subtriangular, about 1.5 times longer than wide (Fig. 67A); genital complex more than half length of cephalothorax; abdomen distinct, 1-segmented, about 1.4 times longer than wide; carrying caudal rami on posterior margin, either side of anal slit. Antenna with well-developed, pointed, posterior process on proximal segment. Tine of post-antennal process slightly curved; associated papillae multisensillate. Posterior tooth on anterior sclerite overlapping base of posterior process of maxillule (Fig. 67B). Sternal furca with straight, divergent, tapering tines. Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal margin spine 1 longest (Fig. 67C), spines 2 and 3

each with accessory process and ornamented with serrations; seta 4 just shorter than spine 3. Outer margin of first endopodal segment of leg 2 ornamented with row of stout teeth (Fig. 67D); second endopodal segment short with hirsute lateral margin. Leg 3 with 2-segmented exopod; first segment bearing strong outer spine and inner plumose seta; compound distal segment bearing total of 9 setal elements (4 spines and 5 setae); endopod 2-segmented; first segment forming short velum and bearing inner plumose seta; compound distal segment with 6 plumose setae. Leg 4 uniramous, 3-segmented (Fig. 67E); first and second exopodal segments armed with I and III spines, respectively; apical spine just longer than second segment, other 2 distal spines less than half length of apical spine. Leg 5 represented by outer papilla bearing protopodal seta and inner papilla bearing 3 plumose setae. Mean body length of adult female 4.20 mm, range 3.85 to 4.44 mm (based on 14 specimens). Mean body length of adult male 2.10 mm, range 2.04 to 2.19 mm (based on 4 specimens).

Remarks. This species was originally described by Heegaard (1943) based on a syntype series taken from *Taeniura lymma* (Forsskål, 1775) caught in the western Pacific off Abemama Atoll in Kiribati (formerly the Gilbert Islands). It was redescribed in detail by Tang *et al.* (2013) who also summarized existing records. The majority of published reports of *L. acutus* are based on specimens removed from diverse elasmobranchs kept in captivity including: *Pteroplatytrygon violacea* (Bonaparte, 1832), *Carcharhinus amblyrhynchos* (Bleeker, 1856), *C. melanopterus* (Quoy & Gaimard, 1824) and *Stegostoma fasciatum* (Hermann, 1783) in the Tropen-Aquarium Hagenbeck in Germany (Kik *et al.*, 2011), *Glaucostegus typus*, *Triaenodon obesus* (Rüppell, 1837) and *Stegostoma fasciatum* in Burger's Zoo, The Netherlands (Kik *et al.*, 2011), and *Manta alfredi* (Kreft, 1868) and *Rhincodon typus* Smith, 1828 held in sea pens off Okinawa-jima Island, Japan (Tang *et al.*, 2013). There is also material in the collections of the Natural History Museum, London, collected from *M. alfredi* in the S.E.A. Aquarium, Singapore (NHMUK Reg No. 2015.567-572). In the wild, *Lepeophtheirus acutus* has also been reported on *Rhinobatos rhinobatos* (Linnaeus, 1758) and *Aetomylaeus bovinus* (Geoffroy Saint-Hilaire, 1817) in Turkish waters (Özak *et al.*, in press.) and on *Rhinobatos annulatus* Müller & Henle, 1841 caught off Muizenberg Beach in South Africa (unpublished data). Rodríguez-Santiago *et al.* (2016) recorded *L. acutus* on the body surface of *Aetobatus narinari* (Euphrasen, 1790) caught in the southern Gulf of Mexico, off Campeche.

This is the first record of *L. acutus* from Moreton Bay and both the hosts, *Aetobatus ocellatus* and *Himantura* cf. *astra*, reported here are new host records. This wide-ranging copepod has not previously been reported from Australian waters.

Lepeophtheirus lagocephali Pillai, 1963

(Fig. 68)

Material examined. 3♀♀from *Lagocephalus lunaris* (Bloch & Schneider, 1801) (TC17899) 5 July, 2016, QM Reg. No. W53124; 1♀ (TC17897) 5 July 2016, 1 ovigerous ♀ (TC17905) 5 July 2016, 1 ovigerous ♀, 4♀♀ immature (TC 17944) 6 July 2016, NHMUK Reg. Nos 2017.343–345.

Site on host. Body surface.

Differential diagnosis. Cephalothorax dorsoventrally flattened with well-developed marginal membranes along lateral margins of dorsal cephalothoracic shield; frontal plates lacking lunules. Genital complex quadrangular (Fig. 68A), just (1.04 times) longer than wide; genital complex about 50% length of cephalothorax; abdomen small, less than 20% of length of genital complex, not clearly delimited from genital complex; caudal rami carried on posterior margin of abdomen, either side of anal slit. Antenna with small, weakly developed process on proximal segment (Fig. 68B). Tine of post-antennal process short and straight; associated papillae unisensillate. Posterior process of maxillule bifid, with tapering inner tine and slender outer tine (Fig. 68B). Sternal furca with straight, divergent, acutely tapering tines (Fig. 68C). Distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal margin spines 1, 2 and 3 similar in length (Fig. 68D); spines 2 and 3 each with accessory process and ornamented with finely serrate membranes; seta 4 just longer than spine 3, ornamented with tiny spinules along one margin. Leg 2 with 3-segmented rami: exopodal segments 1 and 2 armed with straight, bilaterally serrate spines directed disto-laterally away from longitudinal axis of ramus; third exopodal segment with large proximal outer spine overlying larger distal outer spine (Fig. 68E). Leg 3 with well developed apron lacking distinctive ornamentation; rami originating closely together (Fig. 68F): endopod 2-segmented, first segment with very slight lateral expansion forming small velum, armed with inner plumose seta; compound distal segment with

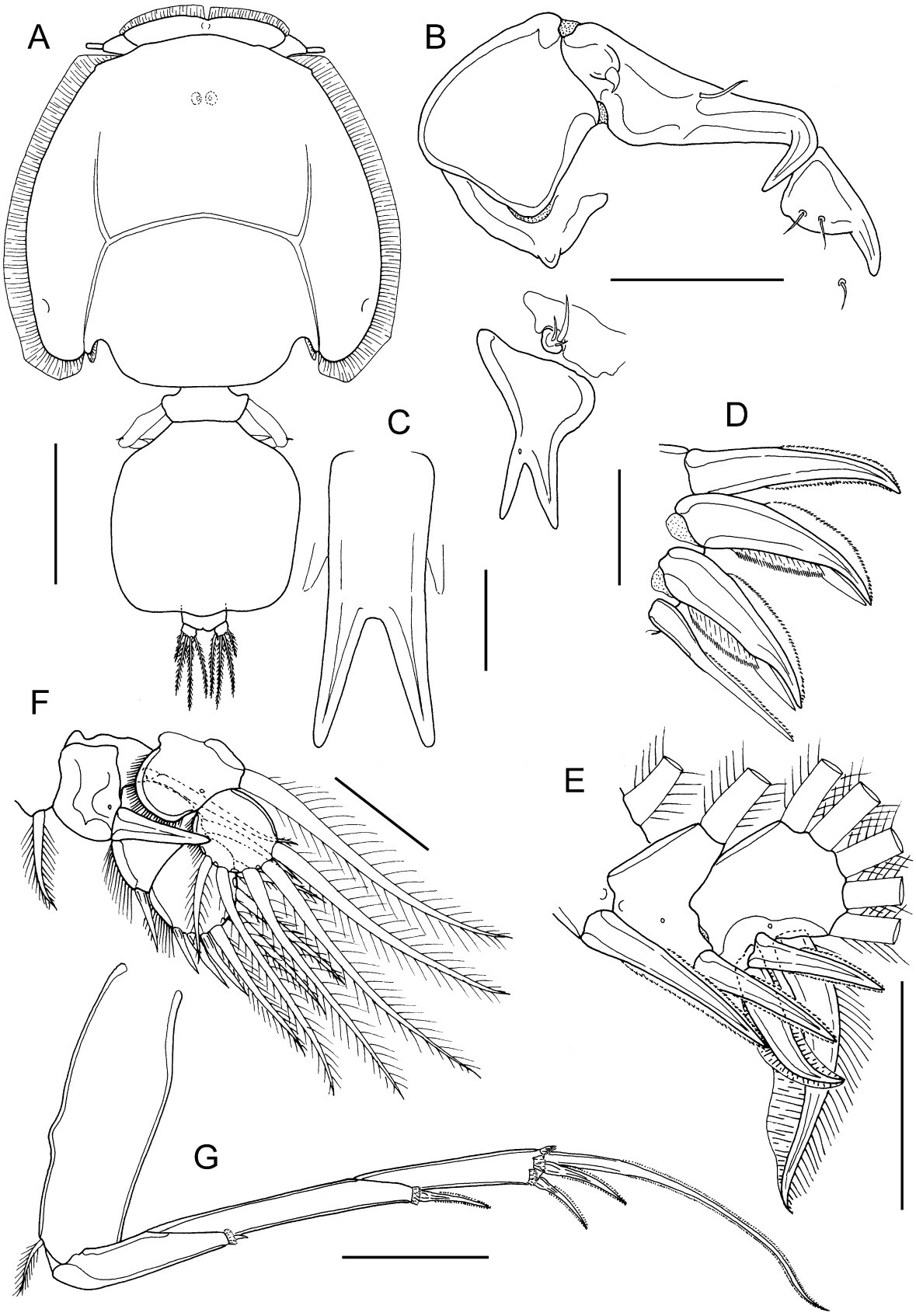

FIGURE 68. *Lepeophtheirus lagocephali* Pillai, 1963, female. A, habitus, dorsal; B, antenna, post-antennal process and maxillule drawn *in situ*; C, sternal furca; D, setation elements on distal margin of leg 1; E, exopod of leg 2; F, rami of leg 3; G, leg 4. Scale bars: 1.0 mm on A, 200 µm on B, E, G, 100 µm on C, F, 50 µm on D.

only 5 plumose setae: exopod 3-segmented; first segment armed with straight outer spine directed obliquely across surface, plus inner plumose seta; second segment with outer spine and inner seta; third with 3 outer spines and 4 plumose setae. Leg 4 uniramous, 4-segmented (Fig. 68G); exopodal segments bearing I; I; III spines: proximal spine on exopod very small, apical claw more than 3 times longer than adjacent distal spines. Mean body length of female 4.85 mm, range 4.39 to 5.10 mm (based on 4 specimens).

Remarks. The form of leg 4 in *L. lagocephali* is typical for the majority of *Lepeophtheirus* species, with a 3-segmented exopod and a I, I, III formula (with the proximal spine minute). The distinctive features of this species include the short abdomen in combination with the configuration of the distal spines on the exopod of leg 1 plus the reduced setation of leg 3. The compound distal endopodal segment of leg 3 bears only 5 plumose setae (Fig. 68F) rather than 6, as is typical for the majority of *Lepeophtheirus* species.

Pillai (1963) based his description of this species on material collected from *Lagocephalus inermis* caught off Kerala, India. In Moreton Bay, this copepod utilizes *L. lunaris* and this constitutes a new host record as well as a first record from Australian waters.

Lepeophtheirus robertae sp. nov.

(Figs. 69–71)

Type material. Holotype ♀, allotype ♂ from *Scarus ghobban* Forsskål, 1775 (TC 16968) 11 January 2016, QM Reg. Nos Holotype ♀ W53125, allotype ♂ W53126.

Type Host. *Scarus ghobban* Forsskål, 1775.

Site on host. Body surface.

Etymology. The new species is named for my wife, Roberta, in recognition of her support and her skills as an illustrator of copepods (e.g. in Boxshall & Montú, 1998).

Description. Holotype adult female (Fig. 69A) body length including caudal rami 2.71 mm. Cephalothorax subcircular (length 2.18 x width 2.20 mm), comprising about 80% of total body length. Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly well beyond rear margins of lateral portions and overlapping anterior half of genital complex. Frontal plates without lunules. Genital complex incorporating fused fourth pedigerous somite; extremely broad (1.07 mm) but short (0.50 mm); with rounded anterolateral corners, convex lateral margins and linear posterior margin bearing prominent spiniform fifth legs (Fig. 69B) extending beyond tips of caudal rami. Copulatory pores located near midline, oviduct openings marked by swellings. Genital complex about 2.5 times longer than abdomen. Abdomen 1-segmented; about 1.3 times wider than long (0.21 x 0.17 mm) in ventral view (Fig. 69B); carrying paired caudal rami distally; anal slit terminal. Caudal rami with parallel sides, about 2.3 times longer than wide (153 μm x 67 μm). Each ramus armed with short hirsute seta at inner distal angle, two short hirsute setae at outer distal angle, and 3 long plumose setae on distal margin.

Antennule (Fig. 69C) 2-segmented; large proximal segment with 25 plumose setae arrayed along anteroventral surface and 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Antenna (Fig. 69D) comprising proximal segment bearing spatulate posteriorly-directed spinous process; middle segment subrectangular, tapering slightly distally, unarmed; terminal segment forming recurved claw bearing weak swelling proximally, and slender seta near anterior margin. Post-antennal process robust, weakly curved; ornamented with 2 multisensillate papillae on basal part and single similar multisensillate papilla on adjacent ventral cephalothoracic surface.

Mandible of typical stylet-like structure, with 12 marginal teeth. Maxillule (Fig. 69D) comprising anterior papilla bearing 3 unequal, tiny naked setae and bifid posterior process, inner tine more slender than outer. Maxilla 2-segmented, comprising elongate syncoxa and basis: syncoxa unarmed; basis (Fig. 70A) bearing membranous flabellum on anterior margin, and terminating in 2 claw-like elements (calamus and canna). Calamus longer than canna, both ornamented with strips of serrated membrane. Maxilliped subchelate (Fig. 70B); proximal segment with small rounded process on myxal surface; distal subchela short, with apical claw separated from proximal segmental part by incomplete suture; armed with slender seta on concave margin.

Sternal furca (Fig. 70C) with short, broad divergent tines, with bluntly rounded tips.

First swimming leg pair (Fig. 70D) with joined by slender intercoxal sclerite; sympod with inner and outer plumose setae derived from basis; endopod represented by unarmed process on posterior margin of basis. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment armed with small outer (anterior) spine

and ornamented with row of setules along middle section of posterior margin; second segment armed with 3 short plumose setae along posterior margin and 4 distal elements along distal margin. Distal elements as follows: spine 1 (anterior-most) robust and slightly curved with minute serrations along concave margin, longer than spine 2; spine 2 markedly longer than spine 3, each with accessory process and with strip of serrated membrane distally; seta 4 shorter than spine 3, naked, and shorter than segment.

Second leg (Fig. 70E) biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by transversely elongate intercoxal sclerite bearing marginal membrane posteriorly. Coxa with plumose seta and surface sensilla. Basis armed with outer naked seta; ornamented with surface sensilla, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. Exopodal segment 1 with bilaterally serrate outer spine and inner plumose seta, ornamented with flap of membrane anteriorly reflexed back across dorsal surface of ramus; segment 2 with outer spine and inner seta; segment 3 with bilaterally serrate proximal spine and curved distal spine ornamented with membrane laterally; apical spine with marginal membrane laterally and pinnules medially, and 5 inner plumose setae. First and second endopodal segments armed with 1 and 2 inner plumose setae, respectively; segment 3 with 6 plumose setae; outer margins of all endopodal segments ornamented with fine setules.

Third leg pair (Fig. 70F) forming large flattened plate closing posterior part of cephalothoracic sucker. Protopodal part flattened joined by plate-like, intercoxal sclerite forming apron, ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate, and outer plumose seta dorsally near base of exopod; sensillae located adjacent to inner coxal seta and adjacent to origin of endopod; rami originating close together. Exopod 2-segmented; first segment (Fig. 70H) almost circular, armed with short claw directed over ventral surface of ramus; outer distal margin of segment ornamented with strip of membrane and 2 long sensillae present on ventral surface of segment; compound distal segment (Fig. 70I), with partial suture marking plane of fusion of former segments; armed with 4 spines and single plumose seta along outer margin. Endopod 2-segmented (Fig. 70G); first segment with weakly expanded lateral margin, forming rudimentary velum ornamented with spinules along free margin, armed with inner plumose seta; distal segment with 4 plumose setae.

Fourth leg (Fig. 71A) 4-segmented, comprising slender protopodal segment and elongate 3-segmented exopod: protopodal segment with smooth outer margin armed with plumose seta distally; first exopodal segment armed with slender minute outer distal spine with pecten at base; second segment with curved outer distal spine with pecten at base; third with 2 long apical spines ornamented with membrane plus shorter curved subapical spine; all spines with pecten at base.

Fifth legs developed as conspicuous tapering posterior processes originating posterolaterally on genital complex (Fig. 69B); each fifth leg comprising anterior seta located on surface of genital complex just lateral to base of tapering process; process representing exopod about 0.45 mm long, armed with long apical plumose seta and 2 subapical setae.

Allotype male (Fig. 71B) body length 1.85 mm including caudal rami. Cephalothorax subcircular as in female (length 1.59 mm x width 1.53 mm). Fourth pedigerous somite incompletely fused to genital complex and concealed in dorsal view beneath thoracic zone of dorsal cephalothoracic shield. Genital complex about 1.3 times wider than long (0.34 x 0.26 mm), measured along mid-line; with parallel lateral margins. Abdomen short, 1-segmented, separated from genital complex dorsally but fused ventrally (Fig. 71C); carrying paired caudal rami distally; anal slit terminal. Caudal rami broad, with convex distal margin twice as wide as base; armed with short plumose seta at inner distal angle, 2 short plumose setae at outer distal angle, and 3 longer plumose setae on distal margin.

Antennule, mandible, maxillule and maxilla as in female. Antenna modified (Fig. 71D); first segment elongate; second segment reflexed, swollen proximally with surface forming corrugated adhesion pads ventrally, plus dorsal pad in distal part; distal segment forming short powerful apical claw, plus accessory claw and armed with 2 setae proximally.

Maxilliped (Fig. 71E) with rounded myxal process on proximal segment; distal subchela longer relative to syncoxa than in female.

Legs 5 and 6 (Fig. 71C) each forming paired conical processes on posterior margin of genital complex. Each leg 5 represented by posterolateral process armed with 1 plumose seta at base, 1 long plumose seta on apex, and 2 subapically. Each leg 6 represented by oblique operculum closing off paired genital aperture and terminating in process armed with 3 short naked setae around apex.

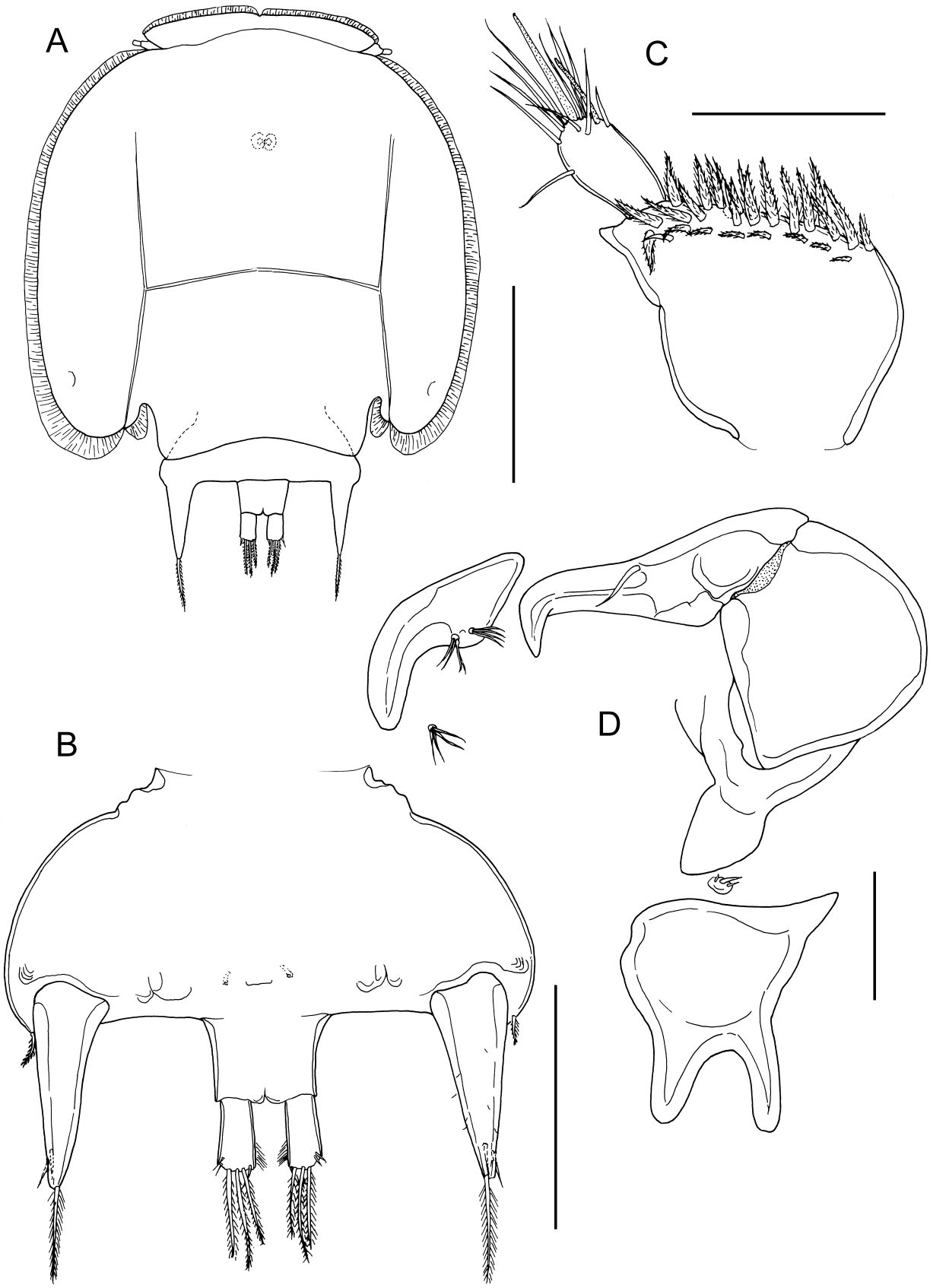

FIGURE 69. *Lepeophtheirus robertae* **sp. nov.**, holotype female. A, habitus, dorsal; B, genital complex, incorporating fourth pedigerous somite, and abdomen, ventral; C, antennule; D, antenna, post-antennal process and maxillule drawn *in situ*. Scale bars: 1.0 mm on A, 0.5 mm on B, 100 µm on C, D.

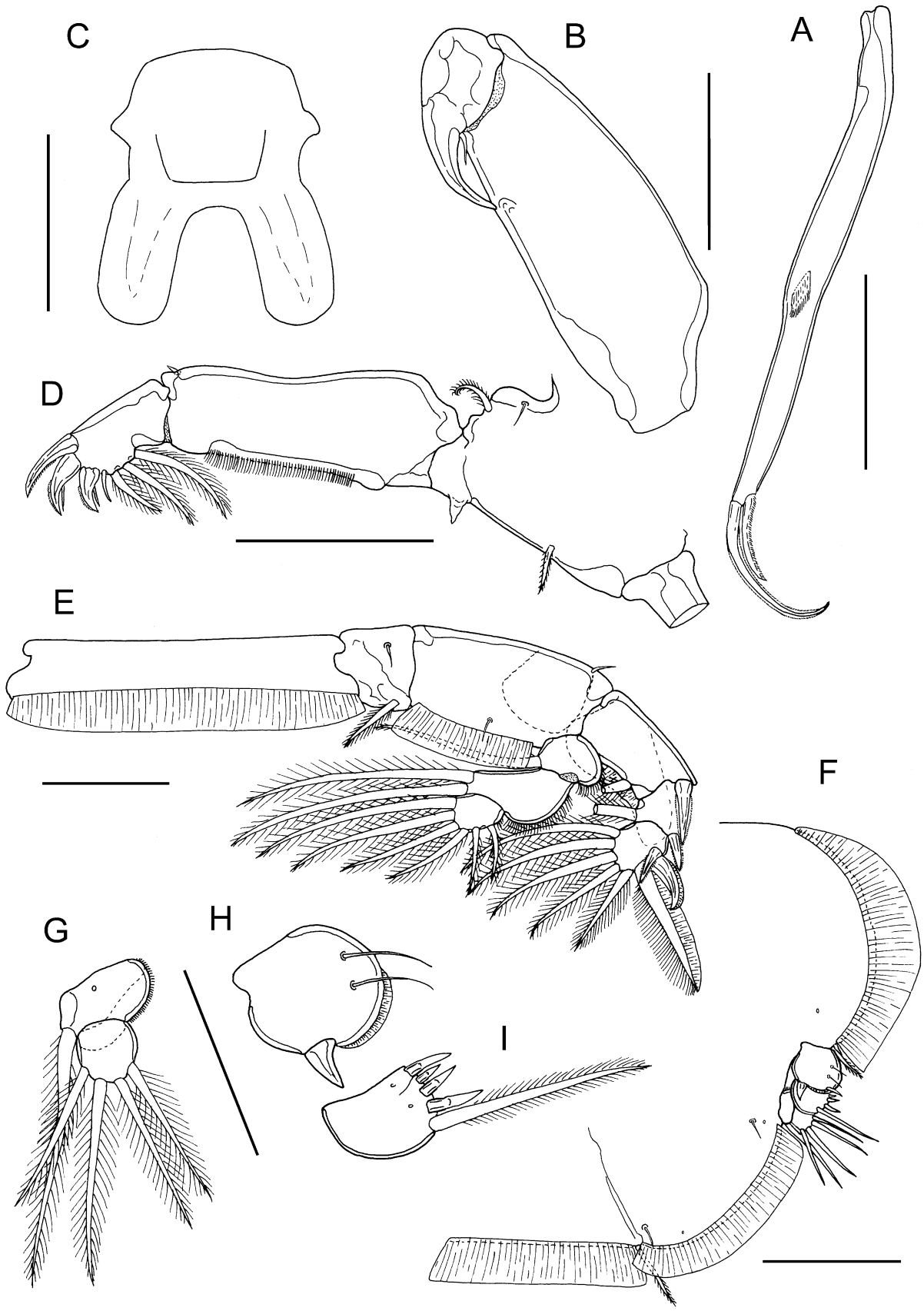

FIGURE 70. *Lepeophtheirus robertae* **sp. nov.**, holotype female. A, brachium of maxilla; B, maxilliped; C, sternal furca; D, leg 1, ventral; E, leg 2, ventral; F, leg 3, ventral; G, endopod of leg 3; H, first exopodal segment of leg 3, I, second exopodal segment of leg 3. Scale bars: 200 μm on A–F, 100 μm on G–I.

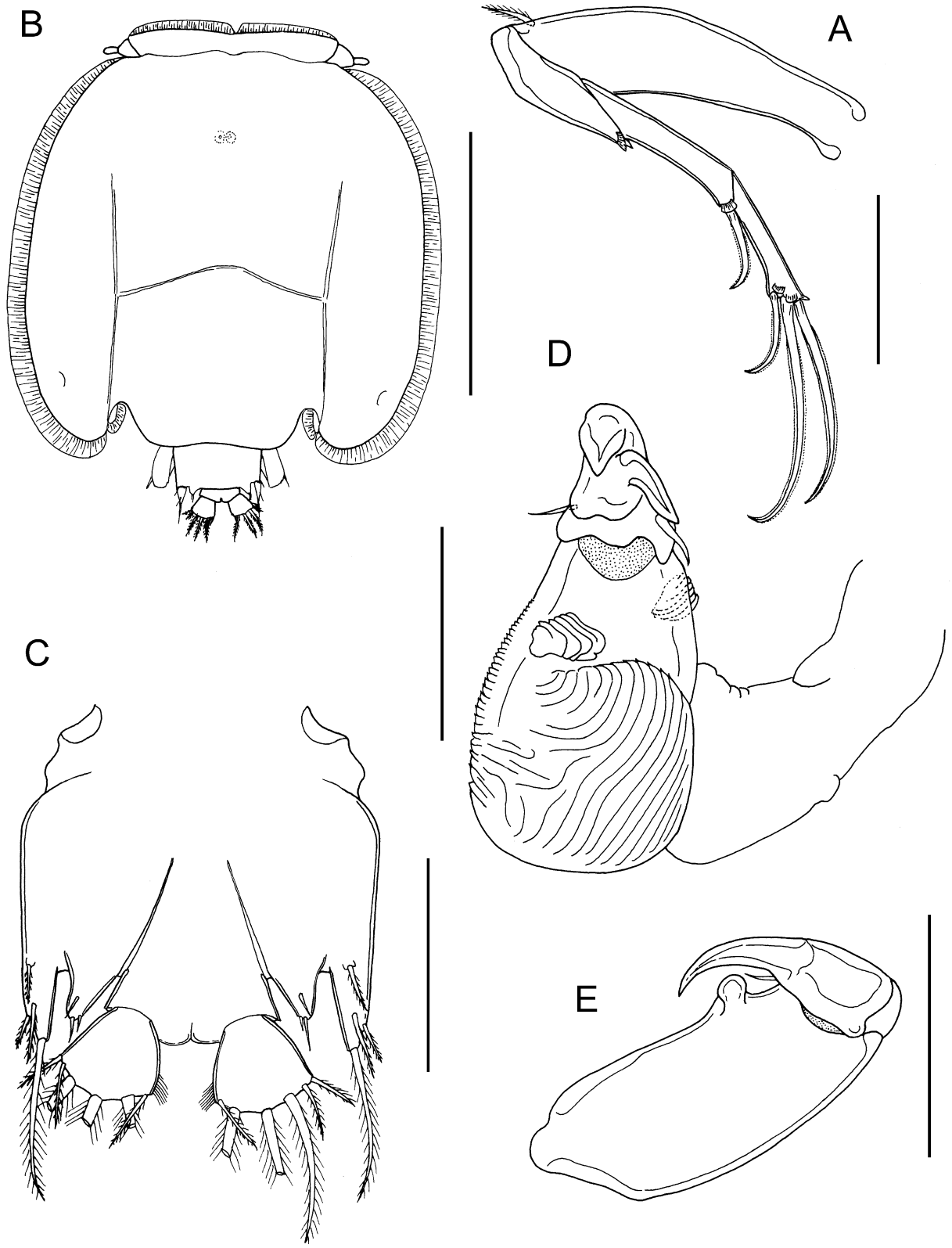

FIGURE 71. *Lepeophtheirus robertae* **sp. nov.**, holotype female. A, leg 4. Allotype male, B. habitus, dorsal; C, fourth pedigerous somite, genital complex and abdomen, ventral; D, antenna; E, maxilliped. Scale bars: 200 μm on A, C, E, 1.0 mm on B, 100 μm on D.

TABLE 8. Species of *Lepeophtheirus* with extreme development of spiniform leg 5 in female.

Species	body length female, mm	Genital complex (W:L ratio)	GC lobes	Caudal rami (L:W ratio)	P3 exopod segments	Exopodal formula	Endopodal formula	Source
L. curtus	3.13 – 3.60	2.1:1	absent	*ca.* 2.0:1	2	I-1; IV,5	0-1; 6	Lewis (1964b)
L. bifurcatus	3.08 – 3.45	1.9:1	absent	*ca.* 2.0:1	3	I-0; I-1; III,4	0-1; 6	Lewis (1964b)
L. lichiae	7.5	1.1:1	present	*ca.* 1.5:1	?	?	?	Barnard (1948)
L. litus	3.45 – 3.90	2.1:1	absent	*ca.* 1.0:1	2	I-1; IV,5	0-1; 6	Lewis (1964b)
L. longicauda	5.6	1.8:1	present	*ca.* 4.0:1	2	I-?; IV,3	0	Cressey (1966)
L. robertae **sp. nov.**	2.71	2.1:1	absent	*ca.* 2.3:1	2	I-0; IV,1	0-1; 4	Present account
L. spinifer	4.0	1.4:1	present	*ca.* 1.0:1	2	I-1; ?*	0-1; ?*	Kirtisinghe (1937)
L. ulua	6.00 – 7.13	1.1:1	present	*ca.* 1.0:1	3	I-0; I-1; III,4	0-1; 6	Lewis (1964b)

*Not clear from description of Kirtisinghe (1937).

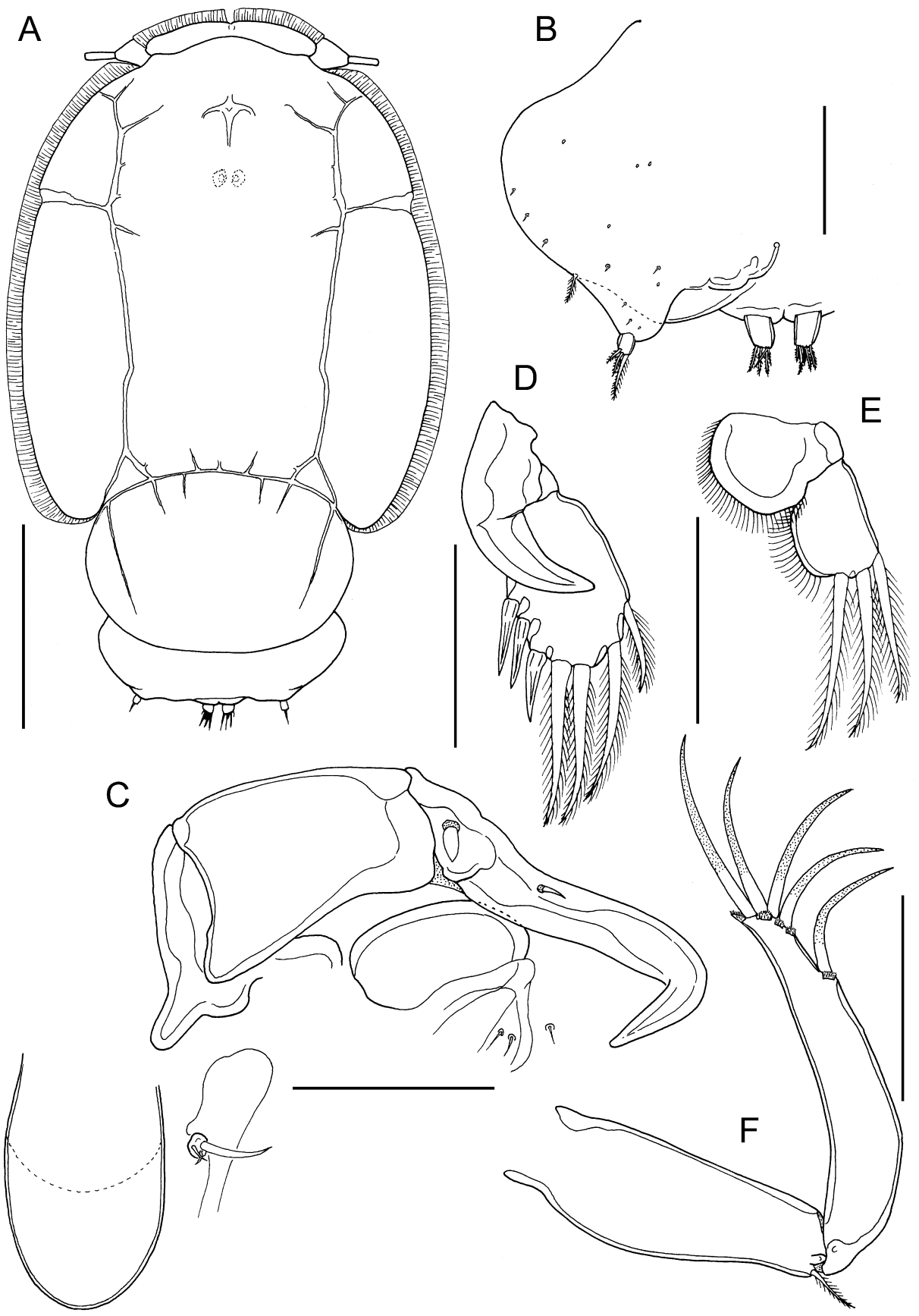

FIGURE 72. *Mappates plataxus* Rangnekar, 1958, female. A, habitus, dorsal; B, right side of genital complex, ventral view showing leg 5; C, antenna, post-antennal process and enlarged, lobate maxillule drawn *in situ*; D, exopod of leg 3; E, endopod of leg 3; F, leg 4. Scale bars: 1.0 mm on A, 250 µm on B, 200 µm on C, F, 100 µm on D, E.

Remarks. The extreme development of the fifth leg of the female is shared with a cluster of seven species within *Lepeophtheirus*, most of which were formerly placed in a separate genus, *Dentigryps* (see Lewis, 1964b). However, *Dentigryps* is no longer regarded as valid (see Dojiri & Ho (2013) for a summary of the taxonomic history of this genus) so these seven species are now considered as belonging to *Lepeophtheirus* as: *L. bifurcatus* (Lewis, 1964), *L. curtus* (Wilson, 1913), *L. lichiae* Barnard, 1948, *L. litus* (Lewis, 1964), *L. longicauda* (Cressey, 1966), *L. spinifer* Kirtisinghe, 1937, and *L. ulua* (Lewis, 1964). Only two of these, *L. litus* and *L. ulua*, have previously been reported from Australian waters (Kabata, 1965a; Ho & Dojiri, 1977). Characteristics of these seven species, together with the new species, are summarised in Table 8.

A dichotomous key to females can be constructed using these character states (Table 8) plus a few supplementary features:

1	Genital complex less than 1.5 times wider than long; genital complex with posterolateral lobes carrying fifth legs	2
-	Genital complex more than 1.8 times wider than long; posterolateral lobes usually absent, sometimes present (in *L. longicauda)*	4
2	Adult body length about 4.0 mm; genital complex 1.4 times wider than long	*L. spinifer*
-	Adult body length about 6.0 to 7.5 mm; genital complex 1.1 times wider than long	3
3	Abdomen 2-segmented; tip of fifth legs not reaching distal margin of caudal rami	*L. lichiae*
-	Abdomen 1-segmented; tip of fifth legs extending well beyond distal margin of caudal rami	*L. ulua*
4	Genital complex with posterolateral lobes carrying fifth legs; caudal rami about 4.0 times longer than wide	*L. longicauda*
-	Genital complex without posterolateral lobes; caudal rami less than 2.5 times longer than wide	5
5	Leg 3 with 3-segmented exopod with setal formula I-0; I-1; III,4	*L. bifurcatus*
-	Leg 3 with 2-segmented exopod (ancestral second and third segments fused) with IV spines plus either 1 or 5 setae on compound distal segment	6
6	Compound distal segment of leg 3 with 5 setae	7
-	Compound distal segment of leg 3 with 1 seta	*L. robertae* **sp. nov.**
7	Proximal (protopodal) segment of leg 4 with spiniform process near middle of outer margin	*L. litus*
-	Proximal (protopodal) segment of leg 4 without process on outer margin	*L. curtus*

The new species shares a number of fine scale features with *L. longicauda*; for example, both species are ornamented with 2 conspicuous sensillae on the surface of the first exopodal segment of leg 3. Both have reduced setation on the compound distal segment of the exopod of leg 3, however, *L. longicauda* has a total of 4 spines and 3 setae (Cressey, 1966), whereas the new species has 4 spines but only a single seta (Fig. 70I). The endopod of leg 3 is reduced to a single unarmed segment in *L. longicauda* whereas it is 2-segmented and has 0-1, 4 setation in the new species. This species brings to 12 the total number of species of *Lepeophtheirus* known from Australian waters.

Genus *Mappates* Rangnekar, 1958

Mappates plataxus Rangnekar, 1958

(Fig. 72)

Material examined. 15♀♀ from *Platax teira* (Forsskål, 1775) (TC16981) 11 January 2016, 8 ♀♀ QM Reg. No. W53127, 7♀♀ NHMUK Reg. Nos 2017.346–352.

Site on host. Attached at mid-length of gill filaments on lateral faces between adjacent filaments.

Differential diagnosis. Cephalothorax elongate (about 1.5 times longer than maximum width), covered by dorsoventrally flattened cephalothoracic shield with marked lateral sutures in anterior third (Fig. 72A); thoracic zone of shield enlarged, completely concealing fourth pedigerous somite and anterior half of genital complex in dorsal view: frontal plates and lateral margins with well-developed marginal membranes; frontal plates without lunules. Genital complex broad, more than twice as wide as long; bearing well defined fifth legs at posterolateral corners (Fig. 72B); leg comprising outer protopodal seta plus exopodal segment bearing 3 plumose setae. Abdomen vestigial, largely incorporated into posterior surface of genital complex. Caudal rami located either side of anal slit on posterior margin. Antenna with posterior process on proximal segment (Fig. 72C). Post-antennal process lacking tine; associated papillae unisensillate. Maxillule with posterior process enlarged to form flattened lobe with rounded apex (Fig. 72C). Maxilliped with smooth myxal margin and large subchela. Sternal furca absent. Leg 1 with vestigial endopod; distal exopodal segment of leg 1 with 3 plumose setae on posterior margin; distal

margin spine 1 longer than spine 2; spines 2 and 3 each with accessory process; seta 4 originating on surface of segment, about as long as spine 3. Leg 2 with 3-segmented rami; outer margin spines on exopodal segments 1 and 2 aligned with long axis of ramus. Leg 3 with 2-segmented rami; first exopodal segment bearing large recurved spine, lacking inner seta (Fig. 72D): compound distal segment bearing 3 spines and 4 setae in total: first endopodal segment unarmed, expanded to form small velum, compound distal segment bearing 3 plumose setae (Fig. 72E). Leg 4 uniramous, 2-segmented (Fig. 72F); exopodal segment compound, bearing 5 subequal spines distally. Mean body length of female 3.34 mm, range 3.18 to 3.49 mm (based on 10 specimens).

Remarks. The female of *M. plataxus* was redescribed in detail by Dojiri & Ho (2013) but the male is still unknown. It is a distinctive species with its elongate dorsal cephalothoracic shield marked with a characteristic pattern of sutures, the lack of a sternal furca, and the flattened lobate form of the posterior process of the maxillule. A second species of *Mappates*, *M. alter* Kabata, 1964, was established by Kabata (1964b) based on material from an ephippid fish host, *Zabidius novenaculeatus* (McCulloch, 1916) (as *Platax novenaculeatus*) caught off Heron Island, Queensland. The two species can be readily distinguished by the size of the posterior zone of the dorsal cephalothoracic shield which completely conceals the genital complex and abdomen in dorsal view in *M. alter* whereas in *M. plataxus* the genital complex extends well beyond the posterior margin of the cephalothoracic shield.

Although *M. plataxus* is known from India (Rangnekar, 1958; Pillai, 1985) and Sri Lanka (Kirtisinghe, 1964) across to Taiwan (Ho & Lin, 2004), this is the first record from Australia. In Moreton Bay it occurred on the type host *Platax teira*, but elsewhere it has been reported from *Platax orbicularis* (Forsskål, 1775) (Ephippidae) (Ho & Lin, 2004) and *Drepane punctata* (Linnaeus, 1758) (Drepaneidae) (Prabha & Pillai, 1983).

Genus *Pupulina* Van Beneden, 1892

Pupulina keiri sp. nov.

(Figs. 74–76)

Type material. Holotype ♀, 2♀♀ paratypes, 1♂ allotype from *Aetobatus ocellatus* (Kuhl, 1823) (TC17932) 5 July 2016, QM Reg. Nos Holotype ♀ W53128, 2 paratype ♀♀ W53129, allotype ♂ W53130; 2♀♀, 2♂♂, 2 immature paratypes (TC17637) 27 June 2016, QM Reg. Nos 2 paratype ♀♀ W53131, 2 paratype ♂♂ W53132, 2 immatures W53133; 2♀♀, 2♂♂, 3 immature paratypes (TC17933) 5 July 2016, NHMUK Reg. Nos 2017.353–356; 2♂♂, 7 immature paratypes (TC17940) 6 July 2016, NHMUK Reg. Nos 2017.357–358.

Type Host. *Aetobatus ocellatus* (Kuhl, 1823).

Site on host. Body surface.

Etymology. The new species is named after Keir Boxshall, a keen diver and observer of elasmobranchs.

Description. Adult female (Fig. 73A) mean body length including caudal rami 5.76 mm, range 5.54 to 5.96 mm (based on 4 ovigerous specimens). Cephalothorax subcircular, comprising about 48% of total body length; surface of dorsal cephalothoracic shield densely ornamented with sensillae near posterolateral corners (Fig. 73B). Free margin of thoracic portion of dorsal cephalothoracic shield extending posteriorly beyond rear margins of lateral portions. Frontal plates without lunules. Free fourth pedigerous somite wider than long. Genital complex about 1.2 times wider than long, with rounded anterolateral corners and linear lateral margins; fifth legs carried ventrolaterally near posterolateral corners (Fig. 73C). Copulatory pores located near midline, oviduct openings marked by swellings. Genital complex about 1.6 times longer than abdomen (including caudal rami). Abdomen elongate; about 2.2 times longer than wide. Caudal rami (Fig. 73D) elongate about 3.1 times longer than wide. Each ramus armed with 1 short, curved plumose seta at inner distal angle, 2 short plumose setae along distal part of lateral margin, and 3 long plumose setae on distal margin; ornamented with linear array of 4 long setules along dorsal midline and 2 short sensillae ventrally.

Antennule (Fig. 73E) 2-segmented; large proximal segment with 1 sensilla plus 22 plumose setae arrayed along anteroventral surface and 2 setae located dorsally; distal segment bearing 12 elements (10 setae plus 2 aesthetascs) around apex, plus isolated seta on posterior margin. Ventral cephalothoracic surface forming spinous process located immediately medial to base of antennule (Fig. 73E). Antenna (Fig. 73F) comprising proximal segment bearing pointed, posteriorly-directed spinous process; middle segment subrectangular, tapering slightly distally, unarmed; terminal segment forming recurved claw bearing seta on weak swelling proximally, and seta near anterior margin. Post-antennal process short, weakly curved; ornamented with 2 multisensillate papillae on large basal part and single multisensillate papilla on adjacent ventral cephalothoracic surface.

Mandible of typical stylet-like structure, with 12 marginal teeth. Maxillule (Fig. 75A) comprising anterior papilla bearing 3 unequal, tiny naked setae, and tapering posterior process with minute subapical tooth. Maxilla 2-segmented, comprising elongate syncoxa and basis (Fig. 74A): syncoxa unarmed; basis bearing membranous flabellum on anterior margin, and terminating in 2 claw-like elements (calamus and canna). Calamus more than twice as long as canna, both ornamented with strips of serrated membrane. Maxilliped subchelate (Fig. 74B); proximal segment slender with smooth myxal surface; distal subchela short, with apical claw separated from proximal segmental part by incomplete suture; slender seta present on concave margin.

Sternal furca absent.

First swimming legs biramous (Fig. 74C); joined by slender intercoxal sclerite; sympod with inner and outer plumose setae derived from basis; endopod 2-segmented: first segment unarmed, second with 3 plumose setae on distal and inner margins. Exopod 2-segmented; directed laterally and forming main axis of leg; first segment armed with small outer (anterior) spine and ornamented with row of setules along middle section of posterior margin; second segment armed with 3 plumose setae along posterior margin and 4 distal elements along distal margin. Distal elements as follows: spine 1 largest, slightly curved and with row of minute serrations along concave margin; spine 2 markedly longer than spine 3, without accessory process and armed with rows of minute serrations; spine 3 short, with accessory process; seta 4 plumose, about as long as spine 3, and shorter than segment; positioned on anterior surface of segment.

Second leg (Fig. 74D) biramous, with flattened protopodal segments and 3-segmented rami. Coxae of leg pair joined by elongate intercoxal sclerite bearing extensive marginal membrane posteriorly. Coxa with plumose seta and surface bisensillate papilla. Basis armed with outer naked seta; ornamented with surface bisensillate papilla near origin of endopod, marginal membrane posteriorly, and flap of membrane anteriorly, reflexed back over dorsal surface of segment. First exopodal segment with bilaterally serrate outer spine directed obliquely across surface of ramus, plus inner plumose seta, and bearing anterior flap of membrane reflexed back over dorsal surface of ramus; second segment with shorter bilaterally serrate spine aligned with long axis of ramus, plus inner seta; third segment with proximal and distal naked outer spines, apical spine ornamented with pinnules bilaterally, and 5 inner plumose setae. First and second endopodal segments armed with 1 and 2 inner plumose setae, respectively; both segments with expanded lateral margins ornamented with setules: third segment with 6 plumose setae.

Third leg pair (Fig. 75B) forming flattened plate closing posterior part of cephalothoracic sucker. Protopodal part flattened and joined by plate-like intercoxal sclerite forming apron, ornamented with marginal membrane posteriorly and along lateral margin anterior to exopod; bearing inner plumose seta at junction with intercoxal plate, and outer plumose seta near base of exopod; sensillae located adjacent to inner coxal seta and adjacent to origin of endopod and scattered over surface; rami originating close together. Exopod 3-segmented (Fig. 75C); first segment armed with straight outer spine and inner plumose seta, plus pecten at outer distal corner of segment; second segment armed with outer spine and inner seta; third segment with 3 short outer spines and 4 plumose setae along distal and inner margins. Endopod 3-segmented; first segment with enlarged lateral margin forming subcircular velum ornamented with spinules along free margin, lacking inner seta; second segment with 2 plumose inner setae; third segment with 4 plumose setae.

Fourth leg (Fig. 75D) 4-segmented, comprising robust protopodal segment and 3-segmented exopod: protopodal segment ornamented with scattered surface spinules and armed with plumose seta distally; first and second exopodal segments each armed with stout outer distal spine with pecten at base; third with long apical spine and 2 shorter spines, one set subapically on lateral margin; spines ornamented with serrated membrane bilaterally; large pecten present at inner distal corner.

Fifth legs developed as conspicuous tapering posterior processes originating posterolaterally on genital complex (Fig. 73C); each fifth leg comprising isolated anterior seta (outer protopodal seta) located on surface of genital complex and small posterior papilla representing exopod, armed with 2 plumose setae.

Allotype male (Fig. 76A) mean body length including caudal rami 4.17 mm, range 4.04 to 4.44 mm (based on 6 specimens). Cephalothorax subcircular as in female. Genital complex (Fig. 76B) about 1.4 times longer than wide, measured along mid-line; with linear lateral margins; ventral surface ornamented with spinules. Abdomen long, 2-segmented; first somite distinctly shorter than second (Fig. 76C), ornamented with surface sensillae; carrying paired caudal rami distally; anal slit terminal. Caudal rami about 3.8 times longer than wide, ornamented with sensillae on ventral surface; armed with short plumose seta at inner distal angle, 2 short plumose setae on distal part of lateral margin, and 3 long plumose setae around distal margin.

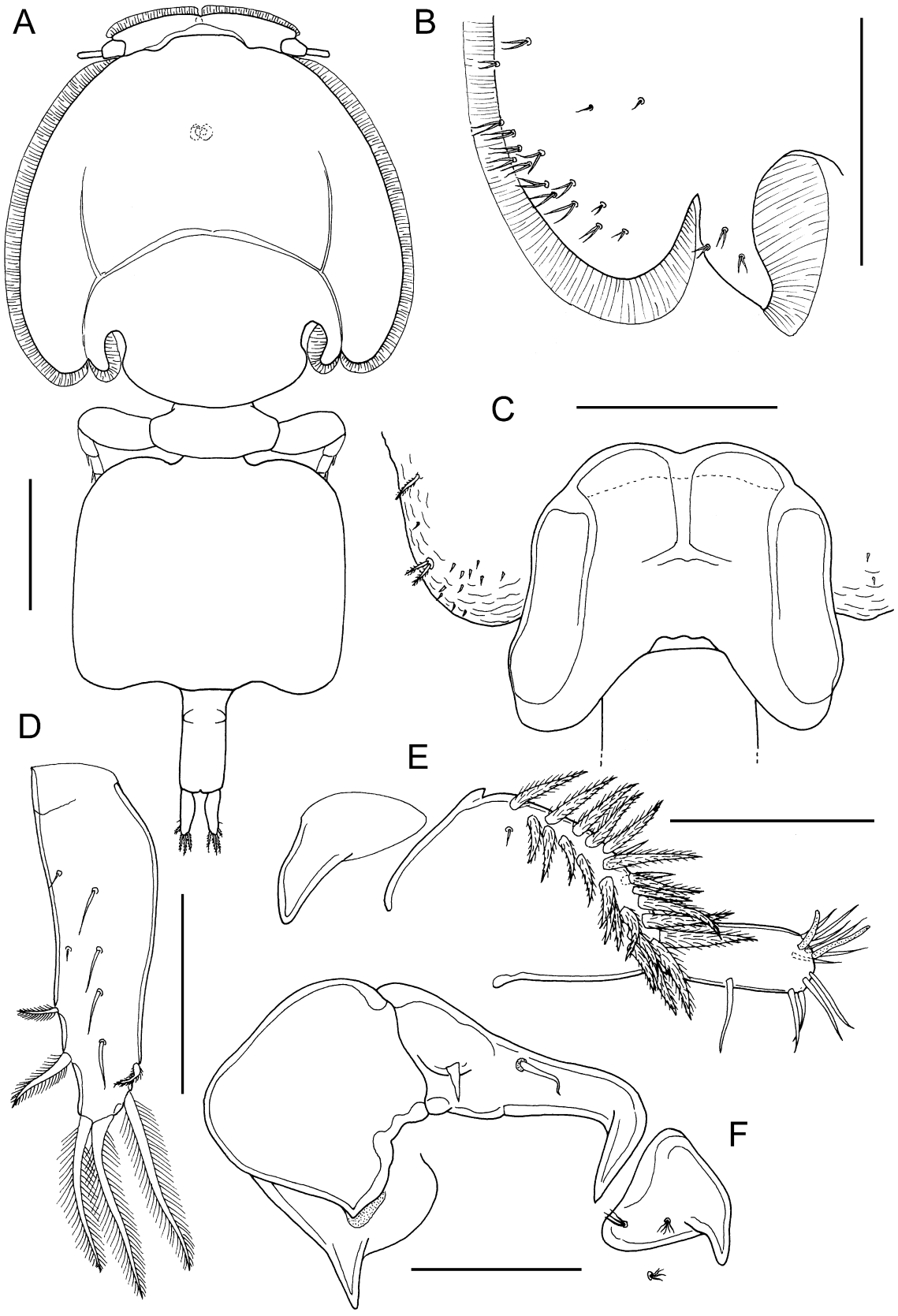

FIGURE 73. *Pupulina keiri* **sp. nov.** paratype female. A, habitus, dorsal; B, left corner of dorsal cephalothoracic shield, dorsal view showing surface ornamentation; C, genital complex, ventral view with spermatophore attached; D, caudal ramus, ventral; E, antennule and adjacent hook on ventral cephalothoracic surface, drawn *in situ*; F, antenna and post-antennal process drawn *in situ*. Scale bars: 1.0 mm on A, 0.5 mm on B, 200 µm on C–F.

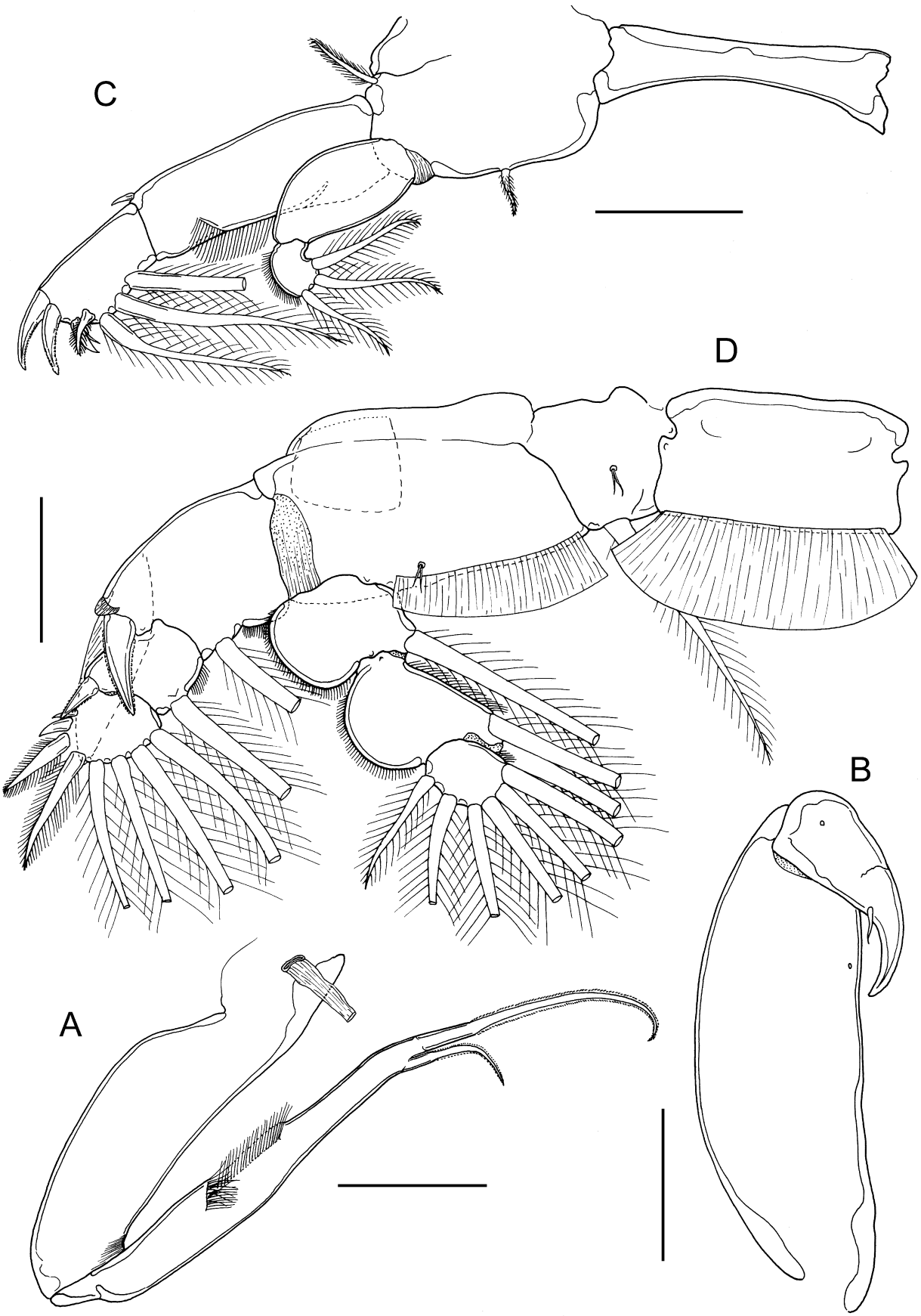

FIGURE 74. *Pupulina keiri* **sp. nov.** paratype female. A, maxilla; B, maxilliped; C, leg 1 and interpodal bar, anterior; D, leg 2, ventral. All scale bars 200 µm.

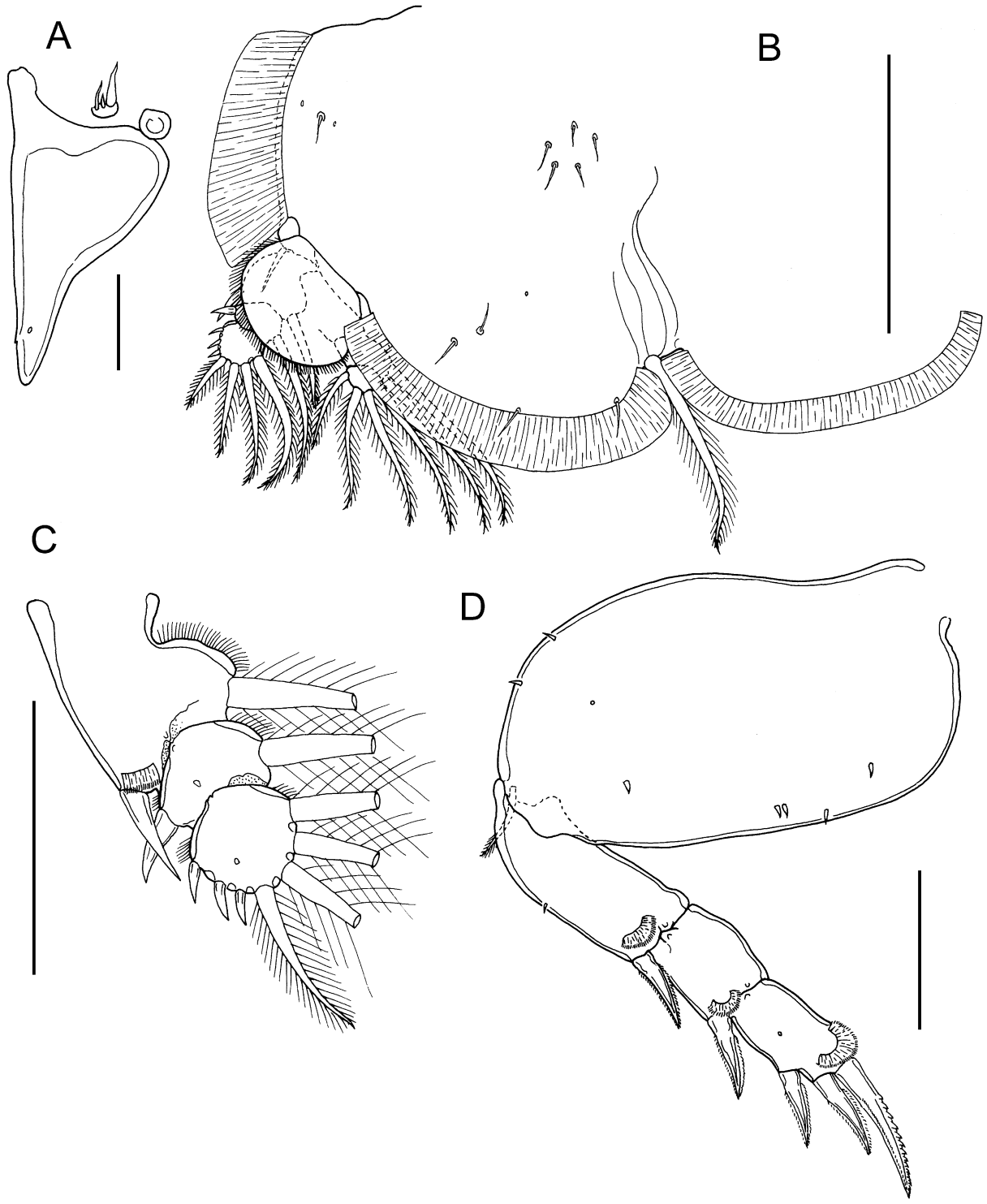

FIGURE 75. *Pupulina keiri* **sp. nov.** paratype female. A, maxillule; B, leg 3, ventral; C, exopod of leg 3, ventral; D, leg 4. Scale bars: 100 μm on A, 0.5 mm on B, 200 μm on C, D.

Antennule, mandible and maxilla as in female. Antenna modified (Fig. 76D); first segment elongate; second segment reflexed, swollen proximally with surface forming corrugated adhesion pads ventrally, plus dorsal pad in distal part; distal segment forming short powerful apical claw, with accessory claw and armed with 2 setae proximally. Maxillule (Fig. 76E) similar to that of female but with small, rounded post-oral process present, plus additional knob-like process on surface sclerite anterior to posterior process.

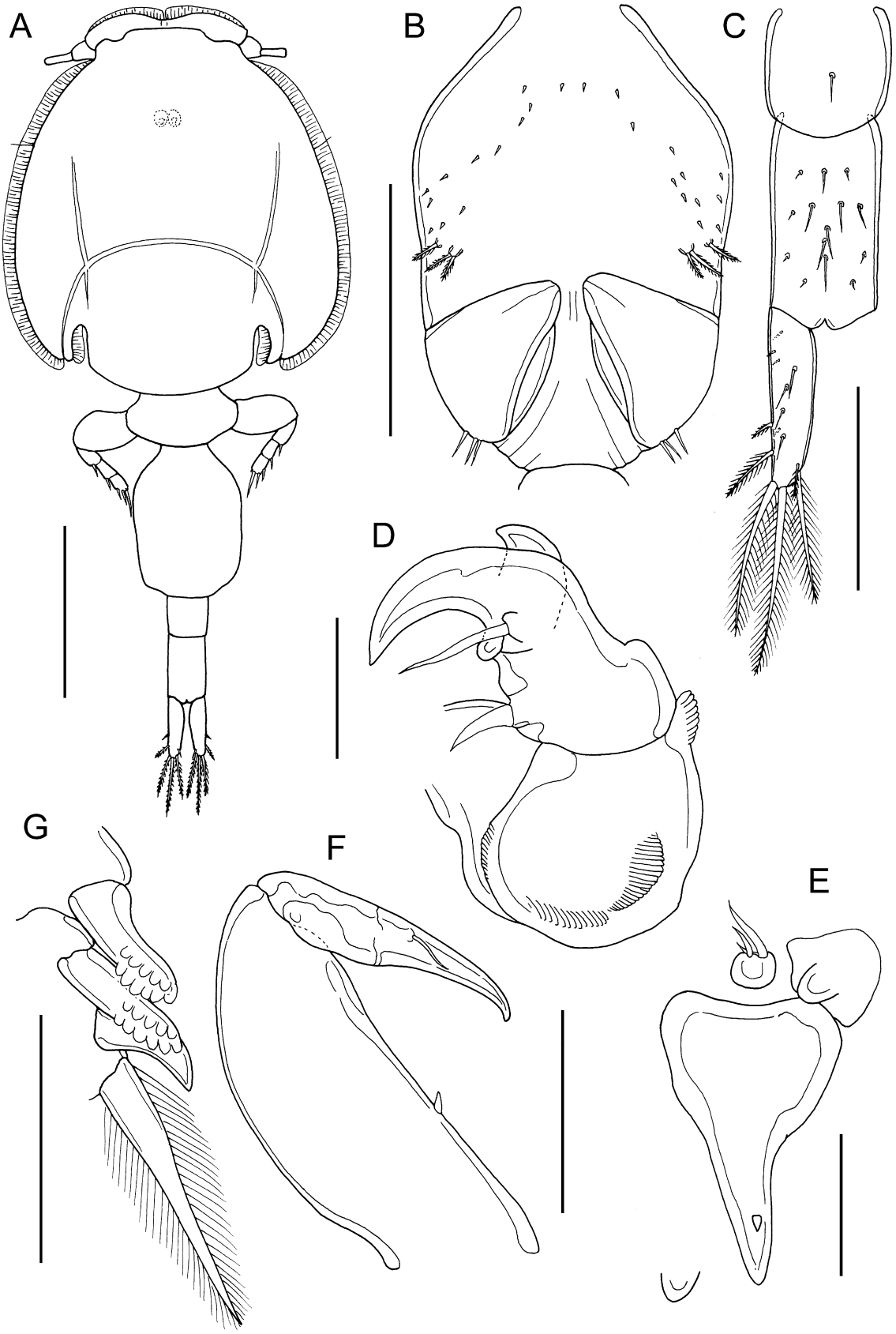

FIGURE 76. *Pupulina keiri* **sp. nov.** paratype male. A, habitus, dorsal; B, genital complex, ventral view; C, free abdominal somites and caudal ramus, ventral; D, antenna; E, maxillule and postoral process; F, maxilliped; G, sexually dimorphic spines on outer margin of exopod of leg 2. Scale bars: 1.0 mm on A, 0.5 mm on B, 200 µm on C, F, 100 µm on D, E, G.

Maxilliped (Fig. 76F) slender, proximal segment bearing small spiniform process on myxal margin; distal subchela longer than in female.

Spines on exopod of leg 2 modified in adult male: outer spine on second exopodal segment and proximal outer spine on third segment both stout and ornamented distally with dual rows of rounded denticles (Fig. 76G). Distal outer spine on third segment about as long as other spines, stout, unornamented.

Fifth legs 5 (Fig. 76B) represented by isolated plumose seta plus posterior lobe bearing 2 plumose setae located ventrolaterally almost at mid-level of genital complex. Sixth legs each represented by oblique operculum closing off genital aperture and armed with 3 short naked setae around apex (Fig. 76B).

Remarks. Only five genera of Caligidae retain a 2-segmented endopod of leg 1 armed with 0-0; 3 setae: *Alebion*, *Avitocaligus* Boxshall & Justine, 2005, *Euryphorus* Milne Edwards, 1840, *Gloiopotes* and *Pupulina* van Beneden, 1892. *Pupulina* can be distinguished from these other four by the combination of the loss of the endopod of leg 4 (*Euryphorus* and *Avitocaligus* have a biramous leg 4 with a 2-segmented endopod), and the lack of paired dorsal plates on the fourth pedigerous somite (dorsal plates are present in *Alebion*, *Euryphorus* and *Gloiopotes*). *Pupulina* currently comprises five valid species: *P. flores* van Beneden, 1892*, P. brevicauda* M.S. Wilson, 1952, *P. minor* M.S. Wilson, 1952, *P. cliffi* Dippenaar & Lebepe, 2013 and *P. merira* Dippenaar & Lebepe, 2013, and these species can be identified using the key provided by Dippenaar & Lebepe (2013). The new species and *P. cliffi* both lack paired posterolateral processes on the female genital complex, while in *P. merira*, the posterolateral corners of the genital complex of the female are very slightly expanded and were considered to represent short, rounded processes by Dippenaar & Lebepe (2013). The other three species each have paired posterolateral processes that reach at least to the middle of the first free abdominal somite.

Female *P. merira* have elongate caudal rami that are about 6.7 times longer than maximum width (at base) and are almost as long as the abdomen. In the new species, the caudal rami are about 3.1 times longer than wide and less than half the length of the abdomen. In addition, the second exopodal segment of leg 4 carries a plumose inner seta as well as an outer spine, whereas in *P. kieri* **sp. nov.** this segment carries only an outer spine.

The new species is most closely related to *P. cliffi* which was described from two species of mobuline rays, *Mobula kuhlii* (Müller & Henle, 1841) and *M. eregoodootenkee* (Bleeker, 1859) caught in South African waters (Dippenaar & Lebepe, 2013). In *P. cliffi* the caudal rami are about 5.3 times longer than wide whereas in *P. kieri* **sp. nov.** the caudal rami are about 3.1 times longer than wide. The abdomen in *P. cliffi* is about as long as the genital complex and is 3.8 times longer than wide, in contrast in the new species the abdomen is less than half the length of the genital complex and is only 2.3 times longer than wide. These differences are sufficient to justify the establishment of a new species to accommodate the material from Moreton Bay.

All previous records of this genus are from rays belonging to the subfamily Mobulinae (family Myliobatidae): *P. flores* on *Manta birostris* (Walbaum, 1792) (C.B. Wilson, 1935; M.S. Wilson, 1952) and ?*Mobula hypostoma* (Bancroft, 1831) (Bere, 1936), *P. brevicauda* from *Mobula thurstoni* (Lloyd, 1908) (as *M. lucasana* Beebe & Tee-Van) (Wilson, 1952) and *M. mobular* (Bonnaterre, 1788) (as *M. diabolus* (Shaw)) (Pillai & Padmanbhan, 1963), *P. minor* also from *M. thurstoni* (as *M. lucasana*) (Wilson, 1952) and *M. mobular* (as *M. diabolus*) (Pillai, 1964b), and both *P. cliffi* and *P. merira* from *M. kuhlii* and *M. eregoodootenkee* (Dippenaar & Lebepe, 2013). The host of the new species from Moreton Bay is *Aetobatus ocellatus*, a member of the subfamily Myliobatinae. This marks a considerable broadening of the known host range of *Pupulina*.

Discussion

Species groups in *Caligus*. *Caligus* is the most species rich genus in the order Siphonostomatoida: it currently comprises 254 valid species and another nine new species are added here. A further species (*C. alepicolus* **nom. nov.**) is transferred into *Caligus* from *Caligodes*, a second species is transferred from *Parapetalus* (as *C. seriolicolus* **nom. nov.**) and *Parapetalus parapetalopsis* is returned to its original combination as *Caligus parapetalopsis*, raising the total number of valid species to 266. It is difficult to navigate around a genus of this size and especially difficult to carry out the comparisons necessary to justify the establishment of any new species. It is possible, however, to recognise some large groups of species, each of which can be defined on the basis of a suite of shared morphological character states. No proposals can be made at this stage to create formal supraspecific names for these groups because, as with many parasitic taxa, there is evidence of convergent reduction within

Caligus. Freeman *et al.* (2013), for example, used molecular data to show that the vestigial condition of leg 4 occurred convergently in different lineages within *Caligus*. The species groups recognised here provide a convenient aid to navigate the genus; they are based on phenotypes and do not necessarily represent monophyletic groups, although some might. The monophyletic status of these groups should eventually be tested using molecular data. Five species groups are recognised in this paper:

***Caligus bonito*-group. Diagnosis.** 3-segmented leg 4 armed with four spines on compound second exopodal segment; three plumose setae present on posterior margin of distal exopodal segment of leg 1; and ornamentation of large denticles present along outer margin of second endopodal segment of leg 2; antenna with process present on proximal segment but often small or weakly developed.

This group includes: *C. bonito*, *C. asperimanus*, *C. asymmetricus*, *C. biseriodentatus*, *C. cossacki*, *C. grandiabdominalis*, *C. hoplognathi*, *C. malabaricus*, *C. mutabilis*, *C. omissus*, *C. phipsoni*, *C. tenuifurcatus*, and *C. triabdominalis*. A few other species share most but not all of the diagnostic features, such as *C. infestans* and *C. chamelensis*, in which the denticles along the margin of the second endopodal segment of leg 2 are not as conspicuously enlarged as in other members of the group.

***Caligus confusus*-group. Diagnosis.** 3-segmented exopod on leg 4 armed with I, I, III spines; raised cuticular rib (often with bifid tip) and circular array of large denticles present on apron of leg 3; outer margin spine on first exopodal segment of leg 3 forming large recurved hook; antenna with posterior process on proximal segment (process typically spatulate); accessory tine present on post-antennal process, and accessory tine present on posterior maxillulary process.

This group includes: *C. confusus*, *C. aesopus*, *C. bicycletus*, *C. brevicaudus*, *C. chorinemi*, *C. cordyla*, *C. equulae*, *C. kurochkini*, *C. lichiae*, *C. lunatus*, *C. platurus*, *C. randalli*, *C. regalis*, *C. spinosus*, *C. tenax* and *C. zylanica*. A few other species share most but not all of the diagnostic features including: *C. clavatus*, *C. fortis*, *C. isonyx* and *C. inopinatus*.

The new species, *C. abigailae* **sp. nov.**, and the three species transferred into *Caligus* from other genera, *C. alepicolus* **nom. nov.**, *C. parapetalopsis*, and *C. seriolicolus* **nom. nov.**, are all recognised as additional members of the *C. confusus*-group.

***Caligus diaphanus*-group. Diagnosis.** 3-segmented exopod on leg 4 armed with I,I,III spines and ornamented with strip of membrane (modified pecten) associated with each spine; three plumose setae present on posterior margin of distal exopodal segment of leg 1; spines 2 and 3 on distal exopodal segment of leg 1 apparently lacking accessory processes; ornamentation of fine setules extending over surface of second and third endopodal segments of leg 2; and with outer spines of first and second exopodal segments of leg 2 aligned close to longitudinal axis of ramus; antenna lacking posterior process on proximal segment; tine on post-antennal process vestigial or weakly developed.

This group includes: *C. diaphanus*, *C. cybii*, *C. kanagurta*, *C. kapuhili*, *C. laticaudus*, *C. macrurus*, *C. pagelli, C. pelamydis, C. platytarsis*, *C. robustus*, *C. rotundigenitalis*, *C. seriolae, C. stromatei, C. tanago*, and *C. tenuis*.

***Caligus macarovi*-group. Diagnosis:** 3-segmented leg 4 with first and second exopodal segments bearing I and III spines; distal exopodal segment of leg 1 armed with 3 posterior margin plumose setae and with spines 1, 2 and 3 all subequal in length, only spines 2 and 3 with accessory processes, and seta 4 markedly longer than spines; antenna with posterior process on proximal segment; distal margin of brachium of maxilla typically ornamented with marginal serrations; abdomen 1-segmented in female.

This group was first established by Boxshall & Gurney (1980) to accommodate 28 species. It now comprises 44 species, as listed in Table 5, one of which is reported as having accessory processes on exopodal spines 1 to 3 of leg 1, rather than only spines 2 and 3 as is typical for the group.

***Caligus productus*-group. Diagnosis.** Posterior margin of distal exopodal segment of leg 1 lacking typical plumose setae, or retaining single vestigial seta; 2-segmented exopod of leg 4 armed with IV spines on compound distal exopodal segment; and with ornamentation of long, tapering spinules present along outer margin of second endopodal segment of leg 2; antenna with well developed posterior process on proximal segment.

This group was established by Boxshall & El-Rashidy (2009) and it now includes: *C. productus*, *C. ariicolus*, *C. affinis* Heller, 1866, C. *alaihi*, *C. bocki* Heegaard, 1943, *C. dakari* van Beneden, 1892, *C. enormis* Wilson, 1913, *C. epinepheli*, *C. lagocephali*, *C. haemulonis* Krøyer, 1863, *C. pagrosomi*, *C. schlegeli*, *C. sciaenops* Pearse, 1952, *C. temnodontis* Brian, 1924, and *C. turbidus* **sp. nov.**

Caligus lethrinicola Boxshall & El-Rashidy, 2009 was placed in the *C. productus*-group as it lacks any trace of

the three plumose setae on the posterior margin of the distal exopodal segment of leg 1. However, it carries only I, III spines on the fourth leg exopod, rather than I, IV found in all other species lacking the leg 1 exopodal setae. Its membership of the group should be tested but it does share some other character states typical of the group, e.g. relatively large lunules, a strongly recurved post-antennal process, and the presence of a small process medial to the post-antennal process.

Caligus tenuicauda (Shiino, 1964) has not previously been included in the *C. productus*-group, largely because it was previously classified as a member of the genus *Pseudocaligus* due to its reduced fourth legs. It was transferred to *Caligus* (see Özak *et al.*, 2013) and can be included in the *C. productus*-group.

The intensive sampling of marine fish at a single locality has significantly added to our knowledge of the Australian sea lice. Prior to this study 69 caligids had been recorded from Australian waters (Table 1): the 50 species reported here include 29 new to Australia, raising that total to 98. Thirteen of these newly-reported species are new to science. Analysis of the composition of the Australian fauna reveals a mix of cosmopolitan species, typically species that utilize large pelagic hosts, Indo-West Pacific species which also occur in India and/or in South East Asia and Japan, and regional species that have thus far only been found in Australian waters. A few records defy categorization: the second ever report of *C. sicarius*, for example, is remote from the type locality in the Red Sea. This species exhibits distinctive features such as the wedge-shaped tines of the sternal furca and a unique leg 4, so the morphology-based identification is robust, but testing such an extreme disjunct distribution with molecular data would confirm its identity.

The cosmopolitan species are *C. bonito* and *C. pelamydis*, both of which typically use wide-ranging scombrid hosts (Cressey *et al.*, 1983). *Caligus longipedis* also has a wide geographical range, which includes isolated records in the Atlantic (Florida and Belize) as well as numerous reports from the Indian Ocean and both North and South Pacific. It occurs on a broad range of hosts but appears to prefer carangids. *Caligodes laciniatus* is found on members of the Belonidae and was regarded as cosmopolitan in distribution by Cressey & Collette (1970). *Lepeophtheirus acutus* uses a variety of large chondrichthyans as hosts and may fall in the same category, however, since so many records are based on fishes held in captivity, the extent of its natural distribution is not yet clear.

The bulk of the species reported here seem to belong to an Indo-West Pacific fauna that extends westwards at least to the west coast of India in the Indian Ocean and eastwards to Taiwan/Japan in the North Pacific. Moreton Bay species that have previously been reported from both India and South East Asia to Japan include: *Abasia platyrostris* (India, Hawaii), *Alebion maculatus* (India, Sri Lanka), *Anuretes branchialis* (India, Taiwan, Japan, Philippines), *A. plectorhynchi* (Japan, Philippines), *A. serratus* (Japan, Hawaii), *Caligus ariicolus* (Thailand), *C. alepicolus* **nom. nov.** (Indonesia), *C. asymmetricus* (Japan, Hawaii), *C. biseriodentatus* (China), *C. brevicaudus* (India), *C. chiastos* (Taiwan), *C. confusus* (India, Taiwan), *C. dasyaticus* (India, Taiwan), *C. elasmobranchi* **sp. nov.** (India), *C. epidemicus* (Taiwan, Philippines), *C. furcisetifer* (India), *C. lagocephali* (India, Japan), *C. laminatus* (India), *C. laticaudus* (India, Taiwan, Japan), *C. malabaricus* (India), *C. oviceps* (Taiwan, Japan), *C. parvilatus* (South Korea), *C. platytarsis* (India), *C. schlegeli* (Taiwan), *C. sclerotinosus* (Taiwan, Japan), *Hermilius longicornis* (India, Sri Lanka, Malaysia), *Lepeophtheirus lagocephali* (India) and *Mappates plataxus* (India, Taiwan).

Regional species known only from Australian waters include most of the new species: *Anuretes amplus* **sp. nov.**, *A. amymichaelae* **sp. nov.**, *Caligus abigailae* **sp. nov.**, *C. hyporhamphi* **sp. nov.**, *C. nataliae* **sp. nov.**, *C. neoaricolus* **sp. nov.**, *C. paranengai* **sp. nov.**, *C. pseudorhombi* **sp. nov.**, *C. turbidus* **sp. nov.**, *C. upenei* **sp. nov.**, *Lepeophtheirus robertae* **sp. nov.**, and *Pupulina keiri* **sp. nov.** as well as *Caligus seriolicolus* **nom. nov.**, *C. triabdominalis* and *Hermilius youngi*.

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