



## A review of the *Caligus productus* species group, with the description of a new species, new synonymies and supplementary descriptions

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### Abstract

The *productus*-group within the sea lice genus *Caligus* Müller, 1785 is characterised by the loss of two and the reduction or loss of the third of the three plumose setae normally carried on the posterior margin of the distal exopodal segment of the first swimming leg. We describe a new species, *Caligus lethrinicola* n.sp., from a lethrinid host collected in New Caledonia. We review the group and recognize 15 species as valid, including the new species. The type material of the three varieties of *Caligus mauritanicus* Brian, 1924 is re-examined and the var. *temnodontis* is here recognized as a distinct species, *Caligus temnodontis* Brian, 1924. The typical and *miniscula* varieties are recognised as synonyms of *Caligus dakari* van Beneden, 1892 and *C. haemulonis* Krøyer, 1863 respectively. Additional synonymies are proposed within the group. Supplementary observations are presented on the morphology of *C. dakari*, *C. haemulonis* and *C. temnodontis*. A brief differential diagnosis is presented for each of the 14 previously described valid species and a key to species has been constructed.

**Key words:** Sea lice, parasite, taxonomy, new species, new synonyms, key to species

## Introduction

The genus *Caligus*, established by O.F. Müller in 1785, is the most speciose genus within the family of sea lice, the Caligidae. It currently comprises more than 220 species reported throughout the oceans and seas of the world and these species utilize a very broad range of fishes as hosts, although the great majority occur on teleosts (Margolis et al. 1975). In recent years several species have emerged as serious pests of finfish in commercial aquaculture facilities (Johnson et al. 2004).

The complex of *Caligus* species referred to as the *productus*-group by Boxshall & Gurney (1980) is characterised by the loss of two and the reduction or loss of the third of the three plumose setae normally carried on the posterior margin of the distal exopodal segment of the first leg. Ho & Lin (2003) listed a total of 16 valid species in the group and added two subspecies of *C. pagrosomi* Yamaguti, 1936 which they recognized and described in detail, *C. pagrosomi pagrosomi* and *C. pagrosomi schelegeli* Ho & Lin, 2003. In addition to the loss or reduction of plumose setae on posterior margin of distal exopodal segment of first leg, we can expand the diagnosis of the *productus*-group to include other typical character states such as: two-segmented exopod of fourth leg armed with I, IV spines (rarely I, III), relatively large lunules, two-segmented abdomen of male, and the fourth leg of both sexes typically carries conspicuous setules on the first and/or second segments (coxo-basis and first exopodal segment respectively). There are some sexually dimorphic characters also: the adult male typically has a pointed process on the myxal area of the maxilliped and an elongate genital complex; and the post-antennal process is also typically sexually dimorphic with the process being larger and more strongly curved in males than in females.

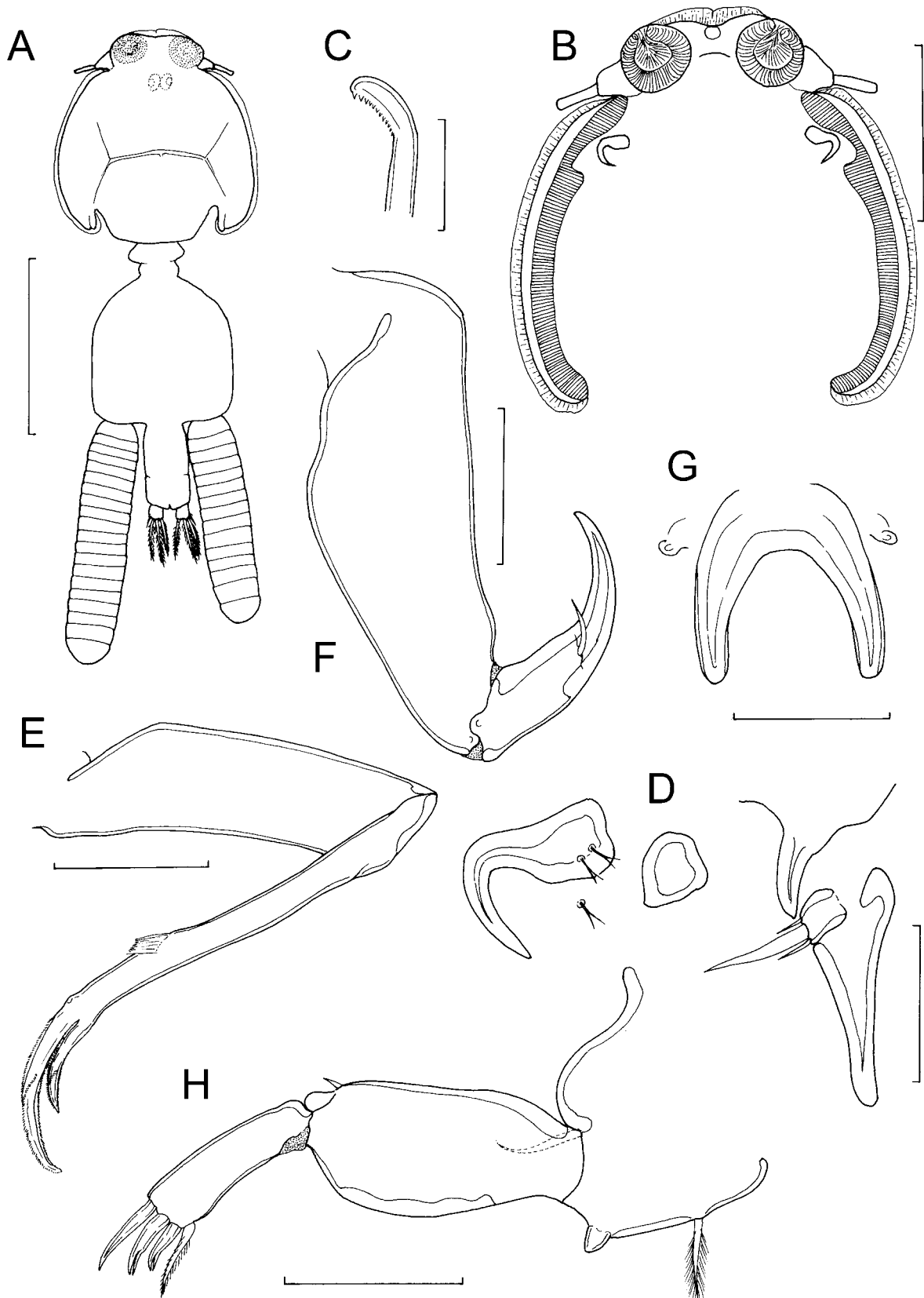
These additional characteristics can be useful in determining whether a species belongs to the group. For example, *Caligus bicycletus* Heegaard, 1945 has two vestigial posterior margin setae on the distal exopodal segment of the first leg, but is here excluded from the *productus*-group because it does not share the other diagnostic characters of the group. In particular, its fourth leg has a three-segmented exopod with a spine formula of I, I, III, rather than the I, IV typical of the group. The new species described below is atypical, having a spine formula of I, III for the exopod of the fourth leg, but shares other character states with the *productus*-group members including the complete loss of the three posterior margin setae on the first leg.

The species of the *productus*-group are not particularly well defined. When addressing the confusion around the species concept of *C. epinepheli* Yamaguti, 1936, Ho & Lin (2003) concluded that there seemed to be “no apparent structural differences” between *C. epinepheli* and *C. affinis* Heller, 1866, *C. annularis* Yamaguti, 1954, *C. ariicolous* Wilson, 1928, *C. chiloscyllii* Pillai, 1967, *C. mauritanicus* Brian, 1924 and *C. paxillifer* Yamaguti, 1954. They further commented that “it is tempting to unify the 7 *Caligus* species mentioned above under the 1<sup>st</sup> reported name, *C. affinis*” but considered such an action inappropriate before reexamination of the type material of each of these species. We have re-examined the type material of *C. mauritanicus* and its varieties *temnodontis* Brian, 1924 and *miniscula* Brian, 1924, in an attempt to resolve some of the uncertainty. In addition we have examined material belonging to other species of the *productus*-group stored in the collections of the Natural History Museum, London

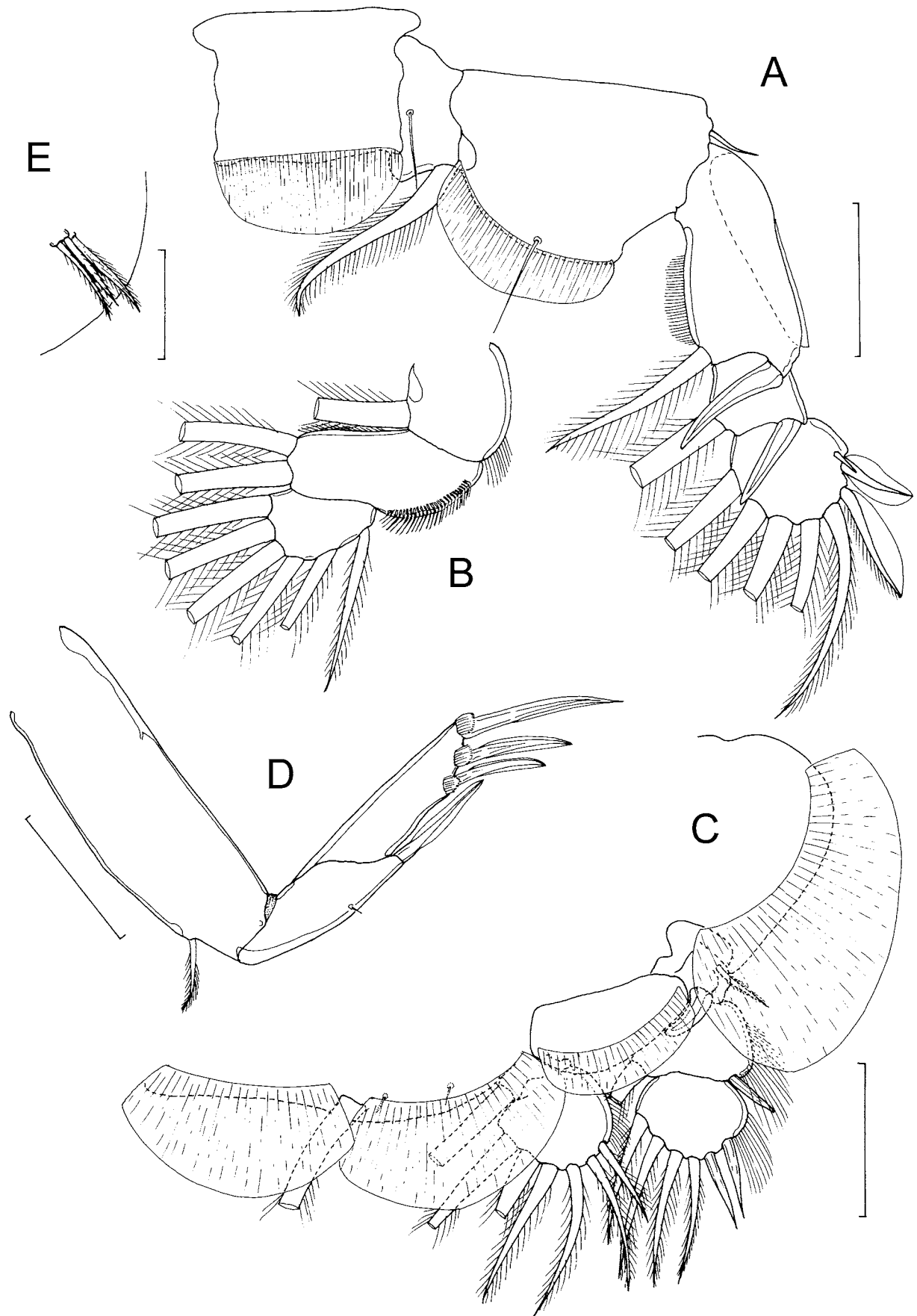
We provide a differential diagnosis for each of the valid species in the *productus*-group and recognize some new synonymies. Observations of new material are provided where this will usefully supplement existing descriptions.

## Materials and methods

The copepods were preserved in 70% ethyl alcohol. Subsequently the specimens were cleared in lactic acid for 2 h, then dissected on a glass slide and mounted as temporary preparations in lactophenol. Measurements were made using an ocular micrometer and drawings were made with the aid of camera lucida on a Leitz Diaplan differential interference contrast microscope. Morphological terminology follows Boxshall (1990) and Huys & Boxshall (1991): host fish names are according to FishBase (Froese & Pauly 2009).



**FIGURE 1.** *Caligus lethrinicola* n. sp. Holotype female. A. body, dorsal view; B. cephalothorax margins, ventral view showing lunules and marginal striations; C. Tip of mandible; D. basal part of broken antenna, post-antennal process and maxillule *in situ*, ventral view; E. maxilla; F. maxilliped; G. sternal furca *in situ*; H. leg 1. Scale-bars: A = 1 mm, B = 500  $\mu$ m, C = 50  $\mu$ m, D-H = 100  $\mu$ m.



**FIGURE 2.** *Caligus lethrnicola* n. sp. Holotype female. A. leg 2, with endopod detached; B. endopod of leg 2; C. leg 3, ventral view; D. leg 4; E. leg 5, ventral view. Scale-bars: A-D = 100 µm, E = 50 µm.

***Caligus lethrinicola* n. sp.**

**Type material:** Holotype female, partly dissected in alcohol, reg. No. MNHN-Cp2969.

**Type locality:** Récif au large de Nouméa, New Caledonia, 22°34.529'S 166°32.974'E. Collected on 27 November 2003 by J.-L. Justine (JNC 988C).

**Host:** on gills of *Lethrinus rubrioperculatus* Sato, 1978

**Etymology:** the species name is based on the generic name of its host, *Lethrinus* and *-icola*, meaning inhabitant.

Female body (Fig. 1A) dorsoventrally flattened, caligiform; body length 2.75 mm; maximum width of cephalothoracic shield 1.10 mm. Cephalothorax incorporating first to third pedigerous somites; dorsal cephalothoracic shield provided with conspicuous marginal membrane laterally and with well defined striated border located ventrally internal to lateral margins of dorsal cephalothoracic shield (Fig. 1B). Frontal plates carrying large lunules and provided with marginal membrane. Nauplius eye visible dorsally through cuticle (Fig. 1A). Fourth pedigerous somite forming narrow 'waist' between cephalothorax and genital complex. Genital complex longer than wide; length 0.91 mm and width 0.80 mm. Abdomen 2-segmented (Fig. 1A) longer than wide, length 0.54 mm and width 0.25 mm. Caudal rami dorsoventrally flattened, armed with 2 small and 4 large plumose setae (Fig. 1A).

Antennule typical for family; 2-segmented with tapering first segment and elongate second segment.

Antenna damaged on both sides; basis with spinous process near inner distal corner (Fig. 1D). Post-antennal process strongly recurved; 2 bi-setulate papillae present on basal part of process plus 1 on adjacent surface; small process located on ventral cephalothoracic surface just medial to process (Fig. 1D).

Oral cone typical for genus: mandible stylet-like (Fig. 1C) bearing 12 teeth on one side near apex.

Maxillule with basal portion incorporated into ventral cephalothoracic wall; anterior papilla bearing 3 unequal setae; posterior lobe forming tapering spiniform process (Fig. 1D).

Maxilla (Fig. 1E) well developed, brachiform, comprising unarmed syncoxa (lacertus) and basis (brachium) bearing long calamus and shorter canna at apex, plus flabellum just distal to mid-length on anterior margin. Flabellum comprising serrated membrane.

Maxilliped comprising slender corpus (Fig. 1F) and distal subchela representing fused endopodal segments plus heavily sclerotized terminal claw. Corpus unarmed. Subchela subdivided by irregular suture line; bearing single seta about at level of suture.

Sternal furca with slightly incurved tines (Fig. 1G); pair of small sclerotized swellings located on ventral cephalothoracic wall either side of furca.

Leg 1 (Fig. 1H) with sympod bearing outer and inner plumose setae. Endopod vestigial. Exopod 2-segmented; large, robust first segment carrying outer distal spine, and with smooth inner margin; second segment with 3 distal margin spines, outer most simple, second and third with bifid tips (Fig. 1H), plus inner distal angle seta located on ventral surface close to distal margin, inner margin naked.

Leg 2 biramous (Fig. 2A-B); protopod comprising coxa and basis; coxa short, bearing long, plumose seta on posterior margin; basis long, armed with short, naked, outer distal seta and provided with extensive reflexed flap of marginal membrane along inner margin and another reflexed flap of membrane dorsally, along outer margin (not figured). Both rami 3-segmented. First exopodal segment elongate, with large outer spine reflexed over middle segment, and inner plumose seta; inner margin setulose. Second segment with reflexed outer spine. Third segment with tiny naked spine proximally, adjacent spine with broad flanges bilaterally, and terminal spine (flanged along outer margin and plumose along inner). Endopod (Fig. 2B) directed medially; first segment with inner seta and with lateral margin ornamented with distal tuft of fine pinnules; second segment elongate, with thickened lateral margin ornamented with row of spinules along outer edge, and 2 inner plumose setae; third segment with 6 plumose setae.

Leg 3 pair (Fig. 2C) fused with expanded, flattened intercoxal sclerite to form broad transverse plate. Intercoxal sclerite with extensive flap of membrane along posterior margin. Coxa and basis incompletely fused, with large plumose (coxal) seta located posteriorly. Basis with plumose outer seta; posterior and lateral

margins each with extensive flap of membrane. Rami originating close together on basis, base of exopod concealed ventrally by flap-like velum, ornamented with membrane along free margin. Exopod broad, 3-segmented; first segment short and highly sclerotised, small, reflexed, outer spine lying transversely across ventral surface of ramus; second segment armed with outer spine and inner plumose seta, plus long setules along outer margin; third segment armed with 2 naked outer spines plus 4 short, plumose inner setae. Endopod 2-segmented, comprising small, proximal segment with inner plumose seta, and distal segment armed with 6 plumose setae (Fig. 2C).

Leg 4 uniramous (Fig. 2D); coxa and basis fused, bearing plumose basal seta laterally. Exopod 2-segmented: first exopodal segment armed with long outer spine and ornamented with single marginal setule; distal segment bearing 3 flanged spines, distalmost longest; each spine with pecten at base.

Leg 5 comprising outer basal seta on lateral surface of genital complex plus 2 (exopodal) plumose setae located immediately medial to isolated seta (Fig. 2E). Leg 6 represented by paired, unarmed lobes closing off genital apertures.

**Remarks:** In common with *Caligus productus* Dana, 1852, the new species lacks any trace of the three plumose setae on the posterior margin of the second exopodal segment of leg 1. However, it differs from all other species that share this character in the spine formula of the fourth leg exopod – which bears I, III spines rather than I, IV found in all other species lacking the leg 1 setae. This combination of characters is unique in the genus, and allows us to identify this species as new despite the incomplete state of the antennae and the lack of a male. It shares some other characters typical of the *productus*-group species, such as the relatively large lunules, the strongly recurved postantennal process, the presence of a small process medial to the post-antennal process, and the presence of a marginal setule on the first exopodal segment of the fourth leg.

An interesting character present in the new species is the striated ventral border extending around the lateral margins of dorsal cephalothoracic shield internal to the margin membrane. It is distinctly notched in the vicinity of the post-antennal processes. We infer that this border enhances attachment to the surface of the host. This striated border has not been discussed extensively but we note that it also occurs in *Caligus epinepheli* Yamaguti, 1936, *C. pagrosomi* Yamaguti, 1939, and *C. schelegeli* Ho & Lin, 2003 (see figures in Ho & Lin 2003), and *C. sciaenops* Pearse, 1952 (see figures in Pearse 1953). We suspect this character is more widely distributed in the group, but for most species only dorsal views are given and its presence cannot be confirmed.

## Species of the *Caligus productus*-group

### *Caligus productus* Dana, 1852

Syn: *C. alalongae* Krøyer, 1863

*C. dentatus* Heegaard, 1962

*C. katuwo* Yamaguti, 1936

*C. lobatus* Wilson, 1935

*C. microdontus* Heegaard, 1964

*C. monacanthi* Krøyer, 1863

*C. mirabilis* Leigh-Sharpe, 1934

nec *Caligus productus* O.F. Müller, 1785 (= *Dinemoura producta*)

**Differential diagnosis:** Female genital complex and abdomen combined just longer than cephalothorax; body length 4.0–5.5 mm. Male body length 4.07 mm. Female genital complex produced into distinct postero-lateral lobes; abdomen 2-segmented, first segment just shorter than second. Male abdomen 2-segmented; second segment about twice length of first. Post-antennal process sexually dimorphic, larger and more strongly curved in male. No additional process present between post-antennal process and base of antenna. Sternal furca with straight, slightly divergent tines. Female maxilliped with small tooth-like process on myxal margin.

Male maxilliped with small process on myxal margin as in female. Exopod of leg 1 with seta at inner distal angle longer than segment, no posterior margin setae. Outer margin of second endopodal segment of leg 2 ornamented with large denticles. Leg 4 ornamented with marginal setules on first exopodal segment; distal margin spines stout, increasing in length towards terminal spine.

**Material examined:** 4 adult females and 1 male collected from *Coryphaena hippurus* caught off Tahiti by K. Rohde: stored in collections of the Natural History Museum, London Reg. Nos. 1979.482-486.

1 male collected from *Thunnus albacares* (Bonnaterre, 1788) caught off South Africa by R. van der Elst: stored in collections of the Natural History Museum, London Reg. Nos. 1979.916.

2 females and 1 male collected from *Thunnus albacares* caught off Cape Vidal, South Africa by R. Bray: stored in collections of the Natural History Museum, London Reg. Nos. 1984.130.

**Distribution:** cosmopolitan.

**Hosts:** Balistidae: *Balistes polylepis* Steindachner, 1876 (as *Verrunculus polylepis*), *Balistes* sp., *Pseudobalistes flavimarginatus* (Rüppell, 1829) (as *Balistes flavomarginatus*);

Carangidae: *Naucrates ductor* (Linnaeus, 1758), *Seriola lalandi* Valenciennes, 1833 (as *S. dorsalis*);

Centropomidae: *Centropomus* sp.;

Coryphaenidae: *Coryphaena hippurus* Linnaeus, 1758, *Coryphaena* sp.;

Elopidae: *Elops saurus* Linnaeus, 1766;

Monacanthidae: *Monacanthus* sp.;

Polynemidae: *Polydactylus opercularis* (Gill, 1863);

Sciaenidae: *Pogonias cromis* (Linnaeus, 1766);

Scombridae: *Auxis thazard* (Lacepède, 1800), *Euthynnus affinis* (Cantor, 1849) (as *Euthynnus yaito*), *Katsuwonus pelamis* (Linnaeus, 1758) (as *Katsuwonus vagans* and as *Thynnus pelamys*), *Scomber scombrus* Linnaeus, 1758, *Scomberomorus cavalla* (Cuvier, 1829), *S. maculatus* (Mitchill, 1815), *S. niphonius* (Cuvier, 1832), *S. sierra* Jordan & Starks, 1895, *Sarda orientalis* (Temminck & Schlegel, 1844), *S. sarda* (Bloch, 1793), *Thunnus alalunga* (Bonnaterre, 1788), *T. albacares* (Bonnaterre, 1788) (as *Neothunnus albacore* and as *N. macropterus*), *T. obesus* (Lowe, 1839), *T. thynnus* (Linnaeus, 1758);

Serranidae: *Paralabrax clathratus* (Girard, 1854), *P. maculatofasciatus* (Steindachner, 1868);

Sparidae: *Calamus brachysomus* (Lockington, 1880);

Sphyraenidae: *Sphyraena argentea* Girard, 1854.

*Caligus productus* utilizes a wide range of fish hosts but the most commonly reported host families are the Scombridae and Coryphaenidae (Margolis et al. 1975; Ho & Lin 2004).

**Remarks:** Despite its long list of synonyms, this species is easy to distinguish from the other members of the species group by the combination of characters in the differential diagnosis. In particular, it is the only species in the group, apart from *C. bocki* Heegaard, 1943, which has produced lobes at the postero-lateral angles of the female genital complex. It differs from *C. bocki* in the possession of bifid rather than a spine-like sternal furca.

In their review of the genus *Caligus*, Margolis et al. (1975) listed *C. monacanthi* Krøyer, 1863, *C. lobatus* Wilson, 1935 and *C. katuwo* Yamaguti, 1936 as synonyms. Four further species were recognized as synonyms by Cressey (1991), *C. alalongae* Krøyer, 1863, *C. mirabilis* Leigh-Sharpe, 1934, *C. dentatus* Heegaard, 1962 and *C. microdontus* Heegaard, 1964, and these were all accepted as synonyms in Ho & Lin's review of the sea lice of Taiwan (Ho & Lin 2004).

### ***Caligus affinis* Heller, 1866**

Syn: nec *Caligus affinis* Kurian, 1961

nec *Caligus* cf. *affinis*: Kensley & Grindley, 1973

**Differential diagnosis:** Female genital complex and abdomen combined about 1.2 times longer than cephalothorax; body length 3.3–5.45 mm. Male body length 4.36 mm. Female genital complex without distinct postero-lateral lobes. Abdomen 2-segmented, first segment about twice as long as second. Male abdomen 2-segmented; first segment just shorter than second. Post-antennal process large and strongly curved in both sexes. Additional process present between post-antennal process and base of antenna in female. Sternal furca with strongly incurved tines and wide gape. Female maxilliped with smooth medial margin. Male maxilliped with large pointed process on myxal margin, opposing tip of claw. Exopod of leg 1 with seta at inner distal angle longer than longest spine but shorter than segment; no vestiges of posterior margin setae; first exopodal segment broad, with strongly convex posterior margin. Outer margin of second endopodal segment of leg 2 ornamented with denticles. Leg 4 with outer spine on second exopodal segment short, not reaching base of outer distal margin spine; outer and middle distal spines of similar length and distinctly shorter than terminal spine.

**Material examined:** none

**Distribution:** Mediterranean Sea.

**Hosts:** Sciaenidae: *Umbrina cirrosa* (Linnaeus, 1758), *Umbrina canariensis* Valenciennes, 1843.

**Remarks:** Brian (1935) gave a relatively good description of *C. affinis* based on a single female collected from the type host, *Umbrina cirrosa*, at Genoa. Cressey (unpublished) found and described in detail the same species on *Umbrina canariensis* from the type locality, the Adriatic Sea. The material reported by Kensley & Grindley (1973) as *Caligus* cf. *affinis* is not *C. affinis*. The body proportions of the adult female are different; the genital complex and abdomen are about twice as long as the cephalothorax, a vestigial seta is present on the posterior margin of the second exopodal segment of leg 1, and the proportional lengths of the spines on the exopod of leg 4 are not the same as in *C. affinis*. The South African material of Kensley & Grindley (1973) most closely resembles *C. pagrosomi* and *C. temnodontis* (see below). The plumose seta on the posterior margin of leg 1 exopod is more strongly reduced than in *C. pagrosomi*, and Özak et al. (submitted) tentatively attributed this material to *C. temnodontis*.

*Caligus affinis* is most closely related to the widely distributed *C. epinepheli* but can be distinguished from it by the shape of the sternal furca, with its more strongly incurved tines and wider gape, and by the strongly recurved post-antennal process of the female. Thus far *C. affinis* is only confirmed as parasitic on species of *Umbrina* in the Adriatic Sea.

### *Caligus alaihi* Lewis, 1968

**Differential diagnosis:** Female genital complex and abdomen combined shorter than cephalothorax; body length 2.77 mm. Male body length 2.07 mm. Female genital complex lacking distinct postero-lateral lobes; abdomen apparently 1-segmented, about half as long as genital complex. Male abdomen 2-segmented; second segment almost twice length of first. Post-antennal process sexually dimorphic, larger and more strongly curved in male. Sternal furca with straight, strongly divergent tines. Female maxilliped with smooth medial margin. Male maxilliped with slight rounded swelling in myxal area. Exopod of leg 1 with seta at inner distal angle about as long as segment, single plumose seta on posterior margin about as long as shortest distal spine. Outer margin of second endopodal segment of leg 2 ornamented with denticles. Leg 4 ornamented with marginal setules on protopodal segment but none figured on exopodal segments: outer spine on second exopodal segment reaching well beyond base of adjacent distal margin spine; terminal spine about twice as long as other 2 distal margin spines.

**Material examined:** none

**Distribution:** Eniwetok Atoll.

**Hosts:** Holocentridae: *Neoniphon samara* (Forsskål, 1775) (as *Holocentrus samara*).

**Remarks:** This species can be readily distinguished within the group by the short, 1-segmented abdomen of the adult female. It differs from *C. enormis* in which the abdomen is even more reduced and fused to genital



complex and which lacks a sternal furca. It carries a single, well developed plumose seta on the posterior margin of the distal exopodal segment of leg 1 as in *C. pagrosomi*. In *C. enormis* this seta is present but is spinulate, rather than plumose, and one of the distal margin spines is lacking (Ho & Bashirullah 1977).

### ***Caligus ariicolus* Wilson, 1928**

**Differential diagnosis:** Female genital complex and abdomen combined about 1.5 times longer than cephalothorax; body length 3.75–4.25 mm. Male length 3.0 mm. Female genital complex large, lacking distinct postero-lateral lobes; only slightly longer than abdomen; abdomen 2-segmented, first segment about 3 times longer than second. Male genital complex slender: abdomen 2-segmented; second segment longer than first. Post-antennal process sexually dimorphic, larger and more strongly curved in male. Sternal furca with incurved tines but narrow gape. Female maxilliped with smooth medial margin. Male maxilliped with process on myxal margin, opposing tip of claw. Exopod of leg 1 with seta at inner distal angle longer than longest distal spine but shorter than segment; no setae on posterior margin. First exopodal segment of leg 4 with large outer spine reaching nearly to tip of outer spine on second segment; outer spine on second exopodal segment long, about equal in length to outer and middle spines on distal margin; terminal spine distinctly longer than other 2 distal margin spines.

**Material examined:** none

**Distribution:** Thailand.

**Hosts:** Ariidae: *Nemapteryx caelata* (Valenciennes, 1840) (as *Arius caelatus*).

**Remarks:** This species has a large genital complex and abdomen and is similar in body proportions to *Caligus fugu* Yamaguti & Yamasu, 1959. However, it differs in the absence of the spinous process on the medial margin of the maxilliped of the female. The sternal furca of *C. ariicolus* has incurved tines whereas those of *C. fugu* are straight and tapering. *Caligus ariicolous* Wilson, 1928 was described from a catfish caught off Paknam, Thailand, and has not been reported since.

### ***Caligus bocki* Heegaard, 1943**

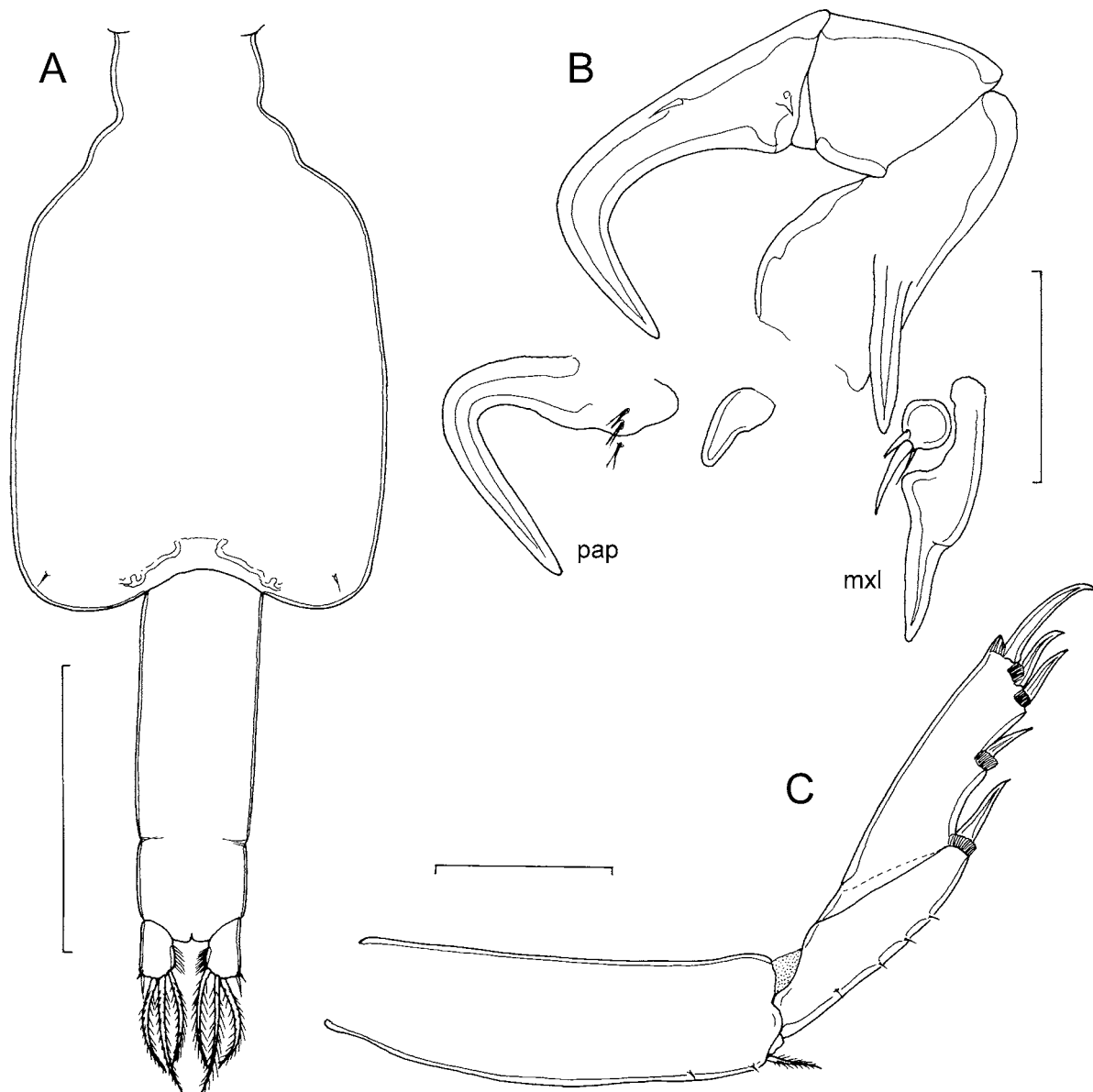
**Differential diagnosis:** Female genital complex and abdomen combined just slightly shorter than cephalothorax; body length 2.6–2.8 mm. Female genital complex produced into distinct postero-lateral lobes; abdomen apparently 2-segmented, first segment very much shorter than second. Post-antennal process not strongly recurved in female. Sternal furca with tines apparently fused to form median tapering spine. Female maxilliped with small tooth-like process on myxal margin. Leg 4 with long distal spines, terminal spine slightly longer than other 2 distal margin spines. Male unknown.

**Material examined:** none

**Distribution:** Gilbert Islands.

**Hosts:** Carcharhinidae: *Carcharhinus falciformis* (Müller & Henle, 1839) (as *Eulamia menisorrah* (Müller & Henle)).

**Remarks:** The original description is of extremely poor quality and is inconsistent: the body length of the single holotype female is given as 2.6 mm and also as 2.8 mm by Heegaard (1943) in different parts of the text. Although described as having a 1-segmented abdomen, we consider the abdomen 2-segmented with the short base illustrated as carrying the large free segment being interpreted here as a short first free abdominal segment. As well as being the only species in the group, other than *C. productus* itself, to possess postero-lateral lobes on the genital complex, this species shares a second similarity, namely the tiny process on the medial margin of the female maxilliped. This at least raises the possibility that the type specimen could be an aberrant individual of *C. productus*, found on an unusual host, the shark *Carcharhinus falciformis*. The form of the sternal furca, with its fused tines, is a unique apomorphy for this species within the group.



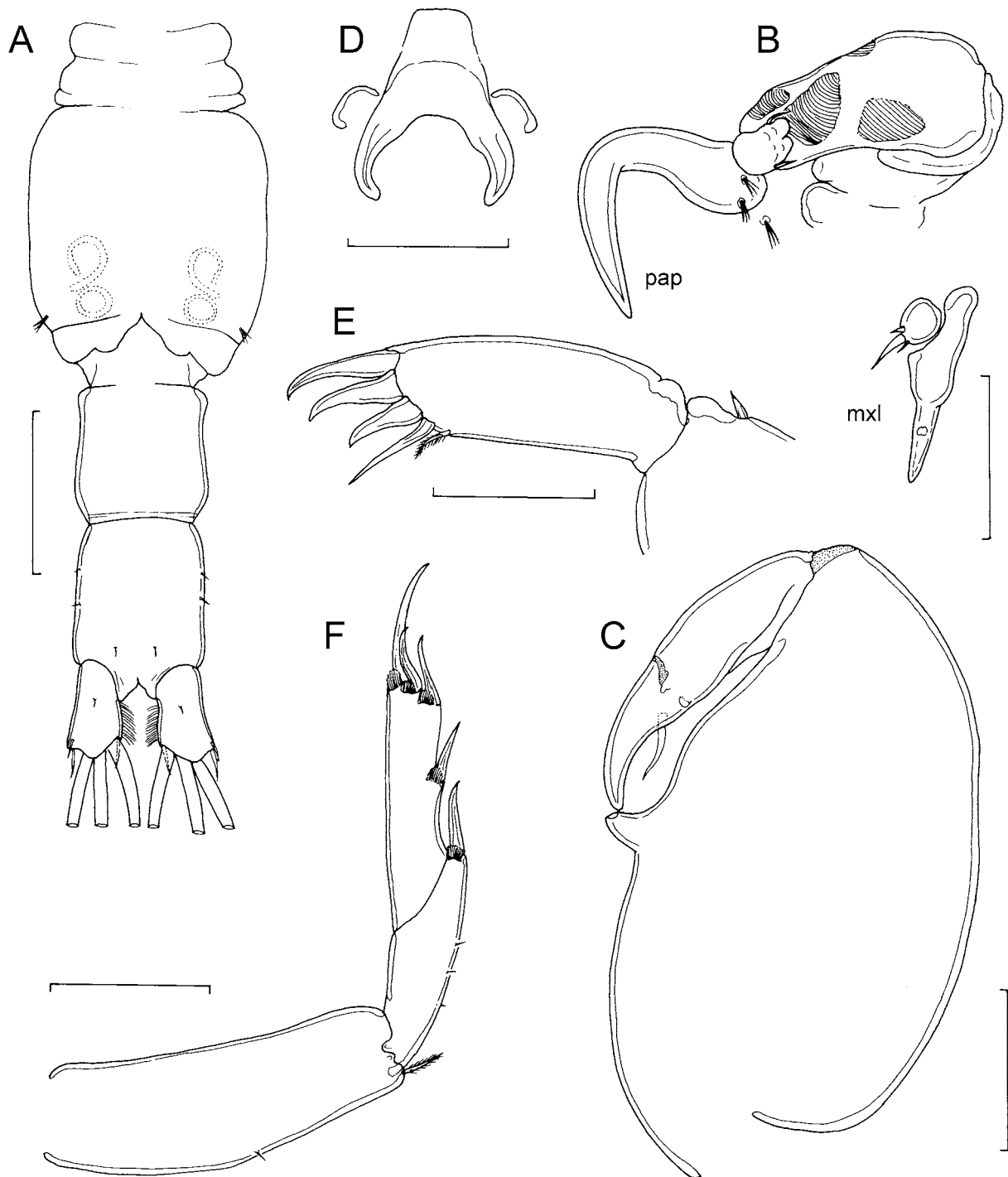
**FIGURE 3.** *Caligus dakari* van Beneden, 1892 female. A. genital complex and abdomen, ventral view; B. antenna, post-antennal process (pap) and maxillule (mxl), ventral view *in situ*; C. leg 4. Scale-bars: A = 1 mm, B = 200  $\mu$ m, C = 250  $\mu$ m.

### *Caligus dakari* van Beneden, 1892

Syn: *Caligus mauritanicus* typical form Brian 1924

**Differential diagnosis:** Female genital complex and abdomen combined about 1.5 times longer than cephalothorax; body length 6.0–6.5 mm. Male body length 5.0 mm. Female genital complex (Fig. 3A) elongate with parallel lateral margins and narrow waist-like region anteriorly, lacking distinct postero-lateral lobes: abdomen 2-segmented, first segment nearly three times longer than second. Male abdomen 2-segmented (Fig. 4A); second segment longer than first. Post-antennal process large and strongly curved in both sexes (cf. Figs 3B, pap; 4B, pap). Additional process present between post-antennal process and base of antenna in female (Fig. 3B). Posterior process of maxillule (Fig. 4B, mxl) with distinct narrowing between proximal and distal parts; male with tiny blunt accessory process. Sternal furca with strongly incurved tines and

wide gape; transverse thickenings of body surface present either side of furca (Fig. 4D). Female maxilliped with smooth medial margin. Male maxilliped with pointed process on myxal margin (Fig. 4C), opposing tip of claw; process minutely concave at tip. Exopod of leg 1 with seta at inner distal angle shorter than segment and about as long as terminal spine on distal margin; posterior margin with single plumose seta less than half length of adjacent seta (Fig. 4E). Exopod of leg 4 distinctive in both sexes (Fig. 3C, 4F): first exopodal segment large with marginal setules, second segment with concave margin proximal to first marginal spine: exopodal spines relatively stout, outer 2 spines of similar length and markedly shorter than terminal spine.



**FIGURE 4.** *Caligus dakari* van Beneden, 1892 male. A. genital complex and abdomen, ventral view; B. antenna, post-antennal process (pap) and maxillule (mxl) *in situ*, ventral view; C. maxilliped; D. sternal furca *in situ*; E. second exopodal segment of leg 1 showing distal armature; F. leg 4. Scale-bars: A = 500  $\mu$ m, B, C, D, F = 250  $\mu$ m, E = 100  $\mu$ m.

**Material examined:** 30 female and 3 male syntypes labeled *Caligus mauritanicus*, in 2 vials deposited in the collections of the Museum National d'Histoire Naturelle in Paris, registration numbers, MNHN Cp.278 and Cp.280.

**Distribution:** Eastern South Atlantic: Mauritania, Senegal.

**Hosts:** Carangidae: *Lichia amia* (Linnaeus, 1758);

Sciaenidae: *Argyrosomus regius* (Asso, 1801) (as *Sciaena aquila*).

**Remarks:** The original description of *C. dakari* was incomplete and inadequate by modern standards and even though Brian (1924) recognised a remarkable similarity in gross form between *C. mauritanicus* and *C. dakari*, he preferred to establish a new species. Van Beneden's (1892) description specified that the plumose setae were absent on the posterior margin of the distal exopodal segment of leg 1 of *C. dakari*, which allows us to place it in the *productus*-group. In addition, this is an unusually large species of *Caligus*. These two nominal species are the only species currently known from the Atlantic coast of Africa that lack these setae, share this shape of genital complex and elongate abdomen, and have a female body length of about 6.0 mm. We consider these species to be identical. The oldest available name for this species is *C. dakari* and we here recognise the typical form of *Caligus mauritanicus* Brian, 1924 as a junior subjective synonym.

Kirtisinghe (1964) considered that the specimens of *Caligus arii* Bassett-Smith, 1898 reported from South Africa by Barnard (1955) belonged to *C. dakari*.

### ***Caligus enormis* Wilson, 1913**

**Differential diagnosis:** Female genital complex and abdomen combined slightly longer than cephalothorax; body length 2.15 mm. Male body length 1.6 mm. Female genital complex large, with parallel sides, rounded corners and narrow waist-like region anteriorly; without distinct postero-lateral lobes, fused to extremely short unsegmented abdomen. Male genital complex elongate; free abdomen 1-segmented, about 1.5 times longer than wide. Post-antennal process sexually dimorphic, much larger and more strongly curved in male. No additional process present between post-antennal process and base of antenna in female. Sternal furca lacking. Female maxilliped with smooth medial margin. Male maxilliped with large pointed process on myxal margin, opposing tip of claw, and smaller rounded process located more distally on medial margin. Exopod of leg 1 lacking spine at anterodistal angle; seta at inner distal angle about as long as segment; one short spinulate seta present on posterior margin. Outer margin of second endopodal segment of leg 2 ornamented with fine setules. Leg 4 with strongly produced outer margin on first exopodal segment; outer and middle spines on distal margin markedly shorter than terminal spine.

**Material examined:** none

**Distribution:** Jamaica.

**Hosts:** Scaridae: *Sparisoma viride* (Bonnaterre, 1788).

**Remarks:** Despite its name, this is a small species with a female body length of about 2.15 mm. It is the large size of the post-antennal process in the male that gives this species its name (Wilson 1913).

*Caligus enormis* is an atypical member of the *productus*-group which can be distinguished from all other members of the group by the extremely short abdomen of the female that appears fused to the genital complex. In addition it lacks a sternal furca, as confirmed by Ho & Bashirullah (1977), and lacks the anterior-most of the terminal spines on the distal exopodal segment of leg 1 (Ho & Bashirullah 1977: Fig. 5C) while retaining one posterior margin seta, albeit spinulate rather than plumose. These are unusual characters. With reference to leg 3, Wilson (1913) stated "the endopod contains but one partial joint, which is fused to the basal plate". This joint carries an inner plumose seta (Wilson 1913: Fig. 121). The type material of *C. enormis* was re-studied by Ho & Bashirullah (1977) but was not in good condition and they provided no further information on leg 3, but they commented that *C. enormis* was "not a species of *Caligus*" as it lacks an endopod in leg 3. The partial loss of the endopod of leg 3, even if it is not based on an aberrant or damaged individual, might merely be an autapomorphy of the species. It cannot be inferred from this one reduced

character state, that *C. enormis* should be placed in a different genus. We retain this species within the *productus*-group, with which it shares important apomorphies including the segmentation and armature of leg 4, and the sexual dimorphism of the post-antennal processes.

### ***Caligus epinepheli* Yamaguti, 1936**

Syn: *C. annularis* Yamaguti, 1954

*C. chiloscyllii* Pillai, 1967

*C. minutus* Pillai, 1963

*C. paxillifer* Yamaguti, 1954

*C. sciaenae* Gnanamuthu, 1947

nec *Caligus epinephali* [sic]: Cressey, 1991

**Differential diagnosis:** Female genital complex and abdomen combined about 1.2 times longer than cephalothorax; body length 2.20–3.10 mm. Male body length 2.3 mm. Female genital complex without distinct postero-lateral lobes. Abdomen 2-segmented, first segment about twice as long as second. Male abdomen 2-segmented; first segment just shorter than second. Post-antennal process sexually dimorphic, larger and more strongly curved in male. Additional process present between post-antennal process and base of antenna in female. Sternal furca with slightly incurved tines. Female maxilliped with smooth medial margin. Male maxilliped with large pointed process on myxal margin, opposing tip of claw. Exopod of leg 1 with seta at inner distal angle longer than longest spine but shorter than segment; no vestiges of posterior margin setae; first exopodal segment broad, with strongly convex posterior margin. Outer margin of second endopodal segment of leg 2 ornamented with fine denticles. First exopodal segment of leg 4 with long spine reaching almost to tip of short outer margin spine on second segment, ornamented with marginal setule; all 3 distal margin spines on second exopodal segment differing in length, increasing towards terminal spine.

**Material examined:** 1 adult female collected from *Epinephelus merra* Bloch, 1793 caught off Green Island, Queensland, Australia by P.C. Young and identified by Z. Kabata: stored in collections of the Natural History Museum, London Reg. No. 1965.4.7.5.

**Distribution:** Indo-West Pacific; Japan, Taiwan, Malaysia, Australia.

**Hosts:** Carangidae: *Scomberoides lysan* (Forsskål, 1775) (as *Chorinemus moadetta*), *Scomberoides tala* (Cuvier, 1832);

Drepaneidae: *Drepane punctata* (Linnaeus, 1758);

Haplogenyidae: *Haplogenyus mucronatus* (Eydoux & Souleyet, 1850);

Hemiscyllidae: *Chiloscyllium indicum* (Gmelin, 1789);

Nemipteridae: *Scolopsis vosmeri* (Bloch, 1792);

Sciaenidae: *Johnius dussumieri* (Cuvier, 1830), *J. glaucus* (Day, 1876) (as *Sciaena glauca*), *Pterolithus maculatus* (Cuvier, 1830) (as *Otolithes maculatus*);

Serranidae *Epinephelus septemfasciatus* (Thunberg, 1793), *Epinephelus akaara* (Temminck & Schlegel, 1842), *Epinephelus merra* Bloch, 1793;

Sparidae: *Acanthopagrus schlegelii* (Bleeker, 1854).

*Caligus epinepheli* exploits a range of fish hosts, as summarised by Ho & Lin (2003).

**Remarks:** This species is extremely close to *C. affinis* in female body shape and proportions, especially the relatively short abdomen compared to the genital complex. We maintain it as a separate species on the basis of the difference in shape of the sternal furca, which has strongly incurved tines and a wide gape in *C. affinis* but only slightly incurved tines and a narrower gape in *C. epinepheli*. In addition the female post-antennal process is weakly curved in *C. epinepheli* but strongly curved in *C. affinis*. There are also slight differences in the relative lengths of the distal spines on the fourth leg. The two subterminal spines are about equal in length and only slightly shorter than the terminal spine in *C. affinis* but all 3 distal spines differ in length in *C. epinepheli*, increasing in length towards the terminal spine. In this decision we are influenced by

the known distribution patterns: *C. affinis* is only confirmed from the Mediterranean at present while *C. epinepheli* is an Indo-Pacific species unknown from the Atlantic.

*Caligus epinepheli* is a relatively small species with a reported female body length of 2.98–3.1 mm in Japan (Yamaguti 1936; Shiino 1952) and 2.20–2.26 in Taiwan (Ho & Lin 2004). This range is substantially smaller than the 4.5 mm length given by Pillai (1985) for material from Indian waters, and we consider that the specific identity of the material cited by Pillai requires verification.

*Caligus chiloscyllii* Pillai, 1967 is treated here as a synonym of *C. epinepheli*. The adult female has a similar body length (2.4 mm) and the proportional lengths of the cephalothorax, genital complex and abdomen (Pillai 1967) are similar to those of *C. epinepheli*. In addition the shape of the sternal furca, the degree of curvature of the female post-antennal process, the ornamentation on the lateral margin of the second endopodal segment of leg 2, and the relative lengths of the setal elements on the tip of the exopod of leg 1 and the spines on leg 4, are all similar to those described for *C. epinepheli* (Ho & Lin 2003). Although the original description (Yamaguti 1954) contained minimal detail, we also consider that *C. annularis* Yamaguti, 1954 does not differ from *C. epinepheli* in any significant characters. The female body length (2.1 – 2.4 mm) given by Yamaguti (1954) is in accord with the known size range for *C. epinepheli* and the sternal furca is the same shape.

Unfortunately *C. sciaenae* Gnanamuthu, 1947 is based only on the male and the description is inaccurate to the extreme that some figures are un-interpretable (Gnanamuthu 1947). However, it clearly belongs in the *productus*-group and its small body size (1.7 mm), the large, acutely-pointed myxal spine on the maxilliped, and the proportional lengths of the two abdominal somites, provide support for our proposed treatment of this species as a synonym of *C. epinepheli*.

*Caligus paxillifer* Yamaguti, 1954 is tentatively placed in synonymy with *C. epinepheli*, since it does not differ in any substantive characters from Yamaguti's (1936) description. It shares the same body proportions, female body size, shape of sternal furca, even the relative lengths of the three spines on the exopod of leg 4. However, a detailed redescription of *C. paxillifer* is required to confirm this.

### ***Caligus fugu* Yamaguti & Yamasu, 1959**

Syn: *C. lagocephali* Pillai, 1961

**Differential diagnosis:** Female genital complex and abdomen combined nearly twice as long as cephalothorax; body length 3.0–3.7 mm. Male length 2.0–2.4 mm. Female genital complex large, lacking distinct postero-lateral lobes; about 1.6 times longer than abdomen; abdomen 2-segmented, first segment just over twice as long as second. Male genital complex with evenly convex lateral margins: abdomen 2-segmented; second segment just longer than first. Post-antennal process sexually dimorphic, larger and more strongly curved in male. Additional process present between post-antennal process and base of antenna in female. Sternal furca with straight, tapering tines. Female maxilliped with large tapering process proximally on medial margin. Male maxilliped with large, acutely-pointed process on myxal margin, opposing tip of claw. Exopod of leg 1 with seta at inner distal angle as long as longest distal spine but much shorter than segment; no setae on posterior margin. Outer margin of second endopodal segment of leg 2 densely ornamented with fine spinules. Second exopodal segment of leg 4 with short outer margin spine and 3 long distal margin spines, increasing in length slightly towards terminal spine.

**Material examined:** none

**Distribution:** Indo-West Pacific, Japan, India.

**Hosts:** Tetraodontidae: *Takifugu rubripes* (Temminck & Schlegel, 1850) (as *Sphaeroides rubripes*), *Takifugu alboplumbeus* (Richardson, 1845) (as *S. alboplumbeus*), *Takifugu niphobles* (Jordan & Snyder, 1901) (as *S. niphobles*), *Takifugu pardalis* (Temminck & Schlegel, 1850) (as *S. pardalis*), *Lagocephalus inermis* (Temminck & Schlegel, 1850).

All the reported hosts of *C. fugu* are tetraodontids (Yamaguti & Yamasu 1959; Pillai 1961).

**Remarks:** The distinguishing character of this species is the well developed process located proximally on the inner margin of the female maxilliped. This character is shared by *C. lagocephali* and the females of these species have similar body size (2.8 mm) and body proportions. *C. lagocephali* is here placed in synonymy with *C. fugu* since it does not differ in any substantive characters.

### *Caligus haemulonis* Krøyer, 1863

Syn: *C. mauritanicus* var *miniscula* Briani, 1924

**Differential diagnosis:** Female genital complex and abdomen combined about 1.3 times longer than cephalothorax; body length 2.96–3.92 mm. Male body length 1.86–3.26 mm. Female genital complex (Fig. 5A) longer than wide, lacking distinct postero-lateral lobes: abdomen 2-segmented, first segment about 1.4 times longer than second. Male abdomen 2-segmented (Fig. 6A); second segment about 1.6 times longer than first. Female antenna with distal claw strongly curved (Fig. 5B). Post-antennal process large and strongly curved in both sexes (cf. Figs 5B, 6B). Additional process present between post-antennal process and base of antenna in female (Fig. 5B). Posterior process of maxillule with tiny blunt accessory process in male (Fig. 6B). Sternal furca of female with incurved or straight tines (Fig. 5C) and with small rounded processes on body surface either side of furca (Fig. 5C); tines of sternal furca more incurved in male (Fig. 6D). Female maxilliped with smooth myxal margin; with tiny process on inner margin of claw in some specimens (Fig. 5C). Male maxilliped with large, acutely-pointed process on myxal margin (Fig. 6C), opposing tip of claw. Exopod of leg 1 with seta at inner distal angle shorter than segment and about twice long as middle of distal spines; posterior margin with single, naked vestigial seta (Fig. 5E), which can be longer in male (Fig. 6E). Outer margin of second endopodal segment of leg 2 ornamented with typical setules. Leg 4 with robust first exopodal segment bearing marginal setule; second segment with well developed spines (Figs 5F, 6F).

**Material examined:** 2 females and 1 male collected from *Micropogon furnieri* caught off Ubatuba and Santos, Brazil by K. Rohde: stored in the collections of the Natural History Museum, London, Reg. Nos. 1979.610-613.

59 female and 21 male syntypes labeled *Caligus mauritanicus* var *miniscula*; collected from a variety of host fishes as specified by Briani (1924); stored in 7 vials deposited in the collections of the Museum National d'Histoire Naturelle in Paris, registration numbers, MNHN Cp.279, Cp.283 - Cp.289.

2 females and 1 male collected from *Girella tricuspidata* caught off Coff's Harbour, New South Wales, Australia by M. La Spina: stored in the collections of the Natural History Museum, London, Reg. Nos. 1984.12.

**Distribution:** Cosmopolitan.

**Hosts:** Ariidae: *Ariopsis felis* (Linnaeus, 1766) (as *Hexanematichthys felis*, as *Galeichthys felis* and as *Arius felis*), *Arius heudelotii* Valenciennes, 1840, *Bagre marinus* (Mitchill, 1815) (as *Felichthys marinus* and as *Bagre marina*);

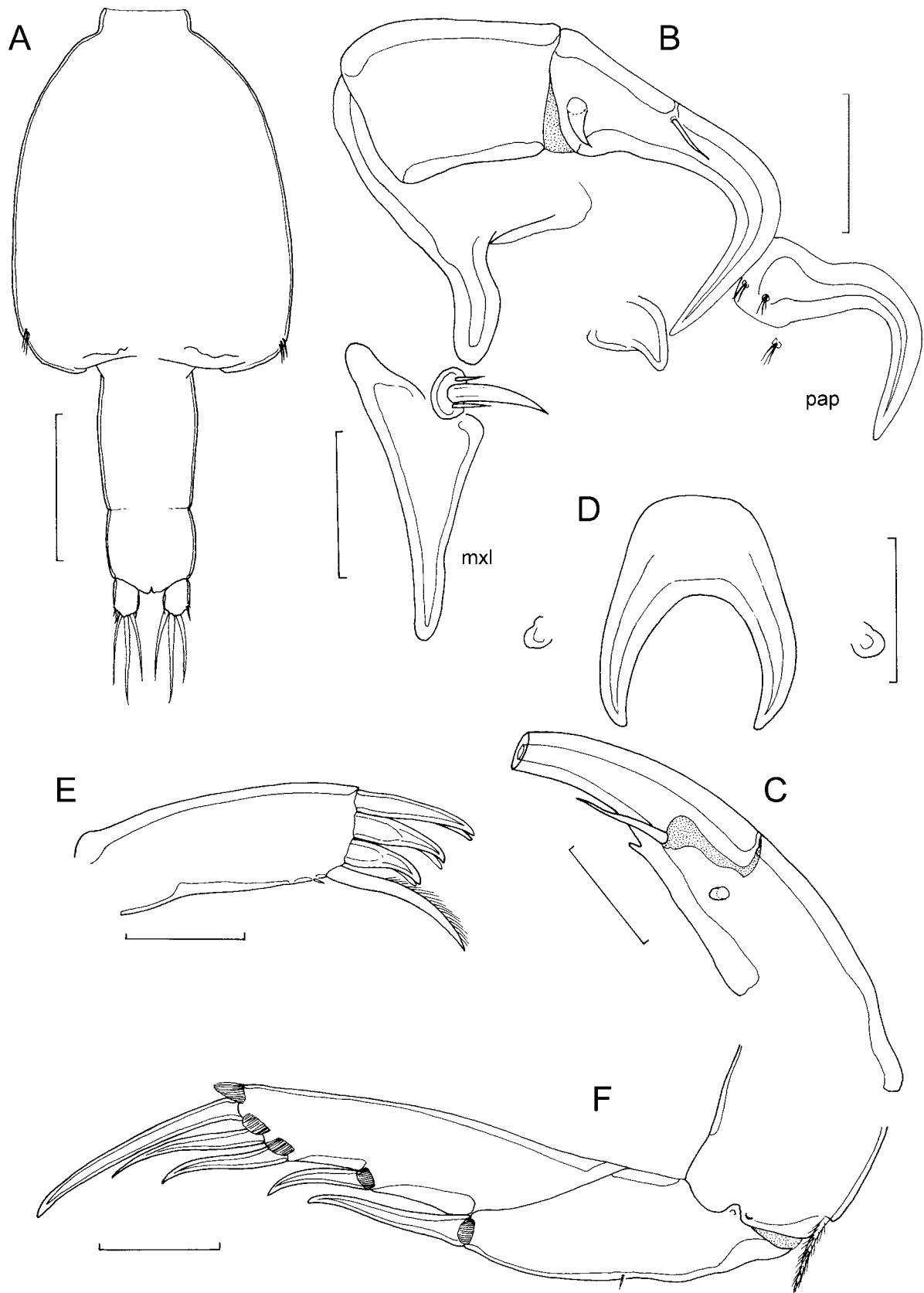
Carangidae: *Caranx* sp., *C. rhonchus* Geoffroy Saint-Hilaire, 1817 (as *C. angolensis*), *Lichia amia* (Linnaeus, 1758) (as *Lichia vadigo*), *Trachurus trachurus* (Linnaeus, 1758);

Ephippidae: *Chaetodipterus faber* (Broussonet, 1782);

Haemulidae: *Anisotremus virginicus* (Linnaeus, 1758), "*Haemulon elegans*", *H. sciurus* (Shaw, 1803), *H. carbonarium* Poey, 1860, *H. plumierii* Lacepède, 1801, *H. macrostomum* Günther, 1859, *H. steindachneri* (Jordan & Gilbert, 1822), *Orthopristis ruber* (Cuvier, 1830), *Plectorhinchus mediterraneus* (Guichenot, 1850) (and as *Diagramma mediterraneum*);

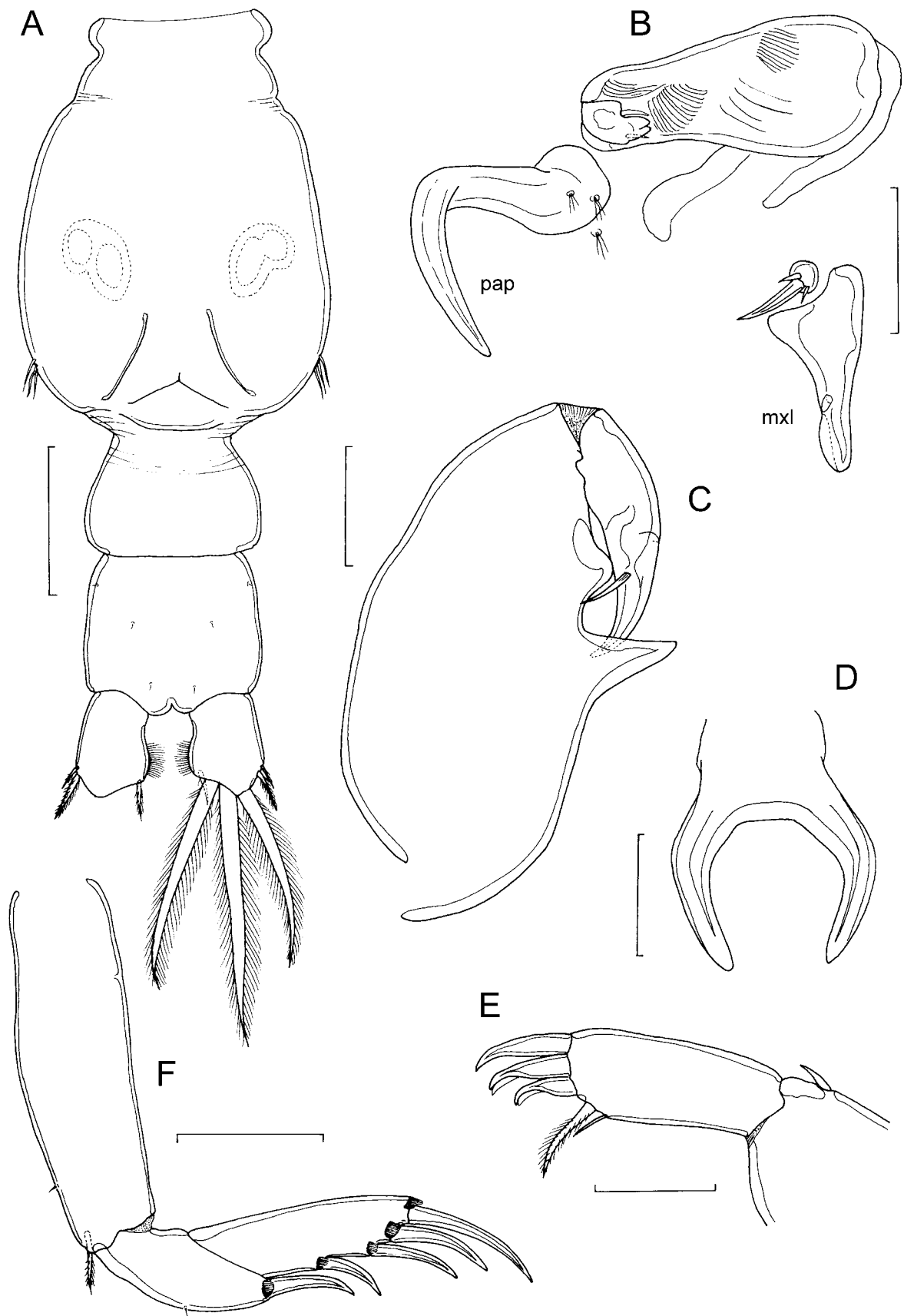
Kyphosidae: *Girella tricuspidata* (Quoy & Gaimard, 1824);

Monacanthidae: *Aluterus schoepfi* (Walbaum, 1792) (as *Aleuterus schoepfi*);



**FIGURE 5.** *Caligus haemulonis* Krøyer, 1863 female. A. genital complex and abdomen, ventral view; B. antenna, post-antennal process (pap) and maxillule (mxl), ventral view *in situ*; C. damaged subchela of maxilliped, showing denticle on concave margin; D. sternal furca *in situ*; E. second exopodal segment of leg 1 showing distal armature; F. exopodal segments of leg 4. Scale-bars: A = 500  $\mu$ m, B, D = 100  $\mu$ m, C, E, F = 50  $\mu$ m.





**FIGURE 6.** *Caligus haemulonis* Krøyer, 1863 male. A. genital complex and abdomen, ventral view; B. antenna, post-antennal process (pap) and maxillule (mxl) *in situ*, ventral view; C. maxilliped; D. sternal furca; E. distal armature on second exopodal segment of leg 1; F. leg 4. *Scale-bars:* A = 200  $\mu$ m, B, C, F = 100  $\mu$ m, D, E = 50  $\mu$ m.

Myliobatidae: *Aetobatus narinari* (Euphrasen, 1790) (as *Stoasodon narinari*);  
Polynemidae: *Polydactylus quadrifilis* (Cuvier, 1829);  
Rachycentridae: *Rachycentron canadum* (Linnaeus, 1766);  
Sciaenidae: *Bairdiella chrysoura* (Lacepède, 1802), “*Corvina cameronensis*”, *Menticirrhus americanus* (Linnaeus, 1758) (as *Menticirrus americanus*), *Micropogonias furnieri* (Desmarest, 1823) (as *Micropogon furnieri*), *Pogonias cromis* (Linnaeus, 1766), *Pseudotolithus elongatus* (Bowdich, 1825) (as *Corvina nigra*), *Sciaenops ocellatus* (Linnaeus, 1766), *Umbrina* sp.;  
Serranidae: *Centropristes striata* (Linnaeus, 1758);  
Sparidae: *Archosargus probatocephalus* (Walbaum, 1792), *Dentex* sp., *D. gibbosus* (Rafinesque, 1810) (as *D. filiosus*), *Pagrus pagrus* (Linnaeus, 1758), *Pagrus* sp.;  
Triglidae: *Trigla lyra* Linnaeus, 1758.  
This is a widespread species that has been reported from a very large range of hosts (Margolis et al. 1975; Luque & Takemoto 1996; Ho & Lin 2003).

**Remarks:** The original description of *C. haemulonis* does not provide a great deal of detail although it does confirm the absence of any large plumose setae from the posterior margin of the second exopodal segment of leg 1 (Krøyer 1863: Tab. IV, Fig. 3c). In 1905 Wilson (Wilson 1905) repeated the description and copied the original figures from Krøyer but subsequently he gave a fuller description based on new material of both sexes from the Atlantic coast of the USA (Wilson 1908). It was described again by Cressey (1991) based on material from Florida and Belize, and by Luque & Takemoto (1996) using material from Brazil. There are slight inconsistencies between these descriptions which, we believe, are more due to the style of drawing than to real differences in characters. Cressey (1991) was the first to figure a tiny naked vestigial seta on the posterior margin of the distal exopodal segment of leg 1.

We place *Caligus mauritanicus* var *miniscula* as a new synonym of *C. haemulonis* because there are no substantive differences between these species, if we use Wilson’s (1908) redescription as the best representation of *C. haemulonis*.

Cressey (1991) placed both *C. sciaenops* Pearse, 1952 and *C. setosus* Pearse, 1953 in the synonymy of *C. haemulonis* with no discussion. As discussed below, we consider that *C. sciaenops* is a valid species most readily distinguished by the unusually long tines on the sternal furca. *Caligus setosus* is treated here as a synonym of *C. sciaenops*.

*Caligus pagrosomi schelegeli* was established by Ho & Lin (2003) as a new subspecies of *C. pagrosomi*, but is treated as a valid species here (see below). Both *C. schelegeli* and *C. haemulonis* share the presence of a tiny, naked vestige of a seta on the posterior margin of the distal exopodal segment of leg 1, but can be distinguished by the shorter genital complex and abdomen of *C. haemulonis* and by the shape of the antennal claw and post-antennal process which are strongly recurved in *C. haemulonis*.

### ***Caligus pagrosomi* Yamaguti, 1939**

**Differential diagnosis:** Female genital complex and abdomen combined nearly twice as long as cephalothorax; body length 3.94–5.30 mm. Male length 2.40–3.46 mm. Female genital complex elongate, lacking distinct postero-lateral lobes; abdomen just shorter than genital complex; 2-segmented, first segment about 2.5 times longer than second. Male genital complex elongate, wider posteriorly; abdomen 2-segmented; second segment nearly twice length of first. Post-antennal process sexually dimorphic, larger and more strongly curved in male. Additional process present between post-antennal process and base of antenna in female. Sternal furca with incurved tines; thickenings lateral to sternal furca forming paired, rounded processes. Female maxilliped with smooth medial margin. Male maxilliped with large, acutely-pointed process on myxal margin, opposing tip of claw. Exopod of leg 1 with seta at inner distal angle longer than longest distal spine but shorter than segment; posterior margin with single plumose seta longer than shortest spine. Outer margin of second endopodal segment of leg 2 ornamented with fine spinules. Leg 4 ornamented

with single marginal setule on first exopodal segment; second exopodal segment with outer and middle spines on distal margin similar in length and distinctly shorter than terminal spine.

**Material examined:** 2 females and 1 male collected from *Argyrosomus hololepidolus* caught off Coff's Harbour, New South Wales, Australia by K. Rohde: stored in the collections of the Natural History Museum, London, Reg. Nos. 1984.52.

**Distribution:** Western North Pacific; Japan, Taiwan, Australia.

**Hosts:** Ariidae: *Arius maculatus* (Thunberg, 1792);

Carangidae: *Caranx ignobilis* (Forsskål, 1755), *Trachinotus blochii* (Lacepède, 1801);

Latidae: *Lates calcarifer* (Bloch, 1790);

Lobotidae: *Lobotes surinamensis* (Bloch, 1790);

Lutjanidae: *Lutjanus russellii* (Bleeker, 1849);

Sciaenidae: *Argyrosomus hololepidolus* (Lacepède, 1801), *Miichthys miiuy* (Basilewsky, 1855), "*Pagrosomus unicolor*".

*Caligus pagrosomi* occurs on a range of teleost fishes from at least six families (Ho & Lin 2003).

**Remarks:** The original description (Yamaguti 1939) was incomplete and the best available description of this species is that of Ho & Lin (2003). The possession of a single well developed plumose seta on the posterior margin of the second exopodal segment of leg 1, in addition to the normal array of 3 spines and one seta on the distal margin, is shared only with *C. alaihi*. In *C. enormis* the single posterior margin seta is spinulate, but one of the distal margin spines is lacking. In *C. dakari* (as re-diagnosed above) and in *C. temnodontis* the plumose seta is reduced to about half the length of the adjacent seta, while in *C. haemulonis* the seta is further reduced to a tiny, naked vestige.

### ***Caligus schelegeli* Ho & Lin, 2003**

Syn: *C. pagrosomi schelegeli* Ho & Lin, 2003

**Differential diagnosis:** Female genital complex and abdomen combined about 1.6 times longer than cephalothorax; body length 3.10–3.88 mm. Male body length 2.28–2.84 mm. Female genital complex longer than wide, lacking distinct postero-lateral lobes: abdomen 2-segmented, first segment about 2.0 times longer than second. Male abdomen 2-segmented; second segment about 1.6 times longer than first. Female antenna with distal claw weakly curved. Post-antennal process curved in both sexes. Additional process present between post-antennal process and base of antenna in female. Posterior process of maxillule with tiny blunt accessory process in male. Sternal furca of female with incurved tines and with small rounded processes on body surface either side of furca. Female maxilliped with smooth myxal margin. Male maxilliped with large, acutely-pointed process on myxal margin, opposing tip of claw. Exopod of leg 1 with seta at inner distal angle shorter than segment but longer than longest of distal spines; posterior margin with single, naked vestigial seta. Outer margin of second endopodal segment of leg 2 ornamented with typical setules. Leg 4 with robust first exopodal segment bearing marginal setule, spine extending beyond base of proximal outer spine of second segment; second segment with distal spines well developed, increasing slightly in length from outer to inner.

**Material examined:** none

**Distribution:** Taiwan.

**Hosts:** Carangidae: *Megalaspis cordyla* (Linnaeus, 1758);

Mugilidae: *Mugil cephalus* Linnaeus, 1758;

Scatophagidae: *Scatophagus argus* (Linnaeus, 1766);

Siganidae: *Siganus fuscescens* (Houttuyn, 1782);

Sparidae: *Acanthopagrus schlegelii* (Bleeker, 1854);

Terapontidae: *Terapon jarbua* (Forsskål, 1775).

Host data from Ho & Lin (2003).

**Remarks:** *C. schelegeli* is closely related to *C. haemulonis* but differs in having a genital complex plus abdomen that, combined, are about 1.6 times longer than the cephalothorax, rather than 1.3 times longer as in *C. haemulonis*.

### ***Caligus sciaenops* Pearse, 1952**

Syn: *C. setosus* Pearse, 1953

*C. cresseyi* Ho & Lin, 2003

*C. epinephali* [sic]: Cressey (1991)

**Differential diagnosis:** Female genital complex and abdomen combined about 1.2 times longer than cephalothorax; body length 3.1–4.2 mm. Male body length unknown. Female genital complex sub-rectangular, without distinct postero-lateral lobes; about as long as abdomen. Abdomen 2-segmented, first segment markedly longer than second. Male abdomen 2-segmented, first segment about half length of second. Post-antennal process large and strongly curved in female. Antenna claw not strongly curved. No additional process present between post-antennal process and base of antenna in female. Sternal furca with long, tapering tines. Female maxilliped with smooth medial margin. Exopod of leg 1 with seta at inner distal angle longer than longest spine but shorter than segment; no vestiges of posterior margin setae; first exopodal segment broad, with strongly convex posterior margin. Outer margin of second endopodal segment of leg 2 ornamented with fine spinules. Distal spines on exopod of leg 4 all similar in length but terminal spine just longer than other 2.

**Material examined:** none

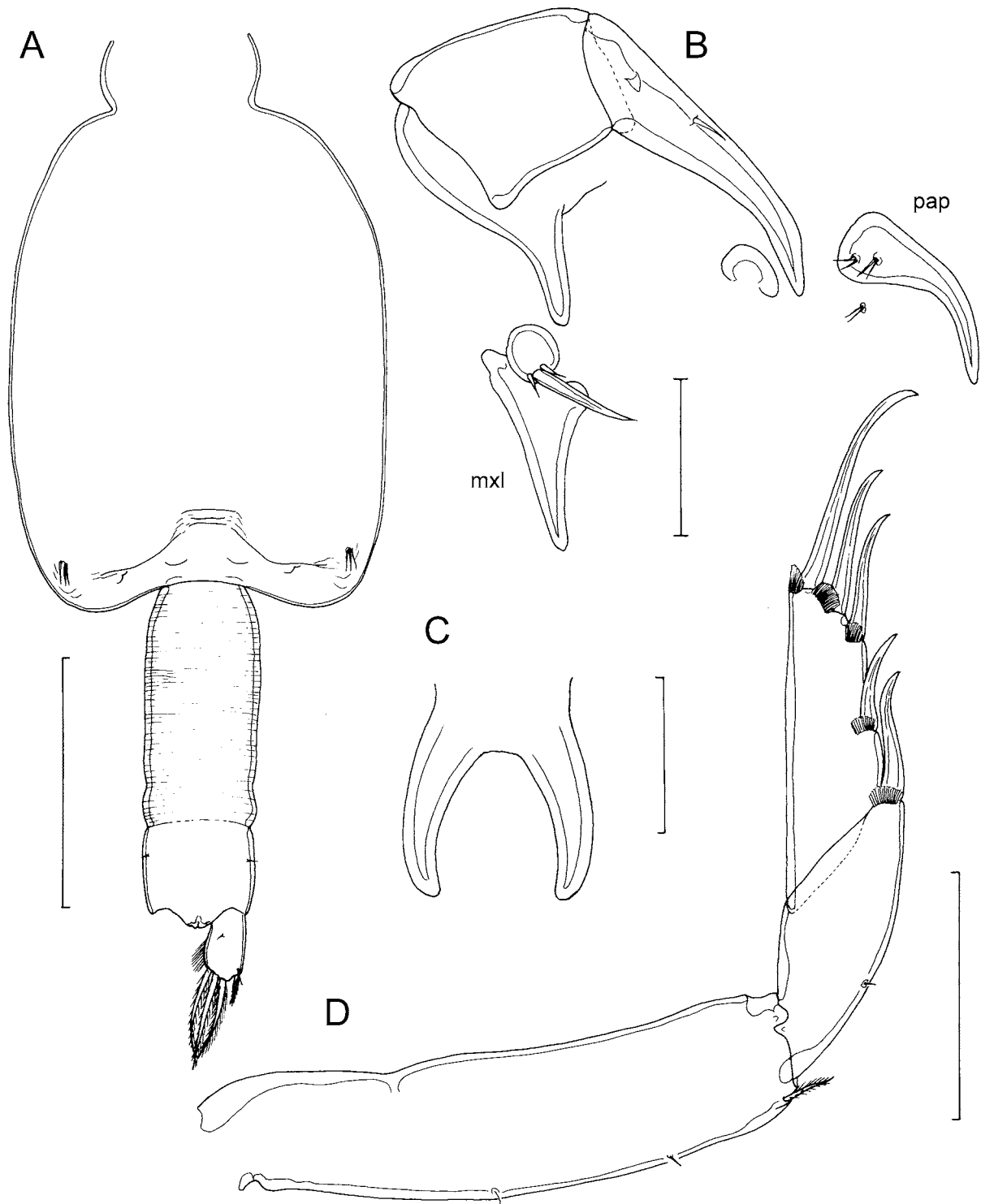
**Distribution:** Jamaica, Gulf of Mexico (Texas coast).

**Hosts:** Sciaenidae: *Sciaenops ocellatus* (Linnaeus, 1766), *Cynoscion nebulosus* (Cuvier, 1830), *Cynoscion nothus* (Holbrook, 1848), *Leiostomus xanthurus* Lacepède, 1802.

The only known hosts of *C. sciaenops* are sciaenids (Pearse 1952; 1953; Cressey 1991).

**Remarks:** Cressey (1991) placed *C. sciaenops* in the synonymy of *C. haemulonis* with no discussion. The general body size and shape given by Pearse (1952) is consistent with *C. haemulonis* and, although the proportional lengths of the two abdominal segments in the female do not match with the description of *C. haemulonis*, the abdomen appears abnormally slender in Pearse's figures of females (Pearse 1952: Fig. 49, 59). The male figured by Pearse (1952: Fig. 58) has a 2-segmented abdomen and the proportional lengths of the two segments match those of *C. haemulonis*. However, we consider the shape of the sternal furca, with its unusually long tines, to be an important distinction between *C. sciaenops* and *C. haemulonis*. In this character, and in other characters such as the strongly recurved post-antennal process and weakly recurved antennal claw, *C. sciaenops* resembles the species described by Cressey (1991) as *C. epinephali* [sic] Yamaguti, 1936. In an earlier study, Ho & Lin (2003) concluded that the *Caligus* material described by Cressey (1991) as *C. epinephali* [sic] was not conspecific with *C. epinepheli* of Yamaguti (1936) and proposed *Caligus cresseyi* Ho & Lin, 2003 as a new name, based on Cressey's description. We consider that the oldest available name for this taxon is *Caligus sciaenops* Pearse, 1952, and we recognise *C. cresseyi* Ho & Lin, 2003 as a junior subjective synonym of *C. sciaenops*.

*Caligus setosus* has a female body length of 3.17 mm, within the range of *C. sciaenops*, the sternal furca has long tapering tines and the post-antennal process is strongly curved in the female (Pearse 1953), as in *C. sciaenops*. On this basis we treat *C. setosus* as a junior subjective synonym of *C. sciaenops*, but this needs confirmation.



**FIGURE 7.** *Caligus temnodontis* Brian, 1924 female. A. genital complex and abdomen, ventral view; B. antenna, post-antennal process (pap) and maxillule (mxl), ventral view *in situ*; C. sternal furca *in situ*; D. leg 4. Scale-bars: A = 500  $\mu$ m, B = 250  $\mu$ m, C = 100  $\mu$ m, D = 200  $\mu$ m.

***Caligus temnodontis* Brian, 1924**

Syn: *C. mauritanicus* var. *temnodontis* Brian, 1924

*C. cf. affinis*: Kensley & Grindley, 1973

**Differential diagnosis:** Female genital complex and abdomen combined about 1.2 times longer than cephalothorax; body length 3.61–5.48 mm. Male body length 2.52–3.85 mm. Female genital complex (Fig. 7A) about 1.5 times longer than wide, narrowing to waist-like region anteriorly, lacking distinct postero-lateral lobes; abdomen 2-segmented, first segment about three times longer than second and ornamented with transverse striated cuticular markings. Cephalothorax lacking striated lateral borders. Male abdomen 2-segmented (Fig. 8A); second segment about 1.6 times longer than first. Female antenna with distal claw only slightly curved (Fig. 7B). Male antenna with complex apical claw (Fig. 8C). Post-antennal process sexually dimorphic, larger and more strongly curved in male (cf. Figs 7B, pap; 8B, pap). Additional rounded process present between post-antennal process and base of antenna in female (Fig. 7B). Posterior process of maxillule tapering evenly (Figs 7B, 8B) in both sexes; with tiny blunt accessory process in male (Fig. 8B, mxl). Sternal furca with straight to slightly incurved tines (Figs 7C, 8E) and with transverse thickenings of body surface either side of furca (Fig. 8E). Female maxilliped with smooth medial margin. Male maxilliped with 2 pointed processes on myxal margin (Fig. 8D), larger, proximal process opposing tip of claw and with slight concavity (possibly a pore) at tip. Exopod of leg 1 with seta at inner distal angle shorter than segment and about as long as middle spine on distal margin; posterior margin with single plumose seta about half length of adjacent seta (Fig. 8F). Outer margin of second endopodal segment of leg 2 ornamented with typical setules. Leg 4 with robust first exopodal segment bearing single marginal setule; second segment with well developed spines in both sexes, increasing in length towards terminal spine (Figs 7D, 8G).

**Material examined:** 13 female and 6 male syntypes labeled *Caligus mauritanicus* var *temnodontis*, in two vials deposited in the collections of the Museum National d'Histoire Naturelle in Paris, registration numbers, MNHN Cp. 281 and Cp.282.

3 adult females and 1 male collected from *P. saltatrix* caught off Mapelane, South Africa, on 30 August 1975 by R. van der Elst: stored in collections of the Natural History Museum, London Reg. Nos. 1979.899-903.

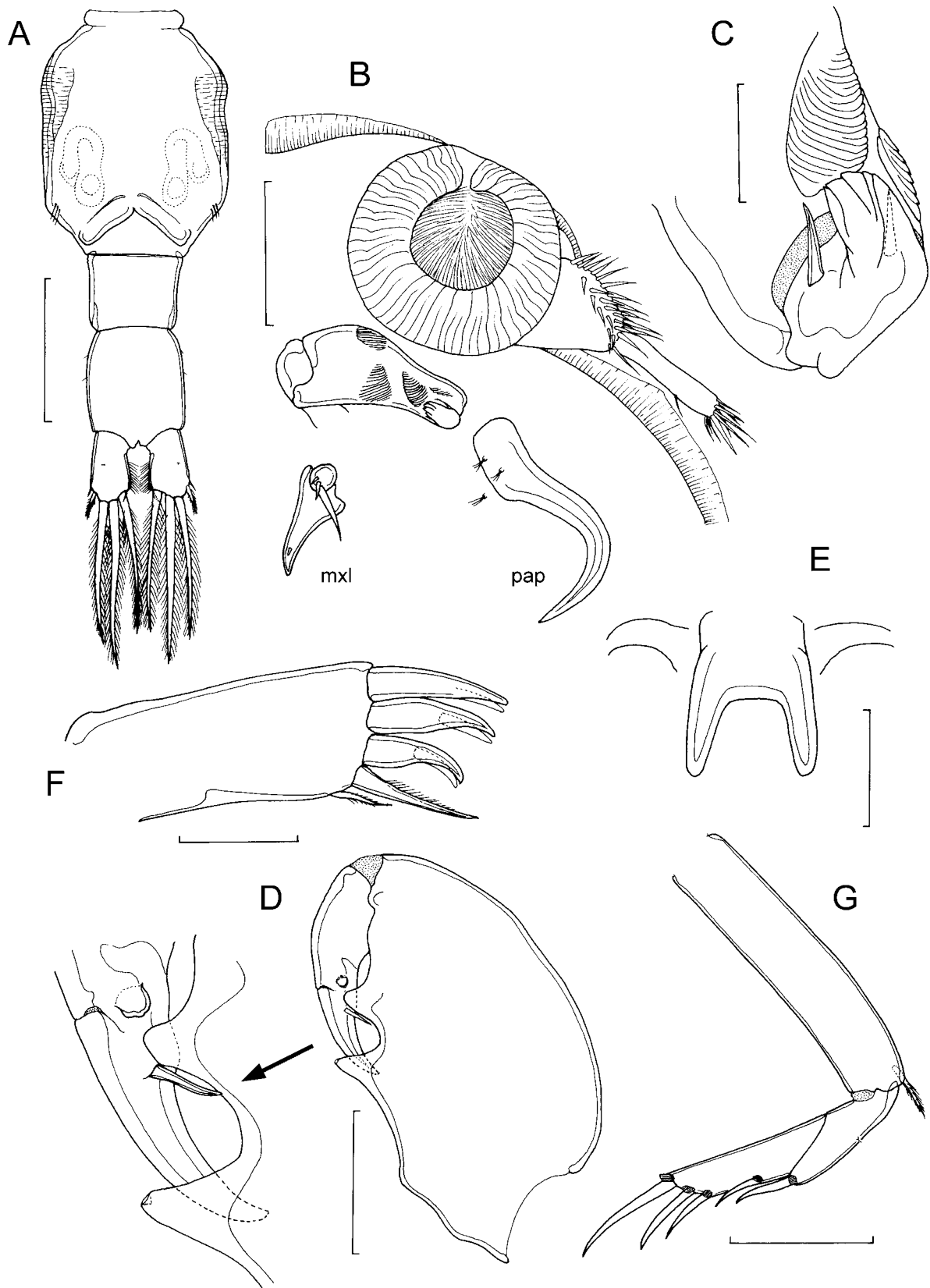
5 adult females collected from *P. saltatrix* caught off Durban, South Africa, by R. Bray: stored in collections of the Natural History Museum, London Reg. Nos. 1984.129.

4 adult females collected from *P. saltatrix* caught off Sodwana, Natal, South Africa, by R. Bray: stored in collections of the Natural History Museum, London Reg. Nos. 1984.133.

**Distribution:** Eastern South Atlantic.

**Host:** Pomatomidae: *Pomatomus saltatrix* (Linnaeus, 1766) (as *Temnodon saltator* and as *Pomatomus saltator*).

**Remarks:** In his survey of the parasitic copepods of Mauritania Brian (1924) described a new species, *Caligus mauritanicus*, from a range of hosts. Brian noted that this form resembled *C. productus* and *C. haemulonis* in the apparent absence of the three large plumose setae from the posterior margin of the distal exopodal segment of the first swimming legs. In his original description, Brian (1924) established *C. mauritanicus* n. sp. and two distinct varieties which he named, *n. varietas miniscula* and *n. varietas temnodontis*. He distinguished the former from 'la forme typique' on the basis of its smaller size and small differences in the relative proportions of genital complex and abdomen. He distinguished the latter on the basis of differences in body shape, in the shape of the post-antennal processes ('hamuli ou secundae maxillae') and in the form of the spines on the distal margin of the first leg exopod. We consider that these three varieties represent three distinct species: the typical form of *C. mauritanicus* is synonymized above with *C. dakari* and the variety *miniscula* was synonymized above with *C. haemulonis*. The variety *temnodontis* is, in our opinion, a valid species characterised by the presence of a small plumose seta on the posterior margin of the distal exopodal segment of leg 1. It shares this character state with *C. dakari* but the leg 4 differs from that of *C. dakari* which has a distinctive shape to the distal exopodal segment. The females of these species can also be distinguished on the basis of size, body proportions and the shape of the antennal claw and post-antennal process.



**FIGURE 8.** *Caligus temnodontis* Brian, 1924 male. A. genital complex and abdomen, ventral view; B. frontal margin of cephalothorax with lunule, antenna, post-antennal process (pap) and maxillule (mxl) *in situ*, ventral view; C. detail of antennal claw armature; D. maxilliped, with inset showing detail of myxal margin; E. sternal furca; F. second exopodal segment of leg 1 showing distal armature; G. leg 4. *Scale-bars:* A = 500  $\mu$ m, B, D, G = 250  $\mu$ m, C = 50  $\mu$ m, E, F = 100  $\mu$ m.

South African *Caligus* material from the type host, *Pomatomus saltatrix*, in the collections of the Natural History Museum, London is identifiable as *C. temnodontis*, and this species has recently been reported from *P. saltatrix* in the eastern Mediterranean (Özak et al. submitted).

We consider that the material identified as *Caligus* cf. *affinis* by Kensley & Grindley (1973) is also, most probably, *C. temnodontis*.

### Key to species of the *Caligus productus*-group (females only):

1. Leg 4 with spine formula I, III on exopod.....*C. lethrinicola* n. sp.  
Leg 4 with spine formula I, IV on exopod..... 2
2. Genital complex with pronounced posterolateral lobes.....3  
Genital complex lacking posterolateral lobes.....4
3. Sternal furca with divergent tines .....*C. productus*  
Sternal furca with tines fused to form median tapering spine .....*C. bocki*
4. Abdomen short, fused to genital complex; sternal furca absent.....*C. enormis*  
Abdomen at least half length of genital complex; sternal furca present.....5
5. Abdomen 1-segmented; genital complex and abdomen combined shorter than cephalothorax .....*C. alaihi*  
Abdomen 2-segmented (sometimes indistinctly); genital complex and abdomen combined as long as or longer than cephalothorax .....6
6. Posterior margin of distal exopodal segment of leg 1 with plumose seta, or with naked vestige of seta.....7  
Posterior margin of distal exopodal segment of leg 1 lacking any vestige of plumose setae.....11
7. Posterior margin of distal exopodal segment of leg 1 with plumose seta.....8  
Posterior margin of distal exopodal segment of leg 1 with naked vestige of seta .....10
8. Plumose seta on posterior margin of distal exopodal segment of leg 1 well developed, about two thirds length of adjacent seta .....*C. pagrosomi*  
Plumose seta small, about half length of adjacent seta.....9
9. Body length 6.0 to 6.5 mm; post-antennal process large and strongly recurved; leg 4 with short spine on first exopodal segment just reaching base of outer margin spine on second segment .....*C. dakari*  
Body length 3.6 to 5.5 mm; antennal claw and post-antennal process only slightly curved; leg 4 with spine on first exopodal segment reaching mid-length of outer margin spine on second segment .....*C. temnodontis*
10. Genital complex and abdomen combined about 1.6 times longer than cephalothorax .....*C. schelegeli*  
Genital complex and abdomen combined typically about 1.3 times longer than cephalothorax .....*C. haemulonis*
11. Maxilliped with large tapering process proximally on medial margin; genital complex and abdomen combined about 2.0 times longer than cephalothorax .....*C. fugu*  
Maxilliped without proximal process on medial margin; genital complex and abdomen combined at most 1.6 times longer than cephalothorax .....12
12. Genital complex and abdomen combined about 1.5 to 1.6 times longer than cephalothorax .....*C. ariicolus*  
Genital complex and abdomen combined typically 1.0 to 1.3 times longer than cephalothorax .....13
13. Sternal furca with long, divergent tines .....*C. sciaenops*  
Sternal furca with relatively short, incurved tines .....14
14. Sternal furca with strongly incurved tines and wide gape; leg 4 with 2 subterminal spines about equal in length and only slightly shorter than terminal spine.....*C. affinis*  
Sternal furca with slightly incurved tines and narrow gape; leg 4 with all 3 spines different, increasing in length towards terminal spine .....*C. epinepheli*

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## References

- Barnard, K.H. (1955) South African Parasitic Copepoda. *The Annals of the South African Museum*, 41, 223–312.
- Van Beneden, P.-J. (1892) Quelques nouveaux Caligidés de la côte d’Afrique et de l’archipel des Açores. *Bulletin de l’Académie royale de Belgique*, Series 3, 24, 241–262, pls I–IV.
- Boxshall, G.A. (1990) The skeletomusculature of siphonostomatoid copepods, with an analysis of adaptive radiation in structure of the oral cone. *Philosophical Transactions of the Royal Society, London*, Series B, 328, 167–212.
- Boxshall, G.A. & Gurney, A.R. (1980) Descriptions of two new and one poorly known species of the genus *Caligus* Müller, 1785 (Copepoda: Siphonostomatoida). *Bulletin of the British Museum (Natural History), Zoology*, 39, 161–178.
- Brian, A. (1924) Parasitologia Mauritanica. *Arthropoda* (1re partie), Copepoda. Copépodes commensaux et parasites des côtes mauritaniennes. *Bulletin du comité d’Etudes Historiques et Scientifiques de l’Afrique occidentale française*, 364–427.
- Brian, A. (1935) *Caligus* parassiti dei pesci del Mediterraneo (Copepodi). *Annali del Museo Civico di Storia Naturale Giacomo Doria*, 57, 152–211.
- Cressey, R. (1991) Parasitic copepods from the Gulf of Mexico and Caribbean Sea, III: *Caligus*. *Smithsonian Contributions to Zoology*, 497, 1–53.
- Froese, R. & Pauly, D. (Eds.) (2008) FishBase. World Wide Web electronic publication. Available from: <http://www.fishbase.org/> (3 November 2008).
- Gnanamuthu, C.P. (1947) *Caligus sciaenae* n. sp. parasitic on *Sciaena glauca* from Madras. *Proceedings of the Indian Academy of Sciences, Section B*, 25, 43–49.
- Heegaard, P. (1943) Parasitic Copepods mainly from Tropical and Antarctic Seas. *Arkiv för Zoologi*, 34A, 1–37.
- Ho, J.-s. & Bashirullah, A.K.M. (1977) Two species of caligid copepods (Crustacea) parasitic on marine fishes of Venezuela, with discussion of *Metacaligus* Thomsen, 1949. *Journal of Natural History*, 11, 703–714.
- Ho, J.-s. & Lin, C.L. (2003) Solution to the taxonomic confusion surrounding *Caligus epinepheli* Yamaguti, a caligid copepod (Siphonostomatoida) parasitic on marine fishes. *Zoological Studies*, 42, 268–283.
- Ho, J.-s. & Lin, C.L. (2004) *Sea Lice of Taiwan (Copepoda: Siphonostomatoida: Caligidae)*. The Sueichan Press, Keelung, 388 pp.
- Huys, R. & Boxshall, G.A. (1991) *Copepoda Evolution*. The Ray Society, London, 468 pp.
- Johnson, S.C., Treasurer, J.W., Bravo, S., Nagasawa, K. & Kabata, Z. (2004) A review of the impact of parasitic copepods on marine aquaculture. *Zoological Studies*, 43, 229–243.
- Kensley, B. & Grindley, J.R. (1973) South African Parasitic Copepoda. *The Annals of the South African Museum*, 62, 69–130.
- Kirtisinghe, P. (1964) A review of the parasitic copepods of fish recorded from Ceylon with descriptions of additional forms. *Bulletin of the Fisheries Research Station Ceylon*, 17, 45–132.
- Krøyer, H. (1863) Bidrag til Kundskab om Snyltekrebsene. *Naturhistorisk Tidsskrift*, series 3, 2, 75–320, pls 1–9.
- Luque, J.L. & Takemoto, R.M. (1996) Parasitic copepods on *Orthopristis ruber* and *Haemulon steindachneri* (Osteichthyes: Haemulidae) from the Brazilian littoral, with the description of a new species of *Caligus* (Siphonostomatoida: Caligidae). *Revista Brasileira de Biologia*, 56, 529–546.
- Margolis, L., Kabata, Z. & Parker, R.R. (1975) Catalogue and synopsis of *Caligus*, a genus of Copepoda (Crustacea) parasitic on fishes. *Bulletin of the Fisheries Research Board of Canada*, 192, 1–117.
- Özak, A.A., El-Rashidy, H.H., Demirkale, I. & Boxshall, G.A. submitted. The discovery of *Caligus temnodontis* Brian, 1924 (Copepoda: Caligidae) from the bluefish, *Pomatomus saltatrix* Linnaeus, in the eastern Mediterranean Sea. *Systematic Parasitology*
- Pearse, A.S. (1952) Parasitic Crustacea from the Texas coast. *Publications of the Institute of Marine Science, The University of Texas*, 2, 5–42.
- Pearse, A.S. (1953) Parasitic Crustacea from Alligator Harbor, Florida. *Journal of the Florida Academy of Science*, 25, 187–243.
- Pillai, N.K. (1961) Copepods parasitic on South Indian fishes. Part I. Caligidae. *Bulletin of the Central Research Institute. University of Kerala (C)*, 8, 87–130.
- Pillai, N.K. (1967) Copepods parasitic on Indian marine fishes. A review. *Proceedings of Symposium on Crustacea. Cochin*, 5, 1556–1680.
- Pillai, N.K. (1985) *Fauna of India. Parasitic copepods of marine fishes*. Zoological Survey of India, Calcutta, 900 pp.
- Shiino, S.M. (1952) Copepods parasitic on Japanese fishes. 1. On the species of *Caligus* and *Lepeophtheirus*. *Report of the Faculty of Fisheries, Prefectural University of Mie*, 1, 79–113.
- Wilson, C.B. (1905) North American parasitic copepods belonging to the family Caligidae. Part 1. The Caliginae. *Proceedings of the United States National Museum*, 28, 479–672, pls 5–29.
- Wilson, C.B. (1908) North American parasitic copepods: new genera and species of Caliginae. *Proceedings of the United*

*States National Museum*, 33, 593–627, pls 49–56.

- Wilson, C.B. (1913) Crustacean parasites of West Indian fishes and land crabs, with descriptions of new genera and species. *Proceedings of the United States National Museum*, 44, 189–277, pls 18–53.
- Yamaguti, S. (1936) Parasitic copepods from fishes of Japan. Part 2. Caligoida, I, 1–22, pls 1–12. [Private publication]
- Yamaguti, S. (1939) Parasitic copepods from fishes of Japan. Part 5. Caligoida, III. In: *Volumen Jubilare pro Prof. Sadao Yoshida*, 2, 443–487, pls 14–33.
- Yamaguti, S. (1954) Parasitic copepods from fishes of Celebes and Borneo. *Publications of the Seto Marine Biological Laboratory*, 3, 375–398.
- Yamaguti, S. & Yamasu, T. (1959) Parasitic copepods from fishes of Japan with descriptions of 26 new species and remarks on two known species. *Journal of Biology, Okayama University*, 5, 89–165.