



Resolving taxonomic and nomenclatural problems in the genus *Caligus* O.F. Müller, 1785 (Copepoda: Caligidae)

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Abstract

Supplementary descriptions are provided for six poorly known species of *Caligus*, based on a study of type and other material carried out by the late Roger F. Cressey but never published. As part of that study new illustrations were produced by Hillary Boyle Cressey who has kindly made these previously unpublished drawings available to this paper. The present account also contains critical re-assessments of the validity of several other species of *Caligus* Müller, 1785. It is proposed to recognise that: *C. glacialis* Gadd, 1910 and *C. raniceps* Heegaard, 1943 are junior subjective synonyms of the type species *C. curtus* Müller, 1785 and we consider the published geographical locality given for *C. raniceps* by Heegaard (1943) to be erroneous; *C. guerini* Guiart, 1913 is a junior subjective synonym of *C. elongatus* von Nordmann, 1832; *C. mordax* Leigh-Sharpe, 1934 is a junior subjective synonym of *C. coryphaenae* Steenstrup & Lütken, 1861; *C. lessonius* Risso, 1826 is not a caligid and is probably a junior synonym of the pandarid *Demoleus heptapus* (Otto, 1821); *C. clavatus* Kirtisinghe, 1964 is a junior subjective synonym of *C. sphyraeni* Pillai, 1963; *C. rotundigenitalis* Yü, 1933 is a junior subjective synonym of *C. torpedinis* Heller, 1865; *C. hyalinae* Heegaard, 1966 is a junior subjective synonym of *C. chelifera* Wilson, 1905; *C. biserioidentatus*, Shen, 1957 is a junior subjective synonym of *C. pauliani* Nuñez-Ruivo & Fourmanoir, 1956; and *C. cornutus* Heegaard, 1962 can be formally treated as a junior subjective synonym of *C. lobodes* (Wilson, 1911) because the name *C. cornutus* belongs with the male holotype; the female allotype collected by Heegaard (1962) remains unidentified. We also conclude that *C. mebachii* Marukawa, 1927 was based on a young male of *Euryphorus brachypterus* (Gerstaecker, 1853) and a male of *Caligus coryphaenae* Steenstrup & Lütken, 1861 which was mistakenly identified as the female. A lectotype is designated for *C. mebachii* and this species is treated as a synonym of *Euryphorus brachypterus*. It is noted that *C. hamatus* Heegaard, 1955 is conspecific with, and has priority over, *C. undulatus* Shen & Li, 1959. However, given that *C. undulatus* is a high profile and well known species, frequently recorded from across the Pacific, Indian and Atlantic oceans, a case has been submitted to the ICZN to grant precedence of *C. undulatus* over *C. hamatus*. We reject the transfer of *Chalimus tenuis* Leidy, 1889 to *Caligus* by Fowler (1912) on the basis of lack of evidence supporting the transfer, and return it to *Chalimus*, where it can be treated as a *species inquirendum* within a genus that is no longer considered as valid. We consider that *C. alalongae* Krøyer, 1863 and *C. gracilis* Dana, 1852 are *species inquirenda*. *Caligus truttiae* is a *nomen nudum* because Giard (1890) provided no morphological information or illustration associated with the new name.

Key words: nomenclature, redescriptions, new synonyms, sea lice

Introduction

Members of the copepod family Caligidae are commonly referred to as sea lice and have considerable economic importance because of their negative impact upon marine finfish farming. Sea lice are ectoparasitic on fish and can cause severe health consequences for their hosts (Rodger *et al.*, 2022). It has been estimated that sea lice cause losses of almost €1 billion p.a. to the commercial culture of Atlantic salmon (*Salmo salar* Linnaeus, 1758) at high latitudes worldwide (Boxaspen *et al.*, 2022), and they are also a major health hazard in the culture of numerous subtropical and tropical marine fish (Johnson *et al.*, 2004).

The family currently comprises 516 species with the great majority belonging to the two largest genera, *Caligus* and *Lepeophtheirus* von Nordmann, 1832, which include 277 and 124 species, respectively (Walter & Boxshall, 2023). We are currently in the process of creating online keys to the genera of Caligidae and for each of these two most speciose genera. This process has involved a critical re-assessment of the validity of all species listed on the World of Copepods website (Walter & Boxshall, 2023) as well as re-examination of specimens of some incompletely known species. The focus of this present account is the genus *Caligus*, which is the most species rich genus in the Order Siphonostomatoida and within the entire subclass Copepoda. The task has been greatly facilitated by reference to the catalogue to species of *Caligus* prepared by Margolis *et al.* (1975) which lists the nominal species at the time and summarises early records, known hosts and existing descriptions. A huge volume of research has been published on *Caligus* since 1975 but this catalogue remains a valuable resource for both taxonomists and parasitologists. Our emphasis has been on “cleaning up *Caligus*” by critically re-evaluating available descriptions and redescrptions, and by re-examination of appropriate material.

Materials and Methods

The six supplementary descriptions included below are based on unpublished observations made by the late Roger F. Cressey and on unpublished drawings made by Hillary Boyle Cressey. They were created as part of a project that was never completed but which was designed to improve knowledge of several extremely poorly known species of *Caligus* originally described from Atlantic fishes, by the re-examination of type material where possible. The original drawings prepared by Hillary Boyle Cressey could not be traced but new plates have been redrawn from photocopies. The drawings lack scale bars but we include the body lengths of the adult females in the figure legends as this provides an approximate indication of scale. Host names are updated following FishBase (Froese & Pauly, 2023).

One male *Caligus coryphaenae* Steenstrup & Lütken, 1861 from The Natural History Museum collection (NHMUK 2012.1041–2) was examined with light microscopy and confocal laser scanning microscopy (CLSM). For light microscopy, the specimen was cleared in lactic acid for approximately 1 h, temporarily mounted on a glass slide, and examined with a Leitz Diaplan microscope equipped with differential interference contrast. For CLSM, the specimen was stained overnight in a saturated solution of Congo Red in 100% ethanol, then rinsed in distilled water until no Congo Red could be seen diffusing and prepared as a temporary mount in a 50% solution of glycerin and distilled water on a glass slide under a coverslip. The specimen was examined using a Leica TCS SP5 equipped with a Leica DM5000 B upright microscope and the Leica Application Suite Advanced Fluorescence software LAS AF 2.2.1. (Leica, Wetzlar, Germany). We used a 561-nm excitation wavelength from a DPSS 10 mW 561 nm laser set at 80% power and collected the emitted fluorescence in two channels: 570–630 nm artificially coloured green and 630–715 nm artificially coloured red. Series of image stacks were collected, and the final images were obtained by maximum projection of the overlaid channels using the same Leica software.

Taxonomy

Supplementary descriptions of poorly known species

Caligus belones Krøyer, 1863

Material examined by R. F. Cressey: One female from *Belone belone* (Linnaeus, 1760) caught in the river Elbe, Germany and stored in the Smithsonian Institution, Washington D.C., USA (Reg. No. USNM 180596).

Supplementary Description: Genital complex of female about 1.2 times longer than wide and about 2.3 times longer than abdomen; genital complex with rounded posterolateral lobes; abdomen about 1.4 times longer than wide, with lateral swellings anterior to midlevel (Fig. 1A). Caudal rami about 1.6 times longer than wide. Antenna (Fig. 1B) with irregularly tapering posterior process on proximal segment; subchela armed with 2 setae located proximally and near anterior margin. Postantennal process (Fig. 1B) with small base and weakly curved tine. Posterior process of maxillule (Fig. 1B) strongly tapering towards acute tip. Sternal furca with widely divergent tines (Fig. 1C). Second exopodal segment of leg 1 (Fig. 1D) armed with 3 plumose setae along posterior margin; distal margin

spines 1 to 3 each with accessory process; seta 4 more than twice as long as spine 1 and longer than segment. Leg 2 (Fig. 1E) with outer margin of second endopodal segment ornamented with setule row; first and second exopodal segments armed with outer spines directed obliquely across surface of ramus; third segment armed with II, I, 5. First exopodal segment of leg 3 (Fig. 1F) lacking inner seta; armed with short, slightly curved, outer spine ornamented with narrow flange along lateral margin, spine not reaching articulation separating second and third segments. Leg 4 (Fig. 1G) with 2-segmented exopod armed with I, IV spines, each with conspicuous pecten at base.

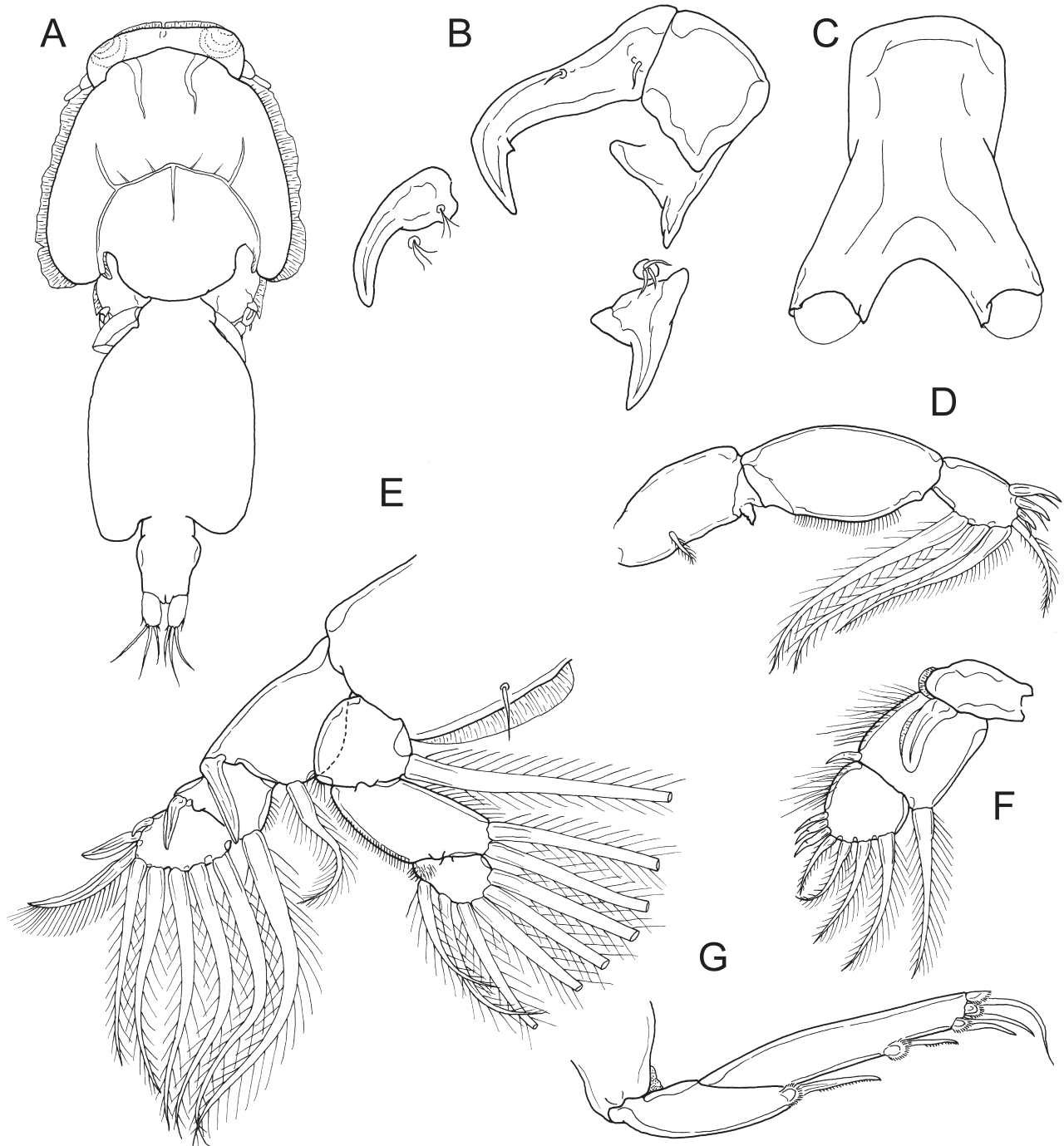


FIGURE 1. *Caligus belones* Krøyer, 1863 adult female (body length 5.7 mm). A, habitus, dorsal; B, antenna, postantennal process and maxillule *in situ*, ventral; C, sternal furca; D, leg 1; E, leg 2; F, exopod of leg 3; G, exopod of leg 4.

Remarks: *Caligus belones* has a complicated history. It was first described by Krøyer (1863) based on females collected from *Belone belone* (as “Hornfisk”) caught in Denmark. Later Wilson (1905) provided a redescription of a species he identified as *C. belones* but unfortunately Wilson’s species has a 2-segmented exopod on leg 4 with a

spine formula of I, III whereas Krøyer (1863: pl. VII, Fig. 1e) shows the formula of *C. belones* as I, IV. The species described by Wilson (1905) was renamed *C. wilsoni* by Delamare Deboutteville & Nuñez-Ruivo (1958) in a paper which provided a partial redescription of true *C. belones*. Other partial descriptions are available (e.g. Cressey & Collette, 1970) but none provides the detail needed for the development of the online key.

***Caligus engraulidis* Barnard, 1948**

Material examined by R. F. Cressey: Holotype female from *Stolephorus holodon* (Boulenger, 1900) (as *Engraulis (Anchoviella) holodon*) caught in the Zwartkops river, Algoa Bay, Republic of South Africa, loaned to R. F. Cressey by the Iziko South African Museum (Reg. No. A6520).

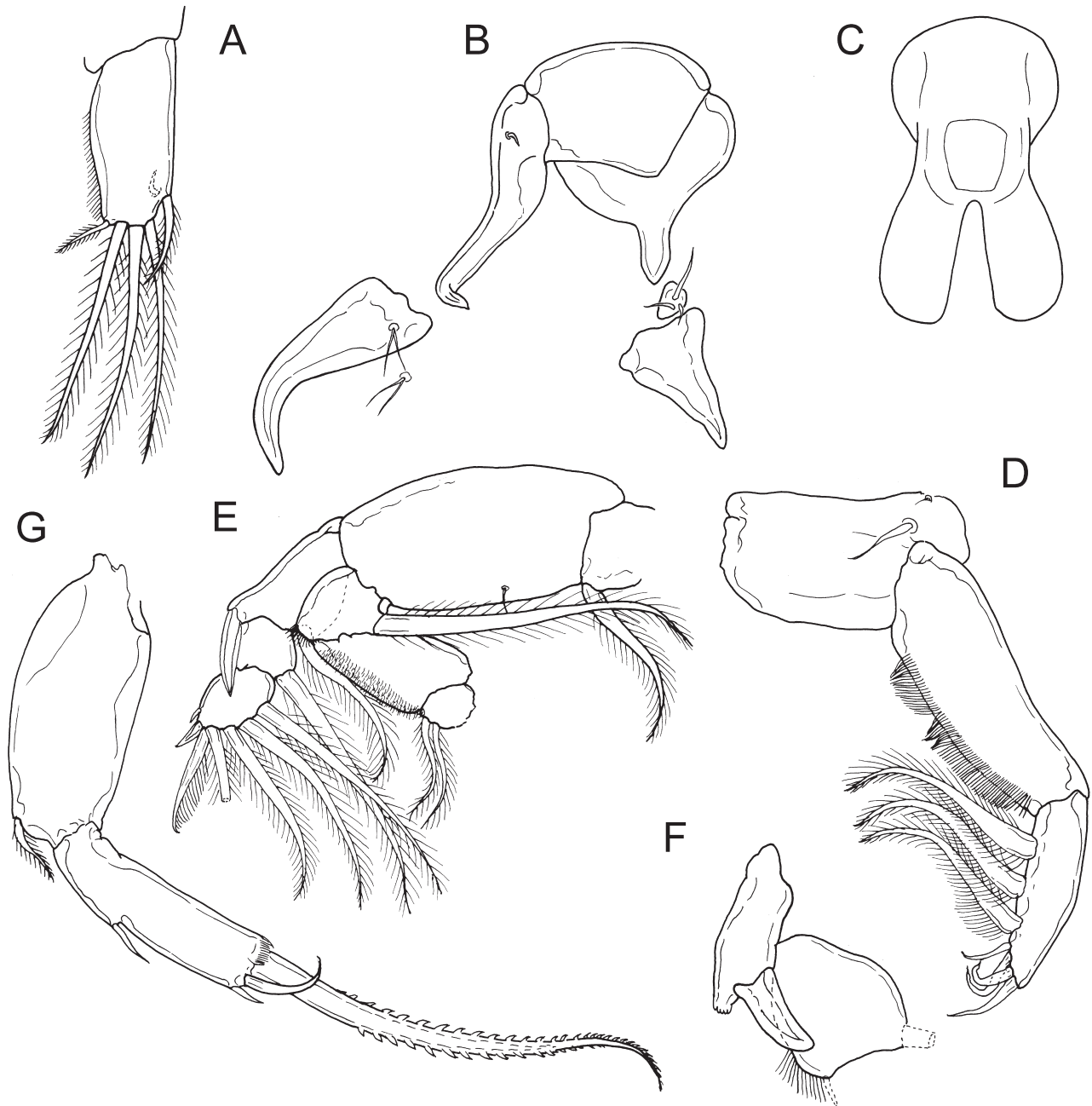


FIGURE 2. *Caligus engraulidis* Barnard, 1948 adult female (body length 3.5 mm). A, caudal ramus; B, antenna, postantennal process and maxillule *in situ*, ventral; C, sternal furca; D, leg 1; E, leg 2 (with some setae missing on endopod); F, first and second exopodal segments of leg 3; G, leg 4.

Supplementary Description: Caudal rami (Fig. 2A) about twice as long as wide, ornamented with short setules along medial margin and armed with 6 setae as typical for genus. Antenna (Fig. 2B) with spatulate process on posterior margin of proximal segment and armed with short seta proximally on subchela. Postantennal process (Fig. 2B) strongly curved and ornamented with bisensillate papillae. Maxillule (Fig. 2B) with simple tapering posterior process. Sternal furca (Fig. 2C) with very broad, blunt-tipped and slightly divergent tines. Leg 1 (Fig. 2D) lacking spinular ornamentation on surface of protopod but bearing single sensilla close to outer protopodal seta; distal exopodal segment armed with 3 plumose setae on posterior margin; distal margin with spines 1 to 3 all subsimilar in length and all lacking accessory process, seta 4 shorter than spines. Leg 2 (Fig. 2E) with setular ornamentation on outer margin of endopodal segment 2 extending slightly over onto surface of segment; outer spine on first exopodal segment large, aligned more closely with outer margin rather than positioned obliquely across ramus; third exopodal segment apparently with II, I, 4 setal formula. First exopodal segment of leg 3 (Fig. 2F) lacking inner seta, armed with short outer spine and with outer margin produced into additional spinous process. Leg 4 (Fig. 2G) 2-segmented, comprising protopodal segment bearing outer plumose seta and compound exopodal segment armed with naked spine near middle of outer margin and 3 spines on distal margin—1 long inner terminal spine ornamented bilaterally with strong denticles, shorter middle spine ornamented with setules bilaterally, and very short naked outer spine.

Remarks: The original description by Barnard (1948) was ultra-brief and was supported only by a sketch of the female genital complex and abdomen, plus the sternal furca and details of the 2 spines he observed on the apex of leg 4. Although no habitus drawing was possible due to damage to the holotype, the re-examination reveals important details of the structure and armature of the antennae, maxillules, sternal furca, legs 1 to 4 and caudal rami. The most significant of these are: the lack of accessory processes on spines 2 and 3 of the distal exopodal segment of leg 1, the presence of an additional spinous process on the outer margin of the first exopodal segment of leg 3, and the 1-segmented state of the exopod of leg 4 which is armed with 1 outer spine and 3 apical spines. Barnard's (1948) original description referred to the presence of only 2 apical spines on the exopod and the segmentation of this taxonomically important limb was depicted inaccurately.

***Caligus hemiconiati* Capart, 1941**

Material examined by R. F. Cressey: Syntype female from *Ehippion guttifer* (Bennett, 1831) (as *Hemiconiatus guttifer*) caught off the coast of Gambia during the Ninth cruise of the "Mercator", loaned to R. F. Cressey by the Musée royal d'Histoire naturelle, Brussels (Reg. No. I.G. 10910).

Supplementary Description: Abdomen broad, tapering slightly towards posterior margin; caudal rami located at small distance medial to posterolateral corners of abdomen. Caudal rami (Fig. 3A) wider than long and armed with 6 setae as typical for genus. Antenna (Fig. 3B) with small, pointed process on posterior margin of proximal segment, and armed with short seta proximally on subchela. Postantennal process (Fig. 3B) strongly curved and ornamented with multisensillate papillae. Maxillule (Fig. 3B) with curved, tapering posterior process. Sternal furca (Fig. 3C) with slender, strongly tapering tines; slightly asymmetrical with one tine straight and other slightly incurved. Second endopodal segment of leg 2 (Fig. 3D) short, broad, and with outer margin ornamented with setules; outer spine on first exopodal segment large and aligned obliquely across surface of ramus, spine on second segment similarly aligned; third exopodal segment with II, I, 5 setal formula. Leg 3 exopod (Fig. 3E) with first segment lacking inner seta, bearing long, slightly curved, outer spine reaching beyond articulation separating second and third segments. Leg 4 (Fig. 3F) comprising protopodal segment and 2-segmented exopod: first exopodal segment armed with long, tapering outer spine reaching almost to tip of ramus; second exopodal segment bearing 3 distal margin spines decreasing in length from inner to outer.

Remarks: The original description was generic and provided few specific details but there were sufficient differences to enable Capart (1941) to distinguish between his new species and *C. balistae* Steenstrup & Lütken, 1861, which shares a similar leg 4. *Caligus hemiconiati* differs from *C. balistae* in numerous characters, in particular the shape of the abdomen and caudal rami. The abdomen is widest posteriorly in *C. balistae* and the caudal rami are located on the posterior margin directly at the posterolateral angles of the abdomen (Cressey, 1991: Fig. 31) whereas in *C. hemiconiati* the abdomen is broadest more anteriorly and the caudal rami are positioned some distance medial to the posterolateral angles of the abdomen. In addition, the caudal rami are about as long as wide in the former species, compared to distinctly wider than long in the latter.

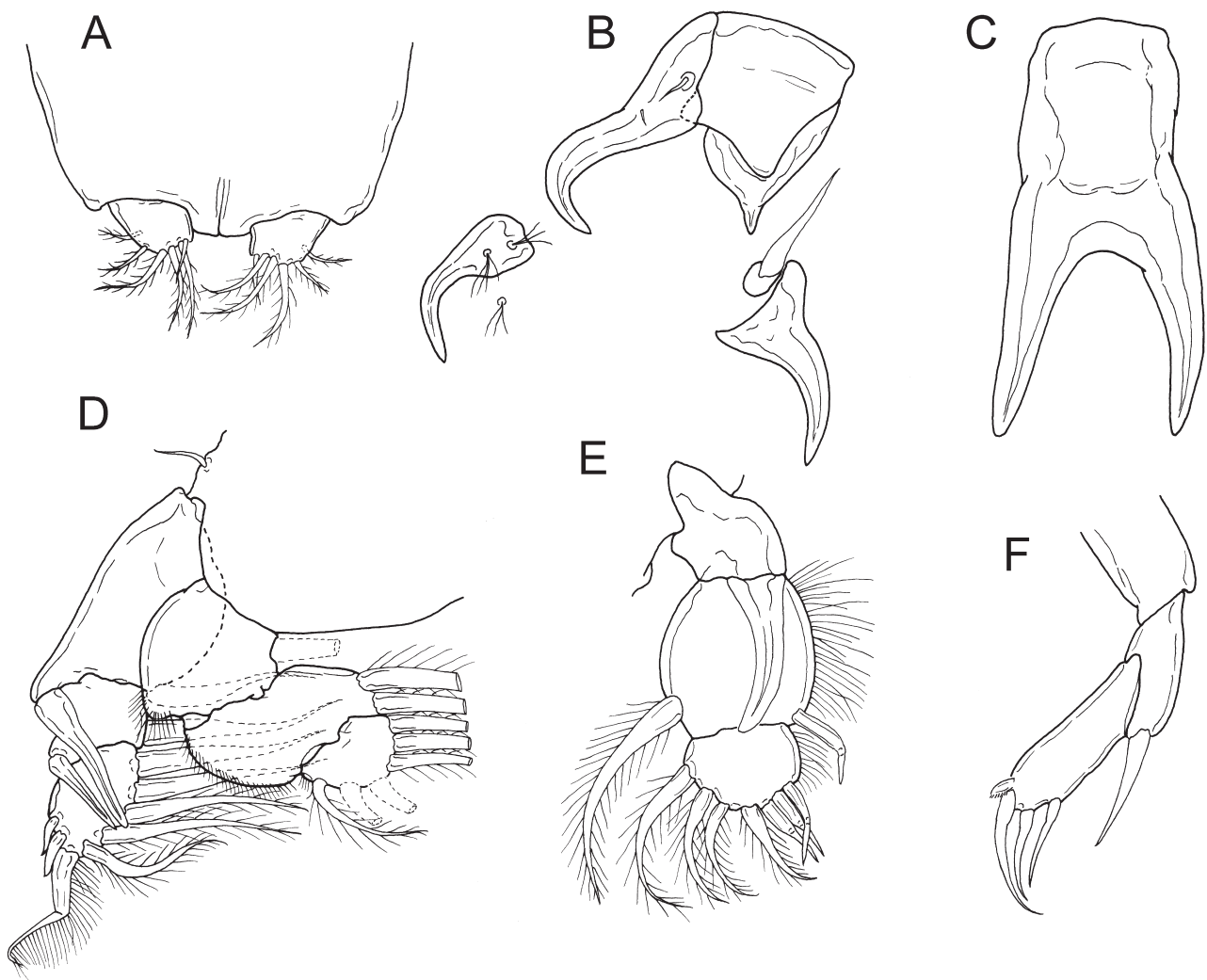


FIGURE 3. *Caligus hemiconiati* Capart, 1941 adult female (body length 3.2 mm). A, distal part of abdomen and caudal rami, dorsal; B, antenna, postantennal process and maxillule *in situ*, ventral; C, sternal furca; D, rami of leg 2 (with some setae missing on endopod); E, exopod of leg 3; F, exopod of leg 4.

***Caligus lacustris* Steenstrup & Lütken, 1861**

Material examined by R. F. Cressey: Syntype female from *Esox lucius* Linnaeus, 1758 caught in “Lake Furr”, Denmark, loaned to R. F. Cressey by the Zoological Museum, Copenhagen. In his unpublished manuscript Cressey stated that the specimen he borrowed from the Zoological Museum was “one of three” syntypes ex *Esox lucius* from “Lake Furr”, Denmark. However, Margolis *et al.* (1975) listed the type locality as “Lake Fuur” and “Lake Tiustrup, Denmark”, while the online catalogue of the Zoological Museum lists only one lot of *C. lacustris* and gives the locality as “Lake Thystrup”. The Reg. No. of this material is NHMD84850 (formerly CRU-007006).

Supplementary Description: Abdomen (Fig. 4A) about 1.5 times longer than wide. Caudal rami about 1.3 times longer than wide and armed with 6 setae as typical for genus. Antenna (Fig. 4B) with slender process on posterior margin of proximal segment and armed with 2 short setae proximally on subchela. Postantennal process (Fig. 4B) curved and ornamented with bisensillate papillae. Maxillule (Fig. 4B) with tapering posterior process. Sternal furca (Fig. 4C) with broad, blunt-tipped, parallel tines. Second exopodal segment of leg 1 (Fig. 4D) with 3 plumose setae along posterior margin; spines 1 to 3 on distal margin subequal, all lacking accessory process; seta 4 about equal in length to spines 1 to 3. Leg 2 (Fig. 4E) with outer margin of endopodal segment 2 ornamented with setules, slightly spreading onto surface; outer spine on first exopodal segment large and aligned obliquely across surface of ramus, spine on second segment small, curved and aligned along lateral margin of segment; third exopodal segment

with II, I, 5 setal formula. Leg 3 exopod (Fig. 4F) with first segment lacking inner seta, bearing long, weakly curved, outer spine almost reaching articulation separating second and third segments. Leg 4 (Fig. 4G) comprising protopodal segment and 2-segmented exopod: first exopodal segment armed with long, outer spine reaching well beyond middle of second segment; second exopodal segment bearing 3 distal margin spines; inner spine longer than segment, middle and outer spines short.

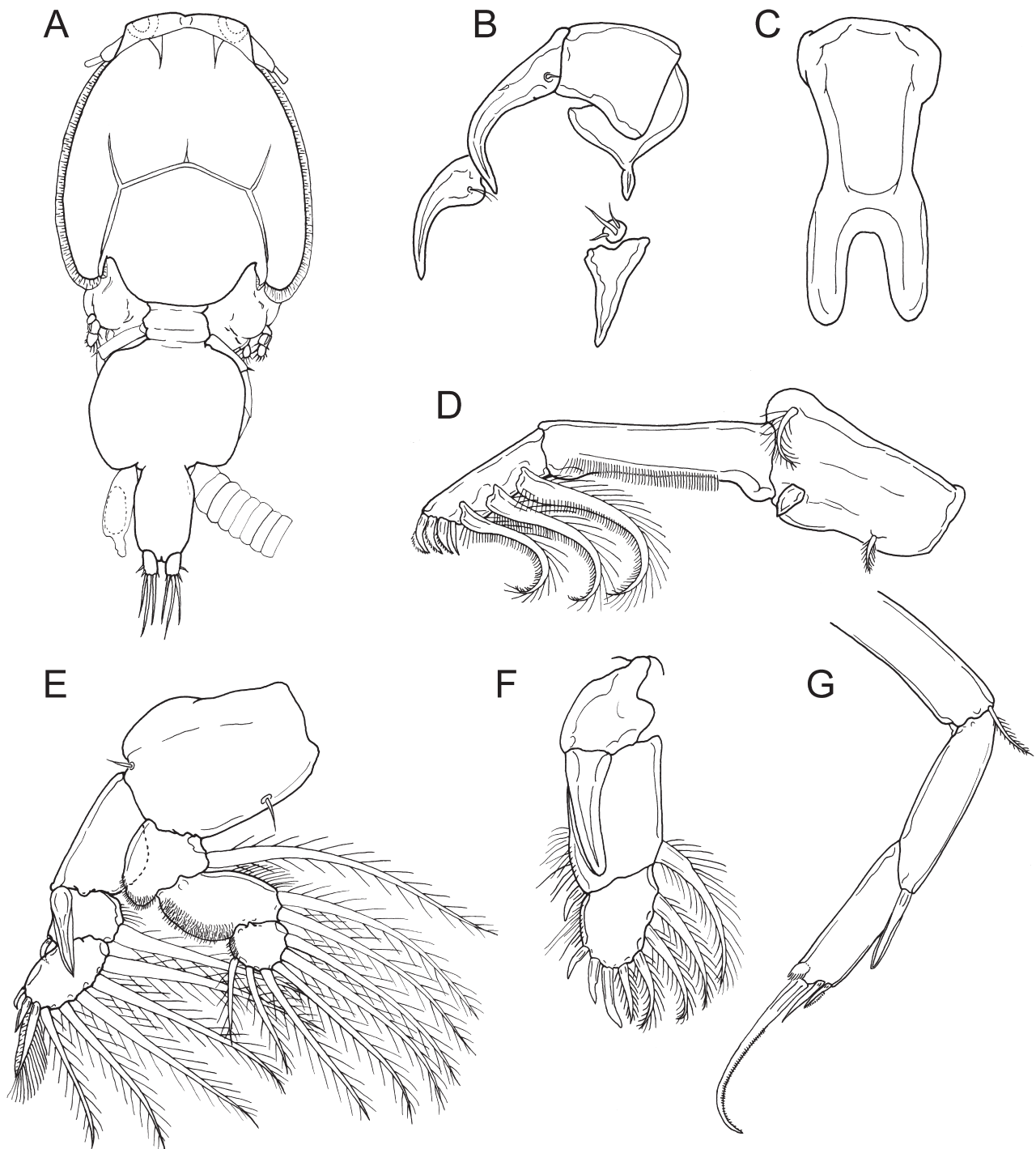


FIGURE 4. *Caligus lacustris* Steenstrup & Lütken, 1861 adult female (body length 6 mm). A, habitus, dorsal; B, antenna, postantennal process and maxillule *in situ*, ventral; C, sternal furca; D, leg 1; E, leg 2; F, exopod of leg 3; G, exopod of leg 4.

Remarks: *Caligus lacustris* is the best known caligid found in fresh water. It has a wide distribution across Northern and Central Europe and western Asia, having been reported from freshwater habitats in Denmark, Germany, The Netherlands, Finland, Sweden, Poland, Ukraine, Russia, Azerbaijan, and Uzbekistan as well as from around the Caspian Sea, Aral Sea, Sea of Azov and Baltic Sea (see References in Margolis *et al.*, 1975). Despite the large number of records of *C. lacustris*, it proved difficult to find reliable descriptive accounts of details of the swimming legs in particular. The supplementary description revealed: the lack of accessory processes on distal spines 2 and 3 on the second exopodal segment of leg 1, the extent of the setular ornamentation on the endopod of leg 2, the small size and unusual configuration of the outer spine on the second exopodal segment of leg 2, the lack of an inner seta on the first exopodal segment of leg 3 and the relative size and ornamentation of the spines on leg 4.

There are interesting and unusual similarities between *C. lacustris* and the type species *C. curtus* O.F. Müller, 1785. Both species share the possession of a large outer spine on the first exopodal segment of leg 2 which is directed somewhat obliquely across the ramus, reaching about to the mid-point of the second segment, combined with an unusually small outer spine on the second exopodal segment. This spine lies parallel with the longitudinal axis of the ramus and curves slightly across the dorsal surface. In addition, spines 1–3 on the second exopodal segment of leg 1 lack an accessory process in both species and seta 4 is only slightly longer than spine 3. Finally, the segmentation and armature of leg 4 is the same in both species. From these morphological similarities, we infer a close phylogenetic relationship between *C. curtus* and *C. lacustris*. The geographical distribution of the former species at high latitudes around the North Atlantic basin is contiguous with that of *C. lacustris* in northwestern Eurasia. We hypothesise that *C. curtus* is the marine sister taxon of the freshwater *C. lacustris* and that timing of the colonization of fresh waters by this lineage might be post-glacial.

***Caligus pageti* Russell, 1925**

Material examined by R. F. Cressey: Syntype female (dissected on slides) from *Mugil capito* Cuvier, 1829 taken from experimental fish culture ponds in Lake Maryût at Mex, near Alexandria in Egypt, loaned to R. F. Cressey by the Natural History Museum, London (Reg. No. BMNH 1958.4.9.1-22).

Supplementary Description: Genital complex about 1.2 times longer than wide and about 2.5 times longer than abdomen; abdomen about as long as wide (Fig. 5A) with angular posterolateral corners. Caudal rami about twice as long as wide. Antenna (Fig. 5B) with rounded swelling proximally and minute seta on anterior margin near middle of subchela. Second exopodal segment of leg 1 (Fig. 5C) with 3 plumose setae on posterior margin; spines 1 to 3 slender, each lacking accessory process; seta 4 just longer than spines 2 and 3 but shorter than segment. Leg 2 (Fig. 5D) ornamented with patches of densely-packed setules extending onto lateral part of endopodal segment 2; outer spine on first exopodal segment lying obliquely across ramus; spine on second segment short and aligned close to lateral margin of ramus. First exopodal segment of leg 3 (Fig. 5E) lacking inner seta, produced into outer distal accessory process ornamented with strip of marginal membrane on apex, and bearing short, slightly curved, outer spine not reaching as far as articulation separating second and third segments. Leg 4 (Fig. 5F) comprising protopodal segment and unsegmented exopod armed with 1 outer and 2 distal spines; outer margin spine unornamented, not reaching distal margin; inner distal spine bilaterally spinulate, longer than exopodal segment, outer distal spine unilaterally spinulate, less than one third length of inner spine; pectens lacking.

Remarks. The original description was based on a large amount of material of both sexes and included developmental stages (Russell, 1925). The species was well characterised and has been recorded since from several other species of mugilids in waters along the Mediterranean coast of North Africa from Egypt to Algeria (Argilas, 1931; Brian, 1935, Raibaut *et al.*, 1971) and from the Mediterranean coast of France (Ben Hassine, 1983). The developmental stages of this species were very well described in the PhD thesis of Ben Hassine (1983) but her thesis is not widely available, so some additional features are highlighted here.

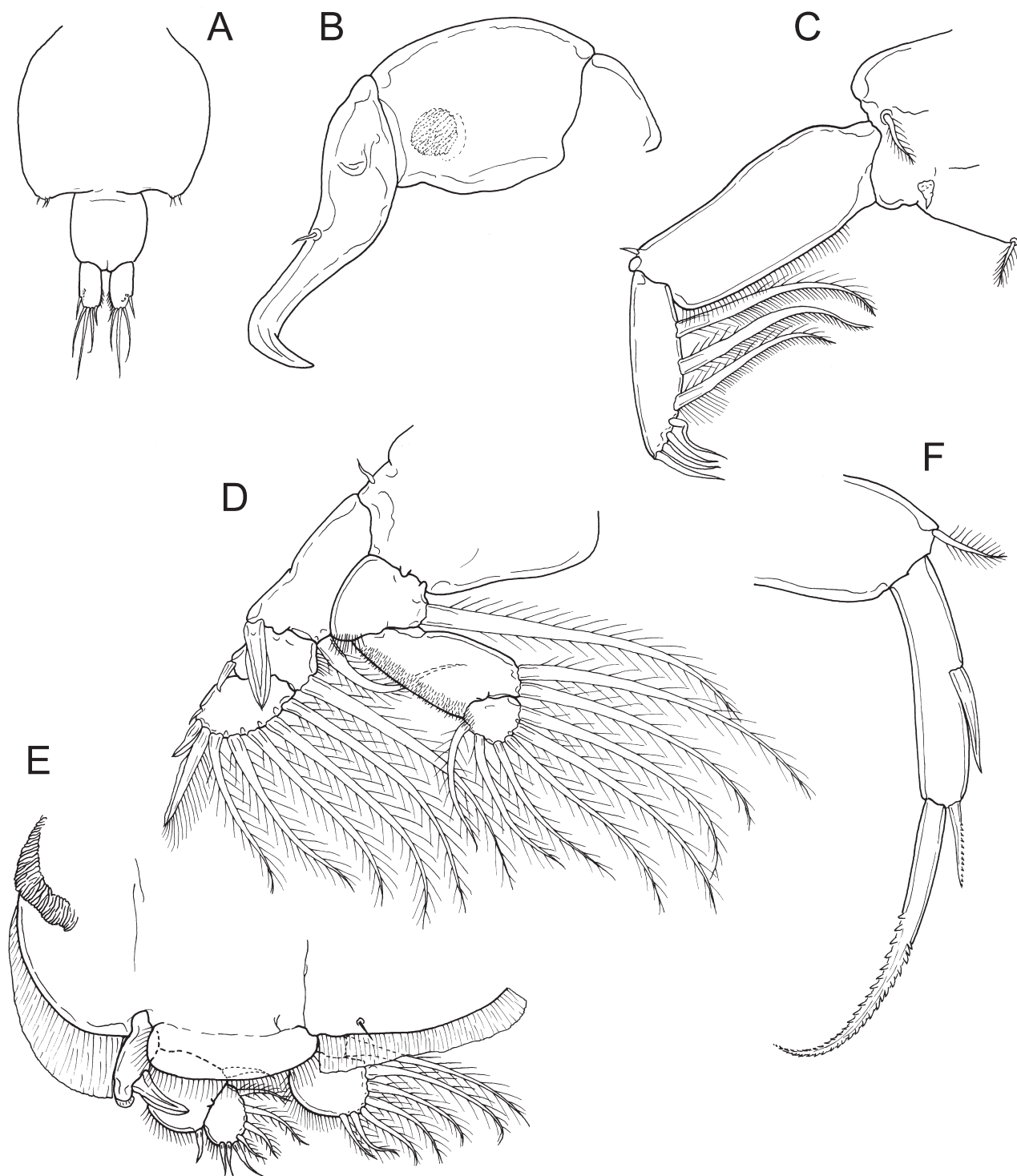


FIGURE 5. *Caligus pageti* Russell, 1925 adult female (body length 5.6 mm). A, genital complex and abdomen, dorsal; B, antenna, ventral; C, leg 1; D, leg 2; E, leg 3; F, exopod of leg 4.

***Caligus pagri* Capart, 1941**

Material examined by R. F. Cressey: Syntype female from *Evynnis ehrenbergi* (Valenciennes, 1830) (as *Pagrus ehrenbergi*) caught off the coast of Gambia, loaned to R. F. Cressey by the Musée royal d’Histoire naturelle, Brussels (Reg. No. I.G. 10910).

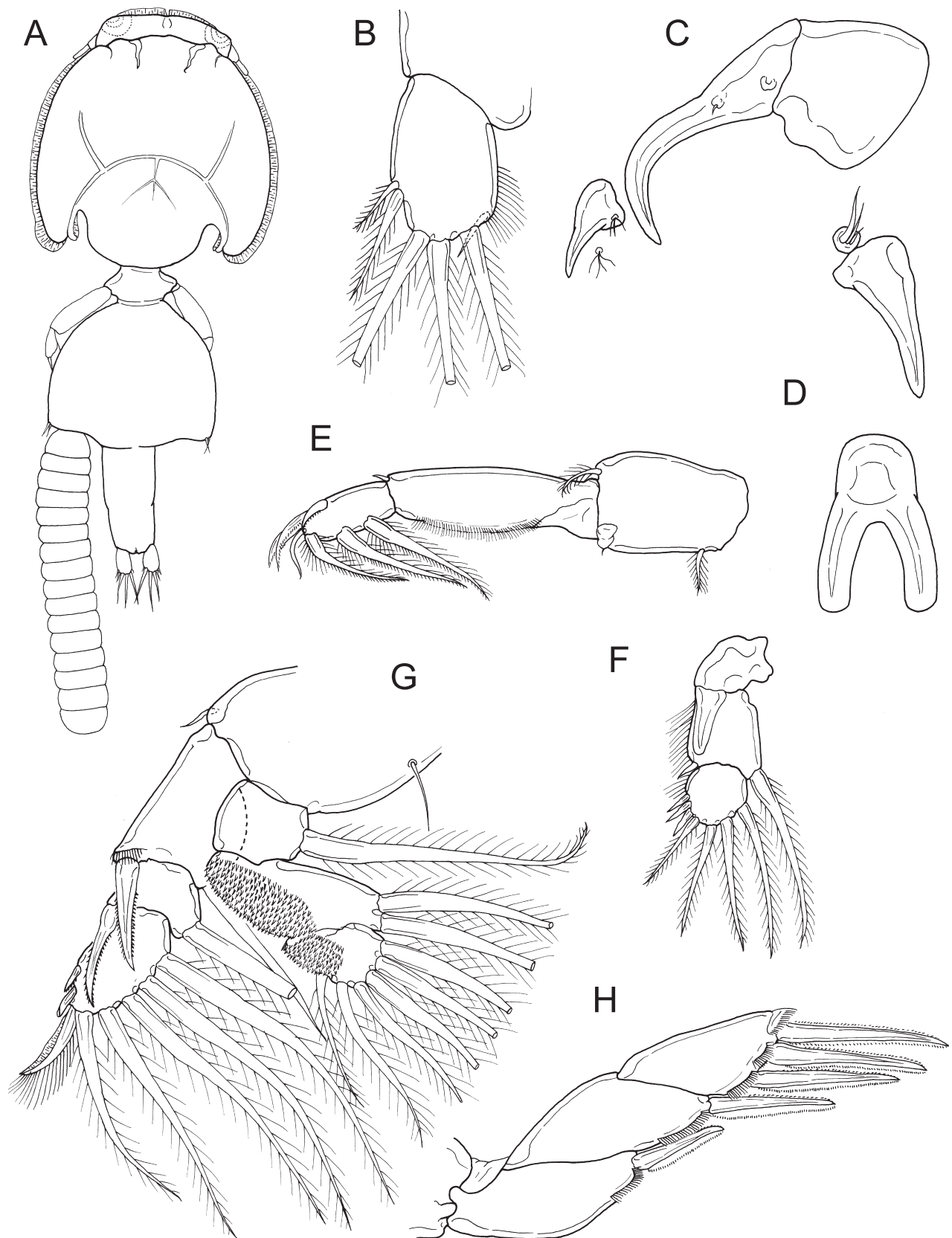


FIGURE 6. *Caligus pagri* Capart, 1941 adult female (body length 2.8 mm). A, habitus, dorsal; B, caudal ramus, dorsal; C, antenna, postantennal process and maxillule *in situ*, ventral; D, sternal furca; E, leg 1; F, leg 2; G, exopod of leg 3; H, exopod of leg 4.

Supplementary Description: Abdomen of female indistinctly 2-segmented (Fig. 6A) with somites separated by shallow groove. Caudal rami (Fig. 6B) about 1.5 times longer than wide and ornamented with long setules on medial margin. Antenna (Fig. 6C) lacking posterior process on proximal segment; subchela armed with 2 minute setal vestiges. Postantennal process (Fig. 6C) with small slightly curved tine, shorter than base. Maxillule (Fig. 6C) with tapering posterior process. Sternal furca (Fig. 6D) with blunt, weakly diverging tines. Second exopodal segment of leg 1 (Fig. 6E) with 3 plumose setae on posterior margin; spines 1 to 3 each lacking accessory process; seta 4 just shorter than spines 2 and 3. Leg 2 (Fig. 6F) ornamented with extensive patches of densely-packed setules extending over lateral part of endopodal segments 2 and 3; outer spines on first and second exopodal segments elongate; spine of first segment weakly oblique, spine on second aligned close to lateral margin of ramus. Leg 3 exopod (Fig. 6G) with first segment lacking inner seta, bearing short, straight, outer spine not reaching as far as articulation separating second and third segments. Leg 4 (Fig. 6H) comprising protopodal segment and 3-segmented exopod armed with I, I, III spines; pectens on exopodal segments modified as linear membranes lying along lateral margin of segment.

Remarks: The original description by Capart (1941) was supported by figures of the dorsal habitus of the female plus individual figures of the maxilla, sternal furca, and legs 1 and 4. This species was not listed by Yamaguti (1963) but was included in the catalogue of Margolis *et al.* (1975). There have been few subsequent mentions of *C. pagri*. Oldewage & van As (1989) listed *C. pagri* from two sparid hosts, *Pagrus caeruleostictus* (Valenciennes, 1830) (as *Sparus caeluleostictus*) and *S. aurata* Linnaeus, 1758, in Gambia and they attributed this record to Capart (1941). However, the two hosts recorded by Capart (1941) were, *Evynnis ehrenbergi* (as *Pagrus ehrenbergi*) and *S. aurata*, so the source of Oldewage & van As's (1989) record from *P. caeruleostictus* is unclear and this host record requires confirmation.

Boxshall (2018) did not include *C. pagri* in the newly defined *C. diaphanus*-species group despite the overall similarity to *C. diaphanus* mentioned by Capart (1941) because too little information was available on its detailed morphology. The new observations confirm the presence of other key character states typical of this species group, namely, the lack of any posterior process on the proximal segment of the antenna, the reduced size of the tine on the postantennal process, the small size of spine 1 on the distal exopodal segment of leg 1 plus the lack of an accessory process on spines 2 and 3, the extensive surface ornamentation on the endopod of leg 2, and the modified linear pectens on leg 4. Given this combination of features, *C. pagri* is a member of the *C. diaphanus*-group.

Synonymies

Caligus glacialis Gadd, 1910 and *Caligus curtus* Müller, 1785

Despite its early twentieth century publication date, the original description of *C. glacialis* by Gadd (1910) provides detailed information on some important morphological features. Comparison of Gadd's description of *C. glacialis* with the redescription of the type species *C. curtus* by Parker *et al.* (1968) reveals numerous detailed similarities. The general habitus of female *C. glacialis* is very similar to that of *C. curtus* and similarities between their appendages include: the presence of a blunt posterior process on the proximal segment of the antenna; a recurved postantennal process; a slender maxilliped lacking any myxal process; a sternal furca with short divergent tines; leg 2 with an unusually large outer spine of the first exopodal segment combined with an inconspicuous outer spine on segment 2, and neither lies obliquely across the surface of the ramus; leg 3 carries a slightly curved outer spine on the first exopodal segment that does not extend as far as the articulation between exopodal segments 2 and 3; and leg 4 is 3-segmented and bears 3 distal margin spines, the innermost of which is more than twice as long as the other 2 spines and longer than the segment. The male, as described by Gadd (1910), also shares numerous detailed features with *C. curtus*, including the presence of 2 well developed digitiform processes on the myxal surface of the maxilliped opposing the tip of the subchela, one proximal to and one distal to the tip of the subchela when adducted.

The female of *C. curtus* attains lengths up to 10.1 mm and the male, unusually for a *Caligus* species, is longer than the female, up to 12.3 mm according to Kabata (1979). The body lengths given by Gadd (1910) for female and male *C. glacialis* were 8.9 mm and 9.9 mm, respectively, and conform to this unusual pattern of gender-based size dimorphism. On the basis of all these similarities, and in the absence of significant differences, we propose to recognise *Caligus glacialis* Gadd, 1910 as a junior subjective synonym of *Caligus curtus* Müller, 1785. This species is widespread at high latitudes in the Arctic-Boreal Atlantic.

***Caligus raniceps* Heegaard, 1943 and *Caligus curtus* Müller, 1785**

The description of *Caligus raniceps* was based on three male specimens stored in the collections of the Swedish Museum of Natural History (Heegaard, 1943). Heegaard's paper states that these males were collected in the "Bay of Bengal" by Captain Sundevall and "host unknown" but it does not specify whether the specimens were taken from the plankton or from an unidentified fish. The description lacks detail but in the features that are mentioned or illustrated, *C. raniceps* appears identical to the male of *C. curtus* as redescribed by Parker *et al.* (1968), as already commented by Pillai (1985). The maxilliped of the male bears distinctive myxal processes opposing the tip of the subchela, one proximal to and one distal to the tip of the subchela when adducted. This configuration is the same in both species. In addition, leg 4 is 3-segmented and bears 3 distal margin spines, the innermost of which is more than twice as long as the other 2 spines and longer than the segment, the sternal furca has short divergent tines, and the body length (given as 9 to 12 mm) is unusually large. With our current state of knowledge, the syntype males of *C. raniceps* are identifiable as *C. curtus* and we consider that *Caligus raniceps* Heegaard, 1943 should be treated as a junior subjective synonym of *Caligus curtus* Müller, 1785.

Caligus curtus is widely distributed in the northern Atlantic region (Parker *et al.*, 1968; Dojiri & Ho, 2013) but has never been reported from the Pacific or Indian Oceans except for Heegaard's (1943) paper. We consider it extremely unlikely that this cold-water Atlantic species occurs in Indian waters. Heegaard's (1943) paper was based on material collected from numerous localities around the world and stored in the Riksmuseum, Stockholm, and we agree with Pillai (1985) who commented "probably there has been some confusion in the labels regarding the collection locality".

***Caligus guerini* Guiart, 1913 and *Caligus elongatus* von Nordmann, 1832.**

The original description of *C. guerini* was based on a single ovigerous female *Caligus* found settled on a *Laminaria* frond collected on the Glenan Islands off the Brittany coast in northern France (Guiart, 1913). The description was very brief and was largely focused on overall body proportions. It was supported by a single illustration showing the type female in dorsal view. Guiart (1913) gave the body length as 6 mm, the width as 2.5 mm, and noted that the genital complex showed spots of reddish pigment. This species has never been reported since the original description although it was listed in Yamaguti's (1963) compendium, in the catalogue of *Caligus* species by Margolis *et al.* (1975), and it is listed on the World of Copepods website (Walter & Boxshall, 2023).

The *Caligus* species found in the waters off northwestern Europe are well known and were reviewed in detail by Kabata (1979) in his landmark monograph. Of these species, *C. elongatus* von Nordmann, 1832 is the closest fit to the inadequately described *C. guerini*. Both species have the same female body length: Kabata (1979) gives the length range for *C. elongatus* as 5 to 6 mm. Female *C. elongatus* also often show reddish-brown pigmentation spots all over the body including the genital complex and have been found free swimming away from any host sufficiently frequently to be included in a student manual for the identification of coastal marine zooplankton (Todd *et al.*, 1996). The size of the abdomen as illustrated for *C. guerini* is smaller relative to the genital complex than in *C. elongatus* but the triangular shape of the abdomen depicted in Guiart's figure is extraordinary and almost certainly inaccurate. Other species in the European fauna that have a short abdomen, such as *C. labracis* T. Scott, 1902, differ in body length (3.5 mm for *C. labracis*) and their general habitus is more squat compared to the elongate habitus of *C. elongatus* and *C. guerini*.

The deposition of the type specimen is unknown (Margolis *et al.*, 1975) and in the absence of any other data, we propose to treat *Caligus guerini* Guiart, 1913 as a junior subjective synonym of *Caligus elongatus* von Nordmann, 1832.

***Caligus mordax* Leigh-Sharpe, 1934 and *Caligus coryphaenae* Steenstrup & Lütken, 1861**

Caligus mordax was described by Leigh-Sharpe (1934) in his account of the commensal and parasitic Copepoda of the Siboga Expedition. Unfortunately, there are no published data on either the host or collection locality for this species. Only a single specimen was recovered and Leigh-Sharpe (1934) concluded that it was a female.

Close examination of Leigh-Sharpe's figures reveals two distinctive character states: firstly, there is no defined postantennal process, and secondly, the outer spine on the first exopodal segment of leg 3 has a particular spatulate shape and extends to the side of the ramus (i.e., it does not overlap onto the surface of the second segment). The same distinctive spine shape and orientation is exhibited by both sexes of *C. coryphaenae* and this species is also one of the very few species of *Caligus* that lack a defined postantennal process (cf. Kabata, 1979; Cressey & Cressey, 1980; Pillai, 1985; Ho & Lin, 2004). Careful comparison reveals that the specimen illustrated by Leigh-Sharpe (1934) is actually a male: the antenna bears an additional process on the subchela, the genital complex is small and rectangular, the free abdomen is 2-segmented, and legs 5 and 6 are represented by separate papillae each bearing setae, some of which are elongate. In the proportions of its 2-segmented abdomen and the configuration of its caudal rami, the illustrated specimen of *C. mordax* conforms closely to the male of *C. coryphaenae* as illustrated by Ho & Lin (2004: Fig. 82). We propose to recognise *Caligus mordax* Leigh-Sharpe, 1934 as a junior subjective synonym of *Caligus coryphaenae* Steenstrup & Lütken, 1861.

***Caligus lessonius* Risso, 1826 and *Demoleus heptapus* (Otto, 1821)**

This species was established by Risso (1826) to accommodate a parasitic copepod found on "squale griset" caught in the Mediterranean. In their catalogue of *Caligus* species, Margolis *et al.* (1975) listed the type host as *Hexanchus griseus* (Bonnaterre, 1788), the bluntnose sixgill shark. *Caligus lessonius* has not been reported since 1826 although it has been listed in regional compendia such as Carus (1885) and Brian (1935), and in taxonomic compendia such as Wilson (1905) and Yamaguti (1963), all of which misspelled the name as *Caligus lessonianus*. Parker (1969) noted that *C. lessonius* did not belong in *Caligus* but he did not specify where it should be placed, and this treatment was followed by Margolis *et al.* (1975). In the absence of any formal transfer out of *Caligus*, this species has remained listed by the World of Copepods website (Walter & Boxshall, 2023).

The very brief original description by Risso (1826) comprises the following (translated from French): an oblong body with a yellow coloration traversed by a brown stripe; cephalothorax heart-shaped, convex, traversed by two longitudinal sutures and ornamented with 2 golden spots which are touching; the eyes are close together; the antennae are small and 3-segmented; the oral cone is long and pointed; there are 7 pairs of legs, the first are short and armed with a curved hook, the third are thick, and the last are ornamented with 2 claws; the abdomen is composed of 4 segments, the first 2 of which are equipped with foliaceous lamellae, and the last is very long and divided into 2 parts each carrying a canaliculate appendage at the base of which are 2 pieces surrounded by spines.

This description includes sufficient characters, especially the presence of foliaceous lamellae on two post-cephalothoracic body segments, to recognise that this species should be transferred to the family Pandaridae. The brief description given by Risso (1826) conforms reasonably closely to that of *Demoleus heptapus* (Otto, 1821) (cf. Kabata, 1979) and this species is known principally as an external parasite of *Hexanchus Rafinesque*, 1810 species (Cressey, 1967). We consider it likely that *Caligus lessonius* Risso, 1826 is a junior synonym of *Demoleus heptapus* (Otto, 1821).

***Caligus clavatus* Kirtisinghe, 1964 and *Caligus sphyraeni* Pillai, 1963**

In 1963 Pillai described *C. sphyraeni* from *Sphyraena acutipinnis* Day, 1876 and *S. jello* Cuvier, 1829 caught in Indian waters off Trivandrum (Pillai, 1963) and the following year Kirtisinghe (1964) described *C. clavatus* from *S. obtusata* Cuvier, 1829 caught in waters off Colombo, Sri Lanka. Pillai (1967; 1985) recognised that these *Caligus* species were synonymous but opted to use *C. clavatus* Kirtisinghe, 1964 for this taxon because of the similarity between his original name and the name of an unrelated congeneric species, *Caligus sphyraenae* Nuñez-Ruivo & Fourmanoir, 1956. This action was followed by Ho & Lin (2004) but both *C. sphyraeni* and *C. clavatus* have continued to be listed as valid in the World of Copepods website (Walter & Boxshall, 2023).

Caligus sphyraeni Pillai, 1963 is not strictly a homonym of Nuñez-Ruivo & Fourmanoir's (1956) species and there is no necessity to suppress Pillai's name, which has priority. We therefore treat *Caligus clavatus* Kirtisinghe, 1964 as a junior subjective synonym of *C. sphyraeni* Pillai, 1963. We note that *Caligus sphyraenae* Nuñez-Ruivo & Fourmanoir, 1956 was considered to be a junior synonym of *C. infestans* Heller, 1865 by Cressey & Cressey (1980) and Pillai (1985).

***Caligus rotundigenitalis* Yü, 1933 and *Caligus torpedinis* Heller, 1865**

Caligus torpedinis has not been reported since its original description by Heller (1865) which was based on a female found on the gills of a species of “*Torpedo*” caught in the Indian Ocean. The brief description can be summarised as follows: “The cephalothorax, which corresponds to two-fifths of the whole length of the body, is almost as wide as long, narrowing somewhat anteriorly and rounded posterolaterally. The frontal margin appears almost straight, not bulging in the middle, and the lunules are small, crescent-shaped, surrounded in front by a somewhat protruding membrane. The antennules are short, comprising two segments about equal in length. The antennae do not reach the margin of the dorsal cephalothoracic shield. The postantennal processes are simple, directed backwards. The first legs are armed with only two spines, plus seta 4 and 3 plumose setae on the terminal segment. Leg 4 is 4-segmented, armed with 5 spines, the last three of which are fairly similar in length. The genital complex is shorter than the cephalothorax, broader than long, with rounded lateral margins and a straight posterior margin. The abdomen is almost the same length as the genital complex, but is very narrow and composed of two somites, the second somite appearing somewhat shorter than the first. The caudal rami are longer than wide and about half the length of the anal somite, and bear three long plumose setae on the distal margin plus a small single seta on the outer margin.” This description is supported by two figures, a dorsal view of the habitus of the female and leg 4 (Heller, 1865: Tab. XV, figs. 6 and 6a).

The form of leg 4, with its 3-segmented exopod bearing I, I, III spines which are all of similar size and all directed obliquely away from the ramus, is shared with members of the *C. diaphanus*-group of species. Within this group of species, *C. torpedinis* closely resembles *C. rotundigenitalis* Yü, 1933 in overall body shape and body proportions, and has the same form of leg 4. Heller (1865) reported only 2 spines on the distal margin of the second exopodal segment of leg 1 but was presumably uncertain about this because he includes a question mark in the Latin diagnosis where he states: “*Pedes primi paris ad apicem duobus aculeis (?)*”. In *C. rotundigenitalis* spine 1 is only half the length of spines 2 and 3 and all 3 spines lie on top of each other in ventral view (cf. Ho & Lin, 2004: fig. 10). It seems probable that Heller (1865) overlooked spine 1. The postantennal processes are typically reduced in members of the *C. diaphanus*-group but Heller’s (1865) description of these processes as simple and directed backwards is in accord with Ho & Lin’s (2004: fig. 8A) redescription of *C. rotundigenitalis*.

On the basis of the available evidence we propose to treat *Caligus rotundigenitalis* Yü, 1933 as a junior subjective synonym of *C. torpedinis* Heller, 1865. This species has an extremely wide range of known hosts having been reported from at least 40 species of teleost fishes representing 26 different families of fishes (as listed by Ho & Lin (2004) and Walter & Boxshall (2023)), although this is the first record from an elasmobranch host.

***Caligus hyalinae* Heegaard, 1966 and *Caligus chelififer* Wilson, 1905**

Caligus hyalinae was originally described from material found in plankton samples. Heegaard’s (1966) material came from plankton tows taken in the Gulf of Mexico off Rockport, Texas. Both sexes were found but Heegaard (1966) noted that the genital complexes of the females did not contain eggs and considered that the very slender shape of the female genital complex may change considerably in “mature” females. The males were adult as indicated by the possession of secondary sexual characters, such as the large myxal process on the maxilliped. Unfortunately, Heegaard’s description lacks certain important details and is almost certainly inaccurate as *C. hyalinae* apparently exhibits multiple extremely unlikely character states, such as the possession of only 1 inner seta on the second endopodal segment of leg 2, the lack of both outer margin spines on the third exopodal segment of leg 2, and the lack of outer margin spines on the second and third exopodal segments of leg 3. Given this level of inaccuracy, it is necessary to interpret this description with caution.

Caligus hyalinae is very similar in gross morphology to *C. chelififer* and the type and only locality of *C. hyalinae* falls within the known distribution range of *C. chelififer* in the western Atlantic. Comparison of *C. hyalinae* with more recent redescriptions of *C. chelififer*, such as that of Kabata (1972), reveals numerous similarities between these two species. The overall body shape is very similar in both species although the free abdomen in both sexes shows a trace of a subdivision in Kabata’s figures of *C. chelififer* whereas no such subdivision is indicated in Heegaard’s (1966) figures of *C. hyalinae*. The caudal rami are elongate in both species. Both species show an unusual configuration of the armature elements on the distal exopodal segment of leg 1, namely, spines 1 to 3 are all subequal in size, seta

4 is more than twice as long as the spines and is longer than the segment, and the 3 plumose setae on the posterior margin are all reduced (i.e. are shorter than the segment). The sternal furca has weakly divergent tines with rounded tips in both species. The maxilliped of the male carries an unusually long, slender myxal process with a divided tip opposing the subchela in both species. This is a robust and rare character state shared by the males of *C. hyalinae* and *C. chelififer*. There are differences between the descriptions; namely, the exopod of leg 4 is shown as 3-segmented by Heegaard (1966) but as only 2-segmented by Kabata (1972), and the myxal process on the female maxilliped is not shown in the *in situ* figure of Heegaard (1966). But, given the numerous inaccuracies in the description of *C. hyalinae* pointed out above, the similarities between these two species provide sufficient evidence for us to propose to recognise *Caligus hyalinae* Heegaard, 1966 as a junior subjective synonym of *Caligus chelififer* Wilson, 1905.

Caligus hyalinae was proposed as a possible member of the *Caligus undulatus*-species group by Ohtsuka *et al.* (2020). We concur and consider its senior subjective synonym, *C. chelififer*, to be a member of the group.

***Caligus biseriodentatus* Shen, 1957 and *Caligus pauliani* Nuñez-Ruivo & Fourmanoir, 1956**

Caligus bioseriodentatus was originally described in detail from material of both sexes taken from a *Scomberomorus commerson* (Lacepède, 1800) (as *Cybiium commersoni*) caught off Hainan Island, China (Shen, 1957). It was not reported widely until 1980 when Cressey & Cressey (1980) recognised *Caligus obovatus* Heegaard, 1962, *Caligus proboscoidatus* Heegaard, 1962 and *Caligus auxisi* Pillai, 1963 as junior synonyms of *C. biseriodentatus*. In the same monograph on scombrid parasites, Cressey & Cressey (1980) redescribed both sexes of *C. biseriodentatus* and also figured an immature male specimen which exhibits several distinctive character states: the abdominal somites are each about 1.5 times longer than wide, and together they are longer than the genital complex; the three posterior margin setae on the second exopodal segment of leg 1 are shorter than the segment and shorter than seta 4, and the distal exopodal segment of leg 4 carries four subequal spines which are smaller than the spine on the first segment (Cressey & Cressey, 1980: Fig. 59c).

In contrast, *C. pauliani* is poorly known and was inadequately described. It is based on five specimens collected from the body surface and around the base of the pelvic and anal fins of *Sphyræna barracuda* (Edwards, 1771) (as *Sphyræna commersonii* Cuvier & Valenciennes) caught off the coast of Madagascar (Nuñez-Ruivo & Fourmanoir, 1956). The specimens were identified as males by Nuñez-Ruivo & Fourmanoir (1956) and their body length was given as 5 mm. The original description is incomplete and is supported by a habitus drawing plus figures of leg 1 and leg 4 only. However, the specimens do exhibit the same distinctive character states as *C. biseriodentatus*: the two free abdominal somites are each about 1.4 to 1.5 times longer than wide, and together they are longer than the genital complex; the three plumose setae on the posterior margin of the second exopodal segment of leg 1 are reduced (all three are shorter than the segment and shorter than seta 4), and the four spines carried on the distal exopodal segment of leg 4 are subequal and smaller than the outer margin spine carried on the first exopodal segment.

We conclude that these two species are synonymous and, unfortunately, the poorly described and virtually unused *Caligus pauliani* Nuñez-Ruivo & Fourmanoir, 1956 has priority over *C. biseriodentatus* Shen, 1957.

Although Cressey & Cressey (1980) and Cressey *et al.* (1983) showed that this is a widespread species occurring across the Indian Ocean (Malagasy Republic, Somalia, Arabian Sea, Sri Lanka, Thailand, Zanzibar) and the Indo-West Pacific (China, Philippines, Indonesia) as far south as Papua New Guinea and Australia, and that it has been recorded from seven species of *Scomberomorus* Lacepède, 1800 as well as from *Auxis thazard* (Lacepède, 1800) (Boxshall, 2018), the name *C. biseriodentatus* has not been mentioned in more than 25 publications by a minimum of ten different authors in the past 50 years. It is, therefore, not possible to maintain prevailing usage under Article 23.9.1.2. of the International Code of Zoological Nomenclature.

***Caligus cornutus* Heegaard, 1962 and *Caligus lobodes* (Wilson, 1911)**

As Pillai (1966) highlighted, the male and the female of *C. cornutus* described and illustrated by Heegaard (1962) are not conspecific. The male described by Heegaard (1962) is readily identifiable as the male of *Caligus lobodes* (Wilson, 1911) (Kirtisinghe, 1964 as *Midias lobodes*; Pillai, 1966 as *M. lobodes*; Boxshall, 2018 as *C. lobodes*). The female of *C. cornutus* was considered to be an immature specimen by Heegaard (1962) and all the appendages

illustrated in his species description were those of the male. The dorsal habitus view currently represents the only data available on the female. Boxshall (2018) concurred that the male described as *C. cornutus* was a misidentified male of *C. lobodes* but he erroneously assumed that the female was the designated holotype and thus maintained the name *C. cornutus* Heegaard, 1962 as valid, based on the female. However, Heegaard (1962) in his record of specimens states “1 male and 1 juvenile female, holotype and allotype, on *Sphyraena*...” and we interpret this as confirmation that the male is the holotype.

Caligus cornutus Heegaard, 1962 can therefore be formally treated as a junior subjective synonym of *Caligus lobodes* (Wilson, 1911) because the name *C. cornutus* belongs with the male holotype. The female specimen collected by Heegaard (1962) is currently unidentified and, since a single habitus drawing provides too little information upon which to make a reliable identification, we propose to leave it unidentified.

***Caligus mebachii* Marukawa, 1927**

Marukawa (1927) established *C. mebachii* based on material collected from *Thunnus obesus* (Lowe, 1839) (as “mebachii” in Japanese) caught in neritic waters of Japan (Nagasawa *et al.*, 2018). The original description was an entry in the *Encyclopedia of the Fauna of Japan* and was very brief. This species has not been reported since, although the original description was reprinted in subsequent editions up to and including the final 1947 revised and enlarged edition (Marukawa, 1947) and again in the 1956 abridged version for students. According to Damkaer & Onbé (2018), Marukawa’s section on copepods was unchanged through all these editions, still reporting the new species of *Caligus*. It was included in the catalogue of *Caligus* species (Margolis *et al.*, 1975) and was listed by Nagasawa *et al.* (2010) in their annotated list of *Caligus* species recorded from Japan and by Nagasawa *et al.* (2018) in their list of parasitic copepods from tuna species.

Translated from the original Japanese, the original description states: “Body flattened, translucent tinged with yellowish. Body length: female 6-7 mm; male 4-5 mm. Cephalothorax oval, separated from third [= fourth] pediger. Fourth pediger wider than long and reduced, with leg 4, located in front of genital complex. Genital complex of female nearly quadrate, gonopore located anteriorly [dubious character state]; that of male widest at mid-length, slightly longer than wide, having four spiniform elements on each side. Abdomen two-segmented in both sexes; anal somite produced posteriorly. Caudal ramus nearly quadrate, with three plumose setae and one outer spine which is longer in male than in female.” The descriptive text is accompanied by two illustrations (Fig. 7A, B), both dorsal habitus views, presumably of the male and female as identified by Marukawa (1927). We consider that these two specimens are not conspecific. The smaller specimen (Fig. 7A) (presumably the male of Marukawa) exhibits an indentation in the lateral margin of the dorsal cephalothoracic shield that is characteristic of species of *Euryphorus* Milne Edwards, 1840. In addition, this figured specimen clearly has a biramous leg 4 and lacks lunules (Marukawa, 1927). This specimen appears to be a young male of *E. brachypterus* (Gerstaecker, 1853), a common parasite of scombrids, including *Thunnus obesus*, in Japanese waters (Nagasawa *et al.*, 2018).

In contrast the larger specimen (Fig. 7B) has paired lunules and a 4-segmented uniramous leg 4 and clearly belongs to the genus *Caligus*. Although Marukawa (1927) identified this specimen as the “female”, the internal structures figured within its genital complex suggest that it is a male containing developing spermatophores. The shape and general proportions of the genital complex and the short, clearly 2-segmented abdomen are also in accord with those of a male. The figure appears to show that the first exopodal segment of leg 3 is armed with a spine which is directed laterally and does not lie across the surface of the ramus as is typical for *Caligus* species. The unusual orientation of this spine is typical of *C. coryphaenae* (e.g., Ho & Lin, 2004: Fig. 81), also a common parasite of scombrids in Japanese waters, including *Thunnus obesus* (Nagasawa *et al.*, 2018). The body length for this specimen given by Marukawa (1927) was 6–7 mm and overlaps with the known body length of male *C. coryphaenae*, given as 4.5 to 6.0 mm by Kabata (1979). The configuration of the setae on the caudal ramus of male *C. coryphaenae* is also unusual (Fig. 7C, D). There are 6 caudal setae, as typical for the genus; 3 long pinnate setae distally, 1 short inner seta and 2 short outer setae. The innermost long pinnate seta is located ventral to the other setae and is ornamented with two rows of pinnules, the pinnules along the inner margin of the seta are particularly long and densely set. The pinnule row along the outer margin does not lie in the same plane as the inner row and is set at about 150° relative to the inner row so it projects ventrolaterally rather than laterally. To the best of our knowledge, the broad extent of the pinnules on this inner distal seta is unique to male *C. coryphaenae* and this arrangement is visible in

Marukawa's (1927) illustration of the "female" (cf. Fig. 7B). However, Marukawa's (1927) figure includes the outlines of two elongate structures originating on the genital complex which we presume represent egg sacs. We suspect that these structures, which are not the correct proportions for egg sacs, were added to the drawing perhaps to indicate the presumed sex of the specimen. We, therefore, tentatively conclude that Marukawa's "female" is a male of *C. coryphaenae* which was mistakenly identified as the female.

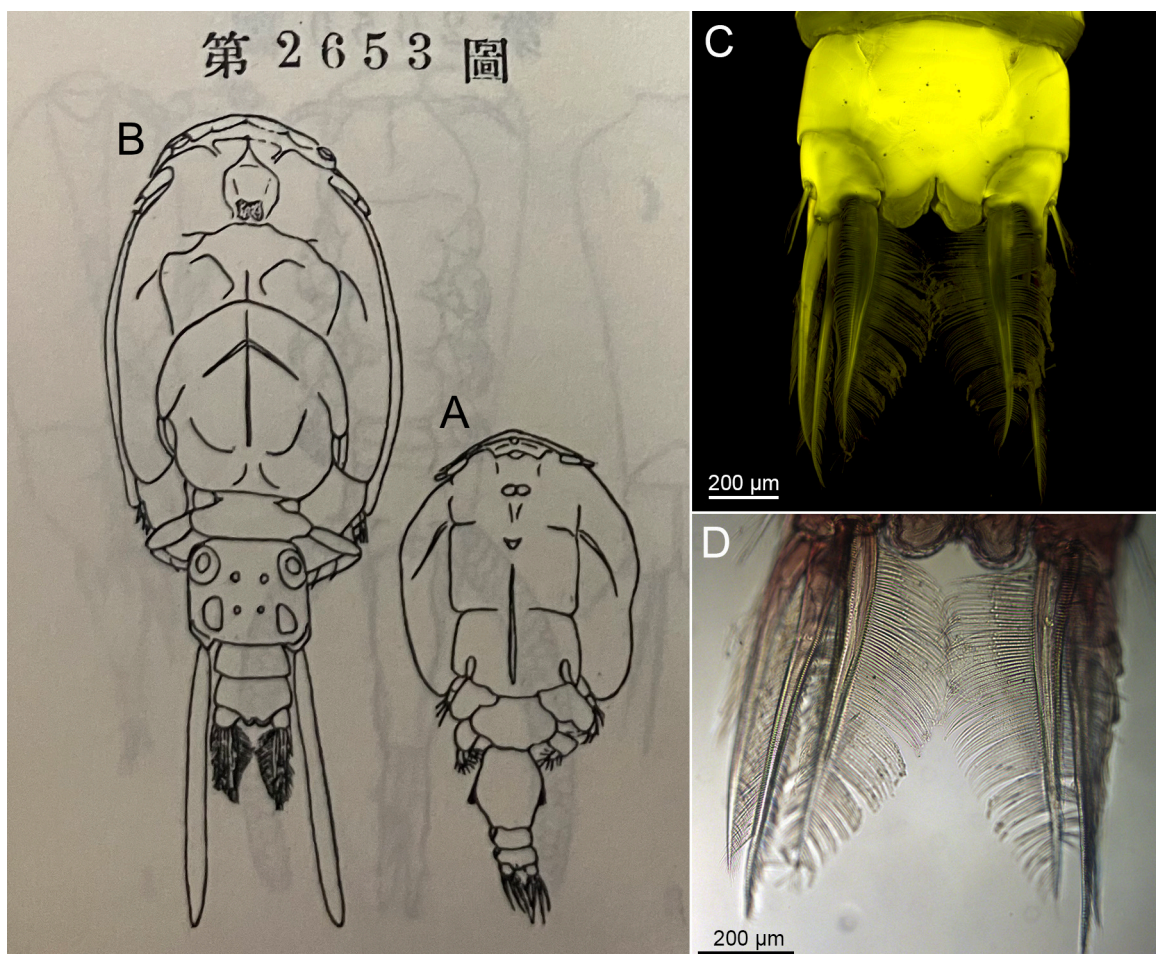


FIGURE 7. A, B, Dorsal habitus views of male (A) and "female" (B) *Caligus mebachii* Marukawa, 1927, illustration from the 1956 abridged edition of Marukawa (1947) [Copyright expired in 2008]; C, Anal somite and caudal rami of male *Caligus coryphaenae* Steenstrup & Lütken, 1861, dorsal view using CLSM; D, Same, using light microscopy.

The type material of *C. mebachii* cannot be traced and without it we cannot resolve the confusion surrounding the sex of the so-called "female". The two specimens illustrated in Marukawa (1927) are effectively syntypes and we here designate the male (Fig. 7A) as the lectotype. Subsequent designation of a lectotype by means of an illustration is permitted under Article 74.4. of the International Code of Zoological Nomenclature (ICZN, 1999), even when the specimens can no longer be traced. The newly designated lectotype of *C. mebachii* is identifiable as a young male of *Euryphorus brachypterus* and we formally propose to treat *Caligus mebachii* Marukawa, 1927 as a junior subjective synonym of *Euryphorus brachypterus* (Gerstaecker, 1853).

Name proposed for reversal of precedence

Caligus hamatus Heegaard, 1955

Caligus hamatus is known from a single male collected in a plankton sample taken at a depth of 20 m in the surface layers of the Bonny River, an arm of the Niger River delta in southern Nigeria, during the Atlantide Expedition

(Heegaard, 1955). It has never been reported since and no host association has ever been reported for *C. hamatus*. The whereabouts of the type specimen is unknown (Margolis *et al.*, 1975) but, fortunately, Heegaard's (1955) description, although inadequate by modern standards, contains sufficient detail to allow comparison with related congeneric species, specifically with *Caligus undulatus* Shen & Li, 1959.

Caligus undulatus was also originally described from zooplankton samples, collected in Qingdao (as Tsingtao) Harbour on the eastern coast of China, and the type material comprised numerous ovigerous females and males (Shen & Li, 1959). Since its description, *C. undulatus* has been reported widely from across the Indo-West Pacific (Pillai, 1966; Venmathi Maran & Ohtsuka, 2008; Venmathi Maran *et al.*, 2012a, b; Venmathi Maran *et al.*, 2016; Moon & Park, 2019) and western Atlantic (Montú, 1982; Suárez-Morales *et al.*, 2012a, b; Ortega *et al.* 2017; Kim *et al.*, 2019). All of these records were based on specimens caught in the plankton and it wasn't until 2020 that this caligid was finally found on a host, the clupeid *Sardinella zunasi* (Bleeker, 1854) caught in Japanese waters (Ohtsuka *et al.*, 2020). It has since been recorded on a second clupeid host, *Konosirus punctatus* (Temminck & Schlegel, 1846) landed at a fish market in southern Korea (Lee *et al.*, 2022).

Comparison of *C. hamatus* with *C. undulatus* reveals that the males of these two species share numerous character states including: broad marginal membrane surrounding the dorsal cephalothoracic shield; first and second free abdominal somites both about twice as long as wide and with the first slightly shorter than the second; male maxilliped with prominent myxal process opposing tip of subchela; sternal furca with parallel to weakly divergent tines separated by narrow gap; second exopodal segment of leg 1 armed with plumose setae on posterior margin that are almost as long as first exopodal segment, and with seta 4 much longer than second segment; leg 2 with outer spine on first exopodal segment passing obliquely across surface of ramus, with outer spine on second segment much smaller and lying close to lateral margin, and with at least one outer spine on third segment apparently missing; leg 3 with weakly curved outer spine on first exopodal segment not reaching articulation between second and third segments; leg 4 with 2-segmented exopod bearing 4 subequal spines on distal segment. On the basis of these similarities in fine details, and in the absence of any significant morphological differences, we conclude that *C. hamatus* and *C. undulatus* are conspecific. Unfortunately, the widely used species name *C. undulatus* was established after *C. hamatus*, which therefore has priority. However, a case has been submitted to the ICZN to propose that *Caligus undulatus* Shen & Li, 1959 be given precedence over the virtually unused *Caligus hamatus* Heegaard, 1955.

Homonymy

Caligus tenuis (Leidy, 1889)

Özak *et al.* (2017) concluded that the genus *Sciaenophilus* van Beneden, 1852 was a synonym of *Caligus* and transferred all four of its species. The type species *Sciaenophilus tenuis* van Beneden, 1852 became *Caligus tenuis* (van Beneden, 1852). This transfer created a secondary homonym since the name *Caligus tenuis* (Leidy, 1889) was used by Fowler (1912). This homonymy has not been addressed.

Leidy (1889) originally established a new species of caligid as *Chalimus tenuis* Leidy, 1889 based on a single unidentifiable chalimus stage. By this date it was quite widely accepted that the chalimus was merely a developmental stage of caligids (e.g., Krøyer, 1837) and the generic name *Chalimus* Burmeister, 1835 had largely fallen into disuse. However, Fowler (1912) in his "*Crustacea of New Jersey*" listed the genus *Chalimus* as a synonym of *Caligus* and transferred Leidy's species, thereby creating the new combination *Caligus tenuis* (Leidy, 1889). This taxon has incorrectly been attributed to Fowler (1912) although Fowler was responsible only for the new combination.

The type specimen, an early chalimus stage found by Leidy (1889), was obtained from the tail fin of a larval fish, *Leptocephalus* sp. The description available is minimal with a single dorsal habitus view showing no rudiments of lunules or any trace of ecdysial extension lobes, typical of many *Caligus* species. We conclude that there is no robust evidence supporting the transfer of *Chalimus tenuis* to *Caligus* as it could equally well belong to another caligid genus. We therefore reject this transfer. *Chalimus tenuis* Leidy, 1889 remains a *species inquirendum* within a genus which is no longer regarded as valid.

Species inquirenda

Caligus alalongae Krøyer, 1863

Krøyer (1863) described *Caligus alalongae* based on material collected from *Thynnus alalunga* (Bonnaterre, 1788) (as *Thynnus alalonga*) from an unknown locality. Wilson (1905) considered *C. carangis* Krøyer, 1863 and *C. alalongae* to be synonymous and used only the latter name in his key to species. Krøyer's (1863) description of *C. alalongae* showed a similar gross morphology to *C. carangis* in terms of body proportions but the only other illustrations (sternal furca and lunule plus antennule) don't provide for easy comparison with those he provided for *C. carangis*. However, one of the reliable diagnostic features for members of the *C. confusus*-species group is the possession of an elongate distal antennular segment. This is illustrated by Krøyer (1863) for *C. carangis* but is not shared by *C. alalongae*. We therefore consider that *C. alalongae* is distinct from *C. carangis*.

Other species have been confused with *C. alalongae*. Kirtisinghe (1937) described both sexes of a caligid identified as "*C. alalongae*" collected from *Alepes djedeba* (Forsskål, 1775) (as *Caranx kalla*) and two "other *Caranx* species" in Sri Lankan waters. As noted by Capart (1953) and Shiino (1959), "*C. alalongae*" of Kirtisinghe (1937) is not conspecific with *C. alalongae* of Krøyer (1863). Pillai (1961) considered that Kirtisinghe's (1937) material represented a new species, *C. confusus* Pillai, 1961 that he had just described based on material collected from *Caranx sansun* (Forsskål, 1775) in Indian waters. Kirtisinghe (1964) subsequently followed Pillai's synonymy. Yamaguti (1954) recorded "*C. alalongae*" on *Elagatis* sp. and *Caranx* sp. caught off Macassar (Indonesia) but his material is not conspecific with *C. alalongae* of Krøyer (1863). Yamaguti's material is also identifiable as *C. confusus*. Lewis (1967) concurred that "*C. alalongae*" of both Kirtisinghe (1937) and Yamaguti (1954) were conspecific with *C. confusus*.

Capart (1953) reported "*C. alalongae*" from *Mobula rochebrunei* (Vaillant, 1879) caught off Gorée in Senegal. This record was based on a single juvenile female for which no description was provided and is considered doubtful. Capart (1959) subsequently reported "*C. alalongae*" from *Thunnus obesus* caught off the west coast of southern Africa but his illustrations clearly show that his species was identifiable as *C. productus* Dana, 1852. Capart (1959) placed the material from his 1953 account in the synonymy of "*C. alalongae*", so we conclude that neither of his records applies to *C. alalongae* of Krøyer (1863).

None of the other records listed for *C. alalongae* by Margolis *et al.* (1975) provides sufficient morphological detail to allow verification. Therefore, the only available description of "typical" *C. alalongae* is the original description by Krøyer (1863) and this does not provide enough detail to allow a robust identification. We therefore consider *C. alalongae* Krøyer (1863) to be a *species inquirendum*.

Caligus gracilis Dana, 1852

In his study of material collected during the U.S. Exploring Expedition, Dana (1852, 1853) described an ovigerous female of *Caligus* taken from the body of a "*Serranus*" caught in the Atlantic off Rio de Janeiro and named it *C. gracilis*. His original description is very brief and is focussed on the body shape and proportions. It provides some detail of the setation of the caudal ramus and notes that the sternal furca has divergent, truncate tines. The text is supported by four figures: the dorsal habitus of the female, the antenna and postantennal process, the maxillule and the maxilliped (Dana, 1855: pl. 94, figs. 5a-d). Parker (1968) included this species in his list of "*nomina nuda* or *species inquirenda*" and was followed in this action by Margolis *et al.* (1975). We continue to treat *C. gracilis* as a *species inquirendum*.

We note that this species is a junior homonym of *Caligus gracilis* van Beneden, 1851 which is now treated as a junior subjective synonym of *Lepeophtheirus thompsoni* Baird, 1850.

Nomen nudum

Caligus truttae Giard, 1890

This species name was proposed for a *Caligus* specimen collected on sea trout (as *Salmo trutta* Linnaeus, 1758) caught in the estuary of the river Wimereux on the channel coast of northwestern France (Giard, 1890). Giard (1890) noted that sea trout were frequently infected by “*Caligus rapax* Milne Edwards, 1840” but commented that this caligid species has been recorded from a “large diversity of fishes including elasmobranchs”. He considered that it was inadequately described and suggested that the parasite found on this salmonid at Wimereux was a distinct species which he named *Caligus truttae*.

The bulk of Giard’s (1890) short paper was devoted to discussion of the application of the study of algae to the understanding of the behaviour of the sea trout. He outlined the timing of the life cycle of *S. trutta* and noted the seasonality of infection by “*Caligus truttae*” and the presence of settlement stages of *Laminaria* species, as well as attached diatoms and the monogenean *Udonella* Johnston, 1835 and its egg capsules. However, nowhere does Giard (1890) provide any descriptive morphological data or illustration associated with the name of his proposed new species. We therefore consider *Caligus truttae* Giard, 1890 to be a *nomen nudum*.

Acknowledgements

We are extremely grateful to Hillary Boyle Cressey for permission to trace and re-use her excellent drawings reproduced here as figures 1 to 6. We are also grateful to Prof. Susumu Ohtsuka (Hiroshima University) for finding and translating the encyclopaedia article concerning *Caligus mebachii* Marukawa, 1927, and to Prof. Kazuya Nagasawa for his comments on this species.

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