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AN UPDATED KEY TO THE GENERA OF CALIGIDAE (COPEPODA: SIPHONOSTOMATOIDA)

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ABSTRACT

Members of the copepod family Caligidae are some of the most common parasites of marine fishes. There are 503 recognized species divided into about 30 genera, with 75% of species belonging to the 2 largest genera, *Caligus* and *Lepeophtheirus*. More than 30 caligid species are known to cause serious pathologic changes as ectoparasites in marine teleost aquaculture. This study was undertaken to provide a key to the valid genera of Caligidae, to examine their morphology in new detail with confocal laser scanning microscopy, and to review uncertainties concerning boundaries between several genera. There have been several substantial changes to the taxonomy of Caligidae over the last decade: *Metacaligus, Sciaenophilus,* and *Sinocaligus* have been synonymized with *Caligus* and the validity of *Midias* has been questioned. Here, we formally propose that *Midias* and *Markevichus* are junior subjective synonyms of *Caligus*. In total, we recognize 27 valid genera; provide a key to these genera; present confocal laser scanning micrographs for 25 of the genera, many of which have never been imaged before; and highlight helpful diagnostic features used in the key. We also discuss some concerns regarding the generic boundaries separating *Belizia, Caritus, Parapetalus, Parechetus, Pseudechetus,* and *Synestius* from *Caligus* and those separating *Anuretes, Pseudanuretes,* and *Mappates* from *Lepeophtheirus*.

Sea lice, members of the family Caligidae Burmeister, 1835, are ectoparasitic copepods found on most groups of marine fishes. Adult caligids typically inhabit the body surface, buccal cavity, or gills of their hosts. These parasites are abundant in natural ecosystems and can cause substantial pathogenesis in aquaculture (Mustafa et al., 2000). Caligids are of major economic significance because several species have emerged as serious pests in marine finfish aquaculture in coastal waters around the world, including cold temperate and subtropical environments (Johnson et al., 2004). These copepods are perhaps most well-known as problematic pathogens in salmon farms, where they are responsible for over $1 billion in losses each year (Boxaspen et al., 2022). It is not uncommon for dozens or even hundreds of individuals to be found on a single fish, feeding on mucus, tissue, and blood and causing substantial pathologic changes (Johnson et al., 1996, 2004; Bravo, 2003; Treasurer and Bravo, 2011; Kodama et al., 2021; Rodger et al., 2022).

Caligids are characterized by the possession of a shield-shaped cephalothorax incorporating the first to third pedigerous somites (i.e., leg-bearing body segments). The cephalothorax typically forms a suction cup, enhanced by a marginal membrane, closed off anteriorly by the paired frontal plates, and delimited posteriorly by the broad, apron-like third swimming legs (Ohtsuka et al., 2021). This sucker is used for host attachment, and the suction force can be rapidly generated and released for attachment or free movement as needed (Ohtsuka et al., 2021). However, there are several interesting and rather extreme deviations from this body plan, which are imaged here with confocal laser scanning microscopy (CLSM) and revealed in new detail.

The most recent key to the genera of Caligidae is from the detailed monographic study of Dojiri and Ho (2013), who considered 31 genera to be valid, but many recent taxonomic changes have occurred since. Dojiri and Ho (2013) synonymized many genera and noted that boundaries between several others were poorly defined. Since then, there have been several revisions, and the genera *Metacaligus* Thomsen, 1949, *Sciaenophilus* van Beneden, 1852, and *Sinocaligus* Shen, 1957 have all been synonymized with *Caligus* Müller, 1785 (Özak et al., 2017, 2024; Boxshall and Barton, 2023). Although Dojiri and Ho (2013) treated *Midias* Wilson, 1911 as valid, we agree with Kabata (1979) and others in regarding *Midias* as a synonym of *Caligus*. We also formally recognize *Markevichus* Özdikmen, 2008 as a junior subjective synonym of *Caligus*. In total, we recognize 27 genera as valid, which collectively include 503 species. Over 75% of caligid species are members of the 2 largest genera, *Caligus* (276 species) and *Lepeophtheirus* von Nordmann, 1832 (124 species), followed by *Anuretes* Heller, 1865 with 21 species (Walter and Boxshall, 2024). The remaining 24 genera have fewer than 10 species each, and 10 genera are monotypic.

Here, we present a new key to genera of Caligidae supported by images generated with CLSM and macrophotography for nearly all valid genera. The goals of this study were to facilitate the identification of the 27 genera, to highlight the morphological diversity of Caligidae, and to discuss limitations in data supporting several taxa. Molecular phylogenetic analyses are needed to establish more stable and robust generic boundaries, but because appropriate specimens for sequencing are not available for most genera and species, a more formal systematic revision awaits the collection of suitable material for sequencing.

MATERIALS AND METHODS

Specimens of 25 of the 27 valid caligid genera were imaged; only *Arrama* Dojiri and Cressey, 1991 and *Dartevellia* Brian, 1939 were not examined. The following specimens were imaged with CLSM: *Abasia platyrostris* Pillai, 1963 (NHMUK 2017.173), *Alanlewisia fallolunulus* (Lewis, 1967) (NHMUK 2010.658), *Alebion gracilis* Wilson, 1905 (NHMUK 2010.974), *Anchicaligus nautili* Stebbing, 1900 (NHMUK 2010.979), *Anuretes heckelii* (Krøyer, 1863) (NHMUK 1979.592), *Belizia brevicauda* Cressey, 1990 (USNM 241670), *Caligodes laciniatus* (Krøyer, 1863) (NHMUK 2017.192), *Caligus diaphanus* von Nordmann, 1832 (NHMUK 1975.180), *Caritus serratus* Cressey, 1967 (USNM 120354), *Echetus typicus* Krøyer, 1864 (USNM 107877), *Euryphorus brachypterus* (Gerstaecker, 1853) (NHMUK 2014.637), *Gloiopotes huttoni* (Thomson, 1890) (from a "sailfish," locality unknown), *Hermilius longicornis* Bassett-Smith, 1898 (NHMUK 2017.334), *Kabataella indica* Prabha and Pillai, 1983 (USNM 268272), *Lepeophtheirus pectoralis* (Müller, 1776) (NHMUK 1975.482), *Mappates plataxus* Rangnekar, 1958 (NHMUK 2017.346), *Paralebion elongatus* Wilson, 1911 (NHMUK 1994.716), *Parapetalus occidentalis* Wilson, 1908 (NHMUK 1984.13), *Parechetus carangis* (Bassett-Smith, 1898) (NHMUK 1999.628), *Pseudanuretes papernai* Kabata and Deets, 1988 (USNM 231871), *Pseudechetus fimbriatus* Prabha and Pillai, 1979 (USNM 274345), *Pupulina flores* van Beneden (1892) (USNM 1087132), *Synestius caliginus* Steenstrup and Lütken, 1861 (NHMUK 1994.1212), and *Tuxophorus caligodes* Wilson, 1908 (NHMUK 1954.9.20.7).

For CLSM, specimens were stained overnight in a saturated solution of Congo Red in 100% ethanol, rinsed in changes of distilled water until no stain could be seen diffusing, and prepared as temporary mounts in a 50% solution of glycerin and distilled water on a glass slide under a coverslip. For thicker specimens, the coverslip was suspended above the specimen with pieces of paraffin or, for the largest specimens, with rubber washers glued to a slide to create a deep well. Specimens were examined with 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 2 channels: 570–630 nm artificially colored green and 630–715 nm artificially colored red. A series of image stacks was collected, and the final images were obtained by maximum projection of the overlaid channels using the same Leica software or ImageJ v2.14. For some specimens, multiple stacks or multiple fields of view were needed to produce high-resolution images of the entire specimen. Multiple stacks were combined using the concatenate tool in ImageJ or manually using Adobe Photoshop v25.0, and multiple fields of view were combined using the ImageJ pairwise stitching plugin (Preibisch et al., 2009) or with Adobe Photoshop.

RESULTS

Systematics

Caligidae Burmeister, 1835

Valid genera: Abasia Wilson, 1908, *Alanlewisia* Boxshall, 2008, *Alebion* Krøyer, 1863, *Anchicaligus* Stebbing, 1900, *Anuretes* Heller, 1865, *Arrama* Dojiri and Cressey, 1991, *Avitocaligus* Boxshall and Justine, 2005, *Belizia* Cressey, 1990, *Caligodes* Heller, 1865, *Caligus* Müller, 1785, *Caritus* Cressey, 1967, *Dartevellia* Brian, 1939, *Echetus* Krøyer, 1863, *Euryphorus* Milne Edwards, 1840, *Gloiopotes* Steenstrup and Lütken, 1861, *Hermilius* Heller, 1865, *Kabataella* Prabha and Pillai, 1983, *Lepeophtheirus* von Nordmann, 1832, *Mappates* Rangnekar, 1958, *Paralebion* Wilson, 1911, *Parapetalus* Steenstrup and Lütken, 1861, *Parechetus* Pillai, 1962, *Pseudanuretes* Yamaguti, 1936, *Pseudechetus* Prabha and Pillai, 1979, *Pupulina* van Beneden, 1892, *Synestius* Steenstrup and Lütken, 1861, and *Tuxophorus* Wilson, 1908.

Remarks

Midias **Wilson, 1911 is a junior subjective synonym of** ***Caligus*** **Müller, 1785**

Before the landmark monograph of Kabata (1979), the genus *Midias* was classified in the family Euryphoridae. However, Kabata (1979) noted that *Midias* could not be validly retained in the Euryphoridae because it lacks the diagnostic dorsal plates on the fourth pedigerous somite. He stated that "except for the shape of the abdomen and the rather prominent fifth legs, it could become a typical member of the genus *Caligus*" (Kabata, 1979, p. 202). Dojiri and Ho (2013) considered the appendages of *Midias* nearly identical to those of *Caligus* but upheld the validity of *Midias* within the Caligidae (now incorporating the genera previously placed in the Euryphoridae) based on 4 characteristics: (1) the bulbous expansion of the first abdominal somite of the female, (2) the setiferous conical projection representing leg 5 of the female, (3) 2 large claw-like outer spines on the first exopodal segment of leg 3, and (4) the spinulose posterolateral processes on the anal somite. Of these characters, only the presence of spinulose posterolateral processes on the anal somite is unique. Even in that case, similar processes are present in *Caligus formicoides* Redkar, Rangnekar and Murti, 1949, but they are unornamented. As detailed below, none of these characters is unique and we consider that they are likely autapomorphies.

Similar lateral expansions of the first abdominal somite of the female are found in several *Caligus* species, including *Caligus alepicolus* Boxshall, 2018, *C. formicoides, Caligus grandiabdominalis* Yamaguti, 1954, *Caligus kurochkini* Kazachenko, 1975, *Caligus parapetalopsis* Hameed and Pillai, 1973, and *Caligus seriolicolus* Boxshall, 2018. These species represent at least 3 different species groups within the genus: *bonito*-group (*C. grandiabdominalis*), *diaphanus*-group (*C. formicoides*), and *confusus*-group (*C. alepicolus, C. kurochkini, C. parapetalopsis,* and *C. seriolicolus*) (Boxshall, 2018), and we infer that such lateral expansions of the abdomen have arisen independently on several occasions within the Caligidae.

A projecting conical fifth leg is also found in several other species of *Caligus*, including: *Caligus cordiventris* Shiino, 1952, *Caligus parvilatus* Kim, 1998, *Caligus praecinctorius* Hayes, Justine and Boxshall, 2012, *Caligus sclerotinosus* Roubal, Armitage and Rohde, 1983, and *Caligus tylosuri* (Rangnekar, 1956). The possession of large conical fifth legs was once used to distinguish members of the genus *Dentigryps* Wilson, 1913 from *Lepeophtheirus,* but as noted by Dojiri and Ho (2013, p. 378), “the taxonomic value of the length of any appendage is highly questionable” and the generic boundary between *Dentigryps* and *Lepeophtheirus* was somewhat arbitrary. Dojiri and Ho (2013) agreed with Hewitt (1971) that *Dentigryps* should be treated as a junior synonym of *Lepeophtheirus*. We consider using the fifth leg to distinguish between *Midias* and *Caligus* to be equally suspect.

The character “presence of two large claw-like outer spines on the first exopodal segment of leg 3” (Dojiri and Ho, 2013, p. 275) requires clarification. Examination of *Midias lobodes* specimens in the collections of the NHM (NHMUK 2010.623-628) reveals that only the larger distal spine is a true armature element articulated at its base. The smaller proximal structure is a spinous outgrowth of the segment itself. Such spinous projections, often ornamented with strips of membrane, are present at the outer distal corner of the first exopodal segment of leg 3 in several *Caligus* species, including *Caligus mortis* Kensley, 1970, *Caligus pageti* Russell, 1925, *C. parvilatus,* and *Caligus saucius* Dojiri, 1989, although they do not curve across the surface of the segment.

In summary, the character states identified by Dojiri and Ho (2013) as diagnostic for *Midias* (when found in combination) are scattered through the morphospace occupied by *Caligus*. Given the variability exhibited within *Caligus,* the largest genus in the entire Copepoda, we consider that none of these characters is robust as a generic-level discriminant. We therefore follow Kabata (1979) and Boxshall and Halsey (2004) in treating *Midias* as a junior subjective synonym of *Caligus*. Furthermore, we consider that its type species, *Midias lobodes,* is probably a member of the *Caligus confusus*-group within *Caligus* because it shares most of the character states diagnostic for the species group, namely, leg 4 is 3-segmented and armed with I, I, III spines; leg 3 bears a rosette and rib on the apron, and the true outer spine on the exopod segment 1 is robust and strongly recurved; and the maxillule bears a small accessory tine. In addition, the distal antennulary segment is quite long, the plumose posterior setae on leg 1 are short, and the outer margin of leg 2 endopod segment 1 is strongly convex, which we note here are all additional states commonly exhibited by members of the *confusus*-group.

Markevichus **Özdikmen, 2008 is a junior subjective synonym of** ***Caligus***

Markevichus is the replacement name proposed for the genus *Caligopsis* Markevitsch, 1940, established to accommodate a single new species, *Caligopsis ponticus* Markevitsch, 1940. As noted by Dojiri and Ho (2013), Markevitsch (1940) distinguished his new genus primarily on the absence of leg 4, and the genus currently remains monotypic (Walter and Boxshall, 2024). Kabata (1979) suggested that *Caligus apodus* (Brian, 1924) (as *Pseudocaligus apodus*) belongs to *Markevichus* (as *Caligopsis*) because this genus lacked leg 4. However, there is still uncertainty regarding the state of leg 4 in this species. A redescription of *C. apodus* (as *P. apodus*) from Tunisia included the presence of vestiges of leg 4 in both sexes (Ben-Hassine, 1983). Subsequently, Özak et al. (2013) re-examined 2 syntype females of *P. apodus* in the collections of the Museum National d’Histoire Naturelle in Paris and found that 1 female lacked any trace of leg 4 while the other carried a minute rod-like vestige, possibly representing leg 4, on 1 side of the body. Özak et al. (2013) also reported that newly collected material of both sexes of *C. apodus* from Turkish waters carried an indistinctly segmented leg 4 in the male, armed with a total of 4 setae, but lacked any obvious trace of leg 4 in the female. It seems possible that the state of the vestigial leg 4 is variable in *C. apodus,* especially in the female. The genus *Pseudocaligus* has been recognized as a junior subjective synonym of *Caligus* based on both morphological (Dojiri and Ho, 2013) and molecular (Freeman et al., 2013) evidence.

Dojiri and Ho (2013, p. 374) raised the key question concerning the validity of this genus, namely, “Even if leg 4 is absent, can *Caligopsis* be considered valid based solely on the absence of leg 4, a characteristic of questionable value?” They then noted that species formerly placed in *Pseudocaligus* form a gradation of progressive reduction of leg 4. This series culminates in the loss of leg 4, as described for *Caligopsis ponticus* by Markevitsch (1940).

Although Dojiri and Ho (2013) clearly articulated the argument against continuing to treat *Markevichus* as valid and they dealt with it in their chapter “Miscellaneous Genera” (which comprised the other genera they considered invalid), they did not formally place *Markevichus* in synonymy with *Caligus*. Here we propose to transfer *Caligopsis ponticus* Markevitsch, 1940 to *Caligus* as *Caligus ponticus* (Markevitsch, 1940) n. comb. and thus treat *Markevichus* as a junior subjective synonym of *Caligus*. We also consider *C. ponticus* (Markevitsch, 1940) n. comb. to be a nomen dubium because it is inadequately described and the types have been lost (Titar, pers. comm. cited by Dojiri and Ho, 2013).

Metacaligus **Thomsen, 1949 is a junior subjective synonym of** ***Caligus***

Metacaligus was originally established by Thomsen (1949) as a subgenus of *Caligus* to accommodate a new species, *Caligus* (*Metacaligus*) *uruguayensis* Thomsen, 1949. It was raised to generic status by Ho and Bashirullah (1977). Until the recent paper by Özak et al. (2024), 5 species were treated as valid (Walter and Boxshall, 2024), namely, *Metacaligus trichiuri* (Krøyer, 1863) (as *M. uruguayensis* (Thomsen, 1949)), *Metacaligus rufus* (Wilson, 1908), *Metacaligus unguidentatus* (Rangnekar and Murti, 1950) (as *Metacaligus hilsae* (Shen, 1957)), *Metacaligus latus* Ho and Lin, 2002, and *Metacaligus yucatanensis* Suárez-

Morales, Kim and Escamilla, 2012. Dojiri and Ho (2013) treated *Metacaligus* as a valid genus and highlighted 4 diagnostic character states, the combination of which could be used to separate this genus from *Caligus*. These states were (1) the absence of a sternal furca; (2) the lack of accessory processes on spines 2 and 3 on the distal margin of the second exopodal segment of leg 1; (3) the 3 plumose setae on the posterior margin of the same segment are short (i.e., shorter than the segment); and (4) the presence of only 1 outer spine on the third exopodal segment of leg 2. Dojiri and Ho (2013) emphasized that all these character states can be found individually in particular species of *Caligus,* but the full combination is found in only species of *Metacaligus*.

Özak et al. (2024) considered the list of characters provided by Dojiri and Ho (2013) to support the validity of *Metacaligus* not to be robust. The sternal furca has been lost or extremely reduced in at least 10 species of *Caligus,* including members of several different species groups: for example, *Caligus enormis* (*Caligus productus*-group), *Caligus yucatanensis* (*Caligus undulatus*-group), and *Caligus afurcatus*. The reduced length of the 3 plumose setae on the posterior margin of the distal exopodal segment of leg 1 is found in about 20 other species of *Caligus*; it is typical of members of the *C. confusus*-group and is found in some other species such as *Caligus paulini* Nuñes-Ruivo and Fourmanoir, 1956, a member of the *Caligus bonito*-group (Ismail et al., 2024). The absence of accessory processes from spines 2 and 3 on the distal exopodal segment of leg 1 is found in over 40 species of *Caligus,* is typical of the *C. diaphanus*-group, and is found in some members of other species groups. The loss of the proximal outer spine of the third exopodal segment of leg 2 is rare in *Caligus*; however, it is lacking in *Caligus chinglonglini* Ohtsuka and Boxshall, 2019 and is reduced in size in members of the *Caligus pseudorhombi*-group and *C. undulatus*-group (Ohtsuka and Boxshall, 2019; Ohtsuka et al., 2020; Özak et al., 2024). In addition, Özak et al. (2024) demonstrated numerous similarities between *M. yucatanensis* and their 2 new species *Caligus izmiriensis* Özak, Kurt, Kamanli, Akbulut, Yanar and Boxshall, 2024, and *Caligus sarosi* Özak, Kurt, Kamanli, Akbulut, Yanar and Boxshall, 2024. These similarities include the loss of the outer margin spine on the second exopodal segment of leg 2, which is shared by *C. sarosi* and *M. yucatanensis*. In light of the numerous shared character states, Özak et al. (2024) transferred *Metacaligus yucatanensis* to *Caligus* as *C. yucatanensis* and placed it in the *C. undulatus*-group established by Ohtsuka et al. (2020). Özak et al. (2024) also proposed to treat *Metacaligus* as a synonym of *Caligus* and recognized the 4 remaining species previously assigned to *Metacaligus* as a new species group, the *Caligus trichiuri*-group. We agree with that proposal.

Caligodes megacephalus **Wilson, 1905 is a junior subjective synonym of** ***Caligodes laciniatus*** **(Krøyer, 1863)**

Dojiri and Ho (2013) noted that these 2 species are very similar, and the main feature distinguishing them is the presence of a posteromedian process on the genital complex in *C. megacephalus*. We examined the holotype of *C. megacephalus* (USNM 6103) and confirmed that, as suggested by Dojiri and Ho (2013), this process was a misinterpretation by Wilson; the suspected process is simply a series of folds in the cuticle on the dorsal surface of the genital complex that intersect posteriorly (as drawn by Pillai, 1961, fig. 15A) rather than an extension of the body (as drawn by Wilson, 1905, fig. 187). The maxillipeds were missing on the type specimen, but we agree with Dojiri and Ho (2013) that the maxillipeds are similar in these 2 species, especially given the more detailed redescription by Pillai (1961). All other appendages were the same between these 2 species, including the unusual setation patterns on legs 1, 2, and 4. We therefore propose to treat *C. megacephalus* as a junior subjective synonym of *C. laciniatus*.

Key to Caligidae genera

1a. Dorsal shield of cephalothorax typical, dorso-ventrally flattened 2
(e.g., Fig 1B-J, L, O-X)
1b. Lateral margins of cephalothorax folded ventrally 22
(e.g., Fig 2A-G)
2a. Leg 1 endopod 2-segmented; Leg 3 endopod 3-segmented 18
(Fig. 3A, B)
2b. Leg 1 endopod unsegmented with reduced or vestigial setal elements; Leg 3 endopod with <3 segments 3
(Fig. 3C, D)
3a. Leg 1 endopod armed with 2 setae + setal vestige; Characteristic rounded, lunule-like projections extending anteriorly from frontal plates near base of antennules .... *Alanlewisia*
(Fig. 1B, 4D)
3b. Leg 1 endopod with vestigial setae only or unarmed; With true lunules or lacking lunules 4
4a. Lunules present 5
(Fig. 4A-C)
4b. Lunules absent 13
5a. Genital complex with long posterior processes (extending almost to, or beyond, caudal rami); Abdomen without plate-like lateral expansions 6
(Fig. 5B-E)
5b. Genital complex with plate-like lateral expansions extending posteriorly (at least one-third the length of the genital complex); Abdomen with plate-like lateral expansions 7
(Fig. 5G, F)
5c. Genital complex without long posterior processes; Abdomen without plate-like lateral expansions 8
6a. Total of 6 processes present (4 on genital complex and 2 on abdomen) .... *Pseudechetus*
(Fig. 5C, D)
6b. Total of 4 processes present (all on genital complex) . ... *Synestius*
(Fig. 5E)
6c. Total of 2 processes present (both on genital complex) .... *Caligodes*
(Fig. 5B)
7a. With elongate "neck" present between cephalothorax and genital complex ("neck" longer than cephalothorax) .... *Parechetus*
(Fig. 1S)
7b. Without elongate "neck" .... *Parapetalus*
(Fig. 1R)

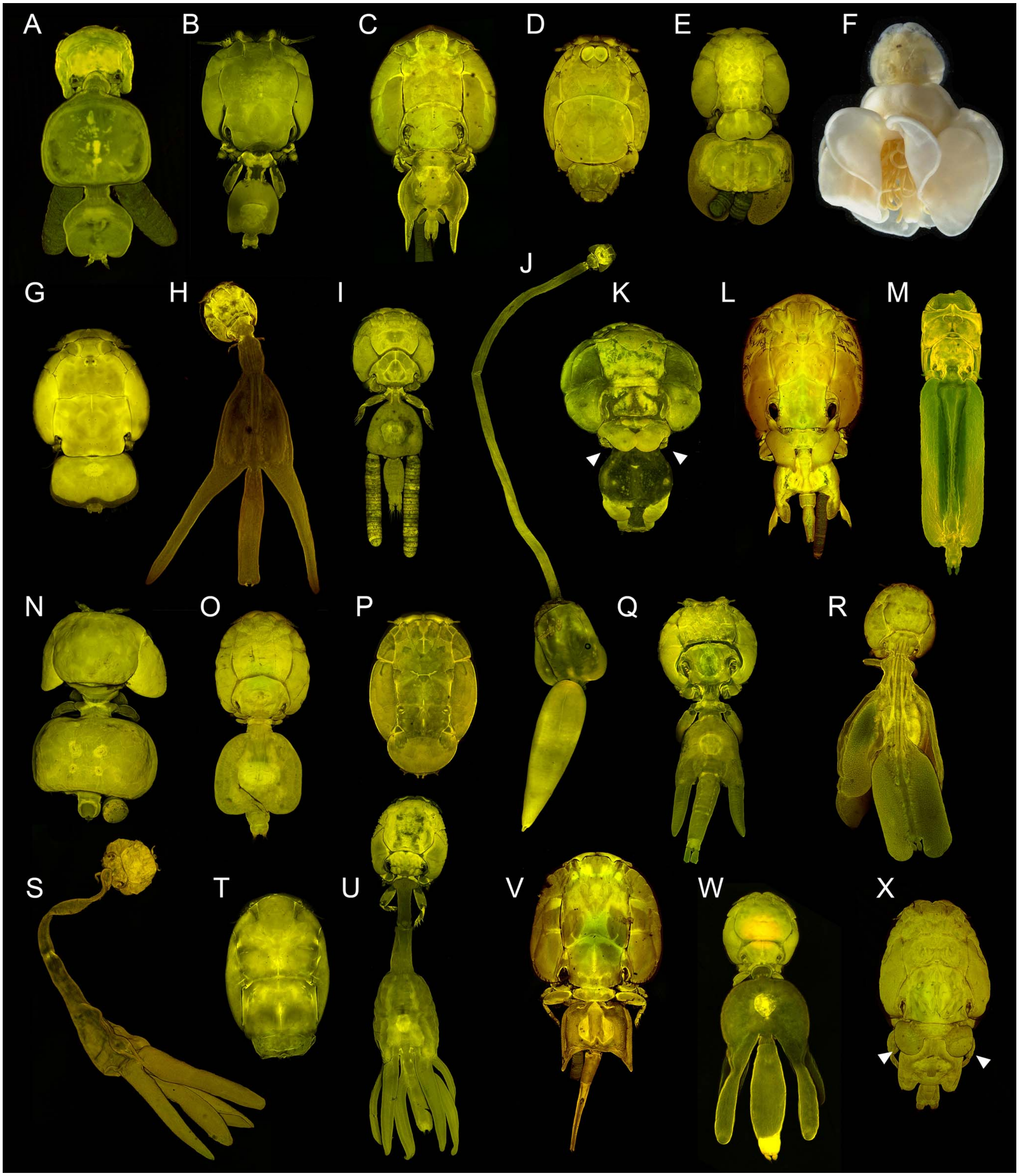

Figure 1. Caligid genera, dorsal view, confocal laser scanning microscopy (except **F**). (**A**) *Abasia platyrostris*. (**B**) *Alanlewisia fallolunulus*. (**C**) *Alebion gracilis*. (**D**) *Anchicaligus nautili*. (**E**) *Anuretes heckelii*. (**F**) *Avitocaligus assurgericola* (macrophotography, holotype MNHN Cp-2185). (**G**) *Belizia brevicauda*. (**H**) *Caligodes laciniatus*. (**I**) *Caligus diaphanus*. (**J**) *Echetus typicus*. (**K**) *Euryphorus brachypterus*; arrowheads indicate dorsal plates on fourth pediger. (**L**) *Gloiopotes huttoni*. (**M**) *Hermilius longicornis*. (**N**) *Kabataella indica*. (**O**) *Lepeophtheirus pectoralis*. (**P**) *Mappates plataxus*. (**Q**) *Paralebion elongatus*. (**R**) *Parapetalus occidentalis*. (**S**) *Parechetus carangis*. (**T**) *Pseudanuretes papernai*. (**U**) *Pseudechetus fimbriatus*. (**V**) *Pupulina flores*. (**W**) *Synestius caliginus*. (**X**) *Tuxophorus caligodes*; arrowheads indicate dorsal plates on fourth pediger. Color version available online.

8a. Fourth pedigerous somite with dorsal aliform plates. .... *Tuxophorus* (Fig. 1X)
8b. Fourth pedigerous somite without dorsal plates 9
9a. Extremely elongate neck present (derived from fourth pedigerous somite and anterior part of genital complex) .... *Echetus* (Fig. 1J)
9b. Lacking extremely elongate neck 10
10a. Thoracic zone of cephalothorax extending posteriorly, completely concealing fourth pedigerous somite .... *Belizia* (Fig. 6F, G)
10b. Thoracic zone of cephalothorax not concealing fourth pedigerous somite 11
11a. Leg 3 endopod lacking setae .... *Caritus*
11b. Leg 3 endopod with 6 setae (or rarely 2–5 setae).......... 12
12a. Nauplius eye with enlarged conical lenses.... *Anchicaligus* (Fig. 1D)
12b. Nauplius eye with small lenses present, or (rarely), if lenses enlarged, lenses extending laterally .... *Caligus* (Fig. 1I)
13a. Abdomen expanded into large paired, flattened processes extending posteriorly, incorporating caudal rami .... *Dartevellia*
13b. Abdomen not expanded into flattened processes extending posteriorly; caudal rami (typically) distinct . 14
14a. Genital complex bearing long digitiform processes extending posteriorly .... *Paralebion* (Fig. 5A)
14b. Genital complex without digitiform posterior processes 15
15a. Dorsal cephalothoracic shield with main transverse supporting rib located posteriorly (almost at tips of lateral thoracic zones of cephalic shield); Posterior process of maxillule forming large rounded lobe .... *Mappates* (Fig. 6D)
15b. Dorsal cephalothoracic shield supported by H-shaped ribs with main transverse rib near mid-level of lateral thoracic zones of cephalic shield; Posterior process of maxillule tapering conical or absent........... 16
16a. First endopodal segment of leg 3 with inner plumose seta .... *Lepeophtheirus* (Fig. 1O, 6C)
16b. First endopodal segment of leg 3 lacking inner plumose seta 17
17a. Antenna of female with accessory claw...... *Pseudanuretes* (Fig. 6B)
17b. Antenna of female without accessory claw .... *Anuretes* (Fig. 6A)
18a. Leg 4 biramous 19
18b. Leg 4 uniramous (lacking endopod) 20
19a. Fourth pedigerous somite lacking flattened dorsal plates; Genital complex with 2 pairs of large leaf-like plates overlying abdomen; Pair of similar, large leaf-like plates on abdomen .... *Avitocaligus* (Fig. 1F)
19b. Fourth pedigerous somite with large, flattened dorsal plates; Genital complex with small lobes, lacking large leaf-like plates; Abdomen without plates .... *Euryphorus* (Fig. 1K)
20a. Leg 4 reduced, 1-segmented; Some outer spines on exopods of legs modified, fan-like....................... *Alebion* (Fig. 1C, 3B)
20b. Leg 4 exopod with 3 segments; No outer spines on exopods of legs fan-like 21
21a. Fourth pedigerous somite with paired dorsal plates; Leg 1 distal exopod segment with spines 2 and 3 at tip of segment bifid and each with medial accessory process; Leg 3 endopod segment 2 enlarged with inflated outer margin .... *Gloiopotes* (Fig. 1L)
21b. Fourth pedigerous somite without dorsal plates; Leg 1 distal exopod segment with spines 2 and 3 at tip of segment simple; Leg 3 endopod segment 2 unmodified, lacking plate-like extension .... *Pupulina* (Fig. 1V)
22a. Leg 3 reduced to minute setiferous lobe, lacking intercoxal plate .... *Arrama*
22b. Leg 3 forming apron with (reduced) intercoxal plate present 23
23a. Antenna terminal segment slender with large accessory claw; Leg 1 distal exopod segment with extremely long spines; Leg 1 distal exopod segment with 3 well-developed plumose setae on posterior margin .... *Hermilius* (Fig. 1M, 2A-C)
23b. Antenna terminal segment lacking accessory claw; Leg 1 distal exopod segment bearing spines shorter than length of segment; Leg 1 distal exopod segment with reduced or vestigial setae on posterior margin 24
24a. Leg 4 with 4 segments .... *Kabataella* (Fig. 2F-H)
24b. Leg 4 reduced (3 segments, 2 segment, vestigial, or absent) .... *Abasia* (Fig. 2D, E)

DISCUSSION

Here, we review questionable evidence supporting the validity of some caligid genera and speculate on potential evolutionary relationships based on new morphological interpretations. Boundaries between many genera are poorly defined and have often been further eroded by the discovery of species exhibiting intermediate combinations of character states. The few morphological features in caligids that have been examined in a molecular phylogenetic context have often been found to be homoplasious. For example, the segmentation of leg 4 was historically used to distinguish the genera *Markevichus, Pseudocaligus,* and *Pseudolepeophtheirus,* which possess a highly reduced leg 4 or lack leg 4 altogether. Although variability in the segmentation of leg 4 remains one of the most useful features for identifying species, molecular phylogenetic studies have revealed that leg 4 has been reduced to a single segment at least 3 times independently

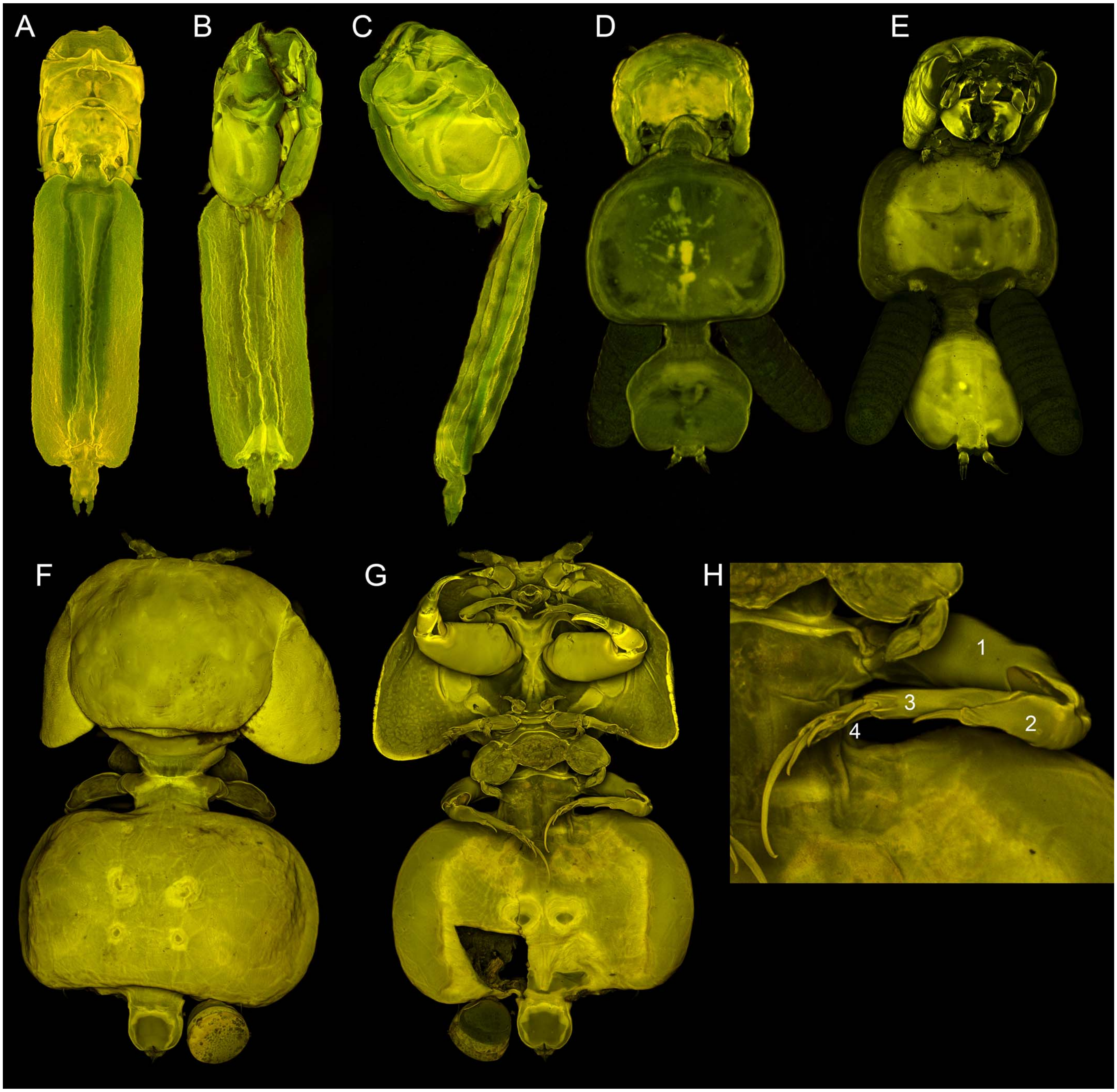

Figure 2. Confocal laser scanning microscopy of caligid genera with ventrally folded cephalothorax (*Arrama* not shown). *Hermilius longicornis*: (**A**) dorsal, (**B**) ventral, (**C**) lateral. *Abasia platyrostris*: (**D**) dorsal, (**E**) ventral. *Kabataella indica*: (**F**) dorsal, (**G**) ventral, (**H**) leg 4 ventral with segments numbered. Color version available online.

(Freeman et al., 2013), providing support for existing synonymies of *Markevichus* and *Pseudocaligus* with *Caligus* and *Pseudolepeophtheirus* with *Lepeophtheirus*.

The presence or absence of the sternal furca is also patchy throughout the Caligidae, and we consider it very likely that this structure also exhibits a high degree of homoplasy. This situation is analogous to that in the genus *Dissonus* Wilson, 1906 (family Dissonidae), the species of which may possess a typical sternal furca or a modified sternal stylet or may lack the sternal furca altogether (Boxshall et al., 2008). Given that what little we know about morphological evolution in caligids suggests there are many instances of convergent evolution, in the interest of taxonomic stability we have avoided making large taxonomic changes until we have evidence from molecular phylogenetic analysis to support or refute clades. We caution that taxonomic changes in this diverse and globally important group should not be made without robust support.

Perhaps the most problematic set of generic distinctions relates to *Anuretes, Pseudanuretes, Mappates,* and *Lepeophtheirus*. These

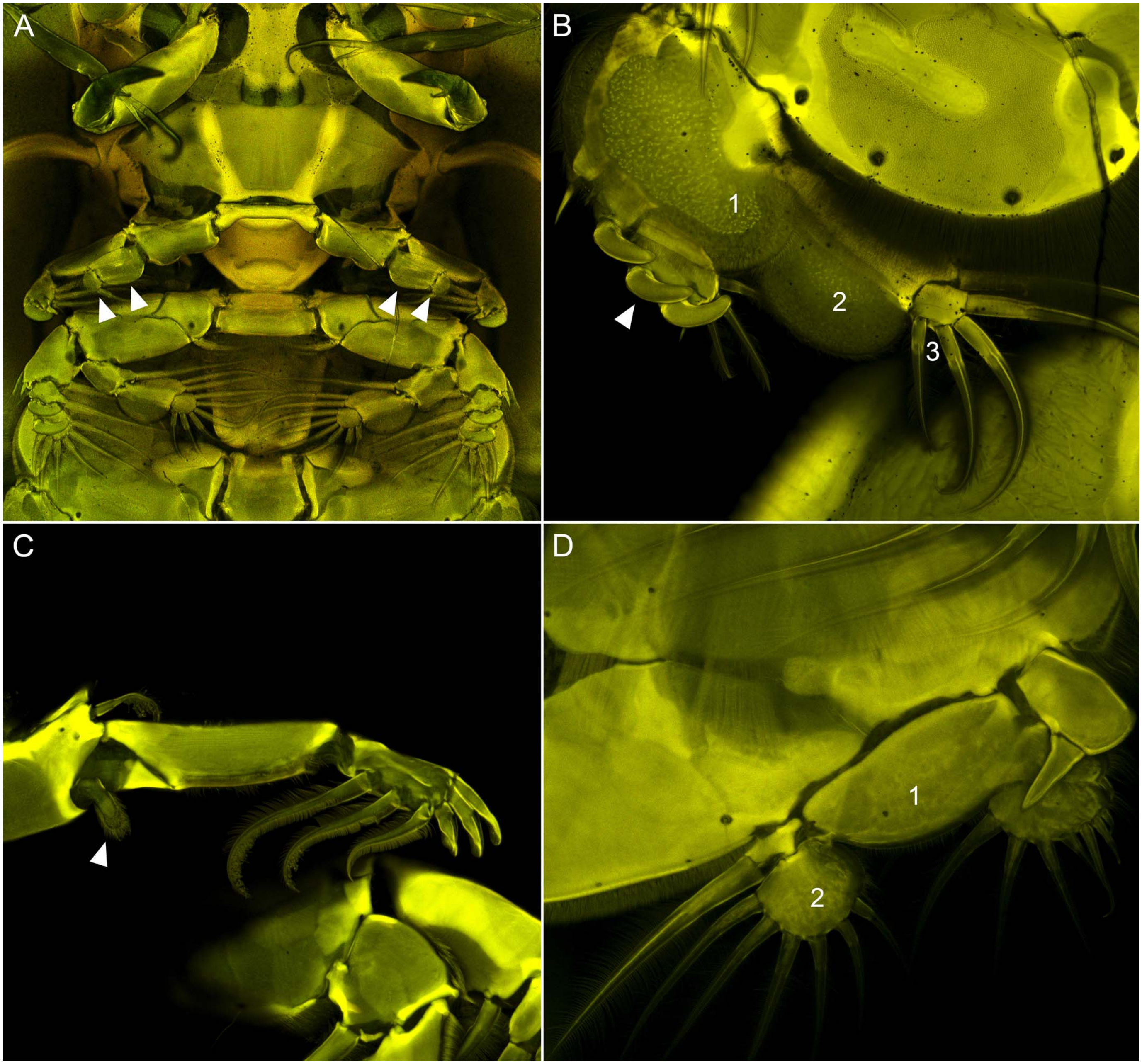

Figure 3. Confocal laser scanning microscopy for comparison of legs 1 and 3. (**A**) Leg 1 with 2-segmented endopod; *Alebion gracilis*, arrowheads indicate segments. (**B**) Leg 3 with 3-segmented endopod in *A. gracilis* with segments numbered, arrowhead indicates 1 of many modified spines characteristic of *Alebion*. (**C**) Leg 1 with unsegmented endopod in *Caligus hirsutus*, endopod indicated with arrowhead. (**D**) Leg 3 with 2-segmented endopod in *Caligus epidemicus* with segments numbered. Color version available online.

genera are traditionally distinguished from each other primarily by the extent of the elongation of the free margin of the thoracic zone of the cephalothorax in the female; however, there is significant overlap in this feature between the genera (e.g., Fig. 6A–D). Dojiri and Ho (2013) included a detailed discussion of this history and evidence, or lack thereof, supporting their separation. These genera already have a complex taxonomic history given that *Anuretes* has already been synonymized with *Lepeophtheirus* and then resurrected (Ho and Dojiri, 1977; Dojiri and Ho, 2013) and that 3 of the 9 currently accepted species of *Pseudanuretes* (Walter and Boxshall, 2024) were considered as questionable by Dojiri and Ho (2013) because their inclusion would require broadening of the generic boundaries. Indeed, it is challenging to key out these genera because virtually every feature used to distinguish *Anuretes* is also found in some species of *Lepeophtheirus* or *Pseudanuretes*. Because there are no molecular data for any species of *Anuretes, Pseudanuretes,* or *Mappates,* we have elected to retain these 3 genera until a molecular phylogenetic analysis can better address the boundaries separating them.

Ten genera appear closely related to *Caligus* based on morphology: *Anchicaligus, Belizia, Caligodes, Caritus, Echetus, Parapetalus, Parechetus, Pseudechetus, Synestius,* and *Tuxophorus*. Despite the

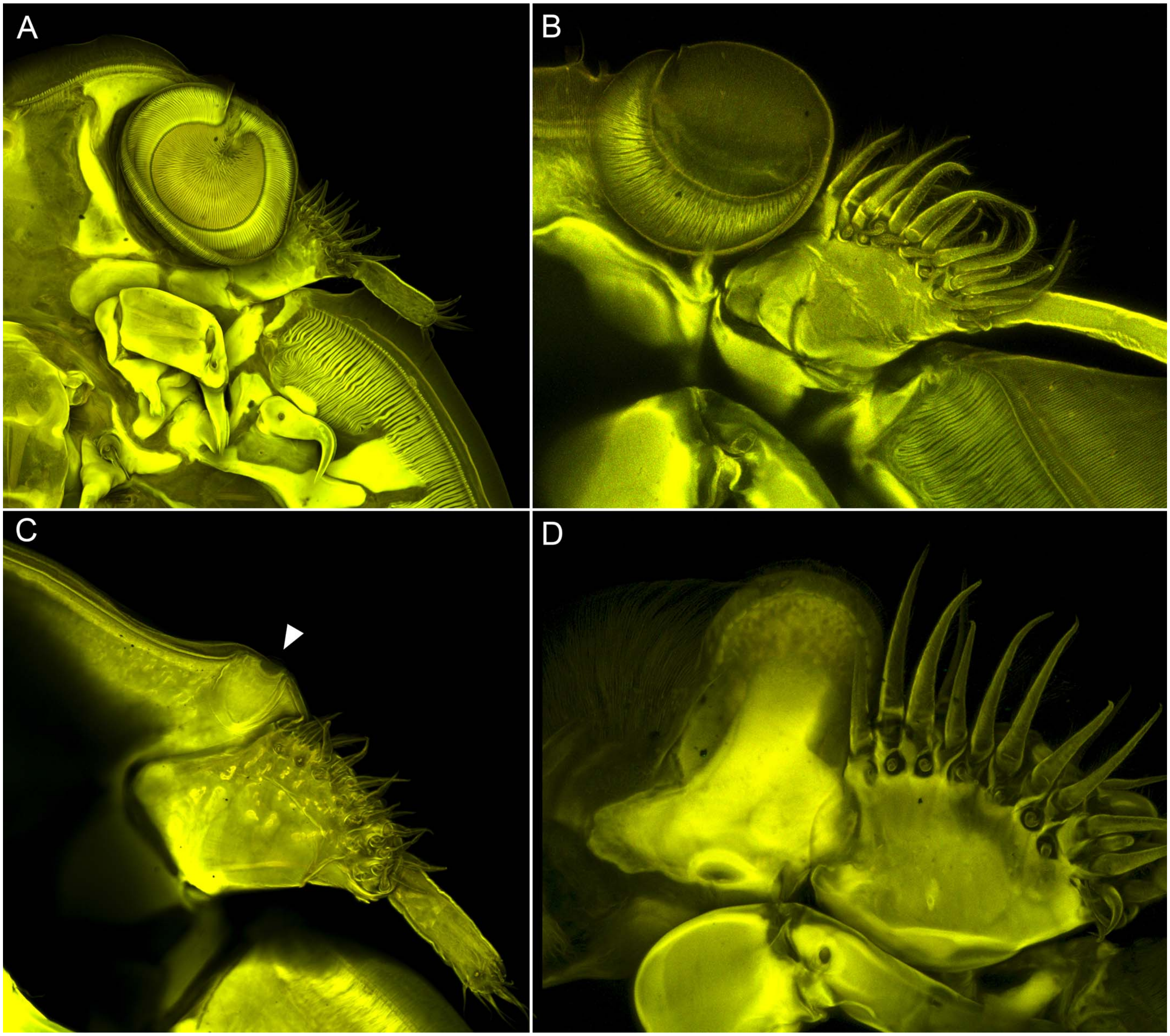

Figure 4. Confocal laser scanning microscopy of lunules and lunule-like structures in the Caligidae. (**A**) *Caligus schlegeli* exhibits relatively large lunules. (**B**) *Caligus confusus* exhibits typical lunules. (**C**) *Caligus furcisetifer* has the smallest lunules in *Caligus*. (**D**) *Alanlewisia fallolunulus* female possesses lunule-like structures that are not true lunules. Color version available online.

occasional dramatic elongations or lateral extensions of body somites (e.g., "necks," waists, and foliaceous processes on the abdomen or genital complex), the appendage structure across these genera is remarkably conserved. They share the same segmentation on all appendages except for leg 4 (there are also rare fusions of the terminal 2 exopodal segments of leg 3 in a few species of *Caligus*) and share the same unique evolutionary novelty—the paired lunules on the frontal plate of the dorsal cephalothoracic shield (Kaji et al., 2012). Essentially all these genera are erected based on a difference in body somites relative to *Caligus*. The following 6 genera are monotypic and based on only autapomorphies relative to *Caligus*: *Anchicaligus, Belizia, Echetus, Parechetus, Pseudechetus,* and *Synestius*. The robustness of all 10 of these genera awaits to be tested in a molecular phylogenetic context. Regardless of their validity, these taxa are very interesting from an evolutionary perspective, and resolution of their phylogenetic relationships will give insights into the evolution of some remarkable body structures (e.g., "necks," foliaceous processes, and enlarged lenses in the nauplius eye), attachment methods and sites (e.g., specialization for attachment to the operculum or to the wall of the buccal cavity by *Echetus, Parapetalus, Parechetus,* and *Pseudechetus,* with a mesoparasitic style in *Echetus*), and host associations (e.g., the colonization of *Nautilus* Linnaeus, 1758 by *Anchicaligus*). We suspect that the divergent morphology of at least some of these taxa is not the result of a unique phylogenetic history but that they are terminal branches of larger clades within

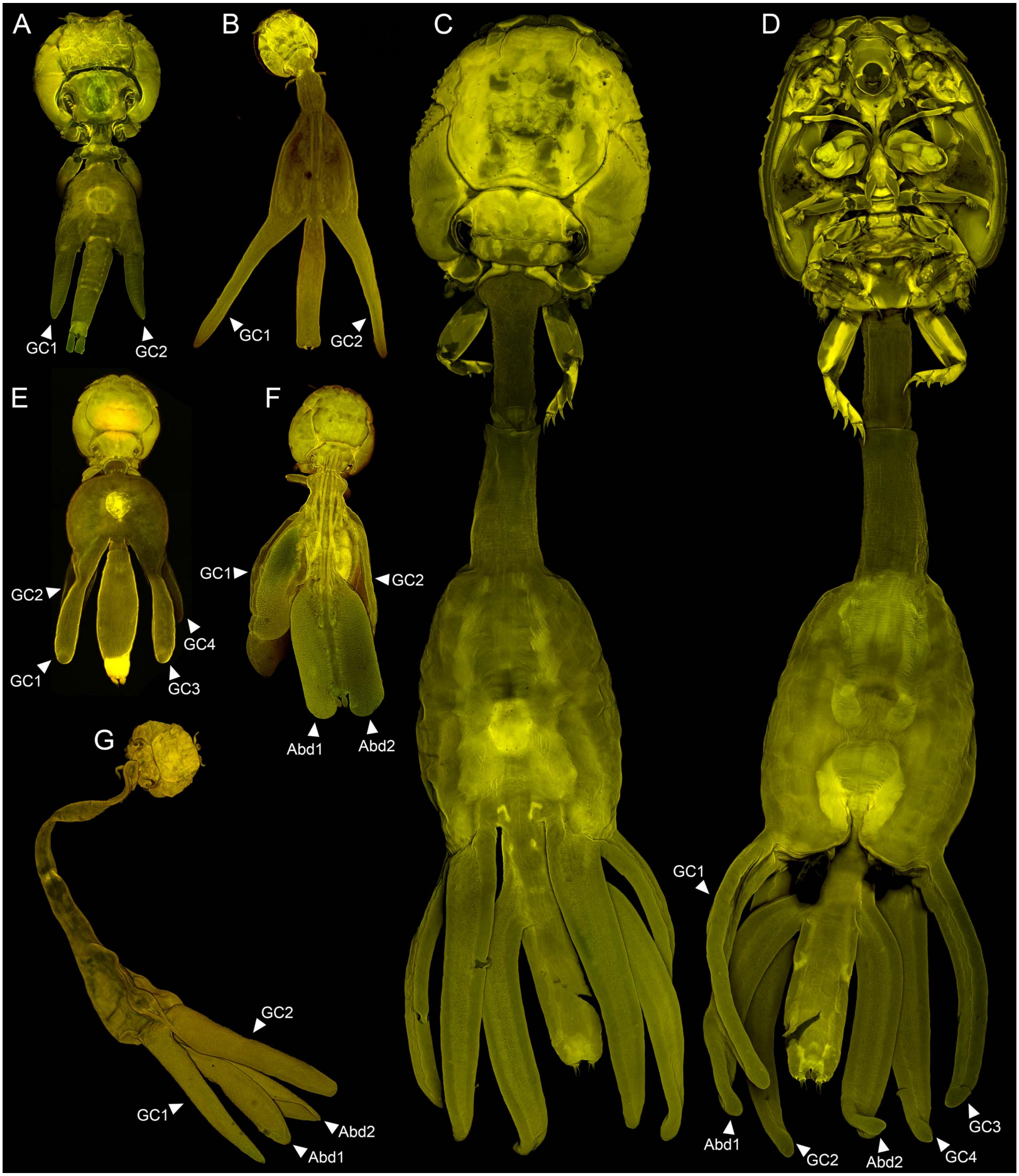

Figure 5. Confocal laser scanning microscopy of posterior processes on caligid genera. (**A**) *Paralebion elongatus*. (**B**) *Caligodes laciniatus*. (**C**) *Pseudechetus fimbriatus*. (**D**) *Pseudechetus fimbriatus* ventral. (**E**) *Synestius caliginus*. (**F**) *Parapetalus occidentalis*. (**G**) *Parechetus carangis*. Abbreviations: GC, processes on genital complex; Abd, processes on abdomen. Color version available online.

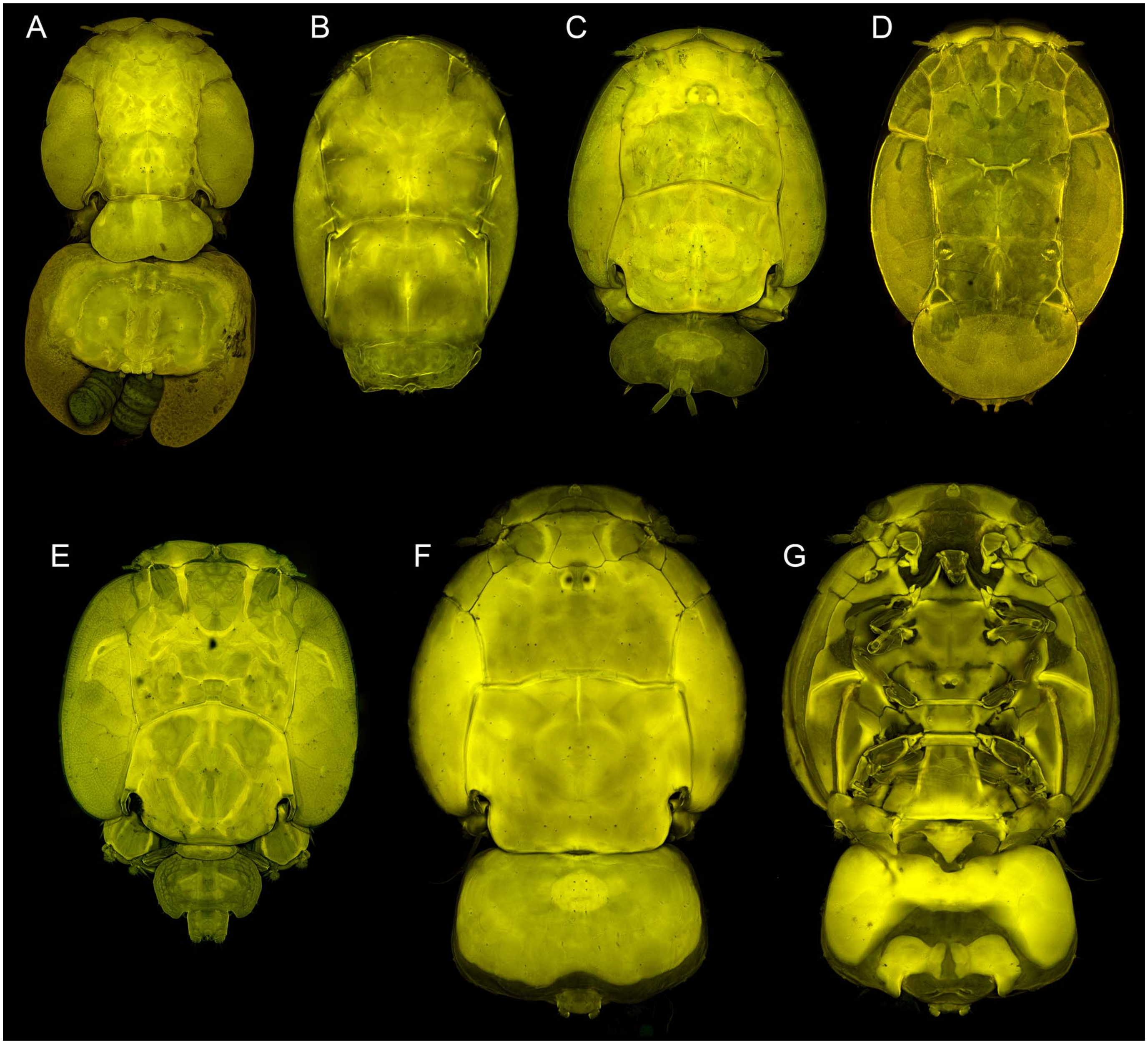

Figure 6. Confocal laser scanning microscopy of caligid genera with dorsal expansion of cephalothoracic shield partially covering pediger 4. (**A**) *Anuretes heckelii*. (**B**) *Pseudanuretes papernai*. (**C**) *Lepeophtheirus atypicus*. (**D**) *Mappates plataxus*. (**E**) *Caligus epidemicus*. (**F**) *Belizia brevicauda*. (**G**) *Belizia brevicauda,* ventral view. Color version available online.

Caligus, and their divergent morphology may be linked to changes in hosts and/or attachment sites.

The distinction between *Belizia* and *Caligus* is similar to that separating *Anuretes, Pseudanuretes,* and *Mappates* from *Lepeophtheirus* in that *Belizia* is distinguished primarily by the extension of the posterior margin of the thoracic zone of the cephalothorax so that it overlaps and conceals the fourth pedigerous somite in dorsal view (Fig. 6F). Cressey (1990) and Dojiri and Ho (2013) further distinguished *Belizia* based on the presence of only 4 setae on the caudal ramus, the sternal furca being reduced to 2 sclerotized knobs (Fig. 6G), the presence of 4 setae on the terminal endopodal segment of leg 3, and the velum not distinctly separated from the first endopodal segment of leg 3. However, we do not find these derived differences particularly robust. The sternal furca is reduced or absent in at least 10 species of *Caligus.* Although most species of *Caligus* have 6 setae on the terminal endopodal segment of leg 3, several species have 5, *Caligus longipes* (Moon and Kim, 2012) and *C. laciniatus* have 4, and *Caligus uniartus* (Ho, Kim, Cruz-Lacierda and Nagasawa, 2004) has 3 (Ho et al., 2004; Moon and Kim, 2012). The velum of leg 3 is not much different from that of most species of *Caligus* except that it is a bit smaller; this is not so surprising given that *Belizia,* at 1.6 mm body length, is 1 of the smallest caligids and has a small leg 3. We suspect molecular phylogenetic analyses will show that

Belizia is a morphologically unusual species of *Caligus,* but we retain it as a valid genus at present.

Caritus also closely resembles *Caligus*. *Caritus serratus,* the type species, was redescribed from type material by Dojiri and Ho (2013) and was distinguished from *Caligus* by the absence of a posterior process on the proximal antennal segment, the absence of the postantennal process, the absence of the sternal furca, the possession of a mandible with an elongate terminal section, the possession of modified exopodal spines on leg 2, the absence of setae on the terminal endopodal segment of leg 3, and the relatively large lobe-like leg 5. This latter character is not particularly robust because several species of *Caligus* and *Lepeophtheirus* have an enlarged lobe-like leg 5, as discussed in detail in the remarks on *Midias,* above. Furthermore, numerous species of genera such as *Abasia* and *Caligus* lack a posterior process on the proximal antennal segment, a postantennal process, or sternal furca and occasionally lack 2 of these 3 features. In fact, the antennal posterior process is very reduced in *Echetus typicus,* and this species also lacks a postantennal process and sternal furca. Although no species of *Caligus* lacks all setae on the leg 3 terminal endopodal segment, several species have fewer than 6, and *C. uniartus* has only 3. *Caritus tolii* Rangnekar, 1984 is relevant to this discussion. Although poorly described, it appears to have the typical complement of 6 setae on the terminal endopodal segment of leg 3, and it appears to lack the large lobe-like leg 5 of the type species (Rangnekar, 1984), further eroding the distinction between *Caritus* and *Caligus*. If *C. tolii* truly lacks the posterior process on the proximal segment of the antenna and lacks the postantennal process, the sternal furca, and the lobe-like leg 5, that would leave the genus distinguished by only modified spines on the exopodal segments of leg 2. We consider that *Caritus tolii* should be placed in *Caligus,* as proposed by Morales-Serna et al. (2024). Indeed, based on these morphological interpretations, we infer that the 2 species of *Caritus* are not sister taxa and that both are nested within *Caligus,* but this hypothesis requires testing with molecular data.

Interestingly, *Midias* (=*Caligus*), *Parapetalus, Parechetus, Pseudechetus,* and *Synestius* share a suite of characters not just with *Caligus* but specifically with the *Caligus confusus*-group. With the addition of *C. lobodes* here, there are now 25 species in the *confusus*-group (Boxshall, 2018), and the group is defined by the following set of characters: antenna with posterior process on proximal segment (process typically spatulate); accessory tine present on postantennal process; maxillulary posterior process bifid; apron of leg 3 with raised cuticular rib and circular array of large denticles (also known as a rosette); outer margin spine on first exopodal segment of leg 3 stout and strongly recurved; leg 4 with 4 segments and with terminal 3 segments bearing spines I, I, III (Boxshall, 2018). In addition, the distal segment of the antennule is nearly always elongated, the setae on the posterior margin of the exopod of leg 1 are usually somewhat reduced in size, and members of the *confusus*-group typically parasitize species of the Carangidae. Although species assigned to the *confusus*-group typically possess this entire suite of character states, some species lack 1 or more of them.

We find it remarkable that many of these *confusus*-group character states are shared with *Parapetalus, Parechetus, Pseudechetus,* and *Synestius*. These genera are distinguished by superficially obvious differences involving processes and expansions on the abdomen or genital complex (Fig. 5C–G). We suspect that these gross differences in body form, currently used as generic discriminants, may not be robust with respect to phylogeny, especially given the larger suite of shared characters detailed below. We have synonymized *Midias* with *Caligus* here but have maintained the other genera until their phylogenetic relationships can be more formally evaluated with molecular data.

Of these 4 *confusus*-like genera, *Pseudechetus* most clearly resembles the *C. confusus*-group. The sole species, *Pseudechetus fimbriatus,* is distinctive because it possesses an elongated waist (also referred to as a neck) between the fourth pedigerous somite and the genital complex and has 6 elongate posterior processes: 4 on the genital complex and 2 on the abdomen (Fig. 5D). Despite these differences in the overall appearance of the body, *P. fimbriatus* possesses all of the *confusus*-group characters listed above, is known from only carangid hosts, and further resembles *C. confusus* itself in that it possesses a postantennal process that has 2 accessory processes (a posterior tine and an additional anterior-lateral tine) rather than the typical single accessory process (Fig. 5D).

Parechetus is easily identified by its possession of an elongated waist and single pair of long processes on the genital complex and abdomen (Fig. 5G), but it also possesses many of the *confusus*-group features. As redescribed by Pillai (1985), the type species *P. carangis* has a bifid postantennal process, a leg 3 protopod with a small rosette, a leg 3 exopod with a stout recurved spine, and a leg 4 typical of the *confusus*-group. It also possesses a long antennule distal segment and has reduced setae on the exopod of leg 1 (in this case, reduced to a single seta), plus it is known from only the carangid *Carangoides ferdau*. Its possession of the remaining *confusus*-group characters cannot be confirmed because Pillai (1985) did not figure the maxillule or the rib on the apron of leg 3.

The status of *Parechetus constrictus* Kirtisinghe, 1964 is uncertain. It is currently treated as a synonym of *P. carangis* (Walter and Boxshall, 2024), but Pillai (1985) did not formally propose a synonymy. He suggested only that the constricted neck in Kirtisinghe's *P. constrictus* might be an artifact, and if so they would likely be synonyms (Pillai, 1985). Dojiri and Ho (2013) also considered that these species were likely synonyms. However, the fact that the NMNH specimen of *P. fimbriatus* imaged here (Fig. 5C) has a constriction in just the same area of the "neck" indicates that this character might not be an artifact. Pillai (1985) specifically stated that he could not synonymize the 2 taxa because he had not looked at Kirtisinghe's types, so both should be treated as valid until further review.

The single species of *Synestius, S. caliginus,* possesses 4 elongate posterior processes on the genital complex (Fig. 5E) but also exhibits many *confusus*-group features. The distal segment of the antennule is elongate; the postantennal process has an accessory process; leg 1 has reduced setae on the posterior margin of the exopod; leg 3 bears a rosette, rib, and robustly recurved exopodal spine; and leg 4 is of the typical form (Dojiri and Ho, 2013). Beyond the 4 large posterior processes on the genital complex, *S. caliginus* differs from typical *confusus*-group species in several notable ways: the postantennal process has an accessory process that is a anterio-lateral knob rather than the typical posteriorly directed pointed process; the maxillulary process is simple rather than bifid and is less elongate; and it is known to parasitize hosts belonging to the families Stromateidae and Lutjanidae but not Carangidae (Walter and Boxshall, 2024).

The situation in *Parapetalus* is more complicated than that of the previous 3 genera because almost since its inception it has comprised a heterogenous group of species loosely united by degrees of expansion of the lateral margins of the abdomen. In the last decade, 7 species previously assigned to this genus have been transferred to *Caligus* (Boxshall, 2018; Boxshall and Barton, 2023; Walter and Boxshall, 2024). The 4 remaining species are *Parapetalus dewani* Pillai and Hameed, 1981, *Parapetalus longipennatus* Rangnekar, 1956, *Parapetalus occidentalis,* and the type species *Parapetalus orientalis* Steenstrup and Lütken, 1861. Each possesses a different number of *confusus*-group characters. *Parapetalus longipennatus* exhibits the most: it has an antennule with an elongate distal segment; an antenna with a broadening posterior process; a post-antennal process bearing an accessory process; a bifid maxillulary process; a leg 3 bearing a rib, rosette, and exopod armed with a robust recurved spine; reduced setae on leg 1; and is so far known only to parasitize carangid hosts (Pillai, 1985; Walter and Boxshall, 2024). *Parapetalus dewani* exhibits the next largest suite of *confusus*-group characters: long antennular distal segment; postantennal process with an accessory tine (although the maxillulary process is not bifid); leg 3 bearing a rosette and robust recurved exopodal spine; and reduced setae on leg 1 (Pillai and Hameed, 1981); it is unclear from available descriptions whether this species possesses a rib on the apron of leg 3. *Parapetalus dewani* is known from only *Rachycentron canadum* (Rachycentridae), and although this host is not in the Carangidae it is a member of the order Carangiformes.

Parapetalus occidentalis and *P. orientalis* share a more reduced suite of *confusus*-group features. They lack an accessory process on the postantennal process, and they have a simple rather than bifid maxillulary process, but they are reminiscent of the *confusus*-group in possessing an elongate distal antennulary segment, reduced setae on the exopod of leg 1, a rib on leg 3, a strongly recurved or oblique spine on the exopod of leg 3, and a leg 4 typical of the group (Ho and Lin, 2004; Dojiri and Ho, 2013). *Parapetalus occidentalis* parasitizes *R. canadum,* and *P. orientalis* parasitizes carangids. Given the suite of shared characters, it is tempting to transfer the remaining species of *Parapetalus* to *Caligus*. However, in the interest of taxonomic stability, until the diagnostic utility of the various *confusus*-group characters can be evaluated in a phylogenetic context or the evolutionary relationships of these species can be directly tested, we have elected to retain these species in *Parapetalus* given their unusual body plans and mosaic of character states.

The variety of posterior foliaceous and digitiform processes among species of *Parapetalus, Parechetus, Pseudechetus,* and *Synestius* (Fig. 5C–G) raises the question: what is their function? Parasites in general, and indeed many caligids, tend to have enlarged reproductive systems that increase their egg production capacity, but the processes on the genital complex of these genera are very flattened and do not appear to contain reproductive tissue. These posteriorly directed processes may serve to protect egg strings, perhaps from the activity of cleaner fish, which has been suggested for similar posterior processes in other groups of copepods such as the Lernanthropidae (Boxshall et al., 2020). All of these genera are relatively large caligids, so the expansions and processes may contribute additional surface area for respiration, but species of *Pupulina* and *Gloiopotes* and even *Caligus curtus* are substantially larger and lack such processes. These 4 genera have modified attachment sites relative to most caligids and live on the interior of the operculum or in the buccal cavity rather than on the body surface or gills. These regions may be more sheltered from shearing forces, which is particularly relevant because these copepods tend to parasitize rapidly swimming fishes. Under reduced shearing forces, the bodies of these copepods may have a broader adaptive landscape. Lastly, it is interesting to speculate that there may be a developmental element to this process. Many body parts in the *confusus*-group have additional processes or extensions: the posterior process of the maxillule and the postantennal process both tend to have accessory tines, and the rib on the apron of leg 3 often has a bifid tip. In *Pseudechetus,* the sternal furca is also bifid. Could there be a signaling pathway that leads to the development of additional axes of growth such as those listed above, and if so might this same process be involved in forming the foliaceous processes on the genital complex and abdomen in *Parapetalus, Parechetus, Pseudechetus,* and *Synestius*?

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