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Copepoda

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Introduction

Because of their size, their diversity, and their abundance, Copepoda have been regarded as “insects of the sea” (e.g. Huys & Boxshall 1991). However, as argued by Schminke (2007), the contrary was more appropriate: insects should be seen as “the terrestrial copepods”, due to the fact that copepods had to face much more impediments in their evolutionary history than the latter but notwithstanding reached the recent quite successful position within the aquatic realm. It is not possible to give an exact number of marine Copepoda, as a huge amount of species is still undescribed. The latest estimation revealed around 11 290 accepted marine species (Costello & Chaudhary 2017), including about 6500 marine benthic Copepoda (Table 27.1; Walter & Boxshall 2018a–f). The number of totally expected copepod species varies remarkably; while Humes (1994) estimated ~75 000 and Appeltans et al. (2012) attain to 50 125, Seifried (2004) speculates about even ~450 000 copepod species.

Morphology

Copepoda are small crustaceans comprising body lengths between 250 µm and ~3.0 cm. Whereas especially parasitic species developed much derived and variegated body shapes, most free-living Copepoda present a “typical” body that can be divided into three morphological tagmata: cephalosome, thorax, and abdomen (Fig. 27.1). In all copepods the 5 cephalic segments are fused to the first thoracic segment to form a **cephalosome** (Fig. 27.2) bearing the following appendages: **antennule (A1)**, **antenna (A2)**, **mandible (md)**, **maxillula (mxl)**, **maxilla (mx)** and **maxilliped (mxxp)**; originally the first thoracic leg). The mouth

is frontally limited by the **labrum** (Fig. 27.2). In several Copepoda the second thoracic somite carrying the first swimming leg P1 is incorporated into the cephalosome, which is then named **cephalothorax (cphth)** (Fig. 27.2). Frontally, the cephalosome/cphth is medially extended. That extension is named **rostrum (R)** (Fig. 27.1). Its length and shape varies between copepod groups, being sometimes fused to the cephalic shield and sometimes distinct. In some species the R is completely incorporated into the cephalosome/cphth. It carries a complex of sensory organs as well as one or more pairs of sensilla and a median tube pore.

The **thorax** encloses those body somites following the cephalosome or cphth bearing the biramous swimming legs (P1/P2–P6). The integument of the thoracic somites is divided into a ventral **sternite** and a dorsal **tergite**. In some species, the tergites are laterally broadened and extended to form **epimeres** or **epimeral plates**. The **abdomen** consists of four limbless somites: the first abdominal somite, which is often fused with the genital somite (last thoracic, P6-bearing somite) in female Neocopepoda to form a **genital double-somite**. This somite is followed by two

Table 27.1. Overview of the number of accepted species of marine benthic Copepoda.

Taxon	Number of benthic species
Calanoida	82
Canuelloida	85
Cyclopoida	~1500
Harpacticoida	~4800
Misophrioida	36
Platycopioida	11
Sum	~6514

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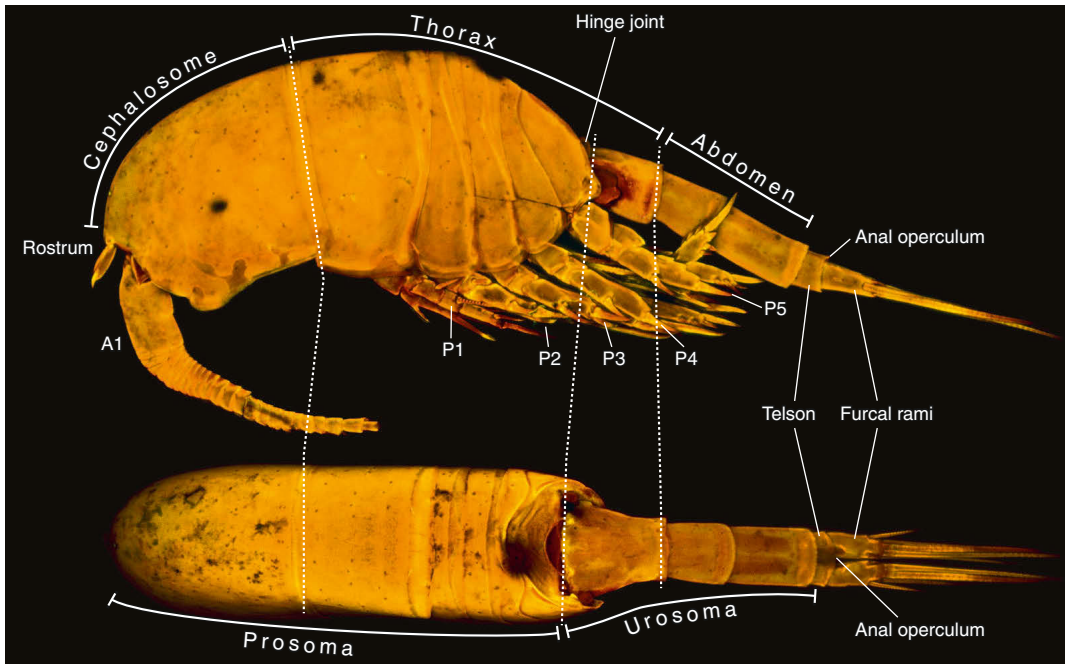


Fig. 27.1. Pseudocyclopidae gen. et sp. nov., lateral and dorsal view, showing the tagmosis and selected body parts. CLSM photo: N. Mercado Salas, original.

further somites and the **telson** (= anal somite) which carries the setiferous **furca**. The furca entails two **furcal rami** (FR) (Fig. 27.1), which are not somitic legs but “telsonic processes” (Schminke 1976, p. 298). In benthic Copepoda the FR present highest diversity in shape and size. Dorsally the telson bears the **anal operculum** that roofs the anus (Fig. 27.1).

The body somites and the segments of the appendages are flexibly hinged by smooth hyaline membranes, which are often turned into posteriorly jagged, often spinulose **hyaline frills** (Fig. 27.3). The shape of these frills shows a high interspecific variability and thus is of remarkable taxonomic importance. In some species, mainly those inhabiting fresh or brackish water, osmoregulatory **integumental windows** are present. These are rounded, sometimes more translucent areas in the integument, which possess ionocytes (Hosfeld, 1999).

Apart from the differentiation of the copepod body into cephalosome/cephalothorax, thorax, and abdomen, a second kind of differentiation divides the body into the anterior **prosoma** and the posterior **urosoma** (Fig. 27.1). Both tagmata are separated by a so-called “prosome-urosome

boundary” (Huys & Boxshall 1991, p. 321), consisting of a “hinge joint” (Fig. 27.1). According to the position of that hinge joint, two types of tagmosis can be recognized. The ancestral **gymnoplean tagmosis** is present in Platycopioidea Fossahagen, 1985 and Calanoida Sars, 1903; the hinge joint is located between the P5 bearing somite and the genital somite. The **podoplean tagmosis** is present in all remaining orders (joint together into the taxon Podoplea) in which the main body articulation is located between the P4- and P5-bearing thoracic somites (Fig. 27.27B).

Body and appendages are more or less densely covered with small to long robust or flexible elements of different origin (e.g. Huys et al. 1996) (Fig. 27.3):

- Spinules** and **setules** are of integumental origin; the cuticula is not perforated at their bases;
- Flexible **setae** and rigid **spines** are similar with respect to their origin: at their bases there is a hole that breaks through the integument (in Copepoda: a chitinous **cuticula**). Both kinds of structure may carry 1 or more rows of pinnules, so there may be described as **bare/**

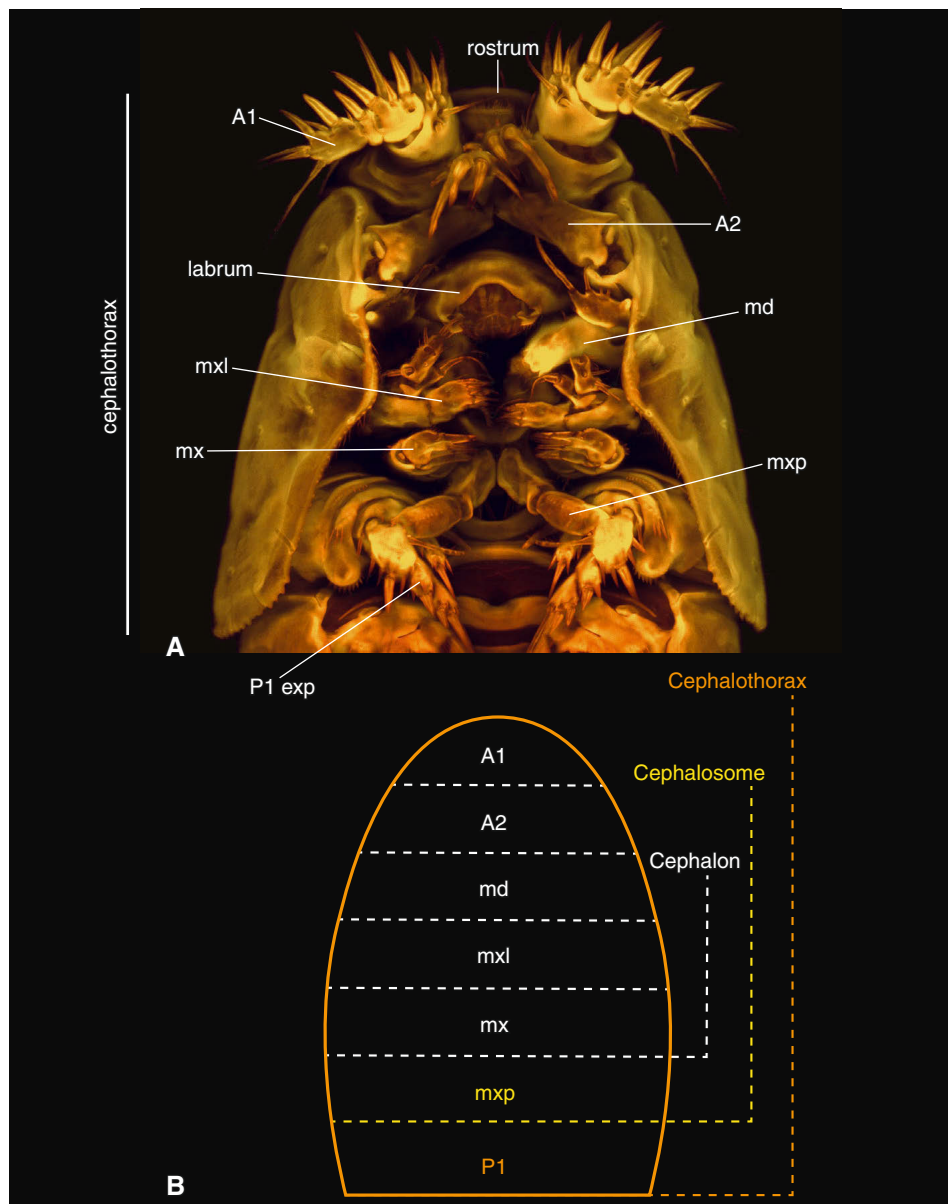


Fig. 27.2. A. *Nannopus* sp., ventral view of cephalothorax showing A1, A2 and mouthparts, and P1; CLSM photo: T. C. Kihara. B. scheme of the copepod cephalosome with indicated appendages; original.

naked, uni- to multipinnate (Fig. 27.3). If the pinnules are fine and hair-like, the respective seta is called (uni- to multi-)plumose. Particular setae may present a straw-like articulation at one side; these are called geniculated setae.

c) **Sensilla** are small filaments located on the body somites that break through the cuticula and may have a sensory function.

The A1 (Fig. 27.4) is the only originally uniramous appendage and highly variable; in females the number of segments may vary between 3

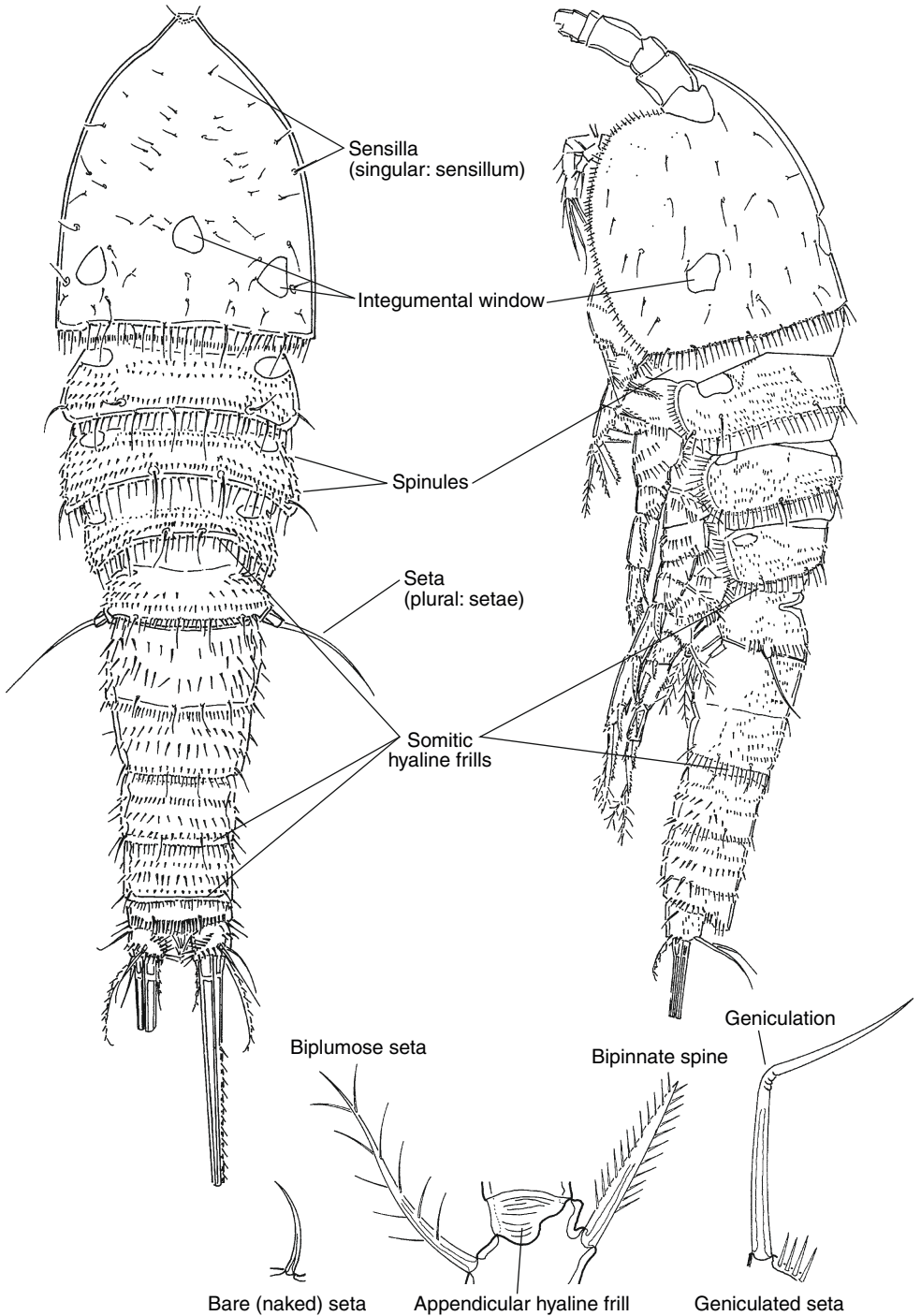


Fig. 27.3. *Microarthridion corbisierae* Kihara & Rocha, 2007, body in dorsal and lateral view, showing dorsal ornamentation and integumental windows; modified from Kihara & Rocha (2007). Details of setae and spines: originals.

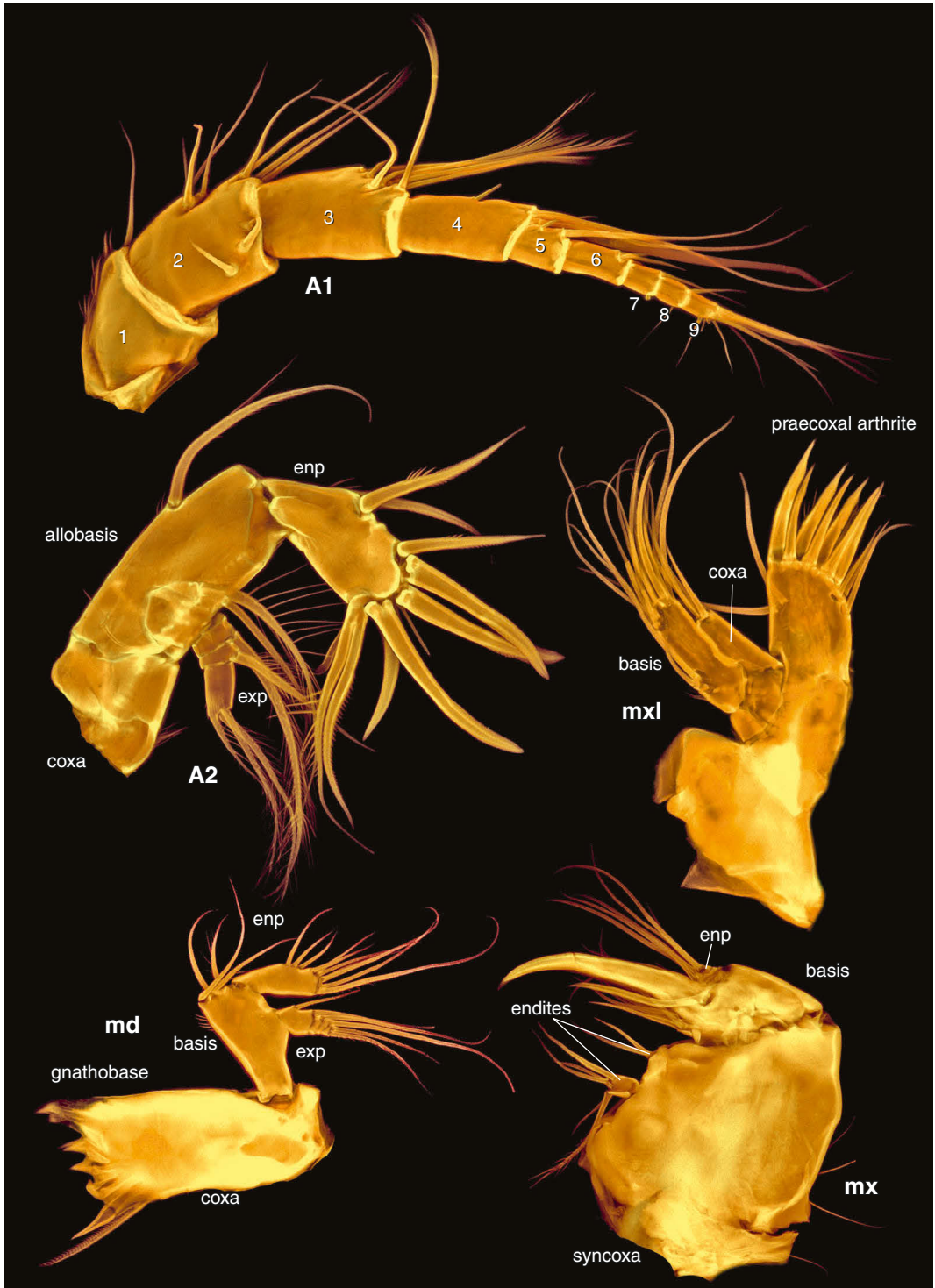


Fig. 27.4. A1 of *Harpacticus* sp. A2, md, mxl, and mx of *Aegisthidae* gen. et sp. nov.; CLSM photos: T. C. Kihara.

(e.g. harpacticoid genera *Ancorabolus* Sars, 1909; *Ceratonotus* Sars, 1909) and 27 (div. Calanoida, Misophrioida). Due to sexual dimorphism, male antennules often differ both in shape and number of segments.

A2–P6 originally are biramous limbs, although not always recognizable as such. Particularly the mouthparts and swimming legs P5 and P6 deviate from the following biramous groundpattern (see below).

The typical biramous limb consists of a 2- to 3-segmented **protopod** enclosing the **praecoxa** (not in A2, md, P6, and sometimes P5), **coxa**, and **basis**. While praecoxa and coxa attach the limb to the body, the basis bears the two lobes that are characteristic for Crustacea: **endopod (enp)** and **exopod (exp)**.

The **A2** (Fig. 27.4) is biramous and carries a 2-segmented protopod (coxa and basis); the enp may enclose up to 4, the exp up to 10 segments. Sometimes the basis is fused with the first endopodal segment, forming then an **allobasis**.

In the biramous **md** (Fig. 27.4) the coxa turned into a large **gnathobase** carrying few to several (multi-)cuspidate teeth. Furthermore it carries a **mandibular palp** consisting of basis, enp, and exp. The latter may show different kinds of deviation: they can each be fused with the basis or be completely lost; otherwise they may present a varying number of segments: enp = 1–2 segments, exp = 1–5 segments.

In the biramous **mxl** (Fig. 27.4) the praecoxa is enlarged, bearing an arthrite that carries several spines and setae. The coxa presents an outer epipodite with up to 9 setae and an inner endite carrying at the most 6 setae. The basis presents up to 2 endites that may, however, be incorporated completely into the segment; the maximum number of basal elements is 9. Enp and exp may consist of at most 1 and 3 segments, respectively, bearing a varying number of setae, but they can be completely fused with the basis, too.

In the (secondary) uniramous **mx** (Fig. 27.4) the exp is lost. The praecoxa carries 2 endites, the proximal one armed with up to 10, the distal one with 3 setae at the most. Also the coxa originally bears 2 endites, each of which armed with 3 setae. However, praecoxa and coxa may be fused, then forming a **syncoxa**. The basis is elongated and equipped with 4 setae, one of which often fused with the basis and transformed into a claw. The enp consists of at the most 4 setae-bearing segments, but it is often reduced, in some species

even being represented by 1 to few setae only (Harpacticoida [part.]).

Also the **mxp** (Fig. 27.5) is a secondary uniramous limb lacking the exopod. In addition to the 3-segmented protopod (praecoxa, coxa, basis) the exp bears up to 6 segments. In many derived Copepoda praecoxa and coxa fused to a syncoxa; furthermore, the number of endopodal segments is strongly reduced, and the limb turns into an organ able to grasp (= a **prehensile** or **subchelate mxp**). That ability is increased by the transformation of at least 1 endopodal element into a strong **claw**. Other maxillipedal forms are called **phyllopodial** (i.e. non-prehensile, segments broad and flattened) and **stenopodial** (i.e. non-prehensile, segments long, narrow).

Swimming legs 1–4 (P1–P4) (Figs. 27.5): The first four pairs of swimming legs present a more or less uniform shape. It is biramous and consists of a 3-segmented protopod whose praecoxa is largely reduced in size, whilst coxa and basis are of highly variable size and shape. The coxa bears at the most 1 inner, and the basis 1 inner and 1 outer seta. Both legs of one somite are linked together by a sclerotized plate that is named **intercoxal sclerite**. That plate inhibits independent moving of the connected legs, resulting in a movement that reminds on rowing (name of the taxon: Copepoda = “rowing feet”!). Like the protopod, also both the enp and exp originally are 3-segmented, carrying each segment 1 to several setae/spines on each the inner and/or outer margin, whose number is variable in different copepod species. While the P2–P4 commonly are of similar shape and setation, the P1 may differ from them in both aspects, particularly in Harpacticoida, where it often turns into a grasping (= prehensile) appendage.

Swimming leg 5 (P5) (Fig. 27.5): While ancestral copepod taxa the P5 resembles the previous swimming legs (Fig. 27.15E), in more derived groups it shows increasing deviation, often depending on its function. For instance, it may be considerably reduced in size. Furthermore, the basis and the enp may be fused, forming a **basoendopod (benp)**. In that case the endopodal lobe may be reduced in size even until its complete loss, giving the P5 a uniramous aspect. Also the exp may show reduction in size and fusion of its segments. At the same time the number of setae/spines may decrease. Finally, also the exp may get fused to the benp. In Calanoida the male P5 is asymmetrically modified (e.g. Fig. 27.17G).

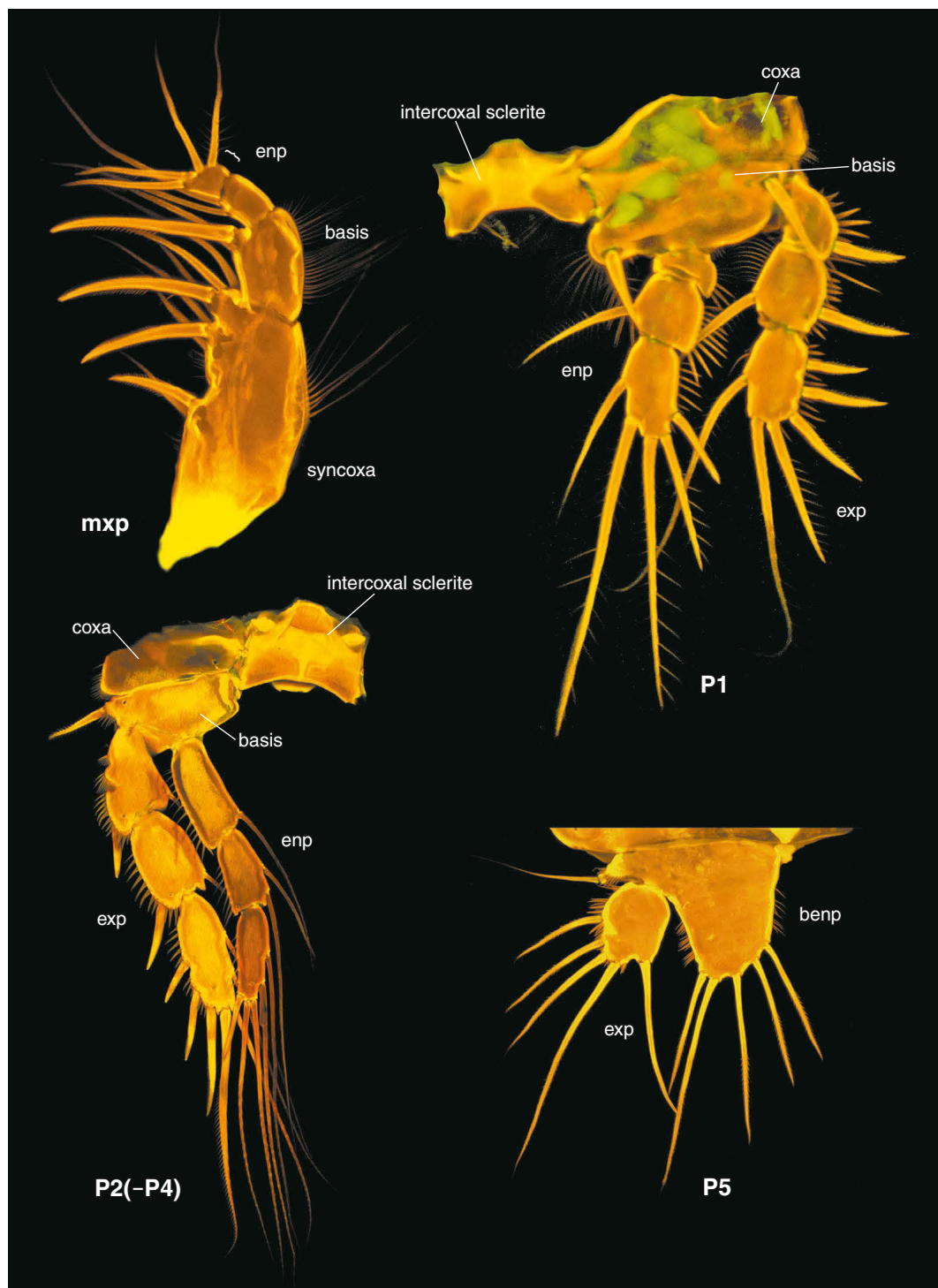


Fig. 27.5. Mxp of *Aegisthidae* gen. et sp. nov., P1 of *Microarthridion littorale* (Poppe, 1881), P2 of *Harpacticus* sp., P5 of *Tigriopus kingsejongensis* Park, Lee S., Cho, Yoon, Y. Lee & W. Lee; CLSM photos: T. C. Kihara.

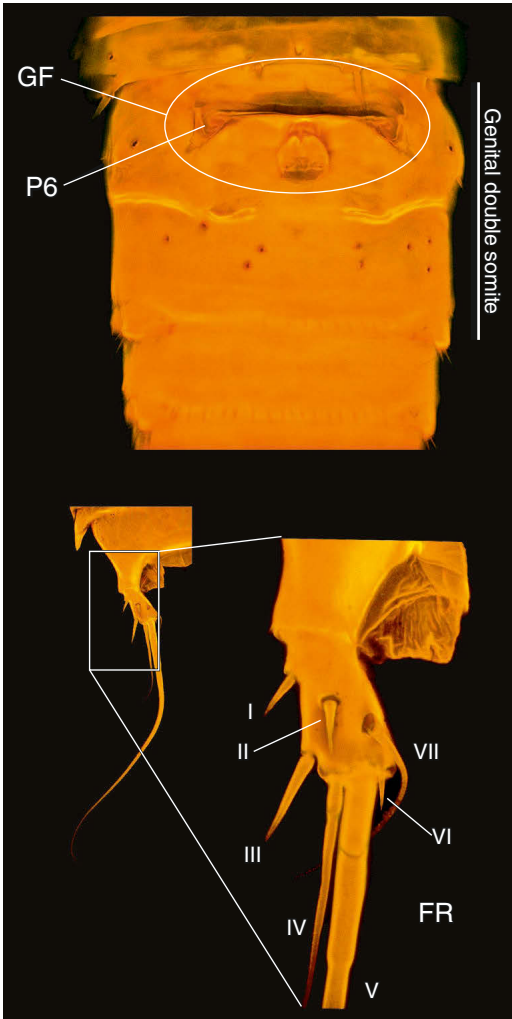


Fig. 27.6. Genital double somite (ventral view) of *Pseudotachidius bipartitus* Montagna, 1980, showing GF and P6; left FR of Aegisthidae gen. et sp. nov. with enumeration of furcal setae; CLSM photos: T. C. Kihara.

Swimming leg 6 (P6): The sixth pair of swimming leg is developed in both sexes as a small flap covering the gonopores and bearing up to 3 setae only. In female, the P6 forms part of the **genital field (GF)** (Fig. 27.6) which also includes the gonopores.

The **furca** consists of a pair of rami (furcal or caudal rami, **FR**) arising posteriorly from the telson (Fig. 27.6). These rami are not derived legs (e.g. uropods) but emerged from originally forked telsonic processes, which “became segmented off

and movable” (Schminke 1976, p. 298). Each furcal ramus in Copepoda bears 7 setae (I–VII) in the groundpattern, however, in many species some setae are reduced.

Life cycle and reproduction

Copepoda have separate sexes and there is always sexual dimorphism between the adult forms. Reproduction is commonly bi-sexual but parthenogenesis has been reported in few freshwater harpacticoid species (Roy 1931, Lang 1935a, Sarvala 1979, see also Dahms & Qian 2004). Benthic Copepoda are mostly sac spawners. Females carry their eggs in a single or in paired sacs attached to the genital pores until the nauplius larvae hatch. The life cycle of a copepod consists of six larval (naupliar; NI–NVI) and six juvenile (copepodid, CI–CVI) stages, the last copepodid stage (CVI) being the adult (Fig. 27.7). A nauplius bears three pairs of appendages only, A1, A2, and md. The naupliar phase is characterized by retention of development: instead of new segments and appendages being added at each moult, only “anlagen” of appendages as well as the FR appear successively (e.g. Dahms 1992). The moult from last naupliar (NVI) and first copepodid (CI) stage is characterized by a profound metamorphosis, at which we observe the simultaneous development of the head-appendages (A1, A2, md, mx1, mx2, mxp) together with the first swimming legs. The number of body somites, swimming legs and their segments starts to develop until reaching the full number in the CVI state (Fig. 27.7).

Males and females of most species present a more or less strong sexual dimorphism (Fig. 27.8). In males, the antennules are often transformed into a grasping organ (only Platycopioidea lacks primarily the antennular geniculation in males), enabling them to secure the female during copulation. Three types of male antennules are distinguished (Lang 1935b): the **haplocer** A1 shows a quite weak transformation only, with no segment being swollen; in the **subchirocer** A1, the last but second segment is clearly swollen, followed by 2–3 segments and presenting an explicitly geniculated union with the subsequent segment (Fig. 27.8.B), whilst in the **chirocer** type, the strongly swollen segment is followed by 1 small segment only. Calanoid males show an antennular sexual dimorphism on the right A1 only, while the left A1 resembles that of the female (Huys & Boxshall 1991). In contrast, males of podoplean copepod

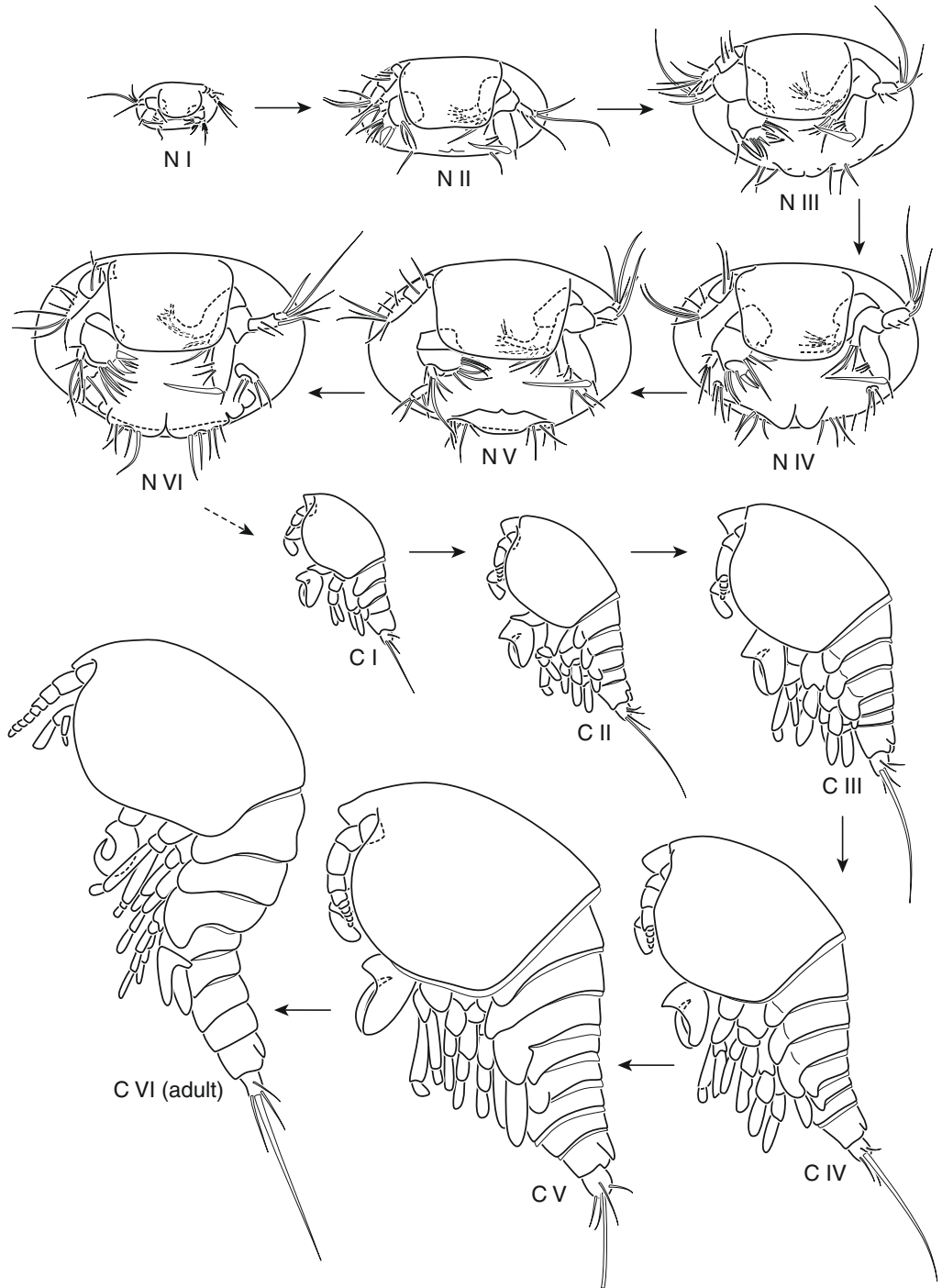


Fig. 27.7. Naupliar development exemplified on the N I-N VI stages of *Paramphiascella fulvofasciata* Rosenfield & Coull, 1974, and copepodid development exemplified on the C I-CV stages of *Thalestris longimana* Claus, 1863. Explanation in the text. No scales; naupliar images modified from Dahms (1990a), copepodid images (C I-CV) modified from Dahms (1990b), adult female (C VI) modified from T. Scott (1903).



Fig. 27.8. Sexual dimorphism in Copepoda, exemplified on harpacticoid species. Female (A) and male (B) antennule of *Heterolaophonte minuta* (Boeck, 1873), female (C) and male (D) P3 endopod as well as female (E) and male (F) P5 of *Ancorabulus chironi* Schulz & George, 2010. No scales. A, B: modified from Dahms (1989); C–F: modified from Schulz & George (2010).

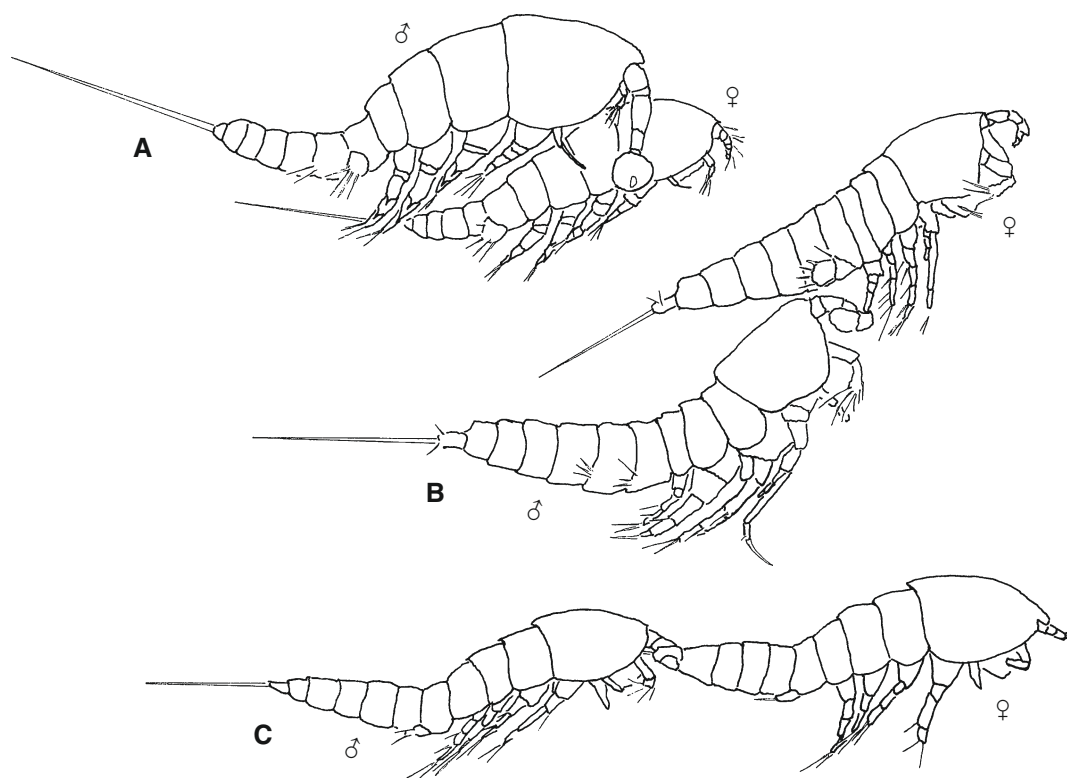


Fig. 27.9. Grasping behaviour in different harpacticoid species. **A.** *Tachidius discipes* Giesbrecht, 1881, male grasping the female cphth. **B.** *Heterolaophonte minuta* (Boeck, 1873), male grasping the female P4. **C.** *Mesochra lilljeborgii* Boeck, 1865, male grasping the female furca; modified from Dürbaum (1998).

orders display antennulary geniculation in both body sides. Loss of the antennulary geniculation in males is a characteristic of the poecilostomes families of the order Cyclopoida, which are parasites or associated to invertebrates. Furthermore, copepod males may show sexually dimorphic swimming legs, mainly the P2, P3, and P5 (the latter also asymmetrical in most calanoid species) (Fig. 27.8). The modified swimming legs are used to attach the spermatophore on the female genital aperture or may have other functions associated to mating behaviour. Most Neocopepodan females present a **genital double somite (GDS)**, which results from a fusion of the P6-bearing last thoracic somite with the first abdominal somite, forming together the genital field (Fig. 27.6).

While males are able to produce several spermatophores and copulate several times during their live, females of the Neocopepoda are equipped with paired seminal receptacles to store the sperms that discharge from the sper-

matophore. The sperms can be stored for months to even years, this allowing desynchronizing copulation from fertilization. The fact that adult females may already contain foreign sperms in the receptacle at the time of copulation provokes competition between males, which has promoted the evolution of mate guarding strategies. The most common ones are precopulatory mate guarding and/or postcopulatory mate guarding (e.g. Dürbaum 1997, 1998).

At the beginning of the copula the male grasps the female with its A1. Calanoid males usually cling to the furcal rami, cyclopoids usually the fifth leg, whereas in Harpacticoida, different body regions are grasped in different species (Fig. 27.9). Afterwards the male turns around and presses its gonoduct carrying the spermatophore against the female genital aperture (e.g. Dürbaum 1997, 1998, Dahms & Qian 2004) (Fig. 27.10). After the attachment of the spermatophore, the male remains clinged for a while until the spermatophore

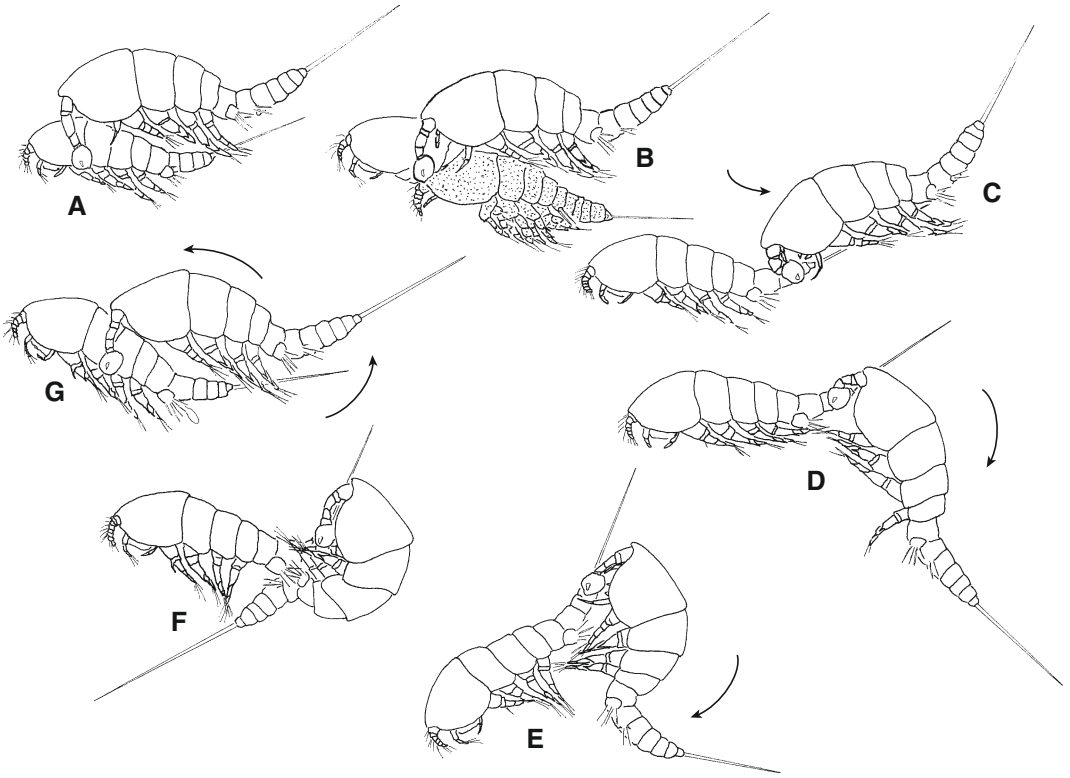


Fig. 27.10. Mating behaviour of *Tachidius discipes* Giesbrecht, 1881. **A.** Male (above) grasps CV female (precopulatory mate guarding). **B.** After final moult of CV female (dotted body = exuvia), male grasps eclosed CVI (= adult) female. **C.** Male moves down the female's body. **D.** Male turns to female's ventral side. **E.** Male presses his underside against female's genital field. **F.** Copula, transfer of spermatophore. **G.** Couple after copulation, male guards female (postcopulatory mate guarding). No scales; modified from Dürbaum (1997).

has been discharged completely (postcopulatory mate guarding) (Dürbaum 1997). Such behaviour ensures that the attached spermatophore cannot be removed by a successional male before all sperms have been transferred into the female's seminal receptacles. In many harpacticoid species the males even grasp juvenile females (CIII–CV) that are not yet fertile (Fig. 27.10B), a strategy named precopulatory mate guarding. The males remain attached to the juvenile female for days or weeks until the last moult of the female CV to the adult stage and then immediately start to transfer the spermatophore (Dürbaum 1997) ensuring paternity of the offspring.

Remarks on the phylogenetic position and internal systematics

Copepoda is a monophyletic group within Pancrustacea and sister-group to a clade comprising Thecostraca + Tantulocarida and Malacostraca (Khodami et al. 2017) (Fig. 27.11). Four major monophyletic infraclasses are defined within Copepoda, the Progymnoplea Lang, 1948, the Neocopepoda Huys & Boxshall, 1991, the Gymnoplea Giesbrecht, 1892 and the Podoplea Giesbrecht, 1892 (Fig. 27.12). The Progymnoplea (including only Platycopioidea Fosshagen, 1985) splits at the root of Copepoda, next to a clade containing Neocopepoda, sister to the reciprocally monophyletic Gymnoplea (including only Calanoida Sars, 1903) and Podoplea (Fig. 27.12). Podoplea contain 8 major clades corresponding to the orders Misophrioida Gurney, 1933, Canuelloidea Khodami, McArthur, Blanco-Bercial &

Martínez Arbizu, 2017, Gelyelloida Huys, 1988, Cyclopoida Burmeister, 1835, Harpacticoida Sars, 1903, Monstrilloida Sars, 1901, Siphonostomatoida Burmeister, 1834 and Mormonilloida Boxshall, 1979. Misophrioida branches off basally within Podoplea (note that Lang (1948a) established an own infraclass Propodoplea for Misophrioida), sister to 2 reciprocally monophyletic clades: “Clade CGCH”, comprising Canuelloida (= Polyarthra Lang, 1944) next to Gelyelloida and a clade with Harpacticoida (= Oligoarthra Lang, 1944) and Cyclopoida (enclosing poecilostomes); “Clade MMS”, containing Mormonilloida sister to Monstrilloida and Siphonostomatoida (Fig. 27.12). The ancestral copepod was presumably hyperbenthic, living in close contact to the sediment but not permanently within it. This life-style is retained in the order Platycopioidea and in the most plesiomorphic representatives of Calanoida, Misophrioida and Cyclopoida, while several habitat-shifts in more derived lineages lead to independent colonization of open waters (plankton) muddy and sandy sediments, and phytal habitats, as well as to different degrees of association with other organisms ranging from loose commensalism to endoparasitism (e.g., George & Schwabe 2019). The most common and diverse order of Copepoda in the interstitial meiofauna is the Harpacticoida, but Canuelloida, Cyclopoida, Misophrioida,

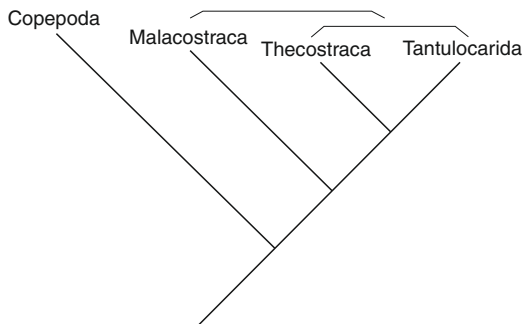


Fig. 27.11. Scheme of phylogenetic relationships of Copepoda according to Khodami et al. (2017); original.

Calanoida and Platycopioidea can also be found in lower individual and species numbers. The order Gelyelloida lives in continental groundwaters only. Mormonilloida and Monstrilloida are strictly planktonic and Siphonostomatoida live in association with invertebrates or fishes. These 4 latter orders will not be treated in this chapter.

Brief reference to ecology

Benthic Copepoda are found in all kinds of marine habitats: from intertidal flats, rock pools (e.g., the adapted *Tigriopus* Norman, 1869), and phytal zones to deep-sea plains and hydrothermal

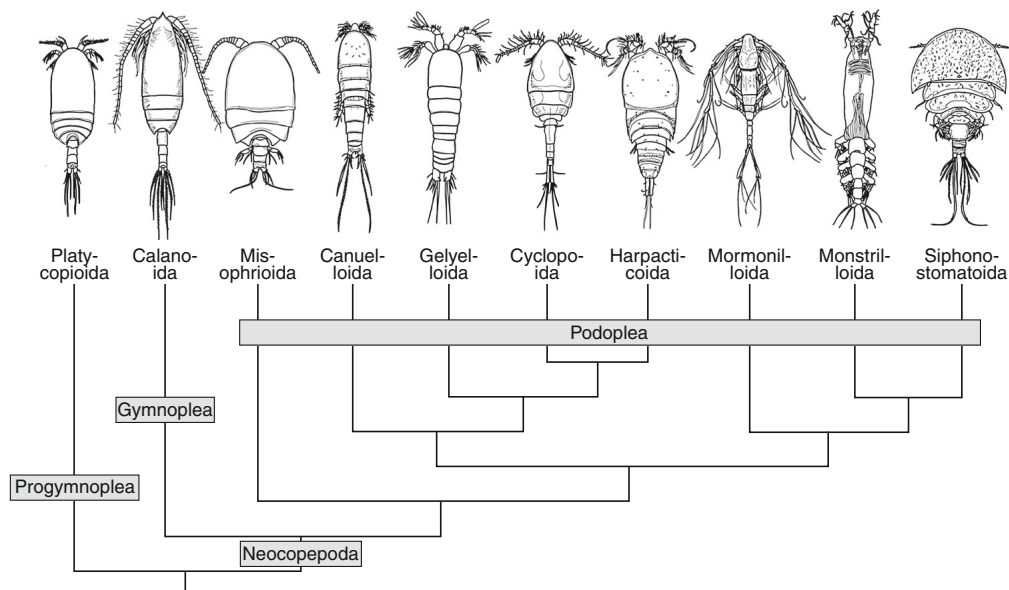


Fig. 27.12. Dendrogram showing the systematic relationships within Copepoda according to Khodami et al. (2017); modified from Khodami et al. (2017).

vents (e.g., the specialised Dirivultidae Humes & Dojiri, 1980). Their preferred habitat can often be deduced from their body shape. Epibenthic species are characterised by fusiform (torpedo-shaped; e.g., Ectinosomatidae Sars, 1903) or pyriform (droplet-like; e.g., Tachidiidae Sars, 1909, Harpacticidae Dana, 1846) body shapes that contribute to their well-developed swimming abilities. Endobenthic groups tend to be cylindrical (e.g., Cletodidae *sensu* Por, 1986), elongated (e.g., Paramesochridae Lang, 1944) or even vermiform (worm-like; e.g., Leptastacidae Lang, 1948). Cylindrical forms typically burrow in muddy areas, while the elongated or vermiform species more often weave **through** the interstitial space amongst coarser sediments. Phylal Copepoda are often dorsoventrally flattened (e.g., Peltidiidae Claus, 1860) or laterally compressed (e.g., Tegastidae Sars, 1904) carrying strongly developed maxillipeds or first swimming legs used to cling to algae, seagrass or mangrove leaves and avoid being drifted away by water movements.

Bacteria, microalgae and detritus are the main food sources of benthic Copepoda (e.g., Rieper 1982, De Troch et al. 2005). Few records indicate that some benthic copepod species may be carnivorous, feeding on mussel tissue or on Nematoda (Bröhdick 2005, Seifried & Dürbaum 2010). Studies on interactions of copepod communities with sediment-modifying macrofauna (e.g. lugworms; so-called “ecosystem engineers”) show that slight changes in environmental settings, such as mean grain size of the sediment or food availability, may lead to differing communities (e.g., Kuhnert et al. 2010).

Role in the meiofaunal community

After Nematoda, Copepoda often constitute the second-most abundant group in marine sediments. Due to their high motility they form one of the most active meiobenthic components. Depending on their body shape members of many families are very good swimmers (Thistle & Sedlacek 2004). Others leave the sediment at least temporarily, e.g. at night time. This behaviour makes them a prey for e.g. fish larvae, small benthic fish or zooplanktic predators (e.g., Schückel et al. 2012). They can thus be regarded as a conveyor of energy to higher trophic levels in benthic food webs. In the deep sea benthic Copepoda may prefer freshly deposited food over more degraded organic matter, which is instead

consumed by Nematoda (Veit-Köhler et al. 2013). However, the role of Copepoda in the remineralisation of degraded organic material at the sea floor is still understudied and not yet quantified.

Brief history of discovery and further research

The history of the discovery and description of copepods diversity was reviewed by David M. Damkaer in his monumental work “The Copepodologist’s Cabinet: A Biographical and Bibliographical History” (Damkaer 2002, 2017). The first volume covers the history since first mentioned by ancient Greeks to approximately 1830. The second volume covers from 1830 to 1890. A third volume is in preparation.

Parasitic copepods are very conspicuous and often discernable without the aid of a microscope. For this reason, parasitic copepods were already reported by Aristotle, who included in his “History of Animals” the first historic mention of a copepod: “The tunny and the sword-fish are infested with a parasite about the rising of the Dog-star; that is to say, about this time both these fishes have a grub beside their fins that is nicknamed the ‘gadfly’. It resembles the scorpion in shape and is about the size of the spider. So acute is the pain it inflicts that the sword-fish will often leap as high out of the water as a dolphin ...”¹ Rondelet (1554) was the first to illustrate a copepod. It was a parasite on the Mediterranean tuna and swordfish known as “oestro” or “asilo” at that time. He referred to Virgil and Pliny, who also reported on this parasite. Redi (1684) on his work “animals living inside other animals” described very small creatures² that he observed with the aid of a microscope and he recovered from inside a “pincio marino” (most probably an ascidian) from the Mediterranean off Italy. According to his drawing the copepod was most probably a notodelphyid Cyclopoida. He already described that these animals infest not only “pincio” (ascidians) but also “mentula” (holothurians) and are most common from January to July. What Boccone (1671) described and illustrated as a “leech with tail feathered on both sides” was indeed a

¹ Book VII, Part 19, Translated by D’Arcy Wentworth Thompson. [https://en.wikisource.org/wiki/History_of_Animals_\(Thompson\)/Book_VIII](https://en.wikisource.org/wiki/History_of_Animals_(Thompson)/Book_VIII).

² “... ne son maggiori di un piccolo granello di grano ...” Redi 1684, p. 186.

pennellid copepod parasitizing on a sword fish.

The first free living copepod was illustrated by Blankaart (1688). It was a limnic cyclopoid copepod. Some 100 years later, the first marine copepod was described by Gunnerus (1770), a calanoid copepod called by him *Monoculus finmarchicus*.

The word “Copepoda” was introduced by Milne Edwards (1830), but he used it only to designate the free-living copepods, as the parasitic ones were classified as “Siphonostoma”. The first ecological study dealing with copepods was probably Jurine’s (1820) work on changes in the population structure of freshwater cyclopids.

The history of classification of Copepoda is marked by the difficult task of recognizing how free-living and parasitic forms are related to each other. Early attempts of systematization divided copepods in 2 groups corresponding to **parasitic** and free-living copepods, respectively. Thorell (1859) basing on differences in mouth-part-morphology introduced the series Gnathostoma (with a large oral cavity and biting mandibles with palp), Siphonostoma (with an oral cone and stylet-like mandibles) and Poecilostoma (with no mandibles). On the contrary Giesbrecht (1883), studying the planktonic copepods of the Gulf of Naples, divided them into Gymnopleoden and Podopleoden, based on the main body tagmosis (see below). G. O. Sars, while preparing his comprehensible “Account of the Crustacea of Norway”, emphasized the study and description of both planktonic and benthic copepods. His new classification divided the Copepoda into 7 groups, the Calanoida (including Platycopiidae), Harpacticoida, Cyclopoida (with the subunits Gnathostoma, Siphonostoma and Poecilostoma), Notodelphoida, Monstrilloida, Caligoida and Lernaoida (e. g., Sars 1903). It was Lang (1948a) who introduced evolutionary thinking into copepod classification which can be summarized with his statement “... *parasitic forms should be classified together with the free-living forms they derived from* ...”. His classification of copepods into Progymnoplea (including only Platycopiidae and being the most basal), followed in this sequence by Gymnoplea (including Calanoida only), Propodoplea (including Misophrioida only) and Podoplea (including the most derived groups) fully agrees with the new phylogenetic tree proposed recently by Khodami et al. (2017) using molecular methods.

A more detailed review of 19th and 20th century classification of copepods can be found in

Huys & Boxshall (1991). This work also includes the most comprehensive homologization of the segmentation and setation of all appendages, body tagmosis and reproductive organs.

In a book about meiofauna, we cannot finish this brief review of the history of discoveries without mentioning the work of Karl Lang (1948b) who in his two volumes of the “Monographie der Harpacticiden” reviewed all the knowledge of that time about harpactoid copepods, the most common group in the meiofauna. He presented drawings, notes on ecology and distribution, and identification keys to all (over 3000) marine and fresh water species described until then.

Geographic distribution

Copepoda are aquatic organisms, which results in a multitude of habitats they can colonize. Fresh-water copepods occur for example in lakes (Servala 1998), rivers (Gaviria 1998), springs, groundwaters, and even in so called semi-terrestrial habitats like phytotelmata in bromeliads (Suárez-Morales et al. 2010), forest litter and, on mosses. Distribution of freshwater species and genera is often restricted by geographical barriers. In contrast, for most marine benthic copepods (Gheerardyn & Veit-Köhler 2009; Menzel et al. 2011) no such barriers exist, and many families and even species show a cosmopolitan distribution (Chertoprud et al. 2010, George 2017), mainly defined by habitat characteristics like sediment grain size, temperature, and oxygen concentration. Consequently, several typical deep-sea taxa also occur in shallow-water areas of the Arctic seas (Chertoprud et al. 2010) as well as in caves (Janssen et al. 2013) due to deep-sea like conditions in these regions.

In contrast to this for the families, the distribution pattern of most species level is difficult to assess. Extreme environmental conditions may facilitate specialised communities that are more stable over larger distances: communities from the intertidal of the German and Southern Bight of the North Sea equal those around the British Isles more than subtidal communities in the same areas (Veit-Köhler et al. 2010). Restricted distribution areas recorded for certain species are very likely an artefact of limited sampling in certain geographical areas or difficult to access habitats. For example, for the deep sea – even though increased studies on benthic Copepoda around

the world are carried out – the area sampled is extremely small compared to the world's ocean and within one sample, more than 90 % of the species identified may be new to science (e.g., George et al. 2014). But with ongoing investigations, it was possible to show that even species restricted to shallow-water habitats have a cosmopolitan distribution (Packmor et al. 2015, Packmor & Riedl 2016, George 2017). Several dispersal methods like emergence, rafting and drifting have already been discussed (Gerlach 1971, Giere 2009), and also seamounts support the distribution of benthic Copepoda across the oceans as stepping stones or staging posts (George 2013, Packmor et al. 2015).

Preferred extraction method

The extraction method for benthic copepods depends on the nature of the substrate:

1. **In medium to coarse sandy sediments**, the best option is the decantation method (Pfanckuche & Thiel 1988, Giere 2009) where the sample is placed in a recipient with filtered seawater and agitated vigorously enough to suspend the sediment grains. The supernatant is decanted into a stack of sieves ranging from 1000 to 32 μm mesh sizes. If the samples contain fine sediment, it is advisable to insert an intermediate sieve (500 or 300 μm mesh sizes) to minimize the possibility of clogging and the risk of overflow. The coarsest sieve will retain larger pieces of detritus and the material recollected on the finest sieve is then washed into the storage container. The resuspension and decantation should be repeated at least 3 times to maximize extraction of the copepods. In order to detach the copepods from the substrate in live samples, it is advisable to add an anaesthetic (e.g. $\text{MgCl}_2 - 7\%$ solution in seawater) or rinse the sample in freshwater.
2. **In fine sand and muddy sediments**, the copepods can be extracted by hand or by differential flotation and centrifugation of the sample in a colloidal silica gel (Heip et al. 1974, McIntyre & Warwick 1984). Hand-picking a sample is very arduous and time-consuming task, as all the sediment needs to be examined under a stereo-microscope and picked out using fine tip needles. Taxon and operator specific bias has been examined by Rohal et al. (2017). In the centrifugation method, a small amount of the material is first suspended by thorough mixing in a medium of a specific density, which is higher of that of the copepods, so they float (~1.08 to 1.15) but lower than the density of sediment particles, so they sink (~2.5 to 2.8). In order to reduce the settlement time of sediment particles, the solution is centrifuged (10 min at 6000 rpm). The supernatant is then washed onto a 32 μm sieve and transferred to a storage container. This procedure is repeated 3 (after resuspension of the sediment fraction in new silica gel) to ensure a high extraction efficiency. Several colloidal silicas as Ludox® (du Pont), Percoll® (Pharmacia), and Levasil® (Bayer) are used as medium and more detailed information about this technique can be found in Schwinghamer (1981), Pfanckuche & Thiel (1988), Burgess (2001) and Giere (2009).
3. **“Problematic” fine sediment samples:**
 - In sediments rich in clay with clumps or concretions different treatments can be used as: ultrasonic treatment (Thiel et al. 1975), freezing – thawing (Barnett 1980), detergent and water softening detergent addition (Barnett 1980, Cedhagen 1989).
 - In samples with very high silt content (e.g. deep-sea samples), the addition of 1–2 spoons of kaolin powder to the sample before applying centrifugation is recommended, as it helps to separate the sediment from the overlaying solution. Kaolin is among the finest sediment particles and will therefore be the last to settle during centrifugation creating a stable separation to the supernatant liquid phase at the surface of the sediment (Heiner & Neuhaus 2007).
 - Samples with high plant-debris content, (e.g. mangrove samples) can be centrifuged with a mix of kaolin and magnesium sulphate (MgSO_4) of specific density 1.28 (Ladell 1936).
4. **In Phytal samples from macroalgae**, copepods can be extracted by adding an anesthetic (e.g. $\text{MgCl}_2 - 7\%$ solution in seawater), or freshwater to the recipient containing the algae and shaking it vigorously. The water can be decanted into a sieve of 32 μm mesh size. Extraction efficiency is enhanced by repeating the procedure 3 times. In the case of mangrove leaves samples, the shaking can be done using filtered seawater.

Further information on processing copepod samples can be found in Heip et al. (1974), Nichols (1979), Schwinghamer (1981), Pfannkuche & Thiel (1988), Giere (2009), Kihara & Rocha (2009), Boxshall et al. (2016), Rohal et al. (2018).

Important characters for determination

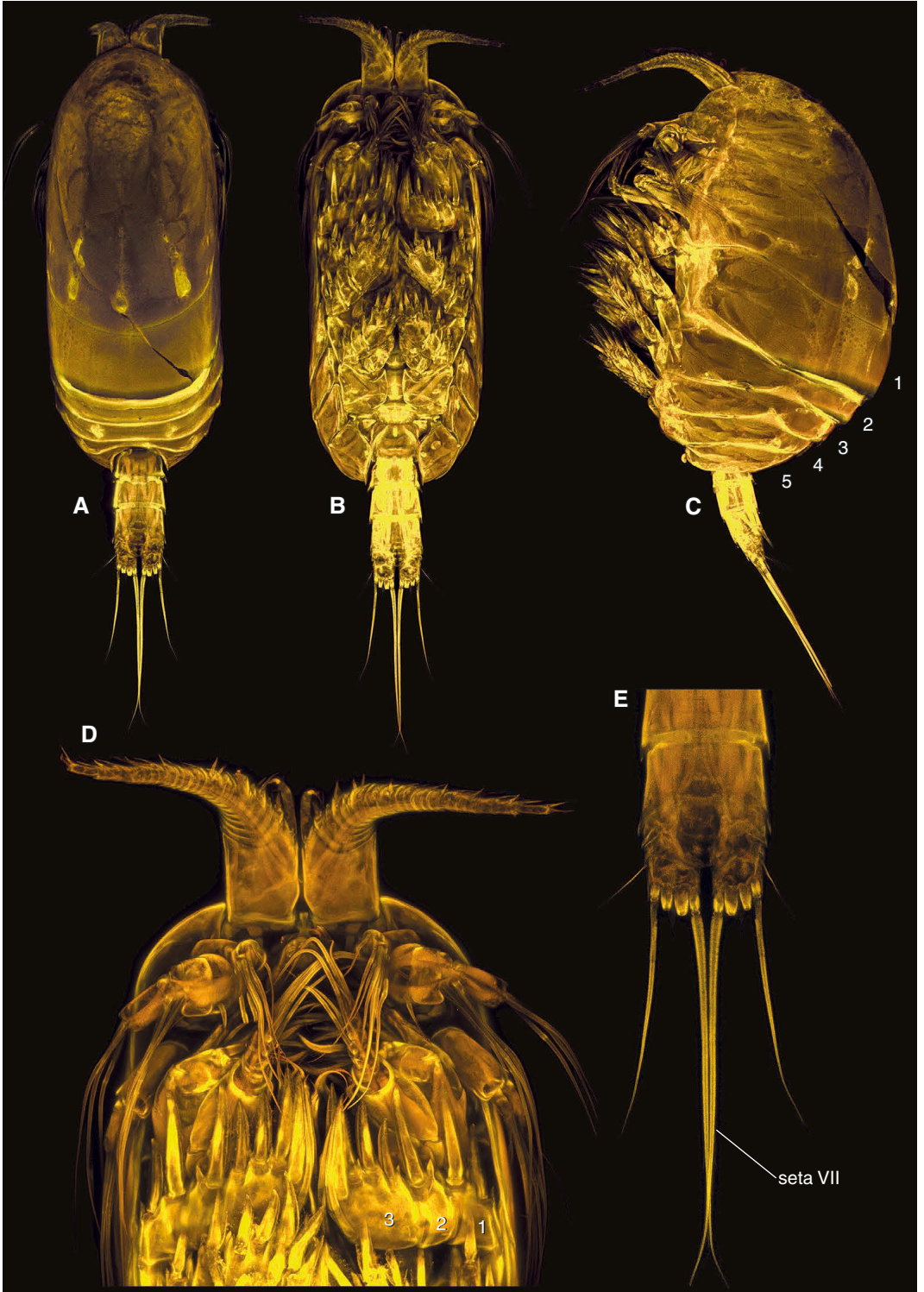
The “typical” adult benthic copepod shows a more or less elongated body with a size of 300–500 µm. Some species are bigger reaching more than 2.0 mm in length (e.g. *Echinopsyllus voightae* George & Müller, 2013 [Harpacticoida]; cf. George & Müller 2013). However, due to specific adaptations to the corresponding habitat, benthic Copepoda present a high variability in their body shape (“Lebensformtypen”, cf. Remane 1952, Noodt 1971) (e.g. Fig. 27.33). Inhabitants of the phytal are often dorsally depressed or laterally compressed or show a cyclopi- or fusiform shape; interstitial species frequently present a slender and flexible vermiform or fusiform body; epibenthic and burrowing species are generally robust cylindrical, pyriform or fusiform. Thus, the body shape may provide first information for the identification. Nevertheless, for an unambiguous determination of a collected specimen, a combined comparison of several morphological characteristics is absolutely indispensable. The shape of the appendages, number of respective segments, and location of setae/spines allow an unequivocal assignment of a found individual to a particular species or the recognition as a so far unknown species. Differentiation between the sexes is possible because of a pronounced sexual dimorphism in almost all species. Generally it is expressed by the formation of a genital double somite in many females, the modification of male antennules in order to grasp the mating partner, development of cuticular processes (**apophyses**) in male P2–P4 enps in many species (see above), and transformation/reduction of the male P5 and P6 (see above “Remarks on reproduction and life cycle”), the presence of one or two gonopores in female genital somite and the presence of spermatophores in males (not in Platycopioida).

Identification keys

Key to copepod orders

(adopted from Huys et al. 1996, Boxshall & Halsey 2004)

- 1 Gymnoplean tagmosis: Prosome-urosome boundary between P5-bearing somite and genital somite (Figs. 27.13C, 27.16). 2
 - Podoplean tagmosis: Prosome-urosome boundary between P4- and P5-bearing somite (e.g., Figs. 27.21D, 27.27B). 3
- 2 Male A1 and P5 bilaterally symmetrical; P2–P4 bases with inner spine, exps-1 with 2 outer spines (Fig. 27.15F). Platycopioida
 - Male A1 and P5 bilaterally asymmetrical (Figs. 27.18, 27.17G); P2–P4 bases without inner spine, exps-1 with 1 outer spine. Calanoida
- 3 Cphth reaching half of body length, A1 at most 5-segmented in both sexes, A2 and mouthparts missing. Monstrilloida
 - These characters not combined. 4
- 4 A2 exp 8-segmented in female, 9-segmented in male, apical segment in female with 3 setae only. Mormonilloida
 - A2 exp at most 8-segmented in both sexes, apical segment in female with 4 setae. 5
- 5 P1–P3 lacking intercoxal sclerites. Gelyelloida
 - P1–P4 with intercoxal sclerites. 6
- 6 A2 exp commonly with 2 or more segments; if absent or 1-segmented, P5 benp developed, with 2 or more setae. 7
 - A2 exp 1-segmented or absent; P5 enp represented by 1 seta or absent. 9
- 7 Female A1 at least 16-segmented. Misophrioida
 - Female A1 at most 9-segmented. 8
- 8 A2 exp at least 6-segmented; P1 coxa with inner seta/spine. Canuelloida
 - A2 exp at most 4-segmented; P1 coxa without inner seta/spine. Harpacticoida



- 9 Labrum and labium (= fused paragnaths) forming oral cone, P4 exp-3 with 1 terminal and 3 outer spines. Siphonostomatoida
- Oral cone absent; paragnaths separated, no antennary exopodal segment, P4 exp-3 with 1 terminal and 2 outer spines³, fith leg without any vestige of endopod. Cyclopoida

Order Platycopioidea Fosshagen, 1985

(Pedro Martínez Arbizu, Alejandro Martínez and Sahar Khodami)

Platycopioidea are the most basal copepods. The 4 genera described so far are grouped into a single family Platycopiidae G. O. Sars 1911. *Antriscopia* Fosshagen, 1985 (Fig. 27.14A) and *Nanocopia* Fosshagen, 1988 (Figs. 27.14B–C) are monotypic and are known from a single anchialine cave (Road Side Cave) in Bermuda Island (Fosshagen & Il-life 1985, 1988). These species are considered as critically endangered. *Sarsicopia* Martínez Arbizu, 1997 (Figs. 27.14D,E) is also monotypical and the deepest record of the order, found at 534 m depth in the Barent Sea on soft sediments covered by a dense mat of sponge spicula (Martínez Arbizu 1997d). *Platycopia* Sars, 1911 (Fig. 27.15) is the most diverse genus (8 species). They live in shallow water hyperbenthic habitats (up to 120 m depth), preferring biogenic sands. They have been recorded from both margins of the North Atlantic and Iceland, Bahamas, Mauritania and Japan (Ohtsuka et al. 1998).

Platycopioidea can be easily recognized by the combination of following characters: Gymnoplean tagmosis (Figs. 27.13A–C), presence of inner setae on the basis of P2–4 (Fig. 27.15F), no inner seta on coxa in any swimming leg, no outer seta on basis of P1, presence of 2 spines on outer margin of exp-1 at least on P2–3 (Figs. 27.15D–F), location of furcal seta 7 on distal inner margin of furca (not in

³ One terminal and 3 outer spines may be present in *Cyclopicina toyoshioae* and *Paracyclopina nana*, but this should be considered an atavism.

dorsal position, Fig. 27.13E), antennules at most 23 segmented in female and 20 segmented in males. Platycopioidea are the only copepods to exhibit an exite on the basis of the maxillule. Swimming legs are always biramous, P1 with 2-segmented endopod, other legs with 3-segmented endopods. Rostrum always fused to cephalosome. Males and females of Platycopioidea are difficult to differentiate, as females lack a genital double somite, and males lack a spermatophore. Also, males of *Platycopia* and *Nanocopia* lack a geniculated antenna. Some grasping capabilities were described from the bilaterally symmetrical male antennules of *Antriscopia* (Figs. 27.14A,F) and *Sarsicopia* (Figs. 27.14G), but the function is unknown. Male fith leg is symmetrically transformed in *Platycopia* (Figs. 27.15D).

Key to genera of Platycopioidea

- 1 P1 enp-1 without inner seta, P1 enp-2, or homologous, with 3 setae, male antennule not geniculated, P5 sexually dimorphic (Figs. 27.15D,E). 2
 - P1 enp-1 with inner seta, P1 enp-2 or homologous with at least 6 setae, P5 not sexually dimorphic. 3
- 2 P1 exp with 3-segmented endopod. *Nanocopia*
(single species *Nanocopia minuta*)
 - P1 exp with 2-segmented rami. *Platycopia*
- 3 Antennary exp 8-segmented, mandibulary exp 5-segmented, P1 enp-2 with 7 setae, P5 exp-1 with inner seta, P2–P4 enp-2 with 1 inner setae. *Antriscopia*
(single species *Antriscopia prehensilis*)
 - Antennary exp 7-segmented, mandibulary exp 5-segmented, P1 enp-2 with 6 setae, P5 exp-1 without inner seta, P2–P4 enp-2 with 2 inner setae. *Sarsicopia*
(single species *Sarsicopia polaris*)

Order Calanoida Sars G. O., 1903

(Nancy Mercado-Salas and Pedro Martínez Arbizu)

The order Calanoida is diagnosed by the combination of the following characters: prosome comprising cephalosome and 5 free pedigerous somites (gymnoplean tagmosis, Fig. 27.1),

◁ Fig. 27.13. Platycopioidea. Undescribed species of *Platycopia* from the Mediterranean Sea. A. Dorsal habitus. B. ventral habitus. C. lateral habitus. D. close up, ventral, showing P2 with 2 spines on outer margin of exp-1. E. urosome and furca, dorsal view, showing seta VII on terminal inner margin. CLSM photos: A. Martínez.

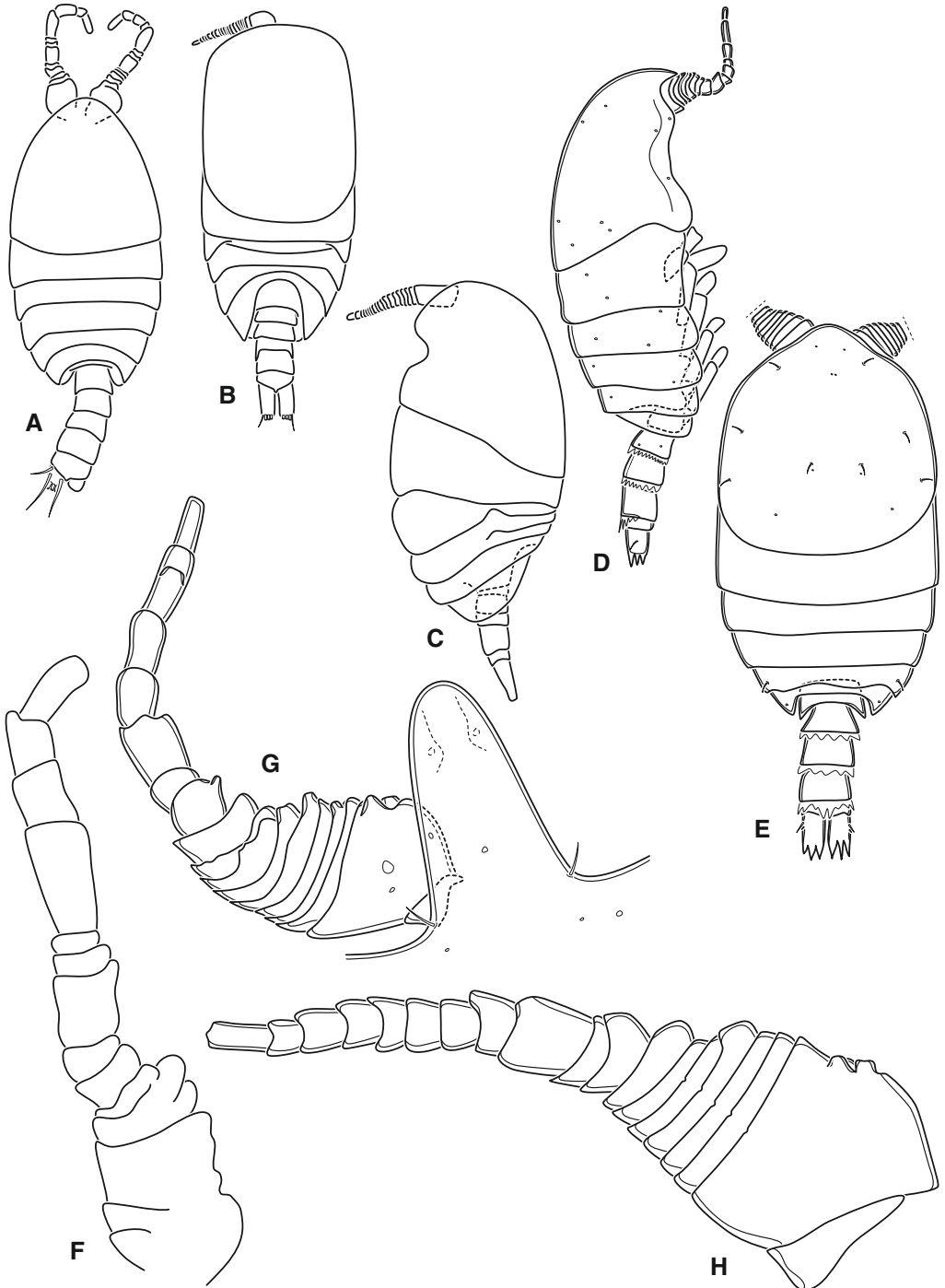


Fig. 27.14. Platycopeioida. Habitus. **A.** *Antrisocopia prehensilis* Fosshagen, 1985, dorsal. **B.** *Nanocopia minuta* Fosshagen, 1988, dorsal. **C.** *N. minuta*, lateral. **D.** *Sarsicopia polaris* Martínez Arbizu, 1997, lateral. **E.** *S. polaris*, dorsal. **F.** male A1 of *A. prehensilis*. **G.** male A1 of *S. polaris*. **H.** female A1 of *S. polaris*. No scales. A, F, modified from Fosshagen & Iliffe (1985); B, C, modified from Fosshagen & Iliffe (1988); D, E, G, H, modified from Martínez Arbizu (1997d).

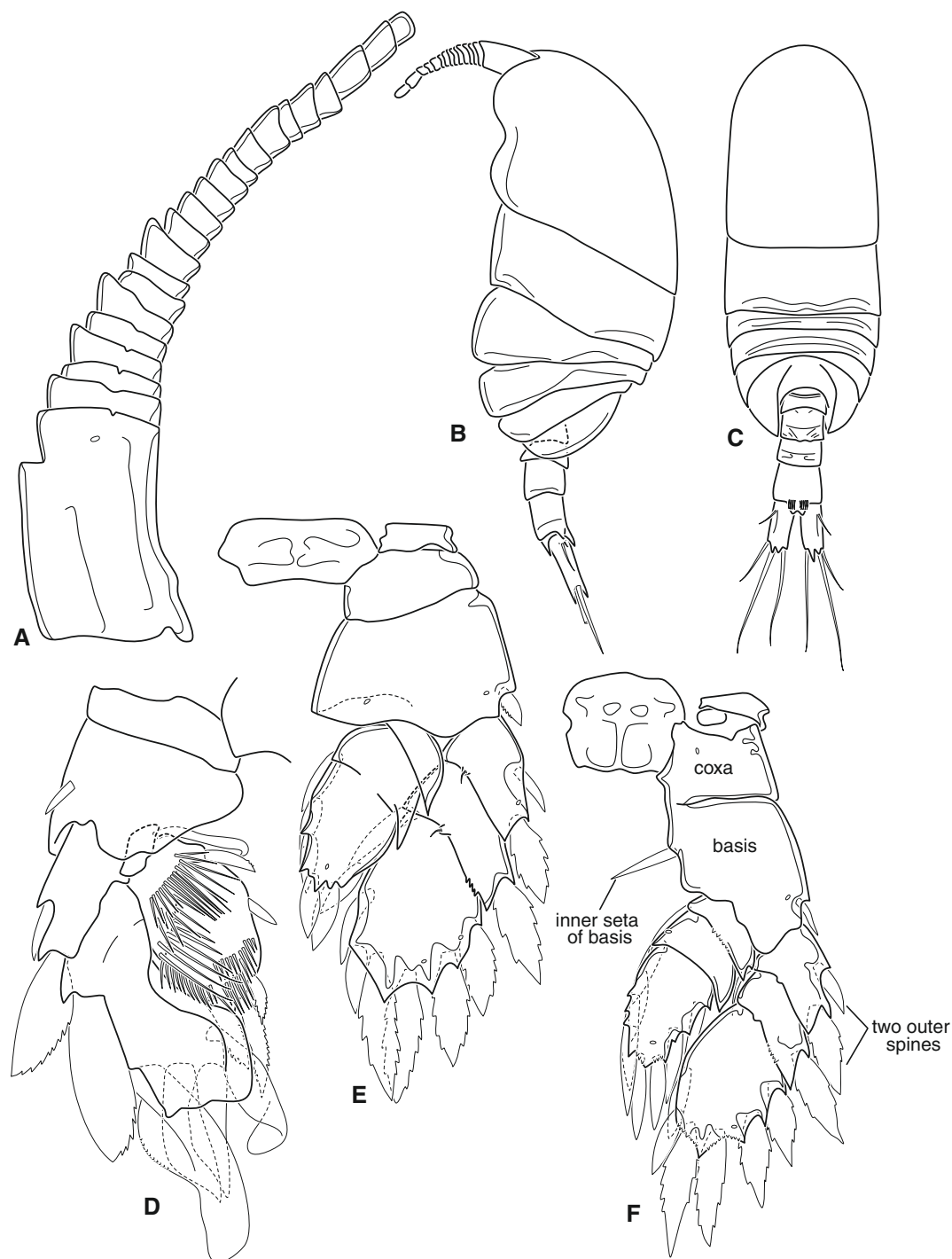


Fig. 27.15. Platycopioida. **A.** Female A1 of *Platycopia compacta* Ohtsuka, Soh & Ueda, 1998. **B.** lateral habitus of *Platycopia orientalis* Ohtsuka & Boxshall, 1994. **C.** dorsal habitus of *P. orientalis*. **D.** male P5 of *P. compacta*; **E.** female P5 of *P. orientalis*; **F.** P3 of *P. orientalis*, showing 2 outer spines on exp-1 and 1 inner seta on basis. No scales. A, D, modified from Ohtsuka et al. (1998); B, C, E, F: modified from Ohtsuka & Boxshall (1994).

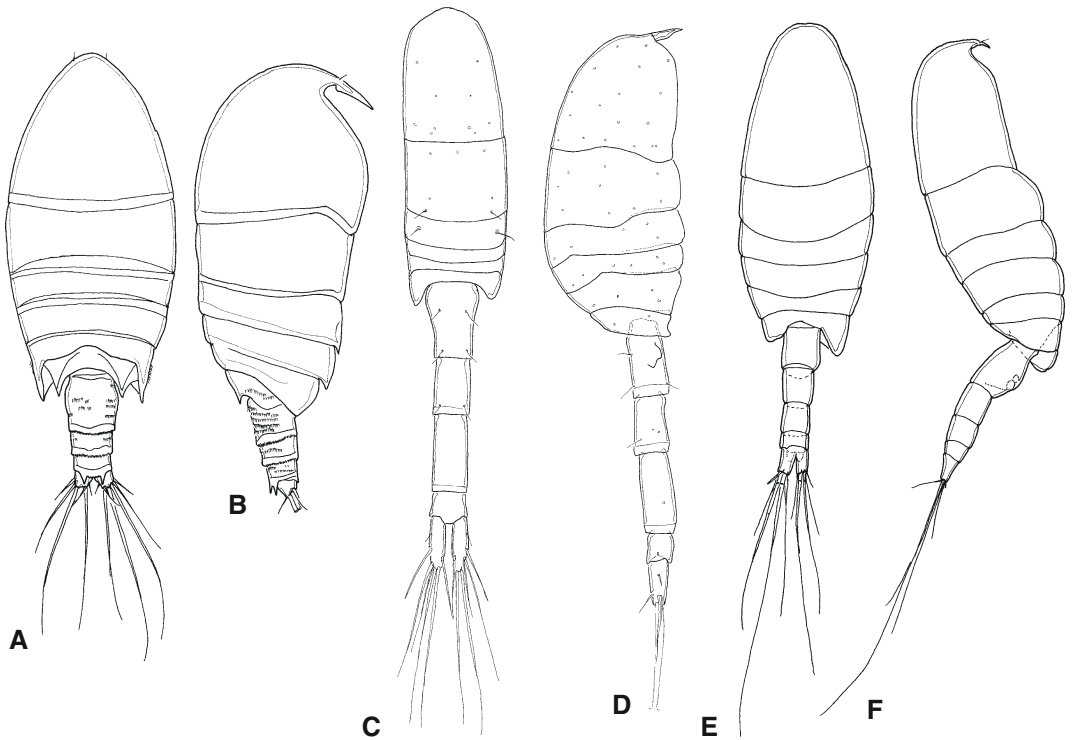


Fig. 27.16. Calanoida. Habitus. **A.** *Pseudocyclops ornatacaudata* Ohtsuka, Fosshagen & Putchakarn, 1999, dorsal. **B.** *P. ornatacaudata*, lateral. **C.** Pseudocyclopiidae gen. et sp. nov., dorsal. **D.** Pseudocyclopiidae gen. et sp. nov., lateral. **E.** *Robpalmeira asymmetrica* Fosshagen & Iliffe, 2003, dorsal. **F.** *R. asymmetrica*, lateral. No scales. A, B, modified from Ohtsuka et al. (1999); C, D, originals; E, F, modified from Fosshagen & Iliffe (2003).

presence of 1 outer spine on the first exopodal segment of P2 and P5, fusion of genital and first abdominal to form a genital double somite in females, and the presence of a maximum of 2 setae on the terminal endopodal segment of the maxilla. A main characteristic of Calanoida is the presence of asymmetrical sexual dimorphism in males. Only 1 gonoduct is functional, producing 1 spermatophore at a time. Spermatophores are transferred by the males with the aid of a modified P5, which is also asymmetrical. When present, the male grasping antennula is modified only on one. Calanoids are the most abundant metazoans in the marine plankton, occurring from the surface to abyssal depths in the water column. However, the ancestral habitat of Calanoida is considered to be the hyperbenthos, retained in some pleuromorphic families, such as Pseudocyclopiidae, Pseudocyclopiidae and Arietellidae. Members of the Family Pseudocyclopiidae can be considered as benthic and can be found sporadically in

meiofauna samples. Some species have enlarged outer exopodal spines on the swimming legs, or display robust modified endopod of P1, and in some species, the antennules are very short or even asymmetrically developed, have been interpreted as an adaptation for digging into the sediments. Most of the species of Pseudocyclopiidae (Fig. 27.16) have been reported from shallow benthopelagic or anchialine cave habitats. Some species such as *Placocalanus* and *Pseudocyclops* have small, compressed and slender body shapes; unusual first swimming legs that seems to be used for digging or holding to the substrate more than for a swimming function and, in the case of *Placocalanus* a modified first antenna with the first segment forming a plate-like structure that seems to be used as a digging organ. The family Pseudocyclopiidae includes 82 valid species arranged in 14 genera: *Badijella* Krsini, 2005 (1 species); *Boholina* Fosshagen, 1989 (5); *Brattstromia* Fosshagen, 1991(6); *Exumella* Fosshagen, 1970 (4); *Exumellina*

Fosshagen, 1998 (1); *Hondurella* Suárez-Morales & Iliffe (1), 2003; *Normancavia* Fosshagen & Iliffe, 2003 (1); *Pinkertonius* Bradford-Grieve, Boxshall & Blanco-Bercial, 2014 (1); *Placocalanus* Fosshagen, 1970 (5); *Pseudocyclops* Brady, 1872 (40); *Ridgewayia* Thompson I. & Scott A., 1903 (14); *Robpalmeria* Fosshagen & Iliffe, 2003 (1), *Stargartia* Fosshagen & Iliffe, 2003 (1) and; *Stygoridgewayia* Tang, Barron & Goater, 2008 (1). The synapomorphic characters of the family can be found in the revision made by Bradford-Grieve (2014).

Key to genera of Pseudocyclopidae

(adopted from Ohtsuka et al. 1996, Boxshall & Halsey 2004)

- 1 Female P5 with exp-3 in normal position (Fig. 27.17C), females retaining the plesiomorphic stage of pair genital apertures. 2
 - Female P5 usually with exp-3 offset on inner-distal margin of second segment (Fig. 27.17D), females with derived stage of one genital aperture. 4 (former *Ridgewayiidae*)
- 2 Female A1 bearing 24–27 segments (Fig. 27.18A); A2 exp 8-segmented (setal formula 1,1,1,1,1,1,4) 3
 - Female A1 up to 17-segmented; A2 exp 5-segmented (setal formula 1,1,4,1,5). *Pseudocyclops*
- 3 Female A1 27-segmented; Male A1 with multiple aesthetascs in segments III (3), V (2) and VII (2); A2 compound distal segment without small serrated process on medial margin; P1 exp-1 with inner seta (Fig. 27.19G); P2–P4 with knob-like projections on outer borders of exps-2,3. *Pinkertonius*
 - Female A1 24–25-segmented; Male A1 without multiple aesthetascs in segments III, V and VII; A2 compound distal segment ornamented with a small serrated process on medial margin; P1 exp-1 lacking inner seta (Fig. 27.19H); P2–P4 without knob-like projections on outer borders of exps-2,3. *Boholina* (former *Boholinidae*)
- 4 Body not laterally compressed (Fig. 27.16E,F); A1 in both sexes long, reaching to or beyond end of prosome, first segment not modified, cylindrical (Fig. 27.18A); P1 enp usually 3-segmented, when reduced without acute distal process; animals commonly found in shallow waters, karstic caves or continental groundwaters. 5
 - Body laterally compressed (Fig. 27.16C,D); A1 in both sexes short, reaching at most the first pedigerous somite, and having the first segment strongly developed and extended forming a triangular expanded plate (Fig. 27.18C); P1 enp 2-segmented, enp-2 unarmed and modified, with a long acute distal process (Fig. 27.19I); animals found in hyperbenthic sandy-bottoms. *Placocalanus*
- 5 P3 and P4 with only 2 outer spines on exp-3 (Fig. 27.17A). 6
 - P3 and P4 with 3 outer spines on exp-3 (Fig. 27.17B). 8
- 6 Md enp-2 and mxl free endopodal segments forming large flattened plates (Fig. 27.19B), with reduced setation; female P5 biramous; male P5 enp-2 or 3-segmented; species found in anchialine caves. 7
 - Md and mxl unmodified cylindrical segments (Fig. 27.19C), female P5 uniramous (Fig. 27.17F); male P5 enp 1-segmented; species found in continental groundwaters. *Stygoridgewayia*
- 7 P5 with exp-3 not markedly offset at its articulation with second segment; mxl enp 3-segmented. *Stargartia*
 - P5 with exp-3 markedly offset at its articulation with second segment; mxl enp 2-segmented. *Exumellina*
- 8 Rostrum without filaments; mxp not reflexed. 9
 - Rostrum with pair filaments (Fig. 27.19A); mxp powerfully developed, reflexed. 11
- 9 Mxp enp bearing modified setae with comb-like tip (Fig. 27.19F). 10
 - Mxp enp without modified setae. *Ridgewayia*
- 10 Rostrum produced ventrally to rounded simple tip; P1 without process on basis; female P5 enp reduced into a 1-segmented unarmed structure (Fig. 27.17E); female P5 exp-3 with armature formula II, I, 4. *Hondurella*

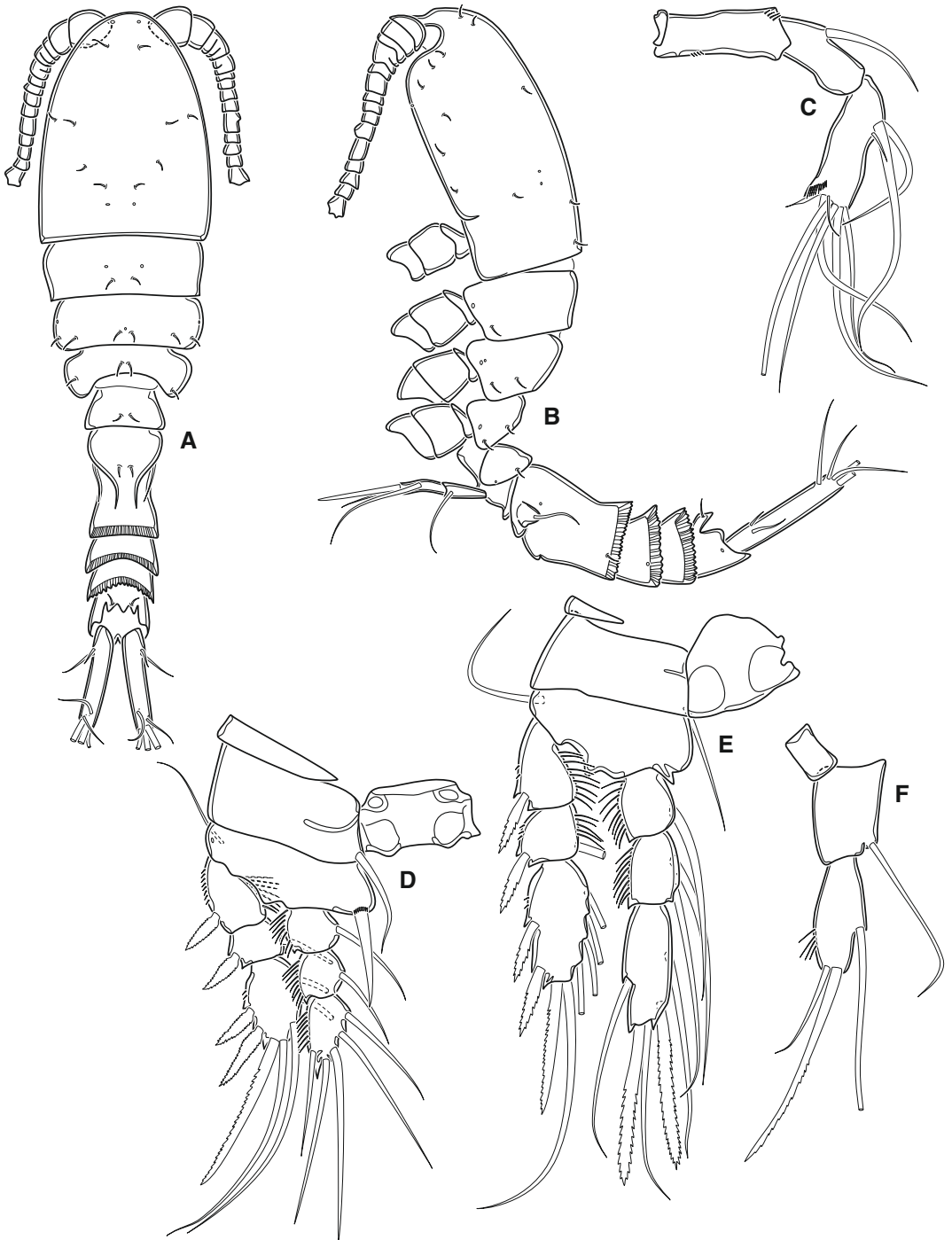


Fig. 27.17. Calanoida. **A.** P3 of *Stargatia palmeri* Fosshagen & Iliffe, 2003. **B.** P3 of *Normancavia minuta* Fosshagen & Iliffe, 2003. **C.** female P5 of *Pseudocyclops ensiger* Ohtsuka, Fosshagen & Putschakarn, 1999. **D.** female P5 of *Pseudocyclopidae* gen. et sp. nov.. **E.** female P5 of *Hondurella verrucosa* Suárez-Morales & Iliffe, 2007. **F.** female P5 of *Stygoridgewayia trispinosa* Tang, Barron & Goater, 2008. **G.** male P5 of *Pseudocyclops bahamensis* Fosshagen, 1968. No scales. A, B, modified from Fosshagen & Iliffe (2003); C, modified from Ohtsuka et al. (1999); D, original; E, modified from Suárez-Morales & Iliffe (2007); F, modified from Tang et al. (2008); G, modified from Huys & Boxshall (1991).

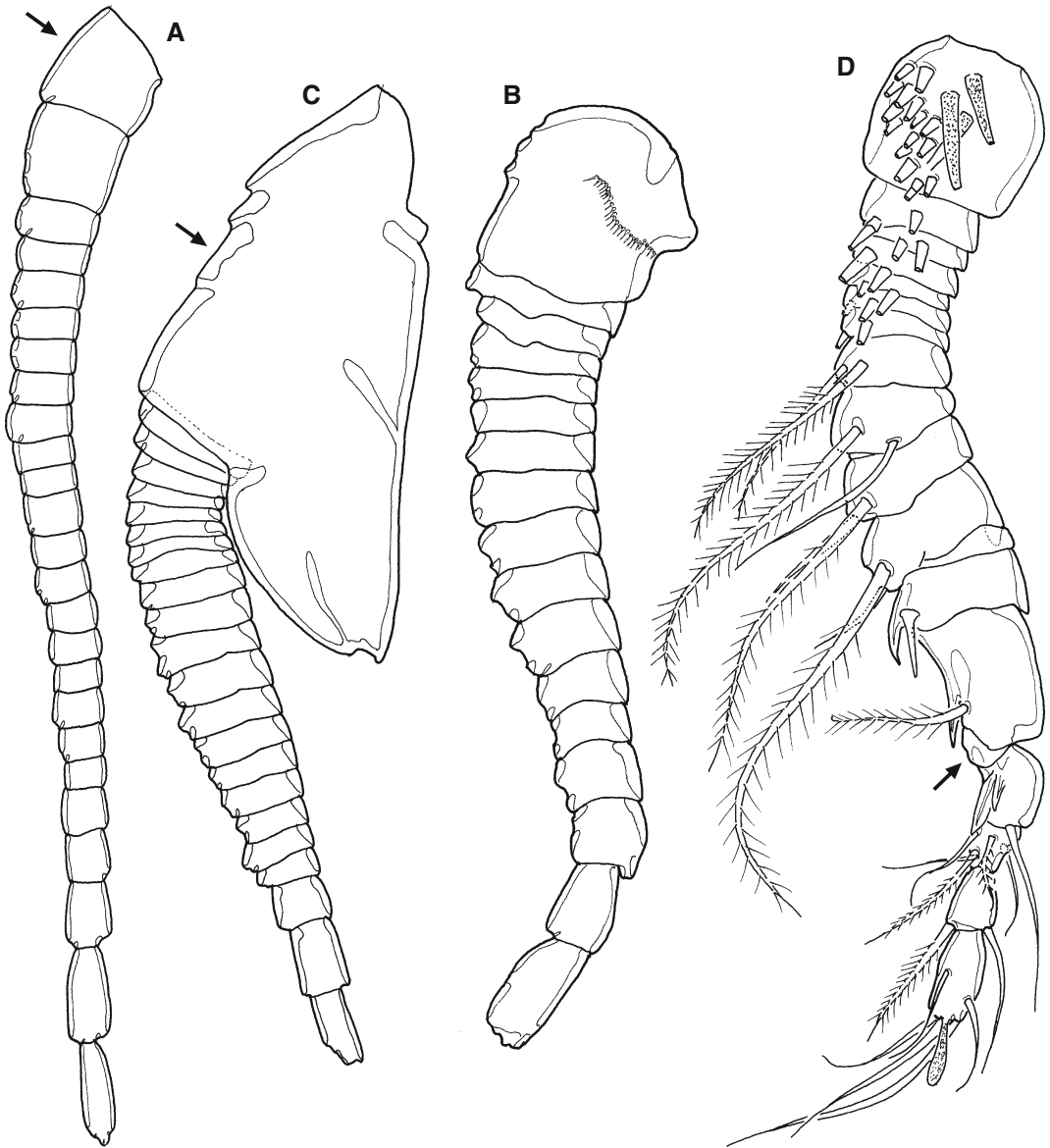


Fig. 27.18. Calanoida. A1. **A.** *Stygoridgewayia trispinosa* Tang, Barron & Goater, 2008, female. **B.** *Pseudocyclops bahamensis* Fosshagen, 1968, female. **C.** *Placocalanus insularis* Fosshagen, 1970, female. **D.** *Pseudocyclops bahamensis* Fosshagen, 1968, male. No scales. A, modified from Tang et al. (2008); B–D, modified from Huys & Boxshall (1991).

- Rostrum bifurcate at tip; P1 with strong process on basis; female P5 enp 3-segmented; female P5 exp-3 with armature formula II, II, 4. *Brattstromia*
- 11 Md palp with reduced enp, setae on basis absent (Fig. 27.16D); male P5 with enp 3-segmented. *Exumella*
- Md palp with well-developed enp and armed with 1–2 setae on basis (Fig. 27.16E); male P5 with lobate or at most 2-segmented enp. 12

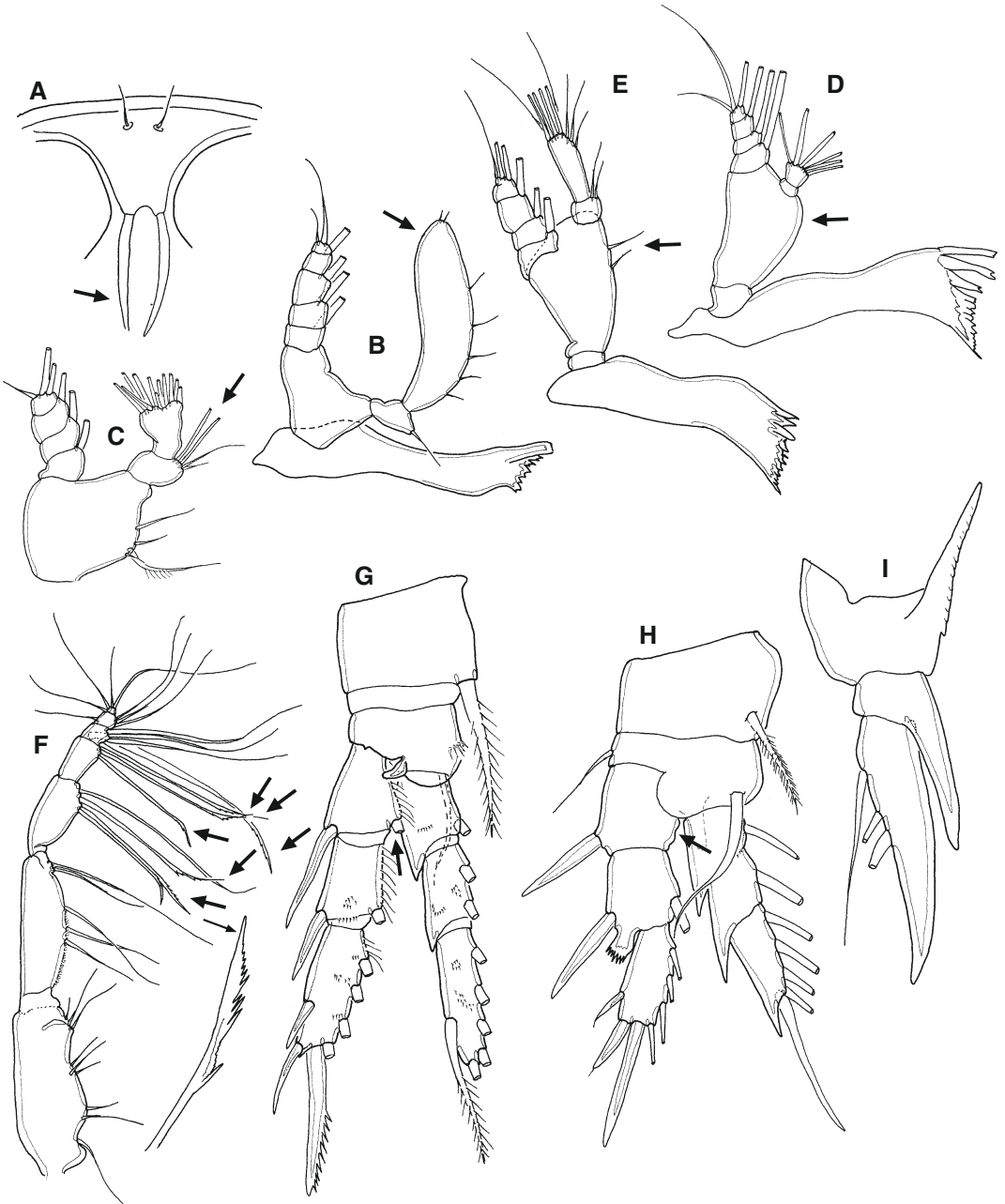


Fig. 27.19. Calanoida. **A.** Rostrum of *Badijella jalzici* Kršinic, 2005. **B.** md of *Exumellina bucculenta* Fosshagen & Iliffe, 1998. **C.** md palp of *Stygoridgewayia trispinosa* Tang, Barron & Goater, 2008. **D.** md of *Exumella polyarthra* Fosshagen, 1970. **E.** md of *Robpalmeria asymmetrica* Fosshagen & Iliffe, 2003. **F.** mxp of *Brattstromia longicauda* Fosshagen & Iliffe, 1991. **G.** P1 of *Pinkertonius ambiguus* Bradford-Grieve, Boxshall & Blanco-Bercial, 2014. **H.** P1 of *Boholina crassicephala* Fosshagen & Iliffe, 1989. **I.** P1 of *Placocalanus longicauda* Ohtsuka, Fosshagen & Soh, 1996. No scales. **A,** modified from Kršinic (2005); **B,** modified from Fosshagen & Iliffe (1998); **C,** modified from Tang et al. (2008); **D,** modified from Fosshagen (1970); **E,** modified from Fosshagen & Iliffe (2003); **F,** modified from Fosshagen & Iliffe (1991); **G,** modified from Bradford-Grieve et al. (2014); **H,** modified from Fosshagen & Iliffe (1989); **I,** modified from Ohtsuka et al. 1996.

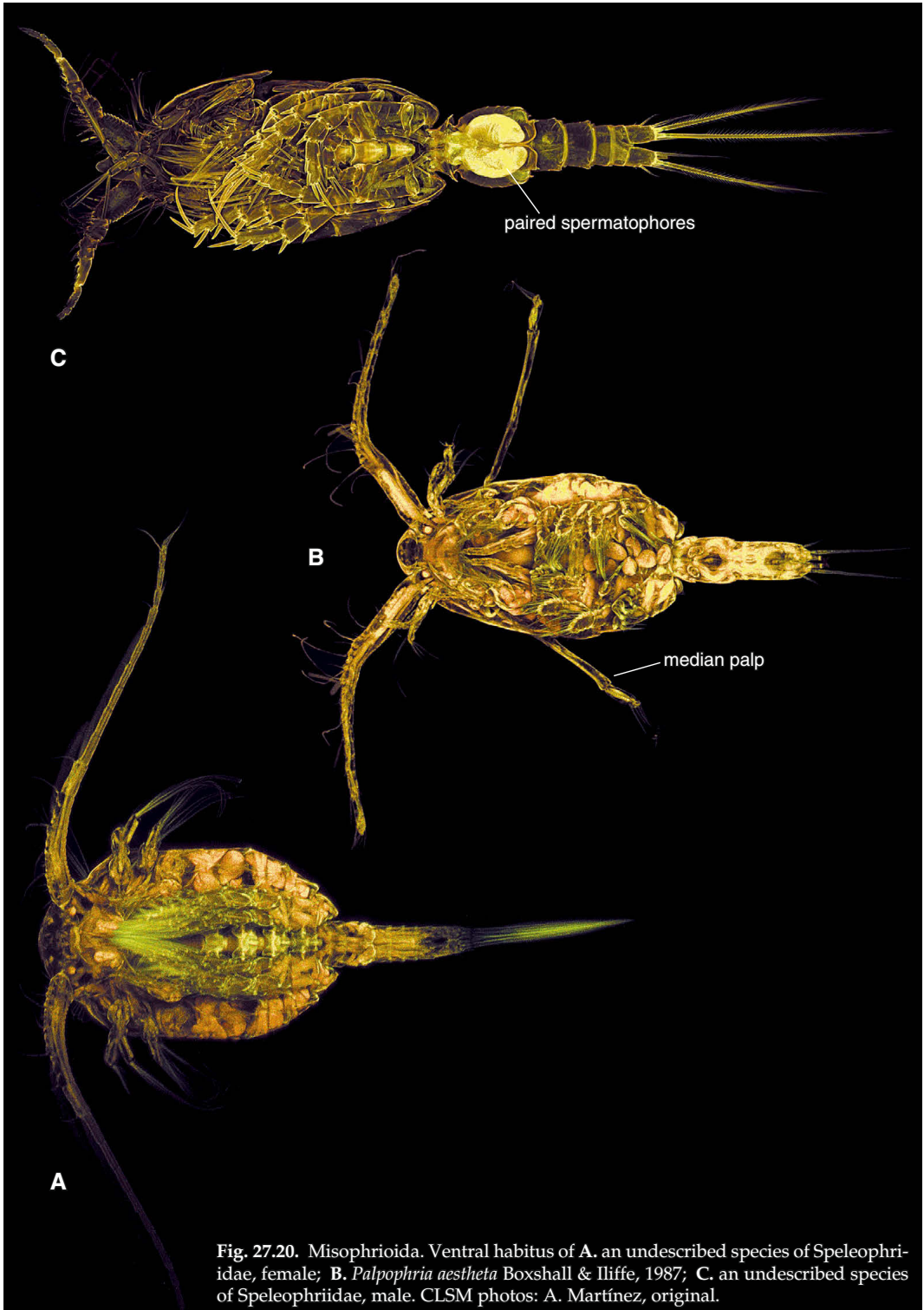


Fig. 27.20. Misophrioida. Ventral habitus of **A.** an undescribed species of Speleophriidae, female; **B.** *Palpophria aestheta* Boxshall & Iliffe, 1987; **C.** an undescribed species of Speleophriidae, male. CLSM photos: A. Martínez, original.

- 12 Md distal enp elongated; female P5 biramous, female P5 exp-3 armed with 4 spines and 3 setae. 13
- Md distal enp not elongated; female P5 uniramous, lacking enp; female P5 exp-3 armed with 3 spines and 2 setae. *Normancavia*
- 13 Female last prosomal somite asymmetrical (Fig. 27.16E); male P5 enp reduced to minute rounded bulb in both sides, mxl enp 1-segmented. *Robpalmeria*
- Female last prosomal somite symmetrical; male P5 with 2-segmented enp, bearing 4 distal setae on enp2; mxl enp 3-segmented. *Badijella*

Order Misophrioida Gurney, 1933

(Pedro Martínez Arbizu, Alejandro Martínez, Nancy Mercado-Salas and Sahar Khodami)

Misophrioida is the first offshoot of the Podoplea. They are exclusively hyperbenthic or dwelling in the water column of anchialine caves. No Misophrioida is known from interstitial habitats or ocean surface waters. They can be found sporadically as a by-catch in meiofauna samples, for instance in the deep-sea or in caves (Martínez Arbizu & Seifried 1996, Martínez Arbizu & Jaume 1999, Boxshall & Jaume 2000).

The order is divided into 3 families, the Misophriidae Brady, 1878 (19 species), the Speleophriidae Boxshall & Jaume, 2000 (21) and the monotypic Palpophriidae Boxshall & Jaume, 2000 (single species *Palpophria aestheta* Boxshall & Iliffe, 1987 living in the anchialine lava tunnel Jameos del Agua, Lanzarote, Spain; Figs. 27.20B, 27.22C). Misophriidae comprises 8 genera, mainly hyperbenthic. The genera *Benthomisophria* Sars G. O., 1909, *Misophria* Boeck, 1865, *Misophriella* Boxshall, 1983, and *Misophriopsis* Boxshall, 1983 (Fig. 27.21D) are common in near bottom deep-sea waters. *Arcticomisophria* Martínez Arbizu & Seifried, 1996 and *Fosshageniella* Jaume & Boxshall, 1997 inhabit shallow water hyperbenthic habitats at higher latitudes. *Dimisophria* Boxshall & Iliffe, 1987 and *Stygomisophria* Ohtsuka, Huys, Boxshall & Ito, 1992 inhabit the water column of anchialine caves. Boxshall and Halsey 2004 suggested that *Dimisophria* might be a late copepodid stage of another misophrioid genus. It is excluded therefore from the key below.

The Speleophriidae comprises 8 genera, from which only *Archimisophria* Boxshall, 1983 is the only hyperbenthic deep-sea representative, being the remaining 7 genera (*Boxshallia* Huys, 1988, *Expansophria* Boxshall & Iliffe, 1987, *Huysia* Jaume, Boxshall & Iliffe, 1998, *Mexicophria* Boxshall, Zylinski, Jaume, Iliffe & Suárez-Morales, 2014, *Protospeleophria* Jaume, Boxshall & Iliffe, 1998, *Speleophria* Boxshall & Iliffe, 1986 and *Speleophriopsis* Jaume & Boxshall, 1996) exclusive from the water column of anchialine caves and cenotes.

Morphological based phylogenesis recovered Seleophriidae, including most anchialine species and the marine hyperbenthic *Archimisophria*, as sister to a clade with the monotypic cave-dwelling Palpophriidae splitting next to the marine Misophriidae (Boxshall & Jaume 2000). However recent molecular results suggest that *Palpophria* is a derived genus within Speleophriidae and *Archimisophria* should rather be assigned as a basal member of the Misophriidae (Khodami, pers. comm.).

Hyperbenthic misophrioids are probably omnivorous, feeding on algae as well as preda-ting on smaller copepods and plankton (Martínez Arbizu & Jaume 1999, Ohtsuka et al. 2018). Cave misophrioids are probably scavengers or predators as they get attracted by baited traps.

Key to Misophrioida families and genera

(modified from Martínez Arbizu & Seifried 1996, Boxshall & Halsey 2004)

- 1 Female A1 26 to 27-segmented (Fig. 27.22G), 23 to 25-segmented in male, A2 exp 6 to 8-segmented (Fig. 27.22F), P5 enp represented at most by a small lobe bearing 1 seta, md palp biramous, habitus like in Figs. 27.22D,E. 2 Speleophriidae
- Female A1 17- to 19-segmented (Fig. 27.21A), 12 to 15-segmented in male, A2 exp 6-segmented (Fig. 27.21F), P5 enp represented at most by a small lobe bearing 2 setae (Figs. 27.21C,E), md palp biramous (Fig. 27.21B), habitus like in Fig. 27.21D. 8 Misophriidae
- Female A1 26-segmented (Fig. 27.22C), A2 exp 7-segmented (Fig. 27.22A), P5 reduced to a lobe with a single seta (Fig. 27.22B), md palp uniramous and extremely elongated (Fig. 27.22C). Palpophriidae
- 2 P1 enp 3-segmented. 3
- P1 enp 2-segmented. 6

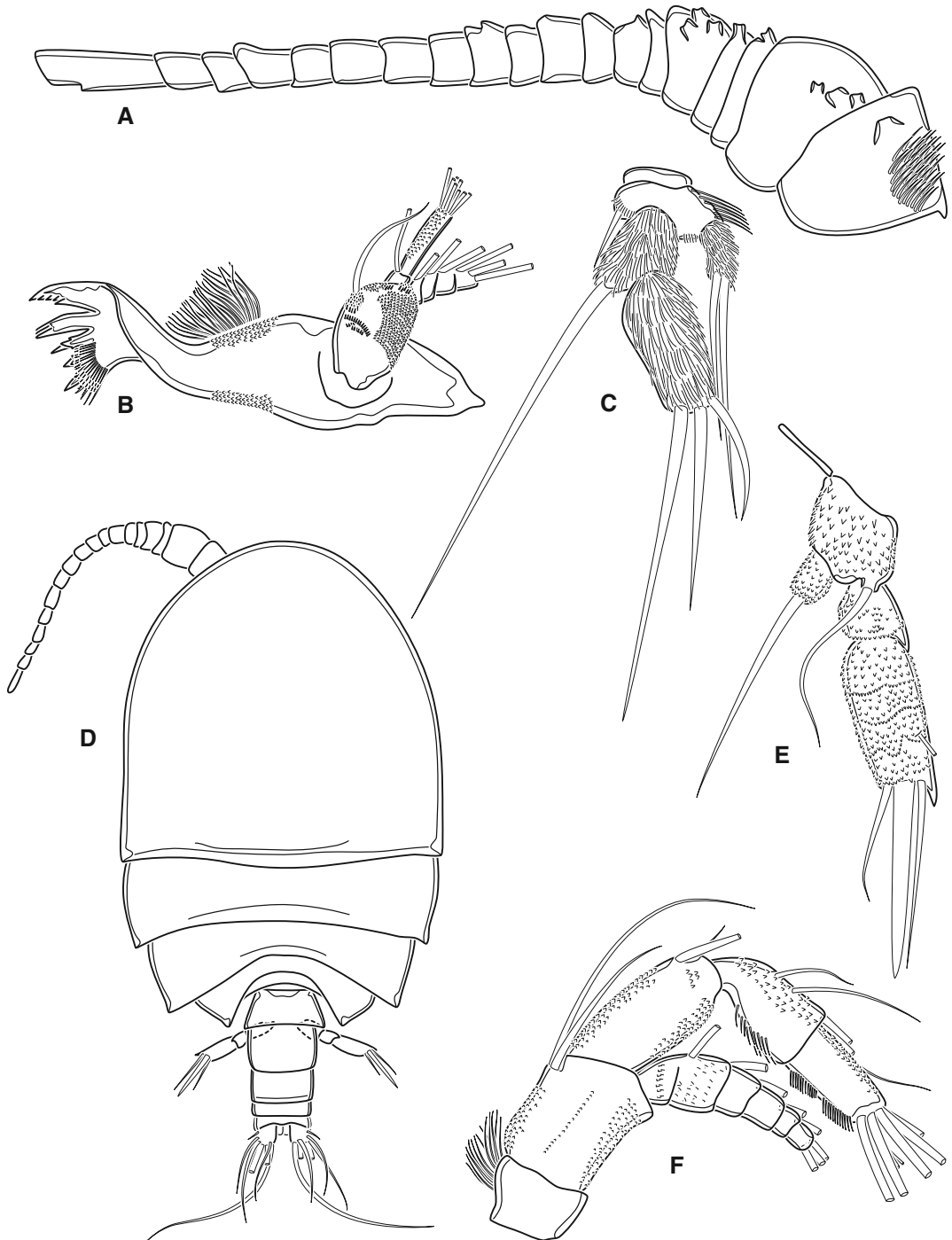


Fig. 27.21. Misophrioida. A. Female A1 of *Arcticomisophria bathylaptevensis* Martínez Arbizu & Seifried, 1996. B. md of *Misophriopsis polaris* Martínez Arbizu & Jaume, 1999. C. female P5 of *A. bathylaptevensis*. D. dorsal habitus of *M. polaris*. E. Female P5 of *M. polaris*. F. A2 of *M. polaris*. No scales. A, C, modified from Martínez Arbizu & Seifried (1996); B, D, E, F, modified from Martínez Arbizu & Jaume (1999).

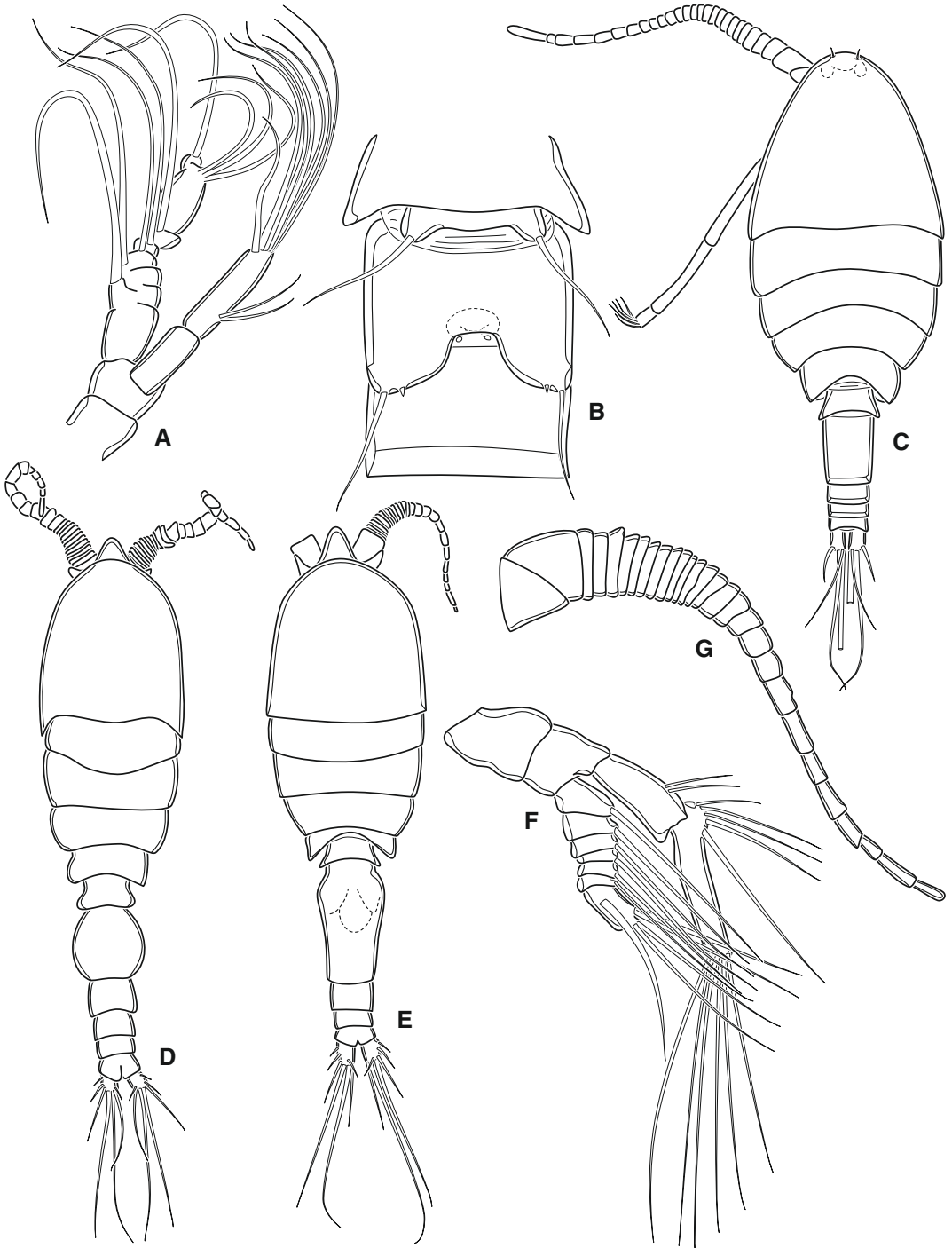


Fig. 27.22. Misophrioida. **A.** A2 of *Palpophria aestheta* Boxshall & Iliffe, 1987. **B.** female P5 and P6 of *P. aestheta*, ventral. **C.** dorsal habitus of *P. aestheta*. **D.** dorsal habitus of *Speleophriopsis mljetensis* Kršinić, 2017, male. **E.** dorsal habitus of *S. mljetensis*, female. **F.** A2 of *S. mljetensis*. **G.** female A1 of *S. mljetensis*. No scales. A–C, modified from Boxshall & Jaume (2000); D–G, modified from Kršinić (2017).

- 3 First pedigerous somite free but concealed beneath carapace-like extension of posterior rim of cephalosome. *Archimisophria*
 – First pedigerous somite free but not concealed beneath carapace-like extension of cephalosome. 4
- 4 Female A1 27-segmented with swelling on proximal segment, P5 enp represented by inner seta on basis. 5
 – Female A1 26-segmented without swelling on proximal segment, P5 without any vestige of enp. *Expansophria*
- 5 P1 enp 3-segmented, P5 exp 2-segmented.
 *Boxshallia bulbantennulata*
 – P1 enp 2-segmented, P5 exp 1-segmented.
 *Mexicophria cenotocola*
- 6 P5 enp 1-segmented bearing 1 seta.
 single species *Huysia bahamensis*
 from Exuma Cays in the Bahamas
 – P5 lacking enp. 7
- 7 P4 with 5 setae on inner margin of exp-3.
 *Speleophriopsis*
 – P4 with 4 setae on inner margin of exp-3.
 *Speleophria*
 – P4 with 3 setae on inner margin of exp-3.
 *Protospeleophria lucayae*
- 8 P1 with 2 setae on inner margin of enp-2. 9
 – P1 with 1 seta on inner margin of enp-2.
 *Arcticomisophria*
- 9 A2 with 5-segmented exp. P5 reduced, bilobed, with an at most 1-segmented exp.
 *Benthomisophria*
 – A2 with 6-segmented exp. P5 with an at least 2-segmented exp. 10
- 10 Female A1 17-segmented. *Misophria*
 – Female A1 at least 18-segmented. 11
- 11 Female A1 19-segmented. 12
 – Female A1 18-segmented. 13
- 12 P5 with distinct endopodal segment bearing 2 seta. *Fosshageniella glabra*
 – P5 lacking any vestige of the enp.
 *Misophriella*

- 13 P5 exp-1 with outer seta.
 *Stygomisophria kororiensis*
 – P5 exp-1 without outer seta. *Misophriopsis*

Order Cyclopoida Burmeister, 1834

(Pedro Martínez Arbizu, Nancy Mercado-Salas and Sahar Khodami)

Cyclopoids are characterized by a prosome comprising cephalosome and 4 free pedigerous somites (podoplean tagmosis), males A1 geniculated on both sides (geniculation lost in poecilostomes families), A2 exp represented by up to 3 setae on basis (no exopodal segment remains; Fig. 27.23B), no remain of enp on P5 (Fig. 27.23F) in both sexes, P4 exp-3 with 1 terminal spine and only 2 outer spines (Figs. 27.27E, 27.27E), gonopores of female on lateral position, always paired eggs sacs (if present). The order Cyclopoida includes more than 3000 marine species. Most of them (>2250 species) unified as 'poecilostomes families' are parasites or associated with other organisms. Members of Cyclopoida are the most abundant and successful group in continental waters with more than 900 species belonging to the family Cyclopidae Rafinesque, 1815, but the order also includes species from brackish coastal and marine habitats, anchialine caves, as well as parasitic forms. In the plankton, the most common cyclopoids are the Oithonidae Dana, 1853 and Oncaidae Giesbrecht, 1893. However, the most plesiomorphic members of the order Cyclopoida inhabit hyperbenthic environments, moving near to the bottom or penetrating the upper layers of the muddy sediments. In the brackish coastal environments (including mangroves) members of the families Euryteidae Monchenko, 1974, Halicyclopidae Kiefer, 1927, Cyclopidae and Cyclopinidae Sars G. O., 1913 can be found; in anchialine systems species in addition the families Speleoithonidae Rocha & Iliffe, 1991 and some members of Cyclopettidae Martínez Arbizu, 2000 are present; some Hemicyclopinidae Martínez Arbizu, 2001 are adapted to interstitial coastal groundwaters; in hyperbenthic and benthic marine habitats (including interstices of submerged marine sands) species of the families Cyclopettidae, Cyclopinidae, Giselinidae Martínez Arbizu, 2000, Psammocyclopinidae Martínez Arbizu, 2001, Schminkepinellidae Martínez Arbizu, 2006 and Smirnovipinidae Khodami, Vaun MacArthur, Blanco-Bercial & Martínez Arbizu, 2017 can be typically found. Some cyclopoids display

morphological adaptations that allowed them to colonize interstices of marine sands, among these changes are the elongation and compression of body shapes, the reduction of the number of eggs per egg-sac, the shortened antennules and the reduction of armature in swimming legs.

The systematic relationships and inner taxonomy of Cyclopoida is in the state of flux, which makes it difficult to provide a complete key to all the families. An initial morphological revision of the order was undertaken by Martínez Arbizu (1997a,b,c, 2000a,b 2001a,b, 2006) basically subdividing the paraphyletic Cyclopinidae into monophyletic units which were later corroborated by molecular methods by Khodami et al (2017). Recently, Khodami et al (in press) proposed a new high level phylogeny of Cyclopoida based on molecular data. They divide the cyclopoida into 4 suborders, (1) Cyclopicinoidea, to allocate the single monotypic family Cyclopicinidae Khodami, Vaun MacArthur, Blanco-Bercial & Martínez Arbizu, 2017 (genus *Cyclopicina* Lindberg, 1953), (2) Ergasiloidea, to allocate the marine free-living families Giselinidae (deep-sea) and Schminkepinellidae (deep-sea and anchialine caves) together with the so called poecilostome families, (3) Cyclopoidea, to allocate the marine Euryteidae (loose associated invertebrates), the brakish water living Halicyclopidae and the fresh-water Cyclopidae, together with some parasitic families (see below), and (4) Oithonoidea to allocate the marine free-living families (see below) together with some planktonic and invertebrate associated families.

The so called poecilostome families are all associated with or parasites on other organisms.

The key to free-living marine Cyclopoida presented below includes only the families underlined in the following systematic account.

Cyclopicinoidea: Cyclopicinidae.

Ergasiloidea: Giselinidae, Schminkepinellidae and poecilostome families (Abrsiidae Karanovic, 2008, Anchimolgidae Humes & Boxshall, 1996, Anomoclausidae Gotto, 1964, Antheacheridae M. Sars, 1870, Anthessiidae Humes, 1986, Bomolochidae Claus, 1875, Bradophilidae Marchenkov, 2002, Catiniidae Bocquet & Stock, 1957, Chondracanthidae Milne Edwards, 1840, Clausidiidae Embleton, 1901, Clausiidae Giesbrecht, 1895, Corallovexiidae Stock, 1975, Corycaeidae Dana, 1852, Echiurophilidae Delamare Deboutteville & Nunes-Ruivo, 1955, Entobiidae Ho,

1984, Erebonasteridae, Ergasilidae Burmeister, 1835, Eunicolidae G. O. Sars, 1918, Gadilicolidae Boxshall & O'Reilly, 2015, Gastrodelphyidae List, 1889, Herpyllobiidae Hansen, 1892, Intramoligidae Marchenkov & Boxshall, 1995, Iveidae Tung, Cheng, Lin, Ho, Kuo, Yu & Su, 2014, Jasmineiricolidae Boxshall, O'Reilly, Sikorski & Summerfield, 2015, Kelleriidae Humes & Boxshall, 1996, Lamippidae Joliet, 1882, Leaniricolidae Huys, 2016, Lichomolgidae Kossmann, 1877, Lubbockidae Huys & Böttger-Schnack, 1997, Macrochironidae Humes & Boxshall, 1996, Makrostrotidae Huys, Fatih, Ohtsuka & Llewellyn-Hughes, 2012, Mesoglicolidae Zulueta, 1911, Mycolidae Yamaguti, 1936, Mytilicolidae Bocquet & Stock, 1957, Nereicolidae Claus, 1875, Octopicolidae Humes & Boxshall, 1996, Oncaeidae Giesbrecht, 1893, Paralubbockidae Boxshall & Huys, 1989, Philichthyidae Vogt, 1877, Philoblennidae Izawa, 1976, Phyllocolidae Delamare Deboutteville & Laubier, 1961, Pionodesmotidae Bonnier, 1898, Polyankyliidae Ho & Kim, 1997, Praxillinicolidae Huys, 2016, Pseudanthessiidae Humes & Stock, 1972, Rhynchomolgidae Humes & Stock, 1972, Sabelliphilidae Gurney, 1927, Saccopsidae Lützen, 1964, Sapphirinidae Thorell, 1859, Serpulidicolidae Ho, 1979, Shiinoidae Cressey, 1975, Spiophanicolidae Ho, 1984, Splanchnotrophidae Norman & T. Scott, 1906, Strepidae Cheng, Liu & Dai, 2016, Synapticolidae Humes & Boxshall, 1996, Synaptiphilidae Bocquet & Stock, 1957, Taeniacanthidae C. B. Wilson, 1911, Telsidae Ho, 1967, Thamnomolgidae Humes & Boxshall, 1996, Urocopiidae Humes & Stock, 1972, Vahiniidae Humes, 1967, Ventriculinidae Leigh-Sharpe, 1934, Xarifiidae Humes, 1960, Micrallectidae Huys, 2001 and Xenocoelomatidae Bresciani & Lützen, 1966).

Cyclopoidea: Ascidicolidae Thorell, 1859, (Buppridae Thorell, 1859, Enterognathidae Illg & Dudley, 1980, and Enteropsidae Thorell, 1859 are considered as lineages of Ascidicolidae (Illg and Dudley, 1980; Boxshall and Halsey, 2004)), Cyclopidae (Cyclopinae + Eucyclopinae), Euryteidae, Halicyclopidae, Lernaeidae, Ozmanidae Ho & Thatcher, 1989, Fратиidae Ho, Conradi & López-González, 1998, Botryllophilidae G. O. Sars, 1921.

Oithonoidea Dana, 1853: Archinotodelphyidae Lang, 1949, Chitonophilidae Avdeev & Sirenko, 1991, Chordeumiidae Boxshall, 1988, Cucumari-
colidae Bouligand & Delamare-Deboutteville, 1959, Cyclopettidae, Cyclopinidae, Hemicyclopi-

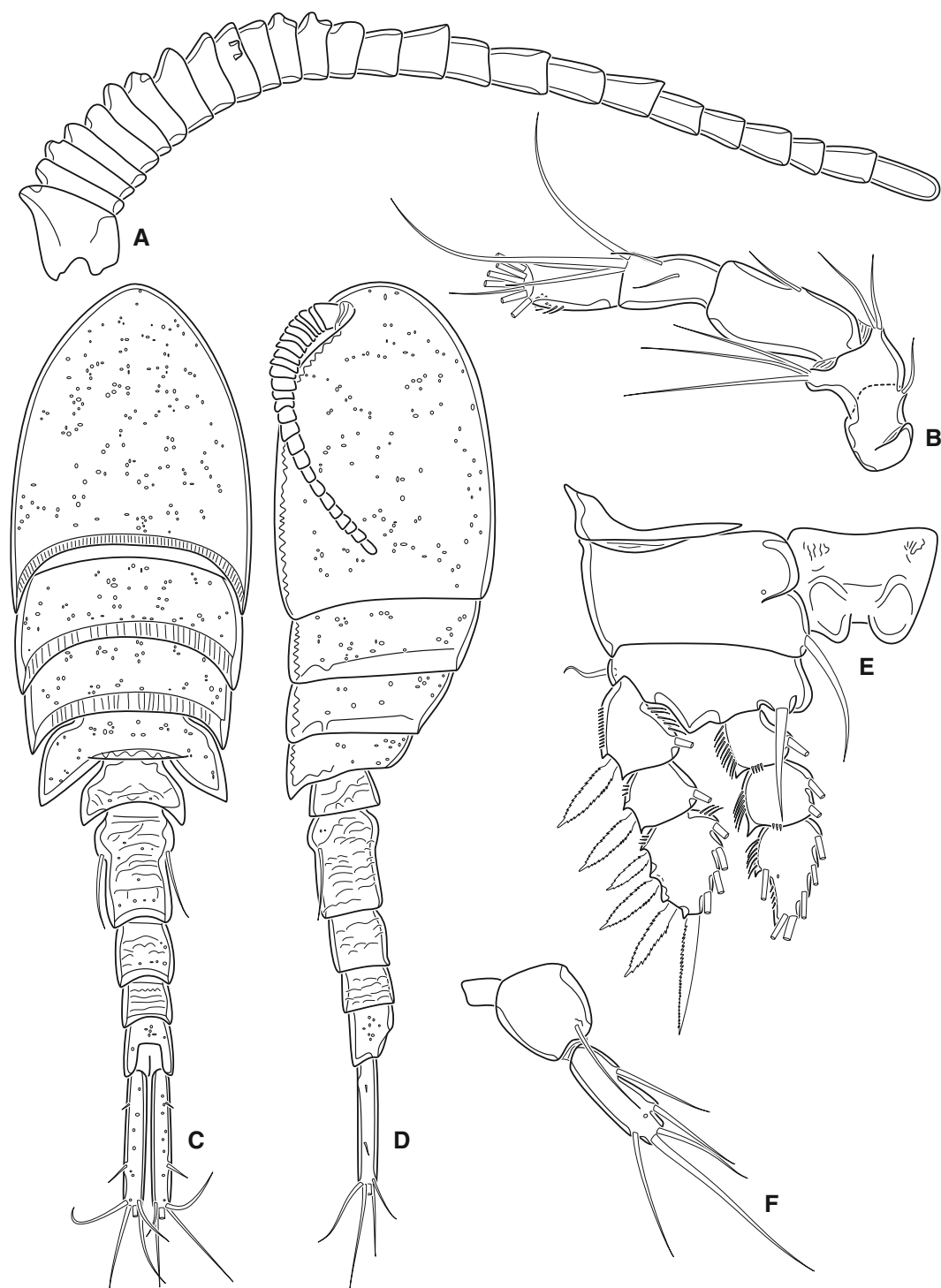


Fig. 27.23. Cyclopoida. *Cyclocpicina toyoshioae* Ohtsuka, Tanaka & Boxshall, 2016. A. female A1. B. A2. C. dorsal habitus, female. D. lateral habitus, female. E. P1. F. female P5. No scales. A-F, modified from Ohtsuka et al. (2016).

nidae, Mantridae Leigh-Sharpe, 1934, Notodelphyidae Dana, 1853, Oithonidae, *Psammocyclopinidae*, *Pterinopsyllidae*, *Smirnovipinidae*, *Speleoithonidae* and *Thaumatopsyllidae* Sars G. O., 1913.

Key to benthic and hyperbenthic free living marine Cyclopoida

- 1 Female A1 26-segmented (Fig. 27.23A), exp A2 represented by 2–3 seate (Fig. 27.23B), A2 coxa with 1 seta (Fig. 27.23B).
..... Cyclopicinidae (only genus *Cyclopicina*)
– These characters not combined. 2
- 2 Md palp reduced to 1 segment (at most) with up to 3 setae (Fig. 27.24D–F), male A1 geniculated (sexually dimorphic), female genital apertures (gonopores) ventrally (Fig. 27.25 D–H). 3 Cyclopoidea
– Md palp reduced to 1 segment (at most) with up to 4 setae (or absent), A1 male not geniculated, A1 at most 8-segmented in both sexes, A2 without exp, female genital apertures (gonopores) laterally or dorso-laterally.
..... poecilostome families
– Md palp with basis and enp (exp reduced or with up to 4 segments). 4
- 3 Marine and estuarine species; A1 18–21-segmented; mxp with 2 curved claws on apical enp segment (Fig. 27.25A); P5 intercoxal sclerite always present; female P5 exp bearing 4 elements (Fig. 27.25D).
..... Euryteidae
– Predominantly brackish water species; A1 up to 15-segmented; mxp with 1 straight claw on apical enp (Fig. 27.25B); P5 intercoxal sclerite present (Fig. 27.25E) or absent (Fig. 27.25F); female P5 exp bearing 4 or 5 elements.
..... Halicyclopidae
– Predominantly freshwater species; A1 up to 17-segmented; P5 intercoxal sclerite always absent (fused to 5th pedigerous somite); female P5 exp bearing up to 3 elements (Figs. 27.25G,H). Cyclopidae
- 4 P1–P4 exp-1 without inner seta, P1 enp-2 with only 1 inner seta (Fig. 27.27D), P4 exp-3 at least terminal outer seta and distal inner seta transformed into spines (Fig. 27.27E).
..... 5 (Ergasiliioidea in part)
– These characters not combined.
..... 6 Oithonoidea
- 5 P1 fused to cephalosome (Fig. 27.27A–B), P1 enp-3 with only 2 inner setae (5 setae in total), P1 exp-3 with only 2 outer spines (3 spines and 4 setae in total) (Fig. 27.27D), A2 without palp (Fig. 27.27C), furcal setae I and III located on dorsal margin. Giselinidae
– P4 end-2 distal inner seta transformed into a spine, P4 enp-3 with all setae transformed into spines (Fig. 27.27E), md palp with distinct basis and enp (Fig. 27.28B), female P5 exp with 3 spine and 1 seta (Fig. 27.28D).
..... Schminkepinellidae
- 6 Body form elongated, harpacticoid-like (Figs. 27.29A, 27.30G). 7
– Body form cyclopoid-like (Figs. 27.29F, 27.30A, 27.31A,F). 8
- 7 A1 short, at most 10- or 11-segmented in female (Figs. 27.29A,B), P2–P3 exp-3 with 2 outer spines, female P5 with distinct coxa (bearing 1 inner seta) and basis (Fig. 27.29C), living in interstices of sublittoral sands.
..... Psammocyclopinidae
– A1 11- to 19-segmented in female, P2–P3 exp-3 with 3 outer spines, female P5 with fused coxa and basis (coxal seta on inner margin present or absent), enp-2 and enp-3 of mxp elongated (twice as long as wide) (Fig. 27.30E), living in marine coastal groundwaters.
..... Hemicyclopinidae
(in part: *Procyelopina*, *Hemicyclopinina*, *Neocyclopinina*, *Glareolina*, *Parapseudocyclopinodes*)
- 8 A1 16- to 18-segmented in female, 8th most and 5th most distal A1 segments with 1 seta (Fig. 27.30B), P1 exp-3 with 3 outer spines and 5 setae (Fig. 27.30D), female P5 with inner coxal seta (coxa and basis fused or separated) (Fig. 27.30C). Hemicyclopinidae
(in part: *Cyclopinodes*, *Pseudocyclopinina*)
– First pedigerous somite free, female A1 18- or 19-segmented, with traces of subdivision on 3rd and 4th (double segments) and 7th (triple segment) segments, 8th most and 5th most distal A1 segments without setae (Fig. 27.29E), female P5 with distinct coxa (without inner seta) and basis (Fig. 27.29D), furca usually elongated (Fig. 27.29F). Smirnovipinidae
– These characters not combined. 9

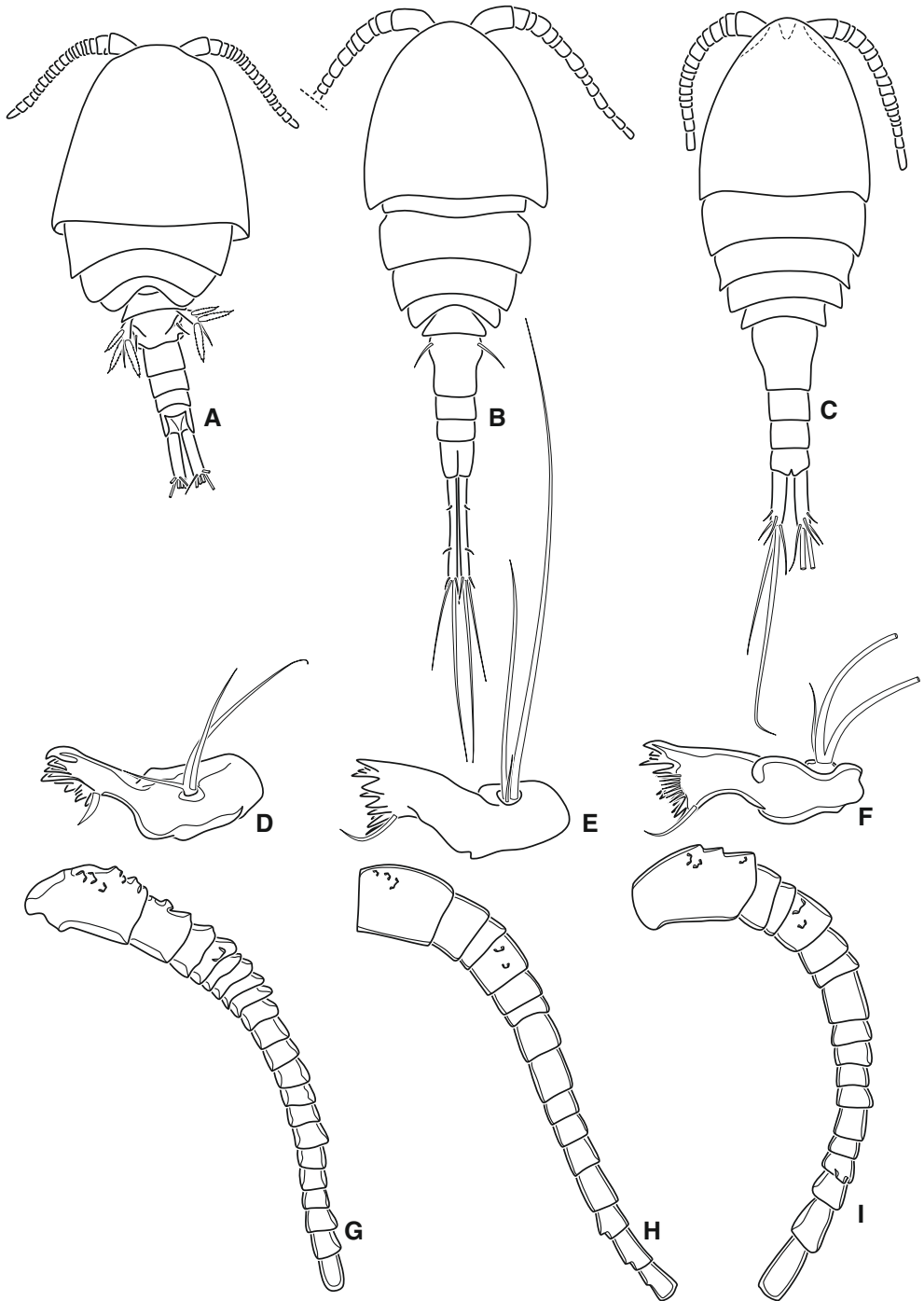


Fig. 27.24. Cyclopoida. **A.** Dorsal habitus of *Euryte koreana* Karanovic 2014. **B.** dorsal habitus of *Troglodyclops janstocki* Rocha & Iliffe, 1994. **C.** dorsal habitus of *Acanthocyclops americanus* (Marsh, 1893). **D.** md of *E. koreana*, **E.** md of *T. janstocki*. **F.** md of *A. americanus*. **G.** female A1 of *E. koreana*. **H.** female A1 of *T. janstocki*. **I.** female A1 of *A. americanus*. No scales. A,D,G, modified from Karanovic (2014); B,E,H, modified from Rocha & Iliffe (1994); C,F,I, modified from Miracle et al. (2013).

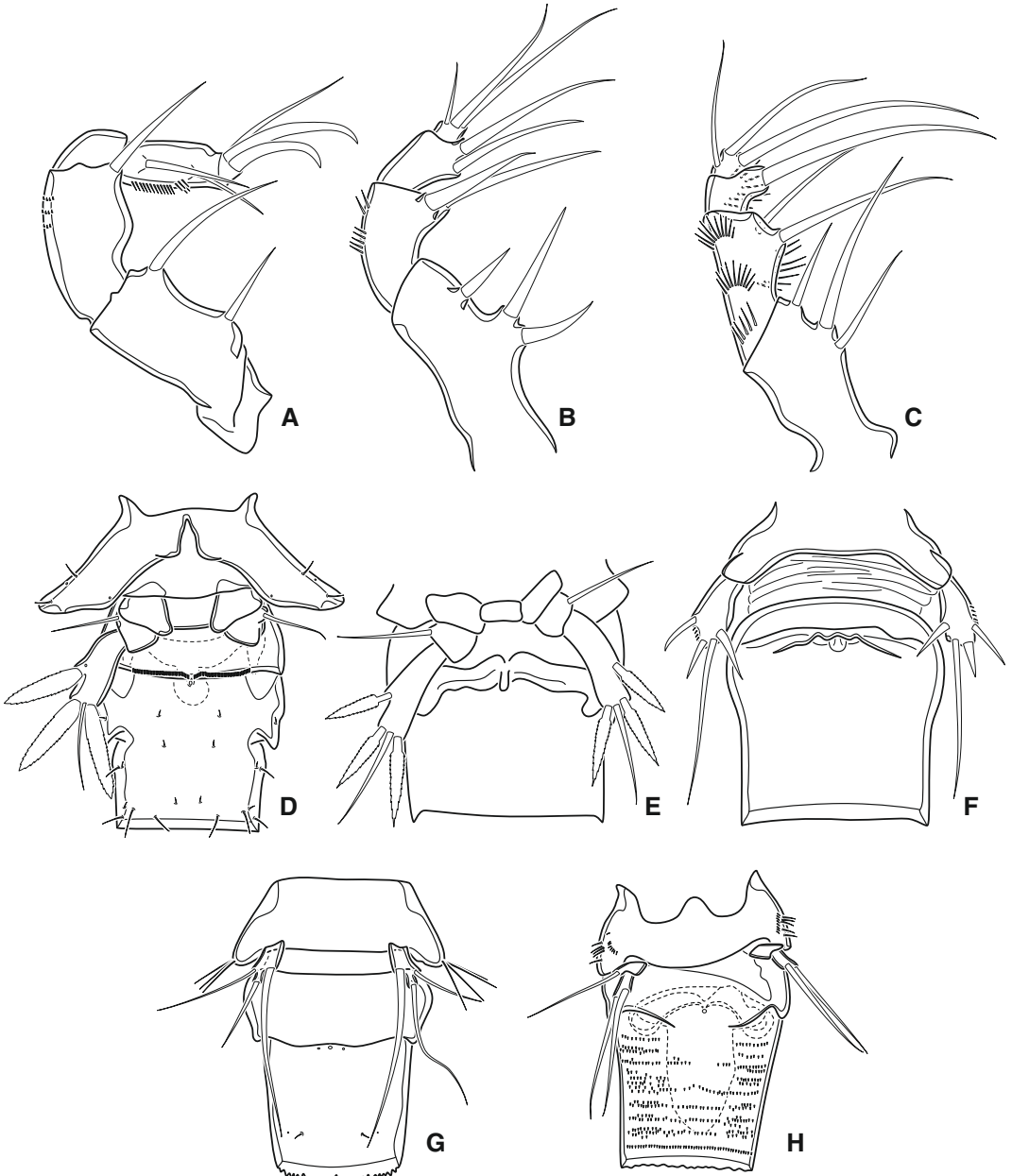


Fig. 27.25. Cyclopoida. **A.** Mxp of *Euryte robusta* Giesbrecht, 1900. **B.** mxp of *Neocyclops hoonsooi* Lee & Chang, 2015. **C.** mxp of *Diacyclops chakan* Fiers et al., 1996. **D.** female genital somite and P5 of *E. robusta*. **E.** female genital somite and P5 of *Neocyclops stocki* Pesce, 1985. **F.** female genital somite and P5 of *Halicyclops cenoticola* Rocha et al., 1998. **G.** female genital somite and P5 of *Eucyclops edytiae* Tang & Knoot, 2009. **H.** female genital somite and P5 of *Mesocyclops granulatus* Holynska et al. 2003. No scales; A, D, modified from Huys & Boxshall (1991); B, modified from Lee & Chang (2015); C, modified from Fiers et al. (1996); E, modified from Pesce (1985); F, modified from Rocha et al. (1998); G, modified from Tang & Knoot (2009); H, modified from Holynska et al. (2003).



Fig. 27.26. Cyclopoida. Female habitus of undescribed species of *Neocyclops*. A. ventral. B. dorsal. CLSM photos: A. Martínez.

- 9 A1 female 9-segmented, P1 exp-3 with 3 outer spines and 5 setae, female P5 without coxal seta, P5 exp 1-segmented with 4 elements (1 outer and 1 outer distal spine and 1 inner distal and 1 inner seta), copulatory pore ventrally.
 ... Hemicyclopinidae (in part: *Monchenkiella*)
- A1 at most 12 segmented (can be reduced to 8-11 segments), the 6th segment elongated (4-7× longer than wide) (Fig. 27.31E), if A1 9-segmented, the 5th, if 8-segmented the 4th is elongated, P1 exp-3 with 4 spines and 4 setae (Fig. 27.31H), female P5 exp 1-segmented with just 3 elements (one terminal seta in between of one inner and one outer spine) (Fig. 27.31G), copulatory pore ventrally. Cyclopinidae
 - A1 7-, 9-, 15- or 17-segmented, P5 located in lateral margin, without intercoxal sclerite joining them, protopod of P5 fused to somite

so that exopod arises directly from somite (Fig. 27.32C), no ventrally located copulatory pore in female (displaced to lateral position) (Figs. 27.32A,B), enp of mxp 2-segmented. ..
 Cyclopettidae

- Body robust (Fig. 27.31A), A1 short, 8-segmented in female, with broad very ornamented setae (Fig. 27.31D), P5 ventrally located, with distinct coxa (with 1 inner seta) and basis (Fig. 27.31C), copulatory pore ventral, P4 exp-3 with only 1 outer and 1 terminal spine (Fig. 27.31B), distal outer spine transformed into a seta located on anterior surface of segment, P4 end 2-segmented in female (Fig. 27.31B). Pterinopsyllidae

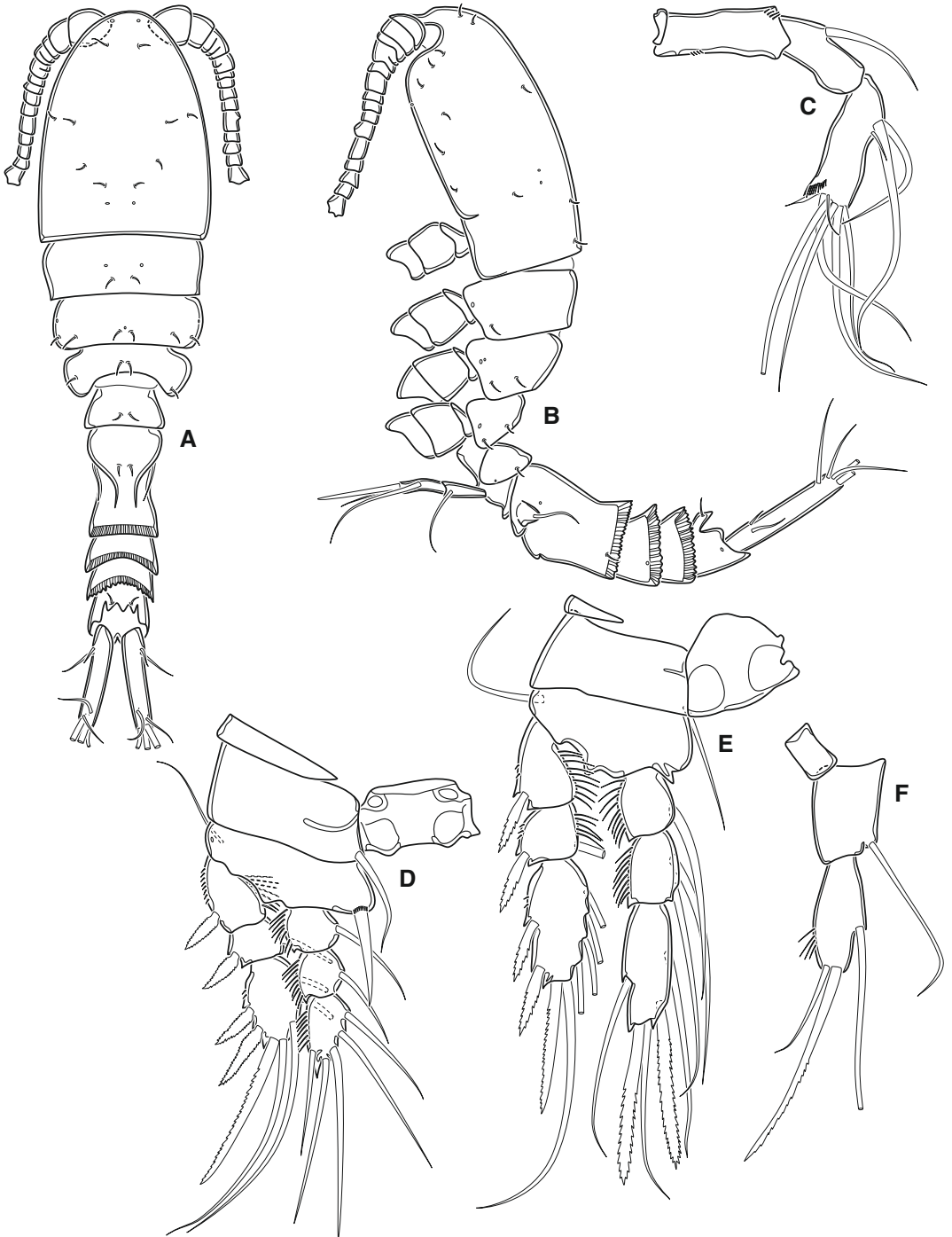


Fig. 27.27. Cyclopoida. *Giselina cristata* Martínez Arbizu, 2000, female. A. Dorsal habitus. B. Lateral habitus. C. A2. D. P1. E. P4. F. P5. No scales. A-F, modified from Martínez Arbizu (2000a).

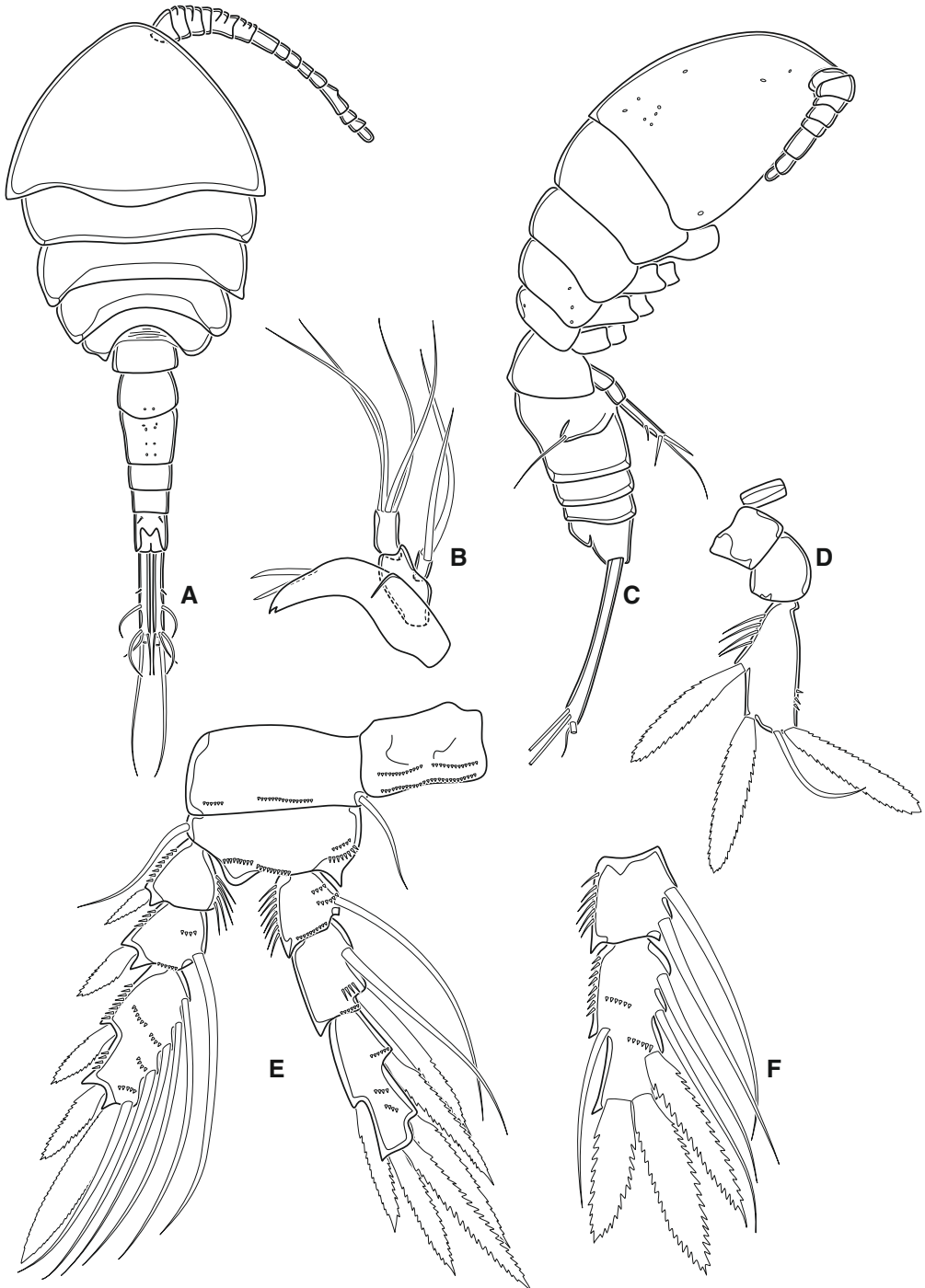


Fig. 27.28. Cyclopoida. **A.** Dorsal habitus of *Muceddina multispinosa* Jaume & Boxshall, 1996. **B.** md of *Schminkepinella plumifera* Martínez Arbizu, 2006. **C.** lateral habitus of *S. plumifera*. **D.** female P5 of *Einslepinella mediana* Martínez Arbizu, 2006. **E.** P4 of *M. multispinosa*. **F.** enp 2-3 of P3 of *M. multispinosa*. No scales. A, E, F, modified from Jaume & Boxshall (1996); B-D, modified from Martínez Arbizu (2006).

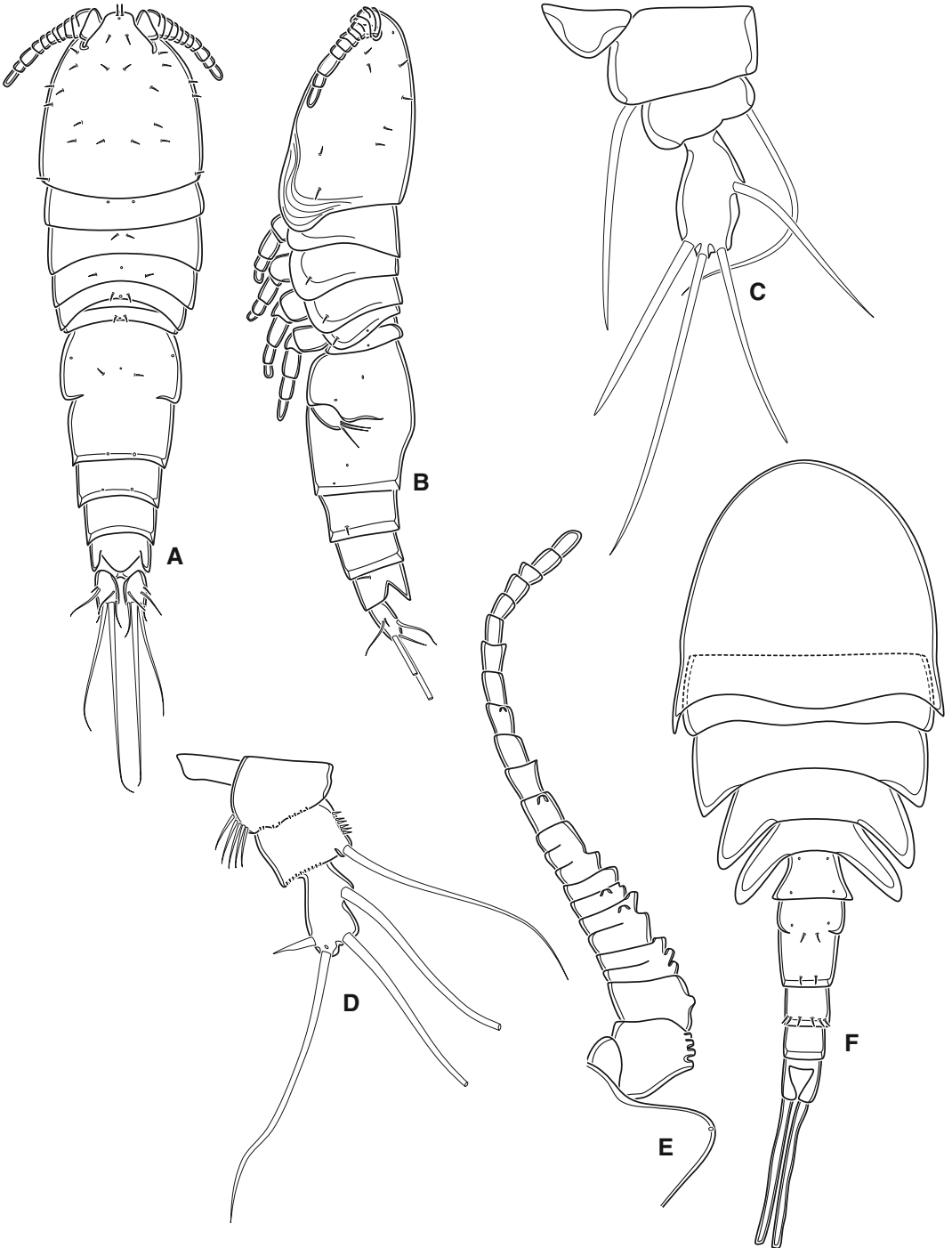


Fig. 27.29. Cyclopoida. **A.** Dorsal female habitus of *Psammocyclopina georgei* Martínez Arbizu, 2001. **B.** lateral female habitus of *P. georgei*. **C.** female P5 of *P. georgei*. **D.** female P5 of *Smirnovipina barentsiana* (Smirnov, 1931). **E.** female A1 of *S. barentsiana*. **F.** dorsal habitus of *S. barentsiana*, female. No scales. A–C, modified from Martínez Arbizu (2001b); D–F, modified from Martínez Arbizu (1997c).

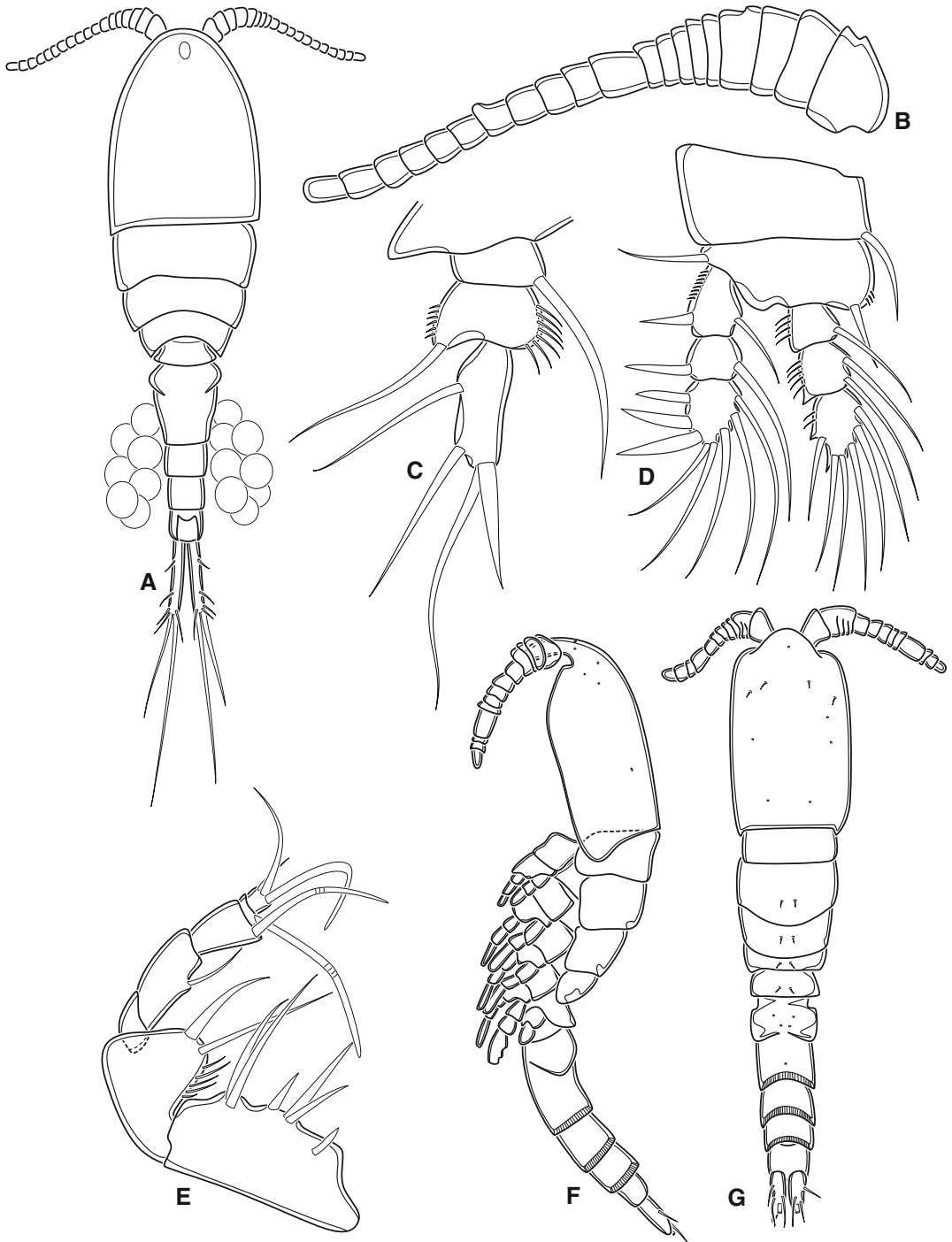


Fig. 27.30. Cyclopoida. A. Dorsal female habitus of *Cyclopinodes elegans* (Scott, T., 1894). B. female A1 of *C. elegans*. C. female P5 of *C. elegans*. D. P1 of *C. elegans*. E. mxp of *Hemicyclopina begoniae* Martínez Arbizu 2001. F. lateral female habitus of *H. begoniae*. G. dorsal habitus of *H. begoniae*, female. No scales. A-D, modified from Sars (1913); E-G, modified from Martínez Arbizu (2001a).

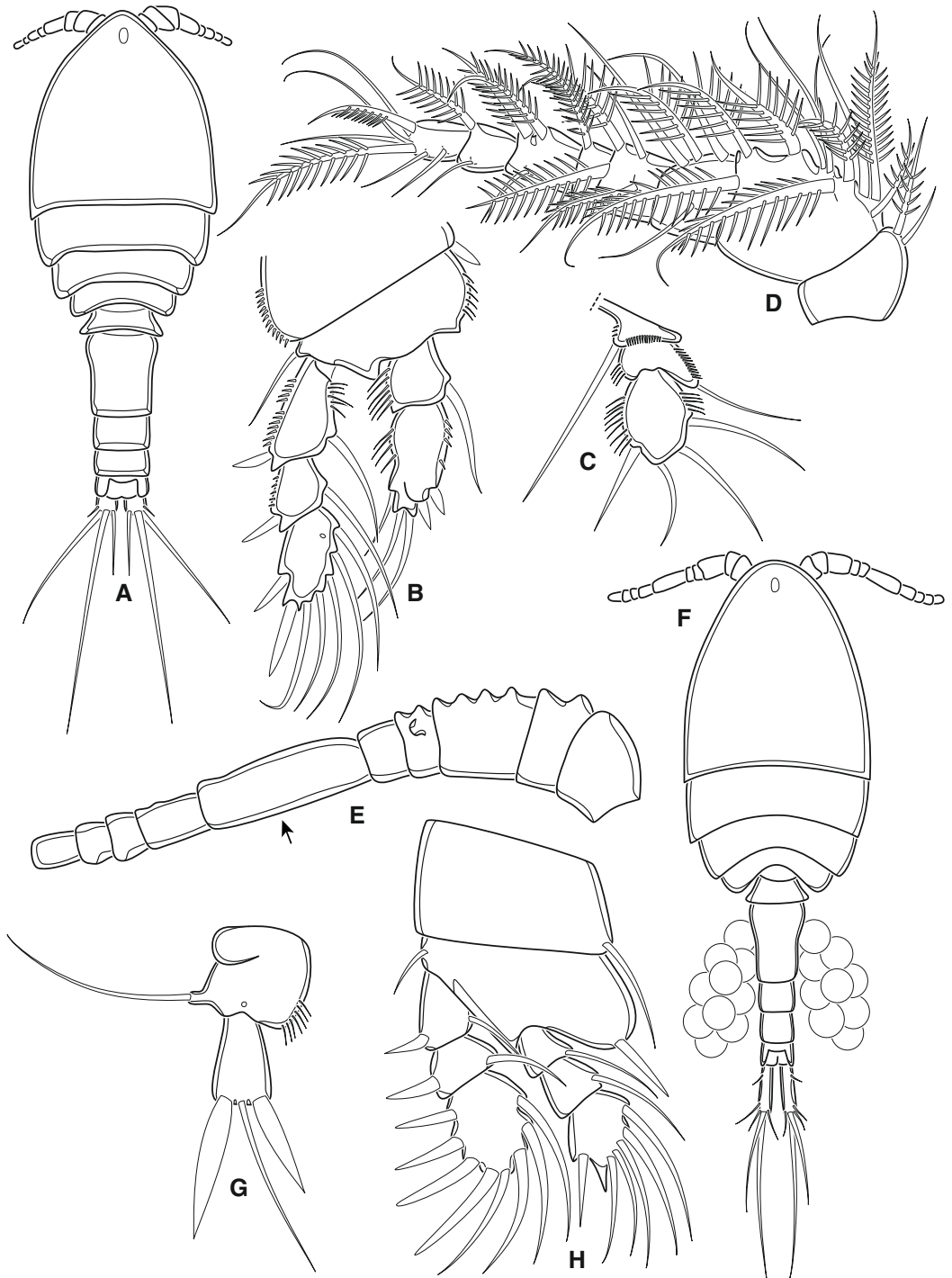


Fig. 27.31. Cyclopoida. **A.** dorsal female habitus of *Pterinopsyllus insignis* (Brady, 1878). **B.** P4 of *P. insignis*. **C.** female P5 of *P. insignis*. **D.** female A1 of *P. insignis*. **E.** female A1 of *Cyclopina gracilis* Claus, 1863. **F.** dorsal female habitus of *C. gracilis*. **G.** female P5 of *C. gracilis*. **H.** P1 of *C. gracilis*. No scales. A-F, modified from Sars (1913).

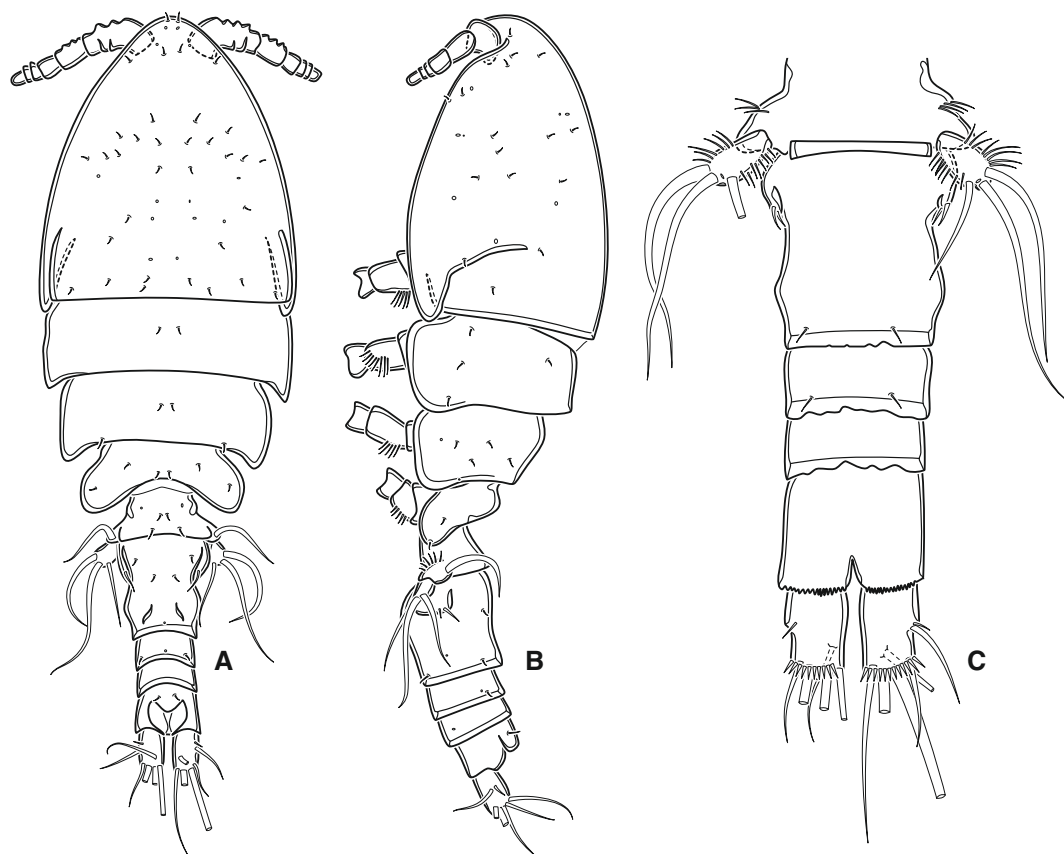


Fig. 27.32. Cyclopoida. *Cyclopetta boetiussae* Martínez Arbizu, 2000, female. A. Dorsal habitus. B. lateral habitus. C. urosome, ventral. No scales. A–C, modified from Martínez Arbizu (2000b).

Order Harpacticoida Sars, 1903 (Kai Horst George and Karin Pointner)

Harpacticoida Sars, 1903 is the copepod order with most representatives in the meiofaunal communities. At the moment, the order contains about 4000 marine benthic species, belonging to 555 genera and 54 families (Walter & Boxshall 2018d).

Harpacticoids are characterized by a prosome comprising cephalosome and 4 free pedigerous somites (podoplean tagmosis), A1 at most 9-segmented in females and 14-segmented in males; A2 with 4-segmented exp and 2-segmented enp; P5 basis and enp fused to benp.

This group is widespread across the world, from tropical to Polar Regions with some genera being considered cosmopolitan and other showing a more restricted distribution. Marine

harpacticoids are mainly bottom-living copepods and successfully exploited a wide variety of environments that include deep sea, hydrothermal vents, sea ice, the phytal, mangroves, brackish and shallow waters, interstices of submersed sands and groundwaters (Seifried 2003) (Table 27.2).

The harpacticoids can be very abundant in soft coarse grain sediments and macroalgae. These small copepods (0.2 to 2.5 mm) are usually the second most abundant meiofaunal taxon (after Nematoda) with densities ranging from tens to thousands inds./cm². In marine ecosystems, harpacticoids flexibility in nutritional demands play an important role in aquatic food webs by coupling nutrients with higher trophic levels, and also structure benthic and pelagic links (Hicks & Coull 1983).

Key to harpacticoid families

(adopted from Lang 1948b, Huys et al. 1996, Boxshall & Halsey 2004, Wells 2007)

- 1 Commensal on baleen whales, sirenians, turtles. Balaenophilidae
- Not commensal on baleen whales, sirenians, turtles. 2
- 2 Body short, laterally strongly compressed, amphipod-like (Figs. 27.33A,B). Tegastidae (Figs. 27.33A,B)
- Body broad, rounded/ovoid, strongly dorsoventrally compressed (Figs. 27.33C,D). 3
- Body different: elongated, cylindrical, fusiform, or vermiform (Figs. 27.33E-S). 5
- 3 Body ovoid; integument strongly chitinized, often with sclerotized ridges (Fig. 27.33C); P1 principally as in Fig. 27.34A. Peltidiidae (Peltidiinae) (Fig. 27.33C)
- Body shield-shaped, prosoma large, with broad epimeral plates, urosoma small (Fig. 27.33D). 4
- 4 P1 principally as in Fig. 27.34B; P5 large, without endopod, exp extending until telson and completing ovoid body shape. Porcellidiidae (Fig. 27.33D)

Fig. 27.33. Body shapes (habitus) of Harpacticoida. **A.** Tegastidae dorsal. **B.** Tegastidae lateral. **C.** Peltidiidae. **D.** Porcellidiidae. **E.** Aegisthidae (Cerviniopsinae). **F.** Aegisthidae (Cerviniinae). **G.** Ectinosomatidae. **H.** Tachidiidae. **I.** Argestidae. **J.** Ancorabolinae (*Ceratonotus*-group). **K.** Cylindropsyllidae. **L.** Louriniidae. **M.** Cletodidae. **N.** Metidae. **O.** Orthopsyllidae. **P.** Nannopodiidae. **Q.** Ancorabolinae (*Ancorabolutus*-lineage). **R.** Pseudotachidiidae. **S.** Tetragonicipitidae. No scales. CLSM photos: A, L, N, O, F. Nazari; B-I, K, M, P-S, T. C. Kihara; J, S. Durst, J. Schuckenbrock; material of C kindly provided by S. Rossel, material of I kindly provided by C. Schmidt.

- P1 as in Fig. 27.34C; P5 with distinct exp and benp, outer basal seta arising from long setophore. Hamondiidae (*Hamondia*)
- 5 P1 principally as in Figs. 27.34D,J; not or weakly prehensile; basis may be laterally elongated; enp and exp 1-3-segmented, enp-1 not surpassing length of exp-1 and exp-2 together, endopodal segments of nearly the same length. 6
- P1 principally as in Fig. 27.34E; exp and/or enp clearly prehensile, rami slender or robust; basis may be laterally elongated; enp-1 at least as long as exps-1 and -2 together, enp-2 and/or enp-3 (if present) smaller than enp-1; last segment with at least 1 claw. 30

Table 27.2. List of marine environments and the most common harpacticoid families encountered in these habitats.

Environment	Families
Shallow waters	
Coarse grained sandy sediments (epibenthic species)	Cletodidae, Danielsseniinae, Ectinosomatidae, Harpacticidae, Laophontidae, Miraciidae, Tachidiidae, Thomspsonulidae
Fine to medium sandy sediments (interstitial species)	Ameiridae, Canthocamptidae, Cylindropsyllidae, Ectinosomatidae, Leptastacidae, Nannopodiidae, Paramesochridae, Rhizothrichidae
Mud substrates (epibenthic and interstitial species)	Ectinosomatidae, Cletodidae, Miraciidae, Tachidiidae
Brackish waters	Ameiridae, Canthocamptidae, Cletodidae, Ectinosomatidae, Miraciidae, Nannopodiidae, Tachidiidae
Mangroves	Canthocamptidae, Cletodidae, Darcythompsoniidae, Pseudotachidiidae
Phytoplankton	Harpacticidae, Laophontidae, Peltidiidae, Porcellidiidae, Tegastidae, Thalestridae, Tisbidae
Anchialine caves	Novocriniidae, Rotundiclipeidae, Superornatiremidae
Sea ice	Ectinosomatidae, Harpacticidae, Thalestridae, Tisbidae
Hydrothermal vents	Aegisthidae, Ancorabolidae, Argestidae, Ectinosomatidae, Laophontidae, Tisbidae, Pseudotachidiidae (Donsiellinae)
Deep sea	Aegisthidae, Tisbidae, Ancorabolinae, Argestidae, Cletodidae, Ectinosomatidae, Neobryidae, Ameiridae, Miraciidae, Danielseninae, Pseudotachidiinae, Thalestridae, Rometidae, Parameiropsidae



- 6 Body somewhat pyriform, pro- and urosoma clearly distinguishable, prosome sometimes with strong projections; A2 exp 3-4-segmented; md palp 3-4-segmented; mxp with 2-segmented exp, enp-1 with 3 setae, enp-2 with 1 inner and 1 outer seta and 2 apical spines. ...
 Aegisthidae (3 subfamilies:
 Aegisthinae, Cerviniinae (Fig. 27.33F),
 and Cerviniopsinae (Fig. 27.33E);
 systematics unresolved)
 - These characters not combined. 7
- 7 A2 and md with 4-segmented exp; mxp phyllopodial. 8
 - A2 exp 4-segmented; md exp 2-segmented; cphth circular, remaining body tapering distally; md gnathobase forming stylet; P1 exp and enp 1-segmented (Fig. 27.34F).
 Rotundiclipeidae
- 8 A2 and md exp at most 3-segmented. 9
 - Body slender, mostly cylindrical; anal operculum absent; mxp enp 2-segmented; P1 exp-1 without inner seta, exp-3 with 3 outer spines.
 Neobradylidae
 - Body fusiform, cphth frontally butt; anal operculum present; mxp enp 1-segmented; P1 exp-1 with inner seta, exp-3 with 2 outer spines. Rometidae
 - Body fusiform, cphth tapering frontally; md enp 2-segmented; mxp prehensile.
 Novocriiniidae
- 9 Body distinctly fusiform or cylindrical (Fig. 27.33G); A1 very short; mx principally as in Figs. 27.34G,H; P5 of characteristic shape (Fig. 27.34I), with 2 setae on benp, and 3-4 setae on exp, one of which often on exopodal surface. Ectinosomatidae (Fig. 27.33G)
 - These characters not combined. 10
- 10 Body cycloform, pro- and urosoma clearly distinguishable (Fig. 27.33H); cphth and prosomal somites laterally with integumental windows (Fig. 27.37C); A2 exp 1-2-segmented; P1-P4 regularly 3-segmented, P1 principally as in Figs. 27.34D,J.
 Tachidiidae (Fig. 27.33H)
 - These characters not combined. 11
- 11 Body cylindrical, slightly depressed; cphth and most body somites with lateral globular glands (Fig. 27.35A); P1 exp 2-segmented, enp 1-2-segmented (Fig. 27.35B).
 Adenopleurellidae
 - These characters not combined. 12
- 12 Body cylindrical, integument weakly sclerotized, so gut content regularly visible, body often equipped with many spinules (Figs. 27.33I, 27.35C); telson large, mostly square, FR set widely apart and of variable length (Fig. 27.35C); A2 with 1-2-segmented exp; coxae of swimming legs larger than bases, shape and segmentation of swimming legs highly variable. Argestidae (Fig. 27.33I)
 - These characters not combined. 13
- 13 Body cylindrical, slender, cphth and body somites often with dorsal and/or lateral processes; female A1 3-4-segmented; A2 without exp; P1-P4 bases transversely strongly elongated (Fig. 27.35D).
 Ancorabolinae (*Ceratnotus*-group)
 (Fig. 27.33J)
 - These characters not combined. 14
- 14 Body cylindrical, no clear separation between pro- and urosome; female A1 5-segmented; A2 exp 1-segmented, P1-P4 enps 2-segmented. Cletodidae (Fig. 27.33M)
 - These characters not combined. 15
- 15 Body slender, cylindrical to vermiform (Fig. 27.33K); female A1 7-segmented; A2 exp 1-segmented; P1-P4 exps 3-segmented, enps 1-2-segmented.
 Cyliodropsyllidae (Fig. 27.33K)
 - These characters not combined. 16
- 16 Body of variable shape, often robust; rostrum well-developed, shovel-like; FR short (Fig. 27.35E); female A1 4-6-segmented; A2 exp usually 3-segmented (*Carolinicola*: 1-segmented); md, mxl and/or mx occasionally with aesthetasque-like elements (Figs. 27.35F-H); P1 exp 3-segmented, enp 2-segmented, with enp-2 longer than enp-1; P2-P4 with 3-segmented exps, enps absent or 1-3-segmented; P5 with broad benp and smaller square exp.
 Pseudotachidiidae (Danielsseniinae)
 (Fig. 27.33R)
 - These characters not combined. 17

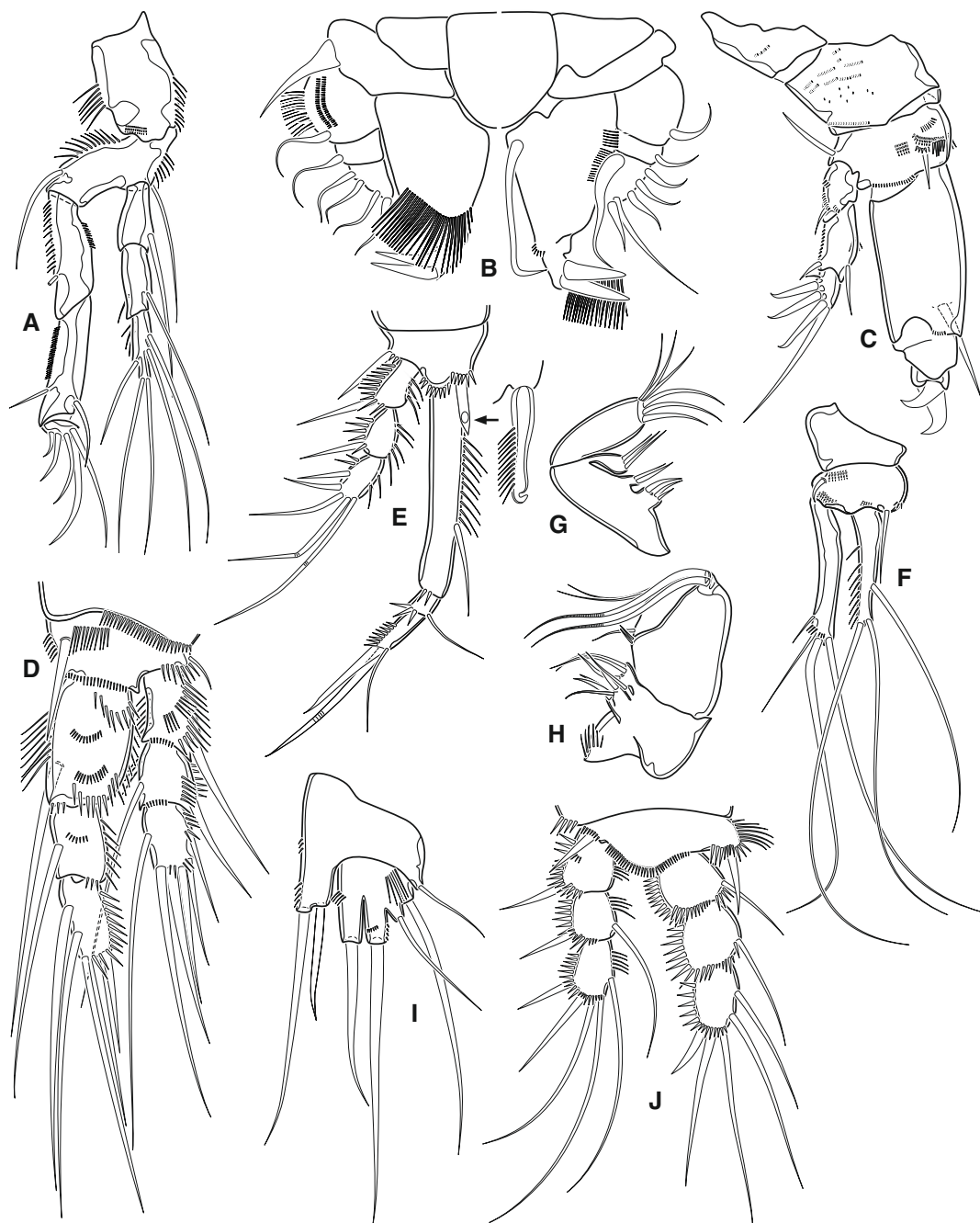


Fig. 27.34. Harpacticoida. A. P1 of *Altheuta polarsternae* Dahms, 1992. B. P1 of *Brevifrons faviolatum* Harris, 1994 (left ventral, right dorsal view). C. P1 of *Hamondia superba* Huys, 1990. D. P1 of *Ectinosoma nonpectinatum* Mielke, 1979. E. male P1 of *Ameira longipes* Boeck, 1865. F. P1 of *Rotundiclipeus canariensis* Huys, 1988. G. mx of *Signatidium parvulum* Mielke, 1974. H. mx of *Ectinosoma nonpectinatum* Mielke, 1979. I. female P5 of *Ectinosoma nonpectinatum* Mielke, 1979. J. P1 of *Tachidius discipes* (Giesbrecht, 1881). No scales. A, modified from Dahms (1992); B, modified from Harris (1994); C, modified from Huys (1990a); D, H, modified from Mielke (1979); E, modified from Mielke (1974); detailed modified inner basal seta of *A. listensis* modified from Mielke (1973); F, modified from Huys (1988); G, modified from Mielke (1974); I, modified from Mielke (1979); J, modified from Mielke (1975).

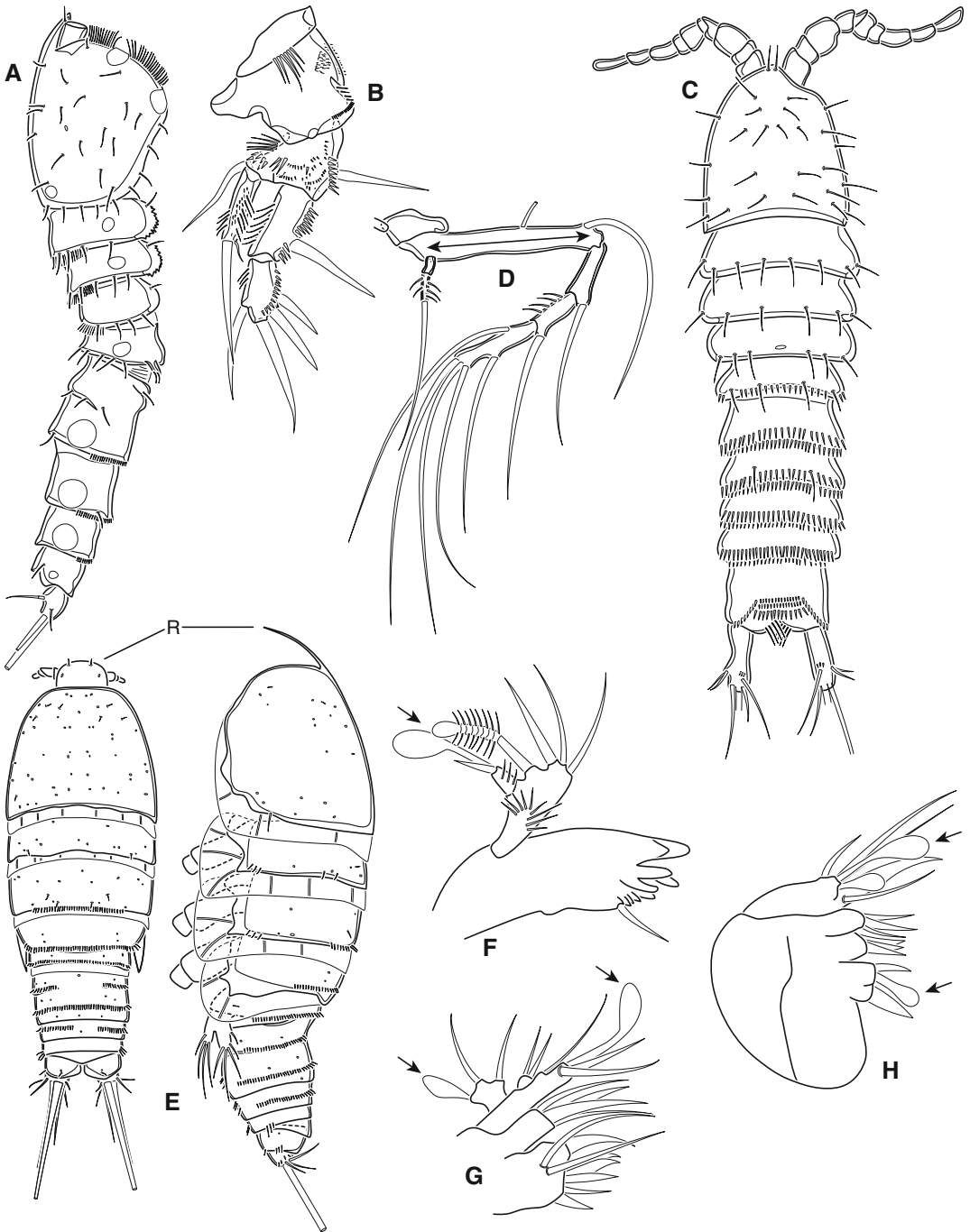


Fig. 27.35. Harpacticoida. **A.** Lateral female habitus of *Adenopleurella brevipes* Huys, 1990. **B.** P1 of *Adenopleurella brevipes* Huys, 1990. **C.** dorsal male habitus of *Bodinia meteorensis* George, 2004. **D.** female P4 of *Ceratonotus tauroides* George, 2006. **E.** dorsal and lateral female habitus of *Fladenia robustus* (Sars, 1921); R = rostrum. **F.** md of *Paradanielssenia biclavata* Gee, 1988. **G.** mx1 of *Paradanielssenia biclavata* Gee, 1988. **H.** mx of *Paradanielssenia biclavata* Gee, 1988. No scales. A, B, modified from Huys (1990b); C, modified from George (2004a); D, modified from George (2006); E, modified from Gee and Huys (1990); F–H, modified from Gee (1988).

- 17 Body slender, cylindrical to vermiform; female A1 5-7-segmented; A2 exp 0-2-segmented; mxp reduced or even absent; P1 exp 3-, enp 1-2-segmented; P5 small or absent, if present, benp and exp fused. Darcythompsoniidae
 - These characters not combined. 18
- 18 Body slender, cylindrical; female A1 7-segmented; A2 exp 1-segmented; female P5 with large benp and distinct ovoid exp; in male P5 benp and exp fused, small.
 Louriniidae (Fig. 27.33L)
 - These characters not combined. 19
- 19 Body compact, strongly pyriform, strongly tapering distally; A2 short, robust, exp represented by seta; mouthparts reduced in size; P1 exp 3-segmented, enp short, 2- to 3-segmented (Fig. 27.36B).
 Metidae (Fig. 27.33N)
 - These characters not combined. 20
- 20 Body fusiform; FR short; female A1 5-9-segmented; A2 exp 1-segmented; P1-P4 with 2-3-segmented exps and 0-2-segmented enps; in some genera, P1 strongly modified; P5 regularly with weakly developed benp and small distinct exp.
 Nannopodiidae (Fig. 27.33P)
 - These characters not combined. 21
- 21 Body cylindrical; female A1 4-6-segmented; A2 1-segmented; P1 exp 3-, enp 2-segmented, enp-2 with 1-2 brush setae; exp-3 with 2 brush setae. 22
 - These characters not combined. 23
- 22 A1 with spinous process on second segment; P1 enp-2 with 1 brush seta (Fig. 27.36C); male P3 with strong apophysis.
 Orthopsyllidae (Fig. 27.33O)
 - A1 lacking spinous process; P1 enp-2 with 2 brush setae (Fig. 27.36D); male P3 without strong apophysis. Rhizotrichidae
- 23 Body cylindrical, telson longer than preceding somite, tapering distally; female A1 8-segmented; A2 robust, with strong bipinnate spines, dorsally bent, sticking out laterally in dorsal view (Fig. 27.36E); mxp prehensile; P1-P4 with 3-segmented exps and enps.
 Parameiropsidae
 - These characters not combined. 24
- 24 Body pyriform, pro- and urosoma clearly distinguishable; rostrum large, square; A2 exp 2-segmented; FR with apical setae IV and V of rat-tailed shape (Fig. 27.36F).
 Pseudotachidiidae (Pseudomesochrinae)
 - These characters not combined. 25
- 25 Body pyriform, robust, pro- and urosoma clearly distinguishable; rostrum large and bell-shaped; A1 short, with abundant pinnate setae/spines (Fig. 27.36G); A2 exp 2-3-segmented; P1 exp 3-, enp 2-3-segmented; P5 short but laterally elongated, exp widely apart from benp.
 Pseudotachidiidae (Pseudotachidiinae)
 - These characters not combined. 26
- 26 Body pyriform (Fig. 27.36H); md enp elongated and twisted, apically with long setae (Fig. 27.36I). Miraciidae (Steneliinae)
 - These characters not combined. 27
- 27 Body fusiform, pro- and urosoma clearly distinguishable (Fig. 27.37A); mouthparts forming oral cone; P1 exp and enp 3-segmented, at least some segments with supernumerary setae or spines (Fig. 27.37B).
 Superornatiremidae
 - These characters not combined. 28
- 28 Body fusiform, tapering both anteriorly and posteriorly; rostrum large; FR broader than long (Fig. 27.37D); female A1 5-6-segmented; A2 exp 3-segmented; mxp prehensile, enp slender, apically with 1 claw and 4-5 setae (Fig. 27.37E); P1-P4 with 3-segmented exps and enps, enps longer than exps (Fig. 27.37F).
 Thompsonulidae
 - Body cylindrical, pro- and urosoma clearly distinguishable, posterolateral margins of cphth and free thoracic somites with irregular extensions (Fig. 27.37G); A1 short, with 6-8 segments; A2 exp 3-segmented; in lateral view, mouthparts of characteristic bulbous aspect (Fig. 27.37H); mxp stenopodial (Fig. 27.37I); P1-P4 with 3-segmented exps and 2-3-segmented enps; P5 limbs fused medially, benp tiny, exp distinct. Zosimeidae
- 30 P1 enp 3-segmented. 31
 - P1 enp 2-segmented. 36

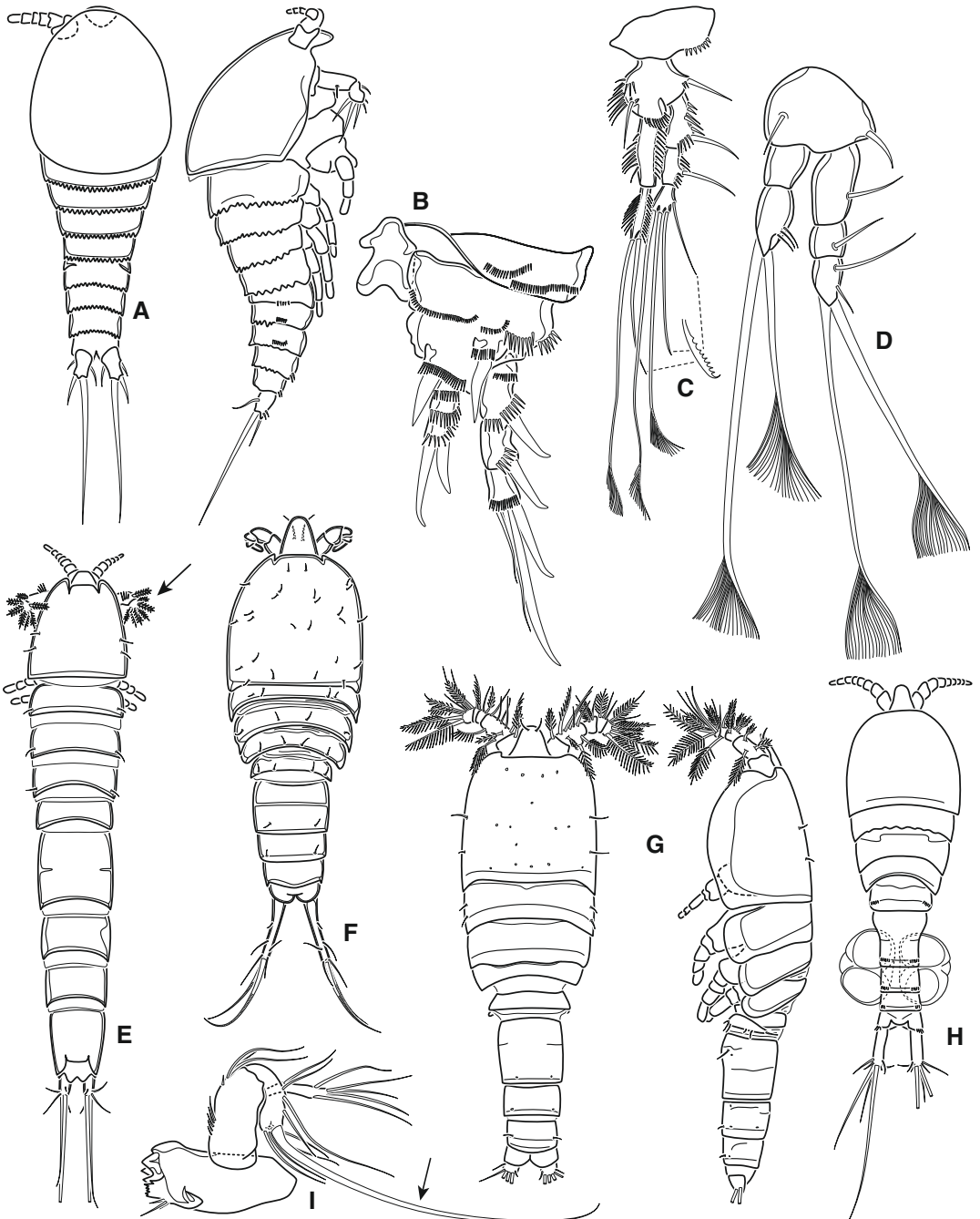


Fig. 27.36. Harpacticoida. **A.** Dorsal and lateral female habitus of *Laubieria corallicola* Soyer, 1966. **B.** P1 of *Laubieria terciara* Fiers, 1992. **C.** female P1 of *Orthopsyllus linearis illgi* (Chappuis, 1958). **D.** female P1 of *Tryphoema bocqueti* (Božić, 1953). **E.** dorsal female habitus of *Parameiopsis magnus* Itô, 1983. **F.** dorsal female habitus of *Pseudomesochra gertwilleni* Willen, 1996. **G.** dorsal and lateral female habitus of *Pseudotachidius bipartitus pacificus* Itô, 1983. **H.** dorsal female habitus of *Delavalia longipilosa* (Lang, 1965). **I.** md of *Delavalia oblonga* (Lang, 1965). No scales. A, modified from Soyer (1966); B, modified from Fiers (1992); C, modified from Lang (1965); D, modified from Mielke (1975); E, modified from Itô (1983); F, modified from Willen (1996); G: modified from Itô (1983); H, I, modified from Lang (1965).

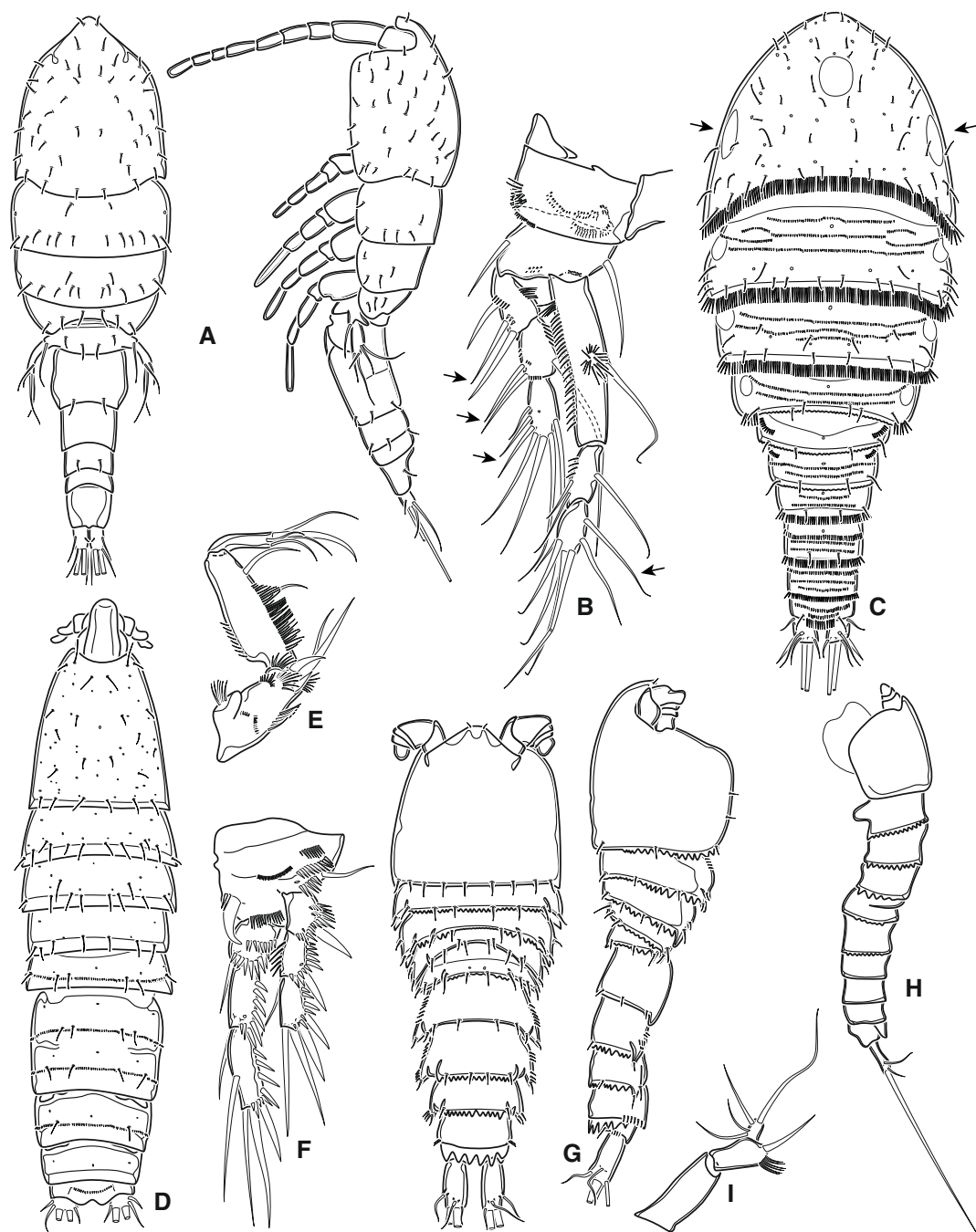


Fig. 27.37. Harpacticoida. **A.** Dorsal and lateral female habitus of *Neoechinophora daltonae* Huys, 1996. **B.** P1 of *Superornatirems mysticus* Huys, 1996. **C.** female dorsal habitus of *Neotachidius coreanus* Huys, Ohtsuka, Conroy-Dalton & Kikuchi, 2005. **D.** female dorsal habitus of *Thompsonula hyaenae* (Thompson, 1889). **E.** mxp of *Thompsonula hyaenae* (Thompson, 1889). **F.** female P1 of *Thompsonula hyaenae* (Thompson, 1889). **G.** dorsal and lateral habitus of *Zosime pacifica* Fiers, 1991. **H.** lateral female habitus of *Zosime paramajor* Bodin, 1968. **I.** mxp of *Zosime atlantica* Bodin, 1968. No scales. A, modified from Huys (1996); B, modified from Huys & Boxshall (1991); C, modified from Huys et al. (2005); D, E, modified from Huys et al. (1996); F, modified from Huys & Gee, 1990; G, modified from Fiers (1991); H, I, modified from Bodin (1968).

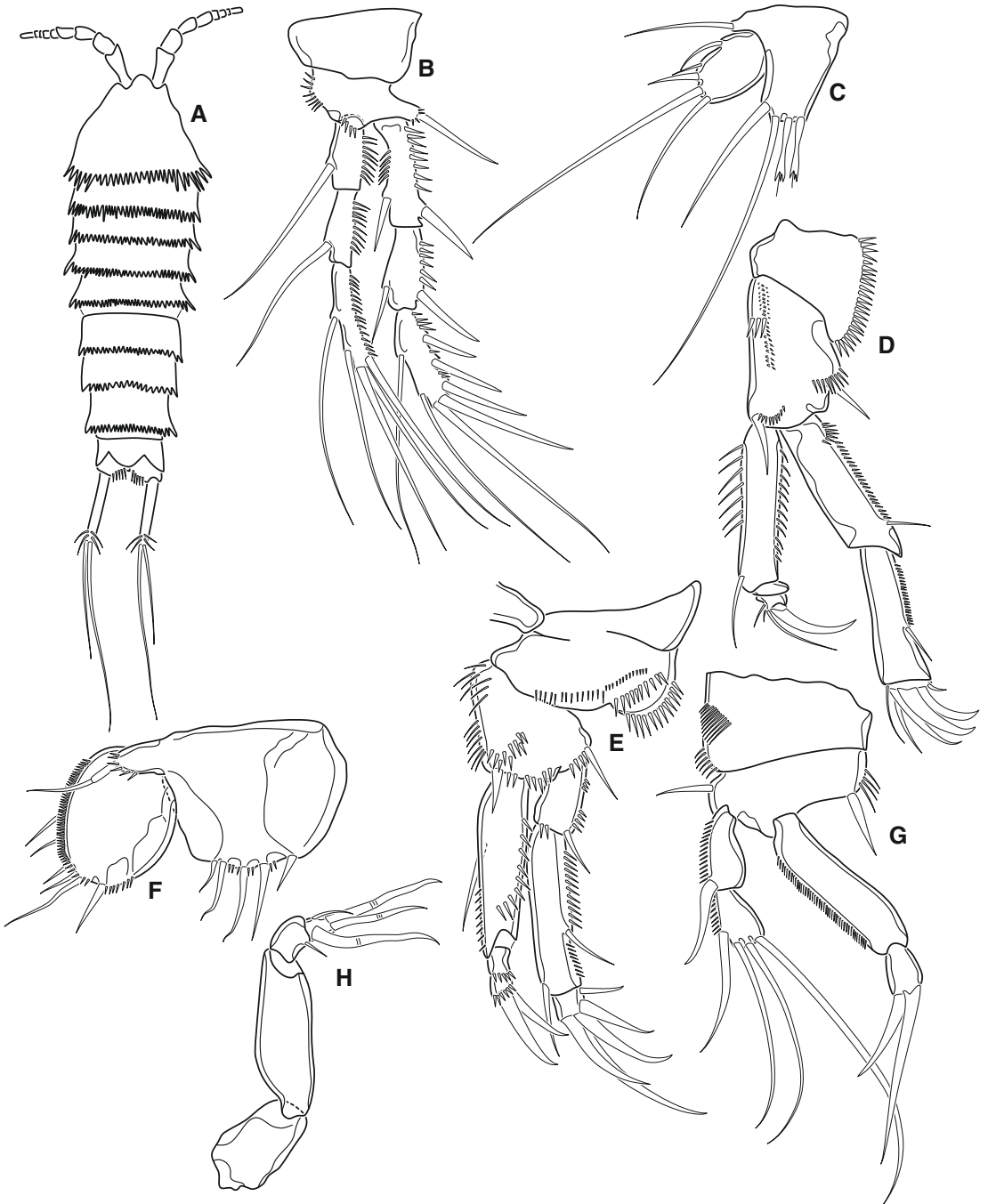


Fig. 27.38. Harpacticoida. **A.** Dorsal female habitus of *Stenocopia reducta* Cottarelli, Saporito & Puccetti, 1986. **B.** female P2 of *Stenocopia reducta* Cottarelli, Saporito & Puccetti, 1986. **C.** female P5 of *Ameira parvula nana* Willey, 1935. **D.** female P1 of *Harpacticus chelifer* (Müller, 1776). **E.** female P1 of *Amenophia orientalis* Ho & Hong, 1988. **F.** female P5 of *Amenophia orientalis* Ho & Hong, 1988. **G.** female P1 of *Paramesochra mielkei* Huys, 1987. **H.** mxp of *Paramesochra mielkei* Huys, 1987. No scales. A, B, modified from Cottarelli et al. (1986); C, modified from Dinet (1971); D, modified from Huys et al. (1996); E, F, modified from Ho & Hong (1988); G, H, modified from Huys (1987a).

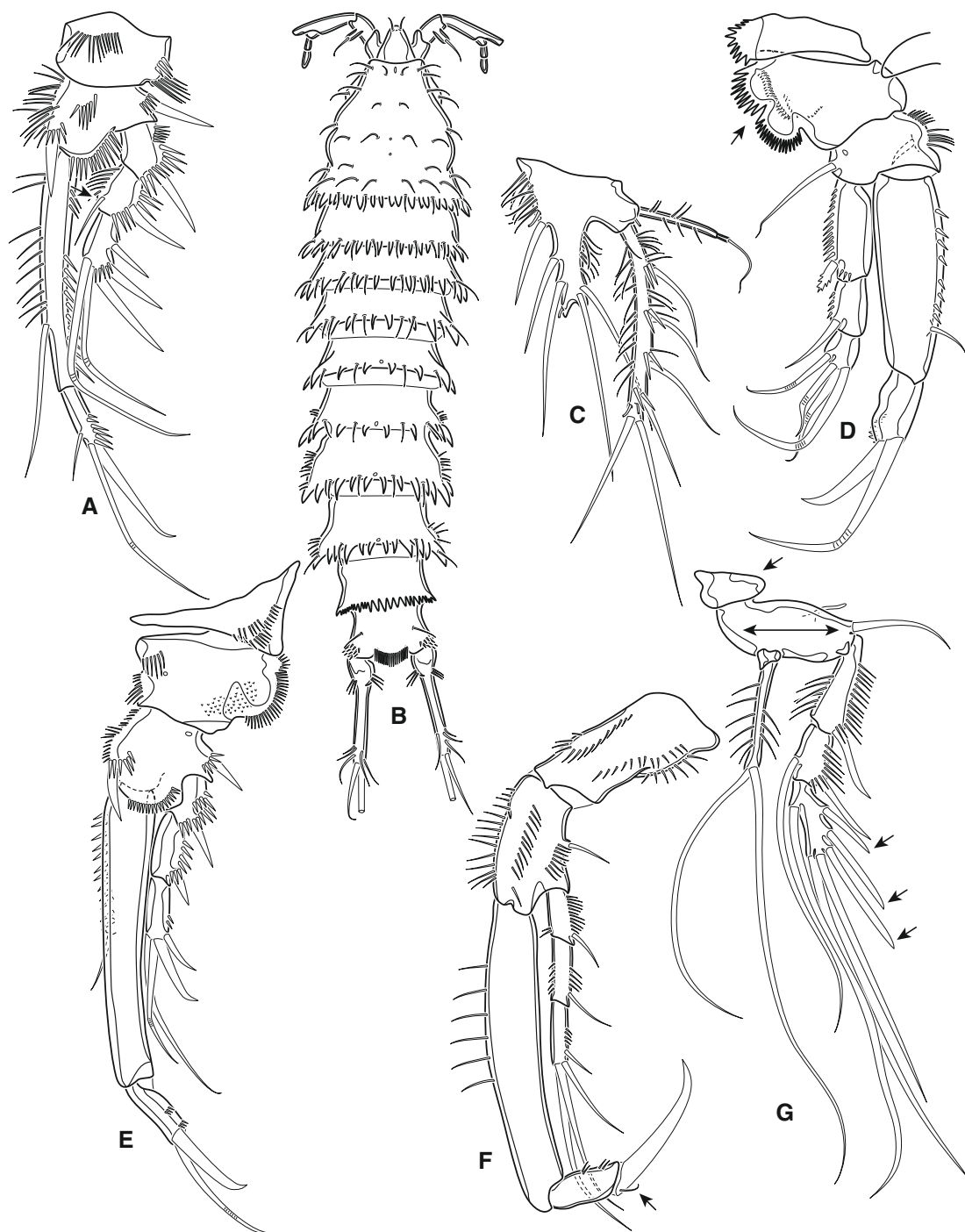


Fig. 27.39. Harpacticoida. **A**. P1 of *Normanella dubia* Brady and Robertson in Brady, 1880. **B**. dorsal female habitus of *Bathycletopsyllus hexarthra* Huys & Lee, 1999. **C**. female P5 of *Bathycletopsyllus hexarthra* Huys & Lee, 1999. **D**. female P1 of *Noodtorthopsyllus psammophilus* (Noodt, 1955). **E**. female P1 of *Aculeopsis longisetosa* Huys & Willems, 1989. **F**. female P1 of *Laophonte acutirostris* Lang, 1965. **G**. female P2 of *Laophontodes horstgeorgei* George & Gheerardyn, 2015. No scales. A–C, modified from Huys & Lee (1999); D, modified from Huys (1990c); E, modified from Huys & Willems (1989); F, modified from Lang (1965); G, modified from George & Gheerardyn (2015).

- 31 P1 exp 3-segmented, exp-2 with inner seta, enp-1 as long as exp, males with modified inner basal seta (often “bottle opener”-shaped) (Fig. 27.34E). 32
 – These characters not combined. 33
- 32 Body shape robust, integument weakly sclerotized, FR long and slender (Fig. 27.38A); A1 first segment elongated; A2 exp 1-2-segmented; P2–P4 large, bases sometimes transversely elongated, enps 2-3-segmented, shifted outwardly (Fig. 27.38B); male P3 exp without apophysis; P5 exp distinct, long and slender. Ameiridae (Stenocopiinae; only one genus: *Stenocopia*)
 – Body rather slender, cylindrical, FR at most 2× longer than wide; A1 first segment not elongated; P2–P4 enps not shifted outwardly, P5 benp tapering, exp distinct, ovoid (Fig. 27.38C). Ameiridae (Ameirinae)
- 33 P1 principally as in Fig. 27.38D: exp 3-segmented, exp-1 and exp-2 long, exp-3 small, with 5 claws; enp half as long as exp, enp-1 long, with inner subapical seta, enp-2 and enp-3 small, enp-2 with small inner seta, enp-3 with 2 claws and small inner seta. Harpacticidae
 – P1 different. 34
- 34 P1 principally as in Fig. 27.38E; exp 2-3-segmented, exp-2 with inner seta, much longer than exp-1 and exp-3, exp-3 with strong outer and terminal spines; enp-1 long, inner seta arising medially, enp-2 and enp-3 small, enp-2 without seta, enp-3 longer with 2 strong curved claws; mxp strong, prehensile; P2–P4 with 3-segmented rami, enps smaller than exps, endopodal respectively exopodal segments of nearly same size; female P5 large and broad, exp distinct, ovoid (Fig. 27.38F). .. Thalestridae
 – P1 different. 35
- 35 P1 principally as in Fig. 27.38G; exp 1-3-segmented, enp with 3 segments, as long as or longer than exp, terminal segment with 1-2 strong setae, sometimes additionally with small seta; body variable, mostly cylindrical to vermiform; mxp with 1-2-segmented enp, with 2-3 strong spines and/or 1-2 strong geniculate setae and 1-2 small seta (Fig. 27.38H); P2–P4 small, exps 3-, enps 0-3-segmented. Paramesochridae
 – These characters not combined. 36
- 36 P1 principally as in Fig. 27.39A: exp-2 with inner seta; enp-1 as long as or longer than exp, with inner seta, enp-2 small, apically with 1 claw and 1 geniculate seta, additionally with 1-2 tiny inner setae. 37
 – P1 principally as in Fig. 27.39A, but exp-2 without inner seta; enp-2 with at most 1 tiny inner seta. 38
- 37 Body cylindrical, tapering distally, posterior margins of cpht and body somites dentate or crenulate (Fig. 27.39B); female A1 4-6-segmented, second segment with 2 conical projections, each bearing a seta; A2 exp 1-segmented with 2 setae; P1 enp-1 inner seta small, enp-2 with 1-2 tiny inner setae; P2–P4 enps 2-segmented; female P5 benp with long outer basal setophore, exp elongate, rectangular (Fig. 27.39C). Cletosyllidae
 – Cphth and body somites lacking dentate or crenulate posterior margins; female A1 5-6-segmented, without any conical projections; A2 exp 1-segmented with 3-4 setae; P1 as in Fig. 27.39A, inner seta on enp-1 long, enp-2 with only 1 tiny inner seta; female P5 exp not rectangular. Normanellidae
 – Body fusiform, slender, R well developed, distinct (Fig. 27.42F); female A1 9-segmented; A2 exp 2-segmented; P1 exp 3-segmented, exp-2 with inner seta, exp-3 with 4 setae/spines, enp 2-segmented, enp-1 longer than exp, inner seta in proximal half, enp-2 small, with 2 claws and 1 small seta (Fig. 27.42G); female P2–P4 with 3-segmented rami; female P5 broad, exp ovoid, distinct (Fig. 27.42H), male P5 exp 0-3(!)-segmented (Fig. 27.42I). .. Parastenheliidae
- 38 Body cylindrical, R large, broad; female A1 4-segmented, first segment with prominent process; A2 lacking exp; P1 as in Fig. 27.39D: praecoxa and coxa with outer spinous crests, exp-2 without inner seta, enp-2 without tiny inner seta; P2–P4 small, with 1-2-segmented enps; P5 small, exp and benp fused, not distinguishable. Cristacoxidae
 – These characters not combined. 39

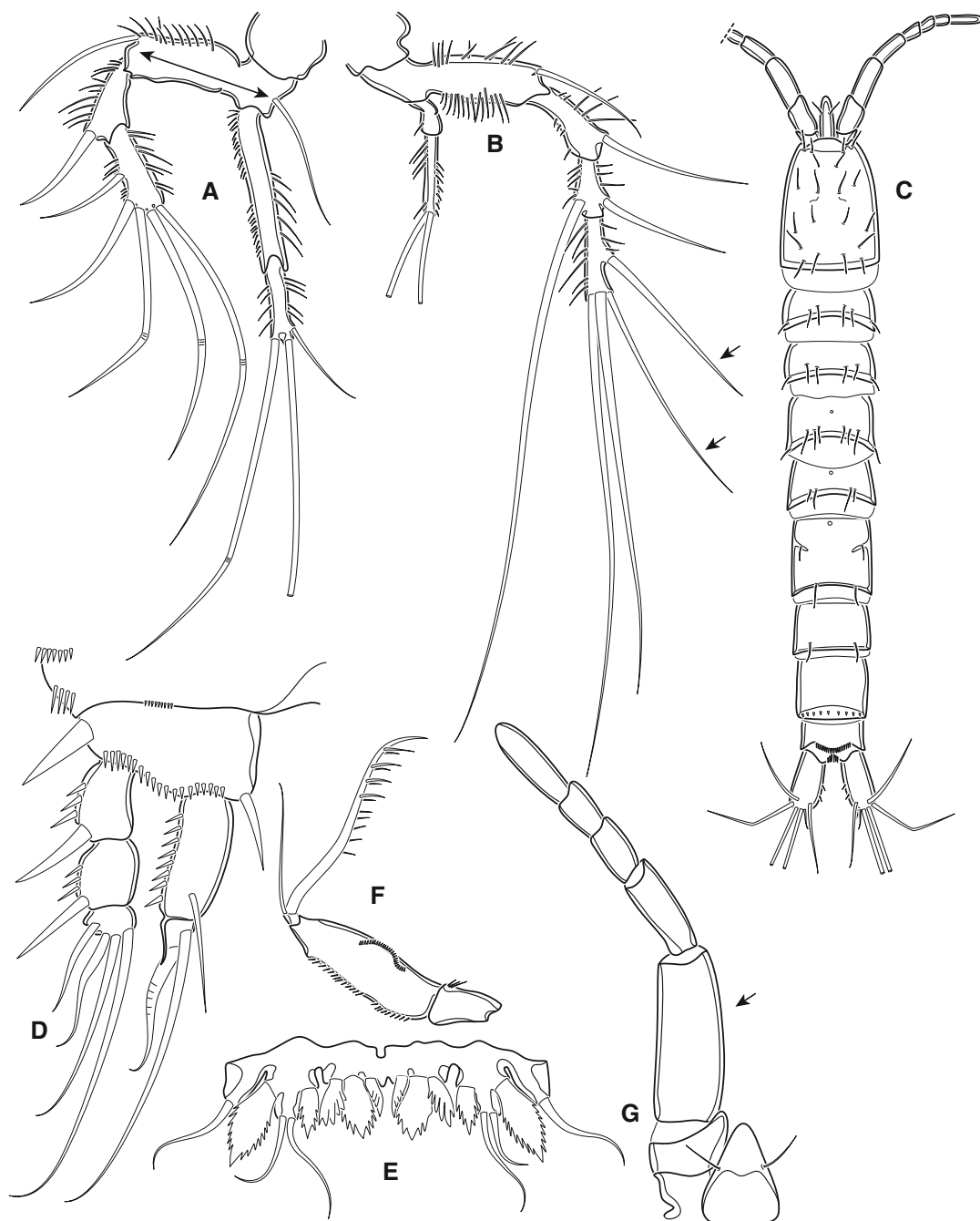


Fig. 27.40. Harpacticoida. **A.** P1 of *Ancorabulus chironi* Schulz & George, 2010. **B.** P2 of *Ancorabulus chironi* Schulz & George, 2010. **C.** dorsal female habitus of *Leptastacus laticaudatus* Nicholls, 1935. **D.** female P1 of *Delamarella excimia* (Božić, 1969). **E.** female P5 of *Arbutifera phyllosetosa* (Kunz, 1984). **F.** mxp of *Leptastacus laticaudatus* Nicholls, 1935. **G.** female A1 and R of *Arenopontia clasingi* Mielke, 1985. No scales. A, B, modified from Schulz & George (2010); C, F, modified from Huys (1987b); D, modified from Božić (1969); E, modified from Huys & Kunz (1988); G, modified from Mielke (1985).

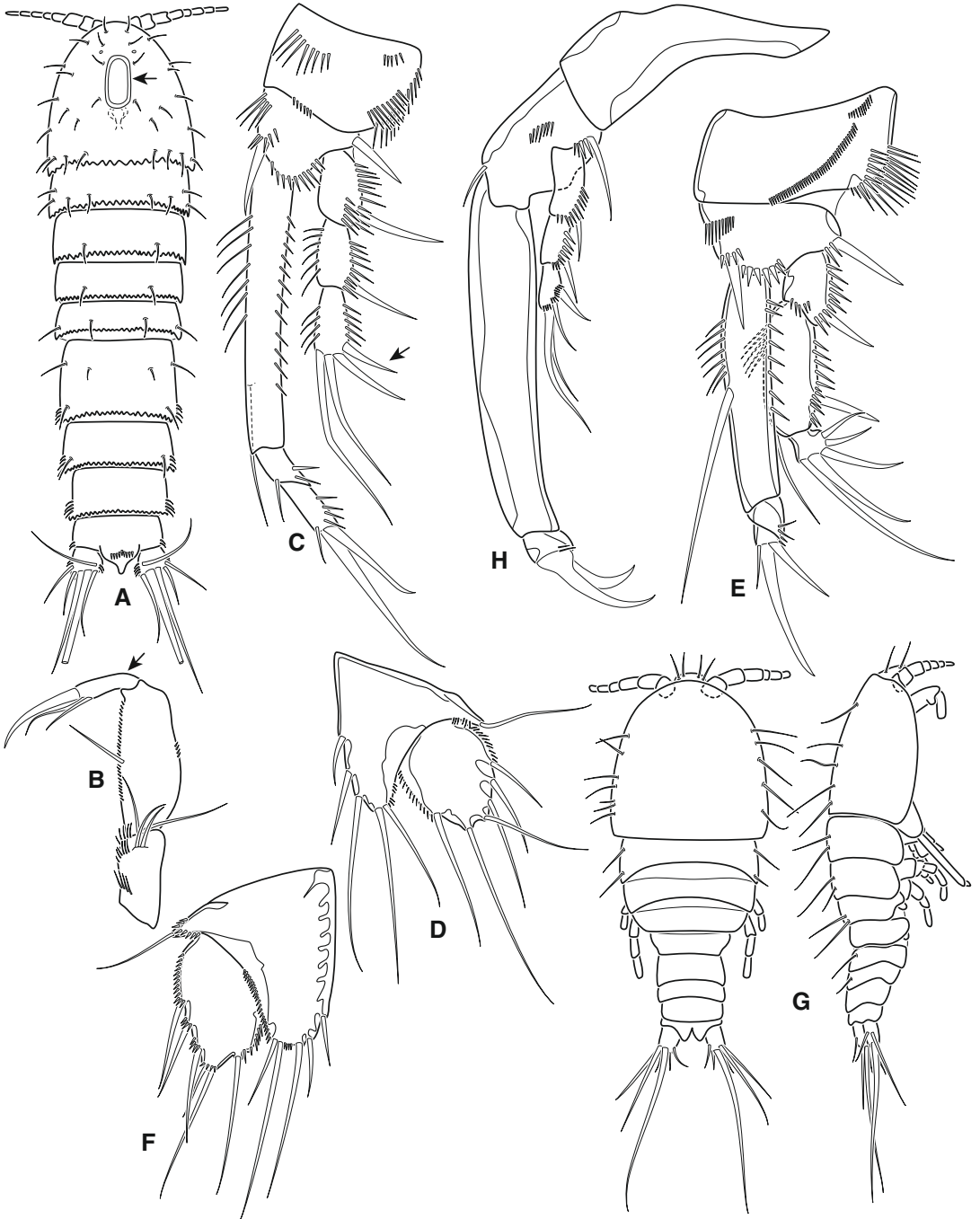


Fig. 27.41. Harpacticoida. **A.** Dorsal female habitus of *Attheyella (Delachauxiella) timmsi* (Hamond, 1987). **B.** mxp of *Amphiascopsis ekmani* (Lang, 1965). **C.** female P1 of *Amphiascoides dimorphus* Lang, 1965. **D.** female P5 of *Sarsamphiascus undosus* (Lang, 1965). **E.** female P1 of *Dactylopusia vulgaris inornata* (Lang, 1965). **F.** female P5 of *Dactylopusia vulgaris inornata* (Lang, 1965). **G.** dorsal and lateral female habitus of *Pseudonsiella aotearoa* Hicks, 1988. No scales. A, modified from Boxshall & Halsey (2004); B-F, modified from Lang (1965); G, modified from Hicks (1988).

- 39 Body cylindrical; R large, broad; female A1 short, 4-segmented, with or without spinous process on first segment; A2 exp 1-segmented, with 4 setae; P1 enp-1 twice as long as exp, with small inner seta, enp-2 with 1 claw and 1 geniculate seta, lacking tiny inner seta (Fig. 27.39E). Laophontopsidae
 – These characters not combined. 40
- 40 P1 as in Fig. 27.39F: exp small, 1-3-segmented, enp-1 strongly developed, lacking inner seta, enp-2 with 1 strong claw accompanied by minute seta; P2-P4 bases transversely not elongated. Laophontidae
 – These characters not combined. 41
- 41 P2-P4 coxae very small; bases transversely elongated (Fig. 27.39G; cf. also Fig. 27.35D).
 42
 – P2-P4 coxae of normal size; bases not transversely elongated. 43
- 42 Body cylindrical, tapering posteriorly; female A1 4-5-segmented, fourth segment very small and partly overlapped by previous segment; A2 with knob-like 1-segmented exp with 1 tiny seta, or represented by 1 small seta; P1 basis not transversely elongated; P2-P4 exp-3 with 3 outer spines (Fig. 27.39G).
 Laophontodinae
 (Ancorabolinae and Laophontodinae were merged to the paraphyletic “Ancorabolidae”)
 – Female A1 3-4-segmented; A2 lacking exp; P1 basis transversely elongated (Fig. 27.40A); P2-P4 exp-3 with 2 outer spines (Fig. 27.40B); cphth and/or body somites often with dorsal and/or lateral cuticular processes (Fig. 27.33Q).
 Ancorabolinae (*Ancorabolutus*-lineage)
 (Fig. 27.33Q)
- 43 Body slender, vermiform (Fig. 27.40C). 44
 – Body different. 47
- 44 P1 compact, with 2-3-segmented exp and 2-segmented enp (Fig. 27.40D), enp-2 small, with 1 long subapical seta and 1 geniculate apical claw; P2-P4 with 3-segmented rami, P4 enp 2-3-segmented; P5 short, fused medially, benp and exp also fused (Fig. 27.40E).
 Latiremidae
 – These characters not combined. 45
- 45 Mxp characteristic, prehensile, enp 1-segmented, with long bipinnate sigmoid claw accompanied by long slender seta (Fig. 27.40F).
 Leptastacidae
 – Mxp different. 46
- 46 A1 first segment strongly elongated.
 Leptopontiidae
 – A1 second segment strongly elongated (Fig. 27.40G). Arenopontiidae
- 47 Body cylindrical, cphth mid-dorsally with nuchal organ (Fig. 27.41A), anal operculum well developed; P1 principally as in Fig. 27.34E, but exp-2 without inner seta; P2-P4 usually with 3-segmented rami, enps often sexually dimorphic, particularly enp-3.
 Canthocamptidae
 – These characters not combined. 48
- 48 Body slightly fusiform, R large, triangular and defined at base; A2 exp 3-segmented, middle segment very small, without seta; mxp with slender enp (Fig. 27.41B); P1 enp-1 inner seta inserting at distal half, exp-3 with 4 spines (Fig. 27.41C), sexual dimorphism on male P2 enp; female P5 large, both benp and exp broad (Fig. 27.41D). Miraciidae (Diosaccinae)
 – These characters not combined. 49
- 49 Body robust, fusiform, FR short; female A1 short, however with up to 9 segments; P1 as in Fig. 27.41E: P1 enp-1 longer than exp, inner seta medially, enps 2 and 3 very small, enp-3 with 2 strong claws, exp-2 longer than exps 1 and 3, with inner seta; P2-P4 exps 3-segmented, longer than inner rami, enps 2-3-segmented; P5 large, benp and exp broad, exp distinct (Fig. 27.41F). Dactylopusiidae
 – These characters not combined. 50
- 50 Body pyriform, robust, broadly rounded anteriorly, dorsoventrally compressed (Fig. 27.41G); R distinct; female A1 6-7-segmented, P1 longitudinally elongated, exp 3-segmented, enp 2-segmented, enp-1 much longer than exp, enp-2 with 2 strong claws (Fig. 27.41H); P2-P4 enps 1-3-segmented; female P5 benp broad, exp distinct, small.
 Pseudotachidiidae (Donsiellinae)
 – These characters not combined. 51

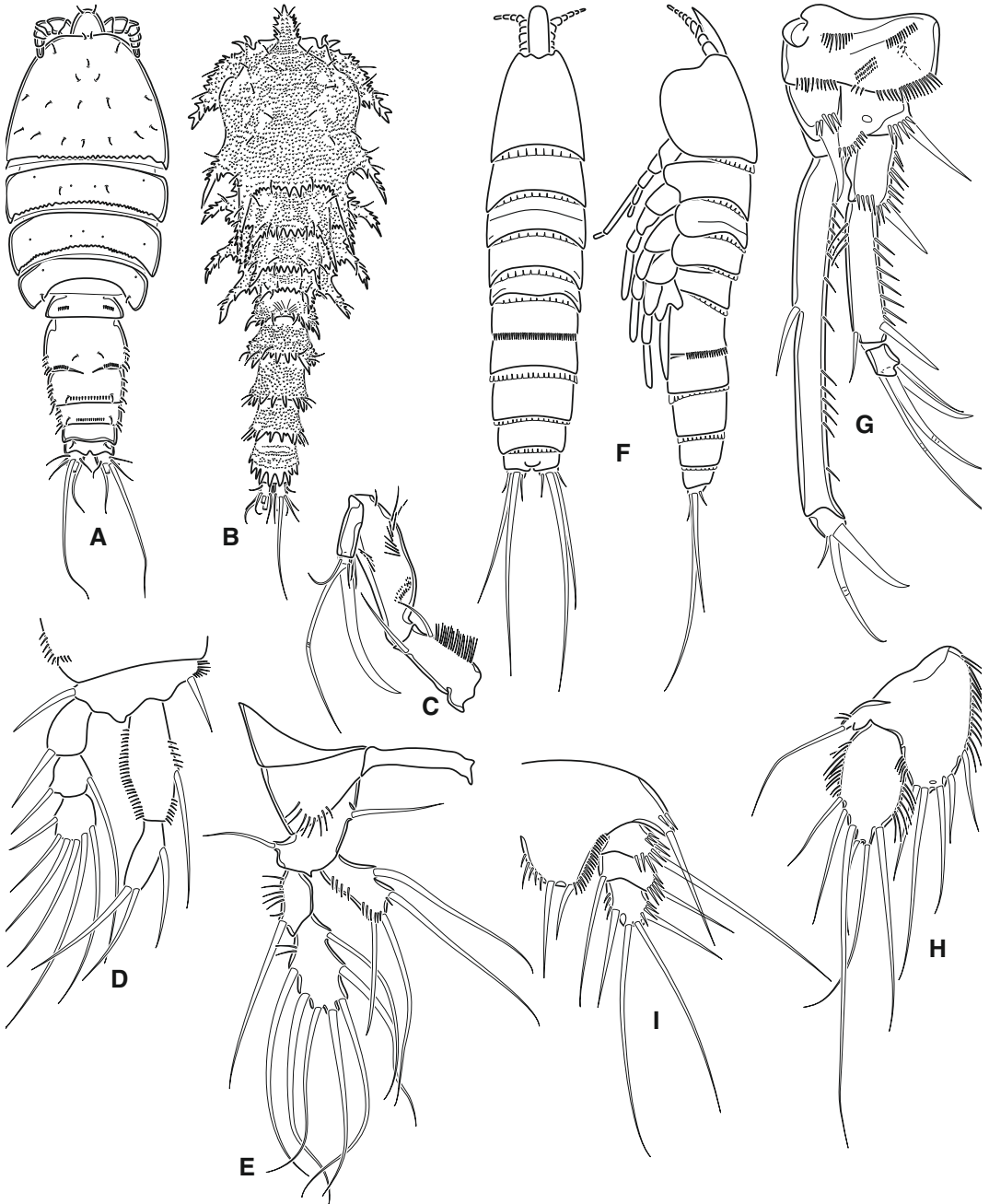


Fig. 27.42. Harpacticoida. **A.** Dorsal female habitus of *Tachidiella kimi* Lee & Huys, 1999. **B.** dorsal female habitus of *Styracothorax gladiator* Huys, 1993. **C.** mxp of *Meteorina magnifica* George, 2004. **D.** female P1 of *Idyellopsis typica* Lang, 1948. **E.** female P1 of *Aspinothorax insolentis* Moura & Martínez Arbizu, 2003. **F.** dorsal and lateral female habitus of *Parastenhelia megarostrum* Wells, Hicks & Coull, 1982. **G.** female P1 of *Parastenhelia costata* Pallares, 1982. **H.** female P5 of *Parastenhelia costata* Pallares, 1982. **I.** male P5 of *Parastenhelia spinosa spinosa* (Fischer, 1860). No scales. A, modified from Lee & Huys (1999); B, modified from Huys (1993); C, modified from George (2004b); D, modified from Gee & Fleeger (1986); E, modified from Moura & Martínez Arbizu (2003); F, modified from Wells et al. (1982); G,H, modified from Pallares (1982); I, modified from Mielke (1974).

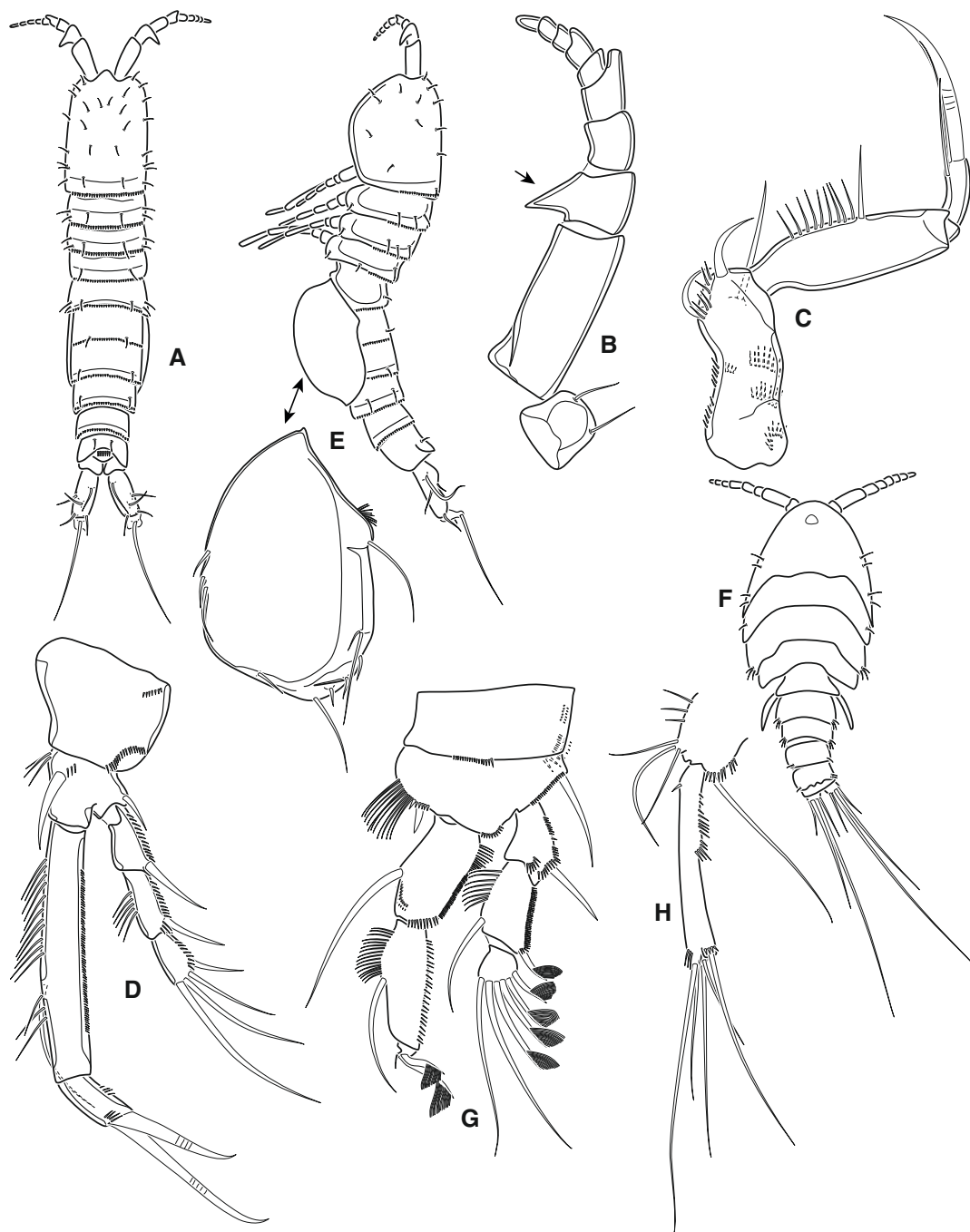


Fig. 27.43. Harpacticoida. A. Dorsal female habitus of *Phyllopodopsyllus setouchiensis* Kitazima, 1981. B. female A1 of *Phyllopodopsyllus carinatus* Mielke, 1992. C. mxp of *Phyllopodopsyllus ancylus* Mielke, 1992. D. female P1 of *Phyllopodopsyllus ancylus* Mielke, 1992. E. female P5 of *Phyllopodopsyllus ancylus* Mielke, 1992. F. dorsal female habitus of *Tisbe furcata* (Baird, 1837). G. female P1 of *Tisbe elanitica* Volkmann, 1979. H. female P5 of *Tisbe longipes* Volkmann, 1979. No scales. A, modified from Kitazima (1981); B-E, modified from Mielke (1992); F, modified from Bergmans (1979); G,H, modified from Volkmann (1979).

- 51 Body cyclopfiform or pyriform (Fig. 27.42A), clear distinction between pro- and urosoma, sometimes cphth and body somites with peculiar cuticular extensions (Fig. 27.42B); female A1 9-segmented; A2 with 1-4-segmented exp; md palp with 1-segmented enp and 1-2-segmented exp; if 2-segmented, then exp-1 elongated; mxp strong, prehensile, with 2-segmented enp and up to 5 claws and setae (Fig. 27.42C); P1 usually as in Fig. 27.42D, with exp-3 bearing 6 setae/spines, but sometimes (e.g. *Aspinothorax*, *Styracothorax*) strongly derived (Fig. 27.42E), enp 1-3-segmented; P2-P4 with 2-3-segmented rami.
 Idyanthidae
- These characters not combined. 52
- 52 Body cylindrical or fusiform, R distinct, rather small (Fig. 27.43A); female A1 7-9-segmented, first segment often elongate, first or second segment often with spinous process (Fig. 27.43B); A2 exp 1-segmented, with 1-3 setae; md with 1-segmented enp and 1-2-segmented exp; mxp with slender, elongated enp, carrying 1 geniculate claw and 1-3 setae (Fig. 27.43C); P1 with 2-3-segmented exp, exp-2 without inner seta, exp-3 with 4 setae/spines, enp 2-3-segmented, enp-1 elongate, with inner seta, following segment(s) small, terminal segment with 2 geniculate setae (Fig. 27.43D); P2-P4 with 3-segmented exps and 1-2-segmented enps; female P5 often forming brood pouch (Figs. 27.43A,E).
 Tetragonicipitidae (Fig. 27.33S)
- Body cyclopfiform, dorsoventrally compressed, R small (Fig. 27.43F); female A1 9-segmented; A2 with 4-segmented exp; md with 1-segmented exp and enp; P1 as in Fig. 27.43G: both rami 3-segmented, exp-1 and exp-2 elongated, exp-2 with inner seta, exp-3 short, with 6 setae/spines, enp-1 and enp-2 extremely elongated, longer than exp, enp-2 with inner seta, enp-3 very small, with 2 densely unipinnate claws and 2 small setae; P2-P4 with 3-segmented rami; P5 benp reduced, exp elongated, displaced laterally (Fig. 27.43H).
 Tisbidae

Order Canuelloida Khodami, Vaun MacArthur, Blanco-Bercial & Martinez Arbizu, 2017
 (Karin Pointner)

The order Canuelloida can be differentiated from other orders by the presence of the following characters: Body form elongated, cylindrical or fusiform with no clear distinction between prosome and urosome (Fig. 27.44C); rostrum dominant and defined at the base; A1 six-segmented; A2 exopod with at least six segments; presence of an inner spine or seta on the coxa of P1; P1-P4 biramous with 3-segmented rami; urosome 5-segmented in female and 6-segmented in male; anal operculum present; caudal rami V-shaped with seven setae (Boxshall & Halsey 2004, Huys et al. 1996, Seifried 2003, pers. observation).

Canuelloida encloses 2 families, the Canuellidae Lang, 1944 (Figs. 27.44C-E) and the Longipediidae Boeck, 1865 (Figs. 27.44A,B), whose synapomorphies are listed in detail by Seifried (2003).

Only marine and brackish species of Canuellidae are known to date, which do not prefer any special type of sediment. Hence, they can be found in mud as well as in coralline sediment, from the interstitial (e.g. *Canuella*, *Microcanuella*) down to the deep sea (e.g. *Brianola*), living epibenthic or interstitial (Boxshall & Halsey 2004). Several species associate with hermit crabs, for detailed information see Boxshall & Halsey (2004). The Canuellidae count 62 species in 18 genera: *Brianola* Monard, 1926 (8 species), *Canuella* Scott T. & A., 1893 (4), *Canuellina* Gurney, 1927 (6), *Canuellopsis* Lang, 1936 (3), *Coullana* Por, 1984 (2), *Echinosunaristes* Huys, 1995 (1), *Elanella* Por, 1984 (3), *Ellucana* Coull, 1971 (2), *Galapacanuella* Mielke, 1979 (1), *Ifanella* Vervoort, 1964 (1), *Indocanuella* Huys, 2016 (1), *Intercanuella* Becker & Schriever, 1979 (1), *Intersunaristes* Huys, 1995 (2), *Microcanuella* Mielke, 1994 (2), *Nathaniella* Por, 1984 (1), *Parasunaristes* Fiers, 1982 (2), *Scottolana* Huys, 2009 (18), *Sunaristes* Hesse, 1867 (4).

Species of Longipediidae are known from the marine and brackish (only *Longipedia corteziensis* Gómez, 2001) environment, and are present from the shallow area down to 150 m below sea surface in a mixture of sand and muddy clay but can also be rarely found on sand, mud, on macroalgae and in the bottom-plankton (Boxshall & Halsey 2004; Huys et al. 1996). The Longipediidae count 23 species in only one genus, *Longipedia* Claus, 1862.



Fig. 27.44. Body shapes of Canuelloida. A. *Longipedia coronata* Claus, 1862, lateral. B. *L. coronata*, ventral. C. *Canuella perplexa* T. & A. Scott, 1893, lateral. D. *C. perplexa*, ventral. E. *Microcanuella secunda* Pointner, 2015, lateral. No scales. CLSM photos: A–D, S. Rossel; E, K. Pointner.

Key to canuelloid families

(adopted from Lang 1948b, Huys et al. 1996, Boxshall & Halsey 2004, Wells 2007)

- 1 P2 **exp3** extremely elongated (Fig. 27.44B). ...
 Longipediidae (single genus *Longipedia*)
- P2 **exp3** not extremely elongated (Fig. 27.44D). Canuelliidae

Key to canuelliid genera

(from Huys 2016, with slight changes)

- 1 Distal segment of P4 enp with 2 setae/spines.
 *Microcanuella*
- Distal segment of P4 enp with 3 setae/spines.
 2
- Distal segment of P4 enp with 4 setae/spines.
 7

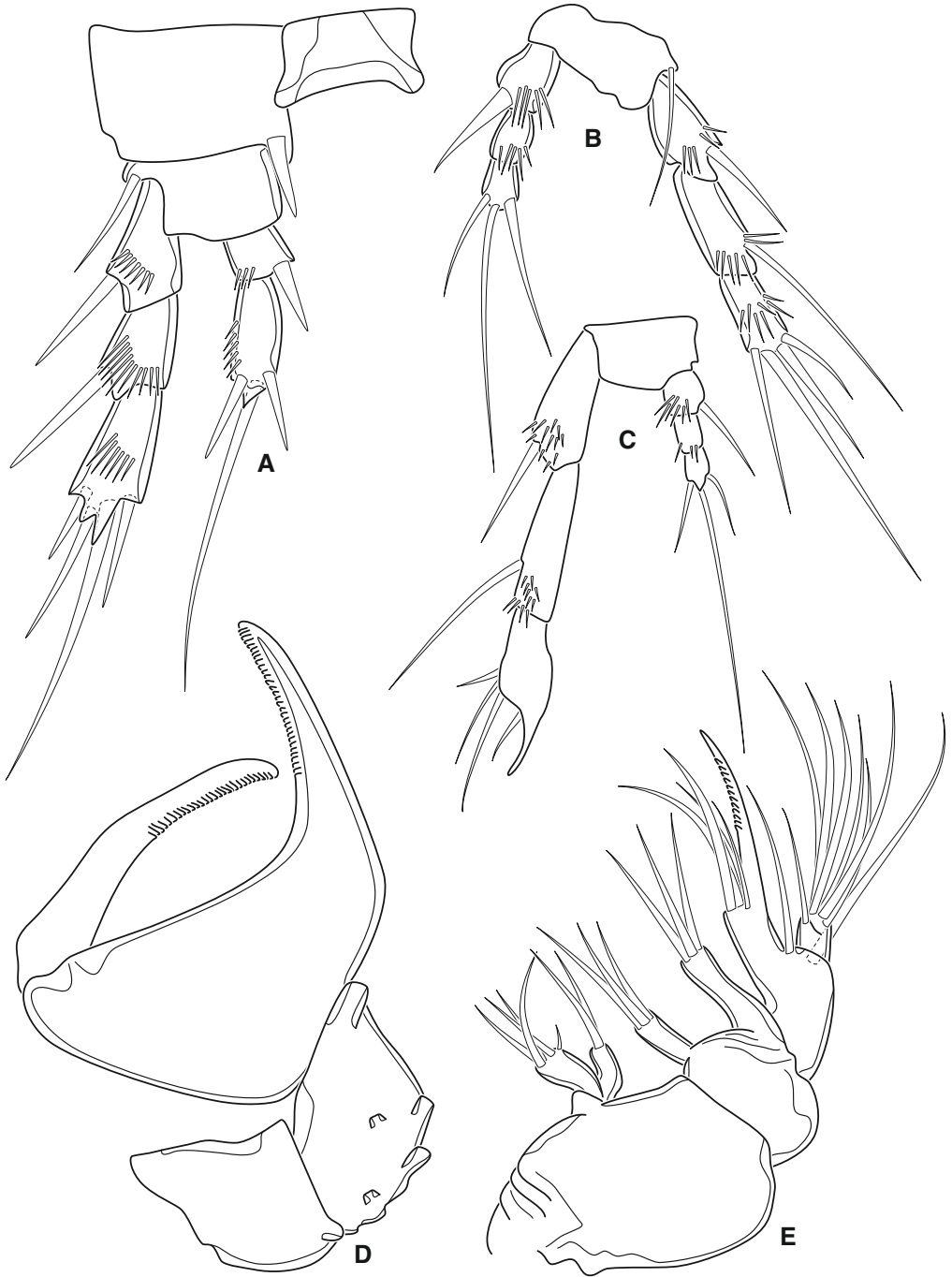


Fig. 27.45. Canuellidae. **A.** P4 of *Ellucana longicaudata* Sewell, 1940. **B.** female P4 of *Canuella canalis* Por, 1969. **C.** male P4 of *C. canalis*. **D.** A1 of *Parasunaristes cucullaris* Fiers, 1982. **E.** mx of *Intersunaristes dardani* (Humes and Ho, 1969). No scales. A, modified from Fiers (1982); B,C, modified from Por (1969); D, modified from Fiers (1982); E, modified from Humes & Ho (1969).

- 2 P1 exp-3 and enp-3 with 6 and 4 setae/spines, respectively; P2 exp-3 and enp-3 with 5 and 4 setae/spines. *Galapacanuella*
 – P1 exp-3 and enp-3 with 7 and 6 setae/spines, respectively; P2 exp-3 and enp-3 with 6-7 and 5 elements, respectively. 3
- 3 P2 exp-3 with 6 elements; distal segments of both rami of P3 with 4 setae/spines; P4 exp-2 without inner seta. 4
 – P2 exp-3 with 7 elements; P3 exp-3 and enp-3 with 5 and 3 setae/spines, respectively; P4 exp-2 with inner seta. 5
- 4 Outer elements on P4 exp-1 and exp-2 short and spiniform (Fig. 27.45A); male genital field with triangular opercula bearing basal styliform element, conspicuous uncinat spine and slender seta. *Ellucana*
 – Outer elements on P4 exp-1 and exp-2 elongate and setiform (Fig. 27.45B); male genital field with different morphology and armature, displaying distinct chitinized patches; P2 exp-3 identical in both sexes, P4 exp-3 occasionally sexually dimorphic (Fig. 27.45C). *Canuellina*
- 5 P4 exp 2-segmented. 6
 – P4 exp 3-segmented. *Sunaristes*
- 6 Mx sexually dimorphic, allobasal claw strongly chitinized, dark brown and recurved in female, much smaller, straight and with blunt teeth in male; A1 with enormous subchela in male (Fig. 27.45D). *Parasunaristes*
 – Mx not sexually dimorphic, allobasal claw short and accompanied at base by 4 accessory setae (Fig. 27.45E); antennule with moderately developed subchela in male. *Intersunaristes*
- 7 P1 exp 2-segmented. *Canuellopsis*
 – P1 exp 3-segmented. 8
- 8 P3 exp-3 with 4 setae/spines. 9
 – P3 exp-3 with 5 setae/spines. 10
- 9 P2 exp-3 with 3 setae/spines. *Indocanuella*
 – P2 exp-3 with 4 setae/spines. *Brianola*
 – P2 exp-3 with 5 setae/spines. *Nathaniella*
 – P2 exp-3 with 6 setae/spines. *Ifanella*
 – P2 exp-3 with 7 setae/spines. *Intercanuella*
- 10 P4 exp-3 with 4 setae/spines. 11
 – P4 exp-3 with 5 setae/spines. 12
- 11 P1-bearing somite fused to cephalosome; P4 exp-3 without inner seta. *Coullana*
 – P1-bearing somite not fused to cephalosome; P4 exp-3 with inner seta. *Scottolana*
- 12 P4 exp-2 without inner seta. 13
 – P4 exp-2 with inner seta. *Elanella*
- 13 Female caudal rami distinctly longer than wide; P3-P4 coxa with inner seta; usually free-living. *Canuella*
 – Female caudal rami not longer than wide; P3-P4 coxa without inner seta; endosymbionts of spatangoid sea-urchins. *Echinosunaristes*

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