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## Chapter 6. Suborder Epicaridea

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### Abstract

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Diagnoses and keys are provided for 15 families, 13 subfamilies and 265 genera of epicaridean isopods. *Alaxphryxus* Boyko and Williams is diagnosed as a new genus of Hemiarthrinae. The ecology and distribution of each taxon are discussed with citation of literature critical for further investigation and identification of species.

### Keywords

Argeiinae, Asconiscidae, Athelginae, Bathygyginae, Bopyridae, Bopyrinae, Bopyroidea, Cabiropidae, Capitoniscidae, Crinoniscidae, Cryptoniscidae, Cryptoniscoidea, Cumoechidae, Cyproniscidae, Dajidae, Entoniscidae, Entophilidae, Hemiarthrinae, Hemioniscidae, Ionidae, Keponinae, Orbioninae, Phyllozurinae, Pleurocryptellinae, Podasconidae, Pseudioninae, Stellatoniscidae, dichotomous keys.

### Introduction

Epicaridea Latreille, 1825 (c. 880 species fide Boyko et al., 2025; c. 8% of all isopods) contains species of isopods that parasitise intermediate and definitive crustacean hosts. Epicaridea is a longstanding name within Isopoda. Based on adult morphology, these parasites were formerly treated as two superfamilies (Bopyroidea Rafinesque, 1815 and Cryptoniscoidea Kossman, 1880) within the suborder Cymothoidea Wägele, 1989 (Brandt and Poore, 2003), a group that contains free-living and ectoparasitic isopods of fishes (see Dreyer and Wägele, 2001). However, molecular data has since provided support for a monophyletic Epicaridea that does not form a sister group relationship with any cymothoid (An et al., 2022; Boyko et al., 2013; Thomas Thorpe, 2024; Yu et al., 2018), calling into question the hypothesis that crustacean parasites evolved from fish parasites. Presently, Epicaridea is recognised as its own suborder of isopods (An et al., 2022).

Epicarideans are endoparasitic, mesoparasitic (with part of the female body embedded in the host) or ectoparasitic (including hyperparasites) on or in a wide range of crustacean definitive hosts; nearly all epicaridean species that have been investigated use a pelagic calanoid copepod as their intermediate host (figs 6.1a–d, 6.2c; Williams and Boyko, 2012; Williams et al., 2022). Within the epicarideans, there are presently 15 families: three in Bopyroidea (figs 6.1a, b, 6.2–6.4: Bopyridae Rafinesque, 1815, Entoniscidae Kossman, 1881, and Ionidae H. Milne Edwards, 1840) and 12 in Cryptoniscoidea (figs 6.1c, d;

6.5, 6.6: Asconiscidae Bonnier, 1900, Cabiropidae Giard and Bonnier, 1887, Capitoniscidae Boyko and Williams, 2023, Crinoniscidae Bonnier, 1900, Cryptoniscidae Kossman, 1880, Cumoechidae Boyko and Williams, 2023, Cyproniscidae Giard and Bonnier, 1887, Dajidae G.O. Sars, 1883, Entophilidae Richardson, 1903, Hemioniscidae Bonnier, 1900, Podasconidae Giard and Bonnier, 1895, and Stellatoniscidae Oanh and Boyko, 2020). Bopyridae is the most speciose group (650 species, Boyko et al., 2025), with ten subfamilies currently recognised: Argeiinae, Athelginae, Bathygyginae, Bopyrinae, Hemiarthrinae, Keponinae, Orbioninae, Phyllozurinae, Pleurocryptellinae and Pseudioninae (figs 6.1a, b, 6.2–6.4).

Adult female epicarideans reach sexual maturity on or in the definitive host (figs 6.1a–d, 6.2a–e, g). Typically, parasitised definitive hosts harbour one female and male pair, but several males may be found, and double infestations of mature females are known (e.g., Williams et al., 2023). The male isopods move into the brood chamber and fertilise the eggs within the marsupium of the female. The fertilised eggs develop into epicaridium larvae (figs 6.1a–d, 6.2b) and are then released into the water column to parasitise the intermediate copepod hosts. The epicaridium larva feeds on the copepod and metamorphoses into a microniscus larva (figs 6.1a–d, 6.2c), and then moults into a cryptoniscus larva (figs 6.1a–d, 6.2d) that detaches and seeks out the definitive crustacean host. The cryptoniscus larva settles on the definitive host and moves to the final attachment site on the host when ectoparasitic or penetrates the host if endoparasitic (figs 6.1a–d, 6.2a). The female cryptoniscus larva

will pierce the host and feed on its hemolymph or ovarian fluids, often shutting down reproduction of the host in the process (see review of life cycle and natural history of Epicaridea in Williams and Boyko, 2012).

The morphology of epicarideans is more highly modified than that of free-living isopods and even that of members of Cymothoidea (ectoparasites of fish) (Dreyer and Wägele, 2001). All epicarideans exhibit sexual dimorphism, with larger females having more modified features than the dwarf males (figs 6.1–6.6). Bopyroids are nearly all ectoparasitic on decapod hosts (figs 6.1a, 6.2a–g), although one family (Entoniscidae: figs 6.1b, 6.4t–y) is exclusively endoparasitic. Cryptoniscoids are endoparasitic, mesoparasitic or ectoparasitic across a diverse assemblage of crustacean definitive hosts (fig. 6.1c), although one family (Dajidae: figs 6.1d, 6.5c, d) is exclusively ectoparasitic. Three families contain hyperparasites (Cabiropidae, Cryptoniscidae and Stellatoniscidae).

Bopyrids are instructive for demonstrating key morphological characters of epicarideans (figs 6.2, 6.3; see also Markham, 1985 and glossary therein, and Ribeiro and Horch, 2023), although these features (e.g. segmentation, pereopods) are further reduced or modified in many groups. Females residing in the branchial chamber of hosts may exhibit some degree of asymmetry (e.g. fig. 6.3a), whereas those ectoparasitic on the abdomens of hosts may be more symmetrical, with pereopods clustered around the head and oostegites extending beyond the margin of the head (fig. 6.2a, e). Although species in most genera exhibit five pairs of large and midventrally overlapping oostegites (fig. 6.3b), females within putatively primitive bopyrid genera (e.g., *Pleurocryptella* Bonnier, 1900) retain seven pairs of oostegites (fig. 6.3e, f). Some genera contain species that have smaller oostegites that do not meet midventrally (fig. 6.3k), thus the marsupium is partially open but eggs/larvae are retained by the host covering. The first oostegite is divided into two lobes (fig. 6.3c, m); typically, the anterior lobe is larger and rounded, whereas the posterior lobe is smaller and rounded or extended into a posterolateral point and the two lobes are divided by an internal ridge that may be smooth (fig. 6.3c) or digitate (fig. 6.3m). The maxilliped is found underneath oostegite 1 (fig. 6.3h) and is composed of two lobes: the anterior lobe, which may possess an articulated or non-articulated palp (fig. 6.3h), and the posterior lobe, exhibiting a spur-like lateral extension. The head is generally rounded and may be partially or completely divided into two lobes (figs 6.3n, 6.4e, p) and often has a frontal lamina extending beyond the anterior margin (e.g. figs 6.2a, 6.3j, 6.4e, m). Eyes are usually lacking but, if present, they are small and irregularly shaped (fig. 6.4h). Body pigmentation is also typically lacking, although some species may exhibit extensive pigmentation on the pereomeres and pleomeres. The posteroventral border of the head exhibits posterolateral projections (termed barbula; figs 6.2h, 6.3g, l) that may be smooth (fig. 6.3g) or digitate (fig. 6.3l) and the posterior margin between the lobes may likewise be smooth or digitate. The antennae (antennula = antenna 1; antenna = antenna 2) are generally reduced to 3–6 articles and often obscured by the frontal lamina and anterior structures (compare with fig. 6.3k). The seven pereomeres may exhibit dorsolateral bosses anterior to tergal projections on each

segment, sometimes with coxal plates on the lateral edge (e.g., fig. 6.3a, j, n). Species in some genera exhibit middorsal projections on the posterior pereomeres and pleomeres (fig. 6.3n). The pereopods of the females are generally gnathopodal and exhibit six articles (dactylus to basis), although in some there is partial fusion of articles. The pleon is typically composed of five pleomeres plus uropods and sometimes a pleotelson extension with an anal cone. The number of pleomeres is variable due to fusion in some groups; the pleomeres may exhibit lateral extensions on the dorsal side (lateral plates), and ventrally they may exhibit pleopods that can be biramous (endopod, inner ramus and exopod, outer ramus) or uniramous (figs 6.2a, 6.3i, j, n). The uropods may also be uniramous or biramous; sometimes being similar in morphology to the pleopods or greatly extended; both pleopods and uropods may be smooth (figs 6.2a, 6.4c, k, p, r), tuberculate (figs 6.3j, k, 6.4g) or highly digitate (figs 6.3n, 6.4a, e). The pleotelson, if present, is generally small and produced into an anal cone; in species of some genera the pleotelson is elongate and large (fig. 6.4r).

Males exhibit a more typical isopod form with distinct segmentation. The head is often fused with the first pereomere (fig. 6.2f) and eyes, if present, range in size from minute to relatively large and irregularly shaped (fig. 6.4l). Body pigmentation may be present as small, scattered groups of pigment. As in females, the antennae are generally reduced to 3–6 articles, with antennulae being overall smaller and with fewer articles than the antennae (fig. 6.2l). Maxillipeds may be present or absent. The seven pereomeres may exhibit midventral projections (tubercles) on some segments (fig. 6.3o). The pereopods of males are generally gnathopodal and have six articles (basis to dactylus; fig. 6.2k), although in some groups articles may be fused. Some species exhibit greatly enlarged anterior pereopods. The pleon exhibits variable degrees of segmental fusion, from being completely fused (figs 6.2f, 6.4d, l, s), fusion with indication of segments (fig. 6.4n), to exhibiting five clearly divided pleomeres plus pleotelson with anal cone (figs 6.2i, j, 6.3o, 6.4f, i, q); in a few groups (e.g. *Pleurocryptella*) the males exhibit “true” articulating uropods. Pleomeres are often produced laterally to a slight degree and more separated than the pereomeres (e.g. figs 6.2i, 6.4j) but some have long lateral extensions (fig. 6.4b). Pleopods may be present on the pleomeres (fig. 6.2i) and midventral tubercles likewise (fig. 6.3o). The pleotelson, if present, may be in the form of two distally rounded lobes (figs 6.2i, 6.4f, i) that in some cases may be greatly elongate (figs 6.2j, 6.4b).

The larval stages of epicarideans are more poorly known than adults for nearly all species; however, they hold key characters, especially for the cryptoniscoids (some of which are known only from the males that retain the cryptoniscus larval stage form when sexually mature; i.e. they are neotenous). The first and second larval stages, the epicaridium and microniscus larvae, are the least studied (Williams et al., 2022) and the micronisci are particularly hard to study due to their short duration and soft cuticle. *Microniscus* Müller, 1871 is also a valid genus name but is functionally a larval group with six included described and named species, all of which are based solely on the epicaridean microniscus stage and will likely not

ever be identifiable to any taxon within Epicaridea. The third and final larval stage, the cryptoniscus larva, is the best studied and can be used to distinguish between some of the groups of bopyroids and cryptoniscoids based on characters such as the antennal article count (figs 6.1a–d, 6.2d1; Boyko et al., 2013; Boyko and Williams, 2015). Additional important characters of the cryptoniscus larva include antennula morphology (fig. 6.2d1), pereopod morphology (fig. 6.2d2, d3) and pleotelson plus uropod morphology (fig. 6.1d4).

Although bopyrid morphology is a good starting point for understanding the overall morphology of epicarideans (including Ionidae and Entophilidae), their form is quite variable and becomes extremely modified in species of some genera and families. In some groups, the females may exhibit so much fusion and reduction of characters (e.g. segmentation, pereopod number) that they can only be identifiable to the species level if males or cryptoniscus larvae are present. This is the case for the bopyroid family Entoniscidae (fig. 6.3t–y) and nearly all of the cryptoniscoids (figs 6.5, 6.6). Among the cryptoniscoids, the

family Entophilidae (fig. 6.5a, b) is unique in that the females and males retain a morphological form that generally matches that described for some bopyroids (e.g. with clear segmentation). Dajidae (fig. 6.5c, d) are all ectoparasitic cryptoniscoids, females of which are ovate in shape, have gnathopodal pereopods or antennae to clutch onto hosts, and retain some degree of segmentation. The rest of the cryptoniscoids (figs 6.5e–t, 6.6) have females with highly reduced bodies: from sac-like and lacking pereopods (figs 6.5e, h, k, t, 6.6a, d, f, i) to stellate-shaped bodies (fig. 6.5n) and males that retain a cryptoniscus larval-type morphology when sexually mature (figs 6.5f, g, m, o, p, r, 6.6b, e, g, j). Some groups contain hyperparasitic species, including Cabiropidae (fig. 6.6c–e) most of which parasitise bopyrid isopods, Cryptoniscidae (fig. 6.6a, b), some of which parasitise rhizocephalan barnacles, and Stellatoniscidae (fig. 6.5n, o) that parasitise entoniscid isopods. Although females of some cryptoniscoids lose all evidence of segmentation, those of Hemioniscidae (fig. 6.5e) and Asconiscidae (fig. 6.5t) retain anterior segmentation when mature.

### Key to superfamilies, families and subfamilies of Epicaridea

Monotypic families and subfamilies with genus shown in parentheses

1. Cryptoniscus larva with antenna of fewer than 9 articles (fig. 6.1a, b) ..... Bopyroidea ... 2
  - Cryptoniscus larva with antenna of 9 (4 basal + 5 flagellar) articles (fig. 6.1c, d) ..... Cryptoniscoidea ... 16
2. Female not vermiform, pereopods, antennulae and antennae articulated. Male with articulated antennulae and antennae. Cryptoniscus larva with antenna of 8 (4 basal + 4 flagellar) articles (fig. 6.1a). Ectoparasitic ... 4
  - Female vermiform, pereopods, antennulae and antennae non-articulated. Male with antennula non-articulated, antennae lacking. Cryptoniscus larva with antenna of 7 or fewer (4 basal + 1 or 3 flagellar) articles (fig. 6.1b). Endoparasitic ..... Entoniscidae ... 14
4. Female with uropods bearing lateral plates, numerous filamentous rami extending from lateral plates. Male with long, slender lateral plates. Cryptoniscus larva with pereopodal dactyli each bearing an elongate dorsomedial seta (fig. 6.4a, b). Ectoparasitic, branchial ..... Ionidae (*Ione*) ... p. 314
  - Female with uropods lacking lateral plates. Male without long, slender lateral plates. Cryptoniscus larva without pereopodal dactyli bearing an elongate dorsomedial seta. Ectoparasitic (figs 6.2, 6.3) ..... Bopyridae ... 5
5. Female with coxal plates large, first 2 pairs medially directed; second oostegites extending beyond anterior margin of head; pleon flexed anterodorsally over pereon. Male with distoventral extension on all propodi, each with slot into which dactylus inserts (fig. 6.4c, d). Ectoparasitic, branchial ..... Bathygyginae (*Bathygyge*) ... p. 249
  - Female with variable coxal plates, if large, first 2 pairs not medially directed; second oostegites not extending beyond anterior margin of head; pleon not flexed anterodorsally over pereon. Male without distoventral extensions on propodi ..... 6
6. Female with pleomeres having extended, digitate or tuberculate lateral plates, usually directed anterolaterally from pleon (fig. 6.4e, f). Ectoparasitic, branchial ..... Keponinae ... p. 270
  - Female with pleomeres having short, simple, non-digitate or tuberculate lateral plates, usually directed laterally, or lateral plates lacking ..... 7
7. Female with marsupium not much enlarged beyond margins of pereon, composed of 5 pairs of loosely fitting subequal oostegites; pleopods, when present, not pedunculate ..... 8
  - Female with marsupium enlarged beyond at least one side of pereon, formed of close-fitting oostegites, usually fewer than 5 pairs, unequal in size; pleopods and lateral plates, when present, pedunculate ..... 12

8. Female with coxal plates and frontal lamina of head greatly enlarged, giving anterior portion of body semicircular shape (fig. 6.4g). Ectoparasitic, branchial ..... Orbioninae ... p. 280  
 – Female with coxal plates and frontal lamina not greatly enlarged, body more linear ..... 9
9. Female with well-developed pleopods. .... 10  
 – Female with small tuberculiform, triangular or ovate pleopods ..... 11
10. Male with unsegmented or reduced maxilliped. Epicaridium larvae without external yolk sac (fig. 6.4h, i). Ectoparasitic, branchial or abdominal ..... Pseudioninae ... p. 287  
 – Male with segmented, setose maxilliped (in some segmentation may appear indistinct). Epicaridium larvae with external yolk sac (fig. 6.4j). Ectoparasitic, branchial ..... Pleurocryptellinae ... p. 284
11. Female with head oval or fusiform, never fused with pereon; lateral plates pedunculate; pleopods knob-like, uniramous (fig. 6.4k, l). Ectoparasitic, branchial ..... Argeiinae ... p. 242  
 – Female with head subrectangular or subtriangular, often fully or partially fused with pereon; lateral plates, if present, not pedunculate; pleopods flap-like, usually biramous (fig. 6.4m, n). Ectoparasitic, branchial ..... Bopyrinae ... p. 250
12. Female with symmetrical to slightly asymmetrical body, brood pouch symmetrical to slightly asymmetrical (if asymmetrical then expanded on one side at posterior margin), formed by oostegites from both sides of body ..... 13  
 – Female with highly asymmetrical body, brood pouch greatly expanded and formed by oostegites from one side of body (fig. 6.4o). Ectoparasitic, abdominal ..... Hemiarthrinae ... p. 260
13. Female with symmetrical body; lateral margins of head not overlapped by forward curved lateral portions of posterior pereomeres; lateral plates and pleopods falcate (fig. 6.4p, q). Ectoparasitic, abdominal ..... Phyllozurinae (*Phyllozurus*) ... p. 283  
 – Female with asymmetrical body; lateral margins of head overlapped by forward curved lateral portions of posterior pereomeres; lateral plates and pleopods variably foliose (thin elongate to broad) (fig. 6.4r, s). Ectoparasitic, abdominal ..... Athelginae ... p. 245
14. Female marsupium formed by close adhesion of oostegites to host membrane. Male with articulated pereopods ..... 15  
 – Female oostegites free, not adhering to host membrane; pleural lamellae absent; female without pereopods. Male with non-articulated pereopods (fig. 6.4t, u). Endoparasitic ..... Entoniscinae ... p. 307
15. Parasitic in decapods other than hermit crabs. Female with well-developed pleural lamellae, with heart tubercle in pleomere 3 (fig. 6.4v, w). Endoparasitic ..... Entioninae ... p. 311  
 – Parasitic in hermit crabs. Female without pleural lamellae, with heart tubercle in pleomere 1 (fig. 6.4x, y). Endoparasitic ..... Diogenioninae ... p. 309
16. Mature female with segmented body; antennae lobe-like; pereopods prehensile; pleopods present. Mature male morphology distinct from cryptoniscus larval form; antennae lobe-like; pereopods prehensile. Cryptoniscus larva with isomorphic pereopods ..... 17  
 – Mature female with unsegmented body; antennae absent or articulate; pereopods absent or styliform; pleopods absent. Mature male morphology similar to cryptoniscus larval form, antennae articulate; pereopods styliform. Cryptoniscus larva without isomorphic pereopods, posterior pairs elongate with long dactyli ..... 18
17. Mature female elongate, body segments distinct in dorsal view, head distinct from pereon, 7 pairs of pereopods equally distributed along body. Male with segmented pleon. Cryptoniscus larva without oral sucker (fig. 6.5a, b). Endoparasitic, abdominal ..... Entophilidae ... p.338  
 – Mature female ovate, body segments indistinct in dorsal view, head and pereon fused, first 5 pairs of pereopods adjacent to each other near head, pereopod 7 usually absent. Male with fused pleomeres. Cryptoniscus larva usually<sup>1</sup> with oral sucker (fig. 6.5c, d). Ectoparasitic ..... Dajidae ... p. 330

18.	Female parasitising thecostracan barnacles .....	19
–	Female parasitising other hosts .....	20
19.	Male (paedomorphic cryptoniscus) with teeth on basal article of antennula (fig. 6.5e, f). Endoparasitic .....	
	..... Hemioniscidae <sup>2</sup> ... p. 340	
–	Male (paedomorphic cryptoniscus) without teeth on basal article of antennula (fig. 6.5g–i). Endoparasitic .....	
	..... Crinoniscidae ( <i>Crinoniscus</i> ) <sup>3</sup> ... p. 322	
20.	Mature female with stellate body, parasitising entoniscid isopods (fig. 6.5n, o). Endoparasitic .....	
	..... Stellatoniscidae ( <i>Stellatoniscus</i> ) ... p. 344	
–	Mature female without stellate body .....	21
21.	Female parasitising ostracods (fig. 6.5j–m). Ectoparasitic .....	Cyproniscidae ... p. 328
–	Female parasitising amphipods (fig. 6.5p, q). Ectoparasitic .....	Podasconidae ... p. 342
–	Female parasitising mysids (fig. 6.5r–t). Ectoparasitic .....	Asconiscidae ( <i>Asconiscus</i> ) ... p. 316
–	Female parasitising other hosts .....	22
22.	Cryptoniscus larva with dactylus and propodus of pereopods 6 and/or 7 fused, forming elongate rapier-like structure. Parasitising rhizocephalans and decapods (fig. 6.6a, b). Endoparasitic or mesoparasitic .....	
	..... Cryptoniscidae ... p. 324	
–	Cryptoniscus larva with dactylus and propodus of pereopods 6 and 7 not fused, dactylus articulating with propodus. ....	23
23.	Cryptoniscus larva head “typical” (frontal margin not projected forward or inflated). Parasitising rhizocephalans and isopods (fig. 6.6c–e). Endoparasitic, mesoparasitic or ectoparasitic ... Cabriopidae ... p. 316	
–	Cryptoniscus larva head atypical (frontal margin either projected forward or inflated) .....	24
24.	Cryptoniscus larva with conical head, posterior margin no wider than pereomere 1; antennular basal article with marginal teeth; dactylus approximately half as long as propodus. Parasitising cumaceans (fig. 6.6f–h). Ectoparasitic .....	Cumoechidae ... p. 327
–	Cryptoniscus larva with inflated, rounded head, posterior margin much wider than pereomere 1; antennular basal article without marginal teeth; dactylus longer than propodus. Parasitising cumaceans (fig. 6.6i, j). Ectoparasitic .....	Capitoniscidae ... p. 322

<sup>1</sup> See remarks in Williams and Boyko (2021).

<sup>2</sup> Cryptothiridae (*Cryptothir* Dana, 1853) was poorly described from the cryptoniscus larva only and is a *nomen dubium*; based on the host barnacle, it is probably synonymous with either Crinoniscidae or Hemioniscidae.

<sup>3</sup> *Proteolepas* Darwin, 1854 is placed in Crinoniscidae but is a *nomen dubium*; it may be synonymous with *Crinoniscus*.

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## Credits

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Fig. 6.1a, c, Williams et al. (2022); b, McDermott et al. (2019); d, Williams and Boyko (2021); insets, Boyko and Williams (2015). Fig. 6.2a–c, e–h, Cericola and Williams (2015); d, i, k, l, Williams et al. (2019); j, Bourdon and Bowman

(1970). Fig. 6.3a, b, h, i, Williams et al. (2019); c–g, Boyko and Williams (2010); j–m, An et al. (2013); n, o, An et al. (2019). Fig. 6.4a, b, Trilles (1999); c, d, Markham (2016); e, f, Bourdon (1983); g, An et al. (2013); h, i, Boyko and Williams (2004); j, Williams et al. (2024); k, Williams et al. (2022); l, An et al. (2015); m, n, Williams and Boyko (2004); o, Boyko and Williams (2004); p, q, Richardson (1905); r, s, Williams and Boyko (2016); t, u, Miyashita (1940); v, w, Uyeno and Boyko (2020); x, y, DeTorre (et al. (2023). Fig. 6.5a–d, Boyko and Williams (2012); e, Trilles (1999); f, Goudeau (1970); g–i, Buhl–Mortensen et al. (2020); j–m, Shiino (1942); n, o, Oanh and Boyko (2020); p, q, Giard and Bonnier (1895); r–t, Sars (1899). Fig. 6.6a, b, Boyko (2014); c–e, Carayon (1942); f–j, Boyko and Williams (2023). Fig. 6.7a–c, An et al. (2015); d, Chopra (1923); e, Nierstrasz and Brender à Brandis (1923); f, g,

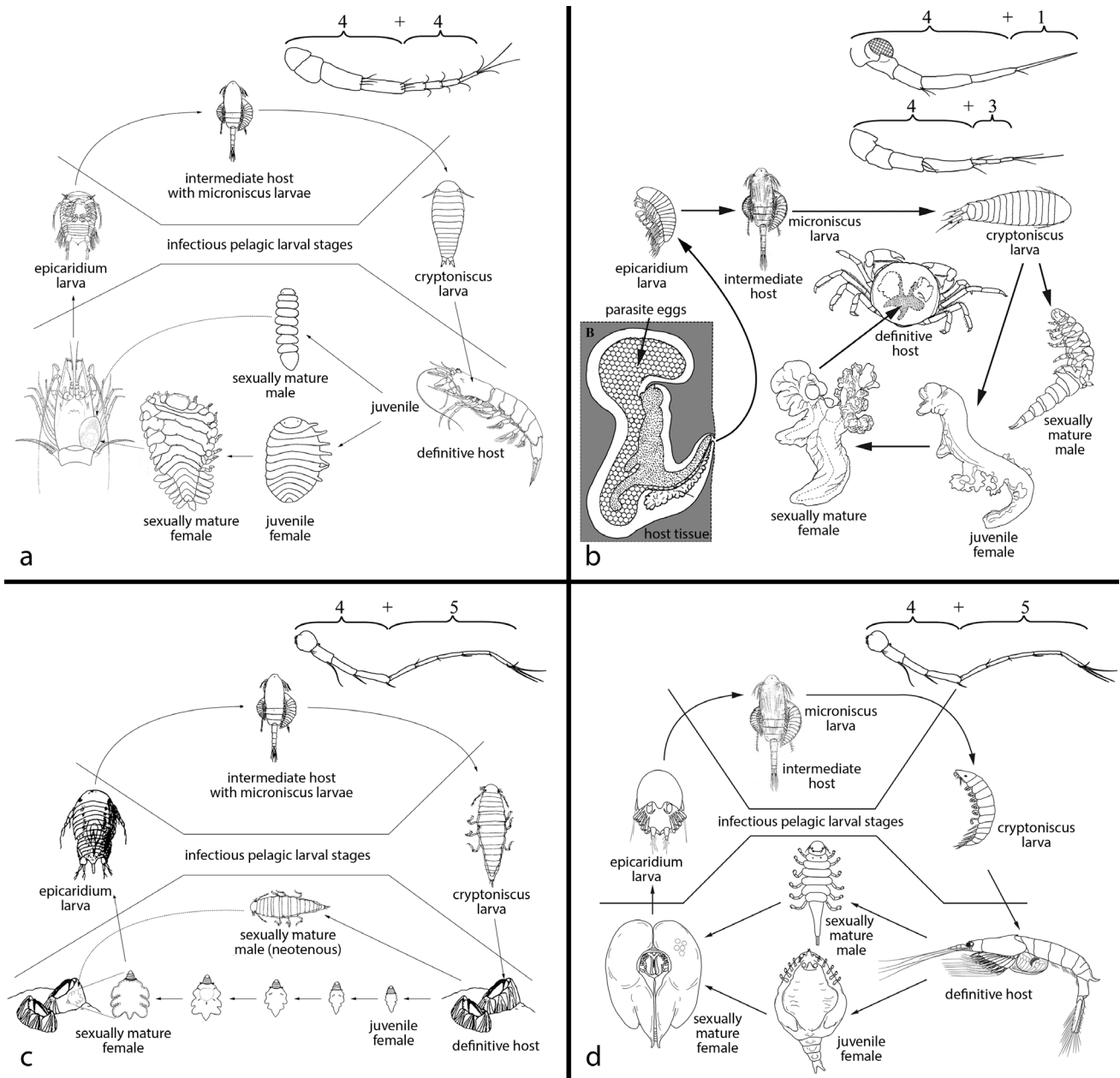


Figure 6.1. Epicaridea (Bopyroidea and Cryptoniscoidea). Representative life cycles (a–d) and antennal articulation of their respective cryptoniscus larvae. a, life cycle of *Argeia pugettensis* Dana, 1853 (Bopyridae, Argeiinae), inset shows 4 peduncular and 4 flagellar articles of cryptoniscus larval antennae. b, life cycle of *Pinnixion sexdecennia* McDermott, Williams and Boyko, 2019 (Entoniscidae, Entioninae), inset shows 4 peduncular and 1 or 3 flagellar articles of cryptoniscus larval antennae in Entoniscidae. c, life cycle of *Hemioniscus balani* Buchholz, 1866 (Cryptoniscoidea, Hemioniscidae), inset shows 4 peduncular and 5 flagellar articles of cryptoniscus larval antenna. d, life cycle of *Prodajus ostendensis* Gilson, 1909 (Cryptoniscoidea, Dajidae), inset shows 4 peduncular and 5 flagellar articles of cryptoniscus larval antenna.

Williams and Boyko (2010); h, i, An et al. (2017); j, Kensley (1974); k, l, Bourdon and Bruce (1983); m, n, Danforth (1970); n, o, Shiino (1958). Fig. 6.8a, b, Markham (1972); c, d, i–o, Williams and Boyko (2016); e–h, Boyko and Williams (2003); p, q, Cericola and Williams (2015). Fig. 6.9a, b, Markham (2016); c, d, An et al. (2015). Fig. 6.10a, b, Bourdon (1968); c, p,

q, Markham (1982); d, Shiino (1933); e, Bourdon (1976); f, g, Markham (1989); h, i, Markham (1988); j, k, Richardson (1904); l, m, Ribeiro et al. (2019); n, o, t, u, Markham (1985); r, s, Adkison (1984); v, w, An et al. (2015). Fig. 6.11a, b, Nierstrasz and Brender à Brandis (1929); c, f, g, Bourdon (1983); d, e, An et al. (2015); h, i, Boyko (2004); j, Bourdon (1968); k,

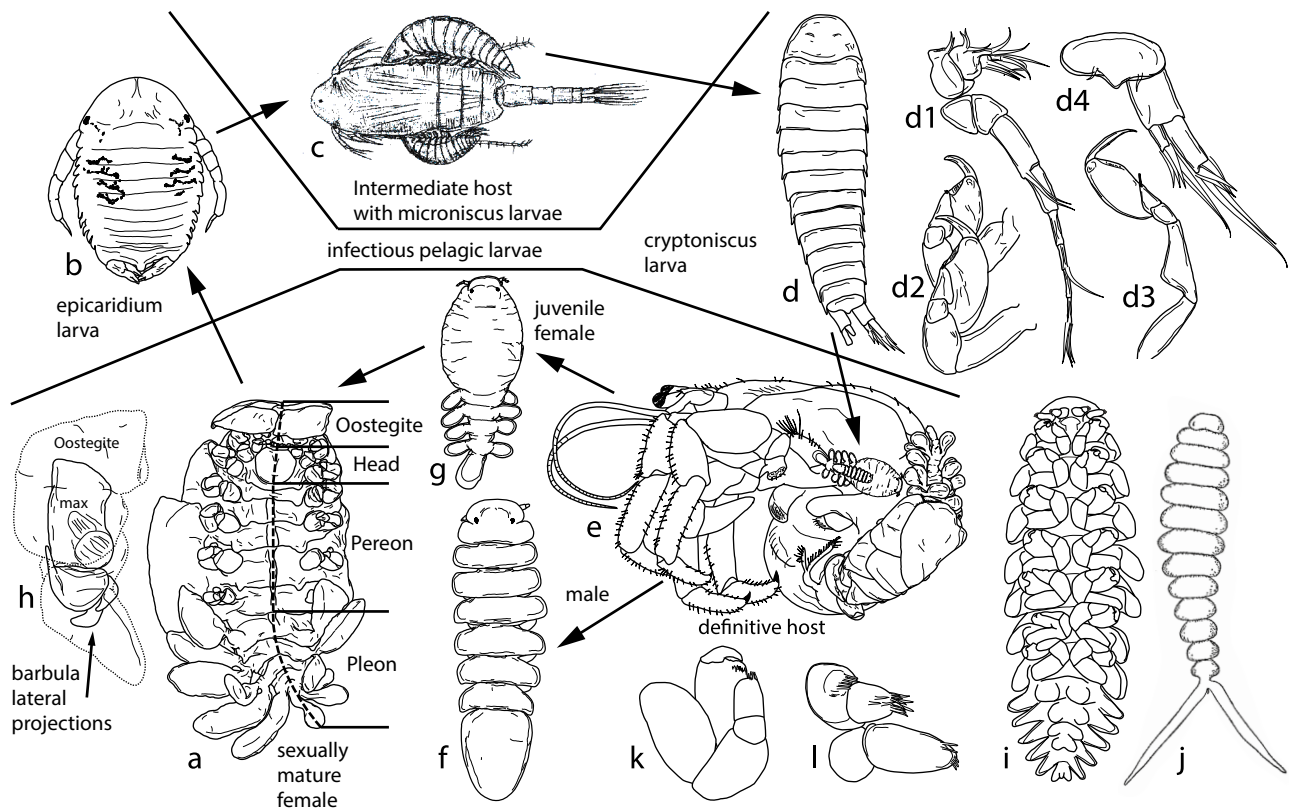


Figure 6.2. Epicaridea (Bopyridae). Life cycle stages and morphology: a, e, adult females; b, epicaridium larva; c, microniscus larva; d, cryptoniscus larva; f, i, j, adult males; g, juvenile female. a, female, ventral view; b, epicaridium larva, dorsal view; c, microniscus larvae on copepod intermediate host; d, cryptoniscus larva, dorsal view and parts (d1, antennula, antenna; d2, pereopods 1, 2; d3, pereopod 7; d4, pleotelson and right uropod); e, adult female plus juvenile female and male pair on hermit crab definitive host; f, male, dorsal view; g, juvenile female; h, maxilliped and lateral extensions of barbula shown within oostegite 1; i, male, ventral view; j, male, dorsal view; k, male, pereopod 1; l, male, antennula and antenna.

Richardson (1904); l, Shiino (1934); m, n, Bourdon and Bruce (1983); o, p, Shimomura et al. (2006); q, r, Markham (1985); s, t, Bourdon (1981); u–w, Bourdon and Markham (1980). Fig. 6.12a, b, Bruce, 1975; c, d, Bruce, 1973b; e, Bruce, 1972b; f, Shiino, 1937; g, Nierstrasz and Brender à Brandis, 1932; h, i, Bruce, 1974; j, Markham, 1985; k, q, r, Shiino, 1934; l, Richardson, 1904; m, Saito, 2020; n, Boyko, 2012; o, Saito, 2015; p, Nierstrasz and Brender à Brandis, 1931; s, An et al., 2015; t, u, Markham, 1972; v, Bruce, 1973a. Fig. 6.13a–d, Markham, 1990; e, Markham, 1972; f, n, Markham, 1985; g, Nierstrasz and Brender à Brandis, 1931; h, i, Saito and Shimomura, 2015; j, Barnard, 1955; k, Markham, 1992; l, Nierstrasz and Brender à Brandis, 1932; m, Boyko and Williams, 2004; o, p, Chopra, 1923. Fig. 6.14a, b, Shiino (1936b); c, Nobili (1906); d, Tattersall (1905); e, f, An et al. (2012); g, h, Bourdon (1968); i, p, q, Shiino (1937); j, k, Shiino (1951); l, An et al. (2019); m, u, Nierstrasz and Brender à Brandis (1931); n, An et al. (2018); o, Shiino (1936b); r, s, Bourdon (1977); t, Nierstrasz and Brender à Brandis (1930a); v, An et al. (2007); w, Uyeno and Boyko (2020); x, Williams et al. (2023). Fig. 6.15a, b, g, h, Nierstrasz and Brender à Brandis (1931); c, d, Shiino (1936a); e, f, Brasil

Lima (1980); i, j, q, r, Danforth (1972); k, Nierstrasz and Brender à Brandis (1930b); l, m, An et al. (2006a); n, o, Bourdon and Bowman (1970). Fig. 6.16a, b, h, Bourdon (1981); c, d, Bourdon (1968); e, Boyko (2003); f, g, k, l, An et al. (2013a); i, j, Bourdon (1982); m, n, Shiino (1950); o, p, Richardson (1904). Fig. 6.17a–c, Richardson (1905). Fig. 6.18a–h, Bourdon (1981); i, Boyko et al. (2024); j–o, Williams et al. (2024); p, q, Bourdon (1979); r, s, Boyko and Williams (2010); t, u, Bourdon (1972b); v, Nierstrasz and Brender à Brandis (1929). Fig. 6.19a, Saito and Moritaki, 2020; b, c, Pérez, 1920; d, e, Boyko and van der Meij, 2018; f, g, Bourdon and Boyko, 2005; h, i, l, o, Shiino, 1933; j, An et al., 2010; k, Markham, 2010; m, n, Williams et al., 2019; p, q, Shiino, 1949. Fig. 6.20a, Dollfus and Carayon, 1942; b, c, An et al., 2016a; d, e, Markham and Boyko, 1999; f, Kensley, 1974; g, Markham, 1979; h, Bourdon, 1972a; i, An et al., 2015; j, Markham, 1999; k, Markham, 1994; l, Van Name, 1920; m, n, Adkison and Heard, 1995; o, An et al., 2016b; p, Bourdon, 1983; q, An et al., 2009; r, Williams and An, 2009; s, t, Markham, 1985; u, SOSA et al., 2025; v, Bourdon, 1968; w, Nobili, 1906. Fig. 6.21a, Nobili, 1906; b, c, Bourdon, 1968; d, e, n, Nierstrasz and Brender à Brandis, 1929; f, Markham, 1978a; g, h, Bourdon,

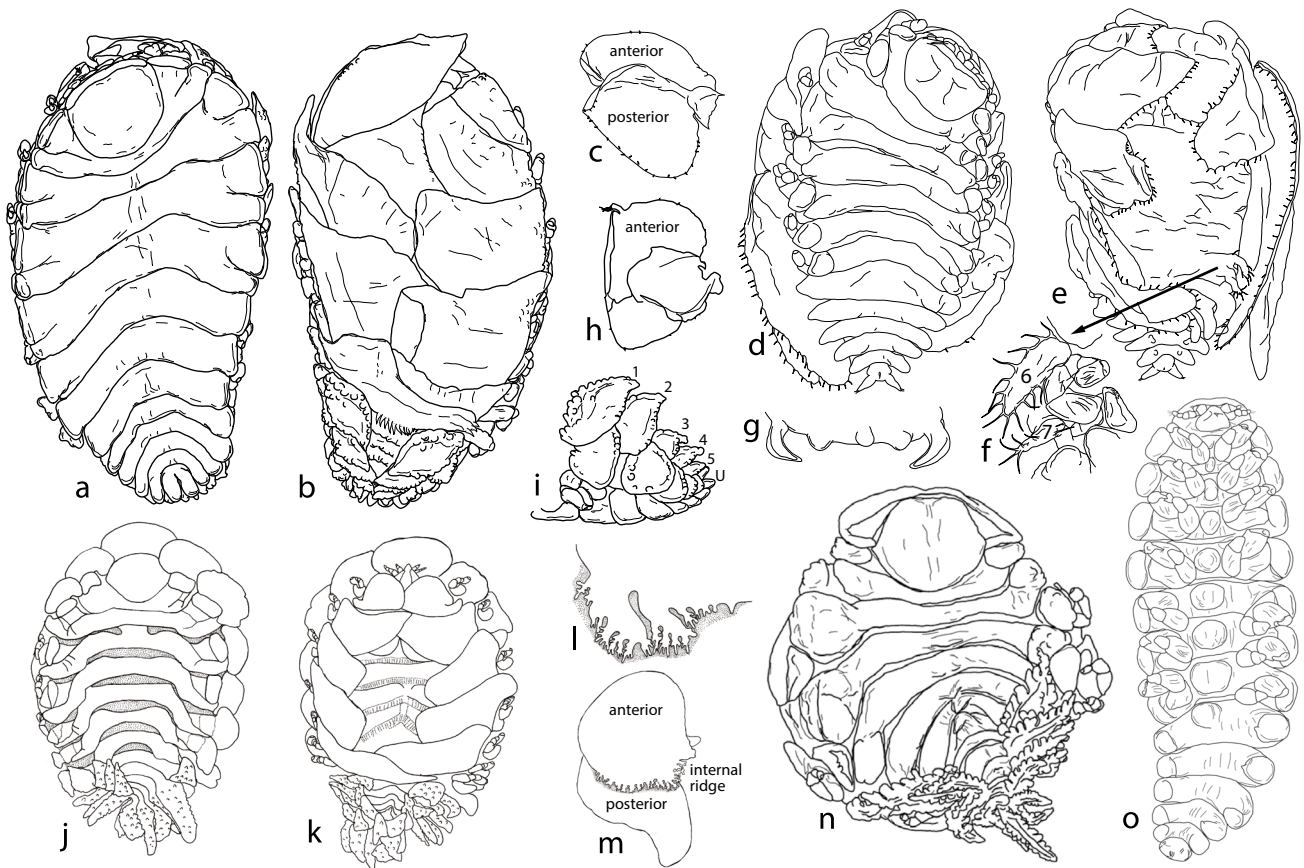


Figure 6.3. Epicaridea (Bopyridae). Representative adult females and males. a, female, dorsal view; b, female, ventral view; c, oostegite 1, internal view; d, female, dorsal view; e, female, ventral view showing oostegites 6 and 7; f, close up of oostegites 6, 7 and pereopod 7; g, barbula, both sides shown; h, maxilliped with palp; i, lateral view of pleon; j, female, dorsal view; k, female, ventral view; l, barbula, only one side shown; m, oostegite 1, internal view; n, female, dorsal view; o, male, ventral view.

1976; i, j, Markham, 1974; k, Richardson, 1910; l, Markham, 2008; m, Román-Contreras and Soto, 2002; n, Román-Contreras, 2008. Fig. 6.22a, Nierstrasz and Brender à Brandis, 1923; b, Román-Contreras and Boyko, 2007; c, d, Shiino, 1934; e, f, Markham, 1988; g, h, Boyko et al., 2018; i, j, Markham, 1975b; k, l, Shiino, 1958; m, n, Markham, 1975a; o, Richardson, 1904; p, Williams and Madad, 2010; q, An et al., 2020; r, Nierstrasz and Brender à Brandis, 1929. Fig. 6.23a, b, Miyashita (1940); c, d, Reinhard (1945); e, f, Codreanu et al. (1960); g–l, Uyeno and Boyko (2020); m–o, McDermott et al. (2019); p, Williams et al. (2023). Fig. 6.24a–g, Bourdon (1968). Fig. 6.25a–g, Sars (1899). Fig. 6.26a, Boyko (2013); b, c, Caullery and Mesnil (1920); d, e, Shiraki and Kakui (2024); f, p, Giard and Bonnier (1895); g, Sars (1883); h–l, Pillai (1966); m, Barnard (1925); n, o, Nierstrasz and Brender à Brandis (1931); q–t, Sassaman (1985); u, v, Hansen (1916); w, x, Rybakov (1990). Fig. 6.27a–f, Bourdon (1972); g–l, Schultz (1977). Fig. 6.28a–h, Buhl–Mortensen et al. (2020). Fig. 6.29a, Pérez (1920); b, c, Peresan and Roccatagliata (2005); d, Fraisse (1878); e–n, Boyko (2014); o, Boyko and van der Meij (2018). Fig. 6.30a–h,

Hansen (1916). Fig. 6.31a–c, Sars (1883); d–i, Shiino (1942). Fig. 6.32a–d, Williams and Boyko (2021); e, f, Shields and Gómez–Gutiérrez (1996); g, p, q, Sars (1885); h, i, Boyko and Williams (2012); j–l, Shimomura et al. (2005); m, Richardson (1909); n, o, Koehler (1911). Fig. 6.33a, f, Richardson (1908a); b–d, Nierstrasz and Brender à Brandis (1923); e, G.O. Sars (1883); g, Schultz (1978); h, Williams and Boyko (2021); i–k, Boyko and Williams (2021b); l–n, Jones and Smaldon (1986); o–q, Nierstrasz and Brender à Brandis (1931). Fig. 6.34a, b, f, g, Markham and Dworschak (2005); c–e, Boyko and Williams (2015); h–j, Richardson (1903); k–n, Bourdon (1976). Fig. 6.35a–d, Grygier (1981a); e, Goudeau (1977); f, g, Goudeau (1970); h, Hosie (2008); i, j, Grygier (1981b). Fig. 6.36a, d–j, Giard and Bonnier (1885); b, c, Giard and Bonnier (1899). Fig. 6.37a–i, Oanh and Boyko (2020). Fig. 6.38a–h, Bourdon (1983); i–q, Schultz (1977). Fig. 6.39a–i, p–s, Schultz (1977); j, k, Nielsen (1967); l–o, Bourdon (1981); t–w, Williams et al. (2022). Fig. 6.40a–d, Bourdon (1967); g–k, Bourdon (1981); l–s, Schultz (1977); t–w, Williams et al. (2024). Fig. 6.41a–m, Schultz (1977); n–q, Schädel et al. (2019).

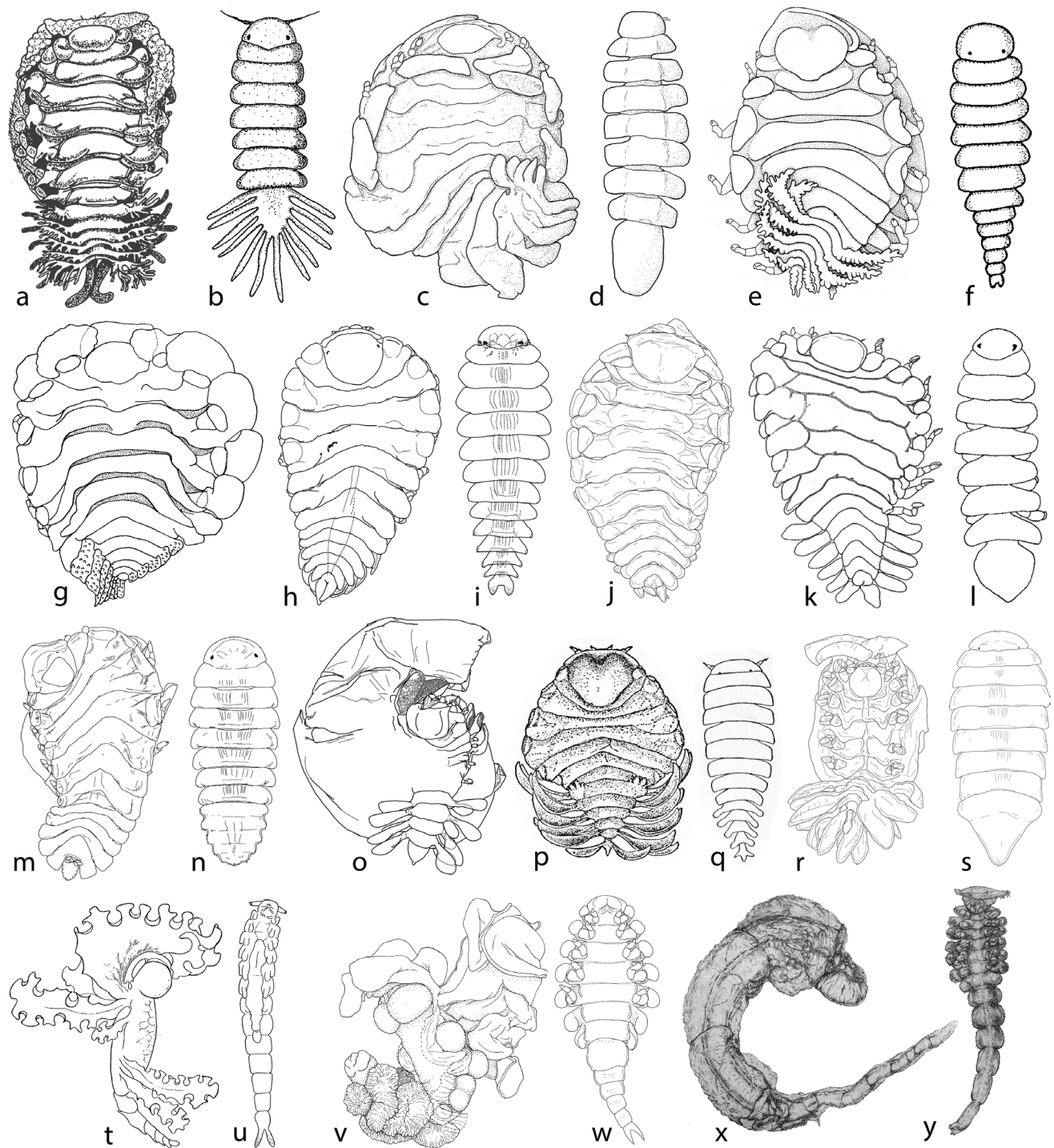


Figure 6.4. Epicaridea (Ionidae, Bopyridae, and Entoniscidae). Representative adult females and males. a, b, Ionidae: *Ione thoracica* (Montagu, 1808); c, d, Bathygyginae: *Bathygyge grandis* Hansen, 1897; e, f, Keponinae: *Dactylokepon semipennatus* Bourdon, 1983; g, Orbioninae: *Parasymmetrorbione bicauda* An, Boyko and Li, 2013; h, i, Pseudioninae: *Pseudione quasimodo* Boyko and Williams, 2004; j, Pleurocryptellinae: *Pleurocryptella poseidon* Williams and Boyko in Williams, Boyko and Stewart, 2024; k, l, Argeiinae: *Argeia pugettensis* Dana, 1853; m, n, Bopyrinae: *Schizobopyrina bombyliaster* Williams and Boyko, 2004; o, Hemiarthrinae: *Hemiarthrus surculus* Boyko and Williams, 2004; p, q, Phyllozurinae: *Phyllozurus abdominalis* Stimpson, 1857; r, s, Athelginae: *Allathelges alisonae* Williams and Boyko, 2016; t, u, Entoniscinae: *Entoniscoides okadai* Miyashita, 1940; v, w, Entioninae: *Allocancrion yunnu* Uyeno and Boyko, 2020; x, y, Diogenioninae: *Diogenion vermifactus* Codreanu, Codreanu and Pike, 1960. a, c, e, g, h, j, k, m, o, p, r, mature female, dorsal view; t, v, x, mature female, lateral view; b, d, f, i, l, n, q, s, male, dorsal view; u, w, y, male, ventral view.

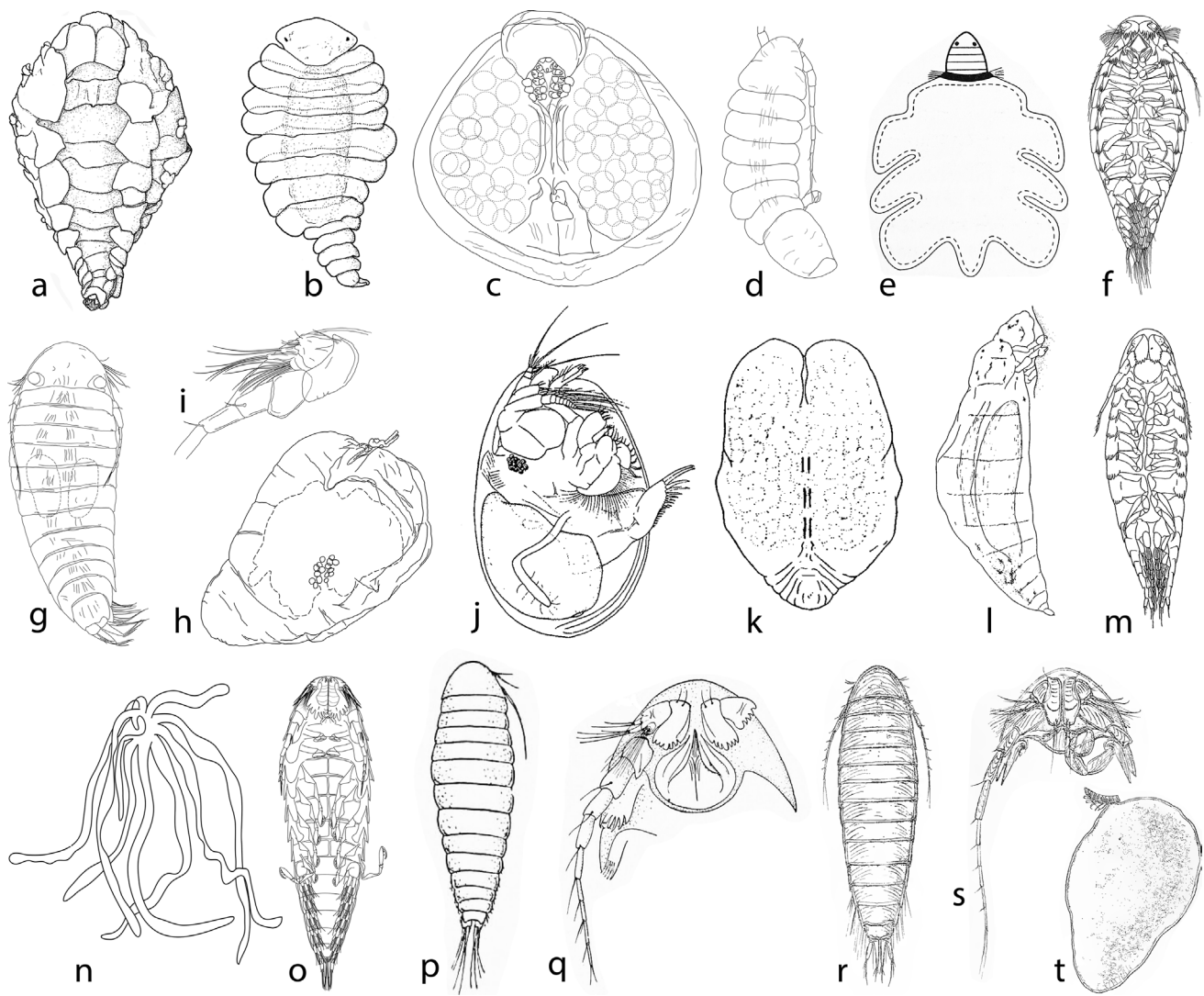


Figure 6.5. Epicaridea (Cryptoniscoidea). Representative adult females and males. a, b, Entophylidae: *Entophylus mirabile dictu* Markham and Dworschak, 2005; c, d, Dajidae: *Aspidophryxus discoformis* Boyko and Williams, 2012; Hemioniscidae: e, f, *Hemioniscus balani* Buchholz, 1866; g–i, *Crinoniscus stroembergi* Buhl-Mortensen, Williams and Boyko, 2020; Cyproniscidae: j–m, *Onisocryptus ovalis* (Shiino, 1942); n, o, Stellatoniscidae: *Stellatoniscus tentaculus* Oanh and Boyko, 2020; p, q, Podasconidae: *Parapodascon stebbingi* (Giard and Bonnier, 1895); r–t, Asconiscidae: *Asconiscus simplex* G.O. Sars, 1899. a, k, mature female, ventral view; b, d, g, p, r, male, dorsal view; c, ovigerous female, ventral view; e, mature female, dorsal view; f, m, o, male, ventral view; h, ovigerous female, lateral view; i, antennula of male; j, mature female within ostracod host; l, immature female, lateral view; n, mature female; q, mouthparts, antennulae, and antenna of male; s, antennulae, antenna, and pereopod 1 of male; t, immature female, lateral view.

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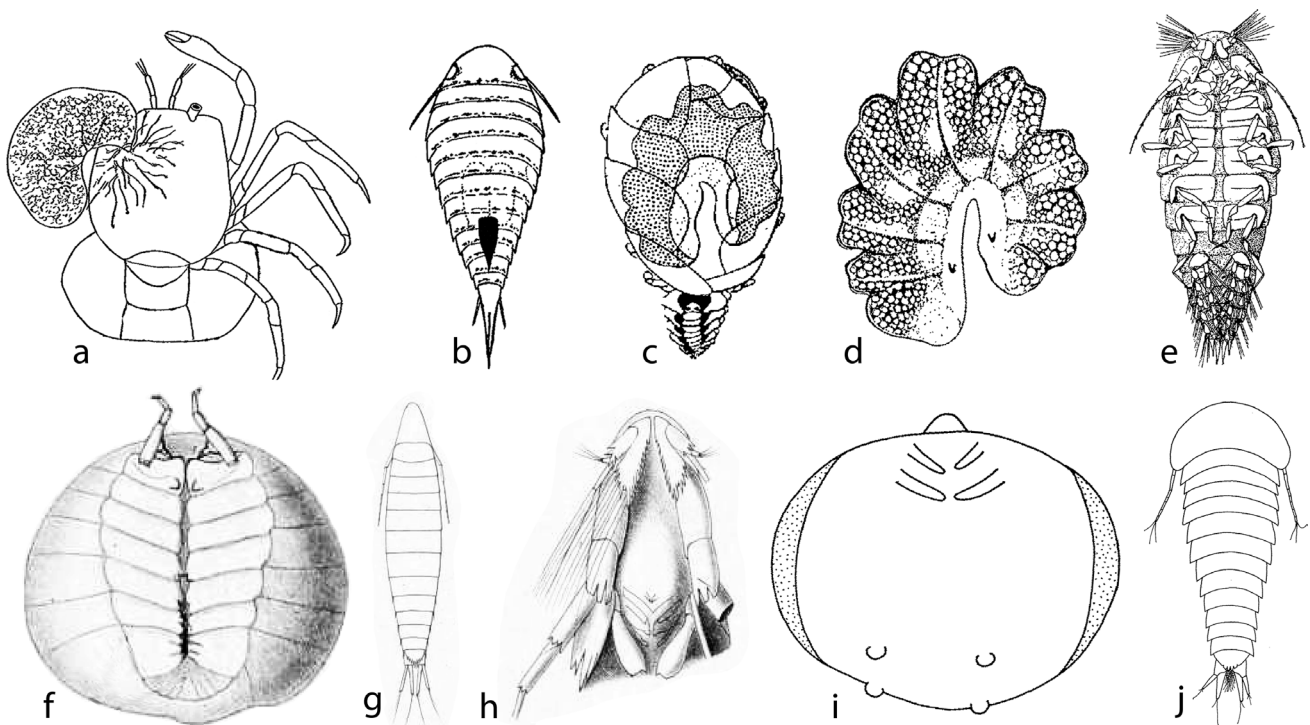


Figure 6.6. Epicaridea (Cryptoniscoidea). Representative adult females and males. a, b, Cryptoniscidae: *Danalia hapalocarcini* Fize, 1955; c–e, Cabiropidae: *Cabirops perezi* Carayon, 1942; f–h, Cumoechidae: *Cumoechus insignis* Hansen, 1916; i, j, Capitoniscidae: *Capitoniscus cumacei* Bourdon, 1972. a, mature females attached to host crab; b, male, ventral view; c, mature female within brood chamber of host; d, ovigerous female, lateral view; e, male, ventral view; f, mature female, ventral view; g, male, dorsal view; h, antennulae and antennae of male; i, mature female, ventral view; j, male, dorsal view.

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## Superfamily Bopyroidea Rafinesque, 1815

The superfamily Bopyroidea contains three families (Bopyridae Rafinesque, 1815, Entoniscidae Kossman, 1881, and Ionidae H. Milne Edwards, 1840), with bopyrids and ionids composed of ectoparasitic (branchial and abdominal) species and entoniscids of solely endoparasitic species. However, it is difficult to diagnose Bopyroidea effectively. Trilles (1999) indicated the following characters as unique to bopyroids: sexually dimorphic with females being much larger than males, often symmetrical, with large broods and oostegites; males being symmetrical and dwarf; the cryptoniscus larva developing into a fourth stage (bopyridium). However, Trilles' (1999) concept of Bopyroidea included Dajidae and Entophilidae, which were subsequently shown to be part of Cryptoniscoidea (Boyko et al., 2013). Therefore, characters of significant sexual dimorphism, hypertrophic, often symmetrical and usually hyperfertile with oostegites apply to members of Bopyroidea and Cryptoniscoidea. In addition, there are symmetrical, dwarf males in both groups, although no species of bopyroids have neotenus males as found in many cryptoniscoids. The “bopyridium” (sometimes referred to as the fourth larval stage) is found in all bopyroids as well as dajids and entophilids.

The only morphological character that appears to be a synapomorphy for bopyroids is the number of articles on the antennae of the cryptoniscus larval stage (four basal plus four or fewer flagellar articles (Boyko and Williams, 2015). This is supported by molecular data that distinguishes the two superfamilies (Boyko et al., 2013). Schädel et al. (2019) stated that “two supposed species of Bopyridae, *Probopyrus pandalicola* and *Probopyrus floridensis*, have five antennal flagellum elements (Dale and Anderson, 1982).” This, however,

is not correct. Dale and Anderson (1982) did state in the text, without comment that the numbers were odd, that both species had five flagellar articles on the antennae, but examination of their illustrations shows that both species clearly have four flagellar articles and do not deviate from the 4+4 or fewer pattern of bopyroid cryptoniscus larvae antennae.

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## Family Bopyridae Rafinesque, 1815

Bopyridae as currently diagnosed is a diverse and heterogeneous taxon (see below) composed of ten subfamilies. Further molecular studies are required to more adequately define the family and some of the subfamilies (e.g. Pseudioninae; Boyko et al., 2017). It is likely that some subfamilies are not monophyletic, whereas others may be raised to family level. All subfamilies are ectoparasitic (branchial or abdominal) on a range of hosts.

**Diagnosis. Female** body ovate to elongate; pereomeres distinct or fused; head shape variable. Frontal lamina present or absent. Eyes present or absent. Barbular lobes present or absent. Antenna and antennula articulated or fused. Maxilliped with or without palp. Marsupium open or closed. 5 or 7 pairs of oostegites; oostegite 1 with anterior and posterior lobes; internal ridge

smooth or digitate. Coxal plates present or absent. Dorsolateral bosses present or absent. Middorsal projections present or absent. 1 to 7 pairs of pereopods. Pleomeres distinct or fused; lateral plates present or absent. Pleopods present or absent. Uropods present or absent. **Male** body elongate; head distinct or fused with pereomere 1. Eyes present or absent. Antennae and antennulae articulated. Midventral tubercles present or absent. 7 pairs of pereopods. Pleomeres distinct or fused; pleopods and uropods present or absent. Ectoparasites. **Cryptoniscus** larva body teardrop shaped, eyes present or absent. Antennula without denticles on basal segment. Oral sucker present or absent. Pereomeres without toothed coxal plates. Pereopods 1–7 subequal in size and shape. 5 biramous pleopods. Uropodal exopod larger and longer than endopod. Pleotelson without teeth.

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## Subfamily Argeiinae Markham, 1977

Figure 6.7

Females of species in Argeiinae are all ectoparasites in the branchial chambers of shrimps and have the posterior lobe of the first oostegite of two main shapes: rounded or with a triangular projection. Males are all similar in shape, with the main differences being seen in the shape of the pleotelson, including: short rounded (fig. 6.7i), short triangular (fig. 6.7o), and elongate (fig. 6.7g). The genus *Bopyrosa* Nierstrasz and Brender à Brandis, 1923 was based solely on a single, clearly immature, female (now lost) from an unknown host. Markham (1977) placed *Bopyrosa* in Argeiinae but it could also belong to Keponinae based on the morphology of the pleon. The family diagnosis and key to genera are modified from An et al. (2017). Males representative of some genera are figured.

*Diagnosis. Female* body rounded, subtriangular to nearly circular; weakly distorted, up to 30°; pereomeres usually

distinct; head wider than long, oval to triangular, head entire or bilobed. Frontal lamina present or absent. Eyes present or absent. Barbula smooth, with 2 or 3 smooth, tapered lobes on each side. Antenna and antennula articulated. Maxilliped with articulated palp or tuft of setae in palp area. Marsupium open or almost closed. 5 pairs of oostegites; oostegite 1 with low rounded or extended triangular posterior lobe; internal ridge smooth. Coxal plates present. Dorsolateral bosses present or absent. Middorsal projections absent. 5 pairs of pereopods. Pleon of 6 pleomeres, lateral plates present or absent. Pleopods uniramous or biramous, 3–5 pairs, tuberculiform, triangular or ovate flaps. Uropods uniramous or biramous. **Male** pereomeres subequal in width, head wider than long. Eyes present or absent. Antenna and antennula articulated. Midventral tubercles absent. 7 pairs of pereopods. Pleomeres fused into single segment, pleopods and uropods absent. Branchial parasites.

### Key to females of genera of Argeiinae

- |    |   |                     |
|----|---|---------------------|
| 1. | Pleomeres with lateral plates .....   | 2                   |
| –  | Pleomeres without lateral plates .....  | 6                   |
| 2. | Pleopods biramous .....   | 3                   |
| –  | Pleopods uniramous .....  | 4                   |
| 3. | Body longer than broad (fig. 6.7a, b) .....   | <i>Argeia</i>       |
| –  | Body broader than long (fig. 6.7d) .....  | <i>Stegoalpheon</i> |
| 4. | Pereon much wider than pleon .....  | 5                   |
| –  | Pereon approximately as wide as pleon (fig. 6.7e) .....                                     | <i>Bopyrosa</i>     |
| 5. | Pleon quadrate, approximately as long as pereon (fig. 6.7f, g) .....                        | <i>Eragia</i>       |
| –  | Pleon triangular, much shorter than pereon (fig. 6.7h, i) .....                             | <i>Paraeragia</i>   |
| 6. | Uropods uniramous .....   | 7                   |
| –  | Uropods biramous (fig. 6.7j) .....  | <i>Argeiopsis</i>   |
| 7. | Pleomeres fused (fig. 6.7k, l) .....  | <i>Gareia</i>       |
| –  | Pleon segmented .....   | 8                   |
| 8. | Brood pouch closed. Maxilliped with articulated palp (fig. 6.7m) .....                      | <i>Parargeia</i>    |
| –  | Brood pouch open (fig. 6.7n, o). Maxilliped without palp or with non-articulated palp ..... | <i>Stegoargeia</i>  |

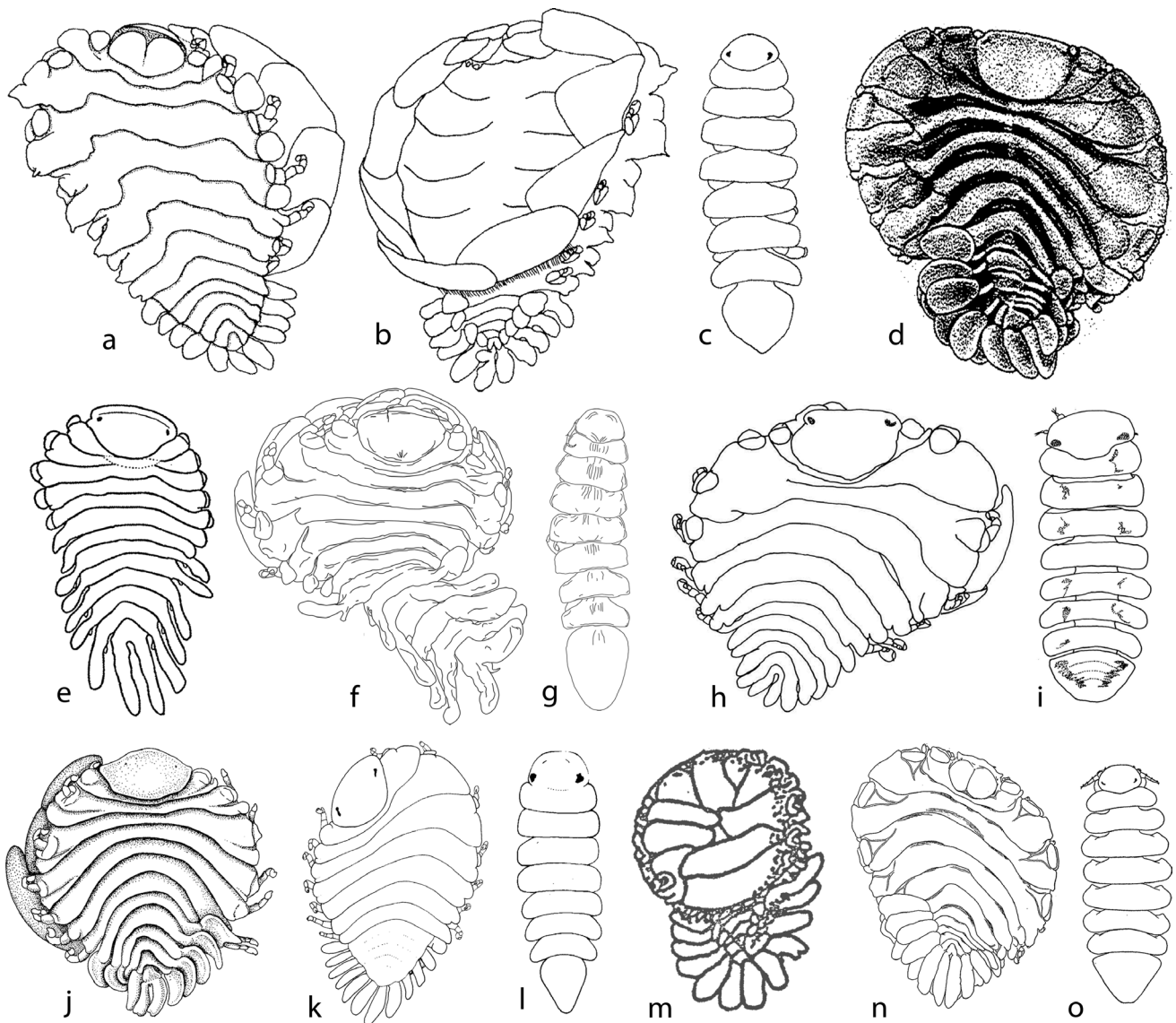


Figure 6.7. Argeiinae. *Argeia pugettensis* Dana, 1853: a, female dorsal view; b, female ventral view; c, male dorsal view. *Stegoalpheon kemp* Chopra, 1923: d, female dorsal view. *Bopyrosa phryxiformis* Nierstrasz and Brender à Brandis, 1923: e, female dorsal view. *Eragia profunda* Markham, 1994: f, female dorsal view; g, male dorsal view. *Paraeragia kiribatiensis* An, Zhang and Paulay, 2017: h, female dorsal view; i, male dorsal view. *Argeiopsis inhacae* Kensley, 1974: j, female dorsal view. *Gareia arafurae* Bourdon and Bruce, 1983: k, female dorsal view; l, male dorsal view. *Parargeia ornata* Hansen, 1897: m, female ventral. *Stegoargeia lowisi* (Chopra, 1923): n, female dorsal view; o, male dorsal view.

### *Argeia* Dana, 1853

**Diagnosis. Female** body ovoid, approximately 3/4 as wide as long, pereomeres distinct; head subrectangular, wider than long, bilobed, not distorted. Frontal lamina present, narrow. Eyes absent. Maxillipedal palp setose, sometimes articulated. Marsupium open. Oostegite 1 with low rounded posterior lobe. Dorsolateral bosses present. Pereopods subequal. Pleon with 5 pairs of uniramous oval to lanceolate lateral plates. 4 or 5 pairs of uniramous knob-like to ovate uniramous pleopods. Uropods uniramous. **Male** with eyes. All pereopods subequal.

Shelf-slope, parasitising crangonid shrimps. Temperate Northern Pacific, Temperate Northern and Tropical Atlantic. 2 species and 1 *taxon inquirendum* (An et al., 2015; Markham, 1977).

### *Argeiopsis* Kensley, 1974

**Diagnosis. Female** body nearly circular to triangular in outline; pereonites distinct; head triangular, not bilobed, not distorted. Frontal lamina present, thin. Eyes present. Barbula with 2 smooth, tapered lobes on each side. Maxilliped with setose,

non-articulated palp. Marsupium open. Oostegite 1 with extended triangular posterior lobe. Dorsolateral bosses present. Pereopods subequal. Pleon without lateral plates. 5 pairs of biramous pleopods as large triangular flaps. Uropods biramous. **Male** head narrower than first pereonite. Eyes present or absent. First pair of pereopods larger than others.

Subtidal, parasitising stenopodid and alpheid shrimps. Western Indo-Pacific. 3 species (An et al., 2017; Boyko and Kazmi, 2005).

#### ***Bopyrosa* Nierstrasz and Brender à Brandis, 1923**

*Diagnosis.* **Female** body outline subrectangular, first 3 pereomeres fused medially; head ovate, not bilobed, distorted 15°. Frontal lamina present, thin. Eyes present. Barbula, antenna, antennula, maxilliped unknown. Marsupium open. Oostegite 1 unknown. Dorsolateral bosses absent. Pereopods unknown. Pleon with 5 pairs of uniramous, elongate lateral plates. 5 pairs of uniramous pleopods as minute flaps. Uropods uniramous. **Male** unknown.

Subtidal, host unknown. Central Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1923).

#### ***Eragia* Markham, 1994**

*Diagnosis.* **Female** pereon rounded, pleon distorted 30°; pereomeres distinct; head quadrilateral in shape, embedded in pereon, not bilobed, not distorted. Frontal lamina present, thin. Eyes absent. Barbula with 2 short, smooth lobes on each side. Maxilliped with setose articulated palp. Marsupium open. Oostegite 1 with extended triangular posterior lobe. Dorsolateral bosses present. Pereopods 1 and 2 smaller than others. Pleon with 5 pairs of uniramous, elongate lateral plates. 5 pairs of uniramous pleopods as minute knobs. Uropods apparently as single uniramous structure. **Male** without eyes. Pereopod 7 with much longer basis and ischium than others.

Bathyal, parasitising crangonid shrimps. Central Indo-Pacific. 1 species (Williams and Boyko, 2010).

#### ***Gareia* Bourdon and Bruce, 1983**

*Diagnosis.* **Female** body ovate, pereomeres distinct; head ovate, not bilobed, distorted approximately 30°. Frontal lamina absent. Eyes present. Barbula with 2 pairs of lobes on each side. Maxilliped with setose non-articulated palp. Marsupium open. Oostegite 1 with low rounded posterior lobe. Coxal plates present but reduced. Dorsolateral bosses indistinct. Pleomeres almost completely fused dorsally, lateral plates absent. 5 pairs of biramous pleopods (exopods ovate, endopods tuberculiform). Uropods uniramous. **Male** with eyes present. Pereopods subequal in size.

Intertidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (Bourdon and Bruce, 1983).

#### ***Paraeragia* An, Zhang and Paulay, 2017**

*Diagnosis.* **Female** body ovate, pereomeres distinct; head subquadrate, not bilobed, distorted approximately 10°. Frontal lamina absent. Eyes present. Barbula with 2 short tapered lobes on each side. Maxilliped with setose articulated palp.

Marsupium open. Oostegite 1 with extended triangular posterior lobe. Dorsolateral bosses present. Pleomeres distinct, 5 pairs of lateral plates. 5 pairs of uniramous tuberculiform pleopods. Uropods uniramous. **Male** with eyes present. Pereopods subequal in size. Pleomeres fused but with faint dorsal indications of segmentation.

Subtidal, parasitising alpheid shrimps. Eastern Indo-Pacific. 1 species (An et al., 2017).

#### ***Parargeia* Hansen, 1897**

*Diagnosis.* **Female** body (exclusive of lateral plates) subtriangular, pereomeres distinct; head ovate, distorted approximately 15°. Frontal lamina thin. Eyes absent. Barbula unknown. Maxilliped with setose articulated palp. Marsupium closed. Oostegite 1 with ovate posterior lobe bearing small distolateral projection. Dorsolateral bosses present. Pleomeres distinct, 5 pairs of lateral plates. 5 pairs of uniramous ovate pleopods. Uropods uniramous. **Male** with eyes absent. Pereopods becoming gradually smaller posteriorly. Pleon much broader than pereon, bearing anterior middorsal tubercle.

Slope, parasitising crangonid shrimps. Tropical Eastern Pacific. 1 species (Hansen, 1897).

#### ***Stegoalpheon* Chopra, 1923**

*Diagnosis.* **Female** body ovate, pereomeres distinct; head ovate, distorted approximately 10°. Frontal lamina present, subquadrate. Eyes absent. Barbula with 2 long tapered lobes on each side. Maxilliped with setose non-articulated palp. Marsupium open. Oostegite 1 with extended triangular posterior lobe. Dorsolateral bosses present. Pleomeres distinct, 5 pairs of uniramous lateral plates. 5 pairs of biramous pleopods. Uropods uniramous. **Male** with eyes present. Pereopods 1 and 2 larger than others.

Intertidal, parasitising alpheid shrimps. Western Indo-Pacific, Temperate Northern Pacific. 1 species (An et al., 2015).

#### ***Stegoargeia* An, Boyko and Li, 2015**

*Diagnosis.* **Female** body ovate, pereomeres distinct; head bilobed, distorted approximately 5°. Frontal lamina present, subquadrate. Eyes absent. Barbula with 3 long tapered lobes on each side. Maxilliped with setose non-articulated palp. Marsupium open. Oostegite 1 with extended triangular posterior lobe. Dorsolateral bosses present. Pleomeres distinct, lateral plates absent. 5 pairs of biramous pleopods. Uropods uniramous. **Male** with eyes. Pereopod proportions unknown. Pleon triangular.

Intertidal, parasitising alpheid shrimps, Western Indo-Pacific, Temperate Northern Pacific. 2 species (An et al., 2015; Shiino, 1958).

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## Subfamily Athelginae Codreanu and Codreanu, 1956

Figure 6.8

The genera of Athelginae can be distinguished from other epicarideans in that the females are abdominal ectoparasites of calcinid, diogenid and pagurid hermit crabs, as well as one species recorded from the abdomen of a hapalogastrid anomuran. No other epicarideans are known as abdominal parasites of hermit crabs or their close relatives. The heads of females are not distorted relative to the pereon but the pleon may be distorted up to 90°, one or more oostegites are typically extended anterior to the head, forming a funnel for aerating the brood and releasing the larvae, and the abdomen usually lacks lateral plates and has biramous ovate or foliose pleopods on four or five pleomeres. All males have fused pleomeres lacking any appendages. The key is modified from Boyko and Williams (2003) and Williams and Boyko (2016). Males of representative genera are figured.

**Diagnosis. Female** body longer than wide, linear or distorted up to 90°; head wider than long or length and width subequal, with subparallel margins, posterior margin convex or straight;

barbula of 1–4 smooth or digitate lobes on each side. Oostegites 1, 2 or 3 extended over head or not anteriorly produced; oostegite 1 with long or short, triangular, recurved or rounded posterior lobe; other oostegites forming large, enclosed marsupium. One or more pereopods anterior to head, at least some pairs adjacent to head, last 2 pairs evenly spaced or distant from first 5 pairs. Pleomeres 1–4 or 1–5 with biramous pleopods arising from common peduncle, lateral plates present or absent. Pleotelson with or without uropods. **Male** body length approximately 2–6 times width, lateral margins of all pereomeres subequal or with some larger, rounded or laterally tapered. Head wider than long, anterior margin rounded. Pereomeres closely approximated or with posterior pereonites more widely spaced. Pleomeres fused into single segment without indication of segmentation or with weak indication of first pleomere, triangular, broadest anteriorly, tapering distally to rounded or subacute tip. Pleopods and uropods absent. Abdominal ectoparasites of anomurans.

### Key to females of genera of Athelginae

- |    |  |                      |
|----|--|----------------------|
| 1. | Lateral plates present .....   | 2                    |
| –  | Lateral plates absent .....  | 7                    |
| 2. | Lateral plates on pleomeres 1–5 .....  | 3                    |
| –  | Lateral plates only on pleomeres 1–3 (fig. 6.8a, b) .....                        | <i>Stegias</i>       |
| 3. | Lateral plates on pleomere 5 similar to lateral plates on other pleomeres. ....  | 4                    |
| –  | Lateral plates on pleomere 5 reduced, globular or scar-like (fig. 6.8c, d) ..... | <i>Pseudostegias</i> |

4.	Pereopods 5 and 6 widely separated (broad pereomeres) .....	5
–	Pereopods 5 and 6 not widely separated (narrow pereomeres) .....	6
5.	Pleopods uniramous (fig. 6.8e, f) .....	<i>Minimathelges</i>
–	Pleopods biramous (fig. 6.8g, h) .....	<i>Anathelges</i>
6.	5 pleomeres (fig. 6.8i) .....	<i>Claustrathelges</i>
–	6 pleomeres (fig. 6.8j, k) .....	<i>Falsanathelges</i>
7.	Uropods uniramous, articulated with terminal pleomere (fig. 6.8l, m) .....	<i>Parathelges</i>
–	Uropods absent or as reduced unsegmented lobes .....	8
8.	Pleopods on pleomere 5 present (fig. 6.8n, o) .....	<i>Allathelges</i>
–	Pleopods on pleomere 5 absent (fig. 6.8p, q) .....	<i>Athelges</i>

### ***Allathelges* Kazmi and Markham, 1999**

**Diagnosis.** **Female** body longer than broad, not distorted; head wider than long, posterior margin slightly convex; barbula of 4 smooth lobes on each side. First oostegites extended over head and reflexed, posterior lobe elongate, triangular. Pereomeres 1, 2 anteriorly concave, posteriorly convex; pereomeres 3–6 anteriorly medially straight and laterally narrowly convex, posteriorly straight and laterally with narrow posteriorly directed lobes; pereomere 5 or 6 largest; pereomere 7 with convex anterior margin and concave posterior margin. Pereopods 1–3 anterior to head, 4–7 evenly spaced. Pleomeres 1–5 with lamellar biramous pleopods arising from common peduncle, lateral plates absent. Pleotelson tapering, uropods absent. **Male** body length approximately 2–3 times width, lateral margins of all pereomeres subequal, rounded. Pereomeres closely approximated. Pleomeres fused into single segment without indication of segmentation or with weak indication of first segment, triangular, broadest anteriorly, tapering distally to rounded tip.

Intertidal–subtidal, parasitising calcinid and diogenid hermit crabs. Western and Central Indo-Pacific. 2 species (Williams and Boyko, 2016).

### ***Anathelges* Bonnier, 1900**

**Diagnosis.** **Female** body distorted sinistrally; head longer than wide, posterior margin slightly convex; barbula of 3 smooth short lobes on each side. First 3 oostegites extended over head, first pair forming conical projection, posterior lobe elongate, triangular. Pereomeres 1–5 anteriorly concave, posteriorly convex; pereomere 6 largest, anterior and posterior margins concave; pereomere 7 with convex anterior margin and concave posterior margins; pereomere 7 similar to 6 but smaller. Pereopods 1, 2 anterior to head, 3–5 parallel to head, 4 and 5 at posterior margin of pereon. Pleomeres 1–5 with lamellar or subovate biramous pleopods and uniramous lateral plates arising from common peduncle. Pleotelson with uniramous, nonpedunculate, uropods. **Male** body length approximately 3 times width, lateral margins of all pereomeres subequal, rounded. Pereomeres separated at lateral margins, especially 5–7. Pleomeres fused into single elongate segment without

indication of segmentation or with weak indications of segmentation, broadest anteriorly, tapering distally to rounded or subacute tip.

Intertidal–subtidal, parasitising pagurid hermit crabs. Temperate Northern and Tropical Atlantic, Tropical Eastern Pacific, Temperate Northern Pacific, Temperate South America. 4 species (Boyko and Williams, 2003).

### ***Athelges* Gerstaecker, 1862**

**Diagnosis.** **Female** body linear or distorted at 90°; head length and width subequal, posterior margin convex; barbula of 2 smooth short lobes on each side. Second pair of oostegites extended over head, oostegite 1 posterior lobe elongate, triangular. Pereomere 1 anteriorly concave, posteriorly convex; pereomeres 2–5 anteriorly medially straight and laterally narrowly convex, posteriorly straight and laterally with narrow posteriorly directed lobes; pereomere 6 largest, anterior margin straight, posterior margin concave; pereomere 7 similar to 6 but shorter. Pereopod 2 anterior to head, pereopods 2 and 3 parallel to head, 6 and 7 at posterior margin of pereon. Pleomeres 1–4 with subovate biramous pleopods, lateral plates absent. Pleotelson without uropods, distal tip slender, rounded or with 2–4 small knobs. **Male** body length approximately 3 times width, lateral margins of all pereomeres subequal, rounded. Pereomeres closely approximated. Pleomeres fused into single elongate segment without indication of segmentation, broadest anteriorly, tapering distally to rounded tip.

Intertidal–slope, parasitising diogenid and pagurid hermit crabs. Temperate Northern Atlantic, Temperate Southern Africa, Temperate Northern Pacific, Central Indo-Pacific, Temperate Australasia. 14 species (Boyko et al., 2024; Shinoda et al., 2026).

### ***Claustrathelges* Williams and Boyko, 2016**

**Diagnosis.** **Female** pereon not distorted, pleon weakly distorted, head length and width subequal, anterior margin weakly convex, posterior margin convex; barbula with 2 digitate lobes on each side. No oostegites extended over head or produced posteriorly; oostegite 1 with short rounded posterior lobe. Pereomeres 1–4 anteriorly concave and posteriorly convex, pereomere 5 with margins nearly straight, pereomeres

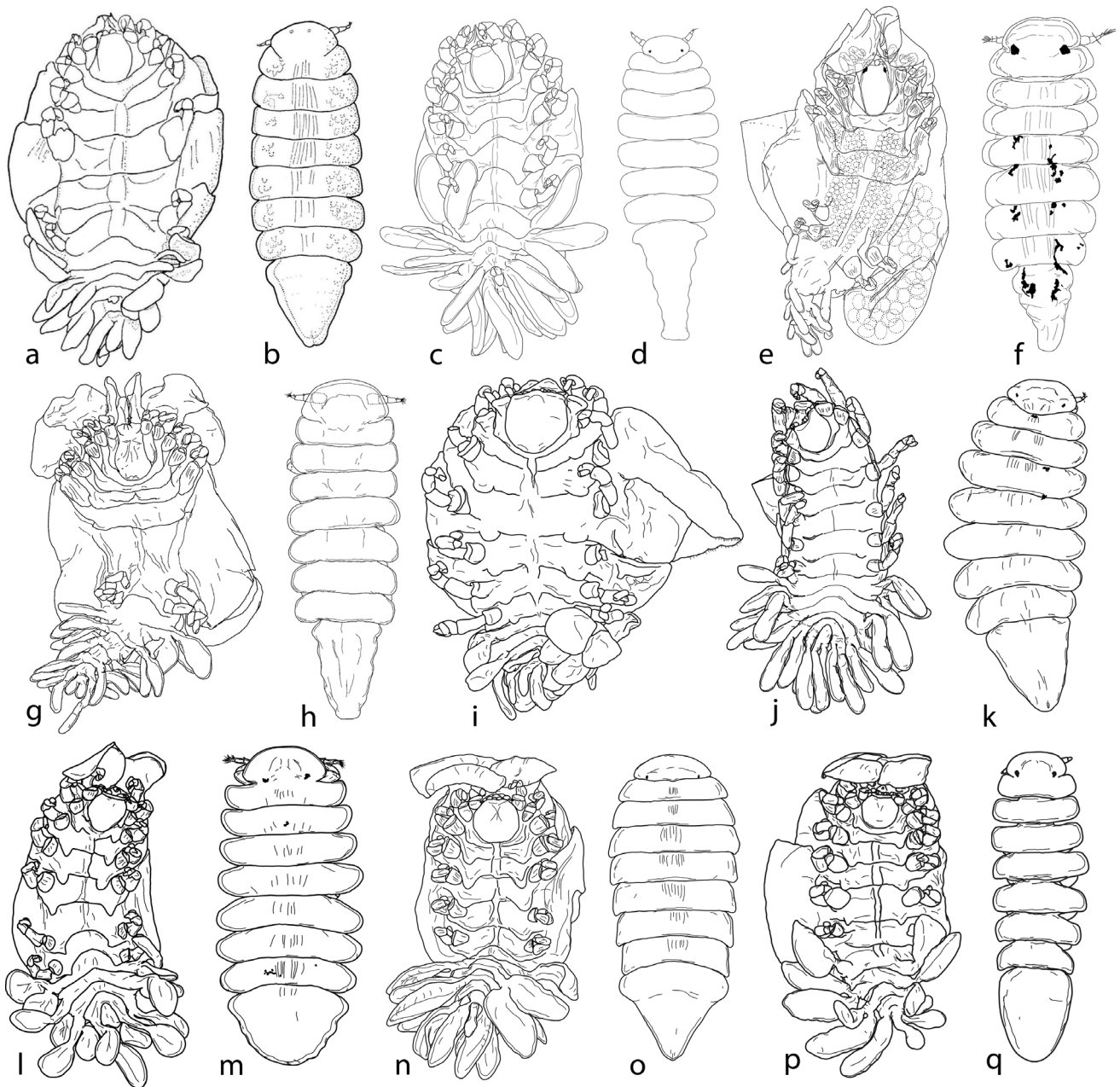


Figure 6.8. Athelginae. *Stegias clibanarii* Richardson, 1904: a, female dorsal view; b, male dorsal view. *Pseudostegias dulcilacuum* Markham, 1982: c, female dorsal view; d, male dorsal view. *Minimathelges nanus* Boyko and Williams, 2003: e, female dorsal view; f, male dorsal view. *Anathelges hyptius* (Thompson, 1902): g, female dorsal view; h, male dorsal view. *Claustrathelges macdermotti* Williams & Boyko, 2016: i, female dorsal view; j, female dorsal view; k, male dorsal view. *Falsanathelges mariae* Williams and Boyko, 2016: j, female dorsal view; k, male dorsal view. *Parathelges aniculi* (Whitelegge, 1897): l, female dorsal view; m, male dorsal view. *Allathelges alisonae* Williams and Boyko, 2016: n, female dorsal view; o, male dorsal view. *Athelges takanoshimensis* Ishii, 1914: p, female dorsal view; q, male dorsal view.

6 and 7 anteriorly convex, posteriorly concave; pereopod 4 broader than other pereopods. Pereopod 1 anterior to head, pereopods 2 and 3 parallel to head, no large gaps between pereopods 4–7. Dorsal surface of first oostegites with pattern of ridges. Pleomeres 1–5 with elongate-ovate biramous pleopods

and uniramous lateral plates, all arising from common peduncle. Pleotelson absent; pleon of 5 pleomeres. **Male** unknown.

Subtidal, parasitizing diogenid hermit crabs. Temperate Australasia. 1 species (Williams and Boyko, 2016).

***Falsanathelges* Boyko and Williams, 2003**

*Diagnosis. Female* body not distorted, head broader than long with convex lateral margins, anterior margin concave, posterior margin convex; barbula of 2 digitate lobes on each side. No oostegites extended over head or produced posteriorly; oostegite 1 with short recurved posterior lobe. Pereomeres 1–3 anteriorly concave and posteriorly convex, pereomere 4 only slightly so, pereomere 5 with more or less straight margins, pereomeres 6 and 7 anteriorly convex and posteriorly concave; pereomeres 3–5 subequal in size and larger than others. Pereopod 1 anterior to head, 2 parallel to head, no large gaps between 4–7. Pleomeres 1–5 with elongate-ovate biramous pleopods and uniramous lateral plates, all arising from common peduncle. Pleotelson with biramous, pedunculate, elongate-ovate uropods. *Male* body length approximately 3.5 times width, lateral margins of pereomeres 3–7 almost parallel, 1, 2 shorter. Pereomeres widely separated. Pleomeres fused into single segment, broadest anteriorly, lateral margins showing residual segmentation, tapering posteriorly to rounded distal tip.

Intertidal–subtidal, parasitizing calcinid and diogenid hermit crabs. Central Indo-Pacific. 3 species (Boyko and Williams, 2003; Shinoda et al., 2025; Williams and Boyko, 2016).

***Minimathelges* Boyko and Williams, 2003**

*Diagnosis. Female* body distorted sinistrally with right side longest; head longer than wide, posterior margin convex; barbula unknown. First two oostegites extended over head, oostegite 1 with long triangular lobe. Pereomeres 1–5 anteriorly concave and posteriorly convex; pereomere 6 largest, anterior and posterior margins subparallel. Pereopod 1 anterior to head, 3 and 4 parallel to head, 6 and 7 at posterior margin of pereon. Pleomeres 1–5 with lamellar uniramous pleopods and uniramous lateral plates, not arising from common peduncle. Pleotelson with uniramous lamellar uropods. *Male* body length approximately 3.1 times width, lateral margins of pereomeres 3–6 almost parallel, 1, 2, 7 shorter. Pereomeres closely approximated. Pleomeres fused into single segment with partial demarcation of at least first pleomere ventrally, broadest anteriorly, lateral margins showing residual segmentation, tapering posteriorly to rounded distal tip.

Intertidal, parasitizing pagurid hermit crabs. Central Indo-Pacific. 2 species (Boyko and Williams, 2003).

***Parathelges* Bonnier, 1900**

*Diagnosis. Female* body slightly to c. 30° distorted dextrally with left side longest; head approximately as long as wide, posterior margin slightly convex; barbula of 2 smooth lobes on each side. First oostegites extended over head, posterior lobe long, triangular, second and third pairs adjacent to head. Pereomere 1 anteriorly concave, posteriorly convex; pereomeres 2–5 anteriorly medially straight and laterally narrowly convex, posteriorly straight and laterally with narrow posteriorly directed lobes; pereomere 6 largest, anterior margin straight, posterior margin concave; pereomere 7 similar to 6 but not as long. Pereopod 1 anterior to head, 2 and 3 parallel to head, 4

and 7 at posterior margin of pereon. Pleomeres 1–4 with lamellar biramous pleopods arising from common peduncle, lateral plates absent. Pleotelson with uniramous lamellar uropods. *Male* body length approximately 2–3 times width, lateral margins of all pereomeres subequal, rounded. Pereomeres closely approximated. Pleomeres fused into single segment without indication of segmentation, triangular, broadest anteriorly, tapering distally to rounded tip.

Intertidal–subtidal, parasitizing calcinid, diogenid and pagurid hermit crabs. Temperate Northern and Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 10 species (Kazmi and Markham, 1999; Markham, 1972).

***Pseudostegias* Shiino, 1933**

*Diagnosis. Female* body not distorted to weakly distorted; head longer than wide, posterior margin straight; barbula of 1–4 smooth or digitate lobes on each side. First oostegites not extended over head, with long triangular posterior lobe. Pereomere 1 anteriorly concave, posteriorly convex; pereomeres 2–5 anteriorly medially straight and laterally narrowly convex, posteriorly straight and laterally with narrow posteriorly directed lobes; pereomere 6 largest, anterior margin straight, posterior margin concave; pereomere 7 similar to 6 but not as long. Pereopod 1 anterior to head, 2 and 3 parallel to head, 6 and 7 at posterior margin of pereon. Pleomeres 1–4 with elongate lateral plates and biramous pleopods; pleomere 5 with pair of rounded or triangular medially positioned lateral plates and biramous pleopods. Pleotelson with uniramous elongate uropods. *Male* body length approximately 3 times width, lateral margins of all pereomeres rounded, pereomere 4 broadest. Pereomeres not closely approximated. Pleomeres fused into single segment with or without indication of segmentation, triangular, broadest anteriorly, tapering distally to rounded or truncate tip.

Intertidal–subtidal, parasitizing calcinid and diogenid hermit crabs and hapalogastrids. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 7 species (Williams and Boyko, 2016).

***Stegias* Richardson, 1904**

*Diagnosis. Female* body slightly distorted sinistrally with right side longest or straight; head longer than wide, posterior margin convex; barbula with 2 short lobes bearing few digitations. First oostegites not extended over head, oostegite 1 with long triangular posterior lobe. Pereomeres 1 and 2 anteriorly concave and posteriorly convex; pereomeres 3–5 anteriorly concave and posteriorly straight; pereomere 6 largest, anterior margin straight, posterior margin concave. Pereopod 1 anterior to head, 3 and 4 parallel to head, 6 and 7 at posterior margin of pereon. Pleomeres 1–3 with lamellar biramous pleopods and uniramous lateral plates, not arising from common peduncle; pleomeres 4 and 5 with biramous pleopods, without lateral plates. Pleotelson with uniramous lamellar uropods. *Male* body length approximately 6 times width, lateral margins of pereomeres 1–4 subequal, straight, those of 5–7 wider and tapered laterally. Pereomeres closely approximated in anterior

half of body. Pleomeres fused into single segment without indication of segmentation, broadest anteriorly, tapering distally and slightly expanded at rounded distal tip.

Subtidal, parasitising diogenid hermit crabs. Tropical Atlantic, Central Indo-Pacific, Tropical Eastern Pacific. 3 species (Nierstrasz and Brender à Brandis, 1931).

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## Subfamily Bathygyginae Markham, 2016

Figure 6.9

The sole genus and species of Bathygyginae is ectoparasitic in the branchial chambers of shrimps. It can be distinguished from other epicarideans in that the females have oostegite 2 extending beyond the anterior margin of the head, the coxal plates of at least pereomeres 1 and 2 extending medially over the pereomeres, and the pleon distorted at approximately 70° (Markham, 2016). The males possess propodal sockets into which the tips of the dactyli are inserted; this character is known from species in a few other genera (e.g. *Asymmetrione*

Codreanu, Codreanu and Pike, 1965). The cryptoniscus larval stage was figured but not described by An et al. (2015).

**Diagnosis. Female** body nearly circular; pereomeres distinct; head much wider than long, oval, deeply embedded in first pereomere and overlapped by second oostegites. Head entire, not distorted. Frontal lamina absent. Eyes absent. Barbula with 2 smooth, tapered lobes on each side. Antenna and antennula articulated. Maxilliped with articulated palp. Marsupium closed. 5 pairs of oostegites; oostegite 1 with extended

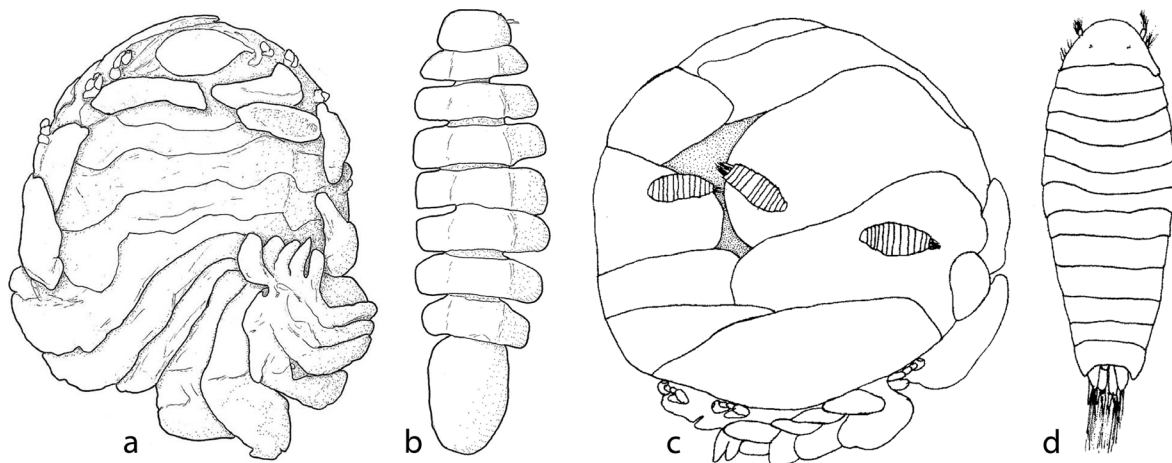


Figure 6.9. Bathygyginae. *Bathygyge grandis* Hansen, 1897: a, female dorsal view; b, male dorsal view; c, female ventral view, with three cryptoniscus larvae; d, cryptoniscus larva dorsal view.

triangular posterior lobe; internal ridge smooth. Coxal plates present, those of pereomeres 1 and 2 (sometimes 3) extending medially over pereomeres. Dorsolateral bosses absent. Middorsal projections absent. 5 pairs of subequal pereopods. Pleon of 6 segments, partially fused, distorted approximately 70°; 5 pairs of uniramous lateral plates present. Pleopods absent. Uniramous uropods present. **Male** body with pereomeres subequal in width; head wider than long, narrower than pereomere 1. Eyes absent. Antenna and antennula articulated. Midventral tubercles absent. 7 pairs of pereopods, dactyli on 1–5 longer than those on 6 and 7; all propodi with sockets for insertion of dactyli. Pereomeres fused into single segment, pleopods and uropods absent. Branchial parasites.

### ***Bathygyge* Hansen, 1897**

*Diagnosis.* As for family.

Bathypelagic, parasitising glyphocrangonid shrimps. Temperate Northern Atlantic, Temperate Southern Africa, Central Indo-Pacific, Temperate Northern Pacific. 1 species

(Hansen, 1897; Markham, 2016).

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## **Subfamily Bopyrinae Rafinesque, 1815**

Figures 6.10, 6.11

Species in the genera of Bopyrinae are all ectoparasitic in the branchial chambers of caridean shrimps, primarily in alpheid and palaemonid hosts. Bodies of females are generally dorsoventrally flattened with slight to moderate distortion of the head relative to the body, weakly developed (or absent) coxal plates and dorsolateral bosses, and a pleon with small, flap-like pleopods; lateral plates, if present, are not pedunculate. Males typically have a fused or partly fused pleon and if pleopods are present, they are sessile and uropods are absent. The key is modified from those in Markham (1985) and An et al. (2015). Males of some representative genera are figured.

*Diagnosis.* **Female** body linear, elongate or ovate, body not distorted to moderately distorted; head distinct from or fused with pereon; frontal lamina present or absent. Eyes present or absent. Antennula and antenna articulated or indistinct. Maxilliped without palp or with articulated or non-articulated

palp. Barbula with 1 or 2 smooth short lobes on each side. Pereomeres distinct or medially fused dorsally. 5 or 7 pairs of oostegites. Oostegites 1 symmetrical or asymmetrical with triangular or ovate posterior lobe, smaller or larger than anterior lobe; internal ridges smooth or digitate. Marsupium open or closed. Coxal plates, dorsolateral bosses and tergal projections present or absent. 5 pairs of pereopods. Pleon narrower or not narrower than pereon, 4–6 distinct or fused pleomeres; 3–5 pairs (sometimes asymmetrical) of smooth uniramous or biramous pleopods; uropods uniramous or absent. **Male** approximately 2–4 times as long as wide, pereomeres narrower or not narrower posteriorly. Head narrower than or subequal in width to pereon. Eyes present or absent. Antennula and antenna articulated or not articulated. Pereopods moderate to large compared to body, subequal or smaller posteriorly. Midventral tubercles present or absent. Pleon fused or of 6 segments; pleopods present or absent. Uropods absent.

### **Key to females of genera of Bopyrinae**

- |    |   |                         |
|----|---|-------------------------|
| 1. | Uropods present .....   | 2                       |
| –  | Uropods absent .....  | 5                       |
| 2. | Uropods biramous, with long, thin rami (fig. 6.10a, b) .....              | <i>Urobopyrus</i>       |
| –  | Uropods uniramous, with long, wide rami .....                             | 3                       |
| 3. | Maxilliped without palp (fig. 6.10c) .....                                | <i>Litobopyrus</i>      |
| –  | Maxilliped with palp .....  | 4                       |
| 4. | Palp without setae; oostegite 1 posterior lobe ovate (fig. 6.10d) .....   | <i>Bopyrinina</i>       |
| –  | Palp with setae; oostegite 1 posterior lobe triangular (fig. 6.10e) ..... | <i>Parapleurocrypta</i> |

5.	All pleopods biramous .....	6
–	Some or all pleopods uniramous .....	13
6.	Head distinctly extended into anterolateral horns (fig. 6.10j, k) .....	<i>Capitetragonia</i>
–	Head not anterolaterally extended .....	7
7.	Head and pereomere 1 separate .....	8
–	Head and pereomere 1 fused at least medially .....	11
8.	Body heart-shaped, barbula with 2 pairs of projections on each side (fig. 6.10l, m) .....	<i>Probopyrus</i>
–	Body not heart-shaped, barbula with 1 pair of projections on each side .....	9
9.	Oostegite 1 without posterolateral point (fig. 6.10n, o) .....	<i>Parabopyriscus</i>
–	Oostegite 1 with posterolateral point .....	10
10.	Pleomeres distinct, separated laterally on both sides (fig. 6.10p, q) .....	<i>Probopyriscus</i>
–	Pleomeres distinct on long side only (fig. 6.10r, s) .....	<i>Probopyrinella</i>
11.	Head fused with pereomere 1 medially. Body oval (fig. 6.10t, u) .....	<i>Ovobopyrus</i>
–	Head completely fused with pereomere 1. Body elongate .....	12
12.	Pleomeres of at least one side fused (fig. 6.10v, w) .....	<i>Bopyrella</i>
–	Pleomeres distinct on both sides (fig. 6.11a, b) .....	<i>Parabopyrella</i>
13.	Pleopods on one side of pleon (fig. 6.10f, g) .....	<i>Palaemonellione</i>
–	Pleopods on both sides of pleon .....	14
14.	Some pleopods biramous .....	15
–	All pleopods uniramous .....	16
15.	Pleopods 1–3 biramous, fourth uniramous (fig. 6.11c) .....	<i>Allobopyrus</i>
–	Pleopods on one side of pleon biramous, on other side uniramous (fig. 6.10h, i) .....	<i>Ogyridione</i>
16.	5 pairs of pleopods .....	17
–	Fewer than 5 pairs of pleopods .....	24
17.	5 pairs of oostegites .....	18
–	7 pairs of oostegites (fig. 6.11d, e) .....	<i>Septembopyrina</i>
18.	Coxal plates absent (fig. 6.11f, g) .....	<i>Probopyrione</i>
–	Coxal plates present .....	19
19.	Coxal plates on pereomeres 1–4 .....	20
–	Coxal plates on pereomeres 2–4 .....	23
20.	Pleopods reduced to tubercles (fig. 6.11h) .....	<i>Bopyroides</i>
–	Pleopods flap-like, not reduced .....	21
21.	Body ovate (fig. 6.11i) .....	<i>Discorsobopyrus</i>
–	Body elongate .....	22
22.	Oostegites 1 symmetrical (fig. 6.11j) .....	<i>Bopyrus</i>
–	Oostegites 1 asymmetrical (fig. 6.11k) .....	<i>Bopyrinella</i>
23.	Pleomeres fused (fig. 6.11l) .....	<i>Parabopyrus</i>
–	Pleomeres distinct (fig. 6.11m, n) .....	<i>Probynia</i>

24.	Pleomeres fused on one side (fig. 6.11o, p) .....	<i>Bopyrina</i>
–	Pleomeres distinct on both sides .....	25
25.	Oostegites 1 asymmetrical (fig. 6.11q, r) .....	<i>Schizobopyrina</i>
–	Oostegites 1 symmetrical .....	26
26.	Head fused with pereomere 1 at least medially (fig. 6.11s, t) .....	<i>Synsynella</i>
–	Head separate from pereomere 1 (fig. 6.11u–w) .....	<i>Bopyrione</i>

### ***Allobopyrus* Bourdon, 1983**

**Diagnosis. Female** linear, body distorted; head distinct from pereon; frontal lamina present. Eyes present. Antennulae and antennae articulated. Maxilliped with setose, non-articulated palp. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegites 1 slightly asymmetrical with triangular posterior lobe, larger than anterior lobe; internal ridges smooth. Marsupium open. Coxal plates and dorsolateral bosses present, tergal projections absent. Pleon not narrower than pereon, 6 pleomeres, fused except at lateral margins; 4 pairs of smooth pleopods: 3 pairs biramous and 1 pair uniramous; uropods absent. **Male** unknown.

Intertidal, parasitising palaemonid shrimps. Central Indo-Pacific. 1 species (Bourdon, 1983).

### ***Bopyrella* Bonnier, 1900**

**Diagnosis. Female** ovate, body slightly distorted; head fused with pereon medially, subquadrate; frontal lamina absent. Eyes present. Antennula and antenna articulated. Maxilliped with setose articulated palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing distal recurved lobe, smaller than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates present and dorsolateral bosses usually present, tergal projections absent. Pleon not narrower than pereon, 4 indistinct pleomeres mostly fused; 5 pairs of smooth biramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles present. Pleon of 6 segments; pleopods absent.

Intertidal–subtidal, parasitising alpheid shrimps. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 7 species (An et al., 2015).

### ***Bopyrina* Kossmann, 1881**

**Diagnosis. Female** elongate, body distorted; head distinct from pereon; frontal lamina present. Eyes present or absent. Antennula and antenna indistinct. Maxilliped without palp. Barbula with 1 smooth lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with posterior elongate ovate lobe larger than anterior lobe; internal ridges smooth. Marsupium open. Coxal plates present, dorsolateral bosses and tergal projections absent. Pleon narrower than

pereon, 5 pleomeres fused on one side or medially; 3 or 4 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately 4 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula articulated; antenna not articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments mostly fused with faint indications of segmentation or distinct; pleopods absent.

Subtidal–shelf, parasitising chlorocellid, hippolytid and palaemonid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Western and Central Indo-Pacific. 5 species (Markham, 1985).

### ***Bopyrinella* Nierstrasz and Brender à Brandis, 1925**

**Diagnosis. Female** elongate, body distorted; head fused with pereon medially; frontal lamina present. Eyes present. Antennula and antenna articulated. Maxilliped with setose articulated palp. Barbula with 1 smooth lobe on each side. Pereomeres fused medially in dorsal view. 5 pairs of oostegites. Oostegites 1 asymmetrical, that on long side of body with triangular posterior lobe, larger than anterior lobe; that on short side of body with ovate or triangular posterior lobe, smaller than anterior lobe; internal ridges smooth. Marsupium open. Small coxal plates, dorsolateral bosses and tergal projections present on short side. Pleon not narrower than pereon, 6 pleomeres fused medially or laterally; 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments fused medially; 5 pairs of sessile pleopods present.

Intertidal–subtidal, parasitising alpheid, ogyridid and thorid shrimps. Tropical Atlantic, Western Indo-Pacific, Temperate Northern Pacific. 7 species (An et al., 2021). This diagnosis is based only on the type species, *Bopyrinella antillensis* Nierstrasz and Brender à Brandis, 1925 (= *B. thorii* (Richardson, 1904)) because the genus does not appear to be monophyletic.

### ***Bopyrinina* Shiino, 1933**

**Diagnosis. Female** elongate ovate, body distorted; head distinct from pereon; frontal lamina present. Eyes absent. Antennula not articulated; antenna articulated. Maxilliped with non-setose unsegmented palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe, smaller than anterior

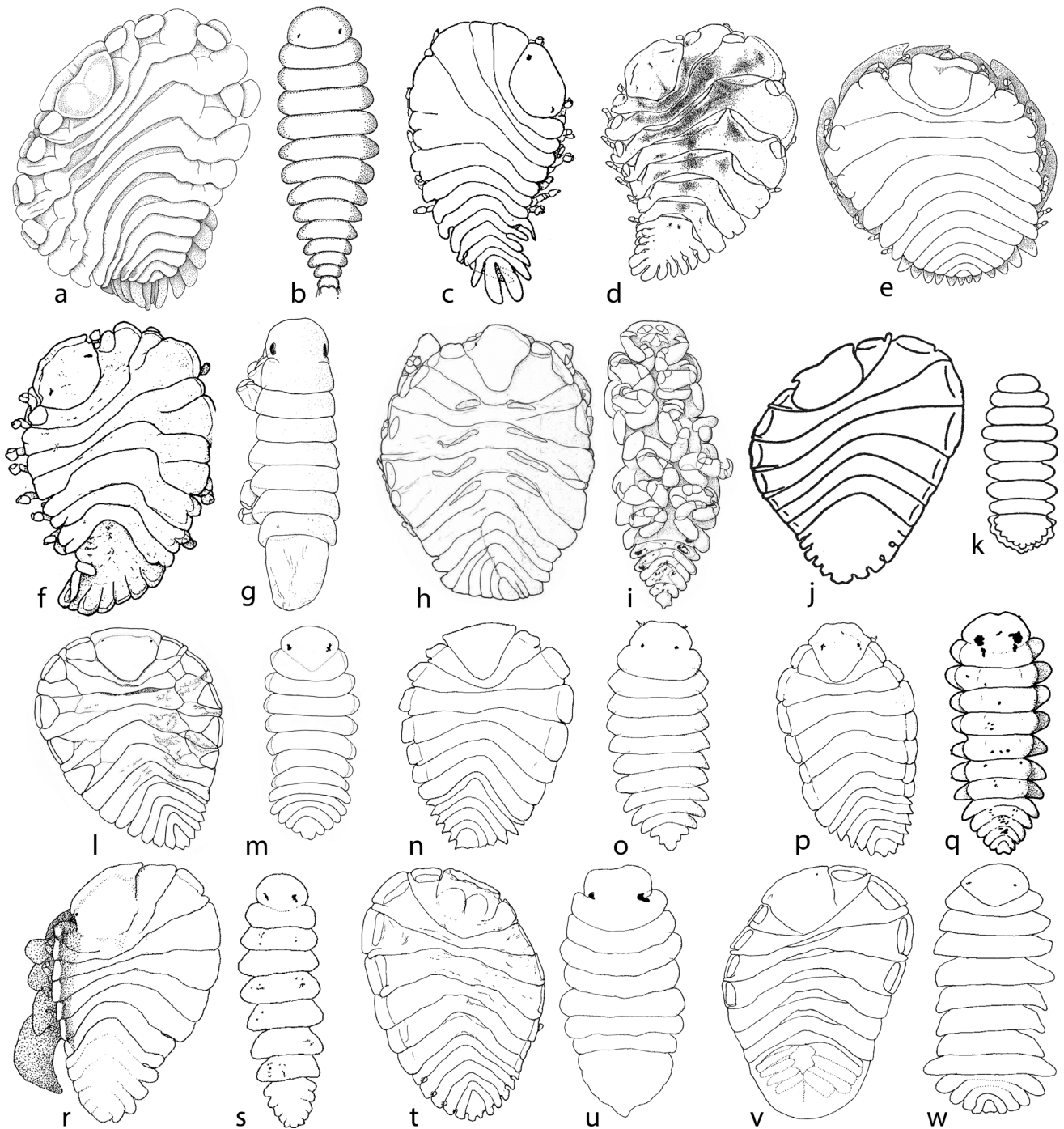


Figure 6.10. Bopyrinae. *Urobopyrus processae* Richardson, 1904: a, female dorsal view; b, male dorsal view. *Litobopyrus longicaudatus* Markham, 1982: c, female dorsal view. *Bopyrinina dorsimaculata* Shiino, 1933: d, female dorsal view. *Parapleurocrypta digitata* Bourdon, 1976: e, female dorsal view. *Palaemonellione cebuensis* Markham, 1989: f, female dorsal view; g, male dorsal view. *Ogyridione caroliniana* Markham, 1988: h, female dorsal view; i, male ventral view. *Capitetragnonia alpei* (Richardson, 1900): j, female dorsal view; k, male dorsal view. *Probopyrus cf. pandalicola* (Packard, 1879): l, female dorsal view; m, male dorsal view. *Parabopyriscus stellatus* Markham, 1985: n, female dorsal view; o, male dorsal view. *Probopyriscus novempalensis* Markham, 1982: p, female dorsal view; q, male dorsal view. *Probopyrinella heardi* Adkison, 1984: r, female dorsal view; s, male dorsal view. *Ovobopyrus alphezemiotes* Markham, 1985: t, female dorsal view; u, male dorsal view. *Bopyrella articulata* An, Boyko and Li, 2015: v, female dorsal view; w, male dorsal view.

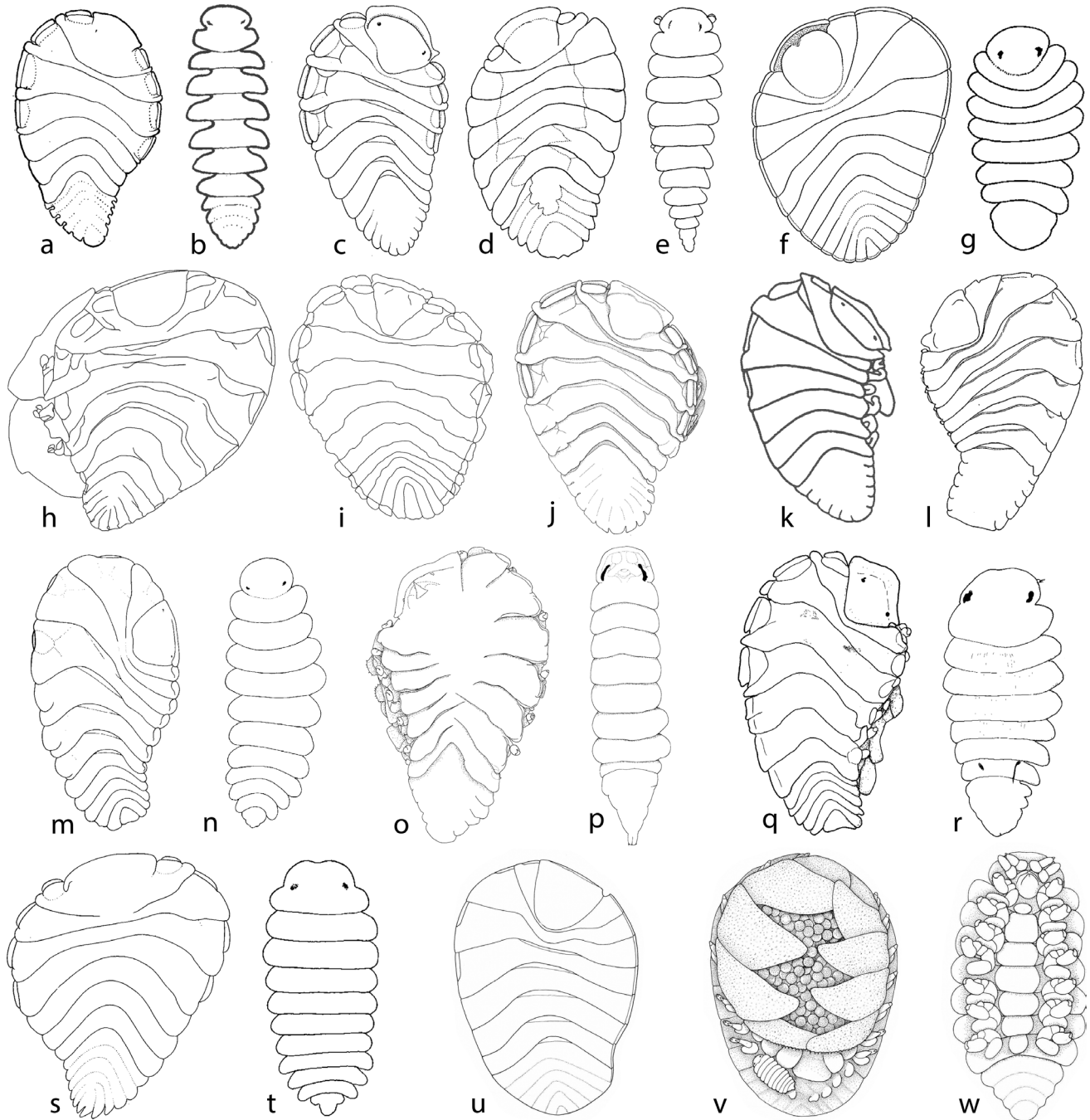


Figure 6.11. Bopyrinae. *Parabopyrella mortenseni* (Nierstrasz and Brender à Brandis, 1929): a, female dorsal view; b, male dorsal view. *Allobopyrus rumphiusi* Bourdon, 1983: c, female dorsal view. *Septembopyrina tozeumaophila* An, Boyko and Li, 2015: d, female dorsal view; e, male dorsal view. *Probopyrione plana* Bourdon, 1983: f, female dorsal view; g, male dorsal view. *Bopyroides hippolytes* (Krøyer, 1838): h, female dorsal view. *Discorsobopyrus stebbingi* (Nierstrasz and Brender à Brandis, 1923): i, female dorsal view. *Bopyrus crangorum* (Fabricius, 1798): j, female dorsal view. *Bopyrinella thorii* (Richardson, 1904): k, female dorsal view. *Parabopyrus kiensis* Shiino, 1934: l, female dorsal view. *Probynia obstipa* Bourdon and Bruce, 1983: m, female dorsal view; n, male dorsal view. *Bopyrina ocellata* (Czerniavsky, 1868): o, female dorsal view; p, male dorsal view. *Schizobopyrina urocaridis* (Richardson, 1904): q, female dorsal view; r, male dorsal view. *Synsynella choprai* (Pearse, 1932): s, female dorsal view; t, male dorsal view. *Bopyrione synalphei* Bourdon and Markham, 1980: u, female dorsal view; v, female ventral view, with male attached and eggs shown in brood chamber; w, male ventral view.

lobe; internal ridge smooth. Marsupium open. Coxal plates present; dorsolateral bosses and tergal projections absent. Pleon narrower than pereon; 6 pleomeres, separated laterally, fused medially; 3 or 4 pairs of smooth uniramous pleopods; uropods present. **Male** approximately 3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon fused; pleopods absent.

Subtidal–slope, parasitising palaemonid shrimps. Central Indo-Pacific, Temperate Northern Pacific. 3 species (An et al., 2021). This diagnosis is based on two of the three described species because *Bopyrinina articulata* An, Xi and Paulay, 2021 does not appear to belong to this genus.

#### ***Bopyrione* Bourdon and Markham, 1980**

**Diagnosis. Female** ovate, body slightly distorted; head distinct from pereon, triangular; frontal lamina absent. Eyes present or absent. Antennula and antenna articulated. Maxilliped without palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger or smaller than anterior lobe; internal ridge smooth. Marsupium open or closed. Coxal plates present; dorsolateral bosses and tergal projections absent. Pleon not narrower than pereon, 5 or 6 indistinct pleomeres; 4 or 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles present. Pleon with 1 or more segments laterally indicated and medially fused, ventrally segmented; pleopods absent.

Subtidal–shelf, parasitising alpheid shrimps. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 5 species (An et al., 2015).

#### ***Bopyroides* Stimpson, 1864**

**Diagnosis. Female** ovate, body slightly distorted; head distinct from pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose non-articulated palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates and dorsolateral bosses present, tergal projections absent. Pleon narrower than pereon, 6 pleomeres, distinct laterally, fused medially or distinct; 4 or 5 pairs of tubercular uniramous pleopods; uropods absent. **Male** approximately 4 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon fused; pleopods absent.

Subtidal–slope, parasitising hippolytid and pandalid shrimps. Arctic Ocean, Temperate Northern Atlantic, Central Indo-Pacific, Temperate Northern Pacific. 3 species (Boyko, 2004).

#### ***Bopyrus* Bosc, 1801**

**Diagnosis. Female** ovate, body distorted; head distinct from pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose non-articulated palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing triangular distal projection; internal ridge digitate. Marsupium open. Coxal plates, tergal projections and dorsolateral bosses present. Pleon narrower than pereon, 6 pleomeres fused medially, distinct laterally; 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately 2.5 times as long as wide, pereomeres narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments fused medially with only lateral indications; 4 pairs of sessile pleopods.

Subtidal, parasitising palaemonid shrimps. Temperate Northern Atlantic, Western Indo-Pacific, Temperate Northern Atlantic. 2 species (Bourdon, 1968).

#### ***Capitragonia* Pearse, 1953**

**Diagnosis. Female** ovate, body slightly distorted; head distinct from or fused with pereon medially; frontal lamina present. Eyes present or absent. Antennula and antenna indistinct. Maxilliped with setose non-articulated palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing triangular distal projection; internal ridge smooth. Marsupium open. Coxal plates and tergal projections present; dorsolateral bosses absent. Pleon not narrower than pereon, 6 pleomeres; 4 or 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately 3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments fused medially with only lateral indications; 4 or 5 pairs of sessile pleopods present.

Subtidal, parasitising alpheid shrimps. Tropical Atlantic, Central Indo-Pacific. 2 species (An et al., 2015; Markham, 1992).

#### ***Discorsobopyrus* Boyko, 2004**

**Diagnosis. Female** ovate, body slightly distorted; head distinct from pereon, triangular; frontal lamina present. Eyes present. Antennula and antenna not articulated. Maxilliped without palp. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge smooth. Marsupium closed. Coxal plates and dorsolateral bosses present; tergal projections absent. Pleon not narrower than pereon; 6 pleomeres; 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna not articulated. Pereopods of moderate size, subequal. Midventral tubercles present. Pleon fused; pleopods absent.

Slope, parasitising pandalid shrimps. Central Indo-Pacific. 1 species (Boyko, 2004).

***Litobopyrus* Markham, 1982**

*Diagnosis. Female* elongate ovate, body distorted; head distinct from pereon; frontal lamina indistinct. Eyes present. Antennula and antenna articulated. Maxilliped without palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates, dorsolateral bosses and tergal projections absent. Pleon narrower than pereon, 6 pleomeres, separated laterally; 5 pairs of smooth biramous pleopods; uropods present. **Male** approximately 3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon fused; pleopods absent.

Intertidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (Markham, 1982).

***Ogyridione* Markham, 1988**

*Diagnosis. Female* ovate, body not distorted; head distinct from pereon; frontal lamina indistinct. Eyes present. Antennula and antenna not described. Maxilliped with setose articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates and dorsolateral bosses present on some pereomeres; tergal projections present or absent. Pleon not narrower than pereon, 6 pleomeres, overlapping laterally; 5 pairs of asymmetrical smooth pleopods (biramous one side, uniramous on other); uropods absent. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of large size, subequal. Midventral tubercles absent. Pleon of 6 segments; sessile pleopods present on pleomeres 1–5.

Intertidal, parasitising ogyridid shrimps. Temperate Northern Atlantic. 1 species (Markham, 1988).

***Ovobopyrus* Markham, 1985**

*Diagnosis. Female* body ovate, length approximately 1.5 times maximum width, head distinct from pereon laterally, fused posteriorly, medially bilobed. Eyes absent. Antennula and antenna each of 2 articles. Maxilliped with non-setose, non-articulating palp. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe, internal ridge smooth. Marsupium open. Coxal plates, dorsolateral bosses, and tergal projections larger on long side of pleomeres 1–4, short side of pleomeres 1–4 with reduced coxal plates and tergal projections, dorsolateral bosses absent. Pleon of 6 pleomeres, separated by lateral notches; 5 pairs of biramous smooth pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres subequal in width. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods large compared to body. Midventral tubercles absent. Pleon without lateral indication of segmentation; 5 pairs of discoid sessile pleopods.

Shelf, parasitising alpheid shrimps. Tropical Western Atlantic. 2 species (Markham, 1985; Modesto et al., 2025).

***Palaemonellione* Markham, 1989**

*Diagnosis. Female* body elongate ovate, moderately distorted; head distinct from pereon; frontal lamina present. Eyes present. Antennula and antenna articulated. Maxilliped with non-setose articulating palp. Barbula not described. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with rounded posterior lobe, smaller than anterior lobe, internal ridge smooth. Marsupium open. Tergal projections present on long side of body; coxal plates and dorsolateral bosses absent. Pleon narrower than pereon, 5 pleomeres, fused medially; pleopods asymmetrical (3 uniramous smooth pleopods on long side, none on short side); uropods absent. **Male** approximately 3 times as long as wide, pereomeres subequal in width. Head as wide as pereon. Eyes present. Antennula and antenna articulated. Pereopods not large compared to body. Midventral tubercles absent. Pleon fused; pleopods absent.

Subtidal, parasitising palaemonid shrimps. Central Indo-Pacific. 1 species (Markham, 1989).

***Parabopyrella* Markham, 1985**

*Diagnosis. Female* body linear to ovate, slightly to moderately distorted; head almost entirely fused with pereon; thin frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose (usually) articulating palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe, internal ridge smooth. Marsupium open. Coxal plates, dorsolateral bosses, and tergal projections usually present on pleomeres 1–4. Pleon subequal in width to pereon or markedly narrower; 6 pleomeres, separated by lateral notches; 5 pairs of biramous smooth pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres subequal in width. Head slightly to markedly narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods large compared to body. Midventral tubercles absent. Pleon partly to completely fused; 5 pairs of sessile pleopods.

Intertidal–shelf, parasitising alpheid, hippolytid and lysmatid shrimps. Tropical Atlantic, Temperate Southern Africa, Western and Central Indo-Pacific, Temperate Northern Pacific. 29 species (An et al., 2015; Markham, 1985; Modesto et al., 2026).

***Parabopyriscus* Markham, 1985**

*Diagnosis. Female* ovate, body not distorted; head distinct from pereon; frontal lamina absent. Eyes absent. Antennula and antenna articulated. Maxilliped with setose, non-articulating palp. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with rounded posterior lobe, subequal in size to anterior lobe, internal ridge smooth. Marsupium open. Coxal plates present on pereomeres 1–6, dorsolateral bosses and tergal projections absent. Pleon subequal in width to pereon; 6 pleomeres, separated by lateral notches; 5 pairs of biramous smooth pleopods; uropods absent.

**Male** approximately twice as long as wide, pereomeres subequal in width. Head markedly narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size. Midventral tubercles absent. Pleon partly fused with lateral indications of segmentation; 5 pairs of sessile pleopods.

Shelf, parasitising alpheid shrimps. Tropical Western Atlantic. 1 species (Markham, 1985).

#### ***Parabopyrus* Shiino, 1934**

*Diagnosis.* **Female** elongate ovate, body distorted; head not fused with pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped without palp. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegites 1 asymmetrical, that on short side of body with triangular posterior lobe, much larger than anterior lobe, that on long side of body with ovate lobe, slightly larger than anterior lobe; internal ridges smooth. Marsupium open. Coxal plates present, dorsolateral bosses and tergal projections absent. Pleon not narrower than pereon; 6 pleomeres, separated laterally, fused medially; 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately 4 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles present. Pleon of 6 segments; pleopods present.

Subtidal, parasitising alpheid and lysmatid shrimp. Central Indo-Pacific, Temperate Northern Pacific. 1 species (Bourdon and Bruce, 1983b).

#### ***Parapleurocrypta* Chopra, 1923**

*Diagnosis.* **Female** elongate ovate, body slightly asymmetrical; head not fused with pereon; frontal lamina present or absent. Eyes absent or present. Antennula and antenna articulated. Maxilliped with setose non-segmented palp. Barbula with 1 or 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates absent or present, dorsolateral bosses present, tergal projections absent. Pleon not narrower than pereon, 6 pleomeres; 5 pairs of smooth uniramous pleopods or pleopods absent; uropods uniramous. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon fused; pleopods and uropods absent.

Subtidal-slope, parasitising alpheid shrimps. Western Atlantic, Western Indo-Pacific. 3 species (Bourdon, 1976; Horch et al., 2024).

#### ***Probopyrinella* Nierstrasz and Brender à Brandis, 1929**

*Diagnosis.* **Female** elongate ovate, body slightly distorted; head fused or not fused with pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose non-articulated palp. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger

than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates, dorsolateral bosses and tergal projections absent. Pleon not narrower than pereon, 6 pleomeres, separated laterally, fused medially; 4 pairs of smooth biramous pleopods and 1 pair of smooth uniramous pleopods; uropods absent. **Male** approximately 3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments; 5 pairs of uniramous pleopods.

Pelagic, parasitising hippolytid shrimps. Temperate Northern Atlantic, Tropical Atlantic. 2 species (Adkison, 1984; Markham, 1985).

#### ***Probopyrione* Bourdon, 1983**

*Diagnosis.* **Female** ovate, body slightly distorted; head not fused with pereon; frontal lamina present. Eyes absent. Antennula and antenna not articulated. Maxilliped without palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium closed. Coxal plates, dorsolateral bosses and tergal projections absent. Pleon not narrower than pereon, 6 pleomeres, separated laterally, fused medially; 5 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna not articulated. Pereopods of moderate size, subequal. Midventral tubercles present. Pleon fused; pleopods absent.

Subtidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (Bourdon, 1983).

#### ***Probopyriscus* Markham, 1982**

*Diagnosis.* **Female** elongate, body not distorted; head distinct from pereon; frontal lamina present. Eyes present. Antennula and antenna articulated. Maxilliped with setose palp. Barbula with 2 smooth very short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegites 1 asymmetrical, triangular posterior lobe on one side larger than anterior lobe, on other side subequal to anterior lobe; internal ridges smooth. Marsupium open. Coxal plates, dorsolateral bosses and tergal projections present. Pleon narrower than pereon, 6 pleomeres, separated laterally; 5 pairs of smooth biramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 6 segments; 5 pairs of uniramous pleopods.

Subtidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (Markham, 1982).

#### ***Probopyrus* Giard and Bonnier, 1888**

*Diagnosis.* **Female** ovate, body slightly distorted; head distinct from pereon; frontal lamina small or absent. Eyes absent. Antennula and antenna articulated. Maxilliped with setose

non-articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing distal triangular projection, larger than anterior lobe; internal ridge smooth or digitate. Marsupium open. Coxal plates and dorsolateral bosses present; tergal projections absent. Pleon not narrower than pereon, 6 pleomeres, distinct or fused medially; 5 pairs of biramous smooth pleopods; uropods present or absent. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 5 or 6 segments; 3–5 pairs of tuberculiform to globose pleopods.

Subtidal, parasitising palaemonid and thorid shrimp. Temperate Northern Atlantic, Tropical Atlantic, Temperate South American, Western and Central Indo-Pacific, Tropical Eastern Pacific. 29 species (Dale and Anderson, 1982; Markham, 1985).

#### ***Probynia* Bourdon and Bruce, 1983**

*Diagnosis.* **Female** elongate ovate, body strongly distorted; head distinct from pereon; frontal lamina present. Eyes present or absent. Antennula and antenna articulated. Maxilliped with setose articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing distal triangular projection, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates present on some pereomeres; dorsolateral bosses and tergal projections present or absent. Pleon narrower than pereon, 6 pleomeres, overlapping laterally; 4 or 5 pairs of uniramous smooth pleopods; uropods absent. **Male** approximately 3 times as long as wide, pereomeres slightly narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 3 free segments and fourth segment fused with lateral indications of segmentation; pleopods present on pleomeres 1 and 2 or 1–3.

Subtidal, parasitising palaemonid shrimp. Tropical Atlantic, Western and Central Indo-Pacific. 3 species (Bourdon and Bruce, 1983a; Romero-Rodríguez and Álvarez, 2021).

#### ***Schizobopyrina* Markham, 1985**

*Diagnosis.* **Female** ovate, body distorted; head distinct from pereon; frontal lamina present. Eyes present or absent. Antennula and antenna articulated. Maxilliped with setose, articulating palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegites 1 asymmetrical, that on short side of body with recurved triangular posterior lobe, larger than anterior lobe, that on long side of body with rounded posterior lobe, subequal to anterior lobe; internal ridges smooth. Marsupium open. Dorsolateral bosses present on pereomeres 1–4, coxal plates and tergal projections absent. Pleon narrower than pereon, 6 pleomeres, overlapping laterally; 4 pairs of uniramous smooth pleopods; uropods absent. **Male** approximately 2–3 times as long as wide, pereomeres subequal in width. Head subequal in width to pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size.

Midventral tubercles absent. Pleon partly fused with lateral indications of segmentation; 3 or 4 pairs of sessile pleopods.

Subtidal, parasitising hippolytid, palaemonid and thorid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Indo-West Pacific, Temperate Northern Pacific. 13 species, including *Schizobopyrina platylobae* (Bourdon in Bourdon and Bruce, 1983), which Boyko and Williams (2023) listed erroneously under *Bopyrina* (Campos and Campos, 1990; Markham, 1985; Williams and Boyko, 2004).

#### ***Septembopyrina* An, Boyko and Li, 2015**

*Diagnosis.* **Female** elongate ovate, body slightly distorted; head fused with pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped without palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 7 pairs of oostegites. Oostegite 1 with elongate triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium open. Dorsolateral bosses present on pereomere 1, coxal plates and tergal projections absent. Pleon slightly narrower than pereon, 5 pleomeres, separated laterally with notches; 5 pairs of uniramous smooth pleopods; uropods absent. **Male** approximately 3 times as long as wide, pereomeres narrower posteriorly. Head narrower than pereon. Eyes present. Antennula and antenna articulated. Pereopods of moderate size, smaller posteriorly. Midventral tubercles absent. Pleon fused with lateral indications of segmentation; pleopods absent.

Shelf, parasitising hippolytid shrimps. Central Indo-Pacific. 1 species (An et al., 2015).

#### ***Synsynella* Hay, 1917**

*Diagnosis.* **Female** elongate ovate, body weakly distorted; head fused with pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose articulated or non-articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with ovate posterior lobe bearing triangular posterior projection, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates and dorsolateral bosses present, tergal projections absent. Pleon narrower than pereon, 6 pleomeres, approximated laterally; 4 pairs of smooth uniramous pleopods; uropods absent. **Male** approximately twice as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods of moderate size, subequal. Midventral tubercles absent. Pleon of 3 free segments and 2 fused segments; 3 or 4 pairs of uniramous pleopods present or absent.

Subtidal–shelf, parasitising alpheid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Temperate Northern Pacific. 5 species (Markham, 1985).

#### ***Urobopyrus* Richardson, 1904**

*Diagnosis.* **Female** ovate, body not distorted; head distinct from pereon; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose non-articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. 5 pairs of oostegites. Oostegite 1 with triangular

posterior lobe, larger than anterior lobe; internal ridge smooth. Marsupium open. Coxal plates and dorsolateral bosses present, tergal projections absent. Pleon narrower than pereon, 6 pleomeres, separated laterally; 5 pairs of smooth biramous pleopods; uropods biramous. **Male** approximately 3 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes absent. Antennula and antenna articulated. Pereopods of moderate size, first 2 pairs much larger than others. Midventral tubercles absent. Pleon of 6 segments; 1 pair of uniramous pleopods.

Shelf, parasitising processid shrimps. Tropical Atlantic, Temperate Northern Atlantic. 1 species (Markham, 1985).

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## Subfamily Hemiarthrinae Markham, 1972

Figures 6.12, 6.13

Genera of Hemiarthrinae can be distinguished from those of other bopyrid subfamilies in that females have slight to extreme distortion of the head relative to the body and have one side of the body formed by greatly expanded oostegites, giving the body a strongly asymmetrical appearance. Species in Hemiarthrinae are ectoparasites of caridean shrimps. Females of most species are found attached to the ventral surface of the abdomen but those in some genera are found in unusual positions: attached to the buccal region (*Orophryxus*), attached to the dorsal or lateral surface of the abdomen (*Filophryxus*, *Metaphryxus*), or in the branchial chamber (*Sigyn*). The key is modified from that of An et al. (2020). *Pliophryxus* Caroli, 1930 is very poorly described and is not included in the key. Representative males are figured.

**Diagnosis. Female** body linear or subovate, elongate or compact, asymmetrical and expanded on convex side, distorted approximately 10–110°; head rounded or elongated, anterolateral margins not produced or produced into anteriorly or anterolaterally directed lobes. Eyes present or absent.

Antennula articulated or non-articulated or absent. Antenna articulated or non-articulated or absent. Barbula with 1–8 smooth short lobes on each side. Maxilliped without palp. Pereomeres distinct on concave side, fused on convex side (sometimes with 1–4 anterior segments distinct), distinct or indistinct dorsally. Marsupium closed. Oostegites 1 asymmetrical; internal ridge smooth; oostegites 2–5 usually present but variable; oostegite 2 recurved over head and covered with cup-like discs or not recurved and smooth. Coxal plates and dorsolateral bosses present or absent. 1–7 pereopods present on concave and convex sides. Pleon of 1–5 pleomeres; 2–5 pairs of uniramous or biramous smooth lateral plates and 2–5 pairs of uniramous or biramous smooth pleopods present or absent. Uropods uniramous or absent. **Male** pereomeres subequal in width or anterior, middle, or posterior pereomeres wider; midventral tubercles absent. Head wider than long. Eyes present or absent. Antennula and antenna articulated or non-articulated. 7 pairs of subequal pereopods. Pleomeres fused into single segment with or without lateral indication of segmentation; pleopods absent. Uropods present or absent.

### Key to genera of Hemiarthrinae

1. Pleon of female without appendages (fig. 6.12a, b) ..... *Orophryxus*
- Pleon of female with appendages ..... 2
2. Coxal plates of female with filiform extensions ..... 3
- Coxal plates of female without filiform extensions ..... 4
3. Female with 3 pairs of uniramous pleopods (fig. 6.12e) ..... *Filophryxus*
- Female with 3 pairs of uniramous pleopods and 4th uniramous pleopod on one side (fig. 6.12o) .....  
..... *Izuohshimaphryxus*
4. Female without lateral plates ..... 5
- Female with lateral plates ..... 7
5. Female with 5 pleomeres ..... 6
- Female with pleon fused, 2 pereopods on convex side of body (fig. 6.12f) ..... *Anomophryxus*
6. Female with 1 pereopod on convex side of body, male without pleonal extensions (fig. 6.12c, d) .....  
..... *Neophryxus*
- 5 pereopods on convex side of body, male with 2 pairs of pleonal extensions (fig. 6.13o, p) .....  
..... *Alaxphryxus* n. gen.
7. Female with fewer than 5 pleomeres ..... 8

–	Female with 5 pleomeres .....	16
8.	Female with fewer than 4 pleomeres .....	9
–	Female with 4 pleomeres .....	12
9.	Female with 1 pleomere .....	10
–	Female with 3 pleomeres .....	11
10.	Female with 3 pairs of uniramous lateral plates (fig. 6.12v) .....	<i>Mesophryxus</i>
–	Female with 4 pairs of uniramous lateral plates (fig. 6.12p) .....	<i>Apophryxus</i>
11.	Female with 3 pairs of uniramous lateral plates (fig. 6.13k, l) .....	<i>Anchiarthrus</i>
–	Female with 2 pairs of uniramous lateral plates (fig. 6.13j) .....	<i>Miophryxus</i>
12.	Female with 4 lateral plates on convex side, 3 on concave side (fig. 6.13n) .....	<i>Azygopleon</i>
–	Female with all lateral plates paired .....	13
13.	Female with 3 pairs uniramous lateral plates (fig. 6.13l) .....	<i>Hypohyperphryxus</i>
–	Female with 4 pairs uniramous lateral plates .....	14
14.	Female with biramous pleopods (fig. 6.12m) .....	<i>Quadripediphryxus</i>
–	Female with uniramous pleopods .....	15
15.	Female with 4 pereopods on convex side (fig. 6.12h, i) .....	<i>Hemiphryxus</i>
–	Female with 2 pereopods plus stub on convex side (fig. 6.13c, d) .....	<i>Mediophryxus</i>
16.	Female with fewer than 5 pereopods on convex side .....	17
–	Female with 5 or 7 pereopods on convex side .....	25
17.	Female with lateral plates biramous to quadriramous .....	18
–	Female with lateral plates uniramous .....	20
18.	Female with oostegite 2 not reflexed over head, 4 biramous pleopods on one side of pleon (fig. 6.12j) .....	19
–	Female with oostegite 2 reflexed over head, 4 biramous pleopods on both sides of pleon (fig. 6.12l) .....	<i>Diplophryxus</i>
19.	Female with 4 biramous pleopods on one side of pleon (fig. 6.12j) .....	<i>Allodiplophryxus</i> <sup>1</sup>
–	Female with 4 biramous pleopods on both sides of pleon (fig. 6.12n) .....	<i>Micropodiphryxus</i>
20.	Female with oostegite 2 reflexed over head .....	21
–	Female with oostegite 2 not reflexed over head .....	22
21.	Female with 4 pairs of biramous pleopods (fig. 6.13f) .....	<i>Hyperphryxus</i> <sup>1</sup>
–	Female with 4 pairs of uniramous pleopods (fig. 6.13m) .....	<i>Hemiarthrus</i>
22.	Female with pleotelson divided (fig. 6.13e) .....	<i>Dicropleon</i>
–	Female with pleotelson undivided .....	23
23.	Female with 5 pairs of lateral plates, uropods present (fig. 6.12g) .....	<i>Epiphryxus</i>
–	Female with 4 pairs of lateral plates, uropods absent .....	24
24.	Female with head c. 80–90° distorted (fig. 6.13g) .....	<i>Metaphryxus</i>
–	Female with head c. 20–30° distorted (fig. 6.13a) .....	<i>Eriphryxus</i>
25.	Female found in host branchial chamber (fig. 6.12s) .....	<i>Sigyn</i>
–	Female found on ventral abdomen .....	26

26. Male with 1 pair of pleonal extensions ..... *Hypophryxus*  
 – Male without pleonal extensions ..... 27
27. Female with biramous lateral plates (fig. 6.12k) ..... *Cataphryxus*<sup>2</sup>  
 – Female with uniramous lateral plates ..... 28
28. Female with terminal pleomere entire or indented but without elongate uropods (figs 6.12q, r, 6.13h, i) .....  
 ..... *Anisarthrus/Eophrixus*<sup>3</sup>  
 – Female with elongate uropods (fig. 6.12t, u) ..... *Loki*

<sup>1</sup> Type species only (genus likely not monophyletic)

<sup>2</sup> Females of *Cataphryxus fiedleri* Markham, 2025 have only 3 pereopods on the convex side of the body; the other two species in the genus have 7 pairs of pereopods; otherwise all three species appear congeneric.

<sup>3</sup> Type species of *Eophrixus* and *Anisarthrus* are very similar; the type species of *Eophrixus* is incompletely described/illustrated and the genus is likely not monophyletic.

### ***Alaxphryxus* Boyko and Williams n. gen.**

(<http://zoobank.org/urn:lsid:zoobank.org:act:40AA0134-BBE7-4167-8D3C-BC1699A94CFB>)

*Type species. Hemiarthrus filiformis* Chopra, 1923 (by original designation and monotypy).

**Diagnosis. Female** body linear, distorted approximately 30°. Eyes absent. Antennula, antenna, barbula and oostegite 1 not described. Pereomeres distinct dorsally only on concave side. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 5 pereopods on convex side. Pleon of 5 pleomeres, lateral plates absent, 4 pairs of smooth biramous pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antennula and antenna articulated. Pleon with segmentation laterally indicated, with 2 pairs of pleonal extensions at anterior end; uropods absent.

Subtidal, parasitising alpheid shrimps, Western Indo-Pacific. 1 species (Chopra, 1923).

**Etymology.** The new genus is named (*ala* = wing + *x* + *phryxus*, a common suffix in hemiarthrine taxa) after the male's pleopodal extensions, which resemble the wings of an X-wing starfighter in the *Star Wars* films.

**Remarks.** The two pairs of extensions on the pleon of the male are unique among hemiarthrine taxa and warrant the erection of a new genus; males in *Hypophryxus* have a single pair of pleonal extensions, but the females in that genus have lateral plates that are lacking in *Alaxphryxus*. There is a record of "*Hypophryxus filiformis* (Chopra, 1923)" from Markham (1992) where the male has two pleonal extensions but the female has lateral plates; this is not likely to be conspecific with *Alaxphryxus filiformis* n. comb. and may not belong to the genus.

### ***Allodiplophryxus* Markham, 1985**

**Diagnosis. Female** body linear, elongate, distorted approximately 90°; head elongated, anterolateral margins not produced. Eyes present. Antennula of 1 or 2 articles; antenna absent. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, larger than anterior lobe, that on concave side with elongate

posterior lobe, larger than anterior lobe. Coxal plates and dorsolateral bosses absent. 5 pereopods present on concave side, 2 plus basal scar of 3 present on convex side. Pleon of 5 pleomeres; 4 pairs of biramous smooth lateral plates and 4 pairs of biramous smooth pleopods on both sides or 4 biramous smooth pleopods on one side only; uropods absent. **Male** with pleomeres subequal in width. Eyes present. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Subtidal, parasitising palaemonid shrimps. Tropical Western Atlantic, Central Indo-Pacific. 2 species (An et al., 2020; Markham, 1985).

### ***Anchiarthrus* Markham, 1992**

**Diagnosis. Female** body subovate, distorted approximately 60°; head embedded in pereon. Eyes absent. Antennae and antennulae absent. Barbula with 1 smooth lobe on each side. Pereomeres indistinct dorsally. Oostegite 1 on concave side with small bilobed posterior lobe, that on convex side larger. Oostegites 2–4 present on both sides. Coxal plates and dorsolateral bosses absent. 7 pereopods present on concave side, 3–6 present on convex side. Pleomeres fused but with indication of 3 pleomeres; 3 pairs of uniramous smooth lateral plates and 3 pairs of biramous smooth pleopods present; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antenna and antennula articulated. Posterior pairs of pereopods slightly longer. Pleon with lateral indications of segmentation; uropods absent.

Intertidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (An et al., 2015).

### ***Anisarthrus* Giard, 1907**

**Diagnosis. Female** body linear, elongate, distorted approximately 40°; head rounded, anterolateral margins produced as anterolaterally directed lobes. Eyes absent. Antennula and antenna articulated. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, smaller than anterior lobe, that on concave side without posterior lobe. Coxal plates absent; dorsolateral bosses present on concave side. 7 pereopods present on both sides. Pleon of 5 pleomeres; pleomeres 1 and 2 with

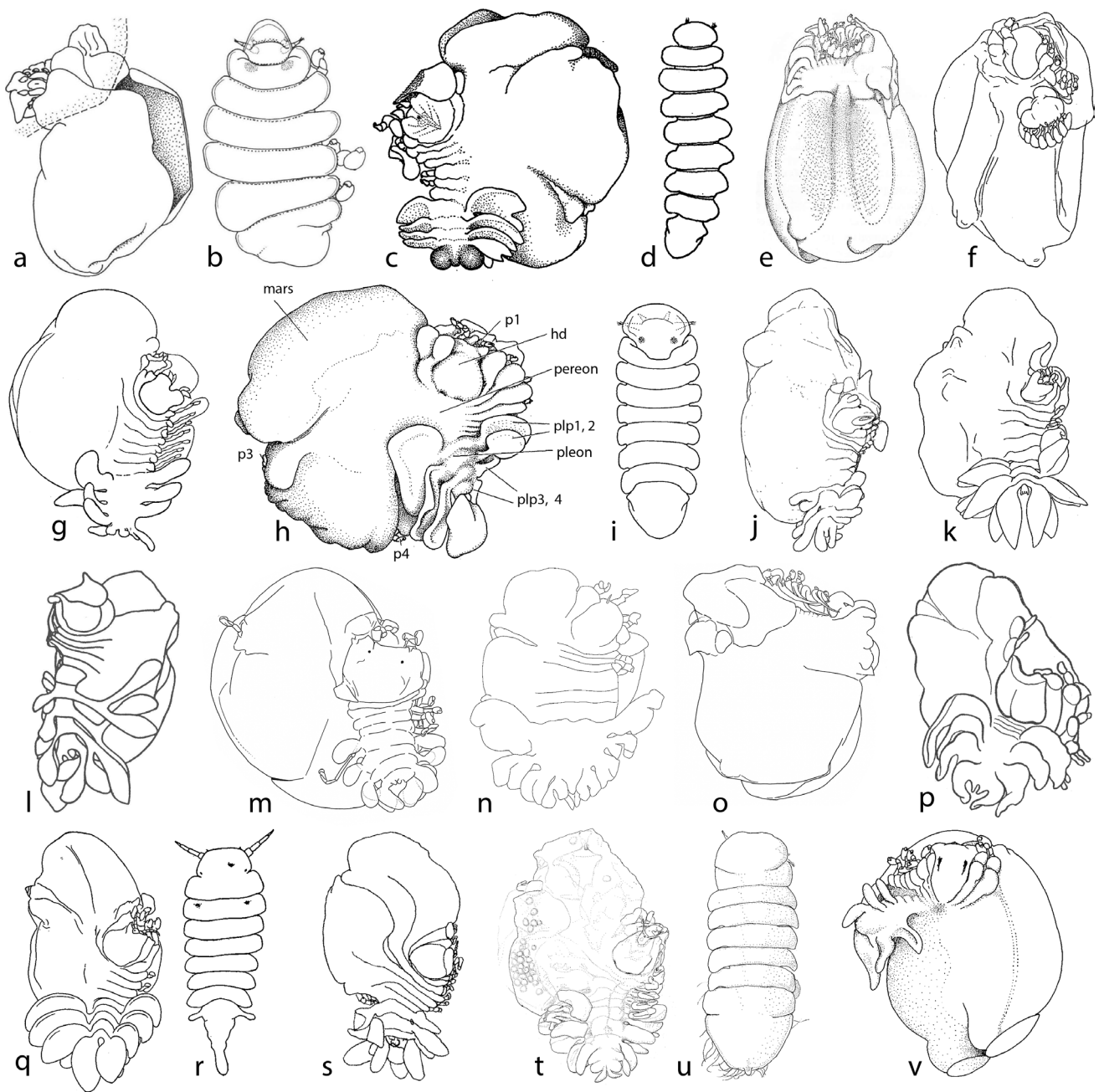


Fig. 6.12. Hemiarthrinae. *Orophryxus shiinoi* Bruce, 1972: a, female dorsal view, host's carapace indicated by broken line; b, male dorsal view. *Neophryxus globicaudatus* (Bruce, 1973): c, female dorsal view; d, male dorsal view. *Filophryxus dorsalis* Bruce, 1972: e, female dorsal view. *Anomophryxus deformatus* Shiino, 1937: f, female dorsal view with male attached. *Epiphryxus adriaticus* Nierstrasz and Brender à Brandis, 1932: g, female dorsal view. *Hemiphryxus malindiae* (Bruce, 1974): h, female dorsal view; i, male dorsal view. *Allodiplophryxus floridanus* Markham, 1985: j, female dorsal view. *Cataphryxus primus* (Shiino, 1934): k, female dorsal view. *Diplophryxus jordani* Richardson, 1904: l, female dorsal view. *Quadripediphyxus mayuzumii* Saito, 2020: m, female dorsal view. *Micropodiphyxus richardsonae* (Chopra, 1930): n, female dorsal view. *Izuohsimaphryxus hoshinoi* Saito, 2015: o, female dorsal view. *Apophryxus philippinensis* Nierstrasz and Brender à Brandis, 1931: p, female dorsal view. *Eophryxus yusakiensis* (Shiino, 1934): q, female dorsal view; r, male dorsal view. *Sigyn branchialis* An, Boyko and Li, 2015: s, female dorsal view. *Loki circumsaltanus* Markham, 1972: t, female dorsal view; u, male dorsal view. *Mesophryxus ventralis* Bruce, 1973: v, female dorsal view. Abbreviations: hd, head; mars, marsupium, p, pereopod; plp, pleopod.

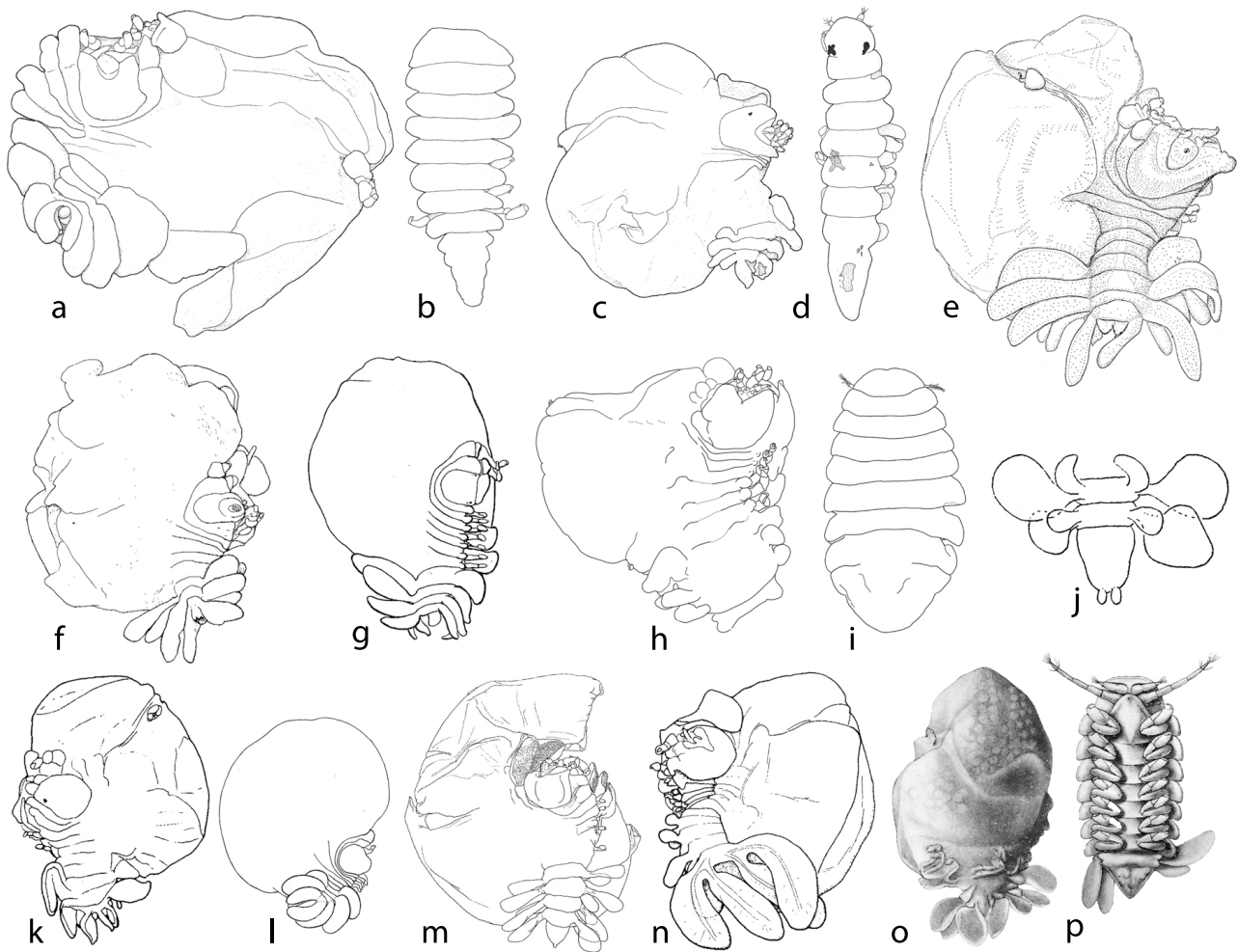


Fig. 6.13. Hemiarthrinae. *Eriphrixus obesus* Markham, 1990: a, female dorsal view; b, male dorsal view. *Mediophrixus pinuum* Markham, 1990: c, female dorsal view; d, male dorsal view. *Dicropleon periclimenis* Markham, 1972: e, female dorsal view. *Hyperphrixus castrensis* Markham, 1985: f, female dorsal view. *Metaphrixus carolii* Nierstrasz and Brender à Brandis, 1931: g, female dorsal view. *Anisarthrus okunoi* Saito and Shimomura, 2015: h, female dorsal view; i, male dorsal view. *Miophrixus latreutidis* Barnard, 1955: j, terminal segments of female pleon. *Anchiarthrus derelictus* Markham, 1992: k, female dorsal view. *Hypohyperphrixus latilamellaris* Nierstrasz and Brender à Brandis, 1932: l, female dorsal view. *Hemiarthrus surculus* Boyko and Williams, 2004: m, female dorsal view. *Azygopleon schmitti* (Pearse, 1932): n, female dorsal view. *Alaxphryxus filiformis* (Chopra, 1923) n. comb.: o, female dorsal view; p, male ventral view.

midventral tubercles; 4 pairs of uniramous smooth lateral plates present; 4 pairs of uniramous smooth pleopods present; uropods absent. **Male** with pereomeres wider posteriorly, pereomeres 7 medially fused with pleon. Eyes absent. Antennula and antenna articulated. Pleon fused with pereomere 7 with slight lateral indication of segmentation; uropods absent.

Subtidal, parasitising alpheid and rhynchocinetid shrimps. Temperate Northern Atlantic, Temperate Northern Pacific. 2 species (Saito and Shimomura, 2015).

#### *Anomophryxus* Shiino, 1937

**Diagnosis. Female** body compact, distorted approximately 60°; head elongate, medially constricted, anterolateral margins not produced. Eyes absent. Antennula papilliform, antenna

articulated. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally and on first 2 pereomeres of convex side. Marsupium formed of 4 oostegites on convex side, 3 on concave side. Oostegite 1 on convex side with ovate posterior lobe, as large as anterior lobe, that on concave side without posterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods present on concave side, 2 present on convex side. Pleon of fused segments; lateral plates absent; 4 pairs of uniramous smooth pleopods, anterior 2 pairs much larger than posterior ones; uropods present. **Male** with pereomeres subequal in width except 7 narrower. Eyes absent. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Shelf, parasitising pandalid shrimps. Temperate Northern Pacific. 1 species (Shiino, 1937).

***Apophrixus* Nierstrasz and Brender à Brandis, 1931**

*Diagnosis.* **Female** body linear, elongate, distorted approximately 30°; head subquadrate, anterolateral margins produced as anterolaterally directed lobes. Eyes absent. Antennula and antenna articulated. Barbula with 1 smooth short lobe and 1 low blunt lobe on each side. Pereomeres indistinct dorsally. Oostegite 1 on convex side with triangular posterior lobe, smaller than anterior lobe, that on concave side with ovate posterior lobe, larger than anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 6 or 7 on convex side. Pleon of single fused segment; 4 pairs of uniramous smooth lateral plates; 4 pairs of uniramous smooth pleopods; uropods present. **Male** with pereomeres subequal in width, pereomeres 6 and 7 fused with pleon in one species. Eyes present or absent. Antennula and antenna articulated. Posterior pairs of pereopods longer. Pleon sometimes fused with pereomeres 6 and 7, with slight lateral indication of segmentation; uropods absent.

Subtidal, parasitising alpheid shrimps. Central Indo-Pacific. 2 species (An et al., 2015).

***Azygopleon* Markham, 1985**

*Diagnosis.* **Female** body linear, compact, distorted approximately 40–90°; head rounded, anterolateral margins not produced. Eyes absent. Antennulae fused, displaced onto dorsal surface of head, antennae as non-articulated lobes. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, as large as anterior lobe, that on concave side with small finger-like posterior lobe, much smaller than anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 1 on convex side. Pleon usually of 4 pleomeres, pleotelson absent; concave side with 4 uniramous smooth lateral plates and 4 uniramous smooth pleopods, convex side with 3 lateral plates and uniramous pleopod on pleomere 4 only; uropods absent. **Male** with pereomeres subequal in width but posterior pereomeres longer than anterior. Eyes absent. Antennula and antenna articulated. Pleon fused without lateral indication of segmentation; uropods absent.

Subtidal–shelf, parasitising alpheid shrimps. Temperate Northern and Tropical Atlantic. 1 species (Markham, 1985).

***Cataphryxus* Shiino, 1936**

*Diagnosis.* **Female** body linear, distorted approximately 35–50°; head ovate, anterolateral margins produced anteriorly. Eyes absent. Antennula and antenna articulated. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. Marsupium formed of 4 or 5 oostegites on both sides. Oostegite 1 on convex side with slender ovate posterior lobe, as large as or smaller than anterior lobe, that on concave side with minute to large posterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on both sides or 3 on one side and 7 on the other. Pleon of 5 pleomeres; 4 pairs of biramous smooth lateral plates; 4 pairs of biramous pleopods, those on pleomeres 2–4 with additional papilla-like appendage; uropods absent but pleotelson with posterior digitiform processes. **Male** with pereomeres subequal

in width. Eyes absent. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Subtidal, parasitising lysmatid shrimps. Temperate Northern Pacific, Tropical Eastern Pacific. 3 species (Romero Rodríguez and Álvarez, 2023; Markham, 2025).

***Dicropleon* Markham, 1972**

*Diagnosis.* **Female** body linear, elongate, distorted approximately 30–50°; head rounded, anterolateral margins produced as anteriorly directed lobes. Eyes absent. Antennula and antenna articulated. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, as large as anterior lobe, that on concave side with small finger-like lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 2 or 3 on convex side. Pleon of 5 pleomeres; pleotelson subdivided; 4 pairs of uniramous smooth lateral plates, 4 pairs of uniramous or biramous or 3 pairs and 1 pair uniramous smooth pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antennulae and antennae articulated. Posterior pairs of pereopods longer. Pleon without indication of segmentation, distal tip cleft; uropods absent.

Subtidal, parasitising palaemonid and processid shrimps. Tropical Atlantic, Western and Central Indo-Pacific. 4 species (An et al., 2015).

***Diplophryxus* Richardson, 1904**

*Diagnosis.* **Female** body linear, compact, distorted approximately 30–100°; head ovate, anterolateral margins not produced. Eyes absent. Antennula non-articulated or articulated; antenna non-articulated. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate elongate posterior lobe, larger than anterior lobe, that on concave side with ovate posterior lobe, smaller than anterior lobe. Oostegite 2 reflexed over head, covered in cup-shaped discs. Pereopods 3–7 on concave side; 1 or 2 on convex side. Pleon of 5 pleomeres, pleotelson elongate with terminal point; 4 pairs of biramous to quadriramous smooth lateral plates and 4 pairs of smooth biramous to quadriramous pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes absent. Antennula and antenna articulated. Pleon without indication of segmentation; uropods absent.

Intertidal–shelf, parasitising alpheid and palaemonid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific, Temperate South America. 8 species (Boyko, 2012; Markham, 1985).

***Eophrixus* Caroli, 1930**

*Diagnosis.* **Female** body linear, compact, not distorted or distorted approximately 40–80°; head bilobate or ovate, anterolateral margins not produced or produced into anteriorly directed lobes. Eyes absent. Antennula articulated or non-articulated; antenna articulated. Barbula with 2 smooth lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, smaller than anterior lobe, that on

concave side with ovate posterior lobe, smaller (sometimes markedly so) than anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 5 or 7 pereopods on convex side. Pleon of 5 pleomeres; 4 pairs of uniramous smooth lateral plates and 3 or 4 pairs of smooth uniramous or biramous pleopods; uropods present or absent. **Male** with pereomeres subequal in width. Eyes present. Antennula and antenna articulated. Pleon without indication of segmentation or with segmentation laterally indicated; uropods absent or present but not elongate.

Subtidal, parasitising alpheid, hippolytid, lysmatid, palaemonid and pasiphaeid shrimps. Temperate Northern Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 11 species (An et al., 2015).

#### ***Epiphrixus* Nierstrasz and Brender à Brandis, 1932**

*Diagnosis.* **Female** body linear, distorted approximately 30°; anterolateral margins of head produced into anteriorly directed lobes. Eyes absent. Antenna and antennula present (non-articulated?). Barbula unknown. Pereomeres distinct dorsally. Oostegites 1 posterior lobes unknown. Oostegites 2–4 present. Coxal plates on pereomeres 1 and 2 of convex side and 1–7 of concave side; dorsolateral bosses absent. 7 pereopods on concave side, 2 on convex side. Pleon of 5 pleomeres; 5 uniramous lateral plates, 5 pairs of uniramous pleopods; uropods present. **Male** unknown.

Intertidal, parasitising alpheid shrimps. Temperate Northern Atlantic. 1 species (Nierstrasz and Brender à Brandis, 1932).

#### ***Eriphrixus* Markham, 1990**

*Diagnosis.* **Female** body ovate, compact, distorted approximately 40°; head rounded, anterolateral margins produced as anteriorly directed lobes. Eyes absent. Antennulae absent; antenna non-articulated. Barbula with 1 smooth short lobe on each side. Pereomeres weakly distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, smaller than anterior lobe, that on concave side unknown. Coxal plates present on concave side; dorsolateral bosses absent. 7 pereopods on concave side, pereopods 1–3 on convex side. Pleon of 5 pleomeres; pleotelson globose; 4 pairs of uniramous smooth lateral plates and 4 pairs of uniramous smooth pleopods; uropods absent. **Male** with anterior pereomeres wider than posterior. Eyes absent. Antennula and antenna articulated. Posterior pairs of pereopods longer. Pleon with lateral indication of segmentation; uropods absent.

Slope, parasitising palaemonid shrimps. Central Indo-Pacific. 1 species (Markham, 1990).

#### ***Filophryxus* Bruce, 1972**

*Diagnosis.* **Female** body linear, compact, distorted approximately 90°; head fused with pereon, anterolateral margins produced as laterally directed lobes. Eyes absent. Antennulae absent; antenna non-articulated. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally, first 2 pereomeres distinct on convex side. Oostegite 1 on convex side with ovate posterior lobe, nearly as large as anterior lobe, that on concave side with ovate posterior lobe, much smaller than anterior lobe. Filiform

coxal plates on pereomeres 1–6 of concave side; dorsolateral bosses absent. 3 pereopods on concave side, 2 pereopods on convex side. Pleon of 1 fused segment; lateral plates absent; 3 pairs of uniramous smooth pleopods; uropods absent. **Male** with anterior pereomeres wider than posterior. Eyes absent. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Slope, parasitising palaemonid shrimps. Temperate Australasia. 1 species (Bruce, 1972a).

#### ***Hemiarthrus* Giard and Bonnier, 1887**

*Diagnosis.* **Female** body linear, elongate, distorted approximately 35–60°; head ovate, anterolateral margins produced into anteriorly directed lobes. Eyes absent. Antennulae and antennae non-articulated. Barbula with 2–4 smooth lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, larger than anterior lobe, that on concave side with finger-like posterior lobe, smaller than anterior lobe. Oostegite 2 reflexed over head and covered with cup-shaped discs; oostegites 3 and 4 with cup-shaped discs on lateral margins. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side; 1 pereopod on convex side. Pleon of 5 pleomeres; 4 pairs of uniramous smooth lateral plates and 4 pairs of smooth uniramous pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antennulae and antennae articulated. Pleon without indication of segmentation or with segmentation laterally indicated; uropods absent.

Subtidal–slope, parasitising alpheid, nematocarcinid, and thoridae shrimps. Temperate Northern Atlantic, Tropical Atlantic, Temperate Southern Africa, Eastern Indo-Pacific. 5 species (An et al., 2020; Markham, 1985).

#### ***Hemiphryxus* Bruce, 1978**

*Diagnosis.* **Female** body linear, compact, distorted approximately 90°; head rounded, anterolateral margins produced as anterolaterally directed lobes. Eyes absent. Antennula as papillae; antenna articulated. Barbula with 1 smooth short lobe on each side. Pereomeres distinct dorsally, first 2 distinct on convex side. Oostegite 1 on convex side with triangular posterior lobe, larger than anterior lobe, that on concave side with ovate posterior lobe, smaller than anterior lobe. Coxal plates present; dorsolateral bosses absent. 7 pereopods on concave side, 4 pereopods on convex side. Pleon of 4 pleomeres; 4 pairs of uniramous smooth lateral plates; 4 pairs of uniramous smooth pleopods; uropods absent. **Male** with pereomeres subequal, head distally expanded and recurved. Eyes present. Antennula and antenna articulated. Pleon with lateral indication of segmentation; uropods absent.

Subtidal, parasitising palaemonid shrimps. Western Indo-Pacific. 1 species (Bruce, 1974).

#### ***Hyperphrixus* Nierstrasz and Brender à Brandis, 1931**

*Diagnosis.* **Female** body linear, elongate, distorted approximately 90°–110°; head elongate-ovate, anterolateral margins not produced. Eyes absent. Antennula and antenna

unknown. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side; 1 or 2 pereopods on convex side. Pleon of 5 pleomeres; 4 pairs of uniramous smooth lateral plates; 4 pairs of biramous smooth pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antennula and antenna articulated. Posterior pairs of pereopods shorter. Pleon without lateral indication of segmentation; uropods absent.

Subtidal, parasitising alpheid and palaemonid shrimps. Tropical Atlantic, Western and Central Indo-Pacific. 3 species (An et al., 2015).

#### ***Hypohyperphrixus* Nierstrasz and Brender à Brandis, 1932**

*Diagnosis.* **Female** body linear, compact, not distorted; head rounded, anterolateral margins not produced. Eyes absent. Antennula and antenna unknown. Barbula unknown. Pereomeres distinct dorsally, 1–4 distinct on convex side. Coxal plates and dorsolateral bosses absent. 7 Pereopods on concave side, 1 on convex side. Pleon of 4 pleomeres; 3 pairs of uniramous smooth lateral plates; 3 pairs of biramous smooth pleopods; uropods present. **Male** unknown.

Subtidal, parasitising alpheid shrimps. Western Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1932).

#### ***Hypophryxus* Shiino, 1934**

*Diagnosis.* **Female** body linear, compact, not distorted or distorted approximately 15°; head bilobate, anterolateral margins produced into anteriorly directed lobes. Eyes absent. Antennula articulated; antenna articulated. Barbula unknown. Pereomeres distinct dorsally. Oostegite 1 unknown. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 7 pereopods on convex side. Pleon of 5 pleomeres; 4 pairs of uniramous smooth lateral plates and 4 pairs of smooth biramous pleopods; uropods present. **Male** with anterior pereomeres widest. Eyes present. Antennula and antenna articulated. Pleon fused with segmentation laterally indicated and pair of pleonal extensions at anterior end; uropods absent.

Subtidal, parasitising alpheid shrimps. Temperate Northern Pacific. 1 species (Shiino, 1934). Markham (1992) confounded the genera *Hypophryxus* and *Hyperphrixus* when trying to resurrect *Hypophryxus* from synonymy with *Eophrixus* (see Caroli, 1949) and An et al. (2015) decided that Caroli's synonym was correct. Re-examination of the description of *H. yusakiensis* Shiino, 1934 and comparison with all hemiarthrine taxa leads us to conclude that Markham (1992) was correct in his intent, if not execution, and we reinstate *Hypophryxus* as a valid genus herein.

#### ***Izuohshimaphryxus* Saito, 2015**

*Diagnosis.* **Female** body subovate, distorted approximately 40°; lateral sides of head produced into expanded lobes. Eyes absent. Antenna absent; antennula non-articulated. Barbula with 2 smooth lobes on each side. Pereomere 1 dorsally distinct on convex side. Oostegite 1 on concave side with minute posterior lobe, that on convex side with posterior lobe subequal in size to

anterior lobe. Oostegites 2–4 present. Coxal plate and dorsolateral boss only on pereomere 1 of convex side. 7 pereopods on concave side, 2 pereopods on convex side; filiform coxal plates at base of pereopods on concave side, stout extensions on convex side. Pleon of 1 fused segment. Lateral plates absent; 4 uniramous pleopods on concave side, 3 on convex side; uropods absent. **Male** unknown.

Shelf, parasitising palaemonid shrimps. Temperate Northern Pacific. 1 species (Saito, 2015).

#### ***Loki* Markham, 1972**

*Diagnosis.* **Female** body linear, compact, not distorted or distorted approximately 40°; head rounded, anterolateral margins produced as anteriorly directed lobes. Eyes absent. Antennula and antenna articulated. Barbula with 1 smooth long lobe on each side. Pereomeres distinct or weakly distinct dorsally. Oostegite 1 on convex side unknown, that on concave side with subquadrate posterior lobe approximately as large as anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on both sides. Pleon of 5 pleomeres; 3 or 4 pairs of uniramous smooth lateral plates, 3 or 4 pairs of uniramous smooth pleopods; uropods present. **Male** with all pereomeres subequal in width. Eyes present or absent. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Subtidal, parasitising alpheid and thorid shrimps. Tropical Atlantic, Western Indo-Pacific. 2 species (An et al., 2020; Markham, 1985).

#### ***Mediophrixus* Markham, 1990**

*Diagnosis.* **Female** body linear, compact, distorted approximately 80°; head rounded, anterolateral margins produced as anteriorly directed lobes. Single eye present. Antennula and antenna absent. Barbula with 1 smooth short lobe on each side. Pereomeres weakly distinct dorsally. Oostegite 1 on convex side with triangular expanded posterior lobe, larger than anterior lobe, that on concave side unknown. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 2 pereopods on convex side. Pleon of 4 pleomeres; pleotelson absent; 4 pairs of uniramous smooth lateral plates, and 4 pairs of uniramous smooth pleopods; uropods absent. **Male** with all pereomeres subequal in width. Eyes present. Antennula and antenna articulated. Pleon with lateral indication of segmentation; uropods absent.

Intertidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (Markham, 1990).

#### ***Mesophryxus* Bruce, 1973**

*Diagnosis.* **Female** body linear, compact, distorted approximately 55°; head elongate, anterolateral margins produced as anterolaterally directed lobes. Eyes present. Antennula papilliform; antenna articulated. Barbula with 2 smooth short lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with ovate posterior lobe, larger than anterior lobe, that on concave side without posterior lobe. Coxal plates present at base of all fully developed pereopods; dorsolateral bosses absent. 7 pereopods on concave side, 2 pereopods on convex

side. Pleon of 1 fused segment; 3 pairs of uniramous smooth lateral plates; 3 pairs of uniramous smooth pleopods; uropods absent. **Male** with pereomeres narrower posteriorly. Eyes absent. Antennula non-articulated; antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Subtidal, parasitising palaemonid shrimps. Western Indo-Pacific. 1 species (Bruce, 1973a).

#### ***Metaphrixus* Nierstrasz and Brender à Brandis, 1931**

*Diagnosis.* **Female** body linear, elongate, distorted approximately 70–90°; head rounded, anterolateral margins not produced. Eyes present or absent. Antennula articulated; antenna articulated or non-articulated. Barbula with 1 smooth slender and 1 short blunt lobe on each side or 2 smooth slender lobes. Pereomeres distinct dorsally. Oostegite 1 on convex side with subquadrate posterior lobe, as large as anterior lobe, that on concave side with small finger-like posterior lobe. Coxal plates absent; dorsolateral bosses present on concave side or absent. 7 pereopods on concave side, 2 or 3 pereopods on convex side. Pleon of 5 pleomeres; 4 pairs of uniramous smooth lateral plates; 4 pairs of uniramous smooth pleopods; uropods absent. **Male** with middle pereomeres widest. Eyes present. Antennula and antenna articulated. Pleon without lateral indication of segmentation; uropods absent.

Subtidal-Shelf, parasitising hippolytid and palaemonid shrimps. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 5 species (Ribeiro et al., 2024; Shimomura et al., 2006).

#### ***Micropodiphryxus* Boyko, 2012**

*Diagnosis.* **Female** body ovate, distorted approximately 10°; head ovate, anterolateral margins not produced. Eyes present or absent. Antennula and antenna unknown. Barbula unknown. Pereomeres distinct dorsally. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 4 pereopods on convex side. Pleon of 5 pleomeres; 4 pairs of biramous smooth lateral plates; 4 pairs of biramous smooth pleopods; pleotelson bifid; uropods absent. **Male** unknown.

Subtidal, parasitising crangonid shrimps. Western Indo-Pacific. 1 species (Boyko, 2012).

#### ***Miophrixus* Barnard, 1955**

*Diagnosis.* **Female** with 7 pereopods on concave side, 2 pereopods on convex side. Pleon of 3 pleomeres; 2 pairs of uniramous smooth lateral plates; 2 pairs of uniramous smooth pleopods; uropods present. [Other characters not known.] **Male** with eyes present. Uropods absent. [Other characters not known]

Subtidal, parasitising hippolytid shrimps. Western Indo-Pacific. 1 species (Barnard, 1955).

#### ***Neophryxus* Bruce, 2007**

*Diagnosis.* **Female** body linear, distorted approximately 70°; head rounded. Eyes absent. Antennula absent; antenna non-articulated. Barbula with 2 smooth long lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on convex side with large ovate posterior lobe, larger than anterior lobe, that on concave side with elongate, rounded posterior lobe larger than

anterior lobe. 4 oostegites on convex side, 5 on concave side. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 1 on convex side. Pleon of 5 pleomeres; lateral plates absent, 4 pairs of uniramous smooth pleopods; uropods present. **Male** with pereomeres subequal in width. Eyes absent. Antennula articulated; antenna of 1 segment. Pleon with lateral indication of segmentation, uropods absent.

Intertidal, parasitising palaemonid shrimps. Western Indo-Pacific. 1 species (Bruce, 1973b).

#### ***Orophryxus* Bruce, 1972**

*Diagnosis.* **Female** body linear, distorted approximately 90°; head fused to pereon, indistinct. Eyes present. Antennula as articulated flattened plate; antenna as large tubular segment with additional small distal segment. Barbula unknown. Pereomeres distinct dorsally, feebly distinct on concave side. 4 oostegites on convex side of body, 3 on concave side. Coxal plate and dorsolateral boss presence/absence unclear. 2 pereopods on concave side; 4 on convex side. Pleon a small non-articulated lamina; lateral plates, pleopods, and uropods absent. **Male** unknown.

Intertidal, parasitising palaemonid shrimps. Western Indo-Pacific. 1 species (Bruce, 1972b).

#### ***Pliophrixus* Caroli, 1930**

*Diagnosis.* **Female** with 7 pereopods on concave side, 3 on convex side. [Other characters not known.] **Male** unknown.

Subtidal, parasitising processid shrimps. Temperate Northern Atlantic. 1 species (Caroli, 1930).

#### ***Quadripediphryxus* Saito, 2020**

*Diagnosis.* **Female** body linear, distorted approximately 10°; head subquadrate. Eyes present. Antenna and antennula articulated. Barbula with 2 smooth short lobes on each side. Pereomeres 1–3 fused to head, 4–7 distinct dorsally and on concave side. Oostegite 1 on concave side with minute posterior lobe, that on convex side with posterior lobe subequal in size to anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on concave side, 4 on convex side. Pleon of 4 pleomeres; pleotelson minute; 4 pairs of uniramous oval lamellar lateral plates and 4 pairs of biramous pleopods; minute dorsally positioned lobes (uropods?) on terminal pleomere present. **Male** with pereomeres subequal in width. Eyes present. Antenna and antennula articulated. Uropods absent.

Subtidal, Temperate Northern Pacific, parasitising alpheid shrimp. 1 species (Saito, 2020).

#### ***Sigyn* An, Boyko and Li, 2015**

*Diagnosis.* **Female** body linear, distorted approximately 90°; head rounded. Eyes absent. Single pair of articulated antennae present (antennulae absent). Barbula with 7 or 8 smooth short acute lobes on each side. Pereomeres distinct dorsally. Oostegite 1 on concave side with small triangular posterior lobe, that on convex side with elongate, distally acute posterior lobe subequal in size to anterior lobe. Coxal plates and dorsolateral bosses absent. 7 pereopods on both sides, crowded together on concave

side. Pleon of 5 pleomeres, terminal pleomere (pleotelson?) as sphere covered with tubercles; 4 pairs of uniramous lamellar smooth lateral plates and 4 pairs of uniramous smooth pleopods; uropods absent. **Male** with pereomeres subequal in width. Eyes present. Antenna and antennula articulated. Pleon without lateral indications of segmentation; uropods absent.

Intertidal, parasitising alpheid shrimps. Central Indo-Pacific. 1 species (An et al., 2015).

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## Subfamily Keponinae Boyko, Moss, Williams and Shields, 2013

Figures 6.14, 6.15

Species in the genera of Keponinae are all branchial ectoparasites of brachyuran crabs, with the exception of one species of *Dactylokepon*, which parasitises slipper lobsters, species of *Coxalione*, *Hemicepon* and *Procepon*, which parasitise gebiids, and both species of *Castrione*, which parasitise axiids. Bodies of mature females are generally dorsoventrally inflated with slight to moderate distortion of the head relative to the body, often have middorsal projections on one or more of the posterior pereomeres, and usually have elongate uniramous lateral plates and pleopods with digitate margins. Females of species in some genera (e.g. *Carcinione*, *Coxalione*) deviate considerably from the typical members of the subfamily. Males usually have a pleon with distinct segmentation, often have midventral tubercles on the pereon and/or pleon, and if pleopods are present they are typically sessile and uropods are absent. The sole species of *Hemicepon* was described based on a mature male and a male in the process of transitioning to a female; no additional specimens have been reported and placement in Keponinae is tentative. The key is modified from that of An et al. (2020). The subfamily Keponinae includes *Cardiocepon* Nobili, 1906, the only semiterrestrial epicaridean, parasitic on gecarcinid crabs.

**Diagnosis. Female** body ovate and/or elongate, body weakly to not distorted; head distinct from pereon, bilobed or not bilobed;

frontal lamina present or absent. Eyes present or absent. Antennula and antenna articulated. Maxilliped with setose or non-setose articulated or non-articulated palp or without palp. Barbula with 2–5 short smooth or with crenulate/digitate bumps or lobes on each side. Pereomeres distinct dorsally, with middorsal projections on pereomeres 5, 6 and/or 7 or without middorsal projections. 5 pairs of oostegites. Oostegite 1 with triangular, subquadrate or ovate posterior lobe, larger, smaller or subequal to anterior lobe; internal ridge smooth or digitate/tuberculate. Marsupium closed. Coxal plates, dorsolateral bosses and tergal projections present or absent. Pleon of 6 pleomeres, narrower or not narrower than pereon; middorsal projection on pereomere 1 present or absent. 5 pleomeres with elongated uniramous smooth or tuberculate lateral plates with digitate, crenulate or smooth margins or lateral plates absent; 5 pairs of uniramous or biramous smooth or tuberculate pleopods with smooth or digitate margins; uropods uniramous or biramous, smooth or tuberculate, with smooth to digitate margins. **Male** approximately 2–7 times as long as wide, pereomeres narrower or not narrower posteriorly. Head narrower than pereon. Eyes present or absent. Antennula and antenna articulated. Pereopods subequal or anterior pairs 1–4 larger. Midventral tubercles present or absent. Pleon segmented or fused; lateral plates present or absent; pleopods present or absent; posterolateral corners of pleomere 6 rounded or produced into lobes; uropods present or absent.

### Key to genera of the subfamily Keponinae

The key is based on female and male characters. *Hemicepon* is excluded (see above).

- |    |   |                    |
|----|---|--------------------|
| 1. | Pereomere 2 of female reduced (fig. 6.14a, b) .....                     | <i>Onychocepon</i> |
| –  | All pereomeres of female normally developed .....                       | 2                  |
| 2. | 1 pair of lateral plates on all pleomeres of female .....               | 3                  |
| –  | 2 pairs of lateral plates on all pleomeres of female (fig. 6.14c) ..... | <i>Cardiocepon</i> |
| 3. | Female with middorsal projections on some pereomeres .....              | 4                  |
| –  | Female without middorsal projections on any pereomeres .....            | 12                 |
| 4. | Pleopods of female with well-developed endopods .....                   | 5                  |
| –  | Pleopods of female with reduced or absent endopods .....                | 8                  |
| 5. | Some pleomeres of male fused (fig. 6.14d) .....                         | <i>Scyracepon</i>  |
| –  | All pleomeres of male distinct .....                                    | 6                  |
| 6. | Female with middorsal projection on pleomere 1 (fig. 6.14e, f) .....    | <i>Megacepon</i>   |
| –  | Female without middorsal projection on any pleomere .....               | 7                  |
| 7. | Male without pleopods (fig. 6.14g, h) .....                             | <i>Ergyne</i>      |
| –  | Male with pleopods (fig. 6.14i) .....                                   | <i>Allokepon</i>   |
| 8. | Pleopods of female without endopods (fig. 6.14j, k) .....               | <i>Mesocepon</i>   |
| –  | Pleopods of female with reduced endopods .....                          | 9                  |

9.	Middorsal projections on more than pereomeres 6 and 7 of female .....	10
–	Middorsal projections only on pereomeres 6 and 7 of female .....	11
10.	Lateral plates and pleopods of female with digitate margins (fig. 6.14l) .....	<i>Cancricepon</i>
–	Lateral plates and pleopods of female with smooth margins (fig. 6.14m) .....	<i>Paracepon</i>
11.	Pereomere 6 of female with more than 1 projection (fig. 6.14n) .....	<i>Tylokepon</i>
–	Pereomere 6 of female with 1 projection (fig. 6.14o) .....	<i>Grapsicepon</i>
12.	Pleopods of female with well-developed endopods, at least on anterior pleopods .....	13
–	Pleopods of female all with very reduced endopods .....	21
13.	Lateral plates and pleopods of female with smooth margins .....	14
–	Lateral plates and pleopods of female with digitate margins .....	16
14.	Male with lateral plates (fig. 6.14p, q) .....	<i>Procepon</i>
–	Male without lateral plates .....	15
15.	Female with wide lamellar lateral plates, male with slender uropods (fig. 6.14r, s) .....	<i>Coxalione</i>
–	Female with narrow lateral plates, male with stout uropods (fig. 6.14t) .....	<i>Hypocepon</i>
16.	Head of female with bilobate anterior margin .....	17
–	Head of female with convex anterior margin .....	18
17.	Surfaces of lateral plates and pleopods of female covered with tubercles, margins sparsely digitate (fig. 6.14u) .....	<i>Anacepon</i>
–	Surfaces of lateral plates and pleopods of female medially smooth, margins densely digitate .....	20
18.	Coxal plates smooth (fig. 6.14v) .....	<i>Dactylokepon</i>
–	Coxal plates covered with tubercles .....	19
19.	Coxal plates swollen (fig. 6.14w) .....	<i>Kepon</i>
–	Coxal plates not swollen, with crenulate surfaces and small thin projections (fig. 6.14x) .....	<i>Rhizophoracepon</i>
20.	Male without pleopods (fig. 6.15a, b) .....	<i>Metacepon</i>
–	Male with pleopods (fig. 6.15c, d) .....	<i>Heterocepon</i>
21.	Female with 5 pairs of biramous pleopods and uropods (fig. 6.15e, f) .....	<i>Castrione</i>
–	Female with 5 pairs of uniramous pleopods and uropods .....	22
22.	Lateral plates of female with smooth margins .....	23
–	Lateral plates of female with digitate margins .....	24
23.	Pleopods of female with exopods slightly shorter than corresponding lateral plates (fig. 6.15g) .....	<i>Metathelges</i>
–	Pleopods of female with exopods much shorter than corresponding lateral plates (fig. 6.15h) .....	<i>Atypocepon</i>
24.	Male with all pleomeres fused (fig. 6.15i, j) .....	<i>Hypercepon</i>
–	Male with some pleomeres separated .....	25
25.	Female with reduced frontal lamina (fig. 6.15k) .....	<i>Apocepon</i>
–	Female with well-developed frontal lamina .....	26
26.	Female with tuberculate frontal lamina (fig. 6.15l, m) .....	<i>Onkokepon</i>
–	Female with smooth frontal lamina .....	27
27.	Male with long uropods (fig. 6.15n–p) .....	<i>Leidya</i>
–	Male with short uropods (fig. 6.15q, r) .....	<i>Trapezicepon</i>

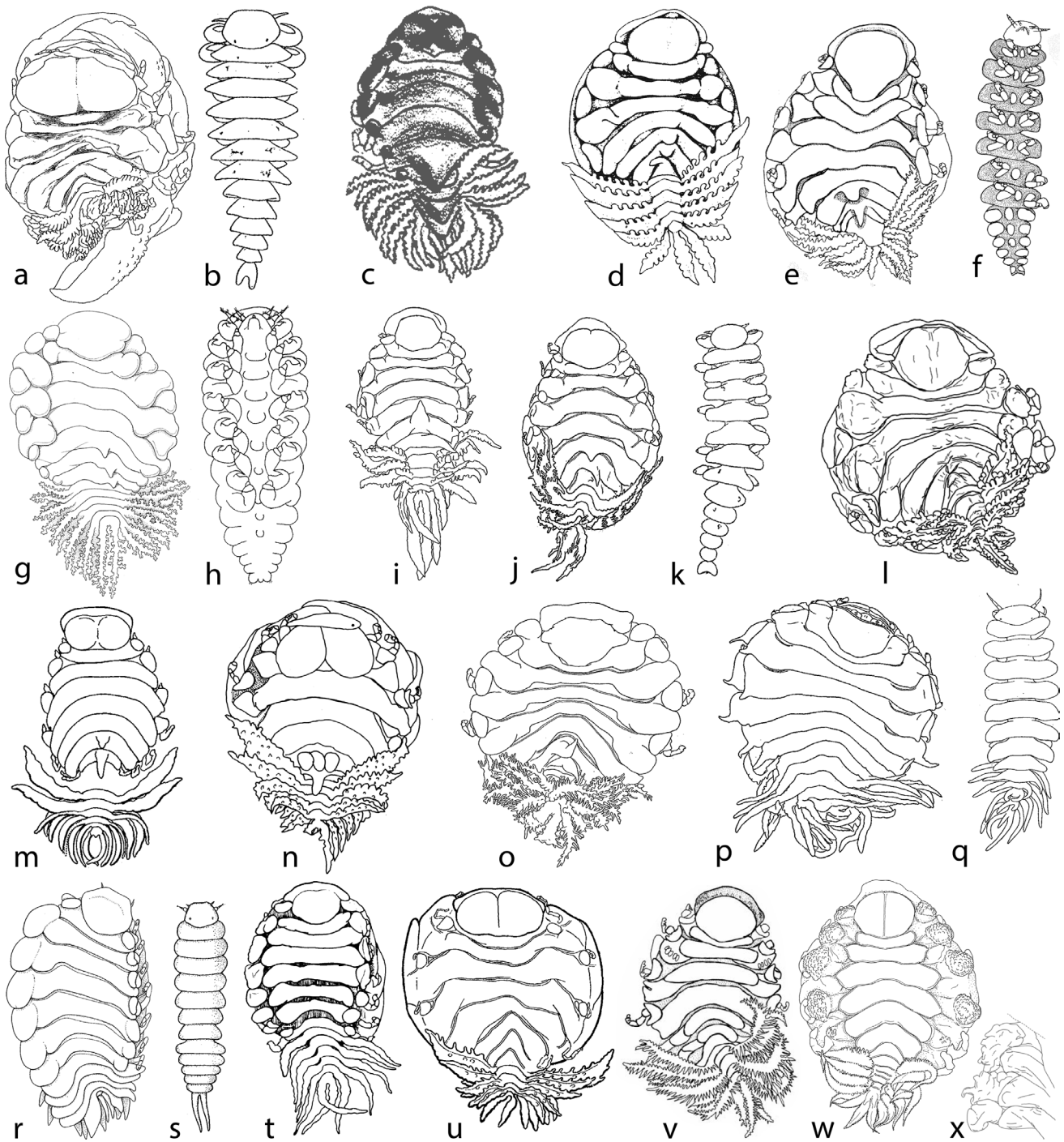


Figure 6.14. Keponinae. *Onychocepon resupinum* Shiino, 1936: a, female dorsal view; b, male dorsal view. *Cardiocepon pteroides* Nobili, 1906: c, female dorsal view. *Scyracepon tuberculosa* Tattersall, 1905: d, female dorsal view. *Megacepon sheni* An, Boyko and Li, 2012: e, female dorsal view; f, male ventral view. *Erygne cervicornis* Risso, 1816: g, female dorsal view; h, male ventral view. *Allokepon tiariniae* (Shiino, 1937): i, female dorsal view. *Mesocepon tosizimensis* Shiino, 1951: j, female dorsal view; k, male dorsal view. *Cancricepon castroi* An, Wang, Boyko and Williams, 2019: l, female dorsal view. *Paracepon stebbingi* Nierstrasz and Brender à Brandis, 1931: m, female dorsal view. *Tylokepon bonnieri* Stebbing, 1904: n, female dorsal view. *Grapsicepon rotundum* Shiino, 1936: o, female dorsal view. *Procepon insolitum* Shiino, 1937: p, female dorsal view; q, male dorsal view. *Coxalione inaequalis* Bourdon, 1977: r, female dorsal view; s, male dorsal view. *Hypocepon enoensis* Nierstrasz and Brender à Brandis, 1930: t, female dorsal view. *Anacepon sibogae* Nierstrasz and Brender à Brandis, 1931: u, female dorsal view. *Dactylokepon richardsonae* Stebbing, 1910: v, female dorsal view. *Kepon grapsi* (Nobili, 1905): w, female dorsal view. *Rhizophoracepon magnagibbus* Williams, Boyko and Tri, 2023: x, female coxal plates and tergal projections on pereopods 5–7.

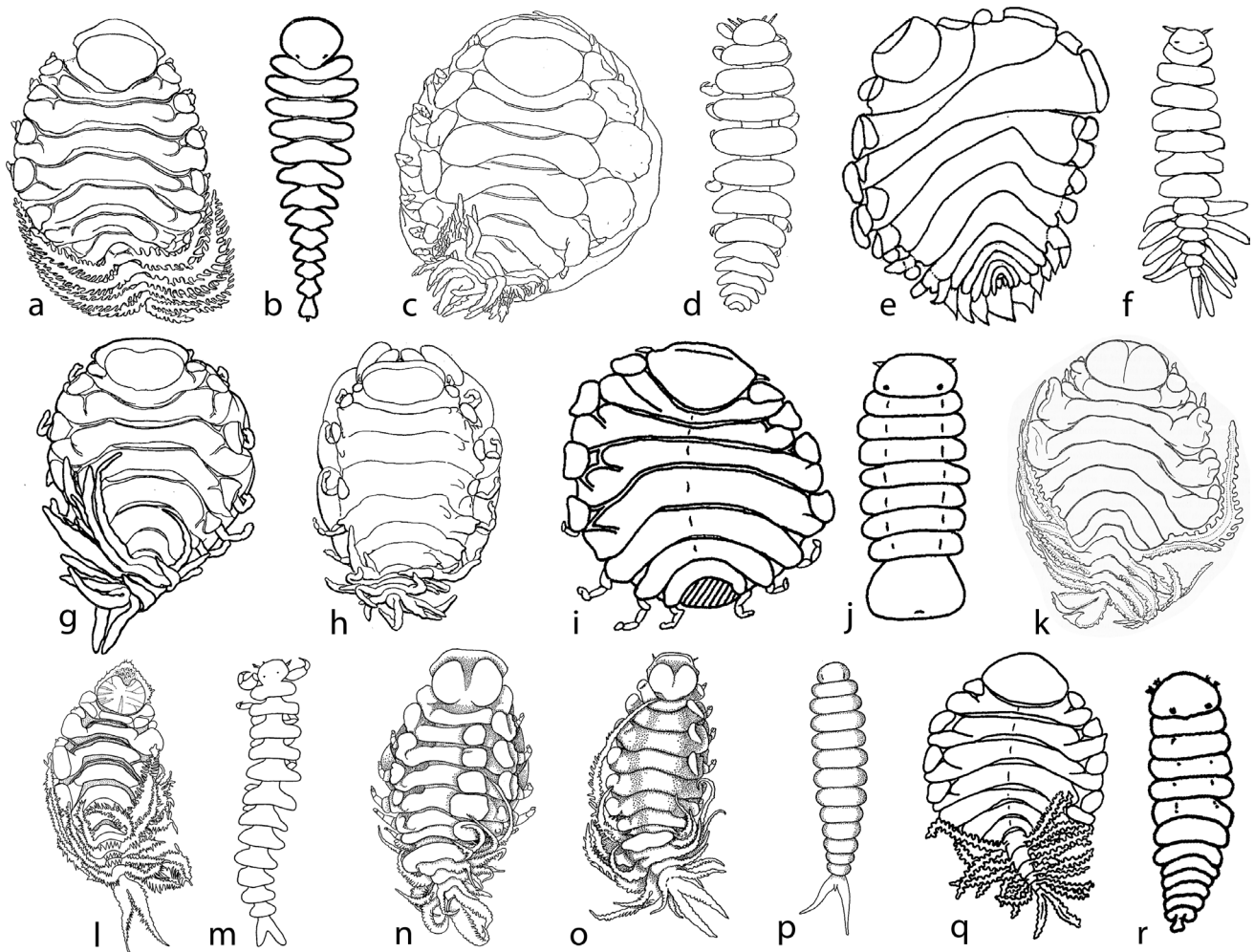


Figure 6.15. Keponinae. *Metacepon leidyi* Nierstrasz and Brender à Brandis, 1931: a, female dorsal view; b, male dorsal view. *Heterocephon marginatum* Shiino, 1936: c, female dorsal view; d, male dorsal view. *Castrione longicaudata* Brasil Lima, 1980: e, female dorsal view; f, male dorsal view. *Metathelges japonicus* (Nierstrasz and Brender à Brandis, 1931): g, female dorsal view. *Atypocephon intermedium* Nierstrasz and Brender à Brandis, 1931: h, female dorsal view. *Hypercephon guamensis* Danforth, 1972: i, female dorsal view, hatched area shows where pleopods are missing; j, male dorsal view. *Apocephon pulcher* Nierstrasz and Brender à Brandis, 1930: k, female dorsal view. *Onkocephon articulatus* An, Yu and Li, 2006: l, female dorsal view; m, male dorsal view. *Leidya distorta* (Leidy, 1855): n, female dorsal view; o, immature female dorsal view; p, male dorsal view. *Trapezicepon domeciae* Danforth, 1972: q, female dorsal view; r, male dorsal view.

#### ***Allokepon* Markham, 1982**

**Diagnosis. Female** ovate, body weakly to not distorted; head bilobed or not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 short smooth lobes on each side. Middorsal projections on pereomeres 6 and 7. Oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates present or absent; dorsolateral bosses and tergal projections absent. Pleon narrower than pereon. Lateral plates smooth, with digitation on margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 3–4 times as long as wide, pereomeres narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present. Pleon of 6

segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–shelf, parasitising epialtid, inachoidid and portunid crabs. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 5 species (Duan et al., 2008; Markham, 1982).

#### ***Anacepon* Nierstrasz and Brender à Brandis, 1931**

**Diagnosis. Female** elongate, body not distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated or non-articulated palp. Barbula with 2 short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with triangular posterior lobe, larger than anterior

lobe; internal ridge digitate. Dorsolateral bosses, coxal plates and tergal projections present. Pleon narrower than pereon. Lateral plates smooth, with digitate margins, first pair extremely long; pleopods smooth, biramous, exopods elongate with digitate margins, endopods rudimentary; uropods smooth, uniramous, with crenulated margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 4 or 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into lobes; uropods absent.

Shelf, parasitising parthenopid crabs. Central Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1931).

#### ***Apocepon* Nierstrasz and Brender à Brandis, 1930**

*Diagnosis.* **Female** elongate, body not distorted; head distinct from pereon, bilobed; frontal lamina present. Eyes absent. Antennula and antenna articulated. Maxilliped with setose articulated or non-articulated palp. Barbula with 2 short lobes on each side. Pereomeres distinct dorsally, without middorsal projections. 5 pairs of oostegites. Oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge digitate. Marsupium closed. Dorsolateral bosses, coxal plates and tergal projections present. Pleon narrower than pereon, 5 pleomeres with strongly elongated lateral plates smooth, with digitation on margins, first pair extremely long; 5 pairs of biramous smooth pleopods, exopods elongate with digitate margins, endopods rudimentary; uropods uniramous, smooth, broad, with crenulated margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Head narrower than pereon. Eyes absent. Antennula and antenna articulated. Pereopods subequal. Midventral tubercles absent. Pleon segmented; pleopods as small lobes on pleomeres 1–4 or 1–5; posteroventral corners of pleomere 6 produced into lobes; uropods absent.

Shelf, parasitising leucosiid crabs. Central Indo-Pacific. 3 species (An et al., 2006b).

#### ***Atypocepon* Nierstrasz and Brender à Brandis, 1931**

*Diagnosis.* **Female** ovate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Antennula and antenna not described. Maxilliped not described. Barbula not described. Pereomeres without middorsal projections. Oostegite 1 not described. Dorsolateral bosses present; tergal projections and coxal plates absent. Pleon narrower than pereon. Lateral plates smooth, with smooth margins; pleopods smooth, biramous (exopod large, endopod rudimentary) with smooth margins; uropods smooth, uniramous, with smooth margins. **Male** unknown.

Slope, host unknown. Central Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1931).

#### ***Cancericepon* Giard and Bonnier, 1887**

*Diagnosis.* **Female** ovate, body weakly distorted; head bilobed or not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 short smooth

lobes on each side. Large middorsal projections present on pereomeres 5–7. Oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Dorsolateral bosses present, tergal projections present or absent, coxal plates absent. Pleon narrower than pereon. Lateral plates digitate, with digitate margins; pleopods digitate, biramous; uropods digitate, uniramous. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Eyes present or absent. Anterior 3 or 4 pairs of pereopods larger than posterior pairs. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 slightly produced into lobes or rounded; uropods absent.

Intertidal–shelf, parasitising dacyropilumnid, domeciid, eriphiid, panopeid, pilumnid, pseudothombiliid, scalopidid, trapeziid and xanthid crabs. Temperate Northern Atlantic, Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 11 species (An et al., 2019).

#### ***Cardiocepon* Nobili, 1906**

*Diagnosis.* **Female** elongate, body not distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose, non-articulated palp. Barbula not described. Middorsal projections present on pereomeres 6 and 7. Oostegite 1 with ovate posterior lobe, much larger than anterior lobe; internal ridge with few small lobes. Coxal plates present; tergal projections and dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates tuberculate, with digitate margins. Pleopods tuberculate, biramous, with digitate margins; uropods tuberculate, uniramous, with digitate margins. **Male** unknown.

Semiterrestrial, parasitising gecarcinid crabs. Central Indo-Pacific. 1 species (Boyko, 2003).

#### ***Castrione* Brasil Lima, 1980**

*Diagnosis.* **Female** ovate, body weakly to not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose, non-articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe, larger than anterior lobe; internal ridge with few small lobes. Coxal plates and tergal projections present; dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, uniramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of elongate uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods uniramous.

Subtidal–shelf, parasitising micheleid shrimps. Tropical Atlantic, Central Indo-Pacific. 2 species (Markham, 1995).

#### ***Coxalione* Bourdon, 1977**

*Diagnosis.* **Female** elongate, body weakly distorted; head not bilobed; frontal lamina indistinct. Eyes absent. Maxilliped without palp. Barbula with 2 short lobes on each side, outer

lobe smooth, inner lobe crenulate. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe with distal triangular projection, smaller than anterior lobe; internal ridge tuberculate. Coxal plates and dorsolateral bosses present; tergal projections absent. Pleon not narrower than pereon. Lateral plates smooth, with smooth margins; pleopods smooth, biramous, with smooth margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 3–4 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleonite 6 rounded; uropods uniramous, elongate.

Subtidal, parasitising laomediid shrimps. Central Indo-Pacific. 1 species (Bourdon, 1977).

#### ***Dactylokepon* Stebbing, 1910**

*Diagnosis. Female* elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose non-articulated palp. Barbula with 2 digitate short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe bearing distal triangular extension, subequal to anterior lobe; internal ridge digitate. Dorsolateral bosses and tergal projections present, coxal plates absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods digitate, biramous; uropods smooth, uniramous with digitate margins. **Male** approximately 3–4 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods 1 and 2 larger than others. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into lobes or rounded; uropods absent.

Shelf, parasitising leucosiid, pilumnid, pinnotherid, portunid, tetraliid, trapeziid and xanthid crabs, and scyllarid lobsters. Temperate Northern Atlantic, Tropical Atlantic, Western and Central Indo-Pacific. 11 species (An et al., 2007).

#### ***Ergyne* Risso, 1816**

*Diagnosis. Female* elongate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose non-articulated palp. Barbula with 2 smooth bumps or short lobes on each side. Middorsal projections present on pereomeres 5–7. Oostegite 1 with ovate posterior lobe bearing distal triangular extension, smaller than anterior lobe; internal ridge with few low bumps, not digitate. Dorsolateral bosses and coxal plates present, tergal projections absent. Pleon not narrower than pereon. Lateral plates smooth, with digitate margins; pleopods digitate, biramous; uropods smooth, uniramous, with digitate margins. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; pleopods absent; posterolateral corners of pleomere 6 produced into short lobes; uropods absent.

Subtidal, parasitising portunid crabs. Temperate Northern Atlantic. 1 species (Bourdon, 1968).

#### ***Grapsicepon* Giard and Bonnier, 1887**

*Diagnosis. Female* ovate, body not or weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Antennula and antenna not described. Maxilliped with setose articulated palp. Barbula with 2 pairs of smooth lobes on each side. Middorsal projections present on pereomeres 6 and 7. Oostegite 1 with ovate posterior lobe bearing triangular distal process, smaller than anterior lobe; internal ridge digitate. Dorsolateral bosses and coxal plates present; tergal projections absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods digitate, biramous; uropods smooth, uniramous, with digitate margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising grapsid, majid, mithracid, tetraliid, and xanthid crabs. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific. 6 species (Markham, 1988).

#### ***Hemicepon* Lemos de Castro and Brasil-Lima, 1980**

*Diagnosis. Transitional male to female* elongate, body not distorted; head not bilobed; frontal lamina absent. Eyes present. Maxilliped with distally bifurcated articulated palp. Barbula not described. Pereomeres without middorsal projections. No oostegites (not mature). Dorsolateral bosses, tergal projections and coxal plates absent. Pleon not narrower than pereon. Lateral plates smooth, with smooth margins; pleopods smooth, biramous, with smooth margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 6–7 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 weakly produced; uropods absent.

Intertidal, parasitising upogebiid shrimps. Tropical Atlantic. 1 species (Lemos de Castro and Brasil-Lima, 1980).

#### ***Heteroepon* Shiino, 1936**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 pairs of smooth lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Dorsolateral bosses and tergal projections absent; coxal plates present. Pleon narrower than pereon. Lateral plates smooth, with crenulated margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with weakly crenulate margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising pinnotherid crabs. Temperate Northern Pacific, Central Indo-Pacific. 2 species (Boyko and Williams, 2024; Janssen and Brandt, 1994; Shiino, 1936a).

***Hypercepon* Danforth, 1972**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Antennula and antenna present. Maxilliped not described. Barbula not described. Pereomeres without middorsal projections. Oostegite 1 not described. Dorsolateral bosses and tergal projections present; coxal plates absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, uniramous, with digitate margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods not described in detail. Midventral tubercles absent. Pleon fused; lateral plates absent; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising trapeziid crabs. Eastern Indo-Pacific. 1 species (Danforth, 1972).

***Hypocepon* Nierstrasz and Brender à Brandis, 1930**

*Diagnosis. Female* ovate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 2 pairs of smooth lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe bearing small triangular projection, subequal in size to anterior lobe; internal ridge digitate. Coxal plates present; tergal projections and dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates smooth, with slightly crenulate margins; pleopods smooth, biramous, finger-like, with smooth margins; uropods smooth, biramous, with crenulate margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising pinnotherid crabs. Central Indo-Pacific. 1 species (Boyko and Williams, 2024; Markham, 1992).

***Kepon* Duvernoy, 1840**

*Diagnosis. Female* ovate, body weakly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose non-articulated palp. Barbula with 2 pairs of digitate lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with triangular posterior lobe, subequal in size or larger than anterior lobe; internal ridge digitate. Coxal plates present, covered in tubercles; tergal projections and dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates tuberculate, with digitate margins; pleopods tuberculate, biramous, with digitate margins; uropods tuberculate, uniramous, with digitate margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 strongly produced; uropods absent.

Intertidal–shelf, parasitising grapsid, majid and varunid crabs. Western and Central Indo-Pacific. 4 species (Uyeno and Boyko, 2020).

***Leidya* Cornalia and Panceri, 1861**

*Diagnosis. Female* elongate, body weakly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 pairs of smooth elongate lobes on each side. Middorsal projections present or absent. Oostegite 1 with elongate ovate posterior lobe, larger than anterior lobe; internal ridge digitate. Coxal plates present; tergal projections and dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 4–5 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods long, filamentous, uniramous.

Intertidal, parasitising grapsid and ocypodid crabs. Temperate Northern and Tropical Atlantic, Temperate Northern Pacific. 4 species (Markham, 2002).

***Megacepon* George, 1947**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose, non-articulated palp. Barbula with 2 smooth long lobes on each side. Middorsal projection on pereomere 6. Oostegite 1 with elongate posterior lobe, much larger than anterior lobe; internal ridge digitate. Dorsolateral bosses and tergal projections present; coxal plates absent. Pleon narrower than pereon; middorsal projection on pleomere 1. Lateral plates smooth, with digitate margins; pleopods digitate, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 4–5 times as long as wide, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 weakly produced; uropods as sessile, ventrally displaced discs or absent.

Intertidal–subtidal, parasitising sesarmid and varunid crabs. Western and Central Indo-Pacific, Temperate Northern Pacific. 6 species (An et al., 2012).

***Mesocepon* Shiino, 1951**

*Diagnosis. Female* elongate, body weakly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with setose, non-articulated palp. Barbula not described. Middorsal projections on pereomeres 5–7. Oostegite 1 with subquadrate posterior lobe bearing distal rounded lobe, subequal to anterior lobe; internal ridge digitate. Dorsolateral bosses and tergal projections present; coxal plates absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, uniramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 4 times as long as wide, pereomeres not narrower posteriorly. Eyes absent. Pereopod 1 larger than others. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; pleopods absent; posterolateral corners of pleomere 6 weakly produced; uropods absent.

Subtidal, parasitising leucosiid crabs. Temperate Northern Pacific. 1 species (Shiino, 1951).

***Metacepon* Nierstrasz and Brender à Brandis, 1931**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with non-setose, non-articulated palp. Barbula with 2 smooth short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with triangular posterior lobe, subequal to or smaller than anterior lobe; internal ridge slightly tuberculate. Dorsolateral bosses and coxal plates present; tergal projections absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, uniramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 3 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 weakly to moderately produced; uropods absent.

Subtidal–shelf, parasitising matutid and pilumnid crabs. Central Indo-Pacific. 2 species (Bourdon and Stock, 1979; Markham, 1992).

***Metathelges* Nierstrasz & Brender à Brandis, 1923**

*Diagnosis. Female* ovate/elongate, body not distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose non-articulated palp. Barbula with 2 smooth bumps or short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe bearing distal triangular extension, smaller than anterior lobe; internal ridge smooth. Dorsolateral bosses, coxal plates and tergal projections present. Pleon narrower or not narrower than pereon. Lateral plates smooth, with smooth margins; pleopods smooth, biramous, with smooth margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods 1 and 2 larger than others. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into lobes; uropods absent.

Shelf–slope, parasitising cyclodorippid crabs. Central Indo-Pacific, Temperate Northern Pacific. 4 species (Boyko, 2024, 2025; Boyko and Williams, 2021).

***Onkokepon* An, Yu and Li, 2006**

*Diagnosis. Female* elongate, body not distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 pairs of digitate lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with subquadrate posterior lobe bearing triangular projection, subequal to anterior lobe; internal ridge digitate. Coxal plates absent; tergal projections and dorsolateral bosses present. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 4–5 times as long as wide, pereomeres not

narrower posteriorly. Eyes present. Pereopods 1 and 2 larger than posterior pairs. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into lobes; uropods absent.

Shelf, parasitising leucosiid crabs. Central Indo-Pacific. 2 species (An et al., 2006a).

***Onychocepon* Pérez, 1921**

*Diagnosis. Female* ovate, body not distorted to strongly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 2 digitate short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with subquadrate posterior lobe, subequal to anterior lobe; internal ridge with few small lobes. Coxal plates present; tergal projections and dorsolateral bosses absent. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 2–3 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods 1 and 2 larger than posterior pairs. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into short lobes; uropods absent.

Subtidal, parasitising pinnotherid crabs. Central Indo-Pacific, Temperate Northern Pacific. 3 species (Shiino, 1936b).

***Paracepon* Nierstrasz and Brender à Brandis, 1931**

*Diagnosis. Female* elongate, body not distorted; head bilobed; frontal lamina present. Eyes absent. Antennula and antenna not described. Maxilliped not described. Barbula not described. Middorsal projections on pereomeres 6 and 7. Oostegite 1 not described. Coxal plates and tergal projections absent; dorsolateral bosses present. Pleon narrower than pereon. Lateral plates tuberculate, with undulating (not digitate) margins; pleopods smooth, biramous, with undulating (not digitate) margins; uropods smooth, uniramous, with undulating (not digitate) margins. **Male** elongate, approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Antennula and antenna not described. Eyes absent. Pereopods not described. Midventral tubercles not described. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 produced into short lobes; uropods absent.

Slope, parasitising inachid crabs. Western and Central Indo-Pacific. 2 species (Nierstrasz and Brender à Brandis, 1931; Pillai, 1954).

***Procepon* Shiino, 1937**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present. Maxilliped without palp or with setose non-articulating palp. Barbula with 2–5 crenulate short lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with ovate posterior lobe bearing triangular lobe, smaller or larger than anterior lobe; internal ridge with few tubercles or highly digitate. Dorsolateral bosses

absent; coxal plates and tergal projections present. Pleon not narrower than pereon. Lateral plates smooth, with smooth margins; pleopods smooth, biramous, with smooth margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 2–3 times as long as wide, pereomeres narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates present; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods uniramous.

Subtidal, parasitising upogebiid shrimps. Western and Central Indo-Pacific, Temperate Northern Pacific. 3 species (An et al., 2009).

#### ***Rhizophoracepon* Williams, Boyko and Tri, 2023**

**Diagnosis. Female.** Head subovate, frontal lamina thin, extending to lateral margin of head. Eyes absent. Barbula with 2 slender subequal falcate pointed lateral projections on each side, middle region smooth. Maxilliped with large non-setose palp. Coxal plates on pereomeres 1–7 rounded with crenulate surface and small thin projections; dorsolateral bosses and tergal projections absent. Pereomeres without middorsal projections. Oostegite 1 with subcircular anterior article, subequal in size to posterior article, internal ridge digitate, posterior article rounded with distolateral triangular projection. Pereopods subequal in structure, posterior pairs slightly longer than anterior. Pleomeres 1–5 each bearing a pair of biramous digitate pleopods and uniramous digitate lateral plates, surfaces crenulate. Endopods, exopods, and lateral plates subequal in size. Uropods uniramous, surface smooth, margins slightly crenulate. **Male.** Pereomeres not narrower posteriorly. Head ovate, distinctly separated from pereomere 1. Eyes present. Pleon without midventral tubercles. Pereopods subequal in size and structure except anterior three pairs with longer dactyli. Pleomeres 1–5 each with low, rounded pleopods bearing nipple-like extension, pleomeres 1–4 with midventral tubercles; pleomere 6 posterolaterally extended into 2 flat, broad, smooth rami separated by large triangular median indentation; uropods absent.

Intertidal, parasitising pinnotherid crabs. Central Indo-Pacific. 1 species (Williams et al., 2023).

#### ***Scyracepon* Tattersall, 1905**

**Diagnosis. Female** ovate, body weakly to moderately distorted; head bilobed or not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 or 3 pairs of smooth lobes on each side. Pereomeres with or without middorsal projections. Oostegite 1 with triangular or subrectangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates absent; tergal projections and dorsolateral bosses present. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods digitate, biramous; uropods smooth, uniramous, with digitate margins. **Male** approximately 2–3 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments, distinct ventrally but fused dorsally; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal–slope, parasitising corystid, epialtid, eriphiid, geryonid, goneplacid, macrophthalmid, majid, portunid and xanthid crabs. Temperate Northern Atlantic, Temperate Southern Africa, Indo West-Pacific, Temperate Northern Pacific. 11 species (An et al., 2020).

#### ***Trapezicepon* Bonnier, 1900**

**Diagnosis. Female** ovate, body weakly to moderately distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 pairs of smooth lobes on each side. Pereomeres without middorsal projections. Oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates absent; tergal projections and dorsolateral bosses present. Pleon narrower than pereon. Lateral plates smooth, with digitate margins; pleopods smooth, biramous, with digitate margins; uropods smooth, uniramous, with digitate margins. **Male** approximately 3–4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising domeciid and trapeziid crabs. Western and Eastern Indo-Pacific. 2 species (An et al., 2019).

#### ***Tylokepon* Stebbing, 1904**

**Diagnosis. Female** ovate, body weakly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose non-articulated palp. Barbula with 2 or 3 pairs of smooth lobes on each side. Pereomeres 6 and 7 with middorsal projections. Oostegite 1 with ovate or triangular posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates and tergal projections absent; dorsolateral bosses present. Pleon narrower than pereon. Lateral plates tuberculate or smooth, with smooth margins; pleopods smooth, biramous, with smooth to slightly undulating margins; uropods smooth, uniramous, with smooth margins. **Male** approximately 4 times as long as wide, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 segments; lateral plates absent; 5 pairs of sessile uniramous pleopods; posterolateral corners of pleomere 6 slightly produced; uropods ventrally displaced, uniramous.

Subtidal–shelf, parasitising epialtid, majid and parthenopid crabs. Central Indo-Pacific, Temperate Northern Pacific. 5 species (An et al., 2018).

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## Subfamily Orbioninae Codreanu, 1967

Figure 6.16

Genera in Orbioninae can be distinguished from those of other bopyrid subfamilies in that females have little to no distortion of the head and pleon relative to the pereon but the coxal plates and often the dorsolateral bosses are much larger on one side of the body; the frontal lamina is also well developed. Species in Orbioninae are the only known bopyrid ectoparasites in the branchial chambers of penaeoid shrimp; some species are also found on aristeid, solenocerid, and sicyoniid shrimp hosts. An et al. (2022) questioned the monophyly of *Orbione*. The key is modified from An et al. (2022). Males of representative genera are figured.

**Diagnosis.** **Female** body ovate; all pereomeres distinct or with median regions of some fused; head ovate, not bilobed; frontal lamina large. Eyes present or absent. Antennula and antenna articulated. Barbula with 2 digitate lobes on each side.

Maxilliped with articulated or non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate or smooth. Coxal plates present, larger on one side of pereon. Dorsolateral bosses present. 5 pairs of subequal pereopods or posterior pereopods larger or smaller than anterior pairs. Pleon of 5 or 6 segments, not distorted or distorted up to 30°. 5 pairs of tuberculate biramous pleopods; 5 pairs of smooth or tuberculate lateral plates or lateral plates absent; uropods uniramous or biramous, smooth or tuberculate. **Male** pereomeres subequal in width or with 3–5 broader, head wider than long. Eyes present or absent. Antennula and antenna articulated. Midventral tubercles present or absent. 7 pairs of subequal pereopods or anterior pairs larger or posterior pairs larger. Pleomeres fused into single segment, sometimes with traces of segmentation, pleopods and uropods present or absent.

### Key to females of genera of Orbioninae

- |    |  |                           |
|----|--|---------------------------|
| 1. | 5 pleomeres .....  | 2                         |
| –  | 6 pleomeres .....  | 3                         |
| 2. | Pleomeres 2–4 with rudimentary lateral plates; pereomeres medially fused (fig. 6.16a, b) .....                     | <i>Anisorbione</i>        |
| –  | All pleomeres with well-developed lateral plates; pereomeres distinct (fig. 6.16c, d) .....                        | <i>Epipenaeon</i>         |
| 3. | Body asymmetrical .....  | 4                         |
| –  | Body symmetrical .....   | 5                         |
| 4. | Uropods uniramous (fig. 6.16e) .....   | <i>Asymmetrorbione</i>    |
| –  | Uropods biramous (fig. 6.16f, g) .....   | <i>Parasymmetrorbione</i> |
| 5. | Coxal plates and lateral plates reduced; short side of body with coxal plates only on pereomere 1 (fig. 6.16h) ... | <i>Minicopenaeon</i>      |
| –  | Coxal plates and lateral plates well developed; short side of body without coxal plates on pereomere .....         | 6                         |
| 6. | Body ovate; pleomere 6 with lateral plates (fig. 6.16i, j) .....   | <i>Orbione</i>            |
| –  | Body oblong; pleomere 6 without lateral plates .....   | 7                         |
| 7. | All pereomeres of both sides with subequal coxal plates (fig. 6.16k, l) .....                                      | <i>Parapenaeonella</i>    |
| –  | Only first two pereomeres with subequal coxal plates .....   | 8                         |
| 8. | Lateral plates of pleomeres well developed, lamellar, margins serrated (fig. 6.16m, n) .....                       | <i>Aparapenaeon</i>       |
| –  | Lateral plates of pleomeres reduced to narrow strips, margins not serrated (fig. 6.16o, p).....                    | <i>Parapenaeon</i>        |

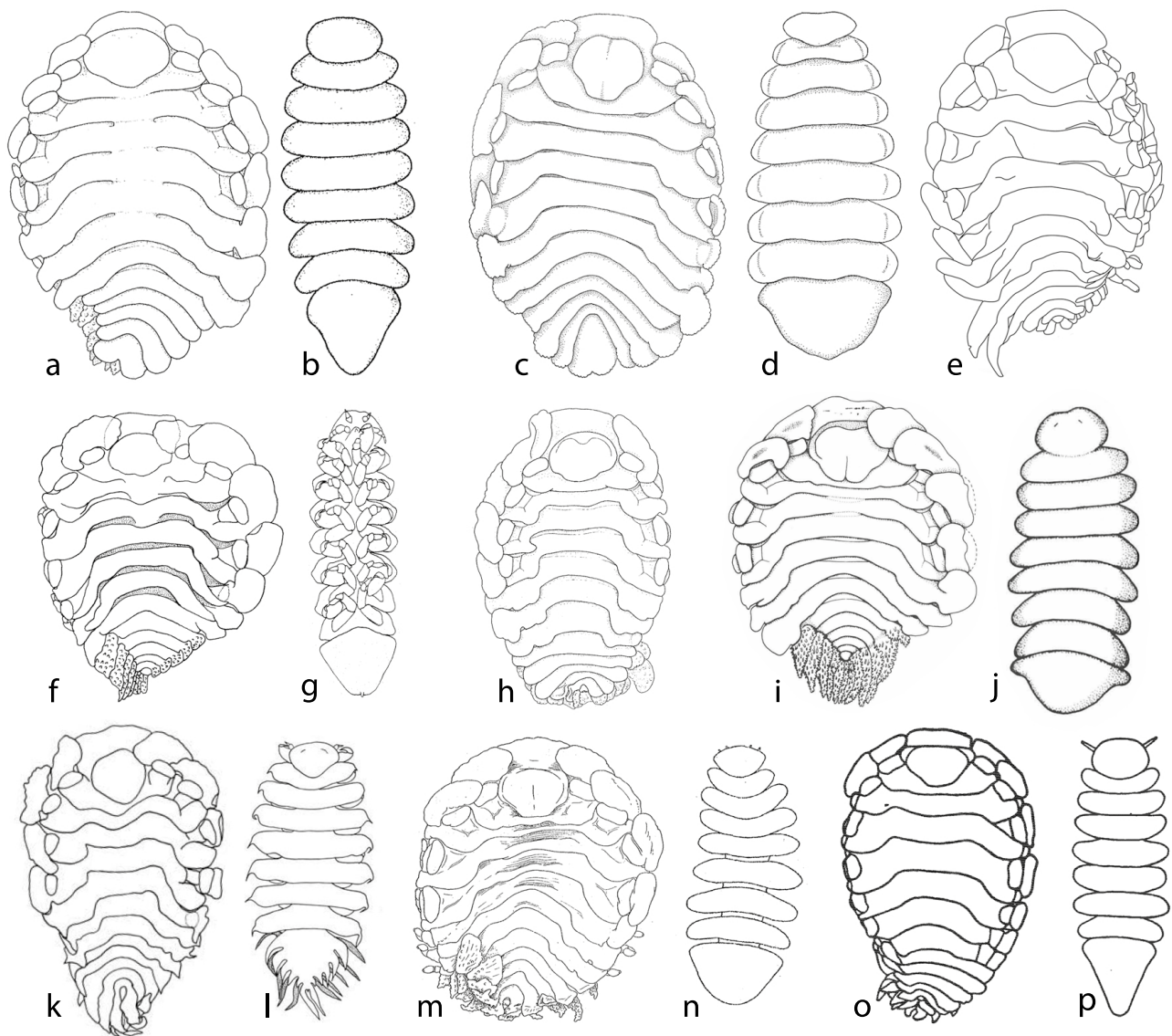


Figure 6.16. Orbioninae. *Anisorbione curva* Bourdon, 1981: a, female dorsal view; b, male dorsal view. *Epipenaeon ingens* Nobili, 1906: c, female dorsal view; d, male dorsal view. *Asymmetrorbione drepanopleon* Boyko, 2003: e, female dorsal view. *Parasymmetrorbione bicaudata* An, Boyko and Li, 2013: f, female dorsal view; g, male ventral view. *Minicopenaeon crosnieri* (Bourdon, 1979): h, female dorsal view. *Orbione digitata* Bourdon, 1982: i, female dorsal view; j, male dorsal view. *Parapenaeonella distincta* Shiino, 1949: k, female dorsal view; l, male dorsal view. *Aparapenaeon japonica* (Thielemann, 1910): m, female dorsal view; n, male dorsal view. *Parapenaeon consolidata* Richardson, 1904: o, female dorsal view; p, male dorsal view.

### *Anisorbione* Bourdon, 1981

**Diagnosis. Female** with pereomeres fused medially; head not distorted. Eyes absent. Maxilliped with non-articulated palp. Marsupium closed. Oostegite 1 internal ridge slightly digitate. 5 pairs of subequal pereopods. Pleon of 5 pleomeres, distorted 30°. Lateral plates absent; uropods biramous, tuberculate. **Male** with pereomeres subequal in width. Eyes absent. Midventral tubercles absent. 7 pairs of subequal pereopods. Pleomeres fused into single segment, pleopods and uropods absent.

Shelf, parasitising penaeid shrimps. Central Indo-Pacific. 1 species (Bourdon, 1981).

### *Aparapenaeon* An, Yin, Chen, Boyko and Liu, 2022

**Diagnosis. Female** with all pereomeres distinct or with median regions of some fused. Eyes absent. Maxilliped with non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate. Pereomeres 1–4 with dorsolateral bosses and large coxal plates on long side of body, but only pereomeres

1 and 2 with large coxal plates on short side of body, coxal plates on pereomeres 3 and 4 small or absent. 5 pairs of pereopods, posterior pereopods larger or smaller than anterior pairs. Pleon of 6 segments, not distorted or distorted up to 30°; pleomeres 1–5 with lamellar lateral plates, margins serrated, sometimes covered with small tubercles. 5 pairs of tuberculate biramous pleopods. Uropods biramous. **Male** with pereomeres subequal in width or with 3–5 broader. Eyes absent. Midventral tubercles absent. 7 pairs of subequal pereopods or anterior pairs larger. Pleopods and uropods absent.

Shelf, parasitising penaeid shrimps. Western and Central Indo-Pacific, Temperate Northern Pacific. 4 species (An et al., 2022).

#### ***Asymmetrorbione* Boyko, 2003**

*Diagnosis.* **Female** with all pereomeres distinct; one side of pereon and pleon distinctly longer than other, head weakly distorted. Eyes present or absent. Maxilliped with non-articulated palp. Marsupium open. Oostegite 1 internal ridge smooth. 5 pairs of pereopods, posterior pairs larger. Pleon of 6 segments, not distorted. 5 pairs of smooth uniramous lateral plates, larger on longer side; uropods uniramous, smooth. **Male** with pereomeres 3–5 broadest. Eyes absent. Midventral tubercles absent. 7 pairs of subequal pereopods. Pleomeres fused into single segment, pleopods and uropods absent.

Subtidal–slope, parasitising sicyoniid shrimps, Western and Central Indo-Pacific. 2 species (Boyko, 2003).

#### ***Epipenaeon* Nobili, 1906**

*Diagnosis.* **Female** with all pereomeres distinct; head not distorted. Eyes present or absent. Maxilliped with non-articulated palp. Marsupium open. Oostegite 1 internal ridge digitate. 5 pairs of pereopods, posterior pairs larger. Pleon of 5 segments, weakly distorted. 5 pairs of smooth uniramous lateral plates, larger on one side of pleon; uropods biramous, tuberculate. **Male** with pereomeres subequal in width. Eyes present or absent. Midventral tubercles absent. 7 pairs of pereopods, posterior pairs larger. Pleomeres fused into single segment, sometimes with traces of segmentation, pleopods and uropods absent.

Shelf, parasitising penaeid shrimps. Temperate Northern Atlantic (Mediterranean, introduced), Temperate Southern Africa, Western and Central Indo-Pacific. 7 species (An et al., 2022).

#### ***Minicopenaeon* Bourdon, 1981**

*Diagnosis.* **Female** with all pereomeres distinct; head not distorted. Eyes absent. Maxilliped with non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate. 5 pairs of pereopods, posterior pairs smaller. Pleon of 6 segments, not distorted. 5 pairs of smooth uniramous lateral plates, larger on one side of pleon; uropods biramous, tuberculate. **Male** with pereomeres subequal in width. Eyes absent. Midventral tubercles absent. 7 pairs of subequal pereopods. Pleomeres fused into single segment, sometimes with traces of segmentation, pleopods and uropods absent.

Shelf–slope, parasitising penaeid shrimps. Western and Central Indo-Pacific. 4 species (An et al., 2013b).

#### ***Orbione* Bonnier, 1900**

*Diagnosis.* **Female** with all pereomeres distinct; head not distorted. Eyes absent. Maxilliped with non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate. 5 pairs of pereopods, posterior pairs larger. Pleon of 6 segments, not distorted. 5 pairs of tuberculate uniramous lateral plates; uropods uniramous, tuberculate. **Male** with pereomeres subequal in width. Eyes present. Midventral tubercles absent. 7 pairs of pereopods, posterior pairs larger. Pleomeres fused into single segment, sometimes with traces of segmentation, pleopods and uropods absent.

Shelf, parasitising aristeid, penaeid and solenocerid shrimps. Western and Central Indo-Pacific, Temperate Northern Pacific. 8 species (Boyko et al., 2025).

#### ***Parapenaeon* Richardson, 1904**

*Diagnosis.* **Female** body with all pereomeres distinct; head not distorted. Eyes absent. Maxilliped with non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate. Pereomeres 1–4 with dorsolateral bosses and large coxal plates on long side of body, pereomeres 1 and 2 with large coxal plates on short side of body. 5 pairs of pereopods, posterior pairs larger. Pleon of 6 segments, not distorted or weakly distorted. 5 pairs of smooth uniramous lateral plates, larger on one side of pleon; uropods biramous, tuberculate. **Male** with pereomeres subequal in width. Eyes present or absent. Midventral tubercles absent. 7 pairs of pereopods, anterior pairs larger. Pleomeres fused into single segment, sometimes with traces of segmentation, pleopods and uropods absent.

Shelf, parasitising penaeid shrimps. Western and Central Indo-Pacific, Temperate Northern Pacific. 6 species (An et al., 2022).

#### ***Parapenaeonella* Shiino, 1949**

*Diagnosis.* **Female** body with all pereomeres distinct; head not distorted. Eyes absent. Maxilliped with non-articulated palp. Marsupium open or closed. Oostegite 1 internal ridge digitate. 5 pairs of pereopods, posterior pairs larger. Pleon of 6 segments, not distorted. 5 pairs of tuberculate or smooth uniramous lateral plates; uropods uniramous, tuberculate. **Male** with pereomeres subequal in width. Eyes present. Midventral tubercles present or absent. 7 pairs of subequal pereopods. Pleomeres fused into single segment with lateral indications of segments, broad anteriorly, tapering distally, pleopods and uropods uniramous.

Shelf–slope, parasitising penaeid shrimps. Western and Central Indo-Pacific, Temperate Northern Pacific. 6 species (An et al., 2022).

#### ***Parasymmetrorbione* An, Boyko and Li, 2013**

*Diagnosis.* **Female** body with all pereomeres distinct except 1 and 2; one side of pereon and pleon distinctly longer than other; head weakly distorted. Eyes absent. Maxilliped with articulated

palp. Marsupium open. Oostegite 1 internal ridge digitate. 5 pairs of pereopods, posterior pairs larger. Pleon of 6 segments, not distorted. 5 pairs of tuberculate uniramous lateral plates, larger on longer side; uropods biramous, tuberculate. **Male** with pereomeres subequal in width. Eyes absent. Midventral tubercles absent. 7 pairs of subequal pereopods. Pleomeres fused into single segment, pleopods and uropods absent.

Shelf, parasitising solenoceraid shrimps. Central Indo-Pacific. 1 species (An et al., 2013a).

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## Subfamily Phyllozurinae Markham, 1977

Figure 6.17

The sole genus and species in Phyllozurinae is an ectoparasite on the abdomens of upogebiids. It can be distinguished from other epicarideans in that the females have a linear, non-distorted body, smooth (outer) and tuberculate (inner) barbula lobes, ischia of posterior pairs of pereopods extremely elongate, first pleomere bearing papillose processes, and a triangular pleon bearing 5 pairs of uniramous falcate lateral plates and pleopods. Males have the posterior 5 pleomeres with posterolaterally extended tapered lateral lobes and 5 pairs of uniramous sac-like pleopods.

*Phyllozurus abdominalis* Stimpson, 1857 is known with certainty only from the Pacific coast of North America, from southern British Columbia to Baja California (Markham, 1977, 2005). There are reports of a “*Phyllozurus* sp.” from Japan (e.g. Itani, 2004) and another is known from southeastern Australia but these specimens have neither been described nor illustrated, their identity is unclear, and the genus is at present monotypic.

**Diagnosis. Female** (fig. 6.17a, b) body subtriangular; pereomeres distinct; head longer than wide, triangular, not bilobed, not distorted. Frontal lamina present. Eyes absent. Barbula with 1 smooth tapered outer lobe and 1 tuberculate tapered inner lobe on each side. Antennula and antenna articulated. Maxilliped without articulated palp. Marsupium closed. 5 pairs of oostegites; oostegite 1 with extended triangular posterior lobe; internal ridge smooth. Coxal plates present. Dorsolateral bosses present. Middorsal projections absent. 7 pairs of pereopods,

dactyli and propodi subequal in size, ischia progressively longer in posterior pairs. Pleon of 6 segments, triangular, narrower than pereon; pleomere 1 with dorsal papillose process on each side of anterior margin; 5 pairs of uniramous smooth falcate lateral plates. 5 pairs of uniramous smooth pleopods as elongate, falcate lobes. Uropods uniramous, smooth, falcate on sharply pointed pleotelson. **Male** (fig. 6.17c) pereomeres subequal in width, head wider than long. Eyes present. Antennula and antenna articulated. Midventral tubercles absent. 6 pairs of pereopods, dactyli and propodi subequal. Pleon of 6 pleomeres, posterior 5 with posterolaterally extended tapered lateral lobes, 5 pairs of uniramous sac-like pleopods, uropods absent. Abdominal parasites.

### *Phyllozurus* Stimpson, 1857

**Diagnosis.** As for family.

Intertidal, parasitising upogebiid shrimps. Temperate Northern Pacific. 1 species (Markham, 1977).

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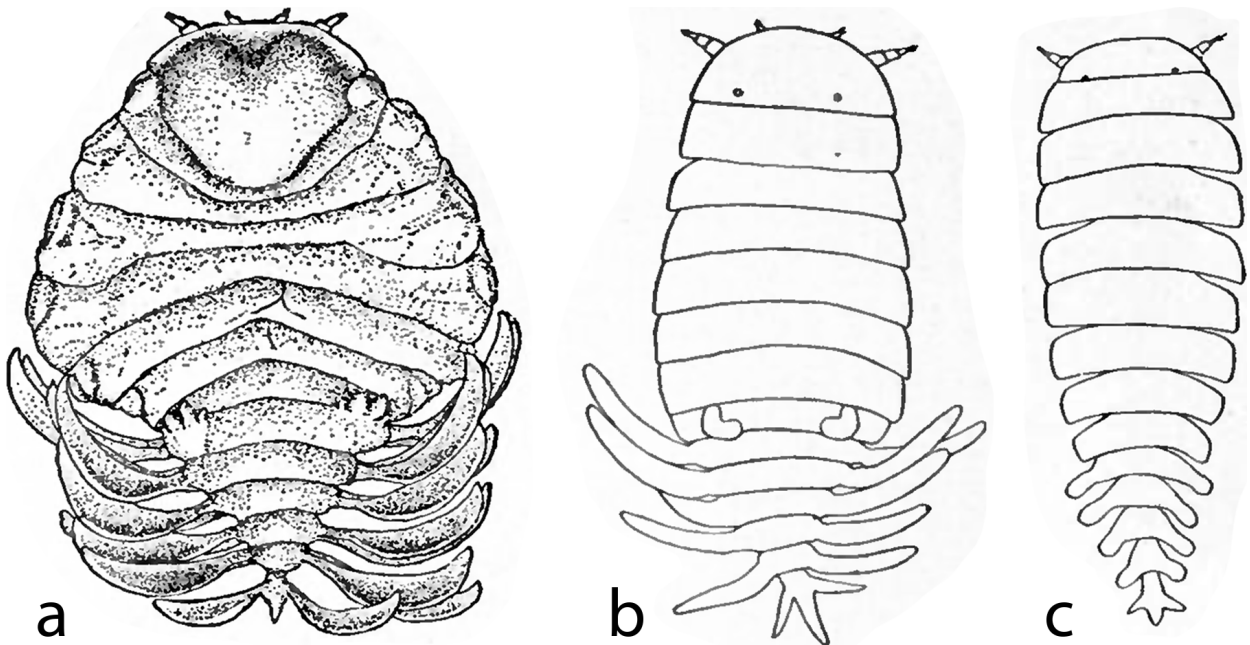


Fig. 6.17. Phyllodurinae. *Phyllodurus abdominalis* Stimpson, 1857: a, female dorsal view. b, juvenile female dorsal view. c, male dorsal view.

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### Subfamily Pleurocryptellinae Williams and Boyko in Williams, Boyko and Stewart, 2024

#### Figure 6.18

Members of Pleurocryptellinae are branchial ectoparasites of chirostyliid, munidid, and munidopsid squat lobsters. The genera in Pleurocryptellinae can be distinguished from all other bopyrid genera in that the epicaridium larvae have teardrop-shaped bodies with a large yolk sac extending between the uropods. Females of species in *Pleurocryptella* and *Pagurocryptella* have 7 pairs of oostegites; the only other genera that contain species with this character are *Septembopyrina* An, Boyko and Li, 2015 and *Bopyrinella* Nierstrasz and Brender à Brandis, 1925 (Bopyrinae); females of species in *Paragigantione*, *Parapleurocryptella*, and *Pleurocryptina* have the typical 5 pairs of oostegites. Males of all species in Pleurocryptellinae have segmented maxillipeds and those in *Pleurocryptella*, *Paragigantione* and *Pleurocryptina* have articulated uropods.

**Diagnosis. Female** body elongate or ovate, weakly distorted to distorted; head bilobed or not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose articulated and segmented palp, setose non-articulated palp, or without palp. Barbula with 1 or 2 long smooth lobes or 1 long lobe and 1 small nub on each side or 1 short smooth lobe on each side, median

region smooth. 5 or 7 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller, subequal to or larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections present or absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower or not narrower than pereon. Lateral plates absent or reduced; 4 or 5 pairs of smooth biramous pleopods or 4 pairs of smooth biramous pleopods and 1 pair of smooth uniramous pleopods or 3 pairs of biramous and 2 pairs of smooth uniramous pleopods, pleopods of 1 or 2 segments; uropods uniramous, smooth, distally bilobed or entire. **Male** approximately 2–4 times as long as wide, head narrower or as wide as pereon, pereomeres narrower or not narrower posteriorly. Eyes present or absent. Maxillipeds segmented, distally setose (in some species the maxilliped segmentation may be indistinct). Pereopods 1 and 2 larger than other pairs or all pereopods subequal. Midventral tubercles present or absent. Pleon of 6 pleomeres; 5 pairs of pleopods; posterolateral corners of pleomere 6 rounded or indented; uropods present, articulated or non-articulated. **Epicaridium larva** body teardrop shape with large yolk sac, extending between uropods.

**Key to females of genera of Pleurocryptellinae**

- |    |  |                            |
|----|--|----------------------------|
| 1. | 7 pairs of oostegites .....                            | 2                          |
| –  | 5 pairs of oostegites .....                            | 3                          |
| 2. | 5 pairs of biramous pleopods (fig. 6.18j–o) .....      | <i>Pleurocryptella</i>     |
| –  | 3 or 4 pairs of biramous pleopods (fig. 6.18p–s) ..... | <i>Pagurocryptella</i>     |
| 3. | Uropods distally bilobed (fig. 6.18a–i) .....          | <i>Paragigantione</i>      |
| –  | Uropods not distally bilobed .....                     | 4                          |
| 4. | 5 pairs of biramous pleopods (fig. 6.18t, u) .....     | <i>Parapleurocryptella</i> |
| –  | 4 pairs of biramous pleopods (fig. 6.18v) .....        | <i>Pleurocryptina</i>      |

***Pagurocryptella* Boyko and Williams, 2010**

**Diagnosis. Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp or with setose non-articulated palp. Barbula with 1 long smooth lobe and 1 small nub on each side, median region smooth. 7 pairs of oostegites; oostegite 1 with ovate posterior lobe, larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 4 pairs of smooth biramous pleopods or 3 pairs of biramous and 2 pairs of uniramous smooth pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleon of 5 or 6 pleomeres; pleopods, posterolateral corners of pleomere 6 and uropods unknown.

Shelf–bathyal, parasitising pagurid and parapagurid hermit crabs. Temperate Northern Atlantic, Central Indo-Pacific. 2 species (Boyko and Williams, 2010; Kato et al., 2018; Kokasko et al., 2025).

***Paragigantione* Barnard, 1920**

**Diagnosis. Female** ovate-elongate, body weakly distorted to distorted; head not bilobed. Maxilliped without palp. Barbula with 1 long smooth lobe on each side. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, larger than anterior lobe. Lateral plates reduced; 5 pairs of smooth biramous pleopods; uropods uniramous, distally bilobed. **Male** approximately 2–3 times as long as wide, head narrower than pereon. Pereopods subequal. Posterolateral corners of pleomere 6 rounded.

Slope, parasitising munidid squat lobsters. Temperate Northern Atlantic, Tropical Atlantic, Temperate Southern Africa, Central Indo-Pacific, Temperate Australasia. 5 species (Bourdon, 1981; Boyko et al., 2024).

***Parapleurocryptella* Bourdon, 1972**

**Diagnosis. Female** ovate or elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated and segmented palp. Barbula with 1 short smooth lobe on each side, median region smooth.

5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller or larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower or not narrower than pereon. Lateral plates absent; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Maxilliped segmented. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods present.

Slope, parasitising chirostyliid and munidopsid squat lobsters. Tropical Atlantic, Central Indo-Pacific, Temperate Australasia. 3 species (Bourdon, 1972; Kokasko et al., 2025).

***Pleurocryptella* Bonnier, 1900**

**Diagnosis. Female** elongate or ovate, body weakly distorted; head bilobed or not bilobed. Maxilliped with setose articulated and segmented palp. Barbula with 2 long smooth lobes or 1 long lobe and 1 small nub on each side. 7 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller or subequal to anterior lobe. Lateral plates absent or reduced; 5 pairs of smooth biramous pleopods or 4 pairs of smooth biramous pleopods and 1 pair of smooth uniramous pleopods, pleopods of 1 or 2 segments; uropods uniramous, smooth, distally not bilobed. **Male** approximately 3–4 times as long as wide, head as wide as pereon. Pereopods 1 and 2 larger than other pairs. Posterolateral corners of pleomere 6 rounded or indented.

Shelf–abyssal, parasitising chirostyliid, munidid, and munidopsid squat lobsters. Temperate Northern Atlantic, Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific, Tropical Eastern Pacific. 11 species and 1 subspecies (Williams et al., 2020, 2024).

***Pleurocryptina* Nierstrasz and Brender à Brandis, 1929**

**Diagnosis. Female** ovate, body weakly distorted; head bilobed; frontal lamina present. Eyes present. Maxilliped with setose non-articulated palp. Barbula with 1 long smooth lobe and 1 nub on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, larger than anterior lobe;

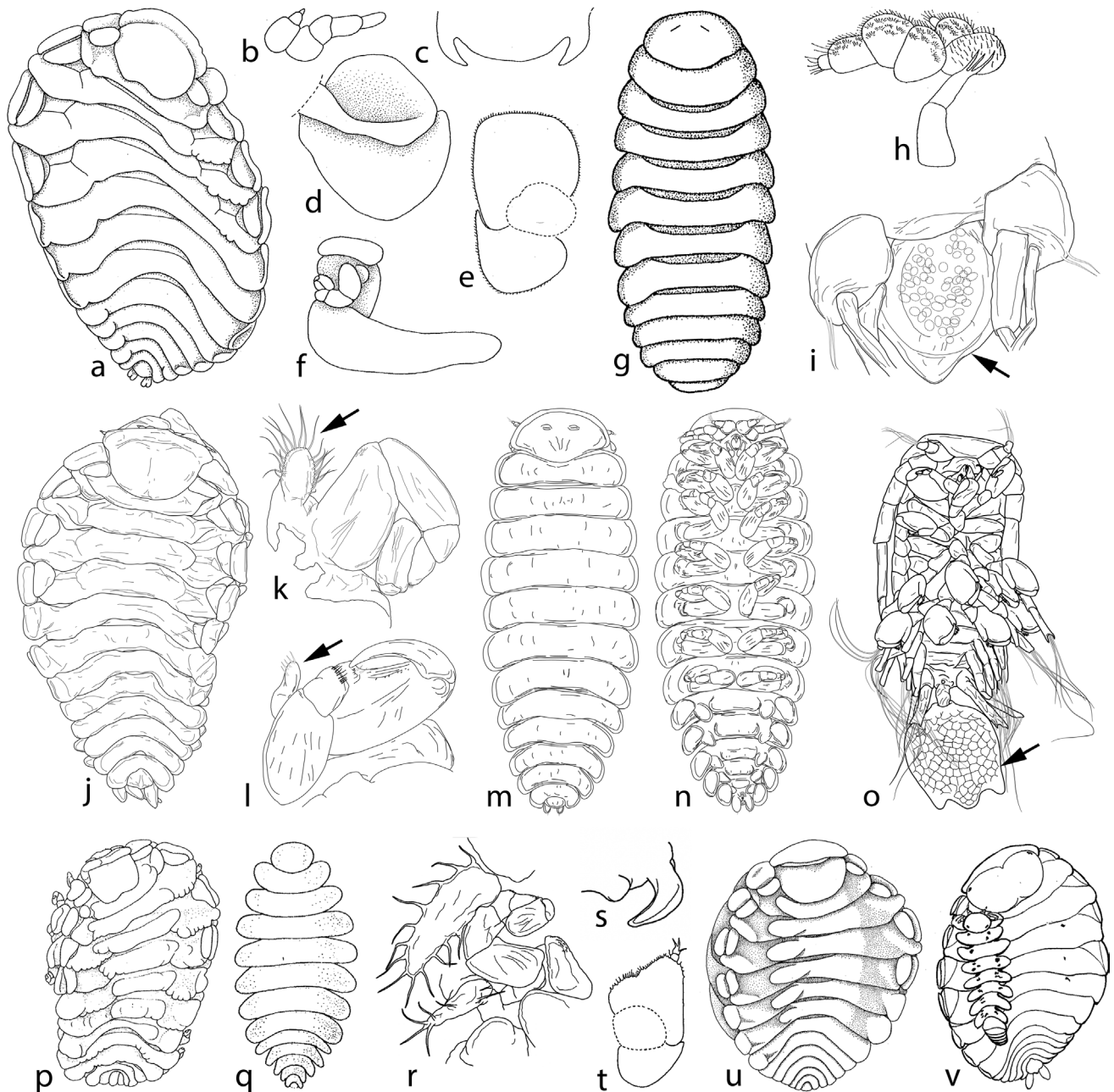


Fig. 6.18. Pleurocryptellinae. *Paragigantione europaea* Boyko et al., 2024: a, female dorsal view; b, female left antennae; c, female barbula; d, female left oostegite 1, inner view; e, female left maxilliped; f, female right oostegite 5 and pereopod 5; g, male dorsal view; h, male right antenna, antennula and maxilliped. *Paragigantione americana* (Markham, 1974): i, epicaridium larvae, ventral view of uropods and yolk sac (arrow). *Pleurocryptella poseidon* Williams and Boyko in Williams, Boyko and Stewart, 2024: j, female dorsal view; k, female left pereopod 7 with oostegite (arrow); l, female left pereopod 1 and maxilliped (arrow); m, male dorsal view; n, male ventral view; o, epicaridium larva with yolk sac (arrow). *Pagurocryptella paguri* (Bourdon, 1979): p, female dorsal view; q, male dorsal view. *Pagurocryptella holthuisi* Boyko and Williams, 2010: r, left pereopod 7 and oostegites 6 and 7; s, left side of barbula. *Parapleurocryptella minuta* Bourdon, 1972: t, female maxilliped; u, female dorsal view. *Pleurocryptina indica* Nierstrasz and Brender à Brandis, 1929: v, female dorsal view, with male attached.

internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates small; 4 pairs of smooth biramous pleopods and 1 pair of smooth uniramous pleopods; uropods uniramous, smooth. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Segmented maxillipeds present. Pereopods 1 and 2 larger than other pairs. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of pleopods; posterolateral corners of pleomere 6 rounded; uropods present.

Shelf, parasitising galatheid squat lobsters. Central Indo-Pacific. 1 species (Bourdon and Stock, 1979; Kokasko et al., 2025).

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## Subfamily Pseudioninae Codreanu, 1967

Figures 6.19–6.22

Pseudioninae was considered the ancestral taxon within Bopyridae (Markham, 1986; Shiino, 1965) but that was based on the inclusion of *Pleurocryptella* in the subfamily; that genus is now placed in Pleurocryptellinae. As can be seen from the diagnosis below, nearly every character is variable within Pseudioninae and no synapomorphies can be identified. Species in Pseudioninae are also found parasitising the widest range of definitive hosts of any epicaridean group, being found as ectoparasites on species in Achelata, Anomura, Astacidea, Axiiidea, Brachyura, Caridea and Gebiidea. The subfamily and several included genera are doubtfully monophyletic and in need of revision. Boyko et al. (2017) defined *Pseudione sensu stricto* to contain only eight species (with one subsequently described), and the diagnosis below reflects this, as well as the recent removal of 13 species to the genus *Cryptione* Hansen, 1897. The remaining species parasitising galatheoids and unknown hosts are considered *Pseudione sensu lato* and are also in need of revision; they will not key out to *Pseudione*.

**Diagnosis. Female** body ovate to elongate, not distorted to highly distorted (c. 120°); head bilobed or not bilobed; frontal

lamina present or absent, expanded or not expanded laterally. Eyes present or absent. Maxilliped with setose or non-setose, articulated or non-articulated, segmented or non-segmented palp or palp absent. Barbula with 1–4 long or short smooth, digitate or tuberculate lobes on each side or without lobes, median region smooth or digitate. Oostegite 1 with triangular, oblong, ovate or subquadrate posterior lobe or ovate posterior lobe bearing triangular, recurved or finger-like distal projection, larger, subequal or smaller than anterior lobe; internal ridge smooth or digitate. Coxal plates, dorsolateral bosses and tergal projections present or absent. Mediodorsal lobes present or absent. Pereopods elongate or not elongate, with or without propodal sockets. Pleon abruptly narrower or not narrower than pereon. Lateral plates slender, tubular or broad, large or reduced, or absent; 3–5 pairs of smooth or tuberculate uniramous or biramous pleopods, 1 or 2-segmented, with smooth or crenulate margins; uropods smooth or tuberculate, uniramous, biramous, or uniramous and bifid distally, smooth or crenulate margins, or absent. **Male** approximately 1–5 times as long as wide, head narrower than pereon or as wide as pereon, pereomeres narrower or not narrower posteriorly. Eyes present or absent. Segmented

maxillipeds present or absent. Pereopods subequal or some pairs larger. Midventral tubercles present or absent. Pleon of 1–6 pleomeres; lateral plates present or absent; 3–5 pairs of uniramous or biramous pleopods or pleopods absent; posterolateral corners of pleomere 6 rounded or extended; uropods articulated, rounded or bifid, or absent.

### Key to genera of the subfamily Pseudioninae

(Based on female and male characters; modified from Williams et al., 2019.)

1.	Abdominal parasites .....	2
–	Branchial parasites .....	4
2.	Under folded abdomen of pinnotherid or cryptochirid hosts, pleopods biramous .....	3
–	Under abdomen of caridean shrimps, pleopods uniramous (fig. 6.19a) .....	<i>Pleonobopyrus</i>
3.	Head of female rounded, oostegite 1 with sharp point on posterior margin, coxal plates well developed, pereopods isomorphic, uropods posteriorly extended and foliaceous (fig. 6.19b, c) .....	<i>Rhopalione</i>
–	Head of female subquadrate, oostegite 1 with rounded posterior margin, coxal plates small, pereopod 1 approximately half as large as pereopod 7, uropods short, rounded lateral lobes (fig. 6.19d, e) .....	<i>Spathione</i>
4.	Body of female fully enclosed within branchial chamber of host .....	5
–	Body of female partly within branchial chamber and extending onto abdomen of host (fig. 6.19f, g) .....	<i>Bopyrophryxus</i>
5.	Females parasitising hermit crabs or king crabs .....	6
–	Females parasitising other hosts .....	14
6.	Females greatly distorted, typically 90° or more and/or with propodal sockets on pereopods .....	7
–	Females less distorted (generally <70°) or nearly symmetrical, lacking propodal sockets on pereopods .....	8
7.	Females with propodal sockets on pereopods (fig. 6.19h, i) .....	<i>Asymmetrione</i>
–	Females without propodal sockets on pereopods, body strongly distorted (fig. 6.19j) .....	<i>Parasymmetrione</i>
8.	Females with biramous uropods .....	9
–	Females with uniramous uropods or uropods absent .....	10
9.	Females with 6 pairs of pleonal lateral plates (fig. 6.19k) .....	<i>Pagurion</i>
–	Females with 5 pairs of pleonal lateral plates (fig. 6.19l) .....	<i>Parapagurion</i>
10.	Females with pleomere 6 ventrally displaced, not visible in dorsal view .....	11
–	Females with pleomere 6 not ventrally displaced, visible in dorsal view .....	12
11.	Males with uniramous pleopods (fig. 6.19m, n) .....	<i>Bopyrissa</i>
–	Males with biramous pleopods (fig. 6.19o) .....	<i>Propseudione</i>
12.	Females with 5 pairs of biramous pleopods .....	13
–	Females with some pleopods uniramous (fig. 6.19p, q) .....	<i>Pseudionella</i>
13.	Males with uniramous pleopods (fig. 6.20a) .....	<i>Eremitione</i>
–	Males without pleopods (fig. 6.20b, c) .....	<i>Paguristione</i>
14.	Females with long, extended, blunt ended anterolateral projections on head, coxal plates completely covering both sides of each pereomere, parasitising sand crabs (Hippoidea) (fig. 6.20d, e) .....	<i>Albunione</i>
–	Females lacking anterolateral projections on head .....	15
15.	Females parasitising caridean shrimps .....	16
–	Females parasitising other hosts .....	20

16.	Females with 5 pleomeres (fig. 6.20f) .....	<i>Nikione</i>
–	Females with 6 pleomeres .....	17
17.	Females with 5 pairs of uniramous pleopods (fig. 6.20g) .....	<i>Pontobopyrus</i>
–	Females with some pleopods biramous .....	18
18.	Females with 5 pairs of biramous pleopods .....	19
–	Females with pleopods 1 and 2 biramous, others uniramous (fig. 6.20h) .....	<i>Shiinoella</i>
19.	Uropods biramous (fig. 6.20i) .....	<i>Paranikione</i>
–	Uropods uniramous (fig. 6.20j) .....	<i>Cryptione</i>
20.	Females parasitising axiideans, gebiideans, or brachyurans .....	21
–	Females parasitising other hosts .....	34
21.	Pleon of female highly compressed, parasitising axiideans (fig. 6.20k) .....	<i>Ionella</i>
–	Pleon of female elongate .....	22
22.	Females with lateral plates .....	23
–	Females without lateral plates .....	31
23.	Females with distinct constrictions along length of lateral plates and pleopods, parasitising axiideans and gebiideans (fig. 6.20l) .....	<i>Acrobelione</i>
–	Females without distinct constrictions along length of lateral plates and pleopods (may have crenulate edges and tubercles) .....	24
24.	Pleomeres of male widely separate, distolateral margins extended, parasitising axiideans (fig. 6.20m, n) .....	<i>Robinione</i>
–	Pleomeres of male not widely separate, distolateral margins not extended .....	25
25.	Females with small coxal plates on pereomeres 1–4 .....	26
–	Females with elongate, sickle-shaped coxal plates on pereomeres 1–4, parasitising axiideans and brachyurans (fig. 6.20o) .....	<i>Gigantione</i>
26.	Females parasitising brachyurans (fig. 6.20p) .....	<i>Carcinione</i>
–	Females parasitising other hosts .....	27
27.	Males with articulated uropods .....	28
–	Males without articulated uropods .....	29
28.	Maxilliped with palp, oostegite 1 internal ridge margin and barbula digitate, parasitising axiideans and gebiideans (fig. 6.20q) .....	<i>Progebiophilus</i>
–	Maxilliped without palp, oostegite 1 internal ridge margin and barbula smooth, parasitising gebiideans (fig. 6.20r) .....	<i>Orthione</i>
29.	Body of male with pleon wider than pereon, parasitising gebiideans (fig. 6.20s, t) .....	<i>Upogebione</i>
–	Body of male with pleon narrower than pereon .....	30
30.	Females with irregular protuberances on dorsolateral margins of pleomeres 1–6 (fig. 6.20u), parasitising axiideans .....	<i>Zeaione</i>
–	Females without irregular protuberances, parasitising axiideans and astacideans (fig. 6.20v) .....	<i>Pseudione sensu stricto</i>
31.	Females with elongate pleopods and uropods, visible in dorsal view .....	32
–	Females with short elongate pleopods and uropods, not visible in dorsal view .....	33
32.	Females with posterior margin of head not reaching posterior margin of pereomere 1, head triangular with	

	eyespot, parasitising gebideans (fig. 6.20w) .....	<i>Aporobopyroides</i>
–	Females with posterior margin of head reaching posterior margin of pereomere 1, head subquadrate, eyespots absent, parasitising gebideans (fig. 6.21a) .....	<i>Upogebiophilus</i>
33.	Females with 6 distinct pleomeres, uropods absent, parasitising gebideans (fig. 6.21b, c) .....	<i>Gyge</i>
–	Females with fusion, fewer than 6 pleomeres, uropods present, parasitising gebideans (fig. 6.21d, e) .....	<i>Pauperella</i>
34.	Females with 5 pleomeres .....	35
–	Females with 6 pleomeres .....	38
35.	Females without uropods, parasitising porcellanids (fig. 6.21f) .....	<i>Kolourione</i>
–	Females with uniramous or biramous uropods .....	36
36.	Males with 5 pleomeres, parasitising porcellanids (fig. 6.21g, h) .....	<i>Allorbimorphus</i>
–	Males with fewer than 5 pleomeres .....	37
37.	Females with uniramous uropods, parasitising munidid squat lobsters (fig. 6.21i, j) .....	<i>Balanopleon</i>
–	Females with biramous uropods, parasitising porcellanids (fig. 6.21k) .....	<i>Orbimorphus</i>
38.	Barbula of female with 1 elongate lateral projection on each side .....	39
–	Barbula of female with 2 or more elongate lateral projections on each side .....	41
39.	Females without uropods, parasitising porcellanids (fig. 6.21l) .....	<i>Discomorphus</i>
–	Females with uropods .....	40
40.	Females with enlarged lateral plates, parasitising munidid and munidopsid squat lobsters (fig. 6.22b) .....	<i>Bathione</i>
–	Females without enlarged lateral plates, parasitising munidid squat lobsters (fig. 6.21m) .....	<i>Galathocrypta</i>
41.	Females with bilobed head .....	42
–	Females without bilobed head .....	43
42.	Females with oostegite 1 posterior lobe subquadrate, internal ridge smooth, pleopodal endopod and exopod slender, parasitising munidid squat lobsters (fig. 6.21n) .....	<i>Goleathopseudione</i>
–	Females with oostegite 1 posterior lobe ovate with triangular extension, internal ridge digitate, pleopodal endopod and exopod lamellar, parasitising porcellanids, eumunidid and munidid squat lobsters (fig. 6.22a) .....	<i>Parionella</i>
43.	Females with well-developed lateral plates .....	44
–	Females without well-developed lateral plates .....	46
44.	Males with midventral tubercles, parasitising porcellanids and munidid squat lobsters (fig. 6.22c, d) .....	<i>Aporobopyrina</i>
–	Males without midventral tubercles .....	45
45.	Females with well-developed uniramous or biramous uropods, parasitising porcellanids, galatheids and munidid squat lobsters (fig. 6.22e, f) .....	<i>Pleurocrypta</i>
–	Females with minute uniramous uropods or without uropods, parasitising porcellanids, galatheids and munidid squat lobsters (fig. 6.22g, h) .....	<i>Anuropodione</i>
46.	Females with biramous uropods, parasitising munidid squat lobsters (fig. 6.22i, j) .....	<i>Munidion</i>
–	Females with uniramous uropods or without uropods .....	47
47.	Females without uropods, body of males broad, squat (width >1/2 of length), parasitising munidid squat lobsters (fig. 6.22k, l) .....	<i>Ovoionella</i>
–	Females with uniramous uropods, body of males elongate (width ~1/3 of length) .....	48

48.	Females without coxal plates, parasitising porcellanids (fig. 6.22m, n) .....	<i>Astalione</i>
–	Females with coxal plates .....	49
49.	Females with small coxal plates .....	50
–	Females with well-developed coxal plates .....	51
50.	Females with small lateral plates, males with 5 pleomeres, parasitising porcellanids and munidid squat lobsters (fig. 6.22o) .....	<i>Parione</i>
–	Females with moderately developed lateral plates, pyriform body, males with 6 pleomeres, parasitising porcellanids (fig. 6.22p) .....	<i>Aporobopyrus</i>
51.	Males with pleopods, parasitising porcellanids (fig. 6.22q) .....	<i>Parioninella</i>
–	Males without pleopods, parasitising galatheids (fig. 6.22r) .....	<i>Parionina</i>

### *Acrobelione* Bourdon, 1981

**Diagnosis. Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated or non-articulated palp. Barbula with 2 long digitate lobes on each side, median region digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge digitate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present, slender; 5 pairs of crenulate biramous pleopods; uropods uniramous, crenulate. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 5 or 6 pleomeres; uniramous pleopods or pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–shelf, parasitising callianassid and upogebiid shrimps. Temperate North Atlantic, Tropical Atlantic, Central Indo-Pacific. 4 species (Boyko et al., 2017).

### *Albunione* Markham and Boyko, 1999

**Diagnosis. Female** elongate, body not distorted; head not bilobed; frontal lamina present, expanded laterally into large flaps. Eyes absent. Maxilliped with setose articulated or non-articulated palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, subequal to or smaller than anterior lobe; internal ridge digitate. Coxal plates and tergal projections present, dorsolateral bosses absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present, slender; 5 pairs of crenulate biramous pleopods; uropods uniramous, crenulate. **Male** approximately 3–4 times as long as wide, head as wide as pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present or absent. Pleon of 6 pleomeres; lateral plates elongate; pleopods uniramous; posterolateral corners of pleomere 6 extended; uropods absent.

Shelf, parasitising albuneid sand crabs. Tropical Atlantic, Central Indo-Pacific. 3 species (Markham and Boyko, 2003).

### *Allorbimorphus* Bourdon, 1976

**Diagnosis. Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp or with setose non-articulated palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates reduced; 4 or 5 pairs of smooth biramous pleopods; uropods uniramous or biramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. First 3 pairs of pereopods larger. Midventral tubercles absent. Pleon of 3–6 pleomeres; pleopods uniramous or absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–shelf, parasitising porcellanid crabs. Western and Central Indo-Pacific, Temperate Australasia. 5 species (An et al., 2012; Bourdon, 1976).

### *Anuropodione* Bourdon, 1967

**Diagnosis. Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge digitate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods absent. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleon of 1–6 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Shelf–slope, parasitising munidid squat lobsters. Temperate Northern Atlantic, Tropical Atlantic. 5 species (Alves-Júnior et al., 2019; Boyko et al., 2018).

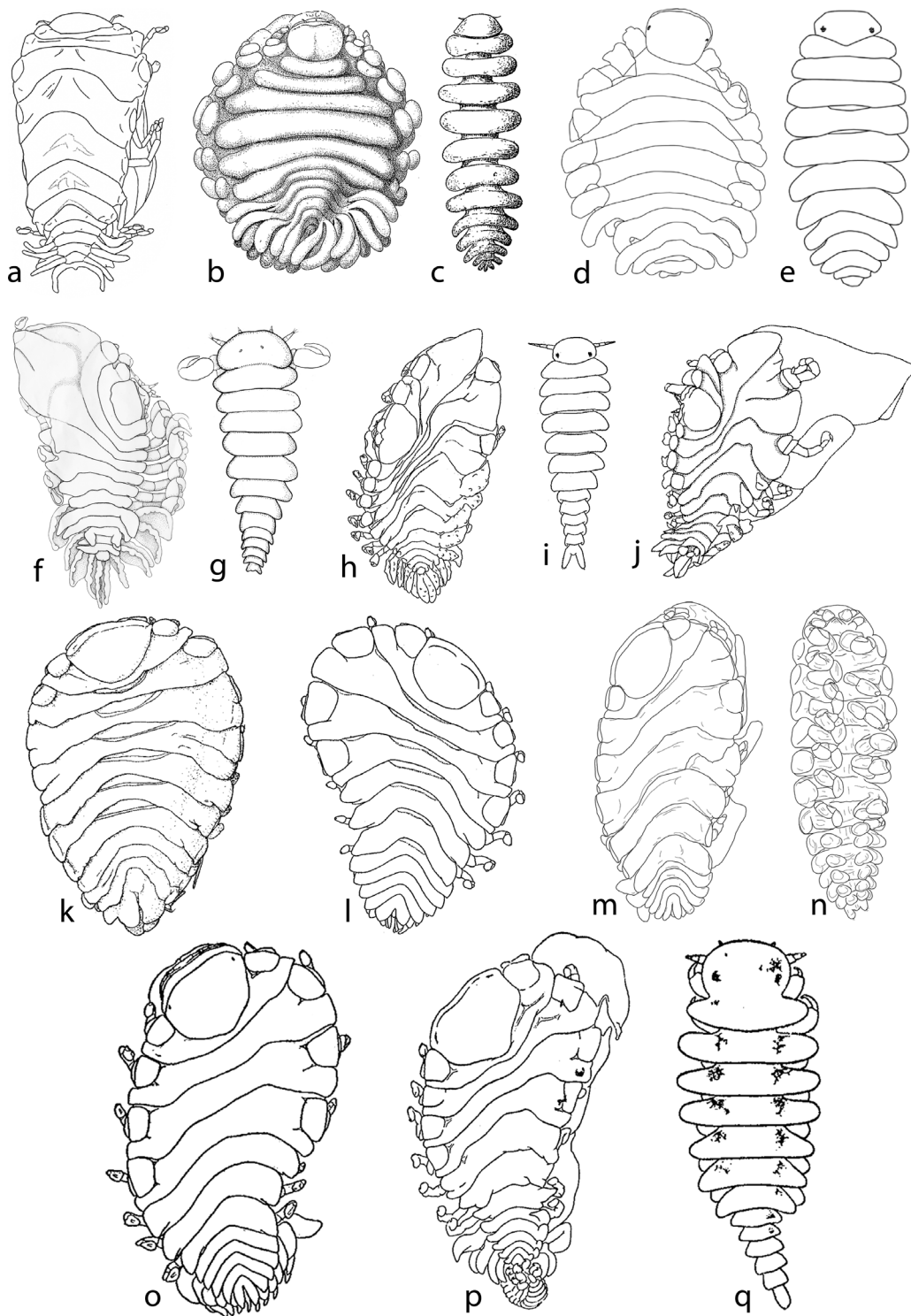


Figure 6.19. Pseudioninae. *Pleonobopyrus kumanonadensis* Saito and Moritaki, 2020: a, female dorsal view. *Rhopalione uromyzon* Pérez, 1920: b, female dorsal view; c, male dorsal view. *Spathione aprosdovrima* Boyko and van der Meij, 2018: d, female dorsal view; e, male dorsal view. *Bopyrophryxus branchiabdrominalis* Codreanu, 1965: f, female dorsal view; g, male dorsal view. *Asymmetrione asymmetrica* (Shiino, 1933): h, female dorsal view; i, male dorsal view. *Parasymmetrione tuberculineata* An, Markham and Yu, 2010: j, female dorsal view. *Pagurion tuberculata* Shiino, 1933: k, female dorsal view. *Parapagurion calcinicola* Shiino, 1933: l, female dorsal view. *Bopyrissa magellanica* Nierstrasz and Brender à Brandis, 1931: m, female dorsal view; n, male ventral view. *Propseudione rhombicosoma* Shiino, 1933: o, female dorsal view. *Pseudionella attenuata* Shiino, 1949: p, female dorsal view, with male attached to pleopods; q, male dorsal view.

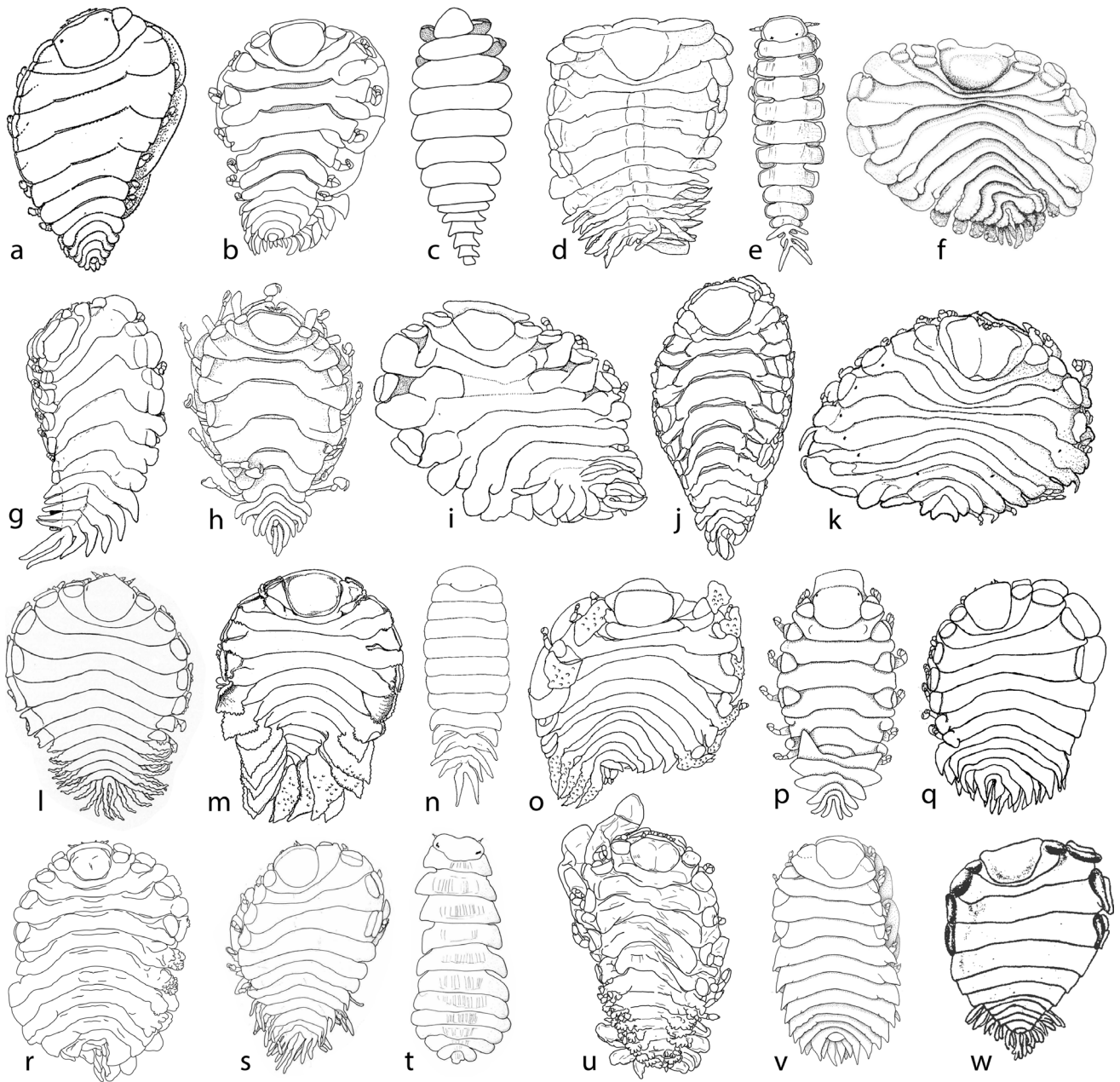


Figure 6.20. Pseudioninae. *Eremittone hyndmanni* (Bate and Westwood, 1867): a, female dorsal view. *Paguristione uniropodus* An, Zhao and Markham, 2016: b, female dorsal view; c, male dorsal view. *Alburnione indecora* (Markham, 1988): d, female dorsal view; e, male dorsal view. *Nikione natalensis* Kensley, 1974: f, female dorsal view. *Pontobopyrus abyssorum* Markham, 1979: g, female dorsal view. *Shiinoella gracilipes* Bourdon, 1972: h, female dorsal view. *Paranikione sibogae* An, Boyko and Li, 2015: i, female dorsal view. *Cryptione elongata* Hansen, 1897: j, female dorsal view. *Ionella maculata* Markham, 1994: k, female dorsal view. *Acrobelione langi* (Van Name, 1920): l, female dorsal view. *Robinione overstreerti* (Adkison and Heard, 1995): m, female dorsal view; n, male dorsal view. *Gigantione tuberculata* An, Williams and Jiang, 2016: o, female dorsal view. *Carcinione platypleura* Bourdon, 1983: p, female dorsal view. *Progebiophilus sinicus* Markham, 1982: q, female dorsal view. *Orthione griffenis* Markham, 2004: r, female dorsal view. *Upogebione phuketensis* Markham, 1985: s, female dorsal view; t, male dorsal view. *Zeaione everta* Boyko and Williams in Andrade et al., 2025: u, female dorsal view. *Pseudione callianassae* Kossmann, 1881: v, female dorsal view. *Aporobopyroides upogebiae* Nobili, 1906: w, female dorsal view.

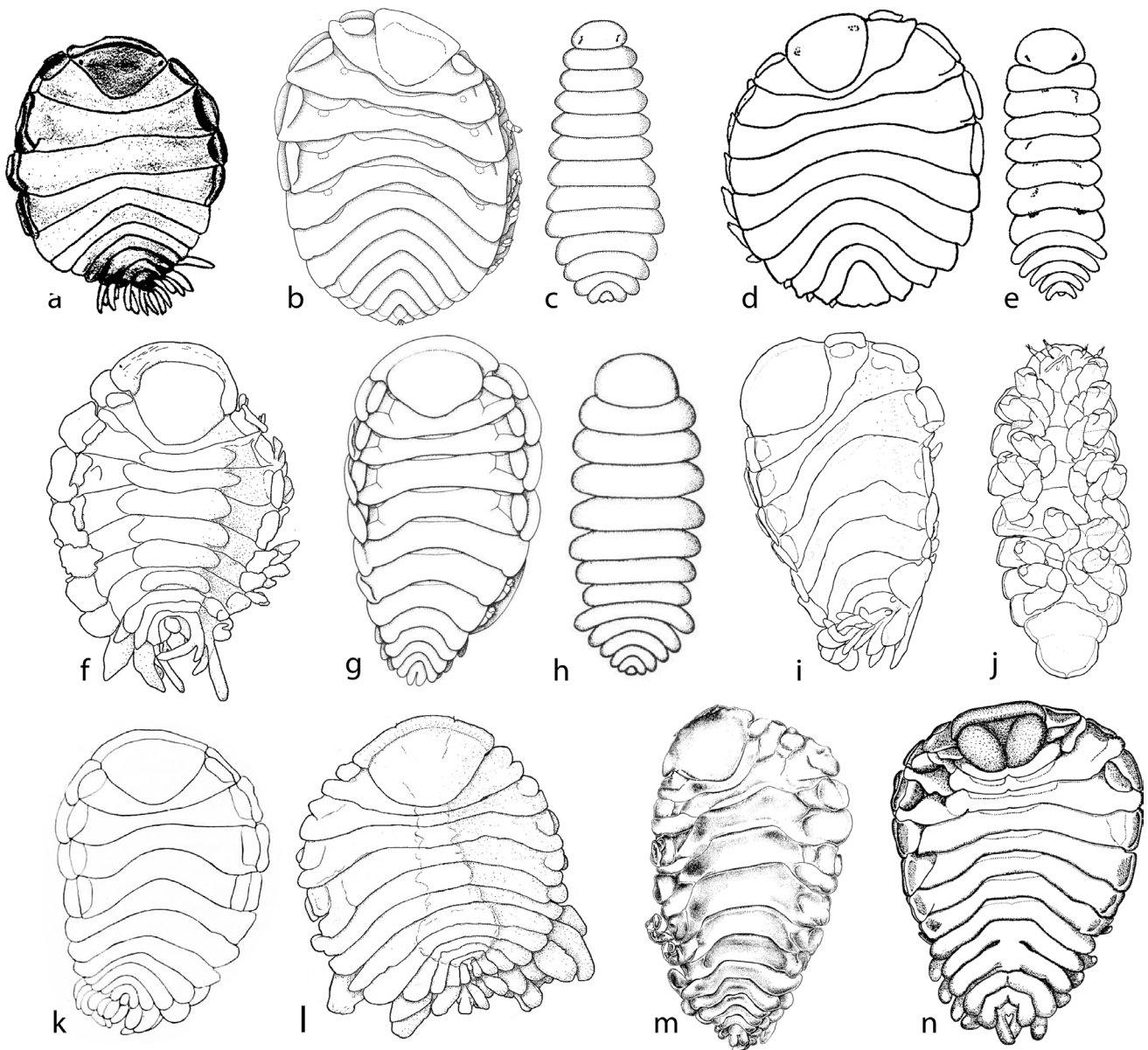


Figure 6.21. Pseudioninae. *Upogebiophilus rhadames* Nobili, 1906: a, female dorsal view. *Gyge branchialis* Cornalia and Panceri, 1861: b, female dorsal view; c, male dorsal view. *Pauperella rotunda* Nierstrasz and Brender à Brandis, 1929: d, female dorsal view; e, male dorsal view. *Kolourione premordica* Markham, 1978: f, female dorsal view. *Allorbimorphus lamellosus* (Nierstrasz and Brender à Brandis, 1923): g, female dorsal view; h, male dorsal view. *Balanopleon tortuganus* Markham, 1974: i, female dorsal view; j, male ventral view. *Orbimorphus constrictus* Richardson, 1910: k, female dorsal view. *Discomorphus magnifolius* Markham, 2008: l, female dorsal view. *Galathocrypta acaudata* Román-Contreras and Soto, 2002: m, female dorsal view. *Goleathopseudione bilobatus* Román-Contreras, 2008: n, female dorsal view.

#### *Aporobopyrina* Shiino, 1934

**Diagnosis. Female** elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose, non-articulated palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge smooth or with weak digitations. Coxal plates, dorsolateral bosses, and

tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present, small; 5 pairs of smooth biramous pleopods; uropods biramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present. Pleon of 4–6 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

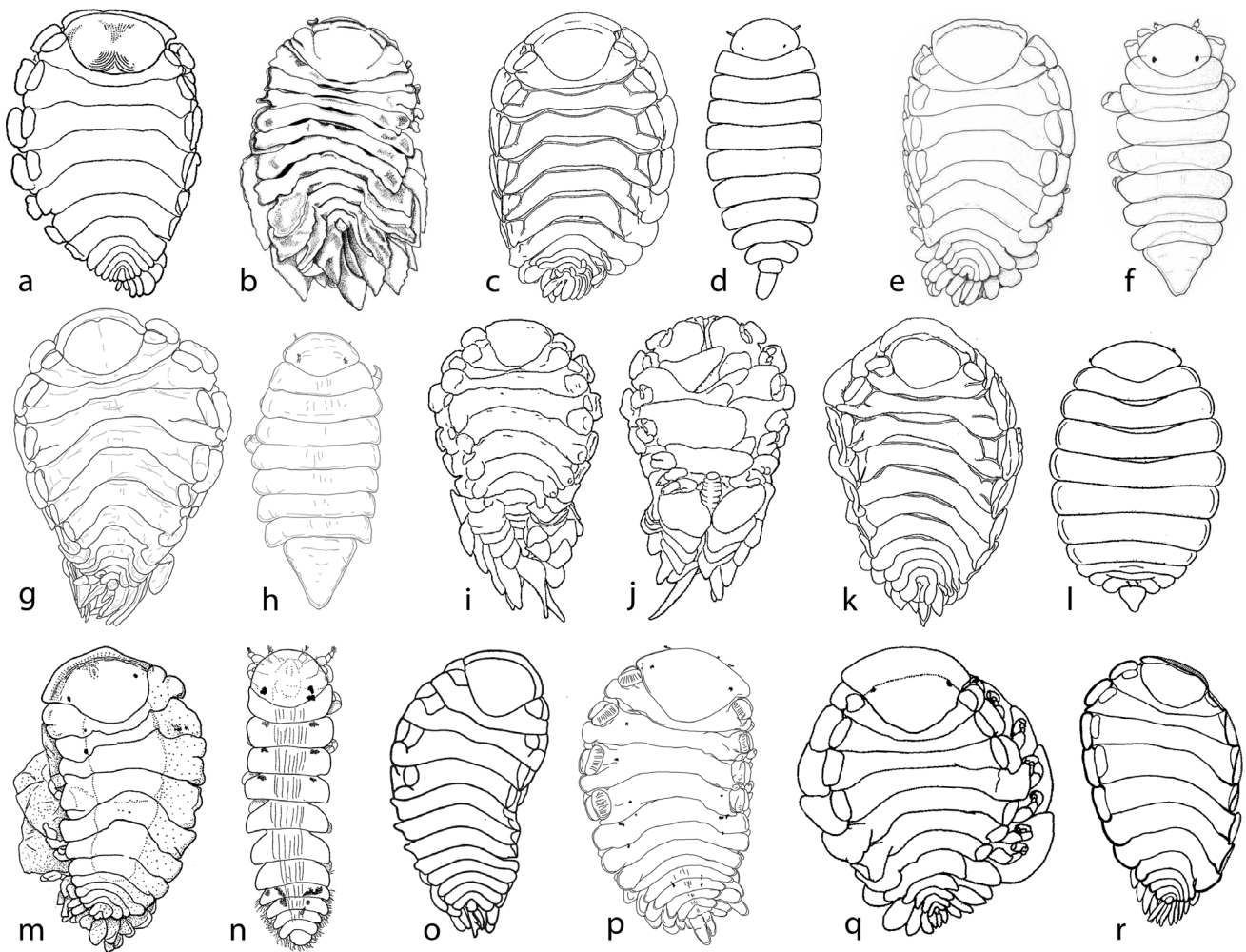


Figure 6.22. Pseudioninae. *Parionella richardsonae* Nierstrasz and Brender à Brandis, 1923: a, female dorsal view. *Bathione magnafolia* Román-Contreras and Boyko, 2007: b, female dorsal view. *Aporobopyrina lamellata* Shiino, 1934: c, female dorsal view; d, male dorsal view. *Pleurocrypta petrolisthis* Markham, 1988: e, female dorsal view; f, male dorsal view. *Anuropodione ampliandra* (Codreanu, Codreanu and Pike, 1966): g, female dorsal view; h, male dorsal view. *Munidion princeps* Hansen, 1897: i, female dorsal view; j, female ventral view, with male positioned among pleopods. *Ovoionella obovata* (Shiino, 1958): k, female dorsal view; l, male dorsal view. *Astalione cruciaria* Markham, 1975: m, female dorsal view; n, male dorsal view. *Parione paucisecta* (Richardson, 1904): o, female dorsal view. *Aporobopyrus galleonus* Williams and Madad, 2010: p, female dorsal view. *Parioninella astridae* Nierstrasz and Brender à Brandis, 1930: q, female dorsal view. *Parionina pacifica* Nierstrasz and Brender à Brandis, 1929: r, female dorsal view.

Intertidal–slope, parasitising munidid squat lobsters and porcellanid crabs. Tropical Atlantic, Western and Central Indo-Pacific. 4 species (Bourdon, 1983).

#### *Aporobopyroides* Nobili, 1906

**Diagnosis. Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-articulated palp. Barbula not described. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing recurved distal projection, smaller than anterior lobe; internal ridge smooth. Coxal plates present; dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral

plates absent; 5 pairs of biramous pleopods with crenulate margins; biramous uropods with crenulated margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 5 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising upogebiid shrimps. Temperate Northern Atlantic. 1 species (Nobili, 1906).

#### *Aporobopyrus* Nobili, 1906

**Diagnosis. Female** ovate to elongate, body weakly to moderately distorted; head not bilobed; frontal lamina present

or absent. Eyes present or absent. Maxilliped with setose non-articulating palp or without palp. Barbula with 1–3 tuberculate or smooth lobes on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 ovate with triangular distal projection posterior lobe, subequal to anterior lobe; internal ridge smooth or digitate. Coxal plates present, dorsolateral bosses present or absent, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth or tuberculate biramous pleopods with smooth or crenulate margins; uniramous uropods smooth or tuberculate with smooth or crenulate margins. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal or first 2 pairs larger. Midventral tubercles present or absent. Pleon of 5 pleomeres; 5 pairs of uniramous ovate pleopods; posterolateral corners of pleomere 6 rounded or slightly extended; uropods absent.

Intertidal–slope, parasitising porcellanid crabs and galatheid and munidid squat lobsters. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific, Tropical Eastern Pacific. 21 species (An et al., 2026; Bourdon, 1976; Williams and Madad, 2010).

#### ***Astalionae* Markham, 1975**

**Diagnosis. Female** elongate, body distorted ca. 40°; head not bilobed; frontal lamina present. Eyes present. Maxilliped without palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates absent; 5 pairs of smooth biramous pleopods with smooth margins; smooth uniramous uropods with smooth margins. **Male** approximately 3–4 times as long as wide, head as wide as pereon, pereomeres not narrower posteriorly. Eyes present. First pair of pereopods larger than others. Midventral tubercles absent. Pleon of 5 pleomeres, fringed with setae; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal, parasitising porcellanid crabs. Tropical Atlantic. 1 species (Markham, 1975a).

#### ***Asymmetrione* Codreanu, Codreanu and Pike, 1965**

**Diagnosis. Female** elongate, body not distorted to strongly distorted up to c. 90°; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped without palp. Barbula with 1 or 2 short smooth or digitate lobes on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular or fingerlike distal projection, smaller than or subequal to anterior lobe; internal ridge smooth or digitate. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; with propodal sockets. Pleon not narrower than pereon. Pleomeres 1–4 with flattened lateral plates and rounded lateral plates on pleomere 5 or 5 pairs of flattened lateral plates;

5 pairs of smooth or tuberculate biramous pleopods; uniramous or biramous smooth or tubercular uropods. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres narrower or not narrower posteriorly. Eyes present or absent. Pereopods subequal but propodi and dactyli of first two pairs proportionately larger than others. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of round pleopods; posterolateral corners of pleomere 6 rounded or extended; uropods present or absent.

Intertidal–shelf, parasitising calcinid, diogenid and pagurid hermit crabs. Temperate North Atlantic, Tropical Atlantic, Western and Central Indo-Pacific, Temperate Northern Pacific, Temperate South America. 12 species (Williams et al., 2019).

#### ***Balanopleon* Markham, 1974**

**Diagnosis. Female** elongate, body distorted c. 30°; head not bilobed; frontal lamina present. Eyes absent. Maxilliped not described. Barbula with 1 short smooth lobe and 1 stub on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates small; 5 pairs of smooth biramous pleopods with smooth margins; smooth uniramous uropods with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 2 pleomeres, distinct dorsally, fused ventrally; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Shelf, parasitising porcellanid crabs. Tropical Atlantic. 1 species (Markham, 1974).

#### ***Bathione* Román-Contreras and Boyko, 2007**

**Diagnosis. Female** ovate to elongate, body weakly distorted or not distorted; head not bilobed, fused medially with pereomere 1; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 1 long smooth lobe on each side, median region digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing small distolateral slender lobe, smaller than anterior lobe; internal ridge digitate. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates greatly enlarged, edges crenulate; 5 pairs of large smooth or tuberculate biramous pleopods with crenulate margins; uniramous uropods large, smooth. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Slope, parasitising munidid and munidopsid squat lobsters. Temperate Northern Pacific, Temperate South America. 2 species (Román-Contreras and Boyko, 2007).

***Bopyrissa* Nierstrasz and Brender à Brandis, 1931**

*Diagnosis. Female* elongate, body weakly to strongly distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped without palp or with setose articulated or non-articulated palp. Barbula with 1 long tuberculate lobe and 1 short tuberculate lobe on each side or 1 long smooth or tuberculate lobe on each side, median region smooth or tuberculate. 5 pairs of oostegites; oostegite 1 ovate with triangular projection, posterior lobe larger, smaller than or subequal to anterior lobe; internal ridge digitate or smooth. Coxal plates absent, dorsolateral bosses present or absent, tergal projections present or absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth or tuberculate biramous pleopods or 4 pairs biramous and 1 pair uniramous; uropods uniramous, smooth or tuberculate. **Male** approximately 2–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present or absent. Pleon of 6 pleomeres; 4 or 5 pairs of round or sessile pleopods; posterolateral corners of pleomere 6 rounded or weakly or strongly extended; uropods absent.

Intertidal–subtidal, parasitising calcinid and diogenid hermit crabs. Temperate Northern Atlantic, Tropical Atlantic, Central and Eastern Indo-Pacific, Temperate Northern Pacific, Tropical Eastern Pacific. 14 species (Williams et al., 2019).

***Bopyrophryxus* Codreanu, 1965**

*Diagnosis. Female* elongate, body distorted c. 80°; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 1 short smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates large; 5 pairs of tuberculate uniramous pleopods with tuberculate margins; uniramous uropods tuberculate with tuberculate margins. **Male** approximately 2–3 times as long as wide, head as wide as pereon, pereomeres not narrower posteriorly. Eyes present. Pereopod 1 much larger than posterior pereopods. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of ovoid pleopods; posterolateral corners of pleomere 6 extended; uropods absent.

Intertidal–slope, parasitising parapagurid and pagurid hermit crabs. Central Indo-Pacific. 1 species (Bourdon and Boyko, 2005).

***Carcinione* Bourdon, 1983**

*Diagnosis. Female* elongate, body not distorted; head not bilobed; frontal lamina present. Eyes present. Maxilliped without palp. Barbula without lobes, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent.

Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates well developed with crenulate edges; 1 pair of biramous pleopods and 4 pairs of uniramous pleopods with crenulate edges; uropods uniramous with crenulate edges. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising cryptochirid crabs. Central Indo-Pacific. 1 species (Boyko and van der Meij, 2018).

***Cryptione* Hansen, 1897**

*Diagnosis. Female* elongate, body nearly straight to distorted (<55°); head not bilobed; frontal lamina present, narrow to wide. Maxilliped with setose palp, some species with setose region below palp. Barbula with 1 or 2 lobes on each side. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distolateral projection, smaller than anterior lobe; internal ridge smooth or digitate. Pereopods increasing in size posteriorly; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of biramous pleopods decreasing in size posteriorly, endopods smaller than exopods; uropods uniramous or reduced. **Male** approximately 4–7 times as long as wide, head subobovate, as wide as pereon, pereomeres not narrower posteriorly. Eyes present or absent. Maxillipeds absent. Pereopods subequal. Pleon of six pleomeres; 5 pairs of uniramous pleopods; posterolateral corners of pleomere 6 extended; uropods absent.

Subtidal–bathyal, parasitising caridean shrimps. Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Central Indo-Pacific, Temperate Northern Pacific, Tropical Eastern Pacific, Temperate Australasia. 11 species (Williams et al., 2024).

***Discomorphus* Markham, 2008**

*Diagnosis. Female* ovate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 1 minute nub on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates reduced, tergal projections present, dorsolateral bosses absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods absent. **Male** unknown.

Intertidal, parasitising porcellanid crabs. Temperate Northern Pacific. 1 species (Markham, 2008).

***Eremitione* Williams, Boyko and Madad, 2019**

*Diagnosis. Female* elongate, body weakly to strongly distorted or not distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose non-articulated or articulated palp or palp absent. Barbula with 1 long smooth lobe and 1 short smooth or tuberculate lobe on each side or

short lobe absent, median region smooth or tuberculate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular or distal recurved projection or lobe triangular, subequal to or larger than anterior lobe; internal ridge digitate. Coxal plates present or absent, dorsolateral bosses present or absent, tergal projections present or absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes present or absent. Pereopods subequal or pereopod 1 smaller. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile or raised pleopods; posterolateral corners of pleomere 6 rounded or weakly or strongly extended; uropods absent.

Subtidal–slope, parasitising calcinid, diogenid, pagurid and pylochelid hermit crabs and lithodid king crabs. Temperate Northern Atlantic, Tropical Atlantic, Temperate South America, Central Indo-Pacific, Temperate Northern Pacific. 11 species (Golovan et al., 2024; Williams et al., 2019).

#### ***Galathocrypta* Román-Contreras and Soto, 2002**

*Diagnosis. Female* elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 1 long smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with oblong posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates, dorsolateral bosses and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates reduced; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Slope, parasitising munidopsid squat lobsters. Tropical Atlantic. 1 species (Román-Contreras and Soto, 2002).

#### ***Gigantione* Kossmann, 1881**

*Diagnosis. Female* ovate, body slightly distorted, symmetrical or asymmetrical; head bilobed or not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 1 smooth lobe on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than or subequal to anterior lobe; internal ridge smooth or digitate. Coxal plates present, narrow and extended, dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates slender and tapering; 5 pairs of smooth or digitate biramous pleopods with smooth or digitate margins; uropods smooth, biramous or uniramous but distally bifid, with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres narrower or not narrower posteriorly. Eyes present or absent. Pereopods subequal.

Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of uniramous or biramous pleopods; posterolateral corners of pleomere 6 rounded; uropods distally rounded or weakly bifid.

Intertidal–slope, parasitising carpiliid, dromiid, euryplacid, goneplacid, pilumnid and xanthid crabs and axiid shrimps. Temperate Northern Atlantic, Central and Eastern Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 18 species (An et al., 2016a).

#### ***Goleathopseudione* Román-Contreras, 2008**

*Diagnosis. Female* elongate, body slightly distorted; head bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 3 smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with subquadrate posterior lobe, larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth biramous slender pleopods with smooth margins; uropods smooth, uniramous, slender with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles present. Pleon of 6 pleomeres; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 extended; uropods absent.

Abyssal, parasitising munidopsid squat lobsters. Temperate Northern Pacific. 1 species (Román-Contreras, 2008).

#### ***Gyge* Cornalia and Panceri, 1861**

*Diagnosis. Female* ovate to subquadrate, body slightly distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped without palp. Barbula with 2 short digitate lobes on each side, median region digitate. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge digitate. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates absent; 3 or 4 pairs of smooth uniramous or biramous pleopods with tuberculate margins; uniramous uropods smooth with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile pleopods or pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal–subtidal, parasitising upogebiid shrimps. Temperate Northern Atlantic, Western and Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 6 species (An et al., 2009; Boyko and Williams, 2025; Markham, 2004).

#### ***Ionella* Bonnier, 1900**

*Diagnosis. Female* ovate, body weakly distorted; head weakly bilobed or not bilobed; frontal lamina absent. Eyes present or absent. Maxilliped without palp, densely lined on margin by short setae. Barbula with 2 short, notched lobes on each side,

median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge digitate. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates absent; 5 pairs of digitate biramous pleopods; uropods uniramous, slender, smooth. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; pleopods uniramous, biramous or mixed; posterolateral corners of pleomere 6 rounded; uropods uniramous.

Intertidal–shelf, parasitising callianassid shrimps. Central and Eastern Indo-Pacific, Temperate Northern Pacific, Temperate South America. 5 species (Markham, 1994; Romero-Rodríguez and Álvarez, 2025).

#### ***Kolourione* Markham, 1978**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 very short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Pleomeres 1 and 2 with lateral plates; 4 pairs of smooth biramous pleopods; uropods absent. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleomeres fused; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–shelf, parasitising porcellanid crabs. Tropical Atlantic. 1 species (Markham, 1978a).

#### ***Munidion* Hansen, 1897**

*Diagnosis. Female* elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing acute triangular projection, smaller than anterior lobe; internal ridge digitate. Coxal plates, dorsolateral bosses, and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates tuberculate; 5 pairs of smooth biramous pleopods; uropods biramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present. Pleomeres fused, often with lateral indications of segmentation; pleopods absent; posterolateral corners of pleomere slightly rounded; uropods absent.

Shelf–slope, parasitising munidid squat lobsters. Tropical Atlantic, Central Indo-Pacific, Tropical Eastern Pacific, Temperate Australasia, Temperate Northern Pacific. 9 species (Katsuragawa et al., 2025; Markham, 1975b; Williams et al., 2026).

#### ***Nikione* Kensley, 1974**

*Diagnosis. Female* ovate, body distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 3 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates, dorsolateral bosses, and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates tuberculate; 5 pairs of tuberculate biramous pleopods; uropods biramous, tuberculate. **Male** approximately 3–4 times as long as wide, head as wide as pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; pleopods absent; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Shelf, parasitising processid shrimps. Temperate Southern Africa. 1 species (Kensley, 1974).

#### ***Orbimorphus* Richardson, 1910**

*Diagnosis. Female* elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, subequal to anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates small; 4 pairs of smooth biramous pleopods; uropods biramous, smooth. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 1 pleomere with lateral indication of segmentation; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal, parasitising porcellanid crabs. Tropical Eastern Pacific. 1 species (Bourdon, 1976).

#### ***Orthione* Markham, 1988**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 1 long smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of uniramous sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods uniramous.

Intertidal, parasitising upogebiid shrimps. Temperate

Northern Atlantic, Temperate Northern Pacific, Temperate South America. 3 species (Markham, 2004).

#### ***Ovoionella* Boyko, 2004**

*Diagnosis. Female* elongate-ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-articulated palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distal projection, smaller than anterior lobe; internal ridge digitate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods absent. **Male** approximately 1–2 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present or absent. Pleon of 4 pleomeres; 3 pairs of uniramous pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Shelf, parasitising munidid squat lobsters. Central Indo-Pacific, Temperate Northern Pacific. 1 species (Boyko, 2004).

#### ***Pagurion* Shiino, 1933**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 1 long tuberculate lobe on each side, median region tuberculate. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge digitate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of tuberculate biramous pleopods; uropods biramous, tuberculate. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present. Pleon of 6 pleomeres; 5 pairs of sessile or elongate pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal–slope, parasitising calcinid hermit crabs. Central Indo-Pacific, Temperate Northern Pacific. 1 species (Williams et al., 2019).

#### ***Paguristione* An, Zhao and Markham, 2016**

*Diagnosis. Female* elongate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 2 long smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Pleomeres 1–3 with lateral plates; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head

narrower than pereon, pereomeres narrower posteriorly. Eyes absent. Pereopods 3–5 larger than other pairs. Midventral tubercles absent. Pleon of 6 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Shelf, parasitising diogenid hermit crabs. Temperate Northern Pacific. 1 species (An et al., 2016b).

#### ***Paranikione* An, Boyko and Li, 2015**

*Diagnosis. Female* elongate-ovate, body distorted; head bilobed or not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, larger than anterior lobe; internal ridge smooth. Coxal plates, dorsolateral bosses, and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 5 pairs of tuberculate biramous pleopods; uropods biramous, tuberculate. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of tubercular pleopods; posterolateral corners of pleomere 6 extended into lobes; uropods absent.

Shelf, parasitising processid shrimps. Central Indo-Pacific, Temperate Northern Pacific. 2 species (An et al., 2015).

#### ***Parapagurion* Shiino, 1933**

*Diagnosis. Female* elongate, body weakly or strongly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose non-articulated palp or without palp. Barbula with 1 short or long smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing distal triangular projection, subequal to anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods uniramous or biramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 rounded or weakly extended; uropods absent.

Subtidal–slope, parasitising calcined, diogenid, and parapagurid hermit crabs. Tropical Atlantic, Temperate Northern Pacific. 2 species (Markham 1978b).

#### ***Parasymmetrione* An, Markham and Yu, 2010**

*Diagnosis. Female* elongate, body extremely distorted (~120°); head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 2 smooth lobes and 1 nub on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with rounded posterior lobe bearing triangular distal projection, smaller than or subequal to anterior lobe; internal ridge digitate. Coxal plates and tergal projections

present, dorsolateral bosses absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; pleopods, 5 pairs tuberculate pleopods, 4 pairs biramous and 1 pair uniramous; uropods tuberculate, uniramous. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopod 1 larger than others. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of flap-like pleopods; posterolateral corners of pleomere 6 rounded; uropods present.

Intertidal, parasitising diogenid hermit crabs. Central Indo-Pacific. 1 species (An et al., 2010).

#### ***Parione* Richardson, 1910**

*Diagnosis. Female* elongate, body slightly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-articulated palp. Barbula with 1 smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with rounded posterior lobe bearing triangular distal projection or triangular lobe, smaller than or subequal to anterior lobe; internal ridge smooth. Coxal plates present, dorsolateral bosses present or absent, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates short; 5 pairs of smooth biramous slender pleopods with smooth margins; uropods smooth, uniramous, slender with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present. Pleon of 5 or 6 pleomeres; 4 or 5 pairs of sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–slope, parasitising munidid squat lobsters and porcellanid crabs. Temperate South America, Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 5 species (Bourdon, 1976).

#### ***Parionella* Nierstrasz and Brender à Brandis, 1923**

*Diagnosis. Female* elongate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped without palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates present, dorsolateral bosses present or absent, tergal projections present or absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates short; 4 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods 1–3 larger than others. Midventral tubercles present. Pleon of 5 pleomeres, medially separated or fused; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal–slope, parasitising eumunidid and munidid squat lobsters and porcellanid crabs. Central Indo-Pacific, Temperate Northern Pacific. 4 species (Bourdon, 1972b).

#### ***Parionina* Nierstrasz and Brender à Brandis, 1929**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped not described. Barbula not described. Oostegites not described. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present or absent; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods not described. Midventral tubercles not described. Pleon of 4 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Slope, parasitising galatheid squat lobsters. Central Indo-Pacific, Temperate Northern Pacific. 2 species (Nierstrasz and Brender à Brandis, 1931).

#### ***Parioninella* Nierstrasz and Brender à Brandis, 1930**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped without palp. Barbula with 1 tubercle on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates reduced; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of uniramous pleopods; posterolateral corners of pleomere 6 rounded or slightly extended; uropods absent.

Intertidal–subtidal, parasitising porcellanid crabs. Central Indo-Pacific. 3 species (An et al., 2020).

#### ***Pauperella* Nierstrasz and Brender à Brandis, 1929**

*Diagnosis. Female* ovate, body weakly distorted; head not bilobed; frontal lamina absent. Eyes present. Maxilliped not described. Barbula not described. Oostegites not described. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon, first 2 pleomeres distinct, others fused with pleotelson. Pleomeres 1 and 2 with lateral plates; 3 pairs of smooth biramous pleopods; uropods absent. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods not described. Midventral tubercles not described. Pleon of 6 pleomeres; pleopods not described; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal, parasitising upogebiid shrimps. Central Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1929).

***Pleonobopyrus* Saito and Moritaki, 2020**

*Diagnosis. Female* elongate, body not distorted; head not bilobed; frontal lamina absent. Eyes absent. Maxilliped without palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge smooth. Dorsolateral bosses present, coxal plates and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 4 pairs of smooth uniramous pleopods; uropods uniramous, smooth. **Male** unknown.

Slope, parasitising crangonid shrimps. Temperate Northern Pacific. 1 species (Saito and Moritaki, 2020).

***Pleurocrypta* Hesse, 1865**

*Diagnosis. Female* elongate or ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose non-articulated palp or palp absent. Barbula with 2 long or short smooth or tuberculate lobes on each side, median region smooth or tuberculate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular projection, subequal to anterior lobe; internal ridge tuberculate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates small or large; 5 pairs of smooth or tuberculate biramous pleopods; uropods uniramous or biramous, smooth or tuberculate. **Male** approximately 2–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods 1–3 larger than others. Midventral tubercles absent. Pleon of 1–6 partly to entirely fused pleomeres (often appearing as single pleomeres with lateral undulations); pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Intertidal–shelf, parasitising galatheid and munidid squat lobsters and porcellanid crabs. Temperate Northern Atlantic, Tropical Atlantic, Central Indo-Pacific. 12 species (Markham, 1988).

***Pontobopyrus* Markham, 1979**

*Diagnosis. Female* elongate, body distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 2 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates and tergal projections present, dorsolateral bosses absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present; 5 pairs of smooth uniramous pleopods; uropods uniramous, smooth. **Male** unknown.

Abyssal, parasitising crangonid shrimps. Temperate Northern Atlantic. 1 species (Markham, 1979).

***Progebiophilus* Codreanu and Codreanu, 1963**

*Diagnosis. Female* ovate or elongate, body not distorted; head not bilobed; frontal lamina present. Eyes present or absent.

Maxilliped with setose articulated or non-articulated palp or palp absent. Barbula with 1–3 smooth or digitate lobes on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distolateral projection, subequal to anterior lobe; internal ridge digitate. Coxal plates present, dorsolateral bosses present or absent, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present or absent; 5 pairs of smooth or tuberculate biramous pleopods; uropods uniramous or biramous, smooth or tuberculate. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present or absent. Pleon of 6 pleomeres; 5 pairs of tubercular uniramous pleopods present; posterolateral corners of pleomere 6 rounded or extended; uropods present or absent.

Intertidal–subtidal, parasitising upogebiid shrimps. Temperate Northern Atlantic, Tropical Atlantic, Temperate Southern Africa, Western and Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 13 species (An et al., 2009; Markham, 2005).

***Propseudione* Shiino, 1933**

*Diagnosis. Female* elongate, body distorted; head not bilobed; frontal lamina present. Eyes present. Maxilliped with setose non-articulated palp. Barbula with 1 digitate lobe and 1 smooth lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distolateral projection, larger than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present but not well developed; 5 pairs of large smooth biramous pleopods with smooth margins; uropods small, smooth, uniramous with smooth margins. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of tubercular biramous pleopods; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Subtidal, parasitising calcinid hermit crabs. Temperate Northern Pacific. 1 species (Shiino, 1933).

***Pseudione* Kossmann, 1881 *sensu stricto***

*Diagnosis. Female* elongate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated or non-articulated palp adjacent to setose lobe. Barbula with 1 smooth lobe and 1 smooth nub present or absent on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular distolateral projection, smaller than anterior lobe; internal ridge smooth or digitate. Coxal plates, dorsolateral bosses and tergal projections present. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates present, large; 5 pairs of

large smooth or tuberculate biramous pleopods with smooth or crenulate margins; uropods smooth or tuberculate, uniramous or biramous, with smooth margins. **Male** approximately 2–5 times as long as wide, head as wide as pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; 5 pairs of sessile uniramous pleopods present or absent; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Intertidal–slope, parasitising axiid and callianassid shrimps and nephropid lobsters. Temperate Northern Atlantic, Tropical Atlantic, Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific. 9 species (Boyko et al., 2017).

#### ***Pseudione* Kossmann, 1881 *sensu lato***

**Diagnosis. Female** elongate, body weakly to moderately distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose articulated or non-articulated palp or palp absent. Barbula with 2 smooth or digitate lobes on each side, median region smooth or digitate. 5 pairs of oostegites; oostegite 1 posterior lobe ovate or ovate with triangular posterior distal projection, subequal to or smaller than anterior lobe; internal ridge digitate. Coxal plates present or absent, dorsolateral bosses present, tergal projections present or absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present, small or large, smooth or tuberculate; 5 pairs of smooth or tuberculate pleopods with smooth or crenulate margins; uropods uniramous, smooth or tuberculate, with smooth or crenulate margins. **Male** approximately 3–4 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present or absent. Pereopods subequal. Midventral tubercles present or absent. Pleon of 6 pleomeres; 4 or 5 pairs of sessile or raised uniramous pleopods; posterolateral corners of pleomere 6 rounded or slightly to moderately extended; uropods absent.

Subtidal–slope, parasitising galatheid, munidid and munidopsid squat lobsters. Temperate Northern Atlantic, Tropical Atlantic, Temperate Southern Africa, Western and Central Indo-Pacific, Temperate Australasia, Temperate Northern Pacific, Temperate South America. 18 species (Boyko et al., 2017 ; Williams et al., 2026).

#### ***Pseudionella* Shiino, 1949**

**Diagnosis. Female** elongate, body distorted; head not bilobed; frontal lamina present. Eyes present or absent. Maxilliped with setose non-articulated palp. Barbula with 2 short digitate lobes and 1 short smooth lobe on each side, median region digitate. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates not well developed; 5 pairs of smooth pleopods with smooth margins, 2 biramous and 3 uniramous; uropods smooth, uniramous, with smooth margins. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres narrower posteriorly. Eyes present. Pereopods subequal or pereopods 1–3 larger. Midventral tubercles absent. Pleon of 6

pleomeres; 5 pairs of tubercular or flap-like uniramous pleopods; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Intertidal–shelf, parasitising calcinid and pagurid hermit crabs. Temperate Northern Atlantic, Tropical Atlantic, Western, Eastern and Central Indo-Pacific, Temperate Northern Pacific, Temperate Southern Africa. 6 species (An et al., 2013; Boyko and Williams, 2001; Brandt et al., 2024).

#### ***Rhopalione* Pérez, 1920**

**Diagnosis. Female** ovate, body not distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with non-setose non-articulated palp or without palp. Barbula with 1 long and 1 short smooth lobe or 1 long lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing small triangular distal projection, subequal to anterior lobe; internal ridge with few small digitations. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates smooth, tubular; 5 pairs of smooth tubular biramous pleopods; uropods uniramous, smooth, tubular. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 6 pleomeres; uniramous sessile pleopods; posterolateral corners of pleomere 6 rounded or extended; uropods absent.

Intertidal–subtidal, parasitising pinnotherid crabs. Western and Central Indo-Pacific, Temperate Australasia. 7 species (Ahyong and Boyko, 2019; Boyko and Williams, 2024).

#### ***Robinione* Boyko, Williams and Shields, 2017**

**Diagnosis. Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with setose articulated palp. Barbula with 2 smooth or digitate lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing triangular projection, smaller than anterior lobe; internal ridge digitate. Coxal plates and tergal projections present, dorsolateral bosses absent. Pereopods elongate; without propodal sockets. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates greatly enlarged, tuberculate; 5 pairs of tuberculate biramous pleopods; uropods uniramous, tuberculate. **Male** approximately 3–4 times as long as wide, head narrower than or as wide as pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 5 or 6 pleomeres; 5 pairs of uniramous pleopods; posterolateral corners of pleomere 6 extended; uropods absent.

Intertidal, parasitising callianassid and callichirid shrimps. Temperate Northern Atlantic, Temperate South America. 2 species (Boyko et al., 2017).

#### ***Shiinoella* Bourdon, 1972**

**Diagnosis. Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with

setose non-articulated palp. Barbula with 1 long and 1 short digitate lobe on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, smaller than anterior lobe; internal ridge with few small tubercles. Coxal plates and dorsolateral bosses present, tergal projections absent. Pereopods elongate; without propodal sockets. Mediodorsal lobes absent. Pleon narrower than pereon. Lateral plates smooth; 2 pairs of smooth biramous pleopods, 3 pairs of smooth uniramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes absent. Pereopods subequal, elongate. Midventral tubercles absent. Pleon of 6 pleomeres with posterior 3 nearly fused; pleopods absent; posterolateral corners of pleomere 6 slightly extended; uropods absent.

Slope, parasitising alpheid shrimps. Western Indo-Pacific. 1 species (Bourdon, 1972a).

#### ***Spathione* Boyko and van der Meij, 2018**

**Diagnosis. Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present. Maxilliped without palp. Barbula with 3 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates and tergal projections present, dorsolateral bosses absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not narrower than pereon. Lateral plates smooth; 4 pairs of smooth tubular biramous pleopods, 1 pair of smooth uniramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 5 pleomeres; pleopods absent; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising cryptochirid crabs. Central Indo-Pacific. 1 species (Boyko and van der Meij, 2018).

#### ***Upogebione* Markham, 1985**

**Diagnosis. Female** ovate, body moderately distorted; head not bilobed; frontal lamina present. Eyes absent. Maxilliped with articulated palp. Barbula with 2 short smooth lobes on each side, median region digitate. 5 pairs of oostegites; oostegite 1 with triangular posterior lobe, subequal to anterior lobe; internal ridge digitate. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates present; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** approximately 2–3 times as long as wide, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles present or absent. Pleon of 5 pleomeres; 4 pairs of uniramous sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods absent.

Subtidal, parasitising upogebiid shrimps. Tropical Atlantic, Central Indo-Pacific. 4 species (An et al., 2009).

#### ***Upogebiophilus* Nobili, 1906**

**Diagnosis. Female** ovate, body weakly distorted; head not bilobed; frontal lamina present. Eyes present. Maxilliped without palp. Barbula with 3 or 4 short smooth lobes on each side, median region not described. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe bearing small triangular distal projection, subequal to anterior lobe; internal ridge smooth. Coxal plates present, dorsolateral bosses and tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon narrower than pereon. Lateral plates absent; 5 pairs of smooth biramous pleopods; uropods uniramous, smooth. **Male** size not described, head narrower than pereon, pereomeres not narrower posteriorly. Eyes present. Pereopods subequal. Midventral tubercles absent. Pleon of 5 pleomeres; 4 pairs of uniramous sessile pleopods; posterolateral corners of pleomere 6 rounded; uropods uniramous.

Subtidal, parasitising upogebiid shrimps. Western Indo-Pacific. 1 species (Nobili, 1906).

#### ***Zeaione* Boyko and Williams in Andrade et al., 2025**

**Diagnosis. Female** elongate, body weakly distorted; head weakly bilobed; frontal lamina present. Eyes absent. Maxilliped with articulated non-segmented palp. Barbula with 3 short smooth lobes on each side, median region smooth. 5 pairs of oostegites; oostegite 1 with ovate posterior lobe, smaller than anterior lobe; internal ridge smooth. Coxal plates and dorsolateral bosses present, tergal projections absent. Mediodorsal lobes absent. Pereopods not elongate; without propodal sockets. Pleon not markedly narrower than pereon; dorsolateral margins of pleomeres 1–6 with numerous, irregular, mostly semi-spherical protuberances. Lateral plates broad, lamellar, with scalloped posterior margins; 5 pairs of smooth biramous pleopods with bilobed endopods; uropods biramous, smooth. **Male** approximately 3 times as long as wide, head narrower than pereon, pereomeres slightly narrower posteriorly. Eyes present. Maxillipeds segmented. Pereopods subequal. Midventral tubercles absent. Pleon of six pleomeres; 5 pairs of uniramous sessile pleopods; posterolateral corners of pleomere 6 extended; uropods absent.

Subtidal, parasitising eucalliacid shrimps. Temperate Australasia. 1 species (Andrade et al., 2025).

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## Family Entoniscidae Kossmann, 1881

Figure 6.23

Entoniscidae is a relatively small group (45 species) of endoparasites that reside in the visceral cavities of anomuran, brachyuran and shrimp hosts. Characters of females, males, epicaridium larvae and cryptoniscus larvae are included in the diagnoses when known, because all these life history stages exhibit informative traits. Entoniscid females are highly modified, with bulbous heads positioned in the host's gonad or hepatopancreas, reduced or absent pereopods, and a variable number of oostegites that form the brood chamber. Presently, three subfamilies are recognised: Diogenioninae (2 species), Entoniscinae (8 species) and Entioninae (35 species), differing in morphology of the female marsupium, oostegites, and pleural lamellae and the pereopod structure of males. Most mature entoniscid females exhibit one or more projections containing ovarian tissue on the pereomeres called ovarian processes; these are located on five possible positions of the pereon: anterior dorsolateral, dorsal, lateral, posterolateral and ventral. Dorsal ovarian processes are found only in *Entione* and *Cancrion* (Adkison, 1990). However, dorsal ovarian processes could easily be confused with anterior dorsolateral ovarian processes, especially considering that it is likely that all ovarian processes vary in size and/or shape according to the development of the female. In contrast, the presence of unpaired ventral ovarian processes appears to be a more consistent feature. Males exhibit a less modified isopod body plan with distinct segmentation, but those of all species lack pereopods on pereomere 7 or have them highly reduced. Some males possess medioventral spines (= hypospheonians or midventral hooks) on posterior pereomeres or anterior pleomeres.

Epicaridium larvae of entoniscids exhibit a modified pereopod 6; in some genera this includes an elongate pereopod 6 with unique propodal extensions. The life cycle has not been completely worked out for any entoniscid, but a copepod host is assumed to be involved in most cases (see life cycle in McDermott et al., 2019). One entoniscid species (*Entionella fluviatilis* Miyashita, 1941) is known to bypass the copepod

intermediate host; females of this species brood their larvae until they reach the cryptoniscus stage, which are then released and find new definitive hosts (Miyashita, 1941). This the only documented case of such an abbreviated life cycle in epicarideans. Cryptoniscus larvae typically have antennae with seven segments (four peduncular and three flagellar) but in at least one case the flagellar segments are reduced (Boyko and Williams, 2015). Much investigation remains to be done on the diversity of the group, with multiple undescribed species and cryptic species likely in all subfamilies (e.g. Adkison, 1990; DeTorre et al., 2023). Note that the diagnosis of *Entionella* is based only on the type species (*E. fluviatilis*), because the other species in this genus differ markedly in the morphology of pereopod 6 of the epicaridium larvae. The key is based on male and female characters (modified from DeTorre et al., 2023).

**Diagnosis** (modified from Adkison, 1990). **Female** body symmetrical, body regions distinct, segments often indistinct. Head bulbous, rounded, with or without dorsal groove; antennae reduced to 2 unsegmented ridges on anterior margin of head. Maxilliped not lamellar, development variable, in mature specimens well-developed with 3 lobes present, exopod largest, other lobes reduced. Oral cone present, reduced in size. Eyes absent. Pereopods with reduced segmentation or absent. Ovarian processes often present in anterior dorsolateral, dorsal, lateral, posterolateral and ventral locations. Brood pouch formed by up to 7 oostegites or by oostegites and host-derived sheath. Oostegite 1 often greatly developed with up to 3 lobes (ascendant, transverse and recurrent). Pleon of 6 segments. Pleural lamellae (= lamina) development variable from absent to simple lobes to complexly folded. Pleopods uniramous, up to 5 pairs. Uropods present or absent. **Male** head often fused with pereomere 1. Antennula and antenna present or reduced to pair of antennula in form of unsegmented lobes with tuft of setae. Pereopods of 6 pairs, with or without distinct segments. Pereomere 7 pereopods reduced to small protuberances or

absent. Medioventral spine present or absent on medioventral surface of posterior pereomeres or anterior pleomeres. Pleon with 6 segments, without pleopods. Posterior margin of pleomere 6 entire or bifid. **Epicaridium larva** (fig. 6.23k, n) with pereopod 6 similar in size (e.g., fig. 6.23l) to preceding pereopods or dissimilar in size (some greatly elongate, e.g., fig. 6.23o, p) and form (carpus and propodus typically fused,

reduced dactylus, sometimes with processes). Pleopods of 5 uniramous or biramous pairs. Uropods biramous, peduncle shorter than rami. **Cryptoniscus larva** antenna typically of 7 segments – 4 peduncular and 3 flagellar (rarely 1 flagellar segment). Pereopod 7 longer, more slender than anterior pereopods. Pleopods of 5 pairs; 1–4 uniramous, 5 uniramous or biramous.

### Key to genera of Entoniscidae

1. Marsupium of female formed by close adhesion of oostegites to host membrane; males with segmented pereopods (fig. 6.23f) ..... 2
  - Oostegites free, not adhering to host membrane (fig. 6.23a), pleural lamellae absent, females without pereopods, males with unsegmented pereopods (fig. 6.23b) ..... Entoniscinae ... 3
2. Parasitic in hermit crabs; females without pleural lamellae, female with heart in pleomere 1 (fig. 6.23e) ..... Diogenioninae ... 18
  - Parasitic in other decapods; females with well-developed pleural lamellae, female with heart in pleomere 3 (fig. 6.23g) ..... Entioninae ... 6
3. Parasitic in hermit crabs; oostegite 1 of female largest with ascendant and recurrent lobes, oostegites 2–5 at posterior end of pereon (fig. 6.23c); male with antennae not projecting beyond margin of head (fig. 6.23d) ..... *Paguritherium*
  - Parasitic in other decapods ..... 4
4. Female without maxilliped (fig. 6.23a); terminal segment of male bifurcated (fig. 6.23b) ..... *Entoniscoides*
  - Female with maxilliped (fig. 6.23h); pleotelson of male undivided ..... 5
5. Female with more than 2 pairs of oostegites; unpaired dorsal ovarian processes ..... *Entoniscus*
  - Female with oostegite 1 absent; only 2 pairs of oostegites forming brood pouch ..... *Synalpheion*
6. Males with 5 pairs of pereopods (fig. 6.23j); pereon of female with pairs of lateral ovarian processes and without unpaired ventral or dorsal processes (fig. 6.23g–i) ..... *Allocancrion*
  - Males with 6 pairs of pereopods (fig. 6.23m) ..... 7
7. Pereon of female without ovarian processes ..... 8
  - Pereon of female with at least 1 ovarian process ..... 9
8. Female with 2 transverse lobes on oostegite 1 and fused oostegites 2–5; males with pair of lateral expansions on each of first 2 pleomeres (fig. 6.23m) ..... *Pinnixion*
  - Female with 1 transverse lobe on oostegite 1 and separate oostegites 2–5; males with pair of expansions only on pleomere 1 ..... *Entionella*
9. Mature female with dorsal ovarian processes of variable number, rarely absent ..... 10
  - Mature female without dorsal ovarian processes ..... 12
10. Mature female with 2 ventral ovarian processes ..... *Entione*
  - Mature female without ventral ovarian processes ..... 11
11. Epicaridium larvae with elongate pereopod 6 (long merus and carpus) (fig. 6.23p) ..... *Cancrion*
  - Epicaridium larvae with short pereopod 6 (short merus and carpus) (compare to fig. 6.23l) ..... *Cryptocancrion*
12. Female with dorsolateral ovarian processes ..... 13
  - Female without dorsolateral ovarian processes ..... 15

- |     |  |                      |
|-----|--|----------------------|
| 13. | Pereon of female with 1 unpaired dorsolateral ovarian process .....  | <i>Micippion</i>     |
| –   | Pereon of female with paired dorsolateral ovarian processes .....  | 14                   |
| 14. | Female with 1 pair of dorsolateral ovarian processes .....   | <i>Portunion</i>     |
| –   | Female with 2 pairs of dorsolateral ovarian processes .....  | <i>Priapion</i>      |
| 15. | Female with 1 unpaired ventral ovarian process .....   | <i>Xanthion</i>      |
| –   | Female with 2 unpaired ventral ovarian processes .....   | 16                   |
| 16. | Oostegite 1 of female without transverse lamellae (compare to fig. 6.23i) .....                                      | <i>Pinnotherion</i>  |
| –   | Oostegite 1 of female with transverse lamellae .....   | 17                   |
| 17. | Posterior oostegites of female reduced, not enclosing recurrent lamella of oostegite 1 (compare to fig. 6.23i) ..... | <i>Tiarinion</i>     |
| –   | Posterior oostegites of female enclosing recurrent lamella of oostegite 1 .....                                      | <i>Achelion</i>      |
| 18. | Female with marsupium formed by oostegites 1–4, pleopods absent .....  | <i>Diogenion</i>     |
| –   | Female with marsupium formed by oostegites 1–7, pleopods present .....   | <i>Paradiogenion</i> |

### Subfamily Diogenioninae DeTorre, Williams and Boyko, 2023

#### *Diogenion* Codreanu, Codreanu and Pike, 1960

**Diagnosis.** **Female** head with dorsal groove; antennula broad, antenna reduced; maxilliped small. Oostegites 1–7 present; oostegite 1 without ascendant lobe, with strongly developed recurrent lobe lined with pleat-like folds; brood pouch formed by overlapping of oostegites 1–4, oostegites 5–7 reduced. Pereopods 1–7 present. Pleon slender, heart in pleomere 1; pleural lamellae, pleopods and uropods absent. **Male** with antennula and antenna, antennula projecting beyond margin of head; head not fused with pereomere 1. Pereopods 1–6 present, multisegmented; pereopod 7 absent or greatly reduced. Pleon of 5 pleomeres plus pleotelson, medioventral spines absent, pleotelson bifurcated, uropods absent. **Epicaridium larva** with pereopods 1–6 isomorphic; pereopod 7 absent; pereopod 6 subequal in length to pereopod 5. Pleon with 5 pairs of biramous pleopods. Telson tapering to point. Uropods with endopod slightly longer than exopod. **Cryptoniscus larva** unknown.

Subtidal, parasitising diogenid hermit crabs Western Indo-Pacific. 1 species (Codreanu et al., 1960; DeTorre et al., 2023).

#### *Paradiogenion* Shinoda and Shimomura in Shinoda, Takiyama, Fujita, Nakano and Shimomura, 2026

**Diagnosis.** Female head with dorsal groove; antennula broad, antenna reduced; maxilliped small. Oostegites 1–7 present; oostegite 1 without ascendant lobe, with strongly developed recurrent lobe lined with pleat-like folds; brood pouch formed by overlapping of oostegites 1–7. Pereopods 1–7 present. Pleon slender, heart in pleomere 1; 4 uniramous pleopods, pleural lamellae and uropods absent. **Male** with antennula and antenna, antennula projecting beyond margin of head; head not fused with pereomere 1. Pereopods 1–6 present, multisegmented; pereopod 7 absent. Pleon of 5 pleomeres plus pleotelson, medioventral spines absent, pleotelson distally bifurcated, uropods absent. **Epicaridium larva** with pereopods 1–6 isomorphic; pereopod 7 absent; pereopod 6 subequal in length to pereopod 5. Pleon with 5 pairs of biramous pleopods. Telson tapering to point. Uropods with endopod slightly longer than exopod. **Cryptoniscus larva** unknown.

Subtidal, parasitising diogenid hermit crabs Temperate Northern Pacific. 1 species (Shinoda et al., 2026).

### Subfamily Entoniscinae Kossmann, 1881

#### *Entoniscoides* Miyashita, 1940

**Diagnosis.** **Female** head with dorsal groove; maxilliped present. Pereon without ovarian processes; pereopods absent; brood pouch formed by 5 pairs of oostegites, oostegites deeply divided or notched; oostegite 1 forming part of brood pouch. Heart in pleomere 1; 5 pairs of uniramous pleopods; posterior margin of pleomere 6 entire; uropods absent. **Male** head fused with pereomere 1; antenna elongate, projecting well beyond margin of head; pereopods unsegmented; medioventral spines and pleopods

absent; posterior margin of pleomere 6 deeply notched, uropods present. **Epicaridium larva** not present as free-swimming stage; larvae released from brood chamber as cryptoniscus larva; pereopod 6 subequal in length to pereopod 5. **Cryptoniscus larva** with eyes present; antennula with basal segment not enlarged into plate, without teeth; antenna of 5 segments: 4 peduncular and 1 flagellar. Pereonal coxal plates without teeth. Pleon with 5 pairs of uniramous pleopods; uropods biramous.

Intertidal–subtidal, parasitising xanthid crabs. Temperate Northern Pacific. 1 species (Miyashita, 1940).

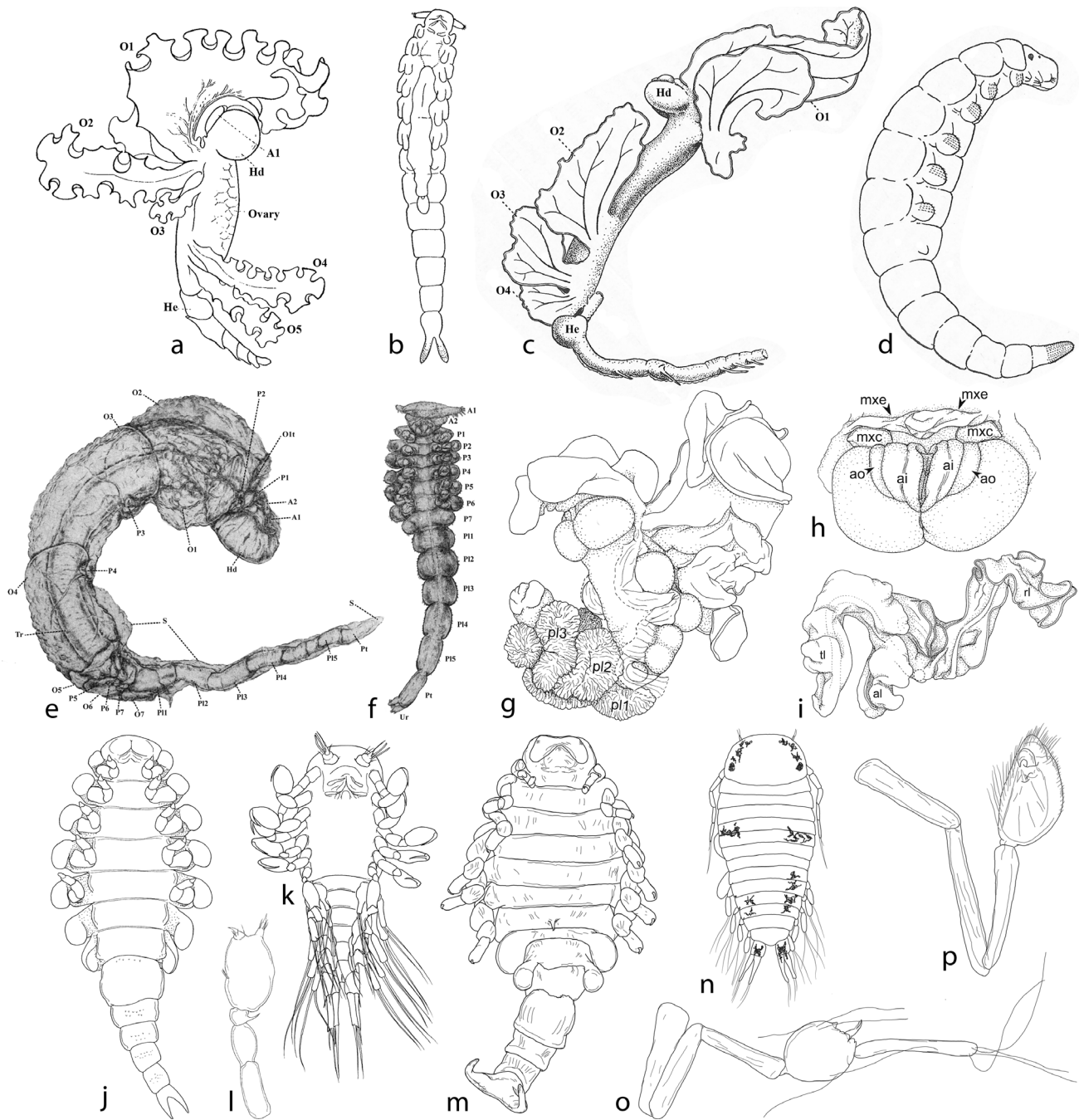


Figure 6.23. Entoniscidae (a–d, Entoniscinae; e, f, Diogenioninae; g–p, Entioninae). *Entoniscoides okadai* Miyashita, 1940: a, female lateral view; b, male ventral view. *Paguritherium alatum* Reinhard, 1945: c, female lateral view; d, male lateral view. *Diogenion vermifactus* Codreanu, Codreanu and Pike, 1960: e, female lateral view; f, male ventral view. *Allocancrion yunnu* Uyeno and Boyko, 2020: g, female lateral view; h, head; i, oostegite 1; j, male ventral view; k, epicaridium larva ventral view; l, pereopod 6 of epicaridium larva. *Pinnixion sexdecennia* McDermott, Williams and Boyko, 2019: m, male ventral view; n, epicaridium larva dorsal view; o, pereopod 6 of epicaridium larva. *Cancrion carolinus* Pearse and Walker, 1939: p, pereopod 6 of epicaridium larva. Abbreviations: al, ascendant lobe; A1, antennula; A2, antenna; Hd, head; He, heart; mx, maxilliped exopod; mxc, maxilliped coxopod; O1–O7, oostegites 1–7; O1r, transverse plate of oostegite 1; P1–P7, pereopods 1–7; P11–P15, pleopods 1–5; Pt, pleotelson; rl, recurrent lobe; S, host sheath; tl, transverse lobe; Tr, ovarian thoracic trunk; Ur, uropods.

***Entoniscus* Müller, 1862**

*Diagnosis. Female* head with strong dorsal groove; maxilliped absent; pereopods present; number of oostegites variable; ovarian processes unpaired, dorsal, number variable; heart in pleomere 1; number of pleopods variable; posterior margin of pleomere 6 variable; uropods absent. *Male* antenna projecting beyond margin of head; pereopods unsegmented; medioventral spines and pleopods absent; posterior margin of pleomere 6 variable; uropods absent. ***Epicaridium larva*** with pereopod 6 subequal in length to pereopod 5, dactylus reduced. Pleopods 1–4 with medial angle of peduncle bearing 1 seta, exopod bearing 3 long setae; pleopod 5 smaller than pleopod 4, medial angle peduncle bearing 1 rudimentary seta, exopod bearing 3 rudimentary setae. ***Cryptoniscus larva*** unknown.

Intertidal–subtidal, parasitising porcellanid crabs. Temperate Northern Atlantic, Temperate South America, Temperate Northern Pacific. 4 species (Shiino, 1942).

***Paguritherium* Reinhard, 1945**

*Diagnosis. Female* head with dorsal groove; antennula and antenna present as fused pads; maxilliped present. Pereon without ovarian processes; oostegites 1–5 present, oostegite 1 largest, ascendant and recurrent lobes present; other oostegites on posterior of pereon, multilobed, directed dorsally; oostegite 5 reduced. Heart in pleomere 1; 5 pairs of pleopods; posterior margin of pleomere 6 entire; uropods absent. *Male* antenna projecting beyond margin of head; pereopods unsegmented; medioventral spines and pleopods absent; posterior margin of

pleomere 6 entire. ***Epicaridium larva*** with pereopod 6 subequal in length to pereopod 5, dactylus reduced; pleopods 1–3 each with medial angle of peduncle bearing 1 long seta, exopod bearing 3 long setae; pleopod 4 with medial angle of peduncle bearing 1 short seta, exopod bearing 3 long setae; pleopod 5 reduced, setae absent. ***Cryptoniscus larva*** unknown.

Intertidal–shelf, parasitising pagurid hermit crabs. Temperate Northern Atlantic. 2 species (DeTorre et al. 2023; Reinhard, 1945).

***Synalpheion* Coutière, 1908**

*Diagnosis. Female* head without dorsal groove; maxilliped absent. Pereon with 2 pairs of posterolateral ovarian processes; brood pouch formed by 2 pairs of oostegites; 1 oostegite on each ovarian process; oostegites multilobed, folded; oostegite 1 absent. Heart in pleomere 1; 5 pairs of uniramous pleopods; posterior margin of pleomere 6 entire; uropods absent. *Male* antenna slightly projecting beyond margin of head; pereopods unsegmented; pereomeres without lateral projections; medioventral spines and pleopods absent; posterior margin of pleomere 6 entire; uropods absent. ***Epicaridium larva*** with pereopod 6 subequal in length to pereopod 5, carpo-propodus with 2 processes; pleopods 1–4 each with medial angle of peduncle bearing 1 long seta, exopod bearing 3 long setae; pleopod 5 with medial angle of peduncle bearing 1 seta, exopod bearing 3 long setae. ***Cryptoniscus larva*** unknown.

Subtidal, parasitising alpheid shrimps. Tropical Atlantic. 1 species (Coutière, 1908).

**Subfamily Entioninae Codreanu, Codreanu and Pike, 1960*****Achelion* Hartnoll, 1966**

*Diagnosis. Female* oostegite 1 with well-developed ascendant, transverse and recurrent lobes, oostegites 2–5 delicate, fused. Thorax with 2 large midventral ovarian processes, dorsal ovarian processes absent. Heart in pleomere 3. Pleural lamellae 1–4 convoluted, 5 simple. *Male* head fused with pereomere 1. Pereomeres with flattened lateral expansions. Medioventral spines on pleomeres 1 and 2. Pleomere 6 bifid. ***Epicaridium larva*** with pereopod 6 much longer than others, carpo-propodus with well-developed terminal process, dactylus reduced. ***Cryptoniscus larva*** unknown.

Subtidal, parasitising mithracid crabs. Tropical Atlantic. 1 species (Hartnoll, 1966).

***Allocancrion* Uyeno and Boyko, 2020**

*Diagnosis. Female* with body U-shaped. Head oval with 2 bulbous cephalic lobes; 2 pairs of antennal lobes. Maxillipeds paired, uniramous. Pereon with 4 pairs of ventrolateral ovarian processes, without ventral processes; pereopods absent. Oostegite 1 well developed, composed of ascendant lobe, elongate transverse lobes, and large recurrent lobe. Oostegites 2–5 fused into single large membranous flap covering oostegite 1. Pleon not distinctly segmented, bulbous heart in pleomere 3, 5

pairs of uniramous pleopods; pleomeres 1–3 with pair of pleural lamellae; pleopods 1–4 with oval lobes; pleopod 5 as small lobe. Terminal pleomere with 2 pairs of tapered projections. *Male* with ovoid head, incompletely fused to pereomere 1. Eyes present. Antennula as bulbous lobe with cluster of setae. Antenna absent. Maxilliped a conical projection with apical element. Pereon with 7 pereomeres, 1–5 each with pair of pereopods. Pereopods increasing in size posteriorly, all segments distinct. Pereomere 7 with pair of lateral gonopores. Pleon with 5 pleomeres plus pleotelson; pleopods absent; pleotelson with pair of tapering lateral lobes, uropods absent. ***Epicaridium larva*** antennula with 3 articles. Antenna elongate, with 6 articles. Mandible 2 segmented. Maxilla slender with apical long seta. Maxilliped with 2 apical setae. Pereon with 6 pairs of pereopods. Pereopods 1–6 subequal in size with all articles distinctly separated except carpus fused to propodus. Pereopod 6 with small dactylus incompletely fused to carpo-propodus. Pleon with 6 pleomeres and pleotelson. 5 pairs of uniramous pleopods. Terminal pleomere with biramous uropods; exopod and endopod subequal in length with 2 setae each and sharp processes on distal tip. ***Cryptoniscus larva*** unknown.

Intertidal, parasitising plagusiid crabs. Central Indo-Pacific. 1 species (Uyeno and Boyko, 2020).

***Cancrion* Giard and Bonnier, 1887**

*Diagnosis. Female* with dorsal ovarian processes, ventral processes absent; oostegite 2 covering basal part of oostegite 1. Pleural lamellae of pleomeres 1 and 2 complex, pleomeres 3 and 4 complex or simple. *Male* without ventromedial spines on pleon. ***Epicaridium larva*** with pereopod 6 much longer than pereopod 5, distodorsal margin of carpo-propodus with well-developed flange-like process. ***Cryptoniscus larva*** with 7 pairs of isomorphic pereopods.

Intertidal-subtidal, parasitising panopeid, pilumnid, portunid, and xanthid crabs. Temperate Northern and Tropical Atlantic, Temperate South America, Temperate Northern Pacific, Central Indo-Pacific, Temperate Australasia. 8 species (Oanh and Boyko, 2020).

***Cryptocancrion* Williams, Boyko, Tepolt and Blakeslee, 2023**

*Diagnosis. Female* with sheath secreted by host surrounding parasite except for perforation at posterior end. Head as 2 bulbous lobes, bearing 2 pairs of antennae, 1 pair of minute maxillipeds. Pereon compact, with variable (0–4) numbers of dorsal ovarian processes; pereopods absent. 5 pairs of oostegites forming brood pouch; oostegite 1 with ascendant lobe projecting anteriorly and dorsally, 2 simple transverse lobes, 1 recurrent lobe extending entire length of pereon; oostegites 2–5 fused in mature females. Pleon composed of 5 segments with overlapping uniramous pairs of pleopods, terminal pair expanded laterally. 2 pairs of complex pleural lamellae on pleomeres 1 and 2; bulbous heart in pleomere 3. Distal end of pleon with 2 finger-like projections. *Male* head fused with pereomere 1, pereomeres 2–7 distinct dorsally. Head with pair of large eyes. Antennulae as large, separate ovate lobes, with short setae; antennae absent. Maxillipeds absent. Pereopods 1–6 with propodus and carpus fused; pereopod 7 reduced to rounded nub. Pleon of 5 segments plus pleotelson; pleomeres distinctly narrower posteriorly, pleopods absent. Pleotelson with 2 short, distally rounded, lobes; uropods absent. ***Epicaridium larva*** with antennula of 3 articles; antenna elongated, approximately half length of body, of 6 articles. Oral cone with sucker-shaped structure at terminus. Pereopod 6 subequal in length to other pereopods, propodus bearing long digitiform process tipped with long terminal setae and small pointed dactylus. ***Cryptoniscus larva*** unknown.

Intertidal, parasitising panopeid crabs. Temperate Northern Atlantic. 1 species (Williams et al., 2023).

***Entione* Kossmann, 1881**

*Diagnosis. Female* with 2 large unpaired ventral ovarian processes, posterior process slightly longer than anterior; 2 pairs of large dorsolateral ovarian processes surrounding 2 pairs of small tubercles. Oostegite 1 with ascendant and recurrent lobes. Pleural lamellae well developed (2 or 3 pairs), pleopods reduced, lamellar. *Male* with jointed pereopods. Terminal pereonal segment and pleomeres 1 and 2 with medioventral spines. ***Epicaridium larva*** pereopod 6 subequal in length to pereopod 5. ***Cryptoniscus larva*** unknown.

Subtidal, parasitising inachid and grapsid crabs. Temperate South America, Temperate Northern Atlantic. 2 species (Giard and Bonnier, 1887).

***Entionella* Miyashita, 1941**

*Diagnosis. Female*, first oostegite with well-developed ascendant, lateral and recurrent lobes. Thorax without ovarian processes. Heart in pleomere 3. *Male* with jointed pereopods. Pereomeres expanded laterally as flat plates. Pleomeres 1–4 with medioventral spines. ***Epicaridium larva*** with pereopod 6 subequal in size to others, dactylus reduced (note: above is for the type species, others with pereopod 6 longer than 5). ***Cryptoniscus larva*** body elongate, fusiform. Antennula of 3 segments, basal joint not toothed; antenna of 5 segments, reaching to pereomere 3. Coxal plates narrow, without teeth. 7 pairs of pereopods present, anterior 4 pairs with stout propodi, last 3 pairs more elongate with slender propodi and elongated dactyli. Pleon of 5 segments, each with pair of pleopods. Uropodal inner ramus longer than outer ramus; each ramus with 1 long and 1 short seta.

Intertidal–subtidal, freshwater and marine, parasitising eriphiid, majid, sesarmid and varunid crabs. Temperate Northern Atlantic, Temperate Northern Pacific. 4 species (Demassieux and Veillet, 1980).

***Micippion* Shiino, 1942**

*Diagnosis. Female* with 2 ventral ovarian processes and one dorsal ovarian process. Marsupium complete, oostegite 1 enclosed by oostegite 2, which is completely fused with oostegite 3; oostegites 4 and 5 separate. Pleural lamellae of pleomeres 1–4 folded. *Male*, head fused with pereomere 1; pleomere 1 with medioventral spines. ***Epicaridium larva*** with pereopod 6 well developed, propodus bearing terminal process. ***Cryptoniscus larva*** unknown.

Subtidal, parasitising majid crabs. Temperate Northern Pacific. 1 species (Shiino, 1942).

***Pinnixion* McDermott, Williams and Boyko, 2019**

*Diagnosis. Female* with sheath secreted by host surrounding entire parasite except for perforation at posterior end. Head rounded, dorsally distinctly divided into 2 bulbous lobes, bearing 2 pairs of antennae. Maxilliped with subquadrate curved coxopod, lamellar exopod. Pereon without ovarian processes, pereopods absent. 5 pairs of oostegites forming brood pouch, margins entire. Oostegite 1 with 1 ascendant lobe, 2 transverse lobes, 1 recurrent lobe; oostegites 2–5 fused in mature females, covering oostegite 1. Pleomeres 1–3 each with distinct uniramous flattened pair of pleopods overlaying one another; pleomeres 4, 5 with reduced pleopods. 2 pairs of complex pleural lamellae positioned medially on pleon. Bulbous heart in pleomere 3. Terminal pleomere with pair of anteroventral lobes, 2 long, tapered lateral projections, 4 distal finger-like projections. *Male* with pereomere 1 ventrally fused with trapezoidal head. Head with pair of mediolateral cephalic slits, eyes present. Antennulae as large ovate lobes fused medially; antenna absent. Pair of mitten-shaped maxillipeds at base of

oral cone. Pereomere 7 with small, setose medioventral spine. 6 pairs of pereopods with dactylus; propodus, carpus fused into 1 cylindrical segment. Pleomeres 1, 2 with large lateral hemispherical lobes, lobes on pleomere 1 more than twice as large as those on pleomere 2. Pleotelson with 2 elongated tapered posterolateral lobes. **Epicaridium larva** with antennula of 2 rounded articles, antenna elongated, approximately half length of body, of 6 articles. Pereopod 6 greatly elongated with long, cylindrical process, articulated with propodus/carpus dorsal to dactylus. **Cryptoniscus larva** unknown.

Subtidal, parasitising pinnotherid crabs. Temperate Northern and Tropical Atlantic. 1 species (McDermott et al., 2019).

#### ***Pinnotherion* Giard and Bonnier, 1889**

*Diagnosis. Female* with 2 ventral ovarian processes, dorsal processes absent. Marsupium closed, oostegite 1 without transverse lamella, enclosed by other pairs. Pleural lamellae folded in pleomeres 1–4. *Male* head fused with pereomere 1; pleomeres with ventromedial processes. **Epicaridium larva** with pereopod 6 not prehensile or longer than others, rudimentary dactylus present. **Cryptoniscus larva** body elongate, fusiform; 7 pairs of pereopods, 1–6 each with short dactyli, pereopod 7 with elongate dactylus.

Subtidal, parasitising inachid and pinnotherid crabs. Temperate Northern Atlantic, Temperate Northern Pacific. 2 species (Shiino, 1942).

#### ***Portunion* Giard and Bonnier, 1886**

*Diagnosis. Female* with 2 ventral and 1 pair of anterodorsal ovarian processes. Marsupium complete; ascendant lamellae of oostegite 1 entirely covered by oostegite 2. Pleomeres 1–4 with folded pleural lamellae. *Male* head fused or distinct from pereomere 1; pleon with medioventral spines. **Epicaridium larva** with pereopod 6 not prehensile or longer than others; propodus with simple process at tip and rudimentary dactylus. **Cryptoniscus larva** body elongate, fusiform; 7 pairs of pereopods, 1–6 each with short dactyli, pereopod 7 with elongate dactylus.

Subtidal, parasitising carcinid, epialtid, grapsid, polybiid and varunid crabs. Temperate Northern Atlantic (including Mediterranean Sea), Indo-West Pacific, Temperate Northern Pacific. 10 species (Chaix and Veillet, 1981; Huang et al., 2025; Oanh and Boyko, 2026).

#### ***Priapion* Giard and Bonnier, 1888**

*Diagnosis. Female* with anterior pair of dorsolateral ovarian processes, 2 unpaired ventral ovarian processes; last pereomere with 2 large, rounded bulges. Pleural lamellae of pleon and pleopods highly developed on lateral edges of pleon, terminal segment with 2 symmetrical, quadrangular parts, joined to each other along almost entire length. *Male* head not fused with pereomere 1; pleomere 1 with elongate penis. **Epicaridium larva** unknown. **Cryptoniscus larva** unknown.

Subtidal, parasitising polybiid crabs. Temperate Northern Atlantic. 1 species (Giard and Bonnier, 1888).

#### ***Tiarinion* Shiino, 1942**

*Diagnosis. Female* with 2 ventral processes, dorsal processes absent. Oostegite 1 with well-developed ascendant lamella, smaller transverse and recurrent lamellae that may be fused. Oostegite 1 largely uncovered by oostegite 2; oostegites 3–5 small, rudimentary; oostegite 6, 7 present or absent. Pleural lamellae folded on pleomeres 1, 2, simple on pleomeres 3, 4. *Male* head fused with pereomere 1; pleomeres 1, 2 with medioventral spines or spines absent. **Epicaridium larva** with pereopod 6 much longer than others, strongly prehensile, propodus bearing well-developed terminal process. **Cryptoniscus larva** antennula of 6 segments. Maxilliped present. Merus of first pereopod with 1 spine on outer side and 1 seta on inner side. Pleon with shallow median notch on posterior margin.

Subtidal, parasitising epialtid crabs. Temperate Northern Pacific, Central Indo-Pacific. 2 species (Shields and Ward, 1998).

#### ***Xanthion* Shiino, 1942**

*Diagnosis. Female* with single ventral process. Marsupium incompletely closed, ascendant lamella of oostegite 1 largely uncovered by oostegite 2. Pleural lamellae of pleomeres 1–4 folded. *Male* head fused with pereomere 1; pleon ventromedial spines absent. **Epicaridium larva** with pereopod 6 much longer than others, strongly prehensile, propodus bearing well-developed terminal process. **Cryptoniscus larva**, body wider anteriorly than posteriorly. Basal 2 joints of antennula denticulate on posterior margins. Maxilla and maxilliped absent. Coxal plates entire on posterior border. Propodus of pereopods 1–6 more or less crenulate on distal margin, carpus very thin, tipped with 1 short spine, merus tipped with 1 long, sharp spine. Pleopods 1–4 with protopod nearly quadrate, bearing 3 long plumose setae and 1 short non-plumose seta at inner distal angle and 2 simple setae at inner proximate angle; exopod with 1 long plumose and 1 short simple seta. Triangular protopod of pleopod 5 with endopod bearing 2 setae.

Subtidal, parasitising xanthid crabs. Temperate Northern Pacific. 1 species (Shiino, 1942).

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## Family Ionidae H. Milne Edwards, 1840

Figure 6.24

All members of the Ionidae are branchial ectoparasites of callinassid shrimps. The only species in Ionidae with well-described females, males and cryptoniscus larvae is *Ione thoracica* (Montagu, 1808). This species, and perhaps all the species in the genus, possess the ability for differentiated males to undergo a sex change based on environmental conditions (i.e. loss of the mature female in the branchial chamber of the host); the reverse (females changing to males) may also occur (Reinhard, 1949; Reverberi and Pittoti, 1943). The ramified lateral plates of females and the elongate lateral plates of males are distinctive, as are the denticles on the basal articles of the antennulae of cryptoniscid larvae (bopyroid cryptoniscus larvae typically have smooth basal articles on the antennulae).

**Diagnosis. Female** (fig. 6.24a, c, d) body elongate; pereomeres distinct; head wider than long, oval, partly embedded in pereomere 1. Head entire, not distorted. Frontal lamina present, extending laterally as 2 tapered lobes. Eyes absent. Barbula with 3 smooth, tapered lobes on each side.

Antennula and antenna articulated. Maxilliped without palp. Marsupium open or closed. 5 pairs of oostegites; oostegite 1 with short, rounded posterior lobe; internal ridge smooth or digitate. Pereomeres 1–4 with coxal plate and dorsolateral bosses. Middorsal projections absent. 7 pairs of pereopods, progressively longer posteriorly. Pleon of 6 distinct pleomeres; 5 pairs of uniramous lateral plates, each divided into numerous distal rami. 5 pairs of pleopods, usually biramous (1 or 2 pairs sometimes uniramous). Uropods uniramous. **Male** (fig. 6.24b) body with pereomeres subequal in width or widest at middle; head wider than long, narrower than or subequal in width to pereomere 1. Eyes present or absent. Antennula and antenna articulated. Midventral tubercles absent. 7 pairs of pereopods, posterior pairs larger. Pleomeres 1–6 distinct or medially fused, all with elongate lateral plates; pleopods and uropods absent. **Cryptoniscus larva** (fig. 6.24e–g) body teardrop-shaped, eyes present. Antennula with denticles on basal article, without large teeth. Oral sucker absent. Pereomeres without toothed coxal plates. Pereopods 1–7 subequal in size and

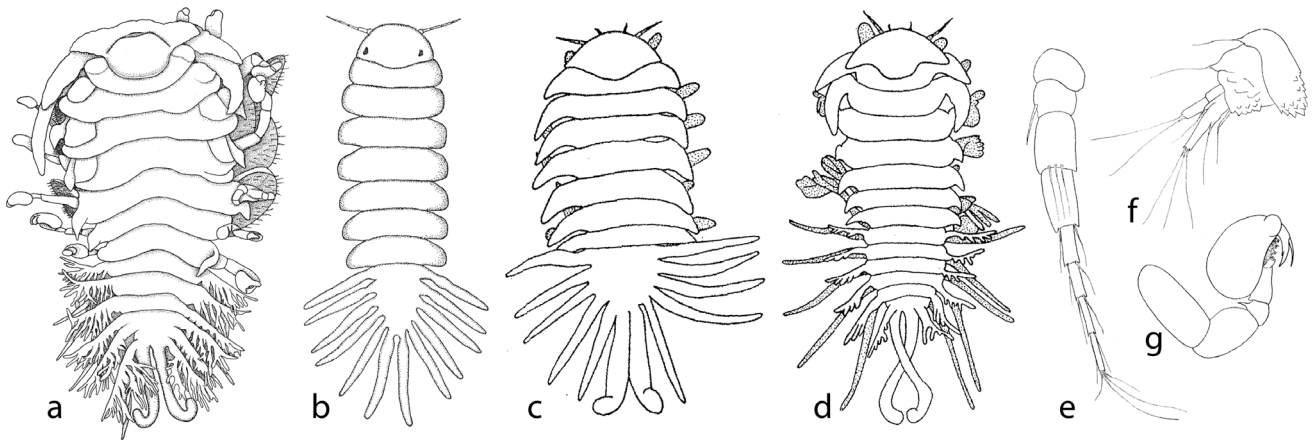


Figure 6.24. Ionidae. *Ione thoracica* (Montagu, 1808): a, female dorsal view; b, male dorsal view; c, d, juvenile females dorsal view; e, cryptoniscus larva antenna; f, cryptoniscus larva antennula; g, cryptoniscus larva pereopod.

shape, dactyli weakly bifid with large dorsal seta, propodi with stout setae on margin. 5 biramous pleopods. Uropodal exopod larger and longer than endopod. Pleotelson heart-shaped, without teeth. Branchial parasites.

#### *Ione* Latreille, 1818

*Diagnosis.* As for family.

Intertidal, parasitising callianassid shrimps. Temperate Northern Atlantic, Western and Central Indo-Pacific, Temperate Northern and Tropical Eastern Pacific, Temperate South America. 7 species (Hernández et al., 2023).

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### Superfamily Cryptoniscoidea Kossmann, 1880

As with Bopyroidea, Cryptoniscoidea is difficult to diagnose. Cryptoniscoids exhibit a wide range of associations with definitive hosts (endoparasitic, mesoparasitic and ectoparasitic, including some hyperparasites). Trilles (1999) stated that all cryptoniscoids are protandrous hermaphrodites (the cryptoniscus larva transforms into a functional male that attaches to a definitive host and become female if one is not present) with species in only one genus, *Scalpelloniscus*, being possibly gonochoristic (Grygier, 1981). However, Trilles (1999) did not include Dajidae and Entophilidae in Cryptoniscoidea, and data for sexual development in most cryptoniscoid species have not been recorded. Functionally adult males (i.e. capable of fertilisation) appear externally indistinguishable from the cryptoniscus larval stage in most families, but in Dajidae and Entophilidae males are of a distinct morphotype and similar to those in Bopyroidea. Females of species in many genera are greatly modified, with body shapes partly or wholly sac-like (Hemioniscidae), globular (Crinoniscidae) or stellate (Stellatoniscidae). However, females in Dajidae and Entophilidae

are similar to those in Bopyroidea (i.e. with clear body segmentation and pereopods).

The only morphological character that appears to be a synapomorphy for cryptoniscoids is the number of articles of the antenna of the cryptoniscus larval stage (4 basal plus 5 flagellar articles) (Boyko and Williams, 2015). This is supported by molecular data that distinguishes the epicaridean superfamilies (Boyko et al., 2013).

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## Family Asconiscidae Bonnier, 1900

Figure 6.25

The sole species in Asconiscidae can be distinguished from other cryptoniscoid epicarideans by the form of the female, which is reduced to an irregular sac that is extruded from the ventral surface of the cryptoniscus larval stage to which it remains attached, as well as by the strong cuticular ridges on the first two segments of the antennula and the three long thick setae on the first segment of the antennula (Sars, 1899). The sole species is an ectoparasite of mysids.

**Diagnosis. Male** (paedomorphic cryptoniscus larva) (fig. 6.25c–g) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth but with strong cuticular striations, three large setae near posterior margin, article 2 with strong cuticular striations. Coxal plates without teeth. Pereopods 1 and 2 gnathopodal, pereopods 3–7 ambulatory; propodi of pereopods 3–5 quadrate distally, pereopods 6 and 7 tapering distally. Pleotelson margin smooth. **Immature females** with slight indication of segmentation (fig. 6.25a). **Mature females** (fig. 6.25b) without segmentation, sac-like, extending ventrally and attached to cryptoniscus larval body. Ectoparasitic.

### *Asconiscus* G.O. Sars, 1899

**Diagnosis.** As for family.

Subtidal–bathyal, parasitising *Boreomysis arctica* (Krøyer, 1861) (Mysida). Temperate Northern Atlantic. 1 species (Nielsen and Strömberg, 1973a, b; Sars, 1899).

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## Family Cabiropidae Giard and Bonnier, 1887

Figure 6.26

As can be seen from the diagnosis below, Cabiropidae is something of a “wastebasket” family in Cryptoniscoidea. The family contains members that are endoparasitic, mesoparasitic or ectoparasitic (including hyperparasites) in the marsupium of isopods and other hosts. Two genera are known from cryptoniscus larvae only and a third is known from cryptoniscus larvae and immature females only, while five other genera are known only from females, which are highly reduced in morphology. It is likely that some if not most genera in this family will eventually be placed elsewhere in Cryptoniscoidea. If discussing only those genera that share characters with the type genus *Cabirops* (*Arcturocheres*, *Bourdonia*, *Perezina* and *Rolandoniscus*), these five genera can be distinguished from other epicarideans in that the females are compressed laterally and recurved and found unattached in the marsupia of their hosts and pass through 4 stages of development, including a stage with pronounced dorsal lobes and a mature form with a row of chitinous plates along the ventral margin in the centre of the body (the mature stage has not been observed in *Arcturocheres*).

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with or without prominent cuticular striations. Head wider than long, oral cone directed anteriorly or posteriorly. Eyes present or absent. Antennula article 1 with 3–11 posterior teeth or lacking teeth. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal or ambulatory (if ambulatory, propodi quadrate distally), dactyli bifid or entire; pereopods 3–7 ambulatory; propodi of 3–5 quadrate distally, 6 and 7 tapering distally. Pleotelson margin with or without teeth. **Immature female** body compressed laterally, recurved, with numerous dorsal lobes, segmentation indistinct or dorsoventrally compressed, with segmentation visible or body subdivided into 2 portions: a 2-pronged posterior portion anchored in the host’s visceral cavity and a segmented anterior end; head distinct with mouthparts and pair of reduced pereopods surrounding it, or indistinct. **Mature female** compressed laterally and recurved, with row of chitinous plates along ventral margin in centre of body or dorsoventrally compressed and rounded, elongate, or quadrate; segmentation present or absent; lobes present or absent; appendages or mouthparts present or absent. Endoparasitic, mesoparasitic and ectoparasitic.

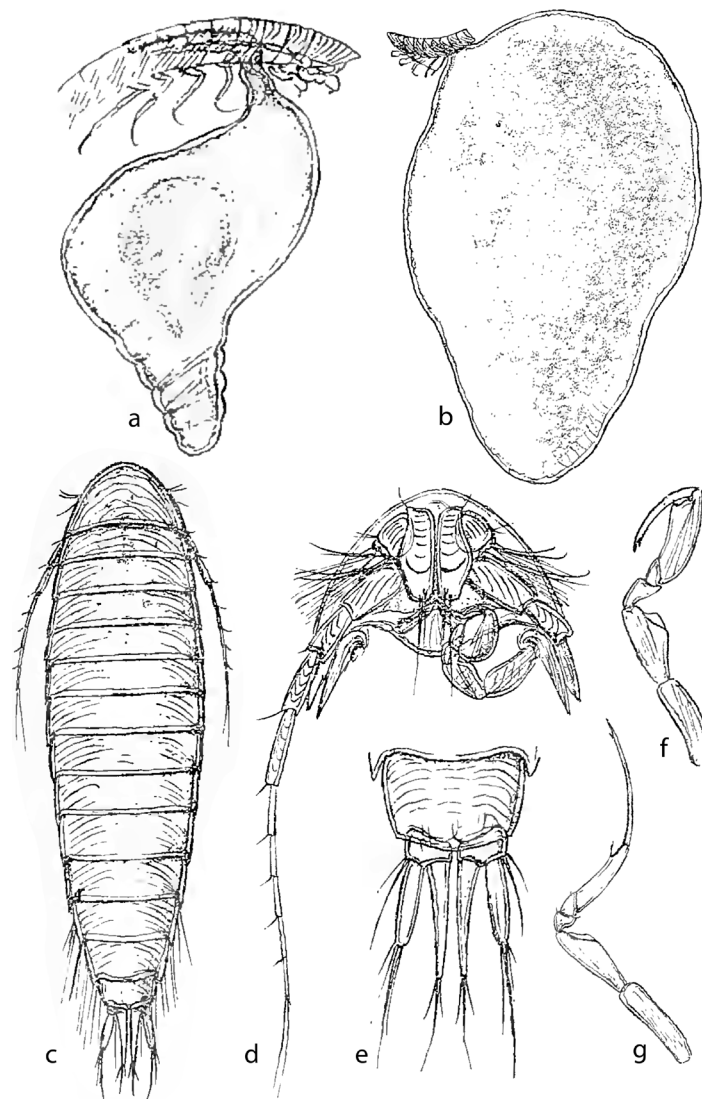


Figure 6.25. Asconiscidae. *Asconiscus simplex* G. O. Sars, 1899: a, immature female lateral view; b, mature female lateral view; c, male dorsal view; d, male head, ventral view; e, male pleon, dorsal view; f, male pereopod 3; g, male pereopod 7.

### Key to genera of Cabiropidae

*Cironiscus*, *Pleuroniscus*, *Podoniscus* and *Rolandoniscus* are not in the key to genera; they are known only from cryptoniscus larvae.

1. Body of mature female body embedded in host ..... 2
- Body of mature female not embedded in host ..... 3
2. Body of mature female (fig. 6.26a) entirely within host rhizocephalan ..... *Perezina*
- Approximately half of body of mature female (fig. 6.26b, c) embedded in host isopod ..... *Ancyroniscus*
3. Body of mature female compressed dorsoventrally, not recurved ..... 4
- Body of mature female compressed laterally, recurved ventrally ..... 10
4. Body of mature female (fig. 6.26d, e) elongate, with lateral bulges ..... *Anthuroniscus*
- Body of mature female not elongate, without lateral bulges ..... 5

- |     |   |                      |
|-----|---|----------------------|
| 5.  | Body of mature female body heart-shaped .....   | 6                    |
| –   | Body of female not heart-shaped .....   | 7                    |
| 6.  | Mature female (fig. 6.26f) hyperparasitising cryptoniscoid epicarideans on amphipods .....  | <i>Gnomoniscus</i>   |
| –   | Mature female (fig. 6.26g) parasitising asellote isopods .....  | <i>Munnoniscus</i>   |
| 7.  | Body of mature female (fig. 6.26h; see also male fig. 6.26i–l) much longer than wide; found in marsupium of host cirolanid isopods .....                          | <i>Cirolaniscus</i>  |
| –   | Body of mature female length and width subequal .....   | 8                    |
| 8.  | Body of mature female (fig. 6.26m) with flap-like lateral lobes; found in marsupium of host aegid isopods .....   | <i>Aegoniscus</i>    |
| –   | Body of mature female with ovate lateral lobes .....  | 9                    |
| 9.  | Mature female (fig. 6.26n, o) with pereopods; found in marsupium of host nebaliceans .....  | <i>Apocumoechus</i>  |
| –   | Mature female (fig. 6.26p) without pereopods, found in marsupium of host isopods .....  | <i>Clypeoniscus</i>  |
| 10. | Cryptoniscus larva (figs. 6.6e, 6.26r–t; see also female, figs. 6.6c, d, 6.26q) with dactylus of pereopod 1 bifurcated at tip; parasites of bopyrid isopods ..... | <i>Cabirops</i>      |
| –   | Cryptoniscus larva with dactylus of pereopod 1 not bifurcated at tip .....  | 11                   |
| 11. | Cryptoniscus larva (fig. 6.26v; see also female, fig. 6.26u) with dactylus of pereopod 6 deeply bifurcated; parasites of antarcturid isopods .....                | <i>Arcturocheres</i> |
| –   | Cryptoniscus larva (fig. 6.26x; see also female, fig. 6.26w) with dactylus of pereopod 6 not bifurcated, parasites of bopyrid isopods .....                       | <i>Bourdonia</i>     |

### ***Aegoniscus* Barnard, 1925**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) not known. **Mature female** dorsoventrally compressed, ventral surface with medial line of 6 pairs of lobes, later margins with row of larger lobes.

Slope, parasitising aegid isopods. Temperate Southern Africa. 1 species (Barnard, 1925).

### ***Ancyroniscus* Caullery and Mesnil, 1919**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body teardrop-shaped (cuticular striations not described). Oral cone not described. Eyes present. Antennula article 1 with 11 posterior teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid, 3–7 ambulatory. Pleotelson margin with or without teeth. **Immature female** body subdivided into 2 parts: 2-pronged posterior portion anchored in the host's visceral cavity and segmented anterior end, with mouthparts and 2 pairs of rudimentary pereopods, projecting into the marsupium. **Mature female** without appendages or mouthparts; posterior and anterior portions subdivided into multiple rounded lobes filled with eggs.

Subtidal, parasitising aegid and sphaeromatid isopods (egg predators). Temperate Northern Atlantic, Temperate Australasia. 2 species (Bourdon and Bruce, 1980; Caullery and Mesnil, 1919).

### ***Anthuroniscus* Shiraki and Kakui, 2024**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body teardrop-shaped without prominent cuticular striations. Head wider than long, oral cone directed posteriorly. Eyes absent.

Antennula article 1 with 8 posterior teeth. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid; pereopods 3–7 ambulatory; propodi of 3–5 quadrate distally, 6 and 7 tapering distally. Pleotelson margin with or without teeth. **Mature female** dorsoventrally compressed, elongate; 6 pairs of lateral bulges indicating segmentation; mouthparts absent; appendages reduced to single putative pereopod 1 stub.

Subtidal, parasitising anthurid isopods (probable egg predators). Central Indo-Pacific. 3 species (Shiraki and Kakui, 2024).

### ***Apocumoechus* Nierstrasz and Brender à Brandis, 1931**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) not known. **Mature female** without segmentation, body fused into large marsupium with long median slit extending nearly entire length; 2 pairs of (apparently posterior) pereopods near oral area.

Subtidal, parasitising nebaliceans. Tropical Atlantic. 1 species (Nierstrasz and Brender à Brandis, 1931).

### ***Arcturocheres* Hansen, 1916**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Oral cone directed anteriorly. Eyes absent. Antennula article 1 with 6 posterior teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid, 3–7 ambulatory; dactylus of pereopod 6 bifurcated. Pleotelson margin smooth. **Immature female** segmented, body recurved; **mature female** not known.

Slope–bathyal, parasitising antarcturid isopods. Arctic, Southern Ocean. 2 species (Boyko, 2013).

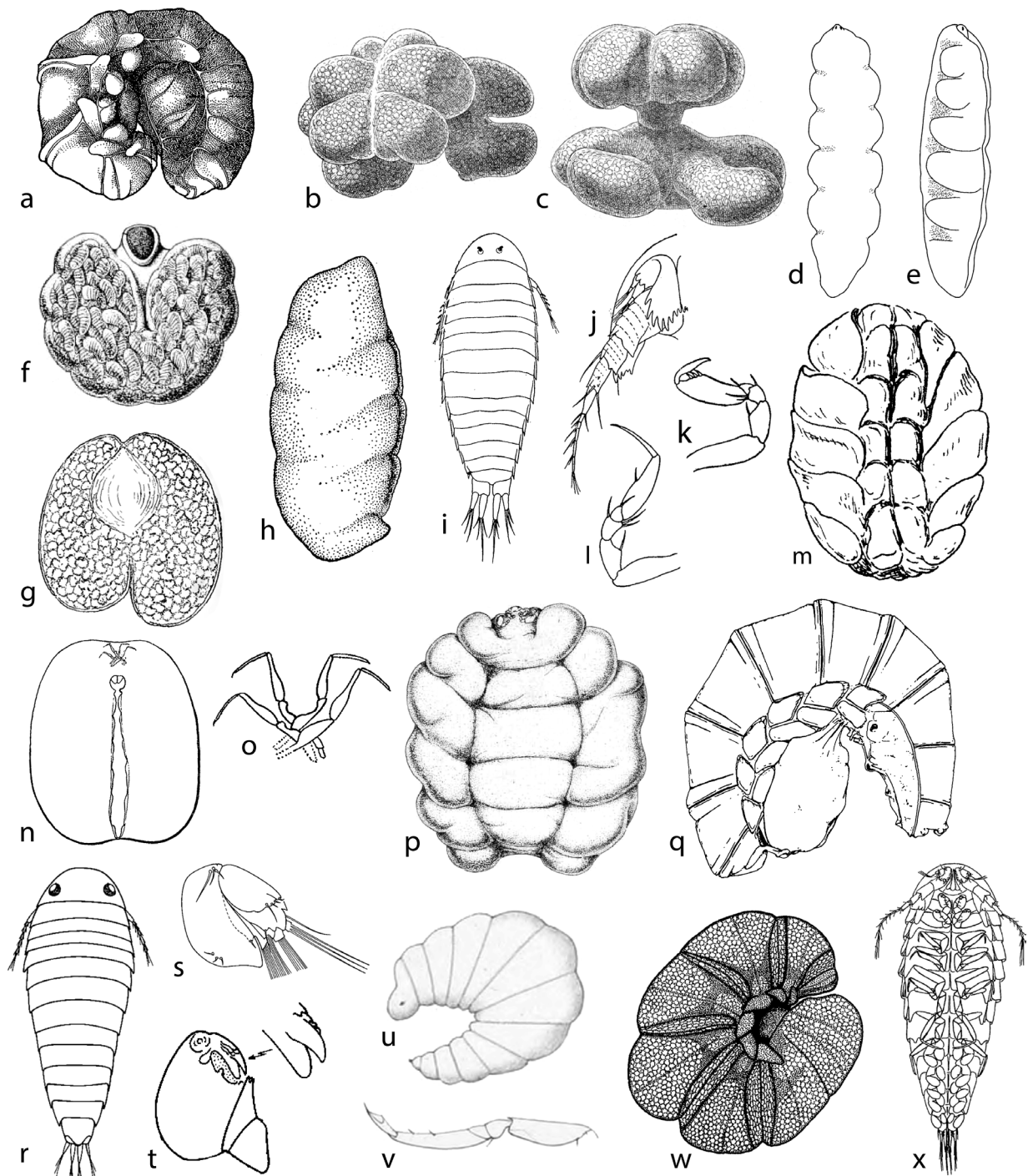


Figure 6.26. Cabiropidae. *Perezina gregaria* (Nierstrasz and Brender à Brandis, 1929): a, female lateral view. *Ancyoniscus bonnieri* Caullery and Mesnil, 1919: b, female dorsal view (segmented region extends from isopod host body); c, female lateral view (top portion extends from isopod host body, bottom portion within body of host). *Anthuroniscus* Shiraki and Kakui, 2024: d, female ventral view; e, female lateral view. *Gnomoniscus podasconis* Giard and Bonnier, 1895: f, female lateral view showing dorsal organ, anterior opening of marsupium and developing embryos. *Munnoniscus marsupialis* (G.O. Sars, 1883): g, female lateral view showing developing embryos in marsupium. *Cirolaniscus willeyi* Pillai, 1966: h, female lateral view; i, male dorsal view; j, male pereopod 1; k, male pereopod 7. *Aegoniscus gigas* Barnard, 1925: m, female ventral view. *Apocumoechus paranebaliae* Nierstrasz and Brender à Brandis, 1931: n, female ventral view; o, female pereopods (originally labelled incorrectly as first and second antennae). *Clypeoniscus hanseni* Giard and Bonnier, 1895: p, female ventral view. *Cabirops montereyensis* Sassaman, 1985: q, female lateral view; r, male dorsal view; s, male antennula; t, male pereopod 1, inset shows bifid tip of dactyl; *Arcturocheres pulchripes* Hansen, 1916: u, female lateral view; v, male pereopod 6. *Bourdonia tridentata* Rybakov, 1990: w, female lateral view; x, male ventral view.

***Bourdonia* Rybakov, 1990**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Oral cone directed anteriorly. Eyes absent. Antennula article 1 with 3 blunt posterior teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid, 3–7 ambulatory. Pleotelson margin smooth. **Mature female** with segmentation visible, body recurved, row of chitinous plates along ventral margin in centre of body.

Subtidal, slope, hyperparasitising bopyrid isopods. Temperate Australasia, Temperate Northern Pacific. 2 species (Boyko, 2013; Boyko et al., 2024).

***Cabirops* Kossmann, 1884**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Oral cone directed anteriorly. Eyes present. Antennula article 1 without teeth. Pereopods 1 and 2 gnathopodal, dactylus bifid, 3–7 ambulatory, dactylus less than half length of propodus; 6 and 7 with dactylus as long as propodus. Pleotelson margin smooth. **Immature female** body recurved with numerous dorsal lobes, segmentation indistinct; **mature female** body recurved with segmentation visible, row of chitinous plates along ventral margin in centre of body.

Subtidal–slope, hyperparasitising bopyrid isopods. Tropical and Temperate Northern Atlantic, Temperate Southern Africa, Central Indo-Pacific, Temperate Northern Pacific. 15 species (Boyko, 2013).

***Cirolaniscus* Pillai, 1966**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped (cuticular striations not described). Oral cone not described. Eyes present. Antennula article 1 with 8 posterior teeth. Pereopods 1–7 ambulatory, dactylus not bifid; propodus of pereopod 1 quadrate distally, 7 tapering distally (other pereopods not described). Pleotelson margin smooth. **Mature female** quadrate, vestigial segmentation visible; anterior 2/3 of body with 2 large rectangular lobes nearly meeting in midline; appendages absent.

Subtidal, parasitising cirolanid isopods. Indo-West Pacific. 1 species (Pillai, 1966).

***Cironiscus* Nielsen, 1967**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped without prominent cuticular striations. Oral cone directed posteriorly. Eyes absent. Antennula article 1 with 8 posterior teeth. Pereopods 1 and 2 gnathopodal, dactylus not bifid, 3–7 ambulatory; dactyli of 3–5 shorter than propodi, slightly recurved, 6 and 7 longer than propodi, straight. Pleotelson margin with teeth. **Female** not known.

Subtidal, parasitising cirolanid isopods. Temperate Northern Atlantic. 1 species (Nielsen, 1967).

***Clypeoniscus* Giard and Bonnier, 1895**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped without cuticular striations. Oral cone directed posteriorly. Eyes absent. Antennula article 1 with 11 posterior

teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid, 3–7 ambulatory; dactyli of 3–5 less than half as long as propodi, 6 and 7 with dactyli 3/4 as long as propodi. Pleotelson margin with teeth. **Immature female** dorsoventrally compressed with segmentation visible, head distinct, surrounded by pair of reduced pereopods; **mature female** without segmentation, compressed dorsoventrally, ventral surface with median slit along entire length, dorsal surface with median groove along half of length and rounded “dorsal organ.”

Subtidal–slope, parasitising asellote and vaviliferan isopods. Arctic, Temperate Northern Atlantic, Temperate Southern Africa, Temperate Northern Pacific. 5 species (Barnard, 1920; Bourdon, 1967; Giard and Bonnier, 1895; Nielsen and Strömberg, 1973a, b; Nierstrasz and Brender à Brandis, 1929a). We herein designate *Clypeoniscus hansenii* Giard and Bonnier, 1895 as the type species of the genus.

***Gnomoniscus* Giard and Bonnier, 1895**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) not known. **Mature female** without segmentation; body compressed dorsoventrally, rounded with 2 large lateral lobes semi-divided by median groove; anterior end raised on short stalk.

Subtidal, hyperparasitising cryptoniscoid isopods. Temperate Northern Atlantic. 1 species (Boyko, 2013; Giard and Bonnier, 1895).

***Munnoniscus* Giard and Bonnier, 1895**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) not known. **Mature female** without segmentation; body compressed dorsoventrally, rounded with 2 large lateral lobes completely divided by median groove; anterior end not raised on short stalk.

Subtidal, parasitising asellote isopods. Temperate Northern Atlantic. 2 species (Boyko, 2013; Giard and Bonnier, 1895; Sars, 1899). We herein designate *Cryptothiria marsupialis* G.O. Sars, 1883 as the type species of the genus.

***Perezina* Nierstrasz and Brender à Brandis, 1930**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) not known. **Mature female** with segmentation visible, body recurved, row of chitinous plates along ventral margin in centre of body.

Subtidal, hyperparasitising rhizocephalan barnacles. Temperate Northern Atlantic. 1 species (Boyko, 2013; Nierstrasz and Brender à Brandis, 1929b).

***Pleuroniscus* Williams and Boyko in Williams, Boyko and Stewart, 2024**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body cylindrical with prominent cuticular striations. Oral cone directed anteriorly. Eyes absent. Antennula article 1 with 7 posterior teeth. Pereopods 1, 2 gnathopodal, 3–7 ambulatory, dactyli not bifid; 1–4 with toothed coxal plates; propodi of 3–5 quadrate distally; 6, 7, tapered distally; dactyli of 1–5 shorter than propodi, 6 and 7 as long as propodi. Pleotelson margin without teeth. **Mature female** not known.

Bathyal, hyperparasitising bopyrid isopods. Indo-West Pacific. 1 species (Williams et al., 2024).

**Podoniscus Bourdon, 1981**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Oral cone directed anteriorly. Eyes absent. Antennula article 1 with 8 posterior teeth. Pereopods 1–7 ambulatory, dactyli not bifid; propodi of 1–5 quadrate distally; dactyli of 1 and 2 as long as propodi, 3 and 4 as long as propodi and carpi combined, 5–7 as long as propodi, carpi and meri combined. Pleotelson margin with teeth. **Female** not known.

Bathypelagic, host(s) unknown. Southern Ocean. 1 species (Bourdon, 1981).

**Rolandoniscus Boyko, 2013**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped (cuticular striations not described). Oral cone not described. Eyes absent. Antennula article 1 with 8 posterior teeth. Pereopods 1 and 2 gnathopodal, dactyli not bifid, 3–7 ambulatory; dactyli of 3–5 shorter than propodi, 6 and 7 longer than propodi. Pleon with 5 medioventral tubercles. Pleotelson margin indented medially, smooth. **Female** poorly known (based on single damaged specimen), body with bilobed marsupium and lateral plates.

Slope, hyperparasitising bopyrid isopods. Temperate Northern Atlantic. 1 species (Bourdon, 1967; Boyko, 2013).

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## Family Capitoniscidae Boyko and Williams, 2023

Figure 6.27

Members of Capitoniscidae are ectoparasitic in the marsupium of cumaceans and an unknown host. They can be distinguished from other epicarideans by the greatly swollen head, lack of teeth on antennula segment 1, lack of teeth on the coxal plates, and morphology of pereopods 1 and 2 of the cryptoniscus larvae; the female appears to be spheroid and unsegmented with some appendages present, but is poorly described (Bourdon, 1972; Boyko and Williams, 2023).

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body elongate. Head wider than long, inflated anteroposteriorly, posterior margin wider than pereomere 1; eyes absent.

Antennula article 1 short, rounded, without marginal teeth; dense setal brush present. Coxal plates with weak marginal crenulations but without teeth. Pereopods 1–3 gnathopodal, 1 and 2 with globular propodi and thick dactyli extending to distal margin of merus, pereopod 3 with ovate propodus and slender dactylus extending to distal margin of carpus; pereopods 4–7 ambulatory with propodi tapering distally; each pereopodal dactylus bearing a distal tooth. Pleotelson triangular, with or without distal row of few stout teeth. **Mature female** spheroid in dorsal view, unsegmented, possibly with two pairs of pereopods and two pairs of posterior tubercles. Ectoparasitic.

### Key to cryptoniscus larvae of genera of Capitoniscidae

1. Cryptoniscus larva (fig. 6.27a–e; see female fig. 6.27f) pleotelson with terminal teeth, pereopods 3–5 of similar structure and segment proportions and different from pereopods 6 and 7; parasites of cumaceans ..... *Capitoniscus*
- Cryptoniscus larva (fig. 6.27g–l) pleotelson without terminal teeth, pereopods 3 of different structure and proportions than pereopods 4–7, all similar; host unknown ..... *Carocryptus*

### *Capitoniscus* Bourdon, 1972

**Diagnosis. Male** (paedomorphic cryptoniscus larva) pereopods 3–5 of similar structure and segment proportions and different from those of pereopods 6 and 7. Pleotelson triangular, with distal row of few stout teeth.

Bathypelagic, parasitising cumaceans, Temperate Southern Africa, Southern Ocean, Temperate South America. 3 species (Bourdon, 1972, 1981; Menzies and George, 1972).

### *Carocryptus* Schultz, 1977

**Diagnosis. Male** (paedomorphic cryptoniscus larva) pereopod 3 of different structure and segment proportions from pereopods 4–7. Pleotelson triangular, without distal row of teeth.

Bathypelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

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## Family Crinoniscidae Bonnier, 1900

Figure 6.28

Members of Crinoniscidae are endoparasitic and can be distinguished from other isopod parasites of barnacles by the lack of teeth on the basal segment of the antennula in males (= cryptoniscus larval stage); females are egg predators (Williams and Boyko, 2006; Buhl-Mortensen et al., 2020).

**Diagnosis. Male** (paedomorphic cryptoniscus larva) (fig. 6.28d–h) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes present. Antennula article 1 without posterior teeth. Coxal

plates without teeth. Pereopods 1 and 2 gnathopodal, pereopods 3–7 ambulatory; propodi of pereopods 3–5 quadrate distally with dactyli shorter than propodi, pereopods 6 and 7 tapering distally, dactyli subequal to propodi in length. Pleotelson margin smooth. **Immature female** (fig. 6.28b, c) segments incompletely fused, lacking appendages except for unarticulated antenna in some species, mandibles and elongate second pereopods. **Mature female** (fig. 6.28a) fusiform or anteriorly globose, posteriorly annulated, lacking appendages (remnants of pereopod 2 present in some species). Endoparasitic.

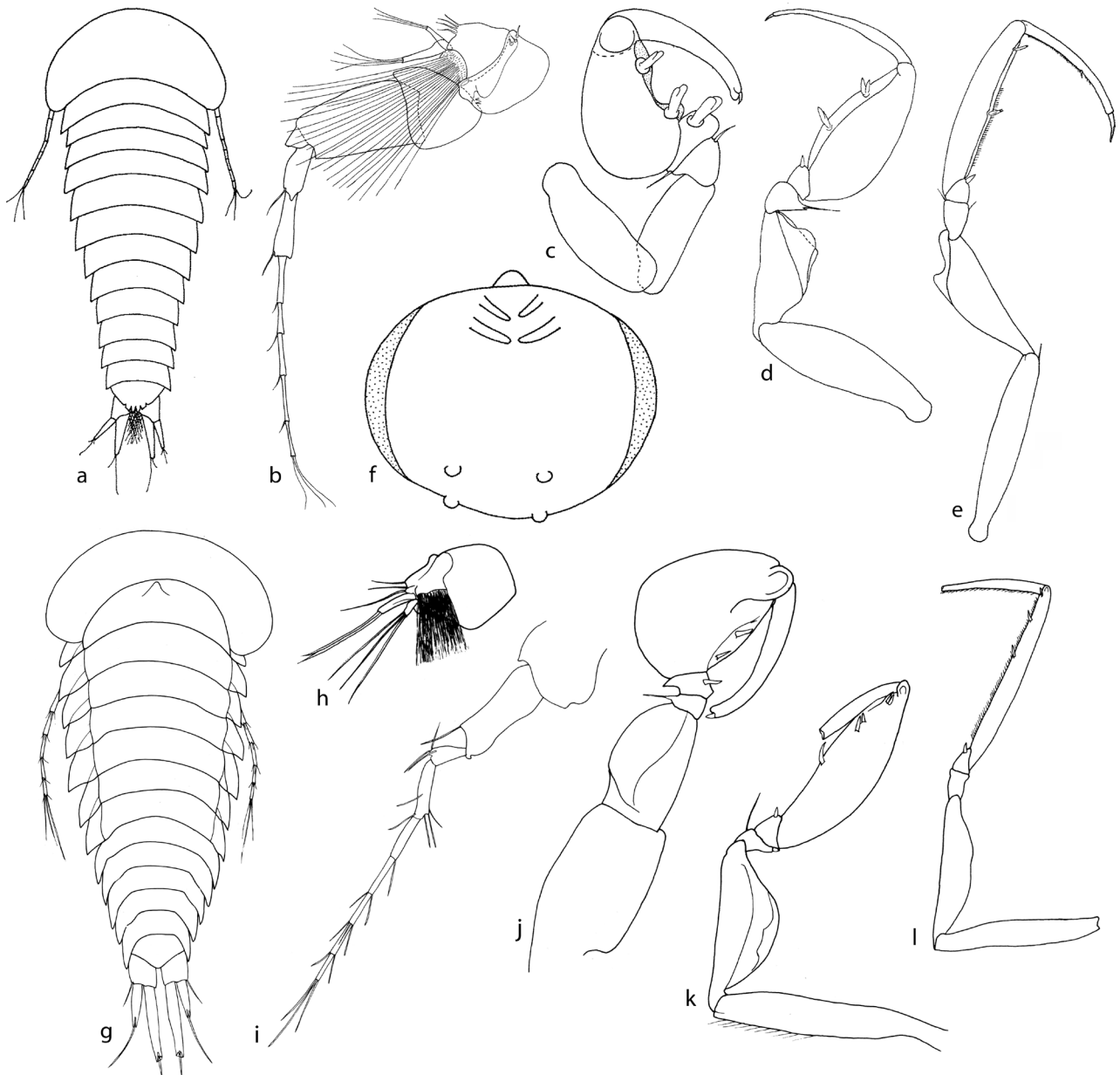


Figure 6.27. Capitoniscidae. *Capitoniscus cumacei* Bourdon, 1972: a, male dorsal view; b, male antennula and antenna; c, male pereopod 1; d, male pereopod 3; e, male pereopod 7; f, female ventral view. *Carocryptus laticephalus* Schultz, 1977: g, male dorsal view; h, male antennula; i, male antenna; j, male pereopod 1; k, male pereopod 3; l, male pereopod 7.

### *Crinoniscus* Pérez, 1900

*Diagnosis.* As for family.

Subtidal–slope, parasitising sessile and pedunculate barnacles. Temperate Northern Atlantic, Temperate Australasia. 5 species (Buhl-Mortensen et al., 2020).

### *Proteolepas* Darwin, 1854 *nomen dubium*

*Diagnosis.* As for family (only the immature female is known and is indistinguishable from those of *Crinoniscus* spp.).

Subtidal, parasitising pedunculate barnacles. Tropical Atlantic. 1 species (Buhl-Mortensen et al., 2020).

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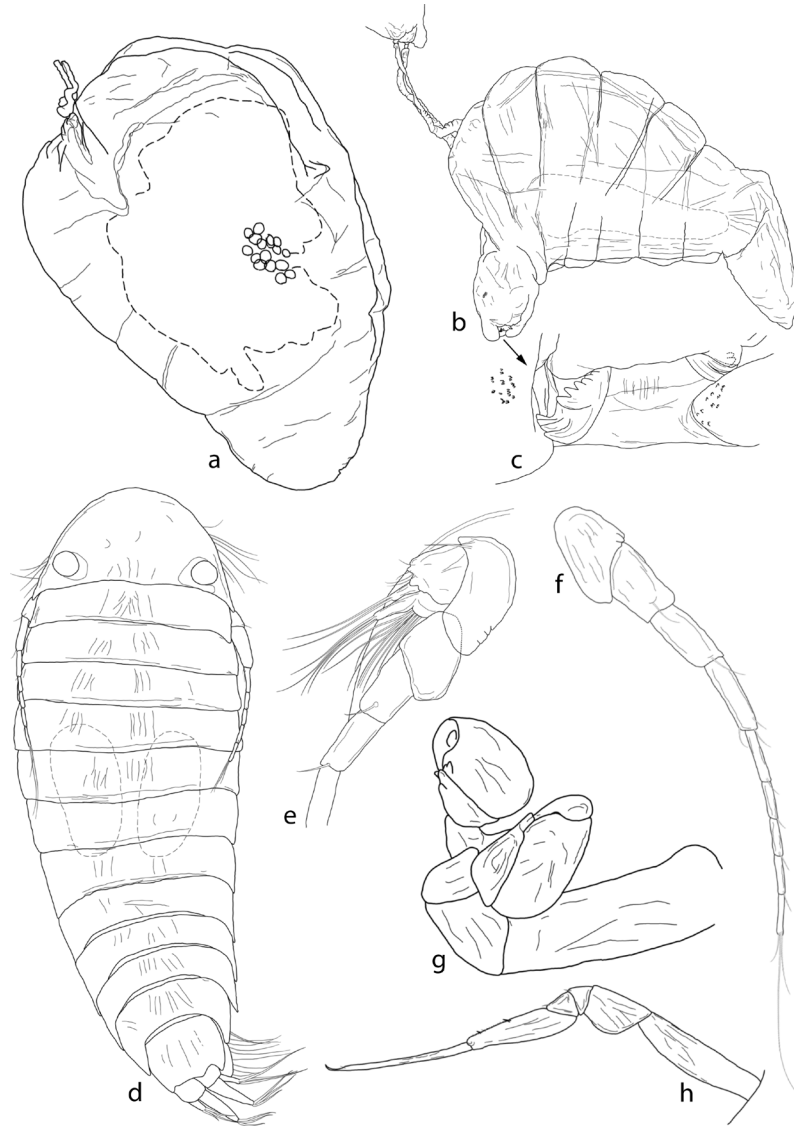


Figure 6.28. Crinoniscidae. *Crinoniscus stroembergi* Buhl-Mortensen, Williams and Boyko, 2020: a, mature female lateral view; b, immature female lateral view; c, close-up of mandibles of immature female; d, male dorsal view; e, male antenna; f, male antenna; g, male pereopods 1 and 2; h, male pereopod 7.

## Family Cryptoniscidae Kossmann, 1880

Figure 6.29

Members of Cryptoniscidae are endoparasitic or mesoparasitic, and can be distinguished from other epicarideans by the presence of an elongate rapier-like dactylus (or dactylus and propodus) on at least the seventh (sometimes also the sixth) pereopod of males (= cryptoniscus larval stage). In addition, in

at least one genus (*Liriopsis*) the epicaridium larvae exhibit a modified pereopod 6, the dactyl of which is needle-like (Fraisie, 1878; Peresan and Roccatagliata, 2005). Aside from Entoniscidae, this is the only group of epicarideans presently known to exhibit such modification of the sixth legs of

epicaridium larvae. Mature females (except for those of species in *Liriopsis*) have a subdivided attachment process inserted into the host (Boyko, 2014; Peresan and Roccatagliata, 2005). It should be noted that several genera lack a description of one of the life history stages (male, immature female and/or mature female) and their placement in this family is tentative. Some cryptoniscids are hyperparasites of rhizocephalan barnacles.

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped without prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes present. Antennula article 1 without teeth. Coxal plates without teeth. Pereopods 1 and 2 gnathopodal; pereopods 3–5 or 3–6 ambulatory, propodi tapering or quadrate distally, dactyli shorter than propodi; if 3–5 ambulatory then pereopod 6 of 3 segments (third segment extremely long and slender, tapering toward recurved tip, more than twice as long as ischium and

basis combined) or 4 segments (terminal segment long and slender, tapering toward tip, approximately as long as ischium and basis combined or terminal segment long and slender, acute at tip, twice as long as all other segments combined) or 6 segments (terminal segment long and slender, acute at tip, as long as all other segments combined); pereopod 7 of 4 segments (terminal segment elongate or globular, undivided or divided, tapering to distal tip, recurved at tip) or 6 segments (propodus tapering distally, dactylus elongate, slender, longer than propodus or as long as all other segments combined). Pleotelson margin smooth. **Mature female** linear (flattened dorsoventrally with 5 lateral lobes on each side or as an elongate smooth sac), recurved strongly (dorsal margin smooth or divided into 6–10 lobes) or body divided by narrow neck into anchor portion embedded in host body and subspherical portion (marsupium) extending from host mantle. Attachment trunk, if present, with 2 or 4 attachment lobes. Mesoparasitic or endoparasitic.

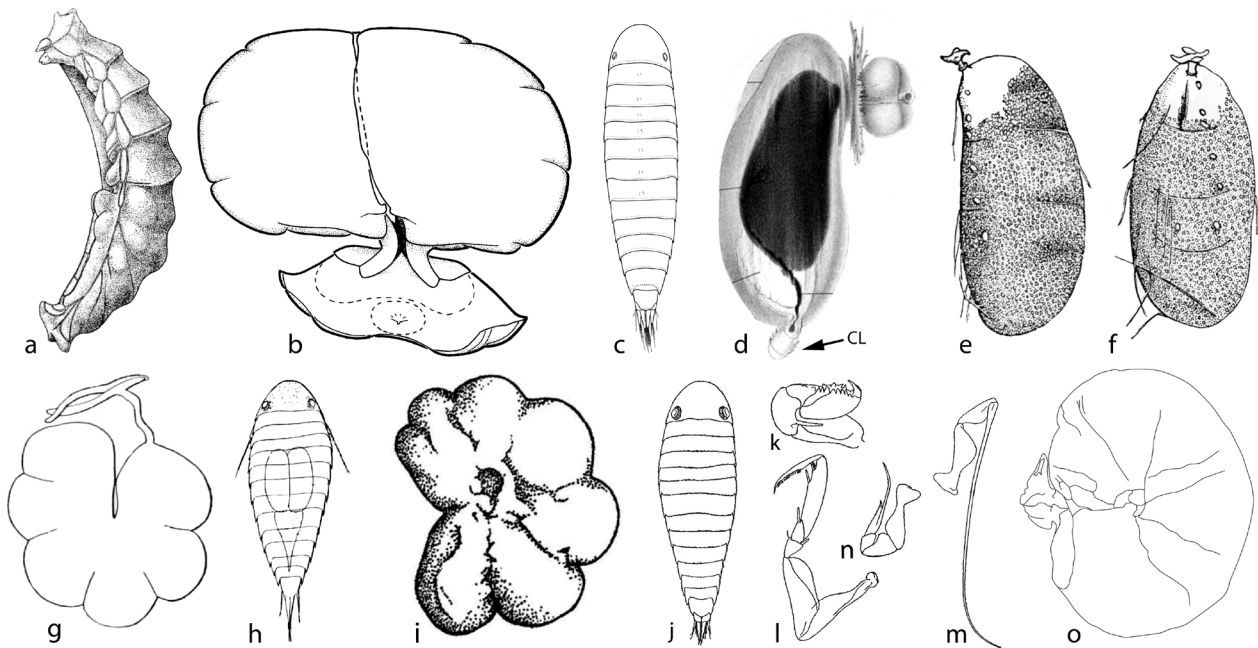


Figure 6.29. Cryptoniscidae. *Enthylacus trivinctus* Pérez, 1920: a, female lateral view. *Liriopsis pygmaea* (Rathke, 1843): b, mature female ventral view; c, male dorsal view. *Cryptoniscus paguri* Fraisse, 1878: d, female lateral view. *Zeuxokoma setosa* (Nierstrasz and Brender à Brandis, 1930): e, female lateral view; f, female ventral view. *Danalia curvata* (Fraisse, 1878): g, mature female lateral view; h, male dorsal view. *Avada kedavra* Boyko, 2014: i, mature female lateral view; j, male dorsal view; k, male pereopod 2; l, male pereopod 4; m, male pereopod 6; n, male pereopod 7. *Cabirnalina nausicaa* Boyko and van der Meij, 2018: o, mature female lateral view. Abbreviations: CL, cryptoniscus larva.

### Key to mature females of genera of Cryptoniscidae

*Eumetor* not included in key; it was poorly described and placement in Cryptoniscidae is not certain.

1. Found inside of host body unattached (fig. 6.29a) ..... *Enthylacus*
- External to host and attached to host body ..... 2
2. Approximately half of body (fig. 6.29b; see also male, fig. 62.8c) embedded in host; attachment process lacking ..... *Liriopsis*
- Most of body not embedded in host; attachment via process with terminal lobes ..... 3

- |    |  |                      |
|----|--|----------------------|
| 3. | Body of mature female not recurved .....   | 4                    |
| –  | Body of mature female recurved .....   | 5                    |
| 4. | Body (fig. 6.29d) attached to host by short process with 2 terminal bulbous lobes .....                                | <i>Cryptoniscus</i>  |
| –  | Body (fig. 6.29e, f) attached to host by short process with 4 terminal hook-like lobes .....                           | <i>Zeuxokoma</i>     |
| 5. | Body (fig. 6.29g; see also male, fig. 6.29h) attached to host with long process bearing 4 terminal slender lobes ..... | <i>Danalia</i>       |
| –  | Body attached to host with short process bearing stout terminal lobes .....  | 6                    |
| 6. | Attachment process (fig. 6.29i; see also male, fig. 6.29j–n) with 4 hook-like terminal lobes .....                     | <i>Avada</i>         |
| –  | Attachment process (fig. 6.29o) with 2 flattened, triangular, terminal lobes .....                                     | 7                    |
| 7. | Dorsal margin of body smooth, terminal lobes triangular .....  | <i>Cabirnalía</i>    |
| –  | Dorsal margin of body lobed, terminal lobes ovate .....  | <i>Cryptodanalia</i> |

### ***Avada* Boyko, 2014**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body with striations not described. Head anterior margin with triangular median region reflexed posteroventrally (visible in ventral view). Coxal plates not described. Pereopods 3–5 ambulatory, propodi tapering distally; pereopod 6 of 3 segments, segment 3 extremely long and slender, tapering toward recurved tip, more than 2 times as long as ischium and basis combined; pereopod 7 of 4 segments, terminal segment long, slender, subdivided by median slit into ventral and dorsal portions, dorsal portion twice length of ventral, recurved at tip. **Mature female** with strongly convex smooth dorsal margin smooth or divided into 7–9 lobes, ventral side shorter, shallow medial indentation present. Attachment trunk short with 4 short strongly sclerotised attachment lobes.

Intertidal, parasitising sacculinid rhizocephalans, and anomuran and brachyuran decapods. Central Indo-Pacific, Temperate Northern Pacific, and Eastern Indo-Pacific. 3 species (Boyko, 2014).

### ***Cabirnalía* Boyko and van der Meij, 2018**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) not described. **Mature female** body recurved strongly, circular in outline; strongly convex dorsal margin without lobes but with cuticular indentations indicating segmentation; ventral sides meeting medially, with several small, platelike areas demarcated at midpoint. Attachment trunk short, with 1 attachment lobe, medially divided and expanded into 2 broad sections.

Subtidal, parasitising cryptochirid crabs. Eastern Indo-Pacific. 1 species (Boyko and van der Meij, 2018).

### ***Cryptodanalia* Williams, Boyko and Zheng, 2026**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) not described. **Mature female** body recurved strongly, U-shaped in outline; strongly convex dorsal margin with lobes; ventral sides not meeting medially, with several small, platelike areas demarcated at midpoint. Attachment trunk short, with 2 ovate, swollen attachment lobes.

Slope, parasitising galatheid squat lobsters. Temperate Australasia. 1 species (Williams et al., 2026).

### ***Cryptoniscus* Müller, 1864**

**Diagnosis. Male** coxal plates not described. Pereopods 3–6 ambulatory, propodi quadrate distally, dactyli shorter than propodi; pereopod 7 of 6 segments, propodus tapering distally, dactylus elongate, slender, longer than propodus. **Immature females** vermiform, swollen; head as pair of inflated lobes extending through cuticle of host. **Mature female** body flattened dorsoventrally with 5 lateral lobes on each side; anterior and posterior ends tapered, anterior end more strongly; ventral surface with medial slit terminating in rounded area where head extends out through body wall of host.

Subtidal, parasitising rhizocephalan barnacles on hermit crabs. Tropical Atlantic, Temperate North Atlantic. 2 species (Fraisie, 1878).

### ***Danalia* Giard, 1887**

**Diagnosis. Male** oral cone not described. Pereopods 3–5 ambulatory, propodi quadrate distally; pereopod 6 of 4 segments, terminal segment long and slender, tapering toward tip, approximately as long as ischium and basis combined; pereopod 7 of 4 segments, terminal segment elongate, undivided, tapering to distal tip, recurved at tip. **Mature female** elongate and strongly recurved; strongly convex dorsal margin with 6–10 weakly to moderately pronounced lobes, ventral side strongly concave, with large median gap between lobes. Attachment trunk variable in length with 4 short to elongate flexible and fragile attachment lobes. Thickened anteroventral shield area small to moderate in size.

Subtidal, parasitising galatheid squat lobsters, brachyuran crabs, and rhizocephalans on brachyuran crabs. Tropical Atlantic, Temperate Northern Atlantic, Western and Central Indo-Pacific, Eastern Indo-Pacific. 14 species (Boyko, 2014).

### ***Enthylacus* Pérez, 1920**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body cuticular striations not described. Oral cone not described. Antennula not described. Coxal plates not described. Pereopods 3–5 ambulatory; propodi of 3–5 tapering distally; pereopod 6 of 4 segments, terminal segment long and slender, acute at tip,

twice as long as all other segments combined; pereopod 7 of 4 segments, terminal segment globular at base, tapering in distal half to acute tip, undivided, recurved at tip. Pleotelson margin not described. **Immature female** with dorsal segmentation and ventral medial lobes, body recurved slightly; anterior and posterior ends with triangular shield-like projection. **Mature female** not described.

Subtidal, parasitising rhizocephalan barnacles on brachyuran crabs. Western Indo-Pacific. 1 species (Pérez, 1920).

### ***Eumetor* Kossmann, 1872**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) illustrated but with relevant characters not described. **Mature female** not described but Kossmann (1872) noted the mature female differed little from *Liriopsis pygmaea* (Rathke, 1843).

Subtidal, parasitising rhizocephalans on brachyuran crabs. Central Indo-Pacific. 1 species (Kossmann, 1872).

### ***Liriopsis* Schultze in Müller, 1859**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) pereopods 3–5 ambulatory, propodi quadrate distally; pereopods 6 and 7 of 6 segments each, terminal segment long and slender, acute at tip, as long as all other segments combined. **Mature female** body divided by narrow neck into anchor portion embedded in host body and subspherical portion (marsupium) extending from host mantle; anchor portion with 3 parallel hollow bars, ventral surface concave; marsupium ventral surface with longitudinal median slit bearing finger-shaped process at anterior end and 6 internal digitations at posterior end.

Subtidal, parasitising rhizocephalans on hermit crabs and king crabs. Temperate Northern Atlantic and Pacific, Temperate South America. 2 species (Peresan and Roccatagliata, 2005).

### ***Zeuxokoma* Grygier, 1993**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) not described. **Mature female** body elongate, relatively linear

## **Family Cumoechidae Boyko and Williams, 2023**

Figure 6.30

Members of Cumoechidae are ectoparasitic in the marsupium of cumacean hosts. They can be distinguished from other isopod parasites by a conical head and an elongate antennular segment 1 with c. 16 acute marginal teeth of the cryptoniscus larva and the shape of the female body with a long median cleft bearing antennae and pereopods at the anterior end (Hansen, 1916).

**Diagnosis. Epicaridium larva** (fig. 6.30h) with antenna as long as body; setae on antenna and uropodal exopod and endopod as long as or longer than body. **Male** (paedomorphic cryptoniscus larva) body elongate (fig. 6.30b–g). Head longer than wide, conical, posterior margin no wider than pereomere 1; eyes absent. Antennula article 1 elongate with c. 16 marginal acute teeth. Coxal plates with posterior margins toothed. Pereopods 1–3 gnathopodal, pereopods 4–7 ambulatory with

smooth sac with pronounced thickened anteroventral shield; internal subdivisions present but external lobes lacking; trunk short relative to body with 4 stout strongly sclerotized attachment hooks.

Subtidal–slope, parasitising caridean shrimps. Tropical Atlantic, Central Indo-Pacific, Temperate Northern Pacific, Eastern Indo-Pacific. 6 species (Boyko, 2014).

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propodi tapering distally, dactyli as long as propodi. Pleotelson margin with 10 teeth, distalmost pair longest. **Mature female** (fig. 6.30a) spheroid in dorsal view, compressed dorsoventrally, segmented, ventral surface with long median cleft and raised segmented pad surrounding cleft; anterior region with reduced antennae and pair of pereopods. Ectoparasitic.

### ***Cumoechus* Hansen, 1916**

**Diagnosis.** As for family.

Slope–bathyal, parasitising cumaceans. Arctic. 1 species (Boyko and Williams, 2023; Hansen, 1916).

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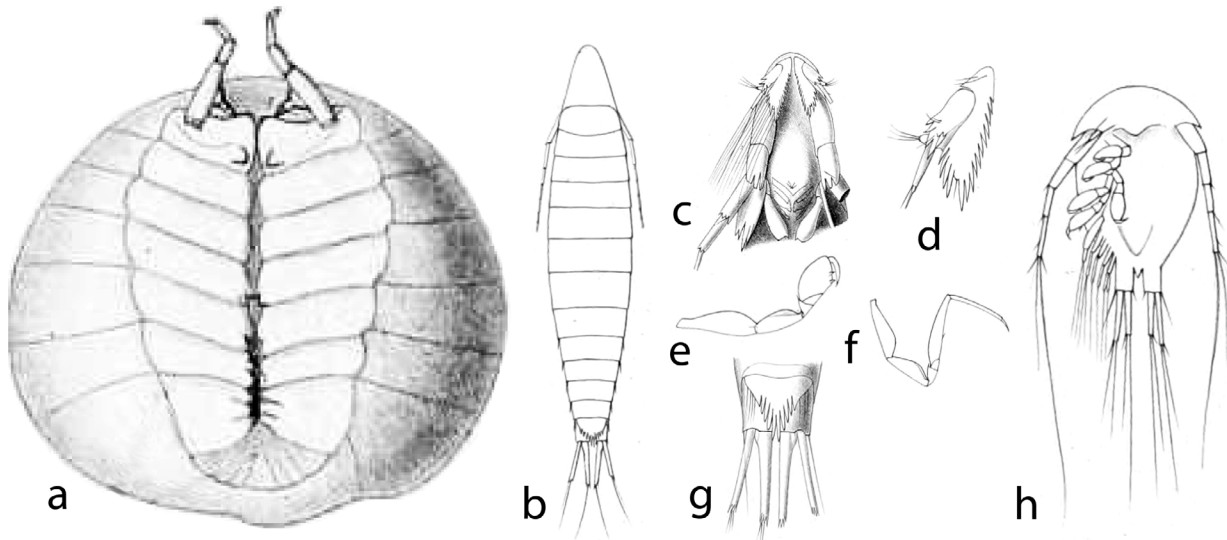


Figure 6.30. Cumoechidae. *Cumoechus insignis* Hansen, 1916: a, female dorsal view; b, male dorsal view; c, male head, ventral view; d, male antennula; e, male pereopod 1; f, male pereopod 7; g, male pleon, dorsal view; h, epicaridium larva ventral view.

## Family Cyproniscidae Giard and Bonnier, 1887

Figure 6.31

Members of Cyproniscidae are ectoparasitic within the carapace of ostracod hosts; no other epicarideans are known to parasitise ostracods. There are no clear synapomorphies for the family because the two genera have very different cryptoniscus larval and female morphologies, as well as feeding strategies (Hosie, 2008; Buhl-Mortensen et al., 2020).

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly or posteriorly. Eyes

present or absent. Antennula article 1 with 6–12 posterior teeth. Coxal plates with 5–8 teeth. Pereopods 1 and 2 gnathopodal, subequal in size or with 2 much larger than 1; pereopods 3–7 ambulatory, propodi of pereopods 3–5 distally quadrate, 6 and 7 tapering distally or 3–7 all tapering distally. Pleotelson margin with or without teeth; anal tube present or absent. **Mature females** with or without rudimentary segmentation; rudimentary mouthpart and pereopodal appendages present or absent. Attachment tube to host present or absent. Ectoparasitic.

### Key to genera of Cyproniscidae

1. Cryptoniscus larvae (fig. 6.31c) without anal tube; mature female (fig. 31a, b) attached to host via slender tube; direct feeding on host. .... *Cyproniscus*<sup>1</sup>
- Cryptoniscus larvae (fig. 6.31g–i) with anal tube; mature female (fig. 6.31d–f) not attached to host via slender tube; cryptoniscus larvae are egg predators. .... *Oniscryptus*

<sup>1</sup> Four species described in *Cyproniscus* do not belong to this genus: *C. binoculis* Menzies and George, 1972 was transferred to *Scalpelloniscus* (Hemioniscidae) by Grygier (1981), *C. peruvicus* Menzies and George, 1972 was transferred to *Capitoniscus* Bourdon, 1972 (Capitoniscidae) by Boyko and Williams (2023); *C. decemspinus* Menzies and George, 1972 and *C. octospinosus* Menzies and George, 1972 are left in *Cyproniscus* for now because there is no other taxon to accommodate them and erecting a new genera is unwarranted until they are fully redescribed. We do not consider the characters of the latter two species in the diagnosis for *Cyproniscus*.

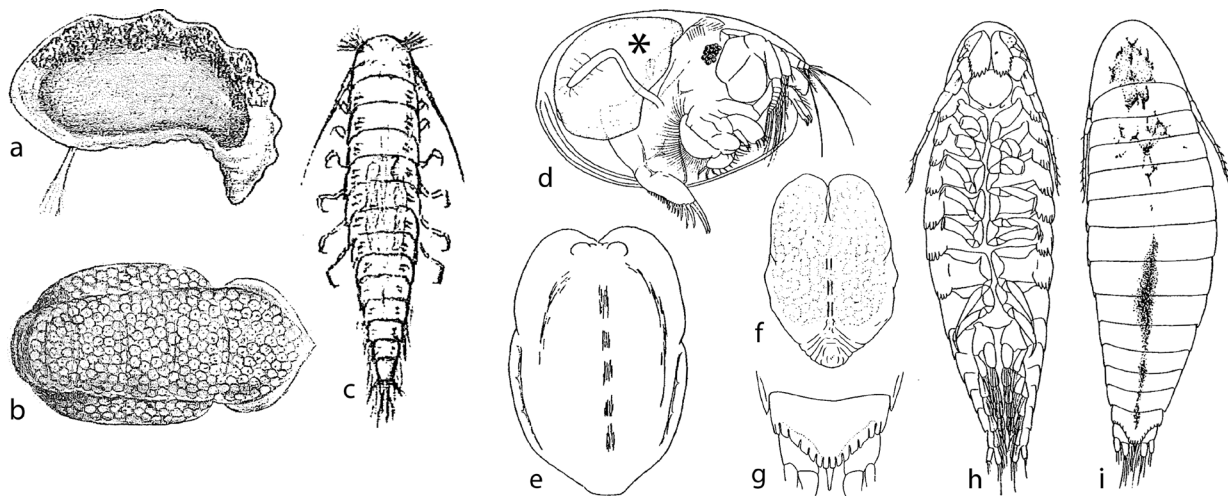


Figure 6.31. Cyproniscidae. *Cyproniscus cypridinae* (G.O. Sars, 1883): a, female lateral view; b, ovigerous female dorsal view; c, male dorsal view. *Onisocryptus ovalis* (Shiino, 1942): d, female within host ostracod (parasite shown by asterisk); e, female dorsal view; f, female ventral view; g, male pleon and anal tube, dorsal view; h, male ventral view; i, male dorsal view.

### *Cyproniscus* Kossmann, 1884

**Diagnosis. Male** (paedomorphic cryptoniscus larva) oral cone directed anteriorly. Eyes absent. Antennula article 1 with 6–10 posterior teeth. Coxal plates with 8 teeth. Pereopods 1 and 2 gnathopodal, subequal in size; pereopods 3–7 ambulatory, propodi of pereopods 3–5 distally quadrate, 6 and 7 tapering distally. Pleotelson margin without teeth; anal tube absent. **Mature female** with rudimentary segmentation, pleon recurved, much smaller than pereon; mouthpart and pereopodal appendages lacking. Attachment tube to host present.

Subtidal–shelf, parasitising ostracods. Temperate Northern Atlantic, Temperate Southern Africa, Southern Ocean. 4 species and 1 subspecies (Nielsen and Strömberg, 1973a, b; Sars, 1899).

### *Onisocryptus* Schultz, 1977

**Diagnosis. Male** (paedomorphic cryptoniscus larva) oral cone directed posteriorly. Eyes present or absent. Antennula article 1 with 10–12 posterior teeth. Coxal plates with 5 teeth. Pereopods 1 and 2 gnathopodal, pereopod 2 much larger than 1; pereopods 3–7 ambulatory, subequal in size and shape, propodi of pereopods 3–7 tapering distally or 3–5 distally quadrate and 6 and 7 tapering distally. Pleotelson margin with teeth; anal tube present. **Mature female** without distinct segmentation; some rudimentary mouthpart and pereopodal appendages at anterior end present. Attachment tube to host absent; egg predators.

Subtidal–bathyal, parasitising ostracods. Temperate Northern Pacific, Southern Ocean. 3 species (Abe and Horiuchi, 2000; Strömberg, 1983).

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## Family Dajidae G.O. Sars, 1883

Figures 6.32, 6.33

Dajidae is a rather heterogeneous grouping of ectoparasitic genera with body shapes ranging from dorsoventrally flattened and ovate to heart-shaped, elongate, pyriform or spheroid. Future analyses, using molecular data and morphological data from presently unknown cryptoniscus larvae will, at a minimum, change the allocation of species to genera and likely break up the taxon into two or more families. Characters of females, males and cryptoniscus larvae are included, as all these life history stages exhibit phylogenetically informative traits; those of epicaridium larvae may also be informative but they are known from too few species to warrant inclusion here. Females of species in some genera, such as *Akrophryxus* and *Telephryxus*, are radically divergent from the “typical” “back-pack isopod” shape seen in species of *Holophryxus* and *Zonophryxus*, whereas species in other genera (e.g. *Antephrya* and *Streptodajus*) are very similar to each other.

**Diagnosis.** **Female** body semicircular, heart-shaped, elongate, pyriform, ovate or spheroid, pereomeres segmented or unsegmented; head visible or not visible dorsally (with or without frontal lamina), displaced facing anteriorly, or internalised into pereon; anterolateral corners of lateral lobes rounded or modified into recurved, elongate lobes with spoon-like tips. Eyes absent. Antennula present (segmented or unsegmented) or absent; antenna present (segmented or

unsegmented) or absent. Oral sucker present or absent. 4–6 pairs of oostegites or oostegites fused. 4–6 pairs of gnathopodal pereopods, subequal in size and shape, or pereopod 5 modified into large clasper, all at anterior end of pereon, pereopods 1–4 at anterior end and 5 at posterolateral margin, or widely spaced. Pleon segmented, unsegmented, vermiform, or modified into thickened plate with medial holes; pleopods and uropods present or absent. **Male** body flat or recurved, pereomeres subequal in width, head wider than long, rounded or triangular, distinct from or fused with pereomere 1. Eyes present or absent. Antennula and antenna unsegmented or segmented. Pereomere 7 distinct from or fused to pleon. 6 or 7 pairs of pereopods (7 reduced or absent). Pleon segments distinct or fused, pleopods absent, anal cone and uropods present or absent. **Cryptoniscus larva** body teardrop-shaped or elongate, head with posterolateral lobes or not, head rounded, horseshoe-shaped, helmet-shaped, or triangular, eyes present or absent. Antennula with or without teeth on basal segment. Oral sucker present or absent. Pereomeres with toothed, serrate or smooth coxal plates. Pereopods 1, 1 and 2, or 1–6 gnathopodal, others ambulatory, longer, anterior pairs with or without multifid setae on propodi and carpi, posterior pairs always with multifid setae on propodi and carpi. Pleotelson rounded, quadrate, or triangular, with or without teeth. Ectoparasitic.

### Key to females of genera of Dajidae, including some characters of males

*Cryptociscus*, *Dolichophryxus*, *Neritoniscus* and *Paraspidophryxus* are not in the key to genera; they are known only from cryptoniscus larvae. For these genera see figs 6.38 and 6.39.

1. Body of mature female spherical ..... 2
  - Body of mature female not spherical, compressed dorsoventrally ..... 3
2. Mature female (fig. 6.32a) without antennula, attachment plate (pleon) triangular, male (fig. 6.32b) with 6 pairs of pereopods; parasites of brachyurans (Ethusidae, Goneplacidae and Palicidae) ..... *Akrophryxus*
  - Mature female (fig. 6.32c) with antennula, attachment plate (pleon) subquadrate, male (fig. 6.32d) with 7 pairs of pereopods (seventh pair reduced); parasites of anomurans (Munidopsidae) ..... *Telephryxus*
3. Mature female with attachment processes ..... 4
  - Mature female without attachment processes ..... 5
4. Mature female (fig. 6.32e, f) with attachment processes at anterior end, male with rudimentary pereopod 7; parasites of euphausiids ..... *Oculophryxus*
  - Mature female (fig. 6.32g) with attachment processes at posterior end, male with well-developed pereopod 7; parasites of euphausiids ..... *Heterophryxus*
5. Mature female (fig. 6.32h; see also male, fig. 6.32i) pleon modified as slender, whip-like structure used by males for attachment; parasites of mysids ..... *Aspidophryxus*
  - Mature female pleon not modified as slender, whip-like structure ..... 6
6. Mature female pleotelson distinct, bilobed, posterolateral margins of marsupium extend posteriorly to or beyond pleotelson ..... 7
  - Mature female pleotelson indistinct, posterolateral margins of marsupium not extending posteriorly to or beyond pleotelson ..... 8

7. Mature female (fig. 6.32j–l) body unsegmented, heart-shaped; parasites of mysids ..... *Prodajus*  
 – Mature female (fig. 6.32m) body segmented anteriorly and posteriorly, ovate; parasites of mysids .....  
 ..... *Prophryxus*
8. Mature female with segmented pleon ..... 9  
 – Mature female with unsegmented pleon ..... 13
9. Mature female (fig. 6.32n; see also male, fig. 6.32o) with lateral portions of marsupium directed laterally, host(s) unknown ..... *Allophryxus*  
 – Mature female with lateral portions of marsupium directed medioventrally, meeting in midline of ventral surface or nearly so ..... 10
10. Mature female with pleon indistinctly segmented dorsally ..... 12  
 – Mature female with pleon distinctly segmented dorsally ..... 11
11. Mature female (fig. 6.32p, q) marsupium with distinct anterior “shoulders” extending anterior to frontal margin of head, male with unsegmented pleon; parasites of mysids ..... *Dajus*  
 – Mature female (fig. 6.33a) marsupium without distinct anterior “shoulders,” head and anterolateral margins of marsupium on same plane, male with segmented pleon; parasites of lophogastrids ..... *Arthropryxus*
12. Mature female (fig. 6.33b–d) with pereopods and mouthparts directed anteriorly; parasites of mysids .....  
 ..... *Streptodajus*  
 – Mature female (fig. 6.33e) with pereopods and mouthparts directed ventrally; parasites of mysids and euphausiids ..... *Notophryxus*
13. Mature female with distinct dorsal pereon segmentation ..... 14  
 – Mature female with indistinct or absent dorsal pereon segmentation ..... 15
14. Mature female (fig. 6.33f) with 5 distinct pereon segments indicated dorsally; host(s) unknown .....  
 ..... *Colophryxus*  
 – Mature female (fig. 6.33g) with three distinct pereon segments indicated dorsally; host(s) unknown .....  
 ..... *Antephrya*
15. Mature female (fig. 6.33h) length and width approximately subequal; parasites of aegid isopods ..... *Aegophila*  
 – Mature female longer than wide ..... 16
16. Mature female (fig. 6.33i, j; see also male fig. 6.33k) with posterior margin of body bearing row of triangular processes; parasites of caridean shrimps ..... *Zonophryxus*  
 – Mature female with posterior margin of body smooth ..... 17
17. Mature female (fig. 6.33l, m; see also male fig. 6.33n) with frontal lamina projecting anterior to head, posterior lobe extending beyond posterior margins of marsupium; parasites of dendrobranchiate and caridean shrimps ..... *Holophryxus*  
 – Mature female (fig. 6.33o, p; see also male, fig. 6.33q) without frontal lamina or posterior lobe extending beyond posterior margins of marsupium; parasites of euphausiids ..... *Branchiophryxus*

### *Aegophila* Bresciani, 1966

**Diagnosis.** **Female** body semicircular, wider than long; pereomeres with faint dorsal indications; head subsumed into pereon, not extending anteriorly beyond anterior margins of lateral lobes. Eyes absent. Antennula and antenna absent. Oostegites 1 large, ovate, 2–5 small, slender to subquadrate. Pereopods 1–5 gnathopodal, subequal in size and shape; distoventral margin of propodi expanded into cup to receive tips of dactyli. Pleon minute, vermiform, segments fused. **Male** with

pereomeres subequal in width, head wider than long, fused with pereomere 1. Eyes absent. Antennula of one segment; antenna segmented, short. Pleon segments fused, pleopods absent, anal cone present, uropods absent. **Cryptoniscus larva** body teardrop-shaped, eyes absent. Antennula without teeth on basal segment. Oral sucker present. Pereomeres without toothed coxal plates. Pereopods 1 gnathopodal, dactyli short, slightly curved, propodus inner margin folded, bearing 2 flat multifid setae; carpus without multifid setae. Pereopods 3–6 dactyli more elongate than 1 and 2, propodi more elongate, narrower than 1

and 2, bearing 2 flat multifid setae; carpi without multifid setae. Pereopod 7 dactylus and propodus subequal in length to those of pereopods 3–5, propodus bearing 2 large, erect, multifid setae, carpus without multifid setae. Pleotelson without teeth.

Slope, parasitising aegid isopods. Arctic, Temperate Northern Pacific. 2 species (Williams and Boyko, 2021).

#### ***Akrophryxus* Williams and Boyko, 2021**

*Diagnosis. Female* body spheroid, unsegmented; head not visible externally. Eyes absent. Antennula absent; antenna as oblong flat plate lateral to oral cone. Oostegite 1 largest, ovate with small posterior accessory lobe; oostegites 2–5 small, becoming larger posteriorly. Pereopods 1–5 gnathopodal, subequal in size and shape. Pleon modified as oblong, narrow, thickened plate with 3 circular medial holes, largest surrounding antennula of host. *Male* with pereomeres subequal in width, head wider than long, fused with pereomere 1. Eyes absent. Antennula of few small, stacked, disc-like segments; antenna as broad elongate lobes lateral to oral cone. Pereomere 7 fused to pleon. 6 pairs of subequal pereopods (pereopod 7 absent). Pleon segments fused, pleopods, anal cone, and uropods absent. **Cryptoniscus larva** body teardrop-shaped, eyes present. Antennula without teeth on basal segment. Oral sucker absent. Pereomeres without toothed coxal plates. Pereopods 1 and 2 subequal, dactyli short, slightly curved, propodus inner margin folded, bearing 2 flat multifid setae; carpus with 1 distal multifid seta. Pereopods 3–5 dactyli more elongate than 1 and 2, curved, propodi more elongate, narrower, than 1 and 2, inner margin of each folded, bearing 2 flat multifid setae; carpi each with 1 distal multifid seta. Pereopod 6 dactylus subequal in length to those of pereopods 3–5, propodus more elongate and narrower than those of pereopods 3–5, inner margin slightly folded, bearing 2 erect, multifid setae, carpus with 1 distal multifid seta. Pereopod 7 similar to pereopod 6 but with elongate dactylus extending to distal margin of merus, carpus with 1 flat multifid seta. Pleotelson without teeth.

Slope, parasitising ethusiid, goneplacid, and palicid brachyurans. Western and Central Indo-Pacific, Temperate Northern Pacific. 3 species (Williams et al., 2022).

#### ***Allophryxus* Koehler, 1911**

*Diagnosis. Female* body heart-shaped; pereomeres indicated dorsally and ventrally; head with subquadrate frontal lamina, directed anteriorly, extending well beyond anterior margins of lateral lobes. Antennula (or antenna) of 1 segment, other absent. 5 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in size. Pleon segmented, extending posteriorly beyond posterior margins of lateral lobes; pleomeres 1–3 with medial projection. Possible pleopods present on last 2 pleomeres; uropods present, displaced to same side of pleotelson. *Male* body recurved with pereomeres subequal in width, head wider than long, fused to pereomere 1. Eyes absent. Antennula not described; antenna segmented. Pleon large, triangular, segments fused; pleopods and anal cone absent; minute uropods present. **Cryptoniscus larva** unknown.

Mesopelagic–bathypelagic, host(s) unknown. Temperate Northern Atlantic. 1 species (Koehler, 1911).

#### ***Antephrya* Schultz, 1978**

*Diagnosis. Female* body elongate ovate, tapering posteriorly; some pereomeres indicated dorsally; head with frontal lamina scarcely visible dorsally, directed anterodorsally, extending anteriorly slightly beyond anterior margins of lateral lobes. Antennula and antenna not described. Oral sucker present. Oostegites not described. Pereopods 1–5 gnathopodal, subequal in size, displaced to anterior margin below head. Pleon not segmented, extending posteriorly beyond posterior margins of lateral lobes; pleomeres with 4 medial irregular projections. Pleopods and uropods absent. **Male** and **cryptoniscus larva** unknown.

Bathypelagic, host(s) unknown. Southern Ocean. 1 species (Schultz, 1978).

#### ***Arthropryxus* Richardson, 1908**

*Diagnosis. Female* body ovate; pereomeres segmented dorsally; head without frontal lamina, not extending beyond anterior margins of lateral lobes. Eyes absent. Antennula as 1 flat lobe, antenna segmented. 5 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in size and shape. Pleon segmented, pleopods and uropods absent. *Male* body recurved, pereomeres subequal in width; head triangular, wider than long, fused with pereomere 1. Eyes absent. Antennula and antenna not described. 7 pairs of pereopods. Pleon segmentation visible dorsally, pleopods, anal cone and uropods absent. **Cryptoniscus larva** unknown.

Bathypelagic, parasitising lophogastrids. Temperate Northern Pacific. 1 species (Richardson, 1908a).

#### ***Aspidophryxus* G.O. Sars, 1883**

*Diagnosis. Female* body heart-shaped; pereomeres with faint dorsal indications; head with subquadrate frontal lamina, ventrally directed, slightly extending anteriorly beyond anterior margins of lateral lobes. Eyes absent. Antennula and antenna of one segment each. Oostegites fused. Pereopods 1–5 gnathopodal, ischia progressively longer in posterior pairs. Pleon vermiform, segments fused. *Male* with pereomeres subequal in width, head wider than long, distinct from pereomere 1. Eyes absent. Antennula of one segment; antenna segmented, long. Pleon segments fused, pleopods absent, anal cone and uropods present. **Cryptoniscus larva** body teardrop-shaped, eyes absent. Antennula without teeth on basal segment. Oral sucker present. Pereomeres without toothed coxal plates. Pereopods 1–5 not described. Pereopod 6 dactylus elongate, propodus bearing 3 short, multifid setae, carpus with 1 simple(?) seta. Pereopod 7 similar to pereopod 6 but propodus bearing 2 large, erect multifid setae, carpus with 1 simple(?) seta. Pleotelson without teeth.

Subtidal–shelf, parasitising mysids, Tropical Atlantic, Temperate Northern Atlantic, Temperate Northern Pacific. 5 species (Shimomura, 2017).

#### ***Branchiophryxus* Caullery, 1897**

*Diagnosis. Female* body elongate ovate; pereomeres indicated dorsally only in median; head without narrow frontal lamina, not extending anteriorly beyond anterior margins of lateral

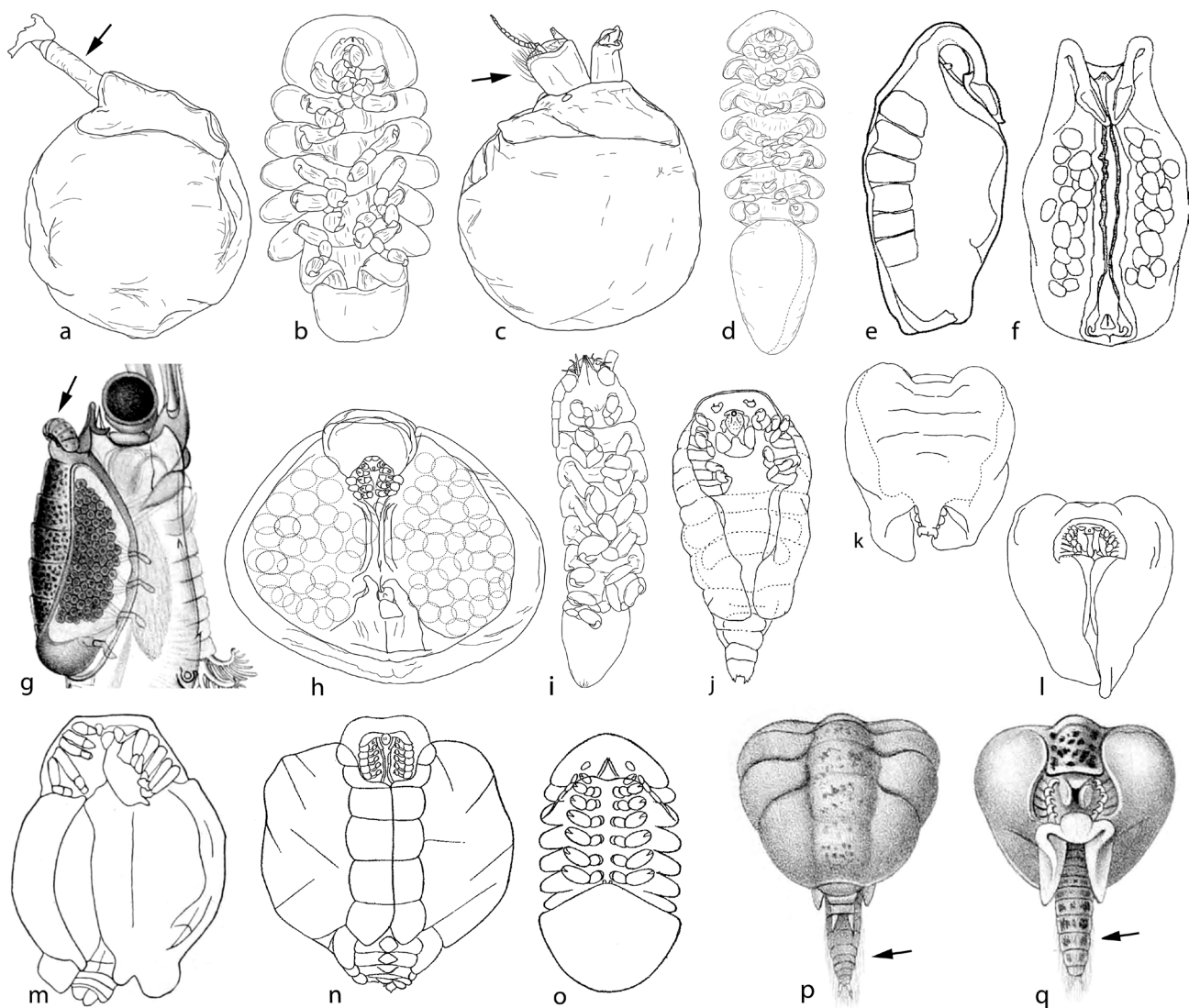


Figure 6.32. Dajidae. *Akrophryxus milvus* Williams and Boyko, 2021: a, female lateral view, shown attached to host antenna (arrow); b, male ventral view. *Telephryxus clypeus* Williams and Boyko, 2021: c, female lateral view, shown attached to host antennula (arrow); d, male ventral view. *Oculophryxus bicaulis* Shields and Gómez-Gutiérrez, 1996: e, female lateral view; f, female ventral view. *Heterophryxus appendiculatus* G.O. Sars, 1885: g, female lateral view, shown attached to host *Euphausia pellucida* Dana, 1850, male shown by arrow. *Aspidophryxus discoformis* Boyko and Williams, 2012: h, female ventral view; i, male ventral view. *Prohajus curviabdominalis* Shimomura, Ohtsuka and Naito, 2005: j, immature female (stage 2) ventral view; k, mature female dorsal view; l, mature female ventral view. *Prophryxus alascensis* Richardson, 1909: m, mature female ventral view. *Allophryxus ruber* Koehler, 1911: n, female ventral view; o, male ventral view. *Dajus siriellae* G.O. Sars, 1885: p, female dorsal view, arrow shows male attached; q, female ventral view, arrow shows male attached.

lobes. Antennula as flat plates, antenna absent. 4 pairs of oostegites. Pereopods 1–4 gnathopodal, subequal in size. Pleon minute, fused; pleopods and uropods absent. **Male** body flattened with pereomeres subequal in width, head wider than long, posterior margin raised and sloping towards anterior margin, fused to pereomere 1. Eyes absent. Antennula rudimentary, antenna segmented. Pleon rounded, unsegmented; pleopods, anal cone and uropods absent. **Cryptoniscus larva** body elongate, head triangular; eyes absent. Antennula basal segment not described. Oral sucker present. Pereomere coxal

plates not described. Pereopods 1–5 short, 6 and 7 greatly elongated (pereopods otherwise not described). Pleotelson without teeth.

Shelf–bathypelagic, parasitising euphausiids. Temperate Northern Atlantic. 3 species (Nierstrasz and Brender à Brandis, 1931).

#### *Colophryxus* Richardson, 1908

**Diagnosis.** **Female** body ovate; pereomeres indicated dorsally; head with narrow frontal lamina, directed anteriorly and

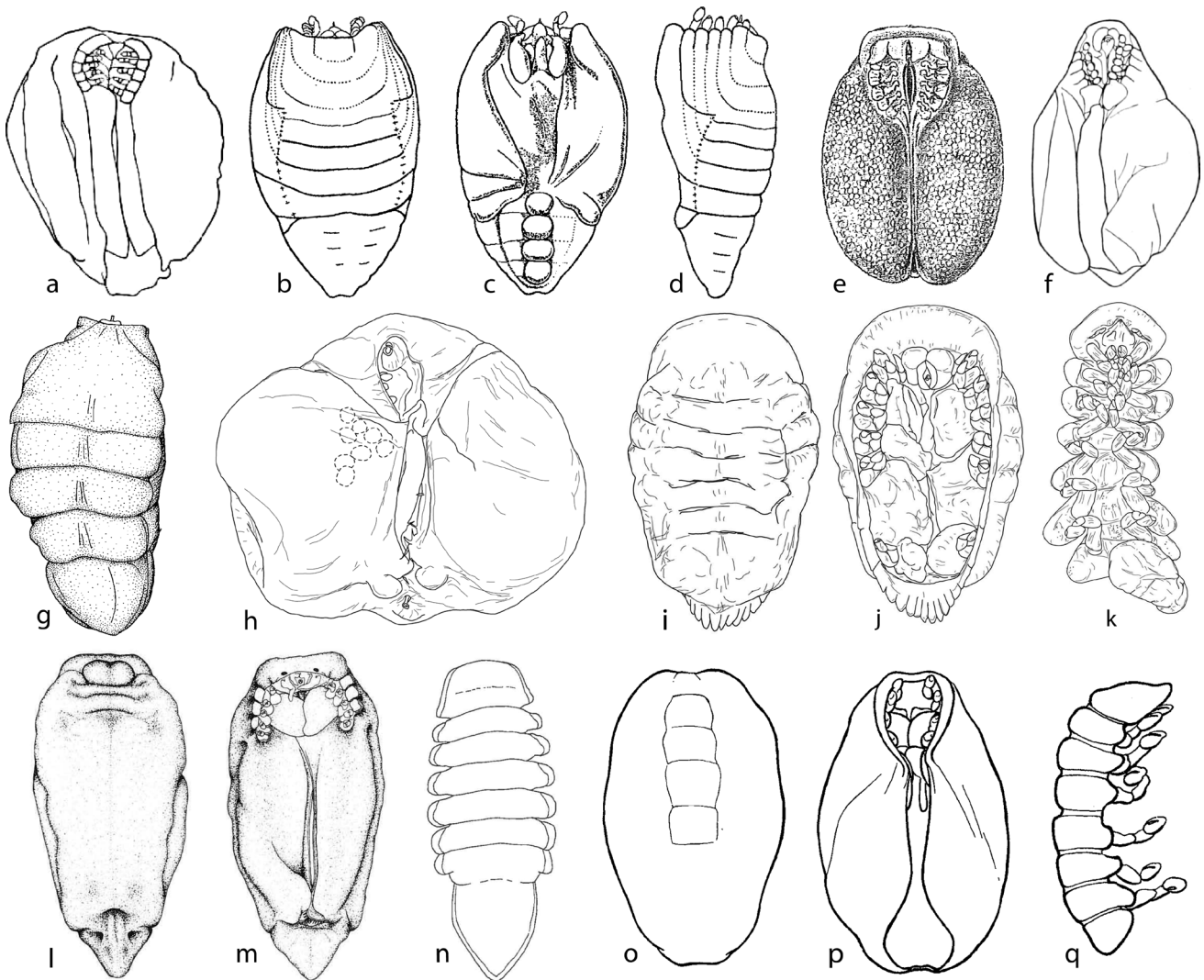


Figure 6.33. Dajidae. *Arthropryxus beringanus* Richardson, 1908: a, female ventral view. *Streptodajus equilibrans* Nierstrasz and Brender à Brandis, 1923: b, female dorsal view; c, female ventral view; d, female lateral view. *Notophryxus ovoides* G.O. Sars, 1883: e, female with brood of eggs, ventral view. *Colophryxus novangliae* Richardson, 1908: f, female ventral view. *Antephyria limacis* Schultz, 1978: g, female dorsal view. *Aegophila cappa* Williams and Boyko, 2021: h, female ventral view. *Zonophryxus probisowa* Boyko and Williams, 2021: i, female dorsal view; j, female ventral view; k, male ventral view. *Holophryxus acanthephyrae* Stephensen, 1912: l, female dorsal view; m, female ventral view; n, male dorsal view. *Branchiophryxus koehleri* Nierstrasz and Brender à Brandis, 1931: o, female dorsal view; p, female ventral view; q, male lateral view.

extending well beyond anterior margins of lateral lobes. Antennula and antenna not described. 4 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in size. Pleon fused, extending slightly beyond posterior margins of lateral lobes; pleopods and uropods absent. **Male** body recurved with pereomeres subequal in width, head wider than long, posterior margin raised and sloping towards anterior margin, fused to pereomere 1. Eyes absent. Antennula and antenna not described. Pleon large, swollen, indistinctly segmented; pleopods, anal cone and uropods absent. **Cryptoniscus larva** unknown.

Bathypelagic, host(s) unknown. Temperate Northern Atlantic. 1 species (Richardson, 1908b).

#### ***Cryptoniscus* Schultz, 1977**

**Diagnosis. Female and male unknown. *Cryptoniscus larva*** body elongate, head horseshoe-shaped; eyes absent. Antennula without teeth on basal segment. Oral sucker absent. Pereomeres with serrate coxal plates margins, without teeth. Pereopods 1–6 gnathopodal, 1 shorter than 2–6, dactyli stout, ventrally serrate; 1 with stout setae on propodus and carpus, 2–6 propodi with 2 erect multifid setae, carpus with 1 multifid seta; pereopod 7 ambulatory, dactylus, propodus and ischium long; dactylus smooth ventrally, bearing distal tooth; propodus with 2 erect multifid setae ventrally and row of spines dorsally, carpus with 1 erect multifid setae. Pleotelson with distomedial region

quadrate, bearing 1 small spine at each posterolateral corner.

Shelf–bathypelagic, host(s) unknown. Southern Ocean. 1 species (Schultz, 1977).

#### ***Dajus Krøyer, [1842]***

*Diagnosis. Female* body heart-shaped; pereomeres with dorsal segmentation; head with narrow frontal lamina, directed anteriorly, not extending beyond anterior margins of lateral lobes. Eyes absent. Antennula and antenna segmented. 5 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in shape, all at anterior end. Pleon segmented, pleopods present as 1 pair of large lobes on pleomere 1 and rudimentary pairs on other pleomeres, uropods present. *Male* with pereomeres subequal in width, head wider than long, rounded, fused to pereomere 1. Eyes absent. Antennula and antenna segmented. Pleon unsegmented, pleopods absent and anal cone absent (anal slit present), rudimentary uropods present. **Cryptoniscus larva** body teardrop-shaped, eyes absent. Antennula with teeth on basal segment. Oral sucker present. Pereomeres with serrations on coxal plates but without teeth. Pereopods 1 and 2 gnathopodal, dactylus stout, without robust setae on propodi or carpi. Pereopods 3–7 ambulatory, 3–5 subequal in size, 6 and 7 with longer ischia; setal patterns of 3–5 unknown; 6 and 7 with 2 large erect multifid setae on propodus, 1 large erect multifid seta on carpus. Pleotelson posterior margin rounded, without teeth.

Subtidal–bathypelagic, parasitising mysids. Temperate Northern Atlantic, Arctic, Western Indo-Pacific. 4 species (Pillai, 1964).

#### ***Dolichophryxus Schultz, 1977***

*Diagnosis. Female* and *male* unknown. **Cryptoniscus larva** body teardrop-shaped, head helmet-shaped with small lobes at posterolateral corners; eyes absent. Antennula with teeth on basal segment. Oral sucker present. Pereomeres with serrate coxal plates margins, without teeth. Pereopod 1 gnathopodal, dactylus short, large setae on propodus or carpus absent; pereopods 2–6 ambulatory, dactyli long, ventrally smooth with distal tooth; propodi with 2 erect multifid setae; carpi with 1 erect multifid seta; pereopod 7 ambulatory, dactylus long; dactylus setose ventrally, subdivided at midlength; propodus with 2 erect multifid setae ventrally and row of spines dorsally, carpus with 1 erect multifid setae. Pleotelson with distomedial region triangular.

Mesopelagic–bathypelagic, host(s) unknown. Southern Ocean. 1 species (Schultz, 1977).

#### ***Heterophryxus G.O. Sars, 1885***

*Diagnosis. Female* body elongate ovate; pereomeres with medial dorsal segmentation; head with square frontal lamina, projecting beyond anterolateral margins of pereon. Eyes absent. Antennula absent; antenna rudimentary. 5 pairs of oostegites. Pereopods 1–4 gnathopodal, subequal in shape and size, widely spaced along pereon; pereopod 5 modified into enlarged clasper at posterior end of body. Pleon small, fused, rounded, projecting slightly posteriorly beyond lateral lobes, pleopods and uropods absent. *Male* with pereomeres subequal in width, head wider than long, rounded, fused to pereomere 1. Eyes absent. Antennula

and antenna segmented. Pleon fused, rounded, swollen; pleopods, anal cone, and uropods absent. **Cryptoniscus larva** unknown.

Subtidal–bathypelagic, parasitising euphausiids. Central Pacific Ocean, Temperate Southern Pacific, Southern Ocean. 4 species (Ariyama et al., 2016).

#### ***Holophryxus Richardson, 1905***

*Diagnosis. Female* body elongate ovate; pereomeres with faint or no dorsal segmentation; head with rounded or square frontal lamina, projecting beyond anterolateral margins of pereon. Eyes absent. Antennula and antenna rudimentary. 5 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in shape. Pleon fused, projecting posteriorly beyond lateral lobes, pleopods and uropods absent. *Male* with pereomeres subequal in width, head wider than long, fused to pereomere 1. Eyes absent. Antennula 2 segmented. Antenna unsegmented. Pleon fused, elongate, pleopods and uropods absent. Anal cone present. **Cryptoniscus larva** body teardrop-shaped, eyes absent. Antennula without teeth on basal segment. Oral sucker absent. Pereomeres without toothed coxal plates. Pereopods 1–6 gnathopodal, 1 shorter than 2–6, dactyli stout, ventrally serrate; 1 with stout setae on propodus and carpus, 2–6 with 2 transverse rows of 1 to several setae on propodi, carpi with stout bifid seta; 7 dactylus, propodus, ischium longer than 1–6, dactylus smooth ventrally, propodus with 2 erect multifid setae, carpus with 1 bifid seta. Pleotelson without teeth.

Mesopelagic–bathypelagic, parasitising sergestoid and caridean shrimps. Temperate Northern Atlantic, Central Atlantic, Central Indo-Pacific, Temperate Northern Pacific, South Pacific, Temperate South America. 10 species (Boyko and Williams, 2021a; Huys et al., 2023).

#### ***Neritoniscus Schultz, 1977***

*Diagnosis. Female* and *male* unknown. **Cryptoniscus larva** body teardrop-shaped, eyes present with multiple ocelli. Antennula without teeth on basal segment. Pereomeres without toothed coxal plates. Pereopods 1 smallest, dactylus shorter than propodus, propodus bearing 2 erect, multifid setae, carpus with 1 multifid seta; pereopods 2–7 subequal in size, dactyli approximately as long as propodi, propodi each bearing 2 erect, multifid setae, carpi each with 1 multifid seta. Pleotelson without teeth.

Shelf, host(s) unknown. Temperate South America. 1 species (Schultz, 1977).

#### ***Notophryxus G.O. Sars, 1883***

*Diagnosis. Female* body ovate; pereomere segmentation visible medially on dorsal surface; head with broad lamina, extending beyond anterior margins of lateral lobes. Eyes absent. Antennula segmented, antenna absent. Oostegites fused into single unit. Pereopods 1–5 gnathopodal, subequal in size. Pleon segmented, terminal segment bifurcated; pleopods and lateral plates present. *Male* body recurved with pereomeres subequal in width, head wider than long, fused to pereomere 1; anterior margin sloping. Eyes absent. Antennula unsegmented, antenna segmented. 7 pairs of pereopods, pereopods 1–4 smaller than

5–7. Pleon segmented or unsegmented; pleopods, anal cone, and uropods absent. **Cryptoniscus larva** unknown.

Subtidal–bathypelagic, parasitising mysids and euphausiids. Temperate Northern Atlantic, Tropical Atlantic, Southern Ocean, Western Indo-Pacific, Temperate Northern Pacific. 9 species (Shimomura and Ohtsuka, 2011).

#### ***Oculophryxus* Shields and Gómez-Gutiérrez, 1996**

*Diagnosis.* **Female** body pyriform; pereomere segmentation absent; head without frontal lamina, not extending beyond anterior margins of lateral lobes. Antennula of 1 segment, antenna absent. Anterolateral margins of body modified into recurved, elongate lobes with spoon-like tips. Oostegites fused into 1 unit. Pereopods 1–4 gnathopodal, subequal in size; pereopod 5 absent. Pleon fused with pereon; pleopods and uropods absent. **Male** body flat with pereomeres subequal in width, head wider than long, fused to pereomere 1; anterior margin with medial indentation. Eyes absent. Antennula and antenna segmented. 6 pairs of subequal fully developed pereopods; pereopod 7 reduced, of 2 segments, dactylus absent. Pleon large, ovate, segments fused; pleopods, anal cone, and uropods absent. **Cryptoniscus larva** unknown.

Shelf, parasitising euphausiids. Tropical Atlantic, Central Indo-Pacific, Tropical Eastern Pacific. 1 species (Shields and Gómez-Gutiérrez, 1996).

#### ***Paraspidophryxus* Schultz, 1977**

*Diagnosis.* **Female** and **male** unknown. **Cryptoniscus larva** body elongate, head triangular; eyes absent. Antennula not described. Oral sucker present. Pereomeres with coxal plates not described. Pereopod 1 gnathopodal, dactylus stout; 2–6 ambulatory, dactyli longer than propodi, propodi with 2 erect multifid setae, carpus with 1 multifid seta; 7 ambulatory, dactylus, propodus and ischium long; dactylus smooth ventrally, bearing 1 distal tooth; propodus with 2 erect multifid setae ventrally, carpus with 1 erect multifid setae. Pleotelson with distomedial region rounded, smooth.

Mesopelagic–bathypelagic, host(s) unknown. Southern Ocean. 1 species (Schultz, 1977).

#### ***Prodajus* Bonnier, 1903**

*Diagnosis.* **Female** body heart-shaped; pereomeres with faint or no dorsal segmentation; head with subquadrate frontal lamina, directed ventrally, not extending beyond anterior margins of lateral lobes. Eyes present or absent. Antennula 1 or 4 segmented. Antenna absent or 4 segmented. 5 pairs of oostegites. Pereopods 1–5 gnathopodal, subequal in shape, pereopod 1 slightly smaller than 2–5. Pleon of 3 or 4 pleomeres plus pleotelson, pleopods absent, pair of recurved posterolateral lobes (“uropods”) present. **Male** with pereomeres subequal in width, head wider than long, fused to pereomere 1. Eyes present or absent. Antennula 2 segmented. Antenna of 5 or 6 segments. Pleon 1 or 2 segmented, pleopods absent. Anal cone absent (anal slit present). Pair of tapered posterolateral lobes (“uropods”) present, distal tips bifurcated. **Cryptoniscus larva** body teardrop-shaped, eyes present or absent. Antennula with teeth

on basal segment. Oral sucker present. Pereomeres with toothed coxal plates. Pereopod 1 gnathopodal, dactylus stout, without robust setae on propodus or carpus. Pereopods 2–7 ambulatory, subequal in size except 7 with longer ischium; pereopods 2–6 each with 2 stout setae on propodus, 1 stout seta on carpus; pereopod 7 with 2 large erect multifid setae on propodus, 1 large erect multifid seta on carpus. Pleotelson with or without teeth.

Subtidal, parasitising mysids. Temperate Northern Atlantic, Western Indo-Pacific, Temperate Northern Pacific. 7 species (Shimomura et al., 2005).

#### ***Prophryxus* Richardson, 1909**

*Diagnosis.* **Female** body irregularly ovate; pereomeres 1–3 segmented, 4–7 with indications of segmentation dorsally; head with thin frontal lamina, head and pereomeres 1–3 extending beyond anterior margins of lateral lobes. Eyes absent. Antennula and antenna not described. Oostegites not described. Pereopods 1–5 gnathopodal, subequal in size and shape. Pleon segmented, pleopods rudimentary (number unknown), uropods not described but possibly present. **Male** and **cryptoniscus larva** unknown.

Bathypelagic, parasitising a “schizopod” (euphausiid or mysid; species of both were collected at the type locality). Temperate Northern Pacific. 1 species (Richardson, 1909).

#### ***Streptodajus* Nierstrasz and Brender à Brandis, 1923**

*Diagnosis.* **Female** body ovate, tapering posteriorly; pereomeres indicated dorsally; head with frontal lamina not visible dorsally, directed anterodorsally, extending anteriorly slightly beyond anterior margins of lateral lobes. Oral sucker present. Antennula (or antenna) of 1 segment, other absent. Oostegites of 1 pair, large, fused. Pereopods 1–5 gnathopodal, subequal in size, displaced to anterior margin below head. Pleon indistinctly segmented dorsally and ventrally, segmented ventrally, extending posteriorly beyond posterior margins of lateral lobes; pleomeres 1–4 with medial rounded projections. Pleopods and uropods absent. **Male** and **cryptoniscus larva** unknown.

Bathypelagic, parasitising mysids. Central Indo-Pacific. 1 species (Nierstrasz and Brender à Brandis, 1923).

#### ***Telephryxus* Williams and Boyko, 2021**

*Diagnosis.* **Female** body spheroid, unsegmented; head not visible. Eyes absent. Antennula as 1 flat triangular plate; antenna as 1 flat rectangular plate lateral to oral cone. Oostegite 1 largest, broadly ovate with large triangular posterior accessory lobe; oostegites 2–4 flat, ovate; oostegite 5 flat, tapering. Pereopods 1–5 gnathopodal, subequal in size and shape. Pleon modified as subquadrate, broad, thickened plate with 2 circular medial holes, subequal in size; hole surrounding distal portion of host antennular peduncle with 1 small additional hole on each lateral margin. **Male** with pereomeres subequal in width; head wider than long, triangular, fused with pereomere 1. Antennula as 1 ovate plate lateral to and extending posterior to oral cone; antenna of 2 segments. Pereomeres 2–7 distinct, lateral margins recurved ventrally. Pereopods 1–6 subequal in size and shape; pereopod 7 reduced to stub. Pleon tapering to rounded tip, all segments fused, distinct from pereomere 7; pleopods, anal cone,

and uropods absent. **Cryptoniscus larva** body teardrop-shaped, head extended posterolaterally; eyes present. Antennula without teeth on basal segment. Oral sucker absent. Pereomeres without toothed coxal plates. Pereopod 1 with short, slightly curved dactylus, propodus semi-spherical bearing 2 stout, simple setae, carpus with 1 stout simple seta; pereopods 2–6 each with more elongate curved dactyli, propodi progressively more elongate, bearing 2 stout simple setae, carpi each with 1 stout, simple seta. Pereopod 7 with long, slightly curved dactylus, propodus elongate with 2 large multifid setae near base of dactylus; carpus with 1 distal large multifid seta; merus triangular with anterodorsal edge extending into spine-like extension. Pleotelson without teeth.

Abyssal, parasitising munidopsid squat lobsters. Tropical Atlantic. 1 species (Williams and Boyko, 2021).

### **Zonophryxus Richardson, 1903**

**Diagnosis. Female** body ovate; pereomeres with faint dorsal indications; head with large frontal lamina, fused with lateral margins of pereomeres. Eyes absent. Antennula as recurved flat lobe; antenna small, digitiform. 6 pairs of oostegites, sixth pair fused to fifth. Pereopods gnathopodal, 5 or 6 pairs, sixth pair (if present) near posterior margin of body at base of oostegite 6. Pleon without pleopods or uropods. Posterior margin of pleon with row of triangular-shaped processes. **Male** body flattened; head ovate, fused with pereomere 1. Eyes absent. Antennula minute, rounded; antennae elongate, blade-like. Pereon with 6 free segments. 7 pairs of subequal pereopods. Pleomeres fused; pleopods, anal cone, and uropods absent. Type 1 male head sloping from anterior to posterior, smooth. Pereomere 7 smaller than pereomere 2. Pleon extending posteriorly from pereomere 7. Type 2 male head with distinct medial and lateral lobes. Pereomere 7 larger than pereomere 2. Pleon ventrally displaced under pereomere 7. **Cryptoniscus larva** body teardrop-shaped, eyes absent. Antennula without teeth on basal segment. Pereomeres without toothed coxal plates. Pereopods 1 and 2 subequal, dactyli short, slightly curved, propodus bearing 2 stout, simple setae; carpus without setae. Pereopods 3–5 dactyli more elongate, curved, propodi more elongate, narrower, bearing 2 stout simple setae; carpi without setae. Pereopod 6 and 7 dactyli subequal in length to those of pereopods 3–5, propodi more elongate and narrower than those of pereopods 3–5, bearing 2 erect, multifid setae, carpus with 1 distal multifid seta. Pleotelson without teeth.

Shelf–bathypelagic, parasitising caridean shrimps. Tropical Atlantic, Temperate Northern Atlantic, Temperate Southern Africa, Southern Ocean, Central and Eastern Indo-Pacific, Temperate Northern Pacific, Temperate South America. 7 species (Williams and Boyko, 2021b).

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## Family Entophilidae Richardson, 1903

### Figure 6.34

Members of Entophilidae are endoparasitic; they can be distinguished from all other epicarideans by the symmetrical body form of the females, the pleopods and lateral plates forming a cylindrical tube surrounding the pleomeres, and thread-like form of some pleopodal endopods and/or uropods. Within Epicaridea, entoniscids are the only other fully internal parasites; female entoniscids are vermiform (Boyko and Williams, 2015; McDermott et al., 2019).

**Diagnosis. Female** body nearly symmetrical, ovoid with tapering posterior end. Pereomeres distinctly segmented dorsally; head bilobed, not distorted. Frontal lamina present. Eyes absent. Barbula with single (irregularly shaped or smooth) lobe on each side. Antennula as rounded unsegmented flap, antenna as elongate, unsegmented flap or 2-segmented. Maxilliped without palp. Marsupium closed. 5 pairs of oostegites; oostegite 1 with triangular or ovate posterior lobe; internal ridge smooth. Coxal plates present. Dorsolateral bosses absent. Middorsal projections absent. 7 pairs of subequal pereopods. Pleon of 5 or 6 segments, pleomeres 1 and 2 with

medioventral tubercles or tubercles absent; uniramous lateral plates on pleomeres 1–4 or 1–5. Biramous pleopods on pleomeres 1–4 or 1–6, exopods lamellar, unsegmented or 2-segmented, endopods long and thin; pleopod 5 uniramous, lamellar or thread-like. Pleopods and lateral plates forming cylindrical tube surrounding pleomeres. Slender or thread-like uniramous uropods inserted ventrally between fifth pleopods. **Male** with pereomeres slightly narrowing posteriorly or with tubular body shape. Head wider than long, diamond-shaped or ovate; eyes present or absent. Antennula rounded, unsegmented lobe, sparsely setose, antenna absent or antennula and antenna as bilobed flaps, densely setose. Midventral tubercles absent. 6 pairs of subequal pereopods plus pereopod 7 as an unsegmented stub or 7 pairs of subequal pereopods. 6 distinct pleomeres, pleopods present on pleomeres 1–4 as rounded stubs, pleomere 5 without pleopods or bilobed flap-like pleopods present on pleomeres 1–5. Pleotelson ovate, with pair of slender uropods inserted posteromedially or posterolaterally, with or without scales, marginally setose. Endoparasitic.

### Key to genera of Entophilidae

1. Mature female (fig. 6.34a–d) with unsegmented antenna, 5 pairs of biramous pleopods, pleopod 5 a stout tapered lobe, male (fig. 6.34f, g) with antenna as pair of simple flaps, pereopod 7 reduced to stub, 4 pairs of uniramous pleopods. .... *Axiophilus*
- Mature female (fig. 6.34h–k) with 2-segmented antenna, 6 pairs of pleopods, pleopod 5 minute and thread-like, male (fig. 6.34l–n) with antenna as 2 pairs of bilobed flaps, pereopod 7 not reduced, 5 pairs of uniramous pleopods. .... *Entophilus*

### *Axiophilus* Boyko and Williams, 2015

**Diagnosis. Female** with barbula as single irregularly shaped lobe on each side. Antennula and antenna as elongate, unsegmented flaps. Oostegite 1 with triangular posterior lobe. Pleon of 5 segments, medioventral tubercles absent; uniramous lateral plates on pleomeres 1–4. Biramous pleopods on pleomeres 1–4, exopods lamellar, 2-segmented, endopods long and thin; pleopod 5 uniramous, lamellar (lacking endopod).

Uropods slender, uniramous, inserted ventrally between fifth pleopods. **Male** with pereomeres slightly narrowing posteriorly. Head diamond-shaped; eyes present. Antennula a rounded, unsegmented lobe, sparsely setose; antenna absent. Midventral tubercles absent. 6 pairs of subequal pereopods plus pereopod 7 as unsegmented stub. Pleopods present on pleomeres 1–4 as rounded stubs, pleomere 5 without pleopods. Pleotelson with slender uropods inserted posteromedially, without scales.

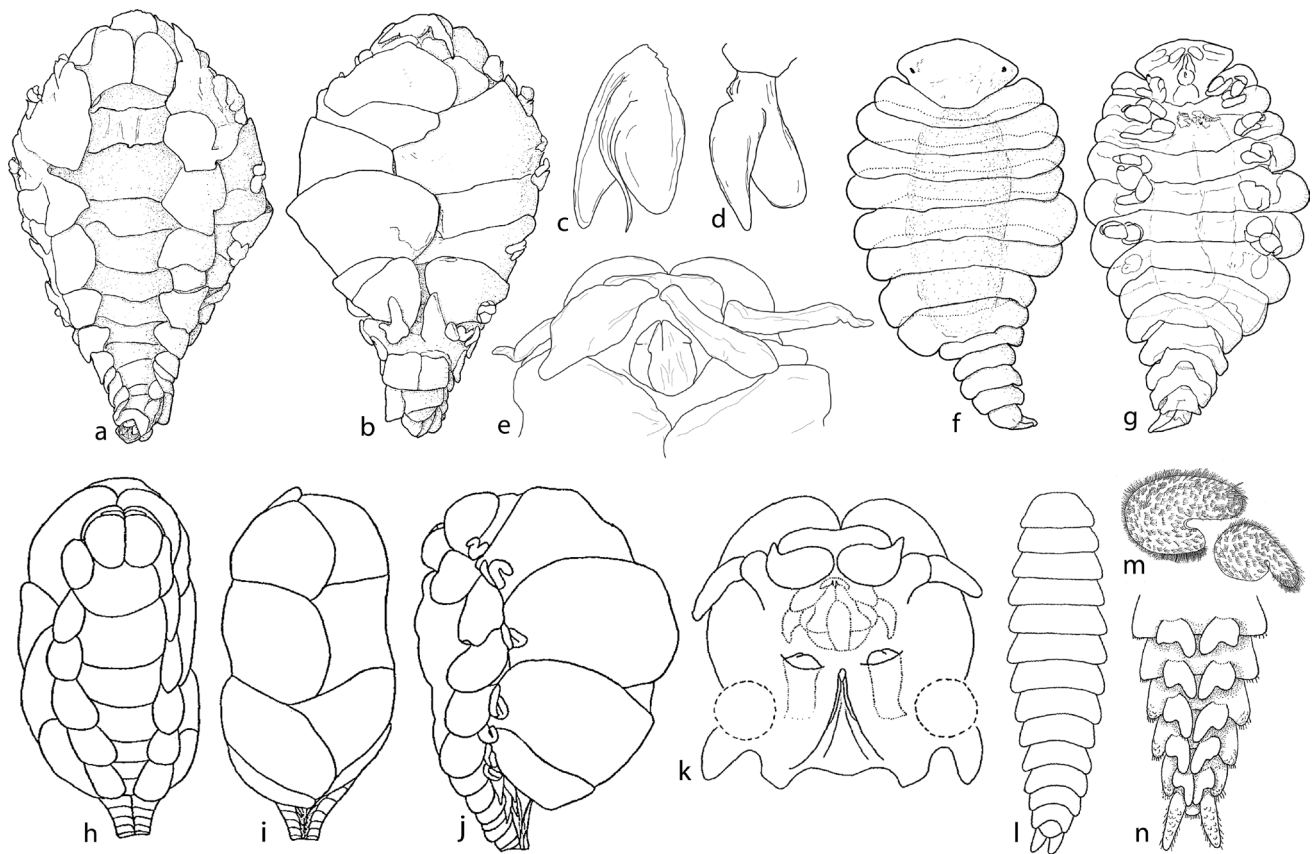


Figure 6.34. Entophilidae *Axiophilus mirabilectus* (Markham and Dworschak, 2005): a, female dorsal view; b, female ventral view; c, female pleopod 4; d, female, pleopod 5 and terminal pleomere, lateral view; e, female head, ventral view; f, male dorsal view; g, male ventral view. *Entophilus omnitectus* Richardson, 1903: h, female dorsal view; i, female ventral view; j, female lateral view; k, female head, ventral view; l, male dorsal view; m, male antennula and antenna; n, male pleon, ventral view.

Subtidal, parasitising callianassid shrimps. Western Indo-Pacific. 1 species (Boyko and Williams, 2015).

### *Entophilus* Richardson, 1903

**Diagnosis. Female** with barbula as single, smooth lobe on each side. Antennula as rounded, unsegmented flap; antenna with 2-segments. Oostegite 1 with ovate posterior lobe. Pleon of 6 segments, medioventral tubercles on pleomeres 1 and 2; uniramous lateral plates on pleomeres 1–5. Biramous pleopods on pleomeres 1–6, exopods and endopods lamellar, unsegmented; pleopod 5 minute, thread-like (lacking endopod). Uropods uniramous, minute, thread-like. **Male** with tubular body shape, pereomere and pleomere width subequal. Head ovate; eyes absent. Antennula and antenna as bilobed flaps, densely setose. Midventral tubercles absent. 7 pairs of subequal pereopods. Bilobed flap-like pleopods present on pleomeres 1–5. Pleotelson with slender uropods inserted posterolaterally, with scales.

Shelf-Slope, parasitising munidid squat lobsters. Tropical Atlantic, Temperate Northern Atlantic, Western and Eastern Indo-Pacific. 1 species (Boyko and Williams, 2015).

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## Family Hemioniscidae Bonnier, 1900

Figure 6.35

Members of Hemioniscidae are endoparasitic. They can be distinguished from other isopod parasites of barnacles by the presence of distinct teeth on the basal segment of the antennula in males (= cryptoniscus larval stage) (Buhl-Mortensen et al., 2020; Williams and Boyko, 2006).

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head

wider than long, oral cone directed anteriorly. Eyes present or absent. Antennula article 1 with 5–9 posterior teeth. Coxal plates with or without teeth. Pereopods 1 and 2 gnathopodal, pereopods 3–7 ambulatory, pereopods 3–5 with propodi quadrate distally, 6 and 7 tapering distally. Pleotelson margin smooth. **Mature females** with some segmentation visible, most of body fused into large marsupium. Endoparasitic.

### Key to genera of Hemioniscidae

*Cryptothir taxon inquirendum* excluded

1. Cryptoniscus larva (fig. 6.35b, c) antennular basal segment with fewer than 6 teeth (fig. 6.35d); mature female spheroid with dorsal segmentation, lacking appendages (fig. 6.35a); parasitic in ascothoracicans ..... *Gorgoniscus*
- Cryptoniscus larva antennular basal segment with more than 6 teeth; mature female retains some cryptoniscus segmentation with appendages (fig. 6.35e, h) ..... 2
2. Cryptoniscus larva (fig. 6.35f, g) antennular basal segment with 7 teeth, female (fig. 6.35e) parasitic in balanid, lepadid and trypetesid cirripedes ..... *Hemioniscus*
- Cryptoniscus larva (fig. 6.35i, j) antennular basal segment with 8 or 9 teeth, female (fig. 6.35h) parasitic in scalpellid cirripedes ..... *Scalpelloniscus*

### *Cryptothir* Dana, 1853 (*taxon inquirendum*)

**Diagnosis.** As for family (only the cryptoniscus larva is known and was described and figured incompletely).

Subtidal, parasitising pyrgomatid barnacles. Eastern Indo-Pacific. 1 species (Williams and Boyko, 2006).

### *Gorgoniscus* Grygier, 1981

**Diagnosis. Male** (paedomorphic cryptoniscus larva) eyes absent. Antennula article 1 with 5 posterior teeth. Coxal plates longitudinally ridged, posterior margins smooth. Pleotelson margin smooth. **Mature female** spheroid in dorsal view, compressed dorsoventrally with anterior and posterior ends curled ventrally; cryptoniscus segmentation not retained, lacking appendages.

Slope, parasitising ascothoracican barnacles. Eastern Indo-Pacific. 1 species (Grygier, 1981a).

### *Hemioniscus* Buchholz, 1866

**Diagnosis. Male** (paedomorphic cryptoniscus larva) eyes present. Antennula article 1 with 7 bluntly rounded teeth. Coxal plates with or without teeth. Pleotelson with smooth evenly rounded distal margin. **Mature female** with anterior segments unmodified from cryptoniscus form; posterior segments fused into enlarged marsupium.

Intertidal–subtidal, parasitising acrothoracican, lepadid and sessile thoracican barnacles. Central Indo-Pacific, Temperate Northern Pacific, Temperate Northern Atlantic, and Temperate

Southern Africa. 3 species and 1 subspecies (Goudeau, 1967, 1970, 1972; Williams and Boyko, 2006). *Leponiscus* Giard, 1887 is treated here as a junior subjective synonym.

### *Scalpelloniscus* Grygier, 1981

**Diagnosis. Male** (paedomorphic cryptoniscus larva) eyes absent. Antennula article 1 with 8 or 9 bluntly rounded teeth. Coxal plates with teeth. Pleotelson with bell curve-shaped posterior lobe. **Mature female** with anterior segments as in cryptoniscus larva; posterior segments as in cryptoniscus larva dorsally (sac-like ventrally) or entirely sac-like.

Slope–abyssal, parasitising pedunculate thoracican barnacles. Temperate Southern Africa, Temperate Australasia, Temperate South America. 4 species (Grygier, 1981b; Hosie, 2008).

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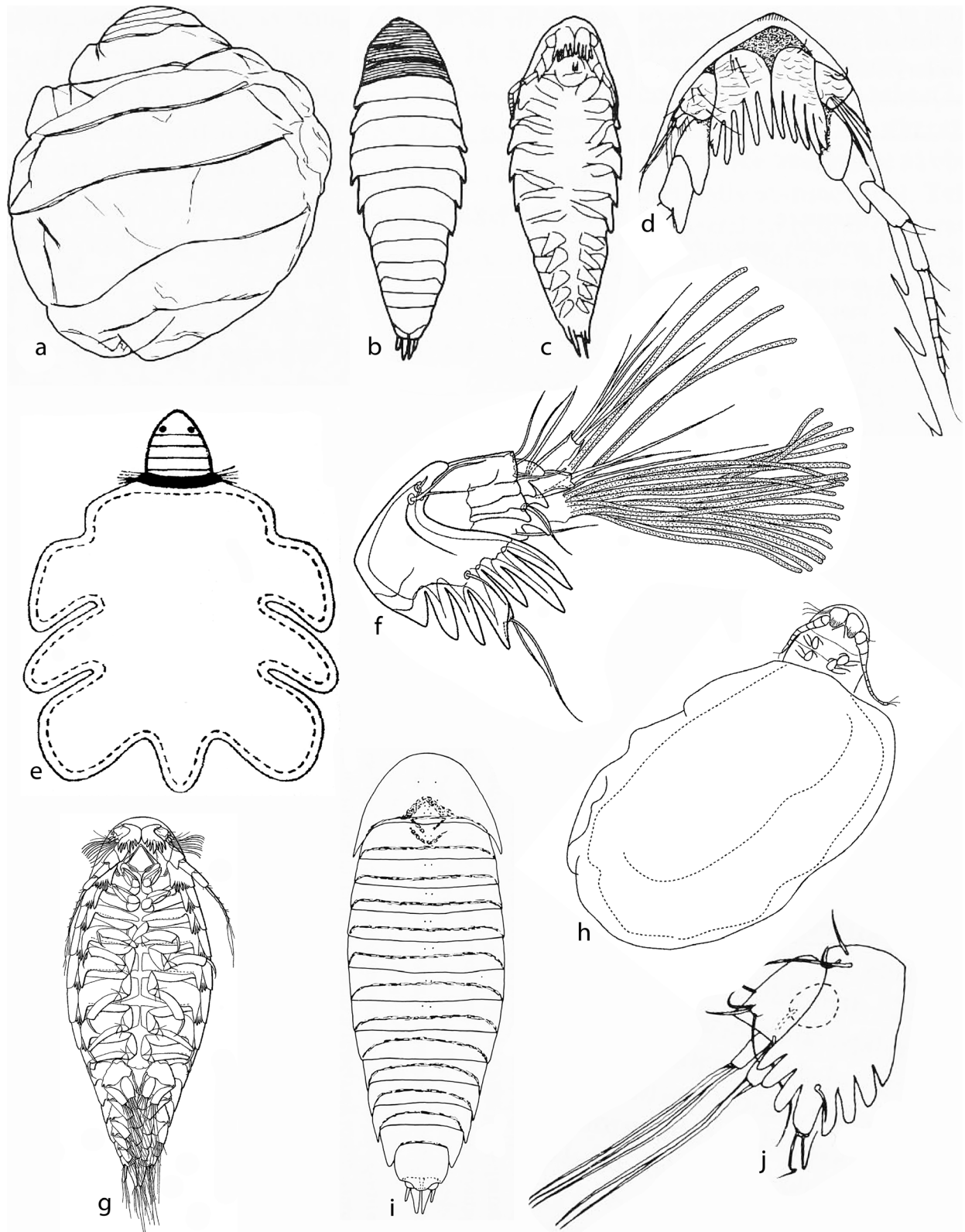


Figure 6.35. Hemioniscidae. *Gorgoniscus incisodactylus* Grygier, 1981: a, female dorsal view; b, male dorsal view; c, male ventral view; d, male head, ventral view showing antennulae and antenna. *Hemioniscus balani* Buchholz, 1866: e, female dorsal view; f, male antennula; g, male ventral view. *Scalpelloniscus nieli* Hosie, 2008: h, female ventral view. *Scalpelloniscus penicillatus* Grygier, 1981b: i, male dorsal view; j, male antennula.

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## Family Podasconidae Giard and Bonnier, 1895

Figure 6.36

Members of Podasconidae are the only known direct epicaridean ectoparasites of amphipods (*Gnomoniscus podasconis* Giard and Bonnier, 1895 is a hyperparasite of *Podascon haploopsis* Giard and Bonnier, 1895; fig. 6.36a) (Giard and Bonnier, 1895; Hansen, 1916). It is possible, however, that the two included genera do not belong to the same family or even that the family is not valid; they were likely placed in the same family on the basis of host choice rather than morphological affinities. Females of species of *Podascon* are very similar to those of *Cirolanoniscus* (Pillai, 1966; Cabiropidae) but cryptoniscus larvae are not known from either

genus. The females of species of *Parapodascon* are similar to those of *Cumoechus* (Cumoechidae) but the cryptoniscus larvae are very different. A complete redescription of species in both genera is needed, as well as collection of material for molecular analysis, to determine their relationships to each other and to other cryptoniscoids. The family-level diagnosis below includes only the characters for the type genus.

**Diagnosis. Male** (paedomorphic cryptoniscus larva) unknown. **Mature female** ovate, swollen dorsoventrally, dorsal surface with segmentation, marsupium closed by 2 large smooth lateral lobes; pleon distinct, segmented. Ectoparasitic.

### Key to mature females of genera of Podasconidae

1. With dorsal segmentation; ventrally with 2 large lateral lobes meeting in midline; pleon distinguishable (fig. 6.36a–d) ..... *Podascon*
- Without any segmentation; ventrally with narrow slit in midline; pleon indistinguishable (fig. 6.36e–j) ..... *Parapodascon*

### *Parapodascon* Hansen, 1916

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body teardrop-shaped with poorly developed cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 with 7 posterior teeth. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal, pereopods 3–7 ambulatory; propodi of pereopods 3–5 quadrate distally, 6 and 7 tapering distally; dactylus of pereopods 5 and 7 with terminal spine, that of pereopod 6 with 1 long dorsal spine and 1 short ventral spine. Pleotelson margin smooth. **Mature female** ovate, without any segmentation, lacking most appendages; median half of ventral surface with longitudinal slit flanked by 5 pairs of rounded lobes and bearing minute conical antennae at anterior end; pleon indistinguishable.

Intertidal–slope, parasitising lysianassoid amphipods.

Arctic. 1 species (Coyle and Mueller, 1981; Hansen, 1916).

### *Podascon* Giard and Bonnier, 1889

**Diagnosis. Mature female** ovate, swollen dorsoventrally, dorsal surface with segmentation; pleon distinct.

Subtidal, parasitising lysianassoid amphipods. Temperate Northern Atlantic. 3 species (Giard and Bonnier, 1895).

### References

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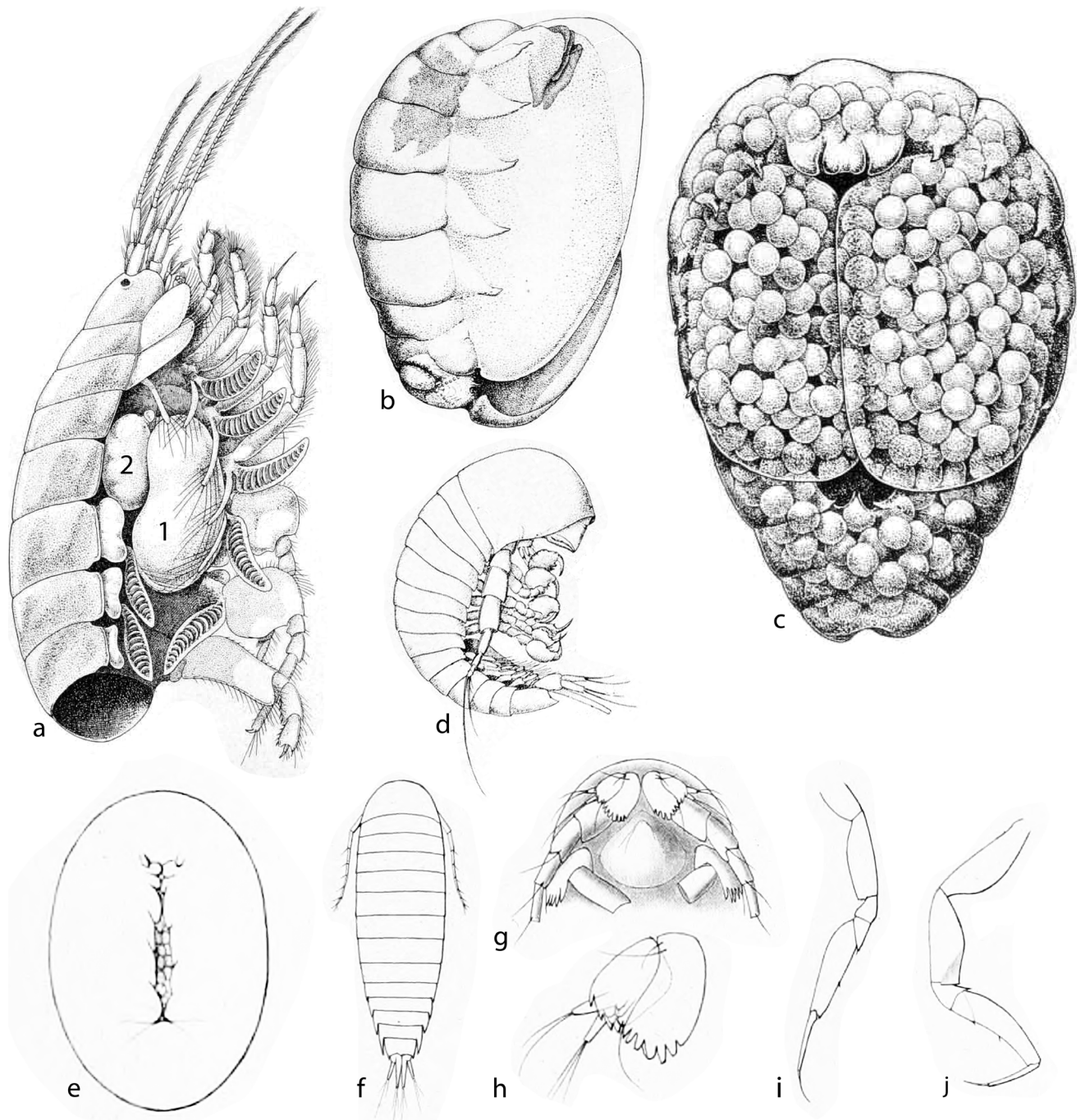


Figure 6.36. Podasconidae. a, host amphipod with *Podascon haploopsis* Giard and Bonnier, 1895 (labeled 1) and hyperparasitic cabriopid isopod *Gnomoniscus podasconis* Giard and Bonnier, 1895 (labeled 2), lateral view of host and parasites. *Podascon dellavallei* Giard and Bonnier, 1889: b, female lateral view; c, ovigerous female ventral view. *Podascon chevreuxi* Giard and Bonnier, 1895: d, epicaridium larvae, lateral view. *Parapodascon stebbingi* (Giard and Bonnier, 1895): e, female ventral view; f, male dorsal view; g, male head, ventral view; h, male antennula; i, male pereopod 5; j, male pereopod 7.

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## Family Stellatoniscidae Oanh and Boyko, 2020

Figure 6.37

Members of Stellatoniscidae are ectoparasitic in the marsupium of entoniscid isopods as hyperparasites. They can be distinguished from other epicaridean parasites by the mature females possessing numerous thin tentacular extensions and the cryptoniscus larva having a mesial demarcated area on antennular segment 1, pereomere 7 lacking coxal plates, pereopod 1 with a ridged surface on the carpus and merus, and pereopods 1 and 2 dissimilar (Oanh and Boyko, 2020).

**Diagnosis. Epicaridium larva** (fig. 6.37e) antenna approximately 3/4 as long as body. 6 pairs of gnathopodal pereopods subequal in size and shape; pleon with 5 pairs of biramous pleopods; uropods biramous. **Male** (paedomorphic cryptoniscus larva; fig. 6.36e–j), body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes present. Antennula article 1 with 6 or 7 posterior teeth and mesial demarcated area. Coxal plates 1–6 entire, covered with scales, pereomere 7 lacking coxal plate. Pereopods 1 and 2 gnathopodal, pereopod 2 larger than 1 and with greatly enlarged dactylus; pereopod 1 carpus and merus with ridged surface, pereopods 3–7 ambulatory, subequal in size and shape, propodi

subquadrate distally, ischia and bases with mediodorsal lobes. Pleotelson margin smooth. **Immature female** (fig. 6.37b–d) developing from 4-lobed stage to 4 lobes with short thin mediodistal extensions to reduced body with 8 short tentacular extensions; **mature female** (fig. 6.37a) with 10 tentacular thin extensions radiating out from central body. Ectoparasitic.

### *Stellatoniscus* Oanh and Boyko, 2020

**Diagnosis.** As for family.

Subtidal, parasitising entoniscid isopods. Central Indo-Pacific. 2 species (Oanh and Boyko, 2020).

### Reference

Oanh, L.T.K., and Boyko, C.B. 2020. *Cancrion khanhensis* sp. nov. (Crustacea: Isopoda: Entoniscidae) infesting *Monomia haanii* (Stimpson, 1858) (Crustacea: Brachyura: Portunidae) from Nha Trang Bay, Khanh Hoa, Vietnam, with remarks on larval stages of entoniscids and description of a new family, genus and two new species of hyperparasites infesting entoniscids. *Zootaxa* 4894(3): 366–386. <https://doi.org/10.11646/zootaxa.4894.3.4>

## Cryptoniscoidea genera known only from cryptoniscus larvae

Figures 6.38–6.41

Some epicaridean species and 20 genera have been described solely from the cryptoniscus larval stage and, as such, present some difficulties in taxonomic placement. Although some have characters that allow them to be included in existing families (with unclear position), others are of uncertain placement within Cryptoniscoidea. *Vacuotheca* Schädel, Perrichot and Haug, 2019, a monotypic genus known only from fossil cryptoniscus specimens that was not placed within a superfamily when described, is clearly a member of Cryptoniscoidea (4 basal + 5 flagellar antennal segments; fig. 6.41o). Due to the lack of knowledge of adult stages, it is unknown if species in these genera are endoparasitic, mesoparasitic or ectoparasitic associates of definitive hosts.

The following key includes taxa known only from cryptoniscus larval stages. Users should be aware that unknown cryptoniscus larvae they encounter may correspond to taxa

included here, or possibly to those covered in preceding sections for which adult forms may be known. The key is intended as a practical tool to aid in narrowing down identifications and encouraging comparison across cryptoniscoid genera. We hope to facilitate efforts to link cryptoniscoid larval and adult stages, resolve taxonomic placement, and expand understanding of their life histories and host associations. Researchers should also be aware that findings of cryptoniscus larvae on female epicarideans may represent hyperparasites (e.g., Cabiropidae) rather than recently settled larva of the same species.

The cryptoniscus larvae of the type species of the monotypic *Eumetor* Kossman, 1872 (Cryptoniscidae?) and *Cryptothir* Dana, 1853 (Cryptothiridae; possible synonym of Crinoniscidae or Hemioniscidae) are poorly described and not included in the key.

Diagnoses are given below only for genera placed *incertae sedis*. For all others, see Cabiropidae and Dajidae.

### Key to genera known only from cryptoniscus larvae

- |    |  |   |
|----|--|---|
| 1. | Oral sucker (fig. 6.38b, j, o) present ..... | 2 |
| –  | Oral sucker absent .....                     | 4 |

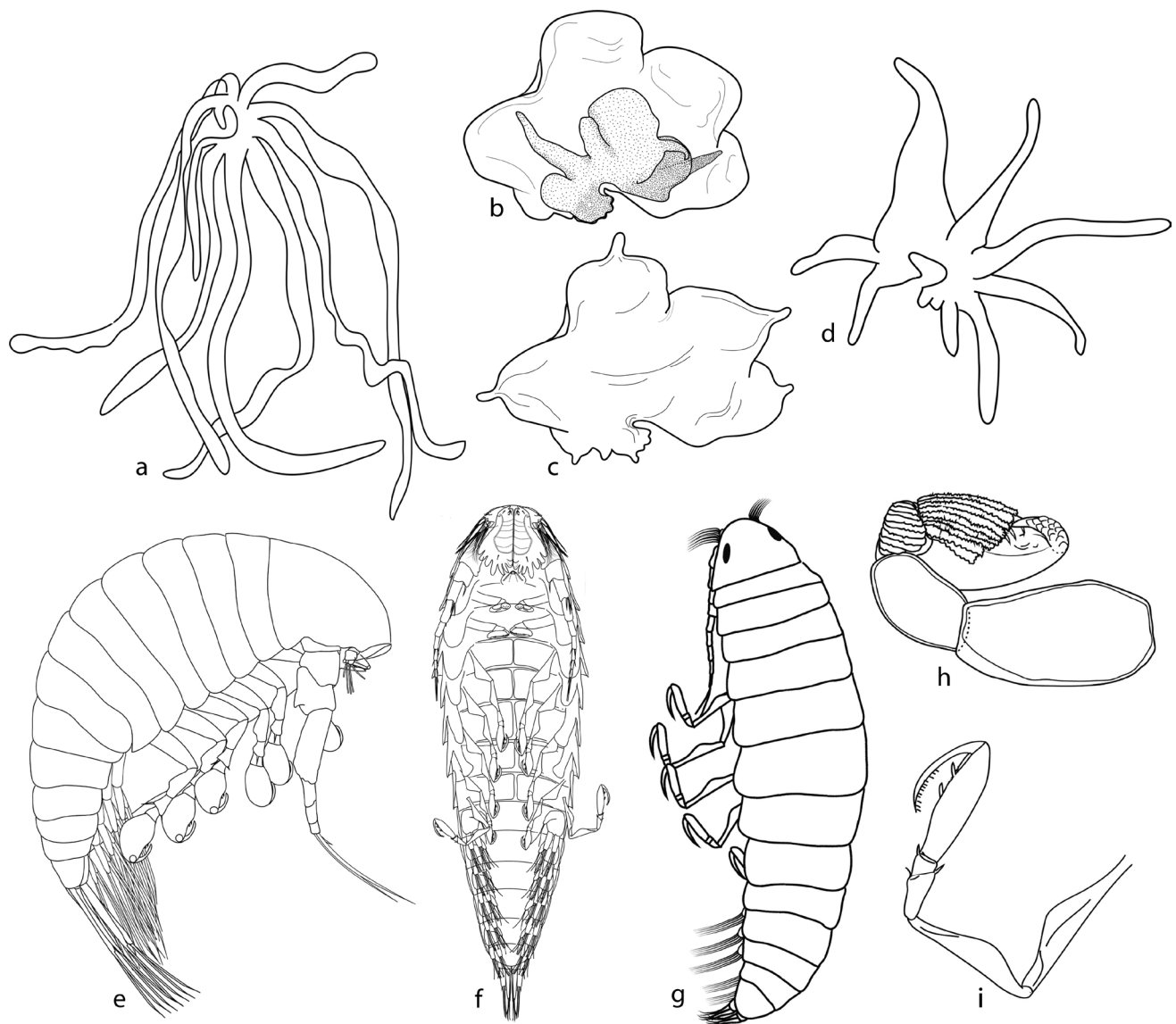


Figure 6.37. Stellatoniscidae. *Stellatoniscus tentaculus* Oanh and Boyko, 2020: a, mature female; b, immature female (stage 1); c, immature female (stage 2); d, immature female (stage 3); e, epicaridium larva lateral view; f, male ventral view; g, male dorsolateral view; h, male pereopod 1; i, male pereopod 7.

- |    |  |  |
|----|--|--|
| 2. | Pereopod 7 with large multifid teeth on propodus and carpus .....  | 3                                      |
| –  | Pereopod 7 (fig. 6.38h) without large multifid teeth on propodus and carpus (see also fig. 6.38a–g) .....  | <i>Thermaloniscus (incertae sedis)</i> |
| 3. | Antenna (fig. 6.38i, n) reaching past anterior margin of pleomere 1, dorsal margin of pereopod 7 (fig. 6.38m) propodus spinose (see also fig. 6.38j–l) ..... | <i>Dolichophryxus</i> (Dajidae)        |
| –  | Antenna (fig. 6.38o) reaching past anterior margin of pereomere 5; dorsal margin of pereopod 7 (fig. 6.38q) propodus smooth (see also fig. 6.38p) .....      | <i>Paraspidophryxus</i> (Dajidae)      |
| 4. | Pereopod 7 with large multifid teeth on propodus and carpus (fig. 6.39d, h) .....  | 5                                      |
| –  | Pereopod 7 without large multifid teeth on propodus and carpus .....   | 6                                      |
| 5. | Coxal plate margins smooth (figs. 6.39a–d) .....   | <i>Neritoniscus</i> (Dajidae)          |

–	Coxal plate margins serrated (figs. 6.39e–i) .....	<i>Cryptociscus</i> (Dajidae)
6.	Antennular basal segment with marginal teeth (fig. 6.39k, m, u) .....	7
–	Antennular basal segment smooth .....	13
7.	Pleotelson posterior margin with teeth (fig. 6.39j, n) .....	8
–	Pleotelson posterior margin without teeth .....	10
8.	Pleotelson (fig. 6.39j) posterior margin with fewer than 10 teeth .....	9
–	Pleotelson (fig. 6.39n) posterior margin with more than 10 teeth (see also fig. 6.39l, m, o) .....	<i>Podoniscus</i> (Cabiropidae)
9.	Dactylus of pereopods 6 and 7 (fig. 6.39k) as long as propodus, pleotelson (fig. 6.39j) posterior margin with 5 teeth .....	<i>Cironiscus</i> (Cabiropidae)
–	Dactylus of pereopods 6 and 7 (fig. 6.41p) shorter than propodus, pleotelson (fig. 6.41n, q) posterior margin with 6 teeth (see also fig. 6.41o) .....	<i>Vacuotheca</i> ( <i>incertae sedis</i> )
10.	Coxal plate margins with 4 or fewer teeth .....	11
–	Coxal plate (compare to fig. 6.39f) margins with more than 10 teeth (see also fig. 6.39p–s) .....	<i>Osicryptus</i> ( <i>incertae sedis</i> )
11.	Pleon with medioventral tubercles; pleotelson (fig. 6.40d) medially indented (see also fig. 6.40a–c, e, f) .....	<i>Rolandoniscus</i> (Cabiropidae)
–	Pleon without medioventral tubercles; pleotelson rounded .....	12
12.	Coxal plate margins on pereomeres 5–7 lacking teeth (fig. 6.40w; see also fig. 6.40t–v) .....	<i>Pleuroniscus</i> (Cabiropidae)
–	Coxal plate margins with 3 or 4 teeth on pereomeres 5–7 (fig. 6.39w; see also fig. 6.39t–v) .....	<i>Chimaeroniscus</i> ( <i>incertae sedis</i> )
13.	Antennula (fig. 6.40g) with large subquadrate basal plate (see also fig. 6.40h–k) .....	<i>Trisopodoniscus</i> ( <i>incertae sedis</i> )
–	Antennula without large subquadrate basal plate .....	14
14.	Head inflated and posterolaterally extended (fig. 6.40l, p) .....	15
–	Head not inflated or posterolaterally extended .....	16
15.	Pleotelson (fig. 6.40l) triangular with marginal teeth (see also fig. 6.40m–o) .....	<i>Nalocryptus</i> ( <i>incertae sedis</i> )
–	Pleotelson (fig. 6.40p) subquadrate with smooth margins (see also fig. 6.40q–s) .....	<i>Onocryptus</i> ( <i>incertae sedis</i> )
16.	Propodus of pereopod 6 (fig. 6.41d) greatly reduced, dactylus more than 4 times as long as propodus (see also fig. 6.41a–c, e) .....	<i>Nococryptus</i> ( <i>incertae sedis</i> )
–	Propodus of pereopod 6 not greatly reduced, dactylus less than twice as long as propodus .....	17
17.	Pereopod 3 similar in shape and size to pereopods 1 and 2 (fig. 6.41f–i) .....	<i>Cryptocotitus</i> ( <i>incertae sedis</i> )
–	Pereopod 3 similar in shape and size to pereopods 4–7 (fig. 6.41j–m) .....	<i>Elocryptus</i> ( <i>incertae sedis</i> )

***Chimaeroniscus* Williams, Boyko and Moritaki, 2022**

**Diagnosis. Male** (paedomorphic cryptoniscus larva) body linear with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 with teeth. Coxal plates with teeth. Pereopods 1–2 gnathopodal,

3–7 ambulatory; propodi of 3–7 rounded distally, dactyli shorter than propodi in anterior pairs, gradually becoming longer than propodi in posterior pairs. Pleotelson margin smooth.

Slope, parasitising dajid isopods. Central Indo-Pacific, Southern Ocean. 1 species (Williams et al., 2022).

***Cryptocotitus* Schultz, 1977**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 with few low bumps, without large teeth. Coxal plates with teeth. Pereopods 1–3 gnathopodal, 4–5 ambulatory, propodi quadrate distally; propodi of 6 and 7 tapering distally, dactylus of 6 as long as propodus, dactylus of 7 as long as propodus, merus, and carpus combined. Pleotelson margin smooth.

Bathypelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

***Elocryptus* Schultz, 1977**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body widest at pereomere 5, tapering anteriorly and posteriorly with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth. Coxal plates without teeth. Pereopods 1–2 gnathopodal, 3–7 ambulatory, propodi quadrate distally; dactyli of 3–5 shorter than propodi, 6 and 7 longer than propodi. Pleotelson margin smooth.

Mesopelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

***Nalocryptus* Schultz, 1977**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body linear with prominent cuticular striations. Head much wider than long with posterolateral tapered extensions directed posteriorly, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth. Coxal plates with teeth. Pereopods 1–3 gnathopodal, 4–7 ambulatory; propodi of 4–7 tapering distally, dactyli shorter than propodi. Pleotelson margin triangular, with teeth.

Mesopelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

***Nococryptus* Schultz, 1977**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal, 3–7 ambulatory; propodi of 3 broadly quadrate distally, distal end wider than proximal end; propodi of 4 and 5 narrowly quadrate distally, distal end approximately as wide as proximal end; propodus of pereopod 6 short, rounded, as long as carpus and merus combined, dactylus slender, elongate, as long as all other segments combined; pereopod 7 subequal to 4 and 5 in shape and size. Pleotelson margin smooth.

Slope, host unknown. Southern Ocean. 1 species (Schultz, 1977).

***Onocryptus* Schultz, 1977**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head much wider than long with posterolateral tapered extensions directed

posteriorly, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal, 3–7 ambulatory; propodi of 3–5 rounded distally, dactyli shorter than propodi, recurved; propodus of 6 tapering in middle then slightly expanded to distal rounded tip, dactylus as long as propodus, straight; propodus of 7 tapering distally, dactylus as long as propodus, recurved. Pleotelson margin smooth.

Bathypelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

***Osicryptus* Schultz, 1977**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 with teeth and robust setal brush. Coxal plates with teeth. Pereopods 1 and 2 gnathopodal, 3–7 ambulatory; propodi of 3–6 quadrate distally, dactyli shorter than propodi; propodus of 7 rounded distally, dactylus shorter than propodus. Pleotelson margin smooth.

Bathypelagic, host unknown. Southern Ocean. 1 species (Schultz, 1977).

***Thermaloniscus* Bourdon, 1983**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly, oral sucker present. Eyes present. Antennula article 1 without teeth. Coxal plates without teeth. Pereopods 1 and 2 gnathopodal, 3–7 ambulatory; propodi of 3–7 quadrate distally, dactyli longer than propodi. Pleotelson margin smooth.

Bathyal, host unknown. Tropical Eastern Pacific. 1 species (Bourdon, 1983).

***Trisopodoniscus* Bourdon, 1981**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 without teeth. Coxal plates without teeth. Pereopods 1–3 gnathopodal, 4–7 ambulatory; propodus of 4 quadrate distally, dactylus shorter than propodus; propodi of 5–7 elongate, tapering distally, dactyli approximately 1/4 of propodus length. Pleotelson margin smooth.

Bathypelagic, host unknown. Southern Ocean. 1 species (Bourdon, 1981).

***Vacuotheca* Schädel, Perrichot and Haug, 2019<sup>†</sup>**

*Diagnosis. Male* (paedomorphic cryptoniscus larva) body teardrop-shaped with prominent cuticular striations. Head wider than long, oral cone directed anteriorly. Eyes absent. Antennula article 1 with teeth. Coxal plates with teeth. Pereopods 1–3 gnathopodal, 4–7 ambulatory; dactyli of all pereopods shorter than propodi. Pleotelson margin with teeth.

Fossil only, host unknown. Ex Vendean amber (France). 1 species (Schädel et al., 2019).

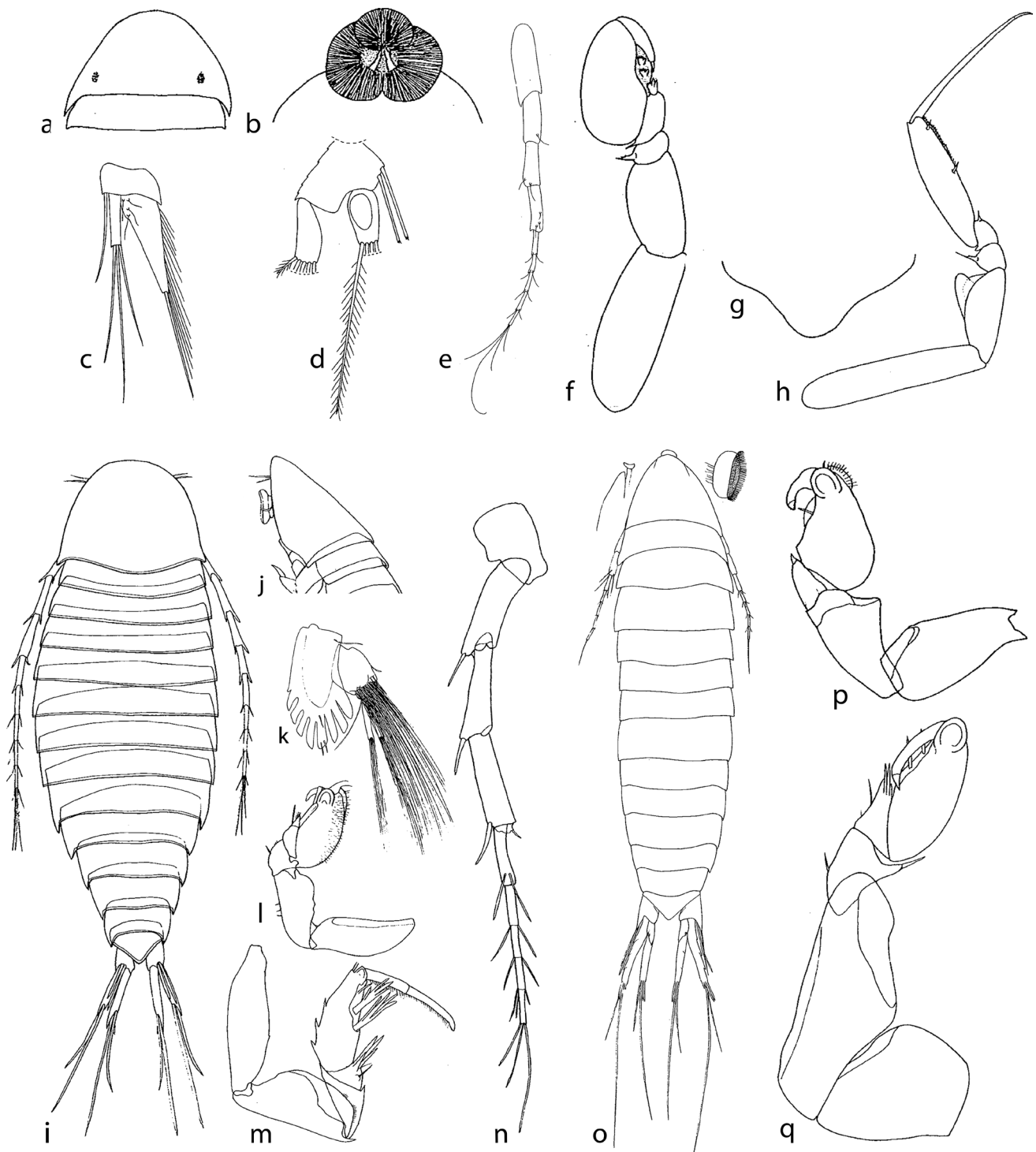


Figure 6.38. Cryptoniscoidea known only from cryptoniscus larvae. *Thermaloniscus cotylophorus* Bourdon, 1983: a, head dorsal view; b, oral sucker; c, uropod; d, pleopod 1; e, antenna; f, pereopod 1; g, pleotelson dorsal view; h, pereopod 7. *Dolichophryxus geminatus* Schultz, 1977: i, dorsal view; j, head and oral sucker lateral view; k, antennula; l, pereopod 1; m, pereopod 7; n, antenna. *Paraspidothryx terminalis* Schultz, 1977: o, dorsal view with close-ups of oral sucker in lateral view; p, pereopod 1; q, pereopod 6.

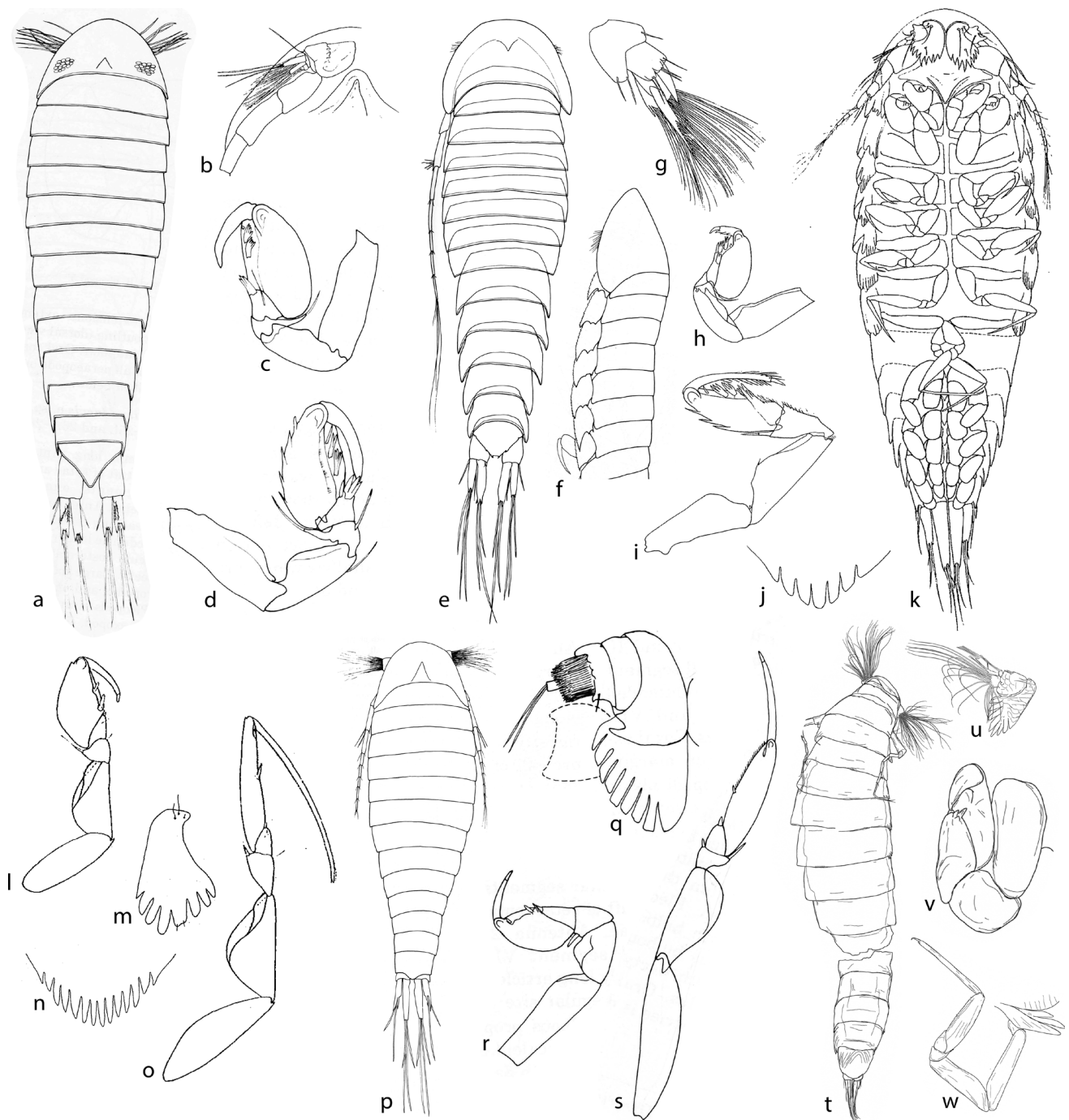


Figure 6.39. Cryptoniscoidea known only from cryptoniscus larvae. *Neritoniscus euphoticus* Schultz, 1977: a, dorsal view; b, antennula, oral cone and part of antenna; c, pereopod 1; d, pereopod 7. *Cryptociscus laevis* Schultz, 1977: e, dorsal view; f, lateral view of head and pereon showing serrated coxal plates; g, antennula; h, pereopod 1; i, pereopod 7. *Cironiscus dahli* Nielsen, 1967: j, pleotelson, dorsal view; k, ventral view. *Podoniscus multidentatus* Bourdon, 1981: l, pereopod 1; m, basal article of antennula; n, pleotelson, dorsal view; o, pereopod 7. *Osicryptus hirsutus* Schultz, 1977: p, dorsal view; q, antennula; r, pereopod 1; s, pereopod 7. *Chimaeroniscus spheramator* Williams, Boyko and Moritaki, 2022: t, dorsal view; u, antennula; v, pereopod 1; w, pereopod 7.

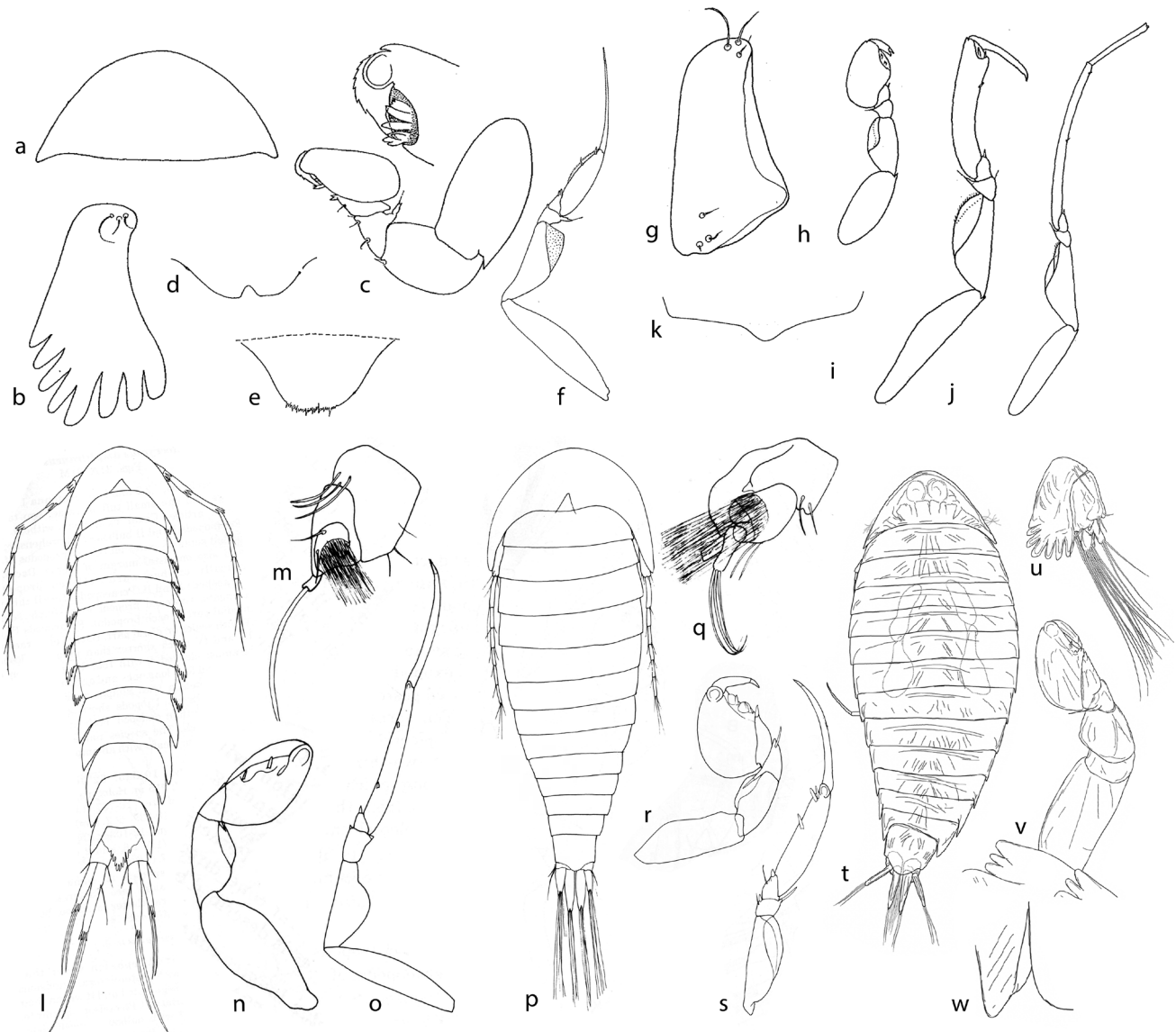


Figure 6.40. Cryptoniscoidea known only from cryptoniscus larvae. *Rolandoniscus serratus* (Bourdon, 1967): a, head, dorsal view; b, basal article of antenna; c, pereopod 1 and close-up; d, pleotelson, dorsal view; e, midventral tubercule; f, pereopod 7. *Trisopodoniscus abyssorum* Bourdon, 1981: g, basal article of antennula; h, pereopod 1; i, pereopod 4; j, pereopod 7; k, pleotelson dorsal view. *Nalocryptus longicaudatus* Schultz, 1977: l, dorsal view; m, antennula; n, pereopod 1; o, pereopod 7. *Onocryptus alatus* Schultz, 1977: p, dorsal view; q, antennula; r, pereopod 1; s, pereopod 7. *Pleuroniscus bellisamans* Williams and Boyko in Williams, Boyko and Stewart, 2024: t, dorsal view; u, antennula; v, right pereopod 2, base shown with coxal plates 1 and 2; w, coxal plate 5.

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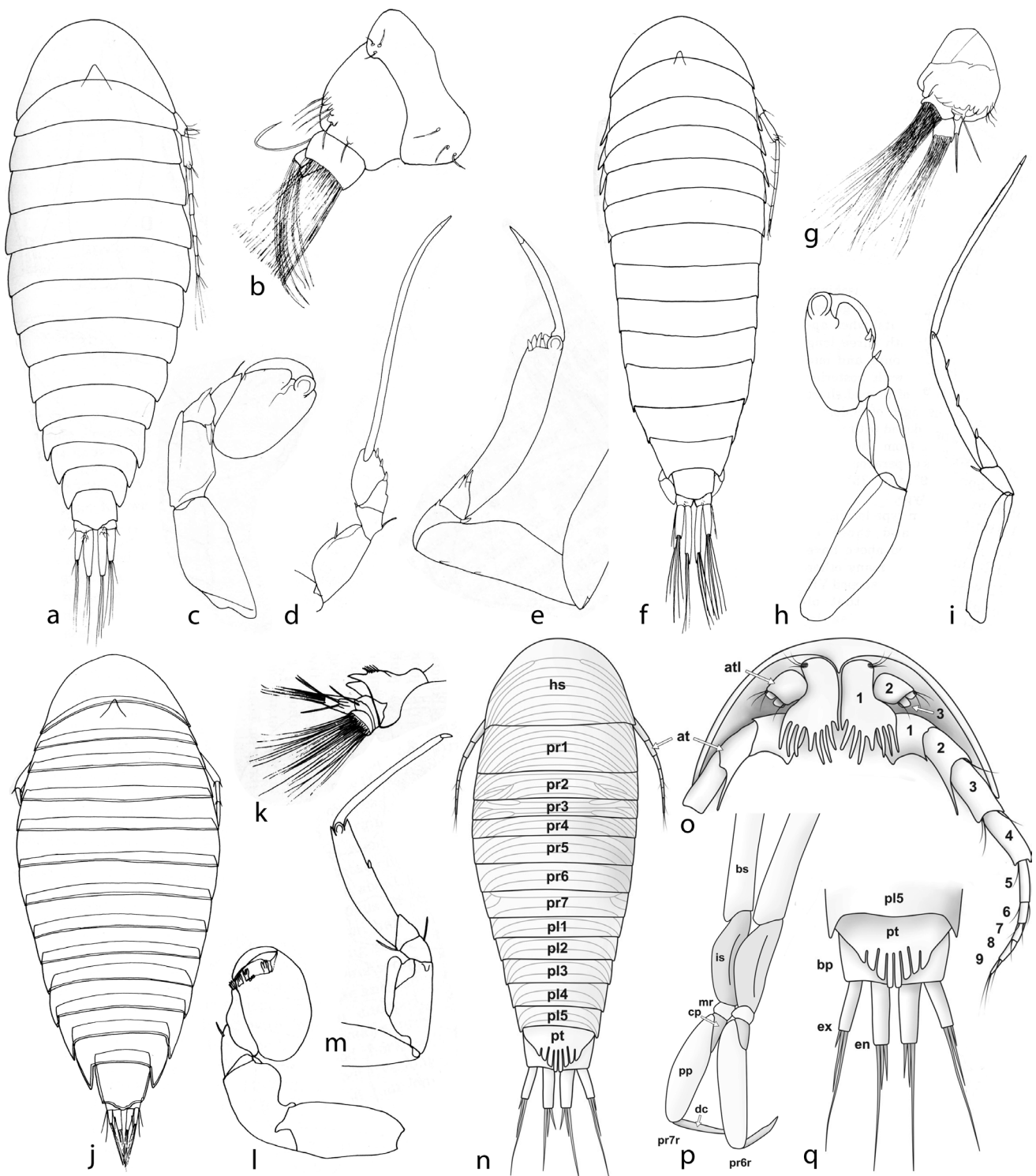


Figure 6.41. Cryptoniscoidea known only from cryptoniscus larvae, including the fossil genus *Vacuothecha* Schädel, Perrichot and Haug, 2019. *Nococryptus angustus* Schultz, 1977: a, dorsal view; b, antennula; c, pereopod 1; d, pereopod 6; e, pereopod 7. *Cryptocotilus acus* Schultz, 1977: f, dorsal view; g, antennula; h, pereopod 1; i, pereopod 7. *Elocryptus amplitruncus* Schultz, 1977: j, dorsal view; k, antennula; l, pereopod 1; m, pereopod 7. *Vacuothecha dupeorum* Schädel, Perrichot and Haug, 2019: n, dorsal view; o, antennulae and antennae; p, pereopods 6 and 7; q, pleotelson and uropods, dorsal view. Abbreviations: at, antenna (with number of articles indicated); atl, antennula (with number of articles indicated); bp, basipod of uropod; bs, basis; cp, carpus; dc, dactylus; en, endopod of uropod; ex, exopod of uropod; hs, head shield; is, ischium; mr, merus; pl1–5, pleomeres 1–5; pr1–7, pereomeres 1–7; pp, propodus; pr6r, right pereopod 6; pr7r, right pereopod 7; pt, pleotelson.

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