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Chapter 5. Suborder Cymothoida

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Abstract

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Diagnoses and illustrated keys are provided for one superfamily of six families, and the remaining nine families, comprising in total 180 marine genera of the Isopoda suborder Cymothoida. The ecology and distribution of each taxon are discussed with citation of literature critical for further investigation and identification to species.

Keywords

Aegidae, Antheluridae, Anthuridae, Anthuroidea, Anuropidae, Barybrotidae, Cirolanidae, Corallanidae, Cymothoidae, Cymothoidea, Expanathuridae, Gnathiidae, Hyssuridae, Leptanthuridae, Paranthuridae, Protognathiidae, Tridentellidae, dichotomous keys

Introduction

The Cymothoida Wägele, 1989 include those families of the former Flabellifera that are scavengers, ectoparasites, blood-suckers or predators (Dreyer and Wägele, 2001). According to these authors, the group has evolved from the scavenging and predatory feeding strategy towards parasitism on fish and other Crustacea. In the most basal families (e.g. Cirolanidae), the mandibular molar is an articulating toothed blade. This structure and the whole mandible is variously modified and reduced to a more piercing structure in the more parasitic families.

Brandt and Poore (2003) summarised the nomenclatural history of Flabellifera to which this suborder formerly belonged. Their morphological cladistic analysis, building on those of Wägele (1989) and Brusca and Wilson (1991), has given rise, more or less, to the accepted classification. Brandt and Poore (2003) assumed the monophyly of the easily recognisable superfamily Anthuroidea. They found the remaining cymothoidan families, including the Epicaridea, to be polyphyletic. They treated Epicaridea collectively as two monophyletic superfamilies Bopyroidea and Cryptoniscoidea within Cymothoida, following Dreyer and Wägele (2001). More recently, molecular data has provided support for a monophyletic Epicaridea that does not form a sister group relationship with any cymothoidan (An et al., 2022; Thomas Thorpe, 2024; Yu et

al., 2018), meaning that parasitism of Crustacea was separately derived from parasitism of fishes.

Diagnosis. Head-pereonite 1 free. Dorsal pereopodal coxal plates present (secondarily reduced in some species); coxal plate of pereopod 1 fused to tergite; coxal plate 7 present; ventral coxal plates 1–7 (medial extension of coxa replacing sternite) obsolete (not distinguished from sternite). Pleotelson incorporating pleonite 6 only, pleonites 1–5 free. Pleotelson underside flat, without ventrolateral ridges (pleopods not enclosed laterally). Penial processes medial, closer to midpoint than to pereopods. Mandibular lacinia mobilis absent; molar flat triangular blade-like or conical process, or sometimes reduced or absent, or absent (rarely); palp present. Maxilla trilobed (reduced in Anthuroidea, absent Gnathiidae). Maxillipedal endite rarely longer than palp article 1 (or absent), distally tapering and with few setae. Pereopods 1–3 more or less prehensile or ambulatory, directed anteriorly; pereopods 4–7 directed posteriorly. Pleopodal exopods uniarticulate. Pleopod 1 biramous. Pleopod 2 biramous. Pleopod 3 biramous; endopod more or less oval or rectangular, rounded distally. Telsonic region of pleotelson elongate, anus situated anteriorly on pleotelson. Uropod inserted ventrally or anterolaterally on pleotelson; peduncle not operculate; rami ventral to pleotelson, articulating from side to side in vertical axis inside branchial chamber.

Key to superfamilies and families of Cymothoidea

1. Body elongate, cylindrical. Pereopodal coxal plates without free ventrolateral margin. Uropodal endopod terminal, exopod more or less dorsally and proximally displaced, sometimes mesially directed or erect (except *Leipanthuria*) (figs 5.1–5.10) Anthuroidea ... 2
- Body flattened or weakly vaulted, somewhat cylindrical in Gnathiidae. Pereopodal coxal plates with free ventrolateral margin. Uropodal endopod distal; exopod set distally or proximolaterally on peduncle, laterally or posteriorly directed (figs 5.11–5.35) 7
2. Pleonites 1–5 free and as long as wide. Slender body form (pereonite 7 longer than wide, little or not shorter than pereonites 6) (fig. 5.7a). Pleopods 1–5 equal (fig. 5.7k, l). Pereopods 2 and 3 with carpus produced posterodistally (fig. 5.7n) Hysuridae ... p. 154
- Pleonites 1–5 free or fused, some at least shorter than wide. Body form not exceptionally slender (at least pereonite 7 wider than long) (figs 5.1–5.6, 5.8–5.10). Pleopod 1 exopod at least slightly wider than rami of other pleopods (fig. 5.6h–j). Pereopods 2 and 3 with carpus rarely produced posterodistally (fig. 5.4i–k) 3
3. Mouthparts not strongly and acutely produced (fig. 5.2m); mandible compact, incisor usually transverse and weakly toothed (fig. 5.2n–x) 4
- Mouthparts strongly and acutely produced (fig. 5.8b); mandible tapering, incisor a simple spike (fig. 5.8f–h) 6
4. Pair of statocysts at base of telson. Pleonites 1–5 fused (or weakly indicated even though immobile) (fig. 5.2b, c, e, f, j). Pereopods 4–7 propodi with no or one posterodistal robust seta, rarely one posterior. Pereopod 7 propodus without anterodistal lateral serrate seta (fig. 5.4l–p) Anthuridae ... p. 140
- Single medial (fig. 5.1c–e) or no statocyst (fig. 5.5a, b) at base of telson. Pleonites 1–5 free (rarely fused) (fig. 5.5a, b, f). Pereopods 4–7 propodi with at least one posterior seta in addition to posterodistal robust seta (fig. 5.90–q). Pereopod 7 propodus usually with anterodistal lateral serrate seta or setae (if not, one of other characters apply) (fig. 5.1g, h) 5
5. Telson without statocyst (fig. 5.5a, b). Maxilliped usually with narrow acute endite and narrow tapering palp of 4–5 articles (fig. 5.5q) or single broad article or vestigial (fig. 5.5p, q). Uropodal exopod typically leaf-like (fig. 5.5a, f) or with strong dorsal spike (fig. 5.5b, h–j) Expanathuridae ... p. 150
- Telson with single medial statocyst (fig. 5.1a–e). Maxilliped usually with broad short endite and broad palp of 5 articles (fig. 5.1f). Uropodal exopod typically leaf-like, never with strong dorsal spike (fig. 5.5a–d) Antheluridae ... p. 138
6. Telson without statocyst (fig. 5.10a–g). Pereopod 1 palm without tooth or strong proximal angle (except *Cruregens*) and without even row of robust setae (fig. 5.10m, n) Paranthuridae ... p. 162
- Telson with one medial statocyst at base of telson, usually opening to pore (fig. 5.8a, n). Pereopod 1 palm with tooth or strong proximal angle and with even row of robust simple or complex setae (fig. 5.9a, b, d, f, h, i, k, m, n) Leptanthuridae ... p. 157
7. Uropod concealed ventrally by pleotelson, similar to pleopods (fig. 5.13) Anuropidae ... p. 169
- Uropod exposed lateral to pleotelson, more sclerified than pleopods 8
8. Pereopod 7 absent in adults 9
- Pereopod 7 present in adults 10
9. Mandibles in males only carried anterior to head; molar obsolete. Maxilla usually absent (small if present). Pereopod 1 usually modified as operculate pylopod (figs 5.31, 5.32) Gnathiidae ... p. 220
- Mandibles carried ventral to head; molar bladelike. Maxilla usually with one endite. Pereopod 1 ambulatory (fig. 5.33) Protognathiidae ... p. 225
10. Pereopods 4–7 prehensile (dactyli longer than propodi). Antennula and antenna reduced, without distinction between peduncle and flagellum. Maxilliped palp of 2 articles (figs 5.23–5.30) Cymothoidea ... p. 198
- Pereopods 4–7 ambulatory (dactyli shorter than propodi). Antennula and antenna with distinct peduncle and flagellum. Maxilliped palp of 2–5 articles 11
11. Maxillipedal endite elongate, more than half as long as palp. Maxilla comprising 1 endite with numerous subapical serrated scales (fig. 5.34) Tridentellidae ... p. 226

- Maxillipedal endite absent or short, little longer than palp article 1. Maxilla with one or 2 endites, with or without terminal robust setae 12
- 12. Mouthparts forming buccal cone. Mandible without lacinia mobilis. Maxillula, maxilla, maxilliped with apical recurved or flat robust setae (fig. 5.12) 13
- Mouthparts not forming buccal cone. Mandible with lacinia mobilis. Maxillula, maxilla, maxilliped with apical setae not recurved (figs 5.11, 5.12, 5.14) 14
- 13. Pereopods 4–7 ambulatory, with cylindrical basis. Mandible without molar. Maxillula comprising styliiform endite with apical recurved robust setae. Maxilla with stout apical recurved robust setae (figs 5.11, 5.12) Aegidae ... p. 165
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- 14. Pereopods 1–3 ambulatory. Mandible incisor wide; molar blade-like. Maxillula margins setose (figs 5.15–5.21) Cirolanidae ... p. 171
- Pereopods 1–3 weakly prehensile. Mandible incisor narrow; molar vestigial or absent. Maxillula endite often forming large recurved spine (fig. 5.22) Corallanidae... p. 195

Contributions of the authors

GCBP was the leading author for Anthuroidea, Anuropidae, Barybrotidae, Corallanidae, Gnathiidae, Protognathiidae and Tridentellidae, while NLB was the leading author for Aegidae, Cirolanidae and Cymothoidea.

Credits

Most line illustrations in this chapter are assembled tracings of figures in the literature, all more or less simplified, undertaken by GCBP using Adobe Illustrator®. Others, listed below, are reprinted directly with permission of the publisher and/or author or are in the public domain. The references cited can be found in sections dealing with relevant families.

Fig. 5.2a, Poore and Lew Ton (1986); b, Poore and Kensley (1981). Fig. 5.5a, Poore and Kensley (1981); b, c, Poore and Lew Ton (2002). Fig. 5.7a, Poore and Lew Ton (1988). Fig. 5.8a, b, Poore and Lew Ton (1990). Fig. 5.10a, Poore (1984b). Fig. 5.11a, b, d–g, Bruce (2009); c, Ho and Tonguthai (1992); h, Bruce (1993). Fig. 5.13a, Lincoln and Jones (1973). Fig. 5.14a, Pillai (1967). Fig. 5.15a, Jones and Icely (1981); b, Bruce and Bussawarit (2004); c, Bruce (1995a); d, Bruce (2004); e, Moore and Brusca (2003); f, i, Bruce (1986); g, Bruce and Jones (1981); h, Barnard (1920); j, Bruce (1980); k, Bruce (2003); l, Brusca et al. (1995); m, Bruce (1995c); n, Bruce (1996); o, Bruce and Javed (1987); p, Jansen (1978). Fig. 5.16o, Moore and Brusca (2003); r, Bruce (1986). Fig. 5.17d–h, Bruce (1985). Fig. 5.18b, Bowman (1977); l, Bruce (2004); m, Bruce and Rodcharoen (2021); n, Bruce (1986); o, Bruce (1981); p, q, Bruce (2004); r, Bruce (1994). Fig. 5.19a, h, l, Bruce (2004); b, m, Bowman et al. (1981); c, d, f, g, Bruce (1986); e, Sidabalok and Bruce (2018c); i, Bruce and Rodcharoen (2021); j, Bruce (2003); k, p, Bruce (1993); n, Sidabalok and Bruce (2018c); q, Moore and Brusca (2003). Fig. 5.20a, Bruce (1993); b, Bruce and Svavarsson (2004); c, m, Bruce (1986); d, n, Bruce (2004); e, Brusca et al. (1995); f, Bruce and Olesen (2002); g, Bruce (2003); h, Sidabalok and Bruce (2015); i, k, Kensley (1978); j, Bruce (1993); o, Bruce and Soares (1996). Fig. 5.21a, Bruce and Javed

(1987); b, Bruce and Soares (1996); c, Brusca et al. (1995); d, Bruce and Rodcharoen (2021); e, Bruce (2003); f, Bruce (1986); g, Riseman and Brusca (2002); h, Jansen (1978); i, Bruce (2004). Fig. 5.22a, Muller (1991); b, c, Santos Silva and Souza-Filho (2017). Fig. 5.23a, b, Bruce (1987a); c, Bruce et al. (2019); d, Bruce (1990); e–g, Bruce (1987b); h, Aneesh et al. (2020); i, Aneesh et al. (2025); j, Bunkley–Williams and Williams (1986). Fig. 5.24a, b, e, Bruce (1990); c, Aneesh et al. (2025); d, Helna et al. (2023); f, Williams and Williams (1985); g, h, Bruce (1986); i, j, Williams and Williams (1994); k, Aneesh et al. (2024). Fig. 5.25a, Martin et al. (2015); b, Martin et al. (2016); c, Trilles (2007); d, Martin et al. (2014); e, Avdeev (1975); f, Hale (1926). Fig. 5.26a, Martin et al. (2015); b, Hadfield et al. (2010); c, d, j, Martin et al. (2016); e, Schioedte and Meinert (1883, redrawn); f, Bruce and Bowman (1989); g, Aneesh et al. (2021); h, Martin et al. (2014); i, Bruce (1990); k, Trilles (2007). Fig. 5.27a, b, f, Bruce (1987a); c, d, h, i, Bruce (1987c); e, Hadfield et al. (2017); g, Bruce (1987b). Fig. 5.28a, c, f–i, Bruce (1990); b, Bowman and Tareen (1983); d, j, Bruce (1986); e, Aneesh et al. (2024). Fig. 5.30a–d, k, Bruce (1987a); e, g, j, o, p, Bruce (1990); f, Martin et al. (2015); h, Pillai (1964); i, Bruce (1987c); l, Bruce et al. (2019); m, Hadfield et al. (2010); n, Bruce et al. (2016). Fig. 5.31a–c, Erasmus et al. (2023). Fig. 5.32a, c–e, Cohen and Poore (1994); b, Beddard (1886). Fig. 5.34a, Wägele and Brandt (1988). Fig. 5.35a, Brandt and Poore (2001).

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Superfamily Anthuroidea Leach, 1814

Anthuroids, for many years treated as the suborder Anthuridea of Isopoda, are recognisable initially from their elongate cylindrical bodies. This general form is combined with the attitude of the uropodal exopod variously elevated and sitting over or alongside the pleotelson. Only one exception, *Leipanthura casuarina* Poore, 2009, has more typical flat posteriorly directed uropodal rami. Some anthuroid families have compact mouthparts but others have the mandible, maxillula and maxilliped produced as interacting stylets. These particularly are micropredators feeding by sucking fluids and tissue from their prey (Wägele, 1982, 1985). Anthuroids are protogynous hermaphrodites in which the terminal phase is a male with large eyes, extended swimming limbs and more numerous aesthetascs on the antennulae. The basis for systematics of the groups was established 100 years ago (Barnard, 1925). Wägele (1981) undertook a thorough review of the phylogeny and systematics of the group, generating many insights into its biology. The most recent synthetic review of the taxonomy of all families was by Poore (2001); few genera and species have been added since.

Diagnosis. Freelifving, predators or ectoparasitic on fishes or invertebrates. Body elongate, cylindrical. Antennula, antenna well developed. Mandibular molar absent or reduced; lacinia mobilis and spine row more or less fused into a lamina dentata; incisor process blunt or acute. Maxilla absent, fused into hypopharynx. Pereopods 1 or 1–3 more or less prehensile;

pereopodal coxal plates without free ventrolateral margin. Pleopod 1 exopod operculiform, pleopods 2–4 rami lamellate, or pleopods 1–5 biramous, rami lamellate (Hyssuridae only). Uropodal endopod terminal; exopod more or less dorsally and proximally displaced, sometimes mesially directed or erect (except *Leipanthura*).

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Antheluridae Poore and Lew Ton, 1988

Figure 5.1

Antheluridae are a small family with mouthparts not produced anteriorly in a cone and a single median telsonic statocyst. All have a row of serrate setae along the extensor margin of pereopod 7 (Poore, 2001; Poore and Lew Ton, 1988).

Diagnosis. Body 10–15 times as long as wide, non-males rarely more elongate (pereonite 7 wider than long, much shorter than pereonite 6); pleonites with plumose setae on margins of epimera or posterior margins of pleonite 5 and sometimes pleonite 4;

pleonites 1–5 together not more than twice as long as wide; pleonites 1–5 free and articulating (fig. 5.1b); telson statocyst single. Antennal flagellum of numerous articles. Mouthparts not produced anteriorly. Mandible compact and with weakly-toothed transverse incisor. Maxillipedal palp broad (c. twice as long as wide; fig. 5.1f). Pereopods 2–3 carpus not or weakly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae present (fig. 5.1g, h). Pleopod 1 exopod operculiform alone.

Key to genera of Antheluridae

1. Pereopods 4–7 carpus much longer than wide (fig. 5.1h). Telson with longitudinal ridge and no statocyst pore (fig. 5.1d) *Anthelura*
- Pereopods 4–7 carpus about as long as wide (fig. 5.1g). Telson domed or flat and with statocyst pore (fig. 5.1c, e) 2
2. Telson domed, with slit-like pore (fig. 5.1c). Antennal flagellum of male of 5 or more articles *Ananthura*
- Telson flat, with small pore (fig. 5.1e). Antenna flagellum of male of 2 or 3 articles *Anthomuda*

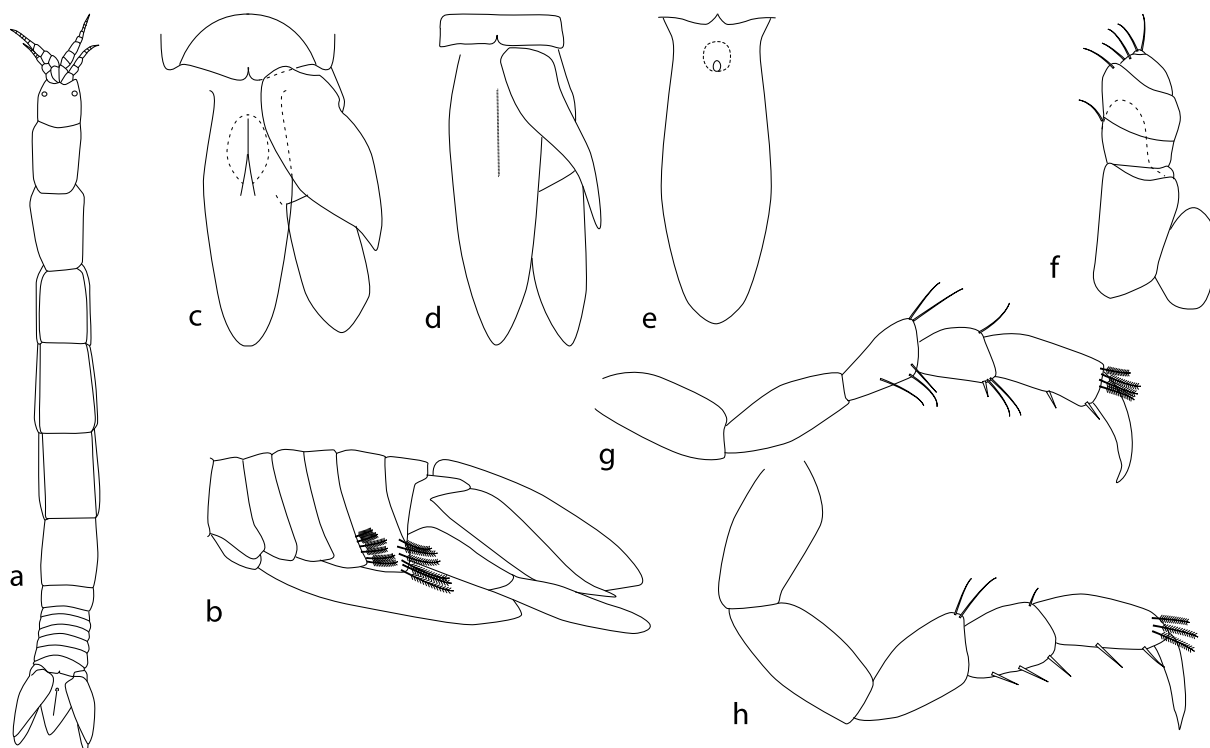


Figure 5.1. Antheluridae. a, dorsal habitus, *Ananthura*. b, lateral pleon, left uropod endopod, telson, right uropod exopod, *Ananthura*. Telson, right uropod: c, *Ananthura*; d, *Anthelura*. e, telson, *Anthomuda*. f, maxilliped, *Anthelura*. Pereopod 7: g, *Ananthura*; h, *Anthelura*.

***Ananthura* Barnard, 1925**

Diagnosis. Body not pigmented. Eyes present in both sexes. Pereopod 1 merus as wide as narrow propodus. Pereopods 4–7 carpus longer than wide, with 2 robust setae along cutting edge. Telson twice as long as wide, with slit-like pore. Uropodal rami tapering to narrow apices.

Shelf–abyssal. Temperate Northern Atlantic, Temperate Northern W Pacific, Temperate Australasia, Southern Ocean. 9 species (Barnard, 1925; Negoescu, 2005; Poore and Lew Ton, 1988).

***Anthelura* Norman and Stebbing, 1886**

Diagnosis. Body not pigmented. Eyes absent. Antennal flagellum of male of 1 basal article + c. 20 aesthetasc articles.

Pereopod 1 merus broader than tapering propodus. Pereopods 4–7 carpus longer than wide, with 4 robust setae along cutting edge. Telson 2.5 times as long as wide, with slit-like pore. Uropodal rami tapering to narrow apices.

Shelf–abyssal. Temperate Northern NE Atlantic. 1 species (Kensley, 1994; Wägele, 1980).

***Anthomuda* Schultz, 1979**

Diagnosis. Body not pigmented, or pigmented. Eyes present in both sexes. Antennal flagellum of male of 1 basal article + c. 10 aesthetasc articles. Pereopod 1 merus as wide as narrow propodus. Pereopods 4–7 carpus about as long as wide, with short anterior margin, with 2 robust setae along cutting edge. Telson 2.5 times as long as wide, with small pore. Uropodal rami apically rounded.

Subtidal, shelf. Tropical Atlantic, Indo West-Pacific, Temperate Southern Africa. 8 species (Kensley, 1994; Müller, 1990).

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Anthuridae Leach, 1814

Figures 5.2–5.4

Anthurids are more or less cylindrical isopods with a tail fan comprising telson and uropods with the exopod held dorsally (with one exception). The mouthparts do not produce forwards. The telson has two basal statocysts (Poore, 2001). Adults are benthic, sometimes building tubes in all forms of sediment from estuarine mud to coral rubble. They appear to be predators on micro-invertebrates or scavengers. As far as is known, anthurids are protogynous hermaphrodites, that is, juvenile develop into females after the manca stage and later become males (Burbanck and Burbanck, 1974). Males are rarer than females and are differentiated from other stages, as in all anthurids, by the possession of long antennulae with numerous aesthetascs, large eyes, and a more elongate body form. Males are presumed swimmers (Burbanck et al., 1979; Wägele, 1979, 1980a).

Diagnosis. Body 10–15 times as long as wide, non-males rarely more elongate (pereonite 7 wider than long, much shorter than pereonite 6); pleonites without marginal plumose setae on pleonal epimera or posterior borders of pleonites 4 and 5; pleonites 1–5 together not more than twice as long as wide; pleonites 1–5 fused; telson statocysts paired. Antennal flagellum of fewer than 10 articles, shorter than peduncle. Mouthparts not produced anteriorly. Mandible compact and with weakly toothed transverse incisor. Maxillipedal palp broad (c. twice as long as wide). Pereopods 2–3 carpus not or weakly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae

absent. Pleopod 1 exopod operculiform alone.

Implicit generic attributes. Body of usual proportions; total length of adult more than 4 mm; smooth. Head more or less parallel-sided in both sexes (not wider anteriorly), without produced chin. Pleonites 1–5 together as long as or longer than greatest width, fused, sutures visible only laterally. Pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson. Antennular flagellum in juvenile and female of 3–4 articles (second longest). Eyes present. Mandibular incisor directed transversely (exceeded by palp); molars blunt; palp of 3 articles; palp article 3 with 1–4 setae on distal margin. Maxillipedal endite obsolete or absent. Pereopod 1 subchelate, dactylus and terminal unguis closing on axial palm, carpus and propodus separated by suture; propodus swollen, subchelate, overlapping merus; propodus palm straight or sinuous, without prominent tooth; palm without strong proximal seta; dactylus smooth, closing on palm. Pereopods 2–7 merus-propodus setose on posterior margin, group of setae on anterodistal margin of merus. Pereopods 2, 3 carpus without robust seta posterodistally. Pereopods 4–7 carpus with 1 robust seta on posterodistal angle. Pereopods 4–7 propodus with 1 posterodistal robust seta only. Pereopod 7 present on adults. Pleopod 1 endopod apically rounded. Uropodal exopod leaf-shaped, articulating along peduncle.

Key to genera of Anthuridae

1. Uropodal exopod terminal, cylindrical (fig. 5.2f, g) *Leipanthura*
- Uropodal exopod subterminal, dorsal, leaf-like (fig. 5.2a–e, h–j) 2
2. Pereopods 4–7 with carpus twice as wide as propodus, rectangular, with obvious free distal margin (usually with row of pectinate setae) defined by stout seta on posterodistal angle (fig. 5.4o). Maxillipedal endite half as long as palp, distally rounded; palp articles 1 and 2 separated by suture (4 or 5 articles visible) (fig. 5.3k) ...
..... *Quantanthura*

- Pereopods 4–7 with carpus of similar width to propodus, or if wider triangular, with short free distal margin between base of dactylus and stout seta (fig. 5.4l–o, p). Maxillipedal endite weak or absent, acute if present; palp articles 1–2 and 4–5 fused (maximum of 3 articles visible) (fig. 5.3a–j) 3
- 3. Pereopods 2–7 ischium-propodus bearing long setae on flexor and extensor margins (fig. 5.4k). Blind or eyes weakly pigmented 4
- Pereopods 2–7 ischium-propodus bearing few short setae, most on flexor margin (merus-carpus posteriorly lobed and setose in some *Apanthura*). Eyes usually pigmented 5
- 4. Pereopods 4–7 carpus longer and wider than propodus (fig. 5.4k). Mandibular palp of 3 articles *Notanthura*
- Pereopods 4–7 carpus shorter than propodus. Mandibular palp of 2 articles (fig. 5.2s) *Cortezura*
- 5. Pereopods 4–7 with carpus more or less triangular, extensor margin much shorter than flexor margin, distal margin oblique and with posterodistal lobe (fig. 5.4l, m, p) 6
- Pereopods 4–7 with carpus more or less rectangular, extensor margin nearly as long as flexor margin, distal margin transverse and without posterodistal lobe (fig. 5.4n) 16
- 6. Pereopod 4–7 carpus with one distal robust seta on extensor margin (fig. 5.4l) 7
- Pereopod 4–7 carpus without distal or marginal robust seta on extensor margin (fig. 5.4m, p) 13
- 7. Pereopod 1 palm straight, without step or prominent tooth (fig. 5.4h) *Tinggianthura*
- Pereopod 1 palm with step or prominent tooth (fig. 5.4a, f) 8
- 8. Maxillipedal palp articles 1–2 fused, 3 free, fused articles 4–5 at least one third as long as article 3 (fig. 5.3i) 9
- Maxillipedal palp articles 1–2 fused, 3 free, fused articles 4–5 minute, without a free mesial margin between its suture and distal group of setae (fig. 5.3b) 10
- 9. Pereopod 1 chelate, propodus palm produced distally, dactylus with complexly ridged distal margin, unguis subterminal, carpus and propodus fused (fig. 5.4d) *Chelanthura*
- Pereopod 1 subchelate, dactylus and terminal unguis closing on axial palm, carpus and propodus separated by suture (fig. 5.4f) *Mesanthura*
- 10. Maxillipedal palp with fused articles 1–2 longer than broad. Mandibles asymmetrical, left molar with tooth fitting socket of right molar (fig. 5.2o, p). Pereopods 2 and 3 with propodus discoid (fig. 5.4i) *Apanthuopsis*
- Maxillipedal palp with fused articles 1–2 broader than long (fig. 5.3b). Mandibles symmetrical (fig. 5.2n). Pereopods 2 and 3 with propodus linear 11
- 11. Pleonites 1–5 separated by sutures dorsally and laterally except dorsally between pleonites 4 and 5 (fig. 5.2c) *Amakusanthura*
- Pleonites 1–5 indicated by shallow notches only ventrally (fig. 5.2e) 12
- 12. Antennal flagellum with 3 or 4 articles. Antennular flagellum of male with one basal + 10 aesthetasc-bearing articles, as long as head (fig. 5.2k). Head without produced chin except in some males *Apanthura*
- Antennal flagellum with 1 or 2 articles. Antennular flagellum of male with one basal + 1–2 short aesthetasc-bearing articles, never as long as head (fig. 5.2l). Head with produced chin in both sexes (fig. 5.2m) *Skuphonura*
- 13. Maxillipedal endite absent; palp articles 1–2 fused, 3 free, fused articles 4–5 at least as long as article 3 (fig. 5.3f) 14
- Maxillipedal endite present as triangular lobe; palp articles 1–5 fused (fig. 5.3j) 15
- 14. Uropodal exopod leaf-shaped, articulating along peduncle (fig. 5.2e). Marine and estuarine *Cyathura*
- Uropodal exopod linear, articulating transversely (fig. 5.2j). Stygobiont in Caribbean *Stygocyathura*
- 15. Pleon shorter than wide. Mandibular palp of one article with long seta (fig. 5.2v) *Pendanthura*
- Pleon longer than wide (fig. 5.2b). Mandibular palp of 3 articles *Sauranthura*

16. Maxilliped with endite; palp of 3 articles of similar length (fig. 5.3c). Mandible with spike-like molar on right side, absent on left (fig. 5.2q). Pleonite 6 not separated from telson by transverse ridge (fig. 5.2d) *Apanthuroides*
- These characters not in combination. Mandible with triangular or blunt molar, symmetrical 17
17. Maxillipedal palp with articles 1–2 fused, 3 free, 4–5 fused or articles 3–5 fused; endite triangular or absent (fig. 5.3d, e, h) 18
- Maxillipedal palp with articles 1–3 fused and 4–5 fused, or all articles fused; endite absent (fig. 5.3a, d, g) 21
18. Maxillipedal palp with fused articles 4–5 contributing to mesial margin of palp, with setae on mesial margin (fig. 5.3h). Telson with longitudinal middorsal ridge. Uropodal endopod short, oblique (fig. 5.2h) *Indanthura*
- Maxillipedal palp with fused articles 4–5 minute, triangular or semicircular, not contributing to mesial margin of palp, with setae on distal or distomesial margin (fig. 5.3d, e). Telson broadly rounded, rarely with longitudinal middorsal ridge. Uropodal endopod at least as long as wide, its suture with peduncle more or less transverse 19
19. Pereopod 1 merus barely touching cylindrical propodus on extensor margin (fig. 5.4c). Maxillipedal endite absent (fig. 5.3e). Antennular flagellum of male of 10 articles *Cetanthura*
- Pereopod 1 merus cupping swollen subchelate propodus (fig. 5.4a). Maxillipedal endite present (fig. 5.3b). Antennular flagellum of male of 20 articles 20
20. Body covered at least in part with setules; pleonites 1–5 with sutures indicated dorsally (fig. 5.2i). Antennal flagellum of 7 articles. Eyes absent *Pilosanthura*
- Body smooth, without setules; pleonites 1–5 without sutures indicated dorsally. Antennal flagellum of 5 articles. Eyes present *Malacanthura*
21. Pereopod 1 palm with strong proximal seta about as long as unguis (fig. 5.4b). Maxillipedal palp with fused articles 4–5 small, transverse, lateral to distomesial lobe of fused articles 1–3 (fig. 5.3d). Mandibular palp of 1 or 2 articles (fig. 5.2r) *Caenanthura*
- Pereopod 1 palm without strong proximal seta. Maxillipedal palp with fused articles 4–5 oblique (fig. 5.3g) or fused. Mandibular palp of 3 articles (fig. 5.2u, v) 22
22. Maxillipedal palp with articles 1–3 fused and 4–5 fused (fig. 5.3g) 23
- Maxillipedal palp with articles 1–5 fused (fig. 5.3a) 24
23. Pereopod 1 propodus swollen, subchelate; dactylus simple and closing on palm (fig. 5.4e). Body of usual proportions, rarely slender *Haliophasma*
- Pereopod 1 propodus cylindrical; dactylus with teeth along flexor margin, not closing on palm (fig. 5.4g). Body slender, c. 20 times as long as wide *Nemanthura*
24. Mandibular palp of 3 articles *Anthura*
- Mandibular palp of 1 article (fig. 5.2x) 25
25. Pereopod 7 present *Ptilanthura*
- Pereopod 7 absent *Exallanthura*

***Amakusanthura* Nunomura, 1977**

Diagnosis. Body not darkly pigmented. Head with produced chin in males. Pleonites 1–5 fused (but separated by folds dorsally and laterally except dorsally between 4 and 5) or fused, sutures visible only laterally. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Maxillipedal

endite present as a triangular lobe, or reaching palp article 3; palp articles 1–2 fused, 3 free and 4–5 fused; palp article 3 barely produced medially beyond articles 4–5 (if at all); palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

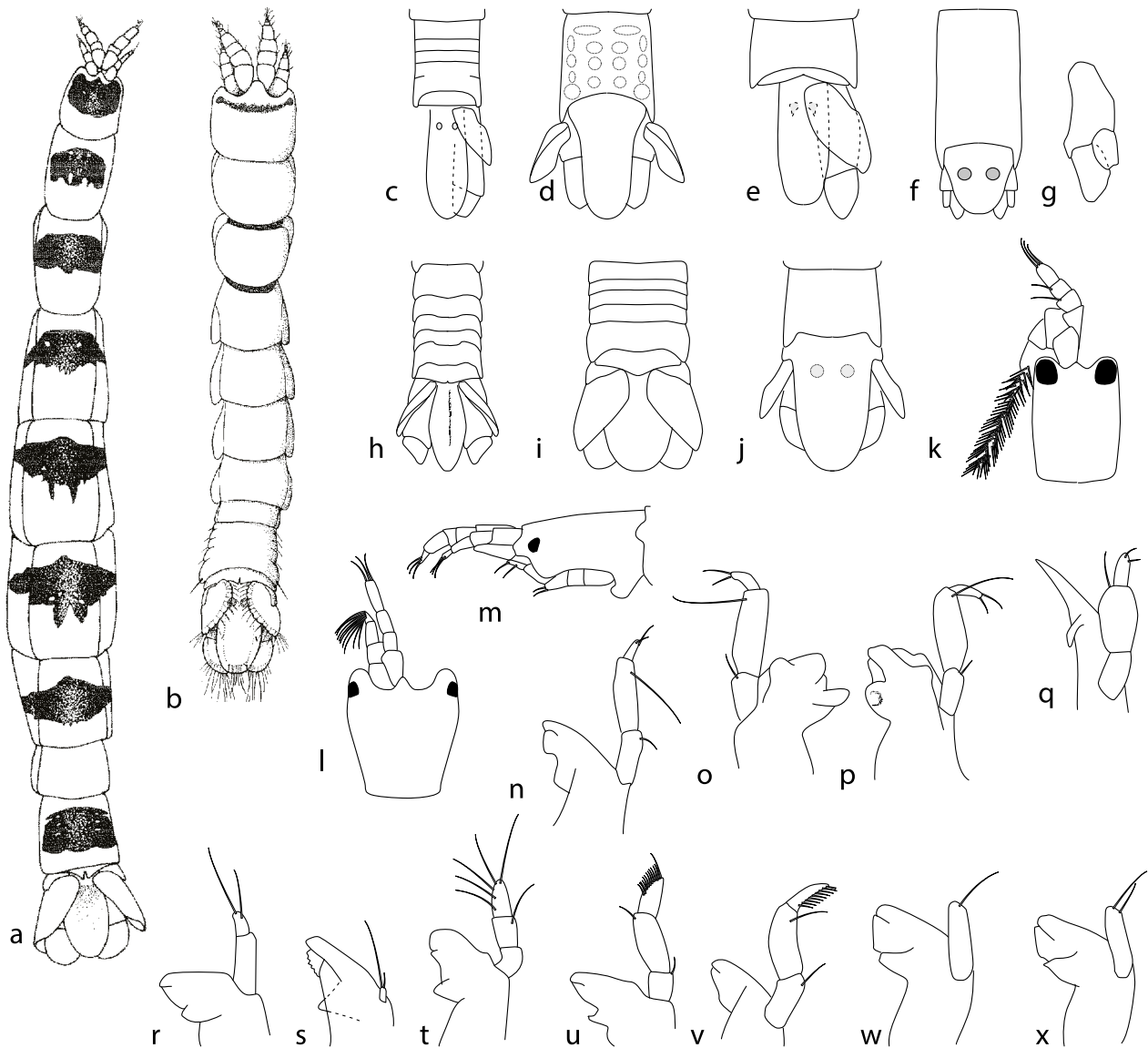


Figure 5.2. Anthuridae. a, *Chelanthura calaena* (Poore and Lew Ton, 1986); b, *Sauranthura goldmanorum* Poore and Kensley, 1981. Pleon, pleotelson, uropod: c, *Amakusanthura*; d, *Apanthuroides*; e, *Cyathura*; f, g, *Leipanthura* (with uropod); h, *Indanthura*; i, *Pilosanthura*; j, *Stygocyathura*. Male head, antennula, antenna: k, *Apanthura*; l, *Skuphonura*. m, male head, antennula, antenna, *Skuphonura*. Mandible: n, *Apanthura*; o, p, *Apanthuopsis* (pair); q, *Apanthuroides*; r, *Caenanthura*; s, *Cortezura*; t, *Haliophasma*; u, *Mesanthura*; v, *Pendanthura*; w, *Pilosanthura*; x, *Ptilanthura*.

Intertidal–bathyal. Temperate Northern and Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia. 48 species (Poore and Lew Ton, 1988a: rediagnosis, key to Australian species; Müller, 1992; Negoescu, 2004: comments on status of genus; Kim and Yoon, 2021: key to species in Far East).

Anthura Leach, 1814

Diagnosis. Body irregularly darkly pigmented. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 7–9 articles, longer than article 5 of

peduncle. Maxillipedal palp articles 1–5 fused. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Intertidal, subtidal. Temperate Northern Atlantic. 1 species (Wägele, 1980b: redescription, figures).

Apanthura Stebbing, 1900

Diagnosis. Body not darkly pigmented or irregularly darkly pigmented. Head with produced chin in males. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles.

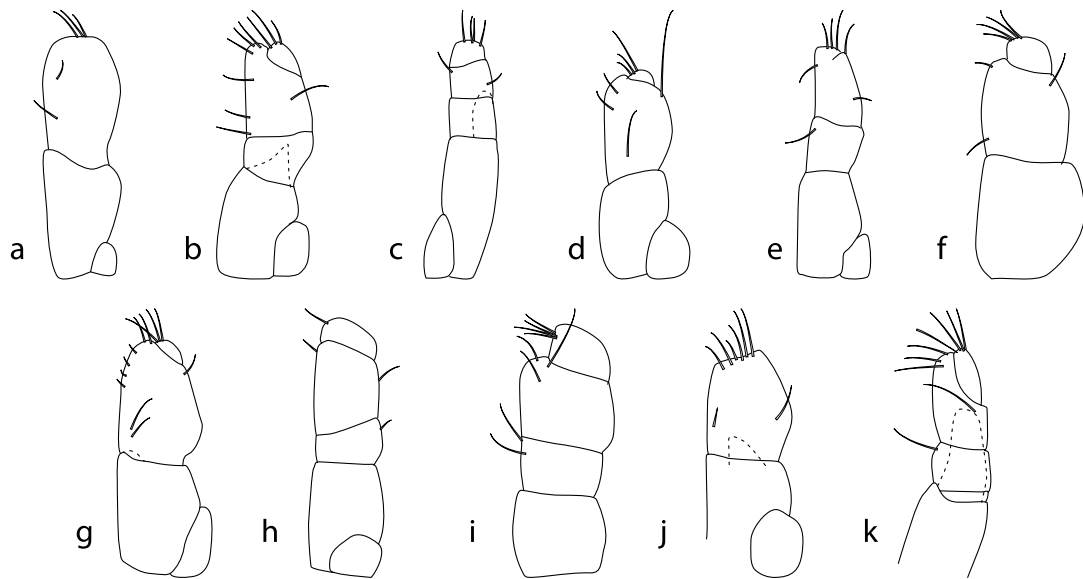


Figure 5.3. Anthuridae. Maxilliped: a, *Anthura*; b, *Apanthura*; c, *Apanthuroides*; d, *Caenanthura*; e, *Cetanthura*; f, *Cyathura*; g, *Haliophasma*; h, *Indanthura*; i, *Mesanthura*; j, *Pendanthura*; k, *Quantanthura*.

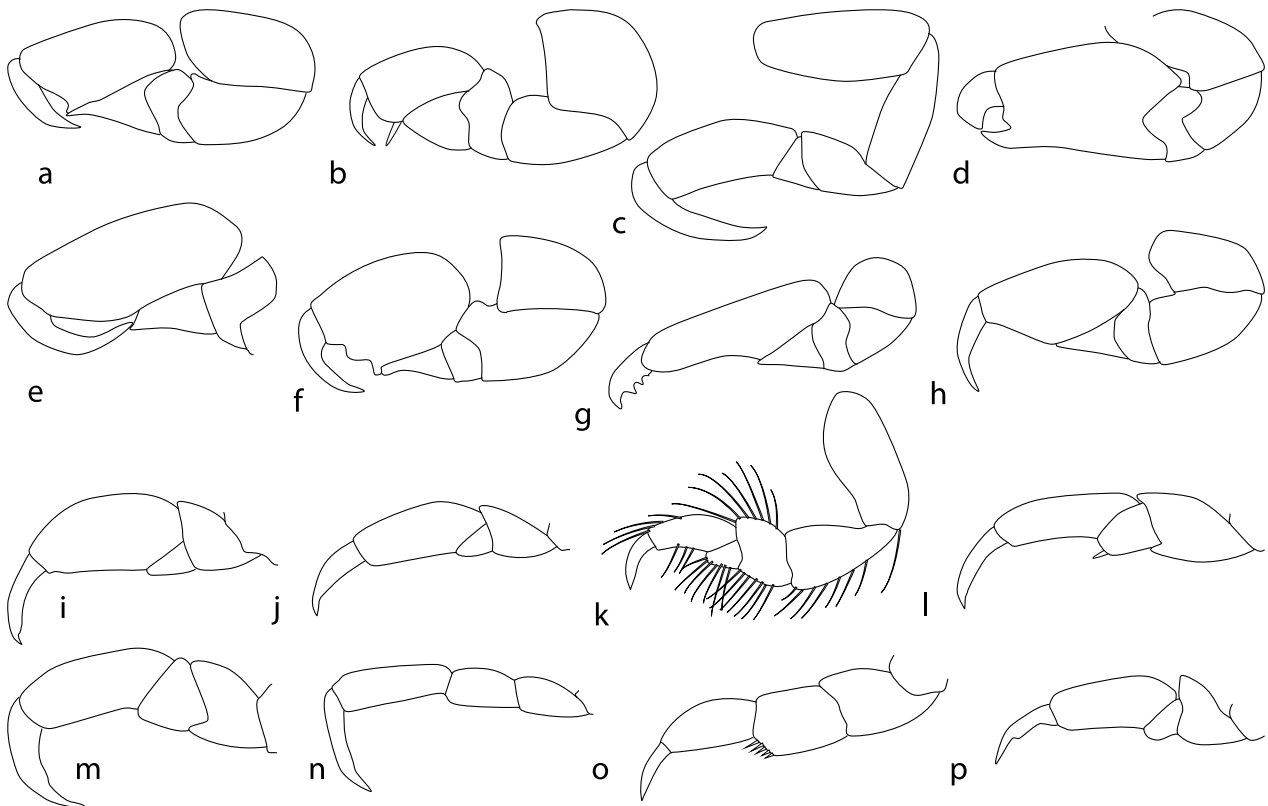


Figure 5.4. Anthuridae. Pereopod 1: a, *Apanthura*; b, *Caenanthura*; c, *Cetanthura*; d, *Chelanthura*; e, *Haliophasma*; f, *Mesanthura*; g, *Nemanthura*; h, *Tinggianthura*. Pereopod 2: i, *Apanthuopsis*; j, *Haliophasma*; k, *Notanthura*. Pereopod 7: l, *Apanthura*; m, *Cyathura*; n, *Haliophasma*; o, *Quantanthura*; p, *Pendanthura*.

Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Maxillipedal endite present as a triangular lobe; palp articles 1–2 fused, 3 free and 4–5 fused; palp article 3 barely produced medially beyond articles 4–5 (if at all); palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Indo West-Pacific, Temperate Southern Africa, Temperate Australasia. 46 species (Poore and Lew Ton, 1988a: rediagnosis, key to Australian species; Kim and Yoon, 2021: key to species of Far East).

***Apanthuroides* Menzies and Glynn 1968**

Diagnosis. Body not darkly pigmented, pitted. Pleotelson without indication of posterior margin of pleonite 6. Antennular flagellum of male of 1 basal + 6–7 aesthetasc-bearing articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Mandibular incisor produced anteriorly (beyond palp); molar spike-like on right side, absent on left. Maxillipedal endite reaching palp article 3; palp articles 1–2 fused, 3 free and 4–5 fused; palp article 3 well exceeded by distal articles; palp terminal articles (4–5) subcircular, transverse. Pereopod 1 propodus cylindrical, not in contact with merus. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Indo West-Pacific, Temperate Southern Africa. 9 species (Kensley and Schotte, 2000: rediagnosis, key to Indian Ocean species; Nunomura, 2013).

***Apanthuropsis* Poore and Lew Ton, 1985**

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular molars asymmetrical, left molar with tooth fitting socket of right molar. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 barely produced medially beyond articles 4–5 (if at all); terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Shelf. Temperate Australia. 1 species (Poore and Lew Ton, 1985b).

***Caenanthura* Kensley, 1978**

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 1–2 articles, very short. Mandibular palp of 1 or 2 short article. Maxillipedal palp articles 1–3 fused, 4–5 fused; article 3 produced as lobe beyond distolateral articles 4–5; terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 palm

with strong proximal seta (about as long as unguis). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Subtidal. Western and Central Indo-Pacific. 6 species (Poore, 2001: rediagnosis, synonymy; Song and Min, 2015: key to species).

***Cetanthura* Kensley, 1982**

Diagnosis. Body not darkly pigmented, pitted. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular incisor produced anteriorly (beyond palp). Maxillipedal palp articles 1–2 fused, 3–5 fused. Pereopod 1 propodus cylindrical, not in contact with merus. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin. Pereopod 7 absent on adults.

Bathyal. Temperate Southern Africa. 1 species (Kensley, 1982).

***Chelanthura* Poore and Bardsley, 1990**

Diagnosis. Body with dark species-specific pigment pattern. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular palp article 3 with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 well exceeded by distal articles; terminal articles (4–5) at least one third as long as penultimate article (3), almost as long as broad, with a free mesial margin between its suture and distal group of setae. Pereopod 1 chelate, propodus produced posterodistally, dactylus with complexly ridged distal margin, unguis subterminal, carpus and propodus fused. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Shelf. Temperate Australasia. 4 species (Poore and Bardsley, 1990).

***Cortezura* Schultz, 1977**

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + 1 or 2 short aesthetasc-bearing articles. Antennal flagellum of 1–2 articles, very short. Eyes weakly pigmented. Mandibular molar a triangular blade; palp of 2 articles, second very setose. Maxillipedal endite present as a triangular lobe; palp articles 1–3 fused, 4–5 fused, or 1–5 fused. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 2–7 merus-propodus bearing long setae on upper and lower margins. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Intertidal, subtidal. Tropical Atlantic, Temperate Northern Pacific. 4 species (Jarquín-Martínez and García-Madrugal, 2021; Kensley, 1978; Schultz, 1977).

***Cyathura* Norman and Stebbing, 1886**

Diagnosis. Body irregularly darkly pigmented, smooth or covered at least in part with setules (fur). Pleonites 1–5 together

shorter than wide. Pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson, or without indication of posterior margin of pleonite 6. Antennular flagellum of male of 4–5 aesthetasc-bearing articles, retractile. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular palp article 3 with 1–4 setae on distal margin, or with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–3 fused, 4–5 fused; article 3 well exceeded by distal articles; terminal articles (4–5) at least one third as long as penultimate article (3), almost as long as broad, with a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin, without robust seta on posterior margin or on posterodistal angle.

Freshwater, estuarine, marine intertidal–bathyal. Arctic, Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific, Central Indo-Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia. 31 species (Bamber, 2008; Cruz et al., 2003; Ferreira et al., 2004). Species of *Cyathura* range from freshwater lakes (Nunomura and Hagino, 2000), through estuaries (e.g. Nunomura, 1977; Poore and Lew Ton, 1985a) to shallow marine sediments (most species) and even to 1000 m depth (Kensley, 1982). The biology of some species has been studied (e.g., Burbank, 1962; Marques et al., 1994).

***Exallanthura* Kensley 1980**

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Mandibular palp of 1 article. Maxillipedal palp articles 1–5 fused. Pereopod 1 propodus cylindrical, not in contact with merus. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe. Pereopod 7 absent on adults. Uropodal exopod broad, apically concave.

Shelf. Western Indo-Pacific. 1 species (Kensley, 1980).

***Haliophasma* Haswell, 1881**

Diagnosis. Body not darkly pigmented, pitted. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Mandibular palp article 3 with row of 10–15 setae on distal oblique margin (sometimes fewer). Maxillipedal endite obsolete or absent; palp articles 1–3 fused, 4–5 fused; palp article 3 barely produced medially beyond articles 4–5 (if at all), or well exceeded by distal articles; palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 39 species (Poore, 1975: rediagnosis; Poore and Lew Ton, 1988b: key to 16 Australian species).

***Indanthura* Pillai and Eapen, 1966**

Diagnosis. Body not darkly pigmented. Pleonites 1–5 fused, sutures visible only laterally or sutures all indicated dorsally and laterally. Antennular flagellum in juvenile and female of c. 5–7 articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Mandibular palp article 3 with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 well exceeded by distal articles; terminal articles (4–5) at least one third as long as penultimate article (3), almost as long as broad, with a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Shelf. Temperate Northern and Tropical Atlantic, Western Indo-Pacific. 4 species (Pillai and Eapen, 1966; Poore, 2001: rediagnosis, synonymy).

***Leipanthura* Poore, 2009**

Diagnosis. Body total length of adult less than 3 mm; irregularly darkly pigmented. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Maxillipedal palp articles 1–5 fused. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin, without robust seta on posterior margin or on posterodistal angle. Pereopod 7 absent on adults. Uropodal exopod cylindrical, articulating distally in same horizontal plane as endopod.

Subtidal (coral reefs). Central Indo-Pacific. 1 species. *Leipanthura* differs from all other anthurids in having a typically “flabelliferan” uropod, the exopod being terminal on the peduncle rather than dorsal as in all others (Poore, 2009).

***Malacanthura* Barnard, 1925**

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 20 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Maxillipedal endite reaching palp article 3; palp articles 1–2 fused, 3 free and 4–5 fused; palp article 3 barely produced medially beyond articles 4–5 (if at all); palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Intertidal–bathyal. Western Indo-Pacific, Temperate South America (S Atlantic), Temperate Southern Africa. 5 species (Bamber, 2000; Barnard, 1925; Kensley and Schotte, 2000).

***Mesanthura* Barnard, 1914**

Diagnosis. Body with dark species-specific pigment pattern. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular palp article 3 with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 well exceeded by distal articles; terminal articles (4–5) at least one third as long as

penultimate article (3), almost as long as broad, with a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male); dactylus often with complex toothed surface at base of unguis. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Intertidal–shelf. Tropical Atlantic, Temperate Northern Pacific, Indo West-Pacific, Tropical Eastern Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 54 species (Poore and Lew Ton, 1986a: rediagnosis; Jarquín-Martínez and García-Madrigal, 2021; Müller, 1993). Species of *Mesanthura* differ from most anthurids in having permanent species-specific colour patterns. One species has been introduced to the Mediterranean (Lorenti et al., 2009).

***Nemanthura* Wägele, 1981**

Diagnosis. Body very slender (c. 20 times as long as wide); not darkly pigmented. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Maxillipedal palp articles 1–3 fused, 4–5 fused; article 3 well exceeded by distal articles; terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 dactylus with tubercular teeth along lower margin. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Shelf. Tropical Atlantic. 1 species (Paul and Menzies, 1971: description of type species as *Haliophasma*; Wägele, 1981).

***Notanthura* Monod, 1927**

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 4–5 aesthetasc-bearing articles, retractile. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular molar a triangular blade; palp article 3 with 1–4 setae on distal margin, or with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–3 fused, 4–5 fused; article 3 barely produced medially beyond articles 4–5 (if at all); terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 2–7 merus-propodus bearing long setae on upper and lower margins. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe. Pleopod 1 endopod tapering to digitiform apex.

Intertidal, subtidal. Temperate Northern and Tropical Atlantic, Temperate Southern Africa. 4 species (Wägele and Platvoet, 1982: as *Monodanthura*; Poore, 2001: rediagnosis, synonymy).

***Pendantthura* Menzies and Glynn 1968**

Diagnosis. Body total length of adult less than 3 mm; irregularly darkly pigmented. Pleonites 1–5 together much shorter than wide. Pleotelson without indication of posterior margin of pleonite 6. Antennular flagellum of male of 4–5 aesthetasc-

bearing articles, retractile. Antennal flagellum of 1–2 articles, very short. Mandibular palp of 1 article. Maxillipedal endite present as a triangular lobe; palp articles 1–5 fused. Pereopods 2, 3 carpus without robust seta posterodistally. Pereopods 4–7 carpus triangular, without free anterior margin, without robust seta on posterior margin or on posterodistal angle.

Shelf. Tropical Atlantic, Tropical Eastern Pacific, Indo West-Pacific. 11 species (Kensley and Schotte, 2000; Chew et al., 2016: rediagnosis, key to species; Annisaqois and Wägele, 2021).

***Pilosanthura* Wägele, 1989**

Diagnosis. Body not darkly pigmented, covered at least in part with setules (fur). Pleonites 1–5 sutures all indicated dorsally and laterally. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Eyes absent. Maxillipedal endite reaching palp article 3; palp articles 1–2 fused, 3 free and 4–5 fused; palp article 3 barely produced medially beyond articles 4–5 (if at all); palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Bathyal. Temperate Northern Atlantic. 2 species (Wägele, 1980b: description of type species; 1989; Negoescu, 2002).

***Ptilanthura* Harger, 1878**

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Mandibular palp of 1 article. Maxillipedal palp articles 1–5 fused. Pereopods 4–7 carpus more or less rectangular, anterior (upper) margin nearly as long as posterior (lower) margin, distal margin transverse and without posterodistal lobe.

Shelf. Temperate Northern and Tropical Atlantic. 2 species (Kensley, 1996).

***Quantanthura* Menzies and George, 1972**

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles; in juvenile and female of c. 5–7 articles. Antennal flagellum of 7–9 articles, longer than article 5 of peduncle. Maxillipedal endite reaching palp article 3; palp articles 1–5 free, or minute article 5 fused with article 4; palp article 3 barely produced medially beyond articles 4–5 (if at all); palp terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus twice width of propodus, rectangular, with obvious free distal margin (usually with row of pectinate setae) defined by stout seta on posterodistal angle, with robust seta on posterior margin and on posterodistal angle. Pereopods 4–7 propodus with 1 robust setae on posterior margin (in addition to posterodistal robust seta).

Subtidal–bathyal. Temperate Northern and Tropical Atlantic, Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia. 13 species (Poore and Lew Ton, 1986b: key to Australian species; Poore, 2001: rediagnosis, synonymy).

Sauranthura Poore and Kensley, 1981

Diagnosis. Body total length of adult less than 3 mm, with dark species-specific pigment pattern. Pleonites 1–5 together shorter than wide. Antennal flagellum of 1–2 articles, very short. Maxillipedal endite present as a triangular lobe; palp articles 1–5 fused. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 2, 3 carpus with robust seta posterodistally. Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin, without robust seta on posterior margin or on posterodistal angle.

Subtidal (coral reefs). Central Indo-Pacific, Temperate South America. 2 species (Poore and Kensley, 1981; Shiraki et al., 2025).

Skuphonura Barnard, 1925

Diagnosis. Body not darkly pigmented. Head much wider anteriorly in male, with produced chin in males. Antennular flagellum of male of 1 basal + 1 or 2 short aesthetasc-bearing articles. Antennal flagellum of 3–4 articles, shorter than article 5 of peduncle. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 barely produced medially beyond articles 4–5 (if at all); terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin.

Shelf. Tropical Atlantic, Temperate South America (W Atlantic). 6 species (Brusca and Müller, 1991; Jarquín-Martínez and García-Madrugal, 2021: comparison of 4 species).

Stygocyathura Botosaneanu and Stock, 1982

Diagnosis. Body not darkly pigmented. Pleonites 1–5 together shorter than wide. Pleotelson without indication of posterior margin of pleonite 6. Antennular flagellum of male of 1 basal + c. 10 aesthetasc-bearing articles. Antennal flagellum of 1–2 articles, very short. Eyes absent. Mandibular palp article 3 with 1–4 setae on distal margin, or with row of 10–15 setae on distal oblique margin. Maxillipedal palp articles 1–2 fused, 3 free and 4–5 fused; article 3 barely produced medially beyond articles 4–5 (if at all); terminal articles (4–5) at least one third as long as penultimate article (3), almost as long as broad, with a free mesial margin between its suture and distal group of setae. Pereopod 1 propodus palm with step or prominent tooth (more pronounced in male). Pereopods 4–7 carpus more or less pentagonal, anterior margin half length of posterior margin, without robust seta on posterior margin or on posterodistal angle. Uropodal exopod linear, articulating transversely.

Freshwater and brackish stygobiont. 23 species (Wägele et al., 1987). Species of *Stygocyathura* are found over a wide ecological range, from subterranean fresh water (Andreev, 1982; Argano, 1972) to brackish water (Botosaneanu, 1987). Some authors have treated the genus as a subgenus of *Cyathura*.

Tinggianthura Chew, Rahim and bin Haji Ross, 2014

Diagnosis. Body not darkly pigmented. Antennular flagellum of male of 1 basal + 1 or 2 short aesthetasc-bearing articles.

Antennal flagellum of 1–2 articles, very short. Maxillipedal palp articles 1–3 fused, 4–5 fused; article 3 barely produced medially beyond articles 4–5 (if at all); terminal articles (4–5) oblique, without a free mesial margin between its suture and distal group of setae. Pereopods 4–7 carpus triangular, without free anterior margin.

Subtidal. Central Indo-Pacific. Malaysia. 2 species (Chew et al., 2014).

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Expanthuridae Poore, 2001

Figures 5.5, 5.6

Expanthurids are distinguished from anthurids, which they resemble superficially, by the absence of statocysts, usually free pleonites, and the primitive condition of the maxilliped (presence of an endite and palp of five articles), anterodistal serrate setae on the propodus of pereopod 7, and the weakly operculiform pleopod 1. Some genera have a highly ornamented telson and uropodal margins not seen in other families (Poore, 2001; Poore and Lew Ton, 2002).

Diagnosis. Body 10–15 times as long as wide, non-males rarely more elongate (pereonite 7 wider than long, much shorter than pereonite 6); pleonites with plumose setae on margins of epimera or posterior margins of pleonite 5 and sometimes pleonite 4; pleonites 1–5 together not more than twice as long as wide; pleonites 1–5 free and articulating, or fused; telson statocysts absent. Antennal flagellum of fewer than 10 articles, shorter than peduncle, or of numerous articles. Mouthparts not produced anteriorly. Mandible tapering and incisor simple, or compact and with weakly-toothed transverse incisor (rarely). Maxillipedal palp narrow and tapering distally to rounded apex (c. 3 times as long as wide), or reduced, digitiform (*Eisothistos*).

Pereopods 2–3 carpus not or weakly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae present. Pleopod 1 exopod and endopod together weakly operculiform, or pleopod 1 exopod operculiform alone (*Expanthura* only).

Implicit generic attributes. Body typically elongate (pereonite 1 longer than wide); setation body and limbs not covered by scattered long setae. Pleonites 1–5 free and articulating, together longer than wide in juvenile. Antennular flagellum of male of 6–7 aesthetasc-bearing articles. Mouthparts not produced anteriorly. Maxillipedal palp narrow and tapering distally to apex (at least twice as long as wide); articles 1 and 2 separated by suture. Pereopods 1–3 only slightly differentiated from posterior pereopods, propodi not more swollen than merus. Pereopod 1 palm of dactylus smooth; propodus cylindrical, palm smooth. Pereopod 1 merus narrower than swollen propodus. Pereopods 1–7 merus without robust seta on anterior margin. Pereopods 4–7 propodus with 1 distal robust seta on cutting edge. Distal palmar robust setae on pereopods 2–7 propodus and 4–7 carpus simple or flagellate. Apices of rami without serrate robust seta.

Key to genera of Expanthuridae

1. Pereopods 1–3 only slightly differentiated from posterior pereopods, propodi not swollen (fig. 5.6a–c). Pleopod 1 rami fused in juveniles (fig. 5.6h). Female pereon and pereopods covered with long setae, body becoming extremely elongate after spawning (fig. 5.5b, c) *Eisothistos*
- Pereopods 1–3 well differentiated from posterior pereopods, propodi swollen. Pleopod 1 rami free. Female pereon and pereopods not covered with long setae, never elongate 2
2. Pleonites 5 and 6 not longer than pleonites 1–4; pleonite 6 clearly fused dorsally to telson. Uropodal exopod a simple narrow leaf (fig. 5.5a) *Coralanthura*
- Pleonites 5 and 6 longer than pleonites 1–4 or all pleonites fused. Pleonite 6 usually marked off dorsally from telson. Uropodal exopod broad or complex 3

- | | | |
|----|---|--------------------|
| 3. | Uropodal exopod with spike-like dorsal lobe, rami and telson with dentate margins (fig. 5.5h–j) | 4 |
| – | Uropodal exopod with obsolete dorsal lobe, rami and telson with entire or dentate margins (fig. 5.5f, g) | 6 |
| 4. | Uropodal exopod spike shorter than proximal plate (fig. 5.5i). Mandibular palp with 3 articles (fig. 3.0). Maxillipedal endite short or absent (fig. 5.5p) | <i>Heptanthura</i> |
| – | Uropodal exopod spike shorter or longer than proximal plate (fig. 5.5h, j). Mandibular palp with fewer than 3 articles (fig. 5.5m). Maxillipedal endite prominent (fig. 5.5q, r) | 5 |
| 5. | Telsonic apex tapering to point from midpoint (fig. 5.5g). Mandibular palp of 2 articles (fig. 5.5n). Maxillipedal palp broad (fig. 5.5r) | <i>Rhiganthura</i> |
| – | Telsonic apex apically rounded (fig. 5.5h). Mandibular palp of one seta only (fig. 5.5m). Maxillipedal palp acute (fig. 5.5q) | <i>Minyanthura</i> |
| 6. | Pereopod 1 propodus broader than that of pereopod 2, strongly tapering, obscurely dentate proximally (fig. 5.6d, e). Antennular flagellum of male with basal article short, with numerous aesthetascs (fig. 5.5d) | <i>Expanathura</i> |
| – | Pereopod 1 propodus similar to that of pereopod 2, scarcely tapering, palm smooth (fig. 5.6f, g). Antennular flagellum of male with rows of aesthetascs on all articles (fig. 5.5e) | <i>Panathura</i> |

***Coralanthura* Poore and Kensley, 1981**

Diagnosis. Pleonites of similar lengths, with plumose setae on ventral margins of all epimera; pleotelson without indication of posterior margin of pleonite 6. Palp of 3 articles. Maxillipedal endite apically rounded, reaching to palp article 3; palp broad (1.5–2 times as wide as long), article 4 semicircular. Pereopod 1 palm of dactylus tuberculate. Pereopods 1–7 merus with robust seta on anterior margin. Pleopod 1 weakly operculiform in both sexes, with exopod slightly wider than endopod but not enclosing it totally. Uropodal exopod a narrow leaf articulating proximally. Apices of rami without serrate robust seta. Telson with smooth distal margin.

Subtidal (coral reef). Central Indo-Pacific. 1 species (Poore and Kensley, 1981; Poore and Lew Ton, 2002).

***Eisothistos* Haswell, 1884**

Diagnosis. Body of postspawning female grossly elongate; of juvenile and male of usual proportions; setation areas of body and bases of some limbs of female covered with scattered long setae. Pleonites 1–5 free and articulating and fused in postspawning female, together longer than wide in male and much wider than long in juvenile and prespawning female, pleonites 1–3 longer than 4 and 5 in male and manca, all of similar lengths in juvenile and female, with plumose setae on ventral margins of all epimera; pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson, or without indication of posterior margin of pleonite 6. Antennular flagellum of male of 1 very short basal article bearing numerous aesthetascs and c. 7 longer articles each with 1–2 aesthetascs (or 7 longer articles, second with bunches of aesthetascs). Mandible and maxilla produced anteriorly beyond rostrum. Palp absent. Maxillipedal endite obsolete or absent; palp of 1–5 weakly differentiated narrow articles. Pereopods 1–3 only slightly differentiated from posterior pereopods,

propodi not more swollen than merus. Pereopod 1 merus as wide as narrow propodus. Pleopod 1 weakly operculiform, with rami fused in juvenile and prespawning female. Uropodal exopod with strong apical spike, with serrate margin; with serrate lateral lobe between articulation and apical spike. Endopod and spike of exopod with apical serrate robust seta. Telson with dentate distal margin.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific, Indo West-Pacific, Temperate South America, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 31 species (Knight-Jones and Knight-Jones, 2002; Poore and Lew Ton, 2002; Wägele, 1979).

***Expanathura* Wägele, 1981**

Diagnosis. Pleonites 5 and 6 longer than pleonites 1–4, with plumose setae on dorsal and lateral margins of pleonite 5 (at least in some life stages); pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson. Antennular flagellum of male of 1 very short basal article bearing numerous aesthetascs and c. 7 longer articles each with 1–2 aesthetascs (or 7 longer articles, second with bunches of aesthetascs). Palp of 3 articles. Maxillipedal endite tapering to acute apex, reaching to at least palp article 4; palp articles 1 and 2 separated by suture. Pereopod 1 propodus as broad as long, triangular, palm dentate proximally. Pereopods 4–7 propodus with row of robust setae along cutting edge (at least 1 in addition to distal seta). Pleopod 1 exopod operculiform alone and enclosing narrower endopod in both sexes. Uropodal exopod a broad leaf articulating longitudinally, with smooth margin; without serrate lateral lobe. Telson with smooth distal margin.

Intertidal–shelf. Indo West-Pacific, Southern Ocean. 8 species (Poore and Lew Ton, 2002: rediagnosis, key to 6 species; Annisakis and Wägele, 2021: differences between species; Shiraki et al., 2021: key to 7 species).

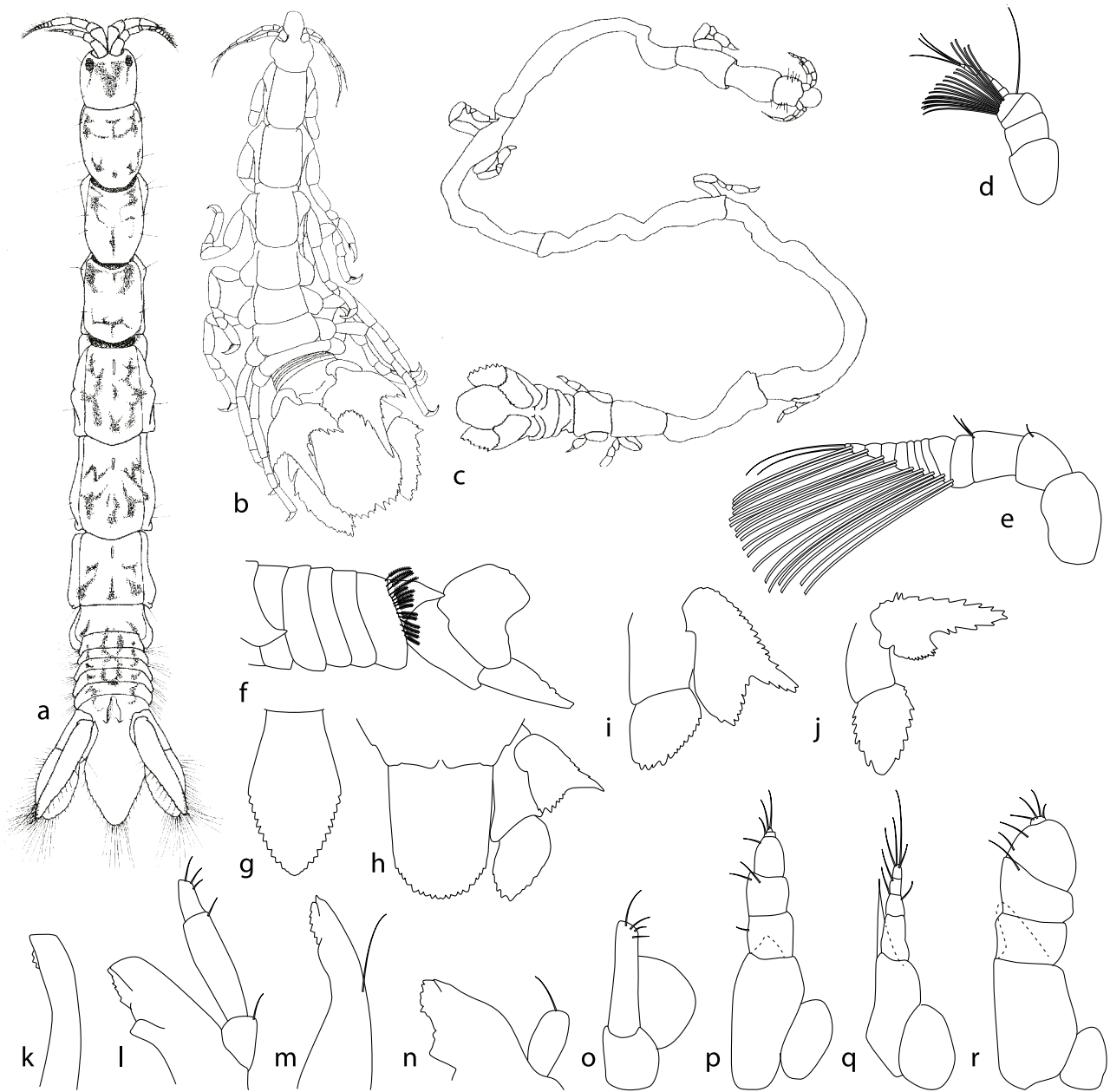


Figure 5.5. Expanthuridae. a, *Coralanthura endeavourae* Poore and Kensley, 1981; b, *Eisothistos bellonae* Poore and Lew Ton, 2002; c, *Eisothistos* sp. (post-spawning female). Male antennula: d, *Expanathura*; e, *Panathura*; f, pleon, uropod, *Expanathura*; g, telson, *Rhiganthura*; h, telson, uropod, *Minyanthura*. Uropod: i, *Heptanthura*; j, *Rhiganthura*. Mandible: k, *Eisothistos*; l, *Heptanthura*; m, *Minyanthura*; n, *Rhiganthura*. Maxilliped: o, *Eisothistos*; p, *Heptanthura*; q, *Minyanthura*; r, *Rhiganthura*.

Heptanthura Kensley, 1978

Diagnosis. Pleonites 1–5 free and articulating or fused, pleonites 5 and 6 longer than pleonites 1–4, with plumose setae on dorsal and lateral margins of pleonite 5 (at least in some life stages); pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson. Palp of 3 articles, or absent. Maxillipedal endite short or absent; palp articles 1–2 fused. Pereopods 1–3

only slightly differentiated from posterior pereopods, propodi not more swollen than merus. Distal palmar robust setae on pereopods 2–7 propodus and 4–7 carpus bifid and blade-like. Pleopod 1 weakly operculiform in both sexes, with exopod slightly wider than endopod but not enclosing it totally. Uropodal exopod with strong apical spike, with serrate margin; without serrate lateral lobe. Telson with dentate distal margin.

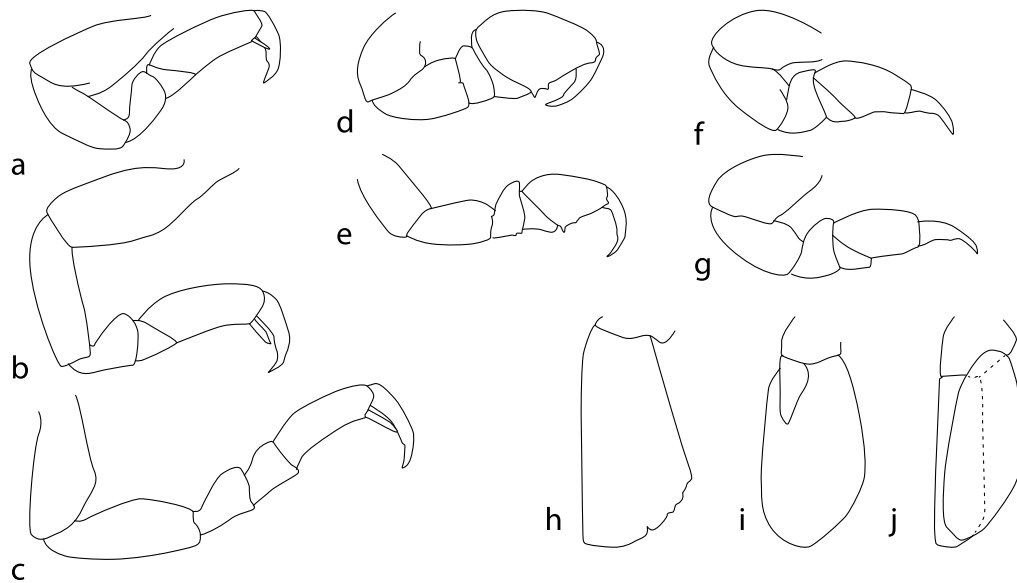


Figure 5.6. Expanthuridae. a, b, c, pereopods 1, 2, 4, *Isothistos*. d, e, pereopods 1, 2, *Expanathura*. f, g, pereopods 1, 2, *Panathura*. Pleopod 1: h, *Isothistos*; i, *Expanathura*; j, *Heptanthura*.

Intertidal–shelf. Temperate Northern and Tropical Atlantic, Central Indo-Pacific, Temperate Australasia. 10 species (Kensley and Schotte, 2000: rediagnosis; Poore and Lew Ton, 2002: synonymy).

Minyanthura Kensley, 1982

Diagnosis. Body compact (pereonite 1 shorter than wide) and total length less than 4 mm. Pleonites 1–5 fused, together wider than long in both sexes, with plumose setae on dorsolateral and lateral margins of pleonites 4 and 5; pleotelson without indication of posterior margin of pleonite 6. Palp of 1 seta. Maxillipedal endite tapering to acute apex, reaching to at least palp article 4. Pleopod 1 weakly operculiform in both sexes, with exopod slightly wider than endopod but not enclosing it totally. Uropodal exopod with strong apical spike, with serrate margin; without serrate lateral lobe. Telson with dentate distal margin.

Intertidal, subtidal. Tropical Atlantic, Eastern Indo-Pacific, Temperate Southern Africa. 3 species (Kensley, 1982; Müller, 1993).

Panathura Barnard, 1925

Diagnosis. Pleonites 5 and 6 longer than pleonites 1–4, with plumose setae on dorsolateral and lateral margins of pleonites 4 and 5; pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson. Palp of 3 articles. Maxillipedal endite apically rounded, reaching to palp article 3. Pereopod 1 merus as wide as narrow propodus. Pleopod 1 weakly operculiform in both sexes, with exopod slightly wider than endopod but not enclosing it totally. Uropodal exopod a broad leaf articulating longitudinally, with smooth margin; without serrate lateral lobe. Telson with smooth distal margin.

Subtidal–slope. Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 6 species (Poore and Lew Ton, 2002: rediagnosis, key to 5 species).

Rhiganthura Kensley, 1978

Diagnosis. Body compact (pereonite 1 shorter than wide) and total length less than 4 mm. Pleonites 1–5 together wider than long in both sexes, pleonites 5 and 6 longer than pleonites 1–4 and pleonite 1 very short, concealed dorsally, with plumose setae on dorsal and lateral margins of pleonite 5 (at least in some life stages); pleotelson without indication of posterior margin of pleonite 6. Palp of 1 or 2 articles. Maxillipedal endite apically rounded, reaching to palp article 3; palp broad (1.5–2 times as wide as long), article 4 semicircular; palp articles 1–2 fused. Pereopod 1 palm of dactylus tuberculate and sometimes carpus and propodus tuberculate. Pereopods 4–7 propodus with row of robust setae along cutting edge (at least 1 in addition to distal seta). Pleopod 1 weakly operculiform in both sexes, with exopod slightly wider than endopod but not enclosing it totally. Uropodal exopod with strong apical spike, with serrate margin; with serrate lateral lobe between articulation and apical spike. Telson with dentate distal margin.

Intertidal–shelf. Central Indo-Pacific, Temperate Australasia. 2 species (Poore and Lew Ton, 2002).

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Hyssuridae Wägele, 1981

Figure 5.7

Members of the Hyssuridae are distinguished from other anthuroids by the absence of a telsonic statocyst, free pleonites, non-operculiform first pleopods (all pleopods are similar) and small size (Müller, 1990; Poore, 2001; Poore and Lew Ton, 1988; Wägele, 1981).

Diagnosis. Body slender (pereonite 7 longer than wide, little or no shorter than pereonite 6); pleonites without marginal plumose setae on pleonal epimera or posterior borders of pleonites 4 and 5; pleonites 1–5 together 3 times as long as wide; pleonites 1–5 free and articulating; telson statocysts absent. Antennal flagellum of fewer than 10 articles, shorter than peduncle. Mouthparts not produced anteriorly. Mandible compact and with weakly-toothed transverse incisor. Maxillipedal palp broad (c. twice as long as wide). Pereopods 2–3 carpus strongly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae absent. Pleopods 1–5

similar, none operculiform.

Implicit generic attributes. Eyes absent. Antennular flagellum article 1 shorter than wide. Antenna flagellum of more than 6 articles, first shorter than others together. Mandibular palp of 3 articles. Maxillipedal endite a short triangular lobe with distal seta(e). Pereopod 2 carpus acutely produced, smooth; propodal palm axial or slightly oblique. Pereopod 3 merus and carpus without tufts of long marginal setae; carpus bluntly produced posterodistally, as in pereopod 2. Pereopods 4–7 propodi without pectinate setae along mesiodistal margin; carpus triangular, with 1 marginal robust or simple seta. Pereopod 7 dactylus narrow, almost as long as propodus. Pleopodal endopods with several marginal setae; pleopod 1 endopod longer and broader than exopod, marginal setae shorter than endopod length. Uropodal endopod free.

Key to genera of Hyssuridae

1. Uropodal exopod as broad or broader than long, endopod fused to peduncle (fig. 5.7b, e). Pleopodal endopods with single apical seta (fig. 5.7m). Mandibular palp of 1 article with seta (fig. 5.7h) 2
 - Uropodal exopod longer than wide, endopod free (fig. 5.7c, d). Pleopodal endopods with several marginal setae (fig. 5.7k, l). Mandibular palp of 3 articles (fig. 5.7f, g) 3
2. Pereopod 3 merus and carpus with tufts of long setae (fig. 5.7q). Telson short, excavate apically (fig. 5.7e). Eyes present *Xenanthura*
 - Pereopod 3 merus and carpus acutely produced posterodistally (fig. 5.7n). Telson with apical projection (fig. 5.7b). Eyes absent *Belura*
3. Uropodal exopod linear, its mesial margin and lateral margins of telson with cuticular spines (fig. 5.7d) *Neohyssura*
 - Uropodal exopod linear or with lateral lobe, unarmed. Telson unarmed (fig. 5.7c) 4
4. Pereopods 4–7 with carpus quadrangular, with 2–3 marginal spiniform setae (fig. 5.7o). Mandibular molar acute (fig. 5.7f) *Hyssura*

- Pereopods 4–7 with carpus triangular, with 1 marginal spiniform seta (fig. 5.7p). Mandibular molar blunt (fig. 5.7g) 5
- 5. Pleopod 1 endopod about as long and broad as exopod (fig. 5.7l). Maxillipedal endite prominent (fig. 5.7j) *Kupellonura*
- Pleopod 1 endopod shorter and narrower than exopod (fig. 5.7k). Maxillipedal endite absent (fig. 5.7i) *Galziniella*

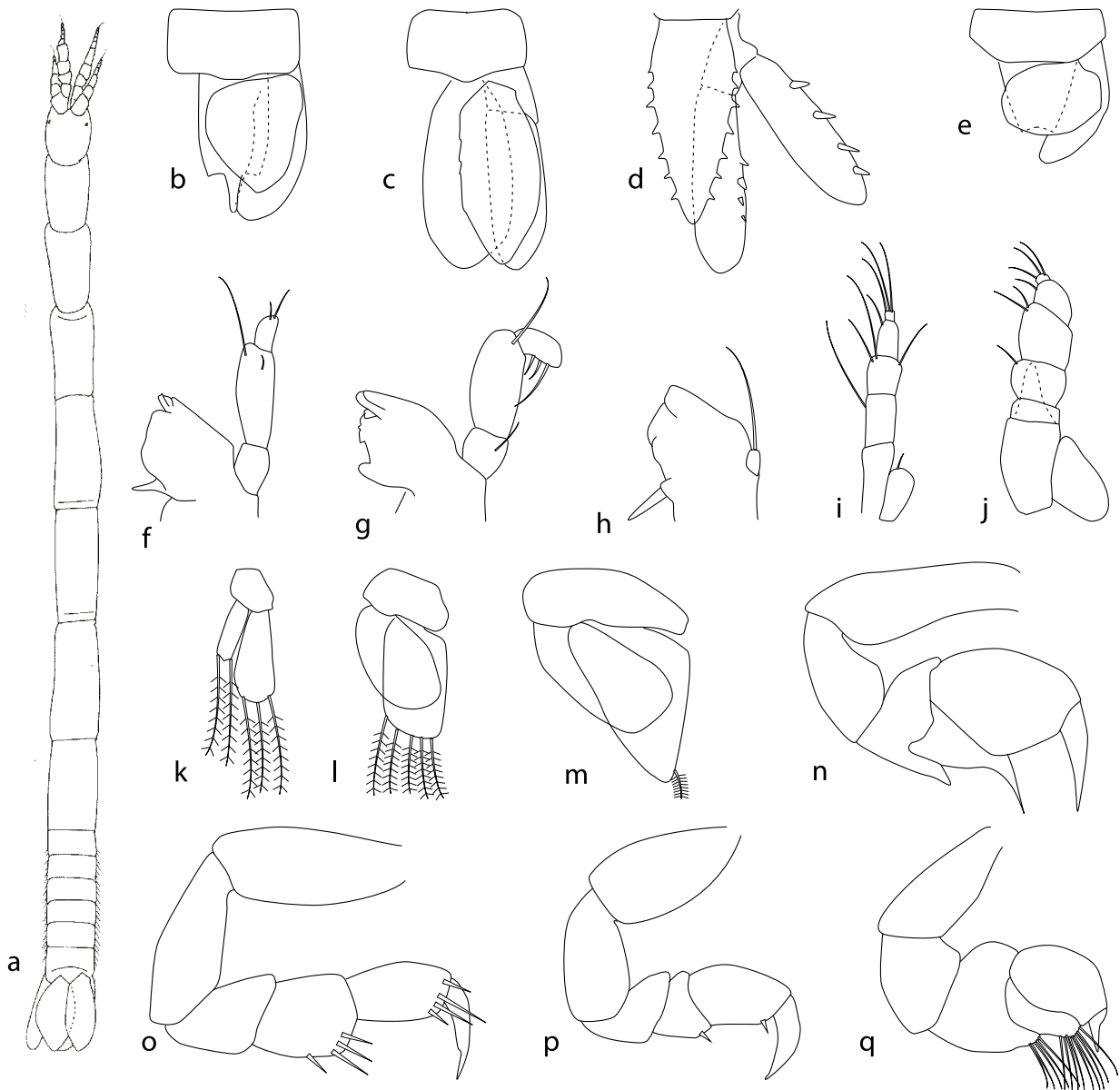


Figure 5.7. Hyssuridae. a, *Kupellonura biriwa* Poore and Lew Ton 1988. Pleonite 6, telson, right uropod: b, *Belura*; c, *Kupellonura*; d, *Neohyssura*; e, *Xenanthura*. Mandible: f, *Hyssura*; g, *Kupellonura*; h, *Xenanthura*. Maxilliped: i, *Galziniella*; j, *Kupellonura*. Pleopod 1: k, *Galziniella*; l, *Kupellonura*; m, *Xenanthura*. n, pereopod 3, *Belura*. o, pereopod 7, *Hyssura*. p, pereopod 4, *Kupellonura*. q, pereopod 3, *Xenanthura*.

Belura Poore and Lew Ton, 1988

Diagnosis. Antenna flagellum of 5 articles, first longer than remaining 4. Mandibular molar an articulating cirolanid-type blade; palp of 1 article with 1 seta or of seta alone. Maxillipedal palp of single fused article. Pereopod 2 carpus a bluntly produced blade, weakly to strongly crenulate; propodus without robust setae on cutting edge. Pereopod 3 carpus acutely produced posterodistally, different from pereopod 2. Pereopods 4–7 propodi with 1 distal robust seta on cutting edge. Pereopod 7 dactylus stout, less than two thirds length of propodus. Pleopodal endopods with single apical seta. Uropodal endopod fused to peduncle; exopod ovoid; rami and telson margins with cuticular spines (especially exopod mesial margin); telson with medial projection on excavate apex.

Subtidal, shelf. Temperate Australasia, Southern Ocean. 2 species (Poore and Lew Ton, 1988).

Galziniella Müller, 1991

Diagnosis. Mandibular molar obsolete, with strong seta reaching near tip of incisor. Maxillipedal endite absent; palp with articles 1 and 2 fused, 3–5 free. Pereopod 2 propodus without robust setae on cutting edge. Pereopods 4–7 propodi with at least 3 robust setae along cutting edge. Pleopod 1 endopod shorter and narrower than exopod, marginal setae longer than endopod length. Uropodal exopod narrowly leaf-shaped; rami and telson margins entire; telson ovoid, with rounded apex.

Intertidal. Eastern Indo-Pacific. (French Polynesia). 1 species (Müller, 1991).

Hyssura Norman and Stebbing, 1886

Diagnosis. Mandibular molar spike-like. Maxillipedal palp of 5 free articles. Pereopod 2 propodus with robust flagellate setae along cutting edge. Pereopods 4–7 propodi with 1 distal robust seta on cutting edge; with short transverse row of 1–3 pectinate setae along mesiodistal margin; carpus quadrangular, wider than propodus, with or without 2 or more pectinate setae along free distal margin. Uropodal exopod with lateral lobe; rami and telson margins entire, or dentate; telson triangular, or ovoid, with rounded apex.

Bathyal. Tropical Atlantic, including Mediterranean, Central Indo-Pacific. 7 species (Kensley, 1978; 1982a: as *Ocsanthura*; Poore and Lew Ton, 1988: rediagnosis).

Kupellonura Barnard, 1925

Diagnosis. Eyes present. Mandibular molar blunt. Maxillipedal palp of 5 free articles. Pereopod 2 propodus with robust flagellate setae along cutting edge. Pereopods 4–7 propodi with 1 distal robust seta on cutting edge. Uropodal exopod narrowly leaf-shaped, or with lateral lobe; rami and telson margins entire, or dentate; telson ovoid, with rounded apex.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, North W Pacific, Central and Eastern Indo-Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean. 19 species (Kensley, 1982b; Poore and Lew Ton, 1988: rediagnosis; Shiraki et al., 2022).

Neohyssura Amar, 1953

Diagnosis. Mandibular molar spike-like. Maxillipedal palp of 5 free articles. Pereopod 2 propodus with robust flagellate setae along cutting edge. Pereopods 4–7 propodi with 1 distal robust seta on cutting edge. Uropodal exopod narrowly leaf-shaped; rami and telson margins with cuticular spines (especially exopod mesial margin); telson triangular.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Western and Central Indo-Pacific, Temperate Southern Africa. 6 species (Wägele, 1987; Poore and Lew Ton, 1988: rediagnosis).

Xenanthura Barnard, 1925

Diagnosis. Eyes present. Antennular flagellum article 1 twice as long as wide. Antenna flagellum of 5 articles, first longer than remaining 4. Mandibular molar an articulating cirolanid-type blade; palp of 1 article with 1 seta or of seta alone. Maxillipedal palp of single fused article. Pereopod 2 carpus a bluntly produced blade, weakly-strongly crenellate; propodal palm transverse, crenellate; propodus without robust setae on cutting edge. Pereopod 3 merus and carpus with tufts of long marginal setae; carpus not produced. Pereopods 4–7 propodi without robust setae on cutting edge (few tubercles on merus-propodus instead); with short transverse row of 1–3 pectinate setae along mesiodistal margin. Pereopod 7 dactylus stout, less than two thirds length of propodus. Pleopodal endopods with single apical seta. Uropodal endopod fused to peduncle; exopod ovoid; rami and telson margins entire; telson short, excavate apically (without medial projection).

Intertidal–shelf. Tropical Atlantic, Western and Central Indo-Pacific, Temperate South America, Temperate Australasia. 7 species (Poore and Lew Ton, 1988: rediagnosis; Müller, 1990).

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Leptanthuridae Poore, 2001

Figures 5.8, 5.9

Leptanthurids have a single telsonic statocyst and an even row of robust setae, often complex, along the palm of pereopod 1, which is usually defined proximally by a square angle or a protruding tooth (Poore, 2001). Leptanthurids are probable predators (Wägele, 1981, 1985a).

Diagnosis. Body 10–15 times as long as wide, non-males rarely more elongate (pereonite 7 wider than long, much shorter than pereonite 6); pleonites without marginal plumose setae on pleonal epimera or posterior borders of pleonites 4 and 5; pleonites 1–5 together not more than twice as long as wide; pleonites 1–5 free and articulating, or fused; telson statocyst single. Antennal flagellum of fewer than 10 articles, shorter than peduncle, or of numerous articles. Mouthparts acutely produced anteriorly. Mandible with acute anteriorly directed incisor. Maxillipedal palp narrow, tapering to acute apex, of fewer than 4 articles (c. 3 times as long as wide). Pereopods 2–3 carpus not or weakly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae absent. Pleopod 1 exopod

operculiform alone.

Implicit generic attributes. Pleonites 1–5 free and articulating; pleotelson with posterior margin of pleonite 6 indicated dorsally, delineated from telson. Eyes well developed. Antennular and antennal peduncle articles compact. Antennal peduncle without sucker-like cuticular structures; flagellum of 5–8 articles, shorter than peduncle; flagellum articles cylindrical and free. Mandibular palp of 3 articles; article 3 with row of 7 or more setae on oblique apex. Maxillipedal palp almost as long as basis. Pereopods 1–3 propodi without rolled tessellated margin. Pereopod 1 carpus, posterior margin without short robust setae; propodus significantly larger than propodus of pereopods 2 and 3; palm axial or oblique; palm with proximal tooth (defined by clear angle to palm). Pereopods 2 and 3 carpus margin without robust setae. Pereopodal propodi 2 and 3 ovate, 4–7 linear. Pereopods 4–7 carpus quadrangular or elongate, with free anterior margin. Pereopod 7 present on adults.

Key to genera of Leptanthuridae

1. Pereopod 7 absent on adults. Pereopodal propodi 2–6 similar, much narrower than long (fig. 5.9i, j) *Curassanthura*
- Pereopod 7 present on adults. Pereopodal propodi 2 and 3 differentiated from 4–7, even slightly 2
2. Maxillipedal endite reaching at least end of first palp article (fig. 5.8i–k) 3
- Maxillipedal endite absent or obsolete (fig. 5.8l, m) 9
3. Pleonites 1–5 fused; pleonite 6 not distinguishable from telson (fig. 5.8n). Pereopods 1–3 similar, propodus with rolled tessellated palm and strong proximal thumb (fig. 5.9a) *Aenigmathura*
- Pleonites free and articulating (rarely 1–5 fused); pleonite 6 marked off dorsally from telson (fig. 5.8a, b). Pereopods 2 and 3 or 3 only differentiated from pereopod 1, none with rolled tessellated propodal palm 4
4. Antennae 1 and 2 flagella of >12 articles, longer than or equal to peduncles (fig. 5.8a, b) 5
- Antennae 1 and 2 flagella of c. 12 articles, shorter than peduncles (fig. 5.8c, d, e) 6
5. Antennal peduncle with sucker-like cuticular structures (fig. 5.8e) *Negoescuanthura*
- Antennal peduncle without sucker-like cuticular structures *Accalathura*
6. Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles (fig. 5.9o, q) *Albanthura*
- Pereopods 4–7 carpus quadrangular or elongate, with free anterior margin (fig. 5.9p) 7
7. Maxillipedal palp of 5 articles (fig. 5.8j). Pereopod 2 much more elongate than pereopod 1 (fig. 5.9b, c) *Bourbonanthura*

- Maxillipedal palp of 3 articles (fig. 5.8k). Pereopod 2 similar to but smaller than pereopod 1 8
- 8. Eyes poorly developed. Pereopod 1 carpus without robust setae on posterior margin; palm with row of similar simple robust setae (fig. 5.9h) *Calathura*
- Eyes well developed. Pereopod 1 carpus with robust setae on posterior margin; palm with row of complex robust setae and distinctive seta on tooth (fig. 5.9n) *Virganthura*
- 9. Mandibular palp of 3 articles 10
- Mandibular palp of 1 article 12
- 10. Maxillipedal palp fused to basis and all articles (except sometimes for minute distal article) (fig. 5.8m) *Neoanthura*
- Maxillipedal palp free from basis, with articles 1–3 or 1–4 fused, article 5 minute if visible (fig. 5.8l) 11
- 11. Antennular and antennal peduncles articles elongate (fig. 5.8c). Pereopods 1 and 2 both with strong proximal thumb on propodal palm (fig. 5.9f, g) *Bunderanthura*
- Antenna 1 and 2 peduncles articles compact (fig. 5.8d). Pereopods 1 and 2 with short proximal thumb on propodal palm (fig. 5.9k, j) *Leptanthura*
- 12. Pereopod 1 propodus much larger than that of pereopod 2 (fig. 5.9d, e). Mandibular palp of one article with one seta (fig. 5.8f) *Bullowanthura*
- Pereopods 1 and 2 or 1–3 similar. Mandibular palp of one article without seta or absent 13
- 13. Pereopods 1 and 2 similar, enlarged, propodus grossly produced at proximal end of palm so that palm is transverse (fig. 5.9m). Pereopods 4–7 with merus not distally lobed on flexor margin. Mandibular palp absent (fig. 5.8g) *Psittanthura*
- Pereopods 1–3 similar, propodus with small thumb at proximal end of axial palm. Pereopods 4–7 with merus lobed (fig. 5.9q). Mandibular palp a simple article (fig. 5.8h) *Ulakanthura*

***Accalathura* Barnard, 1925**

Diagnosis. Antennal flagellum of 13–20 articles, longer than or slightly shorter than peduncle. Maxillipedal endite reaching middle of second fused segment; palp free from basis, with articles 1–2 fused and 3–5 fused. Pereopod 1 palm with even marginal row of short complex robust setae along length; without distinctive robust setae on proximal tooth.

Intertidal–bathyal. Tropical Atlantic, Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia, Southern Ocean (Wägele, 1985a; Poore and Lew Ton, 1990: rediagnosis, key to 13 Australian species; King, 2008: redescription of type species).

***Aenigmathura* Thomson, 1951**

Diagnosis. Pleonites 1–5 fused (or sutures immoveably indicated); pleotelson without indication of posterior margin of pleonite 6. Antennal flagellum articles short and fused. Maxillipedal endite reaching at least article 3; palp free from basis, with articles 1–2 fused and 3–5 fused. Pereopods 1–3 propodi with rolled tessellated margin. Pereopod 1 palm with even marginal row of short complex robust setae along length; with 1–2 distinctive robust setae on tooth.

Intertidal–bathyal. Temperate Australia. 4 species (Poore and Lew Ton, 1986).

***Albanthura* Wägele, 1985**

Diagnosis. Eyes absent. Mandibular palp article 3 with fewer than 4 terminal setae. Maxillipedal endite reaching at least article 3; palp free from basis, with articles 1–2 fused, 3–4 and 5 free. Pereopod 1 palm defined proximally by angle distant from palm of carpus; with even marginal row of short complex robust setae along length; with 1 larger simple robust seta on proximal angle. Pereopods 2 and 3 carpus margin with 1–2 robust setae (as in propodus). Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles.

Shelf–bathyal. New Zealand. 2 species (Wägele, 1985b).

***Bourbonanthura* Müller, 1990**

Diagnosis. Eyes poorly developed, or absent. Maxillipedal endite reaching at least article 3; palp free from basis, of 5 free articles. Pereopod 1 palm with even marginal row of short complex robust setae along length; without distinctive robust setae on proximal tooth.

Intertidal, subtidal. Eastern Indo-Pacific, Temperate Southern Africa. 2 species (Müller, 1990, 1993).

***Bullowanthura* Poore, 1978**

Diagnosis. Eyes absent. Antennal flagellum rudimentary (fewer than 5 articles), shorter than last article of peduncle. Mandibular

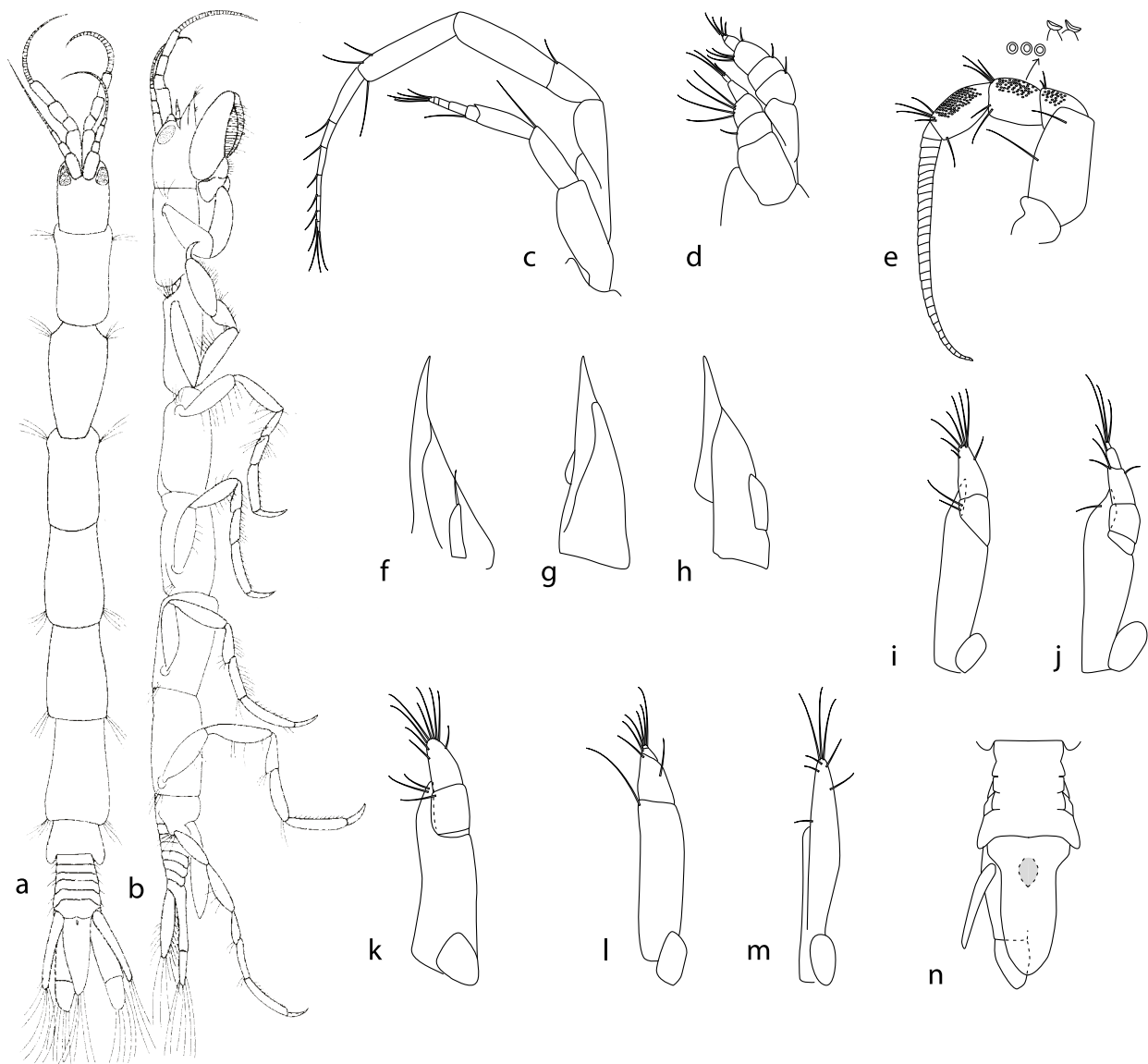


Figure 5.8. Leptanthuridae. a, b, *Accalathura themeda* Poore and Lew Ton, 1990. Left antennula, antenna: c, *Bunderanthura*; d, *Leptanthura*. e, antenna with detail of sucker-like cuticular structures, *Negoescuathura*. Mandible: f, *Bullovanthura*; g, *Psittanthura*; h, *Ulakanthura*. Maxilliped: i, *Aenigmathura*; j, *Bourbonanthura*; k, *Calathura*; l, *Leptanthura*; m, *Neoanthura*. n, pleon, telson, uropod, *Aenigmathura*.

palp of 1 article. Maxillipedal endite absent or obsolete; palp one-third as long as basis, palp free from basis, with articles 1–2 fused and 3–5 fused. Pereopod 1 carpus, posterior margin with short robust setae (as on propodus); palm with even marginal row of short complex robust setae along length; palm with 1–2 distinctive robust setae on tooth. Pereopods 2 and 3 carpus margin with 1–2 robust setae (as in propodus). Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles.

Subtidal–bathyal. Temperate Northern Atlantic, Temperate Australasia. 5 species (Negoescu, 2005; Poore, 1978).

***Bunderanthura* Poore and Humphreys, 2013**

Diagnosis. Antennular and antennal peduncle articles longer than wide. Maxillipedal endite absent or obsolete; palp one third as long as basis, palp free from basis, with articles 1–2 fused, articles 3–5 minute, free. Pereopod 1 palm and pereopod 2 palm with proximal tooth; with even marginal row of short complex robust setae along length; with 1 larger simple robust seta on proximal angle.

Anchialine sinkhole near coast. NW Australia. 1 species (Poore and Humphreys, 2013).

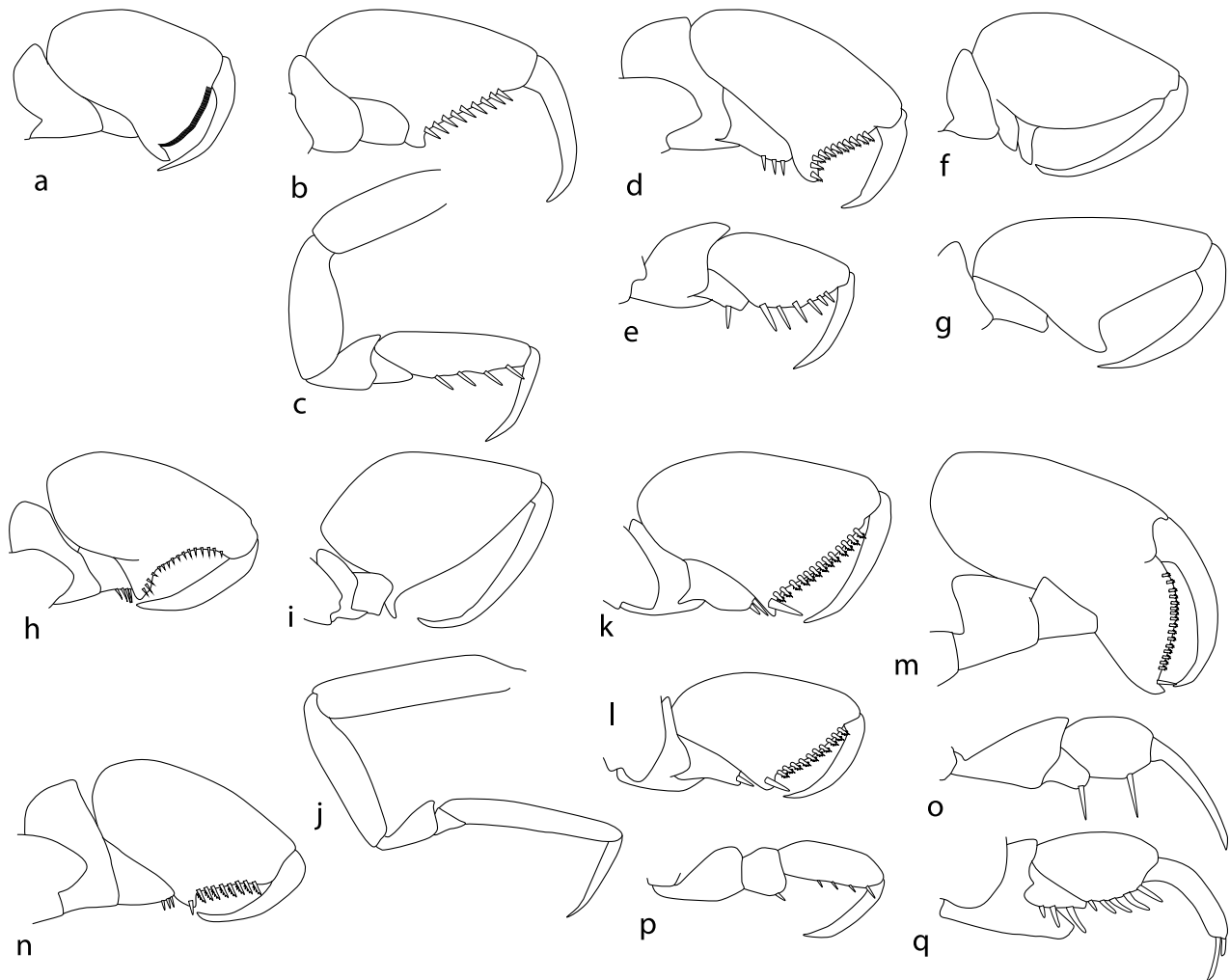


Figure 5.9. Leptanthuridae. Pereopod 1 or 1 and 2: a, *Aenigmathura*; b, c, *Bourbonanthura*; d, e, *Bullowanthura*; f, g, *Bunderanthura*; h, *Calathura*; i, j, *Curassanthura*; k, l, *Leptanthura*; m, *Psittanthura*; n, *Virganthura*. Pereopod 4: o, *Albanthura*; p, *Calathura*; q, *Ulanthura*.

***Calathura* Norman and Stebbing, 1886**

Diagnosis. Maxillipedal endite reaching at least article 3; palp one third as long as basis, palp free from basis, of 5 free articles. Pereopod 1 palm with even marginal row of closely set simple robust setae; without distinctive robust setae on proximal tooth.

Subtidal–bathyal. Temperate Northern Atlantic. 2 species (Brandt and Negoescu, 1997: redescription of type species).

***Curassanthura* Kensley, 1981**

Diagnosis. Eyes poorly developed. Mandibular palp article 3 with fewer than 4 terminal setae. Maxillipedal endite reaching at least article 3; palp free from basis, of 5 free articles. Pereopod 1 palm with even marginal row of short complex robust setae along length; without distinctive robust setae on proximal tooth, or with 1–2 distinctive robust setae on tooth. Pereopodal propodi 2–6 similar, much narrower than long. Pereopod 7 absent on adults.

Hypogean in beach sand. Tropical Atlantic. 5 species (Wägele, 1985c; Wägele and Brandt, 1985).

***Leptanthura* Sars, 1897**

Diagnosis. Eyes poorly developed, or absent. Antennal flagellum rudimentary (fewer than 5 articles), shorter than last article of peduncle. Mandibular palp article 3 with fewer than 4 terminal setae. Maxillipedal endite absent or obsolete; palp one third as long as basis, palp free from basis, with articles 1–3 fused, 5 minute if visible or free from basis, with articles 1–4 fused and 5 minute if visible. Pereopod 1 carpus, posterior margin with short robust setae (as on propodus); palm defined proximally by angle distant from palm of carpus; palm with even marginal row of short complex robust setae along length, with 1 larger simple robust seta on proximal angle. Pereopods 2 and 3 carpus margin with 1–2 robust setae (as in propodus). Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles.

Intertidal–bathyal. Arctic, Temperate Northern and Tropical Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia. 43 species (Kensley and Schotte, 2000; Müller, 1992; Negoescu, 2007).

***Negoescuanthura* Jarquín-Martínez and García-Madrigal, 2021**

Diagnosis. Antennal peduncle with sucker-like cuticular structures; flagellum of more than 30 articles, longer than peduncle. Maxillipedal endite reaching middle of second fused segment; palp free from basis, with articles 1–2 fused and 3–5 fused. Pereopod 1 palm with even marginal row of short complex robust setae along length; without distinctive robust setae on proximal tooth.

Subtidal. Tropical Eastern Pacific. 2 species (Jarquín-Martínez and García-Madrigal, 2021).

***Neanthura* Menzies, 1956**

Diagnosis. Eyes absent. Antennal flagellum rudimentary (fewer than 5 articles), shorter than last article of peduncle. Maxillipedal endite absent or obsolete; palp one third as long as basis, palp fused to basis and all articles (except sometimes for minute distal article).

Bathyal. Tropical Atlantic. 1 species (Menzies, 1956).

***Psittanthura* Wägele, 1985**

Diagnosis. Eyes absent. Mandibular palp absent. Maxillipedal endite absent or obsolete; palp one third as long as basis, palp free from basis, with articles 1–4 fused and 5 minute if visible. Pereopod 1 propodus narrower than on similarly shaped pereopod 2; palm transverse, its proximal angle strongly produced away from carpus; palm defined proximally by angle distant from palm of carpus; palm with even marginal row of short complex robust setae along length; palm with 1 larger simple robust seta on proximal angle. Pereopodal propodus 2 similar to propodus of pereopod 1, propodus 3 smaller, with transverse palm. Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles.

Bathyal. New Zealand. 1 species (Wägele, 1985b).

***Ulakanthura* Poore, 1978**

Diagnosis. Pleonites 1–5 free and articulating. Eyes absent. Antennal flagellum rudimentary (fewer than 5 articles), shorter than last article of peduncle. Mandibular palp of 1 article. Maxillipedal endite absent or obsolete; palp one third as long as basis, palp free from basis, with articles 1–3 fused, 5 minute if visible. Pereopod 1 carpus, posterior margin with short robust setae (as on propodus); propodus narrower than on similarly shaped pereopod 2; palm defined proximally by angle distant from palm of carpus; palm with even marginal row of short complex robust setae along length; palm with 1 larger simple robust seta on proximal angle. Pereopodal propodi 2 and 3 similar to propodus 1 (bases of these limbs much longer and broader than in pereopod 1). Pereopods 4–7 carpus triangular, enclosed anteriorly by surrounding articles.

Subtidal. Temperate Australasia. 7 species (Poore, 1978).

***Virganthura* Kensley, 1987**

Diagnosis. Mandibular palp article 3 with c. 5 setae in longitudinal row. Maxillipedal endite reaching at least article 3; palp free from basis, with articles 1–2 fused, 3–4 and 5 free. Pereopod 1 carpus, posterior margin with short robust setae (as on propodus); palm with even marginal row of short complex robust setae along length; palm with 1–2 distinctive robust setae on tooth.

Shelf. Tropical Atlantic. 1 species (Kensley, 1987).

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Paranthuridae Menzies and Glynn, 1968

Figure 5.10

The family Paranthuridae was introduced to include all anthuroids with “piercing” mouthparts, that is, with the labrum, mandible and maxilliped produced forward as cone comprising acute stylets (Menzies and Glynn, 1968). Poore (2001) separated most of these as Leptanthuridae, retaining Paranthuridae for six genera lacking statocysts and without complex robust setae along the palm of pereopod 1. Shiraki et al. (2022) added another genus. Shiraki et al. (2026) provided a key to genera. Many species are darkly pigmented. The family includes one endemic New Zealand species from interstitial fresh water, *Cruregens fontanus* Chilton, 1882.

Diagnosis. Body 10–15 times as long as wide, non-males rarely more elongate (pereonite 7 wider than long, much shorter than pereonite 6); pleonites without marginal plumose setae on pleonal epimera or posterior borders of pleonites 4 and 5; pleonites 1–5 together not more than twice as long as wide; pleonites 1–5 free and articulating, or fused; telson statocysts

absent. Antennal flagellum rudimentary (fewer than 5 fused articles), shorter than last article of peduncle. Mouthparts acutely produced anteriorly. Mandible with acute anteriorly directed incisor (often secondarily blunt). Maxillipedal palp narrow, tapering to acute apex, of fewer than 4 articles (c. 3 times as long as wide). Pereopods 2–3 carpus not or weakly produced posterodistally. Pereopod 7 propodus anterodistal serrate setae absent. Pleopod 1 exopod operculiform alone.

Implied generic characters. Body pigmented; pleonite 1 mid-dorsal length as long as pleonite 2; pleonites articulating; pleonite 6 posterior margin indicated dorsally, delineated from telson; pleotelson oval. Eyes well developed. Antennal flagellum articles cylindrical and free. Mandibular palp absent. Pereopod 1 palm without proximal tooth (palm more or less continuous with that of carpus). Pereopodal propodi 2 and 3 ovate, 4–7 linear. Pereopod 7 absent in adults.

Key to genera of Paranthuridae

1. Pereopod 7 present in adults. Pereopod 1 propodus without proximal row of closely set setae on mesial surface (fig. 5.10p). Mandible with 3-articled palp (fig. 5.10m) 2
- Pereopod 7 absent in adults. Pereopod 1 propodus without or with row of closely set setae on mesial surface (fig. 5.10o). Mandible without palp (fig. 5.10l) 4
2. Pleonites free or fused; pleonite 6 articulating with pleon, usually distinct from telson; telson oval. Uropodal exopod linear or leaf-shaped (fig. 5.10a). Antenna flagellum plate-like, of short fused articles (fig. 5.10j) *Paranthura*
- Pleonites fused but with sutures visible; pleonite 6 not articulating with pleon; telson triangular. Uropodal exopod reduced (fig. 5.10g, h). Antenna flagellum articles cylindrical (fig. 5.10j) 3
3. Eyes present. Pleonites 1–5, pleotelson fused (sutures visible; fig. 5.10g) *Deltanthura*
- Eyes absent. Pleonites 1–5, pleotelson fused (sutures barely visible; fig. 5.10h) *Pseudanthura*
4. Pereonite 7 very short, not visible laterally (fig. 5.10b–d). Head as long as wide 5

- Pereonite 7 one third as long as pereonite 6 (fig. 5.10e, f). Head longer than wide 6
- 5. Pleonites 1–5 separated by integumental folds dorsally; pleonite 1 twice as long as pleonite 2 (fig. 5.10d)
..... *Colanthura*
- Pleonites 1–5 fused, rarely with integumental folds dorsally; pleonites of similar lengths (fig. 5.10b, c)
..... *Califanthura*
- 6. Pleonites 2–5 only fused (fig. 5.10d). Marine or estuarine. Eyes present *Cruranthura*
- Pleonites all free (fig. 5.10f). Hypogean freshwater. Eyes absent *Cruregens*

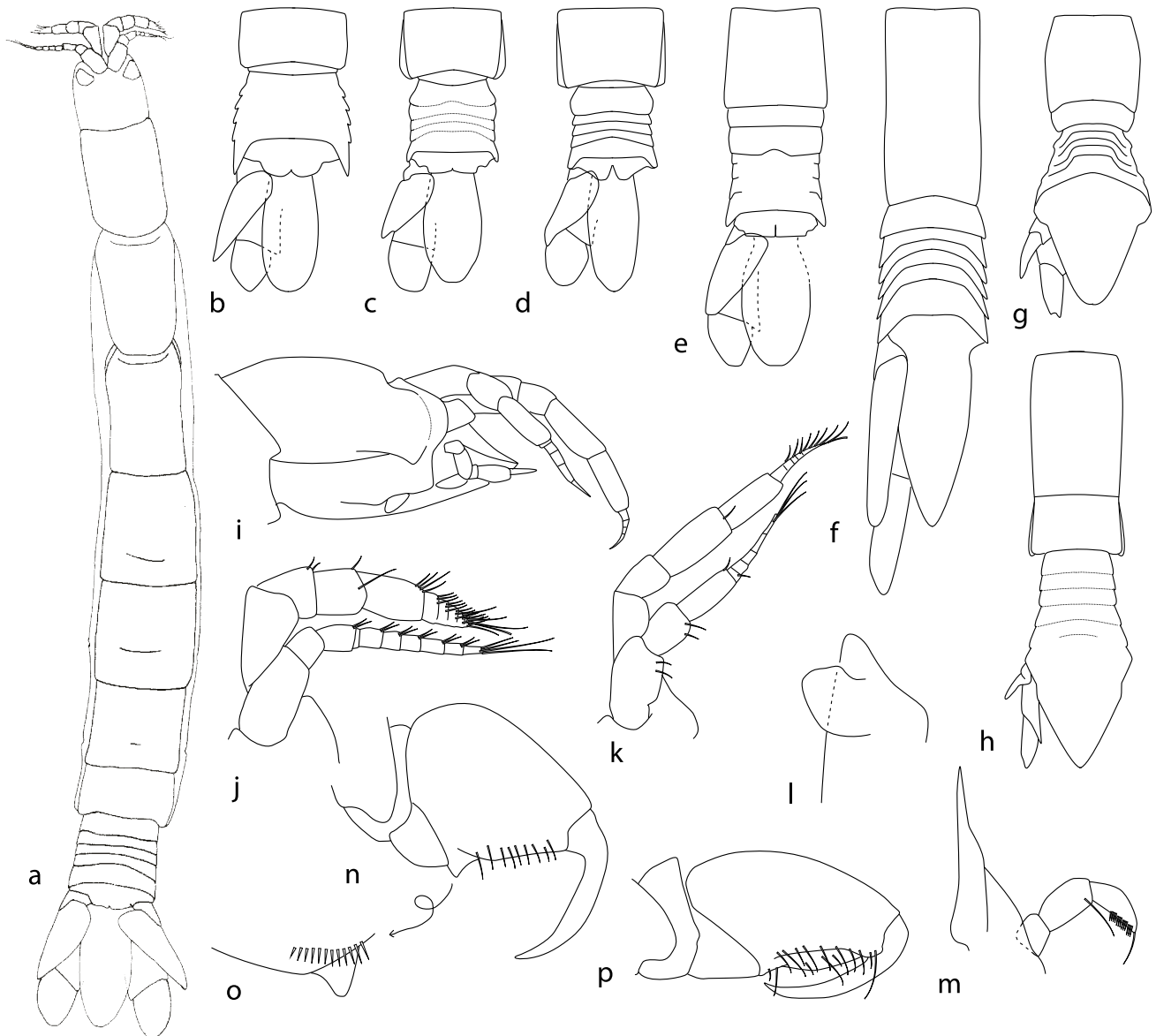


Figure 5.10. Paranthuridae. a, *Paranthura acacia* Poore, 1984. Pereonites 6, 7, pleon, pleotelson, uropod: b, c, *Califanthura*; d, *Colanthura*; e, *Cruranthura*; f, *Cruregens*; g, *Deltanthura*; h, *Pseudanthura*. i, head, mouthparts, antennula, antenna, lateral, *Pseudanthura*. Antennula, antenna: j, *Paranthura*; k *Pseudanthura*. Mandible: l, *Califanthura*; m, *Pseudanthura*. n, o, *Califanthura*, pereopod 1 palm with thumb and row of setae. p, *Paranthura*.

***Califanthura* Schultz, 1977**

Diagnosis. Pereonite 7 extremely reduced, hidden except dorsally; pleonites 1–5 fused (or sutures immoveably indicated). Pereopod 1 propodus with row of closely set setae confined proximally on mesial surface. Uropodal exopod narrowly leaf-shaped.

Intertidal–bathyal. Tropical Atlantic, Temperate South America, Temperate Australasia, Southern Ocean. 9 species (Poore, 1984a: rediagnosis).

***Colanthura* Richardson, 1902**

Diagnosis. Pereonite 7 extremely reduced, hidden except dorsally; pleonites 1–5 fused but indicated by folds dorsally and laterally; pleonite 1 middorsal length longer than pleonite 2, swollen laterally. Pereopod 1 propodus with row of closely set setae confined proximally on mesial surface. Uropodal exopod narrowly leaf-shaped.

Intertidal–bathyal. Temperate Northern and Tropical Atlantic, Temperate Northern Pacific, Indo West-Pacific, Temperate Southern Africa. 14 species (Poore, 1984a: rediagnosis).

***Cruranthura* Thomson, 1946**

Diagnosis. Pereonite 7 one third as long as pereonite 6; pleonites 1 free, 2–5 not indicated by folds dorsally. Pereopod 1 propodus with row of closely set setae confined proximally on mesial surface. Uropodal exopod narrowly leaf-shaped.

Intertidal, subtidal. Temperate Northern Atlantic, Central Indo-Pacific, Temperate Australasia. 4 species (Poore, 1984a: rediagnosis).

***Cruregens* Chilton, 1882**

Diagnosis. Body not pigmented; pereonite 7 one third as long as pereonite 6; pleonites 1–5 free and articulating; pleonites fused; pleonite 6 not delineated from pletelson. Eyes absent. Pereopod 1 propodus with setae on mesial surface evenly spaced along palm; palm with proximal tooth (defined by clear angle to palm). Pereopodal propodi 2–6 similar, much narrower than long. Uropodal exopod linear, apically rounded.

Freshwater stygobiont. New Zealand endemic. 1 species (Wägele, 1982: redescription of type species).

***Deltanthura* Shiraki, Shimomura and Kakui, 2022**

Diagnosis. Body not pigmented; pereonite 7 half as long as pereonite 6; pleonites 1–5 fused (sutures visible); pleonites fused; pleonite 6 not delineated from pletelson; pletelson triangular. Mandibular palp of 3 articles. Pereopod 1 propodus with setae on mesial surface evenly spaced along palm. Pereopodal propodi 2–6 similar, much narrower than long. Pereopod 7 present on adults. Uropodal exopod elongate-triangular, reaching beyond end of peduncle.

Slope. Temperate Northern Pacific. 1 species (Shiraki et al., 2022, 2026).

***Paranthura* Bate and Westwood, 1866**

Diagnosis. Pereonite 7 half as long as pereonite 6; pleonites 1–5 free and articulating, or 1–5 fused (or sutures immoveably indicated), or 1 free, 2–5 not indicated by folds dorsally. Antennal flagellum articles plate-like, of short fused articles. Mandibular palp of 3 articles. Pereopod 1 propodus with setae on mesial surface evenly spaced along palm. Pereopod 7 present on adults. Uropodal exopod narrowly leaf-shaped, or broad and more or less notched.

Intertidal–bathyal. Cosmopolitan except Arctic. 68 species (Poore, 1984b: key to 13 species from SE Australia).

***Pseudanthura* Richardson, 1911**

Diagnosis. Body not pigmented; pereonite 7 half as long as pereonite 6; pleonites 1–5 fused (or sutures immoveably indicated); pleonites fused; pleonite 6 not delineated from pletelson; pletelson triangular. Eyes absent. Mandibular palp of 3 articles. Pereopod 1 propodus with setae on mesial surface evenly spaced along palm. Pereopod 7 present on adults. Uropodal exopod linear, tapering, as long as or shorter than peduncle.

Shelf–abyssal. Tropical Atlantic, Indo West-Pacific, Temperate South America, Temperate Australasia. 5 species (Poore and Lew Ton, 1986: rediagnosis, key to species).

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Remaining Cymothoida Wägele, 1989

The remaining Cymothoida is a polyphyletic grouping that includes all predatory, parasitic, blood-sucking or scavenging cymothoidan isopods except anthuroids. They are best defined by the absence of the extreme mouthpart modifications and reductions seen in Anthuroidea. Brandt and Poore (2003) treated them as two superfamilies, Cirolanoidea and “Cymothooidea”. They include the former suborder Gnathiidea, now treated as a derived and specialised family (Brandt and Poore, 2003; Brusca and Wilson, 1991).

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Aegidae White, 1850

Figures 5.11, 5.12

Aegidae are associates of fishes, almost exclusively attaching temporarily to the external skin surface. A few species are associated with other invertebrates, notably sponges, which might be used as refugia. Aegids are regarded as micropredators rather than parasites, feeding on blood or mucus temporarily and never attaching permanently (Bruce, 2009). Many species are relatively large (1–7 cm) and can be recognised as belonging to this family by the prehensile dactyli on pereopods 1–3 and the large dark eyes, sometimes meeting, or almost meeting, at the midline of the head. Species of the family are occasionally pests of aquaculture fishes. The family is almost exclusively marine, with the monotypic *Alitropus* H. Milne Edwards, 1840 the only genus occurring in fresh water.

Earlier keys to genera included *Barybrotus* Schioedte and Meinert, 1879, now in its own family Barybrotidae Hansen, 1890 (Bruce, 2009), or were limited to seven marine genera.

Diagnosis. Eyes large, often medially united. Mouthparts forming buccal cone; maxillula styliform, with terminal and

mesial robust setae; maxilla with single distomesial basal endite; maxilliped palp with conspicuous recurved (“hooked”) robust setae. Pereopods 1–3 robust, with dactylus as long as or longer than propodus, usually strongly recurved.

Implicit generic attributes. Head overlapped laterally by anterior angles of pereonite 1. Antennulae and antennae well developed; division between peduncle and flagellum distinct. Frontal lamina present, varied in shape, occasionally absent, usually not abutting clypeus. Clypeus and labrum present, often indistinct. Mandible incisor narrow, small molar process present, occasionally absent, laminar and triangular when present; lacinia mobilis and spine row absent. Maxillula styliform, with flattened terminal robust setae, may be distally hooked. Maxilliped endite present (*Aega* group of genera and *Rocinela*) or absent (*Syscenus* and *Xenuraega*); palp with 3–5 articles, at least articles 3 and 4 with large, hooked robust setae. Penial processes flush.

Key to genera of Aegidae

1. Pleonite 1 abruptly narrower than pereonite 7. Pleonite 5 lateral margin entirely free. Eyes usually absent (fig. 5.11f–h) 2
- Pleonite 1 not abruptly narrower than pereonite 7. Pleonite 5 lateral margin partly or entirely overlapped by pleonite 4. Eyes present, often large (fig. 5.11a–e) 3
2. Frontal lamina present (fig. 5.11u). Uropodal rami both laminar (fig. 5.11f) *Syscenus*
- Frontal lamina absent (fig. 5.11v). Uropodal endopod stub-like, exopod filamentous or both rami elongate (fig. 5.11h) *Xenuraega*
3. Body dorsally compressed (fig. 5.11e). Frontal lamina slender, lanceolate (fig. 5.11q). Rostrum anteriorly widely rounded or truncate (fig. 5.11q, s, t). Maxilliped palp 3-articled (fig. 5.12p, q) 4
- Body dorsally moderately to strongly vaulted (fig. 5.11b). Frontal lamina wide (fig. 5.11n, o). Rostrum narrowly rounded, subtruncate or acute (fig. 5.11a, b, r). Maxilliped palp 5-articled; article 5 may be minute or fused to article 4 (fig. 5.12k–n) 5

4. Coxae of pereonites 5–7 as long or longer than respective segment (fig. 5.11d, e). Frontal lamina small but obvious (fig. 5.11t). Maxilliped endite present (fig. 5.12p). Plane of uropodal endopod set oblique to exopod. Marine *Rocinela*
- Coxae of pereonites 5–7 distinctly shorter than respective segment (fig. 5.11c). Frontal lamina minute (fig. 5.11q). Maxilliped endite absent. Uropodal rami coplanar. Estuarine and freshwater, Australasia *Alitropus*
5. Frontal lamina ventrally flat, not strongly narrowed posteriorly. Antennula peduncle articles 1 and 2 flattened (fig. 5.11n, o) 6
- Frontal lamina with free posterior margin and/or narrowed posteriorly (fig. 5.11p r). Antennula peduncle articles 1 and 2 not flattened or expanded (fig. 5.11p r) 7
6. Uropodal rami coplanar, extending to or beyond pleotelson apex; uropodal endopod lateral margin usually without distinct excision. Pleotelson posterior margin not distinctly produced, with or without median point, may be concave or truncate (fig. 5.11a) *Aega*
- Uropodal endopod at oblique angle to exopod, rami usually not extending to pleotelson apex; uropodal endopod lateral margin usually with distinct excision. Pleotelson apex forming distinct point, usually produced (fig. 5.11i, j) *Aegapheles*
7. Rostrum bent ventrally or ventroposteriorly (fig. 5.11l, p). Maxilliped palp article 5 longer than wide, not fused to article 4 (fig. 5.12m, n) *Aegiochus*
- Rostrum minute, not projecting, not visible in dorsal view (fig. 5.11m, r). Maxilliped palp article 5 minute, less than 0.3 width of article 4 (fig. 5.12o) *Epulaega*

***Aega* Leach, 1815**

Diagnosis. Body dorsally vaulted; rostral point large, dorsal, rostral point apex shape acute. Coxae 5–7 as long or longer than respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes large, occupying 50% or more of head. Antennula peduncle article 1 close-set or together, articles 1 and 2 short, dorsoventrally flattened. Antennal peduncle articles 1–3 short, 4 and 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina posteriorly wide, separate from clypeus. Mandible incisor bicuspid. Maxilliped endite present; palp 5-articled, article 1 present. Pleopod 2 appendix masculina inserted basally; pleopods 3 and 4 endopods same size as exopod, with few plumose marginal setae at distolateral angle only. Uropodal rami with distinct apex, rami coplanar.

Subtidal–abyssal (to 2148 m). Cosmopolitan. 37 species (Brusca, 1983: key to 11 species of eastern Pacific; Bruce, 2009: rediagnosis, key to 7 New Zealand species).

***Aegapheles* Bruce, 2009**

Diagnosis. Body dorsally vaulted; head overlapped laterally by anterior angles of pereonite 1; rostral point large, dorsal, rostral point apex shape acute. Coxae 5–7 as long or longer than respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes large, occupying 50% or more of head. Antennula peduncle article 1 close-set or together, articles 1 and 2 short, articles 1 and 2 dorsoventrally flattened. Antennal peduncle articles 1–3 short, 4 and 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina posteriorly wide, separate from clypeus. Mandible incisor bicuspid. Maxilliped endite present; palp 5-articled, article 1 present. Pleopod 2

appendix masculina inserted basally; pleopods 3 and 4 endopods same size as exopod, with few plumose marginal setae at distolateral angle only. Uropodal rami with distinct apex, rami exopod at oblique angle to endopod.

Subtidal–bathyal (70–1140 m). Cosmopolitan. 17 species (Bruce, 2004: description of 21 species as “*Aega deshaysiana* (Milne Edwards, 1840) group”; Bruce, 2009: diagnosis, key to 7 New Zealand species).

***Aegiochus* Bovallius, 1885**

Diagnosis. Body dorsally vaulted; rostral point large, dorsal, rostral point apex shape narrowly rounded. Coxae 5–7 as long or longer than respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes often large, sometimes medially united. Antennula peduncle article 1 separated by rostrum, articles 1 and 2 short, cylindrical. Antennal peduncle articles 1–3 short, 4 and 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina wide, posteriorly narrow, forming stem. Mandible incisor bicuspid. Maxilliped endite present; palp 5-articled, article 1 present. Pleopod 2 appendix masculina inserted basally; pleopods 3 and 4 endopods same size as exopod, with plumose marginal setae. Uropodal rami with distinct apex, rami coplanar.

Subtidal–abyssal (shallow–3461 m). Cosmopolitan. 38 species (Brusca, 1983: description of 5 species as *Aega* (*Rhamphion*) Brusca, 1983), junior synonym; Bruce, 2009: rediagnosis, key to 15 NZ species).

***Alitropus* H. Milne Edwards, 1840**

Diagnosis. Body dorsally depressed; rostral point small, dorsal, rostral point apex shape acute. Coxae 5–7 shorter than

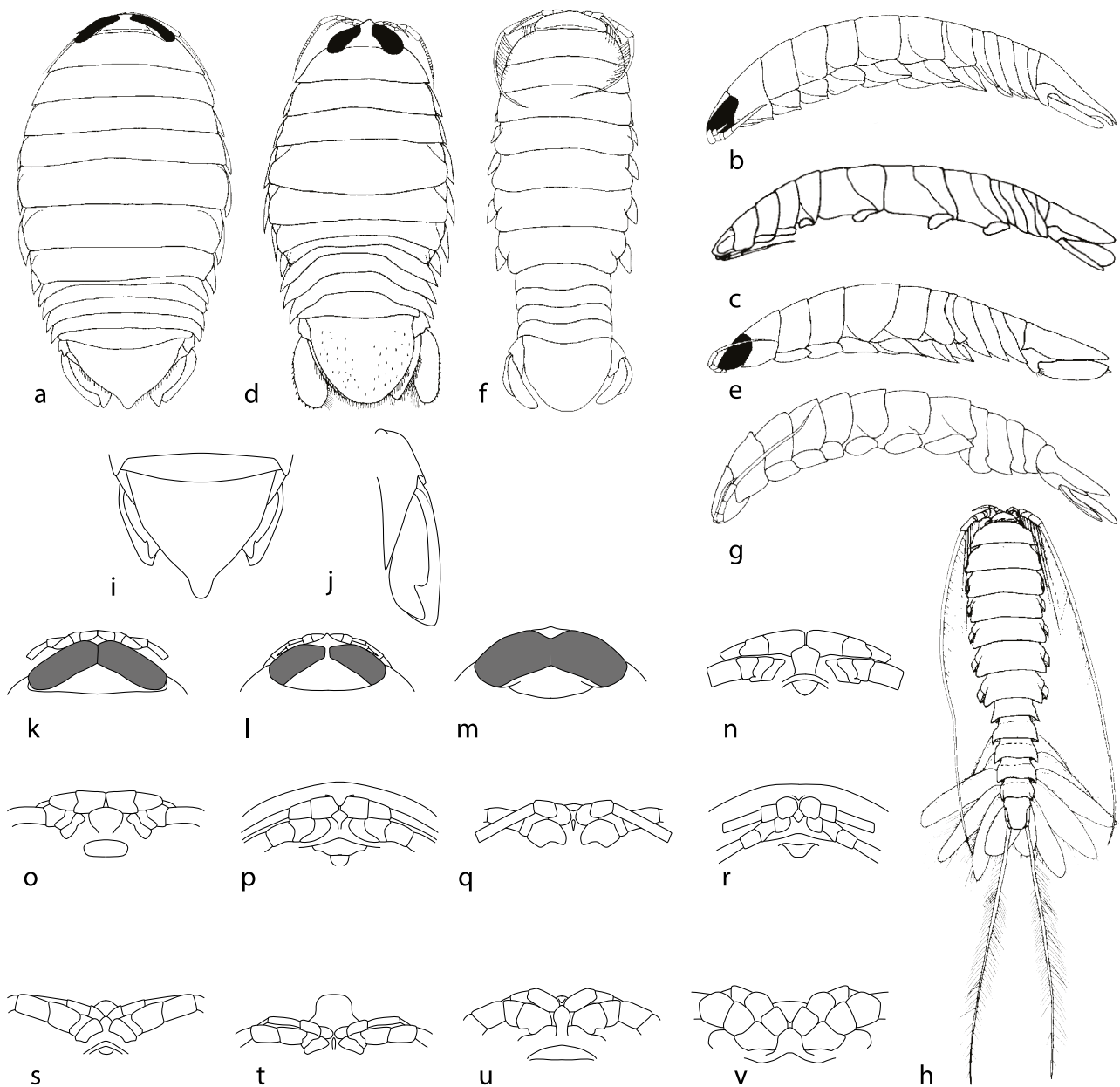


Figure 5.11. Aegidae. a, b, *Aega falklandica* Kussakin, 1967; c, *Alitropus typus* H. Milne Edwards, 1840; d, e, *Rocinela bonita* Bruce, 2009; f, g, *Syscenus kapoo* Bruce, 2009; h, *Xenuraega ptilocera* Tattersall, 1909. i, j, pleonite 5, pleotelson, uropods, *Aegapheles*. Head, eyes, antennae, dorsal: k, *Aegapheles*; l, *Aegiochus*; m, *Epulaega*. Antennulae, antennae, frontal lamina: n, *Aega*; o, *Aegapheles*; p, *Aegiochus*; q, *Alitropus*; r, *Epulaega*; s, t, *Rocinela*; u, *Syscenus*; v, *Xenuraega*.

respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes large, occupying 50% or more of head. Antennula peduncle article 1 close-set or together, articles 1 and 2 short, articles 1 and 2 cylindrical. Antennal peduncle articles 1–3 short, 4 and 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina slender, elongate, posteriorly narrow, forming stem. Mandible incisor unicuspid. Maxilliped endite absent; palp articles 3-articled, article 1

indivisibly fused. Pleopod 2 appendix masculina inserted sub-basally; pleopods 3 and 4 endopods smaller than exopod, without plumose marginal setae. Uropodal rami rounded, without distinct apex, rami exopod at oblique angle to endopod.

Freshwater, estuarine. Central Indo-Pacific (S and SE Asia, tropical Australia). 1 species (Ho and Tonguthai, 1992: figures of only species). *Alitropus typus* H. Milne Edwards, 1840 is an ectoparasitic pest on cultured fish in SE Asia (Bhakta et al., 2021; Shah et al., 2017; Wang et al., 2008).

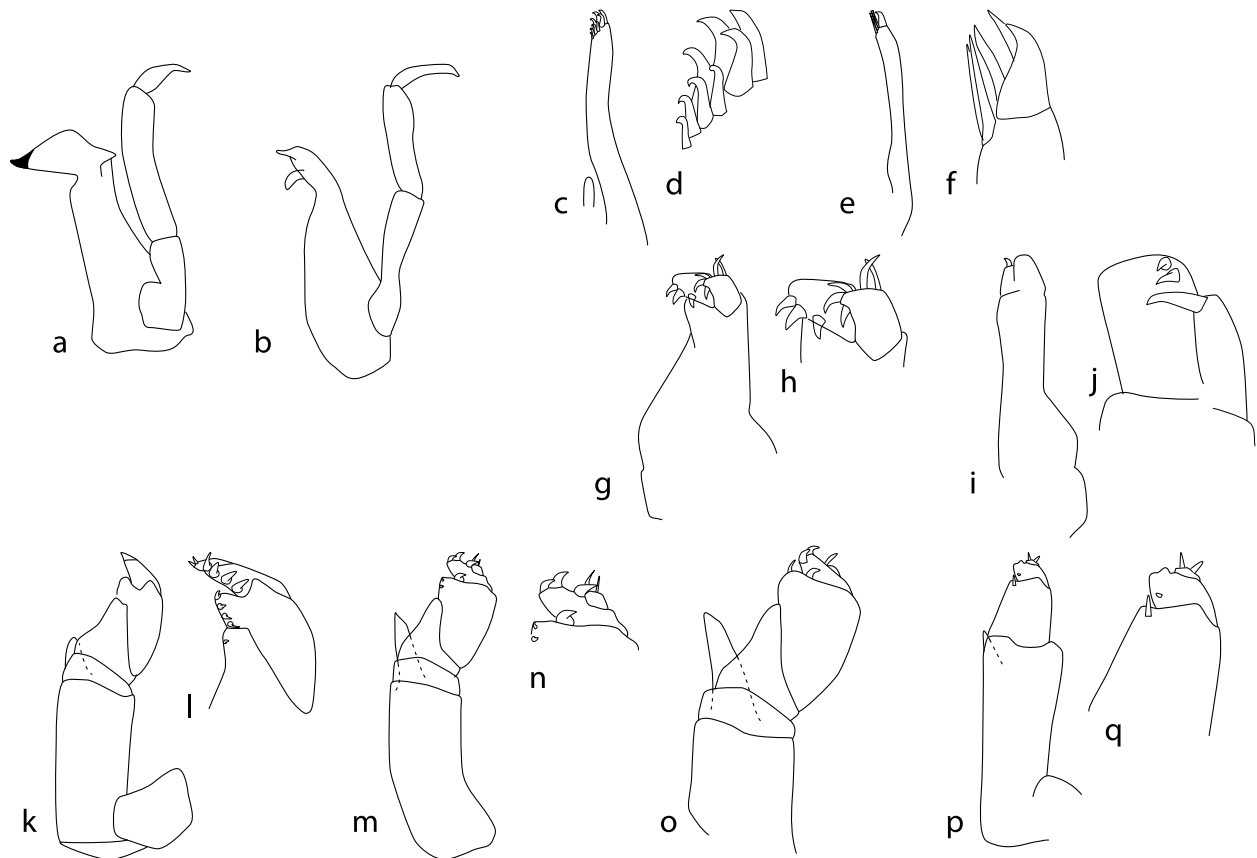


Figure 5.12. Aegidae. Mandible: a, *Aega*; b, *Rocinela*. Maxillula, detail of apex: c, d, *Aega*; e, f, *Rocinela*. Maxilla, detail of apex: g, h, *Aega*; i, j, *Rocinela*. Maxilliped, detail of apex: k, l, *Aega*; m, n, *Aegiochus*; o, *Epulaega*; p, q, *Rocinela*.

***Epulaega* Bruce, 2009**

Diagnosis. Body dorsally vaulted; rostral point small, anteroventral, rostral point apex shape acute. Coxae 5–7 as long or longer than respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes large, occupying 50% or more of head. Antennula peduncle article 1 close-set or together, articles 1 and 2 short, cylindrical. Antennal peduncle articles 1–3 short, 4 and 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina wide, posteriorly narrow, forming stem. Mandible incisor bicuspid. Maxilliped endite present; palp 5-articled, article 1 present. Pleopod 2 appendix masculina inserted basally; pleopods 3 and 4 endopods same size as exopod, with plumose marginal setae. Uropodal rami with distinct apex, rami coplanar.

Subtidal–slope (to 500 m); associated with sponges. Central Indo-Pacific, Temperate Southern Africa, Temperate Australasia. 5 species (Bruce, 2009).

***Rocinela* Leach, 1818**

Diagnosis. Body dorsally depressed; rostral point large, dorsal, rostral point apex shape broadly to narrowly rounded.

Coxae 5–7 as long or longer than respective pereonite. Pleon not distinctly narrower than pereonite 7; pleonite 5 lateral margins largely or wholly overlapped by pleonite 4. Eyes large, occupying 50% or more of head. Antennula peduncle article 1 close-set or together, articles 1 and 2 elongate, cylindrical. Antennal peduncle articles 1 and 2 short, 5 longest, articles 4 or 4 and 5 without long plumose setae. Frontal lamina slender, elongate, posteriorly narrow, forming stem. Mandible incisor unicuspid. Maxilliped endite present, or absent; palp articles 3-articled, article 1 indivisibly fused. Pleopod 2 appendix masculina inserted sub-basally; pleopods 3 and 4 endopods smaller than exopod, without plumose marginal setae. Uropodal rami rounded, without distinct apex, exopod at oblique angle to endopod.

Subtidal–abyssal (103–1976 m). Cosmopolitan. 42 species (Brusca and France, 1992: key to eastern Pacific species; Bruce, 2009: rediagnosis, key to 7 New Zealand species).

***Syscenus* Harger, 1880**

Diagnosis. Body dorsally vaulted; head not overlapped laterally by anterior angles of pereonite 1; rostral point small, anteroventral, rostral point apex shape narrowly rounded.

Coxae 5–7 shorter than respective pereonite. Pleon distinctly narrower than pereonite 7; pleonite 5 lateral margins free. Eyes usually absent (present in 2 species). Antennula peduncle article 1 close set or together, articles 1 and 2 elongate, articles 1 and 2 cylindrical. Antennal peduncle articles 1 and 2 short, 5 longest, articles 4 or 4 and 5 with long plumose setae. Frontal lamina wide, posteriorly wide, separate from clypeus. Mandible incisor unicuspid. Maxilliped endite absent; palp 3-articled or 2-articled, article 1 indivisibly fused. Penial processes flat lobes. Pleopod 2 appendix masculina inserted subproximally; pleopods 3 and 4 endopods smaller than exopod, without plumose marginal setae. Uropodal rami coplanar.

Mesopelagic (704–4609 m). Cosmopolitan. 9 species (Brandt and Andres, 2008; Bruce, 2009).

Xenuraega Tattersall, 1909

Diagnosis. Body dorsally vaulted; head not overlapped laterally by anterior angles of pereonite 1; rostral point small, anteroventral, apex narrowly rounded. Coxae 5–7 shorter than respective pereonite. Pleon distinctly narrower than pereonite 7; pleonite 5 lateral margins free. Eyes absent. Antennula peduncle article 1 close set or together, articles 1 and 2 elongate, articles 1 and 2 cylindrical. Antennal peduncle articles 1 and 2 short, 5 longest, articles 4 or 4 and 5 with long plumose setae. Frontal lamina wide, posteriorly wide, separate from clypeus. Mandible incisor unicuspid. Maxilliped endite absent; palp 3-articled or 2-articled, article 1 indivisibly fused. Penial processes flat lobes. Pleopod 2 appendix masculina inserted sub-basally; pleopods 3 and 4 endopods smaller than exopod, without plumose marginal setae. Uropod with one or both rami elongate (0.2–0.8 body length) or filamentous.

Mesopelagic (310–1250 m). Temperate Northern Atlantic, Temperate Northern Pacific. 2 species (Bruce, 1993; Shimomura and Bruce, 2019).

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Anuropidae Stebbing, 1893

Figure 5.13

Anuropids are unique in having the uropods concealed by the pleotelson, almost identical to pleopods 1–5 and presumably performing a respiratory function. The uropods do, however, move laterally as is typical in cymothoidans (Jansen, 1982). All species have been taken from midwater oceanic environments or at the surface from the guts of oceanic albatrosses and petrels (Lincoln and Jones, 1973; Sivertsen and Holthuis, 1980). Anuropids are probable symbionts of scyphozoans (Barham and Pickwell, 1969). Individuals are large isopods, up to 70 mm long.

Diagnosis. Eyes widely separated, lateral, sometimes small or absent. Antennula of 2 articles with second article expanded

and scalloped. Mandibular incisor blade-like; lacinia mobilis and spine row present; molar blade-like. Maxillipedal endite absent; palp of 1 article. Pereopod 1 subchelate, pereopods 2–7 ambulatory. Uropod folded ventrally below pleotelson, resembling pleopods.

Anuropus Beddard, 1893

Meso- and bathypelagic. Arctic, Temperate Northern Pacific, Western Indo-Pacific, Tropical Eastern Pacific, Temperate South America, Temperate Australasia, Southern Ocean. 10 species (Jansen, 1982; key to 7 species; Brandt and Retzlaff, 2002).

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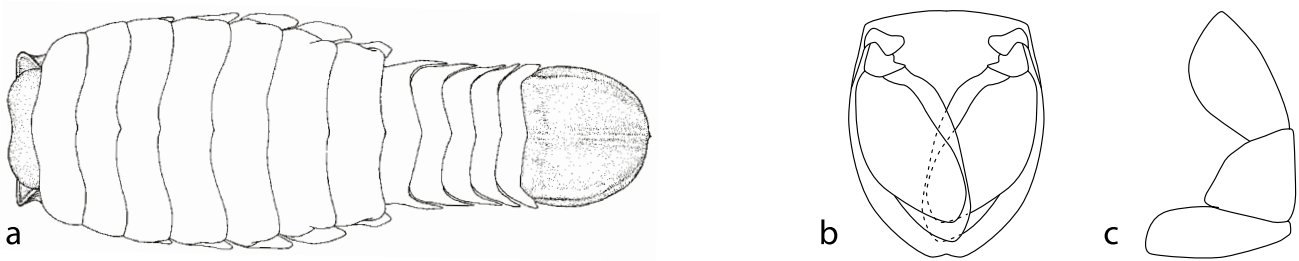


Figure 5.13. Anuropidae. a, *Anuropus pacificus* Lincoln and Jones, 1973. *Anuropus*: b, pleotelson, uropods, ventral view; c, maxilliped.

Barybrotidae Hansen, 1890

Figure 5.14

The only species *Barybrotus indus* Schioedte and Meinert, 1879 has long been considered a member of Aegidae but shares few characters with this family (Bruce, 2009). While the mouthparts are similar, they are not homologous. The maxilla is minute and the maxilliped has only four articles. The species is a probable micropredator of fishes.

Diagnosis. Eyes widely separated. Mouthparts forming buccal cone. Mandibular incisor broad, tridentate; lacinia mobilis and spine row absent; molar blade-like. Maxillula outer endite styliform, with flattened terminal robust setae. Maxilla with 1 endite with terminal sharp recurved robust setae. Maxillipedal endite absent; palp of 4 articles, article 2–4 with hooked robust setae. Pereopods 1–3 with prehensile dactylus, 4–7 natatory,

with flattened bases with fringe of plumose setae.

Barybrotus Schioedte and Meinert, 1879

Slope. Western and Central Indo-Pacific. 1 species (Pillai, 1967: figures; Bruce, 2009: rediagnosis of family).

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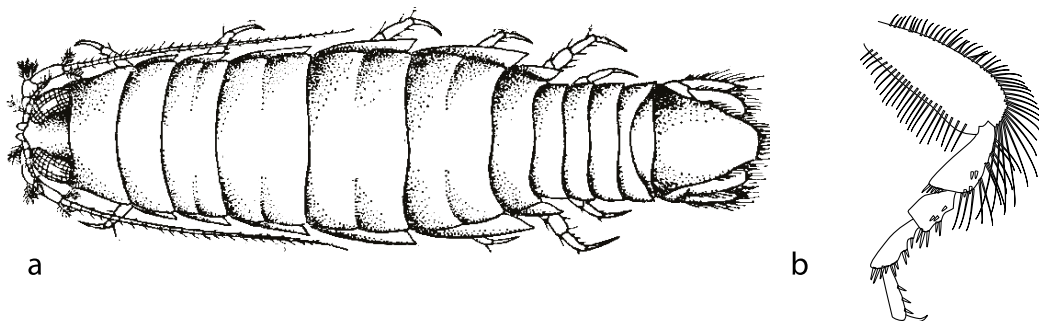


Figure 5.14. Barybrotidae, *Barybrotus indus* Schioedte and Meinert, 1879. a, habitus; b, pereopod 7.

Family Cirolanidae Dana, 1852

Figures 5.15–5.21

The Cirolanidae is the second-largest family of the aquatic Isopoda with 535 species in 64 genera, of which 466 species in 39 genera are marine or estuarine (on 31 December 2025). The family is found in all marine and estuarine waters. Almost 70 species belonging to 25 genera (plus others from predominantly “marine or brackish-water genera”) occur only in fresh water, springs, anchialine caves, marine “blue holes” and ground waters, largely in Central America, Europe and lands surrounding the Mediterranean. These genera are not included in this chapter.

Marine cirolanids occur worldwide, with highest diversity within the tropics, and are largely absent from polar waters. The family is dominated by four marine genera, *Cirolana* Leach, 1818, *Eurydice* Leach, 1816 (on sand beaches and subtidal sands), *Metacirolana* Kussakin, 1979 (particularly on coral reefs) and *Natanolana* Bruce, 1981; these large genera comprise 76% of all marine cirolanid species. The family is near exclusively scavenging and predatory in feeding habits (see Bruce 1986; Brusca et al., 1995), with two species known to be commensals of other invertebrates, namely *Cartetolana integra* (Miers, 1884) which associates with crinoids, and *Neocirolana hermitensis* (Boone, 1919) which associates with hermit crabs of the genus *Dardanus* and is probably an egg predator. The scavenging species, which occur in their thousands at times, play a probably important ecological role in marine environments from the intertidal to the upper continental slope. Cirolanids are generally scarce at depths greater than 500 m, and rare beyond 1000 m; 27 species (7%) are known from depths of 1000 m or more, and of these only nine species are known from more than 2000 m depth.

Diagnosis. Eyes widely separated, lateral, sometimes small or absent. Antennular peduncle 3-articled. Antenna with peduncle and flagellum distinct. Mouthparts not forming a buccal cone; mandibular incisor broad, tridentate, wider than 50% width (rarely less) of mandible body; lacinia mobilis indistinct or absent, spine row present; molar, large, bladeliike, anterior margin usually toothed. Maxillula lateral endite with 10–13 acute, often keratinised, robust setae. Maxilla with 1 or 2 endites. Maxillipedal endite as long as palp article 1; palp of 5 articles. Pereopods 1–3 ambulatory with robust dactyli or sub-prehensile; pereopods 4–7 ambulatory or natatory.

Implicit generic attributes. Body not elongate, < 4 times as long as wide. Dorsum vaulted, dorsal surface smooth. Pleon (pleonites 1–5, excluding pleotelson) short, < 20% body length, usually 10–14% body length, with 5 visible segments. Antennular peduncle articles 1–3 colinear; peduncle articles 1 and 2 short, article 3 longest. Antennal peduncle articles 1–3 short, 4 and 5 subequal in length and longest. Mandible incisor not massive; wide, > 0.55 times basal width. Pereopods 1–3 propodus ambulatory, dactylus less than 0.55 length of propodus; dactylus not extending to carpus when folded; inferior margin of merus without connate spines (spines without suture at base). Pleopod 1 rami not (rarely) operculate; endopod 0.50–0.68 as wide as exopod. Pleopods without respiratory branchiae. Pleopods 2–5 peduncle lateral margins without well-developed laminar lobe. Uropod peduncle posterior mesial margin produced. Uropod rami as long as mesial length of peduncle; endopod lateral margin without excision; exopod laminar, rami subequal in length. Pleotelson posterior margin without prominent spines.

Key to the marine and estuarine genera of Cirolanidae

Priority has been given to using characters that can be seen without dissection, so use of mouthparts has been minimised; the key is therefore not subjectively phylogenetic. Maxillipedal palp article 5 is either distally rounded (fig. 5.18l, n), or quadrate (fig. 5.18m), which can be used to confirm genus identity, with most genera of Eurydicinae showing a quadrate or subquadrate article 5.

BL = body length. The pleon refers to pleonites 1–5, excluding pleotelson. Five genera cannot be clearly placed within subfamilies and do not appear in the key. They are diagnosed under the heading “Unassigned to subfamily”: *Bathylana* Kensley, 1989; *Scutulana* Bruce, 1996; *Seychellana* Kensley and Schotte, 1994; *Sululana* Bruce and Shimomura, 2019; and *Xylolana* Kensley, 1979.

1. Clypeus ventrally flat (fig. 5.18c, d). Pleon short (< 20% BL, usually 10–14%) (fig. 5.15c, d). Pleonite 4 may be laterally enclosed by pleonite 3. Pleonite 5 laterally enclosed by pleonite 4 (fig. 5.16e, h, i) 2
- Clypeus with ventrally- or antero-ventrally projecting blade (best viewed laterally; fig. 5.18f, g, h). Pleon long (10–35% BL, usually 15–35% BL) (fig. 5.15f, g, j). Pleonites 4 and 5 with free lateral margins or with free posterolateral angle (pleonite 5 rarely laterally enclosed by pleonite 4) (fig. 5.16k, l) Eurydicinae ... 3
2. Pereopods 1–3 with ischium and merus superodistal angles strongly produced (fig. 5.19f), without blunt or molariform robust setae. Pereopods 5–7 with numerous slender setae and acute robust setae (fig. 5.19o); dactylus secondary unguis absent or slender (fig. 5.19j). Antennal peduncle articles 3 and 4 subequal in length and shorter than article 5 (fig. 5.17k) Conilerinae ... 13

- Pereopods 1–3 with ischium and merus superodistal angles not or weakly produced, inferior margins usually with blunt robust or molariform robust setae (fig. 5.19a). Pereopods 5–7 usually with few slender setae and acute robust setae (fig. 5.19k, l); dactylus secondary unguis usually robust (fig. 5.19h) or absent. Antennal peduncle articles 1–3 short, 4 and 5 subequal in length and longest (fig. 5.17j) Cirolaninae ... 19

Eurydicinae Stebbing, 1905

3. Antennular peduncle articles 2 and 3 set at right angles to article 1 (fig. 5.17l). Uropod peduncle posterior mesial margin not produced (fig. 5.21b). Male pleopod 2 endopod with appendix masculina attached mid-length on mesial margin (fig. 5.20m) *Eurydice*
- Antennular peduncle articles 1–3 colinear (fig. 5.17i, m). Uropod peduncle posterior mesial margin produced (fig. 5.21d) or not. Male pleopod 2 endopod with appendix masculina attached mesially or sub-basally (fig. 5.20j–l) 4
4. Pleon of 2 or 3 visible segments (short, 5–10% BL) (fig. 5.15e) *Colopisthus*
- Pleon of 4 or 5 visible segments (variable 10–35% BL) (e.g., fig. 5.15g, j) 5
5. Pleonite 5 laterally enclosed by pleonite 4 (fig. 5.16o, p) 6
- Pleonite 5 with free lateral margins, or free posterolateral point (fig. 5.16k, l) 8
6. Pleotelson lateral margins sinuate, posterior margins narrowly rounded (fig. 5.16o). Anterior pereopods with connate spines (marginal spines without suture at base) (fig. 5.19q) *Aphantolana*
- Not as above 7
7. Pleon 10–15% BL (fig. 5.15o). Antennular peduncle article 2 without process. Uropodal exopod cylindrical, exceeding endopod length, exopod 1.3–2.2 times as long as endopod (fig. 5.21a). Pleotelson posteriorly narrow, lateral margins concave (fig. 5.15o) *Atarbolana*
- Pleon 15–18% BL (fig. 5.15p). Antennular peduncle article 2 with prominent, posteriorly directed acute process (fig. 5.17n). Uropodal exopod laminar with lateral margin indented (fig. 5.21h), rami subequal in length. Pleotelson lateral margins evenly convex (linguiform) (fig. 5.15p) *Pseudaega*
8. Rostrum large, extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases, often anteriorly dilated (fig. 5.16c, d) 9
- Rostrum small or absent, not extending to anterior of margin antennula (fig. 5.15f, j) 11
9. Rostrum anteriorly truncate in dorsal view (fig. 5.16d). Adult male antennular peduncle dilated; antennular and antennal flagella extending beyond pleotelson posterior margin (fig. 5.15m) [pelagic; nektonic] *Pontogelos*
- Not as above 10
10. Pleonites 1 and 2 narrower than pleonites 3–5 (fig. 5.15a). Frontal lamina extended anteriorly, usually visible in dorsal view, not fusing or abutting rostrum. Rostrum acute, not anteriorly dilated (fig. 5.16q). Uropodal endopod lateral margin without excision. Head and pereonites 1 or 2 may have horn-like processes (fig. 5.15a) *Annina*
- Pleonites 1 and 2 subequal in width to pleonites 3–5 (fig. 5.15g). Frontal lamina extended anteriorly, usually visible in dorsal view, usually fusing or abutting rostrum. Rostrum truncate or anteriorly dilated (fig. 5.16c). Uropodal endopod lateral margin with excision. Head and pereonites 1 and 2 without horn-like processes (fig. 5.15g) *Exciorolana*
11. Frontal lamina ventral margin linear, blade-like (fig. 5.18k) *Pseudolana*
- Frontal lamina ventrally flat, wide anteriorly, posteriorly with stem (fig. 5.18h) 12
12. Pereopod 1 propodus subchelate (fig. 5.19e, i). Pereopods 2–7 slender, with few robust and slender setae (fig. 5.19n) *Metacirolana*
- Pereopod 1 ambulatory (fig. 5.19b). Pereopods 2–7 stout, with numerous robust and slender setae (fig. 5.19m) *Eurylana*

Conilerinae Kensley and Schotte, 1989

13. Uropodal endopod lateral margin with distinct notch (fig. 5.21g) 14
 – Uropodal endopod lateral margin without notch, inflected or convex (fig. 5.21e) 15
14. Frontal lamina short, as long as posterior width, triangular (fig. 5.18j) *Orphelana*
 – Frontal lamina elongate, > 3 times as long as posterior width (fig. 5.18i) *Politolana*
15. Body elongate, 4.0–5.6 times as long as wide (fig. 5.15l). Pleopod 1 peduncle quadrate or elongate, 0.9–1.3 as long as wide (fig. 5.20e, f). Pleopod 1 exopod or both rami operculate (fig. 5.17g, h) 16
 – Body not elongate, < 4.0 times as long as wide (fig. 5.15k). Pleopod 1 peduncle usually < 0.9 times as long as wide (fig. 5.20g). Pleopod 1 rami not operculate (fig. 5.17e) 17
16. Pleopod 1 peduncle 1.3 times as long as wide (fig. 5.20e); rami subequal, both rami forming operculum (fig. 5.17h) *Conilera*
 – Pleopod 1 peduncle quadrate, about as long as wide; exopod large, forming operculum (fig. 5.20f) *Conilorpheus*
17. Frontal lamina broad (2.4–4.0 times posterior width), anteriorly flat, posteriorly with ventrally directed process (horn) (fig. 5.18e). Pleonite 3 laterally large, with carina (fig. 5.16j) *Dolicholana*
 – Frontal lamina slender (3.8–7.6 times posterior width) (fig. 5.18i), ventrally flat, ventrally without posteriorly directed process. Pleonite 3 not laterally large, without lateral carina (fig. 5.16m) 18
18. Pereopod 1 dactylus haptorial (as long as propodal palm) (fig. 5.19g) *Sintorolana*
 – Pereopod 1 dactylus ambulatory, < 0.7 length of propodal palm (fig. 5.19f) *Natatolana*

Cirolaninae Dana, 1852

19. Body length “huge”, adults 70–>300 mm (fig. 5.15b). Pleopods with respiratory branchiae (fig. 5.20c, o) 20
 – Body length “normal”, adults 3–30 mm, rarely to 70 mm. Pleopods without respiratory branchiae (fig. 5.20a, b, d) 21
20. Body length 70–80 mm. Pleopod branchiae on pleopod 1 peduncle and at base of pleopods 1 and 2 exopods (fig. 5.20o). Pleotelson posterior margin without prominent spines *Parabathynomus*
 – Body length 70–>300 mm. Pleopod branchiae at base of pleopods 1 and 2 exopods only (fig. 5.20c). Pleotelson posterior margin with prominent spines (fig. 5.15b) *Bathynomus*
21. Mandible large, conspicuous in dorsal view. Frontal lamina dorsally displaced, visible in dorsal view (fig. 5.15h) (monotypic South African endemic) *Gnatholana*
 – Not as above. Mandible not large, not visible in dorsal view. Frontal lamina not dorsally displaced 22
22. Pleopod 1 exopod or both rami operculate (fig. 5.17f–h) 23
 – Pleopod 1 rami not operculate (fig. 5.17d, e) 24
23. Pleonite 5 as wide or slightly wider than pleotelson anterior margin (fig. 5.15d, l). Pleopod 1 exopod forming operculum (fig. 5.17g) *Oncilorpheus*
 – Pleonite 5 distinctly narrower than pleotelson anterior margin (fig. 5.17o). Pleopod 1 exopod and endopod forming operculum (fig. 5.17f) *Calyptolana*
24. Pleonite 3 epimeron broad, expanded, with setose longitudinal carina, extending posteriorly beyond pleonite 5 (fig. 5.16e, n). Anterior margin of head medially indented, without rostrum (fig. 5.16a) 25
 – Pleonite 3 epimeron not markedly expanded, not extending or extending posteriorly beyond pleonite 5 (fig. 5.16f, h, i). Anterior margin of head not medially indented, with or without rostrum (fig. 5.16b) 26
25. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae (fig. 5.19p). Pleopod 1 peduncle quadrate (fig. 5.20i). Penial process absent, openings flush with sternite 7 *Plakolana*
 – Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae (fig. 5.19k). Pleopod 1 peduncle shorter than wide (fig. 5.20a). Penial processes quadrate (fig. 5.17a) *Aatolana*

26. Head fused to pereonite 1. Rostrum and frontal lamina both produced, forming 2 horn-like processes (fig. 5.18b). Pleonite 3 epimeron dorsoventrally expanded (fig. 5.16g) *Ceratolana*
- Head not fused to pereonite 1 (fig. 5.16b). Rostrum small or absent, frontal lamina not strongly produced (fig. 5.18a, c, d, g). Pleonite 3 epimeron not dorsoventrally expanded (fig. 5.16f, h, i) 27
27. Frontal lamina with 2 parts, flat anterior part and ventrally produced posterior part (fig. 5.18a). Pleonite 3 epimeron with ventral margin with ventral blade-like process (fig. 5.16f). Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe (fig. 5.20k) *Booralana*
- Frontal lamina ventral surface all flat (fig. 5.18c, d, g). Pleonite 3 ventrolateral margin without process (fig. 5.16h, i). Pleopod peduncles lateral margin without laminar lobe (fig. 5.20j, l, n) 28
28. Pleopod 1 peduncle quadrate or subquadrate (c. 0.75–1.0 times as long as wide) (fig. 5.20h, j) 29
- Pleopod 1 peduncle short (0.45–0.70 times as long as wide) (fig. 5.20d) 30
29. Pleopod 1 endopod narrow (0.26–0.42 times width of exopod) (fig. 5.20b). Appendix masculina submesially attached (fig. 5.20j). Penial processes distally rounded, flat (fig. 5.17b) *Baharilana*
- Pleopod 1 endopod 0.62–0.68 times as wide as exopod (fig. 5.20h). Appendix masculina basally attached. Penial processes papilliform or absent *Odysseylana*
30. Dorsum strongly vaulted (fig. 5.16r). Mandible massive, prominent in ventral view, incisor bicuspid, heavily keratinised (fig. 5.18o) [associate of crinoids] *Cartetolana*
- Dorsum not strongly vaulted. Mandible not massive (fig. 5.18p–r), left incisor tricuspid (fig. 5.18p), not heavily keratinised 31
31. Dorsum flattened. Head widest anteriorly, anterior margin straight (fig. 5.15i). Pereopod 1 robust, propodus subprehensile, 0.8 times as wide as long, dactylus extending to carpus when folded (fig. 5.19c). Appendix masculina unknown *Hansenolana*
- Dorsum vaulted. Head widest mid-length, anterior margin convex (fig. 5.16b). Pereopod 1 propodus stout, c. 0.55 times as wide as long, dactylus not extending to carpus when folded (fig. 5.19a). Appendix masculina basal (fig. 5.20l) or sub-basal 32
32. Mandible incisor narrow, less than half basal width (fig. 5.18r) (head therefore appearing relatively narrow). Uropodal endopod lateral margin with or without prominent excision on lateral margin (fig. 5.21f) *Neocirolana*
- Mandible incisor more than half basal width (fig. 5.18p) (head not appearing relatively narrow). Uropodal endopod lateral margin without prominent excision (fig. 5.21i) 33
33. Pereopod 1 merus inferior margin without molariform robust setae; dactylus with slender secondary unguis (fig. 5.19d). Frontal lamina posteriorly narrowed (abutting clypeus) (fig. 5.18g). Penial processes as flat articulating lobes *Limicolana*
- Pereopod 1 merus inferior with molariform robust setae (fig. 5.19a); dactylus with stout secondary unguis (fig. 5.19h). Frontal lamina posteriorly wide or slightly narrower than at mid-length (fig. 5.18c,d). Penes usually opening flush with sternite 7 (fig. 5.17c) *Cirolana*

Subfamily Conilerinae Kensley and Schotte, 1989

Diagnosis. Clypeus ventrally flat. Pleon short, < 20% BL, usually 10–14%. Pleonite 4 sometimes laterally enclosed by pleonite 3. Pleonite 5 laterally enclosed by pleonite 4. Pereopods 1–3 with ischium and merus superodistal angles strongly produced, without blunt or molariform robust setae. Pereopods 5–7 with numerous slender setae and acute robust setae; dactylus secondary unguis absent or slender. Antennal peduncle articles 3 and 4 subequal in length and shorter than article 5.

Conilera Leach, 1815

Diagnosis. Body elongate, 4.0–6.5 times as long as wide; BL 7–24 mm. Head anterior margin medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, or absent. Pleon < 20% BL, usually 10–14% BL; pleonites 1 and 2 subequal in width to pleonites 3–5; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 acute, not extending beyond

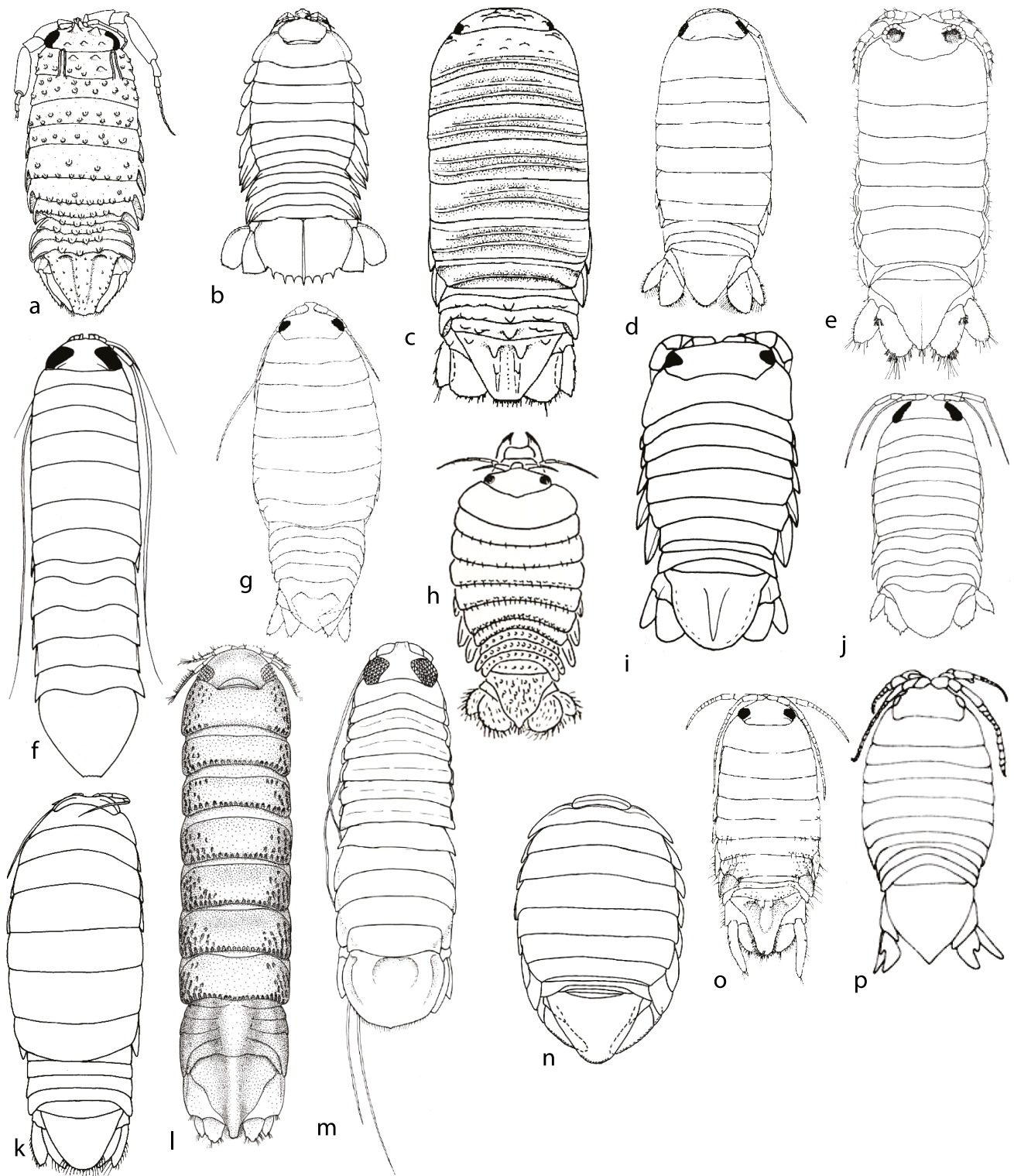


Figure 5.15. Cirolanidae. a, *Annina lacustris* Budde-Lund, 1908; b, *Bathynomus lowryi* Bruce and Bussarawit, 2004; c, *Cirolana cristata* Bruce, 1995; d, *Cirolana kokoru* Bruce, 2004; e, *Colopisthus parvus* Richardson, 1902; f, *Eurydice wongat* Bruce, 1986; g, *Excirolana chiltoni* Richardson, 1909; h, *Gnatholana mandibularis* Barnard, 1920; i, *Hansenolana anisopous* Stebbing, 1900; j, *Metacirolana serrata* (Bruce, 1980); k, *Natatolana rekoahu* Bruce, 2003; l, *Oncilorpheus jerrybarnardi* Brusca, Wetzter and France, 1995; m, *Pontogelos asegekeros* Stebbing, 1910; n, *Scutulana pezata* Bruce, 1996; o, *Atarbolana exoconta* Bruce and Javed, 1987; p, *Pseudaega punctata* Thomson, 1884.

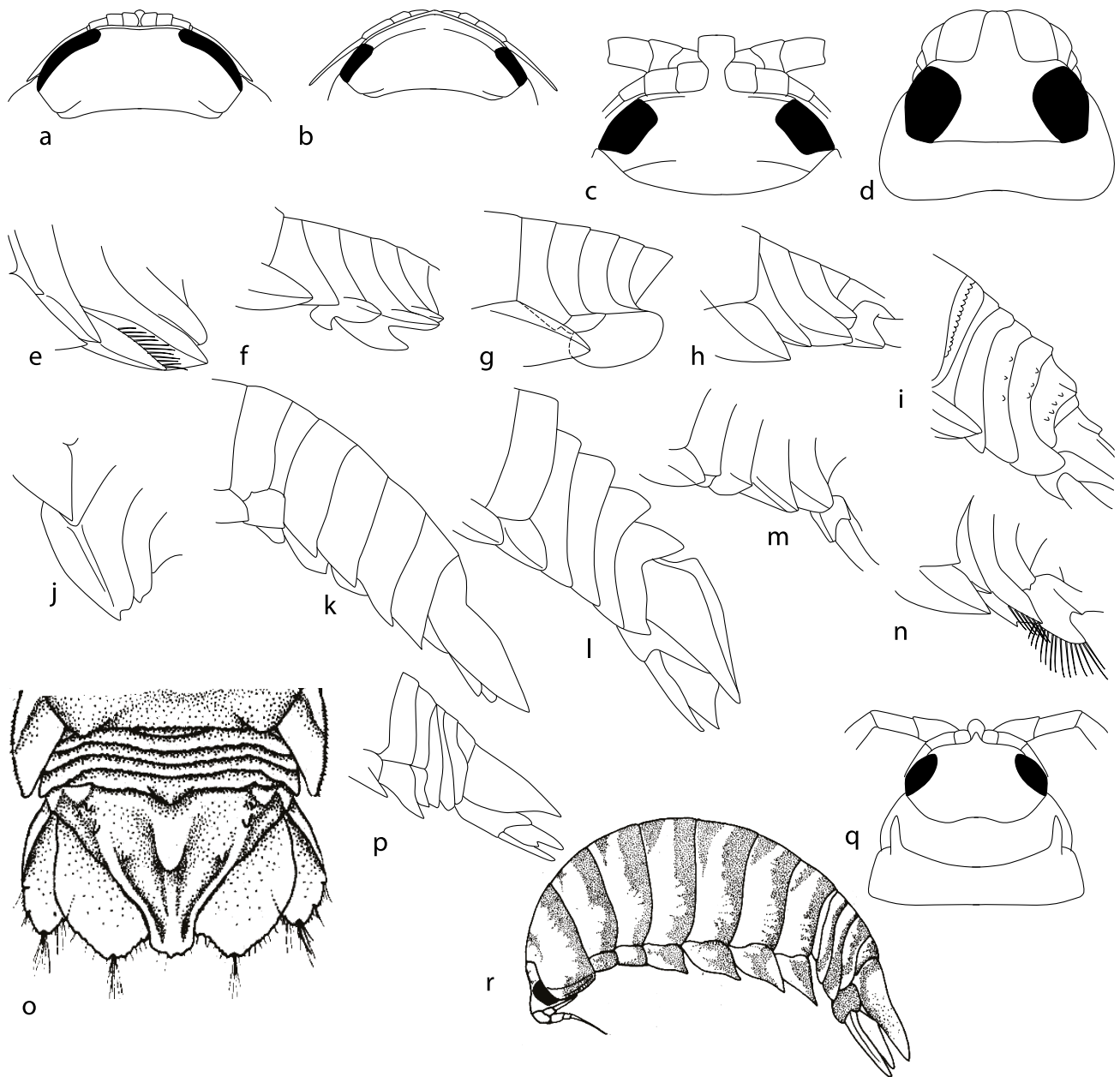


Figure 5.16. Cirolanidae. Head, dorsal view: a, *Aatolana rapax* Bruce, 1993; b, *Cirolana kokoru* Bruce, 2004; c, *Excirolana orientalis* (Dana, 1852); d, *Pontogelos asegokeos* Stebbing, 1910. Pleon lateral view: e, *Aatolana rapax* Bruce, 1993; f, *Booralana bathynella* (Bruce, 1981); g, *Ceratolana papuae* Bowman, 1977; h, *Cirolana kokoru* Bruce, 2004; i, *Cirolana parawongat* Rodcharoen and Bruce, 2021; j, *Dolicholana enigma* Keable, 1999; k, *Eurydice acuticauda* Bruce, 1981; l, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021; m, *Natatolana rekohu* Bruce, 2003; n, *Plakolana accola* Bruce, 1993; o, *Aphantolana costaricensis* Moore and Brusca, 2003, pleon and pleotelson, dorsal view; p, *Pseudaega punctata* Thomson, 1884, pleon, lateral view; q, *Annina fustis* Bowman and Iliffe, 1991, head, dorsal view; r, *Cartetolana integra* (Miers, 1884), habitus, lateral view.

posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded, or with apical point; lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest; flagellum not extending

beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly, usually visible in dorsal view, not fused to or abutting rostrum; ventral surface flat; narrowing posteriorly, not stem-like, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus secondary unguis not known; merus inferior margin without molariform

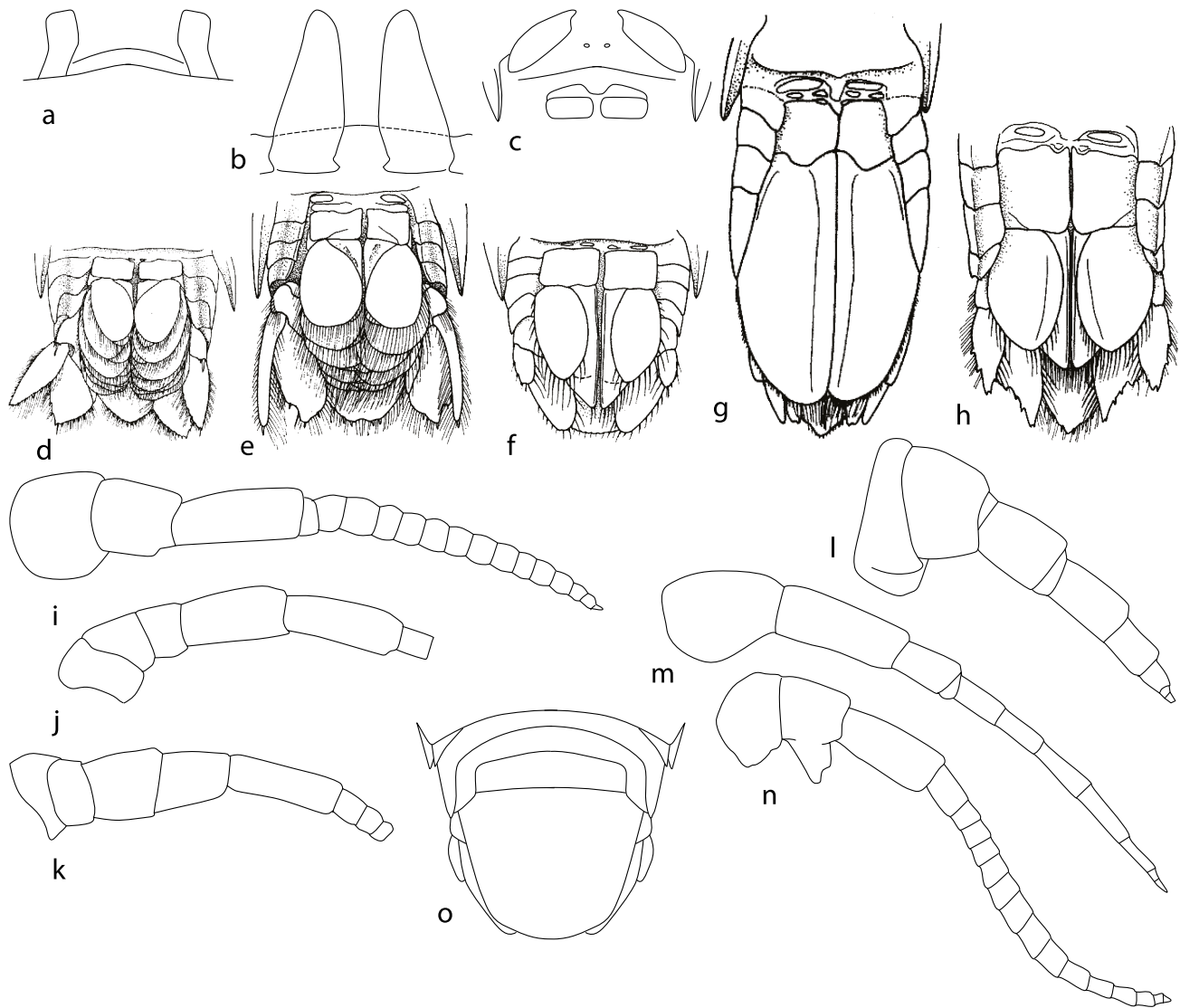


Figure 5.17. Cirolanidae. Penial processes: a, *Aatolana rapax* Bruce, 1993; b, *Baharilana richmondi* Bruce and Svavarsson, 2004; c, *Cirolana kokoru* Bruce, 2004, sternite 7. Pleon, ventral view: d, *Cirolana cranchii* Leach, 1818; e, *Politolana concharum* (Stimpson, 1853); f, *Calyptolana hancocki* Bruce, 1985; g, *Oncilorpheus stebbingi* Paul and Menzies, 1972; h, *Conilera cylindracea* (Montagu, 1805). i, *Cirolana kokoru* Bruce, 2004, antennula; j, *Cirolana kokoru* Bruce, 2004, antenna peduncle; k, *Natatolana rekohu* Bruce, 2003, antennal peduncle; l, *Eurydice kenselyi* Bruce and Soares, 1996, antennula; m, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021, antennula; n, *Pseudaega punctata* Thomson, 1884, antennula; o, *Calyptolana hancocki* Bruce, 1985, pleon, dorsal.

robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus with long robust setae and long slender setae. Penes low tubercles. Pleopod 1 peduncle 1.3 times as long as wide; rami operculate, with both rami forming operculum; endopod not narrow, 0.50–0.7 times as wide as exopod. Male pleopod 2 appendix masculina attached basally, sub-basally, or submesially.

Subtidal–slope (1–510 m). North Atlantic, Tropical Eastern Pacific (Americas). 3 species (Brusca et al., 1995).

***Conilorpheus* Stebbing, 1905**

Diagnosis. Body elongate, 6 times as long as wide; dorsal surfaces smooth, with or without nodules; BL 6–10 mm, rarely longer. Head anterior margin with rostrum. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view, acute, not anteriorly dilated. Pleon < 20% BL, usually 10–14% BL, with 2 or 3 visible segments; pleonites 3 and 4 not extending beyond posterior margin of pleonite 5; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson

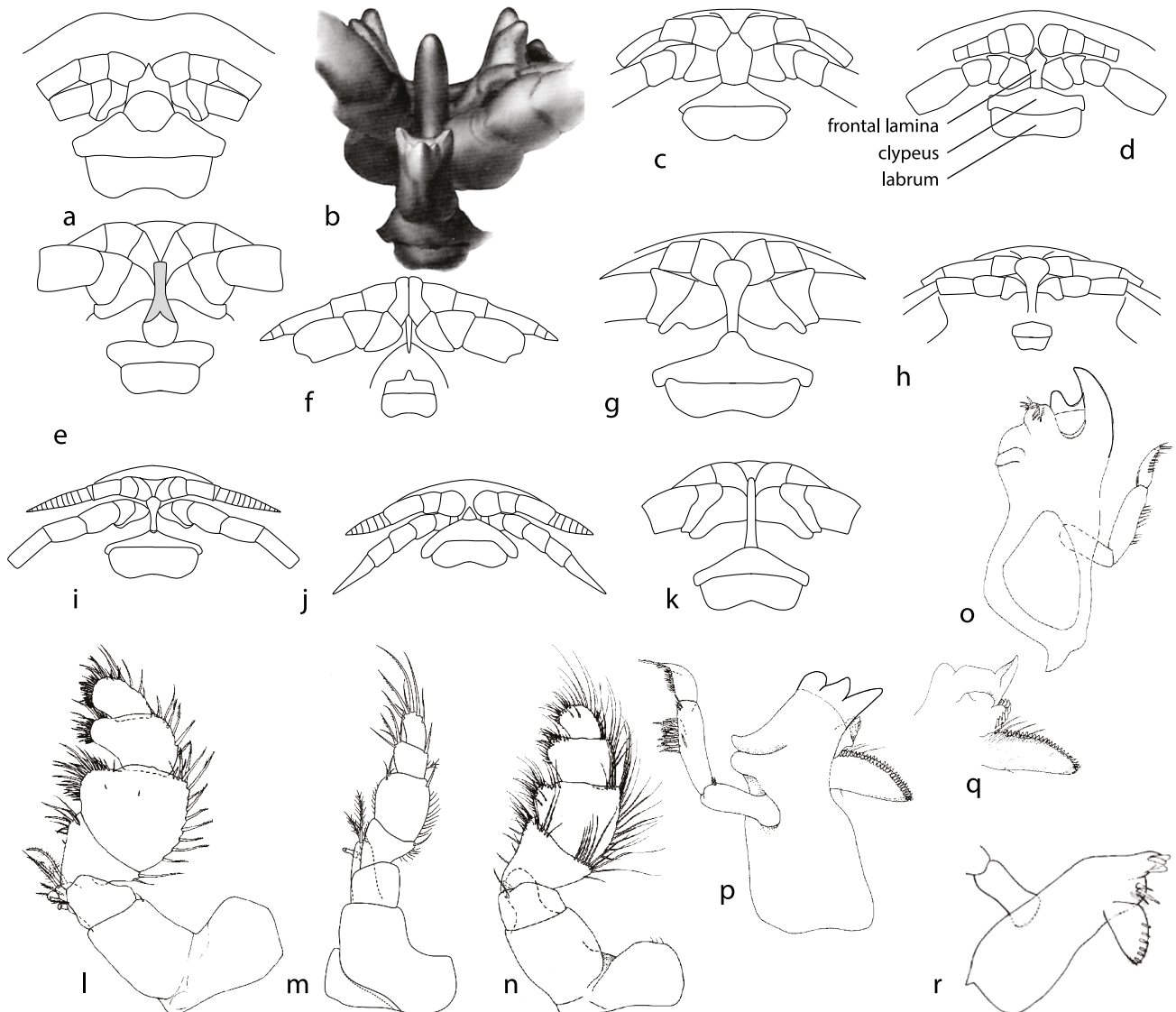


Figure 5.18. Cirolanidae. Frons (comprising rostrum, antennulae, antennae, frontal lamina, clypeus and labrum): a, *Booralana wundurra* Bruce, 1986; b, *Ceratolana papuae* Bowman, 1977; c, *Cirolana kokoru* Bruce, 2004; d, *Cirolana merlion* Sidabalok and Bruce, 2018; e, *Dolicholana elongata* Milne-Edwards, 1840; f, *Eurydice longicornis* (Studer, 1882); g, *Limicolana dinjerra* Bruce, 1986; h, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021; i, *Natatolana rekohu* Bruce, 2003; j, *Orphelana perplexa* Bruce, 1981; k, *Pseudolana towrae* Bruce, 1983. Maxilliped: l, *Cirolana kokoru* Bruce, 2004; m, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021; n, *Limicolana dinjerra* Bruce, 1986. Mandible: o, *Cartetolana integra* (Miers, 1884); p, q, *Cirolana kokoru* Bruce, 2004 (right, left); r, *Neocirolana salebra* Bruce, 1994.

linguiform; posterior margin narrowly rounded or truncate; lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest; flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly usually visible in dorsal view, not fused to or abutting rostrum, ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 merus superodistal angle moderately produced. Pereopods 2–7 usually with slender

setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus with long robust setae and long slender setae. Pleopod 1 peduncle about as long as wide; rami operculate (not indurate); with exopod forming operculum; endopod narrow, 0.26–0.45 times width of exopod. Uropod exopod notably shorter in length than endopod.

Subtidal, shelf (1–41 m). Western and Central Indo-Pacific (South Africa, Sri Lanka and Thailand). 3 species. The genus is almost certainly not monophyletic and species other than the type species are inadequately described. Diagnosis primarily based on type species from redescription by Bruce and Olesen (2002).

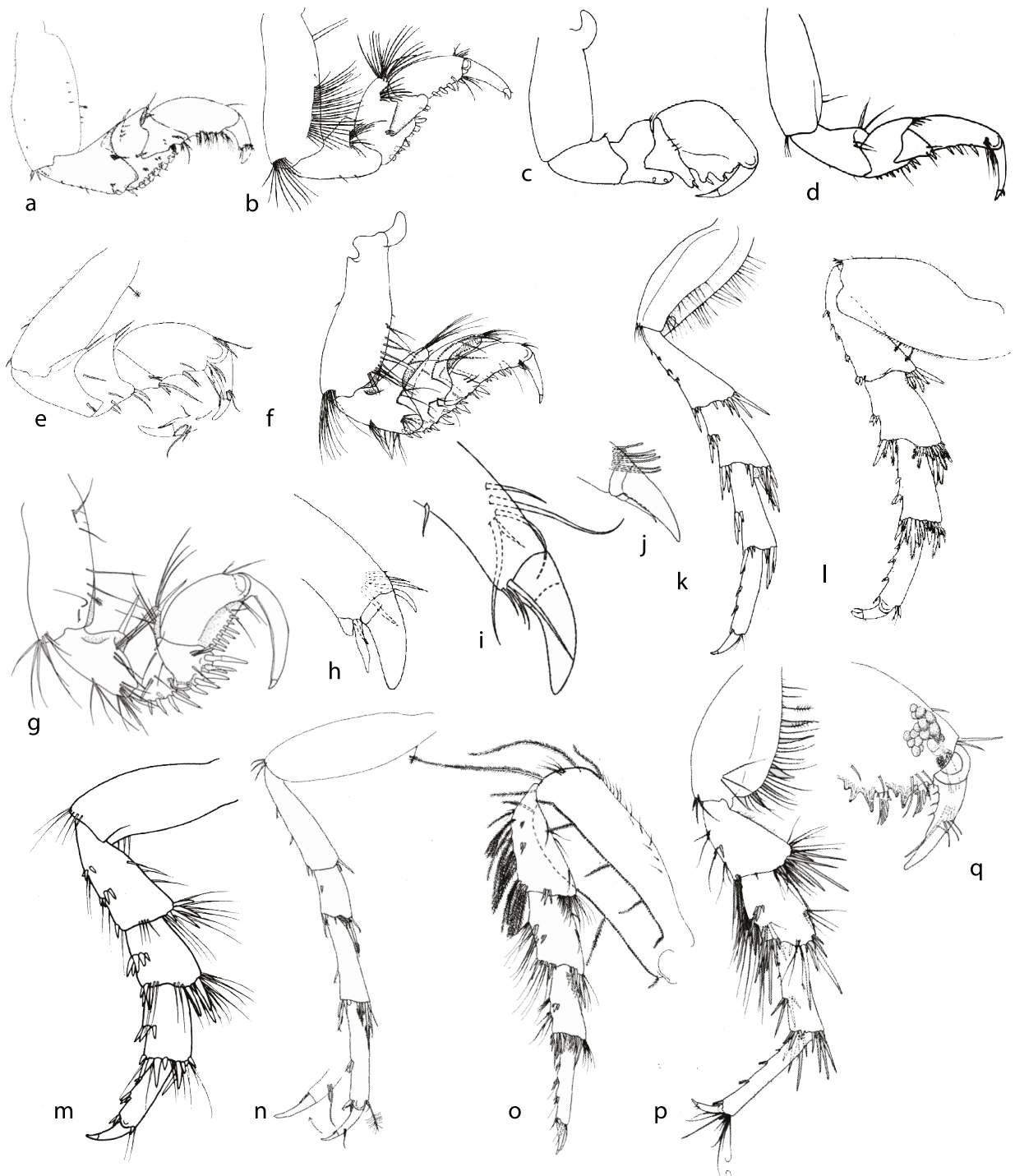


Figure 5.19. Cirolanidae. Pereopod 1: a, *Cirolana kokoru* Bruce, 2004; b, *Eurylana arcuate* (Hale, 1925); c, *Hansenolana anisopous* Stebbing, 1900; d, *Limicolana dinjerra* Bruce, 1986; e, *Metacirolana lombok* Sidabalok and Bruce, 2018; f, *Limicolana dinjerra* Bruce, 1986; g, *Sintorolana atrox* Bruce, 1996. Pereopod 1, dactylar unguis: h, *Cirolana kokoru* Bruce, 2004; i, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021; j, *Natatolana rekohu* Bruce, 2003. Pereopod 7: k, *Aatolana rapax* Bruce, 1993; l, *Cirolana kokoru* Bruce, 2004; m, *Eurylana arcuate* (Hale, 1925); n, *Metacirolana lombok* Sidabalok and Bruce, 2018; o, *Natatolana rekohu* Bruce, 2003; p, *Plakolana accola* Bruce, 1993; q, *Aphantolana costaricensis* Moore and Brusca, 2003.

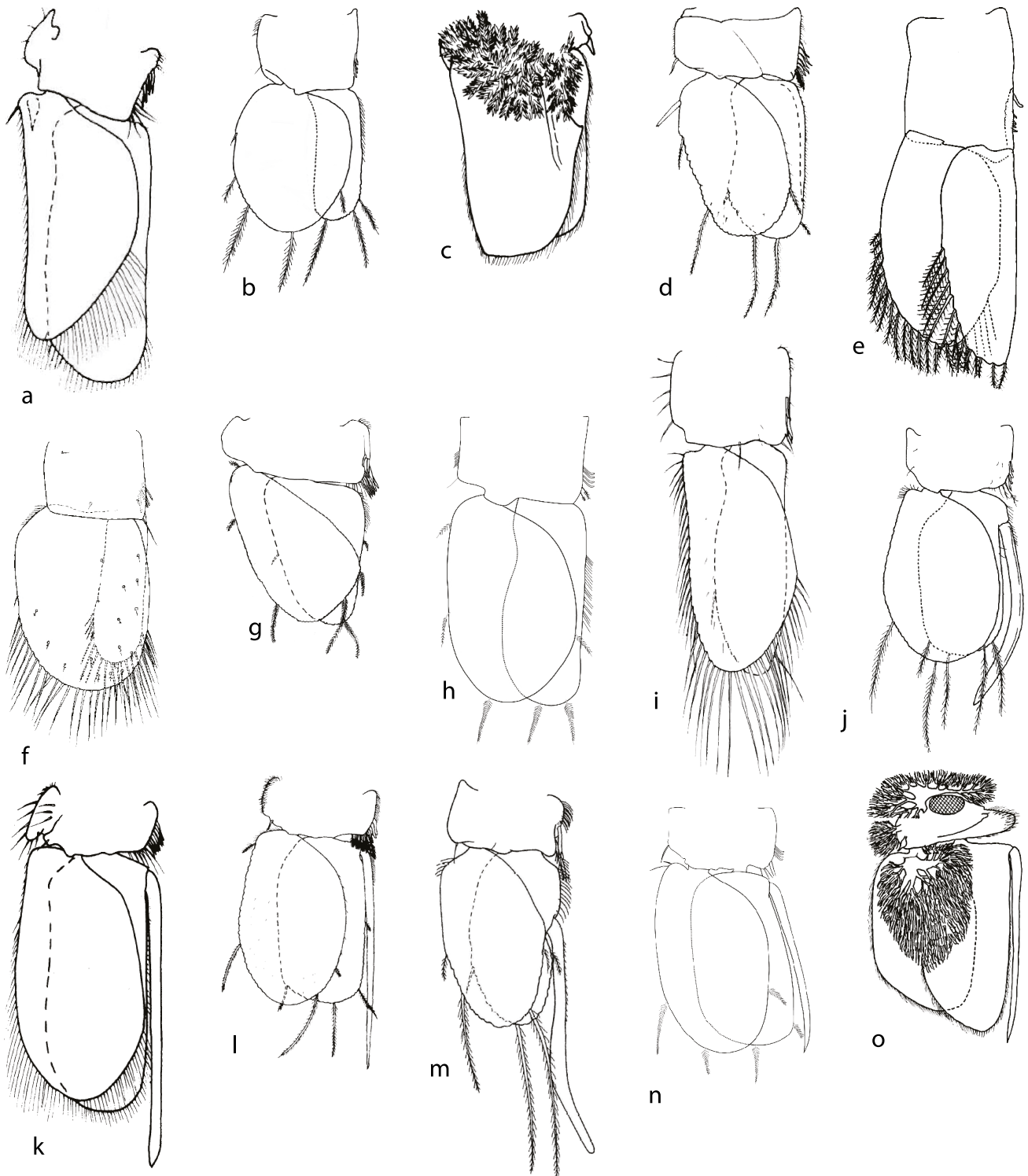


Figure 5.20. Cirolanidae. Pleopod 1: a, *Aatolana rapax* Bruce, 1993; b, *Baharilana richmondi* Bruce and Svarrsson, 2004; c, *Bathynomus immanis* Bruce, 1986; d, *Cirolana kokoru* Bruce, 2004; e, *Conilera bullisi* Brusca et al., 1995; f, *Conilorpheus herdmani* Stebbing, 1905; g, *Natatolana rekohu* Bruce, 2003; h, *Odysseylana temesak* Sidabalok and Bruce, 2015; i, *Plakolana accola* Bruce, 1993. Male pleopod 2: j, *Baharilana richmondi* Bruce and Svarrsson, 2004; k, *Booralana bathynella* (Bruce, 1981); l, *Cirolana kokoru* Bruce, 2004; m, *Eurydice kensleyi* Bruce and Soares, 1996; n, *Odysseylana temasek* Sidabalok and Bruce, 2015; o, *Parabathynomus natalensis* Barnard, 1924.

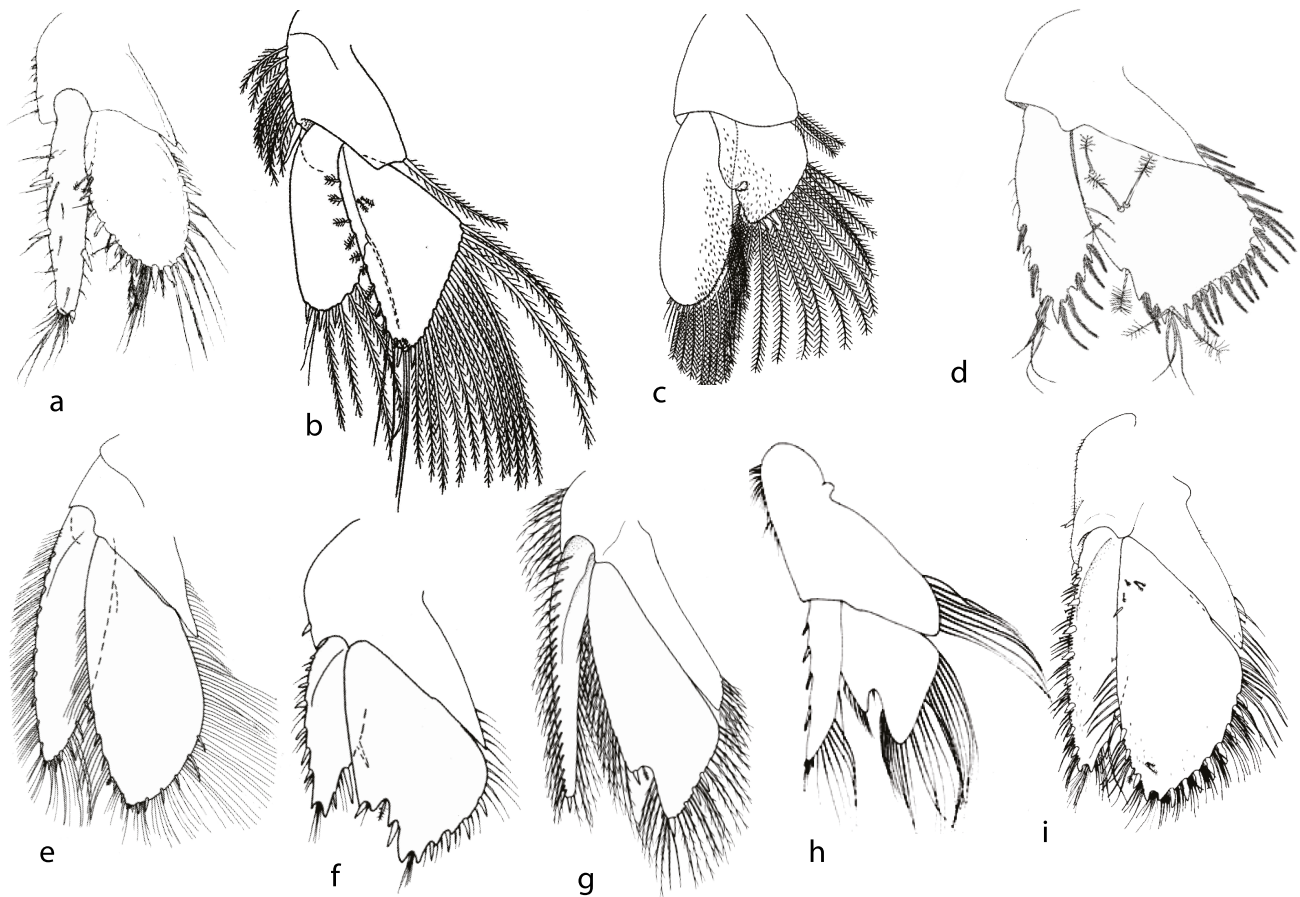


Figure 5.21. Cirolanidae. Uropod: a, *Atarbolana exoconta* Bruce and Javed, 1987; b, *Eurydice kensleyi* Bruce and Soares, 1996; c, *Excirrolana braziliensis* Richardson, 1912 (Brusca et al. 1995); d, *Metacirolana nicosmiti* Bruce and Rodcharoen, 2021; e, *Natatolana rekoahu* Bruce, 2003; f, *Neocirolana excisa* (Richardson, 1910); g, *Politolana concharum* (Stimpson, 1853); h, *Pseudaega melanica* Jansen, 1978; i, *Cirolana kokoru* Bruce, 2004.

***Dolicholana* Bruce, 1986**

Diagnosis. Body about 3–4 times as long as wide; BL 6–40 mm. Head anterior margin without rostrum, medially indented. Pleon < 20% BL, usually 10–14% BL, with 4 or 5 visible segments; pleonite 3 epimeron broad, acute, dorsoventrally expanded, with longitudinal carina, extending posteriorly or not beyond pleonite 5; posterolateral margin of pleonite 4 acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin sometimes overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, < 0.9 times width of anterior margin of pleotelson. Pleotelson posterior margin with apical point or broadly rounded; lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest; flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina extended anteriorly, usually visible in dorsal view, not fused to or abutting rostrum; ventral surface flat or

posterior margin with downwardly directed process (horn); posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with or without secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus with long robust setae and long slender setae. Penes usually absent. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached basally, sub-basally, or submesially.

Subtidal–slope (6–508 m). Tropical Atlantic (Brazil), Indo West-Pacific. 5 species (Bruce 1986; Keable, 1999a; Paiva and Souza-Filho, 2015, 2023a).

***Natanolana* Bruce, 1981**

Diagnosis. Body dorsal surfaces polished in appearance or sparsely punctate; BL 8–40 mm. Head anterior margin with or without rostrum, medially or not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view. Pleon < 20% BL, usually 10–14% BL, with 4 or 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, narrowly rounded or acute; posterolateral margin of pleonite 4 narrowly rounded or acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson linguiform, lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest; flagellum usually not extending posteriorly beyond pereonite 3 but may extend beyond posterior of pleotelson. Frontal lamina extended anteriorly, slightly visible or not visible in dorsal view, slender (3.8–7.6 times posterior width), ventrally flat, without posteriorly directed process; posteriorly as wide or wider than at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae. Penes absent or flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally. Uropod endopod lateral margin with or without prominent excision.

Subtidal–abyssal (1–6000 m). Cosmopolitan. 75 species (Keable, 2006; Paiva and Souza-Filho, 2023a).

***Orphelana* Bruce, 1981**

Diagnosis. Body dorsum strongly vaulted; BL 11 mm. Head anterior margin widest anteriorly; anterior margin without rostrum, not medially indented. Pleon 14% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, rounded; posterolateral margin of pleonite 4 rounded, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, < 0.9 width of anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina short (as long as posterior width), triangular, not visible in dorsal view, ventral surface flat. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae. Penes absent. Pleopod 1 peduncle quadrate, about as long as wide; rami not

operculate; endopod narrow, 0.4 times width of exopod. Male pleopod 2 appendix masculina attached submesially. Uropod endopod lateral margin with prominent excision.

Shelf (15 m). Temperate Australasia (Victoria, Australia). 1 species (Bruce, 1986; rediagnosis).

***Politolana* Bruce, 1981**

Diagnosis. Body elongate, 4.0–6.5 times as long as wide; dorsal surfaces smooth, polished or sparsely punctate; BL 9–46 mm. Head anterior margin markedly widest anteriorly; anterior margin without rostrum, medially indented. Pleon 6–15% BL, with 3–5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 4; posterolateral margin of pleonite 4 narrowly rounded, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin varied, narrowly rounded, truncate, medially indented, with or without apical point; lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest; flagellum not extending beyond pereonite 2. Frontal lamina extended anteriorly, slightly or not visible in dorsal view, elongate, > 3 times as long as posterior width; ventral surface flat, narrowest at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally (where described). Uropod endopod lateral margin with prominent excision.

Shelf, slope (9–1301 m). Tropical and temperate Atlantic, Central Indo-Pacific. 15 species (Paiva and Souza-Filho, 2023a; Riseman and Brusca, 2002; Sidabalok and Bruce, 2016).

***Sintorolana* Bruce, 1996**

Diagnosis. Body dorsal surfaces polished in appearance; BL 5 mm. Anterior margin without rostrum, not medially indented. Pleon 16% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 4; pleonite 4 posterolateral margin posteriorly broad, rounded, extending slightly beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins evenly convex. Antennal peduncle articles 3 and 4 subequal in length, 5 longest. Antennal flagellum not extending beyond posterior margin pereonite 2. Frontal lamina extended anteriorly, not visible in dorsal view, slender (3.8–7.6 times posterior width), ventrally flat, narrowest at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1

propodus haptorial (dactylus as long as propodal palm); dactylus with or without secondary unguis; dactylus extending to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods

6 and 7 ischium, merus and carpus not flattened, with short robust setae. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally.

Slope (1639 m). Central Indo-Pacific (New Caledonia). 1 species (Bruce, 1996).

Subfamily Eurydicinae Stebbing, 1905

Diagnosis. Clypeus with ventrally- or antero-ventrally projecting blade. Pleon usually long (usually 15–35% BL). Pleonites 4 and 5 with free lateral margins or with free posterolateral angle (pleonite 5 rarely laterally enclosed by pleonite 4). Pereopods 1–3 with ischium and merus superodistal angles not or weakly produced; dactylus secondary unguis robust or slender (may be absent). Pereopods 5–7 usually with slender setae and acute robust setae. Antennal peduncle of 4 or 5 visible articles.

Annina Budde-Lund, 1908

Diagnosis. Body length 5–10 mm, < 4 times as long as wide. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented; pereonites 1 and 2 (and head) may have horn-like processes. Rostrum large, extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases, not anteriorly dilated. Pleon usually long, 14–25% BL, with 5 visible segments; pleonites 1 and 2 narrower than pleonites 3–5; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 acute, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins distinctly sinuate or evenly convex. Antennular peduncle articles slender. Antennal peduncle of 4 visible articles, 1 and 2 short, 4 as long as 2; flagellum not extending beyond pleotelson posterior margin of pereonite 6. Frontal lamina extended anteriorly usually visible in dorsal view, not fusing to or abutting rostrum; ventral surface flat, elongate, > 3 times as long as posterior width; narrowing posteriorly, stem-like, not abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle short, usually < 0.9 times as long as wide.

Freshwater, estuarine, marine, intertidal, subtidal. Western and Central Indo-Pacific (mangroves). 6 species (Bowman and Iliffe, 1991; Khalaji-Pirbalouty, 2013; Mitra and Tabassum, 2020; Schotte, 1994).

Aphantolana Moore and Brusca, 2003

Diagnosis. Body dorsum flat or weakly vaulted; dorsal surfaces smooth or sparsely punctate; BL 3–10 mm, rarely longer. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view. Pleon 10–12% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, narrowly rounded; posterolateral margin of pleonite 4 narrowly rounded, not extending beyond posterior margin of pleonite 5 (or slightly beyond); pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 narrower than 4, with free posterolateral point, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins distinctly sinuate. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, not or slightly visible in dorsal view, posteriorly narrowed, not abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 propodus subchelate (dactylus c. 0.8 length of propodus); dactylus with slender secondary unguis; merus inferior margin with molariform robust setae. Pereopod 1 dactylus with slender secondary unguis. Pereopods 1–3 with ischium and merus superodistal angles not produced; with connate spines. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Male pleopod 2 appendix masculina attached submesially.

Intertidal, subtidal. Indo West-Pacific, Tropical Eastern Pacific (coral reefs). 4 species (Anil and Jayaraj, 2020; Moore and Brusca, 2003).

Atarbolana Bruce and Javed, 1987

Diagnosis. Body dorsal surfaces punctate, or coarsely pitted; BL 3–8 mm. Head anterior margin widest at mid-length; anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view, not anteriorly dilated. Pleon 10–15% BL, with 4 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 posteriorly broad, truncate, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior

margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins distinctly sinuate or concave. Antennular peduncle articles progressively shorter distally. Antennal peduncle of 4 visible articles, 2 and 3 short. Frontal lamina extended anteriorly, slightly visible in dorsal view; ventral surface flat; narrowing posteriorly, not stem-like, abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Antennal flagellum not extending beyond anterior margin of pereonite 4. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopod 1 peduncle short, usually < 0.9 times as long as wide. Male pleopod 2 appendix masculina attached mid-length. Uropod peduncle posterior mesial margin weakly produced; rami as long as mesial length of peduncle; exopod cylindrical, 1.3–2.2 times as long as endopod.

Intertidal, subtidal. Western Indo-Pacific. 4 species (Bruce and Javed, 1987; Castelló, 2017; Castelló et al., 2020; Khalaji-Pirbalouty et al., 2015).

***Colopisthus* Richardson, 1902**

Diagnosis. Body dorsum flat or weakly vaulted; dorsal surfaces sparsely punctate; BL 3–10 mm, rarely longer. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, acute, not anteriorly dilated. Pleon 5–10% BL, with 2 or 3 visible segments; pleonites 1 and 2 narrower than pleonites 3–5; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 narrowly rounded, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, < 0.9 times width of anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins distinctly sinuate. Antennular peduncle article 1 shortest, articles 2 and 3 subequal. Antennal flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat, narrowing posteriorly, stem-like, not abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 propodus subchelate, dactylus c. 0.8 times length of propodus, with slender secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced; inferior margin of merus with connate spines. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopod 1 peduncle short, usually < 0.9 times as long as wide. Male pleopod 2 appendix masculina attached submesially.

Intertidal. Tropical Atlantic. 5 species (Moore and Brusca, 2003); also Senegal, West Africa (Monod, 1952).

***Eurydice* Leach, 1815**

Diagnosis. Body 3–4 times as long as wide (female usually proportionally shorter than male); BL 3–8 mm. Head anterior margin widest mid-length; anterior margin with rostrum, medially indented; pereonite 1 without horn-like process. Rostrum small, not extending to anterior margin of antennular peduncle. Pleon long, 18–35% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins, or with free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded or truncate; lateral margins evenly convex. Antennular peduncle articles with articles 2 and 3 set at right angles to article 1. Antennal peduncle of 5 visible articles, 1 and 2 short, 4 as long as 2, 5 longest; flagellum long, may extend beyond pleon and pleotelson, but usually shorter. Frontal lamina extended anteriorly, not visible in dorsal view, slender (3.8–7.6 times posterior width), ventrally flat, not strongly anteriorly produced beyond antennula; narrowing posteriorly, stem-like, not abutting clypeus. Clypeus with ventrally or anteroventrally directed triangular blade. Maxilliped palp article 5 distal margin rounded. Pereopod 1 propodus subchelate (dactylus c. 0.8 length of propodus); dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae. Penes flat lobes. Pleopod 1 peduncle about as long as wide. Male pleopod 2 appendix masculina attached mid-length. Uropod peduncle posterior mesial margin not produced; rami subequal in length, as long as mesial length of peduncle; exopod laminar.

Intertidal; sandy beaches. Cosmopolitan, nocturnal surface plankton to more than 2000 m. 57 species (Bruce 1986; Brusca et al. 1995).

***Eurylana* Jansen, 1981**

Diagnosis. Body length 6–19 mm. Head anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view. Pleon long, 15–18% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 narrowly rounded; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins or free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 4. Frontal lamina extended anteriorly, slightly visible in dorsal view, ventral surface flat; narrowing posteriorly, not stem-like, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 2 and 3 merus moderately produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6

and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide. Male pleopod 2 appendix masculina attached mid-length.

Estuarine, marine, intertidal, subtidal (0–9 m). Central Indo-Pacific, Temperate South America (Chile), Temperate Australasia. 3 species; one species introduced to California (Bowman et al., 1981; Bruce, 1982; Bruce 1986; Jansen, 1981).

***Excirolana* Richardson, 1912**

Diagnosis. Body length 3–15 mm, rarely longer. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum large, extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases, sometimes anteriorly dilated or anteriorly truncate in dorsal view. Pleon usually long, 12–26% BL, with 5 visible segments; pleonites 1 and 2 narrower than pleonites 3–5; pleonite 3 epimeron not markedly expanded, narrowly rounded not extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 acute, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins or free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin not narrowly rounded; lateral margins evenly convex. Antennular peduncle articles progressively shorter distally or article 1 shortest, articles 2 and 3 subequal. Antennal peduncle of 4 visible articles, 1 and 2 short; flagellum not extending beyond posterior margin of pereonite 4. Frontal lamina extended anteriorly, usually visible in dorsal view, usually fusing or abutting rostrum; ventral surface flat, or elongate, > 3 times as long as posterior width, narrowing posteriorly, not stem-like, abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 dactylus with robust secondary unguis, not extending to carpus when folded; merus inferior margin with or without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Pleopods 2–5 peduncle lateral margin with or without well-developed laminar lobe. Male pleopod 2 appendix masculina attached submesially. Uropod endopod lateral margin usually with prominent excision.

Intertidal–shelf (0–16 m). Tropical Atlantic, Indo West-Pacific; sandy beaches. 14 species (Brusca et al., 1995; Jones, 1971). *Pontogeloides* Barnard, 1914 is a synonym.

***Metacirolana* Kussakin, 1979**

Diagnosis. Body dorsal surfaces smooth or sparsely punctate, occasionally with nodules; BL 2–10 mm, rarely shorter or longer. Head anterior margin markedly widest anteriorly, not medially indented, with rostrum. Pereonite 1 may have horn-like processes. Rostrum small, not extending to anterior margin of antennular peduncle, acute, not anteriorly dilated. Pleon usually long, 21–35% BL, with 5 visible segments; pleonite 3 epimeron

not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 acute, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins or free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin rounded, narrowly rounded or truncate; lateral margins evenly convex. Antennular peduncle article 2 longest. Antennal flagellum not extending beyond posterior margin of pereonite 6, usually shorter. Frontal lamina extended anteriorly, slightly or not visible in dorsal view; ventral surface flat, narrowing posteriorly, stem-like, not abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 propodus subchelate (dactylus c. 0.8 times length of propodus); dactylus with slender secondary unguis; dactylus may extend to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with sparse slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally.

Anchialine caves, intertidal–slope (0–2049 m). Temperate to tropical oceans; speciose in coral reefs. 38 species (Bruce, 1986; Bruce and Rodcharoen, 2021, 2023; Brusca et al., 1995; Paiva and Souza-Filho, 2023b; Sidabalok and Bruce, 2018b).

***Pontogelos* Stebbing, 1910**

Diagnosis. Body length 4–8 mm. Head anterior margin with rostrum, not medially indented. Rostrum large, extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases, anteriorly truncate in dorsal view. Pleon long, 35% BL, with 5 visible segments; pleonite 3 epimeron not expanded, not extending posteriorly beyond pleonite 4, narrowly rounded; pleonite 4 not overlapped by pleonite 3; lateral margin free, acute; pleonite 5 with free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennular peduncle article 3 extremely short (rudimentary in male), peduncle articles progressively shorter distally. Flagella of both antennula and antenna extending beyond pleotelson in male (shorter in female). Frontal lamina extended anteriorly, not visible in dorsal view, narrowing posteriorly, stem-like, not abutting clypeus. Clypeus with anteroventral triangular blade. Maxilliped palp article 5 quadrate. Pereopod 1 dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae, without long plumose setae. Penes flat lobes. Pleopod 1 peduncle short, < 0.9 times as long as wide. Male pleopod 2 appendix masculina attached sub-basally. Uropod peduncle posterior mesial margin weakly produced; rami as long as mesial length of peduncle; exopod laminar, exopod notably shorter in length.

Pelagic, nektonic. Indo West-Pacific. 1 species (Bruce, 1995c).

***Pseudaega* Thomson, 1884**

Diagnosis. Body length 3–9 mm. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, acute, not anteriorly dilated. Pleon 12–17% BL, with 4 or 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 narrowly rounded or acute, not extending beyond posterior margin of pleonite 5, pleonite 4 lateral margin partly overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin with apical point; lateral margins evenly convex. Antennular peduncle article 2 with prominent, posteriorly directed acute process. Antennal flagellum not extending beyond pereonite 4, usually shorter. Frontal lamina elongate, > 3 times as long as posterior width, usually visible in dorsal view, not fusing or abutting rostrum; ventral surface flat; posteriorly as wide or widest at mid-length, abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with slender secondary unguis (not clear in original figures); merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles moderately produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide. Male pleopod 2 appendix masculina attached mid-length. Uropod endopod lateral margin with prominent excision.

Intertidal–shelf (0–55 m). Temperate Australasia (New Zealand). 5 species (Jansen, 1978).

***Pseudolana* Bruce, 1979**

Diagnosis. Body length 5–10 mm. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum acute, not anteriorly dilated. Pleon long, 16–22% BL, with 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 4, acute; posterolateral margin of pleonite 4 acute, not extending beyond posterior margin of pleonite 5; pleonite 4 posterolateral margin, free, not overlapped by pleonite 3; pleonite 5 with free lateral margins or free posterolateral point, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin not narrowly rounded; lateral margins evenly convex. Antennular peduncle article 2 longest. Antennal flagellum not extending beyond pereonite 6, usually shorter. Frontal lamina, blade-like, extending anteriorly, not visible in dorsal view; abutting clypeus. Clypeus with ventrally or anteroventrally triangular blade. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles weakly produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide. Male pleopod 2 appendix masculina attached mid-length.

Intertidal, subtidal (0–14 m). Central Indo-Pacific (Papua New Guinea, Australia only). 7 species (Bruce, 1986).

Subfamily Cirolaninae Dana, 1852

Diagnosis. Clypeus ventrally flat. Pleon short, < 20% BL, usually 10–14%. Pleonite 4 sometimes laterally enclosed by pleonite 3. Pleonite 5 laterally enclosed by pleonite 4. Pereopods 1–3 with ischium and merus superodistal angles not or weakly produced, inferior margins usually with blunt robust or molariform robust setae; dactylus secondary unguis usually robust or absent. Pereopods 5–7 usually with few slender setae and acute robust setae. Antennal peduncle articles 1–3 short, 4 and 5 subequal in length and longest.

***Aatolana* Bruce, 1993**

Diagnosis. Body length 8–40 mm. Head anterior margin medially indented, without rostrum. Pleon short, < 20% BL; pleonite 3 epimeron broad, acute, dorsoventrally expanded, with setose longitudinal carina, extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 narrowly rounded, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin may be overlapped by pleonite 3; pleonite 5

laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson linguiform, posterior margin with apical point; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 6. Frontal lamina extended anteriorly, slightly visible in dorsal view; ventral surface flat or posterior margin with downwardly directed process (horn); posteriorly abutting clypeus, as wide or wider at mid-length. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle short, usually < 0.9 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached basally or sub-basally.

Shelf (16–200 m). Indo West-Pacific. 3 species (Bruce, 1993; Keable, 1998).

***Baharilana* Bruce and Svavarsson, 2003**

Diagnosis. Body length 5–10 mm. Head anterior margin without rostrum, not medially indented. Pleon 7–15% BL, with 4 or 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 narrowly rounded or acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson linguiform; posterior margin narrowly rounded or truncate; lateral margins distinctly sinuate or evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin with molariform robust setae. Pereopods 2 and 3 merus moderately produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, distally widest, with long robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle quadrate, about as long as wide; rami not operculate; endopod narrow, 0.26–0.45 times width of exopod. Male pleopod 2 appendix masculina attached submesially.

Intertidal, subtidal, shelf (0–70 m, one species at 1850 m). Western Indo-Pacific. 5 species (Bruce and Svavarsson, 2003; Khalaji-Pirbalouty and Wägele, 2011; Schotte and Kensley, 2005).

***Bathynomus* A. Milne Edwards, 1879**

Diagnosis. Body dorsal surfaces smooth or punctate; BL 70–300 mm or more. Head anterior margin markedly widest anteriorly; anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, acute, not anteriorly dilated. Pleon long, usually 15–35% BL, with 5 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin may be overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, < 0.9 width of anterior margin of pleotelson. Pleotelson posterior margin truncate, with prominent spines; lateral margins evenly convex. Antennular peduncle articles progressively shorter distally. Antennal flagellum not extending beyond posterior margin of pereonite 4, usually shorter. Frontal lamina extended anteriorly, usually visible in dorsal view, usually fused to or abutting rostrum; frontal lamina ventral surface flat, broad (2.4–4.0 times posterior width); posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 triangular. Pereopod 1 dactylus with or without secondary unguis, extending to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3

with merus superodistal margin strongly produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopods with respiratory branchiae at base of pleopods 1 and 2 exopods. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached submesially.

Shelf–bathyal (100–2500 m, occasionally at 20 m). Cosmopolitan, 35°N to 35°S. 22 extant species. Lowry and Dempsey (2006) characterised two groups of species: “giants”, with a length range of 80–140 mm, and “supergiants”, 150–500 mm (Huang and Bruce, 2024; Huang et al., 2022; Kou et al., 2017; Shipley et al., 2016; Sidabalok et al., 2020).

***Booralana* Bruce, 1986**

Diagnosis. Body dorsal surfaces smooth or sparsely punctate; BL 20–60 mm. Head anterior margin widest at mid-length; anterior margin without rostrum, medially indented. Pleon 12–18% BL; pleonite 3 epimeron ventral margin with ventral blade-like process, narrowly rounded; posterolateral margin of pleonite 4 narrowly rounded; pleonite 4 lateral margin may be overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin truncate, or broadly rounded; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina posterior margin with downwardly directed process (horn); posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with or without secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles strongly produced. Pereopods 2–7 slender, with few robust and slender setae. Penes flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached basally or sub-basally.

Shelf, slope (22–610 m). Tropical western Atlantic, Temperate Australasia. 4 species (Bruce, 1986; Camp and Heard, 1988; Shipley et al., 2024).

***Calyptolana* Bruce, 1985**

Diagnosis. Body dorsum strongly vaulted; BL 3–4 mm. Head anterior margin with rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view. Pleon 8% BL, with 4 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, rounded; posterolateral margin of pleonite 4 rounded, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennular peduncle articles 1 and 2 fused. Antennal flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly, not visible in

dorsal view, ventral surface flat, widest at mid-length, abutting clypeus. Clypeus narrow, less than half basal width; ventral surface flat. Maxilliped palp article 5 subquadrate or rounded. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Pleopod 1 peduncle short, usually < 0.9 times as long as wide; both rami forming operculum; endopod 0.50–0.68 times as wide as exopod. Uropod endopod shorter than mesial length of peduncle; exopod laminar, much shorter than endopod.

Subtidal, shelf (1–43 m). Tropical Atlantic (Netherlands Antilles and Caribbean Colombia). 1 species (Bruce, 1985; Müller 1993).

***Cartolana* Bruce, 1981**

Diagnosis. Body dorsum strongly vaulted; BL 9–12 mm. Head anterior margin without rostrum, not medially indented. Pleon 13% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, narrowly rounded; not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin laterally overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins evenly convex. Antennular peduncle articles 1 and 2 short, fused, article 3 longest. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, not visible in dorsal view, ventral surface flat; posteriorly as wide as mid-length, abutting clypeus. Clypeus ventral surface flat. Mandible incisor massive, not visible in dorsal view. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 pereopods 2 and 3 merus moderately produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute short robust setae. Pleopod 1 peduncle short, 0.43 times as long as wide. Male pleopod 2 appendix masculina unknown.

Subtidal, shelf (1–23 m); commensal with Crinoidea. Central Indo-Pacific. 1 species (Bruce, 1986).

***Ceratolana* Bowman, 1977**

Diagnosis. Body dorsal surfaces sparsely punctate, with nodules; BL 22–34 mm. Head anterior margin with rostrum, medially indented; posterior margin fused to pereonite 1 (not clear according to Bruce, 1995b). Rostrum large, extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases, not anteriorly truncate in dorsal view, acute. Pleon 11% BL; pleonites 1 and 2 about as wide as pleonites 3–5; pleonite 3 epimeron ventral margin with ventral blade-like process, rounded; posterolateral margin of pleonite 4 acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, < 0.9 times width of anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral

margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina extended anteriorly, visible in dorsal view, not fusing or abutting rostrum; ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus; anterior part a horn-like process. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis, not extending to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes low tubercles. Pleopod 1 peduncle short, 0.36 times as long as wide. Male pleopod 2 appendix masculina attached submesially.

Intertidal; in mangroves. Central Indo-Pacific (Malaysia, southeastern Papua New Guinea). 1 species (Bowman, 1977; Bruce, 1995b).

***Cirolana* Leach, 1818**

Diagnosis. Body sparsely punctate or nodular; BL 3–30 mm. Head anterior margin widest at mid-length; anterior margin with or without rostrum, not medially indented. Rostrum small, not extending to anterior margin of antennular peduncle, not anteriorly truncate in dorsal view, acute, not anteriorly dilated. Pleon < 20% BL, usually 10–14% BL, with 4 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, rounded, narrowly rounded or acute; posterolateral margin of pleonite 4 rounded, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin sometimes overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson linguiform; posterior margin narrowly rounded or truncate; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina extended anteriorly, slightly or not visible in dorsal view, ventral surface flat, broad (2.4–4.0 times posterior width); posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with slender acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes absent, or low tubercles, which may be medially united. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally.

Freshwater, caves, estuarine, marine, intertidal–shelf. All oceans from 72°S (Ross Sea) to 53°N (Ireland). 146 species, with several distinct groups that could be defined as genera in the future. Thirteen species occur below 100 m depth, and three species below 1,000 m. Bruce (1981, 1986) and Brusca et al. (1995) gave genus reviews and diagnoses. Recent significant species accounts were by Bruce (1995a: Papua New Guinea), Schotte and Kensley (2005: Indian Ocean), Sidabalok and Bruce (2017, 2018a: Indonesia), Rodcharoen et al. (2016, 2017: Thailand) and Rodcharoen and Bruce (2021: Thailand).

***Gnatholana* Barnard, 1920**

Diagnosis. Body dorsal surfaces sparsely punctate; BL 5.5 mm. Pleon 23% BL, with 4 visible segments; narrowly rounded; posterolateral margin of pleonite 4 narrowly rounded, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin with apical point; lateral margins distinctly sinuate. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, usually visible in dorsal view, not fusing or abutting rostrum, dorsally displaced by mandible. Clypeus ventral surface flat. Mandible incisor massive, visible in dorsal view, narrow, distally acute, less than half basal width.

Shelf (155 m). Western Indo-Pacific (South Africa). 1 species (Barnard, 1920). *Gnatholana mandibularis* Barnard, 1920 needs redescription.

***Hansenolana* Stebbing, 1900**

Diagnosis. Body dorsum flat or weakly vaulted; dorsal surfaces smooth or sparsely punctate; BL 6–10 mm. Head anterior margin markedly widest anteriorly, transversely straight, not medially indented. Rostrum small, acute, not extending to anterior margin of antennular peduncle. Pleon 12% BL, with 4 visible segments; pleonites 1 and 2 narrower than pleonites 3–5; pleonite 4 clearly extending beyond posterior margin of pleonite 5, pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly not visible in dorsal view, ventral surface flat; narrowing posteriorly, not stem-like, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 quadrate or subquadrate. Pereopod 1 propodus subchelate (dactylus c. 0.8 length of propodus); dactylus with small slender secondary unguis (blunt on pereopod 2); dactylus extending to carpus when folded; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pleopod 1 peduncle short, 0.45 as long as wide; rami not operculate; endopod narrow, 0.45 width of exopod. Uropod peduncle posterior mesial margin weakly produced; rami as long as mesial length of peduncle, subequal; exopod laminar.

Intertidal. Central Indo-Pacific. 1 species (Bruce, 1986).

***Limicolana* Bruce, 1986**

Diagnosis. Body dorsal surfaces polished in appearance; BL 13–15 mm. Anterior margin with rostrum, medially indented. Rostrum acute, not anteriorly dilated. Pleon 17% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 4, acute; posterolateral margin of pleonite 4 acute, clearly extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior

margin with apical point; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina extended anteriorly, slightly visible in dorsal view; ventral surface flat; narrowing posteriorly, not stem-like, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 propodus subchelate (dactylus c. 0.8 length of propodus); dactylus without secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle short, 0.45–0.70 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached submesially.

Intertidal; mangroves. Central Indo-Pacific (northern Australia). 1 species (Bruce, 1986).

***Neocirolana* Hale, 1925**

Diagnosis. Body dorsal surfaces smooth, or punctate; BL 3–10 mm. Head widest anteriorly or widest at mid-length; anterior margin with rostrum, not medially indented. Rostrum small, acute, not extending to anterior margin of antennular peduncle, not anteriorly dilated. Pleon < 20% BL, usually 10–14% BL, with 4 visible segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 narrowly rounded, not extending beyond posterior margin of pleonite 5, lateral margin may be overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded, or truncate; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 5 (usually shorter). Frontal lamina extended anteriorly, not visible in dorsal view, ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Mandible incisor not massive; narrow, less than half basal width. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin with or without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes absent. Pleopod 1 peduncle short, usually < 0.9 times as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally. Uropod endopod lateral margin with or without prominent excision.

Subtidal, shelf (1–49 m). Tropical Atlantic, Indo West-Pacific. 11 species (Bruce 1986; Bruce and Hughes, 2020).

***Odyseylana* Malyutina, 1995**

Diagnosis. Body length 5–11 mm. Head anterior margin without rostrum, not medially indented. Pleon < 20% BL, usually 10–14% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 rounded, clearly extending beyond posterior

margin of pleonite 5; pleonite 4 lateral margin sometimes overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson linguiform; posterior margin narrowly rounded or truncate; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; dactylus extending to carpus when folded; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles moderately produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes absent, or low tubercles. Pleopod 1 peduncle quadrate, about as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally.

Subtidal–slope (3–300 m). Central Indo-Pacific. 4 species (Sidabalok and Bruce, 2015).

***Oncilorpheus* Paul and Menzies, 1971**

Diagnosis. Body elongate, 4.0–6.5 times as long as wide; dorsal surfaces smooth or coarsely pitted; BL 8–15 mm. Head anterior margin markedly widest anteriorly; anterior margin with or without rostrum, medially indented or not. Rostrum small, not extending to anterior margin of antennular peduncle. Pleon 11% BL, with 5 visible or medially fused segments; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 4; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, slightly wider than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins distinctly sinuate, or evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina not visible in dorsal view; ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with small blunt secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and long slender setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75–1.0 times as long as wide; rami operculate; with exopod forming operculum; endopod narrow, 0.26–0.45 times width of exopod. Male pleopod 2 appendix masculina attached basally or sub-basally. Uropod peduncle posterior mesial margin weakly produced; rami shorter than mesial length of peduncle, subequal in length; exopod laminar.

Shelf (28–73 m). Tropical Atlantic, Tropical Eastern Pacific (Central America). 2 species (Brusca et al., 2015). *Oncilorpheus* has some distinctive uniting and probably apomorphic characters, but the genus is highly unusual in that one species *O. jerrybarnardi* Brusca, Wetzer and France, 1995 has all pleonites medially fused, whereas the other has five unfused pleonites.

***Parabathynomus* Barnard, 1924**

Diagnosis. Body length 70–80 mm. Head anterior margin widest posteriorly, margin without rostrum, not medially indented. Pleon 17% BL, with 5 visible segments; pleonite 3 epimeron not markedly expanded, extending to posterior of pleonite 5, narrowly rounded; posterolateral margin of pleonite 4 narrowly rounded, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin truncate; lateral margins not distinctly sinuate. Antennal flagellum not extending beyond posterior margin of pereonite 4. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat; posteriorly as wide or wider at mid-length, abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 triangular. Pereopod 1 dactylus not extending to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with merus superodistal margin strongly produced. Pereopods 2–7 usually with slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae. Penes flat lobes. Pleopods with respiratory branchiae on pleopod 1 peduncle and at base of pleopods 1 and 2 exopods. Pleopod 1 peduncle short, 0.5 times as long as wide. Pleopods 2–5 peduncle lateral margin with well-developed laminar lobe. Male pleopod 2 appendix masculina attached basally.

Slope (230–766 m). Temperate Southern Africa (E coast). 1 species (Kensley, 1978).

***Plakolana* Bruce, 1993**

Diagnosis. Body length 6–15 mm. Head anterior margin widest at mid-length; anterior margin without rostrum. Pleon 11–13% BL, with 4 or 5 visible segments; pleonite 3 epimeron broad, dorsoventrally expanded, with longitudinal carina, extending posteriorly beyond pleonite 5; posterolateral margin of pleonite 4 posteriorly broad, truncate, extending slightly beyond posterior margin of pleonite 5; pleonite 4 lateral margin overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, as wide as or slightly narrower than anterior margin of pleotelson. Pleotelson posterior margin narrowly rounded; lateral margins evenly convex, converging to apical point. Antennal flagellum not extending beyond posterior margin of pereonite 5. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat, slender (3.8–7.6 times posterior width), posteriorly as wide as at mid-length, abutting clypeus. Maxilliped palp article 5 distal margin rounded. Pereopod 1 dactylus with or without secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus flattened, with long acute robust setae. Penes flat lobes. Pleopod 1 peduncle about as long as wide. Male pleopod 2 appendix masculina attached basally or sub-basally.

Subtidal–slope (8–450 m). Central Indo-Pacific. 6 species (Bruce, 1993; Keable, 1997; 1999b).

Unassigned to subfamily

Bathylana Kensley, 1989

Diagnosis. Body length 3–4 mm. Head anterior margin without rostrum, not medially indented. Pleon long, 20% BL, with 5 visible segments; pleonites 1 and 2 narrower than pleonites 3–5; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 acute, not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4 (with free posterolateral points), as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennal flagellum not extending beyond posterior margin of pereonite 3. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat; narrowing posteriorly, stem-like, not abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 subquadrate. Pereopod 1 propodus subchelate (dactylus c. 0.8 times length of propodus); dactylus with slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Penes short lobes. Pleopod 1 peduncle short, 0.5 times as long as wide. Male pleopod 2 appendix masculina attached submesially. Uropod peduncle posterior mesial margin weakly produced; rami as long as mesial length of peduncle, subequal in length; exopod laminar.

Slope (1000–1450 m). Temperate Southern Africa (Saint Paul and Amsterdam Islands). 1 species (Kensley, 1989). The pereopods, pleopods, maxilliped and frontal lamina all accord with *Metacirolana*; most reliable characters point to Eurydicinae; the frontal lamina appears posteriorly stemmed and not abutting the clypeus, but the clypeus lacks a ventral blade-like projection.

Scutulana Bruce, 1996

Diagnosis. Body short, BL < 4 mm, less than twice as long as wide, dorsum flat. Head anterior margin not medially indented, with small rostrum not extending to anterior margin of antennular peduncle. Pleon 9% BL; pleonites 1 and 2 wider than pleonites 3–5; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, pleonites 3–5 narrow, pleonite 5 narrowest; pleonites 4 and 5 laterally enclosed by pleonite 3, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennular peduncle article 1 shortest, articles 2 and 3 subequal. Antennal flagellum not extending beyond posterior margin of pereonite 2. Frontal lamina extended anteriorly, not visible in dorsal view; ventral surface flat; narrowing posteriorly, stem-like, not abutting clypeus. Clypeus ventral surface flat. Mandible incisor not massive, narrow, less than half basal width. Maxilliped palp article 5 quadrate. Pereopod 1 slender, dactylus with prominent slender secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender

setae. Pereopods 6 and 7 ischium, merus and carpus with both (but few) long robust and long slender setae. Pleopod 1 peduncle subquadrate, c. 0.7 times as long as wide; rami not operculate; endopod narrow, 0.40–0.45 times width of exopod. Uropod exopod notably shorter than endopod.

Slope (440 m). Central Indo-Pacific (New Caledonia). 1 species (Bruce, 1996). Pereopods are of the Cirolaninae form; the pleon is short, with 5 pleonites, but pleonites 3–5 are narrow and overlapped by pleonite 2, with pleonites 4 and 5 subequal in width and laterally enclosed by pleonite 3; the frontal lamina is posteriorly stemmed, but the clypeus does not laterally enclose the labrum; the pereopods have a stout secondary unguis.

Seychellana Kensley and Schotte, 1994

Diagnosis. Body length 6.0–6.6 mm. Head anterior margin without rostrum, not medially indented. Pleon long, 18% BL, with 5 visible segments; pleonite 3 epimeron broad, dorsoventrally expanded, extending posteriorly beyond pleonite 5; pleonite 4 posteriorly rounded; not extending beyond posterior margin of pleonite 5; pleonite 4 lateral margin overlapped by pleonite 3; pleonite 5 with free lateral margins (but laterally overlapped by pleonite 3), as wide as or slightly wider than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennular peduncle articles with articles 2 and 3 weakly offset to article 1. Antennal peduncle articles 3 and 4 subequal in length, 5 longest. Antennal flagellum not extending beyond pereonite 5. Frontal lamina extended anteriorly, visible in dorsal view, not fusing or abutting rostrum; > 3 times as long as posterior width; narrowing mid-length, stem-like, not abutting clypeus. Clypeus ventral surface flat. Maxilliped palp article 5 quadrate. Pereopod 1 propodus subchelate; dactylus c. 0.8 length of propodus, without secondary unguis; merus inferior margin without molariform robust setae. Pereopods 1 merus superodistal angle moderately produced. Pereopods 2–7 with numerous slender setae and acute robust setae. Pereopods 6 and 7 ischium, merus and carpus weakly flattened, with long acute robust setae; pereopod 6 markedly shorter than pereopod 7. Penes low tubercles. Pleopod 1 peduncle short, 0.40 times as long as wide. Male pleopod 2 appendix masculina attached sub-basally. Uropod rami inflected or convex.

Shelf (30 m). Western Indo-Pacific (Seychelles). 1 species (Kensley and Schotte, 1994). While superficially similar to *Eurydice*, many differences indicate it is not close to that genus, nor to others of the Eurydicinae. The antennal peduncle and uropod are of the Conilerinae form, as is the basal appendix masculina; the pleon is long and pleonite 5 has free lateral margins; pereopod 1 and other pereopods are *Plakolana*-like; while pereopod 1 merus has the superodistal margin produced, but pereopod 2 does not. Pleopods are generally similar to Cirolaninae with a basally attached appendix masculina. Penial processes are absent, but low tubercles are present. The strongest characters pointing to Eurydicinae are the frontal lamina being posteriorly stemmed, the shape and narrowness of the clypeus, the long pleon, and pleonite 5 with free lateral margins.

***Sululana* Bruce and Shimomura, 2019**

Diagnosis. Body dorsal surfaces polished smooth; BL < 3 mm. Head anterior margin medially indented, with small rostrum not extending to anterior margin of antennular peduncle. Pleon 11% BL; pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5, acute; posterolateral margin of pleonite 4 acute, pleonite 4 lateral margin free, not overlapped by pleonite 3; pleonite 5 with free lateral margins, wider than anterior margin of pleotelson. Pleotelson posterior margin broadly rounded; lateral margins evenly convex. Antennular peduncle article 2 longest. Antennal peduncle articles 1–3 short, 4 longer, article 5 longest; flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina extended anteriorly, not visible in dorsal view, ventral surface flat. Clypeus ventral surface flat, anteriorly narrowed, not projecting ventrally. Mandible incisor not massive, wide, > 0.55 times basal width; left mandible bicuspid. Maxilliped palp article 5 subquadrate. Pereopod 1 propodus haptorial (dactylus as long as propodal palm); dactylus without secondary unguis; dactylus extending to carpus when folded; merus inferior margin without molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 slender, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus with long robust setae and long slender setae (very few setae). Pleopod 1 peduncle sub-quadrate, about 0.7 as long as wide; rami operculate; with exopod forming operculum; endopod narrow, 0.22 times width of exopod; uropodal rami as long as mesial length of peduncle; exopod laminar, exopod notably shorter in length.

Slope (1012–1016 m). Central Indo-Pacific (Sulu Sea). 1 species (Bruce and Shimomura, 2016). *Sululana* seem closer to *Metacirolana* than to other genera on the basis of antennular peduncle article 2 being longest and the characters of the pleon, maxilliped and pereopods, but has an operculate pleopod 1 (among other characters) that exclude the only species from that genus.

***Xylolana* Kensley, 1987**

Diagnosis. Body about 4 times as long as wide; BL < 4 mm. Head anterior margin with large, anteriorly dilated rostrum extending anteriorly to anterior margin of antennular peduncle, wholly separating antennular bases; anteriorly truncate in dorsal view; rostrum and frontal lamina together produced, forming horn-like process (abutting but not fused). Pleon 9% BL; pleonites 1 and 2 narrower than pleonites 3–5 (pleonite 1 narrowest); pleonite 3 epimeron not markedly expanded, not extending posteriorly beyond pleonite 5; pleonite 4 posterolateral margin posteriorly broad, truncate (expanded), clearly extending beyond posterior margin of pleonite 5, lateral margin free, not overlapped by pleonite 3; pleonite 5 laterally enclosed by pleonite 4, distinctly narrower than anterior margin of pleotelson. Pleotelson posterior margin truncate; lateral margins straight. Antennal peduncle articles progressively increasing in length; flagellum not extending beyond posterior margin of pereonite 1. Frontal lamina not visible. Clypeus ventral surface flat, anteriorly conical anteriorly produced and acute. Mandible incisor not massive, wide, about half width.

Left mandible bicuspid. Maxilliped palp article 5 subquadrate. Pereopod 1 dactylus with robust secondary unguis; merus inferior margin with molariform robust setae. Pereopods 1–3 with ischium and merus superodistal angles not produced. Pereopods 2–7 robust, with few robust and slender setae. Pereopods 6 and 7 ischium, merus and carpus not flattened, with short robust setae and few long slender setae. Penes flat lobes. Pleopod 1 peduncle subquadrate, c. 0.75 times as long as wide. Male pleopod 2 appendix masculina attached subdistally. Uropod peduncle posterior mesial margin moderately produced; rami as long as mesial length of peduncle, subequal in length; exopod laminar.

Intertidal; mangroves. Tropical Atlantic (Belize). 1 species (Kensley, 1987). This genus does not belong in the Eurydicinae, as placed by Kensley and Schotte (1989), and is here regarded as *incertae sedis*. Pleonite 5 is fully enclosed by pleonite 4, and the pleon is “short”. The clypeus does have an anteriorly produced apex, but not a ventrally projecting blade, and the appendix masculina is subdistal in position; the pereopods have stout robust setae and molariform setae on the pereopod 1 merus and the dactylus has a secondary unguis; these and the pleon characters indicate Cirolaninae is more appropriate. The present interpretation is that the labrum is relatively wide, and the clypeus is ventrally flat with an anterior projection (similar to some Cirolaninae) that abuts the rostrum; it seems that the frontal lamina is lost or hidden from view.

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Corallanidae Hansen, 1890

Figure 5.22

Corallanidae is a small family of six genera and 84 species (including three *incertae sedis* species), primarily occurring in tropical and subtropical shallow waters (Delaney, 1989). Some species are symbionts of fishes feeding on fish mucus and fish blood, while others are associated wholly or occasionally with sponges. The biology of many species is not known, though it is probable that some species of *Lanocira* Hansen 1890 feed on polychaetes. At least one species of *Argathona* Stebbing, 1905 is known to attach to fish gills, and others occupy the nasal passages of fish. The genus *Tachaea* Schioedte and Meinert, 1879 is primarily freshwater (one marine species) and is a micropredator of freshwater shrimp (e.g. Mariappan et al., 2003). *Excorallana* Stebbing, 1904 is exclusively New World in distribution (Santos Silva and Souza-Filho, 2017; Vigneshwaran et al., 2021). Species of the family are occasionally pests of aquaculture fishes (e.g. Kua and Bruce, 2010). The mandibular incisor in this family is narrow, giving a typically “narrow-headed appearance”, but the buccal cone is not as distinct as in the Aegidae and Cymothoidae, and the pereopod dactyli, while sometimes distally curved, are not prehensile. In comparison to the Cirolanidae, corallanids are generally more dorsally setose and have somewhat larger eyes, in *Excorallana* the eyes of some species being medially united (Bruce et al., 1982).

The species-level taxonomy is difficult, with rather many unrecognizable species and several species incorrectly placed in genera (Anil et al., 2022; Bruce et al., 2022). The genera are most reliably identified by the mouthpart characters, but the key below

uses some characters that are more easy to observe. Several of the species of Corallanidae described from Japan by Nunomura (1988, 1994, 2006a) were incorrectly identified at genus level.

Diagnosis. Eyes well developed; dorsum often ornamented with setae, spines, tubercles or carinae; head may have well-developed anteriorly produced rostrum (*Argathona*, *Lanocira*); sexual dimorphism in ornamentation common. Antennula peduncle 2- or 3-articulate, basal article sometimes expanded (*Corallana*, *Tachaea*). Antenna peduncle articles 1–3 short, 4–5 elongate. Frontal lamina and clypeus always flat. Mandibular always narrow, less than 0.4 basal width, incisor variously truncate, bidentate, tridentate or falcate; lacinia mobilis absent, molar process reduced occasionally absent. Maxillula lateral lobe with 1–2 large falcate apical spines, with 0–5 smaller subapical (accessory) spines in some genera; mesial lobe with simple, sparsely setose. Maxilla uniramous, minute, 1–3-articulate; apex morphology various, devoid of robust setae, sparsely setose. Maxilliped without endite; palp slender, 5-articulate, with occasional partial fusion of articles, without apical acute or hooked robust setae; various maxilliped articles elongate in different genera.

Additional characters. Many species are often dorsally setose, usually on the pleotelson, pleon and posterior margin of the pereonites, sometimes over the entire dorsum. Several species have a strongly developed rostrum, nodules or process on the head, pereonite 1, posterior pereonites and sometimes the pleon. The frons is always narrow, with a narrow mandibular incisor.

Key to genera of Corallanidae

1. Pleotelson lateral margin with (fig. 5.22b), rarely without (fig. 5.22c), incision. Eyes large, separated by less than half head width to medially contiguous (fig. 5.22b, c). Maxilliped elongate, palp article 3 elongate, about twice as long as wide (fig. 5.22u) *Excorallana*
- Pleotelson lateral margin without incision. Eyes small (“cirolanid-sized”) to moderate in size, separated by more than 0.45 head width (fig. 5.22a). Maxilliped palp article 3 not elongate, less than twice as long as wide (fig. 5.22s) 2

2. Maxilliped slender, basis elongate, 2–4 times as long as wide; palp articles subquadrate (fig. 5.22t). Frontal lamina small, variously shaped but not elongate, or absent (fig. 5.22e, f) *Corallana*
- Maxilliped not slender, palp articles 2–5 short (fig. 5.22s, v), articles 2–5 partly or wholly fused. Frontal lamina variously shaped, elongate (fig. 5.22d, g) 3
3. Mandibular trunk wide (fig. 5.22h); incisor narrow, bi- or tridentate; molar process present (fig. 5.22i). Maxillula lateral lobe with single large terminal robust seta and several subapical smaller robust setae on mesial margin. Maxilla a single rounded or subtruncate article (fig. 5.22o) *Argathona*
- Mandibular trunk and incisor narrow, bi-dentate or unicuspid; molar process absent (fig. 5.22j). Maxillula lateral lobe with large terminal robust setae or with 1 or 2 stout curved terminal robust setae 4
4. Mandible mesial margin serrate (fig. 5.22j). Maxillula lateral lobe with single large terminal strongly hooked robust seta (fig. 5.22l). Maxilla 2- or 3-articled, terminal article sublinear, with prominent terminal setae (fig. 5.22p) *Lanocira*
- Mandible without serrations. Maxillula lateral lobe with 1 or 2 large stout, curved robust setae. Maxilla short, rounded lobe (fig. 5.22n, q) 5
5. Mandibular incisor unicuspid, acute or narrowly rounded. Maxilliped palp margins quadrate (fig. 5.22w). Maxillula lateral lobe with 1 large stout, curved robust seta (fig. 5.22m). Pereopod 1 dactylus simple (fig. 5.22y). Body dorsal surfaces not setose (mainly freshwater on decapod crustaceans) *Tachaea*
- Mandibular incisor truncate or weakly bi-dentate. Maxilliped palp lateral margins convex, (fig. 5.22r). Maxillula lateral lobe with 2 large stout, curved robust setae, with accessory setae in between. Pereopod 1 dactylus with well-developed spines (fig. 5.22x). Body dorsal surfaces often setose *Alcirona*

***Alcirona* Hansen, 1890**

Diagnosis. Eyes normal in size, less than half head width. Pleotelson lateral margin without excision. Antennula article 1 not anteriorly produced. Mandibular incisor bicuspid or truncate; molar process present. Maxillula lateral lobe with 2 stout curved robust setae, with accessory setae between. Maxilla small short rounded lobe. Maxillipedal palp short, articles with lateral margins convex, not fused; article 3 less than twice as long as wide; article 5 longer than article 4. Pereopod 1 dactylus ambulatory, shorter than propodus; inferior margin with comb-like row of spines. Uropodal rami subequal in length.

Intertidal, shelf (to 106 m). Cosmopolitan in tropical and temperate shallow waters. 9 species (Koenig, 1979; Nunomura, 2006b).

***Argathona* Stebbing, 1905**

Diagnosis. Eyes normal in size, less than half head width. Pleotelson lateral margin without excision. Antennula article 1 not anteriorly produced. Mandibular incisor tridentate or bicuspid; molar process present. Maxillula lateral lobe with single stout curved robust seta and 1–4 mesial accessory setae. Maxilla small subtruncate lobe. Maxillipedal palp short, articles with lateral and mesial margins straight; articles not fused; article 3 less than twice as long as wide; article 5 longer than article 4. Pereopod 1 dactylus ambulatory, shorter than propodus; inferior margin even, without row of spines.

Uropodal rami subequal in length.

Intertidal–slope (to 267 m; one species at 760 m) (Bruce et al. 2022; Longstaff et al., 2025). Indo-West Pacific. 20 species; several species strongly associated with fish as commensals or micropredators (Bruce et al., 2022).

***Corallana* Dana, 1853**

Diagnosis. Eyes normal in size, less than half head width. Pleotelson lateral margin without excision. Antennula article 1 not anteriorly produced. Mandibular incisor tridentate, bicuspid or elongate, falcate; molar process present. Maxillula lateral lobe with single stout curved robust seta, without accessory setae. Maxilla small, elongate (longer than basal width) rounded lobe. Maxillipedal palp elongate, articles quadrate, not fused; article 3 less than twice as long as wide; article 5 shorter than article 4. Pereopod 1 dactylus ambulatory, shorter than propodus; inferior margin even, without row of spines. Uropodal exopod of adult male longer than endopod.

Intertidal–shelf (marine and estuarine, to 106 m). Indo-West Pacific (SE Africa to Philippines). 16 species (Delaney, 1989; Müller, 1991).

***Excorallana* Stebbing, 1904**

Diagnosis. Eyes large, occupying half or more than half head width. Pleotelson lateral margin with or without excision. Antennula article 1 expanded. Mandibular incisor elongate, falcate; molar process present or absent. Maxillula lateral lobe

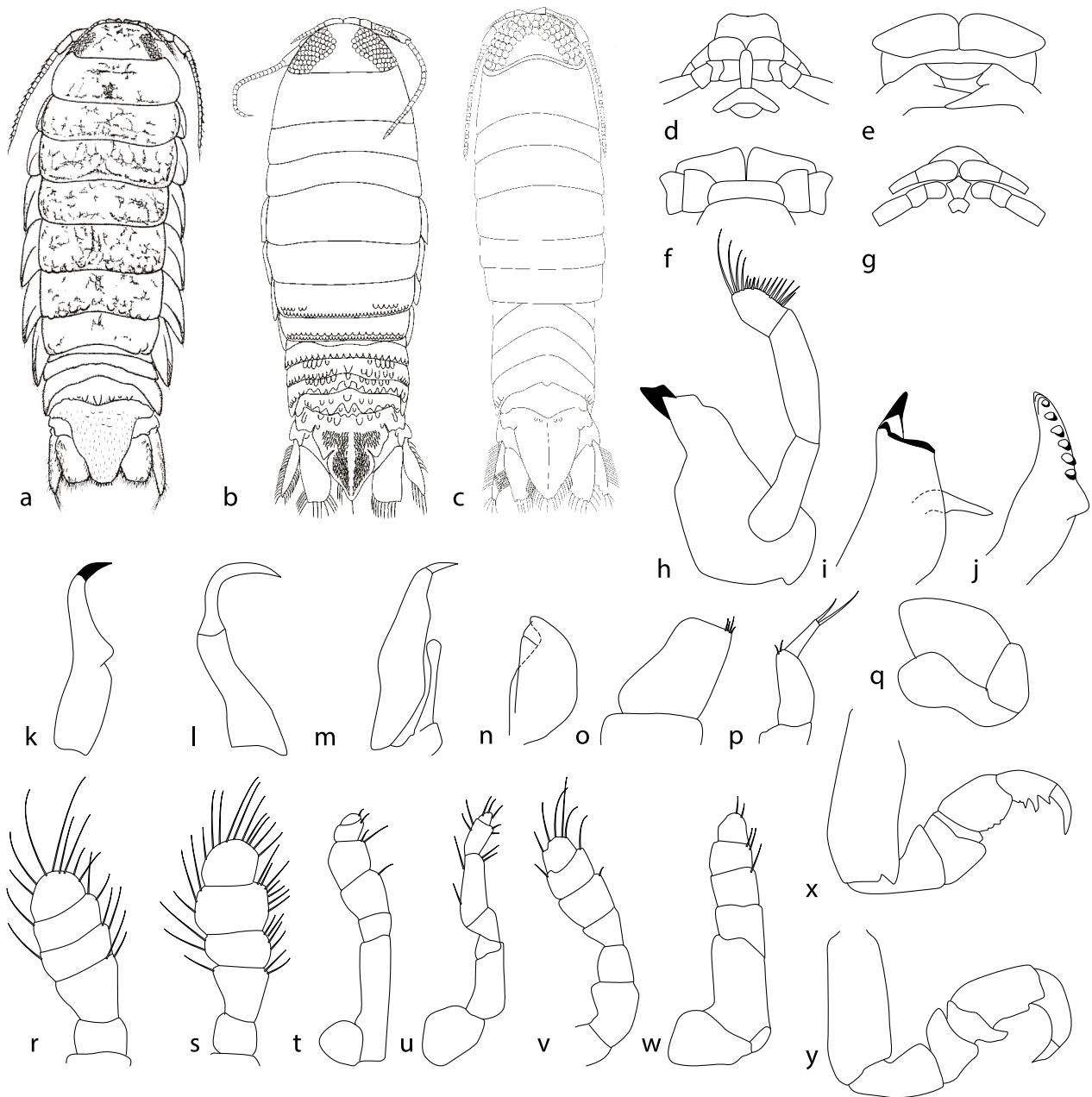


Figure 5.22. Corallanidae. a, *Corallana societensis* Müller, 1991; b, *Excorallana oculata* (Hansen, 1890); c, *Excorallana warmingii* (Hansen, 1890). Frons: d, *Argathona*; e, f, *Corallana*; g, *Lanocira*. Mandibles: h, i, *Argathona*; j, *Lanocira*. Maxillula: k, *Corallana*; l, *Lanocira*; m, *Tachaea*. Maxilla: n, *Alcirona*; o, *Argathona*; p, *Lanocira*; q, *Tachaea*. Maxilliped: r, *Alcirona*; s, *Argathona*; t, *Corallana*; u, *Excorallana*; v, *Lanocira*; w, *Tachaea*. Pereopod 1: x, *Alcirona*; y, *Tachaea*.

with single stout curved robust seta and 1–4 mesial accessory setae, or with large strongly hooked robust seta. Maxilla with 2 small, short, rounded lobes. Maxilliped palp elongate, articles quadrate, not fused; article 3 twice as long as wide; article 5 shorter than article 4. Pereopod 1 dactylus ambulatory, shorter than propodus; inferior margin even, without spines. Uropodal rami subequal in length.

Intertidal–shelf (to 183 m). Tropical Atlantic, Tropical Eastern Pacific (Americas). 23 species (Delaney, 1984; Stone and Heard, 1989; key to 8 species without lateral incision on pleotelson; biology; Santos Silva and Souza-Filho, 2017; descriptions and key to 12 species from Brazil). All records from the Indo-West Pacific are misidentifications.

Lanocira Hansen, 1890

Diagnosis. Eyes normal in size, less than half head width. Pleotelson lateral margin without excision. Antennula article 1 not anteriorly produced. Mandibular incisor bicuspid; molar process present. Maxillula lateral lobe with large strongly hooked robust seta. Maxilla 2- or 3-articled, terminal article linear. Maxilliped palp short, articles with lateral margins convex, not fused; article 3 less than twice as long as wide; article 5 longer or shorter than article 4. Pereopod 1 dactylus subprehensile, subequal in length to dactylus, strongly recurved; inferior margin even, without spines. Uropodal rami subequal in length.

Intertidal–shelf (to 120 m). Indo-West Pacific, Tropical Western Atlantic; primarily on or around coral reefs. 9 species (Bruce and Sidabalok, 2011).

Tachaea Schioedte and Meinert, 1879

Diagnosis. Eyes normal in size, less than half head width. Pleotelson lateral margin without excision. Antennula article 1 anteriorly produced. Mandibular incisor truncate; molar process absent. Maxillula lateral lobe with large strongly hooked robust seta. Maxilla small short rounded lobe. Maxilliped palp short, articles with lateral and mesial margins straight; articles 2–5 variably fused; article 3 less than twice as long as wide; article 5 longer than article 4. Pereopod 1 dactylus subprehensile, subequal in length to dactylus, strongly recurved; inferior margin even, without spines. Uropodal exopod of adult male longer than endopod.

Primarily freshwater (3 estuarine species). Temperate Northern Pacific, Western and Central Indo-Pacific (India, SE Asia, East Asia, tropical Australia); micropredator of shrimps. 8 species (Vigneshwaran et al., 2021).

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Cymothoidae Leach, 1814

Figures 5.23–5.30

Cymothoidae are one of the largest families of aquatic Isopoda with 47 genera holding 394 accepted species names (including *species inquirenda* and *nomina dubia*), of which 38 genera and

about 350 species are marine or estuarine (Boyko et al., 2026, at 31 Dec 2025). Cymothoids are all obligate and exclusively fish parasites, occupying four sites of attachment on the body of their

host, namely: externally or “scale attaching”; buccal or mouth attaching (“tongue replacement” cymothoids of Brusca and Gilligan, 1983); gill or opercular cavity attaching; and flesh burrowing (see Smit et al., 2014; fig. 2). Attachment site and host taxon is reflected in the body shape of cymothoid genera and species, and historically body shape and attachment site also influenced the interpretation of phylogenetic relationships between of genera (e.g. Brusca, 1981), although it had become apparent by the 1990s that position of attachment did not reflect phylogeny (Bruce, 1990; Smit et al., 2014). Most recently, molecular analyses have strongly and consistently demonstrated that body shape and attachment site are independent of phylogeny with, for example, the generally similar-looking and tongue-attaching genera *Ceratothoa* Dana, 1852 and *Cymothoa* Fabricius, 1873 consistently being basally separated (e.g. Fujita et al., 2023; Hata et al., 2017; Martin et al., 2024).

The family primarily occurs in marine waters and to a far lesser degree in estuaries or euryhaline environments. It is only in South America that there is a diverse freshwater cymothoid fauna composed of ten endemic genera and 33 species (Thatcher, 1991, 1993a, 1993b). Marine cymothoids occur from cool temperate waters to tropical waters worldwide, with highest diversity within the tropics, and are entirely absent from polar waters. The family is strongly depth limited, being largely confined to the continental shelf, with fewer than ten species recorded from a depth greater than 500 m (Smit et al., 2014). In common with many taxa, the large species from commercially fished hosts were historically described first; at present, little is known about those species that use small tropical and coral reef fishes as hosts. The family is dominated by seven large (with more than 20 species) marine genera: *Anilocra* Leach, 1818, *Ceratothoa*, *Cymothoa*, *Elthusia* Schioedte and Meinert, 1884, *Mothocya* Costa in Hope, 1851, *Nerocila* Leach, 1818 and *Renocila* Miers, 1880, together comprising 66% of all marine cymothoid species.

The Cymothoidae is one of the earliest described families of the Isopoda. The family concept was framed in a global series of comprehensive monographs by Schioedte and Meinert (1881, 1883, 1884), which clearly established the family as obligate parasites of fishes, and the unity of the family has remained. Subsequently, there were few further global revisions, but several regional revisions of significance were published,

notably by Hale (1926, 1940) on Australian cymothoids. Trilles (1971–2014) published extensively on the taxonomy of many taxa, accompanied by comprehensive synonymies and literature citations; most notably his *Prodromus* (Trilles, 1994) is a highly useful resource for all known genera and species to that date. Brusca (1981) revised the Cymothoidae of the tropical eastern Pacific. Contemporaneously, Williams and Williams began their ongoing revisions of Caribbean and Japanese isopods (Williams and Bunkley-Williams publishing between 1978 and 2000), while Bruce (1987–1990) revised the Australian externally attaching and gill attaching genera. In the twenty-first century there have been significant regional contributions on the cymothoids of South Africa (Hadfield, with Smit and Bruce, 2010–2021), Australia (Martin et al., 2013–2016), and India (Aneesh and co-authors, 2013–2025). Smit et al. (2014) gave a more detailed review of the history of discovery in the Cymothoidae.

Diagnosis (of adult female). Fish parasites. Body dorsum weakly to strongly vaulted. Pleon (pleonites 1–5 without pleotelson) with 5 unfused somites. Eyes widely separated, lateral, often with indistinct ommatidia, sometimes small or absent. Antennula and antenna not differentiated into peduncle and flagellum. Mouthparts forming a buccal cone; mandibular incisor narrow, usually unidentate; lacinia mobilis and spine row absent; molar process absent or represented by small flat lobe. Maxillula lateral endite with 3–5 terminal flat robust setae. Maxilla with 1 subapical endite; both lobes usually with 1–3 recurved (“hooked”) robust setae. Maxilliped without endite; palp of 2 articles, article 2 or 3 with apical recurved robust setae. Pereopods 1–7 with prehensile dactyli. Pleopods without plumose marginal setae.

Implicit generic attributes. Pereonite 1 anterior margin not incised. Pleonites without sublateral gaps. Coxae 5–7 not strongly produced ventrally. Pleonites not strongly produced ventrally. Pleonites 1 and 2 ventrolateral margins not produced. Pleonites 3–5 or 4 and 5 more than half width (c. 0.7) of pereon. Pleotelson lateral margins symmetrical. Antennae both slender. Antennula with more than 5 articles; article 3 not anteriorly lobed. Pereopod 1 propodus without robust setae.

In the diagnoses below the size of the eye is given as “small” or “large” defined by whether it is less than or more than 40% of the head width.

Practical key to marine genera of Cymothoidae

This key applies only to ovigerous adult female cymothoids, those that have oostegites. Males cannot be determined using this key. Cymothoid genera can, fairly consistently, be grouped into four modes of attachment to the fish host: externally attaching; gill attaching; buccal attaching (mostly on the tongue, but also the roof or side of the mouth); and flesh burrowing. A few genera have species that attach to both the mouth and gills. One such is *Catoessa*, which therefore appears twice in the key. One species of *Nerocila* has been recorded from the host gills; it too appears twice in the key.

The key must be used with some cautionary provisos. One is that cymothoid species are truly variable in many aspects of their morphology, and within the large genera one or more species may not show all the genus characters. Identifications should therefore be made on the overall balance of characters. Secondly, any generic identification should be compared to the most recent detailed generic description. Thirdly, new genera of Cymothoidae are still being discovered and revealed through revisions, with four genera established since 2019 (*Bambalocra*, *Brucethoa*, *Gibbothoa*, *Glyptothoa* and *Sandythoa*). Species therefore may be encountered that do not “key out” to any genus.

Host data are not given because cymothoid genera are not specific to particular fish taxa, although a few (such as *Mothocya*, which prefers species of Beloniformes as host) show a family-level preference. In contrast, host identity is critical in aiding species-level identification. Similarly, defined depth range is largely unknown for most genera because for the most part it has not been recorded.

Exclusions. Two monotypic genera are insufficiently characterised and not included in the key: *Lathreana* Schioedte and Meinert, 1881, *Riothra* Schioedte and Meinert, 1884. *Aegathoa* Dana, 1853 is a “form genus” based in immature specimens and is also excluded. The otherwise South American freshwater genus *Telotha* Schioedte and Meinert, 1884 includes *Telotha indica* Nierstrasz, 1915, reported from a marine location in Indonesia, but not adequately described and could equally belong to *Ichthyoxenos* Herklots, 1870 or other similar genus.

- | | | |
|----|---|-------------------|
| 1. | Attaching within buccal cavity (i.e. mouth), gill chamber or burrowing in flesh | 2 |
| – | Attaching to host body external surfaces (above eye, external gill operculum, fins, caudal peduncle etc.) | 4 |
| 2. | Burrowing in host body tissues (fig. 5.25f) | <i>Ourozeukes</i> |
| – | Not burrowing in host body; attached within buccal cavity or gills | 3 |
| 3. | Attached to host gills | 11 |
| – | Attached to buccal cavity, on tongue, roof or sides of mouth | 28 |

Externally attaching genera

- | | | |
|-----|--|----------------------|
| 4. | Head posterior margin trisinate (figs 5.23e, f, 5.27c). Coxae 5–7 as long as or longer than respective pereonite (fig. 5.23f, g, 5.27h) (except <i>Nerocila lomatia</i> Bruce, 1987) | 5 |
| – | Head posterior margin not or weakly trisinate (figs 5.23a, b, 5.27a). Coxae 5–7 manifestly shorter than respective pereonite (fig. 5.23b, 5.27g, i) | 8 |
| 5. | Pleonites 1 and 2 ventrolateral margins produced (fig. 5.27d) | <i>Nerocila</i> |
| – | Pleonites 1 and 2 ventrolateral margins not produced (fig. 5.27b) | 6 |
| 6. | Body dorsal surface strongly vaulted. Coxae 5–7 ventrally directed; pleonites strongly produced ventrally (fig. 5.23g) | <i>Plotor</i> |
| – | Body dorsal surface weakly vaulted. Coxae 5–7 posteriorly directed; pleonites not strongly produced ventrally | 7 |
| 7. | Uropod rami long, extending well beyond posterior of pleotelson. Coxae conspicuous in dorsal view (fig. 5.27h) | <i>Amblycephalon</i> |
| – | Uropod rami short, not extending beyond posterior of pleotelson. Coxae inconspicuous in dorsal view (fig. 5.27i) | <i>Creniola</i> |
| 8. | Head without distinct rostrum, or rostrum not projecting between antennula bases (fig. 5.29c). Antennula broader than and as long as, or longer than antenna (fig. 5.29h). Posterolateral margins of pereonites 5–7 moderately to strongly produced (fig. 5.27g) | <i>Renocila</i> |
| – | Rostrum folded under, projecting between antennula bases (fig. 5.29a). Antennula more slender than and shorter than antenna. Posterolateral margins of pereonites 6 and 7 produced (<i>Bambalocra</i>) or not produced (fig. 5.23a, c) | 9 |
| 9. | Coxae ventral in position, not or barely visible in dorsal view. Posterolateral margins of pereonites 6 and 7 posteriorly produced, rounded (fig. 5.23c). Pleopods 3–5 endopods with weak lobes; pleopods hardly visible in dorsal view (fig. 5.30l) | <i>Bambalocra</i> |
| – | Coxae lateral in position, largely not visible in dorsal view (fig. 5.23a, b), posterolateral margins of pereonites 5–7 not produced (fig. 5.23b). Pleopod 5 only with prominent folded fleshy lobes; pleopods clearly visible in dorsal view (fig. 5.30k) | 10 |
| 10. | Mandible palp article 3 shorter than article 2 (fig. 5.30a). Antennula articles 4–8 short (fig. 5.27a). Pleonites 3–5 or 4 and 5 more than half width (c. 0.7) of pereon (fig. 5.23a). Maxilla with 2 short, hooked robust setae each on mesial and lateral lobe, mesial lobe partly fused to lateral (fig. 5.30b) | <i>Anilocra</i> |
| – | Mandible palp article 3 longer than article 2 (fig. 5.30d). Antennula articles 4–8 elongate (fig. 5.27e). Pleonites 3–5 or 4 and 5 less than half width (c. 0.45) of pereon (fig. 5.27f). Maxilla with 2 large nodular robust setae each on mesial and lateral lobe, mesial lobe distinct (fig. 5.30c) | <i>Pleopodias</i> |

Gill attaching

- | | | |
|-----|--|-------------------------------|
| 11. | Pleonites 1 and 2 with ventrolateral processes (fig. 5.27d) | <i>Nerocila</i> (one species) |
| – | Pleonites 1 and 2 without ventrally directed processes (fig. 5.24b, f) | 12 |
| 12. | Body strongly bilaterally distorted, asymmetrical; pereon or pleon may be hunched in lateral view (figs 5.23i, 5.24c) | 13 |
| – | Body not distorted, bilaterally symmetrical or weakly asymmetrical; body not hunched in lateral view (figs 5.23h, 5.24a, e, g) | 17 |
| 13. | Pleon hunched in lateral view; body weakly twisted. (fig. 5.24j). Antennula with 4 articles (fig. 5.29i) | <i>Kuna</i> |
| – | Pleon not hunched; body asymmetrical or circular in outline (fig. 5.24b, i). Antennula with more than 5 articles | 14 |
| 14. | Pereon not hunched in lateral view. Coxae greatly enlarged on one side (fig. 5.23j) | <i>Cterissa</i> |
| – | Pereon hunched in lateral view. Coxae subequal on both sides or, if larger on one side, not conspicuous in dorsal view (figs 5.23i, 5.24c) | 15 |
| 15. | Body weakly asymmetric, near circular in outline; lateral margins of all pereonites not notably expanded (fig. 5.24i) | <i>Ryukyua</i> |
| – | Body strongly asymmetric; lateral margins of some pereonites notably expanded on one side (figs 5.23i, 5.24c) | 16 |
| 16. | Lateral margin of pereonites 3–5 strongly expanded on one side (fig. 5.23i). Head without dorsally visible rostral point. Brood pouch not strongly protruding (fig. 5.24b) | <i>Agarna</i> |
| – | Lateral margin of pereonites 4–7 strongly expanded on one side (fig. 5.24c). Head with minute dorsally visible rostral point. Brood pouch strongly protruding (fig. 5.24h) | <i>Gibbothoa</i> |
| 17. | Head with rostral point (may be ventrally directed) (fig. 5.28e) | 18 |
| – | Head without rostral point, anterior margin variously narrowly rounded to subtruncate (fig. 5.28a, d) | 22 |
| 18. | Brood pouch extending strongly ventrally (fig. 5.24h) | 19 |
| – | Brood pouch extending weakly ventrally (fig. 5.24b) | 20 |
| 19. | Pleopods not visible in dorsal view. All coxae visible dorsally. Pleon 1.0–1.2 times as wide as widest pereonite (fig. 5.24d) | <i>Glyptothoa</i> |
| – | Pleopods visible in dorsal view. Coxae of pereonites 6 and 7 not visible in dorsal view. Pleon 0.9 times as wide as widest pereonite (fig. 5.23h) | <i>Brucethoa</i> |
| 20. | Body dorsum not or weakly vaulted. Short gaps between pleonites; pleonite 1 narrow, not laterally extended (figs 5.24k, 5.28g) | <i>Sandythoa</i> |
| – | Body dorsum vaulted. No gaps between pleonites; pleonite 1 weakly to moderately laterally extended | 21 |
| 21. | Body ovate (fig. 5.24e). Pleonite 1 not markedly narrower than pleonite 2, partly laterally overlapped by pereonite 7 (fig. 5.24e). Pereopod ischium to carpus flattened, widest distally, dactylus short (fig. 5.30g) | <i>Ichthyoxenos</i> |
| – | Body not strongly ovate. Pleonite 1 narrower than pleonite 2; pleon not immersed in pereon. Pereopod ischium to carpus not widest distally, dactylus long | <i>Idusa</i> |
| 22. | Head posterior margin trilobed (fig. 5.28c). Pleonites 1–5 progressively narrower (fig. 5.28h). Pleopod peduncles with lamellar or fleshy lateral lobe; rami with fleshy lobes (fig. 5.30o, p) | 23 |
| – | Head posterior margin not trilobed. Pleonites 1–5 not progressively narrower; pleopod peduncles and rami without lateral, fleshy lobes | 24 |
| 23. | Head posterior margin strongly trilobed (fig. 5.28c). Pleonites 1–3 lateral margins bilobed (fig. 5.28i). Pleopodal peduncles with branchiae (fig. 5.30p) | <i>Livoneca</i> |
| – | Head posterior margin weakly trilobed. Pleonites 1–3 lateral margins not bilobed. Pleopodal peduncle without branchiae | <i>Norileca</i> |

24. Head laterally enclosed by pereonite 1 anterolateral margins. Pereonites 2 and 3 coxae inflated, much larger than remaining coxae (fig. 5.28b) *Joryma*
 – Head and coxae not as above 25
25. Pereopods with many fine robust setae. Pereopods 4–6 merus inferior margin with distinct blade (fig. 5.30h) *Pseudirona*
 – Pereopods not setose. Pereopods 4–6 merus without distinct blade 26
26. Small gap between pleonites (fig. 26i). Body bilaterally symmetrical; dorsum vaulted. All coxae small. Head not deeply immersed in pereonite 1. Pleon rotationally twisted with narrow pleonite 1 (fig. 5.23d) *Catoessa*
 – No gap between pleonites. Body weakly to moderately asymmetrical; dorsum not or weakly vaulted. Posterior coxae often large. Head immersed in pereonite 1. Pleon not rotationally twisted, pleonite 1 variable in width (fig. 5.24a, b, g) 27
27. Uropods short, not reaching posterior of pleotelson (fig. 5.28f). Pleon greater than 0.75 maximum width of pereon (fig. 5.28f). Antennula slender, shorter than antenna (fig. 5.29f) *Elthusa*
 – Uropods usually longer, reaching or extending posterior to pleotelson; pleon half as wide to as wide as pereon (fig. 5.28j). Antennula thicker and longer than antenna (fig. 5.29g) *Mothocya*

Buccal attaching

28. Head posterior margin trisinate (fig. 5.26h). Pereon and pleon strongly colinear (fig. 5.25d). Brood pouch with posterior pocket; oostegites of coxae 6 forming most of marsupium (fig. 5.30j) *Smenispa*
 – Head posterior margin concave or straight (fig. 5.26a, d). Pereon and pleon weakly colinear (fig. 5.25a, b). Brood pouch without posterior pockets; oostegites arising from coxae 1–6, all forming marsupium (fig. 5.30i) 29
29. Pleotelson posterior margin subtriangular. Body widest at pereonite 6 (figs 5.25c, 5.26k) *Olencira*
 – Pleotelson posterior margin rounded or subtruncate. Body usually widest at pereonite 4 or 5 (fig. 5.25a, b, d) 30
30. Antennula longer than antenna (fig. 5.29d). Pereopod 5–7 basis without well-developed carina (fig. 5.30e). Pleon and pleotelson axially twisted (“rotated”) against plane of pereon (fig. 5.26i) *Catoessa*
 – Antennula shorter than antenna (fig. 5.29b, e). Pereopods 5–7 basis with well-developed carina (fig. 5.30f). Pleon and pleotelson not axially twisted against pereon 31
31. Antennae thick and expanded. Antennula bases contiguous (fig. 5.29e). Head not or weakly immersed in pereonite 1 (fig. 5.26a) 32
 – Antennae slender. Antennula bases separated (fig. 5.29b). Head deeply immersed in pereonite 1 (fig. 5.26c, d) 34
32. Rostrum dorsally not projecting between antennae (fig. 5.26e) *Emetha*
 – Rostrum dorsally projecting between antennae (fig. 5.26a, f) 33
33. Pereonite 1 anterolateral margins projecting forward, without slight sublateral incision, anteromesial margin concave (fig. 5.26a) *Ceratothoa*
 – Pereonite 1 anterolateral margins projecting laterally, with slight sublateral incision, anteromesial margin straight or concave (fig. 5.26f) *Glossobius*
34. Body weakly vaulted. Anterior margin of head with distinct rostrum. Anterolateral margins of pereonite 1 extending anteriorly beyond eyes, with prominent lobes (fig. 5.26g) *Lobothorax*
 – Body strongly vaulted. Anterior margin of head without distinct rostrum. Anterolateral margins of pereonite 1 minute or reaching anterior margin of head, without prominent lobes (fig. 5.26b, c, d) 35
35. Head quadrate. Pleonites subequally wide (fig. 5.25e) *Tetragonocephalon*
 – Head not quadrate (fig. 5.26c), anterior margin narrow to moderately broad (fig. 5.26d). Pleonite 1 or 1–3 narrower than remaining pleonites (fig. 5.26j) 36

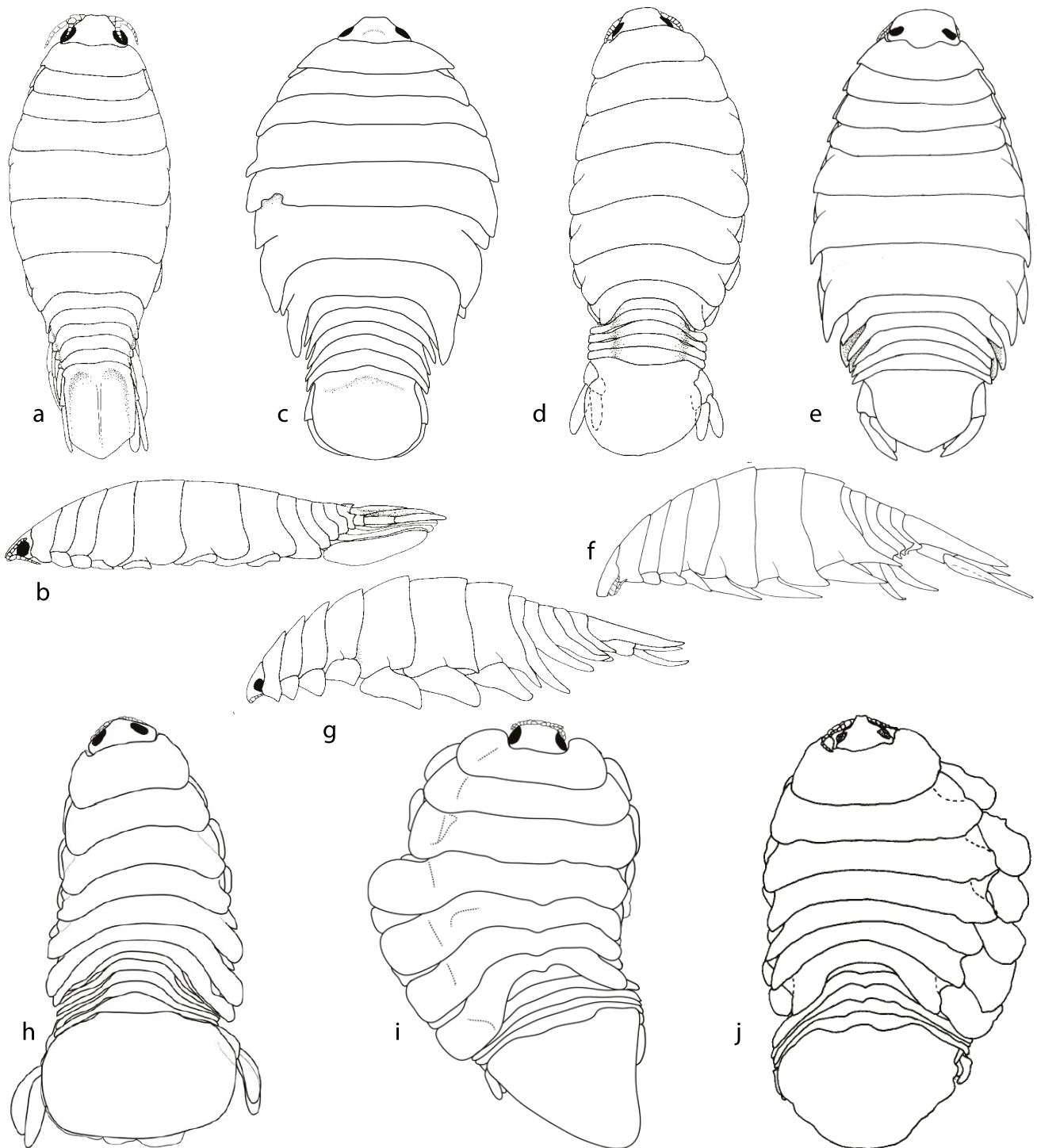


Figure 5.23. Cymothoidae. Externally attaching genera, habitus dorsal and lateral: a, *Anilocra nemipteri* Bruce, 1987a; b, *Anilocra nemipteri* Bruce, 1987a; c, *Bambalocra intwala* Bruce, Welicky, Hadfield and Smit, 2019; d, *Catoessa ambassae* Bruce, 1990; e, *Nerocila orbigny* (Guérin-Méneville, 1832); f, *Nerocila orbigny* (Guérin-Méneville, 1832); g, *Plotor indus* Schioedte and Meinert, 1881. Gill-attaching genera, habitus: h, *Brucethoa bharata* Aneesh, Hadfield, Smit, and Biju Kumar, 2020; i, *Agarna cumulus* (Haller, 1880); j, *Cterissa sakaii* Bunkley-Williams and Williams, 1986.

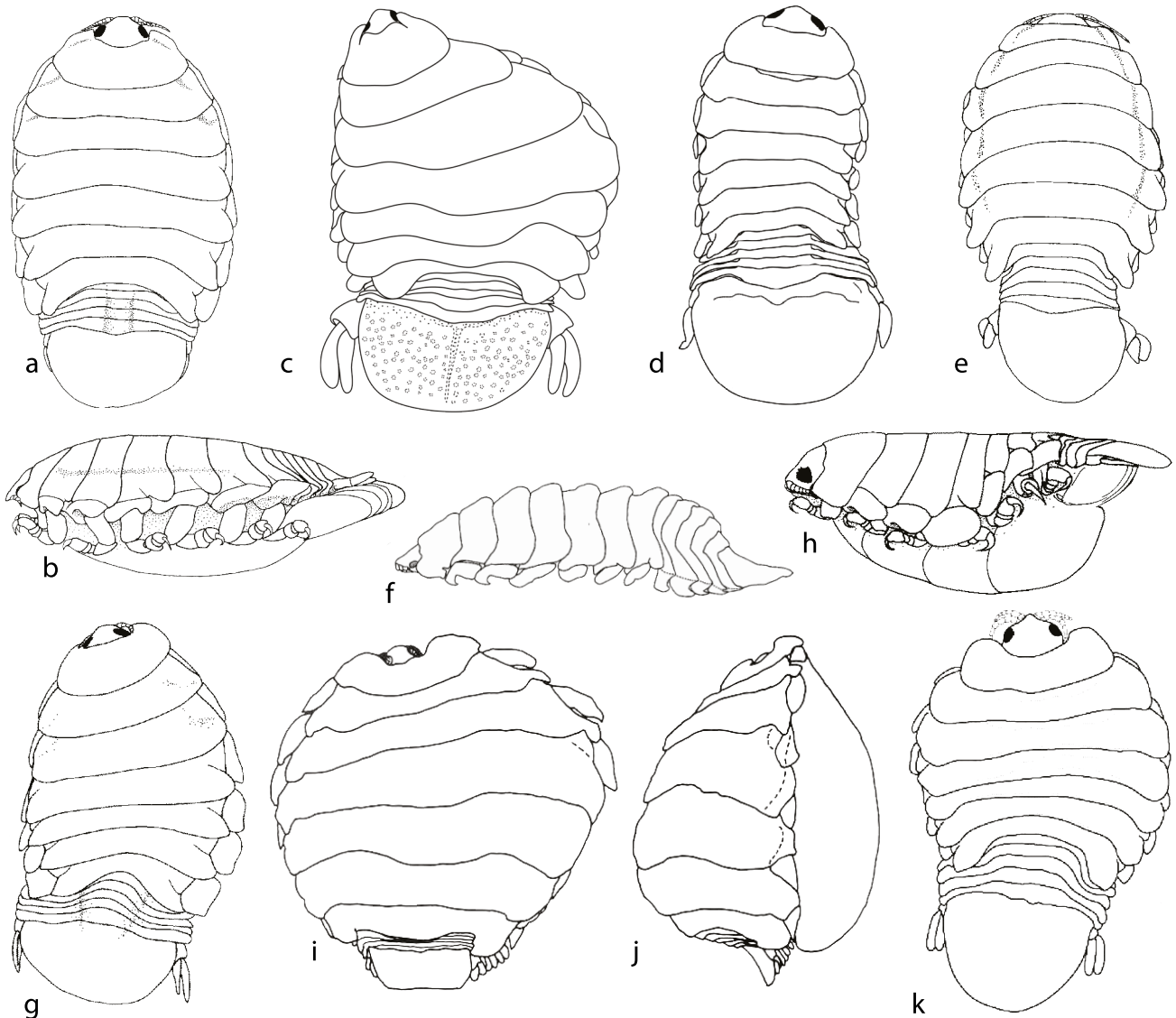


Figure 5.24. Cymothoidae. Gill-attaching genera, habitus dorsal and lateral (continued): a, *Elthusa raynaudii* (Milne Edwards, 1840); b, *Elthusa sigani* Bruce, 1990; c, *Gibbothoa malayi* Aneesh, Hadfield, Smit, and Biju Kumar, in press; d, *Glyptothoa sagara* Helna, Aneesh, Biju Kumar and Ohtsuka, 2023; e, *Ichthyoxenos minabensis* (Shiino, 1951); f, *Kuna insularis* Williams and Williams, 1985; g, *Mothocya melanosticta* (Schioedte and Meinert, 1881); h, *Mothocya melanosticta* (Schioedte and Meinert, 1881); i, *Ryukyua globosa* Williams and Williams, 1994; j, *Ryukyua globosa* Williams and Williams, 1994; k, *Sandythoa tiranga* Aneesh, Bruce, Helna and Biju Kumar, 2024.

- 36. Anterior margin of head subacute (fig. 5.26b). Body ovate, less than 1.5 times as long as greatest width. Pleopods 3–5 without fleshy folds (fig. 5.30n) *Cinusa*
- Anterior margin of head broadly subtruncate. Body subparallel or weakly ovate, more than 1.5 times as long as greatest width (fig. 5.26d, j). Pleopods 3–5 with fleshy folds (fig. 5.30m) *Cymothoa*

Agarna Schioedte and Meinert, 1884

Diagnosis. Attached to host gills. Body strongly asymmetrical or distorted; lateral margins strongly hunched on one side; dorsum strongly vaulted. Rostrum distinct, rounded, ventrally directed. Head partially immersed in pereonite 1, posterior

margin straight, lateral margin convex. Eye small. Coxae unequal on both sides of body; coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite, strongly ventrally directed, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin rounded and appearing to encompass

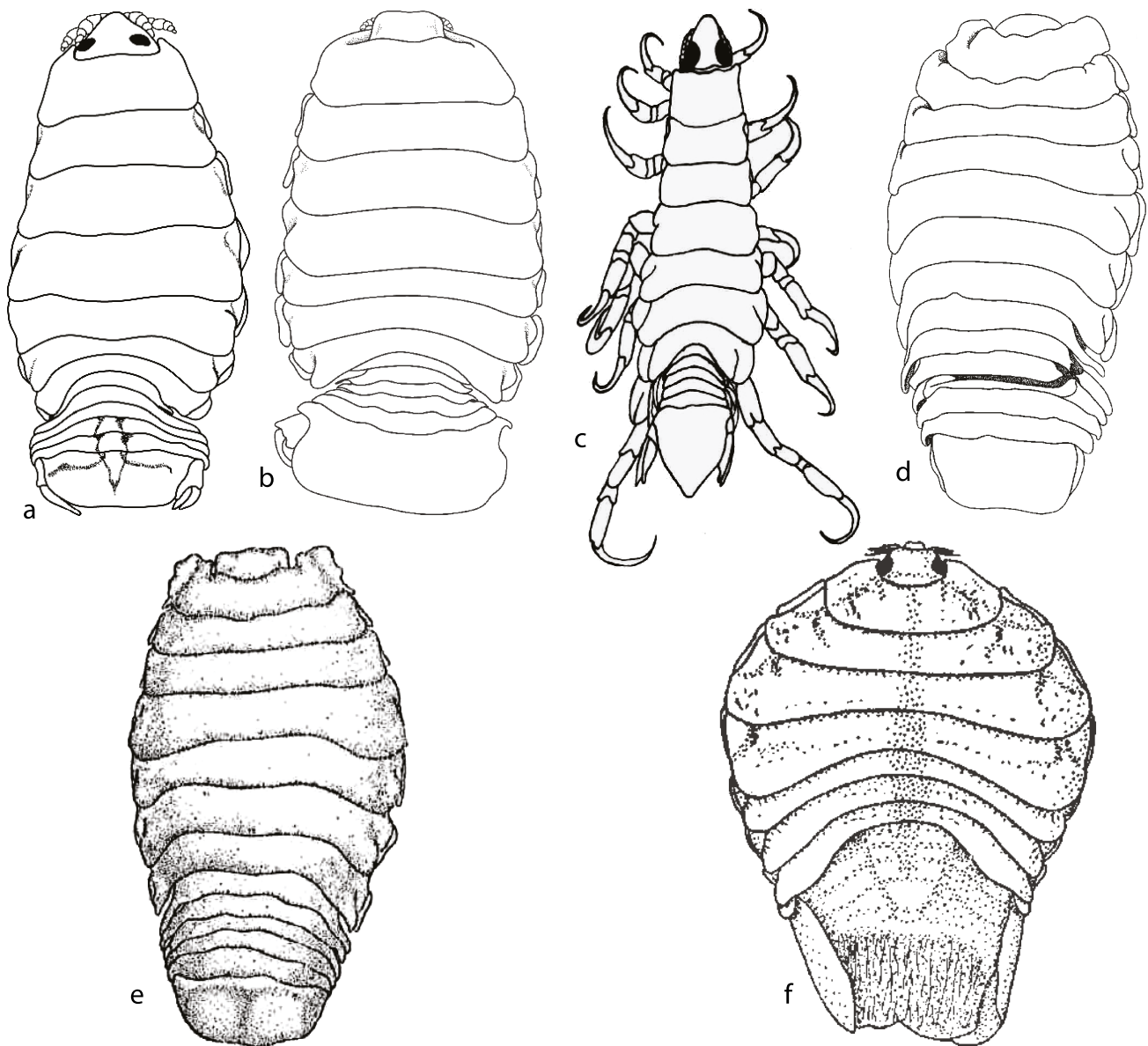


Figure 5.25. Cymothoidea. Buccal-attaching genera, habitus: a, *Ceratothoa banksii* (Leach, 1818); b, *Cymothoa eremita* (Brünnich, 1783); c, *Olencira praegustator* (La Trobe, 1802); d, *Smenispa irregularis* (Bleeker, 1857); e, *Tetragonocephalon lutianus* Avdeev, 1975; f, *Ourozeuktes bopyroides* (Lesueur, 1814).

head (partly encompassing). Pereonites 1–4 of hunched side laterally much expanded from pereopodal bases; posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon about as wide as pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson lateral margins asymmetrical; narrower than pereonite 7 (slightly). Antennula longer than antenna; narrowly separated; articles 1–4 short; terminal article short, nearly reaching or reaching head

posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific. 4 species (Aneesh et al., 2026).

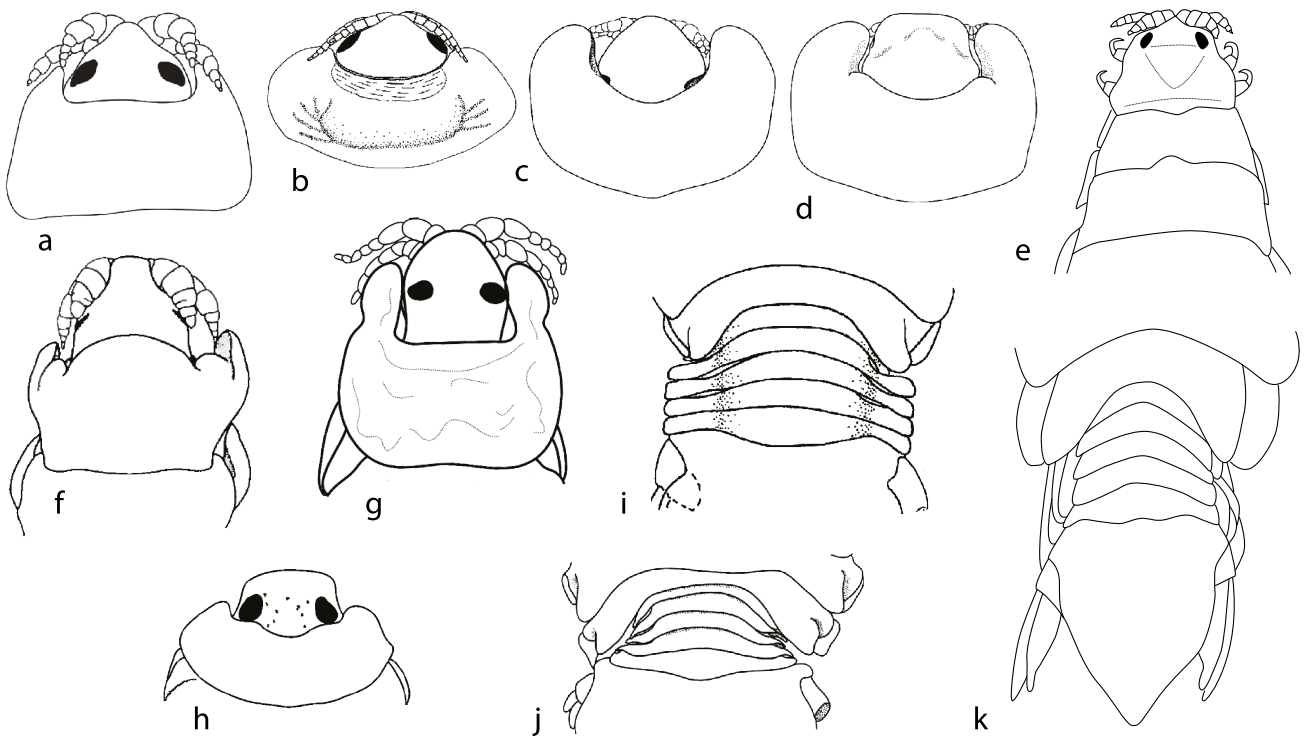


Figure 5.26. Cymothoidae. Buccal-attaching genera, head and pleon: a, *Ceratothoa imbricata* (Fabricius, 1775), head and rostrum; b, *Cinusa tetodontis* Schioedte and Meinert, 1884, head dorsal; c, *Cymothoa carangi* Avdeev, 1979; d, *Cymothoa eremita* (Brünnich, 1783); e, *Emetha audouini* Schioedte and Meinert 1883, anterior dorsal; f, *Glossobius impressus* (Say, 1818), head and pereonite 1; g, *Lobothis nicosmiti* Aneesh, Bruce, Biju Kumar, Bincy and Sreenath, 2021, anterior dorsal; h, *Smenispa irregularis* (Bleeker, 1857), head; i, *Catoessa ambassae* Bruce, 1990, pereonite 7, pleon; j, *Cymothoa eremita* (Brünnich, 1783), pereonite 7, pleon; k, *Olencira praegustator* (La Trobe, 1802), pereonite 7, pleon, pleotelson.

Anilocra Leach, 1818

Diagnosis. Attached to host external body surfaces. Body symmetrical; lateral margins subparallel, or ovate; dorsum strongly vaulted. Rostrum distinct, usually rounded or truncate, ventrally and posteriorly folded, projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin straight or convex, lateral margin convex. Eye large. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than respective pereonite (coxae 2 and 3 shorter than 4); coxae 5–7 shorter than pereonite, not strongly ventrally directed posteriorly, posteriorly narrowly rounded, partially visible in dorsal view (barely for coxae 6 and 7). Pereonite 1 anterolateral margin not produced, flat. Posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonite 1 visible, wider than other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna, bases narrowly separated; article 3 anterodistal margins produced or not; articles 4–8 short: terminal article short, nearly reaching or reaching head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused, with 2 short, hooked robust setae each on mesial and lateral lobe. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin

without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopod 5 only with prominent fleshy ridges; peduncles without lateral lamellar lobes. Uropodal rami long, extending beyond pleotelson posterior margin.

Estuarine, subtidal, shelf (to 550 m). All oceans, except cold and polar waters. 60 species (Bruce, 1987a; Uyeno and Tosuji, 2023; Welicky and Smit, 2019).

Amblycephalon Pillai, 1954

Diagnosis. Attached to host external body surfaces. Body symmetrical; lateral margins subparallel; dorsum not vaulted. Head without rostrum, anterior margin broadly projecting, not immersed in pereonite 1, posterior margin weakly trisinate, lateral margin straight. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 longer than pereonite, not strongly ventrally directed posteriorly, posteriorly narrowly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Posterolateral margins of pereonites 6 and 7 weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonite 1 visible, as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula broader than and longer than antenna; bases widely separated; articles 1–4 short; terminal article short, nearly reaching or

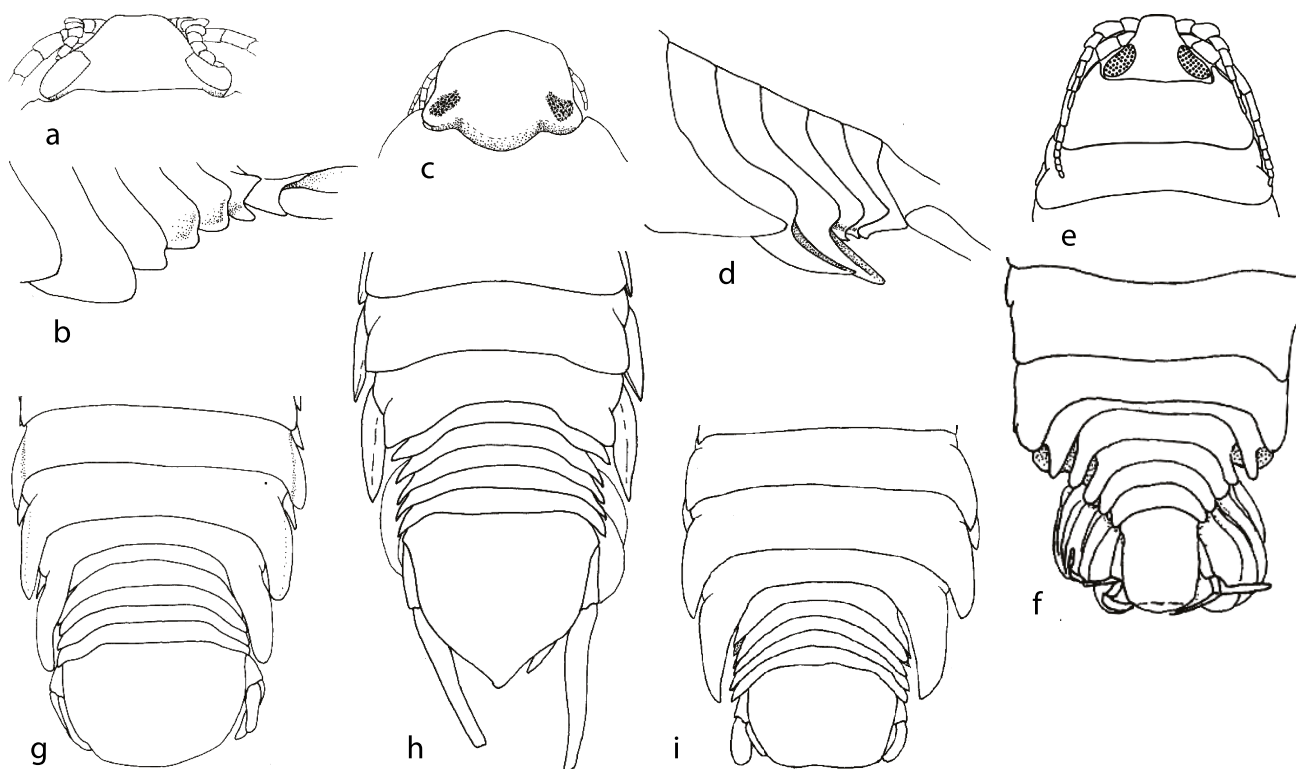


Figure 5.27. Cymothoidae. Externally attaching genera, head and pleon: a, *Anilocra nemipteri* Bruce, 1987, head; b, *Anilocra nemipteri* Bruce, 1987; pleon lateral; c, *Nerocila orbigny* (Guérin-Méneville, 1832), head dorsal; d, *Nerocila orbigny* (Guérin-Méneville, 1832), pleon lateral; e, *Pleopodias elongatus* Richardson, 1910, head, pereonites 1, 2, antennae, dorsal; f, *Pleopodias* sp., pereonites 6, 7, pleon, pleotelson, dorsal; g, *Renocila ovata* Miers, 1880, pereonites 5–7, pleon, pleotelson, dorsal; h, *Amblycephalon schadleri* (Nierstrasz, 1915), pereonites 5–7, pleon, pleotelson, dorsal; i, *Creniola laticauda* (Schioedte and Meinert, 1881), pereonites 5–7, pleon, pleotelson, dorsal.

reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Uropodal rami long, extending beyond or well beyond pleotelson posterior margin.

Subtidal. Western Indo-Pacific. 2 species. The genus is in need of redescription (Bruce, 1987c; Pillai, 1966).

***Bambalocra* Bruce, Welicky, Hadfield and Smit, 2019**

Diagnosis. Attached to host external body surfaces. Body symmetrical; lateral margins ovate; dorsum weakly vaulted. Rostrum distinct, truncate, ventrally and posteriorly folded, projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin concave, lateral margin convex. Eye small. Coxae 2 and 3 smaller than other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 as long as pereonite, not strongly ventrally directed posteriorly, posteriorly prominent and acute, all coxae ventral positioned, not dorsally visible. Pereonite 1 anterolateral margin not produced, flat. Posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 visible, wider than other pleonites;

ventrolateral margins of pleonites 1 and 2 not produced. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles 4–8 short; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with weak fleshy ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Temperate Southern Africa (only from northern Indian Ocean coast of South Africa). 1 species (Bruce et al., 2019).

***Brucethoa* Aneesh, Hadfield, Smit and Kumar, 2020**

Diagnosis. Attached to host gills. Body weakly asymmetrical; lateral margins subparallel (widening posteriorly); dorsum weakly vaulted. Head with distinct rostrum, triangular, ventrally and posteriorly folded, projecting between antennulae bases, not immersed in pereonite 1, posterior margin straight, lateral

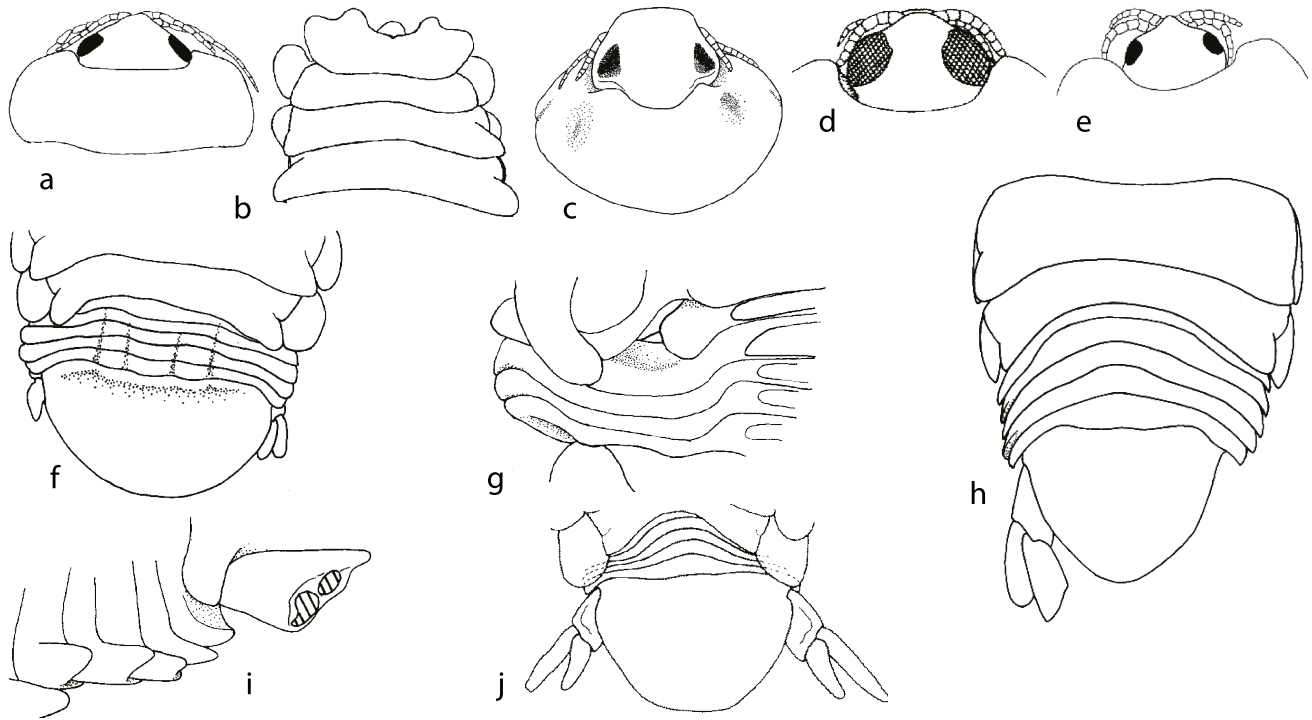


Figure 5.28. Cymothoidae. Gill-attaching genera, head and pleon: a, *Ichthyoxenos minabensis* Shiino, 1951, head, pereonite 1; b, *Joryma sawayah* Bowman and Tareen, 1983, head, anterior pereonites; c, *Livoneca redmanii* Leach, 1818, head, pereonite 1; d, *Mothocya parvostis* Bruce, 1986, head; e, *Sandythoa tiranga* Aneesh, Bruce, Helna and Biju Kumar, 2024, head; f, *Elthusa raynaudii* (Milne Edwards, 1840), pereonite 7, pleon, pleotelson, uropods, dorsal; g, *Elthusa turgidula* (Hale, 1926), pleonites ventral; h, *Livoneca redmanii* Leach, 1818, pereonites 6, 7, pleon, pleotelson, uropod, dorsal; i, *Livoneca redmanii* Leach, 1818, pleonites ventrolateral; j, *Mothocya halei* Bruce, 1986, pereonite 7, pleon, pleotelson, uropod, dorsal.

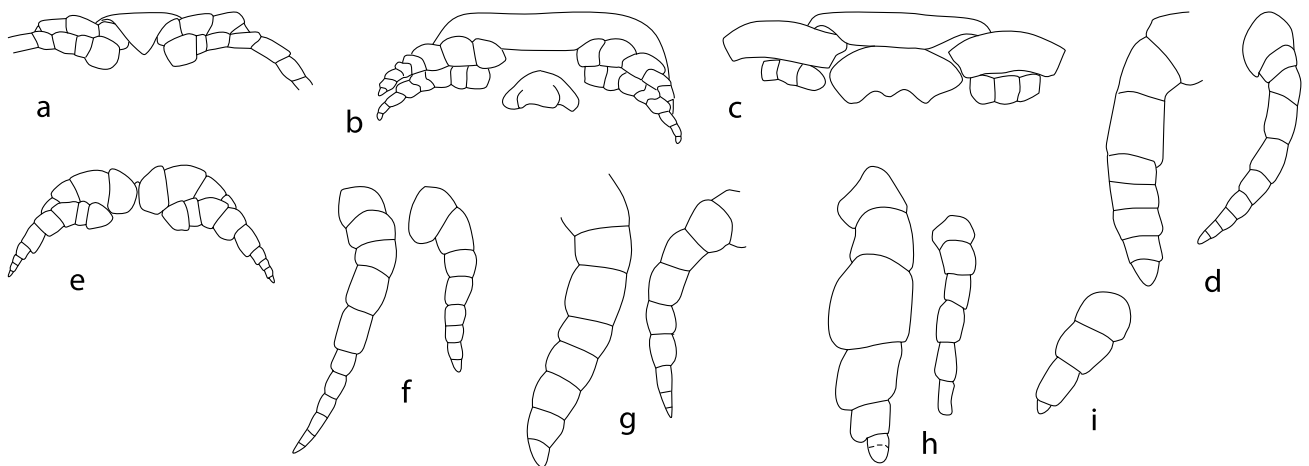


Figure 5.29. Cymothoidae. Frons and antennae: a, *Anilocra nemipteri* Bruce, 1987, frons; b, *Cymothoa eremita* (Brünnich, 1783), antennae ventral; c, *Renocila ovata* Miers, 1880, head ventral; d, *Catoessa ambassae* Bruce, 1990, antenna, antennula; e, *Ceratothoa nipaluna* Bruce, Smit and Hadfield, 2025, antennulae, antennae; f, *Elthusa raynaudii* Milne Edwards, 1840, antenna, antennula; g, *Mothocya colettei* Bruce, 1986, antenna, antennula; h, *Renocila ovata*, Miers, 1880, antenna, antennula; i, *Kuna insularis* (Williams and Williams, 1985), antennula.



Figure 5.30. Cymothoidae. Appendages and brood pouch: a, *Anilocra nemipteri* Bruce, 1987, mandibular palp; b, *Anilocra nemipteri* Bruce, 1987, maxilla apex; c, *Pleopodias* sp., maxilla apex; d, *Pleopodias* sp., mandibular palp; e, *Catoessa ambassae* Bruce, 1990, pereopod 7; f, *Ceratothoa imbricata* (Fabricius, 1775), pereopod 7; g, *Ichthyoxenos minabensis* Shiino, 1951, pereopod 7; h, *Pseudirona laeopsi* Pillai, 1964, pereopod 7; i, *Ceratothoa banksii* (Leach, 1818), brood pouch; j, *Smenispa irregularis* (Bleeker, 1857), posterior pocket. Pleopods: k, *Anilocra nemipteri* Bruce, 1987, pleopod 5; l, *Bambalocra intwala* Bruce, Welicky, Hadfield and Smit, 2019, pleopod 4; m, *Cymothoa rhina* Schioedte and Meinert, 1884, pleopod 5, dorsal; n, *Cinusa tetrodontis* Schioedte and Meinert, 1884, pleopod 5 dorsal; o, *Livoneca redmanii* Leach, 1818, pleopod 1; p, *Livoneca redmanii* Leach, 1818, pleopod 2, dorsal/posterior.

margin convex. Eye large. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin anteriorly acute. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 moderately to strongly produced, posteriorly rounded; pereonite 7 extending past pleonite 1. Pleon as wide as pereon; pleonites with sublateral gaps. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson wider than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles 1–4 short; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch ventrally strongly protruding. Pleopods readily visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami extending slightly beyond pleotelson posterior margin.

Slope (300–600 m). Western Indo-Pacific (India). 1 species (Aneesh et al., 2020).

***Catoessa* Schioedte and Meinert, 1884**

Diagnosis. Attached to host gills or buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum strongly vaulted. Rostrum truncate, not ventrally and posteriorly folded. Head not immersed in pereonite 1, posterior margin straight, lateral margin concave. Eye large or small. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than or as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes convex and progressively increasing; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon; rotationally twisted; pleonites with sublateral gaps. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson as wide as or wider than pereonite 7. Antennula subequal to antenna; bases widely separated; articles 1–3 long; terminal article long, extending beyond head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not or extending slightly beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific. 4 species (Bowman and Tareen, 1983; Bruce, 1990; Trilles et al., 2012).

***Cinusa* Schioedte and Meinert, 1884**

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum strongly vaulted. Rostrum indistinct, triangular, not posteriorly folded.

Head not immersed in pereonite 1, posterior margin concave, lateral margin concave. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes deeply convex and progressively increasing in size; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson as wide as pereonite 7. Antennula broader than and as long as or longer than antenna; bases narrowly separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with large blade-like carina, inferior margin with weak carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf. Temperate Northern W Pacific; Temperate Southern Africa (South Africa, Japan); from puffer fish. 2 species (Hadfield et al., 2010; Nagasawa, 2021).

***Ceratothoa* Dana, 1852**

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel or ovate; dorsum strongly vaulted. Rostrum distinct, triangular, not ventrally and posteriorly folded. Head not or partially immersed in pereonite 1, posterior margin straight, lateral margin straight or concave. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced or anteriorly acute or rounded and appearing to encompass head or lobed. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon as wide as or narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson narrower than or as wide as pereonite 7. Antennae thick and expanded. Antennula broader than and as long as, longer or shorter than antenna; bases in contact; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with large blade-like carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges, with weak unthickened ridge; peduncles without lateral lamellar lobes. Uropodal rami extending slightly beyond pleotelson posterior margin.

Estuarine, subtidal, shelf (shallow to about 100 m). All oceans except polar seas. 27 species (Hadfield et al., 2014, 2016; Martin et al., 2015b).

***Creniola* Bruce, 1987**

Diagnosis. Attached to host external body surfaces. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum weakly vaulted. Head without rostrum, anterior margin truncate, not ventrally and posteriorly folded, not immersed in pereonite 1, posterior margin trisinate, lateral margin concave. Eye small, partially visible. Coxae 2 and 3 smaller than other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, strongly ventrally directed, posteriorly prominent and acute, not visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 moderately to strongly produced, posteriorly rounded; pereonite 7 extending past pleonite 1. Pleon almost as wide as or narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7, or visible, as wide as other pleonites; 1 and 2 ventrolateral margin not produced. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases widely separated; articles 4–8 short; terminal article long, extending beyond head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 longer than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with weak fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf (shallow to 133 m). Central and Eastern Indo-Pacific, Temperate Australasia. 3 species (Bruce, 1987c).

***Cterissa* Schioedte and Meinert, 1884**

Diagnosis. Attached to host gills. Body twisted to one side; lateral margins ovate or somewhat asymmetric; dorsum not vaulted. Rostrum distinct; triangular or truncate, ventrally and posteriorly folded, projecting between antennulae bases. Head immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye small. Coxae unequal on both sides of body; coxae 2 and 3 similar to other coxae; coxae 2–4 longer than respective pereonite; coxae 5–7 longer than pereonite, posteriorly broadly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin rounded and appearing to encompass head. Pereonites 1–4 of hunched side not expanded from pereopodal bases; posterolateral lobes deeply convex and progressively increasing in size; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson wider than pereonite 7. Antennula shorter than antenna; bases widely separated; articles short; terminal article nearly reaching or reaching head posterior margin. Antenna long, extending beyond

pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch ventrally not or weakly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf. Indo-West Pacific. 4 species (Bunkley-Williams and Williams, 1986). The genus needs revision.

***Cymothoa* Fabricius, 1793**

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel; dorsum strongly vaulted. Rostrum indistinct, anterior margin truncate, rounded or concave, ventrally folded, weakly projecting between antennulae bases. Head three quarters immersed in pereonite 1, posterior margin straight, lateral margin concave. Eye absent. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin anteriorly acute or rounded, appearing to encompass head. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson as wide as or narrower than pereonite 7. Antennula shorter than antenna; bases widely separated; articles 1–4 short; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct or partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with large blade-like carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with well developed fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Estuarine, subtidal, shelf. World oceans except polar waters. 42 species (Hadfield et al., 2013; Martin et al., 2016).

***Elthusa* Schioedte and Meinert, 1884**

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum weakly vaulted. Rostrum distinct, truncate, ventrally and posteriorly folded, projecting between antennulae bases or not ventrally and posteriorly folded. Head three quarters immersed in pereonite 1, posterior margin straight, lateral margin concave. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite, not strongly ventrally directed posteriorly, posteriorly broadly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin anteriorly acute or rounded. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7

extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as or narrower than other pleonites (usually slightly narrower). Pleotelson as wide as or narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with or usually without carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf and slope (shallow to about 1000 m). Worldwide, except polar waters. 34 species. The most recent revision of the genus is that of Aneesh et al. (2020). Since then, several species have been removed to other genera (*Brucethoa*, *Glyptothoa* and *Sandythoa*) and direct comparison to the diagnoses of those recently described genera is advised (Aneesh et al., 2020).

***Emetha* Schioedte and Meinert, 1883**

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum strongly vaulted. Rostrum distinct, triangular, not ventrally and posteriorly folded; dorsally not projecting between antennae. Head partially immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson narrower than pereonite 7. Antennae thick, expanded. Antennula shorter than antenna; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal. Pereopods 5–7 basis superior margin with large blade-like carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view, peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Temperate North Atlantic. 2 species. The genus potentially differs from *Ceratothoa* by a single character; no modern revision or redescription exists and many generic characters are unknown (Trilles, 1994).

***Gibbothoa* Aneesh, Hadfield, Bruce, Helna, Smit and Biju Kumar, 2026**

Diagnosis. Attached to host gills. Body strongly asymmetrical or distorted; lateral margins strongly hunched on one side; dorsum

strongly vaulted. Rostrum indistinct, weakly ventrally folded. Head partially immersed in pereonite 1, posterior margin concave (arc to posterior), lateral margin convex. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, conspicuous in dorsal view. Pereonite 1 anterior margin deeply incised, anterolateral margin produced or anteriorly acute. Pereonites 1–4 of hunched side laterally much expanded from pereopodal bases; posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 moderately to strongly produced, or not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson narrower than pereonite 7. Antennula much shorter than antenna; bases narrowly separated; articles short; terminal article nearly reaching or reaching head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopod 5 only with prominent fleshy ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Shelf. Central Indo-Pacific (India). 1 species (Aneesh et al., 2026).

***Glossobius* Schioedte and Meinert, 1883**

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel; dorsum strongly vaulted. Rostrum distinct, triangular or truncate, not ventrally or posteriorly folded. Head not immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than or as long as respective pereonite; coxae 5–7 shorter than pereonite, not strongly ventrally directed posteriorly, posteriorly broadly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin not produced; flat or laterally lobed. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending or not extending laterally past pleonite 1. Pleon as wide as or narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7 or visible, narrower than other pleonites. Pleotelson as wide as or wider than pereonite 7. Antennae thick and expanded. Antennula shorter than antenna; bases in contact; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis superior margin with large blade-like carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with weak fleshy ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Shelf. Pelagic. Tropical Atlantic, Temperate Northern W Pacific, Tropical Eastern Pacific, Indo-West Pacific (world

oceans; primarily on pelagic hosts). 8 species (Bruce and Bowman, 1989; Martin et al., 2015a).

***Glyptothoa* Helna, Aneesh, Kumar and Ohtsuka, 2023**

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum weakly vaulted. Rostrum distinct; small, acute, anteriorly projecting between antennulae. Head three quarters immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye large. Coxae 2 and 3 larger than other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced. Pereonites 1–4 of hunched side not expanded from pereopodal bases; posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon wider than pereon; pleonites with sublateral gaps. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson as wide as pereonite 7. Antennula shorter than antenna; bases narrowly separated; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis margins without carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf and slope (shallow to 650 m). Temperate Northern W Pacific, Indo-West Pacific. Northwestern Pacific. 4 species (Helna et al., 2023).

***Ichthyoxenos* Herklots, 1870**

Diagnosis. Attached to host gills or buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum strongly vaulted. Rostrum indistinct, triangular or rounded, ventrally and posteriorly folded, weakly projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, strongly ventrally directed, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as or slightly narrower than other pleonites. Pleotelson as wide as or narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles short; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis margins without carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods

lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf and slope (shallow to at least 366 m). Temperate Northern W Pacific, Indo-West Pacific. Marine species reported primarily from the Pacific Ocean; freshwater species from continental Africa and Asia. 27 species (4 marine). The genus includes freshwater flesh-burrowing species and marine buccal-attaching species, and is likely not monophyletic (Boyko and Bruce, 2026). This diagnosis applies only to the marine species (Bruce, 1990; Mitra and Chowdhury, 2024). The name has sometimes been misspelled as *Ichthyoxenus*.

***Idusa* Schioedte and Meinert, 1884**

Diagnosis. Attached to host gills or buccal cavity. Body symmetrical, weakly asymmetrical or twisted to one side; lateral margins ovate; dorsum strongly vaulted. Rostrum triangular. Head partially immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 of hunched side not expanded from pereopodal bases; posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated. Pereopods 5–7 basis margins without carina. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Temperate North Atlantic, Tropical Eastern Pacific, Mediterranean. 3 species. Generic position of the one East Pacific species is doubtful. No detailed generic or species descriptions exists so many characters are unknown (Bruce, 1990).

***Joryma* Bowman and Tareen, 1983**

Diagnosis. Attached to host gills (inner surface of operculum). Body twisted to one side; lateral margins somewhat asymmetric; dorsum weakly or strongly vaulted. Rostrum indistinct, rounded, weakly ventrally folded. Head three quarters immersed in pereonite 1, posterior margin convex, lateral margin convex. Eye small. Coxae 2 and 3 larger than other coxae; coxae 2–4 longer than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin lobed. Pereonites 1–4 of hunched side not expanded from pereopodal bases; posterolateral lobes deeply convex and progressively increasing in size; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon as wide as pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases widely separated; articles short; terminal article nearly

reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp stout, articles wholly or partly fused. Maxilla mesial lobe partially fused. Maxilliped without oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific. 6 species (Aneesh et al., 2019).

***Kuna* Bunkley-Williams and Williams, 1986**

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins subparallel; dorsum strongly vaulted. Rostrum indistinct, rounded, ventrally and posteriorly folded, projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite, not strongly ventrally directed posteriorly, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon about as wide as pereon. Pleonites 1–5 strongly produced ventrally; pleonite 1 visible, as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; widely separated; fewer than 5 short articles; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin without carina. Brood pouch not known. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Temperate Northern W Pacific. 1 species (Williams and Bunkley-Williams, 1986; Williams and Williams, 1985).

***Livoneca* Leach, 1818**

Diagnosis. Attached to host gills. Body symmetrical, weakly asymmetrical or twisted to one side; lateral margins ovate; dorsum weakly vaulted. Head without rostrum, anterior margin truncate. Head not immersed in pereonite 1, posterior margin trisinate, lateral margin straight. Eye small. Coxae 2 and 3 smaller than other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 as long as pereonite or longer than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna;

widely separated; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with well developed fleshy ridges; pleopods 2–5 peduncle with well developed branchiae; peduncles with lateral lamellar lobes. Uropodal rami extending slightly beyond pleotelson posterior margin.

Estuarine and subtidal. Temperate North Atlantic, Tropical western Atlantic. 3 species. The genus is New World Atlantic in distribution, with one introduced species now widely reported from Egypt and the Suez Canal region (Bruce, 1990; Mahmoud et al., 2023).

***Lobothorax* Bleeker, 1857**

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel; dorsum strongly vaulted. Rostrum distinct, triangular, not ventrally and posteriorly folded. Head three quarters immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye small. Coxae 2 and 3 smaller than other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterior margin with prominent anterolateral lobes, anterolateral margin lobed. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon subequal to pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson wider than pereonite 7. Antennula longer than antenna; bases widely separated; articles 1–3 long; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin with weak carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 4 and 5 with very weak fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami extending slightly beyond pleotelson posterior margin.

Subtidal, shelf. Temperate Northern W Pacific; Central Indo-Pacific. 4 species (Aneesh et al., 2021).

***Mothocya* Costa in Hope, 1851**

Diagnosis. Attached to host gills (occasionally buccal cavity). Body symmetrical, weakly asymmetrical or twisted to one side; lateral margins ovate; dorsum not vaulted. Rostrum indistinct, narrowly rounded or truncate, ventrally and posteriorly folded. Head three quarters immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye large. Coxae more-or-less equal on both sides of body (slightly larger on convex side in some species); coxae 2 and 3 smaller than other coxae; coxae 2–4 longer than respective pereonite; coxae 5–7 longer than or as long as pereonite, posteriorly broadly rounded, conspicuous in

dorsal view. Pereonite 1 anterolateral margin rounded, sometimes partly encompassing head. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon about as wide as pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; narrower than other pleonites. Pleotelson as wide as or wider than pereonite 7. Antennula broader than, as long as or longer than antenna; bases widely separated; articles short; terminal article nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch strongly ventrally protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without or with weak lateral lamellar lobes. Uropodal rami long, extending beyond pleotelson posterior margin.

Estuarine and subtidal (to at least 908 m). Worldwide except polar waters. 30 species. The genus primarily uses Beloniformes as hosts (Bruce, 1986; Hadfield et al., 2015; van der Wal et al., 2021).

***Nerocila* Leach, 1818**

Diagnosis. Attached to host external body surfaces. Body symmetrical or weakly asymmetrical; lateral margins subparallel or ovate; dorsum not vaulted. Head without rostrum; anterior margin weakly rounded or truncate. Head not immersed in pereonite 1, posterior margin trisinate, lateral margin convex. Eye large or small. Coxae 2 and 3 smaller than other coxae; coxae 2–4 as long as or longer than respective pereonite; coxae 5–7 longer than or as long as pereonite, not strongly ventrally directed posteriorly, posteriorly prominent and acute or narrowly rounded or broadly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 variably produced, sometimes acute; pereonite 7 extending laterally past pleonite 1, or not. Pleon narrower than pereon. Pleonite 1 visible, as wide as or wider than other pleonites (usually slightly wider); pleonites 1 and 2 ventrolateral margin strongly produced. Pleotelson narrower than pereonite 7. Antennula ranging from shorter to longer than antenna; bases widely separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal or 2 slightly longer. Maxilla mesial lobe usually distinct. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods 3–5 with weak fleshy ridges, or endopod 5 only with prominent fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami long, extending beyond pleotelson posterior margin.

Estuarine, subtidal, shelf. World-wide except polar and subpolar seas. 41 species. While readily recognised by the conspicuous ventrolateral processes on pleonites 1 and 2, other characters, such as the extent to which the posterolateral

margins of pereonites 6 and 7 and the coxae are posteriorly produced, vary considerably (Aneesh, Helna et al., 2017; Aneesh, Valarmathi et al., 2017; Bruce, 1987c).

***Norileca* Bruce, 1990**

Diagnosis. Attached to host gills. Body twisted to one side; lateral margins ovate (weakly ovate on one side); dorsum weakly vaulted. Head with distinct rostrum in ventral view; rostrum truncate, ventrally and posteriorly folded, projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin concave, lateral margin straight. Eye large. Coxae 2 and 3 smaller than other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1 or extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 visible, as wide as or wider than other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than or as long as antenna; bases widely separated; articles 1–3 long; terminal article long, extending beyond head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped without oostegite lobe. Pereopod 1 propodus with robust setae present or absent; pereopods 5–7 basis superior margin without carina or with carina, inferior margin with weak carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopod 5 only with prominent fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific. 4 species (Bruce, 1990; Nashad et al., 2022; van der Wal et al., 2017).

***Olencira* Leach, 1818**

Diagnosis. Attached to host gills or buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel; dorsum strongly vaulted. Head without rostrum. Head not immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye large. Coxae 2 and 3 larger than other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter and stouter than antenna; bases in contact; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 longer than article 2. Maxilla mesial lobe distinct. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch ventrally strongly protruding. Pleopods barely

visible in dorsal view; endopods 3–5 with well developed fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf. Temperate North Atlantic, Tropical Atlantic (Atlantic coast of North America and northern Caribbean). 1 species (Trilles, 2007).

***Ourozeuktes* Milne Edwards, 1840**

Diagnosis. Burrowing into flesh of host. Body symmetrical or weakly asymmetrical; lateral margins strongly ovate; dorsum weakly vaulted. Head without rostrum. Head partially immersed in pereonite 1, posterior margin concave, lateral margin convex. Eye small. Coxae 2 and 3 similar to or smaller than other coxae; coxae 2–4 longer than respective pereonite; coxae 5–7 as long as pereonite, strongly ventrally directed, posteriorly narrowly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon; pleonites fused, without lateral gaps. Pleonites 1 and 2 ventrolateral margin not produced. Pleotelson narrower than pereonite 7. Antennula broad, shorter than antenna; bases widely separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 2 oostegite lobes. Pereopods 5–7 basis superior margin without carina, inferior margin with large blade-like carina (also on ischium). Pleopods barely visible in dorsal view, peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Temperate Australasia (Australian endemic hosted especially by leatherjackets, family Monacanthidae). 1 species (Hale, 1926). The only species *O. bopyroides* (Lesueur, 1814) needs redescription.

***Pleopodias* Richardson, 1910**

Diagnosis. Attached to host external body surfaces. Body symmetrical; lateral margins subparallel or weakly ovate; dorsum strongly vaulted. Head with distinct rostrum; rostrum truncate in dorsal view, triangular or truncate, ventrally and posteriorly folded, projecting between antennulae bases. Head not immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye large. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, not visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonites 3–5 or 4 and 5 less than half width (c. 0.45) of pereon. Pleonite 1 visible, not laterally produced; pleonites 1 and 2 lateral margin ventrally produced. Pleotelson posteriorly narrowing strongly; narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles 1–3 long; article 3 anterodistal

margins produced; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct; with 2 large nodular robust setae each on mesial and lateral lobe. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods readily visible in dorsal view; endopod 5 only with prominent fleshy ridges (weak lobes); peduncles without lateral lamellar lobes. Uropodal rami long, extending slightly or well beyond pleotelson posterior margin.

Subtidal, shelf and slope (to 380 m). Temperate Northern W Pacific, Indo-West Pacific, Temperate Southern Africa. 4 species (Bruce, 1987a; Hadfield and Smit, 2017).

***Plator* Schioedte and Meinert, 1881**

Diagnosis. Host attachment not known, but here assumed as external. Body symmetrical; lateral margins ovate; dorsum strongly vaulted. Head without rostrum. Head not immersed in pereonite 1, posterior margin trisinate, lateral margin convex. Eye small. Coxae 2 and 3 smaller than other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 longer than pereonite, strongly ventrally directed, posteriorly broadly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonites 1–5 strongly produced ventrally; pleonite 1 visible, wider than other pleonites; pleonites 1 and 2 ventrolateral margin not produced. Pleotelson narrower than pereonite 7. Uropodal rami extending slightly beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific (distribution quoted as “Indian Ocean”; likely coastal Papua or West Papua, Indonesia). 1 species. The genus and species are effectively undescribed (Bruce, 1987c).

***Renocila* Miers, 1880**

Diagnosis. Attached to host external body surfaces. Body symmetrical or weakly asymmetrical; lateral margins subparallel or convex; dorsum weakly vaulted. Head with or without ventral rostrum; anterior margin folded. Head not immersed in pereonite 1, posterior margin straight, lateral margin straight. Eye small. Coxae 2 and 3 larger than other coxae; coxae 2–4 as long as respective pereonite, or longer than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly prominent, acute or rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin not produced, flat. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 produced; pereonite 7 extending laterally past pleonite 1 or not. Pleon narrower than pereon. Pleonite 1 visible or partially visible, laterally concealed by pereonite 7; as wide as or wider than other pleonites. Pleotelson narrower than pereonite 7. Antennula broader than and as long as antenna; bases widely separated; article 5 long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than or subequal to article 2. Maxilla mesial

lobe distinct, or partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin without carina, inferior margin without or with weak carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopod 5 only with prominent fleshy ridges; peduncles without lateral lamellar lobes. Uropodal rami extending slightly beyond or not extending beyond pleotelson posterior margin.

Subtidal, shelf. Tropical Atlantic and Indo-West Pacific (shallow-water tropical coastal habitats). 20 species. Many characters vary suggesting that the genus is probably not monophyletic (Aneesh et al., 2022; Bruce, 1987b).

Ryukyua Williams and Bunkley-Williams, 1994

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins ovate (strongly); dorsum strongly vaulted. Head without distinct rostrum; anterior margin rounded, folded, ventrally projecting between antennulae bases. Head partially immersed in pereonite 1, posterior margin straight, lateral margin convex. Eye large. Coxae 2 and 3 similar to other coxae; coxae 2–4 longer than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin lobed. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 produced, posteriorly rounded; pereonite 7 extending past pleonite 1. Pleon narrower than pereon. Pleonite 1 partially visible, laterally concealed by pereonite 7; as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula longer than antenna; bases widely separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe partially fused. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis superior margin with carina, inferior margin with weak carina. Brood pouch ventrally strongly protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal. Indo-West Pacific (India, southern Japan). 2 species (Williams and Bunkley-Williams, 1994).

Pseudirona Pillai, 1964

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins ovate. Head without distinct rostrum. Head partially immersed in pereonite 1, posterior margin weakly convex, lateral margin convex. Eye large. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly narrowly rounded, conspicuous in dorsal view. Pereonite 1 anterolateral margin anteriorly acute. Pereonites 1–4 posterolateral lobes convex and consistent; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon as wide as pereon. Pleonite 1 not visible, completely concealed by pereonite 7; narrower than other pleonites. Pleotelson wider than pereonite 7. Antennula longer than antenna; articles 1–3 long; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1

anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Maxilliped with 2 oostegite lobes. Pereopod 1 propodus with robust setae; pereopods 5–7 basis superior margin without carina; pereopods 4–7 ischium and merus with conspicuous blade-like carina, inferior margin without carina. Pleopods barely visible in dorsal view. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal (274 m). Western Indo-Pacific (Trivandrum, Kerala Coast, India). 1 species. The setose pereopods and carinate ischium and merus on the posterior pereopods are distinctive. The only species *P. laeopsi* Pillai, 1964 needs redescription (Pillai, 1964; Ravichandran et al., 2019).

Sandythoa Aneesh, Bruce, Helna and Biju Kumar, 2024

Diagnosis. Attached to host gills. Body symmetrical or weakly asymmetrical; lateral margins ovate; dorsum weakly vaulted. Head with rostral point; rostrum rounded or acute, not ventrally and posteriorly folded. Head partially immersed in pereonite 1, posterior margin concave, lateral margin convex. Eye small. Coxae 2 and 3 similar to other coxae; coxae 2–4 shorter than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced. Pereonites 1–4 posterolateral lobes convex and consistent, or deeply convex and progressively increasing in size; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending past pleonite 1. Pleon narrower than pereon; pleonites with sublateral gaps. Pleonite 1 partially visible, laterally concealed by pereonite 7; much narrower than other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases narrowly separated; articles short; terminal article short, nearly reaching or reaching head posterior margin. Antenna short, nearly reaching or reaching pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal. Maxilla mesial lobe distinct. Maxilliped with 1 oostegite lobe. Pereopods 5–7 basis margins without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopods lamellar, without fleshy lobes or thickened ridges; peduncles without lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf and slope (shallow to 401 m). Indo-West Pacific. 5 species (Aneesh et al., 2024).

Smenispa Özdikmen, 2009

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; dorsum strongly vaulted. Head without rostrum; partially immersed in pereonite 1, posterior margin concave, lateral margin convex. Eye small or partially visible. Coxae 2 and 3 similar to other coxae; coxae 2–4 as long as respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced or rounded, appearing to encompass head. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 extending laterally past pleonite 1 or not. Pleon narrower than pereon. Pleonite 1

visible, as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; bases widely separated; articles 1–3 long; terminal article short, nearly reaching or reaching head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp articles 2 and 3 subequal. Maxilla mesial lobe partially fused. Maxilliped not described. Pereopods 5–7 basis superior margin with carina, inferior margin without carina. Brood pouch not ventrally protruding. Pleopods barely visible in dorsal view; endopod 5 only with prominent fleshy ridges or endopods 3–5 with well developed fleshy ridges; peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal, shelf. Tropical Eastern Pacific; Eastern Indo-Pacific (east Pacific off coast of North America, Central America and northern South America). 2 species (Bruce, 1990; Martin et al., 2014). The genus was previously known as *Enispa* Schioedte and Meinert, 1884.

***Tetragonocephalon* Avdeev, 1975**

Diagnosis. Attached to host buccal cavity. Body symmetrical or weakly asymmetrical; lateral margins subparallel. Head without rostrum. Head three quarters immersed in pereonite 1, posterior margin concave (arc to posterior), lateral margin straight. Eye absent. Coxae 2 and 3 larger than other coxae; coxae 2–4 as long as or longer than respective pereonite; coxae 5–7 shorter than pereonite, posteriorly broadly rounded, partially visible in dorsal view. Pereonite 1 anterolateral margin produced. Pereonites 1–4 posterolateral lobes smooth and straight; posterolateral margins of pereonites 6 and 7 not or weakly produced; pereonite 7 not extending laterally past pleonite 1. Pleon narrower than pereon. Pleonite 1 visible, as wide as other pleonites. Pleotelson narrower than pereonite 7. Antennula shorter than antenna; articles short; terminal article long, extending beyond head posterior margin. Antenna long, extending beyond pereonite 1 anterior margin. Mandible palp article 3 shorter than article 2. Maxilla mesial lobe distinct. Pereopods 5–7 basis superior margin without carina, inferior margin with weak carina. Pleopods barely visible in dorsal view, peduncles with lateral lamellar lobes. Uropodal rami not extending beyond pleotelson posterior margin.

Subtidal or shelf (depth unknown). Indo-West Pacific (known only from type locality). 1 species (Avdeev, 1975).

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Gnathiidae Leach, 1814

Figures 5.31–5.33

Gnathiids are most unusual isopods, polymorphic in the extreme. Males are immediately recognisable by their large mandibles directed forwards from the cephalosome (figs 5.31a, 5.32). The first pereopods are usually modified as “pylopods”, operculate and protecting the other mouthparts (Cohen and Poore, 1994). The pereon bears only 5 pairs of walking legs, pereopod 7 being absent in adults. Males settle after their final instar in crevices in the sediment, mud, submerged wood, sponges, coral rubble or cavities in the reef, do not feed, and may gather a harem of females in their “home” (Klitgaard, 1997; Smit et al., 2003; Tanaka, 2007; Wägele, 1988). Females have more reduced jaws and a thorax swollen with ovary or eggs, sometimes more than a hundred (fig. 5.31b). The juveniles, or praniza larvae (fig. 5.31c), pass through three instars in the only species studied (Juilfs and Wägele, 1987; Wägele, 1988), each feeding on blood as ectoparasites of fishes (Smit and Davies, 2004). The role of the praniza stage (to describe a juvenile with a gut full of blood) and the zuphea (the unfed stage) as ectoparasites of fishes is well studied. The larvae use their sharp mouthparts to penetrate skin and suck blood. They are important ectoparasites, especially on coral reefs (Grutter, 1996, 1999; Smit, 2000; Smit and Davies, 2004; Smit et al., 2003; Tanaka, 2006).

The taxonomy of Gnathiidae was the subject of a monograph by Monod (1926) and was revised more extensively by Cohen

and Poore (1994). These authors justified new genera on a cladistic analysis using morphological characters. Since then, Kensley et al. (2009), Smit and coauthors and Svavarsson and Bruce (2019) have added many species. A key to genera similar to the one below can be found in Ota et al. (2025).

Diagnosis. Males with enlarged head, anteriorly directed mandibles, pereonite 1 short, fused into cephalosome; pereonite 7 shorter than pereonites 2–6; females with pereon swollen with ovary or embryos. Eyes contiguous or almost contiguous anterodorsally and extending from anterior margin to posterior margin of head (*Tenerognathia* only), or widely separated, lateral, sometimes small or absent. Mandibles in males enlarged, projecting anteriorly and together forceps-like. Maxillula usually absent. Pereopod 1 modified as pylopod ventrally overlying mouthparts, pereopod 7 absent as adults. Ectoparasitic as juveniles, usually on fishes.

Implicit generic attributes. Eyes present. Paraocular ornamentation on cephalosome absent. Mandibular incisor absent. Maxillula absent. Maxilliped 5-articled, external margins of articles 2–5 bearing plumose setae. Pereonite 1 not produced laterally, immersed in cephalosome. Pereonite 3 without large anteriorly directed projection. Pleon not folded under pereon.

Key to genera of Gnathiidae (adult males only)

1. Pylopod large, distinct (fig. 5.33e–j, m–p, r). Maxillipedal palp 4-articled (fig. 5.33b–d) 2
- Pylopod thin, elongate (difficult to see even under dissecting microscope) (fig. 5.33l, r). Maxilliped absent or reduced (fig. 5.33k, q) 11
2. Pylopod of 5–6 visible articles; basis distinct (fig. 5.33f, g, j, n, o) 3
- Pylopod of 1–3 visible articles; basis fused to pereonite (fig. 5.33e, d, h, i, m) 7
3. Frontal border with processes, transverse; with pronounced paraocular ornamentation (fig. 5.32b)
..... *Euneognathia*
- Frontal border without processes, rounded or produced, or minute process; lacking paraocular ornamentation
..... 4
4. Pylopod pereopod-like, not operculate (fig. 5.33g). Pereonite 1 greatly produced dorsoposteriorly (fig. 5.32n) ...
..... *Bythognathia*
- Pylopod operculate. Pereonite 1 not greatly produced 5
5. Pylopod 6-articled, ischium longer than wide, merus free, short, more distal articles ovoid (fig. 5.33o).
Mandibular blade dentate (fig. 5.32l). Total length <5 mm *Paragnathia*
- Pylopod 5- or 6-articled, merus fused with distal articles forming triangular operculum (fig. 5.33f, n).
Mandibular blade smooth or absent (fig. 5.32g, k). Total length >5 mm 6
6. Mandible without blade. Buccal cavity wall extension visible at the end of pronounced rostrum (fig. 5.32g) ...
..... *Bathygnathia*
- Mandibular blade smooth. Frontal border rounded, without buccal cavity wall protrusion (fig. 5.32k)
..... *Monodgnathia*
7. Cephalosome spherical, eyes occupying entire side (fig. 5.32m) *Tenerognathia*
- Cephalosome box-like; eyes occupying fraction of side 8
8. Pylopod of a single operculate plate (fig. 5.33e). Maxillula present (fig. 5.33a) *Afrignathia*
- Pylopod of 2 or 3 articles (fig. 5.33h, d, m). Maxillula absent 9
9. Frontal border without frontal process, often rounded; cephalosome lacking paraocular ornamentation and
dorsal sulcus (fig. 5.32a, h) *Caecognathia*
- Frontal border with frontal processes, often transverse; cephalosome may possess paraocular ornamentation
and/or a dorsal sulcus 10
10. Frontal border not deeply excavated. Mandibles not elongate (fig. 5.32d, j) *Gnathia*
- Frontal border excavated. Mandibles long, lacking dentate blade (fig. 5.32i) *Elaphognathia*
11. Pereon smooth, oval; pereonite 3 without dorsal, anteriorly-directed projection; pereonite 7 not visible.
Pleon often folded under pereon. Antennae curved under mandibles (fig. 3.0). Mandible blade crenulate;
incisor present (fig. 5.32e) *Thaumastognathia*
- Pereon covered in granules and setae, rectangular; pereonite 3 with large dorsal, anteriorly-directed
projection; pereonite 7 visible, small. Mandibular blade reduced or absent; incisor absent (fig. 5.32c)
..... *Gibbagnathia*

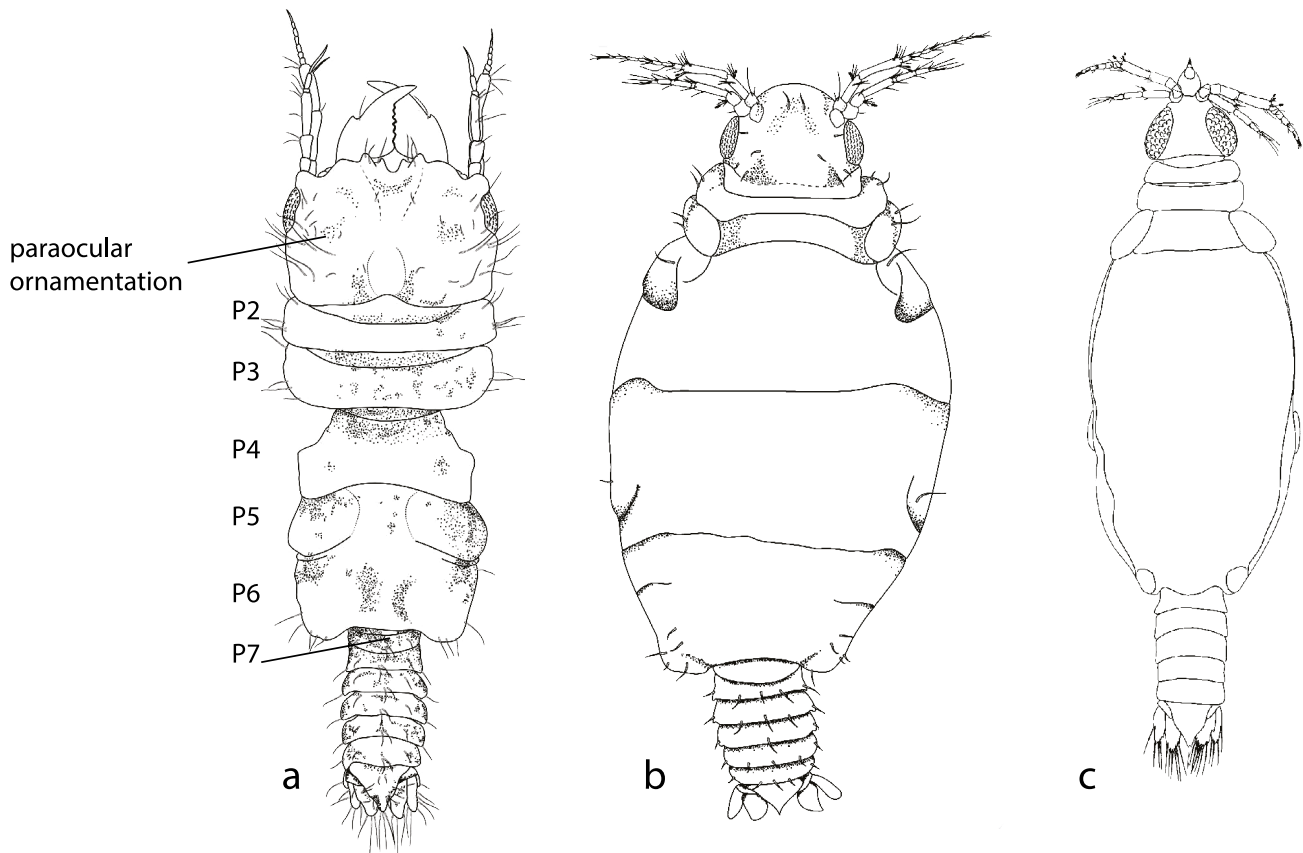


Figure 5.31. Gnathiidae. *Gnathia jimmybuffetti* Erasmus, Hadfield, Sikkell and Smit, 2023: a, adult male; b, female; c, praniza larva (not to same scale).

***Afrignathia* Hadfield and Smit, 2008**

Diagnosis. Frontal border excavated, processes present. Mandibular blade with 2 rows of teeth. Maxillula present. Pylopod comprising single fused article, operculate. Length of male less than 3 mm.

Shelf. Temperate Southern Africa. 1 species (Hadfield and Smit, 2008).

***Bathygnathia* Dolfuss, 1901**

Diagnosis. Eyes present, or absent. Frontal border produced as rostrum, processes absent. Mandibular incisor slight, or absent; blade absent. Pylopod basis free, distal 3 articles triangularly operculate. Length of male 5–10 mm.

Bathyal, abyssal. North and South Atlantic, New Zealand, subantarctic, Indian Ocean basins, Central Indo-Pacific, Southern Ocean. 15 species (Cohen and Poore, 1994: rediagnosis; key to 5 species from Australia and New Zealand; Shimomura, 2008: 2 species).

***Bythognathia* Camp, 1988**

Diagnosis. Eyes absent. Frontal border produced as rostrum, processes absent. Mandibular blade smooth. Pylopod of 4

articles, filiform. Pereonite 1 produced (partially obscuring pereonite 2). Length of male about 20 mm.

Bathyal. Caribbean. 1 species (Camp, 1988: diagnosis, description of type species; Cohen and Poore, 1994: rediagnosis).

***Caecognathia* Dolfuss, 1901**

Diagnosis. Frontal border transverse, processes absent. Mandibular blade smooth. Pylopod basis free, remaining articles triangularly operculate. Length of male less than 5 mm.

Subtidal–bathyal. Cosmopolitan. 48 species (Cohen and Poore, 1994: rediagnosis, key to 10 species from Australia; Ota et al., 2025: key to species from Japan).

***Elaphognathia* Monod, 1926**

Diagnosis. Frontal border excavated, processes present. Mandibular blade absent. Pylopod of 2 or 3 visible articles, triangularly operculate. Length of male less than 5 mm.

Intertidal–shelf. Temperate Northern Atlantic, Temperate Northern Pacific, Western and Central Indo-Pacific, Temperate Australasia. 24 species (Cohen and Poore, 1994: rediagnosis, key to 5 species from Australia; Kensley et al., 2009: key to 6 species from Indian Ocean).

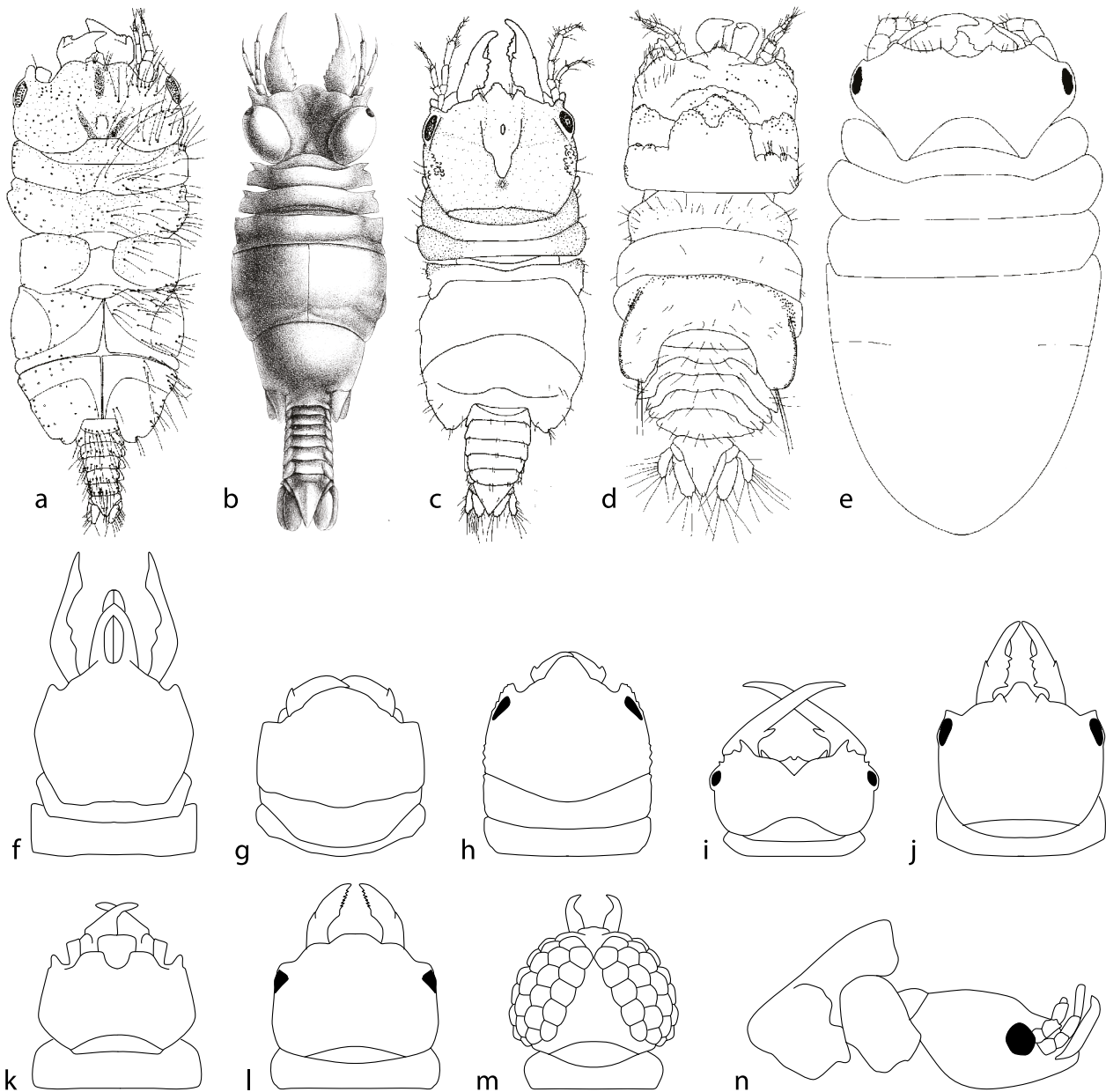


Figure 5.32. Gnathiidae. a, *Caecognathia huberia* Cohen and Poore, 1994; b, *Euneognathia gigas* (Beddard, 1886); c, *Gibbagnathia europalothrix* Cohen and Poore, 1994; d, *Gnathia camponotus* Cohen and Poore, 1994; e, *Thaumastognathia metaphone* Cohen and Poore, 1994. Pereonites 1, 2 head, mandibles: f, *Afrignathia*; g, *Bathygnathia*; h, *Caecognathia*; i, *Elaphognathia*; j, *Gnathia*; k, *Monodgnathia*; l, *Paragnathia*; m, *Tenerognathia*. n, pereonites 1–3, head, antennae, mandibles, lateral, *Bythognathia*.

Euneognathia Stebbing, 1893

Diagnosis. Frontal border transverse, processes present. Mandibular blade crenulate. Pylopod basis free, remaining 4 articles forming triangular operculum. Length of male 5–10 mm.

Shelf. Southern Ocean. 1 species (Beddard, 1886: figure of type species, *Anceus gigas* Beddard, 1886; Cohen and Poore, 1994: rediagnosis).

Gibbagnathia Cohen and Poore, 1994

Diagnosis. Frontal border slightly produced, processes absent. Mandibular blade absent. Maxilliped reduced, of 2 articles. Pylopod of 4 articles, filiform. Pereonite 3 with large anteriorly directed projection partially overhanging pereonites 1 and 2 (clear in lateral view). Length of male less than 3 mm.

Shelf. Temperate SE Australia. 1 species (Cohen and Poore, 1994).

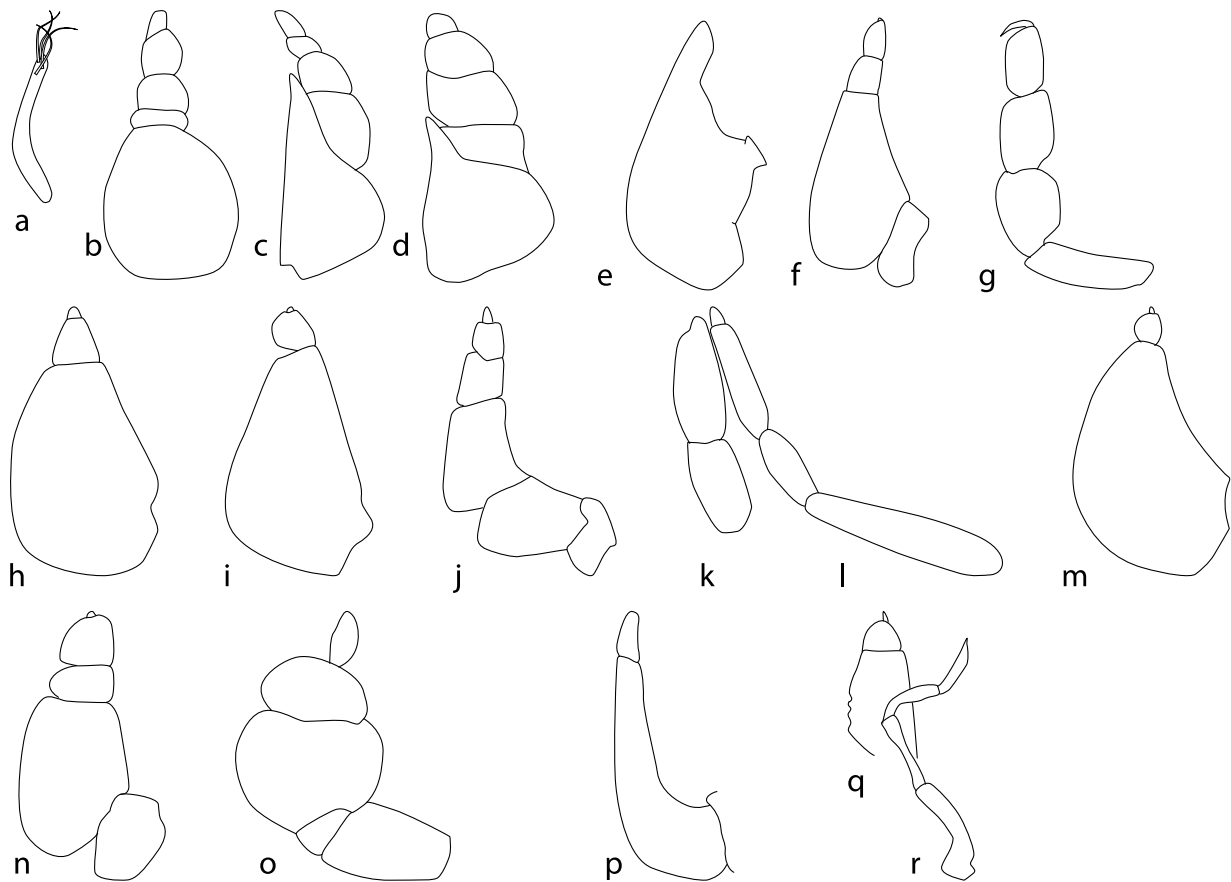


Figure 5.33. Gnathiidae. a, maxilla, *Afrignathia*. Maxilliped: b, *Afrignathia*; c, *Caecognathia*; d, *Elaphognathia*; k, *Gibbagnathia*; q, *Thaumastognathia*. Pylopod: e, *Afrignathia*; f, *Bathygnathia*; g, *Bythognathia*; h, *Caecognathia*; i, *Elaphognathia*; j, *Euneognathia*; l, *Gibbagnathia*; m, *Gnathia*; n, *Monodgnathia*; o, *Paragnathia*; p, *Tenerognathia*; r, *Thaumastognathia*.

***Gnathia* Leach, 1814**

Diagnosis. Frontal border produced as rostrum, processes present; paraocular ornamentation on cephalosome absent, or granules posterior to eye. Mandibular incisor slight, or pronounced; blade dentate. Pylopod of 2 or 3 visible articles, triangularly operculate. Length of male less than 5 mm.

Intertidal–bathyal. Cosmopolitan. 144 species (Cohen and Poore, 1994: rediagnosis, key to 20 species from Australia; Kensley et al., 2009: key to 20 species from Indian Ocean; Svavarsson and Bruce, 2019: descriptions of 10 species; Ota et al., 2025: key to species from Japan).

***Monodgnathia* Cohen and Poore, 1994**

Diagnosis. Eyes absent. Frontal border produced as rostrum, processes absent. Mandibular blade smooth. Pylopod basis free, distal 3 articles triangularly operculate. Length of male 5–10 mm.

Bathyal. Temperate Northern and Tropical Atlantic, Western Indo-Pacific, Temperate Australasia. 4 species (Cohen and Poore, 1994: key to 2 species from Australia).

***Paragnathia* Omer-Cooper and Omer-Cooper, 1916**

Diagnosis. Frontal border produced as rostrum, processes absent. Mandibular blade crenulate. Pylopod ischium and merus free, distal articles oval-operculate. Length of male less than 5 mm.

Subtidal. Temperate Northern E Atlantic. 1 species (Monod, 1926: description of only species).

***Tenerognathia* Tanaka, 2005**

Diagnosis. Eyes occupying whole of side of cephalosome. Frontal border produced as rostrum, processes absent. Mandibular blade smooth. Pylopod of 2 narrow tapering articles. Length of male less than 3 mm.

Shelf. Temperate Northern W Pacific. 2 species (Tanaka, 2005, 2024).

***Thaumastognathia* Monod, 1926**

Diagnosis. Frontal border transverse or slightly produced, processes present or absent. Mandibular blade crenulate. Maxilliped absent, or reduced, of 2 articles. Pylopod of 4 articles, filiform. Pleon folded under pereon. Length of male less than 3 mm.

Bathyal. Temperate Northern W Pacific, Temperate Australasia. 5 species (Cohen and Poore, 1994: rediagnosis, key to 4 species; Shimomura and Tanaka, 2008: 5th species).

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Protognathiidae Wägele and Brandt, 1988

Figure 5.34

Wägele and Brandt (1988), recognising the affinities of *Cirolana bathypelagica* Schultz, 1977 to Gnathiidae and Cirolanidae, separated it as its own genus *Protognathia* and family. The mandibular incisor is acute rather than bladelike as in cirolanids; it is not held anteriorly as in Gnathiidae. Pereopod 7 is absent as in Gnathiidae.

Diagnosis. Eyes widely separated, lateral, sometimes small or absent. Mandibular incisor enlarged, distally with acute point;

molar bladelike. Maxilla with 1 endite. Maxillipedal endite as long as palp article 1; palp of 5 articles. Pereopod 7 absent as adults.

Protognathia Wägele and Brandt, 1988

Meso- and bathypelagic. Southern Ocean. 2 species (Wägele and Brandt, 1988: diagnosis, redescription of type species; Kussakin and Rybakov, 1995: second species).

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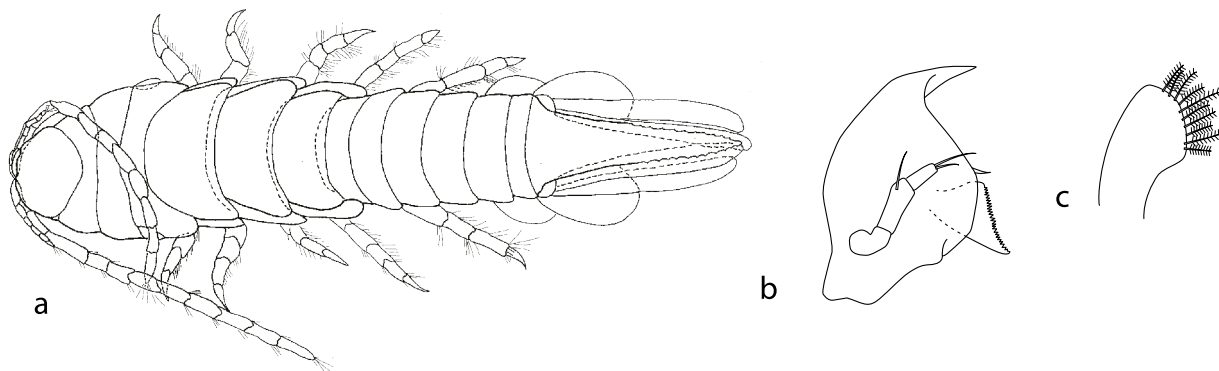


Figure 5.34. Protognathiidae. a, *Protognathia bathypelagica* (Schultz, 1977). *Protognathia*: b, mandible; c, maxilla.

Tridentellidae Bruce, 1984

Figure 5.35

The Tridentellidae are a small family with one genus (Bruce, 1984). Tridentellids are similar to the micropredatory families Aegidae and Corallanidae but are differentiated from them by an elongate maxillipedal endite that extends beyond the third palp article, and simple maxilla provided with numerous serrated scales, but without recurved spines or hooked robust setae. Many species of *Tridentella* are highly ornamented, some with cephalic processes or heavily spinose dorsal surfaces. The pleotelson often has longitudinal ridges and serrate lateral margins. Brandt and Poore (2001) listed the 16 species of *Tridentella* then known and provided a key, but several have been described since (Bruce, 2002, 2008; Bruce and Svavarsson, 2018).

Diagnosis. Eyes widely separated, lateral, sometimes small or absent (rarely contiguous). Mandibular incisor narrow; lacinia mobilis and spine row absent; molar present. Maxillula comprising 1 styliform endite with mesial and terminal robust setae. Maxilla with 1 endite, distal region with small spines or scalelike setae. Maxillipedal endite elongate; palp of 5 articles. Pereopods 1–7 ambulatory, dactyli 1–3 stout, recurved. Ectoparasitic, usually on fishes, or freeliving scavengers.

Tridentella Richardson, 1905

Shelf, slope. Temperate Northern and Tropical Atlantic, Temperate Northern W Pacific, Central Indo-Pacific, Tropical Eastern Pacific, Temperate Southern Africa, Temperate Australasia. 23 species.

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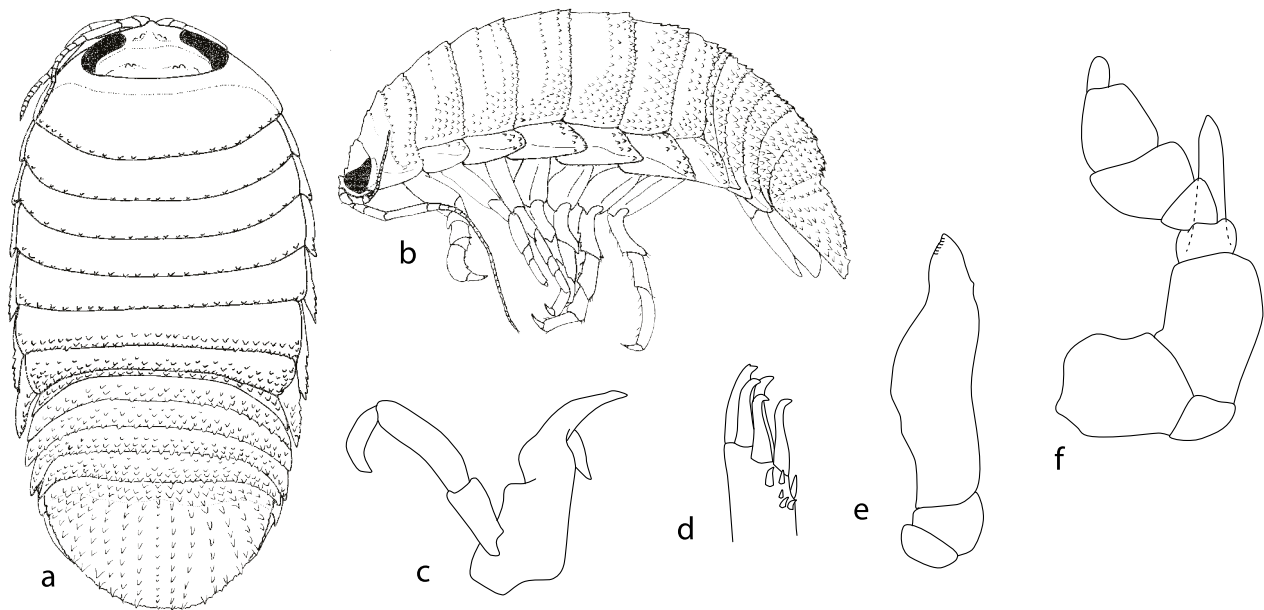


Figure 5.35. Tridentellidae. a, b, *Tridentella namibia* Brandt and Poore, 2001. *Tridentella*: c, mandible; d, maxillula apex; e, maxilla; f, maxilliped.

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