

Out on a limb: novel morphology and position
on appendages of two new genera and three new species
of ectoparasitic isopods (Epicaridea: Dajidae)
infesting isopod and decapod hosts

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COUVERTURE / *COVER*:

Akrophryxus milvus n. gen., n. sp., holotype female, MNHN-IU-2014-20314, attached to *Ethusa machaera* Castro, 2005, macropod images.

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Out on a limb: novel morphology and position on appendages of two new genera and three new species of ectoparasitic isopods (Epicaridea: Dajidae) infesting isopod and decapod hosts

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ABSTRACT

Adult female dajid isopods are ectoparasites found on carapaces, within marsupia, or rarely attached to the eyestalks or pereopods of crustacean hosts. We describe two new genera and species whose females exhibit a novel spheroid shape and envelope antennules of hosts: *Akrophryxus milvus* n. gen., n. sp. parasitizing *Ethusa machaera* Castro, 2005 (Madagascar, c. 900 m) and *Telephryxus clypeus* n. gen., n. sp. parasitizing *Munidopsis crassa* Smith, 1885 (Caribbean, c. 5000 m). Females of both species differ from other dajid species in their spheroid shape and a plate partially surrounding the host antennule; males are distinguished by reduction of pereopods. Females of *A. milvus* n. gen., n. sp. are distinguished from those of *T. clypeus* n. gen., n. sp. in possessing antennules and a triangular attachment plate with three holes (*T. clypeus* n. gen., n. sp. lacks antennules and the broad attachment plate has two medial holes). Males of *A. milvus* n. gen., n. sp. are distinguished from those of *T. clypeus* n. gen., n. sp. in having only six pairs of pereopods, rudimentary antennules, single segmented antennae, and pleon fused to pereomere 7 (*T. clypeus* n. gen., n. sp. with rudimentary seventh pair of pereopods, large single segmented antennules, two segmented antennae, and pleon distinct from pereomere 7). Pre-molt epicaridium larvae and cryptoniscus larvae of *T. clypeus* n. gen., n. sp. are described. We also describe *Aegophila cappa* n. sp. found on pereopods of the isopod *Aegiochus symmetrica* (Richardson, 1905) (Bering Sea, c. 650 m), distinguished from the type species of *Aegophila* Bresciani, 1966 by oostegite morphology of the female, form of the antennae, and shape of the pleon of males. Tables with comparative characters for genera of Dajidae G. O. Sars, 1883 are provided. Dajid life cycles and development are reviewed.

KEY WORDS

Abyssal,
Aegiochus,
antennule parasite,
Ethusa,
Isopoda,
life cycle,
Munidopsis,
new species,
new genus.

RÉSUMÉ

Suspendu à un fil : nouvelle morphologie et position sur les appendices de deux nouveaux genres et trois nouvelles espèces d'isopodes ectoparasites (Epicaridea: Dajidae) infestant des hôtes isopodes et décapodes.

Les femelles adultes d'isopodes dajides sont des ectoparasites que l'on trouve sur les carapaces, au sein de marsupiums, ou plus rarement attachés aux pédoncules oculaires ou aux péréopodes des crustacés hôtes. Nous décrivons deux nouveaux genres et espèces dont les femelles présentent une forme sphérique nouvelle et enveloppent les antennules des hôtes : *Akrophryxus milvus* n. gen., n. sp. parasite d'*Ethusa machaera* Castro, 2005 (Madagascar, c. 900 m) et *Telephryxus clypeus* n. gen., n. sp. parasite de *Munidopsis crassa* Smith, 1885 (Caraïbes, c. 5000 m). Les femelles des deux espèces se distinguent des autres espèces de dajides par leur forme sphérique et une plaque entourant partiellement l'antennule de l'hôte; les mâles se distinguent par la réduction des péréopodes. Les femelles de *A. milvus* n. gen., n. sp. se distinguent de celles de *T. clypeus* n. gen., n. sp. par la présence d'antennules et par une plaque de fixation triangulaire à trois orifices (*T. clypeus* n. gen., n. sp. n'a pas d'antennules et la large plaque de fixation a deux orifices médians). Les mâles de *A. milvus* n. gen., n. sp. se distinguent de ceux de *T. clypeus* n. gen., n. sp. par leur nombre réduit de péréopodes (seulement six paires), des antennules rudimentaires, des antennes unisegmentées et un pléon fusionné au péréomère 7 (*T. clypeus* n. gen., n. sp. a une septième paire de péréopodes rudimentaires, de grandes antennules unisegmentées, deux antennes segmentées et un pléon distinct du péréomère 7). Les larves epicaridium de pré-mues et les larves cryptoniscus de *T. clypeus* n. gen., n. sp. sont décrites. Nous décrivons également *Aegophila cappa* n. sp. trouvé sur les péréopodes de l'isopode *Aegiochus symmetrica* (Richardson, 1905) (mer de Béring, c. 650 m), et qui se distingue de l'espèce type d'*Aegophila* Bresciani, 1966 par la morphologie des oostégites de la femelle, la forme des antennes et la forme du pléon des mâles. Des tableaux avec des caractères comparatifs pour les genres de Dajidae G. O. Sars, 1883 sont fournis. Les cycles de vie et le développement des dajides sont passés en revue.

MOTS CLÉS

Abyssal,
Aegiochus,
antennule parasite,
Ethusa,
Isopoda,
cycle de vie,
Munidopsis,
espèces nouvelles,
genres nouveaux.

INTRODUCTION

Attachment to the extremities, including appendages such as antennae and legs, would seem a risky strategy for ectoparasites of aquatic hosts. Although some protozoans and other small ectoparasites and epibionts are commonly found on such host structures or their setae (e.g. Lom 2005; Heiner & Kristensen 2005), macroparasites are rarely attached in such positions. Rather, the bodies of most ectoparasites are closely applied to the bodies of their hosts or within protected regions (e.g. branchial chambers) and often exhibit adaptations (e.g. dorsoventral flattening, modified attachment structures) to withstand the hydrodynamic pressures that would otherwise dislodge them from hosts (e.g. Boxshall 2005a, b; Smit *et al.* 2014; Baillie *et al.* 2019). Other unusual sites of attachment are on the eye stalks of their crustacean hosts (Shields & Gómez-Gutiérrez 1996). Crustacean parasites that themselves parasitize other crustaceans are likewise usually found attached to the bodies of their hosts, either on the dorsal or ventral surfaces of the cephalon, the pereon or the pleon; however, there are a few highly modified spheroid or ovate macroparasites, such as certain rhizocephalans, tantulocarids, and copepods, that are known from extremities (e.g. antennules, antennae and pereopods) of their crustacean hosts (Boxshall & Hayes 2019).

Rhizocephalans (Rhizocephala Müller, 1862) are mesoparasitic barnacles that include colonial forms, of which some species (e.g. *Thompsonia japonica* Häfele, 1911; *Thylacoplethys porcellanus* Hiller, Williams & Boyko, 2015) can occur on the pereopods as well as the body of the host. An additional species, *Thompsonia chuni* Häfele, 1911, is known from the eyestalks of its hermit crab host (Häfele 1911; Hiller *et al.*

2015). Each mature externa (the reproductive portion of the body) of a colonial rhizocephalan is approximately 1–2 mm in length and is attached by a short stalk to an appendage of its host; however, it does not surround the appendage (Hiller *et al.* 2015). The spheroid externae of these species, like all rhizocephalans, erupt from the body of the host and are connected to an internal root system; they are not originally attached to the appendages (aside from the larval phase that is responsible for injection of the primordial cells and may settle on an appendage prior to the injection; see life cycles in Høeg & Lützen 1995; Baeza *et al.* 2018).

Tantulocarids (Tantulocarida Boxshall & Lincoln, 1983) are ectoparasites on a range of small crustacean hosts (copepods, peracarids and ostracods) and their life cycle includes sac-like adult female stages attached to the host (both parthenogenetic females and females in the sexual stage are sac-like; see background and life cycles in Huys *et al.* 1993; Boxshall 2005c; Baeza *et al.* 2018). Several species of tantulocarid parasites (e.g. *Amphitantulus harpiniacheres* Boxshall & Vader, 1993; *Microdajus tchesunovi* Kolbasov & Savchenko, 2009; *M. langi* Greve, 1965) attach to the antennules, antennae and/or pereopods of their tanaid or amphipod hosts. However, these species have also been found attached to the main body of their hosts (Grygier & Sieg 1988; Boxshall & Vader 1993; Kolbasov & Savchenko 2009). There are a few tantulocarid species (e.g. *Microdajus aporosus* Grygier & Sieg, 1988) that have only been reported from appendages (pereopods) of tanaids (Grygier & Sieg 1988). Species of *Microdajus* Greve, 1965 are minute (< 1 mm in length) and are attached by a stalk to the appendage of their hosts (Boxshall & Hayes 2019; Boyko *et al.* in press).

The only other previously known crustacean parasites that may be appendage specialists are some species of mesoparasitic nicothoid copepods (Nicothoidae Dana, 1852; see review in Kakui 2016). In particular, two species (*Nicorbiza humesi* Lincoln & Boxshall, 1983 and *N. rockallensis* Lincoln & Boxshall, 1983) are found attached to the bases of pereopods 3-6 of their asellote isopod hosts (Lincoln & Boxshall 1983). Adult females of *Nicorbiza* Lincoln & Boxshall, 1983 and other genera in the “*Rhizorhina* group” (*sensu* Boxshall & Halsey 2004) superficially resemble rhizocephalans, including convergently possessing an absorptive rootlet system within the host. These copepods are spheroid, relatively small (400-600 µm in length) and attach to hosts by a modified oral cone. The point of attachment to hosts for some nicothoids (e.g. species of *Diexanthema* Ritchie, 1975; see Boxshall & Harrison 1988) remains unknown and other species might be found to vary in their position on hosts (sampling has been low for many) but none are known to surround the appendages of their hosts.

Among the parasitic isopods (Epicaridea Latreille, 1825), which likewise exclusively parasitize other crustaceans, there were no species previously found attached to the antennules and only one known to attach to pereopods of their hosts. Epicaridea contains two superfamilies (Bopyroidea Rafinesque, 1815 and Cryptoniscoidea Kossmann, 1880), species of which nearly all externally parasitize calanoid copepod hosts as their intermediate hosts and then parasitize one or more of a wide range of crustaceans (cirripedes, decapods, euphausiids, mysids, ostracods, peracarids) as definitive hosts. The most diverse family within Bopyroidea is Bopyridae Rafinesque, 1815 with over 600 species (Boyko *et al.* 2008a onwards), which are mostly ectoparasites in the branchial chambers of their definitive hosts, although some are also found attached to the ventral surfaces of host abdomens and a very few occur on other parts of hosts or are endoparasites (Trilles 1999; Williams & Boyko 2012). Females of most bopyrid species have a dorsoventrally flattened form, as do those of species in Ionidae H. Milne Edwards, 1840 which are exclusively branchial chamber parasites (see Boyko *et al.* 2013), whereas females of species in Entoniscidae Kossmann, 1881 are endoparasitic and vermiform. Among the cryptoniscoids, there are many species in which sexually mature females exhibit a sac-like form (Trilles 1999), but they are irregular in shape, do not form a spheroid, and are typically found in the brood chamber or shell (for the case of barnacles) of hosts as primary parasites or hyperparasites of a wide range of hosts (Williams & Boyko 2012).

Within Cryptoniscoidea the family Dajidae G. O. Sars, 1883 (Boyko *et al.* 2013) presently contains 56 species that typically possess a cryptoniscus larval stage with an oral sucker (see more in Remarks under *Telephryxus clypeus* n. gen., n. sp.) used to attach to the definitive host (see Gilson 1909; Coyle & Mueller 1981; Gómez-Gutiérrez *et al.* 2017). Most species in this group are attached as adults to the dorsal carapace of their hosts, typically on caridean shrimp and euphausiids or occur in the marsupia of mysids (see G. O. Sars 1898; Wasmer 1988; Shimomura *et al.* 2005; Gómez-Gutiérrez *et al.* 2017; de Almeida Alves-Júnior *et al.* 2019). One species (*Oculophryxus bicaulis* Shields & Gómez-Gutiérrez 1996)

uses modified antennae to attach to the eyestalk peduncle of euphausiid hosts, whereas species of *Heterophryxus* G. O. Sars, 1885 also attach to eyestalks but do so with their fifth pereopods. However, species of *Heterophryxus* and *Oculophryxus* Shields & Gómez-Gutiérrez 1996 retain the dorsoventrally flattened typical dajid form as adult females and are closely applied to the host body. *Aegophila socialis* Bresciani, 1966 is the sole dajid as well as epicaridean known to parasitize the pereopods of its host, a species of aegid isopod; the body of females is more flattened than is typical of other dajids but is otherwise quite similar. *Notophryxus lateralis* G. O. Sars, 1885, is found attached to an appendage, either the endopod of the sixth pereopod or the sixth gill (G. O. Sars 1885; Field 1969; Gómez-Gutiérrez *et al.* 2017) but this species is in a very protected position on the ventral surface of its host.

Herein, we report on two new species of dajids that exhibit an unusual spheroid morphology and novel attachment position partially surrounding the antennules of their decapod hosts. In contrast to the highly modified female morphology, the males, epicaridium and cryptoniscus larvae of these species are typical of dajids in gross morphological details. One species was collected from the western Indian Ocean off Madagascar in nearly 1000 m depth, whereas the other was obtained in exceptionally deep (*c.* 5000 m) waters from the southern Caribbean. We also describe a third species of dajid, a new species of the genus *Aegophila* Bresciani, 1966 from the Bering Sea, found attached to a pereopod of an aegid isopod host. Although the morphology of females of this species is atypical of dajids and apparently specialized for attachment to the legs of hosts, females of this species do not exhibit the spheroid shape found in females of the two new genera attached to host antennules. The present study thus expands our knowledge of the morphological diversity and host attachment strategies within Dajidae, as well as parasitic isopods in general.

MATERIAL AND METHODS

Methods of specimen collection are indicated in the “Type Material” sections below; data on collections (e.g. longitude and latitude coordinates, depth) are provided from the original records where possible. Carapace length (CL) of hosts was measured from the anterior end of the rostrum to the posterior edge of the carapace and carapace width (CW) was measured as the maximum width of carapace, using calipers. Isopod parasite size is given as maximal diameter for females of the two new genera (*Akrophryxus* n. gen. and *Telephryxus* n. gen.) and maximal length for all males and females of *Aegophila* (from anterior border of cephalon to terminus of uropods). All measurements were made with a micro-scale tool, ocular micrometer, or from drawing tube sketches.

Line drawings of parasites were made by sketching specimens using drawing tubes attached to Olympus compound and dissecting microscopes and using Adobe Illustrator to trace original sketches and produce final figures. Light micrographs were created with a Macropod Pro kit (MacroscopicSolutions) and resulting pictures were aligned and stacked with the focus

stacking software Zerene Stacker (10–65 images from bottom to top of specimens). For Scanning Electron Microscopy (SEM) preparation of epicaridium larvae, specimens were dehydrated in an ascending ethanol (EtOH) series, starting with 70% EtOH and ending with 100% EtOH. Specimens were then dried in a Samdri 795 Critical Point Dryer, mounted on aluminum stubs, coated with gold using an EMS-550 Sputter coater, and viewed with a FEI Quanta 250 SEM.

All specimens were deposited in the Museum National d’Histoire Naturelle, Paris, (MNHN) and National Museum of Natural History, Smithsonian Institution, Washington D.C., (USNM). References are provided for taxonomic authorities of parasite taxa but not for those of hosts.

SYSTEMATICS

Family DAJIDAE G. O. Sars, 1883

Genus *Aegophila* Bresciani, 1966

TYPE SPECIES. — *Aegophila socialis* Bresciani, 1966

Aegophila cappa n. sp.
(Figs 1; 2)

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“parasite” – Richardson 1909: 125, figs 49, 50.

“eine Form ohne Namen auf dem Isopode *Aega symmetrica* vom Behring-Meer” – Nierstrasz & Brender à Brandis 1931: 220.

“*Aegophila socialis* sp. nov.?” – Bresciani 1966: 108–109, fig. 6 (after Richardson 1909) (not *A. socialis* Bresciani, 1966).

TYPE MATERIAL. — **Holotype.** Bering Sea • USNM 39524; ovigerous female (3.4 mm W, 2.4 mm L); attached to pereopod of *Aegiochus symmetricus* (Richardson, 1905) (USNM 39293); Sta. 4772; 54°30'30"N, 179°14'E; “Bowers Bank”; 344–372 fathoms (= 629–680 m); coll. United States Bureau of Fisheries steamer *Albatross*, taken by 12-foot Tanner beam trawl (Anonymous 1907); 4.VI.1906. **Allotype.** Bering Sea • USNM 1616634; mature male (920 µm L); same data as for holotype.

TYPE LOCALITY. — 54°30'30"N, 179°14'E, “Bowers Bank”, Bering Sea, 629–680 m.

TYPE HOST. — *Aegiochus symmetrica* (Richardson, 1905) [Crustacea: Isopoda: Aegidae] (originally as *Aega symmetrica* in Richardson, 1909; see WoRMS 2008b onwards).

ETYMOLOGY. — The species name is derived from the Latin for cloak or cape (*cappa*), in reference to the fused oostegite 5 and lateral body wall of the female’s resemblance to a cloak drawn around the body. The gender is feminine.

DISTRIBUTION. — Known only from the type locality and type host.

DESCRIPTION

Female

Body (Fig. 1A, B) semicircular, approximately 1.25 times as wide as maximum length, dorsoventrally flattened, with pair

of broad lateral lamellae filled with numerous embryos; lateral lamellae not reaching beyond frontal margin of cephalon. Cephalon (Fig. 1A–C) indistinctly dorsally separated from pleon, without eyes. Antennules and antennae apparently absent. Oral cone (Fig. 1B, D) with flaring rounded mandibles, extended, distal surface covered with scale-like structures; posterior margin of oral cone with two finger-like projections. Maxillipeds subquadrate (Fig. 1E). Pereon with few faint transverse and longitudinal folds in cuticle (Fig. 1A). Pereopods 1–5 subequal in size and shape, without setae (Fig. 2F–I, K); dactylus short but highly recurved, propodus and carpus fused, carpus expanded into cup receiving tip of dactylus, basis elongate. Oostegite 1 ovate, expanded, few small setae on posterior margin (Fig. 1H); oostegite 2 slender, rounded at narrowed distal tip, fringe of setae on proximoventral margin (Fig. 1I); oostegite 3 broader than 2, fringe of thick setae on proximoventral margin (Fig. 1J); oostegite 4 subquadrate, fringe of thick setae on proximoventral margin (Fig. 1K); oostegite 5 fused with lateral pleon, medioventral area with region of setae and small, rounded lobe (Fig. 1B, L). Pleon segments fused, minute, vermiform, without lateral plates or pleopods (Fig. 1B).

Male

Body not recurved ventrally (Fig. 2A). Cephalon wider than long (Fig. 2A, B), fused with pereomere 1, anterior margin rounded, posterolateral margins (pereomere 1) as small, rounded lobes; lacking eyes, cephalic slits present. Antennules each as single flattened lobe with five or six long setae on medial and distal margins (Fig. 2B, C). Antennae of three segments each with single distal thin flagellum (Fig. 2B, C). Oral cone triangular (Fig. 2B, C). Pereomeres 2–7 distinct, 4–6 subequal in width, others narrower (Fig. 3B); lateral margins of pereomeres 2–7 extended ventrally, with multiple thin setae on margins (Fig. 2B, E). Pereopods with all segments distinct; 1, 2 each with recurved dactylus approximately as long as rounded propodus (Fig. 2B–D), 3–7 with recurved dactylus approximately 25% as long as slender elongate propodus (Fig. 2E); all ischia and bases elongate. Pleon elongate, subtriangular, segments fused but faint indication of pleomere 1 by rounded lobes and presence of lateral setae similar to those on pereomeres 2–7 (Fig. 2A, B); pleon tapering posteriorly with small distal rounded protrusion bearing terminal setae surrounding anal slit (Fig. 2A, B); pleopods lacking.

REMARKS

The new species is clearly conspecific with *Aegophila socialis*; females of both species show dorsoventral compression of the body, lack of antennules and antennae, expanded, club-like mandibles, the same arrangement of oostegites 1–4, the presence of a rounded knob and fringe of thin papillae on the medioventral margin of oostegite 5, as well as fusion of the fifth oostegites with the ventral body wall, and the pleon being a small, unsegmented protuberance. Males of the two species are similar in having fusion of the cephalon with the first pereomere and presence of rounded posterolateral lobes

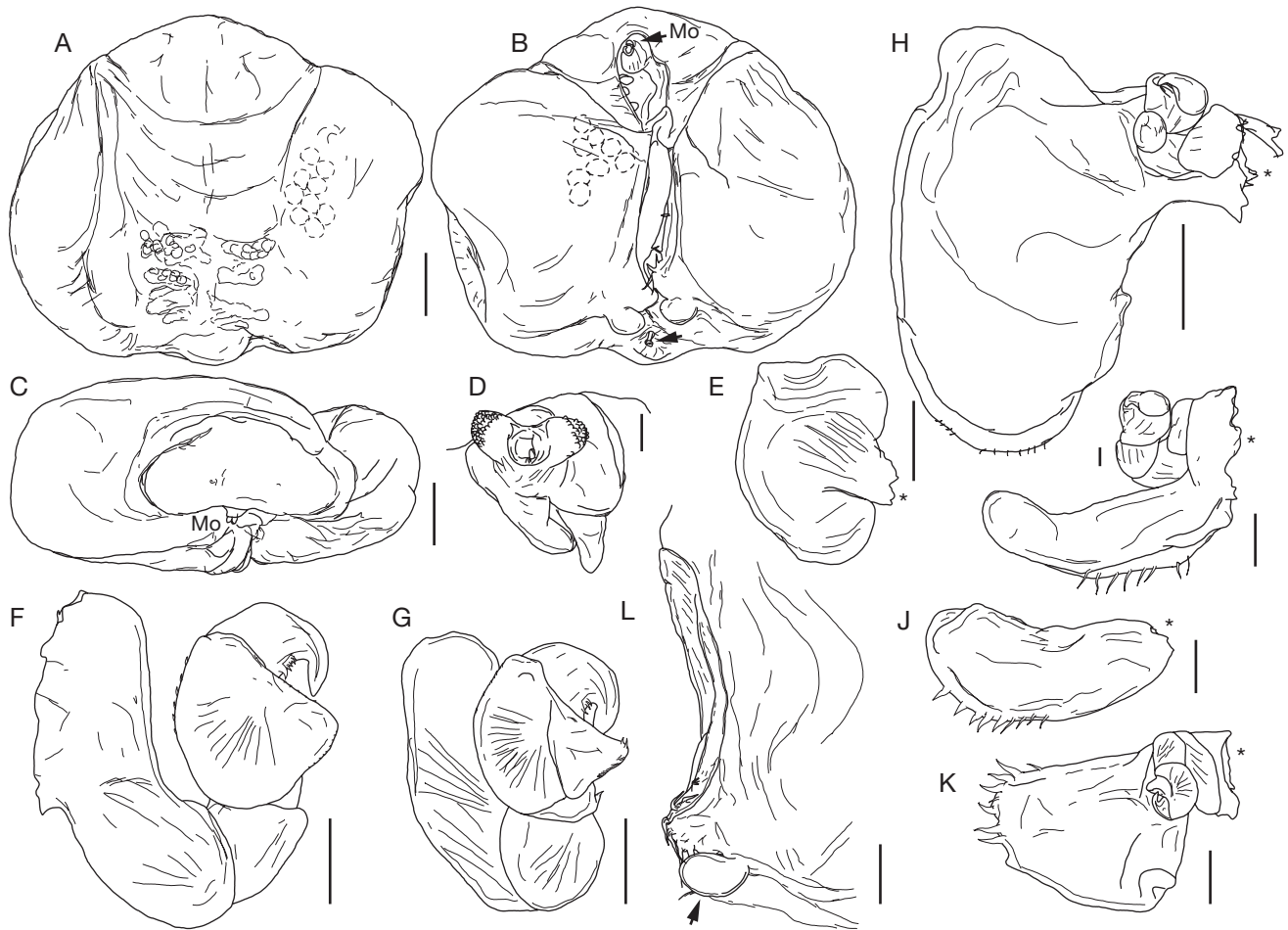


FIG. 1. — *Aegophila cappa* n. sp., holotype female, USNM 39524: **A**, dorsal view; **B**, ventral view (showing mouthparts, **Mo**; **arrow** indicates pleon); **C**, anterior end, *en-face* (showing mouthparts, **Mo**); **D**, mouthparts; **E**, left maxilliped, outer view; **F**, left pereopod 3; **G**, left pereopod 4; **H**, left oostegite 1 and pereopod 1; **I**, left oostegite 2 and pereopod 2; **J**, left oostegite 3; **K**, left oostegite 4 and pereopod 4; **L**, left oostegite 5, external view of medial edge and posterior end with rounded lobe (**arrow**). In figures E and H-K asterisks show site of attachment for structures dissected from body of parasite. Scale bars: A-C, 500 μ m; D, F, G, 50 μ m; E, H, L, 250 μ m; I-K, 125 μ m.

corresponding to the side of pereomere 1, the antennules as unsegmented flaps fringed by setae, and the pleon with all segments fused and lacking pleopods.

Diagnostic differences between females of the two species include: oostegite 1 large, ovate in *A. cappa* n. sp. (small, “spoon-like” in *A. socialis*), oostegite 2 narrow in *A. cappa* n. sp. (broad in *A. socialis*), and oostegite 4 subquadrate in *A. cappa* n. sp. (ovate in *A. socialis*). Bresciani (1966) described *A. socialis* as lacking maxillipeds, but they are clearly present in *A. cappa* n. sp. and it is unclear if he overlooked them or if they are truly lacking in *A. socialis*; the latter appears unlikely since maxillipeds are required for oxygenation of the brood (Gilson 1909; Cericola & Williams 2015). Bresciani (1966) described the pereopods of *A. socialis* as “small and badly segmented, and do not show any special characters” but did not illustrate them well. In *A. cappa* n. sp., the pereopods have highly recurved dactyli and show fusion only of the propodus and carpus, with the carpus inner margin being expanded as a cup for insertion of the dactylus.

The males of the two species differ in the form of the antennae (multisegmented with a single flagellum in *A. cappa* n. sp. vs a single segment with a single flagellum in *A. socialis*) and the shape of the pleon (much longer than wide in *A. cappa* n. sp. vs length and width subequal in *A. socialis*). Bresciani (1966) did not describe the pereopods in detail but did illustrate them. His illustrations appear to show a difference in pereopods 1 and 2 (rounded propodus with typically recurved dactylus) vs 3-7 (elongate propodus and highly recurved dactylus) that is also seen in *A. cappa* n. sp. However, he drew pereopod 1 as having the propodus and carpus fused whereas in *A. cappa* n. sp., they are distinct.

It is not clear which specimen of *Aegiochus symmetrica* was the host of *A. cappa* n. sp. as all of the potential host aegids collected at the parasite’s type locality (Sta. 4772, USNM 39293) have their legs intact and no evidence of damage is visible; however, a label reading “1 sent to W. W. Alpatov / Jan 1923” is present in the jar and it is possible that this gifted specimen was the (now lost) host specimen of the holotype of *A. cappa* n. sp.

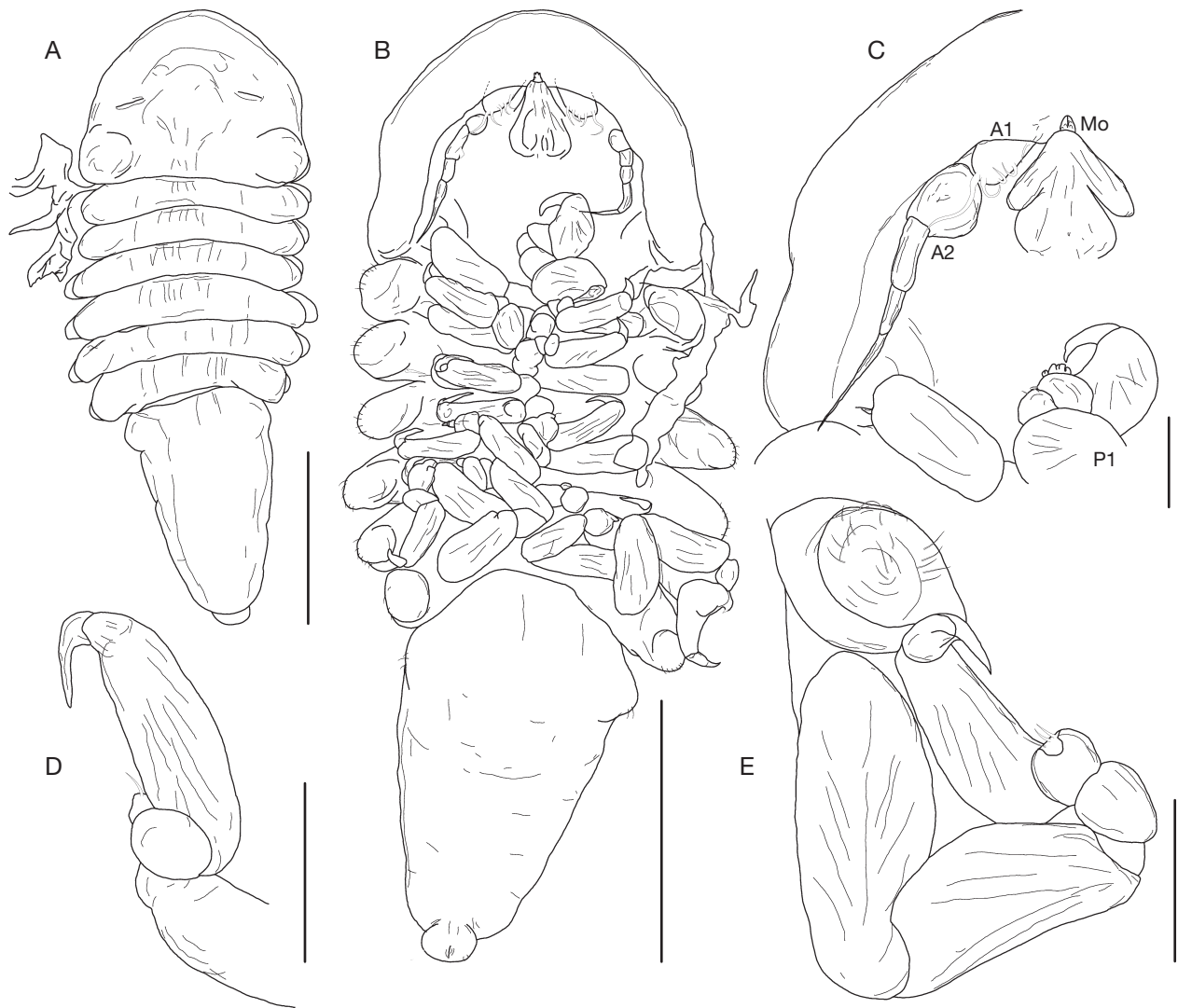


FIG. 2. — *Aegophila cappa* n. sp., allotype male, USNM 1616634: **A**, dorsal view; **B**, ventral view; **C**, right antennule (**A1**), antenna (**A2**), mouthparts (**Mo**) and pereopod 1 (**P1**); **D**, pereopod 2; **E**, pereopod 7 and side of pereomere 7. Scale bars: A, B, 250 µm; C-E, 50 µm.

Genus *Akrophryxus* n. gen.

[urn:lsid:zoobank.org:act:223FBBB0-B294-4C38-ADEA-37C5E561BCB0](https://doi.org/10.2223/FBBB0-B294-4C38-ADEA-37C5E561BCB0)

TYPE SPECIES. — *Akrophryxus milvus* n. sp.

ETYMOLOGY. — The genus name is derived from the Greek prefix ἀκρο- (ákro-), meaning “limb” or “extremity” in reference to the specialization of the female of the species on the antennule of the host crab rather than on the host body, in combination with *-phryxus*, from the Boeotian prince Phryxus (Φρίξος) of Greek mythology, a common ending for dajid, as well as some bopyrid, genera. The gender is masculine.

INCLUDED SPECIES. — *Akrophryxus milvus* n. sp. (type species).

DIAGNOSIS. — **Female.** Body spheroid; cephalon externally indistinguishable from pereon. Antennules absent, antennae each as oblong flat plate lateral to oral cone. Maxillipeds ovate with

recurved digitiform extension. Pereopods 1-5 subequal in size and shape. Oostegite 1 largest, broadly ovate with small posterior accessory lobe; oostegites 2/3, 4, 5 progressively larger; oostegite 2 thin and closely applied to oostegite 3. Pleon apparently modified as oblong, narrow, thickened plate with three circular medial holes: largest surrounding antennule of host, smallest hole at midpoint of plate, intermediate sized hole farthest from mouthparts of parasite.

Male. Cephalon fused with pereomere 1; cephalic slits present. Antennules of three stacked discs, flagella absent; antennae broad elongate lobes lateral to oral cone, flagella absent. Pereomeres 2-6 distinct; pereomere 7 fused with pleon, lateral margins recurved ventrally. Pereopods 1-6 subequal in size and shape; pereopod 7 lacking. Pleon rounded, all segments fused and fused with pereomere 7; pleopods lacking.

REMARKS

See Remarks below under *Akrophryxus milvus* n. gen., n. sp. for comparison of female and male characters of *Akrophryxus* n. gen., *Telephryxus* n. gen., and other dajid genera.

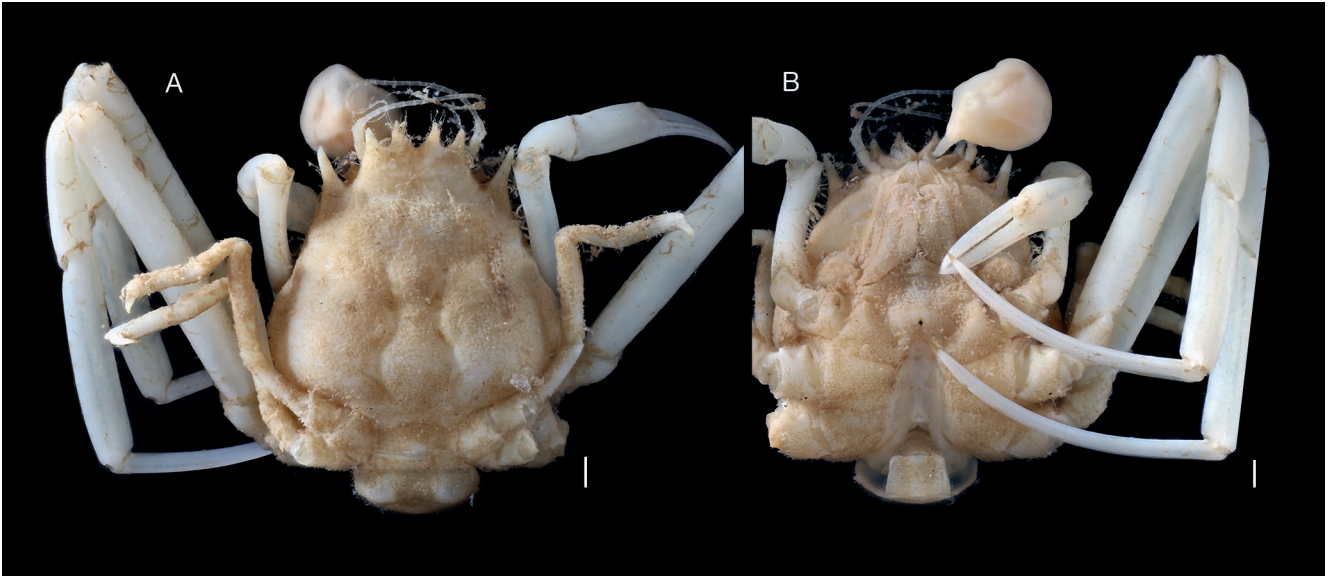


FIG. 3. — *Akrophryxus milvus* n. gen., n. sp., holotype female, MNHN-IU-2014-20314, attached to *Ethusa machaera* Castro, 2005, macropod images: **A**, dorsal view of host, showing parasite attached to left antennule; **B**, ventral view of host, lateral view of parasite showing attachment to left antennule. Scale bars: A, B: 1 mm.

Akrophryxus milvus n. sp.
(Figs 3-5, 11Q, R)

[urn:lsid:zoobank.org:act:AC0E5AFB-69BB-434D-86A6-A679F9EACDBC](https://doi.org/10.21203/rs.3.rs-1000000/v1)

“sacculinid (? parasite attached to antennular fossa)” – Castro 2013: 443.

TYPE MATERIAL. — **Holotype.** Madagascar • MNHN-IU-2014-20314; ovigerous female (3.1 mm diameter), attached to left antennule of male *Ethusa machaera* Castro, 2005 (9.2 mm CL, 9.0 mm CW; MNHN-IU-2010-1997); Sta. CP 3595; 25°35'28.2012”S, 44°15'25.2”E; south of Pointe Barrow; 821-910 m; coll. Bouchet *et al.* on the shrimper *Nosy Be 11*; ATIMO VATAE expedition, collected by trawling; 12.V.2010.

Allotype. Madagascar • MNHN-IU-2014-20315; mature male (740 µm L); same data as for holotype.

TYPE LOCALITY. — 25°35'28.2012”S, 44°15'25.2”E, Madagascar, south of Pointe Barrow, 821-910 m.

TYPE HOST. — *Ethusa machaera* Castro, 2005 [Crustacea: Brachyura: Ethusidae].

ETYMOLOGY. — The species name is derived from the Latin for “kite” in reference to the plate partially surrounding the host antennule that is reminiscent of the shape of a kite shield, defensive armor used primarily in Western Europe in the 10th-13th centuries. The gender is masculine.

DISTRIBUTION. — Known only from the type locality and type host.

DESCRIPTION

Female

Body spheroid, length and width nearly equal, filled with numerous eggs (Figs 3A, B; 4A, C-G). Cephalon externally indistinguishable from pereon, without eyes. Antennules absent, antennae each as oblong flat plate lateral to oral cone, covered with minute scales (not shown) (Figs 4G; 5G). Oral

cone rounded (Fig. 4G); mouthparts indistinct. Maxillipeds ovate with recurved digitiform extension (Fig. 5H). Pereopods 1-5 subequal in size and shape, without setae (Figs 4G; 5E, F); dactylus short, recurved, propodus carpus and merus fused, ischia and bases stout. Oostegite 1 largest (Figs 4G; 5J), broadly ovate with small posterior accessory lobe, broad lobe medially divided in lateral view (Fig. 5K); oostegites 2/3, 4, 5 progressively larger; oostegite 2 present, thin and closely applied to oostegite 3, lobes subequal in size and shape (Fig. 5L); oostegite 3 subtriangular (Fig. 5L), expanded posteriorly, medial and anterior finger-like extensions present with small setae distally, oostegites 4 and 5 subquadrate, small setae on medial and posterior margins (Fig. 5M). Pleon presumably modified (see Discussion) as oblong, narrow, thickened plate (Fig. 4A-G) partially surrounding host antennule of host and closest to mouthparts of parasite, smallest hole at midpoint of plate, intermediate sized hole farthest from mouthparts of parasite.

Male

Body not recurved ventrally (Fig. 5A, B). Cephalon fused with pereomere 1 (Fig. 5A, B), anterior margin rounded, posterolateral margins evenly rounded; lacking eyes, cephalic slits present. Antennules reduced, each apparently composed of three flattened disc-shaped segments (Fig. 5C); antennae each as single broad elongate lobes lateral to oral cone, flagella absent (Fig. 5C). Oral cone triangular (Fig. 5B, C). Pereomeres 2-6 distinct, 4-6 subequal in width, others slightly narrower (Fig. 5A, B); pereomere 7 fused with pleon, lateral margins recurved ventrally. Pereopods 1-6 subequal in size and shape, all segments distinct, carpi rounded, ischia short, bases elongate; dactylus, propodus and carpus with isolated marginal setae (Fig. 5B-D); pereopod 7 lacking. Pleon com-

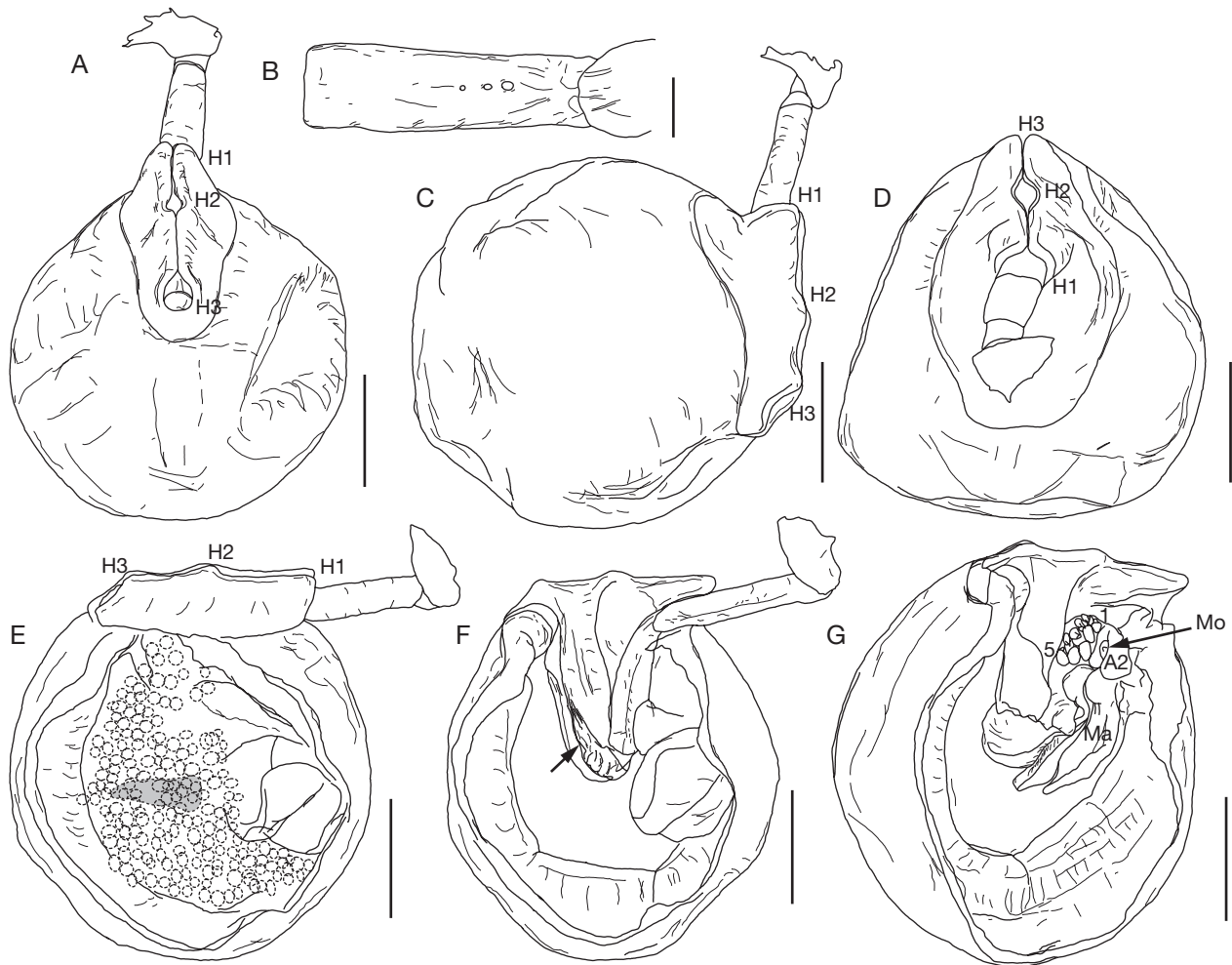


FIG. 4. — *Akrophryxus milvus* n. gen., n. sp., holotype female, MNHN-IU-2014-20314: **A**, posterior view, proximal end of host antenna extending from body of parasite at top; **B**, host antenna, middle segment showing attachment sight of parasite with three holes created by mouthparts; **C**, lateral view, left side showing proximal end of host antenna extending from body of parasite; **D**, anterior view (opposite side to that shown in **A**; proximal end of host antenna facing viewer); **E**, lateral view, right side, outer membrane of parasite removed showing brood of developing eggs (dashed circles) and position of male shown by grey outline; **F**, lateral view, right side with eggs removed and showing position of host antenna (arrow indicates distal end); **G**, lateral view, right side with host antenna and eggs removed showing mouthparts (**Mo**), antenna (**A2**), maxilliped (**Ma**) and pereopods (1 and 5 labeled). In figures **A**, **C**, **D**, and **E**, the three circular medial holes in pleon are labeled (hole surrounding antennule of host and closest to mouthparts, **H1**; hole at midpoint, **H2**; hole farthest from mouthparts, **H3**). Scale bars: **A**, **C**-**G**, 1 mm; **B**, 250 μ m.

pact, rounded, all segments fused and fused with pereomere 7, rounded posteriorly; anal slit and pleopods lacking (Fig. 5A, B).

REMARKS

The female of *Akrophryxus milvus* n. gen., n. sp. is very different from those in all other dajids, excepting *Telephryxus clypeus* n. gen., n. sp. (Table 1). The spheroid shape of the body and possession of a plate partially surrounding the host antennule are shared only by these two genera. The male of *A. milvus* n. gen., n. sp. is likewise very different from those in all other dajid genera (Table 2), including *T. clypeus* n. gen., n. sp. in having only six pairs of pereopods with no trace of the seventh pair (pereopod 7 of two elongate segments in the sole species of *Oculophryxus* and of one or two stub-like segments in *T. clypeus* n. gen., n. sp.). The male of *A. milvus* n. gen., n. sp. also differs from those in most genera in having the pleon fused with pereomere 7 (distinct from pereomere 7

in males in all other genera except *Holophryxus* Richardson, 1905 and *Oculophryxus*), and from all other genera in having a reduced antennule and an antenna with a single large segment (males of other genera with antennules of at least one well-developed segment and all with antennae segmented and with distal flagella).

The female of *A. milvus* n. gen., n. sp. can be distinguished from that of *T. clypeus* n. gen., n. sp. in lacking antennules and in having three medial holes on the narrow, triangular attachment plate partially surrounding the host antennule with no additional lateral holes (*T. clypeus* n. gen., n. sp. has flattened antennules and a broad, subquadrate attachment plate partially surrounding the host antennule and having two large medial holes, the largest with two additional small lateral holes). The male of *A. milvus* n. gen., n. sp. can be distinguished from that of *T. clypeus* n. gen., n. sp. in having only six pairs of pereopods (six fully-developed pairs plus a rudimentary seventh pair of one

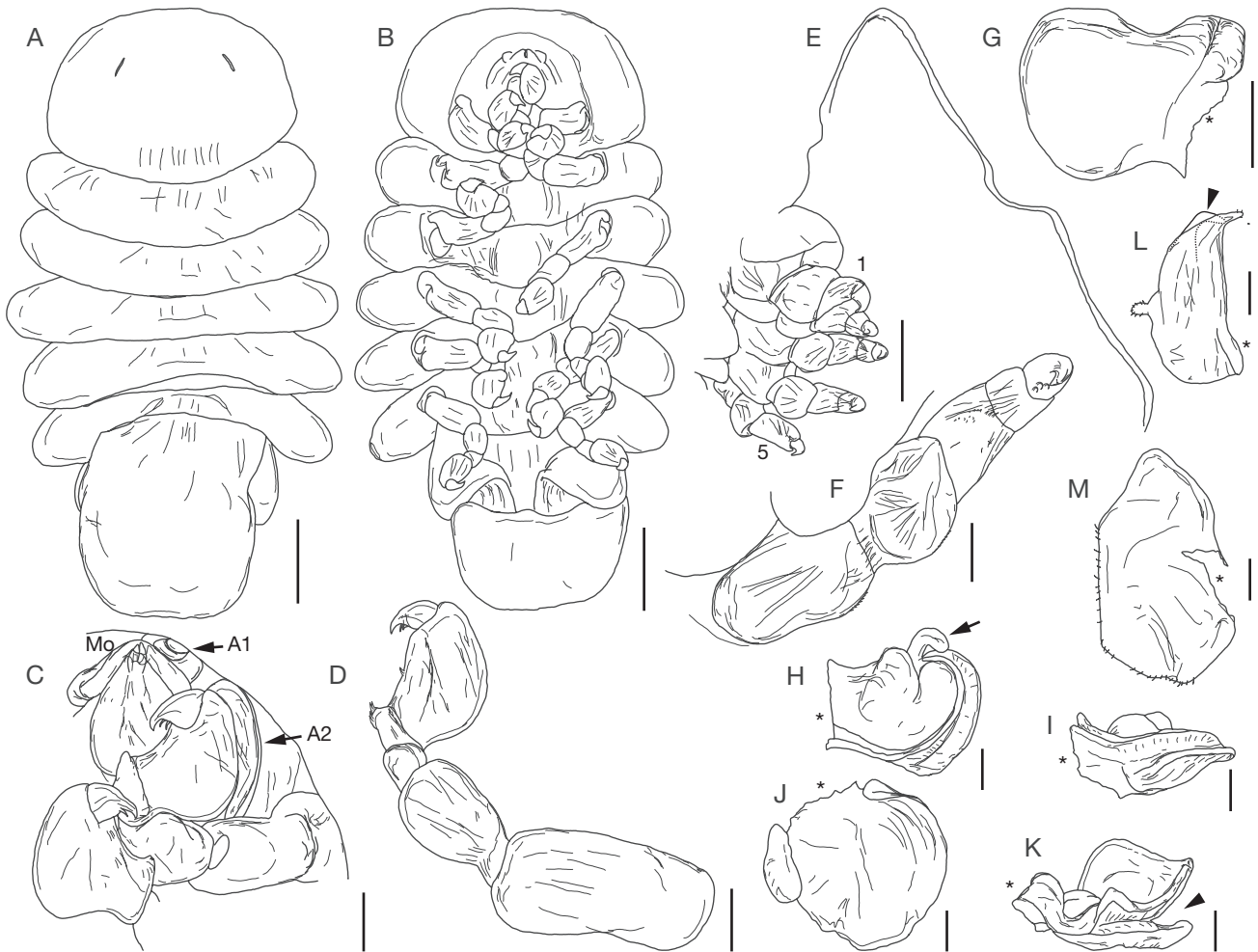


FIG. 5. — *Akrophryxus milvus* n. gen., n. sp., allotype male (A–D; MNHN-IU-2014-20315) and holotype female (E–M; MNHN-IU-2014-20314): A, dorsal view; B, ventral view; C, ventral view of anterior end showing left antennule (A1), left antenna (A2), mouthparts (Mo) and first pereopods; D, right pereopod 6; E, pereopods 1–5 from left side (1 and 5 labeled with numbers); F, pereopod 3 from left side; G, antenna from left side, covered in scales (not shown); H, left maxilliped, ventral view, arrow shows digitiform extension that is inserted in fold of oostegite 1 in part K (shown by arrowhead); I, left maxilliped, lateral view; J, left oostegite 1, ventral view; K, left oostegite 1, lateral view showing fold where digitiform extension of maxilliped resides (arrowhead); L, left oostegite 3, anterior portion of oostegite 2 shown by arrowhead and in dashed line; M, left oostegite 5. In Figures 2G, H–K, and M asterisks show site of attachment for structures dissected from body of parasite. Scale bars: A, B, G, L, M, 100 μ m; C, D, 25 μ m; E, H–K, 250 μ m; F, 50 μ m.

or two small segments in *T. clypeus* n. gen., n. sp.), a reduced antennule and a single segmented antenna (large ovate single segmented antenna and two segmented short antennae in *T. clypeus* n. gen., n. sp.), and the short and rounded pleon fused to pereomere 7 (pleon distinct from pereomere 7, elongate and tapered pleon in *T. clypeus* n. gen., n. sp.).

Genus *Telephryxus* n. gen.

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TYPE SPECIES. — *Telephryxus clypeus* n. sp.

ETYMOLOGY. — The genus name is derived from the Greek prefix τηλε- (tele-), meaning “far away” in reference to the specialization of the female of the species on the antennule of the host crab rather than on the host body (as in “far away from the host’s body”) as

well as to the occurrence of the sole species in the abyssopelagic zone (far away from the habitat of most dajids), in combination with *-phryxus*, from the Boeotian prince Phryxus (Φρίξος) of Greek mythology, a common ending for dajid, as well as some bopyrid, genera. The gender is masculine.

INCLUDED SPECIES. — *Telephryxus clypeus* n. sp. (type species).

DIAGNOSIS. — **Female.** Body spheroid; cephalon externally indistinguishable from pereon. Antennules each as flat triangular plate; antennae each as flat rectangular plate lateral to oral cone. Maxillipeds inflated, rectangular, each with recurved maxilliped digitiform extension (“appendix”) at posterolateral corner. Pereopods 1–5 subequal in size and shape. Oostegite 1 largest, broadly ovate with large triangular posterior accessory lobe; oostegites 2–4 flat, ovate; oostegite 5 flat, tapering. Pleon apparently modified as subquadrate, broad, thickened plate with two circular medial holes, subequal in size; hole surrounding distal portion of host antennular peduncle with one small additional hole on each lateral margin.

Male. Cephalon fused with pereomere 1; cephalic slits present. Antennules each as single ovate plate lateral to and extending posterior to oral cone; antennae of two segments each, flagella absent. Pereomeres 2-7 distinct, lateral margins recurved ventrally. Pereopods 1-6 subequal in size and shape; pereopod 7 reduced, single rounded stub on right side, rounded stub plus dactylus on left side. Pleon tapering to rounded tip, all segments fused, distinct from pereomere 7; pleopods lacking. Cryptoniscus larva: Body tear-drop shaped. Cephalon medial region of posterior margin convex, lateral regions concave, posterolateral margins extended posteriorly. Antennules of three articles each, basal article triangular, article 2 quadrate, article 3 digitiform, inserted into article 2 distoventrally. Antennae of nine articles each, peduncular articles subequal in size; flagellar articles approximately half width of peduncular articles. Oral cone lacking oral sucker (possible artifact due to loss during collection). Pereomeres 1-7 with entire coxal plates. Pereopod 1 with short, slightly curved dactylus, propodus semi-spherical; pereopods 2-6 with more elongate curved dactyli, propodi progressively more elongate. Pereopod 7 with long, slightly curved dactylus, propodus elongate with two large multifid setae near base of dactylus; carpus with distal large multifid seta; merus triangular with anterodorsal edge extending into spine-like extension, ischium triangular, basis cylindrical. Pleon with five pairs of biramous pleopods, endopods cylindrical, exopods triangular. Pleotelson oval. Uropods biramous, sympod broad, endopod slightly longer than exopod.

REMARKS

See Remarks above under *Akrophryxus milvus* n. gen., n. sp. for comparison of female and male characters of *Akrophryxus* n. gen., *Telephryxus* n. gen., and other dajid genera.

Telephryxus clypeus n. sp.
(Figs 6-10; 11N)

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“remarkable isopod parasite (Dajidae?)” – Gore 1983: 207.

TYPE MATERIAL. — **Holotype.** Caribbean Sea • USNM 1163461; female (8.0 mm diameter) with pre-molt epicaridean larvae, attached to right antennule of female *Munidopsis crassa* Smith, 1885 (40.9 mm CL, incl. rostrum; USNM 204595); NORDA Sta. 99; 14°51.70'N, 67°27.8'W; Venezuela Basin, north of Islas de Aves; 4956-4997 m; coll. United States Navy research vessel USNS *Bartlett*, taken by 45 ft balloon net trawl (Gore 1983); 3.XII.1981.

Allotype. Caribbean Sea • USNM 11616635; mature male (2.4 mm L); same data as for holotype.

Paratype. Caribbean Sea • USNM 11616636; cryptoniscus larva (0.9 mm L); same data as for holotype.

ADDITIONAL MATERIAL. — USNM 11616637, c. 30 pre-molt epicaridium larvae, same data as for holotype (on SEM stubs).

TYPE LOCALITY. — 14°51.70'N, 67°27.8'W, Venezuela Basin, Caribbean Sea, 4956-4997 m (*vide* Gore, 1983).

TYPE HOST. — *Munidopsis crassa* Smith, 1885 [Crustacea: Anomura: Munidopsidae].

ETYMOLOGY. — The species name is derived from the Latin for “shield” in reference to the broad subquadrate plate that partially surrounds the host antennule and is reminiscent of the shape of a shield. The gender is masculine.

DISTRIBUTION. — Known only from the type locality and type host.

DESCRIPTION

Female

Body spheroid (Figs 6; 7A, B), length and width nearly equal, filled with numerous pre-molt epicaridium larvae (see description below). Cephalon externally indistinguishable from pereon, without eyes. Antennules (Fig. 7F) each as flat triangular plate covered with minute scales (not shown); antennae each as rectangular flat plate lateral to oral cone (Fig. 7E, G), covered with minute scales (Fig. 7G inset). Oral cone rounded (Fig. 7E); mouthparts indistinct. Maxillipeds inflated, rectangular, each with recurved maxilliped digitiform extension (“appendix”) at posterolateral corner (Figs 6E, 7E, H, K), “appendix” extending into groove of oostegite 1 (Fig. 7K). Pereopods 1-5 subequal in size and shape, without setae (Fig. 7E); dactylus short, recurved, propodus carpus and merus fused (indistinct ventral indication of segmentation on some pereopods), ischia and bases stout. Oostegite 1 largest, broadly ovate with large triangular posterior accessory lobe (Figs 6E; 7I, J, K), broad rounded lobe medially divided in lateral view, forming groove (Fig. 7J, K); oostegites 2-4 flat, ovate, posterior pairs progressively slightly larger (Fig. 7K); oostegite 5 flat, elongate, tapering, lacking marginal setae (Fig. 5L). Pleon presumably modified (see Discussion) as subquadrate, broad, thickened plate (Figs 6A-D; 7A, B, D) partially surrounding host antennule with two circular medial holes, subequal in size; hole surrounding basal antennular peduncle of host closest to mouthparts of parasite, hole surrounding distal portion of host antennular peduncle with one small additional hole on each lateral margin.

Male

Body not recurved ventrally (Fig. 8A, B). Cephalon fused with pereomere 1 (Fig. 8A-C), anterior margin subtriangular, posterolateral margins evenly rounded; faint unpigmented eyes, cephalic slits present. Antennules each as single ovate plate lateral to and extending posterior to oral cone, with minute lateral projection bearing terminal setae (Fig. 8C); antennae lateral to antennules, of two segments each with distal setae (Fig. 8C), flagella absent. Oral cone subtriangular (Fig. 8B, C). Pereomeres 2-7 distinct, 2-6 subequal in width, 7 slightly narrower, lateral margins recurved ventrally (Fig. 8A, B). Pereopods 1-6 subequal in size and shape (Fig. 8B-D), ischia and bases fused, carpi rounded, ischia/bases elongate; dactylus and propodus with isolated marginal setae; pereopod 7 reduced, single rounded stub on right side, rounded stub plus dactylus on left side. Pleon elongate (Fig. 8A, B), tapering to rounded tip, all segments fused, distinct from pereomere 7; anal slit and pleopods lacking.

Cryptoniscus larva

Body tear-drop shaped (Fig. 9A, B), length 0.9 mm, maximum width at pereomere 3. Cephalon anterior margin round, medial region of posterior margin convex, lateral regions concave, posterolateral margins extended posteriorly (Fig. 9A); eyes round, unpigmented. Body pigmentation lacking. Antennules of three articles each (Fig. 9C), basal article triangular with five stout distal setae, article 2 quadrate with four stout distal

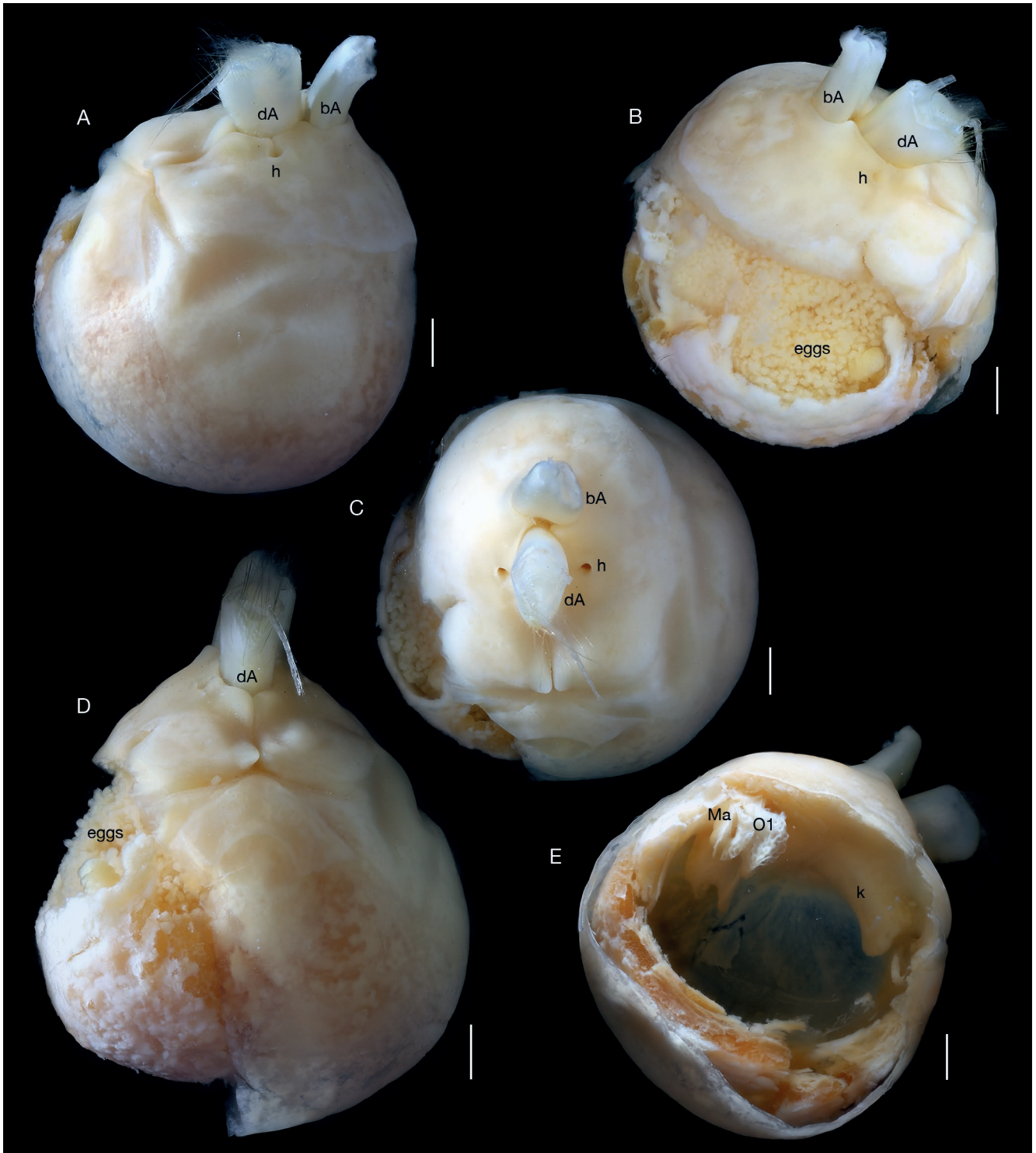


FIG. 6. — *Telephryxus clypeus* n. gen., n. sp., holotype female, macropod images, USNM 1163461: **A**, lateral view, right side showing host antennule extending from top (remains of distal end of host antennule to left, basal end of host antennule to right); **B**, oblique view of left side, outer membrane of parasite removed, showing brood of eggs; **C**, top down view, showing lateral openings in parasite body to side of host antennule; **D**, posterior view, membrane of parasite removed on left side, showing brood of eggs; **E**, lateral view, left side with eggs removed showing maxillipeds (**Ma**), oostegite 1 (**O1**) and raised keel-like structure (**k**) that extends posteriorly. In figures **A-D**, the basal antennular peduncle of host (**bA**), distal portion of host antennular peduncle (**dA**), and small additional hole in pleon (**h**) are labeled. Scale bars: A-E, 1 mm.

setae and several low, rounded bumps, article 3 digitiform, inserted into article 2 distoventrally, less than half width of article 2, with two distal setae (Fig. 9C). Antennae of nine

articles each (four peduncular and five flagellar) (Fig. 9B, D), all articles cylindrical, peduncular articles subequal in size with minute, distal setae (at least on articles 3 and 4); flagellar

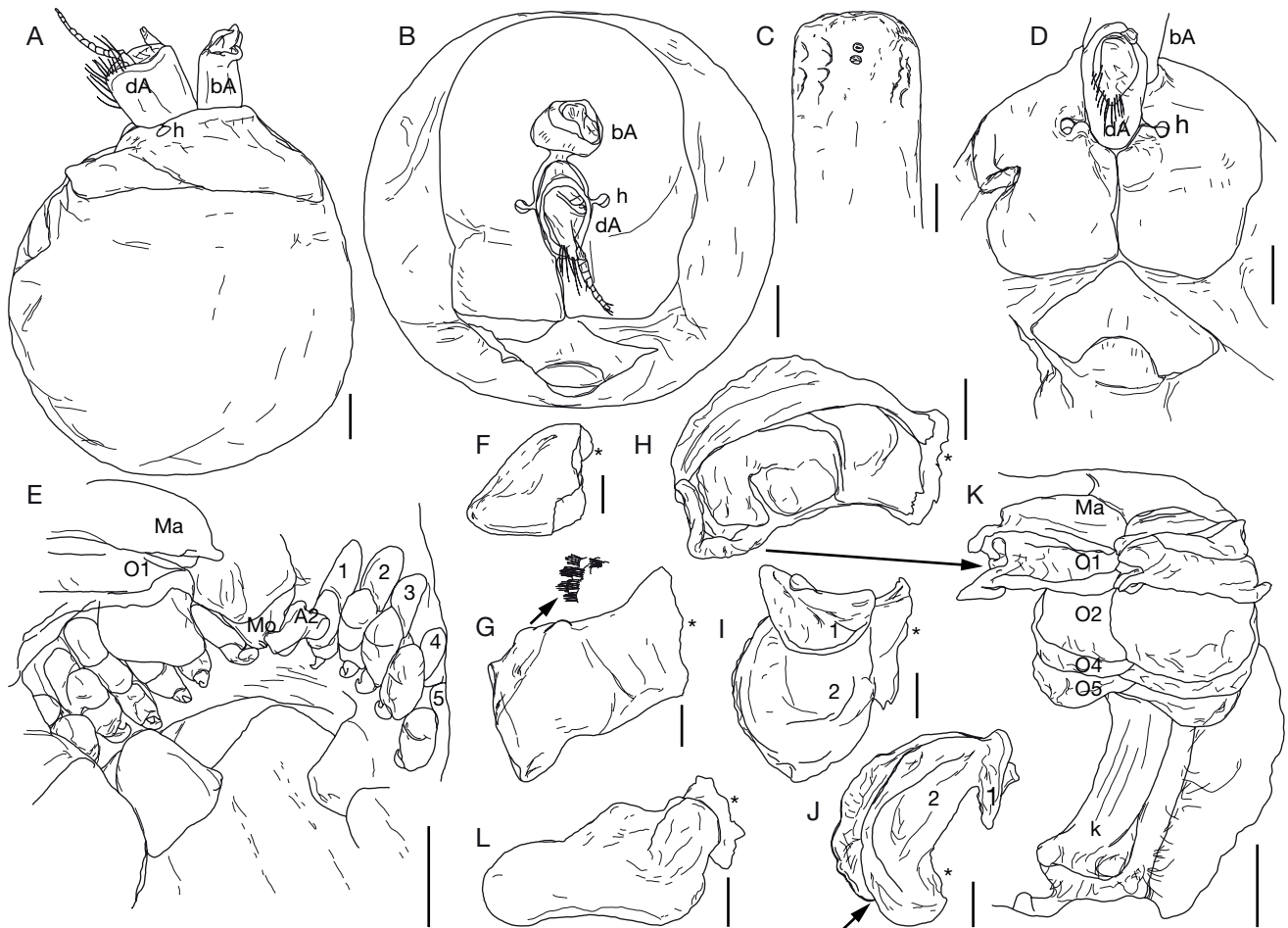


FIG. 7. — *Telephryxus clypeus* n. gen., n. sp., holotype female, USNM 1163461: **A**, lateral view, right side showing host antennule extending from top (remains of distal end of host antennule to left, basal end of host antennule to right); **B**, top down view (remains of distal end of host antennule to top, basal end of host antennule to bottom); **C**, host antennule showing attachment sight of parasite with two holes created by mouthparts and rows of scars from pereopods; **D**, posterior view, showing lateral openings in parasite body to side of host antennule; **E**, ventral view showing showing mouthparts (**Mo**), antenna (**A2**), maxilliped (**Ma**) and pereopods (1-5 labeled); **F**, antennule; **G**, antenna, **arrow** shows magnified view of scales that cover both antennae; **H**, right maxilliped, **arrow** shows position of curved digitiform extension and where it is inserted in fold of oostegite 1 in part **K**; **I**, right oostegite 1, showing two lobes (1 and 2); **J**, right oostegite 1, view showing two lobes (1 and 2) and fold along edge within which digitiform extension of maxilliped resides; **K**, ventral view of body showing maxillipeds (**Ma**), oostegite 1 (**O1**) and pereopods (1-5 labeled) and raised keel-like structure (**k**) that extends posteriorly; **L**, left oostegite 5. In figures **A**, **B**, and **D**, the basal antennular peduncle of host (**bA**), distal portion of host antennular peduncle of host (**dA**), and small additional hole in pleon (**h**) are labeled. In figures **F**-**J**, and **L** asterisks show site of attachment for structures dissected from body of parasite. Scale bars: **A**, **B**, **D**, **E**, **K**, 1 mm; **C**, **H**, **I**, **J**, **L**, 500 μ m; **F**, **G**, 200 μ m.

articles approximately half width of peduncular articles, with minute terminal setae, distalmost article with two long terminal setae (Fig. 9D). Oral cone triangular, anteriorly directed, lacking oral sucker (see Remarks) (Fig. 9B, E). Pereomerites 1-7 with entire (not toothed) coxal plates (Fig. 9B). Pereopod 1 with short, slightly curved dactylus, propodus semi-spherical with distoventral ridge corresponding to dactylus tip position bearing stout, simple setae; carpus with distal seta; merus and ischium rounded, basis cylindrical (Fig. 9D, E). Pereopods 2-6 with more elongate curved dactyli, propodi progressively more elongate with distoventral ridge corresponding to dactylus tip position bearing stout, simple setae; each carpus with distal seta; meri and ischia rounded, bases cylindrical (Fig. 9E, F). Pereopod 7 with long, slightly curved dactylus, propodus elongate with distoventral ridge corresponding to dactylus tip position, with two large multifid setae and one simple seta near

base of dactylus; carpus with distal large multifid seta; merus triangular with anterodorsal edge extending into spine-like extension closely applied to propodus dorsal margin, ischium large, triangular, basis long, cylindrical (Fig. 9G). Pleon with five pairs of biramous pleopods, endopods cylindrical, exopods triangular, both with long terminal setae (Fig. 9H). Pleotelson oval, with rounded distomedial margin (Fig. 9A, I). Uropods biramous, composed of wide sympod with lateral projection and seta, endopod slightly longer than exopod, pair of long distal setae on endopods and exopods, short seta at distolateral margin of endopods and exopods (Fig. 9I).

Pre-Molt Epicaridium Larva

Length $228.1 \pm 13.7 \mu\text{m}$ ($n = 30$) from anterior margin of cephalon to end of pleotelson. Body ovoid (Fig. 10A), covered in wrinkled cuticle, obscuring segmentation of append-



FIG. 8. — *Telephryxus clypeus* n. gen., n. sp., allotype male, USNM 1616635: **A**, dorsal view; **B**, ventral view; **C**, ventral view of anterior end showing mouthparts, antennules (**A1**), antenna (**A2**) and left first pereopod (**P1**); **D**, left pereopod 6; **E**, left pereopod 7. Scale bars: A, B, 250 μ m; C-E, 50 μ m.

ages. Cephalon large, rounded anteriorly; in ventral view, broad and extending laterally, appearing fused with antennules (Fig. 10B, D). Antennule triangular with large basal portion, two distal lobes and additional smaller extensions (Fig. 10B, D F). Antenna long, approximately $\frac{3}{4}$ length of body (Fig. 10A, B, E) with small distal lobes (Fig. 10C, G). Oral region inflated, no distinct oral cone, with pair of lobes (maxillipeds) anterior to pair of smaller lobes (Fig. 10B, D). Six pairs of rounded, broadly hooked pereopods, subequal in size, segmentation not visible (Fig. 10B, D, E). In lateral view, sides of pereomeres and pleomeres with thin extensions; anterior pleomeres 3-5 with crenulate margins (Fig. 10E, G). Pleon with 5 pairs of pleopods (Fig. 10B, C, G); pleopods 1-4 biramous, bearing three long terminal setae on each exopod and two long terminal setae on each endopod; pleopod 5 reduced, uniramous, lacking long terminal setae. Uropods biramous, endopods slightly shorter

than exopods, both ending in two short lobes, terminal setae lacking (Fig. 10D, G).

REMARKS

See Remarks under *Akrophryxus milvus* n. gen., n. sp. for comparison with *Telephryxus clypeus* n. gen., n. sp. and other dajids. The maxilliped digitiform extension (“appendix” of Rustad 1935) appears homologous with the lateral lobes of the barbula found in bopyrids (Markham 1985). As in bopyrids, the maxillipeds are used to pump water through the brood chamber, oxygenating the eggs or larvae (Gilson 1909; Cericola & Williams 2015). However, in the case of females of species in the two new genera, the digitiform extension of the maxilliped also fits into the groove of oostegite 1, thus further aiding in oxygenation by moving the whole first oostegite. It may also aid in maintaining larvae in the brood chamber prior to release (Cericola & Williams 2015).

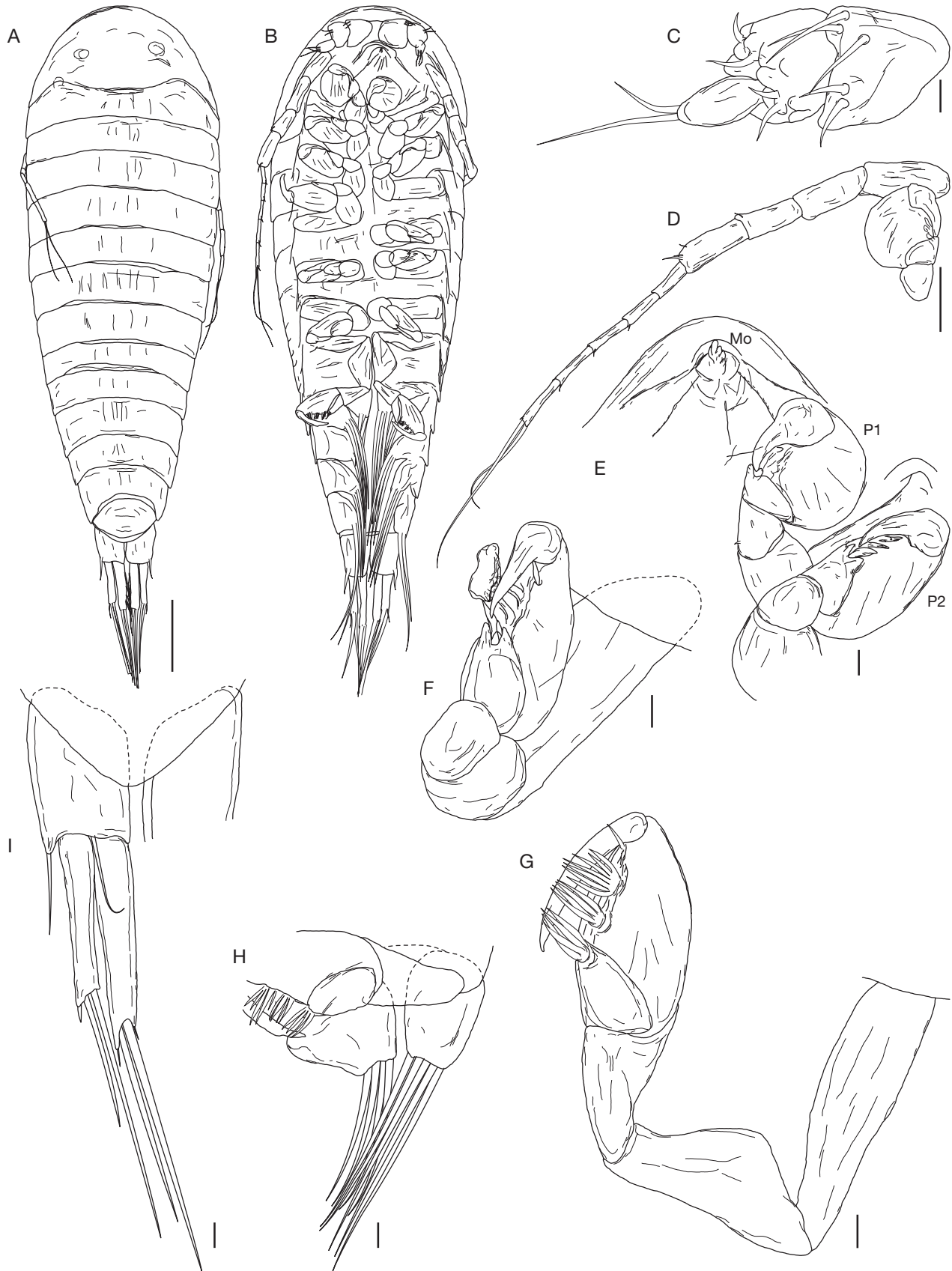


FIG. 9. — *Telephryxus clypeus* n. gen., n. sp., paratype cryptoniscus larva, USNM 1616636: **A**, dorsal view; **B**, ventral view; **C**, left antennule; **D**, left antenna and pereopod 1; **E**, ventral view of mouthparts (**Mo**), right pereopod 1 (**P1**), right pereopod 2 (**P2**); **F**, left pereopod 6; **G**, left pereopod 7; **H**, left pleopod 1 and part of left pereopod 7; **I**, pleotelson and left uropod, dorsal view. Scale bars: A, B, 100 μ m; C, E-I, 10 μ m; D, 50 μ m.

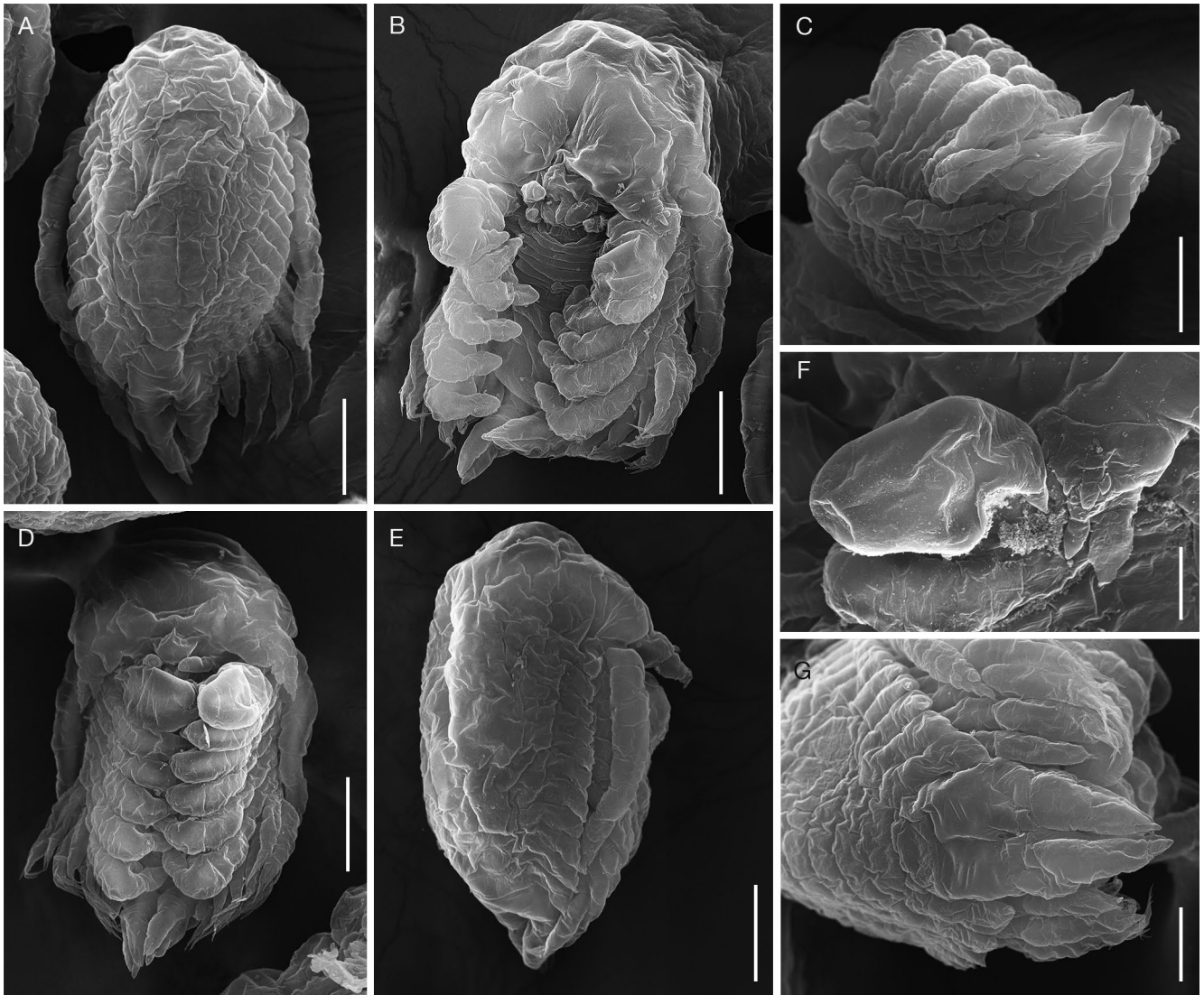


FIG. 10. — *Telephryxus clypeus* n. gen., n. sp., epicaridium larvae, USNM 1616637: **A**, dorsal view; **B**, ventral view; **C**, oblique, lateral view; **D**, ventral view; **E**, lateral view; **F**, left pereopod 1 and antennule; **G**, posterior end, dorsal view. Scale bars: A-E, 50 μ m; F, 15 μ m; G, 25 μ m.

The epicaridium larvae of *Telephryxus clypeus* n. gen., n. sp. were in pre-molt, having a wrinkled cuticle (particularly evident surrounding the cephalon, antennae and pereopods) similar to that shown in larvae of other dajid species (G. O. Sars 1898: pl. 94; Gilson 1909: figs 10, 11; Shimomura *et al.* 2005: fig. 12). As discussed by Gilson (1909), there are two stages of epicaridium larvae: the first is maintained within the brood chamber of the female and the second is released from the female as the planktonic phase prior to attachment to a copepod intermediate host (Fig. 11A-G). In addition to the yolk provisioned endogenously to the epicaridium larvae, they may also be provisioned with exogenous sources of nutrition taken up across the embryonic epithelial layer (as discussed by Strömberg [1971] and shown to occur in cryptoniscoids by Goudeau [1977]) that fuel their final development prior to release into the water column. After molting, the second stage (mature) epicaridium larvae of

dajids show distinct segmentation of appendages (e.g. G. O. Sars 1898; Gilson 1909; Tattersal 1911; Taberly 1957a). The pleopods of the epicaridium larvae of *T. clypeus* n. gen., n. sp. all appear biramous (as they do in other pre-molt larvae previously described; e.g. Stephensen [1913], Shimomura *et al.* [2005]). However, it is not clear if any or all of these will remain biramous or become uniramous in the mature epicaridium larvae. Pleopods of mature epicaridium larvae of dajids have been described with both uniramous and biramous states: pleopods 1-5 uniramous (Gilson 1909) or pleopods 1-4 biramous and 5 uniramous (Taberly 1957a; Coyle & Mueller 1981).

The uropods of the pre-molt epicaridium larvae of *T. clypeus* n. gen., n. sp. are biramous, as are those of the mature epicaridium larvae described by Taberly (1957a). However, the orientation of the endopod and exopod of the uropods is ninety degrees rotated (“superposées” of Trilles 1999) from

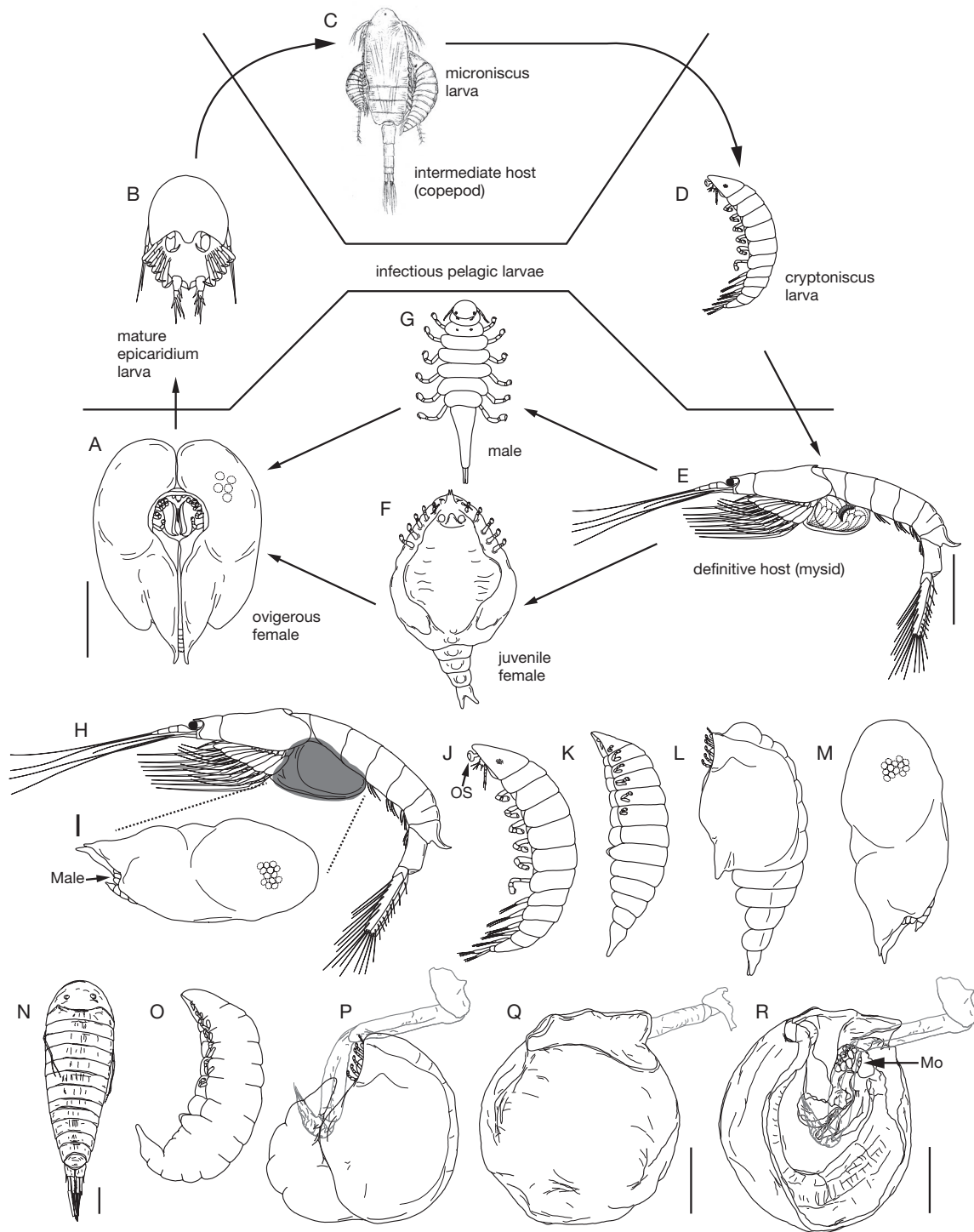


FIG. 11. — Life-cycle diagram of the dajid isopod *Prodajus ostendensis* Gilson, 1909 parasitizing the opossum shrimp *Gastrosaccus spinifer* (Goës, 1864): **A**, ovigerous female, ventral view. Eggs (shown in **dashed circles**) develop into early epicaridium larvae and then molt once; **B**, mature epicaridium larvae released into the water column; **C**, mature epicaridium larvae find copepod intermediate host, attach and metamorphose into an ectoparasitic microniscus larva. Microniscus larva transforms into a cryptoniscus larva that detaches and is free-swimming; **D**, cryptoniscus larva settles on host mysid and invades marsupium; **E**, within the host marsupium the cryptoniscus larva transforms into a juvenile female; **F**, juvenile female, ventral view; **G**, another cryptoniscus larva (or larvae) settles and transforms into a dwarf male; **H**, host *G. spinifer* with ovigerous female *P. ostendensis* (in **grey**) occupying the marsupium; **I**, ovigerous female, lateral view with one dwarf male partially visible and eggs shown in dashed circles; **J-M**, developmental series of females of *P. ostendensis*, all in lateral view: **J**, cryptoniscus larva with oral sucker (**OS**); **K**, early juvenile female (second phase *vide* Gilson 1909); **L**, later juvenile female (third phase *vide* Gilson 1909); **M**, ovigerous female; **N-R**, proposed developmental series of females of *Akrophryxus milvus* n. gen., n. sp. and *Telephryxus clypeus* n. gen., n. sp.: **N**, cryptoniscus larva of *T. clypeus* n. gen., n. sp., dorsal view; **O**, hypothetical early juvenile female, lateral view; **P**, hypothetical later juvenile female of *A. milvus* n. gen., n. sp. attached to antennule of host (shown in **grey**), lateral view; **Q**, ovigerous female of *A. milvus* n. gen., n. sp. attached to antennule of host (shown in **grey**), lateral view; **R**, ovigerous female of *A. milvus* n. gen., n. sp. dissected to show attachment to antennule of host (shown in **grey**) with mouth (**Mo**) of parasite noted, lateral view (A, B, D-M, modified from figures in Gilson (1909); C, from G. O. Sars (1898)). Scale bars: A, Q, R, 1 mm; E, 3 mm; N, 100 µm; rest not to scale.

TABLE 1. — Comparative characters of females in the 20 genera of Dajidae G. O. Sars, 1883. Higher level host taxon and the position on hosts or attachment site of the parasites, if known, is indicated in the first column. Two genera have no described females. Species of *Dolichophryxus* Schultz, 1977 and *Paraspidophryxus* Schultz, 1977 described from cryptoniscus larva only, hosts are unknown.

Genus	Host taxon (position on host)	Distinct cephalon	Pereon Segmented	Number of pereopod pairs	Number of oostegite pairs	Number of pleomeres	Number of pleopod pairs	Uropods
<i>Aegophila</i> Bresciani, 1966	Isopoda (pereopod)	Yes	Rudimentary	5	5	1 (fused)	0	No
<i>Akrophryxus</i> n. gen.	Brachyura (antennule)	No	No	5	5	1 (fused into plate)	0	No
<i>Allophryxus</i> Koehler, 1911	Unknown	Yes	Yes	5	5	5 or 6	2	Yes
<i>Antephyra</i> Schultz, 1978	Unknown	Yes	Yes	5	?	1 (fused)	0	No
<i>Arthrophryxus</i> Richardson, 1908a	Lophogastrida (unknown)	Yes	Yes	4	5	5	0	No
<i>Aspidophryxus</i> G. O. Sars, 1883	Mysida (between eyestalks, carapace, thorax)	Yes	Rudimentary	5	1	1 (fused; vermiform)	0	No
<i>Branchiophryxus</i> Caullery, 1897	Euphausiacea (gills)	No	Rudimentary	4	4	1 (fused)	0	No
<i>Colophryxus</i> Richardson, 1908b	Unknown	Yes	Yes	5	?	1 (fused)	0	No
<i>Dajus</i> Krøyer, [1842]	Mysida (in marsupium)	Yes	Yes	5	5	4	1+	Yes
<i>Heterophryxus</i> G. O. Sars, 1885	Euphausiacea (eyestalks; attaches with 5th pereopods)	No	Yes	5 (terminal pair highly modified)	5	1 (fused)	0	No
<i>Holophryxus</i> Richardson, 1905	Caridea & Sergestoidea (carapace)	Yes	Rudimentary	5	5	1 (fused)	0	No
<i>Notophryxus</i> G. O. Sars, 1883	Euphausiacea (abdomen, carapace, gill, pereopod)	Yes	Yes	5	1 (fused)	1 (fused)	0	No
<i>Oculophryxus</i> Shields & Gómez-Gutiérrez, 1996	Euphausiacea (eyestalks; attaches with antennae)	No	Rudimentary	4	1 (fused)	1 (fused)	0	No
<i>Prodajus</i> Bonnier, 1903	Mysida (in marsupium)	Yes	No	5	5	4 or 5	0	Yes
<i>Prophryxus</i> Richardson, 1909	Unknown	Yes	Yes	5	2?	5	Rudimentary?	?
<i>Streptodajus</i> Nierstrasz & Brender à Brandis, 1923	Mysida (unknown)	No	Yes	5	?	1 (fused, with slight dorsal indications)	0	No
<i>Telephryxus</i> n. gen.	Anomura (antennule)	No	No	5	5	1 (fused into plate)	0	No
<i>Zonophryxus</i> Richardson, 1904	Caridea (carapace)	No	Rudimentary	5	5	1 (fused)	1	No

the lateral orientation that is typical for other epicarideans (“côte à côte” of Trilles 1999). The two segments can only be distinguished in lateral view (Taberly 1957a: fig. 1; Coyle & Mueller 1981: fig. 1E). Some mature dajid larvae have been illustrated with what appear to be uniramous uropods (G. O. Sars 1898; Gilson 1909) but, as suggested by Taberly (1957a), these larvae may not have been observed in the proper orientation. Tattersall (1911) considered uniramous pleopods and uniramous uropods a defining characteristic for dajids; however, the key of Bourdon in Trilles (1999) is probably more accurate for dajid characters (pleopods and uropods both biramous).

The cryptoniscus larva of *T. clypeus* n. gen., n. sp. lacks an oral sucker, a characteristic found in most dajid species

for which larvae have been examined (Fig. 11J). However, we think this represents a case where the attachment structure fell off prior to or during collection. As noted by Taberly (1957b), the oral sucker of dajids is easily detached. Other records of dajid cryptoniscus larvae lacking an oral sucker (e.g. *Holophryxus alaskensis* Richardson, 1905, *Zonophryxus quinquidens* Barnard, 1914) should be considered as possible instances where this structure was detached. Although Coyle & Mueller (1981) collected several cryptoniscus larvae of *H. alaskensis* and reported they lacked an oral sucker, we suggest collection of new material of all such species is needed to confirm absence or presence of the oral sucker in cryptoniscus larvae across dajid taxa.

TABLE 2. — Comparative characters of males in the 20 genera of Dajidae G. O. Sars, 1883 (five genera have no described males: *Antephyra* Schultz, 1978, *Prophryxus* Richardson, 1909, and *Streptodajus* Nierstrasz & Brender à Brandis, 1923 are known from females only; species of *Dolichophryxus* Schultz, 1977 and *Paraspidophryxus* Schultz, 1977 are known from cryptoniscus larvae only).

Genus	Antennule (= antenna 1)	Antennae (= antenna 2)	Terminal pereomere fused with first pleomere	Number of pereopod pairs	Number of pleomeres	Uropods
<i>Aegophila</i> Bresciani, 1966	Single lobe	2 or 4 segments	No	7	1 (fused)	No
<i>Akrophryxus</i> n. gen.	3? segments	Single lobe	Yes	6	1 (fused)	No
<i>Allophryxus</i> Koehler, 1911	Single lobe?	5 segments	No	7	4 (partly fused)	Rudimentary
<i>Arthrophryxus</i> Richardson, 1908	Unknown	Unknown	No	7	6	No
<i>Aspidophryxus</i> G. O. Sars, 1883	1 or 2 segments	8 or 9 segments	No	7	1 (fused)	Yes
<i>Branchiophryxus</i> Caullery, 1897	Rudimentary (1 segment?)	9 segments	Unknown	7	1 (fused)	No
<i>Colophryxus</i> Richardson, 1908	Unknown	Unknown	No	7	5 or 6	No
<i>Dajus</i> Krøyer, [1842]	Rudimentary (1 segment?)	9 segments	No	7	1 (fused)	Rudimentary
<i>Heterophryxus</i> G. O. Sars, 1885	1-3 segments	5 segments	No	7	1 (fused)	No
<i>Holophryxus</i> Richardson, 1905	1-3 segments	Longer, 1-3 segments?	Yes	7	1	No
<i>Notophryxus</i> G. O. Sars, 1883	1 or 2 segments	5 or 6 segments	No	7	1 (fused)	No
<i>Oculophryxus</i> Shields & Gómez-Gutiérrez, 1996	2 segments	5 segments	Yes	7	1	No
<i>Prodajus</i> Bonnier, 1903	2 segments	5 or 6 segments	No	7	1 or 2	Yes (biramous)
<i>Telephryxus</i> n. gen.	1 large segment	2 segments	No	6 + reduced pair	1 (fused)	No
<i>Zonophryxus</i> Richardson, 1904	1 segment	6 segments	No	7	1 (fused)	No

DISCUSSION

Female epicaridean parasites exhibit an amazing degree of morphological diversity that has likely evolved as varied adaptations to their highly specialized parasitic lifestyle, from forms that are not widely divergent from the typical isopod bauplan (i.e., with seven clearly identifiable pereomeres and segmented pereopods) to those that are nearly unrecognizable as isopods to the untrained eye (i.e., exhibit a sac-like body lacking any segmentation) (e.g. Trilles 1999; Williams & Boyko 2012; Buhl-Mortensen *et al.* 2020). The present study adds two new genera and three new species to the family Dajidae, increasing the total number of genera from 18 to 20 and bringing the total number of species in the family to 59. The findings expand the morphological boundaries of dajids – a group of parasites historically known primarily from the carapaces of shrimp-like hosts and the marsupia of mysids (Boxshall & Hayes 2019; Williams & Bunkley-Williams 2019). The females of the two newly described genera are nearly perfect spheres encompassing a portion of the antennules of their decapod hosts, a position and morphology previously unknown among dajids (Table 1) and only rarely reported in some other groups of crustacean parasites (see review in Introduction). Although these unusual parasites show no external signs of being epicarideans, upon dissection they exhibit the characteristic five pairs of segmented pleopods and other taxonomically important features of dajids. The males of both species are similar to other dajids in most characters (Table 2); although they are found inside the brood chambers of their female partners, as are the males of many other dajid species, they are essentially

entombed by the fusion of the female’s pereomeres and pleon around the antennae of hosts. Although the females of both new genera are superficially similar in many aspects (Table 1), the males show distinct, generic-level differences (Table 2). The similarity of the females’ spheroid morphology could either be due to a shared common ancestor or to convergent adaptations for parasitizing antennules of their hosts. More specimens and, ideally, molecular data would be needed to address these possibilities.

Dajid life cycles, such as that of *Prodajus ostendensis* Gilson, 1909 from the opossum shrimp host *Gastrosaccus spinifer* (Goës, 1864), show that the female parasites reach sexual maturity and release epicaridium larvae that seek out a calanoid copepod, pass through a microniscus larval stage that feeds on copepod hemolymph, and ultimately transform into a cryptoniscus larva that seeks out and settles on a definitive host (Fig. 11A-G). The cryptoniscus larva likely settles on the host (possibly in the branchial chamber) and then moves to its final destination (see Coyle & Mueller 1981). Unlike in other epicaridean parasites that exhibit protandric hermaphroditism (Williams & Boyko 2012), the cryptoniscus larvae of dajids are supposedly of separate sexes and males do not turn into females (Gilson 1909); larvae either become juvenile females (Fig. 11F) or males (Fig. 11G); this, however, needs more study for confirmation. Males move onto females, eventually entering the brood chamber and fertilizing the eggs of sexually mature females (Fig. 11A, H, I). Some researchers (Gómez-Gutiérrez *et al.* 2010; 2017) have suggested the cryptoniscus larvae of dajids can act as micropredators (feeding transiently on multiple hosts) but this has not been definitively demonstrated.

Additionally, Gómez-Gutiérrez *et al.* (2017) stated that one of the three main feeding strategies for dajids was “eating the eggs from the crustacean’s ovigerous sacs, which so far is only observed in Dajidae infesting mysids (Shimomura *et al.* 2005; Shimomura & Ohtsuka 2008).” No such observation was reported by either Shimomura *et al.* (2005) or Shimomura & Ohtsuka (2008). However, Ohtsuka *et al.* (2007) reported on a copepod (*Neomysidion rahotsu* Ohtsuka, Boxshall & Harada, 2005) that competed with a dajid (*Prodajus curviabdominalis* Shimomura, Ohtsuka & Saito, 2005) for space in a mysid marsupium. This copepod was indeed observed to consume mysid eggs and Ohtsuka *et al.* (2007) stated “both of these parasites [dajid and copepod] utilise the lumen of the mysid marsupium as a microhabitat and its eggs (and embryos) as food (Ohtsuka *et al.* 2005; Shimomura *et al.* 2005)” but, once again, there is no data given in Ohtsuka *et al.* (2007) or either of the papers cited therein to show that dajids actually consume eggs. The sentence in Ohtsuka *et al.* (2007) “No host eggs remained when a fully mature female isopod was present within the marsupium, suggesting that all eggs in a brood were consumed by the isopod” indicates that these authors were speculating on the reason for the lack of host eggs and did not actually observe any predation by the dajids and that the copepod is the only egg predator in this relationship. We are unaware of any published data showing that dajids consume host eggs, although some cryptoniscoids are known to do so (reviewed in Buhl-Mortensen *et al.* 2020).

We propose the hypothetical life cycle and developmental transformation as the pathway by which females of *Akrophryxus milvus* n. gen., n. sp. and *Telephryxus clypeus* n. gen., n. sp. come to exhibit their spheroid morphology. In both new taxa, the life cycle is similar to that described above for dajids in general (Fig. 11A-G). However, the cryptoniscus larvae (Fig. 11N) either settle in the branchial chamber and then move onto the antennule or they may settle directly on an antennule. After attachment using their pereopods (and possibly the oral sucker) to the antennule, the body of a cryptoniscus larva that is transitioning to a juvenile female begins to dorsoventrally flex and the sides of the body expand (Fig. 11O). Eventually the pleon meets the anterior end and the two coalesce, as do the sides of the body (Fig. 11P). Thus, the plate (or “shield”) partially surrounding the host antennule appears to be a highly modified pleon which gradually surrounds the host antennule during development of the parasite (Fig. 11P-R). Alternatively, the plate could be an anterior extension of the cephalon or sides of the body. These appear less likely scenarios considering the shape and orientation of the features. The holes in the plate (Figs 4; 7) represent areas where complete fusion between the cephalon, pleon, and sides of the body has not occurred yet and it is through these openings that the epicaridium larvae of the dajids are likely released. The males reside in the brood chamber of females (as seen in many other dajids although, as mentioned, they are trapped by the fusion of the female body) and fertilize the brood (Gilson 1909). The feeding biology and nutrition of males remains unknown; they may be non-feeding and derive nutrition from stores remaining from the cryptoniscus larval stage.

The male and larval characters (epicaridium and cryptoniscus larvae) display characteristic dajid features. However, the males are unique in their degree of posterior pereopod reduction: lacking a seventh pereopod (*Akrophryxus milvus* n. gen., n. sp.) or seventh pereopod reduced to one or two stub-like segments (*Telephryxus clypeus* n. gen., n. sp.), a feature previously recorded in only one other dajid (*Oculophryxus bicaulis*, with the seventh pereopod reduced to two elongate segments). Finally, the cryptoniscus larval specimen of *T. clypeus* n. gen., n. sp. did not possess an oral sucker, but we suggest this is likely an artifact due to loss of the structure during handling as the suckers are fragile and break off easily (see Taberly 1957b). Future research should examine the life history of these species to document the changes in form of the female through development to sexual maturity and verify the ontogenetic origin of the plate partially surrounding the host antennule (see Fig. 11N-R), as well as clear up remaining questions on larval characters, such as the presence or absence of a sucker in the cryptoniscus stage and the characters of molted (second stage) epicaridium larvae.

The abyssopelagic specimens of *T. clypeus* n. gen., n. sp., being found on a host collected from 4956-4997 m, are the deepest known of any dajid species; the prior record was the type specimens of *Arthrophryxus beringanus* Richardson, 1908, found at 2700 fathoms (4938 m) in the Bering Sea parasitizing *Eucopia australis* Dana, 1852 [Peracarida: Lophogastrida] (Richardson, 1908a). In fact, there is only one record of any epicaridean from deeper waters, that of *Pleurocryptella altalis* Williams, Boyko & Marin, 2020 found on a *Munidopsis petalorhyncha* Baba, 2005 (originally as *M. subsquamosa* Birstein & Zarenkov, 1970) [Anomura: Munidopsidae] from the Kurile-Kamchatka Trench at 5025-5210 m depth (Birstein & Zarenkov 1970 ; Williams *et al.* 2020).

Due to the fact that these are parasites of deep-water hosts, it is unlikely that any questions regarding ontogeny can be tested experimentally (i.e., via rearing). Instead, these questions will most likely need to be addressed with newly fixed material of these dajids in their various larval and developmental stages as obtained from other studies. We therefore urge researchers to retain decapods with unidentified parasites, particularly those found on antennules, properly fix them for morphological and molecular studies and, most critically, deposit them in museums for later analysis.

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