Two New Species of Spheroid Ectoparasitic Isopods (Epicaridea: Dajidae) Attached to the Antennules of Brachyuran Crab Hosts, with Description of a New Genus and Species of Hyperparasite (Epicaridea: Cryptoniscoidea)

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(Received 18 January 2022; Accepted 19 April 2022)

In this paper, we describe two new species of dajid isopods found enveloping the antennules of decapod hosts: *Akrophryxus acinaces* sp. nov. parasitizing *Pycnoplax surugensis* (Rathbun, 1932) (off Pacific coast of central Japan, approximately 200 m depth) and *A. pallipalicus* sp. nov. parasitizing *Parapalicus armatus* Castro, 2000 (South China Sea, approximately 410 m depth). Females of both species exhibit the characteristic spheroid shape found in the genus *Akrophryxus* Williams and Boyko, 2021. Females of the three species in *Akrophryxus* can be distinguished by several characters, including form of the pleon and oostegite 5. Males can be distinguished by head/pereomere 1 to pereomere 2 ratio and posterolateral margin shape, and pereopod 6 dactylus and ischiium size. The three species of *Akrophryxus* not only differ in morphological characters but parasitize species belonging to three different heterotreme brachyuran families. The first described crypotoniscus larval stage for any species in the genus is described for *A. acinaces* sp. nov. We also describe a new cryptoniscoid, *Chimaeroniscus spheramator* gen. et sp. nov., the first hyperparasite described from any dajid host (*A. pallipalicus* sp. nov. on the host *Pa. armatus*). This hyperparasite is a putative egg predator of its dajid host and exhibits a unique combination of generic level characters including: pleon markedly narrower than pereon, antennule with large teeth on basal segment and with setal brush, 3 or 4 coxal teeth on all pereomeres, pereopods 3–7 isomorphic and dissimilar from pereopods 1 and 2, telson with smooth distomedial projection, and uropodal exopods half-length of endopods. Finally, we address some taxonomic issues within Cryptoniscoidea, moving two genera (*Neritoniscus* Schultz, 1977 and *Cryptotaxis* Schultz, 1977) known only by cryptoniscus larval characters from Cryptoniscoidea incertae sedis to Dajidae and synonymize *Cryptonus* Schultz, 1977 with *Holophryxus* Richardson, 1905.

**Key Words:** egg predation, hyperparasitism, Isopoda, *Parapalicus armatus*, *Pycnoplax surugensis*.

Introduction

Isopods of the family Dajidae are a relatively small group with 60 described species of ectoparasites that live on a wide range of definitive crustacean hosts (Boyko et al. 2008a). The best studied members of the group attach as adults to the dorsal carapace of caridean shrimp or euphausiid hosts, e.g., Wasmer (1988), Gómez-Gutiérrez et al. (2017), Alves-Júnior et al. (2018), and Boyko and Williams (2021a, b), or occur in the marsupia of mysids, e.g., Schultz and Allen (1982), Shimomura et al. (2005), and Williams and Boyko (2012). In contrast to these more well-known sites of attachment, Williams and Boyko (2021) reported on a novel attachment position for dajids with females of two new species found surrounding the antennules of hosts. These species also exhibited a unique spheroid morphology and were placed in two genera: *Akrophryxus* *milvis* Williams and Boyko, 2021 parasitizing the brachyuran crab *Ethusa mach-
ate hosts involved, remain poorly known.

Herein, we report on two new species of dajids belonging to the genus Akrophyxus Williams and Boyko, 2021 that attach to the antennules of their decapod hosts. The females and males for both species are described, and the first description of a cryptoniscus larva of a species in this genus is given. A female of one of the dajids was found to contain a hyperparasitic isopod (secondary parasite; see Freeman 2005) which is described and is a presumed egg predator of its host dajid. This study also led to clarification of the status of three cryptoniscoid genera now recognized as members of Dajidae with one genus synonymized with Holophryxus Richardson, 1905.

Materials and Methods

Hosts crabs [Pycnoploca surugensis (Rathbun, 1932) and Parapalicus armatus Castro, 2000] were collected by bottom trawl net (200 m depth) and beam trawl (410–412 m), respectively (see Materials examined for locality and additional data). The parasitized specimen of Py. surugensis was kept alive at the ToBa Aquarium at 10°C in an attempt to observe release of epicaridium larvae from the female dajids. Carapace length (CL) and width (CW) of brachyuran hosts were measured using calipers. Isopod parasite size is given as maximal body diameter for females when in lateral view and maximal body length (not including setae of uropods) for males and cryptoniscus larvae. All measurements were made with an ocular micrometer, from drawing tube sketches, or from scale bars in SEM images.

Line drawings of parasites were made by sketching specimens using drawing tubes attached to Olympus compound microscope (CX31) and Olympus dissecting microscope (SZX12). Scans of original sketches were traced with Adobe Illustrator to 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 (10–20 images from bottom to top of specimens).

For Scanning Electron Microscopy (SEM) preparation of cryptoniscus larvae, specimens were dehydrated in an ascending ethanol (EtOH) series 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 Seto Marine Biological Laboratory, Kyoto University (SMBL), Japan, and Lee Kong Chian Natural History Museum (formerly the Raffles Museum of Biodiversity Research) (ZRC), Singapore.

Taxonomy

Order Isopoda Latreille, 1817
Infraorder Epicaridea Latreille, 1825
Superfamily Cryptoniscoidea Kossmann, 1880
Family Dajidae G. O. Sars, 1883
Genus Akrophyxus Williams and Boyko, 2021

Type species. Akrophyxus milvis Williams and Boyko, 2021, fixed by original designation.

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 progressively larger; oostegite 5 present or absent. Pleon modified as oblong, narrow, thickened plate with two or three circular medial holes, largest surrounding antennule of host. Male: cephalon fused with pereomere 1; cephalic slits present. Antennules reduced, flagellae absent; antennae of one or two 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; pereopod 7 lacking. Pleon rounded, all segments fused and fused with pereomere 7; pleopods lacking. Cryptoniscus larva: body tear-drop shaped. Cephalon anterior margin round, posterolateral margins extending posteriorly; eyes unpigmented. Antennules of three articles each, without teeth. Antennae of nine articles each. Pereomeres 1–7 with smooth coxal plates, each pereomere notched medially. Pereopods 1 and 2 subequal, dactyls short, slightly curved, propodus inner margin folded, bearing two flat, multifid setae; carpus with single distal multifid seta. Pereopods 3–5 dactyls more elongate, curved, propodi more elongate, narrower, inner margin of each folded, bearing two flat, multifid setae; carpi each with single distal multifid seta. Pereopod 6 dactylus subequal in length to those of pereopods 3–5, propodus more elongate and narrower than those of pereopods 3–5, inner margin slightly folded, bearing two stout, multifid setae, carpus with single distal multifid seta. Pereopod 7 similar to pereopod 6 but with elongate dactylus extending to distal margin of merus, carpus with single flattened multifid seta.

Remarks. The below description of the cryptoniscus larval stage is the first for this genus. The cryptoniscus is similar to that described for the closely related T. clypeus; the principal differences being that the cryptoniscus of A. acinaces sp. nov. has a notch on the lateral margin of each pereomere (lacking in T. clypeus), the antennule segments are flatter and smoother (thicker and more sculptured in T. clypeus), and the dactyl of pereopod 7 is proportionally much longer, the propodus thinner, and the multifid spines on the propodus and carpus are much smaller than those of T. clypeus (Williams and Boyko 2021).

The three species of Akrophyxus are not only different in several morphological characters of females and males but
were found parasitizing hosts belonging to three different heterotreme brachyuran families: Ethusidae, Goneplacidae, and Palicidae from Madagascar (821–910 m), Japan (200 m), South China Sea (410–412 m), respectively (Williams and Boyko 2021).

**Akrophrysus acinaces** sp. nov.

[New Japanese name: Tsumenaga-kan-no-hana-chochin] (Figs 1–5)

**Material examined.** Holotype: mature female (SMBL-V0649; 4.5 mm diameter) with developing eggs, attached to right antennule of *Pycnoplax surugensis* (Rathbun,1932) (type host, SMBL-V0653; female, 26.2 mm CL, 35.1 mm CW); 34°08′49.0″N, 136°33′25.0″E, Kumano-nada Sea off Kii Nagashima, Kihoku, Mie prefecture, Pacific coast of central Japan (type locality), approximately 200 m depth, bottom trawl net, fishing trawler Jinsho-maru, 3 June 2020 (fixed 14 September 2020).

Allotype: mature male (SMBL-V0650; 0.65 mm) from female holotype; same data as for holotype.

Paratypes: four cryptoniscus larvae (SMBL-V0651; 1 on SEM stub, rest in ethanol) from ovigerous female holotype; one mature female (SMBL-V0652; 4.0 mm diameter) attached to left antennule of same host specimen as holotype, same data as for holotype.

**Etymology.** The species name is a noun in apposition derived from the Latin for "scimitar" in reference to the strongly recurved and elongate dactyl of the posterior pairs of pereopods of the male.

**Derivation of Japanese name.** We propose the new Japanese name *Tsumenaga-kan-no-hana-chochin* which refers to elongate dactyl of the male ("Tsumenaga" means "long claws") and appearance of the female on the host ("hana-chochin" means "snot bubble").

**Distribution.** Known only from the type locality and type host.

**Description of female.** Body spheroid, length and width nearly equal (maximal diameter in lateral view = 4.5 mm), filled with developing eggs in ovary (Figs 1, 2A–F). 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) (Fig. 3E, F). Oral cone rounded (Figs 2E, 3B), mouthparts indistinct. Maxillipeds ovate with recurved digitiform extension (Fig. 3G, H), extending into groove of oostegite 1. Pereopods 1–5 subequal in size and shape (Figs 2E, F, 3A–C); recurved dactylus short with setae and scales on ventral surface, propodus, carpus and merus fused, ischia and bases stout (Fig. 3D). Oostegite 1 largest (Fig. 3B, I, J), broadly ovate with small posterior accessory lobe, broad lobe medially divided in lateral view (Fig. 3I); oostegites 2–4, progressively larger, thin and closely applied to each other (Fig. 3K); oostegites 2 and 3 subrectangular (Fig. 3K, L), expanded posteriorly with small setae distally, oostegite 4 (Fig. 3M) subquadrate, small setae on medial and posterior margins. Oostegite 5 absent or extremely reduced. Pleon modified (see Remarks) as oblong, narrow, thickened plate (Figs 1D–F, 2A–D) partially surrounding host antennule (Fig. 2G) with two large circular medial holes: largest surrounding antennule of host and closest to mouthparts of parasite, smaller hole farthest from mouthparts of parasite (Fig. 3E). Larger hole flanked by two minute perforations (Fig. 2B, C).

**Description of male.** Body recurved ventrally (Fig. 4A), when flattened approximated 0.65 mm in length. Cephalon fused with pereomere 1 (Fig. 4A), anterior margin rounded and inflated dorsosventrally, posterolateral margins evenly rounded; lacking eyes, cephalic slits present. Antennules reduced, broadly conical, apparently of two segments, terminal segment minute with setae (Fig. 4A); antennae not observed. Oral cone triangular (Fig. 4A). Pereomeres 2–6 distinct, 4–6 subequal in width, others slightly narrower (Fig. 4A); pereomere 7 fused with pleon, lateral margins recurved ventrally (Fig. 4A). Pereopods subequal in size and shape, all segments distinct, carpi rounded, ischia short, bases elongate (Fig. 4A, C); dactyls of pereopods 4–6 similar to 1–3 but with much longer dactylus extending past distal margin of carpi (Fig. 4A, C, D); pereopod 7 lacking. Pleon compact, rounded, all segments fused and fused with pereomere 7, rounded posteriorly; anal slit and pleopods lacking (Fig. 4A).

**Description of cryptoniscus larva.** Body tear-drop shaped (Figs 4E, 5A, B), length (not including long uropodal setae) = 0.46 ± 0.03 mm (n = 4), pereomere 4 widest (Fig. 5A), anterior and posterior segments slightly narrower. Median region of pereomeres 2–6 containing pair of oval-shaped testes (Fig. 4E). Cephalon anterior margin round, medial region of posterior margin convex, lateral regions concave, posterolateral margins extended posteriorly (Fig. 4E); eyes round, unpigmented. Body pigmentation lacking. Antennules of three articles each (Fig. 5C), basal article triangular with two stout simple setae, article 2 quadrate with four marginal simple setae and few low, rounded bumps, article 3 digitiform, inserted into article 2 distoventrally, less than half width of article 2, with three long distal simple setae, lateral “flagellum” with three or four long simple setae (Fig. 5C). Antennae of nine articles each (four peduncular and five flagellar) (Fig. 4F), all articles cylindrical, basal peduncular article broader, next segment longest, distalmost two segments subequal in size and approximately half the length of second segment; minute, distal simple setae on article 4; flagellar articles approximately half width of peduncular articles, with minute terminal simple setae, distalmost article with four long terminal simple setae and two short simple setae (Fig. 4F). Oral cone triangular, anteriorly directed, lacking oral sucker (Figs 4E, 5A). Pereomeres 1–7 with smooth coxal plates, each with distinct distomedial notch (Fig. 5H), and small indentation lateral to notch. Pereopods 1 and 2 (Fig. 5A, C, D) each with short, slightly curved dactylus; propodus semi-spherical, inner margin folded, bearing two flat, multifid setae and one stout simple seta; carpi triangular, distally expanded with single distal multifid seta; meri and ischia rounded, bases cylindrical. Pereopods 3–5 (Fig. 5A, E–G, I) with more elongate curved dactylus, propodi more elongate and narrower, inner mar-
gin of each folded, bearing two flat, multifid setae and one stout simple seta (Fig. 5I); carpi triangular, distally expanded with single distal multifid seta; meri and ischia rounded, bases cylindrical. Pereopod 6 (Fig. 5G) dactylus subequal in length to those of pereopods 3–5, propodus more elongate and narrower than those of pereopods 3–5, inner margin slightly folded, bearing three stout, multifid setae; carpus triangular, with distal setae; merus and ischium rounded, basis cylindrical. Pereopod 7 (Fig. 5G, J) subequal to pereopod 6 but with elongate dactylus extending to distal margin.

Fig. 1. *Akrophryxus acinaces* sp. nov., holotype (SMBL-V0649) and paratype (SMBL-V0652) females, attached to the right and left antennules of host, *Pycnoplax surugensis* (Rathbun, 1932), respectively; images taken while alive. A, Dorsal view; B, en-face view; C, close-up of paratype on left antennule; D, posterior view of holotype attached to host antennule; E, lateral view of holotype, removed from host; F, posterior view of holotype, removed from host. Scale bars: 3 mm (A, B); 1 mm (C–F).
Two new dajid isopods and a new hyperparasite of merus. Pleon (Figs 4G, 5A) with five pairs of biramous pleopods, endopods cylindrical, exopods triangular, both with long terminal plumose setae (Fig. 4G). Pleotelson not observed (obscured by pleomeres). Uropods biramous (Fig. 4G), composed of wide sympod and cylindrical endopod slightly shorter than spatulate exopod; endopods and exopods terminally setose (Figs 4H, 5K).

Remarks. As discussed by Williams and Boyko (2021) for other spheroid dajids, the female of *A. acinaces* sp. nov. has a body showing fusion of pereomeres and pleon (i.e., lacking segmentation when viewed externally) and the plate or shield-like structure surrounding the host antennule is interpreted as the pleon. The female of *A. acinaces* sp. nov., can be distinguished from that of the type species, *A. milvus* as well as *A. pallipalicus* sp. nov. by the following characters: modified pleon with two holes and subtriangular in lateral view (*A. milvus* with three holes and trapezoidal in lateral view; *A. pallipalicus* sp. nov. with two holes and trapezoidal in lateral view), two small perforations lateral to hole closest to mouthparts (no holes present in *A. milvus* or *A. pallipalicus* sp. nov.), and oostegite 5 absent or extremely reduced (present and well-developed in *A. milvus*; absent or reduced in *A. pallipalicus* sp. nov.). The male of *A. acinaces* sp. nov., can be distinguished from that of *A. milvus* and *A. pallipalicus* sp. nov. by the following characters: head/pereomere 1 approximately as wide as pereomere 2, posteralateral margins expanded (head/pereomere 1 narrower than pereomere 2, posteralateral margins not expanded in *A. milvus*; head/pereomere 1 approximately as wide as pereomere 2, posteralateral margins expanded in *A. pallipalicus* sp. nov.), dactylus of pereopod 6 elongate, reaching beyond distal margin of carpus (dactylus of pereopod 6 short, reaching at most midpoint of propodus in *A. milvus* and *A. pallipalicus* sp. nov.), ischium of pereopod 6 less than twice as long as wide (less than twice as long as wide in *A. milvus*; more than twice as long as wide in *A. pallipalicus* sp. nov.). The cryptoniscus larval stage is only known from *A. acinaces* sp. nov.

Video evidence showed the host *Py. surugensis* repetitively used both its third maxillipeds and chelipeds, unsuccessfully, to remove the dajids attached to its antennules (see Appendix 1). Decapods are known to groom their appendages (Bauer 1981, 1989) for removal of fouling organisms and parasites (Ritchie and Høeg 1981). However, the female dajids were not dislodged by these attempts, showing the tenacity of their attachment to the antennules through the use of their pereopods and also because the whole body of
the female dajid encapsulates the host antennule. Although isolated alive for 80 and 103 days, respectively, for the specimens on the left antenna of the host (SMBL-V0652) and right antennae of the host (SMBL-V0649), no larvae were released. Only the holotype female was paired with a male; this female had developing eggs (0.10 ± 0.01 mm, n = 10; across long axis) and also four cryptoniscus larvae within the marsupium.

The cryptoniscus larva of *A. acinaces* sp. nov. lacks an oral sucker and this character state is also found in the cryptoniscus larvae of the closely related spherical dajid *T. clypeus*. The presence of oral suckers on cryptoniscus larvae has long been used as a de facto synapomorphy for Dajidae, e.g., Tattersall (1911) and Schultz (1977), but there is a growing body of evidence that the presence/absence of a sucker is variable within the family. In some species it appears the sucker is more easily broken off (Taberly 1957); however, none of the four cryptoniscus larvae of *A. acinaces* sp. nov. had a sucker or even trace of one. We suggest it represents one of the dajid species where the structure is never developed in the cryptoniscus (see Williams and Boyko 2021 for a more detailed discussion of this issue).

**Akrophryxus pallipalicus** sp. nov.

(Figs 6–8)

**Material examined.** Holotype: mature female (ZRC 2022.0001; 1.8 mm diameter) attached to left antennule of female *Parapalicus armatus* Castro, 2000 (type host, ZRC 2016.0412; 9.0 mm CL, 11.9 mm CW), Sta. CP 4152, 16°2′N, 113°53′E–16°5′N, 113°55′E, Macclesfield Bank (Zhangsha Island), South China Sea (type locality), 410–412 m, beam trawl, flat rocky bottom, coll. ZhongSha 2015, 27 July 2015, host identified by P. Castro, July 2016.

Allotype: mature male (ZRC 2022.0002; 0.54 mm), same data as for holotype.

**Etymology.** The species name is a compound noun in apposition of the Latin pallium (covering) and the second part of the genus name of the host.

**Description of female.** Body spheroid, length and width nearly equal (maximal diameter in lateral view = 1.8 mm) (Figs 6, 7A–C). Cephalon externally indistinguishable from pereon, without eyes. Antennules absent, antennae each as recurved flat plate lateral to oral cone, covered with minute scales (not shown) (Fig. 7E). Oral cone rounded (Fig. 7E); mouthparts indistinct. Maxillipeds ovate with recurved digitiform extension (Fig. 7F, G), extending into groove of oostegite 1. Pereopods 1–5 subequal in size and...
Fig. 4. *Akrophryxus acinaces* sp. nov., allotype male (A–D; SMBL-V0650) and paratype cryptonicus larva (E–H; SMBL-V0651). A, Lateral view, dashed line showing part of shed cuticle attached to head; B, left antenna; C, left pereopods 1 and 2; D, left pereopod 6; E, dorsal view, dashed line shows testes; F, right antenna; G, posterior end, ventral view showing uropods and terminal pleopods; H, exopod of left uropod. Scale bars: 50 µm (A, E); 10 µm (B–D); 20 µm (F–H).
shape (Fig. 7D, J, K); recurved dactylus short with setae and scales on ventral surface, propodus carpus and merus partly fused, ischia and bases stout (Fig. 7J, K). Oostegite 1 largest (Fig. 7H, I), broadly ovate with small posterior accessory lobe, broad lobe medially divided in lateral view (Fig. 7H); oostegites 2–4, progressively larger, thin and closely applied to each other (Fig. 7D); oostegites 2 and 3 subrectangular, expanded posteriorly with small setae distally, oostegite 4 subquadrate, small setae on medial and posterior margins, oostegite 5 absent or extremely reduced. Pleon modified (see Remarks under A. acinaces sp. nov.) as oblong, narrow, thickened plate (Figs 6C, D, 7A–D) partially surrounding host antennule (Figs 6A, B, 7A–D) with two large circular medial holes: largest surrounding antennule of host and

Fig. 5. Akrophyxus acinaces sp. nov., paratype cryptonicus larva (A–J; SMBL-V0651), SEM. A, Ventral view; B, lateral view; C, ventral view of cephalon showing antennules, mouthparts and first pereopods; D, right pereopod 2; E, left pereopod 3; F, right pereopod 4; G, right pereopods 5–7; H, lateral view of pereomeres 6 and 7 showing distinct notch and indentation; I, multifid setae of left pereopod 4; J, multifid setae of left pereopod 7; K, posterior end, ventral view. Scale bars: 100 µm (A, B); 50 µm (C, K); 30 µm (D–F); 20 µm (G); 10 µm (H–J).
Two new dajid isopods and a new hyperparasite

Closest to mouthparts of parasite, smaller hole farthest from mouthparts of parasite (Fig. 7B).

Description of male. Body not recurved ventrally (Fig. 8A). Cephalon fused with pereomere 1, anterior margin rounded and inflated dorsoventrally (Fig. 8A, B), posterolateral margins evenly rounded, slightly expanded at proximolateral corners; lacking eyes, cephalic slits present (Fig. 8A). Antennules reduced, broadly conical, apparently of one segment (Fig. 8C); antennae of two segments, basal segment subquadrate, distal segment elongate, tapering (Fig. 8C). Oral cone triangular (Fig. 8C). Pereomeres 2–6 distinct, 3 and 4 subequal in width, others slightly narrower (Fig. 8A, B); pereomere 7 partly fused with pleon, lateral margins of all pereomeres recurved ventrally (Fig. 8B). Pereopods subequal in size and shape, all segments distinct; dactyli of all pereopods subequal, short and slightly recurved; propodi narrow, longer than wide; carpi ovate, each with small distoventral projection; meri ovate; ischia and bases cylindrical, elongate, ischia narrower than bases (Fig. 8D); pereopod 7 lacking. Pleon (undergoing molt) compact, rounded, all segments fused and fused with pereomere 7, rounded posteriorly; anal slit and pleopods lacking (Fig. 8B).

Remarks. See Remarks under A. acinaces sp. nov. for a discussion of the characters that distinguish A. pallipalicus sp. nov. from that species as well as the type species, A. milvus. The female had eggs (0.12 ± 0.01 mm, n = 29; across long axis) within the marsupium.

Superfamily Cryptoniscoidea Kossman, 1880
Family incertae sedis
Genus Chimaeroniscus gen. nov.

Type species. Chimaeroniscus spheramator sp. nov., by original designation herein.

Etymology. The genus name is a combination of chimaera (a mythical beast of mixed morphology) and -oniscus (a common suffix for isopod genera) and refers to the unique mixture of characters present in the cryptoniscus.

Fig. 6. Akophryxus pallipalicus sp. nov. Macropod photographs of holotype (ZRC 2022.0001) attached to left antennule of Parapalicus armatus Castro, 2000 (ZRC 2016.0412), macropod images taken after fixation. A, Dorsal view of host with holotype attached to the left antennule; B, ventral view of host with holotype attached to the left antennule; C, lateral view of holotype, removed from host; D, top down of holotype, removed from host. Scale bars: 5 mm (A, B); 1 mm (C, D).
larva. The gender is masculine.

Diagnosis. Cryptoniscus larva: body cylindrical, elongate, pleomeres markedly narrower than pereomeres. Cephalon anterior margin round, posterolateral margins not extended posteriorly; eyes absent. Cuticle striated. Antennules of three articles each, basal article triangular with eight large teeth on margin, surface striated; article 3 with brush of numerous long simple setae. Antennae of nine articles each, first two articles subquadrate, distal two articles cylindrical. Pereomeres 1–7 with toothed coxal plates (first with 3 teeth, second–sixth with 4 teeth, seventh with 3 teeth). Pereopods 1 and 2 each with short, slightly curved dactylus, propodus semi-spherical. Pereopods 3–7 dactyli slender, elongate, reaching articulation of carpus/merus, distal tips ventrally indented. Pleon with five pairs of biramous pleopods, som- pod bearing two long slender setae with minutely multifid tips. Pleotelson subquadrate with distomedial rounded projection. Uropodal exopod half as long as endopod.

Remarks. The cryptoniscus larva (and only known life history stage) of the hyperparasite described from the marsupium of *A. pallipalicus* sp. nov. possesses a combination of characters not found in any other cryptoniscoid genus and so a new genus is erected for it. Presently, 60% (42/70) of the genera within Cryptoniscoidea are monotypic (Boyko et al. 2008b) but this is likely to be an artifact of poor sampling of these organisms, many of which are minute and cryptic as adults as well as larvae.

The combination of characters that justify this new genus includes: dorsal cuticle striated, pleomeres markedly narrower than pereomeres, antennule with large teeth on basal segment, surface striated; article 3 with brush of numerous long simple setae. Antennae of nine articles each, first two articles subquadrate, distal two articles cylindrical. Pereomeres 1–7 with toothed coxal plates (first with 3 teeth, second–sixth with 4 teeth, seventh with 3 teeth). Pereopods 1 and 2 each with short, slightly curved dactylus, propodus semi-spherical. Pereopods 3–7 dactyli slender, elongate, reaching articulation of carpus/merus, distal tips ventrally indented. Pleon with five pairs of biramous pleopods, som- pod bearing two long slender setae with minutely multifid tips. Pleotelson subquadrate with distomedial rounded projection. Uropodal exopod half as long as endopod.

Oscryptus hirsutus Schultz, 1977 (Cryptoniscoidea, family incertae sedis; monotypic) is perhaps the most similar genus and species to the present material (cuticle striated, pleomeres markedly narrower than pereomeres, teeth on antennule with large teeth on basal segment, strong setal brush on distal segment, pereopods 1 and 2 similar, pereopods 3–7 isomorphic and dissimilar from 1 and 2, telson...
without marginal teeth and with smooth distomedial projection) but *O. hitatus* has numerous small teeth on all coxal plates (vs. 3 or 4 stout teeth in the new species), much more robust setae on the ventral margin of the pereopodal dactyli (pair of minute setae in the new species), and pleopodal sympods bearing long thin simple setae (without multifid tips as in the new species).

Another genus and species that is somewhat similar to the present material is *Gorgoniscus incisodactylus* Grygier, 1981 (Cryptoniscoidea, family incertae sedis; monotypic) which shares with the present specimen a striated cuticle, teeth on the basal segment of the antennule (albeit fewer

Fig. 8. *Akrophryxus pallipalicus* sp. nov., allotype male (A–D), ZRC 2022.0002. A, Dorsal view; B, dorsal view; antenna; C, left antennule (A1), antenna (A2), and pereopod 1; D, right pereopod 6. Scale bars: 100 µm (A, B); 50 µm (C, D).
and slenderer), similar structure and form of all the pereopods, including the small size of the setae on the ventral margins of the propodi on pereopods 3–7, and shape of the telson. However, the pleomeres of *G. incisodactylus* are not markedly narrower than the pereomeres and it does not have a similarly robust setal brush on the antennae, lacks coxal teeth on any of the pereomeres, and has plumose setae on the pleopods. *Gorgoniscus incisodactylus* is a hyperparasite of ascothoracican barnacles (*Gorgonolaureus muzikae* Grygier, 1981) living in paramuriceid gorgonians from Hawaii (366 m) (Grygier 1981a, b). Based on the fact that infested barnacle hosts lacked eggs and the hyperparasite was “free” within the dajid host (not attached by mouthparts), Grygier (1981a) indicated that *G. incisodactylus* might be an egg predator (see more on egg predation in Remarks below).

As with the two species *Chimaeroniscus spheramator* gen. et sp. nov. is compared to above, it is also placed incertae sedis within Cryptoniscoidea. Molecular data as well as discovery of the form of the female are necessary to determine to what other cryptoniscoid taxa it is most closely related.

*Chimaeroniscus spheramator* sp. nov.  
(Fig. 9)

**Material examined.** Holotype: cryptoniscus larva (ZRC 2022.0003; 1.4 mm total length) from marsupium of female *Akrophryxus pallipalicus* sp. nov. (type host, ZRC 2022.0001; 1.8 mm diameter), attached to the host *Parapalicus armatus*, Sta. CP 4152, 16°2’N, 113°53’E–16°5’N, 113°55’E, Macclesfield Bank (Zhanga Island), South China Sea (type locality), 410–412 m, beam trawl, flat rocky bottom, coll. ZhongSha 2015, 27 July 2015.

**Etymology.** The species name is a compound noun in apposition of the Latin *sphaer-* (sphere) and *amator* (lover) and refers to the finding of the species in the marsupium of a spheroid dajid.

**Description of cryptoniscus larva.** Body cylindrical, elongate (Fig. 9A), length 1.4 mm, pereomere 5 widest (Fig. 9A), anterior and posterior pereomeres slightly narrower, pleomeres markedly narrower than pereomeres. Cephalon anterior margin round, medial region of posterior margin convex, posterolateral margins not extended posteriorly.

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**Fig. 9.** *Chimaeroniscus spheramator* gen. et sp. nov., holotype cryptoniscus larva, ZRC 2022.0003. A, Dorsal view (specimen broken across pleomere 2); B, right antennule; C, left antenna; D, left pereopod 1; E, left pereopod 3; F, left pereopod 7; G, terminal pleomere, dorsal view; H, left uropod, dorsal view; I, left pleopod 2. Scale bars: 200 µm (A); 50 µm (B–I).
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(Fig. 9A); eyes absent. Cuticle striated (Fig. 9A, G), body pigmentation lacking. Antennules of three articles each (Fig. 9B), basal article triangular with eight large teeth on margin, surface striated, anteromedial corner with two stout simple setae; article 2 quadrate with two anterodistal small simple setae, surface striated; article 3 rounded, inserted into article 2 distoventrally, less than half width of article 2, with brush of numerous long simple setae, lateral "flagellum" basal segment with two long simple setae, second segment with three long simple setae, terminal segment with five long simple setae (Fig. 9B). Antennae of nine articles each (four peduncular and five flagellar) (Fig. 9C), first two articles subquadrilateral, distal two articles cylindrical, basal peduncular article broadest, third segment longest, distalmost segment slightly narrower than third segment, minute, distal simple setae on articles 2–4; flagellar articles approximately half width of distal peduncular article, with minute terminal setae, distalmost article with two long terminal simple setae and short simple setae (Fig. 9C). Oral cone triangular, anteriorly directed. Pereomeres 1–7 with toothed coxal plates (first with 3 teeth, second–sixth with 4 teeth, seventh with 3 teeth) (Fig. 9D–F). Pereopods 1 and 2 (Fig. 9D) each with short, slightly curved dactyli, propodus semi-spherical, inner margin smooth; carpus triangular, distal margin with stout setae; merus rounded; ischium and basis cylindrical. Pereopods 3–7 (Fig. 9E, F) dactyli slender, elongate, reaching articulation of carpus/merus, distal tips ventrally indented with single simple seta inserted at notch; propodi slender, elongate, each with two small stout setae on ventral margin; carpi and meri subtriangular; ischia and bases elongate, slender, subequal in size. Pleon with five pairs of biramous pleopods (Fig. 9I), sympod rounded, bearing two long slender setae with minutely multifid tips; endopods cylindrical, bearing five long simple setae, exopods triangular, bearing four long simple setae. Pleotelson (Fig. 9G) subquadrate with disto-medial rounded projection. Uropods biramous (Fig. 9H), composed of subquadrilateral sympod bearing two long simple setae on distal corners and cylindrical exopod bearing two distal long simple setae approximately half as long as endopod bearing three distal long simple setae and one short simple seta on proximal dorsal surface.

Remarks. See Remarks under *Chimaeroniscus* gen. nov. for a review of the unique combination of morphological features of this species. This is the first hyperparasite (=secondary parasite) described from any dajid host (=primary parasite); *Pa. armatus* is the host of the dajid.

The phenomenon of egg predation in Cryptoniscoidea was reviewed by Buhl-Mortensen et al. (2020); cryptoniscus larvae of some species have been confirmed to actively feed on eggs or young embryos as observed by Bocquet-Vedrine and Bocquet (1972a, b) and Abe and Horiiuchi (2000). This feeding stage is relatively short lived (approximately 1 week), with the female transitioning to a mature, non-feeding stage and thus is easily overlooked in preserved samples. Other cryptoniscoid species are suspected to be egg predators based on their morphology, particularly the lack of piercing mouthparts to feed on host hemolymph or a specialized attachment organ for internal penetration of the host marsupium and subsequent loss of host brood (Holdich 1975). Some females of this group are found unattached within the hosts’ marsupia and include species in Cabiropodiidae, Crinonisciidae, and Podasconidae, as well as several genera that are incertae sedis within Cryptoniscoidea. Buhl-Mortensen et al. (2020) speculated that species of *Onisocryptus* Schultz, 1977 (Cyroniscidae) might also be egg predators; this was indeed shown to be the case in the overlooked study by Abe and Horiiuchi (2000) who indicated that *O. ovalis* (Shiino, 1942) could ingest nearly the whole brood of its ostracod host. *Chimaeroniscus spheramator* gen. et sp. nov. is suspected to be an egg predator by virtue of it being collected in the marsupium of a dajid where, upon the host’s egg production, the hyperparasite would have ample food for its own development.

**Discussion**

During examination of specimens of other dajid larvae as well as a review of the literature, we agree with Trilles (1999) that all dajid cryptoniscus larvae possess a synapomorphy of seven pairs of pereopods with similar morphology (although the posterior five pairs are usually somewhat larger) with at least the posterior pair (and often other pairs) bearing two large multifid setae on the ventral margin of each propodus and one large multifid seta on the distoventral margin of the carpus. This pattern of large multifid setae on the propodi and carpi is not found in any other epicaridean cryptoniscus larvae described to date. The cryptoniscus larvae of *Bopyroides cluthae* (Scott, 1902) and *Cryptobopyus elongatus* Schultz, 1977, both in Bopyridae, have multifid setae on some propodi but the structure is different than those seen on dajids and the setae are not multifid on the posterior pereopods (see Bourdon 1968: fig. 168; Schultz 1977: figs 36, 37). In addition, cryptoniscus of both these species have four peduncular and four flagellar segments in contrast to the four peduncular and five flagellar segments found in dajids and other cryptoniscoids (Boyko and Williams 2015).

Another cryptoniscus character, presence of an oral sucker, was usually thought to be a synapomorphy for Dajidae (Tattersall 1911; Schultz 1977; Boyko and Williams 2015; but not Trilles 1999). However, there are several reports of such larvae lacking these suckers, e.g., Richardson (1905), Barnard (1914), and Coyle and Mueller (1981), possibly because they do not develop them or because they are easily broken off in collection (Tableerly 1957). In addition, there are other non-dajid species that also possess oral suckers, e.g., *Thermaloniscus cotylophorus* Bourdon, 1983 (Cryptoniscoidea, family incertae sedis) (see Bourdon 1983: fig. 1d), *Bopyroides hippolytes* (Kröyer, 1838) (Bopyridae) (see Hansen 1916: pl. 15, fig. 11a), and *B. cluthae* (Bopyridae) (see Bourdon 1968: fig. 168c), thus, this feature appears to have been independently derived multiple times within Epicaridea. The suckers of these other species, e.g., *Bopyroides* spp. appear thinner than those of dajids (Hansen 1916) and may not provide the same force for attachment as is suspect-
ed to be the case in dajids. Functional morphology studies are needed to examine this issue and whether the suckers employ muscle-facilitated suction (see Müller et al. 2008).

As a result of our review of cryptopsincus larvae, we consider *Neritomisicus euthaphus* Schultz, 1977 and *Cryptopsicus laevis* Schultz, 1977 (described in Cryptopsiculoidea but without placement to family) to be members of Dajidae and we transfer them accordingly. Additionally, we find that the cryptopsincus larva of *Cryptopus truncatus* Schultz, 1977, is so similar to that described by Coyle and Mueller (1981) for *Holophryxus alaskensis* Richardson, 1905, that we must synonymize the monotypic *Cryptopus* Schultz, 1977 with *Holophryxus*; the correct name for the species is *H. truncatus* (Shultz, 1977) comb. nov. It is possible that *H. truncatus* is the larva of one of the four species of *Holophryxus* known from adult specimens collected in the southern hemisphere (see Boyko and Williams 2021a) but none of those species have been collected quite as far south (62°04′ S, 75°18′ W) as the types of *H. truncatus* comb. nov.

**References**


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This research was supported, in part, by a grant to JDW from the National Science Foundation (DBI-1337525).

**Acknowledgments**

Thanks to Drs. Peter K. L. Ng and Jose C. E. Mendoza (ZRC) who hosted a visit by the authors to study their collections in July 2016 and facilitated the loan of specimens. We thank Shigemi Nakashima for the video of *Akrophryxus acinaces* sp. nov. on the antennules of *Pycnotopax surugensis*. We also thank the two anonymous reviewers and Species Diversity Associate Editor Dr. Naoya Ohtsuchi for their valuable comments.

This research was supported, in part, by a grant to JDW from the National Science Foundation (DBI-1337525).


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**Appendix**

Supplemental Material 1. Video of the live host *Pycnoplasma suragensis* (Rathbun, 1932) in an aquarium at 10°C showing the crab repetitively using its third maxillipeds and chelipeds, unsuccessfully, to remove the female dajids, *Arkophryxus acinaces* sp. nov, from its antennules. [https://doi.org/10.6084/m9.figshare.19610214](https://doi.org/10.6084/m9.figshare.19610214)