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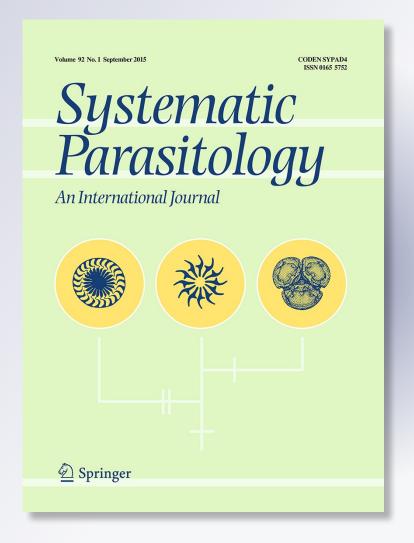
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A new genus for *Entophilus mirabiledictu* Markham & Dworschak, 2005 (Crustacea: Isopoda: Cryptoniscoidea: Entophilidae) with remarks on morphological support for epicaridean superfamilies based on larval characters

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Abstract A detailed reexamination of male and female Entophilus mirabiledictu Markham Dworschak, 2005 (an endoparasite of callianassid shrimp), resulted in recognition of seven female and five male characters that separate the species from its sole congener, E. omnitectus Richardson, 1903 (an endoparasite of munidid squat lobsters). These characters show that the two species are so different as to warrant E. mirabiledictu being placed in its own genus within the Entophilidae. Additionally, a review of the morphological features of entophilid cryptoniscus larvae led to the finding that the number of flagellar segments on the second antenna offers morphological support for a recent molecular phylogeny of epicaridean taxa that rearranged the component families within the two recognised superfamilies. This work highlights the power of using larval characters in testing hypotheses on the evolutionary relationships of epicaridean taxa.

Introduction

Reexamination of *Entophilus mirabiledictu* Markham & Dworschak, 2005 resulted in recognition of several female and male characters whose importance in distinguishing the species from its sole congener *E. omnitectus* Richardson, 1903 was not previously recognised. These characters, including those of antennae, pereopods, pleomeres, pleopods, and uropods, are resdescribed based on scanning electron and light microscopy. Using this data we were able to clarify some misinterpretations in the original description of *Entophilus mirabiledictu* (see Markham & Dworschak, 2005) and show that *E. mirabiledictu* warrants its own genus within the Entophilidae, resulting in the new combination *Axiophilus mirabiledictu* (Markham & Dworschak, 2005).

Axiophilus mirabiledictu is found in the ghost shrimp Callianassa aqabaensis Dworschak (Axiidea: Callianassidae), whereas E. omnitectus is found in squat lobsters (Anomura: Munididae). Although the two species are endoparasites of distantly related host taxa, both species belong to the Entophilidae. To date, A. mirabiledictu has only been found in the one callianassid species from the Red Sea off Jordan at depths of 4–30 m, whereas E. omnitectus has been found in five species of munidids

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in the genera *Agononida* Baba & de Saint Laurent and *Munida* Leach in both the Atlantic (Gulf of Mexico and Azores) and Pacific (Hawaii and Madagascar) at depths of 310–1,010 m (Markham, 1994; Dworschak, 2003; Markham & Dworschak, 2005; Boyko & Williams, 2011; Boyko et al., 2012). Note that Markham (1994) questioned whether the specimen of *Munida incerta* Henderson, a species previously known to host *E. omnitectus*, reported from the Chesterfield Islands was correctly identified. He suggested that it possibly represented a sixth munidid host. Subsequently, Macpherson (1994) concluded that the identification of the specimen as *Munida incerta* was correct.

The present study led to the observation that the cryptoniscus larvae of *E. omnitectus* possess nine second antennal segments (four basal + five flagellar) (Adkison & Collard, 1990), a characteristic shared with all known cryptoniscus larvae of species in the Cryptoniscoidea. Our findings provide morphological support for the placement of Entophilidae in Cryptoniscoidea as shown by the molecular phylogeny of Epicaridea (Boyko et al., 2013).

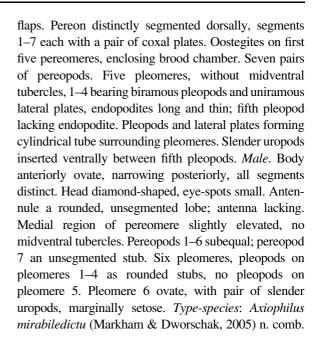
Materials and methods

Line drawings were made with a drawing tube attachment; original sketches were scanned and traced with Adobe Illustrator. Preserved specimens were prepared for SEM by dehydrating in an ascending ethanol series (70 to 100% EtOH), ending with four changes of 100% EtOH. A Samdri 795 Critical Point Dryer was used to dry specimens that were then mounted on aluminium stubs, coated with gold using an EMS-550 Sputter coater, and viewed with a Quanta-250 FEI scanning electron microscope. Carapace length (CL) is provided as an indicator of size for hosts. Isopod size is given as total body length (TL = anterior margin of head to posterior margin of pleotelson). Measurements were made to 0.01 mm using an ocular micrometer. Hosts and parasites were borrowed from the collection of the Naturhistorisches Museum, Wien (NHMW).

Axiophilus n. g.

Diagnosis

Female. Body nearly symmetrical, elliptical. Head bilobed; antennule and antenna elongate, unsegmented



Etymology: Derived from Axiidea (name of the infraorder to which the host belongs) combined with philos (Greek, lover), referring to the parasite being found on an axiidean host, as opposed to the habitat of *E. omnitectus*, which is from munidid squat lobsters.

Remarks

Axiophilus n. g. is distinguished from Entophilus Richardson, 1903 by at least seven female and five male characters (Table 1). Other differences also exist, such as the digitate (Axiophilus) vs smooth (Entophilus) surface of the female's barbula, a deeply triangular internal ridge of the female's oostegite 1 (Axiophilus) vs a straight internal ridge (Entophilus), and the male's first pereopod being smaller than the sixth (Axiophilus) vs being larger than the sixth (Entophilus); however, these are likely specific characters and not generic-level distinctions.

Axiophilus mirabiledictu (Markham & Dworschak, 2005) n. comb.

Syns "Unidentified bopyrid isopod" of Dworschak (2003); Entophilus mirabiledictu Markham & Dworschak, 2005

Type-host: Callianassa aqabaensis Dworschak.



Table 1 Comparison of characters for females and males of the species in Axiophilus and Entophilus

Character	Axiophilus	Figure	Entophilus	Figure
	Female		Female	
Antenna (A2)	unsegmented	Fig. 1B	2-segmented	Fig. 1A
Pleomeres 1–2	without medioventral tubercles	Markham & Dworschak (2005): figure 1B	with medioventral tubercles	Bourdon (1976): figure 22B
Pleopods	5 pairs	Fig. 1H-M	6 pairs	Bourdon (1976): figure 22B
Pleopod 1 exopod	2-segmented	Fig. 1H	1-segmented	Bourdon (1976): figure 22B
Pleopods 1–4 exopods and endopods	dissimilar in width (endopod slender)	Fig. 1H, J–L	subequal in width	Bourdon (1976): figure 22B
Pleopod 5	stout tapered lobe	Fig. 1M	minute and threadlike	Bourdon (1976): figure 22B
Uropods	slender lobes, marginally setose	Fig. 1N, Q	minute and threadlike	Bourdon (1976): figure 22B
	Male		Male	
Body shape	broad then narrowed	Fig. 2A	tubular	Fig. 1C
Antennae	1 pair simple flaps with sparse setae	Fig. 2B	2 pair bilobed flaps, densely setose	Fig. 1D
Pereopod 7	reduced stub	Fig. 2F	not reduced	Bourdon (1976): Figure 23D
Pleopods	4 pairs uniramous	Fig. 2F	5 pairs bilobed	Fig. 1E
Uropods	inserted posteromedially, without scales	Fig. 2G	inserted posterolaterally, with scales	Fig. 1E

Type-locality: Aqaba, Gulf of Aqaba, Red Sea, Jordan, 29.4708N, 34.9738E.

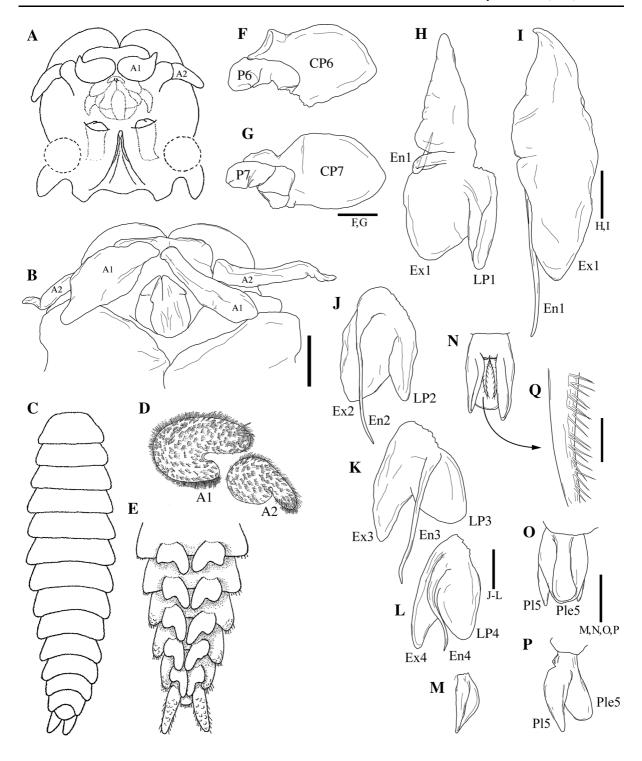
Material examined: Two male and female paratype pairs infecting Callianassa aqabaensis, Royal Diving Club, Aqaba, Gulf of Aqaba, Red Sea, Jordan, 29.4708N, 34.9738E, 28–31 October 2002, P. C. Dworschak, coll. and det. of hosts (NHMW 16785; anterior ends of females damaged, not measured; males 1.0 mm TL; one male on SEM stub).

Description (Figs. 1B, F-Q, 2)

Female (Fig. 1B, F–Q). Body elliptical, broadest at third pereomere. Body axis nearly linear. Head obscured by first coxal plates, anterior margin bilobed, subquadrate lobe present ventrally between antennae and distal margin of head (Fig. 1B). Antennule (antenna 1) an elongate, unsegmented flap, expanded medially, tapering distally; antenna (antenna 2) an

elongate, unsegmented, slender flap, narrower than antennule (Fig. 1B). Maxilliped posterior article irregularly ovate, anterior article chevron-shaped, lateral margins deeply convex at junction of articles; palp and plectron lacking. Barbula with medial crenulate lobe and one tapered irregular projection with small marginal extensions laterally on each side. Pereon distinctly segmented dorsally, segments 1–7 each with a pair of coxal plates, largest anteriorly and tapering posteriorly (Fig. 1F, G). Oostegites on first five pereomeres, overlapping and completely enclosing brood chamber. First oostegite with irregularly shaped anterior lobe and triangular posterior lobe, internal ridge between segments smooth, second through fifth oostegites subequal in size, larger than first. Pereopods small. Pleon of five pleomeres, 1-4 bearing biramous pleopods and uniramous lateral plates. First pleopod endopodite long and thin, extending posteriorly beyond border of exopodite; exopodite lamellar,





tapered anteriorly and posteriorly; lamellar lateral plate attached to posterior portion of exopodite, width less than that of exopodite (Fig. 1H, I). Second pleopod similar to first in form but lacking anterior

extension of exopodite, lateral plate similar to that of first pleomere (Fig. 1J). Third and fourth pleopods similar to second in form, lateral plate broader than exopodite of corresponding pleopod (Fig. 1K, L).



▼Fig. 1 Entophilus omnitectus Richardson, 1903 (A, C, D, E) and Axiophilus mirabiledictu (Markham & Dworschak, 2005) n. comb., NHMW16785 (B, F-Q). A, Female head, ventral view; B, Female head, ventral view; C, Male, dorsal view; D, Male antennule (A1) and antenna (A2); E, Male pleon, ventral view; F, Female, coxal plate 6, inner view; G, Female, coxal plate 7, inner view; H, Female, pleopod 1, inner view (note twisted endopodite, En1); I, Female, pleopod 1, outer view; J, Female, pleopod 2, inner view; K, Female, pleopod 3, inner view; L, Female, pleopod 4, inner view; M, Female, pleopod 5, outer view; N, Reconstruction of the female sixth pleomere, pleopods 5 and uropods, ventral view; O, Female terminal pleomere and pleopods 5, dorsal view; P, Female terminal pleomere and pleopod 5, lateral view; Q, Close-up view of middle portion of uropod. Abbreviations: A1, antenna 1 (antennule); A2, antenna 2; CP, coxal plate; En, endopod; Ex, Exopod; LP, lateral plate; P, pereopod; Pl, pleopod; Ple, pleomere. Scale-bars: B, F, G, H-M, N, O, P, 250 μ m; Q, 50 μ m; rest not to scale. A, C–E modified from Bourdon (1976)

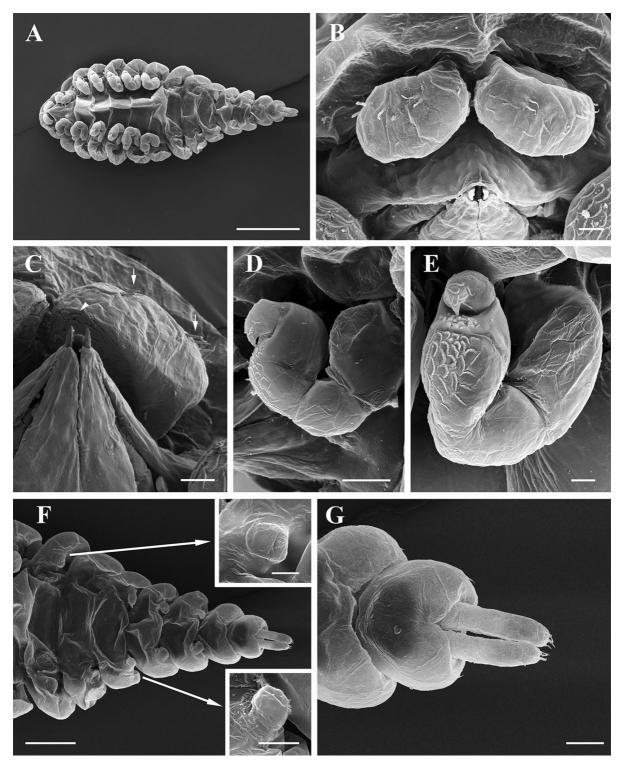
Fifth pleopod lacking endopodite, exopodite of similar shape to those of pleopods 3 and 4 (Fig. 1M, P). Fifth pleomere ovate with dorsolateral folds that may represent fused lateral plates (Fig. 1O, P). Pleopods and lateral plates forming cylindrical tube surrounding pleomeres. Subterminal slender uropods inserted ventrally between fifth pleopods, shorter than fifth pleopods, marginally setose (Fig. 1N, Q).

Male (Fig. 2). Anterior 2/3 of body ovate, broadest at fourth percomere, narrowing posteriorly (Fig. 2A). Length 1.0 mm, maximal width 0.5 mm at fourth segment (Fig. 2A). All segments distinct (Fig. 2A, F), no body pigmentation. Head a compressed diamond shape, widest medially, narrower than anterior margin of pereomere 1, separated from pereon by lateral notches. Eyes near mediolateral margin. Single antenna (?antennule) a rounded, unsegmented lobe with sparse stout setae and scales on surface, scales most pronounced on surface facing oral cone (Fig. 2B, C); second antenna (?antenna) lacking. Medial region of pereomere slightly elevated dorsally and ventrally (Fig. 2A); no midventral tubercles. Pereopods 1–6, subequal in size and shape (Fig. 2A, D, E); dorsal surface of dactylus and ventral surface of carpus and merus with scales (Fig. 2D, E); pereopod 7 an unsegmented stub (Fig. 2F, upper inset). Pleon of 6 pleomeres, tapering posteriorly, dorsal anterior and posterior margins not curved, ventral margins concave posteriorly. Pleopods on pleomeres 1-4, as rounded stubs slightly raised off of ventral surface (Fig. 2F and lower inset), no pleopods on pleomere 5. Pleomere 6 ovate, with pair of slender, elongate, distally setose uropods deeply embedded in posterior margin (Fig. 2G).

Remarks

There are a number of discrepancies between the male and female characters of this species as described by Markham & Dworschak (2005) compared to our present findings. For the female, Markham & Dworschak (2005) indicated the antenna (antenna 2) was "obscure"; however, it is present as a pronounced elongate flap. Markham & Dworschak (2005) stated that there were seven pairs of coxal plates and seven pairs of oostegites. There are seven pairs of coxal plates but only five pairs of oostegites, the same as found in E. omnitectus (see Bourdon, 1976). On pereomeres 6 and 7 the coxal plates have a semibilobed structure (Fig. 1F, G) that resembles a coxal plate plus a very reduced oostegite, but closer examination shows they are clearly part of the same structure. Therefore, Markham & Dworschak's (2005) figure 1I ("oostegite 7") is actually the coxal plate on pereomere 7. Markham & Dworschak (2005) also misinterpreted some aspects of the pleopods. Their figure 1L (pleopod 1) looks correct but incomplete; it is lacking the long thin endopod. Their figure 1M ("pleopod 7") is either pleopod 2 or 3; there is no pleopod 7. They stated: "first pleopod ... produced into pointed exopodite extending over surface of seventh oostegite". However, it is actually the triangular anterior extension of pleomere 1 extending over the surface of the fifth oostegite. Markham & Dworschak (2005) stated that pleopods 2–5 had long slender endopodites; however, they are present on pleopods 1–4. Pleopod 5 was stated to be biramous but is uniramous and their description of the uropods as "tiny uniramous flaps inside end of that tube" (tube formed by pleonal appendages) is incorrect. They were likely looking at the 5th pleopods. The uropods and the long thin exopodites of the fourth pleopods are hidden because they are covered by the preceding pleopods.





For the male, Markham & Dworschak (2005) labeled antenna 2 (which we interpret as antenna 1 based on its position) as having a minute distal second

article on the posterior edge; we did not find this article. They also stated that pleopods were absent in the males but they are present on pleomeres 1–4.



◄ Fig. 2 Axiophilus mirabiledictu (Markham & Dworschak, 2005) n. comb., scanning electron micrographs of male, NHMW16785. A, Ventral view, whole body; B, ?Antennule (A1) and mouthparts; C, ?Antennule (A1) and mouthparts (arrowheads indicate scales on medial posterior surface, arrows indicate groups of setae); D, Left pereopod 1, lateral view; E, Left pereopod 6; F, Pleomere 7 (reduced left pereopod 7 shown in top inset) and pleon (second right pleopod shown in bottom inset); G, Pleomeres 5, 6 and uropods. Scale-bars: A, 250 μm; B, C, E, 10 μm; D, G, 25 μm; F, 100 μm

Discussion

Previous authors showed that the number of cryptoniscus larvae antennal segments was a useful character to place larvae at the family-level (e.g. Tattersall, 1911; Schultz, 1977). It has not, however, been considered as a character to support epicaridean taxonomy or phylogeny, which has always been based on the adult form. During our review of the literature, we noted that the number of flagellar segments of antenna 2 for *Entophilus omnitectus* is five (Adkison & Collard, 1990), which contrasts with the four antennal flagellar segments found in all other bopyrid

cryptoniscus larvae. Traditionally, epicarideans were divided into two superfamilies: Cryptoniscoidea (seven families) and Bopyroidea (three families). Bopyroidea contained the Bopyridae, Dajidae, and Entoniscidae, with Entophilinae being considered a subfamily of the Bopyridae (see Boyko et al., 2013). A recent molecular phylogeny of epicaridean taxa (Boyko et al., 2013) radically rearranged the component families within the two recognised superfamilies, moving Dajidae and Entophilinae (as Entophilidae) into Cryptoniscoidea and recognising the bopyrid subfamily Ioninae as a family within Bopyroidea. Analysis of the antenna 2 flagellar segment counts (data from Tattersall, 1911; Schultz, 1977; Adkison, 1990; Adkison & Collard, 1990) shows that all taxa in the Cryptoniscoidea (including Dajidae and Entophilidae) have cryptoniscus larvae with nine antennal segments (four basal + five flagellar), while all taxa in the Bopyroidea have eight antennal segments or fewer (four basal + four flagellar for all Bopyridae and Ionidae; four basal + one or three flagellar for Entoniscidae) (Fig. 3). Thus, number of antennal flagellar segments offers a morphological character

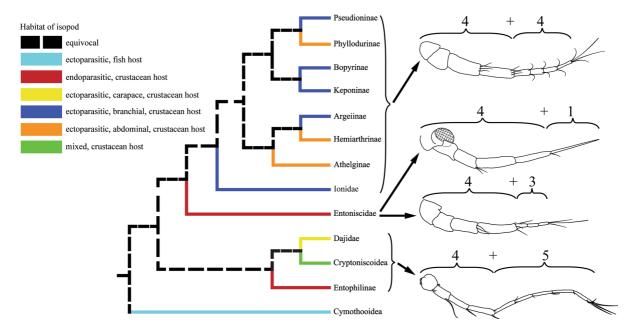


Fig. 3 Habitat of family-level and higher isopod taxa plus antennal segmentation patterns for epicaridean taxa mapped onto a phylogeny derived from 18S rDNA analysis (Boyko et al., 2013). Mixed = examples of ecto-, endo- and mesoparasitism within the taxon. Second antennae of (top to bottom) *Cancricepon elegans* Giard & Bonnier, 1887, *Entoniscoides okadai* Miyashita, 1940, *Xanthion spadix* Shiino, 1942, and *Entophilus omnitectus* Richardson, 1903 [line drawings of antennae modified from Bourdon (1968), Miyashita (1940), Shiino (1942) and Adkison & Collard (1990), respectively]



that supports the recent molecular phylogeny of epicaridean taxa (Boyko et al., 2013).

This study shows that larval characters can be informative in phylogenetic studies of epicarideans, as has been found in other parasitic crustacean groups like rhizocephalan barnacles (see Rybakov et al., 2002; Boyko & Williams, 2009; Glenner et al., 2010). Unfortunately few detailed descriptions of epicaridean larvae (epicaridium, microniscus, and cryptoniscus) exist (but see Anderson & Dale, 1981; Dale & Anderson, 1982; Williams & An, 2009; Cericola & Williams, 2015). Future researchers should examine these life history stages, with particular focus on their antennae and other taxonomically important features to further test hypotheses on the evolutionary relationships of epicaridean taxa.

Key to epicaridean cryptoniscus larvae

Tattersall (1911) constructed a key to cryptoniscus larvae based on second antenna segmentation by which he separated Cryptoniscina (= Cryptoniscoidea) and Bopyrina (Dajidae, Bopyridae, Entoniscidae). This key was also used by Schultz (1977), albeit without entoniscids included. The key is modified herein to conform to modern terminology:

- 1. Antenna of nine (4 basal + 5 flagellar) segments
 - a. Oral sucker lacking Cryptoniscoidea
 - b. Oral sucker present Dajidae
- 3. Antenna of seven or fewer (4 basal + 1 or 3 flagellar) segments Entoniscidae

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Conflict of interest The authors declare that they have no conflict of interest.

Compliance with ethical standards All applicable institutional, national and international guidelines for the care and use of animals were followed.

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