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A NEW SPECIES OF *ENTOPHILUS* RICHARDSON, 1903 (ISOPODA: BOPYRIDAE: ENTOPHILINAE) FROM THE GULF OF AQABA, JORDAN

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A B S T R A C T

Entophilus mirabiledictu, new species, is described as a parasite of *Callianassa aqabaensis* Dworschak, 2003, in shallow water on the Jordanian coast of the Gulf of Aqaba. It is compared with the only species previously known from the genus or subfamily Entophilinae Richardson, 1903, *Entophilus omnitectus* Richardson, 1903, a parasite of several species of the galatheid anomuran genus *Munida* in water deeper than 300 m at widespread localities around the world. Information on the prevalence of the parasite and its effects on its hosts is provided.

The epicaridean family Bopyridae currently contains over 500 described parasitic species whose definitive hosts are decapod crustaceans (Markham, 1994, 2001; Trilles, 1999). All known species but one infest their hosts externally, most of them branchially, the others abdominally. The only internally-occurring bopyrid heretofore known is *Entophilus omnitectus* Richardson, 1903, found inside the visceral cavity of its host.

Recent studies by one of us (PCD) in the Gulf of Aqaba in 2000, 2001, and 2002 turned up numerous specimens of callianassid shrimps. The most common species, which proved to be new to science, was described as *Callianassa aqabaensis* Dworschak, 2003. Because the presence of both female and male gonopores in individuals of *C. aqabaensis* (see Dworschak, 2003) made it difficult to determine their sex, one specimen was dissected in a search for ovaries or testes. This led to the discovery of a bopyrid parasite inside the host. During subsequent sampling in 2002, this parasite was specifically sought, and it was determined to be a new species of *Entophilus* occurring at a rather high prevalence. This paper deals with the description of the new species and provides additional information on its prevalence and its effects on its callianassid host.

Materials and Methods

Specimens of *Callianassa aqabaensis* were collected with a yabby pump while SCUBA diving between 4 and 30 m (for details see Dworschak, 2003). In 2002, live specimens were inspected for parasites, and photographic color slides were made of them. Infected specimens were chilled on ice and then fixed in 4% formaldehyde. In the laboratory, host shrimps were examined and measured under a stereoscopic microscope and photographed with a digital camera attached to the microscope. The following parameters were determined for all animals: 1) sex, based on the appearance of the first and second pleopods (see Dworschak, 2003); 2) carapace length (cl in mm) from the tip of the rostrum to the end of the carapace; 3) palm length of the propodus of the major cheliped (plma in mm) in the middle line from the carpus to the insertion of the dactylus; 4) palm width of the major cheliped (pwma in mm) in the middle of the propodus, ventral to dorsal margin. Regression lines were calculated using SigmaPlot 2000 and statistical comparison among parasitized specimens, unparasitized males and unparasitized females was by analysis of covariance (ANCOVA) (Zar, 1984). The ANCOVA requires an initial test for homogeneity between slopes, and, if nonsignificant, a second test compares between elevations. All data were $\log_{10}(x+1)$ transformed to reduce heteroscedastity. If the ANCOVA tests revealed significant differences, a Tukey's post-hoc pairwise comparison was performed to determine statistically significant differences among groups.

Several infected shrimp were cut open ventrally, and the parasite was removed, dissected and illustrated using stereoscopic dissecting and compound microscopes equipped with drawing tubes.

Type-specimens have been deposited in the Naturhistorisches Museum Wien, Austria (NHMW), the Muséum National d'Histoire Naturelle, Paris, France (MNHN), the Nationaal Natuurhistorisch Museum, Leiden, The Netherlands (RMNH), and the Senckenbergmuseum, Frankfurt/M, Germany (SMF).

Results

Systematics

Family Bopyridae Rafinesque, 1815
Subfamily Entophilinae Richardson, 1903
Genus *Entophilus* Richardson, 1903

Type-species, by original designation, *Entophilus omnitectus* Richardson, 1903. Number of species previously recorded, one, cosmopolitan in moderately deep waters, infecting *Munida* species.

Entophilus mirabiledictu, new species
Figs. 1–3

"Unidentified bopyrid isopod:"—Dworschak, 2003: 424 [Gulf of Aqaba, Red Sea; infecting specimen in non-type material of *Callianassa aqabaensis* Dworschak, 2003].

Material Examined.—Infecting *Callianassa aqabaensis* Dworschak, 2003, completely enclosed within second abdominal somite of each host. Royal Diving Club, about 15 km south of town of Aqaba, Gulf of Aqaba, Red Sea, Jordan, 29.470°N, 34.973°E, 28–31 October 2002, P. C. Dworschak, coll. and det. of hosts: holotype, 1♀, NHMW 16781; allotype, 1♂, NHMW 16781; paratypes, 1♀, 1♂, MNHN Ep 1008; 1♀, 1♂, RMNH I 7232; 1♀, 1♂, SMF 30021. [Host shrimps deposited under NHMW 16778] Non-type material: 2♀, 2♂: NHMW 16767, 4 November 2001; NHMW 16777, 10 November 2001; 23 pairs of parasites left in their hosts: NHMW16783–16788, 26 October–5 November 2002.

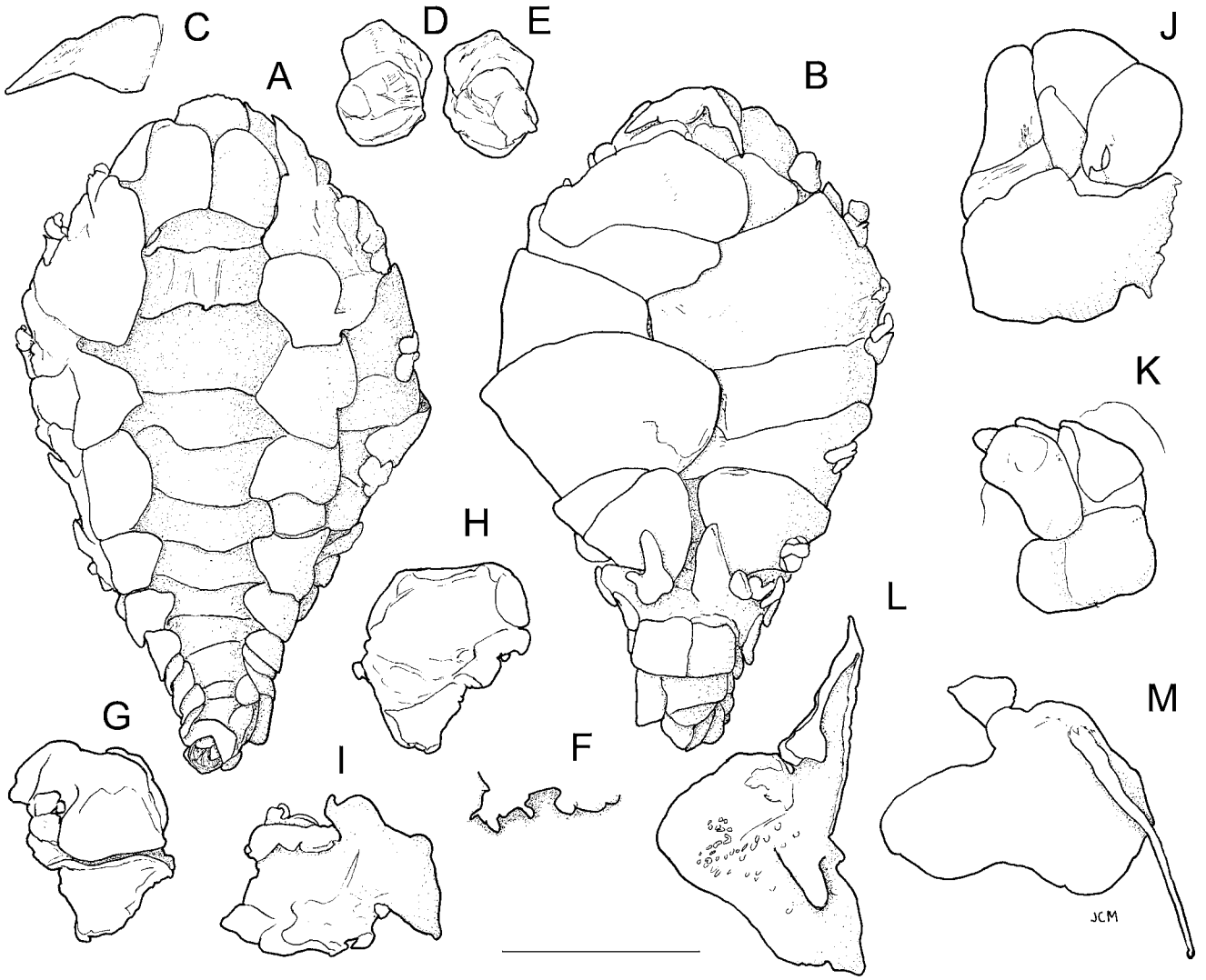

Fig. 1. *Entophilus mirabiledictu*, new species. Holotype female. A. Dorsal. B. Ventral. C. Right antenna 2. D. Maxilliped, external view. E. Same, internal view. F. Right side of barbula. G. Oostegite 1, external view. H. Same, internal view. I. Oostegite 7, external view. J. Right pereopod 1. K. Right pereopod 7. L. Pleopod 1, internal view. M. Pleopod 7, internal view. Scale: 2.00 mm for A, B, G, H; 1.00 mm for C–F, I; 0.89 mm for L, M; 0.36 mm for J. K.

Description of Holotype Female (Fig. 1)

Body elliptical, broadest slightly forward of midline. Body length 6.6 mm, maximal width 3.8 mm, pleon length 1.8 mm. Body axis distortion 6° (Fig. 1A, B).

Head largely concealed by first coxal plates, anterior margin covered by long frontal lamina. Antennae 1 obscure, antennae 2 (Fig. 1C) sharply pointed uniramous lanceolate flaps covering anteroventral region of head, extending backward over first oostegites. Maxilliped (Fig. 1D, E) asymmetrical, posterior article displaced laterally of indistinctly separated chevron-shaped anterior article, nearly circular posterior article, both markedly convex externally; no palp or plectron. Barbula (Fig. 1F) with single broad posterolaterally directed lateral extension on each side, that sparsely fringed by narrow flaps; middle projection broad, short, trilobed.

Pereon distinctly segmented dorsally, all pereomeres bearing paired coxal plates, largest at front and progressively smaller posteriorly, each overlapping that posterior to it, rows covering about one-third of dorsal surface of body. Oostegites on all 7 pereomeres, largely overlapping and completely enclosing brood chamber. First oostegite (Fig. 1G, H) irregularly triangular externally, articles separated by deep but unornamented groove internally; second through fifth oostegites about same size, much larger than others; seventh oostegite (Fig. 1I) irregularly quadrilateral. Pereopods (Fig. 1J, K) relatively reduced, many with articles reduced and/or absent or misshapen, dactyli ending in very blunt points.

Pleon of 6 distinct pleomeres, each of first five bearing biramous pleopods and connected uniramous lateral plates wrapping around sides; lateral plates continuing lines of pereonal coxal plates along dorsolateral margins of pleon; pleopods completely covering ventral surface of pleon. First pleopod (Fig. 1L) produced into pointed endopodite extending over surface of seventh oostegite; endopodites of other pleopods (Fig. 1M) in form of very slender threadlike processes posteriorly directed and aligned

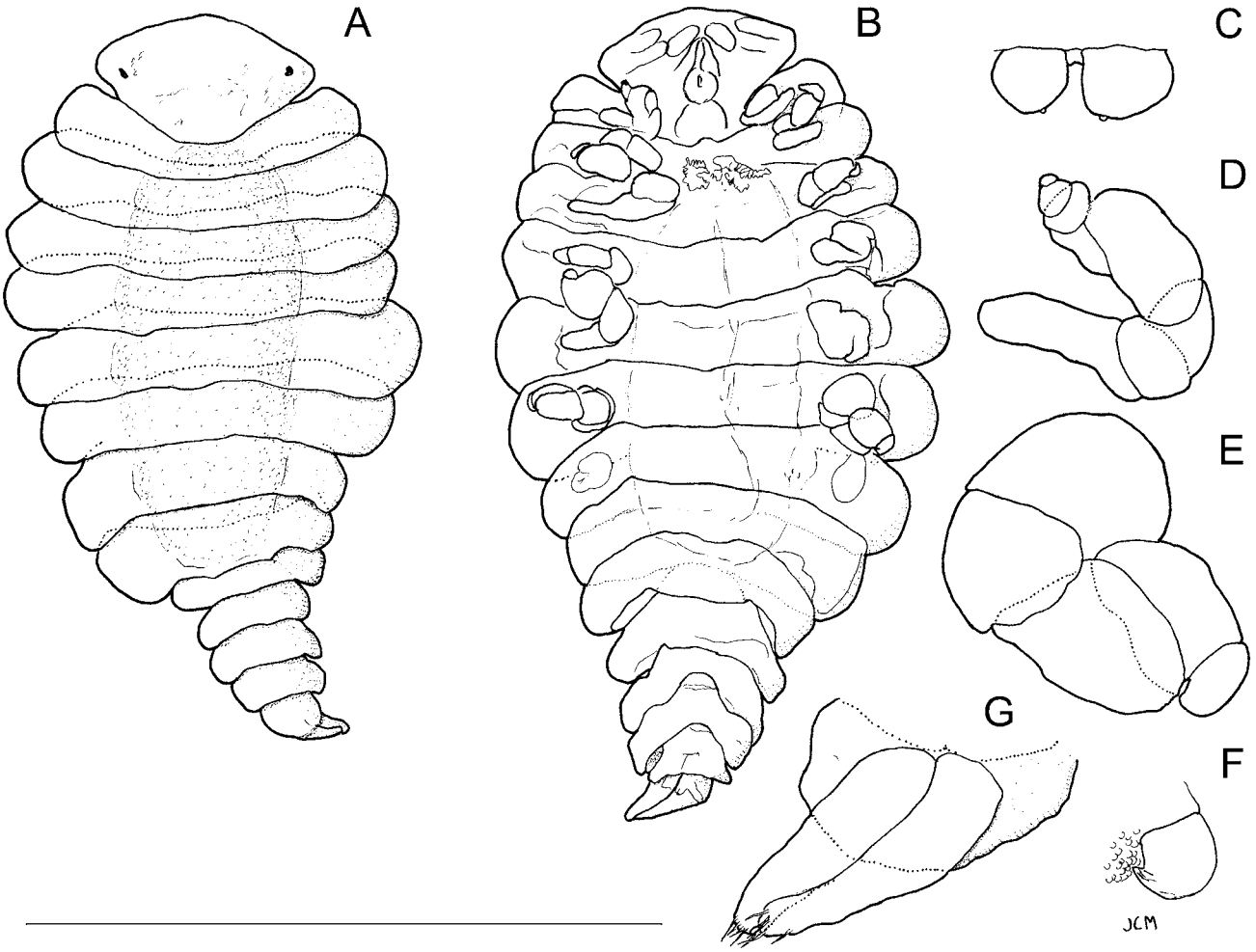

Fig. 2. *Entophilus mirabiledictu*, new species. Allotype male. A. Dorsal. B. Ventral. C. Right antennae 2. Right pereopod 1. D. Left pereopod 6. E. Dacytlus of same. F, G. Pleomere 6 and uropods, ventral view. Scale: 1.00 mm for A, B; 0.50 mm for C–F; 0.25 mm for F, G.

together under exopodites. Pleonal appendages forming cylindrical tube surrounding posterior end of body. Uropods as tiny uniramous flaps inside end of that tube.

Description of Allotype Male (Fig. 2)

Body outline subelliptical, narrower posteriorly. Length 1.15 mm, maximal width 0.61 mm, head length 0.21 mm, head width 0.34 mm, pleon length 0.40 mm. Body axis continuously curved. All body regions and segments distinctly separated (Fig. 2A, B). No pigmentation aside from small eyespots.

Head elliptical, extended into rounded angles laterally, narrower than anterior of pereomere 1 and laterally separated from it by deep notches. Eyes near lateral angles. Antennae 1 obscure, antennae 2 (Fig. 2C) as sessile flaps posteriorly directed, with minute distal second articles on posterior edges.

Pereon suboval, tapering jaggedly both forward and backward from pereomere 5, each pereomere overlapping that behind it. Slightly raised oval central regions both dorsally and ventrally. No midventral tubercles. Pereopods 1–6, all irregularly shaped, gradually larger posteriorly (Fig. 2D, E); tips of short dactyli reflexed onto scaly anterior edges of meri (Fig. 2F); pereopods of seventh pair as unisegmented stubs.

Pleon tapering posteriorly, of 6 pleomeres, first nearly as wide and as long as pereomere 7, others much shorter and narrower; dorsally, front and back edges nearly straight across, ventrally, pleomeres 1–5 markedly concave posteriorly. No pleopods. Final (sixth) pleomere strongly angled to one side, split into two posteriorly directed lanceolate uropods, their posterior borders sparsely setose (Fig. 2G).

Etymology.—Latin phrase *mirabile dictu* meaning "strange to tell" selected to stress the remarkable nature of this species and its unexpected discovery.

Comparison of Paratypes.—Both the females and males are very similar to the respective types. The three paratypic females are 4.36, 5.33, and 5.51 mm long respectively. Two bear early-stage eggs, the third late-stage larvae. One has a much more elaborate barbula. One has pereopods 5–7 tightly clustered together, pereopods 7 being reduced and ventrally placed. The three paratype males are 0.84, 1.02, and 1.24 mm long. One has an oval head not pointed laterally, prominent eyes, rudimentary seventh pereopods, and a straight pleon; the other two have pleons bent to the

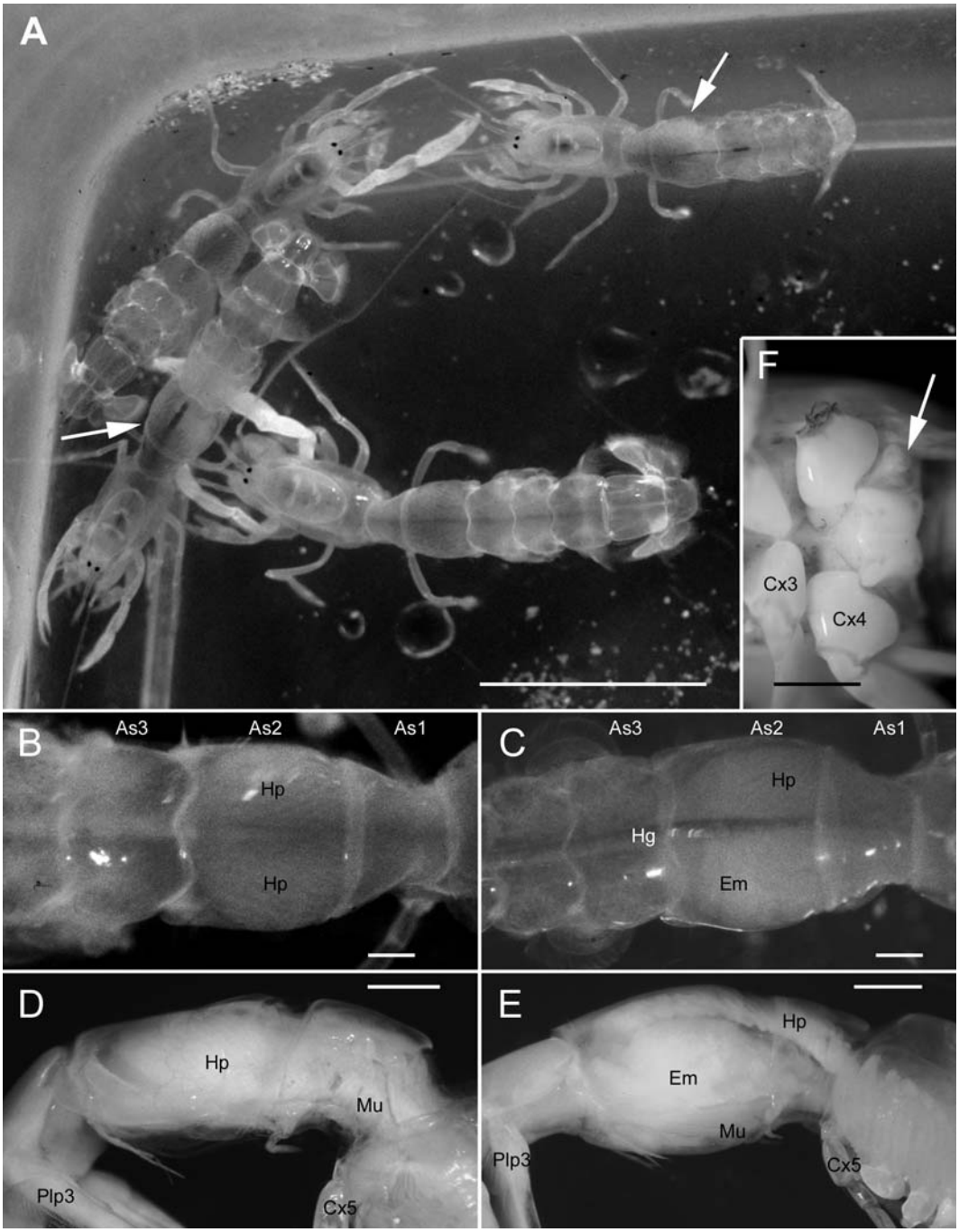

Fig. 3. A. Four live specimens of *Callianassa aqabaensis* Dworschak, 2003, two (indicated by arrows) infested by *Entophilus mirabiledictu*, new species. Detail of abdominal somites of live host shrimp without (B) and with (C) bopyrid, in dorsal view. Lateral view of abdomen of nonparasitized (D) and parasitized (E) Formalin-fixed *Callianassa*. F. Ventral view of host's thoracomeres 3 and 4 showing exit pore of parasite (arrow). Scale: 1 cm for A, 1 mm for B–F. Cx3–5: coxa of third, fourth and fifth pereopod. As1–4: first to fourth abdominal somites. Hp: hepatopancreas. Hg: hindgut. Plp3: third pleopod. Em: *Entophilus mirabiledictu*.

right like the allotype but tapered more smoothly than the allotype's instead of abruptly narrowing posteriorly.

Occurrence on Host.—The parasites occurred entirely within the bodies of their hosts. Each female occupied the second abdominal somite of its host and extended into the first abdominal somite with its narrowing posterior end reaching into the ventral part of the cephalothorax. The dorsal surface of each female faced the ventral side of its host. The body of each female was fixed in place and completely unable to move. Each accompanying male was located at the ventral side of the female near its pleon.

Prevalence.—Of the nine shrimp specimens collected in 2000, none was infested. In 2001, two specimens (one male and one female) of the 33 collected (6%) had the parasite. In

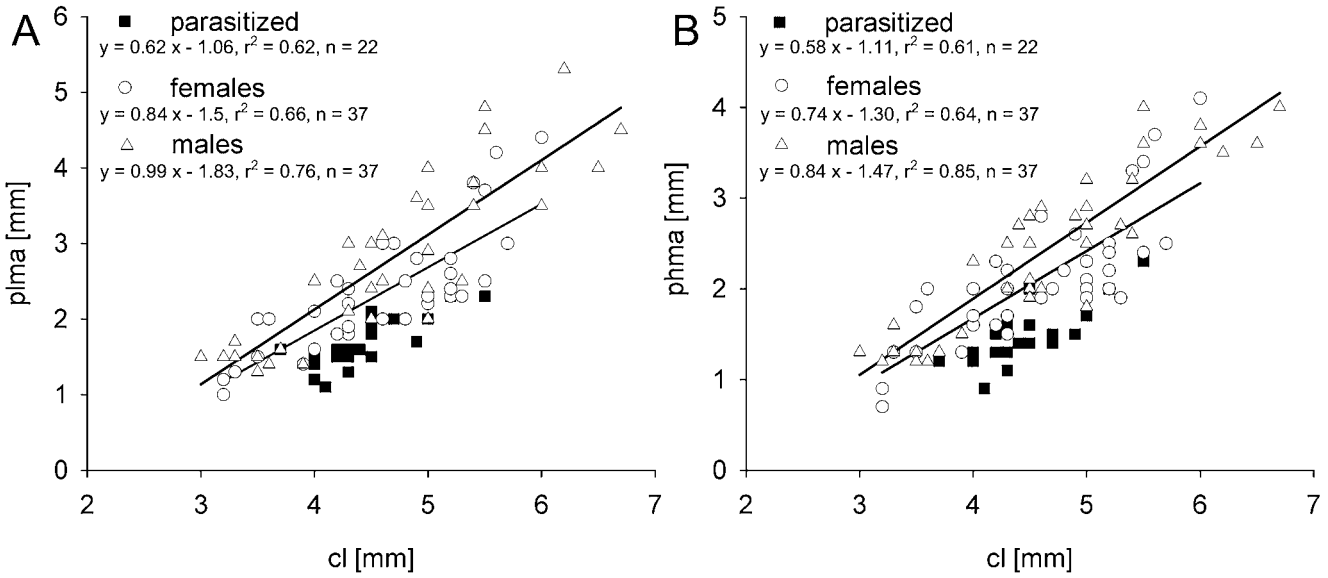

Fig. 4. Relationship between (A) propodus length and (B) propodus height of major chelipeds against carapace length of parasitized specimens and nonparasitized males and females of *Callianassa aqabaensis*.

2002, 28 *C. aqabaensis* (one male, 27 females) of 96 examined were parasitized by the bopyrid, for a prevalence of 29%.

Effects of the Parasite on the Host.—In live specimens of *C. aqabaensis*, infestation by the bopyrid can easily be recognized in dorsal view (Fig. 3A–C) by the slightly swollen first and second abdominal somites, the asymmetrical hepatopancreas and the hindgut which is visible in the second abdominal somite. In unparasitized shrimps, the entire abdominal somites 1 and 2 are completely filled with the yellow to orange hepatopancreas, which obscures the hindgut (Fig. 3B). In infected animals, most of the hepatopancreas is atrophied, and the hindgut is dislocated towards the tergites (Fig. 3C). The swelling of the abdominal somites caused by the presence of the parasite is clearly visible in lateral view (see Fig. 3D, E). The abdominal musculature also atrophies and is thinner than in unparasitized specimens. The female parasite produces an obscure exit pore near the coxae of the fourth pereopods of the host (Fig. 3F); presumably, it is through this pore that the prospective male finds its mate and the larvae are released. Remarkably, the parasites seem to diminish the activity levels of their hosts very little. Infested animals were evidently as active as others, and they were able to reburrow and to construct new burrows within a few hours in aquaria. The bopyrids, however, do cause castration and feminization of their hosts. Diagnostic of this feminization is the allometric growth of the major cheliped (Fig. 4), the propodus of which is much reduced in both length and height in parasitized specimens; its condition in both sexes approaches that of nonparasitized females. The first stage of the ANCOVA indicated homogeneity among slopes ($P > 0.05$) both for propodus length and height against carapace length. The results from the second-stage ANCOVA test revealed a highly significant difference in elevations ($P < 0.01$) among all three groups for both propodus measurements. A Tukey's post-hoc test revealed that the propodus of parasitized specimens was significantly smaller than that of nonparasitized females and nonparasitized males ($P < 0.05$); no significant difference was detected between unparasitized males and nonparasitized females ($P > 0.05$).

Discussion

The only other species of the genus *Entophilus* or its bopyrid subfamily Entophilinae is *E. omnitectus* Richardson, 1903. It has been recorded as a deep-water parasite (from 300 to over 1000 m) of various species of the galatheid genus *Munida* from Hawai'i (Richardson, 1903), Madagascar (Bourdon, 1976), the Azores (Bourdon, 1979), the Gulf of Mexico (Adkison and Collard, 1990), and the Chesterfield Islands of Australia (Markham, 1994). In each case, it occurred inside the visceral cavity of its host, a position unique for a bopyrid. Thus the occurrence of *E. mirabiledictu* entirely within the body of its host is consistent with that of its congener, but it differs from *E. omnitectus* in occurring in the abdomen rather than the thorax of its host. More remarkably, it occurs in a completely different species of host, a thalassinidean rather than an anomuran, and it is known only from shallow water, facts which inspired the selection of its name.

The best description of *Entophilus omnitectus* that has been published is that of Bourdon (1976), so we are using it as the basis of comparison with *E. mirabiledictu*. Females of both species have nearly identical body shapes and proportions and look much alike dorsally, in having large overlapping centrally-directed coxal plates lining the front of both sides of the dorsal surface of the pereon and their lines continued by similarly placed lateral plates. Their antennae are all unisegmented flaps; their maxillipeds are strangely asymmetrical and lack palps and plectrons; their reduced pereopods lack some articles and have dactyli lacking sharp points; all seven pairs of oostegites are equally developed; and their pleopodal endopodites extend posteriorly into overlapping sharp points. All those characters are

unique to the Entophilinae. The female of *E. omnitectus*, in contrast with that of *E. mirabiledictu*, has a barbula produced into simple unadorned projections; its first oostegite bears a distinct internal ridge extended into a sharp point; the articles of its pereopods are more regular; its pleopodal endopodites are lanceolate rather than threadlike; and the posterior end of its pleon is not surrounded by a tube formed by the endopodites. Males of both species have unisegmented antennae, all pereomeres and all six pleomeres strongly separated, and uropods large, pointed and prominently extended. The males are otherwise quite different, that of *E. omnitectus* being very slender, lacking eyes, and bearing five pairs of prominent bilobed pleopods.

Bopyrid parasites of thalassinideans, many species of which infest both callianassids and upogebiids, constitute a unique assemblage of species that has been designated the "Thalassindean Transition" (Markham, 1986, 2001), because it appears to represent an evolutionary link between the subfamilies Pseudioninae (otherwise mostly parasites of anomurans) and the Ioninae (otherwise mostly parasites of brachyurans) and comprises those genera morphologically evidently ancestral within both subfamilies. Another parasite of thalassinideans is the monotypic *Phyllodurus abdominalis* Stimpson, 1857, the sole member of the subfamily Phyllodurinae, frequently found as a parasite of a number of species of the genus *Upogebia* along the eastern Pacific coast (Markham, 1977, 2001). Morphologically, *P. abdominalis* is more similar to branchially-occurring bopyrids, even though it infests its hosts abdominally; it may represent a link between subfamilies whose species exhibit those two different modes of infestation. It is very different from *Entophilus*. The new species, *Entophilus mirabiledictu*, is difficult to fit into this scheme, primarily because it is congeneric with a species found on very different hosts, as discussed above. Because we have so far collected 29 pairs of *E. mirabiledictu* only as parasites of *Callianassa aqabaensis* over three years, and *E. omnitectus* has been collected several times, always as a parasite of a *Munida* species, it is clear that neither species' host selection can be considered an "accidental" occurrence.

The occurrence of these two species of *Entophilus* entirely within the bodies of their decapod hosts is unique within the Bopyridae, but reminiscent of the mode of infection of parasitic isopods in the closely related family Entonscidae (see Trilles, 1999), species of which occupy the visceral cavities of some brachyurans and form similar exit pores for release of larvae from their hosts' bodies. Entoniscid females, however, are morphologically much more modified for parasitic existence than any bopyrids, their bodies consisting of little more than reproductive sacs that are difficult even to recognize as isopods. It would be of interest to learn whether comparable studies of the life-histories of the Entonscidae and Entophilinae might show similarities in their invasion methods, reproductive strategies, and effects on their hosts.

Although the total number of *C. aqabaensis* collected differed considerably from year to year, prevalence of its parasite seems to have increased from 2000 to 2002. Unfortunately, we did not return to the Gulf of Aqaba thereafter. The prevalence observed for *E. mirabiledictu* in 2002 is much higher than those reported for external bopyrids on other callianassids. For instance, *Ione thoracica* (Montagu, 1808) infests *Callianassa tyrrhena* (Petagna, 1792) or *Callianassa subterranea* (Montagu, 1808) only up to 12% (Bourdon, 1968; Rowden and Jones, 1994; Dworschak, 1998).

Feminization and parasitic castration by external bopyrids has been observed in a number of thalassinideans, for instance in *Upogebia pusilla* (Petagna, 1792) (reported as *U. littoralis* by Tucker, 1930) and in *Callianassa tyrrhena* (Petagna, 1792) (reported as *C. laticauda* by Reverberi, 1942); see also the summaries by Bourdon (1968). Similarly, *Entophilus mirabiledictu*, though found internally, affects the external secondary sexual characters of its hosts. All except one infected shrimp had feminized pleopods, and the dimensions of their chelipeds were always closer to those of nonparasitized females and often even more weakly developed than the latter.

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