AN UNEXPECTED PARASITIC RELATIONSHIP BETWEEN A NEW SPECIES OF *ANTHESSIUS* (COPEPODA: CYCLOPOIDA) AND A DECAPOD CRUSTACEAN, *ALPHEUS MACROCHELES* (HAILSTONE, 1835) FROM THE NW MEDITERRANEAN SEA

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ABSTRACT

We describe from the NW Mediterranean Sea a new copepod species of Anthessiidae, *Anthessius alpheusicolous*, found in association with the snapping shrimp *Alpheus macrocheles* (Hailstone, 1835). The new species is differentiated from its 40 congeners by the formula of the third segment of the fourth exopod, the number and morphology of the terminal claws on the antenna, the armature of the mandible, and the length of leg 5. A key to the 41 species currently included in *Anthessius* is presented. The relationship between *A. alpheusicolous* and its decapod host likely arose through host switching, and the known symbiotic relationships between the species of *Anthessius* and their respective hosts are reviewed within this frame. Additionally, the synonymy between *A. projectus* Kim, 1993 and *A. kimjensis* Suh, 1993 is here reported for the first time.

KEY WORDS: *Alpheus*, *Anthessius*, Copepoda, Cyclopoida, host-switching

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INTRODUCTION

The evolutionary history of Copepoda demonstrates that this group has been highly successful in forming associations with other marine organisms; they parasitize members of virtually every animal phylum, from sponges and cnidarians to vertebrates (including mammals). Most are external parasites, living on the surface of their hosts or colonizing more sheltered microhabitats (such as gills, nostrils, mantle cavities, genital bursae), while others have even became endoparasites, burrowing into muscles, living within body cavities, or inhabiting digestive tracts of their hosts (Huys and Boxshall, 1991).

Among symbiotic copepods, parasitic species from 11 families are known to occur on crustaceans, including seven families of harpacticoids, two of siphonostomatoids, and two of cyclopoids (Boxshall and Halsey, 2004). These families have different host specificities and, thus, different host ranges, varying from strictly monoxenous (strictly occurring on a single host species) to polyxenous (occurring on a wide range of phylogenetically unrelated hosts) (Boxshall, 1998). Most of these families have been reported as occasional crustacean associates, among other marine invertebrates, but only one family, the siphonostomatoid Nicothoidae Dana,

1852, is known to exclusively utilize crustaceans as hosts (Boxshall, 2005).

For the cyclopoid Anthessiidae Humes, 1986, there are no previous reports of crustacean symbionts. In fact, the whole family is considered to show a high degree of host-specificity for molluscs (Ho, 1997; Boxshall and Halsey, 2004; Huys et al., 2007). However, during a broad survey on symbiotic shrimps, several specimens of *Athessius* were found attached to a specimen of the Mediterranean snapping shrimp *Alpheus macrocheles* (Hailstone, 1835). The present study describes these specimens as a new species, compares them with congeners, and discusses host specificity patterns among symbiotic anthessiids.

MATERIAL AND METHODS

The hosts were collected in the vicinity of the Medes Islands, in the Mediterranean just off the Spanish coast northeast of, under stones at a depth of 10 m on September 9, 2009. The host snapping shrimp was transported alive to the laboratory and gently anaesthetised prior to taking digital images to show the position of the parasitic copepods. Then, the host shrimp and copepods were fixed in 70% ethanol.

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Selected specimens were dissected in lactic acid prior to staining with Chlorazol black E (Sigma® C-1144), examined as temporary mounts in lactophenol, and finally sealed with Entellan as permanent mounts. All figures were drawn with the aid of a camera lucida on a Leica DMLB differential interference stereomicroscope. Mean body length (MBL) was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. All appendage segments and setation elements are named and numbered according to Huys and Boxshall (1991). All observations were carried out under a Leica DM5500 B automated Upright Microscope.

The type series is deposited in the Museo Nacional de Ciencias Naturales, Madrid (MNCN) and in the collection of the "Biodiversidad y Ecología de Invertebrados Marinos" research group of the University of Sevilla (BEIM).

SYSTEMATICS

Anthessius alpheusicolous n. sp.
Figs. 1-5

Types.—Holotype female (MNCN 20.04/8572), associated with the crustacean *Alpheus macrocheles*, collected by I. Marin, September 9, 2009, 10 m. NW Mediterranean Sea, Medes Islands; MNCN 20.04/8573 allotype, adult male, same sampling data as holotype; four paratypes, BEIM (COP 99), two adult females and two adult males, same sampling data as type material. One additional female was present on the host *in vivo*, but was lost during sample handling.

Female.—Body similar to other species of *Anthessius* (Fig. 1A). MBL = 1.35 mm (1.48-1.53 mm), maximum width 0.77 mm (0.77-0.78 mm), based on three specimens in lactic acid. Cephalosome and first pedigerous somite discernible from each other. Prosome length/width ratio = 1.16:1. Prosome/urosome length ratio = 1.45:1. Urosome 5-segmented (Fig. 1B) comprising leg 5-bearing somite, genital double-somite, and three free abdominal somites. Somite of leg 5 bell-shaped, slightly wider than long. Genital double somite (Fig. 1A, B) 1.26 times wider than long, widest at middle, i.e., genital area, constricted posteriorly. Each genital area (Fig. 1D) with two short, naked setae and a small spiniform process. Egg sacs extending to tips of caudal setae, each about 60 × 30 mm. Three free abdominal somites each wider than long (Fig. 1A, B). Caudal ramus (Fig. 1A, B), 134 μm long, 3.3 times longer than wide, with six terminal setae. Outer lateral and dorsal setae naked, similar in length. Outermost terminal seta with setules on internal margin; innermost terminal seta plumose. Two median terminal setae plumose, 400 μm (outer) and 583 μm (inner) long. Urosome with minute fringes (Fig. 1A, B).

Antennule (Fig. 1E) 610 μm long, with seven segments measuring (along posterior, non-setiferous margin): 40 (80 μm along anterior margin), 130, 45, 150, 140, 55, and 50 μm, respectively. Formula for armature: 4, 16, 3 + 1 spiniform seta, 3, 4 + 1 aesthete, 2 + 1 aesthete, and 8 setae. All setae naked. Surface of antennule with small fringes.

Antenna (Fig. 1C) 3-segmented, 312 μm long (claws excluded), with second segment longest. First two segments each with one naked seta on inner margin. Terminal segment with one naked seta on inner margin and three subterminal

setae in a row close to inner margin. Outer corner with a row of spinules, two setae each with strong spinules at base, and one spiniform seta. Four unequal terminal claws, two of them long, slender, seta-like; other two more unguiform, sclerotized, with narrow interruption of inner-side sclerotization at mid-length; latter two claws with a row of spines (outermost) and a small sclerotized lobe with spinules (innermost), giving them a subchelate appearance. Labrum (Fig. 2F) with two posteroventral lobes each one bearing a paragnath (Fig. 2E) as a small sclerotized lobe with tiny spinules.

Mandible (Fig. 2C) a flat plate, with thick cuticle along anterior and posterior margins. Appendage with one long lash, two proximal elements on the ventral margin and an articulated dorsal seta well developed. Lash with long row of spines on outer margin, a few small terminal spinules on inner margin, a small patch of spinules, and three hyaline lamellae (two mid-sized, one flat, and one triangular, between the lash and the dorsal seta; one bigger, posterior to lash base) at its base. Two proximal elements pectinated.

Maxillule (Fig. 2A) bilobed distally; outer lobe more sclerotized than inner one, with smooth, slender seta, a short spine, two unequal setae, and small spiniform process; inner lobe with two prominent, strong elements and small spiniform process. Distal segment of maxilla (Fig. 2B) with six strong teeth on distal medial margin (first one small with a tiny basal spinule, sixth one highly sclerotized with few basal spinules on outer margin), rounded, well-sclerotized protuberance with spine bearing spinules on posterior surface, and tiny spine on proximal median surface. Maxilliped (Fig. 2D) with two lateral constrictions as rudiments of segmentation, with spines on surface of second and third segments and third segment with one small terminal spine.

Swimming legs 1-4 (Fig. 3A-D) biramous with 3-segmented rami, intercoxal sclerite and a characteristic spine and setal formula (Table 1).

Coxae with spinule rows around outer margin and inner plumose seta (this seta smaller on fourth coxa). Basis of legs with small setae on inner margin and an outer naked seta.

Leg 5 (Fig. 1A, B) 5.5 times longer than wide, 225 × 41 μm, with row of spinules on outer basal and inner distal margins, three spines, and one seta.

Male.—Body 1.15 mm (1.26-1.31 mm) long, based on three specimens in lactic acid (Fig. 4A). Prosome 1.43 times relatively longer than wide. Urosome 6-segmented (Fig. 4A, B), with few setules, longer than in female. Genital somite slightly wider than long. Fourth postgenital somite slightly wider than long. Caudal ramus 2.6 times longer than wide, armed as in females.

Antennule (Fig. 4C) as in females, but armature of last three segments different: 5, 2 + 1 aesthete, and 8 + 1 aesthete. Antenna, labrum, mandible, maxillule, and maxilla as in females. Maxilliped (Fig. 4D) 4-segmented including claw. First segment with a distolateral lobe with row of long spinules. Second segment bearing two dorsomedial unequal setae and two dense, conspicuous patches of moderately blunt, somewhat digitiform spinules. Third segment shortest, distally armed with one small naked seta and one longer pointed process. Claw arched, longer than second segment, with spinulose medial margin and one very small seta.
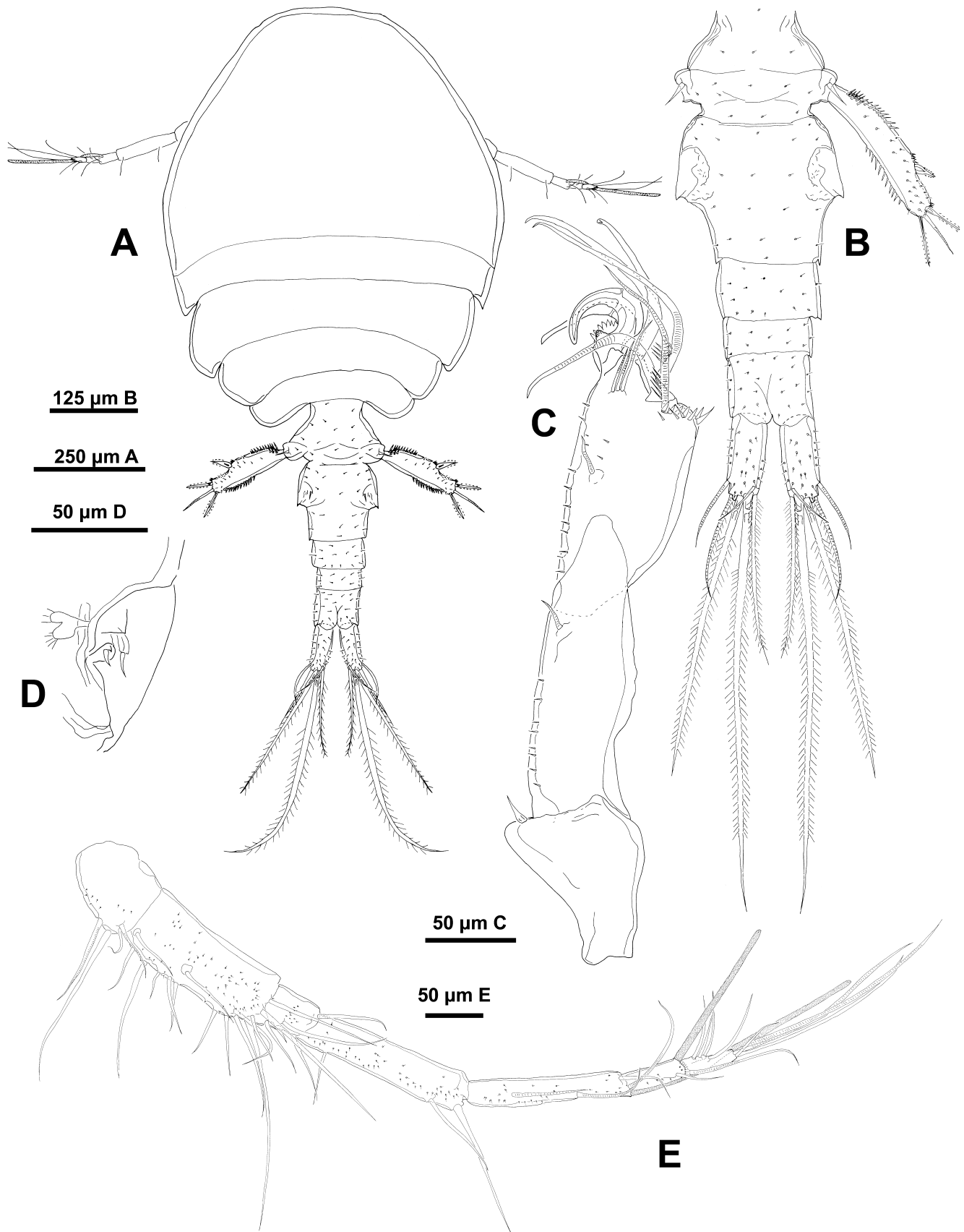
Fig. 1. *Anthessius alpheusicolous* n. sp. (female). A, habitus, dorsal; B, urosome, dorsal; C, antenna; D, genital area; E, antennule.
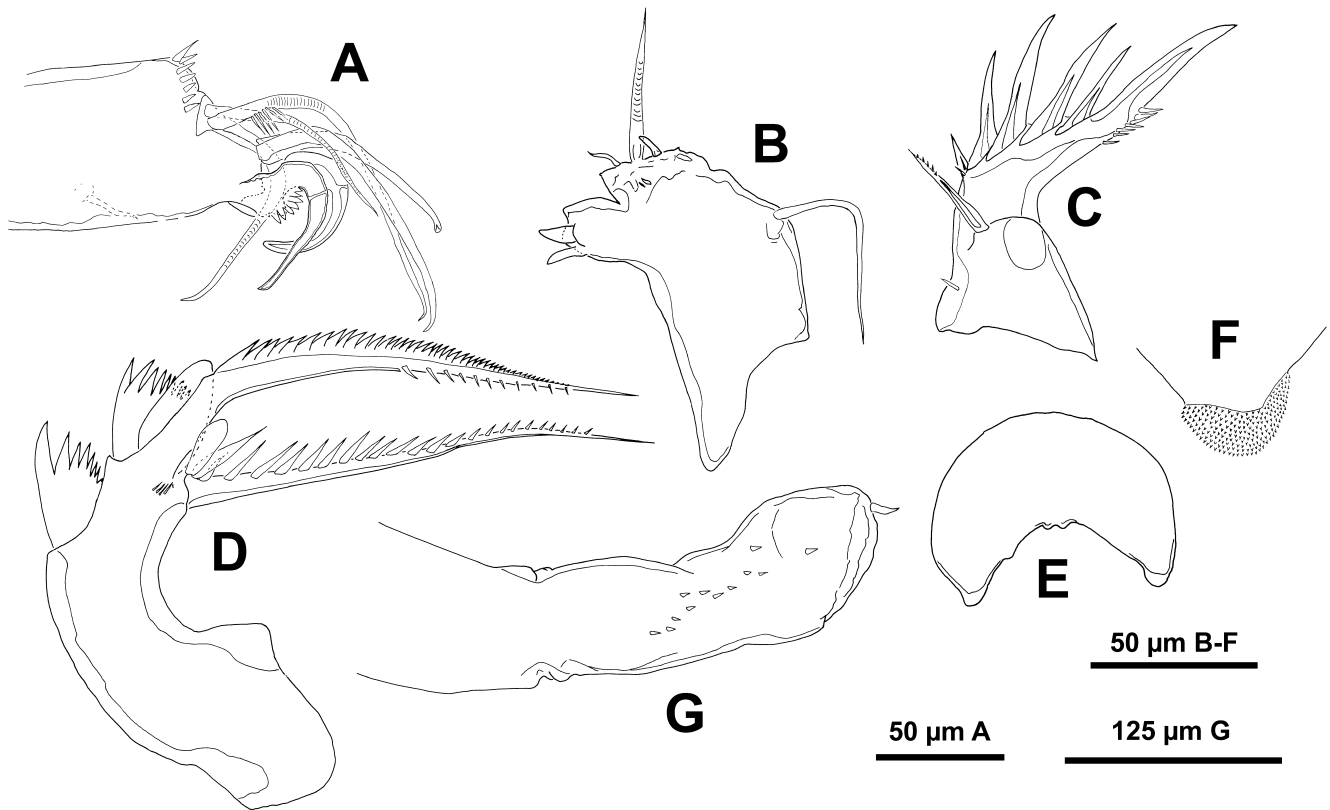
Fig. 2. *Anthessius alpheusicolous* n. sp. (female). A, last segment of the antennule; B, maxillule; C, maxilla; D, mandible; E, maxilliped; F, paragnath; G, labrum.

Legs 1-4 as in females. Leg 5 (Fig. 4B) with marginal spinules, about 4.3 times longer than wide. Leg 6 (Fig. 4B) represented by two pairs of unequal setae on posterolateral corners of genital somite.

Ecology.—The host was found in shallow water, 10 m deep beneath boulders, the typical habitat of *Alpheus macrocheles*. This shrimp is common in the Mediterranean, mainly inhabits sand or gravel substrates, often hiding under large boulders or coralline algae aggregates and burrowing galleries in the sediment. Seven specimens of the symbiotic copepod (three males and four females) were attached to the pleopods and uropods of a male shrimp (Fig. 5). The copepods were similar in colour. A female shrimp, probably a mate, collected under the same boulder had no symbiotic copepods attached.

Etymology.—The specific name "*alpheusicolous*" (adjective) is derived from *Alpheus*, the generic name of the host.

Distribution.—Known only from the type locality.

Taxonomic Remarks.—*Anthessius* Della Valle, 1880 is a fairly homogeneous group comprising 41 species [*A. projectus* Kim, 1993 is a synonym of *A. kimjensis* Suh, 1993, I. H. Kim, personal communication], which are often recognized on the basis of rather subtle differences (Humes and Ho, 1965). According to the formula of the third segment of the fourth swimming leg's exopod, these species can be divided into two groups, one with III, I, 5 and the other with II, I, 5. The following key is partially based on Stock (1960), as well as on some of the morphological features used by Ho (1997) in his phylogenetic analysis of the genus.

Artificial Key to Species of *Anthessius*, Female
(Except for *A. investigatoris*, the Female of which Is Unknown)

1a. Armature formula of third segment of exopod of 4th leg: II, I, 5 2
1b. Armature formula of third segment of exopod of 4th leg: III, I, 5 17
2a. Antenna tipped with 4 claws 3
2b. Antenna tipped with fewer than 4 claws 14
3a. Caudal ramus shorter than anal somite 4
3b. Caudal ramus longer than anal somite 9
4a. Mandible unarmed at base of the lash . . . .
. . . .*A. varidens* Stock, Humes, and Gooding, 1963
4b. Mandible armed with one, simple or divided, or two hyaline lamellae base of the lash 5
5a. Mandible armed with one, either simple or divided, at base of the lash 6
5b. Mandible armed with 2-3 hyaline lamellae at base of the lash 7
6a. Mandible armed with one simple lamella base of the lash . .*A. sensitivus* Stock, Humes, and Gooding, 1963
6b. Mandible armed with one divided lamella base of the lash . . .*A. proximus* Stock, Humes, and Gooding, 1963
7a. Mandible armed with two hyaline lamellae at base of the lash 8

125 μm
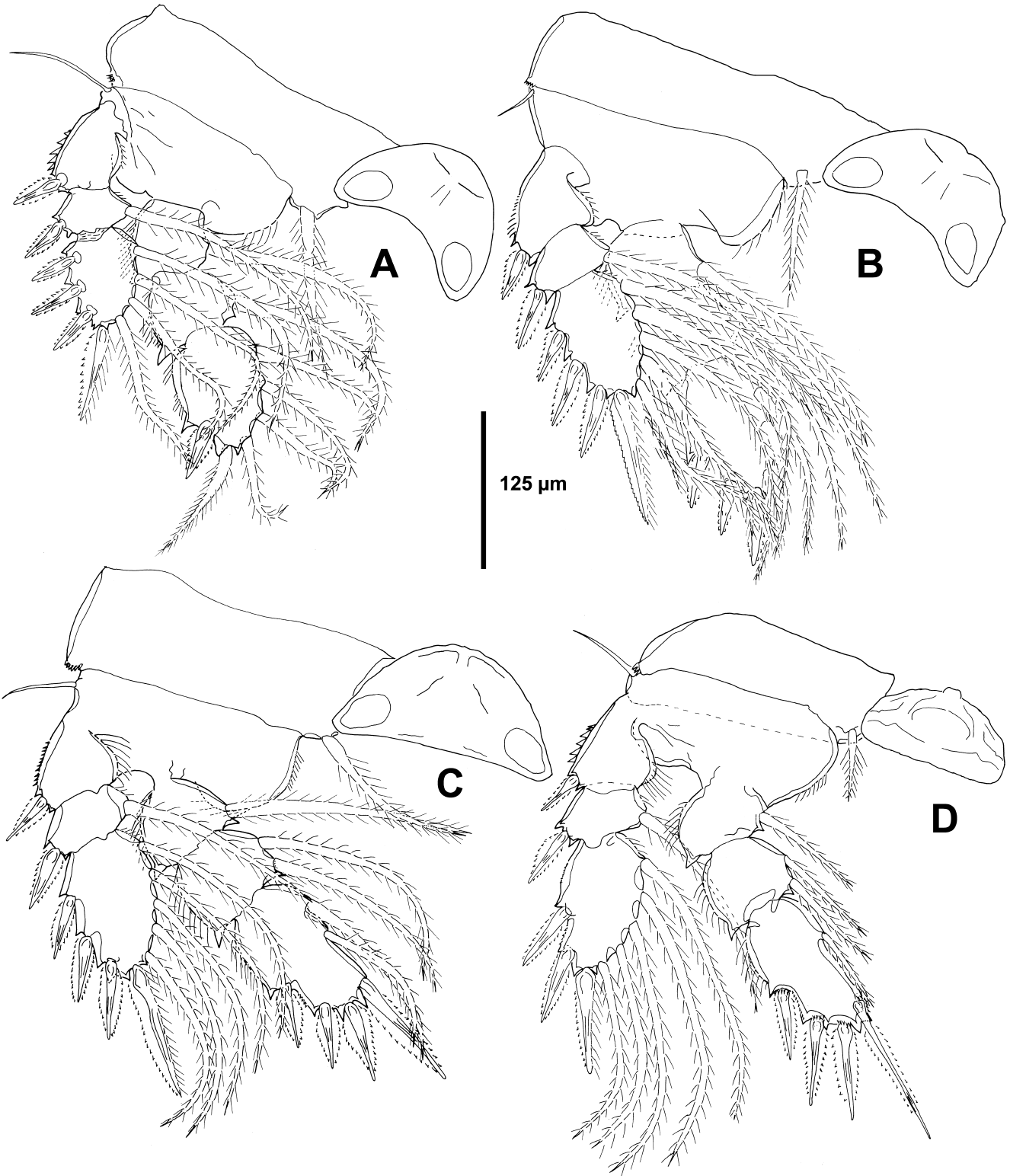
Fig. 3. *Anthessius alpheusicolous* n. sp. (female). A, leg 1; B, leg 2; C, leg 3; D, leg 4.

7b. Mandible armed with three hyaline lamellae at base of the lash . . . . *A. alpheusicolous* sp. nov

8a. Leg 5 nearly 3 times longer than wide . . . . *A. dolabellae* Humes and Ho, 1965

8b. Leg 5 less than 3 times longer than wide . . . . *A. navanacis* (C. B. Wilson, 1935)

9a. Mandible unarmed at base of the lash 10

9b. Mandible armed at base of the lash 12

Table 1. Spine and setal formula for swimming legs 1 to 4 of *Anthessius alpheusicolous*, n. sp.

	Coxa	Basis	Exopodal segments	Endopodal segments
Leg 1	0-1	1-0	I-0; I-1; III, I, 4	0-1; 0-1; I, 5
Leg 2	0-1	1-0	I-0; I-1; III, I, 5	0-1; 0-2; III, 3
Leg 3	0-1	1-0	I-0; I-1; III, I, 5	0-1; 0-2; IV, 2
Leg 4	0-1	1-0	I-0; I-1; II, I, 5	0-1; 0-2; IV, 1

10a. Free segment of leg 5 less than three times longer than wide . . . . *A. graciliunguis* Do and Kajihara, 1984

10b. Free segment of leg 5, three o more times longer than wide 11

11a. Terminal segment of antenna at least 2 times longer than wide . . . . *A. leptostylis* (G. O. Sars, 1916)

11b. Terminal segment of antenna as long as wide . . . . *A. lophiomi* Avdeev and Kazatchenko, 198

12a. Mandible armed with one forked hyaline lamella base of the lash . . . . *A. saecularis* Stock, 1964

12b. Mandible armed with one simple hyaline lamella at base of the lash 13

13a. Terminal segment of antenna about 1.5 times longer than wide, with 4 strong claws equal in length . . . . *A. longipedis* Ho and Kim, 1992

13b. Terminal segment of antenna as long as wide, with 4 articulated claw-like elements varying much in size . . . . *A. nortoni* Illg, 1960

14a. Antenna tipped with just one claw . . . . *A. pinnae* Humes, 1959

14b. Antenna tipped with 3 terminal claws 15

15a. Mandible unarmed at base of the lash . . . . *A. dilatatus* (G. O. Sars, 1918)

15b. Mandible armed at base of the lash 16

16a. Caudal ramus shorter than anal somite . . . . *A. kimjensis* Suh, 1993

16b. Caudal ramus longer than anal somite . . . . *A. atrinae* Suh and Choi, 1991

17a. Antenna tipped with four claws 18

17b. Antenna tipped with fewer than four claws 32

18a. Caudal ramus shorter than anal somite 19

18b. Caudal ramus longer than anal somite 23

19a. Maxillar terminal process with fewer than 10 teeth 20

19b. Maxillar terminal process with more than 10 teeth . . . . *A. distensus* Humes and Ho, 1965

20a. Mandible unarmed at base of the lash . . . . *A. minor* Stock, 1969

20b. Mandible armed with two hyaline lamellae base of the lash 21

21a. Free segment of leg 5 about 4 times longer than wide . . . . *A. lighti* Illg, 1960

21b. Free segment of leg 5 discoid, about as long as wide or slightly longer than wide 22

22a. Mandible armed with 2 unequal hyaline lamellae at base of the lash . . . . *A. discipedatus* Humes, 1976

22b. Mandible armed with 2 equal hyaline lamellae at base of the lash . . . . *A. amicalis* Humes and Stock, 1965

23a. Free outer margin of leg 5 without spinules or setae . . . . *A. groenlandicus* (Hansen, 1921)

23b. Free outer margin of leg 5 with spinules or/and setae 24

24a. Mandible unarmed at base of the lash 25

24b. Mandible armed at base of the lash 28

25a. Inner margin of leg 5 with distal group of slender spinules at distal third and a group of slender spinules in middle of segment 26

25b. Inner margin of leg 5 with only distal group of slender spinules at distal third, no spinules in middle of segment 27

26a. Free segment of leg 5 with three setiform and plumose spines . . . . *A. arenicolous* (Brady, 1878)

26b. Free segment of leg 5 with three strong spines . . . . *A. nosybensis* Kim, 2009

27a. Ventral surface of abdominal segments 1, 2, and 3 with tooth-like projections; that of abdominal segment 4 with two rows of strong spinules . . . . *A. solenocurtis* Della Valle, 1880

27b. Ventral surface of abdominal segment 4 with two rows of hardly discernable spinules; other abdominal segments without armature . . . . *A. teissieri* Bocquet and Stock, 1958

28a. Caudal ramus more than three times longer than wide 29

28b. Caudal ramus less than three times longer than wide 31

29a. Mandible armed with two hyaline lamellae at base of the lash 30

29b. Mandible armed with one hyaline lamella at base of the lash . . . . *A. mytilicolus* Reddiah, 1966

30a. Body habitus very modified, cephalosome much expanded in outline, thoracic segments with widely extending epimera . . . . *A. fitchi* Illg, 1960

30b. Body in general approaching typical cyclopoid habitus . . . . *A. solidus* Humes and Stock, 1965

31a. Maxillar terminal process with fewer than 10 teeth . . . . *A. stylocheili* Humes and Ho, 1965

31b. Maxillar terminal process with more than 10 teeth . . . . *A. alatus* Humes and Stock, 1965

32a. Antenna with two curved claws on its terminal segment . . . . *A. brevifurca* Sewell, 1949

32b. Antenna tipped with three terminal claws 33

33a. Caudal ramus shorter than anal somite 34

33b. Caudal ramus longer than anal somite 37

34a. Mandible armed with 1 hyaline lamella at base of the lash . . . . *A. brevicauda* (Leigh-Shape, 1934)

34b. Mandible armed with pectinate process at base of the lash 35

35a. Distal pointed segment of maxilliped unarmed . . . . *A. ovalipes* Stock, Humes, and Gooding, 1963

35b. Distal pointed segment of maxilliped with one small subterminal seta 36
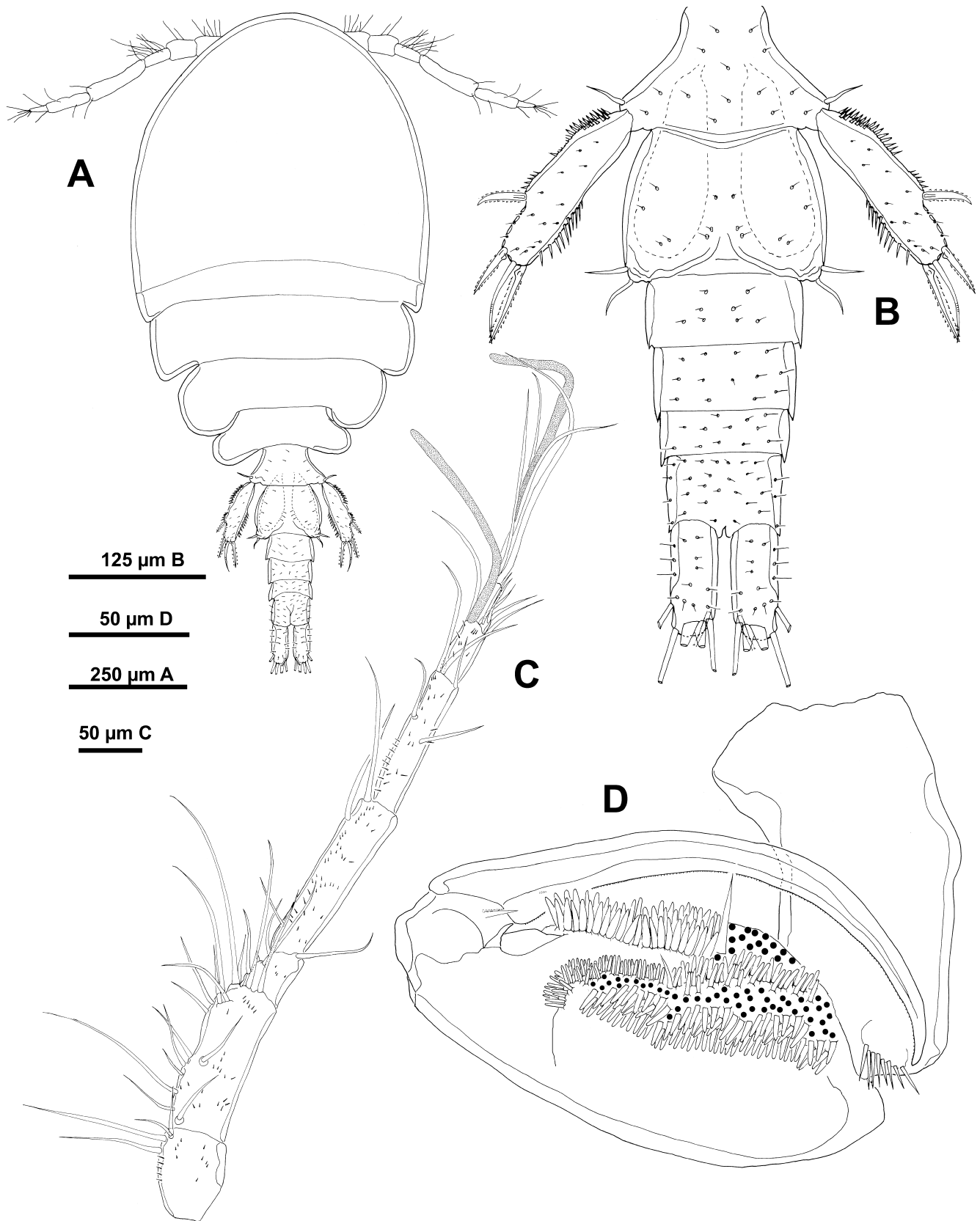
Fig. 4.   *Anthessius alpheusicolous* n. sp. (male). A, habitus, dorsal; B, urosome, dorsal; C, antennule; D, maxilliped with dots represent showing locations of omitted setae.
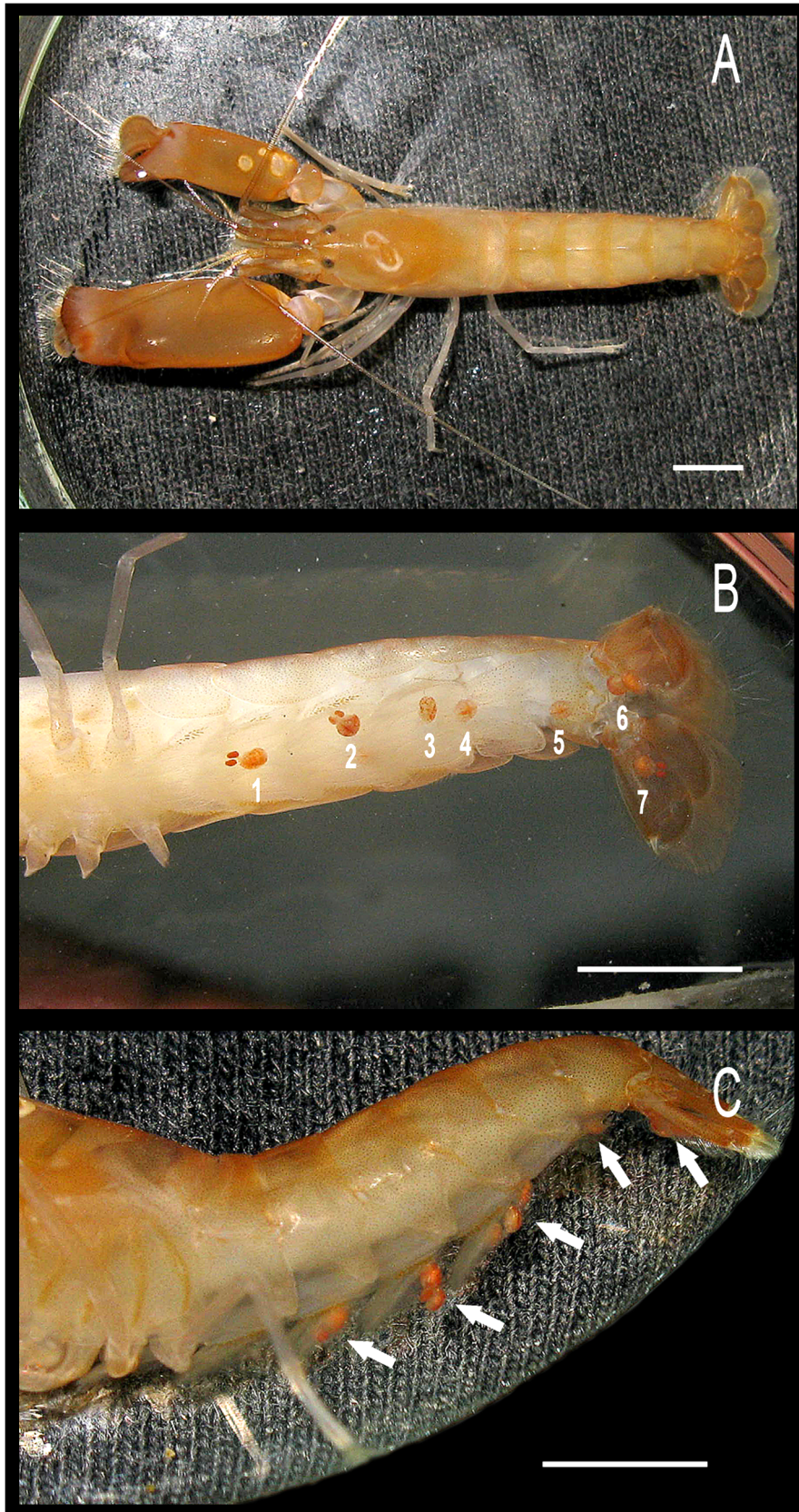
Fig. 5. *Anthessius alpheusicolous* n. sp. on its host *Alpheus macrocheles*. A, *A. macrocheles* in dorsal view; B, position of the parasites (numbered from 1 to 7) on *A. macrocheles* in lateral view; C, position of the parasites (white arrows) on *A. macrocheles* in ventral view. Scale bars 5 mm.

36a. Free segment of leg 5 with three serrated spines and one seta . . . . *A. arcuatus* López-González, Conradi, Naranjo, and García-Gómez, 1992

36b. Free segment of leg 5 with three slender setiform spines and one seta . . . . *A. obtusispina* Ho, 1983

37a. Maxillar terminal process with fewer than 10 teeth 38

37b. Maxillar terminal process with more than 10 teeth 39

38a. Mandible armed with hyaline plate at base of the lash . . . .*A. pinctadae* Humes, 1973

38b. Mandible armed with a pectinate process at base of the lash. . . . . *A. hawaiiensis* (C. B. Wilson, 1921)

39a. Mandible unarmed at base of the lash . . . .*A. pectinis* Tanaka, 1961

39b. Mandible armed with pectinate process at base of the lash 40

40a. Free segment of leg 5 less than three times longer than wide . . . .*A. coccinus* (A. Scott, 1909)

40b. Free segment of leg 5 at least three times longer than wide. . . . .*A. pleurobranchiae* Della Valle, 1880

The group with III, I, 5 contains 25 species, and that with II, I, 5, 16, including our new species. Among the latter, *A. atrinae*, *A. dilatatus*, and *A. kimjensis* are clearly distinguishable from *A. alpheusicolous* by having three terminal claws on the antenna (G. O. Sars, 1918; Suh and Choi, 1991; Suh, 1993). *Anthessius pinnae* differs strikingly from the new species in having only two claws on the antenna (Humes, 1959) instead of four. Eleven species of the second group have the same number of claws on the antenna as the new species, but none of them presents the two unguiform and ornamented claws (one with a row of spinules and the other with a small sclerotized lobe with setules) characteristic of *A. alpheusicolous*. Furthermore, *A. graciliunguis*, *A. leptostylis*, *A. ophioni*, and *A. varidens* have the mandible unarmed at the base of the lash (G. O. Sars, 1916; Stock et al., 1963; Do and Kajihara, 1984; Avdeev and Kazatchenko, 1985). *Anthessius longipedis*, *A. nortoni* and *A. sensitivus* have one membranous or hyaline lamella there, and a leg 5 that is more than three times but less than five times longer than wide (Illg, 1960; Stock et al., 1963; Ho and Kim, 1992).

Anthessius proximus and *A. saecularis* have a divided hyaline lamella and a leg 5 that is scarcely three times longer than wide (Stock et al., 1963; Stock, 1964). Finally, *A. dolabellae* and *A. navanacis* have two hyaline lamellae and a leg 5 2.8 and 1.8 times longer than wide, respectively (Illg, 1960; Humes and Ho, 1965).

The typical mandible of Anthessidae represents, together with those of Myicolidae, an intermediate stage in the gradual incorporation of the five ancestral gnathobase elements to form the lash. The mandibles of antessiids have a dominant lash with spinulose margins, two proximal elements on the ventral margin (which are sometimes reduced), and a well development dorsal seta separate from those elements (Huys and Boxshall, 1991). The addition of either a hyaline plate or a pectinate process at the base of lash is considered a further development towards a parasitic mode of life, with

the development of the former being considered to be more specialized than that of the latter (Ho, 1997).

DISCUSSION

The anthessiids currently includes 50 species, grouped into six genera. The single known species of *Rhinomolgus* G. O. Sars, 1918 was collected from dredged material, and those of *Katanthessius* Stock, 1960, *Neanthessius* Izawa, 1976, and *Panaietis* Stebbing, 1900 parasites of molluscs. *Discanthessius* Kim, 2009 has recently been described as living on a scleractinian coral. The 41 species of *Anthessius* were recovered from weed washes (one species), to the marine plankton (four species), and as parasites of mollusc (35 species) or fish (one species).

The species reported without an specific association to a given host are: *Rhinomolgus anomalus* G. O. Sars, 1918, with "a considerable number of specimens" found in dredged material containing, among others animals, some crinoids of the genus *Antedon* (Sars, 1918), two females and eight males of *A. concinnus* found in plankton samples from the East Pacific (A. Scott, 1909); one female of *A. dilatatus* from a fjord in Norway (G. O. Sars, 1918); three females of *A. groenlandicus* in a fishing net from west Greenland (Hansen, 1923); and one female of *A. brevifurca*; and one male of *A. investigatoris* in weed washings from tropical waters of the Indian Ocean (Sewell, 1949). With the single exception of *R. anomalus*, all these species have been reported only once and in low numbers.

Some species of *Anthessius* are known from non-mollusc hosts. For instance, *A. alatus* usually parasitizing giant clams in the Indo-West Pacific, was collected on a sea star, *Acanthaster planci* (L., 1758), and in a sponge, *Stylissa carteri* (Dendy, 1889), reported as *Acanthella auranta* (Dendy, 1889) in the Red Sea (Humes and Stock, 1965). *Anthessius obtusispina* was first collected in the gill cavity of an embiotocid surf perch before being described from a notaspidean sea slug in California (Ho, 1983). Furthermore, *A. lophiomi* was found on the gills and in the mouth of the fish *Lophiomus stigerous* (Vahl, 1797) (Avdeev and Kazatchenko, 1985) and has not been collected anywhere else. Except for this last specimen, all these findings were occasional and included a low number of specimens: only one of *A. alatus* (in the sponge) and *A. obtusispina* (in the surf perch) and three of *A. alatus* (in the sea star). Accordingly, anthessiid copepods are considered as molluscan parasites (Ho, 1997; Boxshall and Halsey, 2004; Huys et al., 2007), having a relatively high degree of specificity and occurring mainly on/in gastropod and bivalve hosts.

Having three-segmented rami and well-developed plumose setae on their swimming legs (as typical planktonic copepods), anthessiids appear to retain the potential to wander off their normal mollusc hosts (Ho, 1997). The repeated and seasonal presence of *A. graciliunguis* in plankton samples during different years, suggests that its planktonic phase may not be accidental, with foraying away from its host being a normal part of its life habit (Ueda et al., 2006). Such behaviour might be related to release of nauplii or to changes in host's condition (Ueda et al., 2006). Assuming that such behaviour could be generalized for the entire family, many species may then have the potential ability to settle on dif-

ferent hosts, with their recurrent use eventually leading to permanent host switching.

A possible example host switching was the description of *A. graciliunguis* living in association with the mussel *Mytilus galloprovincialis* (Do and Kajihara, 1984), which was considered a fortuitous association, since a single female was discovered after examining about 2000 mussels. Later on, the species was collected from three scallops, *Patinopecten yessoensis* (Jay, 1857), *Pecten albicans* (Schöter, 1802), and *Chlamys squamata* (Gmelin, 1791) from Korea (Kim, 1998), as well as from plankton in Japan (Ueda et al., 2006).

Host-parasite associations result from co-evolutionary events, categorized differently depending on the author (Mitter and Brooks, 1983; Brooks, 1988; Page and Charleston, 1998; Paterson and Banks, 2001; Johnson et al., 2003; Desdevises, 2007). There is, however, a general agreement in considering host switching, i.e., colonisation of new hosts, as an important process for triggering co-evolutionary events. Tight co-evolution results in high host-specificity, while frequent host switching leads to low host-specificity (Barker, 1991). As in many other parasites, the potential to disperse and to come into contact with several potential host species (Baer, 1957; Kennedy, 1975; Price, 1980; Noble et al., 1989) undoubtedly facilitates host switching in anthessiids. Colonization of new hosts may be easiest when several suitable host species, i.e., with a mode of life similar to the parasite's present host and thus providing it those with similar living conditions, are available (Poulin, 1992). As Gotto (1998) admirably explained, host switching can be presumed to have occurred when copepods apparently confined to one host group are revealed to have one or a few representatives associated with hosts of different groups. Host-switching, not only expands greatly the ecological niche (*sensu* Elton, 1927) of a given species, it also favours the establishment of new symbiotic associations, this being one of the major factors leading to the formation of new species by sympatric speciation (Via, 2001; Conradi et al., 2004).

Despite clear evidence for host switching, most attempts to correlate morphological characteristics of the species of *Anthessius* with their host preferences have failed (Illg, 1960; Humes and Ho, 1965). However, Ho (1987) followed his earlier suggestion that the six species associated with notaspidean sea slugs (*A. concinnus*, *A. hawaiiensis*, *A. obtusispina*, *A. ovalipes*, *A. pleurobrancheae*, and *A. arcuatus*) have evolved from bivalve-associated *Anthessius*-like copepods (see Ho, 1983), which generally supportive phylogenetic analysis together with evidence that *A. concinnus* is also a sea slug parasite, not a free-living, planktonic species (Ho, 1987).

Not all copepod associations with new potential hosts result in new permanent alliances. Most of them should be considered as either as occasional, i.e., as steps in the host-switching processes, or as temporary, i.e., as intermediary steps in the normal course of their life cycles. It is conceivable that most species of *Anthessius* associated with non-mollusc hosts (including the new one here described) could fall into one of these categories. There is, however, a single remarkable exception. The finding of 136 females and 30 males of *A. lophiomi* on nine specimens of the fish

Lophiomus stigerous (Vahl, 1797) was not considered as accidental (Nair, 1988), and so this fish is considered to be that copepod's definitive host (Poulin, 1992).

In agreement with the suggestion of Boxshall and Halsey (2004), we affirm that the unusual host-symbiont relationship between *A. alpheusicolous* and its non-mollusc host, *Alpheus macrocheles* could be the result of host switching. Based on our data, however, no definitive conclusion may be proposed about the nature of this new relationship. Further studies should be addressed to decide whether that finding represents the starting point of a host-switching process or a permanent, well established host-symbiont association.

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