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Systematics of the genus *Heterolaophonte* (Crustacea, Copepoda, Harpacticoida), with redescription of *H. uncinata* and *H. curvata*

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Abstract

Both sexes of *Heterolaophonte uncinata* (Cherniavski, 1868) and *H. curvata* (Douwe, 1929) are redescribed based on newly collected material from the Black Sea and Mediterranean coasts of Turkey in view of the fact that there has been no detailed redescription since their original descriptions. Neotypes are also designated for both species. Detailed comparisons of the characters displayed among *Heterolaophonte* Lang, 1948 species reveal that the genus cannot be defined by any unique apomorphy. We propose that the structure of the male appendages, especially the swimming legs, can provide a considerable number of significant characters that are valuable both for taxonomic identification and phylogenetic inferences. In addition, several mistakes leading to a great confusion in the accurate interpretation of the relationships among species within *Heterolaophonte* are discovered in earlier species descriptions. Therefore, *H. rottenburgi* (T. Scott, 1912), *H. exigua* (T. Scott, 1912), *H. australis* (T. Scott, 1912), and *H. insignis* (T. Scott, 1914) are removed from the genus and placed as incertae sedis in Laophontidae. We also conclude that *H. phycobates* (Monard, 1935), *H. pygmaea* (T. Scott, 1893), *H. tupitskyi* Chislenko, 1976, and *H. curvata micarthros* Marcus & Por, 1960, which still need further taxonomic investigation, have doubtful identity within the genus, and we place them as species inquirendae.

Key words: Laophontidae, neotype, taxonomy, Turkey

Introduction

The family Laophontidae T. Scott 1903 is a large and heterogeneous group, at present including 69 genera and about 300 species (Wells 2007; Gherardyn *et al*. 2007; Cottarelli *et al.* 2008; Huys & Lee 2009). Laophontids are essentially marine, free-living and benthic, and mainly inhabit the intertidal zone or shallow subtidal habitats and are frequently found among algal assemblages (Huys *et al*. 1996). The main problem surrounding laophontid taxonomy is that relationships between the genera are usually not well documented and justified. The origin of this problem lies in the outdated practice of defining a new genus by the particular combination of characters it displays rather than by autapomorphies. Many genera in the family such as the type genus *Laophonte* Philippi 1840 are therefore housing unnatural, polyphyletic assemblages of species (Huys & Lee 2000). Although the boundaries between genera are historically subjective, it is now widely accepted that a genus should constitute a monophyletic group. It is also recognized that formal taxonomic names and classifications should ideally be consistent with the phylogeny of the group. Moreover, there should be convincing phylogenetic reasons and/or an unequivocal unique definition before a new genus is established (Holm & Schoeman 1999).

Lang (1944) did create the name *Heterolaophonte* but, since he did not name a type-species, it was only validated in 1948 when he did nominate a type species for the genus. Hence the date of authorship is 1948, not 1944 (Huys 2009). On the other hand, Huys (2008) noticed that the genus-group names *Mesolaophonte* Nicholls 1941 and *Monolaophonte* Nicholls 1941 were senior subjective synonyms of *Heterolaophonte* since no type species was fixed. Therefore, Huys (2008) requested to ICZN that the generic name *Heterolaophonte* should be conserved, giving it precedence over the unused senior names whenever these names are considered to be synonyms. Huys' (2008) request to ICZN was granted in 2010 (ICZN 2010).

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At present *Heterolaophonte* is one of the three most speciose genera in the Laophontidae, despite the fact that the "*quinquespinosa*" species group was later removed from *Heterolaophonte* and included in *Quinquelaophonte* (Wells *et al*. 1982). The genus currently accommodates 34 valid species and five subspecies (including nominate subspecies) (Wells 2007; Varela & Ortiz 2008; Bang *et al*. 2011), and has been recorded from all oceanic basins including the Antarctic Ocean (Apostolov & Pandourski 2000). The genus is diagnosed by the cylindrical body, cylindrical caudal rami with at least 1 well-developed terminal seta, 6–7 segmented female antennule with aesthetasc on the fourth segment, reduced antennary exopod, 3-segmented P2-P4 exopod (P3 exopod always, P2-P4 exopods sometimes more developed in the male), P2-P4 endopod (first endopod segment without inner seta, endopods sometimes differently built in the male), reduced plate-like P5 of male.

None of these diagnostic characters can define *Heterolaophonte* as a monophyletic group. Although the reduced antennary exopod and rudimentary plate-like form of male P5 have been used as reliable characteristics to assign the newly described species into the genus (Mielke 1981), these characters are either plesiomorphic or homoplastic, since they are also observed in the genera *Quinquelaophonte* Wells, Hicks & Coull, 1982 and *Platychelipus* Brady, 1880. On the other hand, either the use of the above mentioned diagnostic features or the mistaken inclusion of some species into the genus (see discussion) resulted in grouping phylogenetically unrelated species within the genus *Heterolaophonte*. The removal of "*quinquespinosa*" species group to the genus *Quinquelaophonte* by Wells *et al*. (1982) has not been sufficient to render *Heterolaophonte* a natural group, since the position of certain *Heterolaophonte* species remains doubtful. The deficient descriptions of certain species and the lack of information on male characteristics hinder a robust phylogenetic analysis to solve the taxonomic problems surrounding this genus.

Heterolaophonte uncinata and *H. curvata* are two of the many species within the genus that are in need of urgent redescription. Detailed descriptions of both sexes of these *Heterolaophonte* species will contribute in solving taxonomic problems since especially the male swimming legs contain several phylogenetically informative characters. Here we provide detailed redescription of both sexes of the two species, based on material collected along the Turkish Coast.

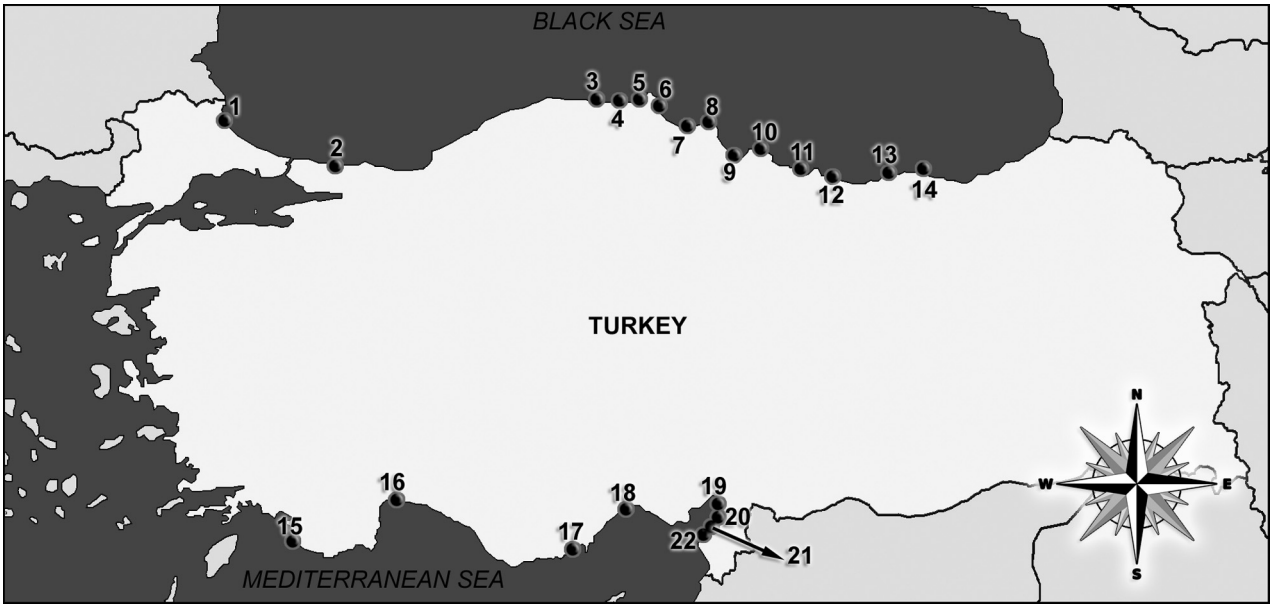

FIGURE 1. Map of sampling stations (coordinates of station numbers in Table 1).

Material and methods

Phytal samples were collected by hand from supra-littoral rocky shores at 22 stations (Table 1, Fig. 1). All samples were immediately preserved in either 4% formalin or 70% ethanol solutions. Copepods were extracted from the algae under OLYMUS SZX-12 or SZX-16 stereo microscopes and stored in 70% ethanol. Selected specimens were dissected in lactic acid and parts were mounted on slides in lactophenol mounting medium. Glass fibres were added

to prevent the animal and appendages from being compressed by the coverslip and to facilitate rotation and manipulation, allowing observation from all angles. Preparations were subsequently sealed with Entellan. Identifications were made under OLYMPUS BX-50 or BX-51 microscopes equipped with differential interference contrast (DIC). The descriptive terminology is adopted from Huys *et al.* (1996). Specimens were examined with a Zeiss SUPRA 55VP (FESEM) scanning electron microscope in Mersin University Advanced Technology Education, Research and Application Center (MEITAM). Specimens were prepared by dehydration through graded acetone, critical point dried, mounted on stubs and sputter-coated with platinum. Materials are deposited in the collection of NHM (the Natural History Museum, London) and in the Zoological Museum at the Biology Department of Mersin University.

TABLE 1. Names and coordinates of sampling stations.

No	Station Name	Coordinates
1	İğneada Beach, Kırklareli	41º53.366'N 28º00.059'E
2	Akçakoca Beach, Düzce	41º05.135'N 31º05.513'E
3	Doğanyurt Beach, Kastamonu	42º00.481'N 33º27.505'E
4	Güzelkent Beach, Sinop	41º57.133'N 34º23.516'E
5	Aliköyü Beach, Sinop	41º56.499'N 34º39.437'E
6	Karakum Beach, Sinop	42º00.938'N 35º11.536'E
7	Fatsa Beach, Ordu	41º04.601'N 37º26.448'E
8	Beyazkum Beach, Ordu	41º06.806'N 37º43.037'E
9	Tirebolu Beach, Giresun	41º00.249'N 38º48.473'E
10	İsmailbeyli Village Beach, Giresun	41º02.198'N 38º56.901'E
11	Yaroz Feneri Village Beach, Trabzon	41º05.677'N 39º23.718'E
12	Akçaabat Beach, Trabzon	41º03.152'N 39º32.227'E
13	Rize Beach, Rize	41º01.039'N 40º22.165'E
14	Kapısuyu Beach /Bartın	41°50.847'N 32° 45.177'E
15	Kalkan Beach, Antalya	36°13.722'N 29°26.955'E
16	Krizantem Hotel Beach, Alanya, Antalya	36°32.066'N 32°02.028'E
17	Nato Port, Silifke Mersin	36°17.094'N 33°49.928'E
18	Alata Beach, Mersin	36°36.866'N 34°19.702'E
19	Kurtpınarı Beach, Hatay	36°53.409'N 35°56.775'E
20	Arsuz, Hatay	36°14.008'N 35°50.220'E
21	Samandağ Beach, Hatay	36°08.315'N 35° 54.598'E
22	Samandağ Beach, Hatay	36°05.783'N 35° 56.182'E

Results

Order Harpacticoida Sars 1903

Family Laophontidae T. Scott 1905

Genus *Heterolaophonte* Lang 1948

Type species. *H. stroemii* (Baird, 1837)

Other species and subspecies. *Heterolaophonte bisetosa* Mielke, 1975; *H. brevipes* Roe, 1958; *H. campbelliensis* (Lang, 1934); *H. curvata* (Douwe, 1929); *H. c. micarthros* Marcus & Por, 1960; *H. denticulata* Roe, 1958; *H. discophora* (Willey, 1929); *H. furcata* Noodt, 1958; *H. hamatus* Jakobi, 1954; *H. hamondi* Hicks,

1975; *H. heejinae* Bang, Lee & Lee, 2011; *H. lalanai* Varela & Ortiz, 2008; *H. letovae* Huys, 1990; *H. littoralis* (T. & A. Scott, 1893); *H. livingstoni* Apostolov & Pandourski, 2001; *H. longisetigera* (Klie, 1950); *H. manifera* (Wilson, 1932); *H. mendax* (Klie, 1939); *H. minuta* (Boeck, 1873); *H. murmanica* Letova, 1982; *H. norvegica* Drzycimski, 1968; *H. oculata* (Gurney, 1927); *H. pauciseta* (Lang, 1936); *H. serratula* Mielke, 1981; *H. stroemii* (Baird, 1834); *H. s. brevicaudata* (Monard, 1926); *H. s. paraminuta* Noodt, 1955; *H. s. stroemii* (Baird, 1834); *H. tenuispina* (Lang, 1934); *H. uncinata* (Czerniavski, 1868); *H. variabilis* Lang, 1965.

Species incertae sedis. *Cleta setigera* Kričagin, 1873; *Heterolaophonte australis* (T. Scott, 1912); *H. exigua* (T. Scott, 1912); *H. insignis* (T. Scott, 1914); *H. manifera sulamericana* Jakobi, 1954; *H. rottenburgi* (T. Scott, 1912); *Laophonte laurentica* Nicholls, 1939.

Species inquirendae. *H. curvata micarthros* Marcus & Por, 1960; *H. phycobates* (Monard, 1935); *H. pygmaea* (T. Scott, 1893); *H. tupitskyi* Chislenko, 1976; *Heterolaophonte sp.* Roe, 1960; *Heterolaophonte sp.* Wells, 1961; *Heterolaophonte sp.* Yoo & Lee, 1995.

Heterolaophonte uncinata (Czerniavski, 1868)

(Figs. 2–9)

Synonymy. *Cleta uncinata* Czerniavski, 1868, p 42, plate I, Figures 19–29.

Neotype designation. With the type materials lost, a neotype is designated here in order to clarify the taxonomic status of *H. uncinata*. Neotype is a female, collected on 10.09.2002 from Tirebolu Beach (St. 9), Giresun province, Turkey (41º00.249'N 38º48.473'E), dissected on eight slides (deposited in the NHMUK reg. no. 2014.1).

Material examined. St.9, one ♀ dissected on two slides (deposited in the NHMUK reg. no. 2014.2), two ♀, (deposited in the NHMUK reg. no. 2014.3–4), one adult ♂ dissected on eight slides (deposited in the NHMUK reg. no. 2014.5), one ♂ (deposited in the NHMUK reg. no. 2014.6); St.1, two ♀ (16.09.2001), three ♀ (10.08.2002); St.5, two ♀ and two ♂ (09.07.2001), two ♀ (13.09.2002); St.6, two ♀, two ♂ (13.09.2002); St.7, one ♀ (11.09.2002); St.10, one ♀, two ♂ (10.09.2002); St.15, one ♀ (14.04.2007); St.17, five ♀ (27.11.2007); St.20, four ♀ (07.04.2007) deposited in the collection of Zoological Museum at the Biology Department of Mersin University. Undissected materials are whole mounted on slides.

Redescription of female (based on neotype). Body (Fig. 2A, B). Total body length 518–656 µm (n = 10, mean = 563 µm). Largest width at posterior margin of cephalic shield. Urosome gradually tapering posteriorly. All somites covered with hardly visible minute spinules (as arrowed in Fig. 2A). Rostrum triangular (Fig. 2A), with pair of sensilla near apex; midventral tube-pore in subapical position; completely defined at base. Cephalothorax with posterior margin fringed with small spinules; pleural areas well developed and rounded with lobate posterolateral angles; and pattern of sensillae as in Fig. 2A, B. All prosomites without defined hyaline frills; posterior margins fringed with small spinules. Urosome (Fig. 2A, B) 5-segmented, comprising P5-bearing somite, genital double-somite and 3 free abdominal somites. Ventral surface of abdominal half of genital double-somite, second and third abdominal somites with rows of spinules (Fig. 3A). Hyaline frills of urosomites not distinct. Genital double-somite with transverse surface ridge dorsally and laterally (Fig. 2A, B), 2 pairs of pores located ventrally in the middle; completely fused ventrally (Fig. 3A). Genital field (Fig. 3A) with medium-sized copulatory pore located in median depression; gonopores fused medially forming single genital slit covered on either side by operculum derived from sixth leg; P6 with small protuberance bearing 2 bare setae. Anal somite with 2 pairs of ventral tube-pores (Fig. 3A); anal operculum flanked by pair of sensilla; anal opening bordered by well-developed frill bearing long setular extensions (Fig. 3B).

Caudal rami (Fig. 3A, B) short, cylindrical, slightly longer than wide; each ramus with 7 bare setae: seta I inserted subventrally, bare and shortest; setae II and III bare; setae IV and V fused basally, and with fracture planes; seta VII tri-articulate at base; each ramus with small spinules on dorsal surface; additional spinular ornamentation present around ventral and dorsal distal margins; long tube-pore present near ventral distal margin.

Antennule (Fig. 4A, B) seven-segmented; spinular ornamentation on segments 1–4 as figured. Segments 1–2 without spinous processes. Segment 4 with aesthetasc fused basally to seta and arising from distinct pedestal. Armature formula: 1-[1], 2-[8], 3-[7], 4-[1 + (1 + ae)], 5-[1], 6-[2], 7-[7 + acrothek]. Apical acrothek consisting of small aesthetasc fused basally to 2 naked setae.

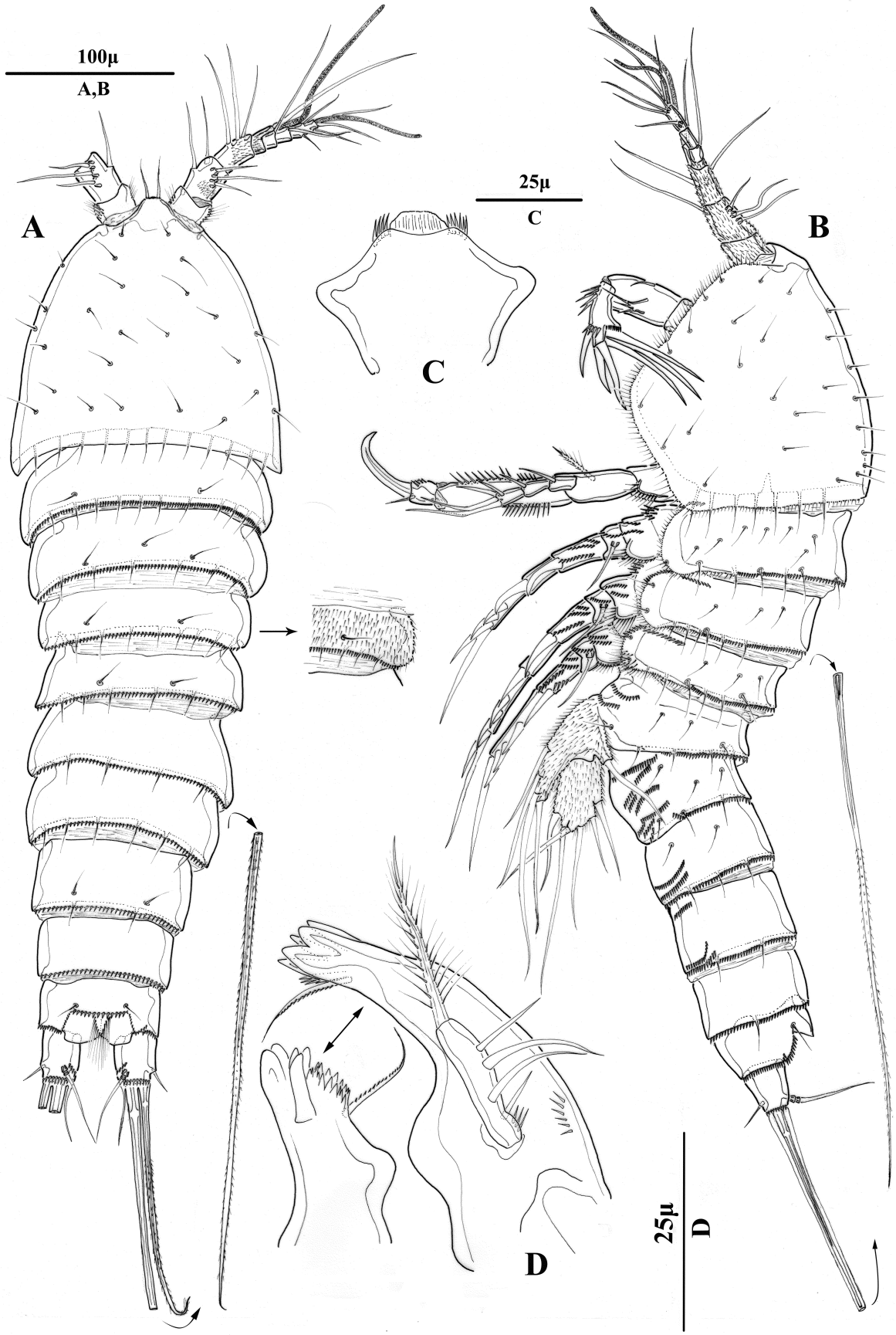

FIGURE 2. *Heterolaophonte uncinata,* ♀. A, habitus, dorsal (arrow indicates ornamentation of body); B, habitus, lateral; C, labrum, anterior; D, mandible, ventral.

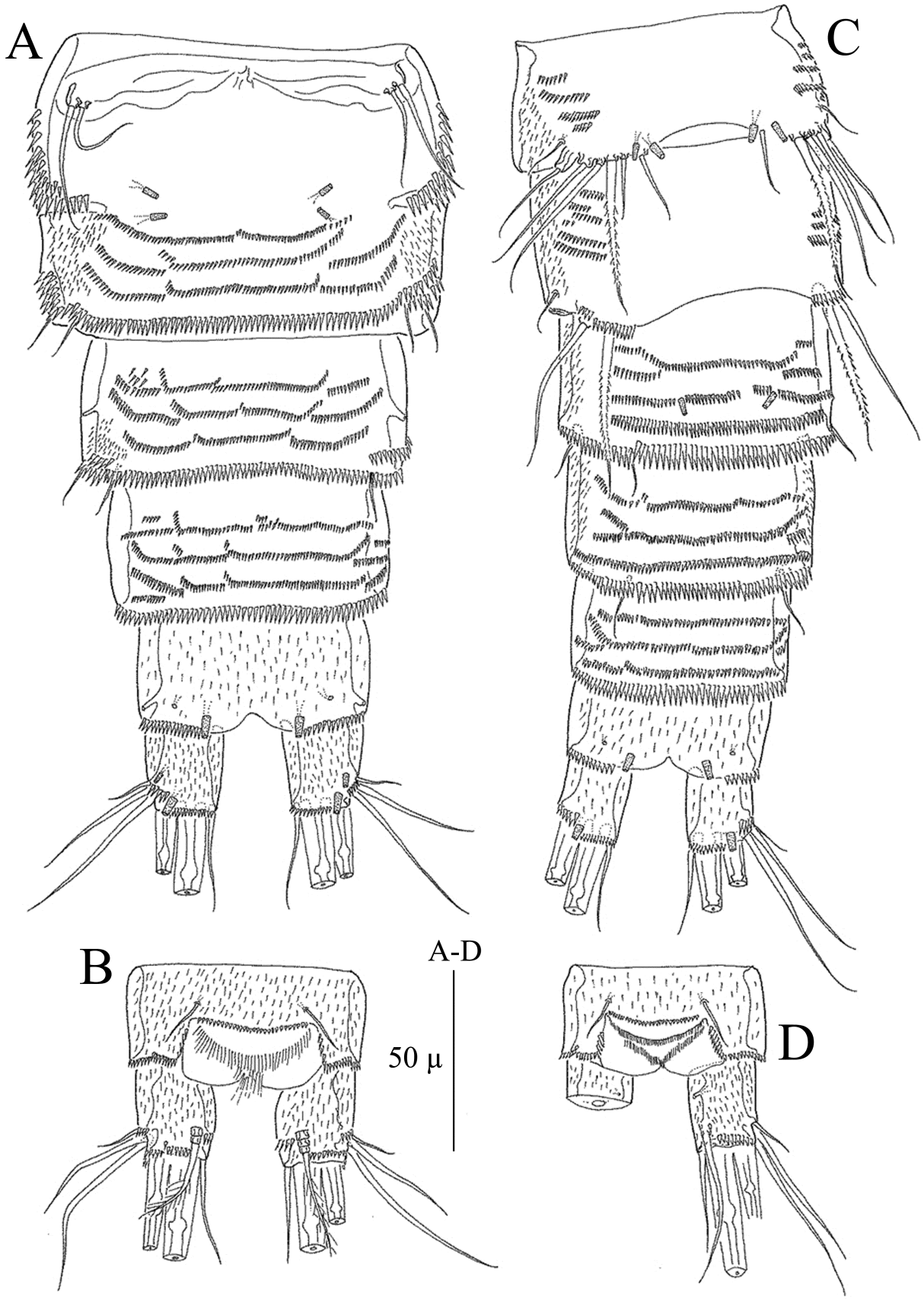

FIGURE 3. *Heterolaophonte uncinata.* A, ♀ urosome and P6, ventral; B, ♀ anal somite and caudal rami, dorsal; C, ♂ urosome, P5 and P6; D, ♂ anal somite and caudal rami, dorsal.

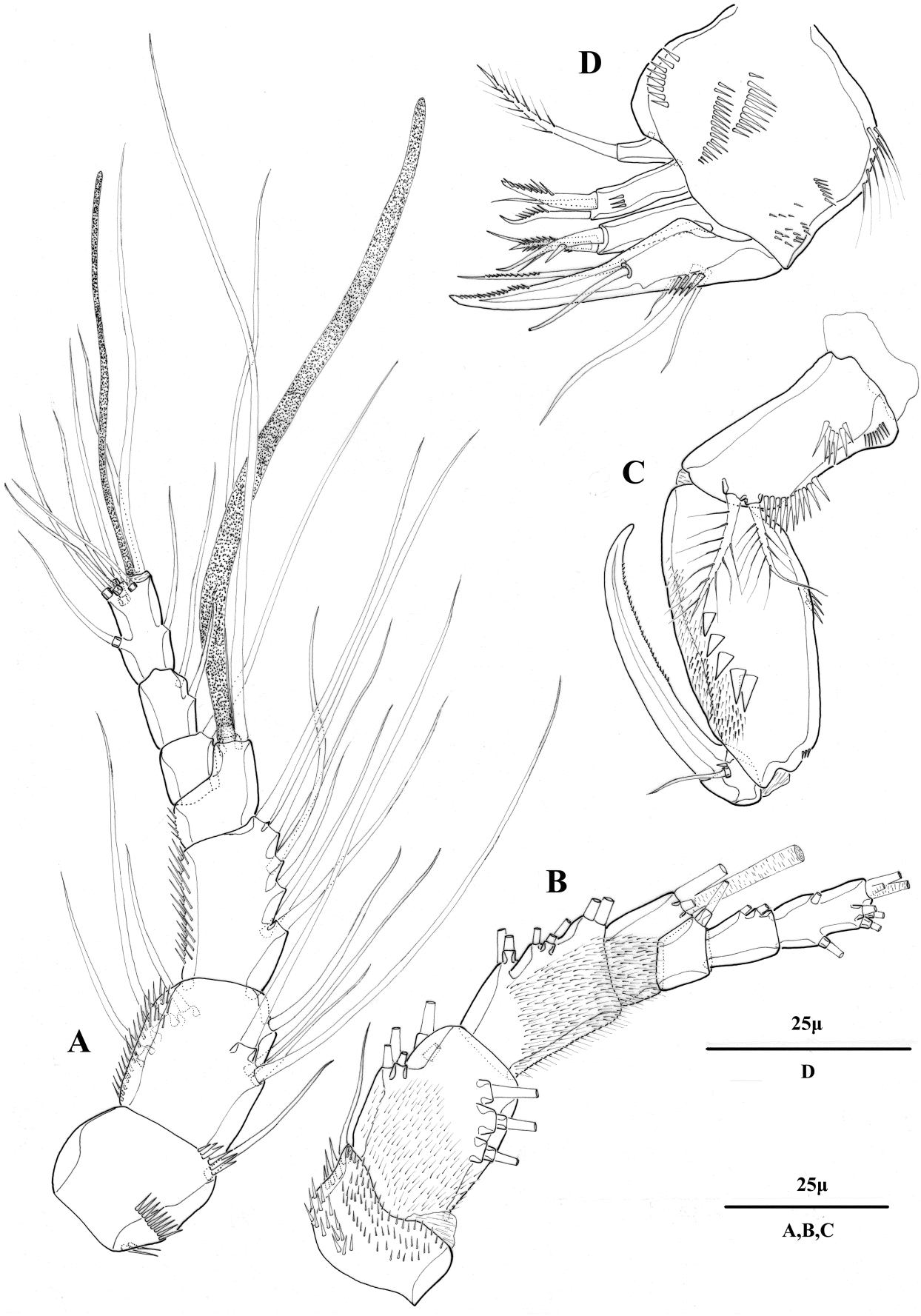

FIGURE 4. *Heterolaophonte uncinata,* ♀. A-B, antennule; C, maxilliped; D, maxilla.

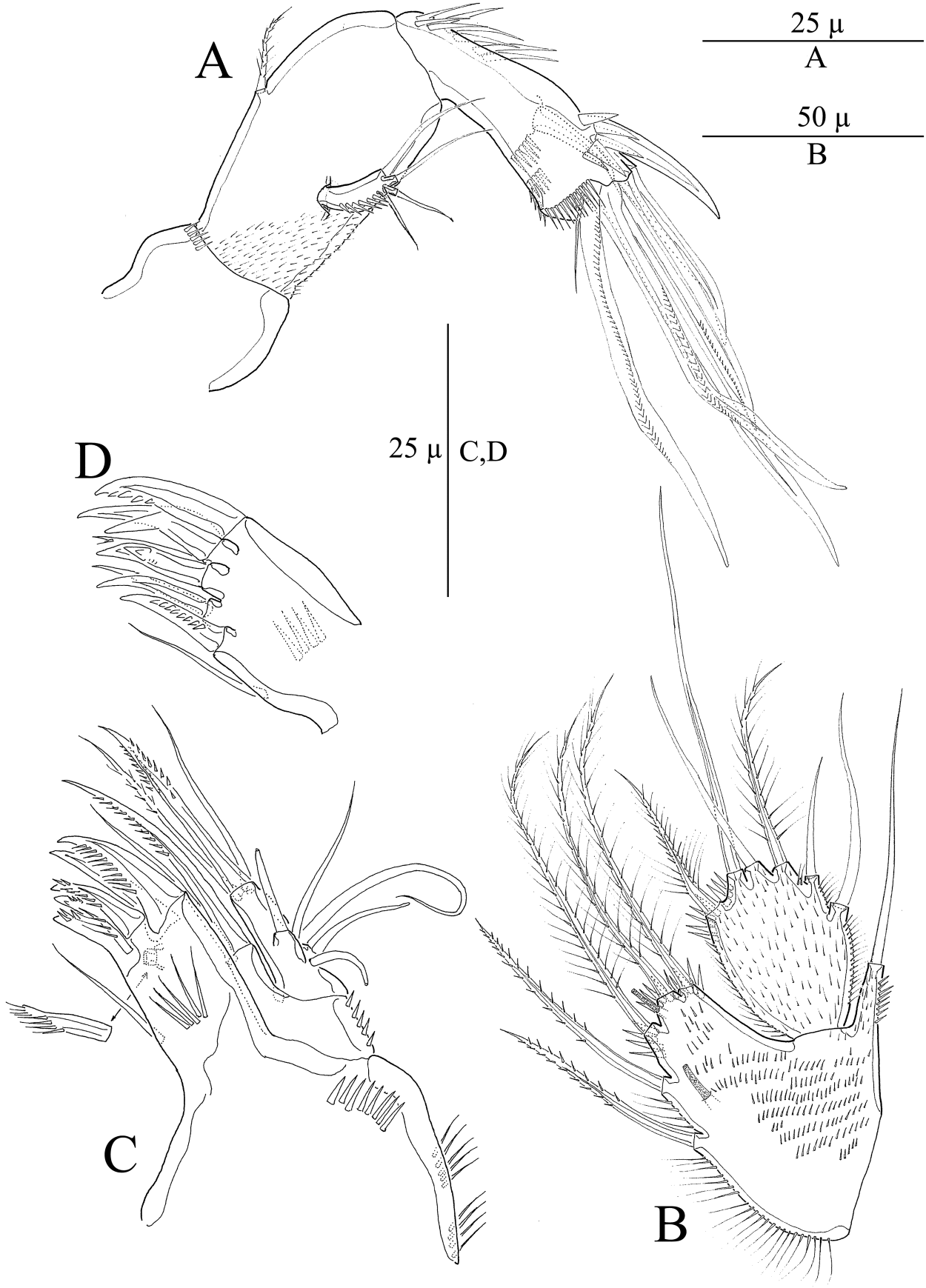

FIGURE 5. *Heterolaophonte uncinata,* ♀. A, antenna; B, P5, anterior; C, maxillule; D, maxillulary arthrite.

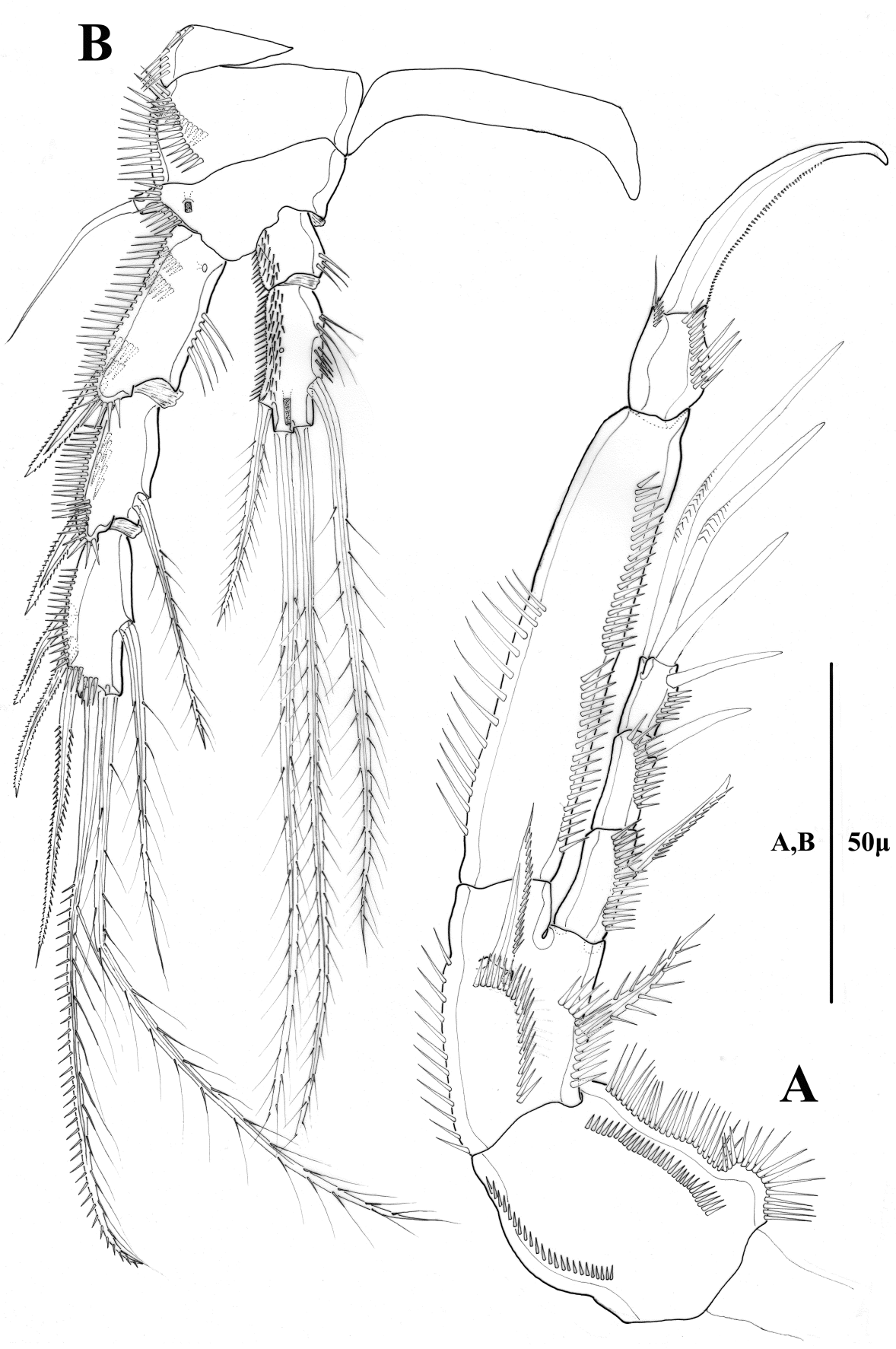

FIGURE 6. *Heterolaophonte uncinata,* ♀. A, P1, anterior; B, P4, anterior.

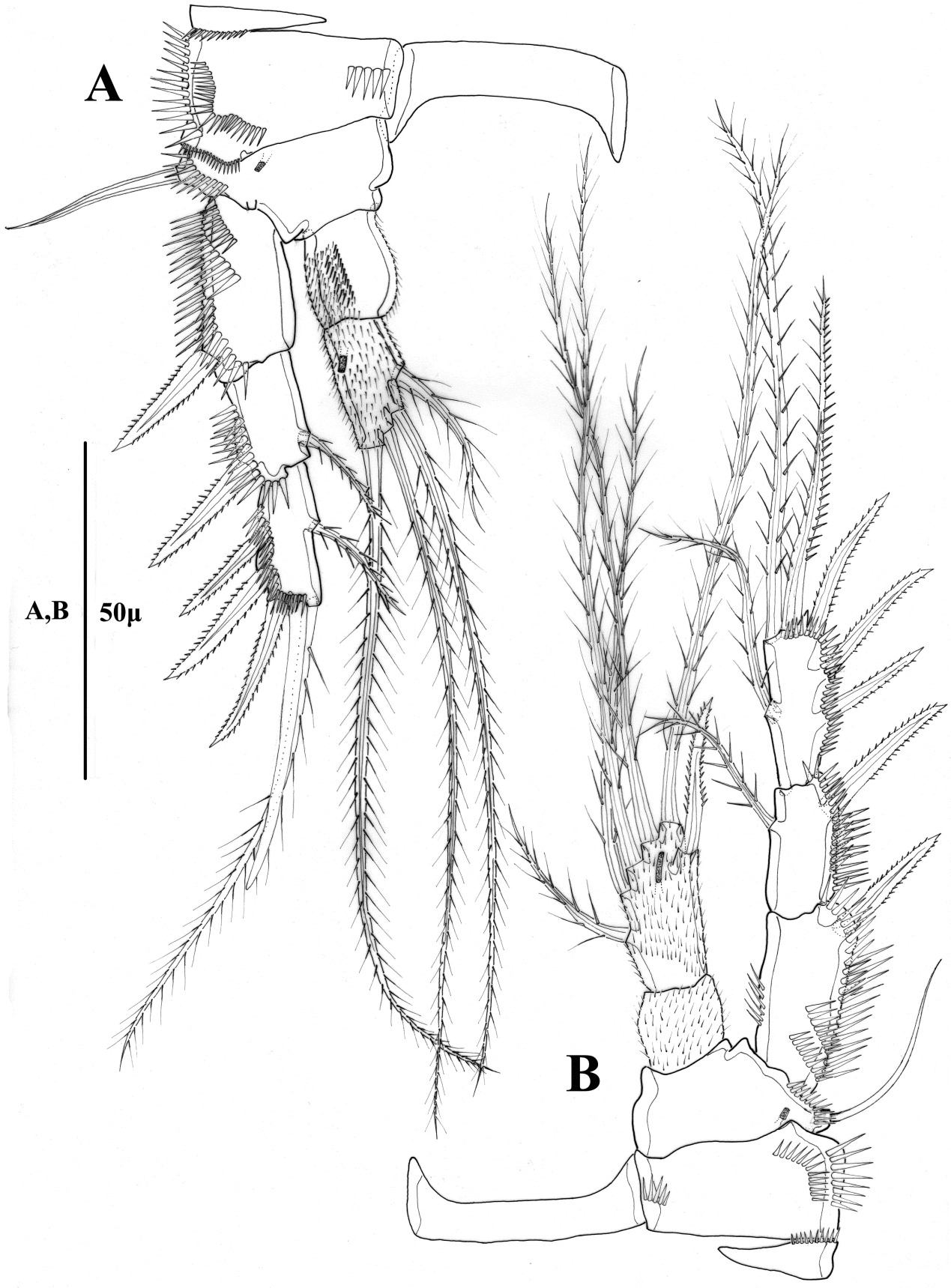

FIGURE 7. *Heterolaophonte uncinata,* ♀. A, P2, anterior; B, P3, anterior.

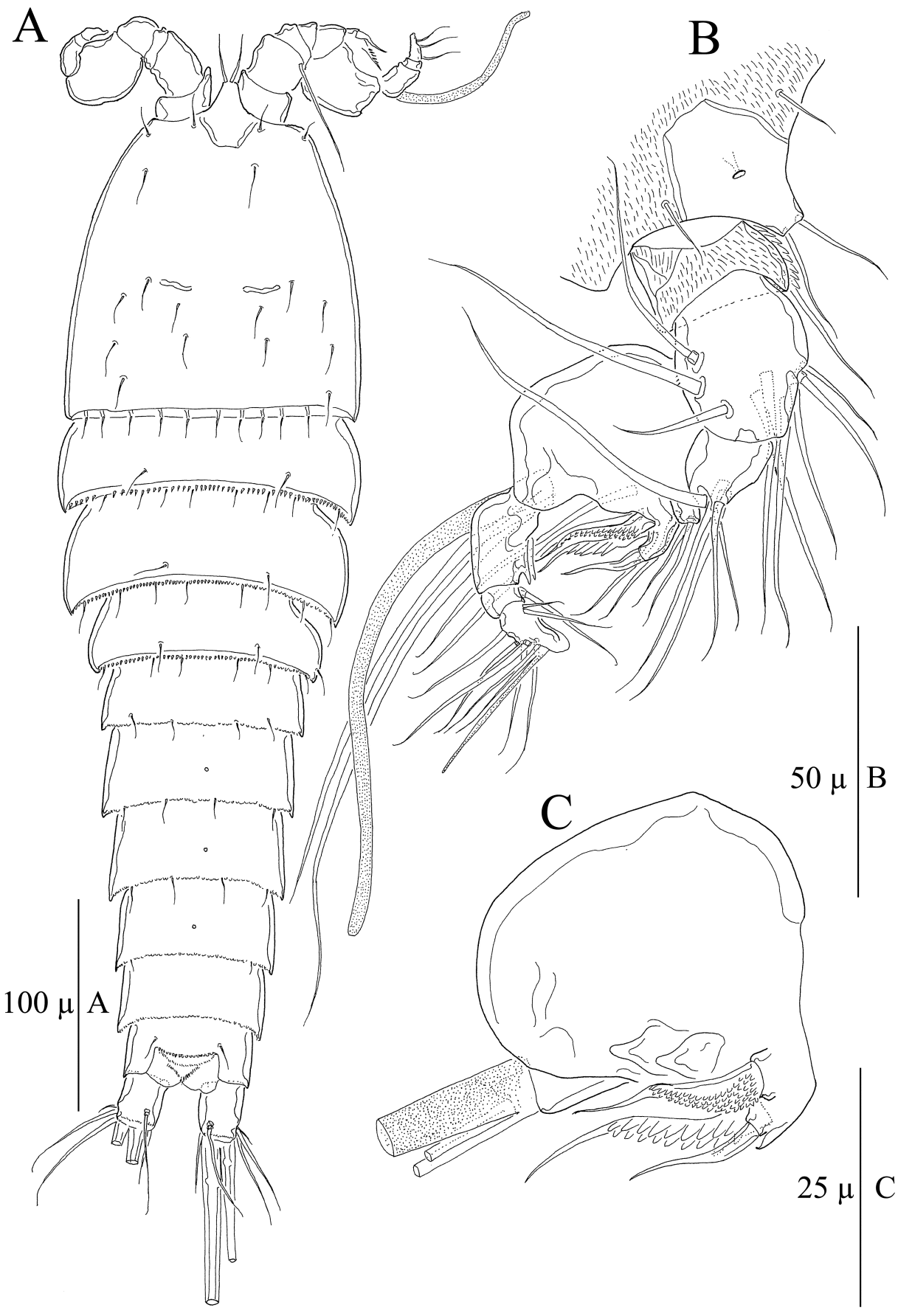

FIGURE 8. *Heterolaophonte uncinata,* ♂. A, habitus, dorsal; B, rostrum and antennule, dorsal; C, fifth antennulary segment.

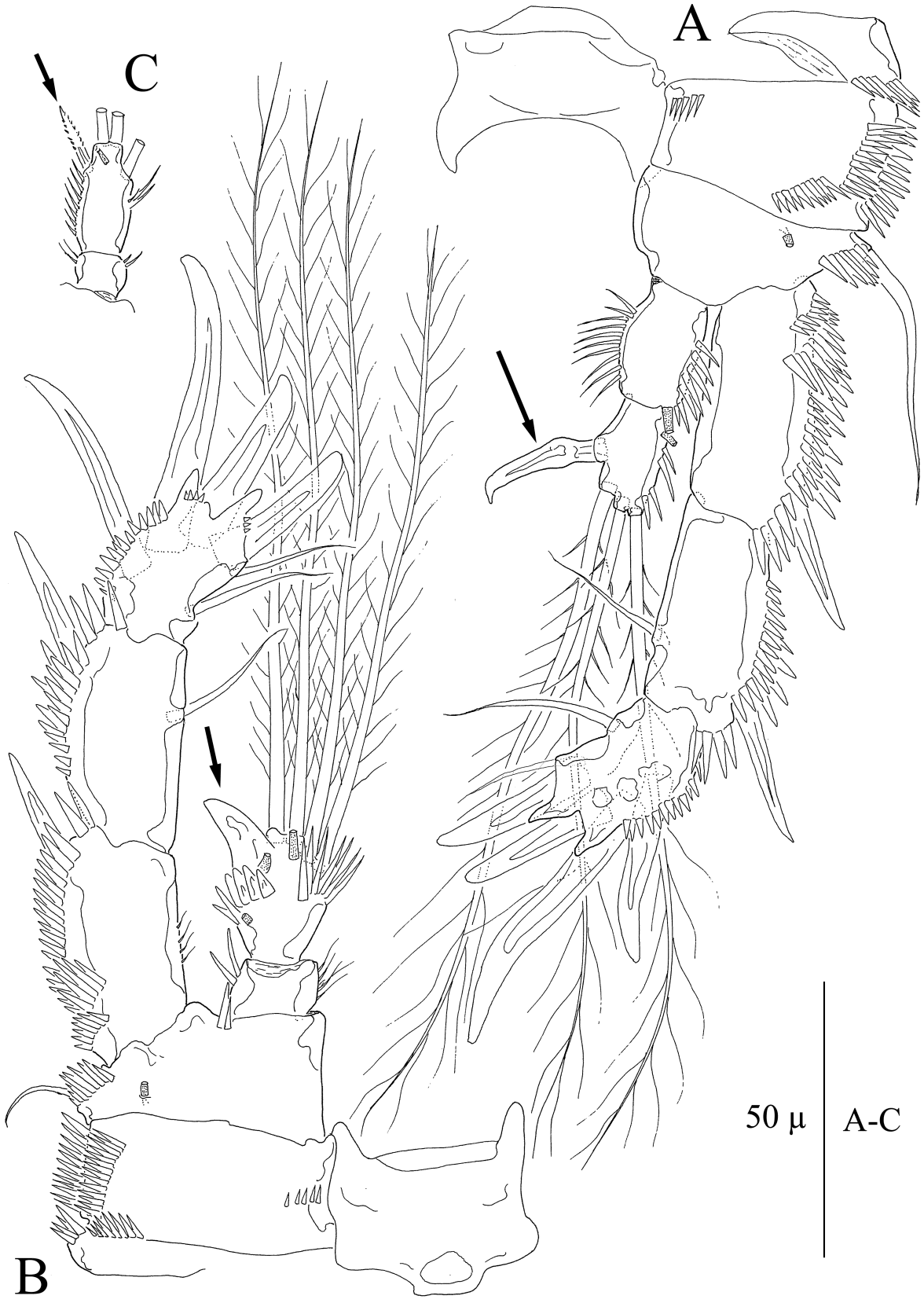

FIGURE 9. *Heterolaophonte uncinata,* ♂. A, P2, anterior (arrow indicates modified seta); B, P3, anterior (arrow indicates modified seta); C, P4 endopod, anterior.

Antenna (Fig. 5A). Three-segmented, comprising coxa, allobasis and free 1-segmented endopod. Coxa small, with row of small spinules. Allobasis not elongate; without distinct surface suture marking original segmentation; with 1 abexopodal bipinnate seta near middle, with patch of fine spinules proximally near base of exopod. Exopod very small, with 4 naked small setae (2 apically and 2 subapically); 1 row of coarse spinules on posterior surface. Endopod about as long as allobasis; lateral armature inserted in distal half, consisting of 1 seta flanked by 2 strong spines; apical armature consisting of 2 strong spines and 3 geniculate setae (one geniculate seta fused basally to a short seta). Endopod with 1 row of long spinules in proximal half and row of spinules subapically.

Labrum well developed; spinular ornamentation on anterior surface as in Figure 2C. Mandible (Fig. 2D) with well developed gnathobase bearing several multicuspidate teeth on distal margin as figured and 1 unipinnate seta at dorsal corner; palp elongate bearing 4 naked and 1 apical plumose seta, with spinules near base.

Maxillule (Fig. 5C, D); praecoxa with several spinules around outer margin; arthrite strongly developed, with 1 naked seta on dorsal surface and 8 spines/setae around distal margin; 1 transverse row of long spinules on posterior surface. Coxa with cylindrical endite bearing 1 naked seta and 1 curved pinnate spine; with 1 spinular row on outer margin. Basis with cylindrical endite bearing 1 naked, 1 plumose setae and 1 pinnate spine. Endopod completely incorporated into basis, forming cluster of 2 tube-like and 1 naked setae; exopod 1-segmented but fused to basis, with 1 tube-like and 1 naked setae.

Maxilla (Fig. 4D). Syncoxa with 3 endites; with several rows of spinules on posterior surface as figured; praecoxal endite small and cylindrical, with 1 plumose seta; both coxal endites with 2 pinnate setae and 1 naked seta; proximal coxal endite with 1 row of spinules posteriorly. Allobasis drawn out into 1 strong, slightly curved, distally pinnate claw; accessory armature consisting of 2 setae. Endopod represented by 3 naked setae, surrounded by spinules near base.

Maxilliped (Fig. 4C). Syncoxa elongate, with 2 plumose setae and 3 rows of spinules. Basis with row of strong spinules along palmar margin next to patch of fine spinules. Endopod drawn out into 1 long distally pinnate claw; with 1 short accessory seta anteriorly.

Swimming legs. P1–P4 (Figs. 6A, B; 7A, B), with wide naked intercoxal sclerites and triangle praecoxae. Praecoxae with spinules along outer margin. Exopods 3-segmented, endopods 2-segmented.

P1 (Fig. 6A). Coxa large; with 2 spinular rows on anterior surface and 1 spinular row along outer margin. Basis with strong unipinnate seta near insertion of endopod, long spinules along inner margin, 1 spinular row on anterior surface and 1 bipinnate spine and 1 spinular row along outer margin. Exopodal segments with spinules along outer margins. Exp-1 with 1 bipinnate spine; exp-2 with 1 naked outer spine; exp-3 with 2 naked outer spines and 2 geniculate apical setae. Enp-1 about 4.5 times as long as wide, and about twice as long as exopod, with long spinules along proximal half of inner margin, and with spinules along outer margin; enp-2 with 1 strong, minutely denticulate claw, and 1 small naked seta; several spinules along outer margin and around inner distal corner.

P2–P4 (Figs 6B; 7A, B). Coxae and bases with spinular rows along outer margin, on anterior and posterior surfaces; basis with tube-pore on anterior surface (P2,P3); exopods with 3 segments, exopodal segments with similar width/length ratio; outer margin of basis with naked seta; exopodal and endopodal segments with elaborate spinular/setular ornamentation as figured. P2–P4 enp-1 shorter than enp-2 (P2 enp-1 as long as enp-2) and without seta; enp-2 with tube pore. Spine and setal formulae of swimming legs as follows:

	Exopod	Endopod
P2	0.1.123	0.220 [0.220 ♂]
P3	0.1.123	0.321 [0.220 ♂]
P4	0.1.123	0.121

Fifth pair of legs (Fig. 5B). Baseoendopods not fused medially. Exopod and baseoendopod discrete, each with pattern of spinules on anterior surface as figured. Baseoendopod forming, outer setophore bearing basal naked seta; with 2 tube pores on anterior surface; endopodal lobe extending middle of exopod, with 2 apical and 3 medial bipinnate setae, two proximal setae with small pinnules. Exopod with 2 plumose terminal setae, 2 naked terminal setae and 2 subapical outer naked setae.

Redescription of male (based on material from St.9). Body (Fig. 8A). 495–574 μm (n = 5; mean 524 μm). Largest width at posterior margin of cephalic shield. Urosome narrower than prosome. Prosome (Fig. 8A) 4-

segmented, comprising cephalothorax and 3 free pedigerous somites. Free pedigerous somites with spinulate posterior margin; whole surface covered with tiny spinules as in ♀. Rostrum, antenna, mouth parts and P1 as in female. Urosome 6-segmented (Fig. 8A), comprising P5-bearing somite, genital somite and 4 abdominal somites, ornamented with spinular rows ventrally as figured. All urosomites with surface ornamentation consisting of tiny spinules dorsally and laterally.

Antennule (Fig. 8B, C). Eight-segmented, subchirocer. Segment 1 covered with groups of spinules along anterior margin as figured. Segment 5 swollen (Fig. 8B, C). Segmental homologies: 1-(I), 2-(II–VIII), 3-(IX–XII), 4-(XIII), 5-(XIV–XX), 6-(XXI–XXII), 7-(XXIII), 8-(XXIV–XXVIII). Armature formula: 1-[1], 2-[9], 3-[5], 4-[2], 5-[8 + 5 modified + (1 + ae)], 6-[1 + 2 modified spinous elements], 7-[1], 8-[7 + acrothek]. Apical acrothek consisting of aesthetasc and 2 naked setae.

Swimming legs P2–P4 (Fig. 9A, B, C) with 2-segmented endopods and 3-segmented exopods. Surface ornamentation of intercoxal sclerites and protopods generally as in ♀. Many modifications on P2-P4 exopodal and endopodal segments. P2-P3 (Fig. 9A, B). All exopod segments more robust; inner setae and outer spines naked. Exp-3 curved and sclerotised, outer spines naked and robust, outer terminal seta modified into 1 naked spine, inner terminal setae reduced as 2 smaller naked setae.

P2 (Fig. 9A). Enp-1 elongated with long spinules along inner and outer margins, enp-2 with long spinules along outer margin, innermost seta transformed into 1 naked spine (arrowed in Fig. 9A).

P3 (Fig. 9B). Enp-1 with long spinules along inner and outer margins. Enp-2 with long fine spinules along inner margin; with very stout spinular row near outer margin; with 3 tube-pores on anterior surface. Enp-2 produced distally into short, spiniform outer apophysis (homologous with outer spine of enp-2 in ♀, arrowed in Fig. 9B); innermost seta lost.

P4 (Fig. 9C). Enp-1 with 2 spinules on inner and outer distal margins. Enp-2 with spinules on inner and outer margins; inner seta reduced to 1 small spine (arrowed in Fig. 9C).

Fifth pair of legs (Fig. 3C). Baseoendopods fused medially, with setophore bearing outer naked basal seta and with 5 setae; with 2 pair of tube-pores.

Sixth pair of legs (Fig. 3C). Symmetrical; represented by 1 plate fused to ventral wall of supporting somite; outer distal corner produced into small process bearing several spinules at base, 1 bipinnate inner and 1 naked outer seta.

Variability. No significant variation was observed among the examined specimens.

Distribution. Based on the examined materials, it can be assumed that *H. uncinata* has a wide distribution both in the Black Sea and the Mediterranean Sea.

Remarks. *Heterolaophonte uncinata* was originally described as *Cleta uncinata* from Cape St. John in the Black Sea. Cape St. John (now more often called "Cape Monastery"), located in Yalta, in the Crimea peninsula (Czerniavski 1868) and it has been reported from few localities since then (Lang 1948; Bodin 1997). *Heterolaophonte uncinata* is one of the species of the genus *Heterolaophonte* which requires urgent redescription. Unfortunately the type material is lost (personal communication with Prof. Dr. Rony Huys) and therefore a neotype is designated here to help in solving the taxonomic problem surrounding *H. uncinata*. Unfortunately figures of the original description lack sufficient detail to make meaningful comparisons with the present redescription. On the other hand, the old figures prepared by Czerniavski (1868) can still provide us many surprising details which are overlooked even in some recent publications. For example, the structure of the modified inner spine on P2 enp-2 of the male was well documented and figured. We believe that structure of this modified spine is a diagnostic feature for *H. uncinata* (arrowed in Figure 9A) and provides strong support that the redescribed specimens are conspecific with Czerniavski's specimens.

There is some significant degree of variation among some previous reports (Petkovski 1954; Marcus & Por 1960; Apostolov & Marinov 1988). Petkovski (1954) recorded *H. uncinata* from the Adriatic, but this species cannot be attributed to *Heterolaophonte* as it has very unusual characteristics. For example, P4 exp-2 has an abnormal process terminally carrying a plumose seta on the second exopodal segment; this is not found in any harpacticoid species. Apostolov & Marinov (1988) provided a supplementary description of *H. uncinata* from the Black Sea. According to Apostolov & Marinov (1988) the first seta on the plate of male P5 exopod is longer than the second seta, and the third seta is given as very long. In the present description of *H. uncinata* the first outer seta is shorter than the second seta, and the third seta is shorter than the second. The first inner lateral seta of P5 endopod lobe is given as naked but it is pinnate in the present specimen. The unipinnate spine of P1 basis was possibly overlooked by Apostolov & Marinov (1988). Another report of *H. uncinata* from the Black Sea (Yalta,

Crimea) was provided by Marcus & Por (1960). But this report almost certainly represents a different species since it has 5 setae/spines on P2-P4 exp-3 of the female instead of 6 setae/spines in the present redescription, and also has 5 setae/spines on P2-P3 exp-3 and 4–5 setae/spines on P4 exp-3 of the male. In conclusion, the variation among previous *H. uncinata* reports (Petkovski 1954; Marcus & Por 1960; Apostolov & Marinov 1988) is noteworthy. It can be speculated that *H. uncinata* may well be a species complex in which each population can only be separated from each other by the detailed comparisons.

Heterolaophonte curvata (Douwe, 1929)

(Figs. 10–21)

Synonymy. *Laophonte curvata*, Douwe (1929), p. 286, figs. 4–9.

Neotype designation. With the type materials lost, a neotype is designated here in order to clarify the taxonomic status of *H. curvata*. Neotype is a female, collected on 10.09.2002 from a beach in Yaroz Feneri Village (St. 11), Trabzon province, Turkey (41º05.677'N 39º23.718'E), dissected on 8 Slides (deposited in the NHMUK reg. no. 2014.7).

Material examined. St.11 (10.09.2002), one ♀ and one ♂, each dissected on eight slides (deposited in the NHMUK reg. no. 2014.8-9); St.2, one ♀ dissected on four slides, four ♀, one ♂, (01.05.2001); St.4, three ♀, two ♂ (13.09.2002); St.7, three ♀ (11.09.2002); St.8, six ♀ (1 ♀, dissected on 1 slide) and one ♂ (11.09.2002), St.12, one ♀ (dissected on 2 slides), three ♂ (10.09.2002); St. 13, two ♀ (09.09.2002); St. 14, three ♀, one ♂ (14.09.2002); St. 16, one ♂ (29.11.2007); St. 18, one ♀ (26.11.2007); St. 19, two ♀, one ♂ (08.04.2007), one ♀ (25.11.2007); St.20, two ♀ (24.11.2007); St. 21, one ♂ (24.11.2007); St. 22, one ♀ (24.11.2007). All other materials are deposited in the collection of Zoological Museum at the Biology Department of Mersin University. Undissected materials are whole mounted on slides.

Redescription of female (based on neotype). Body (Fig. 10A, B). Total body length 686–706 μm (n = 20; mean = 694 μm). Shape, ornamentation and structure of body, rostrum and cephalothorax as in *H. uncinata*. Entire surface covered with tiny spinules (see insert on Fig. 10A). Rostrum triangular (Fig. 12A), with 1 pair of well-developed sensilla near apex; midventral tube-pore in subapical position; with transverse incomplete surface ridge dorsally indicating original articulation; with ovoid patch of fine spinules located centrally. All prosomites without defined hyaline frills; posterior margins fringed with small spinules. Urosomites (Fig. 11A) with several rows of spinules on ventral surface extending laterally (Fig. 10B). Genital double-somite with transverse surface ridge dorsally and laterally (Fig. 10A, B), 2 pairs of pores located medially; completely fused ventrally (Fig. 11A). Copulatory pore located in proximal depression; gonophores fused medially forming single genital slit covered on either side by operculum derived from sixth leg; P6 with small protuberance bearing 1 bare seta (Fig. 11A). Anal somite (Fig. 11A, B); anal operculum flanked by 1 pair of sensilla; anal opening bordered by 1 frill bearing fine setular extensions. Caudal rami (Fig. 11A, B). Divergent, cylindrical, about twice as long as wide; each ramus with 7 bare setae: seta I subventral, bare and shortest; setae II and III bare; setae IV and V fused basally, and with fracture planes; seta VII tri-articulate at base with spinular row near insertion. Each ramus covered with hardly visible spinules on dorsal surface; additional spinular ornamentation present around ventral and dorsal distal margins; long tube-pore present near ventral distal margin.

Antennule (Fig. 12B) 7-segmented; segmentation, setation and ornamentation as in *H. uncinata* except for 1 plumose seta on segment 2. Antenna (Fig. 17C); segmentation, setation and ornamentation as in *H. uncinata* except for allobasis with 1 transverse proximal spinular row near base of exopod. Mandible, maxillule, maxilla, maxilliped as in *H. uncinata*.

Swimming legs P2–P4 (Fig. 14B; 16A, B) with wide intercoxal sclerites bearing hardly visible spinules and with well developed praecoxae. Praecoxae with spinules along outer margin. Exopods 3-segmented, endopods 2-segmented.

P1 (Figs. 14A; 15A, B, C) with 2-segmented exopod. Ornamentation of intercoxal sclerite and praecoxae as in other swimming legs. Coxa large; with 3 spinular rows on anterior surface, inner and outer margins as figured. Basis with bipinnate seta near insertion of endopod; with spinular rows on anterior surface, along inner and outer margins; with bipinnate seta at outer margin. Exopodal segments with spinular rows as figured. Exp-2 (Figs. 14A; 15C) about twice as long as exp-1. Enp-1 about 5 times as long as width (Fig. 15A), and about 3 times as long as

exopod, with spinular row located medially on anterior surface; enp-2 with one strong, minutely denticulate claw, and 1 small naked seta (arrowed in Fig. 15B); several spinules along outer margin and around inner distal corner.

P2–P4 (Figs 14B; 16A, B). Coxae and bases with spinular rows along outer margin and on anterior surface; basis with tube-pore on anterior surface; outer margin of basis with bipinnate seta; exopodal and endopodal segments with elaborate spinular/setular ornamentation along outer margins as figured; outer half of endopod segments of P2-P3 covered with fine spinules. P3–P4 enp-1 shorter than enp-2, P3 enp-2 about as long as enp-1, P2-P4 enp-1 without seta; P2 and P4 enp-2 with tube pore located terminally on anterior surface. Spine and setal formulae of swimming legs as follows:

	Exopod	Endopod
P2	0.1.023	0. 211
P3	0.1.023	0. 221
P4	0.1.022 [0.1.022 ♂]	0. 020 [0.120 ♂]

Fifth pair of legs (Fig. 17B). Similar to that of *H. uncinata*. Exopod and baseoendopod each with pattern of spinules on anterior surface as figured. Baseoendopod with 3 tubepores on anterior surface; endopodal lobe extending to middle of exopod, with 2 apical and 3 medial bipinnate setae, outermost minutely pinnate seta shortest, 2 proximal setae minutely pinnate. Exopod with 6 setae (one of which naked).

Redescription of male (based on material from St.11). Body (Figs. 17A; 18A) similar to *H. uncinata*. Body length 638–670 μm (n=10; mean 650 μm). Rostrum narrower than female (Fig. 12C) with 1 pore (arrowed in Fig. 18B), surface with 1 group of spinules on anterior surface as figured . All urosomites with several spinular rows centrally, some rows extending laterally. Caudal rami as in female (Figs. 11C, D; 18A, D).

Antennule (Fig. 12C; 13A, B, C) 8-segmented; subchirocer with geniculation between segments 5 and 6. Segment 1 with spinules along anterior margin and covered with tiny spinules dorsally as figured. Segment 5 swollen with 1 robust spinulose seta swollen at base (Fig. 12C; arrowed in Fig. 13A) with 1 long aesthetasc (arrowed in Fig. 13C) and 1 semispinulose seta. Segment 6 with 2 modified spinous element (arrowed in Fig. 13B). Segmental homologies: 1-(I), 2-(II–VIII), 3-(IX–XII), 4-(XIII), 5-(XIV–XX), 6-(XXI–XXII), 7-(XXIII), 8-(XXIV–XXVIII). Armature formula: 1-[1], 2-[9], 3-[6], 4-[2], 5-[11 + 1 modified + (1 + ae)], 6-[2 modified spinous elements], 7-[1], 8-[7 + 1 modified + acrothek]. Apical acrothek consisting of 1 aesthetasc and 2 naked setae (Fig. 12C). Surface ornamentation of intercoxal sclerites and protopods of P1–P4 (Figs 16C; 19A, B) generally as in ♀. Many modifications on P1-P4.

P2 (Fig. 19A). Exopod segments more robust than female. Exp-3 more sclerotised, outer spines stouter and naked, innermost spine remarkably shorter and stouter (homologous to terminal bipinnate spine of female). Enp-1 terminally elongated as 1 apophysis carrying 1 pore at tip and with 1 group of spinules along inner and outer margins. Enp-2 with longer spinules along outer margin, terminal seta longer and bipinnate, proximal inner seta transformed into 1 naked spine (arrowed in Fig. 19A; indicated with upper right arrows in Fig 20A).

P3 (Fig. 19B). Exp-3 slightly curved and sclerotised, outer spines naked and robust (posterior fine spinular ornamentations only visible with SEM, arrowed in Fig. 20D), middle outer spine modified into 1 longer naked spine, outer terminal spine modified into 1 shorter naked spine. Enp-1 with long setules along inner margin. Enp-2 with long spinules along inner margin, outermost seta transformed into 1 apophysis (arrowed in Fig. 19B; indicated with lower left arrow in Fig. 20A), anterior surface with 2 stout spinules.

P4 (Fig. 16C). Inner seta of exp-2 minutely pinnate and smaller than that of female. Terminal inner spine of female reduced to 1 small naked seta. Enp-1 with 2 small inner spinules. Enp-2 ornamented with long spinules along outer margin and 1 patch of anterior minute spinules near base of tube pore; with small pinnate inner seta; terminal seta semispinulose about twice longer than outer terminal seta.

Fifth pair of legs (Fig. 11C). Baseoendopods fused medially (Figs. 11C; 18C), with setophore bearing outer naked basal seta; endopodal and exopodal lobes vestigial bearing 2 and 4 small naked setae respectively; with spinules and 1 tube-pore near base of setophore (indicated with upper arrow in Fig. 20B). Sixth pair of legs (Fig. 11C) symmetrical; represented by 1 plate fused to ventral wall of supporting somite (Figs. 11C; 18C); outer distal corner produced into small process bearing several spinules at base and 2 naked setae (indicated with lower arrow in Fig. 20B).

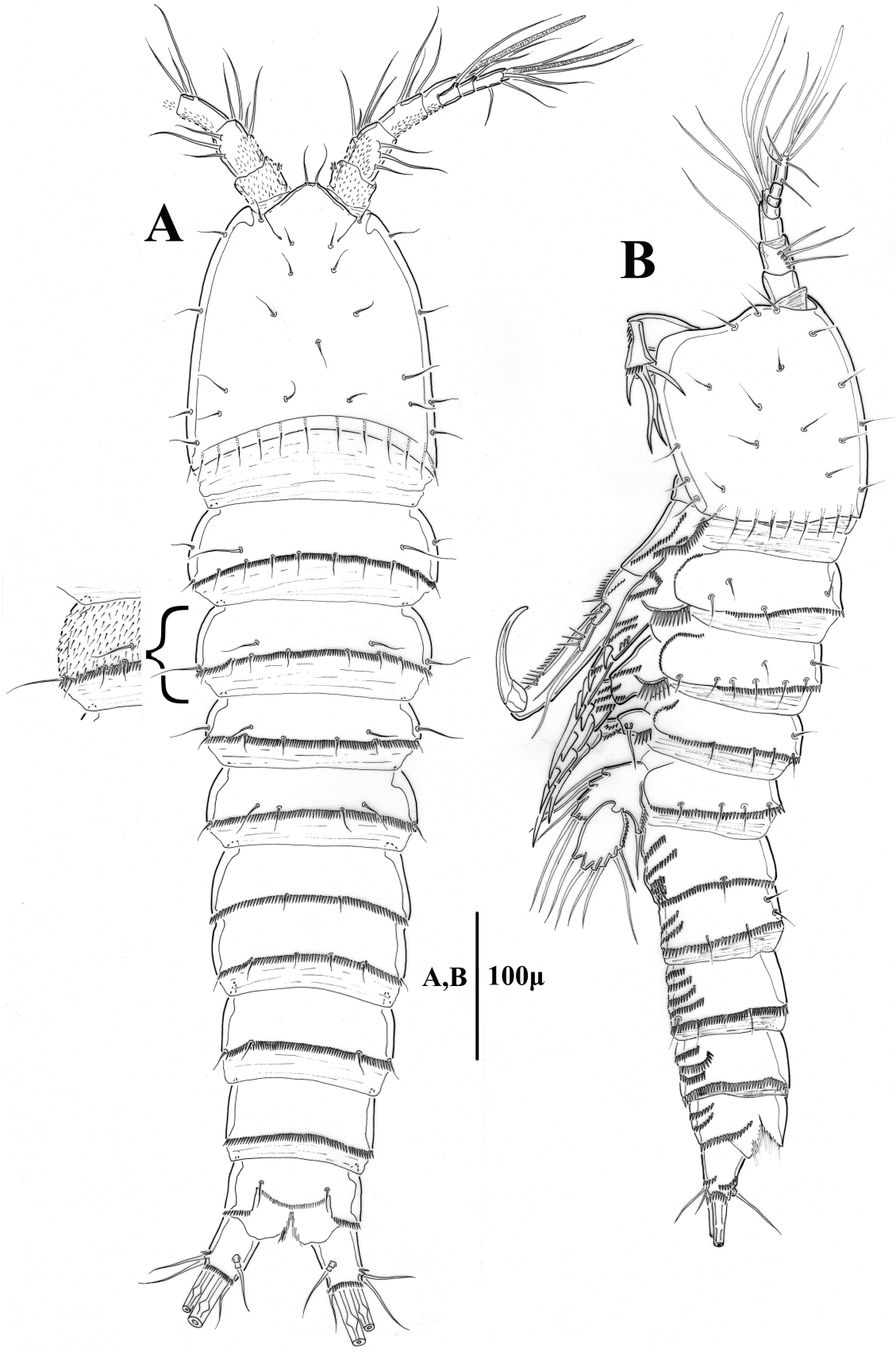

FIGURE 10. *Heterolaophonte curvata,* ♀. A, habitus, dorsal (insert indicates ornamentation on the body surface); B, habitus, lateral.

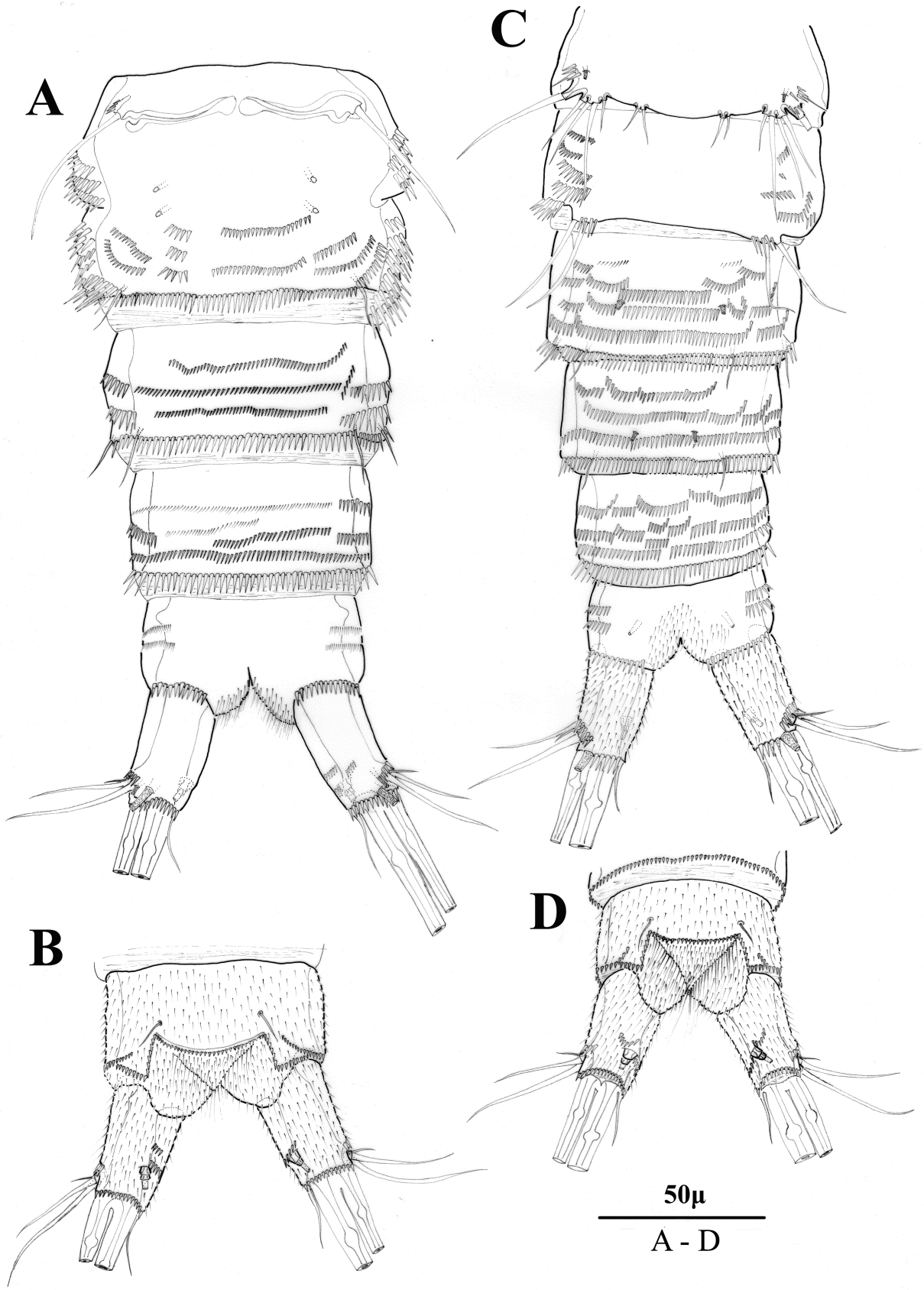

FIGURE 11. *Heterolaophonte curvata.* A, ♀ urosome, ventral; B, ♀ anal somite and caudal rami, dorsal; C, ♂ urosome, P5 and P6, ventral; D, ♂ anal somite and caudal rami, dorsal.

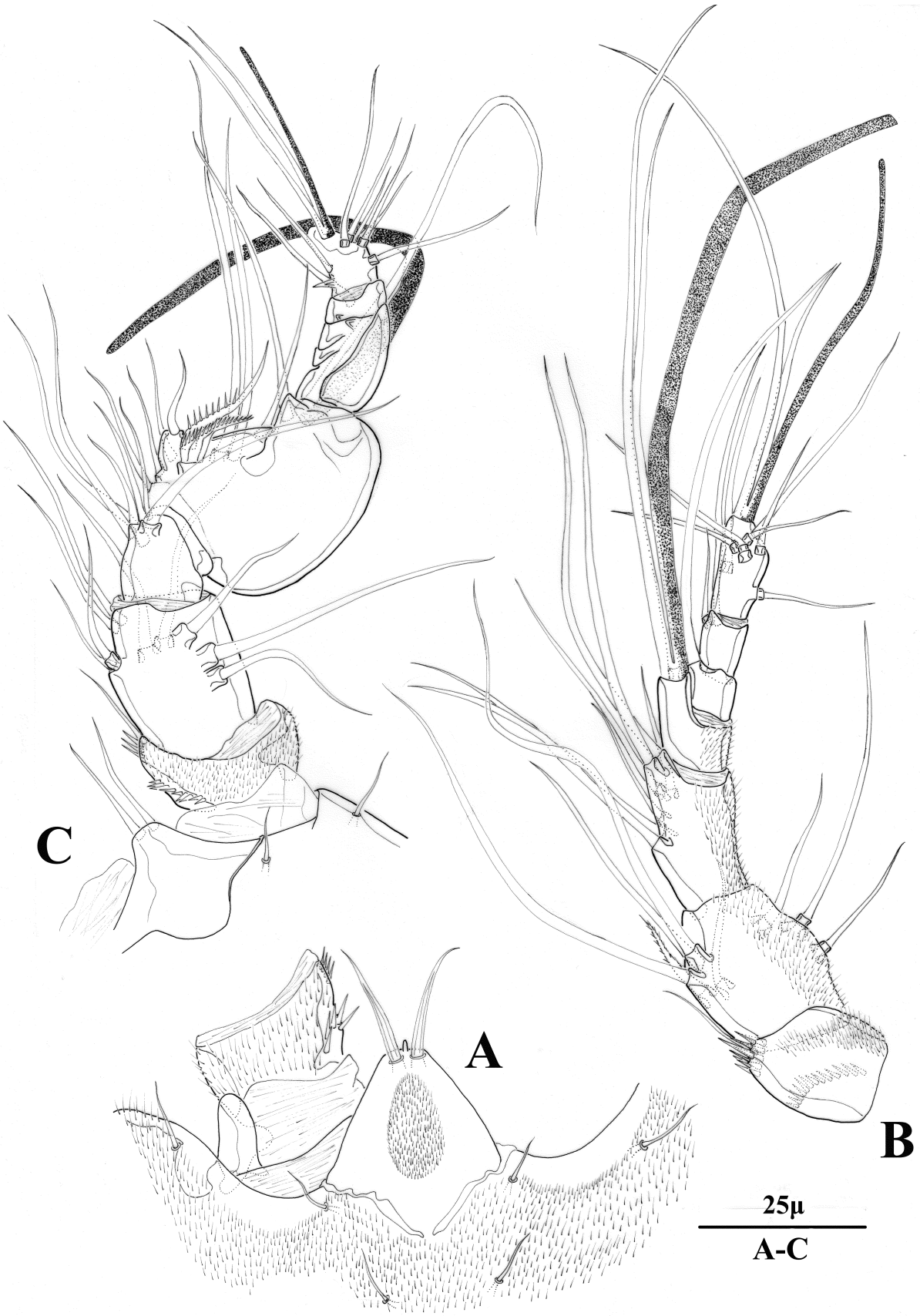

FIGURE 12. *Heterolaophonte curvata.* A, ♀ rostrum, dorsal; B, ♀ antennule, ventral; C, ♂ antennule and rostrum, dorsal.

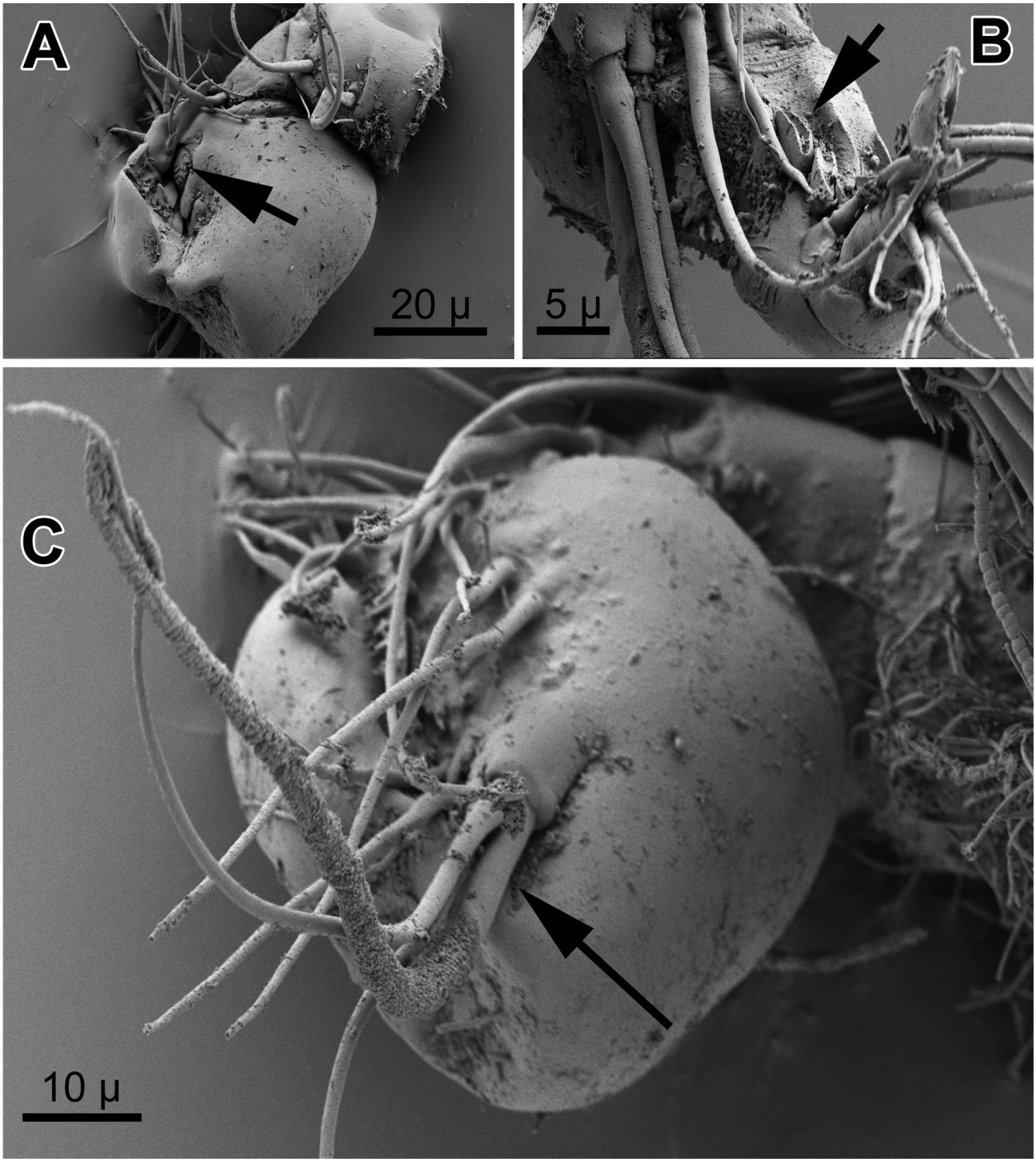

FIGURE 13. *Heterolaophonte curvata,* ♂. SEM micrographs of antennule. A, dorsal (arrow indicates the modified seta); B, distal portion (arrow indicates the modified elements on segment 5); C, swollen segment 5 (arrow indicates the aesthetasc).

Variability. No significant variation was observed among the examined specimens.

Distribution. Based on the examined materials and confirmed records, it can be assumed that *H. curvata* has a wide distribution both in the Black Sea and the Mediterranean Sea.

Remarks. *Heterolaophote curvata* was originally described from Bay of Cavaliere and Cette along the Mediterranean French coast by Douwe (1929). The present specimens differ from the original description in the presence of four setae (instead of one) on antennary exopod and in having one small inner terminal seta on the third exopodal segment of the male P3. But, it is highly possible that these setae have been overlooked by Douwe (1929). Further comparisons about the spinular ornamentation on the appendages cannot be made since the original

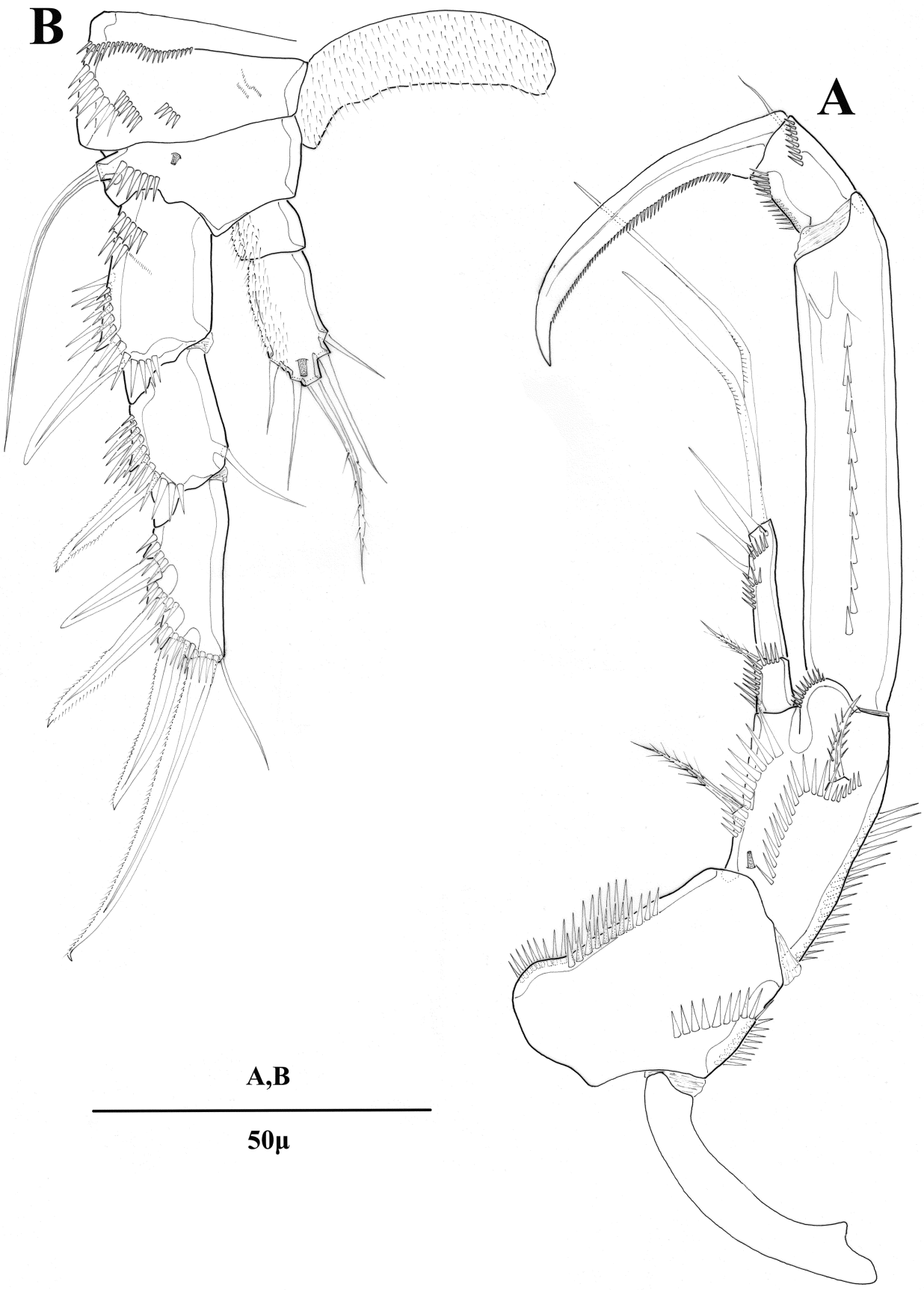

FIGURE 14. *Heterolaophonte curvata,* ♀. A, P1, anterior; B, P3, anterior.

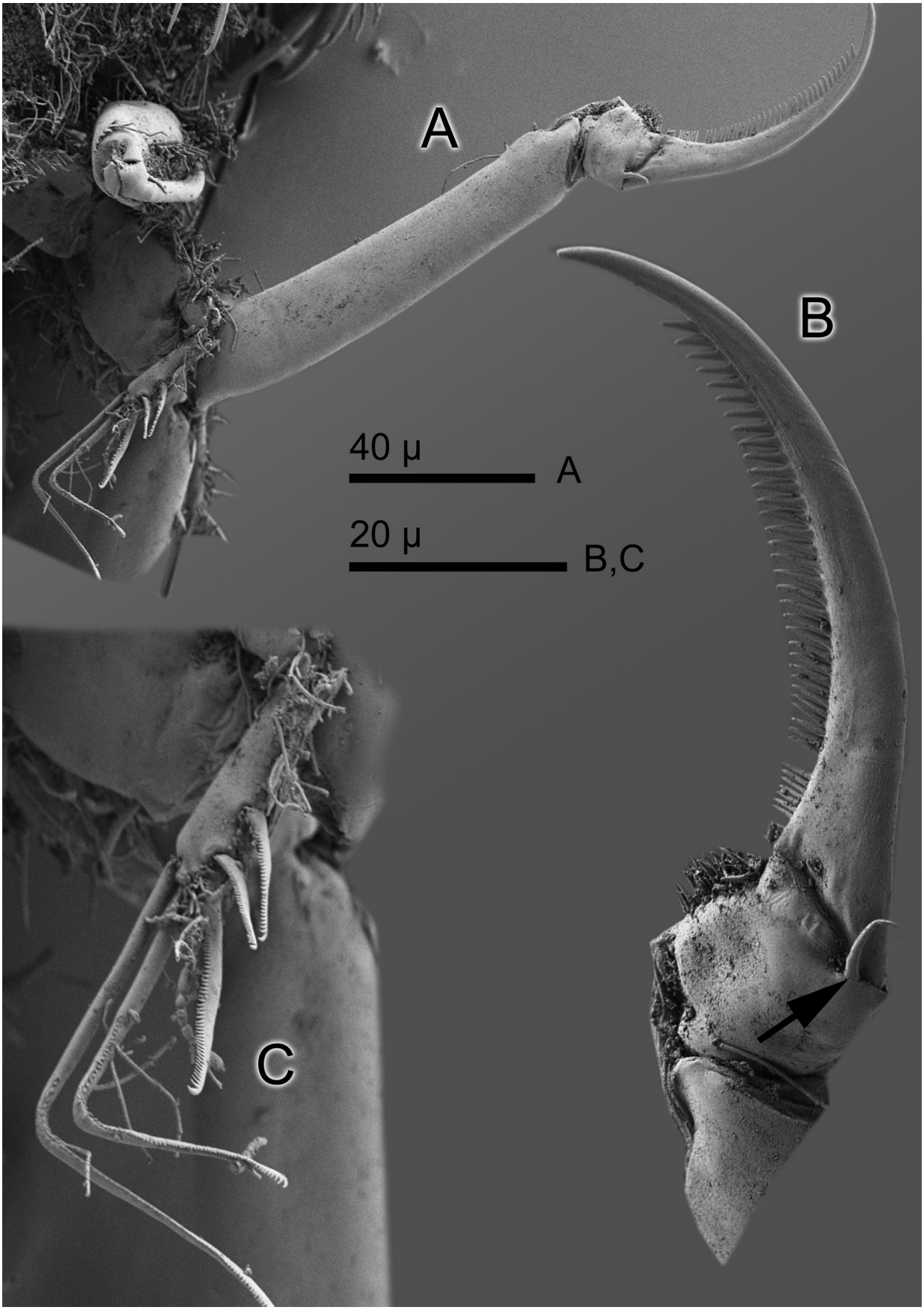

FIGURE 15. *Heterolaophonte curvata,* ♀. SEM micrographs of P1. A, exopod and endopod; B, terminal endopod segment and the distal claw (arrow indicates the small seta); C, exopod.

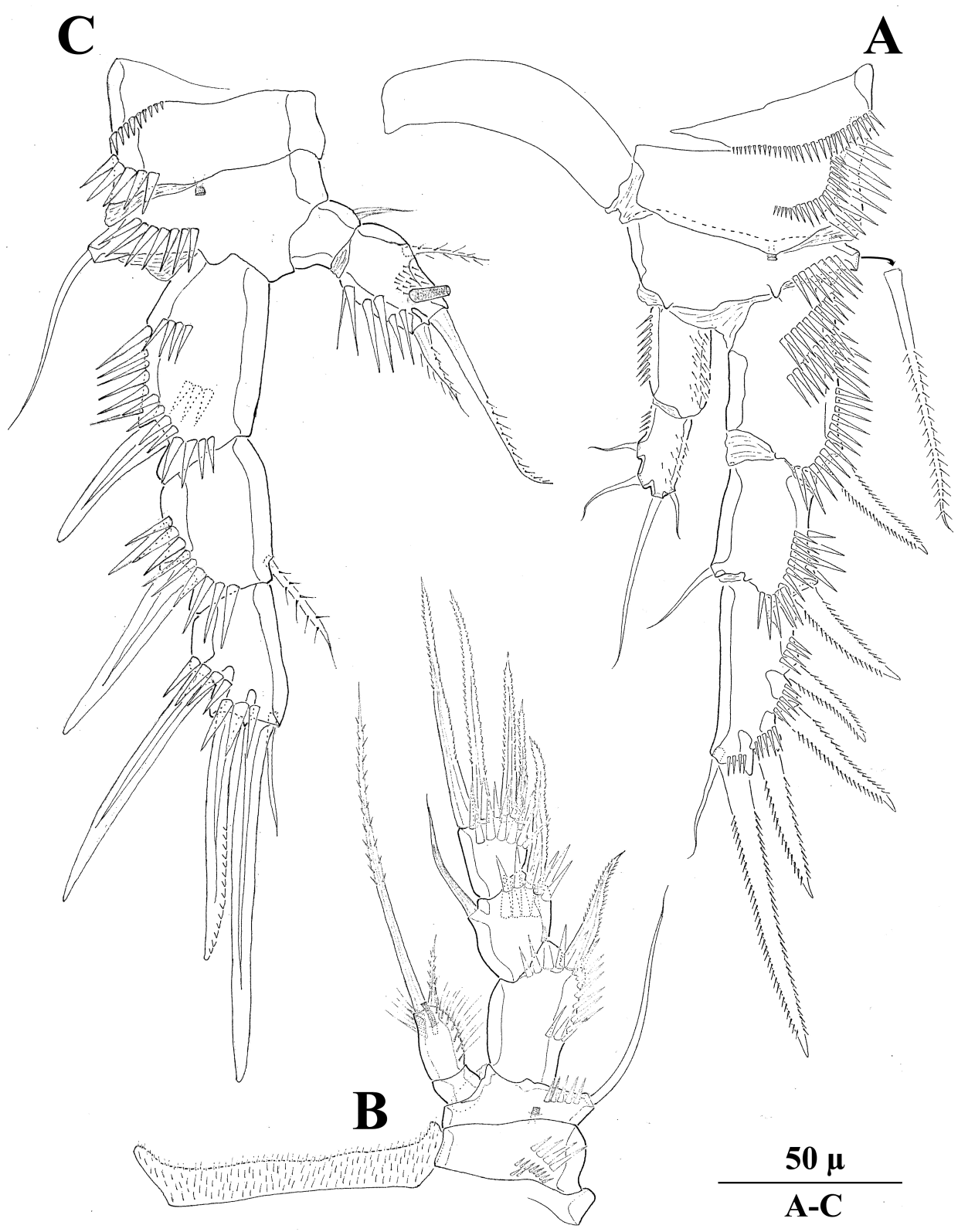

FIGURE 16. *Heterolaophonte curvata.* A, ♀ P2, anterior; B, ♀ P4, anterior; C, ♂ P4, anterior

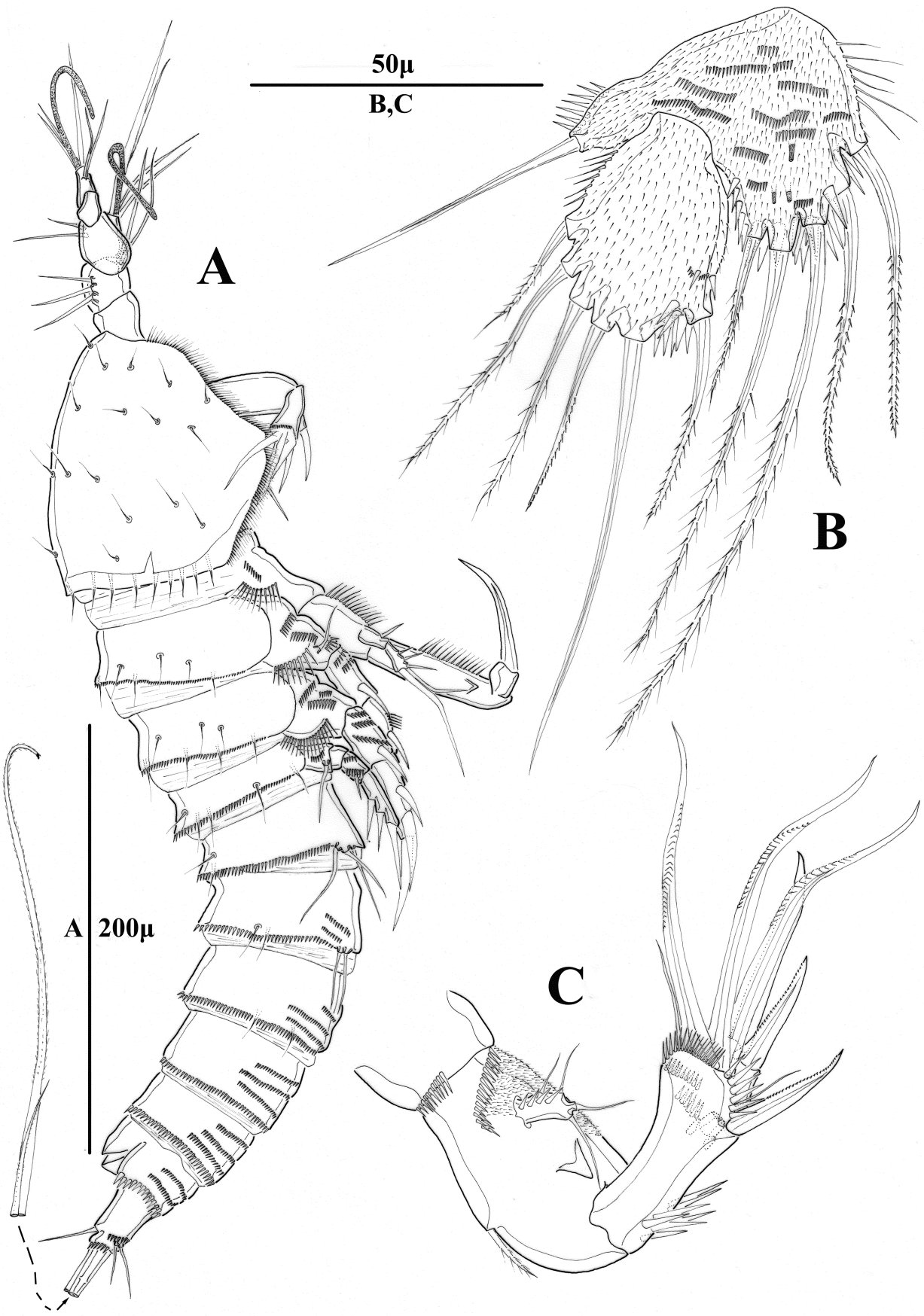

FIGURE 17. *Heterolaophonte curvata.* A, habitus, lateral ♂; B, ♀ P5, anterior; C, ♀ antenna.

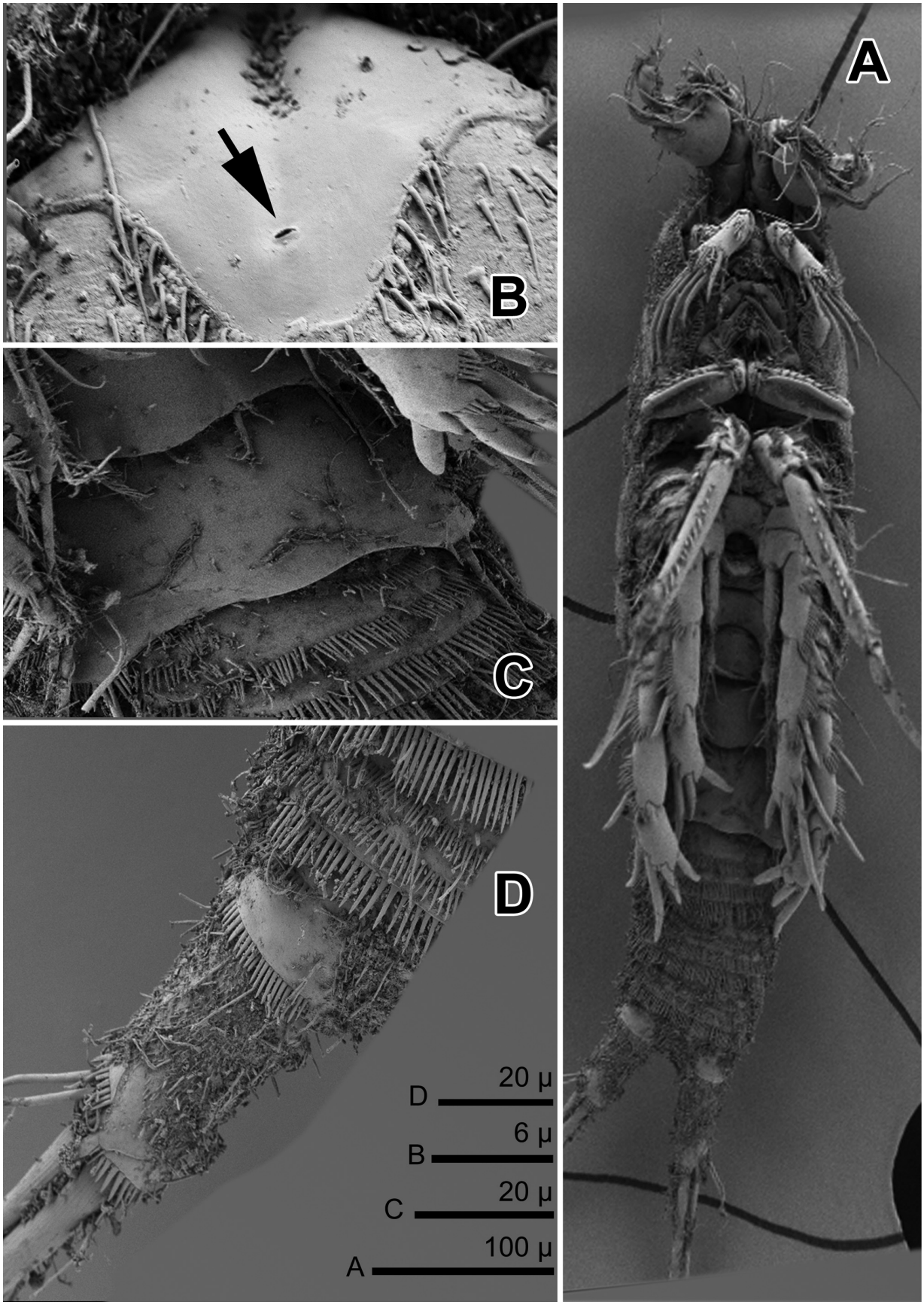

FIGURE 18. *Heterolaophonte curvata,* ♂. SEM micrographs. A, habitus, ventral; B, rostrum, dorsal (arrow indicates the pore); C, plate-like structure of P6; D, caudal rami, ventral.

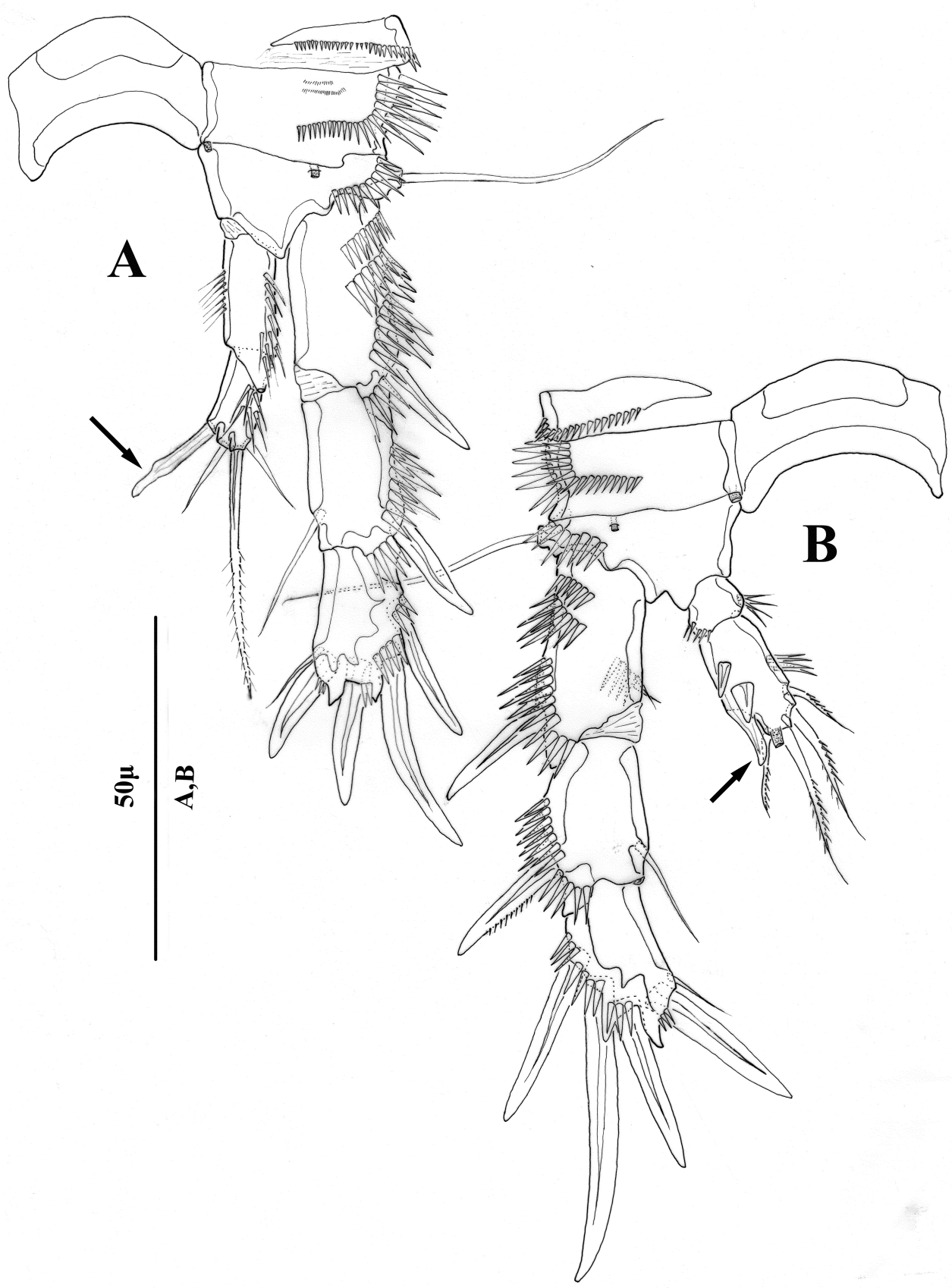

FIGURE 19. *Heterolaophonte curvata,* ♂. A, P2, anterior (arrow indicates modified seta); B, P3, anterior (arrow indicates apophysis).

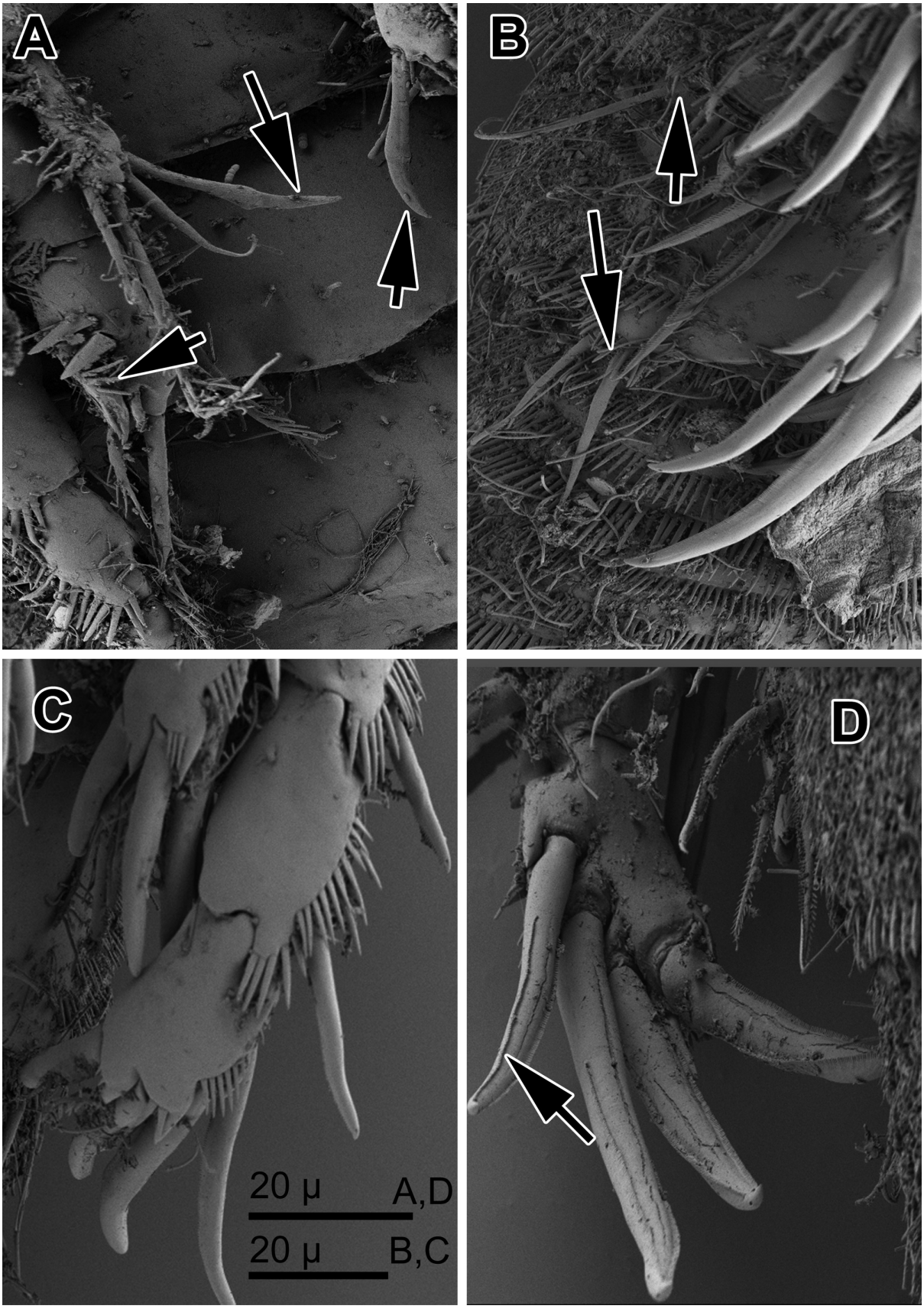

FIGURE 20. *Heterolaophonte curvata,* ♂. SEM micrographs. A, modified element on P2 endopod (indicated with 2 upper arrows) and straight, spiniform apophysis on P3 endopod surrounded at base by row of coarse spinules (indicated with a lower arrow); B, setal elements on P5 and P6 (indicated with arrows); C, P3 exopod, anterior; D, exopodal spines of P3 exp-3, posterior (arrow indicates the minute pinnules).

figures lack sufficient detail. On the other hand our specimens match well with the previous descriptions (Lang 1948; Apostolov 1990; Apostolov & Marinov 1988). But, the setation on the figures and the setal formulae given in the text by Apostolov & Marinov (1988) contain several discrepancies which might have resulted from typing errors. Therefore the population reported by Apostolov & Marinov (1988) from the Black Sea is accepted as conspecific with the present species presented herein.

The subspecies *H. curvata micrarthros* has an interesting history of description. This subspecies was originally created as a new variety of *H. curvata* from Yalta (Crimea) by Marcus & Por (1960). But, they determined that a previous report of *H. curvata* by Por (1960) from Romanian Black Sea coast (Eforie) was conspecific with the specimens from Yalta. Although Por (1960) noted some differences between Romanian specimens and the typical *H. curvata* he decided at that time that creating a new variety was not justified since he had only male specimens from a single locality. Later Marcus & Por (1960) found female specimens in Yalta (Crimea) and created *H. curvata* var. *micrarthros* and concluded that their specimens differed from typical *H. curvata* by the following five features: **i**) Exopod of the antenna more developed than as that described by Douwe (1929) and bearing 4-5 setae instead of one, **ii**) terminal exopod segment of P3 has an extra seta and the P3 enp-2 a very weak thumb-shaped spine, **iii**) anal operculum with spinules on free border, **iv**) inner modified spine of P2 enp-2 of the male is less chitinized and weaker, **v**) the P4 endopod of the male is 2-segmented instead of one. But, these diagnostic features of *H. curvata micrarthros* are also found in the present redescription of *H. curvata*. On the other hand, several new differences can now be defined between *H. curvata micrarthros* and presently redescribed *H. curvata*; **i**) caudal rami shorter in female, **ii**) terminal exopodal segment of P4 with 5 setae/spines in male, **iii**) P4 enp-2 of male with one long seta, **iv**) structure and the ornamentation of setal elements of female P5 are different. On the other hand, it should be pointed out that the setal formula of P4 differs between female and male of *H. curvata micrarthros*, viz, terminal exopodal segment of P4 with 5 setae/spines in female but with 4 setae/spines in male and P4 enp-2 of male with one long seta in female but with 2 setae in male. This might mean that *H. curvata micrarthros* was described on the basis of male and female specimens belonging to different species. As mentioned above, the female specimens of *H. curvata micrarthros* were collected from Eforie (Romania) but the male specimens were obtained from Yalta. The description of the male possibly belongs to a taxon closely related to *H. curvata* (Por, 1960) but the female specimens described from Yalta (Marcus & Por 1960) may not even belong to the genus *Heterolaophonte* but another genus such as *Paralaophonte*. Therefore, the position of *H. curvata micrarthros* within the genus should provisionally be considered doubtful. The reports of *H. curvata micrarthros* given by Marinov (1971) and Apostolov & Marinov (1988) should also be confirmed.

Discussion

The insufficient descriptions of many species are a main obstacle in testing the monophyletic status of several genera in the family Laophontidae (Huys & Lee 2000). One example is the genus *Heterolaophonte* in which the descriptions of many species are insufficient and vague. Detailed redescriptions are therefore urgently needed in order to support a robust phylogeny-based classification and to identify more accurate diagnostic characters for this genus. It has been shown in this study that the sexual dimorphism shown by the male appendages, especially those of the swimming legs, provide a considerable number of significant characters that are valuable for both taxonomic identification and phylogenetic inferences. For example the following male characters seem to be reliable modifications that can be used as the autapomorphies of *Heterolaophonte*: **i**) modified inner spine on the P2 enp-2 (arrowed in Fig. 9A and 19A), **ii**) 2-segmented P3 endopod and **iii**) the modification of the inner seta on P3 enp-2 into a spine in the male (arrowed in Fig. 9B and 19B). The significant modifications on the swimming legs in the male have also been noticed by Lang (1965) who stressed the phylogenetic importance of such dimorphisms in solving the taxonomic grouping problem in the genus. But testing the monophyletic status of *Heterolaophonte* will invariably involve other related genera such as *Quinquelaophonte* Wells, Hicks & Coull, 1982 and *Platychelipus* Brady, 1880. The best evidence for this is that *H. littoralis* and *H. longisetigera* share important characteristics with species of *Platychelipus*, especially with that of *P. littoralis* Brady 1880. In these species proximal inner seta of the male P2 enp-2 is not modified, second segment of the 3-segmented P3 endopod bears an apophysis and P4 endopod is reduced. For this reason, *H. littoralis* and *H. longisetigera* may form separate lineage together with *Platychelipus*. On the other hand the males of all species of *Heterolaophonte*, *Quinquelaophonte* and *Platychelipus*

possess a rudimentary plate-like P5 indicating that they come from the same ancestral stock. The genus *Quinquelaophonte* is defined by the 6-segmented female antennules, reduced antennary exopod, caudal rami with a single well developed terminal seta (V), broad female P5 endopodal lobe, unmodified male P2 endopod, sexually dimorphic P2-P4 exopods and reduced male P5 represented by five setae arising from the somatic margin. But only the 6-segmented female antennules and caudal rami with a single well developed terminal seta (V) are autapomorphic states defining *Quinquelaophonte*, the other characters are also found in *Heterolaophonte* species.
When Lang (1944) first created the genus *Heterolaophonte*, he divided the genus into seven species-groups: (1) *stroemii*-group, (2) *minuta*-group, (3) *littoralis*-group, (4) *quinquespinosa*-group, (5) *discophora*-group, (6) *campbelliensis*-group and (7) *tenuispina*-group. Wells *et al*. (1982) proposed a new genus *Quinquelaophonte* to include *quinquespinosa*-group. Nowadays, Lang's other species-groups are no longer recognised as taxonomically useful units (Wells 2007). Furthermore, the inclusion of certain species in *Heterolaophonte* by Lang (1944, 1948) was clearly erroneous. Firstly, *H. rottenburgi* is the only species in the genus with a well-developed spiniform process on the second antennulary segment. This species was originally described as *Laophonte rottenburgi* from the South Orkney Island (Antarctica) on the basis of female specimens by Scott (1912) and has not been reported anywhere else since then. Scott (1912) only figured the antennule, maxilliped, P1, P3, P5, anal somite and caudal rami. According to Lang (1944, 1948) the reduced antennary exopod and rudimentary plate-like form of male P5 were sufficient enough to assign species into *Heterolaophonte*. It is clear that *H. rottenburgi* does not belong to *Heterolaophonte* and it should be placed as species *incertae sedis* within Laophontidae. In the same study, again on the basis of female specimens, Scott (1912) described two more new species namely *L. exigua* and *L. australis* from Antarctica. Two years later Scott (1914) described *H. insignis* from the Falkland Islands. But the figures provided for these species are insufficient to allow generic diagnosis. However, Lang (1944, 1948) assigned these three species to *Heterolaophonte* for the same reason ("small" antennary exopod). In their present state of knowledge, therefore, these three species should also be considered as *incertae sedis* within Laophontidae.

On the other hand, the position of *Heterolaophonte pygmaea*, *H. phycobates* and *H. tupitskyi* (the males are unknown) within the genus should provisionally be considered doubtful. *H. pygmaea* was originally described as *Laophonte pygmaea* by Scott (1894) from São Thomé Island in the Gulf of Guinea and has also been reported from the Red Sea (Scott 1902). The description of *H. pygmaea* is very concise, presenting illustrations of the female antennule, P1, P4, P5, caudal ramus and anal somite. The antennary exopod of *H. pygmaea* was not illustrated, and the structure and ornamentation of anal somite more resemble that of *Paralaophonte brevirostris* (Lang, 1948) than any species in the genus *Heterolaophonte*. *H. phycobates* and *H. tupitskyi* also suffer from similar problems to those discussed for *H. pygmaea*. In the lack of male descriptions and on the basis of present knowledge, the inclusion of *H. pygmaea*, *H. phycobates* and *H. tupitskyi* in the genus *Heterolaophonte* is not fully justified.

In conclusion, the genus *Heterolaophonte* as it is defined (Lang 1965; Mielke 1981) is not monophyletic (possibly para/polyphyletic). It is also clear that several lineages can be identified among the species of *Heterolaophonte*, *Quinquelaophonte* and *Platychelipus*. Whether each of these lineages belongs to a different taxonomic category should be re-examined when more detailed morphological data becomes available. Detailed descriptions of both sexes, especially those of sexually dimorphic characters on the swimming legs, of *H. curvata* and *H. uncinata* revealed many characteristics which will certainly help in solving the taxonomic problem surrounding the genus *Heterolaophonte*.

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