



Description of a new species of *Onychostenhelia* Itô (Copepoda, Harpacticoida, Miraciidae) from the Bohai Sea, China

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Abstract

Onychostenhelia bispinosa **sp. nov.** is described from material collected from the Bohai Sea, China. It differs from the type and only known species of *Onychostenhelia* in the setal formula of the swimming legs, the form of the setae on the baseoendopod of P5 in both sexes, the female rostrum, the structure of the sexually dimorphic P4 exopod in the male, and size.

Onychostenhelia, *Cladorostrata* and *Delavalia* belong to a core group within the Stenheliinae that exhibits an unusual morphology in the maxillule, the exopod and endopod being confluent at base but not actually fused to the supporting basis. Based on this circumstantial evidence it is postulated that in biramous limb patterning both exopodal and endopodal primordia are recruited from a common precursor and, consequently, patterns of axial diversification in crustacean limbs and the mechanisms of segmentation that establish them may have to be reinterpreted.

Previously published evidence supporting the monophyly of the Stenheliinae is reviewed and a dichotomous key to the nine genera of the subfamily Stenheliinae provided.

Key words: *Onychostenhelia bispinosa* **sp. nov.**, Harpacticoida, Miraciidae, Stenheliinae, taxonomy, limb patterning, Bohai Sea, China

Introduction

The genus *Onychostenhelia* was proposed by Itô (1979) for a new species, *O. falcifera*, based on five specimens dredged from a sandy substratum off Oshoro, Hokkaido, Japan. Its relationships clearly lie with the subfamily Stenheliinae (Miraciidae) because of the dorsolateral position of the female genital apertures on the genital double-somite. Itô (1979) suggested that, within this subfamily, *Onychostenhelia* most closely resembled *Pseudostenhelia* in the segmentation and armature of the swimming legs, and that the female P5 was similar to that found in *Delavalia cornuta* (Lang, 1936). However, the genus clearly differed from any other harpacticoid in the peculiar transformation of the P4 exopod in the male.

Specimens belonging to the Stenheliinae were relatively common in the Bohai Sea samples. Most of these belonged to various species of the genera *Stenhelia* Boeck, 1865 and *Delavalia* Brady, 1869 (Mu & Huys 2002). However, one of the most abundant animals could clearly be assigned to the monotypic genus *Onychostenhelia* and comparison with the very detailed description of *O. falcifera* unequivocally indicated that it should be placed in a new species, which is described below.

Materials and methods

Specimens were collected during an ongoing sampling survey in 1997–1999 in the central region of the Bohai Sea (38°30' N, 120° E), China. Sediments range from muddy sand to mud. Sediment samples were collected at an average depth of 20 m (range 11–70 m) with a 0.1 m² box corer. Harpacticoid copepods were extracted using a 48 µm sieve and subsequent flotation-centrifugation employing the colloidal silica polymer LUDOX, from a standard subsample taken from the box core by three 26 mm diameter plastic tubes inserted to a depth of 5 cm.

Samples were fixed in 10% formalin. Specimens were preserved in 4% formalin. Before dissection the habitus was drawn from whole specimens temporarily mounted in lactophenol. Specimens were dissected in lactic acid, and the parts individually mounted in lactophenol under coverslips, which were subsequently sealed with transparent nail varnish. All drawings were prepared using a camera lucida on a Zeiss Axioskop differential interference contrast microscope. The terminology of the body and appendage morphology follows that of Huys and Boxshall (1991) and Huys *et al.* (1996). Abbreviations used in the text and figures are *P1-P6* for thoracopods 1–6; *exp(enp)-1(-2-3)* to denote the proximal (middle, distal) segment of a ramus; and *ae* for aesthetasc. Body length was measured from the anterior margin of the rostrum to the posterior margin of the caudal rami. Scale bars in all illustrations are in µm. Type material is deposited in the Natural History Museum, London (NHM).

Systematics

Order Harpacticoida Sars, 1903

Family Miraciidae Dana, 1846

Subfamily Stenheliinae Brady, 1880

Genus *Onychostenhelia* Itô, 1979

Amended diagnosis. Stenheliinae. Anal operculum absent. Caudal rami about 3 times as long as anal somite; seta V swollen in proximal part. Rostrum bell-shaped, with bifid or rounded tip. Antennule ♀ 7-segmented with aesthetasc on segments 4 and 7; haplocer in ♂; segments 1–2 with spinous process on posterior margin in both sexes. Antenna with allobasis; exopod 3-segmented with setation formula [1,1,(1 + 3 apical)]. Mandible with elongate basis bearing 3 setae; exopod with 6 setae; endopod with 2 lateral setae, and 6 setae apically (none of which modified into a lash, two of them fused). Maxillule without modified elements on arthrite; endopod and exopod confluent at base. Maxilliped subchelate; syncoxa with 3 setae; basis with 2 setae; endopod slender, bearing claw and 2 accessory setae.

P1 with slender, elongate rami; not sexually dimorphic; exopod 3-segmented, endopod 2-segmented; exp-2 with inner seta, exp-3 with 4 setae, outer elements long and setiform; enp-1 distinctly longer than enp-2; enp-2 with 3 slender setae apically. P2–P4 with 3-segmented exopod and 2-segmented endopods; all segments strongly chitinized; P2 exopod abbreviated, about as long as endopod, P3–P4 exopods distinctly longer than endopods. P2 endopod not sexually dimorphic. Inner element of ♀ P3–P4 enp-1 spiniform, absent in ♂. P4 exopod sexually dimorphic; longer in ♂ due to elongation of exp-2; exp-2 ♂ with modified outer spine; exp-3 with 3 well developed inner setae in both sexes, in ♂ with cup-shaped chitinous projection along outer margin. P1-P4 armature formula:

	Exopod	Endopod
P1	0.1.121	1.120
P2	0.1.223	0.221
P3	0.1.32(2-3)	1.321 [σ° : 0.321]
P4	0.1.32(2-3)	1.221 [σ° : 0.321]

Fifth pair of female legs with free exopods and medially fused baseoendopods; exopod drawn out into a conspicuous terminal spinous process (derived from incorporated spine), with 3 inner and 2 outer setae; baseoendopod with 5 elements. Male P5 with free exopod modified into a claw-like outwardly directed segment with 2 outer setae; baseoendopod fused medially, endopodal lobe vestigial, with inner spine and outer seta. Male P6 with 3 setae, innermost not modified.

Egg-sacs elongate and uniseriate.

Note that Itô (1979) stated in the original diagnosis that the proximal aesthetasc in the female antennule arises from the fifth segment. This must be an inadvertent slip of the pen.

Type species. *Onychostenhelia falcifera* Itô, 1979 (by monotypy)

Other species. *O. bispinosa* **sp. nov.**

***Onychostenhelia bispinosa* sp. nov.**

(Figs 1–8)

Material examined. Holotype: adult ♀ dissected on 20 slides (NHM reg. no 2002.662). Paratypes: 1 ♂ dissected on 20 slides (NHM reg. no 2002.663), 10 ♀♀ and 2 ♂♂ preserved in alcohol (NHM reg. no 2002.664–674). One ♀ and 1 ♂ prepared for SEM, mounted on stub but not registered.

Description. The present species is very similar to *O. falcifera*, which Itô (1979) described in great detail. Therefore, the following description is confined to those features which are different to, or which were not described for, *O. falcifera*. Unfortunately the type material of the latter is no longer available for re-examination.

FEMALE. Body (Fig. 1A–B). Length 500–610 µm (mean 557 µm, n = 11), shape and general body facies as in *O. falcifera*.

Rostrum (Figs 1A, 6A, 8C–D) clearly defined at base and extending beyond second antennular segment; triangular, with concave lateral margins and distinctly bifid tip; furnished with numerous integumental pits and a central tube-pore on dorsal surface and with a pair of lateral sensilla just below apex.

Caudal ramus (Fig. 6B) elongate, cylindrical, 8 times longer than basal width with a row of spinules on distal ventral margin; seta I and seta II well-developed, inserted at 90% of ramus length on dorsolateral outer margin; seta III slender, about as long as caudal rami, inserted subapically on outer distal margin; distal seta IV somewhat longer than caudal ramus, seta V thickened proximally, about 3 times as long as caudal ramus and seta VI minute, closely set to seta V; seta VII triarticulate at base, inserted on inner margin opposite setae I and II.

Antennule (Fig. 2A–B) 7-segmented with aesthetasc on fourth and distal segments. Segments 1–4 with pitted region on dorsal surface. Segment 1 longest, with three rows of spinules on anterior margin, segments 1 and 2 with a strong, chitinous spur on distal posterior margin. All setae naked except for 1 plumose seta on each of segments 2, 3 and 7. Apical acrothek consisting of aesthetasc and 2 setae. Setal formula as follows: 1-[1], 2-[9], 3-[9], 4-[4 + (1 + ae)], 5-[2], 6-[4], 7-[7 + (2 + acrothek)].

Antenna (Fig. 3A) as in *O. falcifera* except for subdistal inner corner of endopod with 2 spines and 2 setae. It is conceivable, however, that Itô (1979) overlooked one of the setae.

Mandible (Fig. 3B–C) as in *O. falcifera*.

Maxillule (Fig. 3D) as in *O. falcifera* except for 11 elements present on arthrite (7 spines and 2 setae on distal edge, 2 parallel setae on anterior surface); exopod and endopod fused basally, forming a bilobate structure (Figs 8A–B).

Maxilla (Fig. 3E) as in *O. falcifera* except for basis armed with 2 claws (one of them fused with segment) and 4 setae.

Maxilliped (Fig. 3F) as in *O. falcifera* except for outer and distal edge of basis with a row of long spinules.

P1 (Fig. 4A). As in *O. falcifera*

P2–P4 (Figs 4B, 5A–B). Segment shapes as in *O. falcifera*, except for P2 coxa which is not laterally expanded. Distribution of ornamentation elements slightly different; P2 with long setules along inner margins of basis and enp-1; presence of pores on anterior face of distal segment of rami not mentioned by Itô (1979). P3–P4 exp-3 with only 2 outer spines (3 outer spines in *O. falcifera*) and ornamentation of terminal setae on distal segments of rami slightly different (biserrate instead of with unilateral membranous flange). Setal formula as follows:

	Exopod	Endopod
P1	0.1.121	1.120
P2	0.1.223	0.221
P3	0.1.322	1.321 [0.321]
P4	0.1.322	1.221 [0.321]

[formulae in brackets denote male condition]

P5 (Fig. 6C). Baseoendopods fused medially. Exopod not fused to baseoendopod; longer than in *O. falcifera*; basal fusion of largest laterodorsal seta (on outer margin) was not mentioned by Itô (1979) but from his figure 15-3, it seems as if this seta is not fused to the ramus. Outer basal seta plumose. Armature of baseoendopod distinctly different: outer two elements well developed, second outer minutely pinnate (both small, slender and naked in *O. falcifera*); middle element a well developed seta with hyaline border on one side and minute pinnules on other (same length but naked in *O. falcifera*); second inner as long as middle seta but innermost seta less than one third length of middle seta (in *O. falcifera* second inner element is a short pectinate spine and inner element a long serrate spine).

MALE. Sexual dimorphism in antennule, P3 endopod, P4 rami, P5, P6, and in urosomal segmentation and ornamentation.

Body. Length 440–560 μm (mean = 500 μm , n = 3).

Rostrum (Fig. 7G) bifid. Note that the female of *O. falcifera*, as described by Itô (1979), possesses a rostrum with rounded tip, while the male of that species possesses a rostrum with bifid tip similar to that found in *O. bispinosa*. Re-examination of topotypes of *O. falcifera* is desirable to verify whether the bifid condition of the female rostrum of *O. falcifera* was overlooked by Itô (1979).

Antennule (Fig. 2C–D). Indistinctly 8-segmented, haplocer, segment 5 moderately swollen, geniculation between segments 6 and 7; proximal 2 segments with chitinous hook, segment 1 with 2 anterior rows of spinules; modified elements on segments 5, 6 and 7, aesthetascs on segments 3, 5 and as part of acrothek on segment 8. Setal formula as follows: 1-[1], 2-[9], 3-[7 + ae], 4-[2], 5-[8 + (1 + ae)], 6-[4 + 3 spinules], 7-[3], 8-[7 + acrothek]. Itô (1979) did not figure the small fourth segment nor the aesthetasc on the terminal segment, and illustrated 3 segments distal to the geniculation (instead of 2 in *O. bispinosa*). Re-examination of the topotype material of *O. falcifera* is required to confirm these discrepancies.

P3 (Fig. 5C). Endopod as in ♀ except enp-1 without inner element and enp-2 proportionally longer with shorter outer spinous process. Exp-3 as in ♀ (shape sexually dimorphic in *O. falcifera*).

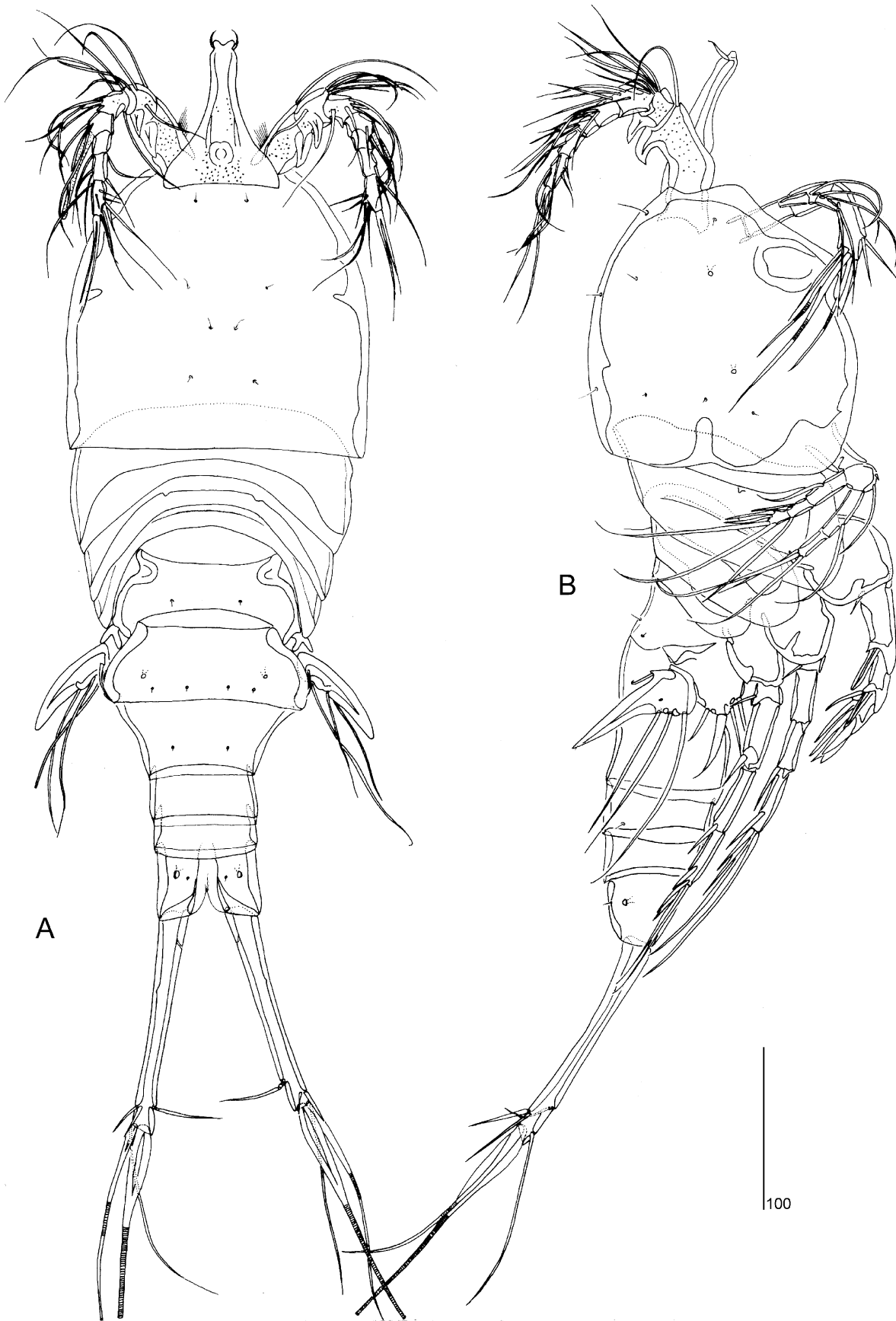


FIGURE 1. *Onychostenhelia bispinosa* sp. nov. (holotype ♀; NHM reg. no 2002.662): (A) habitus, dorsal; (B) habitus, lateral.



FIGURE 2. *Onychostenhelia bispinosa* sp. nov.: (A) antennule ♀, ventral (armature omitted); (B) antennule ♀, ventral (disarticulated); (C) antennule ♂, ventral (armature omitted); (D) antennule ♂ ventral (disarticulated). [(A)–(B): holotype ♀, NHM reg. no 2002.662; (C)–(D): paratype ♂, NHM reg. no 2002.663].

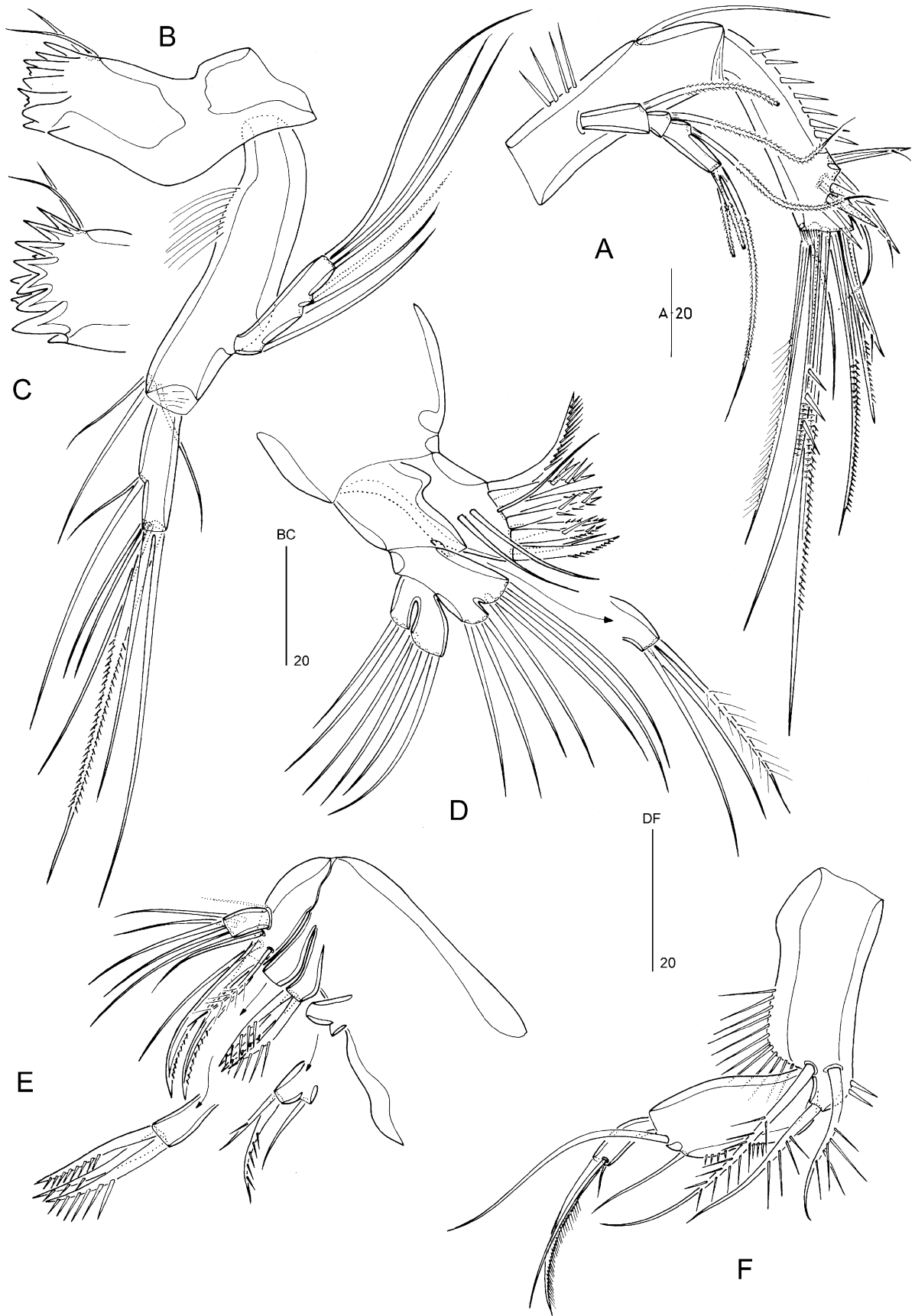


FIGURE 3. *Onychostenhelia bispinosa* sp. nov. (holotype ♀; NHM reg. no 2002.662): (A) antenna; (B) mandible; (C) mandibular gnathobase; (D) maxillule, anterior [inset showing proximal endite of syncoxa]; (E) maxilla, anterior; (F) maxilliped, anterior.



FIGURE 4. *Onychostenhelia bispinosa* sp. nov. (holotype ♀; NHM reg. no 2002.662): (A) P1, anterior; (B) P2, anterior.



FIGURE 5. *Onychostenhelia bispinosa* sp. nov.: (A) P3 ♀, anterior; (B) P4 ♀, anterior; (C) P3 endopod ♂, anterior. [(A)–(B): holotype ♀, NHM reg. no 2002.662; (C): paratype ♂; NHM reg. no 2002.663].

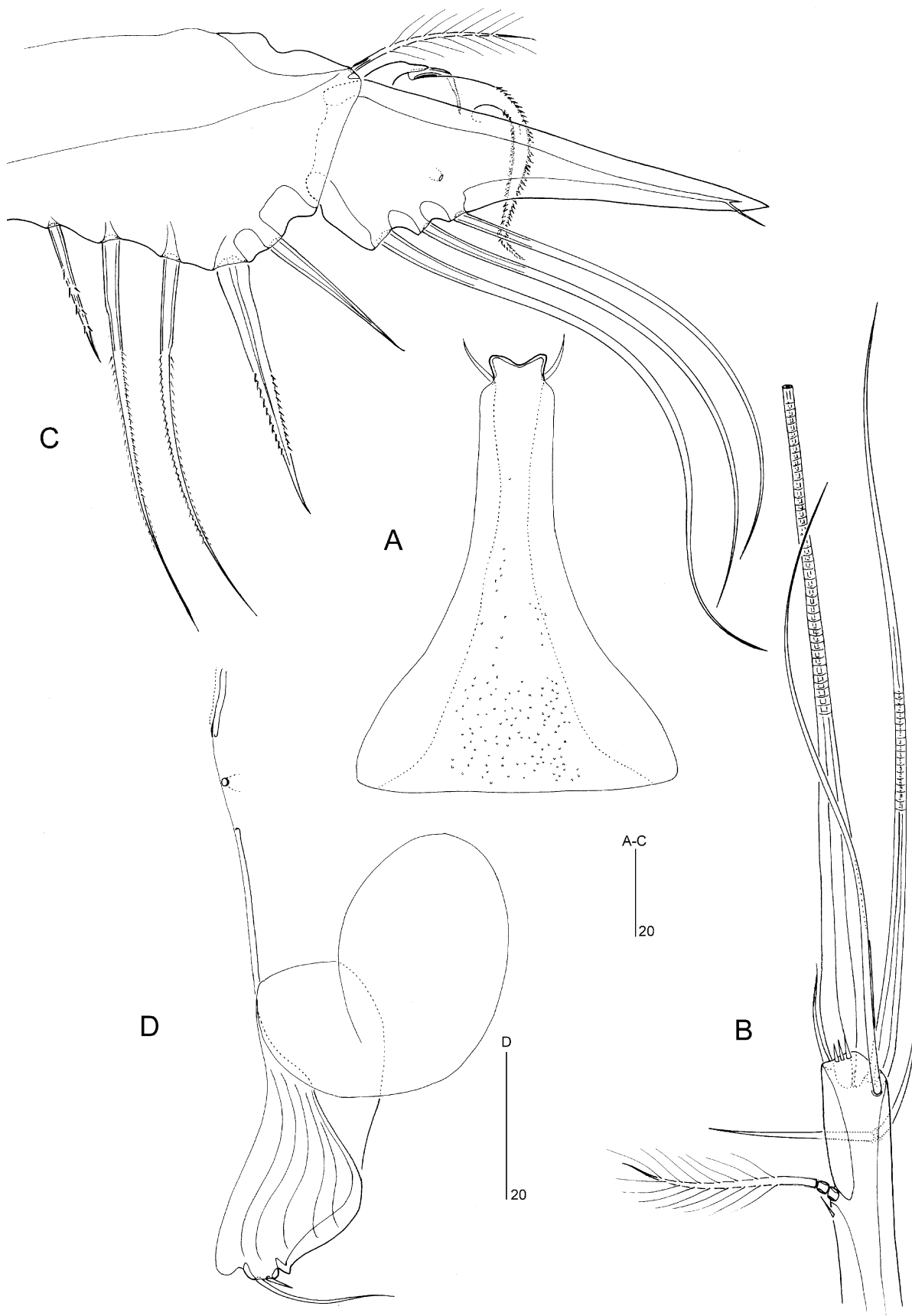


FIGURE 6. *Onychostenhelia bispinosa* sp. nov. (holotype ♀; NHM reg. no 2002.662): (A) rostrum, dorsal; (B) distal part of caudal ramus, ventral; (C) P5, anterior; (D) genital field.

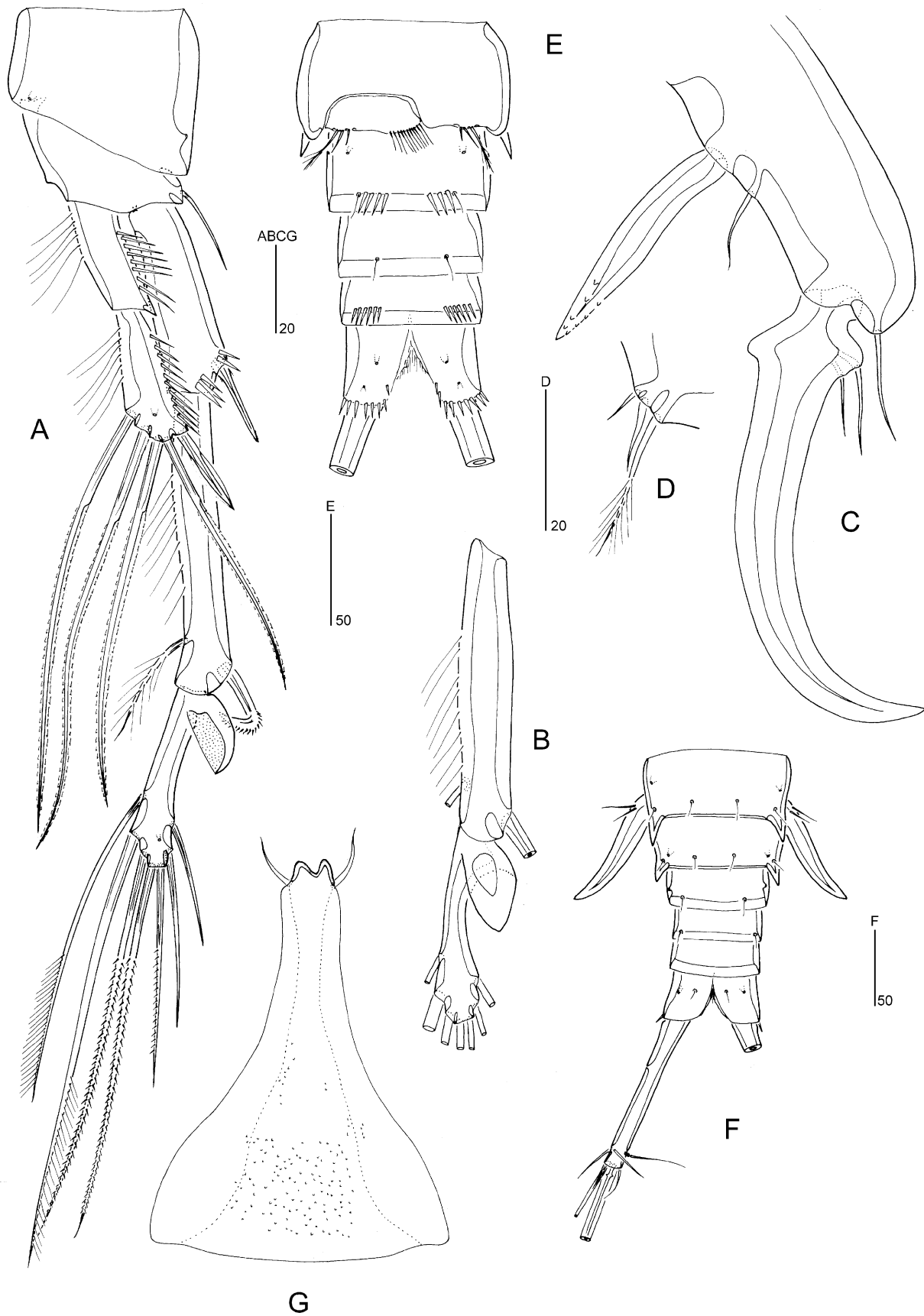


FIGURE 7. *Onychostenhelia bispinosa* sp. nov. (paratype ♂; NHM reg. no 2002.663): (A) P4, anterior; (B) P4 endopod viewed from another angle (setae not drawn at full length); (C) P5, anterior; (D) armature elements of P6; (E) urosome, ventral; (F) urosome, dorsal; (G) rostrum, dorsal.

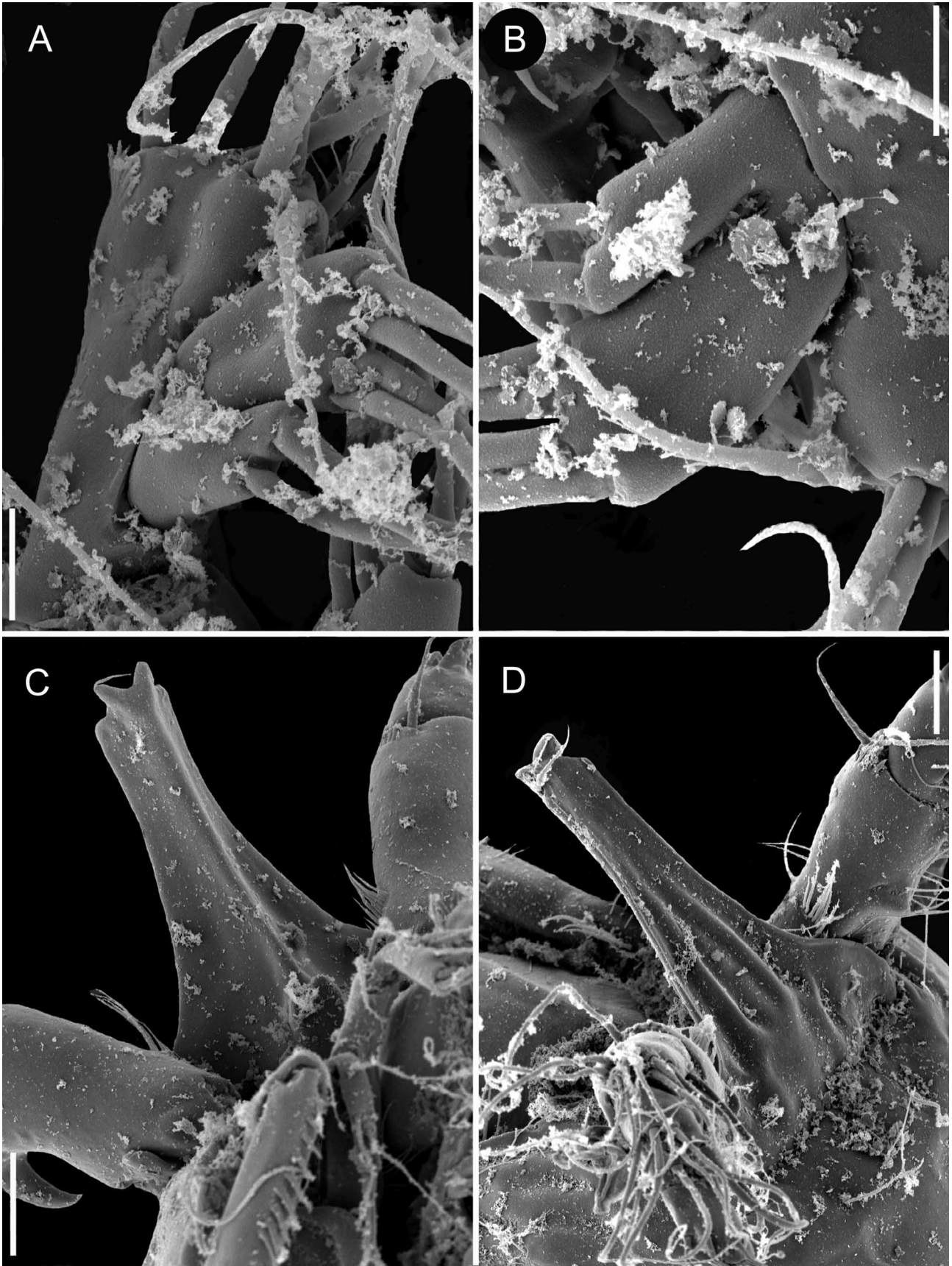


FIGURE 8. *Onychostenhelia bispinosa* sp. nov. (♀): (A) maxillary palp, showing basally fused exopod and endopod; (B) same, different angle; (C) rostrum, ventral; (D) rostrum, dorsal. Scale bars: 2 m (A–B), 10 μ m (C–D).

P4 (Fig. 7A–B). Exopod modified. Exp-1 as in female. Exp-2 much longer and more slender than in female; outer margin straight (with pointed process in *O. falcifera*), outer spine distinctly recurved and relatively slender (a thick straight spine in *O. falcifera*). Exp-3 less curved than in *O. falcifera* and proximal outer element larger; on proximal outer margin, with a chitinous, recurved projection, being concave (cup-shaped) and filled with semi-hyaline granular material; arrangement of setae on distal margin as in female. Endopod as in female except proportionally shorter and enp-1 without inner element.

P5 (Fig. 7C). Baseoendopods forming single plate without setular ornamentation around free margin (present in *O. falcifera*), exopods discrete. Exopods as in *O. falcifera* but distal half more strongly curved outwardly. Endopodal armature distinctly different; outer element a small seta (well developed in *O. falcifera*); inner element a virtually straight, short, very stout spine with dentate margin near tip (much more elongate, distally curved and more slender in *O. falcifera*).

P6 (Fig. 7D–E) asymmetrical, with right side fused to somite and left side represented by articulating operculum closing off functional gonopore, with a row of long setules around inner distal corner; each side with 3 elements, outermost plumose, others short and smooth. Itô's (1979: Fig. 18-2) drawing gives a distorted view of the sixth pair of legs and it is not clear whether each leg has one or two spinular rows.

Urosome (Fig. 7E–F). Urosomites 2 and 3 with a distinct process on each laterodorsal corner (weak ones present in *O. falcifera*). Penultimate somite with paired spinule rows on ventral surface (absent in *O. falcifera*).

Etymology. The specific name refers to the presence of only two outer spines on P3 and P4 exp-3.

Discussion

Relationships. *Onychostenhelia bispinosa* can be distinguished from *O. falcifera* by (a) the setal formula of the swimming legs, (b) the relative length of the setae on the baseoendopod of P5 in both sexes, (c) the structure of the sexually dimorphic P4 exopod in the male, (d) size (♀♀: 500–610 µm vs 840 µm; ♂♂: 440–560 m vs 810 m), and possibly (e) the female rostrum, and (f) the number of antennular segments, and number of segments distal to the geniculation in the male.

In the female, *O. bispinosa* has only two outer spines on the P3 and P4 exp-3 and the anterior margin of the rostrum is distinctly bifid, whereas in *O. falcifera* there are three outer spines on P3 and P4 exp-3 and Itô (1979) shows the anterior tip of the female rostrum as rounded, although he illustrates a bifid rostrum in the male. The differences in the armature elements of the P5 baseoendopod in both sexes are discussed in the description above.

In the male, the P3 exp-3 in both species is the same as their respective females but there are significant differences in the structure of P4. In *O. bispinosa* the outer margin of exp-2 is straight and not modified and the outer spine is distinctly recurved and marginal in position. In *O. falcifera* the outer margin has a marked invagination in the distal half forming a hooked spinous process, while the strong outer spine on exp-2 is thicker and more heavily chitinized than that in the female and arises from the posterior face rather than the lateral margin. On P4 exp-3, the outer falciform projection in *O. falcifera* does not have a granular central portion as described for *O. bispinosa*. Further, the sexually dimorphic number of armature elements on P4 exp-3 in *O. falcifera* raises the question whether the proximal falciform process in the male is homologous with the proximal outer spine of the female as there are only seven additional elements on this segment in the male. However, the condition in *O. bispinosa*, where there are seven elements in both the male and the female but the falciform process is still present in the male, would indicate that the process is not setal in origin but must be an outward extension of the segment margin.

Both species of *Onychostenhelia* exhibit an unusual morphology in the maxillule, the exopod and endopod being confluent at base but not actually fused to the supporting basis (Fig. 8A–B). Such bilobate structure

is also a diagnostic character for the genus *Delavalia* (see e.g. Lang 1965; Willen 2002, 2003). According to Shen & Tai's (1963) illustrations of the maxillule in *Cladostrota brevipoda* the rami are fused to the basis; examination of an as yet undescribed species of *Cladostrota* from the Mandovi River (central west coast India) (cf. Ansari & Parulekar 1993) revealed a similar condition as in *Onychostenhelia* and *Delavalia*. The maxillary rami are completely discrete at the base and not fused to each other in *Stenhelia* (e.g. Mu & Huys 2002), *Beatricella* (R. Huys, pers. observ.), *Melima* (e.g. Willen 2002) and the recently established genera *Ani-sostenhelia* Mu & Huys, 2002 (Thistle & Coull 1979) and *Hicksia* Mu & Huys, 2002 (Hicks 1988). Published descriptions of *Pseudostenhelia* species (Wells 1967, 1971; Coull & Fleegeer 1977; Ranga Reddy 1984; Gómez 2000) are inconclusive with regard to the condition of the maxillary rami, however re-examination of paratype material of *P. prima* Wells, 1967 (NHM reg. nos 1967.8.4.45) and *P. secunda* Wells, 1971 (NHM reg. nos 1969.5.30.5-6) revealed the exopod and endopod are discrete at the base. The proximally confluent condition of the maxillary exopod and endopod has to our knowledge not been reported in any extant copepod or crustacean. The limb patterning pathway underlying the fusion of the exopod and endopod of a biramous appendage is difficult to explain. Based on the observations above the only plausible explanation is that both exopodal and endopodal primordia are recruited from a common precursor but failed to separate completely in some stenheliinid genera. If this interpretation is correct this may have profound implications for our understanding of patterns of axial diversification in crustacean limbs and the mechanisms of segmentation that establish them. The confluent condition of the maxillary rami therefore clearly represents a robust synapomorphy grouping *Onychostenhelia*, *Cladostrota* and *Delavalia* within the Stenheliinae. Based on this, Itô's (1979) assertion that there is a resemblance in leg segmentation and armature between *Onychostenhelia* and *Pseudostenhelia* has therefore little phylogenetic significance. Similarly, the resemblance in leg 5 between *Onychostenhelia* and certain members of *Delavalia* [e.g. female *D. cornuta* (Lang, 1936) and males of most members of the *D. clavus*-group (Wells & Rao, 1987; Willen, 2002)] is to be regarded a product of convergence.

Remarks on monophyly of Stenheliinae. In a recent phylogenetic analysis of the Thalestridimorpha, Willen (2000) recognized eight apomorphic character states in support of the monophyly of the Stenheliinae:

(1) ancestral segments 7 and 8 fused, forming a compound segment in both sexes; this character evolved convergently in the Miraciinae;

(2) modified setation pattern on distal segment of female antennule, including an enlarged seta 2 (numbering according to Willen 2000: Fig. 10), loss of seta 5 and (almost always) seta 4, and a tendency towards reduction of the terminal aesthetasc. The significance of this composite character is limited since many species display exceptions, casting doubt on the validity of the stenheliinid groundpattern reconstructed by Willen (2000), which is confusingly depicted with four posterior setae in her Fig. 9 (matching the oligarthran groundpattern) but with only three setae in her Fig. 10. Various species have retained four setae along the posterior margin of the distalmost segment, including *Stenhelia sheni* (cf. Mu & Huys 2002) and the species figured by Willen (2000: Fig. 10) under the *nomen nudum* *S. paradivergens*. Seta 2 is not enlarged in many species and varies significantly in size and shape within the subfamily. Likewise, the aesthetasc is well developed in a wide range of stenheliinid taxa such as *O. bispinosa* and *S. sheni*;

(3) 2-segmented exopod of mandibular palp with displaced setae. Willen (2000) refers to her Fig. 28 to illustrate this condition but this figure is in reality a duplication of her Fig. 27, which does not include the stenheliinid pattern. In many taxa one of the lateral setae is indeed displaced to the outer margin but this condition is by no means absolute as shown in e.g. the genera *Onychostenhelia*, *Pseudostenhelia* and *Melima* (Itô 1979; Gómez 2000; Willen 2002; present account);

(4) mandibular gnathobase with small, stout and blunt teeth; the phylogenetic usefulness of this character is limited since many transitional stages exist within the subfamily ranging from small and blunt as in *Melima* and some *Delavalia* species to large and pointed as in *Onychostenhelia*;

(5) maxilliped with only 3 syncoxal setae, both palmar setae on basis closely positioned to one another and setation of ancestral enp-2 lost;

(6) P5 of female with laterally directed exopod and flattened baseoendopod;

(7) P2 sexual dimorphism. Willen (2000) was unable to reconstruct the stenheliinid groundpattern for this character since at least three different types of modifications of the male P2 endopod exist in the subfamily. She pointed out that the male P2 types could not be derived from the groundpattern of the Thalestroidea but unfortunately refrained from stating which characters in the stenheliinid male P2 endopod support the monophyly of the subfamily;

(8) Rostrum broadly triangular and bifid apically; although not all stenheliinids display this condition and often different rostrum types occur in the same genus Willen (2000) believed a genetic basis for such a rostrum somehow seems to be present in the stenheliiniine [*sic*] groundpattern and its special shape can therefore be regarded an autapomorphy of the Stenheliinae.

Willen (2002) reiterated her argumentation in support of stenheliinid monophyly but did not list the mandibular exopod condition (character 3 above) as one of the autapomorphies.

Dahms *et al.* (2005) studied the naupliar development of *Stenhelia peniculata* (Lang, 1965) and compared it with previously published naupliar descriptions of *Delavalia palustris* Brady, 1869 (cf. Dahms & Bresciani 1993) and new data on *Pseudostenhelia wellsi* Coull & Fleeger, 1977. They recognized a number of stenheliinid apomorphies based on naupliar morphology (their Table 3) but admittedly cautioned subsequent workers their own inferences were derived from a limited dataset:

(1) lateral margin of naupliar shield with unique lobate protuberances;

(2) antennary gnathobase (masticatory process) characteristically fan-shaped distally;

(3) antennary exopod strongly developed, dorsally recurved and with reduced segmentation (3- instead of 4-segmented);

(4) mandible with characteristic shape and orientation (laterodistally elongated basipod, strongly chitinized exopod);

(5) posterolateral field of mandibular endopod with remarkably strong, inner spinulose spine;

(6) distal three spines on mandibular exopod with unique morphology (possibly involved in performing vigorous crawling strokes).

In their discussion Dahms *et al.* (2005) also listed a number of other unique characters shared by *Stenhelia*, *Delavalia* and *Pseudostenhelia*, including the extremely foreshortened cephalic shield, the presence of a spinous process on the distal third of the second (their figures show it on the middle third) and of a particularly notched inner distal seta on the third antennular segment (it is not clear from the text or the accompanying illustrations which seta or naupliar stage they refer to), and a lobate outer protuberance on the first segment of the antennary exopod. It is debatable how much phylogenetic significance can be attributed to these characters, however, at present they appear to be unique within the Harpacticoida.

Willen (2000, 2002) reviewed character state transformations in thalestridimorph appendage morphology and some additional structures such as the rostrum and caudal rami (it should be noted that at least one page (between pp 178–179) is missing in her section 6.12) but excluded the female genital somite from her analysis. Here we add the laterally displaced gonopores as a unique apomorphic condition for the Stenheliinae. In females the genital apertures have migrated to the lateral surface of the genital double somite and each has become elongated transversely round the side of the somite. The dorsal part of the aperture is closed off by setose flaps derived from the sixth legs and the egg sacs are extruded from this part. Spermatophores discharge via a spermatophore tubule, which extends into subventral part of the aperture where the isolated copulatory pore leading to the copulatory duct and seminal receptacle is located.

Key to genera of Stenheliinae

Willen (2000) assigned *Stenhelia*, *Pseudostenhelia*, *Onychostenhelia* and *Melima* to the subfamily Stenheliinae. Wells and Rao (1987) had relegated the latter genus to a junior synonym of *Stenhelia*, and a formal justification for its subsequent resurrection was not published until Willen (2002) who described a new species, *M. papuaensis*, and revised the genus. Willen (2000) also listed *Cladorostrata* as a candidate member of the Stenheliinae but expressed the need of re-examination of Shen and Tai's (1963) material in a later paper (Willen 2002). Mu and Huys (2002) abandoned the traditional subgeneric division of *Stenhelia* and upgraded *Delavalia* to genus level. They also reinstated *Beatricella* and created two new genera, *Hicksia* and *Anisostenhelia* for *Stenhelia xylophila* Hicks, 1988 and *S. asetosa* Thistle & Coull, 1979, respectively, raising the number of genera in the subfamily to nine.

1. P1 endopod 3-segmented2.
P1 endopod 2-segmented5.
2. P1 exp-2 with inner seta; P2–P4 enp-1 with inner seta modified into short (P2–P3) or long lanciform (P4) spine; P4 enp-2 without inner seta..... *Hicksia* Mu & Huys, 2002.
P1 exp-2 without inner seta; P2–P4 enp-1 inner seta not modified; P4 enp-2 with inner seta.....3.
3. P2–P4 exp-1 with inner seta; P4 endopod not sexually dimorphic4.
P2–P4 exp-1 without inner seta; outer spine of P4 enp-3 modified into characteristic sickle-shaped element *Anisostenhelia* Mu & Huys, 2002.
4. P2 exp-3 with 6 setae/spines; P3 exp-3 with 7 setae/spines; ♂ P5 exopod and baseoendopod distinct; anal operculum absent..... *Stenhelia* Boeck, 1865.
P2 exp-3 with 7 setae/spines; P3 exp-3 with 8 setae/spines; ♂ P5 exopod and baseoendopod confluent; anal operculum present..... *Beatricella* T. Scott, 1905.
5. P2–P4 endopods 2-segmented6.
P2–P4 endopods 3-segmented7.
6. Antennule ♀ 5-segmented, without spinous processes on segments 1–2 in either sex; P5 ♂ fully incorporated into somite, with 2–3 setae *Pseudostenhelia* Wells, 1967.
Antennule ♀ 7-segmented, with spinous processes on segments 1–2 in both sexes; P5 ♂ represented by distinct baseoendopod and recurved, triangular exopod..... *Onychostenhelia* Itô, 1979.
7. P1 exp-3 with 5 setae/spines8.
P1 exp-3 with 4 setae/spines9.
8. Antennary exopod 1-segmented *Cladorostrata* Shen & Tai, 1963.
Antennary exopod 3-segmented *Delavalia* Brady, 1869 [Group I].
9. P2–P4 exp-3 with 2, 2, 2 outer spines, respectively *Melima* Por, 1964.
P2–P4 exp-3 with 3, 2, 2 outer spines, respectively *Delavalia* Brady, 1869 [Group II].
P2–P4 exp-3 with 3, 3, 2 outer spines, respectively *Delavalia* Brady, 1869 [Group III].
P2–P4 exp-3 with 3, 3, 3 outer spines, respectively *Delavalia* Brady, 1869 [Group IV].

Species composition of *Delavalia*-groups:

Group I: *D. reflexa* Brady & Robertson in Brady (1880); *D. bifidia* (Coull, 1976); *D. lima* (Becker & Schriever, 1979);

Group II: *D. longifurca* (Sewell, 1934); *D. ornamentalia* (Shen & Tai, 1965); *D. madrasensis* (Wells, 1971); *D. golikovi* (Chislenko, 1978);

Group III: *D. palustris* Brady, 1869; *D. incerta* (Por, 1964); *D. unisetosa* (Wells, 1967); *D. clavus* (Wells & Rao, 1987); *D. paraclavus* (Wells & Rao, 1987); *D. valens* (Wells & Rao, 1987); *D. schminkei* (Willen, 2002);

Group IV: *D. longicaudata* (Boeck, 1873); *D. giesbrechti* (T. & A. Scott, 1896); *D. arctica* T. Scott, 1899; *D. inopinata* A. Scott, 1902; *D. minuta* A. Scott, 1902; *D. normani* T. Scott, 1905; *D. magnacaudata*

(Monard, 1928); *D. polluta* (Monard, 1928); *D. tethysensis* (Monard, 1928); *D. arenicola* (C.B. Wilson, 1932); *D. acutirostris* (Willey, 1935); *D. cornuta* (Lang, 1936); *D. latisetosa* (Sewell, 1940); *D. truncatipes* (Sewell, 1940); *D. confluens* (Lang, 1948); *D. hanstromi* (Lang, 1948); *D. elisabethae* (Por, 1960); *D. latipes* (Lang, 1965); *D. longipilosa* (Lang, 1965); *D. oblonga* (Lang, 1965); *D. mastigochaeta* (Wells, 1965); *D. nuwukensis* (M.S. Wilson, 1965); *D. bermudensis* (Coull, 1969); *D. bocqueti* (Soyer, 1972); *D. coineauae* (Soyer, 1972); *D. diegensis* (Thistle & Coull, 1979); *D. latioperculata* (Itô, 1981); *D. adriatica* (Marinov & Apostolov, 1981); *D. intermedia* (Marinov & Apostolov, 1981); *D. islandica* (Schriever, 1982); *D. noodti* (Schriever, 1982); *D. stephensoni* (Greenwood & Tucker, 1984); *D. saharae* (Marinov & Apostolov, 1985); *D. fustiger* (Wells & Rao, 1987); *D. hirtipes* (Wells & Rao, 1987); *D. breviseta* (Wells & Rao, 1987); *D. mixta* (Wells & Rao, 1987); *D. andamanica* (Rao, 1993); *D. gundulae* (Willen, 2003).

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