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New species of *Stenhelia* (Copepoda, Harpacticoida, Diosaccidae) from the Bohai Sea (China) with notes on subgeneric division and phylogenetic relationships

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Abstract: Two new species of *Stenhelia* (Copepoda, Harpacticoida, Diosaccidae) are described from subtidal sediments in the Bohai Sea, China. The traditional subgeneric division of *Stenhelia* is abandoned since both subgenera, *Stenhelia* (*Stenhelia*) and *Stenhelia* (*Delavalia*), are polyphyletic taxa. The latter is tentatively upgraded to generic rank pending a phylogenetic analysis of the Stenheliinae. The genus *Stenhelia* is restricted to a core group of species formerly allocated to the subgenus *Stenhelia* (*Stenhelia*), including *S. gibba*, *S. proxima*, *S. curviseta*, *S. divergens*, *S. peniculata*, *S. pubescens* and both new species from the Bohai Sea, *S. sheni* sp. nov. and *S. taiae* sp. nov., which are most closely related to *S. pubescens*, described from the Sea of Japan. The genus *Beatricella*, erroneously considered a junior objective synonym of *Stenhelia*, is reinstated to accommodate *S. aemula* as the type species. The problematic *S. asetosa* is transferred to a new genus *Anisostenhelia* primarily on account of the sexual dimorphism of the swimming legs and is regarded as the sistergroup of *Stenhelia*. The P1 endopod of the bathyal *S. diegensis* is reinterpreted and consequently the species is re-assigned to the genus *Delavalia* where it is most closely related to other deepwater species. *S. xylophila* is designated as the type of a new genus *Hicksia*. Swimming leg morphology suggests a close relationship with *Delavalia hanstromi* and *D. bocqueti*, indicating at least a dual origin of the 2-segmented P1 endopod in the Stenheliinae.

Résumé : *Nouvelles espèces de* Stenhelia *(Copepoda, Harpacticoida, Diosaccidae) de la mer de Bohai (Chine) et notes sur les divisions subgénériques et les relations phylogénétiques*. Deux nouvelles espèces de *Stenhelia* (Copepoda, Harpacticoida, Diosaccidae) sont décrites des sédiments infralittoraux dans la mer de Bohai. La subdivision traditionelle de *Stenhelia* en sous-genres est abandonée puisque les deux sous-genres *Stenhelia* (*Stenhelia*) et *Stenhelia* (*Delavalia*) sont des taxons polyphylétiques. Le dernier est provisoirement élevé au rang générique, en attendant une analyse phylogénétique des Stenheliinae. Le genre *Stenhelia* est limité à un groupe d'espèces rattachées au sous-genre *Stenhelia* (*Stenhelia*), incluant *S. gibba*, *S. proxima*, *S. curviseta*, *S. divergens*, *S. peniculata*, *S. pubescens* et les deux nouvelles espèces de la mer de Bohai, *S. sheni* sp. nov. et *S. taiae* sp. nov. qui sont très proches de *S. pubescens* décrite de la mer du Japon. Le genre *Beatricella*, considéré à tort comme un synonyme de *Stenhelia*, est rétabli avec *S. aemula* comme espèce type. L'espèce problématique *S. asetosa* est transférée dans un nouveau genre *Anisostenhelia* principalement en raison du dimorphisme sexuel des pattes natatoires. L'endopodite de P1 de l'espèce bathyale *S. diegensis* est réinterprété et en conséquence l'espèce est à nouveau assignée au genre *Delavalia* où elle est étroitement associée à d'autres espèces profondes. *Stenhelia xylophila* est désignée comme type d'un nouveau genre *Hicksia*. La morphologie des pattes natatoires suggère une étroite parenté avec *Delavalia hanstromi* et *D. bocqueti*, indiquant au moins une origine double de l'endopodite à deux articles de P1 chez les Stenheliinae.

Keywords: Copepoda, Harpacticoida, *Stenhelia*, *Delavalia*, *Beatricella*, *Anisostenhelia* gen. nov., *Hicksia* gen. nov., China.

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Introduction

Boeck (1865) established the genus *Stenhelia* for the type and only species *S. gibba* Boeck, 1865. Soon after, Brady (1869) proposed another monotypic genus, *Delavalia*, for a new species *D. palustris*. In Brady's (1880) classification both genera, together with *Ameira* Boeck and *Jonesiella* Brady, were placed in the new subfamily Stenheliinae within the order Harpacticoida (then treated as a family Harpacticidae). Sars (1906*b*) considered the generic distinction as insufficient and consequently relegated *Delavalia* as a junior subjective synonym and *Beatricella* T. Scott as a junior objective synonym of *Stenhelia*. The latter was placed in the newly established family Diosaccidae and the older subfamily name Stenheliinae was abandoned (Sars, 1906*a*). In Monard's (1927, 1928) system, *Delavalia* was reinstated as a subgenus of *Stenhelia*, and this course of action was adopted by Lang (1944, 1948). The genus *Melima* Por was considered as valid by Lang (1965) but Wilson (1965) and Coull (1976) expressed doubts about its distinctiveness and regarded it as a possible synonym of *Stenhelia*. Wells & Rao (1987) formally relegated *Melima* to a junior subjective synonym of the latter, referring the two known species (Por, 1964; Coull, 1971) and the closely related *S. ovalis* Wells & Rao, 1987 to the subgenus *Delavalia*. Willen (2000) recognized a taxon Stenheliinae within the family Diosaccidae, accommodating the genera *Stenhelia*, *Cladorostrata* Shen & Tai, *Melima*, *Pseudostenhelia* Wells and *Onychostenhelia* Itô. No explicit reasons were given for the reinstatement of *Melima* at the time, but a strong recommendation was given in a later contribution (Willen, 2002).

Lang's (1948) monograph listed 19 valid species of *Stenhelia* in two subgenera (*S. divergens* Nicholls, 1939, *S. latisetosa* Sewell, 1940 and *S. truncatipes* Sewell, 1940 were overlooked). The genus has seen the addition of over 40 species since (Bodin, 1997), the great majority of which has been placed in the subgenus *Delavalia*. Two species listed by Willen (2000), *S. infiernensis* and *S. paradivergens*, are *nomina nuda* (Gómez, pers. comm.). Subgeneric assignment of species has traditionally been based only on the segmentation of the P1 endopod. The use of a single discriminant without considering additional characters of higher phylogenetic significance raises doubts about the monophyletic status of both subgenera. Willen (2000) pointed out that the P2 sexual dimorphism could provide an indication for the artificiality of this subdivision. However, species currently included in the subgenus *Delavalia* display also a huge disparity in maxillipedal structure, swimming leg armature pattern, P5 setation and segmentation, caudal ramus shape and the detailed morphology of the P1 endopod and anal operculum. The variation contained in these characters strongly suggests that *Delavalia* is a polyphyletic amalgamate, combining different evolutionary lineages with a 2-segmented P1 endopod.

The nominate subgenus *Stenhelia* is diagnosed by the plesiomorphic 3-segmented condition of the P1 endopod. Lang (1948) used the absence of the inner seta on the middle exopod segment of P1 as an additional diagnostic character but this is no longer exclusive since some species of *Stenhelia* (*Stenhelia*) display it (Thistle & Coull, 1979; Hicks, 1988) and some species of *Stenhelia* (*Delavalia*) have secondarily lost it (Sewell, 1940; Shen & Tai, 1965; Wells, 1971; Coull, 1976; Marinov & Apostolov, 1985; Rao, 1993). Thistle & Coull (1979) reviewed the subgenus and provided a key to species. Two species have been described since (Chislenko, 1978; Hicks, 1988), raising the total number to ten. Careful comparison of the published descriptions in conjunction with re-examination of type material revealed that *Stenhelia* (*Stenhelia*) is also polyphyletic. The discovery of two new species from the Bohai Sea, China provided us with the incentive to redefine the boundaries of the genus *Stenhelia*. In this paper we upgrade both *Stenhelia* and *Delavalia* to generic level, and discuss the phylogenetic relationships of some problematic species previously assigned to the subgenus *Stenhelia*.

Material and methods

Specimens were collected during an ongoing sampling survey in 1997 - 1999 from 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 m^{-2} box corer. Harpacticoid copepods were extracted using a 48 µm sieve and Ludox centrifugation flotation, 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%, and 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 differential interference contrast microscope. The terminology for body and appendage morphology follows that of Huys & Boxshall (1991) and Huys *et al.* (1996). Abbreviations used in the text and tables are P1-P6 for thoracopods 1-6; exp(enp)-1(-2-3) to denote the proximal (middle, distal) segment of a ramus; CR for caudal rami; and ae for aesthetasc. Body length was measured from the anterior margin of the cephalic shield to the posterior margin of the caudal rami. Scale bars in all illustrations are in µm. Type material was deposited in the Natural History Museum, London.

Taxonomy

Order Harpacticoida Sars, 1903
Family Diosaccidae Sars, 1906*a*
Genus *Stenhelia* Boeck, 1865

Stenhelia sheni sp. nov.

Material examined

Holotype: adult ♀ dissected on 20 slides (NHM reg. no. 2002.204). Paratypes: 1 ♂ dissected on 20 slides (NHM reg. no. 2002.205), 10 ♀♀ and 5 ♂♂ preserved in alcohol (NHM reg. nos 2002.206-220).

Description

Female (Figs 1A-E; 2A, B; 4A-D; 5A-C; 6A-B; 7A-B; 8A-C; all based on holotype)

Body length 650 - 830 µm (n = 10, mean = 731 µm).

Body (Fig. 1A-C). Distinct separation between prosome and urosome. Cephalic shield increasing in width posteriorly; thoracic and urosome somites both tapering posteriorly. Original segmentation of genital double-somites marked by discontinuous internal chitinous rib dorsolaterally and laterally (Fig. 1A-C). Hyaline frills plain, faintly striated (Fig. 1D). Anal somite medially cleft; anal operculum absent; anus terminal.

Body ornamentation (Fig.1A-C). All somites except for penultimate furnished with sensillae. Pores distributed on ventral surface of all urosomites and also dorsal and lateral surface of anal somite. Prosome without spinule rows. Distribution of spinules on urosome as follows: urosomite-1 with short paired lateral rows; posterior margin of genital double-somite with paired dorsolateral rows; urosomite-4 with paired dorsolateral rows; penultimate somite with short lateral rows; anal somite with dorsal, lateral and ventral rows at base of caudal rami.

Rostrum (Fig. 1E). Demarcated from cephalothorax, broadly triangular with bifid tip, with a pair of sensillae subapically.

Antennule (Fig. 2A, B) with 8 distinct short segments. Armature: 1-[1]; 2-[11]; 3-[9]; 4-[5 + (1+ae)]; 5-[3]; 6-[4]; 7-[4]; 8-[4+(2+ae)].

Antenna (Fig. 4 A, B). Coxa small, with spinule row. Allobasis with spinules at proximal half of abexopodal margin; abexopodal seta long and bipinnate. Exopod and endopod slender. Exopod 3-segmented, with 1-1-(1+3) setae; all setae pinnate; exp-1 with short spinules on distal margin; exp-2 short; exp-3 with spinules apically and along inner and outer edge. Endopod with 3 spinule rows; lateral armature consisting of 2 smooth setae and 2 stout pinnate spines; apical armature consisting of 7 elements: 1 pinnate spine, 4 geniculate pinnate setae and 2 slender pinnate setae, one of which is fused basally to outermost geniculate seta.

Mandible (Fig. 4 C). Gnathobase with row of 5 pointed teeth superimposed on a second row of 4, ventral corner with small semi-hyaline projection, dorsal corner with 1 pinnate and 1 smooth seta; with spinule row near insertion of palp. Palp biramous. Basis large, elongate; with 5 rows of spinules and 3 smooth setae subdistally. Exopod well developed, implanted on small pedestal arising from basis; with 6 setae: 4 pinnate, 2 naked. Endopod recurved and twisted over exopod, with 3 smooth marginal setae and 5 terminal elements: 2 terminal setae lash-like and largely fused to segment, one of which modified into an extremely large spine furnished with twisted hyaline flange in middle part; other 3 terminal setae pinnate.

Maxillule (Fig. 5A). Praecoxa and coxa demarcated. Praecoxal arthrite with 9 spines and 1 seta around distal margin, with 2 setae (1 pinnate, 1 smooth) on anterior surface; with row of spinules around medial margin. Coxal endite with 1 smooth and 2 pinnate setae. Basis with row of spinules along inner margin, with two endites; proximal endite with 2 pinnate and 2 smooth setae; distal endite with 3 pinnate setae. Endopod broader and longer than exopod, with 3 smooth and 1 pinnate setae. Exopod with 1 pinnate and 1 smooth seta.

Maxilla (Fig. 5B, C). Syncoxa with 3 rows of spinules around outer margin and 3 endites; proximal endite with 1 lateral and 2 apical pinnate setae; middle endite with 3 distal pinnate setae; distal endite with 1 smooth and 2 pinnate setae distally. Allobasis drawn out into curved claw; accessory armature consisting of claw-like spine and 4 smooth setae. Endopod 1-segmented, with 2 pinnate and 3 smooth setae.

Maxilliped (Fig. 4D) subchelate. Syncoxa with 3 rows of spinules and 3 strong pinnate setae, one of which arising from distal corner, the other two subdistally. Basis compact, with 2 rows of long spinules; with 2 long smooth setae near distal margin. Endopod slender, with a smooth seta subapically and a claw-like spine distally.

All swimming legs with well developed praecoxae and 3-segmented rami. P2-P4 endopods decreasing in length (relative to exopod) posteriorly.

P1 (Fig. 6A) smaller than other swimming legs. Coxa with 3 rows of long spinules and 1 row of tiny spinules on anterior surface. Basis with pinnate outer seta and strong bipinnate inner spine; with spinular pattern as figured. Inner margin of coxa and basis with long setules. Exopodal segments about equally long; outer and distal margin with spinules; exp-1 and exp-2 with pinnate outer spine; exp-2 inner margin with row of setules; exp-3 with 2 pinnate outer spines, 1 multipinnate and 1 unipinnate distal seta. Enp-1 elongate, reaching beyond distal margin of exp-2; about 1.7 times longer than enp-2 and enp-3 combined; with pinnate inner seta subapically; outer and distal margin with spinular row, inner margin with setules; enp-2 short, with spinules on outer margin and short plumose inner seta; enp-3 slightly

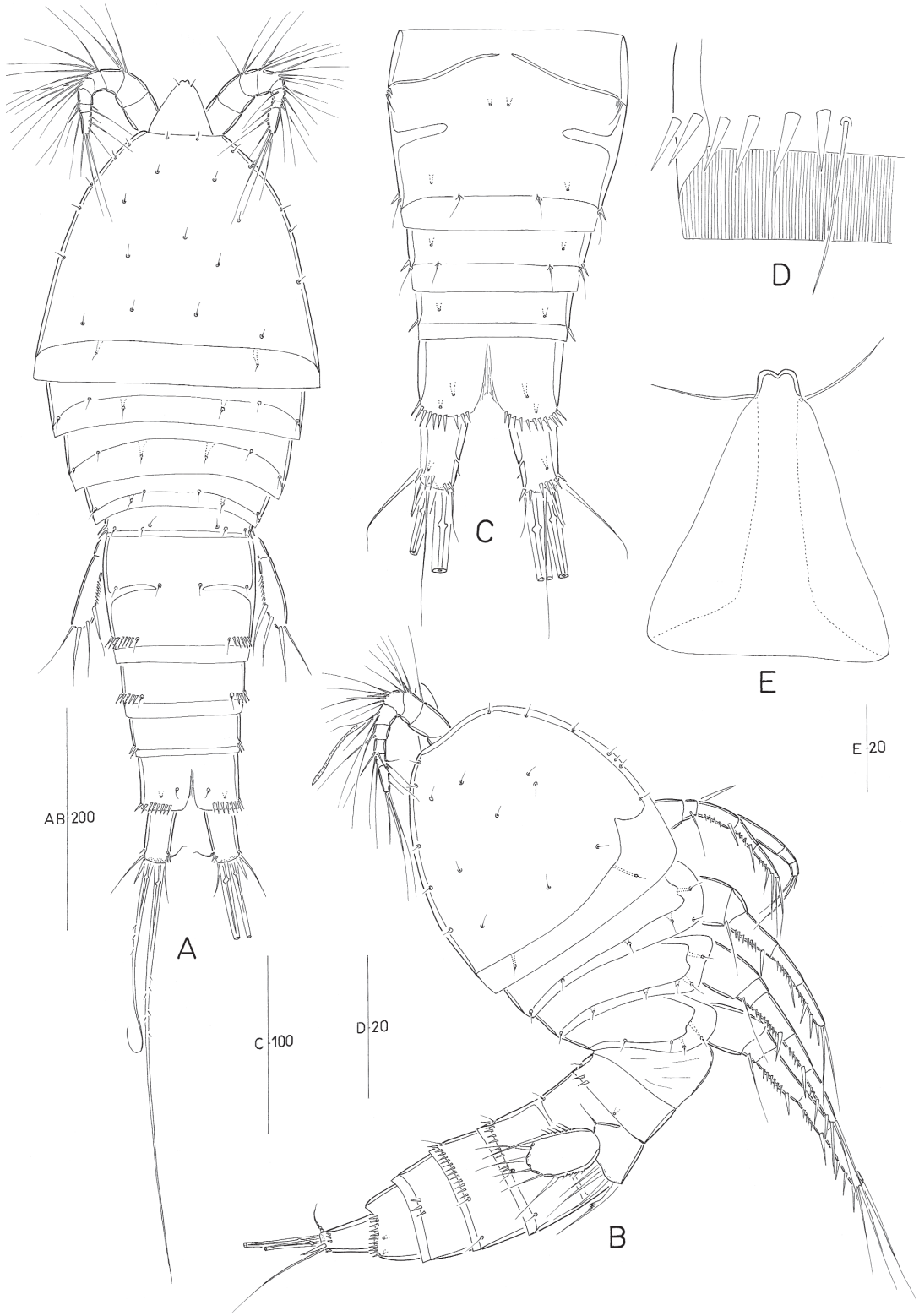


Figure 1. *Stenhelia sheni* sp. nov. (♀). **A.** habitus, dorsal; **B.** habitus, lateral; **C.** urosome (excluding P5-bearing somite), ventral; **D.** striated hyaline frill; **E.** rostrum, dorsal.

Figure 1. *Stenhelia sheni* sp. nov. (♀). **A.** habitus, vue dorsale ; **B.** habitus, vue latérale ; **C.** urosome (sauf le somite portant P5), vue ventrale ; **D.** bord hyalin strié ; **E.** rostre, vue dorsale.

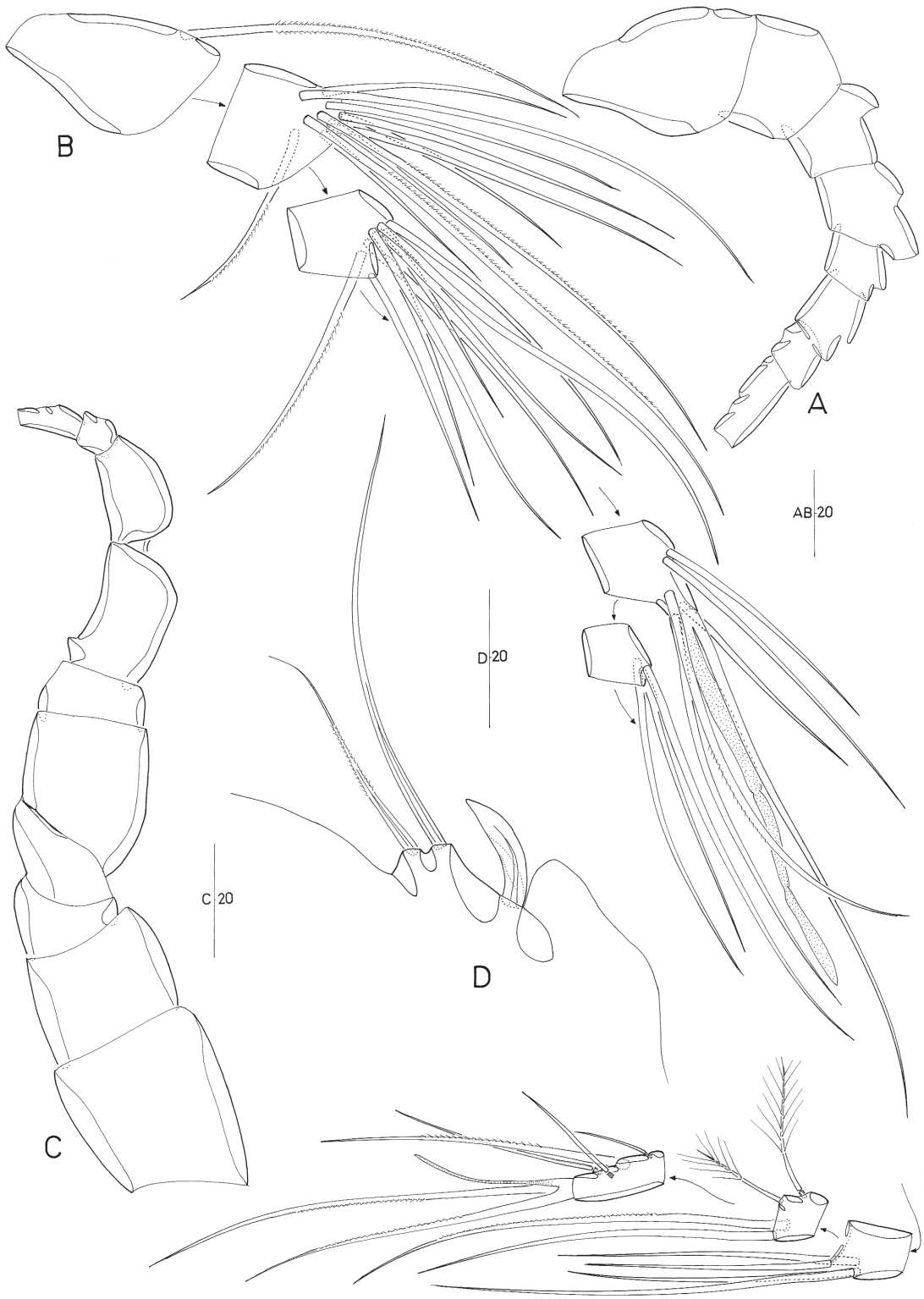


Figure 2. *Stenhelia sheni* sp. nov. **A.** antennule ♀ (armature omitted); **B.** antennule ♀ (disarticulated); **C.** antennule ♂ (armature omitted); **D.** P6 ♂.

Figure 2. *Stenhelia sheni* sp. nov. **A.** antennule ♀ (armature omise) ; **B.** antennule ♀ (désarticulée) ; **C.** antennule ♂ (armature omise) ; **D.** P6 ♂.

Figure 3. *Stenhelia sheni* sp. nov. (♂). **A.** antennule (disarticulated), ventral; **B.** antennulary segments 4-8, anterior; **C.** P3 basis and endopod, anterior.

Figure 3. *Stenhelia sheni* sp. nov. (♂). **A.** antennule (désarticulée), vue ventrale ; **B.** articles antennulaires 4-8, vue antérieure ; **C.** base et endopodite de P3, vue antérieure.

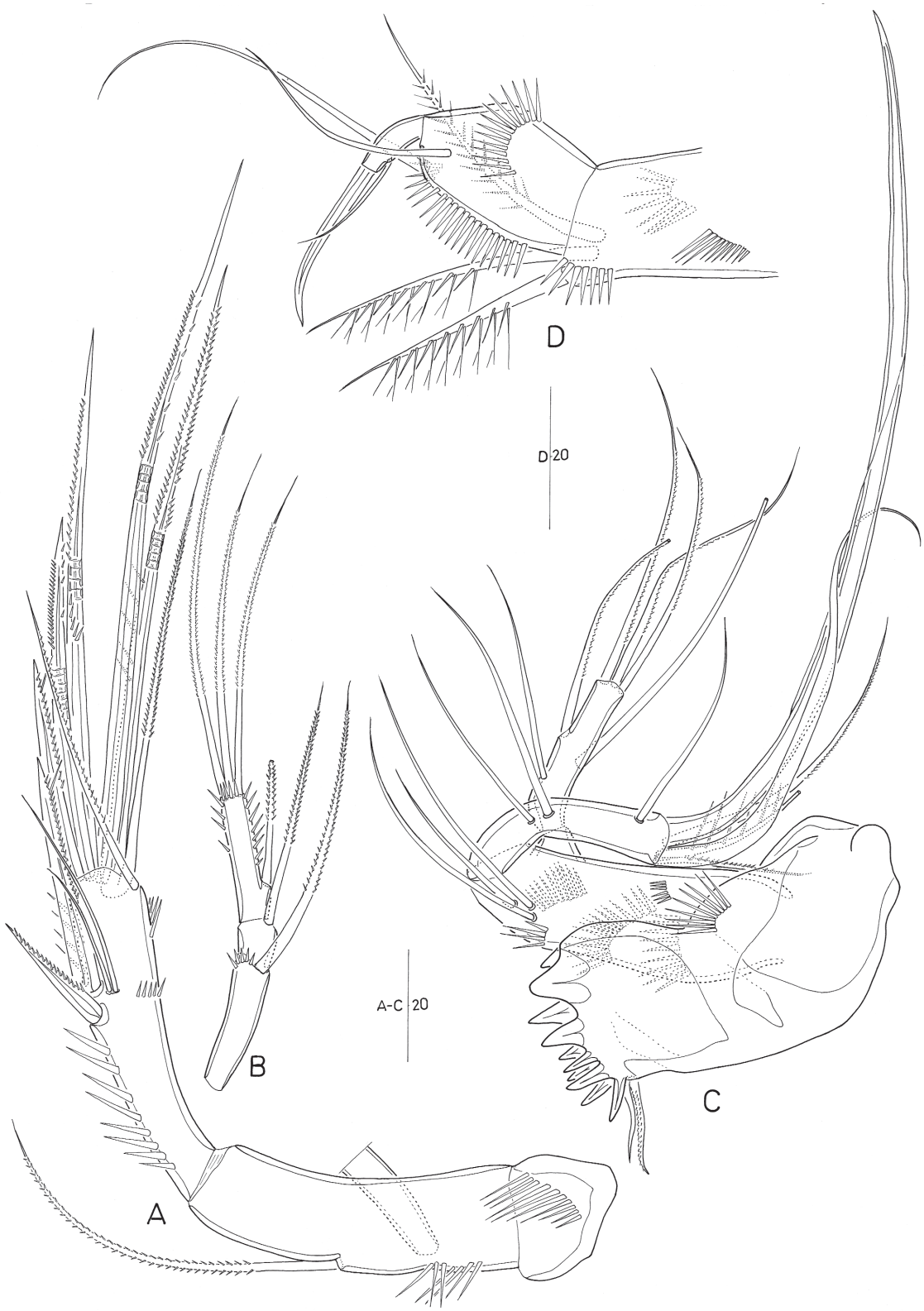


Figure 4. *Stenhelia sheni* sp. nov. (♀). **A.** antenna (exopod omitted); **B.** antennary exopod; **C.** mandible; **D.** maxilliped.
Figure 4. *Stenhelia sheni* sp. nov. (♀). **A.** antenne (exopodite omis) ; **B.** exopodite de l'antenne ; **C.** mandibule ; **D.** maxillipède.

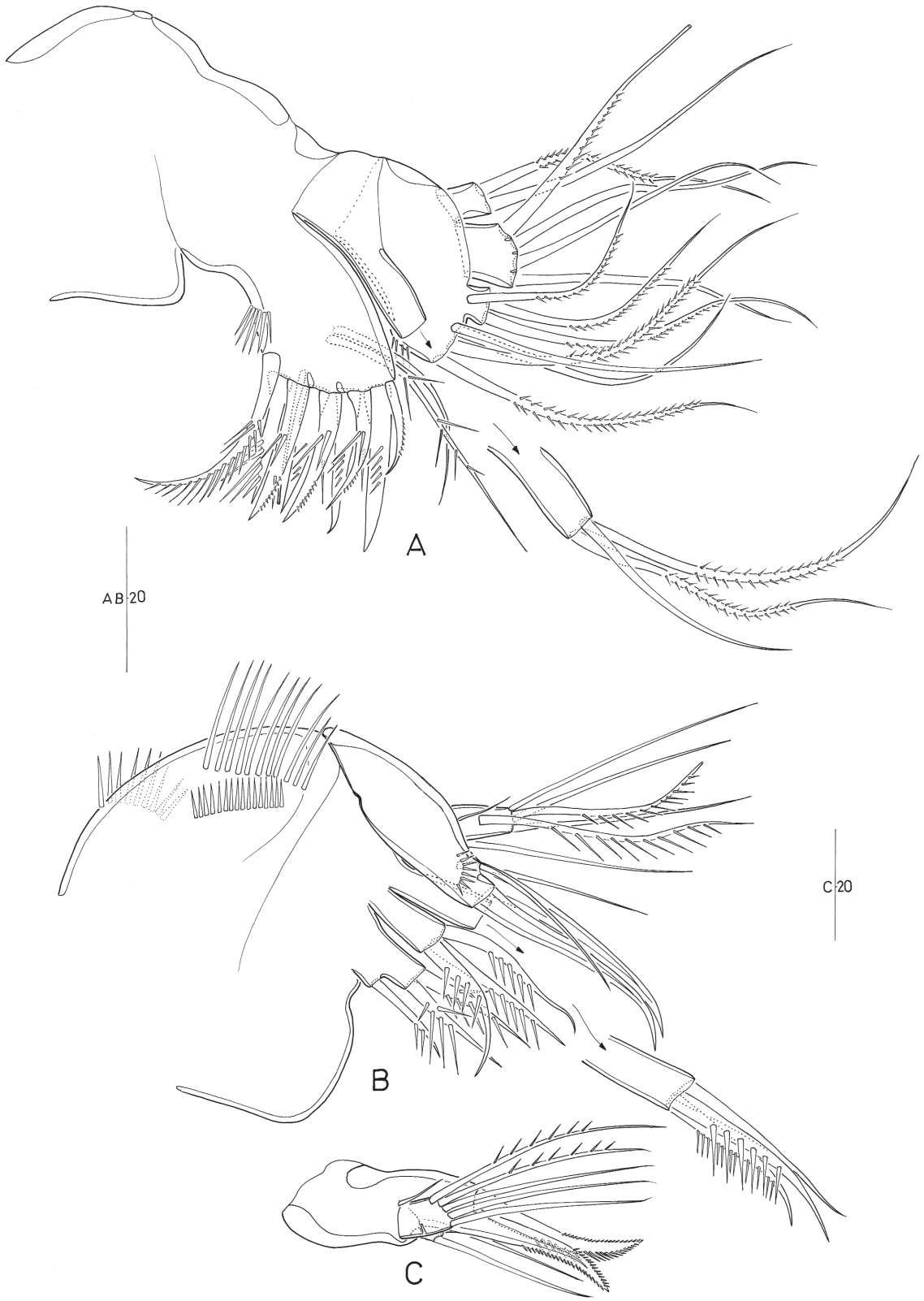


Figure 5. *Stenhelia sheni* sp. nov. (♀). **A.** maxillule; **B.** maxilla; **C.** maxillary allobasis and endopod.
Figure 5. *Stenhelia sheni* sp. nov. (♀) **A.** maxillule ; **B.** maxilla ; **C.** allobase et endopodite de la maxille.

longer than enp-2, with spinules on outer and distal margin and 3 elements apically: 1 unipinnate outer spine, 1 long and 1 short unipinnate seta.

P2-P4 (Figs 6B; 7A-B). Coxa with spinular pattern as figured. Basis with pinnate (P2) or plumose (P2-P3) outer seta; inner distal corner produced into spinous process (decreasing in size from P2 to P4), in P4 overlying larger rounded process arising from posterior surface; distal margin between rami forming blunt or spinous process. Outer distal corner of exp-1 (except P4) and -2 produced into spinous process. Endopods with broad proximal and middle segments in P2-P3, each with curved spinous process on both inner and outer distal corners; enp-3 produced into outer apical process, displacing outer spine to apical position and both apical setae to inner margin. P4 endopod markedly smaller; spinous processes as in preceding legs but less well developed; enp-1 inner seta not modified.

P1-P4 armature formulae as follows:

	Exopod	Endopod
P1	0.0.022	1.1.120
P2	1.1.123	1.2.121
P3	1.1.223	1.1.321
P4	1.1.323	1.1.221

Fifth pair of legs (Fig. 8A) not fused medially; baseoendopod and exopod separate. Baseoendopod wide, endopodal lobe with 5 terminal setae; second innermost seta shorter than others, proximal part styliform, middle part strongly pinnate and with transverse serrate comb on posterior surface (as in *S. taiae* sp. nov.: Fig. 13C), distal part flagellate; other setae slightly pinnate, outer 3 swollen at base. Exopod oval, about 1.6 times as long as broad, with long spinules around inner and outer margins; with 1 pore on anterior surface and 1 on distal margin; with 6 setae, second innermost seta smooth, others slightly pinnate, swollen at base and with fine tip.

Genital field (Fig. 8D). Gonopores separate, located anteriorly, wide, closed by P6 bearing a plumose seta and two small spines.

Caudal rami (Fig. 8B, C) 1.9 times as long as broad; with few spinules around distal margin and 3 pores on ventral surface; with 7 well developed setae. Setae I-II positioned at outer distal corner; seta I short and stout, pinnate, with subapical flagella; seta II smooth, about 1.2 times caudal ramus length; seta III displaced to subdistal ventral margin, smooth, about 1.7 times caudal ramus length; setae IV-V well developed, slightly pinnate (Fig. 1A), bases covered by transparent membrane ventrally; seta VI short and smooth, located at inner corner, fused basally to seta V; seta VII tri-articulate, plumose, arising from inner subdistal corner.

Male (Figs 2C-D, 3A-C, 6C, 8E, 9A-C)

Body length 550 - 700 µm (n = 7, mean = 611 µm). Sexual dimorphism in antennule, P2 endopod, P3, P5, P6, genital segmentation and urosome ornamentation.

Antennule (Figs 2C; 3A, B). Haplocer; 10-segmented. Armature formula: 1-[1], 2-[11], 3-[7 + ae], 4-[2], 5-[5 + (1 + ae], 6-[1], 7-[4], 8-[1 + 2 modified], 9-[4], 10-[4 + (2 + rudiment)]. Segments 1 and 7 with row of spinules. Rudiment on segment 10 representing vestigial aesthetasc.

P2 (Fig. 6C). Protopod and exopod as in ♀. Endopod modified, 2-segmented. Enp-1 with a pinnate inner seta and long spinules on outer margin, outer distal corner with a semi-transparent blunt projection, inner distal corner with spinous process, anterior surface with a pore. Enp-2 elongate, tapering distally to basally fused pinnate spine bearing stiff medially directed spinules in middle third; with 3 pinnate inner setae; outer margin with hyaline flange.

P3 (Fig. 3C). Inner distal process of basis smaller than in ♀ and with semi-transparent flanges. Spinules on outer margin of endopodal segments longer and more slender than in ♀; both outer and inner distal processes on enp-2 much smaller than in ♀.

P5 (Fig. 8E). Baseoendopods fused medially, each with 2 endopodal setae, inner one styliform at base, with transverse serrate comb in middle part, and flagellate distal part; outer one short, about one third length of inner seta, pinnate. Exopod demarcated from baseoendopod, about 1.2 times as long as broad; outer margin with few spinules; with 2 inner setae and 2 outer spines, innermost seta located proximally, short and plumose, distal seta pinnate; spines subequal in length, bipinnate.

P6 (Figs 2D; 9C) asymmetrical, with non-functional member fused to somite; with 3 elements each, innermost modified into outwardly recurved spine, middle seta smooth and about 1.8 times as long as minutely pinnate outer one.

Urosome ornamentation (Fig. 9A-C). Distribution of spinules on urosome as follows: urosomite-2 with dorsolateral rows, urosomites-3 to 5 each with lateral rows partly extending dorsally and ventrally; urosomite-5 also with ventral row; anal somite with spinules all around posterior margin.

Etymology. The species is named after Dr Chia-jui Shen, in recognition of his numerous contributions to the freshwater and marine harpacticoid fauna of China.

Stenhelia taiae sp. nov.

Material examined

Holotype: adult ♀ dissected on 20 slides (NHM reg. no. 2002.221). Paratypes: 1 ♂ dissected on 17 slides (NHM reg. no. 2002.222), 2 ♀♀ and 5 ♂♂ preserved in alcohol (NHM reg. nos 2002.223-229).

Figure 6. *Stenhelia sheni* sp. nov. **A.** P1 ♀, anterior; **B.** P2 ♀, anterior; **C.** P2 basis and endopod ♂, anterior.
Figure 6. *Stenhelia sheni* sp. nov. **A.** P1 ♀, vue antérieure ; **B.** P2 ♀, vue antérieure ; **C.** P2 base et endopodite ♂, vue antérieure.

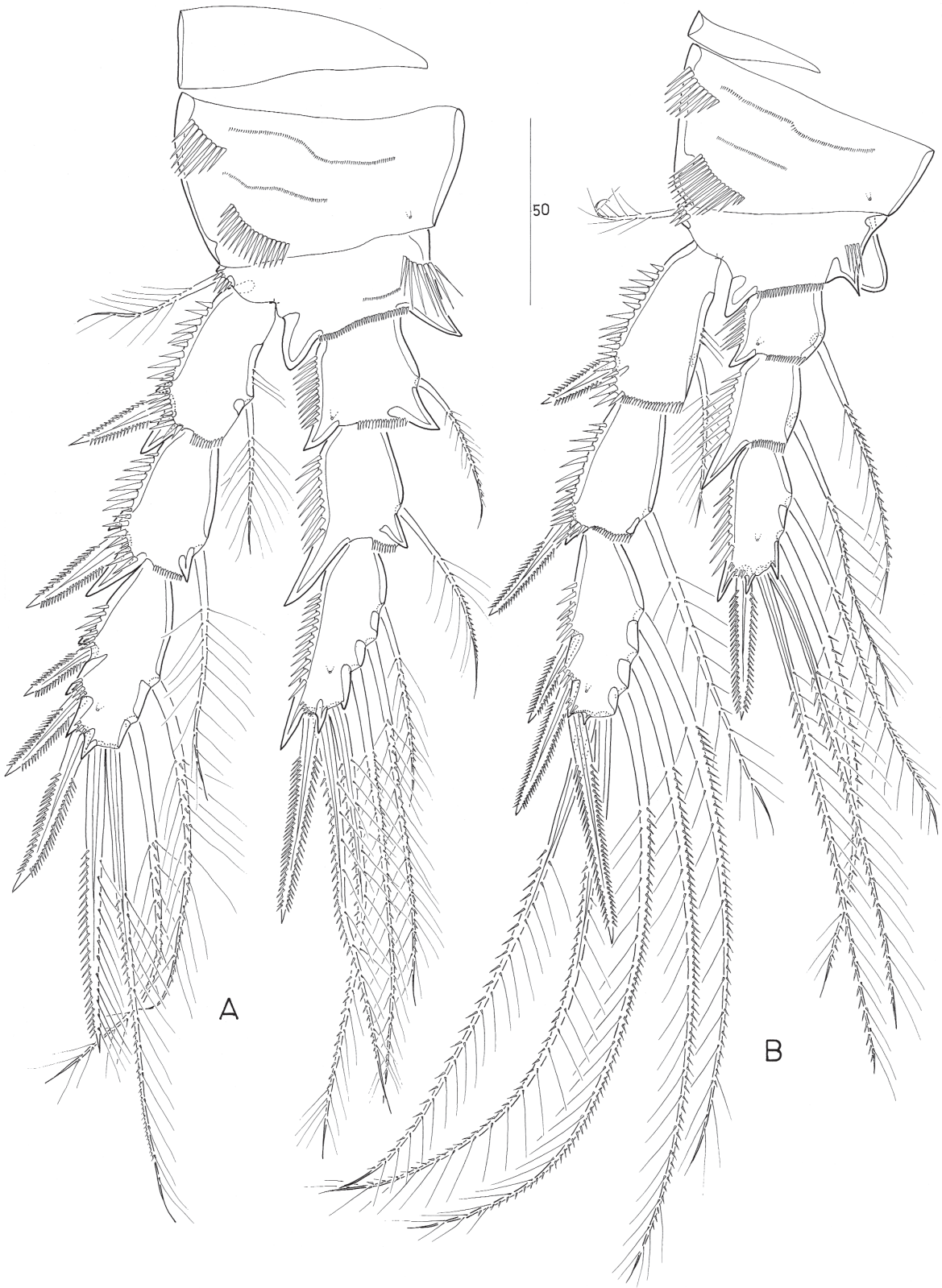


Figure 7. *Stenhelia sheni* sp. nov. (♀). **A.** P3, anterior; **B.** P4, anterior.
Figure 7. *Stenhelia sheni* sp. nov. (♀). **A.** P3, vue antérieure ; **B.** P4, vue antérieure.

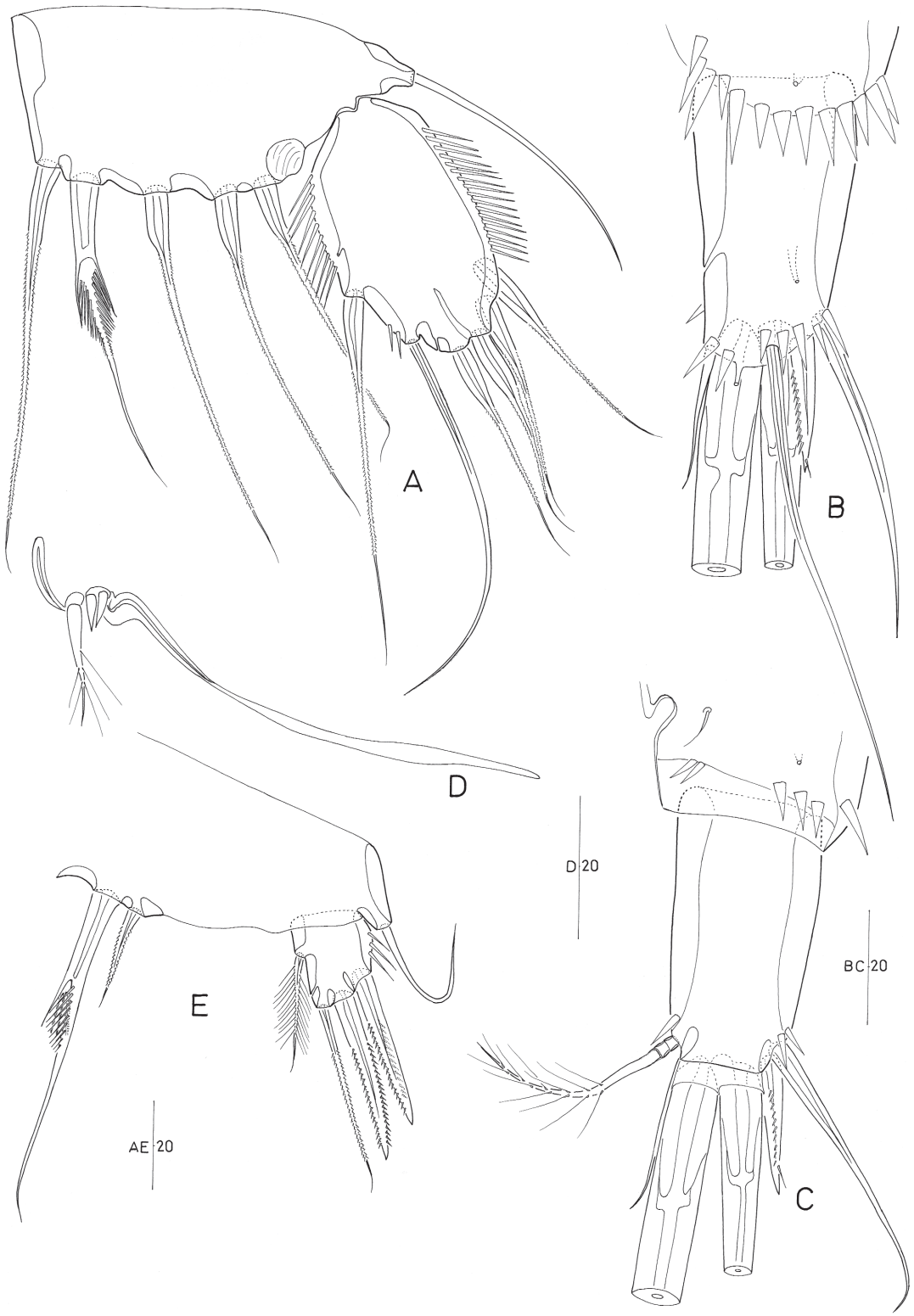


Figure 8. *Stenhelia sheni* sp. nov. **A.** P5 ♀, anterior; **B.** caudal ramus ♀, ventral; **C.** caudal ramus ♀, dorsal; **D.** genital field ♀; **E.** P5 ♂, anterior.

Figure 8. *Stenhelia sheni* sp. nov. **A.** P5 ♀, vue antérieure ; **B.** rame caudale ♀, vue ventrale ; **C.** rame caudale ♀, vue dorsale ; **D.** aire génitale ♀ ; **E.** P5 ♂, vue antérieure.

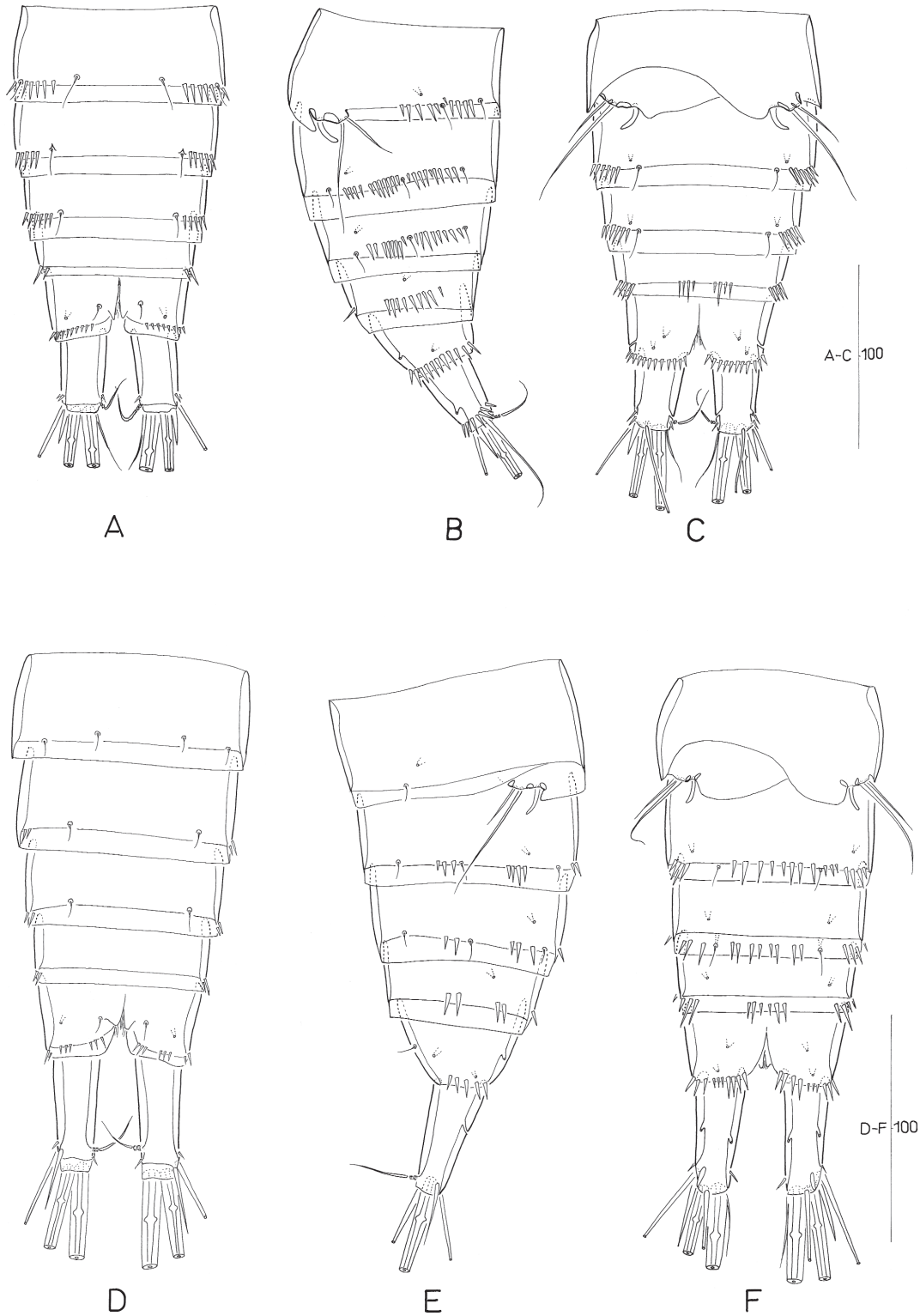


Figure 9. A.-C. *Stenhelia sheni* sp. nov. (♂) urosome (excluding P5-bearing somite). **A.** dorsal; **B.** lateral; **C.** ventral. **D.-F.** *Stenhelia taiae* sp. nov. (♀) urosome as in A.-C. **D.** dorsal; **E.** lateral; **F.** ventral.

Figure 9. A.-C. *Stenhelia sheni* sp. nov. (♂) urosome (sauf le somite portant P5). **A.** vue dorsale ; **B.** vue latérale ; **C.** vue ventrale. **D.-F.** *Stenhelia taiae* sp. nov. (♂) urosome comme en A-C. **D.** vue dorsale ; **E.** vue latérale ; **F.** vue ventrale.

Description

Female (Figs 10A-C,11A-B,12A-B, 13A-C; all based on holotype)

Body length 560 - 660 m (n = 3; mean = 593 μm).

Body ornamentation (Fig. 10A-C). Hyaline frills finely striated as in *S. sheni* sp. nov. Distribution of spinules on urosome as following: urosomite-1 with paired lateral rows of tiny spinules; posterior margin of genital double-somite, urosomite-4 and penultimate somite each with short paired lateral rows; anal somite with dorsal, lateral and ventral rows at base of caudal rami.

Rostrum, antennule, antenna and mouthparts as in *Stenhelia sheni* sp. nov.

P1 (Fig. 11A). Smaller than other swimming legs. Coxa with 3 rows of long spinules and 3 rows of tiny spinules on anterior surface. Basis with pinnate outer seta and inner spine; with spinular pattern as figured. Inner margin of coxa and basis with long setules. Exp-1 and exp-2 with pinnate outer spine; outer and distal margin with spinules; exp-2 inner margin with setules; exp-3 with 2 pinnate outer spines and 2 plumose distal setae, outer margin with spinules. Enp-1 as long as exp-1 and exp-2 combined, about 1.5 times as long as enp-2 and enp-3 combined; with pinnate inner seta subapically; outer and distal margin with row of spinules, inner margin with row of long setules; enp-2 with coarse spinules on outer margin and short plumose inner seta; enp-3 slightly longer than enp-2, with coarse spinules on outer and distal margin and 3 apical elements: outer unipinnate spine, 1 short and 1 long pinnate seta.

P2-P4 (Figs 11B; 12A-B). Coxa with spinular pattern as figured. Basis with pinnate (P2-P3) or plumose (P4) outer seta; inner distal corner produced into strong spinous process (decreasing in size from P2 to P4), in P4 overlying rounded process arising from posterior surface; distal margin between rami forming spinous process. Outer distal corner of exp-1 and -2 produced into spinous process (but much smaller than in *S. sheni* sp. nov.). Middle endopodal segment with strong spinous process at outer distal corner; inner distal corner of P2 enp-2 and -3 also produced; enp-3 produced into outer apical process. P4 endopod markedly smaller.

P1-P4 spine and seta formulae as in *S. sheni* sp. nov.

Fifth pair of legs (Fig. 13C) not fused medially. Baseoendopod and exopod separate. Baseoendopod wide, armed with five endopodal setae; innermost seta longest and pinnate; second innermost seta stouter than others, middle part strongly pinnate and with transverse serrate comb on posterior surface; remaining setae minutely pinnate. Exopod about 1.4 times as long as broad; with spinules around outer margin and one pore on anterior surface; with 6 setae, second innermost seta smooth, others minutely pinnate.

Genital field as in *S. sheni* sp. nov.

Caudal rami (Fig. 13A-B) 2.4 times as long as broad; with few spinules around distal margin; ventral surface with 1 pore; with 7 setae, position and ornamentation as in *S. sheni* sp. nov. Seta I spiniform but more slender and relatively longer than in *S. sheni* sp. nov.; seta II about 1.9 times as long as caudal ramus; seta III about 2.8 times as long as caudal ramus.

Male (Figs 9 D-F, 11C, 13D)

Body length 530 - 620 μm (n = 5, mean = 562 μm) Sexual dimorphism in antennule, P2 endopod, P5, P6, genital segmentation and urosome ornamentation.

P2 (Fig. 11C) with protopod and exopod as in ♀. Endopod modified, 2-segmented; morphology as in *S. sheni* sp. nov. but enp-2 more compact and stiff spinules on distal spine coarser.

P5 (Fig. 13D). Baseoendopods fused medially, each with 2 endopodal setae; inner one stout, middle part strongly pinnate and with transverse serrate comb on posterior surface, distal part flagellate; outer one short and finely pinnate. Exopod demarcated from baseoendopod, about 1.2 times as broad as length; inner element spine-like, smooth; distal margin with 2 pinnate subequal spines (inner one about twice the length of outer) and 1 smooth seta.

P6 as in *S. sheni* sp. nov.

Urosome ornamentation (Fig. 9 D-F) sparser than in *S. sheni* sp. nov. but generally more pronounced midventrally. Distribution of spinules on urosome as follows: urosomites-3 to -5 each with two short paired rows laterally and one median row ventrally; anal somite with dorsal, lateral and ventral row at base of caudal rami.

Etymology. The species is dedicated to Dr Ai-yun Tai, in recognition of her contributions to the taxonomy of Chinese harpacticoid copepods.

Discussion

The sole basis for justifying the current subgeneric division of *Stenhelia* is the difference in segmentation of the P1 endopod with the plesiomorphic 3-segmented condition being diagnostic for *Stenhelia* (*Stenhelia*) and the apomorphic 2-segmented state defining *Stenhelia* (*Delavalia*). In addition, comparison of other phylogenetically informative characters clearly indicate that both subgenera represent polyphyletic assemblages and are in urgent need of redefinition. In order to redefine the genus *Stenhelia* unambiguously, the subgeneric classification is abandoned here and *Stenhelia* (*Delavalia*) is excluded by elevating it to generic rank. This is a temporary course of action pending a phylogenetic analysis of the Stenheliinae required to resolve the polyphyletic status of *Delavalia* grad. nov.

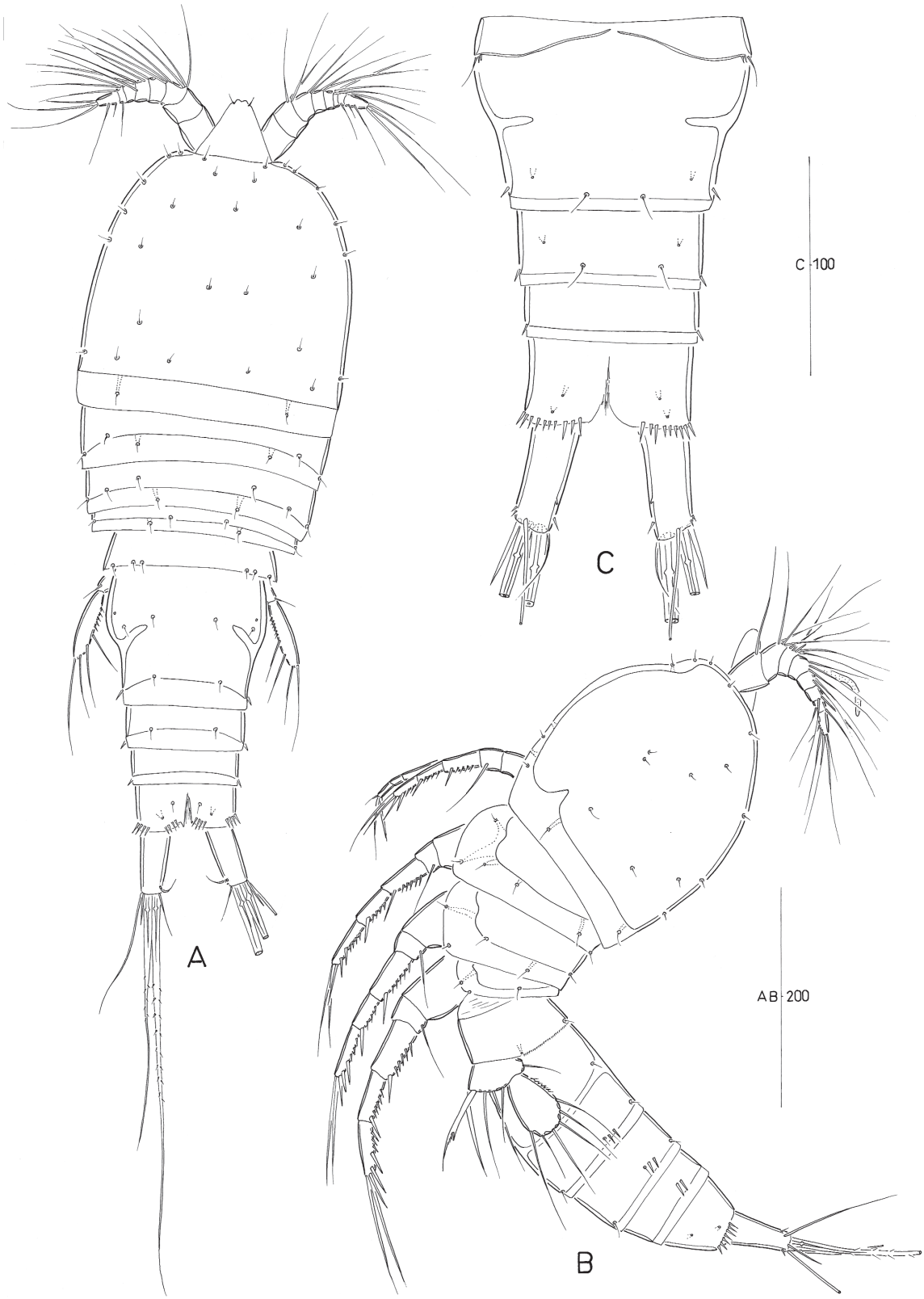


Figure 10. *Stenhelia taiae* sp. nov. (♀). **A.** habitus, dorsal; **B.** habitus, lateral; **C.** urosome (excluding P5-bearing somite), ventral.
Figure 10. *Stenhelia taiae* sp. nov. (♀). **A.** habitus, vue dorsale ; **B.** habitus, vue latérale ; **C.** urosome (sauf le somite portant P5), vue ventrale.

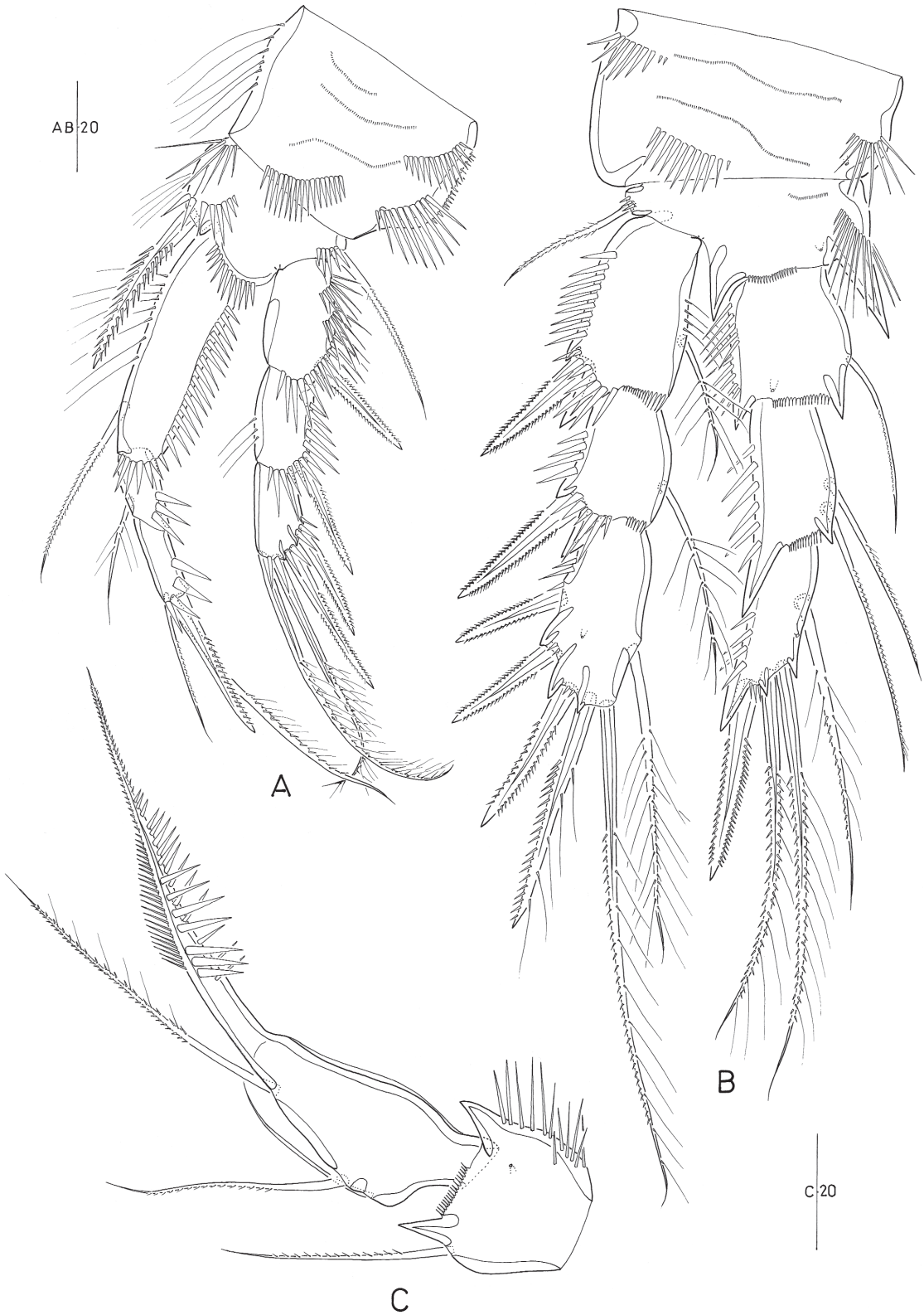


Figure 11. *Stenhelia taiae* sp. nov. **A.** P1 ♀, anterior; **B.** P2 ♀, anterior; **C.** P2 endopod ♂, anterior.
Figure 11. *Stenhelia taiae* sp. nov. **A.** P1 ♀, vue antérieure ; **B.** P2 ♀, vue antérieure ; **C.** endopodite de P2 ♂, vue antérieure.

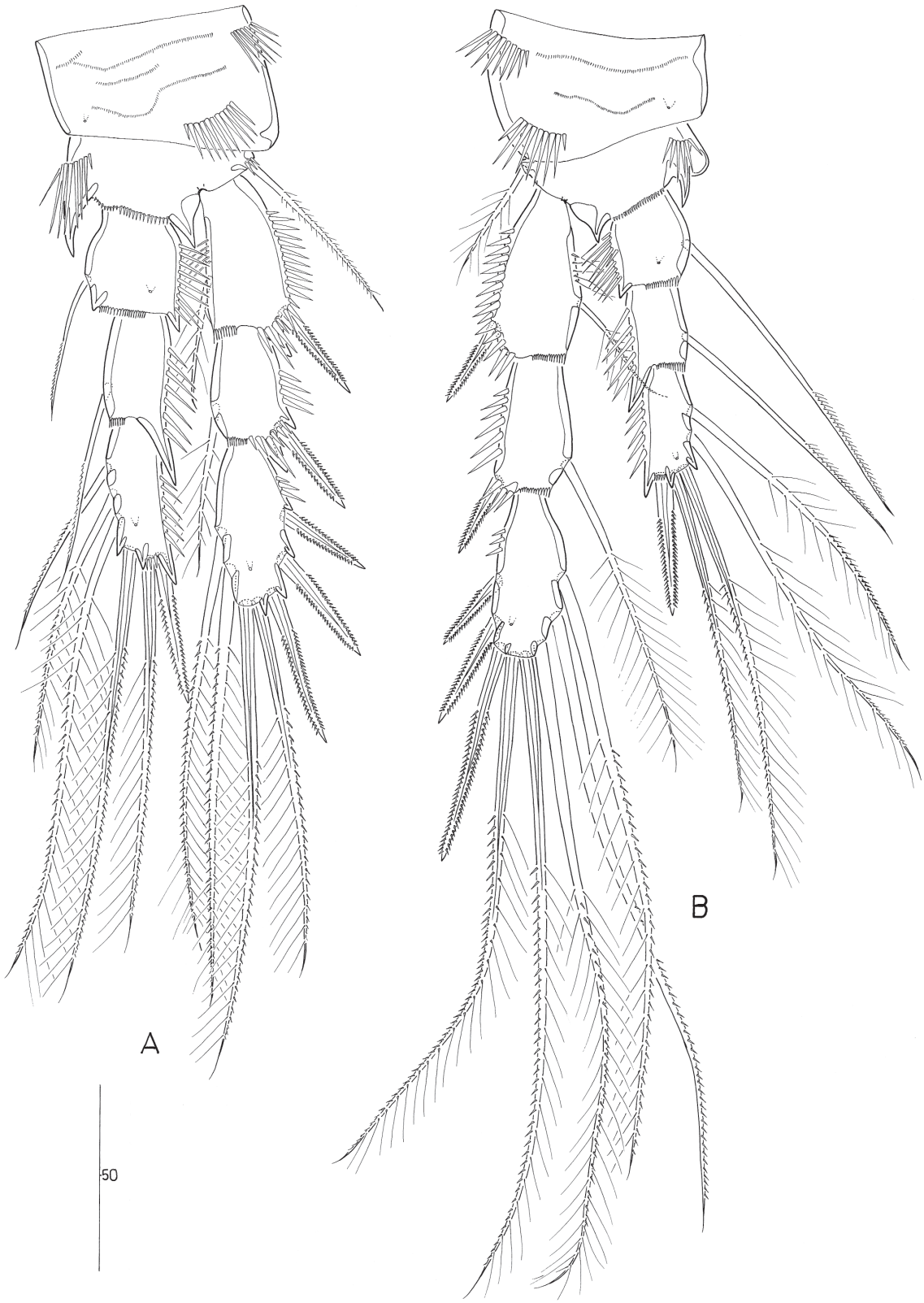


Figure 12. *Stenhelia taiae* sp. nov. (♀). **A.** P3, anterior ; **B.** P4, anterior.
Figure 12. *Stenhelia taiae* sp. nov. (♀). **A.** P3, vue antérieure ; **B.** P4, vue antérieure.

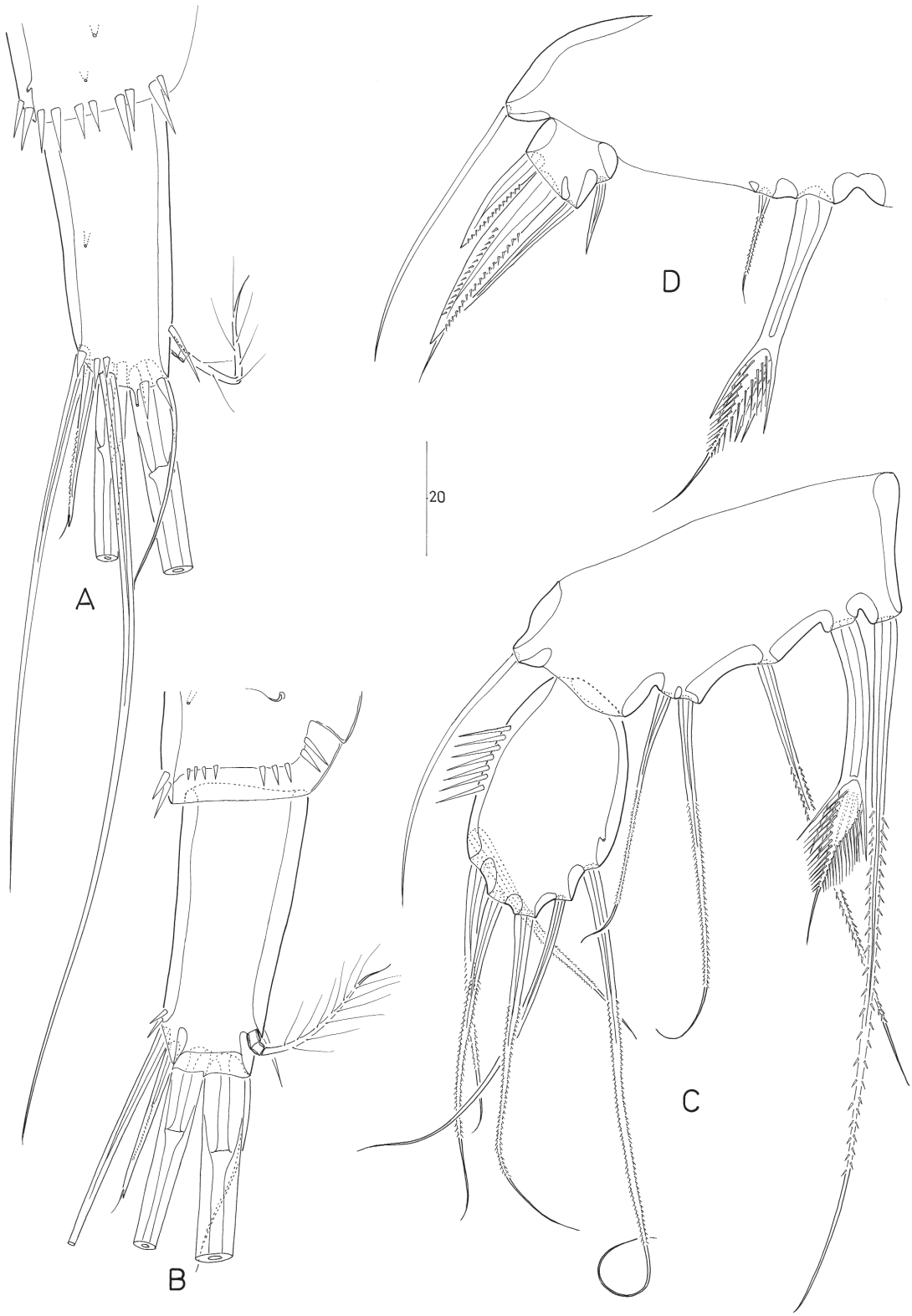


Figure 13. *Stenhelia taiae* sp. nov. **A.** caudal ramus ♀, ventral; **B.** caudal ramus ♀, dorsal; **C.** P5 ♀, anterior; **D.** P5 ♂, anterior.

Figure 13. *Stenhelia taiae* sp. nov. **A.** rame caudale ♀, vue ventrale ; **B.** rame caudale ♀, vue dorsale ; **C.** P5 ♀, vue antérieure ; **D.** P5 ♂, vue antérieure.

Redefinition of *Stenhelia* Boeck, 1865

The genus *Stenhelia* is restricted to a core group of species formerly allocated to the subgenus *Stenhelia* (*Stenhelia*). This core group includes the type species *S. gibba* and seven additional species: *S. proxima* Sars, 1906*b*; *S. curviseta* Lang, 1936; *S. divergens* Nicholls, 1939; *S. peniculata* Lang, 1965; *S. pubescens* Chislenko, 1978, and both new species from the Bohai Sea. The monophyly of this species group is substantiated by the presence of a modified seta on the P5 baseoendopod of both sexes, being the second innermost in the ♀ and the innermost in the ♂. This seta bears a transverse serrate comb across the posterior surface (Fig. 13C), marking the transition between the styliform proximal part and the setiform middle part. The diagnostic value of this seta was first noticed by Lang (1965) in his description of *S. peniculata* and re-examination of material has confirmed its presence in *S. divergens*, *S. gibba* and *S. proxima*. Chislenko's (1978) description of *S. pubescens* is not conclusive in this respect but in view of the close relationship between this species and *S. sheni* sp. nov. we assume it to be present.

The genus *Stenhelia* shares a sistergroup relationship with *S. asetosa* Thistle & Coull, 1979 which is designated below as the type of a new genus *Anisostenhelia*. Both genera display the following synapomorphies:

(1) P2 exp-3 with 123 formula (loss of 1 inner seta).

(2) P3 exp-3 with 223 formula (loss of 1 inner seta).

(3) P2-P3 enp-3 produced into an outer apical spinous process, displacing the outer spine to an apical position and both apical setae to the inner margin.

(4) ♂ P2 endopod with outer distal corner of enp-2 drawn out into long ornate process with flagellate distal portion; this process is homologous to the outer spine of the female and is characteristically armed with stout spinules along the outer margin (Figs 6C; 11C); the outer margin of the segment typically has a hyaline flange in *Stenhelia*. The males of *S. curviseta*, *S. divergens* and *S. pubescens* are unknown but based on other morphological similarities it is conceivable that they exhibit the same type of sexual dimorphism. Lang (1965) shows the outer spine in the male of *S. peniculata* as an articulated element but this may be an observational error. An incomplete surface suture marking the original point of articulation was observed in the male of *S. taiae* (Fig. 11C); excessive squashing during mounting may accentuate such surface suture, creating the false impression that it is a functional articulation. Examination of developmental stages of both *S. gibba* and *S. sheni* has confirmed the presence of this seta in copepodid V.

(5) ♂ P5 exopod with two outermost elements modified into spines.

(6) ♂ P6 with innermost element modified into outwardly recurved spine.

(7) anal operculum completely absent.

All *Stenhelia* species have lost the inner seta on P1 exp-2 but this character is shared with *S. aemula* and *S. asetosa*, constituting a potential synapomorphy for *Stenhelia*, *Anisostenhelia* and *Beatricella* (see below). In his description of *S. divergens* Nicholls (1939) illustrates a seta-like element on this segment but does not refer to it in the text. He also states that the types are represented by two ovigerous females and that the male is unknown. The type material deposited in the Natural History Museum (reg. no. 1940.5.1.17) consists of a single copepodid V male. Re-examination of this specimen confirmed Lang's (1965) supposition that the setiform element figured by Nicholls (1939) represents one of several setules commonly found in this position (Figs 6A; 11A). According to Thistle & Coull's (1979) setal formula table, *S. divergens* possesses 2 inner setae on P2 enp-3 which contradicts Nicholls' (1939) description and our observation.

Genus *Stenhelia* Boeck, 1865

Diagnosis

Stenheliinae. Anal operculum absent. Caudal rami at most slightly longer than anal somite; setae not modified. Rostrum bell-shaped, usually with bifid tip. Antennule ♀ 8-segmented with aesthetasc on segments 4 and 8. Antennary exopod 3-segmented with setation formula [1,1,(1 + 3 apical)]. Mandible with elongate basis bearing 3 setae; exopod with 6 setae; endopod with 3 lateral setae, and 1 very long and 1 shorter lash plus 3 accessory setae apically. Maxillule without modified elements on arthrite. Maxilliped subchelate; syncoxa with 3 setae; basis with 2 setae; endopod slender, bearing claw and 1 accessory seta. P1 with 3-segmented rami; not sexually dimorphic; exp-2 without inner seta; enp-1 usually distinctly longer than enp-2 and -3 combined; enp-3 with 3 elements apically. P2 endopod ♂ 2-segmented; enp-2 tapering distally, with 3 inner setae and drawn out into slender bipinnate process bearing large stiff spinules along outer margin. P4 exp-3 with 3 well developed inner setae; enp-1 with normal plumose seta. P1-P4 armature formula:

	Exopod	Endopod
P1	0.0.022	1.1.3
P2	1.1.123	1.2.121*
P3	1.1.223	1.1.(2-3)21*
P4	1.1.323	1.1.221

* enp-3: outer spine typically displaced to apical position, and both apical setae to inner margin

P5 ♀ with 6 setae on exopod; baseoendopod with 5 setae, outermost well developed, second innermost modified bearing transverse serrate comb on posterior surface. P5 ♂

Table 1. Swimming leg setal formulae of species previously allocated to the subgenus *Stenhelia*.
Tableau 1. Formules sétales des pattes natatoires des espèces préalablement placées dans le sous-genre *Stenhelia*.

	P1	P1		P2		P3		P4	
	enp-1:enp-(2+3)	exp	enp	exp	enp	exp	enp	exp	enp
gibba	>>	0.0.022	1.1.3	1.1.123	1.2.121[a]	1.1.223	1.1.221[a]	1.1.323	1.1.221
proxima	>>	0.0.022	1.1.3	1.1.123	1.2.121[a]	1.1.223	1.1.221[a]	1.1.323	1.1.221
curviseta	>	0.0.022	1.1.3	1.1.123	1.2.121[a]	1.1.223	1.1.221[a]	1.1.323	1.1.221
divergens	=	0.0.022[b]	1.1.3	1.1.123	1.2.121[a]	1.1.223	1.1.321[a]	1.1.323	1.1.221
peniculata	>>	0.0.022	1.1.3	1.1.123	1.2.121[a]	1.1.223	1.1.321[a]	1.1.323	1.1.221
pubescens	>>	0.0.022	1.1.3	1.1.123	1.2.121[a]	1.1.223	1.1.321[a]	1.1.323	1.1.221
sheni sp. nov.	>>	0.0.022	1.1.3	1.1.123	1.2.121[a]	1.1.223	1.1.321[a]	1.1.323	1.1.221
taiae sp. nov.	>>	0.0.022	1.1.3	1.1.123	1.2.121[a]	1.1.223	1.1.321[a]	1.1.323	1.1.221
asetosa	<	0.0.022[b]	1.1.3	0.1.123	1.2.121[a]	0.1.223	1.1.321[a,c]	0.1.323	1.1.221
aemula	<	0.0.022	1.1.3	1.1.223	1.2.121	1.1.323	1.1.321	1.1.323	1.1.221
xylophila	<<	0.1.022	1.1.3	1.1.223	1.2.121	1.1.323	1.1.221	1.1.323	1.0.221
diegensis	not applicable[d]	0.1.022	1.3[d]	1.1.223	1.1.121[e]	1.1.323	1.1.221	1.1.323	1.1.221

[a]: outer spine positioned terminally, displacing 2 apical elements to inner margin
[b]: the inner seta on exp-2 originally reported in these species (Nicholls, 1939; Thistle & Coull, 1979) is an ornamentation element
[c]: the report of 2 inner setae on enp-2 in the ♂ (Thistle & Coull, 1979) is erroneous
[d]: the 3-segmented P1 endopod figured by Thistle & Coull (1979) is here re-interpreted as 2-segmented
[e]: Thistle & Coull (1979) show 2 inner setae on enp-1 but this is based on an observational error

with free exopod bearing 2 spiniform outer elements and 2 setiform inner elements; inner endopodal spine modified, with serrate comb as in ♀. P6 ♂ with 3 setae, innermost spiniform and outwardly recurved.
Type species: *Stenhelia gibba* Boeck, 1865 (by monotypy)
Other species: *S. proxima* Sars, 1906*b*; *S. curviseta* Lang, 1936; *S. divergens* Nicholls, 1939; *S. peniculata* Lang, 1965; *S. pubescens* Chislenko, 1978; *S. sheni* sp. nov.; *S. taiae* sp. nov.

The genus *Stenhelia* can be divided in two species groups on the basis of the number of inner setae on the distal endopod segment of P3 (Table 1). *S. gibba*, *S. proxima* and *S. curviseta* have two inner setae on this segment. Thistle & Coull (1979) remarked that the distinction between the latter two species is based solely on the shape of the setae on the ♀ P5 baseoendopod and may not be sufficient to warrant distinct specific status for *S. curviseta*. Although the curved nature of the inner baseoendopodal seta (cf. name) is probably based on an artefact, we believe conspecificity is ruled out by differences in the length of the P1 endopod and in the spacing and relative size of the endopodal setae on the ♀ P5.

The second group unites all remaining species that display three inner setae on P3 enp-3. The only Atlantic species in this group, *S. divergens*, can be readily differentiated from its four North Pacific congeners (*S. pubescens*, *S. peniculata*, *S. sheni* sp. nov., *S. taiae* sp. nov.) by the short P1 endopod. The latter can be differentiated by morphometric differences in the P1 endopod and the caudal rami (Table 2).

S. sheni appears most similar to *S. pubescens*, described from the Sea of Japan (Chislenko, 1978). It differs from the latter mainly by (1) P1 enp-1 shorter, only 1.6 times as long

Table 2. Morphometric comparison of P1 endopod and caudal ramus between Chinese and closely related species
Tableau 2. Comparaison morphométrique de l'endopodite des P1 et des rames caudales entre les espèces chinoises et les autres espèces apparentées.

	*S. peniculata**	*S. pubescens**	*S. sheni*	*S. taiae*
P1: length ratio enp-1/ (enp-2+enp-3)	2.1	2.2	1.6	1.5
CR: length/width ratio	1.1	1.5	1.9	2.4

*: morphometric data based on original descriptions by Lang (1965) and Chislenko (1978)

as enp-2 and enp-3 combined (about 2.2 times in *S. pubescens*), (2) processes on outer distal corner of P2-P4 endopodal segments distinctly larger, (3) most setae on ♀ P5 with swollen base (normal setae in *S. pubescens*), (4) setae II-III of caudal ramus smooth (conspicuously plumose in *S. pubescens*), and (5) caudal rami distinctly longer in *S. sheni* (Table 2).

S. taiae is closely related to *S. sheni* but differs from the latter primarily in (1) ornamentation pattern on urosome of both sexes (Fig. 1A-B; 9A-F; 10A-B), (2) ♀ P5 without basally swollen setae and innermost seta of baseoendopod much longer than others (about equally long in *S. sheni*), (3) caudal ramus longer (Table 2) and seta I slender (stout in *S. sheni*), (4) ♂ P5 exopod innermost seta spiniform (plumose seta in *S. sheni*), outermost spine about half the length of adjacent spine (subequal in *S. sheni*), (5) ♂ P5 exp broader, about 1.2 times as wide as long (about 1.2 times as long as wide in *S. sheni*).

Key to species of *Stenhelia* Boeck, 1865

1. P3 enp-3 with 2 inner setae (formula 221) ..... 2.
   P3 enp-3 with 3 inner setae (formula 321) ..... 4.
2. P1 enp-1 reaching to distal margin of exp-2; innermost seta of ♀ P5 benp longer than twice length of adjacent seta/spine ..... *S. curviseta* Lang, 1936.
   P1 enp-2 reaching well beyond distal margin of exp-2; innermost seta of ♀ P5 benp at most slightly longer than adjacent seta/spine ..... 3.
3. P1 enp-1 at least as long as exopod; elements of ♀ P5 benp all abbreviated, outermost two very short, middle one shorter than comb-bearing seta and spiniform ..... *S. gibba* Boeck, 1865.
   P1 enp-1 distinctly shorter than exopod; elements of ♀ P5 benp all well developed, middle one longer than comb-bearing seta and spiniform ..... *S. proxima* Sars, 1906b.
4. P1 enp-1 distinctly shorter than exp-1 and -2 combined ..... *S. divergens* Nicholls, 1939.
   P1 enp-1 at least as long as exp-1 and -2 combined ..... 5.
5. Caudal rami at most 1.5 times as long as wide; P1 enp-1 at least twice as long as enp-2 and -3 combined ..... 6.
   Caudal rami at least 1.5 times as long as wide; P1 enp-1 distinctly shorter than twice length of enp-2 and -3 combined ..... 7.
6. Caudal rami 1.5 times as long as wide with setae II and III conspicuously plumose ..... *S. pubescens* Chislenko, 1978.
   Caudal rami almost squarish with setae II and III at most sparsely ornate ..... *S. peniculata* Lang, 1965.
7. ♀ P5 without basally swollen setae and innermost seta of baseoendopod much longer than others; ♂ P5 exopod innermost seta spiniform, outermost spine about half the length of adjacent spine ..... *S. taiae* sp. nov.
   ♀ P5 with basally swollen setae and elements of baseoendopod about equally long; ♂ P5 exopod innermost seta plumose, outer spines subequal in length ..... *S. sheni* sp. nov.

Status of *Stenhelia* (*Stenhelia*) *asetosa* Thistle & Coull, 1979

The original description of this species shows several unusual features which require clarification before its taxonomic position can be re-assessed. A re-examination of the type material deposited in the National Museum of Natural History, Washington, D.C. (NMNH reg. nos 169876-169877) revealed the following discrepancies with Thistle & Coull's (1970) figures:

(1) The rostrum is bifid at the tip and the antennule bears a tiny aesthetasc on the terminal segment forming part of the apical acrothek.

(2) The mandibular endopod has 5 terminal elements (as in *S. sheni*): 2 terminal setae lash-like and largely fused to segment, one of which modified into an extremely large spine furnished with twisted hyaline flange in middle part; other 3 terminal setae pinnate.

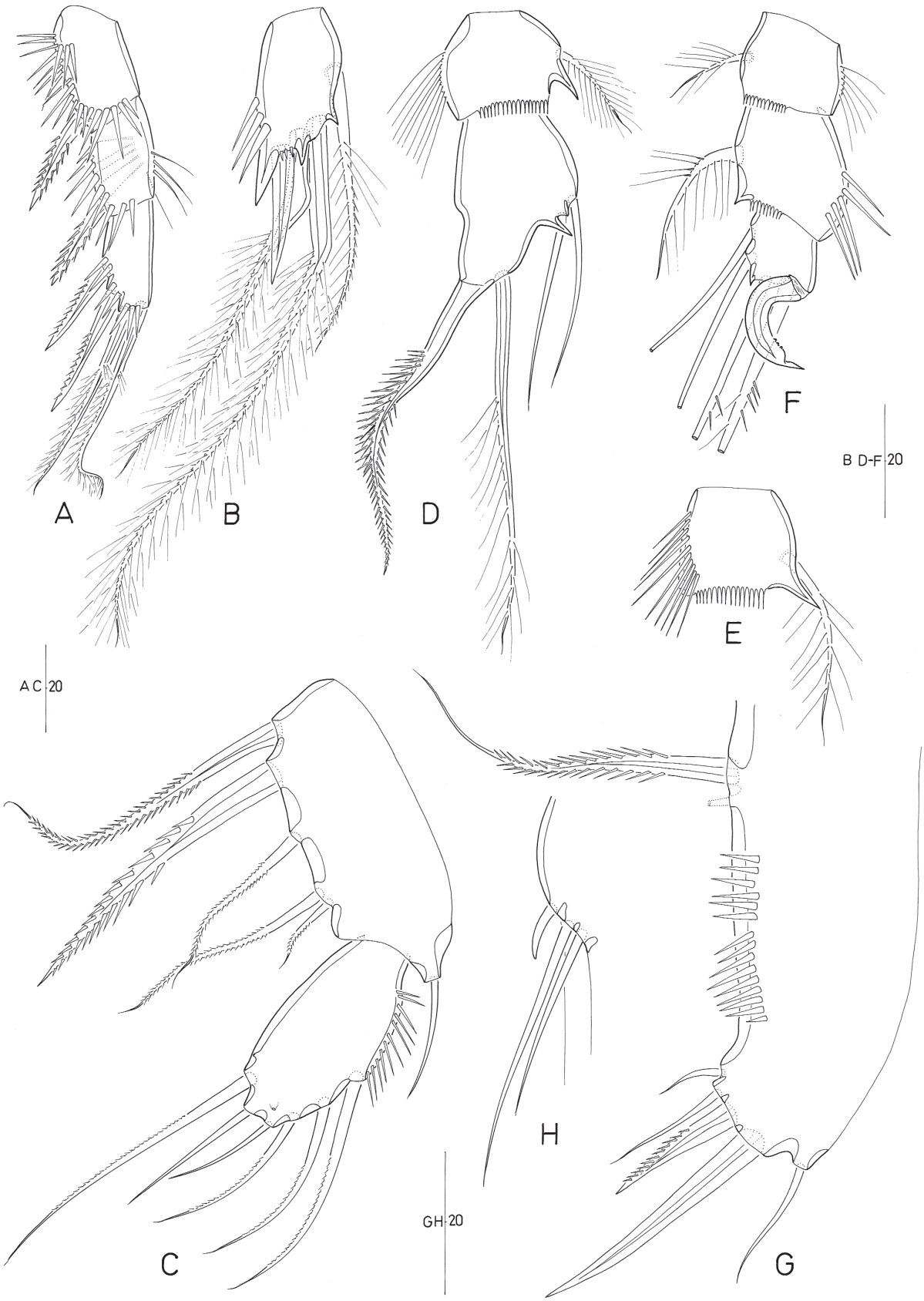
(3) The maxilliped has the same armature pattern as in *Stenhelia* with 3 setae on the syncoxa and 2 on the basis.

(4) There is some confusion surrounding the armature of the P1 exopod. Thistle & Coull figured a thin inner seta on exp-2 which they also mentioned in the text description but in their setation table the formula is listed as 0.0.022. Re-examination revealed this element to be one of the long setules found along the inner margin and posterior surface of this segment (Fig. 14A).

(5) The two apical setae on P2 enp-3 in the ♀ have a characteristically swollen basal part and are much longer than figured in the original description (Fig. 14B).

(6) The outer distal corner of the ♂ P2 enp-2 is drawn out into long ornate process as in *Stenhelia*; it bears a double row of spinules along the middle outer margin but the spinules are not as coarse as in *Stenhelia*; the outer margin of the segment has no hyaline flange as in *Stenhelia* (Fig. 14D).

(7) Thistle & Coull reported a remarkable sexual dimorphism in the P3 endopod. The middle segment of P3 endopod displays 2 inner setae in the male instead of one in the female; no other species within the Stenheliinae has


A
B
D
F
B D-F 20
E
A C 20
C
H
GH 20
G

more than one seta on this segment in either sex. Re-examination showed that the spinous outgrowth at the inner distal corner was mistaken for a setation element (Fig. 14E) and that there is no sexual dimorphism.
(8) The outer spine on the ♂ P4 enp-3 is articulating at the base, strongly recurved, bears denticles around the distal outer margin and tapers abruptly in a sharp tip (Fig. 14F).
(9) The detailed ornamentation of the setae on the ♀ P5 is shown in Fig. 14C. The stout baseoendopodal spine is not modified as in *Stenhelia* but bears strong spinules bilaterally.
(10) The ♂ P5 bears 2 outer spines on the exopodal lobe (as in *Stenhelia*) and the long endopodal spine is not modified (Fig. 14G).
(11) The innermost element on the ♂ P6 is an outwardly recurded spine (as in *Stenhelia*) (Fig. 14H).
(12) The anal operculum is completely absent as in *Stenhelia*.

S. asetosa is closely related to the genus *Stenhelia* (see synapomorphies above) but cannot be accommodated in this genus because of the unmodified endopodal spine in the P5 of both sexes. It is designated here as the type of a new genus *Anisostenhelia* defined by the following apomorphies: (1) loss of inner seta on P2-P4 exp-1; (2) modification of both terminal setae on ♀ P2 enp-3; (3) sexual dimorphism of P4 endopod; and, (4) fusion of ♂ P5 exopod and baseoendopod.

Genus *Anisostenhelia* gen. nov.

Diagnosis
Stenheliinae. Anal operculum absent. Caudal rami shorter than anal somite; setae not modified. Rostrum bell-shaped, tip bifid. Antennule ♀ 8-segmented with aesthetasc on segments 4 and 8. Antennary exopod 3-segmented with setation formula [1,1,(1 + 3 apical)]. Mandible with short basis bearing 3 setae; exopod with 6 setae; endopod with 3 lateral setae, and 1 very long and 1 short lash, plus 3 accessory setae apically. Maxillule without modified elements on arthrite. Maxilliped subchelate; syncoxa with 3 setae; basis with 2 setae; endopod small, bearing claw and 1 accessory seta. P1 with 3-segmented rami; not sexually dimorphic; exp-2 without inner seta; enp-1 about as long as enp-2 and -3 combined; enp-3 with 1 subapical and 2 apical elements. P2-P4 endopods distinctly shorter than exopods. Outer spine of P2-P3 enp-3 positioned terminally, displacing apical elements to inner margin. P2 endopod ♂ 2-segmented; enp-2 tapering distally, with 3 inner setae and drawn out into slender bipinnate process bearing double row of spinules along outer margin. P4 exp-3 with 3 well developed inner setae; enp-1 with short pinnate seta; enp-3 outer spine modified and strongly recurved in ♂. P1-P4 ♀ armature formula:

	Exopod	Endopod
P1	0.0.022	1.1.120
P2	0.1.123	1.2.121*
P3	0.1.223	1.1.321*
P4	0.1.323	1.1.221

* enp-3: outer spine typically displaced to apical position, and both apical setae to inner margin

P5 ♀ with 6 setae on exopod; baseoendopod with 5 setae, outermost small, second innermost very large and spiniform but not modified. P5 ♂ with confluent exopod and baseoendopod; exopod with 2 spines, 1 short and 1 longer seta; inner endopodal spine not modified. P6 ♂ with 3 setae, innermost spiniform and outwardly recurved.
Type and only species: *Stenhelia* (*Stenhelia*) *asetosa* Thistle & Coull, 1979 = *Anisostenhelia asetosa* (Thistle & Coull, 1979) comb. nov.

Etymology. The generic name is derived from the Greek *anisos* (unequal) and refers to the sexual dimorphism displayed in P2-P4. Gender: feminine.

Status of *Stenhelia* (*Stenhelia*) *aemula* (T. Scott, 1893) and *Beatricella* T. Scott, 1905

This species shares with *Stenhelia* spp. and *Anisostenhelia asetosa* the absence of the inner seta on P1 exp-2 but differs in most other aspects. It exhibits a more primitive swimming leg setal formula, including the presence of 2 inner setae (instead of 1) on P2 exp-3 and 3 inner setae (instead of 2) on P3 exp-3. The second innermost seta on the female P5 baseoendopod is not modified (Sars, 1906*b*) and the inner element on the male P6 is small and setiform (Bodin, 1970) rather than spiniform and inwardly directed. Bodin's (1970) redescription of the male showed the inner baseoendopodal seta to be superficially similar to that found

Figure 14. *Anisostenhelia asetosa* (Thistle & Coull, 1979) comb. nov. **A.** P1 exopod ♀, anterior; **B.** P2 enp-3 ♀, anterior; **C.** P5 ♀, anterior; **D.** P2 endopod ♂ anterior; **E.** P3 enp-2 ♂, anterior; **F.** P4 endopod ♂ anterior; **G.** left P5 ♂, anterior; **H.** left P6 ♂, anterior.

Figure 14. *Anisostenhelia asetosa* (Thistle & Coull, 1979) comb. nov. **A.** exopodite de P1 ♀, vue antérieure; **B.** P2 enp-3 ♀, vue antérieure ; **C.** P5 ♀, vue antérieure ; **D.** endopodite de P2 ♂, vue antérieure ; **E.** P3 enp-2 ♂, vue antérieure ; **F.** endopodite de P4 ♂, vue antérieure ; **G.** P5 gauche ♂, vue antérieure ; **H.** P6 gauche ♂, vue antérieure.

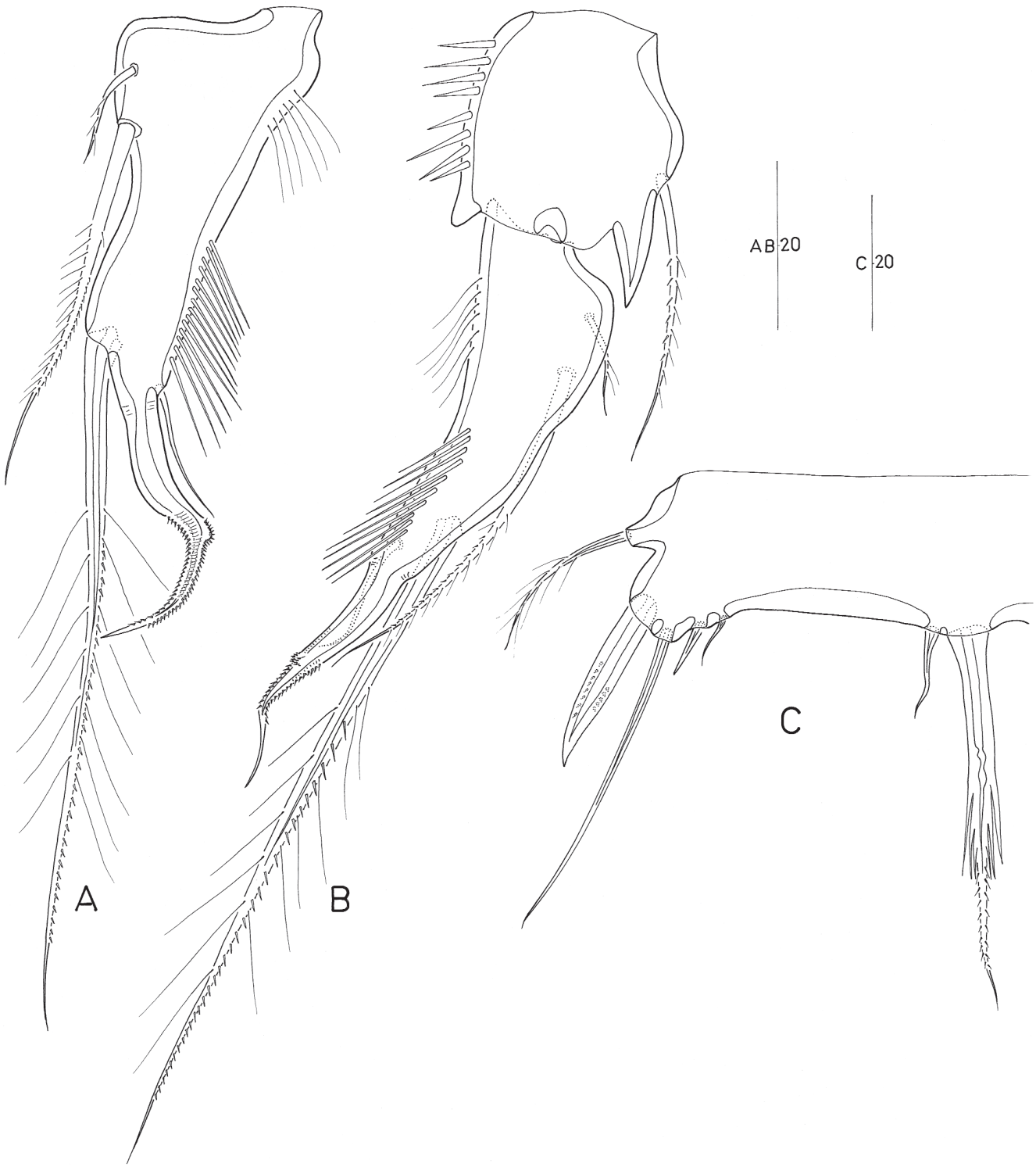


Figure 15. *Beatricella aemula* (T. Scott, 1893) comb. nov. (♂). **A.** P2 enp-2, lateral; **B.** P2 endopod, anterior; **C.** P5, anterior.
Figure 15. *Beatricella aemula* (T. Scott, 1893) comb. nov. (♂). **A.** P2 enp-2, vue latérale ; **B.** endopodite de P2, vue antérieure ; **C.** P5, vue antérieure.

in species of *Stenhelia*. The seta is illustrated with a biserrate region halfway down its length, i.e. at exactly the same position where the modification is expressed in *Stenhelia* spp. Re-examination of specimens collected in Salcombe (30 June 1875) and Plymouth (02 August 1889) by T. Scott (NHM Norman collection; reg. nos 1911.11.8.43615-624) confirmed that the shape of this element is exactly as shown by Bodin (1970) and clearly lacks the transverse serrate comb across the posterior surface (Fig. 15C). The male P5 exopod also deviates from the typical *Stenhelia* condition by its complete fusion to the baseoendopod and in the presence of only one outer spine, the second outermost element being long and setiform. The male P2 endopod resembles that displayed by *Stenhelia* and *Anisostenhelia* but differs in the absence of stiff spinules along the outer margin of the distal process (instead there is an additional outer spinular row on the segment; Fig. 15A-B) and in the presence of an accessory setiform element.

S. aemula does not display any of the seven synapomorphies supporting the sistergroup relationship between *Stenhelia* and *Anisostenhelia* (see above) and consequently it cannot be placed in either genus. T. Scott (1905) introduced a new genus *Beatricella* to accommodate *Delavalia mimica* T. Scott, 1897 and a second species which was cited in a footnote (p. 569) as "*Delavalia* (*Beatricella*) *æmula*". It is conceivable that the parentheses in Scott's citation were only meant to allude to the new combination proposed for *D. aemula*, and not to indicate subgeneric rank of *Beatricella*. Sars (1906*b*) not only showed that *D. mimica* was merely a junior subjective synonym of *Stenhelia gibba* but also claimed that *Beatricella* was a junior objective synonym of *Stenhelia* since it was "... founded upon the type of the latter genus". In reality, T. Scott (1905) did not fix a type species nor is there any report of subsequent type designation. Since Sars' (1906*b*) course of action does not necessarily invalidate the genus *Beatricella*, we prefer to reinstate it here by fixing *D. aemula* T. Scott, 1893 as the type species rather than to introduce a new generic name for this species.

Genus *Beatricella* T. Scott, 1905

Diagnosis

Stenheliinae. Anal operculum present, not modified. Caudal rami about as long as anal somite; setae not modified. Rostrum bell-shaped with bifid tip. Antennule ♀ 8-segmented with aesthetasc on segments 4 and 8. Antennary exopod 3-segmented with setation formula [1,1,(1 + 3 apical)]. Mandible with elongate basis bearing 3 setae; exopod with 6 setae; endopod with 3 lateral setae, and 1 very long lash, one equally long dilated seta plus 3 accessory setae apically. Maxillule without modified elements on arthrite. Maxilliped subchelate; syncoxa with 3 setae; basis with 2 setae; endopod slender, bearing claw and 1 accessory seta. P1 with 3-segmented rami; not sexually dimorphic; exp-2 without inner seta; enp-1 about as long as enp-2 and -3 combined; enp-3 with 3 elements apically. P2 endopod ♂ 2-segmented; enp-2 tapering distally, with 3 inner setae (proximal one minute) and drawn out into sigmoid process bearing accessory seta at base; outer margin of enp-2 with spinule row in distal half. P4 exp-3 with 3 well developed inner setae; enp-1 with very long stout seta. P1-P4 armature formula:

	Exopod	Endopod
P1	0.0.022	1.1.3
P2	1.1.223	1.2.121
P3	1.1.323	1.1.321
P4	1.1.323	1.1.221

P5 ♀ with 6 setae on exopod; baseoendopod with 5 setae, outermost very small, second innermost not modified. P5 ♂ with confluent exopod and baseoendopod; exopod with strong outer spine, 1 long seta and 2 minute elements; inner endopodal spine biserrate around mid-region. P6 ♂ with 3 setae, innermost rudimentary.

Type and only species *Delavalia aemula* T. Scott, 1893 = *Beatricella aemula* (T. Scott, 1893) comb. nov.

Species inquirenda: *Stenhelia aemula* sensu Marinov (1977)

Marinov's (1977) record of *S. aemula* from off the coast of the Spanish Sahara probably refers to a different species. The P1 endopod is distinctly longer, the ♀ P5 exopod is more elongate and the innermost seta on the ♀ P5 baseoendopod is well developed and not vestigial as in *S. aemula*. The male P5 illustrated by Marinov, showing the strong outer exopodal spine and the fused baseoendopod and exopod, leaves no doubt that this species belongs to *Beatricella*. Bodin (1970) showed unequivocally that Lang's (1936) variety *S. aemula* var. *bifida* has no right of existence.

The genus *Beatricella* can be defined by the following apomorphies: (1) P2 enp-2 ♂ drawn out into sigmoid finely pinnate process; outer margin with row of long spinules (Fig. 15A-B); (2) P4 enp-1 with very long stout seta; and (3) P5 exopod ♂ incorporated in baseoendopod; outermost element modified into strong spine (Fig. 15C).

Re-allocation of *Stenhelia* (*Stenhelia*) *diegensis* Thistle & Coull, 1979

This bathyal species was placed in the subgenus *Stenhelia* (*Stenhelia*) on account of the 3-segmented P1 endopod. Thistle & Coull (1979) remarked that the endopod could also be viewed as 2-segmented if the apical element is regarded as a massive bi-articulated seta. We regard this interpretation more plausible since accepting the endopod as being 3-segmented would imply that there is an outer seta

on the middle segment. Except for the family Superornatiremidae (Huys, 1996), where the presence of one or two setae on the outer margin of this segment represents a secondary state originated within the Harpacticoida, no other extant copepod has an outer seta on the second endopodal segment of P1 (Huys & Boxshall, 1991). On the basis of the 2-segmented condition of the P1 endopod *S. diegensis* is transferred to the genus *Delavalia*. The characteristic P1 endopod (enp-2 reduced with 3 elements, the apical one being multiplumose and flagellate) and the elongate caudal rami indicate a relationship with certain other deepwater *Delavalia* species such as *D. noodti* (Schriever, 1982) comb. nov. (500 m), *D. islandica* (Schriever, 1982) comb. nov. (500 m) and possibly *D. lima* (Becker & Schriever, 1979) comb. nov. (920 m). The fact that these unifying characters are also displayed by *D. longipilosa* (Lang, 1965) comb. nov., *D. coineauae* (Soyer, 1971) comb. nov. and *D. intermedia* (Marinov & Apostolov, 1981) comb. nov. suggests that the deepwater lineage originated from a shallow water ancestral stock. Such depth zone transition is demonstrated by *D. mastigochaeta* (Wells, 1965) comb. nov. which was originally described from 101-146 m depth from Loch Nevis and the Fladen Ground (Wells, 1965) but has since then been recorded from much shallower depths (J.M. Gee, pers. commn). Thistle & Coull (1979: Fig. 2D) show 2 inner setae on the proximal endopod segment of P2 and confirm this number in the setal formula table. Since no other copepod has more than one seta on this segment, this observation must either be erroneous or based on an aberrant specimen.

Affinities of *Stenhelia xylophila* Hicks, 1988

The description of *S. xylophila* was based on two females collected from teredinid bored submerged wood recovered off the northwest coast of New Zealand. Hicks (1988) pointed out the unique position of the species within the subgenus *Stenhelia* (*Stenhelia*). In addition to the absence of the inner seta on P4 enp-2 mentioned by Hicks (1988), *S. xylophila* differs from other *Stenhelia* spp. also in other swimming leg aspects. The endopods in P2-P3 are longer than the respective exopods and the outer distal corner of the proximal and middle segments are characteristically attenuated. The inner seta of enp-1 is modified into a short stout spine in P2-P3 and a long lanciform spine in P4. It is noteworthy that the same swimming leg morphology is also displayed by two species currently assigned to the subgenus *Stenhelia* (*Delavalia*). *S.* (*D.*) *hanstromi* Lang, 1948 and *S.* (*D.*) *bocqueti* Soyer, 1971 are known exclusively from females and represent the only species within the subgenus that display a spiniform element on P2-P4 enp-1. In the latter the spine on P4 enp-1 is remarkably similar in size and form to that found in *S. xylophila*. The close relationship between both *Delavalia* species was pointed out by Soyer (1971) who drew attention to the shared presence of basally confluent setae IV-V on the caudal rami and the close similarity in swimming leg armature. Soyer (1971) differentiated both species on the basis of the number of setae on P2 enp-2 and the shape of the endopodal lobe of the female P5. The first character is invalidated by Drzycimski's (1969) observations of *D. hanstromi* which confirmed the presence of only one seta on this segment, contrary to Lang's (1948) original statement that this species displays the same armature formula as *S. aemula* (and therefore should have 2 setae on P2 enp-2). The second character requires confirmation since Soyer's illustrations of the urosome (his Fig. 4A-B) show that the genital and first abdominal somites are not fused, and the fifth pair of legs is not demarcated at the base. These observations suggest that the description of *D. bocqueti* may have been based on a copepodid V, in which case the endopodal lobe of the P5 may not have attained its final (adult) shape.

It is conceivable that the *D. hanstromi* - *bocqueti* lineage and *S. xylophila* represent sistergroup taxa derived from a common ancestor which already displayed the spinous modifications on P2-P4 and had lost one of the endopodal setae on the female P5. This would imply that the 2-segmented condition in the P1 endopod of the former evolved independently of that in other *Delavalia* species. Such a dual origin lends support to the suggested diphyletic (or polyphyletic) status of the subgenus. In order to reflect the transitionary position of *S. xylophila* we propose a new genus to accommodate this species.

Genus *Hicksia* gen. nov.

Diagnosis

Stenheliinae. Anal operculum large, with produced laterodistal corners. Caudal rami short, about as long as anal somite; setae not modified. Rostrum bell-shaped, weakly indented apically. Antennule ♀ 8-segmented with aesthetasc on segment 4, distinctly pinnate setae on segments 1 and 8, and basally swollen setae on segments 5 and 6. Antennary exopod 3-segmented with setation formula [1,1,(1 + 3 apical)]. Mandible with moderately elongate basis bearing 3 setae; exopod with 6 setae; endopod with 3 lateral setae, and 1 very long lash, one short basally dilated seta plus 3 accessory setae apically. Maxillule without modified elements on arthrite. Maxilliped subchelate; syncoxa with 3 setae; basis with 2 setae; endopod slender, bearing claw and 1 accessory seta. P1 with 3-segmented rami; not sexually dimorphic; exp-2 with inner seta; enp-1 about as long as enp-2; enp-3 with 1 subapical and 2 apical elements. P2-P3 enp-1 with short stout spine. P2 endopod ♂ unconfirmed. P4 exp-3 with 3 well developed inner setae; enp-1 with very long lanciform spine; enp-2 unarmed. P1-P4 armature formula:

	Exopod	Endopod
P1	0.1.022	1.1.120
P2	1.1.223	1.2.121
P3	1.1.323	1.1.221
P4	1.1.323	1.0.221

P5 ♀ with 6 setae on exopod; baseoendopod with 4 setae, second innermost not modified.

Type and only species: *Stenhelia xylophila* Hicks, 1988 = *Hicksia xylophila* (Hicks, 1988) comb. nov.

Etymology. The genus is dedicated to Dr Geoffrey Hicks in recognition of his numerous contributions to the ecology and systematics of marine harpacticoid copepods. Gender: feminine.

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