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A NEW FAMILY OF CALANOID COPEPODS, THE HYPERBIONYCIDAE, COLLECTED FROM THE DEEP-SEA HYPERBENTHIC COMMUNITY IN THE NORTHEASTERN ATLANTIC

SUSUMU OHTSUKA, HOWARD S. J. ROE & GEOFFREY A. BOXSHALL

SARSIA

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A new family Hyperbionycidae (Copepoda: Calanoida) is established to accommodate *Hyperbionyx pluto* gen. et sp. nov., which was collected from the deep-sea hyperbenthic layer in the North-east Atlantic. The new family is closely related to the family Arietellidae, sharing several apomorphic characters, but can be readily distinguished by the highly modified maxilla. Relationships between the new family and other families in the superfamily Arietelloidea are also discussed.

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INTRODUCTION

Shallow-water hyperbenthic calanoid copepods have been intensively investigated in the Atlantic by SARS (1903, 1921) and FOSSHAGEN (1968a, b, 1970a, b, 1973, 1978, 1983) and in the Pacific by OHTSUKA 1984, 1985, 1992), OHTSUKA & al. (1987, 1990, 1991) and BARR & OHTSUKA (1988). In contrast, deep-sea hyperbenthic calanoids have scarcely been studied because of the difficulties of collection. The only taxonomic studies on deep-sea hyperbenthic calanoids were carried out by GRICE (1973a, b), GRICE & HULSEMANN (1970) and ROE (1986) in the Atlantic and by BRADFORD (1969) and FLEMINGER (1983) in the Pacific. The deep-sea hyperbenthic calanoid copepod community is dominated by such families as the Aetideidae, Arietellidae, Bathypontiidae, Diaixidae, Phaennidae, Spinocalanidae and Tharybidae (cf. BRADFORD 1969; GRICE & HULSEMANN 1970; GRICE 1973b; FLEMINGER 1983).

Between 1976 and 1985 the Institute of Oceanographic Sciences Deacon Laboratory carried out a series of cruises in the northeastern Atlantic sampling midwater animals at discrete depth intervals throughout the water column to depths in excess of 5000 m. In the course of this sampling programme various techniques were developed to allow accurate trawling with midwater trawls to within 10 m of the sea bed (see ROE & DARLINGTON 1985). The near-bottom hauls yielded large numbers of deep-sea hyperbenthic copepods many of which are new to science (ROE 1986).

The present paper describes a new family of Calanoida represented by a single species from hauls made at the start of this sampling programme, and also considers the relationships between the new family and related families.

MATERIAL AND METHODS

The samples were taken with the acoustically controlled RMT 1+8 system (BAKER & al. 1973) fitted with a bottom indicator switch and fished as described by BOXSHALL & ROE (1980). Station data for the specimens described here are shown in Table 1.

As discussed by BOXSHALL & ROE (1980) the absolute depths sampled may be inaccurate but the relative depths off bottom are accurate. The single specimen caught at Stn 9131#19 was very badly damaged and could conceivably have been caught in the preceding haul (9131#18) and hung up in the net.

The samples were preserved on board ship in 5 % formalin and subsequently transferred to a preserving fluid. The copepods described here were picked out from the total RMT 8 catch; dissected appendages were mounted in polyvinyl lactophenol and stained with lignin pink or mounted in Gum-chloral. A slightly damaged adult fe-

Table 1. Station data of the hauls in which *Hyperbionyx pluto* gen. et sp. nov. was collected on 21 November 1976.

Station number	Locality	Sounding range (m)	Mean sounding (m)	Depth off bottom of sample (m)
9131#18	20°7.7′ N, 21°32.9′ W 20°9.1′ N, 21°40.4′ W	3870–3896	3884	20–100
9131#19	20°14.4′ N, 21°47.0′ W 20°23.8′ N, 21°49.4′ W	3957–4036	3998	100–500

male collected from Stn 9131#18 was observed with a scanning electron microscope (HITACHI S-800). Type specimens are deposited in the Natural History Museum, London.

The morphological terminology of copepods is based on HUYS & BOXSHALL (1991).

SYSTEMATICS

Family Hyperbionycidae fam. nov.

The diagnostic characters of the new family are given below as shown in the diagnosis for the new genus.

Type genus. – *Hyperbionyx* gen. nov. (monotypic).

Genus *Hyperbionyx* gen. nov.

Diagnosis. – Body widest at midlength of cephalosome; prosome tapering posteriorly; cephalosome separate from first pedigerous somite; fourth and fifth pedigerous somites fused; posterolateral corner of last pedigerous somite slightly produced outwards. Genital double somite of female with functional left and non-functional right gonopores, ventrolaterally. Caudal rami asymmetrical, right longer than left. Rostrum triangular, with pair of long filaments. Right antennule of female indistinctly 27-segmented, shorter than left. Antenna with indistinctly 3-segmented endopod and incompletely 9-segmented exopod. Mandibular gnathobase with 2 strong teeth and palp comprising 2-segmented endopod and indistinctly 5-segmented exopod. Maxillule with 7 spines and 6 setae on praecoxal arthrite, 3 setae on coxal endite and 2 setae on coxal epipodite; endopod elongate, 1-segmented with 5 setae; exopod incompletely fused with basis, bearing 2 terminal setae. Maxilla well developed; second coxal endite with stout, serrate spine; basal endite considerably produced anteriorly, bearing chitinized spine; first endopod segment produced, having chitinized spine; terminal endopod segments relatively reduced. Maxilliped: syncoxa and basis bearing 4 and 3 setae, respectively; terminal endopod segment carrying relatively well developed, serrate seta.

Leg 1: basis lacking outer seta; distal 2 endopod segments completely or incompletely separate; first exopod segment with long spiniform outer seta; second lacking outer spine; third with 2 lateral and 1 terminal spines. Leg 3 with 1 small outer seta on posterior surface of basis. Leg 4 with inner coxal seta. Leg 5 of female uniramous, nearly symmetrical, lacking endopod; 1-segmented exopod with 2 lateral spines and 1 terminal and 2 inner setae. Leg 5 of male uniramous, asymmetrical; right basis with inner projection derived from endopod; distal 2 exopod segments of right leg expanded, lamellar.

Type species. – *Hyperbionyx pluto* gen. nov. sp. nov.

Etymology. – The new generic name, '*Hyperbionyx*' is derived from the Greek *hyperbios* meaning very powerful and the Greek *onyx* meaning claw, and refers to the stout spines on the maxilla of the new genus. The specific name, '*pluto*' (Greek, meaning God of the dark underworld) alludes to the relatively large size of the new species from the deep-sea hyperbenthic layer.

Hyperbionyx pluto gen. et sp. nov. (Figs 1–8)

Material examined. – 4 ♀♀, body length 9.96 mm (holotype), 10.10, 10.84 mm (paratypes). ♂, body length 8.40 mm. All from Stn 9131#18. ♀, cephalosome only from Stn 9131#19.

Types. – Holotype: ♀, dissected and mounted on glass slides, BM (NH) Registration No. 1993. 12. Paratypes: ♀, appendages dissected and mounted on glass slides, body proper preserved in 70 % ethanol, ♂, dissected and mounted on glass slides, ♀, whole specimen, BM (NH) Registration Nos 1993. 13–15.

Description. – Female. Body (Fig. 1A, B) widest at midlength of cephalosome, prosome tapering posteriorly; cephalosome and first pedigerous somite separate; fourth and fifth pedigerous somites fused, posterior corner, in dorsal view, directed slightly outwards. Rostrum (Fig. 1D) triangular, with pair of long filaments. Genital double somite (Figs 1C, 8A) as long as 2 following somites combined. Genital apertures asymmetrically located, anterior to fold line marking plane of fusion between genital and first abdominal somites (Fig. 8B). Left aperture (Fig. 8D) more anteriorly located than right, with laterally directed, chitinized projection, copulatory pore located at anteromedial inner corner of aperture; well developed muscular bands present; seminal receptacle on left side sigmoid, almost as long as genital double somite. Right genital aperture (Fig. 8C) lacking laterally directed process; copulatory pore slit-like, located along inner margin of aperture; no muscles associated with gonopore and no seminal receptacle present. Anal somite (Fig. 1H) separate from caudal rami; caudal rami asymmetrical, right longer than left; vestigial seta I located at midlength of outer margin, setae II–VI developed, dorsal seta (VII) originating near base of seta VI; inner margin fringed with row of pinnules except anteriorly; gland openings present on outer lateral margin and on both anterior and posterior surfaces; minute spinules near base of seta V.

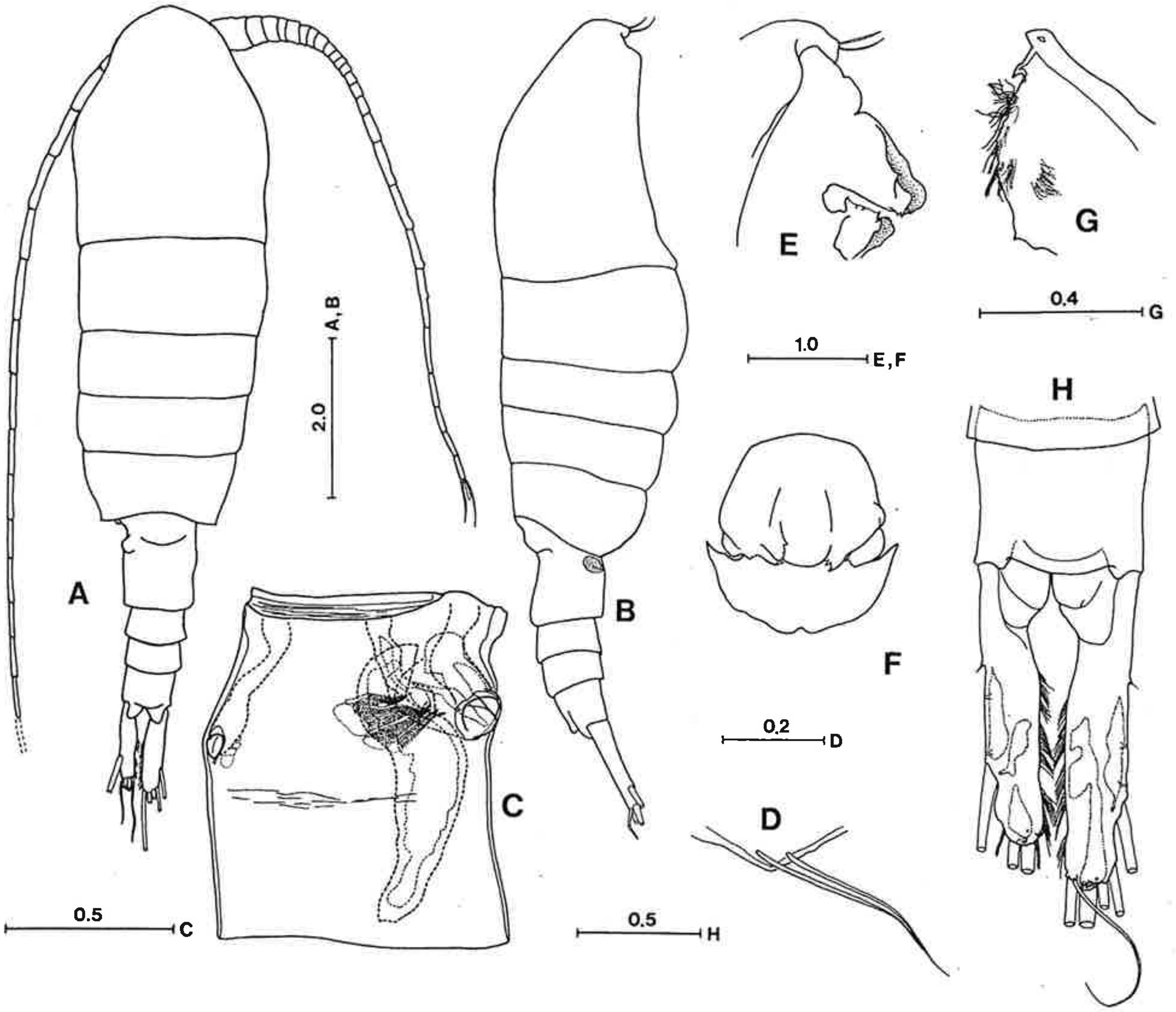


Fig. 1. *Hyperbionyx pluto*, gen. et sp. nov., female (paratype: A, B, E, F; holotype: C, D, G, H). A. Habitus, dorsal view. B. Habitus, lateral view. C. Genital double somite, ventral view. D. Rostrum. E. Labrum and paragnath, lateral view. F. Labrum and paragnath, ventral view. G. Paragnath. H. Anal somite and caudal rami, ventral view. Scales in mm.

Antennule asymmetrical, left longer than right, but terminal segments of left antennule missing in all available specimens. Posterior margin of proximal segments lacking ornamentation. Right antennule (Fig. 2A) indistinctly 27-segmented, reaching to posterior end of genital double somite; armature and fusion pattern of holotype as follows: I–III-5 + 4 aesthetascs (1 element on II and 1 on III missing), IV–1 + aesthetasc (element missing), V-2 + 2 aesthetascs, VI-2 + aesthetasc, VII–2 aesthetascs (2 elements missing), VIII-2 aesthetascs, (element missing), IX-2 aesthetascs (2 elements missing), X-1 + aesthetasc (element missing), XI-1 + aesthetasc (element missing), XII-1 + aesthetasc (element missing), XIII-2 aesthetascs (element missing), XIV-1 + aesthetasc (element missing), XV-aesthetasc (element missing), XVI-1 + aesthetasc (element missing), XVII (3 elements missing), XVIII (3 elements missing), XIX (3 elements missing), XX (3 elements missing), XXI (3 elements missing), XXII–1 (element missing), XXIII–2, XXIV-1 + 1, XXV-aesthetasc (element missing), XXVI (2 elements missing), XXVII–XXVIII-2 (3 elements missing); segments XXVI and XXVII–XXVIII only partly fused.

Left antennule (Fig. 2B) lacking distal segments; armature on segments V, VII, IX and XIII different from that of right antennule. Armature and fusion pattern of holotype as follows: I–III-1 + 2 aesthetascs (4 elements on I, 3 on II and 1 on III missing), IV-aesthetasc (2 elements missing), V-1 (element missing), VI-1 + aesthetasc (element missing), VII-aesthetasc (2 elements missing), VIII-1 (2 elements missing), IX (3 elements missing), X

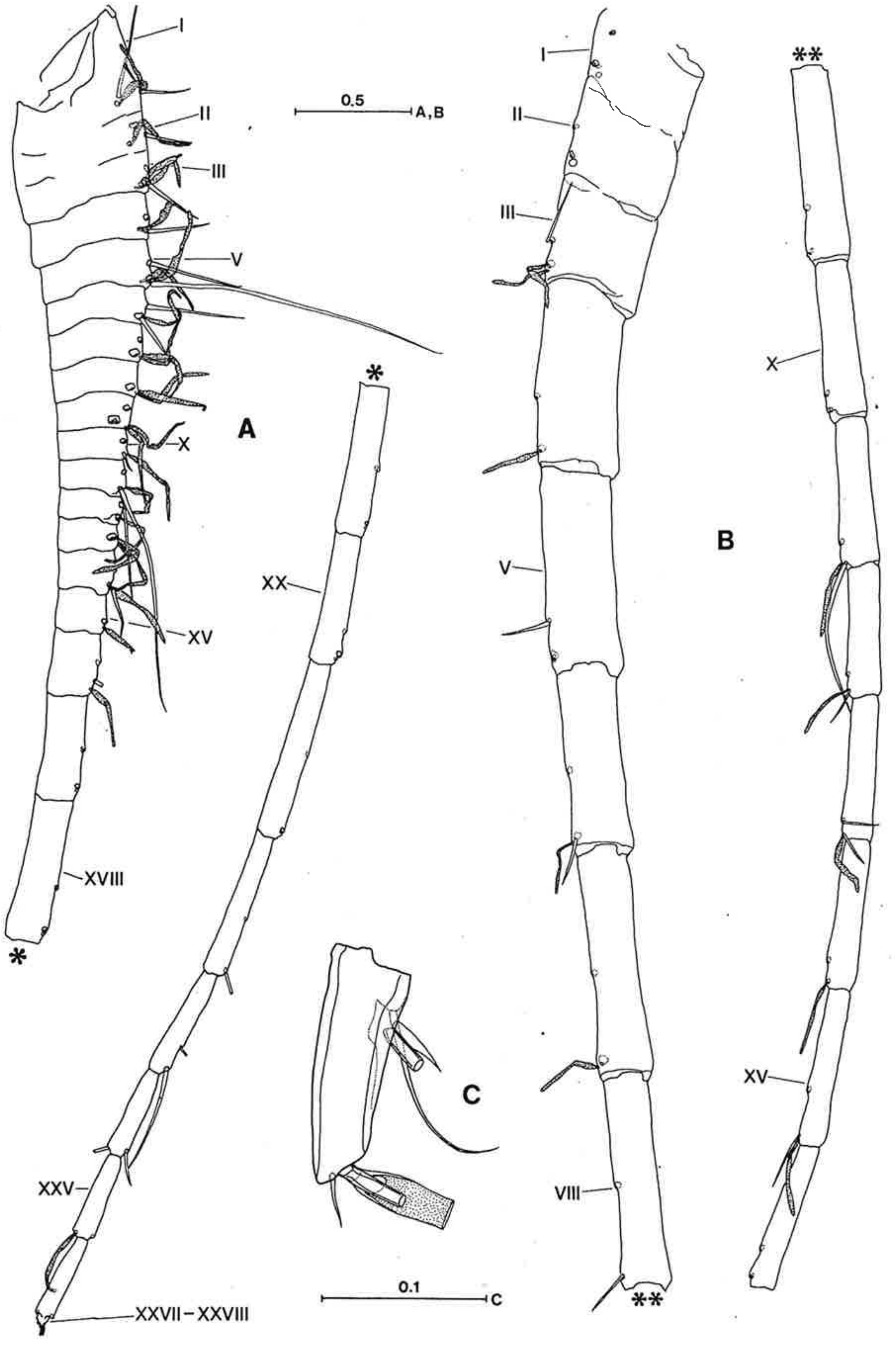


Fig. 2. *Hyperbionyx pluto*, gen. et sp. nov., female (A, B holotype), male (C paratype). A. Right antennule. B. Left antennule. C. Terminal fused segment of left antennule. Scales in mm.

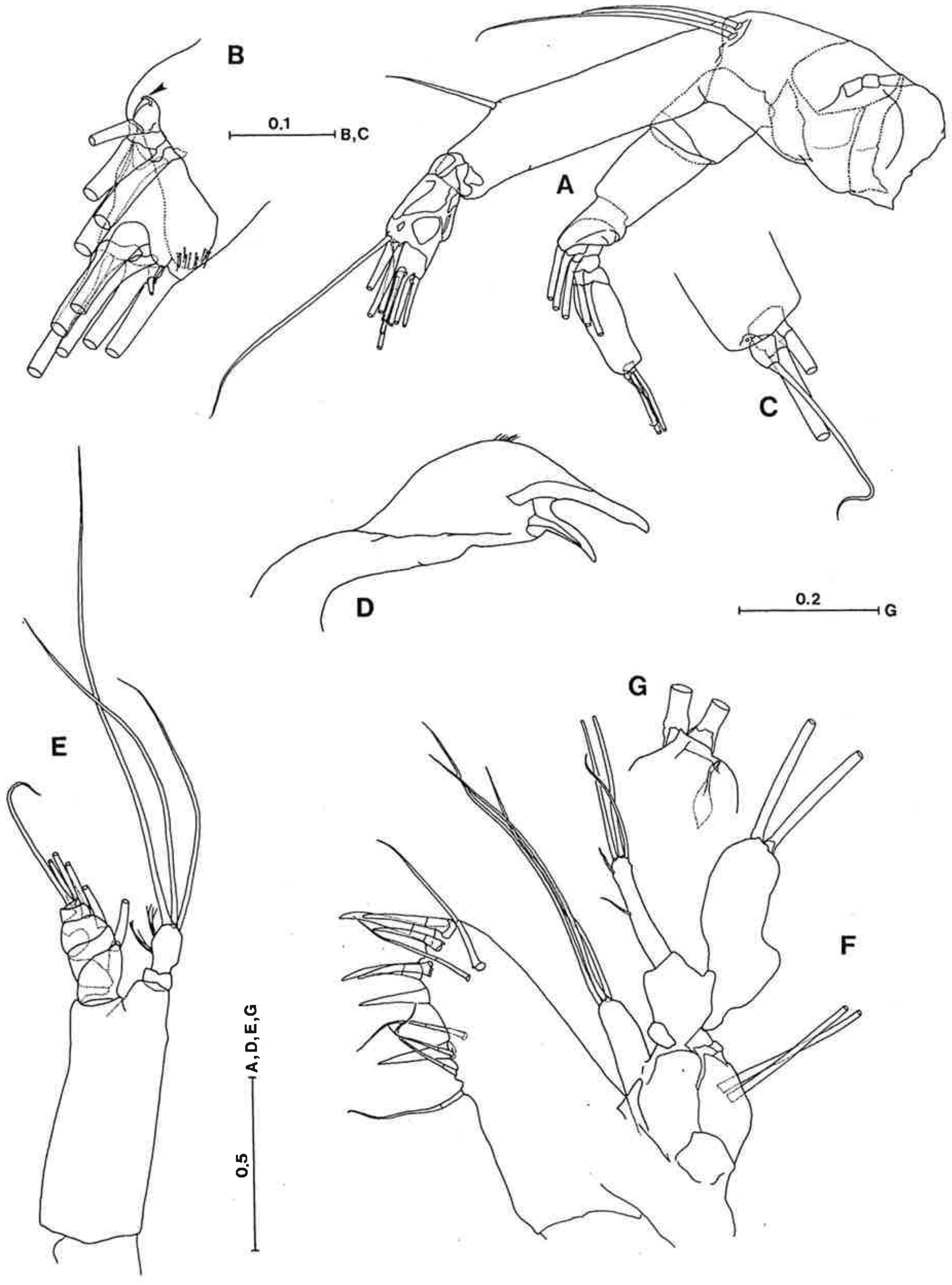


Fig. 3. *Hyperbionyx pluto*, gen. et sp. nov., female (holotype). A. Antenna. B. Terminal part of second endopod segment of antenna, vestigial seta indicated by arrowhead. C. Ninth exopod segment of antenna. D. Mandibular cutting edge. E. Mandibular palp. F. Maxillule. G. Terminal part of maxillulary exopod. Scales in mm.

le.

(3 elements missing), XI-1 + aesthetasc (element missing), XII-1 + aesthetasc (element missing), XIII-2 + aesthetasc, XIV-aesthetasc (2 elements missing), XV–I + aestetasc (element missing), XVI (3 elements missing).

Antenna (Fig. 3A–C): coxa and basis incompletely fused; basis and first endopod segment also incompletely fused; basis bearing 2 unequal setae at inner distal corner; endopod indistinctly 3-segmented, proximal segment with 1 inner seta at three-quarters length, apical segment bilobed, representing incompletely fused ancestral segments II and III–IV: carrying 4 setae and 1 minute setule (indicated by arrowhead in Fig. 3B) on proximal lobe and 6 setae and patch of spinules on apical one; second outermost seta on terminal compound segment with minute tubular secretory pore on base. Exopod 9-segmented, ancestral segments I to V incompletely fused; ninth segment. (Fig. 3C) small, with 3 unequal setae, terminal one of which originated from small bulbous knob; setal formula as follows; 0, 0, 1, 1, 1, 1, 1, 0, 3.

Mandibular gnathobase (Fig. 3D) heavily chitinized, bearing 2 stout teeth and row of setules. Mandibular palp (Fig. 3E): basis elongate, unarmed; endopod distinctly 2-segmented, proximal segment unarmed, apical bearing 3 setae terminally and row of long setules along outer margin; exopod indistinctly 5-segmented, first to fourth each bearing 1 seta and fifth with 2 setae. Labrum (Fig. 1E, F) rounded, posterior margin produced ventrally on both sides. Paragnath (Fig. 1G) more or less chitinized, posterior margin with 2 tooth-like processes and 4 patches of setules.

Maxillule (Fig. 3F, G): praecoxal arthrite produced medially, bearing 7 spines and 6 setae; coxal endite developed, with 3 setae terminally; coxal epipodite with 2 long, plumose setae; first basal endite small, unarmed; second basal endite rudimentary; endopod elongate, 1-segmented, carrying 1 middle, 1 subterminal and 3 terminal setae; exopod expanded, incompletely fused to basis, bearing 2 plumose setae terminally; 1 tube pore at base of outer seta (Fig. 3G).

Maxilla (Fig. 4A–D) well developed: first praecoxal endite with 3 setae and 2 small, spiniform elements, second with 1 serrate seta; first coxal endite having 2 serrate setae; second coxal endite (Fig. 4B) produced anteriorly, with 1 strongly serrate spine and 2 setae terminally; basal endite (Fig. 4C) considerably produced anteriorly, with 1 large, serrate spine terminally and 1 moderate, serrate seta, 2 weak setae and 1 tube pore subterminally. Endopod (Fig. 4D) indistinctly 4-segmented, first well developed, furnished with 1 heavily chitinized spine and 3 weak setae; second bearing 3 setae; third with 1 seta, fourth bearing 2 setae.

Maxilliped (Fig. 4E, F) elongate; syncoxa bearing 1 basal, 1 middle and 2 terminal serrate setae along inner margin; basis with 3 middle setae, each hirsute basally and serrate apically, and row of fine spinules along almost entire length; first endopod segment incompletely incorporated into basis, bearing 2 terminal setae; second with 3 medial and 1 subterminal setae, 2 pores present at base of 2 medial setae; third with 3 medial and 1 elongate, subterminal setae, and with 3 pores at base of terminal seta, (locations of pores shown by arrowheads in Fig. 4E); fourth and fifth each bearing 3 setae, and with 2 and 1 pores respectively; sixth small, with 1 chitinized, serrate spiniform seta and 3 setae of unequal lengths.

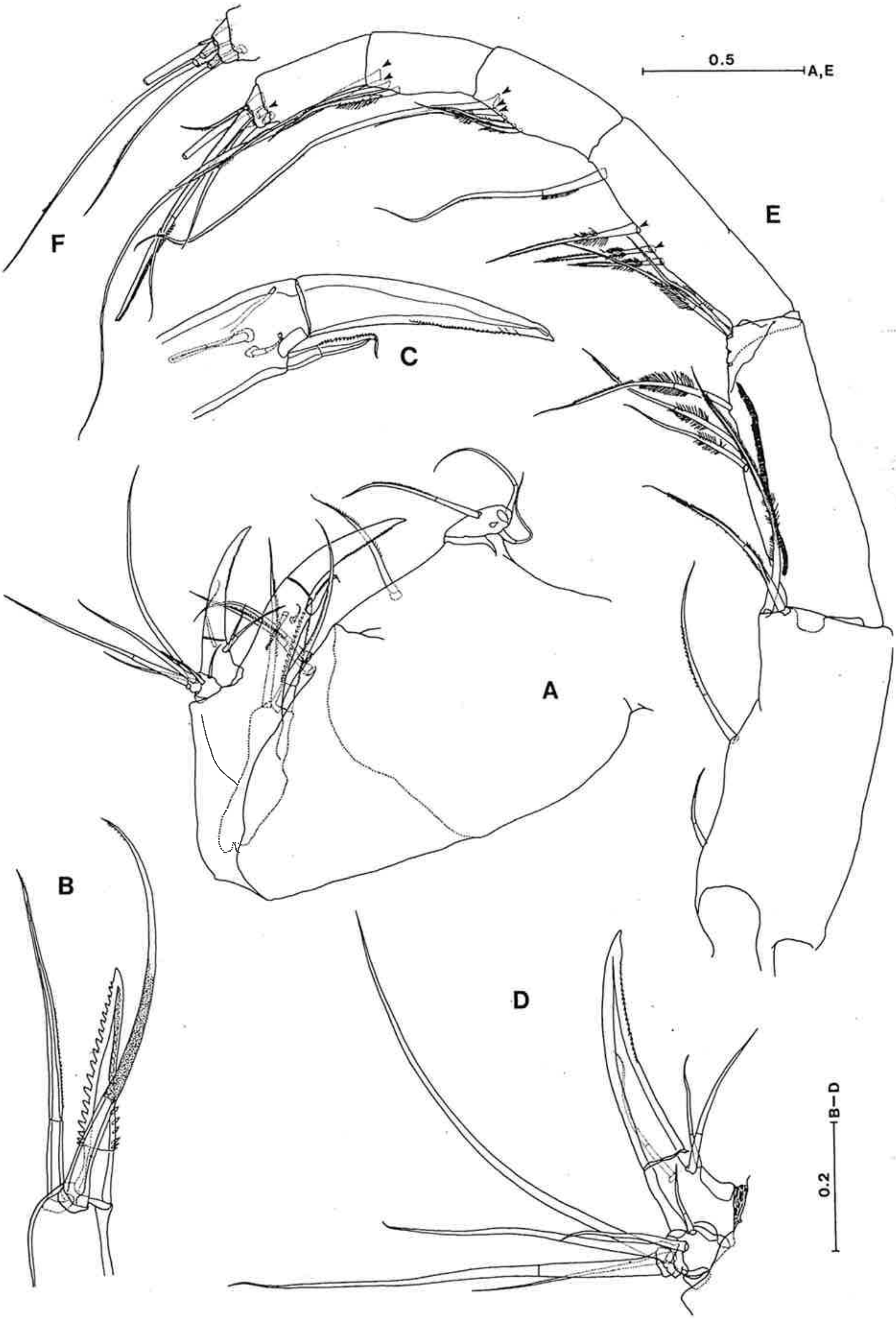
Seta and spine formula of legs 1 to 4 as in Table 2. Leg 1 (Fig. 5A–C): coxa with large, plumose seta at inner angle; basis with hirsute seta at inner angle and 1 process on posterior surface, lacking outer marginal seta. Endopod distinctly 3-segmented on right side (Fig. 5A) and segmentation incomplete on left side (Fig. 5B); first segment expanded, with 5 pores and 3 patches of spinules on anterior surface; distal 2 segments of left endopod incompletely fused and with more spinules on anterior surface than on right. Exopod 3-segmented; first segment with 1 long spiniform seta, its posterior margin bearing row of minute spinules; second produced at outer angle into small process, with spinules along outer margin and row of minute spinules distally (Fig. 5C); third with 2 naked, lateral and 1 finely serrated terminal spines. Five tube pores present on outer margins of second and third

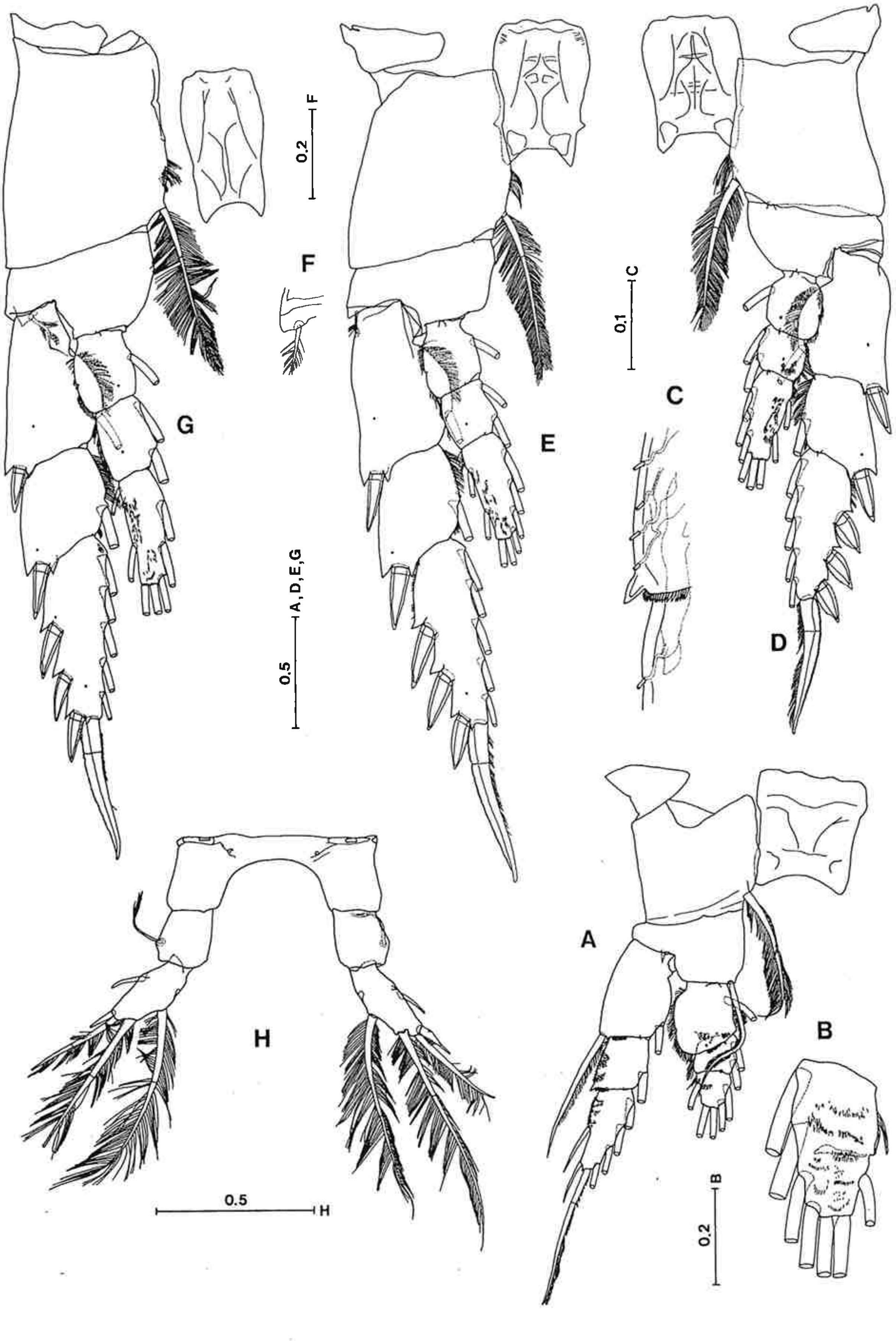
Table 2. *Hyperbionyx pluto* gen. et sp. nov. Spine and seta formula for legs 1–4.

	Coxa	Basis	Exopod segments 1 2 3	Endopod segments 1 2 3
Leg 1	0–1	0–1	I–1;0–1;II,1,4	0–1;0–2;1,2,2
Leg 2	0–1	0–0	I–1;I–1;III,I,5	0–1;0–2;2,2,4
Leg 3	0–1	1–0	I–1;I–1;III,I,5	0–1;0–2;2,2,4
Leg 4	0–1	1–0	I–1;I–1;III,I,5	0–1;0–2;2,2,3

→

Fig. 4. *Hyperbionyx pluto*, gen. et sp. nov., female (holotype). A. Maxilla. B. Second coxal endite of maxilla. C. Basal endite of maxilla. D. Endopod of maxilla. E. Maxilliped, with the locations of pores indicated by arrowheads. F. Fifth endopod segment of maxilliped. Scales in mm.


0.5
A,E
F
E
C
A
B
D
0.2
B–D


G
0.2
F
F
E
0.1
C
C
D
A, D, E, G
0.5
H
A
B
0.5
H
B
0.2

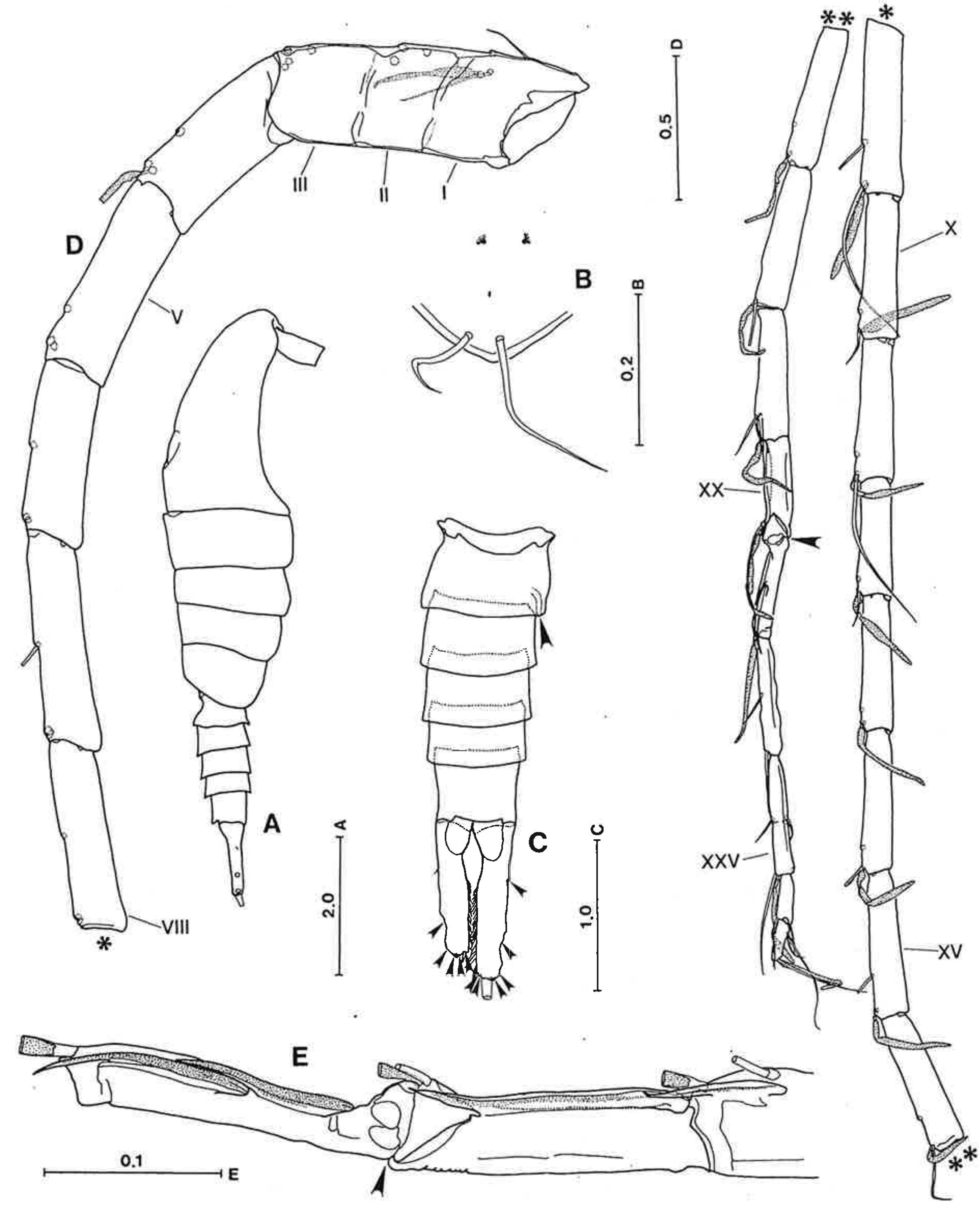


Fig. 6. *Hyperbionyx pluto*, gen. et sp. nov., male (paratype). A. Habitus, lateral view. B. Rostrum. C. Urosome, dorsal view, gonopore indicated by large arrowhead, position of missing caudal seta by small arrowhead. D. Left antennule, geniculation indicated by arrowhead. E. Ancestral segments XIX to XXI, geniculation indicated by arrowhead. Scales in mm.

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Fig. 5. *Hyperbionyx pluto*, gen. et sp. nov., female (holotype). A. Leg 1, anterior surface. B. Distal two endopod segments of left leg 1. C. Outer margin of second and third exopod segments of leg 1. D. Leg 2, anterior surface. E. Leg 3, anterior surface. F. Basal seta of leg 3. G. Leg 4, anterior surface. H. Leg 5, anterior surface. Scales in mm.

exopod segments (Fig. 5C). Leg 2 (Fig. 5D) and leg 3 (Fig. 5E, F) similar, but basis of leg 3 with 1 short, plumose seta (Fig. 5F) and blunt process at outer angle which is lacking in leg 2. Leg 4 (Fig. 5G) bearing inner coxal seta and better developed outer seta on posterior surface of basis than in leg 3.

Leg 5 (Fig. 5H): coxae fused to form common base; basis bearing 1 plumose seta subterminally near outer distal angle; endopod lacking; exopod 1-segmented, with 2 lateral spines, 1 spiniform terminal seta and 2 plumose inner setae; minute prominence present at base of proximal lateral spine.

Male. Body (Fig. 6A) resembling that of female. Urosome (Fig. 6C) 5-segmented; genital somite with gonopore ventrolaterally on right side; right caudal ramus longer than left, as in female. Rostrum (Fig. 6B) as in female.

Left antennule (Figs 2C, 6D, E) geniculate, indistinctly 26-segmented; geniculation between 20th and 21st segments; 19th to 21st segment carrying 1, 1 and 2 modified ridge-like elements, respectively; fusion pattern and armature elements as follows: I–III-2 + aesthetasc (1 element on I, 3 on II and 4 on III missing), IV- aesthetasc (2 elements missing), V-(3 elements missing), VI (3 elements missing), VII-1 (2 elements missing), VIII (3 elements missing), IX-2 + aesthetasc, X-1 + aesthetasc (element missing), XI-1 + aesthetasc (element missing), XII-1 + aesthetasc (element missing), XIII-aesthetasc (2 elements missing), XIV-1 + aesthetasc (element missing), XV-1 + aesthetasc (element missing), XVI-1 + aesthetasc (element missing), XVII – aesthetasc (2 elements missing), XVIII-1 + aesthetasc (element missing), XIX-1 + aesthetasc, XX-1 + aesthetasc, XXI – aesthetasc, XXII–XXIII-2, XXIV–XXV-3 + aesthetasc (element missing), XXVI-2, XXVII–XXVIII-5 + aesthetasc.

Right antennule similar to that of female, distal several segments missing in the only paratypic male; fusion pattern and armature elements as follows: I–III-7 + 4 aesthetascs, IV-1 + aesthetasc (1 element missing), V-1 + 2 aesthetascs (element missing), VI-1 + aesthetasc (element missing), VII-2 aesthetascs (2 elements missing), VIII-2 aesthetascs (element missing), IX-2 aesthetascs (2 elements missing), X-2 + aesthetasc, XI-2 + aesthetasc, XII-2 + aesthetasc, XIII-1 + 2 aesthetascs, XIV-2 + aesthetasc, XV-1 + aesthetasc, XVI-2 + aesthetasc, XVII-2 + aesthetasc, XVIII-aesthetasc (2 elements missing), XIX-aesthetasc (2 elements missing), XX-1 + aesthetasc (element missing), XXI (3 elements missing).

Mouthparts and legs 1–4 similar to those of female except for the following differences. Maxilliped syncoxa and basis asymmetrical, with outer terminal patch of minute spinules near inner distal corner only on left syncoxa (Fig. 7A) and transverse row of minute spinules and small terminal patch of short, minute spinules only on right basis (Fig. 7B); right fifth endopod segment bearing only 2 inner setae. Distal 2 endopod segments of leg 1 incompletely fused on left side, separate on right, as in female. Distal 2 exopod segments of left leg 2 (Fig. 7C): second segment with 3 processes on outer corner and slightly more slender spine than in female; third segment tapering distally, bearing only 4 inner setae and 2 outer spines. Endopods of leg 3: third segment of right leg (Fig. 7E) having only 1 inner and 1 outer seta; left endopod (Fig. 7D) 1-segmented, bulbous. First and third endopod segments of right leg 4 (Fig. 7F) lacking 1 inner seta and 2 inner and 2 terminal setae, respectively; proximal 2 endopod segments of left leg lacking inner setae; third exopod segment of left leg (Fig. 7G) slender medially and lacking 2 inner medial setae and second outer spine reduced.

Leg 5 (Fig. 7H–L) uniramous, asymmetrical. Right leg: coxa completely fused with intercoxal sclerite; basis carrying middle plumose seta on posterior surface and inner blunt process (Fig. 7L) probably representing endopod; exopod indistinctly 3-segmented, distal 2 segments almost fused; first segment produced on outer corner with short, thick spine; fused second and third segments lamellar, forming pocket-like structure fringed by proximal and inner margin; second segment with patch of fine setules on mid-inner margin, naked seta on outer corner and proximal process directed inwards; third segment tapering distally, with circular process and naked seta terminally. Left leg: coxa incompletely separate from intercoxal sclerite; basis expanded anteriorly, bearing plumose medial seta on posterior surface, with vestigial endopod (Fig. 7I) represented by low process on inner angle; exopod 3-segmented, first segment produced on outer corner armed with one spine, second elongate, bearing stout middle spine (Fig. 7K) on knob on posterior surface, third small, tapering distally, curved inwards, with 2 plate-like structures proximally on outer margin and short, thick terminal seta (Fig. 7J) fused to segment basally.

DISCUSSION

The new family can be assigned to the superfamily Arietelloidea Sars, 1902 (Andronov 1991), which had been originally proposed as Augaptiloidea Sars, 1905 by Andronov (1974). Four main diagnostic characters were given for the superfamily by

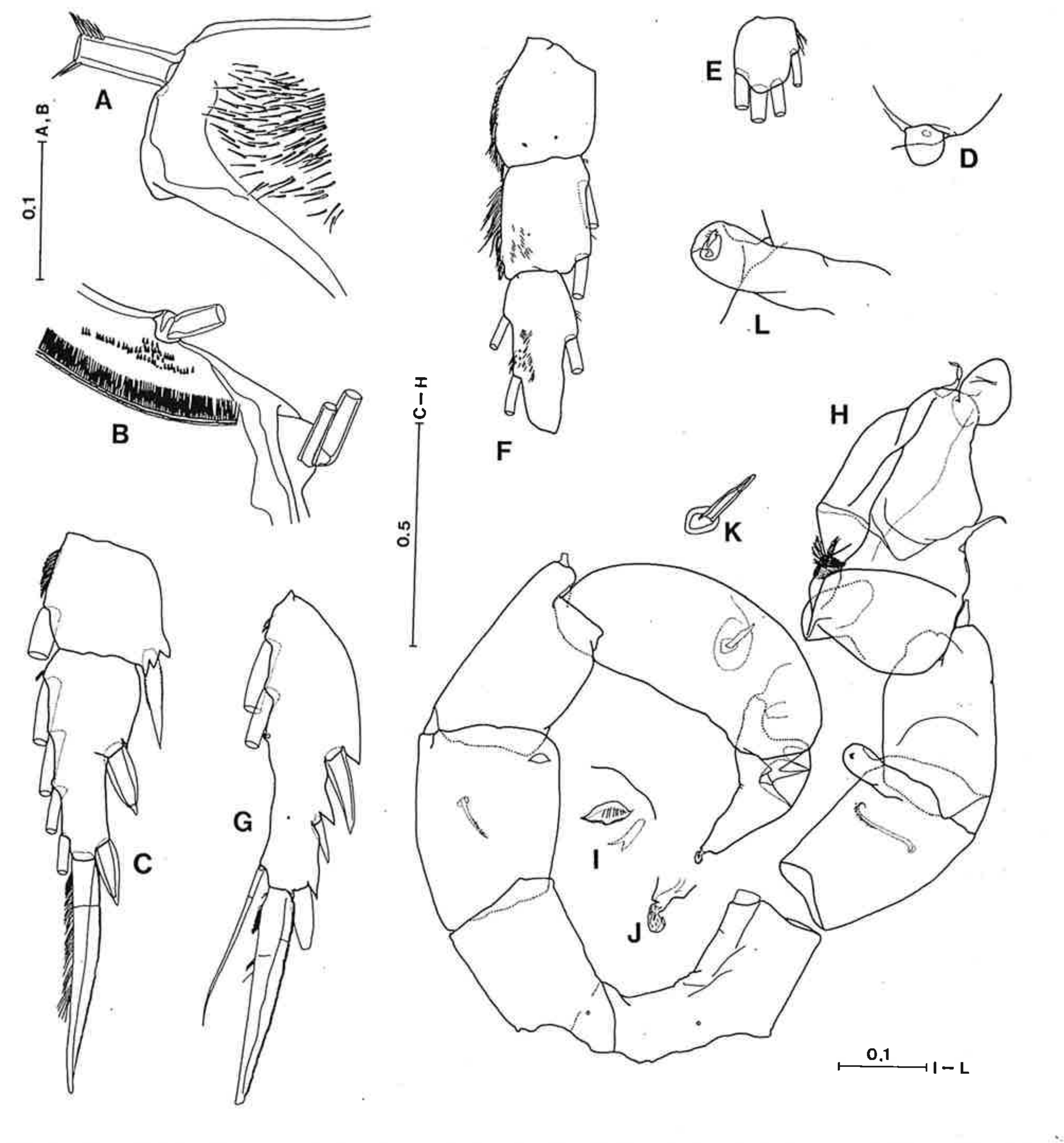

Fig. 7. *Hyperbionyx pluto*, gen. et sp. nov., male (paratype). A. Terminal end of syncoxa of left maxilliped. B. Terminal end of basis of right maxilliped. C. Third exopod segment of left leg 2. D. Endopod of left leg 3. E. Third exopod segment of right leg 3. F. Endopod of right leg 4. G. Third exopod segment of left leg 4. H. Leg 5, anterior surface. I. Vestigial endopod of left leg 5. J. Terminal seta of third exopod segment of left leg 5. K. Medial spine on second exopod segment of left leg 5. L. Vestigial endopod of right leg 5. Scales in mm.

PARK (1986): (1) left antennule of male geniculate; (2) exopodal segments 1–7 of the antenna separate; (3) exopod of maxillule elongate; (4) maxilla long, with a well-developed sixth lobe on the basis (actually, first endopod segment). However, these characters are not shared by all members of the superfamily and the retention of separate exopod segments 1–7 of the antenna is a plesiomorphic character. As PARK (1986) has already suggested, members of the superfamily share many plesiomorphic characters such as 3-segmented rami of the legs and the presence of an outer basal seta on some legs. However, the left geniculate antennule of the male is found solely in the Arietelloidea. These facts

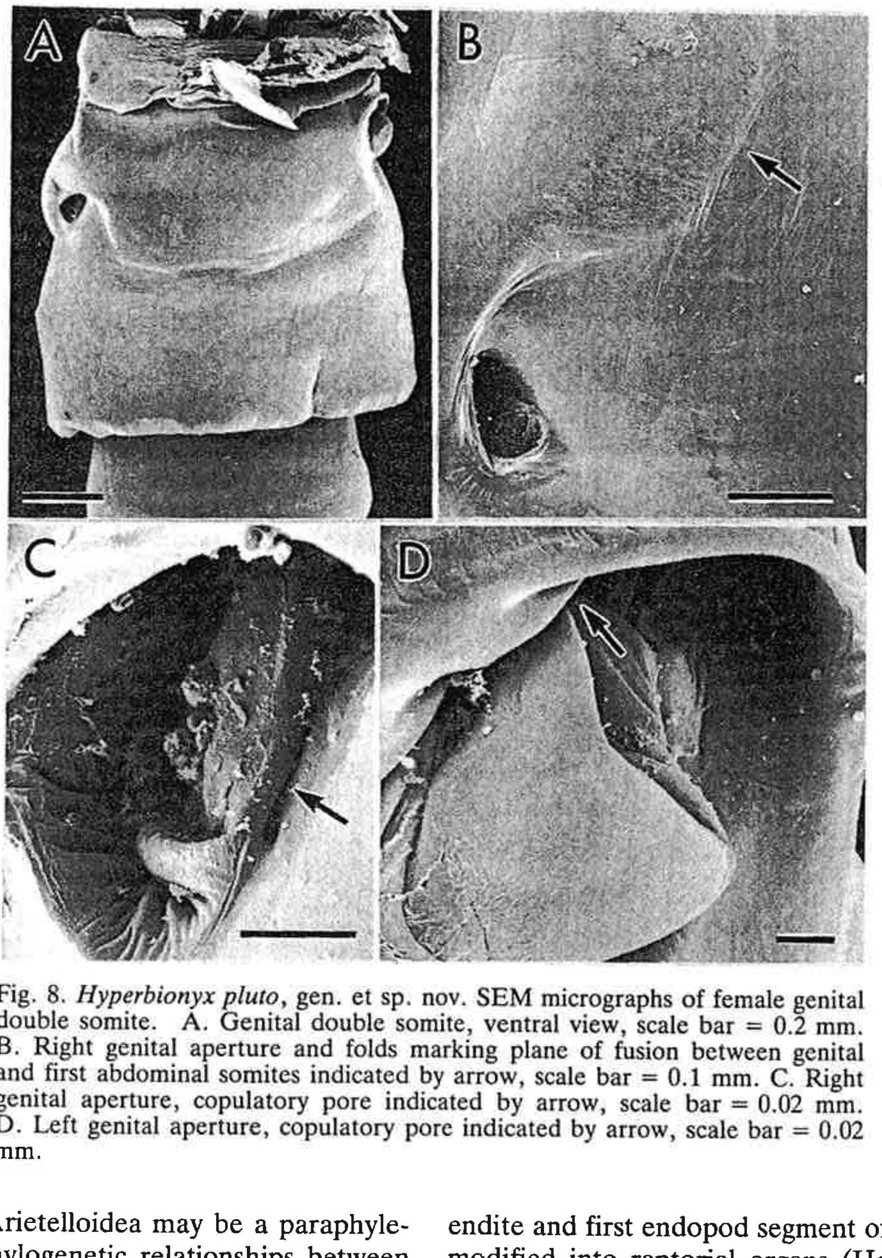

Fig. 8. *Hyperbionyx pluto*, gen. et sp. nov. SEM micrographs of female genital double somite. A. Genital double somite, ventral view, scale bar = 0.2 mm. B. Right genital aperture and folds marking plane of fusion between genital and first abdominal somites indicated by arrow, scale bar = 0.1 mm. C. Right genital aperture, copulatory pore indicated by arrow, scale bar = 0.02 mm. D. Left genital aperture, copulatory pore indicated by arrow, scale bar = 0.02 mm.

suggest that the Arietelloidea may be a paraphyletic group. The phylogenetic relationships between the families in the superfamily will be considered elsewhere.

The new family shares the following apomorphic characters with at least some of the other families (Arietellidae, Augaptilidae, Heterorhabdidae, Metridinidae (replacement name for Metridiidae by DUNN & HULSEMANN (1979)) and Phyllopodidae) in the superfamily Arietelloidea: (1) the number of mandibular teeth is reduced to only a few (Arietellidae and Augaptilidae); (2) the praecoxal arthrite of the maxillule is remarkably expanded (Phyllopodidae); (3) the number of setae on the coxal epipodite of the maxillule is reduced (Arietellidae, Augaptilidae, Heterorhabdidae and Phyllopodiae); (4) the basal exite of the maxillule lacks setae (all families except for the Metridinidae); (5) the basal endite and first endopod segment of the maxilla are modified into raptorial organs (Heterorhabdidae); (6) the maxilliped is elongated (Arietellidae, Augaptilidae and Phyllopodidae); (7) leg 5 of the female is uniramous and the exopod consists of one compound segment (Arietellidae and Metridinidae); (8) the fourth and fifth pedigerous somites are fused (all families). The last apomorphy may represent convergence because fusion between the fourth and the fifth pedigerous somites is widely found in other families of Calanoida.

Within the Arietelloidea the new family Hyperbionycidae is most closely related to the family Arietellidae by virtue of several synapomorphic characters: (1) the asymmetrical antennules of the female with the left longer than the right; (2) the reduced numbers of setae on the coxal epipodite and exopod of the maxillule; (3) the intercoxal sclerite and coxae of leg 5 of the female fused to form a common base; (4) leg 5 of the male with well-developed exopod and vestigial endopod on both sides, the distal two exopod segments of the right leg modified into a lamellar structure.

The following characters are also common to both families although they represent the plesiomorphic state: (1) the presence of one pair of rostral filaments; (2) the genital double somite of the female with paired gonopores ventrolaterally; (3) the setation on the maxilliped, except for the presence of praecoxal seta; (4) the segmentation and setation of legs 1 to 4 except for the absence of an outer basal seta on leg 1, the incomplete fusion of the two terminal endopod segments of leg 1 and the presence of a basal seta on leg 3. The female of the new species has paired genital apertures, but based on the reduced internal structures on the right side, only the left one is functional (apparently a derived character). In contrast to the new species, some arietellids have paired functional gonopores. For example, the female of *Paramisophria japonica* OHTSUKA, FOSSHAGEN & GO has a pair of gonopores ventrolaterally, each of which is closed off with an operculum, paired seminal receptacles, and a ventromedial copulatory pore which is connected to both seminal receptacles by paired copulatory ducts (OHTSUKA & al. 1991). In some species of *Metacalanus,* the female carries a pair of genital apertures ventrolaterally but lacks a ventromedial copulatory pore (CAMPANER 1984; OHTSUKA 1985).

Several autapomorphic characters are found in the Hyperbionycidae, and serve to distinguish it from Arietellidae: (1) the asymmetrical caudal rami; (2) the presence of a quadrithek on several segments of the antennules; (3) the formation of the allobasis in the antenna; (4) only 2 teeth on the mandibular gnathobase; (5) the expanded praecoxal arthrite of the maxillule; (6) the strongly developed basal endite and first endopod segment of the maxilla; (7) the absence of an outer basal seta and outer spine on the second exopod segment of leg 1; (8) incomplete fusion of the 2 terminal endopod segments of the left leg 1; (9) numerous gland openings on appendages. Most of these characters are widely found in other, less closely related families of Calanoida, but they are most likely products of convergent evolution.

The modification of the maxilla is important when considering relationships between the new family described here and other families. In the Arietellidae all setae on the maxillary endopod are well developed, heavily chitinized, and ornamented with serrate inner margin. By contrast, the maxilla of the Hyperbionycidae exhibits some similarities with that of the family Heterorhabdidae, in particular, the genus *Heterorhabdus*: the praecoxal and first coxal endites and the terminal three endopod segments are weakly developed; only the second coxal and basal endites and the first endopod segment are highly specialized for grasping prey organisms. The developed elements are the same in both families (see HUYS & BOXSHALL 1991, pp. 345–347; GIESBRECHT 1892, plate 20, figs 15, 16 and 18): in the basal endite the seta 'A' is most developed into a heavily chitinized grasping spine; in the first endopod segment the seta 'I' is most developed. The differences between these two families lie in the armature elements on the second coxal endite: in the Hyperbionycidae only the innermost seta is modified into a heavily chitinized, serrate spine, while in the Heterorhabdidae the innermost and outermost setae are relatively developed and furnished with minute spinules but they are not so heavily chitinized as in the Hyperbionycidae. Although the dissected holotypic female and paratypic male of *H. pluto* had an empty gut, the heavily chitinized spines on the basal endite and the first endopod segment of the maxilla indicate that it is a raptorial carnivore.

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