Copepoda (Poecilostomatoida and Siphonostomatoida) from deep-sea hydrothermal vent areas off British Columbia, including *Amphicrossus altalis*, a new species of Erebonasteridae, with notes on the taxonomic position of the genus *Tychidion* Humes

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HUMES, A. G., and HUYS, R. 1992. Copepoda (Poecilostomatoida and Siphonostomatoida) from deep-sea hydrothermal vent areas off British Columbia, including ***Amphicrossus altalis***, a new species of Erebonasteridae, with notes on the taxonomic position of the genus *Tychidion* Humes. Can. J. Zool. **70**: 1369–1380.

Amphicrossus altalis, n.sp., belonging to the primitive poecilostomatoid family Erebonasteridae, was found at a depth of 2420 m at the Juan de Fuca Ridge off British Columbia. The male of an *Amphicrossus* species is described for the first time. The new copepod differs from the two recognized species of *Amphicrossus* in its body surface being not highly ornamented with spinules, its smooth anterior surface of the labrum, and the dimensions of the fifth leg. New records for *Benthoxynus spiculifer* Humes, 1984, *Aphotopontius forcipatus* Humes, 1987, and *Stygiopontius quadrispinosus* Humes, 1987, are included. The clausidiid genus *Tychidion* is redescribed and its taxonomic position discussed.

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Une espèce nouvelle, ***Amphicrossus altalis***, appartenant à la famille primitive des Erebonasteridae (Poecilostomatoida), est trouvée à une profondeur de 2420 m le long de la crête Juan de Fuca, au large de la Columbie Britannique. Le mâle d'*Amphicrossus* est décrit pour la première fois. Le nouveau copépode diffère des deux espèces déjà connues d'*Amphicrossus* par l'abondance moins grande de spicules à la surface de son corps, par la surface antérieure lisse de son labre et par les dimensions de sa cinquième patte. Trois autres copépodes, *Benthoxynus spiculifer* Humes, 1984, *Aphotopontius forcipatus* Humes, 1987, et *Stygiopontius quadrispinosus* Humes, 1987, ont été trouvés également. Le genre *Tychidion* (Clausidiidae) est redécrit et sa position taxonomique est examinée.

Introduction

As a result of biological exploration of deep-sea hydrothermal vents in the Pacific and elsewhere, a large number of copepods, mostly Poecilostomatoida and Siphonostomatoida, have been discovered (Humes 1984, 1987, 1988*a*, 1988*b*, 1988*c*, 1988*d*, 1989*a*, 1989*b*, 1989*c*, 1990*a*, 1990*b*, 1990*c*, 1991*a*, 1991*b*; Humes and Dojiri 1980*a*, 1980*b*). Among these copepods from such spatially limited and rigorous habitats are members of the family Erebonasteridae Humes, 1987. These are primitive poecilostomatoid copepods distinguished from all other families by a unique and remarkable palp on the mandible. The paired midventral copulatory pores separated from the gonopores (Huys and Boxshall 1990) further attest to the primitive nature of the Erebonasteridae and indicate the origin of the family early in the evolution of the Poecilostomatoida.

The first erebonasterid to be described, *Erebonaster protentipes* Humes, 1987, both females and males, came from a depth of 2002–2022 m in the Guaymas Basin in the lower Gulf of California (Humes 1987). This discovery was followed by the description of *Erebonaster spinulosus* Humes, 1989*c*, female only, from 3266 m depth, at the West Florida Escarpment cold seeps (Humes 1989*c*). *Centobnaster humesi* Huys and Boxshall, 1990 was described from one female collected at 500 m depth east of southern New Caledonia. One female *Amphicrossus pacificus* Huys, 1991 was found at 155 m depth north-northwest of New Caledonia (Huys 1991). *Erebonaster spinulosus* was transferred by Huys to the genus *Amphicrossus* Huys, 1991 as *Amphicrossus spinulosus* (Humes, 1989).

Materials and methods

The description of the new species is based on five specimens from the Juan de Fuca Ridge. Specimens of *Benthoxynus spiculifer*, *Aphotopontius forcipatus*, and *Stygiopontius quadrispinosus* came from a wide range of localities also on the Juan de Fuca Ridge. All copepods were sent to us by Dr. Verena Tunnicliffe, University of Victoria, Victoria, British Columbia. The copepods were recovered from sediments, in both a sediment box core (A2252-989) and a push core (A2251-903), through which vent water was flowing. At the type locality, washings from Vestimentifera did not yield these copepods.

The copepods were measured and dissected in lactic acid, according to the method described by Humes and Gooding (1964). The upper case letters in the figure captions denote the scale at which the figure was drawn.

Poecilostomatoida Thorell, 1859
Erebonasteridae Humes, 1987
Amphicrossus Huys, 1991
Amphicrossus altalis, n.sp.
Figs. 1*a*–1*f*, 2*a*–2*h*, 3*a*–3*h*, 4*a*–4*g*

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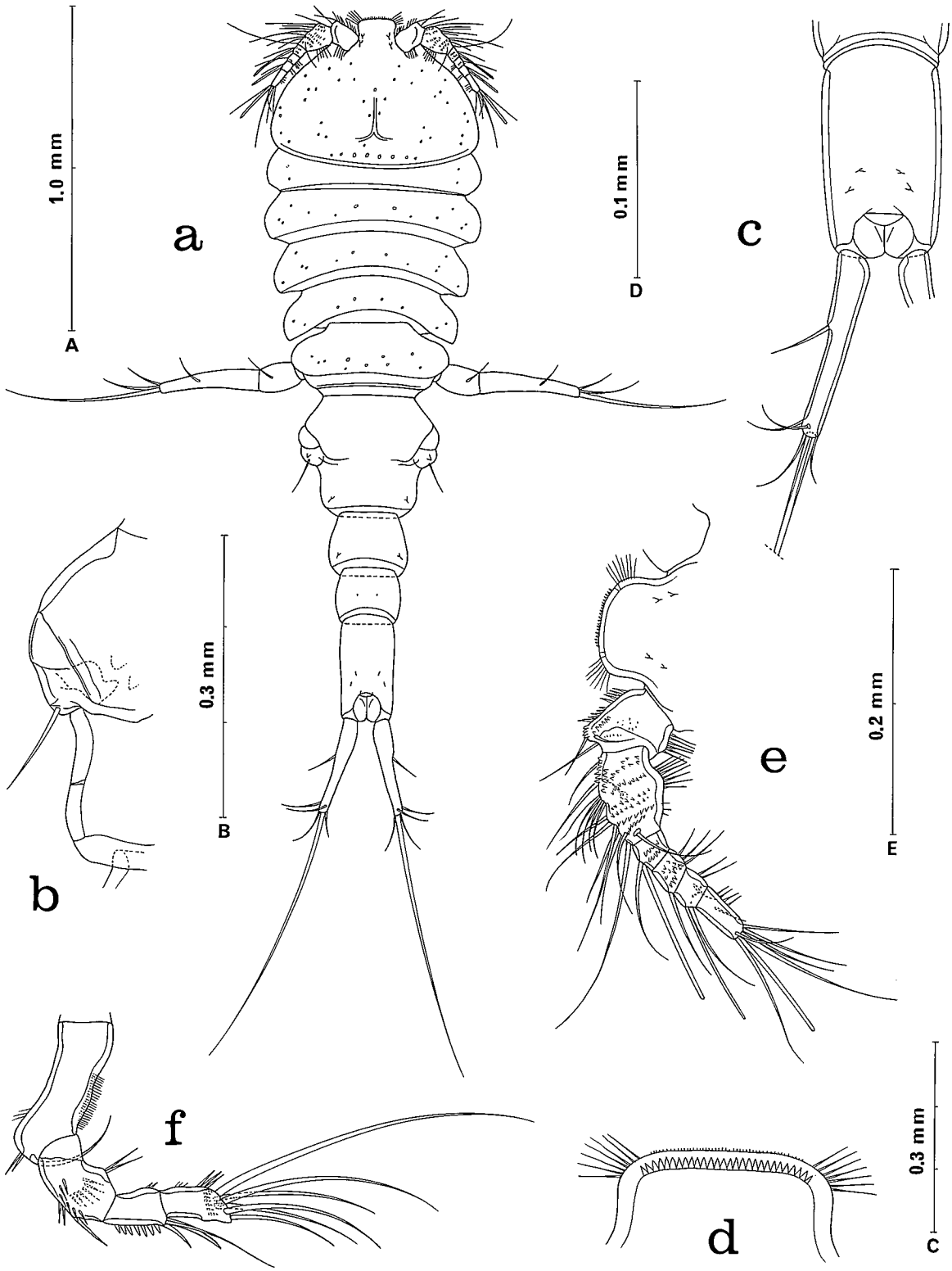

FIG. 1. *Amphicrossus altalis* n.sp., female. (*a*) Dorsal view (scale A). (*b*) Genital area, dorsal view (B). (*c*) Anal segment and caudal ramus, dorsal view (C). (*d*) Rostrum, ventral view (D). (*e*) Rostrum and antennule, dorsal view (B). (*f*) Antenna, posterior view (E).

TYPE MATERIAL: Two ♀♀, 3 ♂♂, at 2420 m, Peanut Mound, High Heat Flow Area, Middle Valley, Juan de Fuca Ridge, 48°27.5′N, 128°42.5′W, 6 August 1990. Holotype ♀ (United States National Museum (USNM) 257120), allotype ♂ (USNM 257121), and 1 paratype ♂ (USNM 257122) deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C. Remaining paratypes (dissected) are in the collection of the first author.

Female

Body (Fig. 1*a*) elongate and moderately flattened. Prosome widest at level of somite bearing leg 2. Length (not including

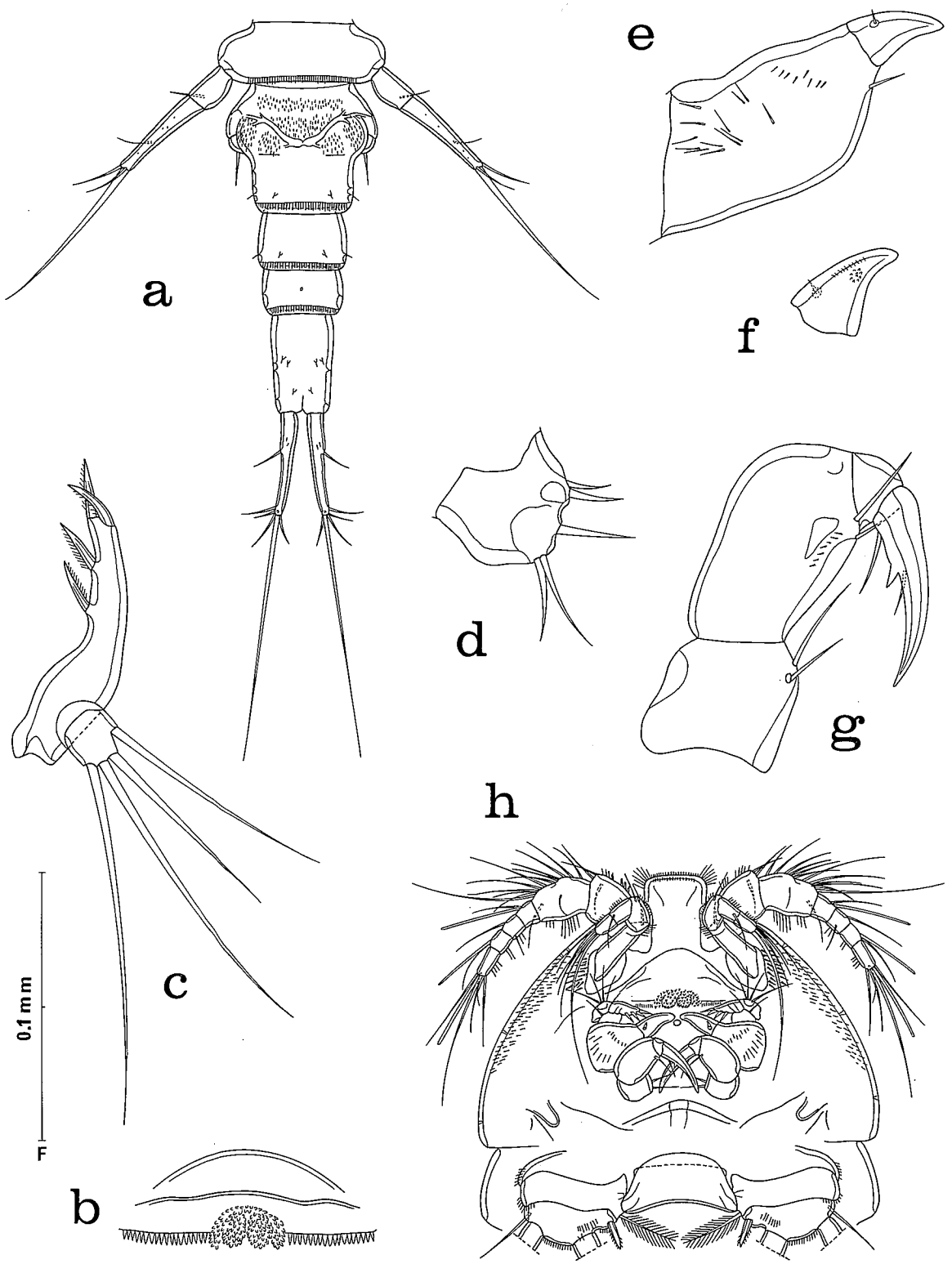

FIG. 2. *Amphicrossus altalis* n.sp., female. (*a*) Urosome, dorsal view (scale A). (*b*) Labrum, ventral view (E). (*c*) Mandible, posterior view (F). (*d*) Maxillule, anterior view (F). (*e*) Maxilla, ventral view (D). (*f*) Claw of second maxilla, dorsal view (D). (*g*) Maxilliped, posterior view (D). (*h*) Cephalosome, ventral view (C).

setae on caudal rami) 2.44 mm (2.41−2.46 mm) and greatest width 0.65 mm (0.64−0.66 mm), based on 2 specimens. Somite bearing leg 1 clearly separated dorsally from cephalosome. Epimera of somites bearing legs 1−4 rounded. Ratio of length to width of prosome 1.75:1. Ratio of length of prosome to that of urosome 0.90:1.

Somite bearing leg 5 (Fig. 2*a*) 198 × 572 μm. Genital double somite 363 μm long, broader in anterior half, 484 μm, with rounded lateral margins, than in posterior half, 350 μm, with parallel lateral margins. Anterior half showing ventrally internal broadly U-shaped sclerotization (representing copulatory ducts) and ventral surface with many small spinules.

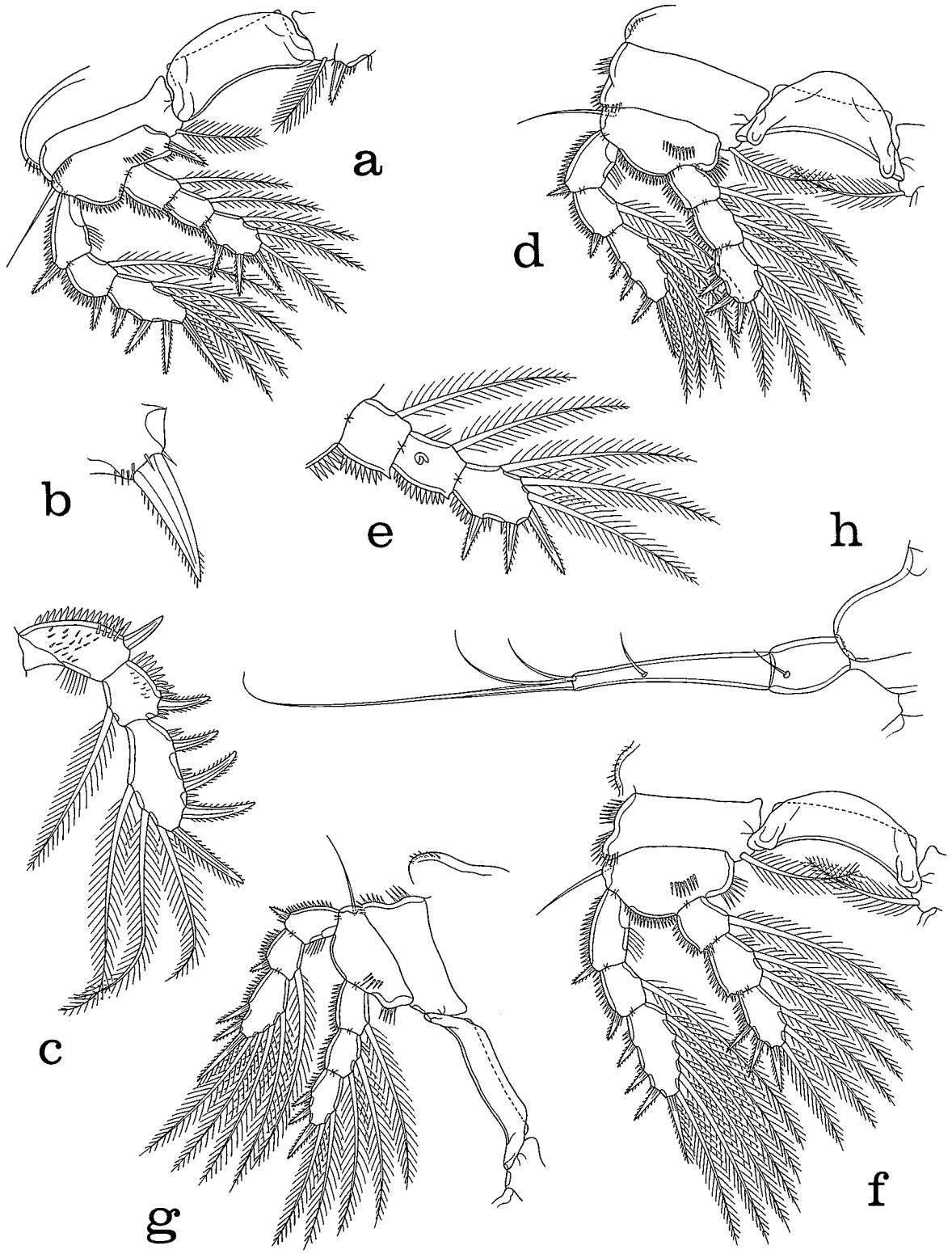

FIG. 3. *Amphicrossus altalis* n.sp., female. (*a*) Leg 1 and intercoxal plate, anterior view (scale B). (*b*) Inner spine on basis of leg 1, anterior view (B). (*c*) Exopod of leg 1, posterior view (E). (*d*) Leg 2 and intercoxal plate, anterior view (B). (*e*) Endopod of leg 2, posterior view (E). (*f*) Leg 3 and intercoxal plate, anterior view (B). (*g*) Leg 4 and intercoxal plate, anterior view (B). (*h*) Leg 5, dorsal view (C).

Gonopores located laterally just anterior to junction of two halves. Each gonopore (Fig. 1*b*) covered by operculum with conspicuous seta 104 μm long and minute spiniform process. Three postgenital somites from anterior to posterior 187 × 286, 165 × 230, and 319 × 187 μm. Genital double somite and first two postgenital somites with transverse postero-ventral hyaline frill.

Caudal ramus (Fig. 1*c*) elongate, unornamented, 297 μm long, 52 μm in greatest width proximally, 35 μm wide at outer seta, and 29 μm wide distally, ratio 7.6:1 (using average width

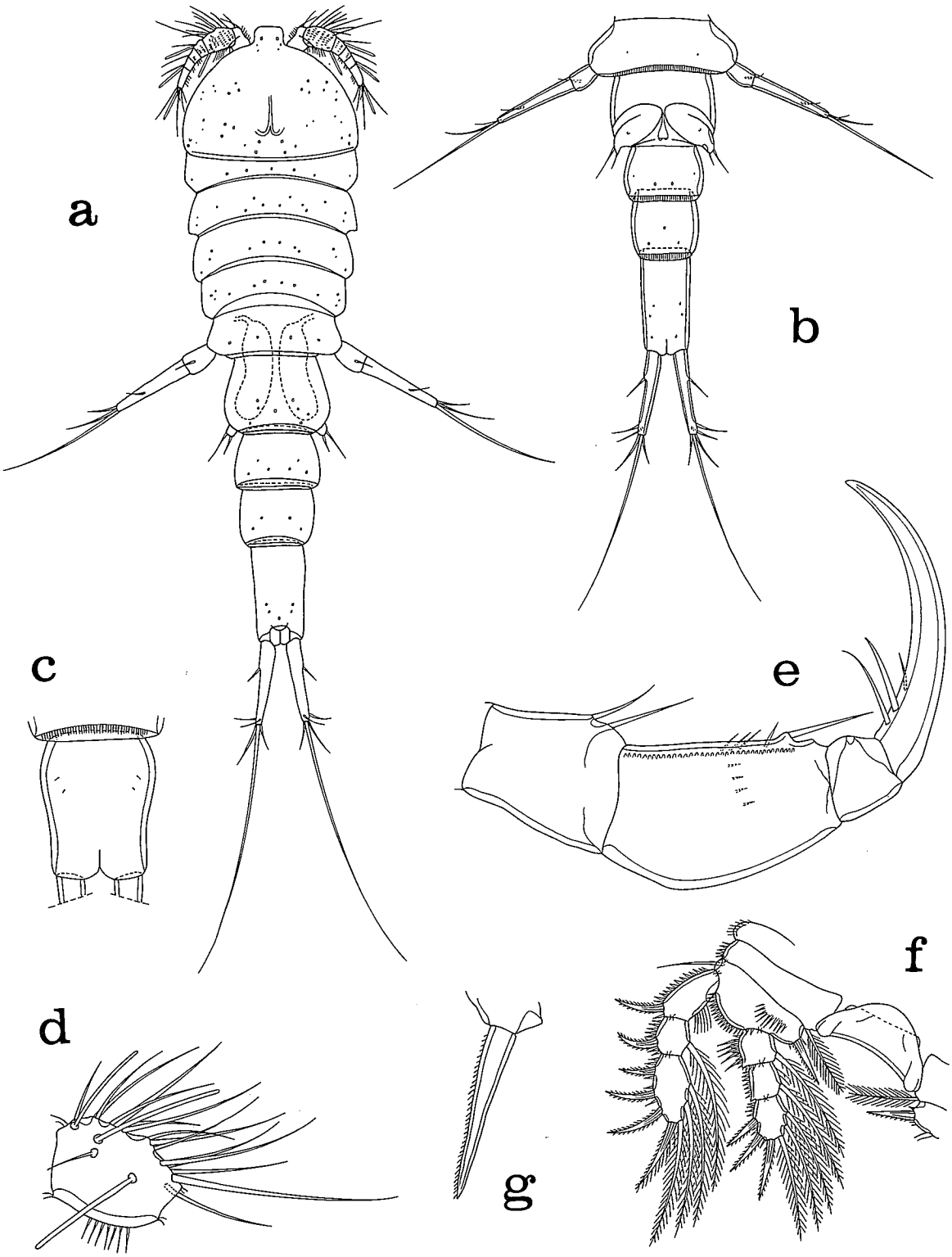

FIG. 4. *Amphicrossus altalis* n.sp., male. (*a*) Dorsal view (scale A). (*b*) Urosome, ventral view (A). (*c*) Anal segment, ventral view (B). (*d*) Second segment of antennule, ventral view (E). (*e*) Maxilliped, posterior inner view (D). (*f*) Leg 1 and intercoxal plate, anterior view (B). (*g*) Inner spine on basis of leg 1, anterior view (F).

of 39 μm). Outer lateral seta (II) 88 μm, located at approximately midlength. Outermost terminal seta (III) subterminal in position, 88 μm, and innermost terminal seta (VI) 75 μm. Two terminal setae very unequal, 109 μm (outer) and 890 μm (inner) (IV and V, respectively). Dorsal seta (VII) 86 μm. All setae smooth.

Dorsal body surface with many scattered sensilla on prosome, few on urosome (Fig. 1*a*). Ventral surface of cephalosome on both sides with submarginal elongated patch of spinules and group of larger spinules external to insertion of antenna (Fig. 2*h*).

Egg sac unknown.

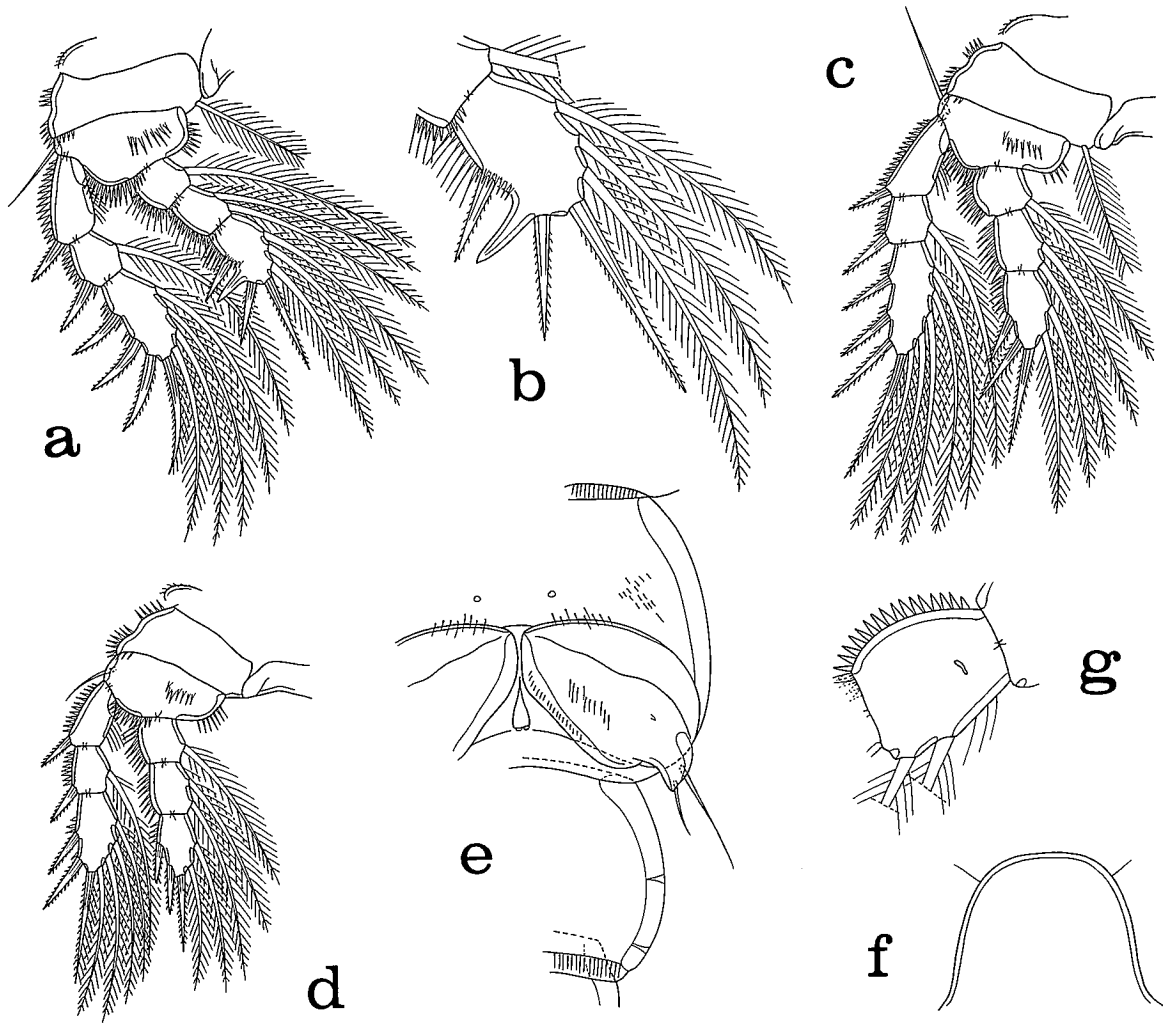

FIG. 5. (*a*–*e*) *Amphicrossus altalis* n.sp., male. (*a*) Leg 2, anterior view (scale B). (*b*) Third segment of endopod of leg 2, anterior view (D). (*c*) Leg 3, anterior view (B). (*d*) Leg 4, anterior view (B). (*e*) Leg 6, ventral view (B). (*f* and *g*) *Erebonaster protentipes* Humes, 1987, paratype female. (*f*) Rostrum, ventral view (D). (*g*) Second segment of endopod of leg 2, posterior view (F).

Rostrum (Figs. 1*d*, 2*h*) with truncate anterior margin bearing lateral groups of long setules; medially with marginal row of minute spinules and ventrally with subterminal row of dentiform spinules.

Antennule (Fig. 1*e*) 6-segmented, 275 μm long, not including terminal setae. First 2 segments larger than others. Lengths of segments (measured along their posterior non-setiferous margins): 47 (83 μm along anterior margin), 85, 23, 26, 31, and 55 μm. Formula for armature: 3, 16, 1 + 1 aesthete, 2, 2 + 1 aesthete, and 7 + 1 aesthete. All setae smooth. Various long setules on both anterior and posterior margins of first segment, and on posterior margins of remaining segments. Dorsal surface of segments 1–5 ornamented with small spines; ventral surface smooth except for 1 seta on segment 2.

Antenna (Fig. 1*f*) 4-segmented. Protopod with inner seta. Endopod 3-segmented, with formula 1, 3, and 6 (2 + 4). Two of 3 setae on endopod segment 2 slightly blunt, third longer and attenuated. All segments ornamented with setules or spinules as illustrated.

Labrum (Figs. 2*b*, 2*h*) with median spinulose region composed of 2 oval areas surrounded anteriorly and laterally by more similar spinules; lateral to spinulose region, row of larger dentiform spinules on both sides. Anterior face smooth.

Mandible (Fig. 2*c*) slender with 4 unilaterally pectinate spines distally and having large proximal palp bearing 4 long smooth setae. Paragnaths weakly developed. Maxillule (Fig. 2*d*) with 5 smooth setae. Maxilla (Fig. 2*e*) with large syncoxa bearing 1 seta and 2 groups of slender setules, those in dorsal group small, those in proximal group larger. Basis represented by stout claw (Fig. 2*f*) 57 μm long, with 1 proximal seta; distally with small patch of minute spinules and row of very small setules. Maxilliped (Fig. 2*g*) 4-segmented. First segment (syncoxa) with 2 inner setae. Second segment (basis) with 2 distal inner setae and short row of minute spinules. Small third segment (endopod 1) unarmed. Fourth segment (endopod 2) forming claw 103 μm long, bearing 2 setae and having marginal spiniform process.

Arrangement of appendages on cephalosome as shown in Fig. 2*h*.

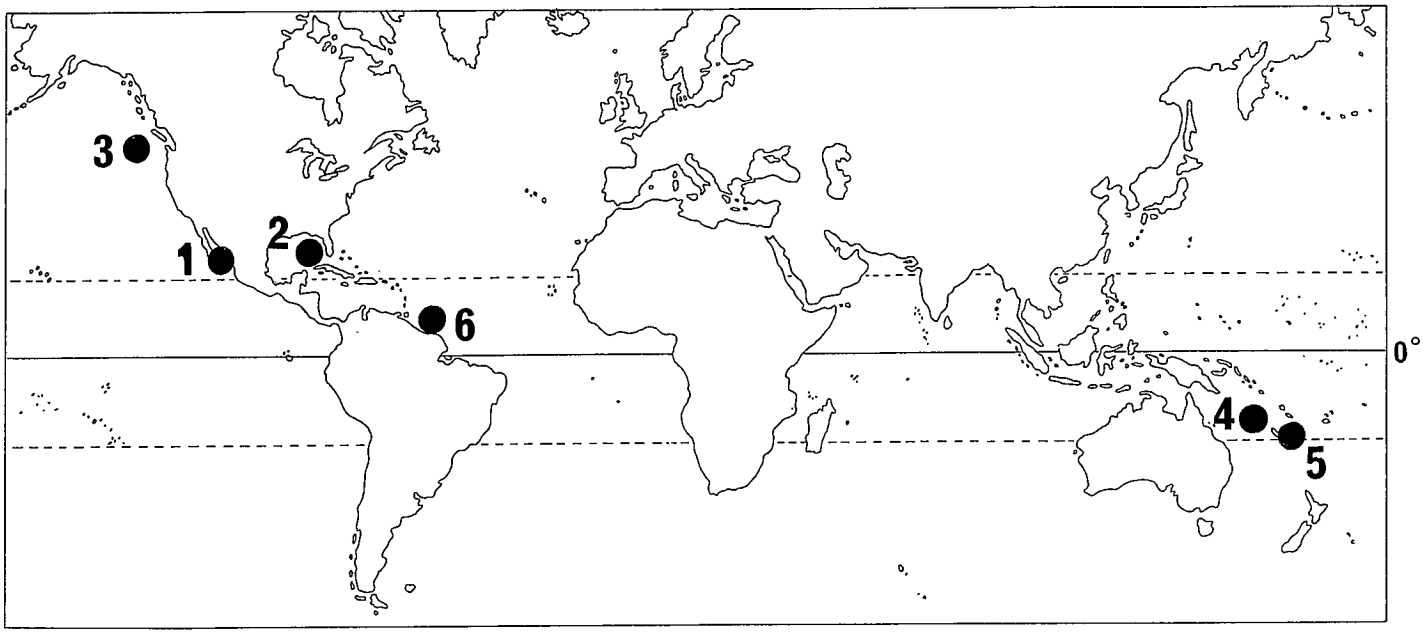

FIG. 6. World distribution of the Erebonasteridae. 1, *Erebonaster protentipes* Humes, 1987, Guaymas Basin, Gulf of California; 2, *Amphicrossus spinulosus* Humes, 1989, West Florida Escarpment; 3, *Tychidion guyanense* Humes, 1973, Guyana; 4, *Amphicrossus pacificus* Huys, 1991, New Caledonia; 5, *Centobnaster humesi* Huys and Boxshall, 1990, New Caledonia; 6, *Amphicrossus altalis*, n.sp., British Columbia.

Legs 1–4 (Figs. 3*a*, 3*d*, 3*f*, 3*g*) with 3-segmented rami. Spine and setal formula as follows (Roman numerals indicate spines and Arabic numerals setae):

P_1	coxa 0-1	basis 1-I	exp I-0;	I-1;	III, I, 3
			enp 0-1;	0-1;	II, I, 3
P_2	coxa 0-1	basis 1-0	exp I-0;	I-1;	III, I, 4
			enp 0-1;	0-2;	II, I, 3
P_3	coxa 0-1	basis 1-0	exp I-0;	I-1;	III, I, 5
			enp 0-1;	0-2;	II, I, 3
P_4	coxa 0-0	basis 1-0	exp I-0;	I-1;	II, I, 4
			enp 0-1;	0-2;	II, I, 2

Coxae in legs 1–3 with plumose inner seta, but this seta absent in leg 4. Basis of leg 1 with inner spine (Fig. 3*b*) 49 μm long, with minute spinules. Posterior surfaces of first 2 exopod segments of legs 1–4 with small setules as in leg 1 (Fig. 3*c*). Posterior surface of second endopod segment of leg 2 with minute sclerotized (sensory) area (Fig. 3*e*). All 4 legs ornamented with setules and spinules as illustrated.

Leg 5 (Fig. 3*h*) 2-segmented, unornamented, in preserved specimens held erect from body or nearly so. First segment (basis) 109 μm along anterior margin, 120 μm along posterior margin, 86 μm wide, with 1 dorsal seta approximately 52 μm long. Second segment (exopod) 319 μm long, tapered, 56 μm wide proximally, 29 μm wide distally, with dorsal seta approximately 57 μm and 3 terminal setae 99, 180, and 540 μm long. All setae smooth.

Leg 6 probably represented by seta and process on genital area (Fig. 1*b*).

Color of living specimens unknown.

Male

Body (Fig. 4*a*) resembling that of female in general form. Length (excluding setae on caudal rami) 2.06 mm (1.98–2.13 mm) and greatest width 0.51 mm (0.45–0.57 mm), based on 3 specimens in lactic acid. Ratio of length to width of prosome 1.57:1. Ratio of length of prosome to that of urosome 0.67:1, urosome being longer than prosome.

Somite bearing leg 5 (Fig. 4*b*) 143 × 429 μm. Genital somite 253 × 341 μm, slightly wider than long. Three postgenital somites from anterior to posterior 187 × 275, 198 × 240, and 308 × 176 μm. Anal somite in 1 male shorter, 218 × 185 μm (Fig. 4*c*).

Body surface ornamented as in female.

Rostrum like that of female. Antennule resembling that of female, but second segment (Fig. 4*d*) bearing 3 aesthetes. Antenna as in female.

Labrum, mandible, maxillule, and maxilla like those of female. Maxilliped (Fig. 4*e*) larger than in female. Syncoxa with 2 setae. Basis with 2 setae, few slender setules, and long row of small blunt spinules. Small third segment (endopod 1) unarmed. Claw (endopod 2) 150 μm long with 3 proximal setae.

Legs 1–4 (Figs. 4*f*, 5*a*, 5*c*, 5*d*) segmented and armed as in female. Basis of leg 1 with inner spine (Fig. 4*g*) 61 μm long. Spines on exopods of all 4 legs relatively slightly longer than in female. Other sexual dimorphism in long setules as well as spines on first and second segments of endopod of leg 2. Most striking dimorphism in development of long (31 μm) spiniform process on third segment of endopod of leg 2 (Fig. 5*b*).

Leg 5 resembling that of female.

Leg 6 (Fig. 5*e*) usual posteroventral flap on genital segment bearing 2 setae 42 μm and 104 μm long, and groups of small slender setules as illustrated.

Spermatophore not seen except inside body of male (Fig. 4*a*).

Color of living specimens unknown.

ETYMOLOGY: The specific name is formed from Latin *altum*, a poetic name for the deep sea, and the suffix *alis*, "pertaining to."

Remarks

The three genera of the Erebonasteridae, *Erebonaster* Humes, 1987, *Amphicrossus* Huys, 1991, and *Centobnaster* Huys and Boxshall, 1990 were compared by Huys and Boxshall (1990). The new species from the Juan de Fuca Ridge possesses most of the characters that they listed for *Amphicrossus*. There are, however, several differences. In the new species the body surface is not highly ornamented with spinules, but instead has a moderate number of small pores or sensilla. The anterior face of the labrum is not spinulose but smooth. Leg 5 is smooth, not highly ornamented, and extends to the posterior margin of the genital double somite; the exopod (second segment) is approximately 2.7 times the length of the protopod (first segment); and the terminal seta is 1.7 times the length of the exopod. These differences are considered to be derived rather than primitive, and are probably to be regarded as important at the species level rather than at the genus level. The size and form of leg 5 in other poecilostomatoid families often vary widely interspecifically. It seems prudent, at least for the present, to conclude that the new species belongs to the genus *Amphicrossus*. The discovery of males of *Amphicrossus pacificus* and *A. spinulosus* may verify their relationships.

Reexamination of paratypes of *Erebonaster protentipes* shows the presence of a single long setule on both corners of the rostrum (Fig. 5*f*), rather than a group of setules as in *Amphicrossus*. In addition, there is a minute sclerotization on the second segment of the endopod of leg 2 (Fig. 5*g*), as in *Amphicrossus*.

The occurrence of two widely separated species of *Amphicrossus*, *A. spinulosus* in the Guaymas Basin and *A. altalis* at the Juan de Fuca Ridge, may be a further instance of vicariance between the two vent systems (see Humes 1991*b*; Tunnicliffe 1988). The presently known distribution of the Erebonasteridae is indicated in Fig. 6. Future investigations will undoubtedly expand the range of this primitive family.

The Erebonasteridae is considered to be the first offshoot of the main poecilostomatoid lineage (Huys and Boxshall 1990). Its primitive position is supported by various plesiomorphic characters, such as the retention of a discrete palp on the mandible, the ventral position of the copulatory pores, and the ancestral setation of the maxillae and maxillipeds. The last character is also found in most Clausidiidae, and Huys and Boxshall (1990) pointed out the striking similarity in structure of the fifth leg between the erebonasterid *Centobnaster* and the clausidiid *Hemicyclops*. The sharing of these primitive characters does not necessarily indicate a close relationship between both families. However, it illustrates the primitive position of the Clausidiidae within the Poecilostomatoida, or as Huys and Boxshall stated, "... the Clausidiidae occupies a pivotal position. ..." Members of the Erebonasteridae are presumably loose associates of deep-sea invertebrates and seem to have been successful in the exploration of hydrothermal vents and cold seeps (Humes 1987, 1989*c*; Huys 1991; Huys and Boxshall 1990; present study). A survey of the clausidiid genera reveals a wider range of hosts, but only one of them, *Tychidion* Humes, is associated with Vestimentifera, which are a typical faunal element of hydrothermal vents. Closer inspection of the type material of *T. guyanense* revealed some previously overlooked structures indicating a close affinity with the erebonasterid genera. A concise redescription of the relevant structures is presented below.

Redescription of *Tychidion guyanense* Humes, 1973

Humes (1973) reported 2 males and 3 copepodids, but reexamination of the adult specimens found off Guyana (Crust. F795 and F796, deposited in the Rijksmuseum van Natuurlijke Historie, Leiden) proved them to be females. The second somite of the 5-segmented urosome represents a genital double somite derived by fusion of the genital somite and the first abdominal somite. It shows a spinous process on either lateral margin. Both the dorsolateral gonopores and the paired copulatory pores are located on the anterior third of the genital double somite (Fig. 8*b*). Each gonopore is closed off by an operculum derived from the sixth leg and bearing 2 small spines and a long seta (Fig. 8*d*). The paired copulatory pores are closely set to the ventral midline in a common median depression and lead to heavily sclerotized copulatory ducts (Fig. 8*c*).

Labrum (Fig. 7*a*) with smooth anterior surface; anterior margin denticulate and with weakly defined median process consisting of slightly larger spinules; each lateral margin provided with a large spinous process accompanied by a secondary process medially.

Mandible (Fig. 7*b*) with strong gnathobase and small unisegmented palp. Gnathobase with strong unipinnate spine dorsally and 4 closely set spinous processes medially, the largest one being pectinate along the dorsal margin. Palp emerging from foramen formed by lateral margin of labrum and anterior surface of maxillule (Fig. 7*a*); with a lateral seta and 1 vestigial plus 2 long setae apically.

Maxillule (Fig. 7*a*) slightly bilobed with armature consisting of inner group with 2 short spines and outer group with 3 pinnate setae.

Maxilla (Fig. 7*c*) 2-segmented; proximal segment (syncoxa) robust and bearing vestigial endite represented by 1 small seta; distal segment, representing basis, produced into several spinous processes distally and with 1 long and 2 small setae.

Maxilliped (Fig. 7*d*) 4-segmented, comprising syncoxa, basis, and 2-segmented endopod. Syncoxa with 1 larger and 1 vestigial seta along inner margin and some tiny spinules on anterior surface. Basis large, inner half of anterior surface densely covered with fine spinules, with 1 inner seta on both anterior and posterior surfaces. First endopod segment without armature. Second segment produced into robust, distally serrated claw with 1 long seta and 2 rudimentary setae proximally.

Fifth pair of legs (Fig. 8*a*) located at ventral hind margin of fifth pedigerous somite; legs 2-segmented, uniramous, joined by well-developed intercoxal sclerite. Undivided protopod with 1 outer midmargin seta (41 μm; derived from basis). Exopod with 1 lateral spine at outer margin and with 1 smooth seta flanked by 2 large spines at distal margin; spines with lateral strips of serrated membrane; inner margin with few spinules.

Caudal ramus (Fig. 8*e*) 3.7 times as long as maximum width, with 7 setae. Seta I diminutive, setae IV and V strongly developed; setae II, III, and VI composed of a short proximal part with which the distal pinnate (II, III) or filiform (VI) part articulates; dorsal seta VII swollen. Ramus with tiny spinules in dorsal anterior half; ventral hind margin irregularly serrated.

The affinity of *Tychidion guyanense* to other erebonasterid genera is unequivocally defined by the following diagnostic characters: the presence of a discrete mandibular palp, paired copulatory pores located in a common midventral depression

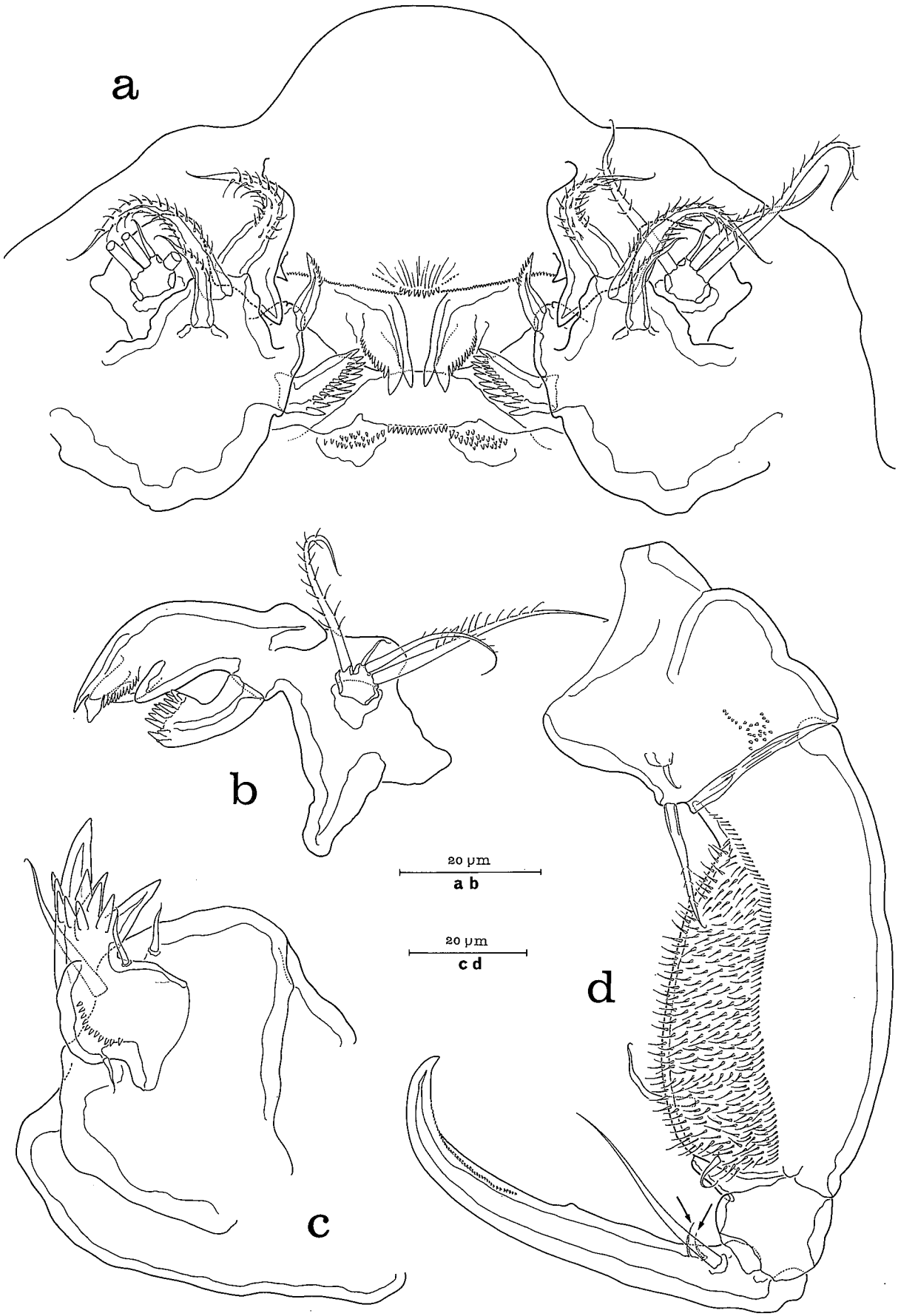

FIG. 7. *Tychidion guyanense* Humes, 1973, female. (*a*) Oral area, including maxillules, ventral view. (*b*) Mandible. (*c*) Maxilla. (*d*) Maxilliped.

remote from the dorsolateral gonopores, and segmental homologies of the antennule (see Fig. 2.10.6 in Huys and Boxshall 1991). Within the Erebonasteridae, *Tychidion* is particularly close to the genus *Centobnaster*, whose type species, *C. humesi*, is the most primitive poecilostomatoid described thus far (Huys and Boxshall 1990). They share the most primitive fifth legs of the order, i.e., located ventrally and connected by a small intercoxal sclerite. Only the males of some Serpulidicolidae have ventral fifth legs that still show a vestige of an intercoxal sclerite (e.g., Southward 1964). Other common characters include the 7-segmented antennules, the lateral processes on the genital double somite, the composite setae II, III, and VI of the caudal ramus (although II and III were lost in the holotype of *C. humesi*), and the gnathobase of the mandible. The genera of the Erebonasteridae can be distinguished by the following key.

Key to the genera of the Erebonasteridae

1. Antennules 7-segmented in both sexes; fifth legs of female ventrally located and joined by intercoxal sclerite 2
   Antennules 6-segmented in both sexes; fifth legs laterally located and intercoxal sclerite absent 3
2. Urosome of female with 5 somites ..... *Tychidion* Humes, 1973
   Urosome of female with 4 somites ..... *Centobnaster* Huys and Boxshall, 1990
3. Epimera of somites bearing P2–P4 expanded posteriorly; armature formula of distal exopodal segment of P4 II,I,3 ..... *Erebonaster* Humes, 1987
   Epimera of somites bearing P2–P4 not expanded posteriorly; armature formula of distal exopodal segment of P4 II,I,4 ..... *Amphicrossus* Huys, 1991

The reallocation of *Tychidion* to the Erebonasteridae and the earlier removal of *Myzomolgus* and *Cotylomolgus* to the catiniid "complex" (Ho 1984) narrow considerably the boundaries of the Clausidiidae. Taking into account the recent establishment of *Doviella* (da Rocha 1986), and *Hyphalion* (Humes 1987) and the doubtful status of *Hersiliodes* and *Giardella*, the family currently embraces eight valid genera which can be differentiated by the following key, which is applicable to both sexes.

Key to the genera of the Clausidiidae

1. Antennules 7-segmented in both sexes 2
   Antennules 6-segmented in both sexes 3
2. Endopods of swimming legs P1–P4 with sucking discs; middle exopod segment of P1 without inner seta; urosome with 3 somites in female, with 5 somites in male ..... *Clausidium* Kossmann, 1874
   Swimming legs P1–P4 without sucking discs; middle exopod segment of P1 with inner seta; urosome with 5 or 6 somites in female, with 6 somites in male ..... *Hemicyclops* Boeck, 1872 (partim)
3. Antenna 3-segmented; urosome with 6 somites in female 4
   Antenna 4-segmented; urosome 5-segmented in female 5
4. Urosome with 5 somites in male; P1 endopod in male not modified, 3-segmented; antenna with 3 sickle-shaped claws (longer than distal endopod segment) ..... *Hyphalion* Humes, 1987
   Urosome with 6 somites in male; P1 endopod in male modified, 2-segmented; antenna without such claws ..... *Doviella* da Rocha, 1986
5. Distal exopod segment of P4 with 9 spines or setae in total ..... *Conchyliurus* Bocquet and Stock 1957
   Distal exopod segment of P4 with 8 spines or setae at most 6
6. Maxilla with endites on syncoxa ..... *Hemicyclops* Boeck, 1872 (partim)[1]
   Maxilla without endites on syncoxa 7
7. Maxilliped rudimentary in female; middle endopod segment of P4 with 1 seta ..... *Leptinogaster* Pelseneer, 1929
   Maxilliped well developed in female; middle endopod segment of P4 with 2 setae ..... *Hippomolgus* Sars, 1917

[1] *H. latericius* (Grube, 1869) and *H. ctenidis* Ho and Kim, 1990 possess 6-segmented antennules, owing to fusion of segments 3 and 4.

Siphonostomatoida Thorell, 1859
Dirivultidae Humes and Dojiri, 1980
Benthoxynus spiculifer Humes, 1984

SPECIMENS STUDIED: 233 ♀♀, 146 ♂♂, depth 1780 m, Crab Vent, Explorer Ridge, 49°45.6′N, 130°16.1′W, 5 July 1984, P1979-808 (75 ♀♀, 20 ♂♂ deposited in the Canadian Museum of Nature, Ottawa, and 100 ♀♀, 90 ♂♂ in the National Museum of Natural History, Smithsonian Institution, Washington, D.C.).

These specimens have slightly smaller dimensions than those given for the type specimens of *B. spiculifer*. The average length of 25 females was 1.36 mm (1.23–1.47 mm), contrasting with 1.68 mm (1.61–1.79 mm) in the original description. In 80 ovigerous females there was a single egg in each egg sac, in contrast with 2 or 3 eggs in the type specimens. No external anatomical differences could be found between the original description and the present specimens. (Type specimens of this species, deposited in the National Museum of Natural History, Ottawa, NMC-C-1984, 1097, 1098, 1099, were found at the Axial Seamount, Juan de Fuca Ridge; Humes 1984.)

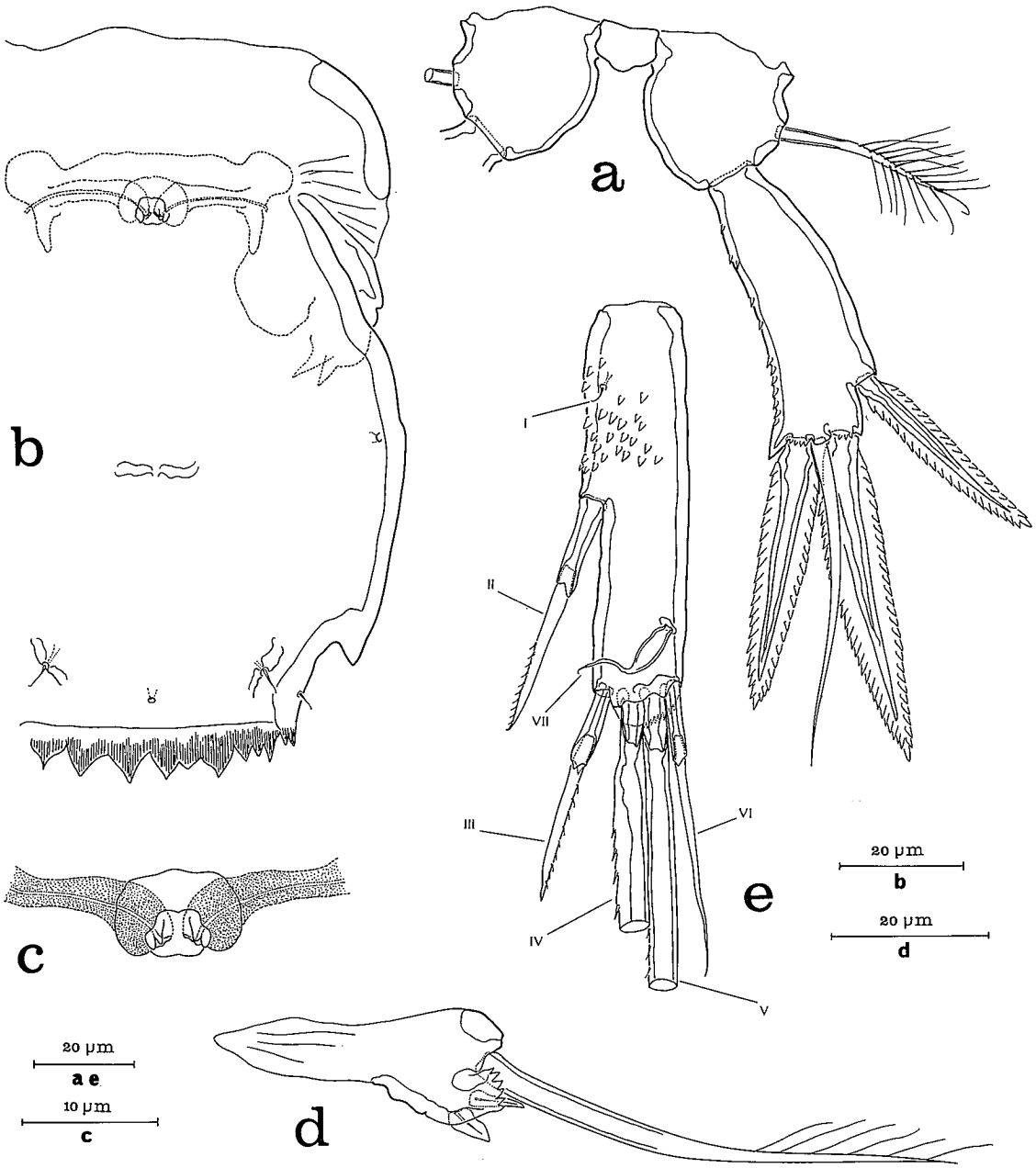

FIG. 8. *Tychidion guyanense* Humes, 1973, female. (*a*) Leg 5. (*b*) Genital double somite. (*c*) Copulatory pores. (*d*) Operculum closing off gonopore. (*e*) Caudal ramus.

OTHER SPECIMENS: 6 ♀♀, 6 ♂♂, depth 1570 m, Mushroom Vent, Axial Seamount, Juan de Fuca Ridge, 45°55′N, 130°03′W, 18 July 1986, P1722-889 (1 ovigerous ♀ with 2 eggs in egg sac); 1 ♀, depth 1570 m, Southern Axial, Mushroom Vent, Axial Seamount, Juan de Fuca Ridge, 45°55.4′N, 130°01.7′W, 18 July 1986, P1722-885 (this female with 2 eggs in egg sac); 1 ♀, depth 1780 m, Crab Vent, UMN, Explorer Ridge, 49°45.6′N, 130°16.1′W, 4 July 1984, P1494-817; 2 ♀♀, depth 1570 m, Mushroom Vent, Axial Seamount, Juan de Fuca Ridge, 45°55′N, 130°03′W, 17 July 1986, P1921-904; 1 ♀, 9 ♂♂, depth 2280 m, Hidden Vent, Megaplume Site, Juan de Fuca Ridge, 44°57.6′N, 130°13.8′W, 20 August 1988, A2092-895; 4 ♀♀, depth 2420 m, Heineken Hollow, High Heat Flow Field, Juan de Fuca Ridge, 48°27.5′N, 128°42.5′W, 5 August 1991, A2251-910; 2 ♂♂, depth 2420 m, Heineken Hollow, Middle Valley, Juan de Fuca Ridge, 48°27.5′N, 128°42.5′W, 6 August 1990, A2251-904.

Aphotopontius forcipatus Humes, 1987

SPECIMENS STUDIED: 3 ♀♀, depth 1570 m, Mushroom Vent, Axial Seamount, Juan de Fuca Ridge, 45°55.4′N, 130°01.7′W, 18 July 1986, P1722-889; 1 ♀, depth 1780 m, Crab Vent, UMN, Explorer Ridge, 49°45.6′N, 130°16.1′W, 4 July 1984, P1494-817; 2 ♀♀, 1 ♂, depth 1570 m, Hammond's Hell, Axial Seamount, Juan de Fuca Ridge, 45°55′N, 130°03′W, 20 July 1986, P1724-905. (Type specimens of this species, USNM 231927, 231928, and 231929, deposited in the National Museum of Natural History, Washington, D.C., were found at the Explorer Ridge (Humes 1987).)

Stygiopontius quadrispinosus Humes, 1987

SPECIMENS STUDIED: 524 ♀♀, 56 ♂♂, depth 1780 m, Crab Vent, Explorer Ridge, 49°45.6′N, 130°16.1′W, 18 July 1986, P1722-889; 2 ♀♀, depth 2250 m, Cleft Segment, S. Juan de Fuca, Plume, 48°38′30″N, 130°22′20″W, 24 October 1984, A1457-P-844; 2 ♀♀, depth 2200 m, Endeavor Segment, 47°57′N, 129°05′W, 1 September 1984, A1445-821; 1 ♀, depth 1570 m, Mushroom Vent, Axial Seamount, Juan de Fuca Ridge, 45°55.4′N, 130°01.7′W, 18 July 1986, P1722-889; 2 ♀♀, depth 2280 m, Hidden Vent, Megaplume Site, Juan de Fuca Ridge, 44°57.6′N, 130°13.8′W, 20 August 1988, A2092-895; 1 ♀, 1 ♂, depth 2420 m, Middle Valley, Juan de Fuca Ridge, 48°27.5′N, 128°42.5′W, 5 August 1991, A2251-910; 3 ♀♀, depth 1570 m, Mushroom Vent, Axial Seamount, Juan de Fuca Ridge, 45°55′N, 130°03′W, 17 July 1986, P1921-706; 2 ♀♀, depth 2420 m, Heineken Hollow, High Heat Flow Area, Middle Valley, Juan de Fuca Ridge, 48°27.5′N, 128°42.5′W, 5 August 1990, A2251-901; 20 ♀♀, 5 ♂♂, depth 2420 m, Heineken Hollow, Middle Valley, Juan de Fuca Ridge, 48°27.5′N, 128°42.5′W, 6 August 1990, A2251-904. (Type specimens of this species, USNM 231955, 231956, 231957, deposited in the National Museum of Natural History, Washington, D.C., were found at the Explorer Ridge (Humes 1987).)

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