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Discovery of hydrothermal vent Tantulocarida on a new genus of Argestidae (Copepoda: Harpacticoida)

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Abstract: Preliminary investigations of hydrothermal vent harpacticoids from the Galapagos Rift resulted in the discovery of a new genus and species of Tantulocarida. *Rimitantulus hirsutus* gen. et sp. nov. is described on the basis of the tantulus larva and the male at an early stage of development. It is the first record of the subclass from hydrothermal vent habitats and is placed in the Basipodellidae which exclusively utilize copepods as hosts. The harpacticoid host *Argestoides prehensilis* gen. et sp. nov., which is known only from the male, shows affinities with both the Ameiridae and Argestidae and is placed *genus incertae sedis* in the latter primarily on account of the complete lack of sexual dimorphism on the swimming legs.

Résumé : Une étude préliminaire des Harpacticoïdes des sources hydrothermales de la faille des Galapagos a conduit à la découverte d'un nouveau genre et d'une nouvelle espèce de Tantulocaride. *Rimitantulus hirsutus* gen. et sp. nov. est décrit à partir de la larve tantulus et d'un mâle à l'un des premiers stades du développement. Il s'agit du premier signalement de cette sous-classe dans les biotopes des sources hydrothermales ; le genre est placé dans les Basipodellidae qui utilisent exclusivement les Copépodes comme hôtes. L'Harpacticoïde hôte, *Argestoides prehensilis* gen. et sp. nov., dont on ne connaît que le mâle, présente des affinités à la fois avec les Ameiridae et avec les Argestidae ; il est considéré comme *genus incertae sedis* dans cette dernière famille essentiellement en raison de l'absence totale de dimorphisme sexuel sur les pattes natatoires.

Keywords : Tantulocarida, Harpacticoida, *Rimitantulus* gen. nov., *Argestoides* gen. nov., hydrothermal vents, Galapagos Rift.

Introduction

Since their formal recognition as a new class of ectoparasitic Crustacea in 1983 (Boxshall & Lincoln, 1983) numerous new genera and species of Tantulocarida have been discovered from a wide variety of marine crustacean hosts, habitats and localities. Initially regarded as a typical cold water-inhabiting taxon primarily occurring in deep-sea or high latitude environments, subsequent sampling in other habitats such as coral reef sands (Huys, 1990*a*), anchihaline lava pools (Boxshall & Huys, 1989) and shallow subtidal localities (Huys *et al.*, 1994) has indicated that they can be found over a wide range of temperatures. This has led to the suggestion that they are probably very widespread and ubiquitous, their current distribution picture and grossly underestimated number of species being solely the result of scant collecting and their extremely small size.

The present account records the first tantulocarid discovered in the hydrothermal vent habitat. It was discovered in the course of examining a series of copepod

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samples collected from the vent fields of the Galapagos Rift by the deep-sea submersible ALVIN during one of its visits in 1979. The Galapagos Rift vent site, lying at about 700 km west of Ecuador, retains a special significance since it is the location of the first discovery of hydrothermal venting and its associated fauna (Corliss *et al.*, 1979). The tantulocaridan is parasitic on a new genus of harpacticoid copepod which is tentatively assigned to the family Argestidae. Other harpacticoid families previously recorded as tantulocaridan hosts include Longipediidae (Huys, 1990*a*), Canuellidae (Boxshall & Huys, 1989; Huys, 1991), Tisbidae (Boxshall & Lincoln, 1983; Huys, 1990*b*), Diosaccidae (Boxshall, 1988; Huys, 1990*a*; Huys *et al.*, 1994), Huntemanniidae (Becker, 1975; Schriever (in Grygier & Sieg, 1988)), Tetragonicipitidae (Huys *et al.*, 1994), Styracothoracidae (Huys, 1993; Huys *et al.*, 1993) and the interstitial families Paramesochridae, Cylindropsyllidae and Leptopontiidae (Huys & Boxshall, 1988; Huys & Ohtsuka, 1993; Huys *et al.*, 1994). The tantulocaridan has been identified as a new genus and species of Basipodellidae, a family which utilizes exclusively copepods as hosts. This paper describes the tantulus larva and immature male of the new tantulocaridan as well as the adult male of the new argestid.

Methods

Specimens were cleared in lactic acid and subsequently placed in lactophenol mounting medium. Preparations were sealed with glyceel (Gurr®, BDH Chemicals Ltd, Poole, England). All drawings have been prepared using a camera lucida on a Zeiss Axioskop microscope equipped with differential interference contrast.

The descriptive terminology applied to segmentation and setation of body appendages of the harpacticoid host is adopted from Huys & Boxshall (1991) except for the swimming leg formula which follows Lang (1948). Abbreviations used in the text and figures are: ae, aesthetasc; P1 - P6, first to sixth thoracopods; exp, exopod; enp, endopod; exp(enp)-1(-2, -3), to denote the proximal (middle, distal) segment of a ramus. Pore signature terminology for the tantulocarid head shield follows Boxshall & Vader (1993).

Type material is deposited in the collections of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (NMNH).

Systematics

DESCRIPTION OF HARPACTICOID HOST

Family ARGESTIDAE Por, 1986

Argestoides gen. nov.

Diagnosis. [based on ♂ only]. - Argestidae. Cephalothorax and body somites without dorsal spinous processes. Prosome slightly wider than urosome. Urosomites with distinct pattern of fine spinules dorsally and coarse spinules ventrally. Anal operculum minutely serrate. Caudal rami short; with 7 setae; setae IV and V multipinnate.

Rostrum small, with 2 long sensillae. Antennule 11-segmented in ♂, with geniculation located between segments 8 and 9, and modified joint between segments 9 and 10; aesthetasc present on segment 6 and as part of apical acrothek on segment 11. Antenna with incompletely fused allobasis; exopod 2-segmented with armature formula [1, 2]. Mouthparts not atrophied in ♂. Mandibular palp biramous, with 1-segmented rami; basis with 2 spines; endopod with 1 lateral and 5 apical setae, exopod with 3 setae. Maxillule with free bisetose exopod; endopod represented by 2 setae incorporated into trisetose basis. Maxilla with tiny proximal endite (with 1 seta) and trisetose distal endite on syncoxa; allobasis with accessory spine and seta; endopod completely incorporated, represented by 2 setae. Maxilliped with 1 seta on syncoxa; basis unarmed; endopod with 1 accessory seta.

Swimming legs with 3-segmented rami; no sexual dimorphism discernible.

P1. Inner basal spine long, unipinnate with subapical flagellate tip. Exp-3 with 1 long bipinnate seta and 3 geniculate spines. Endopod prehensile, distinctly longer than exopod; enp-3 with 1 plumose and 2 geniculate setae.

Armature formula of swimming legs:

	Exopod	Endopod
P1	0.1.121	1.1.021
P2	0.1.223	1.1.121
P3	0.1.323	1.1.221
P4	0.1.323	1.1.221

Fifth pair of legs largely free medially in ♂; baseoendopod and exopod free; endopodal lobe moderately developed, with 2 spines; exopod with 6 setae/spines.

Sixth pair of legs slightly asymmetrical; each P6 with inner bipinnate spine and outer naked seta.

Type and only species. - *Argestoides prehensilis* gen. et sp. nov.

Argestoides prehensilis gen. et sp. nov.

Type locality. - Galapagos Rift, Stn 986: 0° 47.89'N, 86° 09.21'W; depth 2494 m.

Material. - Holotype (dissected on 7 slides (NMNH reg. no. 284161); in 0.297 mm fraction of mussel bucket washings; 03 December 1979; collected by *Alvin*.

Description

Female. Unknown.

Male.

Total body length measured from anterior tip of rostrum to posterior margin of caudal rami: 340 µm. Maximum width measured at posterior margin of cephalothorax. Anal operculum finely serrate.

Caudal ramus (Figs 4F, 6B-C) slightly longer than wide; with 7 setae. Seta I vestigial; setae II and III slender and naked; seta IV well developed, multipinnate; seta V very long, 80% of total body length (Fig. 2A), multipinnate; seta VI short and naked, fused basally to inner distal corner; seta VII bi-articulate at base, naked. Spinules present around ventral rear margin and around base of seta II; secretory pores located as in Figs 4F and 6B-C.

Rostrum (Fig. 3A) small, fused to dorsal cephalic shield; with 2 long sensillae apically; ventral surface forming lobate wing-like processes; pore not discernible.

Antennule (Fig. 2B-D) slender, 11-segmented; haplocer, with geniculation located between segments 8 and 9; modified joint present between segments 9 and 10. Segment 1 with posterior row of long setules; segment 3 longest; segment 5 vestigial, represented by U-shaped sclerite and discernible in anterior aspect only (Fig. 2D); segment 6 with long, swollen aesthetasc (100 µm) fused basally to very long, naked seta; distal margin of segment 9 produced ventrally forming curved process bearing long seta. Spine- and seta formula: 1-[1 pinnate], 2-[1 pinnate], 3-[6 + 2 pinnate], 4-[4 + 2 vestigial], 5-[1 + 1 vestigial], 6-[2 + 3 pinnate + 1 modified spine + (1 + ae)], 7-[1 + 1 modified spine], 8-[2 + 1 modified spine + 1 fused spine], 9-[1 + 3 fused spines], 10-[4]; 11-[5 + acrothek]. Modified spines on segments 6-8 (Fig. 2D) short and stubby, multispinulose, with flagellate tip; fused spines of segments 8 and 9 bare (Fig. 2C-D), with median pore (not figured). Apical acrothek on segment 11 (Fig. 2C) consisting of 1 long and 1 short naked seta fused basally to aesthetasc (34 µm).

Antenna (Fig. 3B). Coxa with spinular row. Basis and proximal endopod segment incompletely fused forming allobasis; original segmentation marked by tiny surface sutures; abexopodal margin with several groups of spinules. Exopod 2-segmented; exp-1 about 3 times as long as exp-2, with 3 spinule groups and 1 multipinnate spine; exp-2 with 1 subapical and 1 apical multipinnate spine and row of strong spinules. Free endopod 1-segmented, outer margin with 2 hyaline frills; lateral armature consisting of 2 unipinnate spines; distal armature consisting of 3 geniculate setae, 2 geniculate spines and 1 slender seta (fused basally to longest geniculate seta and bearing tube pore plus setular tuft at its base).

Labrum (Fig. 3C) a well developed lobe; distal (ventral) margin with transverse row of strong spinules and accessory row of tiny spinules.

Mouthparts fully developed; not atrophied.

Mandible with well developed gnathobase (Fig. 4A) bearing large isolated tooth ventrally and series of closely set multicuspidate (medially) or simple (dorsally) teeth around distal margin; dorsal corner with strong unipinnate seta. Palp (Fig. 4B) biramous, comprising basis and 1-segmented rami; basis with short, unipinnate, proximal spine and stout, pectinate, distal spine; exopod smaller than endopod, with setules along distal outer margin, 1 lateral and 2 apical naked setae; endopod with 1 unipinnate seta laterally and 5 naked setae around distal margin.

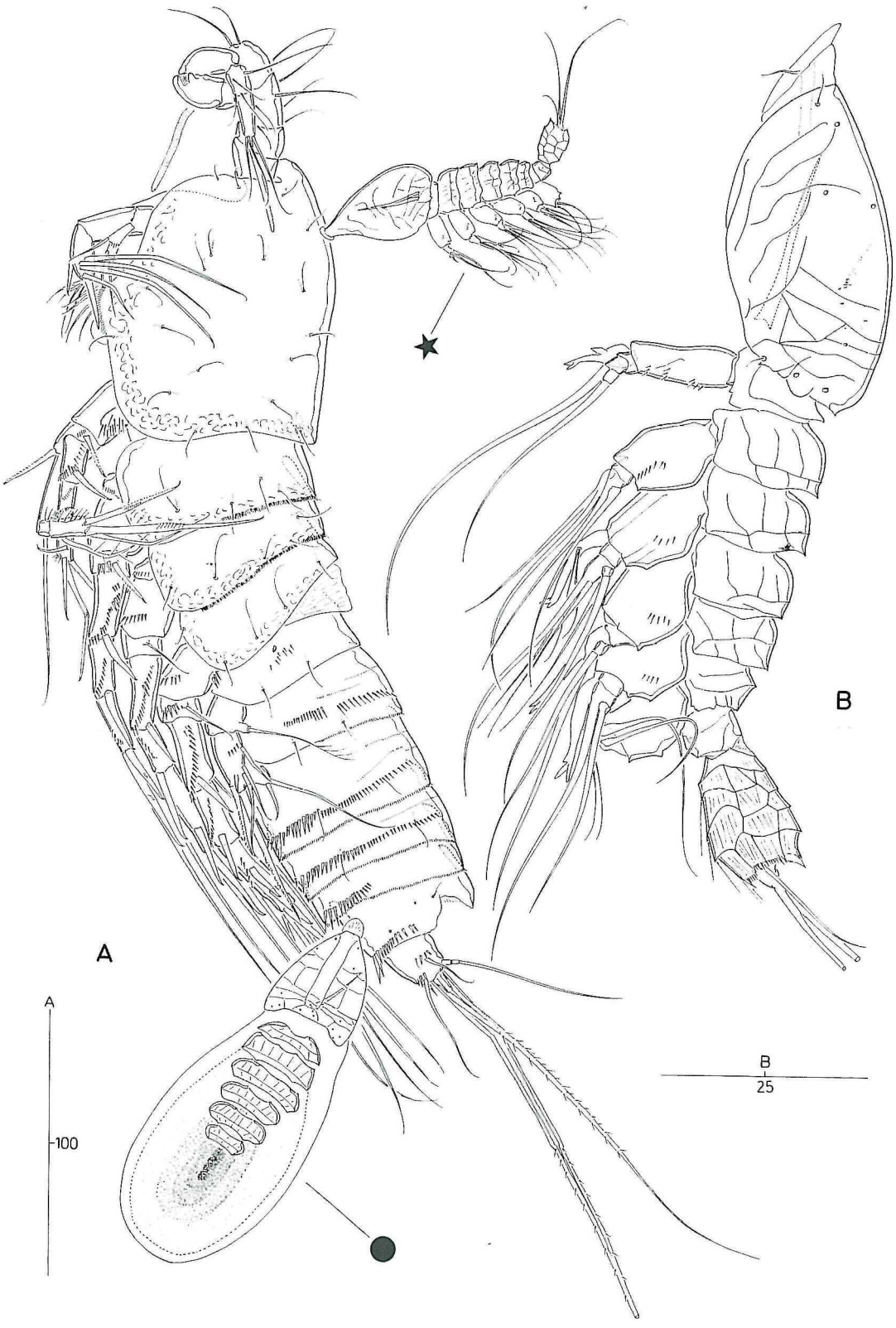
Paragnaths (Fig. 3D) represented by paired, well developed lobes bearing rows of strong spinules laterally and patch of fine, densely packed setules medially; lobes separated by median swelling bearing short spinules around distal margin and larger spinules on anterior surface.

Maxillule (Fig. 4C). Praecoxa produced medially forming long subrectangular arthrite; outer distal corner with few spinules; arthrite armature consisting of 2 parallel setae on anterior surface, 2 unipinnate, non-articulating setae medially along inner margin, and 6 spines around distal margin. Coxa forming medial endite bearing 4 naked setae and 1 weakly geniculate, unipinnate claw distally. Basis subrectangular; baso-endites reduced, probably represented by 2 slender setae apically (proximal endite?) and bipinnate seta laterally (distal endite?). Endopod completely incorporated into basis, represented by 2 bipinnate setae. Exopod represented by small segment, wider than long; with 2 bipinnate setae apically. [An alternative interpretation could be that the exopod is lost, the articulating segment therefore representing the endopod, the 2 bipinnate setae the distal baso-endite and the 3 setae referred to as basal above the proximal baso-endite].

Maxilla (Fig. 4D). Syncoxa with outer margin bearing distal group of short setules and proximal group of long setules; with 2 (coxal) endites; proximal endite vestigial, with 1 naked seta; distal endite with 2 naked setae and 1 short, apically serrate spine. Allobasis drawn out into acutely tapering claw bearing spinules along distal third of inner margin; accessory armature consisting of naked anterior seta and unipinnate posterior spine. Endopod incorporated into allobasis; represented by 2 naked setae arising from common minute knob.

Maxilliped (Fig. 4E). Syncoxa with long bipinnate seta; anterior surface with 2 spinular rows. Basis with proximal group of long setules and distal group of spinules; palmar margin with spinular row; no armature. Endopod represented by long, unipinnate, acutely curved claw bearing short naked seta at base.

Swimming legs with 3-segmented rami (Figs 3E, 5, 6A); apparently without sexually dimorphic features. Intercoxal sclerites wide, without ornamentation. Praecoxae well developed, with anterior spinular row.


A
B
A
100
B
25

P1 (Fig. 3E). Coxa with spinular pattern as figured; outer margin with 2 slight setulose bulges. Basis with bipinnate outer spine; unipinnate inner spine provided with subapical flagellate tip. Exopod with long outer spines; exp-3 with 3 geniculate spines and 1 long bipinnate seta. Endopod prehensile, distinctly longer than exopod; enp-1 elongate but shorter than exopod, inner seta plumose and very long; enp-2 shortest, inner seta plumose; enp-3 with 1 plumose and 2 geniculate setae.

P2-P4 (Figs 5A-B; 6A). Coxae with anterior spinular pattern as figured; posterior surface with 1 row of coarse spinules. Bases with outer bipinnate spine (P2) or naked seta (P3-P4); inner subdistal corner naked (P3-P4) or with 3 long spinules arising from minute protuberance (P2). Large secretory pores present anteriorly on bases (near insertion of outer seta/spine), exp-2 and -3, and enp-3. Exopods markedly longer than endopods; inner setae slender and plumose except for proximal and middle inner setae of P4 exp-3 which are swollen and unipinnate; apical elements of exp-3 setiform, pinnate along outer margin, plumose along inner margin; outer spines minutely bipinnate, those of exp-3 gradually increasing in length distally. Endopods with outer distal corners of enp-1 and -2 slightly attenuated; inner elements of enp-1 and -2 plumose or setulose proximally and unipinnate distally, distinctly spiniform in P2; inner setae and inner apical seta of enp-3 bipinnate; outer apical seta of enp-3 pinnate along outer margin (P2) or plumose (P3-P4); outer spine of enp-3 minutely bipinnate. Posterior spinule rows present on P2-P4 enp-2 and -3, P4 enp-1 and P2-P4 exp-1.

Fifth pair of legs largely free medially (fusion only discernible at base of baseoendopods; concealed under ventral hind margin of somite) (Fig. 6B); comprising baseoendopod and free 1-segmented exopod. Outer basal seta sparsely plumose, arising from short semi-articulating pedestal. Endopodal lobe moderately developed; with 2 bipinnate spines, inner one longest. Exopod with distinctly stepped inner margin; outer margin with proximal bipinnate spine and 2 naked setae; inner margin with bipinnate seta proximally and bipinnate spine distally; apex with long bipinnate seta. Large secretory pores present anteriorly on both exopod and endopodal lobe.

Sixth pair of legs (Fig. 6B) slightly asymmetrical; largest (functional) member delimited at base; outer distal corner produced into cylindrical process bearing inner bipinnate spine and outer naked seta.

Spermatophore ovoid (Fig. 6B); length 58 µm.

Etymology. The specific name is derived from the Latin *prehendere*, meaning to seize, and refers to the prehensile endopod of the P1.

Discussion

The taxonomic position of *Argestoides prehensilis* is enigmatic. *Argestoides* gen. nov. bears close similarities with some ameirid genera, particularly in the setation and segmentation of the antennary exopod, the structure of the mouthparts and the facies of the prehensile P1 endopod. It differs from male Ameiridae by the absence of sexual dimorphism on leg 1.With the exception of some neotenic genera such as *Psammonitocrella* Rouch, 1992 and a few deepwater genera of doubtful affinity (e.g. *Malacopsyllus* Sars, 1911; *Anoplosoma* Sars, 1911; *Parameiropsis* Becker, 1974) all Ameiridae exhibit a modified inner basal spine on the male P1. This character is regarded here as the primary synapomorphy diagnosing exclusively true ameirids. It will prove crucial in future revisions of the family by serving as a unique sift criterion to either include or exclude taxa. Although this might potentially lead to problems in assigning certain taxa known only from females, accepting this as the cut-off point is the sole alternative to avoid further blurring of the family boundaries. On similar grounds Fiers (1990) recently transferred two genera associated with land crabs, *Cancrincola* Wilson, 1913 and *Antillesia* Humes, 1958, from the Ameiridae and placed them in a new family Cancrincolidae. In *A. prehensilis* the inner basal spine of leg 1 is very well developed and clearly not transformed. The genus is therefore excluded from the Ameiridae even though similarities in leg 1 and mouthparts are striking. The prehensile nature of the P1 endopod has, however, evolved on numerous occasions during harpacticoid evolution - sometimes convergently within the same family such as in the Ameiridae - and does not necessarily indicate phylogenetic affinity.

The complete absence of swimming leg sexual dimorphism in conjunction with the 3-segmented condition in both rami of P1-P4, suggests a relationship with the genera currently accommodated in the Argestidae. The only other family which primitively displays this combination is the Ectinosomatidae which differs profoundly from *Argestoides* in body shape, mouthpart structure and P5. The Argestidae, a primarily deepwater inhabiting family, was recently established by Por (1986) as a result of his subdivision of the polyphyletic family Cletodidae. In addition to the type genus *Argestes* Sars, 1910 the following genera were included: *Fultonia* T. Scott, 1902; *Eurycletodes*

Figure 1. *Argestoides prehensilis* (♂). A, habitus, lateral [with tantulocarids attached (●: young ♂ enclosed in trunk sac of preceding tantulus larva; ★: tantulus larva)]. *Rimitantulus prehensilis* (tantulus larva). B, habitus, lateral.

Figure 1. *Argestoides prehensilis* (♂). A, habitus, vue latérale [avec tantulocarides attachés (● : ♂ juvénile à l'intérieur du sac du tronc de la larve tantulus précédente ; ★ : larve tantulus)]. *Rimitantulus prehensilis* (larve tantulus). B, habitus, vue latérale.

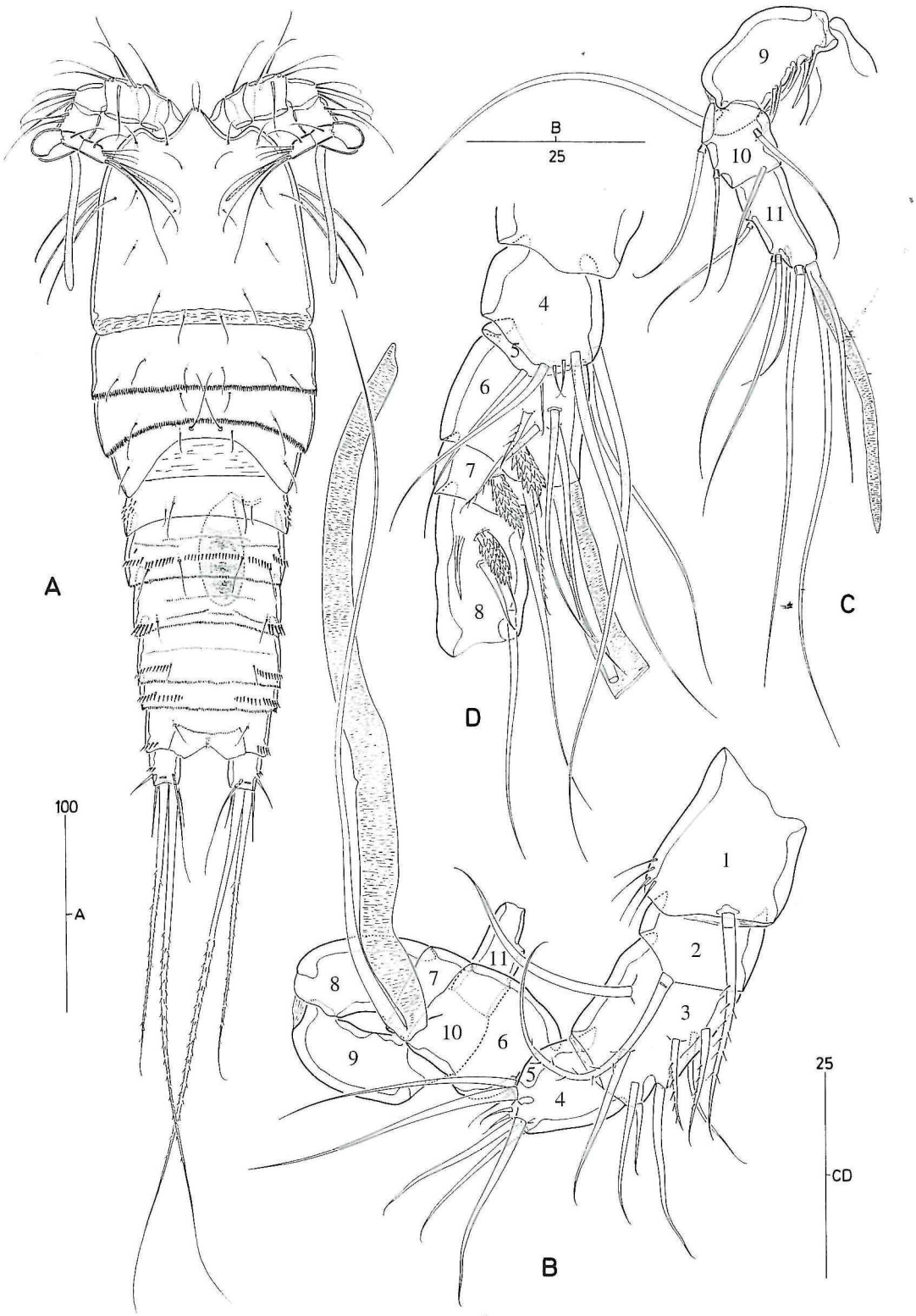


Figure 2. *Argestoides prehensilis* (♂). A, habitus, dorsal [with tantulocarids detached]; B, antennule, ventral [armature of segments 6-11 omitted]; C, antennulary segments 9-11, dorsal; D, antennulary segments 4-8, anterior.

Figure 2. *Argestoides prehensilis* (♂). A, habitus, vue dorsale (avec tantulocarides détachés) ; B, antennule, vue ventrale [armature des articles 6-11 omise] ; C, articles antennulaires 9-11, vue dorsale ; D, articles antennulaires 4-8, vue antérieure.

Sars, 1909; *Mesocletodes* Sars, 1909; *Leptocletodes* Sars, 1920; *Argestigens* Willey, 1935; *Hemicletodes* Lang, 1936; *Parargestes* Lang, 1944; *Odiliacletodes* Soyer, 1964; *Coralliclетodes* Soyer, 1966; *Neoargestes* Drzycimski, 1967; *Hypalocletodes* Por, 1967; *Dizahavia* Por, 1979 and *Megistocletodes* Por, 1986. The description of the monotypic genus *Austrocletodes* Pallares, 1979 was not available to Por (1986), however, there seems to be sufficient evidence indicating its affinity with the other argestid genera. Finally, the deepwater genus *Abyssameira* Itô, 1983, formerly placed in the Ameiridae, has recently been transferred (Huys *et al.*, 1996: 112) to the Argestidae.

Within the Argestidae only the monotypic genus *Dizahavia* shows a prehensile P1 endopod. *D. halophila* Por, 1979, which is known from females only, was described from the shallow metahaline Di Zahav pool on the Sinai coast of the Gulf of Elat (Por, 1979). Apart from a striking difference in habitat utilization, it can be distinguished from *A. prehensilis* primarily by the 2-segmented endopod of P1 and P4, the presence of an inner seta on P2-P4 exp-1 and particularly the antennary exopod. The 2-segmented, trisetose antennary exopod is the stumbling block to formal recognition of *Argestoides* as a genuine argestid since in all other members of the family the exopod is at most 1-segmented and carries a maximum of 2 setae (e.g. *Megistocletodes, Mesocletodes*). This condition is even displayed in the most primitive genera such as *Argestigens* and *Neoargestes* which have a more plesiomorphic swimming leg setal formula than *Argestoides*. On the basis of this discrepancy *Argestoides* is only tentatively placed in the Argestidae as *genus incertae sedis* pending a thorough revision of the family.

Becker (1974) has already remarked on the similarities between the Ameiridae and the "cletodid" genera related to *Argestigens*. In fact, he recognized an evolutionary lineage consisting of *Parameiropsis*, which he considered as very similar to Lang's (1948) hypothetical ameirid ancestor, and *Argestes*, *Parargestes* and *Argestigens*, which according to Becker (1974) could not be retained in the Cletodidae and should instead be placed in the Ameiridae. In a later paper he (Becker, 1979) reinforced this idea by stating that only lack of information on the undiscovered males prevented him from allocating these genera to a separate family closely related to the primitive Ameiridimorpha. The subsequent discovery of various deepwater genera (Becker, 1979; Itô, 1983) has further blurred the boundaries between the Ameiridae and the Cletodidae (read "Argestidae") since. The taxonomic interface between these families is now clearly "*incertae sedis* land" which can only be elucidated by a redefinition of their respective diagnoses. It is conceivable that *Argestoides* forms part of a lineage that holds an intermediate position between the Ameiridae and Argestidae and which eventually will be accorded family rank. We regard it unlikely that the absence of sexual dimorphism in *A. prehensilis* is secondary as a result of neotenic development since no other indication of heterochrony could be observed in those appendages that are usually affected by such a process, for example in the fifth legs or the antennules.

A second alternative hypothesis is that the only known male of *A. prehensilis* represents an aberrant intersex individual displaying a mozaic of both male and female characters. Intersexuality is rare in harpacticoids (Huys & Gee, 1993), however, where present it is usually expressed in more than one somite or appendage. The probability that the holotype of *A. prehensilis* is an intersex specimen, exhibiting the female condition of the inner basal spine, is unlikely since no other aberrations could be detected in e.g. the antennules, P5, P6 or the separation of the genital and first abdominal somites.

Except for some undescribed Ectinosomatidae which have been recorded from around the foot of black smokers at the East Pacific Rise (Alain Dinet, pers. comm. in Grassle (1986)), identified harpacticoid records from vent and cold seep habitats are still non-existent. *A. prehensilis* is the first harpacticoid described from hydrothermal vents. It was infested by two stages of an unknown tantulocarid which is described below.

DESCRIPTION OF TANTULOCARIDAN

Family BASIPODELLIDAE Boxshall & Lincoln, 1983

Rimitantulus gen. nov.

Diagnosis [based on tantulus larva]. Basipodellidae. Cephalic shield with paired subdorsal longitudinal lamellae and pattern of connecting oblique and transverse lamellae dorsally and laterally. Cephalic pore formula as follows: A_{I-IV}, L_{I-IV}, D_{I-IV}. Cephalic stylet straight. Thoracic tergites with transverse and longitudinal surface lamellae. Thoracopods 1-5 with medial protopodal endite. Thoracopod 1 biramous; endopod short, without armature; exopod indistinctly 2-segmented, with 2 long terminal setae and 1 short inner seta. Thoracopods 2-5 with long endopod bearing 2 setae; exopod 2-segmented, with 4 (thoracopod 2) or 5 well developed setae (thoracopods 3-5). Thoracopod 6 with 2 curved setae. Abdomen with 4 transverse lamellae; dorsal surface with several longitudinal lamellae primarily in distal half and numerous minute surface striations; ventral surface with long cuticular hairs. Caudal rami with long lateral seta; terminal setae not modified.

Hosts: Harpacticoida (Argestidae?).

Type and only species. - *Rimitantulus hirsutus* gen. et sp. nov.

Rimitantulus hirsutus gen. et sp. nov.

Type locality. - As for host harpacticoid.

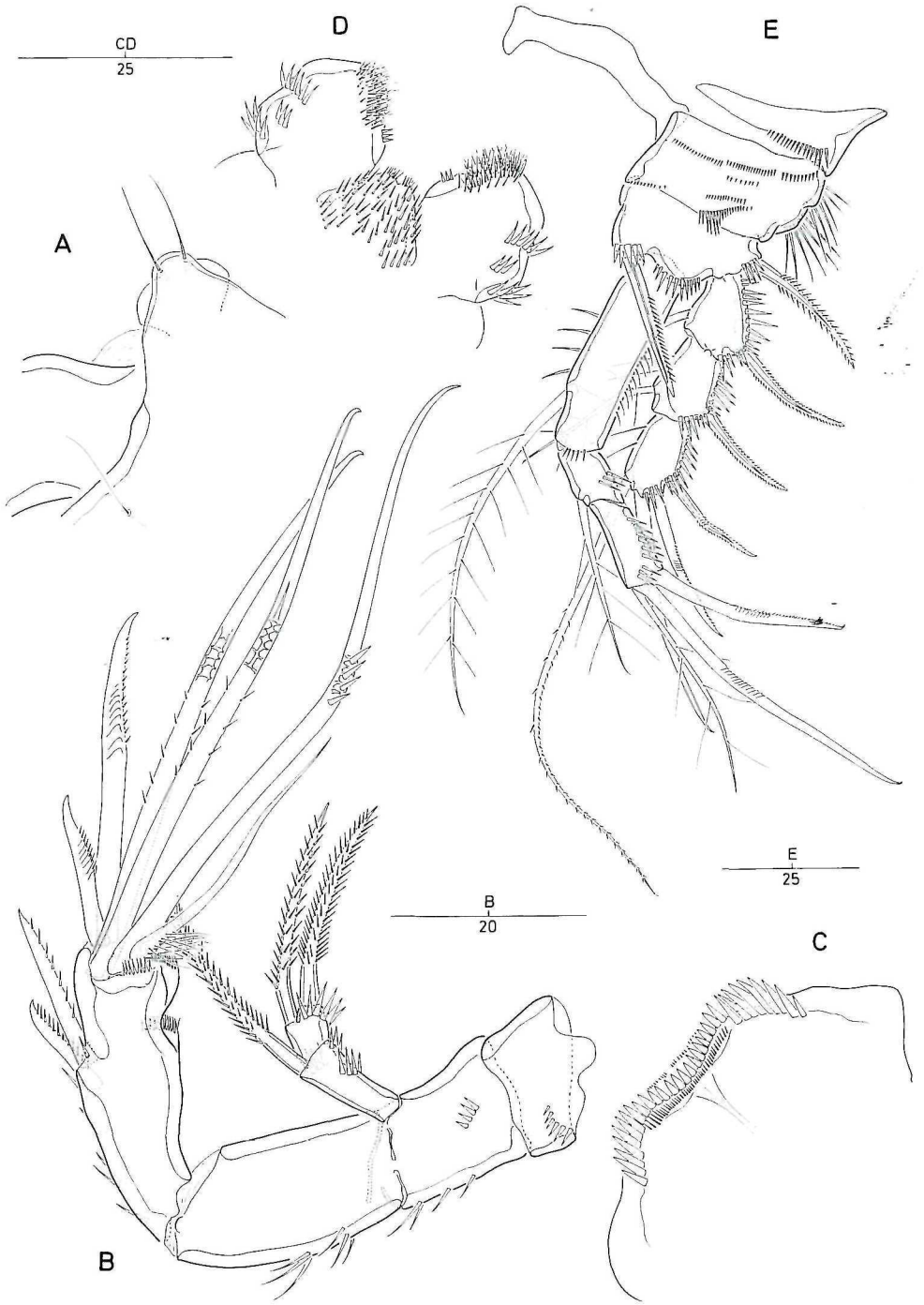


Figure 3. *Argestoides prehensilis* (♂). A, rostrum, dorsal; B, antenna; C, labrum, anterior; D, paragnaths, anterior; E, P1, anterior.
Figure 3. *Argestoides prehensilis* (♂). A, rostre, vue dorsale ; B, antenne ; C, labre, vue antérieure ; D, paragnathes, vue antérieure ; E, P1, vue antérieure.

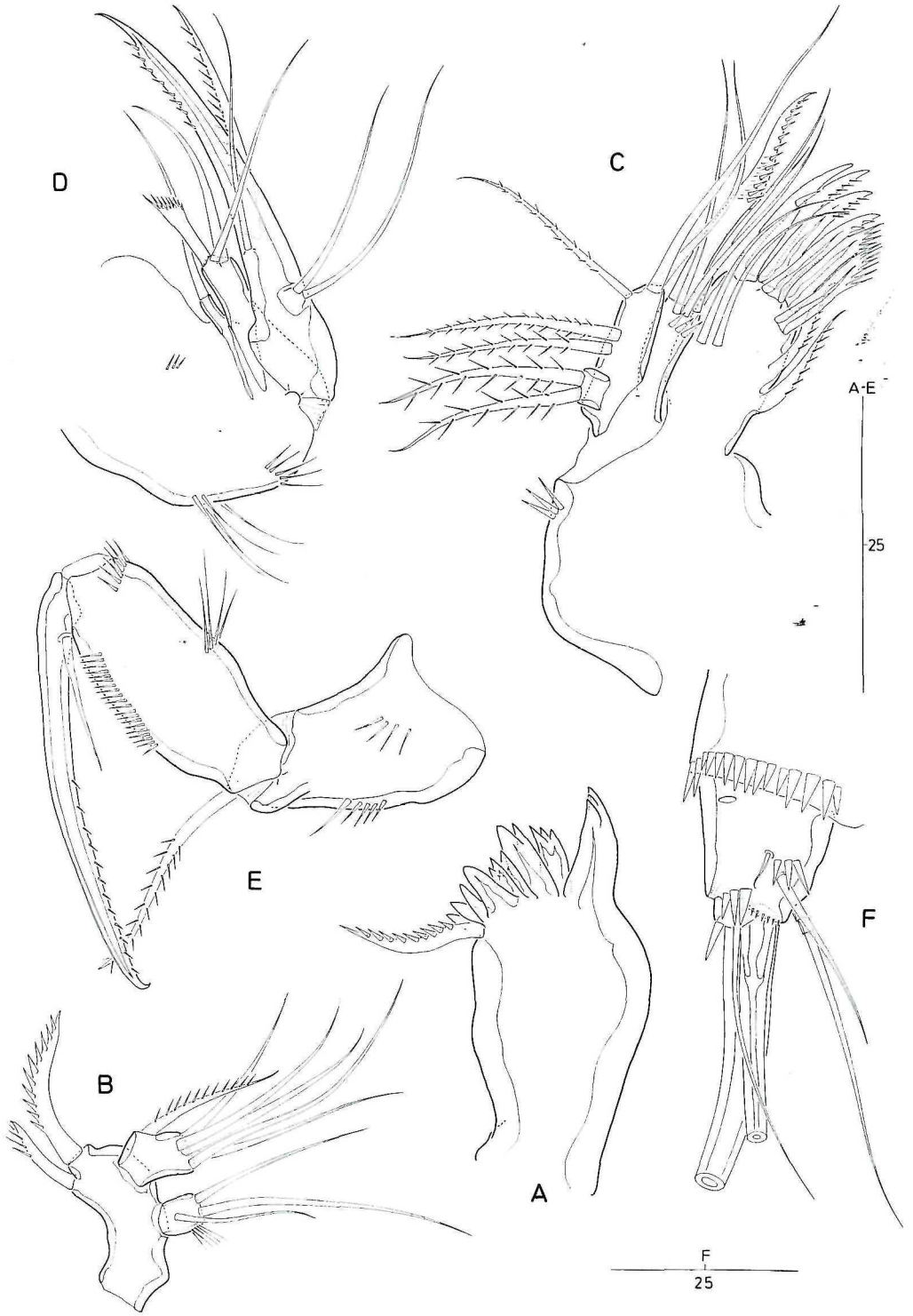


Figure 4. *Argestoides prehensilis* (♂). A, mandibular gnathobase; B, mandibular palp; C, maxillule, anterior; D, maxilla; E, maxilliped, anterior; F, left caudal ramus, lateral.

Figure 4. *Argestoides prehensilis* (♂). A, gnathobase mandibulaire ; B, palpe mandibulaire ; C, maxillule, vue antérieure ; D, maxille ; E, maxillipède, vue antérieure ; F, rame caudale gauche, vue latérale.

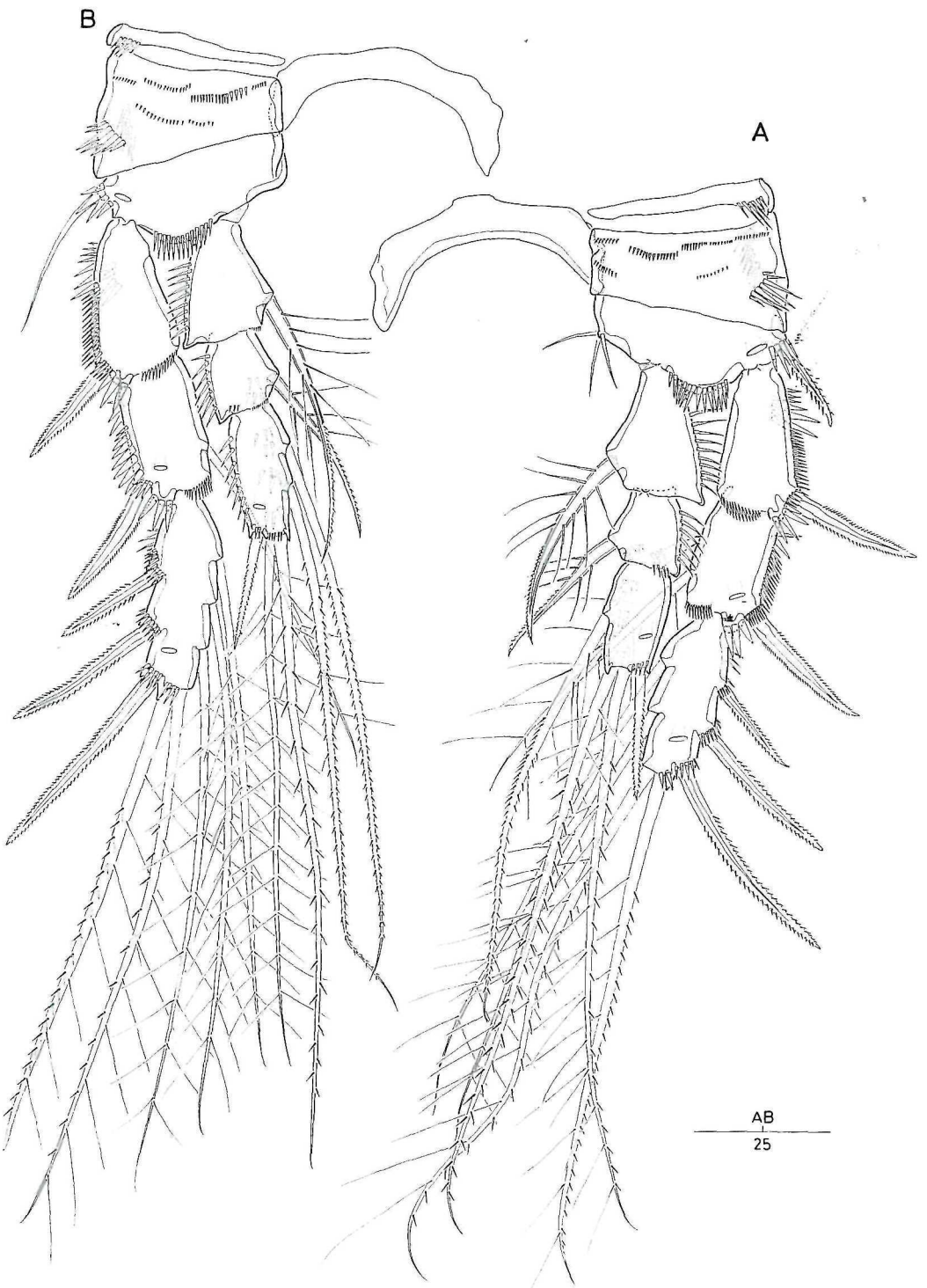


Figure 5. *Argestoides prehensilis* (♂). A, P2, anterior; B, P3, anterior.
Figure 5. *Argestoides prehensilis* (♂). A, P2, vue antérieure ; B, P3, vue antérieure.

Etymology. - The generic name is derived from the Latin *rima*, meaning rift, cleft, and tantulus, which forms part of the name of the subclass Tantulocarida, and refers to the hydrothermal vent habitat of its type species.

Material. - Holotype ♂ enclosed in trunk sac of metamorphosed tantulus (NMNH reg. no. 284162), attached to left side of anal somite of host; mounted on slide. Paratype tantulus (NMNH reg. no. 284163) attached to dorsal surface of cephalic shield; mounted on slide.

Description

Tantulus larva

Body consisting of cephalon covered by dorsal shield, 6 pedigerous somites and 2-segmented limbless urosome; body length about 108 µm, measured from anterior tip of cephalon to posterior margin of caudal rami (Fig. 1B). Cephalon (Fig. 1A-B) tapering anteriorly with 1 pair of longitudinal epicuticular lamellae extending dorsally from posterior end of cephalon to anterior sensilla; lateral surface with anastomotic pattern of transverse and oblique epicuticular lamellae. Cephalic shield about 1.1 times as long as wide (37 µm x 34 µm); Oral disc about 14 µm in diameter, anteroventrally positioned; partly covered anteriorly by membranous extension of cephalon (Fig. 1B). Ventral pores and M-pores missing. Cephalic pore formula as follows: A_{I-IV}, L_{I-IV}, D_{I-IV}. Cephalic stylet 23 µm long, more or less straight; hollow at base. Eight glandular structures (arranged in pairs) discernible in posterior half of cephalon (not figured in Fig. 1B).

Thoracic somites 1 to 6 (Fig. 1B) each provided with well developed tergite and pair of thoracopods. First tergite largely concealed beneath posterior rim of cephalon. Tergites with distinct surface ornamentation consisting of short longitudinal ridges arranged both anterior and posterior of transverse surface lamella. Thoracopods with minute spinules along lateral margin of protopod (Fig. 1B).

Thoracopod 1 (Fig. 7D) with unsegmented protopod bearing medial endite and well developed rami. Endopod represented by digitiform segment, with proximal half swollen midway and distal half slightly bifid apically; outer margin without armature. Exopod indistinctly 2-segmented; segments separated posteriorly by oblique suture; proximal segment small, drawn out into short setiform process at inner distal corner; distal segment forming two cylindrical processes, each with long terminal seta, inner seta with spinous process at base.

Thoracopods 2 to 5 (Fig. 7E-F) similar, with large unsegmented protopod, wider than that of thoracopod 1 and with angular inner expansion; medial endite lobate, with at least 1 grappling spine. Endopod 1-segmented, elongate and slender, with 2 outer setae midway; apex with 2 processes. Exopod 2-segmented; proximal segment unarmed; distal segment with 2 long and 2 (thoracopod 2; Fig. 7E) or 3 (thoracopods 3-5; Fig. 7F) fine setae terminally; distal segment of thoracopod 2 also with accessory setule along outer margin (Fig. 7E).

Thoracopod 6 (Fig. 7G) with undivided protopod lacking endite, but having 2 coupling spinules midway the inner margin; inner distal corner spinous; vestigial segment with 2 setae and short spinous process; inner seta shorter than outer, more or less chitinized and curved inwards.

Urosome (Figs. 1B; 7B-C) consisting of small seventh thoracic somite and large unsegmented abdomen; about 19 µm in length. Seventh thoracic somite tapering anteriorly, with 1 longitudinal and 2 transverse lamellae dorsally. Abdomen longer than wide, 45 µm long; with 4 distinct, transverse lamellae dorsally (Fig. 7B) and ventrally (Fig. 7C), connected by short longitudinal lamellae laterally (Fig. 1B) and dorsally (Fig. 7B); dorsal and lateral surfaces with numerous minute longitudinal striations; ventral surface with long cuticular hairs medially and shorter ones in distal fifth (Fig. 7C); dorsal posterior margin with series of minute processes (Fig. 7B). Caudal rami small, each with 1 relatively long lateral seta and 2 long medial setae with common base; medial setae not modified or spiniform (Fig. 7B-C).

Male

Male at early stage of development enclosed in reflexed position within expanded trunk sac of preceding tantulus larva (Figs. 1A; 7A); metamorphosed tantulus about 150 µm in length. Trunk sac expanded dorsally, with major swelling posterior to sixth tergite; additional swelling occurring between posterior rim of cephalon and first thoracic tergite and between individual tergites. Cephalon, rest of thorax including thoracopods, and urosome remaining unchanged from preceding tantulus larva. Metamorphosing male supplied with nutrients via large tissue connection (umbilical cord) containing larval stylet and connecting ventral side of cephalothorax with larval oral disc. Differentiation of tagmosis not discernible yet. Anlagen of 6 pairs of thoracopods, penis and caudal rami present but armature not developed. Cephalothorax with 3 pairs of aesthetascs. Male connected with larval urosome via tissue strand.

Etymology. The specific name is derived from the Latin *hirsutus,* meaning shaggy, and alludes to the presence of long cuticular hairs on the ventral surface of the abdomen.

Discussion

The new tantulocaridan is placed in the family Basipodellidae, redefined by Huys (1990b), on the basis of the 2-segmented urosome, the absence of a rostrum, the segmentation of the rami of the thoracopods in the tanulus larva, and the position of the expanded trunk sac containing the developing male. In all genera of the Basipodellidae the

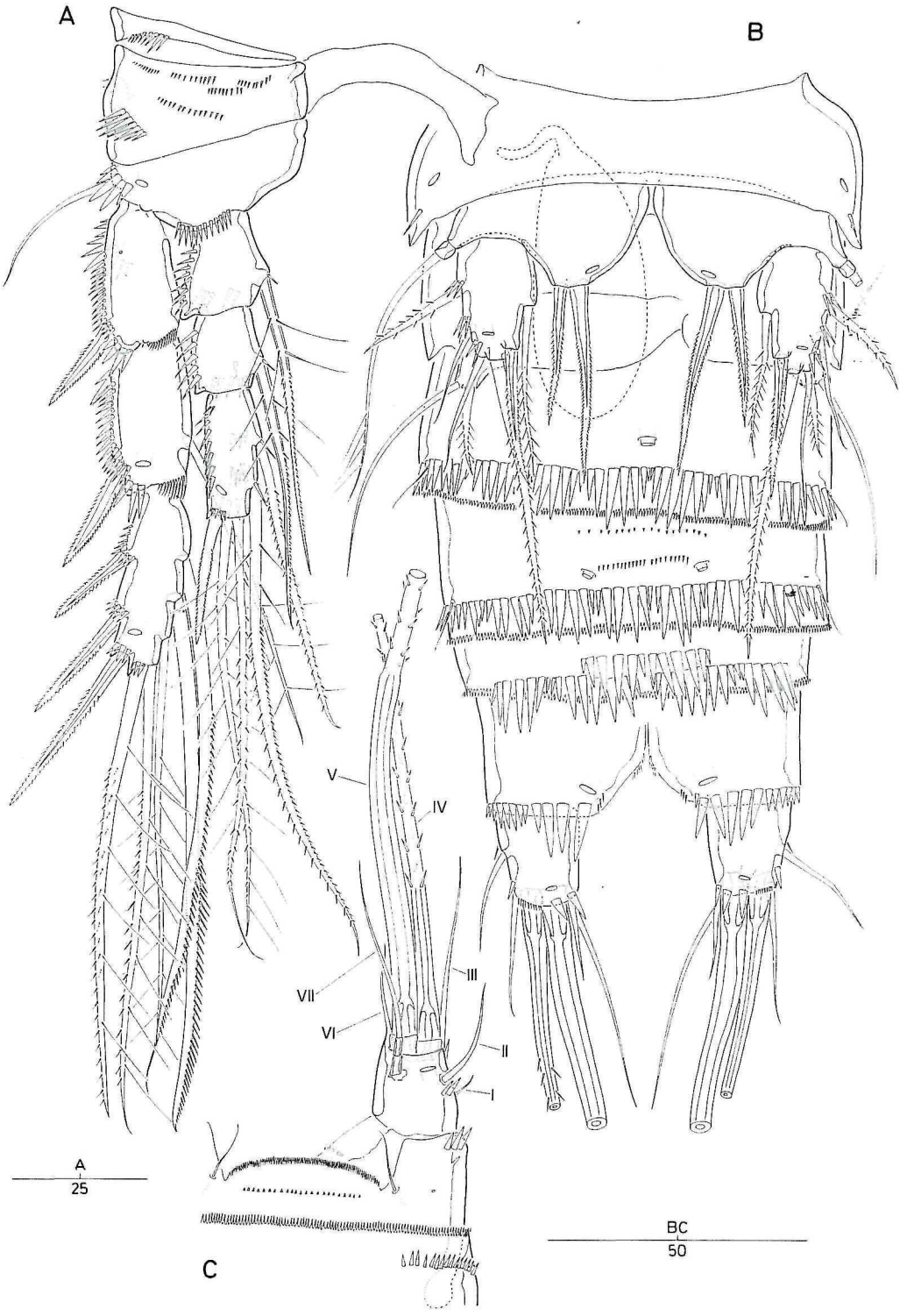


Figure 6. *Argestoides prehensilis* (♂). A, P4, anterior; B, urosome, ventral; C, anal somite and left caudal ramus, dorsal.
Figure 6. *Argestoides prehensilis* (♂). A, P4, vue antérieure ; B, urosome, vue ventrale ; C, somite anal et rame caudale gauche, vue dorsale.

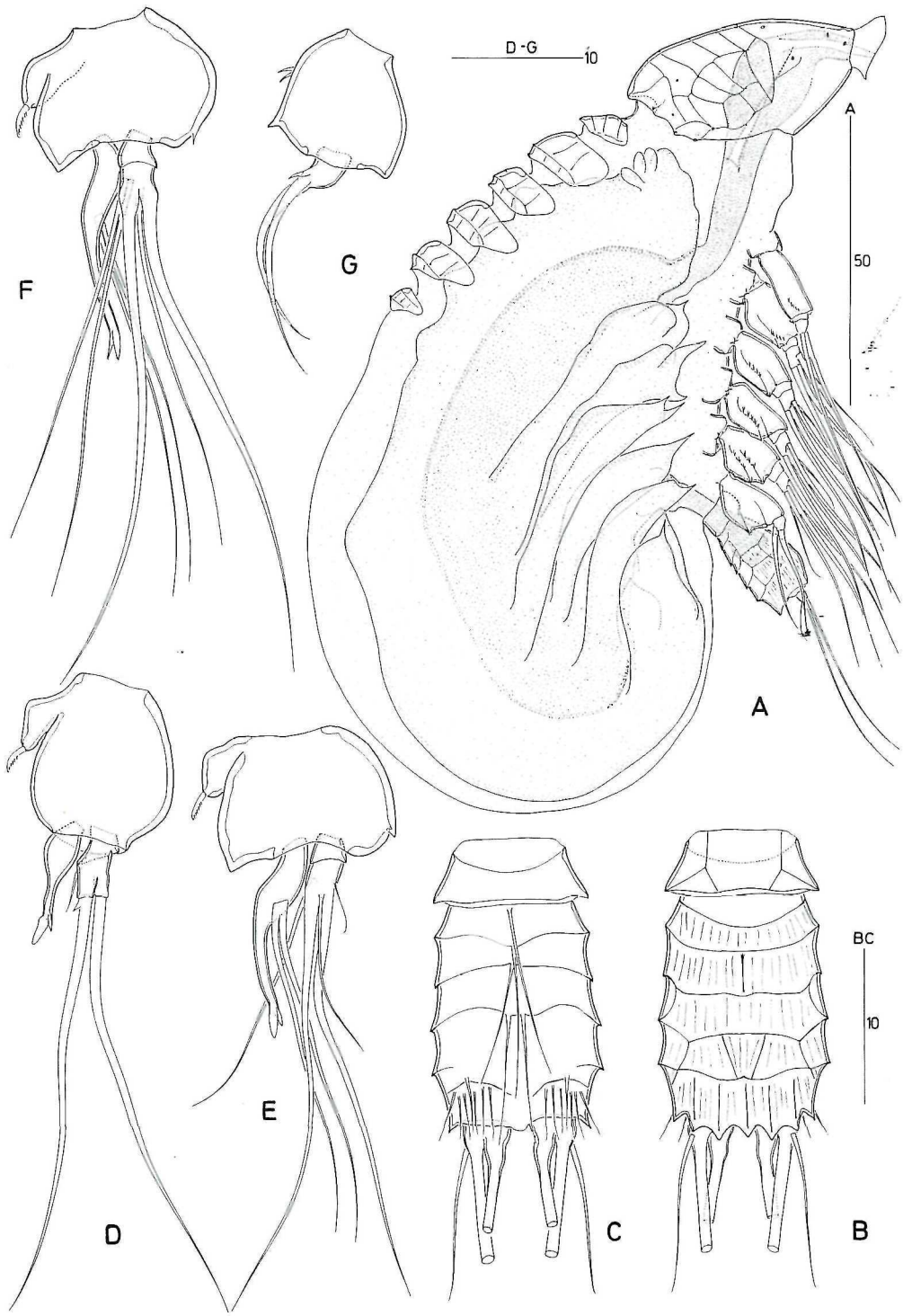


Figure 7. *Rimitantulus hirsutus*. A, young ♂ enclosed in trunk sac of preceding tantulus larva; B, urosome, dorsal; C, urosome, ventral; D, thoracopod 1; E, thoracopod 2; F, thoracopod 3; G, thoracopod 6.

Figure 7. *Rimitantulus hirsutus*. A, ♂ juvénile à l'intérieur du sac du tronc de la larve tantulus précédente ; B, urosome, vue dorsale ; C, urosome, vue ventrale ; D, premier thoracopode ; E, second thoracopode ; F, troisième thoracopode ; G, sixième thoracopode.

male trunk sac is formed dorsally by major swelling posterior to the sixth tergite (as in other families except for the Doryphallophoridae: cf. Huys (1990b)) and by minor swelling anterior to the first tergite (unique to Basipodellidae). The separation of the first tergite from the cephalic shield occurs very early in the metamorphosis and allows for rapid and unequivocal identification of young basipodellid males since in all other families this tergite remains largely concealed beneath the head shield during the process of trunk sac formation.

The Basipodellidae currently comprise five species which were all discovered during examination of their copepod hosts (Becker, 1975; Boxshall & Lincoln, 1983; Boxshall & Huys, 1989; Huys *et al.*, 1994; Ohtsuka & Boxshall, in press). The three species belonging to the genera *Basipodella* Becker and *Stygotantulus* Boxshall & Huys exclusively utilize harpacticoids as hosts. Both *Basipodella harpacticola* Becker, described from several life-cycle stages collected in the Peru Trench (Becker, 1975) and *B. atlantica* Boxshall & Lincoln, known only from a parthenogenetic female found southwest of the Azores (Boxshall & Lincoln, 1983), were discovered on deep-sea harpacticoid copepods. *Stygotantulus stocki* Boxshall & Huys was described from an anchihaline lava pool on Lanzarote and also utilizes harpacticoid hosts (Boxshall & Huys, 1989). The other two genera *Nipponotantulus* Huys, Ohtsuka & Boxshall and *Hypertantulus* Ohtsuka & Boxshall are monotypic genera described from Japanese waters. *N. heteroxenus* Huys, Ohtsuka & Boxshall appears to exhibit a low level of host specificity, occurring on calanoids (Pseudocyclopiidae), cyclopoids (Cyclopinidae) and at least five families of harpacticoids (Diosaccidae, Tetragonicipitidae, Paramesochridae, Cylindropsyllidae, Leptopontiidae) (Huys & Ohtsuka, 1993; Huys *et al.*, 1994). *H. siphonicola* Ohtsuka & Boxshall infests at least two genera of shallow-water siphonostomatoid copepods (family Asterocheridae) (Ohtsuka & Boxshall, in press). Another new basipodellid collected from the Northeast Water Polynya (NEW) on the East Greenland shelf has been described recently (Huys *et al.*, 1997).

Rimitantulus can be readily distinguished from the other basipodellid genera by the presence of 5 setae on the distal exopod segment of thoracopods 3-5. This is the maximum number found in any tantulocarid and has been recorded thus far only in both genera of the Doryphallophoridae and in some representatives of the Deoterthridae (e.g. *Deoterthron* Bradford & Hewitt, *Aphotocentor* Huys, *Amphitantulus* Boxshall & Vader). In other basipodellids the exopod of these thoracopods bears 4 setae (*Basipodella, Stygotantulus, Hypertantulus*) or is reduced even further to 3 elements in the anterior thoracopods (*Nipponotantulus*). Within the Basipodellidae the new tantulocarid also displays the maximum number of setae on the exopod of thoracopod 1. The short accessory seta arising from the inner distal corner of the proximal segment is likely to be the homologue of the slender inner seta found on the unsegmented exopod of the deoterthrids *Boreotantulus kunzi* Huys & Boxshall and *Aphotocentor styx* Huys. Another unique character of *R. hirsutus* is the conspicuous surface ornamentation on the abdomen consisting of very long cuticular hairs arising from the ventral midline and supplementary setules arranged in paired patches near the ventral posterior margin.

Nipponotantulus differs from *Rimitantulus* in the presence of modified medial setae on the caudal ramus and the absence of oblique and transverse epicuticular lamellae on the cephalic shield. *Basipodella* and *Stygotantulus* can be differentiated from *Rimitantulus* by the 1-segmented exopod of thoracopod 1. Finally, *Hypertantulus* differs from the new genus and all other known basipodellids in the presence of an inner seta on the endopod of thoracopod 1.

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