

STYGOFAUNA OF THE CANARY ISLANDS, 10

ROTUNDICLIPEIDAE FAM. NOV. (COPEPODA, HARPACTICOIDA)
FROM AN ANCHIHALINE CAVE ON TENERIFE, CANARY
ISLANDS

BY

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SUMMARY

A new family Rotundiclipeidae is proposed for an anchihaline cave-dwelling harpacticoid *Rotundiclipeus canariensis* gen. nov., sp. nov. from Tenerife, Canary Islands. It is suggested that the family should be placed in the Cervinioidea grouping also the chiefly deep-sea Cerviniidae and the mesopelagic Aegisthidae. Because of numerous unique and unusual derived traits, the small-sized Rotundiclipeidae are regarded as the advanced sistergroup of the Cerviniidae-Aegisthidae complex whilst the Cerviniidae are standing closest to the cervinioid ancestor. In the context of Stock's (1986) conclusion it is postulated that both the cave-dwelling Rotundiclipeidae and the deep-sea Cerviniidae are originated from a common shallow water ancestor.

RÉSUMÉ

On propose la nouvelle Rotundiclipeidae pour un Harpacticoïde cavernicole anchihaline, *Rotundiclipeus canariensis* gen. nov., sp. nov., de Tenerife (Canaries). On suggère que la famille doit prendre place dans les Cervinioidea comprenant aussi les Cerviniidae (formes surtout abyssales) et les Aegisthidae (mésopélagiques). A cause de nombreux caractères apomorphes uniques et remarquables, les Rotundiclipeidae — formes de petite taille — sont considérés comme groupe-frère plus apomorphe du complexe Cerviniidae-Aegisthidae, dont les Cerviniidae sont plus proches de l'ancêtre cervinioïde.

Dans le contexte de la conclusion de Stock (1986) on suppose que les Rotundiclipeidae cavernicoles et les Cerviniidae abyssaux ont leur origine dans un ancêtre commun d'eaux peu profondes.

INTRODUCTION

The extent of our knowledge concerning the harpacticoid copepod fauna of the Canary Islands is almost entirely confined to the major island, Tenerife. I.C. Thompson (1887) in the first study strictly devoted to this area presented some preliminary results of a faunal survey in the Canary Islands and Madeira. That paper and a later one (I.C. Thompson, 1888) dealt with 17 species of Harpacticoida obtained from the northern coast of Tenerife near Puerto de la Cruz (Puerto Orotava); all these species, however, had been fre-

quently reported before in earlier studies of the North Sea and adjacent estuaries. The only other publication before the turn of the century was that of Richard (1898), recording *Canthocamptus palustris* (= *Nitocra spinipes*) in association with *Artemia salina* in the semi-enclosed lagoon of Janubio on Lanzarote.

The most meaningful data came from Noodt (1955, 1958) who identified 51 species and described several new Darcythompsoniidae and Laophontidae from sandy beaches on Tenerife. Schminke (1971) described two new Parastenocarididae, *Parastenocaris ursulae* and *P. inferna*, from Barranco del Infierno, Tenerife. Marinov (1973) described *Phyllopodopsyllus laspalmensis* from a coarse sandy beach in Las Palmas on Gran Canaria. Finally, Kunz (1978) reported *Leptocaris biscayensis* from El Medano and described the male of *L. minimus* from material collected at Punta del Hidalgo, Tenerife.

A series of samples, gathered during the Amsterdam Expedition to the Canary Islands, was kindly placed at my disposal by Prof. J.H. Stock. Harpacticoid copepods were collected in anchihaline caves (sensu Stock et al., 1976) situated on Tenerife and El Hierro. Thus far, only calanoids (Yeatman, 1980; Barr, 1984; Fosshagen & Iliffe, 1985), platycopioids (Fosshagen & Iliffe, 1985) and misophrioids (Boxshall & Iliffe, 1986) have been described from "marine" caves. This paper is the first of a series dealing exclusively with anchihaline cave-dwelling Harpacticoida.

MATERIAL AND METHODS

Before dissection, the habitus was drawn in lactophenol and body length measurements were made. Specimens were dissected in lactic acid and the dissected parts were individually positioned in lactophenol mounting medium. Preparations were sealed with glyceel.

Rotundiclipeus canariensis gen. nov., sp. nov. was examined by scanning electron microscopy (SEM) with a JEOL JSM-840 microscope. A single male was prepared by dehydration through graded ethanol, critical point dried, mounted on stubs and sputter coated with gold.

All figures have been prepared using a camera lucida. The terminology and presentation of the setal formulae are adopted from Lang (1948, 1965). The terms pars incisiva, pars molaris and lacinia mobilis are omitted in the description of the mandibular gnathobasis (Mielke, 1984). Boxshall's (1985: 341-344) terminology for the mandible and the maxilliped and that of Huys (1988) for the caudal ramus structure are followed.

Abbreviations used in the text and figures are: P1-P6. Type-specimens are deposited in the collections of the Zoölogisch Museum, Amsterdam (ZMA).

SYSTEMATICS

Family **Rotundiclipeidae** fam. nov.

Diagnosis.- Habitus cerviniid-like, tapering gradually posteriorly. Cephalosoma forming sub-circular shield covering second thoracic somite. P1-bearing somite not fused with cephalosoma. Genital double-somite without any trace of subdivision. Ventral abdominal muscles inserting at about two-thirds the length of anal somite. Anal operculum lacking. Caudal rami short, furnished with 7 setae; inner terminal seta (V) strongly developed.

Rostrum diminutive, fused with cephalosoma, without sensillae. Antennulae with smooth setae, first segment shorter than second one; 8-segmented in female, 4th and 8th segments with aesthetasc; 10-segmented and haplocer in male, 2nd, 3rd, 4th and 10th segments with aesthetasc. Antenna with allobasis (without setae); endopodite 1-segmented; exopodite 4-segmented, segment 1 bare, segments 2-4 with 1 seta. Labrum well developed, triangular, unarmed. Mandibular gnathobasis strikingly elongated, forming stylet with 1 seta at cutting edge; palp strongly elongated, 2-segmented, distal segment with geniculate setae. Maxillula with long praecoxal arthrite; coxal endite with bulb-shaped processus, epipodite absent; basis with 2 endites and geniculate setae; endopodite 1-segmented with geniculate setae; exopodite incorporated into basis, represented by 2 setae. Maxillar syncoxa with one bilobed endite; basis forming into a geniculate claw and with an aesthetasc; endopodite 3-segmented. Maxilliped prehensile; with unarmed syncoxa and basis; 1-segmented endopodite with straight claw and 2 setae.

Swimming legs with well developed intercoxal plates. Leg 1 with both rami 1-segmented. P2-P4 with 3-segmented exopodites and 2-segmented endopodites. P5 in both sexes represented by 2 setae, no segmental boundaries. Genital complex simple, with 1 seta at either side. Sixth pair of legs reduced, symmetrical, represented as a single seta.

Sexual dimorphism in antennula, P5, P6 and genital segmentation; 1 spermatophore.

Anchihaline, cave-dwelling.

Type and unique genus.- *Rotundiclipeus* gen. nov.

Genus **Rotundiclipeus** gen. nov.

Diagnosis.- As for family.

Etymology.- The generic name is formed from the Latin *rotundus* (= round) and *clipeus* (= shield), and alludes to the presence of the sub-circular cephalic shield of the cephalosome which is covering almost entirely the first pedigerous somite; gender masculine.

Type and unique species.- *Rotundiclipeus canariensis* gen. nov., sp. nov.

Rotundiclipeus canariensis sp. nov.

Type locality.- Amsterdam Expedition to the Canary Islands, Sta. 87-127. Tenerife, Cueva del Agua (at El Balayo, = WSW of Iguete; fig. 1); shallow cave just above the high tide mark; the cave contains a number of cemented pools and basins, catching fresh groundwaters; these pools are influenced by sea water during stormy weather; light penetrates in the cave; the sample was taken by handnet in a marginal gully of the basins, closest to the sea; bottom sand and stones, no algae; depth 0-20 cm; temperature 18.6° C; conductivity 15.40 mS/cm (= ca. 12.3 ppt salinity); 14 May 1987; coll. J.H. Stock & E. Sánchez. Accompanying fauna; oculate Cirolanidae (Isopoda), Coleoptera, Ostracoda, Oligochaeta, mosquito larvae.

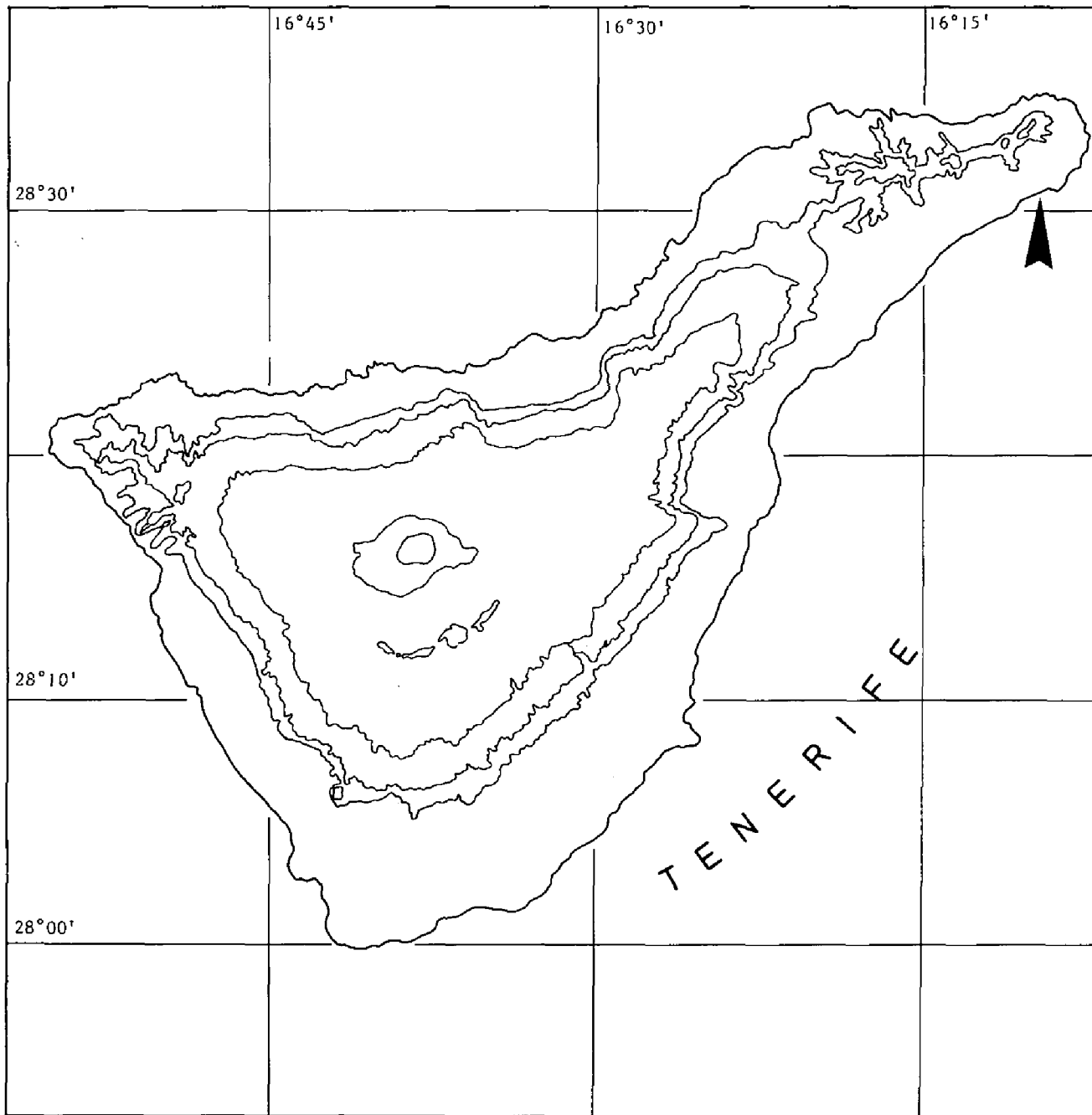


Fig. 1. Type locality of *Rotundiclipeus canariensis* gen. nov., sp. nov.

Material.- Two females and three males. One female (holotype, ZMA Co. 102.807a) and one male (allotypic paratype, ZMA Co. 102.807b) dissected and mounted on three slides each; other paratypes are one female (preserved in alcohol, retained in personal collection of the author) and one male (dissected on slide, ZMA Co. 102.807c).

Etymology.- The specific name *canariensis* refers to the archipelago where the species was found.

Description.-

Female (holotype; figs. 2A-B).- Body length: 330 μm rostrum and caudal rami excluded, 345 μm rostrum and caudal rami included; largest width measured at posterior margin of second free thoracic somite; following somites tapering gradually in posterior direction; distinct articulation between prosome and urosome.

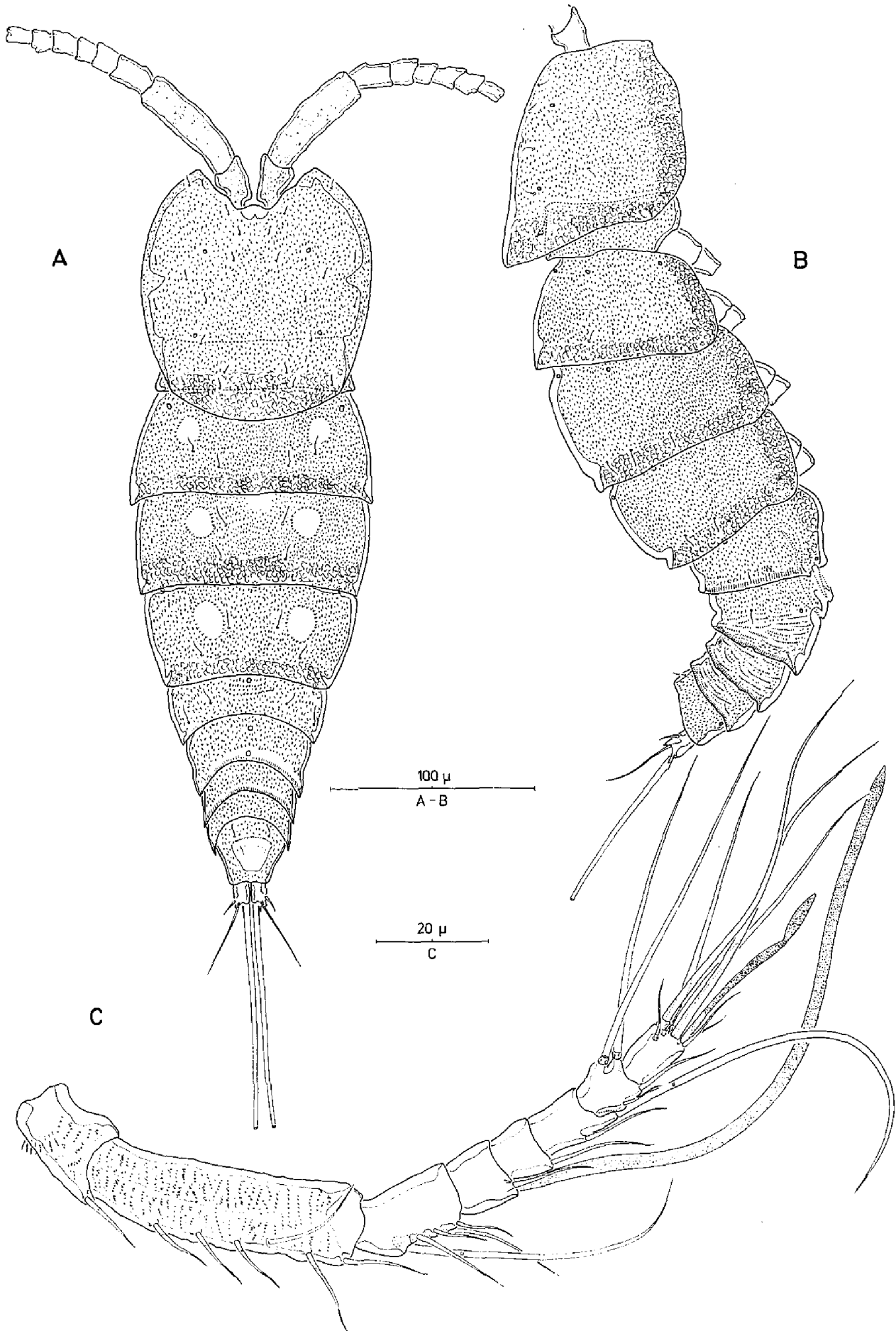


Fig. 2. *Rotundiclipeus canariensis* gen. nov., sp. nov.: A, habitus of female, dorsal view; B, habitus of female, lateral view; C. antennula of female.

Body cerviniid-like; cephalosome forming a subcircular shield which is deeply incised anteriorly and covering almost entirely the first pedigerous somite; first pedigerous (= second thoracic) somite not fused with cephalosome (fig. 8A), without sensillae; pleurotergites of remaining metasomites strongly developed; 3rd-5th thoracic somites with a smooth circular area on either laterodorsal side (fig. 9B), 4th one also with a smooth mid-dorsal plate (fig. 9D).

Except for sensillar pattern genital double-somite without any trace of subdivision; antepenultimate and penultimate somites smallest; anal somite trapezium-shaped, anal operculum lacking; integument of cephalosome and all somites provided with diminutive teeth densely arranged in an irregular pattern; nauplius eye not observed.

Rostrum (fig. 4D) diminutive, situated in the anterior cephalosomic incision; with two small processes; without sensillae.

Caudal rami (figs. 3D-E) parallel, rectangular, about twice as long as maximum width, furnished with 2 tubular pores and 7 setae: anterolateral accessory seta (I) smallest, anterolateral (II) and posterolateral (III) setae short and bare, outer terminal seta (IV) spiniform and confluent at base with inner terminal seta (V) which is strongly developed and spinulose, terminal accessory seta (VI) very small and smooth, dorsal seta (VII) long and slender and originating beneath a bifid dorsal processus of the posterior margin of the caudal ramus.

Antennula (fig. 2C) 8-segmented, directed laterally and dorsally; 1st segment shorter than 2nd one, furnished with a spinular row, several minute teeth and a geniculate seta at the inner distal corner; 2nd segment longest, about 4 times as long as greatest width, surface covered with dense pattern of minute teeth which are separated in 2 fields by a median furrow, armed with 6 slender setae, most of which being geniculate; 3rd segment without surface ornamentation and furnished with a long geniculate seta and 4 additional simple ones; 4th one bearing a long, slender aesthetasc accompanied at base by a small seta; 5th segment with 1 seta; 6th one with a long geniculate seta at the inner proximal corner and a smaller one at about middle inner edge; 7th segment provided with 2 long outer setae and 2 smaller inner ones; terminal segment bearing 7 setae of different lengths and a small indistinctly bilobated aesthetasc.

Antenna (figs. 4A, 8E) slender. Coxa slightly developed. Basis fused with first endopodite segment and forming a long, narrow allobasis which is furnished with an outer spinular row in the distal half and a 4-segmented exopodite inserting at about 1/3 distance of the proximal margin. Exopodite segments 2-4 with a slender plumose seta each; segment 1 bare and showing a small pit in the outer chitinous rim. Second endopodite segment with 3 setae at about the middle inner edge, 2 spinular rows in the distal half and 6 non-geniculate setae at the distal margin.

Labrum (fig. 5B) triangular, unarmed, protruding ventrally.

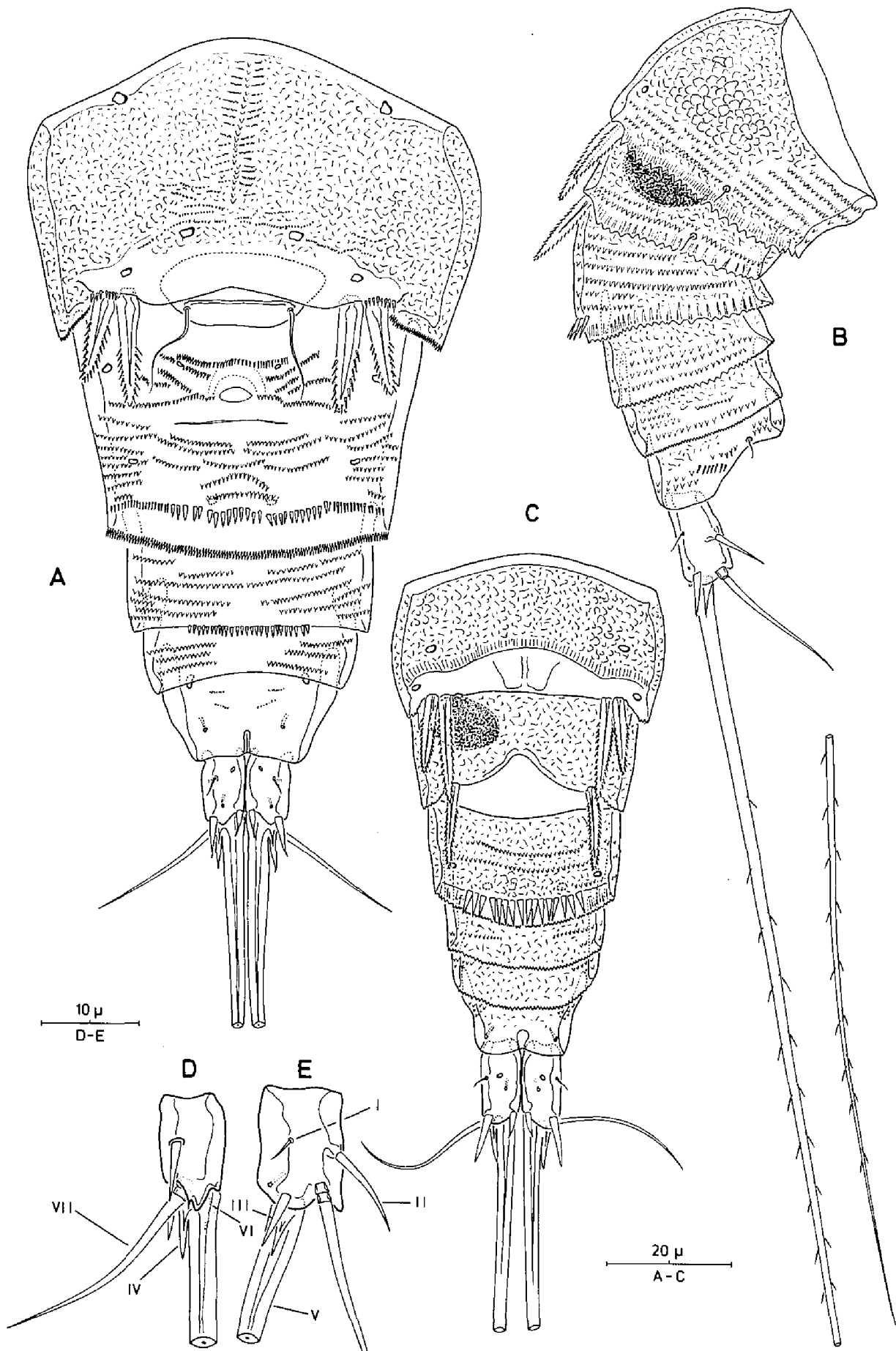


Fig. 3. *Rotundiclipeus canariensis* gen. nov., sp. nov.: A, urosome of female, ventral view; B, urosome of male, lateral view; C, urosome of male, ventral view; D, caudal ramus, dorsal view; E, caudal ramus, lateral view.



Fig. 4. *Rotundiclipeus canariensis* gen. nov., sp. nov.: A, antenna (arrow indicating small pit in chitinous rim of proximal exopodite segment); B, mandible; C, maxillula; D, anterior part of cephalosome showing rostrum and proximal segments of antennulae.

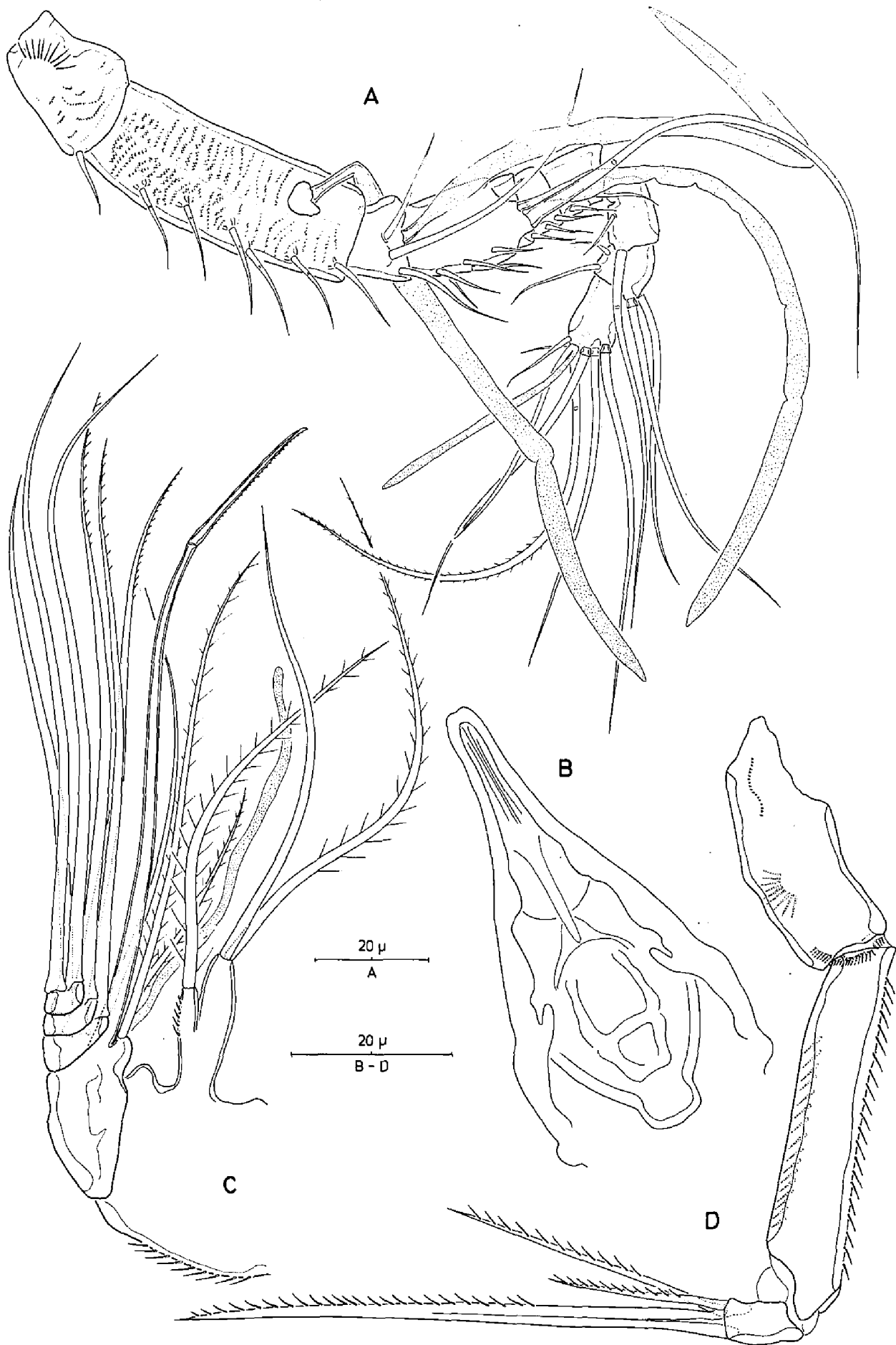


Fig. 5. *Rotundiclipeus canariensis* gen. nov., sp. nov.: A, antennula of male; B, labrum; C, maxilla; D, maxilliped.

Mandible (fig. 4B) with extremely long and narrow gnathobasis which is bearing a pinnate seta at the distal cutting edge. Palp extraordinary elongated, 2-segmented, uniramous. First segment (= basis) making up nearly 7/8 of the palp; spinulose along outer margin and distal half of inner margin; furnished with a set of long spinules at the middle. Distal segment (= endopodite?) with a short inner seta and 4 long medially geniculate setae at the top.

Maxillula (figs. 4C, 8D) well developed. Praecoxal arthrite long and narrow; densely spinulose at part of the posterior surface; provided with 2 parallel setae at anterior surface; distal edge with 2 strong claws, 1 subapical and 3 apical setae. Coxa with inner margin spinulose; endite swollen and bearing a distinct lobe at the posterior surface, furnished with 5 slender setae and a spirally pinnate claw; epipodite absent. Basis with 2 endites; proximal endite

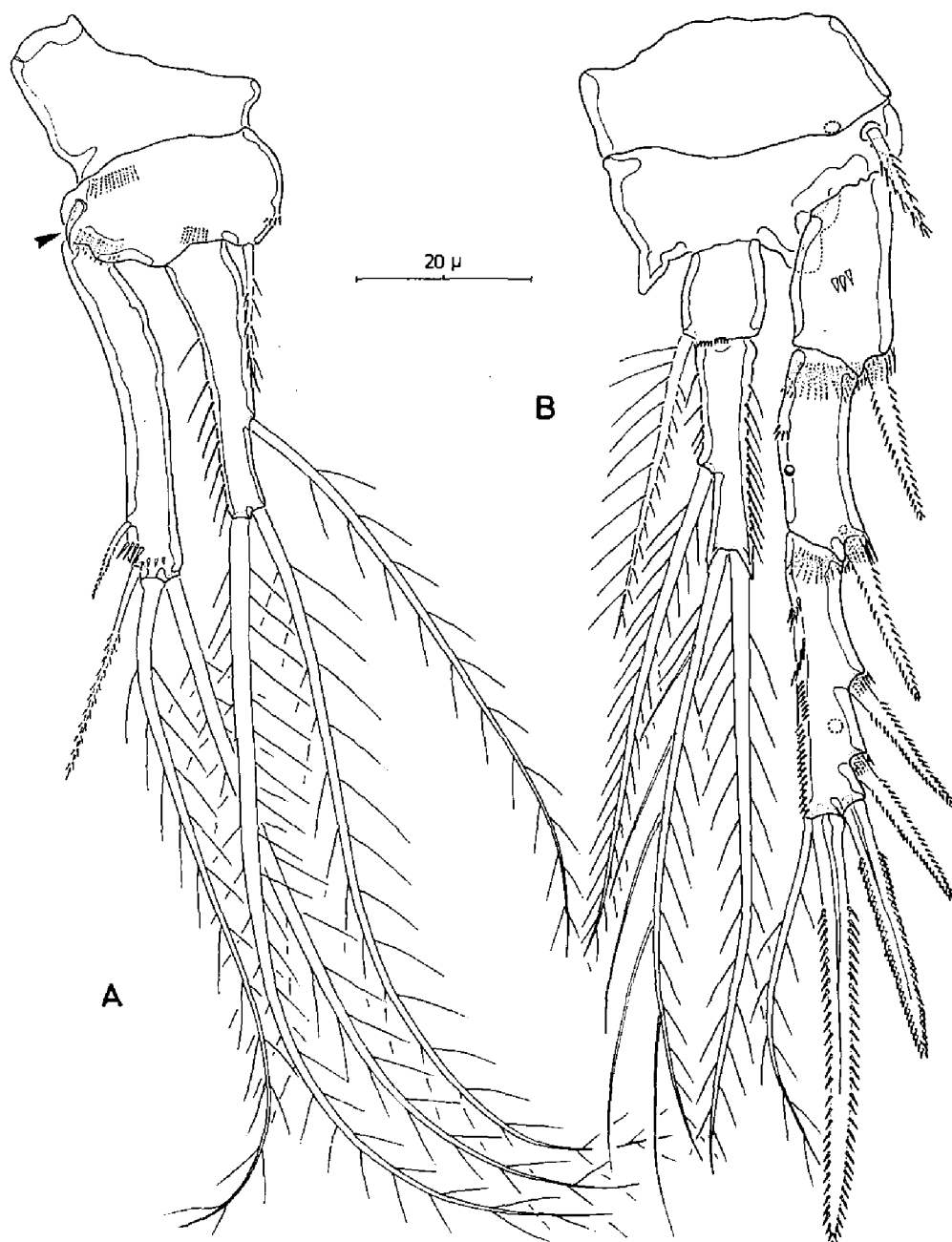


Fig. 6. *Rotundiclipeus canariensis* gen. nov., sp. nov.: A, P1; B, P2.

with 2 setae, distal one with 5 setae. Endopodite unisegmented and armed with 2 lateral and 4 distal setae. Exopodite incorporated in the basis and represented by 2 small setae. Both the basal endites and the endopodite show setae which are bi-geniculate.

Maxilla (fig. 5C). Syncoxa spinulose along outer edge and having a bilobed endite and a weakly defined lobe near junction with basis; proximal lobe of endite largest and having 2 long setae, distal lobe spinulose and with a terminal seta. Basis forming into an extremely long geniculate claw which is spinulose along the distal part and accompanied at base by a slender seta; inner lobe small and bearing 2 plumose setae and a long aesthetasc. Endopodite 3-segmented; each segment with 2 slender setae.

Maxilliped (figs. 5D, 9F) prehensile, slender. Syncoxa devoid of setation; armed with some spinular rows. Basis elongated, without setae; spinulose

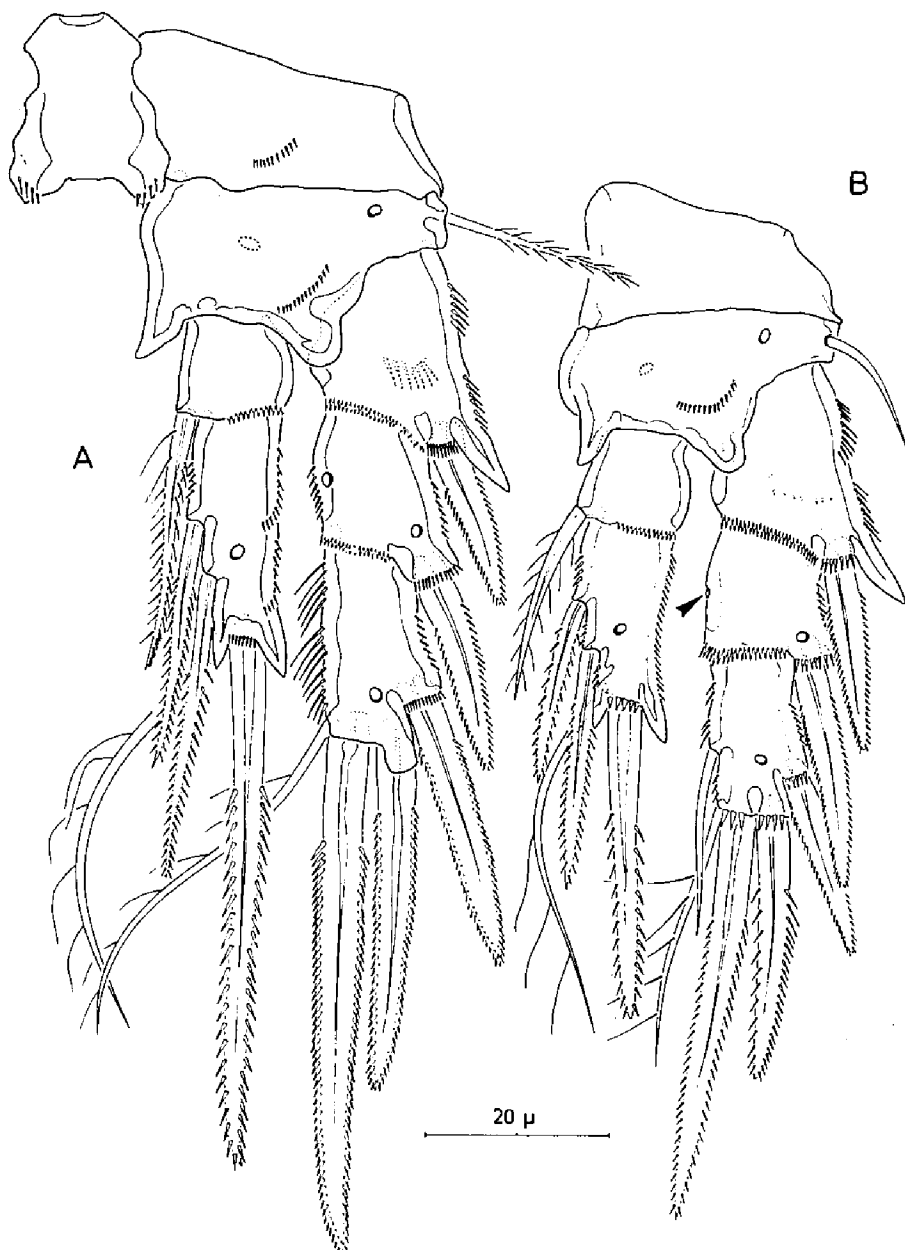


Fig. 7. *Rotundiclipeus canariensis* gen. nov., sp. nov.: A, P3; B, P4.

along outer and inner margins. Endopodite unisegmented and bearing a long, straight and spinulose claw and 2 pinnate setae.

Swimming legs (figs. 6, 7) with well developed intercoxal plates (interpodal bar).

P1 (fig. 6A). Praecoxa not observed. Coxa unarmed. Basis with some spinular rows on anterior surface, a curved spine at the outer edge and a pinnate seta at the inner distal corner. Exopodite unisegmented, somewhat directed inwards; furnished with 2 pinnate setae along the outer margin, 1 basally swollen seta at the top and 1 plumose seta at the inner subdistal corner. Endopodite unisegmented, a little shorter than exopodite; furnished with 2 inner seta and 1 apical one.

P2-P4 (figs. 6B, 7A-B, 10A-C) with 3-segmented exopodites and 2-segmented endopodites. P2 slender, P3-P4 robust. Coxa almost unarmed. Basis forming into a strong process at the inner distal corner and a rounded projection between exo- and endopodite; furnished with 1-2 secretory pores; outer side with a bipinnate (P2-P3) or smooth (P4) seta. Surface of exopodital segments 2-3 and distal endopodital segment with large secretory pores; outer distal corner of exopodital segments forming a strong pointed (segment 1) or truncate (segments 2 and 3) process. Proximal endopodital segment square, distal one long and having 2 distinct processes at the top. Seta and spine formulae are shown in table I.

Table I

Seta and spine formula of *Rotundiclipeus canariensis* gen. nov., sp. nov.

	exopodite	endopodite
P1	- - 112	- 210
P2	0.0.113	1.120
P3	0.0.112	1.220
P4	0.0.212	1.220

P5-bearing somite (fig. 3A) with 3 pairs of large secretory pores and a distinct median ridge at the ventral side. Fifth pair of legs forming a smooth common plate which is incorporated into the ventral integument; represented by 2 strong bipinnate setae on either side.

Genital double-somite (fig. 3A) with 3 pairs of secretory pores and a median copulatory pore; genital pores fused to a common median slit; P6 represented as 1 slender seta on either side.

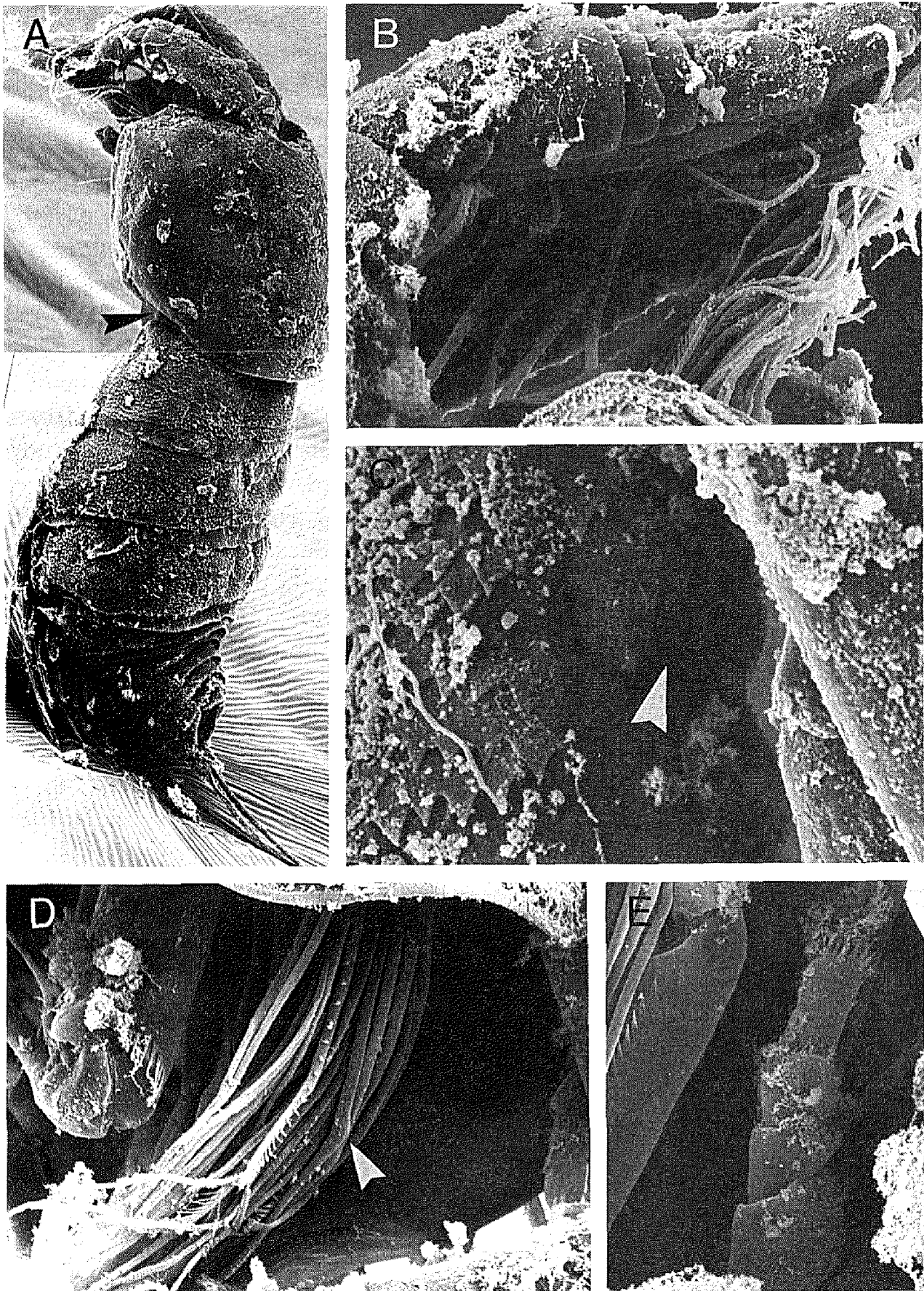


Fig. 8. *Rotundiclipeus canariensis* gen. nov., sp. nov. (SEM-photography of male): A, habitus, lateral view (arrow indicating free P1-bearing somite); B, antennula; C, detail of second antennular segment (arrow indicating aesthetasc originating beneath operculum); D, geniculate setae of maxillula; E, antennal exopodite.

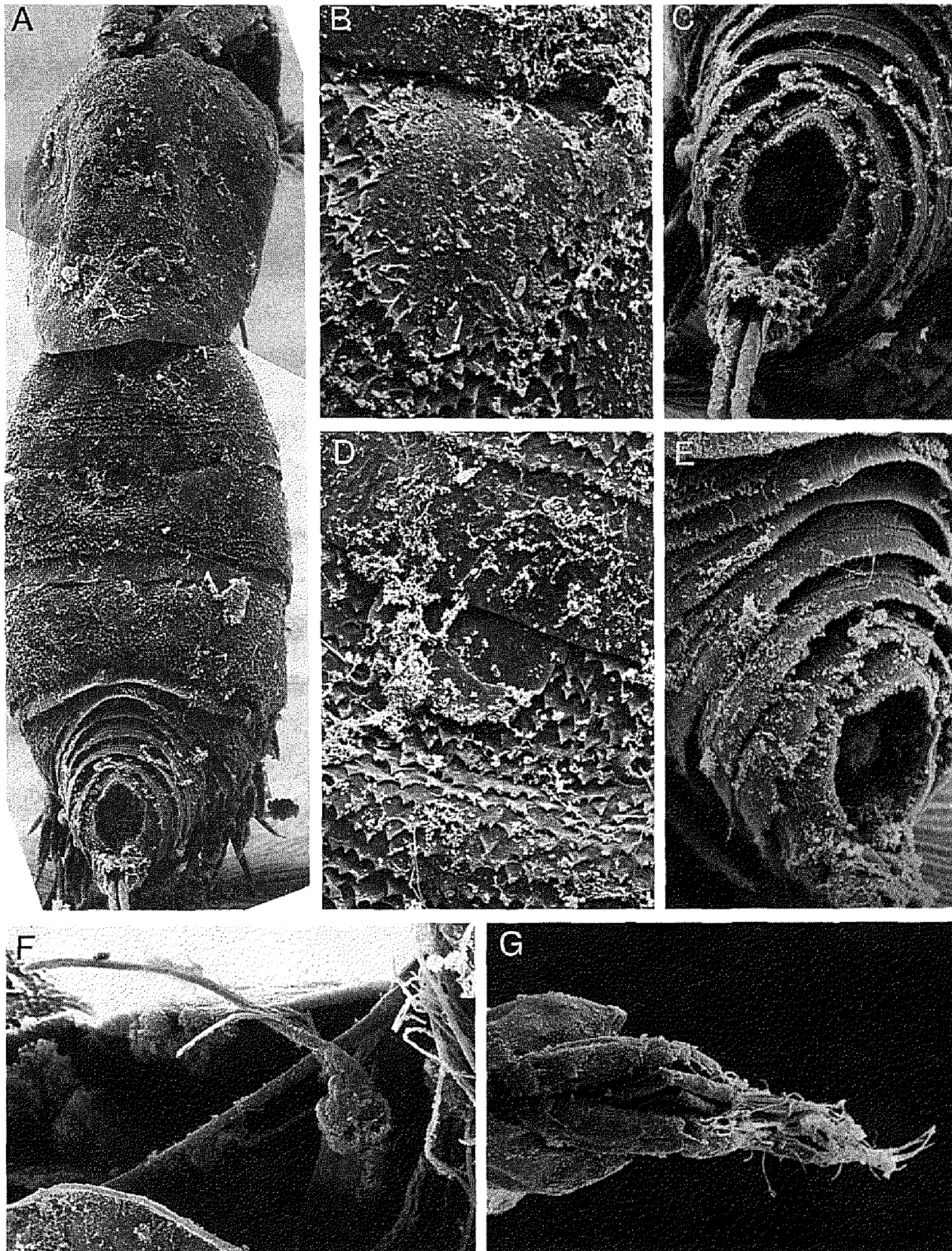


Fig. 9. *Rotundiclipeus canariensis* gen. nov., sp. nov. (SEM-photography of male): A, habitus, dorsal view; B, smooth laterodorsal area of third pleurotergite; C, urosome, dorsal view; D, smooth middorsal plate of third pleurotergite; E, urosome, laterodorsal view; F, maxilliped; G, antennulae and antennae, dorsal view.

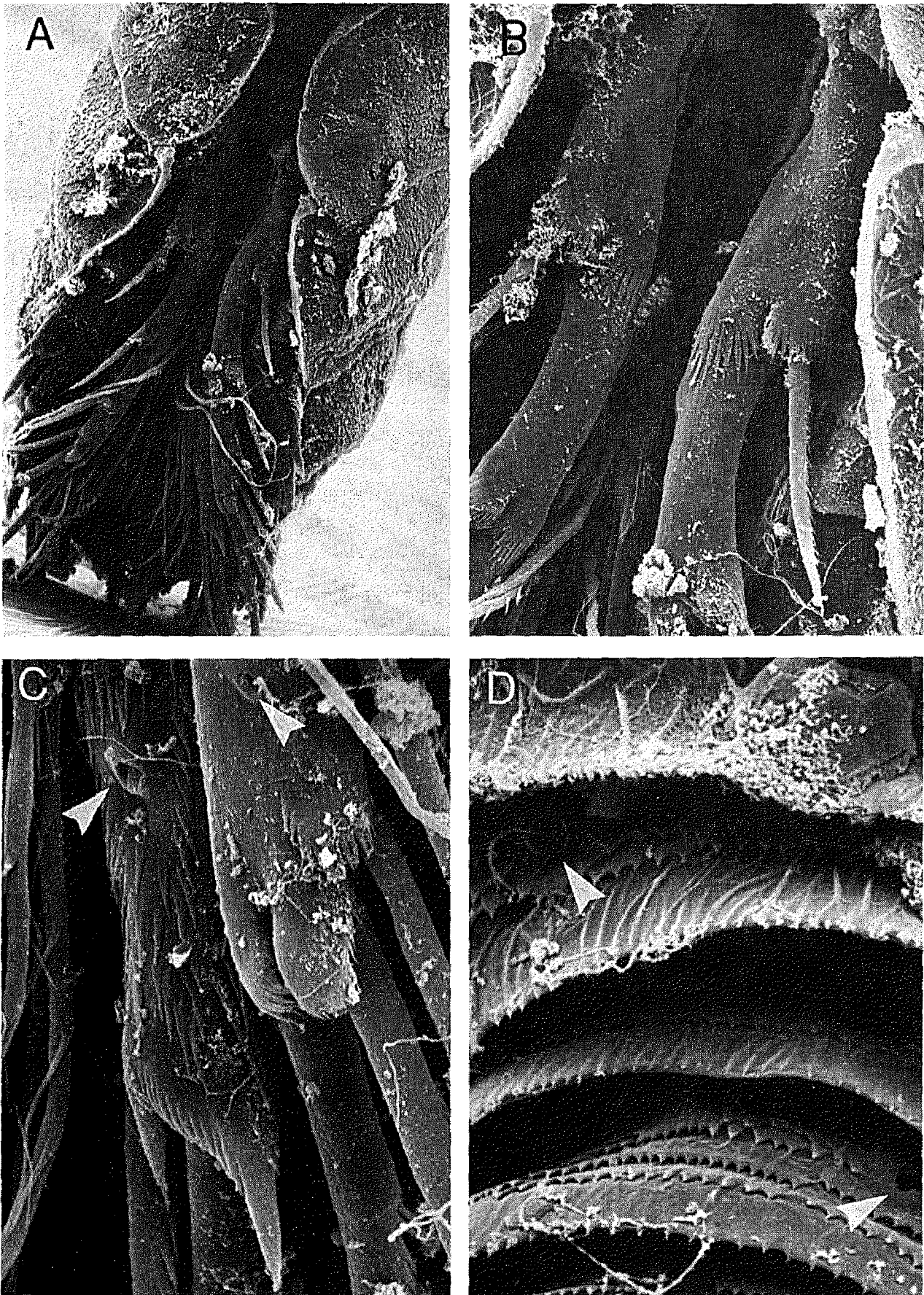


Fig. 10. *Rotundiclipeus canariensis* gen. nov., sp. nov. (SEM-photography of male): A, metasome, ventral view; B, P2, proximal and middle segments of exopodite; C, distal exopodite segments of P2 and P3 (arrow indicating tube pores); D, detail of integument of urosomal somites (arrows indicating middorsal pore and laterodorsal sensilla).

Male.- Body length: 300 μm rostrum and caudal rami excluded, 315 μm rostrum and caudal rami included. Habitus as in the female except for the free genital somites (figs. 3B-C). Sexual dimorphism in the antennula, fifth and sixth legs.

Antennula (figs. 5A, 8B-C, 9G) 10-segmented, haplocer; 1st segment furnished with an inner seta and some spinular rows; 2nd segment longest, armature as in the female except for the large aesthetasc which is originating near the distal margin and covered by a small smooth operculum; 3rd segment with 3 bare setae and a large aesthetasc at the anterior margin; 4th segment bearing 5 small setae along the inner margin and forming a sub-cylindrical process on which a geniculate seta and a long aesthetasc is implanted; 5th and 6th segments small, with 1 and 2 setae, respectively; segments 7 and 8 forming haplocer apparatus and having 2 setae each; 9th segment with 2 inner and 2 outer setae; distal segment with 7 slender setae of which one is fused at the base with a small aesthetasc.

P5-bearing somite (figs. 3B-C) with 2 pairs of large secretory pores. Fifth pair of legs as in female except for the spines which are more slender.

P6 (figs. 3B-C) fused with somitic wall; represented on either side by a bipinnate spine.

DISCUSSION

The Rotundiclipeidae exhibit many unusual, and in some cases unique characters which provide many clues as to their phylogenetic relationships. The possession of a slender aesthetasc on the basis of the maxilla is to my knowledge unique among harpacticoid copepods. Thus far aesthetascs on postantennular appendages have been reported only in some "tachidiid" genera. Soyer (1970b), in describing *Paradanielssenia kunzi* from Banyuls-sur-Mer, mentioned the presence of "addendes en massue" on the mandibular endopodite, maxillular basis and maxillar endopodite. Similarly, *P. biclavata* (Gee, 1988) shows these club-shaped appendages on the mandible (exo- and endopodite), maxillula (basis, exopodite) and maxilla (proximal endite, endopodite). Mielke (1975) reported similar "Klöppelborsten" in two new species of *Micropsammis*. It is, however, clear that there exist no close relationships between these genera and *Rotundiclipeus*.

The first leg with reduced unisegmented rami is an unusual feature among harpacticoids, generally being considered to be diagnostic for the Tegastidae and further only found in *Anoplosoma* where it constitutes a secondarily derived trait within the family Ameiridae.

There is a close resemblance in general morphology of the buccal structure between *Tisbe* and *Rotundiclipeus*. In both genera the labrum, mandible and maxillula are elongated and project ventrally as a conical structure showing a superficial similarity with the buccal siphon of the Siphonostomatoida. Obviously, the stylet-like structure of the extremely elongated mandibular

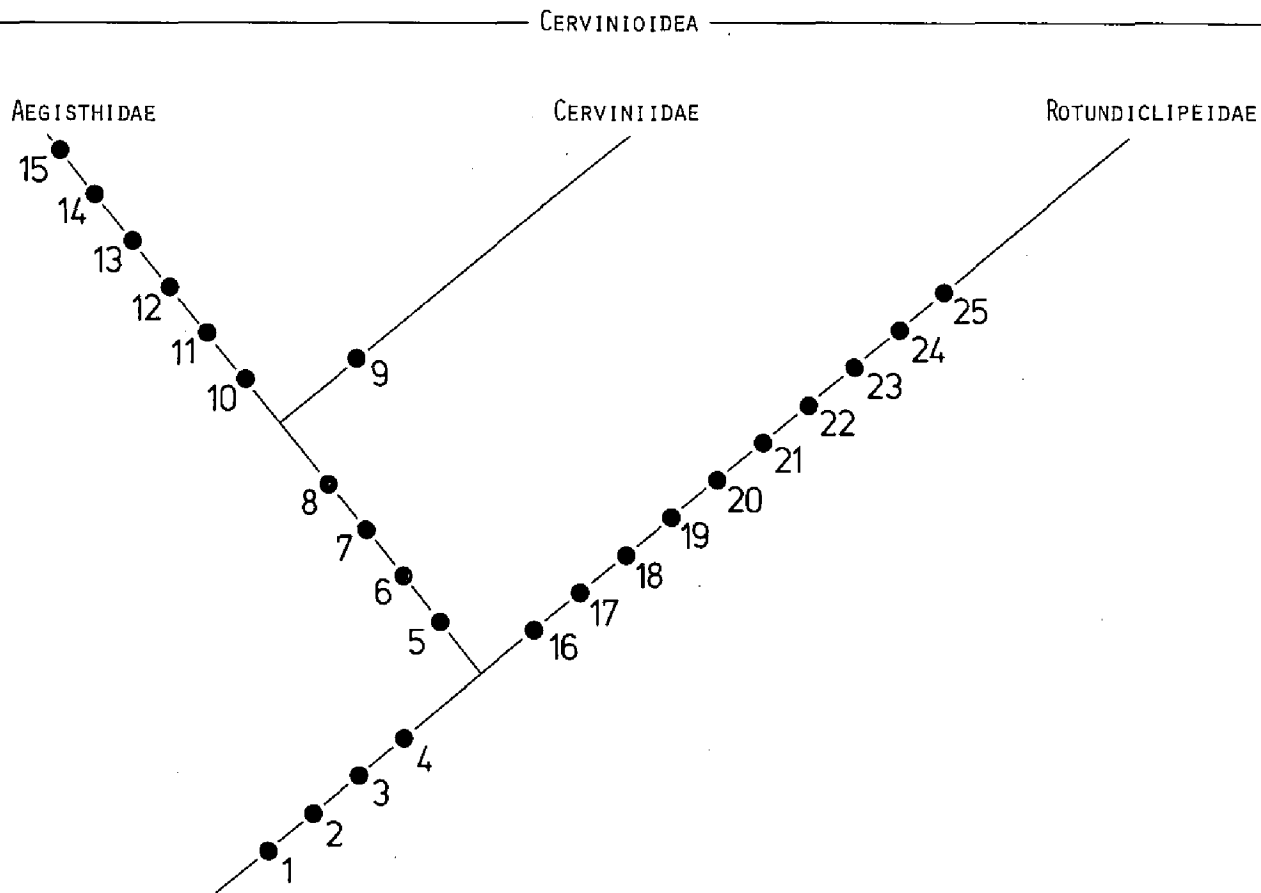


Fig. 11. Cladogram depicting the phylogenetic relationships of the cervinioid families. Synapomorphies are (1) loss of endopodite P5, (2) antennula 8-segmented in female; 10-segmented in male (with 4 aesthetascs), (3) maxillula with reduced exopodite, (4) rostrum fused with cephalosoma, (5) elongation of caudal rami, (6) incorporation of maxillular endopodite into basis, (7) antennula 8-segmented in male, (8) female P6 forming elongated, narrow segment, (9) first pedigerous somite smaller than following, partially covered by cephalosoma, (10) antennula 6- or 7-segmented in female, (11) antenna with allobasis, exopodite 2 segmented, (12) sexual dimorphism in all postantennal cephalosomic appendages (reduced in male), (13) mandibular palp absent, (14) maxilliped 3-segmented, (15) caudal rami extremely elongated, (16) allobasis of antenna devoid of setae, (17) mandible stylet-like, palp reduced and elongated, (18) maxillula without epipodite, exopodite incorporated into basis, (19) maxilla with 1 endite, basis with geniculate claw and slender aesthetasc, (20) maxilliped prehensile, with syncoxa and asetose basis, (21) P1 with unisegmented rami, first exopodite segment without inner seta, (22) P2-P4 with 2-segmented rami, (23) genital double-somite completely fused, (24) P5 alike in both sexes, strongly reduced, (25) P6 in both sexes represented by 1 seta or spine.

gnathobasis seems to be preadapted for piercing the skin of a presumed host or prey. Though this facultative feeding behaviour is reported in *Tisbe* (Marcotte, 1977), there is at present no factual justification for such feeding mechanism in the Rotundiclipeidae.

The non-fused P1-bearing somite is of little assistance in the assessment of phylogenetic affinities since it is shared by several harpacticoid copepods: Canuellidae, Phyllognathopodidae, Chappuisiidae, some Latiremidae, *Cubanocleta*, *Noodtortopsyllus*, Cerviniidae and Aegisthidae. Despite the presence of several derived traits, the resemblance in general body facies, the detailed structure of some of the mouthparts and the reduction of the fifth leg all

indicate a close relationship with the cervinioid lineage (Cerviniidae, Aegisthidae). The ancestor of this cerviniidimorphic assemblage typically had an 8-segmented antennula in the female. This condition is retained in the Rotundiclipeidae and most Cerviniidae. In the Aegisthidae (Lang, 1948; Boxshall, 1979; Huys, in prep.) and some Cerviniidae (*Cerviniopsis*, *Cervinia* (part.), *Tonpostratiotes*) a secondary reduction took place and the number of antennular segments never exceeds 7. The ancestral male condition is found only in *Rotundiclipeus*, viz. 10-segmented with aesthetascs on segments 2, 3, 4 and 10. The same aesthetasc arrangement is found among male Cerviniidae (e.g. *Pontostratiotes*; Itô, 1982), however the antennula is primitively 8-segmented due to fusion of segments 6-7 and 9-10 (the annulated 4th segment of male *Pontostratiotes robustus*, Itô, 1982 indicates that the number of segments in the ancestral cerviniid antennula may have to be increased to 11).

In males of Cerviniidae (Huys, unpubl.), Aegisthidae (Huys, in prep.) and Rotundiclipeidae (present account) the most proximal aesthetasc is not arising from a distal process or from the anterior margin of the segment; here the aesthetasc is associated with a distinct integumental aperture and covered at base by a small smooth operculum.

All three families share the reduced exopodite (not endopodite as mentioned by Itô, 1982, 1983) of the maxillula, being a minute segment with at most 3 setae in the Cerviniidae or entirely incorporated into the basis in Rotundiclipeidae and Aegisthidae.

Another synapomorphic character is the loss of the endopodite in the fifth pair of legs. In Aegisthidae and Cerviniidae the exopodite is well developed in both females (1-segmented) and males (at most 3-segmented in *Eucanuella*); in *Rotundiclipeus* the P5 is further reduced and represented by only 2 setae. Finally, the monophyly of the cervinioid families can be substantiated by the rostrum which is fused with the cephalosome, being strongly developed in both Cerviniidae and female Aegisthidae, but diminutive in *Rotundiclipeus*.

It is beyond doubt that the Cervinioidea (= Cerviniidimorpha sensu Lang, 1948) constitute an early offshoot in the mainstream of harpacticoid evolution. This is for instance clearly illustrated through the misophrioid-like stenopodial maxilliped, the multisegmented male exopodite of the 5th leg and the absence of profound sexual dimorphism on the swimming legs, a character generally regarded as being typical for the hypothesized benthic "Archicopepod" (Boxshall et al., 1984). Within the Cervinioidea sexual dimorphism is primitively restricted to the antennulae (Cerviniidae, Rotundiclipeidae) or to all cephalic appendages (Aegisthidae; Huys, in prep.). Examples of secondarily evolved but generally overlooked (e.g. Dinét, 1977) sexual dimorphism are found only in the Cerviniidae; viz. middle segment of P4 with supplementary seta in *Pontostratiotes*, *Stratiopontotes* (Itô, 1982); Montagna (1979, 1981) found 3-segmented endopodites P1-P4 and reductions in the postantennal cephalic appendages of male *Cervinia magna*.

Within the Cervinioidea (= Cerviniidimorpha) the Cerviniidae are without doubt the most primitive group because of (1) an antenna with basis; this ancestral condition is retained in some *Cervinia* species, (2) a mandible with primitive biramous palp (exopodite 4-segmented, endopodite 1-segmented), (3) a maxillula with epipodite (up to 2 setae in *Cerviniopsis*) and defined exopodite, (4) a stenopodial maxilliped with 2-segmented endopodite.

The Aegisthidae — Cerviniidae complex constitutes the primitive sistergroup of the Rotundiclipeidae. Its monophyletic status can be defined by (1) elongation of the caudal rami (in *Rotundiclipeus* the caudal rami are very short but the inner terminal setae (V) are extremely long in order to take over the balancing function of the cerviniid caudal ramus), (2) incorporation of the maxillular endopodite into the basis, (3) male antennula at most of 8 segments, (4) female P6 forming a long, narrow segment which is projected ventrally.

The Cerviniidae themselves share the state of the first pedigerous somite which is much smaller than the following and at least in part covered by the cephalosomic shield. In Aegisthidae the P1-bearing somite is almost equal in size to the following somite, like in e.g. Phyllognathopodidae.

In addition to the sexual dimorphism (viz. reduction in the male) in the antenna, mandible, maxillula, maxilla and maxilliped (Huys, in prep.) the monophyletic status of the Aegisthidae can be established on the basis of (1) the 6- or 7-segmented antennula in the female, (2) antenna with allobasis and 2-segmented exopodite, (3) mandible palp absent, (4) 3-segmented maxilliped, (5) extremely elongated caudal rami (not the furcal setae as mentioned by previous authors by rightly rectified by Boxshall, 1979).

Finally, the Rotundiclipeidae exhibit a tremendous series of advanced characters such as (1) allobasis of antenna devoid of setae, (2) mandible with stylet-like gnathobasis and reduced, elongated palp, (3) exopodite of maxillula incorporated into the basis, without epipodite, (4) maxilla with 1 endite and basis with geniculate claw and slender aesthetasc, (5) maxilliped prehensile, with syncoxa and asetose basis, (6) P1 with unisegmented rami, first exopodite segment without inner seta, (7) P2-P4 with 2-segmented endopodites, (8) P5 alike in both sexes, reduced, (9) genital double-somite completely fused, (10) P6 in both sexes represented by 1 seta or spine. With regard to the rotundiclipeid maxilliped it should be stressed that the prehensile type has originated at numerous occasions during harpacticoid evolution. A detailed study of the maxilliped within the harpacticoid families will certainly shed more light on the validity of these taxa in particular and on the harpacticoid phylogeny in general (Huys, in prep.). The relationships of the cervinioid families are summarized in fig. 11.

Again it is shown that cavernicolous organisms often have deep-sea inhabitants as their closest relatives (see Hart et al., 1985 for a review). A number of authors has postulated a deep-sea origin of cave faunas or assumed that species-groups could form a continuum reaching from island caves — via

crevicular habitats in the rock — into the deep waters (Ilfte et al., 1983, 1984; Hart et al., 1985).

Stock (1986) on the contrary, rejected this supposition because the anoxia stages of the middle Tertiary have eliminated the Tethyan deep-sea fauna. The author re-confirmed that a modern deep-sea fauna evolved from shallow water ancestors. On the basis of cladistic and biogeographic arguments Stock (1986) extended his hypothesis also to the stygofauna, or as he put it: "...the undeniable taxonomic relationship between certain anchihaline cave taxa and Recent bathyal animals, must point to a common ancestry, not to an origin from (taxonomically quite different, extinct) Tethyan deep water biotas".

Though the cladistic analysis shows more plesiomorphies for the deep-sea Cerviniidae than for the cave-dwelling Rotundiclpeidae, it is striking that the latter family exhibits certain clear plesiomorphies which are definitely absent in both Cerviniidae and Aegisthidae. Following Iliffe et al.'s (1984) supposition it would be very difficult to accept that the Cerviniidae are the ancestors of the Rotundiclpeidae. In this respect it is noteworthy that the most primitive cerviniid genera (e.g. *Eucanuella*, *Cerviniopsis*, *Cervinia* part.) are principally found on the continental shelf, as shallow as 30 m (Lang, 1948; Soyer, 1970a; Huys, unpubl.). These members are adapted to a burrowing existence and are characterized by robust antennulae, short caudal rami and a high ratio between body length and caudal ramus length (Montagna, 1982). Otherwise, the truly deep-sea Cerviniidae (e.g. *Pontostratiotes*, *Stratiopontotes*, *Tonpostratiotes*, *Herdmaniopsis*) have long antennulae and caudal rami, a low ratio between body length and caudal ramus length and exhibit a lengthening and narrowing of the swimming legs; they are typically adapted for an epipelagic mode of life "spider effect"; Por, 1964).

Finally, one more (reinforcing) comment has to be made concerning Stock's (1986) hypothesis. If indeed the anchihaline cave taxa would have descended from shallow water (infra- and circalittoral zones) ancestors, than cave biota would not have a restricted distribution but may be present in similar habitats on other islands as well. Preliminary results revealed the presence of closely allied representatives of the Rotundiclpeidae in Lanzarote and Bermuda (Roadside cave). A common pattern is found for another new family to be described from anchihaline caves on the Bahamas, Bermuda and Lanzarote (Huys & Iliffe, in prep.).

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