



Description of *Ancorabolus hendrickxi* sp. nov. (Copepoda: Harpacticoida: Ancorabolidae) from the neotropics and notes on caudal ramus development within oligoarthran harpacticoids

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Abstract: A single female specimen of *Ancorabolus hendrickxi* sp. nov. (Harpacticoida: Ancorabolidae) was found in meiofauna samples taken off Sinaloa (North-western Mexico) at a depth of 1985 m. Parsimony analysis of the *Ancorabolus*-lineage including this new species, confirmed Conroy-Dalton & Huys' (2000) conclusions on the monophyly of *Ancorabolus* and the validity of both *Breviconia* and *Juxtaramia*, and identified the Scandinavian *Ancorabolus confusus* as the closest relative of *A. hendrickxi* sp. nov. Both species show close similarity in the general body shape, length and pattern of integumental processes on the cephalothorax and body somites, elongate and slender caudal rami, absence of proximal recurved process on posterior margin of second antennular segment and presence of an inner seta on the second endopodal segment of the second swimming leg. *Ancorabolus hendrickxi* sp. nov. can be readily differentiated from its congeners by the complete lack of a maxillary coxal endite, the mandibular palp with five setae, and the very reduced proximal endite of the maxillary syncoxa bearing only one seta. Re-evaluation of the taxonomic status of the recently described species *A. ilvae* from the Magellan Straits, Chile demonstrates that it can only be regarded as *species inquirenda* in *Ancorabolus*. An updated generic diagnosis of *Ancorabolus* is provided. Postembryonic caudal ramus development within oligoarthran harpacticoids is analysed, based on observations of *A. confusus*, *Macrosetella gracilis* and *Microarthridion* sp., and additional literature data. A generalized developmental pattern of caudal rami, based on vertical tracking of the homology of caudal setae I-VII throughout ontogeny is proposed.

Résumé : Description de *Ancorabolus hendrickxi* sp. nov. (Copepoda : Harpacticoida : Ancorabolidae) des sédiments profonds néotropicaux et notes sur le développement des rames caudales chez les harpacticoides oligoarthres. Une femelle adulte d'*Ancorabolus hendrickxi* sp. nov. (Harpacticoida : Ancorabolidae) a été récoltée dans des échantillons de méiofaune obtenus en face de la côte de Sinaloa (nord-ouest du Mexique) à 1985 m de profondeur. L'analyse parcimonieuse d'*Ancorabolus* a confirmé les conclusions de Conroy-Dalton & Huys (2000) au sujet de la monophylie d'*Ancorabolus*, la validité de *Breviconia* et *Juxtaramia*, et a identifié *A. confusus* de Scandinavie comme l'espèce la plus proche d'*A. hendrickxi* sp. nov.. Ces espèces partagent la structure générale du corps, longueur et arrangement des excroissances tégumentaires sur le céphalothorax et les segments libres du corps, rame caudale allongée et étroite, absence d'une excroissance recourbée sur la marge postérieure du deuxième segment de l'antennule, et présence d'une soie interne sur le deuxième segment de l'endopodite de la deuxième patte. *Ancorabolus hendrickxi* sp. nov. peut être séparée des autres espèces d'*Ancorabolus* par l'absence de l'endite de la coxa de la maxillule, le palpe de la mandibule avec cinq soies, et l'endite proximal de la syncoxa de la maxille ne portant qu'une soie. La réévaluation du statut taxonomique d'*A. ilvae*, connue du Détroit de Magellan, Chili,

a démontré que cette espèce doit être considérée comme *species inquirenda* dans le genre *Ancorabolus*. Une diagnose générique actualisée d'*Ancorabolus* est proposée. Le développement postembryonnaire des rames caudales chez les harpacticoides oligoarthres a été étudié à partir de quelques observations sur *A. confusus*, *Macrosetella gracilis* et *Microarthridion* sp. et d'après des données supplémentaires. Un modèle général de développement des rames caudales, basé sur le suivi vertical des homologies des éléments I-VII est proposé.

Keywords: Copepoda, Harpacticoida, Ancorabolidae, Systematics, Phylogeny, México

Introduction

A new representative of Ancorabolinae, *Ancorabolus hendrickxi* sp. nov. was found in sediment samples taken during the sampling campaign "Talud V" at a depth of 1985 m off Sinaloa, in the framework of the project CONACyT 31805-N (Biocenosis and chemical composition of benthic and pelagic deep water invertebrates in the southern Gulf of California in relation to environmental conditions), sponsored by the National Council of Science and Technology (CONACyT) and the Institute of Marine Sciences and Limnology (National Autonomous University of Mexico).

Since its proposal by Sars (1909) to accommodate *Ancorabolus mirabilis* Norman, 1903 and three new genera, the Ancorabolinae has undergone significant changes resulting from the phylogenetic analysis of relationships within this subfamily (Conroy-Dalton & Huys, 2000; Conroy-Dalton, 2001). Members of this subfamily have typically been found at high latitudes (see Conroy-Dalton & Huys, 2000, Table 1). However, recent evidence indicates that the Ancorabolinae are widely distributed, probably continuously from the Arctic to the Antarctic (Conroy-

Dalton & Huys, 2000). The discovery of *A. hendrickxi* sp. nov. lends support to this hypothesis, and suggests that the discontinuous distribution of this genus and many other harpacticoid taxa is merely the result and a reflection of our patchy knowledge of neotropical harpacticoid fauna. Such data are crucial for a better understanding of the historical biogeography of harpacticoid copepods.

Caudal ramus development in the Harpacticoida and the homologization of individual caudal setae have repeatedly been a subject of discussion, resulting in the proposal of several developmental models (eg. Huys & Böttger-Schnack, 1994; Dahms, 1992). A controversial model was recently proposed by George (2001) based on the copepodid development of *Ancorabolus ilvae*. Contrary to Huys & Boxshall (1991), George (2001) claimed that a reduction from 7 to 6 caudal ramus setae can also result from the loss of seta IV, and not exclusively of seta I as generally accepted. A revision of George's (2001) and some other models through careful examination of copepodid and intermoult stages for a range of harpacticoid taxa is presented.

Table 1. Post-maxillipedal leg pattern development from CI to CVI for a) *Enhydrosoma lacunae* Jakubisiak, 1933 (modified from Fiers, 1996); b) *Ancorabolus ilvae* George, 2001; and c) *Ancorabolus confusus* Conroy-Dalton & Huys, 2000, and *A. inermis* Conroy-Dalton & Huys, 2000 (present study). Terminology after Ferrari (1998). b = leg bud, exopodal + endopodal segments; ? = data not mentioned by George (2001); - = unknown.

Tableau 1. Développement des pattes P1-P4 aux stades CI à CVI chez a) *Enhydrosoma lacunae* Jakubisiak, 1933 (modifié d'après Fiers, 1996) ; b) *Ancorabolus ilvae* George, 2001 ; et c) *Ancorabolus confusus* Conroy-Dalton & Huys, 2000, and *A. inermis* Conroy-Dalton & Huys, 2000 (cette étude). Terminologie d'après Ferrari (1998). b = bourgeon des pattes, segments de l'exopode + endopode ; ? = données non mentionnées par George (2001) ; - = inconnu.

	a) <i>Enhydrosoma lacunae</i>				b) <i>Ancorabolus ilvae</i>				c) <i>A. confusus</i> + <i>A. inermis</i>			
Stage	P1	P2	P3	P4	P1	P2	P3	P4	P1	P2	P3	P4
CI	1+1	1+1	b		1+1	1+1	b?		-	-	-	
CII	2+2	2+2	1+1	b	2+2	2+2	1+1	?	-	-	-	-
CIII	2+2	2+2	2+2	1+1	-	-	-	-	-	-	-	-
CIV	2+2	2+2	2+2	2+2	2+2	2+2	2+2	2+2	-	-	-	-
CV	2+2	2+2	2+2	2+2	2+2	2+2	2+2	2+2	2+2	2+2	2+2	2+2
CVI	3+2	3+2	3+2	3+2	-	-	-	-	2+2	3+2	3+2	3+2

Material and methods

Triplicate sediment samples for meiofaunal analyses were taken during the sampling campaign Talud V carried out during December 2000 on board the research vessel “El Puma” of the National Autonomous University of Mexico. Sediment cores were taken at depths ranging from about 500 to 2000 m using a multiple sediment corer equipped with six cores of 30 cm in length and sampling surface of 3.9 cm². The recovered cores were slowly frozen at –20 °C. When frozen, the cores were opened longitudinally using a circular saw fixed to a working table. Each sediment core was then divided vertically into separate sediment slices as follows: 0–1 cm, 1–2 cm, 2–3 cm, 3–5 cm, 5–7 cm, and 7–10 cm depth. Meiofauna samples were fixed in 10% formalin, sieved through 500 and 40 µm sieves to separate macro- and meiofauna, preserved in 70% ethanol and stained with Rose Bengal. Meiofauna was sorted and quantified at a magnification of 40X.

The only specimen of *Ancorabolus hendrickxi* sp. nov. and its dissected parts were illustrated at a magnification of 1000X using a Leica DMLB microscope equipped with a drawing tube. Additional observations were made at magnifications of up to 1200X. The dissected parts were mounted on separate slides in glycerin. Other material examined in this study includes type material of *Ancorabolus inermis* Conroy-Dalton & Huys, 2000 (NHM, reg. no. 2000.1062-1117), *A. confusus* Conroy-Dalton & Huys, 2000 (NHM reg. no. 2000.1121-1168), and unregistered specimens of *Microarthridion* sp. (coll: T. Chandler, 10.06.98; from aquaculture tanks; Dept. ENHS, University of South Carolina, Columbia, U.S.A.), all held in the collections of the Natural History Museum (NHM) London, U.K. For this harpacticoid material specimens were cleared in lactic acid and temporarily mounted whole in lactophenol. Drawings were made using a camera lucida on a Leitz Diaplan differential interference contrast microscope.

The terminology of Huys & Boxshall (1991) and Ferrari (1988, 1998) was adopted for descriptive morphology and post-maxillipedal leg development, respectively. Abbreviations used in the text and figures: P1–P6, first to sixth swimming legs; ae, aesthetasc, exp, exopod; enp, endopod; Md, mandible; Mx, maxilla.

The phylogenetic software package PAUP 3.1.1 written by David Swofford was used to analyse phylogenetic relationships within the *Ancorabolus*-group.

Type material was deposited in the collections of the Mazatlán Marine Station of the Institute of Marine Sciences and Limnology.

Systematics

Family ANCORABOLIDAE Sars, 1909
Subfamily ANCORABOLINAE Sars, 1909
Genus *Ancorabolus* Norman, 1903
Ancorabolus hendrickxi sp. nov.

Figs 1–6

Type locality. Off Sinaloa, North-western Mexico (23°54'N, 110°11'W); collected at a depth of 1985 m; found in surface layer of sediment (0–1 cm deep into the sediment); oxygen content and temperature of water column at a depth of 1970 m, 0.73 mlO₂ l⁻¹ and 2.6 °C.

Type material. Female holotype (EMUCOP-171200-01) dissected onto seven slides; 17th December 2000; Project: CONACyT-31805-N (Biocenosis and chemical composition of benthic and pelagic deep water invertebrates in the southern Gulf of California in relation to environmental conditions); coll. S. Gómez.

Description

Female

Total body length 717 µm from tip of rostrum to posterior end of caudal rami. Body (Fig. 1A) dorsoventrally depressed, tapering posteriorly; without clear division between pro- and urosome; with smooth somatic frills, weakly developed and difficult to discern.

Rostrum fused to cephalic shield (Fig. 1A, 2A); subapical ventral displacement creating a false impression of demarcation at base, bifid apically, with 2 lateral sensillae in distal half, 2 lateral pointed membranous projections in proximal half, and 1 long midventral tube-pore subapically; ornamented with several long setules. Cephalothorax and body somites strongly chitinized and ornamented with 24 pairs of simple and branched processes (numbered from 1 to 24 in Fig. 1A), pattern identical with that of *A. confusus*. Anal somite with rounded and bare anal operculum; with 2 longitudinal rows of small spinules in middle; ventrally with 2 pores and spinules along posterior margin. Caudal rami (Fig. 1) divergent, cylindrical and long; about 10 times as long as wide (taking width at its widest part proximally); slightly convex; with spinule patches along outer margin proximally and around insertion sites of setae I and II; with minute spinules dorsally and ventrally. Seta I arising ventrolaterally halfway outer margin; seta II arising laterally at same level as seta I, twice as long as seta I; seta III subapical in position, about same length as seta II; seta IV fused at base to seta V (Fig. 1C); seta VI arising from inner distal corner of caudal ramus and as long as seta IV; seta VII dorsal, triarticulate at base and arising sub-apically.

Antennule (Fig. 2) 3-segmented. Segment 1 about 3.8 times as long as wide (taking width at its widest part distally), with 1 dorsal sub-apical seta arising from spinous projection (arrowed in Fig. 2A, B). Segment 2 barely longer

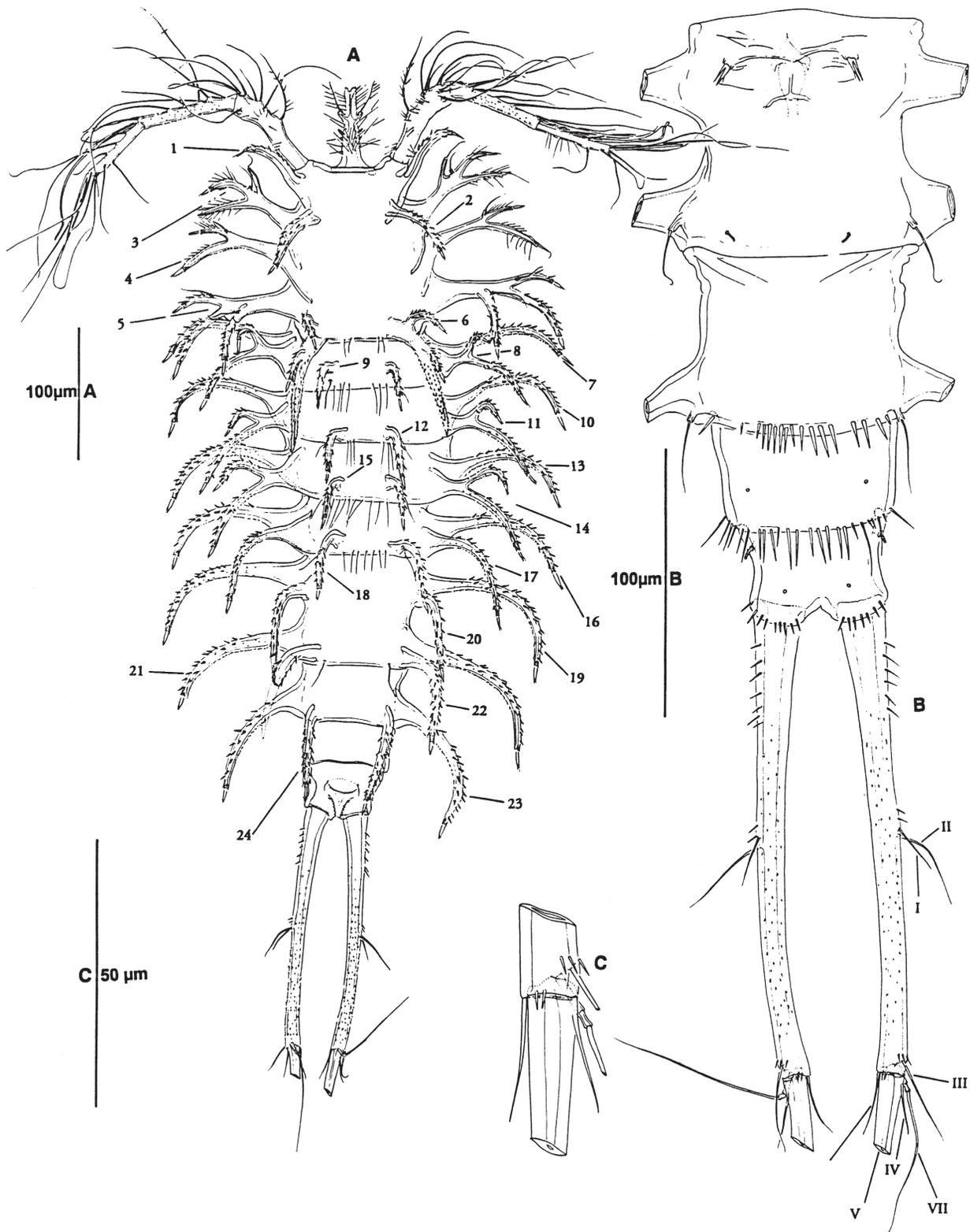


Figure 1. *Ancorabolus hendrickxi* sp. nov., adult female, holotype. **A** habitus, dorsal; **B** urosome, ventral (P5-bearing somite omitted); **C** distal part of left caudal ramus, ventral.

Figure 1. *Ancorabolus hendrickxi* sp. nov., femelle adulte, holotype. **A** habitus, vue dorsale ; **B** urosome, vue ventrale (le segment qui porte P5 a été omis) ; **C** partie distale de la furca gauche, vue ventrale.

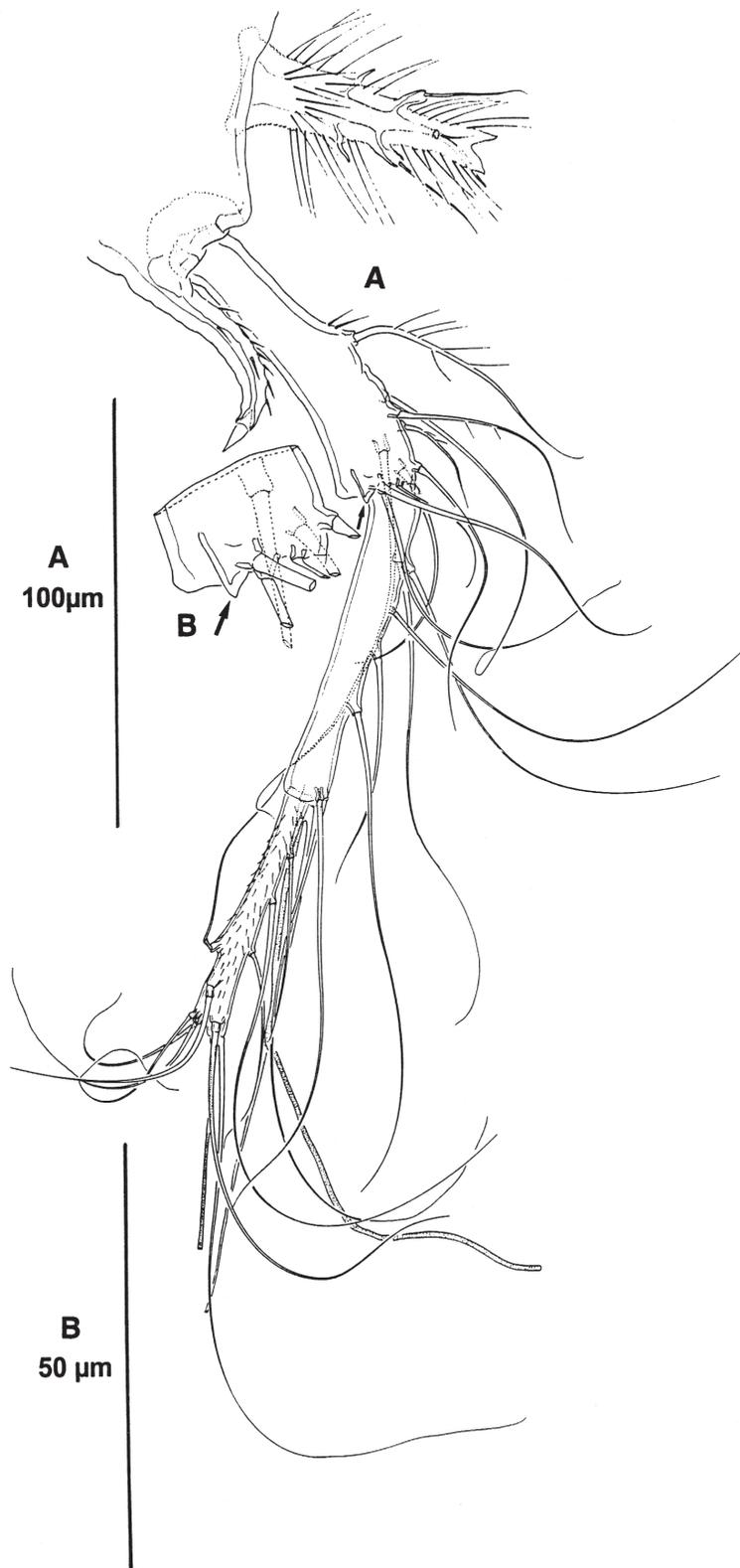


Figure 2. *Ancorabulus hendrickxi* sp. nov., adult female, holotype. **A** antennule and rostrum; **B** distal part of first antennular segment.
Figure 2. *Ancorabulus hendrickxi* sp. nov., femelle adulte, holotype. **A** antennule et rostre ; **B** partie distale du premier segment de l'antennule.

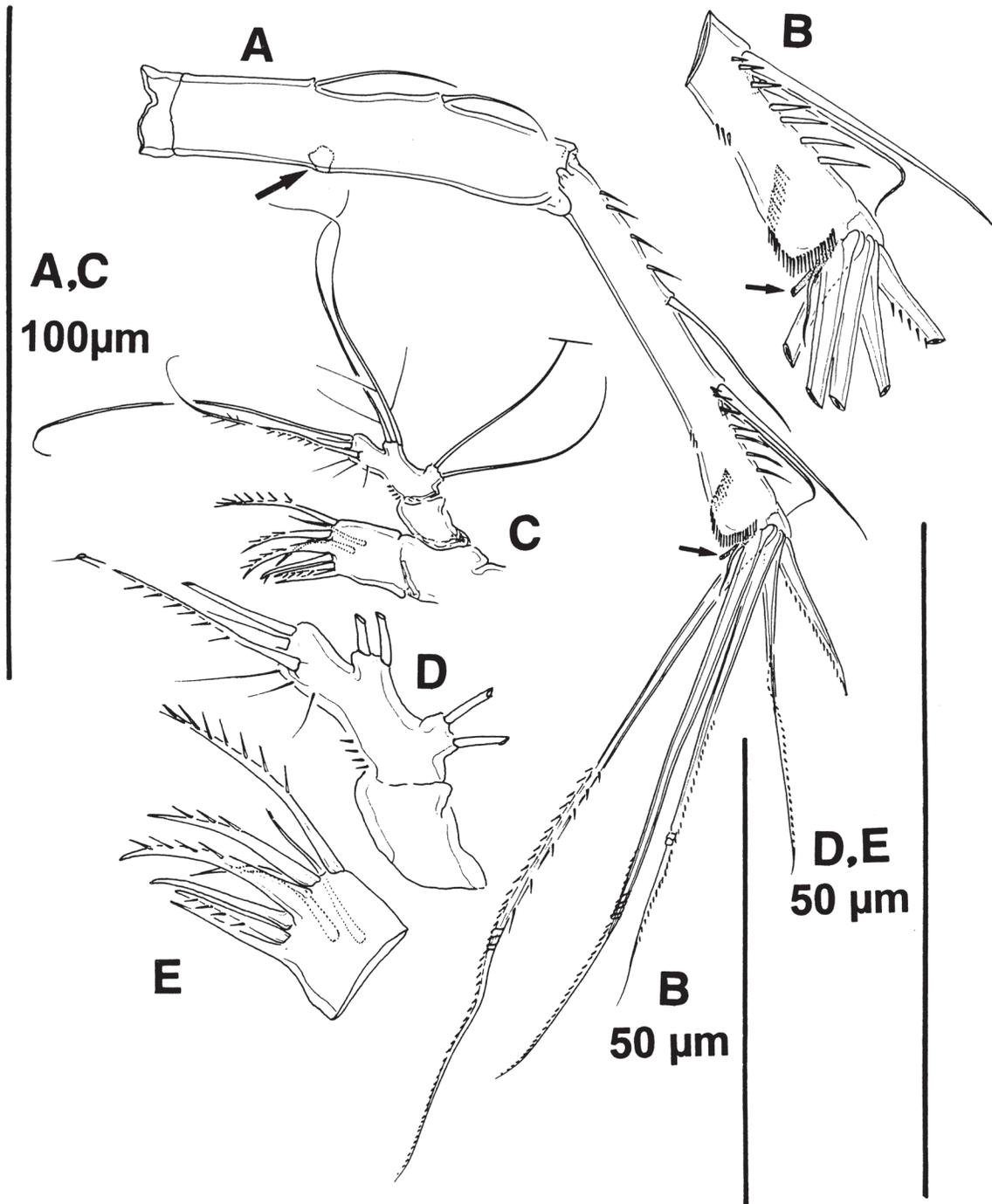


Figure 3. *Ancorabolus hendrickxi* sp. nov., adult female, holotype. **A** antenna; **B** distal part of endopodal segment of antenna; **C** maxillule; **D** maxillular coxa and basis with fused endopod and exopod; **E** maxillular arthrite.

Figure 3. *Ancorabolus hendrickxi* sp. nov., femelle adulte, holotype. **A** antenne ; **B** partie distale du segment de l'endopode de l'antenne ; **C** maxillule ; **D** coxa et basis de la maxillule avec l'endopode et l'exopode fusionnés ; **E** arthrite de la maxillule.

than first, about 6 times as long as wide. Segment 3 shortest, about 8 times as long as wide (taking width at its widest part distally). Armature formula: 1-(10), 2-[7+(1+ae)], 3-

(9+acrothek). Acrothek consisting of aesthetasc and 1 slender seta.

Antenna (Fig. 3A, B) with long allobasis (about 4.5 times

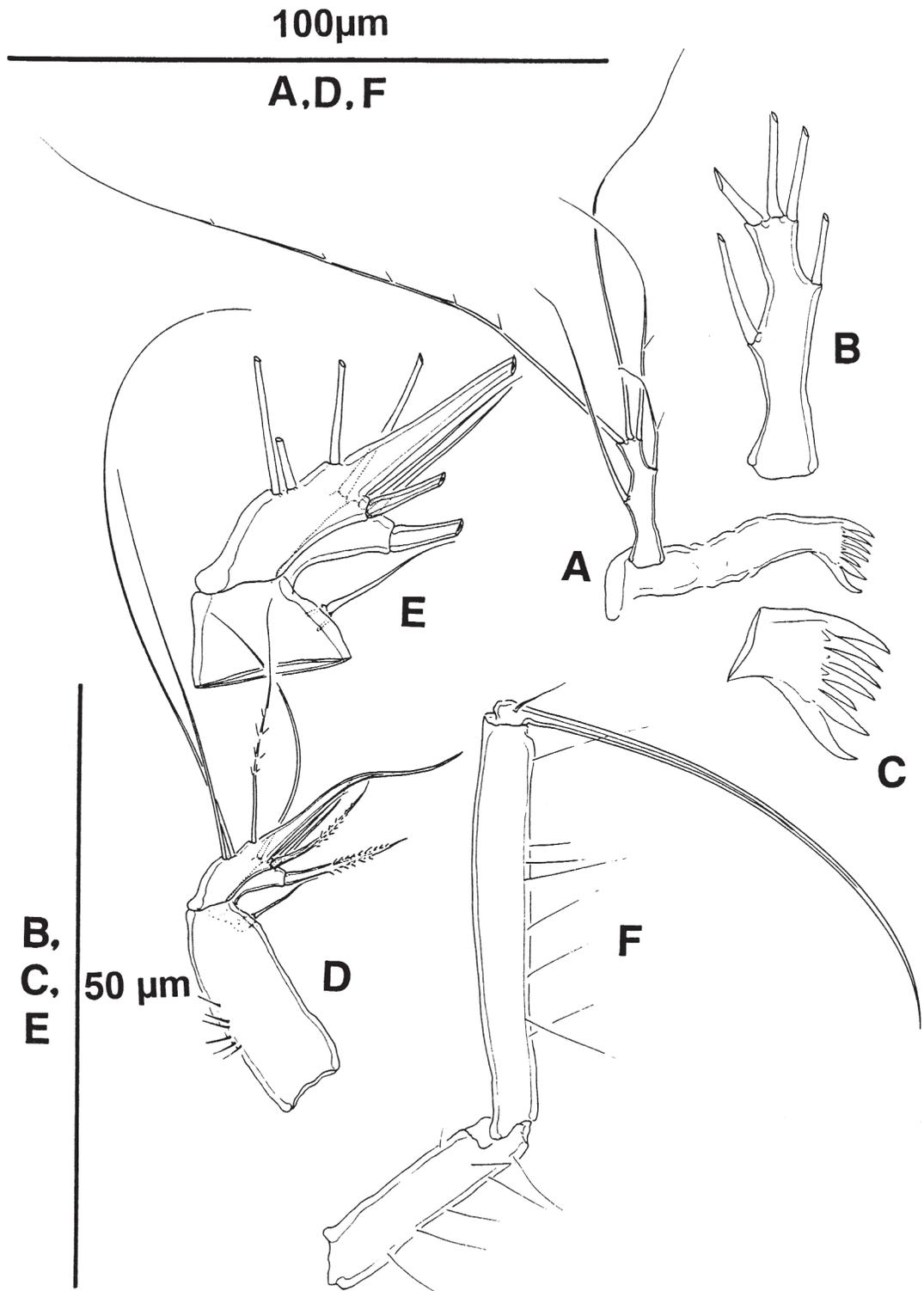


Figure 4. *Ancorobolus hendrickxi* sp. nov., adult female, holotype. **A** mandible; **B** mandibular palp; **C** distal part of mandibular gnathobase; **D** maxilla; **E** distal part of maxillary syncoxa showing proximal and distal endites, and allobasis; **F** maxilliped.

Figure 4. *Ancorobolus hendrickxi* sp. nov., femelle adulte, holotype. **A** mandibule ; **B** palpe mandibulaire ; **C** partie distale de la mandibule ; **D** maxille ; **E** partie distale de la syncoxa de la maxille avec les endites proximal et distal, et l'allobasis ; **F** maxillipède.

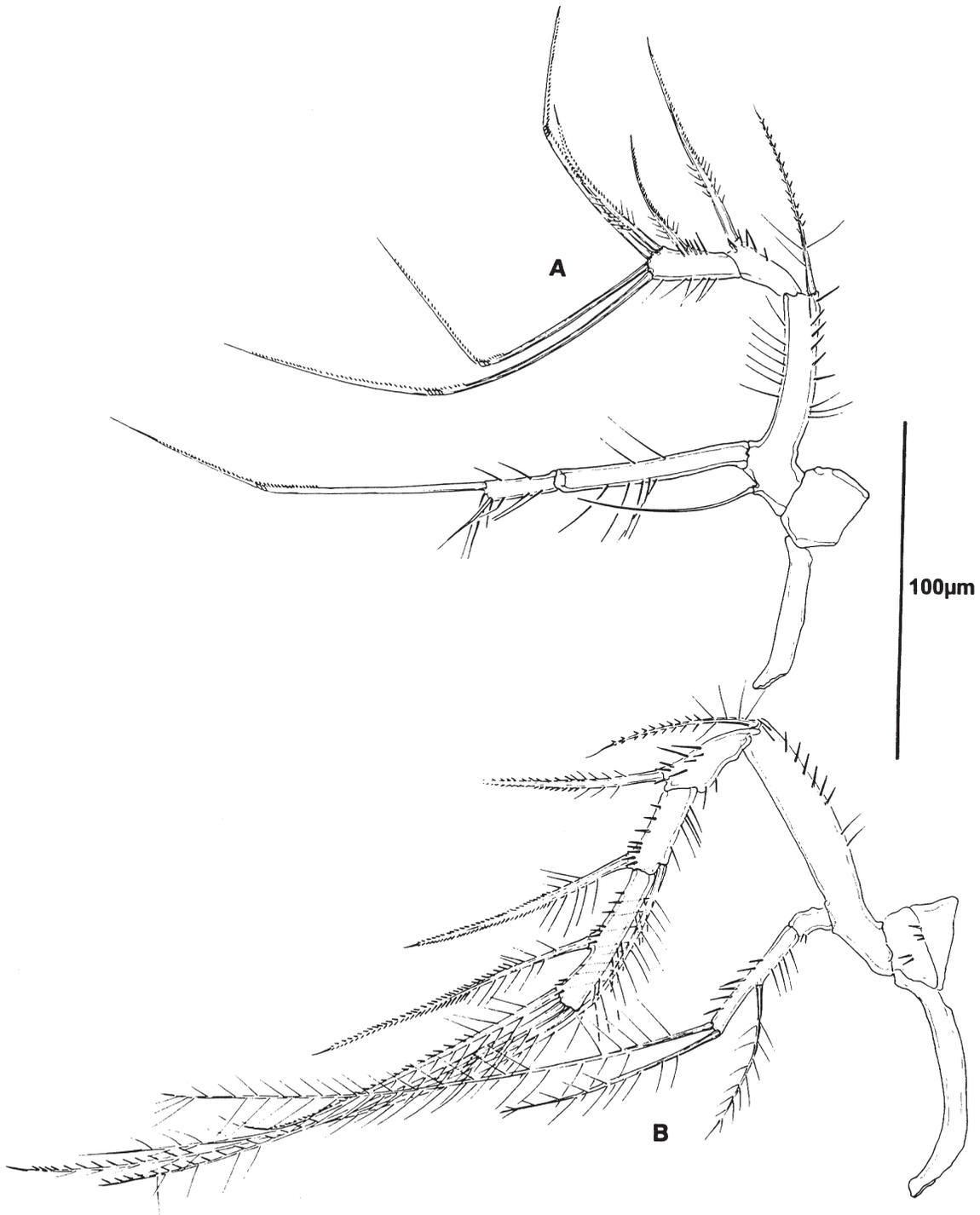


Figure 5. *Ancorobolus hendrickxi* sp. nov., adult female, holotype. **A** P1; **B** P2.

Figure 5. *Ancorobolus hendrickxi* sp. nov., femelle adulte, holotype. **A** P1; **B** P2.

longer than wide) bearing 2 slender abexopodal setae; with membranous insert halfway marking original position of exopod (arrowed in Fig. 3A); exopod absent. Endopod

segment slightly longer than allobasis, about 9.5 times as long as wide; with some spinules along inner margin and with 2 spines and 1 seta laterally; outer margin with distal

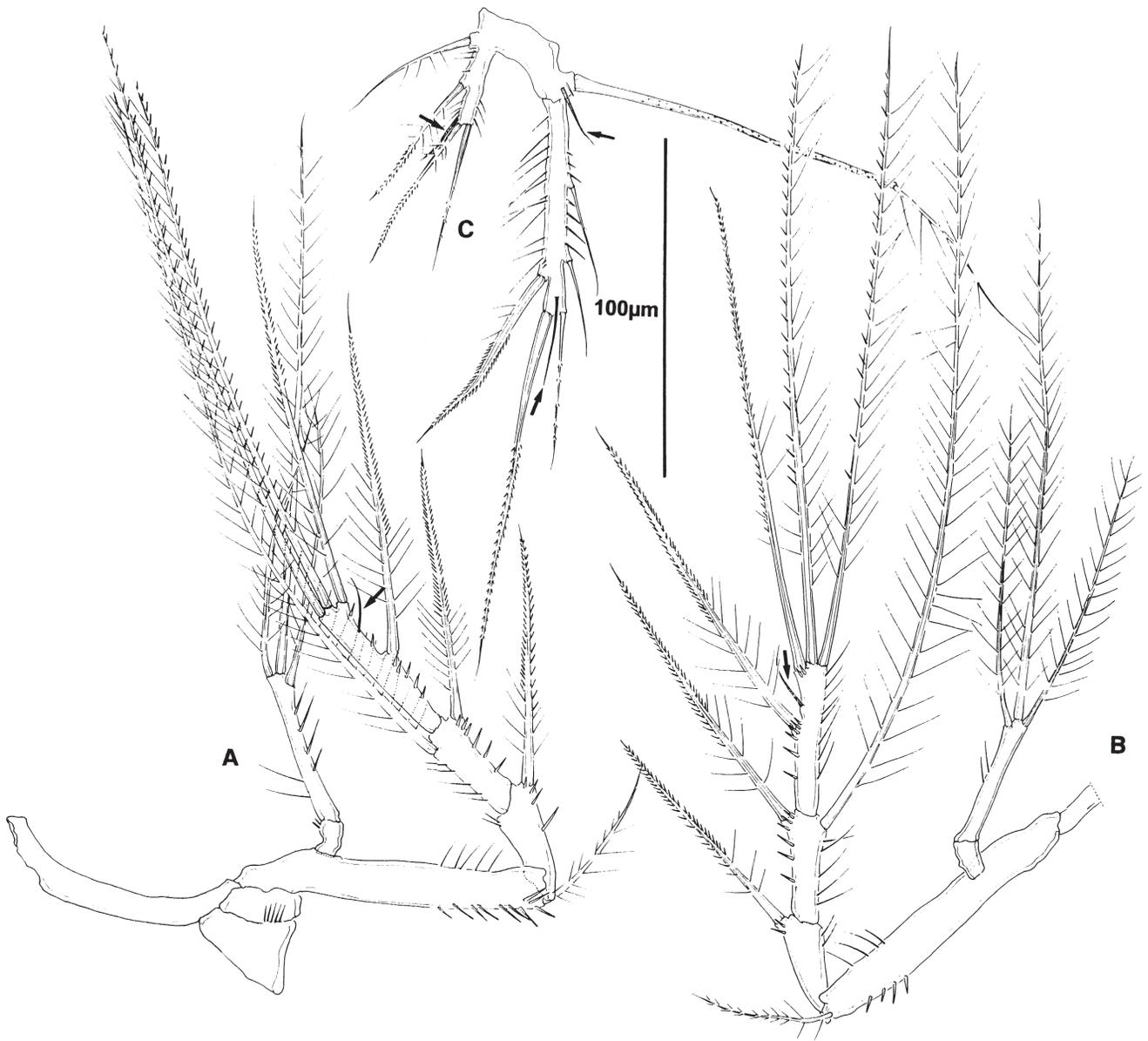


Figure 6. *Ancorabolus hendrickxi* sp. nov., adult female, holotype. **A** P3; **B** P4; **C** P5.

Figure 6. *Ancorabolus hendrickxi* sp. nov., femelle adulte, holotype. **A** P3; **B** P4; **C** P5.

surface frill; with 6 apical elements, of which 3 outermost geniculate and longest one fused basally to vestigial seta and tube-pore (arrowed in Fig. 3A, B).

Mandible (Fig. 4A, B, C) with slender coxa; gnathobase with incised teeth and with strong element at dorsal corner. Palp well developed 1-segmented, with 1 exopodal, 1 basal seta and 3 apical (endopodal) setae.

Maxillule (Fig. 3C, D, E) with praecoxal arthrite bearing 2 surface setae and 6 distal elements, innermost fused to arthrite. Coxal endite absent. Basis with 2 endites; proximal

and distal endite with 3 and 2 setae, respectively. Exopod incorporated into basis and represented by 2 setae; endopod not represented by any elements.

Maxilla (Fig. 4D, E), syncoxa with sparse spinules along outer margin; with 2 endites, proximal endite reduced to small tubercle bearing 1 naked seta, distal endite well developed with 1 pinnate and 2 bare elements. Allobasis drawn into long and slender claw, with 2 accessory setae and 1 spine. Endopod represented by 2 setae.

Maxilliped (Fig. 4F) subchelate, slender and elongate. Syncoxa without armature. Basis without armature and ornamented as syncoxa. Endopod drawn into long and slender claw with 1 accessory seta.

P1 (Fig. 5A) with long and narrow intercoxal sclerite. Basis transversely elongate bearing pinnate outer seta and bare inner element; outer and inner margins with row of spinules and setules, respectively. Exopod 2-segmented; segment 1 with outer spine; segment 2 with 3 geniculate setae and 2 spines. Endopod 2-segmented; about 1.8 times longer than entire exopod; segment 1 longer than entire exopod, about 8.5 times longer than wide, without armature, with only few fine setules along outer and inner margins; segment 2 about 1/3 length of first segment and armed with three apical elements.

P2-P4 (Figs 5B, 6A, B) with wide intercoxal sclerites. Praecoxae and coxae with some spinules. Bases transversely elongate. Exopods 3-segmented. Segments 1 and 3 without inner elements, segment 2 with long inner seta; segment 3 with four elements and with (P3-P4) or without (P2) long outer tube-pore (arrowed in Fig. 6A, B). Endopods 2-segmented; segment 1 small, about twice as long as wide, without armature; endopod 2 with 1 inner and 2 apical setae (P2) or with 1 subapical outer and 2 distal setae (P3-P4). Armature formula of P1-P4 as follows:

	EXP	ENP
P1	I-0; II+1,2,0	0-0; 0,2,1
P2	I-0; I-1; I,2,0	0-0; 0,2,1
P3	I-0; I-1; I,2,0	0-0; 1,2,0
P4	I-0; I-1; II,2,0	0-0; 1,2,0

P5 (Fig. 6C) with long tube-pore at distal outer corner of baseoendopod halfway between insertion site of exopod and outer seta. Exopod long and slender, about 9 times longer than wide, with long spinules along outer margin and slender setules along inner margin; with 2 outer, 1 strong inner and 2 apical setae; with long tube-pore subapically (arrowed in Fig. 6C). Endopodal lobe with few spinules close to insertion site of outer seta and some slender spinules along inner and outer margin; with 2 lateral and 2 apical elements, and one long tube-pore subapically.

Genital field (Fig. 1B) with fused gonopores covered by genital operculum derived from vestigial sixth legs. P6 (Fig. 1B) each with 3 basally fused minute elements. Copulatory pore (Fig. 1B) moderately large.

Male. Unknown.

Etymology: the species is named in honour of Dr Michel Hendrickx Reners (Mazatlán Marine Station of the Institute of Marine Sciences and Limnology, National Autonomous University of Mexico), head of the project "Biocenosis and chemical composition of benthic and pelagic deep water

invertebrates in the southern Gulf of California in relation to environmental conditions".

Discussion

Generic diagnosis of Ancorabolus Norman, 1903 and validity of A. ilvae George, 2001

Sars (1909) established the family Ancorabolidae to accommodate *Ancorabolus mirabilis*, *Arthropysyllus* Sars, 1909, *Ceratonotus* Sars, 1909 and *Echinopsyllus* Sars, 1909. Lang (1936, 1944, 1948) significantly changed the familial concept by incorporating *Laophontodes* T. Scott, 1894 (previously placed in the Laophontidae T. Scott) and by the subsequent division into two subfamilies, the Ancorabolinae and the Laophontodinae. As a result of thorough investigation of extant material of *Ancorabolus mirabilis* from the collections of A. M. Norman, G. O. Sars and K. Lang, Conroy-Dalton & Huys (2000) found this material to consist of three new species different from *A. mirabilis*: *A. inermis*, *A. confusus*, and *Juxtaramia polaris* Conroy-Dalton & Huys, 2000. They also designated the specimen illustrated by Norman (1911, Plate 29, Figs. 1-2) as the lectotype of *A. mirabilis* and gave a brief diagnosis of the species based on some differences between Norman's (1903, 1911) descriptions, and both *A. inermis* and *A. confusus*. Following the discovery of *A. hendrickxi* sp. nov., the generic diagnosis proposed by Conroy-Dalton & Huys' (2000) requires some minor amendments: (1) "...Mandible with slender coxa; palp 1-segmented, uniramous with a maximum of 5 setae (always with 3 setae apically)...", and (2) "...Maxillary syncoxa with 2 endites; distal endite well developed with 3 elements; proximal endite either well developed (with 3 setae) or reduced (with 1 seta);...".

Recently, George (2001) established *Ancorabolus ilvae* explicitly on the basis of a fifth copepodid female (CV), differing markedly from its congeners by the 2-segmented condition of the exopods of P2-P4. In order to incorporate this variation, George (2001) suggested altering the generic diagnosis accordingly. For reasons outlined below his amendment is not adopted here, not least because the specific status of *A. ilvae* appears to be controversial.

Although alluding to some of the risks involved in establishing species descriptions on juvenile stages, George (2001) claims however that the fifth copepodid may be used for species description and identification since several characters are already fully developed at this stage. As examples of such characters George mentions the body shape, body ornamentation and the segmentation and setation of appendages. Although this crude assumption may be valid for some taxa, accepting it uncritically would require oversimplifying the phylogenetic significance of heterochrony and ignoring the plasticity of terminal

developmental processes. Furthermore, George's (2001) inferences were based solely on observations of the copepodid stages of a single species, *A. ilvae*. In the absence of data on the adult of this species and of comparative ontogenetic information for other species of *Ancorabolus*, statements of this kind should be regarded as speculative.

Body shape and ornamentation frequently remain unchanged at the final moult, particularly in taxa that display a relatively unmodified body plan. It would, however, be naive to extend this rule to those families displaying an elaborate body morphology such as the Ancorabolidae, some Laophontidae T. Scott and Cerviniidae Sars. In many cases significant reorganization takes place at the final moult, generating the primary diagnostic characters necessary for separation of closely related species or even for generic placement. For example, copepodid stages of *Probosciphontodes ptenopostica* Fiers, 1988 and *P. stellata* Fiers, 1988 (Laophontodinae) are virtually indistinguishable. At the final moult from copepodid V to adult, *P. ptenopostica* develops additional lateral pleural extensions on the prae-anal somite which are absent in the closely related *P. stellata*. It is likely that the absence of these processes in the latter results from terminal deletion, either by progenesis (early offset), post-displacement (late initiation) or neoteny (slower developmental rate). It is also possible that the observed discrepancy in body process patterns between these species has resulted from terminal addition in *P. ptenopostica* due to a peramorphic event such as hypermorphosis. In the absence of the outgroup of *Probosciphontodes* it is at present impossible to determine which developmental process is underlying the expression or suppression of prae-anal processes (Fiers, 1988).

Another example demonstrates that knowledge of adult morphology is an essential prerequisite for correct generic assignment. Fiers (1991a) elucidated interspecific relationships by comparing the development of cephalothoracic structures in copepodids of *Xanthilaophonte trispinosa* (Sewell, 1940) and three species of *Echinolaophonte* Nicholls (*E. armiger* (Gurney, 1927), *E. mirabilis* (Gurney, 1927) and *E. tropica* Ummerkutty, 1970). The cephalic mediodorsal rounded swelling found in adult *X. trispinosa* bears little resemblance to the elaborate spinous process exhibited by *Echinolaophonte*, but Fiers (1991a) showed that it is however identical to the structure found in CV stages of the latter. Fiers' (1991a) ontogenetic data highlighted the sister-group relationship between *Xanthilaophonte* Fiers and *Echinolaophonte*. Considering the developmental pattern in *Echinolaophonte* as ancestral he concludes that the morphology of the cephalic shield is postdisplaced in *Xanthilaophonte*.

The terminal addition of body processes in *Ancorabolus* is of particular relevance to the validity of *A. ilvae*. Our

observations of copepodid stages of both *A. inermis* and *A. confusus* indicate that ignorance of adult body morphology can lead to erroneous identification. In both species the full complement of body processes is present in CV female (albeit less developed, most notably in *A. inermis*) except on the second abdominal somite, where no processes are present. The processes found in the adult female on this somite (1 lateral + 1 laterodorsal pair) are therefore only expressed at the final moult (when also the genital and first abdominal somites fuse, and the penultimate and anal somite separate). Also, it is precisely the process pattern on the second abdominal somite that displays sexual dimorphism in adult *Ancorabolus* species where males are known (second abdominal somite male: *A. inermis* without processes; *A. confusus* with paired laterodorsal processes only). Critical changes in body morphology (with particular reference to pattern and degree of development of body processes) therefore do occur between the CV stage and adults of *Ancorabolus* species, contrary to George's (2001) supposition.

From documented swimming leg developmental patterns (Ferrari, 1988, 1998; Fiers, 1990, 1991a, 1996; Dahms, 1990, 1993a, b) it is clear that copepodid V exopodal segmentation of P2-P4 does not necessarily correspond to that found in the adults as George (2001) postulates. A striking similarity in swimming leg development between *Enhydrosoma lacunae* Jakubisiak, 1933 (see Fiers, 1996) and *A. ilvae* (George, 2001) is shown in Table 1. The single difference is the adult state of the P1 exopod, being 3-segmented in *E. lacunae* and 2-segmented in *A. ilvae*. Unfortunately the CIII of *A. ilvae* remains unknown, and George (2001) makes no comment on the presence/absence of primary buds of P3 and P4. However, it is highly probable that the leg development of CIII of *A. ilvae* is similar to that of *E. lacunae*. According to Ferrari (1988, 1998) a delayed pleiotropic regulatory process seems to affect the morphology of all rami synchronically from CIV to CV (the simultaneous addition of the third exopodal segment is delayed). During the last moult (from CV to adult [CVI]) a second regulatory process affects only the morphology of endopods of P1-P4 (the simultaneous addition is suspended), whereas the last addition in the exopod takes place in *E. lacunae*. A similar scenario obviously occurs in *A. ilvae* (see Table 1) except that the second regulatory process affects the morphology of the P1 exopod as well (the last addition is suppressed).

Female CV stages of *A. inermis* and *A. confusus* display (a) a 2-segmented condition P2-P4 exopods (Fig. 7B, Table 1) with full complement of armature elements as in the adult and (b) a P5 exopod which is not discrete from the baseopod (although an indication of the line of separation is discernible (Fig. 7C insert)). In contrast to George's (2001) assumptions, it is evident therefore that

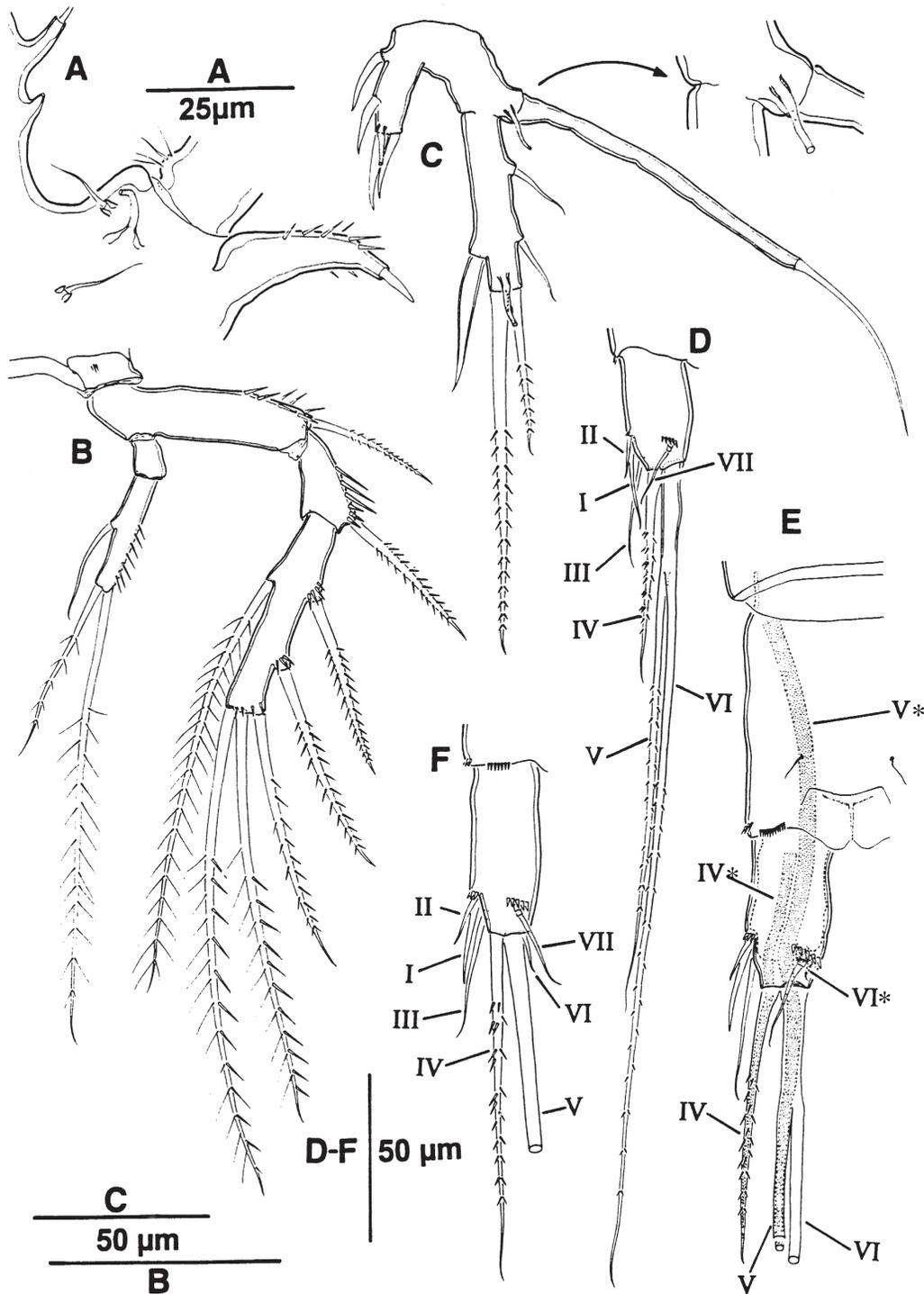


Figure 7. *Ancorabolus confusus*. **A** anterior corner of cephalic shield female, dorsal; **B** P2, CV, female, anterior; **C** P5, CV, female, anterior (insert showing area between baseoendopod and exopod); *Macrosetella gracilis*. **D** left caudal ramus, CI, dorsal; **E** anal somite (part) and left caudal ramus, CI intermolt (asterisks indicating precursors of setae IV – VI), dorsal; **F** left caudal ramus, CII, dorsal.

Figure 7. *Ancorabolus confusus*. **A** angle antérieur du bouclier céphalique, femelle, vue dorsale; **B** P2, CV, femelle, vue antérieure; **C** P5, CV, femelle, vue antérieure (l'encart indique la partie entre le baseoendopode et l'exopode); *Macrosetella gracilis*. **D** rame caudale gauche, CI, vue dorsale; **E** somite anal et rame caudale gauche, CI intermue (les astérisques indiquent les précurseurs des soies IV – VI), vue dorsale; **F** rame caudale gauche, CII, vue dorsale.

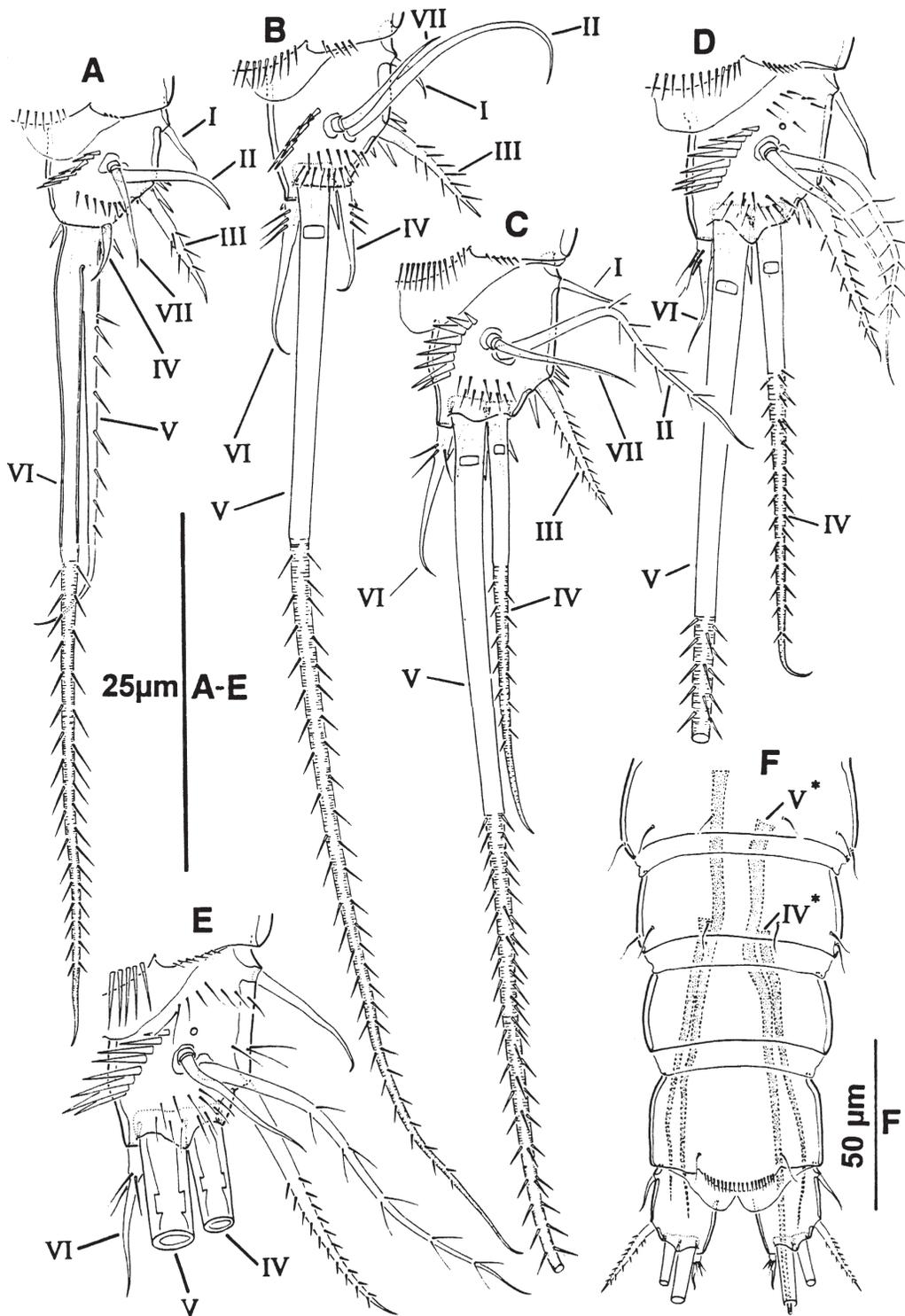


Figure 8. *Microarthridion* sp. **A** right caudal ramus, CI, dorsal; **B** right caudal ramus, CII, dorsal; **C** right caudal ramus, CIII, dorsal; **D** right caudal ramus, CV, dorsal; **E** right caudal ramus, adult, dorsal; **F** urosome, CV intermolt (asterisks indicating precursors of setae IV – V), dorsal.

Figure 8. *Microarthridion* sp. **A** rame caudale droite, CI, vue dorsale; **B** rame caudale droite, CII, vue dorsale; **C** rame caudale droite, CIII, vue dorsale; **D** rame caudale droite, CV, vue dorsale; **E** rame caudale droite, adulte, vue dorsale; **F** urosome, CV intermue (les astérisques indiquent les précurseurs des soies IV – V), vue dorsale.

exopodal differentiation in P2-P5 does occur at the final moult in *Ancorabolus*, i.e. exp-3 separates in P2-P4 (rami becoming 3-segmented) and P5 exopod becomes defined as a discrete segment.

George (2001) lists 8 characters (a combination of both plesiomorphies and apomorphies) differentiating *A. ilvae* from its congeners, directly cited below as follows:

- 1) Presence of large frontal tube pores (apomorphic)
- 2) Retention of 1 exopodal seta on the mandibular palp (plesiomorphic)
- 3) Loss of seta on the cutting edge of the Md (apomorphic)
- 4) Retention of third endopodal (?) seta on allobasis Mx (plesiomorphic)
- 5) Proximal endite of Mx with only 1 seta (apomorphic)
- 6) Distal endite of Mx with only 2 setae (apomorphic)
- 7) Possession of 2-segmented exps in P2-P4 (apomorphic)
- 8) Fusion of exp and benp of female P5 (apomorphic)

Characters (7) and (8) have been demonstrated above as juvenile characters and should therefore be disregarded. The large cephalic frontal pores, character (1), is shared by nearly all members of the *Ancorabolus*-group. Conroy-Dalton & Huys (2000) figured it in all species they directly observed and is shown here more clearly in Fig. 7A for *A. confusus*. Only in *Breviconia australis* (George, 1998) are these structures unconfirmed, being neither mentioned in the text or figured in the original description, and verification in the present study was not possible despite several attempts to gain access to the type material held in the collections of Carl von Ossietzky University, Oldenburg, Germany. The presence of these cephalic tube pores is an apomorphy shared by all members of the *Ancorabolus*-group, moreover it is probably a synapomorphy for a much larger group of taxa, having also been observed in *Arthricornua* Conroy-Dalton, 2001, *Ceratonotus pectinatus pectinatus* Sars, 1909; *Dorsiceratus octocornis* Drzycimski, 1967; *D. triarticulatus* Coull, 1973 and *Echinopsyllus normani* Sars, 1909 (Conroy-Dalton, 2001; pers. obs.).

Characters (2) and (5) are shared by *A. ilvae* and *A. hendrickxi* (see description above). Of the remaining three characters, (3) and (6) should be viewed with caution. The elements referred to are often reduced and can easily be overlooked or misinterpreted [(3) the mandibular seta is often closely adpressed to the gnathobase; (6) in the *Ancorabolus*-group the two outer elements found on this endite are typically tiny and superimposed]. Verification of these characters in *A. ilvae* was not possible by either comparative analysis (in particular to *A. hendrickxi* with which it shows several similarities) nor from direct observations of type material (which was not made available for study, see above). Characters (3) and (6) should therefore be at best regarded as questionable. Consequently, the specific status of *A. ilvae* is tenuous,

being supported by only 1 plesiomorphic character (4). There is no doubt that *A. ilvae* belongs to the genus *Ancorabolus* but the current information does not allow for unequivocal specific identification. Based on all the evidence presented above, we consider *A. ilvae* George, 2001 as *species inquirenda* until discovery of adult female and/or male specimens and the designation of a neotype in terms of Article 75.5 of the International Code of Zoological Nomenclature (1999).

Ancorabolus hendrickxi sp. nov. can be readily differentiated from its congeners on the basis of the following characters: (a) mandibular palp with a total of 5 setae [1 exopodal, 1 basal and 3 apical endopodal setae]; (b) maxillule, coxal endite completely absorbed and without armature; (c) maxilla, proximal syncoxal endite very reduced bearing 1 naked seta. It appears most closely related to *A. confusus* (from Norway and Sweden) based on the following combination of characters: (1) pattern, degree of development and length of body processes; (2) elongate and slender nature of the caudal rami; (3) cephalothorax with pair of dorsal backwardly directed processes in anterior half; (4) shape and size of rostrum; (5) A1 female segment 2 without proximal recurved process near posterior margin; (6) maxillule, incorporated endopod not represented by armature elements; (7) P2 enp-2 with inner seta.

Phylogenetic Analysis of the Ancorabolus-group

Characters and Taxa

The taxonomic position of *A. hendrickxi*, the monophyly of the genus *Ancorabolus* and the validity and relationships of the genera belonging to the *Ancorabolus*-group were assessed using parsimony analysis. Conroy-Dalton & Huys' (2000) character set was updated to include *A. hendrickxi*, with the addition of five phylogenetically informative characters (characters: 11, 12, 14, 19 and 25) listed here in Table 2. A total of 25 morphological characters was used in the final analysis, all of which were set irreversible which suppresses reversals at the expense of introducing extra convergences and consequently increasing tree-length. For detailed methodology, scoring of characters and trends in cephalic sensillar group (I-V) patterns see Conroy-Dalton & Huys (2000).

Results

Parsimony analysis identified a single fully resolved, most parsimonious tree with a tree length of 43 steps, a consistency index 0.744 and a retention index of 0.900 (Fig. 9, Table 3). Homoplasy is encountered in 5 characters (12, 14, 15, 16b, 20) and is largely concentrated on branches leading to terminal taxa.

The cladogram depicted in Fig. 9 is completely congruent with the phylogenetic tree obtained by Conroy-Dalton & Huys (2000), reinforcing the phylogenetic

Table 2. Morphological characters used in the phylogenetic analysis (see also Conroy-Dalton & Huys, 2000). Apomorphic states are referred to in square brackets.

Tableau 2. Caractères morphologiques utilisés dans l'analyse phylogénétique (voir aussi Conroy-Dalton & Huys, 2000). Les caractères apomorphes sont indiqués entre crochets.

-
1. Rostrum female lateral margins forming rectilinear contour with anterolateral portions of cephalic shield [1: with clear basal constriction forming subrectangular rostrum; 2: additional constriction and elongation + sensillae on distinct conical projections].
 2. Cephalic shield without pair of dorsal processes in anterior half [paired dorsal processes present].
 3. Lateral wing-like processes on second abdominal somite present in both sexes [1: absent in male].
 4. Body somites female without distinct laterodorsal and dorsolateral processes [2 pairs (1 laterodorsal, 1 dorsolateral) present on somites bearing P2-P5; additional development of 1 pair of laterodorsal processes in both anterior and posterior halves of genital double-somite; addition of 1 pair on second abdominal somite].
 5. Pedigerous somites without dorsal processes [1 pair present on somites bearing P2-P4].
 6. Process bearing cephalothoracic sensillar group I blunt and small [more produced and spinous].
 7. Cephalothoracic sensillar group II: all sensillae and tube-pores arising from single lobate process [sensillae *b-c* and posterior tube-pore arising from individual thorn-like processes; anterior tube-pore raised].
 8. Cephalothoracic sensillar group III: all sensillae arising from weakly or strongly bilobate process [processes thorn-like and elongate].
 9. Cephalothoracic sensillar group IV: sensillae *c-e* arising from conical processes [1: development of third process bearing sensilla *a-b*; 2: constriction and allometric growth resulting in distad displacement of sensilla(e) *a* (and *d*)].
 10. Cephalothoracic sensillar group V: all sensillae arising from posterior margin [1: formation of spinous extension between sensillae *c* and *d*, and development of tubercles bearing sensillae *a* and *c*; 2: enlargement of tubercles; 3: displacement of sensillae *a-c* (with associated processes) onto spinous extension].
 11. Cephalothoracic sensillar group V: when present spinous extension moderately developed [extension extremely elongate].
 12. Antennular segments 1 and 2 partially free [segments fused].
 13. Antennule female segment 2 (or equivalent when segments 1 and 2 are indistinctly fused) with armature formula 9 + (1+ae) [loss of 2 setae resulting in 7 + (1+ae)].
 14. Antennule female segment 2 (or equivalent when segments 1 and 2 are indistinctly fused) without recurved processes [posterior margin with recurved process proximally].
 15. Seta representing mandibular exopod present [absent].
 16. Mandibular palp with 2 basal setae [1: with 1 seta; 2: both setae absent].
 17. Coxal endite of maxillule with 2 setae [1: with 1 seta; 2: both setae absent].
 18. P1 exp-2 distal outer element spiniform, not modified [setiform and geniculate].
 19. P2-P4 exopodal outer elements spiniform [elongate and setiform].
 20. P2 enp-2 inner seta present [absent].
 21. P3 enp-2 inner seta present [absent].
 22. P4 female enp-2 inner seta present [absent].
 23. P4 enp-2 outer element not sexually dimorphic [setiform in female, spiniform in male].
 24. P5 male inner baseopodal seta not modified [spiniform and serrate].
 25. Produced body processes bearing unmodified sensillae [1: sensillae arising from body processes in pleural areas modified; 2: sensillae arising from all body processes modified].
-

positions of all genera (see also Table 3). *Arthropysyllus* is the most primitive offshoot and *Uptionyx* Conroy-Dalton & Huys, 2000 and *Breviconia* Conroy-Dalton & Huys, 2000 diverge from intermediate nodes. According to the topology obtained in Fig. 9, modified sensillae (character 25) have evolved convergently in the ancestor of *Ancorabolus* and in *Uptionyx verenae* Conroy-Dalton & Huys, 2000. This character was scored as a multistep character with the presence of modified sensillae restricted to the pleural areas as the derived state 1 (in *Uptionyx*) and the modification of additional sensillae on the dorsal processes of the cephalothorax and body somites as the further derived state 2 (in *Ancorabolus*). An alternative hypothesis is that modified sensillae were already present in the ancestor of the *Ancorabolus*-lineage and that its disjunct distribution in the currently known extant descendants is due to secondary reduction (*Uptionyx*) or complete loss (*Arthropysyllus*,

Breviconia, *Juxtaramia* Conroy-Dalton & Huys, 2000). In order to test this hypothesis we have scored this character unordered and ordered in subsequent trial analyses but this resulted in the same topology as depicted in Fig. 9, confirming the independent acquisition of modified sensillae in *Uptionyx* and *Ancorabolus*. The seemingly articulated sensillae figured by George (1998: Fig. 2B) for *Breviconia australis* are not considered as homologous here because they are of a different structure and, according to the original description, are restricted to the lateral processes of the genital double-somite.

Juxtaramia and *Ancorabolus* share a sistergroup relationship, forming the terminal clade of the tree (Fig 9). They represent the two most ornate genera and their sister group relationship is supported by the following synapomorphies: (1) elongation of anterolateral processes of sensillar group I, (2) sensillar group II with several thorn-

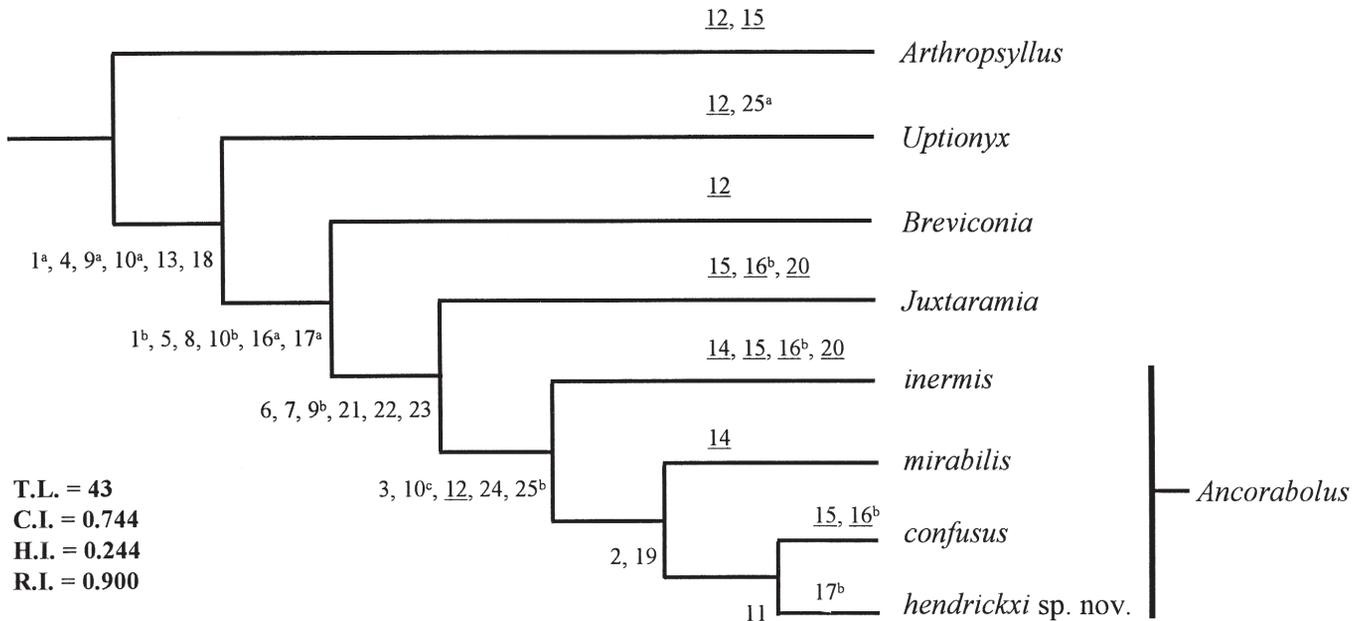


Figure 9. Phylogenetic tree depicting relationships between species of the *Ancorabolus*-group. Superscript letters refer to multistep character changes [^a: 0→1; ^b: 1→2; ^c: 2→3]. Underlined numbers refer to convergences. For explanation see Tables 2-3 and text.

Figure 9. Arbre phylogénétique montrant les relations entre les différentes espèces du groupe *Ancorabolus*. Les lettres en exposant se réfèrent aux changements de caractère multiétats [^a: 0→1; ^b: 1→2; ^c: 2→3]. Les chiffres soulignés se réfèrent aux convergences. Voir Tableaux 2-3 et texte pour explication.

Table 3. Character data matrix [0 = ancestral (plesiomorphic) state, 1-3 = derived (apomorphic) states, ? = missing data].

Tableau 3. Matrice de caractères [0 = état ancestral (plésiomorphe), 1-3 = états dérivés (apomorphes), ? = données absentes].

Character	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
<i>Ancorabolus inermis</i>	2	0	1	1	1	1	1	1	2	3	0	1	1	1	1	2	1	1	0	1	1	1	1	1	2
<i>A. confusus</i>	2	1	1	1	1	1	1	1	2	3	1	1	1	0	1	2	1	1	1	0	1	1	1	1	2
<i>A. hendrickxi</i>	2	1	?	1	1	1	1	1	2	3	1	1	1	0	0	1	2	1	1	0	1	1	?	?	2
<i>A. mirabilis</i>	2	1	?	1	1	1	1	1	2	3	0	1	?	1	?	?	?	?	1	?	?	?	?	?	2
<i>Arthropysyllus</i>	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Breviconia australis</i>	2	0	?	1	1	?	?	1	1	2	0	1	1	0	0	1	1	1	0	0	0	0	?	?	0
<i>Juxtaramia polaris</i>	2	0	0	1	1	1	1	1	2	?	0	0	1	0	1	2	1	1	0	1	1	1	1	1	0
<i>Uptionyx veranae</i>	1	0	?	1	0	0	0	0	1	1	0	1	1	0	0	0	0	1	0	0	0	0	?	?	1

like processes, (3) allometric growth in sensillar group IV, (4) loss of inner seta of P3 enp-2, (5) loss of inner seta of P4 enp-2 and (6) sexual dimorphism in P4 enp-2 outer element (for an explanation on sensillar group nomenclature see Conroy-Dalton & Huys, (2000).

Referring to Conroy-Dalton & Huys' (2000) cladogram, George (2001) claims that there is only a single apomorphy

supporting the genus *Juxtaramia*. However, Conroy-Dalton & Huys (2000) explicitly state in the text that only phylogenetically informative characters were considered in their analysis. One category of uninformative characters omitted by the authors, were autapomorphies since they only increase the tree length without any additional resolution. Parsimony analysis of any data matrix having a

less than optimal fit between taxa and character states (i.e. consistency index < 1) leads to a homoplastic distribution of apomorphic states on the tree(s) either on internal nodes (synapomorphies) or terminal branches (autapomorphies). In Conroy-Dalton & Huys' (2000) analysis the apomorphic state of their character 17 (loss of P2 enp-2 inner seta) occurred convergently on the terminal branches leading to *Ancorabolutus inermis* and *Juxtaramia polaris* and can be considered as an autapomorphy in addition to those which are unique to either of these taxa but were not included in the analysis. Conroy-Dalton & Huys (2000: p. 395) listed no less than six autapomorphies which are exclusive to *Juxtaramia*. These characters were obviously not considered by George (2001) and we therefore consider his reservations about the validity of *Juxtaramia* unfounded.

Ancorabolutus represents the most advanced genus in the group and its monophyly is substantiated by (1) the absence of lateral wing-like processes on the second abdominal somite in the male, (2) displacement of sensillae a-c in cephalic sensillar group V (with associated tubercles) onto the spinous extension, (3) modification of male P5 inner endopodal element into spiniform and serrate spine and (4) all sensillae arising from produced integumental processes are modified. George (2001) suggests that two of these characters [(1) and (3) above] should be abandoned since they are sexually dimorphic and males are not known for all species of *Ancorabolutus*. The discovery of new taxa known only from one sex does not invalidate apomorphic characters based on the other sex. Whether constant sexually dimorphic characters that cannot be verified in all taxa should be excluded from cladistic analysis is obviously irrelevant to the issue since the phylogenetic significance of every single character, male, female or juvenile, has to stand trial by future discovery of closely related taxa.

Within the genus, *A. hendrickxi* and *A. confusus* are most closely related on account of the extreme elongation of the spinous extension of cephalic sensillar group V. The presence of paired dorsal processes in the anterior half of the cephalothorax in combination with the setiform nature of the outer exopodal spines in P2-P4 indicates an affinity between these two species and *A. mirabilis*.

Caudal ramus development in oligoarthran harpacticoids

Dahms (1992) studied intermoult stages of *Amonardia normani* (Brady, 1872), attempting to trace the homology of individual caudal ramus setae between the naupliar and copepodid phases. His proposed developmental scenario is based on three inferences. Firstly, Dahms concluded that the long caudal seta of the sixth nauplius (NVI) develops into a branched seta in the first copepodid (CI). This setal complex he regarded as the common precursor of both principal setae IV and V in the later copepodid stages and the adult.

Secondly, the outer distal seta in NVI was considered as being the precursor of seta VI, generally known as the accessory terminal seta which is typically positioned at the inner distal corner in later stages. In order to explain this positional difference between CI and CII, Dahms (1993a) had to assume that seta VI shifts medially and, simultaneously, both principal setae IV and V shift outwardly during this moult. Finally, comparison of setal numbers between NVI and CI led Dahms to assume that two setae developed *de novo* at CI, i.e. setae II and VII (p. 230). This contradicts his later statement (p. 232) that seta VII already appears at NIII in Oligoarthra, representing the only caudal ramus element that can be traced with certainty from the naupliar to the copepodid phase without the need of supporting evidence from intermoult stages.

Huys & Böttger-Schnack (1994) proposed an alternative scenario for caudal ramus development based on the study of intermoult stages of *Macrosetella gracilis* (Dana, 1847). They unequivocally demonstrated that no setal displacement takes place around the rear margin of the caudal ramus between CI and CII and that the longest seta in the former (seta VI) is not homologous to the longest seta in the latter (seta V). Since extreme reduction of the inner branch of the seta-complex coincides with extensive elongation of the outer branch it is clear that size in itself is not a reliable criterion for correct homologization between stages. Huys & Böttger-Schnack (1994) did not reject Dahms' (1992, 1993a) proposed patterns of caudal ramus development, presuming that deviations may occur in certain groups. New evidence accumulated since demonstrates that Dahms' assumptions are no longer tenable and that Huys & Böttger-Schnack's scenario is applicable to most harpacticoid families, if not the entire Oligoarthra.

The presence of only one principal seta (or branch) in the early copepodids has undoubtedly played a deceptive role in past attempts to homologize the setae around the posterior margin. Given that the total number of setae remains constant between CI and CII, the difference in position of the principal seta could only be explained by accepting that some degree of displacement of individual setation elements had occurred (Dahms, 1992, 1993a), or alternatively and more implausible, by assuming that there is a loss of the outer distal seta (IV) and a synchronous gain of the inner terminal seta (VI) at CII (Fiers, 1996; George, 2001). In both assumptions the fate of seta IV and the homology of the principal seta between CI and CII are central. The latter cannot only be falsified by the examination of intermoult stages (Huys & Böttger-Schnack, 1994) but the true ontogenetic trajectory of seta IV can also be traced by using a particular reference point. In the majority of harpacticoid copepods setae IV and V can readily be identified by the presence of predesigned fractures planes around the base

(Fig. 8E). Vertical backtracking of seta IV in *Microarthridion* sp. shows that this fracture plane first appears at CIII (Fig. 8A-E). At this stage seta VI has the same characteristic form and shape as in the adult, a condition which is already attained by CII when seta IV is much smaller than in the successive stages. Further backtracking to CI (Fig. 8A) demonstrates that seta IV is even more minute and cannot possibly be homologous with the outer branch of the setal complex. This outer branch is not only distinctly longer but also lacks a fracture plane. To homologize this branch with seta IV (Dahms, 1992, 1993a) would mean that it undergoes gross reduction at CII and subsequently enlarges again to its original size at CIII. This is extremely unlikely and is incongruent with the results obtained from intermoult stages. The principal seta (or inner branch of the setal complex) at CI can be identified as seta VI and is about twice the length of the inner branch (seta V). At CII (Fig. 8B) the latter acquires the fracture plane and dramatically increases in length, whereas seta VI undergoes extreme reduction in size. This pattern is not only characteristic for the Tachidiidae Sars but also for several other families such as the Diosaccidae Sars (Rosenfield & Coull, 1974), Canthocamptidae Sars (Itô & Takashio, 1981), Tisbidae Stebbing (Dahms & Bergmans, 1988), Parastenheliidae Lang (Dahms, 1993a) and Harpacticidae Sars (Itô & Fukuchi, 1978). The same pattern is found in the Cletodidae T. Scott (Fiers, 1991b, 1996) except that seta IV fuses to seta V at CII and retains its original minute size during the succeeding stages (Fiers, 1991b, 1996). In some harpacticoids (Fig. 8F) setae IV and V fuse at the terminal moult. This is a novel character acquired typically at the final moult and not a juvenile attribute (see also *Cerconeotes* Huys, 1992).

Conroy-Dalton & Huys (2000) questioned George's (1998) interpretation of the caudal ramus in *Breviconia australis* (George, 1998). The author claimed that this species possessed only 6 setae and inferred from their individual positions that seta IV is absent and seta II is displaced to the hind margin. In accordance with the high conservativeness in the caudal ramus setal pattern within the *Ancorabolus*-lineage, Conroy-Dalton & Huys (2000) suspected that seta I was overlooked in George's (1998) original description and figures, accounting for the erroneous homologization of setae II-IV. In a recent paper, George (2001) rejects this criticism and attempts to reinforce at length his earlier conviction by incorporating ontogenetic data. However, since he erroneously assumed that seta VI is missing at CI, all other setae (except VII) were also incorrectly identified at this stage. This error is perpetuated in his interpretation of the CII condition where he invokes the loss of seta IV and the simultaneous expression of seta VI as the explanation for the "constant" relative position of the single principal seta. In reality, the

ancorabolid ontogenetic pattern is identical to that of the Cletodidae. The element identified by George (2001) as the tube pore in close proximity to seta "I" in *A. ilvae* is most likely seta I whereas his setiform element identified as seta I is in reality seta II.

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