The phylogenetic position of the bathyal harpacticoids *Aspinothorax* gen. n. and *Styracothorax* HUYS (Crustacea: Copepoda)

by Gisela MOURA & Pedro MARTÍNEZ ARBIZU

Abstract

Aspinothorax insolentis gen. et sp. n. is described from abyssal sites in the Laptev Sea (Arctic Ocean). The new genus is closely related to *Styracothorax* HUYS. The presence of a characteristic sexual dimorphism on endopod of the second leg of male *Aspinothorax* gen. n. demonstrates its phylogenetic relationship with *Idyella* (Idyanthinae: Tisbidae). As a consequence the harpacticoid family Styracothoracidae HUYS is rejected, and its only genus and species *Styracothorax gladiator* HUYS is transferred to the Idyanthinae together with the new genus. As a result of a re-evaluation of the family Tisbidae, the family Porcellidiidae is rejected, because its members are closely related with the tisbid genera *Sacodiscus* and *Scutellidium*.

Key-words: *Aspinothorax insolentis* gen. sp. n. Styracothoracidae, Tisbidae, Harpacticoida, Copepoda, phylogenetic systematics.

Resumen

Se describe *Aspinothorax insolentis* gen et sp. n. colectado en una estación abisal en el Mar de Laptev (Océano Artico). El nuevo género está emparentado con *Styracothorax* HUYS. La presencia de un característico dimorphismo sexual en el endópodo de la segunda pata en el macho de *Aspinothorax* demuestra la relación filogenética con *Idyella* (Idyanthinae: Tisbidae). En consecuencia la familia Styracothoracidae HUYS debe ser abolida y su único género y especie *Styracothorax gladiator* transferida junto con el nuevo género a los Idyanthinae. Como resultado de una reevaluación de la familia Tisbidae, se propone la abolición de la familia Porcellidiidae, ya que sus miembros están intimamente emparentados con géneros de Tisbidae *Sacodiscus* y *Scutellidium*.

Palabras llave: *Aspinothorax insolentis* gen. sp. n. Styracothoracidae, Tisbidae, Harpacticoida, Copepoda, sistemática filogenética.

Introduction

Harpacticoid copepods are usually the dominant arthropod group in marine benthic habitats. They have been reported from shallow waters to depths greater than 10,000 m (BELYAEV, 1972). Deep-sea harpacticoid species usually belong to the families Argestidae (e.g. *Argestes*, *Mesocletodes*), Paranannopidae (e. g. *Cylindronannopus*, *Bathypsammis*, *Pseudomesochra*), Tisbidae Idyanthinae (e. g. *Zosime*), and Cerviniidae (e. g. *Pontostratiotes*) (e. g. BECKER, 1972, 1974; DINET, 1978; ITÔ, 1982, 1983). Recently a new deep see family, Styracothoracidae has been described (HUYS, 1993) on the base of a single female specimen collected from an abyssal site off the Philippine west coast. In the course of study of Arctic copepod biocenoses, minute harpacticoid specimens were discovered in deep waters of the Laptev Sea. Close examination of these specimens revealed them to belong to a new genus *Aspinothorax* gen. n., closely related to *Styracothorax* HUYS. The discovery of male *Aspinothorax* gen. n. allows a re-evaluation of the phylogenetic position of *Styracothorax*, to be discussed in the present contribution.

The currently accepted system of Harpacticoida is based on LANG (1948). Unfortunately, LANG's system was not produced using the methods of the phylogenetic systematic (e. g. HENNIG, 1982), therefore it contains some polyphyletic and paraphyletic groups. In the present contribution the families Tisbidae (in the sense of LANG, 1948) and Porcellidiidae are re-evaluated using a phylogenetic argumentation.

Material and Methods

Meiofauna samples were taken during the German-Russian expedition to the Arctic Ocean ARK-IX/4 (Aug./Sept. 1993), on board of RV *Polarstern*, using a Multicorer and a Giant-Box-Corer. Samples were fixed immediately after collection using formalin at a final concentration of about 4%. Specimens were extracted by differential flotation using Levasil and transferred to glycerine for slide preparation. All drawings were made with a Leitz Dialux phase contrast microscope using a camera lucida. The type material is stored in the Senckenberg Museum in Frankfurt, Germany.

Description

Aspinothorax gen. n.

Harpacticoida Oligoarthra. First thoracic somite fused to cephalosome. Rostrum small, fused to cephalothorax (Fig. 8 D). Furca about 14 times longer than median wide, with 7 setae. Male antennule 10-segmented, with aesthetascs on 6th and distal segments. Female antennule 7-segmented, with aesthetascs on 4th and distal segments. Antennary exopod 1-segmented, carrying 6 setae. Mandibulary exopod 1-segmented, with 5 setae. Maxillulary exopod with 3 setae. Maxilliped coxa with 2 setae, basis asetose, first and second endopodal segments not separated, with 2 claw-like setae subterminally and 2 slender setae terminally. Leg 1 with 2-segmented exopod and 1-segmented endopod, second exopodal segment with 7 bipinnate setae. Leg 2 with 3-segmented exopod and 2-segmented endopod, distal endopodal segment with 3 inner, 2 terminal and 1 outer seta in female; sexually dimorphic in male, with outer seta transformed into a short apophysis, outer terminal seta minute, and without inner setae. Leg 3 with 3-segmented exopod and 2-segmented endopod. Leg 4 with 2-segmented exopod and 1-segmented endopod. Leg 5 with fused coxa, basis, exopod and endopod; female with 1 outer basal seta, 3 exopodal setae and 1 endopodal seta; male as female, but with 4 exopodal setae. Leg 6 asetose in both sexes.

TYPE SPECIES

Aspinothorax insolentis sp. n.

ETYMOLOGY

The generic name is built by combining the Latin lexemes «*a*», «*spina*» and «*thorax*», meaning «back without spikes», and makes reference to the absence of horn-like processes on tergites, that are characteristic of its closest relative *Styracothorax* HUYS.

Aspinothorax insolentis sp. n.
(Figs 1-9)

MATERIAL

Holotype one female, collected in the continental slope of the Laptev Sea at a depth of 3,428 m, September the 3rd 1993 (coordinates 79°39,00'N, 130°36,10'E), dissected and mounted in 18 slides (coll. no. SMF 28977), allotype one male collected in the continental slope of the Laptev Sea at a depth of 3,211 m, September the 12th 1993 (coordinates 79°07,72'N, 122°52,10'E), dissected and mounted on 6 slides, (coll. no. SMF 28978).

FEMALE

Body length 340 μm from tip of rostrum to posterior rim of telson (Fig. 1 A-B). Furca elongate, about 14 times longer than median wide, ornamented with longitudinal rows of spinules, with 7 setae. Two setae inserting on outer margin, 2 setae subterminally on dorsal margin, 3 setae terminally (Fig. 7 A-B).

Antennule 7-segmented, setal formula beginning with proximal segment 1, 6, 3, 2 + aesthetasc, 1, 2, 9 + aesthetasc (Fig. 6 B). Seta on first segment arising from a horn-like pointed process. Similar but minor processes on segments 2, 3, 4, and 5.

Antenna (Fig. 2 A) with defined asetose coxa and basis, and 2-segmented endopod. First endopodal segment with one outer seta pointing to inner margin, second compound segment ornamented with rows of spinules, with 3 lateral and 7 terminal setae. Exopod elongate, 1-segmented, with 3 lateral and 3 terminal setae.

Mandible (Fig. 3 B), basis with 3 lateral setae, endopod 1-segmented, with 1 lateral and 5 terminal setae. Exopod elongated, 1-segmented with 3 lateral and 2 terminal setae.

Maxillule (Fig. 2 C), praecoxal arthrite with 10 terminal spines and 2 surface setae, coxal endite with 1 spine and 5 setae. Basis and endopod indistinctly fused with a total of 12 setae, exopod bearing 3 setae.

Maxilla (Fig. 3 A), syncoxa with 4 endites. Proximal endites fused together, with 3 setae and 2 setae and a claw. Distal endites with 2 setae and a claw each. Baseoendopod with one strong claw flanked by 3 setae, additionally with 3 endopodal slender setae on inner margin, and one endopodal seta on anterior distal margin. Endopod indistinctly 3- segmented, with 2 geniculated setae on proximal and middle segments and one geniculated seta and 3 slender setae on distal segment.

Maxilliped (Fig. 2 B), syncoxa with 2 pinnate setae on inner margin. Basis asetose, with rows of spinules along outer and inner margins. Endopod 1-segmented with a claw arising from anterior margin on the middle of the segment, a stronger claw subterminally on inner margin and 2 slender setae terminally, which are apparently confluent at base.

Leg 1 (Fig. 4 A) with well developed praecoxa, coxa and basis. Basis slightly transversely elongated, with an inner spine arising from a small protuberance and one outer seta. Endopod 1-segmented with 4 bipinnate setae. Exopod 2-segmented, proximal segment with outer bipinnate seta, distal segment with 7 setae in total, all of them being slender and bipinnate.

Leg 2-4 (Figs. 5 A-B, 6 A) with transversely elongated bases, outer basal setae arising from a small protuberance on anterior margin.

Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
leg 1	0-0	1-I	1-0; 3,1,3	1,1,2
leg 2	0-0	1-0	I-1; I-1; III,I,3	0-1; 1,2,3
leg 3	0-0	1-0	I-1; I-1; II,I,4	0-1; 0,2,2
leg 4	0-0	1-0	I-0; III,I,2	0,1,2

Fifth leg with baseoendopod and exopod fused together (Fig. 7 A-B), bearing one outer basal seta, 3 setae on the exopodal lobe, and 1 seta on the endopodal lobe. With one
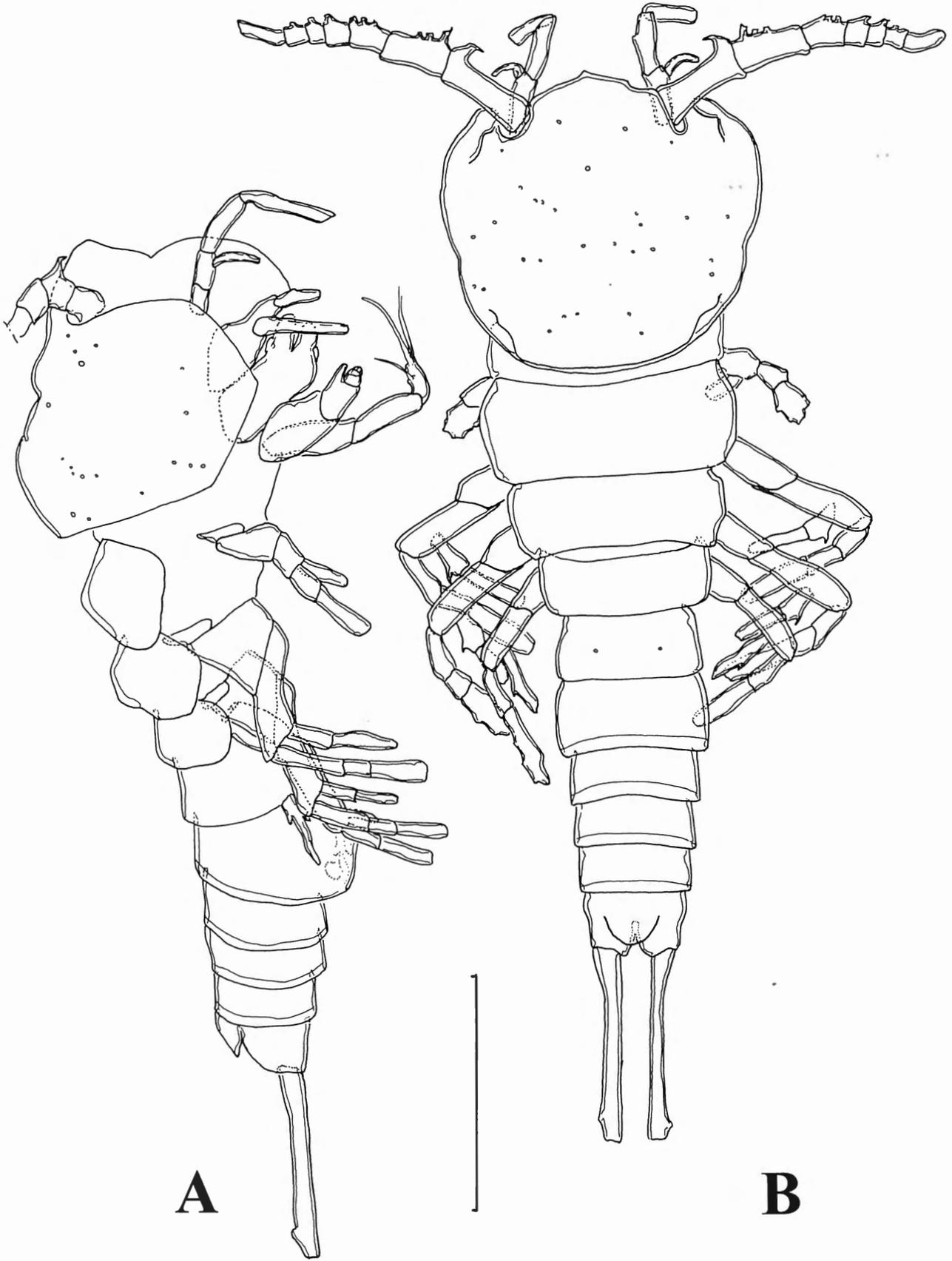
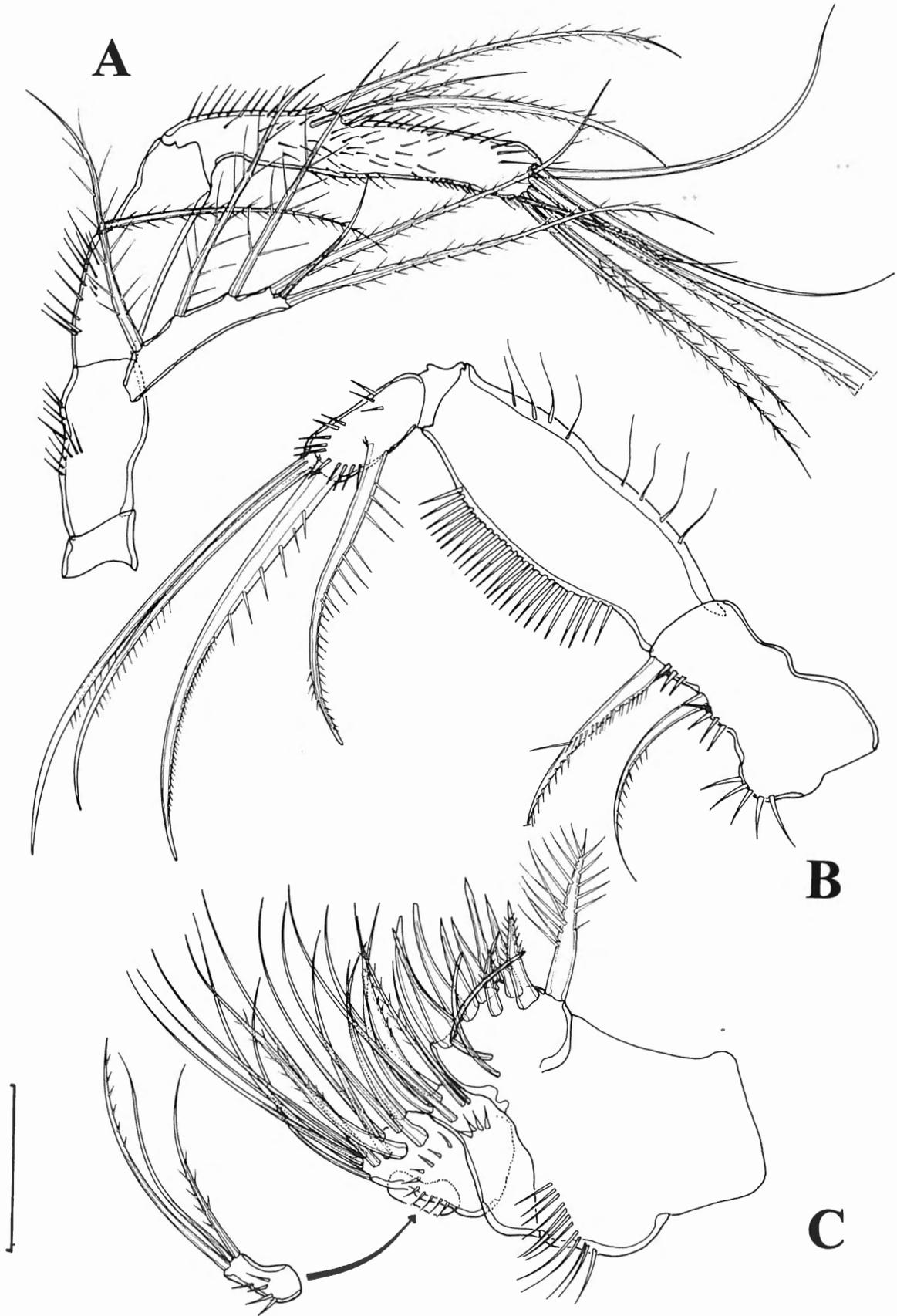Fig. 1. *Aspinothorax insolentis* gen. et sp. n. Female habitus. A: lateral view, B: dorsal view. Scale bar 100 μm.

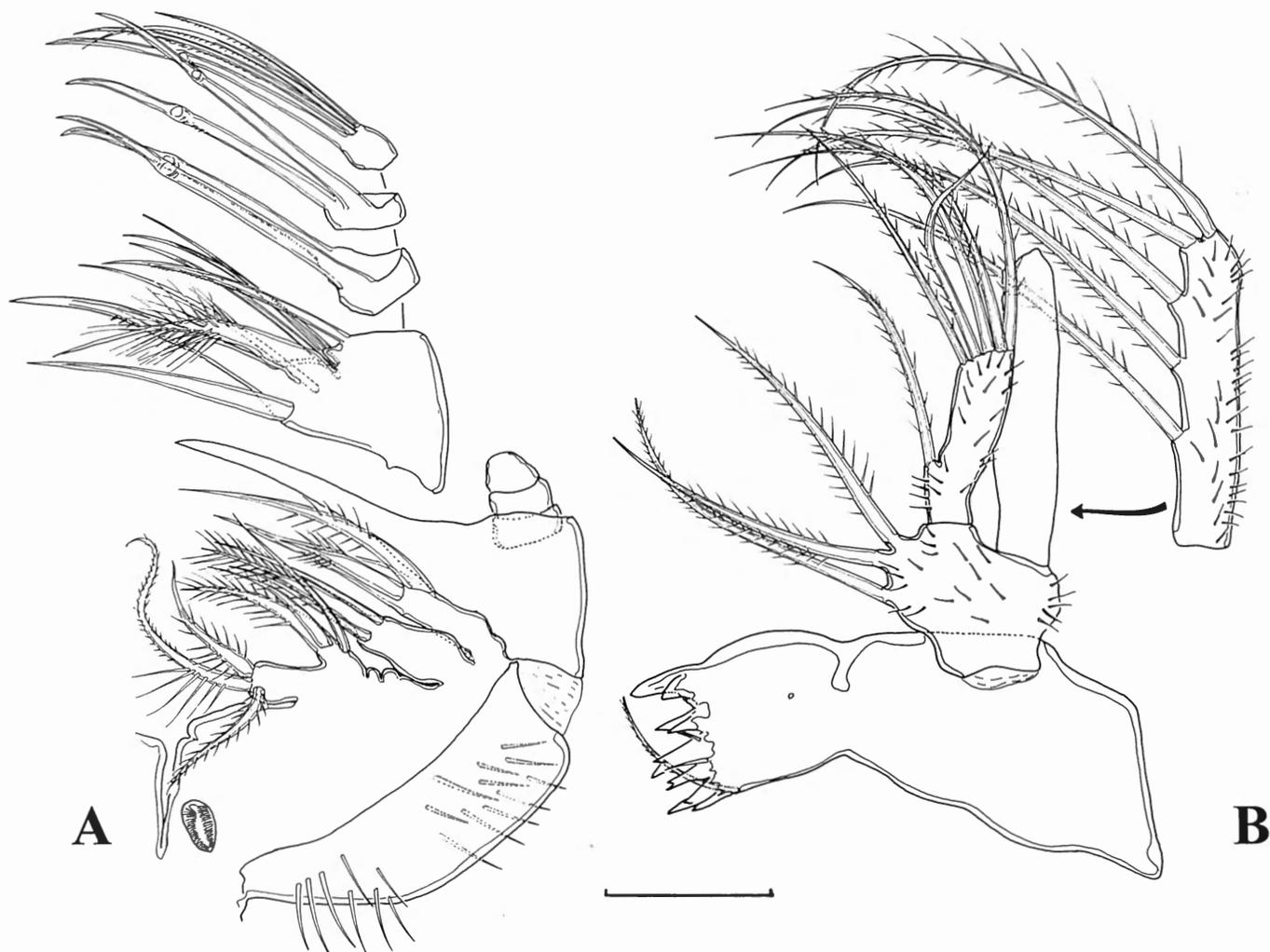Fig. 2. *Aspinothorax insolentis* gen. et sp. n. Female. A: Antenna, B: Maxilliped, C: Maxillule. Scale bar 20 μm.

Fig. 3. *Aspinothorax insolentis* gen. et sp. n. Female. A: Maxilla, with disclosed baseoendopod and endopal segments, B: Mandible, with disclosed exopod. Scale bar 20 μm.

integumental pore beneath the outer basal seta on anterior margin. Intercoxal sclerite not discernible.

Genital somite produced ventrally, not fused to first abdominal somite (Fig. 7 B). Genital pore and setae representing sixth legs not discernible. Seminal receptacle bilobate (Fig 7 A).

MALE

Differing from female in the following characters:

Body length 250 μm from tip of rostrum to posterior rim of telson.

Antennule 10-segmented (Fig. 8 C), setal formula beginning with proximal segment 1, 1, 5, 5, 1, 4 + aesthetasc, 2, 5, 3, 9 + aesthetasc.

Endopod of second leg 2-segmented (Fig. 8 A-B). Proximal endopodal segment with 1 inner seta, distal segment consisting of fused middle and distal segments of a 3-segmented endopod. Proximal part corresponding to middle endopodal segment with 2 inner setae, distal part corresponding to distal segment with a strongly pointed cuticular outgrowth on outer distal margin, outer seta transformed into a bulbous spine,

outer terminal seta extremely reduced, having the appearance of a little spiniform process, inner terminal seta normally developed, inner setae absent.

Fifth leg with an additional seta on proximal inner margin of the exopodal lobe (Fig. 9 A).

Genital somite with rudimentary sixth legs forming two asetose plates (Fig. 9 A-B). One spermatophore.

ETYMOLOGY

The specific name is derived from the Latin «*insolens*» meaning «impertinent», and makes reference to the unexpected taxonomic changes provoked by its discovery.

Discussion

THE PHYLOGENETIC POSITION OF *ASPINOTHORAX* GEN. N.

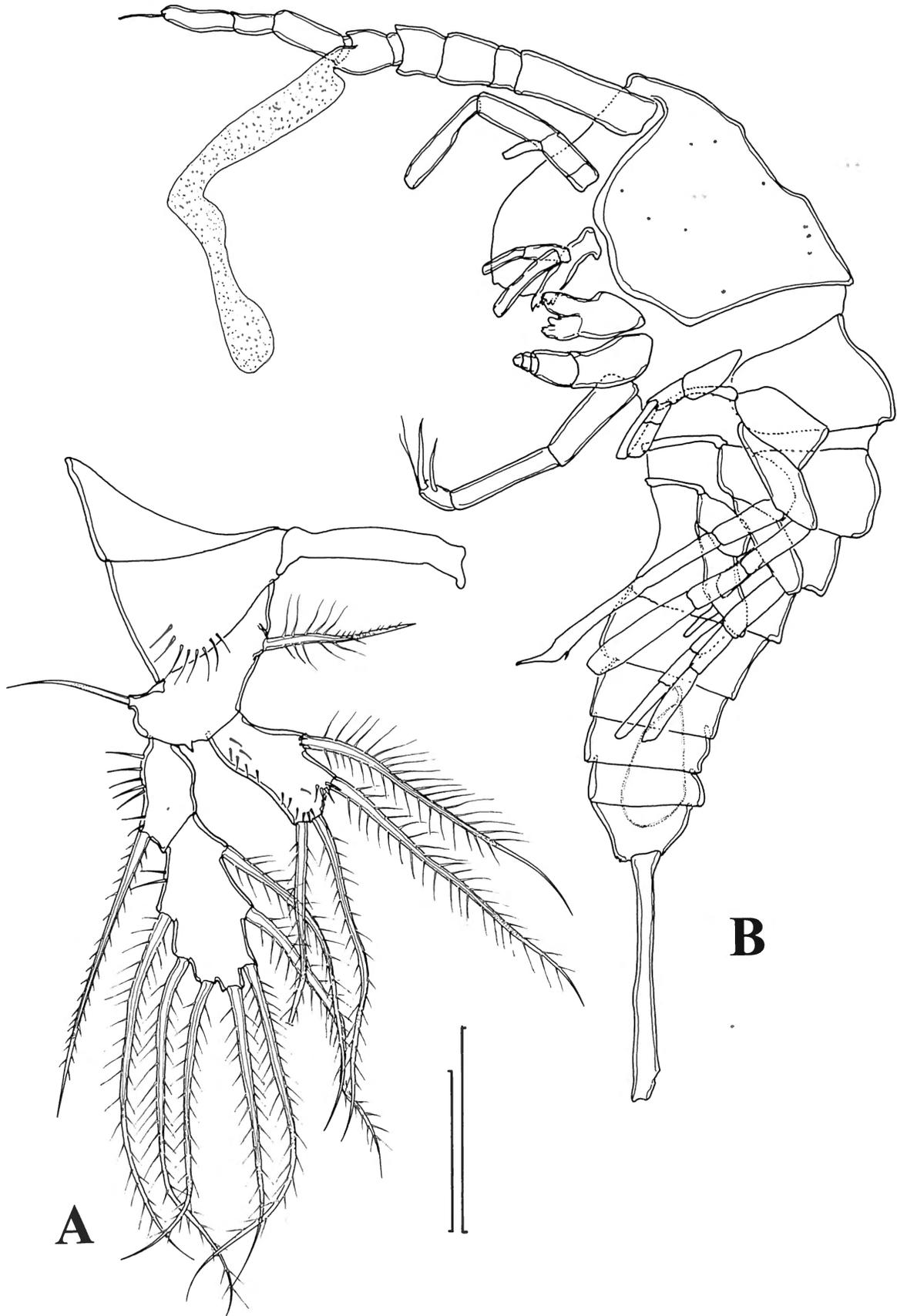*Aspinothorax* gen. n. resembles *Styracothorax* Huys in many respects. The female antennule is 7-segmented in both

Fig. 4. *Aspinothorax insolentis* gen. et sp. n. Female, A: first leg. Scale bar (left) 20 μm. Male, B: habitus, lateral view. Scale bar (right) 50 μm.
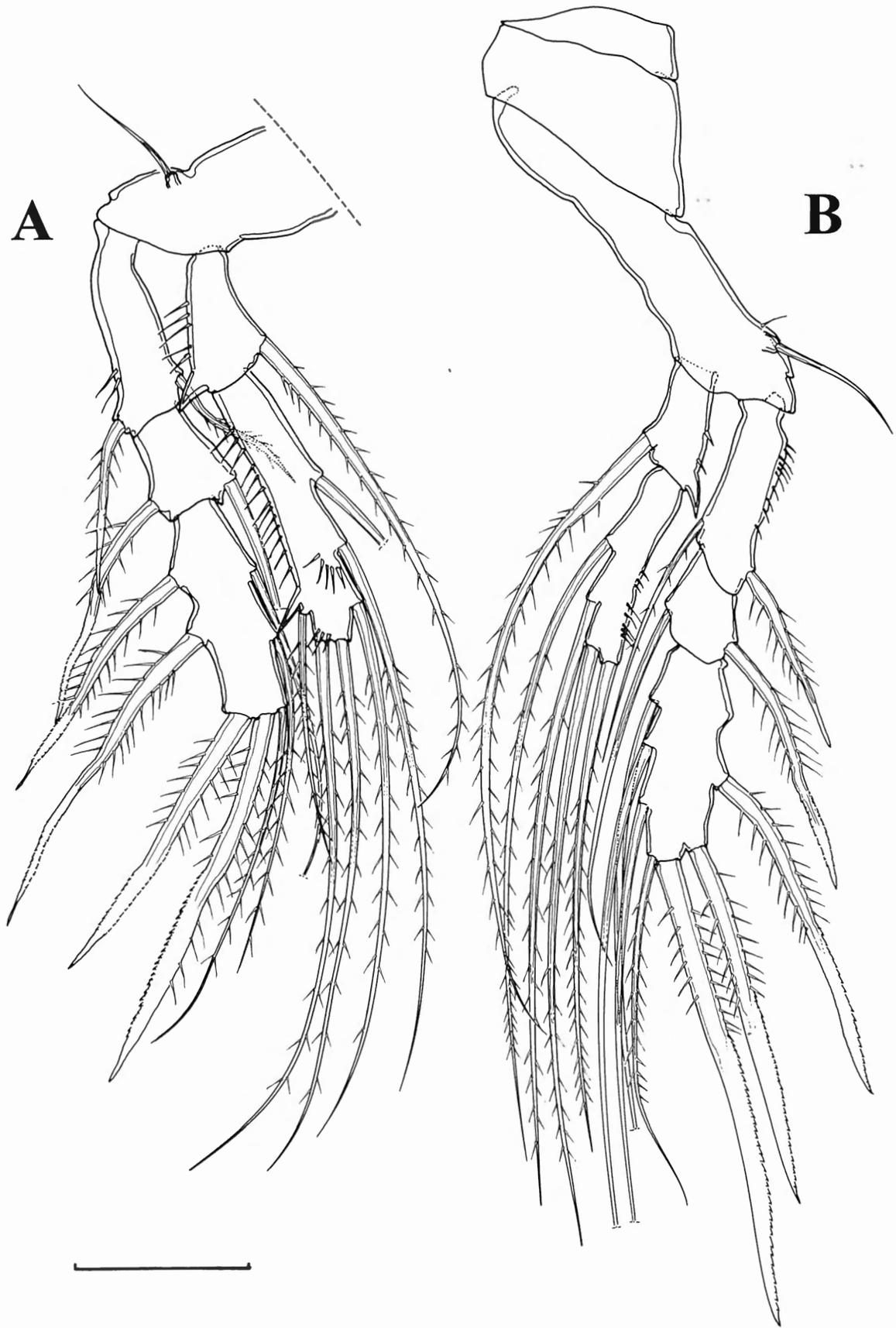
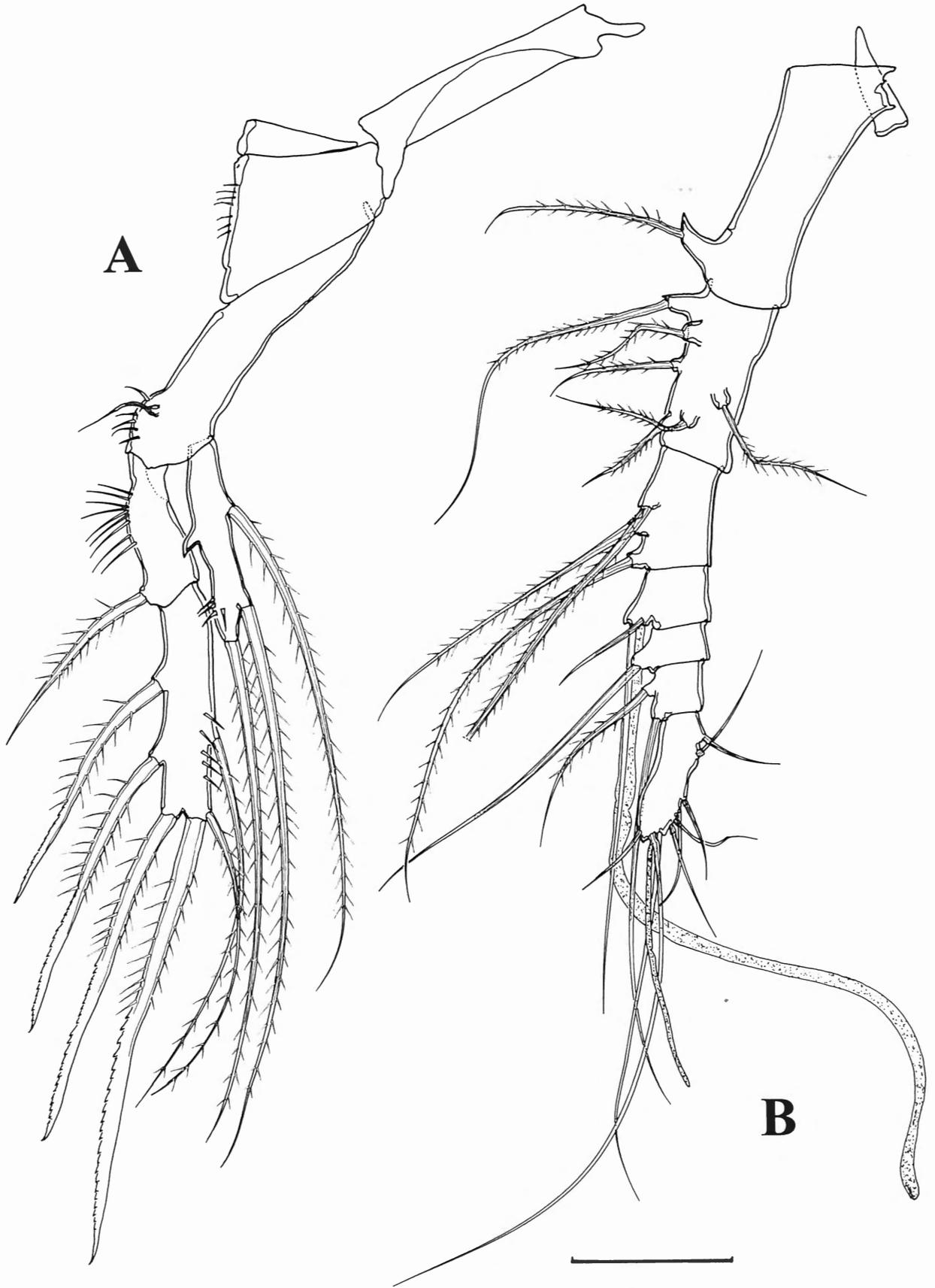Fig. 5. *Aspinothorax insolentis* gen. et sp. n. Female. A: leg 2, B: leg 3. Scale bar 20 μm.

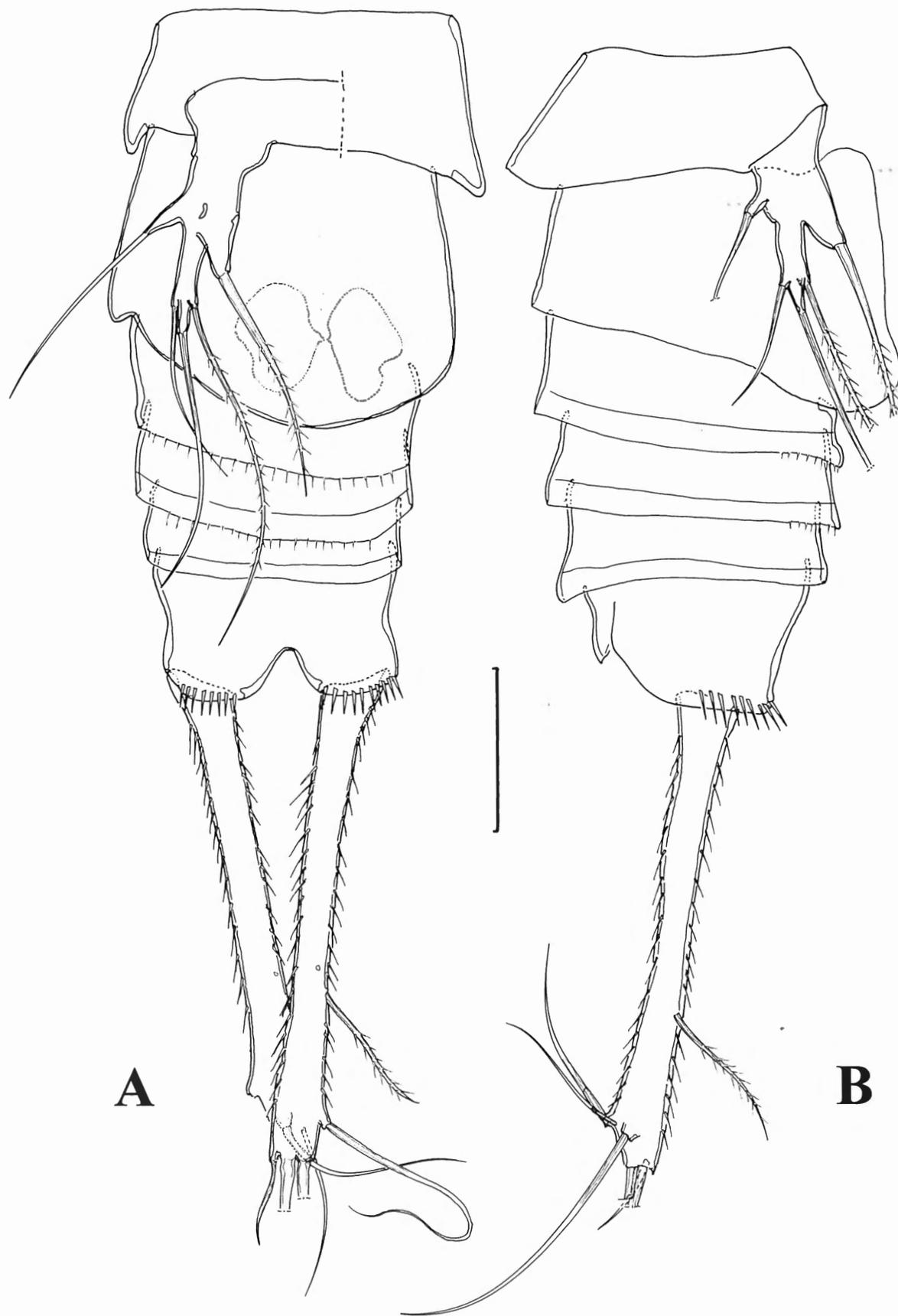Fig. 6. *Aspinothorax insolentis* gen. et sp. n. Female, A: leg 4. Male, B: Antennule. Scale bar 20 μm.

Fig. 7. *Aspinothorax insolentis* gen. et sp. n. Female. A: urosome and leg 5, ventral view, B: urosome and leg 5, lateral view. Scale bar 20 µm.
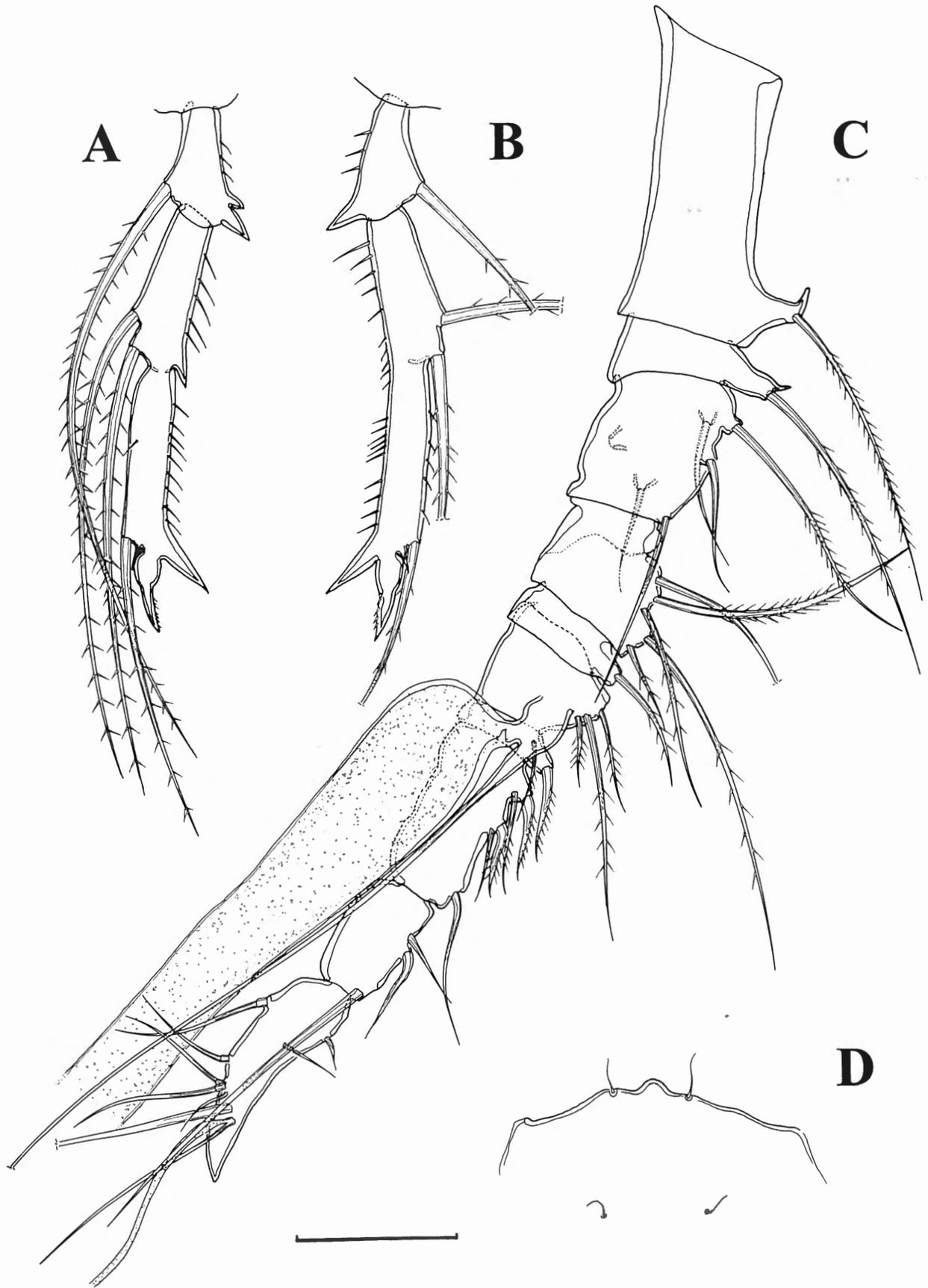
Fig. 8. *Aspinothorax insolentis* gen. et sp. n. Male, A: left endopod leg 2, B: right endopod leg 2, C: Antennule. Female, D: rostrum. Scale bar 20 μm.
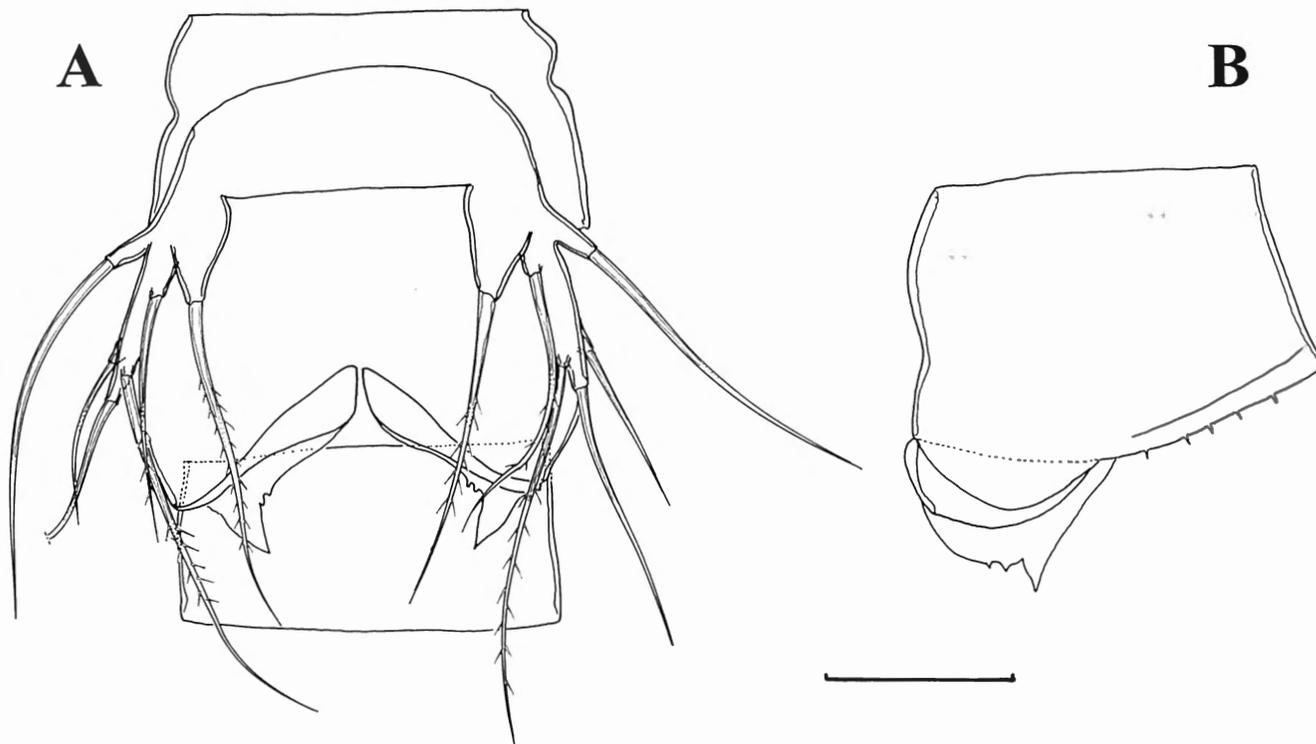
Fig. 9. *Aspinothorax insolentis* gen. et sp. n. Male. A: Leg 5 and leg 6, ventral view, B: Leg 6, lateral view. Scale bar 20 μm.

genera, these segments being homologue, although *Aspinothorax* gen. n. has less armature elements in some segments. The setae on the antennulary segments arise from protuberances on the dorsal surface in both genera.

The antenna is almost identical in both genera, including an asetose coxa and basis, first endopodal segment with 1 seta bending inwardly to inner margin, and second endopodal segment with 3 setae laterally and 7 setae terminally. The antennary exopod is 1-segmented in both genera, but *Aspinothorax* gen. n. displays 6 setae, while only 2 setae are present in *Styracothorax*.

The mandible is very similar in these genera, having a biramous palp, although some differences have to be noticed. In *Aspinothorax* gen. n. the basis has 3 setae, while no seta is present in *Styracothorax*; the 1-segmented endopod bears 1 lateral and 5 distal setae in *Aspinothorax* gen n., while 2 lateral and 4 distal setae are present in *Styracothorax*, and the exopod consists of an elongate segment with 3 lateral and 2 distal setae in *Aspinothorax* gen. n., while in *Styracothorax*, it consists of a proximal elongated segment bearing 4 lateral setae and a small distal segment with 2 setae.

Maxillule and Maxilla are almost identical in these genera. A striking similarity is the structure of the surface setae on the maxillulary praecoxal arthrite, the proximal surface seta being geniculated in both genera. The maxillule of *Aspinothorax* gen. n. differs from that of *Styracothorax* in that the endopod is apparently confluent with the basis and the exopod bears 3 setae in the first genus, while the endopod is defined, and the exopod bears 2 setae in the latter genus. The maxillary baseoendopod of Aspinothorax gen. n. displays a total of 7 setae in addition to the claw, while only 6 setae and a claw are present in Styracothorax. Remarkably, Aspino-

thorax is the first Harpacticoida known to display the full arrangement of 4 armature elements on the first maxillary endopodal segment, a character previously known from calanoid copepods only. Similar in *Aspinothorax* gen. n. and *Styracothorax* is the presence of an allobasis and an indistinctly 3-segmented endopod.

The maxilliped is completely homologue in terms of segmentation and setation in *Aspinothorax* gen. n. and *Styracothorax*. It consists of a syncoxa with 2 setae, an asetose basis and a 1-segmented endopod bearing 4 elements. The distal claw of *Styracothorax* is homologue with the subdistal claw of *Aspinothorax* gen n., while both the proximal claw and the terminal setae of *Aspinothorax* gen. n. are reduced in size in *Styracothorax*.

The swimming legs are very alike in these genera, both having a reduced first leg, and legs 2-4 with transversely elongated bases. The first leg has a 2-segmented exopod which is not a common character within Harpacticoida; all outer setae of exopod segments 1 and 2 are transformed into flexible bipinnate setae, while these elements are rigid spines in the ground pattern of Harpacticoida. The endopod of the first leg is 2-segmented, with 1 and 3 setae in *Styracothorax*, while it is 1-segmented with 4 setae in *Aspinothorax* gen. n. Legs 2-4 differ in segmentation and setation in these genera, *Aspinothorax* gen. n. displaying a derived condition.

A remarkable similarity is present between the female fifth legs of these genera. In both genera baseoendopod and exopod are fused to form an elongated plate having a proximal outer basal seta and three exopodal setae terminally. Differences in this limb are that *Styracothorax* has an additional outer exopodal seta proximally and no endopodal seta, while *Aspinothorax* gen n. has no proximal exopodal seta, but an

endopodal element is present. The conical process at about one-third distance from base on inner margin present in *Styracothorax* is, without any doubt, homologue with the endopodal lobe as present in *Aspinothorax* gen. n.; the pore on the tip of this process being the insertion point of the endopodal seta, which is absent or lost in *Styracothorax*.

As for genital field structures, both genera exhibit circular seminal receptacles, but no setae corresponding to sixth legs could be discerned in *Aspinothorax* gen n., while 3 setae are present in *Styracothorax*. In addition, in *Styracothorax*, as in the great majority of harpacticoids, female genital somite is fused with the first abdominal somite to form a genital double-somite. This is not the case in *Aspinothorax* gen. n., where these somites are completely separated. We interpret this as a secondary condition. Secondary absence of genital double-somite has been reported from some harpacticoids belonging to the families Latiremidae and Cancrincollidae. Own observations reveal a secondary absence of a genital double-somite in the diosaccid *Psammotopa* also. According to FIERS (1990) the absence of a genital double somite can be the result of a failure of fusion during ontogeny, as the genital somite becomes fused to the first abdominal somite only during the last moult from copepodid V to the adult.

Finally, both genera have a rostrum confluent with cephalothorax, although they are very different in shape, and the furca of *Aspinothorax* gen. n. is elongated, while it is almost quadratic in *Styracothorax*.

By far the most evident difference between these genera is the presence of elaborate conical processes on the tergites of *Styracothorax*, which are not present in *Aspinothorax* gen. n. The nature of the sexual dimorphism on the second leg of *Aspinothorax insolentis* gen. et sp. n. is the clue to the phylogenetic position of this genus, and by extension of the genus *Styracothorax*. In male *Aspinothorax* gen n. the endopod of second leg displays following modifications on distal segment i) outer outgrowth of the segment more strongly developed than in female, ii) outer seta transformed into a spine, confluent with the segment, iii) outer terminal seta very reduced in size, having the appearance of a little spine, confluent with the segment, and iv) loss of 2 inner setae, which are homologous with the inner setae of the distal endopodal segment of a 3-segmented limb. The 2 proximal inner setae present in *Aspinothorax* gen. n. are homologous with the 2 inner setae present on the middle segment of a 3-segmented limb. This is evidenced by the presence of suture lines on the posterior surface of the second endopod segment, demarcating the former division of the middle and the distal endopods of a 3-segmented limb, and by the presence of spinous outgrowth at midlength on outer margin on the endopod of left leg (Fig. 8 A), obviously being homologue to the distal outer outgrowth of the middle segment of a 3-segmented limb. This type of sexual dimorphism is well known from male harpacticoids belonging to the tisbid subfamily Idyanthinae. The condition present in male *Idyella* cfr. *kunzi* (Fig. 10 B) agrees with that of male *Aspinothorax* gen. n. in every detail. Comparison with the female (Fig. 10 C) and the male fifth copepodid stage of *Idyella* cfr. *kunzi* (Fig. 10 A) allows a precise homologisation of the setae involved and shows that the final condition present in adult males is a product of a modification in 2 steps. In the first step the outer

setae becomes stout and strong, this condition is already present in the fifth male copepodid stage. The second step involves the fusion of this seta with the segment, the reduction in size of the outer terminal seta, the loss of the 2 inner setae, and the fusion of the middle and distal endopodal segments, all this fulfilled during the moult from the fifth copepodid stage to the adult. *Idyella*, as well as *Idyanthe* resembles *Aspinothorax* gen. n. and *Styracothorax* in many respects concerning the shape and armature of antenna, mouthparts, and swimming legs. Most of these characters are symplesiomorphies, so that an intensive discussion of these characters would be of less phylogenetic significance. Therefore, we will centre on only some remarkable characters that are potential synapomorphies.

In addition to the specific nature of the sexual dimorphism of the leg 2, these taxa share the presence of only 2 setae on the maxillipedal syncoxa, the loss of setae in the maxillipedal basis, the elongation of the basis on legs 2 to 4 (less pronounced in *Idyella* and *Idyanthe*), reduction of the size of the endopodal lobe of the fifth swimming leg, and the sexual dimorphism on the exopod of this limb, the male having an additional seta on proximal inner margin.

In the preceding paragraphs we have presented derived characters arguing for a sister-group relationship between *Aspinothorax* gen n. and *Styracothorax*, and, on the other hand, the phylogenetic position of *Aspinothorax* gen. n. within a monophyletic group including *Idyella* and *Idyanthe*. As a result both *Aspinothorax* gen n. and *Styracothorax* must be included into the Idyanthinae.

HUYS (1993) proposed a new family Styracothoracidae for the genus *Styracothorax*, and placed this family into the superfamily Cervinoidea. Following the arguments proposed above, the family Styracothoracidae has to be refuted. HUYS' decision to create a new family to accommodate *Styracothorax gladiator* was, in our opinion, precipitate. Not because the diagnosis of the family is based on a single specimen, but because the family was erected before the discovery of males. Morphology of male specimens in regards of the shape of the antennule and eventual sexual dimorphisms in the swimming legs are often the strongest characters to asses phylogenetic relationships at familiar and even suprafamiliar level within Harpacticoida. Even the total absence of sexual dimorphism in swimming legs (provided they have not been secondarily lost) is a powerful information, because it can exclude the specimens studied from a great number of monophyletic groups

HUYS (1993) accommodated «Styracothoracidae» within the superfamily Cervinoidea based on 4 characters, i.e. i) fusion of the rostrum with cephalosome, ii) presence of only 3 setae on lateral margin of second antennary endopodal segment, iii) maxillary exopod reduced to small trisetose lobe, and iv) fifth leg uniramous in both sexes, with no trace of baseoendopodal lobe. In our opinion, none of these 4 characters give sufficient evidence to include *Styracothorax* into Cervinoidea.

The presence of a rostrum which is confluent with the dorsal margin of the cephalosome is a character difficult to polarize. The rostrum is articulated in a great number of harpacticoid families (LANG, 1948) including for instance Canuellidae, Longipediidae, Paranannopidae, Diossaccidae, Ameiridae,
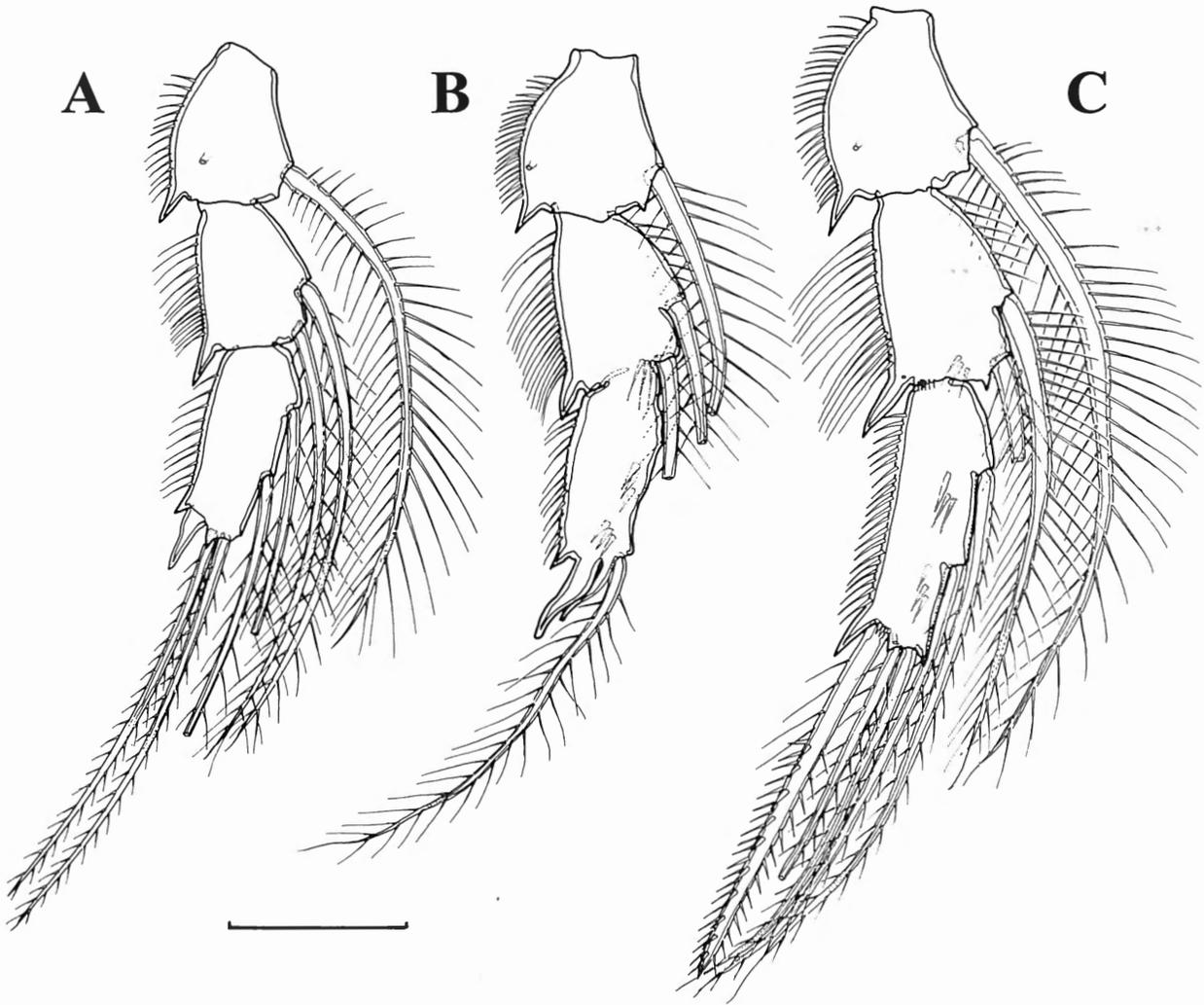
Fig. 10. *Idyella* cfr. *kunzi*. A: Male copepodid V, endopod of leg 2, B: adult male, endopod of leg 2, C: adult female, endopod of leg 2. Scale bar 20 μm.

and Lourinidae, but it is confluent with the cephalosome in a great number of relatively primitive families including Tisbidae, Paramesochridae, Cerviniidae, Chappuisiidae, Phyllognathopodidae, Neobradyidae, etc. The rostrum is not articulated in copepods belonging to the orders Platycopioida, Cyclopoida, Mormonilloida, Mostrilloida, Siphonostomatoida, and in most Calanoida and Misophrioida, so that we may conclude from outgroup comparison that this condition is symplesiomorphic for Harpacticoida as well. The presence of a non-articulated rostrum in Cervinidae, Aegesthidae and *Styracothorax*, when being considered a symplesiomorphy, has no phylogenetic value.

The presence of only 3 setae on the lateral margin of second antennary endopodal segment is an autapomorphy compared with up to 5 setae present at this site in Polyarthra, but this reduction has developed convergently in different harpacticoids lineages, being present, for instance, in *Idyella*, *Idyanthe*, *Aspinothorax* gen. n. and *Styracothorax*.

The third character i.e. maxillulary exopod reduced to a small trisetose lobe is also shared by the members of the Idyanthinae (at least described for *Idyella* and *Idyanthe* so

far), and is therefore a weak indicator of a cervinoidean affinity in *Styracothorax*.

Finally, the complete absence of baseoendopodal lobe in the fifth leg is, in our opinion, a character not shared by *Styracothorax*, because, as argumented above, the conical process on the inner margin of its fifth leg is homologue with the baseoendopodal lobe.

Recently, Seifried (2003) provided independent evidence to exclude «Styracothoracidae» from Cervinoidea.

REMARKS ON LANG´S TISBID CONCEPT

In Lang´s (1948) concept the Tisbidae consisted of two subfamilies, i. e. Tisbinae and Idyanthinae. These subfamilies evolved from an «ancestral form» that combines the primitive characters of both lineages. According to Lang, the Tisbinae are characterized by the presence of 2 inner setae on middle endopodal segment of leg 4, the absence of sexual dimorphism on leg 2, and the presence of only 2 endites on maxillary protopod. The Idyanthinae are characterized by the presence of only 1 inner seta on middle endopodal segment

of leg 4, the presence of sexual dimorphism on leg 2, and the presence of 4 endites on maxillary protopod. Despite the fact that the diagnoses of both subfamilies include potential apomorphic characters, no evidence was provided by Lang to demonstrate the sistergroup relationship of this subfamilies, i. e. the monophyly of the family Tisbidae. We have also been unable to discover any synapomorphic character and thus we believe that Tisbinae and Idyanthinae are unrelated phylogenetically. On the other hand, Idyanthinae (including *Aspinothorax* and *Styracothorax*) shares the reduction in size of the terminal outer seta on male distal segment of leg 2 endopod with Rhyncothalestridae (sensu WILLEN, 2000) and Tachidiidae (LANG, 1948), which may be interpreted as a synapomorphy of these families.

The sistergroup of the Tisbidae is the family Porcellidiidae SARS according to Lang. Porcellidiidae are characterized by an elipsoid, dorso-ventrally flattened habitus and by an elaborated sucker that allows them to attach to algae or other substrates. The morphology and histology of the porcellidiid sucker was studied in detail by TIEMANN (1984). Labrum (anteriorly), mandibulary palps (laterally), and first legs (posteriorly) form a ring, that is sealed by acid mucopolysaccharides attached to the strongly pinnate setae on these appendages and modified spinules on labrum; a ring of strong muscles lift the center of the sucker, causing the necessary low pressure inside it to produce the adhesive effect. Maxillule, maxilla, and maxillipeds are not involved in forming the sealing ring, yet they are located inside the sucker, which allows the animal to eat while it is attached to the substrate. In conclusion, in terms of limbs morphology, the evolution of the porcelidiid sucker requires mainly the modification of mandible and first legs. The mandibulary gnathobasis remains unchanged, while the palp becomes extremely elongated and flattened, basal endite, endopod, and exopod are armed with densely plumose setae. The first leg has a very broadened first endopodal segment, and the distal endopodal segment bears two characteristic seta, which are short but possess a dense row of long subordinate spinules, the exopods have plumose outer spines, and both sides of the first legs together have a semi-elipsoid appearance forming the posterior half of the sucking ring. However, these characteristic modifications did not evolve de novo in Porcellidiidae from a more generalized ancestral form, but are the end stage of a step by step transformation series within Tisbinae resulting in a more specialized adaptation to a phytal way of live. The specialized setae on the distal endopodal segment of leg 1 are already present in *Tisbe*, but they become more densely pinnate in *Scutellidium*. Both taxa have elongated first and second endopodal segments, but the first endopodal segment becomes broadened at its base in *Scutellidium*. Continuing this transformation series, *Sacodiscus* reduces the length of the second endopodal segment, while the first one acquires the typical trapezoidal appearence as present in *Porcellidium*. Finally, the middle endopodal segment is not present in *Porcellidium*. What concerns the mandibulary palp, preludes of the modifications present in *Porcellidium* can be discerned in *Scutellidium* and are more obvious in *Sacodiscus*. TIEMANN (1984) regarded the suckers of adult *Scutellidium* and *Sacodiscus* to be prob-

ably homologous, but not as perfectly as the sucker of *Porcellidium*. Because of these characters the familiar status of Porcellidiidae has to be reconsidered. *Porcellidium* is a highly derived genus within Tisbinae, most probably the sister-group of *Sacodiscus*. Consequently applying the methods of phylogenetic systematics, the family Porcellidiidae has to be refuted to accommodate its species within Tisbinae. Not doing so Tisbidae (Tisbinae) would remain a paraphyletic taxon. It becomes clear that the family Tisbidae deserves a phylogenetic revision, but this will only be feasible following a comprehensive revision of the Exanechentera as a whole.

Acknowledgements

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Gisela MOURA & Pedro MARTÍNEZ ARBIZU*
FB7/ AG. Zoomorphologie
Carl v. Ossietzky Universität Oldenburg,
26111 Oldenburg, Germany.

*Present address: DZMB-Forschungsinstitut Senckenberg
Schleusenstrasse 1
D-26382 Wilhelmshaven, Germany.
Email: pmartinez@senckenberg.de