



# Notes on the systematic position of the Stenheliinae (Copepoda, Harpacticoida) within the Thalestridimorpha and description of two new species from Motupore Island, Papua New Guinea

Elke WILLEN

Deutsches Zentrum für Marine Biodiversitätsforschung, c/o Carl v. Ossietzky Universität Oldenburg, AG Zoosystematik  
und Morphologie, 26111 Oldenburg, Germany

Fax: (49)-0441-798-3162 - E-mail: elke.willen@mail.uni-oldenburg.de

**Abstract:** Two new species of Stenheliinae, *Stenhelia* (*D.*) *schminkei* sp. nov. and *Melima papuaensis* sp. nov. are described from intertidal mud and algal washings from Motupore Island, Papua New Guinea. *S. schminkei* can be assigned to a species group also containing *S. clavus*, *S. paraclavus* and *S. valens* all described from the Andaman Islands. They share an apomorphic setation pattern of the swimming legs, a confluent female P5 and the special shape of the male P5. The group seems to have only a restricted distribution within the Indo-Pacific region. In describing *Melima papuaensis* sp. nov. the genus *Melima* is reinstated as a first step towards a revision of the paraphyletic genus *Stenhelia*. Autapomorphies for this taxon are defined. A key to the females of *Melima* is provided. In the course of a phylogenetic analysis of the Thalestridimorpha it turned out, that the “*Stenhelia*-group” within the traditional Diosaccidae forms a monophylum which can be assigned together with the remaining species of the Diosaccidae and the species of the former family Miraciidae to a common taxon Miraciidae within the Thalestridimorpha. A historical overview and a summary of the discussion is given and an attempt is made to identify some monophyletic subtaxa within the Stenheliinae.

**Résumé:** Notes sur la position systématique des Stenheliinae (Copepoda: Harpacticoida) dans les Thalestridimorpha et description de deux nouvelles espèces de l'île de Motupore, Papouasie Nouvelle Guinée. Deux espèces nouvelles de Stenheliinae *Stenhelia* (*D.*) *schminkei* sp. nov. et *Melima papuaensis* sp. nov. sont décrites, en provenance des algues et de la vase intertidale de l'île de Motupore, Papouasie Nouvelle Guinée. *Stenhelia schminkei* sp. nov. appartient à un groupe d'espèces contenant aussi *S. clavus*, *S. paraclavus* et *S. valens* toutes décrites des Iles Andaman. Ces espèces ont en commun des caractères apomorphes tels que la disposition des soies sur les pattes natatoires, des P5 confluentes chez la femelle et la forme spéciale des P5 du mâle. La distribution de ce groupe d'espèces paraît se limiter à la région Indo-Pacifique. Le rétablissement du genre *Melima* marque le point de départ d'une révision du genre *Stenhelia* qui est paraphylétique. Les autapomorphies de *Melima* sont définies. Une clef pour la détermination des femelles de *Melima* est donnée. Au cours d'une analyse phylogénétique récente des Thalestridimorpha il est apparu que “le group *Stenhelia*” dans la famille traditionnelle des Diosaccidae représente un taxon monophylétique qui, avec le reste des Diosaccidae et avec les espèces de l'ancienne famille des Miraciidae, forme un taxon commun du nom de Miraciidae dans les Thalestridimorpha. Un aperçu historique et un résumé de la discussion sont donnés et un premier essai est fait pour identifier des subtaxa monophylétiques dans les Stenheliinae.

**Keywords :** Copepoda, Harpacticoida, Stenheliinae, *Stenhelia*, *Melima*, Papua New Guinea, phylogeny.

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## Introduction

Several authors (Monard, 1935; Por, 1964; Wells, 1967; Dahms & Bresciani, 1993) have questioned the assignment of the “*Stenhelina*-group” (including *Stenhelina* Boeck, 1865 and the more recently described genera *Melima* Por, 1964, *Onychostenhelina* Itô, 1979 and *Pseudostenhelina* Wells, 1967) to the Diosaccidae sensu Lang (1944) and suggested to exclude it from that family because of its derived and “aberrant” morphology as compared to the other species of the Diosaccidae. However, in the first place this only means that the “*Stenhelina*-group” displays many autapomorphies which do not necessarily exclude phylogenetic relationships with the traditional Diosaccidae. To find characters linking higher taxa at different levels of inclusiveness and to reconstruct their groundpatterns in order to find monophyletic groups and to avoid typological categories, a phylogenetic study within a larger context has to be undertaken.

In the course of a phylogenetic analysis of the Thalestridomorpha Lang, 1944 (Willen, 2000), the position of the “*Stenhelina*-group” has been re-evaluated. It turned out that the “*Stenhelina*-group” indeed forms a monophyletic taxon which remains more closely related to the species of the traditional Diosaccidae than to any other taxon within the Thalestridomorpha. In what follows the discussion will be summarized and viewed in a historical context. Furthermore, the systematic status of *Stenhelina* will be discussed and an attempt be made to uncover monophyletic subtaxa within the Stenhelinae. Two new species, *Stenhelina* (*D.*) *schminkei* sp. nov. and *Melima papuaensis* sp. nov. from Motupore Island, Papua New Guinea, are described in the present paper.

## Material and methods

Holotypes and allotypes were preserved in 5% buffered formalin and subsequently transferred to glycerine. Drawings were made with the aid of a camera lucida on Leitz Diaplan microscopes equipped with a phase contrast 100x objective and with an interference contrast 100x objective, respectively. The dissected parts are mounted on several slides. All specimens are in the collection of the AG Zoosystematik und Morphologie, C.v.O. Universität Oldenburg (UNIOL).

The terminology is adopted from Lang (1948, 1965) except for the segmental composition of mandible and maxilliped and the numbering of the furcal setae, in which cases Huys & Boxshall (1991) are followed. The abbreviations used in the text and Figures are: aes: aesthetasc, benp: baseoendopodite of P5, Ceph: cephalothorax, enp: endopodite, “enp1”: first segment of

endopodite, exp: exopodite, f.r.: furcal rami, Md: mandible, Mx: maxilla, Mxl: maxillula, Mxp: maxilliped, P1-P6: swimming legs 1-6, Ro: rostrum.

The term groundpattern is used in the sense of “Grundmuster” (Ax, 1984, p.156). For type localities see descriptions of the new species. The specimens involved in the phylogenetic analyses are listed in Willen (2000).

## Descriptions

### *Stenhelina* (*Delavalia*) *schminkei* sp. nov.

Figs 1 - 8

*Type locality.* Motupore Island, near the Marine Biological Station of the University of Papua New Guinea. The sample site was intertidal, located between sandy and muddy bottom; the upper centimetres of sediment were washed in seawater. A sample was taken in autumn 1984 during high tide by Prof. H. K. Schminke. Several females and males were collected.

*Type specimens.* Female holotype, catalogue no. UNIOL 2001.018; male allotype, catalogue no. UNIOL 2001.019; one male and one female paratypes, catalogue no. UNIOL 2001.020.

*Etymology:* the species is dedicated to Prof. H.K. Schminke, Oldenburg.

#### *Description of the female holotype*

Body length (incl. ro and f. r.): 475 µm

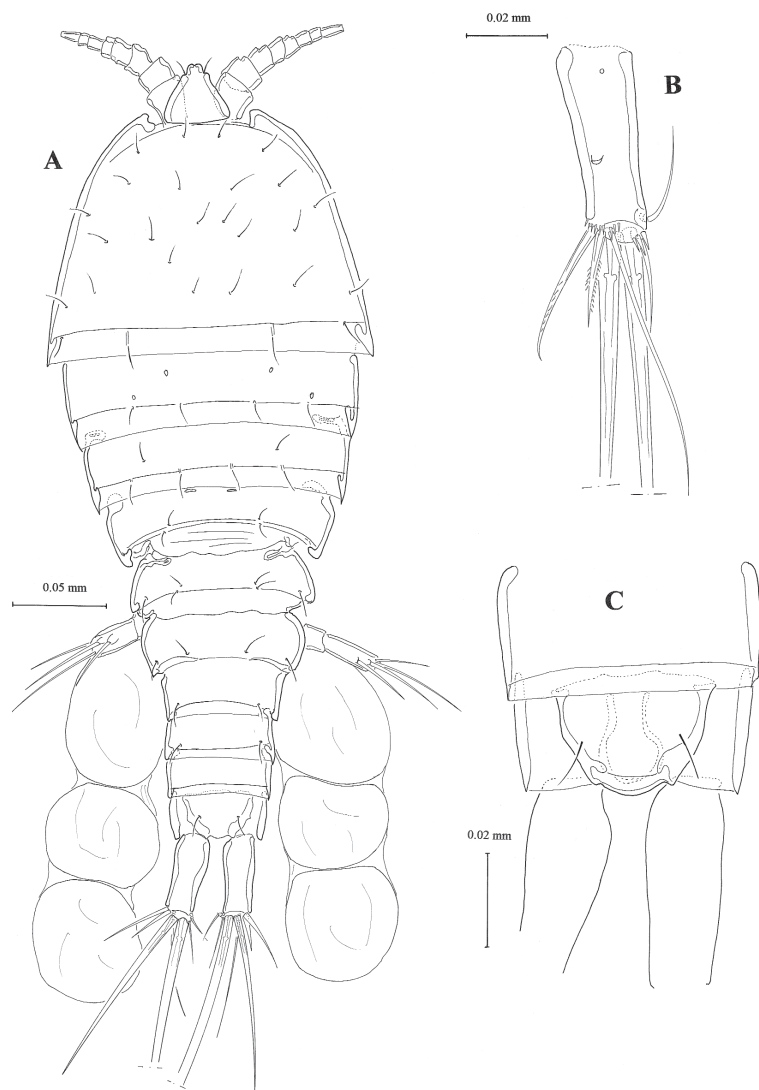
Rostrum: 35 µm

Furcal rami length: 47,5 µm

*Rostrum* (Figs 1A, 2): broadly triangular with bifid tip, demarcated from cephalothorax, with one pair of sensillae subapically.

*Body* (Figs 1A, 8A): distinct separation between broad prosome and smaller urosome. Cephalothorax clearly broader than long, cephalic shield with pattern of sensillae. Posterior margin of each body somite (excl. anal and penultimate somite) with sensillae, somites dorsally without spinules, hyaline frills smooth; genital double-somite (free somites 5 and 6) not completely fused, for genital field see Fig. 8A; urosome (Fig. 8A) smooth, ventrally without spinules; anal operculum (Fig. 1A, C) sclerotized, large and prominent, bearing two sensillae; furcal rami (Figs 1A, C, 8A) 2.9 times as long as broad, all furcal setae located terminally, I and II at outer edge, III slightly displaced ventrally, IV and V well developed, VI located at inner edge, VII biarticulated, subterminally on dorsal surface; two pores present on ventral surface of ramus.

*Antennule* (Figs 1, 2): with eight short segments. Armature: I(1); II(11); III(8); IV(6+aes); V(3); VI(4); VII(4); VIII(5, aes absent).



**Figure 1.** *Stenhelia schminkei* sp. nov., female: **A** Habitus, dorsal view, **B** Left caudal ramus, **C** Anal operculum.

**Figure 1.** *Stenhelia schminkei* sp. nov., femelle : **A** Habitus, vue dorsale, **B** Rame caudale gauche, **C** Somite anal.

*Antenna* (Fig. 4): allobasis with abexopodal pinnate seta in distal half; exp 3-segmented, with 1-1-(1+3) setae; third segment with two spinule rows, one apically, the other one medially; enp with two spinule rows, one subapically, the other one more proximally; subapical armature consisting of two spines and two slender, juxtaposed setae; apically with seven setae, two smaller geniculate ones, three large geniculate setae, outermost at base fused with a slender naked seta and one additional slender naked seta.

*Mandible* (Fig. 3): with compact gnathobase with short and broad teeth on the outer and more slender and pointed

teeth on the inner side of the biting edge, the inner side also carrying a compact, pinnate seta; basis large and compact, with spinule rows and three subdistal setae; enp enlarged, as long as two thirds of the basis and folded back towards the basis, with three marginal and five terminal setae, one of which modified into an extremely large spine being fused to the enp; exp well developed with six setae altogether.

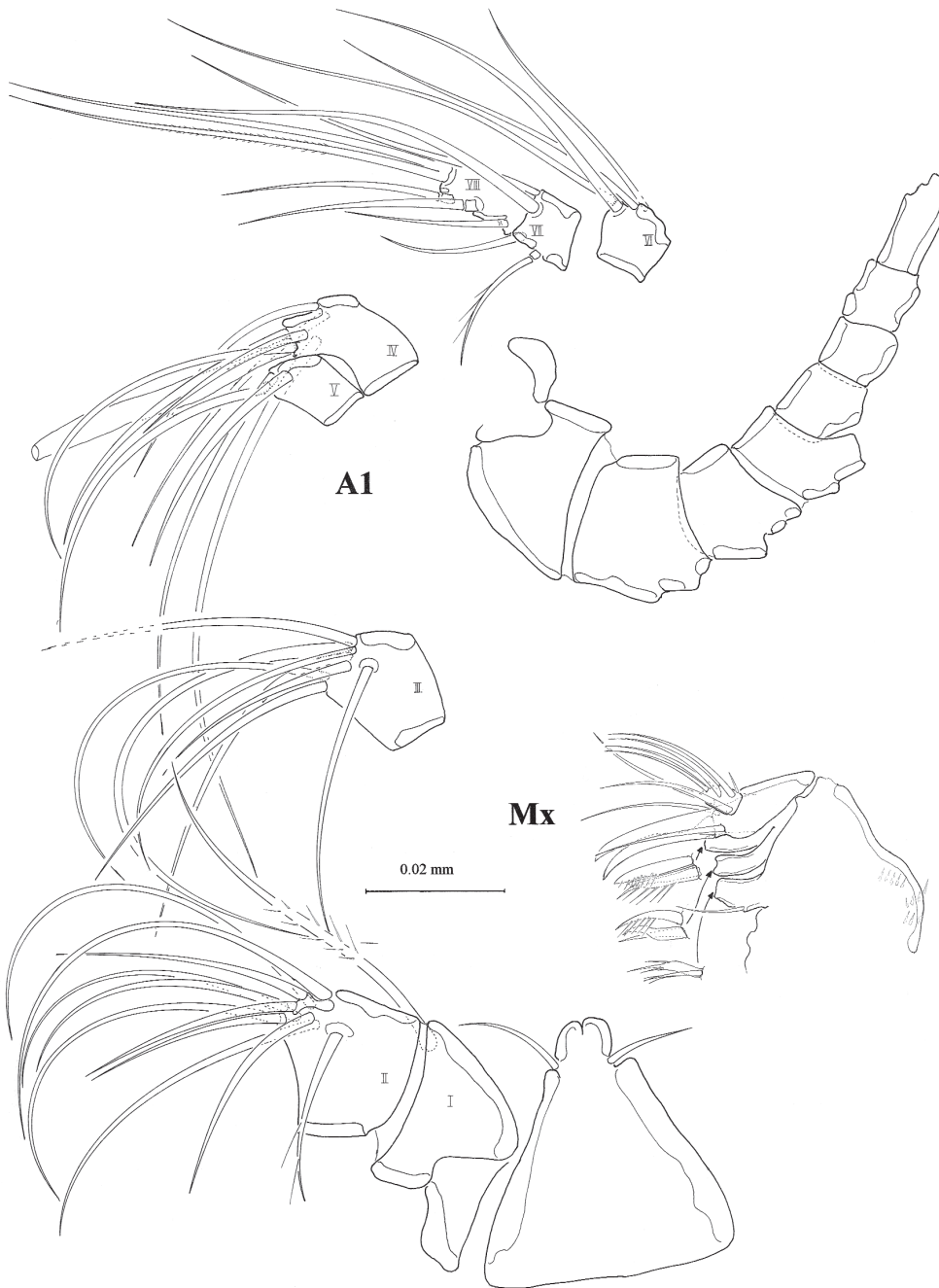
*Maxillule* (Fig. 3): arthrite of praecoxa with nine apical spines and two juxtaposed setae on surface; coxa demarcated from basis, coxal endite with three setae; basis with two distinguishable endites, bearing 3 + 4 setae, respectively; exp cylindrical with two setae, enp broader with four setae, exp and enp confluent.

*Maxilla* (Fig. 2): syncoxa with spinules and three endites; proximal endite with two apical and one subapical seta, middle endite with three setae one of which pinnate, distal endite with three setae, two of which pinnate; basal endite with two claw-like setae, one of which fused with basis and accompanied by two slender naked setae; enp unisegmented, with one minute and six larger setae.

*Maxilliped* (Fig. 3): syncoxa more than twice as long as basis, with three well developed pinnate setae located at distal margin, basis reduced and globular, bearing four basal and two endopodal setae on apical margin, two of which larger and pinnate, enp incorporated into basis, represented by the two above mentioned setae.

*P1* (Fig. 4): coxa of rectangular shape with spinule row on outer margin. Basis with short pinnate outer seta and inner flagellated spine; terminal margin with spinules. Exp 3-segmented, outer margins with hairs, terminal ones with spinules; exp1 and 2 each with one outer pinnate spine, exp2 with short inner seta; exp3 with two outer spines, one terminal spine and one longer pinnate seta; enp 2-segmented; enp1 with strong spinules along outer and distal margin and naked inner seta; enp2 slightly longer, with two inner brush-like setae, terminally with one outer spine and one inner pinnate seta.

*P2-P4* (Figs 4, 6, 7): exps and enps 3-segmented. Intercoxal sclerites with two lateral pointed projections. Coxae of almost rectangular shape with few spinule rows each. Basis with small and slender outer seta, and spinulose along inner margins and near implantation of outer setae. Enp and exp of equal length in P2 and P3, enp shorter in P4. Setal formulae (after Lang, 1948):



**Figure 2.** *Stenhelium schminkei* sp. nov., female. Antennule with rostrum and maxilla.

**Figure 2.** *Stenhelium schminkei* sp. nov., femelle. Antennule, rostre et maxille.

	Exp	Enp
P2	0-1-1, 2, 3	1-1-1, 2, 1
P3	0-0-2, 2, 3	1-1-1, 2, 1
P4	0-0-2, 2, 2	1-0-1, 2, 1

*P5* (Fig. 3): pair of legs fused medially, endopodal lobe not quite prominent with four setae, innermost serrate and strong; exp ovoid with four terminal and one outer subterminal seta arising from distinct cylindrical projection on posterior surface.

*Description of male allotype*

Body length (incl. ro and f. r.): 425  $\mu$ m

Rostrum: 32.5  $\mu$ m

Furcal rami length: 50  $\mu$ m

*Body*: as in female, except somites 5 and 6 completely separated, urosome (Fig. 8B) ventrally without spinules, except for spinule rows along the distal margin of anal somite.

*Antennule* (Fig. 5): haplocer, 9-segmented, setal armature as follows:

I(1); II(12); III(7+aes); IV(7 + 1+aes); V(1);

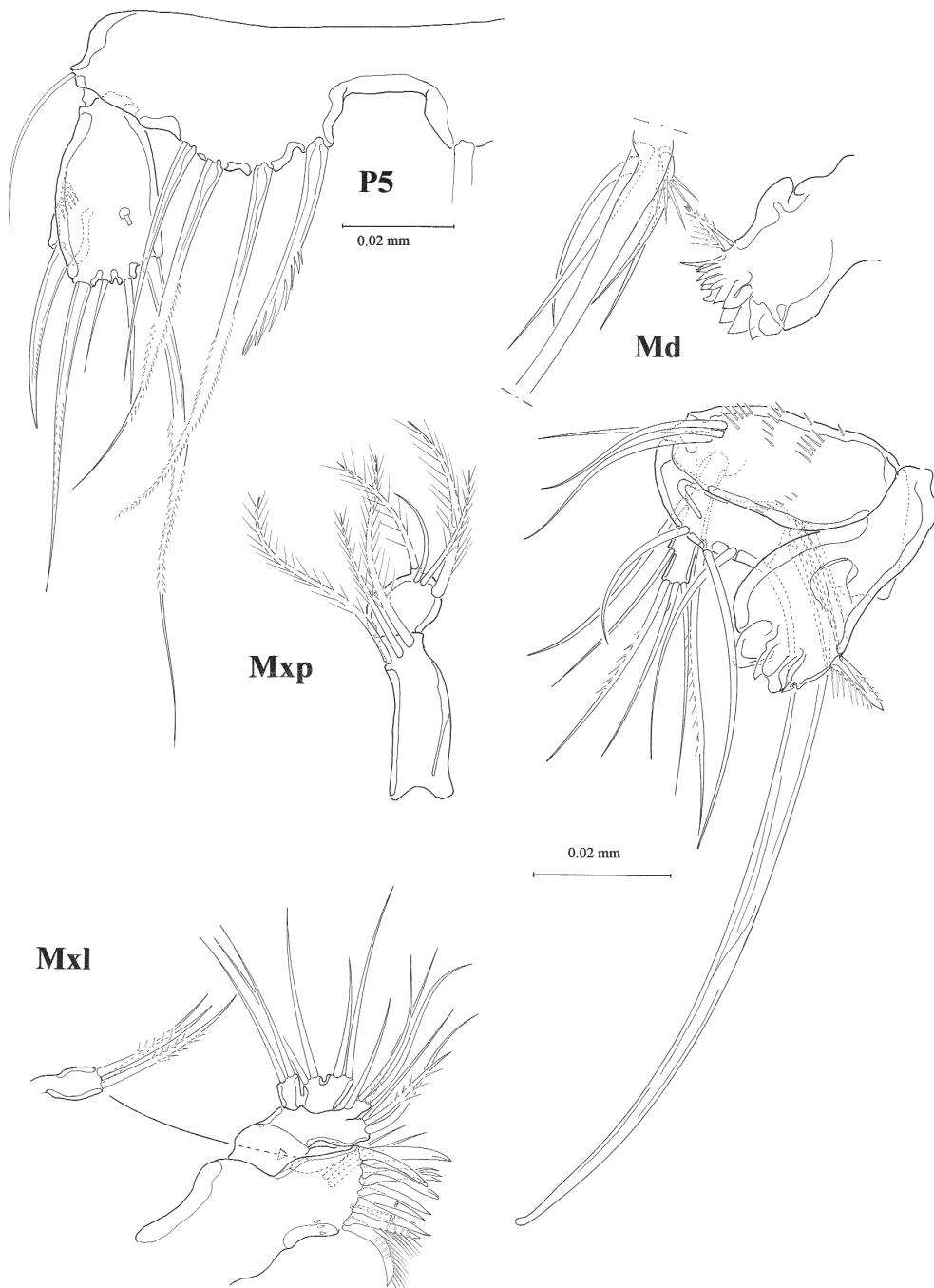
VI(1); VII(1); VIII(3); IX(5, aes absent).

*A2, mouthparts, Mxp and P1*: as in female.

*P2enp* (Fig. 4A): 2-segmented, one inner seta inserting above an inner median projection of the segment marking the distal margin of the middle segment of the female homologue; terminal margin with two setae, the outer of which modified, setae on P2enp2 generally thickened compared to the female.

*P3* (Fig. 6A): inner seta and terminal setae of enp3 and inner and terminal setae on P3exp3 (fig 6B) thickened compared to the female condition.

*P4* (Fig. 7): enp1 inner seta minute; enp3 all setae thickened and shortened compared to their female homologue; exp2 with modified outer segmental margin;



**Figure 3.** *Stenhelia schminkei* sp. nov., female. P5, mandible, maxilliped and maxillule.

**Figure 3.** *Stenhelia schminkei* sp. nov., femelle. P5, mandibule, maxillipède et maxillule.

exp3 with one inner seta less than female, lower inner seta and terminal setae also thickened.

*P5* (Fig. 6): pair of legs medially fused, endopodal part on both sides represented by an inner strong serrate seta and

a minute outer seta respectively; exp small with four elements: three inner slender setae and one outer extremely enlarged spine being fused with exp.

*P6* (Fig. 8): consisting of two lobes with three lateral setae each, innermost seta very short.

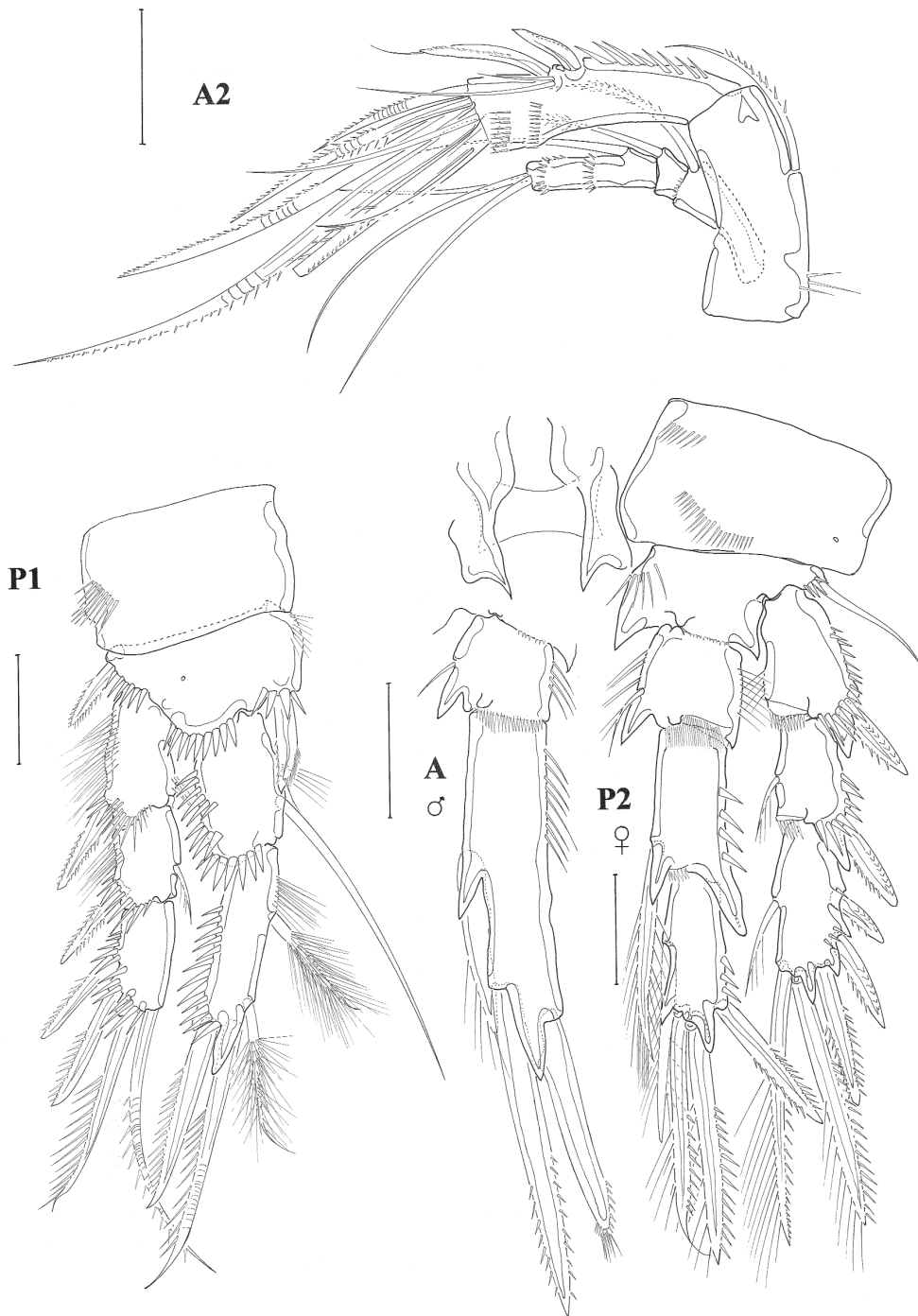
### Discussion

The species being most closely related to *Stenhelia schminkei* sp. nov. are without doubt *S. clavus* Wells & Rao, 1987, *S. valens* Wells & Rao, 1987 and *S. paraclavus* Wells & Rao, 1987, all of which have been described from the Andaman Islands (India). The following characters are shared by all these species:

P2-P4exp1 without inner seta ; P2exp3 with at most one inner seta; P3exp3 with at most two inner setae, P3enp3 with at most one inner seta; P4exp3 with only two outer spines, the distalmost inner seta on P4exp3 missing, P4enp 2 asetose, P4enp3 with at most one inner seta; female P5 confluent with an angled or rounded median gap (in *S. paraclavus* only the male has been described); the modified thorn on the male P5 exp, presumably representing a homologous seta (since the male P5 exp shows an identical distribution of setae in all species), is present in *S. clavus*, *S. schminkei* sp. nov. and

*S. paraclavus* (in *S. valens* the male is still unknown); basis and enp of Mxp fused, allobasis of globular shape.

*S. schminkei* sp. nov. differs from *S. clavus* in the following aspects: in *S. schminkei* the cephalothorax and



**Figure 4.** *Stenhelia schminkei* sp. nov., female. Antenna, P1, P2. A, male: Endopod of P2. Scale bars = 0.02 mm.

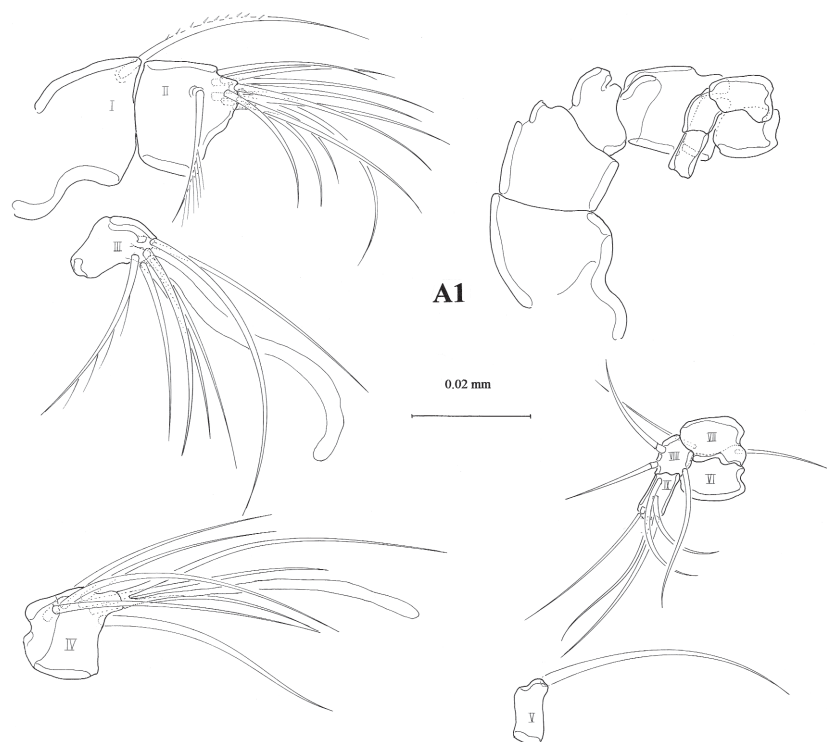
**Figure 4.** *Stenhelia schminkei* sp. nov., femelle. Antenne, P1, P2. A, mâle : Endopodite de P2. Echelles = 0,02 mm.

the caudal rami are much shorter; the genital double-somite is dorsally completely divided (fused in *S. clavus*); Mxp syncoxa elongated (almost as short as basis in *S. clavus*);

P1enp2 inner and terminal inner setae brush-like ornamented (naked in *S. clavus*); P2enp2 with one seta (two setae in *S. clavus*); P3exp3 with two setae (one seta in *S. clavus*); P3exp2 inner margin asetose (with one inner seta in *S. clavus*); P4enp3 with one inner seta (asetose inner margin in *S. clavus*); female P5 without thorn-like modified seta, shape and length of exopodal and baseoendopodal setae very different from *S. clavus*; male P2 enp2 with only three setae (four setae in *S. clavus*).

*Stenhelia paraclavus*, for which the female is unknown, lacks the brush-like ornamentation on P1enp2 and the hairy ornamentation on exp1 and exp2 which is present in *S. schminkei* and *S. clavus*. Moreover, *S. schminkei* sp. nov. shows a much more elaborate sexual dimorphism on the swimming legs: male P3enp2 and 3, P3exp3 and P4enp3 bear thickened inner setae compared to the female (Fig. 6); P4enp1 inner seta is enlarged in the female and vestigial in the male; P4exp3 lacks the upper inner seta in the male and the inner and outer terminal setae are thickened compared to the female (Fig. 7). The segmental projection on the male P4exp2, which is also present in *S. paraclavus* is much more developed in *S. schminkei*.

*Stenhelia schminkei* sp. nov. differs from *S. valens* in bearing four setae on the maxillipedal allobasis (only three in *S. valens*), in the shape of the female P5 showing different



**Figure 5.** *Stenhelia schminkei* sp. nov., male. Antennule.

**Figure 5.** *Stenhelia schminkei* sp. nov., mâle. Antennule.

length proportions of the setation of both benp and exp, the different shape of the outermost exopodal and innermost baseoendopodal seta, respectively and in having an angled gap between the pair of legs (a rounded gap in *S. valens*).

The “*clavus*-group” seems to be restricted in its distribution to the Indo-Pacific region (Andaman Islands and Papua New Guinea).

***Melima papuaensis* sp. nov.**

Figs 9 - 13

*Type locality.* Motupore Island, near the Marine Biological Station of the University of Papua New Guinea in autumn 1984, collected by H.K. Schminke. Rhizomes of *Zostera* and leaves were washed out during low tide (depth app. 50 cm). Two female specimens were collected.

*Type specimens.* Female holotype, catalogue no. UNIOL 2001.021; female paratype, catalogue UNIOL no. 2001.022.

*Etymology:* the species name refers to Papua New Guinea, where it has been collected.

*Description of the female holotype*

Body length (incl. ro and f. r.): 475 µm

Rostrum: 37,5 µm

Furcal rami length: 45 µm

*Rostrum* (Figs 9, 10): broadly triangular, with one pair of sensillae subapically, demarcated from the cephalothorax, tip rounded and notched.

*Body* (Figs 9, 13): clear constriction between broad prosome and slender urosome. Cephalothorax longer than broad, dorsally with sensillae. Posterior margin of each body somite (excl. anal- and penultimate somite) with setules, somites dorsally without spinules, hyaline frills smooth; genital double somite (Fig. 13) (free somites 5 and 6) not completely fused; urosome (Fig. 13) ventrally without spinules except anal somite carrying spinules on distal margin; anal operculum smooth, not prominent, flanked by two lateral sensillae; furcal rami (Fig. 13) 2.9 times as long as broad, furcal setae: I minute, II long and slender, III, VI and VII slender, IV + V well developed.

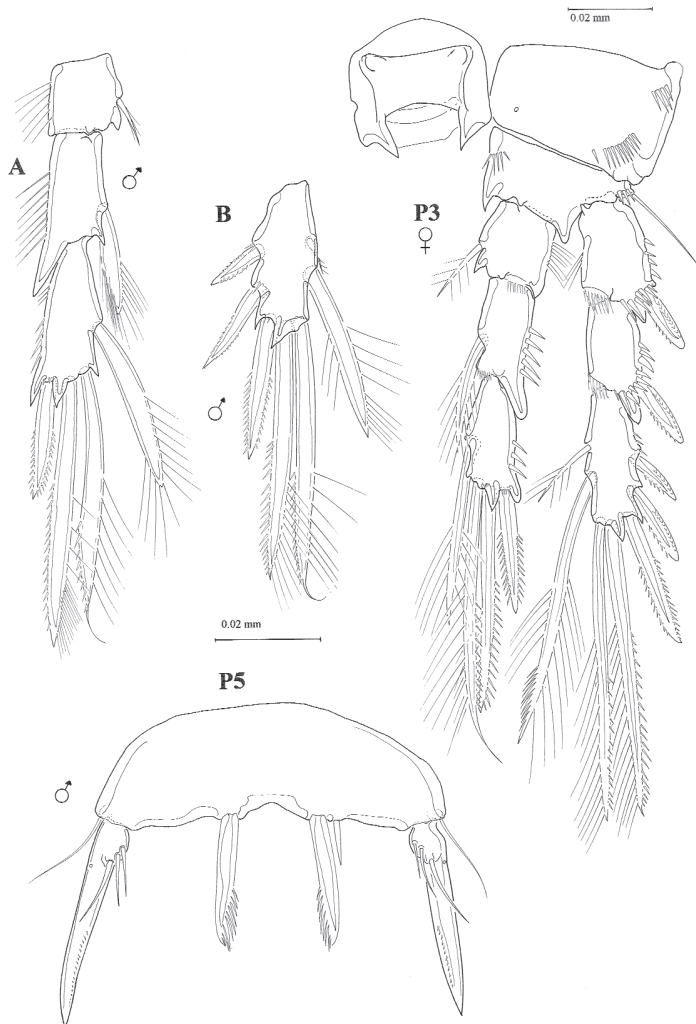
*Antennule* (Fig. 10): 8-segmented; II elongated; setal armature as follows: I(1); II(11); III(9); IV(4 + 1+aes); V(2); VI(4); VII(4); VIII(6).

*Antenna* (Fig. 12): with allobasis bearing one abexopodal seta in distal half; exp 3-segmented, with 1-1-4 setae; enp distal part elongated, with two spinule rows, two almost spine-like and two long and slender setae along inner margin; apically one spine-like seta, three geniculate setae, each of different length; one geniculate seta basally fused with one slender naked seta; additionally one single pinnate seta and one tubular pore.

*Mandible* (Fig. 11): with elongated and massively built basis bearing three subdistal setae; enp enlarged and curved back towards basis, with three marginal setae and two strongly modified apical setae; exp long and slender, with six setae; coxa short and stout, gnathobase with short and blunt teeth being sharply dented on inner side.

*Maxillule* (Fig. 12): arthrite of praecoxa apically with ten spines and setae respectively and two naked slender setae on surface; coxal endite with three slender, long setae; basis with two distinguishable endites bearing four and three setae respectively; enp with three slender naked setae and one large spinulose seta; exp with two modified setae being fused basally and of hyaline and amorphous appearance.

*Maxilla* (Fig. 11): syncoxa with four endites, proximal two being fused basally and carrying two setae each; middle endite with three pinnate setae one of which curved



**Figure 6.** *Stenhelia schminkei* sp. nov., female: P3. Male: **A** P3 endopod, **B** P3 exopod 3 and P5.

**Figure 6.** *Stenhelia schminkei* sp. nov., femelle : P3. Mâle : **A** Endopodite de P3, **B** Exopodite 3 de P3 et P5.

upwardly; distal endite with three setae, two of which strong and pinnate, the uppermost claw-like; basal endite with claw being demarcated from the basis and with three accompanying setae, one of which located near enp; enp unisegmented with seven setae, most proximal one being tiny.

*Maxilliped* (Fig. 13): praecoxa present, coxa with three apical setae; basis with spinule rows and distally two long, slender setae inserting closely to each other; enp well developed with one terminal unarmed claw and one subterminal slender naked seta.

*P1* (Fig. 11): coxa and basis with spinule rows; outer basal seta reaching to end of exp2; enp 2-segmented, enp1 massive and as long as whole exp, with one small seta near distal margin; enp2 much smaller, of irregular shape, with one slender inner terminal seta, one outer terminal and one outer seta, the latter two being of flap-like shape; exp 3-segmented, segments small and slender, exps1 and two with reduced outer spines, exp2 with minute inner seta; exp3 with two slender outer spines, one outer terminal spine and one long, geniculate seta.

*P2-P4* (Figs 12, 9, 13): exps and enps 3-segmented. Intercoxal sclerites with two pointed projections. Coxae of almost rectangular shape with few spinule rows each. Basis with small and slender setae. Enp and exp of equal length in P2 and P3, enp shorter in P4.

	Exp	Enp
P2	1-1-1, 2, 2	1-1-0, 2, 1
P3	1-1-3, 2, 2	1-1-2, 2, 1
P4	1-1-2, 2, 2	1-0-1, 2, 1

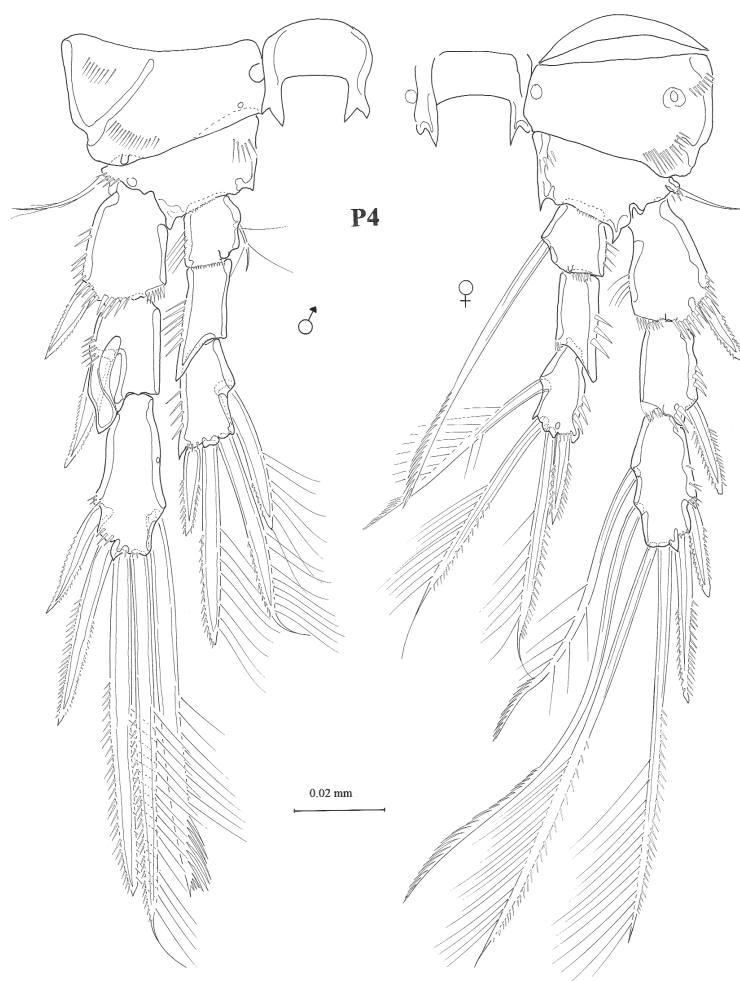
*P5* (Fig. 9): pair of legs not fused medially; benp slightly prominent with four setae, second outermost stronger and pinnate, the other three slender and shorter; exp narrow and long with 4 (second female specimen with 5) terminally located setae, the innermost stronger and pinnate; exp spread outwardly in the characteristic stenheliid manner.

*Male*: unknown.

## Discussion

Several authors (Wilson, 1965, Coull, 1976, Wells & Rao, 1987) have discussed the validity of *Melima* Por, 1964 and have criticized Por's decision to establish a new genus because of the specialized P1, the advanced reduction of the setation of the swimming legs and the lack of sexual dimorphism in the male P2. Por (1964) considered this a first step to the separation of the "highly peculiar *Stenhelia*-like Harpacticoida from the other Diosaccidae". Finally, Wells & Rao (1987) synonymized *Melima* with *Stenhelia*. They redescribed the "intermediate" *Stenhelia indica* Krishnaswamy, 1957, showing a P1 not as specialized as in *Melima* but also lacking sexual dimorphism on the swimming legs, having a male P5 and P6 similar to that of *Melima caulerpae* Por, 1964, showing setal reductions in the swimming legs and therefore "blurring" the differences between *Melima* and the other *Stenhelia* species. The species *Melima caulerpae*, *M. bisetosa* Coull, 1971, *M. ovalis* Wells & Rao, 1987 and *Stenhelia indica* can well be united as a monophyletic taxon *Melima*, within the Stenheliinae. Since the characters which





**Figure 7.** *Stenhelia schminkei* sp. nov., P4 male and female.  
**Figure 7.** *Stenhelia schminkei* sp. nov., P4 mâle et femelle.

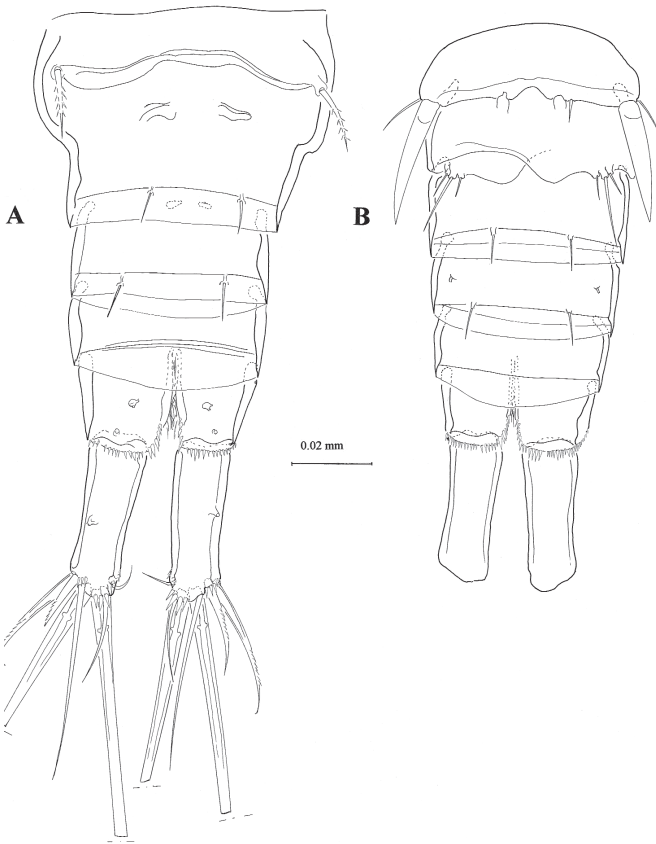
have always been diagnostic for *Stenhelia* are actually symplesiomorphies of the higher taxon Stenheliinae, the genus is left without real autapomorphies (see discussion below). A first step towards a systematic revision of the obviously paraphyletic taxon *Stenhelia* is the recognition and characterization of monophyletic subgroups. The reinstatement of *Melima* has to be regarded within this context.

The following apomorphic characters are shared by all species of *Melima* including *M. indica*:

Md basis massively built and considerably longer than the coxa and gnathobase (Fig. 11), which is not the case in the other Stenheliinae; Mx1 enp bears three slender naked setae and one modified (strong and spinulose) outer seta, both exopodal setae are also modified being irregularly shaped and of hyaline-like appearance, basally fused in *Melima papuaensis* sp. nov. (Fig. 12) (even fused with the

exp in *M. ovalis* according to Wells & Rao (1987); distal part of A2 enp2 elongated, leaving the subterminal four spines/setae almost in a submedian position (Fig. 12); P1 enp 2-segmented, first segment longer than second (except in *M. ovalis*), the latter bearing three setae. In *M. indica* (according to the illustration by Wells & Rao (1987), p. 299, Fig. 75B) the P1 seems already to be differentiated towards the *Melima*-type modification: the terminally located seta (former anterior claw of the stenheliid groundpattern) of the enp2 armature has already been displaced towards the outer margin, the exopodal outer spines, above all of exps1 and 2, are slightly reduced and the outer basal seta is elongated. The most extreme state of P1 modification, however, is found in the other *Melima*-species (Fig. 11): enp1 massive and very broad with inner seta either lost (in *M. indica*) or miniaturized, shape of enp2 slightly distorted, outer and terminal setae (representing the former anterior claw and the middle geniculate seta of the "prehensile" groundpattern, respectively) being flap-like and of hyaline shape (different setae in *M. caulerpae*?, compare Wells & Rao (1987), p. 302, Fig. 78d and Por (1964), p. 84, Fig. 115); compared to the enp, the whole exp is reduced in size, outer spines are small, basal outer seta elongated; P2-P4 exp3 with only two outer spines; setal formulae of P2-P3: single inner setae missing on P2 exp3 and P3 enp3; female P5 benp with only four setae, exp with five setae; male P5 is a single plate with up to 3 + 1 basal setae (in *M. caulerpae*). P6 seems to be completely asetose (at least clearly in *M. indica*). However, since only the males of two species are known (*M. caulerpae* and *M. indica*) more descriptions have to be awaited; in *M. ovalis* and *M. papuaensis* sp. nov. the upper seta of the middle syncoxal endite of the Mx is curved upwardly. For *M. bisetosa* the Mx is not described. In *M. indica* this character is not so clearly pronounced. (The latter two characters can only be clearly confirmed when more descriptions are available).

The complete absence of swimming leg sexual dimorphism in *Melima* is a character which has also to be regarded as autapomorphic, considering the groundpattern of the Thalestridomorpha displaying at least a 2-segmented P2 enp in the male. There are only few exceptions (e.g. in some *Parastenhelia* species and *Hamondia superba* Huys, 1990) and in all cases, including *Melima*, the respective species belong to well characterized groups and their nearest relatives always show the respective taxon specific sexual dimorphism (Willen, 2000).



**Figure 8.** *Stenhelium schminkei* sp. nov., **A** female urosome. **B** Male urosome.

**Figure 8.** *Stenhelium schminkei* sp. nov., **A** Urosome de la femelle. **B** Urosome du mâle.

Primitive characters of *Melima* within the Stenheiliinae are the Mxl praecoxal arthrite bearing ten apical spines/setae (Fig. 12), the proximal syncoxal endite of the Mx being still divided and bearing four setae (Fig. 11), the well developed and not substantially reduced Mxp (in *M. papuaensis* sp. nov. the syncoxa is even still divided in “praecoxa” and “coxa”, Fig. 13) and the still prominent P5 benp in the female.

*M. indica* seems to be the plesiomorphic sister taxon of the other *Melima*-species which are united by the more strongly modified P1, the rounded rostrum, the upper seta of the middle syncoxal endite of the Mx being upwardly curved and the loss of the inner seta on P2 enp3.

*Melima papuaensis* sp. nov. differs from *M. caulerpae* in that the second segment of the female antennule is clearly longer than the first (almost as long as the first in *M. caulerpae*), the Mxl praecoxal arthrite bears ten apical spines/setae in *M. papuaensis* (seven in *M. caulerpae* (according to Wells & Rao (1987), p.301, Fig.

J), P2 exp3 bearing one seta in *M. papuaensis* (no seta in *M. caulerpae*) and P3 exp3 bearing three setae in *M. papuaensis* (one in *M. caulerpae*), female P5 exp with four setae in *M. papuaensis* (five setae in *M. caulerpae*). Both species share a slightly modified seta on P2enp2 showing a brush-like tip.

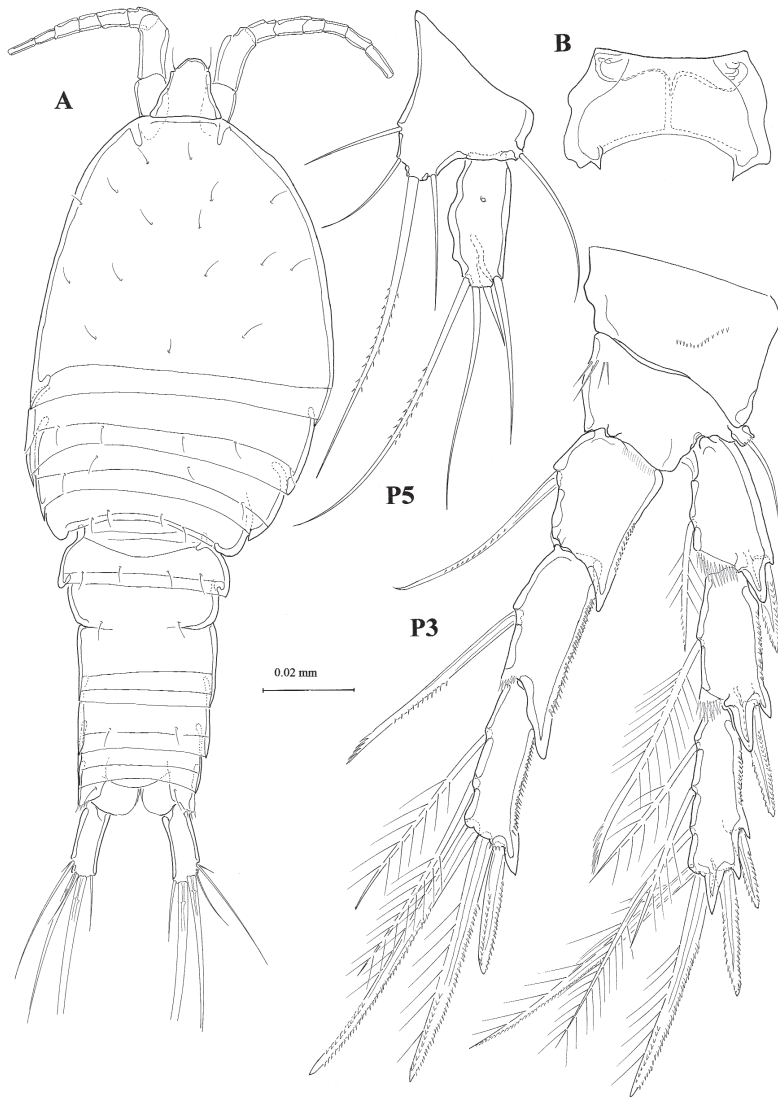
*M. papuaensis* sp. nov. shows the same symplesiomorphic setal formulae of the swimming legs as *M. bisetosa*. Differences can be found in the female A1, the first two segments being of equal length in *M. bisetosa* whereas the second segment is clearly longer than the first in *M. papuaensis* sp. nov.. According to the description and figure of Coull (1971) the enp of the Md bears terminally only one modified spine in *M. bisetosa* whereas two spines are present in *M. papuaensis* sp. nov. (Fig. 11). The three syncoxal setae of the Mxp are all “normally” developed in *M. papuaensis* sp. nov. whereas one of them seems to be spine-like modified and shortened in *M. bisetosa* (Coull, 1971). The anal operculum is smooth in *M. papuaensis* but “finely spinulose” in *M. bisetosa*, according to Coull (1971).

*M. papuaensis* sp. nov. differs from *M. ovalis*, according to the description by Wells & Rao (1987) at least in the following aspects: female A1 I + II of equal length in *M. ovalis*, versus segment II elongated in *M. papuaensis*; Md in *M. ovalis* the modified apical endopodal seta of Md is fused to the enp, versus not fused in *M. papuaensis* Mxl; the two exopodal setae of Mxl are fused to the exp and the endopodal modified seta is considerably shortened in *M. ovalis*, versus only fused to each other and endopodal modified seta long and spinulose in *M. papuaensis*; in *M. papuaensis* enp1 of P1 is approximately twice as long as enp2, versus much shorter compared to enp2 and much broader in *M. ovalis*; single inner setae are missing in *M. ovalis*, versus present in *M. papuaensis* on P2 exp3, P3 exp3, respectively; female P5 exp less than twice as long as broad (1,6x) in *M. ovalis*, with five setae, versus more than twice as long as broad (2,3x) with four setae (with outer spine absent) in *M. papuaensis*.

Both species share the naked elongated seta on P4enp1 which is shorter and plumose in the other species according to Wells & Rao (1987). In *M. papuaensis* sp. nov. the middle inner seta on P4exp3 is large, naked and distally serrated, whereas in the other species it is either short and naked in *M. bisetosa* or “normally” ornamented in the other species. *M. papuaensis* lacks the outer spine of the female P5 exp which is present in all other species.

#### Key to the species of *Melima* (females)

1. P1enp2 setae of “normal” shape, distal edge of segment with a mucroniform process, outer spines of all exopod segments and of some endopod segments of P2-P4 massive



**Figure 9.** *Melima papuaensis* sp. nov., female: **A** Habitus, dorsal view, **B** Intercoxal sclerite of P3, P4, P5.

**Figure 9.** *Melima papuaensis* sp. nov., femelle : **A** Habitus, vue dorsale, **B** Sclérite intercoxal de P3, P4, P5.

and broadly pectinate, P2enp3 with 1 inner seta present, innermost seta of female P5benp elongated and enlarged.  
 ..... *Melima indica* Krishnaswamy, 1957

P1enp2 terminal and outer setae of hyaline structure, distal edge of segment rounded, without process, outer spines of P2-P4 exopods “normally” spinulose, inner margin of P2enp3 asetose, innermost seta of female P5benp as long as second innermost seta  
 ..... 2.

2. P2exp3 inner margin asetose, P3exp3 with only 1 or 2 setae  
 ..... 3.

P2exp3 inner margin with 1 seta, P3exp3 with 3 inner setae  
 ..... 4.

3. P1enp1 broad, of oval shape, app. 1.6 times as long as broad, P1enp1 only approximately 1,6 times as long as enp2, P3exp3 with 2 inner setae, outermost seta of Mx1 enp very short, P2 and P3 of robust appearance, female P5 exp with second outermost seta approximately twice as long as outermost seta  
 ..... *M. ovalis* Wells & Rao, 1987

P1enp1 of more elongate shape, at least 2 times as long as enp2, P3exp3 with 1 inner seta, P2 and P3 of less robust appearance, P2enp2 inner seta slightly enlarged, with brush-like tip, female P5 exp with second outermost seta not longer than outermost seta  
 ..... *M. caulerpae* Por, 1964

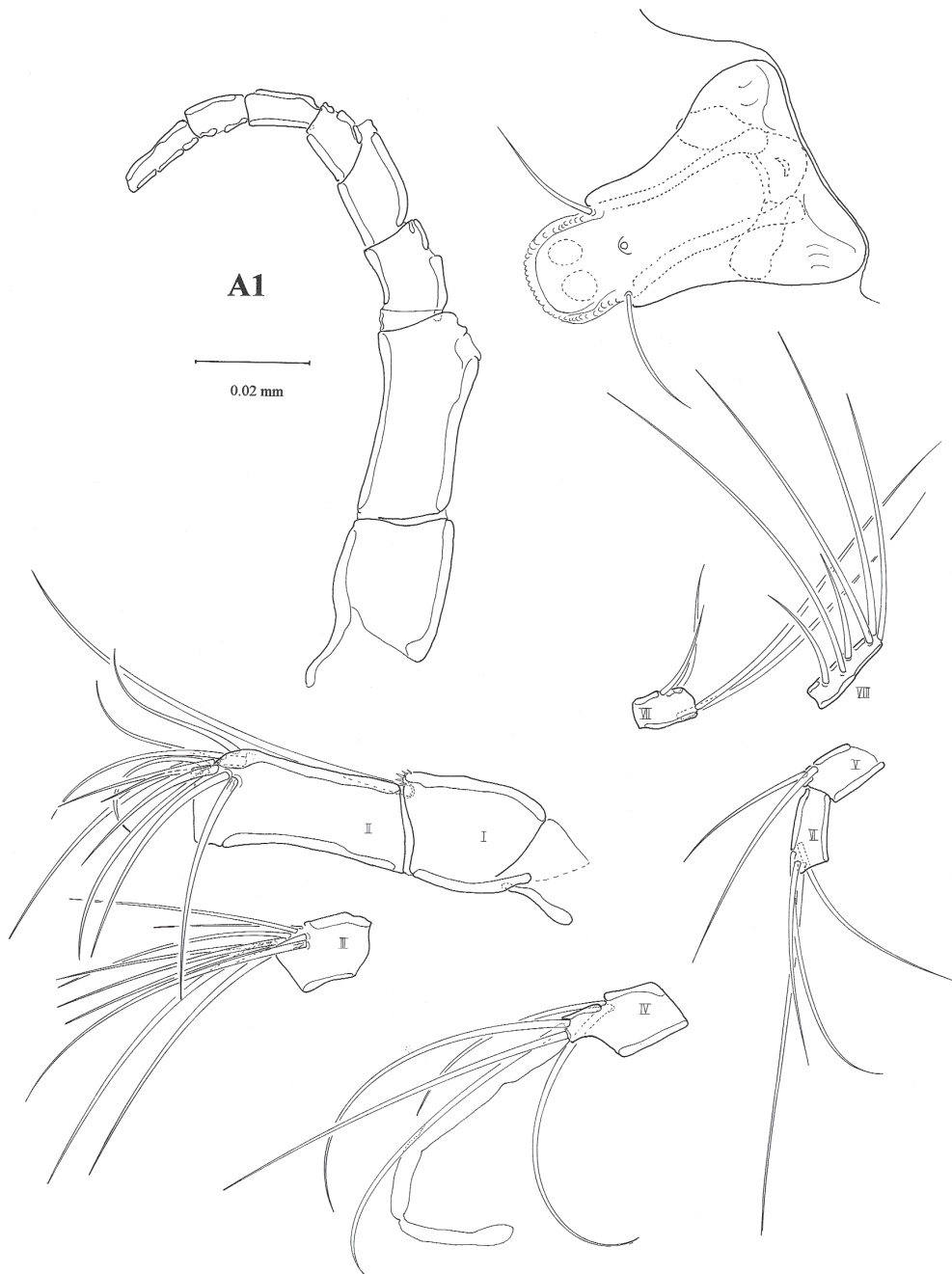
4. First and second segment of female antennule of equal length, female P5 exp with 5 setae, P4exp3 “middle” inner seta naked and shorter than the other inner setae of this segment (specimens of Wells & Rao, 1987), Md enp with only 1 enlarged and modified terminal spine ..... *M. bisetosa* Coull, 1971

Second segment of female antennule much longer than first segment, female P5 exp with only 4 setae (outermost seta lacking), P4exp3 “middle” inner seta large and serrated, Md enp with 2 enlarged and modified terminal spines  
 ..... *M. papuaensis* sp. nov.

**Notes on the systematic position of the Stenheliinae within the Oligarthra**

Brady (1880) established a subfamily Stenheliinae within his system of Harpacticidae (= Harpacticoida) including the genera *Stenhelia* Boeck, 1865 (both species being described in that paper were subsequently placed into other genera, see Sars, 1906; Lang, 1948), *Ameira* Boeck, 1865, *Jonesiella* Brady, 1880 and *Delavalia* Brady, 1869.

In 1906, Sars united the genera *Diosaccus* Boeck, 1873, *Amphiascus* Sars, 1905, *Stenheliopsis* Sars, 1906 (junior synonym of *Pseudomesochra* T. Scott, 1902) and *Stenhelia* within the new family Diosaccidae, characterizing it by the



**Figure 10.** *Melima papuaensis* sp. nov., female. Antennule and rostrum.

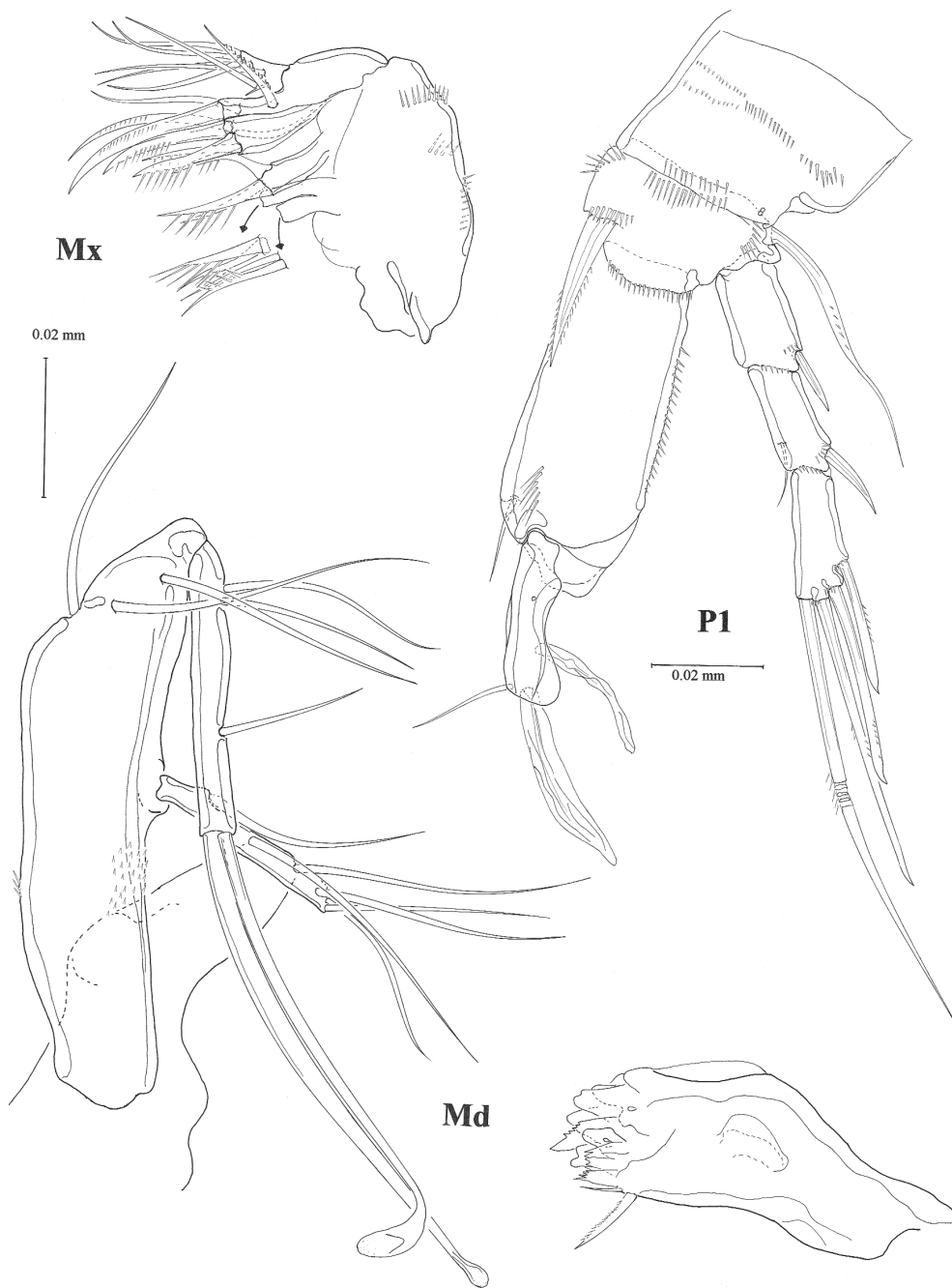
**Figure 10.** *Melima papuaensis* sp. nov., femelle. Antennule et rostre.

paired egg-sacs, the P1 being less prehensile than in the Thalestridae and the shape of the transformed male P2enp. In addition he synonymized *Delavalia* and *Beatricella* T. Scott, 1905 with *Stenhelia*.

Monard (1927, 1928) principally followed Sars' classification but reintroduced *Delavalia* as a subgenus

within *Stenhelia*. Nicholls (1941) subdivided the Diosaccidae into three subfamilies one of which being the Stenheliinae containing only *Stenhelia* and *Pseudomesochra*.

Finally, in the Lang's system of the Diosaccidae (1948, pp 762-763), which was still valid until recently, *Stenhelia*



**Figure 11.** *Melima papuaensis* sp. nov., female. Maxilla, P1 and mandible.

**Figure 11.** *Melima papuaensis* sp. nov., femelle. Maxille, P1 et mandibule.

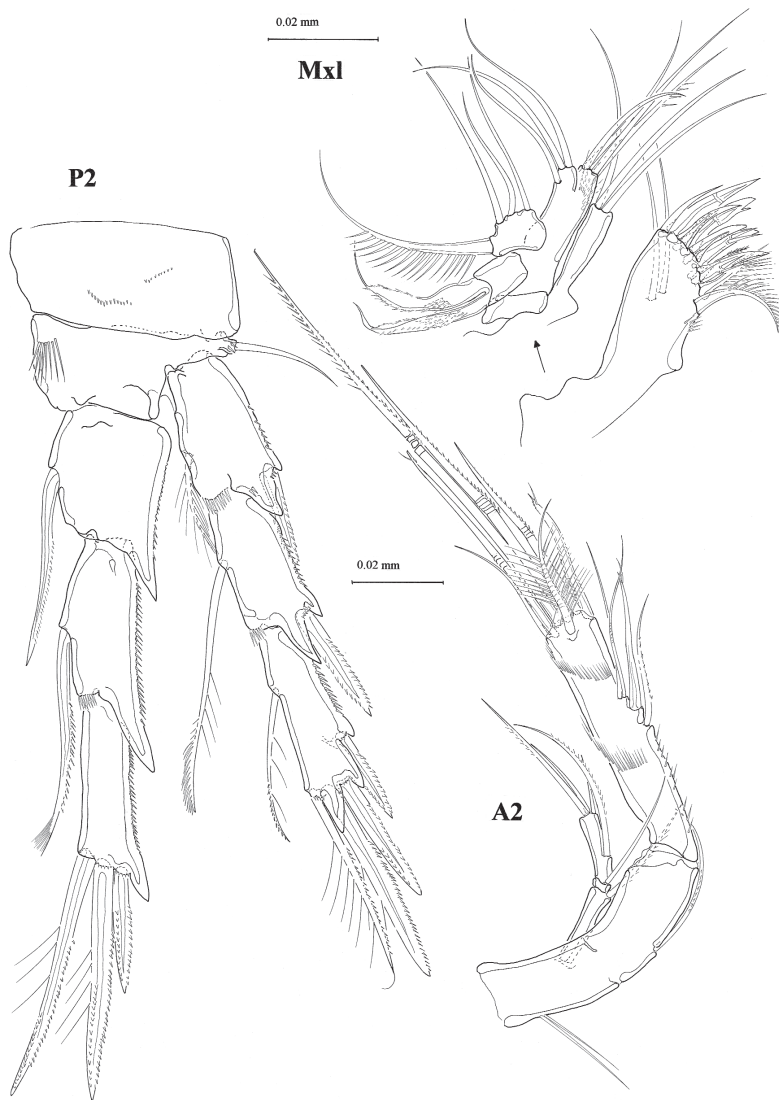
formed a group together with *Pseudomesochra* within a lineage containing also *Pseudodiosaccus-Amonardia-Ialysus* and *Diosaccopsis-Pseudodiosaccopsis-Tydeanella*. However, Lang himself was uncertain about the position of *Stenhelia-Pseudomesochra*, which perhaps merited an own subfamily, but he generally resisted from erecting

subfamilies within the Diosaccidae because of this and other uncertainties (pp. 764-765).

In any case, a close relationship of *Stenhelia* and *Pseudomesochra* is very doubtful. Both genera show convergent similarities in the habitus and in the P1 (subgenus *S. Delavalia*). The 2-segmented P1 enp has developed within the genus *Stenhelia* from a "prehensile" P1 (being a plesiomorphic ground-pattern character of the Miraciidae retained from the Podogennonta (Willen, 1999) and a second time in *Pseudomesochra* as part of the groundpattern shared with the Paranannopinae Por, 1986 within the Pseudotachidiidae (compare Willen, 1996, 1999, 2000). *Stenhelia* does not share any of the apomorphies of the Pseudotachidiidae and vice versa. Therefore a closer relationship of both groups seems to be rather unlikely.

Several authors (Por, 1964, Wells, 1967, Monard, 1935, Dahms & Bresciani, 1993) have questioned the assignment of the "*Stenhelia*-group" to the Diosaccidae sensu Lang (1944) and proposed its exclusion from the family and the erection of a family Stenheliidae Brady, 1880.

In the course of revising the Thalestridimorpha, applying the method of Phylogenetic Systematics originally introduced by Hennig (1966), it turned out that the "*Stenhelia*-group" has indeed not evolved within the traditional Diosaccidae but is nevertheless closely related to them. In the new phylogenetic system of the Thalestridimorpha published by Willen (2000) the stenheliid taxa are united in a subfamily Stenheliinae within



**Figure 12.** *Melima papuaensis* sp. nov., female. Maxillule, antenna and P2.  
**Figure 12.** *Melima papuaensis* sp. nov., femelle. Maxillule, antenne et P2.

the Miraciidae Dana, 1846, whereas the remaining genera traditionally belonging to the Diosaccidae are placed into another subfamily Diosaccinae. As the Miraciidae have also been assigned to the Diosaccidae (see Willen, 2000) the family name Diosaccidae has become a junior synonym and has to be replaced by the older name Miraciidae.

Stenheliinae, Diosaccinae and Miraciinae share the following apomorphies characterizing the Miraciidae within the Thalestridimorpha (Willen, 2000): the loss of an inner seta on P2enp3, the loss of the proximal seta on A2exp1, Mxl exp with only two setae, inner seta of P1enp1 inserting in the distal quarter of the segment, loss of the inner seta on P1enp3, and male P5benp with only two setae.

On the other hand, the Diosaccinae show apomorphies

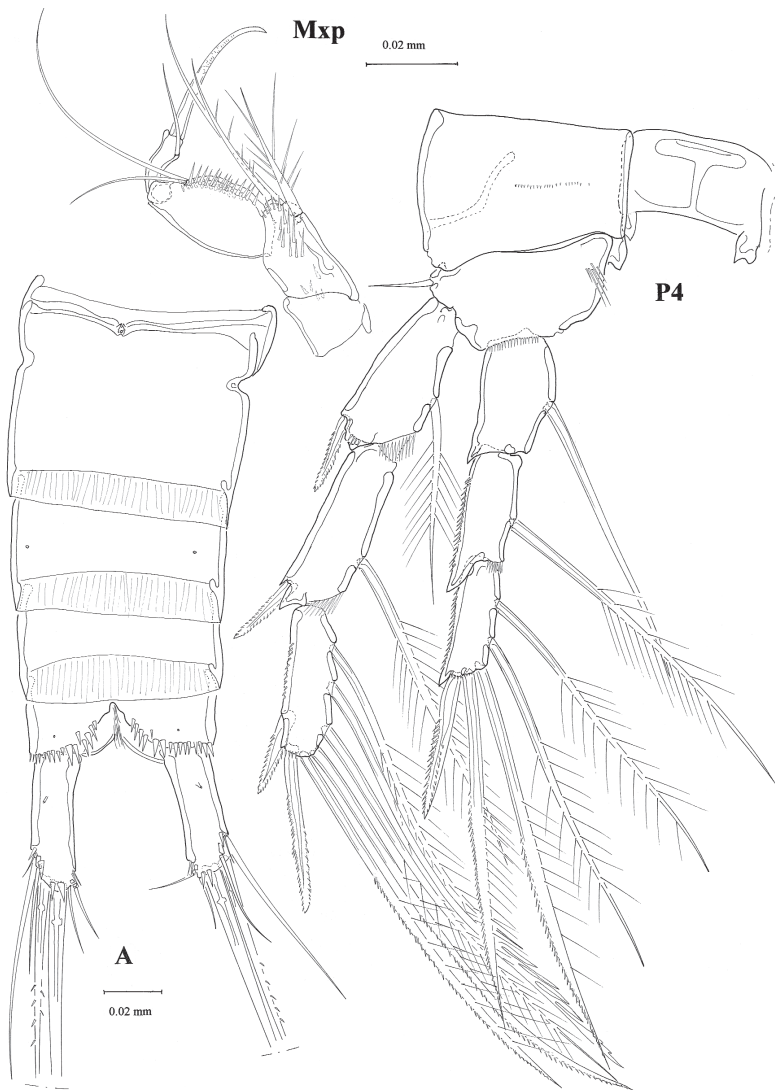
which are not shared by the Stenheliinae: the setation of the female antennule segment 4 is reduced in a characteristic way, one flagellate seta is missing on the coxal proximal endite of the Mx, the male P1 basis bears at most three large “Nebendornen” and a “nose-like” segmental projection.

The Stenheliinae themselves share the following apomorphic characters: bifid, broad triangular rostrum, male and female antennule segments 7+8 always fused, male and female antennule segment 9 with modified setation as described in Willen (2000), Md gnathobase with blunt teeth. Concerning the shape of maxilliped: the Diosaccinae and Miraciinae have retained one enp2-seta inserting terminally on the endopod segment, whereas in the Stenheliinae the complete enp2 setation is lost, the two basal setae are close to one another near the distal inner margin and one seta is missing of the distal coxal pair of setae. Further autapomorphies are the shape of the female P5 and of the male P2enp. The female P5benp is flattened or at least not so well developed as in the Diosaccinae (e.g. in *Melima*, Fig. 9) and the exp is displaced in a characteristic manner. All the characters summarized above, including the sexual dimorphism of the male P2enp, have already been discussed in more detail in the overall context of the new thalestridimorphan system in Willen (2000).

Based on this characterization, the following genera can be assigned to the Stenheliinae: *Stenhelia*, *Pseudostenhelia*, *Onychostenhelia*, *Melima*. The genus *Cladorostrata* Shen & Tai, 1963 also appears to be a member of the Stenheliinae. According to the illustrations by Shen & Tai (1963),

*Cladorostrata brevipoda* possesses an elongated mandibular basis and an enlarged enp as well as the stout coxa and gnathobase, and the typical “pear-shaped” body (typical female P5?). However, re-examination of the material is necessary. Within the Stenheliinae the genera *Onychostenhelia* and *Pseudostenhelia* can be well characterized by several autapomorphies.

Three species of *Pseudostenhelia* have been described: *P. prima* Wells, 1967 (Mozambique), *P. secunda* Wells, 1971 (Southeast India), redescribed by Ranga-Reddy (1984) from a predominantly freshwater lake connected to the Bay of Bengal and *P. wellsi* Coull & Fleeger, 1977 (South Carolina, USA, Western North Atlantic), redescribed from Mexico by Gómez (2000). These species are linked by the



**Figure 13.** *Melima papuaensis* sp. nov., female. Maxilliped, P4 and A Urosome.

**Figure 13.** *Melima papuaensis* sp. nov., femelle. Maxillipède, P4 et A Urosome.

following autapomorphic characters: P2 - P4 enps are 2-segmented, male P5 confluent, consisting only of two basal/exopodal setae and one median basendopodal seta, female A1 only 5-segmented, anal somite almost completely divided, Mxp syncoxa with only two setae, female P5 benp with only 4 setae, male P2 enp2 with outer seta sexually dimorphically modified.

The monotypic genus *Onychostenhelia* has been established by Itô (1979) for *O. falcifera*, which was collected from a sandy bottom off Oshoro, Hokkaido (Japan). This highly aberrant species shows many derived

characters within the Stenheliinae, according to the very detailed description by Itô (1979): body and swimming legs strongly sclerotized, female A1 7-segmented, A1 of both sexes with large, thorn-like projections on segments I + II, first abdominal somite in the female with two sclerotized ventral protuberances on the anterior border, anal operculum not developed, furcal rami elongated, swimming legs of aberrant shape: P1 with elongated coxa and exp1, all setae incl. outer spines on exp slender, naked and elongated; P2-P4 2-segmented, enps1 and 2 of equal length, enps2 with modified and spatially displaced seta of which all (excl. outer terminal seta) are elongated, naked and located terminally. P2 is more strongly modified than P3 and P4: enp1 large and asetose, enp2 with flap-like outer seta, exopodal segments slightly compressed; male P4 extremely modified: segments distorted and outer spines strongly modified, male and female P5 with a thorn-like modified setae fused to the exp. This latter character is also known from some *Stenhelia* species, e.g. *S. schminkei* sp. nov. and *S. saharae* (see description by Marinov & Apostolov (1985)). However, the involved seta is obviously not always homologous, although the genetic basis for developing such an unusual modification of the P5 seems to be generally present in several Stenheliinae.

More complications arise when looking at the large genus *Stenhelia* containing most of the stenheliid species. The most important diagnostic characters for *Stenhelia* have traditionally been the modified Md palp and the peculiar shape of the female P5 (e.g. Sars, 1906, Monard, 1928). However, these characters are actually subfamily characters and the genus is left without real autapomorphies. Moreover, both the most extreme state of mandibular modification (e.g.

*S. schminkei*, Fig. 3) and the less pronounced and almost unmodified states (e.g. *S. coineauae* and *S. bifida*, see descriptions by Soyer (1972) and Coull (1976) respectively) occur within *Stenhelia*. Thus it is not quite obvious which state is part of the Stenheliinae groundpattern. There are more indications that not only *Stenhelia* but also the two subgenera *Stenhelia* and *Delavalia* are paraphyletic. The male P2 enp sexual dimorphism apparently involves non-homologous structures not only just within the genus *Stenhelia* but also generally within the Stenheliinae. The most common type is

present in species of both subgenera *Stenhelia* and *Delavalia* suggesting a closer relationship between these species rather than between all the species of the subgenus *Delavalia* (Willen, 2000).

However, before the genus *Stenhelia* can be revised, re-descriptions and re-evaluations of characters are necessary. In the case of *Melima*, its clear autapomorphies justify the reinstatement of this genus as a start of such a revision.

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