

***Paramesochra* T. Scott, 1892 (Copepoda, Harpacticoida): a revised key, including a new species from the SW Dutch coast and some remarks on the phylogeny of the Paramesochridae**

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Abstract

Paramesochra mielkei sp.n. is described and figured from the interstices of subtidal sandy sediments off the SW Dutch coast. Kunz' (1981) phylogenetic scheme of the Paramesochridae Lang, 1948 is re-examined and it is suggested that the family comprises two phyletic lines which originated early in paramesochrid evolution. Translation into Linnean hierarchies implies the establishment of two new sub-families. Within the primitive Diarthrodellinae subfam. n., *Tisbisoma* Bozic, 1964 is ancestral to *Diarthrodella* Klie, 1949 s.l. and *Rossopsyllus* Soyer, 1975. *Remanea* Klie, 1929 is transferred to the Paramesochrinae subfam. n. which comprises the genera of both the *Scottopsyllus*- and the *Paramesochra*-group. The aberrant genus *Caligopsyllus* Kunz, 1975, standing close to *Apodopsyllus*, is removed from the *Paramesochra*-group. *P. brevifurca* Galhano, 1970 is splitted into two subspecies and replaced in the genus *Paramesochra*. An attempt is made to assess the phyletic interrelationships of the *Paramesochra*-species and the resulting cladogram splits the genus into four species-groups. *P. mielkei* sp.n. is referred to the *dubia*-group and seems to be closely related to *P. borealis* Geddes, 1981. Finally, an amended diagnosis and a revised key to the species of the genus *Paramesochra* are presented.

Introduction

According to the species checklist of Heip *et al.* (1983), many mesopsammic harpacticoid copepods are known from the Southern Bight of the North Sea. Especially along the Dutch and Belgian coasts, subtidal copepod communities are often dominated by *Cylindropsyllidae* and *Paramesochridae* which are characteristic inhabitants of fine sandy sediments. In spite of this, except for Willems (1981) and Willems & Claeys (1982), no taxonomic studies on benthic copepods have so far been done in this area.

As part of a comprehensive investigation of meiobenthic community structure off the SW Dutch coast, the present paper deals with a new *Paramesochra*-species collected in several shallow subtidal localities. *P. mielkei* sp.n. is often found in great abundance of over 750 ind./10 cm² and co-

occurs with *P. helgolandica helgolandica* Kunz, 1936, *Kliopsyllus holsaticus holsaticus* (Klie, 1929), *K. constrictus constrictus* (Nicholls, 1935) and *Scottopsyllus (Scottopsyllus) minor* (T. & A. Scott, 1895).

In his taxonomic study of the harpacticoid fauna of the isle of Sylt, Mielke (1975) presented drawings of one female specimen of an unknown *Paramesochra*-species. A comparison with the Dutch specimens proved that the two taxa are conspecific.

At present fourteen valid species and subspecies are referred to *Paramesochra* T. Scott, 1892. Since the last review of the genus (Kunz, 1981) three species have been added: *P. unaspina* Mielke, 1984, *P. helgolandica galapagoensis* Mielke, 1984 and *P. kunzi* Mielke, 1984. Most couplets of Kunz' (1981) key are based entirely on female morphology and in consequence his key cannot be used for identifying

males. Therefore, a revised key is presented in which I have tried to use characters common to both sexes or a combination of both female and male characteristics.

Though the phylogenetic method of Hennig has been proved to be a critical instrument for examination and hence has been widely accepted, few copepodologists (Boxshall, 1979; Kunz, 1981, 1984; Tiemann, 1984) have used cladism in harpacticoid taxonomy. Recently, Kunz (1981) presented a phylogenetic approach to the classification of the Paramesochridae Lang, 1948. The description of several new species of paramesochrids since then and a critical evaluation of the genera have caused me to challenge part of Kunz' (1981) phylogenetic scheme.

Materials and methods

Specimens were fixed in 7% formalin and preserved in 70% alcohol, containing a drop of glycerin. Before dissection the habitus was drawn both laterally and dorsally and body-length measurements were made. Specimens were dissected in lactic acid and mounted in polyvinyl lactophenol on Cobb-slides. All figures have been prepared using a camera lucida. Abbreviations used throughout the text and figures are: A2=antenna, Md=mandible, P1–P6=first to sixth leg, exp=exopodite, enp=endopodite, benp=baseopodite. The terminology and presentation of the setal formulae are adopted from Lang (1948, 1965). The terms *pars incisiva*, *lacinia mobilis* and *pars molaris* are omitted in the description of the mandible (Mielke, 1984c). Following Bowman (1971), the term caudal rami is used instead of furca.

Material examined

1. Southern Bight of North Sea, SW Dutch coast (off Delta region), 51°36'04''N, 03°35'47''E (*locus typicus*; 06.09.84), medium sand (Md: 0.310 mm; 5.06% mud), depth 12 m: extremely abundant.

Designated as type-material and deposited in the collection of the Recent Invertebrates Section of the 'Koninklijk Belgisch Instituut voor Natuurwetenschappen', Brussels (IG 27010):

- Holotype female dissected on 3 slides;
- Paratypes: 1 male (allotype) and 1 female dissected on 3 slides; other paratypes (10 females, 10 males) spirit preserved.

Of holotype female were drawn: habitus, antenna, mandible, maxillula, P1–P5, urosoma.

2. North of Westerschelde mouth, 51°28'25''N, 03°28'10''E (06.07.83 and 08.08.83), fine sand (Md: 0.235 mm; 0.39% mud), depth 7.5 m. 6 females.

3. Off Hoek van Holland, 52°29'02''N, 02°58'57''E (18.06.84), medium sand (Md: 0.284 mm; 0.28% mud), depth 32 m. 4 females, 2 males.

4. From Dr. W. Mielke: 1 female dissected on slide. Collected from sandy beach, List/Sylt, Germany (Mielke, 1975).

Other specimens than the type-series are retained in the author's collection.

Results

Paramesochra mielkei sp.n.

Synonymy: *Paramesochra* spec. (in Mielke, 1975)

Etymology: In honour of Dr. W. Mielke (Göttingen) who first encountered this species.

Description

Female

Body-length: 270 μm –305 μm (n=10); \bar{x} = 285 μm ; Holotype: 280 μm) rostrum and caudal rami excluded; 290 μm –330 μm (n=10; \bar{x} = 310 μm ; Holotype: 305 μm) rostrum and caudal rami included.

Body (Fig. 1A, B) slightly depressed dorsoventrally, almost colorless and semi-transparent, distinctly tapering posteriorly, constricted between somites. Thoracic somites 3–5 as broad as cephalothorax. Distinct separation between anterior and posterior body, anal somite narrowest. Cephalothorax about 1.25 times as long as two succeeding somites combined. Genital double-somite longest, without any trace of subdivision. Anal somite shortest. Nauplius eye absent.

Rostrum (Fig. 1A; 3B) diminutive, tip pointing downwards, fused with cephalosoma, without any sensillae.

Except for third and fourth free thoracic somites,

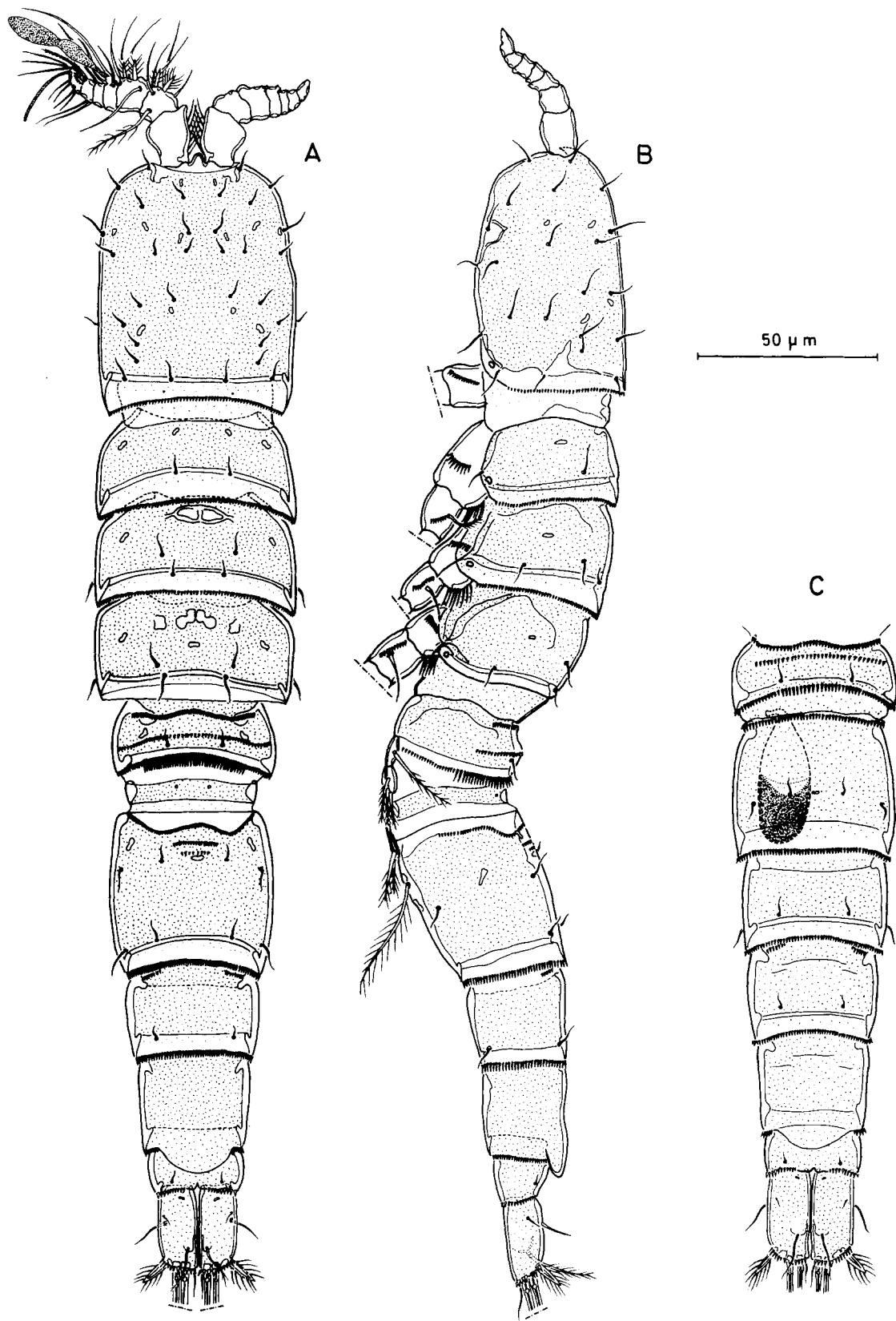


Fig. 1. *Paramesochra mielkei* sp. n. — A. Habitus, dorsal side (♀). — B. Habitus, lateral side (♀). — C. Urosoma, dorsal side (♂).

posterior margin of all body-somites provided dorsally and laterally with minute spinules (=somatic hyaline frill). Integument of caudal rami and somites dorsally and laterally granulated, urosoma and caudal rami also ventrally granulated.

Cephalic shield rectangular, about 1.25 times as long as maximum width, occupying 1/5 of total body-length, furnished with three sets of pores and seven groups of delicate sensillae; posterior margin dorsally and laterally fringed with spinules.

Pleurotergite of first thoracic somite not covered with cephalic integument. Cephalic shield and pleurotergites of second, third and fourth thoracic somites provided with a pore near lateroventral margin. Fifth thoracic somite furnished with three transverse spinular rows, the anterior two restricted to the dorsal side and composed of diminutive spinules, the posterior one formed by long spinules dorsally and minute ones laterally.

Genital double-somite armed with some dorsal spinules in anterior half. Penultimate somite without sensillae. Ventral hind edge of anal somite furnished laterally with some spinules. Pseudopericulum semi-circular, without any spinules or hairs.

Caudal rami (Fig. 1A, B, C; 3C, D; 5A) parallel, about 2.2–2.5 times as long as greatest width; furnished in proximal half with a fine setula ventrally and a bare seta dorsally near outer edge. Posterior margin of caudal ramus armed ventrally with several spinules of which the outermost fine, the inner ones strong and closely set to each other. Dorsal seta plumose, triarticulated at base and arising from a chitinous outgrowth. Subapical outer seta stout, short and two-sided spinulose (SEM examination revealed that the spinules are flattened in a plane perpendicular to the length axis of the seta). So-called principal terminal seta well-developed and accompanied with a long outer seta which is plumose along outer edge, and a fine basally geniculate small seta (proximal part cylindrical and closely set to principal terminal seta) on inner side.

Antennula (Fig. 2A) eight-segmented, short, robust. First segment longest, inner margin with long spinules, furnished with one short spiniform seta near distal margin. Second segment with eight setae, of which one slender and plumose, two thick, short and spinulose, the others slender and bare. Third segment, provided with four long bare setae and two short bilaterally spinulose setae along inner side. Inner distal corner of fourth segment

forming a sub-cylindrical process provided with a thick aesthetasc (L: 36 μm) and a long slender seta which are confluent at base; two bilaterally spinulose setae at base of processus. Fifth segment with a slender bare seta arising from a sub-cylindrical inner outgrowth. Sixth segment similar, but seta two-sided spinulose. Seventh one very small, furnished with a thick two-sided spinulose seta near distal edge, two slender bare seta along outer margin and a slender spinulose seta at inner subdistal corner. Last segment longer than wide, furnished with seven setae and a subapical slender aesthetasc (L: 26 μm).

Antenna (Fig. 3A). Coxa well-defined, squarish, unornamented. Basis slightly widening distally, approximately 1.6 times as long as maximum width, without any spinules or setae. Exopodite unisegmented, sub-cylindrical, slightly bending outwards, about 4 times as long as wide; inner side furnished with one bare seta and two smaller one-sided spinulose setae; apex provided with a stout bare seta accompanied at base by a short outer seta and a minute spinule. First endopodite-segment shortest, furnished with one unilaterally spinulose seta on about middle inner edge. Anterior margin of second endopodite-segment furnished subdistally with some spinules and three bare setae of which distalmost two arising from a small common protuberance; posterior margin with some diminutive spinules and a slender seta; distal edge furnished with five geniculate setae, the posterior one longest and confluent at base with a slender bare seta.

Mandible (Fig. 2B1, B2). Praecoxa (corpus mandibulae) long and narrow. Cutting-edge with one bidentate thick spine, one smaller bidentate spine, about 7 long teeth and one slender bare seta on the dorsal side. Palp well-developed. Coxa-basis long, much widening distally, furnished with three bare setae. Exopodite unisegmented, with four bare setae and two diminutive spinules. Endopodite long, three-segmented; first segment about 3.8 times as long as greatest width, with two bare setae at subdistal corner; second segment approximately 2.5 times as long as greatest width, without any ornamentation; distal segment square, with two bare setae at subproximal corner and three slender apical setae of which at least two confluent at base.

Maxillula (Fig. 2C). Praecoxa squarish, inner edge with a few long fine spinules subdistally. Arthrite of praecoxa about 1.4 times as long as

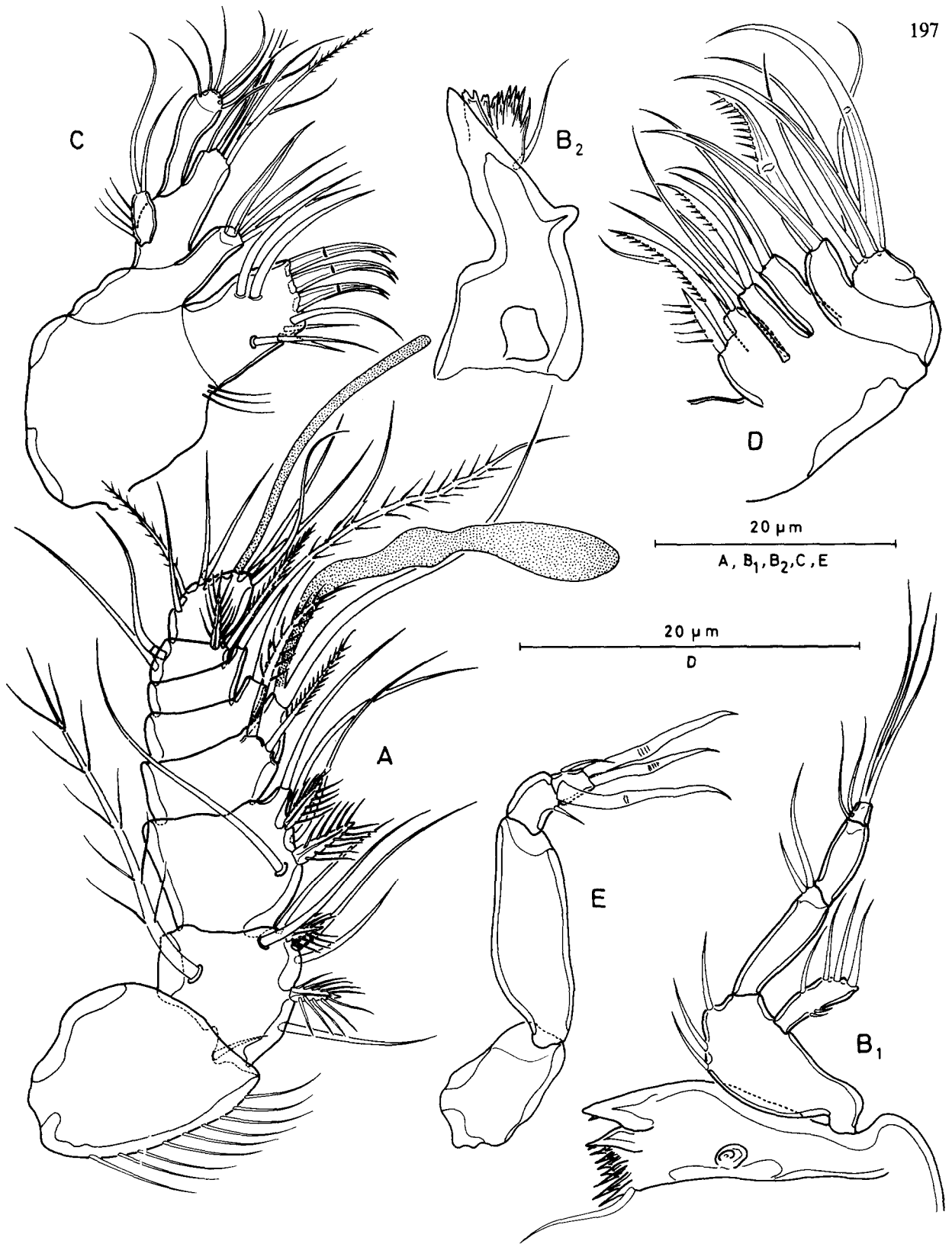


Fig. 2. *Paramesochra mielkei* sp. n. (♀). — A. Antennula. — B1. Mandible. — B2. Corpus mandibulae (Praecoxa). — C. Maxillula. — D. Maxilla. — E. Maxillipede.

greatest width, armed with three pairs of curved spines and one slender seta on apical edge, two closely set short setae and one slender seta on dorsal edge, two juxtaposed slender setae on anterior surface near ventral edge. Inner process of coxa long and cylindrical, furnished with three closely set setae apically and one subapical stout spine. Inner process of basis extending beyond coxal inner process, armed with five closely set setae apically (of which one spinulose) and one slender subdistal seta on ventral edge. Endopodite long, unisegmented, distal part swollen and furnished with six bare setae. Exopodite represented by a small segment, provided with some fine spinules along outer edge and two slender setae of different lengths, distally.

Maxilla (Fig. 2D). Syncoxa with thickly chitinous outer rim and furnished with three endites. Proximal endite clearly bilobed, armed with two unilaterally spinulose stout setae on dorsal lobe, with two slender setae on ventral lobe. Second endite sub-cylindrical, close to second endite, armed apically with two slender setae and one spinulose seta. Distal endite clearly separated from middle one, sub-cylindrical, furnished with three closely set setae apically. Basis armed apically with one stout bare seta and one, medially geniculate, strong claw which is spinulose along distal inner edge. Endopodite undistinctly subdivided, furnished with three slender setae, one stout seta and one geniculate claw-like seta.

Maxillipede (Fig. 2E). Basis approximately 1.7 times as long as maximum width, unornamented. Endopodite three-segmented (?). First segment longest, about 2.9 times as long as greatest width, without any spinules or hairs. Second segment with one spiniform short seta. Third segment minute, with two apical geniculate claws, one setula on outer edge and a geniculate strong spine near junction with second segment.

Natatorial legs (Fig. 4) with two-segmented endopodites, except for P1 always shorter than three-segmented exopodites.

P1 (Fig. 4A). Coxa well-developed, furnished with some spinules on outer subdistal edge and two oblique spinular rows in proximal half of anterior surface and near outer margin. Basis somewhat shorter than coxa; outer edge armed with a short bare seta, inner edge furnished with a thick unilaterally spinulose seta and a few spinules. Exopodite two-segmented, much shorter than en-

dopodite: proximal segment longer than distal one, somewhat swollen distally and about 2 times as long as greatest width, fringed with spinules along outer edge and provided with a spinulose seta at subdistal outer corner; distal segment armed with three apical one-sided plumose slender setae of different lengths and a spinulose stout seta on outer subdistal edge, outer margin fringed with fine spinules. Endopodite two-segmented, demarcation between segments not clearly defined, possibly prehensile; proximal segment longest, approximately 4 times as long as maximum width and exceeding exopodite, except for spinulose outer margin unarmed; second segment 1/4 the length of preceding one, armed with two stout claw-like setae which are medially geniculate and spinulose along subdistal edge.

P2 (Fig. 4B). Free edge of intercoxal plate clearly swelling out bilaterally, ventral side concave. Coxa markedly protruded outwards over basis; furnished with an arched row of fine spinules near subdistal outer corner. Inner lobe of basis provided with long spinules; outer margin armed with a short bilaterally spinulose stout seta and a row of fine spinules in distal part. Exopodite three-segmented: first segment armed with a one-sided spinulose stout seta, inner and outer margin fringed with spinules; second segment shortest, forming spinous projection and incised appendicular hyaline frill at inner distal corner, outer margin spinulose and furnished with a stout seta subdistally; distal segment longest, about 2.4 times the length of preceding one, outer margin spinulose and armed with two stout setae arising from clearly stepped edge, apical part with a long medially geniculate strong seta, an outwards curved spinous projection and an inner slender plumose seta subdistally. Endopodite about two-thirds the length of exopodite, two-segmented, both segments equally long: inner margin of first segment forming a rudimentary spinous projection, outer margin spinulose; second segment swollen, wider than first one, furnished with an arched row of spinules on anterior surface, fine spinules along outer margin and a two-sided spinulose outer seta subapically.

P3 (Fig. 4C). Ventral edge of intercoxal plate more concave than in preceding leg. Coxa and basis as in P2 except for outer seta of basis which is longer, slender, plumose and biarticulated at base. General form and setation of exopodite as in P2;

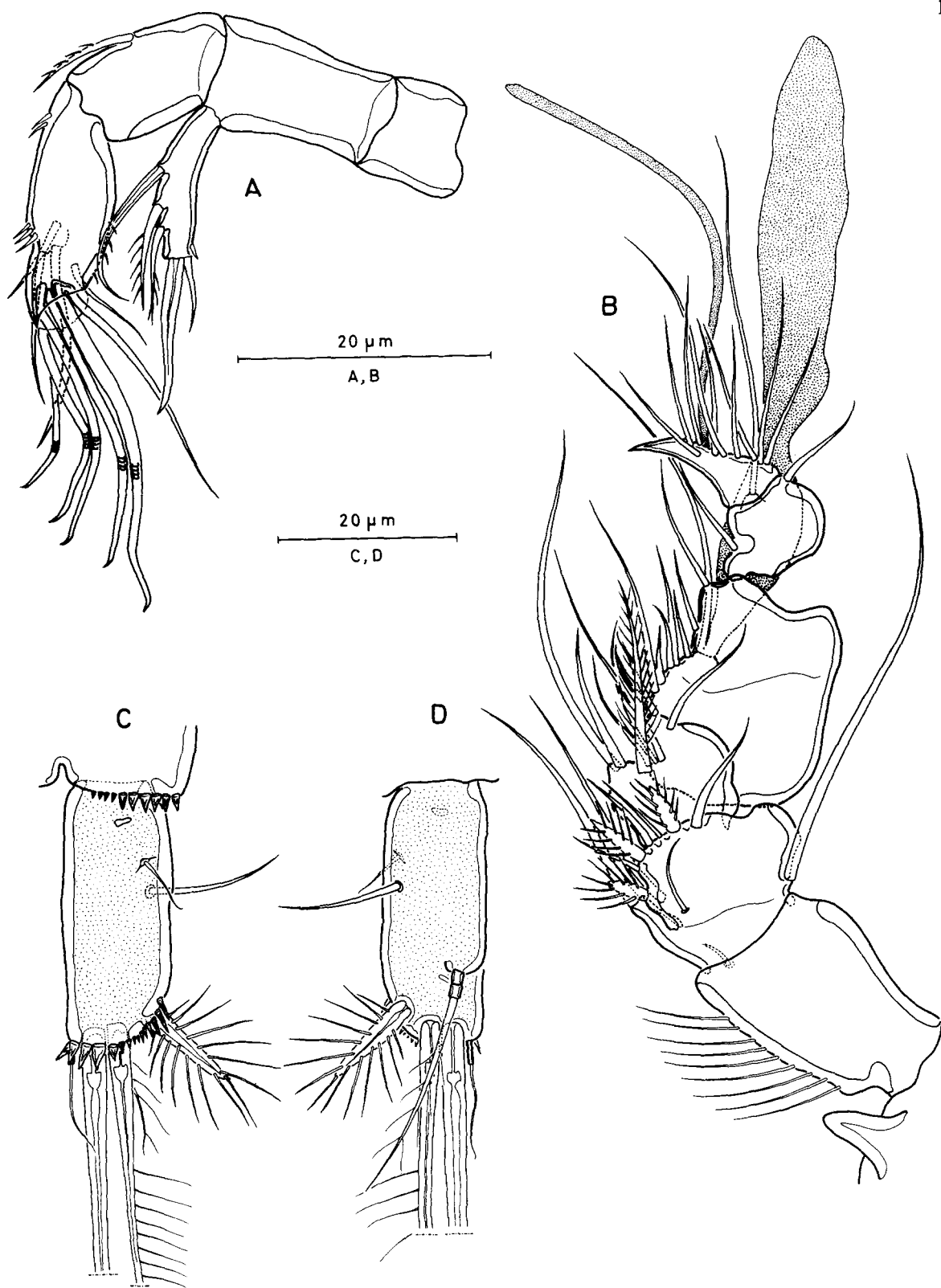


Fig. 3. *Paramesochra mielkei* sp. n. - A. Antenna (♀). - B. Antennula (♂). - C. Caudal ramus, ventral side. - D. Caudal ramus, dorsal side.

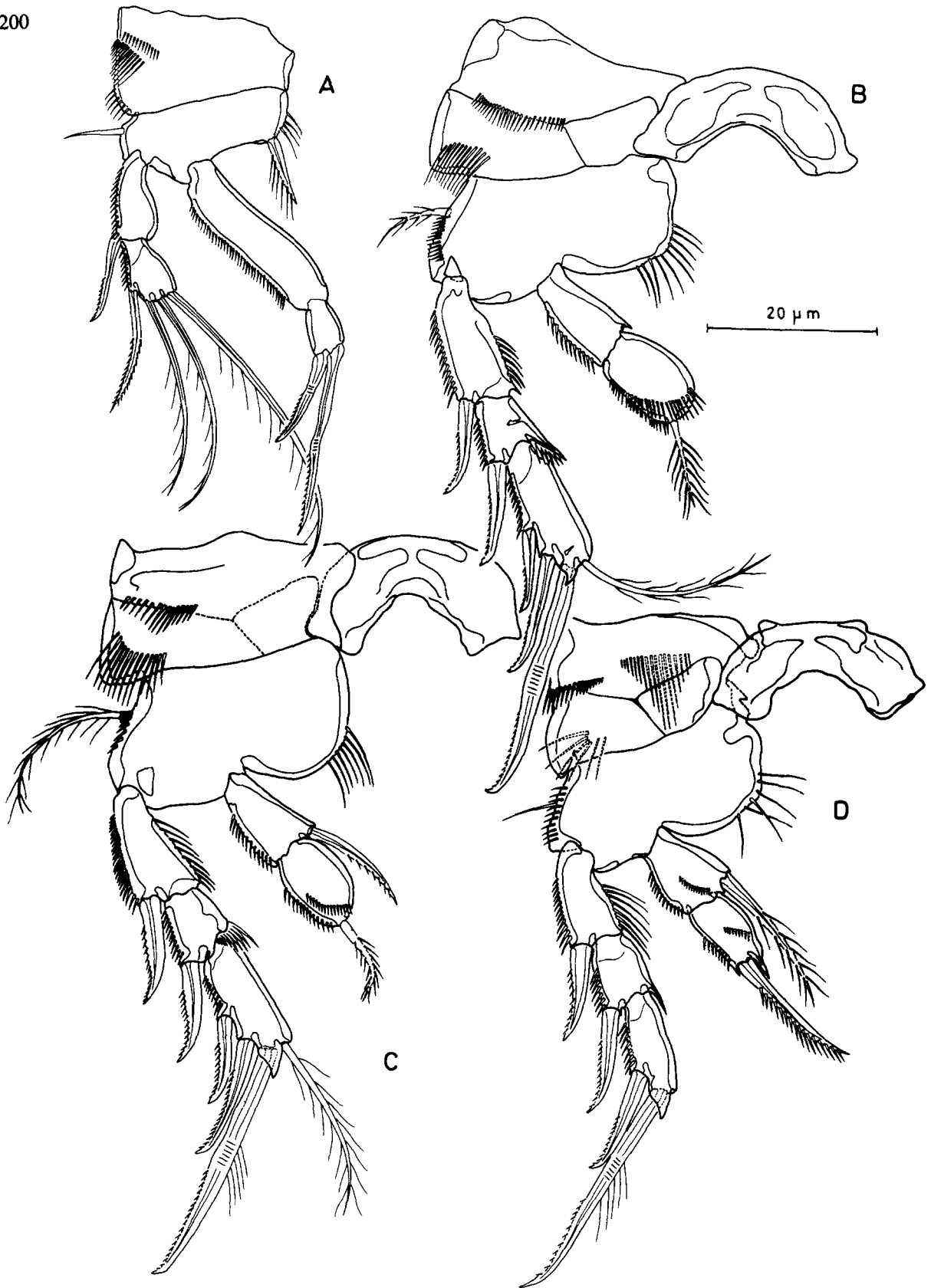


Fig. 4. *Paramesochra mielkei* sp. n. (♀). - A. P1. - B. P2. - C. P3. - D. P4.

spinous projection of distal segment strongly developed, not observed in middle segment. Endopodite two-segmented: first segment slightly longer than distal one, armed with a strong spinulosa seta on inner subdistal corner and diminutive spinules along outer margin; second one ovoid in shape, with an outer spinulose seta subapically, an arched spinular row in distal half of anterior surface and fine spinules along outer edge.

P4 (Fig. 4D). Free edge of intercoxal plate as in *P2*, dorsal edge bilaterally forming a reduced projection. Coxa provided with a row of long spinules in both proximal and distal half of posterior surface and an oblique row of short spinules on posterior surface near middle outer margin. Except for the short bare seta on middle outer edge, armature and general form of basis as in preceding leg. Exopodite three-segmented: proximal segment with inner and outer margin spinulose and a strong spinulose seta at outer subdistal corner; middle segment shorter, forming an inner spinous projection, outer edge provided with minute spinules and a stout seta subdistally; distal segment narrowest with outer side spinulose and a stout seta arising from stepped edge, apical margin forming a well-developed spinous outgrowth and armed with a long medially geniculate seta. Endopodite as in preceding leg except for distal segment which is forming a spinous inner projection.

Leg 5 (Fig. 5B). Baseoendopodites of fifth pair of legs confluent, forming a very large plate, extending beyond exopodite, each with a long slender plumose seta lateral to exopodite. Baseoendopodital plate distinctly narrowing apically and bilobed at distal edge; each lobe furnished with a short inner and a longer outer seta, both bilaterally spinulose and stout. Exopodite small, sub-circular in shape; inner edge spinulose; armed with three setae, the proximal long and finely spinulose along outer edge, the middle straight, shorter and bilaterally spinulose, the distal stout and two-sided spinulose.

Genital complex (Fig. 5A). *P6* forming a small transverse plate, bilaterally furnished with a long plumose seta just inside outer corner and two inner spiniform setae; distal edge crenellate.

Male

Body-length: 270 μm –300 μm (n = 10; \bar{x} = 275 μm) rostrum and caudal rami excluded; 290 μm –320 μm (n = 10; \bar{x} = 300 μm) rostrum

and caudal rami included.

General body-shape, colour, ornamentation and sensillar pattern as in female. Sexual dimorphism in antennula, fifth and sixth leg; genital segmentation (Fig. 1C). Last thoracic somite (= *P6*-bearing somite) with a mediodorsal pore, two dorsal and two ventrolateral sensillae. Genital somite with two dorsal and two lateral sensillae.

Antennula (Fig. 3B) six-segmented, short, robust; subchirocer; antennular hyaline frill not observed. First and fourth segments longest. Distal edge of first segment with a minute spiniform seta, inner margin provided with long fine spinules. Middle inner margin of second segment forming a sub-cylindrical processus from which a slender bare seta arises; anterior margin furnished with three thick bilaterally spinulose setae, one long and four short bare setae; a fine seta arises from dorsal surface. Third segment armed with eight setae, one of which is two-sided plumose. Fourth segment swollen; inner edge provided with eight setae, most of which are spiniform and short, anterior margin forming a concave depression in which fifth segment articulates (subchirocer apparatus); ventral surface furnished with a constricted sausage-shaped aesthetasc (L: 50 μm) and a slender bare seta which are confluent at base and arising from a small protuberance near middle inner edge. Penultimate segment shortest, with a short bare seta on both inner middle edge and outer proximal corner; anterior margin with a long slender seta arising from a small processus. Last segment triangular, furnished with nine bare setae and a slender aesthetasc (L: 37 μm).

Leg 5 (Fig. 5C). Baseoendopodite confluent, forming a large unarmed plate, extending just beyond exopodites, each with one slender plumose outer seta lateral to exopodite. Exopodite small, subcircular, furnished with four setae: two outer unilaterally spinulose setae, one bilaterally spinulose subapical short seta and one long bilaterally spinulose seta apically; inner margin armed with diminutive spinules.

Leg 6 (Fig. 5D). Sixth pair of legs not confluent. Exopodite and baseoendopodite forming an elongate triangular plate which is provided with a slender plumose seta at subproximal outer corner and two juxtaposed spinulose short setae near middle of distal edge. Distal margin forming a hyaline lobe devoid of punctuations.

Spermatophore (Fig. 1C; 5E). Ovoid, approxi-

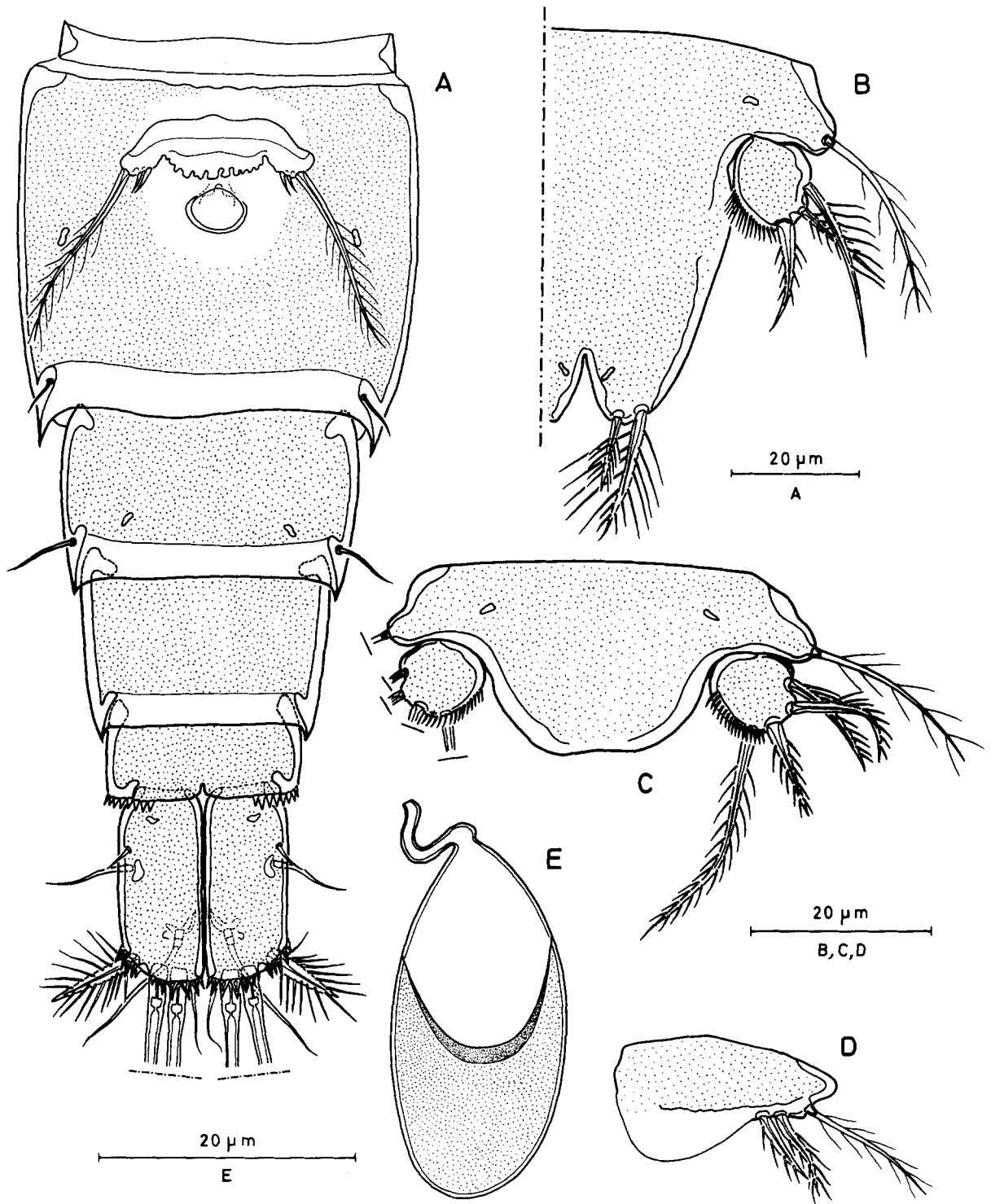


Fig. 5. *Paramesochra mielkei* sp. n. — A. Urosoma, ventral side (♀). — B. P5 (♀). — C. P5 (♂). — D. P6 (♂). — E. Spermatophore.

mately 2 times as long as maximum width; 1/9 of total body-length.

Variability

Except for the body-length and the length:width ratio of the caudal rami, no conspicuous variability in the size and the ornamentation of the appendages was detected.

Distribution

Germany: List/Sylt (Mielke, 1975; as *Paramesochra* spec.);

The Netherlands: off Hoek van Holland, N. of Westerschelde-mouth, off shore Delta area;

Belgium: coastal zone;

France: Douarnenez Bay (Bodin, 1984; as *Paramesochra* sp. Mielke, 1975).

Discussion

1. The phylogenetic position of *Paramesochra* T. Scott, 1892 within the *Paramesochridae*

Kunz (1981) reviewed the main characteristics and the taxonomy of the *Paramesochridae* and as a result proposed a scheme of the evolutionary pathways within the family. Since then a number of interesting species have been described (Mielke, 1984a, b; 1985) which makes the cladogram capable of adaptation to the knowledge now available. Through out-group comparison with *Tachidiopsis* (Tisbidae), Kunz deduced the plesiomorphic characters that were present in the ancestor of the *Paramesochridae*: three-segmented condition in exopodite of antenna and mandible, in endopodite of mandible and maxilla, in endopodite and exopodite of P1–P4; baseoendopodite and exopodite P5 not fused in both sexes; distal segment of exopodite P1–P4 with 8 setae; distal segment of endopodite P2–P4 with 5 setae.

According to Kunz (1981) *Rossopsyllus kerguelenensis kerguelenensis* Soyer, 1975 is closer to the ancestral form than any other species because of the plesiomorphous three-segmented condition in exopodite and endopodite of mandible, maxillar endopodite, exopodite P2–P4 and endopodite P3–P4. On the other hand, the biarticulated an-

tennal exopodite, the two-segmented condition in exopodite P1 and endopodite P1–P2, the reduced setation of distal podomeres in P2–P4 (5 setae in exopodite, 3 in endopodite) and the fused leg 5 in both sexes can be considered to be apomorphies.

Unquestionably, the discovery of *R. kerguelenensis quellonensis* Mielke, 1985 from Chile throws some doubt on the validity of Kunz' (1981) conclusions on the separate phylogenetic position of *Rossopsyllus* Soyer, 1975. In this subspecies the mandibular palp possesses a unisegmented exopodite and a two-segmented endopodite (the distal segment being the basal fusion of the apical setae).

In Kunz' (1981) cladogram the other *paramesochrid* genera are referred to three groups: the *Diarthrodella*-group (*Diarthrodella* Klie, 1949; *Tisbisoma* Bozic, 1964; *Remanea* Klie, 1929; *Paramesochra brevifurca* Galhano, 1970), the *Paramesochra*-group (*Paramesochra* T. Scott, 1892; *Kliopsyllus* Kunz, 1962; *Kunzia* Wells, 1967; *Caligopsyllus* Kunz, 1975) and the *Scottopsyllus*-group (*Scottopsyllus* (*Scottopsyllus*) Kunz, 1962; *Scottopsyllus* (*Intermedopsyllus*) Kunz, 1962; *Scottopsyllus* (*Wellsopsyllus*) Kunz, 1981; *Leptopsyllus* (*Leptopsyllus*) T. Scott, 1894; *Leptopsyllus* (*Paraleptopsyllus*) Lang, 1948; *Apodopsyllus* Kunz, 1962). His conclusion, however, that the *Scottopsyllus-Paramesochra* branch is ancestral to the *Diarthrodella*-group because of a shared three-segmented mandibular endopodite, cannot be maintained. Recently, Mielke (1984a) described *Diarthrodella parorbiculata pacifica* which has a triarticulated mandibular endopodite. A similar characteristic has been found in the nominate subspecies *D. parorbiculata parorbiculata* Wells, 1963 from Northern Ireland (pers. observ.). Since the distal endopodital segment is diminutive, it can be presumed that the absence of the plesiomorphous state in some species with a bi-segmented endopodite (e.g. *D. psammophila* Bocquet & Bozic, 1955) is due to deficiencies in the description. Hence, it is clear that phylogenetic inferences based on comparative mandibular palp morphology must be made with caution.

According to Kunz (1981) the *Paramesochra*-group and the *Scottopsyllus*-group are linked to each other by the two-segmented maxillar endopodite, the three-segmented mandibular endopodite and the structure of the fifth leg in both sexes. The latter two similarities are real, but it is erroneous to

PARAMESOCHRIDAE

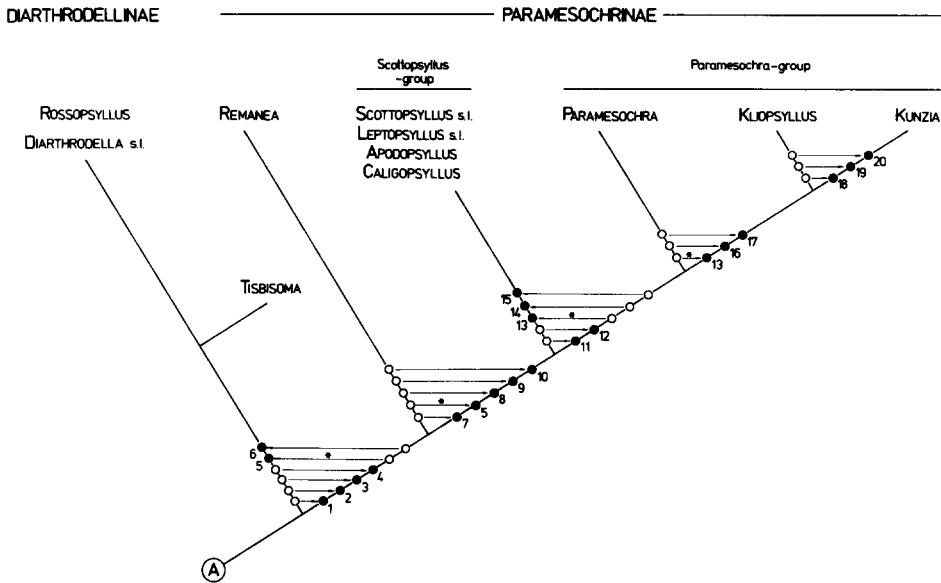


Fig. 6. Cladogram of the Paramesochridae, based on the following apomorphies: 1=enp P2–P4 2-segmented; 2=exp A2 2-segmented; 3 = reduction in setation of distal segment exp (5-5-5) and enp (3-3-3) P2–P4; 4 = proximal segment enp P2–P4 without inner seta; 5 = exp P1 2-segmented; 6 = reduction benp P5; 7 = reduction in setation of distal segment exp (4-4-4) and enp (2-2-2) P2–P4; 8 = distal segment exp P1 with 5 setae; 9 = proximal segment enp P1 without inner seta; 10 = middle segment exp P2–P4 without inner seta; 11 = exp A2 1-segmented; 12 = exp Md 1-segmented; 13 = distal segment exp P1 with 4 setae; 14 = enp P2–P3 1-segmented; 15=reduction in setation of distal segment exp (2-2-2) and enp (1-1-1) P2–P4; 16=enp P2–P4 1-segmented; 17=distal segment exp P4 with 3 setae; 18 = exp P1 1-segmented; 19 = enp P1 unarmed lobe; 20 = distal segment exp P4 with 2, enp P4 with 1 seta. * = parallel evolution (cf. 5 and 13), A = ancestor.

interpret them as evidence of close phylogenetic affinity (monophyly), because they are symplesiomorphies and may just represent a common point through which all paramesochrid genera passed. The biarticulated condition in the maxillar endopodite cannot be considered as a strict apomorphy, since in some species (e.g. *Kliopsyllus panamensis* Mielke, 1984; *K. unguiseta* Mielke, 1984) the plesiomorphous state is reflected in the indistinctly subdivided proximal (or distal) endopodital segment.

The Paramesochridae comprise two branches (= adelphotaxa sensu Ax, 1984) which diverged early in the evolution of the family – the plesiomorphous line (Diarthrodellinae subfam. n.) represented by *Diarthrodella* Klie, 1949, *Tisbisoma* Bozic, 1964 and *Rossopsyllus* Soyer, 1975, the apomorphous sister-group (Paramesochrinae subfam. n.) formed by the *Scottopsyllus*-group, the *Paramesochra*-group and the genus *Remanea* Klie, 1929.

The Paramesochrinae subfam. n. are defined by at least four apomorphies: (1) antennal exopodite two-segmented; (2) endopodite P2–P4 two-segmented; (3) absence of inner seta on proximal segment of exopodite P2–P4; (4) reduction in setation of distal exopodital (5 setae) and endopodital (3 setae) segment of P2–P4. The plesiomorphous alternatives of these characters (antennal exopodite three-segmented, endopodite P2–P4 three-segmented, presence of inner seta on proximal segment of exopodite P2–P4, primitive setation of distal exopodital (6–8 setae) and endopodital (4–5 setae) segment of P2–P4) occur in the Diarthrodellinae subfam. n. which constitutes a monophyletic taxon (= monophylum sensu Ax, 1984) by reason of two apomorphies: (1) reduction of the baseoendopodite P5 leading to the extreme condition in e.g. *Diarthrodella lancifera* Kunz, 1983 and *D. galapagoensis* Mielke, 1984; (2) two-segmented exopodite P1. The latter is an apomorphous character that has, however, arisen twice

during paramesochrid evolution (parallel evolution).

Within the Diarthrodellinae subfam. n. the genus *Tisbisoma* is undoubtedly more plesiomorphous than any other species. The three-segmented condition in antennal exopodite, exopodite P2–P4 and endopodite P1–P4, and the primitive setation of the distal exopodital (7–8 setae) and endopodital (4–5 setae) segment in P2–P4 relate the genus closely to the paramesochrid stem species. The unisegmented mandibular palp probably constitutes an autapomorphy for *Tisbisoma*, however, a critical redescription of *T. spinisetum* remains indispensable to elucidate the structure of the mouthparts within this genus. The apomorphous branch of the Diarthrodellinae subfam. n. unites the more advanced genera *Diarthrodella* and *Rossopsyllus*. Having compared the different species of the genus *Diarthrodella*, my conclusion is that the genus is by no means a monophyletic group. Even the recent division by Kunz (1981, 1983) into an *orbiculata*-group and a *secunda*-group failed to elucidate the interspecific phyletic relationships within this artificial genus. Following Mielke (1985), *D. chilensis* Mielke, 1985 is more closely related to the genus *Rossopsyllus* than to any other species of the *orbiculata*-group. Clearly, a thorough revision of *Diarthrodella* s.l. (Huys, in prep.) has to confirm the polyphyletic status of this genus and as a result will amend the generic diagnosis.

Contrary to Kunz (1981), the genus *Remanea* and *Paramesochra brevifurca* Galhano, 1970 are referred to the apomorphous sister-group of the Diarthrodellinae subfam. n. This is in complete agreement with Soyer's (1975) statement that 'nous avons un groupe *Tisbisoma-Rossopsyllus-Diarthrodella-Idyanthopsis* à affinités indiscutables, avec une forme de transition vers les autres Paramesochridae, le genre *Remanea*' (Kunz (1962) regards *Idyanthopsis* Bocquet & Bozic, 1955 as a synonym of *Diarthrodella*). The triarticulated exopodite P1 in *Remanea* represents a unique character within the Paramesochridae. This plesiomorphous condition relates the genus closely to the hypothetical ancestor and moreover, offers support for the hypothesis that the two-segmented exopodite P1 occurred independently in each sub-family (parallel evolution). Within the Paramesochrinae subfam. n., *Remanea* forms the plesiomorphous branch and shares at least four advanced characters (synapomorphies) with the apomorphous lineage of the sub-family,

which are sufficient to falsify Kunz' (1981) hypothesis.

In Kunz' cladogram (Kunz, 1981), *Paramesochra brevifurca* stands apart as the apomorphous adelphotaxon of *Remanea*. In spite of this the author hesitated in establishing a new genus. The present author, however, must agree with Galhano (1970) and places the species in the genus *Paramesochra* T. Scott, 1892 (see below).

The apomorphous branch within the Paramesochrinae subfam. n. is defined by at least five apomorphies: (1) two-segmented exopodite P1 (= parallel evolution); (2) absence of inner seta on proximal endopodital segment P1; (3) reduction of distal setation in exopodite (4 setae) and endopodite (2 setae) P2–P4; (4) exopodite P1 with at most 5 setae on distal segment; (5) absence of inner seta on middle exopodital segment P2–P3.

Caligopsyllus Kunz, 1975 is the weakest component in Kunz' (1981) phylogenetic system of the Paramesochridae because of its combination of plesiomorphic characters (inner seta on middle segment and 3 setae on distal segment of exopodite P2–P3) and autapomorphies. As a result of its presumed ectoparasitic existence (Kunz, 1981) this monotypic genus displays an extensive set of autapomorphies (absence endopodite P2–P4; exopodite P1 and P4 unisegmented; endopodite P1 with 2 strong curved claws; both P5 forming a common plate in both sexes). Despite some fundamental differences (cyclopid-like, dorsoventrally flattened (= fusiform depressed sensu Coull (1977) habitus, unisegmented exopodite P4), Kunz (1975) initially related *Caligopsyllus* to *Apodopsyllus* because of the loss of the endopodite P2–P4. Later on, Kunz (1981) himself pointed out that it would be unwise, however, to select the superficial similarity of the swimming-legs as evidence of affinity as this might be the product of convergent evolution. Considering the structure of the exopodite P2–P3 (3 setae on distal segment) Kunz (1981) found a weakly defined similarity with *Kliopsyllus* (partim) and placed the genus in the *Paramesochra*-group. In his phylogenetic scheme, *Caligopsyllus* constitutes the apomorphous sister-group of the *Kliopsyllus-Kunzia* complex. Kunz' idea, however, cannot be correct since synapomorphic characters which can substantiate the monophyletic status of the *Kliopsyllus-Kunzia* branch are not present in his cladogram.

In spite of the profound modifications upon the

basic functional plan, I believe *Caligopsyllus* should be incorporated into the *Scottopsyllus*-group. This hypothesis is supported by re-examination of the types of *C. primus* Kunz, 1975 (Huys, in prep.). The P2 figured by Kunz (1975: p. 204, Abb. 202) clearly shows: (1) an inner seta on the middle segment of exopodite P2–P3, (2) 3 setae (the outer of which is spiniform and small) on distal segment exopodite P2–P3. Within the Paramesochrinae subfam. n. the former plesiomorphic character is further only found in the genus *Remanea*. Detailed examination of the holotype of *C. primus*, however, revealed that the strongly developed appendicular hyaline frill (see also *Apodopsyllus panamensis* Mielke, 1984b) of podomeres II and III of P2–P3 has been misinterpreted by Kunz (1975) as setae. As a result one can postulate that *Caligopsyllus* and *Apodopsyllus* form a monophyletic group of which the former genus constitutes the apomorphous line which has by no means affinity with *Kliopsyllus*.

In the remaining genera of the Paramesochrinae subfam. n., two groups can be recognised which evolved from a common ancestor. The *Paramesochra*-group unites the genera *Paramesochra* (incl. *P. brevifurca*), *Kliopsyllus*, and *Kunzia*, and represents the apomorphous branch. The plesiomorphous *Scottopsyllus*-group formed by the genera *Scottopsyllus*, *Leptopsyllus*, *Apodopsyllus* and *Caligopsyllus* stands apart by three apomorphies: (1) endopodite P2–P3 unisegmented (parallel evolution with *Kliopsyllus-Kunzia*), (2) reduction in distal setation of exopodite (2, 2 and 2 setae, resp.) and endopodite (1 seta) in P2–P4, (3) distal segment exopodite P1 with 4 setae. The genera of the *Paramesochra*-group are linked to each other by the unarticulated condition in the antennal and mandibular exopodite (synapomorphy). The hypothesis that the plesiomorphous alternative occurred in the stem species of the *Scottopsyllus*-group is supported by the presence in some species of a two-segmented exopodite in the antenna (e.g. *Leptopsyllus* (L.) *dubaty* Soyer, 1975; *Apodopsyllus vermiculiformis* Lang, 1965) or in the mandible (e.g. *Scottopsyllus* (S.) *pararobertsoni* Lang, 1965; *Apodopsyllus unguiformis* Coull & Hogue, 1978; *A. africanus listensis* Mielke, 1975).

A detailed scheme of the evolutionary pathways within the *Scottopsyllus*-group will be given in a subsequent paper (Huys, in prep.).

Within the *Paramesochra*-group the genus *Paramesochra* constitutes without doubt the plesiomorphous branch. The apomorphous branch is formed by the genera *Kliopsyllus* and *Kunzia* of which the latter is more advanced by reason of the reduced structure of leg 1: (1) exopodite unisegmented; (2) endopodite an unarmed lobe. Kunz (1981) had some doubt about the systematic position of *Kliopsyllus spiniger spiniger* Wells, Kunz & Rao, 1974 and *K. idiotes* Wells, 1967 since these species show an aberrant setation of leg 4, being more primitive than in all other members of the genus *Kliopsyllus*. At present *K. idiotes* and *K. panamensis* Mielke, 1984 possess 3 setae (instead of 2) on the distal exopodital segment P4; *K. holsaticus varians* Kunz, 1951, *K. spiniger spiniger*, *K. spiniger ornatus* Kunz, 1981, *K. similis* Mielke, 1984, *K. unguiseta* Mielke, 1984 and probably *K. californicus* Kunz, 1981 possess 2 setae (instead of 1) on the distal endopodital segment P4.

It is clear that all *Kliopsyllus*-species can be derived by reduction from an ancestor with 3 and 2 setae on distal exopodite- and endopodite-segment P4, respectively. The derived condition (2 and 1 setae, resp.) then constitutes not only a third autapomorphy for the genus *Kunzia*, but, also evolved independently in *Paramesochra* sensu Kunz, 1981 (= excl. *P. brevifurca* Galhano, 1970). In consequence the genus *Paramesochra* and the branch *Kliopsyllus-Kunzia* must share a common ancestor with at least 3 and 2 setae on distal exopodital and endopodital segment P4, respectively. Such plesiomorphous characteristic is found in *P. brevifurca* Galhano, 1970 (4 and 3 setae, resp.) which belongs undoubtedly to the *Paramesochra*-group. The pentasetose condition in the distal exopodite-segment of leg 1 is clearly a plesiomorphy, absent in all other relatives of the group. Since inflation of taxa should be avoided whenever possible, I include *P. brevifurca* in the genus *Paramesochra*, rather than erecting a new genus. The lineage *Kliopsyllus-Kunzia* then is defined by the following apomorphies: (1) endopodite P2–P4 unarticulated; (2) exopodite P1 with 4 setae on distal segment (parallel evolution in *Scottopsyllus*-group); (3) distal segment exopodite P4 with 3 setae.

As a result of these considerations, a cladogram (Fig. 6) can be drawn. Translation into Linnean hierarchies implies the establishment of two sub-

families: Diarthrodellinae subfam. n. and Paramesochrinae subfam. n.

Among them, the latter is clearly the most successful group and until now comprises over 80% of the 116 valid species and subspecies. Regarding the cyclopid-like habitus of the primitive Paramesochridae (e.g. *Tisbisoma spinisetum* Bocquet & Bozic, 1955), one can assume that the family evolved from an ancestor which lived on or near the surface of the substratum and not within it (cf. *Tachidiopsis* Sars, 1911). Exploitation of the pore system between the sand grains, presenting as it does an endless labyrinth with many niches, has led to an explosive speciation of interstitial forms. In consequence their life cycle offers the potential of specializations for interstitial existence. Epibenthic species could occupy the interstitial habitat permanently by maturing at a larval or juvenile level. As Kunz (1981) pointed out, it is striking that in highly specialized Paramesochridae (e.g. *Apodopsyllus*, *Leptopsyllus*) with extreme reduction in the pereopods 'noch relativ ursprüngliche Gliederungen im Bau der Mundwerkzeuge zu erkennen sind'. Although the postembryonic development of interstitial species is unknown (except for *Arenopontia* (*Neoleptastacus*) *indica* Rao, 1967), most larval de-

velopment studies support the fact that the adult morphology and setation of the mouthparts is attained in the first copepodid stage. This means, that paedomorphosis could be a main principle in the evolution of the Paramesochrinae subfam. n., or as Gould (1977) put it, 'a rigid requirement for small size must be the primary determinant of progenesis among interstitial organisms'. The term paedomorphosis is used here as a general term for the presence of ancestral larval characters in adult descendants.

Especially in the *Scottopsyllus*-group, there is evidence that certain taxa have undergone paedomorphic evolution. *Scottopsyllus*, *Leptopsyllus* (*Leptopsyllus*), *Leptopsyllus* (*Paraleptopsyllus*) and *Apodopsyllus* can easily be included in a morphological series with increasingly pronounced larval characters.

2. Phylogeny of the genus *Paramesochra* T. Scott, 1892

Within the genus *Paramesochra*, *P. brevifurca* Galhano, 1970 represents undoubtedly the plesiomorphic branch (Fig. 7). The apomorphic branch then, stands apart by three apomor-

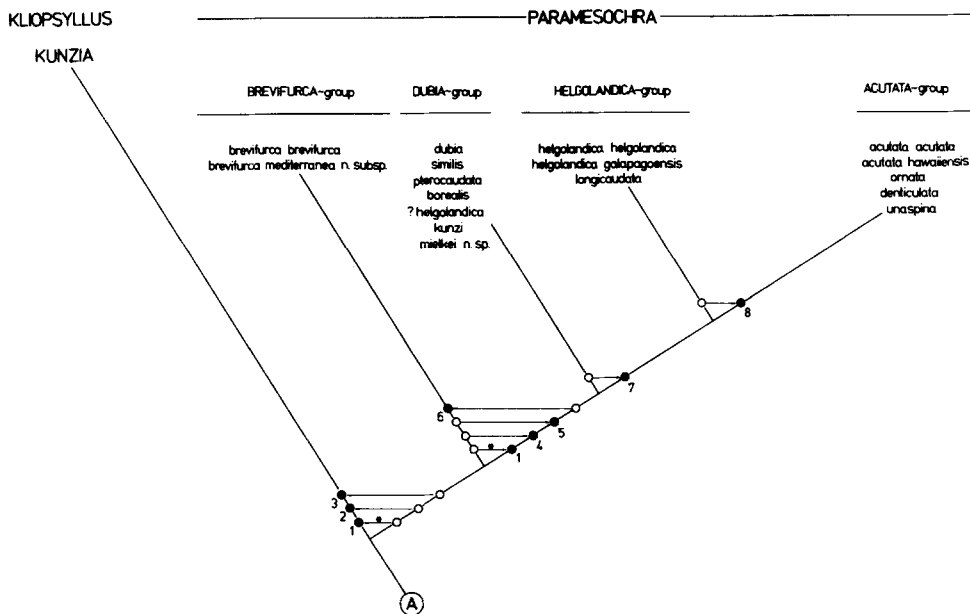


Fig. 7. Cladogram of the genus *Paramesochra* T. Scott, 1892, based on the following apomorphies: 1 = distal segment exp P1 with 4 setae; 2 = enp P2–P4 1-segmented; 3 = distal segment exp P4 with 3 setae; 4 = distal segment enp P2–P4 with 1 seta; 5 = distal segment exp P4 with 2 setae; 6 = enp Md 2-segmented; 7 = absence inner seta proximal segment enp P3; 8 = absence inner seta proximal segment enp P4.

* = parallel evolution (cf. 1); A = ancestor.

phies: (1) distal segment exopodite with 4 setae (= parallel evolution in *Kliopsyllus-Kunzia*); (2) endopodite P2–P4 one-segmented; (3) distal segment exopodite P4 with 3 setae. The two-segmented mandibular endopodite, might be an autapomorphy for the *brevifurca*-group. At present *P. brevisfurca* has been recorded from Porto, Portugal (Galhano, 1970) and Sassari, Sardinia, Italy (Cottarelli, 1970). Cottarelli's specimens, however, show some differences: mandibular endopodite one-segmented (instead of two-), rostrum not almost extending to first antennular segment, differences in setation of maxilla and maxillula. Though these specimens are without doubt closely related to Galhano's material, I prefer to establish a new subspecies *P. brevisfurca mediterranea* subsp. n. for the Sardinian specimens.

Based on the presence or absence (apomorphy) of the inner seta in the proximal segment of endopodite P3–P4, one can distinguish three species-groups which are phylogenetically related to each other. Inside the *dubia*-group, the plesiomorphous state is retained in both P3 and P4, and a progressive elongation of the caudal rami occurred, resulting in the extreme condition in e.g. *P. similis* Kunz, 1936 and *P. pterocaudata* Kunz, 1936. The apomorphic branch then, is formed by the *helgolandica-acuteata* complex in which the inner seta disappeared in leg 3 (synapomorphy). Within the latter, the *helgolandica*-group constitutes the plesiomorphous lineage and unites three very closely related species (see Mielke, 1984a). In the apomorphic *acuteata*-group, species are linked by the absence of the inner seta in endopodite P4. Several remarkable reduction phenomena occurred in this branch (e.g. endopodite P1 with one claw in *P. unaspina* Mielke, 1984a; reduction baseoendopodite P5 in *P. denticulata* Rao & Ganapati, 1969 and *P. ornata* Krishnaswamy, 1957), however, the present state of knowledge does not enable us to define the evolutionary pathways within the *acuteata*-group.

As a result of these considerations, an amended generic diagnosis is required for *Paramesochra*:

Paramesochridae. Paramesochrinae subfam. n. Body depressed, broad anteriorly and slightly tapering posteriorly. Genital double-somite broader and longer than any of the more posterior somites. Rostrum small. Antennula 7–8-segmented in female, 6-segmented and subchirocer in male. Antenna with basis; first endopodite-segment with

inner seta; exopodite uniarticulated, with 3–5 setae. Mandible with well-developed praecoxa; endopodite 1–3-segmented; exopodite 1-segmented. Maxillula with well-developed praecoxal arthrite; exopodite 1-segmented. Maxilla with 3 endites, endopodite 1–2-segmented. Maxillipede with 2–3-segmented endopodite. Exopodite of P1 2-segmented, distal segment with 4–5 setae; endopodite 2-segmented, prehensile, proximal segment long and devoid of inner seta, distal segment small and with 1–2 setae or claws. P2–P4 with 3-segmented exopodites, proximal and middle segment without inner seta, distal segment with 4, 3–4 and 2–4 setae, resp.; endopodite P2–P4 2-segmented, proximal segment with 0, 0–1 and 0–1 setae, distal segment with 1–2 setae. Baseoendopodites P5 confluent, each with 0–2 setae in both sexes; exopodites small, with 3–4 setae in female, 2–4 setae in male.

Type-species: *P. dubia* T. Scott, 1892.

3. Interspecific relationships of *P. mielkei* sp. n. and a revised species key

The presence of an inner seta on the proximal segment of endopodite P3 and P4 relates *P. mielkei* sp. n. without doubt to the *dubia*-group. At present six other species are referred to this species-group: *P. dubia* T. Scott, 1892; *P. similis* Kunz, 1936; *P. pterocaudata* Kunz, 1936; *P. borealis* Geddes, 1981; *P. ? helgolandica* Mielke, 1975 and *P. kunzi* Mielke, 1984.

The presence of a strong distal hook on the first antennular segment, the lateral spiny projection of the cephalothorax and the long caudal rami differentiate *P. dubia* clearly from the new species. *P. pterocaudata* differs in the lateral posteriorly directed processus of the anal somite and the length:width ratio of the caudal rami. *P. similis* can be distinguished from *P. mielkei* n. sp. by the structure of the caudal rami (length 3.8 times the width, but one terminal seta well-developed) and the antennal exopodite (4 setae). *P. kunzi* differs primarily in the length of the caudal rami, the male exopodite P5 (3 setae) and the two claws (instead of setae) on the distal endopodital segment of leg 1. In List/Sylt Mielke (1975) found a female specimen which he tentatively identified as *P. ? helgolandica*. This species, however, belongs unquestionably to the *dubia*-group and is easily distinguishable from

P. mielkei sp. n. in the length of the caudal rami (L:W ratio = 3.7).

P. borealis comes close to the new species in the structure of the caudal rami, however, differs markedly in the baseoendopodite male P5 which has 2 setae on either side and in the terminal seta of the endopodites P2–P3 which is accompanied by a spinose lobe. These characteristics might be an indication that *P. borealis* stands close to the ancestral stem species of the *dubia*-group. Indeed, the spinose lobe probably represents a modified short second seta, a character also found in the *brevifurca*-group besides the shared short caudal rami.

Mielke's (1975) figures of the caudal ramus and the P4 can be completed with the present description. The author overlooked the small ventral setula in the proximal half of the caudal ramus and figured the accessory two-jointed inner setula of the principal terminal seta as a short spinule. The outer subapical seta of the third segment of the exopodite P4 is situated more distally.

The discovery of new species from Galapagos and Panama (Mielke, 1984a, b), the subspecific subdivision of *P. brevisfurca* and the description of the present species have made Kunz' key (Kunz, 1981) out of date. Moreover, this key is not applicable to male specimens since some couplets are exclusively based on female morphological characters (cf. P5). I, therefore, present a revised key in which I tried to avoid the single use of either female or male characteristics.

Key to the species of *Paramesochra* T. Scott, 1892

1. Distal segment exopodite P1 with 5 setae . 2
Distal segment exopodite P1 with 4 setae . 3
2. Endopodite of mandible palp 2-segmented;
caudal rami 1.5 times as long as maximum
width .. *brevifurca brevisfurca* Galhano, 1970
Endopodite of mandible palp 1-segmented;
caudal rami 1.1 times as long as maximum
width *brevifurca mediterranea* subsp. n.
3. Distal segment endopodite P1 with 1 claw ...
unaspina Mielke, 1984
Distal segment endopodite P1 with 2 claws or
setae 4
4. Cephalothoracic somite produced laterally
into posteriorly directed projection .. *dubia*
T. Scott, 1892

- Cephalothoracic somite without this projection 5
5. Anal somite produced laterally into posteriorly
direction projection *pteroaudata* Kunz, 1936
Anal somite without this projection 6
 6. Proximal segment endopodite P4 without inner
seta 7
Proximal segment endopodite P4 with inner
seta 10
 7. Exopodite P1 1-segmented; posterior margin
of caudal rami not prolonged dorsally into
hyaline triangular lappet 8
Exopodite P1 2-segmented; posterior margin
of caudal rami prolonged dorsally into hyaline
triangular lappet 9
 8. Body-length (excluding caudal setae) exceeding
900 μm ; distal segment exopodite P2–P4 with
2 setae *ornata* Krishnaswamy, 1957
Body-length (excluding caudal setae) about
320 μm ; distal segment exopodite P2–P4 with
4 setae .. *denticulata* Rao & Ganapati, 1969
 9. Distal segment exopodite P3 with 3 setae; an-
tennular exopodite with 3 setae *acutata*
hawaiiensis Kunz, 1981
Distal segment exopodite P3 with 4 setae; an-
tennular exopodite with 3 setae *acutata*
hawaiiensis Kunz, 1981
 10. Proximal segment endopodite P3 without in-
ner seta 11
Proximal segment endopodite P3 with inner
seta 13
 11. Exopodite female P5 with 4 setae, exopodite
male P5 with 2 setae *longicaudata* Nicholls,
1945
Exopodite female P5 with 3 setae, exopodite
male P5 with 3 setae 12
 12. Body-length (excluding caudal setae)
310–330 μm ; distal segment endopodite
P2–P3 swollen .. *helgolandica helgolandica*
Kunz, 1936
Body-length (excluding caudal setae)
210–250 μm ; distal segment endopodite
P2–P3 not swollen *helgolandica galapagoen-*
sis Mielke, 1984
 13. Terminal seta of endopodite P2–P3 accompa-
nied with a spinose lobe *borealis* Geddes, 1981
Terminal seta of endopodite P2–P3 not ac-
companied with a spinose lobe 14
 14. Antennular exopodite with 3 setae; endopodite
P1 with 2 terminal claws; exopodite male P5

- with 3 setae *kunzi* Mielke, 1984
 Antennal exopodite with 4 setae; endopodite
 P1 with 2 terminal setae; exopodite male P5
 with 4 setae *similis* Kunz, 1936
 Antennal exopodite with 5 setae 15
 15. Caudal rami 3.7 times as long as greatest
 width (?)*helgolandica* Mielke, 1975
 Caudal rami 2.2–2.5 times as long as greatest
 width *mielkei* sp. n.

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