TRACING THE ROUTES OF SPECIATION IN *MESOCYCLOPS WOUTERSI*–SUPERSPECIES (COPEPODA: CYCLOPOIDA)

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Abstract.— Morphological comparisons among three allopatric representatives of the *Mesocyclops thermocyclopoides*–group – *Mesocyclops parentium* **sp. nov.** (southern India, Sri Lanka), *Mesocyclops woutersi* Van de Velde, 1987 (New-Guinea–Indochina–Ryukyu Is.) and *Mesocyclops dissimilis* Defaye et Kawabata, 1993 (Honshu, Kyushu Is.) – revealed a very slight degree of divergence, as compared to that of sympatric species of the group. Clear-cut differences in some characters (presence/absence of spinules at base of antero- and posterolateral furcal setae, hair rows on dorsum of pediger 5) do nevertheless indicate genetic discontinuity among the species. The separation of *M. dissimilis* is also expressed in quantitative traits, some of them (increase of relative length of the apical exopod and baseoendopod setae of leg 5, the dorsal furcal setae and third endopodal segment of leg 4) being very probably adaptations for pelagic life. *Mesocyclops guangxiensis* Reid et Kay, 1992 is synonymyzed with *M. woutersi* Van de Velde, 1987, **syn. nov**.

Parsimony, zoogeographical and ecological considerations leave two hypotheses of relationships within the trio likely: either the ancestor of the group was *M. parentium*–like; or the ancestor was different from all three.

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Key words.— Copepoda, *Mesocyclops parentium sp. nov.*, speciation, pelagic adaptations, Asia.

INTRODUCTION

All the species (ca. 60) of the genus *Mesocyclops* Sars, 1918, as generally species of the subfamily Cyclopinae that they belong to, live in inland waters. Their ability to enter dormancy has been already observed in *M. leuckarti* (Claus, 1857) (Fryer and Smyly 1954), *M. edax* (Forbes,1890) (Dobrzykowski and Wyngaard 1993), *M. dissimilis* Defaye et Kawabata, 1993 [referred to by Kawabata (1989) as *M. thermocyclopoides* Harada, 1931], *M. aspericornis* (Daday, 1906), *M. australiensis* (Sars, 1908), *M. darwini* Dussart et Fernando, 1988, and *M. guangxiensis* Reid et Kay, 1992 (Zhen et al. 1994). These well-studied species are the focus of either limnological studies, or mosquito control research, so we can assume with rather great certainty, that dormancy also occurs in the other, poorly known representatives of the genus. No exact data on salinity tolerance of different *Mesocyclops* species are known to me, but the types of biotopes from where they have been recorded show that a good few do tolerate oligohaline (*M. brasilianus* Kiefer, 1933, *M. meridianus* (Kiefer, 1926), *M. longisetus longisetus* (Thiébaud, 1914), *M. ellipticus* Kiefer, 1936 – Reid 1985; *M. dissimilis* – Ishida (in litt.); *M. chaci* Fiers, 1996, *M. yut-*

sil Reid, 1996 – Fiers et al. 1996), or even saline waters (*M. ogunnus* Onabamiro, 1957, *M. salinus* Onabamiro, 1957 – Van de Velde, 1984). This broad salinity tolerance and the capability to enter diapause can promote long-distance dispersal through, or even between, continents.

Mesocyclops woutersi Van de Velde 1987, *M. guangxiensis*, *M. dissimilis* and a new species from Sri Lanka and southern India, whose relationships and speciation are discussed below, belong to the speciose (18 spp.) *thermocyclopoides*–group (Holynski and Fiers 1994, Holynska in press). The complex, confined mainly to Afro-Asia, has three representatives in Australia (*M. notius* Kiefer, 1981, *M. australiensis*, and *M. brooksi* Pesce et al., 1996), probably one – of still unsettled taxonomic position, referred to by Collado et al. (1984) as *M. thermocyclopoides* – in Central America, and one pantropical species (*M. aspericornis*).

Since the original description of *M. woutersi* from the North-coast of Papua New Guinea, no more record of this species appeared in the literature. Reid and Kay (1992) described *M. guangxiensis* from samples collected in China (Nanning), North Vietnam (Hanoi), and Laos (Vientiane). Rather far from these localities, Ishida (in litt.) found the species in Japan, in the Ryukyu (Iriomote, Ishigaki Is.) and Honshu Islands. In 1989 Kawabata

Table 1. Material examined. (For taxonomic status of *M. guangxiensis* see text.)

	Coordinates	Coll. date	Biotope	Specimens
M. woutersi				
holotype				
Papua New Guinea				
Madang Pr., Warawaranga	04° 14'S-144°56'E	02 Jun 1982	coral gravel pit	1 (KBIN,26528/A 3291)
paratypes				
Papua New Guinea				
Madang Pr., Warawaranga	04° 14'S-144°56'E	02 Jun 1982	coral gravel pit	2 (KBIN, 26528/B-C 3291)
non-types				
Papua New Guinea				
Madang Pr., 'Jp. airstrip'	04° 47'S-145°40' E	04 Mar 1989	pond	7 (MH)
M. guangxiensis				
paratypes				
China				
Guangxi Pr., Nanning	22°50'N-108°19'E	25 Nov 1990	culture	9 (USNM,251622)
non-types				
Laos				
Vientiane, Sisavath	18°00'N-102°38'E	03 Jun 1993	—	14 (USNM, 259637)
Vietnam				
Ha Bac Pr., Phu Hoa	21°00'N-106°13'E	02 Nov 1994	concrete tank	2 (USNM, 271912)
Hai Hung Pr.	21°N-106°E	12 Sep 1994	concrete tank	2 (USNM, 271917)
Hai Hung Pr., Di Su	21°N-106°E	23 Jun 1994	concrete tank	2(USNM, 271920)
Hai Hung Pr., Di Su	21°N-106°E	23 Jun 1994	pond	2 (USNM, 271923)
Hanoi	21°00'N-105°51'E	25 Jun 1994	lake	4 (USNM, 271919)
Japan, Ryukyu Is.				
Ishigaki	24°30'N-124°10'E	12 May 1996	—	11 (TI)
Ishigaki., Nakura	24°30'N-124°10'E	12 May 1996	small stream	2 (TI)
Iriomote	24°20'N-123°50'E	13 May 1996	ditch in ricefield	34 (TI)
Iriomote, O-hara	24°20'N-123°50'E	13 Jan 1989	small pond	1 (TI)
M. dissimilis				
holotype				
Japan, Honshu				
Lake Biwa	35°00'N-135°53'E	11 Jul 1988	pelagic, S-Basin	1 (MNHN,Cp. 941)
paratype				
Japan, Honshu				
Lake Biwa	35°00'N-135°53'E	11 Jul 1988	pelagic, S-Basin	1 (MNHN, Cp. 943)
non-types				
Japan, Honshu				
Lake Biwa	35°00'N-135°53'E	11 Jul 1988	pelagic, S-Basin	4 (MNHN)
Lake Biwa	35°10'N-136°00'E	27 Jul 1995	pelagic, N-Basin	10 (MilZ)
Lake Biwa	35°03'N-135°53'E	22 May 1988	littoral, S-Basin	9 (TI)
Japan, Honshu				
Lake Kitaura	35°59'N-140°35'E	28 Oct 1987	littoral	1 (TI)
M. parentium sp. nov.				
Holotype				
India, Kerala				
Chalakudy	10°18'N-76°22'E	02 Sep 1992	marsh	1 (MilZ)
Paratypes				
India, Kerala				
Chalakudy	10°18'N-76°22'E	02 Sep 1992	marsh	2 (MilZ, MH)
Sri Lanka		07 Feb -		
Central	—*	08 Mar 1896	marsh	3 (HNHM, MH)

Abbrevations used: KBIN – Koninklijk Belgisch Insituut voor Natuurwetenschappen, Brussels, Belgium; MH – Author's collection deposited in Museum i Instytut Zoologii PAN, Warsaw, Poland; TI – collection of Teruo Ishida, Irifunecho, Hokkaido, Japan; USNM – National Museum of Natural History, Smithsonian Institution, Washington, U. S. A.; MNHN – Museum National d'Histoire Naturelle, Paris, France; MilZ – Muzeum i Instytut Zoologii PAN, Warsaw, Poland; HNHM – Magyar Természettudományi Múzeum, Budapest, Hungary; 'Jp airstrip' – Japanese airstrip; Pr. -province; Coll. date – date of collection

*: Precise locality data are not available.

changed the taxonomic position of the *Mesocyclops* living in Lake Biwa (Japan, Honshu) and mentioned in previous limnological literature as *M. leuckarti*, to *M. thermocyclopoides* Harada, 1931. Having compared this animal with topotypes of *M. thermocyclopoides*, however, Defaye and Kawabata (1993) came to the conclusion that the *Mesocyclops* in question actually represents a new species, and named it *M. dissimilis*. In a vial of the Collectio Dadayana (Hungarian Natural History Museum) labelled as *"Mesocyclops leuckarti"* from Sri Lanka, and in a sample sent by Dr. Sunny George from southern India I found a species, which showing minute but clear-cut differences from *M. woutersi* is considered as new, and is described here.

Comparison of the morphological features, completed with simple analysis of some morphometric characteristics, and evaluation of the zoogeographical distribution patterns and habitat preference data provide an opportunity to formulate a hypothesis of speciation of the three *Mesocyclops* species mentioned above.

MATERIALS AND METHODS

The material examined is shown in Table 1.

Only adult females have been used in the morphological comparisons. All the observations and measurements, with exception of preparata of *M. woutersi* from Ishigaki Island, mounted in gum chloral, were made on specimens in glycerine. Drawings were done by camera lucida attached to a Wild M 20 microscope. Measurements were taken following the method of Koźmiński (1933), however the length of the pediger 5 was not taken into consideration in either the body or urosome length. The width of the third endopodal segment of the leg 4 was measured across its widest part. All the linear dimensions were measured with an accuracy of 1 μm except for the length of the body, urosome, and inner terminal furcal seta, where an accuracy of 5 μm was used.

I made pair-wise comparisons of six traditionally used body ratios and the body length between *M. dissimilis*, *M. woutersi*, and *M. parentium*. The sample of *M. dissimilis* was divided into two subsamples, one including specimens collected from the shore, the other from the pelagic region. Specimens belonging to the pelagic group and found in the more shallow, southern basin of Lake Biwa, were collected ca. 500 m from the nearest (western) shore in 2 meters deep water, where the bottom is usually covered with rooted, submerged macrophytes, but in the upper open water planktonic organisms are present (Kawabata in litt.). In the northern basin of L. Biwa the collecting site was 3 km from the western shore, and 75 m deep (Kawabata in litt.).

In the graphic representation (Dice-Leraas diagrams) (Fig. 25), the mean, range and confidence intervals (± 2SE) of those linear dimensions from which the particular body ratio is derived are shown. If these intervals do not overlap in two samples, we can assume that the difference between the means is significant. This method makes rapid recognition of significant changes in body parameters possible, and also shows the component of the body ratio, the shift of which is actually responsible for the change in proportions. The method has however its own limitations, when the sizes and/or standard errors of the samples are too different. Therefore a t-test has been used as well to compare the means of the ratios. The t formula adapted for comparison of small samples (Simpson and Roe, 1939) is as follows:

$$t = \frac{(M_1 - M_2)\sqrt{N_1 N_2/(N_1+N_2)}}{\sqrt{(N_1\sigma_1^2 + N_2\sigma_2^2)/(N_1+N_2-2)}} \qquad df = N_1+N_2$$

in which M_1, N_1 and σ_1 are respectively the mean, total frequency, and standard deviation for one sample and M_2, N_2, and σ_2 are the same for the other sample, df is degree of freedom. Basic statistical data are shown in Appendix 1–4.

Abbreviations used in the text: enp=endopod; s=seta; sp=spine; ae=aesthetasc.
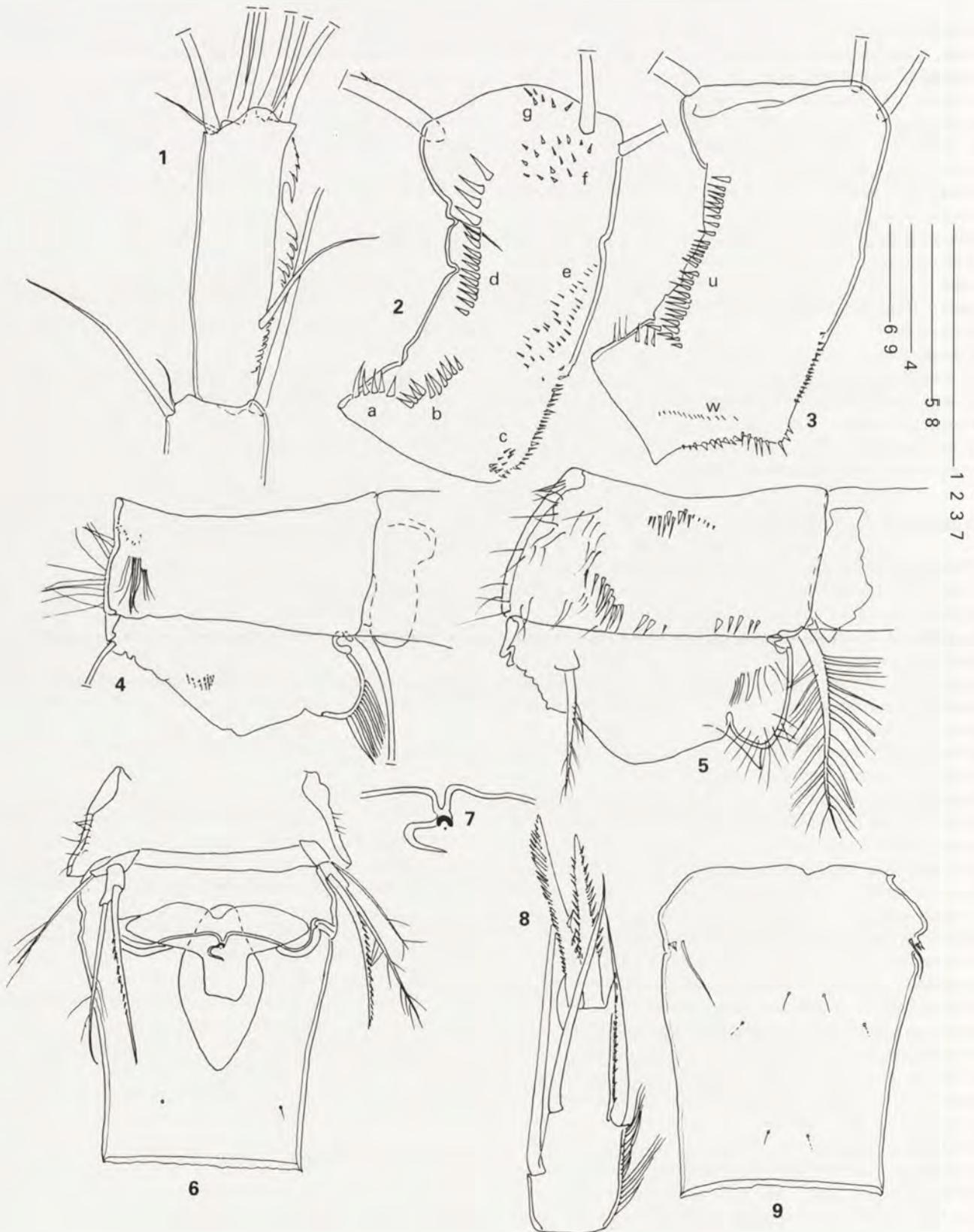
Mesocyclops parentium sp. nov.

Mesocyclops woutersi: Holynski 1994: 58–63, Figs 30. A–C,E, 31. A,C, 32. A,C,F

Types. Holotype (♀) India, Kerala, Chalakudy, 10°18'N–76°22'E, in marsh. Leg. Dr. Sunny George, 02 September 1992. Two paratypes (♀) of same origin as holotype, three paratypes (♀) from Sri Lanka, found together with *M. ogunnus*, *M. cf. pehpeiensis*, *M. splendidus* Lindberg, 1943 and *M. isabellae* Dussart et Fernando 1988 in a vial (No: III–253) deposited in "Collectio Dadayana", Hungarian Natural History Museum, Budapest. From the note *"Cyclops leuckarti* 1070 1896. Ceylon. Madarász" on the original label of the vial I infer that the collection data of *"Cyclops leuckarti"* collected by J. Madarász in Sri Lanka 1896 published in Daday's paper (1898), concern these paratypes. Daday mentioned swamp areas at Madatugama, Kalawewa (nearby localities in central Sri Lanka, coordinates: 7°58' N–80°33'E) and the River Mahaweli as collecting sites of *"Cyclops leuckarti"*. All types are dissected and mounted on two slides each: the first one contains A1–P4, the second P5–abdomen. Holotype and one paratype (Sri Lanka) are deposited in the Museum and Institute of Zoology PAS, Warsaw. Two paratypes (one from India and one from Sri Lanka) each are in the Hungarian Natural History Museum, Budapest and in the author's collection (deposited in the Museum and Institute of Zoology, PAS, Warsaw). No male found.

Description of the holotype (female)

Length of the body=1050 μm; prosome/urosome=1.70; cephalothorax length/width=1.20

Antennula. 17-segmented, last two segments with hyaline membrane. Hyaline membrane of segment 17 with one large notch (Fig. 1). Articles 1, 4, 5, 7–13 anteriorly adorned with spinule rows, segments 1, 4, 5 with scattered

Figures 1–9. *Mesocyclops parentium* sp. nov., female. 1–3, 5–9 Holotype; 4. Paratype (South-India). (1) last antennulary segment; (2) antennary basis – caudal; (3) antennary basis – frontal; (4) leg 1 coxa, basis – caudal; (5) leg 4 coxa, basis – caudal; (6) pediger 5, genital double somite – ventral; (7) copulatory pore, copulatory and transverse ducts; (8) leg 4 enp3; (9) genital double somite – dorsal. Scales: 50 μm.
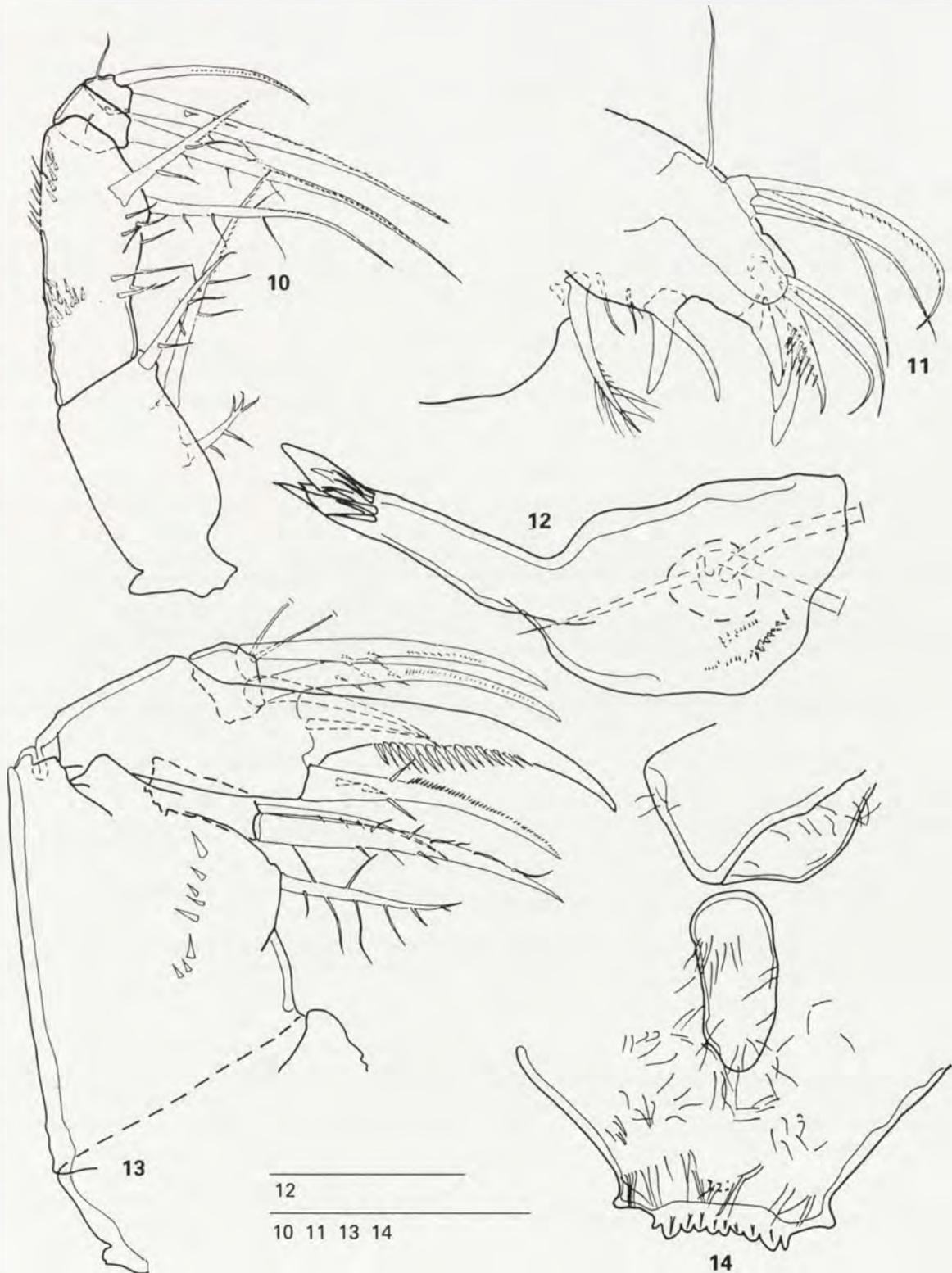
Figures 10–14. *Mesocyclops parentium* sp. nov., female. 10–13 Holotype; 14 Paratype (Sri Lanka). (10) maxilliped – frontal; (11) maxillula – frontal; (12) mandibula – caudal; (13) maxilla – frontal; (14) labrum, epistoma, rostrum – ventral. Scales: 50 μm.

shallow pits on posterior surface. Armature formula as *M. leuckarti* and *M. thermocyclopoides*: 8s, 4s, 2s, 6s, 4s, 1s+1sp, 2s, 1s, 1s, 0, 1s, 1s+1ae, 1s, 1s, 2s, 2s+1ae, 7s+1ae.

Antenna. Coxa, basis, and three-segmented endopod with 0, 3, 1, 7, 7 setae respectively.

Basis, caudal spinule pattern (Fig. 2): "*Leuckarti*-type" spinule pattern, which includes groups **a**, **b**, **c**, **d** and **e** supplemented with two fields of spinules (groups **f** and **g**) next to implantation of inner setae and near distal rim of segment; 16 spinules of distally increasing size (largest/smallest=2) in group **d**.

Basis, frontal spinule pattern (Fig. 3): 30 spinules in longitudinal row on outer rim (group **u**); no spinule group next to implantation of exopod seta; transverse row of tiny spinules near base of segment (group **w**)

Labrum. (Fig. 14) On external surface, scattered and transverse row of hairs above the moustache-like hair row overhanging the toothed distal rim. Epistoma and the vertical cleft separating epistoma from rostrum also hairy.

Mandibula. (Fig. 12) Gnathobase with strongly chitinized teeth. One-segmented palp with two long and one short setae. Near the palp three groups of spinules.Those forming transverse row next to praecoxal-coxal boundary conspicuously larger than others.

Maxillula. (Fig. 11) Praecoxal arthrite with three distal claws, at their base one spiniform seta on ventral surface. Two medium-sized, three small spiniform setae, and one large setulose seta on inner rim, and one small spine at base of praecoxal arthrite. Palp with one spine and two setae apically, one outer seta proximally, and three setae on outer lobe. No spinules on palp.

Maxilla. (Fig. 13) Syncoxa, basis and one-segmented endopod. Praecoxa bears one endite with two setae (not shown on the drawing), coxa has one endite with one seta at distal third, and one distal endite with one strong spiniform and one slender setae, ca. half as long as spiniform seta. Basis with two setae, shorter seta placed caudally, longer seta inserted in front of the claw-like basal endite, which is armed with strong teeth. One-segmented endopod with five setae. Coxa with longitudinal spinule row on frontal surface.

Table 2. Armature of leg 1-4 of *Mesocyclops parentium* sp. nov. (Spines are denoted by Roman, setae by Arabic numerals. The armature on the outer margin of any segment is given first, followed by the elements on the apical and inner margins.)

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

Maxilliped. (Fig. 10.) Syncoxa, basis and two-segmented endopod. Syncoxa with three setae. Basis with one long inner seta at distal third and one spiniform seta displaced to frontal surface. Long spinules on medial margin and frontal surface below insertion of the basal setae, and two groups of scale-like spinules caudally and on outer margin. Enp1 bearing one stout seta and few spinules on frontal surface. Enp2 with three setae of medially increasing length.

Leg 1-4. (Figs 4, 5, 8) Spine and seta formula as in *M. leuckarti* and *M. thermocyclopoides* (Table 2).

Lateral rim of leg 1–4 coxa with hairs. Intercoxal sclerites of all swimming legs naked on both frontal and caudal surface. Leg 1 basis frontally adorned with small spinules in semicircular arch.

Apical hairs on medial expansion of basis present in leg 1–4, supplemental caudal group of hairs in leg 4. Two small acute outgrowths on distal rim of intercoxal sclerite of leg 4. Coxal seta conspicuously (1.4x) longer than height of medial expansion of leg 4.

Caudal ornamentation of leg 4 coxa: intermittent group of spinules (3+5) near distal rim; oblique row of long spinules (9) at outer distal angle; dense group of hairs on and next to lateral rim; conspicuously large spinules in outer half of spinule row near proximal rim.

Leg 4 enp3 (Fig. 8): length/width=2.50; inner apical spine/outer apical spine=1.10; inner apical spine/length of enp3=0.86; outer edge of inner apical spine with few (4) teeth in proximal half.

Leg 5. (Fig. 6) Segmentation and setation typical of the genus. Length of medial and apical exopod setae and baseoendopod seta 86 μm, 83 μm, and 59 μm respectively.

Leg 6. (Fig. 9) Long medial seta and two short spines of about equal length.

Pediger 5. (Figs 6, 15) Lateral hairs continue as regular hair rows on dorsum. Two sensilla medially and two on outer distal angle on dorsal surface.

Genital double somite (Figs 6, 9) Dorsum naked, only six sensilla present. Ventrally two sensilla at distal fourth.

Receptaculum seminis (Figs 6, 7): Lateral arms short, weakly curved posteriorly; anterior margin of proximal part concave in the middle; one circular pore posterior to horseshoe-shaped copulatory pore; transverse ducts form acute angle before their connection with strongly curved copulatory duct; part of copulatory duct connecting copulatory pore and transverse ducts ('joint canal') seems to be short (the virtual length depends on the angle between the duct and the plane of observation), but recognizable.

Anal segment. (Figs 18, 19) Spinules on distal margin present ventrally and dorsally, absent laterally.

Furca. (Figs 18, 19) Length/width=3.10; dorsal seta/posterolateral seta=0.73; length of terminal setae from innermost to outermost: 200 μm, 440 μm, 310 μm, 90 μm; inner terminal seta/urosome=1.20. Spinules at implantation of posterolateral furcal setae only. No hairs on furca.
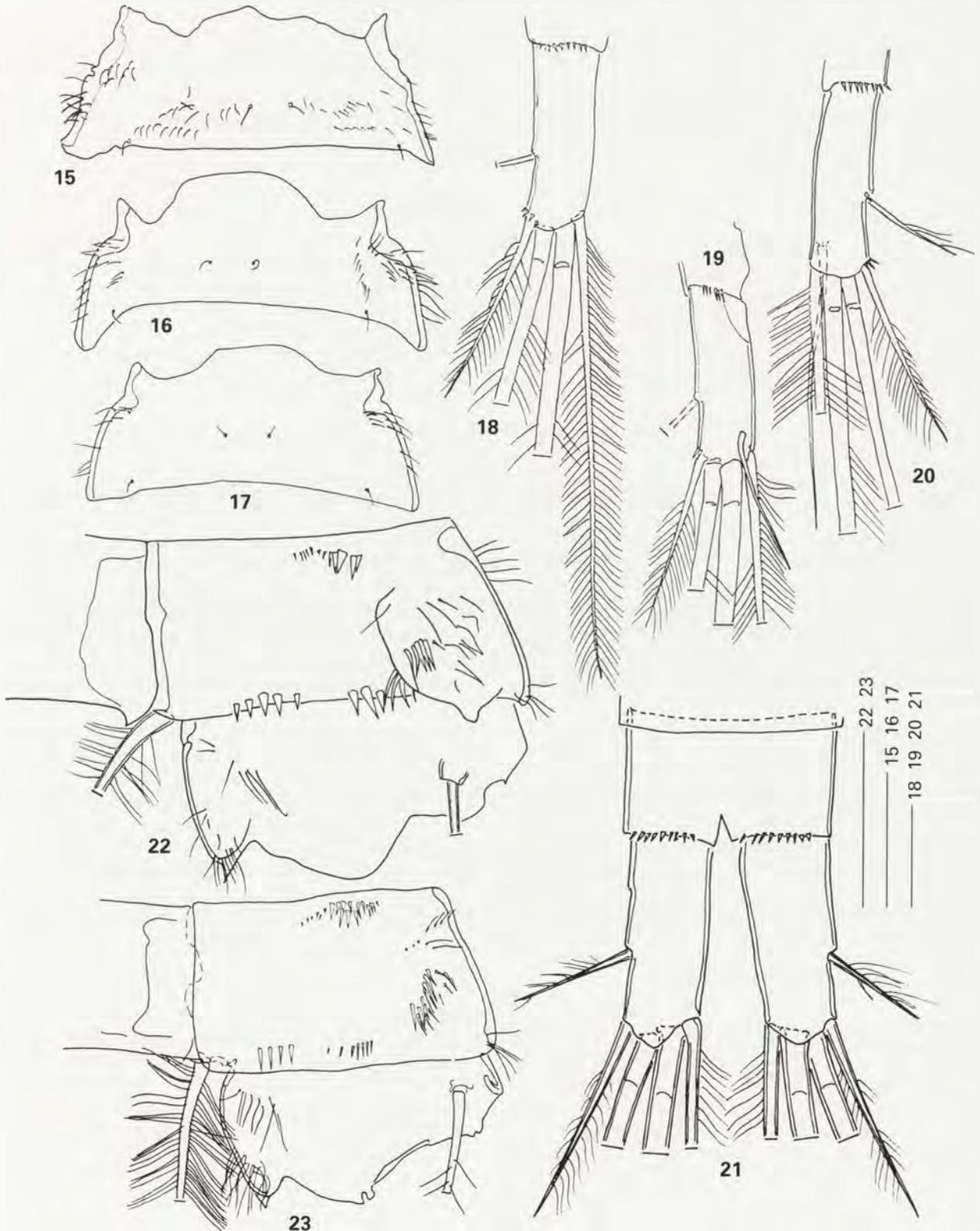
Figures 15–23. *Mesocyclops* spp., females. 15, 18, 19. *M. parentium* sp. nov. (Holotype); 16, 21, 22. *M. woutersi* (Papua New Guinea); 17, 20, 23. *M. dissimilis* (L. Biwa, pelagic region). 15–17. pediger 5 – dorsal; 18–21. furcal rami: (18) ventral; (19) dorsal; (20) ventral; (21) ventral; 22,23. leg 4 coxa, basis – caudal. Scales: 50 μm.

Variability

The variability in body ratios is shown in Table 3.

Table 3. Morphometrical variability of *Mesocyclops parentium* sp. nov. (Characteristics compared in the interspecific morphometric analysis are not shown here. In parentheses the numbers of specimens measured).

	Range	Average
Cephthx l/w (5):	1.20-1.23	1.21
Gen dos l/w (6):	1.17-1.30	1.27
Pros/Uros (6):	1.63-2.00	1.81
P4 enp3		
ap sp, in/out (6):	1.05-1.17	1.10
in ap sp/ enp3 l (6):	0.81-0.94	0.88
Furcal s		
ter acces (5):	200-265 μm	232 μm
out ter (4):	310-390 μm	350 μm
Ant lat s/furca l (3):	0.43-0.64	0.53

Abbreviations: cephthx=cephalothorax, l=length, w=width, gen dos=genital double somite, pros=prosome, uros=urosome, P4=leg 4, enp3=third segment of endopod, ap=apical, sp=spine, in=inner, out=outer, s=seta, ter=terminal, acces=accessory, ant=antero, lat=lateral.

In specimens from Sri Lanka the circular pits on the anterior surface of the antennula are confined to the first segment or are absent. No variability in spinule pattern of the antennary basis has been observed, only the number of spinules in certain groups changes, e. g. there are 13–16 and 25–31 spinules in group **d** and **u**, respectively (Figs 2, 3). In 5 of 6 specimens, the spinule ornamentation on the posterior surface of the leg 4 coxa is the same, only the number of spinules varies, e.g. there are 4–8 spinules in the row parallel to the distal rim. In one animal from Sri Lanka, the basic pattern is supplemented with a group of hairs near the medial rim and an oblique hair row starting from the inner distal angle on coxal plate of the right-hand side. On the outer edge of inner apical spine of leg 4 enp3 there are 1–8 teeth. In one specimen from Sri Lanka the distal rim of the anal segment is ornamented with spinules laterally as well as ventrally and dorsally.

Diagnosis

Mesocyclops parentium sp. nov. can be distinguished from other congeners by the following combination of characters: no spine on medial expansion of the leg 1 basis; intercoxal sclerite of leg 4 naked, outgrowths small; lateral hairs of pediger 5 continue dorsally as regular hair rows; receptaculum seminis with short and wide lateral arms, transverse ducts directed at acute angle to one another before the connection with strongly curved copulatory duct; proximal and distal group of hairs on medial expansion of leg 4 basis, spinule ornamentation of the antennary basis and leg 4 coxa, furca without hairs, spinules at implantation of posterolateral furcal setae only.

RELATIONSHIPS

Mesocyclops parentium belongs to the *thermocyclopoides*-group as evidenced by the absence of a spine on the medial expansion of leg 1 basis, the frontal spinule ornamentation of the antennary basis, short outgrowths on leg 4 intercoxal sclerite, presence of lateral hairs on pediger 5, shape of receptaculum seminis and caudal hair ornamentation on medial expansion of leg 4 basis, as polythetic character-assemblage, and the presence of a distinct spinule row on the frontal surface of the maxillary-coxa as a strongly diagnostic, synapomorphic feature. Within the complex, *M. parentium*, *M. woutersi* and *M. dissimilis* are united by almost identical caudal ornamentation of the leg 4 coxa (Figs 5, 22, 23). The conspicuous similarity of the spinule pattern on the leg 4 coxa in the three allopatric *Mesocyclops* species, a feature that I (Holynska in press) suppose to be a tactile part of the "Specific Mate Recognition System" suggests relatively recent separation of these species, or at least that they have never been sympatric. One element of this pattern, the shape of the spinule row next to the proximal rim, showing perceptible variability in members of the *thermocyclopoides*-group, seems to have special diagnostic value. This spinule group is represented by numerous large outer and very small inner spinules in all specimens of *M. parentium*, *M. woutersi* and *M. dissimilis*, but, except for a few specimens of *M. ogunnus*, I have not found a similar instance outside the trio.

The *M. parentium-woutersi-dissimilis* clade can be easily recognized by a combination of characters (the caudal spinule ornamentation of the antennary basis, the seven setae on the second endopodal segment of the antenna, and the V-shaped connection of transverse ducts), which nevertheless are not synapomorphies of the trio. Taking into consideration the simple caudal spinule ornamentation of the antennary basis in other genera of the subfamiliy Cyclopinae (Fiers and Van de Velde 1984), I assume the more complex pattern to be more advanced in the genus *Mesocyclops*. However, the addition of group "**f**" and "**g**" (Fig. 2) to the *leuckarti*-type spinule pattern, a characteristic of *M. parentium*, *M. woutersi* and *M. dissimilis*, is not an unique feature of these taxa. Spinules in the same position also appear in several species within (*M. isabellae*, *M. aequatorialis similis*, *M. affinis*, *M. tobae*, *M. aspericornis*, *M. brooksi*), and outside (*M. ruttneri*, *M. papuensis*) the *thermocyclopoides*-group, indicating their plesiomorphic or homoplasic states. Similarly, the V-shaped connection of the transverse ducts present in the three species in question is also shared by many species within (*M. microlasius*, *M. aspericornis*, *M. kieferi*, *M. granulatus*, *M. arcanus*, *M. brooksi* and *M. notius*) and outside (e.g. *M. ruttneri*, *M. papuensis*, *M. brevisetosus*, *M. salinus*, *M. tenuisaccus* and *M. rarus*) the *thermocyclopoides*-group in the Old World. The tendency toward repeated reductions in the number of setae on the second endopodal segment of the antenna, observed in cyclopoids

in general (Huys and Boxshall 1991), holds within the genus *Mesocyclops* as well. Seven setae, which represent an advanced state in comparison with the eight- or nine-seta states often occurring in this genus, are common both within (*M. isabellae*, *M. aequatorialis*, *M. thermocyclopoides*, *M. affinis*, *M. tobae*, *M. microlasius*) and outside (e. g. *M. leuckarti*, *M. pehpeiensis*, *M. ruttneri*, *M. papuensis*, *M. salinus*, *M. brasilianus*) the *thermocyclopoides*–group.

The low degree of the morphological differentiation between *M. parentium*, *M. woutersi* and *M. dissimilis*, in comparison with that between other, sympatric representatives of the *thermocyclopoides*–group, is striking. In Table 4 I give a list of the differences observed between the species.

Table 4. Characters showing differentiation in *M. parentium* sp. nov., *M. woutersi* and *M. dissimilis*. +: feature present; –: feature absent; +/–: intraspecific variability. Number of spinules (character 3) counted on antennae of both left and right side. (Characteristics compared in the interspecific morphometric analysis are not shown here. In parentheses the number of specimens examined.)

	parentium	*woutersi*	*dissimilis*
1. Notches on hyaline membrane of A1	1(6)	1(79)	1(22)/2(1)
2. Spinules on 14. antennulary segment: Antennary basis, spinule group **d**	–(6)	+(5)/–(51)	+(6)/–(13)
3. - Number - range; mean:	13-16; 14.4(9)	13-25; 19.0(73)	13-21; 15.1(22)
4. - Largest/smallest - range; mean:	1.9-2.2; 2.1(6)	2.1-4.6; 3.4(16)	1.4-2.2; 1.8(10)
5. Antennary basis, group **g**: Leg 4 enp3	+(6)	+(48)/–(11)	+(2)/–(16)
6. - Teeth on outer edge of inner apical spine	1–8(6)	0-whole length(73)	7-whole length(22)
7. Anal segment, distal rim, lateral spinules:	+(1)/–(4)	+(1)/–(70)	+(22)
8. Pores posterior to leg 6	6(1)	6(6)	8(5)
9. Pediger 5, dorsum, hair rows:	+(6)	–(56)	–(13)
10. Spinules at base of anterolateral furcal setae:	–(6)	–(93)	+(26)
11. Spinules at base of posterolateral furcal setae	+(6)	–(93)	+(26)

Comparisons made between Chinese, Laotian, Vietnamese and Japanese (Ryukyu Is.) material identified by J. Reid and T. Ishida as *M. guangxiensis*, clearly suggest that these specimens are conspecific with *M. woutersi*. As such *M. guangxiensis* is considered here a junior synonym of the latter. The identity in the majority of the features, and great variability (e. g. number of teeth on outer margin of inner apical spine of the leg 4 enp3 in *M. woutersi*, or the extension of distal spinulation (group **f**) on caudal surface of the antennary basis in *M. guangxiensis*) of the rest, observed even within one population, have not let me find a single character by which these animals can be distinguished from each other. Therefore in Table 4 the characteristics of *M. guangxiensis* from the above-mentioned localities and of *M. woutersi* from Papua New Guinea have been combined under the latter name.

Clear-cut differences between *M. parentium*, *M. woutersi* and *M. dissimilis* have been found only in the last four characters shown in Table 4. Although Reid (1992) observed spinules at the implantation of posterolateral furcal setae in two of fourteen specimens of "*M.*

guangxiensis" collected in That Luang village (Laos, Vientiane), in the material examined by me there was no specimen having those spinules. Eight pores posterior to leg 6 very rarely occur in Old World *Mesocyclops*: besides *M. dissimilis*, *M. aequatorialis similis* is the only taxon known to me, where this feature is also present in some specimens (others show the 6-pore state). The occurrence of six pores in *Thermocyclops* species (*T. neglectus*, *T. dybowskii*, *T. oithonoides*) suggests that the eight-pore state is derived. On the other hand, I see no way to polarize characters 10 and 11 (Table 4) *a priori*. The alternate states (spinules present/absent) of both characters unite otherwise unrelated species. A reason for the mysterious character-state distribution may be that these characters, as part of SMRS, are controlled by strong disruptive selection during the final, sympatric phase of speciation. Neither do I consider *a priori* polarization of character 9 to be well established in the present stage of analysis.

DISTRIBUTION

Fig. 24 shows the geographical distribution of the three taxa. *Mesocyclops parentium* is known so far only from Sri Lanka and southern India. Besides Lake Biwa, where it is one of the dominant plankters, *M. dissimilis* has been collected from shallow lakes (L. Kitaura, Ishida in litt; L. Teganuma, Kawabata in litt.) and small ponds in Honshu (unpublished record of Taira, Ishida in litt.) and Kyushu (Ueda et al. in press) also. The huge distributional area of *M. woutersi* stretches from New Guinea, through Indochina at least to the Ryukyus. Ishida (in litt.) identified "*M. guangxiensis*" from a stream in Hyogo (Honshu), but I have not seen the specimen. The lack of records of *M. woutersi* from the Malay Archipelago should not be interpreted as a real distributional hiatus until a thorough faunistical survey in this region has been accomplished.

Experiments done on Chinese "*M. guangxiensis*" specimens (Zhen et al. 1994) showed that supposedly both adults and copepodids of *M. woutersi* can survive disappearance of free water in sediment even with low (15–20%) water content at 28°C. The desiccation tolerance of the species decreased with the decrease of temperature. These facts support the possibility of long-distance passive dispersal within the tropics. Transport organisms may be birds that migrate to New Guinea from the northern hemisphere to winter. A significant part of northern migrants in New Guinea are waders which, visiting different freshwater biotopes, have a good chance to encounter *Mesocyclops* and carry them on their legs or feathers. Habitat preference and range data of New Guinean birds
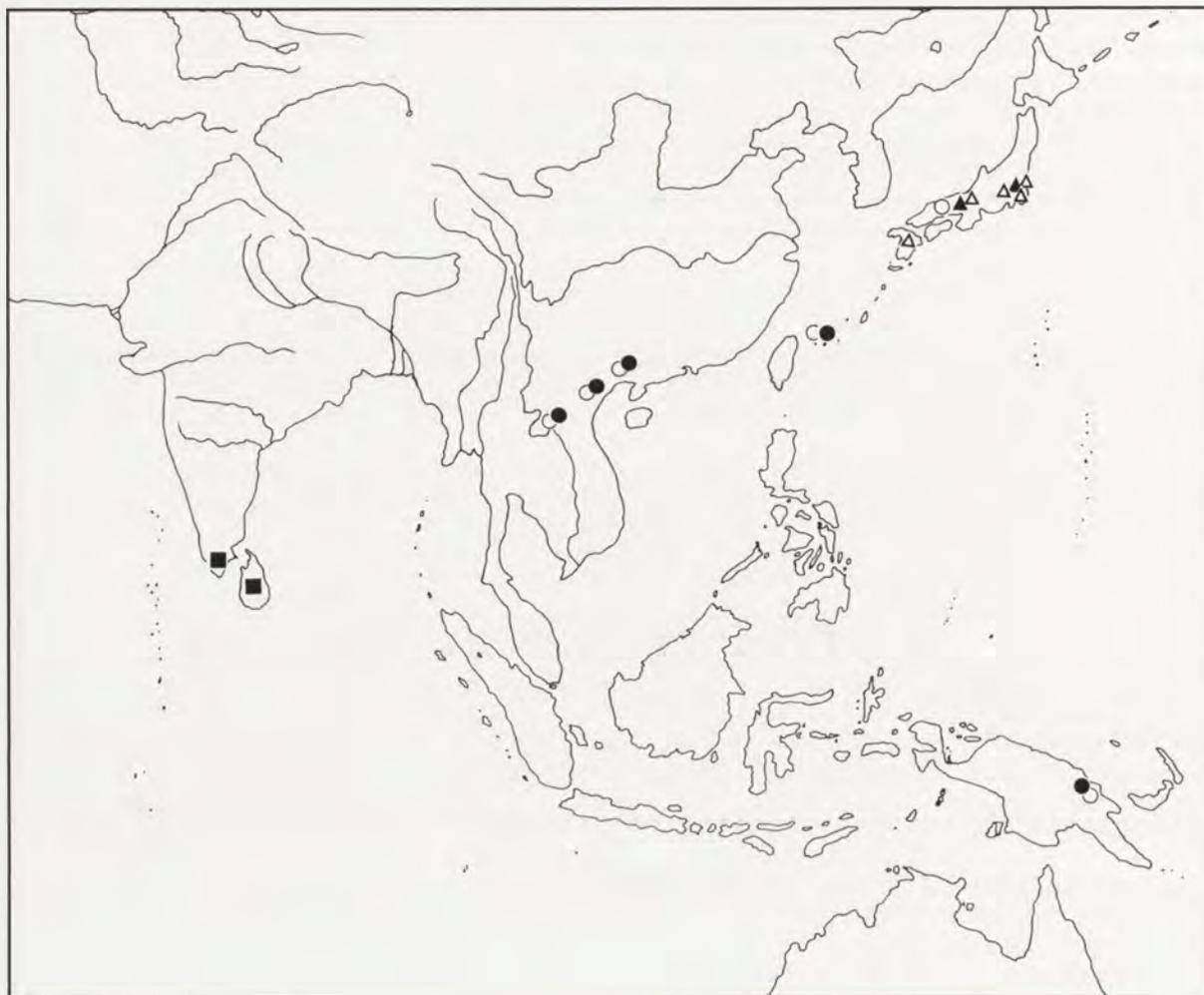
Figure 24. Distribution of *M. parentium* (square), *M. woutersi* (circle) and *M. dissimilis* (triangle). Empty symbols: literature data, or unpublished records not checked by me; Filled symbols: records checked.

(Beehler et al.1986), let us select some candidates for copepod transport: the wood sandpiper (*Tringa glareola*), grey-tailed tattler (*Tringa brevipes*), common sandpiper (*Tringa hypoleucos*), sharp-tailed sandpiper (*Calidris acuminata*), red-necked stint (*Calidris ruficollis*), and the greater sand plover (*Charadrius leschenaultii*). In another zoogeographic region, but probably also a result of passive dispersal, is the occurrence of two neotropical species (*M. longisetus curvatus* Dussart, 1987, and *M. venezolanus* Dussart, 1987) in a tundra depression far North (Yukon Territory, Canada) (Reid and Reed, 1994).

MORPHOMETRIC TRAITS AND HABITAT PREFERENCES

Results of the morphometrical comparisons made by graphic estimation and t-test (Figs 26–32; Appendix 5) can be summarized as follows:

1. The graphical method shows a constant pattern (pelagic *M. dissimilis* → littoral *M. dissimilis* → *M. woutersi* → *M. parentium*) of the differences in body
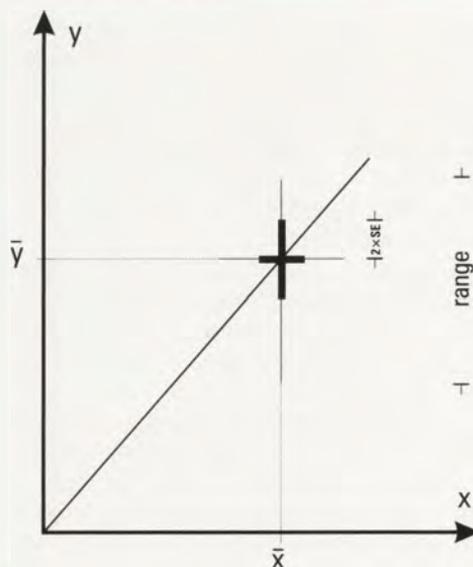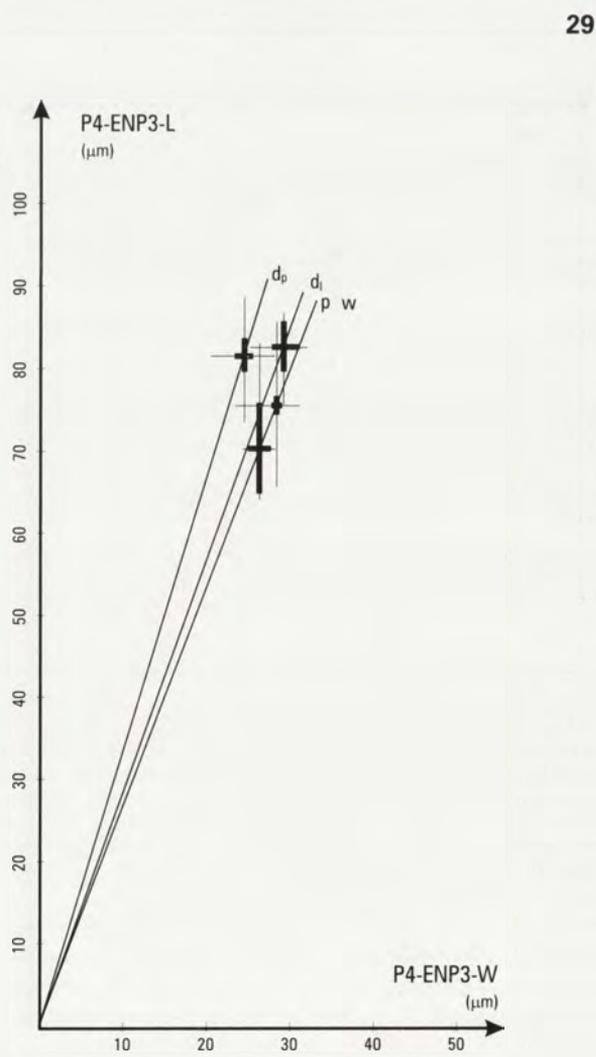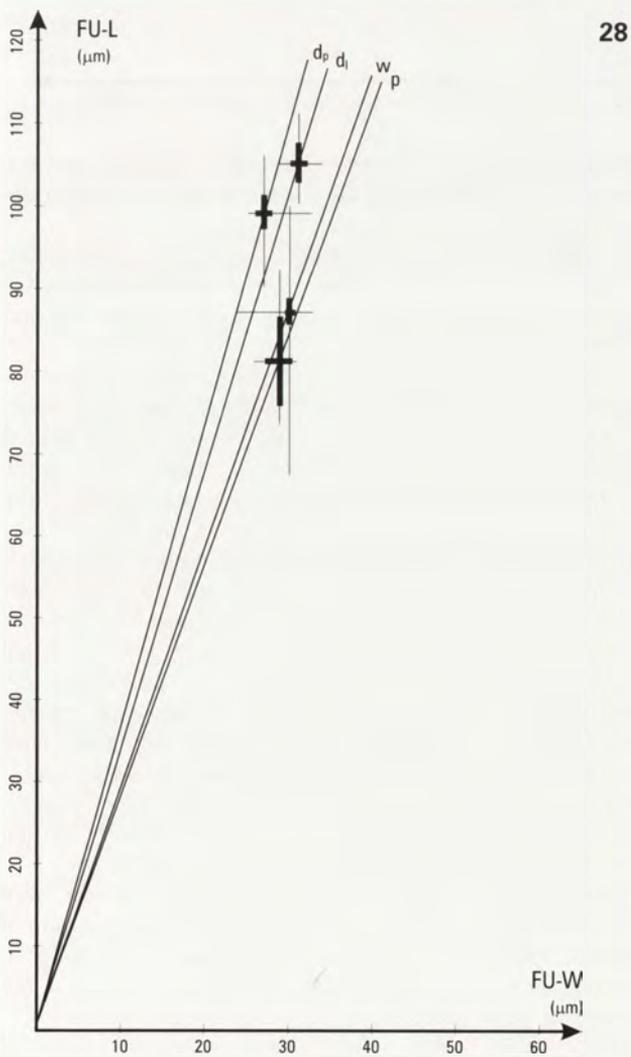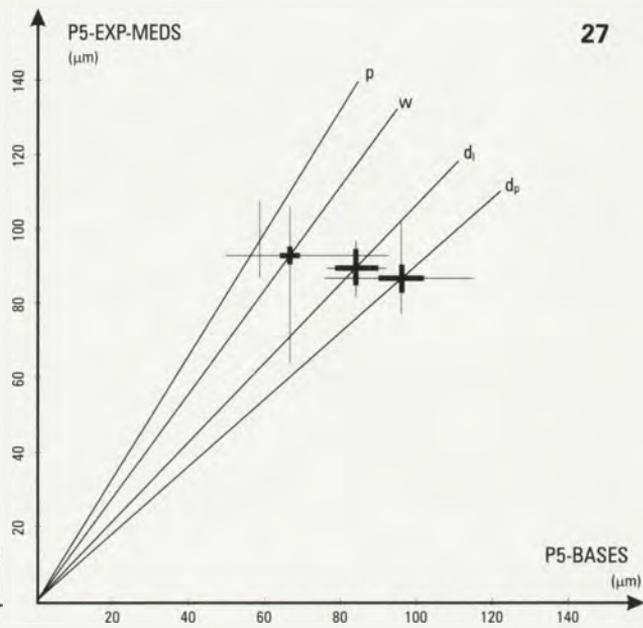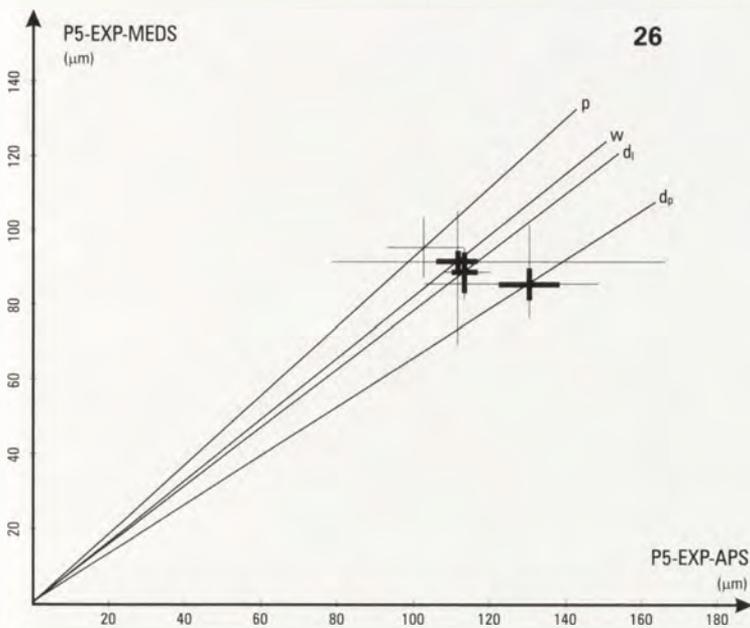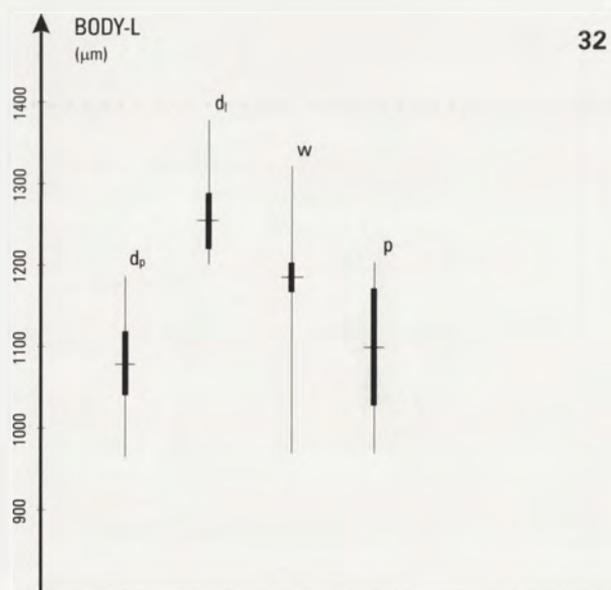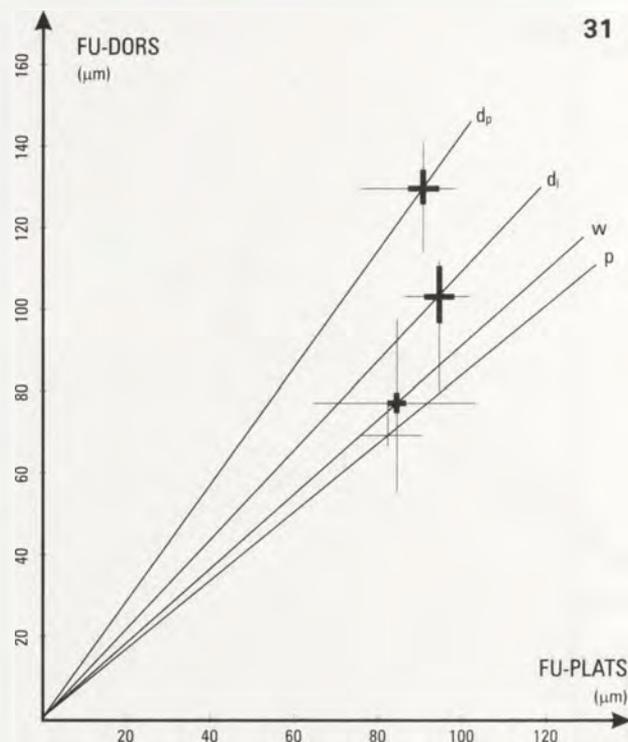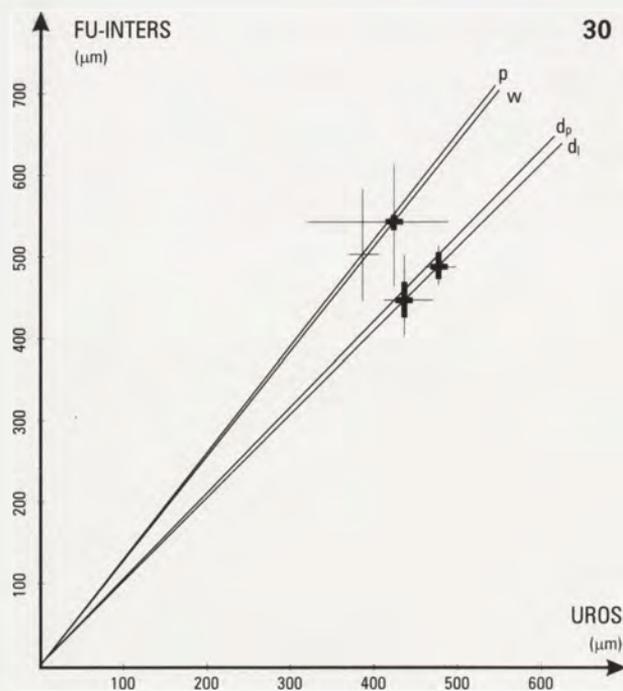
Figure 25. Schematic representation of diagrams used in graphic comparisons of body ratios between *M. dissimilis*, *M. woutersi* and *M. parentium*. SE: Standard error; x̄, ȳ: mean values

Figures 26–32. Change of body length and proportions in *M. dissimilis*, pelagic form (**d$_p$**) *M. dissimilis*, littoral form (**d$_l$**), *M. woutersi* (**w**) and *M. parentium* (**p**). Abbreviations of linear dimensions see in Appendix 1. Because of the very low frequencies, standard errors of length of leg 5 setae, urosome and furcal (inner terminal, dorsal and posterolateral) setae in *M. parentium* are not counted and shown here.

ratios. The only exception to this rule is the FU INTERS/UROS ratio (for abbreviations see Appendix 1), where the pelagial and littoral forms of *M. dissimilis* exchange places.

2. The t-test has not confirmed significant differences between *M. woutersi* and *M. parentium* in any body ratio,

which, considering the above-mentioned repeating pattern, can however be explained by the small size of the *M. parentium* sample (Appendix 4).

3. The tendency in body length (pelagic *M. dissimilis*, *M. parentium* < *M. woutersi* < littoral *M. dissimilis*) is totally different from those in body ratios, suggesting that the body ratios studied here are not size-correlated.

4. Except for FU INTERS/UROS, body ratios (in particular P5 MEDS/APS and P4 ENP3 L/W) of *M. dissimilis* specimens collected from littoral zone conspicuously shifted toward *M. woutersi*. This observation suggests that while FU INTERS/UROS is presumably a species-specific, non-environment-dependent feature, the remaining 5 body ratios are elastic, environment-dependent in *M. dissimilis*.

5. A tendency to elongation has been observed from *M. parentium* toward the pelagic *M. dissimilis*: relative lengths of apical exopod and baseondopod setae of leg 5, and the dorsal furcal setae increase, furcal rami and third endopodal segment of leg 4 also lengthen (probably all the other leg segments show the same tendency, but no measurements have been made). The only trait not fitting in the general trend is FU INTERS/UROS. In comparison with *M. parentium* and *M. woutersi*, the inner terminal furcal setae significantly shorten in both littoral and pelagic groups of *M. dissimilis*.

Shifts in body proportions similar to those shown here as well within one species (*M. dissimilis*) as in a group of closely related species (*M. parentium*, *M. woutersi*, *M. dissimilis*) characterize other genuine plankters of the genus also (see Table 5).

The data in Table 5 give strong support for increase of relative lengths of the apical exopod and baseoendopod

Table 5. Shifts of body ratios in planktonic *Mesocyclops* taxa. [Closely related, reference taxa used in the comparisons: *M. aequatorialis similis*[1] (*M. aequatorialis s. str.*), *M. affinis*[2] (*M. tobae*) and *M. reidae*[3] (*M. yutsil*) +: tendency agrees with that observed in *M. dissimilis*; –: tendency does not agree with that observed in *M. dissimilis*)

	aequatorialis s. str.[1] L. Kivu,Tanganyika	tobae[2] L. Toba	yutsil[4] Large hypogean lakes
P5 MEDS/BASES	+	+	+
P5 MEDS/APS	+	+	+
FU L/W	+?	–	–
P4 ENP3 L/W	+	+	+
FU DORS/PLATS	+	+	+
FU INTERS/UROS	no data	–	–

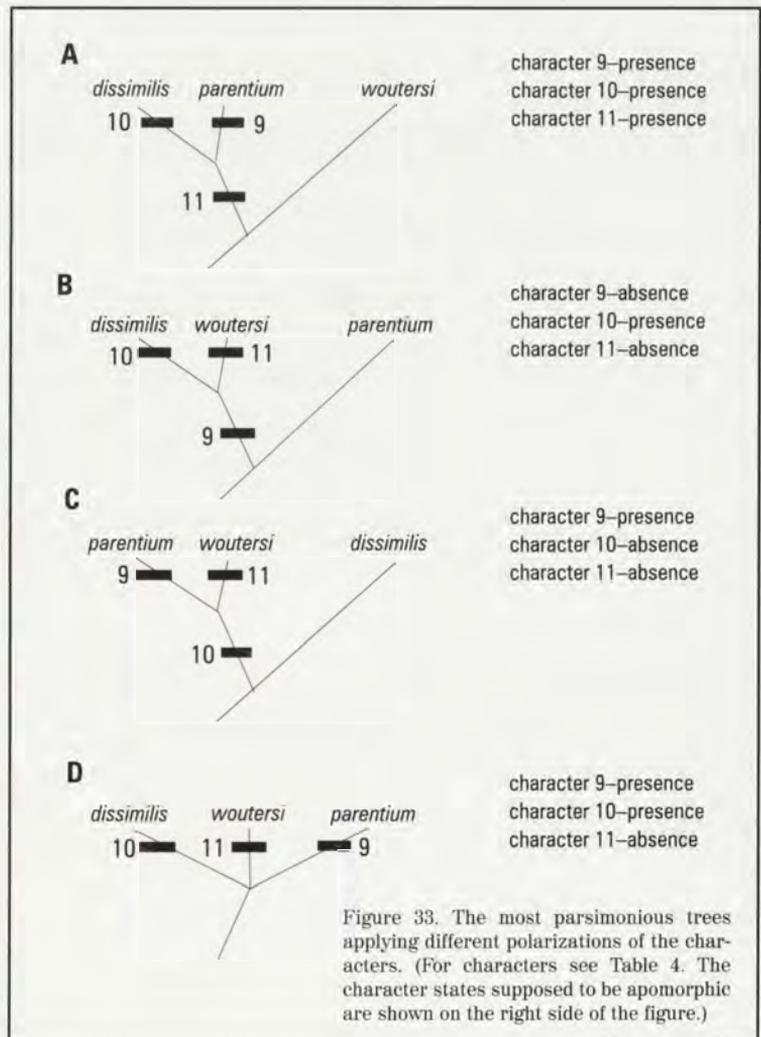[1]: After Van de Velde 1984; [2]: After Holynski 1994; [3]: After Reid 1993; [4]: After Fiers et al. 1996.

setae of leg 5, the dorsal furcal setae and the third endopodal segment of leg 4, as adaptations to the pelagic mode of life.Whereas, the decrease of relative length of the inner terminal furcal setae and elongation of furcal rami as pelagic characteristics remain questionable.

Conclusions

There was insufficient information to polarize characters 9, 10, 11 showing clear-cut differences among *M. parentium*, *M. woutersi* and *M. dissimilis* (see Table 4) *a priori*, therefore I examined all (24 = three different bifurcating trees for three taxa x 8 different combinations of polarities in three characters with two states each) possibilities of character evolution using just paper and pencil. Three dichotomous and one polytomous tree emerge as the shortest trees, with a length of three steps (Fig. 33A–D).

Distribution and ecological characteristics make *M. dissimilis* unlikely to be closest to the ancestor of the trio (Fig. 33C). The species, which lives at the northern boundary of the distributional area inhabited by the *thermocyclopoides*-group, and adapted to the pelagic way of life of large deep lakes (a special environment conquered by only few *Mesocyclops* species), supposedly represents the most advanced form in the clade *M. parentium–woutersi–dissimilis*. The scenario with a *woutersi*-like ancestor and a clade consisting of two extremes both in ecological and zoogeographical sense (*dissimilis–parentium*) (Fig. 33A) is not plausible either. Two competing hypotheses remain: one assumes a *parentium*-like ancestor and *M. woutersi–dissimilis* clade (Fig. 33B), while the other supposes separate divergence of all three species from the ancestral stock (Fig. 33D). The difference between these two branching patterns

resulted from opposite polarization of the dorsal hair ornamentation of pediger 5. As both states (hair rows present/absent) of this character appear in several species within the *thermocyclopoides*-group, and the relationship of *M. parentium–woutersi–dissimilis* group with those species has not yet been analyzed thoroughly, the choice of a convenient outgroup to polarization is problematic. However, the presence of regular hair rows in species (*M. granulatus, M. aspericornis, M. ogunnus*) that in having more than seven setae on the second endopodal segment of the antenna are probably close to root of *thermocyclopoides*-group points rather to plesiomorphy of this feature. Also the gradual reduction of hairiness on pediger 5 from *M. parentium* through *M. woutersi* to *M. dissimilis* (Figs 15–17), coinciding with series of changes in morphometric traits showing most advanced state in *M. dissimilis*, suggests the same polarization as above. As long as the phylogenetic relationships within *thermocyclopoides*-group are obscure, and knowledge of the distribution of *M. parentium* is poor, it is reasonable to keep both hypotheses in mind.

Figure 33. The most parsimonious trees applying different polarizations of the characters. (For characters see Table 4. The character states supposed to be apomorphic are shown on the right side of the figure.)

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Appendix 1. Basic statistical data of *M. dissimilis*, pelagic form.

	P5-EXP-APS	P5-EXP-MEDS	P5-BASES
Total frequency	13	15	14
Mean (μm)	131	86	97
Std dev. (μm)	13.5	7.45	12.1
Minimun (μm)	103	76	76
Maximum (μm)	149	101	116

FU-L	FU-W	P4-ENP3-L	P4-ENP3-W
16	16	15	15
99	27	81	24
3.70	2.00	3.68	1.89
90	25	73	20
106	33	88	28

FU-INTERS	UROS	FU-DORS	FU-PLATS
14	12	15	15
447	427	129	90
32.4	17.6	8.03	6.75
400	400	113	75
500	460	140	98

BODY-L
14
1081
68.8
965
1185

P5 MEDS/APS	P5 MEDS/BASES	FU L/W	P4 ENP3 L/W
13	14	16	15
0.660	0.898	3.73	3.40
0.069	0.090	0.219	0.250
0.510	0.710	3.10	2.79
0.830	1.03	4.00	3.90

FU INTERS/UROS	FU DORS/PLATS
12	15
1.04	1.44
0.069	0.149
0.94	1.22
1.16	1.77

Abbreviations used: P5-EXP-APS=length of apical seta of leg 5 exopod; P5-EXP-MEDS=length of medial seta of leg 5 exopod; P5-BASES =length of baseoendopodal seta of leg 5; FU-L=length of furca; FU-W=width of furca; P4-ENP3-L=length of third endopodal segment of leg 4; P4-ENP3-W=width of third endopodal segment of leg 4; FU-INTERS=length of inner terminal furcal seta; UROS=length of urosome; FU-DORS=length of dorsal furcal seta; FU-PLATS=length of posterolateral furcal seta; BODY-L=length of body; P5 MEDS/APS=ratio of length of medial and apical setae of leg 5 exopod; P5 MEDS/BASES=ratio of length of medial exopodal and baseoendopodal setae; FU L/W=ratio of length and width of furca; P4 ENP3 L/W=ratio of length and width of third endopodal segment of leg 4; FU INTERS/UROS=ratio of length of inner terminal furcal seta and urosome; FU DORS/PLATS=ratio of length of dorsal and posterolateral furcal setae

Appendix 2. Basic statistical data of *M. dissimilis*, littoral form.
(Abbreviations used are the same as in Appendix 1.)

	P5-EXP-APS	P5-EXP-MEDS	P5-BASES
Total frequency	6	6	5
Mean (μm)	114	89	85
Std dev. (μm)	3.95	5.90	5.80
Minimun (μm)	108	81	79
Maximum (μm)	121	96	93

FU-L	FU-W	P4-ENP3-L	P4-ENP3-W
10	10	9	9
105	31	82	29
3.85	1.36	4.27	2.21
100	29	75	25
111	34	86	32

FU-INTERS	UROS	FU-DORS	FU-PLATS
5	5	9	9
485	477	103	94
16.7	9.80	9.78	4.91
460	465	79	86
510	495	111	101

BODY-L
9
1256
47.1
1200
1375

P5 MEDS/APS	P5 MEDS/BASES	FU L/W	P4 ENP3 L/W
6	5	10	9
0.782	1.04	3.36	2.78
0.073	0.088	0.143	0.110
0.69	0.92	3.00	2.60
0.86	1.19	3.52	3.00

FU INTERS/UROS	FU DORS/PLATS
5	9
1.02	1.10
0.034	0.088
0.97	0.92
1.07	1.22

Appendix 3. Basic statistical data of *M. woutersi* (including *M. guangxiensis*) (Abbreviations used are the same as in Appendix 1.)

	P5-EXP-APS	P5-EXP-MEDS	P5-BASES
Total frequency	39	51	50
Mean (μm)	112	92	67
Std dev. (μm)	16.9	8.97	9.47
Minimun (μm)	79	63	50
Maximum (μm)	167	105	93

FU-L	FU-W	P4-ENP3-L	P4-ENP3-W
90	90	81	81
87	30	75	28
7.06	1.87	5.13	1.75
67	24	65	23
100	33	85	31

FU-INTERS	UROS	FU-DORS	FU-PLATS
76	67	72	77
540	418	76	84
37.1	31.9	10.2	8.29
460	315	54	64
610	480	95	103

BODY-L
57
1185
65.3
970
1320

P5 MEDS/APS	P5 MEDS/BASES	FU L/W	P4 ENP3 L/W
38	50	90	81
0.834	1.40	2.92	2.72
0.091	0.187	0.218	0.170
0.62	1.10	2.39	2.27
0.98	1.85	3.63	3.10

FU INTERS/UROS	FU DORS/PLATS
67	72
1.30	0.903
0.114	0.128
1.04	0.56
1.80	1.21

Appendix 4. Basic statistical data of *M. parentium* sp. nov. (Standard deviations not counted for the linear dimensions measured in very few specimens)

(Abbreviations used are the same as in Appendix 1.)

	P5-EXP-APS	P5-EXP-MEDS	P5-BASES
Total frequency	3	3	2
Mean (μm)	103	96	59
Std dev. (μm)	—	—	—
Minimun (μm)	83	86	59
Maximum (μm)	114	107	59

FU-L	FU-W	P4-ENP3-L	P4-ENP3-W
6	6	6	6
81	29	70	26
6.07	1.77	6.15	1.34
73	26	64	24
92	31	83	28

FU-INTERS	UROS	FU-DORS	FU-PLATS
4	4	3	3
502	387	69	82
—	—	—	—
440	365	66	75
580	405	75	90

BODY-L
6
1100
80.2
970
1205

P5 MEDS/APS	P5 MEDS/BASES	FU L/W	P4 ENP3 L/W
3	2	6	6
0.940	1.54	2.85	2.67
0.082	0.075	0.241	0.248
0.84	1.46	2.52	2.40
1.04	1.61	3.10	3.12

FU INTERS/UROS	FU DORS/PLATS
4	3
1.31	0.853
0.112	0.099
1.20	0.72
1.45	0.96

Appendix 5. t-test results. (+++: difference significant at $P<0.001$; ++: difference significant at $0.001<P<0.01$; +: difference significant at $0.01<P<0.05$; —: no significant difference at $P>0.05$.

(Abbreviations used are the same as in Appendix 1.)

P5 MEDS/APS

	diss p	diss l	wout	par
diss p	*			
diss l	++	*		
wout	+++	—	*	
par	+++	+	—	*

P5 MEDS/BASES

	diss p	diss l	wout	par
diss p	*			
diss l	+	*		
wout	+++	+++	*	
par	+++	+++	—	*

FU L/W

	diss p	diss l	wout	par
diss p	*			
diss l	+++	*		
wout	+++	+++	*	
par	+++	+++	—	*

P4 ENP3 L/W

	diss p	diss l	wout	par
diss p	*			
diss l	+++	*		
wout	+++	—	*	
par	+++	—	—	*

FU INTERS/UROS

	diss p	diss l	wout	par
diss p	*			
diss l	—	*		
wout	+++	+++	*	
par	+++	++	—	*

FU DORS/PLATS

	diss p	diss l	wout	par
diss p	*			
diss l	+++	*		
wout	+++	+++	*	
par	+++	++	—	*

BODY-L

	diss p	diss l	wout	par
diss p	*			
diss l	+++	*		
wout	+++	++	*	
par	—	+++	++	*