Mesocyclops (Crustacea, Copepoda, Cyclopidae) in the South Pacific islands

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Mesocyclops (Crustacea, Copepoda, Cyclopidae) in the South Pacific islands

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A B S T R A C T

Based mainly on recently collected material, we discuss the taxonomy and zoogeography of a (sub)tropical genus, Mesocyclops, in the South Pacific. A new species, Mesocyclops roberti sp. nov. is described from Fiji and the Wallis Islands. New data on the geographic distribution and morphology are reported for Mesocyclops mediadis, Mesocyclops woutersi and Mesocyclops aspericornis. Phylogenetic reconstructions coding the intraspecifically variable characters by different methods (unordered, unscaled and scaled coding) support close relationship of M. roberti with two Australian species (Mesocyclops brooki and Mesocyclops notios). Both the “unordered” and “scaled” analyses show monophyly of a group composed of Australian (Mesocyclops australiensis, M. brooki, M. notios, and Mesocyclops pubiventris) and South Pacific (M. mediadis and M. roberti sp. nov.) taxa. None of the analyses supports a sister relationship of M. roberti with M. mediadis (New Caledonia, Vanuatu), the only other species restricted to South Pacific, which suggests that Mesocyclops invaded the South Pacific from Australia at least twice. The sister relationship of the Australian-South Pacific clade remains unresolved, yet all reconstructions suggest a link with Asian Mesocyclops sp.

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1. Introduction

In the latest monograph of the zoogeography of the freshwaters, Bănărescu (1990, 1991, 1995) recognized eight zoogeographic regions and two transitional areas, the delimitations of which in certain details differ from the system that is used in many textbooks and some recent papers of the geographical distribution of the freshwater organisms (e.g. Boxshall and Defaye, 2008). Among others, the Pacific region, [this term was used in the publications of the “Freshwater Animal Diversity Assessment” project (Balian et al., 2006)] is referred by Bănărescu as the Indo-West Pacific region, but the latter entity also includes the Philippines, Wallacea (the East Indonesian archipelago between the Sunda shelf and the continental shelf of Australia), and the circum-Antarctic islands (in the cold zone of the southern Pacific and Indian Ocean). In the present study we will follow the Bănărescu system. The Indo-West Pacific region (or “peripheral areas”; the term Bănărescu preferred) is characterized by the relative paucity of the primarily freshwater taxa, and domination by lineages of marine origin (Bănărescu, 1995).

The Cyclopidae with ca. 990 (sub)species is one of the largest crustacean families in continental waters. Most of this cosmopolitan group live in fresh waters, only a small percentage is marine (Euryteinae, 11 species), or occur in brackish coastal and/or saline water bodies (most Halicyclopsinae and the cyclopine Apocylops Lindberg, 1942). From the Indo-West Pacific region merely 36 cyclopod species have been reported so far (Table 1), of which: 6 occur in the Philippines, 5 in Wallacea, and 2 in the circum-Antarctic, but not in the Pacific islands; and 23 species occur in islands of the Pacific Ocean (Dussart and Defaye, 2006; Schabetsberger et al., 2009; unpublished data of the senior author). As a comparison, in the similarly rich Cyprididae, an ostracod family with ca. 1000 species worldwide, 23 species occur in the Pacific (Meisch et al., 2007; the Philippines, Wallacea, and the circum-Antarctic islands were not included). That is, in both predominantly non-marine families approximately 2% of the species have invaded the Pacific archipelagoes. Most islands in the Indo-West Pacific region are located in the tropical belt, therefore mainly the “tropical” genera (Hołyńska, 2011) [Halicyclops Norman, 1903 (3), Ectocylops Brady, 1904 (2), Tropocylops Kiefer, 1927 (4), Bryocylops Kiefer, 1927 (2), Cryptocylops G.O. Sars, 1927 (1), Mesocylops G.O. Sars, 1914 (8), Metacyclops Kiefer, 1927 (1), Microcylops Claus 1893 (2), and Thermocylops Kiefer 1927 (5)] are represented there, although a few “tropical/temperate” [Eucyclops Claus, 1893 (1), Paracyclops Claus, 1893 (2), Gonicyclops Kiefer, 1955 (1)] and “temperate” [Diacyclops Kiefer, 1927 (1), Acanthocylops Kiefer, 1927 (1), and Mixocylops Kiefer, 1944 (1)] groups also occur. None of these genera is endemic to the Indo-West Pacific, but 11 species only occur in one or few islands of the region (Philippines: 2; Sulawesi: 2; New Caledonia (with Vanuatu): 3;
Fiji (with Tonga and Samoa): 2; circum-Antarctic: 2). The relative species richness of *Mesocyclops* in the Indo-West Pacific may partly be due to the fact, that the taxonomy/zoogeography of this group, in comparison to other tropical groups, is better known. *Mesocyclops* is also the only cyclopoid genus in which comprehensive analysis of the phylogeny has been attempted (Holyńska, 2006).

In 2004 Robert Schabetsberger and Gabrielle Drozdowski organized a collecting trip in the South Pacific and sampled 39 water bodies on 18 islands. Preliminary identification of the cyclopoid material was done by one of us (F.S.) and published by Schabetsberger et al. (2009). Of the 12 species reported there, 5 taxa belonged to *Mesocyclops*: *Mesocyclops aspericornis* (Fisk, 1906), *Mesocyclops woutersi* Van de Velde, 1987, M. sp. 1 aff. *woutersi*, M. sp. 2 aff. *woutersi*, M. sp. 3 aff. *woutersi*.

The aims of this paper are: (i) to perform a detailed morphological analysis of the material of the genus *Mesocyclops* reported in Schabetsberger et al. (2009); (ii) to search for the closest relatives of the South Pacific endemic species in a phylogenetic analysis that includes the Old World representatives of the genus; and (iii) to formulate a hypothesis about the origin of *Mesocyclops* in the South Pacific islands.

2. Materials and methods

Selected specimens were dissected in glycerin, and mounted on slides in glycerin medium. Slides were sealed with nail polish. The remaining specimens were stored in 70% ethanol with 10% glycerin added. Drawings were made with the aid of a camera lucida,

![Table 1](https://example.com/table1.png)

**Table 1**

<table>
<thead>
<tr>
<th>Indo-West Pacific</th>
<th>Extralimital</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phil.</td>
<td>Wall.</td>
</tr>
<tr>
<td><strong>Halicyclops</strong></td>
<td></td>
</tr>
<tr>
<td><em>H. thermophilus</em> Kiefer, 1929</td>
<td>+</td>
</tr>
<tr>
<td><em>H. spinifer</em> Kiefer, 1935</td>
<td>+</td>
</tr>
<tr>
<td><em>H. septentrionalis</em> Kiefer, 1935</td>
<td></td>
</tr>
<tr>
<td><strong>Eucyclops</strong></td>
<td></td>
</tr>
<tr>
<td><em>E. neocaledoniensis</em> Dussart, 1984</td>
<td>+</td>
</tr>
<tr>
<td><strong>Australoecyclops</strong></td>
<td></td>
</tr>
<tr>
<td><em>A. aff. timmi</em></td>
<td>+</td>
</tr>
<tr>
<td><strong>Paracyclops</strong></td>
<td></td>
</tr>
<tr>
<td><em>P. chiltoni</em> (Thomson, 1882)</td>
<td>+</td>
</tr>
<tr>
<td><em>P. eucyclopoides</em> Kiefer, 1929</td>
<td>+</td>
</tr>
<tr>
<td><strong>Ectocyclus</strong></td>
<td></td>
</tr>
<tr>
<td><em>E. phaleratus</em> (Koch, 1838)</td>
<td>+</td>
</tr>
<tr>
<td><em>E. rubescens</em> Brady, 1904</td>
<td>+</td>
</tr>
<tr>
<td><strong>Tropicyclops</strong></td>
<td></td>
</tr>
<tr>
<td><em>T. prasinus</em> (Fischer, 1860)</td>
<td>+</td>
</tr>
<tr>
<td><em>T. p. meridionalis</em> Kiefer, 1931</td>
<td>+</td>
</tr>
<tr>
<td><em>T. confinis</em> (Kiefer, 1930)</td>
<td>+</td>
</tr>
<tr>
<td>&quot;<em>T. matanensis</em> Dussay, 2007&quot;</td>
<td>+</td>
</tr>
<tr>
<td><strong>Microcyclus</strong></td>
<td></td>
</tr>
<tr>
<td><em>M. varicans</em> (G.O. Sars, 1863)</td>
<td>+</td>
</tr>
<tr>
<td>&quot;<em>M. microsetus</em> Yeatman, 1983&quot;</td>
<td>+</td>
</tr>
<tr>
<td><strong>Mesocyclops</strong></td>
<td></td>
</tr>
<tr>
<td><em>M. aspericornis</em> (Daday, 1906)</td>
<td>+</td>
</tr>
<tr>
<td>&quot;<em>M. microlasius</em> Kiefer, 1981&quot;</td>
<td>+</td>
</tr>
<tr>
<td>&quot;<em>M. friendorum</em> Holyńska, 2000&quot;</td>
<td>+</td>
</tr>
<tr>
<td>&quot;<em>M. medialis</em> Dussay, 2001&quot;</td>
<td>+</td>
</tr>
<tr>
<td><em>M. agamus</em> Onabamiro, 1957</td>
<td>+</td>
</tr>
<tr>
<td>M. affinis Van de Velde, 1987</td>
<td>+</td>
</tr>
<tr>
<td><em>M. thermocyclopoides</em> Harada, 1931</td>
<td>+</td>
</tr>
<tr>
<td><em>M. woutersi</em> Van de Velde, 1987</td>
<td>+</td>
</tr>
<tr>
<td><strong>Bryocyclus</strong></td>
<td></td>
</tr>
<tr>
<td><em>B. anninae</em> (Menzel, 1926)</td>
<td>+</td>
</tr>
<tr>
<td>&quot;<em>B. fidei</em> Lindberg, 1954&quot;</td>
<td>+</td>
</tr>
<tr>
<td><strong>Cryptocyclus</strong></td>
<td></td>
</tr>
<tr>
<td><em>C. linjanticus</em> (Kiefer, 1928)</td>
<td>+</td>
</tr>
<tr>
<td><strong>Dicycyclus</strong></td>
<td></td>
</tr>
<tr>
<td>&quot;<em>D. miryri</em> (Borutzky and Vinogradov, 1957)&quot;</td>
<td>+</td>
</tr>
<tr>
<td><strong>Acanthocyclus</strong></td>
<td></td>
</tr>
<tr>
<td><em>A. robustus</em> (?) (G. O. Sars, 1863)</td>
<td>+</td>
</tr>
<tr>
<td><strong>Metacyclops</strong></td>
<td></td>
</tr>
<tr>
<td><em>M. mendocinus</em> (Wierzejski, 1889)</td>
<td>+</td>
</tr>
<tr>
<td><strong>Mixocyclus</strong></td>
<td></td>
</tr>
<tr>
<td>&quot;<em>M. crrozensis</em> Kiefer, 1944&quot;</td>
<td>+</td>
</tr>
<tr>
<td><strong>Thermocyclus</strong></td>
<td></td>
</tr>
<tr>
<td><em>T. crassus</em> (Fischer, 1853)</td>
<td>+</td>
</tr>
<tr>
<td><em>T. decipiens</em> (Kiefer, 1929)</td>
<td>+</td>
</tr>
<tr>
<td><em>T. operculifer</em> (Kiefer, 1930)</td>
<td>+</td>
</tr>
<tr>
<td>&quot;<em>T. philippinensis</em> (Marsh, 1932)&quot;</td>
<td>+</td>
</tr>
<tr>
<td><em>T. woutercki</em> Kiefer, 1938</td>
<td>+</td>
</tr>
<tr>
<td><strong>Goniocyclus</strong></td>
<td></td>
</tr>
<tr>
<td>&quot;<em>G. arenicola</em> Dussart, 1984&quot;</td>
<td>+</td>
</tr>
</tbody>
</table>

Phil., Philippines; Wall., Wallacea; Paci., Pacific islands; C.-Ant., Circum-Antarctic; AUS, Australian; ETH, Ethiopian; HOL, Holarctic; MAL, Malagasy; MID, Middle American transitional; NEO, Neotropical; SIN, Sinoindian; WAT, Western Asian transitional (Dussart and Defaye, 2006; Schabetsberger et al., 2009; own data). Taxa that are endemic to the Indo-West Pacific region are marked by asterisk.
using Olympus BX50 microscope equipped with Nomarski optics. All measurements were taken with an ocular micrometer.

The following abbreviations are used in the descriptions: ae, aesthetasc; enp, endopodite; exp, exopodite; P1–P6, leg 1–leg 6; MIZ, Museum and Institute of Zoology Warsaw; MNHN, Muséum national d’Histoire naturelle Paris.

Type specimens as well as all the material examined are deposited at the Museum and Institute of Zoology of the Polish Academy of Sciences, Warsaw, Poland.

Except for those specimens which were collected by others than Schabetsberger and Drozdowski, collecting data were taken from Schabetsberger et al. (2009). Shallow water bodies were sampled from the shore, while in larger lakes the samples were taken from 0 to 5 m depth (Schabetsberger et al., 2009).

In the phylogenetic reconstructions the criterion of the global parsimony was applied using Hennig86 version 1.5 (Farris, 1988). The analysis included all Old World taxa (48 species) lacking medial spine on P1 basipodite. Monophyly of this group has been supported by both morphological (Holyńska, 2006) and combined (morphology + nuclear genes) analyses (Wyngaard et al., 2010). Collecting sites of the taxa included in the phylogenetic reconstructions are those given by Holyńska (2006), as well as those provided herein. The morphological characters used in the analysis (Appendix A) are the same as in Holyńska (2006), with the exception of the modifications of the character states of characters 25 and 79. Character 25, modified character state (0): aesthetasc on penultimate antennular segment is long, reaching to about the middle of the terminal segment; character 79, modified character state (3): 2 sets of spinules present on antennular segments 1 and 12–14. The character matrix (Appendix B) was extracted from what has already been published by Holyńska (2006), but was supplemented with new data on Mesocyclops roberti sp. nov., Mesocyclops bosuntwii Mirabullayaye, Sanful and Frempong, 2007 and Mesocyclops mediialis Defaye, 2001.

Altogether six separate analyses were run treating polymorphic characters in three different ways (unordered, unscaled and scaled coding – Campbell and Frost, 1993; Mabee and Humphries, 1993; Wiens, 2000) and using two different sets of the terminal taxa. For a comparison of the accuracies of different coding methods of the polymorphic characters to recover clades of taxa with known phylogenies, see Wiens (2000). The three coding methods recognize a polymorphic state as a separate state, the differences between these coding methods are in the presumed numbers of character state transformations. In the unordered coding the numbers of transformations are the same between any character states (“fixed absent”, “polymorphic”, and “fixed present”). In unscaled coding the states “fixed absent”, “polymorphic”, and “fixed present” are ordered, the traits pass through a polymorphic stage between absence and fixed presence (a change from “fixed absent” to “fixed present” involves two steps); yet those characters, in which polymorphic stage was not observed, are not assumed to pass through the polymorphic stage (a change from “fixed absent” to “fixed present” involves one transformation). In the scaled method the states “fixed absent”, “polymorphic”, and “fixed present” are ordered; in those characters in which polymorphic stage was not observed, it is assumed that polymorphic stage was present but unobserved (a change from “fixed absent” to “fixed present” involves two transformations). That is, fixed characters get a weight of 2 with the scaled method (relative to characters with polymorphic states), and a weight of 1 with unscaled method.

In the “unordered” analysis, all characters (both those which are intraspecifically variable, and those which are not) were coded as unordered, and given a weight of one. In the “unscaled” run, characters 6, 8–11, 14, 17, 23, 50, 53, 54, 63 and 79 were coded as unordered, and all others those with intraspecific variation, as well as some fixed characters with serially homologous receptive states (chars 22, 68) were coded as ordered, and all characters were given a weight of one. In the “scaled” analysis, characters 6, 8–11, 14, 15, 17, 23, 50, 53, 54, 63 and 79 were coded as unordered, and all others were coded as ordered; the fixed characters 4, 6–12 14, 17, 21–23, 25, 28, 37, 38, 41–45, 47, 50, 53–55, 57, 59–63, 68, 74, 75, 77, 79 and 81 were given a weight of 2, and polymorphic characters were given a weight of one.

For each type of coding of polymorphic characters, two parallel analyses were run: one which was extended to include all Old World taxa lacking medial spine on P1 basipodite, including also M. bosuntwii, a taxon recently described from Ghana (Africa); and one, which excluded M. bosuntwii from the above mentioned group, as the states of several characters are still unknown in this species.

In tree building a heuristic search was employed using mheinn* bb* commands. In the analysis of character transformations and editing of the trees we used WinClada (Nixon, 1999–2002).

3. Results

3.1. M. roberti sp. nov.

Type material. Holotype (female, MIZ: 300001) from Wal lis Island (France), Lac Lanutuli [18], 17°13′W, 13°19′S, alt. 10 m, area 0.001 ha, water depth 1 m, fishless, volcanic crater lake with submerged vegetation, temp. 33.9 °C, pH 4.14, cond. 30 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 02 November 2004 – referred by Schabetsberger et al. (2009) as M. sp. 2 aff. woutersi Van de Velde, 1987.

Paratypes. 3 females (MIZ: 300002–300004) and 1 male (MIZ: 300005) from the same locality as the holotype, and 6 females (MIZ: 300006–300011) and 4 males (MIZ: 300012–300015) from Fiji, Vanua Levu, Navesiwaka [14], 17°40′E, 16°25′S, alt. 230 m, lake with fish (tipilas) and without submerged vegetation, area 1.5 ha, depth 8 m, temp. 27.5 °C, pH 7.4, cond. 41 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 15 October 2004 – referred by Schabetsberger et al. (2009) as M. sp. 3 aff. woutersi Van de Velde, 1987.

Etymology. The species is named in honour of Dr. Robert Schabetsberger, who collected the species described herein.

Female (Fig. 1A and B; unless otherwise stated, description refers to holotype) – body length 990 μm; length of prosome/length of urosome: 1:84; width of cephalothorax/width of genital double-somite: 2:93; cephalothorax, length/width: 1:14.

Pediger 5 (Fig. 2B) bearing long hairs laterally and rows of short hairs dorsally near distal margin; two medial and two laterodistal hair-sensilla present on dorsal surface. Genital double-somite 1.2 times as long as wide, with few groups of very tiny hairs/spinules (Fig. 2B, with arrowheads) on dorsolateral surface. These groups of hairs are difficult to notice on intact specimens, yet it is rather easy to observe the hair ornamentation in the female in which the genital double-somite is dorso–ventrally compressed. Ventral surface of genital double-somite (Fig. 1E) with pits, no hairs or spinules present. Anterior part of seminal receptacle (Fig. 1E) with wide lateral arms, sinuate in the middle; posterior part long. Medial copulatory pore horsehoe-shaped, single circular pore next to copulatory pore. Copulatory duct strongly but not sinuously curved, duct-like transverse structures V-shaped next to copulatory pore. Anal operculum (Fig. 2A) weakly developed, proctodenum without hairs or spinules, posterior margin of anal somite with continuous row of spinules. Caudal rami 2.75 times as long as wide, no medial hairs. Both ventral and dorsal surface of rami ornamented with small spinules (Fig. 2A). Larger spinules present at insertion of lateral and lateralmost terminal caudal setae. Lateral caudal seta 0.55 times as long as ramus, and inserted at distance of 0.4 length of the caudal ramus, measured from posterior end of ramus. Dorsal
caudal seta 1.03 times as long as lateralmost terminal caudal seta. Relative length of the terminal caudal setae from medialmost to lateralmost: 3.4, 6.1, 4.3, 1.0. Inner median (longest) terminal caudal seta 1.24 times as long as urosome.

Antennule reaching slightly beyond cephalothorax in females from Wallis Island (Fig. 1A), or beyond pediger 2 in females from Fiji (Fig. 1B); 17-segmented, armature formula as usual in the genus: 1 – [8], 2 – [4], 3 – [2], 4 – [6], 5 – [4], 6 – [2], 7 – [2], 8 – [1], 9 – [1], 10 – [0], 11 – [1], 12 – [1 + ae], 13 – [0], 14 – [1], 15 – [2], 16 – [2 + ae], 17 – [7 + ae] (Fig. 3A, B and D). Aesthetasc on segment 12 reaching (or slightly beyond) distal margin of segment 13 in specimens from Wallis and Fiji (Fig. 3B and C). Aesthetasc on segment 16 short, not reaching insertion of medial seta of segment 17. Segments 1, 4–5, and 7–13 with spinules on anterior surface. Segments 16 and 17 with serrate hyaline membrane, that on article 17 extending almost whole length of segment and bearing one or two small notches (one notch in the holotype).
Antenna (Fig. 4A) composed of coxobasis and 3-segmented endopodite, with 3, 1, 9, and 7 setae, respectively. Lateral (exopodal) seta of coxobasis reaching beyond distal margin of third endopodal segment (seta broken off in the holotype, character verified in the paratypes). Long row of spinules (24) present next to lateral margin on frontal surface of antennal coxobasis, spinules absent near insertion of exopodal seta. Spinule ornamentation on caudal surface of coxobasis (Fig. 4B–D) consisting proximal spinules on lateral margin (group a), oblique row of larger spinules (8) next to former group (group b), wide oblique field of small spinules starting ca. in middle of segment (group c), spinules along medial rim (group d), longitudinal row (23 spinules) near lateral margin (group e), and field of small spinules at implantation of mediiodistal setae (group f).

Labrum (Fig. 4E) undivided lobe extending posteroventrally between antennae, with long distal hairs arranged in arc, rounded lateral protuberances smooth (indicated by arrowhead in Fig. 4E). Epistoma, median hump between labrum and rostrum, with fine hairs (indicated by arrowhead in Fig. 4E), row of long hairs present laterally to epistoma. Armature of paragnaths (Fig. 5A) as usual in the genus: spinules present in distal half, on inner (dorsal) surface; fine hairs appear whole length of paragnath (Fig. 5A shows hairs on the medial margin only) on outer (ventral) surface; four medial spines inserted in proximal half, on inner surface; mediiodistal lobe with hairs.

Mandibular palp (Fig. 5B) with two long and one short setae; gnathobase bearing three groups of spinules on anterior surface close to insertion of palp, spinules in transverse proximal row much larger than those in other two groups.

Maxillule (Fig. 5C and D) with armature as common in genus: arthrite ending in three distal claw-like setae with one ventral seta at their base; four paired setae (one pair large and one pair small), one small and bare, and one robust feathered seta on medial margin of arthrite; and one small spine lateroproximally to large feathered seta. Maxillulary palp (Fig. 5D) bare, with one proximal and three apical setae, and with three setae on lateral lobe of the palp.

Maxilla (Fig. 5E) with praecoxopodite and coxopodite fused on frontal surface, articulation between segments present on caudal surface; praecoxopodite with one endite bearing 2 setae, coxopodite with median and distal endite with 1 and 2 setae, respectively. Distinct row of fine spinules presents on frontal surface of coxopodite (Fig. 5A). Basipodite (Fig. 5E) with one short seta inserted on caudal surface at base of medial claw-like attenuation of segment, and one long seta. Endopodite apparently one-segmented: arthrodidal membrane between second (terminal) endopodal segment and large distal seta fails to form, therefore two smaller setae appear as if inserted on base of large distal seta.

Maxilliped (Fig. 6B) with syncoxopodite, basipodite and 2-segmented endopodite, bearing 3, 2, 1 and 3 setae, respectively. No ornamentation on frontal surface of syncoxopodite. Spinules on caudal surface of basipodite arranged in two groups near lateral margin. On frontal surface, long hair-like spinules present near medial margin of basipodite and median part of first (proximal) endopodal segment.

Armature of swimming legs (Table 2 and Figs. 6C and D and 7A–E), as common in genus. Couplers of P1–P4 without hairs/spinules on caudal and frontal surfaces. P4 coupler (Fig. 7C and F) with small and obtuse protuberances. P1 basipodite lacking medial spine (Fig. 6C), spinules on frontal
Fig. 6. Mesocyclops roberti sp. nov., female: (A) maxilla syncxopodite, frontal; (B) maxilliped, frontal; (C) leg 1, frontal; and (D) leg 2 (caudal). Except for (A) showing a paratype (Wallis, MIZ: 300002), all drawings show holotype. Scale bars: 50 μm.

Table 2
Armature of legs 1–4 in Mesocyclops roberti sp. nov. Spines are denoted by Roman, setae by Arabic numerals. The armature on the lateral margin of any segment is given first, followed by the elements on the apical and medial margins.

<table>
<thead>
<tr>
<th>Coxopodite</th>
<th>Basipodite</th>
<th>Exopodite</th>
<th>Endopodite</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leg 1</td>
<td>0–1</td>
<td>0–0</td>
<td>0–1; 1–1; 1–2; 2–2</td>
</tr>
<tr>
<td>Leg 2</td>
<td>0–1</td>
<td>1–0</td>
<td>1–1; 1–1; 1–2; 1–3</td>
</tr>
<tr>
<td>Leg 3</td>
<td>0–1</td>
<td>1–0</td>
<td>1–1; 1–1; 1–2; 1–3</td>
</tr>
<tr>
<td>Leg 4</td>
<td>0–1</td>
<td>1–0</td>
<td>1–1; 1–1; 1–2; 1–3</td>
</tr>
</tbody>
</table>

surface arranged in arch between insertion of exo- and endopodite. Basipodite of P1–P3 with long hair-like spinules on frontal surface near lateral margin (indicated by arrowhead in Fig. 6D). Medial expansion of P1 basipodite with medial and apical hairs, those on P2–P4 only apically pilose. Hair-like spinules on caudal surface of medial expansion of P3 basipodite (indicated by arrowhead in Fig. 7A) present only on leg of left side. Proximal hairs on caudal surface of medial expansion of P4 basipodite (indicated by arrowhead in Fig. 7C) appear on legs of left and right side. Caudal surface of P4 coxopodite (Fig. 7C) adorned with intermittent row of spinules (10–11) next to distal margin (group a), group of elongate spinules at laterodistal angle (group b), median row of spinules (8–9) near proximal margin (group c), fine hairs at proximolateral angle (group d) and next to lateral margin (group e). Group of hairs/spinules also presents on anterolateral surface of pediger 4 (Fig. 7F). P4 enp3 (Fig. 7D) 2.9 times as long as wide, terminal spines of equal length, 3/4 of segment length. Lateral margin of medial (inner) spine with single or no teeth. P5 2-segmented, apical seta of segment 2 1.1–1.5 times as long (1.1 in holotype), and lateral seta of segment 1 0.8–1.1 times (broken off in holotype) as long as medial spine on segment 2. P6 (Fig. 2B) bearing long medial setae reaching about middle of genital double-somite, and two short lateral spines.

Male (paratypes from Wallis and Fiji) – body length larger in specimen from Wallis (640 μm – one specimen) than in males from Fiji (547 μm – mean of four specimens) (Fig. 1C and D) – for morphometric data see Table 3. Pediger 5 (Fig. 8A) with long lateral hairs, no hairs/spinules on dorsal surface, only 2 median and 2 laterodistal hair-sensilla present. Posterior margin of anal somite with continuous row of spinules. Caudal rami shorter (length/width: 2.33–2.56) than in females, no medial hairs. Spinules present at implantation of lateral and lateralmost terminal caudal setae. Dorsal caudal seta slightly longer (dorsal/lateralmost: 1.28–1.63), and medialmost terminal caudal seta shorter (medialmost/lateralmost: 2.6–2.8), than in female.

Antennule 16-segmented with incomplete subdivision of compound apical segment, armature formula as common in genus: 1 – [8 + 3 ae], 2 – [4], 3 – [2], 4 – [2+ ae], 5 – [2], 6 – [2], 7 – [2], 8 – [2], 9 – [1+ spine + ae], 10 – [2], 11 – [2], 12 – [2], 13 – [2+ ae], 14 – [2], 15 – [1+ ae], 16 – [4 + ae], 7 + ae]. Plate-like structures with pore (1 large plate on segment 14 and 2 smaller ones on segment 15) and short conical elements (one on segment 14 and 15 each) present at distal geniculation. Spinules on anterior surface present only on first segment of antennule.

Table 3
Variation of the morphometric characters in male of Mesocylops roberti sp. nov. Numbers in parentheses show where the number of specimens measured is less than four.

<table>
<thead>
<tr>
<th>Character</th>
<th>Wallis (1 male)</th>
<th>Fiji, Vanua Levu (4 males)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range</td>
<td>Mean</td>
</tr>
<tr>
<td>1</td>
<td>640</td>
<td>525–570</td>
</tr>
<tr>
<td>2</td>
<td>1.32</td>
<td>1.14–1.4(3)</td>
</tr>
<tr>
<td>3</td>
<td>1.87</td>
<td>1.72–1.85</td>
</tr>
<tr>
<td>4</td>
<td>1.1</td>
<td>1.10–1.20</td>
</tr>
<tr>
<td>5</td>
<td>2.56</td>
<td>2.33–2.50</td>
</tr>
<tr>
<td>6</td>
<td>0.67</td>
<td>0.57–0.65</td>
</tr>
<tr>
<td>7</td>
<td>0.43</td>
<td>0.33–0.43</td>
</tr>
<tr>
<td>8</td>
<td>1.35</td>
<td>1.28–1.63</td>
</tr>
<tr>
<td>9</td>
<td>2.6</td>
<td>2.6–2.8</td>
</tr>
<tr>
<td>10</td>
<td>5.3</td>
<td>5.7–6.6</td>
</tr>
<tr>
<td>11</td>
<td>3.9</td>
<td>4.2–4.8</td>
</tr>
<tr>
<td>12</td>
<td>1.67</td>
<td>1.40–1.55</td>
</tr>
<tr>
<td>13</td>
<td>2.67</td>
<td>2.9–3.1</td>
</tr>
<tr>
<td>14</td>
<td>1.1</td>
<td>1.04–1.07</td>
</tr>
<tr>
<td>15</td>
<td>0.82</td>
<td>0.69–0.81</td>
</tr>
<tr>
<td>16</td>
<td>1.7</td>
<td>1.4–1.9</td>
</tr>
<tr>
<td>17</td>
<td>3.0</td>
<td>4.7(1)</td>
</tr>
</tbody>
</table>

1, body length (μm); 2, cephalothorax, length/width; 3, length of prosome/length of urosome; 4, length of longest terminal caudal seta/length of urosome; 5, caudal ramus, length/width; 6, length of lateral caudal seta/length of caudal ramus; 7, distance of insertion of lateral caudal seta, measured from posterior end of ramus/length of caudal ramus; 8, caudal setae, dorsal/lateralmost; 9, terminal caudal setae, medialmost/lateralmost; 10, terminal caudal setae, inner medial (longest)/lateralmost; 11, terminal caudal setae, outer median/lateralmost; 12, P4, length of coxopodite seta/height of medial expansion of basipodite; 13, P4 enp3, length/width; 14, P4 enp3, medial terminal spine/lateral terminal spine; 15, length of longer terminal spine/length of P4 enp3; 16, P6, length of median seta/length of medial spine; 17, P6, length of lateral seta/length of medial spine.

Antenna (Fig. 8B) with coxobasis and 3-segmented endopodite, bearing 3, 1, 6, and 7 setae, respectively. Spine ornamentation of coxobasis (Fig. 8B) similar to female, but fewer spines present in particular groups; ‘group c’ (cf. Fig. 4B) never forms field yet fine row present, ‘group I’ (cf. Fig. 4B) missing or present with few spines.

Labrum with long distal hairs, epistoma bare in both Wallis and Fiji. Paragynaths, mandible, maxillule and maxilliped as in female. Setation of maxilla as in female, but spines on frontal surface of coxopodite missing or very tiny.

Armature of swimming legs as in female. Couplers of P1–P4 without hairs/spinules, protuberances of P4 coupler small and obtuse. Basipodite of P1–P4 without laterofrontal spines. Proximal hairs (Fig. 8C, with arrowhead) on caudal surface of medial expansion of basipodite present only on P4. Medial expansion of basipodite apically pilose in P1–P4. Pediger 4 bearing row of spinules/hairs on anterolateral surface. Spine ornamentation on caudal surface of P4 coxopodite (Fig. 8C) similar to that in female, yet ‘group d’ (cf. Fig. 7C) absent, or present with few short hairs, and ‘group e’ (cf. Fig. 7C) absent. P4 enp3 (Fig. 8D) 2.7–3.1 times as long as wide; terminal spines subequal, or medial spine slightly longer than lateral, medial terminal spine 0.7–0.8 times as long as segment. No, or just few (1–3) teeth on lateral margin of medial spine. Except for one medial pore, no surface ornamentation on P6 flap (Fig. 8A). P6 with middle seta 1.4–1.9 times as long as medial spine, and lateral seta 3.0–4.7 times as long as medial spine.

3.1.1. Intraspecific variation

Beyond the body size, other morphometric traits, such as length and width ratio of the caudal ramus, and relative lengths of the dorsal caudal seta and coxopodite seta of P4, differ between the Wallis and Fiji populations (Table 4) as well. The spine ornamentation on the caudal surface of antennal coxobasis varies: in ‘group e’ (cf. Fig. 4B) there are more spinules (≥20) in the specimens from Wallis than in females from Fiji (13–16); spinules in ‘group c’ can appear in a wide oblique field, or almost single line in both Wallis and Fiji.
and Fiji population. In the longitudinal row on the frontal surface of antennal coxobasis (Fig. 4A, with arrowhead), spines are less in females from Fiji (20–23 spines) than in females from Wal- lis (24–25). Epistoma pilose in females from Wallis (Fig. 4E), yet bare in females from Fiji (Fig. 4F, with arrowhead). Hair-like spinules on the caudal surface of the medial expansion of P3 basipodite (Fig. 7A, with arrowhead) appear asymmetrically (only on one side of the paired legs) in 2 of 4 females from Wallis, and present on both sides in 1 of 6 females verified from Fiji – the group is absent in 7 of 10 females from Wallis and Fiji. Lateral pilosity on the caudal surface of P4 coxopodite (Fig. 7C, ’group e’) scarce or missing in females from Fiji.

3.1.2. Diagnosis (female)

The species can be distinguished from its congeners by the following combination of characters: Small to medium-sized (0.7–1.1 mm) species. Pediger 5 with long hairs laterally, and rows of short hairs dorsally. Hairs present on anterolateral surface of pediger 4. Few groups of spinules/hairs present on laterodorsal surface of genital double-somite. Seminal receptacle with wide lateral arms, posterior part long. Duct-like transverse structures V shaped next to copulatory pore, copulatory duct strongly, but not sinuously curved. Caudal rami relatively short, 2.5–2.9 times as long as wide, no hairs on medial margin. Spinules present at insertion of lateral and lateralmost terminal caudal setae.

Antennular segments 1, 4–5, and 7–13 with spinules on anterior surface. Serrate hyaline membrane of terminal antennal segment extending almost the whole length of article, with one or two small notches. Second endopodal segment of antenna with 9 setae. On caudal surface of antennal coxobasis, group of small spinules present near insertion of mediodistal setae (‘group f’, cf. Fig. 4B), ‘group c’ can be wide field or single row (Fig. 4B–D). Mandible with three groups of spinules near palp, on anterior surface. Maxillulary palp bare. Maxilla with distinct row(s) of spinules on frontal surface of coxopodite. P1 basipodite lacking median spine. P4 coupler bare, protuberances small and obtuse. Medial expansion of P4 basipodite with apical hairs, and proximal hairs on caudal surface. Terminal spines on P4 enp3 subequal (medial/lateral: 1.0–1.2), teeth absent or only few (1–6) on lateral margin of medial spine.

The adult female of _M. roberti_ sp. nov. can be distinguished from the closest, Australian relatives (see Section 4), _M. notius_ Kiefer, 1981 and _M. brooksi_ Pesce, De Laurentis and Humphreys, 1996, by: pilosity of the dorsal surface of the genital double-somite (restricted to few spots in _M. roberti_ and _M. brooksi_, yet extended to both anterior and posterior half of double-somite in _M. notius_); number of setae on the second endopodal segment of antenna (9 in _M. roberti_, 8 or 7 in _M. brooksi_, and 7 in _M. notius_); the size of spinules near implantation of the mediodistal setae (group f) on the caudal surface of antennal coxobasis (spinules are much smaller than those in the longitudinal row (group e) in _M. roberti_ and _M. brooksi_, yet spinules are at least as large as those in longitudinal row in _M. notius_); lateral edge of medial terminal spine of P4 enp3 smooth or with few teeth in _M. roberti_ (many teeth in _M. brooksi_, few or many in _M. notius_); length of terminal spines of P4 enp3 (while in _M. roberti_ the medial spine longer or as long as lateral spine, in _M. notius_ and _M. brooksi_ it is usually shorter than lateral one). There are also some characters in the male that aid in distinguishing the new species from the closely related Australian taxa: middle seta of P6 conspicuously (1.4–1.9 times) longer than medial spine (subequal in _M. notius_); lateral edge of medial terminal spine of P4 enp3 without teeth or just few (1–3) teeth present (many teeth in _M. brooksi_ and _M. notius_); medial terminal spine of P4 enp3 longer or as long as lateral terminal spine (shorter than lateral in _M. brooksi_ and _M. notius_).

3.2. _M. medialis_ Defaye, 2001

_Vanaxu_. Epi, Lake Imao. 32. 168°13’E, 16°46’S, alt. 280 m, 0.7 ha, depth 1 m, with submerged vegetation, temp. 27.7 °C, pH 6.65, cond. 41 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 22 December 2004, 2 females (MIZ: 300016–300017), 1 male (MIZ: 300018); Espiritu Santo, Blue Hole near Shark Bay, [30] 16°10’E, 15°19’S, alt. 5 m, 0.2 ha, depth 10 m, temp. 26.5 °C, pH 7.13, cond. 1070 μS cm⁻¹, with fish, leg. R. Schabetsberger & G. Drozdowski, 11 December 2004, 2 males (MIZ: 300019–300020), 1 CV female (MIZ: 300021) – referred to by Schabetsberger et al. (2009) as _M. sp. 2 aff. woutersi_ Van de Velde, 1987.

**Distribution.** Known only from the South Pacific (New Caledonia and Vanuatu).

**Comments.** Examination of the Vanuatu material provided some additional information on morphology of the male, which so far has been known only from New Caledonia (Defaye, 2001). Here we list only those data which are new, or differ from those of the New Caledonian males.

Body length smaller, 735–760 μm (New Caledonia, mean: 784 μm). Length of prosome/length of urosome: 1.7–2.0. Hairs on dorsal surface of pediger 5, present in female, absent in male. Hairs present on anterolateral surface of pediger 4, Furcal rami 2.6–3.0 times as long as wide (2.3 in New Caledonia). Spinules present at insertion of lateral and lateralmost terminal caudal setae (spinules absent at insertion of lateral caudal seta in allotype from New Caledonia). Relative length of terminal caudal setae from medialmost to lateralmost: 2.3–2.8, 4.9–5.3, 3.6–4.1, and 1.0. Inner median (longest) terminal caudal seta 1.1–1.2 times as long as urosome. On anterior surface of antennule (Fig. 9A), spinules present on segments 1, 12–14. Caudal surface of antennal coxobasis (Fig. 9B) with group of small spinules near implantation of mediodistal setae (cf. Fig. 4B, group f); this group also presents in females from Vanuatu and New Caledonia. Epistoma bare. In females from Vanuatu and New Caledonia epistoma pilose, and row of long hairs also presents laterally to epistoma, similarly to female in _M. roberti_ sp. nov. (cf. Fig. 4E). Protuberances on P4 coupler small and acute (acute
3.3. M. woutersi Van de Velde, 1987

Vanuatu. Gaua, Lake Letas [31], 16°32′E, 14°17′S, volcanic crater lake, alt. 418 m, area 1900 ha, depth 360 m, temp. 26.7 °C, pH 8.9, cond. 555 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 15 December 2004, 3 females (MIZ: 300022–300024).

Distribution. North Australia (Kimberley region, Queensland), Papua New Guinea, Vanuatu, Cambodia (R. Chaicharoen, pers. comm., 2009), Laos, Vietnam, South China, Taiwan, Japan (the Ryukyus, possibly Honshu) and Korea.

Comments. No characters were found in which the Vanuatu specimens differed from the Asian and Australian populations (Holyńska et al., 2003).

3.4. M. aspericornis (Daday, 1906)

Wallis, Lake Lanutavake [16], 176°13′W, 13°19′S, alt. 5 m, area 5 ha, temp. 30.6 °C, pH 8.85, cond. 88 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 01 November 2004, 2 males (MIZ: 300025–300026); Lake Lalolalo [17], 176°14′W, 13°18′S, alt. 2 m, area 18 ha, depth 70 m, temp. 30.2 °C, pH 8.79, cond. 1583 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 02 November 2004, 1 female (MIZ: 300027), 1 male (MIZ: 300028); Lake Nanumaha [19], 176°13′W, 13°19′S, alt. 35 m, area 1.5 ha, depth <5 m, temp. 34.7 °C, pH 8.85, cond. 28 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 02 November 2004, 1 female (MIZ: 300029).


Cook Islands, Mitiaro, Vaie Marere [5], 157°43′W, 19°52′S, alt. 5 m, area 0.008 ha, depth <3 m, temp. 23.6 °C, pH 7.76, cond. 2560 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 24 September 2004, 1 female (MIZ: 300032), 1 male (MIZ: 300033); Mitiaro, Lake Rotono [6], 157°41′W, 19°52′S, alt. 1 m, area 100 ha, depth 2 m, temp. 26.1 °C, pH 8.28, cond. >4000 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 25 September 2004, 1 female (MIZ: 300034); Atiu, Lake Tirote [10], 158°07′W 20°01′S, alt. 20 m, area 3 ha, depth 7 m, temp. 27.5 °C, pH 8.54, cond. >4000 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 28 September 2004, 1 male (MIZ: 300035).

Tahiti, Vaihiria [1], 149°25′W, 17°41′S, alt. 380 m, area 0.6 ha, depth <5 m, temp. 25.0 °C, pH 7.47, cond. 97 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 17 September 2004, 1 male (MIZ: 300037) – referred to by Schabetsberger et al. (2009) as M. sp. 1 aff. woutersi Van de Velde, 1987; Lac Bleu, [2] 149°25′W, 17°41′S, alt. 380 m, area 0.6 ha, depth <5 m, temp. 25.0 °C, pH 7.47, cond. 97 μS cm⁻¹, leg. R. Schabetsberger & G. Drozdowski, 17 September 2004, 1 male (MIZ: 300037) – referred to by Schabetsberger et al. (2009) as M. sp. 1 aff. woutersi Van de Velde, 1987.


Distribution. Pantropical.

Comments. The female morphology is rather uniform, although the species occurs throughout the tropics. Only the number of setae on the second endopodal segment of antenna, and the spinule ornamentation of the antennal coxobasis show regional differences. While in the South and East Asian populations, and tropical Australian populations most often 8 or 9 setae inserted on the second endopodal segment of the antenna, and the 7-setae state very rarely occurs, in South and Middle America the 7-setae state is more common, and the 8- or 9-setae states are rare. The spinule ornamentation of the antennal coxobasis shows a geographic pattern similar to that mentioned above: while the females from South and Middle America, and West Africa often have an additional group of spinules on the caudal surface, near the distal margin, this group very rarely occurs in the East African, South and East Asian, and tropical Australian populations. The females from the South Pacific islands show the “eastern” character states: the second endopodal segment of the antenna bears 8 or 9 setae (the 7-setae state appears on one of the two antennae in a single female from the Easter Island); and spinules are absent on the caudal surface of the coxobasis, near the distal margin (Fig. 9D – arrowhead shows the site where spinules are usually present in the Neotropical, West African and East Asian females).

4. Discussion

4.1. Mesocyclops in the South Pacific: taxonomy and geographic distribution

The geographic distribution of Mesocyclops in the South Pacific Islands is shown in Fig. 10. Of the 76 (sub)species of this predominantly (sub) tropical genus, we only found four taxa, M. aspericornis, M. woutersi, M. medialis and M. roberti sp. nov., in this region.

A relatively frequent occurrence of M. aspericornis was expected in the South Pacific. The species is circumtropical in distribution, and it has been reported from several islands (Mariana, Marshall and Hawaiian) of the North Pacific (Kiefer, 1981). Historically interesting, the very first large-scale field studies on the use of copepods in mosquito control were made in French Polynesia (Tahiti), and tested just M. aspericornis (Rivière and Thirel, 1981). As to the ecological traits, from usually low density of the species but wide variety of the habitats where it is able to thrive, Reid and Saunders (1986) inferred that M. aspericornis would be an example of “fugitive species”, characterized by good dispersal power but poor competitive ability. Although the close phylogenetic relationships of M. aspericornis are not understood yet, this circumtropical species clearly groups with the Old World (mainly Asian and Australian) taxa in the phylogenetic reconstructions (Holyńska, 2006).

The zoogeographic distribution of M. woutersi is an interesting case. This species is one of the more common Mesocyclops taxa in east Asia (South Korea, Ryukyus Is., South China), Indochina (Vietnam, Laos, Cambodia) and Taiwan, and also occurs in tropical Australia (incl. Papua New Guinea) and Vanuatu, yet it has never been reported from either the Malay Peninsula or the Greater or Lesser Sunda Islands (Holyńska, 2000; Holyńska and Brown, 2003; Holyńska et al., 2003). The uniform morphology of M. woutersi from South Korea to North Australia, however, indicates uninterrupted gene flow rather than separation between the Asian and Australian populations.
Fig. 10. Geographic distribution of Mesocyclops in the South Pacific.

populations. Might this contact between the northern and southern hemisphere faunas be across Taiwan, Philippines and the Moluccas, instead of the Sunda Islands? In comparison to the Sunda Islands, our knowledge of the fauna of the Philippines and Moluccas unfortunately is very poor. From the Philippines only three Mesocyclops sp., Mesocyclops ogunnus Onabamiro, 1957 and Mesocyclops microlausius Kiefer, 1981 from Luzon, and M. aspericornis from Luzon and Mindanao have been reported (Holyńska, 2000; unpublished data), and the Mesocyclops fauna of the Moluccas is completely unknown. The poor zoogeographic data do not allow us to either to support or reject a Taiwan – Philippines – Moluccas – New Guinea (and North Australia) – Solomon Islands – Vanuatu dispersal route. Finally, the possibility of an introduction of M. woutersi in the South Pacific volcanic lakes through the practice of fish stocking cannot be ruled out (Schabetsberger et al., 2009).

M. roberti sp. nov. and M. medialis seem to be endemic to the South Pacific. Our study revealed the occurrence of M. medialis in Vanuatu, so far known only from New Caledonia (Defaye, 2001). A previous phylogenetic analysis (Holyńska, 2006) grouped M. medialis together with species that are endemic to Australia.

M. roberti sp. nov. lives in Fiji (Vanua Levu) and Wallis islands, which are at a distance of approximately 280 km from each other. The females from Fiji and Wallis differ conspicuously in body length (Table 4) and also other morphometric characters (length and width proportion of the caudal rami, relative length of the dorsal caudal seta and P4 coxopodite seta), which might suggest that we have two species in hand. The Wallis and Fiji forms have been referred to by Schabetsberger et al. (2009) as M. sp. 2 aff. woutersi and M. sp. 3 aff. woutersi, respectively. On the other hand, we could find only one qualitative character which might separate these two populations. The only exception is the ornamentation character of the epistoma in the female, which is pilose in Wallis, and bare in the Fiji population. Presence or absence of hairs on the epistoma is a stable feature in most Mesocyclops sp., yet this character does show intraspecific variation (Holyńska, 2006) in two Australian taxa, M. brooksi and M. notius, both of which morphologically very close to M. roberti. This fact hints that ornamentation of the epistoma could be an intraspecifically variable character in M. roberti as well.

To interpret the divergence of the Fiji and Wallis populations in morphometric characters, some earlier observations of other Mesocyclops taxa can be helpful. Comparisons of the littoral (or eutrophic) and pelagic (or oligotrophic) populations among species that are not closely related species, such as Mesocyclops leuckarti Claus, 1857, and Mesocyclops dissimilis Defaye and Kawabata, 1993, revealed, among others, significant inter-population differences in body length, the relative length of caudal rami, and dorsal caudal setae (Einsle, 1968; Kiefer, 1978; Holyńska, 1997). While in the proportions of the caudal rami the trends are different among different species [the pelagic forms may have longer or shorter rami in comparison to the littoral (small pond) forms], the shifts in the body length and dorsal caudal seta are in the same direction in every species investigated, i.e. specimens living in the plankton (or oligotrophic environment) have smaller body length and longer dorsal caudal setae, than those of the littoral [eutrophic] waters. The characteristics of the sampling sites in Wallis (small, shallow pond with submerged vegetation) and Fiji (lake), and the morphometric features of Mesocyclops living in these habitats correspond with the trends observed in other taxa. Thus we assigned the differences in these morphometric characters less weight, and considered the Wallis and Fiji populations to be conspecific.

apomorphies [char 9(0), char 27(3)] (only those apomorphies are mentioned here and later in the discussion, which are present in all the trees of a reconstruction), the M. notius—M. roberti clade is present only in the unordered analyses, and this group is supported by a single apomorphy [char 19(0)]. Dorsal pilosity of the genital double-somite, which is restricted to just few groups of hairs [char 9(0)] (Fig. 2B), is an unique synapomorphy of M. roberti and M. brooksi, also in the genus as a whole. The other diagnostic character [char 27(3)] of the roberti–brooksi clade is the presence of 7 or 8 setae on the second endopodal segment of the antenna; this character state is preserved in M. brooksi, and the 9-setae state appears in M. roberti. The number of setae on the second endopodal segment of the antenna is a less stable feature in Mesocyclops. Some Old World species (e.g. M. aspericornis, M. acanthoramus and M. ogumus) show large intraspecific variation, as any character state between 7- and 9-setae state can occur.

The presumed synapomorphy of the M. notius–M. roberti clade is the fixed presence of spines at the insertion of the lateral caudal seta (Fig. 2A, with arrowhead). Frequent occurrence of this character state in other Old World species, as well as, the presence of spines in the copepodid stages of Mesocyclops (also in those species where the spines are missing in the adult female), however, suggest that the feature shared by M. notius and M. roberti [char 19(0)] is an ancestral state rather, than a derived one.

It is important to note here that two South Pacific endemics, M. medialis and M. roberti never form a clade (or even a paraphyletic group) in any of our reconstructions (Fig. 11), which indicates that the ancestors of M. medialis and M. roberti reached the South Pacific from Australia independently. The morphological divergences between M. medialis, M. roberti and their Australian close relatives are so slight, that relatively recent eastward (Australia > South Pacific) long-distance dispersals seem to be more plausible explanations for the evolution of the South Pacific taxa than older vicariance events. New Caledonia had continental contact with Australia in the Late Cretaceous (ca. 80 MYA) (Sanmartín and Ronquist, 2004), although some authors (e.g. Ladiges and Cantrill, 2007) suggest such contact existed even in the Paleocene/Eocene. Vanuatu and Fiji, along with the Solomon and Tonga Islands, are parts of the East Melanesian Arc, which appeared as a continuous island chain in the Eocene but remained mainly submarine until early Miocene (De Boer, 1995). The Wallis Island emerged recently, mainly due to Pleistocene volcanism (Stearns, 1945).

Both “unordered” reconstructions and one of the “scaled” analyses (Fig. 11) support monophyly of the group comprising Australasian (M. australiensis, M. brooksi, M. notius and M. pubiventris) and South Pacific taxa (M. medialis and M. roberti). Maximum parsimony analysis that sampled all species in the genus and used the scaled coding for the polymorphic characters (Holyńska, 2006) has also shown monophyly of the above mentioned group. The Australian–South Pacific clade is supported by only one apomorphy in the unordered reconstructions [char 38(0)]; bare vertical cleft (anteriorly to epistoma) [Fig. 4E, with arrowhead] and by three apomorphies in the scaled analysis [char 8(3): pilose genital double-somite; char 24(3): polymorphic state of the notches on the hyaline membrane of the last antennular segment (Fig. 3D, with arrowhead); and char 67(3): polymorphic state of the distal protuberances of P4 coupler (Fig. 7C, with arrowhead)]. None of these character states is unique apomorphy in the Old World Mesocyclops. In both “unordered” analyses, the Afro-Asian dussartii-clade (Mesocyclops dussartii Van de Velde, 1984, Mesocyclops dadayi Holyńska, 1997, Mesocyclops isabellei Dussart and Fernando 1988 and Mesocyclops thermocyclopooides Harada, 1931) appears as the closest relative of the Australian–South Pacific clade. The sister relationship is supported by two apomorphies [char 1(1,2): lateral pilosity of pediger 4 (Fig. 7F, with arrowhead); char 8(3): pilose genital double-somite], none of which is unique in the

Fig. 11. Clades that appeared more than once in the strict consensus trees of the parsimony analyses using different codings of the polymorphic characters (explanations of the coding in Section 2) and two sets of the terminal taxa. Black and white rectangles indicate if a clade is present or absent, respectively. Clade 1: (M. notius, M. roberti); clade 2: (M. brooksi, M. roberti); clade 3: (M. brooksi, M. notius, M. roberti); clade 4: (M. australiensis, M. medialis, M. pubiventris, M. brooksi, M. notius, M. roberti); clade 5: (M. australiensis, M. medialis, M. pubiventris, M. brooksi, M. notius, M. roberti) (M. dussartii, M. dadayi, M. isabellei, M. thermocyclopooides). *: M. bosumtwii included in the reconstruction.

4.2. Phylogenetic relationships and origin of M. roberti

Morphological characters indicated a close relationship of M. roberti with the Australian Mesocyclops australiensis (Sars, 1908) [Tasmania, Victoria, New South Wales, Northern Territory(?)]. M. brooksi [Western Australia, Queensland], M. notius [Western Australia, Northern Territory, Queensland, New South Wales], Mesocyclops pubiventris Holyńska and Brown 2003 [Queensland] and M. medialis [New Caledonia and Vanuatu]. To test this, we ran three analyses that coded the polymorphic characters by three different methods (unordered, unscaled and scaled coding, for details see Material and Methods), and used two sets of terminal taxa. M. bosumtwii, a recently described African species and supposedly close relative of the African-Madagascan major-clade, was included or excluded from the reconstructions. Although we focused on the relationships of a small group of taxa, the reconstructions included all Old World species (48) lacking medial spine on P1 basipodite. The relatively large number of taxa added to our reconstructions is justified, because the phylogenetic relationships in the Old World Mesocyclops remained largely unresolved in previous analyses (Holyńska, 2006).

There are a few clades in the Australian–South Pacific group, which appear at least twice in the strict consensus trees of the six reconstructions (Fig. 11).

The clade which is the least sensitive to coding of the polymorphic characters and taxon sampling includes M. notius, M. brooksi and the new species, M. roberti (Fig. 11). There is one apomorphy [char 70(3)] that repeats in all the trees supporting the brooksi–notius–roberti clade, and another apomorphy [39(1)], which appears in majority of the trees in one reconstruction (“scaled”, M. bosumtwii added) and always present in the trees of the other four reconstructions where this clade appears. Interestingly, the states diagnosing this clade are just the polymorphic one in both characters. Polymorphic appearance of proximal hairs [char 70(3): hairs present or absent] on the caudal surface of the medial expansion of P3 basipodite (Fig. 7A) is unique in the Old World group and the genus in general. Polymorphic appearance of hairs on the epistoma [char 39(1): hairs present or absent] (Fig. 4E vs. F) is also very rare in Mesocyclops. The polymorphic state, beyond the brooksi–notius–roberti clade, occurs only in Mesocyclops kieferi (Africa, Yemen, Israel).

As to the sister relationship of M. roberti sp. nov. [Fiji, Wallis], M. brooksi [Western Australia, Queensland] seems to be a more likely candidate than M. notius [Western Australia, Northern Territory, Queensland, New South Wales]. While the M. roberti–M. brooksi clade appears in two different codings (unscaled and scaled) of the polymorphic characters, and the group is supported by two different clades among the reconstructions using different codings of the polymorphic characters (explanations of the coding in Section 2) and two sets of the terminal taxa. Black and white rectangles indicate if a clade is present or absent, respectively. Clade 1: (M. notius, M. roberti); clade 2: (M. brooksi, M. roberti); clade 3: (M. brooksi, M. notius, M. roberti); clade 4: (M. australiensis, M. medialis, M. pubiventris, M. brooksi, M. notius, M. roberti); clade 5: (M. australiensis, M. medialis, M. pubiventris, M. brooksi, M. notius, M. roberti) (M. dussartii, M. dadayi, M. isabellei, M. thermocyclopooides). *: M. bosumtwii included in the reconstruction.
Old World Mesocyclops. The clade comprising the dussarti and the Australian–South Pacific group (*M. australiensis, M. pubiventris, M. notius, M. brooksi, and *M. medialis*) appears in most of the trees in a previous parsimony analysis (all Mesocyclops sp. included, different outgroup choices, scaled coding of the polymorphic characters) (Holyńska, 2006). In another reconstruction that used the corrected distance method (MICSEQ) (Holyński, 2001; Holyńska, 2006), the Australian–South Pacific clade is the sister of a larger group of species, most of which are distributed in the Asian mainland and Malay Archipelago. Though the sister relationship of the Australian–South Pacific clade remains ambiguous, all these reconstructions suggest a link with Asian *Mesocyclops* sp. Australia fully separated from Antarctica in the Eocene (52–35 MYA) and drifted toward Asia relatively quickly. Nevertheless it has been isolated from Asia for long time. It could be that in the Miocene (25 MYA), a long chain of islands formed on the north of Australia, resulting in a discontinuous link between Southeast Asia, Melanesia and Australia (Hall, 1998). The contact between the Asian and Australian faunas, however, could be strongly limited, as the deep sea basins, some of which were just formed in the Miocene, could have been insurmountable barrier to dispersal in many groups. A more intensive influx of the Oriental elements to Australia could have taken place in the last 5 MY, when land areas surrounding SE Asia significantly increased, and new dispersal routes (e.g. across Taiwan–Philippines–North Moluccas–New Guinea, or through the Sunda Islands and the South Moluccas) opened up between the northern and southern continents (Hall, 1998).

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Appendix A. (Figures refer to those in Holyńska, 2006)

List of characters

Tergites

(1) Hairs or spinules on lateral and dorsal surfaces of pedigers 3–4: (0) absent; (1) absent or present on lateral surface of pediger 4; (2) present on lateral surface of pediger 4; (4) present on lateral and dorsal surfaces of pediger 4; (6) present on lateral and dorsal surfaces of pediger 4 and lateral surface of pediger 3; and (8) present on dorsal and lateral surfaces of pedigers 3–4.

Notes. Hairs do not occur on pediger 2 and cephalothorax. Plisosity patterns observed in various New- and Old-World species show that dorsal and lateral surface ornamentation of particular segment and hair ornamentation of the two proso- mal segments are not independent features. Plisosity reduction proceeds from pediger 3 to pediger 4, and from the dorsal to lateral. There is an exception to this rule in *M. pubiventris*, in which pediger 3 pilose, yet pediger 4 has only lateral hairs. Assuming that character transformations as formulated above are additive, the character state (hairs present on lateral surfaces of pedigers 4–3) occurring in *M. pubiventris* can be derived at shortest by one step (loss of dorsal hairs on pediger 4) from character-state 6, therefore *M. pubiventris* are assigned ‘6’ in the matrix.

Intraspecific variability (pedigers 3–4 without hairs/spinules, or lateral spinules present only on pediger 4) occur in two Australian species, *M. brooksi and M. australiensis*.

(2) Pediger 5, hairs or spinules: (0) absent [Fig. 23B]; (1) absent or present on lateral surface; (2) present on lateral surface; (3) present only on lateral surface, or on lateral and dorsal surfaces; and (4) present on lateral and dorsal surfaces [Fig. 23A and G].

Notes. *Mesocyclops brevisetosus* (no lateral hairs, dorsal ornament unknown) is assigned ‘0’ in the matrix.

(3) Pediger 5 dorsal surface, lateral hair-sensilla [Fig. 23C, arrowed]; (0) present; (1) present or absent; and (2) absent.


(4) Pediger 5 dorsal surface, laterodistal hair-sensilla [Figs. 23B and 36D, arrowed]; (0) present and (1) absent.


(5) Pediger 5 dorsal surface, median hair-sensilla [Fig. 36D, arrowed]; (0) present; (1) present or absent; and (2) absent.


(6) Hairs/spinules along posterior margin of pediger 5: (0) present on dorsal and ventral surfaces [Fig. 23C]; (1) present only on ventral surface; and (2) absent.

Note. *M. microcalius* (dorsal surface ornamentation unknown, spinules absent on ventral surface) is assigned ‘2’.

(7) Group of spinules anteriorly to implantation of P5 [Fig. 36B, arrowed]; (0) absent and (1) present.

Urosomites

(8) Surface ornamentation of genital double-somite: (0) no rows of spinules, hairs or ridges; (1) transverse rows of ridges present [Fig. 23A]; (2) transverse rows of spinules present [Fig. 23D]; and (3) hairs present [Fig. 23E–G].

(9) If hairs present on genital double-somite, they appear: (0) in few rows on dorsal surface [Fig. 23E]; (1) dorsally, on anterior half [Fig. 23F]; (2) dorsally, on anterior and posterior halves; and (3) on dorsal and ventral surfaces.

(10) Anal somite, surface ornamentation of proctodeum: (0) no ornamentation [Fig. 26E and F]; (1) with tiny spinules [Fig. 26G]; and (2) with long spinules or hairs [Fig. 26D].


(11) Suture cord on ventral surface of genital double-somite, between legs 6: (0) present [Fig. 24F, arrowed]; (1) reduced to short medial section [Fig. 25B and D]; and (2) absent.

Seminal receptacle.

(12) Lateral arms: (0) narrow [Fig. 25E, arrowed] and (1) wide [Fig. 25B–D, F, and G; arrowed on Fig. 25D].

(13) Transverse duct-like structures medially meet at: (0) acute angle [Fig. 25F, arrowed]; (1) acute, or obtuse angle; and (2) straight or obtuse angle [Fig. 25G, arrowed].

Notes. *Mesocyclops spinosus* (transverse duct-like structures run beside each other before their fusion, attaching by medial walls of the canals) is assigned ‘0’. *M. dussarti*: data from Van de Velde, 1984.

(14) Copulatory duct: (0) not curved sinuously in sagittal plane [Fig. 25F]; (1) with slight sinuous curvature in sagittal plane; and (2) with strong sinuous curvature in sagittal plane [Fig. 25G and H].

(15) Transverse duct-like structures medially meet: (0) before copulatory pore (‘joint-canal’ present) [Fig. 25E, arrowed]; (1) before or next to copulatory pore; and (2) next to copulatory pore (‘joint-canal’ absent) [Fig. 25F].

(16) Posterior margin of anal somite: (0) with continuous row of spinules [Fig. 26G]; (1) with row of spinules, which is either continuous or laterally intermittent; (2) with laterally intermittent row of spinules; (3) with row of spinules, which is either laterally or both laterally and dorsally intermittent; (4) with row of spinules, which is both laterally and dorsally intermittent [Fig. 26F].

Notes. Mesocyclops cuttacutae in which any character state can appear, is assigned ‘?’. Presence/absence of the spinules on the ventral, lateral and dorsal surfaces are not independent features, but different states of one character. This could be inferred from the clear tendency of their reduction: the lateral spinules disappear at first, followed by reduction on the dorsal surface, but spinules on the ventral surface always remain. We did not meet any species having later but not dorsal and ventral spinules, or having dorsal but not ventral spinules. If spinulation varies within species, this same sequence of reduction occurs.

Caudal rami

(17) Medial pilosity: (0) no hairs; (1) hairs present anteriorly and posteriorly to implantation of lateral seta [Fig. 26A]; and (2) hairs present anteriorly to implantation of lateral seta [Fig. 26B, arrowed].

(18) Transverse lateral row of spinules between anterior margin and implantation of lateral seta: (0) present [Fig. 26C and E, arrowed]; (1) present or absent; and (2) absent.


(19) Spinules at implantation of lateral caudal seta [Fig. 26C, arrowed]: (0) present; (1) present or absent; and (2) absent.

(20) Spinules at implantation of lateralmost terminal caudal seta [Fig. 26C, arrowed]: (0) present; (1) present or absent; and (2) absent.

(21) Medialmost terminal caudal seta/lateralmost terminal caudal seta: (0) ≤1.8 [Fig. 26C] and (1) >1.8.

Antennule

(22) Hyaline membrane, present: (0) on last three segments; (1) on last two segments [Fig. 27B]; (2) on terminal segment only; and (3) absent.


(23) Hyaline membrane of terminal segment: (0) serrate, proximally not extending beyond implantation of medial seta [Fig. 27B]; (1) serrate, intermittent at implantation of medial seta, and smooth beyond it [Fig. 27E]; (2) serrate in whole length of segment, but intermittent at implantation of medial seta; and (3) serrate, continuous, proximally extending beyond implantation of medial seta [Fig. 27C].


(24) Deep notches on serrate hyaline membrane of terminal segment: (0) absent [Fig. 27B]; (1) absent, or 2 or more notches; (2) 2 or more notches [Fig. 27E]; (3) 2 or more notches, or 1 large notch; (4) 1 large notch [Fig. 27C].

Notes. M. leuckarti and M. kieferi, where any character state can occur, are assigned ‘?’.

(25) Aesthetasc on penultimate segment: (0) long, reaching to about middle of terminal segment [Fig. 27B] and (1) reduced [Fig. 27E].


(26) Ventral spinules present on segment(s): (0) 1 only; (2) 1, 4–5, 7–10, and 12–13; (3) 1, 4–5, 7–10, and 12–13, or 1, 4–5, 7–13; (4) 1, 4–5, 7–13; (5) 1, 4–5, 7–13, or 1, 4–5, 7–14; (6) 1, 4–5, 7–14; and (8) 1–14 [Fig. 27A].

Notes. It is supposed here that the autapomorphic character-states: spinules present on segments 1, 7–10, and 12–13 [M. cuttacutae] derived from character state ‘2’; spinules present on segments 1, 4–13 [M. brevisetosus], and spinules present on segments 1–5, 7–13 or 1, 4–5, 7–13 [M. brooksii] derived from character state ‘4’; when Hennig86 is applied, these species are assigned those character states which are closest to their autapomorphic character states.

Antenna

(27) Number of setae on endopodite 2 (third segment) [Fig. 29C, arrowed]: (0) 9; (1) 9 or 8; (2) 8; (3) 8 or 7; (4) 7; and (5) 7 or 6.

Notes. Those species (e.g. M. aspericornis, M. ogunnus, M. acanthoramus), in which intraspecific variability includes 9–7 setae states, are assigned ‘?’

(28) Spinules near median margin, on caudal surface of endopodite 1 [Fig. 28C, arrowed]: (0) present and (1) absent.

Spinule pattern on caudal surface of coxobasis:

(29) Oblique row/field starting ca. at midlength of medial rim [group c] [Fig. 28B]: (0) absent; (1) absent or distinct row; (2) distinct row; (3) distinct row or oblique field; and (4) oblique field.

Note. In this paper (see Fig. 4B) it is also indicated as group c.

(30) Group of spinules at height of exopodite seta (group f) [Fig. 28A and E]: (0) absent; (1) present or absent; and (2) present.

Note. This group of spinules is absent in the Australian–South Pacific clade.

(31) Spinules near implantation of medial setae (group g) [Fig. 28A and B]: (0) absent; (1) absent or tiny in field/row; (2) tiny in field/row; (3) tiny in field/row or large in row; and (4) large in row.

Note. In this paper (see Fig. 4B) this group is indicated as group f.

(32) Spinules near distal margin (group h) [Fig. 28A and B]: (0) absent; (1) present or absent; and (2) present.

(33) Group of spinules (group i) between proximal oblique and longitudinal row near lateral margin [Fig. 28A and B]: (0) absent; (1) present or absent; and (2) present.

(34) Oblique row/field of spinules (group j), below insertion of inner medial seta [Fig. 28A and C]: (0) absent; (1) absent or present; and (2) present.

Spinule pattern on frontal surface of coxobasis:

(35) Group of spinules near implantation of exopodite seta [Fig. 29D, arrowed]: (0) absent; (1) present or absent; and (2) present.

(36) Longitudinal row near lateral margin: (0) number of spinules less than 20 [Fig. 29D]; (1) number of spinules sometimes less than 20, sometimes 20 or more; and (2) number of spinules not less than 20 [Fig. 29E].

Mouthparts

(37) Paragnaths, spinules on mediodistal angle: (0) present [Fig. 30F, arrowed] and (1) absent [Fig. 30E].

(38) Vertical cleft, spinules or hairs: (0) absent and (1) present [Fig. 31E and F, arrowed].

(39) Epistoma, spinules or hairs [Figs. 30C and 31E, arrowed]: (0) absent; (1) absent or present; and (2) present.

(40) Transverse field/row of spinules or hairs between epistoma and distal fringe hairs [Fig. 31E, arrowed]: (0) absent; (1) absent or present; and (2) present.

(41) Distal fringe hairs of labrum: (0) arranged in triangular field [Fig. 30B, arrowed]; (1) arranged in arc [Fig. 31E and F].
(42) Rounded lateral protuberances of labrum: (0) with tiny teeth [Fig. 30B and D, arrowed] and (1) smooth [Fig. 30C].

Mandible, spinule ornamentation on anterior surface, next to palp:
(43) Group a [Figs. 31C and D and 32A–F]: (0) absent and (1) present.
(44) Group b [Figs. 31A and B and 32A–C, E and F]: (0) absent and (1) present.
(45) Group c [Fig. 32A–C, E, and F]: (0) absent and (1) present.
(46) Group d [Figs. 31B–D and 32A]: (0) absent; (1) absent or present; and (2) present.
(47) Spinules proximally to palp [Figs. 31A and D and 32A–C, E, and F, arrowed]: (0) absent and (1) present.

Maxillula.

(48) Palp: (0) bare; (1) bare or with spinules; and (2) with spinules [Fig. 33B, arrowed].
(49) Tiny spinules on anterior surface of praecoxopodite, next to palp [Fig. 33B, arrowed]: (0) absent; (1) absent or present; and (2) present.
(50) Spinules on posterior surface of praecoxopodite: (0) absent; (1) small [Fig. 33A, arrowed]; and (2) long [Fig. 33C, arrowed].
(51) Proximalmost seta of lateral lobe of palp [Fig. 33B]: (0) without setules [Fig. 33B]; (1) with or without long setules; and (2) with long setules [Fig. 33C].

Maxilla.

(52) Longitudinal field of spinules on frontal surface in median third of coxopodite: (0) absent or just tiny spinules [Fig. 33G, arrowed]; (1) absent or just tiny spinules, or hair-like spinules; (2) hair-like spinules [Fig. 33F, arrowed]; (3) hair-like or robust spinules; and (4) robust spinules [Fig. 33D, arrowed].

Notes. Any character-state can occur in *Mesocyclops brooksi*, and it is assigned ‘?’.
(53) Spinules on frontal surface of praecoxopodite, next to longitudinal ridge: (0) absent; (1) small [Fig. 33G, arrowed]; and (2) long, hair-like [Fig. 33F, arrowed].
(54) Basipodite seta inserted in front of claw-like endite, spinulation on distal half: (0) absent; (1) spinule only on posterior edge [Fig. 33E, arrowed]; and (2) spinule on both anterior and posterior edge.
(55) Endopodite: (0) two-segmented [Fig. 33E] and (1) one-segmented [Fig. 33D].

The distal arthrodial membrane of the terminal endopodal segment fails to form (the terminalmost terminal claw-like seta incorporates the terminal endopodal segment) in species with ‘one-segmented’ state.

Maxilliped.

(56) Caudal surface of basipodite: (0) with three groups of spinules [Fig. 34C]; (1) with three or two groups; and (2) with two groups of spinules [Fig. 34B].
(57) Frontal surface of syncoxopodite, spinules at height of insertion of proximalmost seta, next to hump near lateral margin: (0) large [Fig. 33C, arrowed] and (1) absent or very tiny [Fig. 33B, arrowed].
(58) Syncoxopodite, group of spinules near base on marginal margin: (0) absent and (1) present or absent.


Legs 1–5

(59) P1 basipodite medial spine: (0) present and (1) absent.

(60) Medial spine of P1 basipodite: (0) spinulose [Fig. 35B, arrowed] and (1) setulose [Fig. 35A, arrowed].
(61) P1 basipodite frontal surface, spinules arranged in arc or oblique row between insertions of exo- and endopodite (group ‘a’): (0) absent or tiny [Fig. 35A] and (1) large [Figs. 34E and 35C and D].
(62) P1 basipodite frontal surface, distinct arc of spinules medially to group ‘a’ (group ‘b’): (0) absent or tiny [Fig. 35A] and (1) large [Fig. 35B–D].
(63) P1 basipodite frontal surface, spinules medi distally to group ‘a’ (group ‘c’): (0) absent or tiny [Fig. 35A–D]; (1) large and arranged in group (2) large and arranged in arc [Fig. 34D].

Notes. To establish homologies of particular group of spinules, two reference points were used: insertion of the medial spine of P1 basipodite [groups ‘a’ and ‘b’ are below, and group ‘c’ is at height of the insertion of the medial spine]; halfway line of the basipodite [group ‘b’ reaches halfway line, group ‘a’ is laterally to it].
(64) P1 third segment of exopodite, middle element on apical margin, few setules on proximal half of lateral edge [Fig. 34A, arrowed]: (0) absent; (1) absent or present; and (2) present.
(65) Spinules on distal protuberances of couplers: (0) present on P1–P4 [Fig. 36A]; (2) present on P1–P3; (4) present on P2–P3; (6) sometimes present on P2; and (7) absent.
(66) Acute protuberances on distal margin of P3 coupler: (0) absent; (1) absent or present; and (2) present.
(67) P4 coupler, protuberances on distal margin: (0) absent (not protruding beyond distal margin of coupler) [Fig. 36C]; (1) absent or obtuse; (2) obtuse; (3) obtuse or acute; and (4) acute [Fig. 36E].

Notes. Any character state can occur in *Mesocyclops brooksi*, and it is assigned ‘?’.
(68) Spinules/hairs on caudal surface of couplers: (0) present on P1–P4 [Fig. 36A]; (1) present on P2–P4; (2) present on P3–P4; (3) present on P4 only; and (4) absent.
(69) Distal hairs/spinules on medial expansion of basipodites of P1–P4 [Fig. 36C and E, arrowed]: (0) present on P1–P4; (1) present on P1–P4 or P1–P3; (2) present on P1–P3; and (4) present on P1 only.
(70) Group of proximal hairs on caudal surface of medial expansion of basipodite [Fig. 36C, arrowed]: (0) present on P1–P4; (2) present on P3–P4; (3) present on P3–P4 or only on P4; (4) present only on P4; (5) present only on P4 or absent; and (6) absent.
(71) Long latero frontal spinules of basipodite present [Fig. 35A, arrowed]: (0) on P1–P4; (1) on P1–P4 or at least on one of P1–P3; (2) at least on one of P1–P3; (3) at least on one of P1–P3 or absent; and (4) absent.

P4 coxopodite, caudal surface ornamentation:
(72) Spinules along distal margin [Fig. 36C, arrowed]: (0) many (15–25); (1) many or few; and (2) few (<15).
(73) Group of spinules on laterodistal angle [Fig. 36C, arrowed]: (0) present; (1) present or absent; and (2) absent.
(74) Spinules near proximal margin: (0) in 1 group (lateral) and (1) in 2 groups (lateral + medial) [Fig. 36C, arrowed].

Note. The ‘lateral’ group is at ca. half length of the segment.
(75) Hairs near medial margin [Fig. 36A, arrowed]: (0) absent and (1) present.
(76) P4 enp3, apical spines: (0) subequal (medial/lateral 0.8–1.3); (1) subequal or of conspicuously different sizes; and (2) of conspicuously different sizes.
(77) P5, terminal segment: (0) with three appendages and (1) with two appendages.
(78) P5, medial spine(s) of terminal segment: (0) at most 1.5 times as long as segment; (1) longer or shorter than 1.5 length.
of terminal segment; and (2) more than 1.5 times longer than terminal segment.

(79) Male antenna, transverse rows of spinules present on segment(s): (0) 1 only; (1) 1, 15, 16 [Fig. 27D]; (2) 1, 12–15; (3) 1, 12–14; and (4) 1, 12–13.

Note. M. kieferi; data from Van de Velde, 1984.

(80) M∞∞ antenna, number of setae on the second endopodal segment: (0) 9; (1) 9 or 8; (2) 8; (3) 8 or 7; (4) 7; (5) 7 or 6; and (6) 6.

(81) Number of elements (setae + spines) on third exopodal segments of P1–P4: (0) 8988; (1) 8987; (2) 6777; and (3) 7887.

Notes. This character is informative in phylogeny of Cyclopidae, a scope wider than what is applied here. Relying upon Ferranti’s studies (1998) on the developmental patterns of cyclopoid throrcopods, we applied internal rooting (O’Grady and Deets, 1987) of the ordered character states: state ‘1’, present in Macrocyclops albidus, is the pleiomorphic condition; state ‘0’, [e.g. Cyclops strenuus] and state ‘2’ [all Mesocyclops] derived from the ancestral developing pattern; state ‘3’, [e.g. Diacyclops dispinosus], derived (reversal) from state ‘2’.

Appendix B.
References


