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

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ABSTRACT

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 medialis*, *Mesocyclops woutersi* and *Mesocyclops aspericornis*. Phylogenetic reconstructions coding the intraspecifically variable characters by three different methods (unordered, unscaled and scaled coding) support close relationship of *M. roberti* with two Australian species (*Mesocyclops brooksi* and *Mesocyclops notius*). Both the "unordered" and "scaled" analyses show monophyly of a group composed of Australian (*Mesocyclops australiensis*, *M. brooksi*, *M. notius*, and *Mesocyclops pubiventris*) and South Pacific (*M. medialis* and *M. roberti* sp. nov.) taxa. None of the analyses supports a sister relationship of *M. roberti* with *M. medialis* (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.

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., 2008)] 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 Halicyclopinae and the cyclopine *Apocyclops* Lindberg, 1942). From the Indo-West Pacific region merely 36 cyclopid 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), *Ectocyclops* Brady, 1904 (2), *Tropocyclops* Kiefer, 1927 (4), *Bryocyclops* Kiefer, 1927 (2), *Cryptocyclops* G.O. Sars, 1927 (1), *Mesocyclops* G.O. Sars, 1914 (8), *Metacyclops* Kiefer, 1927 (1), *Microcyclops* Claus 1893 (2), and *Thermocyclops* Kiefer 1927 (5)] are represented there, although a few "tropical/temperate" [*Eucyclops* Claus, 1893 (1), *Paracyclops* Claus, 1893 (2), *Goniocyclops* Kiefer, 1955 (1)] and "temperate" [*Diacyclops* Kiefer, 1927 (1), *Acanthocyclops* Kiefer, 1927 (1), and *Mixocyclops* 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;

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Table 1
List of the cyclopid species occurring in the Indo-West Pacific region.

	Indo-West Pacific				Extralimital
	Phil.	Wall.	Paci.	C.-Ant.	
Halicyclops					
H. thermophilus Kiefer,1929			+		ETH, MAL, SIN
H. spinifer Kiefer, 1935			+		WAT, SIN, AUS, NEO
H. septentrionalis Kiefer, 1935			+		HOL
Eucyclops					
**E. neocaledoniensis* Dussart, 1984			+		
Australoeucyclops					
A. aff. *timmsi*			+		?
Paracyclops					
P. chiltoni (Thomson, 1882)			+	+?	Cosmopolitan
P. eucyclopoides Kiefer, 1929		+			Greater Sunda Is.
Ectocyclops					
E. phaleratus (Koch, 1838)	+				Cosmopolitan
E. rubescens Brady, 1904			+		Cosmopolitan
Tropocyclops					
T. prasinus (Fischer, 1860)	+				Cosmopolitan
T. p. meridionalis Kiefer, 1931			+		NEO
T. confinis (Kiefer, 1930)			+		ETH, MAL, WAT, SIN, NEO
**T. matanoensis* Defaye, 2007		+			
Microcyclops					
M. varicans (G.O. Sars, 1863)	+		+		Cosmopolitan
**M. microsetus* Yeatman, 1983			+		
Mesocyclops					
M. aspericornis (Daday, 1906)	+	+	+		Pantropical
**M. microlasius* Kiefer, 1981	+				
**M. friendorum* Hołyńska, 2000		+			
**M. medialis* Defaye, 2001			+		
M. ogunnus Onabamiro, 1957	+				Afro-Asian
M. affinis Van de Velde, 1987		+			AUS, SIN
M. thermocyclopoides Harada, 1931		+			SIN
M. woutersi Van de Velde, 1987			+		AUS, SIN
Bryocyclops					
B. anninae (Menzel, 1926)			+		Java
**B. fidjiensis* Lindberg, 1954			+		
Cryptocyclops					
C. linjanticus (Kiefer, 1928)			+		ETH, MAL, WAT, HOL, SIN
Diacyclops					
**D. mirnyi* (Borutzky and Vinogradov, 1957)			+		
Acanthocyclops					
A. robustus (?) (G. O. Sars, 1863)			+		HOL
Metacyclops					
M. mendocinus (Wierzejski, 189)			+		NEO, MID
Mixocyclops					
**M. crozetensis* Kiefer, 1944				+	
Thermocyclops					
T. crassus (Fischer, 1853)	+		+		Old World
T. decipiens (Kiefer, 1929)	+		+		Pantropical
T. operculifer (Kiefer, 1930)		+	+		SIN
**T. philippinensis* (Marsh, 1932)	+				
T. woltereckі Kiefer, 1938	+				SIN, AUS
Goniocyclops					
**G. arenicola* Dussart, 1984			+		

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.

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 cyclopid genus in which comprehensive analysis of the phylogeny has been attempted (Hołyńska, 2006).

In 2004 Robert Schabetsberger and Gabriele Drozdowski organized a collecting trip in the South Pacific and sampled 39 water bodies on 18 islands. Preliminary identification of the cyclopid 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* (Daday, 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, 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 (Hołyńska, 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 Hołyńska (2006), as well as those provided herein. The morphological characters used in the analysis (Appendix A) are the same as in Hołyńska (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): transverse rows of spinules present on antennular segments 1 and 12–14. The character matrix (Appendix B) was extracted from what has already been published by Hołyńska (2006), but was supplemented with new data on *Mesocyclops roberti* sp. nov., *Mesocyclops bosumtwii* Mirabdullayev, Sanful and Frempong, 2007 and *Mesocyclops medialis* 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 state (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 encaptive 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, 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. bosumtwii*, a taxon recently described from Ghana (Africa); and one, which excluded *M. bosumtwii* 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 mhennig* 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 Wallis Island (France), Lac Lanutuli [18], 176°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], 179°40′E, 16°25′S, alt. 230 m, lake with fish (tilapias) 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 horseshoe-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, proctodeum 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

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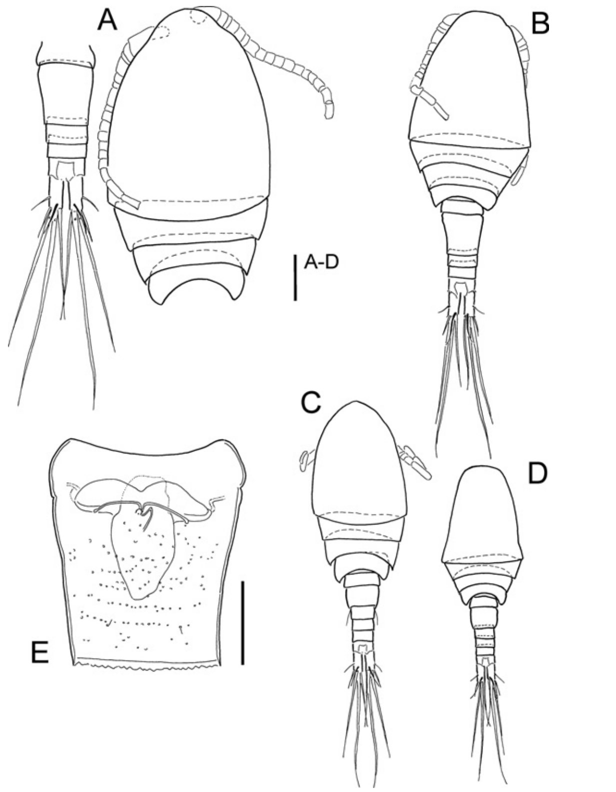

Fig. 1. *Mesocyclops roberti* sp. nov., female: (A) prosome and urosome, Wallis (MIZ: 300003); (B) habitus, Fiji (MIZ: 300009); and (E) genital double-somite, ventral (holotype). Male, habitus: (C) Wallis (MIZ: 300005) and (D) Fiji (MIZ: 300015). Scale bar to (A)–(D): 100 μm and scale bar to (E): 50 μm.

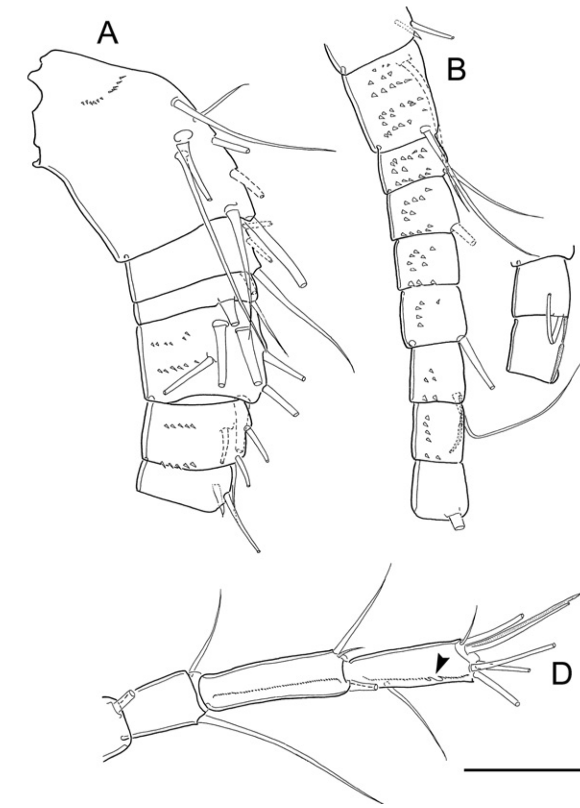

Fig. 3. *Mesocyclops roberti* sp. nov., female antennule: (A) segments 1–6, anterior; (B) segments 7–14, anterior; (C) segments 12–13, posterior; and (D) segments 15–17, anterior. (A, B and D) Holotype and (C) paratype (Wallis, MIZ: 300003). Scale bar: 50 μm.

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).

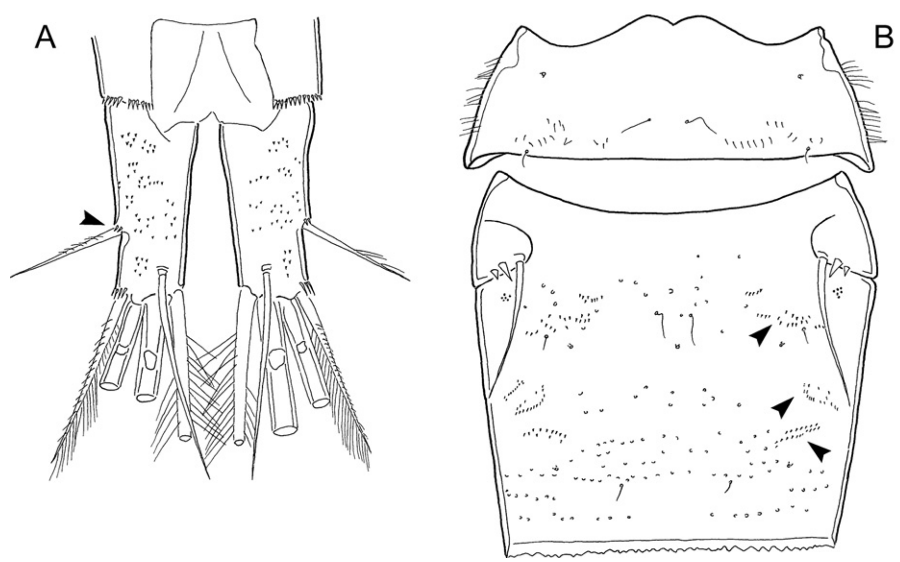

Fig. 2. *Mesocyclops roberti* sp. nov., female: (A) anal somite and caudal rami, dorsal (Wallis, MIZ: 300002) and (B) pediger 5 and genital double-somite, dorsal (Wallis, MIZ: 300002). Scale bar: 50 μm.

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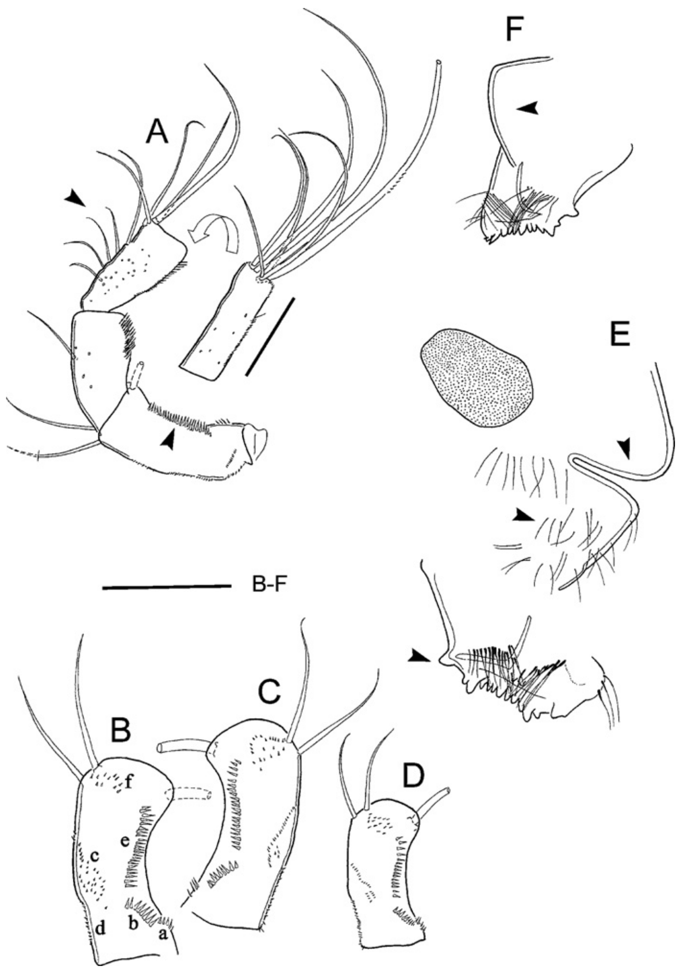

Fig. 4. *Mesocyclops roberti* sp. nov., female: (A) antenna, frontal (holotype); (B)–(D) antennal coxobasis, caudal surface: (B) holotype; (C) paratype, Wallis (MIZ: 300003); and (D) paratype, Fiji (MIZ: 300008). (E and F) Labrum and epistoma: (E) holotype, dotted oval spot shows site of insertion of antennule and (F) paratype, Fiji (MIZ: 300010). Scale bars: 50 μm.

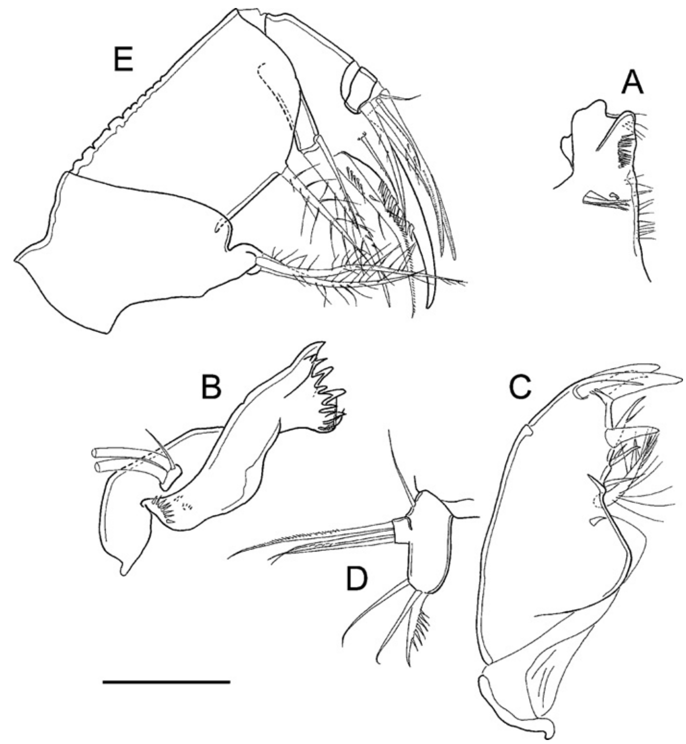

Fig. 5. *Mesocyclops roberti* sp. nov., female: (A) paragnath inner (dorsal) surface; (B) mandible, anterior; (C) maxillule, caudal (palp not shown); (D) maxillulary palp; and (E) maxilla, caudal. Except for (D) showing a paratype (Wallis, MIZ: 300002), all drawings show holotype. Scale bar: 50 μm.

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 mediodistal 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; mediodistal 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. 6A). 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: arthrodial 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

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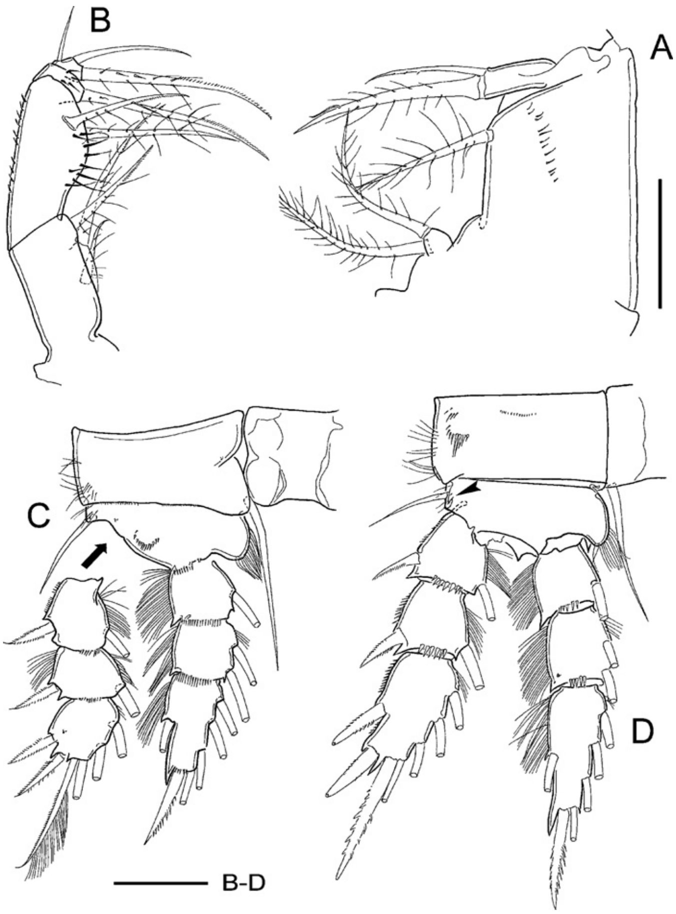

Fig. 6. *Mesocyclops roberti* sp. nov., female: (A) maxilla syncoxopodite, frontal; (B) maxilliped, frontal; (C) leg 1, frontal; and (D) leg 2 (caudal). Except for (A) showing a paratype (Wallis, MIZ: 300002), all drawings show holotype. Scale bars: 50 μm.

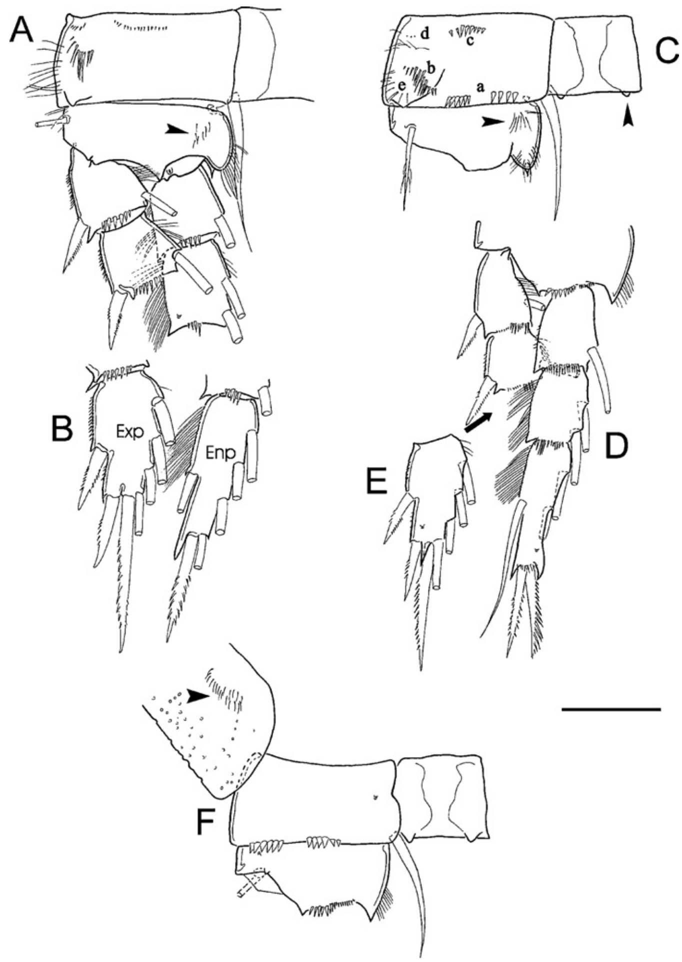

Fig. 7. *Mesocyclops roberti* sp. nov., female: (A) leg 3, protopodite, exp1–2, enp1–2, caudal; (B) leg 3, exp3, enp3, caudal; (C) leg 4, protopodite, caudal; (D) leg 4, exp1–2, enp1–3, frontal; (E) leg 4, exp3, frontal; and (F) lateral part of pediger 4, and leg 4 protopodite, frontal. Except for (C) showing a paratype (Wallis, MIZ: 300003), all drawings show holotype. Scale bar: 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.

	Coxopodite	Basipodite	Exopodite	Endopodite
Leg 1	0-1	1-0	I-1; I-1; I-I, 2-2	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

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 seta 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 *Mesocyclops roberti* sp. nov. Numbers in parentheses show where the number of specimens measured is less than four.

Character	Wallis (1 male)	Fiji, Vanua Levu (4 males)		
		Range	Mean	SD
1	640	525–570	547	21
2	1.32	1.14–1.4(3)	1.27	0.13
3	1.87	1.72–1.85	1.81	0.06
4	1.1	1.10–1.20	1.16	0.05
5	2.56	2.33–2.50	2.39	0.08
6	0.67	0.57–0.65	0.63	0.04
7	0.43	0.33–0.43	0.39	0.05
8	1.35	1.28–1.63	1.44	0.15
9	2.6	2.6–2.8	2.72	0.10
10	5.3	5.7–6.6	6.1	0.42
11	3.9	4.2–4.8	4.6	0.27
12	1.67	1.40–1.55	1.49	0.06
13	2.67	2.9–3.1	3.0	0.08
14	1.1	1.04–1.07	1.06	0.015
15	0.82	0.69–0.81	0.74	0.05
16	1.7	1.4–1.9	1.6	0.22
17	3.0	4.7(1)		

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 median (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.

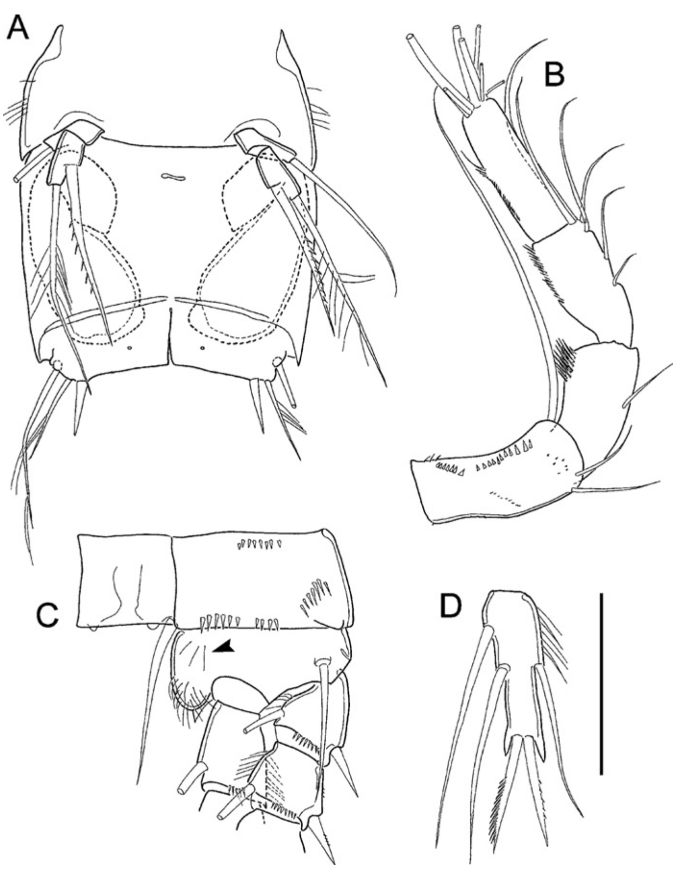

Fig. 8. *Mesocyclops roberti* sp. nov., male: (A) pediger 5 and genital somite, ventral; (B) antenna, caudal; (C) leg 4 protopodite, exp1–2, enp1, caudal; and (D) leg 4 enp3, caudal. All drawings show paratype (Wallis, MIZ: 300005). Scale bar: 50 μm.

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

Labrum with long distal hairs, epistoma bare in both Wallis and Fiji. Paragnaths, mandible, maxillule and maxilliped as in female. Setation of maxilla as in female, but spinules 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 spinules. 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. Spinule 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 spinule 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

Table 4
Variation of the morphometric characters in female of *Mesocyclops roberti* sp. nov. Numbers in parentheses show the number of specimens measured.

Character	Wallis			Fiji, Vanua Levu		
	Range	Mean	SD	Range	Mean	SD
1	990–1110(3)	1058	61.7	740–780(6)	762	16.0
2	1.14–1.29(3)	1.23	0.08	1.09–1.16(6)	1.12	0.023
3	1.13–1.20(2)	–	–	1.11–1.24(6)	1.17	0.052
4	1.84–2.05(3)	1.94	0.11	1.75–1.85(6)	1.79	0.04
5	1.16–1.24(3)	1.19	0.04	1.08–1.20(5)	1.15	0.043
6	2.92–2.93(2)	–	–	2.88–3.17(6)	2.97	0.104
7	2.75–2.91(4)	2.83	0.09	2.56–2.73(7)	2.64	0.066
8	0.55–0.58(4)	0.56	0.013	0.42–0.63(6)	0.53	0.068
9	0.37–0.43(4)	0.40	0.025	0.38–0.43(6)	0.42	0.019
10	1.0–1.1(4)	1.07	0.05	1.25–1.37(3)	1.27	0.087
11	3.2–3.5(4)	3.35	0.13	3.1–3.7(6)	3.32	0.227
12	5.7–6.1(3)	6.0	0.23	5.7–6.9(6)	6.3	0.40
13	4.1–4.3(3)	4.2	0.12	4.3–5.2(7)	4.66	0.292
14	1.69–1.81(4)	1.74	0.055	1.47–1.67(6)	1.56	0.074
15	2.50–2.91(4)	2.67	0.18	2.47–3.00(7)	2.83	0.182
16	1.0–1.13(4)	1.03	0.065	1.07–1.17(7)	1.12	0.042
17	0.75–0.85(4)	0.79	0.043	0.70–0.89(7)	0.77	0.063

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

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and Fiji population. In the longitudinal row on the frontal surface of antennal coxobasis (Fig. 4A, with arrowhead), spinules are less in females from Fiji (20–23 spinules) than in females from Wallis (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 antennular 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 medial 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 Laurentiis 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*).

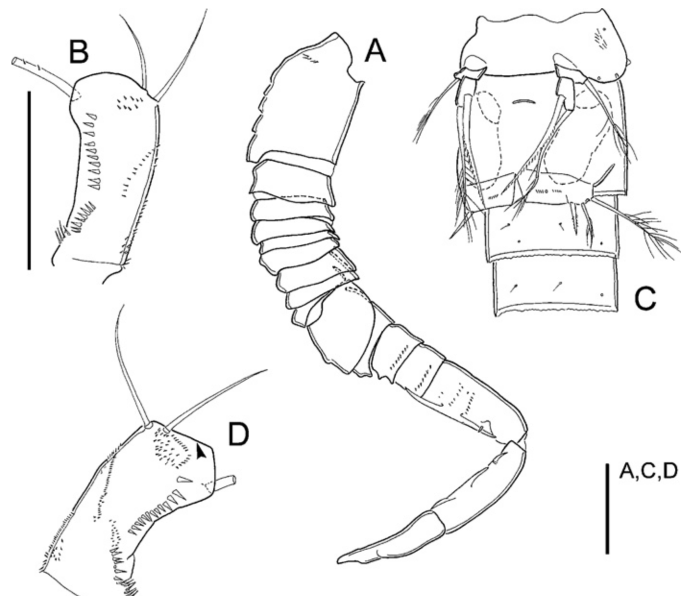

Fig. 9. *Mesocyclops medialis* Defaye, 2001, male: (A) antennule, anterior (Vanuatu, MIZ: 300020); (B) antennal coxobasis, caudal (Vanuatu, MIZ: 300020); and (C) pediger 5 and genital segment, ventral (Vanuatu, MIZ: 30020). *Mesocyclops aspericornis* (Daday, 1906), female. Cook Islands: (D) antennal coxobasis, caudal (Mitiaro, MIZ: 300032). Scale bars: 50 μm.

3.2. *M. medialis* Defaye, 2001

Vanuatu. 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] 167°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, and 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 or obtuse in female in Vanuatu). P4 coxopodite seta 1.5–1.7 times as long as medial expansion of basipodite (ca. 1.9 times as long in female from Vanuatu). Lateral hairs of P4 coxopodite (cf. 'group e' in Fig. 7C), present in female, absent in male. P4 enp3 2.8–2.9 times as long as wide [4.3 in New Caledonian allotype (Defaye, 2001)]; length proportion of medial and lateral terminal spines, 0.98–1.05. Lateral edge of medial terminal spine with many teeth. P6 flap (Fig. 9C) adorned with fine spinules, P6 with middle seta 1.0–1.3 times as long, and lateral seta 2.5 times as long as medial spine.

Female morphology has already been discussed by Defaye (2001), Hołyńska et al. (2003) and Hołyńska (2006) in detail. Females from Vanuatu show a morphology that largely fits the description of this species from New Caledonia, the terra typica. The two Vanuatu females only seem to have more slender P4 enp3 (length/width: 3.0–3.1 in Vanuatu, 2.4–2.7 in New Caledonia) and shorter terminal caudal setae (relative length from medialmost to lateralmost: 2.4, 4.6, 3.5, and 1.0 in Vanuatu, 2.7–2.9, 5.2–5.6, 3.8–4.2, and 1.0 in New Caledonia).

3.3. *M. woutersi* Van de Velde, 1987

Vanuatu. Gaua, Lake Letas [31], 167°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) South Korea.

Comments. No characters were found in which the Vanuatu specimens differed from the Asian and Australian populations (Hołyńska 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 Lanumaha [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).

American Samoa, Tutuila Island, Malaeimi, residual pool in concrete-lined roadside drainage ditch, leg. T. Lemisio, 18 September 2008, 6 females (2 females in MIZ collection: 300030-300031).

Cook Islands, Mitiaro, Vai 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 Rotonui [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 Tiroto [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. 473 m, area 16–22 ha, depth 22 m, temp. 23.4 °C, pH 9.75, cond. 86 μS cm^{-1}, leg. R. Schabetsberger & G. Drozdowski, 17 September 2004, 1 female (MIZ: 300036) – 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.

Easter Island, leg. Lardeux, 1987?, Don. Prod'hon, 4 females, dissected by Danielle Defaye (MNHN, 129-132).

Hawaii, leg. Martens, 27 April 1984, 2 females (MNHN, Cp. 857).

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 West 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 (Hołyńska, 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 (Hołyńska, 2000; Hołyńska and Brown, 2003; Hołyńska 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

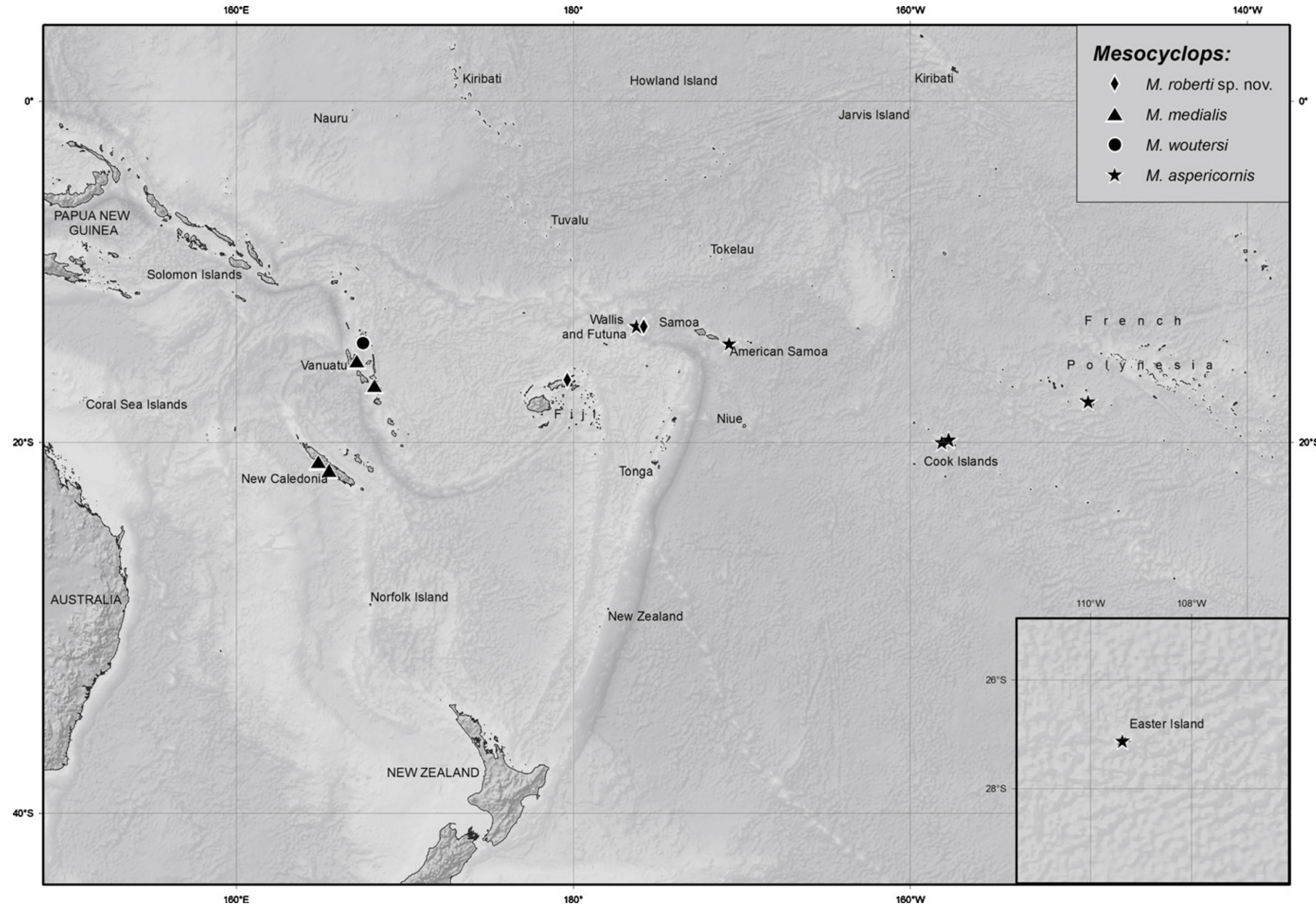

Fig. 10. Geographic distribution of *Mesocyclops* in the South Pacific.

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 microlasius* Kiefer, 1981 from Luzon, and *M. aspericornis* from Luzon and Mindanao have been reported (Hołyńska, 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 (Hołyńska, 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 (Hołyńska, 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; Hołyńska, 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.

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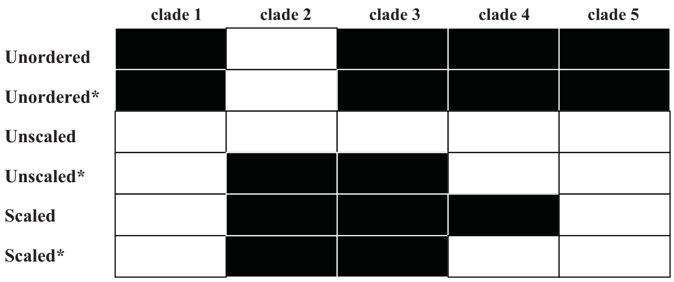

Fig. 11. Clades that appeared more than once in the strict consensus trees of the parsimony analyses using different codings of the polymorphic characters (explanations of the coding in Section 2) and two sets of the terminal taxa. Black and white rectangles indicate if a clade is present or absent, 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. dussarti*, *M. dadayi*, *M. isabellae*, *M. thermocyclopoides*)). *: *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* Hołyńska and Brown 2003 [Queensland] and *M. medialis* [New Caledonia and Vanuatu]. To test this, we ran some 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 (Hołyńska, 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 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. ogunnus*) 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 spinules 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 spinules in the copepodid stages of *Mesocyclops* (also in those species where the spinules 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) suppose 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 Australian (*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 (Hołyńska, 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 *dussarti*-clade (*Mesocyclops dussarti* Van de Velde, 1984, *Mesocyclops dadayi* Hołyńska, 1997, *Mesocyclops isabellae* Dussart and Fernando 1988 and *Mesocyclops thermocyclopoides* 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

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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) (Hołyńska, 2006). In another reconstruction that used the corrected distance method (MICSEQ) (Hołyński, 2001; Hołyńska, 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).

Acknowledgements

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Appendix A. (Figures refer to those in Hołyńska, 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. Pilosity 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 prosomal segments are not independent features. Pilosity 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].

Note. 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.

Note. M. dussarti: data from Van de Velde, 1984.

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

Note. M. dussarti: data from Van de Velde, 1984.

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

Note. M. dussarti: data from Van de Velde, 1984.

(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. microlasius (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].

Notes. Mesocyclops pseudospinosus – observation made by J. Reid; *M. kieferi* – Van de Velde, 1984; *M. dussarti* – Van de Velde, 1984.

(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) Tranverse 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 cuttacuttae* 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 lateral 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.

Notes. *M. kieferi* and *M. dussarti* data from Van de Velde, 1984; *Mesocyclops arcanus* data from Defaye, 1995.

(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) $\leq$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.

Note. *M. arcanus*: data from Defaye, 1995.

(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].

Note. *M. dussarti*: data from Van de Velde, 1984.

(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].

Note. *M. arcanus*: data from Defaye, 1995.

(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. cuttacuttae*] 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. brooksi*] 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. 29G, 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 medial 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) absent or present; 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 *M. aspericornis*, *M. ogunnus*, and *M. acanthoramus*, and they are 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) spinulose only on posterior edge [Fig. 33E, arrowed]; and (2) spinulose 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 lateralmost 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 medial margin: (0) absent and (1) present or absent.

Note. *M. arcanus*: data from Defaye, 1995.

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 mediodistally to group 'a' (group 'c'): (0) absent or tiny [Fig. 35A–D]; (1) large and arranged in group and (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 laterofrontal 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(seta) 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 antennule, 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) Male 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) 8998; (2) 6777; and (3) 7887.

Notes. This character is informative in phylogeny of Cyclopidae, a scope wider than what is applied here. Relying upon Ferrari's studies (1998) on the developmental patterns of cyclopid thoracopods, we applied internal rooting (O'Grady and Deets, 1987) of the ordered character states: state '1', present in *Macrocyclops albidus*, is the plesiomorphic 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.

Character matrix of the Old World *Mesocyclops* sp. lacking medial spine on P1 basipodite. (Hennig86 counts first character as '0', so to keep the same character numbering in the matrix and the character description, we added a 'dummy' character with a state '0' in all species'.)

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               111111111122222222223333333333444444444455555555556666666666777777777788
     0123456789012345678901234567890123456789012345678901234567890123456789012345678901
CUTT 000202200?221000?0200110002010010000200001110000000000112101?10007024064200001 1??2
MAJO 0842021132021100102101134144120000202?0?0111110100000112101?100270430222011012462
PILO 00420211 0?02120022220113414412000020201 20?1111000000000112101?100270430402011012??2
INSU 00420211 0?0212020221011341441202002000120111110000000001 12101?100270430422011012062
BOSU 0?????11??02120222022211341421200000000???????????0?000011 2?01????2704324?2010012?62
MARI 0?4202200???12101222111311 24?20000000??0011111?000000?112101?100070440 6?2000012062
LEUC 000202200?021220002001 13?1241200000001000011111000000000112101?100070440642000012062
MONG 000202200?02122000200113312412000000010000111110000000001 12101?100070440642000012062
AMER 000202200?0212000021111341251000000001000011111000000000112101?100070440642000012062
PSES 000202200?02100002200113414212020000 20?20111110000000001 12101?100070442442000012??2
SHEN 000202200?0210000220011341421202000020?2011111000000000112101?100070442442000012??2
SALI 000200200?0210003022011321441010000201000111110010120011 2101?1000704306400001 12??2
YENA 000202200?0112020000001341201000000111000111110000020021 2101?100070442640000212042
BREV 000202200?011100000000134140100000001100011111000002002121 01?100070440640000212042
REST 0?0202200???100200200113314 4?20200?02????1111100000000?112??1?100070440 6?200001 2??2
SPIN 002202200?02100022210113412412000000 20?0?111110000000001 12101?100070440442000012??2
YESO 000202200?021201002001134124130000002000011111000000000111101?100070440642000012062
PESC 000202200?02120200200113413412000000 1?0201111100000000011?101?100070440641000012062
FERJ 000202200?0210020020011341441202002020000111110000000001 12101?100070440642000012??2
PAPU 000202200?02100200200113414412021000200001111100000000 0112101?100070442642000012062
PEHP 000202200?021002002001134144120110001000011111000000?0112101?100070442642000012062
MICR 0????2200???10001221011341 44?10200001??2???111??0??04?1121?1?100???440??????012??2
GEMI 002202200?0210000220011341441204000002?1201111 10?00004011 2101?100070440402000012062
ASPE 023202200?02100101200113414?1202120011022111111000000?0112101?100070440422000112062
DADA 024202203102120121220113416412021000201211111100000040112101?10007033044200001 2??2
OGUN 004202200?021102002101134 14?1304000020120111110020 00?0112101?100070340412000012052
KIEF 0?0202202?0?100?00200113?140?20000001??1011111?000004?1121?1?100070440 4?20000120?2
GRAN 004202202?021002302221131140120000002 0?0011111010000401 12101?100070440642000012??2
ARCA 0?4202202???1002302221131140?20000002?00011111010??04?112101?100???4406?2000012262
BROO 01220222030021001102101133143120200002001011111000000401 12101?100070?403120001 12062
ROBE 024202203002100200200113314013020000200101111100000030112101?100070240322000012062
THER 044202203102120240222113414412041000201201111100000030112101?100070240442000012062
ISAB 004202203102120240222113416412022200 20?201111100000020112101?100070440442000012??2
NOTI 0242022032021001002001133144120400002001011111000000301 12101?100070340332000012062
DUSS 0?42022032 0?1202402201?3416??20400002??????111??0???4?11?1?1?1000??340??2001012??2
AUST 0132022032021202002101134144120200002002011111000000101 12101?100070340422000112362
MEDI 024202203202100210210113314412020000200201111100000020112101?100070340422000012362
AEQU 002202200?021200001001134154121110001012211111000000401 12101?100070340422000112062
AFFI 022202200?021202002101134144121210002012211111000000401 12101?100070340412000112062
TOBA 000202200?021202102101133143111110000100111110000003011 2101?100070440522000012?62
FRAN 004202200?021000102201134142120200002012211111000000401 12101?100070440422000012??2
FRIE 004202200?021000002001134144130200002012011111000000401 12101?100070440422000012??2
PARE 004202200?021000102201134144140220002012211111000000401 12101?100070440422000012??2
WOUT 002202200?0211011022211341541402100020122111110000004011 2101?100070340422000012062
DISS 002202200?121000002001133154130210002012211111000000401 12101?100070340422000012462
ACAN 002202200?021001002001134 14?1202000010000111110000 00?0112101?100070440422000012052
PUBI 064202203302110200220113314112020000200201111100000020112101?100070340422000012??2
KAYI 08420220 1?0212100122211341201404000011 12011111000000000112101?100070440602000012??2
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ACAN: *M. acanthoramus* Holynska and Brown, 2003
AEQU: *M. aequatorialis* Kiefer, 1929
AFFI: *M. affinis* Van de Velde, 1987
AMER: *M. americanus* Dussart, 1985
ARCA: *M. arcanus* Defaye, 1995
ASPE: *M. aspericornis* (Daday, 1906)
AUST: *M. australiensis* (Sars, 1908)
BOSU: *M. bosumtwii* Mirabdullayev Sanful and Frempong 2007
BREV: *M. brevisetosus* Dussart and Sarnita, 1987
BROO: *M. brooksi* Pesce, De Laurentiis and Humphreys, 1996
CUTT: *M. cuttacuttae* Dumont and Maas, 1985
DADA: *M. dadayi* Holynska, 1997
DISS: *M. dissimilis* Defaye and Kawabata, 1993
DUSS: *M. dussarti* Van de Velde, 1984
FERJ: *M. ferjemurami* Holynska and Vu, 2000,
FRAN: *M. francisci* Holynska, 2000
FRIE: *M. friendorum* Holynska, 2000
GEMI: *M. geminus* Holynska, 2000
GRAN: *M. granulatus* Dussart and Fernando, 1988
INSU: *M. insulensis* Dussart, 1982
ISAB: *M. isabellae* Dussart and Fernando, 1988
KAYI: *M. kayi* Holynska and Brown, 2003
KIEF: *M. kieferi* Van de Velde, 1984
LEUC: *M. leuckarti* (Claus, 1857)
MAJO: *M. major* Sars, 1927
MARI: *M. mariae* Guo, 2000
MEDI: *M. medialis* Defaye, 2001
MICR: *M. microlasius* Kiefer, 1981
MONG: *M. mongoliensis* Kiefer, 1981
NOTI: *M. notius* Kiefer, 1981
OGUN: *M. ogunnus* Onabamiro, 1957
PAPU: *M. papuensis* Van de Velde, 1987
PARE: *M. parentium* Holynska, 1997
PEHP: *M. pehpeiensis* Hu, 1943
PESC: *M. pescei* Petkovski, 1986
PILO: *M. pilosus* Kiefer, 1930
PSES: *M. pseudospinosus* Dussart and Fernando, 1988
PUBI: *M. pubiventris* Holynska and Brown, 2003
REST: *M. restrictus* Dussart and Fernando, 1985
ROBE: *M. roberti* sp. nov.
SALI: *M. salinus* Onabamiro, 1957
SHEN: *M. shenzhenensis* Guo, 2000
SPIN: *M. spinosus* Van de Velde, 1984
THER: *M. thermocyclopoides* Harada, 1931
TOBA: *M. tobae* Kiefer, 1933
WOUT: *M. woutersi* Van de Velde, 1987
YENA: *M. yenae* Holynska, 1998
YESO: *M. yesoensis* Ishida, 1999

References

Balian, E.V., Leveque, C., Segers, H., Martens, K. (Eds.), 2008. Freshwater Animal Diversity Assessment. Hydrobiologia, p. 595.

Bănărescu, P., 1990. Zoogeography of Fresh Waters. Vol. 1 General Distribution and Dispersal of Freshwater Animals. AULA-Verlag, Wiesbaden.

Bănărescu, P., 1991. Zoogeography of Fresh Waters. Vol. 2 Distribution and Dispersal of Freshwater Animals in North America and Eurasia. AULA-Verlag, Wiesbaden.

Bănărescu, P., 1995. Zoogeography of Fresh Waters. Vol. 3 Distribution and Dispersal of Freshwater Animals in Africa, Pacific Areas and South America. AULA-Verlag, Wiesbaden.

Boxshall, G.A., Defaye, D., 2008. Global diversity of copepods (Crustacea: Copepoda) in freshwater. Hydrobiologia 595, 195–207.

Campbell, J.A., Frost, D.R., 1993. Anguid lizards of the genus *Abronia*: revisionary notes, descriptions of four new species, a phylogenetic analysis, and key. Bull. Am. Mus. Nat. Hist., 216.

De Boer, A.J., 1995. Islands and cicadas adrift in the West-Pacific. Biogeographic patterns related to plate tectonics. Tijdschr. Entomol. 138, 169–244.

Defaye, D., 1995. The cyclopoid (Crustacea, Copepoda) fauna of the inland water of Israel. Hydrobiologia 310, 11–18.

Defaye, D., 2001. A new *Mesocyclops* (Copepoda, Cyclopidae) from New Caledonian fresh waters. Crustaceana 74, 647–658.

Dussart, B., Defaye, D., 2006. World Directory of Crustacea Copepoda of Inland Waters II Cyclopiformes. Backhuys Publishers, Leiden.

Einsle, U., 1968. Die Gattung *Mesocyclops* im Bodensee. Arch. Hydrobiol. 64, 131–169.

Farris, J.S., 1988. Hennig86 Reference, Version 1.5. Author, Port Jefferson, New York.

Ferrari, D.F., 1998. Setal developmental patterns of thoracopods of the Cyclopidae (Copepoda: Cyclopoida) and their use in phylogenetic inference. J. Crustacean Biol. 18, 471–498.

Hall, R., 1998. The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. In: Hall, R., Holloway, J.D. (Eds.), Biogeography and Geological Evolution of SE Asia. Backhuys Publishers, Leiden, pp. 99–131.

Hołyńska, M., 1997. Tracing the routes of speciation in *Mesocyclops woutersi*-superspecies (Copepoda: Cyclopoida). Ann. Zool. (Warszawa) 47, 321–336.

Hołyńska, M., 2000. Revision of the Australasian species of the genus *Mesocyclops* Sars, 1914 (Copepoda: Cyclopidae). Ann. Zool. (Warszawa) 50, 363–447.

Hołyńska, M., 2006. Phylogeny of *Mesocyclops* (Copepoda: Cyclopidae) inferred from morphological characters. Zool. J. Linn. Soc. Lond. 147, 1–70.

Hołyńska, M., 2011. Latitudinal gradients in diversity of the freshwater copepod family, Cyclopidae (Crustacea, Copepoda). In: Defaye, D., Suárez-Morales, E., von Vaupel Klein, C. (Eds.), Studies on Freshwater Copepoda. Crustaceana Monographs 16. , pp. 245–269.

Hołyńska, M., Brown, M., 2003. Three new species of *Mesocyclops* G.O. Sars, 1914 (Copepoda, Cyclopoida) from Australia and Burma, with comments on the *Mesocyclops* fauna of Australia. Crustaceana 75, 1301–1334.

Hołyńska, M., Reid, J.W., Ueda, H., 2003. Genus *Mesocyclops* Sars, 1914. In: Ueda, H., Reid, J.W. (Eds.), Guides to the Identification of the Microinvertebrates of the Continental Waters of the World, vol. 20. Copepoda: Cyclopoida. Genera Mesocyclops and Thermocyclops. Backhuys Publishers, Leiden, pp. 12–213.

Hołyński, R.B., 2001. MICSEQ, a new method of phylogenetic analysis, with example reconstruction of *Dicercomorpha* Deyr. (Coleoptera: Buprestidae). Ann. Upper Silesian Mus. (Entomol.) 10–11, 139–168.

Kiefer, F., 1981. Beitrag zur Kenntnis von Morphologie, Taxonomie und geographischer Verbreitung von *Mesocyclops leuckarti* auctorum. Arch. Hydrobiol. Suppl. 62, 148–190.

Kiefer, F., 1978. Das Zooplankton der Binnengewässer. Freilebende Copepoda. Die Binnengewässer XXVI/2. E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, pp. 1–343.

Ladiges, P.Y., Cantrill, D., 2007. New Caledonia–Australian connections: biogeographic patterns and geology. Aust. Syst. Bot. 20, 383–389.

Mabee, P.M., Humphries, J., 1993. Coding polymorphic data: examples from allozymes and ontogeny. Syst. Biol. 42, 166–181.

Meisch, C., Mary-Sasal, N., Colin, J.-P., Wouters, K., 2007. Freshwater Ostracoda (Crustacea) collected from the islands of Futuna and Wallis, Pacific Ocean, with check-list of the non-marine Ostracoda of the Pacific Islands. Bull. Soc. Nat. Luxemb. 108, 89–102.

Nixon, K.C., 1999–2002. WinClada Ver. 1.0000. Author, Ithaca, New York.

O'Grady, R.T., Deets, G.B., 1987. Coding multistate characters, with special reference to the use of parasites as characters of their hosts. Syst. Zool. 36, 268–279.

Reid, J.W., Saunders III, J.F., 1986. The distribution of *M. aspericornis* (von Daday) in South America. J. Crustacean Biol. 6, 820–824.

Rivière, F., Thirel, R., 1981. La prédation du copépode *Mesocyclops leuckarti pilosa* (Crustacea) sur les larves de *Aedes* (*Stegomyia*) *aegypti* et de *Ae.* (St.) polynesiensis (Dip.: Culicidae). Essais préliminaires d'utilisation comme agent de lutte biologique. Entomophaga 26, 427–439.

Sanmartín, I., Ronquist, F., 2004. Southern hemisphere biogeography inferred by event-based models: plant versus animal patterns. Syst. Biol. 53, 216–243.

Schabetsberger, R., Drozdowski, G., Rott, E., Lenzenweger, R., Jersabek, C.D., Fiers, F., Traunspurger, W., Reiff, N., Stoch, F., Kotov, A.A., Martens, K., Schatz, H., Kaiser, R., 2009. Losing the Bounty? Investigating species richness in isolated freshwater ecosystems of Oceania. Pac. Sci. 63, 153–179.

Stearns, H.T., 1945. Geology of the Wallis Islands. Geol. Soc. Am. Bull. 56, 849–860.

Van de Velde, I., 1984. Revision of the African species of the genus *Mesocyclops* Sars, 1914 (Copepoda: Cyclopidae). Hydrobiologia 109, 3–66.

Wiens, J.J., 2000. Coding morphological variation within species and higher taxa for phylogenetic analysis. In: Wiens, J.J. (Ed.), Phylogenetic Analysis of Morphological Data. Smithsonian Institution Press, Washington, pp. 115–145.

Wyngaard, G.A., Hołyńska, M., Schulte II, J.A., 2010. Phylogeny of the freshwater copepod *Mesocyclops* (Crustacea: Cyclopidae) based on combined molecular and morphological data, with notes on biogeography. Mol. Phylogenet. Evol. 55, 753–764.

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