

An overview of the limnetic Cyclopidae (Crustacea, Copepoda) of the Philippines, with emphasis on *Mesocyclops*

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ABSTRACT

Approximately 120 (sub)species of Cyclopidae have been reported from South and Southeast (SE) Asia, where the Philippine archipelago – with 16 (including two endemic) taxa – is one of the least explored parts of the region. Our study, part of current efforts to assess freshwater biodiversity, was undertaken to update the diversity and geographic distribution of the cyclopoid copepods living in the limnetic zone of the freshwater lakes in the Philippines. Examination of the samples from 22 lakes in five islands (Luzon, Mindoro, Cebu, Leyte and Mindanao) revealed a novel species from lake Siloton (Mindanao), *Mesocyclops augusti* n. sp. The new species can be distinguished from the congeners by the surface ornamentation of the hindgut, among others. The same character state was found in a *Mesocyclops* from North Vietnam, which is provisionally identified as *M. augusti* n. sp., though the Vietnam and Mindanao specimens differ in a few (yet polymorphic in the close relatives) characters. *Mesocyclops microlasius* Kiefer, 1981 endemic to the Philippines is redescribed, based on females and males from lake Paoay (North Luzon). Sister relationships of *M. augusti* n. sp. and *M. microlasius* were tested in a phylogenetic analysis that included the closely related Old World representatives of the genus. The max. parsimony trees show *M. dissimilis* Defaye et Kawabata, 1993 (East Asia) as the closest relative of *M. augusti* n. sp. (Mindanao, Vietnam), and support sister relationship between *M. geminus* Holyńska, 2000 (East Borneo) and *M. microlasius* (Luzon, Mindanao). A mainland clade (*M. francisci*, *M. parentium*, *M. woutersi*, *M. dissimilis*, *M. augusti*) appears in most reconstructions; all members of the clade occur in continental Asia though some species also live in islands that have never been connected to the SE Asian shelf. In most trees with the mainland clade the insular taxa (*M. microlasius*, *M. geminus*, *M. friendorum*) form either a paraphyletic (basal to mainland) or monophyletic sister group of the mainland clade. We also established the first records of *Thermocyclops taihokuensis* (Harada, 1931) in the Philippines (Luzon), so far known from East and Central Asia. In all, 11 taxa [*Mesocyclops* (4), *Thermocyclops* (4), *Microcyclops* (1), *Tropocyclops* (1) and *Paracyclops* (1)] including only one endemic species (*M. microlasius*) have so far been found in the limnetic waters. We expect significantly higher diversity and higher rate of endemism of the freshwater cyclopids in the littoral (paludal) and subterranean habitats in the Philippines.

Key words: Biodiversity, tropical lakes, Luzon, Mindanao, zoogeography.

Received: January 2013. Accepted: June 2013.

INTRODUCTION

Cyclopidae [~1010 (sub)species], as one of the largest crustacean families, is represented by ~120 (sub)species in South and Southeast (SE) Asia (Boxshall and Defaye, 2008; MH's personal database), and only 39 species have so far been reported from the insular Indo-West Pacific region (Holyńska and Stoch, 2011). As a dominant component of the lake zooplankton community, cyclopoid copepods are considered important prey of larval and adult zooplanktivorous fish (Papa *et al.*, 2008). Their abundances (together with cladocerans) when compared to calanoid copepods are often related to lake nutrient levels and water temperatures, as they have been revealed by long-term investigations of the zooplankton community responses to eutrophication and climate change (Anneville *et al.*, 2007; Chih-hao *et al.*, 2011). Furthermore,

Mesocyclops (and at least one *Thermocyclops*) species have potential use as biological control agents of Dengue-carrying mosquitoes (*Aedes* spp.). Experiments on the use of copepods in mosquito control have been conducted in several countries including the Philippines, Vietnam, and Australia (Nam *et al.*, 1999; Dussart and Defaye, 2001; Ueda and Reid, 2003; Panogadia-Reyes *et al.*, 2004).

The Philippine archipelago (comprising 7107 islands) are located on the fringe of SE Asia, yet remained separated (though by a narrow strait between the present Borneo and Palawan islands) from the Asian mainland even during the largest sea-level drop during last glaciation (Voris, 2000; Sathiamurthy and Voris, 2006). Diverse connections of the Philippines caused them to be allocated to various biogeographic regions. The Philippines are part of the Oriental region in the Sclater-Wallace system, while the archipelago (except for Palawan) is taken out from the

Oriental region in the Huxley-scheme. Botanists consider the Philippines as part of Malesia (also including the Malay peninsula, Indonesian archipelago and New Guinea), while in the latest monograph of the zoogeography of the continental waters, the southern and southwestern Philippines (Palawan, Calamianes, Mindoro, Sulu and Mindanao islands) belong to the South Asian subregion (that largely fits the Oriental region) of the Sino-Indian region, and the northern Philippines are part of the Indo-West Pacific *peripheral areas* also including Wallacea, the Pacific islands and few islands in the cold zone of southern hemisphere (Bănărescu, 1992, 1995). The insular character has favoured a high species richness and endemism in flora and fauna, thus making the Philippines one of the most interesting regions worldwide (Jones and Kennedy, 2008). It is, unfortunately, also recognised as a biodiversity hotspot, due to the high rate of habitat destruction and loss (Ong *et al.*, 2002; Sinha and Heaney, 2006). Inland waters are among the least studied and most threatened habitats for Philippine biodiversity. In other parts of the world they have been found to host a variety of interesting plants and animal taxa (Balian *et al.*, 2008), but have so far escaped the attention of the Philippine biologists. In the Philippines, studies on limnology and freshwater biodiversity have been fragmentary and inadequate, which often led to the formulation of poorly-prepared conservation and management plans, including those for approximately 70 lakes throughout the archipelago (Papa and Mamaril Sr., 2011).

The current body of knowledge on freshwater zooplankton diversity in the Philippines has mostly been made up of contributions of western scientists. In 1872, Carl Semper described a spherical rotifer, *Trochosphaera aequatorialis*, from rice fields in Mindanao island (southern Philippines) (de Elera, 1895; Mamaril Sr. and Fernando, 1978). This survey was followed by the descriptions of new species and the listing of new records in many lakes and other freshwater ecosystems during the Wallacea-expedition, including the cyclopoid copepods *Mesocyclops microlasius* Kiefer, 1981 and *Thermocyclops wolterecki* Kiefer, 1938 (Brehm, 1938, 1942; Kiefer, 1938a, 1938b, 1981; Hauer, 1941; Woltereck *et al.*, 1941). Two of the most comprehensive and important papers on Philippine freshwater zooplankton were published by a Filipino – Mamaril Sr. – who listed a total of nine copepod species (Mamaril Sr. and Fernando, 1978; Mamaril Sr., 1986). Only a few researchers have added new species or locality records since then (Petersen and Carlos, 1984; Tuyor and Baay, 2001; Aquino *et al.*, 2008; Papa and Zafaralla, 2011). At present, 16 freshwater cyclopoid species have been recorded in the Philippines (Tab. 1), yet some of those species certainly do not occur in the archipelago, or their taxonomic identity needs further verification. On the other hand, hardly anything is known about the cope-

pods of the small water bodies, swamps and subterranean waters of the Philippines, which may be home to a much richer fauna including several endemic and/or relict taxa (Brancelj *et al.*, 2013; Van Damme *et al.*, 2013). A focus on the lake plankton forms can only be justified as the first step of a long-term research project on the freshwater copepod fauna of the Philippines.

Here we present an overview of the species diversity and geographic distribution of the cyclopoid copepods collected from the limnetic zone of 22 lakes distributed in five major islands (Luzon, Mindoro, Cebu, Leyte and Mindanao) of the Philippines. Among these are lakes where efforts to conserve biodiversity have to be balanced with the need to provide sustainable fisheries-based livelihoods, and where the recent increase in under-regulated aquaculture practices have led to a decline in water quality and increased eutrophication (Tamayo-Zafaralla *et al.*, 2002; Palerud *et al.*, 2008).

A large part of the paper deals with the systematics of a single group, the genus *Mesocyclops*, and the reasons for this are twofold: i) *Mesocyclops* is one of the most common and most species-rich components of the tropical lake plankton; ii) the taxonomy of the genus is relatively well understood to pose questions on the phylogenetic relationships/origin of the Philippine species. We describe a new *Mesocyclops* species from Mindanao, provide an amended diagnosis of the endemic *M. microlasius*, and discuss phylogenetic relationships of these *Mesocyclops* taxa.

METHODS

In total, 43 samples collected from 22 lakes were analysed: 15 lakes in Luzon, 4 in Mindanao and 1 each in Cebu, Leyte, and Mindoro islands (Fig. 1; Supplementary Material A). Samples were collected between 2006 and 2011. Plankton sampling was done by towing 50, 80 and 100 µm mesh-size plankton nets from several transects perpendicular to the lake shore. Littoral and limnetic samples were stored separately unless there was no clear demarcation between littoral and limnetic areas of the lake. The samples were fixed in 10% formalin and later transferred to 5% formalin with Rose Bengal dye. Selected specimens from the limnetic samples were dissected and mounted in a glycerin medium. Slides were sealed with nail polish. Dissections were made under an Olympus SZ11 stereomicroscope (Olympus, Tokyo, Japan). Specimens were examined in bright-field and differential interference contrast optics and drawn using a *camera lucida* attached to an Olympus BX50 compound microscope (Olympus). Telescoping body segments were measured separately. Setae of the caudal rami are denoted by Roman numerals, following the scheme applied by Huys and Boxshall (1991).

With few exceptions, only the females could be identified as available identification keys rarely include characters of the male. Identifications were based on Karaytug

Tab. 1. List of cyclopid species so far reported from the Philippine islands.

Notes	Geographic distribution in the Philippines										Extralimital identification key	Descriptions and/or	
	Lu	Mi	Ne	Le	Ce	Ca	Mn	Jo	distribution				
<i>Cryptocyclops linjanticus</i> (Kiefer, 1928)						2					Afro-Asian	Urazova and Mirabdullayev (2007)	Genus needs revision; Philippine record needs confirmation
<i>Ectocyclops phaleratus</i> (Koch, 1838)	6,7,9	6		6,8		6,7					Cosmopolitan?	Fryer (1955)	Genus needs revision; Philippine records need confirmation
<i>Eucyclops serrulatus</i> (Fischer, 1851)	7,8,9	6				6,7					Palaearctic	Alekseev and Defaye (2011)	Very likely it does not occur in the Philippines
<i>Microcyclops varicans</i> (G. O. Sars, 1863)	2,6,7,8	6	6	6,8	6	2	6,7			Restricted to Europe (Mirabdullayev <i>in litt.</i> , 2012)			Genus needs revision; the <i>M. varicans</i> records likely refer to other species in the Philippines
<i>Mesocyclops aspericornis</i> (Daday, 1906)	8,10									Pantropical		Holyńska (2000)	
<i>Mesocyclops leuckarti</i> (Claus, 1857)*	2,6,7	6	2,6	6	6	2	6,7			Palaearctic	Van de Velde (1984); Holyńska <i>et al.</i> (2003)		All <i>M. leuckarti</i> records refer to other species (see Discussion)
<i>Mesocyclops microlasius</i> Kiefer 1981*	5,8,10						8			Endemic		Holyńska (2000)	
<i>Mesocyclops ogunnus</i> Onabamiro, 1957	10									Afro-Asian		Holyńska (2000)	
<i>Mesocyclops thermocyclopoides</i> Harada, 1931*	8						8			SE and E Asia		Holyńska (2000)	
<i>Paracyclops affinis</i> (G. O. Sars, 1863)	8									Old World		Karaytug (1999)	
<i>Paracyclops fimbriatus</i> (Fischer, 1853)	3,6,8,9						3,6			Eurasia		Karaytug (1999)	<i>P. fimbriatus</i> was often confused with other species in the past; the older records in particular need confirmation
<i>Thermocyclops crassus</i> (Fischer, 1853)*	2,4,6,7,8,9	6	2,4,6	6	2,6	2,4,6,7,8	2,4			Old World (including New Guinea, Australia); probably introduced to US and Mexico	Mirabdullayev <i>et al.</i> (2003)		Mirabdullayev <i>et al.</i> (2003) suppose it to be a complex of species
<i>Thermocyclops decipiens</i> (Kiefer 1929)*	4,8,10	2		2,4		8				Pantropical		Mirabdullayev <i>et al.</i> (2003)	
<i>Thermocyclops philippinensis</i> (Marsh, 1932)	1									Endemic		Mirabdullayev <i>et al.</i> (2003)	
<i>Thermocyclops wollecki</i> Kiefer 1938*							2,4			New Guinea, Thailand and Cambodia	Redescription in Chaicharoen <i>et al.</i> (2011)		Limnetic and littoral forms with distinct morphometric characters
<i>Tropocyclops prasinus</i> (Fischer, 1860)*	3,6,7,9			6		3,6,7				Cosmopolitan?	Dumont (2006); Defaye (2007); Lee and Chang (2007)		Genus needs revision; Philippine records need confirmation

Lu, Luzon; Mi, Mindoro; Ne, Negros; Le, Leyte; Ce, Cebu; Ca, Camiguin; Mn, Mindanao; Jo, Jolo; 1, Marsh (1932); 2, Woltereck *et al.* (1941); 3, Mamaril Sr. and Fernando (1978); 4, Kiefer (1938b); 5, Kiefer (1981); 6, Mamaril Sr. (1986); 7, Mamaril Sr. (2001); 8, Tuyon and Baay (2001); 9, Aquino *et al.* (2008); 10, Museum and Institute of Zoology (MIZ) Collection. *Taxa found in limnetic habitats.

(1999), Ueda and Reid (2003) and Hołyńska (1997, 2000, 2006a)

In search of the sister species of *M. augusti* n. sp. and *M. microlasius*, we applied the criterion of the global parsimony using Hennig86 version 1.5. The analyses used 18 morphological characters (46 character states) and included the morphologically close Old World representatives of the genus only (Supplementary Materials B and C). In choice of the ingroup and outgroup taxa we relied upon a former phylogenetic analysis (Hołyńska, 2006b) that included all species of the genus. Phylogenetically informative characters that are fixed in some ingroup species can be intraspecifically variable in other members of the ingroup. Portion of the polymorphic traits can be significant in young groups where most speciations happened relatively recently, and time was too short to reach the fixed condition of a novel character state in each char-

acter. Exclusion of the polymorphic characters from the phylogenetic analysis (means loss of information) would not only result in worse resolution but also false topology of the trees (Wiens, 2000). Eight characters showed intraspecific variation in some species. Data on character polymorphism were taken from earlier publications (Hołyńska *et al.*, 2003; Hołyńska, 2006b), and on observations of the specimens listed herein.

We treated the polymorphic characters in three different ways (*unordered*, *unscaled* and *scaled* coding). All three coding methods recognise a polymorphic condition as a separate state, the differences between these coding methods being in the presumed numbers of transformations between the states *fixed absent*, *polymorphic* and *fixed present* [for more details see Wiens (2000) and Hołyńska and Stoch (2011)]. In the *unordered* run, all characters (both those which are intraspecifically variable,

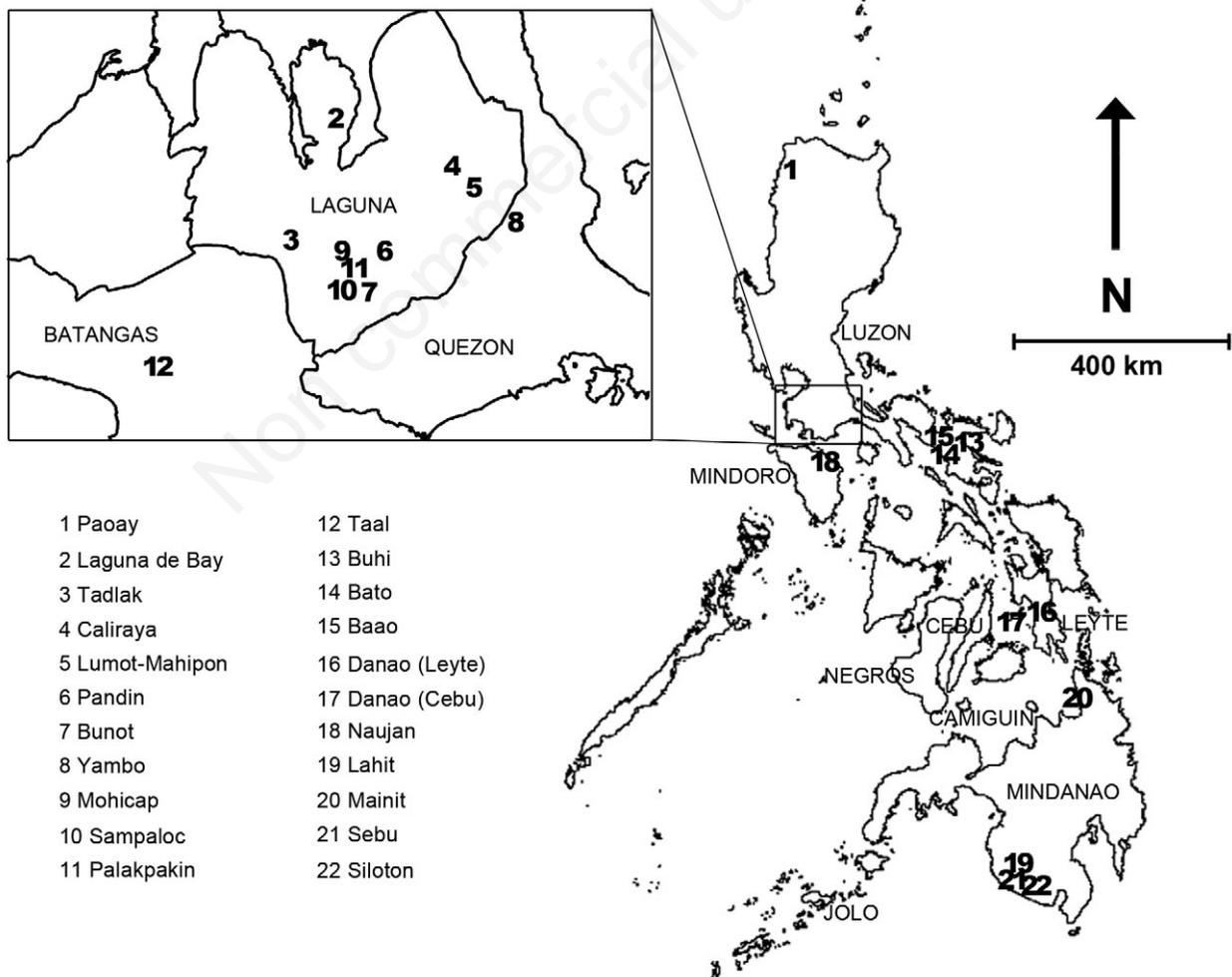


Fig. 1. Map of the Philippine archipelago showing the location of the 22 lakes sampled for this study.

and those which are not) were coded as *unordered*, and given a weight of one. In the *unscaled* run, all characters with intraspecific variation (chars 1, 4, 8-10, 12, 16, and 18), as well as some fixed characters with serially homologous encaptive states (chars 2) were coded as *ordered*, and all characters were given a weight of one. In the *scaled* analysis, characters 1, 2, 4, 8-10, 12, 16, and 18 were coded as *ordered*; the fixed characters 2, 3, 5-7, 11, 13-15 and 17 were given a weight of 2, and polymorphic characters were given a weight of one. In tree building, the *ie* command was applied to produce trees by implicit enumeration, thus the results are in certain to be trees with shortest length. In the analysis of character transformations and editing of the trees we used WinClada (Nixon, 1999-2002).

Specimens were deposited in the Museum and Institute of Zoology (MIZ), Warsaw, Poland, and the University of Santo Tomas Zooplankton Reference Collection (USTZRC), Manila, Philippines.

RESULTS

Taxonomic account

Order Cyclopoida G. O. Sars, 1913

Family Cyclopidae Rafinesque, 1815

Subfamily Cyclopinae Rafinesque, 1815

Genus *Mesocyclops* G. O. Sars, 1914

Mesocyclops augusti n. sp.

Types: holotype, adult female dissected on two slides (MIZ:5/2013/1), Philippines, Mindanao, lake Siloton, 06°13.55'N, 124°43.85'E, leg. R.D.S. Papa, 27 Oct. 2006. For the physical characteristics of lake Siloton see Supplementary Material A. Paratype, one adult female (USTZRC:0068) from the same locality as the holotype.

Other material: Vietnam, Vĩnh Púc province, Vĩnh Yên 21°18'N, 105°36'E, lake Vac, leg. N.S. Vu & Y.T. Nguyen, 10 Jul. 1996, two adult females (MIZ:5/2013/2; MIZ:5/2013/3), two adult males (MIZ:5/2013/4; MIZ:5/2013/5), one CV female (MIZ:5/2013/6).

Comparative material examined: *M. affinis* Van de Velde, 1987 [AFFI]: Indonesia, Java, Bogor Botanical Garden 06°37'S 106°48'E, big lake, leg. M. & R. Holyńscy, 30 Sep. 1988, one female (♀-1, collection of M.H.).

M. dissimilis Defaye et Kawabata, 1993 [DISS]: Japan, Honshu, lake Biwa: pelagic, North-basin 35°10'N 136°00'E, leg. K. Kawabata, 27 Jul. 1995, three females (♀-1,2,3 collection of M.H.) and three males (♂-1,2,3 collection of M.H.); littoral, South-basin 35°03'N 135°53'E, leg. T. Ishida, 22 May 1988, four females (♀-1,2,3,4, collection of M.H.). China, Jiangsu, Nanjing 32°02'N 118°46'E, leg. G. Xiaoming, Aug. 1995, one female (MIZ:5/2013/7).

M. francisci Holyńska, 2000 [FRAN]: Malaysia, Melaka, Ayer Keroh (12 km N Melaka) 02°18'N 102°15'E, pond shore, leg. M. & R. Holyńscy 19 Sep. 1988, female holotype (MIZ:4644). Indonesia, Sumatra, Collectio Dadayana, III 282, 1 female paratype (MIZ:4646).

M. friendorum Holyńska, 2000 [FRIE]: Indonesia, Celebes, Tambolang (2 km W Rantepao) 02°59'S 119°53', ricefield, leg. R. & M. Holyńscy, 8 Oct. 1988, female holotype, (MIZ:4647), and female paratype (MIZ:4648).

M. geminus Holyńska, 2000 [GEMI]: Indonesia, Borneo, Mahakam river valley, Long Iram 00°02'S 115°37', shallow pool in stream bed, leg. M. & R. Holyńscy, 23 May 1989, female holotype (MIZ:4651).

M. ogunnus Onabamiro, 1957 [OGUN]: Taiwan: Pingtung County, Jiuru Township, abandoned fishfarm [PTjr10]. Leg. K-S Tsai, 28 Jun. 2011, one female (MIZ:5/2013/8); Tainan City, Xinying Dist., fishfarm [TNsy06], leg. K-S. Tsai 01 May 2011, one female (MIZ:5/2013/9). India, Chennai(?), leg. A. Zehra, one female (MIZ:5/2013/10).

M. parentium Holyńska, 1997 [PARE]: India, Kerala, Chalakudy 10°18'N 76°22'E, marsh, leg. S. George, 2 Sep. 1992, female holotype (MIZ:4618).

M. roberti Holyńska et Stoch, 2012 [ROBE]: South Pacific, Wallis Island, Lac Lanutuli 13°19'S 176°13'W, [18], leg. R. Schabetsberger & G. Drozdowski, 2 Nov. 2004, one female paratype (MIZ:300003).

M. thermocyclopoides Harada, 1931 [THER]: Indonesia, Sumatra, Musi river, main stream, 14 Jan. 1976, Mizuno coll. 872, one female (♀-1, MIZ:5/2013/11); Java, Telagwarna, near Chibodus, 17 Dec. 1975, Mizuno Coll. 901. one female (♀-2, MIZ:5/2013/12).

M. woutersi Van de Velde, 1987 [WOUT]: Australia, Queensland, Mount Isa 20°43'N 139°29'E, M62, Fisher/Formax, 24 Feb. 1999, one female (♀-1 MIZ:5/2013/13). Taiwan, Pingtung county, Wutai township, artificial pool [PTwt03], leg. K-S Tsai, 16 Aug. 2011, two females (MIZ:5/2013/14, MIZ:5/2013/15).

Etymology: the species is named in honor of Associate Professor Augustus C. Mamaril Sr. of the University of the Philippines-Diliman, who is considered to be the foremost Filipino zooplanktologist.

Female (unless otherwise stated description refers to the holotype): body length 1080 µm (paratype). Pediger 5 (Fig. 2A, 2C, 2D) laterally pilose, dorsally naked except for two medial and two posterolateral hair-sensilla. Genital double-somite 1.18 times as long as wide, naked (Fig. 2A). Six circular pores (Fig. 2D) posteriorly to leg 6 on laterodorsal surface of somite (paratype). Seminal receptacle (Fig. 2B) with wide lateral arms, anterior margin sinuate in middle, posterior sac large. Copulatory pore horseshoe-shaped, copulatory duct strongly curved, long.

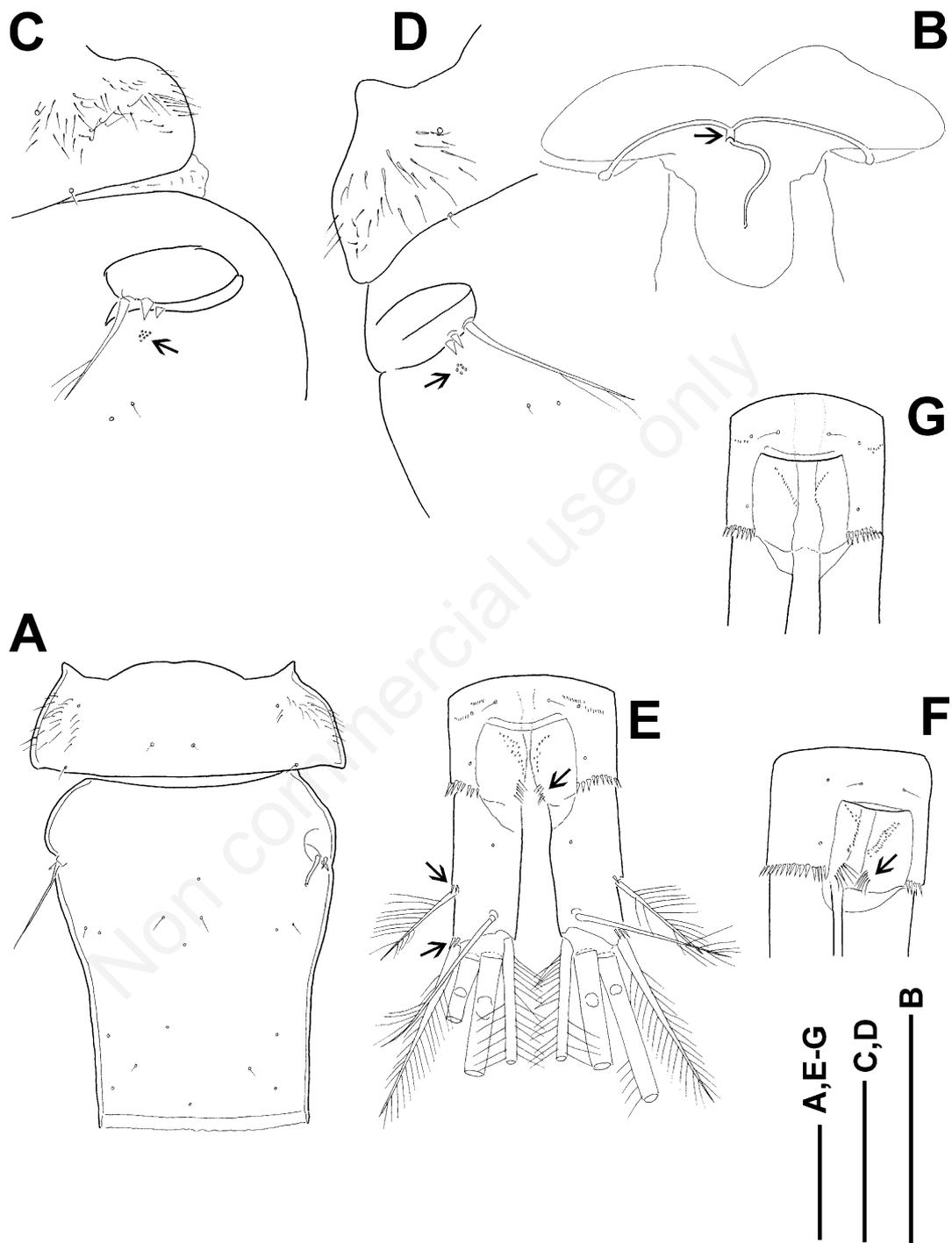


Fig. 2. A-F) *Mesocyclops augusti* n. sp., female; G) *Mesocyclops dissimilis* Defaye et Kawabata, 1993, female (L. Biwa, Japan). A) pediger 5 and genital double-somite, dorsal (Mindanao), holotype; B) seminal receptacle (Mindanao), paratype (arrow points to *joint-canal*); C) pediger 5 and genital double-somite, pores next to leg 6 (Vietnam), MIZ:5/2013/3 (arrow points to eight circular pores); D) pediger 5 and genital double-somite, pores next to leg 6 (Mindanao), paratype (arrow points to six circular pores); E) anal somite and caudal rami, dorsal (Mindanao), holotype (arrows point to long spinules in the hindgut, and spinules at the insertion of caudal setae II and III); F) anal somite, laterodorsal (Vietnam), MIZ:5/2013/3 (arrow points to long spinules in the hindgut); G) anal somite, dorsal, ♀-3. Scale bars: 50 µm.

Single circular pore posterior to copulatory pore in female from Vietnam. Transverse canal-like structures meet anteriorly to copulatory pore at obtuse angle, forming *joint-canal* (Fig. 2B, arrowed). Hindgut (proctodeum) with oblique field of short spinules, and 1-1 row of long spinules near anterior margin of caudal rami (Fig. 2E and 2F, arrowed). Spinules form continuous row on posterior margin of anal somite. Caudal rami (Fig. 2E) 2.52 times as long as wide, without medial hair. Spinules present at insertion of lateral (II) and lateralmost terminal (III) caudal setae. Lateral caudal seta 0.62 times as long as caudal ramus, inserted at distance of 0.41 length measured from posteriormost end of ramus. Dorsal caudal (VII) seta as long as lateralmost terminal (III) caudal seta. Relative length of terminal caudal setae from medialmost (VI) to lateralmost (III): 2.82, 6.64, 4.19, 1.0. Longest terminal (V) caudal seta 1.4 times as long as urosome.

Antennule 17-segmented, with armature formula: 8, 4, 2, 6, 4, 1+ seta transformed to short spine (sp), 2, 1, 1, 0, 1, 1+ aesthetasc (ae), 0, 1, 2, 2+ae, 7+ae. Distal two terminal segments with finely serrate hyaline membrane, that on segment 17 extending beyond insertion of medial seta and bearing one large notch (Fig. 3B, arrowed). Small spinules present on anterior surface of segments 1, 4-5 and 7-13 (Fig. 3A, arrowed). Antenna composed of coxobasis and three-segmented endopodite, with three, one, seven and seven setae, respectively. Caudal surface of antennal coxobasis (Fig. 3C) ornamented with long lateral spinules near base (group a), oblique row of robust spinules (10) near lateral margin (group b), oblique row/field of fine spinules starting near midlength of medial margin (group c), fine spinules on medial margin near base (group d), longitudinal row of spinules (17) of slightly increasing size next to lateral margin (group e), group of small spinules near insertion of medial setae (group f), and few small spinules next to distal margin (group g). Frontal surface adorned with long longitudinal row of small spinules (29) next to lateral margin, and transverse row of fine spinules near base.

Integumental perforation pattern of rostrum as in Fig. 3D. Labrum with 13 teeth on distal edge, lateral lobes smooth (Fig. 3E, arrowed), distal fringe-hair arranged in arc. Shorter spinules (Fig. 3E and 3F, arrowed) present

on both right and left side of labrum, anteriorly to fringe-hair. Epistoma (longitudinal medial hump between labrum and rostrum) pilose (Fig. 3E), hair also present laterally to epistoma. Vertical cleft between epistoma and rostrum pilose (verified in paratype from Mindanao and females from Vietnam) resembling that in *M. micro-lasius*. Mandible (Fig. 4A and 4B) with palp bearing two long and one short setae. Three groups of spinules present on anterior surface of gnathobase near mandibular palp. Maxillule armature as common in genus, palp naked (Fig. 4C). Proximalmost seta of maxillary palp and three setae of lateral lobe without long setules. Maxilla (Fig. 4D and 4E) segmentation and setation as usual in genus. Row(s) of spinules (Fig. 4E, arrowed) present on frontal surface of coxopodite. Maxilliped (Fig. 5A) four-segmented with three, two, one, and three setae, respectively. Lateral seta on terminal segment shorter than $\frac{1}{4}$ length of median seta. No surface ornamentation on frontal surface of syncoxopodite. Caudal surface of basipodite (segment 2) with spinules arranged into two groups (not shown in Fig. 5A), frontal side bearing long and thin spinules near medial margin. First endopodal segment (segment 3) with few short spinules next to distal margin.

Armature formula of swimming legs as in Tab. 2. P1 basipodite (Fig. 5B) lacking medial spine/seta. Medial expansion of basipodite apically pilose in P1-P4. In P4 additional row of long hairs present on caudal surface near medial margin of basipodite (Fig. 5C, arrowed). Long spinules appear on frontal surface of basipodite near lateral margin in P1-P4. Couplers of P1-P4 bare on frontal and caudal surfaces. Outgrowths (Fig. 5C, arrowed) small (*ca.* as long as wide) and acute on distal margin of P4 coupler. Caudal surface of P4 coxopodite bearing intermittent row of spinules (11) along distal margin, group of elongate spinules at laterodistal angle, robust spinules of unequal size in middle near proximal margin of segment, and long hair in lateral part. Lateral margin of P4 first segment of exopodite (exp1) with hair, exp2 and exp3 with spinules (Fig. 5C). P4 third segment of endopodite (enp3) (Fig. 5C) 2.8 times as long as wide, terminal spines subequal, outer margin of medial spine with many (9) spinules. P5 (Fig. 5D) as typical of genus.

Tab. 2. Armature of legs 1-4 in *Mesocyclops augusti* n. sp.

Leg	Coxopodite	Basipodite	Exopodite	Endopodite
1	0-1	1-0	I-1; I-1; I-1,2-2	0-1; 0-2; 1-I,1-3
2	0-1	1-0	I-1; I-1; I-II,1-3	0-1; 0-2; 1-I,1-3
3	0-1	1-0	I-1; I-1; I-II,1-3	0-1; 0-2; 1-I,1-3
4	0-1	1-0	I-1; I-1; I-II,1-3	0-1; 0-2; 1-II-2

Roman numerals denote spines, while Arabic denote setae. The armature on the lateral margin of any segment is given first, followed by the elements on the apical and medial margins.

Male (Vietnam): body length 700-730 μm ; cephalothorax, length/width: 1.1-1.2; prosome length/urosome length: 1.6-1.8. Pediger 5 (Fig. 6A) with sparse short lateral hairs, dorsal surface bare. Hindgut without surface ornamentation. Posterior margin of anal somite with continuous row of spinules. Caudal rami 2.2-2.5 times as long as wide, no medial hair. Spinules present at insertion of lateral (II) and lateralmost terminal (III) cau-

dal setae. Lateral caudal seta 0.5-0.6 times as long as caudal ramus, inserted at distance of 0.42 length measured from posteriormost end of ramus. Dorsal (VII) caudal seta 1.2 times as long as lateralmost terminal (III) caudal seta. Relative length of terminal caudal setae from medialmost (VI) to lateralmost (III): 2.7, 5.2, 3.1-3.3, 1.0. Longest terminal (V) caudal seta as long as urosome.

Antennule 16-segmented, armature as in *M. microla-*

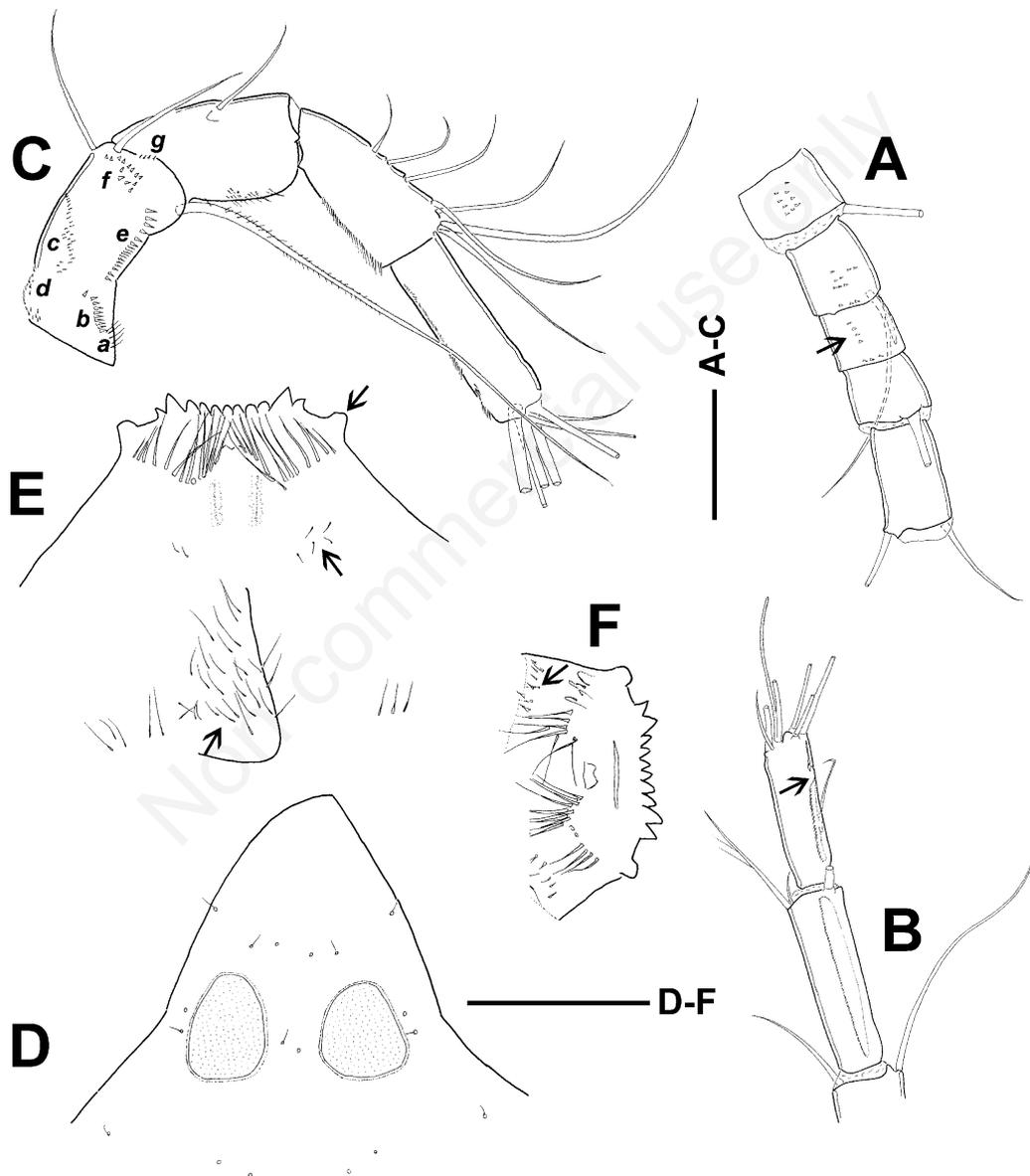


Fig. 3. *Mesocyclops augusti* n. sp., female: antennule, anterior (Mindanao). A-D) show holotype, E) shows paratype, and F) shows Vietnam MIZ:5/2013/3. A) segments 11-15 (arrow indicates small spinules on segment 14); B) segments 16-17 (arrow indicates large notch); C) antenna, caudal (Mindanao) (a-g, groups of spinules); D) rostrum (Mindanao); E) labrum and epistoma, ventral (Mindanao) (arrows point to smooth lateral lobe of labrum, short spinules on labrum, and hairy epistoma); F) labrum, ventral (Vietnam) (arrow points to short spinules). Scale bars: 50 μm .

sius. Spinules present on first antennular segment only. Antenna enp2 with six setae. Caudal surface ornamentation of antennal coxobasis (Fig. 6C) similar to that in female in Vietnam, but differs from female in Mindanao in absence of spinules next to distal margin. Labrum bearing distal fringe hair only, epistoma and vertical cleft bare. Longitudinal rows of spinules absent on frontal surface of maxillary coxopodite. Mandible, maxillule and maxilliped as in female. Armature formula of P1-P4 as in female. Long spinules absent on laterofrontal surface of basipodite in P1-P4. Outgrowths small and acute on distal margin of P4 coupler. Caudal surface ornamentation of P4 coxopodite (Fig. 5E) similar to that in female, but lateral hair restricted to one row in middle. Medial expansion of P4 basipodite apically pilose, oblique row of hairs also present on caudal surface of segment. Lateral margin of P4 exopodal segments with small spinules. P4 enp3 2.7-3.0 times as long as wide. Medial terminal spine 0.9 times as long as lateral spine, longer (lateral) terminal spine 0.9 times as long as segment. Lateral margin of medial spine bearing many spinules. P6 flap (Fig. 6A) with several rows of small spinules, mediolateral angle with small teeth. P6 (Fig. 6D) median seta subequal or slightly shorter than medial spine, lateral seta 2.1 times as long as medial spine.

Intraspecific variation

Variation of the morphometric characters is shown in Tab. 3. Six (single female verified in Mindanao) or eight (two females in Vietnam) pores present posteriorly to P6. Female genital structures: transverse canal-like structures meet at obtuse (Mindanao) or acute (Vietnam) angle. Surface ornamentation of antennule: spinules present on segments 1, 4-5, 7-13 (Mindanao), or 1, 4-5, 7-14 (Vietnam). Spinules present (Mindanao), or absent (Vietnam) next to distal margin of antennal coxobasis (group g; Fig. 3C). Long spinules present on frontal surface of basipodite near lateral margin in P1-P4 (Mindanao) or in P1-P3 (Vietnam).

Mesocyclops microlasius Kiefer, 1981

Mesocyclops microlasius Kiefer (1981); Hołyńska (2000); Hołyńska *et al.* (2003); Tuyor and Baay (2001).

Mesocyclops sp.: Aquino *et al.* (2008)

Material examined: Philippines, Luzon, lake Paoay 18°7.3'N 120°32.4'E, leg. R. Aquino, Apr.-Sep. 2006, 3 females (MIZ:5/2013/16, MIZ:5/2013/17, MIZ:5/2013/18), 3 males (MIZ:5/2013/19, MIZ:5/2013/20, MIZ:5/2013/21). For the physical characteristics of lake Paoay see Supplementary Material A.

Female (*L. Paoay*): body length 980 µm; cephalothorax, length/width: 1.2-1.4; prosome length/urosome length: 1.77-1.84; width of cephalothorax/width of genital double-somite: 2.5-2.9. Pediger 5 (Fig. 7A) with lateral

hair, dorsal surface naked. Genital double-somite 1.2-1.3 times as long as wide, naked, integumental perforation pattern shown in Fig. 7A and 7B. Seminal receptacle as in Fig. 7B, transverse duct-like structures meet anteriorly to horseshoe-shaped copulatory pore, forming *joint-canal*. Hindgut (proctodeum) bearing oblique/longitudinal field of spinules medially, and triangular field of small spinules more laterally near anterior margin of caudal rami (Fig. 7C, left arrowed). Posterior margin of anal somite with continuous row of spinules. Caudal rami (Fig. 7C) 2.4-2.8 times as long as wide. Short hair (Fig. 7C, right arrowed) present on medial margin in anterior half of rami. Spinules present at insertion of lateral (II) caudal setae in one of three females. Spinules present at insertion of lateralmost terminal (III) caudal setae in all specimens. Dorsal (VII) caudal seta 0.81 times as long as lateralmost terminal (III) caudal seta. Lateral (II) seta 0.51-0.63 times as long as caudal ramus, and inserted at distance of 0.41-0.43 length measured from posteriormost end of ramus. Relative length of terminal caudal setae from medialmost

Tab. 3. Variation of the morphometric characters in female of *Mesocyclops augusti* n. sp.

Morphometric characters	Mindanao	North Vietnam
1	1080	1010-1050
2	1.17	0.98
3	1.16-1.18	1.26-1.32
4	1.87	1.58-1.60
5	1.40	1.11
6	2.80	3.50
7	2.48-2.52	3.4-3.5
8	0.58-0.62	0.40
9	0.39-0.41	0.38
10	0.97	1.17-1.21
11	2.84-3.12	2.44-2.81
12	6.6	5.5
13	4.19-4.31	3.33-3.75
14	1.53-1.71	1.86
15	2.57-2.81	2.97-3.35
16	0.97-0.99	0.92-1.02
17	0.83-0.88	0.92-0.94
18	1.23	1.45
19	0.87	0.97

1, body length in 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, fourth leg, length of coxopodite seta/height of medial expansion of basipodite; 15, fourth leg endopodite 3, length/width; 16, fourth leg endopodite 3, medial terminal spine/lateral terminal spine; 17, fourth leg endopodite 3, length of longer terminal spine/length of segment; 18, fifth leg, length of apical seta/length of medial spine; 19, fifth leg, length of lateral seta/length of medial spine.

(VI) to lateralmost (III): 2.4-2.8, 5.5-6.1, 3.9-4.1, 1.0. Longest terminal (V) caudal seta 1.2-1.4 times as long as urosome.

Armature formula of antennule as in *M. augusti* n. sp. Segments 1, 4-5, 7-13 adorned with spinules on anterior surface. Hyaline membrane of last antennular segment with one large notch. Antenna enp2 with seven setae. Caudal surface ornamentation of antennal coxobasis as in Fig. 7E: spinules (11-14) distally increasing slightly in longitudinal row next to lateral margin (Fig. 7E, arrowed).

Frontal surface with long longitudinal row of spinules (24-27) near lateral margin.

Labrum (Fig. 7D) bearing distal fringe of hairs arranged in arc. Spinules/hair absent anteriorly to distal fringe hair (Fig. 3F where spinules are arrowed). Epistoma (longitudinal medial hump between labrum and rostrum) pilose (Fig. 7D, lower arrowed), hair also present laterally to epistoma. Vertical cleft between rostrum and epistoma pilose (Fig. 7D, upper arrowed). Segmentation and setation of mandible, maxillule, maxilla and maxil-

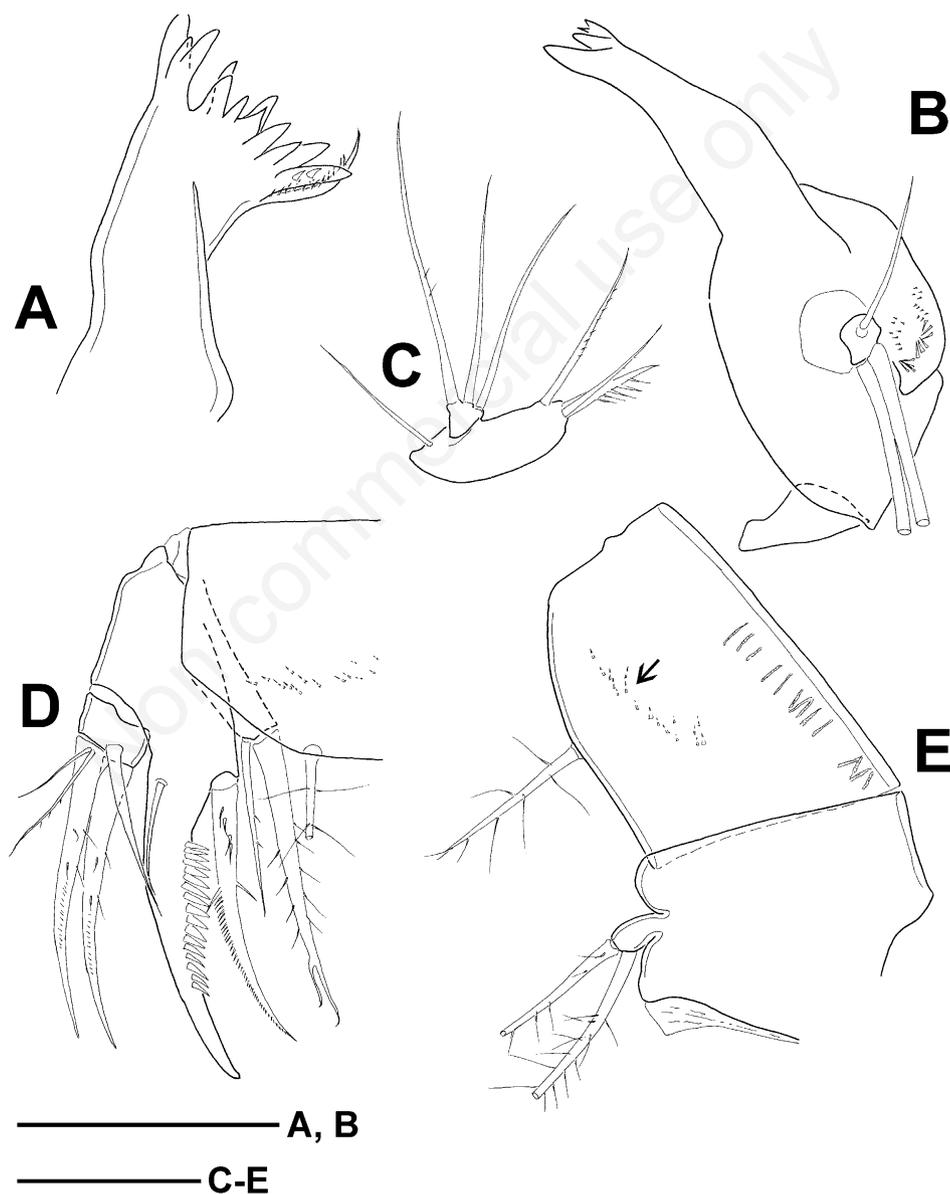


Fig. 4. *Mesocyclops augusti* n. sp., female (Mindanao). Except for A) showing paratype, all drawings show holotype. A and B) mandible; C) maxillulary palp; D-E) maxilla, caudal: D) distal part of coxopodite, basipodite and endopodite, and E) syncoxopodite (arrow indicates rows of spinules). Scale bars: 50 μ m.

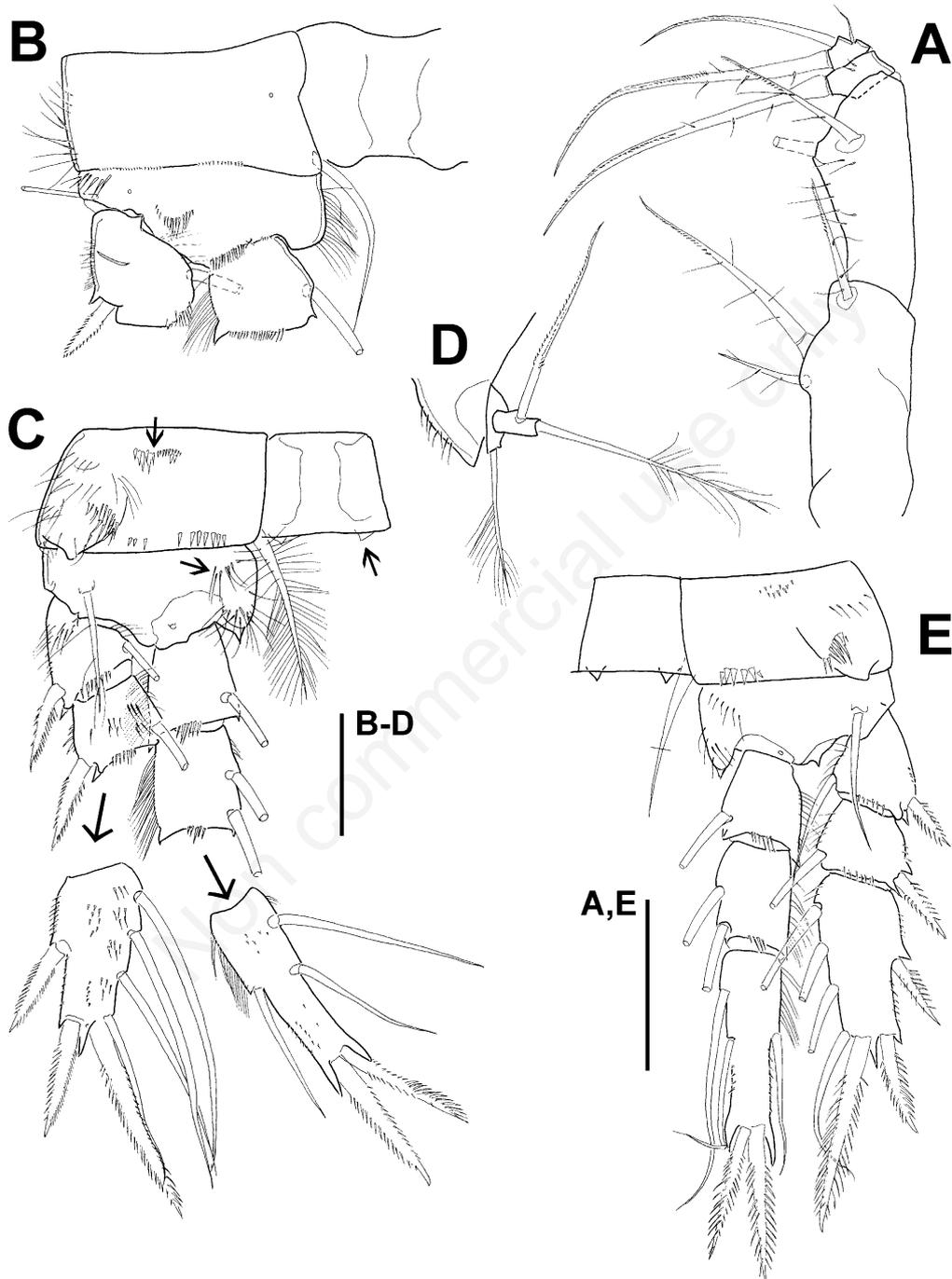


Fig. 5. *Mesocyclops augusti* n. sp.: female. A-C) show holotype, D) shows paratype, and E) shows Vietnam MIZ:5/2013/5. A) maxilliped, frontal, medial seta on basipodite broken off; B) leg 1 protopodite, and first exo- and endopodal segment, frontal; C) leg 4, caudal (short arrows indicate small outgrowths of coupler, spinules of unequal size in proximal row of coxopodite, and row of long hair on basipodite, while long arrows point to terminal segments of exo- and endopodite); D) leg 5, male (Vietnam); E) leg 4 caudal, distal half of coxal seta broken off. Scale bars: 50 μ m.

liped as usual in genus (Figs. 4A-E and 5A). Three groups of spinules present on anterior surface of gnathobase near mandibular palp. Maxillary palp bare. Row(s) of robust spinules present on frontal surface of maxillary coxopodite, similarly to that in *M. augusti* sp. nov. (Fig. 4E, arrowed).

Armature formula of P1-P4 as in *M. augusti* n. sp. (Tab. 2). Basipodite of P1 lacking medial spine. Medial expansion of basipodite apically pilose in P1-P4. Additional row of long medial hair present on caudal surface of segment in P4 (Fig. 8A, arrowed). Couplers of P1-P4 bare on caudal and frontal surfaces. Outgrowths small and acute on distal margin of P4 coupler. Caudal surface ornamentation of P4 coxopodite (Fig. 8A) comprising: robust spinules (7-11) in continuous or intermittent row next to distal margin, group of long spinules at laterodistal angle, row of spinules of unequal size in middle near proximal margin, and hair in lateral part. Lateral margin of P4 exopodal segments with long hair (Fig. 8A). P4 enp3 2.6-3.0 times as long as wide; of terminal spines, medial one 1.0-1.2 times as long as lateral spine, and 0.76-

0.88 times as long as segment. Lateral margin of medial terminal spine of P4 enp3 with 8-15 small spinules. P5 (Fig. 7F) typical of genus, segment 2 with long apical seta almost reaching posterior margin of genital double-somite, and 1.4-1.8 times as long as medial spine. Lateral seta on first segment 0.83-1.35 times as long as medial spine.

Male (*L. Paoay*): body length 625-635 μm , prosome length/urosome length: 1.74-1.77. Pediger 5 with few hairs on lateral surface, dorsal surface naked. Hindgut (proctodeum) (Fig. 8B) bearing oblique/longitudinal rows of hair-like spinules and triangular field of small spinules more laterally near anterior margin of caudal rami. Posterior margin of anal somite with continuous row of spinules. Caudal rami 2.3-2.4 times as long as wide, with group of hair near anterior end of rami. Robust spinules present at insertion of lateral (II) and lateralmost terminal (III) caudal setae. Lateral seta 0.71-0.76 times as long as caudal ramus, and inserted at distance of 0.42-0.45 length measured from posteriormost end of ramus. Dorsal (VII) caudal seta 0.9-1.1 times as long as lateralmost terminal

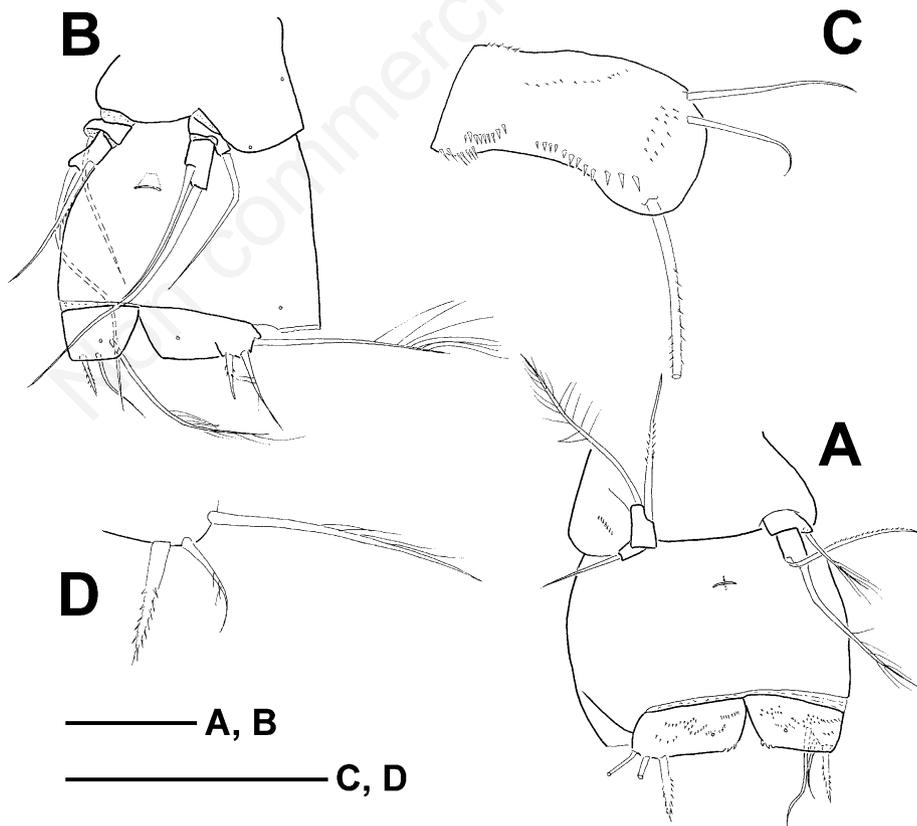


Fig. 6. A, C, D) *Mesocyclops augusti* n. sp., male (Vietnam); B) *Mesocyclops dissimilis* Defaye et Kawabata, 1993, male (L. Biwa, Japan). A) Pediger 5 and genital segment, ventral, MIZ:5/2013/4; B) pediger 5 and genital segment, lateroventral, ♂-3; C) antennal coxobasis, caudal, MIZ:5/2013/5; D) leg 6, MIZ:5/2013/5. Scale bars: 50 μm .

(III) caudal seta. Relative length of terminal caudal setae from medialmost (VI) to lateralmost (III): 2.4-2.5, 5.3-5.7, 3.7-4.0, 1.0. Longest terminal (V) caudal seta 1.1-1.3 times as long as urosome.

Antennule (Fig. 9A-D) 16-segmented, with incomplete subdivision of compound apical segment, with armature formula: 8+3ae, 4, 2, 2+ae, 2, 2, 2, 2, 1+sp+ae; 2, 2, 2, 2+ae, 2, 1+ae, (4+ae, 7+ae). Plate-like structures with pore (one large plate on segment 14 and two smaller ones on segment 15) and short conical elements (one on segment 14 and 15 each) present at distal geniculation. Smooth hyaline membrane present in proximal half of compound apical segment. Spinules present on anterior surface of segment 1 only.

Antenna enp2 with six setae. Caudal surface ornamentation of antennal coxobasis (Fig. 9E) similar to that in female, but number of spinules less in particular groups. On frontal surface 18-20 spinules present in longitudinal row next to lateral margin.

Labrum with 10 distal teeth. Except for fringe hair no ornamentation on labrum, epistoma and vertical cleft naked. Segmentation and setation of mandible, maxillule, maxilla and maxilliped as in female. Spinules tiny or absent on frontal surface of maxillary coxopodite.

Armature formula of P1-P4 as in female. Couplers of P1-P4 naked on frontal and caudal surfaces. Medial pilosity of basipodite of P1-P4 as in female. Outgrowths small and acute on distal margin of P4 coupler. Caudal surface ornamentation of P4 coxopodite (Fig. 8C) similar to that in female but lateral pilosity scarce. Spinules/hair present on lateral margin of second and third exopodal segment of P4, but much shorter than those in female (Fig. 8A and 8C). P4 enp3 2.7-2.8 times as long as wide. Medial terminal spine of P4 enp3 *ca.* 1.1 times as long as lateral spine, and 0.81-0.95 times as long as segment. Lateral margin of medial terminal spine with many fine spinules. P6 flap (Fig. 8D) with few transverse rows of spinules, mediolateral angle with two small teeth. P6 median and lateral seta 1.0-1.2 and 2.5-2.7 times as long as medial spine, respectively.

Comments

This species was originally described from specimens collected from Manila (type locality; cement ponds) and Laguna de Bay during the Wallacea-expedition (Kiefer, 1981). It was later identified from samples collected in lake Sebu (Mindanao), which is the southernmost locality where it has been recorded (Tuyor and Baay, 2001). This is the first time that *M. microlasius* has been reported in northern Luzon, *ca.* 430 km from the type locality. Aquino *et al.* (2008) listed a *Mesocyclops* sp. from lake Paoay but did not identify to species level. The specimen examined here is part of the samples analysed in the aforementioned study.

For an analysis of the phylogenetic relationships of *M. microlasius* see the Discussion.

Geographic distribution of limnetic Cyclopidae in the Philippines

A total of 4 species of *Mesocyclops*, 3 of *Thermocyclops*, and 1 species each of *Microcyclops* and *Paracyclops* were identified (Tab. 4, Fig. 10). Two species (*T. taihokuensis* and *M. augusti* n. sp.) are new records for the Philippines. There was only one male specimen each for *Microcyclops* and *Paracyclops*. The identification of *Microcyclops* sp. to species level was not done due to the absence of a key for male *Microcyclops*. *Thermocyclops crassus* is the most widely distributed species, occurring in 16 lakes found across all five islands followed by *Mesocyclops thermocyclopoides* and *T. taihokuensis*, both occurring in six lakes each. *Thermocyclops taihokuensis*, however, seems to be restricted to Luzon island, while *M. thermocyclopoides*, which occurs mostly in Luzon, was also found in Mindoro island. The endemic *M. microlasius* – which was first collected from the Philippines 80 years ago during the Wallacea-expedition – was found in lake Paoay (northern Luzon). *Thermocyclops decipiens* was only found in three lakes within one small locality in Southwest Mindanao. *Paracyclops fimbriatus* is hereby reported for the first time in lake Mainit together with *Microcyclops* sp. and *Mesocyclops* sp. (Mindanao island).

DISCUSSION

Notes on morphology and phylogenetic relationships of *Mesocyclops augusti* n. sp.

The unique surface ornamentation of the hindgut (oblique field of short spinules, and row of long spinules more posteriorly) distinguishes *M. augusti* n. sp. from all the other *Mesocyclops* species. In many cyclopine and eucyclopine genera (*e.g.* *Acanthocyclops*, *Megacyclops*, *Diacyclops*, *Eucyclops*, *Ectocyclops*, *Macrocyclus* and

Tab. 4. Cyclopidae species identified from the limnetic zone of different freshwater lakes in the Philippines (cf. Fig. 1 and Supplementary Material A).

Cyclopidae species	Lake
<i>Mesocyclops microlasius</i> Kiefer, 1981*	1
<i>M. thermocyclopoides</i> Harada, 1931	2, 4, 5, 11, 13, 18
<i>Mesocyclops</i> sp.	20
<i>Mesocyclops augusti</i> n. sp.°	22
<i>Microcyclops</i> sp. (male only)	20
<i>Paracyclops fimbriatus</i> (Fischer, 1853)	20
<i>Thermocyclops crassus</i> (Fischer, 1853)	1-3, 7-14, 16-20
<i>T. decipiens</i> (Kiefer 1929)	19, 21, 22
<i>T. taihokuensis</i> (Harada, 1931)°	6, 7, 9, 11, 14, 15

*Endemic species; °new record.

Paracyclops) spinules or hair are frequently present in the hindgut (proctodeum), therefore the pilose/spinulose proctodeum supposedly is an ancestral state in Cyclopinae. Hołyńska (2006b) reported surface ornamentation of the hindgut in only few, distantly related *Mesocyclops* taxa [*M. dissimilis* (East Asia) – small spinules; *M. annulatus* (Wierzejski, 1892) (South America) – small spinules; and *M. cuttcuttae* Dumont et Maas, 1985 (Australia) – row of long hair-like spinules], yet we found this feature to be

more common in the genus than previously thought. All members of the *woutersi*-complex (see definition further), as well as *M. francisci*, *M. microlasius*, *M. geminus*, *M. ogunnus* and sometimes *M. pehpeiensis* Hu, 1943 have rows or oblique fields of spinules, though can be tiny and easy to overlook in the hindgut. The conspicuous surface ornamentation present in the Mindanao females from lake Siloton, also appears in two adults and one fifth copepodid stage (CV) female in lake Vac, North Vietnam. The Viet-

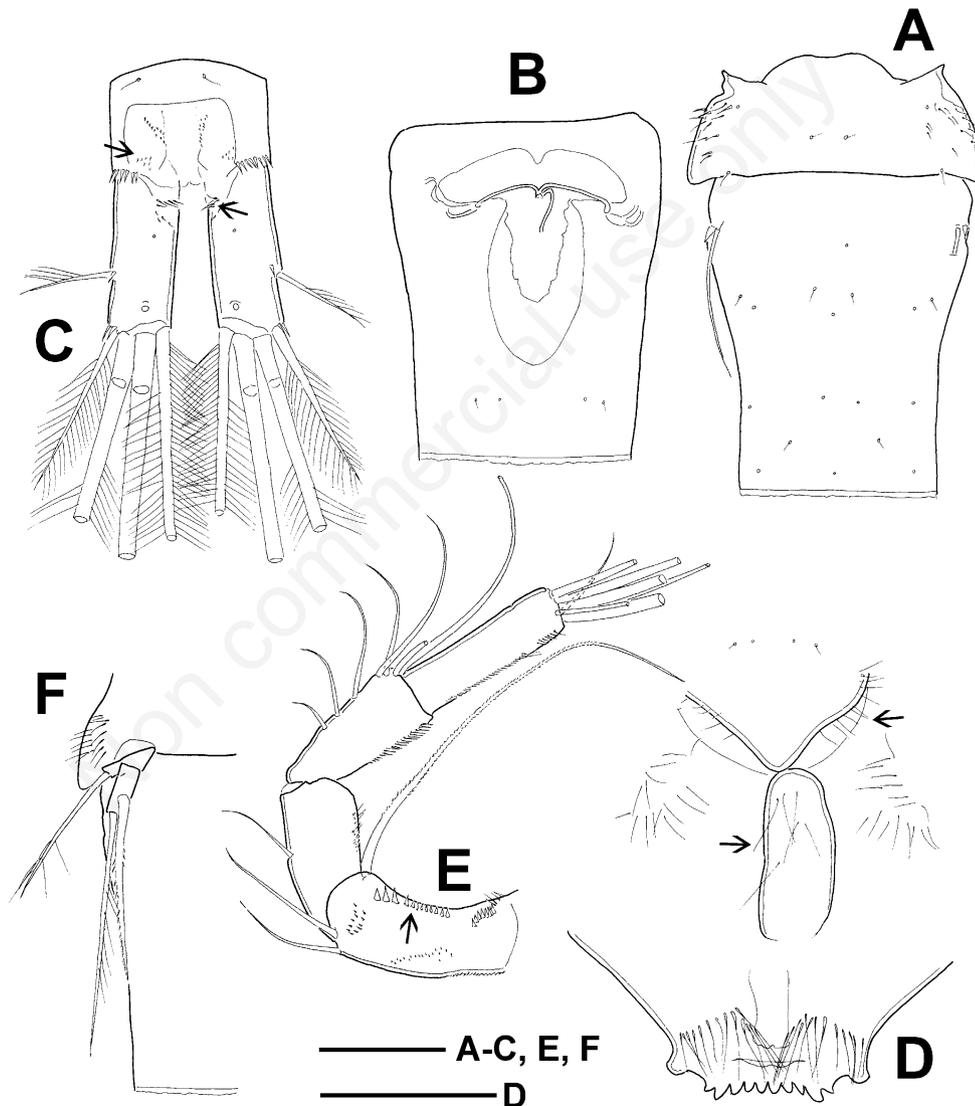


Fig. 7. *Mesocyclops microlasius* Kiefer, 1981, female (L. Paoay, Luzon). A, C, E) show MIZ:5/2013/16, B and F) show MIZ:5/2013/17, and D) shows MIZ:5/2013/18. A) Pediger 5 and genital double-somite, dorsal; B) genital double-somite, ventral; C) anal somite and caudal rami, dorsal (left arrow indicates triangular field of small spinules in hindgut, while right arrow indicates short hair on caudal ramus); D) rostrum, epistoma, and labrum (upper arrow points to hair in vertical cleft, while lower arrow points to hair on epistoma); E) antenna, caudal (arrow indicates longitudinal row of spinules); F) leg 5. Scale bars: 50 μ m.

namese and Mindanao specimens share several other characters as well, therefore we consider them to be conspecific. There are a few features, in which the North Vietnam and Mindanao females seem to be different (cf. intraspecific variation). Most of the qualitative characters differing in these distant populations, however, are intraspecifically variable in the close relatives [surface ornamentation of the antennule and antennal coxobasis (group g) varies within both *M. dissimilis* and *M. woutersi*; female genital structure, transverse canal-like structures form acute or obtuse angle in *M. woutersi*; P4 basipodite, laterofrontal spinules present or absent in *M. ogunus*]. Therefore those differences were given less importance. Nonetheless, with the exception of *M. augusti* n. sp. where the Vietnam and Mindanao females have eight and six pores, respectively, no polymorphism was found in number of the pores posteriorly to P6 (cf. Supplementary Material C) in any taxon included in the present phylogenetic analysis.

It is especially difficult to interpret the morphometric differences (Mindanao 2♀♀, and North Vietnam 2♀♀). Comparisons of the pelagic and littoral populations of *M. dissimilis* in lake Biwa (Japan) revealed significant shifts in the body size and proportions such as the relative length of the leg segments (P4 enp3), caudal rami, and dorsal caudal seta (Hołyńska, 1997), which warned us about the cautious use of the morphometric traits in species identification. We lack strong evidence of a (sub)species-level separation, and the apparent morphological separation of the Mindanao and North Vietnam forms can only be confirmed by the examination of additional material. Also, the Mindanao and North Vietnam findings do not necessarily indicate disjunct distribution until faunistic information on the Philippines (e.g. the Sulu archipelago as a possible dispersal route), Borneo, and Indochinese peninsula are so fragmentary.

Mesocyclops augusti n. sp. is closely related to the *woutersi*-complex coined and defined by Hołyńska (1997, 2000). The group was diagnosed by the characters of the antenna (enp 2 with seven setae; complex spinule ornamentation on the caudal surface of the coxobasis), female genital system (transverse ducts meet at acute angle), and surface ornamentation of P4 coxopodite (spinules of conspicuously different size near proximal margin), and it comprised *M. woutersi*, *M. dissimilis*, *M. parentium* and *M. friendorum*. *Mesocyclops francisci* was hypothesised as the sister of the *woutersi*-complex. A phylogenetic analysis (Hołyńska, 2006b) that included all *Mesocyclops* species (71) showed the *woutersi*-complex *sensu* Hołyńska (2000) para- or polyphyletic rather than monophyletic, while *M. microlasius*, *M. geminus* and *M. ogunus* were united with some members of the *woutersi*-complex in a clade. Our present reconstructions include all the taxa mentioned above, plus some represen-

tatives of three other, relatively closely related groups [Afro-Asian *dussarti*-clade: *M. thermocyclopoides* (SE/E Asia); Afro-Asian *aequatorialis-affinis* clade: *M. affinis* (New Guinea-SE Asia); Australian-South Pacific clade: *M. roberti* (Fiji/Wallis)] as outgroups.

The *unordered* and *scaled* reconstructions and six of the seven shortest trees of the *unscaled* reconstruction show the *woutersi*-complex paraphyletic, yet support monophyly of a predominantly Oriental group (Fig. 11, clade E) comprising: *M. friendorum* (Sulawesi), *M. geminus* (Borneo), *M. microlasius* (Luzon, Mindanao), *M. francisci* (Sumatra, Malaysia Cambodia), *M. parentium* (India, Sri Lanka, Cambodia), *M. woutersi* (Australia, New Guinea, Vanuatu, Laos, Vietnam, Taiwan, South China, Japan, South Korea), *M. dissimilis* [China, Japan, South Korea, Russian Far East (Primorskiy)], and *M. augusti* n. sp. (Mindanao, Vietnam) [occurrence data on Cambodia from Chaicharoen (2011)]. Clade E is supported by at least one apomorphy (Tab. 5) (char 10:0, *joint canal* present). Another derived feature, spinules of unequal size near the proximal margin of P4 coxopodite (char 8:2), also defines this clade in some trees of the *unscaled* run and in most of the *unordered* and *scaled* trees. The character of small spinules in anterior part of proctodeum (char 13:1) as third apomorphy of clade E only shows up in the *unordered* reconstruction. In these reconstructions the unique apomorphy of clade E is the *joint*

Tab. 5. Apomorphies of the clades revealed in phylogenetic reconstructions obtained by applying different coding of the polymorphic characters.

Clades	Unordered [15]	Unscaled [7]	Scaled [3]
A	9 (1>0) 12 (0>1)*	9 (1>0) 12 (0>1)* 16 (2>0)	9 (1>0) 12 (0>1)* 16 (2>0)
B	1(0>1)*	1(0>1)* 11 (1>0)	1(0>1)* 11 (1>0)
C	-	4 (0>1)	4 (0>1)
D	-	6 (0>1) 16 (1>2)	6 (0>1) 16 (1>2)
E	10 (2>0)* 13 (0>1)	10 (2>0)*.°	10 (2>0)*
F	15(0>1)*	-	11 (1>0) 15(0>1)*

-, node was present in some trees, but collapsed in the strict consensus tree. *Unique apomorphies in the group analysed; °clade E was present in six of the seven shortest trees of the unscaled reconstruction. Letters denoting clades refer to the groups indicated in Fig. 11. Only those apomorphic transformations that occur in all shortest trees of a particular reconstruction are listed here. Number of all shortest trees is given in brackets after the name of the reconstruction. For number codes of the characters and character states see Supplementary Material B. Numbers in parentheses show character state transformations.

canal, which is formed by the fusion of the transverse duct-like structures, anteriorly to the copulatory pore. This character state, however, appears in most New World species and also present in several Old World taxa (including the more basal species, e.g. *M. cuttacttae* Dumont et Maas, 1985, *M. rarus* Kiefer, 1981, *M. annae* Kiefer, 1930, *M. splendidus* Lindberg, 1943, *M. salinus* Onabanro, 1957, and *M. brevisetosus* Dussart et Fernando, 1985), which implies that *joint canal* is either a plesiomorphy or a character reversal (apomorphy) in group E. As the outgroups determine the character polarity

and also influence the tree topology, we may need an analysis with larger taxon sampling to verify the diagnostic value of *joint canal* and test the monophyly of group E (this was beyond the goals of this work).

None of the reconstructions supports sister relationships of the two Philippine taxa. Instead, in all analyses the closest relative of *M. augusti* (Mindanao, North Vietnam) is *M. dissimilis* (East Asia), while in all shortest trees of the *unordered* and *scaled* reconstructions and some trees (3 of 7) of the *unscaled* run the sister of *M. microlasius* (Luzon, Mindanao) is *M. geminus* (East Borneo). At

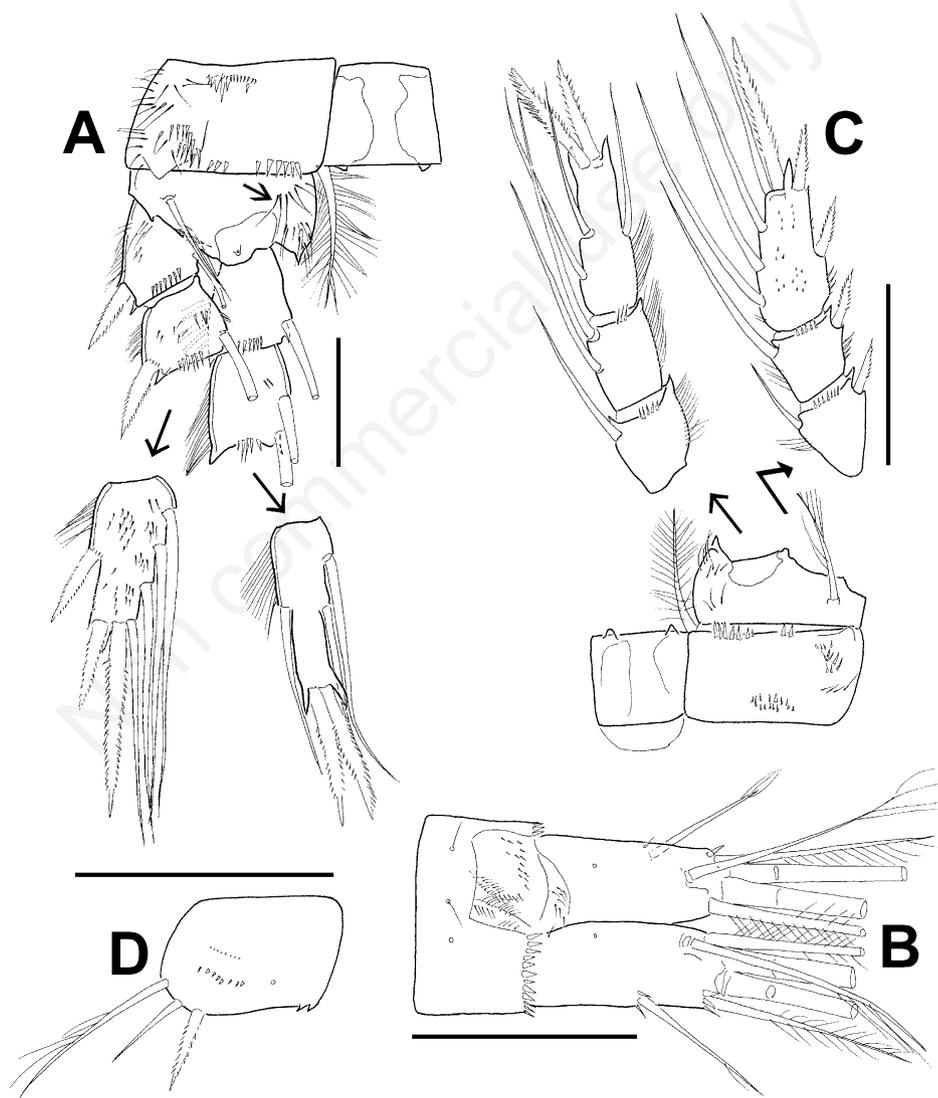


Fig. 8. A) *Mesocyclops microlasius* Kiefer, 1981 (L. Paoay, Luzon): female; *Mesocyclops microlasius* Kiefer, 1981 (L. Paoay, Luzon): male. A) shows MIZ:5/2013/17, B and C) show MIZ:5/2013/19, and D) shows MIZ:5/2013/21. A) leg 4, caudal (short arrow points to row of long medial hair on basipodite, long arrows point to terminal segments of exo- and endopodite); B) anal somite and caudal rami, laterocaudal; C) leg 4, caudal (long arrows indicate exo- and endopodite); D) leg 6. Scale bars: 50 μ m.

least two apomorphies support the *dissimilis-augustus* group (clade A in Fig. 11 and in Tab. 5) (char 9:0, many spinules on lateral margin of medial apical spine of P4 enp3; and char 12:1, eight pores sometimes present posteriorly to P6), while a third apomorphy [char 16:0, spinules present at insertion of lateral (II) caudal setae] also appears in all shortest trees of the *unscaled* and *scaled* reconstructions and in some trees of the *unordered* run. Eight pores posteriorly to P6 is an unique feature of clade A. There are relatively few taxa where this character have been verified, but at least in one species that was not in-

cluded in our analysis, *M. aequatorialis* Kiefer, 1929 (the presumed sister of *M. affinis*), the eight-pore state sometimes occurs. *Mesocyclops augusti* n. sp. differs from *M. dissimilis* in the surface ornamentation of the hindgut in female (long spinules posteriorly present in *M. augusti* yet absent in *M. dissimilis*) (Fig. 2E and 2F vs 2G). There are also four male features that help to distinguish these species: i) the surface ornamentation of the antennular segments (in *M. augusti* spinules present on segment 1 only, while in *M. dissimilis* spinules present on segments 1, and 12-13); ii) length proportions of P6 setae (median

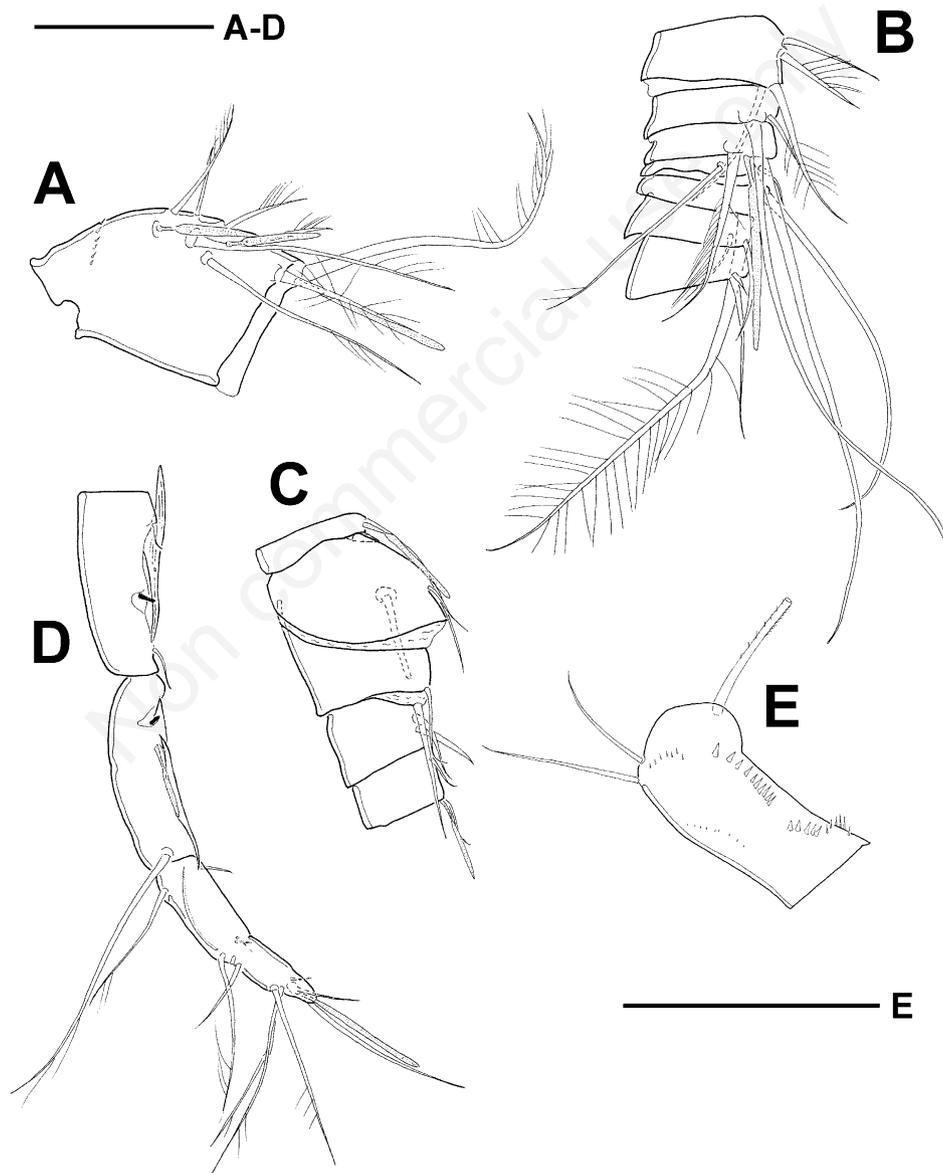


Fig. 9. *Mesocyclops microlasius* Kiefer, 1981, male (L. Paoay, Luzon): antennule, anterior. A-D) show MIZ:5/2013/20, and E) shows MIZ:5/2013/19. A) segment 1; B) segments 2-8; C) segments 9-13; D) segments 14-16; E) antennal coxobasis. Scale bars: 50 μ m.

seta subequal or shorter than medial spine in *M. augusti*, yet min. 1.3 times as long in *M. dissimilis*) (Fig. 6D vs 6B); iii) surface ornamentation of P6 flap (many transverse rows of spinules in *M. augusti*, yet no ornamentation in *M. dissimilis*) (Fig. 6A vs 6B); iv) and lateral pilosity of pediger 5 (short lateral hair in *M. augusti*, no hair in *M. dissimilis*) (Fig. 6A vs 6B).

Clade B (Fig. 11), comprising *M. augusti*, *M. dissimilis* and *M. woutersi* also appears in all the reconstructions. Two apomorphies define this clade in all shortest trees of the *scaled* and *unscaled* run, and in majority (9 of 15) of the trees in the *unordered* run (Tab. 5): spinules can be present on 14th antennular segment (char 1:1), and the pilosity of pediger 5 is reduced to the lateral surface (char 11:0). The presence of spinules on the 14th antennular segment is a unique feature of clade B, and it is a rare character state in the whole genus also. Spinules sometimes present on the 14th antennular segment in *M. aequatorialis*, and always present in the species of the Afro-Asian *dussarti*-clade (but not in *M. thermocycloides* included here).

The *microlasius-geminus* group (clade F in Fig. 11 and Tab. 5) is defined by at least one apomorphy (char 15:1, hair or long spinules present on anterior half of caudal rami). A second (but not unique) apomorphy (char 11:0, pilosity of pediger 5 is restricted to the lateral surface) appears in all trees of the *scaled* run, in majority (9 of 15) of the *unordered* trees, and in three trees of the *unscaled* run where this node shows up. Hair/spinules restricted to anterior half of the caudal rami (unique apomorphy here) only appear in few Old World taxa, *M. pilosus* Kiefer, 1930, *M. insulensis* Dussart, 1982, *M. mariae* Guo, 2000, *M. spinosus* Van de Velde, 1984, *M. shenzhenensis* Guo 2000 and *M. pseudopinosus* Dussart et Fernando 1988. *Mesocyclops microlasius* differs from *M. geminus* in: caudal surface ornamentation of the antennal coxobasis (spinules in group f small in *M. microlasius*, yet large in *M. geminus*); caudal surface ornamentation of P4 coxopodite (spinules of unequal size near proximal margin in *M. microlasius*, yet equal size in *M. geminus*); laterofrontal ornamentation of P4 basipodite (long spinules absent in *M. microlasius*, yet present in *M. geminus*).

The *unscaled* and *scaled* trees and majority (8 of 15) of the trees in the *unordered* run support a *mainland* clade (Fig. 11, clade D), members of which, albeit can also show up in islands that have never been connected to the SE Asian shelf, occur in continental Asia. In most trees with the *mainland* clade (except for one tree in the *unscaled* reconstruction, where *M. geminus* groups with *M. ogunnus* and *M. thermocycloides*) the insular taxa (*M. microlasius*, *M. geminus*, *M. friendorum*) either form a paraphyletic group (basal to *mainland* clade), or constitute a monophyletic group, the sister of the *mainland* clade. Two apomorphies [char 6:1, row of spinules between dis-

tal hair of labrum and epistoma; and char 16:2, spinules absent at implantation of lateral (II) caudal seta] diagnose the *mainland* clade in all trees of the *unscaled* and *scaled* run. From among the eight trees of the *unordered* run where the *mainland* clade appears, in five trees two apomorphies (char 6:1; char 16:2) and in three trees only one apomorphy (char 6:1) supports monophyly of clade D. Nonetheless, to propose a robust hypothesis of the relationship of the *mainland* clade to the insular species, or to answer the question whether the *insular* group would be more basal to the *mainland* group, we need a wider context, *i.e.* an analysis with larger taxon sampling.

Geographic distribution patterns of the limnetic Cyclopidae in the Philippines

Our samplings emphasised the limnetic fauna and our results suggest that interesting taxa may still be found even in this usually less diverse habitat. This is shown with the discovery of two new records including one new species. It also shows how scarce information is on copepods in most Philippine lakes, in spite of their utilisation for local fisheries and aquaculture. Many other lakes and islands have yet to be sampled, which, in time, may yield equally interesting species, and give a more complete picture of the zooplankton fauna of the Philippines.

The endemic *Mesocyclops microlasius* seems to have a wider distribution than previously thought. Our collections reveal that beyond the Manila region (type locality) the species is also present in northern Luzon. The farthest record comes from lake Sebu in Mindanao island (Tuyor and Baay, 2001), yet we could not find the species in our sample (Tab. 4, lake 21). We think that Mindanao occurrence might need further confirmation. Sister relationship of *Mesocyclops microlasius* (Luzon, Mindanao) and *M. geminus* (East Borneo) are in line with the observation made in several primary freshwater fishes, molluscs and crabs in which the Philippine forms (mainly those from the southwestern and southern islands) have their closest relatives in Borneo (Bănărescu, 1992). It is premature to make inferences about the geographic distribution of *M. augusti* sp. n. in the Philippines, yet absence of the species in all the 15 lakes that we sampled in Luzon might indicate that species does not occur in northern Philippines. On the other hand, *M. augusti* sp. n. has been identified from North Vietnam, and its closest relative, *M. dissimilis*, is distributed in East Asia (but not found in Taiwan). Our guess is that *M. augusti* sp. n. might use a southern colonisation route via Borneo between Vietnam and Mindanao.

In contrast, two other cyclopids, *M. thermocycloides* (Luzon and Mindoro) and *T. taihokuensis* (Luzon), have been encountered in the northern islands only, yet scarce sampling in the southern part leave some doubts about the restricted northern distributions of these taxa. At least the study by Tuyor and Baay (2001) reported

M. thermocycloides in Calamba river (Luzon) and lake Mainit (Mindanao). It is possible that some of the previous records of *Mesocyclops leuckarti* (a Palearctic species) in the Philippines (Woltereck *et al.*, 1941; Mamaril Sr. and Fernando, 1978; Mamaril Sr., 1986, 2001) (Tab. 1) may actually refer to *M. thermocycloides*, given the wide distribution of the latter species in Northern Philippines. Also, most localities and lakes where we found *M. thermocycloides* were sites where *M. leuckarti* has been previously recorded from, such as Laguna de Bay and lake Naujan. Based on the widespread occurrence of *M. thermocycloides* among the neigh-

bouring countries such as Indonesia (Flores, Java and Sumatra), Malaysia, Thailand, Cambodia, Vietnam, China and Taiwan (Holyńska *et al.*, 2003; Alekseev and Sanoamuang, 2006; Holyńska and Stoch, 2011; Chaicharoen, 2011), and widespread distribution of the species in Luzon, we think that *M. thermocycloides* is a native species rather than introduced by humans in the Philippines. The distribution of the newly recorded *T. taihokuensis* in the Philippines (Luzon), meanwhile, seems to be restricted to clusters of lakes near one another, as lakes Pandin, Bunot, Mohicap and Palakpakin all located in one town (San Pablo, total area: 214 km²), while lakes

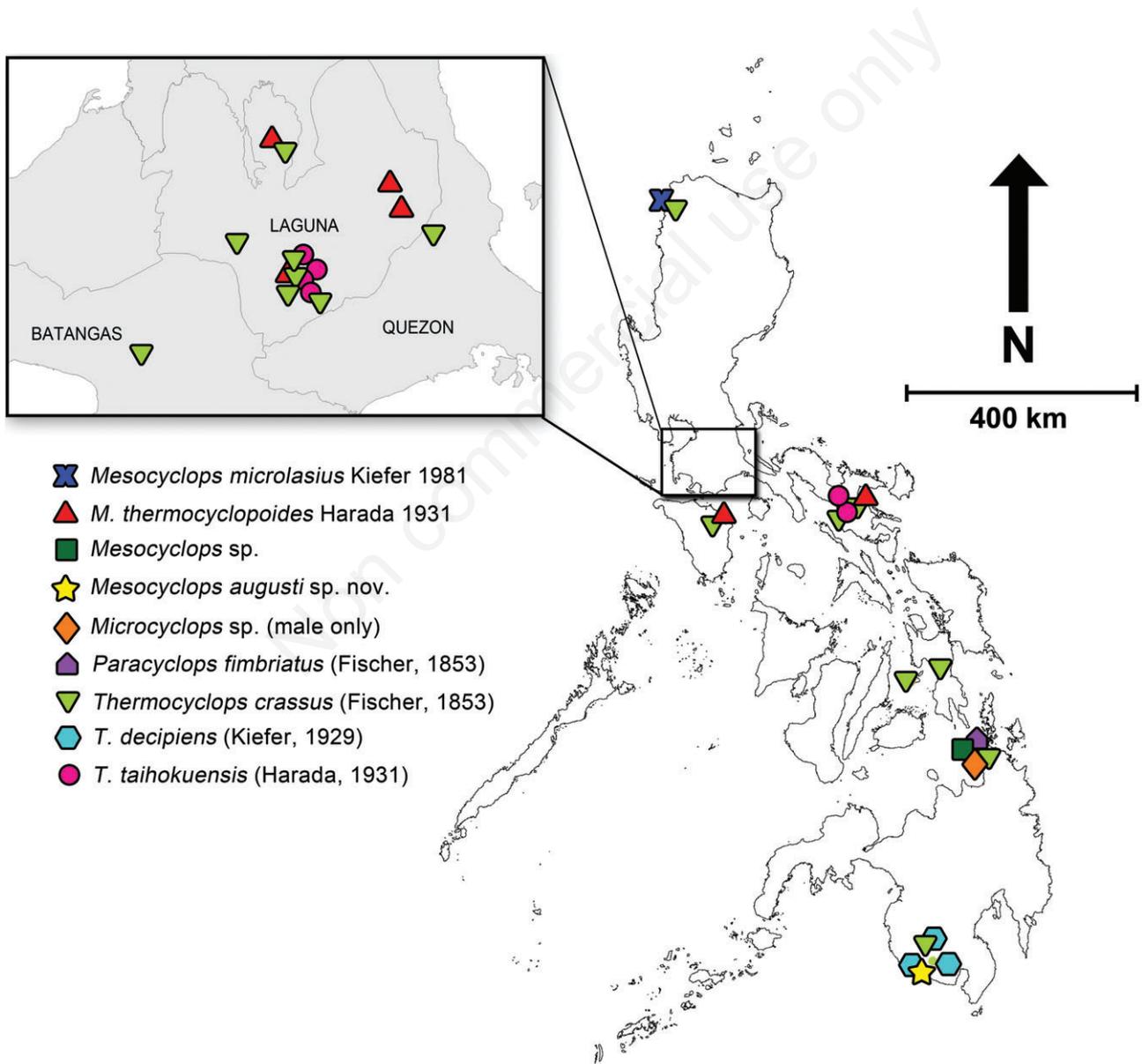


Fig. 10. Distribution map of the nine cyclopoid taxa encountered in the 22 lakes sampled throughout the Philippine archipelago.

Buhi and Baao are approximately 15 km from each other in the province of Camarines Sur. The closest records of East/Central Asian *T. taihokuensis* are those from Vietnam and Taiwan (Mirabdullayev *et al.*, 2003), and we speculate that *T. taihokuensis* reached Luzon from Taiwan.

Colonisation of the northern Philippine Batanes islands from Taiwan has been evidenced in small mammals (shrews) (Esselstyn and Oliveros, 2010).

The ubiquitous nature of *T. crassus* (Old World) in the Philippines is consistent with the results of other studies on

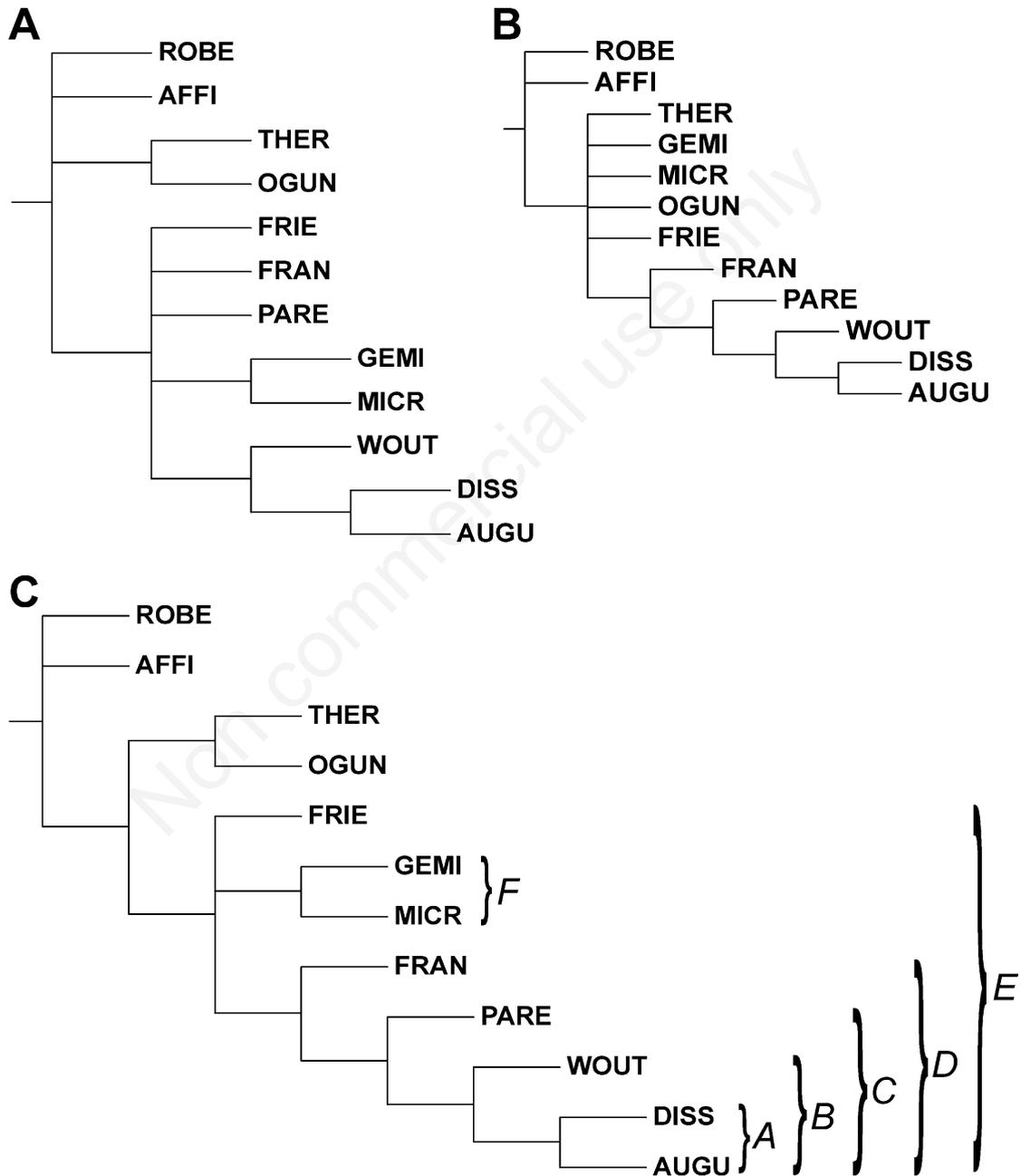


Fig. 11. Strict consensus trees of the parsimony analyses obtained by applying different coding of the polymorphic characters. A) unordered coding [15 shortest trees; length 44; ci: 61; ri: 58]; B) unscaled coding [7 shortest trees, length: 53; ci: 52; ri: 55]; C) scaled coding [3 shortest trees; length 71; ci: 54; ri: 56]. Codes of the taxa are listed under *Comparative material* section in the description of *Mesocyclops augusti* n. sp. (beginning of Results section).

its distribution (Holyńska, 2006a; Chaicharoen *et al.*, 2011). Furthermore, studies in lake Taal have shown how *T. crassus* is the most abundant copepod in the lake compared to calanoids and how this was related to the increased trophic status of the lake from the excessive nutrient inputs in aquaculture areas (Papa and Zafaralla, 2011; Papa *et al.*, 2011).

This is also the second record of *T. decipiens* in Mindanao island, where it has been observed in three lakes within the same locality (South Cotabato). Tuyor and Baay (2001) found *T. decipiens* in lake Mainit, Mindanao, while Holyńska (2006a) reported it from ponds in the town of Dasmariñas (Cavite province, Luzon island). It is not surprising to find more localities with *T. decipiens* in the Philippines (Tab. 1) as it is a widely distributed Pantropical species (Chaicharoen *et al.*, 2011).

We failed to find two species that were also known from limnetic waters in the Philippines. *Thermocyclops wolterecki* Kiefer, 1938 has originally been described from the plankton of lake Lanao (Mindanao), and later reported from lake Pogera in Papua New Guinea (Defaye *et al.*, 1987) and lake La Han in Northeast Thailand (Alekseev and Sanoamuang, 2006). Interestingly, Chaicharoen *et al.* (2011) found the species in small water bodies (canal, stream and temporary pond) in Cambodia. In comparison with the Lanao specimens, the Cambodian females had larger body, shorter caudal setae (V and VII) and slightly different surface ornamentation on the P4 coupler, but the morphology otherwise fit that in the type locality. We suppose that *T. wolterecki* occurs in small waterbodies in the Philippines too, and the small and slender form in lake Lanao is a pelagic ecotype of the species. *Tropocyclops prasinus* (Fischer, 1860) was reported from Luzon, Cebu and Mindanao islands (Tab. 1). The species is recorded from almost every continent, yet recent morphological studies (Lee and Chang, 2007) on the East Asian *T. prasinus*-like forms showed that a few good species with more restricted distribution could be hidden under this name. *Tropocyclops* of the Philippines also needs revision.

In the Philippines, the threat of non-indigenous species taking over native zooplankton fauna has already been observed among calanoid copepods. A Neotropical species, *Arctodiaptomus dorsalis* (Marsh, 1932) was found in most of the lakes sampled in this study. Previously recorded native calanoid copepods have already been displaced by *A. dorsalis* (Papa *et al.*, 2012). Importantly enough, there has been no similar occurrence in the cyclopoid fauna; however, with the presence of aquaculture and its role in the dispersal of non-indigenous zooplankton species (Reid, 2007), in most Philippine lakes the threat still remains.

CONCLUSIONS

Two genera, *Mesocyclops* (4 species) and *Thermocyclops* (4 species), dominate the relatively poor open-water fauna of the lakes in the Philippines (11 species), among

which only one species (*M. microlasius*) seems to be endemic to the archipelago. Our paper currently brings the total number of cyclopoid copepods (including both limnetic and littoral/benthic taxa) known from the Philippines to 18, but more importantly, it highlights the need for more intensive investigations in the small water bodies, paludal and subterranean habitats, which may be home to a significantly richer fauna with higher rate of endemism.

Former phylogenetic analyses that included all species of the genus *Mesocyclops*, and a present reconstruction that was restricted to the Oriental representatives of the genus revealed that: i) all *Mesocyclops* species so far recorded from the Philippines are nested in clades occurring predominantly in the tropical Asian mainland and/or the Greater Sunda islands; ii) the closest relative of *M. augusti* n. sp. (Mindanao, North Vietnam) is *M. dissimilis* (East Asia); and iii) the closest relative of *M. microlasius* (Luzon, Mindanao) is *M. geminus* (East Borneo).

Exploring the species diversity and geographic distribution of Cyclopidae in the Philippines may have implications for human epidemiology as well. The potential use of cyclopoid copepods (*e.g.* *Mesocyclops*), as biological control agents of Dengue-carrying *Aedes* mosquitoes should be considered, as Dengue continues to be one of the leading causes of mortality among Filipinos.

ACKNOWLEDGMENTS

The first author would like to thank D. Tordesillas, H. Li, H. Dumont, J. Briones and B. Han for help in collecting samples from May to November 2011 and University of Santo Tomas undergraduate biology students for sample collection in lakes Paoay and Laguna de Bay in 2006. G. Adorable helped with the sample processing and V. Garcia helped to create the maps. Funds for sample collection were obtained from the Research Center for the Natural and Applied Sciences, University of Santo Tomas, and the Philippine Council for Aquatic and Marine Research and Development. Support from the World Association of Copepodologists to the first author is greatly appreciated for participation in the DEST – Expert-in-Training Program at the Museum and Institute of Zoology, Warsaw, Poland. The programme Southeast Asian – European Year of Science and Technology 2012 European Commission's Seventh Framework Programme for Research and Technological Development (FP7) sponsored the participation of the second author in the FISA workshop.

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