A new cyclopoid copepod from Korean subterranean waters reveals an interesting connection with the Central Asian fauna (Crustacea: Copepoda: Cyclopoida)

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Monchenkocyclops gen. nov. was erected to accommodate *M. changi* sp. nov. from South Korea (type species), *M. mirabdullayevi* sp. nov. from Kazakhstan, *M. biarticulatus* (Monchenko, 1972) comb. nov. from Uzbekistan, and *M. biwensis* (Ishida, 2005) comb. nov. from Japan. The latter species was originally described from surface-water habitats of the ancient Lake Biwa in the genus *Diacyclops* Kiefer, 1927, while two Central Asian species were previously collected from groundwater habitats and assigned to the genus *Acanthocyclops* Kiefer, 1927. *Monchenkocyclops changi* is also found in subterranean waters, and described here in detail. It is morphologically most similar to its Uzbek congener (not to the Japanese one), which rises some interesting zoogeographical questions about the disjunct distribution of this genus. Range fragmentation is a more plausible explanation for this distribution pattern than range expansion, and we emphasize four lines of evidence that support this hypothesis. Four species of *Monchenkocyclops* share not only the same segmentation of the swimming legs, but also the exact same armature formula of all swimming legs, in addition to many other morphological characters, such as the caudal rami shape and armature, absence of exopod on the antenna, similar shape of the seminal receptacle, fifth leg, etc. They can be distinguished mostly by the relative length of different armature elements, such as the innermost terminal caudal setae, and inner setae and apical spines on the third endopodal segment of the fourth leg. A dichotomous key to species is provided.

Keywords: copepod, interstitial, stygofauna, taxonomy, zoogeography

INTRODUCTION

Freshwater cyclopoids in Korea were studied previously predominantly in surface-water habitats, with 50 species recorded so far (Chang, 2009). Only one species, *Acanthocyclops orientalis* Borutzky, 1966, has been reported as an obligate stygobiont, and about six others as stygophiles. In the course of a research project aimed at uncovering Korean invertebrate diversity, and led by the National Institute of Biological Resources (NIBR), subterranean waters were sampled throughout South Korea and identification of cyclopoid copepods was entrusted to the senior author. In one of the river interstitial samples, a new species of the genus *Acanthocyclops* Kiefer, 1927 was discovered, morphologically remarkably similar to *A. biarticulatus* Moncheno, 1972. The latter species was described only from females from subterranean waters in Uzbekistan by Monchenko (1972), and subsequently re-

described also from subterranean habitats in Kazakhstan by Mirabdullayev and Kuzmetov (1997). Mirabdullayev and Kuzmetov (1997) also provided the first description of the male and noted some morphological differences between the Uzbek and Kazakh populations, which they attributed to intraspecific variability. They also noted that the structure of the fifth leg of the Kazakh population is such that it can be attributed both to the genus *Acanthocyclops* and *Diacyclops* Kiefer, 1927, resulting in the difficulty in separating these two genera.

In addition to the description of the Korean new species, we describe here the Kazakh population of *A. biarticulatus* as a new species. We erect a new genus to accommodate these two new species, as well as *Acanthocyclops biarticulatus* from Uzbekistan and *Diacyclops biwensis* Ishida, 2005 from Japan. The latter species was described from surface-waters of the ancient Lake Biwa by Ishida (2005), who was not aware of the publications by Monchenko (1972) or Mirabdullayev and Kuzmetov (1997).

Ishida only compared *D. biwensis* with members of the genus *Diacyclops*, noting its isolated position due to the unusual swimming legs segmentation.

Diacyclops and *Acanthocyclops* are the largest and fourth largest genera of the subfamily Cyclopinae Rafinesque, 1815 respectively (see Boxshall and Halsey, 2004; Walter and Boxshall, 2012), with a long history of taxonomic problems (Karanovic, 2005). Although they are both valid, and their type species are surrounded by large flocks of closely related congeners, unfortunately, both served as taxonomic repositories right from their initial erection as subgenera of the genus *Cyclops* Müller, 1785 by Kiefer (1927). For example, Kiefer (1927) noticed two distinct groups of species within *Diacyclops*: one containing *D. bicuspidatus* (Claus, 1857) [type species], *D. bisetosus* (Rehberg, 1880), *D. crassicaudis* (Sars, 1863), and some others; and the other group including species with a higher degree of appendage oligomerization, like *D. languidus* (Sars, 1863), *D. languidoides* (Lilljeborg, 1901), and *D. stygius* (Chappuis, 1924). Kiefer (1928) was aware of the polyphyletic nature of this genus, which is obvious from his proposed phylogenetic tree (p. 547). Reid and Strayer (1994) noted that the diagnosis of this genus is so broad that it is effectively based on the fifth leg structure only. The genus *Acanthocyclops* shows these problems less obviously due to its smaller size (Monchenko and von Vaupel Klein, 1999), but it is also ill defined and many species were transferred back and forth between *Acanthocyclops* and *Diacyclops* numerous times (see Morton, 1985; Pesce, 1996; Pandourski, 1997; Dussart and Defaye, 2006). Despite that, both genera continued to be repositories for all cyclopoids with even superficially similar fifth leg, a character that was considered probably plesiomorphic by Karanovic (2005; 2006). Ferrari (1991) was probably wrong when he suggested that *Diacyclops* and *Acanthocyclops* belong to two different monophyletic groups of cyclopoids, as he grouped *Acanthocyclops* with *Eucyclops* Claus, 1893 and *Ectocylops* Brady, 1904, both of which belong to a completely different subfamily, and subfamiliar division of Cyclopidae is well supported both by morphological and molecular evidence (see, for example, Ferrari, 1998; Karanovic and Krajicek, 2012a). A proper revision of the *Diacyclops/Acanthocyclops* group would require redescriptions of almost 200 species, not counting the evidence of cryptic speciation in some of the widely distributed taxa (Monchenko, 2000), which seems to be a common phenomenon in freshwater cyclopoids (Karanovic and Krajicek, 2012a). Some recent molecular work suggested that even a well-defined morphological group of the genus *Diacyclops*, within subterranean waters of a well-defined Australian region could be polyphyletic (Karanovic and Krajicek, 2012b). Unfortunately, most of the species of *Acanthocyclops* and *Diacyclops* were described from subter-

ranean habitats, from very few specimens, and for some the types are no longer existent, which all makes a comprehensive revision less plausible. Some initial attempts, however, have been made to separate obviously unrelated species into newly established genera (Lescher-Moutoue, 1976; Reid *et al.*, 1999; Reid and Ishida, 2000; Karanovic, 2000; 2005), and this paper follows the same approach.

MATERIALS AND METHODS

All specimens of the Korean new species were collected by staff of the National Institute of Biological Resources (NIBR) by the Karaman-Chappuis method, i.e. digging a pit in the sandy sediment and decanting the water that drains in though a plankton hand-net (mesh size 38 μm). Animals were fixed in 99% ethanol. Locality data and number of specimens are given in the type material section of the new species below, and all types are deposited in the National Institute of Biological Resources.

Specimens were dissected and mounted on microscope slides in Faure's medium, which was prepared following the procedure discussed by Stock and von Vaupel Klein (1996), and dissected appendages were then covered by a coverslip. For the urosome or the entire animal two human hairs were mounted between the slide and coverslip, so the parts would not be compressed. By manipulating the coverslip carefully by hand, the whole animal or a particular appendage could be positioned in different aspects, making possible the observation of morphological details. During the examination water slowly evaporates and appendages eventually remained in a completely dry Faure's medium, ready for long term depositing. All line drawings were prepared using a drawing tube attached to a Leica MB2500 phase-interference compound microscope, with N-PLAN (5x, 10x, 20x, 40x and 63x dry) or PL FLUOTAR (100x oil) objectives. Specimens that were not drawn were examined in propylene glycol and, after examination, were again preserved in 99.9% ethanol. Specimens for the scanning electron micrography were dehydrated in progressive ethanol concentrations, transferred into pure isoamyl-acetate, critical-point dried, mounted on stubs, coated in gold, and observed under a HITACHI S-2380N microscope on the in-lens detector, with accelerating voltage of 8 kV; black and white photographs were taken on film (Kodak Tri-X 400 pro) and subsequently scanned.

Morphological terminology follows Huys and Boxshall (1991), except for the caudal ramus setae numbering and small differences in the spelling of some appendages (antennula, mandibula, maxillula instead of antennule, mandible, maxillule), as an attempt to standardise the terminology for homologous appendages in different crusta-

cean groups. Biospeleological terminology follows Humphreys (2000). Sensilla and pores on all somites (body segments) were numbered consecutively with Arabic numerals from anterior to posterior part of the body and from dorsal to ventral side, to aid recognition of serially homologous structures and future comparisons with other species; they are not intended as a novel terminology.

SYSTEMATICS

Order Cyclopoida Rafinesque, 1815
Family Cyclopidae Rafinesque, 1815
Sybfamily Cyclopinae Rafinesque, 1815
Genus *Monchenkocyclops* gen. nov.

Diagnosis. Body slender, cyclopiform. Integument weakly sclerotized, smooth, without cuticular pits or cuticular windows, with numerous sensilla and pores. Female genital double-somite large swollen antero-ventrally, widest at first third, with larger anterior part of seminal receptacle and small posterior part; copulatory pore situated at about midlength; ovipores situated dorsolaterally at 2/5 of double-somite length. Anal somite with short medial cleft, and with small and short anal operculum small, not reaching posterior margin of anal somite. Caudal rami cylindrical, parallel, inserted close to each other, from 2.5 to 3.2 times as long as wide and twice as long as anal somite; principal terminal setae with breaking planes, dorsal seta from almost as long as ramus to half as long, outermost terminal seta about 0.7 times as long as ramus, innermost terminal seta shorter or longer than outermost terminal one. Female antennula 11-segmented or 12-segmented, with armature formula 8.4.8 (2.6).4.2.2.3.2+ae. 2.3.7+ae. Male antennula strongly prehensile and digeniculate, 17-segmented, with armature formula 8+3ae.4.2.2 +ae.2.2.2.2.2+ae.2.2.2.2+ae.2.1+ae.4.8+ae. Antenna five-segmented, without exopod, with armature 2.1.9(8). 7. Labrum with two short rows of slender spinules on anterior surface, and ten to 12 sharp teeth between produced and sharply and inwardly pointed lateral corners on cutting edge. Mandibula cutting edge with several slender spinules on anterior surface, eight apical teeth, and dorsalmost bipinnate seta; palp with two long and plumose and one short and smooth setae. Maxillula with four distal spines and six medial elements; palp two-segmented, armed with seven setae. Maxilla five-segmented, with armature formula 2.3.2.2.3. Maxilliped four-segmented, with armature formula 2(3).2.1.3. All swimming legs with three-segmented exopods and two-segmented endopods; first and second exopodal segments of all legs with inner seta and outer spine; first endopodal segment of all legs with inner seta; third exopodal segment spine formula 2.3.3.3 and setal formula 4.4.4.4; second endopodal

segment spine formula 1.1.1.2 and setal formula 5.5.6.5 (4); inner apical spine on second endopodal segment of fourth leg longer than outer apical spine; coxae of all legs with inner seta; bases of all legs with outer seta, basis of first leg additionally armed with stout inner spine. Fifth leg inserted ventro-laterally, small, two-segmented; first segment half as long as greatest width, with single outer slender seta; second segment longer than first and about 1.5 times as long as wide, with apical long seta and subapical inner spine; subapical spine shorter than second segment. Female sixth leg small cuticular plate covering ovipore, with two short and smooth spines and outermost longer and pinnate seta. Male sixth leg larger cuticular plate, with inner spine and two setae on outer distal corner; outermost seta more than twice as long as inner seta and more than three times as long as innermost spine.
Type species. *Monchenkocyclops changi* sp. nov.
Other species. *Monchenkocyclops mirabdullayevi* sp. nov.; *Acanthocyclops biarticulatus* Monchenko, 1972; *Diacyclops biwensis* Ishida, 2005.
Etymology. The new genus is named in honour of Prof. Vladislav I. Monchenko (National Academy of Sciences, Kiev, Ukraine), who described the first species currently included in the genus. His surname is prefixed to the existing generic name *Cyclops* Müller, 1785.

Monchenkocyclops changi sp. nov.
(Figs. 1-8)

Type locality. South Korea, Gangwondo region, Pyeongchang city, Jinbu town, Odae stream, 37° 36′43.5″N 128° 33′09.2″E, 516 m a.s.l., interstitial water from sandy bank.
Type material. Holotype female dissected on two slides (NIBRIV0000232646). Allotype male also dissected on two slides (NIBRIV0000232647). Other paratypes are one male and two females on one SEM stub (NIBRIV00 00232648), one female dissected on one slide (NIBRIV 0000232649); all collected at type locality; leg. J.-L. Cho, 24 April 2010.
Etymology. The new species is named in honour of Prof. Cheon Young Chang (Daegu University, Korea), in recognition of his enormous contribution to our knowledge of freshwater copepods in Korea. The name is a noun in the genitive singular.
Description. Female (based on holotype and three paratypes). Total body length, measured from tip of rostrum to posterior margin of caudal rami (excluding caudal setae), from 789 to 796 μm (792 μm in holotype). Preserved specimens colourless; no live specimens observed. Integument weakly sclerotized, smooth, without cuticular pits or cuticular windows. Surface ornamentation of somites consisting of 111 pairs and 12 unpaired (mid-dorsal) pores and sensilla (numbered with Arabic numerals consecutively from anterior to posterior end of body, and from
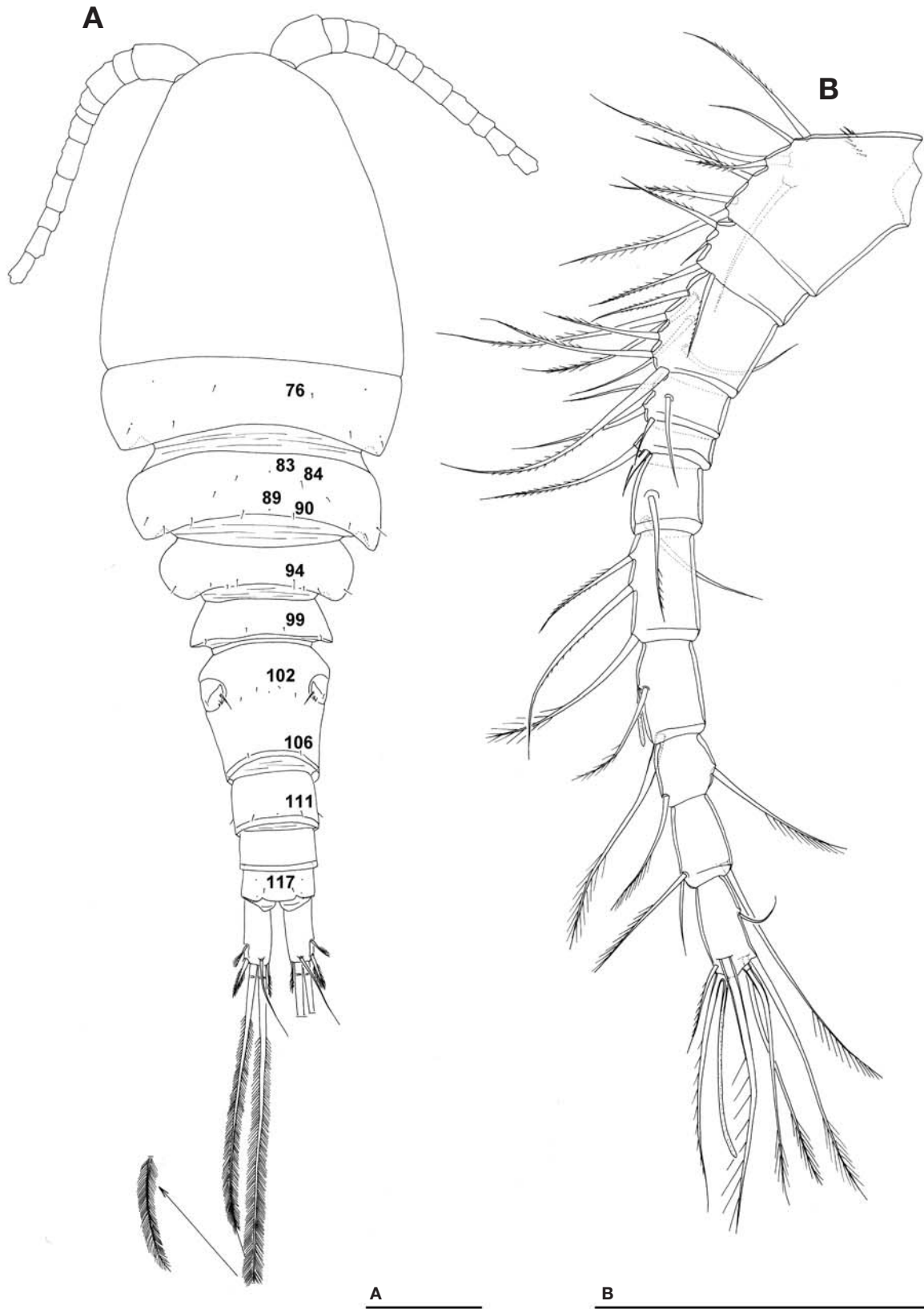
Fig. 1. *Monchenkocyclops changi* gen. et sp. nov., holotype female: A. habitus, dorsal view. B. antennula, dorsal view. Arabic numerals indicating sensilla and pores consecutively from anterior to posterior end of body, and from dorsal to ventral side (excluding appendages; those on cephalothorax not presented). Scale bars 100 μm.
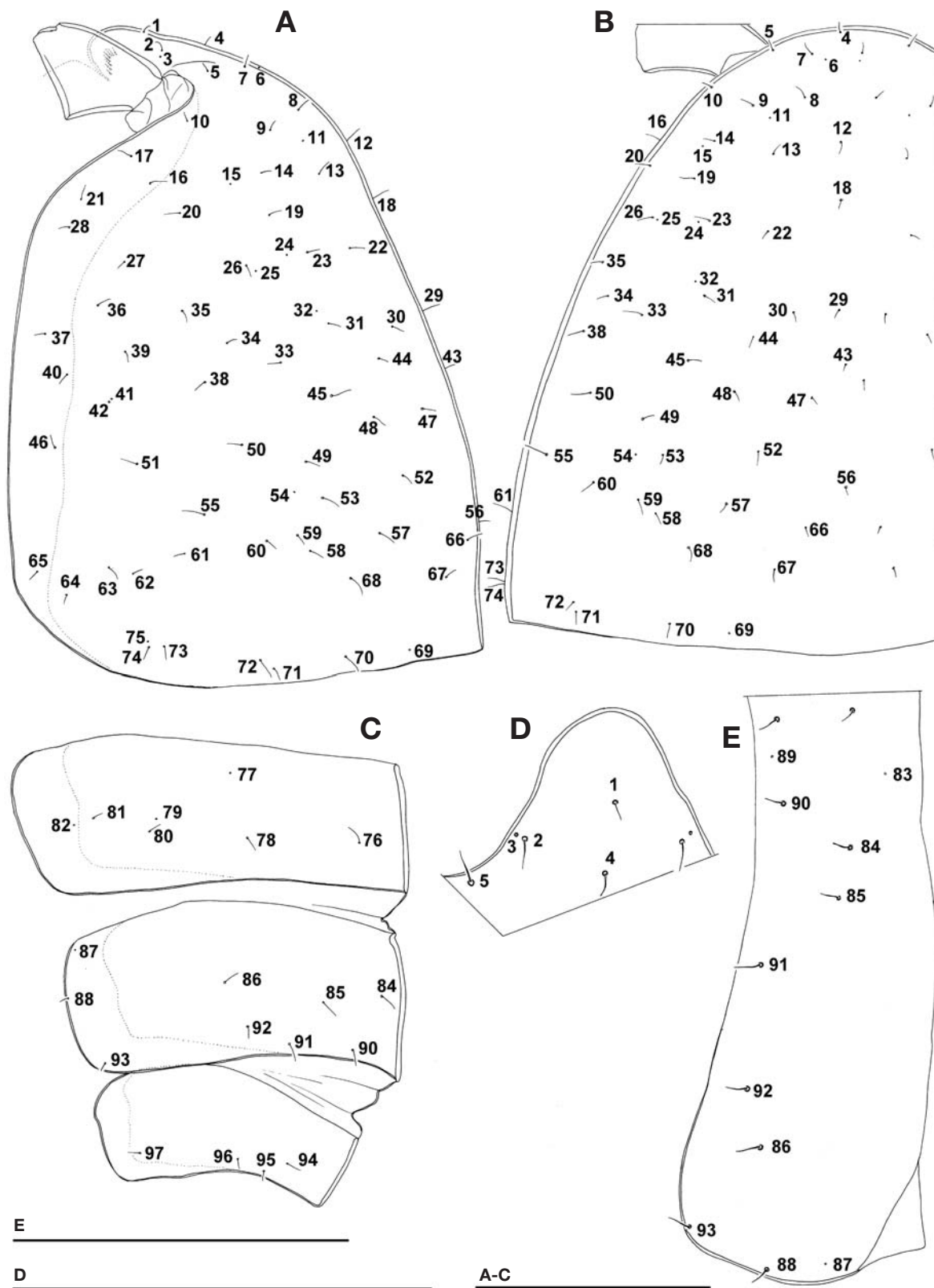
Fig. 2. *Monchenkocyclops changi* gen. et sp. nov., holotype female: A. cephalothoracic shield, lateral view. B. cephalothorax, dorsal view. C. pleurons of free prosomites, lateral view. D. rostrum, dissected and flattened, original anterior view. E. pleuron of second free prosomite (third pedigerous somite), dissected and flattened. Arabic numerals indicating sensilla and pores consecutively from anterior to posterior end of body, and from dorsal to ventral side (excluding appendages). Scale bars 100 μm.

dorsal to ventral side in Figs. 1A, 2A-E, 3A, B, 4A); no spinules except on anal somite, caudal rami, and appendages. Habitus (Fig. 1A) relatively robust, not dorso-ventrally compressed, with prosome/urosome ratio 1.5 and greatest width in dorsal view at posterior end of cephalothorax. Body length/width ratio about three (dorsal view); cephalothorax 2.3 times as wide as genital double-somite. Free pedigerous somites without lateral or dorsal expansions, all connected with well developed arthrodial membranes, and with narrow and smooth hyaline fringes. Pleural areas of cephalothorax and free pedigerous somites relatively well developed, covering insertions of cephalic appendages and praecoxae and partly coxae of swimming legs in lateral view.

Rostrum (Fig. 2D) well developed, membranous, not demarcated at base, broadly rounded and furnished with single central sensilla frontally (no. 1) and one pair of sensilla (no. 2) and pores (no. 3) at its base; latter probably marking boundary between cephalothorax and rostrum.

Cephalothorax (Figs. 1A, 2A, B) as long as its greatest width (dorsal view), much narrower at anterior part and nicely oval; representing 34% of total body length. Surface of cephalic shield ornamented with six unpaired dorsal sensilla (nos. 4, 12, 18, 29, 43, 56) and 66 pairs of long sensilla and small cuticular pores (nos. 4-11, 13-17, 19-28, 30-42, 44-55, 57-75); pores and sensilla 56-75 belong to first pedigerous somite, incorporated into cephalothorax.

Second pedigerous (first free) somite (Figs. 1A, 2C) relatively short, ornamented with four pairs of large sensilla (nos. 76, 78, 80, 81) and three pairs of cuticular pores pores (nos. 77, 79, 82); dorsal pair of sensilla no. 76 probably serially homologous to pair no. 67 on first pedigerous somite, and perhaps pairs no. 78 and no. 70 also serially homologous; others serially homologous pairs much more difficult to reconise.

Third pedigerous somite (Figs. 1A, 2C, E) slightly longer than second and significantly narrower in dorsal view, ornamented with two dorsal unpaired pores (nos. 83, 89), eight pairs of large sensilla (nos. 84-86, 88, 90-93), and one pair of lateral pores (no. 87); recognising serially homologous pairs not easy, but probably sensilla pair no. 84 serially homologous to pair no. 76 on second pedigerous somite.

Fourth pedigerous somite (Figs. 1A, 2C) significantly shorter and narrower than third, ornamented only with four pairs of large sensilla (nos. 94-97); recognising serially homologous pairs much easier than with two previous prosomites (94=90, 95=91, 96=92, 97=93).

Fifth pedigerous (first urosomal) somite (Figs. 3A, B, 4A) short, significantly narrower than fourth pedigerous somite and only slightly wider than genital double-somite in dorsal view, ornamented with one pair of pores (no. 98) and two pairs of large dorsal sensilla (nos. 99, 100); re-

cognising serially homologous pairs not as easy as with two previous somites, but probably 99=94 and 100=96; hyaline fringe smooth and very narrow.

Genital double-somite (Figs. 3A, B, 4A) large, with deep lateral recesses at level of sixth legs and swollen antero-ventrally, widest at first third of its length and gradually tapering posteriorly, about 1.2 times as wide as long (dorsal view), ornamented with one unpaired central dorsal pore (no. 101), two pairs of central dorsal sensilla (nos. 102, 103), one pair of ventro-lateral central pores (no. 104), one unpaired posterior dorsal pore (no. 105), two pairs of posterior sensilla (nos. 106, 108), and two pairs of vento-lateral posterior pores (nos. 107, 109); dorsal sensilla probably serially homologous to those on fifth pedigerous somite (i.e. 102=99, 103=100), but recognising serial homologies of posterior sensilla and pores much harder (perhaps 105=101, 106=103); hyaline fringe deeply and irregularly serrated. Copulatory pore very small, ovoid, situated at about midlength of double-somite ventrally; copulatory duct narrow, siphon-shaped, weakly sclerotized. Seminal receptacle with relatively large anterior expansion and much smaller posterior expansion, representing 49% of double-somite's length; oviducts broad and weakly sclerotized. Ovipores situated dorsolaterally at 2/5 of double-somite length, covered by reduced sixth legs.

Third (ancestral fourth) urosomite (Figs. 3A, B, 4A) relatively short, about 1.7 times as wide as long and only 0.4 times as long as genital double-somite in dorsal view, with also deeply and irregularly serrated hyaline fringe, ornamented with unpaired dorsal posterior pore (no. 110), two pairs of dorso-lateral large sensilla (nos. 111, 112), and two pairs of vento-lateral posterior pores (nos. 113, 114); serially homologous pores and sensilla relatively easy to recognize on genital double-somite (110=105, 111=106, 112=108, 113=107 (?), 114=109).

Fourth (preanal) urosomite (Figs. 3A, B, 4A, 8A) narrower and shorter than third, with also deeply and irregularly serrated hyaline fringe, ornamented only with pair of lateral pores (no. 115) of uncertain serial homology.

Anal somite (Figs. 3A, B, 4A, 8A) slightly narrower and shorter than preanal, with short medial cleft, ornamented with one pair of large dorsal sensilla (no. 117), two pairs of small dorsal pores (nos. 116, 118), one pair of small ventral pores (no. 119), and continous posterior row of large spinules. Anal sinus smooth. Anal operculum small, short, slightly convex, not reaching posterior margin of anal somite, representing 47% of anal somite's width.

Caudal rami (Figs. 3A, B, 4A, 8A) cylindrical, parallel, inserted close to each other, approximately 2.6 times as long as wide (ventral view) and twice as long as anal somite; armed with six setae (one dorsal, one lateral, and four terminal); ornamented with one dorsal pore in ante-
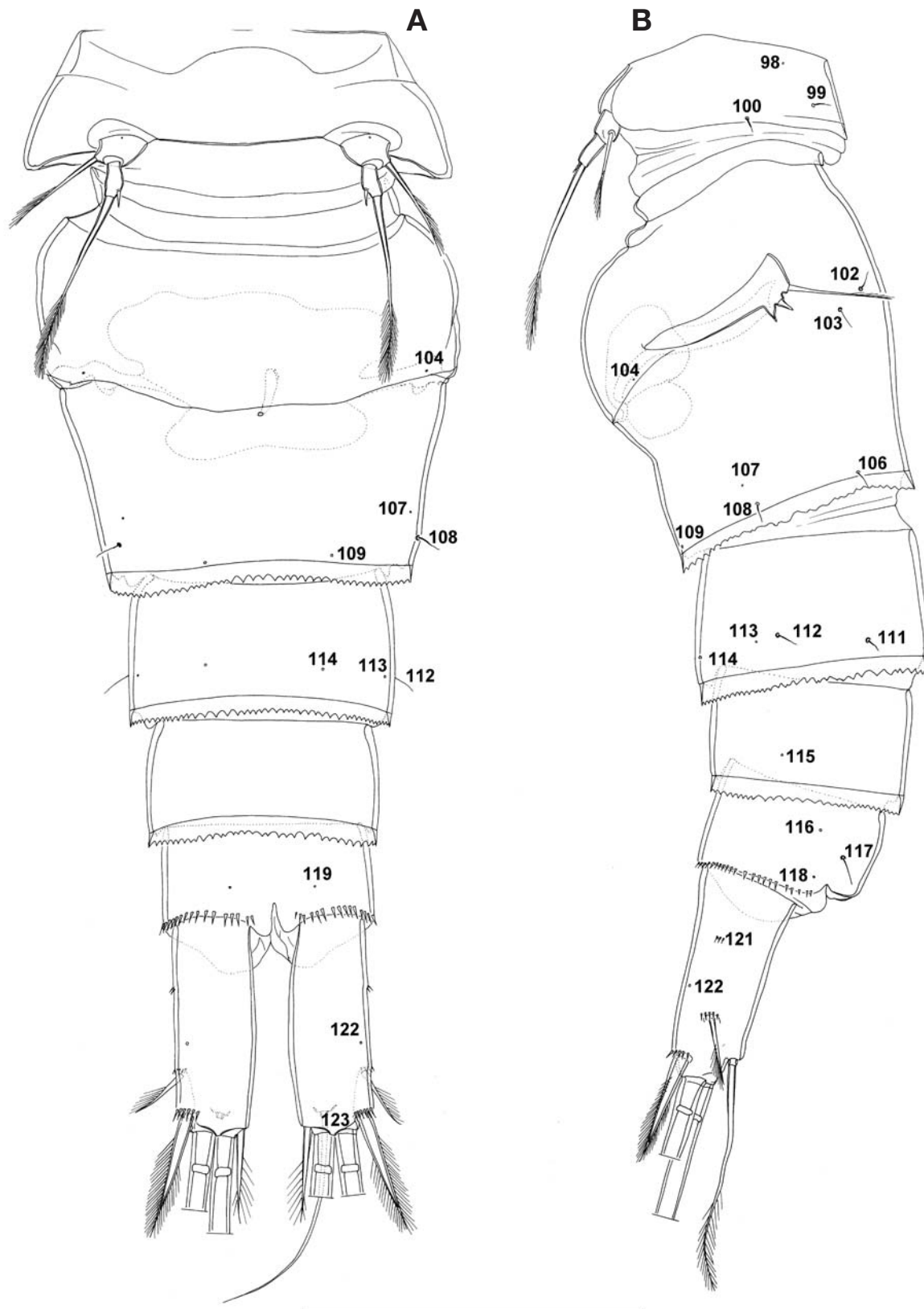
Fig. 3. *Monchenkocyclops changi* gen. et sp. nov., holotype female: A. urosome, ventral view. B. urosome, lateral view. Arabic numerals indicating sensilla and pores consecutively from anterior to posterior end of body, and from dorsal to ventral side (excluding appendages). Scale bars 100 μm.
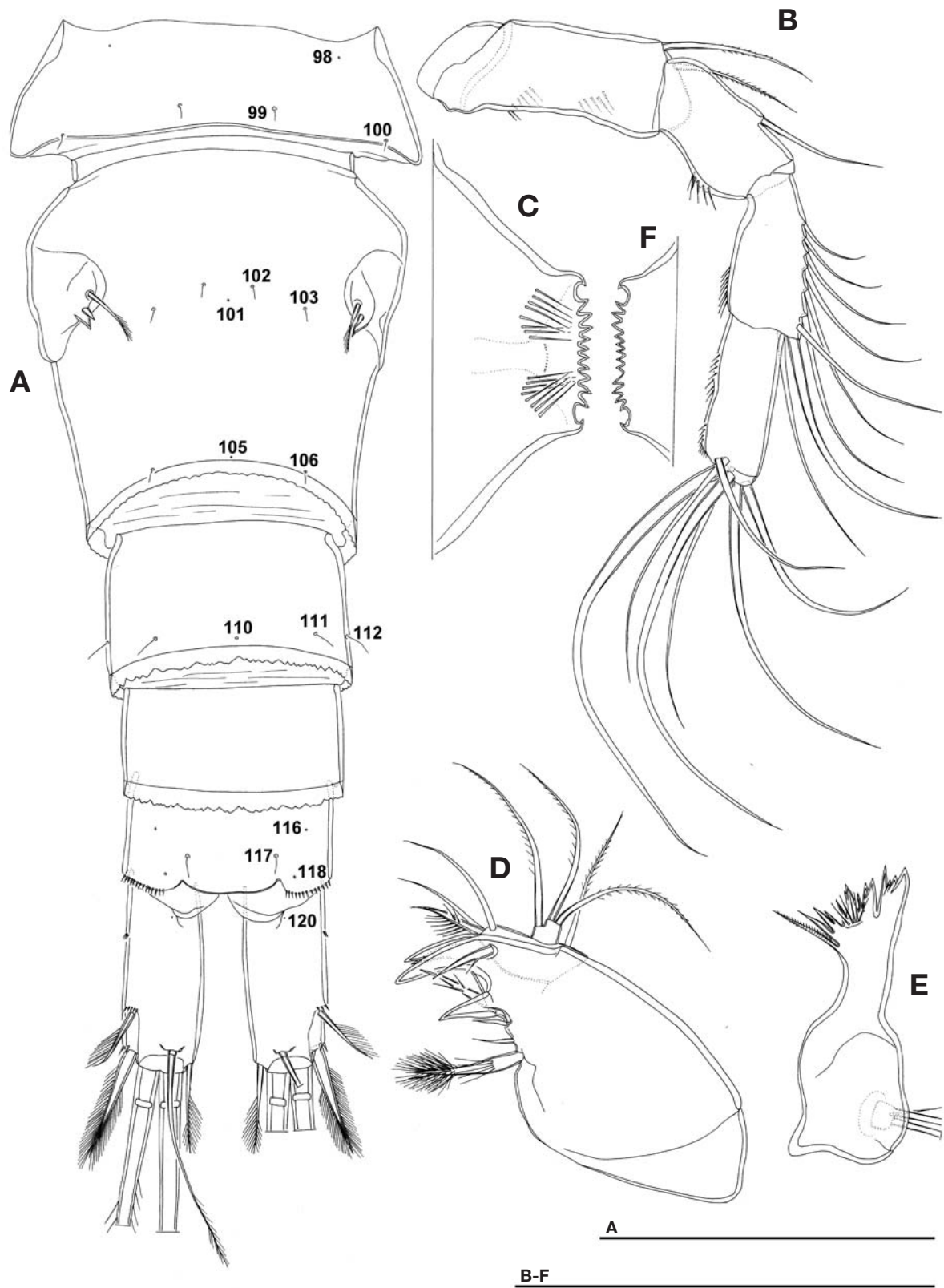
Fig. 4. *Monchenkocyclops changi* gen. et sp. nov., A-E. holotype female. F. paratype female. A. urosome, dorsal view. B. antenna, dorsal view. C. labrum, anterior view. D. maxillula, posterior view. E. mandibula, anterior view. F. cutting edge of labrum, anterior view. Arabic numerals indicating sensilla and pores consecutively from anterior to posterior end of body, and from dorsal to ventral side (excluding appendages). Scale bars 100 μm.

rior part (no. 120), two lateral cuticular pores (nos. 121, 122), one pore on tip of protuberance on distal margin ventrally between two terminal setae (no. 123), rows of small spinules at base of lateral setae, and short row of minute spinules partly covering proximal lateral pore. Dorsal seta about 1.14 times as long as ramus, inserted at 5/6 of ramus' length, biarticulate at base (inserted on small pseudo-joint) and pinnate at distal part. Lateral seta inserted at 2/3 of ramus' length, 0.3 times as long as dorsal seta, unipinnate laterally and uniarticulate at base. Outermost terminal seta stout, spiniform, 0.6 times as long as ramus, densely bipinnate. Innermost terminal (accessory) seta short and slender, sparsely bipinnate, 0.75 times as long as outermost terminal seta. Principal terminal setae with breaking planes, bipinnate; inner principal terminal seta about 1.5 times as long as outer one and nearly seven times as long as caudal rami.

Antennula (Fig. 1B) 11-segmented, slightly curved along caudal margin, directed postero-laterally, not reaching posterior margin of cephalothoracic shield, ornamented just with arched proximo-ventral row of spinules on first segment (no pits or other integumental structures), with armature formula as follows (ae=aesthetasc): 8.4.8.4.2.2.3.2+ae.2.3.7+ae. Only one terminal seta on ultimate segment biarticulating on basal part and most setae sparsely pinnate at distal end; both aesthetascs very slender; aesthetasc on eight segment reaching posterior margin in length. One seta on fifth segment spiniform and short; all other setae slender; one apical seta on eleventh segment fused basally to aesthetasc; second, fourth, and eleventh segments with one short seta, all other setae well developed. Length ratio of antennular segments, from proximal end and along caudal margin, 1:0.4:0.7:0.4:0.3:0.5:0.9:0.8:0.5:0.7:0.8.

Antenna (Fig. 4B) five-segmented, strongly curved along caudal margin, comprising very short coxa, much longer basis and three-segmented endopod. Coxa without armature or ornamentation, about half as long as wide. Basis cylindrical, 2.1 times as long as wide, ornamented with two short, diagonal rows of spinules on ventral surface, armed with two subequal pinnate setae close on distal inner corner (exopodal seta absent). First endopodal segment narrower at basal part but also generally cyclindrical, 1.8 times as long as wide and 0.8 times as long as basis, with inner smooth seta at 2/3 and patch of spinules along caudal margin. Second endopodal segment also with narrow basal part and twice as long as wide, about as long as first endopodal, bearing nine smooth setae along inner margin (which progressively longer from proximal to distal part), ornamented with one row of spinules along caudal margin. Third endopodal segment cylindrical, 2.4 times as long as wide and as long as second endopodal segment, ornamented with two rows of slender spinules along caudal margin, armed with seven smooth

apical setae (four of them strong and geniculate).

Labrum (Fig. 4C, F) relatively large trapezoidal plate, with mascular base and strongly sclerotised distal margin (cutting edge), ornamented with two arched, short rows of eight long and slender spinules each on anterior surface, and central row of minute spinules between them. Cutting edge almost straight, with ten to 12 large and sharp teeth between produced and sharply and inwardly pointed lateral corners.

Mandibula (Fig. 3E, F) composed of coxa and small palp. Coxal gnathobase cutting edge with five slender spinules on anterior surface, eight apical teeth, and dorsalmost bipinnate seta; ventralmost tooth strongest and quadricuspidate, second and fourth teeth from ventral side bicuspidate, all other teeth unicuspidate; three dorsalmost simple teeth partly fused basally and progressively longer from ventral to dorsal. Palp twice as wide as long, unornamented, armed with three apical setae: two long and plumose and one short and smooth; plumose setae subequal in length, directed posteriorly, nearly reaching posterior margin of cephalic shield.

Maxillula (Fig. 4D) composed of praecoxa and two-segmented palp, unornamented. Praecoxal arthrite bearing four very strong distal spines (three smooth, blunt and fused at base; one distinct at base, sharp and with single proximal spinule) and six medial elements (proximalmost one longest and plumose, two distal-most ones with large and strong, three in middle small and slender). Palp composed of coxobasis and one-segmented endopod. Coxobasis with slender proximal seta (probably representing exopod) and three medial setae (two slender and smooth, one strong and bipinnate). Endopod with three slender and pinnate setae.

Maxilla (Figs. 5A) five-segmented but praecoxa partly fused to coxa on anterior surface, unornamented. Proximal endite of praecoxa robust, armed with two subequal, sparsely bipinnate setae; distal endite small, unarmed. Proximal endite of coxa with one bipinnate seta; distal endite highly mobile, elongated and armed apically with two pinnate setae, proximal one somewhat longer and much stronger. Basis expanded into robust claw, and claw furnished with longitudinal row of four strong spinules at midlength, armed with two setae; strong seta about as long as claw, pinnate. Endopod two-segmented, but segmentation not easily discernable; proximal segment armed with two robust, unipinnate setae; distal segment with one robust, unipinnate apical seta and two slender and much shorter subapical setae. Longest seta on distal endopodal segment as long as longer seta on proximal endopodal segment. All strong setae on basis and endopod, as well as basal claw, unguiculate.

Maxilliped (Fig. 5B) four-segmented, composed of syncoxa, basis and two-segmented endopod. Ornamentation consisting of three rows of long and slender spinules on
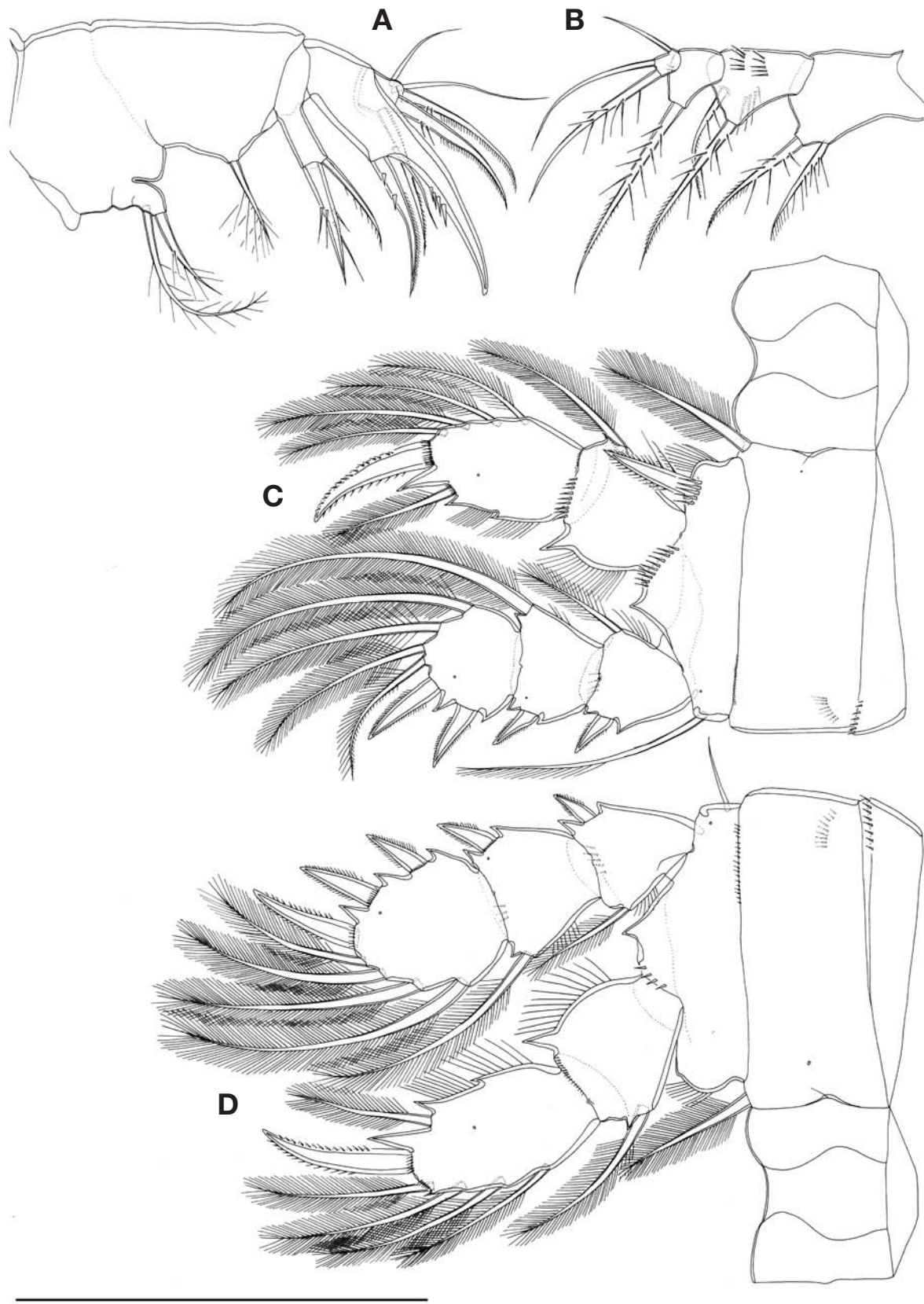
Fig. 5. *Monchenkocyclops changi* gen. et sp. nov., holotype female: A. maxilla, anterior view. B. maxilliped, posterior view. C. first swimming leg, anterior view. D. second swimming leg, anterior view. Scale bar 100 μm.

basis (two on posterior surface close to outer margin and one on anterior surface close to inner margin), as well as one row of two smaller spinules on anterior surface of first endopodal segment. Armature formula: 2.2.1.3. All setae, except two on second endopodal segment, pinnate, and most very strong and unguiculate.

All swimming legs (Figs. 5C, D, 6A-C) relatively large, composed of minute and triangular praecoxa, large and rectangular coxa, short basis, three-segmented exopod and two-segmented endopod. Endopods slightly shorter than exopods. Third exopodal segment spine formula 2.3.3.3 and setal formula 4.4.4.4. All setae on endopods and exopods slender and plumose, except apical seta on exopod of first leg, which pinnate along outer margin and plumose along inner (Fig. 5C); no modified setae observed. All spines strong and bipinnate. Intercoxal sclerite of all swimming legs with slightly concave distal margin and without any surface ornamentation, except on posterior surface of fourth leg.

First swimming leg (Fig. 5C) slightly shorter than other swimming legs; praecoxa unarmed, ornamented with distal row of small spinules on anterior surface; coxa 2.3 times as wide as long, ornamented with short transverse row of spinules on posterior surface close to outer margin, distal row of minute spinules on anterior surface, and small pore on anterior surface close to inner margin, armed with long and plumose seta on inner-distal corner; basis almost pentagonal in shape, 0.8 times as long as coxa, armed with outer long and slender seta, and inner-distal strong and bipinnate element (latter not reaching distal margin of first endopodal segment in length), ornamented with row of slender spinules along inner margin, two posterior rows of shorter and stronger spinules on anterior surface (one at base of inner seta, other at base of endopod), and one cuticular pore on anterior surface close to outer margin; exopod with single outer spine and single inner seta on first and second segment, with two outer spines and four setae (two inner, two apical) on third segment, ornamented with distal rows of spinules on posterior surface of first segment, row of slender inner spinules on first and second segment, single small pore on anterior surface of second and third segments, and extremely minute spinules as base of almost all setae and spines on anterior surface; endopod armed only with inner seta on first segment, second segment with four inner setae, one apical spine, and one outer seta, ornamented with slender spinules along inner margins of both segments, single pore on anterior surface of second segment, with shorter and stronger spinules along distal margins of first segment on anterior surface, and minute spinules at base of most setae and apical spine on anterior surface; apical spine on second endopodal segment outwardly unguiculate, 0.9 times as long as segment and only slightly shorter than inner setae; second endopodal segment about

1.4 times as long as wide and 1.3 times as long as first endopodal segment, with small inner notch showing ancestral segmentation.

Second swimming leg (Fig. 5D) slightly larger than first swimming leg; coxa 2.3 times as wide as long, armed with plumose inner seta (shorter than in first leg), ornamented with short row of strong spinules on posterior surface, in addition to distal row of spinules and small pore on anterior surface; basis with much shorter outer seta than in first leg, and without inner seta, with very small spiniform process instaed; exopod with longer third segment than in first leg, with three outer spines; endopod with longer second segment than in first leg; apical spine on second endopodal segment 0.8 times as long as segment or distal inner seta; second endopodal segment about 1.7 times as long as wide and 1.5 times as long as first endopodal segment.

Third swimming leg (Fig. 6A) extremely similar to second leg, except second endopodal segment with five inner setae and apical spine proportionately shorter; apical spine on second endopodal segment 0.7 times as long as segment and 0.5 times as long as apical seta; second endopodal segment about 1.9 times as long as wide and 1.6 times as long as first endopodal segment.

Fourth swimming leg (Fig. 6B, C), generally similar to third swimming leg, but slightly shorter and more slender, with longer and more plumose setae, with transverse row of long spinules on posterior surface of intercoxal sclerite and another one on posterior margin of coxa, and with second enopodal segment armed with three or four inner setae, two apical spines and one outer seta; second endopodal segment without notch on inner margin, with two pores on anterior surface, about 1.6 times as long as wide, and also 1.6 times as long as first endopodal segment; inner apical spine on second endopodal segment 1.4 times as long as outer apical spine, 0.65 times as long as segment, and less than 0.4 times as long as distal inner seta.

Fifth leg (Figs. 3A, B, 6D) inserted ventro-laterally, relatively small, two-segmented. First segment (possibly protopod) broad and short, almost rhomboidal in shape, half as long as greatest width, ornamented with single pore on anterior surface close to proximal margin, armed with single outer slender seta (probably ancestral outer basal), which inserted on short setophore and unipinnate distally. Second segment (probably exopod) irregularly cylindrical, widest at midlength, 1.2 times as long as first segment and 1.7 times as long as wide, unornamented, armed with apical long seta and subapical inner spine; apical exopodal seta bipinnate distally, 1.4 times as long as basal seta, 4.6 times as long as exopod, and nearly ten times as long as subapical spine, but only reaching midlength of genital double-somite in length; subapical exopodal spine small and slender, smooth, half as long as
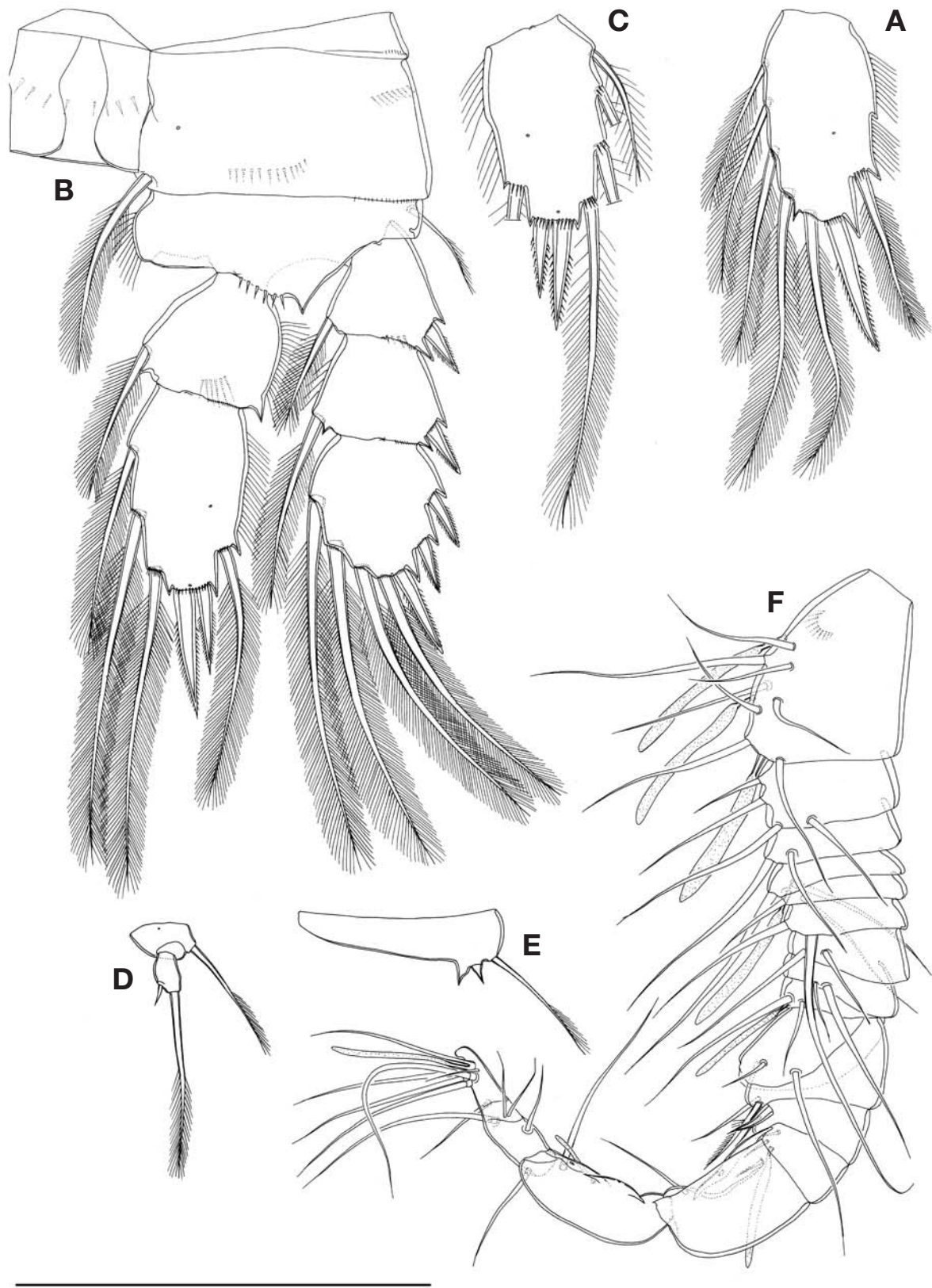
Fig. 6. *Monchenkocyclops changi* gen. et sp. nov., A-E. holotype female. F. allotype male. A. second endopodal segment of third swimming leg, anterior view. B. left fourth swimming leg, anterior view. C. second endopodal segment of right fourth swimming leg, anterior view. D. fifth leg, anterior view. E. sixth leg, lateral view. Scale bar 100 μm.
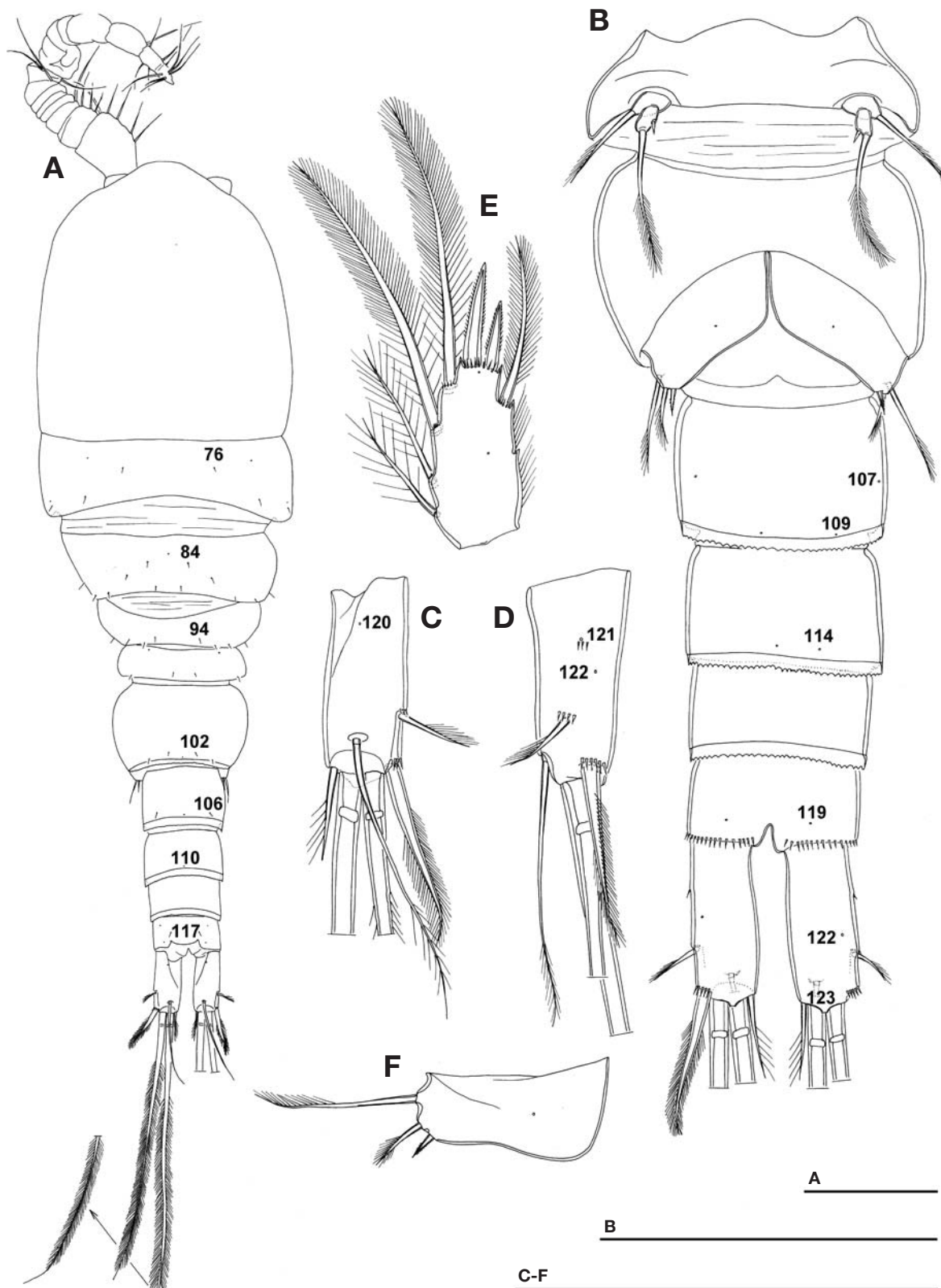
Fig. 7. *Monchenkocyclops changi* gen. et sp. nov., allotype male. A. habitus, dorsal view. B. urosome, ventral view. C. right caudal ramus, dorsal view. D. right caudal ramus, lateral view. E. second endopodal segment of fourth swimming leg, anterior view. F. sixth leg, ventro-lateral view. Arabic numerals indicating sensilla and pores consecutively from anterior to posterior end of body, and from dorsal to ventral side (excluding appendages). Scale bars 100 μm.

exopod and 0.8 times as long as exopod's greatest width.

Sixth leg (Figs. 6E) small, short and broad semicircular cuticular plate, armed with two short and smooth spines and outermost much longer and distally unipinnate seta; inner spine fused to plate, outer articulated basally; outermost seta directed postero-dorsally.

Male (based on allotype and one paratype). Total body length from 640 to 663 µm. Urosome with free genital somite. Habitus (Figs. 7A) much more slender than in female, with prosome/urosome ratio about 1.35 and greatest width in dorsal view at second pedigerous somite. Body length/width ratio 3.3; cephalothorax about 1.9 times as wide as genital somite. Cephalothorax 1.1 times as long as wide (dorsal view); representing 32% of total body length. Ornamentation of cephalothorax and free prosomites (Fig. 7A) and most urosomites (Figs. 7A, B) with same number and distribution of sensilla and pores as in female. Unpaired dorsal pore on genital somite (no. 101) situated more posteriorly than dorsal pair of sensilla no. 102 (more anteriorly in female); ventral pair of pores on fourth urosomite (no. 114) situated closer to each other.

Genital somite (Fig. 7A, B) 1.75 times as wide as long in dorsal view, with finely serrated hyaline fringe dorsally, ornamented with one unpaired dorsal pore (no. 101) and two pairs of dorsal sensilla (nos. 102, 103); no spermatophores visible inside; pair of pores on sixth legs probably homologous to lateral central pores on female genital double-somite (no. 104). Third urosomite homologous to posterior part of female genital double-somite, also ornamented with two pairs of posterior sensilla (nos. 106, 108) and two pairs of posterior ventral pores (nos. 107, 109). Fourth and fifth urosomite as in female. Anal somite (Fig. 7A, B) as in female, except anal operculum slightly narrower and more convex.

Caudal rami (Fig. 7B-D) slightly more slender than in female and with proportionately longer outermost terminal setae, but with very similar ornamentation and armature as in female; outermost terminal seta about nearly twice as long as innermost terminal seta, and only slightly shorter than ramus.
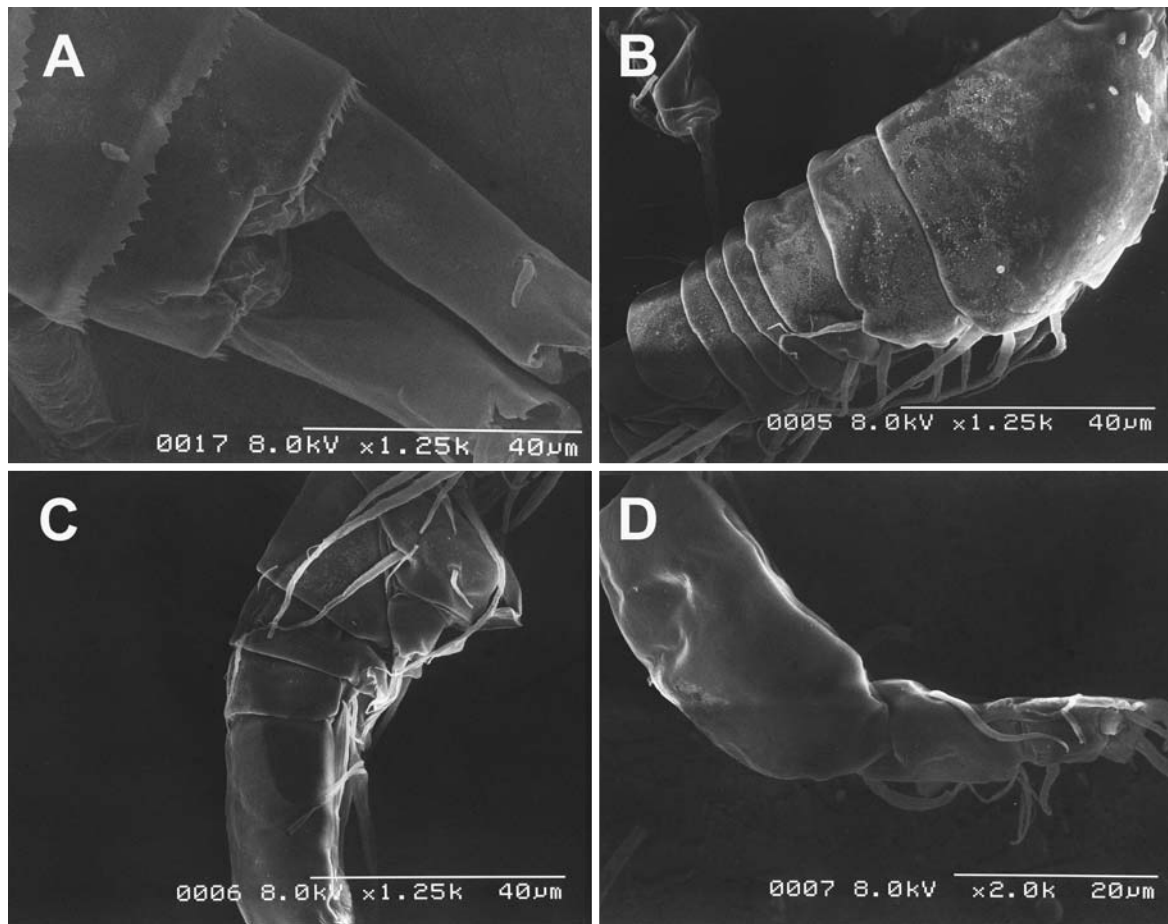

Fig. 8. Scanning electron micrographs of *Monchenkocyclops changi* gen. et sp. nov., A. paratype female. B-D. paratype male: A. anal somite and caudal rami, dorsal view (most caudal setae broken off). B. proximal part of antennula, dorsal view. C. middle part of antennula, dorsal view. D. distal part of antennula, dorsal view. Scale bars 40 µm (A-C) and 20 µm (D).

Antennula (Figs. 6F, 8B-D) strongly prehensile and digeniculate, 17-segmented (but sixteenth and seventeenth segments partly fused on ventral side), ornamented with spinules only on first segment (as in female), with anvil-shaped structures on anterior margin of fourteenth and fifteenth segments (distal geniculation). Armature formula as follows: 8+3ae.4.2.2+ae.2.2.2.2.2+ae.2.2.2.2+ae.2.1+ae.4.8+ae. All aesthetascs linguiform and most relatively long and broad, apical one on seventeenth segment fused basally to one seta; most setae slender and smooth; short smooth setae on eighth (one), ninth (one), tenth (one), twelfth (two), and thirteenth (two) segments; shot pinnate elements on eleventh (one) and fourteenth (one) segments; several seta on seventeenth segment biarticulate distally or with breaking plane.

Antenna, labrum, mandibula, maxillula, maxilla, first swimming leg, second swimming leg, and third swimming leg as in female.

Fourth swimming leg (Fig. 7E) also with similar armature and ornamentation as in female, as well as with similar proportions of spines and setae, except second endopodal segment with four inner setae (instead of three), and two proximal ones shorter, more slender and more sparsely plumose; second endopodal segment more slender than in female, about twice as long as wide.

Fifth leg (Fig. 7B) similar to female, but with slightly shorter apical exopodal seta.

Sixth leg (Fig. 7F) large cuticular plate, ornamented with single pore (probably no. 104) on anterior surface, armed with inner spine and two setae on outer distal corner; outermost seta 2.7 times as long as inner seta and 5.5 times as long as innermost spine.

Monchenkocyclops mirabdullayevi sp. nov.

Synonymy. *Acanthocyclops biarticulatus* Monchenko - Mirabdullayev and Kuzmetov, 1997: p. 11, figs. 1-17. [non] *Acanthocyclops biarticulatus* sp. n. - Monchenko, 1972: p. 83, figs. 1, 2.

Type locality. Kazakhstan, South Kazakhstan Province, Turkestan town, approximately 43° 19′N 68° 12′E, 210 m a.s.l., well.

Type material. Holotype female and allotype male are deposited at Nederlands Centrum voor Biodiversiteit/Naturalis in Leiden (ZMA Co. 203795), formely held at the Zoological Museum in Amsterdam (see Mirabdullayev and Kusmetov, 1997). Paratypes are several males and females together in 4% formaldehyde, deposited at the Institute of Zoology, Uzbek Academy of Sciences, Tashkent, Uzbekistan (Crust/Kz-42). All types were collected at the type locality, 10 June 1995, leg. I.M. Mirabdullayev and A.R. Kuzmetov.

Etymology. The new species is named in honour of Dr. Iskandar M. Mirabdullayev (Institute of Zoology, Academy of Sciences, Uzbekistan), who collected and described specimens of this species. The name is a noun in the genitive singular.

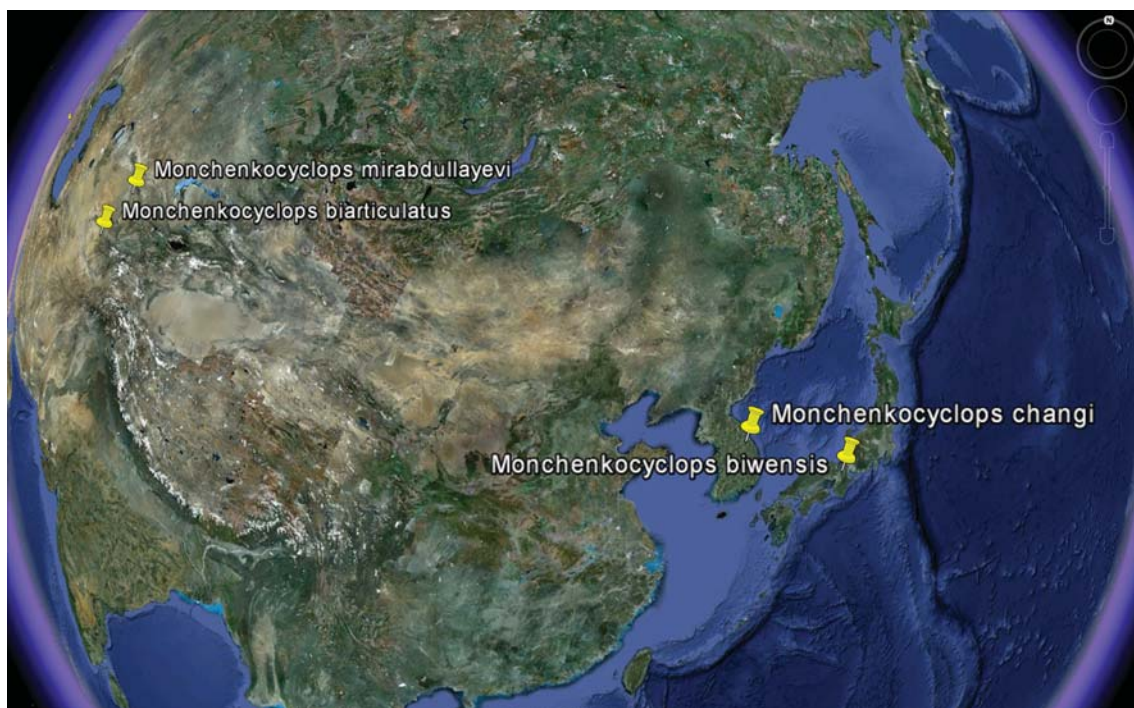**Description.** Female and male as described in Mirabdul-

Fig. 9. Disjunct distribution of the genus *Monchenkocyclops* gen. nov. in East Asia and Central Asia. Map from Google Earth.

layev and Kuzmetov (1997), and illustrated in their figures 1-17 as *Acanthocyclops biarticulatus* Monchenko, 1972.

DISCUSSION

There is no question that all four members of the genus *Monchenkocyclps* gen. nov. are morphologically extremely similar, which implies that they are probably phylogenetically very close. They all not only share the same segmentation of the swimming legs, but also the exact same armature formula of all four swimming legs, in addition to many other morphological characters such as the caudal rami shape and armature, absence of exopod on the antenna, similar shape of the seminal receptacle, fifth leg, etc. The only species that somewhat stands out is the Japanese *Monchenkocyclops biwensis* (Ishida, 2005) comb. nov., with its 12-segmented female antennula. However, this is probably a plesiomorphic character state (all eight setae are still present on the third segment in *M. changi* sp. nov., which was formed by the reduction of arthrodial membrane between the ancestral third and fourth segments), and exclusion of *M. biwensis* just based on this character would probably render the genus *Monchenkocyclops* paraphyletic. One should also not completely discard the possibility that Ishida (2005) illustrated an aberrant specimen, with an atavistic antennula, or perhaps misinterpreted some accidental fold on the surface of the third segment as an arthrodial membrane. These questions would require examination of a larger series of specimens, but *M. biwensis* was described from a single female.

Monchenokocyclops changi differs additionally from *M. biwensis* by longer dorsal caudal setae, fewer elements on the first segment of maxilliped, longer endopod of the fourth leg and its armature, and shorter inner spine on the fifth leg. Ishida (2005) illustrated the antenna of the Japanese species with only eight setae on the second endopodal segment, but he may have overlooked the most terminal seta, which is very slender and usually hidden behind the third endopodal segment. The Korean new species differs from the Uzbek *M. biarticulatus* (Monchenko, 1972) comb. nov. by shorter innermost terminal caudal setae, shorter inner basal spine on the first swimming leg, and shorter apical spines and especially inner setae on the second enopodal segment of the fourth swimming leg. Monchenko (1972) illustrated the antennula of the Uzbek species with fewer setae than in *M. changi*, but that was almost certainly an oversight, as similar antennular armature formula can be found in well studied but only remotely related species of both *Acanthocyclops* and *Diacyclops*. *Monchenokocyclops changi* differs from the Kazakh *M. mirabdullayevi* sp. nov. by shorter innermost terminal caudal setae, longer dorsal caudal setae, and

shorter inner spine on the fifth leg. Mirabdullayev and Kuzmetov (1997) also illustrated the antennula of the Kazakh species with fewer armature elements than in *M. changi*, probably omitting one on the second, sixth, eighth, ninth, and eleventh segments, and two on the fourth segment.

We acknowledge the possibility that subsequent molecular and morphological cladistics analyses of a wider group of Cyclopidae species (especially from the genera *Acanthocyclops* and *Diacyclops*) may suggest one of the members of the *Monchenkocyclops* species as ancestral to some forms with a higher level of the swimming legs oligomerization. However, we don't see that as a real taxonomic problem, as we have no philosophical problems with paraphyletic taxa. We see them as necessary in bridging the gap between the Darwinian concept of speciation, Henningian concept of phylogeny based on character analysis, and Linnean system of nomenclature. One of those species may be the American *Rheocyclops carolinianus* Reid in Reid, Strayer, McArthur, Stibbe and Lewis, 1999, which is the only other cyclopoid with all swimming legs with three-segmented exopods and two-segmented endopods (Reid *et al.*, 1999). This species differs, however, from all members of *Monchenkocyclops* by a number of characters, including: fifth legs inserted ventrolaterally, with fused basal segment and very long and clearly apical inner element on the terminal segment; triangular and very long anal operculum; very short caudal rami; first exopodal segments of all swimming legs without an inner seta; and second endopodal segment of all swimming legs with fewer setae. Unfortunately, males of this species are still unknown. As one can judge from the morphology of adult females alone, it is most likely that the two-segmented state of endopods of the swimming legs evolved convergently in these two lineages.

Monchenkocyclops seems to be relatively closely related to the genus *Zealandcyclops* Karanovic, 2005, with similarly curious disjunct distribution (New Zealand and Lake Baikal), and interspecific variation in the size of the inner spine on the fifth leg (Karanovic, 2005). The two genera, however, differ in the habitus shape, armature of the mandibula and antenna, segmentation of the exopod of the first swimming leg, armature formula of all swimming legs, sexual dimorphism of the third swimming leg, as well as in the size of the basal segment of the fifth leg (Alekseev and Arov, 1986; Boxshall *et al.,* 1993; Karanovic, 2005). The fact that most of these differences are actually reductions in *Zealandcyclops* may indicate that this genus originated from a Monchenocyclops-like ancestor, through a process of neotenic development and further oligomerization of appendages (Monchenko and von Vaupel Klein, 1999). Other more distantly related cyclopoids include European subterranean members of the genus *Acanthocyclops* with more or less oligomerizated

swimming legs, such as *A. reductus* (Chappuis, 1925), *A. propinquus* Pleşa, 1957, or *A. iscrecensis* Pandourski, 1992 (see Pleşa, 1957; 1961; Petkovski, 1972; Pandourski, 1991; 1997; Naidenow and Pandourski, 1992), but they all have different segmentation and armature of the swimming legs, very short genital double-somite, and triangular anal operculum. The latter species (with some others) are sometimes referred to as the *kieferi*-group, but the monophyly of this group has never been tested rigorously; it probably represents a very loose assemblage. Members of the genus *Reidcyclops* Karanovic, 2000 are even more distantly related, with their sexual dimorphism in the swimming legs segmentation, and a very different fifth leg (Karanovic, 2000). All other members of *Acanthocyclops* and *Diacyclops* are only very remotely related to *Monchenkocyclops*. In Korea, all six currently known species of *Acanthocyclps* have three-segmented exopods and endopods of all swimming legs, as well as a 17-segmented antennula (Chang, 2009), and all six species of *Diacyclops* have different segmentation of the swimming legs and much longer inner spine on the fifth leg. Renewed interest in stygofauna here will certainly result in the discovery of many endemic cyclopoid species, as it did recently with some harpacticoid genera (Karanovic and Lee, 2012; Karanovic *et al.,* 2012)

Disjunct distribution of the genus *Monchenkocyclops* in Central Asia and East Asia (Fig. 9) is more probably a result of range fragmentation than range expansion. In support of this hypothesis we can list the following facts:

1. Two Central Asian species do not seem to be more closely related to each other than to their East Asian relatives. In fact, as far as we can judge from their morphology alone and fairly limited original descriptions, the Korean *M. changi* seems to be most closely related to the Uzbek *M. biarticulatus*, while the Japanese *M. biwensis* appears to be more closely related to the Kazakh *M. mirabdullayevi* than to any other congener (here we especially refer to a longer inner spine on the fifth leg in the latter two species).
2. Three of the four species live in subterranean habitats, while *M. biwensis* is only known from the ancient Lake Biwa in Japan, despite the fact that the Japanese cyclopoid fauna is relatively well known (Ishida, 2002). Both subterranean waters and ancient lakes are habitats traditionally considered as refugia (Matzinger *et al.*, 2006; Albrecht and Wilke, 2008), and probably closely connected. Recently, there have been some attempts to explain the role of ancient lakes as biodiversity pumps for subterranean habitats (Karanovic and Abe, 2010).
3. The genus is apparently absent from the ancient Lake Baikal, despite the fact that this lake harbors one of the largest and most diverse suite of species from the *Acanthocyclops*/*Diacyclops* group (Mazepova, 1978; Monchenko and von Vaupel Klein, 1999). As the lake itself was relatively cold in the Quaternaty, and has always been oligotrophic (Prokopenko and Williams, 2003), it is possible that *Monchenocyclops* represents a remnant of a more thermophilic and eutrophic Tertiary fauna.
4. This disjunct distribution pattern is extremely rare in zoogeography, which probably indicates that the four *Monchenkocyclops* species are just chance survivals (=relics). It has to be pointed out that our knowledge of the Asian subterranean fauna is fragmentary, and that some new members of this genus may be expected in the vast expanses of northern and central China.

Key to species of the genus *Monchenkocyclops*

1. Female antennula 11-segmented ···························· 2
− Female antennula 12-segmented ·····························
  ······················*M. biwensis* (Ishida, 2005) comb. nov.
2. Subapical spine on fifth leg shorter than segment's width; innermost terminal caudal seta as long as or shorter than outermost terminal one ······················· 3
− Subapical spine on fifth leg longer than segment's width; innermost terminal caudal seta longer than outermost terminal one ············ *M. mirabdullayevi* sp. nov.
3. Basal inner spine on first leg longer than first endopodal segment; innermost terminal caudal seta as long as outermost terminal one; inner setae on second endopodal segment of fourth leg only slightly reaching beyond tips of apical spines ···
  ········*M. biarticulatus* (Monchenko, 1972) comb. nov.
− Basal inner spine on first leg shorter than first endopodal segment; innermost terminal caudal seta shorter than outermost terminal one; inner setae on second endopodal segment of fourth leg reaching significantly beyond tips of apical spines ········· *M. changi* sp. nov.

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