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The generic concept of Allocyclops Kiefer, : (Copepoda: Cyclopoida: Cyclopidae) an alternative view

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The generic concept of *Allocyclops* Kiefer, 1932: (Copepoda: Cyclopoida: Cyclopidae) an alternative view

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The current systematics of the genus Allocyclops Kiefer, 1932 is a contentious subject. The emended diagnosis proposed in 2001 by Karanovic has not been unanimously accepted and the classical outline and species arrangement has been favoured in the latest update by Dussart and Defaye in 2006. Based on re-examination of types and additional material both concepts are tested and rejected because they are unnatural groupings. The redefined genus absorbs Bacillocyclops Lindberg, 1956 within it, and includes the species Allocyclops chappuisi Kiefer, 1932, Allocyclops cavicola Chappuis, 1951, Allocyclops beadlei (Lindberg, 1956) comb. nov. and Allocyclops botosaneanui Plesa, 1981. Psammocyclops Kiefer, 1955 and Stolonicyclops Reid and Spooner, 1998 are re-instated as separate genera: the former including Psammocyclops excellens Kiefer, 1955 and *Psammocyclops ritae* (Dumont and Lamoot, 1978), the latter including Stolonicyclops heggiensis Reid and Spooner, 1998 only. Hypocyclops gen. nov. is erected to accommodate Hypocyclops kieferi (Petkovski, 1971) comb. nov. and Hypocyclops montenegrinus (Karanovic, 2001) comb. nov. Virbiocyclops gen. nov. is defined for Virbiocyclops silvaticus (Rocha and Bjornberg, 1988) comb. nov. and Olmeccyclops gen. nov. for Olmecyclops veracruzanus (Suárez-Morales, Mendoza and Mercado-Salas, 2010) comb. nov. Speocyclops transsaharicus Lamoot, Dumont and Pensaert, 1981 is allocated to the genus Hesperocyclops Herbst, 1984 and Bryocyclops arenicolous (Fryer, 1956) returned to its initial placement in *Metacyclops* Kiefer 1927. Each of the herein (re)defined genera is representative of a different lineage within Cyclopidae. The status and affinities of Cyclops minutissimus Kiefer, 1933 auct. and Allocyclops (A.) australonipponicus Tomikawa, Ishida and Mawatari, 2005 remain unresolved. They are considered gen. spec. inq.

Keywords: Copepoda; Cyclopidae; *Allocyclops*; leg 5 structure; revision; redescriptions; new genera

Introduction

In its current constitution the genus *Allocyclops* Kiefer, 1932 is an assemblage of small to medium-sized benthic freshwater cyclopines encountered in caves and seeps, the interstitial of river banks and lake shores, and among wet mosses and tropical forest litter. The genus is mainly characterized by the reduced fifth leg morphology in which the two ancestral segments are completely absorbed into the pedigerous somite with the original armature, composed of three elements, located along the lateral and posterior borders of the somite.

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Allocyclops was introduced for Allocyclops chappuisi by Kiefer (1932) in a preliminary report on the diaptomid and cyclopid copepods collected by Ch. Alluaud and P. A. Chappuis in Ivory Coast, part of the region previously known as French West Africa. A slightly amended and illustrated description, annotated with a brief reflection on its possible affinities, figured in the final report (Kiefer 1933). Despite numerous contributions on freshwater Cyclopidae worldwide, the genus Allocyclops has seen few additions. For a long time, seven cyclopines were assigned (Dussart and Defaye 1985): three from Africa (Allocyclops chappuisi, Kiefer 1932, Allocyclops cavicola Chappuis, 1951, Allocyclops ritae Dumont and Lamoot, 1978), two from southeastern Europe (Allocyclops minutissimus (Kiefer, 1933) and Allocyclops kieferi Petkovski, 1971) and two from South America and the Caribbean (Allocyclops silvaticus Rocha and Bjornberg, 1988 and Allocyclops botosaneanui Pleşa, 1981). Allocyclops neotropicalis Dussart, 1984 initially attributed to Allocyclops has been removed (Reid 1988) and is posted in the genus Yansacyclops Reid, 1988.

In an attempt to revise the genus *Allocyclops*, Karanovic (2001) presented a drastic re-arrangement of the systematic landscape: *Psammocyclops* Kiefer, 1955 and *Stolonicyclops* Reid and Spooner 1998 were relegated to *Allocyclops* as subgeneric groups. Members from other genera (*Speocyclops orcinus* Kiefer 1937c, *Speocyclops transsaharicus* Lamoot, Dumont and Pensaert, 1981, *Metacyclops arenicolous* Fryer 1956) were removed from their initial designation and repositioned in one of the three subgenera. *Allocyclops* (*A*). *montenegrinus* Karanovic, 2001, *A.* (*A.*) *austronipponicus* Tomikawa, Ishida and Mawatari, 2005, and *A.* (*P.*) *veracruzanus* Suárez-Morales, Mendoza and Mercado-Salas, 2010 are recent additions. *Allocyclops* (*P.*) *consensus* Karanovic, 2003 has been removed subsequently and is now placed in *Barrowcyclops* Karanovic, Eberhard and Murdoch, 2010, a subgenus of *Dussartcyclops* Karanovic, Eberhard and Murdoch, 2010.

The generic outline of *Allocyclops* as proposed by Karanovic (2001) has not been unanimously accepted. Dussart and Defaye (2006) maintained the classic arrangement with the genera *Allocyclops*, *Psammocyclops* and *Stolonicyclops* as distinct identities and Reid and Williamson (2010), in their recent key to copepod species of North America, maintained *Stolonicyclops* as distinct. The original designation of both members of the genus *Speocyclops* and the position of *Metacyclops arenicolous* Fryer, 1956 in *Bryocyclops* Kiefer, 1927 (Lindberg 1961) was conserved. Fiers and Pandourski (2008) came to similar conclusions when redescribing *Speocyclops orcinus* and promptly reinstated it as a member of the genus *Speocyclops*.

With the ingrained importance attributed to the fifth leg structure in cyclopid systematics (Kiefer 1927, 1928, 1937c) many early descriptions highlighted only a strict minimum of morphological aspects assumed relevant in distinguishing congenerics. The original descriptions of the majority of the species attributed to *Allocyclops* are not different. Apart from *Speocyclops orcinus*, none has been the subject of a redescription or re-examination. Information about mouthparts, the complete leg armament and the male characteristics is only available for four of the 14 species positioned in *Allocyclops* by Karanovic (2001, 2003). The emended generic outline has been exclusively based on information contained in outdated and incomplete descriptions, hence, the reservations expressed in Dussart and Defaye (2006) in relation to the proposed rearrangement and the emended generic definition of *Allocyclops*.

Re-examination of the types revealed that the original concepts of the genera Allocyclops and Psammocyclops have been seriously compromised by subsequent additions. Neither the classic (see Dussart and Defaye 2006) nor the amended (see Karanovic 2001, 2003) systematic outline of the genus *Allocyclops* can be maintained.

Materials and methods

Material examined was obtained from the following institutions: Staatliches Museum für Naturkunde, Karlsruhe, Germany (Friedrich Kiefer Copepod Collection, inventory numbers referred to as FKCC#), the Institute of Speology "Emil Racovitza", Cluj, Romania (ISER), the Royal Museum for Central Africa, Tervuren, Belgium (RMCA#), and the British Museum of Natural History, London, UK (BMNH reg.#). Specimens, previously kept in the collection of H.J. Dumont, University of Ghent, are now hosted at the Royal Belgian Institute of Natural Sciences and incorporated in the copepod collection (inventory numbers: RBINSc COP#). Undissected specimens are stored in 70-75% ethyl alcohol (RMCA and RBINS collections) or glycerin (FKCC collection). Slides from which the mounting medium had evaporated have been refilled with 75% ethyl alcohol, successively replaced by glycerine, and resealed after air bubbles were removed. Observations were made on a Leitz Diaplan, equipped with phase contrast and a camera lucida. Drawings were made at magnifications of $625 \times$ and $1250 \times$. Arabic numerals referring to antennulary segments allude to their position (proximal to distal), reference to the ancestral sequences are given in Roman numerals, segment fusions between [] (see Schultze et al. 2000). Abbreviations used: Aesth, aesthetasc; CR, caudal rami and its armature: Td, dorsal seta; Te, distal lateral seta; Ti, medial terminal seta; Exo, exopodite; End, endopodite; P1–6, legs 1–6; leg armature notation arranged as outer-(distal)-inner element, specified in Table 3 by Roman figures for spines and Arabic figures for setae.

Systematics

Subclass **COPEPODA** Milne Edwards, 1830 Family **CYCLOPIDAE** Rafinesque, 1815 Genus *Allocyclops* Kiefer, 1932 emend.

Allocyclops gen. nov. - Kiefer 1932: 526-527.

Allocyclops Kiefer, 1932 – Kiefer 1934, 1939; Monchenko 1974; Dussart and Defaye 1985, 1995, 2001, 2006; Lescher-Moutoué 1986; Pesce 1996; Boxshall and Halsey 2004; Karanovic 2001, 2004, 2006.

Bacillocyclops gen. nov. - Lindberg 1956a: 26, 27, 32-33.

Bacillocyclops Lindberg, 1956a – Monchenko 1974; Dussart and Defaye 1985, 1995, 2001, 2006; Pesce 1996; Boxshall and Halsey 2004.

non-Allocyclops Kiefer, 1932 - Tomikawa et al. 2005.

Diagnosis

Cyclopidae with typical cyclopine body shape; cephalothorax and urosome prominent, metasome short; genital double-somite longer than wide, without particular surface modifications, and genital complex situated in anterior third; integument of body somites neither modified nor ornamented; caudal border of prosomites straight, caudal border of urosomites with narrow serrate fringe; caudal margin of anal somite with continuous spinule girdle; anal operculum simple with straight or crescentic, naked, border; cylindrical caudal rami without dorsal crest; distal lateral and medial terminal elements long and pinnate; principal terminal setae with breaking plane; antennule 11-segmented with armament (ancestral sequences): 1(8)-2(4)-3(6)-4(2)-5(2)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth); aesthetasc linguiform and stalked on segment 8 (=[XXI-XXIII]), filiform on segment 10 (=[XXV]), tubular and fused with seta on segment 11 (=[XXI-XXVIII]); antennary coxobasis with exopodite remnant and two abexopodal elements; second endopodite segment with nine setae (without exopodite and five setae on second endopodite segment in A. botosaneanui); mandible with two long and one short seta on palp; maxillule and maxilla typical cyclopid, the latter with one-segmented endopodite; maxilliped four-segmented and erect, with 3.2.1.3 armature (3.2.1.2 in A. botosaneanui); legs 1-4 biramous with bimerous rami; exopodite spine formula 3.4.4.3 and seta formula 5.5.5.5/4; armament details in Table 3; armament distribution as shown in Table 1.

Legs 1–4 with medial coxal pinnate seta, and naked intercoxal sclerites with crescentic distolateral edges; leg 1 basis with long, slender and serrate medial spine; medial border of leg 1 basis simple crescentic, of legs 2–4 with short triangular distal structure; leg 5 differentiated as truncate plate, located lateral on pediger, bearing one outer proximal element and two apical elements: outer one setiform, medial one spiniform and robust; leg 6 located dorsolateral with three elements: dorsal one setiform and pinnate, middle and ventral dwarfed, equally sized, with hyaline appearance; genital complex with frontal and caudal expansions.

Male. Urosome with short and wide leg 6-bearing somite; antennule 16-segmented with armament (according to position): 1(8+3 Aesth)-2(4)-3(2)-4(1+1 or 0 (?)Aesth)-5(2)-6(2)-7(2)-8(2)-9(2+1 Aesth)-10(2)-11(2)-12(2)-13(1+Aesth)-14(4)-15(3)-16(11+2 Aesth); setal armament not modified; aesthetascs narrow and long; mouthparts and legs as in female, except leg 4 endopodite lacking folded medial margin of proximal segment; leg 5 as in female; leg 6 bearing two equally long elements: outer one setiform, medial one spiniform, robust and serrate; surface of leg 6 valves smooth.

Type species

Allocyclops chappuisi Kiefer, 1932, type species by monotypy.

Other species

Allocyclops cavicola Chappuis, 1951, *Bacillocyclops beadlei* Lindberg, 1956 comb. nov. and (tentatively) *A. botosaneanui* Pleşa, 1981.

Allocyclops chappuisi Kiefer, 1932 (Figures 1 and 2)

Allocyclops chappuisi sp. nov. - Kiefer 1932: 526-527.

	Exopodite	Endopodite
Genus Allo	cyclops	
P1	1.1–3.2.3	0.1-1.2.3
P2	1.1-3.2.4	0.1 - 1.2.4
P3	1.1-3.2.4	0.1-1.2.3/4
P4	1.0-2.2.4	0.1–1.2.3
Genus Psar	nmocyclops	
P1	1.0-2.2.3	0.1-1.2.2
P2	1.1-2.2.3	0.1-1.2.2
P3	1.1-2.2.3	0.1–1.2.2 or 1.2.3*
P4	1.0-1.2.3	1.1.3
Genus Hyp	ocyclops	
P1	1.0-3.2.3	0.1 - 1.2.2
P2	1.0-3.2.3/4	0.1 - 1.2.2/3
P3	1.0-3.2.3/4	0.1-1.2.3
P4	1.0-2.2.3	0.1-1.2.3
Genus Virb	viocyclops	
P1	1.1-3.2.3	0.1-1.2.2
P2	1.1-2.2.4	0.1-1.2.3
P3	1.1-2.2.4	0.1-1.2.4
P4	1.0-1.2.4	0.1-1.1.3
Genus Olm	eccyclops (female)	
P1	1.0-2.2.2	0.1-1.1.2
P2	1.0-2.2.3	0.1-1.2.2
P3	1.0-2.2.3	0.1-1.2.2
P4	1.0 - 1.2.2	0.1 - 1.1.1
Genus Olm	eccyclops (male)	
P1	1.0-2.2.2	0.1-1.1.2
P2	1.0-2.2.2	0.1-1.2.2
P3	1.0-2.2.2	0.1-1.2.3
P4	1.0-1.2.2	0.1-1.1.1

Table 1. Armament distribution.

*Armament formula for a two-segmented/one-segmented ramus, respectively.

Allocyclops chappuisi Kiefer – Kiefer 1934: 134–136, figs. 37–43; 1939: 132; Petkovski 1971: 109–110, figs. 70–75; Dumont and Lamoot 1978: 25; Pleşa 1981: 31–32; Dussart and Defaye 1985: 146; Dussart and Defaye 1995: 239, fig. L127B; 2001: 286, fig. L136B; 2006: 218; Lescher-Moutoué 1986: 309; Rocha et al. 1988: 445; Reid 1988: 430.

Allocyclops (Allocyclops) chappuisi Kiefer, 1932 - Karanovic 2001: 24; 2003: 148.

Material examined

Type series: two females (FKCC 1820-21 and FKCC 1822-23) and one male (FKCC 1824-1825), all partially dissected. Each slide bears the indication "*typus*".



Figure 1. *Allocyclops chappuisi* Kiefer, 1932. Syntypes. (A) Female urosome, ventral view (genital complex faded); (B) male urosome, ventral view; (C) female antennule, ventral view (A: FKCC 1823; B: FKCC 1825; C: FKCC 1822).

Origin (type locality)

Ivory Coast (Côte d'Ivoire, part of region formerly named French West Africa): laterite springs at foot of hill at Daloa, type locality (city centre approx. 6°53′ N, 6°26′ W) in the Haute-Sassandra Region, Chappuis *leg.*, 18 February 1931 (Chappuis 1934).

Note

The three specimens are partially dissected. Apart from the detached female antennule and antenna the mouthparts were left in place and vaguely visible. Their general



Figure 2. *Allocyclops chappuisi* Kiefer, 1932. Syntypes. (A) Leg 1, frontal; (B) leg 3, frontal; (C) leg 4, caudal; (D) leg 4 intercoxal sclerite; (E) female antenna, frontal (A–E: FKCC 1822).

morphology is identical to that of *A. cavicola*, described below. Details, nowadays impossible to observe, will have to be elucidated when fresh material becomes available.

Redescription

Female. Habitus not observed, but considering the width of the dissected leg 4 pair and that of the fifth pediger, the body has a distinct constriction between prosome and urosome, resembling that of *A. cavicola*, illustrated in Figure 3A. Length, according to Kiefer (1933) between 720 and 740 μ m. Urosome (Figure 1A) tapering, lacking

ornaments on fifth pediger. Genital double-somite slightly wider than long in the preserved specimen (as a result of pressure of the cover glass: fresh specimens would show a somite being longer than wide). Receptacle hardly visible, faded. Copulatory pore, small, leading to a slender duct, forming a loop posteriorly and entering in nearly straight transverse ducts. Hyaline fringe of genital double-somite and following somites irregularly serrate. Anal somite with complete girdle of spinules along posterior margin. Anal operculum crescentic, with smooth margin, covering anal sinus almost completely.

Caudal rami 2.33 times longer than wide, as result of compression by the cover glass. Fresh specimens reported to possess rami 2.5 times as long as wide and cylindrical. Anterolateral seta located at distal end of middle third, without spinules at insertion. Distolateral element (60 μ m long) strong, shorter than ramus, furnished with rigid hairs, and accompanied with five large spines near insertion. Medial seta 1.33 times longer than ramus, dorsal one 1.5 times longer than ramus. Principal middle terminal setae with breaking plane.

Antennule (Figure 1C) 11-segmented with following armament: 1(8)-2(4)-3(6)-4(2)-5(2)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth). Aesthetasc on segment 8 linguiform, on segment 10 and segment 11 tubular. Segment 1 with short comb of long spinules on anterior margin. Distal elements on segments 4 and 5 truncate, with hyaline appearance.

Antenna (Figure 2E) four-segmented. Coxobasis with short plumose exopodal seta, and two equally long abexopodal ones. Endopodite with one, nine and seven elements, respectively. Visible ornamentation of coxobasis located in proximal half of frontal surface of coxobasis: two short rows of spinules parallel to outer margin, one short transverse proximal row, and three slender spinules along outer margin. Caudal surface not clearly visible, furnished, at least, with a short row of spinules parallel to outer margin (not illustrated). Mandible, maxillule, maxilla and maxilliped: see descriptions for *A. cavicola*, below.

Legs 1–4 (Figures 2A–C). Coxa with medial pinnate seta. Intercoxal sclerite with smooth surfaces, without particular produced crescentic distolateral corners (Figure 2D). Medial margin of basis rounded and hairy in leg 1, rounded and furnished with a distal triangular process in legs 2–4. Margin hairy in legs 2 and 3, smooth in leg 4. Medial spine on leg 1 basis present, serrate and reaching halfway to second endopodite segment. Rami two-segmented, with exopodite spine formula 3.4.4.3, and seta formula 5.5.5.5. Complete leg armament in Table 3. Second endopodite segment of leg 4 twice as long as wide, with two terminal spines: outer spine slightly longer than half inner one, the latter as long as segment.

Leg 5 vestiges positioned laterally, segments apparently completely integrated in pediger (when observed ventrally, Figure 1A). Seta representing basal segment moderately long and slender, inserted laterally on pediger, at short distance from medial ones. Elements representing distal segment arising from narrow expansion of posterior margin. Outer element setiform, 1.5 times longer than inner element; the latter spiniform (ornament, if present, nowadays invisible). Leg 6 located in anterior third of genital double-somite, with three elements on valve. Dorsal location of leg 6 results from flattening of the somite by the cover glass.

Male. Habitus not observed. Body length, according to Kiefer (1933), 650 μ m. Urosome (Figure 1B) with fifth pediger devoid of ornamentation. Hyaline fringes of

following urosomites wide, irregular serrate. Posteroventral and posterodorsal margins of anal somite entirely set with small spinules. Anal operculum crescentic, short, with smooth margin.

Caudal rami 2.33 times longer than wide. Anterolateral seta inserted at distal end of median third, with four or five (hardly visible) spinules near insertion. Distolateral element robust, pinnate, as long as ramus, with five spinules at insertion on ventral side of ramus. Medial element 1.25 times longer than ramus. Both principal terminal setae with breaking planes. Dorsal seta as long as medial one.

Antennule typically bi-geniculate, details invisible. Mouthparts not observed. Legs 1–4 as in female.

Leg 5 (Figure 1B) as in female but seta representing basal segment shorter, and elements representing distal segment equally long. Leg 6 vestiges (Figure 1B) with only two elements on outer distal corner of valve: outer one setiform, inner one spiniform and stout, both equally long. Valve with smooth surface.

Remarks

Kiefer (1932, 1934) overestimated the expansion of the anal operculum as he described it as "better developed than normal". Indeed, the operculum appears to be large as it covers the anal sinus partially (compare the retracted position of it in *A. cavicola*, see below). However, the posterior extent of the operculum covering the anal sinus (in the female) or expanding beyond the anal area (in the male) results from flattening of the somites by the pressure of the cover glass.

Allocyclops cavicola Chappuis, 1951 (Figures 3–7)

Allocyclops cavicola sp. nov. - Chappuis 1951: 356-259, figs. 23-28.

Allocyclops cavicola Chappuis – Lindberg 1954: 115; Leleup 1956: 40; Pleşa 1981: 31; Dussart and Defaye 1985: 146; 2006: 198; Lescher-Moutoué 1986: 309; Rocha and Bjornberg 1988: 445.

Allocyclops (Allocyclops) cavicola Chappuis, 1951 - Karanovic 2001: 24; 2003: 148.

Material examined

Type series: three females and one male: one female completely dissected on three slides, two females preserved in alcohol, and one male partially dissected (antennule on slide, prosome and urosome in alcohol), Det. P.A. Chappuis. Stored in the Crustacea collection of the RMCA (no. 45.685 and 45.686); three dissected females with same collection data and formerly hosted in the collection of H. Dumont, now catalogued as RBINSc COP 7664–7666. The specimens (one female, one male, dissected) featuring in the original description were not found and are probably lost.

Origin (type locality)

Democratic Republic of the Congo, Cave "Raymond Lambrechts" 2 km southeast from Lovo village (Basse-Zaire), type locality. N. Leleup leg., 21 August 1949 and



Figure 3. *Allocyclops cavicola* Chappuis, 1951. Syntypes. (A) Female habitus; (B) male habitus; (C) antennary basipodite, frontal view (A, B: RMCA 45.685; C: RBINSc COP 7665).



Figure 4. *Allocyclops cavicola* Chappuis, 1951. Syntypes. (A) Female urosome, dorsal view; (B) idem, ventral view; (C) idem, lateral view (A–C: RMCA 45.685).



Figure 5. *Allocyclops cavicola* Chappuis, 1951. Syntypes. (A) Maxillule (medial element of palp illustrated separately); (B) mandible; (C) maxilliped, frontal; (D) second segment of maxilliped, caudal view; (E) first antennulary segment of female, ventral view; (F) paragnath; (G) male antennule, dorsal view (A–F: RBINSc COP 7664–7666; G: RMCA 45.685).



Figure 6. *Allocyclops cavicola* Chappuis, 1951. Syntypes. (A) Maxilla (proximal part of syncoxa omitted); (B) element of first maxillar endopodite segment, enlarged; (C) labrum; (D) antennary coxobasis, caudal view; (E) leg 1, protopodite and exopodite, caudal; (F) leg 3 endopodite, caudal; (G) leg 4, caudal (A–G: RBINSc COP 7664–7666).



Figure 7. *Allocyclops cavicola* Chappuis, 1951. Syntypes. (A) Male urosome, ventral view; (B) idem, lateral view; (C) female anal somite and caudal rami, dorsal; (D) male anal somite and caudal rami; (E) female copulatory pore area; (F) female leg 6, lateral view; (G) female leg 5 and part of posterior margin of pediger, lateral view (A–G: RMCA 45.685).

28 August 1949 (Leleup, 1956). Detailed description of the site in Heuts and Leleup (1954: referred to as locality B.29).

Description

Female. Habitus (Figure 3A). Typical cyclopid with cephalothorax prominently manifested, almost half as long as entire body (0.45/1). Metasome short, strongly tapering towards principal body articulation. Prosome–urosome transition clearly defined. Genital double-somite longer than wide, widest in anterior third, tapering posteriorly (Figure 4A). Genital area large. Copulatory pore minute, leading to thick-walled S-shaped duct, embedded in a trifoliate area (Figure 7E). Anterior part of receptacle broad ovate, caudal part largely expanded posteriorly, bi-lobed. Integument of body somites smooth. Posterior margins of prosomites and fifth pediger fringeless. Urosomites with wide posterior serrate fringe. Body length: 1 mm.

Anal somite (Figure 4B) with complete girdle of spinules along posterior margin. Anal operculum not expanded, with smooth straight posterior margin. Caudal rami (Figures 4A–C) wide in proximal third, cylindrical distally, roughly 3.15 times as long as wide (possibly furnished with slender setules; Figure 7C). Anterolateral seta inserted at distal end of median third. Distolateral seta (100 μ m) as long as ramus, pinnate, with spinules at insertion. Medial and dorsal setae nearly equally long, both twice as long as ramus, dorsal seta articulating on small basal part. Median terminal seta partially broken in all specimens observed, both with breaking plane.

Antennule reaching end of cephalothorax (Figure 3A), with setal complement as in *A. chappuisi*, except for following details: aesthetasc on segment 8 reaching beyond middle of segment 9, filiform aesthetasc on segment 10 as long as accompanying seta, and aesthetasc on segment 11 considerably longer than accompanying seta. Spinule pattern on segment I present (Figure 5E).

Antenna as in *A. chappuisi*. Frontal surface of coxobasis (Figure 3C) with two oblique rows of slender spinules on inner region of proximal part, two clusters of minute spinules in middle, near outer margin, and cluster of minute spinules near insertion of exopodal seta. Caudal surface (Figure 6D) with cluster of minute spinules near proximal outer corner, a series of spinules in proximal half near outer margin, and two longitudinal series in distal half, near and semi-parallel to outer margin. Abexopodal setae equally long, serrate.

Mandible (Figure 5B): gnathobasis with complex biting edge, and smooth surface. Palp distinct, bearing three elements: two long plumose setae and one short smooth seta. Labrum (Figure 6C) with convex posterior margin, armed with 15 blunt teeth. Ventral surface with long and slender spinules. Paragnath (Figure 5F) with rounded apex, and four strong elements near base. Outer margin furnished with long hairs, inner margin with short row of stiff hairs, inserted sub-apically.

Maxillule (Figure 5A) with robust arthrite bearing seven long elements along lateral margin and three claws and one seta along medial margin. Basis with setae near articulation with arthrite, and three elements (two pinnate setae and one strong serrate terminal spine) on medial border. Palp articulating on basis, bearing three serrate setae.

Maxilla (Figure 6A) with incompletely fused syncoxa. Praecoxal endite typically globular, bearing two long plumose setae; coxal endite represented by large, robust seta. Distal endite with two long serrate elements, proximal one flagellated. Claw of basis rather short, serrate in middle of proximal margin; medial accessorial element

stout with cluster of spinules in proximal half, serrate in distal half (Figure 6B). Endopodite with five elements (three claw-shaped and two slender ones). Onesegmented appearance resulting from the coalescent nature of the three elements and the segment. Principal endopodite elements armed as the medial accessorial element on basis.

Maxilliped (Figure 5C) four-segmented with armament formula: 3.2.1.3. Armature with widely spaced setule ornament in proximal half, discretely serrate in distal half. Frontal surface of basal segments and caudal surface of second segment with spinular patterns. Surfaces of terminal segments smooth (Figure 5D).

Leg 1 (Figure 6E) and legs 2–3 (Figure 6F) as in *A. chappuisi*. Leg 4 (Figure 6G) with distal margin of intercoxal sclerite deeply concave and short coxal medial seta. Caudal surface of leg 4 coxa as in *A. chappuisi* except for presence of an additional row of spinules near outer margin. Outer seta on basis long, reaching beyond middle of terminal exopodite segment. Medial margin of legs 2–4 basis smooth and with distal triangular prominence. Second leg 4 endopodite segment 2.5 times as long as wide. Inner terminal spine shorter than segment (1 : 0.88), twice as long as outer one. Complete armament formula of legs 1–4 in Table 3.

Leg 5 (Figure 4B, 7G) represented as a truncate triangular expansion of pedigerous somite (only visible in lateral view), located lateral on pediger, and bearing two apical elements representing ancestral distal segment: medial one stout, serrate and outer one slender and pinnate, both equally long. Outer seta (of ancestral basal segment) located proximally, 1.5 times longer than apical elements. Both the latter equally long, with medial one spiniform (smooth?) and outer one setiform.

Leg 6 vestige (Figures 4A, B, 7F) situated laterally in anterior third of genital double-somite, in same plane as leg 5 on preceding somite. Valve long ovate with three elements: medial and median one blunt, equally long, with hyaline appearance, outermost element setiform and short.

Male. Habitus (Figure 3B). Body length 895 μ m. Cephalothorax half as long as entire body length. Fifth and sixth pedigers with narrow serrate posterodorsal frill. Urosomites 3–5, parallel-sided, ornamented as in female (Figure 7A, B). Caudal rami with shape, armament and ornamentation as in female (Figure 7D).

Antennule (Figure 5G) 16-segmented, with following complement: 1(8+3Aesth)-2(4)-3(2)-4(1)-5(2)-6(2)-7(2)-8(2)-9(2+Aesth)-10(2)-11(2)-12I(2)-13(1+Aesth)-14(4)-15(3)-16(11+Aesth). Aesthetascs on segments 1. 11 and 13 linguiform and long. Aesthetasc on segment 16 reduced and tubular. Elements on segments 14 and 15 typically transformed in T-shaped plates. Segment 1 with spinule row in proximal half near frontal margin. Antenna, buccal appendages and legs 1-4 as in female.

Leg 5 (Figure 7A, B) as in female, except for the slightly longer median and outer seta. Leg 6 vestige (Figure 7A, B) with two elements on outer proximal corner: medial one spiniform and stout, outer one setiform, slightly shorter than medial element. Surface of valves smooth.

Allocyclops beadlei (Lindberg, 1956) comb. nov.

Bacillocyclops beadlei gen. nov. sp. nov. - Lindberg 1956a: 26, 27, 32-33, figs. 2a-d.

Bacillocyclops beadlei Lindberg, 1956 – Dussart and Defaye 1985: 147; 1995: 239, fig. L127B; 2001: 286, fig. L136A; 2006: 235.

Type specifications

Single female specimen (explicitly reported being damaged and incomplete, current location unknown) from the southeastern branch of the Rushoma marsh (Southwest Uganda), among *Typha* sp. (not examined).

Diagnosis

Female. Large cyclopid (1450 μ m) with distinct constricted urosome (pediger 5 as wide as genital somite) and genital double-somite little longer than wide; urosomites with crenulate hyaline lateral fringe, straight ventrally; anal somite with dense spinule girdle along posterior border; anal operculum crescentic, not produced caudally; caudal rami 2.8 times longer than width, parallel and cylindrical; posterolateral element long, 1.5 times longer than caudal ramus length, slender and pinnate; medial terminal seta close to 2.5 times longer than ramus; dorsal seta nearly as long as caudal ramus (0.95 : 1); antennule (apparently) 11-segmented; mouthparts unknown; coxa of legs 1-4 with medial element, setiform in legs 1-3, spiniform (?) in leg 4; intercoxal sclerites with rounded distolateral edges and smooth surfaces; medial spine on leg 1 basis slender, reaching far beyond middle of second endopodite segment; outer element on leg 2 basis spiniform (?), of legs 1, 3 and 4 setiform; rami of legs bimerous with spine formula 3.4.4.3; seta formula partially known, summarized in Table 3; medial distal spine on leg 4 endopodite 1.56 times longer than outer one, and as long as three-quarters of segment length; leg 5 obsolete with medial spine; median and outer seta detached and lost.

Male. Unknown.

Remarks

Bacillocyclops Lindberg 1956 is one of the most enigmatic and controversial genera erected in Cyclopidae as it was defined upon a single cyclopine female specimen, which was damaged, covered with a layer of detritus, and in a state of decomposition. Its type species, *B. beadlei* Lindberg 1956, stands as the sole member known so far.

Bacillocyclops has gained its status among Cyclopidae (Monchenko 1974; Dussart and Defaye 1985, 2006) and keys out on the basis of the obsolete leg 5 represented by a single element (Dussart and Defaye 1995, 2001; Boxshall and Halsey 2004). Leg 5 of the monospecific *Austriocyclops* Kiefer 1964 resembles that of *Bacillocyclops* and is known to have a variable number of setae (Kiefer 1964). The conservative armature and segmentation of the natatorial legs are obvious differences. *Austriocyclops* is nowadays positioned within Eucyclopinae Kiefer 1927 (Pospisil and Stoch, 1997) and is clearly not related to *Bacillocyclops*.

Lindberg's illustration of the fifth leg of *B. beadlei*, apparently an accurate representation of the appendage on the specimen at hand, is misleading because it depicts the leg only partially. The accompanying text explicitly states that the sole visible element representing leg 5 is the remnant of a ruined and incomplete appendage. Unfortunately, incomplete at both sides (Lindberg 1956a p. 32: "*la cinquième patte parait défectueuse des deux côtés*"). Because of its rigidity, the shortness of its ornamentation, and its position along the posteroventral border of the somite, Lindberg related the remainder as the vestige of the ancestral distal segment. The currently available keys (Dussart and Defaye 1995, 2001; Boxshall and Halsey 2004) refer solely to the original illustration of the leg but omit any comment about its incompleteness.

Attempts to locate the specimen failed. It might be lost. The structure of the mouthparts and details of the other appendages remain as such obscure. However, the appendages detailed in the original description of *B. beadlei* coincide remarkably well with the appendicular morphology known for the two other African species of the genus *Allocyclops*. Given Lindberg's indications, and comparing the leg 5 structure in *A. chappuisi* and *A. cavicola*, it seems reasonable to assume that the two fragile setiform elements (median and outer one) were dislodged during disintegration of the specimen.

Lindberg's interpretation of the robust spiniform armature on leg 2 (basis), leg 4 (coxa) and the leg 5 remnant is undoubtedly a misinterpretation of a bacterial/detritus layer stuck on them. The illustrations provided by Lindberg (his figs. 2c,d) depict elements with a distinct internal volume. The latter is considered herein as the representation of the elements in question, the outer sheet as a coat of detritus.

Consequently, *Bacillocyclops* sinks into synonymy with *Allocyclops*, and *A. beadlei* becomes the third known African representative of the genus *Allocyclops*. The species *A. beadlei* is readily separable from the other species by the setal armament on the terminal exopodite segment of leg 4 (see Table 3) and also deviates significantly from its congeners by the larger dimensions and proportional lengths of the armature on the caudal rami and the leg 4 endopodite. The differences are summarized in Table 2. Affinities between *Allocyclops* and *Bacillocyclops* were assumed previously when Pesce (1996) positioned *Bacillocyclops* along with *Bryocyclops*, *Allocyclops* and *Yansacyclops* Reid 1988 in the *Bryocyclops*-lineage. However, whether *Allocyclops* (inclusive *Bacillocyclops*) is directly related to *Bryocyclops* Kiefer, 1927 and *Yansacyclops* Reid, 1988 is not sustained and is discussed in the section below.

	A. chappuisi	A. cavicola	A. beadlei
Body length (μm)	720-740	1025-1050 (1000*)	± 1450
Caudal rami: L/W	2.33	3.15	2.78
Te/CR	0.86	1.0	1.56
Ti/CR	1.33	2.0	2.4
Td/CR	1.5	2.0	0.95
P4 End ₂ :L/W	2.0	2.5	2.63
P4 End ₂ : L int.ex spine	1.8	2	1.56
P4 End ₂ : L art/int spine	1.0	1.15	1.28

Table 2. Differential dimensions of the females of the three African Allocyclops species.

Note: *Body length of a preserved female type specimen deposited at the RMCA.



Figure 8. *Allocyclops botosaneanui* Plesa, 1981. Syntypes. (A) Female urosome, ventral; (B) female antennule, segments 1–9, dorsal view; (C) antennulary segments 10–11, dorsal view (ISER-collection).

Allocyclops botosaneanui Pleşa, 1981 (Figures 8–10)

Allocyclops botosaneanui sp. nov. - Pleşa 1981: 18, 31-33, figs 61-65.



Figure 9. *Allocyclops botosaneanui* Plesa, 1981. Syntypes. (A) Antenna, frontal; (B) maxillary basis and endopodite; (C) mandibular biting edge; (D) maxilliped; (E) maxillulary palp (ISERcollection).

Allocyclops botosaneanui Pleşa, 1981 – Pleşa 1989: 119 (tbl.); Dussart and Defaye 1985: 146; 2006: 219; Lescher-Moutoué 1986: 309; Rocha and Bjornberg 1988: 445.
Allocyclops (Allocyclops) botosaneanui Pleşa, 1981 – Karanovic 2001: 24; 2003: 148.

Material examined

Type series: two females and one male, all dissected, mounted in glycerine, on three, one and two slides, respectively; stored in the copepod collection at the Speology



Figure 10. *Allocyclops botosaneanui* Plesa, 1981. Syntypes. (A) Leg 1, frontal; (B) leg 2, caudal; (C) leg 3, frontal; (D) leg 4, caudal; (E) male leg 6; (F) outer corner of female fifth pediger with leg 5; (G) idem, of the male (ISER-collection).

Institute "Emil Racovitza", Cluj (Romania). In the absence of type indications on the slides, the specimens are considered here as the syntypes.

Origin (type locality)

Cuba, Province Havana: "Cueva Emilio" (type locality) at Aston (city location appr. 22°47′00″ N, 82°41′00″ W), in pools of phreatic water located in the largest room of the cave. Botosaneanu *leg.* 19 April 1969.

Note

Among the archives left by F. Kiefer copies of the original illustrations and measurements made by Pleşa are present. The original description (Pleşa 1981) principally dealt with the female, the male morphology remaining largely unknown. The redescription below is based on the three available specimens and summarizes the measurements of the five specimens originally collected and published separately (Pleşa 1989).

Amended description

Female. Habitus (see Pleşa 1981: fig. 61) as in the former species. Body length 956 μ m (956–993 μ m, n = 3) with prosome 1.54–1.79 times longer than urosome. Genital double-somite (Figure 7A) tapering, widest in anterior third. Posterior margins of cephalothorax and leg bearing somites straight, lacking fringes. Posterodorsal margin of leg 5 pediger not observed, Genital double-somite and following somites furnished with a wide serrate hyaline fringe. Genital complex expanding over almost entire length of double-somite, with anterior receptacle narrow, wide and ovate, and proximal receptacle long ovate. Copulatory pore leading to S-shaped duct connected to slightly backwards deflected transverse arms. Anal somite with girdle of spinules along posterior margin, interrupted ventrally on left side, uninterrupted on right side. Anal operculum crescentic, not expanded, with naked margin.

Caudal rami (Figure 8A) basically cylindrical, slightly wider at insertion, 2.25 times longer than wide (2.10–2.41) with set of spinules in anterior third of outer margin. Anterolateral seta inserted in second half of margin, accompanied with spinules at insertion. Distolateral element nearly (0.90–0.95 times) as long as ramus. Dorsal seta inserted on basal part, about 2.5 (2.23–2.83) times longer than ramus. Medial seta between 1.58 and 2.14 times longer than ramus. Principal terminal setae with breaking plane. Proportional lengths of terminal setae (outer to medial): 1-4.34-8.45-1.82.

Antennule (Figure 8B, C) 11-segmented, apparently reaching to caudal end of cephalothorax. Armament as in previous species, with the following exceptions: (1) spinule row on segment 1 straight and short; (2) linguiform aesthetasc on segment 8 just reaching beyond segment and as long as accompanying seta, and (3) setae of bithek on terminal segment less than half as long as tubular aesthetasc.

Antenna (Figure 9A) basically as in previous species. Exopodal seta absent, abexopodal margin with two equally sized setae. Spinule pattern on coxobasis either faded or absent, not observable. First endopodite segment with one seta, second segment with six setae. Outer distal one on second segment remarkably wide, robust and

remarkably long, three times terminal segment length at least. The latter with seven terminal setae (fine ornamentation not observable).

Mandible (Figure 9C) basically as in the previous species (complete illustration in Pleşa 1981: fig. 62). Biting edge with remarkably strong and multicuspidate principal teeth. Maxillular arthrite as in previous species. Maxillular palp (Figure 9E) with smooth surface, laterally with outer seta and distinct ramus, bearing three elements. Medial margin with two sub-apical setae and one robust serrate apical spine. Maxilla typical. Syncoxa with smooth surface. Claw of basis (Figure 9B) armoured with large number of slender teeth in mid-section. Accessorial claw with short row of long spinules in proximal third, finely serrate in middle and distal thirds. Endopodite distinctly two-segmented. Proximal and distal segment with one long element ornamented as accessorial claw on basis. Second element on proximal segment, robust, smooth and short (less than half as accompanying element). Setae on distal segment equally sized, short and smooth. Maxilliped (Figure 9D) long, with slender appearance, and setal formula: 3.2.1.2. Proximal segment with frontal cluster of spinules, second segment with frontal and caudal cluster, and terminal segment with short row on frontal surface.

Legs 1–4 (Figures 10A–D) with naked intercoxal sclerites and crescentic distolateral edges. Coxal surface of legs smooth, except for a short spinule row of caudal surface of leg 4. Medial coxal setae present on all legs, pinnate. Medial margin of legs rounded, and hairy, with a small triangular process in legs 2–4. Medial spine of leg 1 basis sturdy, reaching to middle of second endopodite segment. Armature listed in Table 3. Terminal leg 4 endopodite segment 2.59–3.08 times longer than wide, with inner terminal spine equalling (0.96–1.0) segment length. Ratio inner/outer terminal spines: 1.80–2.23/1.

Leg 5 (Figures 8A, 10F) distinctly laterally positioned, with ancestral segments not (?) differentiated from pediger (urosome ventrally viewed). Seta of basal segment rather short, pinnate. Outer element of ancestral terminal segment setiform, little longer than medial prominent spiniform element; the latter apparently naked. Leg 6 vestiges not visible.

Male. Habitus not seen. Body length $815 \,\mu$ m (767–861 μ m, n = 2) with short urosome. Prosome 2.13–2.39 times longer than urosome. Caudal rami as in female, slightly more compact, 2.08–2.28 times longer than wide. Dorsal seta 2.21–2.40 times longer than ramus. Proportional lengths of terminal setae (outer to inner): 1-4.82-broken-2.00. Details of urosome and caudal rami not observable.

Antennule strongly compacted and compressed on slide, segmentation hardly visible, apparently 16-segmented. Segment 1 with three aesthetascs, segments 4, 9 and 13 each with one aesthetasc, all remarkably long and wide (unfortunately partially broken). Aesthetasc on terminal segment tubular.

Mouthparts (as far as observable) and legs as in female. Leg 5 (Figure 10G) represented by three elements as in female. Medial element spiniform, smooth. Leg 6 vestiges (Figure 10E) with smooth valve surface and two elements on outer distal corner: medial one spiniform, outer one setiform, both equally long.

Remarks

The resemblances between *A. botosaneanui* and the African *Allocyclops* species are mainly confined to the similarities of the leg 5, the bimerous aspect of the legs and their

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	Ч	1	P2		Р	3	P	4
	EXO	END	EXO	END	EXO	END	EXO	END
Allocyclops chappuisi	I.1–III.2.3	0.1 - 1.11.3	I.1-III.11.4	0.1 - 1.11.4	I.1–III.I1.4	0.1 - 1.11.4	I.0–II.II.4	0.1 - 1.11.3
A. cavicola	I.1–III.2.3	0.1 - 1.11.3	I.1-III.I1.4	0.1 - 1.11.4	I.1-III.I1.4	0.1 - 1.11.4	I.0-II.I1.4	0.1 - 1.11.3
A. beadlei	?.?-111.2.3	0.1 - 1.11.3	2.2 - 111.11.4	3.2 - 2.2.2	?.?-111.11.4	3.2 - 2.2.2	?.?-II.I1.3	0.1 - 1.11.3
A. botosaneanui	I.1–III.2.3	0.1 - 1.11.3	I.1-III.I1.4	0.1 - 1.11.4	I.1-III.I1.4	0.1 - 1.11.4	I.0-II.I1.4	0.1 - 1.11.3
Metacyclops janstocki	I.1–III.2.3	0.1 - 1.11.3	I.1 - III.I1.4	0.1 - 1.11.4	I.1-III.I1.4	0.1 - 1.11.4	I.1-II.I1.4	0.1 - 1.11.3
Hypocyclops kieferi	I.0-III.2.3	0.1 - 11.1.2	I.0-III.I1.4	0.1 - 1.11.3	I.0-III.I1.4	0.1 - 1.11.3	I.0-II.II.3	0.1 - 1.11.3
H. montenegrinus	I.0-III.2.3	0.1 - 11.1.2	I.0–III.I1.3	0.1 - 1.11.2	I.0-III.I1.3	0.1 - 1.11.3	I.0-II.II.3	0.1 - 1.11.3
Psammocyclops	I.0–II.2.3	0.1 - 1.11.2	I.1–II.II.3	0.1 - 1.11.2	I.1–II.I1.3	0.1 - 1.11.2	I.0–I.II.3	[0.1 - 1.1.2]
excensis Ps. ritae	1.0-11.2.3	0.1-1.11.2	I.1-II.11.3	0.1-1.11.2	L.1-II.11.3	[0, 1–1, 11, 2]	1.0-1.11.3	[0, 1-1, 1, 2]
T/					T 1 TT 1 1			
V trbiocyclops silvaticus	1.1–111.2.3	0.1–1.11.2	I.I-II.II.4	0.1 - 1.11.3	I.1–II.11.4	0.1 - 1.11.4	1.0–1.11.4	0.1-1.1.3
Hesperocyclops pescei	I.1–III.2.3	0.1 - 1.11.3	I.1-III.I1.4	0.1 - 1.11.4	I.1-II.11.4	0.1 - 1.11.4	I.0-II.I1.4	[0.1 - 1.1.3]
H. herbsti	I.1–III.2.3	0.1 - 1.11.3	I.1-III.I1.4	0.1 - 1.11.4	I.1-II.I1.4	0.1 - 1.11.4	I.0-II.I1.4	[0.1 - 1.1.3]
H. transsaharicus	I.1–III.2.3	0.1 - 1.11.2	I.1-III.I1.4	0.1 - 1.11.4	I.1-III.I1.4	0.1 - 1.11.4	I.0-II.I1.4	[0.1 - 1.1.3]
Metacyclops	I.1–III.2.3	0.1 - 1.11.3	I.1-III.I1.4	0.1 - 1.11.4	I.1-II.11.4	0.1 - 1.11.4	I.0-II.I1.4	0.1 - 1.1.3
$denticulatus^*$								
Olmeccyclops	I.0–II.2.2	0.1 - 1.1.2	I.0–II.II.3	0.1 - 1.11.2	I.0–III.I1.3	0.1 - I.I1.2	I.0–I.11.2	0.1 - 1.1.2
veracruzanus q								
0. veracruzanus o ⁷	I.0-II.2.2	0.1 - 1.1.2	I.0-II.I1.2	0.1 - 1.11.2	I.0-II.I1.2	0.1 - 1.11.3	I.0–I.I1.2	0.1 - 1.1.2
M. operculatus	I.0-II.2.3	0.1 - 1.1.2	I.0-II.I1.3	0.1 - 1.11.2	I.0–II.II.3	0.1 - 1.11.2	I.0-I.11.3	0.1 - 1.1.2
Dussartcyclops	I.0–II.2.2	0.1 - 1.11.2	I.0-I.11.3	0.1 - 1.11.2	I.0-I.11.3	0.1 - 1.11.2	I.0–I.II.3	0.1 - 1.1.2
(Barrowcyclops)								
CONSENSUS								
Dussartcyclops	I.0-II.2.2	0.1 - 1.11.1	I.0-I.11.3	0.1 - 1.11.2	I.0–I.II.3	0.1 - 1.11.2	I.0–I.11.3	0.1 - 0.1.2
(D.) mortoni								

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D. (D.) uniarticulatus	I.0–II.2.2	0.1 - 1.11.1	I.0–I.II.3	0.1 - 1.11.2	I.0–I.II.3	0.1 - 0.11.2	I.0–I.II.2	[0.1 - 0.1.2]
Metacyclops arenicolous	I.0–III.2.3	0.1 - 1.11.2	I.0–III.II.4	0.1 - 1.11.3	I.0–III.II.4	0.1 - 1.11.3	I.0–II.II.4	0.1 - 1.11.3
Stolonicyclops heggiensis	I.0–II.2.3	0.1 - 1.11.2	I.0–II.II.3	0.1 - 1.11.2	I.0-II.II.3	0.1 - 1.11.2	I.0–II.II.3	[0.1-1.1.3]
Cochlacocyclops ateles	I.1–III.2.3	0.1 - 1.11.2	I.1–II.II.3	0.1 - 1.11.3	I.1–II.II.3	0.1 - 1.11.3	I.0-I.11.3	[0.1 - 1.1.2]
Goniocyclops primus	I.0-III.2.3	0.1 - 1.11.2	I.0–II.II.3	0.1 - 1.11.2	I.0-II.I1.3	0.1 - 1.11.2	I.0-I.11.3	0.1 - 1.1.2
"Cyclops minutissimusӠ	I.0-III.2.3	0.1 - 1.11.2	I.0–III.II.4	0.1 - 1.11.3	I.0-III.I1.4	0.1 - 1.11.3	I.0–II.II.4	0.1–1.II.3
"Allocyclops australonipponicus"	I.1–III.2.3	0.1–1.11.3	I.1–III.I1.4	0.1 - 1.11.4	I.1–III.I1.4	0.1 - 1.11.3	I.0-II.II.3	0.1–1.11.3
Species names in bold fac	te refer to obser -segmented co	ved material; ar ndition	mature formulae	between [] refer	to the fused cond	ition of the podc	omeres with the a	urrangement

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latter. [†]"*C. minutissimus*" refers to the specimen described in Kiefer, 1937a, b (personal observation) and "*A. minutissimus*" sensu Petkovski, 1971 (*in litt.*).

armature, and the 11-segmented female antennule. However, *A. botosaneanui* deviates from them in several aspects: (1) the large ovate and posteriorly expanded half of the female seminal receptacle with a distinct shaped and caudally directed, copulatory duct, (2) the absence of an antennary exopodite remnant seta, (3) third antennary segment with a reduced number of setae but with the distal element remarkably long, and (4) the presence of two instead of three elements on the proximalmost segment of the maxilliped.

Allocyclops botosaneanui appears to be more closely related to a group of *Metacyclops* species, and more in particular with *Metacyclops janstocki* Herbst, 1990 known from Antigua. Both share, besides the general aspect of the legs, the reduced aspect of the maxilliped (with the loss of the third element on the terminal segment) and third segment setation of the antenna (with six instead of the conservative nine setae). The resemblances of the leg 4, and more particular the proportional lengths of the segment of the second endopodite segment and its armature are remarkable. *Metacyclops janstocki*, however, still has a well-developed distal segment in leg 5, has a 12-segmented antennule and possesses a medial element on the first exopodite segment of leg 4 (which has to be confirmed). The male of *M. janstocki* is unknown. Several other representatives currently attributed to the genus *Metacyclops* are known to occur in the Carribean and adjacent regions (see Dussart and Defaye 2006) but few have been described in detail.

Allocyclops botosaneanui displays a series of characteristics, with the antennary and maxillipedal morphology clearly derived, which indicate that it is not directly affiliated to *Allocyclops*. Within the present systematic concept of the Cyclopidae in which the leg 5 structure is of pivotal importance, *A. botosaneanui* is maintained in the genus *Allocyclops*, but the placement should be considered as provisional.

Key to the species of the genus Allocyclops

1.	Leg 4 second exopodite segment with 5 inner setae, outer distal element on caudal rami as long as ramus, at most
2.	Caudal rami 2.5 times as long as wide, at most
3.	Leg 4 second endopodite segment twice as long as wide, medial seta on caudal rami as long as or slightly longer than ramus

Genus Psammocyclops Kiefer 1955 amend.

Psammocyclops gen. nov. - Kiefer 1955: 229.

Psammocyclops Kiefer 1955 – Kiefer 1956; Dussart 1982; Dussart and Defaye 1985, 2001, 2006; Lescher-Moutoué 1986; Boxshall and Halsey 2004.

Psammocyclops Kiefer 1935 – Karanovic 2001 [grad. nov.]; 2003; Tomikawa et al. 2005; Karanovic 2006.

Diagnosis

Cyclopidae with typical body shape; prosome prominent, urosome short; genital double-somite longer than wide, expanded in middle, with genital complex located in anterior third; integument of genital double-somite and two succeeding somites with pattern of depressions/scars; caudal border of prosomites straight, caudal border of urosomites with narrow irregularly serrate/undulate fringe; caudal margin of anal somite with continuous spinule girdle; anal operculum crescent or rectangular, moderately prominent, with naked border; cylindrical caudal rami with dorsal crest; distolateral and medial terminal elements pinnate, the latter shorter than the former and setiform; principal terminal setae without breaking plane; antennule 11-segmented with armament: 1(5)-2(2 or3)-3(4)-4(2)-5(1)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth); setal armament not modified; antennary coxobasis with exopodite remnant and two abexopodal elements; second endopodite segment with five setae; mandible with two long and one short seta on palp; maxillule and maxilla typical cyclopid, the latter with two-segmented endopodite; maxilliped four-segmented and erect, with 2.2.1.3 armature; legs 1-4 biramus; legs 1 and 2 with bimerous rami; legs 3 and 4 exopodite bimerous, endopodite unimerous or bimerous in leg 3, unimerous in leg 4, both with ancestral segment shape clearly defined; exopodite spine formula 2.3.3.2 and seta formula 5.4.4.4; armament details in Table 3, armament distribution is given in Table 1.

Legs 1–4 with medial pinnate coxal seta, and smooth intercoxal sclerites with crescentic distolateral edges; leg 1 with long, slender and serrate medial spine on basis; medial border of leg 1 basis simple crescent, of legs 2–4 with or without short triangular distal structure; leg 5 obsolete: seta representing ancestral basal segment located laterally on pediger, both elements representing ancestral distal segment located along ventral border of pediger; both slender; leg 6 located dorsolateral with three elements: dorsal one setiform and pinnate, middle and medial one dwarfed, blunt, with hyaline appearance; genital complex with frontal and caudal expanded receptacle.

Male. Urosome with narrow leg 5- and leg 6-bearing somites; antennule typical bi-geniculate, apparently 16-segmented with unmodified setal armament and three aesthetascs on first segment; other details unknown so far; mouthparts and legs as in female, except narrower aspect of leg 4 endopodite; leg 5 as in female, except for longer outer element of ancestral distal segment; leg 6 bearing three elements, all setiform and slender, medial one longest; surface of leg 6 valves smooth.

Type species

Psammocyclops excellens Kiefer 1955 by monotypy.

Other species

Allocyclops ritae Dumont and Lamoot 1978.

Psammocyclops excellens Kiefer 1955 (Figures 11 and 12)



Figure 11. *Psammocyclops excellens* Kiefer, 1955. Syntypes. (A) Female habitus; (B) female urosome, ventral, with two spermatophores attached; (C) male urosome, ventral (A: FKCC vial 2460, B: FKCC 5501, C: FKCC 5503).

Psammocyclops excellens gen. nov., sp. nov. – Kiefer 1955: 229–231, figs 25–30. *Psammocyclops excellens* gen. nov., sp. nov. – Kiefer 1956: 61–63, figs 51–57. *Psammocyclops excellens* Kiefer, 1955 – Dussart 1982: 78, fig. 19B; Lescher-Moutoué

1986: 308; Dussart and Defaye 1985: 146; 1995: 236; 2001: 283; 2006: 235.

Allocyclops (Psammocyclops) excellens (Kiefer, 1955) comb. nov. – Karanovic 2001: 25; 2003: 148.

Psammocyclops primus Kiefer - Dussart and Defaye 1995: 240 [lapsus calami].



Figure 12. *Psammocyclops excellens* Kiefer, 1955. Syntypes. (A) Female antennule, dorsal; (B) antenna, frontal; (C) maxilla; (D) leg 1, frontal; (E) leg 3, second endopodite segment, caudal; (F) leg 4, frontal (A–F: FKCC 5500).

Material examined

One female (FKCC 5500-5501) and one male (FKCC 5502-5503) both partially dissected, labelled "*typus*" and one female (FKCC vial 2460), preserved in glycerine (without type indications on labels).

Origin (type locality)

Madagascar: interstitial in gravel bed of a tributary of the upper L'Onilahy River, along road Ihosy to Betroka, 300 km south of the former, Paulian leg (type reference).

Description

Female. Habitus (Figure 11A). Length (measures and illustrations from female in FKCC vial 2460), 500 μ m. Urosome slightly longer than one-third of entire body length, with wide genital double-somite. Urosomites 4 and 5 short. Posterior margin of anal somite with a continuous row of spinules. Anal operculum slightly caudally produced, semi-rectangular. Integument of genital double-somite with irregular pattern of scars, dorsally and laterally. Hyaline fringe of genital double-somite and following somites irregularly serrate, partially straight.

Caudal rami (Figure 11B) cylindrical, 3.3 times longer than wide without clearly defined dorsal crest. Anterolateral seta arising in middle of median third. Distolateral seta shorter than ramus (0.77:1) nearly twice as long as medial one, and accompanied by strong spinules near insertion. Principal terminal setae without breaking planes. Dorsal seta as long as distolateral one.

Antennule (Figure 12A) 11-segmented, not reaching beyond posterior margin of cephalothorax (Figure 11A). Setal complement: 1(5)-2(3)-3(4)-4(2)-5(1)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth). Aesthetasc on segment 8 linguiform, reaching to middle of segment 9. Segment 10 aesthetasc filiform, tubular on terminal segment, the latter half as long as accompanying seta. Segment 1 with row of spinules in proximal half.

Antenna (Figure 12B) four-segmented, with short serrate exopodal seta and two abexopodal ones. Endopodite segments with one, five and seven setae, respectively. Spinule pattern on coxobasis obscured with, at least, a cluster of minute spinules present near middle of outer margin, on frontal surface.

Mandible with palp, bearing three setae (two long, one short). Maxillule with 10 elements on arthrite, complete palp and endopodite. Maxilla (Figure 12C) with two slender setae on distal endite of syncoxa. Basis with few teeth on claw, accessorial claw broken. Endopodite two-segmented with two and three setae, respectively. Principal ones equally long, serrate in distal half. Maxilliped four-segmented with setal complement: 2.2.1.3, details obscured, not visible.

Leg 1 (Figure 12D): intercoxal sclerite not observed. Coxa with medial pinnate seta. Basis with long outer seta. Serrate medial spine not reaching middle of second endopodite segment. Legs 2 and 3 with medial coxal pinnate seta and naked intercoxal sclerites with rounded distolateral edges. Medial border of basis with small triangular distal process. Rami bimerous. Leg armament in Table 3. Terminal spine on second endopodite segments longer than segment (Figure 12E).

Leg 4 (Figure 12F) with naked intercoxal sclerite and prominent crescentic distolateral edges. Coxa with medial pinnate medial seta, reaching beyond basis. Basis

with crescentic and naked medial margin and a small triangular process close to endopodite articulation. Exopodite two-segmented, endopodite segments with bimerous appearance but coalescent. Discrete sclerotized transverse line as remnant of ancestral articulation present. Terminal spine only little longer than segment. Leg armature summarized in Table 3.

Leg 5 (Figure 11B) represented as a narrow expansion of posteroventral margin of pediger. Outer seta (= ancestral basal segment vestige) located laterally on pediger, elements representing ancestral distal segment with ventral position. Lateral seta twice as long as longest median element, the latter pinnate, distinctly longer than medial one (1.4–1.6 times). Medial element remarkably slender, near to setiform, seta not observable.

Leg 6 (not illustrated) with three elements: outer one setiform, at least twice as long as medial ones, both the latter blunt, equally long, with hyaline appearance. Receptacle largely faded, details not observable, apparently with anterior and caudal expanded parts. Copulatory pore area rather large, not clearly visible because of attached spermatophores.

Male. Habitus not observed, according to Kiefer (1955) body length 510 μ m. Urosomites (Figure 11B) with posterior frills as in female. Caudal rami cylindrical, complemented as in female.

Antennule not observed in detail. Buccal appendages and legs, as in female.

Leg 5 (Figure 11B) with outer seta half as long as in female. Setae representing distal segment arising from distinct semi-ovate protrusion of posteroventral margin of pediger with medial element shorter than outer one. The three leg 5 vestiges with setiform appearance.

Leg 6 vestige (Figure 11B) with three slender elements on outer distal corner. Outermost element shortest, median one 1.5 times longer, and medial twice as long as outermost one reaching to posterior margin of following somite. Medial one inflated near insertion. Valves smooth.

> Psammocyclops ritae (Dumont and Lamoot, 1978) (Figures 13–15)

Allocyclops ritae sp. nov. – Dumont and Lamoot 1978: 22–25, figs 1–2.

Allocyclops ritae Dumont and Lamoot, 1978 – Dussart and Defaye 1985: 146; 2006: 218–219; Lescher-Moutoué 1986: 309; Reid 1988: 430; Rocha and Bjornberg 1988: 445.

Allocyclops (Psammocyclops) excellens – Karanovic 2001: 25; 2003: 148 [comb. nov.]

Material examined

Type series: one female (holotype, not explicitly marked) and one male (paratype), dissected and mounted, inventoried as RBINSc COP 7662 and RBINSc COP 7663.

Additional: two females (topotypic, preserved in alcohol, RBINSc COP 7651) from the collection of Fr. Lescher-Moutoué and collected by G. Kouassi Konan and A. Konan Ndri, 15 May 1998.



Figure 13. *Psammocyclops ritae* (Dumont and Lamoot, 1978). Topotypic. (A) Female urosome, dorsal; (B) idem, lateral; (C) idem, ventral (A–C: RBINSc COP 7651).

Origin

Ivory Coast, Nature Reserve Lamto, Savane du Virage Glissant, 1.5 m long ephemeral pool in granite outcrop near biological research centre, type locality (Lamoot *leg.*). Type series as well as supplementary material.

Description

Female. Habitus as in former species, $600-750 \mu m$ long. Posterior margin of genital double-somite and following somites irregularly serrate. Integument of genital



Figure 14. *Psammocyclops ritae* (Dumont and Lamoot, 1978). Type series. (A) Female antennule; (B) female anal somite and caudal rami, dorsal view; (C) outer corner of female leg 5 pediger with leg 5 vestiges, ventral view; (D) leg 1 protopodite and endopodite, frontal; (E) male urosome, ventral (holotype, A–D: RBINSc COP 7662; paratype, E: RBINSc COP 7663).

double-somite and urosomites 4 and 5 with patterns of scars (partially illustrated). Anal operculum expanded, crescentic in types (Figure 14B), rectangular in supplementary specimens (Figure 13A), border naked. Anal somite with complete girdle of spinules along posterior border.

Caudal rami (Figure 14B) 3.15 times longer than wide, divergent in type specimens, parallel in supplementary specimens. Dorsal surface with longitudinal crest close to, and parallel with, outer margin, and long defined triangular sinus in anterior half of inner margin. Anterolateral seta located in median third, without spinules at insertion. Distolateral seta, 0.75 times the caudal ramus length, with minute spinules near



Figure 15. *Psammocyclops ritae* (Dumont and Lamoot, 1978). Type series. (A) Leg 3 protopodite and endopodite, frontal; (B) female leg 4 protopodite and endopodite, frontal; (C) male leg 4 protopodite and endopodite, caudal; (D) male leg 4 endopodite, frontal (holotype, A, B: RBINSc COP 7662; paratype, C, D: RBINSc COP 7663).

insertion. Medial seta slightly longer than half the distolateral one. Dorsal seta as long as medial one. Principal terminal setae without breaking plane.

Antennule (Figure 14A) 11-segmented, with following setal complement: 1(5)-2(2)-3(4)-4(2)-5(1)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth). Segment 1 with short spinule row in proximal half. Aesthetasc on segment 8 linguiform (very short), on segment 10 filiform, and on segment 11 tubular, shorter (0.75) than accompanying seta.

Antenna and mouthparts as in *P. excellens*.

Leg 1–4 with long medial coxal pinnate seta and naked intercoxal sclerites with crescentic distolateral edges. Legs 2 and 3 basis crescentic, hairy, without triangular distal expansion. Medial spine on leg 1 basis reaching beyond middle of second endopodite segment, slender and serrate (Figure 14D). Legs 1 and 2 bimerous, leg 3 and 4 with bimerous exopodite and endopodite with coalescent segments (Figure 15A–C). Remnant ridge of ancestral articulation visible on frontal surface,
absent on caudal surface. Leg 4 (Figure 15B,C) with spinule row along distal margin of coxal caudal surface. Basis with smooth medial margin, lacking triangular distal process. Complete leg armature listed in Table 3.

Leg 5 (Figure 13B,C) with seta of ancestral basal segment close to three times longer than elements of ancestral distal segment. Both the latter inserted on small expansion of posteroventral border of pediger. Outer seta only little longer than medial spine. The latter slender, serrate (clearly visible in supplementary material). Leg 6 vestige (Figure 13B) as in preceding species. Genital area large with frontal and caudal parts expanded (Figure 13C). Copulatory pore minute, leading to recurved ductus.

Male. Habitus not observed; according to Dumont and Lamoot (1978) between 430 and 450 μ m. Urosome slender, integument with scars. Caudal rami as in female specimen, but parallel as in supplementary females.

Antennule 16-segmented, with three aesthetascs on segment 1. Other details not observable. Mouthparts and legs as in female, except for the bimerous nature of leg 3 and leg 4 endopodite (Figure 15D).

Leg 5 (Figure 14E) with seta representing ancestral basal segment short. Both elements of ancestral distal segment slender, medial one shorter (\pm 0.85 : 1) than outer one. Leg 6 vestige (Figure 14E) with three elements on outer distal corner. Outermost and median one short (equally long?). Medial one three times longer than median element, reaching far beyond posterior margin of following urosomite, and slim. Valves with smooth surface.

Remarks

Psammocyclops ritae and *P. excellens* are very similar and have been considered conspecific (Karanovic 2001). Despite the obvious resemblance they differ in several details: (1) the longitudinal crest on the dorsal surface of the caudal rami in *P. ritae* is far more apparent than in *P. excellens*; (2) the setation of the female antennule is different with on segments I–V (5,2,4,2,1 setae in *P. ritae*, 5,3,4,2,1 in *P. excellens*); (3) the triangular process on the medial margin of leg bases is absent in *P. ritae*, present in *P. excellens*; (4) the considerable longer aspect of the male leg 6 armature in *P. ritae*; and (5) the fused nature of the endopodites in legs 3 and 4 in *P. ritae* instead of in leg 4 only for *P. excellens*.

Species differentiation in semi-subterranean cyclopines is a matter of details and we are ignorant of the morphological variability of both *Psammocyclops* since they are known from a few specimens and from their type locality only. The considerable distance between the two localities (Madagascar versus Ivory Coast) and the quite different habitats (interstitial versus an ephemeral pool in a granitic outcrop) support the supposition that these are separate species.

Genus Hypocyclops gen. nov.

Allocyclops Kiefer 1932 - [partim] Auctorum.

Diagnosis

Female. Cyclopidae with typical body shape; cephalothorax and urosome prominent, metasome short; genital double-somite longer than wide, without particular surface modifications, and genital complex located in anterior third; caudal border of urosomites with narrow undulate fringe; caudal margin of anal somite with continuous spinule girdle; anal operculum crescentic, not expanded, simple, with naked border; cylindrical caudal rami without dorsal crest; distolateral element spiniform, serrate; medial terminal short, setiform; principal terminal setae with breaking plane; antennule 11-segmented with armament (ancestral segmentation sequences): 1(8)-2(4)-3(6)-4(2)-5(2)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth); antennary coxobasis without exopodite remnant. with two abexopodal elements; second endopodite segment with five setae; mandible with single dwarfed seta, lacking distinct palp; maxillule and maxilla typical cyclopid, the latter with one segmented endopodite; maxilliped four-segmented, with 2.2.1.2 armature; legs 1-4 biramous with bimerous rami; exopodite spine formula 3.4.4.3 and seta formula 5.5/4.5/4.4; armament details in Table 3 and armament distribution is shown in Table 1.

Legs 1–4 with medial pinnate coxal seta, and naked intercoxal sclerites with crescentic distolateral edges; leg 1 basis with short, robust and serrate medial spine; leg 1 basis with simple medial border, leg 2–4 basis with minute triangular distal structure; leg 5 differentiated as truncate plate laterally located on pediger with proximal outer element and two apical ones: outer one setiform, medial one spiniform, robust and serrate; leg 6 located dorsolaterally, with three elements: dorsal setiform and pinnate, middle one shorter/less developed than medial one; genital complex expanded caudally (?).

Male. Urosome with short, rather narrow leg 6-bearing somite; antennule 15-segmented with armament (not completely known; listed according to position of segments): 1(8+3Aesth)-2(4)-3(3)-4(1+(?)1Aesth)-5(1)-6(2)-7(2)-8(2+1Aesth)-9(0)-10(4)-11(2)-12(1)-13(3+1Aesth)-14(3)-15(8+2Aesth); setae unmodified; mouthparts and legs as in female, except more slender leg 4 endopodite; leg 5 as in female; leg 6 with three elements: outer one setiform, medial one spiniform and robust, middle one minute; surface of leg 6 valves smooth.

Type species

Allocyclops kieferi Petkovski, 1971, here designated.

Other species

Allocyclops montenegrinus Karanovic, 2001.

Etymology

From the Greek *hypo*, meaning under or below, prefixed to the generic name *Cyclops*. The name refers to the phreatic habitats in which the species thrive. Gender masculine.

Hypocyclops kieferi (Petkovski, 1971) comb. nov. (Figures 16 and 17)

Allocyclops kieferi sp. nov. - Petkovski 1971: 100-104, figs. 49-66.

Allocyclops kieferi Petkovski, 1971 – Kiefer 1978: 215; Dussart and Defaye 1985: 146; 2006: 219; Lescher-Moutoué 1986: 309; Reid 1988: 430; Rocha and Bjornberg 1988: 445.

Allocyclops (s. str.) kieferi Petkovski, 1971 - Karanovic 2001: 24; 2003: 148.

Material examined

One female and one male (topotypic, syntypes?) mounted un-dissected, catalogued RBINSc COP 7034 and RBINSc COP 7035, respectively.

Origin

Republic of Macedonia: pump bore holes (type locality) at Krivogastani (appr. 41°20'7" N, 21°19'49" E, city centre) in the Pelagonian Plain, G. Karaman *leg.*, T. Petkovski *det*.

Differential diagnosis

Medium-sized *Hypocyclops* with caudal rami three times as long as wide. Receptacle with expanded anterior and posterior part. Second exopodite segments of leg 2–4 with five medial setae. Complete leg armament in Table 3. Second endopodite segment of leg 4 twice as long as wide, with inner distal spine shorter than segment, and 1.7 times longer than outer terminal spine. Median seta of leg 5 slightly longer than inner spine. Male leg 6 with two elements: medial one robust spiniform.

Amendments

Petkovski (1971) provided a detailed description, supplementary observations obtained from the two available specimens are given here.

Female. Body 770 μ m long. Posterodorsal margin of leg 5 pediger straight, lateral margins naked. Genital double-somite with faint transverse ridge in anterior third of ventral surface (Figure 16A: marked in dotted line). Genital area not observed, faded. Posterior border of genital double-somite and urosomites 4 and 5 with irregular undulate hyaline fringe. Anal somite with crescent and short operculum. Posterior border with complete girdle of spinules. Caudal rami three times longer than wide, cylindrical, without dorsal longitudinal ridge. Distolateral element about two-thirds of caudal rami length. Medial seta shorter than distolateral one (0.5–0.66 : 1). Dorsal seta longer than ramus. Minute spinules near insertion of lateral elements.

Antennule (Figure 17A) 11-segmented and short, complement as follows: 1(8)-2(4)-3(6)-4(2)-5(2)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth). Aesthetasc on segment 8 linguiform, reaching beyond distal margin of segment. Aesthetasc on segment 10 short and filiform, on segment 11 rather long and tubular. Segment 1 with short spinule row in proximal half.



Figure 16. *Hypocyclops kieferi* (Petkovski, 1971) comb. nov. Topotypic (A) Female urosome, dorsal view; (B) male urosome, dorsal view; (C) outer corner of male fifth pediger with leg 5 vestiges; (D) male leg 6 vestige; (E) outer corner of female fifth pediger with leg 5 vestiges; (F) female leg 6 vestiges (A, E, F: RBINSc COP 7035; B–D: RBINSc COP 7034).



Figure 17. *Hypocyclops kieferi* (Petkovski, 1971) comb. nov. Topotypic. (A) Female antennule, dorsal (arrow heads indicating insertions of lost setae); (B) male antennule, dorsal (arrow indicating distal aesthetasc); (C) female leg 4 endopodite, caudal; (D) male leg 4 endopodite, caudal (A, C: RBINSc COP 7035; B, D: RBINSc COP 7034).

Legs 1–4 with coxal pinnate seta and naked intercoxal sclerites with crescent distolateral border in legs 1–4. Medial spine on leg 1 basis short and stout, as long as first endopodite segment. Medial margin of basis in legs 1–4 crescent, without triangular distal expansion. Exopodite spine formula 3.4.4.3. Leg 4 endopodite distinctly two-segmented with distal segment twice as long as wide (Figure 17C). Length of medial terminal spine equals $\pm 3/4$ of segment length. Outer terminal spine half as long as medial one. Complete armature listed in Table 3.

Leg 5 (Figure 16E) represented as truncate expansion, confluent with pediger, with medial element stout and spiniform, shorter than median seta. Seta representing ancestral basal segment rather short.

Leg 6 vestigial (Figure 16F) with three elements: outermost setiform, twice as long as median and inner one. Both the latter with hyaline appearance and equally long. Medial one slightly more robust than median one.

Male. Body length between 600 and 650 μ m (according to Petkovski 1971). Body ornamentation and caudal rami as in female (Figure 16B).

Antennule (Figure 17B) 15-segmented, geniculate, with following complement (so far as is visible): 1(8+3Aesth)-2(4)-3(3)-4(1)-5(1)-6(2)-7(2)-8(2+Aesth)-9(0)-10(4)-11(2)-12(1)-13(3+Aesth)-14(3)-15(8+2 Aesth). Aesthetascs on segments 1, 8 and 13 linguiform, on segment 15 tubular. Elements on segments 13 and 14 typically plate-shaped.

Legs 1–4 and leg 5 as in female (Figure 16C), leg 6 (Figure 16D) with three elements: outer one setiform and medial one prominent and spiniform; middle one short, transparent, hardly visible (probably overlooked in original description).

Hypocyclops montenegrinus (Karanovic, 2001) comb. nov.

Allocyclops (Allocyclops) montenegrinus, sp. nov. – Karanovic 2001: 21–23, 24, figs. 1–18.

Allocyclops (Allocyclops) montenegrinus Karanovic, 2001 – Karanovic 2003: 148; Tomikawa et al. 2005: 24–25.

Type specifications (material not examined)

Single female specimen collected in small rivulet at the village of Vrela, near Cetinje (Montenegro).

Differential diagnosis

Female. Medium sized *Hypocyclops* with caudal rami 2.7 times as long as wide. Receptacle unknown. Antennule 11-segmented with setal complement as previous species; second exopodite segment of legs 2–4 with four medial setae. Complete leg armature listed in Table 3. Second endopodite segment of leg 4 1.7 times as long as wide, with inner distal spine shorter than segment and 2.4 times longer than outer terminal spine. Leg 5 with median and medial elements equally long.

Male. Unknown.

Genus Virbiocyclops gen. nov.

Allocyclops Kiefer 1933 – [partim] Auctorum. Psammocyclops Kiefer, 1955 – Karanovic 2001, 2003.

Diagnosis

Female. Cyclopidae with typical body shape, and robust appearance; cephalothorax, metasome and urosome equally long; genital double-somite as wide as long, with pattern of crests on dorsal and lateral surface; caudal border of cephalothorax and leg 2-bearing somite straight, caudal border of leg 3-5-bearing somites with narrow serrate fringe, of genital double-somite and both succeeding somites with wide, deep serrate fringe; caudal margin of anal somite with continuous spinule girdle; anal operculum rectangular and caudally expanded with irregular surface and border; cylindrical caudal rami with dorsal crest; distolateral element spiniform serrate/pinnate; medial terminal element shorter than ramus, setiform and pinnate; principal terminal setae without breaking plane; antennule 11-segmented with armament according to ancestral segmentation: 1(7 or 8)-2(2)-3(5)-4(2)-5(2)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth); antennary coxobasis with exopodite remnant and two abexopodal elements; second endopodite segment with five setae; mandible with two long and one short seta on palp; maxillule and maxilla typical cyclopid, the latter with two-segmented endopodite; maxilliped four-segmented and erect, with 2.2.1.3 armature; legs 1-4 biramous with bimerous rami; exopodite spine formula 3.3.3.2 and seta formula 5.5.5.5; leg armament details in Table 3 and armament distribution shown in Table 1.

Legs 1–4 with medial pinnate coxal seta; intercoxal sclerites of legs 1–3 naked, with spinule pattern in leg 4, each with crescent distolateral edges; Basis of leg 1 with long, slender and serrate medial spine and an additional blunt expansion on medial border; medial border of leg 2–4 bases with prominent triangular expansion; leg 5 obsolete, located on lateral expansion of pediger; remnant seta of ancestral basal segment long and sturdy; outer element of ancestral distal segment shorter than medial element; former one slender and setiform, latter one robust, spiniform and serrate; leg 6 located dorsolateral with three elements: dorsal one setiform and pinnate, middle and ventral one dwarfed, equally long, blunt, with hyaline appearance; receptacle of genital complex expanded frontally and caudally with long copulatory duct.

Male. Urosome with laterally expanded leg 6-bearing somite; antennule 16-segmented with armament (according to position): 1(8+3 Aesth)-2(4)-3(2)-4(1+1Aesth)-5(2)-6(2)-7(2)-8(2)-9(2+1 Aesth)-10(2)-11(2)-12(2)-13(1+Aesth)-14(4)-15(3)-16(11+1Aesth); setae not modified; mouthparts and legs 1–4 as in female, except for slender shape and absence of folded medial border of leg 4 endopodite; leg 5 as in female; leg 6 with two elements: outer one setiform, pinnate and half as long as robust medial spiniform element; surface of leg 6 valves rigid and smooth.

Type species

Allocyclops silvaticus Rocha and Bjornberg, 1988, here designated.

Etymology

After *Virbio* or *Virbius*, the Roman woodland god, prefixed to the generic name *Cyclops*; gender masculine.

Virbiocyclops silvaticus (Rocha and Bjornberg, 1988) comb. nov. (Figures 18, 19A–G, 20A–C)

Allocyclops silvaticus sp. nov. - Rocha and Bjornberg 1988: 445-448, figs. 1-20.

Allocyclops (Psammocyclops) silvaticus Rocha and Bjornberg, 1988 comb. nov. – Karanovic 2001: 25; 2003: 148.

Allocyclops silvaticus Rocha and Bjornberg, 1988 – Rocha and Botelho 1998: 141; Schutze et al. 2000: 753, 771, figs. 13, 23, tbl. 1; Dussart and Defaye 2006: 219.

Material examined

Two females and two males, from 2–3 cm deep water in wheel ruts with lush growth of green algae (24°03′17.8″ S, 47°13′07.6″ W), at Iterei farm, Miracuta, State of São Paulo, Brazil. CEF Rocha and JW Reid *leg.*, 13 September 1999. One female and one male dissceted, RBINSc COP 9424 A–D and COP 9425-D, two females and one male preserved, RBINSc COP 9545.

Amendments

The outstanding description by Rocha and Bjornberg (1988) of this species is not repeated here. Only some details are highlighted and compared with those of female specimens of *Hesperocyclops herbsti* Rocha and Bjornberg, 1987 (co-occurring at the same locality, registered RBINSc COP 9423A–D, COP 9426A–D and COP 9546). The antennule (Figure 19I), maxilliped (Figure 19H) and legs 1 and 4 (Figures 20D and E, respectively) of *H. herbsti* are given to facilitate comparison and illustrate the resemblances.

Female. Urosome (Figures 18A–C) with leg 5 pediger considerably wider than genital double-somite, with leg vestiges located distinctly lateral. Genital double-somite, widest in anterior half, with prominent sclerified ridges on dorsolateral surface. Leg 6 located above horizontal plane, with vestigial elements in dorsolateral position. Urosomites 4 and 5 parallel sided. Anal somite with complete girdle of long spinules along posterior margin. Anal operculum produced caudally, covering anal sinus completely, roughly quadrate, and with smooth margin. Integument of urosomites, except pediger 5 with pattern of crescent scars. Posterodorsal margin of pediger 5 indistinct near lateral corners, median part distinct and serrate. Posterior margin of genital double-somite and succeeding somites with prominent serrate hyaline fringe.

Caudal rami, cylindrical, with distinct dorsal ridge in anterior three-quarters. Posteroventral margin straight. Anterolateral seta without spinules at insertion, distolateral element with spinules at insertion. Principal terminal setae without breaking plane. Medial seta shorter than rami.

Antennula (Figure 19A) 11-segmented with short spinular row on segment I, other segments with smooth integument. Complement: 1(8)-2(2)-3(5)-4(2)-5(2)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth). Hyaline structure on segment 5 short and



Figure 18. *Virbiocyclops silvaticus* (Rocha and Bjornberg, 1988) comb. nov. (A) Female urosome, dorsal view; (B) idem, ventral view; (C) idem, lateral view; (D) left leg 5, lateral view; (E) left outer corner of leg 5-bearing somite, dorsal view; (F) right outer corner of leg 5 bearing somite, ventral view (A–F: RBINSc COP 9424).

blunt (Figure 19C). Aesthetasc on segment 8 linguiform, not reaching middle of following segment. Aesthetasc on segment 10, filiform, on segment 11 tubular, nearly as long as accompanying seta.

Antenna with two abexopodal setae and one short exopodite remnant seta on coxobasis. Second endopodite segment with four setae, terminal segment with seven



Figure 19. *Virbiocyclops silvaticus* (Rocha and Bjornberg, 1988) comb. nov. (A) Male urosome, lateral view; (B) female antennule, ventral view; (C) female antennulary segments II–V, dorsal view; (D) antennary coxobasis, frontal; (E) idem, caudal; (F) maxilliped contour, frontal; (G) maxilliped, caudal; *Hesperocyclops herbsti* Rocha and Bjornberg, 1987. (H) maxilliped, frontal; (I) female antennule, dorsal view (A: RBINSc COP 9425; B–G: RBINSc COP 9424, H: RBINSc COP 9423, I: RBINSc COP 9426).



Figure 20. *Virbiocyclops silvaticus* (Rocha and Bjornberg, 1988) comb. nov. (A) Leg 1, frontal (arrow: medial edge of basis enlarged), (B) female leg 4, frontal; (C) Male leg 4 endopodite, frontal; *Hesperocyclops herbsti* Rocha and Bjornberg, 1987. (D) leg 1, frontal (arrow: medial edge of basis enlarged); (E) female leg 4, frontal (A, B: RBINSc COP 9424; C: RBINSc, COP 9425; D, E: RBINSc COP 9423).

setae. Frontal surface of coxobasis (Figure 19D) with small cluster along outer margin and spinular transverse row near inner proximal corner. Caudal surface (Figure 19E) with three clusters of spinules: two in proximal half, one median near outer margin.

Maxilliped (Figure 19F,G) with, from proximal to distal segment, two, two, one and one setae, respectively. Setae flexible, pinnate in proximal half, serrate distally, except for both smooth terminal ones. Surface of second segment furnished with row of slender spinules, parallel to medial margin.

Leg 1 (Figure 20A) with spinules near distal (frontal) outer corner of praecoxa, and near (caudal) outer margin of coxa. Intercoxal sclerite with naked surfaces, distolateral corners crescent. Coxal medial seta long (reaching beyond first endopodite segment) and pinnate. Medial margin of basis with supplementary expansion (see enlargement in Figure 20A) over-reaching main medial margin. Border set with hairs. Medial spine on basis, reaching halfway to second endopodite segment, serrate and sturdy, inserted in front of endopodite. Exopodite with blunt, rigidly sclerified outer corners. Outer distal and subdistal edges of second endopodite segment large, rather blunt. Terminal claw longer than segment, sera minute, not visible in anterior view. Praecoxa, coxa and intercoxal sclerite in legs 2 and 3 as in leg 1, except for additional short (up to 10 spinules) row near distal outer corner of frontal surface. Basis with distinct triangular medial distal corner. Complete leg armament in Table 3.

Leg 4 (Figure 20B) intercoxal sclerite with, on caudal surface, complete transverse row of long spinules in middle and at basis of distolateral crescent edges. Caudal surface of coxa furnished with median row in middle of proximal and distal margin, and two spinular clusters near outer margin. Medial border of basis with narrow triangular outgrowth on distal edge. Medial border of first endopodite segment with supplementary longitudinal ridge on frontal surface. Terminal spine on second segment inserted between two large triangular outgrowths of distal margin, and slightly shorter than segment.

Leg 5 (Figure 18D–F) confluent with pediger. Vestiges located at outermost posterolateral margin of somite. Outer element short and sturdy, arising from truncate expansion of surface. Distal segment vestiges located on small confluent rectangular expansion, discretely outwards positioned, and in equal plane of ventral surface. Outer element slender, shorter than medial element. The latter prominently spiniform and serrate.

Leg 6 long ovate, with three elements: two medial blunt and hyaline structures and one outer seta. Receptacles large. Anterior part ovate, posterior part bi-lobed. Copulatory pore leading to U-shaped caudally directed slender duct, located in a triangular-shaped area of distinctly denser tissue. Lateral arms rather wide.

Male. Urosome (Figure 19A) as in female, except for individualized sixth leg bearing somite. Caudal rami idem. Antennule as described 16-segmented, armament see generic diagnosis. Mouthparts and legs 1–4 as in female, except for proximal leg 4 endopodite segment of leg 4 lacking supplementary crest on frontal surface (Figure 20C).

Antennule 16-segmented with complement listed in generic diagnosis. Aesthetascs on segment 1 linguiform, of normal proportions. Mouthparts and legs as in female, except for absence of crest on proximal leg 4 endopodite segment. Leg 5 (Figure 19A) basically with same structure as in female, but outer seta inserted more directly (lacking prominence) on pediger. Leg 6 represented by two elements: medial one spiniform, at least twice as long as outer pinnate element, both inserted on distinct expansion of outer posterior corner of valve. Surface of valves smooth.

Remarks

The herein examined specimens (from the State of São Paulo) and the originals (from the State of Sergipe, material not examined) differ in the following aspects: (1) the antennule in the Sergipe specimens possess seven and three setae on segments 1 and 2, respectively; females examined by Schutze et al. (2000) and obtained at Comprida Island (State of São Paulo) appear to have eight and three setae on the first and second segments. The females from São Paulo here examined have seven setae on segment 1 although in both an insertion mark of seta 8 is discernable, but the seta is absent in the three specimens examined (marked with dotted lines in Figure 19B) and segment 2 bears only two setae; (2) the intercoxal sclerite of leg 4 is furnished with a supplementary row of spinules in the São Paulo specimens, and the caudal surface of the coxa has a more elaborated spinule pattern than the Sergipe specimens.

Genus Olmeccyclops gen. nov.

Allocyclops - Suárez-Morales, Mendoza and Mercado-Salas, 2010.

Diagnosis

Female. Habitus compact, slightly depressed, with postcephalic somites gently tapering towards anal somite, without distinct cyclopid body constriction at major body articulation; urosomal borders serrate; genital double-somite prominent, wider than long; shape of seminal receptacle unknown; anal operculum caudally expanded, crescentic, with serrate borders; caudal rami short, cylindrical, with dorsal crest, and furnished with a transverse row of long spinules along posteroventral border; distolateral element pinnate; terminal medial element shorter than ramus, setiform; principal terminal setae with breaking plane; antennule, short, 11-segmented with armament according to ancestral segmentation: 1(8)-2(2)-3(5)-4(1)-5(1)-6(2)-7(3)-8(2)-9(2)-10(2)-11(7+Aesth); antennary coxobasis with short exopodite remnant and 2 abexopodal elements; second endopodite segment with 4 setae; mandible with 1 short seta, lacking palp; maxillule and maxilla typical cyclopid, the latter with 2-segmented endopodite; maxilliped 4-segmented and erect, with 2.1.1.2 armature; legs 1-4 biramous with bimerous rami; exopodite spine formula 2.3.3.2 and seta formula 4.4.4.3; armament details in Table 2, armament distribution is shown in Table 1 for both female and male.

Legs 1–4 with pinnate medial coxal seta and naked intercoxal sclerites with crescentic distolateral edges; basis of leg 1 with medial spine; medial border of basis in legs 1–4 crescentic, lacking a triangular distal expansion; outer subdistal element on second endopodite segment of leg 3 modified into prominent serrate spine; leg 5 obsolete, located lateral on pediger, with three elements: one outer proximal seta and two apical

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slender elements, medial one slightly shorter than median one; leg 6 located laterally with three elements: dorsal one setiform, median and medial one short and triangular.

Male. Urosome with lateral expanded leg 6-bearing somite; antennule 15-segmented, typical geniculate, with single short aesthetasc on proximal segment; second segment (=[VI–VII]) with three setae; setation and presence of aesthetascs on following segments not clarified; mouthparts and legs 1 and 4 as in female, but different in legs 2 (exopodite) and 3 (exopodite and endopodite); outer subdistal element of leg 2 second endopodite segment setiform; leg 5 as in female; leg 6 with two elements: outer one setiform, pinnate and equally long as robust medial spiniform element; surface of leg 6 valves rigid and smooth.

Type species

Allocyclops veracruzanus Suárez-Morales, Mendoza and Mercado-Salas, 2010, here designated by monotypy.

Etymology

After *Olmeca*, the mysterious "rubber-people" and ancient Mexican civilization who inhabited the Gulf Coast plain in the region known nowadays as the state of Veracruz (Mexico) and prefixed to the generic name *Cyclops*. Gender masculine.

Olmeccyclops veracruzanus (Suárez-Morales, Mendoza and Marcado-Salas, 2010) comb. nov.

Allocyclops veracruzanus sp. nov. – Suárez-Morales, Mendoza and Marcado-Salas, 2010: 396–400, figs. 1–6.

Type specifications (material not examined)

Female (holotype), male (allotype) and paratypes from aquatic microcosms among leaf axils of the bromeliad *Tillandsia heterophylla* at Racho Viejo near San Andrés Tlalnehuanyocan, at 1420 m above sea level. Material hosted at ECOSUR, Unidad Chetumal (Mexico) and Muséum d'Histoire naturelle de Paris (France).

Remarks

Save the less depressed (flattened) aspect, the habitus of *Olmeccyclops* coincides remarkably well with that of the species assembled in groups I and II of *Bryocyclops* sensu Lindberg, 1956. The voluminous and wide female genital double-somite, the serrate and large anal operculum fitting in a triangular region formed by the dorsal crest on the rami and the slender setiform (distal) vestiges of the obsolete leg 5 are structural similarities which, in case details of the appendages were unknown, would indicate immediate affinity. The morphology of the appendages, however, deviates in many aspects from their counterparts in *Bryocyclops* group I and II (and the other currently included in the genus *Bryocyclops*; see Dussart and Defaye 2006). The striking

resemblances in habitus are seen as an exemplary illustration of convergency in cyclopines thriving in similar habitats (aquatic microcosms of leaf axils). Further conjectures about the affinities of *Olmeccyclops* among the Cyclopinae are discussed below.

Genus Hesperocyclops Herbst, 1984

Hesperocyclops transsaharicus (Lamoot, Dumont and Pensaert, 1981) comb. nov. (Figures 21 and 22)

Speocyclops transsaharicus sp. nov. – Lamoot et al. 1981: 53–57, figs 1–16.

Speocyclops transsaharicus Lamoot et al., 1981 – Dussart and Defaye 1985:138; 2006: 227; Lescher-Moutoué 1986: 311.

Allocyclops (Psammocyclops) transsaharicus comb. nov. – Karanovic 2001: 25; 2003: 148 [lapsus: A. (P.) transsaharicusus].

Material examined

Type series: six slides containing parts of the original single female (designated originally as the holotype) and pair of males, catalogued RBINSc COP 7029-7033, COP 9642.

Origin

Ivory Coast (Côte d'Ivoire): temporary pool 1 km from the village of Guilgo (approx. 6°32' N 7°31' W) in the valley of the Cavally River (type-locality). Lamoot *leg*, January, 1974.

Remarks

The remnants of the three original animals are scattered over six slides, and several body parts are missing. Label indications provide some information about the slide contents but are not sufficiently indicative to relate them to the published illustrations. The original description appears to be a mixture of observations of female and male structures and is, with regard to the natatorial legs and their armament, misleading. The description below is mainly based on the available materials; information extracted from the original description is indicated.

Redescription

Female. Habitus not observed; according to Lamoot et al. (1981), 500 μ m long, with compact appearance and urosome half as long as prosome. Genital double-somite (Figure 21A) distinctly wider than long (L/W ratio: 1.2). Rectangular appearance resulting from compression (compare Figure 21A with text figure 1 in Lamoot et al. 1981). Receptacle not observed, faded. Posterior border of genital double-somite and urosomite 4 and 5 with wide hyaline fringe, serrate, deeply incised. Anal operculum large, crescentic, covering entire anal sinus, and extending far beyond posterior margin of anal somite. Border smooth. Posterolateral and posteroventral margins of anal somite bordered with continuous spinular row.



Figure 21. *Hesperocyclops transsaharicus* (Lamoot et al., 1981) comb. nov. Type series. (A) Female urosome, dorsal view; (B) male anal somite and caudal rami, ventral view; (C) female antennule (holotype, A, B: RBINSc COP 7029–7030; paratype, C: RBINSc COP 7031).

Caudal rami divergent, not quite twice as long as wide, with distinct longitudinal crest on dorsal surface. Anterolateral seta located at distal end of median third of outer margin, without spinules near insertion. Distolateral element robust, as long as



Figure 22. *Hesperocyclops transsaharicus* (Lamoot et al., 1981) comb. nov. Type series. (A) Female leg 1 exopodite, frontal; (B) female leg 1 endopodite, flattened, inner lateral view; (C) female leg 2, caudal; (D) female leg 3 endopodite, caudal; (E) female leg 4, frontal; (F) male leg 4, frontal (arrow indicating setae absent in opposite leg) (holotype, A–E: RBINSc COP 7029–7030; paratype, F: RBINSc COP 7031–7033).

ramus, accompanied with five large spinules near insertion. Medial seta slender and short, less than half length of distolateral one. Principal terminal setae with expanded proximal part. Breaking planes absent. Dorsal seta arising from small elevation formed at proximal end of dorsal sclerotized crest, articulating on single basal part, and about as long as ramus.

Antennule (Figure 21C) 11-segmented with following complement: 1(8)-2(4)-3(6)-4(2)-5(2)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth). Aesthetasc on segment 8 linguiform, on segment 10 filiform, and on segment 11 tubular. No spinule pattern observed on segment 1.

Antenna four-segmented with exopodal seta and two abexopodal setae, the former reaching midway second endopodite segment. Endopodite with one, five and seven setae, respectively. Spinule pattern on coxobasis not observed, either naked or rendered invisible by pressure.

Mandible with distinct palp, bearing one short and two long plumose setae. Maxillular arthrite with 10 elements, medialmost typically claw-shaped. Palp with articulating endopodite segment. Maxilla with two-segmented endopodite and maxilliped four-segmented, armament of both appendages not observed in detail.

Leg 1 (Figure 22A, B) with remarkable rigidly sclerotized rami. Protopodal components not found (according to Lamoot et al. 1981: basis with a normal concave medial margin and a medial element). Corners below insertion of outer spines on exopodite segments prominent, robust and blunt. Distal outer edge of first and second endopodite segment prominent (Figure 18B: distorted by compression, illustration depicts the leg medially). Terminal spine of endopodite remarkable stout, longer than entire endopodite, robust and claw-shaped (ornament not visible).

Leg 2 (Figure 22C) and leg 3 (Figure 22D) with robust appearance. Ornament on coxa and basis not visible, either absent or rendered invisible by pressure. Medial margin of basis expanded, triangular (ornaments not visible). Coxal medial seta present. Intercoxal sclerite with rounded distal edges and smooth surfaces. Outer edges near spine insertions on exopodite prominent, stout and blunt. Apical spine on endopodite of leg 2 slightly longer than segment, of leg 3 as long as segment. Complete leg complement listed in Table 2.

Leg 4 (Figure 22E). Intercoxal sclerite not found. Coxa with medial seta. Medial margin of basis produced in blunt triangular process reaching almost distal margin of first endopodite segment with naked borders. Exopodite two-segmented, rather compact. First endopodite segment inflated and rigidly sclerotized. Frontal surface with rigid crest close to, and parallel with, medial margin. Outer distal edge produced into blunt process. Second endopodal segment truncate in appearance, with three medial setae, one terminal spine (half as long as segment), and one outer subdistal seta. Terminal spine insertion flanked by triangular extensions of segment margin.

Leg 5 (Figure 21A) with basal segment obsolete, represented by a long pinnate seta. Distal segment differentiated as a small rectangular socket, twice as wide as long, faintly separated from pediger and bearing two slender elements: outer one three times as long as inner one.

Leg 6 (Figure 21A) located in anterior third of somite, above frontal plane, with three short blunt elements.

Male. Habitus not observed, (according to Lamoot et al. 1981) similar to that of female and measuring 510 μ m. Anal somite and caudal rami (Figure 21B) as in female. Antennule 16-segmented, with three linguiform aesthetascs of normal length

on segment 1, other details obscured. Mouthparts of one male visible (RBINSc COP 9642: not dislodged) with same appearance as in female. Legs 1–3 not dislodged on slide RBINSc COP 9642. Leg 1 basis with short medial spine and lacking particular expansions of medial margin of basis.

Leg 4 (Figure 22F) with unmodified rami. Intercoxal sclerite not observed. Medial coxal seta present. Medial margin of basis far less produced into triangular outgrowth than in female. Terminal exopodal segment of right leg with 1 (aberrant) additional seta on inner margin (marked with arrow in Figure 22F). First and second endopodal segments with unmodified, flat. Terminal spine nearly as long as second endopodite segment, inserted between pair of distinct triangular outgrowths of segment margin.

Legs 5 and 6 not found, according to Lamoot et al. 1981: leg 5 as in female, leg 6 with two elements only: outer one setiform, inner one spiniform, both equally rather long.

Remarks

Observations on the morphology of the mouthparts other than the antenna are wanting in the original description and the enumeration and representation of the legs appears to be incorrect. Unfortunately, the mounted remains of the type specimens and their labels provide no clarification, rather they sustain the doubts, but it seems obvious that illustration 14 in Lamoot et al. (1981) is the representation of the male leg 4 endopodite (instead of leg 2 as indicated), and in illustration 11 the medial distal seta on the second exopodite segment was overlooked. According to Lamoot et al. (1981), the spine formula in the female would be 3.4.4.3, which could only be confirmed for the male on slide RBINSc COP 9462. The spine formula of the female cannot be confirmed with certainty but is assumed to be identical. The redescription given herein is as complete as possible in so far as the condition of the specimens allowed observation and interpretation. New collections of this animal are required to elucidate the exact morphology of its appendages.

The initial placement of this cyclopine in the genus *Speocyclops* is difficult to comprehend. The justification, based on the resemblance of the prominent nature of the terminal element of the leg 1 endopodite with that of *Speocyclops sardus* Lindberg 1956 and *Speocyclops creticus* Lindberg 1955, is rather thin. Apparently, other potential leads (e.g. *Bryocyclops, Psammocyclops, Cochlacocyclops*) were not considered. The repositioning of the species in *Allocyclops* by Karanovic (2001) has to be seen as an inevitable consequence of the inaccurate original description of the leg 5 morphology, and its assignment to the subgenus *Psammocyclops* because of certain similarities (namely, leg 4 endopodite with a single terminal spine) with *A. silvaticus* (= *Virbiocyclops silvaticus* comb. nov.).

Speocyclops transsaharicus is allocated here to *Hesperocyclops* Herbst, 1984 for obvious reasons: the differentiated distal segment of leg 5, the male leg 6 with two elements, the robustness of the leg 1 exopodite with a claw-shaped spine on the endopodite, the triangular outgrowths on the medial margin of the basis, and the conspicuously inflated nature of the female leg 4 endopodite being unmodified in the male. The placement of *Sp. transsaharicus* in the genus *Hesperocyclops* based on those structural similarities has to be seen as provisional. Compared with *Hesperocyclops pescei* Petkovski, 1988 (RBINSc COP 6999, COP 7657–7661: from Quintana Roo,

Mexico) and *Hesperocyclops herbsti* Rocha and Bjornberg, 1987 (RBINSc COP 9423, COP 9426, COP 9546: from Brazil), *Hesperocyclops transsaharicus* differs by the considerably larger anal operculum, the presence of a distinct longitudinal sclerotized ridge on the dorsal surface of the caudal rami, the hyaline nature and short structure of the three elements on the female leg 6, and the absence of breaking planes in the terminal caudal setae. The most striking differences between *H. transsaharicus* and other *Hesperocyclops* species are (1) the absence of a particular expansion of the medial margin of the leg 1 basis and (2) the considerable enlargement of the medial seta on the first endopodite segment and expands the entire distance between the medialmost border and the insertion of the endopodite. Moreover, the endopodite in *H. transsaharicus* female is much more prominent, and dominates in dimensions the rather short and compact exopodite.

The five species assembled in *Hesperocyclops* (see Galassi and Pesce 1992) are known from the Neotropics (Caribbean and Neogean subregions). *Hesperocyclops transsaharicus* is the first Ethiopian representative and consequently *Hesperocyclops* joins the group of specialized genera with a Transatlantic distribution [e.g. *Bryocyclops* (cfr. Reid 1998), *Haplocyclops* (cfr. Rocha et al. 1998; Fiers 2002; Karanovic 2005), *Reidcyclops* (cfr. Karanovic 2000)]. In view of the insecurities about the exact morphology of *H. transsaharicus*, and consequently its affiliation, biogeographic conjectures about the genus *Hesperocyclops* remain speculative.

Genus *Metacyclops* Kiefer, 1927 *Metacyclops arenicolous* Fryer, 1956 (Figures 23 and 24)

Metacyclops arenicolous sp. nov. – Fryer 1956: 226-229, figs. 1–11.

Metacyclops arenicolous Fryer, 1956 – Fryer 1957: 68, 79; Herbst 1988: 151, 152; Defaye 1992: 149.

Bryocyclops arenicolous (Fryer, 1956) – Lindberg 1961: 132; Dussart and Defaye, 1985: 144; Lescher-Moutoué, 1986: 307.

Bryocyclops (*Bryocyclops*) *arenicolous* (Fryer, 1956) – Dussart and Defaye 2006: 150. *Allocyclops* (s. str.) *arenicolous* (Fryer, 1956) comb. nov. – Karanovic 2001: 24. *Allocyclops* (*Allocyclops*) *arenicolous* (Fryer, 1956) – Karanovic 2003: 148.

Material examined

Type series: two females, labelled syntypes, preserved in alcohol, registered BMNH 1957.2.1.1.

Origin

Malawi, Lake Nyasa (or Lake Malawi): interstitial of fine-grained beach sand at Nkata Bay and interstitial of coarse-grained beach sand at Chikali near Nkata Bay. Label accompanying examined material indicates: Nkata Bay, collected 4 May 1954



Figure 23. *Metacyclops arenicolous* Fryer, 1956. Syntypes. (A) Female habitus, dorsal; (B) idem, lateral; (C) female urosome, lateral (A–C: BMNH 1957.2.1.1).



Figure 24. *Metacyclops arenicolous* Fryer, 1956. Syntypes. (A) Female urosome, dorsal; (B) idem, ventral (A, B: BMNH 1957.2.1.1).

Emended description

Female. Habitus (Figure 23A, B) cyclopid, with urosome less than half entire body length. Transition between prosome and urosome not accentuated. Length 360 μ m (reported 410–490 μ m in Fryer 1956) with largest width, 160 μ m, along posterior margin of cephalothorax. Genital double-somite widest in anterior third, about 1.2 times wider than long, tapering caudally. Anal somite with protruded, smooth, anal operculum and anal sinus with short and sturdy setules. Posterior margin of prosomites smooth, of urosomites without fringe. Integument of pediger 5 smooth. Anal somite with uninterrupted row of spinules along posterior border.

Caudal rami 1.4 times as long as wide, with broad appearance in dorsal view and a distinct triangular depression in anterior half of dorsal surface. Lateral distal element spiniform, about 0.8 times the ramal length. Medial seta half as long as ramus Both

terminal setae with breaking plane, and densely feathered. Dorsal seta slightly longer than ramus.

Antennule 11-segmented, short, reaching end of median third of cephalothorax (Figure 23A). Armature: 1(8)-2(3)-3(5)-4(2)-5(1)-6(2)-7(3)-8(2+Aesth)-9(2)-10(2+Aesth)-11(7+Aesth). Aesthetasc on segment 8 linguiform, reaching to end of segment 9; aesthetasc on 10 filiform, reaching halfway to segment 11; aesthetasc on 11 tubiform and as long as segments 10 and 11 together. Spinule pattern on segment 1 not observed.

Antennary coxobasis without exopodal remnant seta and single abexopodal seta. First endopodite segment with one, second with five and terminal endopodite segment with seven setae. Mandible with palp bearing two long and one short seta. Maxillular palp with three setae, maxillar endopodite two-segmented with two and three elements on proximal and distal segment, respectively. Maxilliped clearly four-segmented with, from proximal to distal, 2-2-1-2 elements.

Legs 1–4 with medial coxal pinnate element. Basis of leg 1 without medial spine. Rami bimerous with armament listed in Table 3. Distal segment of leg 4 endopodite with two terminal spines located between distinct triangular outgrowth of margin. Inner spine 1.5 times longer than outer one, and 0.75 times segment length.

Leg 5 (Figures 23C and 24B) with basal segment represented as a distinct, but confluent, crescentic expansion on posteroventral border of pediger, bearing representative seta of ancestral basal segment. Distal segment slightly longer than wide (in lateral view) with two pinnate elements, both longer than segment: outer one subdistal, medial one inserted distal.

Leg 6 (Figures 23C and 24A) located above sagittal plane, with one seta (outermost) and two hyaline knobs (middle and median element). Copulatory pore leading to anterior directed, S-shaped duct. Lateral arms recurved posteriorly. Anterior part of seminal receptacle laterally expanded, with narrow central part. Posterior part of receptacle ovate, extending far posteriorly.

Males. Not observed. According to Fryer (1956) 370 μ m long, with caudal rami, anal operculum, and leg 5 as in female. Leg 6 vestiges with three (slim ?) elements on outer caudal corner.

Remarks

Lindberg (1961) repositioned *M. arenicolous* in *Bryocyclops* as a consequence of the inaccurate presentation of the leg 5 and its slender armature in combination with the compact, apparently flattened, body shape. Although Herbst (1988) and Defaye (1992) maintained *M. arenicolous* in the initial host genus, the species remained in the nominate subgenus of the genus *Bryocyclops* (Dussart and Defaye, 1985, 2001, 2006). The repositioning of it to *Allocyclops* by Karanovic (2001) has not been properly justified but is undoubtedly a result of the inaccurate description of the appendages.

Metacyclops arenicolous cannot be ascribed to *Allocyclops* or to *Bryocyclops* on the basis of the leg 5 morphology as shown here. Affinities with *Hypocyclops* (part of the so-called European branch of *Allocyclops* in Karanovic 2001) are possible but not evident. *Metacyclops arenicolous* shares with *Hypocyclops* the almost similar leg armature formula, the lack of an exopodal remnant seta on the antennary coxobasis and a reduced armature on the terminal maxillipedal segment (two instead of three).

However, the leg 5 morphology with its distinct terminal segment (although faintly individualized), the complete mandibular palp armature, the presence of two setae on segment 2 of the maxilliped, and the further reduced antennulary armament are indications that *M. arenicolous* is a representative of a different lineage. Apparently, *M. arenicolous* has more in common with *Allocyclops minutissimus* described by Petkovski (1971). In both species, the leg armature formula is identical, the caudal rami have a short and broad appearance, the mandibular palp bears a complete set of setae and the seminal receptacle shows a comparable posterior expansion. Unfortunately, the status of the latter species and its affinities remain mysterious because of the insufficient description of the leg 5 (see discussion in the following paragraphs).

In any case, *M. arenicolous* is returned here to its initial position in the genus *Metacyclops* bearing in mind, however, the artificial nature of the latter (Gurney 1933; Fryer 1956). The affinities with *M. micropus* Kiefer, 1932 as supposed by Fryer (1956) receive more significance with the correction of the original leg 5 description of *M. arenicolous*. Moreover, *M. arenicolous* might turn out to be a junior synonym of *M. micropus* as suggested by Defaye (1992). Nowadays, both species are distinguishable only by the proportional lengths of the caudal rami armament. In the absence of the type specimens (Franke 1989) of *M. micropus*, considering *M. arenicolous* as junior synonym is premature until more information on the morphology of the former becomes available.

Species and genera inquirenda

Cyclops (Diacyclops) ? minutissimus Kiefer, 1933

Citations:

Cyclops (Diacyclops) minutissimus sp. nov. - Kiefer 1933: 277-279, figs. 1-3.

- "Cyclopide" minutissimus Kiefer, 1933 Kiefer 1937a: 18–19, figs. 5–7.
- "Diacyclops" minutissimus Kiefer, 1933 Kiefer 1937b: 81.
- "Cyclops" minutissimus Kiefer, 1933 Kiefer 1937b: 103. Borutzky 1965: 840.
- Allocyclops minutissimus (Kiefer, 1933) Petkovski 1971: 106–108, figs. 67–69.
- Allocyclops minutissimus (Kiefer, 1933) Dussart and Defaye 1985: 146; 2006: 218; Lescher-Moutoué 1986: 309; Rocha and Bjornberg 1988: 445 [part.].
- *Speocyclops minutissimus* (Kiefer, 1933) Borutzky 1965: 840; Kiefer 1967: 179; Kiefer 1978: 215 [part].

Allocyclops (s. str.) minutissimus (Kiefer, 1933) - Karanovic 2001: 24; 2004: 148.

non Speocyclops minutissimus (Kiefer, 1933) – Petkovski 1954: 22–23, figs. 29–33 [= Reidcyclops trajani (Reid and Strayer 1994)].

Material examined

One female and one male, dissected, each mounted on a separate slide (FKCC 2011 and 2012) from the type-locality: wells near Skopje (Republic of Macedonia), Karaman *leg.*, September 1932 (both with completely crystallized mounting medium); One female, dissected and mounted on two slides (FKCC 3388–3389) from Sindelićevo (= Sindjeliceva in Kiefer 1937a) in the vicinity of Skopje (Republic of Macedonia),

Karaman *leg.*, July 1933 (mounting medium on slide 3388 partially, on slide 3389 completely crystallized).

Discussion

Few cyclopines have such a bewildering taxonomic history as "*Cyclops minutissimus*". The confusion has been partially resolved since the recognition of the separate status of *Speocyclops minutissimus* (Kiefer, 1933) *sensu* Petkovski (1954) which figures nowadays as the type species of the genus *Reidcyclops* Karanovic, 2000.

Kiefer (1933) relegated "*Cyclops*" *minutissimus* with *Diacyclops* but left the generic affiliation unsettled subsequently (Kiefer 1937a,b,c) or, following Petkovski (1954), enlisted it as *Speocyclops minutissimus* (Kiefer 1967, 1978). The transfer (Petkovski 1971) to its current position in *Allocyclops* has been generally adopted (Dussart and Defaye 1985; Reid and Strayer 1994; Karanovic 2001, 2003; Dussart and Defaye 2006). Nevertheless, the status and generic affiliation of "*Cyclops*" *minutissimus* Kiefer, 1933 remains, up to now, mysterious.

The original description of "*Cyclops minutissimus*" (Kiefer, 1933) is quite incomplete and subsequent reports (Kiefer 1937a,b) failed to provide more information. Unfortunately, the four slides preserved in the collection of F. Kiefer at Karlsruhe are in very poor condition. The mounting medium has crystallized and obscures the (type) specimens (from Skopje: a female and a male) completely. The Sindelicevo female is partially hidden by crystals, leaving the antennule, antenna and the legs more or less visible but the urosome and leg 5 completely covered. The original set of drawings from the three specimens are absent in Kiefer's archive (sometimes containing additional remarks), but his notes with the meticulous measurements are preserved and reproduced here (original calculations between rounded brackets, supplementary calculations between square ones):

Female (FKCC 2011). Body length, 350 μ m; length caudal rami, 19 μ m, width 11 μ m (L/W ratio: 1/1.721); second endopodal segment of leg 4 length 20 μ m, 13 μ m wide [L/W: 1/1.54]; length of terminal spines, 14.2 and 8.8 μ m [ratio medial/outer: 1/1.48; L medial spine/L segment: 1/0.71].

Male (FKCC 2012). Body length, 300 µm.

Female (FKCC 3388–3389). Body length, 380 μ m; length caudal rami, 19.8 μ m, width, 12.6 μ m (L/W ratio: 1/1.5); second endopodal segment of leg 4 length 21.6 μ m, width 14.4 μ m [L/W: 1.50]; length of terminal spines, 14.4 μ m and 9.0 μ m [ratio medial/outer: 1/1.66; L medial spine/L segment: 1/0.66].

The original description with the measurements located at the end of the text give the impression that they refer to the male specimen. Kiefer's notes establish without doubt that they are female.

It cannot be denied that the specimens from the two localities are very similar. Their descriptions, however, deviate at certain points. Apart from the differences in length/width ratio of the caudal rami, leg 4 endopodite segment and its distal armature, the specimens from the two different localities display noticeable dissimilarities in the anal operculum and caudal rami. The operculum of the Skopje specimens has a straight posterior border and is not particularly enlarged or expanded. The rami are slender cylindrical structures with the usual distance between their medial margins. In contrast, the operculum of the Sindelicevo specimen is illustrated as a crescentic flap, caudally produced and partially covering the anal sinus. The caudal rami are obviously more compact in dorsal view, leaving only a narrow space between them, and have a long triangular medial depression in the anterior half on the dorsal surface. In fact, the shape of the rami and the anal operculum of the Sindelicevo specimen show a remarkable resemblance with those described for *Metacyclops arenicolous* (see above and Figures 23 and 24 herein). Both share a complete identical armament formula of the legs (see Table 3), possess an identical setal armament on the female antennule, and lack an antennary exopodite remnant. Despite the similarities, the fact that the leg 5, head appendages and genital complex of the Sindelicevo specimen cannot be observed makes postulating affinities of this species with *M. arenicolous* rather speculative.

Petkovski (1971) faced comparable problems observing the leg 5 of the animals from Krivogastani in Pelagonia. Only a vague illustration is available, but the description of the leg 5 clearly stipulates the presence of only two elements: an outer element as the remnant seta of the basal segment ("thoraxborste" dixit Petkovski 1971) and a spine, the latter inserted on a minute elevation and considered as a remnant of the ancestral distal segment. The description matches the leg 5 (equally vaguely) depicted for "Cvclops" minutissimus (cfr text figure 3 in Kiefer 1933) from Skopje. Whether Petkovski's specimens are conspecific with "Cyclops" minutissimus remains to be established. The Pelagonian specimens have a caudally expanded anal operculum and have the more robust appearance of the caudal rami as observed in "C." minutissimus from Sindelicevo. Their identical leg armament supports (although weakly) the assumption that the Pelagonian and Sindeliveco specimens are more closely related to each other than to "C." minutissimus from Skopje. The presence of a fully equipped mandibular palp (Petkovski 1971: 102) in addition to the leg armament and shape of the caudal rami also points in the direction of a certain affinity of the Krivogastani specimens to Metacyclops arenicolous.

In any case, assigning "Cyclops" minutissimus to Allocyclops, or to Hypocyclops is speculative at the moment. The status of the few specimens identified as "Cyclops" minutissimus remains questionable.

Allocyclops (Allocyclops) australonipponicus Tomikawa, Ishida and Mawatari, 2005

Allocyclops (Allocyclops) australonipponicus sp. nov. – Tomikawa, Ishida and Mawatari 2005: 20–25, figs 1–4.

Allocyclops australonipponicus Tomikawa, Ishida and Mawatari, 2005 – Dussart and Defaye 2006: 219.

Origin and material (not examined)

Japan, Okinawa Prefecture, Kunigami Village (26°45′34″ N, 128°13′09″ E), Yona River (type locality): under decaying leaves near the river bank. A female holotype and three paratypes dissected, 10 paratype females preserved.

Remarks

Allocyclops australonipponicus is an intriguing form assigned to the genus on the basis of the following combination of characteristics: leg 5 with three elements arising from

a pedestal confluent with the pediger, legs with two-segmented rami, and a short, 11-segmented female antennule.

The description of this form appears to be a compilation of observations on different specimens, some presumably immature or aberrant. Although the illustration of the body in dorsal view depicts an adult female specimen, the presentation of the body in lateral view and of the genital double-somite with the transverse rim in the anterior part of the ventral surface seems to be sub-adult.

The leg 5 of *A. australonipponicus* ought to be a well defined, although not separate, structure on the pediger. The stout appearance of its armament is reminiscent of the leg 5 in *Paracyclops* Claus, 1893. Moreover, the remarkable robustness of the maxillipedal armament in *A. australonipponicus* is reminiscent of the rigidness of the elements in, at least, two eucyclopine genera (*Paracyclops* and *Ectocyclops* Brady, 1904). *Allocyclops australonipponicus* has the conventional erect shape of the maxilliped whereas this appendage has a more compact appearance in the before-mentioned eucyclopine genera.

Allocyclops australonipponicus is not a member of Allocyclops, nor of any of the herein defined genera and is possibly not a member of Cyclopinae. Additional material, including males, is needed to elucidate its status and establish firmly its affinities. For the time being, it should be considered as a *genus et species inquirendum* among Cyclopidae.

Justification and discussion

The key feature for recognizing generic affiliations in Cyclopidae is the structure of the fifth leg. This basic systematic concept in which the number of segments and the number and shape of its armature is fundamental was formalized by Kiefer (1927, 1928, 1937c). The introduction, unfortunately, initiated a drastic erosion of many descriptions with only the most obvious characteristics figured to differentiate species from congenerics. The partial dissections of (type-) specimens from which a few relevant appendages have been dislodged and observed, while the rest of the body has been left unconsidered, are nowadays the witnesses of this practice. Although some of the generic outlines are now ambiguous (Reid and Strayer 1994), these oversights do not appear to have caused systematic problems in the common cyclopines known as plankters or epigene substrate dwellers.

However, the former attitude becomes an acute problem when affinities between highly specialized cyclopines have to be formulated. The earlier criticism about the pivotal value attributed to the leg 5 structure in cyclopine systematics (Gurney 1933; Rylov 1948) is being rekindled (Pesce 1996; Ferrari 1998; Rocha *et al.* 1998; Reid 1993a,b; Reid *et al.* 1999) but an alternative is wanting. The importance of the leg 5 structure as a discriminatory structure among cyclopine genera remains, but its significance in revealing phylogenetic affinities appears to be limited the more the structure deviates (read reduced) from the basic cyclopid leg 5 morphology.

The original description of *A. chappuisi*, type of the genus *Allocyclops*, suffers these deficiencies and is, according to modern standards, incomplete and inaccurate. The same is true for the majority of species subsequently attributed to the genus. Their affinities are principally based on the obsolete nature of the fifth leg with the short female antennulae and the bimerous morphology of the natatorial legs considered as shared character states. However, neither the segmentation of the antennulae nor

that of the legs are strong arguments to postulate a common origin for all the species with a leg 5 morphology apparently similar to that of *A. chappuisi*. In the absence of additional morphological support and considering the incomplete and inaccurate descriptions, the previous (see arrangement in Dussart and Defaye 2006) as well as the recently amended (Karanovic 2001) concept of *Allocyclops* are to be considered as largely conjectural.

To avoid complicated cross-references, the following analysis commences with the systematic arrangement as listed in the compendia of Dussart and Defaye (1985, 2006: herein referred to as "classical"), except for "*Cyclops*" minutissimus Kiefer, 1933 and *A. (P.) australonipponicus* (see preceding section). The amended diagnosis and the rearrangement of genera and species as proposed by Karanovic (2001, 2004, 2006) will be discussed in due course. *Metacyclops arenicolous, Speocyclops transsaharicus* and *Speocyclops orcinus*, still possessing the ancestral distal segment of the leg 5 and which are not affiliated with *Allocyclops*, are omitted in the following discussion. Their transfer has been dealt with in the former section (for *M. arenicolous* and *Sp. transsaharicus*), in Fiers and Pandourski (2008) for *Sp. orcinus* and for *A. (P.) consensus*, now *Dussartcyclops* (*Barrowcyclops*) consensus (Karanovic, 2003), in Karanovic et al., (2010).

Our current perception of the principal diagnostic feature of Allocyclops sens. lat., the leg 5 morphology, is inaccurate. The urosome is commonly observed and depicted in ventral view giving the impression that the three leg 5 vestiges are inserted directly on the pediger. However, examination of the urosome laterally reveals that the constitution of the leg 5 differs among the several species. In Allocyclops sens. nov. leg 5 is present as a relatively large truncate expansion, confluent at its base with the pediger, and furnished with the three remnant setae (see Figure 4A–C). The structure of leg 5 in Hypocyclops is comparable (accurately depicted for H. montenegrinus by Karanovic 2001: figs. 13). In Virbiocyclops and Stolonicyclops a differentiated structural formation representing the leg 5 podomere is absent and the two ancestral constituents are only traceable by two faint expansions (pedestals) on the surface of the pediger, bearing one and two vestiges, respectively (see Figure 18A-C herein and figs 1B, 2I in Reid and Spooner 1998). The leg 5 in *Psammocyclops* is a narrow expansion of the posterolateral margin of the somite, with the two vestiges of the ancestral distal segment located distinctly more medially (having a ventral position) than in the former types (see Figure 13A–C). The situation in *Olmeccyclops* appears to be comparable (see figs. 5A, E in Suárez-Morales et al. 2010). Unfortunately, the correct leg 5 structure of A. botosaneanui is not assessable because of the position of the urosome and the compression of it.

The adult leg 5 morphology, expressed either as a truncate expansion or being obsolete, is the adult expression of two different developmental constraints. The rationale behind this statement is beyond the scope of the present contribution and will be developed elsewhere. In short, the leg 5 in *Allocyclops* and *Hypocyclops* results from an arrested development of the primary bud (which appears at copepodid stage 3) with the addition of a single element in the subsequent stage (copepodid IV). The leg 5 morphology in *Virbiocyclops*, *Stolonicyclops*, *Psammocyclops* and *Olmeccyclops* is to be seen as a secondary transformation in which the differentiation of the distal leg 5 podomere is deleted (a derivation of a *Metacyclops*-like leg 5 basic structure). The progressive suppression of the distal segment as an individual structure is clearly demonstrable along the lineage *Anzcyclops–Dussartcyclops–Barrowcyclops*. The comparable faint, near to undetectable, appearance of the separation between the somite and the distal podomere in *M. arenicolous* and *H. transsaharicus* adds to the assumption that the obsolete nature of the leg 5 has been achieved independently in different lineages.

The genera Allocyclops and Hypocyclops

Allocyclops sens. nov. and *Hypocyclops* are structurally most similar but *Allocyclops*, compared with *Hypocyclops*, occupies a more basal position because of the far less derived complement of the buccal appendages and the legs. Despite the conservative nature of its appendages, the status of *Allocyclops* as a separate genus is, in addition to the conventional diagnostic features, supported by the advanced morphology of the male leg 6 with only two armature elements, and the reduced aspect of the antennulary setation in which segments 3–5 (the sequences [VIII-XI]-[XII-XIII]-[XIV]) bear, respectively, six, two, two elements instead of the ancestral complement with 8.4.2 (the ancestral pattern in 11-segmented antennulae).

Apart from the obsolete leg 5 morphology and the male leg 6, *Allocyclops* coincides almost completely with certain African species currently included in the genus *Metacyclops* Kiefer, 1927 and characterized by two terminal spines on the leg 4 endopodite: *M. aequatorialis* Dussart, 1978 and *M. chelazzi* Dumont, 1981 (*M. tropicus* Kiefer, 1932, *M. micropus* Kiefer, 1932 and *M. arenicolous* Fryer, 1956 posses a leg 6 with three elements, the male of *M. somalicus* Dumont, 1981 is unknown). Whether, *Allocyclops* has direct affinities with a particular lineage confined nowadays within *Metacyclops* remains to be settled. Detailed descriptions with observations on the morphology of the head appendages are wanting for most of the species currently grouped in *Metacyclops*.

It is obvious that *Allocyclops* (except for *A. botosaneanui* of which the affinities remain speculative, see former section) represents a branch with its roots among genera with a basic cyclopine morphology. Among the other less derived features, the body dimensions and shape, the conservative setal complement of the antennary second endopodite segment, and the simple caudal rami with a long medial element, are considered herein as indications that the genus branched off directly from an epigene stock when invading the subterranean realm.

Hypocyclops, unifying *H. kieferi* and *H. montenegrinus*, displays a series of features (antennary exopodite absent, mandibular and maxillipedal armament reduced, medial elements on the proximal exopodite segments absent), which are advanced compared with the conservative nature of their homologues in *Allocyclops* and as such position them outside the generic limits of the latter. Despite the similar leg 5 and antennulary complement, *Allocyclops* and *Hypocyclops* seem not to share a common ancestor. It is suggested here that *Hypocyclops* is a regional offshoot of the cluster of subterranean cyclopines commonly referred to as the "*kieferi*" species-group (Pandourski 1997; Galassi and De Laurentiis 2004; Iepure and Defaye 2008) in the genus *Acanthocyclops* Kiefer, 1927 and of which the systematics is profoundly confusing and in urgent need of revision. The tendency to reduce the leg segmentation from a three-segmented leg segmentation pattern (ex. *A. kieferi* Chappuis, 1925) to a complete two-segmented pattern (ex. *A. biarticulatus* Monchenko, 1972) is obvious. *Hypocyclops* presumably has its roots along this group, but is differentiated from it by the further reduction

of the leg 5. "*Cyclops (Diacyclops) minutissimus*" Kiefer, 1933 is a potential candidate to be placed in the genus, but the uncertainties about its morphology, as discussed in the previous sections, makes a formal incorporation in the genus *Hypocyclops* premature.

The genera Psammocyclops, Stolonicyclops, Olmeccyclops and Virbiocyclops

Psammocyclops is distinct among the three genera characterized by the leg 5 with the vestiges directly inserted on the pedigerous somite. The ventral position of the vestiges representing the ancestral distal segment in *Psammocyclops* and their location at a remote distance from the lateral ancestral basal segment vestige is in sharp contrast with the noticeable lateral position of the three remnant elements in *Stolonicyclops* and *Virbiocyclops*. The position and differentiation of the leg 5 in *Olmeccyclops* is comparable.

Apart from the particular aspect of the leg 5, *Psammocyclops* resembles *Virbiocyclops* to a considerable extent. Both share the typical cyclopine body shape, the sculpted caudal rami, a quadrate prominent anal operculum, and a similar antennary, mandibular and maxilipedal complement. However, they differ considerably in the antennulary setation (segments 1–5: 5.3 or 2.4.2.1 in *Psammocyclops*, 7.2.5.2.2 in *Virbiocyclops*), the leg armature (see Table 3), the number of elements on the male leg 6 (three elements in *Psammocyclops*, two in *Virbiocyclops*), and most of all in the structure of the leg 4 endopodite: in *Psammocyclops* the podomeres have a confluent aspect and there are only two medial setae on the (former) terminal segment. Both genera originated from a different stock, but whereas the kinship of *Virbiocyclops* with *Hesperocyclops* appears to be well supported (see further below), the affinities of *Psammocyclops* to the other cyclopine genera are less obvious.

Two other genera, Goniocyclops Kiefer, 1955 (non Karanovic 2005) and Cochlacocyclops Kiefer, 1955 were erected for cyclopines collected in similar habitats in Madagascar. The differences between them and *Psammocyclops* are subtle and focus mainly on the leg 5 structure and the spine formula of the legs. They share the reduced aspect of the leg 4 endopodite with a single terminal spine inserted between distinct triangular outgrowths of the margin in combination with the presence of only two medial setae on the (former) terminal segment. Goniocyclops differs as follows: the leg 5 with obvious unequal distal elements, a single dwarfed seta on the mandible, antennary exopodite absent, antennulary setation of 1-3 basically 8.4.6 (personal observation: G. primus slides FKCC 5511-5514; G. alter slides KKCC 5417-18, 5499). To what extent *Psammocyclops* and *Cochlacocyclops* Kiefer 1955 are related is difficult, if not impossible, to evaluate. Whether the leg 5 distal segment is differentiated from the pediger in *Cochlacocyclops* remains conjectural (Kiefer 1955), but the conspicuously lateral position of the basal segment vestige and the medial position of the distal part on the ventral surface of the pediger is reminiscent of the situation in *Psammocyclops*. Re-examination of the type specimen of the former (FKCC 5508–5510) confirmed the unfortunate loss of the leg 5 pair, leaving the faint original illustration of it as the only evidence, but revealed the previously overlooked coalescent nature of the leg 4 endopodite segments in which the remnants of the ancestral articulation are only partially present. Cochlacocyclops has, however, a less advanced leg armature (see Table 2), a different antennulary setation pattern on segments 1-5 (8.4.6.2.2), and lacks the exopodite remnant seta on the antennary coxobasis. *Cochlacocyclops* is as such well differentiated from *Psanmocyclops* but whether both share a common origin is speculative in the absence of sufficient details, although the possibility should be considered.

Psammocyclops has a rather particular leg armature in which the medial element on the proximal segment of the leg 1 and leg 4 exopodite is absent, but present in legs 2 and 3. Presence of this medial element in the four legs is the ancestral condition. The loss of the medial seta in leg 4 is common, and advanced cyclopines (the herein discussed *Hypocyclops*, *Olmeccyclops*, *Stolonicyclops*) often lack this element in the four legs. Although the complete setal complement of the legs for many species has not been documented, the pattern with a medial seta only in legs 2 and 3 appears to be uncommon. *Pilbaracyclops* Karanovic, 2006 is the only genus, so far, for which this particular setal complement is known. The taxonomic relevance has to be clarified in the future but is herein included as an advanced character state in support of the separate status of the genus *Psammocyclops*.

Contrary to the number of advanced features, *Psammocyclops* still posseses a rather conservative armament of the mouthparts (antenna with exopodite, mandible fully equipped, maxilliped with 2.2.1.3 setae) and has the ancestral complement on the male leg 6 with three elements contrasting as such significantly from the advanced aspect of leg 5. The conservative nature of these features is assumed here to be evidence that *Psammocyclops* (probably also *Cochlacocyclops*) has affinities among cyclopines with a fairly basic morphology.

The structure of the mouthparts and the male leg 6 armature of *Olmeccyclops* are, compared with their counterparts in *Psammocyclops*, far more advanced. This supports the reservations (Suárez-Morales et al. 2010) of considering *A. veracruzanusis* close to *Psammocyclops excellens*. However, the position of *Olmeccyclops* remains difficult to assess. Although the body of *O. veracruzanus* is remarkably similar to that of certain *Bryocyclops*, direct affinities are not envisaged (namely, the outstanding description of *B. muscicola* by Reid 1999). The absence of a dimorphic armature in the male leg 3, the different spine formula (2.3.3.2 versus 3.3.3.3) and the dimorphic aspects of the setal complement of the exopodites and the leg 2 endopodite, is a unique character combination excluding *O. veracruzanus* from *Bryocyclops*. Although *Bryocyclops* is known to have a circumtropical distribution with two representatives (*B. caroli* Bjornberg, 1985 and *B. campaneri* Rocha and Bjornberg, 1987) known from Brazil, *Olmeccyclops* seems not to be affiliated (the presence of *B. muscicola* in Florida, see Reid 1999, is most likely an introduction).

The simple rounded intercoxal sclerites and the presence of a coxal medial element in each leg, and the leg armature formula of *Olmeccyclops* are comparable with *Muscocyclops* Kiefer, 1937 (redescribed in Rocha and Bjornberg 1987; leg armament in Table 3, personal observation). Presence of an expanded anal operculum, the complete transverse row of spinules along the posteroventral margin of caudal rami and the long nature of the terminal elements on the leg 5 and the male leg 6, the latter with only two appendages, are also in support of affinities between *Olmeccyclops* and *Muscocyclops*. The leg 5 distal podomere still distinct, the dwarfed seventh antennulary segment (sequence [XXI–XXIII]) with two instead of three setae, and the conspicuous transverse comb of spinules/setules on the caudal rami in front of the dorsal seta are characteristic for *Muscocyclops*, but not shared by *Olmeccyclops*.

Virbiocyclops is reminiscent of *Allocyclops* in so far that it still possesses the inner element on the proximal exopodite segments of legs 1–3, has a fully equipped

mandibular palp, an antennary exopodite remnant seta, and a male leg 6 with only two armament elements (the first three to be considered as plesiomorphic, the last one as apomorphic). Nevertheless, based on the nature of leg 5, *Virbiocyclops* is situated among the genera *Stolonicyclops*, *Psammocyclops* and *Olmeccyclops*. Yet, *Virbiocyclops* appears to be most closely related to *Hesperocyclops* as manifested by the presence of the particular outgrowths (additional process in leg 1, conspicuously erected triangular ones in legs 2–4) on the medial border of the basis of the legs. Moreover, habitus and body ornament, caudal rami, anal operculum and the morphology of the buccal appendages are similar in both *Virbiocyclops* and *Hesperocyclops*, demonstrating the sister-group relationship between these genera.

Certain aspects of the appendicular morphology of *Virbiocyclops* adults indicate an arrested development compared with that of *Hesperocyclops*. As demonstrated in Schutze et al. (2000) the antennulary development sequence of *V. silvaticus* is delayed when the nine-segmented condition in copepodid stage III remains unaltered in copepodid stage IV whereas, in *H. improvisus* (syn. *H. stocki*), the number of segments increases from 9 to 10 by the individualization of ancestral segment [XIV] in copepodid stage IV from the sequence [XII–XIV] of stage III. Although the adult antennule in both species is 11-segmented and the segmental sequences are homologous, their development is different. The reduced setal complement of the segments (segments 2 and 3) in adults of *V. silvaticus* points to the stagnation of segmental development and the deletion of setal additions between copepodid stages III and IV (compare Figure 19B and 19I, of *V. silvaticus* and *H. herbsti*, respectively).

The bimerous nature and the untransformed morphology of the leg 4 endopodite in *V. silvaticus* have a similar developmental background. When modification (inflated, particular widening of podomeres) of the leg 4 endopodite in adult females occurs, it is manifested only in the adult stage. Examination of copepodids of species characterized by the presence of a confluent and inflated leg 4 endopodite (*Bryocyclops sens. lat.*, *Hesperocyclops pescei*) revealed that the development of the endopodite (leg 4 appears first at stage II as a bi-lobed bud, from stage III onwards the rami are apparent) shows almost no structural dissimilarities compared with the other legs. Whereas the male leg 4 retains the conventional leg structure, the female leg 4 endopodite becomes drastically reshaped during the transition to the adult stage (terminal acquisition). The unmodified appearance of the leg 4 endopodite in *V. silvaticus* adults is to be seen as the juvenile expression of the leg 4 endopodite of *Hesperocyclops*.

Virbiocyclops and *Hesperocyclops* (except *H. transsaharicus*, see discussion in former section) are essentially Neotropical with the distribution of the latter extended into the Caribbean (Galassi and Pesce 1992; Reid and Strayer 1994) and the Yucatan Peninsula (personal observation). They appear to be most closely related to *Metacyclops denticulatus* Dussart and Frutos, 1985) known from Argentina (Dussart and Frutos 1985; but so far not from Brazil as listed in Dussart and Defaye 2006, see Reid 1987). Only the gross morphology was described. Some morphological aspects have been subsequently documented (Reid 1987) but details of the antennulary setation, the buccal appendages, and of the leg morphology and their complement are still wanting. The male is unknown. The *Metacyclops denticulatus– Hesperocyclops–Virbiocyclops* lineage parallels the same trend demonstrated in the lineage *Anzcyclops–Dussartcyclops–Barrowcyclops*.

The series of advanced character states as displayed in *Stolonicyclops*, namely, the reduced mouthpart armature, absence of the medial element on the proximal exopodite

segments in legs 1–4 combined with the reduced complement of the endopodites, and the absence of the medial coxal element in legs 2–4, support the particular status of this monotypic genus. However, the position of *Stolonicyclops* remains difficult to access. Reid and Spooner (1998) particularly focused on the absence of the coxal elements to assume *Stolonicyclops* as an early derivation of the lineage leading to *Bryocyclops sens. lat., Palaeocyclops* in particular.

Stolonicyclops heggiensis is known from Georgia. A second, yet undescribed species, has been found in the interstitial of a river in Alabama (personal observation). Both localities are situated at the southeastern edge of the Appalachian Mountain chain, which appears to be the "homeland" of a particular, largely undocumented, cyclopine fauna (Reid et al. 1999; Fiers 2011). It seems not impossible that *Stolonicyclops* has its roots among this fauna.

The genera Stolonicyclops and Psammocyclops are very similar. Their comparable leg armament, the confluent nature of the leg 4 endopodite with a single terminal element, and the filiform nature of the leg 5 constituents are the most noticeable. The resemblances do not imply close affinities, but are most likely related to the particular circumstances in which both species live. The habitat of S. heggiensis, known so far only from its type locality at Heggie's Rock in Georgia, is very similar to that in which P. ritae thrives. Both are ephemeral pools/seeps on weathered granite outcrops (monadnocks or inselbergs), islands of crystalline nature amidst plains of different geological origin: Heggie's Rock outcrops in the drainage basin of the Savannah River, Lamto, type locality of *P. ritae*, in that of the Bandama (Ivory Coast). The particular circumstances and highly variable conditions of these habitat types (Jocque et al. 2010) must have been the driving forces towards an accelerated development to grow to maturity and reproduction. The small body size and "immature" appearance of the appendages in both species is a consequence. The similar locomotory appendages, of which the functionality within the limitations of the pool environment is subordinate, must be seen as convergently evolved, and as such are an illustration of the restricted taxonomic relevance of the conventional characteristics in unraveling the phylogenetic relationships among specialized cyclopines.

Conclusion

Apart from the outdated (but still influential) scheme of cyclopid intergeneric relationships proposed by Kiefer (1928) an alternative framework based on a modern synthesis has never been presented. In the absence of a contemporary analysis based on character transformations and polarities, use of a phylogenetic terminology has been avoided in the present contribution.

Any attempt to review a particular group of Cyclopidae faces considerable impediments when features other than the classic diagnostic characteristics have to be considered. The commonly used diagnostic features turn out to be limited in number and, although they are generally accepted, remain unsupported by supplementary morphological data. This narrow view, centralized around the venerated fifth leg structure, widely opens the path to the fallacy of neglecting similar characters derived independently (convergence/homoplasy). Groupings of cyclopids, commonly annotated as specialized representatives, and displaying an appendicular morphology far removed from the groundpattern (cfr. *Acanthocyclops, Cyclops, Macrocyclops*) are particularly vulnerable to definitions based on false assumptions of homology. The burden of the incomplete descriptions of several species left by earlier workers limits any attempt to arrive at a coherent and modern systematic scheme for Cyclopidae.

Since its introduction, the position of the genus *Allocyclops sens. lat.* in Cylopinae has been left unresolved with *Metacyclops* or *Bryocyclops* envisaged as most closely related (Kiefer 1933). Pesce (1996) came to similar conclusions when he positioned *Allocyclops sens. lat.* together with *Bryocyclops* (incl. *Rybocyclops* and *Haplocyclops*), *Bacillocyclops* and *Yansacyclops* in the "*Bryocyclops*-group". *Psammocyclops* figured among the cyclopine genera primarily characterized by a single segmented leg 5 morphology (the "*Microcyclops*-group" in Pesce 1996). *Stolonicyclops* has been seen as an early side branch in the lineage leading to *Bryocyclops* and *Palaeocyclops* (Reid and Spooner 1998) and Karanovic (2001) assumed *Yansacyclops* to be a potential sister-group of *Allocyclops*.

In its classical concept, *Allocyclops sens. lat.* lined up with nine other cyclopine genera mainly defined upon the reduced nature of the leg 5 and the basically bimerous aspect of the natatorial legs: *Bacillocyclops* Lindberg, 1956a, *Bryocyclops* Kiefer, 1927, *Haplocyclops* Kiefer, 1952, *Palaeocyclops* Monchenko,1972, *Psammocyclops* Kiefer, 1955, *Rybocyclops* Dussart, 1982, *Speocyclops* Kiefer, 1937c, *Stolonicyclops* Reid and Spooner, 1998 and *Yansacyclops*, Reid, 1988. The genus *Graeteriella* Brehm, 1926 in which leg 5 possesses only two elements but with the distal podomere still differentiated from the pediger, is commonly associated with this cluster. *Bryocyclops, Speocyclops* and *Graeteriella*, each unifying a significant number of species, are notorious in that their systematics remains confused.

The structural similarities among highly specialized cyclopines has long attracted attention. Chappuis (1927), in following Menzel (1924), championed the hypothesis of a common origin which Brehm (1926) promptly translated in the erection of the genus Graeteriella corralling cyclopines known from Suriname, Europe and Indonesia. Kiefer (1937c), in contrast, regarded the similarities as an inevitable result of comparable circumstances of their habitats, and hence as convergent acquisitions. Both propositions have their merits and advocates, but remain so far speculative in the absence of sufficient corroborating data. The presence and diversity of cyclopines roaming cryptic habitats is still a largely unexplored and most challenging domain (Reid 2001). Our current insight into this fauna is often based on occasional observations, many outdated, and is far from complete. The breakdown of the genus Allocyclops on the basis of morphological characters other than conventional ones aligns with Kiefer's (1937c) assumptions. Moreover, the apparently common origin postulated in lineages as [Metacyclops denticulatus-Hesperocyclops-Virbiocyclops], [Anzcyclops–Dussartcyclops–Barrowcyclops] and the [Acanthocyclops kieferi cluster– *Hypocyclops*] are indications of how ancestral stocks have diversified within a region (area, continent, biogeographic province). The uncertain position of *Stolonicyclops*, Olmeccyclops and Psammocyclops will undoubtedly be settled when more information concerning regional fauna becomes available.

Within this context, the presumed sister-group relationship (Pesce 1996; Karanovic 2001) between *Yansacyclops* and *Allocyclops*, either in its former or in its new definition, cannot be sustained. The leg 5 structure in *Yansacyclops* (Reid 1988: her figs 3 and 19 for the adults, figs 16 and 19 in copepodid stage V) is not comparable with that of *Allocyclops sens. nov.* or *Hypocyclops* but has the undifferentiated obsolete aspect as described for *Virbiocyclops*.

Yansacyclops should not be regarded as a close relative despite the similarites (namely, mouthparts, leg armature: plesiomorphies). The uncommon 10-segmented nature of the female antennule (nine-segmented in copepodid V) and the distal armament of the leg 4 endopodite bearing a spine and a seta are, among other features, indications that *Yansacyclops* is a member of a different evolutionary lineage of Cyclopidae.

Aside from the emendations about the leg 5 structure, the present analyses have emphasized and attributed greater significance in the generic diagnoses to the antennulary setal complement, mouthpart morphology and particular aspects of leg armament. Observations of the copepodid and adult morphology on a range of representatives of most of the cyclopid and of some cyclopinid genera provide sufficient evidence of their systematic importance. Besides filling gaps concerning adult morphology, ontogenetic data appear to be invaluable in evaluating character states. This is of even greater importance because the naturalness of Cyclopinidae Sars, 1913, commonly considered as the most closely related "out-group", has become controversial (see Boxshall and Halsey 2004 and references therein). The existence of basic constraints in copepodid development has been outstandingly documented (Ferrari 1998; Schutze et al. 2000; Ferrari and Dahms 2007), paying considerable tribute to Gurney's (1931) statement that no satisfactory classification of Copepoda will be reached until we have advanced our knowledge of the larval stages.

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