The genus *Haplocyclops* Kiefer, 1952 (Copepoda, Cyclopoida, Cyclopidae): Redescription of the type-species, *H. gudrunae*, and its congeners

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Abstract

The cyclopid genus *Haplocyclops* Kiefer, 1952 has long been a problematic taxon with an uncertain taxonomic position, until it became revalidated recently after the description of the first neotropical representative, *H. torresi* Rocha et al., 1998. This report deals with the redescription of the type-species of the genus, *H. gudrunae* Kiefer, 1952, and of three of its congeners. Specimens from Iran identified as *H. neuter* are considered as a previously unknown species, which is named *H. iranicus* n. sp. *Cyclops* spec. Menzel, 1926, which was included in *Haplocyclops* and named *H. parvulus* Kiefer, 1928, is allocated to the genus *Bryocyclops*. It remains, however, a *species inquirendae*. Based upon these observations the generic diagnosis is updated.

Introduction

With the discovery that cyclopids roam a wide variety of semi-aquatic habitats such as mosses, bromeliads, leaf litter and the interstitial realm of streams, the first half of the former century saw a rapid increase of the number of highly specialized genera. Descriptions, however, were quite concise and certainly inadequate. The contemporary view (Kiefer, 1927, 1928a) that the morphology of the fifth leg represents the key feature in cyclopid systematics, caused a drastice erosion in the completeness and quality of the generic definitions. Until today, with some exceptions, we are still ignorant of most of the morphology of many of these species and genera. Such ignorance fundamentally affects all attempts to arrive at a critical and well-founded analysis of the phylogenetical relationships within the Cyclopidae.

In an attempt to fill certain of these gaps, type series and in some cases additional material of these genera and species deposited in the Friedrich Kiefer Collection (Karlsruhe, Germany) were re-examined. This report deals with observations made on four species, including the type-species *H. gudrunae*, of the genus *Haplocyclops* Kiefer, 1952.

Haplocyclops has been subject to several discussions about its validity and its possible relationship to other cyclopid genera, in particular, the genus *Bryocyclops* Kiefer, 1927. Soon after its erection by Kiefer (1952), Lindberg (1956) dessolved *Haplocyclops* as a species group among five other ones, within the genus *Bryocyclops* Kiefer, 1927. After some hesitation (Kiefer, 1956), Kiefer (1960) followed Lindberg (op. cit.) but maintained *Haplocyclops* as a distinct subgenus within *Bryocyclops*. Despite some amendments of the original descriptions of certain *Bryocyclops* species (Yeatman, 1983; Reid, 1999) and the addition of the subgenera *Rybocyclops* Dussart, 1982 and *Palaeocyclops* Monchenko, 1972, this uncomfortable taxonomic situation remains largely unresolved (Dussart, 1982; Dussart & Defaye, 1985; 1995; Reid, 1999).

With their discovery of the first neotropical representative, *H. torresi*, Rocha et al. (1998) reassessed the genus *Haplocyclops* and brought some intriguing and previously overlooked morphological features to our attention. Their redefinition of the genus is undoubtedly accurate, but was largely based on the information provided in the original descriptions of the species and includes some misinterpretations of the leg

morphology which were introduced into the literature by Lindberg (1956). Following Rocha et al. (1998), the genus was considered valid by Dussart & Defaye (2001).

Material and methods

The material observed herein forms part of the Friedrich Kiefer Copepod Collection (F.K.C.C.) lodged at the "Staatliches Museum für Naturkunde", Karlsruhe (Germany). Generally, the animals were partially dissected and mounted in glycerin with sealed coverglasses. In some cases animals were mounted in Canada balsam. Preserved animals are stored in a drop of glycerin. Observations were made using a Leitz Diaplan Light microscope, equipped with phase contrast and a drawing tube, and at magnifications of 650× and 1250×. Abbreviations used through text and Tables are: Aesth, aesthetasc; End, endopodite; Exo, exopodite; L/W ratio, Length/width ratio.

Systematics

Haplocyclops gudrunae Kiefer, 1952 (Figs 1–3).
Haplocyclops Gudrunae n. g. et n. sp. (Kiefer, 1952: 240–243, Figs. 1–8).
Haplocyclops Gudrunae Kiefer (Kiefer, 1956: 50–53, Figs 15–23).
Bryocyclops gudrunae groupe VI (*Haplocyclops*) (Lindberg, 1956: 77).
Bryocyclops (Haplocyclops) gudrunae (Dussart, 1982: 71, Fig. 17A; Dussart & Defaye, 1985: 143).
Bryocyclops gudrunae (Dussart & Defaye, 1995: 226, Fig. L118).
Haplocyclops gudrunae (Rocha et al., 1998: 3; Dussart & Defaye, 2001: 275, Fig. L124)

Material. (1) slides 5084 (one adult female, holotype) and 5085 (1 copepodid IV), from the interstitial of the river Menarandrana (now Manambahy) near Tranoroa (appr. 24° 45′ S 45° 15′ E), Madagascar. Chappuis *leg.*, January 1952.
(2) Vial 2734 containing six females (one dissected on three slides by the author), from Madagascar. Delamare Deboutteville *leg.*, June 1954 (M39).
(3) Slides 6861–6862: two female specimens, dissected, from a river 7 km south of Tranoroa, Madagascar. Delamare Deboutteville *leg.*, June 1954 (M53).
Description (based on the females from vial 2734)

Female. Habitus (Fig. 1A) compact, with prosome longer than urosome (ratio: 4/3). Length: 304–313 μm. Pedigers 2–4 with rounded pleural regions. Sclerotized pseudosomite prsent between fifth pediger and genital double-somite (Fig. 1B). Genital double-somite, barrel-shaped, wider than long (L/W ratio: 1/0.8) with ovipores situated in median third of lateral margin, and located slightly above frontal plane. Receptacle with anterior part expanded. Posterior part undeveloped. Copulatory pore large, leading to nearly straight and short duct which forms a loop, before entering the lateral arms. Lateral arms crescentic, recurved anteriorly. Total length of next 3 somites shorter than genital double-somite. Integument of somites smooth. Fringes of somites entire.

Anal somite with large triangular anal operculum, reaching towards middle of caudal rami. Apex of operculum bifid (Fig. 1C) or trifid (Fig. 1E). Surface of operculum smooth. Posterodistal margins of somite with spinules laterally and ventrally.

Caudal rami (Figs. 1B–E) cylindrical, twice as long as wide. Lateral seta (12–15 μm) arising in anterior half of ramus, and positioned somewhat dorsolateral. Distolateral seta bipinnate, as long as ramus (25–27 μm). Both principal terminal setae (inner one ± 75 μm, outer one ± 50 μm) bipinnate, lacking breaking planes. Medioterminal seta pinnate, as long as (Fig. 1E) or slightly shorter (0.9, Fig. 1C) than distolateral seta. Dorsal seta less than 1.5 length of distolateral seta. Margins of rami smooth, except for three to four spinules near implantation of distolateral seta.

Antennule (Fig. 2A) 11-segmented, complemented as follows: I(7)-II(2)-III(5)-IV(2)-V(1)-VI(2)-VII(2)-V III(2+Aesth)-IX(2)-X(2+Aesth)-XI(6+Aesth). Element on segment V spiniform. Aesthetascs on segment VIII linguiform, on segment X filiform, and on segment XII tubiform. No spinule comb observed on segment I.

Antenna (Fig. 2I) without exopodal seta, and two abexopodal setae on basipodite. Proximal part of basipodite broken, distal part without ornamentation. Setal complement of endopodal segments: 1, 5, 7.

Mandible (Fig. 2D) with complex biting edge composed of several teeth and 1 biserrate seta. Palp entirely reduced, represented by single short seta. Labrum (Fig. 2C) with convex anterior margin, furnished with about 20 minute sharp teeth between lateral processes. Surface with comb of long slender spinules. Maxillular arthrite (Fig. 2G,H) with three robust medial spines, accompanied by two long ser-
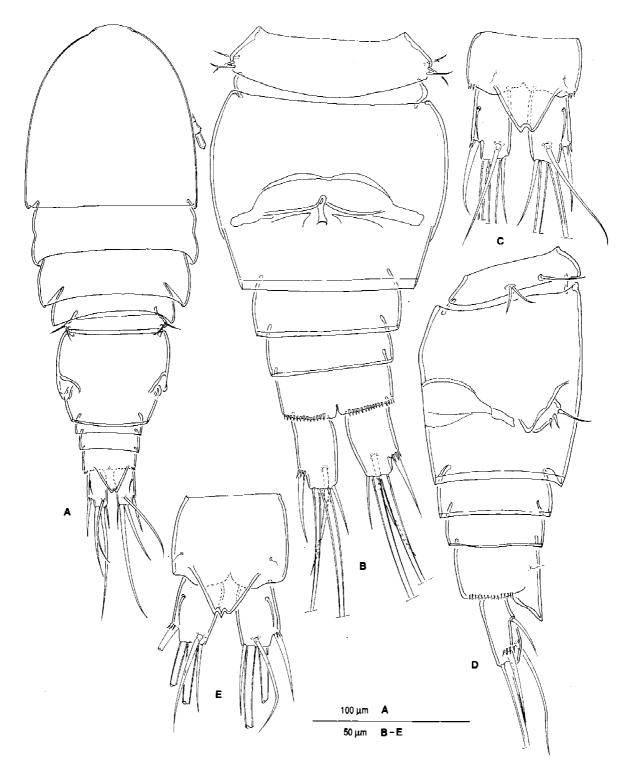
Figure 1. Haplocyclops gudrunae Kiefer, 1952, female (A–E, from vial 2734). A, habitus, dorsal view; B, urosome, ventral view; C, anal somite and caudal rami, dorsal view; D, urosome, lateral view; E, anal somite and caudal rami of other female specimen, dorsal view.
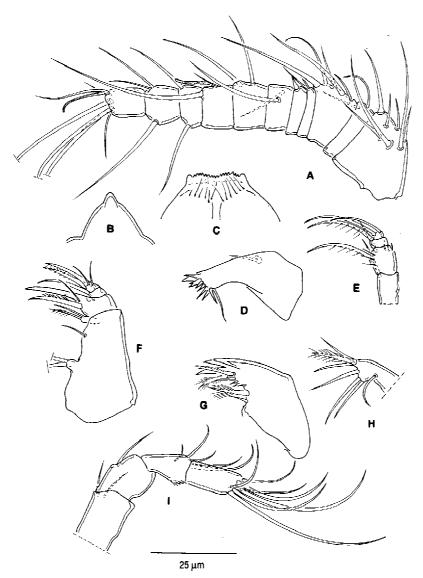
Figure 2. Haplocyclops gudrunae Kiefer, 1952, female (from vial 2734). A, antennule; (B) rostrum; (C) labrum; D, mandible; (E) maxilliped; F, maxilla; G, maxillular arthrite; H, maxillular palp; I, antenna.

rate elements. Lateral margin with six elements: five slender and smooth, one long and bipinnate. Maxillular palp (Fig. 2H) with three elements: two smooth, one bipinnate. One exopodal seta and three endopodal setae. The latter arising from distinct but confluent endopodal palp. Maxilla (Fig. 2F) with three endites on syncoxa, bearing (from proximal to distal one) 2, 1, 2 elements, respectively. Basis with strong claw, one short seta, and one robust serrate element. Endopodite two-segmented with two and three elements, respectively. Maxilliped (Fig. 2E) four-segmented, with (from proximal to distal segment) 1, 1, 1, 2 setae.

All setae, except distalmost, with long setules along dorsally directed margin. Surface of syncoxa and basis with spinules.

Leg 1 (Fig. 3A) with two-segmented rami. Intercoxal sclerite with rounded distal processes. Medial coxal seta present. Outer seta on basis longer than rami, pinnate. Medial basal spine robust, longer than first endopodal segment. Distal spine on terminal endopodal segment as long as segment. Chaetotaxy in Table 2. Leg 2 (Fig. 3D) with two-segmented rami. Medial coxal seta present, and intercoxal sclerite with rounded processes. Medial margin of basis
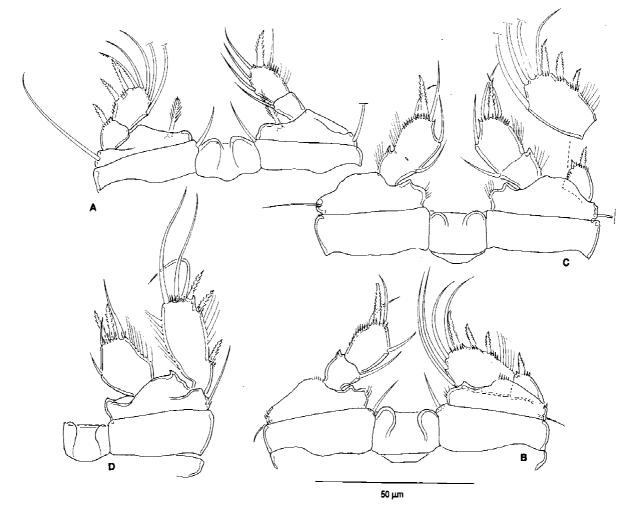
Figure 3. Haplocyclops gudrunae Kiefer, 1952, female (from vial 2734). A, Leg 1, anterior (exopodite of right leg and endopodite of left leg omitted); (B) leg 2, anterior; C; leg 3, anterior; D, leg 4, anterior.

Table 1. Protopodal armament of natatory legs 1–4 for all species of *Halocyclops*, except for *H. neuter* for which the complement is unknown. Notation as follows: outer margin-inner margin coxa: outer margin-inner margin basis. Arabic numerals representing spines, Roman numerals indicating setae

	Leg 1	Leg 2	Leg 3	Leg 4
H. pauliani	0-1:1-I	0-0:1-0	0-0:1-0	0-0:1-0
H. gudrunae	0-1:1-I	0-1:1-0	0-0:1-0	0-0:1-0
H. monodi	0-1:1-I	0-1:1-0	0-0 or 1 :1-0	0-0:1-0
H. iranicus	?	0-1:1-0	0-0:1-0	0-0:1-0
H. torresi	0-1:1-I	0-1:1-0	0-1:1-0	0-1:1:0

Table 2. Ramal chaetotaxy of natatory legs 1–4 in the genus *Haplocyclops* Kiefer, 1952. Arabic numerals representing spines, Roman numerals representing setae

	Exo	End
Leg 1	0-I 3-2-II	1-0 2-1+I+1
Leg 2	0-I 3-1+I-II	1-0 1-1+I-1
Leg 3	0-I 3-1+I-II	1-0 1-1+I-1
Leg 4	2-1+I-II	2-II-1 or 2-1+I-1
Leg 4*	0-I 2-1+I-I	1-0 1-II-1 or 1-1+I-1

*Armament of leg 4 if fusion of the ramal segments had not occurred.

rounded and hairy. Basis with short outer seta. Mediodistal margin of basis rounded. Second exopodal segment with long hairs in proximal half of outer margin. Leg 3 (Fig. 3B) with two-segmented exopodite and one-segmented endopodite. Ancestral division

between both endopodal segments indicated by transverse ridge, or nearly entirely absent. Ornamentation of second exopodal segment as in leg 2. Medial coxal seta absent. Intercoxal sclerite as in leg 2. Basis with long outer seta, medial margin rounded and hairy.

Leg 4 (Fig. 3C) with one-segmented rami. Exopodal segment rather slender, 2.16 times as long as wide. Inner margin and middle part of outer margin furnished with long setules. Endopodite compact, rhomboid. Terminal spines equal in size. Inner subdistal seta slightly shorter than terminal spines, outer subdistal seta distinctly longer than terminal spines. Medial coxal seta absent. Intercoxal sclerite with minute rounded distal processes. Basis with long outer seta, smooth medial margin, and triangular mediodistal process.

Leg 5 (Fig. 1D) entirely obsolete, represented by three setiform elements. Outer seta (remnant of basal segment) 1.5 times longer than medial setae (remnants of distal segment), the latter equally sized. Leg 6 vestige (Fig. 1D) semi-ovate with three appendages, located slightly above the frontal plane of the somite.

Male: Unknown

Discussion

The original description (Kiefer, 1952) of *Haplocyclops gudrunae* was based on a single adult female, which was partially redescribed in a subsequent contribution dealing with the interstitial cyclopid fauna of Madagascar (Kiefer, 1956). The illustrations in both descriptions are identical, except that the medial coxal distal edge of the first leg lacks a seta in the original description (Kiefer, 1952, Fig. 7) while it is present in the redescription (Kiefer, 1956, Fig. 22). The original pencil drawings of the leg 1 protopodite, available in F. Kiefer's archive, show that he observed a seta, but apparently overlooked this element in the preparation of the final draft. Re-examination of the partially dissected female (slide 5084, partially desiccated) revealed the presence of this seta on the P1, but also the presence of an element on the coxa of the second leg. In this aspect, *H. gudrunae* resembles most *H. monodi* and, probably, *H. neuter* (see below for details).

Among all species presently attributed to the genus *Haplocyclops*, *H. gudrunae* is unique because of its large triangular anal operculum with a bifid or trifid apex. All other species posses a crescentic operculum. In this respect, *H. gudrunae* resembles *Bryocyclops*

(*Rybocyclops*) *pauliani* Lindberg, 1954, which is characterized, among other features, by its large bifid anal operculum. The latter, however, differs in some important aspects (spine formula 2222 and absence of an outer subapical element on the terminal endopodal segment in legs 1–4) from *H. gudrunae*, and also from all other species ascribed to *Haplocyclops*.

Haplocyclops pauliani Kiefer, 1955 (Figs 4 and 5).
Haplocyclops Pauliani n. sp. (Kiefer, 1955: 223–224, Figs. 1–5).
Haplocyclops Pauliani n. sp. (Kiefer, 1956: 53–55, Figs. 24–32).
Bryocyclops (Haplocyclops) correctus nov. nom. (Kiefer, 1960: 401).
Bryocyclops (Haplocyclops) correctus (Dussart, 1982: 73, Fig. 18B; Dussart & Defaye, 1985: 144).
Haplocyclops pauliani (Rocha et al., 1998: 3).

Material. Syntypes: slides 5359–5360 (female) and 5361–5362 (male) from the interstitial of the river Sisaony (Madagaskar). Paulian *leg*., 26 February 1952.

Description. Female: Entire habitus not observed. Length, according to Kiefer (1956), 350 μm long. Pseudosomite between fifth pediger and genital double-somite present, sclerotized.

Genital double-somite (Fig. 4A) with conical appearance (L/W ratio: 1/0.75). Anterolateral corners angular. Receptacle with ribbon-shaped anterterior part. Posterior part not developed. Copulatory pore wide, leading to short T-shaped duct. Lateral arms straight, slightly directed posteriorly. Leg 6 vestiges not visible, but clearly present at distal end of median third of double-somite.

Anal somite with large crescentic anal operculum which reaches distal end of anterior third of caudal rami. Posterodorsal margins smooth, posteroventral margins with numerous spinules. Caudal rami 1.7 times as long as wide with crescentic inner margin. Anterolateral seta arising in anterior third of ramus, inserted dorsally. Distolateral seta as long as ramus. Dorsal seta 1.6 times longer than ramus and distolateral seta. Medial seta equaling 75% of ramal length. Outer and inner terminal setae respectively 51 and 71 μm long.

Antennule and other buccal appendages as in *H. gudrunae*.

Coxa of leg 1 with medial seta, legs 2–4 without. Legs 1–2 (Fig. 5A,B) with two-segmented rami, leg 3 (Fig. 5C) with two-segmented exopodite and one-segmented endopodite, leg 4 (Fig. 5D) with both rami
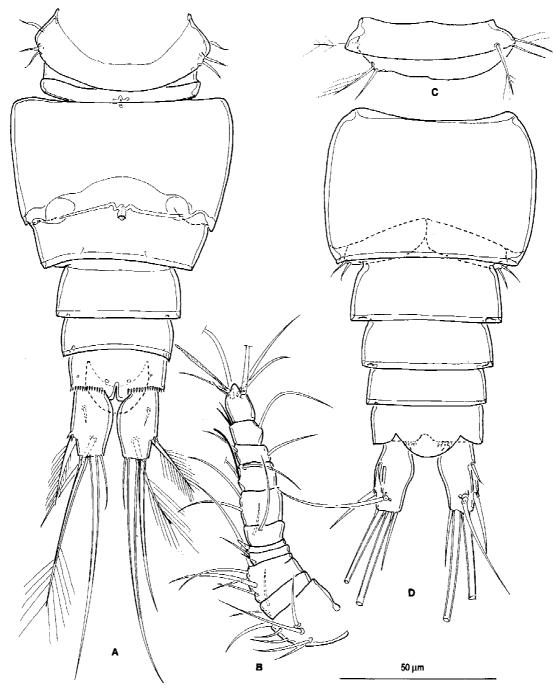
Figure 4. Haplocyclops pauliani Kiefer, 1960, female (A,B, slides 5359 and 5360), male (C,D, slides 5361 and 5362). (A) urosome, ventral view; (B) antennule; (C) fifth pediger, dorsal view; (D) urosome (without fifth pediger), dorsal view.

one-segmented. Endopodite leg 3 with a transverse ridge on frontal surface, remnant of ancestral articulation. Posterior surface without trace of ancestral articulation. Endopodite of leg 4 semi-ovate, 1.5 times as long as wide, with distinct triangular process in middle of medial margin. Terminal spines equal in length, about 80% of ramal length. Outer subdistal seta shorter than twice length of terminal spines.
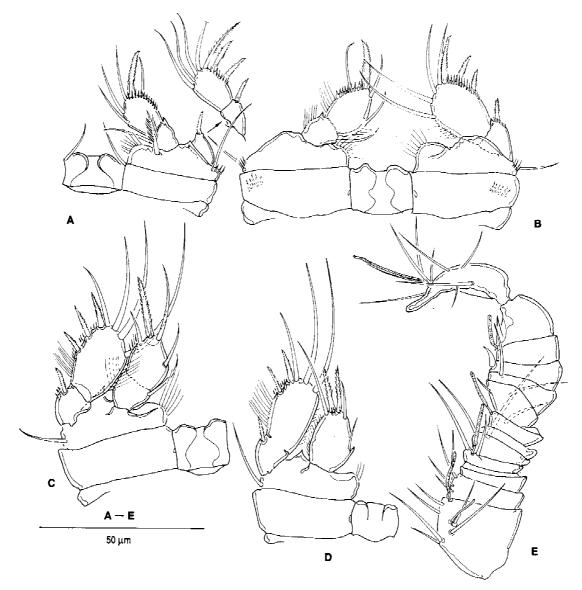
Figure 5. Haplocyclops pauliani Kiefer, 1960, female (A–D, slides 5359 and 5360), male (E, slide 5361). (A) Leg 1, posterior; (B) leg 2, anterior; (C) leg 3, posterior; D, leg 4, posterior; (E) antennule.

Leg 5 (Fig. 4A) obsolete, represented by three slender setae. Remnants of exopodal segment implanted on a (barely visible) elevation.

Male. Habitus not observed. Length, according to Kiefer (1956) 350 μm long. Pseudosomite not observed (fifth pediger and urosome separated on slide). Anal somite with crescentic operculum, the latter far less developed than in the female. Ornamentation of posterior margins as in female.

Caudal ramus more slender than in female, 1.8 times as long as wide. Inner margin less crescentic.

Distolateral seta shorter than ramus, and as long as medial seta.

Antennule (Fig. 5E) 13-segmented, with two aesthetascs on segment I and a single aesthetasc on each of segments IV, VII, XI, and XIII. Exact setal complement not obseved because of compression by cover glass.

Mouthparts (as far as visible on mounted specimen) and legs 1–4 as in female.

Leg 5 (Fig. 4C) obsolete, represented by three equally sized slender setae. Leg 6 vestige (Fig. 4D)

with two setae. Valve strikingly slender and located in far distal half of ventral surface of somite. Surface smooth.

Haplocyclops neuter Kiefer, 1955 (Fig. 6C).
Haplocyclops neuter n. sp. (Kiefer, 1955: 224–225, Figs 6–9).
Haplocyclops neuter n. sp. (Kiefer, 1956: 55–56, Figs 33–38).
Bryocyclops (Haplocyclops) neuter (Dussart, 1982: 71–73, Fig.18A; Dussart & Defaye, 1985: 144).
non *Bryocyclops (Haplocyclops) neuter* (Dussart, 1981: 163–164, Fig. 1.).
Haplocyclops neuter (Rocha et al., 1998: 3).

Material. Holotype: slides 5348–5349 (female) from the interstitial of Maroantsetra Lagoon (Madagascar: Maroantsetra: approx. 15° 26′ S 49° 44′ E). Paulian *leg*., February 1952.

Note: Based on a single female specimen, the original description of this species (Kiefer, 1955) was extremely concise with only four illustrations. The redescription (Kiefer, 1956) is somewhat more detailed and includes three additional illustrations. Most unfortunately is that the female type (FKCC 5349), which has been mounted in Canada balsam, is largely covered with crystals and only the last four segments of the antennule and the last urosomites (Fig. 6C) are fairly visible.

Differential diagnosis

Haplocyclops with slender genital double-somite (length > width); anal operculum crescentic. Caudal rami twice as long as wide. Dorsal seta on caudal ramus 1.5 times as long as distolateral one. Medial coxal seta absent in legs 2–4 (?: to be confirmed later as these structures are barely visible on the mounted specimen). Endopodite of leg 4 short, 1.4 times as long as wide, with two terminal spines, equalling 70% of segment length. Subdistal outer seta of leg 4 endopodite slightly longer than terminal spines.

Male unknown.

Remarks

Dussart (1981) identified a specimen from a high-altitude locality in Iran as *H. neuter*, and provided a short "redescription". The Iranian specimen differs, however, in several aspects from the original descriptions of *H. neuter*. Leaving aside the illustration of the maxilla (indicated as the maxilliped) and the incomplete setal complement of the antennule, other features led us to assume that the Iranian specimen is not conspecific with *H. neuter*.

From all other species assigned to the genus, *H. neuter* is distinctive for its slender female genital double-somite which is slightly longer than wide. The slender appearance is still, although with difficulty, visible in the type-specimen. The genital double-somite as depicted by Dussart (1981) has a more compact appearance, and is as in the other species (only as long as wide), although this appearance my can be a result of compression of the urosome under the coverglass.

The setal armament of the caudal rami depicted in the original description of *H. neuter* is somewhat erroneous, as the insertion place of the dorsal seta is in fact located more closely to the distal end of the rami (see Fig. 6C), as is the case in the specimen from Iran, and all other species of the genus. The proportional lengths of the setae were, however, accurately illustrated. The dorsal seta is about 1.6–1.7 times longer than the distolateral one, while the medial one is rather short (0.67 times the distolateral one).The Iranian specimen has a dorsal seta which is twice as long as the distolateral seta, while the medial one is proportionally longer (medial/distolateral: 0.8).

The fourth leg endopodite in *H. neuter* has a rounded appearance (L/W ratio: 1.37) with two terminal spines equalling about 70% of the segment length. In contrast, the Iranian specimen possesses a leg 4 endopodite which is distinctly slimmer (L/W ratio: 1.63) with terminal spines which are only half as long as the total length of the segment. Secondly, while the outer subapical seta on the leg 4 endopodite of *H. neuter* seems to be only slightly longer than the terminal spines in the original description, this seta is significantly longer in the specimen from Iran. Moreover, the seta in question, which seems to be 2.5 times longer than the terminal spines in the Iranian specimen, is – proportionally – the longest presently known among the species attributed to the genus.

In contrast to all other species of the genus, the iranian specimen seems to bear only three setae on the second exopodal segment of the second leg. However, the apparent absence of this apicalmost seta must be confirmed in the future.

Because species discrimination in *Haplocyclops* is mainly a matter of proportional lengths of the rami and setae of the fourth leg, the specimen described
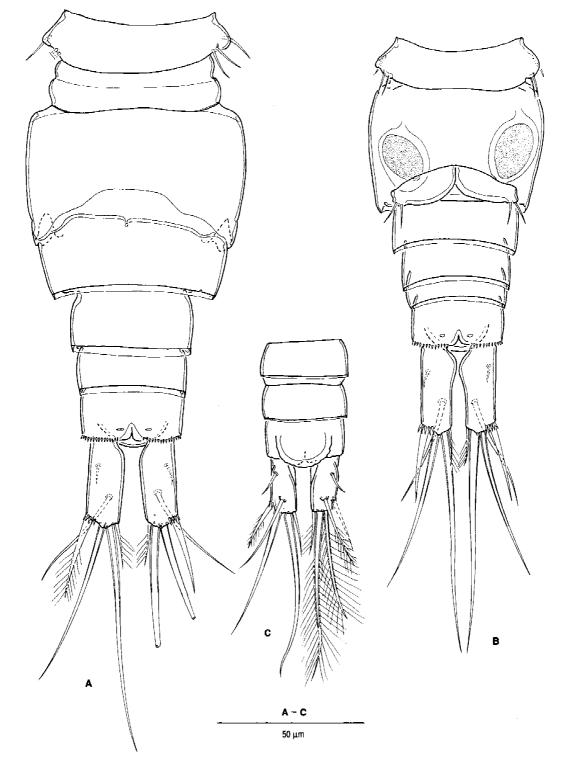
Figure 6. Haplocyclops monodi Kiefer, 1960, female (A, slide 6924), male (B, slide 6933). (A) urosome, ventral view; (B) urosome, ventral view. *Haplocyclops neuter* Kiefer, 1955, female (C, slide 5348). (C) fourth to sixth urosomite and caudal rami, dorsal view.

by Dussart (1981) from Iran is assumed here to be a previously unknown species, and is named:

Haplocyclops iranicus n. sp.
Bryocyclops (Haplocyclops) neuter Kiefer, 1955 (Dussart, 1981: 163–164, Fig. 1).
Bryocyclops (Haplocyclops) neuter Kiefer, 1955 (Dussart & Defaye, 1985: 144 (partim)).
Bryocyclops (Haplocyclops) cf. *neuter* Kiefer (Pesce, 1981: 566).

Etymology. The specific name refers to the type region were the species occurs.

Differential diagnosis. Haplocyclops with compact genital double-somite. Anal operculum crescentic. Caudal rami twice as long as wide, with dorsal seta twice as long as distolateral seta. Medial coxal setae present in legs 1–2, absent in legs 3–4. Endopodite of leg 4 slim, 1.63 times as long as wide, with two terminal spines, both half as long as segment, and a very long subapical outer seta.

Male unknown.

Haplocyclops monodi Kiefer, 1960 (Figs 6A,B and 7).
Bryocyclops (Haplocyclops) monodi n. sp. (Kiefer, 1960: 398–401, Figs 10–22).
Bryocyclops (Haplocyclops) monodi (Dussart & Defaye: 144).
Haplocyclops monodi (Rocha et al., 1998: 3).

Material. Syntypes: slides 6923–6924 (each with one female specimen) and 6933 (male) from the interstitial of a sand spit in the river Niger, near Tilembaya (Niger) (now named Tilembeya in Mali, appr. 14° 09′ N 4° 59′ W). Monod *leg.*, 3 April 1957. Specimens undissected, mounted ventrodorsally.

Description

Female. Habitus as in type-species. Length 367 μm (slide 6923). Pseudosomite between fifth pediger and genital double-somite present, sclerotized. Genital double-somite as long as wide, tapering posteriorly. Receptaculum expanded anteriorly. Posterior part absent. Copulatory pore small, seemingly connected directly to straight lateral arms. Leg 6 vestige located near distal end of median third of somite, not observed in detail.

Anal somite with crescentic operculum reaching slightly beyond proximal margin of somite. Pos-terodorsal margin of somite smooth, posteroventral margin furnished with minute spinules.

Caudal ramus cylindrical, 2.5 times longer than wide. Anterolateral seta positioned on dorsal surfcae, in anterior third. Distolateral element as long as ramus, and twice as long as medial terminal element. Dorsal seta arising at distal end of median third of ramus, 1.5 times longer than ramus. Outer and inner terminal setae pinnate, respectively, 55 and 80 μm long. Integument of rami smooth, except for four to five spinules near implantation of distolateral seta.

Antennule and mouthparts (as far as visible) as in the type-species.

Legs 1 and 2 each with medial coxal seta. One specimen without medial coxal seta on leg 3, but this seta present in the other female specimen. Leg 4 without medial coxal seta. Intercoxal sclerite of legs 1–4 with slightly produced, rounded distolateral corners. Medial margin of basis rounded and hairy in all legs. Mediodistal margin triangular in legs 1 and 4, rounded in legs 2 and 3. Leg 4 rami one-segmented. Endopodite of leg 4 ovate, 1.8 times longer than wide (Fig. 7D). Terminal spines equal in length, slightly longer than half segment length. Outer subdistal element twice as long as terminal spines. Lateral margins of endopodal segment and inner margin of exopodal segment hairy.

Leg 5 (Fig. 6A) obsolete, represented by three equally sized smooth setae.

Male. Body somewhat slimmer than in female, 318 μm long. Anal operculum crescentic, reaching just beyond posterior margin of anal somite. Caudal ramus 2.5 times as long as wide. Inner margin bulbous in anterior third. Setae and proportional lengths as in female (Fig. 6B).

Antennule as in *H. pauliani* (see Fig. 5E), and mouthparts as in the type-species.

Legs 1–3 (Fig. 7A, B) as in female. Protopodite and exopodite of leg 4 as in female (Fig. 7C). Endopodite distinctly longer (nearly 3 times as long as wide), with clear constriction in proximal third. Outer terminal spine slightly longer than inner one. Subdistal outer seta twice as long as outer terminal spine.

Leg 5 (Fig. 6B) represented by 3 subequally long thin setae. Leg 6 vestiges (Fig. 6B) narrow, without integumental ornamentation, and with two equally long setae.

Haplocyclops torresi Rocha, Torres & Maia-Barbosa, 1998
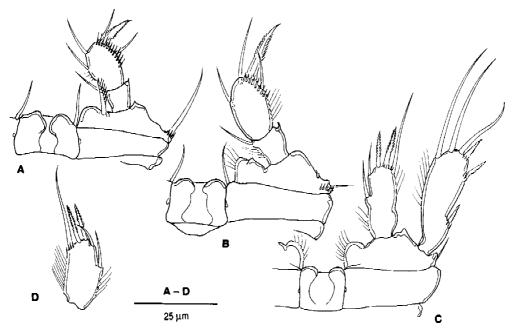*Haplocyclops torresi* sp. n. (Rocha et al., 1998: 3–9, Figs 1–18).

Figure 7. Haplocyclops monodi Kiefer, 1960, male (A–C, slide 6933), female (D, slide 6924). (A) Leg 1, anterior; (B) leg 2 (exopodite omitted), anterior; (C) leg 4, anterior; (D) endopodite of leg 4, anterior.

Differential diagnosis. Haplocyclops with genital double-somite distinctly wider in anterior half. Anal operculum weakly developed, crescentic. Caudal rami twice as long as wide, with dorsal seta slightly longer than distolateral seta, the latter 1.7 times longer than medial one. Coxa of legs 1–4 with medial seta. Endopodite of leg 4 large, equalling 3/4 of exopodite length, and bearing one spine and one seta, terminally. Male with 15-segmented antennule, possessing three aesthetascs on segment I. Leg 4 endopodite large, equalling 2/3 of exopodite length, and bearing one spine and one seta, terminally. Leg 4 exopodite with remnant of articulation between both segments.

Comments

Among the six species presently attributed to the genus, *H. torresi* takes a separate position. The most obvious differences between the latter and its congeners are (1) the presence of a medial element on the coxa of each leg; (2) the leg 4 endopodite with one spine and one seta as terminal elements; (3) the presence of a small knob-like aesthetasc on the penultimate antennular segment of the female; (4) the small anal operculum; and (5) the presence of (remnants of) an articulation between both exopodal segments in the male fourth leg.

Whereas features 1, 4 and 5 clearly represent the plesiomorphic conditions of these character-states, feature 2 is a derived condition. However, the presence in *H. torresi* of a setiform terminal element in the fourth leg cannot be considered as unique, because such a condition is known in other highly specialised cyclopines (e.g., several species presently assigned to *Bryocyclops* (in the sense of Rocha et al., 1998*), Stolonicyclops heggiensis* Reid & Spooner, 1998, among others).

Haplocyclops parvulus (Kiefer, 1928).
Cyclops sp. (Menzel, 1926: 215–216, Fig. 15–17).
Bryocyclops parvulus nov. spec. (Kiefer, 1928b: 102).
Bryocyclops parvulus Kiefer (Kiefer, 1929; Kiefer, 1937: 439).
? *Bryocyclops (Haplocyclops) correctus* (Dussart, 1982: 73).

Although the description of the only specimen is extremely concise, there are, however, sufficient indications that this species should not be assigned to *Haplocyclops* as assumed by Dussart (1982).

(1) The illustration of the caudal rami (Menzel, 1926: Fig. 16) clearly shows a dorsal longitudinal carena. Such modification does not exist in *Haplocyclops* but is a typical feature for the members of the genus *Bryocyclops*.

(2) Secondly, the medial elements of the fifth leg in *Haplocyclops* are slender, equally long, setae. In contrast, the outer medial element of the fifth leg in *H. parvulus* is distinctly shorter than the inner one (Menzel, 1929: Fig. 17) and as such resmble more the fifth leg setation known in the genus *Bryocyclops*.

(3) Finally, the genital double-somite as depicted in Menzel's Fig. 15 is a laterally expanded somite, 1.5 times wider than long, and as such is not comparable with the genital double-somite in *Haplocyclops*. Again, the length/width proportions of *H. parvulus* resemble more those of *Bryocyclops*.

Those three elements appear to be sufficient to exclude *H. parvulus* from the genus *Haplocyclops* and transfer it to *Bryocyclops*. Unfortunately as the original (and sole available) description is inadequate, *B. parvulus* (Kiefer, 1928) comb. nov. cannot be compared with the other species of the genus. It remains a *species inquirendae*.

General discussion

The classic opinions (Lindberg, 1956; Dussart, 1982; Dussart & Defaye, 1985) about the systematic position of the genus *Haplocyclops*, and its relationships to *Bryocyclops* were based completely on the striking resemblances of leg segmentation, chaetotaxy, body shape, and leg dimorphism. Unfortunately, because the original descriptions of several of the species were inadequate, the incorporation of the genus *Haplocyclops* in *Bryocyclops*, and the subsequent subdivision of the latter into species groups as proposed by Lindberg (1956) remained largely based on guesswork.

In contrast with the previous opinions, Rocha et al. (1998) reinstated the genus *Haplocyclops* as a separate taxon from *Bryocyclops* after the discovery of a representative, *H. torresi*, in Brazil. Their detailed observations and comparison with the existing literature revealed a suite of characteristics useful in refining the original generic definition.

In the following paragraphs, it will be shown that the genus *Haplocyclops* can be defined on the basis of several robust apomorphies (including convergent ones): antennule setation, position of the gonopores, the reduced head appendages (antenna, mandible, maxilliped), the reduced setation of the coxae of the legs, the reduced leg 4 endopodite, and the reduced number of appendages in the male sixth leg.

The presence of an extra somite between pediger 5 and the genital somites has been related to the improvement of body flexibility of interstitial cyclopoids (Boxshall et al., 1993, Reid & Strayer, 1994). The presence of such an additional body joint in *Haplocyclops* was first recognized for *H. torresi* by Rocha et al. (1998), and its presence is confirmed here for all other species presently attributed to the genus. However, while this additional body articulation is clearly apparent in female specimens, its presence in males is far less obvious.

The genital double-somite of female *Haplocyclops* is in some aspects quite remarkable. The ground plan location of the sixth vestiges in cyclopine copepods, is invariably in the anterior half of this somite. As discussed at length by Reid & Strayer (1994), adaptation of cyclopines to interstitial habitats involved drastice changes in proportional lengths of the body and tagmata. However, reduction of the genital double-somite appears to remain within certain limits.

Haplocyclops is unique among the cyclopine genera in the position of the sixth leg vestiges, and the medioventral copulatory pore, at the caudal end of the median third of the somite. In contrast, other genera with a strongly reduced genital double-somite (e.g. *Bryocyclops*, *Muscocyclops*, etc) have their leg 6 vestiges and copulatory pore located near the middle of the somite.

The female antennule in *Haplocyclops* is 11-segmented in all species, a condition which is found in several cyclopid genera. This indicates that the reduction of the number of segments has occurred on several occasions (although the patern of reducion might be quite different, cf. Karaytug & Boxshall, 1999; Schutze et al., 2000). However, the setal complement of some of the segments turns out to be of great significance for the generic definition of *Haplocyclops*. Rocha et al. (1998) assumed correctly that the absence of the median caudally directed seta on the ultimate segment represents an apomorphy for the genus. Re-examination of *H. neuter, H. pauliani* and *H. monodi* confirmed their assumption that this is a feature commn to all species attributed to the genus. Moreover, examination (pers. obs.) of the female antennules of representatives from the majority of the other cyclopid genera revealed that the absence of this seta is (probably) a unique condition among the Cyclopidae.

Secondly, the antennular segment VII (representing the ancestral segments XVII–XX) is complemented with only 2 setae in all the species examined, and

this is also the case for *H. torresi*. Comparison (pers. obs.) with representatives of the other cyclopid genera demonstrated that the common armature of this segment is three setae. Thus far, only *Muscocyclops operculatus* (Chappuis, 1917) is known to show the same reduction of the number of setae (according to the illustration by Rocha & Bjornberg, 1987).

The *Haplocyclops* specimens here examined, all possess a seta and a hyaline conical element on the antennular segment IV. The absence of a second element on segment IV in *H. torresi* has to be confirmed. This element, which is rather difficult to observe, has often been overlooked (pers. obs.), even in recent descriptions.

Breaking planes in the principal terminal setae of the caudal rami are a general feature within the Cyclopidae, and probably belong to the groundpattern of cyclopine morphology. Unfortunately, the presence, but more important, the absence of such planes have been mostly ignored in many descriptions. At present only a few cyclopid species are known to lack this setal feature, but personal observations revealed that it is more common than previously thought and that the absence could turn out to be of generic importance in the future.

Recently, Reid (1999) redescribed in detail some members of the genus *Bryocyclops* s. str., and pointed to the particular morphology of the integument characterised by its dense pattern of refractile points. Personal observations revealed the presence of the same type of integument in *B. bogoriensis* (Menzel, 1926), *B. chappuisi* Kiefer, 1928, *B. elachistus* Kiefer, 1935, *B. apertus* Kiefer, 1935, *B. phyllopus* Kiefer, 1939, *B. difficilis* Kiefer, 1935, *B. ankaratranus* Kiefer, 1955 and *B. mandrakanus* Kiefer, 1955 and as such support Reid's assumption that this distinctively structured integument is a typical (and apomorphic) characteristic for *Bryocyclops*. In contrast, the four species of *Haplocyclops* herein examined definitely lack this modification, which further supports the separate status of this taxon.

The typical complement of the cyclopid male sixth leg in cyclopids is three setae/spines arising from the outer caudalmost corner of the leg vestige. In *Haplocyclops* the number is reduced, retaining only two elements (in at least the two species of which the male is known). In contrast, males of *Bryocyclops* still possess the (plesiomorphic) original complement with three elements. Moreover, where the leg 6 setae in *Haplocyclops* are minute elements, those in *Bryocyclops* are still very long setae, a condition which is also found in the less specialized cyclopid genera. The reduction of the original complement to two elements is not unique for *Haplocyclops* as it has been observed in different cyclopine genera: *Allocyclops*, *Goniocyclops*, *Palaeocyclops*, *Rybocyclops*, *Muscocyclops* and is probably achieved among the cyclopid genera several times independently.

Lindberg (1956) stated, either by ignorance or by a slip of the pen, that *Haplocyclops* (his Groupe VI) possess a setal formula of the exopodites of 4443. Rocha et al. (1998) relied on this information to differentiate *H. torresi*, which has a setal complement as 5443, from the other species. It is obvious now that in all *Haplocyclops* species known so far the setal complement of the exopodites is identical: namely 5443.

The affinities of the genus *Haplocyclops* with other cyclopid genera remain unclear, because of our insufficient knowledge of the precise morphology of several species which are characterised by strong reduced appendages. However, the current view that genera such as *Haplocyclops, Bryocyclops*, *Rybocyclops* Dussart, 1982, and *Palaeocyclops* Monchenko, 1972 are closely related (sub)genera probably is untenable.

There are indications that *Haplocyclops* and *Rybocyclops* are more closely related to each other than to any other of these taxa. Features such as the large anal operculum, the dorsal position of the anteromost lateral seta on the caudal rami, the ribbon-shaped receptacle, the reduced armament of the legs, especially the leg 4 morphology with on the (ancestral) terminal exopodal segment only two spines and three setae, plus the reduced number of setae in the male sixth leg may indicate a common ancestry of both genera. *Rybocyclops* differs from *Haplocyclops* because of the loss of the subdistal outer elements on the endopodites of the legs, the absence of the medial spine on the first leg, the spine formula 2222 (all apomorphies), and the barrel-shaped female genital double-somite with the position of the gonopores in the middle of the somite sides (a plesiomorphy). Unfortunately several attempts to locate the specimens of *R. pauliani* (Lindberg, 1954), the sole representative known so far, have failed.

Bryocyclops, in the sense of Reid (1999, and including the several species listed above) is clearly a representative of a different lineage, which certainly includes the genus *Hesperocyclops* Herbst, 1984 (pers. obs.). Four species currently assigned to *Bryocyclops*, namely *B. constrictus* Lindberg, 1947, *B. travancoricus* Lindberg, 1947, *B. africanus* Kiefer, 1932 and *B.*

arenicolous (Fryer, 1956) are most likely representatives of other lineages. Unfortunately, the inadequate descriptions of these species hamper every attempt to locate them correctly within cyclopid systematics. Only re-examination of this material (which is partially in process) will shed light on their relationships with the other cyclopids.

The generic diagnosis of *Haplocyclops* as amended by Rocha et al. (1998) is largely accurate. Based on the observations presented here some additional features can be added: (1) pseudosomite present and sclerotized; (2) terminal setae on caudal rami without breaking planes; (3) female antennule with only two setae on segment VII; and (4) setal formula of exopodites 5443.

A final remark. The spine formula of the exopodites in the diagnosis of the genus is 2332, but as the exopodite of leg 4 is only one-segmented, the indication of the formula should be 2333. However, the outer proximal spine is clearly the outer spine of the ancestral proximal segment of this ramus (as evidenced by its position, and by the remnant of a division line in *H. torresi*). The exclusion of this spine from the formula seems more appropriate for future comparisons of this leg with this appendage in other derived genera.

Acknowledgements

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