

TOWARDS A REVISION OF CYCLOPINAE COPEPODS (Crustacea, Cyclopidae)

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INTRODUCTION

Traditionally the systematic of the cyclopoid copepods, especially at generic level, has established on the structure and armature of the fifth leg (Kiefer 1927; Rylov 1948; Yeatman 1959; Dussart 1969; Monchenko 1974).

However, some authors (Lindberg 1954a; Kiefer 1978; Morton 1985; Petkovski 1986) and recently Reid (1993) suggested that this appendage should be considered a somewhat conservative morphological character among the cyclopoid copepods, as well as it could have a poor taxonomic value as generic discriminant: the fact is that this feature by itself greatly confuses the issue of definition of some genera which remain still vague and controversial (Reid 1994; Fiers et al. 1996).

Moreover, the inadequacy of existing descriptions of numerous species and genera, as well as the recent discovery of several taxa combining morphological characteristics of different genera, such as *Diacyclops* Kiefer, 1927, *Acanthocyclops* Kiefer, 1927, *Megacyclops* Kiefer, 1927, *Allocyclops* Kiefer, 1932, *Mesocyclops* G. O. Sars, 1914 and *Thermocyclops* Kiefer, 1937, further complicate the taxonomic understanding of this group of microcrustaceans (Mazepova 1978; Monchenko 1985; Petkovski 1986; Boxshall et al. 1993; Reid 1993a; Fiers et al. 1996).

The present confusion among the Cyclopinae is also largely due to the fact that certain fundamental micro-characters, such as the ornamentation of the antenna and antennule, and the armature of basis, coxa and couplers of the swimming legs, once considered unimportant, are often neglected in the specific descriptions and illustrations.

In the present paper, because neither recent world review of

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Cyclopinae systematics nor up-to-date identification keys to the currently known genera exist, an attempt has been made to better define the genera in this subfamily by combining the structure and setation of the fifth leg, still of some importance in the cyclopids diagnosis, with other morphological features, such as the number of the segments of the antennula and the oligomerization of the swimming legs.

In this regard, six morphological groups are proposed, and an identification key to all the known cyclopinae genera, including those which have been described after the excellent world check-list by Dussart & Defaye (1985), is provided.

The characters used are mostly taken from the literature, principally after Dussart (1969), Monchenko (1974), Einsle (1993) and Reid (1993); other ones were pointed out from the author's collections.

TAXONOMIC ACCOUNT

Members of the family Cyclopidae are characterized by the antennula composed of 6-21 segments (female) and less than 18 segments (male), antenna 4-segmented (rarely 3-segmented), with or without exopodal vestigial seta and with somewhat reduced armature on the basipodite, mandibular palp reduced, consisting of 1-3 setae implanted on a rudimentary protuberance, or quite lacking in some species, maxillula with endopodite and exopodite fused, maxilliped with reduced endopodite.

The family includes three subfamilies, viz. Halicyclopinae, Eucyclopinae and Cyclopinae. Representatives of the subfamily Cyclopinae share the distal segment of the leg 5 armed with two (rarely one or three) spines/setae, the antennula with 10-17 articles, and a progressive oligomerization of the swimming legs from the plesiomorphic state with 3-segmented rami to an apomorphic condition in which both rami of legs are 2-segmented, or the endopodite and exopodite of leg 4, 1-segmented.

From an ecological point of view the cyclopinae are among the most common and numerous freshwater cyclopoid copepods. They are found in various aquatic biotopes, most of them are planktonic, typical of pelagic lakes, other ones are bottom-dwelling inhabitants of different freshwater bodies and moist semiterrestrial habitats; numerous species and some genera have been reported specifically

from subterranean aquatic habitats, where they usually live within small spaces of coarse substrates rather than in pools. Some large, epigeal species, such as *Acanthocyclops robustus* (G. O. Sars, 1863), *A. vernalis* (Fischer A., 1853), *Diacyclops bicuspidatus odessanus* (Schmankevitch, 1875), *Eucyclops serrulatus* (Fischer, 1851) and *Macrocyclus albidus* (Jurine, 1820) can maintain permanent stygophilic populations in interstitial biotopes, as well (Pesce 1985; Pesce & Maggi 1983).

Although the Cyclopinae phenotype tends to be quite conservative (Chappuis 1920; Reid 1994), several morphological modifications involve the stygobitic members of this subfamily.

Primary changes are related to reduction of the body size and somites. Particularly, most stygobitic species bear a large genital double-somite, generally much wider than long, short caudal rami, reduced antennula and antenna, as well as they undergo attenuation and shortening of the swimming legs, accomplished by fusion or loss of primitive segments.

In some cases reduction in number and length of setae/spines may also occur following oligomerization of the swimming legs (Reid 1994).

Recently, Boxshall et al. (1993) described a secondary pseudosomite anterior to the genital double-somite in females of *Diacyclops biceri* Boxshall et al. 1994, interpreting this feature as an adaptation allowing a greater range of urosomal movements in the interstitial habitat.

At present the subfamily comprises 33 genera and some subgenera which, according to the the number of articles of the antennula, the increasing oligomerization of swimming legs 1-4 and the construction and armature of leg 5, could be classified into six distinct groups, including phenetically allied species viz. *Orthocyclops* Forbes, 1897, *Cyclops* (Kiefer, 1939), *Austriocyclops* Kiefer, 1964, *Mixocyclops* Kiefer, 1944, *Microcyclops* Claus, 1893 and *Bryocyclops* Kiefer, 1927..

The genera *Diacyclops* and *Acanthocyclops* (*Diacyclops-Acanthocyclops* complex), owing to the still preoccupied and debated taxonomy, are provisionally placed partly in the *Cyclops* and *Mixocyclops* groups.

Kiefer (1927) firstly subdivided the above complex into three distinct genera, viz. *Acanthocyclops*, *Megacyclops* and *Diacyclops*; subsequently, the separation of these genera has been questioned by

Reid 1993); other authors (Monchenko 1974; Dussart & Defaye 1985; Einsle 1993) still accept both as valid genera.

Anyway, due to the noteworthy variation among species and the clear overlap between the genera, the complex *Diacyclops-Acanthocyclops* is in urgent need of exhaustive revision.

The first group (*Orthocyclops*-group) is monogeneric, containing only the genus *Orthocyclops*. Members, which are inhabitants of epigeal water bodies, are characterized by the most plesiomorphic condition for all the nominate characters, viz. they show a 16-segmented antennule, swimming legs 1-4 with 3-segmented rami and a 3-segmented leg 5.

Likewise, swimming legs with both rami 3-segmented, are shared by the genera *Austriocyclops*, *Pontocyclops* Reid, 1986 and *Australocyclops* Morton, 1985, whose member species have a variously reduced segmentation of the antennule and leg 5 1-segmented or completely fused to somite (*Austriocyclops*-group).

Other primitive genera [*Cyclops*, *Megacyclops*, *Mesocyclops*, *Thermocyclops*, *Kieferiella* Lescher-Moutoué, 1976, *Diacyclops* (partim), *Acanthocyclops* (partim)] share a plesiomorphic state of most appendages, such as the 12-17 (rarely 11) segmented antennula, the swimming legs with 3-segmented rami, but the leg 5 consisting of two distinct segments. The members of these genera are generally large species, mostly distributed in surface fresh waters, only a few stygobitic or stigophilic species occurring in groundwater biotopes (*Cyclops*-group).

A leg 5 composed of two distinct segments distinguishes also the genera *Caspicyclops* Monchenko, 1986, *Mixocyclops*, *Diacyclops* (partim) and *Acanthocyclops* (partim), but their member species are characterized by 10-11 (rarely 16) segmented antennula and swimming legs with variously reduced number of segments of both exopodite and endopodite. The reduction occurs at first in the anterior swimming legs and endopodites, then in the posterior legs and exopodites. In some apomorphic *Diacyclops* species (*virginianus*-group) the reduction regards anterior and posterior legs, all with 2-segmented rami, or the exopodite of legs 3-4, 3-segmented in some species. The greatest reduction state in the above genus is shown by *D. trajani* (Petkovski, 1954), which has all the swimming legs completely 2-segmented (Reid 1994).

The members of the above genera can be found both in surface

freshwater bodies and in ground waters, with stygophilic or stigobitic species (*Mixocyclops*-group).

The fifth group (*Microcyclops*-group) comprises genera with leg 5 consisting of a single free segment due to the fusion of the proximal segment to the somite. The representatives of this group show a reduced antennula (10-11 segments) and swimming legs 1-4 with both endopodite and exopodite 2-segmented. In the genus *Hesperocyclops* Herbst, 1984 the female leg 4 endopodite is 1-segmented.

In the same group the free segment of leg 5 can bear one (*Cryptocyclops* G. O. Sars, 1927, *Idiocyclops* Herbst, 1987, *Microcyclops* Claus, 1893), two [*Hesperocyclops*, *Graeteriella* Brehm, 1926, with subgenus *Paragraeteriella* Rylov, 1948/63, *Fimbricyclops*, Reid 1993, *Menzeliella* Lindberg, 1954, *Metacyclops* Kiefer, 1927, *Apocyclops* Lindberg, 1942, *Speocyclops*, Kiefer, 1937, *Muscocyclops* Kiefer, 1937, *Goniocyclops* Kiefer, 1955 (= *Psammophilocyclops* Fryer, 1956), and probably *Cochlacocyclops* Kiefer, 1955] or three (*Psammocyclops* Kiefer, 1955) spines/setae.

In some genera the free segment of leg 5 may be also ornamented with an unsocketed spinula, along the middle margin; in the genus *Psammocyclops*, the same segment is composed of fusion of the original segments, therefore it bears 3 setae. Other genera lack the seta on the fifth thoracic somite. In some species of the genus *Speocyclops* the free segment of leg 5 may be partially fused with the somite. In other genera of this group, including *Goniocyclops*, *Muscocyclops* and *Speocyclops*, the anal operculum is considerably produced and, sometimes, toothed or serrate.

As regard the inadequately characterized, monospecific genus *Teratocyclops* Plesa, 1981, long since Dussart & Defaye (1985) noticed its incomplete description and illustrations; later on Reid (1993) too, remarked the absence of adequate figures in Plesa's description, hypothesizing as well that both segments of leg 5 could be distinct in this genus.

Nevertheless, recent re-examination of the type material (Plesa in litt.) revealed that the leg 5 is composed of a single free segment, therefore the nominate genus fits well into the above group, being very close to the genus *Metacyclops*.

All the nominate genera are for the most part stygobitic inhabitants of different groundwater habitats.

The last group (*Bryocyclops*-group) includes more derived genera

whose representatives can be found mostly in ground waters. The members of this group (*Yansacyclops* Reid, 1988, *Allocyclops* Kiefer, 1932, *Bacillocyclops* Lindberg, 1956, *Bryocyclops* Kiefer, 1927 s. l.) show both segments of leg 5 fused to the somite, 1-2 setae, sometimes a little knob, representing the distal segment remaining. In the same genera the antennula and the swimming legs are strongly reduced, viz. the antennula is 10-11-segmented and the swimming legs with both endopodite and exopodite 2-segmented or the endopodite and exopodite of leg 4, 1-segmented.

The genus *Bryocyclops* was firstly divided by Kiefer (1927, 1952) into the subgenera *Bryocyclops* s. str. and *Haplocyclops* Kiefer, 1952. Subsequently, Lindberg (1956) splitted the same genus into six groups (subgenera) according to such characters as the sexual dimorphism, the armature of the leg 1 basipodite, the morphology of the couplers of leg 4, the spines/setae formula of legs 1-4 and the segmentation of the leg 4 exopodite.

At present, according to Dussart (1982), the genus should be divided at least into three morphological subgroups, viz. *Bryocyclops* s. str.-subgroup, whose members are characterized by coxopodite and basipodite of leg 1 with inner spine, and couplers of leg 4 with pointed protuberances; *Rybocyclops*-subgroup, without spine on both coxopodite and basipodite of leg 1, and couplers of leg 4 with little developed, rounded protuberances; *Haplocyclops*-subgroup, with coxopodite and basipodite of leg 1 without or with inner spine, respectively, and couplers of leg 4 little produced, rounded.

Tab.1 – Comparative table of the characters used in the groups definition.

Group	legs 1-4		antennule	leg 5
	enp.	exp.		
<i>Orthocyclops</i>	3.3.3.3	3.3.3.3	16	3
<i>Austriocyclops</i>	3.3.3.3	3.3.3.3	12-17	0-1
<i>Cyclops</i>	3.3.3.3	3.3.3.3	11-17	2
<i>Mixocyclops</i>	2.2.2/3.2/3	2/3.2/3.2/3.2/3	10-11, 16	2
<i>Microcyclops</i>	2.2.2.2/1	2.2.2.2	10-11	1
<i>Bryocyclops</i>	2.2.2.2/1	2.2.2.2/1	10-11	0

Independently of the above morphological groups, further reductions may occur in some species or genera; the most important of

them are the mandibular palp reduced to 1-2 setae (*Allocyclops kieferi* Petkovski, 1971, *Diacyclops imparilis* Monchenko, 1985, *Fimbricyclops*), or completely absent [*Speocyclops demetiensis* (Scourfield, 1932), *Caspicyclops mirabilis* Monchenko, 1986, *Muscocyclops*], the reduced number of setae on the basipodite and second endopodal segment of the antenna, and the reduced or lacking armature of the basis, coxa and couplers of the swimming legs.

The setation of the antenna was firstly recognized as fundamental character by Fiers & Van de Velde (1984), who pointed out distinct patterns of armature (spines/teeth) on the basipodite of numerous species of cyclopinae, as well as they stated that the primitive condition for this appendage is "probably when the whole surface is covered with teeth and /or spines".

Successively, Reid (1991) found losses of one or more setae from the basipodite of the same appendage, including the exopodal vestigial seta, pointing out the great importance of these reductions in the specific diagnosis of the cyclopinae as well as of cyclopoid copepods.

The second endopodal segment of the antenna retains 9 setae (likely plesiomorphic condition) only in few primitive genera, in others the same segment has undergone repeated reduction: eight setae can be found in some species of the genus *Acanthocyclops* and *Megacyclops*, 6-7 setae in species of the genera *Microcyclops*, *Megacyclops*, *Cryptocyclops* and *Diacyclops*, five in *Graeteriella unisetigera* (Graeter, 1908) and *Hesperocyclops venezuelanus* Pesce & Galassi, 1992. To my knowledge, the most apomorphic states can be found in *Diacyclops dimorphus* Reid, 1994 and *Diacyclops paolae* Pesce & Galassi, 1987, with four and three setae, respectively.

Unfortunately, in modern taxonomic accounts of cyclopinae there is almost no description or illustrations of the antenna, as well as of other mouthparts, so that these important features are generally overlooked by the authors.

Einsle (1985) pointed out a further criterion for identification of species in the complicated genus *Cyclops*, considering the patterns of spines on the coxa of leg 4, and coming to the conclusion that the patterns are relatively uniform within the species, but noteworthy variation and reductions exist among species.

Recently, it has been shown that some species of the genera *Bryocyclops*, *Haplocyclops*, *Graeteriella*, *Hesperocyclops*, *Metacyclops* and *Diacyclops* show a sexual dimorphism in the swimming legs con-

sisting in a reduction occurring in the female and primarily in the endopodites of the posterior legs (Reid 1994).

Reid (1991) discovered also elaborate ornamentation of swimming legs couplers and increasing thickness of the same legs in benthic cyclopids.

Some species of the genera *Bryocyclops* and *Muscocyclops* and the species *Fimbricyclops jimhensoni* Reid, 1993 show elaborate arrays of spines and hairs on the swimming legs, anal somite and caudal rami, which Reid (1993) interpreted as a parallel adaptation for life in semiterrestrial habitats.

After all, many species of copepods, including the cyclopinae, are known to possess integumental perforations on the antennule and other appendages (Bresciani 1986), but their function is for the better part unknown.

As regard the cyclopinae, circular pits on the articles of the antennule of some *Mesocyclops* species were firstly pointed out by Von Daday (1906), who interpreted them as integumental tubercles. Reid & Saunders (1986) recognized similar structures in *M. Aspericornis* (Daday, 1906) and in some species of the genus *Thermocyclops*, and considered them as sensory structures, advantageous in spatially restricted habitats. Reid et al. (1989) reported integumental pits also in *Diacyclops navus* Herrik, 1882, confirming as well that such structures can be commonly found in members of the genus *Diacyclops*.

Successively, Pesce et al. (in press) described circular integumental pits both in the antennule and antenna of *Mesocyclops* species from ground waters of Australia.

KEY TO FEMALES OF THE CYCLOPINAE GENERA

1. Antennule 16-segmented; legs 1-4 with 3-segmented ramus, leg 5, 3-segmented *Orthocyclops*-group
2. Antennule 12-17 segmented; legs 1-4 with 3-segmented rami; leg 5 1-segmented, or completely fused to somite..... *Austriocyclops*-group
3. Antennule 11-17 segmented; legs 1-4 with 3-segmented rami; leg 5, 2-segmented ..
..... *Cyclops*-group
4. Antennule 10-11 (rarely 16) segmented; legs 1-4 with variously reduced number of segments; leg 5, 2-segmented *Mixocyclops*-group
5. Antennule 10-11 segmented; legs 1-4 with 2-segmented rami or leg 4 endopodite 1-segmented; leg 5, 1-segmented *Microcyclops*-group
6. Antennule 10-11 segmented; legs 1-4 with 2-segmented rami, or the endopodite/exopodite of leg 4, 1-segmented; both segments of leg 5 fused to somite
..... *Bryocyclops*-group

Orthocyclops-group

1. Legs 1-4 with both rami 3-segmented; antennule, 16-segmented; leg 5, 3-segmented *Orthocyclops*

Austriocyclops-group

1. Leg 5 completely fused to somite *Austriocyclops*
Leg 5 not fused to somite 2
2. Antennule 12-segmented *Australocyclops*
Antennule 17-segmented *Ponticyclops*

Cyclops-group

1. Distal segment of leg 5 with 1 spine and 1 seta 2
Distal segment of leg 5 with 2 setae 5
2. Spine on distal segment of leg 5 long, and distally implanted *Diacyclops* (partim)
Spine on distal article of leg 5 short, and subdistally or medially implanted 3
3. Spine on distal segment of leg 5 subdistally implanted 4
Spine on distal segment of leg 5 medially implanted *Cyclops*
4. Spine on distal segment of leg 5 not articulated; caudal rami with cilia on the inner margin *Megacyclops*
Spine on distal article of leg 5 articulated; caudal rami without cilia on the inner margin *Acanthocyclops* (partim)
5. Distal segment of leg 5 with two distal setae 6
Distal segment of leg 5 with 1 distal and 1 subdistal setae *Mesocyclops*
6. Distal setae of leg 5 of about the same length *Thermocyclops*
Inner distal seta of leg 5 much shorter than outermost *Kieferiella*

Mixocyclops-group

1. Mandibular palp present 2
Mandibular palp absent *Caspicyclops*
2. Leg 4 with 2-segmented rami 3
Leg 4 with 3-segmented rami 4
3. Apical spine on distal segment of leg 5 very reduced *Mixocyclops*
Apical spine on distal segment not reduced, about as long or slightly shorter than article *Diacyclops* (partim)
4. Distal segment of leg 5 with subterminal spine *Acanthocyclops* (partim)
Distal segment of leg 5 with terminal spine *Diacyclops* (partim)

Microcyclops-group

1. Legs 1-3 and exopodite of leg 4 with 2-segmented rami; endopodite of leg 4, 1-segmented *Hesperocyclops*
Legs 1-4 with 2-segmented rami 2
2. Distal segment of leg 5 much enlarged, with 3 setae *Psammocyclops*
Distal segment of leg 5 normally developed, with less than 3 setae 3
3. Distal segment of leg 5 with 2 setae/spines 4
Distal segment of leg 5 with 1 seta 12
4. Fifth thoracic somite without outer seta *Graeteriella*
Fifth thoracic somite with outer seta 5
5. Distal segment of leg 5 with 2 apical setae *Fimbricyclops*
Distal segment of leg 5 with 1 seta and 1 spine 6
6. Spine on free segment of leg 5 stout, and about as long as seta *Menzeliella*
Spine on free segment of leg 5 slender and shorter than seta 7
7. Free segment of leg 5 broad, spine and seta well separated each other *Apocyclops*
Free segment of leg 5 about as long as broad, or slightly longer than broad; spine and seta close together 8

8. Anal operculum well developed.....	9
Anal operculum not well developed	15
9. Anal operculum naked	10
Anal operculum fringed or toothed.....	11
10. Endopodite 3 of leg 4 with 2 apical spines; receptaculum seminis not much developed posteriorly	<i>Goniocyclops</i>
Endopodite 3 of leg 4 with 1 apical spine; receptaculum seminis with well developed, circular posterior end	<i>Cochlacocyclops</i>
11. Anal operculum large, subtrapezoidal, with 2 or more hyaline teeth; free segment of leg 5 quite distinct from somite; lateral seta on somite well separated from the article	<i>Muscocyclops</i>
Anal operculum semicircular or triangular, generally serrate; free segment of leg 5 not completely fused with somite, lateral seta close to the article	<i>Speocyclops</i>
12. Caudal rami with 3 terminal setae	<i>Idiocyclops</i>
Caudal rami with 4 terminal setae	13
13. Receptaculum seminis much elongated posteriorly	<i>Neutrocyclops</i>
Receptaculum seminis not much elongated posteriorly	14
14. Inner spine of the leg 4 endopodite much longer than the outermost; coxal seta short, not overreaching basis	<i>Cryptocyclops</i>
Inner spine of the leg 4 endopodite slightly longer than outermost; coxal seta long, overreaching basis.....	<i>Microcyclops</i>
15. Endopodite 3 of leg 4 with 1 apical slender seta	<i>Teratocyclops</i>
Endopodite 3 of leg 4 with 1 apical spine or with 1 spine and 1 seta ..	<i>Metacyclops</i>

Bryocyclops-group

1. Antennula 10-segmented	<i>Yansacyclops</i>
Antennula 11-segmented	2
2. Leg 5 reduced to a single, stout ciliate spine.....	<i>Bacillocyclops</i>
Leg 5 consisting of 2 setae/spines	3
3. Anal operculum little developed, semicircular or quadrate, smooth	<i>Allocyclops</i>
Anal operculum well developed, triangular, margin smooth or serrated; reduced in subg. <i>Haplocyclops</i>	4 (<i>Bryocyclops</i> s.l.)
4. Couplers of leg 4 with well developed pointed protuberances	<i>Bryocyclops</i> s.str.-subgroup
Couplers of leg 4 with little developed, rounded protuberances.....	5
5. Coxopodite and basipodite of leg 1 without inner spine	<i>Rybocyclops</i> -subgroup
Coxopodite and basipodite of leg 1 without or with inner spine, respectively	<i>Haplocyclops</i> -subgroup

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SUMMARY

The genera of the subfamily Cyclopinae are reviewed. Six morphological groups, according to the oligomerization of the antennula, swimming legs 1-4 and leg 5, are proposed. Other microcharacters useful in the taxonomy of Cyclopinae, viz. spine patterns on the basipodite of antennula and on coxa of leg 4, and the armature of the mandibular palp are pointed out.

An up-to-date key to the genera of the Cyclopinae is presented.

RIASSUNTO

Revisione dei generi della sottofamiglia Cyclopinae (Crustacea, Cyclopidae).

Vengono revisionati i generi della sottofamiglia Cyclopinae (Copepoda, Cyclopidae) e proposti sei gruppi morfologici in relazione all'articolazione dell'antennula, alla oligomerizzazione degli arti toracici 1-4 ed alla conformazione del quinto paio di arti toracici. Microcaratteri utili nella diagnosi dei diversi generi sono anche il palpo mandibolare e la spinulazione sul basipodite dell'antennula e della coxa del quarto paio di arti toracici. Viene presentata una chiave di riconoscimento dei 33 generi della sottofamiglia Cyclopinae.

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