

The neotropical species of *Mesocyclops* (Copepoda, Cyclopoida): an upgraded identification key and comments on selected taxa

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(Accepted 18 April 2006)

Abstract

In this work we present an analysis of upgraded characters used in the taxonomy of cyclopine copepods to provide a new key for the identification of the members of the freshwater genus *Mesocyclops* recorded in the neotropical region. This analysis, which included revision of type and museum specimens, resulted also in the clarification of the taxonomical status of two nominal species not previously revised, *M. varius* Dussart, 1987 and *M. venezolanus* Dussart, 1987. These two species are recognized herein as junior synonyms of *M. brasilianus* Kiefer, 1933. Considering the addition of new records (introduced Afro-Asian or Asian forms), the designation of *M. araucanus* Campos et al., 1974 to species rank, and the conflict of determining the taxonomical status of *M. annulatus diversus*, the number of taxa recognized in the region includes 20 species and one variety. A general morphological analysis of the Old and New World species allowed us to contrast and evaluate some of the differential characters of these two groups. We propose several characters that can be considered as potentially valuable to separate reliably both female and male specimens of the neotropical species. The distribution of selected species or species groups of *Mesocyclops* is also revised in light of this new frame.

Keywords: *Copepoda*, *Cyclopoida*, *distribution*, *Mesocyclops*, *neotropics*, *taxonomy*

Introduction

The world distribution of the freshwater copepod genus *Mesocyclops* G. O. Sars, 1914 is mainly tropical and subtropical (van de Velde 1984; Hołyńska et al. 2003). With more than 70 nominal species, the genus is among the most diverse of the family Cyclopidae (Boxshall and Halsey 2004). Careful morphological analysis of species from Europe, Asia, and Africa

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Published 30 June 2006

ISSN 0022-2933 print/ISSN 1464-5262 online © 2006 Taylor & Francis
DOI: 10.1080/00222930600761837

(Kiefer 1981; van de Velde 1984; Holyńska 2000b) has allowed the identification of useful features for establishing the limits between species.

Around 20 species of *Mesocyclops* have been recorded in tropical America (Gutiérrez-Aguirre and Suárez-Morales 2001b). The morphology and distribution of some of these have been analysed in detail (Reid 1993; Reid and Reed 1994; Fiers et al. 1996; Reid and Moreno 1999; Holyńska et al. 2003). However, the specific determination of many neotropical forms has become a difficult task because they belong to taxonomically complex groups. An example of such a trend is represented by the *M. meridianus*–*brasilianus* complex [including *M. pseudomeridianus*, *M. meridionalis*, and *M. varius* (Holyńska 1994, 2000a)], known mainly from South and Central America (Collado et al. 1984; Dussart 1987) and containing several taxa with an uncertain taxonomical status.

The taxonomical problems of many species may be related to different factors such as the unavailability or loss of type specimens, low sampling efforts, and lack of detailed, upgraded descriptions (Dahms and Fernando 1995). Most of the published descriptions of species of *Mesocyclops* do not include a morphological analysis of males; only female characters are generally used in keys and species diagnoses (Dahms and Fernando 1995). There is an urgent need to increase efforts in order to provide a complete, detailed morphological analysis of taxonomically complex groups. Consistent, robust characters will allow a reliable separation of females and males of tropical American species.

The most recent identification keys that include neotropical *Mesocyclops* were published by Reid (1985), Dussart (1987), and Reid and Pinto-Coelho (1994). However, some of the morphological features used in these works have a relatively low resolution to separate many of these species derived from the current development of the genus taxonomy. This work presents an analysis of new morphological characters for the identification of the neotropical species of *Mesocyclops* based on (1) the analysis of both sexes of each species and (2) a set of the current, upgraded morphological data used in the taxonomy of the genus. Based on this information, the taxonomical status of some species belonging to the *M. brasilianus*–*varius* complex is resolved, thus proposing a new synonymy for these nominal taxa.

Methods

While preparing this key for the identification of the neotropical species of *Mesocyclops*, we analysed and compared the morphological characters that have been proved to be useful to separate species from Europe, Africa, and Australasia, i.e. shape of hyaline membrane of last antennular segment, features of seminal receptacle, ornamentation of thoracic limbs, among others (see Holyńska 2000a, b). Additionally, other complementary features were evaluated as an aid to ease the identification of the neotropical *Mesocyclops*, such as the ornamentation of maxillular coxa, anal somite, intercoxal sclerites, etc., in both females and males.

The morphological structure of several species was examined by light microscopy. This process included observations of type and museum specimens deposited in the collections of different institutions: the Muséum National d'Histoire Naturelle, Paris (MNHN), the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), the Institut voor Systematiek et Populatiebiologie, Amsterdam (ZMA), the Staatliches Museum für Naturkunde, Karlsruhe (SMNK), and the Instituto Nacional de Pesquisas da Amazônia (INPA) (see Table I). The morphological terminology used herein

follows that proposed by van de Velde (1984), Huys and Boxshall (1991), and Hołyńska (1994).

The type specimens of *M. ogunmus*, *M. chaci*, *M. yutsil*, and *M. araucanus* were not observed, but they were included in the key following the descriptions and illustrated features published in van de Velde (1984), Fiers et al. (1996), and Pilati and Menu-Marque (2002). *Mesocyclops annulatus diversus* Herbst, 1962 was excluded from the key because discriminating characters for this species are not defined, i.e. the ornamentation of the frontal surface of the antennal basis, the presence or absence of spines next to the exopodal seta. Also, the depository institution of this material is unknown to us; in fact, the type specimens are probably lost (*M.* Hołyńska, personal communication). The taxonomical status of species belonging to problematic groups was analysed in detail. A general discussion of the geographical distribution of the neotropical species is also presented herein.

Results

Mesocyclops brasilianus Kiefer, 1933

(Figures 1, 2)

M. varius Dussart, 1987, junior synonym.

M. venezolanus Dussart, 1987, junior synonym.

? *M. venezolanus*: Reid and Reid 1994, p 83–87, Figures 3, 4.

The bad condition of the type specimens of *M. brasilianus* prevented a detailed analysis; however, we based our criteria on the observations of 10 adult females from Itacoatiara, Amazonas, Brazil (03°10.807'S, 58°14.631'W, west from Manaus, established by Kiefer 1936 as the type locality).

There is only one female labelled as *M. varius* in the world, from Taxisco, Guatemala (see Table I). Dussart (1987) recognized the resemblance between this specimen and *M. brasilianus*. Hołyńska et al. (2003) stated that its taxonomical status remains questionable; however, they included this species as part of the *M. meridianus*–*brasilianus* complex. Our analysis indicates that the morphological features used by Dussart (1987) to separate these species are not consistent: the presumed absence of an acute angle on the outer margin of the first endopodal segment of the first swimming leg has proved to be erroneous (Figure 1A–C). The same is true with respect to the assumed absence of ornamentation on the coxa and inner margin of the fourth leg basis (Figure 1D–F). The holotype of *M. varius* bears a spermatophore fixed to its genital aperture (Figure 1G), but no differences were observed on the structure of the seminal receptacle between *M. varius* and *M. brasilianus* (Figure 1G, H). Another character used to separate *M. varius* was the length ratio of two caudal setae: dorsal seta/lateral seta [relatively longer in comparison with *M. brasilianus* (Dussart 1987)]. We found that the proportional length observed in the holotype specimen of *M. varius* shows a lower figure than that determined from the original description of *M. brasilianus* (1.2 versus 1.3). In addition, the comparison of the seta length proportions (Figure 2B, E) in different populations of *M. brasilianus* observed here (Table I), through an exploration of frequencies, shows a wide variability, even in the same population (Figure 3); therefore, we consider that this proportion is a weak feature for separating species.

Dussart (1987) described another species, *M. venezolanus*; this was also recognized as being similar to *M. brasilianus*. The description was based on specimens collected in Lake

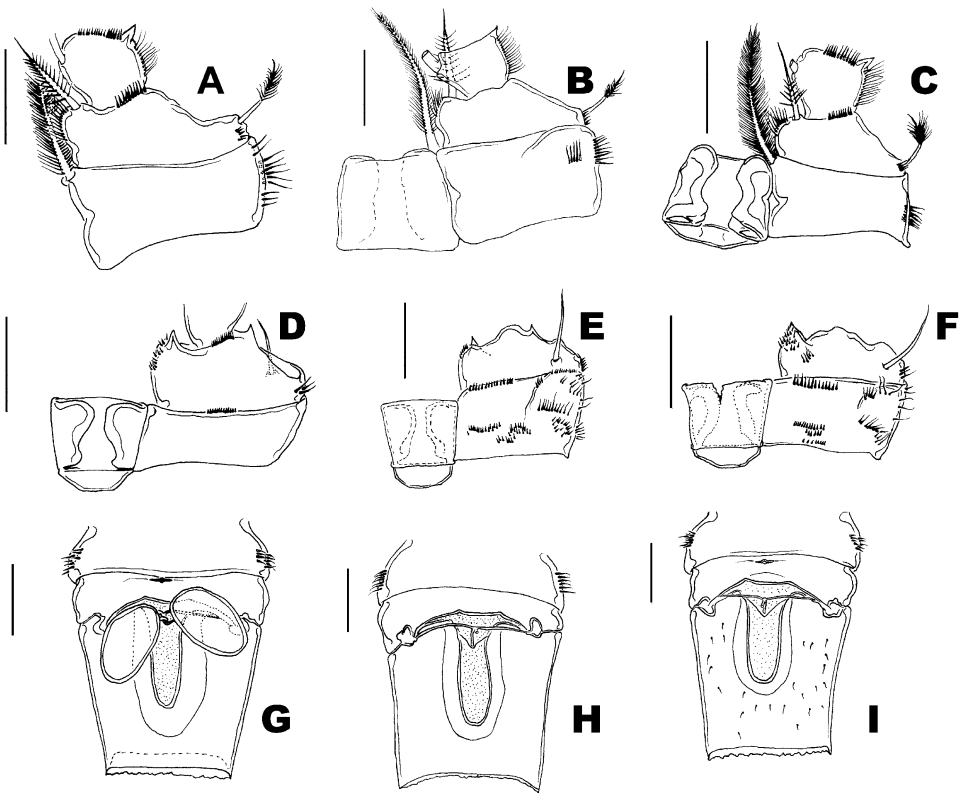


Figure 1. (A) First leg, coxa, basis, and first endopodal segment, frontal (female from Taxisco, Guatemala, MNHN Cp 697, labelled as *Mesocyclops varius*); (B) *Mesocyclops brasilianus*, female from Itacoatiara, Brazil (INPA-1396), first leg, coxa, basis, and first endopodal segment, caudal; (C) first leg, coxa, basis, and first endopodal segment, caudal (female from Mare à Camaguan and Caracas, Venezuela, MNHN-Cp1882, labelled as *Mesocyclops venezolanus*); (D) fourth leg, coxa, and basis, frontal (MNHN Cp 697); (E) *M. brasilianus* (INPA-1396), fourth leg, coxa, and basis, caudal; (F) fourth leg, coxa, and basis, caudal (MNHN-Cp1882); (G) fifth pediger and genital somite, ventral (MNHN Cp 697); (H) *M. brasilianus* (INPA-1396), fifth pediger and genital somite, ventral; (I) fifth pediger and genital somite, ventral (MNHN-Cp1882).

Valencia, Venezuela. The differences by which *M. venezolanus* was separated from *M. brasilianus* were: caudal rami without spines on distal-lateral corner; abdominal somites with serrated hyaline fringe; dorsal seta on caudal rami shorter than outer seta; fifth thoracic somite with dispersed hair-like setae; seminal receptacle with two “bumps”, followed by two curved horns. All these features are present in *M. brasilianus* too (Figures 1B, C, E, F, H, I, 2B, C, E, F), including the lack of spines on the distal-lateral corner of the caudal rami: no adult female of *M. brasilianus* examined here, even the specimens identified by Kiefer, showed those spines. The type specimen is useless for taxonomical analysis, and now we speculate that the spines shown in the illustrations, but not mentioned in the original description of *M. brasilianus*, indicate that this specimen is an immature CV female (Gutiérrez-Aguirre and Suárez-Morales 2003). Another specimen collected in Managuiri, Amazonas, Brazil, and identified by Kiefer (see Table I), does not have these spines. Therefore, the spine presence/absence pattern that would separate *M. brasilianus* and *M. venezolanus* is not a usable character. Therefore, we conclude that both *M. varius* and *M. venezolanus* are junior synonyms of *M. brasilianus* and should be

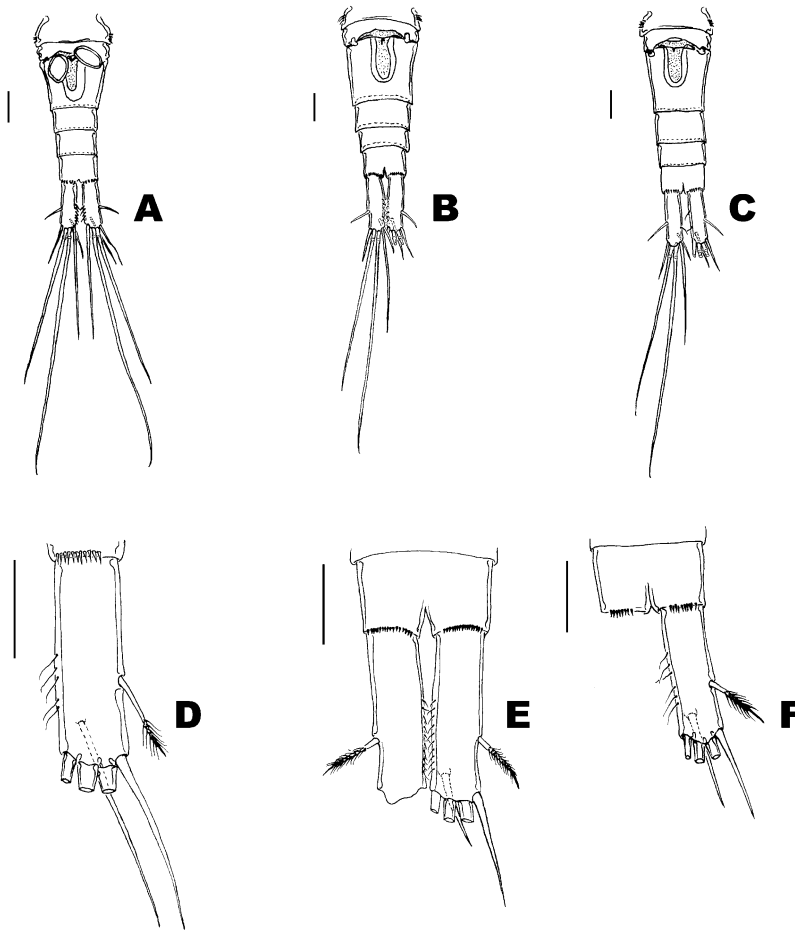


Figure 2. (A) Abdomen ventral (female from Taxisco, Guatemala, MNHN Cp 697, labelled as *Mesocyclops varius*); (B) *Mesocyclops brasilianus*, female from Itacoatiara, Brazil (INPA-1396), abdomen, ventral; (C) abdomen, ventral (female from Mare à Camaguan and Caracas, Venezuela, MNHN-Cp1882, labelled as *Mesocyclops venezolanus*); (D) caudal rami, ventral (MNHN Cp 697); (E) *M. brasilianus* (INPA-1396), anal somite, and caudal rami, ventral; (F) anal somite and caudal rami, view (MNHN-Cp1880).

considered as that in future taxonomic accounts of neotropical *Mesocyclops*. However, the identity of the specimens recorded by Reid and Reed (1994) as *M. venezolanus* from the Yukon Territory remains unverified, taking into account the differences of the hair-ornament observed by Holyńska et al. (2003) in comparison with *M. brasilianus*.

Number of neotropical species of Mesocyclops

Before this study, up to 20 species, two varieties, and one subspecies of *Mesocyclops* had been recorded in the neotropics. With the addition of the recently described *M. evadomingoi* (Gutiérrez-Aguirre and Suárez-Morales 2001a) and the new record of the Asian *M. pephpeiensis* in Mexico (Suárez-Morales et al. 2005), the junior synonymy of *M. varius* and *M. venezolanus* with *M. brasilianus*, the record of *M. kieferi* in Brazil, assignable to *M.*

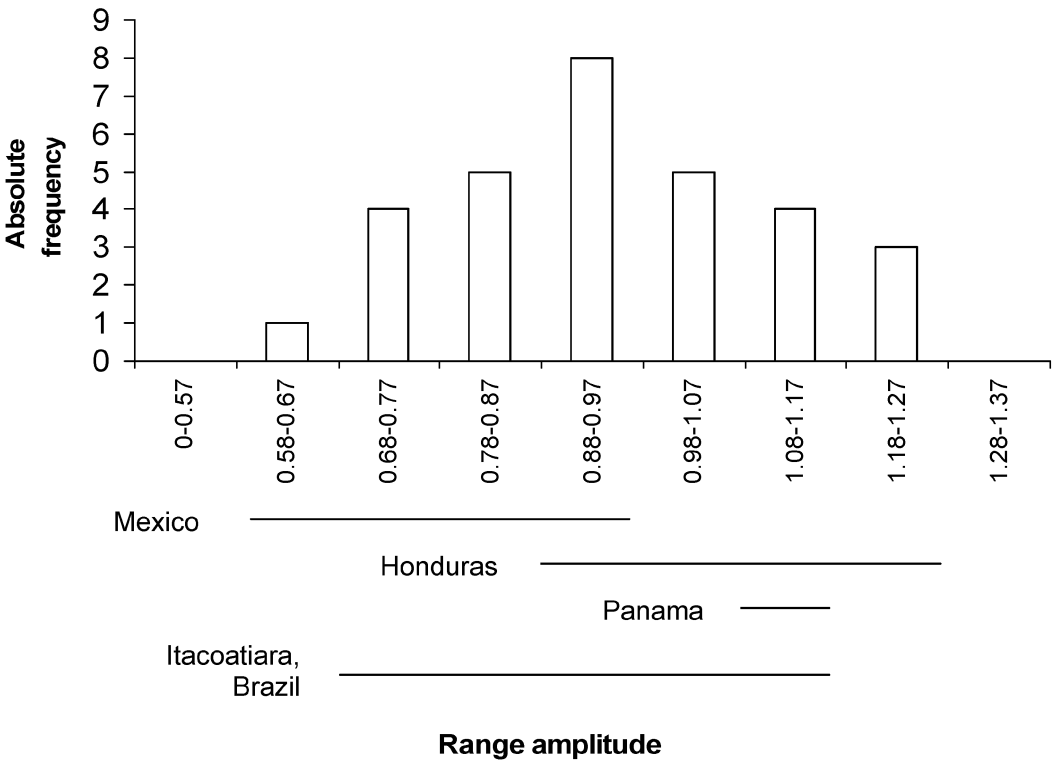


Figure 3. Frequencies of the length ratio of dorsal/lateral caudal setae in the populations of *Mesocyclops brasiliensis* populations examined. Lines refer to the ratio range of each population.

ogunnius (see Gutiérrez-Aguirre et al. 2003a), and the reassignment of *M. longisetus* var. *araucanus* to species rank by Pilati and Menu-Marque (2002), the revised, current account of neotropical records of *Mesocyclops* is: 20 species, one variety, and probably one species known as *M. annulatus diversus* (see section on distributional remarks later).

Key to the neotropical species of *Mesocyclops*

1. Inner basis of first trunk limb without seta (♂♂, ♀♀) (Figure 4A) 2
 - Inner basis of first trunk limb with seta, or spine-like seta (♂♂, ♀♀) (Figure 4B) 6
2. Fifth pediger naked ventrally (Figure 4C); intercoxal sclerite of fourth trunk limb with high, acute projections (♂♂, ♀♀) (Figure 4D) 3
 - Fifth pediger pilose ventrally (Figure 4E); intercoxal sclerite of fourth trunk limb with low, non-acute projection (♂♂, ♀♀) (Figure 4F) 4
3. Ducts connected with genital aperture straight (♀♀) (Figure 4C), inner margin of fourth trunk limb basis pilose (♂♂, ♀♀) (Figure 4D) *M. pescei*
 - Ducts connected with genital aperture directed in rectum angle (♀♀) (Figure 4G), inner margin of fourth trunk limb basis naked (♂♂, ♀♀) (Figure 4H) *M. pehpeiensis*
4. Maxillular palp with spines on inner margin (♂♂, ♀♀) (Figure 5A) *M. ogunnius*
 - Maxillular palp without spines on inner margin (♂♂, ♀♀) (Figure 5B) 5

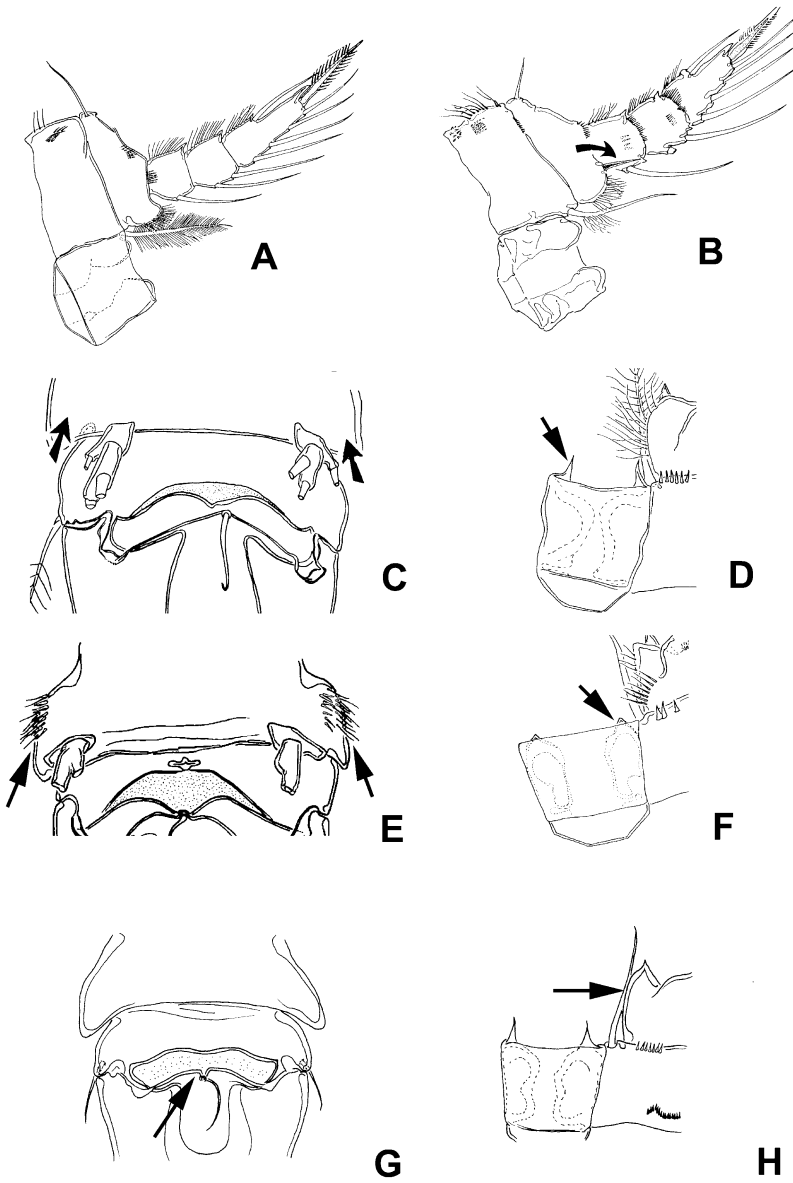


Figure 4. (A) *Mesocyclops thermocyclopoides*, male (ECOCH-Z-01215), first leg, caudal, exopod omitted; (B) *M. brasiliensis*, female (MNHN Cp 821), first leg, frontal, exopod omitted; (C) *M. pescei*, female (ECOCH-Z-01246), fifth pediger, genital somite upper portion, ventral; (D) *M. pescei*, male (ECOCH-Z-01244), fourth leg, intercoxal sclerite; (E) *M. thermocyclopoides*, female (ECOCH-Z-01214), fifth pediger, genital somite upper portion, ventral; (F) *M. aspericornis*, female (ECOCH-Z-01234); (G) *M. pehpehiensis*, female (ECOCH-Z-01667), fifth pediger, genital somite upper portion, ventral; (H) *M. pehpehiensis*, female fourth leg, intercoxal sclerite.

Table I. Material examined, *Mesocyclops* species recorded in neotropical region, and specimens analysed.

| Species | Kind of material | Loan and specimens origin |
|---|-----------------------------------|--|
| <i>M. pescei</i> Petkovski, 1986 | Specimens | •ECOCH-Z-01244–01247, 2♀♀, 2♂♂, Tabasco, Mexico |
| <i>M. pehpeiensis</i> Hu, 1943 | Specimens | •ECO-CHZ-01667, 20♀♀, 2♂♂, pond in Simón Bolívar, Chiapas, Mexico |
| <i>M. thermocycloides</i> (Harada, 1931) | Specimens | •ECOCH-Z-01212–01225, 100♀♀, 16♂♂?, Tabasco, Mexico •ECOCH-Z-01181, 5♀♀, 5♂♂ (USNM-268040 ^a), El Progreso, Honduras •MNHN-Cp833, 1♀, 1♂, Nuñez, Costa Rica |
| <i>M. aspericornis</i> Daday, 1906 | Specimens | •ECOCH-Z-01180 (USNM 216634 ^a), 5♀♀, Anapoima, Colombia •ECOCH-Z-01234, 01235, 2♀♀, Sinaloa, Mexico (granted by M. Silva-Briano) |
| <i>M. edax</i> (S. A. Forbes, 1891) | Specimens | •ECOCH-Z-01259, 15♀♀, 15♂♂, North Carolina, USA (granted by J. W. Reid) |
| <i>M. reidae</i> Petkovsky, 1986 | Specimens | •ECOCH-Z-01253–01255, 5♀♀, 5♂♂ (USNM-268030 ^a), El Progreso, Honduras |
| <i>M. annulatus</i> (Wierzejski, 1892) | Specimens | •MNHN-Cp864, 2♀♀, Adrogué (B. A.), Argentina •ECOCH-Z-01256–01258, 2♀♀ (USNM 278198 ^a), Polavon, Chubut, Argentina •ECOCH-Z-01236–01241, 3♀♀, 2♂♂, Tabasco, Mexico |
| <i>M. longisetus</i> s.str. (Thiébaud, 1912) | Specimens | |
| <i>M. longisetus</i> var. <i>curvatus</i> Dussart, 1987 | Specimens | •MNHN Cp 717, 2♀♀, Amazonas, Brazil •ECOCH-Z-01240, 1♀, Tabasco, Mexico |
| <i>M. araucanus</i> Campos, Bucarey and Arenas, 1974 | Specimens | •ECOCH-Z-01242, 01243, 3♀♀, 1♂♂ (USNM-264237 ^a), Lagoon Las Chulta, Argentina (originally labelled as <i>M. longisetus</i> var. <i>araucanus</i>) |
| <i>M. ellipticus</i> Kiefer, 1936 | Holotype, paratype, and specimens | •SMNK-03153, 03154, Bom Consello, Brazil; 05380, 05381, 05382, Lake Maracaibo, Venezuela. In total 5♀♀ |
| <i>M. intermedius</i> Pesce, 1985 | Holotype and paratypes | •ECOCH-Z-01251, 01252, 5♀♀, Barra Bonita Reservoir, Brazil (granted by M. da Silva) •ZMA Co 102-731, 3♀♀, Klein Bonaire (Netherlands Antilles) |
| <i>M. paranaensis</i> Dussart and Frutos, 1985 | Paratypes and specimens | •MNHN Cp 1883–1885, 3♀♀, Argentina •ECOCH-Z-01248–01250, 2♀♀, 2♂♂ (USNM-285464 ^a), Ceara, Brazil (originally labelled as <i>M. ellipticus</i>) |

Table I. (continued.)

| Species | Kind of material | Loan and specimens origin |
|---|-----------------------------------|--|
| <i>M. meridionalis</i> Dussart and Frutos, 1986 | Holotype | MNHN-Cp718, 1♀, Argentina |
| <i>M. brasiliensis</i> Kiefer, 1933 | Holotype and specimens | <ul style="list-style-type: none"> •SMNK-02050, 1♀, Manaus, Brazil; 05383, 05384, 2♀, Lake Valencia, Venezuela; 05425, 1♀, and 1♂, Barranquilla, Colombia; 05436, 1♀, and 1♂, Taiguaiguai, Venezuela; 08290, 1♀, Lagartijo, Venezuela; •10689, 10690, 2♀, Lake Managuiri, Amazonas, Brazil •INPA-1396 10♀♀ from Itacoatiara, Brazil •ECOCH-Z-01187–01192, 01195–01199, 15♀♀, 3♂♂, Tabasco, Mexico •ECOCH-Z-01260, 1♀ (USNM288061^a), Lake Bayaro, Panama (originally labelled as “<i>M. pseudomeridionalis</i>”) •ECOCH-Z-01261, 5♀♀, 3♂♂ (USNM288057^a), El Progreso, Honduras (originally labelled as “<i>M. venezolanus</i>”) •USNM-204662, 1♂, Lake Valencia, Venezuela •MNHN-Cp821, 2♀, Mantecal, Venezuela |
| <i>M. evadomingoi</i> Gutiérrez-Aguirre, 2001 | Holotype, allotype and paratypes | <ul style="list-style-type: none"> •ECOCH-Z-01157–01161, 8♀♀, 3♂♂, Tabasco, Mexico •MNHN Cp 1915, 3♀♀, 3♂♂, Tabasco, Mexico |
| <i>M. pseudomeridianus</i> Defaye and Dussart, 1988 | Holotype, allotype and specimen | <ul style="list-style-type: none"> •MNHN-Cp708, 1♀, Guyana •MNHN-Cp709, 1♂, Guyana •ECOCH-Z-01278–01279, 1♀, Barra Bonita Reservoir, Brazil (granted by M. da Silva) |
| <i>M. meridianus</i> Kiefer, 1926 | Holotype, paratype, and specimens | <ul style="list-style-type: none"> •MNK-00568, 00569, San Bernardino, Paraguay; 03155, 03156, 03176, 03177, Cachoeira, Brazil. In total 6♀♀ •ECOCH-Z-01193, 01200–01203, 2♀♀, 2♂♂ (USNM-285525^a), 01194, 01204, 01205, 01276, 01277, 10♀♀, Barra Bonita Reservoir, Brazil (granted by M. da Silva) •MNHN-Cp837, 1♂, Río Pacaya, Requena, Peru |
| <i>M. venezolanus</i> Dussart, 1987 | Specimens | <ul style="list-style-type: none"> •ECOCH-Z-01261, 5♀♀, 3♂♂ (USNM-268057^a), El Progreso, Honduras •MNHN-Cp1880, 1882, 2♀♀, Mare à Camaguan and Zuata, near Caracas, Venezuela (specimen from Camaguan labelled as “n. sp.” by Dussart 1987) |
| <i>M. varius</i> Dussart, 1987 | Holotype | •MNHN-Cp697, 1♀, Taxisco, Guatemala |

^aInterchanged material with the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM), and now deposited in the Colección de Zooplankton de El Colegio de la Frontera Sur, Chetumal (ECOCH-Z).

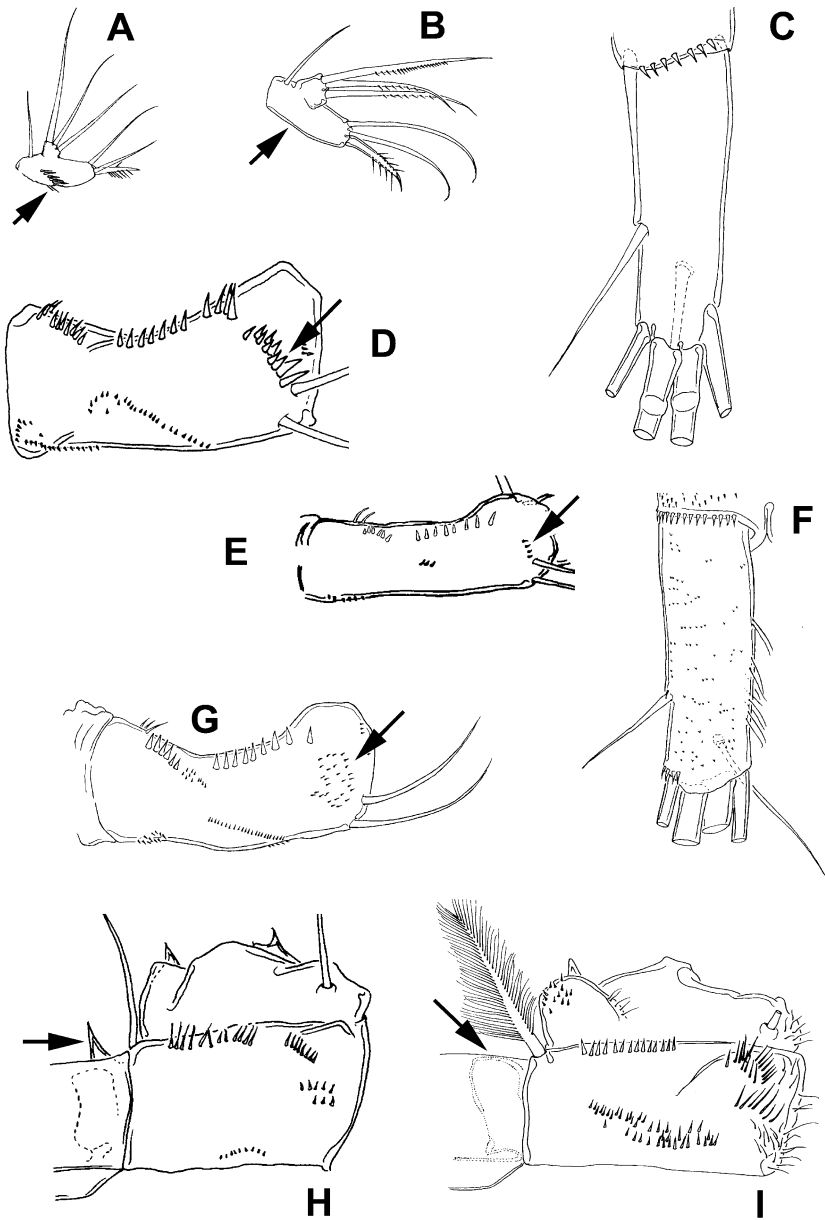


Figure 5. (A) *Mesocyclops ogunnus*, female, maxillular palp (from van de Velde 1984); (B) *M. thermocyclopoides*, female (ECOCH-Z-01214), maxillular palp; (C) caudal rami, ventral; (D) antennal basis, caudal; (E) *M. thermocyclopoides*, male (ECOCH-Z-01215), antennal basis, caudal; (F) *M. aspericornis*, female (ECOCH-Z-01234), caudal rami, ventral; (G) antennal basis, caudal; (H) *M. reidae*, male (ECOCH-Z-01255), fourth leg, intercoxal sclerite, coxa, and basis, caudal; (I) *M. brasilianus*, female (ECOCH-Z-01195), fourth leg, intercoxal sclerite, coxa, and basis, caudal.

5. Inner margin of caudal rami naked ($\sigma\sigma$, $\varphi\varphi$) (Figure 5C). Antennal basis with a row of large spines ($\varphi\varphi$) (Figure 5D) or a row of tiny spines ($\sigma\sigma$) (Figure 5E) near insertion of setae opposite to exopod. *M. thermocyclopoides*
 – Inner margin of caudal rami pilose ($\sigma\sigma$, $\varphi\varphi$) (Figure 5F). Antennal basis with a dense group of tiny spines ($\sigma\sigma$, $\varphi\varphi$) (Figure 5G) near insertion of setae opposite to exopod *M. aspericornis*
6. Intercoxal sclerite of fourth trunk limb with pointed projections ($\sigma\sigma$, $\varphi\varphi$) (Figure 5H) 7
 – Intercoxal sclerite of fourth trunk limb smooth ($\sigma\sigma$, $\varphi\varphi$) (Figure 5I) 17
7. Antennal basis without spines next to exopod ($\sigma\sigma$, $\varphi\varphi$) (Figure 6A) 8
 – Antennal basis with spines next to exopod ($\sigma\sigma$, $\varphi\varphi$) (Figure 6B) 11
8. Inner margin of caudal rami pilose ($\sigma\sigma$, $\varphi\varphi$) (Figure 6C) *M. edax*
 – Inner margin of caudal rami naked ($\sigma\sigma$, $\varphi\varphi$) (Figure 6D) 9
9. Fifth pediger with spines on ventro-lateral margins ($\varphi\varphi$) (Figure 6E) *M. reidae*
 – Fifth pediger naked ventro-laterally ($\varphi\varphi$) (Figure 6F) 10
10. Medial spine longer than apical seta on distal segment of fifth leg ($\sigma\sigma$, $\varphi\varphi$) (Figure 6G) *M. chaci*
 – Medial spine shorter than apical seta on distal segment of fifth leg ($\sigma\sigma$, $\varphi\varphi$) (Figure 6H) *M. yutsil*
11. Intercoxal sclerite of fourth trunk limb with low, non-acute projections ($\sigma\sigma$, $\varphi\varphi$) (Figure 7A) 12
 – Intercoxal sclerite of fourth trunk limb with high, acute projections ($\sigma\sigma$, $\varphi\varphi$) (Figure 7B) 15
12. Anterior margin of seminal receptacle convex, with lateral arms thin ($\varphi\varphi$) (Figure 7C) *M. annulatus*
 – Anterior margin of seminal receptacle concave, wide lateral arms ($\varphi\varphi$) (Figure 7D) 13
13. Lateral arms of seminal receptacle not strongly curved ($\varphi\varphi$) (Figure 7D); inner surface of 16th antennular segment with more than two rows of spines ($\sigma\sigma$) (Figure 7E). Length/width ratio of caudal rami is 3.06 (2.8–3.27) ($\varphi\varphi$) and 2.93 (2.84–3.06) ($\sigma\sigma$); Length/width ratio of third endopodal segment of fourth trunk limb is 2.52 (2.0–2.8) ($\varphi\varphi$) and 2.94 (2.75–3.05) ($\sigma\sigma$); base of lateralmost terminal caudal seta without spines ($\varphi\varphi$) (see Pilati and Menu-Marque 2002) (Figure 7I) *M. longisetus* s. str.
 – Lateral arms of seminal receptacle strongly curved ($\varphi\varphi$) (Figure 7F); inner surface of 16th (Figure 7G) or 15th antennular segment (see Pilati and Menu-Marque 2002) with two rows of spines ($\sigma\sigma$). 14
14. Length/width ratio of third endopodal segment of fourth trunk limb is 2.6–3.2 ($\varphi\varphi$) (Figure 7H); length/width ratio of caudal rami is 2.6–3.2 ($\varphi\varphi$) (Figure 7I) *M. longisetus* var. *curvatus*
 – Length/width ratio of third endopodal segment of fourth trunk limb is 3.48 (3.3–3.8) ($\varphi\varphi$) (Figure 7J) and 3.21 (3.14–3.46) ($\sigma\sigma$); length/width ratio of caudal rami is 3.79 (3.5–4.2) (Figure 7K) ($\varphi\varphi$) and 3.27 (3.13–3.30) ($\sigma\sigma$); base of lateralmost

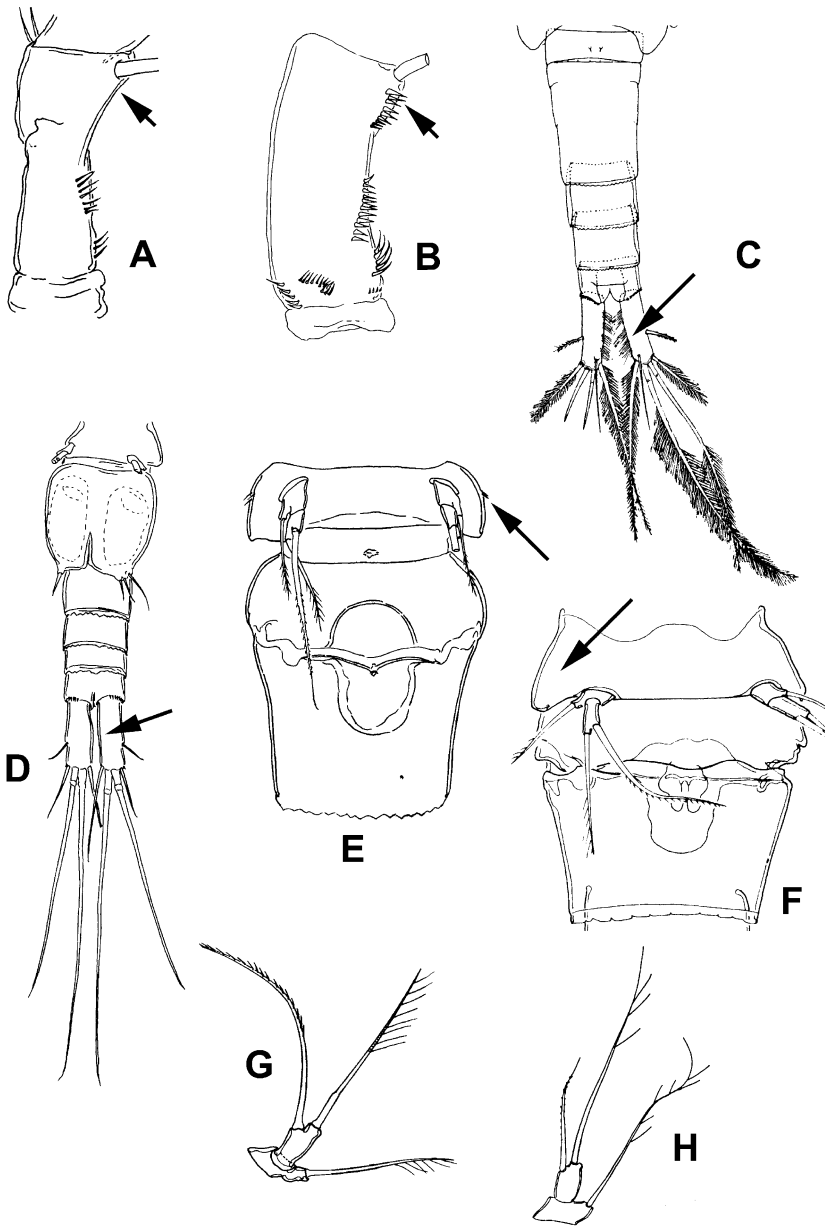


Figure 6. (A) *Mesocyclops reidae*, male (ECOCH-Z-01255), antennal basis, frontal; (B) *M. longisetus* s.str. female (ECOCH-Z-01236), antennal basis, frontal; (C) *M. edax*, female, abdomen (modified from Dahms and Fernando 1995, copyright waiver); (D) *M. reidae*, male (ECOCH-Z-01255), abdomen, ventral; (E) *M. reidae*, female, fifth pediger and genital somite (modified from Reid 1993, copyright waiver); (F) *M. chaci*, female, fifth pediger and genital somite (modified from Fiers et al. 1996, copyright waiver); (G) *M. chaci*, female, fifth leg (modified from Fiers et al. 1996, copyright waiver); (H) *M. yusui*, female, fifth leg (modified from Fiers et al. 1996, copyright waiver).

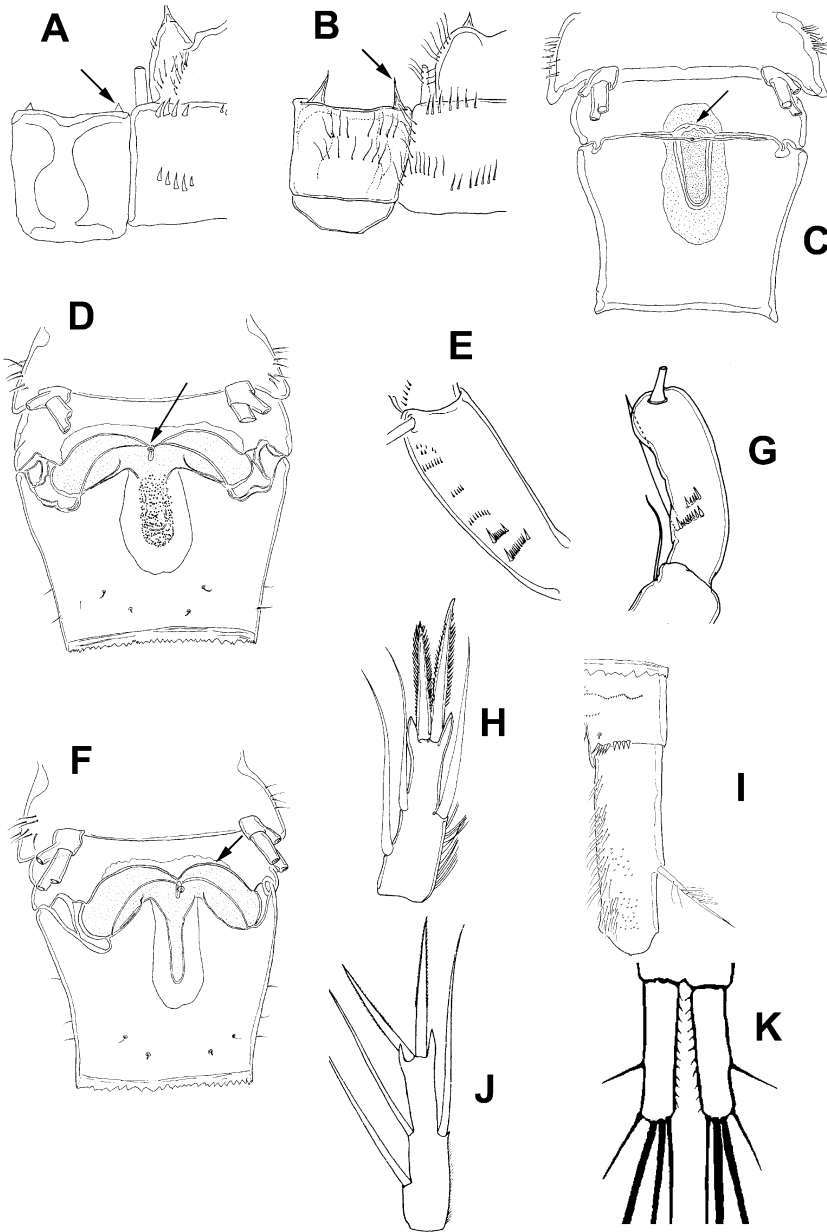


Figure 7. (A) *Mesocyclops annulatus*, female (MNHN Cp 864), fourth leg, intercoxal sclerite; (B) *M. ellipticus*, male (ECOCH-Z-01250); (C) *M. annulatus*, female (MNHN Cp 864), fifth pediger, genital somite, ventral; (D) *M. longisetus* s.str., female (ECOCH-Z-01236), fifth pediger, genital somite, ventral; (E) 16th antennular segment, inner; (F) *M. longisetus curvatus*, female (ECOCH-Z-01240), fifth pediger, genital somite, ventral; (G) *M. longisetus curvatus*, male, 16th antennular segment, inner (from Suárez-Morales et al. 1996, copyright waiver); (H) *M. longisetus curvatus*, female, fourth leg, third endopodal segment (modified from Reid and Reed 1994, copyright waiver); (I) *M. longisetus curvatus*, female (ECOCH-Z-01240), caudal rami, ventral; (J) *M. longisetus araucanus*, female, fourth leg, third endopodal segment (from Löffler 1961); (K) *M. longisetus araucanus*, female, caudal rami, ventral (from Löffler 1961).

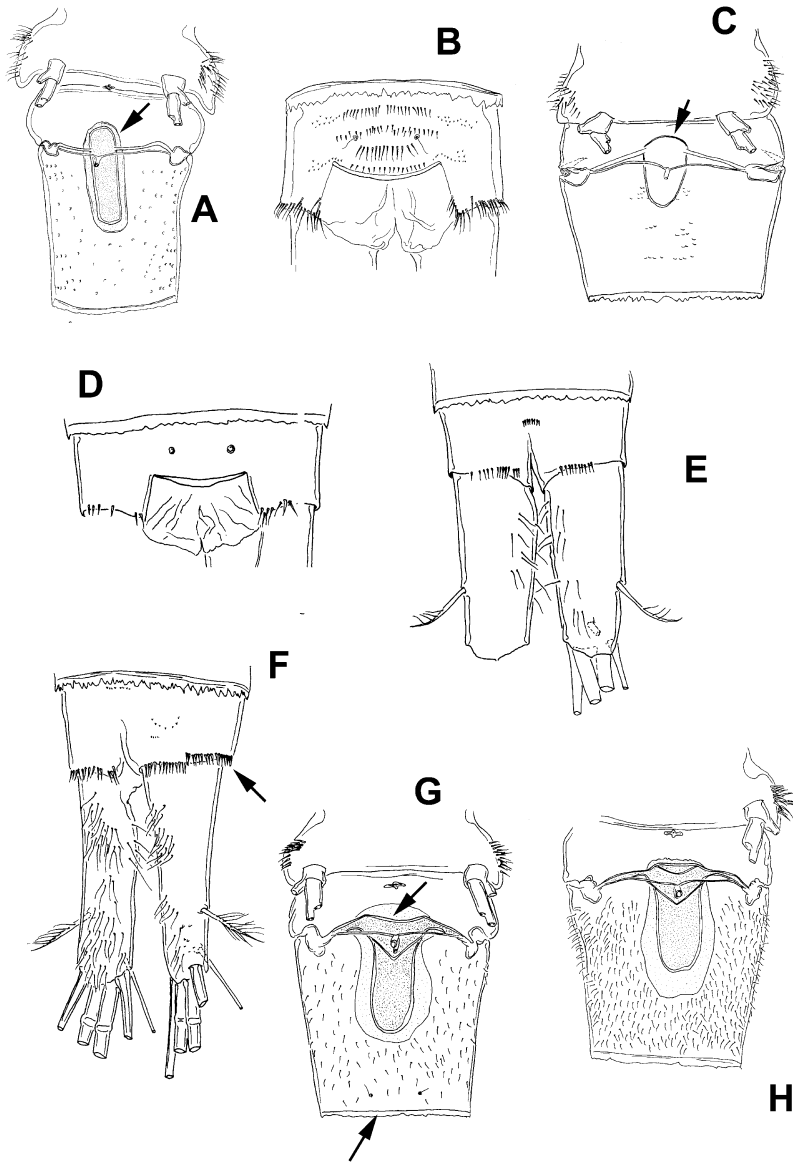


Figure 8. (A) *Mesocyclops ellipticus*, female (ECOCH-Z-01252), fifth pediger, genital somite, ventral; (B) anal somite, dorsal; (C) *M. intermedius*, female (ZMA Co 102-731), fifth pediger, genital somite, ventral; (D) anal somite, dorsal; (E) anal somite, caudal rami, ventral; (F) *M. paranaensis*, female (MNHN Cp 1883), anal somite, caudal rami, ventral; (G) *M. brasilianus*, female (ECOCH-Z-01196), fifth pediger, genital somite, ventral; (H) *M. meridianus*, female (ECOCH-Z-01202).

- terminal caudal seta with spines (♀♀) (see Pilati and Menu-Marque 2002) *M. araucanus*
15. Anterior margin of seminal receptacle strongly convex (Figure 8A), anal somite ornamented dorsally (♀♀) (Figure 8B) *M. ellipticus*
 – Anterior margin of seminal receptacle weakly convex (Figure 8C), anal somite naked dorsally (♀♀) (Figure 8D) 16
16. Row of spines on posterior margin of anal somite not dorso-ventrally continuous (♀♀) (Figure 8E) *M. intermedius*
 – Row of spines on posterior margin of anal somite dorso-ventrally continuous (♀♀) (Figure 8F) *M. paranaensis*
17. Anterior margin of seminal receptacle concave (♀♀) (Figure 8G) 18
 – Anterior margin of seminal receptacle convex (♀♀) (Figure 8H) 19
18. Spines on antennular segments 4–6 (Figure 9A); abdominal somites with a row of setae along posterior margins (♀♀) (Figure 9B) *M. meridionalis*
 – Antennular segments 4–6 without spines (Figure 9C); abdominal somites without a row of setae along posterior margins (♀♀) (Figure 8G) *M. brasilianus*
19. Praecoxal surface of maxillulae with short scales on posterior surface (♂♂, ♀♀) (Figure 9D) *M. evadomingoi*
 – Praecoxal surface of maxillulae with long setae in posterior surface (♂♂, ♀♀) (Figure 9E) 20
20. Caudal rami with inner margin pilose, spines on ventro-posterior surface (♀♀) (Figure 9F) *M. pseudomeridianus*
 – Caudal rami with inner margin naked, scales on entire ventral surface (♀♀) (Figure 9G) *M. meridianus*

Discussion

Distributional remarks

Mesocyclops aspericornis. As well as in Africa (van de Velde 1984) and Asia (Holyńska 2000b), *M. aspericornis* is widely distributed in America: its known distributional range extends from 28°S (Gutiérrez-Aguirre and Suárez-Morales 2001b) to 25°N in the continent (Gutiérrez-Aguirre et al. 2003b), with confirmed records in Argentina, Brazil, Colombia, Venezuela, Antilles, and north-west Mexico. The typical features of the western populations of *M. aspericornis*, i.e. the lower number of setae (seven or eight) on the second antennal endopodal segment and a distal row of spinules near the inner apical seta on the basis, visible in caudal view (van de Velde 1984; Holyńska 2000b), were confirmed in the Mexican and Colombian populations examined here. In addition, other typical features (i.e. shape of seminal receptacle, ornamentation of both the antennal basis and the caudal rami, etc.) used for distinguishing *M. aspericornis* remain as stable characters in the neotropical populations.

Mesocyclops thermocyclopoides complex. *Mesocyclops thermocyclopoides* and *M. ogunnus* are representatives of the *thermocyclopoides*-group in the neotropics. The former species was considered to be an exclusively Asiatic form (van de Velde 1984; Holyńska 2000b),

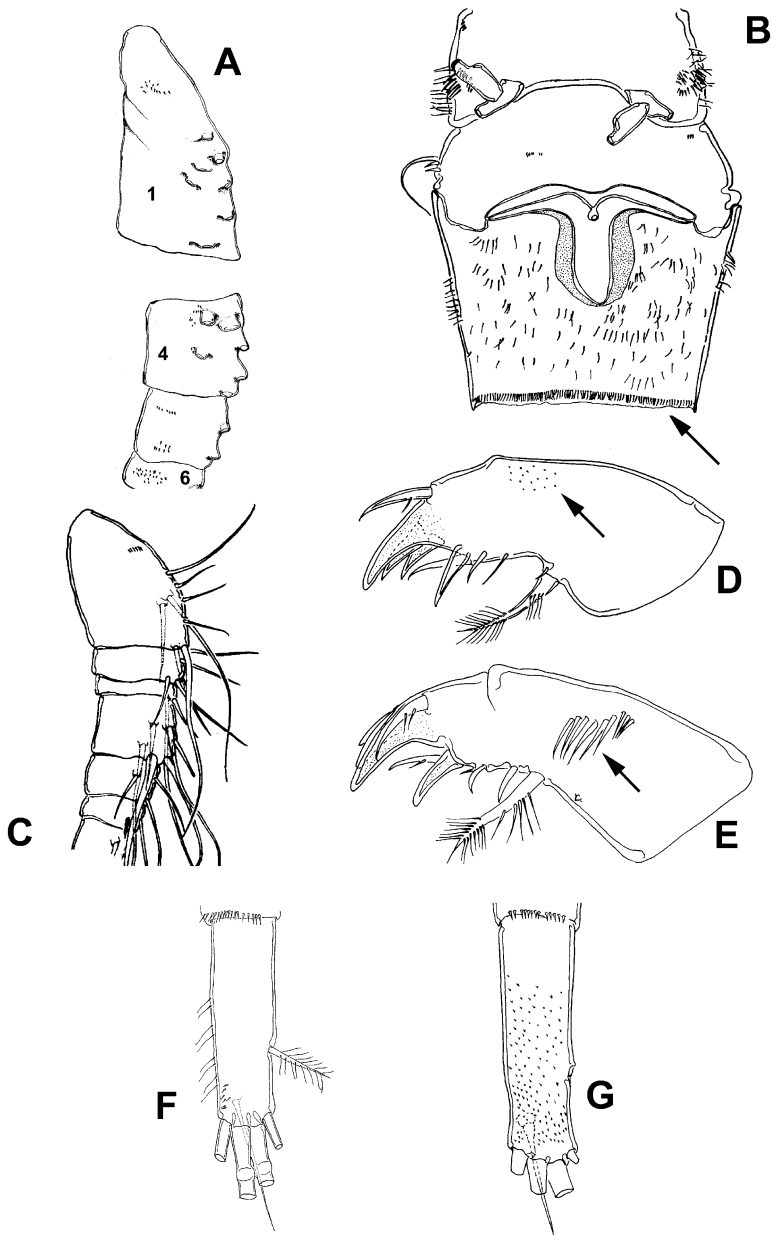


Figure 9. (A) *Mesocyclops meridionalis*, female (MNHN Cp 718), antennular segments; (B) fifth pediger, genital somite, ventral; (C) *M. brasiliensis*, female (MNHN Cp 821) antennular segments; (D) *M. evadomingoi*, female (ECOCH-Z-01157), maxillulae; (E) *M. meridianus*, female (ECOCH-Z-01205), maxillulae; (F) *M. pseudomeridianus*, female (MNHN Cp 708), caudal rami, ventral; (G) *M. meridianus*, female (ECOCH-Z-01204).

but recent evidence confirms its presence in the Americas (see Gutiérrez-Aguirre et al. 2003a). This is another example of a *Mesocyclops* probably introduced by human activity from the Old World to the New World. This species is commonly distributed in natural and artificial ponds, lakes, and reservoirs (Collado et al. 1984). *Mesocyclops ogunnus* has been recorded as an introduced species in the Cayman Islands (Suárez-Morales et al. 1999) and Brazil (Reid and Pinto-Coelho 1994), living in reservoirs and coastal, slightly saline ponds.

Mesocyclops longisetus and related forms. The differences in length/width ratio of the caudal rami, and the third endopodal segment of the fourth leg, as well as the shape of the lateral arms of the seminal receptacle, have been used to separate *M. longisetus* s. str. and *M. longisetus* var. *curvatus* (Dussart 1987; Reid and Pinto-Coelho 1994). The species of *Mesocyclops* are defined by differences in the ornamentation of cephalic or thoracic appendages, or the seminal receptacle shape; therefore, the status in these taxa remain without changes. However, features such as the presence of spines on the base of the lateralmost terminal caudal seta, a higher length/width ratio of caudal rami, and the structure of the third endopodal segment of the fourth leg, were important to distinguish *M. araucanus* as a separate form with species rank, different from *M. longisetus* s. str. (Pilati and Menu-Marque 2002). These forms have a latitudinal distribution between 51°S and 10°N in the Americas: *M. longisetus* s. str. has been recorded in Mexico, the Guadeloupe Islands, Venezuela, and Guatemala, whereas *M. longisetus* var. *curvatus* occurs in Mexico, Panama, Brazil, Guadeloupe Islands, Honduras, southern USA, and Canada. *Mesocyclops araucanus* has a latitudinal distribution between 39°36'S and 51°35'S (Pilati and Menu-Marque 2002). We verified its presence in Las Chulta Lagoon, Argentina (see Table I).

Mesocyclops annulatus diversus. The subspecies was described by Herbst (1962) from specimens collected in Rio Urindéua, Brazil. However, the original description shows morphological differences between the strict form (recorded in Argentina), and the subspecific form: the length ratio of the apical terminal spines on the third endopodal segment of the fourth leg is considerably longer in *M. annulatus diversus* than in *M. annulatus*; the seminal receptacle of the subspecies is more similar to *M. paludosus* Lindberg, 1956, a species restricted to East Africa, with wide arms, instead of the thin arms present in the strict form. Furthermore, *M. annulatus* has hair-like setae on the ventro-lateral surface of the fifth pediger versus a naked condition in *M. annulatus diversus*. It is suggested that the specimen analysed by Herbst (1962) is not a subspecies of *M. annulatus*, but probably a different taxon at a species level. The depository institution of this material is unknown to us; in fact, it is probably lost (M. Holyńska, personal communication). We speculate that a revision of specimens from the type locality would result in the change of its status to become a species. On the other hand, *M. annulatus* appears to be restricted to South America with records in Argentina, Bolivia, Chile, Paraguay, Peru, and Uruguay (Gutiérrez-Aguirre and Suárez-Morales 2001b).

Mesocyclops ellipticus–*M. reidae*. The record of *M. ellipticus* from caves in Yucatan, Mexico by Yeatman (1977) was later assigned to *M. reidae* by Petkovski (1986) and Reid (1993). However, analysis of Yeatman's illustrations clearly shows an intriguing mixture of features of both *M. ellipticus* and *M. reidae* in these cave-dwelling specimens. For instance, presence of two rows of hair-like setae on the fourth intercoxal sclerite, hair-like setae on the inner

margin of the caudal rami, as depicted in the original description of *M. ellipticus* (see Kiefer 1936), and a group of spines next to the insertion of the exopodal seta on the antennal basis (relevant features of *M. ellipticus*). The oval seminal receptacle, and the inner caudal seta short, no more than 1.5 times the length of lateral seta are important features in *M. reidae*. The original material, collected by Yeatman from Grutas Xtacumbilxunam, Campeche, Mexico, is lost (H. C. Yeatman, personal communication). New collection efforts in the same area are likely to produce additional specimens in order to determine the status of the Yucatan record of *M. ellipticus*. The diversification patterns of the genus in the Yucatan Peninsula, with closely related species in geographically restricted areas (Suárez-Morales et al. 2004) suggest that Yeatman's specimens could represent a new, endemic taxon. On the other hand, the record by Herbst (1962) in Amazonas is most probably not referable to *M. ellipticus* because the analysed specimen shows features not present in the species: the seta on the inner basis of P1 is very delicate, the hyaline membrane on antennal segment 17 is completely serrated, without a distal notch, and the fourth intercoxal sclerite lacks cuticular projections and hair-like setae. In fact, the specimen examined by Herbst is very similar to the recently described *M. evadomingoi* (see Gutiérrez-Aguirre and Suárez-Morales 2001a). Finally, we verified that specimens from Barra Bonita Reservoir are actually assignable to *M. ellipticus*; therefore, the distributional range of *M. ellipticus* is extended from Venezuela to Brazil.

Mesocyclops pseudomeridianus, *M. evadomingoi*. The known distributional range of *M. pseudomeridianus* is redefined with the first record of this species in Barra Bonita Reservoir (São Paulo, Brazil). Formerly, the species has been recorded from the type locality only (Mare à lentilles d'eau, rizière Mana French Guyana) (Defaye and Dussart 1988). The distributional range of *M. evadomingoi* is restricted currently to Tabasco, Mexico. This species could be present also in Brazil if the record by Herbst (1962) as *M. ellipticus* in the Amazonian area turns out to be *M. evadomingoi*.

Species with restricted distribution. Several neotropical species still remain known only from the type locality or localities of first description: *M. meridionalis* (Rizièrè près Corrientes, Argentina) (Dussart and Frutos 1985), *M. chaci*, *M. yutuil*, in caves and cenotes from Yucatan, Mexico (Fiers et al. 1996), and *M. intermedius* (hypogean waters from Bonaire) (Pesce 1985). *Mesocyclops paranaensis* appears to be restricted to South America, with valid records in Argentina (Dussart and Frutos 1985) and probably in Brazil, and Paraguay (Lowndes 1934) (see Holyńska et al. 2003). A similar situation is shown by *M. annulatus*, a neotropical species with records in Argentina, Bolivia, Chile, Paraguay, Peru, and Uruguay (Gutiérrez-Aguirre and Suárez-Morales 2001b). *Mesocyclops pescei* is known from the Bahamas, Bonaire, and the Yucatan Peninsula, Mexico (Fiers et al. 2000; Gutiérrez-Aguirre and Suárez-Morales 2001b); therefore, it appears to be restricted to the Caribbean region. The Asian *Mesocyclops pehpeiensis* Hu, 1943 was recorded recently in two ponds of the southeastern zone of the Mexican Pacific coast (Suárez-Morales et al. 2005) as an introduced species.

Species with wide distribution. The distributional patterns of other well-known species of *Mesocyclops* were also revised. For instance, *M. reidae* has been recorded in North and South America, as well as in the Caribbean region (Colombia, Cuba, Haiti, Jamaica), Cayman Islands, Mississippi, and Mexico (Petkovski 1986; Reid 1993). *Mesocyclops edax* is considered to be the most widely distributed species of this genus in the Nearctic region,

but with additional neotropical records in Central America, Antillas (Reid and Moreno 1999), and south-east Mexico (Suárez-Morales et al. 1996).

Morphological remarks

Most Australasian species of *Mesocyclops* show a peculiar combination of features in the trunk limbs: (1) presence of large spines on the medial expansion of the basis, first leg (+); (2) fourth intercoxal sclerite with pointed projections on distal margin (+); and (3) absence of seta on inner margin of the basis, first leg (-). All the species considered as introduced in the neotropics (i.e. *M. aspericornis*, *M. pehepeiensis*, *M. ogunnus*, and *M. thermocyclopoides*), and the recently described *M. pescei*, show the same set of features. Another possible combination [(+), (+), (+)], is very common also in African and Australasian *Mesocyclops* (i.e. *M. darwini* Dussart and Fernando, 1988; *M. dayakorum* Hołyńska, 2000; among others). This combination is shown by the neotropical *M. edax*, *M. ellipticus*, *M. intermedius*, *M. paranaensis*, *M. reidae*, and *M. yutsil*.

One special combination [(-), (+), (+)] is present in 24% of the neotropical taxa (*M. annulatus*, *M. chaci*, *M. longisetus*, *M. araucanus*, and *M. longisetus* var. *curvatus*), and has been observed only in the African *M. rarus* Kiefer, 1981. Finally, one unique combination [(-), (-), (+)] is present in *M. brasilianus*, *M. evadomingoi*, *M. meridianus*, *M. meridionalis*, and *M. pseudomeridianus*. Therefore, in the New World *Mesocyclops*, there is a tendency to reduce the spines on the first leg basis, and a persistence of a seta on the inner margin of the first leg basis; of course, a phylogenetic analysis is urgently required in order to elucidate the evolutionary change of the morphological features of the genus.

In the same sense, the presence of group δ (transversal row of tiny spines) on the antennal basis, caudal surface, together with the shape of the channel connected to the copulatory pore (resembling a “comma”), are features present only in species that probably originated in the Old World (*M. aspericornis*, *M. ogunnus*, *M. pescei*, and *M. thermocyclopoides*). Contrastingly, this group of spines is absent and the channel is wide and bent in most neotropical species.

Another unique feature observed only in neotropical species (except by the Australian *M. darwini* Dussart and Fernando, 1988), is the division of the hyaline membrane at the insertion of the medial seta (on females, last antennular segment). This character is present in *M. brasilianus*, *M. meridianus*, *M. meridionalis*, and *M. pseudomeridianus*. The “incomplete” hyaline membrane (running only from medial seta to distal point of segment) has been observed in the neotropical *M. chaci*, *M. edax*, *M. longisetus*, *M. araucanus*, and *M. longisetus* var. *curvatus*. Only the Asian *M. dayakorum* Hołyńska, 2000 and the Australian *M. pseudoannae* van de Velde, 1987 share this particular feature. All the African species analysed by van de Velde (1984) and most Australasian species observed by Hołyńska (2000b) show the hyaline membrane “complete” along the segmental margin. This condition is present in *M. annulatus*, *M. aspericornis*, *M. evadomingoi*, *M. intermedius*, *M. ogunnus*, *M. paranaensis*, *M. pescei*, and *M. thermocyclopoides*.

The importance of the maxillular ornamentation for distinguishing species was noted only in reference to the palp of the African species *M. ogunnus*. In this study, we found that when it is present, the ornamentation of the praecoxal surface has taxonomic value, similar to that attributed to the ornamentation of maxillar coxa, fourth leg coxa or shape of the seminal receptacle, because this structure (among others) is an important feature for distinguishing *M. brasilianus*, *M. evadomingoi*, and *M. meridianus*.

On the other hand, because many morphological differences were found among the examined species, the following features can be considered as potentially valuable to separate the neotropical species: (1) presence/absence of ornamentation on antennular segments 1, 4, 5, and 6 in the female; (2) presence/absence of ornamentation on antennular segments 15 and 16 in the male; (3) ornamentation on the antennal basis; (4) presence/absence and type of ornamentation on the maxillular praecoxa, posterior surface; (5) ornamentation on both coxa and basis of first and fourth swimming legs; (6) shape of seminal receptacle; (7) ornamentation on abdominal somites; (8) presence/absence of ornamentation on the furca; and (9) presence/absence of ornamentation on the anal somite (posterior margin, and ventral or dorsal surfaces). These features were valuable for the identification of both female and male specimens.

Acknowledgements

We thank C. Quintal-Lizama, A. García-Morales, I. Castellanos-Osorio, and C. Curiel-Mondragón from El Colegio de la Frontera Sur (ECOSUR)-Chetumal, for collecting zooplankton samples in south-east Mexico. Some specimens were a gift from Marcos da Silva (Brazilian copepodologist) and Marcelo Silva-Briano (Universidad Autónoma de Aguascalientes, Mexico). Janet W. Reid (Virginia Museum of Natural History, USA) made some valuable specimens available to us and provided relevant and useful comments on an earlier version of this contribution. Frank Ferrari and Chad Walter kindly authorized the loan of specimens originally deposited in the Smithsonian-NMNH, to the collection at ECOSUR (ECOCH-Z). Danielle Defaye, Muséum National d'Histoire Naturelle, Paris; Dirk Platvoet, Instituut voor Systematiek en Populatiebiologie, Netherlands; and Hans Walter Mittmann, Staatliches Museum für Naturkunde, Karlsruhe, kindly allowed us to review MNHN, ZMA, and SMNK specimens, respectively. Harry C. Yeatman (Sewanee, The University of the South), kindly granted us important information about Mexican specimens. Maria Hołyńska, Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, kindly granted us information, time, and shared with us her broad knowledge of the world species of *Mesocyclops*.

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