

How "Cosmopolitan" are the Continental Cyclopoid Copepods? Comparison of the North American and Eurasian Faunas, with Description of *Acanthocyclops parasensitivus* sp.n. (Copepoda: Cyclopoida) from the U.S.A.

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Abstract. Refinements of alpha-taxonomic methods have resulted in reconsideration and splitting of several "species" of continental (inland-water) cyclopoid copepods (Crustacea). This process should continue as more careful morphological scrutiny, genetic comparisons, and cross-breeding tests are applied to additional taxa. The relative number of taxa supposedly shared between continents, or "cosmopolitan", has been declining upon re-examination; the world cyclopoid fauna is no longer thought to be composed of a significant proportion of relatively few, widespread species. This process is illustrated through inspection of the faunas of North America and Eurasia. Presently a maximum of 32 (28%) of 114 North American cyclopoid species and subspecies is considered to be holarctic, compared to 13 (68%) of the 19 North American species known at the beginning of this century. The species that are presently thought to be holarctic and an additional few morphologically similar, possibly sibling species are listed, and the taxonomic status of some is discussed. *Acanthocyclops parasensitivus* sp.n. from the eastern U.S.A. is described and compared with its European sibling species, *A. sensitivus*.

Key words. *Acanthocyclops*, Crustacea, Cyclopidae, new species, biogeography.

1. INTRODUCTION

A selection of quotes illustrates changes in opinions regarding the extent of cosmopolitanism among continental (inland) cyclopoid copepod crustaceans, and the relationships of the North American fauna to that of other continents, during this century: "It is very evident that most ... American species are identical with those in Europe" (MARSH 1910: 1067). "... there has been misidentification attributable ... to lack of accurate comparison with the Old World copepods" (YEATMAN 1944: 2). "a few species [of cyclopoids] are nearly cosmopolitan ... the list [of characteristic Holarctic species] is likely to grow as the North American fauna becomes more critically understood" (HUTCHINSON 1967: 626). "There's no such thing as a cosmopolitan species" (T. E. BOWMAN, pers. comm. ca. 1990). Carcinologists working with small crustaceans, led by FREY (e.g. FREY 1982, 1986, 1987, 1988) have demonstrated that the names of many,

usually European species have been inappropriately applied to populations on other continents. Several workers have compared European and Asian populations of continental calanoid, harpacticoid, or cyclopoid copepods with some from North America. A number of these have proposed that populations on different continents represent different taxa (DUSSART 1985; ISHIDA 1992a, 1992b, 1993; DODSON 1994; REED 1994; REID & ISHIDA 1996; VYSHKVARTZEVA 1994; S. KARAYTUG, in litt. 1996; F. STOCH, in litt. 1995). On the other hand, several studies have tended to confirm classical suppositions of the conspecificity of some Palearctic and Nearctic taxa, or add new instances of faunal links at the species level (DUSSART & FERNANDO 1990; BORUTZKY et al. 1991; GALASSI 1991; REED 1991; DODSON 1994; REID 1995; H. C. YEATMAN, in litt. 1992-1996). The aim of this paper is to evaluate the proportion of the North American cyclopoid copepod fauna that is currently considered common to the Palearctic Region, to discuss the

effect of recently developed taxonomic criteria and methods for genetic evaluation in changing ideas regarding the species in common, and to exemplify the process by describing and comparing a new North American species of *Acanthocyclops* with its European sister-taxon. The Nearctic and Palearctic Regions were selected for comparison for two reasons. First, knowledge of the copepod faunas is most advanced in those parts of the world. Second, the geographical proximity and, later, understanding of the relative recency of the separation of these regions have led specialists to assume that their faunas would contain a high proportion of taxa in common.

2. MATERIAL AND METHODS

For the taxonomic description, specimens were initially fixed in formalin and transferred to 70% ethanol for long-term storage. Morphological descriptions were made from specimens transferred gradually to glycerin and then to lactic acid, and/or mounted in polyvinyl lactophenol (PVL) with a little chlorazol black E added, or in CMC-10. Measurements and drawings were made using a Wild M30 microscope fitted with a drawing tube, at 600 \times or 1000 \times (oil immersion). The specimens are deposited in the United States National Museum of Natural History, Smithsonian Institution (USNM). To estimate shared faunas, species lists for North American Cyclopidae excluding Euryteinae and Halicyclopiniae from three widely separated dates in this century were compared: those of MARSH (1910) and YEATMAN (1959) and data from 1996. Species and subspecies were counted as separate taxa. The total for 1996 includes ten undescribed species known to me. The numbers of taxa counted as inhabiting both Eurasia and North America in 1910 and 1959 were taken from the discussions of MARSH (1910) and YEATMAN (1959) respectively; for 1996, these taxa have been listed in Tab. 2 and several are discussed. Taxa inhabiting only Mexico are excluded from consideration, as are three species considered to be introduced by human agency into North America (*Megacyclops viridis*, *Mesocyclops rutneri*, and *Thermocyclops crassus*).

3. RESULTS

3.1. *Acanthocyclops parasensitivus* sp.n.

3.1.1. Material examined. Type locality: Jug Bay Wetlands Sanctuary (38 47'N, 76 41'W), Lothian, Anne Arundel County, Maryland, U.S.A. Jug Bay is in the floodplain of the Patuxent River, which enters the east-

ern side of the Chesapeake Bay. Type series: female holotype, USNM 268096, dissected on slide in CMC-10; male allotype, dissected on 2 slides in CMC-10, USNM 278125; 1 female paratype, dissected on 2 slides in CMC-10, and 4 female, 2 male, and 3 copepodid paratypes, ethanol-preserved, USNM 278126; all from Sample 94-C-02, spring in deciduous woods, Jug Bay Wetlands Sanctuary (18 March 1994; coll. A. W. Norden). Accompanying copepod fauna: *Diacyclops* cf. *languidoides* (LILLJEBORG 1901), 1 male, USNM 268097; *Attheyella* (*Mrazekiella*) *spinipes* Reid, 1987, 3 females, 2 males, USNM 268095; *Bryocamptus zschokkei* (Schmeil, 1893), 2 females, USNM 268098; *Bryocamptus* sp. (*minutus*-group), 3 females, 1 male, and 3 copepodids, USNM 268102. 1 female paratype, partly dissected on slide in PVL, USNM 278114 [under right cover slip together with 1 female *Diacyclops nearcticus* (KIEFER 1934), USNM 278115], from Sample "Well 3, 10 cm" in bar of coarse sand with some flattened limestone slabs, less than 1 m above water level of creek, in Buck Creek; (a fifth-order tributary of the Cumberland River) just downstream from Kentucky Route 70 bridge near Somersot (38 17'N, 75 27'W), Pulaski County, Kentucky, U.S.A., 37 14'N, 84 34'W (corresponds to Site 5 of SCHUSTER et al. 1989) (20–21 October 1991; coll. D. L. Strayer).

• Additional material: 1 female and 1 male, both copepodid stage V, and 4 younger copepodids, ethanol-preserved, USNM 278181, from phytotelm in leaves of Northern Pitcher Plant *Sarracenia purpurea* Linnaeus, 1753, Sample 96-VIII-22-11A, bog near Nassawango Creek (38 17'N, 75 27'W), Wicomico County, Maryland (22 August 1996; colls. R. Hamilton IV and R. M. Duffield). Additional material from same site in collection of R. Hamilton IV. Nassawango Creek is an affluent of the Pocomoke River on the eastern side of the Chesapeake Bay.

3.1.2. Description. Female: Length of holotype, excluding caudal setae 892 μ m. Lengths of 4 paratypes from Jug Bay, 760–868 μ m (Tab. 1). Pediger 5 (Fig. 1c) slightly produced laterally, without ornament except normal 2 dorsal sensilla. Abdomen (Fig. 1a,c) short, stout. Genital double somite (Fig. 1a, c) with anterior 1/3 laterally produced, about as broad as length of somite. Seminal receptacle (Fig. 1c) butterfly-shaped, but with arcuate anterior margin in some Maryland

Fig. 1. *Acanthocyclops parasensitivus* sp.n., female; a, b, d, f, holotype (Maryland), USNM 268096; c, g, h, dissected paratype (Maryland), USNM 278126; e, paratype (Kentucky), USNM 278114. a. Urosome, dorsal. b. Middle terminal caudal setae. c. Urosome, ventral. d. Anal somite, dorsal. e. Anal somite, dorsal (from flattened mount). f. Anal somite and caudal rami, ventral. g. Antenna basipodite and endopodite article 1, caudal side. h. Antenna basipodite and endopodite article 1, frontal side. Scale bars: 50 μ m.

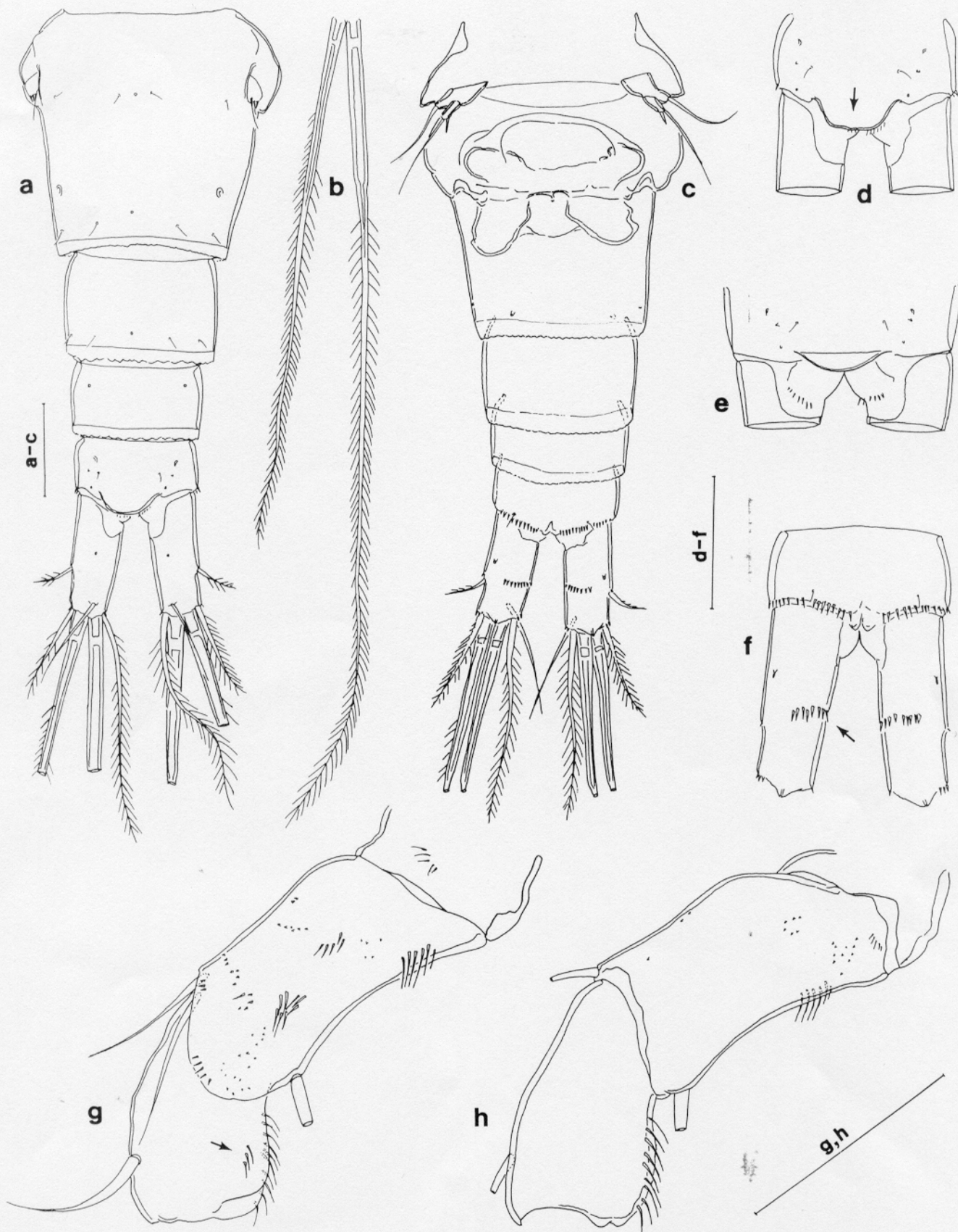


Table 1. Measurements (in μm) of *Acanthocyclops parasensitivus* sp.n. from the type locality. Abbreviations: CR, caudal ramus; Seta 1–4, medialmost to lateralmost terminal caudal setae; Insertion, ls, distance from proximal margin of CR to insertion of lateral seta; P4enp3, leg 4 endopodite article 3; mts, medioterminal seta; lts, lateroterminal seta.

	♀ ♀				♂ ♂			
Body length	892	760	816	760	868	676	620	668
CR length	64	63	55	63	67	56	50	55
CR breadth	26	26	27	24	28	23	22	22
Seta 1	90	130	115	123	117	105	97	103
Seta 2	420	440	420	460	492	408	328	392
Seta 3	292	300	328	284	324	264	b	248
Seta 4	50	68	55	56	61	46	40	41
Dorsal seta	45	42	53	43	51	30	36	34
Insertion, ls	44	41	38	39	45	35	35	34
P4enp3 length	43	45	43	44	47	39	37	37
P4enp3 breadth	28	26	29	30	31	25	23	24
P4enp3 mts	39	37	41	38	40	39	37	37
P4enp3 lts	26	25	27	25	28	24	24	23

specimens as illustrated (seminal receptacle of Kentucky female not clearly visible). Double somite dorsally with row of 2 pairs of hairlike sensilla and pore on midline at level of 6th legs, similar row along posterior margin, and pair of heavily sculptured pores at posterior 3/4; ventrally with 2 pairs of pores near posterior margin. Next posterior somite with row of 2 pairs of sensilla and pore on midline along dorsal posterior margin, no pores visible ventrally. Next somite with only 1 pair of pores dorsally. Anal somite with 3 pairs of pores in diagonal rows lateral to each dorsal sensillum, and 2 sensilla near posterior ventral margin; also with row of spinules along ventral margin, and 2 diagonal rows of perianal spinules. Anal operculum quadrate and produced in all specimens from Maryland (Fig. 1d), crescentic and less produced in specimen from Kentucky (Fig. 1e). Caudal ramus (Fig. 1f) about 2.0–2.6 times longer than broad, with dorsal and ventral pore and transverse row of spinules on ventral surface; also tiny unsocketed spinule above insertion of lateral seta, and few larger spinules anterior to insertion of lateral terminal seta. Lateral seta inserted at posterior 2/3 of ramus. Dorsal seta naked, about as long as or slightly shorter than lateral terminal seta (Fig. 1a, c, Tab. 1). Middle terminal caudal setae (Fig. 1b) longer than abdomen, each seta constricted near beginning of plumage; plumage homogeneous except proximal 1/4 of setules slightly stiffer than distal 3/4. Medialmost terminal caudal seta about 1.4–2.1 times longer than caudal ramus, outermost terminal caudal seta slightly longer to slightly

shorter than ramus. Antennule of 17 articles; long aesthetasc on article 12 reaching just past distal end of article 15. Antenna (Fig. 1g,h), basipodite with 2 setae on anterior distal corner and 1 long (exopodite) seta on posterior distal corner. Endopodite article 1 with 1, article 2 with 9, article 3 with 7 setae. Spinule pattern on basipodite and endopodite article 1 as illustrated. Labrum (Fig. 2a) with 10 tiny teeth between rounded lateral corners. Mandible, maxillule, and maxilla exactly as illustrated for *Acanthocyclops sensitivus* by POSPISIL (1994). Maxilliped (Fig. 2b,c) article 1 with only 2 setae; surface ornamentation as in *A. sensitivus* (as illustrated by POSPISIL 1994). Legs 1–4 (Fig. 2d–f) with rami each of 3 segments. Spine formula 2,3,3,3, seta formula 4,4,4,4. Segments 1 and 2 of endopodite and segment 2 of exopodite of each leg with 1 medial seta; segment 1 of exopodite of each leg lacking medial seta. Setae stout, especially those of legs 3 and 4. Couplers of all legs lacking ornamentation. Leg 1 (Fig. 2d) with stout serrate spine on medial expansion of basipodite, reaching distal end of endopodite article 2. Legs 1 and 4 exopodite article 1 lacking spinules on distal border of caudal side; leg 4 exopodite article 2 with tiny spinules on distal border. Leg 4 endopodite article 3 (Fig. 2e, f) about 1.5–1.7 times longer than broad in Maryland specimens (Tab. 2), 1.56 times longer than broad in Kentucky specimen. Medioterminal spine of this article longer than lateroterminal spine; setae of article considerably longer than article itself in all Maryland specimens, somewhat longer in Kentucky speci-

Fig. 2. *Acanthocyclops parasensitivus* sp.n.; a–e, g, holotype female (Maryland), USNM 268096; f, paratype female (Kentucky), USNM 278114; h, i, allotype male (Maryland), USNM 278125. a. Labrum. b, c. Maxilliped. d. Leg 1 and coupler. e. Leg 4 and coupler. f. Leg 4 endopodite. g. Leg 5. h. Legs 5 and 6. i. Antennule articles 1–6. Scale bars: 50 μm .

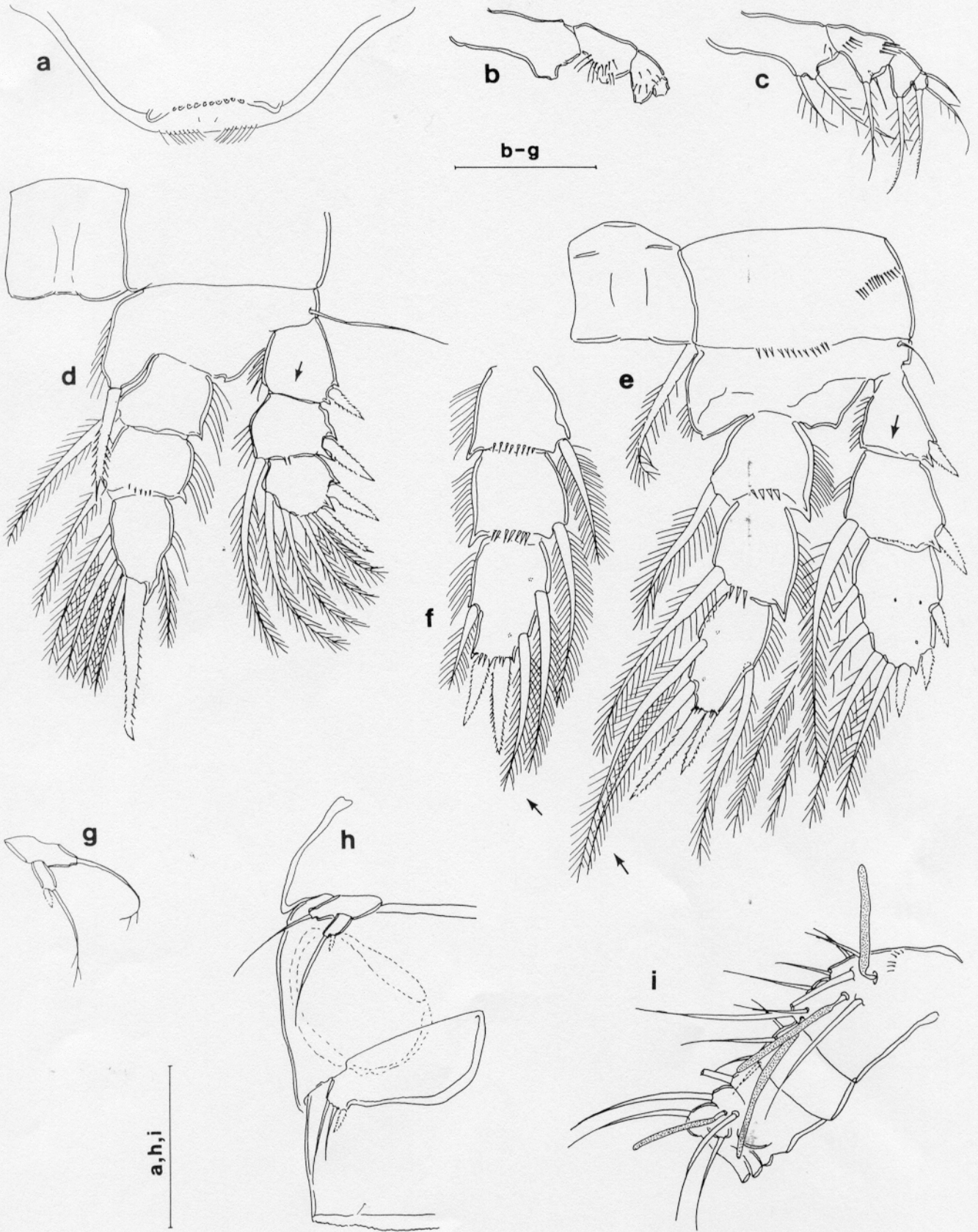


Table 2. Taxa of Cyclopidae presently considered to inhabit both North America and Eurasia. The list does not include introduced species *Megacyclops viridis*, *Mesocyclops ruttneri*, and *Thermocyclops crassus*. ^a indicates species is present in North America only in the extreme northwest.

Eucyclopinae	Cyclopinae
<i>Ectocyclops phaleratus</i>	<i>Acanthocyclops capillatus</i>
<i>Ectocyclops polyspinosus</i>	<i>Acanthocyclops robustus</i>
<i>Ectocyclops rubescens</i>	<i>Acanthocyclops vernalis</i>
<i>Eucyclops agilis</i> (= <i>serrulatus</i>)	<i>Cryptocyclops bicolor</i> ^a
<i>Eucyclops macruroides</i> <i>denticulatus</i>	<i>Cyclops furcifer</i> ^a
<i>Macrocyclus albidus</i>	<i>Cyclops scutifer</i>
<i>Macrocyclus fuscus</i>	<i>Cyclops strenuus</i>
<i>Paracyclops chiltoni</i>	<i>Cyclops vicinus</i>
<i>Paracyclops fimbriatus</i>	<i>Diacyclops bicuspidatus</i>
<i>Paracyclops poppei</i>	<i>Diacyclops bicuspidatus lubbocki</i>
	<i>Diacyclops bisetosus</i>
	<i>Diacyclops crassicaudis</i>
	<i>Diacyclops crassicaudis</i> var. <i>brachycercus</i>
	<i>Diacyclops hypnicola</i>
	<i>Diacyclops languidus</i>
	<i>Diacyclops nanus</i>
	<i>Diacyclops yezoensis</i> ^a
	<i>Megacyclops magnus</i> ^a
	<i>Microcyclus rubellus</i>
	<i>Microcyclus varicans</i>
	<i>Tropocyclops prasinus</i>

men. Leg 5 (Fig. 1c, 2g) of 2 distinct articles, medial subterminal spine finely serrate. Leg 6 consisting of small distinct plate bearing slender dorsal seta and 2 short spines. Egg sacs not present on individuals examined. Preserved specimens colorless.

Male: Length (excluding caudal setae) of allotype 676 µm, of 2 paratypes 620 and 668 µm (Tab. 1). Habitus and caudal setae as in female except for dimorphic features.

Antennule (Fig. 2i) exactly as illustrated by Pospisil (1994) for *A. sensitivus*, i.e. geniculate and composed of 16 articles. Spinule pattern of antenna basipodite not clearly seen, but appearing somewhat simpler than that of female. Leg 6 (Fig. 2h) a broad unornamented plate bearing 1 short serrate medial spine and 2 slender setae, lateral seta longer than middle one.

Etymology: The specific name refers to the close resemblance to *Acanthocyclops sensitivus* (Graeter & Chappuis 1914).

3.1.3. Comparisons. *Acanthocyclops parasensitivus* sp.n. closely resembles the European *A. sensitivus* in its general form, proportions of the caudal rami and

lengths of the caudal setae, number of articles and setation of the antennule, surface ornamentation of the antenna, structure and ornamentation of mouthparts (including maxilliped article 1 with only 2 setae), articulation and major armament of the swimming legs, structure of the 5th legs of both sexes, and the 6th leg of the male, as represented by GRAETER & CHAPPUIS (1914), GURNEY (1933), KIEFER (1935, 1957, 1964), PETKOVSKI (1984), EINSLE (1993), and in most detailed fashion by POSPISIL (1994 and in litt. 1994).

Several slight morphological differences indicate the likelihood of a genetic separation between the North American and European populations. The arcuate anterior expansion of the seminal receptacle of some specimens of *A. parasensitivus* differs from the uniformly butterfly-shaped receptacle of *A. sensitivus* (cf. figures by GRAETER & CHAPPUIS 1914; GURNEY 1933; KIEFER 1957, 1964; PETKOVSKI 1984; EINSLE 1993).

The produced, quadrate anal operculum of the adult specimens from Jug Bay, Maryland, is much larger than the short quadrate opercula represented by KIEFER (1964) and EINSLE (1993). On the other hand, the less produced crescentic operculum of the Kentucky specimen is similar to illustrations by GURNEY (1933) and PETKOVSKI (1984).

All the adult American specimens, and the older copepodids from the Nassawango Creek site, have a transverse row of spinules on the ventral surface of the caudal ramus. Such a feature has never been reported for *A. sensitivus*, and G. L. PESCE (in litt. 1994) and F. STOCH (in litt. 1994) verified that it is not present in their specimens. P. POSPISIL (in litt. 1994) examined females from four populations in the Danube basin, Austria. In three samples no caudal spinule row was found. Four of 25 females from Lobau do possess a row of caudal spinules, but the spinules are more slender and the row extends further dorsally than in the American specimens.

In *A. parasensitivus*, there is a short row of spinules near the distal end of the antenna endopodite article 1 (arrowed in Fig. 1g) that is apparently not present in *A. sensitivus* (POSPISIL 1994).

In *A. sensitivus*, the leg 1 basipodite spine is slender (GURNEY 1933; KIEFER 1957, 1964; PETKOVSKI 1984; EINSLE 1993; POSPISIL 1994). In *A. parasensitivus* the spine is stout. In the Maryland specimens of *A. parasensitivus*, the setae of leg 4 endopodite article 3 are twice as long or longer than the medioterminal spine. The corresponding setae of the Kentucky specimens are not as long, more comparable to those of European specimens, in which the distomedial seta reaches nearly to (POSPISIL 1994) or just past (GURNEY 1933; KIEFER 1935, 1957, 1964; PETKOVSKI 1984; EINSLE 1993) the end of the medioterminal spine. The American specimens lack small spinules along the distal margins of the caudal side of legs 1 and 4 exopodite article

1. The leg 4 exopodite article 2 also lacks distal spinules in the Kentucky female, and the Maryland females have a few minute spinules at this location. European specimens are uniformly represented as having normally developed spinules at these sites (KIEFER 1957, 1964; PETKOVSKI 1984; EINSLE 1993; POSPISIL 1994).

The copepodids from Nassawango Creek, Maryland, are recognizable as *A. parasensitivus* by the ventral transverse row of spinules and the proportions of the caudal ramus, the relative lengths of the caudal setae, the shape of the anal operculum, and the segmentation and setation of the swimming legs. The anal operculum is produced, as in the adults from Jug Bay, Maryland.

Acanthocyclops sensitivus occurs in hypogean situations (dug wells and springs), primarily in the Rhine and Danube basins, with outlying populations in Belgium, France, and southern England (GRAETER & CHAPPUIS 1914; GURNEY 1933; LERUTH 1939; KIEFER 1957, 1964; AMOROS & MATHIEU 1984; PETKOVSKI 1984; POSPISIL 1994). *Acanthocyclops parasensitivus* was collected in a spring, from *Sarracenia* leaves in a bog, and in a stream interstitial habitat, in the Patuxent and Pocomoke Rivers (Atlantic) and Cumberland River (Mississippi) drainage basins respectively. Its broad distribution, and the relatively pristine nature of the sites where it was collected, support the assumption that it is a true member of the North American fauna, not a recent introduction.

Acanthocyclops sensitivus and *A. parasensitivus*, like members of the *Diacyclops languidoides*-group and some other hypogean species, probably descend from Pangaeon populations which began to diverge upon separation of North America from Europe. Transoceanic dispersal of these rare groundwater inhabitants seems unlikely. There are several similar examples of amphiatlantic pairs of continental (inland) crustacean taxa (e.g. STOCK 1993; WÄGELE et al. 1995). The close morphological resemblance of *A. sensitivus* and *A. parasensitivus* attests to the conservative nature of cyclopoid morphology under presumably stable environmental conditions.

3.2. Estimations of shared faunas

With more sophisticated morphological evaluation and the help of some genetic comparisons and crossbreeding attempts, the proportion of Nearctic cyclopoid species considered to be shared with the Palearctic Region has steadily declined in this century. On the other hand, with better collecting the absolute number of supposedly shared species has increased in accordance with HUTCHINSON'S (1967) prediction. MARSH (1910) considered that 13 (68%) of the total of 19 taxa of North American Cyclopidae known at that time also inhabited Eurasia (primarily Europe). In 1959, YEATMAN'S com-

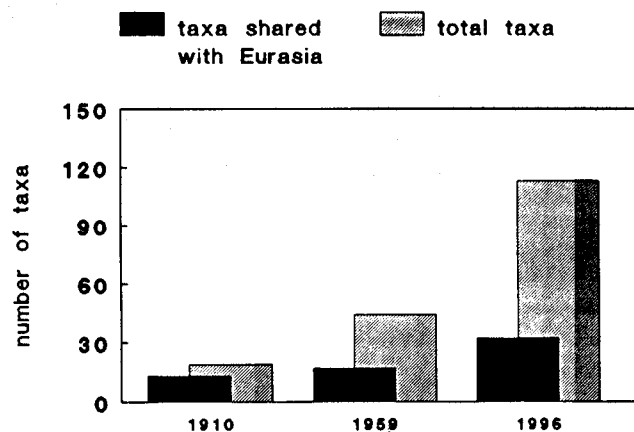


Fig. 3. The number of taxa (species and subspecies) of cyclopoid copepods considered to inhabit both North America and Eurasia (i.e. Holarctic) by MARSH (1910), YEATMAN (1959), and in 1995; and the total number of taxa known from North America in each year. Three species considered to be introduced into North America are excluded (*Megacyclops viridis*, *Mesocyclops ruttneri*, *Thermocyclops crassus*).

prehensive key to North American Cyclopidae listed 17 (of 44, or 39%) supposedly Holarctic taxa. Today a maximum of 31 (27%) of the 114 North American cyclopids known at present may also occur in Eurasia (Fig. 3; Tab. 2). Neotropical species are not considered in this total. Even the 1996 list of "taxa in common" (Tab. 2) is inflated by possible failure to distinguish North American morphs, listing several names for what may be only a single species, and inclusion of a few Eurasian species that are known in North America only from the extreme northwest and apparently do not succeed eastward as members of a true Nearctic fauna. The number of unrecognized sibling taxa cannot be estimated at present, although most putatively Holarctic cyclopids are good candidates for re-examination. An example of the second kind is the species usually known as *Ectocyclops phaleratus* (Koch, 1838). There is probably only one member of this genus on the continent, though DUSSART & FERNANDO (1990) have suggested that it is actually *E. polyspinosus*, and other workers have recorded *E. rubescens* (Brady, 1904). *Diacyclops crassicaudis* (G. O. Sars, 1863) and *D. crassicaudis* var. *brachycercus* (Kiefer, 1927), listed separately, may be ecomorphs (REID 1992). An example of the third kind is *Cryptocyclops bicolor* (G. O. Sars, 1863). YEATMAN (1944, 1959, and in litt. 1995), after discounting other records, still assumed a continent-wide distribution for this species because of the record from Massachusetts by WILSON (1932). However, my inspection of Massachusetts specimens deposited by

WILSON as *Cyclops bicolor* in the collections of the U.S. National Museum of Natural History (USNM 60292) revealed that they are actually *Apocyclops spartinus* RUBER, 1968. A specimen from Alaska determined by YEATMAN represents the only reliable North American record of *C. bicolor* (coll. C. S. WILSON near Circle, in the Yukon River basin, 5 July 1947; USNM 88048). A second species with apparently similar distribution is *Diacyclops yezoensis* (ITO, 1954), known from Japan and Alaska (ISHIDA 1992b). *Eucyclops elegans* (HERRICK, 1884), a species with a long caudal ramus that is serrate invariably along its entire length, appears to be the common American analogue of *E. speratus* (LILLJEBORG, 1901) (E. B. REED & JWR, unpublished data). If all taxa in the second and third categories are eliminated from consideration, the number of true Holarctic species decreases to 24. *Acanthocyclops parasensitivus* and *A. sensitivus* might have been considered members of the same taxon as recently as a decade ago. Demonstrations of the taxonomic value of minor ornamentation of somites and appendages, appendages of mouthparts, integumental pores, and other features usually ignored until recently have provided additional tools for species discrimination; for examples of their use see VAN DE VELDE (1984a), PESCE & GALASSI (1985), DODSON (1994), and ROCHA (1994). However, comparison of the more subtle meristic characters such as antenna spinule patterns is often impossible unless specimens of all species of interest are available, because these features were included in few earlier descriptions. Also, few evaluations of the extent to which such structures can vary have been made (but cf. VAN DE VELDE 1984b; DODSON 1994).

Table 3. Morphologically similar Eurasian and North American species of Cyclopidae. Sources of comparisons: ^a E. B. REED & JWR (unpublished data); ^b S. KARAYTUG (in litt. 1996); ^c REID et al. (1991); ^d PRICE (1958), EINSLE (1992), DODSON (1994); ^e present report; ^f REED (1995); ^g F. STOCH & JWR (unpublished data); ^h REID (1993); ⁱ DUSSART (1985).

Eurasian taxon	North American taxon
Eucyclopinæ	Eucyclopinæ
<i>Eucyclops speratus</i> ^a	<i>Eucyclops elegans</i>
<i>Paracyclops affinis</i> ^b	<i>Paracyclops canadensis</i>
Cyclopinæ	Cyclopinæ
<i>Acanthocyclops phreaticus</i> ^c	<i>Acanthocyclops montana</i>
<i>Acanthocyclops robustus</i> ^d	<i>Acanthocyclops</i> spp.
<i>Acanthocyclops sensitivus</i> ^e	<i>Acanthocyclops parasensitivus</i>
<i>Cyclops kolensis</i> s. str. ^f	<i>Cyclops kolensis alaskaensis</i>
<i>Diacyclops languidoides</i> s. l. ^g	<i>Diacyclops</i> sp.
<i>Diacyclops trajani</i> ^h	<i>Diacyclops virginianus</i>
<i>Mesocyclops leuckarti</i> ⁱ	<i>Mesocyclops americanus</i>

Several investigations have indicated the existence of differences between local North American copepod populations and morphologically similar European forms, suggesting that some may be separate taxa (Tab. 3). PRICE'S (1958) discovery of cryptic speciation in American populations of the *Acanthocyclops vernalis-robustus* group significantly modified previous assumptions of homogenous conspecificity between continents. For instance, DUSSART & FERNANDO (1990) called attention to microcharacter differences between North American (Ontario) and European *Eucyclops serrulatus*. EINSLE (1992) was unable to reconcile the morphology of some American populations of the *A. vernalis-robustus* complex with either of the corresponding European species. CHENGALATH & SHIH (1994) and SHIH & CHENGALATH (1994) noted that western Canadian morphs attributed to *Cyclops scutifer*, *Diacyclops bicuspidatus*, *Eucyclops serrulatus*, and *Macrocyclops albidus* differed slightly from European and some North American descriptions. REED (1995) reviewed morphological differences between the nominate (Eurasian) form of *Cyclops kolensis* and North American populations, known as *C. kolensis alaskaensis*, and concluded that genetic or breeding studies will be necessary to resolve their relationship.

As with cladocerans, the trend in cyclopid alpha-taxonomy has been to give weight to more and more subtle morphological distinctions. The effect has been to "split" species-level taxa that were formerly considered variable. Levels of allopatric speciation between continents are now seen as greater than formerly recognized, and distant populations, particularly those on different continents, are now supposed a priori to be genetically distinct. The simple concept of the continental Cyclopidae as a relatively homogeneous group with many widely distributed species has become outdated. We can expect that additional investigation based on detailed comparisons of type populations with generally similar morphs from other continents will result in recognition of slight but significant distinctions in most cases. The picture of the North American cyclopid assemblage is beginning to resemble that described by FREY (1986) for the cladocerans. Taxa that were on the continent very early, perhaps before the breakup of the Pangaea supercontinent, form the majority of native species, and species with broad inter-continental distributions may be the rare exception.

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REFERENCES

- AMOROS, C. & MATHIEU, J. (1984): Structure et fonctionnement des écosystèmes du Haut-Rhône français. *Hydrobiologia* **108**: 273–280.
- BORUTZKY, E. V., STEPANOVA, L. A. & KOS, M. S. (1991): Revision of the freshwater Calanoida of the U.S.S.R. Nauka, Zoological Institute, Academy of Sciences of the U.S.S.R., St. Petersburg. (In Russian; English abstract.)
- CHENGALATH, R. & SHIH, C.-T. (1994): Littoral freshwater copepods of northwestern North America: northern British Columbia. *Verh. int. Verein. theor. angew. Limnol.* **25**: 2421–2431.
- DODSON, S. (1994): Morphological analysis of Wisconsin (U.S.A.) species of the *Acanthocyclops vernalis* group (Copepoda: Cyclopoida). *J. crust. Biol.* **14**: 113–131.
- DUSSART, B. H. (1985): Le genre *Mesocyclops* (Crustacé, Copépode) en Amérique du Nord. *Can. J. Zool.* **63**: 961–964.
- DUSSART, B. H. & FERNANDO, C. H. (1990): A review of the taxonomy of five Ontario genera of freshwater cyclopoid Copepoda (Crustacea). *Can. J. Zool.* **68**: 2594–2604.
- EINSLER, U. (1992): Nordamerikanischen Arten der Gattungen *Eucyclops* und *Acanthocyclops* (Crustacea, Copepoda) aus alten Proben der Sammlung F. Kiefer. *Andrias* **9**: 195–210.
- EINSLER, U. (1993): Crustacea: Copepoda: Calanoida und Cyclopoida. Süßwasserfauna von Mitteleuropa **8**(4–1): 1–208.
- FREY, D. G. (1982): Questions concerning cosmopolitanism in Cladocera. *Arch. Hydrobiol.* **93**: 484–502.
- FREY, D. G. (1986): The non-cosmopolitanism of chydorid Cladocera; implications for biogeography and evolution. *Crust. Issues* **4**: 237–256.
- FREY, D. G. (1987): The taxonomy and biogeography of the Cladocera. *Hydrobiologia* **145**: 5–17.
- FREY, D. G. (1988): Separation of *Pleuroxus laevis* Sars, 1861 from two resembling species in North America: *Pleuroxus stramineus* Birge, 1879 and *Pleuroxus chiangi* n. sp. (Cladocera, Chydoridae). *Can. J. Zool.* **66**: 2534–2563.
- GALASSI, D. P. (1991): First record of *Diacyclops hypnicola* (Gurney, 1927) (Copepoda, Cyclopidae) from North America. *Crustaceana* **60**: 319–321.
- GRAETER, A. & CHAPPUIS, P. A. (1914): *Cyclops sensitivus* n. sp. *Zool. Anz.* **43**(11): 507–510.
- GURNEY, R. (1933): The British Fresh-water Copepoda. III. The Classification of the Cyclopoida and the Parasitic Forms Derived from Them. xxix + 384 pp., The Ray Society, London.
- HUTCHINSON, G. E. (1967): A Treatise on Limnology. II. Introduction to Lake Biology and the Limnoplankton. ix+1115 pp., John Wiley & Sons, New York.
- ISHIDA, T. (1992a): *Bryocamptus pacificus*, a new harpacticoid copepod (Crustacea) from Japan and the neighboring areas. *Bull. biogeogr. Soc. Japan* **47**: 77–81.
- ISHIDA, T. (1992b): Cyclopoid and harpacticoid copepods (Crustacea) from southeastern Alaska, U.S.A. - *Proc. biol. Soc. Wash.* **105**: 249–254.
- ISHIDA, T. (1993): *Attheyella yesoensis*, a new harpacticoid copepod (Crustacea) from Hokkaido, northern Japan. *Proc. Jap. Soc. Syst. Zool.* **49**: 13–19.
- KIEFER, F. (1935): Zwei seltene Ruderfußkrebse aus dem Grundwasser der oberrheinischen Tiefebene. *Verh. naturw. Ver. Karlsruhe* **31**: 131–136.
- KIEFER, F. (1957). Die Grundwasserfauna des Oberrheingebietes mit besonderer Berücksichtigung der Crustaceen. *Beitr. naturk. Forsch. SüdWdtl.* **16**: 65–91.
- KIEFER, F. (1964). Zur Kenntnis der subterranean Copepoden (Crustacea) Österreichs. *Ann. naturhistor. Mus. Wien* **67**: 477–485.
- LERUTH, R. (1939): La biologie du domain souterrain et la faune cavernicole de la Belgique. *Mém. Mus. r. Hist. nat. Belg.* **87**: 1–506.
- MARSH, C. D. (1910): A revision of the North American species of *Cyclops*. *Trans. Wis. Acad. Sci. Arts Lett.* **16**(2): 1067–1136.
- PESCE, G. L. & GALASSI, D. P. (1985): Due nuovi *Diacyclops* del complesso "languidoides" (Copepoda: Cyclopidae) di acque sotterranee di Sardegna e considerazioni sul significato evolutivo dell'antenna nei copepodi stigobionti. *Bol. Mus. civ. Stor. nat. Verona* **12**: 411–418.
- PETKOVSKI, T. K. (1984): Neue und seltene Copepoden (Crustacea) aus Jugoslawien. 2. *Acanthocyclops sensitivus* (GRAETER ET CHAPPUIS, 1914) aus dem Grundwasser vom Banat. *Acta Mus. maced. Sci. nat.* **17**(6/145): 135–164.
- POSPISIL, P. (1994): Die Grundwassercyclopiden (Crustacea, Copepoda) der Lobau in Wien (Österreich) – faunistische, taxonomische und ökologische Untersuchungen. *Dr. Phil. Diss., Univ. Vienna*. 220 pp.
- PRICE, J. L. (1958): Cryptic speciation in the *vernalis* group of Cyclopidae. *Can. J. Zool.* **36**: 285–303.
- REED, E. B. (1991): *Cyclops furcifer* (Claus, 1857) s.l. from Yukon Territory, Canada: new record for North America (Copepoda, Cyclopoida). *Crustaceana* **60**: 240–245.
- REED, E. B. (1994): *Arctodiaptomus novosibiricus* Kiefer, 1971 in Alaska and Northwest Territories, with notes on *A. arapahoensis* (Dodds, 1915) and a key to New World species of *Arctodiaptomus* (Copepoda: Calanoida). *Proc. biol. Soc. Wash.* **107**: 666–679.
- REED, E. B. (1995): *Cyclops kolensis alaskaensis* Lindberg, 1956, revisited (Copepoda: Cyclopoida). *J. crust. Biol.* **15**(2): 365–375.
- REID, J. W. (1992): Redescription of *Diacyclops nearcticus* (Kiefer, 1934) and description of four similar new congeners from North America, with comments on *D. crassicaudis* (G. O. Sars, 1863) and *D. crassicaudis* var. *brachycercus* (Kiefer, 1927) (Crustacea: Copepoda). *Can. J. Zool.* **70**: 1445–1469.
- REID, J. W. (1993): *Diacyclops virginianus*, a new species of Cyclopoida (Crustacea: Copepoda) from Goose Creek, Virginia. *Md Nat.* **37**(1–2): 36–45.
- REID, J. W. (1995): Redescription of *Parastenocaris brevipes*

- Kessler and description of a new species of *Parastenocaris* (Copepoda: Harpacticoida: Parastenocarididae) from the U.S.A. Can. J. Zool. **73**: 173-187.
- REID, J. W. & ISHIDA, T. (1996): Two new species of *Gulcamptus* (Crustacea: Copepoda: Harpacticoida) from North America. Jap. J. Limnol. **57**: 133-144.
- REID, J. W., REED, E. B., WARD, J. V., VOELZ, N. J. & STANFORD, J. A. (1991): *Diacyclops languidoides* (Lilljeborg, 1901) s.l. and *Acanthocyclops montana*, new species (Copepoda, Cyclopoida), from groundwater in Montana, USA. Hydrobiologia **218**: 133-149.
- ROCHA, C. E. F. (1994): New species of *Metacyclops* (Copepoda, Cyclopidae) from Brazil, with remarks on *M. campestris*. Zool. Scr. **23**: 133-146.
- SCHUSTER, G. A., BUTLER, R. S. & STANSBERRY, D. H. (1989): A survey of the unionids (Bivalvia: Unionidae) of Buck Creek, Pulaski County, Kentucky. Trans. Ky Acad. Sci. **50**: 79-85.
- SHIH, C.-T. & CHENGALATH, R. (1994): Freshwater littoral copepods of British Columbia and Alberta (Canada). Hydrobiologia **292/293**: 379-388.
- STOCK, J. H. (1993): Some remarkable distribution patterns in stygobiont Amphipoda. J. nat. Hist. **27**: 807-819.
- VAN DE VELDE, I. (1984a): Introduction of new identification characters in *Mesocyclops*, with African species as an example. Crustaceana, Suppl. **7**(2): 404-409.
- VAN DE VELDE, I. (1984b): Revision of the African species of the genus *Mesocyclops* Sars, 1914 (Copepoda: Cyclopidae). Hydrobiologia **109**: 3-66.
- VYSHKVA RTZEVA, N. V. (1994): *Senecella siberica* n. sp. and the position of the genus *Senecella* in Calanoida classification. Hydrobiologia **292/293**: 113-121.
- WÄGELE, J. W., VOELZ, N. J. & MCARTHUR, J. V. (1995): Older than the Atlantic Ocean: discovery of a fresh-water *Microcerberus* (Isopoda) in North America and erection of *Coxicerberus*, new genus. J. crust. Biol. **15**: 733-745.
- WILSON, C. B. (1932): The copepods of the Woods Hole region, Massachusetts. Bull. U.S. natn. Mus. **158**: 1-635, plates 1-40.
- YEATMAN, H. C. (1944): American cyclopoid copepods of the *viridis-vernalis* group, (including a description of *Cyclops carolinianus*, n.sp.). Am. Midl. Nat. **32**: 1-90.
- YEATMAN, H. C. (1959): Free-living Copepoda: Cyclopoida. Pp. 795-815 in: EDMONDSON, W. T. (ed.) Ward & Whipple's Fresh-water Biology. 2nd. ed. John Wiley & Sons, New York.

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