

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)

J. W. REID

Research Associate, Department of Invertebrate Zoology, NHB-163, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.

Received September 10, 1991

Accepted February 6, 1992

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.

Diacyclops nearcticus is redescribed from the type specimen, collected in Massachusetts, U.S.A. Four similar new congeners, some previously mistaken for *D. nearcticus*, are described from the U.S.A. and Canada. *Diacyclops harryi* n.sp. occurred in seeps, wells, an acid bog, a pitcher plant, and stream hyporheic zones in the District of Columbia, Maryland, New York, North Carolina, Pennsylvania, and Virginia. *Diacyclops chrisae* n.sp. was collected from the groundwater of Wye Island, Maryland, with a probable record from the hyporheic zone of a stream in Ontario. *Diacyclops sororum* n.sp. occurred in drift in streams in Virginia and Texas. *Diacyclops alabamensis* n.sp. was collected from a well in Alabama. A previous record of *D. nearcticus* from Missouri could not be confirmed. Some morphological details of the probable type specimens of *D. crassicaudis* var. *brachycercus* and of a specimen of *D. crassicaudis* s.str. from Saskatchewan are presented. North American records of *D. crassicaudis* s.str. and *D. crassicaudis* var. *brachycercus* are reviewed.

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.

On trouvera ici une nouvelle description de *Diacyclops nearcticus* basée sur un nouvel examen du spécimen type recueilli au Massachusetts, États-Unis. Quatre nouvelles espèces américaines et canadiennes semblables, certaines préalablement incluses dans *D. nearcticus*, sont également décrites. *Diacyclops harryi* n.sp. a été trouvé dans des eaux d'infiltration, des puits, une tourbière acide, une sarracénie et dans les zones hyporhéiques de ruisseaux, dans le District de Colombie, le Maryland, le New York, la Caroline du Nord, la Pennsylvanie et la Virginie. *Diacyclops chrisae* n.sp. a été recueilli dans une nappe d'eau souterraine dans l'île de Wye, Maryland, et des autres spécimens trouvés dans la zone hyporhéique d'un ruisseau d'Ontario appartient probablement aussi à cette espèce. *Diacyclops sororum* n.sp. a été recueilli dans la dérive, dans des ruisseaux de la Virginie et du Texas. *Diacyclops alabamensis* n.sp. a été trouvé dans un puits d'Alabama. Une mention de *D. nearcticus* au Missouri n'a pu être vérifiée. Certains détails morphologiques des spécimens types probables de *D. crassicaudis* var. *brachycercus* et d'un spécimen de *D. crassicaudis* s.str. de Saskatchewan sont présentés. Les échantillons nord-américains de *D. crassicaudis* s.str. et de *D. crassicaudis* var. *brachycercus* ont fait l'objet d'une révision.

[Traduit par la rédaction]

Introduction

In samples of copepods from Goose Creek, Virginia, collected by Dr. Margaret A. Palmer, there were three previously undescribed species. Two of these, *Diacyclops albus* and *Parastenocaris palmerae*, were described elsewhere (Reid 1992). A more complex problem of identification was presented by the third, a species of *Diacyclops* that greatly resembled existing descriptions of the North American congener *Diacyclops nearcticus* (Kiefer, 1934), but was clearly not the species historically taken to be *D. nearcticus*. The original description of *D. nearcticus* was based on a single female specimen collected in Massachusetts and held in the Friedrich Kiefer Copepod Collection in Germany (Franke 1989; Kiefer 1934). Kiefer's description, although adequate at the time for purposes of discrimination, was brief and incomplete. A detailed redescription by Yeatman (1943, 1944) was based on specimens from North Carolina and understandably did not include a comparison with the type specimen. The only other published figures of *D. nearcticus*, by Strayer (1989b) for material from New York, represented a species very similar to that described by Yeatman (1943). Since both Yeatman's material from North Carolina and the species from Virginia, although clearly representing different taxa, were congruent with most

points of Kiefer's description, the identity of the true *D. nearcticus* came into question.

The type specimen of *D. nearcticus* was obtained from the Kiefer Copepod Collection, now held at the Staatliches Museum für Naturkunde Karlsruhe, Germany. Fortunately the two slides on which the partly dissected type specimen is mounted are still mostly legible, although the medium (probably glycerin jelly) is cracked in numerous places. Three other slides listed in the Catalog of the Kiefer Collection (Franke 1989) as *D. nearcticus* contain females of *D. crassicaudis* var. *brachycercus* (Kiefer, 1927a), and are discussed herein also. The single type female of *D. nearcticus* therefore represents the only existing material of this taxon in the Kiefer Collection. Dr. Harry C. Yeatman provided a series of slides of cyclopoids identified as *D. nearcticus* from various localities, including two slides of the North Carolina specimens that he described in 1943. Other material identified as *D. nearcticus* was made available by Drs. Margaret Palmer, David Strayer, and D. Dudley Williams and Ms. Christine Hakenkamp. Additional specimens in the collections of the National Museum of Natural History, Smithsonian Institution (USNM), were also examined.

Upon comparison of the type specimen of *D. nearcticus*

with this material it was evident that the North Carolina specimens described by Yeatman (1943, 1944) did not represent the same taxon as Kiefer's species. Material in several other collections, especially from groundwater-related habitats, was found to be Yeatman's species. However, the specimens from Goose Creek are a third, distinct species. A specimen from the Neches River, Texas, attributable to this third species was included in the Yeatman slides. Material from Wye Island, Maryland, represents a fourth species, morphologically very similar to Yeatman's species. Specimens from Ontario could be assigned provisionally to this fourth species. A fifth species, collected from a well in Alabama, was also included in Yeatman's collection. This article redescribes *D. nearcticus* and describes the four similar species, summarizing available distribution and habitat data.

Historically there has been some question of the validity of several of the named species and subspecies of the *Diacyclops crassicaudis* complex. I provide notes on some morphological details of the specimens of *D. crassicaudis* var. *brachycercus* from the Kiefer Collection, and on a specimen from Saskatchewan referable to *D. crassicaudis* s.str. These are compared with some other North American populations and to European representations of the nominate species. North American records of the species-complex are listed.

Materials and methods

Specimens treated were fixed in formalin and transferred to 70% ethanol for long-term storage. For taxonomic description, I mounted the specimens temporarily in glycerin or lactic acid, or permanently in commercial polyvinyl lactophenol (PVL) medium with a little chlorazol black E added. Measurements were made of specimens in glycerin unless otherwise noted. Drawings were made at magnifications of 400 \times , 600 \times , or (using an oil-immersion lens) 1000 \times , by means of a Wild M50 microscope fitted with a drawing tube. Where available, information on mounting media and stains used for material from other collections is supplied.

Taxonomic account

- FAMILY Cyclopidae Burmeister, 1834
 GENUS *Diacyclops* Kiefer, 1927b, emend. Morton, 1985, Reid et al. 1989
Diacyclops nearcticus (Kiefer, 1934)
 Figs. 1–10

Synonymy

- Cyclops (Diacyclops) nearcticus* Kiefer, 1934: 270–271, Figs. 3, 4. Yeatman 1943: 27, 28, 30, 31, 35, Figs. 7, 8. Yeatman 1944 (partim): 1, 2, 5, 7, 56–58, Figs. 110, 111. Yeatman 1959 (partim): 807.
Cyclops nearcticus: Franke 1989: 119, 120. Pennak 1953 (partim): 398. Pennak 1963 (partim): 354, 359, Fig. 15. Pennak 1978 (partim): 404, 405, Fig. 281S. Pennak 1989 (partim): 426, 427, Fig. 10S.
Diacyclops nearcticus (partim): Dussart and Defaye 1985: 94. Franke 1989: 49. Hutchinson 1967: 626. Reid 1988a: 36; 1990: 174, 175. Strayer 1989a: 197, 198, 199, 201, 202, 205, Fig. 5, Table IV. Strayer 1989b: 279, 289, 290, Figs. 7f–7h.
 Non *Cyclops nearcticus*: Franke 1989: 101.
 Non *Diacyclops nearcticus*: Williams 1989: 198, 199, 202, 205, 206, Figs. 4, 6b.
 ?*Cyclops nearcticus*: Bunting 1973: 140.

MATERIAL: Type ♀, partly dissected on 2 slides, Mikropräparate 1895 and 1897, from Kiefer Copepod Collection, Staatliches Museum für Naturkunde Karlsruhe. Mikropräparat 1895 contains the cephalosome and the dissected antennules and swimming legs. Mikropräparat 1897 contains the urosome with 5th legs attached. Coll. G. E. Hutchinson, Guildler Pond, Berkshires, Massachusetts. Collection data were taken from the Catalog (Franke 1989), since the slide labels bear only the preparation numbers.

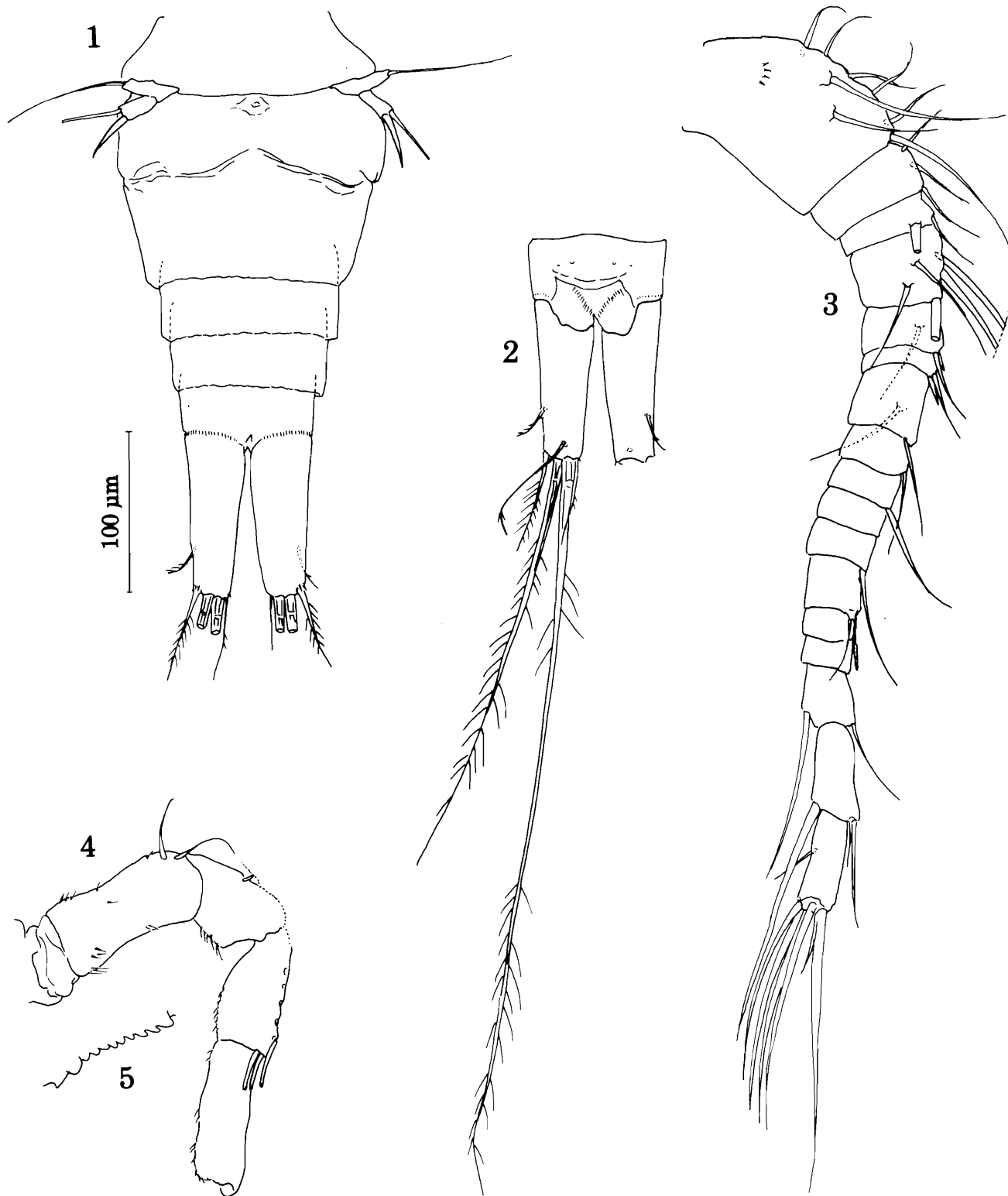
Female

Length (given by Kiefer 1934) 0.8 mm; length of dissected urosome 348 μ m. Lateral corners of pediger 5 (Fig. 1) flattened in mount, rounded, with no keel apparent. Genital segment flattened in mount, anterior half broadened. Details of seminal receptacle indistinct (as also to Kiefer 1934), lateral arms apparently nearly horizontal. Hyaline fringes of urosomites weakly crenulate. Posterior margin of anal somite (Figs. 1, 2) with tiny dorsal spines and larger ventral spines; anal operculum weakly crescentic. Caudal ramus somewhat flattened in mount, reported and figured by Kiefer (1934) as 4 times longer than broad, medial surface naked, lateral surface lacking "comb" or dorsoventral row of small spines present in many congeners. Caudal ramus with few small spines at bases of lateral and lateralmost terminal caudal setae. Lateral seta inserted at posterior 2/3 of caudal ramus. All caudal setae with fine homonomous plumage. Lengths of caudal setae (μ m): lateral 22, dorsal 65, lateralmost to medialmost terminal 52, 256, 444, 40.

Antennule (Fig. 3) of 17 articles, article 5 with small spine, article 6 with larger spine, article 12 with bladelike esthetasc, article 16 with hairlike sensillum; no hyaline membrane visible on distalmost articles. Antennule reaching posterior margin of cephalothorax (Kiefer 1934). Antenna (Fig. 4) lacking exopodite seta; caudal and frontal surfaces of article 1 partly obscured, visible ornament as in figure. Labrum (Fig. 5) with 11 blunt teeth. Remaining mouthparts obscured.

Swimming legs 1–4 (Figs. 6–9) each with triarticulate rami. Legs completely dissected, therefore identity of legs 2 and 3 uncertain. Terminal articles of exopodites with total of 2,3,3,3 spines and 4,4,4,4 setae, respectively. Endopodite article 1 of each leg with 1 seta. Endopodite article 2 of legs 1 and 4 each with 1 seta. Endopodite article 2 of either leg 2 or leg 3 with 2 setae, corresponding article of leg 3 or leg 2 with 1, more distal seta, similar to leg 3 of *D. sororum* (Fig. 51). Endopodite article 3 of legs 1–3 each with 5 setae and 1 spine; leg 4 endopodite 3 with 2 setae on medial margin, 2 terminal spines, and 1 spine on lateral margin. Basipodite of leg 1, medial expansion convex but little developed; spine on medial expansion naked, reaching at least distal margin of article 1, end of spine obscured by cracked medium. Medial expansions of basipodites of legs 2–4 sparsely haired, each with acute oblique process, basipodite of leg 4 less expanded medially than basipodites of legs 2 and 3. Couplers of all swimming legs naked. Leg 4 endopodite 1 medial wall thickened, slightly indented distally. Leg 4 endopodite article 3 about 1.52 times longer than broad, medial terminal spine about 1.52 times longer than lateral terminal spine (measurements from Kiefer 1934, confirmed on specimen); lateral spine and 2 medial setae all reaching past distal end of article.

Medial terminal spine of leg 5 (Figs. 1, 10) about 1.5 times longer than article 2. Both lateral terminal setae of article 2 broken. Lateral seta of article 1 about 2.3 times length of terminal spine.



Figs. 1–5. *Diacyclops nearcticus* (Kiefer, 1934), type female; Figs. 1 and 2: Kiefer Mikropreparat 1897; Figs. 3–5: Kiefer Mikropreparat 1895. Fig. 1. Urosome, ventral. Fig. 2. Anal somite and caudal rami, dorsal. Fig. 3. Antennule. Fig. 4. Antenna, caudal side. Fig. 5. Labrum. Scale bar applies to Fig. 1 only. Figs. 1–4 drawn at 600 \times ; Fig. 5 drawn at 1000 \times ; details of Figs. 3 and 4 confirmed at 1000 \times .

Male

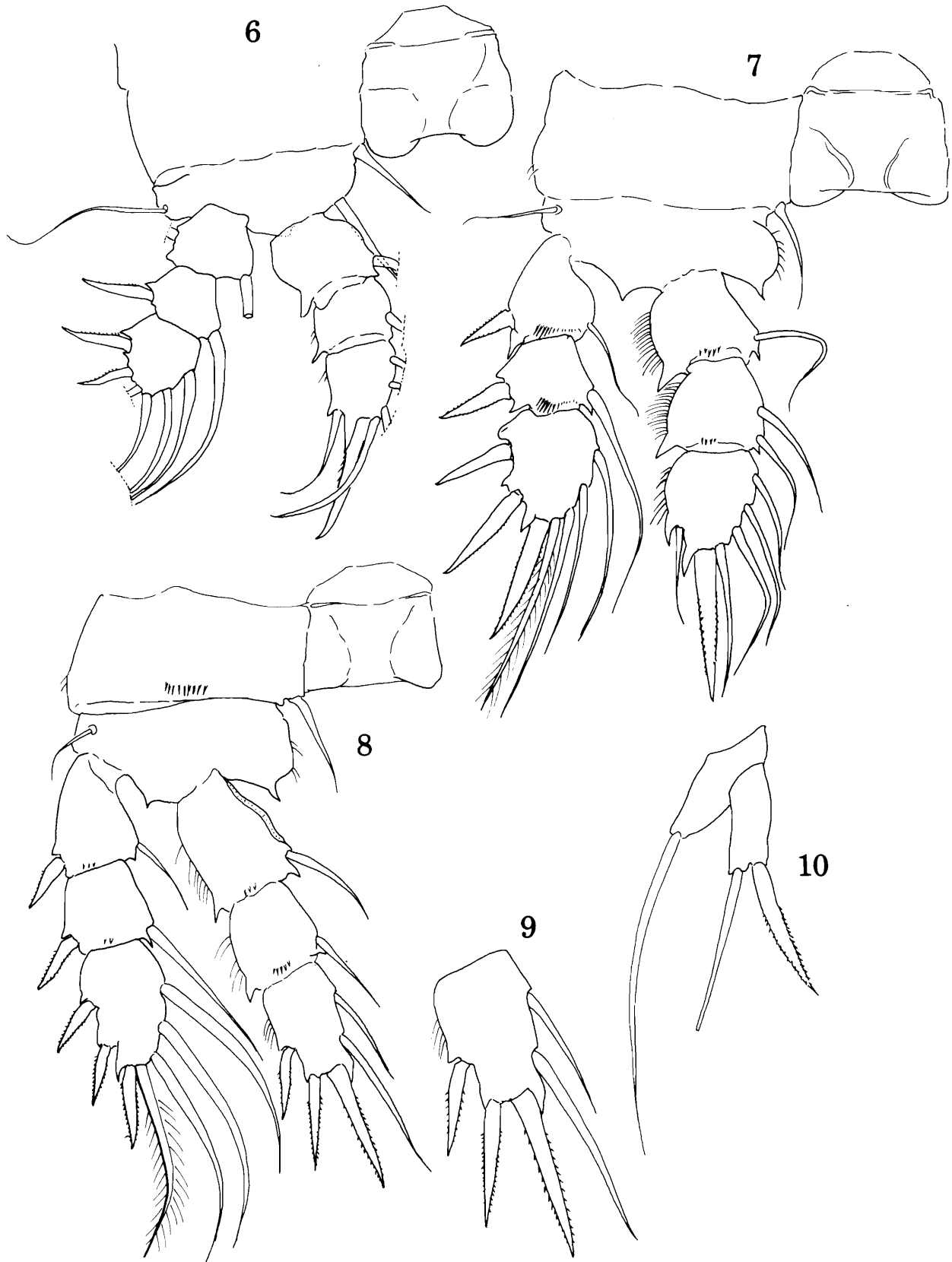
Unknown.

TYPE LOCALITY: Guilder Pond, Berkshires, Massachusetts.

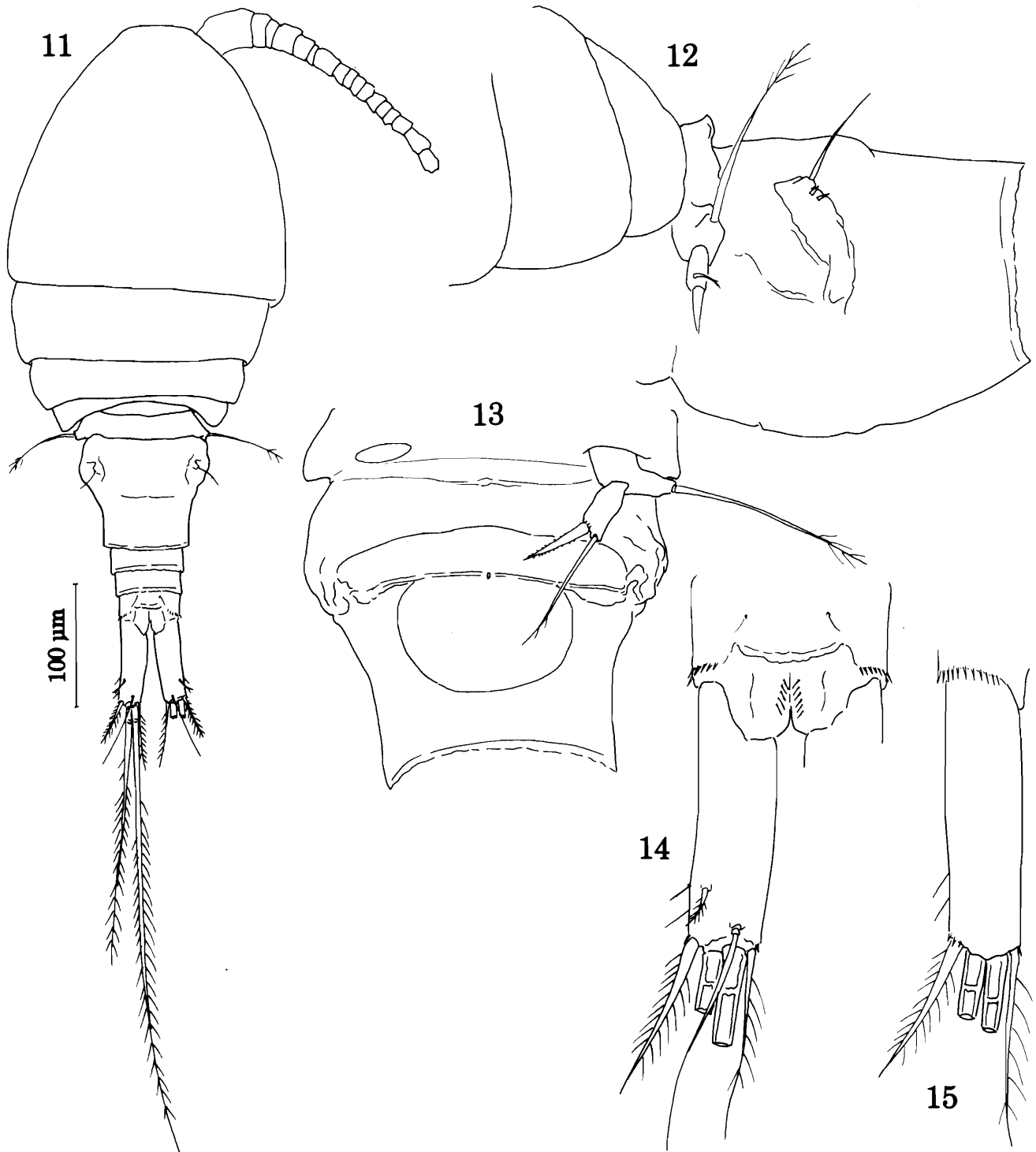
COMPARISONS: *Diacyclops nearcticus* and the four new congeners described herein are compared following the description of *D. alabamensis*.

Ecology and distribution

The only confirmed record of *D. nearcticus* remains that from the type locality, a pond. Dr. Dewey Bunting was unable to supply specimens to confirm his record from Missouri (Bunting 1973; D. L. Bunting, personal communication, 1991). The discovery of several congeners similar to *D. nearcticus* in North America renders this latter record doubtful.



FIGS. 6–10. *Diacyclops nearcticus* (Kiefer, 1934), type female, Kiefer Mikropräparat 1895. Fig. 6. Leg 1 and coupler, posterior (lengths of some setae obscured by drying of medium). Fig. 7. Leg 2 or leg 3 and coupler, posterior. Fig. 8. Leg 4 and coupler, posterior. Fig. 9. Leg 4 endopodite 3, enlarged. Fig. 10. Leg 5. Plumage of most setae of swimming legs is omitted. Figs. 6–9 drawn at 600 \times , details confirmed at 1000 \times ; Fig. 10 drawn at 1000 \times .



Figs. 11–15. *Diacyclops harryi* n.sp., holotype female, USNM 251271. Fig. 11. Habitus, dorsal. Fig. 12. Posterior prosome and anterior urosome, left lateral (spine and seta of article 2 of leg 5 foreshortened). Fig. 13. Pediger 5 and genital segment, ventral. Fig. 14. Anal somite and left caudal ramus, dorsal. Fig. 15. Right caudal ramus, ventral. Fig. 11 drawn at 400 \times ; Figs. 12–15 drawn at 600 \times .

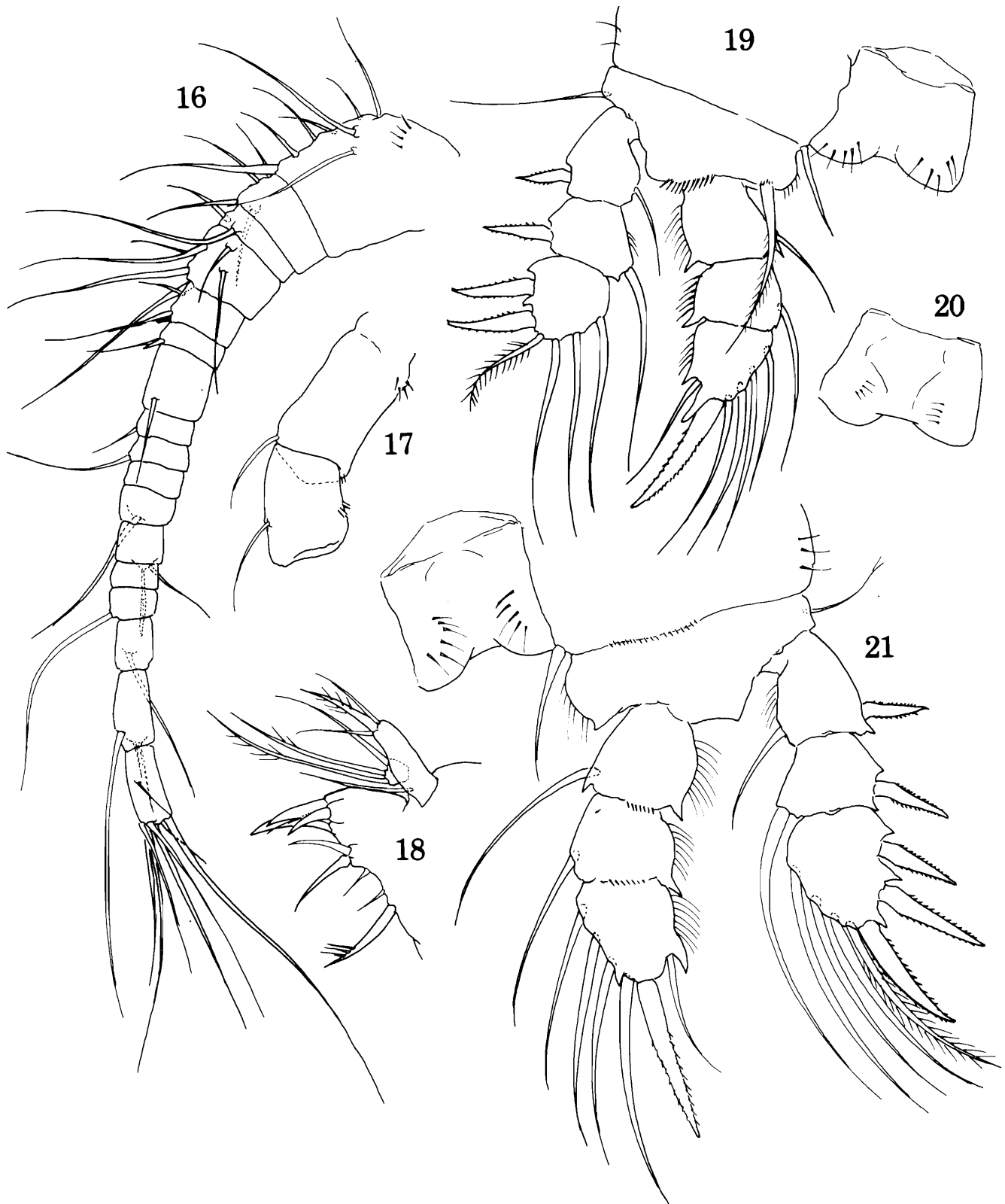
***Diacyclops harryi* n.sp.**
Figs. 11–25

Synonymy

Cyclops (Diacyclops) nearcticus (partim): Yeatman 1943: 27, 28, 30, 31, 35, Figs. 1–6. Yeatman 1944: 1, 2, 5, 7, 56–58, Figs. 110, 111. Yeatman 1959: 807.

Cyclops nearcticus (partim): Pennak 1953: 398; 1963: 354, 359; 1978: 404, 405, Fig. 281S; 1989: 426, 427, Fig. 10S. Yeatman 1964: 98.

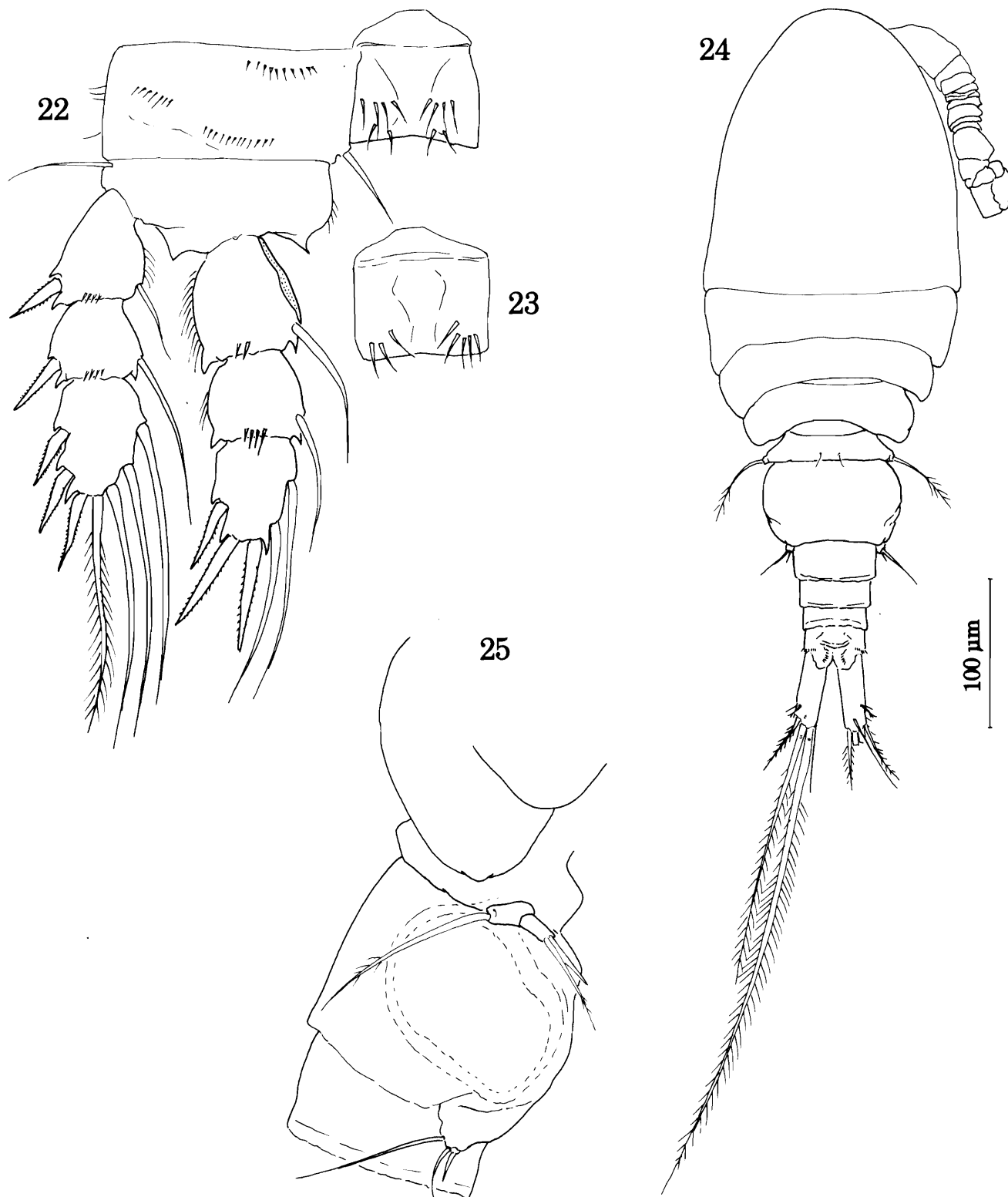
Diacyclops nearcticus (partim): Dussart and Defaye 1985: 94. Hutchinson 1967: 626. Reid 1988a: 36; 1990: 174, 175. Strayer 1989a: 197, 198, 199, 201, 202, 205, Fig. 5, Table IV; 1989b: 279, 289, 290, Figs. 7f–7h.



FIGS. 16–21. *Diacyclops harryi* n.sp. Figs. 16 and 18–21: holotype female, USNM 251271; Fig. 17: female from Gardener's Spring, Maryland, USNM 241930. Fig. 16. Antennule. Fig. 17. Antenna articles 1 and 2, frontal side. Fig. 18. Maxillule. Fig. 19. Leg 1 and coupler, anterior. Fig. 20. Leg 1 coupler, posterior. Fig. 21. Leg 2, anterior. Figs. 16 and 18–21 drawn at 600 \times and details confirmed at 1000 \times ; Fig. 17 drawn at 1000 \times .

MATERIAL: Holotype ♀, USNM 251271; allotype ♂, USNM 251272; each dissected on 1 slide in PVL; paratypes, 9 ♀♀, 14 ♂♂ and 22 copepodids, alcohol preserved, USNM 251270; all from center of Oxon Run Bog, a *Sphag-*

num bog in U.S. Reservation 501, Oxon Run Parkway, SE District of Columbia, 38°48'09"N, 76°58'44"W, 17 June 1991, coll. S. Syphax and A. Veiga. Additional paratypes: 1 ♀, 2 ♂♂ and 2 copepodids, Oxon Run Bog, 4 November



Figs. 22–25. *Diacyclops harryi* n.sp. Figs. 22 and 23: holotype female, USNM 251271; Figs. 24 and 25: allotype male, USNM 251272. Fig. 22. Leg 4 and coupler, posterior. Fig. 23. Leg 4 coupler, anterior. Fig. 24. Habitus, dorsal. Fig. 25. Posterior prosome and anterior urosome, right lateral. Scale applies to Fig. 24 only. Figs. 22, 23, and 25 drawn at 600 \times ; Fig. 24 drawn at 400 \times ; details of Figs. 22 and 23 confirmed at 1000 \times .

1988, coll. S. Syphax, USNM 241931 (reported as *D. nearcticus* by Reid 1990).

Additional, non-paratype material: 2 ♀♀, each partly dissected on 1 slide in glycerin jelly; and 1 ♀ and 2 copepodids, each partly dissected on 1 slide in glycerin jelly, USNM

251294; all from Well Station No. 3, shallow dug well, 1.5 mi (1 mi = 1.609 km) north of Farrington, Chatham County, North Carolina, 25 November 1942, coll. and prep. H. C. Yeatman (reported as *D. nearcticus* by Yeatman 1943, 1944). 2 ♀♀ and 1 ♂, each dissected on 1 slide in PVL, Gardener's

TABLE 1. Measurements of *Diacyclops harryi* n.sp.

| | | N | Range | Mean | SE | CV |
|---------------|--------|----|---------|------|-----|------|
| Total length | ♀ | 10 | 516–568 | 548 | 4.9 | 2.8 |
| | ♂ | 10 | 436–492 | 466 | 6.7 | 4.5 |
| Ramus | | | | | | |
| | Length | ♀ | 63–73 | 71 | 0.9 | 4.3 |
| | ♂ | 10 | 49–66 | 55 | 1.4 | 8.3 |
| Breadth | ♀ | 10 | 18–21 | 19 | 0.4 | 6.1 |
| | ♂ | 10 | 16–17 | 16.5 | 0.2 | 3.2 |
| Seta 1 | ♀ | 10 | 38–53 | 43 | 1.5 | 11.4 |
| | ♂ | 10 | 35–48 | 41 | 1.1 | 9.0 |
| Seta 2 | ♀ | 9 | 320–392 | 353 | 7.2 | 6.1 |
| | ♂ | 10 | 268–364 | 328 | 9.7 | 9.4 |
| Seta 3 | ♀ | 9 | 198–224 | 210 | 2.9 | 4.1 |
| | ♂ | 10 | 148–208 | 185 | 5.4 | 9.2 |
| Seta 4 | ♀ | 10 | 31–50 | 40 | 1.9 | 15.1 |
| | ♂ | 10 | 31–36 | 33 | 0.6 | 5.7 |
| Dorsal seta | ♀ | 10 | 59–75 | 66 | 1.4 | 6.5 |
| | ♂ | 10 | 47–63 | 53 | 1.5 | 9.1 |
| Insertion, ls | ♀ | 10 | 47–55 | 50 | 1.0 | 6.4 |
| | ♂ | 10 | 34–45 | 38 | 1.0 | 8.0 |
| P4 enp3 | | | | | | |
| | Length | ♀ | 24–28 | 26 | 0.5 | 6.2 |
| | ♂ | 10 | 20–24 | 22 | 0.5 | 7.1 |
| Breadth | ♀ | 10 | 21–23 | 22 | 0.2 | 3.1 |
| | ♂ | 10 | 17–19 | 18 | 0.2 | 3.1 |
| P4 enp3 | | | | | | |
| | MTS | ♀ | 25–33 | 29 | 0.8 | 9.5 |
| | ♂ | 10 | 23–28 | 25.5 | 0.5 | 6.5 |
| LTS | ♀ | 10 | 22–31 | 26 | 0.8 | 10.0 |
| | ♂ | 10 | 19–25 | 22 | 0.6 | 8.2 |

NOTE: Dimensions are given in micrometres. Measurements were made from type population from Oxon Run Bog, District of Columbia, 17 June 1991, USNM 251270-251272. P4enp3, leg 4 endopodite 3; insertion, ls, distance along outer margin of caudal ramus from anal somite to insertion of lateral seta; setae 1–4, medialmost terminal to lateralmost terminal setae, respectively; MTS, medial terminal spine; LTS, lateral terminal spine; SE, standard error of mean; CV, coefficient of variation.

Spring, U.S. Reservation 404M, Oxon Hill Farm, small brick pool near end of Woodlot Trail, Prince George's County, Maryland, 38°48'09"N, 77°00'22"W, 4 November 1988, coll. S. Syphax, USNM 241930 (reported as *D. nearcticus* by Reid 1990). 1 ♀, mounted whole on 1 slide, from *Sarracenia purpurea*, Bruce Lake, Promised Land State Park, Pennsylvania, 8 June 1972, coll. D. Fish, prep. H. C. Yeatman, USNM 251312. 1 ♀, 1 ♂, 2 copepodids, partly dissected in CMC on slide No. 54, hyporheic zone of Fishkill Creek at Brinckerhoff's Mills, town of Fishkill, Dutchess County, New York, 5 August 1985; 2 ♀♀, 2 copepodids, some partly dissected in CMC, on slide No. 109, hyporheic zone of Coxing Kill, town of Gardiner, Ulster County, New York, 14 November 1985; 2 ♀♀, 1 ♂, 5 copepodids, some partly dissected in CMC on 2 slides, both numbered 134, hyporheic zone of East Branch of Wappinger Creek, town of Washington, Dutchess County, New York, 25 March 1986; all from D. Strayer collection. 1 ♂ and 1 copepodid, on 1 slide in CMC, Coxing Kill, town of Gardiner, Ulster County, New York, 6 May 1986, coll. and prep. D. Strayer, USNM 236362 (all New York specimens were reported as *D. nearcticus* by Strayer 1989a, 1989b). 1 ♀, dissected on 1 slide, Weir Sample 21C, August 1989; 2 copepodids, Flume Sample 19 NF, 19 June 1990, all from Goose Creek, Virginia, collection of M. A. Palmer. All undissected specimens alcohol preserved.

Description

Dr. H. C. Yeatman donated to the USNM collections two of the slides upon which his description (Yeatman 1943) of *D. harryi* (as *D. nearcticus*) was based. These slides contain three females and one copepodid, each semi-dissected. The specimens are congruent in all respects with the material from other localities assigned to *D. harryi*, except for some mouthparts that cannot be seen clearly on the Yeatman slides. Since more than one specimen is dissected on each of the Yeatman slides, it is uncertain which parts belong together. For this reason and since a good series of specimens was obtained from a federally protected locality in the District of Columbia, these, rather than the North Carolina specimens, are designated the type population herein. The following description is based largely on the District of Columbia material.

Female

Length of holotype and 9 paratype specimens from the District of Columbia 516–568 µm; other body proportions as in Table 1. Length of North Carolina specimens 0.50–0.70 mm (Yeatman 1943). Specimens from New York and Pennsylvania mounted on slides, most partly dissected; measurements of these specimens not presented. Formalin-preserved specimens colorless, transparent. Prosomites (Fig. 11) rounded in dorsal view; in lateral view (Fig. 12), pediger 5 slightly keeled, naked. Genital segment (Figs. 11–13) slightly broader than long, anterior half broadened laterally and ventrally. Seminal receptacle with broad, nearly horizontal anterior expansion, rounded posterior expansion, and nearly horizontal lateral canals; pore canal small, short, not markedly sclerotized. Hyaline fringes of urosomites slightly crenulate. Anal somite (Figs. 11, 14, 15) with strong spines along nearly all of posterior margin, single row of spines on each side of anus, and slightly crescentic, little sclerotized anal operculum. Caudal ramus about 3.7 times longer than broad, medial surface naked, lateral surface usually with 1 or 2 very fine hairs at level of and posterior to lateral seta, otherwise naked, i.e., lacking lateral "comb" or dorsoventral row of small spines present in many congeners, and also lacking spines at bases of lateral and lateralmost terminal setae. Lateral seta inserted at posterior 7/10 of ramus. Dorsal seta with 1 basal articulation, naked, tapering to thin tip. Remaining caudal setae finely and homonomously plumose. Lengths of caudal setae of holotype (µm): lateral 13 (foreshortened in Fig. 14), dorsal 47, lateralmost to medialmost terminal 32, 200, 348, 35.

Antennule (Figs. 11, 16) of 17 articles, not reaching posterior margin of cephalothorax; articles 5 and 6 each with small spine, article 12 with narrow spatulate esthetasc, article 16 with hairlike sensillum, length of sensillum about 1/2 length of article 17. No hyaline membrane visible on distal-most articles of antennule. Antenna (Fig. 17) similar in proportions and ornament to antenna of *D. sororum* (Fig. 41), except lacking not only exopodite seta but also 1 of 2 setae on anterior distal margin, and with only 2 groups of spines on article 1. Mandible, maxilla, and maxilliped as corresponding structures of *D. sororum* (Figs. 44, 45, 47, 48). Maxillule as in Fig. 18, setae of palp long.

Swimming legs 1–4 (Figs. 19–23) all with triarticulate rami, form, ornament and setation of leg 3 identical with leg 2 (illustrated). Terminal articles of exopodites with total of 2,3,3,3 spines and 4,4,4,4 setae, respectively. Endopodites 1 and 2 of all legs each with 1 seta, endopodites 3 of legs 1–3 each with 5 setae and 1 spine. Leg 1 with basipodite little

expanded medially, bearing sparse hairs and slender spine, spine reaching midlength of endopodite article 3. Leg 1 coupler with groups of slender spines on anterior and posterior surfaces; legs 2 and 3 couplers with slender spines on anterior surface only; and leg 4 coupler with groups of broad spines on anterior and posterior surfaces. Leg 4 endopodite 1, medial wall thickened, slightly indented proximally. Leg 4 endopodite 3 about 1.18 times longer than broad, bearing 2 setae on medial margin, 1 spine on lateral margin, and 2 spines on distal margin, distomedial spine always slightly (about 1.1 times) longer than distolateral spine.

Leg 5 (Figs. 12, 13), proximal article with large lateral expansion bearing slender, sparsely plumed seta; distal article bearing subterminal medial spine slightly longer than length of article, and slender, sparsely plumed terminal seta. Leg 6 (Fig. 12) consisting of small flap bearing slender dorsal seta and 2 small spines.

One or 2 fine lateral hairs present on caudal rami of 8 of 10 females examined from type population. Similar hairs visible on female specimen from Goose Creek and on some slide-mounted specimens from North Carolina and New York populations. Estimation of proportion of specimens with these hairs not possible, since several specimens mounted unfavorably. Distal groups of spines on posterior surface of leg 4 coupler (Fig. 22) not present in some female specimens.

Male

Length of allotype and 9 paratype specimens 436–492 μm ; other dimensions as in Table 1. Habitus (Fig. 24), caudal rami, antenna, mouthparts, swimming legs, and leg 5 similar to corresponding structures of female. Antennule (Fig. 24) reaching posterior margin of cephalosome, geniculate, of 17 articles, similar in armament to that of *D. albus* Reid, 1992). Leg 6 (Fig. 25) consisting of small subtriangular flap bearing small ventral spine and 2 dorsal setae, both setae reaching past posterior margin of succeeding somite.

Fine lateral hairs present on caudal rami of 12 of 15 males examined from type population.

TYPE LOCALITY: Oxon Run Bog, U.S. Reservation 501, Oxon Run Parkway, SE District of Columbia.

ETYMOLOGY: The species appellation recognizes Harry C. Yeatman's first description of this species. It is a pleasure to pay a modest tribute to Dr. Yeatman's manifold contributions to the study of North American copepods, through both his own work and his unstinting support of the efforts of many colleagues and students for nearly half a century.

Ecology

Yeatman (1943) first recorded *D. harryi*, as *Cyclops (Diacyclops) nearcticus*, from a shallow dug well, pH 5.8, in North Carolina. The type locality in the District of Columbia is a *Sphagnum* bog, with a small area of open water in the center at the time of collection, water temperature 23°C, conductance 135 $\mu\text{S} \cdot \text{cm}^{-1}$, and pH 3.5. The record in the same collection series by Reid (1990, as *D. nearcticus*) from a spring and the record from the pitcher plant *Sarracenia* in Pennsylvania indicate similar groundwater-related habitats. Records from hyporheic zones of streams include those by Strayer (1989a, 1989b) as *D. nearcticus* from New York and the previously unpublished record herein from the hyporheic zone of Goose Creek, Virginia. As Strayer (1989a, 1989b) concluded, *D. harryi* seems to be a typically but not exclusively subterranean species. It is widespread in groundwater-related

TABLE 2. Measurements of *Diacyclops chrisae* n.sp.

| | | N | Range | Mean | SE | CV |
|---------------|--------|---|----------|-------|------|-----|
| Total length | ♀ | 4 | 644–736 | 680 | 19.7 | 5.8 |
| | ♂ | 2 | 512, 532 | 522 | | |
| Ramus | | | | | | |
| | Length | ♀ | 4 | 72–79 | 76 | 1.5 |
| Breadth | ♂ | 2 | 61, 62 | 61.5 | | |
| | ♀ | 4 | 19–21 | 20 | 0.4 | 4.1 |
| Seta 1 | ♂ | 2 | 18, 18 | 18 | | |
| | ♀ | 4 | 42–49 | 45.5 | 1.7 | 7.7 |
| Seta 2 | ♂ | 1 | 47 | 47 | | |
| | ♀ | 3 | 220–228 | 223 | 2.6 | 2.1 |
| Seta 3 | ♂ | 1 | 310 | 310 | | |
| | ♀ | 3 | 392–440 | 412 | 14.3 | 6.0 |
| Seta 4 | ♂ | 1 | 200 | 200 | | |
| | ♀ | 3 | 39–42 | 40.7 | 0.9 | 3.7 |
| Dorsal seta | ♂ | 2 | 35, 40 | 37.5 | | |
| | ♀ | 3 | 62–67 | 64.3 | 1.4 | 3.9 |
| Insertion, ls | ♂ | 1 | 53 | 53 | | |
| | ♀ | 4 | 50–55 | 53 | 1.2 | 4.6 |
| P4 enp3 | ♂ | 2 | 39, 43 | 41 | | |
| | ♀ | 4 | 23–23 | 23 | 0 | 0 |
| Breadth | ♂ | 2 | 22, 22 | 22 | | |
| | ♀ | 4 | 21–23 | 22 | 0.4 | 3.7 |
| P4 enp3 | ♂ | 2 | 18, 18 | 18 | | |
| | ♀ | 4 | 27–32 | 30.2 | 1.1 | 7.3 |
| MTS | ♂ | 2 | 25, 27 | 26 | | |
| | ♀ | 4 | 22–26 | 23.5 | 0.9 | 7.4 |
| LTS | ♂ | 2 | 22, 23 | 22.5 | | |

NOTE: Dimensions are given in micrometres. For explanation of abbreviations see Table 1. SE and CV were not calculated for males.

habitats in the eastern United States. The species is certainly tolerant of, but not restricted to, acid waters.

Diacyclops chrisae n.sp. Figs. 26–30

Synonymy

Diacyclops sp.: Hakenkamp 1991: 31, Table 2.

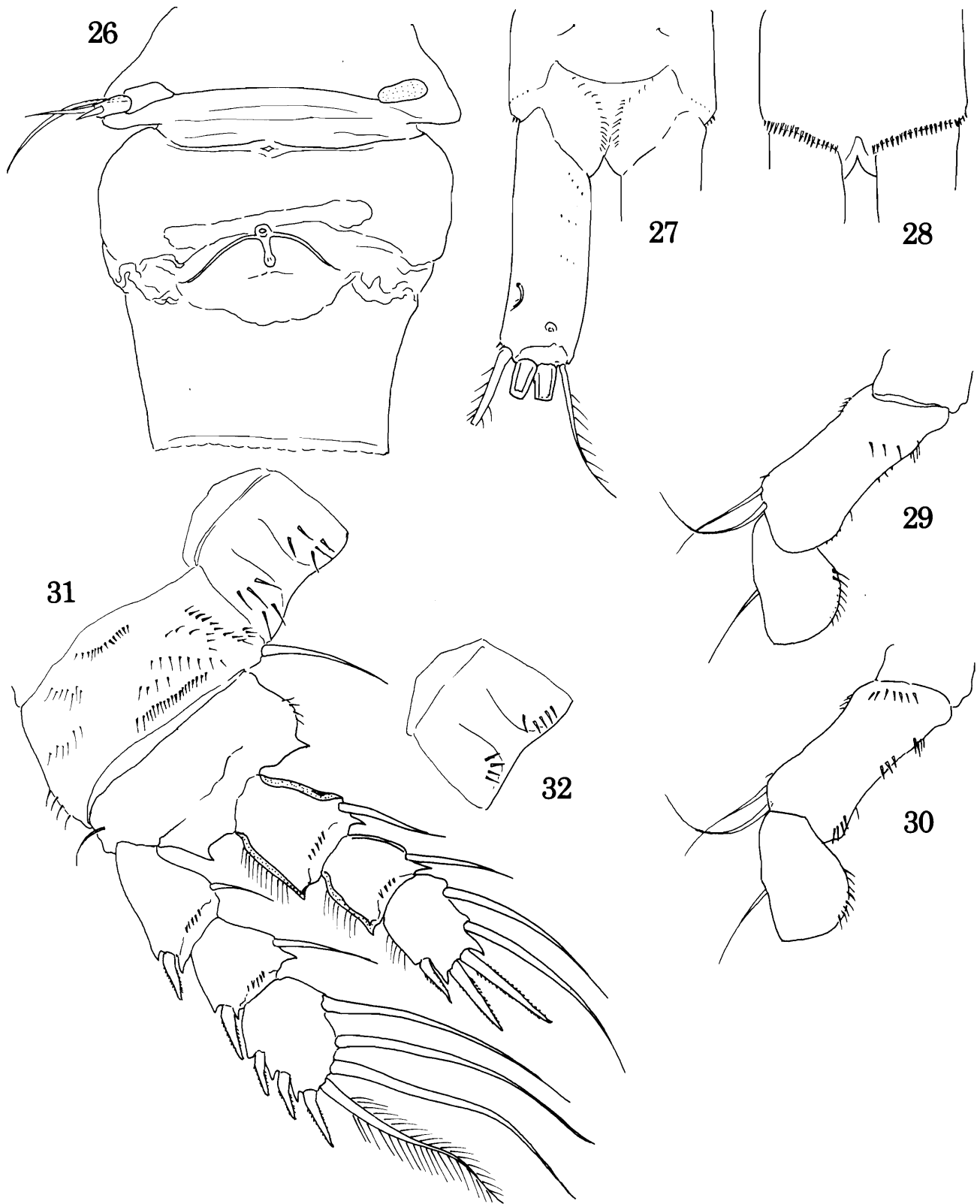
?*Diacyclops nearcticus*: Williams 1989: 198, 199, 202, 205, 206, Figs. 4, 6b.

MATERIAL: Holotype ♀, dissected on 1 slide in PVL, USNM 251284, September 1990; allotype ♂, USNM 251285, June 1990; paratypes: 1 ♀ (damaged), 13 copepodids, September 1990; 3 ♀♀, 1 ♀, 7 copepodids, June 1990, USNM 251286; all from driven well, Sample 1m Far, Intensive Sample Series, Wye Island, Queen Annes County, Maryland, 38°54'N, 76°08'W, coll. C. C. Hakenkamp. Undissected specimens alcohol preserved.

Additional, non-paratype material: specimens from Wye Island in collection of C. C. Hakenkamp. 1 ♂ (damaged), 1 copepodid, 1 nauplius, Sample -1m 30 cm 3; and 9 copepodids (dried), Sample 20 cm 1/ +2 m- Full core, both from Rouge River, Ontario, 27 July 1981, coll. D. D. Williams, USNM 251730.

Female

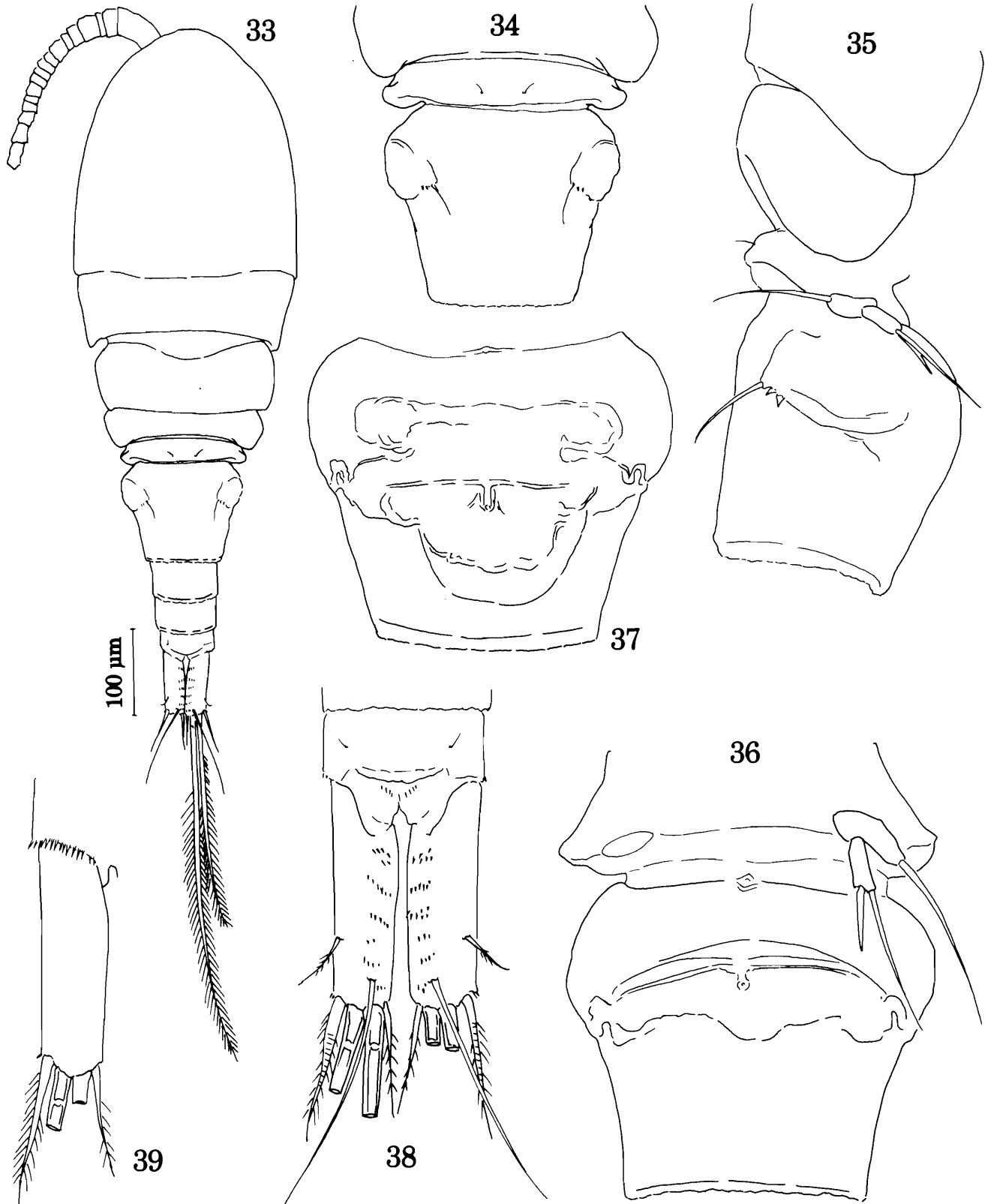
Length of holotype, measured in lactic acid, 672 μm ; range of lengths and other dimensions of holotype and three undamaged paratypes presented in Table 2. Habitus, antennule, mouthparts, legs 1–3 and leg 5 as described for *D. harryi*,



FIGS. 26–32. *Diacyclops chrisae* n.sp., holotype female, USNM 251284. Fig. 26. Pediger 5 and genital segment, ventral (leg 5 fore-shortened). Fig. 27. Anal somite and left caudal ramus, dorsal. Fig. 28. Anal somite, ventral. Fig. 29. Antennule articles 1 and 2, caudal side. Fig. 30. Antennule articles 1 and 2, frontal side. Fig. 31. Leg 4 and coupler, posterior. Fig. 32. Leg 4 coupler, anterior. All figures drawn at 600 \times , details confirmed at 1000 \times .

except pediger 5 without lateral keel. Seminal receptacle (Fig. 26) with anterior and posterior expansions little developed, lateral canals curved posteriorly, pore and pore canal large, sclerotized. Anal somite (Figs. 27, 28) with tiny spines

dorsally and larger spines ventrally along posterior margin. Anal operculum weakly crescentic, unsclerotized, margin smooth. Caudal ramus (Fig. 27) 4 times longer than broad, lateral seta inserted at posterior 2/3. Caudal ramus ornamented



Figs. 33–39. *Diacyclops sororum* n.sp. Figs. 33, 34, 35, and 37: paratype female, USNM 251283; Figs. 36, 38, and 39: holotype female, USNM 251281. Fig. 33. Habitus, dorsal. Fig. 34. Posterior prosome and genital segment, dorsal. Fig. 35. Posterior prosome and genital segment, right lateral. Fig. 36. Posterior prosome and genital segment, ventral. Fig. 37. Genital segment, ventral. Fig. 38. Anal somite and caudal rami, dorsal. Fig. 39. Right caudal ramus, ventral. Scale applies to Fig. 33 only. Fig. 33 drawn at 400 \times ; Figs. 34–39 drawn at 600 \times .

with 3 rows of tiny spines on dorsomedial surface, and few spines near base of lateralmost terminal seta; no spines at base of lateral seta. Most caudal setae of holotype missing or broken; length of medialmost terminal seta 42 μm .

Antenna (Figs. 29, 30) lacking exopodite seta but with 2 setae on anterodistal margin of article 1; frontal and caudal sides of article 1 each with several groups of small spines.

Leg 4 (Figs. 31, 32) with endopodite article 3, length 23 μm ,

breadth 21 μm , thus 1.1 times longer than broad; length of medial terminal spine 31 μm , length of lateral terminal spine 23 μm . Posterior surface of coxopodite with many rows of spines. Lateral and medial walls of endopodites 1 and 2 thickened, medial wall of endopodite 1 slightly indented distally.

Male

Length of allotype 532 μm , of paratype 512 μm ; other measurements presented in Table 2. Habitus, antennule, mouthparts, and legs 1–6 similar to *D. harryi*. Antenna with 2 setae on article 1 and ornament similar to antenna of female. Caudal ramus, like that of female, lacking lateral hairs; no spines visible on surface of caudal rami of either specimen.

Adult male specimen from Ontario slightly damaged, but visible morphological details congruent with paratypes of *D. chrisae*: no spines visible on surface of caudal ramus; antenna with 2 setae on article 1; number of spines and setae on legs 1–4 same as number in paratypes; leg 4 coupler with 2 rows of spines. Lateral terminal spine of leg 4 endopodite article 3 nearly as long as medial terminal spine, therefore relatively slightly longer than corresponding spine in types of *D. chrisae*.

TYPE LOCALITY: Wye Island, Queen Annes County, Maryland.

ETYMOLOGY: Named for the collector, Ms. Christine C. Hakenkamp.

Ecology

Diacyclops chrisae occurred in wells driven to sample the groundwater meiofauna of Wye Island. The following habitat data are abstracted from Hakenkamp (1991): salinities measured in the well water were 0.3–0.6‰ mean pH 4.87, and mean dissolved oxygen content 5.39 $\text{mg} \cdot \text{L}^{-1}$. The sediments consist of poorly sorted sands, median grain size about 400 μm , with little silt or clay content. The species never occurred in surface water adjacent to the locations of the wells (Hakenkamp 1991).

Diacyclops sororum n.sp.

Figs. 33–58

MATERIAL: Holotype ♀, dissected on 1 slide, Sample Weir 5C Time 2, Chamber, control, USNM 251281; allotype ♂, Sample U Cr, Drift, USNM 251282; paratypes: 2 ♀♀, 6 copepodids, Sample U Cr, Drift, USNM 251283; all from Goose Creek, Loudoun County, Virginia, 38°57'N, 77°45'W, August 1989, coll. M. A. Palmer.

Additional, non-paratype material: 1 ♀, mounted whole on 1 slide, Station I (river), Neches River, Orange Co., Texas, 20 January 1952; coll. R. J. Baldauf, prep. H. C. Yeatman, USNM 251295. Undissected specimens alcohol preserved.

Female

Length of holotype, excluding caudal setae, 780 μm ; range of lengths and other body dimensions of holotype and paratypes as in Table 3; length of mounted specimen from Texas 856 μm . Formalin-preserved specimens colorless, transparent. Prosomites (Figs. 33–36) in dorsal view with lateral margins rounded, except pediger 5 with lateral corners slightly keeled and upturned. Lateral margins of pedigers 3 and 4 (Fig. 35) without ornament and rounded except for shallow notch. Genital segment (Figs. 33–37) about as long as broad, anterior half broadened. Seminal receptacle little developed in holotype (Fig. 36), subquadrate in paratypes (Fig. 37), posterior expansion subtriangular, and lateral canals nearly horizontal; pore round, little sclerotized, pore canal short. Hyaline fringes

TABLE 3. Measurements of *Diacyclops sororum* n.sp.

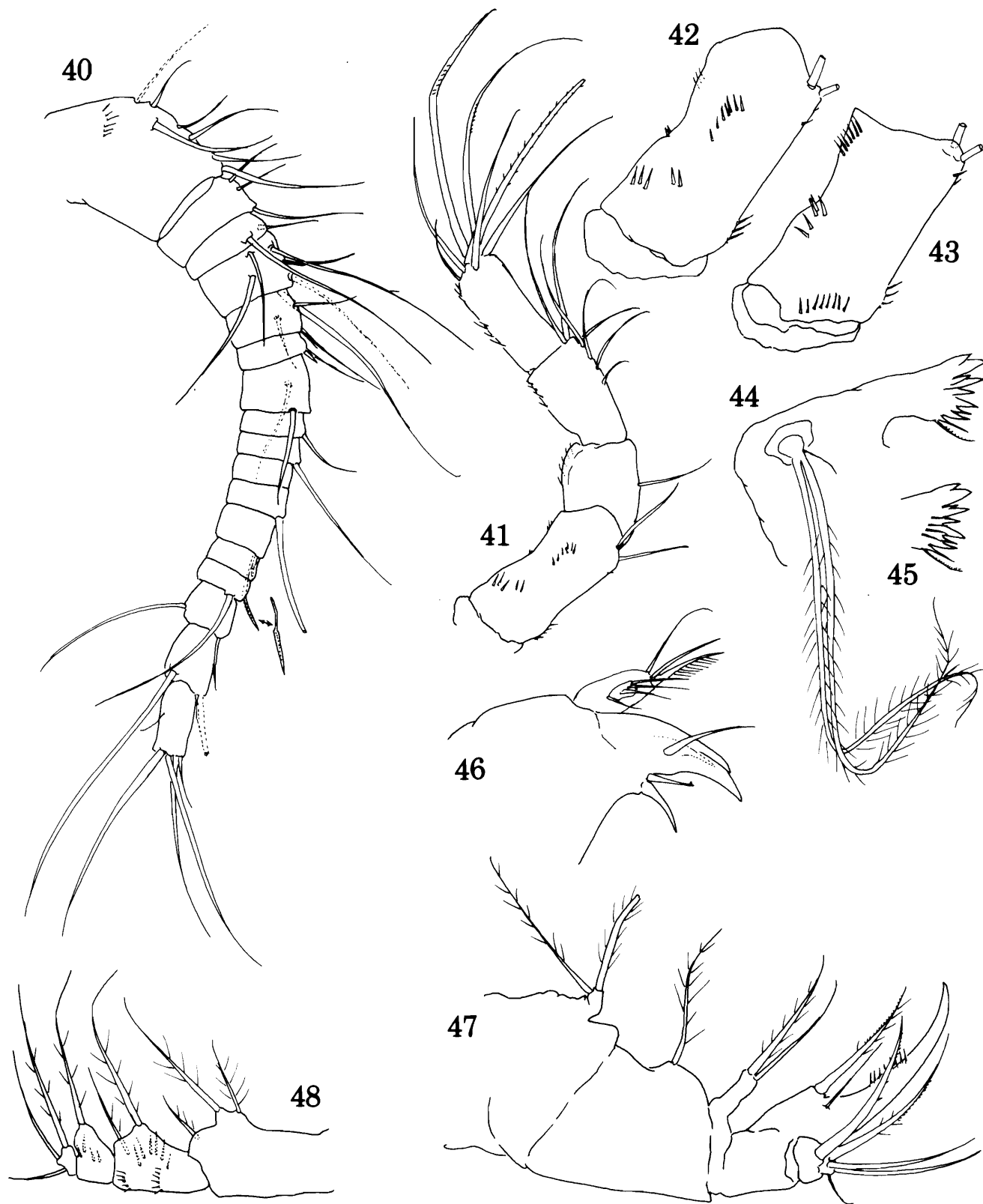
| | | N | Range | Median |
|---------------|--------|---|---------|--------|
| Total length | ♀ | 3 | 624–780 | 732 |
| | ♂ | 1 | 500 | |
| Ramus | | | | |
| | Length | ♀ | 72–80 | 78 |
| | ♂ | 1 | 54 | |
| Breadth | ♀ | 3 | 22–22 | 22 |
| | ♂ | 1 | 16 | |
| Seta 1 | ♀ | 3 | 33–35 | 34 |
| | ♂ | 1 | 28 | |
| Seta 2 | ♀ | 2 | 356–388 | 372 |
| | ♂ | 1 | 296 | |
| Seta 3 | ♀ | 3 | 228–256 | 240 |
| | ♂ | 1 | 172 | |
| Seta 4 | ♀ | 3 | 40–50 | 43 |
| | ♂ | 1 | 37 | |
| Dorsal seta | ♀ | 3 | 74–93 | 80 |
| | ♂ | 1 | 58 | |
| Insertion, ls | ♀ | 3 | 50–55 | 52 |
| | ♂ | 1 | 36 | |
| P4 enp3 | | | | |
| | Length | ♀ | 26–28 | 26 |
| | ♂ | 1 | 23 | |
| Breadth | ♀ | 3 | 21–22 | 21 |
| | ♂ | 1 | 16 | |
| P4 enp3 | | | | |
| | MTS | ♀ | 33–35 | 33 |
| | ♂ | 1 | 23 | |
| LTS | ♀ | 3 | 25–26 | 26 |
| | ♂ | 1 | 20 | |

NOTE: Dimensions are given in micrometres. For explanation of abbreviations see Table 1.

of urosomites weakly crenulate. Posterior margin of anal somite (Figs. 38, 39) without armament dorsally and with large spines laterally and ventrally; anal operculum weakly crescentic, unsclerotized, margin irregular. Caudal ramus (Figs. 38, 39) 3.6 times longer than broad, dorsomedial surface with 6 irregular diagonal rows or groups of small spines, lateral surface lacking “comb,” or dorsoventral row of small spines, present near proximal end of ramus in many congeners. Caudal ramus with small spines at base of lateralmost terminal seta, no spines at base of lateral seta. Lateral seta inserted at posterior 2/3 of ramus. Most caudal setae with fine homonomous plumage, except dorsal seta naked. Dorsal seta tapering to thin whiplike tip. Lengths of caudal setae of holotype (μm): lateral 8, dorsal 80, lateralmost terminal 40, next lateralmost terminal 256, next medialmost terminal broken, medialmost 33.

Antennule (Figs. 33, 40) of 17 articles, length of antennule about 2/3 length of cephalothorax; articles 5 and 6 each with spine, article 12 with esthetasc, article 16 with short hairlike sensillum; no hyaline membrane visible on distalmost articles. Antenna (Figs. 41–43) lacking exopodite seta, bearing 2 setae on distal margin of article 1; caudal and frontal surfaces of article 1 each with several rows of spines. Mandible (Figs. 44, 45) with row of hairs on pars incisiva. Palp of maxillule (Fig. 46) with short setae. Maxilla (Fig. 47) with short row of small teeth at midlength of claw. Maxilliped (Fig. 48) with 2 rows of spines on caudal margin of article 2 in addition to group of spines on frontal margin of same article.

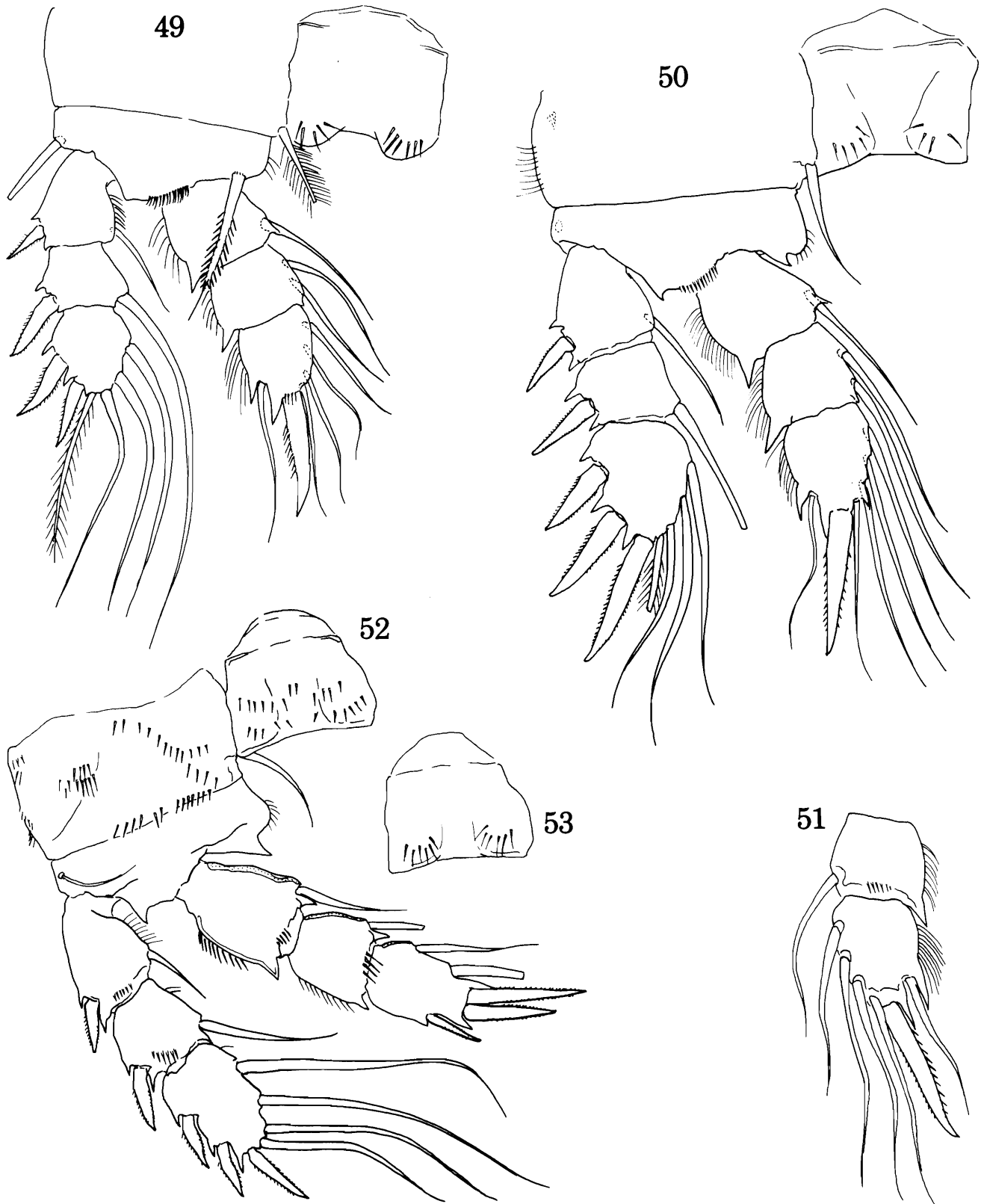
Swimming legs 1–4 (Figs. 49–53) each with triarticulate rami, terminal articles of exopodites with total of 2,3,3,3



Figs. 40–48. *Diacyclops sororum* n.sp., holotype female, USNM 251281. Fig. 40. Antennule. Fig. 41. Antenna, caudal side. Fig. 42. Antenna article 1, caudal side. Fig. 43. Antenna article 1, frontal side. Fig. 44. Mandible. Fig. 45. Pars incisiva of mandible, other side. Fig. 46. Maxillule. Fig. 47. Maxilla. Fig. 48. Maxilliped. Figs. 40, 41, and 44–48 drawn at 600 \times , details confirmed at 1000 \times ; Figs. 42 and 43 drawn at 1000 \times .

spines and 4,4,4,4 setae, respectively. Leg 1 endopodite 2 with 2 setae. Leg 3 identical with leg 2 except endopodite 2 of leg 2 with 2, corresponding article of leg 3 with 1 seta.

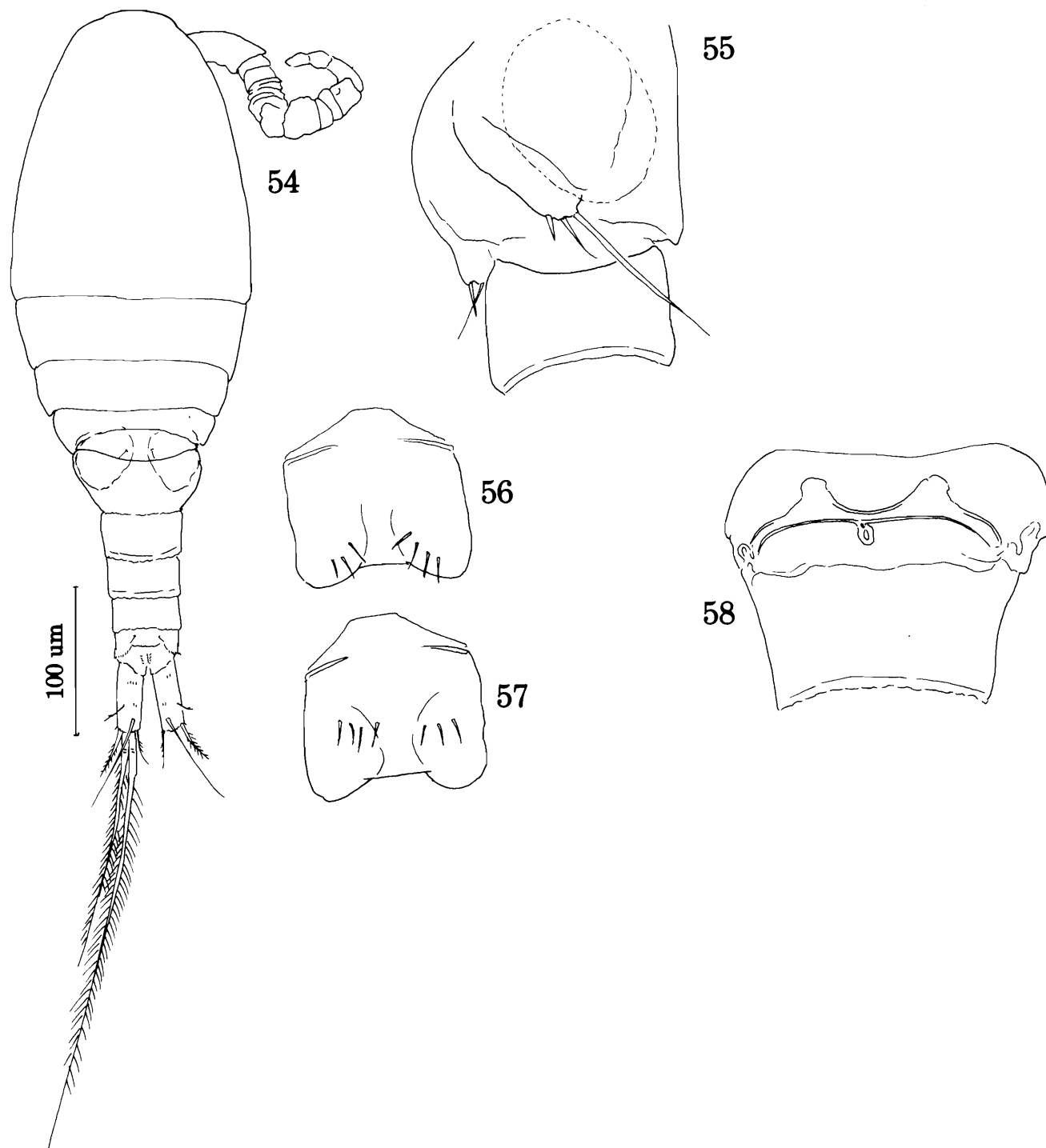
Medial expansion of leg 1 basipodite convex, bearing few hairs and spine, spine reaching past distal end of endopodite article 2, spine with short stiff spinules along middle 1/3 and



FIGS. 49–53. *Diacyclops sororum* n.sp., holotype female, USNM 251281. Fig. 49. Leg 1 and coupler, anterior. Fig. 50. Leg 2 and coupler, anterior. Fig. 51. Leg 3 endopodite articles 2 and 3, posterior. Fig. 52. Leg 4 and coupler, posterior. Fig. 53. Leg 4 coupler, anterior. All figures drawn at 600 \times ; details of Figs. 49, 50, 52, and 53 confirmed at 1000 \times .

thin hairlike tip. Medial expansions of basipodites of legs 2–4 each with acute medially directed process, expansion of basipodite of leg 4 more produced than those of legs 2 and 3. Couplers of legs 1–4 each with 2 groups of long slender

spines on anterior surface near distal margin; coupler of leg 4 additionally with 2 irregular divided rows of fine spines on posterior surface. Leg 4 endopodite, medial wall of article 1 thickened and distal 1/3 indented; medial walls of article 2 and



FIGS. 54–58. *Diacyclops sororum* n.sp. Figs. 54–57: allotype male, USNM 251282; Fig. 58: female from Neches River, Texas, USNM 251295. Fig. 54. Habitus, dorsal. Fig. 55. Anterior urosome, left lateral. Fig. 56. Leg 4 coupler, anterior. Fig. 57. Leg 4 coupler, posterior. Fig. 58. Genital segment, ventral. Scale applies to Fig. 54 only. Fig. 54 drawn at 400 \times ; Figs. 55–58 drawn at 600 \times .

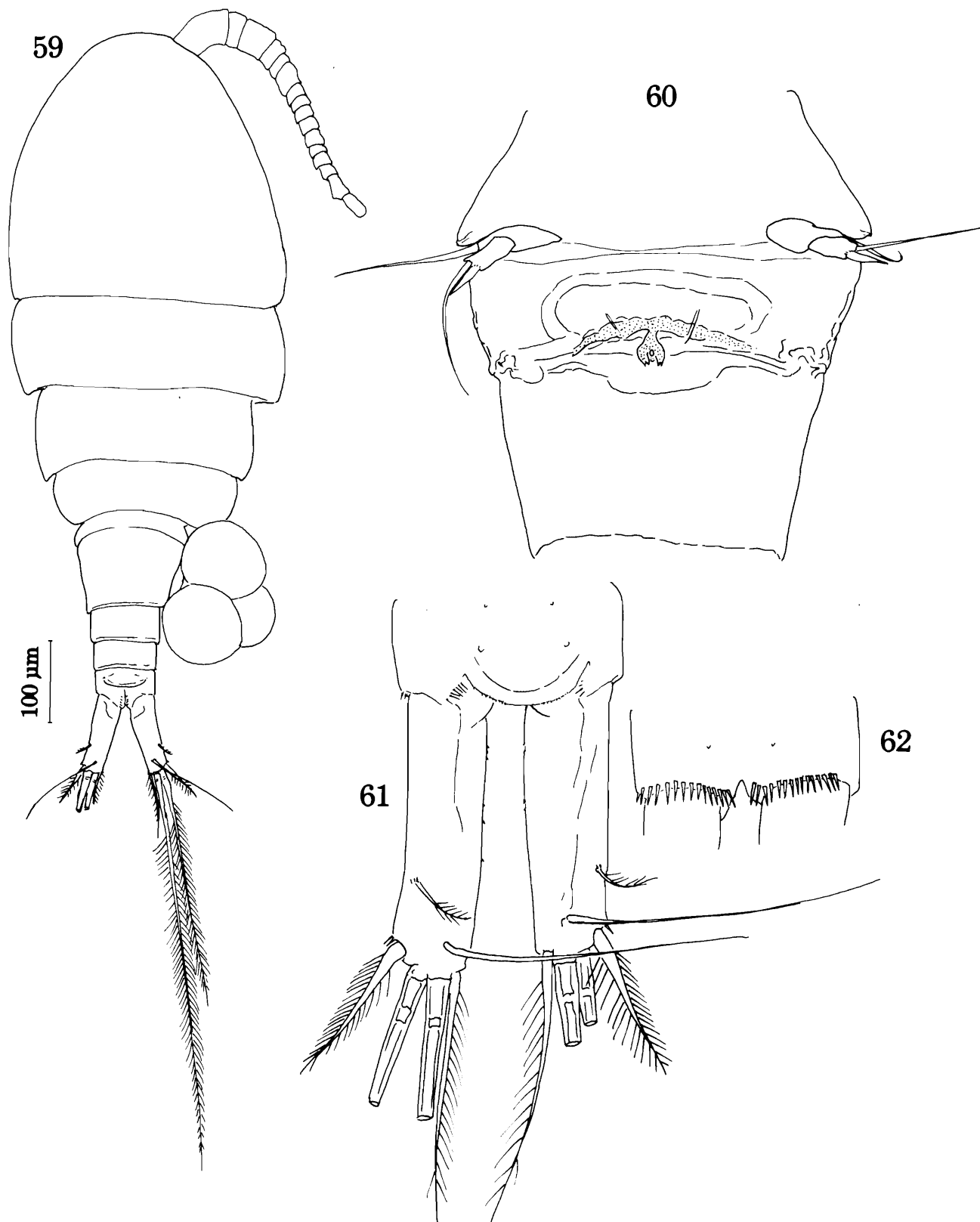
proximal part of article 3 also thickened. Leg 4 endopodite article 3 about 1.27 times longer than broad, with 2 terminal spines, medial terminal spine about 1.3 times longer than lateral terminal spine; this article also with lateral spine and 2 medial setae, all reaching past end of article.

Length of medial terminal spine of leg 5 (Figs. 35, 36) equal to or slightly greater than length of article 2 of leg.

Female specimen from Neches River partly disintegrated, apparently dead when caught, longest caudal setae broken. Specimen mounted whole with appendages down, base of

antenna, mouthparts, and legs 1–3 partly obscured. Medial-most terminal caudal seta slightly longer than lateralmost terminal caudal seta. Seminal receptacle (Fig. 58) with copulatory pore area slightly more sclerotized than in type specimens; anterior expansion of seminal receptacle extended in two diagonal "horns."

The shape of the seminal receptacle and relative lengths of caudal setae vary in other species of *Diacyclops* (Yeatman 1944). The individual from the Neches River is assigned to *D. sororum*, since it is congruent with the specimens from



Figs. 59–62. *Diacyclops alabamensis* n.sp. Fig. 59: holotype female, USNM 251296; Figs. 60–62: paratype female, USNM 251297. Fig. 59. Habitus, dorsal. Fig. 60. Legs 5 and genital segment, ventral (legs 5 slightly foreshortened). Fig. 61. Anal somite and caudal rami, dorsal. Fig. 62. Anal segment, ventral. Scale applies to Fig. 59 only. Fig. 59 drawn at 400 \times ; Figs. 60–62 drawn at 600 \times .

Virginia in the relative length and armament of the antennule, the major armament of the antenna, the setation of leg 4, the ornament of the legs 1–4 couplers, and the proportions and ornament of the caudal ramus.

Male

Length of allotype 500 μm ; other body dimensions as in Table 3. Habitus (Fig. 54), antenna, mouthparts, swimming legs, and leg 5 similar to female. Caudal ramus (Fig. 54) simi-

lar to female except with few tiny spines on surface, which are seen best with the aid of oil immersion. Antennule geniculate, apparently of 17 articles, armament similar to that of antennule of *D. albus* (Reid 1992). Swimming legs similar to those of female except leg 4 coupler (Figs. 56, 57) with only 1 row of slender spines on posterior surface. Leg 6 (Fig. 55) consisting of articulated flap bearing slender ventral spine and median and dorsal setae, dorsal seta reaching past end of succeeding urosomite.

ETYMOLOGY: From Latin *soror*, "sister," in appreciation of the cordiality of the sisters of Notre Dame Academy in permitting access to the study site in Goose Creek.

TYPE LOCALITY: Goose Creek, Loudoun County, Virginia.

Ecology

Goose Creek is a perennial fourth-order, low-gradient stream with a sandy bed. The annual temperature range is about 1–28°C, the mean pH is 7.48, and the mean dissolved oxygen content is 10.4 mg · L⁻¹ (data abstracted from Palmer 1990a, 1990b). The Neches River is a first-order stream draining the pine woodlands of east Texas. No specimens from Goose Creek were collected during intensive sampling of streambed sediments, the few specimens obtained occurring in weir and drift samples. The specimen from the Neches River assigned to *D. sororum* was also collected in drift. *Diacyclops sororum* is therefore unlikely to be a member of the streambed meiofaunal community, but more probably inhabits riparian wetlands.

Diacyclops alabamensis n.sp.

Figs. 59–73

MATERIAL: Holotype ♀, mounted whole in ventral aspect on 1 slide, USNM 251296; paratypes: 1 ♀, completely dissected, and 1 whole ♀, mounted together on 1 slide; 1 ♀ and 1 copepodid stage V ♂, mounted whole together on 1 slide; 1 ♀, completely dissected on 1 slide; 1 ♀, completely dissected on 1 slide; 3 ♂♂, mounted whole together on 1 slide, USNM 251297; all collected with plankton net from old, shallow (ca. 20 ft; 1 ft = 0.3048 m) hand-dug well near McGlendon Cave, 18 mi WSW of the center of Gadsden, St. Clair County, Alabama, 15 June 1967, coll. J. R. Holsinger, D. C. Culver, S. P. Peck, A. Budreau, and A. Fiske, prep. H. C. Yeatman. Specimens mounted in glycerin jelly, holotype unstained, paratypes heavily stained with rose bengal.

Female

Length of holotype 920 μm; lengths of undissected paratypes 744 and 960 μm; other measurements presented in Table 4. Prosomites (Fig. 59) rounded in dorsal view; pediger 5 with small lateral keel. Holotype bearing 3 eggs in lateral sac. Genital segment (Fig. 60, compressed in mount) slightly expanded laterally, seminal receptacle with posterior expansion little developed, pore, pore canal and lateral canals heavily sclerotized. Hyaline fringes of urosomites weakly crenulate. Anal somite (Figs. 61, 62) with no spines dorsally and large spines ventrally along posterior margin; anal operculum sclerotized, crescentic, with few tiny spines along posterior margin, anal operculum in paratypes extending to posterior margin of anal somite, in holotype slightly shorter. Caudal ramus (Figs. 59, 61) about 3.5 times longer than broad, medial surface with few tiny spines, lateral surface lacking "comb," with small spines at bases of lateral and lateralmost terminal setae. Lateral seta inserted at posterior 2/3 of ramus. Dorsal setae naked, tapering to thin hairlike tip, setae extending nearly laterally in all specimens. Remaining

TABLE 4. Measurements of *Diacyclops alabamensis* n.sp.

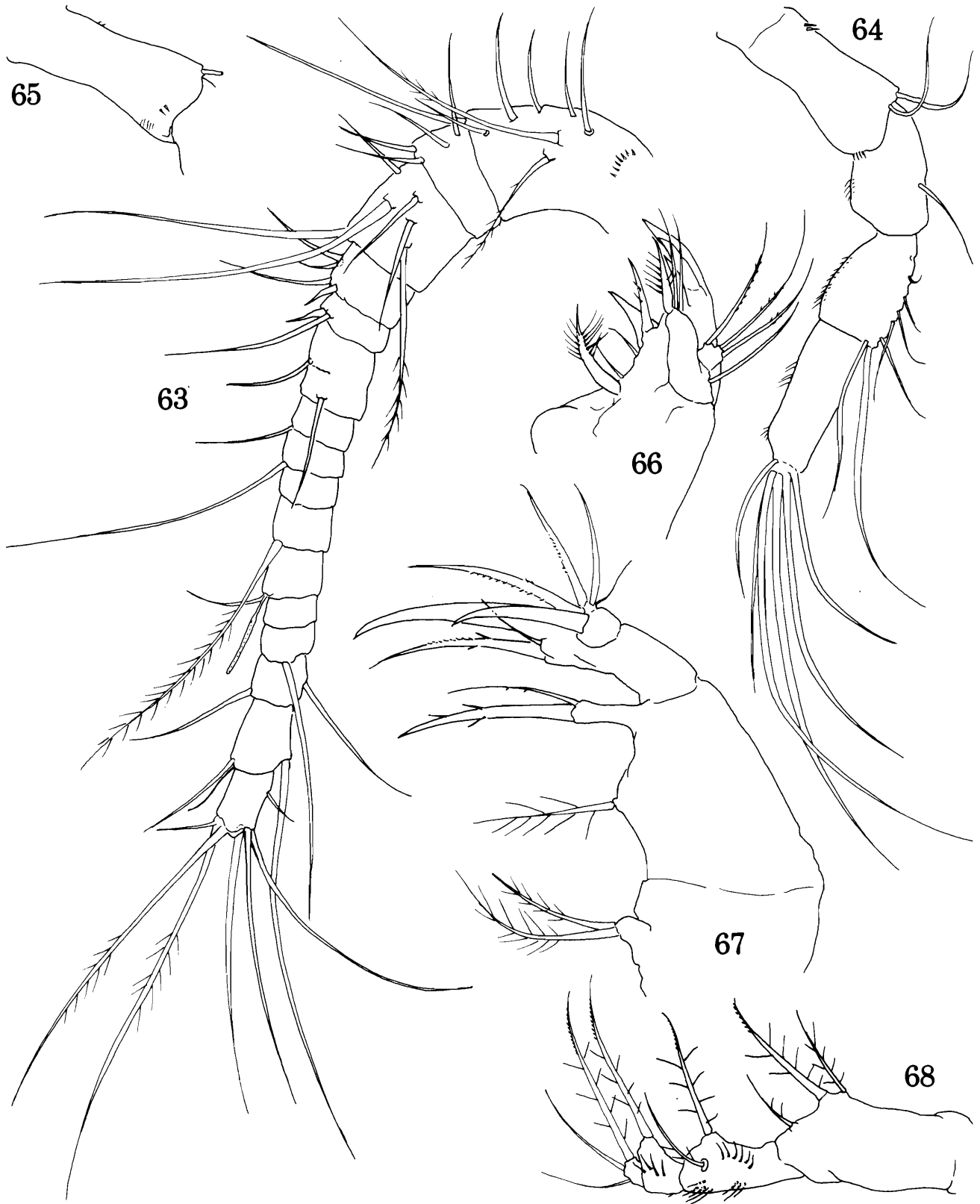
| | | N | Range | Mean | SE | CV |
|---------------|--------|---|---------|------|------|------|
| Total length | ♀ | 3 | 744–960 | 875 | 66 | 13 |
| | ♂ | 3 | 720–788 | 763 | 21.4 | 4.9 |
| Ramus | | | | | | |
| | Length | ♀ | 96–111 | 101 | 2.2 | 5.3 |
| | ♂ | 3 | 77–80 | 78 | 1.0 | 2.2 |
| Breadth | ♀ | 5 | 27–29 | 28 | 0.4 | 3.0 |
| | ♂ | 3 | 22–23 | 23 | 0.3 | 2.5 |
| Seta 1 | ♀ | 6 | 90–105 | 94 | 2.9 | 7.5 |
| | ♂ | 3 | 75–92 | 82 | 5.0 | 10.6 |
| Seta 2 | ♀ | 4 | 520–540 | 530 | 5.8 | 2.2 |
| | ♂ | 2 | 460–480 | 470 | 10.0 | 3.0 |
| Seta 3 | ♀ | 5 | 312–340 | 329 | 5.3 | 3.6 |
| | ♂ | 3 | 280–280 | 280 | 0 | 0 |
| Seta 4 | ♀ | 6 | 52–60 | 58 | 1.3 | 5.4 |
| | ♂ | 3 | 50–58 | 53 | 2.7 | 8.9 |
| Dorsal seta | ♀ | 6 | 90–120 | 105 | 5.0 | 11.7 |
| | ♂ | 3 | 78–87 | 83 | 2.7 | 5.7 |
| Insertion, ls | ♀ | 6 | 67–73 | 70 | 0.9 | 3.0 |
| | ♂ | 3 | 51–52 | 51 | 0.5 | 1.6 |
| P4 enp3 | | | | | | |
| | Length | ♀ | 45–50 | 47 | 0.8 | 4.2 |
| | ♂ | 3 | 35–41 | 38 | 1.7 | 8.0 |
| Breadth | ♀ | 5 | 28–33 | 30 | 0.9 | 6.7 |
| | ♂ | 3 | 23–28 | 25 | 1.4 | 9.9 |
| P4 enp3 | | | | | | |
| | MTS | ♀ | 34–38 | 35 | 0.6 | 4.2 |
| | ♂ | 3 | 30–31 | 30 | 0.3 | 1.9 |
| LTS | ♀ | 6 | 25–30 | 28 | 0.7 | 6.4 |
| | ♂ | 3 | 23–23 | 23 | 0 | 0 |

NOTE: Dimensions are given in micrometres. For explanation of abbreviations see Table 1.

caudal setae with fine homonomous plumage. Lengths of caudal setae of holotype (μm): lateral 28, dorsal 105, lateralmost to medialmost terminal 60, 324, 520, 85.

Antennule (Fig. 63) composed of 16 articles, former articles 3 and 4 fused, bearing together same number of setae as articles 3 and 4 of antennule of *D. nearcticus*. Articles 4 and 5 each with spine, article 6 with shallow groove at midlength, article 12 with spatulate esthetasc, article 15 with long hairlike sensillum. No hyaline membrane visible on distalmost articles. Antenna (Figs. 64, 65) lacking exopodite seta and with few groups of spines on article 1. Mandible similar to that of *D. sororum* except no hairs visible on pars incisiva of any specimen. Maxillule (Fig. 66) with long setae on palp. Maxilla (Fig. 67) lacking teeth on claw. Maxilliped (Fig. 68) with 2 rows of spines on caudal margin.

Swimming legs 1–4 (Figs. 69–72) with triarticulate rami; terminal articles of exopodites with total of 2,3,3,3 spines and 4,4,4,4 setae, respectively. Legs 1–4 endopodites 1 and 2 each with 1 seta. Exopodites of legs 2 and 3 similar to exopodite of leg 4 except lateral spines of legs 2 and 3 slightly stouter. Leg 2 similar to leg 3. Leg 1 with little-developed medial expansion of basipodite bearing few hairs and spine, spine reaching distal end of endopodite 2. Medial expansions of basipodites of legs 2–4 each haired, also with medially directed distal process forming deep notch. Couplers of legs 1–3 naked, coupler of leg 4 with 2 pairs of tiny spines on posterior surface. Leg 4 with lateral and medial walls thickened, medial wall indented along distal 1/2. Leg 4 endopodite 3 about 1.5 times longer than broad, bearing 2 medial setae, 2 terminal spines, medial terminal spine longer than lateral terminal spine, and 1 lateral spine.

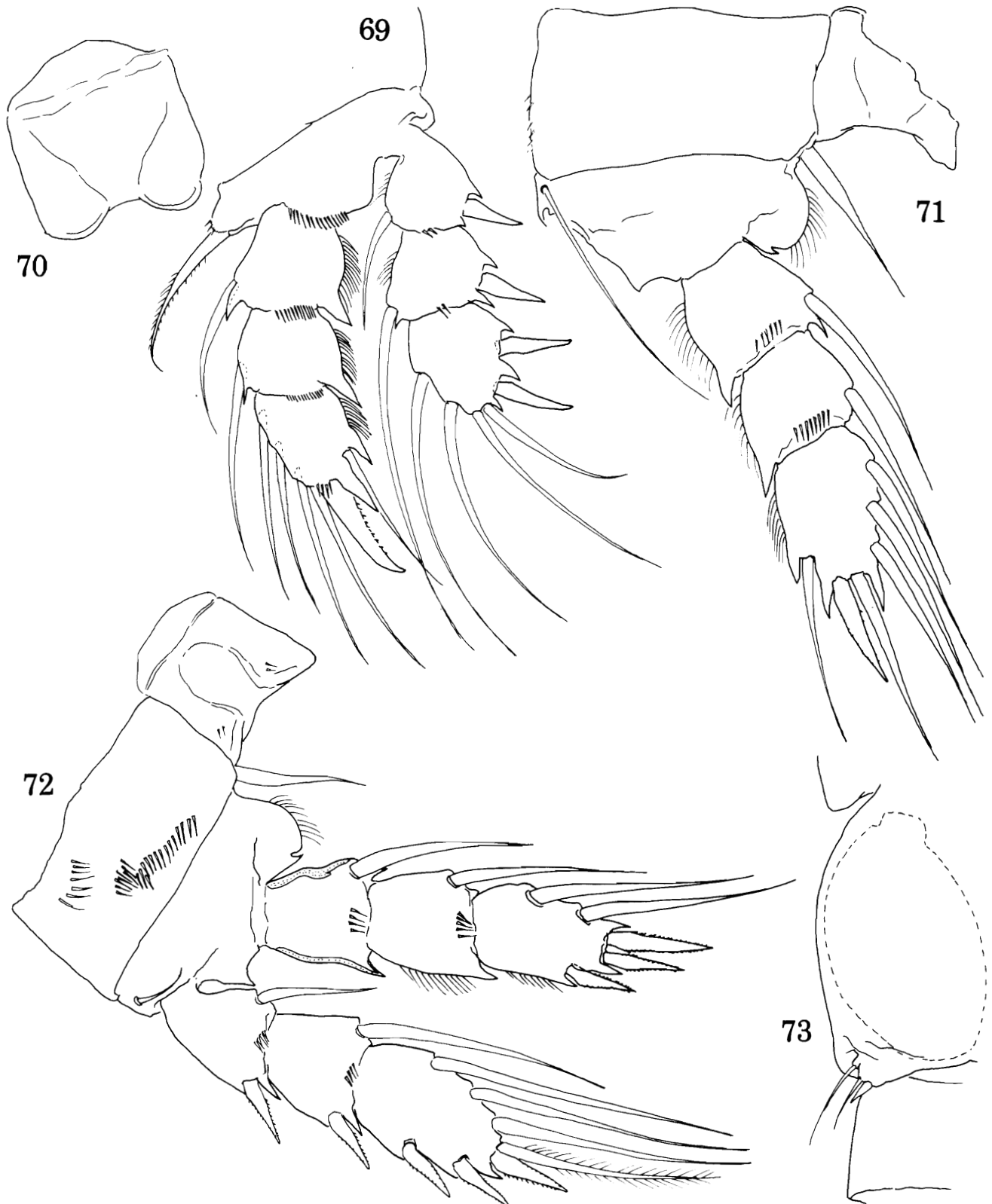


FIGS. 63–68. *Diacyclops alabamensis* n.sp. Fig. 63: holotype female, USNM 251296; Figs. 64–68: paratype female, USNM 251297. Fig. 63. Antennule. Fig. 64. Antenna, caudal side. Fig. 65. Antenna article 1, frontal side. Fig. 66. Maxillule. Fig. 67. Maxilla. Fig. 68. Maxilliped. All figures drawn at 600 \times .

Leg 5 (Fig. 60) with subterminal medial spine slightly shorter than article 2, and setae of articles 1 and 2 subequal in length. Leg 6 similar to that of *D. sororum*.

Male

Lengths of paratypes 720–788 μm . Male specimens mounted more or less in lateral position; few details visible. Habitus



FIGS. 69–73. *Diacyclops alabamensis* n.sp. FIGS. 69–72: paratype female, USNM 251297; FIG. 73: paratype male, USNM 251297. FIG. 69. Leg 1, anterior. FIG. 70. Leg 1 coupler, anterior. FIG. 71. Leg 3 coxo-basipodite, endopodite and coupler (broken), posterior. FIG. 72. Leg 4 and coupler, posterior. FIG. 73. Anterior urosome, left ventral. All figures drawn at 600 \times , details confirmed at 1000 \times .

and antennule similar to those of *D. sororum*. Leg 6 (Fig. 73), small subtriangular flap bearing 1 short medial spine and 2 short setae, neither seta reaching posterior margin of succeeding somite.

ETYMOLOGY: Named for the state where the specimens were collected.

TYPE LOCALITY: Well near McGlendon Cave, St. Clair County, Alabama.

TABLE 5. Principal characters distinguishing *Diacyclops nearcticus* and four similar congeners

| | A1 | A2 | CR spines | P1-4enp2 | P4 coupler |
|--------------------|----|----|-------------|-----------|------------|
| <i>alabamensis</i> | 16 | 2 | Few, tiny | 1,1,1,1 | Spines |
| <i>chrisae</i> | 17 | 2 | Few, tiny | 1,1,1,1 | Spines |
| <i>harryi</i> | 17 | 1 | None | 1,1,1,1 | Spines |
| <i>nearcticus</i> | 17 | 2 | None | 1,2?,1?,1 | Naked |
| <i>sororum</i> | 17 | 2 | Many, large | 2,2,1,1 | Spines |

NOTE: A1, number of articles in antennule; A2, total number of setae on antenna article 1; CR spines, spines on dorsomedial surface of caudal ramus; P1-4enp2, number of setae on medial margin of legs 1-4 endopodite 2 (*D. nearcticus* has 2 setae at this location on either leg 3 or leg 2, and 1 seta on leg 2 or leg 3).

Ecology

Known only from a well.

Comparisons

Diacyclops nearcticus and the four newly described species are similar in having the leg 4 endopodite article 3 moderately short, with 1 lateral and 2 terminal spines; the spine formula 2,3,3,3; and moderately long caudal rami. In addition, all species lack the exopodite seta of the antenna. The consistent presence of the lateral spine on the leg 4 endopodite 3 distinguishes this group of species from all known congeners. One European congener (*D. tantalus* Kiefer, 1937) shows in some populations a tendency for both medial and lateral setae on the distal articles of legs 3 and 4 to be spiniform (Stoch 1987). The armament of the leg 4 endopodite terminal article is not a completely reliable discriminating character, since loss of one of the distal spines on the leg 4 endopodite occurs occasionally in another European species, *D. balearicus* (Lescher-Moutoué 1978/1979). However, intrapopulational variation in these character-states was reported in both these species by Lescher-Moutoué (1978/1979) and Stoch (1987). No variation in the armament of any swimming leg was observed in the American species.

The principal characters distinguishing these five similar congeners are discussed in the following paragraphs and summarized in Table 5.

In the key of Reid (1988a) to North American *Diacyclops*, emended by Reid et al. (1989), *D. alabamensis* keys to *D. languidus* (G. O. Sars, 1863), since only these two species among North American congeners have the antennule composed of 16 articles. *Diacyclops languidus* has a seta, not a spine, on the lateral margin of the leg 4 endopodite article 3, and also differs from *D. alabamensis* in having both rami of leg 1 and the endopodite of leg 2 biarticulate rather than triarticulate.

The remaining four species have the antennule of the female composed of 17 articles. *Diacyclops sororum* is easily distinguished from the other three species by the several rows of prominent spines on the surface of the caudal ramus. The spines on the caudal ramus of *D. alabamensis* and *D. chrisae* are few and small, nearly invisible except with the oil-immersion lens. Two South American congeners have similar rows or groups of prominent spines on the caudal ramus. *Diacyclops hispidus* Reid, 1988b from Colombia differs in having only 3 groups of spines on the ramus and a lateral dorsoventral "comb" or row of spines on the anterior 1/4 of the ramus, the antenna with an exopodite seta, and a lateral seta rather than a spine on the leg 4 endopodite article 3. *Diacyclops uruguayensis* (Kiefer, 1935), described from Uruguay, has 5 or more rows of small spines on the caudal ramus, but in *D. uru-*

guayensis the caudal ramus is 4.4 times longer than broad, the anal operculum is quadrate and strongly sclerotized, and there is a lateral seta rather than a spine on the leg 4 endopodite article 3.

Diacyclops harryi has only 1 seta on the anterodistal margin of the antenna article 1, rather than the 2 setae present in *D. chrisae*, *D. nearcticus*, *D. sororum*, and most known congeners. Reduction from the normal 3 setae borne on the antenna article 1 is a common feature of species of *Diacyclops*. Such reduction also occurs in several other genera of Cyclopinae, more frequently in benthic and subterranean species (Pesce and Galassi 1985; Reid 1991). Of the five species treated here, one of the smallest, *D. harryi*, shows the most reduction in seta number, while the otherwise morphologically very similar *D. chrisae* has 1 more seta on the antenna.

Diacyclops harryi and *D. chrisae* differ from both *D. nearcticus* and *D. sororum* in having 1 seta on both leg 2 and leg 3 endopodite 2, while *D. sororum* has 2 setae on leg 2 endopodite 2, and *D. nearcticus* has 2 setae on either leg 2 or leg 3 endopodite 2. *Diacyclops sororum* has 2 setae on leg 2 endopodite 2, and is also the only species in this group to have 2 setae rather than 1 on leg 1 endopodite 2.

Diacyclops nearcticus lacks ornament on the couplers of the swimming legs, whereas *D. alabamensis*, *D. chrisae*, *D. harryi*, and *D. sororum* all have groups of spines on at least the coupler of leg 4.

Diacyclops harryi is widespread in groundwater-related habitats, its verified range extending from New York to North Carolina. *Diacyclops sororum*, possibly inhabiting riverine wetlands, occurs in Virginia and probably as far as Texas. The similarity between the type specimens of *D. chrisae* and the specimens from Ontario provisionally assigned to this species indicates that *D. chrisae* may also be widely distributed. Both remaining species are known from a single locality. The concentration of reported localities of these species in the eastern and southern United States and southeastern Canada is probably a consequence more of the historically intensive collecting efforts in groundwater-related habitats in the region, rather than of any biogeographic verity.

Diacyclops crassicaudis var. *brachycercus* (Kiefer, 1927a)
Figs. 74-81

Synonymy

Cyclops (*Diacyclops*) *crassicaudis brachycercus* Kiefer, 1927a: 262-264, Figs. 1, 2. Kiefer 1929: xiv, 61. Kiefer 1931: 610, 618. Reddell 1965: 157. Reddell and Mitchell 1969: 7. Yeatman 1944: 2, 5, 8, 16, 57, 60-63, Pl. 9 Figs. 114-121, Table 1. Yeatman 1959: 808.

Acanthocyclops crassicaudis: Pennak 1989: 425.

Acanthocyclops crassicaudis brachycercus: Damian-Georgescu 1963: 144, 145, Fig. 73j. Rylov 1948: 245-248.

Acanthocyclops crassicaudis forma *brachycercus*: Štěrba 1968: 222.

Acanthocyclops crassicaudis var. *brachycercus*: Mäemets and Veldre 1956: 21. Štěrba 1961: 824; 1962: 895. Veldre and Mäemets 1956: 47.

Cyclops bissextilis Willey, 1925: 141, 158, Pl. I Fig. 3. Kiefer 1931: 610, 618. Willey 1929: 529. Yeatman 1959: 808.

Cyclops crassicaudis: Pennak 1953: 398. Willey 1929: 529. *Cyclops* (*Acanthocyclops*) *crassicaudis*: Gurney 1933: 232-234, Figs. 1686-1696 (partim).

Cyclops (*Cyclops*) *crassicaudis*: Coker 1938: 77-79, 85, Figs. 1-13.

Cyclops crassicaudis brachycercus: Bunting 1973: 138. Kiefer 1928: 245. Pennak 1963: 358; 1978: 403. Tash 1971: 95, 96, 115, 118, Tables I, II. Tash and Armitage 1967: 132, 133, 136, Table III. Yeatman 1943: 27, 28, 30, 35; 1964: 98.

Diacyclops crassicaudis brachycercus: Dussart and Defaye 1985: 84. Monchenko 1974: 294–298, Figs. 101, 102. Pesce and Galassi 1987: 207, 211. Pesce et al. 1982: 58, 60, Table II. Reed 1991: 240. Reid 1988a: 36. Strayer 1989a: 201, Table IV. Taylor and Mahoney 1990: 612. Torke 1976: 6, 12. Williams 1989: 189, 197, 202, 205, 206, Fig. 6b.

Diacyclops crassicaudis var. *brachycercus*: Dussart 1969: 153–154.

Non *Cyclops crassicaudis brachycercus*: Harris 1973: 33, Pl. 8 Figs. 48–50. Harris 1978: 28, 32, 33.

MATERIAL: Mikropräparat 762, ♀, partly dissected on slide; Mikropräparate 763 and 766, each consisting of ♀ mounted whole on slide, from Kiefer Copepod Collection, Staatliches Museum für Naturkunde Karlsruhe. These slides are listed in the Catalog of the Kiefer Collection (Franke 1989) as *D. nearcticus*. Each is labeled “*Cyclops crassicaudis nearcticus*, ♀, 2.I.27, Kiefer” on the left label, and “New York, moos, Stadt-Park von Pelhambay (Chappuis)” on the right label. All writing is in ink except the word *nearcticus* in pencil in Kiefer’s handwriting. These label data agree with those given by Kiefer (1927a, p. 262) for *D. crassicaudis brachycercus*, as “von Dr. Chappuis . . . aus nassem Moos von der Umgebung Neuyorks.” Since no other material of *D. crassicaudis brachycercus* is listed in the Kiefer Catalog (Franke 1989), these three specimens are taken to represent the type material of this variety.

ADDITIONAL MATERIAL: 2 ♀♀, partly dissected on 1 slide in CMC, Esopus Creek, town of Shendaken, Ulster Co., New York, 22 October 1985, coll. and det. D. Strayer, USNM 235360. 7 ♂♂, 10 April 1988, USNM 250324; 4 ♀♀, 26 April 1988, USNM 250325; 5 ♀♀ and 8 ♂♂, 3 March 1989, USNM 250326, all from Rainbow Bay, Barnwell Co., South Carolina, coll. B. E. Taylor and G. Wyngaard; alcohol preserved.

Description and comparisons

Kiefer’s (1927a) original description of *D. crassicaudis brachycercus* was brief and included no description of the male. Mikropräparate 762 and 763 are in excellent condition, but the medium on Mikropräparat 766 has dried to the edge of the specimen. The mouthparts are mostly obscured on all the specimens. Coker (1938) and Yeatman (1944) provided excellent descriptions and figures of both sexes from a population in North Carolina. A few possibly useful morphological details mentioned by neither author are apparent on Kiefer’s specimens, and are illustrated herein.

Coker’s and Yeatman’s descriptions are nearly completely congruent with Kiefer’s material. The leg 5 article 2 of the female in Mikropräparat 762 is nearly quadrate, only a little broader than long (Fig. 81), but the corresponding structure as drawn by Coker and Yeatman is slender and about twice as long as broad, which is similar to most representations of the nominate species. Damian-Georgescu (1963, Figs. 73h, 73i) showed 5th legs of two specimens from Europe, one with a similarly short article 2. The anal opercula of the three specimens from the Kiefer Collection are produced, extending to or

past the posterior margin of the anal somite. The antenna (Fig. 74) bears 2 short setae and a long exopodite seta on article 1. The labrum (Fig. 75) has 9 acute teeth between the small blunt lateral expansions. The maxillar claw (Fig. 76) bears a few small teeth near midlength. The medial expansions of the basipodites of legs 1–4 (Figs. 77–80, respectively) are all ornamented, the basipodite of leg 1 with a few coarse hairs, that of leg 2 or leg 3 with a proximally directed knob, that of leg 3 or leg 2 with several small spines, and that of leg 4 with large spines. (It is impossible to determine which is leg 2 and 3, since both legs are completely dissected.) The couplers of legs 1–3 are naked, and the coupler of leg 4 has 2 groups of spines on the posterior surface near the distal margin. Two additional, more proximal groups of very small spines are visible on the posterior surface of the leg 4 coupler of one of the mounted females from New York included in the Strayer collection.

The ornament of the basipodites of the swimming legs is similar to that of *D. crassicaudis* s.str. in Europe (Gurney 1933), except that the leg 2 basipodite is described as being ornamented with spines rather than a knob. I find no previous report of ornament on the leg 4 coupler of either *D. crassicaudis* s.str. or *D. crassicaudis brachycercus*, and Gurney (1933, Fig. 1693) shows the leg 4 coupler of *D. crassicaudis* s.str. as lacking ornament. Damian-Georgescu (1963, Fig. 73c) drew the antenna of *D. crassicaudis* s.str. without setae on articles 1 and 2, but this was possibly an incomplete representation. Pesce and Galassi (1987) provided figures of the antennules of *D. crassicaudis lagreaci* and *D. crassicaudis trinacriae* showing 3 setae on article 1.

Diacyclops crassicaudis (G. O. Sars, 1863) s.str.
Figs. 82–86

Major synonymy

Cyclops crassicaudis G. O. Sars, 1863: 236, 249.

Cyclops (Diacyclops) crassicaudis: Kiefer 1927b: 306.

Acanthocyclops crassicaudis: Rylov 1948: 245–248, Fig. 55.

Reed 1959: 27, 111, 143, Table XVII, Appendix Table B.

Cyclops (Acanthocyclops) crassicaudis: Gurney 1933: 183, 232–234, Figs. 1686–1696 (partim). Reed 1963: 51.

Cyclops crassicaudis brachycercus: Harris 1973: 33, Pl. 8 Figs. 48–50; 1978: 28, 32, 33.

Cyclops Brucei T. Scott, 1899: 93–94, Pl. 6 Figs. 1–6.

Diacyclops crassicaudis: Štěrba 1954: 354, 355–356.

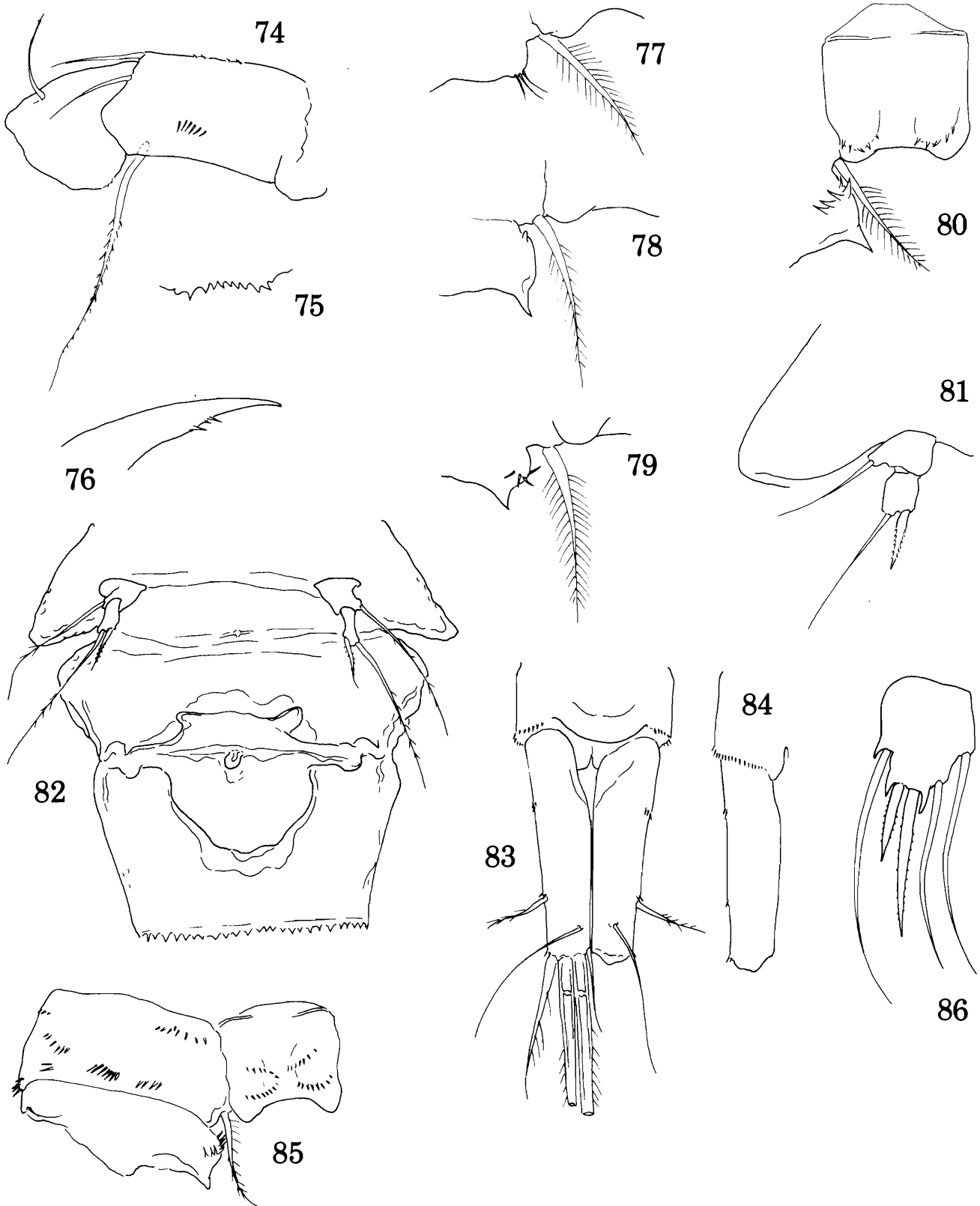
MATERIAL: ♀ and ♂, alcohol preserved, muskeg near Lac La Ronge, Saskatchewan, 3 May 1956, coll. E. B. Reed, USNM 251302.

Female

Similar to description of *D. crassicaudis* by Gurney (1933), except in following details.

Length 764 μm. Pediger 5 and genital segment (Fig. 82) with few round pits on lateral surfaces. Seminal receptacle, anterior expansion with 2 hornlike extensions, posterior expansion rounded, lateral arms horizontal; copulatory pore sclerotized. Caudal ramus (Figs. 83, 84) 4.77 times longer than broad; insertion of lateral seta about at posterior 3/4. Lengths of caudal setae (μm): lateral 21, dorsal 60, lateralmost to medialmost terminal 67, 292, 440, 30. Both median caudal setae telescoped near their bases; medialmost terminal caudal seta closely appressed to next seta, exact length uncertain.

Leg 4 coxopodite (Fig. 85) with 7 groups of spines; coupler



FIGS. 74–86. *Diacyclops crassicaudis* var. *brachycercus* (Kiefer, 1927), female, Kiefer Mikropräparat 762. Fig. 74. Antenna articles 1 and 2, caudal side. Fig. 75. Labrum. Fig. 76. Claw of maxilla. Figs. 77–79. Legs 1–3 basipodite medial expansion and part of coupler, anterior, respectively. Fig. 80. Leg 4 basipodite medial expansion and coupler, anterior. Fig. 81. Leg 5. FIGS. 82–86. *Diacyclops crassicaudis* (G. O. Sars, 1863) s.str., female from Saskatchewan, USNM 251302. Fig. 82. Pediger 5 and genital segment, ventral. Fig. 83. Anal somite and caudal rami, dorsal. Fig. 84. Right caudal ramus, ventral. Fig. 85. Leg 4 coxo-basipodite and coupler, posterior. Fig. 86. Leg 4 endopodite 3. All figures drawn at 600 \times ; details of Figs. 74–81 confirmed at 1000 \times .

with 2 medially divided rows of spines. No ornament visible on couplers of legs 1 and 2; leg 3 coupler with 1 row of spines near distal border. Leg 4 endopodite article 3 (Fig. 86) 28 μm long and 27 μm broad, length:breadth ratio 1.04. Lengths of medial and lateral terminal spines 38 and 21 μm , respectively, ratio of lengths 1.80; ratio of lengths of medial terminal spine and endopodite article 3, 1.35.

Male

Length about 600 μm . Specimen damaged, missing 4th and most of 3rd legs. Antennule similar to that of *D. crassicaudis* as described by Gurney (1933).

Discussion

There are presently 12 named species and subspecies in the *Diacyclops crassicaudis*-complex, most of these stygophil or stygoxene inhabitants of local groundwater systems in Eurasia and North Africa (Lescher-Moutoué 1986; Pesce and Galassi 1987). Only *D. crassicaudis* (G. O. Sars, 1863) and *D. crassicaudis* var. *brachycercus* have been reported from North America. The validity of *D. crassicaudis* s.str., *D. crassicaudis* var. *brachycercus*, and *D. crassicaudis* *cretensis* (Kiefer, 1928), which are all very similar, has been much discussed (Dussart 1969; Gurney 1933; Monchenko 1974; Pesce and Galassi 1987; Rylov 1948; Yeatman 1944). Rylov (1948) summarized the question of the relationship between *D. crassicaudis* and *D. crassicaudis* var. *brachycercus*. The nominate species has the caudal ramus 4.2–5 times, and the variety *brachycercus* 3.2–3.4 times, longer than broad. Other differences mentioned by Yeatman (1944) and others as being characteristic of *D. crassicaudis* var. *brachycercus*, such as 2 spines rather than 1 spine and 1 seta on the leg 3 endopodite 3 of the male, occur also in European populations that are otherwise typical of the nominate species (Gurney 1933; Kiefer 1928). Comparing the morphology of the types and two other North American populations ascribed to *D. crassicaudis* var. *brachycercus* with representations of the nominate species in the literature, I find no meaningful differences except, as before, the slightly shorter caudal ramus. The ornament of the leg 4 coupler, although it is often a useful character in the taxonomy of cyclopoid copepods, is an indistinct feature which is not always indicated in figures. This ornament does vary among populations of this species-complex: Pesce and Galassi (1987) described the leg 4 coupler of *D. crassicaudis lagreaci* as having small spines, but the coupler of *D. crassicaudis trinacriae* as being naked. The leg 4 couplers of *D. karamani* and *D. skopljensis* lack ornament (Kiefer 1932).

The geographical distributions of *D. crassicaudis* s.str. and *D. crassicaudis* var. *brachycercus* seem from presently available information to overlap completely. Populations ascribed to *D. crassicaudis* var. *brachycercus*, i.e., having relatively short caudal rami, have been reported from Europe by Damian-Georgescu (1963, Romania), Mäemets and Veldre (1956, also Veldre and Mäemets 1956, Estonia), Monchenko (1974, Ukraine), and Štěrba (1961, 1962, Czechoslovakia, 1968, Bohemia). Unfortunately, information on other aspects of the morphology of these populations is scanty, and it is uncertain whether they are completely congruent with North American *D. crassicaudis* var. *brachycercus*.

Morphs with long caudal rami ascribable to *D. crassicaudis*

s.str. do occur in North America. Reed (1959, 1963) reported the nominate species from the Adelaide Peninsula in the Canadian Arctic. E. B. Reed (personal communication, 1991) based this decision primarily on caudal ramus length: breadth ratios of about 4 (all were above 3.7 and less than 5). Reed's collection also includes a mounted male taken from St. Mathew Island, Pribilof Islands, Alaska, by Robert and Reggie Rausch. This specimen is ascribed by Reed to *D. crassicaudis* s.str. because the caudal ramus is 4 times longer than broad. Other features of this specimen seem congruent with the nominate species, although no ornament is visible on the medial expansions of the legs 1–4 basipodites (E. B. Reed, personal communication, 1991). The specimen supplied by Reed from Saskatchewan and described herein agrees in most respects with European representations of the nominate species. In the Saskatchewan female the lateral arms of the seminal receptacle are broader, the dorsal caudal seta are relatively longer, the marginal expansions of the leg 4 coupler are more produced, and the medial terminal spine of leg 4 endopodite 3 is relatively longer than in European specimens. There are 2 rows of spines on the leg 4 coupler, which is described as unornamented in specimens of the nominate species from Europe. The meaning, if any, of these differences is unclear, since the range of morphological variation, particularly of subtle meristic characters, has not yet been completely documented in European populations. Although Harris (1973, 1978) collected "*Cyclops crassicaudis brachycercus*" from Mississippi, his figure (Harris 1973, Fig. 48) of the caudal ramus of a female clearly shows the ramus as being 4.2 times longer than broad, just within the range for *D. crassicaudis* s.str.

Available morphological, distributional, and ecological information provides no firm basis for distinguishing two or more morphs of the *D. crassicaudis*-complex at the level of subspecies, at least in North America. As Rylov (1948) noted, variation in the length of the caudal ramus between different populations might be no more significant taxonomically than similar variation in other cyclopoid genera such as *Eucyclops* and *Acanthocyclops*, which occurs with changes in ambient temperatures. Rylov's treatment of *brachycercus* as a variety of *D. crassicaudis* seems to be a reasonable provisional tag for populations with shorter caudal rami. Appropriate comparative studies based on both North American and Eurasian material will be necessary to resolve the problem of the relationships among these and other morphs of the complex. Ideally, such studies should be based on specimens collected year-round from several populations at various latitudes, and will necessitate examination of intra- and inter-populational variations of subtle meristic characters as well as body proportions.

The known distribution of *Diacyclops crassicaudis* s.str. and var. *brachycercus* in North America extends from north of the Arctic Circle to the southern United States. *Diacyclops crassicaudis* s.str. has been collected from the Adelaide Peninsula and St. Mathew Island (Reed 1959, 1963; E. B. Reed, personal communication, 1991), Saskatchewan, and probably Mississippi (Harris 1973, 1978). *Diacyclops crassicaudis* var. *brachycercus* is known from Cape Thompson, Alaska (Tash 1971; Tash and Armitage 1967), the Yukon Territory (Reed 1991), Quebec (Willey 1925), Ontario (Williams 1989), New York (Kiefer 1929; Strayer 1989a), Wisconsin (Torke 1976), North Carolina (Coker 1938; Yeatman 1943, 1944), South

Carolina (Taylor and Mahoney 1990), Tennessee (Bunting 1973), and Texas (Reddell 1965; Reddell and Mitchell 1969). As in Europe, most of the records are from small ephemeral ponds or puddles (Bunting 1973; Coker 1938; Reed 1991; Tash 1971; Tash and Armitage 1967; Taylor and Mahoney 1990; Torke 1976; Willey 1925; Yeatman 1943, 1944), but groundwater-related records are also numerous (Kiefer 1929, moss; Reddell 1965; Reddell and Mitchell 1969, a cave; Reed 1959, 1963, head of a river; Strayer 1989a, springs and seeps; Williams 1989, stream hyporheic zone). The record by Harris (1973, 1978) from plankton in large impoundments is unusual.

It has been repeatedly suggested, most recently by Tash (1971), that *D. crassicaudis* s.l. is cold-stenothermal and that lower-latitude populations are glacial relicts. This theory was denied convincingly by Kiefer (1923) and Rylov (1948), who noted the success of the species in warm waters and the great extent of its range in southern latitudes, i.e., to North Africa Crete, and Taiwan. The several records from the southern United States listed herein add weight to the latter argument.

Acknowledgments

Assembling the specimens and information for this report was possible only through the cordial cooperation of many people. Dr. Hans-Walter Mittmann personally hand-carried material and original drawings from the Kiefer Copepod Collection in the Staatliches Museum für Naturkunde Karlsruhe, Germany. Drs. Margaret A. Palmer, David Strayer, D. Dudley Williams, and Harry C. Yeatman and Ms. Christine Hakenkamp placed at my disposal their collections of material identified as *D. nearcticus*. Dr. Durland Fish provided additional collection data for *D. harryi*, and Dr. John R. Holsinger provided data for *D. alabamensis*; both graciously permitted me to report their previously unpublished records. The sisters of the Notre Dame Academy and Mr. and Mrs. Ridgley White provided Dr. Margaret Palmer access to her study site on Goose Creek, Virginia. Dr. Edward B. Reed supplied extensive drawings and discussions of specimens of *D. crassicaudis* in his collection, and commented helpfully on an interim version of the manuscript. Finally, the contributions of the numerous collectors are gratefully acknowledged.

Bunting, D. L. 1973. The Cladocera and Copepoda of Tennessee. II. Cyclopoid copepods. *J. Tenn. Acad. Sci.* **48**: 138–141.
 Coker, R. E. 1938. Anomalies of crustacean distribution in the Carolinas with list of cyclopoids of the general region of Chapel Hill, N.C. *J. Elisha Mitchell Sci. Soc.* **54**: 76–87.
 Damian-Georgescu, A. 1963. Copepoda, Fam. Cyclopidae (forme de apă dulce). *Fauna Repub. Pop. Romine. Crustacea* No. 4.
 Dussart, B. H. 1969. Les Copépodes des eaux continentales d'Europe occidentale. II. Cyclopoïdes et biologie. Éditions N. Boubée & Cie, Paris.
 Dussart, B. H., and Defaye, D. 1985. Répertoire mondial des Copépodes Cyclopoïdes. Éditions C.N.R.S., Bordeaux.
 Franke, U. 1989. Katalog zur Sammlung limnischer Copepoden von Prof. Dr. Friedrich Kiefer. *Carolinaea*, **5**: 1–433.
 Gurney, R. 1933. British fresh-water Copepoda. III. The Ray Society, London.
 Hakenkamp, C. C. 1991. Community dynamics of groundwater meiofauna and response to nutrient enrichment. M.S. thesis, Department of Zoology, University of Maryland, College Park.
 Harris, M. J. 1973. Calanoid and cyclopoid copepods of northern Mississippi. M.S. thesis, Department of Zoology, Mississippi State University, Mississippi.

Harris, M. J. 1978. Copepoda of northern Mississippi with a description of a new subspecies. *Tulane Stud. Zool. Bot.* **20**: 27–34.
 Hutchinson, G. E. 1967. A treatise on limnology. II. Introduction to lake biology and the limnoplankton. John Wiley & Sons, New York.
 Kiefer, F. 1923. Beitrag zur Kenntnis von *Cyclops crassicaudis* Sars. *Zool. Anz.* **56**: 283–289.
 Kiefer, F. 1927a. Freilebende Süßwasser-Copepoden aus Nordamerika. *Zool. Anz.* **72**: 262–268.
 Kiefer, F. 1927b. Versuch eines Systems der Cyclopiden. *Zool. Anz.* **73**: 302–308.
 Kiefer, F. 1928. Beiträge zur Copepodenkunde (XI). 27. Eine neue Unterart des *Cyclops crassicaudis* Sars (Abb. 1–3). *Zool. Anz.* **79**: 244–250.
 Kiefer, F. 1929. Crustacea Copepoda. 2. Cyclopoida Gnathostoma. *Tierreich*, **53**: 1–102.
 Kiefer, F. 1931. Zur Kenntnis der freilebenden Süßwasser-copepoden, insbesondere der Cyclopiden Nordamerikas. *Zool. Jahrb. Abt. Syst. Oekol. Geogr. Tiere*, **61**: 523–712.
 Kiefer, F. 1932. Neue Süßwassercopepoden aus Jugoslawien. *Zool. Anz.* **101**: 49–60.
 Kiefer, F. 1934. Neue Ruderfusskrebse aus Nordamerika. *Zool. Anz.* **107**: 269–271.
 Kiefer, F. 1935. Neue Süßwassercyclopiden (Crustacea Copepoda) aus Uruguay. *Zool. Anz.* **109**: 181–188.
 Lescher-Moutoué, F. 1978/1979. Cyclopidae des eaux souterraines de l'île de Majorque (Espagne). *Vie Milieu Ser. C*, **28/29**: 83–100.
 Lescher-Moutoué, F. 1986. Copepoda Cyclopoida Cyclopidae des eaux douces souterraines continentales. In: *Stygofauna Mundi*. Edited by L. Botosaneanu. E. J. Brill/Dr. W. Backhuys, Leiden. pp. 299–312.
 Mäemets, A., and Veldre, I. 1956. Eesti NSV vabaltelavad aerjalalised (Eucopepoda). I. Hormikulised (Calanoida). (In Estonian, abstracts in Russian and German.) *Loodusuurijate Selts Eesti NSV Teaduste Akadeemia Juures Abiksloodusevaatlejale Tartu*, **28**: 1–87.
 Monchenko, V. I. 1974. Cyclopidae. *Fauna Ukrainii*, **27**: 1–452.
 Morton, D. W. 1985. Revision of the Australian Cyclopidae (Copepoda, Cyclopoida). I. *Acanthocyclops* Kiefer, *Diacyclops* Kiefer and *Australocyclops*, gen.nov. *Aust. J. Mar. Freshwater Res.* **36**: 615–634.
 Palmer, M. A. 1990a. Temporal and spatial dynamics of meiofauna within the hyporheic zone of Goose Creek, Virginia. *J. North Am. Benthol. Soc.* **9**: 17–25.
 Palmer, M. A. 1990b. Understanding the movement dynamics of a stream-dwelling meiofauna community using marine analogs. *Stygologia*, **5**: 67–74.
 Pennak, R. W. 1953. Fresh-water invertebrates of the United States. The Ronald Press Co., New York.
 Pennak, R. W. 1963. Species identification of the fresh-water cyclopoid Copepoda of the United States. *Trans. Am. Microsc. Soc.* **82**: 353–359.
 Pennak, R. W. 1978. Fresh-water invertebrates of the United States. 2nd ed. John Wiley & Sons, New York.
 Pennak, R. W. 1989. Fresh-water invertebrates of the United States, Protozoa to Mollusca. 3rd ed. John Wiley & Sons, New York.
 Pesce, G. L., and 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. *Boll. Mus. Civ. Stor. Nat. Verona*, **12**: 411–418.
 Pesce, G. L., and Galassi, D. P. 1987. Copepodi di acque sotterranee della Sicilia. *Animalia (Univ. Catania)*, **14**: 193–235.
 Pesce, G. L., Pace, R., and Maggi, D. 1982. Ricerche faunistiche in acque sotterranee freatiche dell' Iran nord-occidentale. *Riv. Idrobiol.* **21**: 37–74.
 Reddell, J. R. 1965. A checklist of the cave fauna of Texas. I. The Invertebrata (exclusive of Insecta). *Tex. J. Sci.* **17**: 143–187.

- Reddell, J. R., and Mitchell, R. W. 1969. A checklist and annotated bibliography of the subterranean aquatic fauna of Texas. Spec. Rep. No. 24, International Center for Arid and Semi-arid Land Studies, Texas Technological College Water Resources Center, Lubbock. pp. 1–48.
- Reed, E. B. 1959. The distribution and ecology of fresh-water Entomostraca in Arctic and Subarctic North America. Ph.D. thesis, Department of Biology, University of Saskatchewan, Saskatoon.
- Reed, E. B. 1963. Records of freshwater Crustacea from Arctic and Subarctic Canada. Nat. Mus. Can. Bull. No. 199. pp. 29–62.
- 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.
- Reid, J. W. 1988a. Copepoda (Crustacea) from a seasonally flooded marsh in Rock Creek Stream Valley Park, Maryland. Proc. Biol. Soc. Wash. **101**: 31–38.
- Reid, J. W. 1988b. Cyclopoid and harpacticoid copepods (Crustacea) from Mexico, Guatemala, and Colombia. Trans. Am. Microsc. Soc. **107**: 190–202.
- Reid, J. W. 1990. Copepoda (Crustacea) from acidic wetlands in the District of Columbia and Maryland, including a description of *Acanthocyclops columbiensis*, new species. Trans. Am. Microsc. Soc. **109**: 174–180.
- Reid, J. W. 1991. Use of fine morphological structures in interpreting the taxonomy and ecology of continental cyclopoid copepods (Crustacea). An. IV Encontro Bras. Plancton. **4**: 261–282.
- Reid, J. W. 1992. *Diacyclops albus* n.sp. and *Parastenocaris palmerae* n.sp. (Crustacea: Copepoda) from the meiofauna of a stream bed in Virginia, U.S.A. (December 1991 issue.) Can. J. Zool. **69**: 2893–2902.
- Reid, J. W., Hare, S. G. F., and Nasci, R. S. 1989. *Diacyclops navus* (Crustacea: Copepoda) redescribed from Louisiana, U.S.A. Trans. Am. Microsc. Soc. **108**: 332–344.
- Rylov, V. M. 1948. Freshwater Cyclopoida. Crustacea. Fauna SSSR. **3**: 1–314. (National Science Foundation, Washington, D.C., and Israel Program for Scientific Translations, Jerusalem, 1963.)
- Sars, G. O. 1863. Oversigt af de indenlandske Ferskvandscopepoder. Forh. Videnskabselsk. Kristiania, 1862: 212–262.
- Scott, T. 1899. Report on the marine and freshwater Crustacea from Franz-Josef Land, collected by Mr. William S. Bruce, of the Jackson–Harmsworth Expedition. J. Linn. Soc. Lond. Zool. **27**: 60–126, Plates 3–9.
- Štěrba, O. 1954. Příspěvek k poznání buchanek (Cyclopidae) z Brněnska a jižní Moravy. Věstn. Česk. Spol. Zool. **19**: 354–364.
- Štěrba, O. 1961. Koryši (Crustacea) z vod náplavů horního toku Laborce. (In Czech, abstracts in Russian and German.) Biológia (Bratisl.), **16**: 821–825.
- Štěrba, O. 1962. Copepoda z intersticiálních vod náplavů některých slovenských toků. (In Czech, abstract in Russian.) Biológia (Bratisl.), **17**: 893–900.
- Štěrba, O. 1968. Příspěvek k poznání klanonožců (Crustacea, Copepoda), zvláště plazivek (Harpacticoida), z Čech. (In Czech, abstract in German.) Acta Univ. Palacki. Olomuc. Fac. Rerum Nat. Biol. **28**: 211–232.
- Stoch, F. 1987. Cave-dwelling cyclopoid (Crustacea, Copepoda) from Venezia Giulia (northeastern Italy). Bull. Zool. Mus. Univ. Amst. **11**: 41–55.
- Strayer, D. 1989a. Crustaceans and mites (Acari) from hyporheic and other underground waters in southeastern New York. (Part 2, 1988.) Stygologia, **4**: 192–207.
- Strayer, D. 1989b. New and rare copepods (Cyclopoida and Harpacticoida) from freshwater interstitial habitats in southeastern New York. (Part 3, 1988.) Stygologia, **4**: 279–291.
- Tash, J. C. 1971. The zooplankton of fresh and brackish waters of the Cape Thompson area, northern Alaska. Hydrobiologia, **38**: 93–121.
- Tash, J. C., and Armitage, K. B. 1967. Ecology of zooplankton of the Cape Thompson area, Alaska. Ecology, **48**: 129–139.
- Taylor, B. E., and Mahoney, D. L. 1990. Zooplankton in Rainbow Bay, a Carolina bay pond: population dynamics in a temporary habitat. Freshwater Biol. **24**: 597–612.
- Torke, B. 1976. A key to the identification of the cyclopoid copepods of Wisconsin, with notes on their distribution and ecology. Wis. Dep. Nat. Resour. Res. Rep. No. 88. pp. 1–15.
- Veldre, I., and Mäemets, A. 1956. Eesti NSV vabaltelevad aerjalalised (Eucopepoda). II. Sõudikulised (Cyclopoida), Rullikulised (Harpacticoida). (In Estonian, abstracts in Russian and German.) Loodusuurijate Selts Eesti NSV Teaduste Akadeemia Juures Abiksoodusevaatlejale Tartu, **29**: 1–128.
- Willey, A. 1925. Northern Cyclopidae and Canthocamptidae. Trans. R. Soc. Can. Ser. 3, **19**: 137–158.
- Willey, A. 1929. Notes on the distribution of free-living copepods in Canadian waters. Part II. Some intertidal harpacticoids from St. Andrews, New Brunswick. Contrib. Can. Biol. Fish. (n.s.), **4**: 529–539.
- Williams, D. D. 1989. Towards a biological and chemical definition of the hyporheic zone in two Canadian rivers. Freshwater Biol. **22**: 189–208.
- Yeatman, H. C. 1943. Rare cyclopoid copepods from wells in North Carolina. J. Elisha Mitchell Sci. Soc. **59**: 27–36.
- 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. In Ward & Whipple's fresh-water biology. 2nd ed. Edited by W. T. Edmondson. John Wiley & Sons, New York. pp. 795–815.
- Yeatman, H. C. 1964. A new cavernicolous cyclopoid copepod from Tennessee and Illinois. J. Tenn. Acad. Sci. **39**: 95–98.