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Diacyclops languidoides (Lilljeborg, 1901) s.l. and *Acanthocyclops montana*, new species (Copepoda, Cyclopoida), from groundwater in Montana, USA

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Abstract

Species of cyclopoid copepods collected from wells on the floodplains of the Flathead and Whitefish Rivers, State of Montana, U.S.A. included *Diacyclops languidoides* s. l. and *Acanthocyclops montana*, new species. New records of *D. languidoides*, recorded for the first time from the U.S.A., are also given from Colorado and Saskatchewan. The first complete description of a North American member of the *D. languidoides* species-complex is furnished. *Acanthocyclops montana* most resembles *A. phreaticus*, but differs in proportions of the caudal setae, terminal spines of leg 4 endopodite 3, and details of the seminal receptacle.

Introduction

Collections from shallow wells located on the alluvial floodplains of the Flathead and Whitefish Rivers, Montana (Stanford & Ward, 1988) revealed an abundant biota including five species of cyclopoid copepods: *Acanthocyclops montana*, new species, *Diacyclops crassicaudis brachycercus* (Kiefer, 1929), *Diacyclops languidoides* (Lilljeborg, 1901) s. l., *Diacyclops thomasi* (S.A. Forbes, 1882), and *Orthocyclops modestus* (Herrick, 1883). Two additional species, *Acanthocyclops vernalis* (Fischer, 1853) and *Eucyclops speratus* (Lilljeborg, 1901) were collected rarely and in small numbers from a well which is in the channel of the Flathead River and is flooded by the river during periods of high water.

The form of *D. languidoides* occurring in the Flathead region differs morphologically from Eurasian subspecies. We describe this form, comparing it to specimens collected in Colorado and recorded here for the first time, and review the few North American records of *D. languidoides*, giving an additional new record from Saskatchewan. We also describe *Acanthocyclops montana*, new species, and furnish a chart to aid in distinguishing North American congeners. The first two authors, Reid and Reed, are the designated authors of the new species.

The wells are located on the floodplains of the Flathead and Whitefish River systems (Fig. 1). The floodplain aquifer is formed by an approximately 10 m thick deposit of Pleistocene and Recent alluvium consisting of cobbles, gravel and sand covered by soil and overlying an impermeable Tertiary clay layer. Aquifer sediments are of high porosity, and dissolved oxygen levels in the monitoring wells exceeded 50% saturation on all sampling dates. Water temperatures varied little (7–9 °C) except in wells near the river where

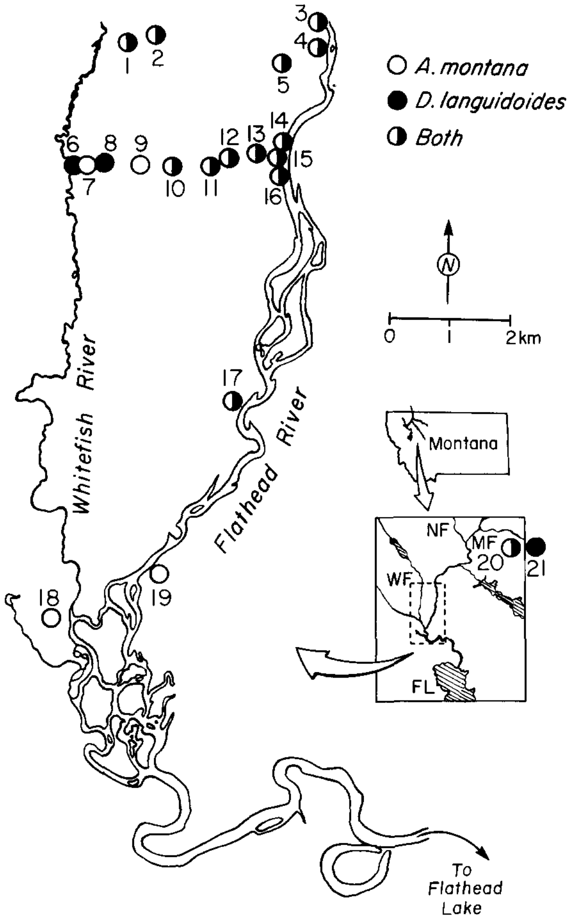


Fig. 1. Wells (numbered locations) in the Kalispell Valley of the Flathead River, State of Montana, U.S.A., where *Diacyclops languidoides* (Lilljeborg) s.l. and *Acanthocyclops montana*, new species, were collected. FL, Flathead Lake; MF, Middle Fork of the Flathead River; NF, North Fork of the Flathead River; WF, Whitefish River.

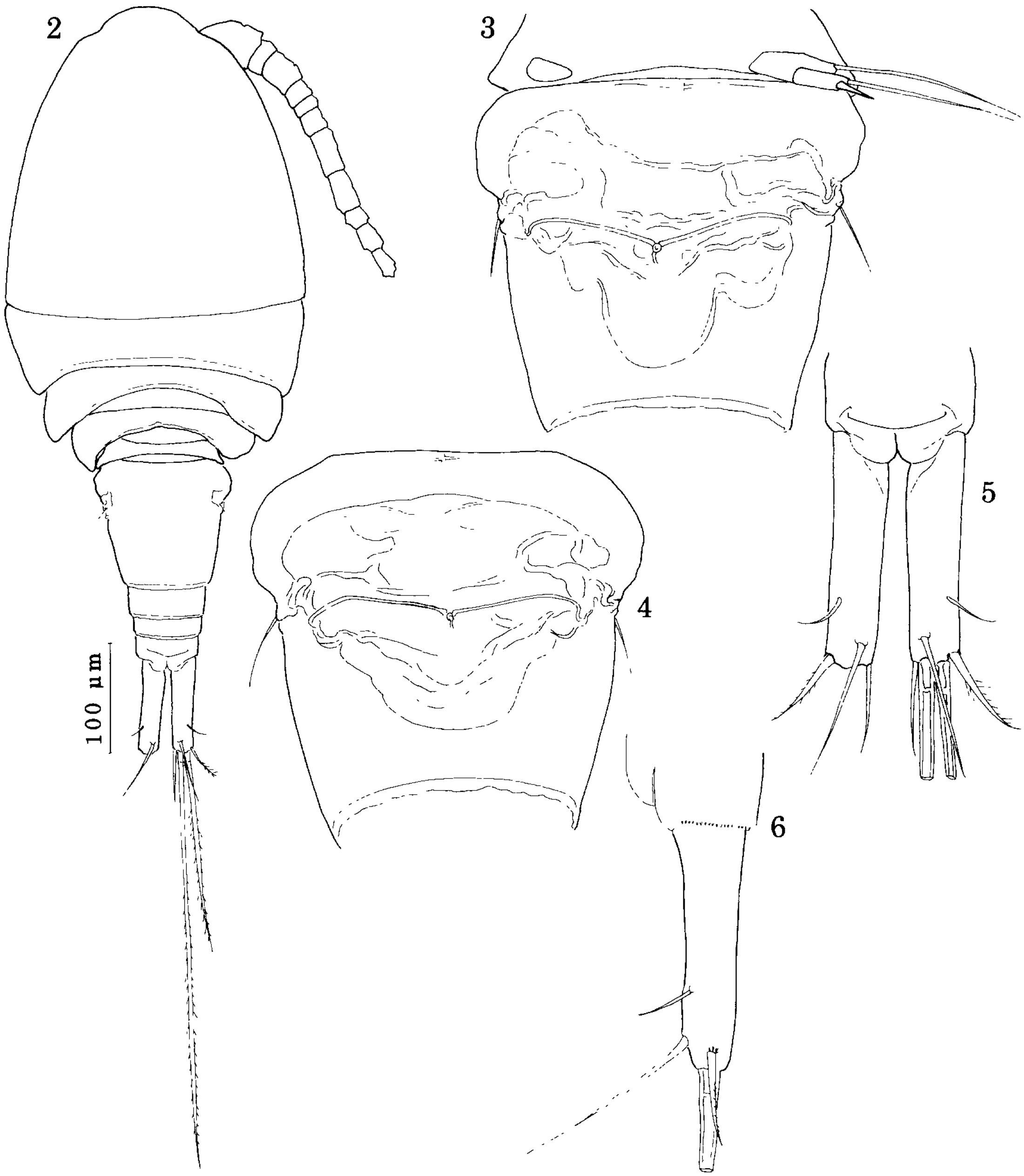
more seasonality was evident (Stanford & Ward, 1988). The groundwater monitoring wells were unscreened PVC pipes 10 cm in diameter, driven to a depth of 8–10 m; wells were capped when not in use. The pipes were perforated along almost their entire length. Specimens were collected by pumping water and sediment from the wells, and passing this water through plankton netting. Specimens were fixed in 5% formalin and later transferred to 70% ethanol. For morphological examination, specimens were placed in a solution of 70% ethanol–10% glycerine, which was allowed to evaporate to nearly pure glycerine. Specimens were then examined in glycerine or lactic acid; dissected specimens were mounted in glycerine jelly or polyvinyl lactophenol. Drawings were made using a Wild M20 compound microscope fitted with a camera lucida. Specimens to be measured were removed from alcohol to water, then into glycerine and water, time allowed for the water to evaporate, and then transferred into individual drops of lactic acid for dissection and measurement.

Diacyclops languidoides (Lilljeborg, 1901), s.l. Figs. 2–23; Table 1

Material. – 16 ♀♀ 37 ♂♂ 23 copepodids, alcohol-preserved, and 2 ♀♀, each dissected on

Table 1. Measurements of *Diacyclops languidoides* from wells in the Kalispell Valley of the Flathead River, Montana. Dimensions are in μm; P4enp3 indicates leg 4 endopodite 3; insertion, ls indicates distance along outer margin of caudal ramus from anal somite to insertion of lateral seta; SE indicates standard error of mean; CV indicates coefficient of variation. Locations (Fig. 1): Well 3, 12 Apr 1988 (14 ♀♀ 13 ♂♂); Well 4, 12 Apr 1988 (10 ♀♀ 10 ♂♂); Well 12, 12 Jun 1988 (2 ♀♀ 3 ♂♂); Well 13, 4 Oct 1988 (2 ♀♀ 13 ♂♂).

Parameter		*N*	Range	Mean	SE	CV
Total length	♀♀	28	593–798	688	10.0	8
	♂♂	39	509–677	600	7.9	8
Ramus length	♀♀	28	75–102	88	1.3	8
	♂♂	39	50– 90	74	1.1	9
Ramus width	♀♀	28	17– 22	19	0.3	9
	♂♂	39	12– 20	16	0.3	10
Inner seta	♀♀	28	25– 42	33	0.8	14
	♂♂	35	20– 40	33	0.4	7
Seta 2	♀♀	20	336–394	368	3.1	4
	♂♂	20	331–383	354	3.6	5
Seta 3	♀♀	26	163–215	186	2.0	6
	♂♂	30	105–189	168	3.0	10
Outer seta	♀♀	28	27– 40	35	0.7	10
	♂♂	37	27– 42	35	0.6	11
Insertion, ls	♀♀	25	52– 72	62	1.0	8
	♂♂	38	37– 65	53	0.9	11
P4 enp3 length	♀♀	26	27– 35	32	0.4	6
	♂♂	25	22– 35	28	0.6	11
P4 enp3 width	♀♀	26	17– 22	21	0.3	8
	♂♂	25	12– 20	17	0.5	14
P4 enp3 inner spine	♀♀	25	25– 30	26	0.4	7
	♂♂	25	17– 27	24	1.3	27
P4 enp3 outer spine	♀♀	25	25– 30	26	0.3	6
	♂♂	25	15– 27	24	1.1	24



Figs. 2–6. Diacyclops languidoides (Lilljeborg), s.l., female: 2, habitus, dorsal; 3, prosomite 5 and genital segment, ventral; 4, genital segment of a second specimen, ventral; 5, caudal rami, dorsal; 6, right caudal ramus, lateral.

1 slide, Well 4, 23 Mar 1988, United States National Museum of Natural History (USNM) 250082; 11 ♀♀ 23 ♂♂ 10 copepodids, alcohol-preserved, Well 11, 12 Feb 1988, USNM 250083; all from the Kalispell Valley of the Flathead River, State of Montana, coll. J.A. Stanford and J.V. Ward. 1 ♀ 3 ♂♂, alcohol-preserved, Bierstadt Lake, Rocky Mountain National Park, Colorado, coll. 10 Oct 1965 by E.B. Reed, USNM 250172. Additional material from Montana in collection of J.V. Ward.

Female. – Mean length of Montana specimens excluding caudal setae 0.687 mm; range 0.593–0.798 mm (Table 1); length of Colorado specimen 0.656 mm. Following description and figures for Montana specimens: body (Fig. 2) widest at prosomite 2, posterior margins of prosomites smoothly rounded; prosomite 5 little expanded laterally, less broad than anterior part of genital segment. Genital segment (Figs. 2–4) expanded anteriorly, tapering posteriorly; seminal receptacle with anterior margin of anterior section convex in most specimens (Fig. 4), sometimes concave (Fig. 3); pore-canal short, appearing straight or slightly curved; posterior expansion of receptacle roughly trapezoidal. Hyaline fringes of urosomites weakly crenulate. Caudal ramus (Figs. 2, 5, 6; Table 1) about 4.6 times longer than broad, inner surface naked; lateral seta inserted at posterior $^1/_4$ of outer margin and somewhat dorsally, length of lateral seta about equal to breadth of ramus; 3 outermost terminal caudal setae finely and homonomously plumed; lengths of terminal caudal setae as in Table 1, dorsal seta about 1.5 times longer than innermost terminal caudal seta.

Antennule (Figs. 2, 7) of 11 articles, when reflexed reaching posterior margin of prosomite 1; articles 4 and 5 each with slender spine; article 8 with esthetasc reaching end of article 9; sensory hair on article 10 about half length of article 11. Antenna (Fig. 8) of 4 articles, article 1 bearing 2 setae on distal anterior margin, 2 groups of few short hairs near proximal anterior and posterior margins, but lacking seta representing exopod. Labrum (Fig. 9) with about 13 teeth between rounded corners. Mandible (Fig. 10) with palp bearing 1 short hairlike and 2 long plumose setae; gnathobase with row of fine subterminal hairs proximal to teeth. Maxillule (Fig. 11) with palp having group of 3 terminal and subterminal setae, 1 seta proximal to endopod, and 3 setae on endopod. Maxilla (Fig. 12) with clawlike expansion having row of fine teeth along middle of inner margin. Maxilliped (Fig. 13) with 3 rows of small spines on surface of article 2, remaining articles without surface ornament.

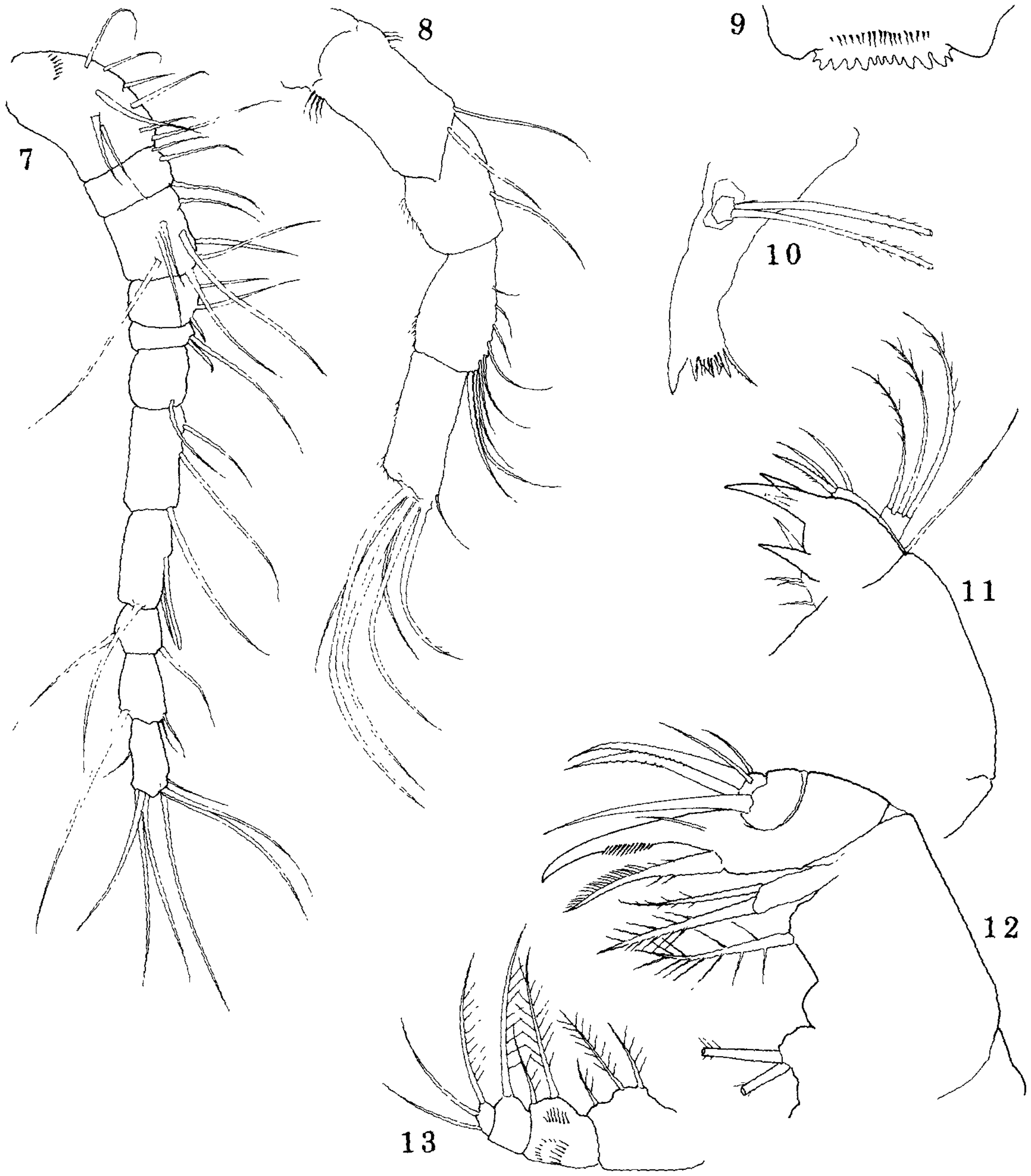
Swimming legs 1–4 (Figs. 14–18) with number of spines on distalmost article of exopodites 3,3,3,3, number of setae 5,4,4,4; leg 1 with rami each of 2 articles; leg 2 with exopodite of 3 articles and endopodite of 2 articles; legs 3 and 4 each with exopodite of 3 articles. Leg 1 with inner margin of basipodite little expanded, bearing long spine reaching nearly to end of endopodite 2. Couplers of legs 1–3 each with 2 groups of fine hairs on anterior surface. Coupler of leg 4 with single row of coarse hairs on posterior surface. Leg 4 coxopodite with 5 groups of coarse hairs or spinules on posterior surface. Leg 4 basipodite medial expansion rounded, lacking acute process often found in congeners. Leg 4 endopodite 3 about 1.5 times longer than broad, inner and outer terminal spines equal in length (Figs. 17, 18; Table 1).

Leg 5 (Figs. 3, 19) consisting of 2 free articles, article 1 with outer expansion bearing single long seta; article 2 bearing inner subterminal spine slightly shorter than length of article, and outer terminal seta approximately equal in length to seta of article 1. Leg 6 (Fig. 20) consisting of triangular plate bearing long dorsal seta and 2 short triangular spines. No specimens examined carried egg sacs.

Morphology of single undissected female specimen from Colorado similar to specimens from Montana regarding habitus, antennule, antenna, swimming legs, and urosome; genital field as in Fig. 4; measured proportions close to means for Montana specimens.

Male. – Mean length of Montana specimens 0.600 mm; range 0.509–0.677 mm (Table 1); range of lengths of Colorado specimens 0.572–0.660 mm. Description and figures for Montana specimens: habitus (Fig. 21) similar to female, except urosomite 1 much expanded. Antennule (Figs. 21, 22) geniculate, of 17 articles, suture between 2 distalmost articles indistinct; article 1 with 2 esthetascs, articles 2, 4, 9, and 13 each with 1 esthetasc; articles 8, 9, and 12 each with spine.

Leg 5 (Fig. 23) similar to leg 5 of female; leg 6 consisting of crescentic plate indistinctly separate from somite, bearing short ventral spine, small

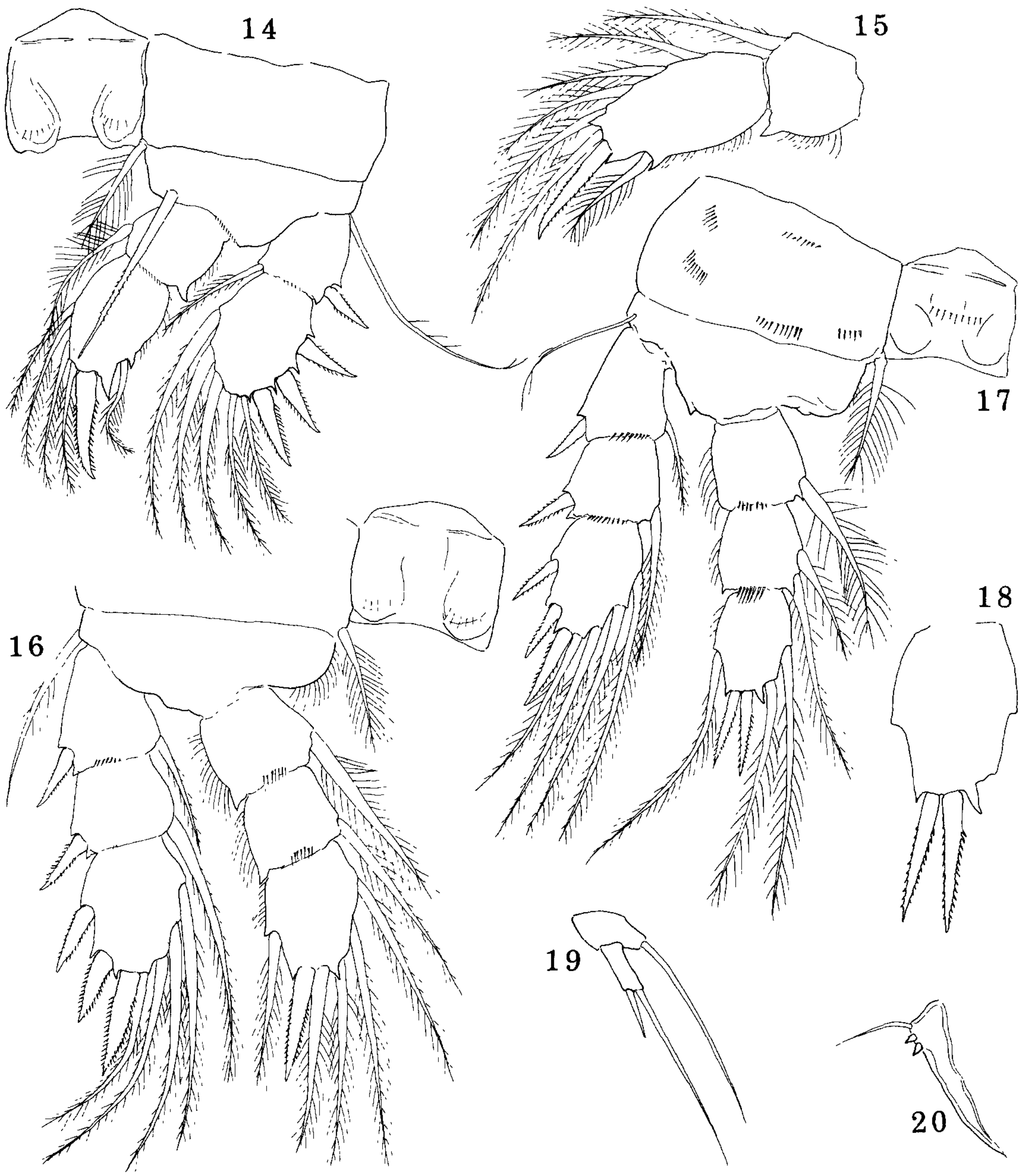


Figs. 7–13. Diacyclops languidoides (Lilljeborg), s.l., female: 7, antennule; 8, antenna; 9, labrum; 10, mandible; 11, maxillule; 12, maxilla; 13, maxilliped.

plumose middle seta, and longer plumose dorsal seta reaching past posterior margin of succeeding somite.

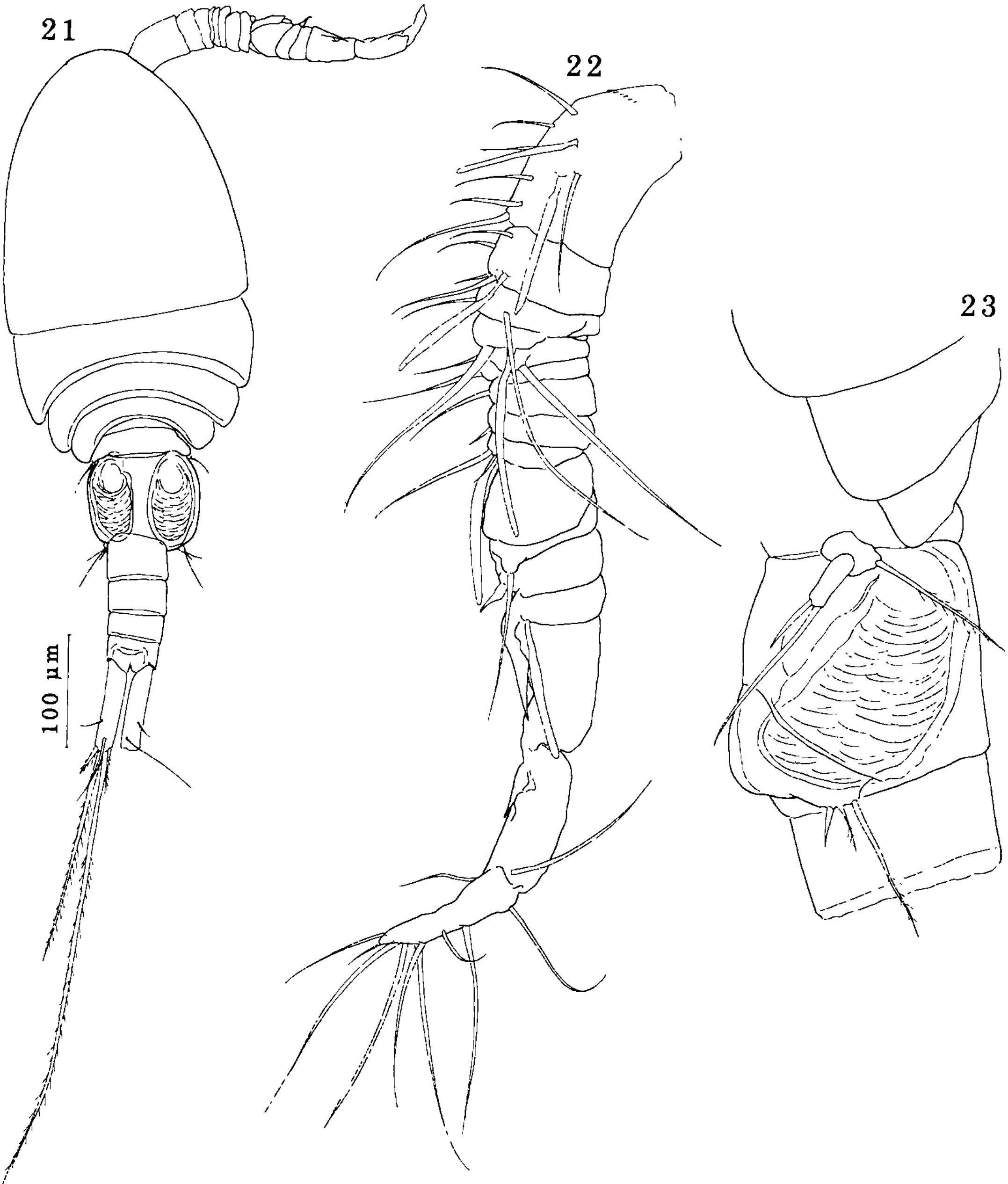
Colorado male specimens similar in morphology and proportions to Montana specimens.

Discussion. – Members of the *Diacyclops languidoides*-complex, although relatively frequently recorded from Europe and northern Asia, have been seldom found in North America; the collections reported here from Montana and Colorado represent the first south of Canada



Figs. 14–20. Diacyclops languidoides (Lilljeborg), s.l., female: 14, leg 1 and coupler, anterior; 15, leg 2 endopodite; 16, leg 3 and coupler, anterior; 17, leg 4 and coupler, posterior; 18, leg 4 endopodite 3; 19, leg 5; 20, leg 6.

(Fig. 24). The earliest North American record is probably that of Willey (1925), who described *Cyclops languidulus* from a single female specimen collected from Long Lake-Lake Obatogamau, Quebec. Although Willey never supplied figures of his specimen, his verbal description clearly indicates a member of the *languidoides*-group. Willey compared his species to *Cyclops* (now *Diacyclops*) *languidus* G.O. Sars, 1863, but was apparently unaware of Lilljeborg's species. *D. languidulus* can be considered a junior synonym of *D. languidoides* s.l., as first noted by Kiefer



Figs. 21–23. Diacyclops languidoides (Lilljeborg), s.l., male: 21, habitus, dorsal; 22, antennule; 23, posterior prosome and anterior urosome, left lateral.

(1929). Reed published the first unequivocal records, as *Cyclops* (*Acanthocyclops*) *languidoides* (Reed, 1959, 1963) or *Cyclops* (*Diacyclops*) *languidoides* (Reed, 1962), from the Colville River area, northern Alaska, and from the Canadian North West Territories (Baffin, Victoria, and King William Islands, Boothia Peninsula, and Adelaide Peninsula). Tash (1971a, b) and Tash and Armitage (1967) recorded the species from the Cape Thompson area, Alaska. Reed (unpublished) found *D. languidoides* in several muskeg samples taken around Lac la Ronge, Saskatche-

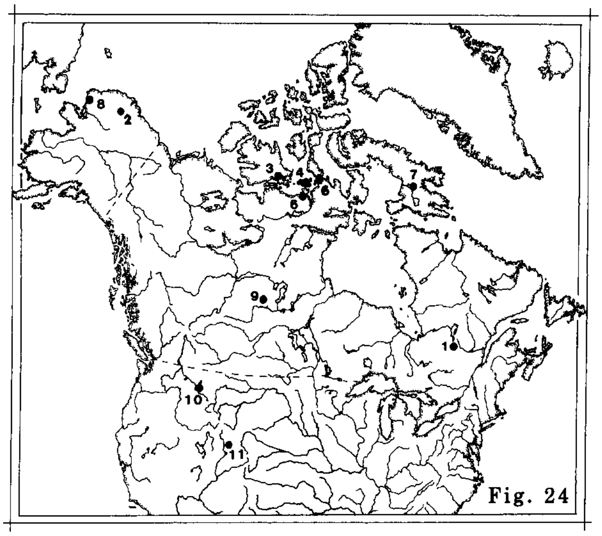


Fig. 24. Collection localities in North America of *Diacyclops languidoides* (Lilljeborg) s.l.: 1, Long Lake-Lake Obatogamau; 2, Colville River area; 3, Victoria Island; 4, King William Island; 5, Boothia Peninsula; 6, Adelaide Peninsula; 7, Baffin Island; 8, Cape Thompson area; 9, Lac la Ronge; 10, Flathead River; 11, Rocky Mountain National Park.

wan, in 1956–1957. Yeatman (1959) included the species in his key to North American Cyclopidae based on Willey's record (H.C. Yeatman, personal communication to J.W. Reid, 1989). *D. languidoides* is not included in Pennak's (1989) key to the Cyclopoida of the United States.

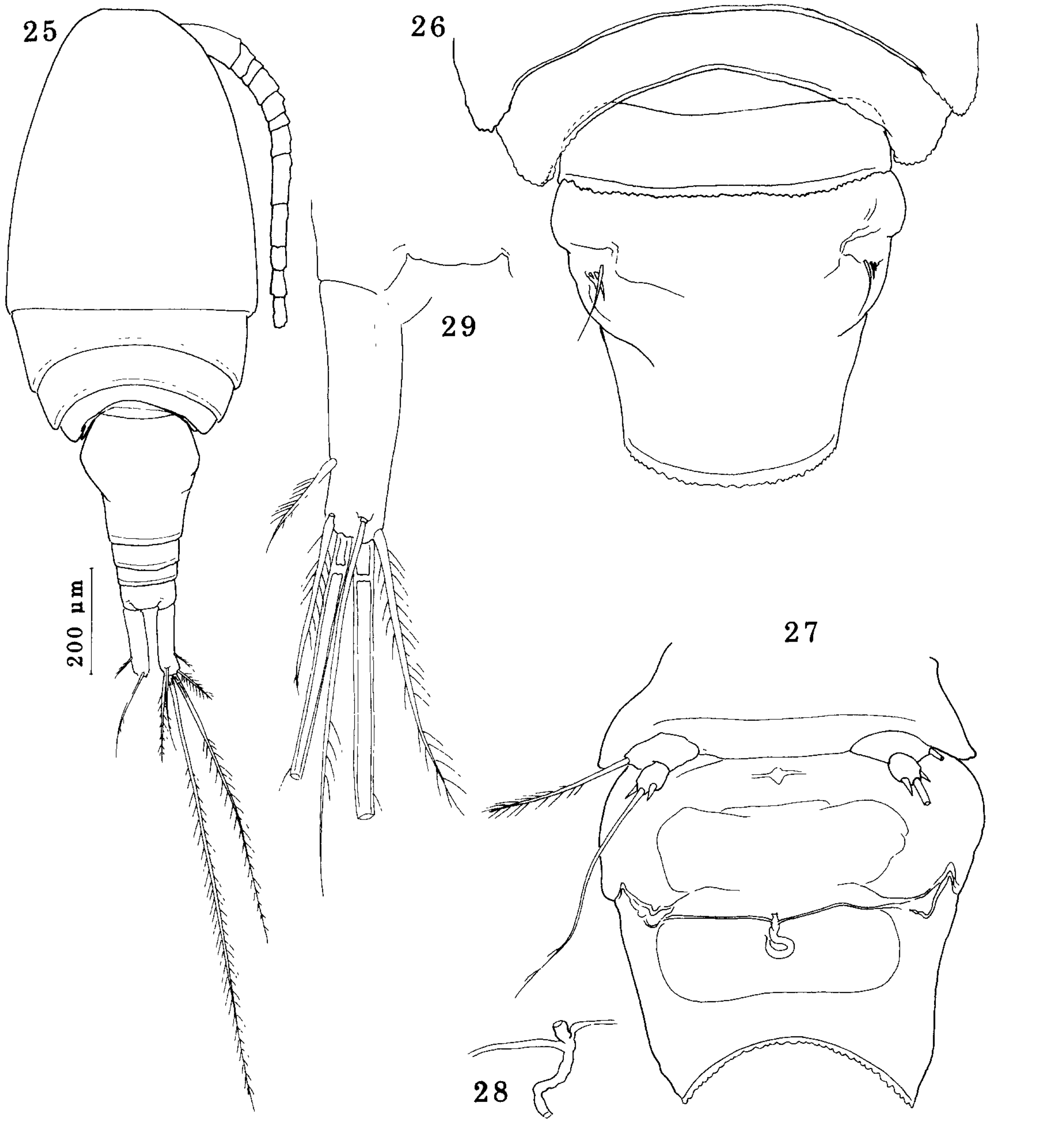
Recorded habitats of members of the *D. languidoides* species-complex in Eurasia are mainly from caves, groundwaters, small ponds, and *Sphagnum* bogs (Dussart, 1969). Most North American records are from small tundra ponds, except the Baffin Island record, from one plankton sample in Lake Nettilling. In the Flathead region, *D. languidoides* occurred in the non-karstic groundwaters of alluvial floodplain gravels, and together with *Acanthocyclops montana* dominated numerically among the cyclopoid copepods collected. The two species usually appeared alone or together, but seldom with other species, and in some cases more than 2 km distant from the river (Fig. 1).

In Europe and Asia, the taxon *D. languidoides* has been 'pulverized' into some 26 subspecies (Dussart, 1969), although diverse opinions exist regarding the synonymies of several (Dussart & Defaye, 1985). Subspecies are distinguished chiefly by differences in the proportions of the caudal ramus, leg 4 endopodite 3 and its terminal spines, and the caudal setae. These differences, in some cases quite subtle, may represent locally adapted, geographically semi-isolated races undergoing radiation and morphological differentiation (Dussart, 1969). The Montana form differs from Eurasian subspecies respecting these characters, but in the absence of a recent revision of this species-complex, rather than applying a subspecies name, we simply present the description for eventual comparison with Eurasian and other North American populations.

Acanthocyclops montana Reid & Reed, new species
Figs. 25–47; Table 2

Material. – Holotype ♀, USNM 250084, allotype ♂, USNM 250085; paratypes: 4 ♀♀ 8 ♂♂ 8 copepodids, unmounted, and 5 ♀♀ 1 ♂, each mounted on 1 slide, Well 4, 23 Mar 1988, USNM 250086; 8 ♀♀ 4 ♂♂ 20 copepodids, Well 11, 12 Feb 1988, USNM 250087; all from the Kalispell Valley of the Flathead River, Montana, coll. J.A. Stanford and J.V. Ward. Additional paratype material in collection of J.V. Ward. Unmounted specimens alcohol-preserved.

Female. – Length of holotype 1.25 mm; lengths of paratypes 1.10–1.27 mm (Table 2). Body widest at posterior margin of prosomite 1 (Fig. 25). Prosomite 5 (Figs. 25, 26) moderately expanded laterally, narrower than anterior part of genital segment. Lateral posterior margins of prosomites 3–5 and hyaline fringes of urosomites crenulate. No cuticular pitting or other conspicuous tegumental ornamentation observed. Genital segment (Figs. 26, 27) broad anteriorly, tapering posteriorly; seminal receptacle with anterior and posterior sections about equally broad, lateral canals nearly horizontal, pore-canal distinct, large, usually recurved anteriorly (Figs. 27, 28). Anal operculum (Fig. 29) weakly



Figs. 25–29. Acanthocyclops montana, new species, female: 25, habitus, dorsal; 26, prosomites 3–5 and genital segment, dorsal; 27, prosomite 5 and genital segment, ventral; 28, pore-canal of seminal receptacle, of another specimen; 29, caudal ramus, dorsal.

convex. Caudal rami (Figs. 25, 29; Table 2) about 4.5 times broader than long; inner surface naked; lateral seta inserted at about posterior $^3/_4$ of outer margin; caudal setae finely and homonomously plumed; innermost terminal seta longer than outermost terminal seta; lengths of terminal caudal setae as in Table 2, lateral seta longer than maximum breadth of ramus, dorsal seta about 1.5 times length of ramus.

Antennule (Figs. 25, 30) of 12 articles, reaching slightly past posterior margin of prosomite 1; articles 5 and 6 each with slender spine, article 9 with esthetasc reaching posterior margin of article; article 11 with sensory hair reaching mid-

Table 2. Measurements of *Acanthocyclops montana*, new species, from wells in the Kalispell Valley of the Flathead River, Montana. Dimensions are in μm; P4enp3 indicates leg 4 endopodite 3; insertion, 1s indicates distance along outer margin of caudal ramus from anal somite to insertion of lateral seta; SE indicates standard error of mean; CV indicates coefficient of variation. Locations (Fig. 1): Well 3, 12 Apr 1988 (3 ♂♂); Well 4, 12 Apr 1988 (10 ♀♀ 7 ♂♂); Well 4, 4 Oct 1988 (2 ♀♀ 1 ♂); Well 5, 10 Feb 1988 (13 ♀♀ 6 ♂♂); Well 12, 12 Jun 1988 (1 ♀ 3 ♂♂); Well 13, 4 Oct 1988 (4 ♀♀ 2 ♂♂).

Parameter		N	Range	Mean	SE	CV
Total length	♀♀	30	1100–1380	1215	15	7
	♂♂	22	860–1070	1008	12	6
Ramus length	♀♀	30	126– 168	136	0.5	2
	♂♂	22	94– 121	108	1.4	6
Ramus width	♀♀	29	26– 37	31	0.7	11
	♂♂	22	21– 31	25	0.6	11
Inner seta	♀♀	29	147– 189	162	2.3	8
	♂♂	22	105– 136	123	2.1	8
Seta 2	♀♀	28	780–1000	880	9.5	6
	♂♂	19	610– 700	672	7.4	5
Seta 3	♀♀	27	470– 620	538	11.5	11
	♂♂	18	360– 440	386	5.0	6
Outer seta	♀♀	29	84– 105	95	1.2	7
	♂♂	22	52– 79	70	1.5	10
Insertion, 1s	♀♀	29	79– 115	98	1.8	10
	♂♂	22	63– 84	75	1.3	8
P4 enp3 length	♀♀	30	67– 95	80	1.0	7
	♂♂	22	60– 72	65	0.9	6
P4 enp3 width	♀♀	30	30– 37	34	0.5	7
	♂♂	22	22– 30	26	0.5	9
P4 enp3 inner spine	♀♀	30	55– 77	66	1.1	6
	♂♂	22	47– 70	57	2.7	11
P4 enp3 outer spine	♀♀	30	55– 75	65	0.8	7
	♂♂	22	47– 62	55	1.1	9

length of article 12. Antenna (Figs. 31, 32) of 4 articles, article 1 with few groups of spinules on frontal and caudal surfaces. Labrum (Fig. 33) with about 12 teeth between rounded corners. Mandible (Fig. 34) with palp bearing 2 long plumose setae (not completely drawn) and 1 short hairlike seta. Maxillule (Fig. 35) with basis of palp furnished apically with 1 sparsely plumed seta and 1 naked seta, and proximally with 1 naked seta; endopod with 3 sparsely plumed setae. Claw of maxilla (Fig. 36) with comb on inner margin consisting of 3–4 short spinules. Maxilliped (Fig. 37) articles 2 and 3 each with 1 group of spinules.

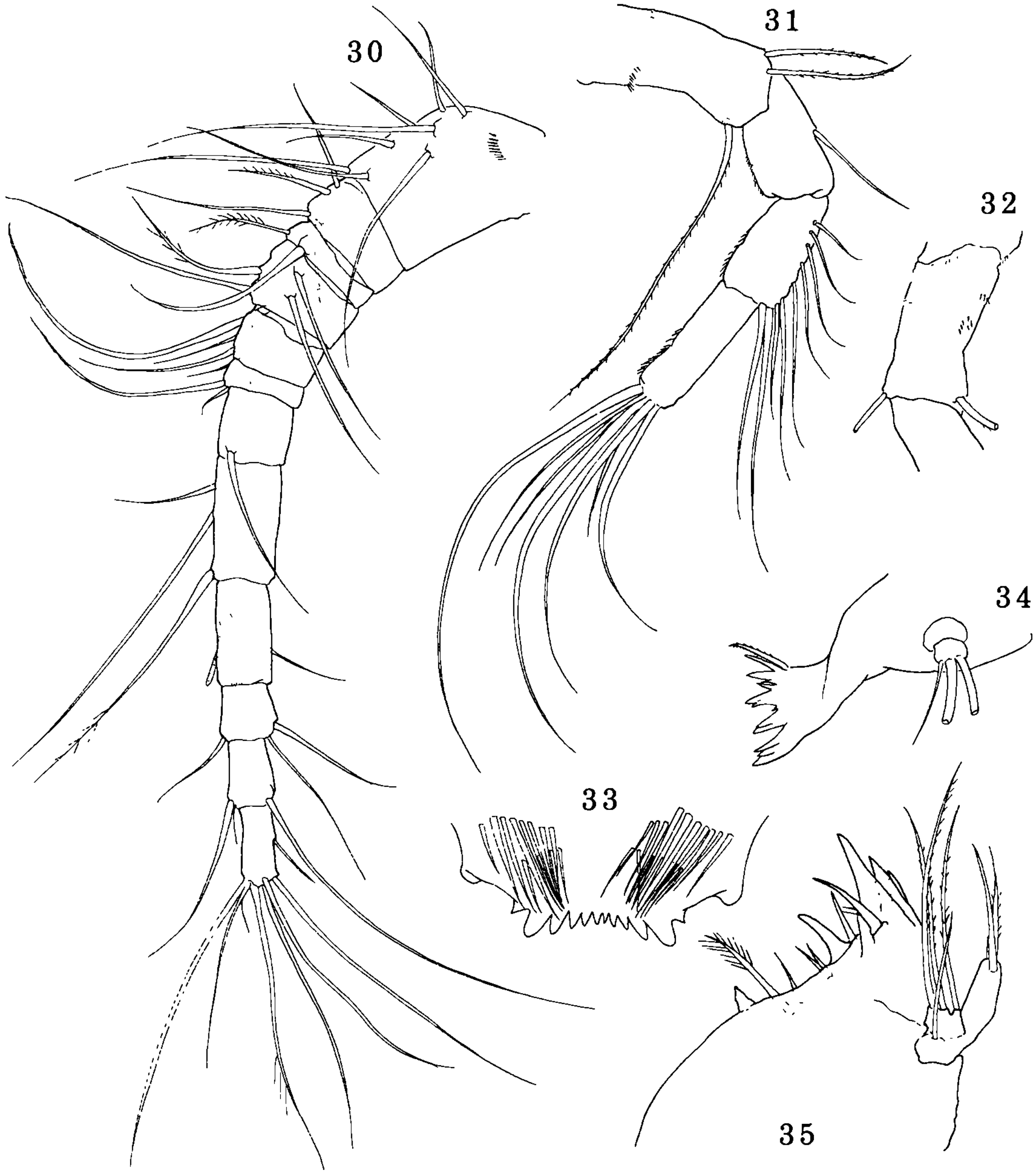
Swimming legs 1–4 (Figs. 38–42) each with rami of 3 articles; number of spines on article 3 of exopodites 3,4,4,4, number of setae 4,4,4,4; leg 3 similar to leg 2. Couplers of all legs without ornament. Leg 1 with inner part of basipodite little expanded, bearing stout spine reaching midlength of endopodite article 2. Leg 4 endopodite 1 inner margin (Figs. 40, 41) slightly concave in distal half. Leg 4 endopodite 3 (Figs. 40, 42; Table 2) about 2.3 times longer than broad; terminal spines of endopodite subequal in length.

Leg 5 (Figs. 27, 43) consisting of 2 free articles, article 1 with lateral expansion bearing long, sparsely plumed seta; article 2 slightly longer than broad, bearing long, sparsely plumed seta apically and stout spine inserted slightly distally to middle of inner margin. Some specimens with additional stout spine inserted on outer margin of article 2, on one or both legs. Leg 6 (Fig. 44) with long, sparsely plumed dorsal seta and 2 short spines, middle spine nearly twice length of ventral spine. No specimens examined carried egg sacs.

Male. – Length of allotype 1.01 mm; lengths of paratypes 0.86–1.07 mm (Table 2). Body form (Fig. 45) similar to female, except urosomite 1 greatly enlarged, nearly as broad as prosomite 4 in dorsal view. Proportions of caudal ramus and lengths of caudal setae much as in female (Table 2). Antennule (Figs. 45, 46) when reflexed reaching slightly past posterior margin of prosomite 1, geniculate, article 1 with 3 esthetascs, articles 4, 9, and 13 each with 1 esthetasc.

Leg 5 (Fig. 47) much as in female, some specimens also with extra spine on outer margin of article 2. Leg 6 consisting of small, indistinctly separated rectangular plate bearing stout inner spine, middle seta nearly twice length of spine and reaching approximately to posterior margin of succeeding urosomite, and long outer (dorsal) seta reaching well past margin of succeeding urosomite.

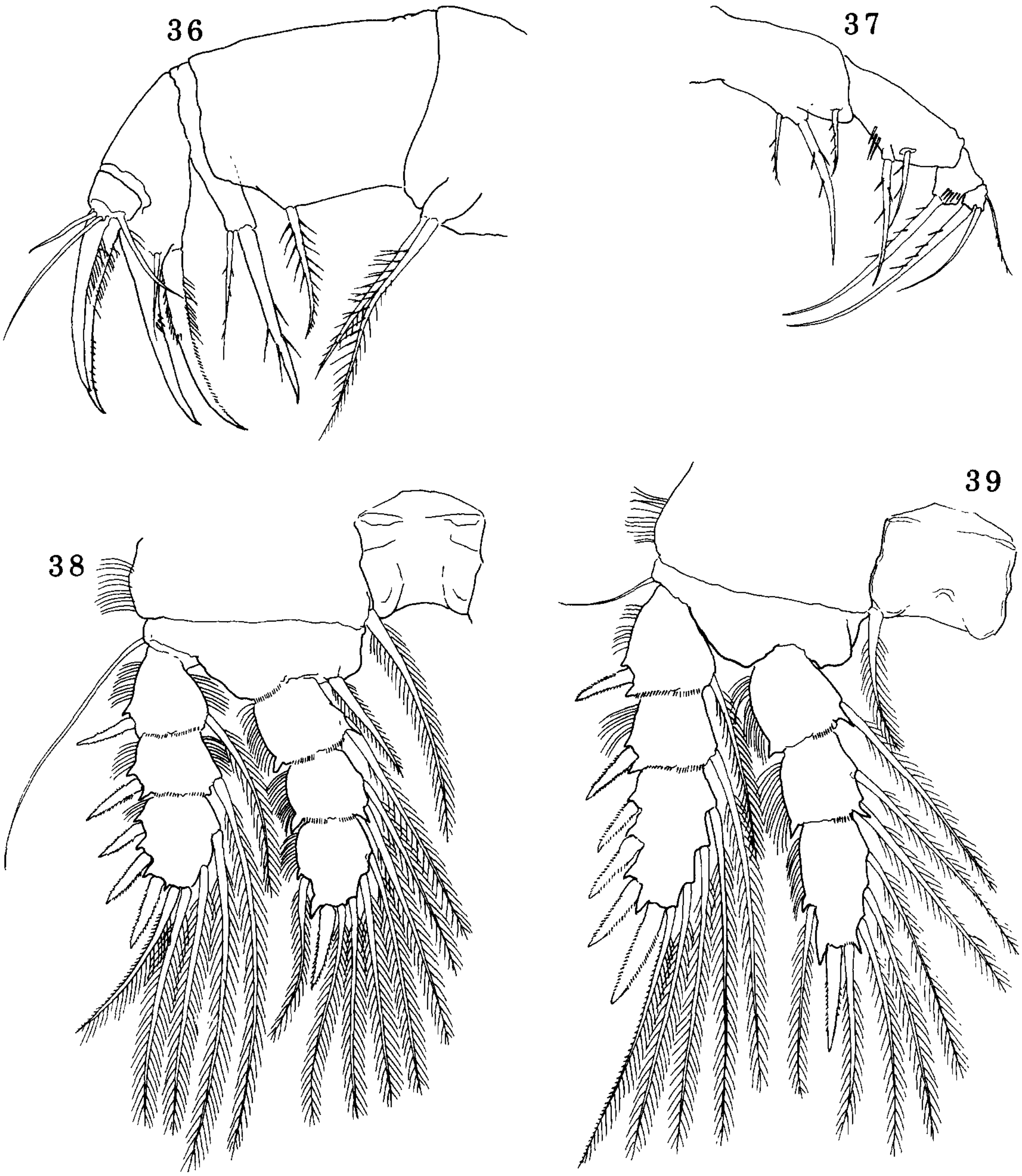
Variation. – Of 22 females examined, 11 had 1 spine on leg 5, and 11 had 2 spines; of 12 males, 3 had 1 spine and 9, 2 spines. A few intergrades with an additional spine on only 1 leg were also observed.



Figs. 30–35. Acanthocyclops montana, new species, female: 30, antennule; 31, antenna, caudal side; 32, antenna article 1, frontal side; 33, labrum; 34, mandible; 35, maxillule.

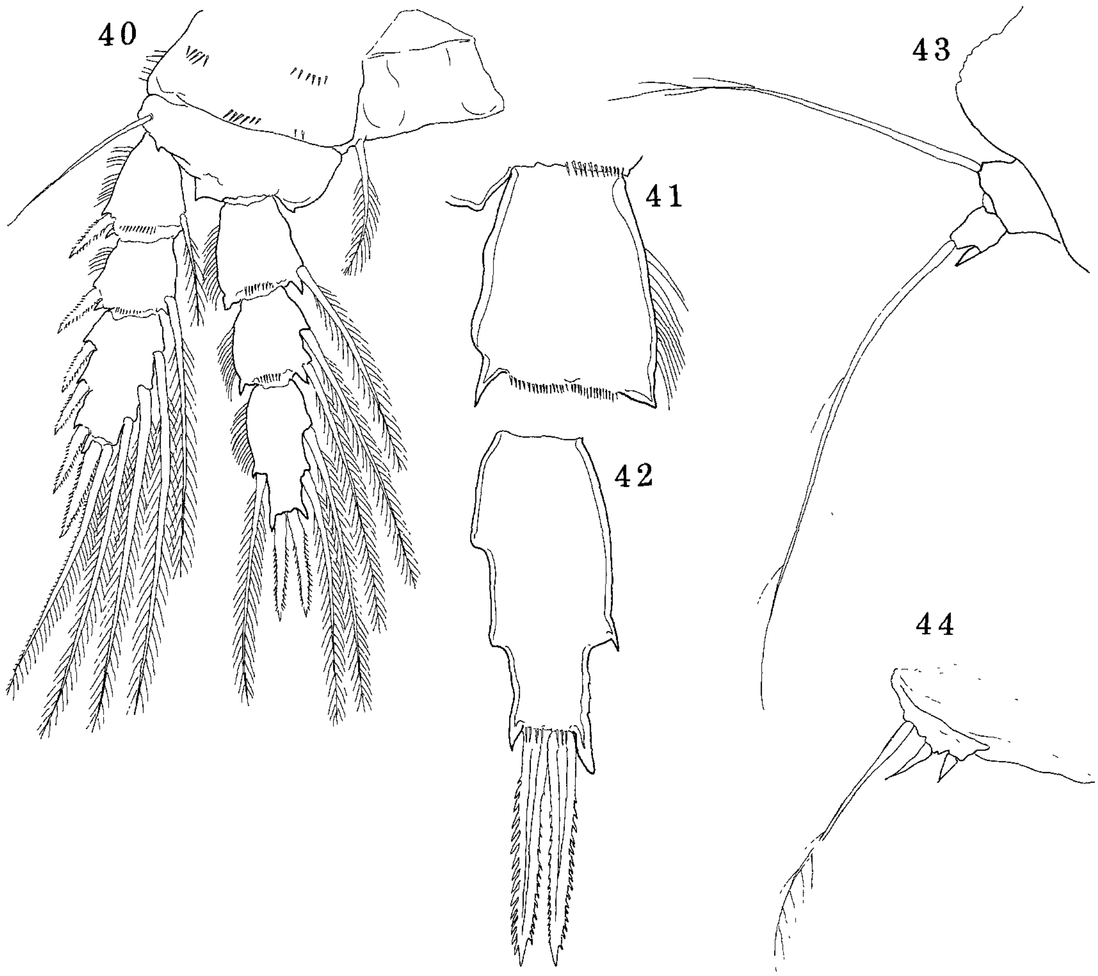
Etymology. – For the specific epithet we propose the name of the state where the species was collected, as a noun in apposition.

Discussion. – Dussart & Defaye (1985) list 32 or 34 species of *Acanthocyclops* sensu Kiefer, 1927, following Kiefer's separation of this group from the related genera *Megacyclops* and *Diacyclops* Kiefer, 1927. The number of species of *Acanthocyclops* depends on whether *A. hispanicus* Kiefer, 1937 and *A. sambugarae* Kiefer, 1981 are considered synonymous with *A. kieferi* (Chappuis, 1925). In addition, subspecies of several species have been distinguished. Of the species listed by



Figs. 36–39. Acanthocyclops montana, new species, female: 36, maxilla; 37, maxilliped; 38, leg 1 and coupler, anterior; 39, leg 3 and coupler, anterior.

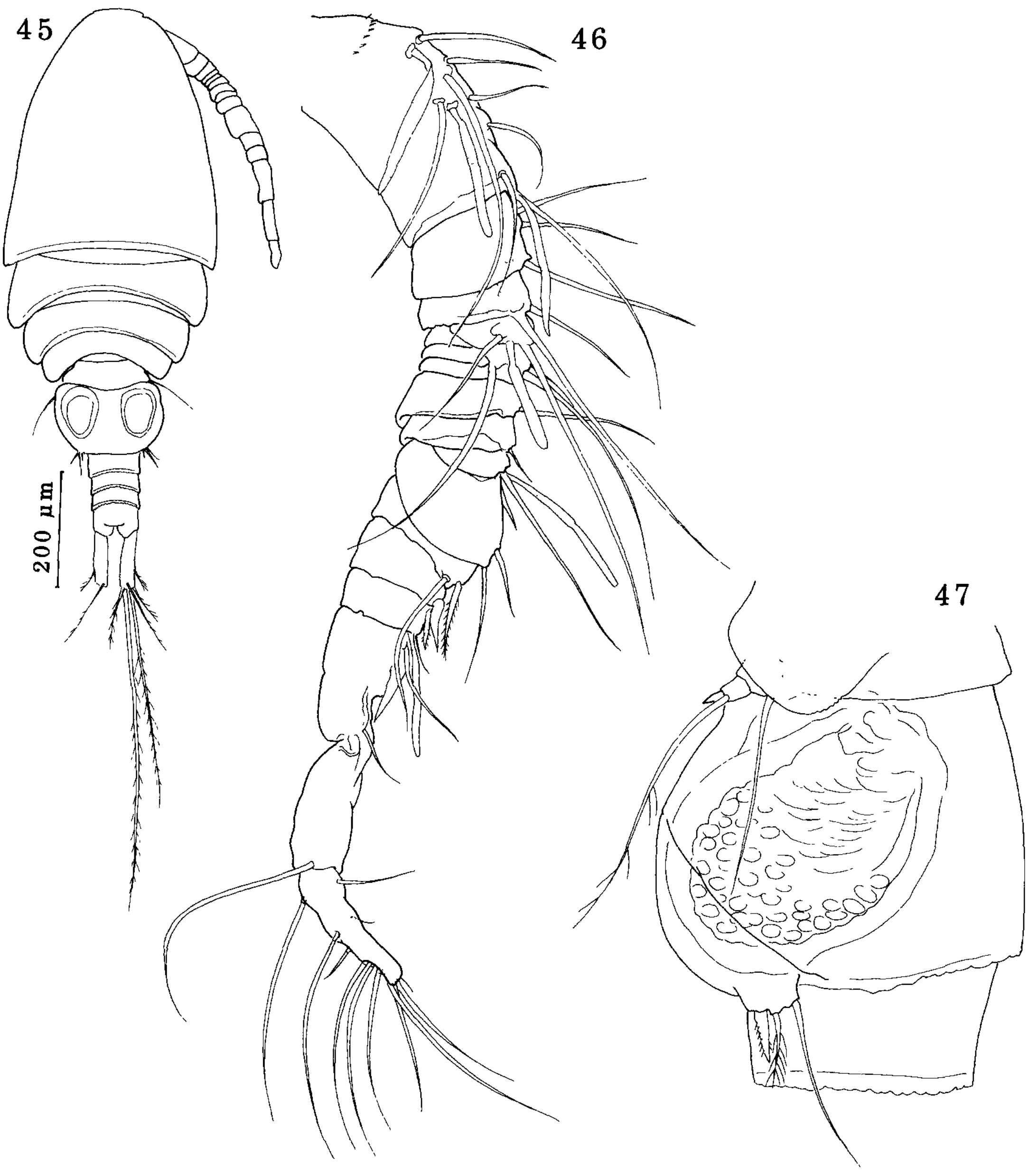
Dussart and Defaye, *A. niceae* (Mann, 1941) has long been considered a synonym of *Megacyclops viridis* (Jurine, 1820) (Lindberg, 1953: 157). The following species are described as having a long inner subterminal spine on leg 5, and therefore should be considered members of the genus *Diacyclops*: *A. mirnyi* Borutzky & Vinogradov, 1957; *A. intermedius* Mazepova, 1952; and *A. tenuispinalis* and *A. longifurcus* Shen & Sung, 1963. The incompletely described *A. plattensis* Pennak & Ward, 1985 is not included here because the descriptions of leg 4 and leg 5 contain unrecon-



Figs. 40–44. Acanthocyclops montana, new species, female: 40, leg 4 and coupler, posterior; 41, left leg 4 endopodite article 1, anterior; 42, left leg 4 endopodite article 3, anterior; 43, leg 5; 44, leg 6.

ciled differences from the generic diagnoses of both *Diacyclops* and *Acanthocyclops*.

Known species of *Acanthocyclops* sensu Kiefer can be distinguished from the Montana species through a series of major characters. Authors of species not listed by Dussart & Defaye (1985) are listed in the References. Species having the antennule composed of 17 articles in the female include *A. vernalis*, *A. robustus* (G.O. Sars, 1863). *A. sensitivus* (Graeter & Chappuis, 1914), *A. carolinianus* (Yeatman, 1944), *A. kagaensis* Ito, 1964, *A. orientalis* Borutzky, 1966, *A. gordani* Petkovski, 1971, and *A. cephallenus* Pesce, 1978 (1979). Species having the antennule apparently always of 11 articles include *A. kieferi*, *A. reductus* (Chappuis, 1925), *A. exilis* (Coker, 1934), *A. hispanicus*, *A. notabilis* Mazepova, 1950, *A. profundus* Mazepova, 1950, *A. biarticulatus* Monchenko, 1972, *A. sambugarae*, *A. petkovskii* Pesce & Lattinger, 1983, *A. similis* Flössner, 1984, and *A. parvulus* Strayer, 1988 (1989). *A. columbiensis* Reid, 1990, has the antennule of the female of 14 articles. Of the two species of which the female is undescribed, *A. skottsbergi* Lindberg, 1949 has the inner margin of the caudal ramus haired; and *A. agamus* Kiefer, 1938 has a short caudal ramus, only 2.3 times longer than broad, and either or both the endopodite and exopodite of legs 1–4 biarticulate. Of the several species having the antennule always or sometimes com-



Figs. 45–47. Acanthocyclops montana, new species, male: 45, habitus, dorsal; 46, antennule; 47, prosomite 5 and anterior urosome, left lateral.

posed of 12 articles, four have a spine formula of 2,3,3,3: *A. michaelseni* (Mrázek, 1901), *A. morimotoi* Ito, 1952, *A. signifer* Mazepova, 1952, and *A. venustoides* (Coker, 1934) and its subspecies. Two species have the lateral seta of the caudal ramus inserted at midlength: *A. capillatus* (G.O. Sars, 1863) and *A. muscicola* (Lastoschkin, 1924). *A. venustus* (Norman & Scott, 1906) and its subspecies have 5 setae on the exopodite 3 of legs 1–4, and the inner surface of the caudal ramus usually haired; and in *A. rupestris* Mazepova, 1950 the inner surface of the caudal ramus is haired. *A. rhenanus* Kiefer, 1936 has the leg 4 endopodite 3 short and armed with 2 terminal spines which are unequal in length. *A. miurai* Ito, 1957 has the leg 4 endopodite 3 armed with a terminal spine and seta.

The status of *A. phreaticus* (Chappuis, 1928) requires discussion. Dussart & Defaye (1985) treated the taxon as a junior synonym of *A. venustus*, apparently following the decision of Rosol & Štěrba (1983). The latter authors, arguing from overlapping dimensions of several morphological characters, synonymized *A. phreaticus* and several other species with *A. venustus*. Lacking material of *A. phreaticus*, which apparently has not been collected again since its original discovery in caves in Romania, Rosol and Štěrba based their treatment on the description and figures supplied by Damian-Georgescu (1963), which consist of a translation into Romanian of Chappuis' original description, plus copies, somewhat redrawn, of Chappuis' figures. For lack of material, Rosol and Štěrba's treatment of *A. phreaticus* is necessarily brief, and their main argument for synonymizing this species with *A. venustus* seems to be a general similarity of proportion, plus an assumption that Chappuis neglected to observe hairs on the inner margin of the caudal rami. We consider these to be inadequate grounds for synonymization, since Chappuis was a meticulous observer and included fine details of the setae and spines of the leg 4 endopodite 3 in his figure for *A. phreaticus*. In addition, Rosol & Štěrba (1983) stated that for the *A. venustus* group, the presence of circular cuticular pitting, lamellar sculpturing, and fine spinules on the dorsal body surface are characteristic, while Chappuis (1928) neither described nor mentioned such structures in *A. phreaticus*. Also, Chappuis (1928) did not give the spine or seta formula for *A. phreaticus*. Pending collection of additional material of *A. phreaticus* for comparison with *A. venustus*, therefore, the former should continue to be considered a valid species.

Of all its congeners, *A. phreaticus*, although incompletely described, most closely resembles the species from Montana in having the antennule of 12 articles; the proportions, naked inner margin, and placement of the lateral seta of the caudal ramus; the general proportion of the leg 4 endopodite 3; and, possibly, in the lack of cuticular ornamentation. There are, however, several differences: the specimens from Montana are larger (females about 1.1–1.4 mm vs. 0.85 mm for *A. phreaticus*); the innermost terminal seta of the caudal ramus is shorter (about 1.2 times the length of the caudal ramus in *A. montana* vs. 2 times longer in *A. phreaticus*); the dorsal caudal seta of *A. phreaticus* is shorter (measured from Chappuis' Fig. 1, 0.5 times the length of the lateral border of the ramus, while the dorsal seta of *A. montana* is about 1.5 times the length of the ramus); and the terminal spines of the leg 4 endopodite 3 are slightly longer in relation to the length of the endopodite 3 (about 0.82 times in *A. montana*, versus about 0.75 times in *A. phreaticus*). Additionally, Chappuis' figure of the seminal receptacle shows a trapezoidal posterior expansion, whereas the posterior expansion is broad and quadrate in the Montana specimens. Chappuis (1928, Fig. 4) gave no indication of the large, usually recurved pore-canal which is prominent in the Montana species. Although these differences may seem small, we believe that they are sufficient to distinguish these taxa. Rather than cause confusion by introducing a probably unjustified extension of the diagnosis of *A. phreaticus*, we have taken the more conservative course of treating the Montana material as a new species.

A. montana is a common inhabitant of the groundwaters of the Flathead system, individuals being present in 18 of 23 wells from which biological samples were taken (only wells containing this species and/or *D. languidoides* are shown in Fig. 1). As many as 117 individuals of *A. montana* were taken in a single sample, although most samples contained fewer than 20 individuals (J.V. Ward and N. Voelz, unpublished). Interestingly, *A. montana* shows no particular morphological adaptation for a groundwater environment, except perhaps the long antennular and dorsal caudal setae of both sexes, and the large seminal vesicles of the male. The high porosity of the alluvium in the Flathead system may account for the success of this relatively large species in a groundwater habitat.

Yeatman (1951) described a new subspecies *bispinosus* of *Acanthocyclops venustoides* (Coker, 1934), based on several populations in Ohio possessing a spine on the outer margin of article 2 of leg 5, in addition to the normal armament of terminal seta and inner subterminal spine. Some specimens had a second, larger spine on the inner margin of article 2. Both forms were found together with 'normal' *A. venustoides*, as well as some intergrades having one leg 5 of each type. Earlier, Willey (1934) (identified as *A. venustus* Norman & Scott, 1906) and Smith & Fernando (1977, 1978) described populations of this species including some specimens with both legs having an extra outer spine, as well as intergrades, from Quebec and Ontario respectively. Strayer (1988 (1989)) reported copepodids of *A. venustoides* having fifth legs bearing an extra outer spine, but found no adults with this feature. Several populations of a species attributed to *A. venustoides bispinosus* and having both inner and outer spines on the fifth legs were reported by Ishida (1984) from Hokkaido. However, it is probable that the Hokkaido specimens are better ascribed to another species of *Acanthocyclops*, since the figures supplied (Ishida, 1984; Fig. 2E, G) show an antennule of 17 articles, a caudal ramus with a single group of hairs on the inner margin, and strikingly long leg 5 spines. The genus *Acanthocyclops* includes several variable species, most notoriously *A. vernalis* and *A. robustus*, which are highly plastic in the armament of the swimming legs. In view of the pattern of occurrence of the extra outer spine of leg 5 in *A. venustoides*, we consider this structure as a variation occurring in some populations of the nominate species, and are therefore of the opinion that the subspecies *bispinosus* should be treated as a junior synonym of *venustoides* s. str. This opinion is reinforced by the occurrence of similar variation of the same structure in several populations of *A. montana*.

Since *A. montana* is the third species of *Acanthocyclops* to have been described recently from North America, it seems useful to present a table to aid in distinguishing species of this region (Table 3); characters selected are primarily those used by Yeatman (1959). Construction of a world key to the genus is made difficult at present by inadequate descriptions of some species, and lack of knowledge of the females of others. In Table 3, *A. vernalis* and *A. robustus* are not separated. Although the two species appear to be ecologically separate in some areas (Fryer, 1985), their distinction on morphological grounds is a difficult and still incompletely resolved question, particularly as regards taxa outside Europe (Kiefer, 1976), and indeed each taxon may represent a group of sibling species (Reed, 1986).

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Table 3. Distinguishing morphological characters of females of species of *Acanthocyclops* recorded from North America. Abbreviations: SEF, setal formula (number of setae on P1–4 exp3 respectively); SPF, spine formula (number of spines on P1–4 exp3 respectively); P1–4, legs 1–4; exp, exopodite; enp, endopodite.

Species	Antennule no. articles	Caudal ramus inner surface	SPF	SEF	P4enp3, lengths of terminal spines
Vernalis, robustus	17–18	Without hairs	Variable	Variable	Subequal
Carolinianus	17	Tufts of hair	Variable	Variable	Subequal
Columbiensis	14	Naked	2,3,3,3	4,4,4,4	Unequal
Montana	12	Naked	3,4,4,4	4,4,4,4	Subequal
Capillatus	12	Naked	3,4,4,4	5,5,5,5	Subequal
Venustoides	12	Finely haired	2,3,3,3	4,4,4,4	Unequal
Venustus	12	Finely haired	3,4,4,4	5,5,5,5	Unequal
Exilis	11–12	Naked	2,3,3,3	4,4,4,4	Unequal
Parvulus	11	Naked	2,3,3,3	4,4,4,4	Subequal

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