Cyclops strenuus (Fischer, 1851) sensu lato in Alaska and Canada, with new records of occurrence

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Abstract: References to *Cyclops strenuus* in the North American literature are reviewed. Male and female specimens of *C. strenuus* sensu lato from 20 sites in Alaska, Yukon, Northwest Territories, and Saskatchewan were measured and compared using several morphological parameters. Two or more phenotypes may be present among the 20 populations. The specimens examined differ sharply from *Cyclops canadensis* Einsle, 1988, especially in the length of the caudal ramus, length of the antennules, width of prosomites 4 and 5, and length of the lateralmost and medialmost terminal caudal setae. Thus, Einsle's conclusion that previous records of *C. strenuus* in North America are likely referable to *C. canadensis* may be premature. New records of *C. strenuus* away from northern coastal areas of Alaska and Canada include Saint Matthew and Nunivak islands, two interior Alaska locations, Galena and Chatanika, and four locations in central and southern Saskatchewan. Passive dispersal via migrating waterfowl may account for the presence of *C strenuus* in Saskatchewan. To date, only a very few individuals of *C. strenuus* s.l. from a very large area in North America have been examined. Final decisions about relationships among Nearctic *C. strenuus* and their relationships to Palearctic congeners must await the examination of many more animals and investigations using biochemical or chromosomal techniques in conjunction with morphology.

Résumé : Les mentions de *Cyclops strenuus* dans la littérature nord-américaine ont été réexaminées. Des mâles et des femelles de *C. strenuus* sensu lato à 20 sites en Alaska, au Yukon, dans les Territoires du Nord-Ouest et en Saskatchewan ont été mesurés et plusieurs de leurs caractéristiques morphologiques ont été comparées. Il semble exister au moins deux phénotypes, peut-être plus, chez ces 20 populations. Les cyclops examinés diffèrent fortement de *Cyclops canadensis* Einsle, 1988, particulièrement par la longueur de leur rame caudale, la longueur de leurs antennules, la largeur de leurs prosomites 4 et 5 et la longueur de leurs soies caudales terminales les plus latérales et les plus médianes. L'hypothèse d'Einsle selon laquelle les *C. strenuus* trouvés préalablement en Amérique du Nord sont probablement des *C. canadensis* semble prématurée. De nouveaux spécimens de *C. strenuus* ont été trouvés loin des régions côtières nordiques de l'Alaska et du Canada, notamment dans les îles Saint Matthew et Nunivak, à deux endroits dans les terres en Alaska, Galena et Chatanika, et à quatre endroits dans le centre et le sud de la Saskatchewan. La dispersion passive par des oiseaux aquatiques en migration pourrait expliquer la présence de *C. strenuus* en Saskatchewan. À ce jour, seuls quelques rares spécimens de *C. strenuus* s.l. provenant d'une vaste zone en Amérique du Nord ont été examinées. L'examen d'dun nombre considérable d'animaux et des études basées sur l'utilisation de techniques biochimiques et chromosomiques combinées à des études morphologiques s'imposent avant qu'il ne soit possible de parvenir à des décisions finales sur les relations entre les *C. strenuus* néarctiques et sur leurs relations avec leurs congénères paléarctiques.
[Traduit par la Rédaction]

Introduction

Cyclops strenuus (Fischer, 1851) was the first species described in the genus now known as *Cyclops* O.F. Müller (sensu restricto Kiefer 1939) (Dussart and Defaye 1985). The members of *Cyclops* s.str. are frequently known collectively as the *C. strenuus*-group (Einsle 1975). The group is widespread geographically and some of its members are quite variable morphologically, leading to the naming of many species, subspecies, and forms; Lindberg (1957) recognized 56 species and subspecies (Einsle 1975). For western Europe, Einsle (1975) reduced the list to 10 species, using characters of chromatin diminution and morphology. Of these 10 taxa, 5 have been reported in North America: *C. strenuus*, *C. scutifer* G.O. Sars, 1863; *C. furcifer* Claus, 1857; *C. vicinus* Uljanin, 1875; and *C. kolensis* Lilljeborg, 1901. The records of *C. vicinus* may be in error and actually refer to *C. kolensis alaskaensis* Lindberg, 1956 (Reed 1968, 1995). Only *C. strenuus* is discussed in this paper.

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Cyclops strenuus was first reported in North America by Marsh (1912), who listed species that he believed were synonymous with Fischer's species: *C. furcifer*, *C. scutifer*, *C. abyssorum*, *C. vicinus*, and *C. kolensis*. Marsh stated that for the most part the synonymy of Schmeil (1891, 1892, 1893) was followed and "granting the limits of variation as stated by him, the species published by Lilljeborg 1901, *scutifer*, *vicinus*, *miniatus*, and *kolensis* should be considered as varieties, and it would be a matter of personal opinion whether or not it is worth-while to recognize them under distinct names" (p. 253).

Marsh (1912) had specimens from Rock Pond, Axton, New York (the United States Postal Service does not now list Axton, N.Y.), which he compared with specimens from Syria that he had identified as *C. strenuus* (Marsh 1926). An indication of the variability Marsh (1912) was willing to give *C. strenuus* may lie in his comparison of caudal rami. Marsh's drawing (1912, Fig. 4) of the ramus of Syrian animals has a length to width ratio of nearly 6.3, while the same ratio of the Axton animals (Fig. 5) is about 4.1. Marsh's habitus figure of the female (Fig. 1) shows prosomites 4 and 5 more similar to *C. scutifer* than *C. strenuus*.

Marsh prepared the section on freshwater Copepoda for the report of the Canadian Arctic Expedition 1913–1918 from specimens collected by Frits Johansen along the northern coasts of Alaska and the Northwest Territories (Marsh 1920). In his report Marsh reiterated his opinion concerning *C. strenuus* and other members of what is now recognized as the genus *Cyclops* s.str.: "This species (*C. strenuus*) is discussed in Marsh, 1912, and its synonymy indicated. Sars, 1913, has been published since the appearance of Marsh's paper, and in that work *C. abyssorum*, *C. lacustris*, and *C. scutifer* are separated from *C. strenuus*. The characteristics which separate these species from *C. strenuus* are difficult to recognize, and do not appear to have even varietal value. In the opinion of the present author these names should be considered synonyms" (Marsh 1920, p. 10*j*).

Marsh (1920) further stated, "This (*C. strenuus*) was, perhaps, the most common form of copepod found in the collections of the expedition." Marsh listed several dates on which *C. strenuus* was collected at Bernard Harbour, N.W.T. These Bernard Harbour specimens may be the source of his habitus figure (Marsh 1920, Fig. 2, p. 23*j*), since he gave length measurements of females from Bernard Harbour (p. 11*j*). This figure and that drawn from New York State animals have been regarded as actually being *C. scutifer*, e.g., Yeatman (1944; H.C. Yeatman, personal communication to K. Elgmork) (Elgmork 1967, p. 967). Marsh's 1920 drawing clearly reveals a specimen flattened by cover glass pressure and could certainly represent *C. scutifer*. However, even if the animal represented as *C. strenuus* in Fig. 2 is *C. scutifer*, this does not mean that all of the *Cyclops* s.str. seen by Marsh were *C. scutifer*. Since Marsh regarded *C. strenuus* and *C. scutifer* as synonymous, his model for Fig. 2 could just as well have come from Bernard Harbour collections as elsewhere.

Johansen (1922) described in considerable detail the bodies of water from which he collected specimens for the Arctic Expedition. From Johansen's description, it is clear that the "big" lakes opposite Bernard Harbour were among the most limnetic-like habitats visited. Many of the waters were paludal, containing higher aquatic macrophytes and supporting a variety of invertebrates commonly regarded as benthic in shallow-water habitats.

Reed (1962) found that in ponds and lakes along the Colville River, Alaska, animals identified as *C. strenuus* usually occurred in weedy shallow waters, while *C. scutifer* tended to be found in more open waters, although the apparent ecological separation was incomplete, since the two species were collected together on two occasions. Considering the number of paludal habitats visited by the Canadian Arctic Expedition and the tendency of *C. strenuus* to be associated with them, it seems almost inevitable that Marsh did in fact see other copepods of the *C. strenuus*-group in addition to *C. scutifer*.

The United States National Museum obtained new collections (Catalog No. 58784) from the big lake opposite Bernard Harbour in 1924 that contained *C. scutifer*, and these specimens were used by Yeatman (1944) in his description of North American *C. scutifer*. The new collections, presumably from the same lake where Johansen had collected in 1915–1916, simply reinforced the belief that Marsh had not seen *C. strenuus* from N.W.T. Given present knowledge of the habitat difference of *C. strenuus* and *C. scutifer* in North America, it is clear that the 1924 efforts might have been more usefully spent on paludal waters if the intent of the collection was to determine if Marsh had really seen *C. strenuus*.

Yeatman (1944) included *C. strenuus* in his treatment of North American cyclopoids, anticipating that it might turn up on the continent, although at that time he knew of no authentic record from North America.

When the second edition of Ward and Whipple's *Freshwater Biology* appeared, Yeatman had examined copepods from Alaska that he identified as *Cyclops strenuus* Fischer, 1851 (Yeatman 1959), including specimens sent to him by E.B.R. from the Colville River area of northern Alaska. Yeatman characterized *C. strenuus* for purposes of his key as follows: "Fourth and fifth metasomal segments not laterally expanded (in contrast to those of *C. scutifer*), but usually with small projections at posterolateral angles of these segments; caudal ramus usually at least 5 to 7 times as long as broad; outer lateral seta attached at a point 73 to 87 percent of distance from base to apex of caudal ramus" (Yeatman 1959, p. 801).

Scheffer (1959) found *C. strenuus* in the Aleutian Islands. Reed (1962) reported *C. strenuus* from 29 different ponds and smaller waters in the Colville River drainage in Alaska. Reed (1963) reported *C. strenuus* from ponds on Prince Patrick Island, Victoria Island, Southampton Island, and Adelaide Peninsula. Tash and Armitage (1967) and Tash (1971) reported *C. strenuus* to be a major species in ponds in the Cape Thompson, Alaska, area, but also occasionally in lakes. Stross and Kangas (1969) mentioned the occurrence of *C. strenuus* in ponds near Imikpuk Lake, Point Barrow, Alaska. Patalas (1975) and Patalas and Patalas (1978) reported *C. s. strenuus* as a minor constituent in the plankton of the western section of Great Slave Lake. Selgeby (1975) reported finding *C. strenuus* in the St. Marys River, the outlet of Lake Superior, Einsle (1988) named *C. canadensis*, a member of the *strenuus*-group, from specimens collected

Table 1. Sites of collection of *Cyclops strenuus* s. measured in this study.

Location	Designation	Coordinates
Alaska		
1. Point Barrow	Barrow	71°23′N, 156°30′W
2. Umiat	Umiat	69°17′N, 152°12′W
3. Anaktuvuk	Anak	69°36′N, 151°32′W
4. Kikiakrorak	Kik	70°01′N, 151°36′W
5. Ocean Point		70°10′N, 151°04′W
6. Oliktok Point	Olik	70°32′N, 150°30′W
7. Chatanika	Chat	65°07′N, 147°31′W
8. Galena	Galena	64°44′N, 156°57′W
9. Saint Matthew Island		60°30′N, 172°45′W
10. Nunivak Island	Nun	60°00′N, 166°30′W
Yukon Territory		
11. Shingle Point	Shingle	68°56′N, 137°15′W
Northwest Territories		
12. Prince Patrick Island		76°30′N, 119°00′W
13. Victoria Island	Vic	69°30′N, 105°00′W
14. Southampton Island	South	64°09′N, 82°53′W
15. Tuktoyaktuk	Tuk	69°27′N, 133°02′W
16. Adelaide Peninsula	Adel	68°09′N, 97°45′W
Saskatchewan		
17. Abbey	Abbey	50°43′N, 108°45′W
18. Leofnard	Leof	52°33′N, 105°43′W
19. Wakaw	Wakaw	52°40′N, 105°35′W
20. Unity	Unity	52°27′N, 109°10′W

Note: "Designation" refers to the abbreviation used in the tables.

near Igloolik, N.W.T. Chenglath and Shih (1994) compiled literature references to freshwater copepods occurring in northwestern North America that included *C. strenuus* from Saskatchewan. C. Shih (personal communication) indicated that the inclusion of Saskatchewan was an error.

The purposes of this paper are to revisit records of *C. strenuus* s.l., a major component of the zooplankton in many northern waters, as they pertain to North America, give new localities of occurrence and add to the stock of morphological information about females begun by Einsle (1988), and provide the first quantitative morphometric data on males.

Uncertainty as to the equivalence of North American species with European species raises problems of nomenclature; to keep terminology simple, names are used as they appear in the North American literature.

Materials and methods

Cyclops strenuus s.l. specimens from 20 sites in Alaska, Northwest Territories, Yukon Territory, and Saskatchewan (Table 1) were examined qualitatively and quantitatively in regard to several morphological characters (Table 2). Material as whole specimens in alcohol or as whole or dissected specimens mounted on permanent microscope slides was available for review in this study. In some instances, specimens measured in earlier studies were no longer extant. The same parameters were considered in all studies over the years; however, not all parameters were measured on all specimens.

Copepods were measured in glycerin and examined in glycerin or lactophenol. Some animals were placed in a weak solution of sodium hypochlorite for up to 1 min before transfer to lactophenol. This treatment essentially removes all soft tissue, leaving the exoskeleton nearly glasslike; a strong solution or protracted immersion may cause disarticulated setae.

When possible, drawings, especially those of the habitus and large appendages, were made without cover slips. Details were checked using oil-immersion lenses. An ocular micrometer was used to obtain data on 18 parameters of female and 19 parameters of male copepods (Table 2). All parameters except total length and the length of the spine on leg 6 (P6 spine in tables) correspond to those used by Kosminski in the 1930s in developing a scheme for systematically measuring adult females of the *Cyclops* s.str. group (Dussart 1958; Einsle 1975; Kiefer 1978).

Clearly, multivariate statistics would be the method of choice in analysis of these data, as measurements were made on several morphological characters. However, numerous missing observations precluded multivariate analysis, therefore univariate analysis of variance (ANOVA) was used (SAS Institute Inc. 1990) to aid in determining whether there were significant differences among animals from different sites.

Results

Our material included unmounted and mounted specimens, raising the question of whether measurements from both could be combined for statistical analysis. Sufficient material from Point Barrow enabled a meaningful comparison of four parameters of each type of material to be made. The total length of 19 unmounted females averagegd 1794 μm and that of 13 mounted females 1704 μm. The t test rejected a null hypothesis of no difference (t = 2.98, P = 0.01), therefore analyses of total length are from unmounted animals only. Mean lengths of the caudal ramus and medialmost and lateralmost terminal caudal setae did not differ significantly (P = 0.05) between mounted and unmounted specimens, therefore analyses of these parameters include mounted specimens that are indicated in the tables.

Qualitative morphology

Female

Length without caudal setae 1350–1960 μm. Body robust, width about 1/3 of length (Figs. 1A, 1B). Cephalothorax widest at hind margin (occasionally at midlength). Posterior margins of prosomites 2 and 3 smoothly rounded. Prosomite 4 width at midlength subequal to width at posterior margin, posterolateral margin produced outwardly in a rounded papilliform projection that may be recurved (Figs. 1C, 1D). Prosomite 5 posterolateral margin produced into two projections, one directed posteriorly, one laterally (Figs. 1C, 1D), greatest width across lateral projections. Genital segment widened anteriorly, width usually exceeding length (Figs. 1A–1D). Posterior margins of urosomites smooth.

Caudal ramus with prominent dorsal chitinous ridge (Figs. 1G, 1H), medial margin hairy, rami slightly to noticeably divergent, lateral seta inserted at about 77–80% of

Table 2. Morphological parameters measured on specimens of *Cyclops strenuus* s. from Alaska and Canada, with abbreviations used in tables.

Parameter	Abbreviation	Females	Males
Distance from most anterior tip of prosome to distal end of caudal ramus	Total length	x	x
Distance from most anterior end of first prosomite to its distal margin	Cephalo length	x	x
Greatest distance across same	Cephalo width	x	x
Greatest distance across prosomite 4	TH4 width	x	x
Greatest distance across prosomite 5	TH5 width	x	x
Distance from anterior margin to posterior margin of genital somite	Genital length	x	x
Greatest distance across genital somite	Genital width	x	x
Distance from anterior margin of caudal ramus to bases of terminal caudal setae	Ramus length	x	x
Greatest width of caudal ramus	Ramus width	x	x
Distance from anterior margin of caudal ramus to insertion of lateral seta as a percentage of ramus length	Insertion	x	x
Length of most mesial terminal caudal seta	Seta 1	x	x
Length of second most mesial terminal caudal seta	Seta 2	x	x
Length of second most lateral terminal caudal seta	Seta 3	x	x
Length of most lateral caudal seta	Seta 4	x	x
Length of terminal article, endopodite, fourth pair of legs	P4 length	x	x
Greatest width of article	P4 width	x	x
Length of mesial terminal spine, same article	P4 inner spine	x	x
Length of lateral terminal spine, same article	P4 outer spine	x	x
Length of spine, leg 6	P6 spine		x

ramus length, length about 5× width. Medialmost terminal caudal seta about 80% of ramus length and about 150% of lateralmost terminal seta.

Swimming legs 1–4 (Figs. 1E, 1F, 2A–2D) with 3,4,3,3 spines on terminal articles of exopodites, number of setae 5,5,5,5. Row of short, stout spinules on upper lateral margin anterior face of coxa leg 3 (Fig. 2C). First article of leg 4 exopodite with J-shaped or slanted row of prominent spinules near distal margin (Fig. 2D). Leg 5 (Fig. 2J) of 2 articles; lateral and terminal setae short; medial slightly longer than width of article 2. Terminal article endopodite leg 4, length about 2.5× width (Figs. 2B, 2D); medial terminal spine about twice length of lateral spine. Coxa leg 4 ornamented with lines or groups of spinules that vary from tooth-like to fine; patterns of ornamentation vary (Figs. 2B, 2D–2H). Coupler of leg 4 with 1, 2, or no lines of hairlike setules (Figs. 2A, 2B, 2D–2H).

Male

Length without caudal setae 1120–1550 μm. Prosomites 4 and 5 lacking lateral expansion (Fig. 2K). Caudal ramus without chitinous ridge, haired on medial margin; lateral seta inserted at about 75% of length; length about 4.8× width. Caudal seta 1 about equal to ramus length and not quite twice length of seta 4.

Number of spines on terminal articles of legs 1–4, 3,4,3,3. Coxa of leg 1 (Fig. 3A) with a cluster of small spinules near lateral margin. Coxa of leg 2 with cluster of stout spinules near lateral margin and proximal group of fine spinules (Fig. 2B). Coxa of leg 3 with line of spinules near upper lateral margin (Fig. 2C). Leg 4 similar to that of female, terminal article exopodite elongated, length 3× width; medial terminal spine shorter than article length (about 2/3), medial spine about twice length of lateral terminal spine; pattern of spinules on coxa (Fig. 3D) similar to that of female. Leg 5 (Fig. 2L) similar to that of female. Leg 6 (Fig. 3E) dorsal and medial setae much longer than spine.

Pooled measurements

About 100 female and 25 male specimens referable to *Cyclops strenuus* s.l. from 20 North American sites (Table 1) were examined. Einsle (1988) pointed out the dearth of quantitative data concerning *C. strenuus* from this continent; hence, considerable effort went into analysing the measurements obtained.

Specimens were pooled by sex (Tables 3 and 4) to gain insight into overall ranges and variations of the parameters measured. Specimens were also segregated by sex and site (Appendix Tables 1 and 2).[1] ANOVA was applied to measurements pooled by sex (Tables 3 and 4).

ANOVA revealed that 12 of 18 morphological parameters measured on females differed at the $P = 0.05$ level, and of these, 10 differed at the $P = 0.01$ level (Table 3). The percentage of variance due to among-site factors clearly exceeded the percentage of within-source variance for five parameters: P4 length, TH5 and genital widths, and cephalo

The Appendix may be purchased from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

Fig. 1. *Cyclops strenuus* s.l., female. (A) Habitus, Oliktok Point. (B) Habitus, Abbey. (C) Prosomites 4 and 5, genital segment, Chatanika. (D) Same, Tuktoyaktuk. (E) Leg 1, Unity. (F) Leg 2, Unity. (G) Caudal ramus, Unity. (H) Same, Point Barrow. Scale bars: *b*, 100 μm; *c*, 200 μm; *d*, 500 μm.

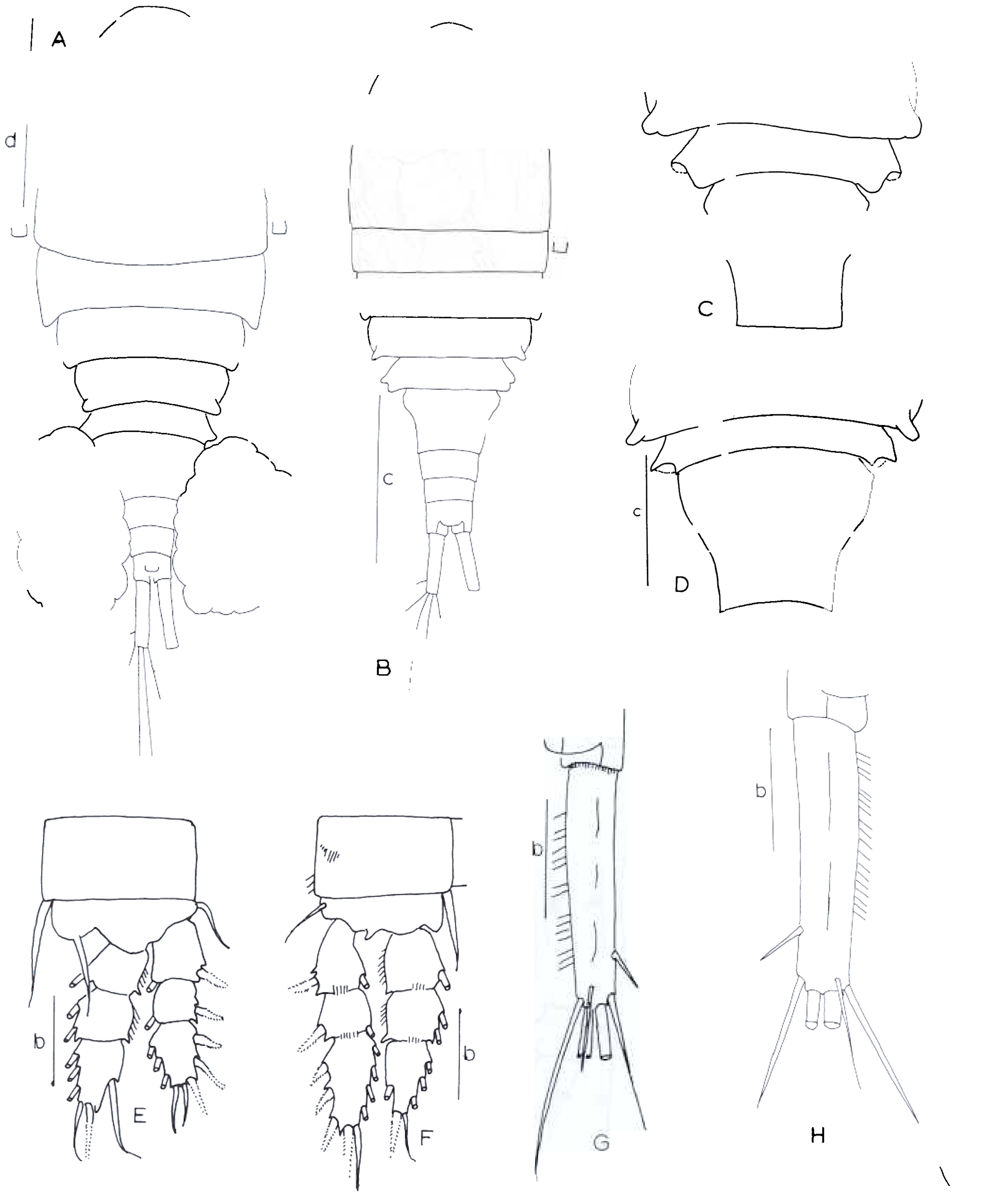

Fig. 2. *Cyclops strenuus* s.l. (A–I). Female. (A) Leg 3, Unity. (B) Leg 4, Unity. (C) Leg 3, Point Barrow. (D) Leg 4, Point Barrow. (E) Coxa, leg 4, Southampton Island. (F) Same, Oliktok Point. (G) Same, Chatanika. (H) Same, Tuktoyaktuk. (I) Leg 5 Unity. (J and K) Male. (J) Habitus, Oliktok Point. (K) Leg 5, Oliktok Point. Scale bars: *a*, 50 μm; *b*, 100 μm; *c*, 400 μm.

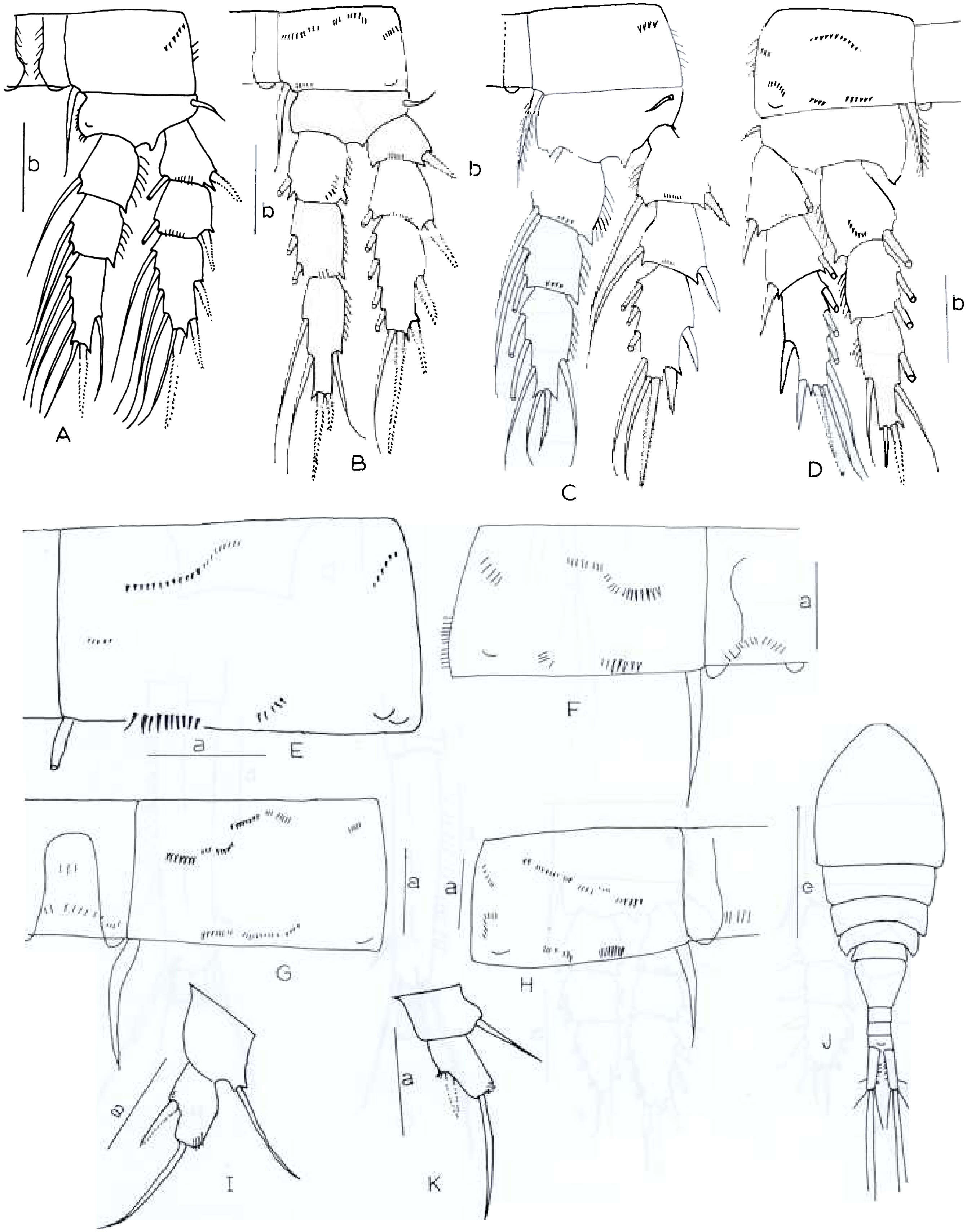

Table 3. Numbers, ranges, means, standard deviations, and coefficients of variation of pooled measurements of female *Cyclops strenuus* s.l. collected in Alaska and Canada.

Parameter	*n*	Range	Mean	SD	CV
Total length	65		1668	92	5.5
Cephalo length	54		638	43	6.8
Cephalo width	32		620	40	6.4
TH4 width	33		389	37	9.5
TH5 width	44		329	34	10.2
Genital length	49		231	23	10.0
Genital width	49		254	35	13.7
Ramus length	88		201	21	10.4
Ramus width	87		37	3	8.3
Insertion	60		75	2	2.8
Seta 1	83		166	19	10.1
Seta 2	60		452	29	6.4
Seta 3	60		393	39	10.1
Seta 4	83		106	12	10.9
P4 length	40		101	9	8.5
P4 width	39		39	5	12.2
P4 inner spine	38		89	9	10.4
P4 outer spine	39		47	7	14.7

Note: Parameters are defined in Table 2. All measurements are given in micrometres.

Table 4. Numbers, ranges, means, standard deviations, and coefficients of variation of pooled measurements of male *Cyclops strenuus* s.l. collected in Alaska and Canada.

Parameter	*n*	Range	Mean	SD	CV
Total length	29	950–1550	1311	141	10.8
Cephalo length	18	400–578	482	34	7.0
Cephalo width	16	400–480	427	21	4.9
TH4 width	11	200–352	248	41	16.5
TH5 width	15	150–226	192	21	10.9
Genital length	18	95–182	125	25	19.8
Genital width	18	137–200	174	19	10.9
Ramus length	29	108–213	143	18	12.6
Ramus width	28	25–38	30	3	10.0
Insertion	18	69–75	73	2	2.7
Seta 1	28	110–178	145	16	11.0
Seta 2	24	200–489	371	48	12.9
Seta 3	23	145–446	305	51	16.7
Seta 4	28	70–112	93	10	10.8
P4 length	16	82–105	90	6	6.7
P4 width	16	25–45	32	5	15.6
P4 inner spine	16	70–100	84	8	9.4
P4 outer spine	16	35–50	42	5	11.9
P6 spine	11	20–32	27	3	11.1

Note: Parameters are defined in Table 2. Measurements are given in micrometres.

length (Table 3). The percentage of within-source variance of total length was larger within sources than among-site variance. The percentages of variance of six parameters showed no clear dominance of either within-source or among-site factors (Table 3).

ANOVA revealed that 10 of 19 morphological parameters measured on males differed at $P = 0.05$; of these, 6 differed at $P = 0.01$ (Table 4). The percentage of variance due to among-sites factors exceeded the percentage of within-source variance for four parameters: total length, TH5 width, P4 inner spine, and seta 4. Percentages of within-source variance were larger than among-sites variance for five parameters: genital length and width, P6 spine, ramus length, seta 1, and P4 inner spine. Percentages were about evenly divided for seta 2 (Table 4).

Site measurements

The Point Barrow females tended to have the greatest mean lengths for several parameters (Appendix Table 1, see footnote 1). Specimens from Unity, Chatanika, Abbey, and Tuktoyaktuk had the smaller mean lengths. The ranges of measurements were much wider at some sites than at others.

Fewer males than females were measured and this may have led to less clear trends for males among sites. Point Barrow males, like the females, tended to have among the larger mean lengths for several parameters (see footnote 1). The few males from Unity and Tuktoyatuk were among the smaller in terms of observed mean length.

Discussion

Point Barrow specimens affected analysis of measurements because of their abundance and their generally large size; for example, the mean total length of all females averaged 1668 μm (Table 3). The mean length of the Point Barrow females was 1794 μm, compared with 1585 μm for females from all other sites. As microscopic examination of copepods proceeded, overall similarity among specimens from all sites emerged for some traits, but at the same time, differences in some morphological characters were noted, suggesting that more than one morphological form seemed to be present. ANOVA revealed statistically significant differences among pooled specimens in regard to some characters (Tables 3 and 4).

Site means and ranges (Appendix Tables 1 and 2, see footnote 1), did not reveal the combination of individual sizes that led to the site population statistics. Frequency distributions which preserved the identity of individual animals suggested that large or small animals tended to be grouped at some sites for some parameters, and that for others, the sizes tended to be more mixed among sites. Table 5 summarizes the trend for females to be predominantly larger or smaller than the parameter mean lengths for populations represented by at least three individuals. Samples from Shingle Point and Southampton Island contained about equal numbers of individuals larger or smaller than the parameter mean length for several characters. Robust animals tended to be found at Point Barrow, Shingle Point, and Southampton Island. More gracile females appeared in Anaktuvuk, Oliktok Point, Nunivak Island, and Chatanika. The Anaktuvuk animals also had relatively long rami.

Lengths of caudal setal characters were well mixed at Shingle Point, Southampton Island, and to a lesser extent at Point Barrow and Tuktoyaktuk. Individuals with long setae predominated in the Victoria Island and Oliktok Point samples, whereas short setae occurred in the Chatanika and Anaktuvuk samples.

Shingle Point and Southampton Island animals were well mixed in sizes of P4 characters. Oliktok Point and Tuktoyak-

Table 5. Sizes of most adult female *C. strenuus* s.l. from sites represented by at least three animals in Canada and Alaska in relation to grand mean lengths.

Parameter	Barrow	Shingle	Vic	South	Anak	Olik	Nun	Chat	Tuk
Total length	L			S	S	S	S	S	
Cephalo width	L		L	S		S		S	
TH5 width	L			L					
Genital length	L		E	L					
Ramus length	L		S	E	L	S		S	S
Seta 1	L		L	E	S	S		S	S
Seta 2	E		L	E	S	L		S	E
Seta 3	L		L	E	E	L		S	E
Seta 4	E		L	S	S	L		S	S
P4 length	E		L	E		E			E
P4 width	L		S	E		S			S
Inner spine	L		E	E		S			S
Outer spine	L		L	E		E			S

Note: Parameters are defined in Table 2 and sites are listed in Table 1. L, most individuals larger than the grand mean length; S, most individuals smaller than the grand mean length; E, individuals about evenly divided.

Table 6. Sizes of most adult male *C. strenuus* s.l. from sites represented by at least two animals in Canada and Alaska in relation to parameter grand mean lengths.

Parameter	Barrow	Olik	Shingle	South
Total length	L	S	S	S
Cephalo width	E	S		E
TH5 width	L	S	S	
Genital length	S	L	S	
Genital width	E	S	S	
Ramus length	L	S	S	E
Seta 1	L	S	E	L
Seta 2	E	E	E	L
Seta 3	L	E	E	E
Seta 4	L	S	E	L
P4 length	L	S		S
P4 width	L	S		S
Inner spine	L	S		S
Outer spine	E	S		L
P6 spine	L	S		L

Note: For an explanation of abbreviations see Tables 1 and 5.

tuk animals had relatively small P4 characters, whereas those of Point Barrow were large.

Thus, more than one form of female *C. strenuus* is statistically and empirically suggested in the data, but the variability which is present means that the forms are not easily defined or geographically delineated except that large, robust animals seemed to occur at Point Barrow, Shingle Point, and Southampton Island. A more slender form(s) seemed to occur at Anaktuvuk, Southampton Island, Oliktok Point, Nunivak Island, and Chatanika. Our samples suggest overlap in traits at Shingle Point and Southampton Island.

Most of the males larger than the parameter mean lengths tended to occur at Point Barrow (Table 6). Oliktok Point males were predominantly among the smaller individuals. Shingle Point and Southampton Island males were mixed. Measurements of males, although fewer than measurements of females, seemed to suggest the existence of two forms, with mixing of the two at Shingle Point and Southampton Island.

Twelve characters of the females (Table 7) and 10 of the males (Table 8) were statistically significant. Most variance seemed to be due to among-site factors, and may be attributable to physical factors such as water temperature or dissolved substances peculiar to each site acting on a single genotype to produce variable phenotypes. Biological factors such as food supply or predation might also contribute to among-site variances. To assume that a single genotype is present at all sites in the absence of data other than morphology alone is highly risky. The investigations of Boileau and Hebert (1991) and Boileau (1991) on other species of freshwater copepods have shown that interbreeding does not occur among forms that are exceedingly similar morphologically. M.G. Boileau (personal communication) has verified, with molecular studies of allozymes, that as many as three forms of *Acanthocyclops* may occur together in one pond without interbreeding and be morphologically identical. Price (1958) determined through breeding trials with individuals of several *Acanthocyclops* populations that reproductive isolation could occur among morphologically indistinguishable forms.

Among the females, within-source variance was greater than among-site variance of total length and P4 width (Table 7). Among the males, within-source variance for genital length and width, ramus length, and length of P6 spine was larger than among-site variance, suggesting the influence of factors that were independent of collection locations.

We suggest that significant variances both among sites and within sources for both sexes raise the possibility of at least two morphological forms of *C. strenuus* s.l. in our data. The simultaneous occurrence of the apparently different forms at some sites further suggests that they may be genotypically as well as phenotypically distinct.

Value of parameters

Historically, copepodologists have paid particular attention to certain morphological features in characterizing females of *Cyclops* spp., such as total length, length of the ramus,

Table 7. ANOVA of pooled measurements of female *Cyclops strenuus* s. collected in Alaska and Canada.

	Model (among sites)			Error (within sources)				Percentage of variance	
Parameter	df	SS	MS	df	SS	MS	*F*	Among sites	Within sources
Total length	11	823985	74907	53	446461	8424	8.89**	36	64
Cephalo length	9	43428	4825	55	78541	1745	2.76*	72	28
Cephalo width	8	45419	5677	24	44405	1850	3.07**	62	38
TH4 width	9	15470	1719	22	28761	1307	1.31	88	12
TH5 width	13	32158	2474	30	33685	1123	2.20*	92	8
Genital length	11	5313	483	37	19764	534	0.09	97	3
Genital width	12	51148	4262	37	44412	1200	3.55**	94	6
Ramus length	15	32667	2178	72	32901	457	4.77**	60	40
Ramus width	15	222	15	71	673	9	1.56	41	59
Insertion	12	49	4	43	234	5	0.75	94	6
Seta 1	15	41231	2749	67	61665	920	2.99**	88	12
Seta 2	15	17684	1179	44	36808	836	1.14	60	40
Seta 3	15	73613	4908	44	69743	1585	3.10**	64	36
Seta 4	15	2260	151	67	88752	131	1.15	92	8
P4 length	8	1667	208	30	2193	73	2.88**	64	31
P4 width	8	569	71	30	302	10	7.06**	40	60
P4 inner spine	8	1828	228	29	1340	46	4.94**	51	49
P4 outer spine	8	865	108	28	878	31	3.45**	62	38

Note: Parameters are defined in Table 2. **, significant at $P = 0.01$; *, significant at $P = 0.05$.

Table 8. Analysis of variance of pooled measurements of male *Cyclops strenuus* s. collected in Alaska and Canada.

	Model (among sites)			Error (within sources)				Percentage of variance	
Parameter	df	SS	MS	df	SS	MS	*F*	Among sites	Within sources
Total length	2	456503	91301	23	103841	4515	20.22**	85	15
Cephalo length	3	4614	1538	14	15106	1079	1.43	15	85
Cephalo width	3	1477	738	13	4959	381	1.94	20	80
TH5 width	4	5397	1349	10	795	79	16.97**	87	13
Genital length	5	9194	1839	12	1372	114	16.08**	12	88
Genital width	5	4823	965	12	1098	92	10.55**	18	82
Ramus length	6	4037	673	22	5026	228	2.94*	38	62
Ramus width	6	63	10	21	224	11	0.98		99
Insertion	5	8	2	13	46	4	0.45	30	70
Seta 1	6	3390	565	21	3791	180	3.13*	41	59
Seta 2	5	51276	10255	15	37080	2472	4.15*	52	48
Seta 3	6	5867	978	16	51171	3198	0.31	20	80
Seta 4	6	1730	288	21	1200	57	5.05**	56	44
P4 length	5	150	30	10	370	37	0.81	15	85
P4 width	5	176	35	10	249	25	1.41	14	86
P4 inner spine	5	687	137	10	319	32	4.42*	58	41
P4 outer spine	5	142	28	10	218	22	1.31	11	89
P6 spine	3	94	31	7	2	29	109.88**	2	98

Note: Parameters are defined in Table 2. **, significant at $P = 0.01$; *, significant at $P = 0.05$.

lengths of seta 1 and 4, and the features of leg 4. In this study, the length of seta 4 did not prove to be of significance in discriminating among populations of females (Table 7). The length and width of the cephalothorax and the length of seta 3 were useful. Males have traditionally received less attention than females. The characters most useful in characterizing the males were total length, greatest distance across prosomite 5, length and width of genital somite, and length of seta 2. Most P4 characters were not useful in characterizing forms.

Comparisons

The relationship of Marsh's (1920) specimens to present specimens is unclear. The specimens on his microscope slides are often heavily obscured by epibionts. Moreover, the preparations have become quite dense over time, presumably because of the stain that Marsh used (personal communication from J.W. Reid). E.B.R. examined some of Marsh's slides around 1960 and drew the ramus of a female that had been collected at Cape Bathurst, N.W.T. (70°35′N, 128°0′W). The dimensions of the ramus and setae 1 and 4

Table 9. Numbers of specimens (*n*) and ranges of measurements (μm) of female *C. strenuus* s. and *C. canadensis*.

	This study		Einsle (1988)		Pond in Poland†		St. Marys River	
Parameter	*n*	Range	*n*	Range	*n*	Range	*n*	Range
Total length	65		13				2	1680–1700
TH4 width	33		13					
TH5 width	44		13					
Genital length	49				5	185–215	2	188–220
Genital width	49				5	220–260	2	195–230
Ramus length	88		13		5	200–225	2	228–235
Seta 1	83		13		5	188–225		Broken
Seta 2	60		13		5	420–536		604
Seta 3	60		13		5	368–436	1	525
Seta 4	83		13		5	125–155	2	130–155
P4 length	40				4	95–100	1	105
P4 width	39				4	38–40	1	32
P4 inner spine	38				4	90–100		115
P4 outer spine	39				4	38–40	1	50

*Measurement is taken from a figure.
†Specimens from U.S. National Museum Accession No. 70708.

are within the ranges of parameters seen in this study (Fig. 3F).

Einsle (1988) named *C. canadensis* from specimens from two ponds near Igloolik, N.W.T. (69°14′N, 81°49′W). He emphasized that the new species was recognizable by (*i*) the antennules not reaching the posterior margin of the cephalothorax, (*ii*) the lateral caudal seta inserted extraordinarily close to the distal end of the caudal ramus (about 78% on drawing), and (*iii*) the shape of the fifth thoracic somite, and stated, "These properties have never been found in European *Cyclops* species . . . ." With respect to these characters, the antennules of the present specimens exceeded the length of the cephalothorax, and the insertion of the lateral caudal seta of the present specimens ranged from 69 to 75% of the ramus length. The shapes of prosomite 5 of the present animals did not appear to differ from Einsle's description or drawings in any significant way. The ranges of several parameters of the present females and Einsle's specimens largely overlap (Table 9). In the present specimens prosomites 4 and 5 appear to be wider and the caudal setae seem to be longer. The present females possessed slenderer and longer setae at the junction of the coupler and coxa of leg 4 than is shown in Einsle's figures of these appendages. Einsle (1988) found that the ornamentation of the coxa and the coupler of leg 4 varied among specimens from Inuvik and Igloolik. Ornamentation of the coxa varied among sites (Figs. 2B, 2D–2H) but overall is similar to patterns shown in Einsle's figures. The inverted L-shaped group of spinules near the lateral distal corner of the Tuktoyaktuk specimens (Fig. 2H) is similar to Einsle's Inuvik specimens. Apparently Einsle's specimens possessed more and longer fine setules on the leg 4 coupler than the present specimens.

While this manuscript was in review, E.B.R. had the opportunity to examine other copepods identified as *C. strenuus*. These included five slides of dissected females identified by Z. Kosminski from a pond near Wigry, Poland, on March 16, 1927 (USNM Catalog No. 70708). The ranges of 11 characters measurable on the five slides are similar to ranges of Canadian and Alaskan females (Table 9). The caudal rami of the Polish specimens had small bumps on the lateral margin at about one-fourth of their length (Fig. 3G). The seta at the junction of leg 4 coupler and coxa was long and slender (Fig. 3H), similar to the setae seen in this study but different from the shorter, thicker seta illustrated by Einsle (1988) for *C. canadensis*.

The ornamentation of the leg 4 coxa of the Polish specimens differed from any pattern observed on Canadian and Alaskan females, especially in regard to the length and robustness of the spinules in the group near the mesial distal margin of the coxa and in the very long setules in the row near the mesial proximal margin. As was the case with many of the Canadian and Alaskan females, no ornamentation was seen on the coupler (Fig. 3H). No important difference was found between leg 5 of the Wigry female (Fig. 3J) and that of the North American specimens.

Einsle (1985) presented figures of the leg 4 coxa ornamentation of females from Norway and Germany, the latter illustrating the seasonal variation found in one lake. These figures are similar to the Wigry females in the pattern of ornamentation and the relatively long slender seta at the junction of the coxa and coupler. The coupler of the Norwegian specimen is not adorned, as is the case with November-caught German specimens. Females caught in April possess two rows of long setules on the couplers.

Selgeby (1975) reported *C. strenuus* from St. Marys River, the outlet of Lake Superior. Identification was confirmed by H.C. Yeatman. We have been able to examine the two undissected specimens seen by Yeatman and we concur that these two females are *C. strenuus* s.l. The antennules extend to about midlength of prosomite 2. Measurements (Table 9) generally fit into the ranges found in the present study. The shapes of prosomite 5 are clearly similar to Einsle's (1988) figure of *C. canadensis* and those of *C. strenuus* s.l. examined in this study.

We believe that our data raise the possibility of more than one genotype among the populations of *C. strenuus* s.l. The apparently uneven distribution in the sizes of several parameters of both females and males suggests the presence of

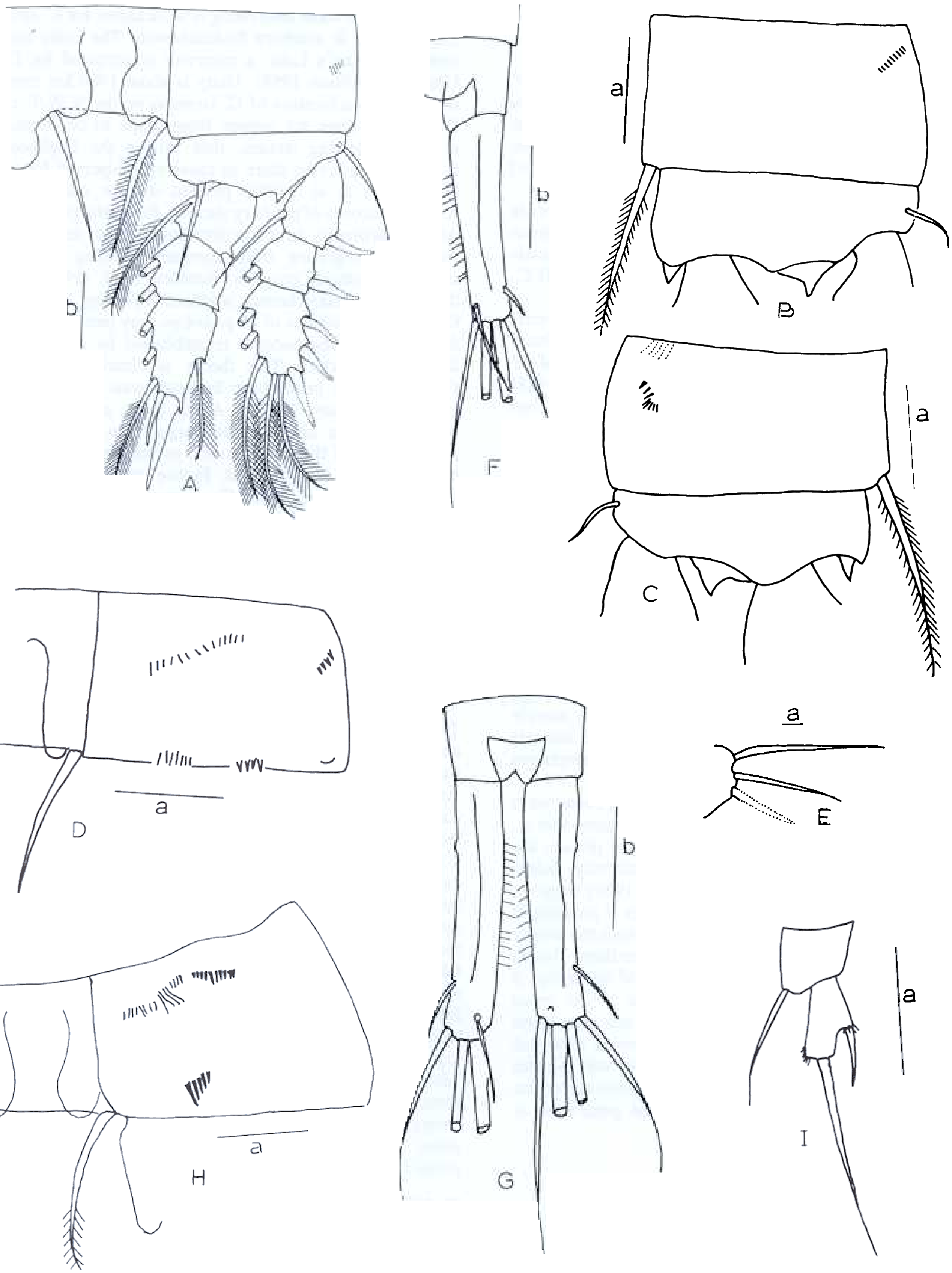

Fig. 3. *Cyclops strenuus* s.l. (A–E) Male. (A) Leg 1, Point Barrow. (B) Coxa, leg 2, Point Barrow. (C) Coxa, leg 3, Point Barrow. (D) Coxa, leg 4, Point Barrow. (E) Leg 6, Oliktok Point. (F–I) Female. (F) Caudal ramus, Cape Bathurst. (G) Same, Wigry pond. (H) Coxa, leg 4, Wigry pond. (I) Leg 5, Wigry pond. Scale bars: *a*, 50 μm; *b*, 100 μm.

"large" and "small" forms that may be genetically distinct. These two forms may well exist in addition to the *C. canadensis* form. Definitive testing of this hypothesis will require data that are independent of morphology and not yet available.

Biology

Relatively little is known about the biology of *C. strenuus* s.l. in North America. *Cyclops strenuus* s.l. occurred in grassy tundra ponds along the Colville River that ranged from as shallow as 10 cm to nearly 1 m deep and ranged from less than 2 m^2 to several hundred square metres in area (Reed 1962).

Collection data with the Chatanika specimens reads "grassy roadside pool." The Galena specimens came from "ponds and pool near river bottom" (Yukon River). Animals from both samples were identified as *C. strenuus* by H.C. Yeatman.

Einsle (1988) gave no ecological data for *C. canadensis*. The tundra ponds along the Colville River and at Point Barrow, Alaska, those described by Johansen (1922), and the ponds at Igloolik and Inuvik mentioned by Einsle (1988) appear to be similar. However, Holmquist (1975) pointed out that while many tundra ponds seem to differ little superficially, they may offer a wider array of habitats than is commonly supposed. Hebert and Hann (1986) pointed to a rather wide spread in thawing index and degree-days among several northern sites in Canada and Alaska.

The records from Great Slave Lake (Patalas 1975; Patalas and Patalas 1978) and from the outlet of Lake Superior (Selgeby 1975) appear to be the only known instances of *C. strenuus* occurring in large lakes in North America. Kiefer (1978) stated that *C. strenuus* occurs in all types of waters ranging from temporary ponds through permanent ponds to large lakes.

Nearly all of the females examined in this study bore egg sacs or contained large eggs in the oviducts. One sample from Point Barrow included seven males. These animals were fully developed except for the lack of spermatophores in their genital segments.

Probably most of the ponds from which *C. strenuus* were taken lack free water during the long winter months; that is, they freeze solid. Therefore, the copepods must possess the capability of withstanding long periods of inactivity. Information on *C. strenuus* elsewhere (Elgmork 1959) suggests that diapause in CIV or a later copepodid stage is possible in Norwegian ponds. This may be the way in which the winter period is survived in tundra ponds of northern North America. As a consequence of long periods of inactivity, it seems unlikely that *C. strenuus* populations in the areas under consideration could produce more than one generation per year. Even if the animals entered diapause as fertilized females, as is known for other species (Naess and Nilssen 1991), the time from spring thaw to autumn freeze-up seems too short for development of more than one generation at arctic temperatures.

Distribution

In addition to the sites shown in Table 1, *Cyclops strenuus* s.l. has been reported from the Aleutian Islands (Scheffer 1959), Cape Bathurst, N.W.T. (Marsh 1920), and the outlet of Lake Superior (Selgeby 1975). The nominate subspecies, *C. s. strenuus*, has been reported from Great Slave Lake (Patalas 1975; Patalas and Patalas 1978). The morphologically similar *C. canadensis* is known from Igloolik and Inuvik, N.W.T. (Einsle 1988).

Perhaps the most interesting new localities for *C. strenuus* s.l. are those in southern Saskatchewan. The Unity animals came from Orr's Lake, a reservoir constructed for Ducks Unlimited (Wilson 1958). Unity is about 1700 km from the nearest known location of *C. strenuus* on the N.W.T. coast. Orr's Lake does not appear from maps to be located on a through-flowing stream, thus raising the likelihood of *C. strenuus* arriving there as passively dispersed founders.

Saunders et al. (1993) pointed out the congruence of southern records of the fairy shrimp, *Branchinecta paludosa*, which is primarily Arctic in distribution, with the flyways of waterfowl migrating from summer breeding grounds to southern wintering grounds. Saunders et al. (1993) suggest that Alberta, Saskatchewan, southern Wyoming, and northern Colorado populations of *B. paludosa* may persist for a time, die out, and then become reestablished by new passively dispersed founders. This theory is clearly applicable to *C. strenuus* s.l. in southern Saskatchewan.

Between Unity and the Arctic coast are thousands of bodies of water ranging from large lakes to small tundra ponds. Most of these waters are, as yet, unknown as far as copepod fauna is concerned. Future collecting may reveal intervening populations of *C. strenuus* s.l.

North of 60°N, North America is an enormous area, rich in freshwater habitats, whose copepod fauna is poorly known. In western Europe, a much smaller area, Einsle (1975) found 10 distinct and stable patterns of chromatin reduction in species of *Cyclops* s.str. There is no reason to suppose that *C. canadensis* and the forms in this study exhaust the potential *C. strenuus* s.l. forms in North America.

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