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First Records of Two Neotropical Species of *Mesocyclops* (Copepoda) from Yukon Territory: Cases of Passive Dispersal?

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ABSTRACT. Two species of neotropical cyclopoid copepod crustaceans, *Mesocyclops longisetus curvatus* and *Mesocyclops venezolanus*, were collected from a pond at Shingle Point, Yukon Territory, Canada, in September 1974. This is the first record of *M. longisetus curvatus* north of the southern United States and the first record of *M. venezolanus* north of Honduras. We provide amplified descriptions of both species. Four additional congeners, *M. americanus, M. edax, M. reidae*, and *M. ruttneri*, are now known from the continental U.S. and Canada. We provide a key to the identification of the six species. We hypothesize that the specimens of *M. longisetus curvatus* and *M. venezolanus* may have been passively transported to Shingle Point by migrant shorebirds.

Key words: Copepoda, Cyclopoida, *Mesocyclops*, new record, Yukon, neotropical, zoogeography, passive dispersal, identification key

RÉSUMÉ. En septembre 1974, on a recueilli deux espèces de copépodes cyclopoïdes néogènes, *Mesocyclops longisetus curvatus* et *Mesocyclops venezolanus*, dans un étang situé à Shingle Point, dans le territoire du Yukon au Canada. Cela représente la première occurrence rapportée de *M. longisetus curvatus* au nord de la partie méridionale des États-Unis, et la première de *M. venezolanus* au nord du Honduras. On donne une description détaillée des deux espèces. On sait maintenant qu'il existe quatre autres congénères, *M. americanus, M. edax, M. reida* et *M. ruttneri*, dans la zone continentale des États-Unis et au Canada. On fournit un code permettant d'identifier les six espèces. On émet l'hypothèse que les spécimens de *M. longisetus curvatus* et de *M. venezolanus* ont pu être transportés de façon passive à Shingle Point par des oiseaux de rivage migrateurs.

Mots clés: copépodes, cyclopoïdes, *Mesocyclops*, nouvelle occurrence rapportée, Yukon, néogène, zoogéographie, dispersion passive, code d'identification

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INTRODUCTION

Between 30 August and 5 September 1974, samples of small crustaceans were collected from ponds in Yukon Territory (Y.T.) and Northwest Territories. Copepods from these samples have been the subjects of previous reports (Reed, 1990, 1991a,b). In this article we note the unexpected presence of two neotropical species of cyclopoid copepods of the genus *Mesocyclops*. These animals were taken from a tundra depression in water not over 10 cm deep at Shingle Point, Y.T. (68°56′N, 137°15′W), 1 September 1974. Moss and gelatinous algal material covered the substratum.

Collected with the two species of *Mesocyclops* were three species of cyclopoids that are widely distributed in northern latitudes but are not necessarily confined to them: *Eucyclops serrulatus* (Fischer, 1851) s. lat., *Macrocyclops albidus* (Jurine, 1820), and *Microcyclops rubellus* (Lilljeborg, 1901) s. lat. The calanoid copepod *Eudiaptomus yukonensis* Reed, 1991, known only from Shingle Point, and ostracodes, likely *Candona rectangulata* or *C. protzi*, also occurred in the same pond. The presence of either of these ostracode species at Shingle Point is not surprising (L.D. Delorme, pers. comm. 1992).

Collections in three nearby ponds did not yield either species of *Mesocyclops* but did contain such typical northern species as *Heterocope septentrionalis* Juday and Muttkowski, 1915, *Megacyclops magnus* (Marsh, 1920), and *Acanthocyclops capillatus* (G.O. Sars, 1863).

The revisions of Kiefer (1981) and Van de Velde (1984) have contributed to a quantum leap forward in species discrimination and consequent understanding of the morphology, biogeography, and general biology of Old World *Mesocyclops*. However, the published descriptions of most New World species do not include many of the meristic details that are now understood to be useful for diagnoses. Accurate taxonomic discrimination of members of this genus is especially desirable because some species are potential biological control agents for anopheline mosquitoes (Marten *et al.*, 1989, 1994). Recent reports have added to the list of congeners now known to occur in Canada and the U.S., seriously outdating available general keys. We take this opportunity to amplify the descriptions of the two species found in Yukon Territory and to provide an updated local key.

TAXONOMIC SECTION

We redescribe both species, giving particular attention to subtle meristic details. The narrative descriptions refer to the redescription of the type-species *Mesocyclops leuckarti* (Claus, 1857) by Van de Velde (1984). Specimens have been deposited in the collections of the U.S. National Museum of Natural History, Smithsonian Institution.

Mesocyclops G.O. Sars, 1914
Mesocyclops longisetus curvatus Dussart, 1987 (Figs. 1, 2)

Description of Female: Large, robust; range of lengths of three adults from Shingle Point, 1.22-1.38 mm; reported lengths of *M. longisetus* s. lat., about 1.1-2.8 mm (Reid, 1985).

Pediger 5 ornamented laterally with two groups of hairlike setae, setae in more dorsal group finer (Fig. 1a,c). Genital segment with group of small spines posterior to leg 6 plate (indicated by arrow in Fig. 1c), otherwise ornamented only by few socketed hairs and hair-bearing papillae in usual

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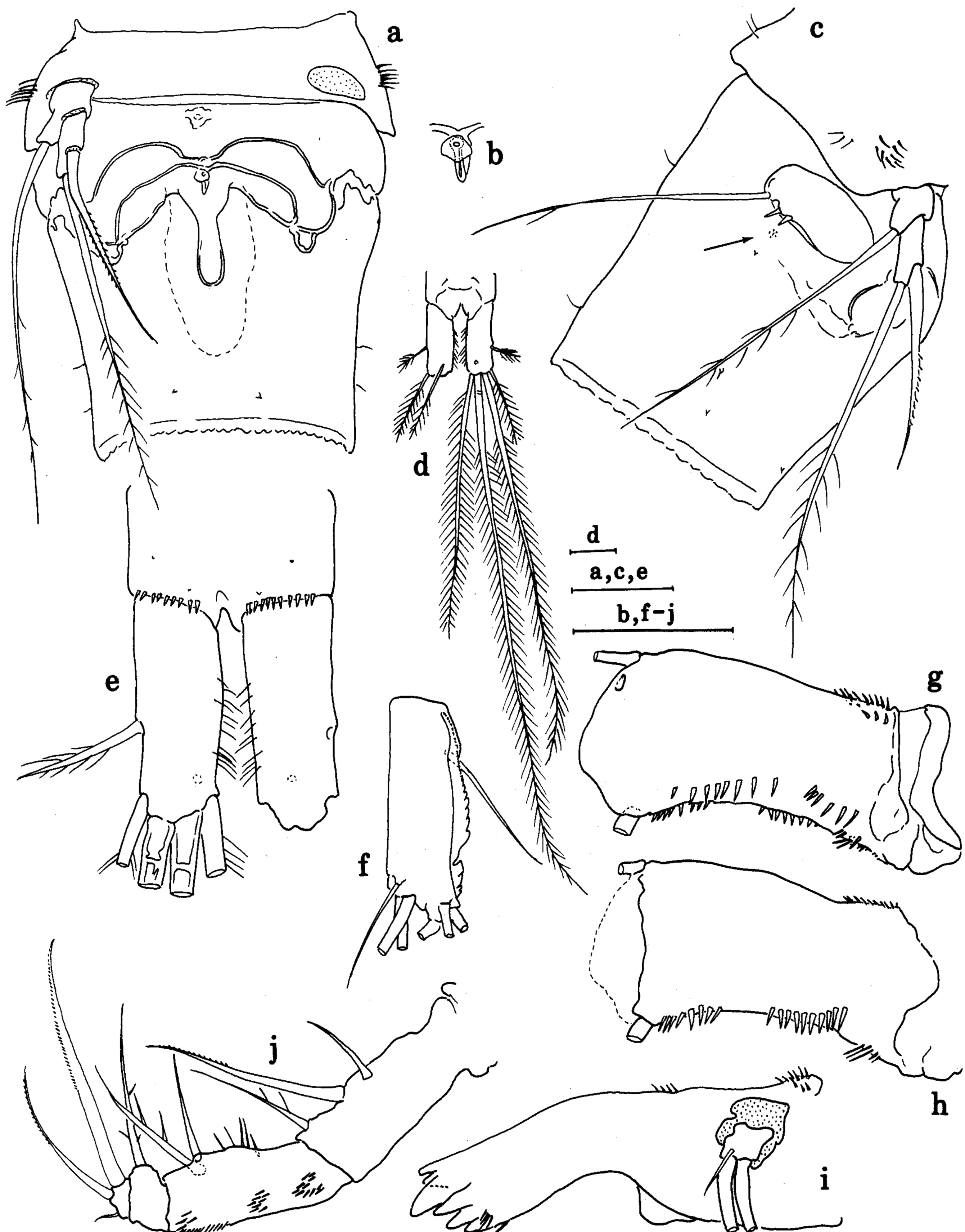

FIG. 1. *Mesocyclops longisetus curvatus*, female from Shingle Point, Yukon Territory: a) Pediger 5 and genital segment, ventral; b) Copulatory pore and pore-canal, enlarged; c) Pediger 5 and genital segment, right lateral; d) Anal somite and caudal rami, dorsal; e) Anal somite and caudal rami, ventral; f) Antennule article 17; g) Antenna article 1 (basipodite), caudal side; h) Antenna basipodite, frontal side; i) Mandible; j) Maxilliped. Scales indicate 50 μm.

pattern for genus. Seminal receptacle (Fig. 1a,b) with broad, strongly recurved lateral arms and lateral canals; anterior margin strongly concave in middle; posterior expansion well developed; copulatory pore surrounded by strongly sclerotized plate, pore-canal recurved anteriorly. Genital segment and succeeding two urosomites with weakly crenate hyaline frills. Anal somite (Fig. 1d,e) ornamented only with few papillae and row of spines along posteroventral margin. Caudal rami (Fig. 1d,e) about 2.6 times longer than broad, sparsely haired along middle half of medial surfaces, lacking spines at bases of lateral and lateralmost terminal caudal setae. Length relationships of caudal setae as in Figure 1d, longest caudal seta about 1.5 times length of urosome.

Antennule as in *M. leuckarti* (see Van de Velde, 1984) except reaching only to pediger 2 and lacking small spines on surfaces of articles present in that species; hyaline membrane of article 17 increasingly strongly serrate distally, with one deep notch (Fig. 1f). Antenna as in *M. leuckarti* except with different spine pattern on basipodite (Fig. 1g,h). Mandible (Fig. 1i) as in *M. leuckarti* except with group of small spines distal to palp, in addition to group of larger spines proximal to palp found in that species. Maxillule and maxilla as in *M. leuckarti*. Maxilliped (Fig. 1j) with three groups of spines on article 2.

Leg 1 (Fig. 2a) as in *M. leuckarti* except with slender, finely denticulate spine on medial expansion of basipodite (spine indicated by arrow in figure). Leg 2 (Fig. 2b) as in *M. leuckarti* except with group of short strong spines on distal half of lateral surface of coxopodite, not present in that species (spines indicated by arrow in figure). Leg 3 as in *M. leuckarti*. Leg 4 (Fig. 2c,d), coupler with two short teeth on distal margin; posterior surface of coxopodite with row of tiny spines near proximal margin, several groups of long spines near and along lateral surface, and row of medium spines along midlength of posterior margin; distal half of medial expansion of basipodite with scattered small spines; exopodite articles 1-3 (only article 1 illustrated) haired on posterior surface; leg 4 endopodite article 3, terminal spines stout and with fine serrations along most of margins, medial terminal spine shorter than lateral terminal spine.

Distribution: *Mesocyclops longisetus* (Thiébaud, 1914) s. lat. is distributed throughout South and Central America, the Antilles, Mexico, and the southern continental U.S. (Reid, 1985, 1993). The southern limits of its distribution are unclear; a named variety, *M. longisetus* var. *araucanus* Löffler, 1961, is planktonic in large lakes of southern Chile and Tierra del Fuego. *Mesocyclops longisetus curvatus* was described from Venezuela and similar morphs are known from as far north as Cuba and as far south as Argentina (Dussart, 1987). Morphs corresponding in most respects to *curvatus* were found more recently in the southern United States (Reid, 1993) and in Honduras, where it is one of the most common species in small ponds (Marten *et al.*, 1994). These morphs were attributed to *curvatus* on the basis of the strongly recurved lateral arms of the seminal receptacle and the proportions of the caudal ramus. *Mesocyclops longisetus curvatus* was originally named as a variety and the genetic relationships of *curvatus* and var. *araucanus* to the nominate species have yet to be determined.

Mesocyclops venezolanus Dussart, 1987 (Figs. 3, 4)

Description of female: Medium-sized, slender; range of lengths of seven adults from Shingle Point, 0.89-1.09 mm; lengths of females from Venezuela, 1.0-1.1 mm (Dussart, 1987). Pediger 5 (Fig. 3a,c,d) with group of hairlike spines on each lateral surface. Genital segment with group of small spines posterior to leg 6 plate (indicated by arrow in Fig. 3c), also with small group of hairs near anterodorsal margin, otherwise with few pairs of socketed hairs and hair-bearing papillae. Seminal receptacle (Fig. 3a,b) with narrow, slightly recurved lateral arms and nearly horizontal lateral canals; anterior margin slightly concave in middle, with characteristic expansion at beginning of each lateral arm; posterior expansion well developed; copulatory pore sclerotized, pore-canal recurved anteriorly. Genital segment and succeeding two urosomites with weakly crenate hyaline frills. Anal somite (Fig. 3e,f) ornamented ventrally with few rows of tiny spines, pair of papillae, and row of spines along posteroventral margin. Caudal rami (Fig. 3e,f) about 2.6 times longer than broad, sparsely haired along middle half of medial surfaces, lacking spines at bases of lateral and lateralmost terminal setae. Length relationships of caudal setae as in Figure 3e, longest caudal seta slightly longer than urosome.

Antennule as in *M. leuckarti* except reaching to pediger 3 and lacking small spines on surfaces of articles present in that species; hyaline membrane of article 17 increasingly strongly serrate distally, with one deep rounded indentation and one or two shallower indentations (Fig. 3g,h). Antenna as in *M. leuckarti* except with different spine pattern on basipodite (Fig. 3i,j). Mandible, maxillule, maxilla and maxilliped as in *M. leuckarti*.

Leg 1 (Fig. 4a) as in *M. leuckarti* except with slender seta on medial expansion of basipodite, this seta with few setules proximally and fine denticles distally. Leg 2 (Fig. 4b) and leg 3 as in *M. leuckarti* except each with coxopodite having row of long rather than tiny spines along proximal margin of posterior surface. Leg 4 (Fig. 4c,d), two crescentic processes on distal margin of coupler small, barely extending past margin; posterior surface of coxopodite with one row and one cluster of small spines near proximal margin, two short rows of long spines near lateral surface, row of fine hairs on lateral surface, and row of medium spines along medial half of posterior margin; medial expansion of basipodite with cluster of small spines on distal half; exopodite articles 1-3 without hairs on posterior surface; leg 4 endopodite article 3, terminal spines subequal in length, finely serrate along most of margins.

Distribution: The specimens from Shingle Point correspond in nearly all particulars to the description of Dussart (1987), except that the crescentic processes on the leg 4 coupler do not extend past the margin of the coupler in Dussart's illustration of a specimen from Venezuela. This may be a function of different angles of view.

The species was described from Venezuela by Dussart (1987). It was subsequently recorded from Colombia (Marten *et al.*, 1989) and Honduras (Marten *et al.*, 1994), where, like *M. longisetus curvatus*, it is one of the most common copepods in small ponds. Both species were

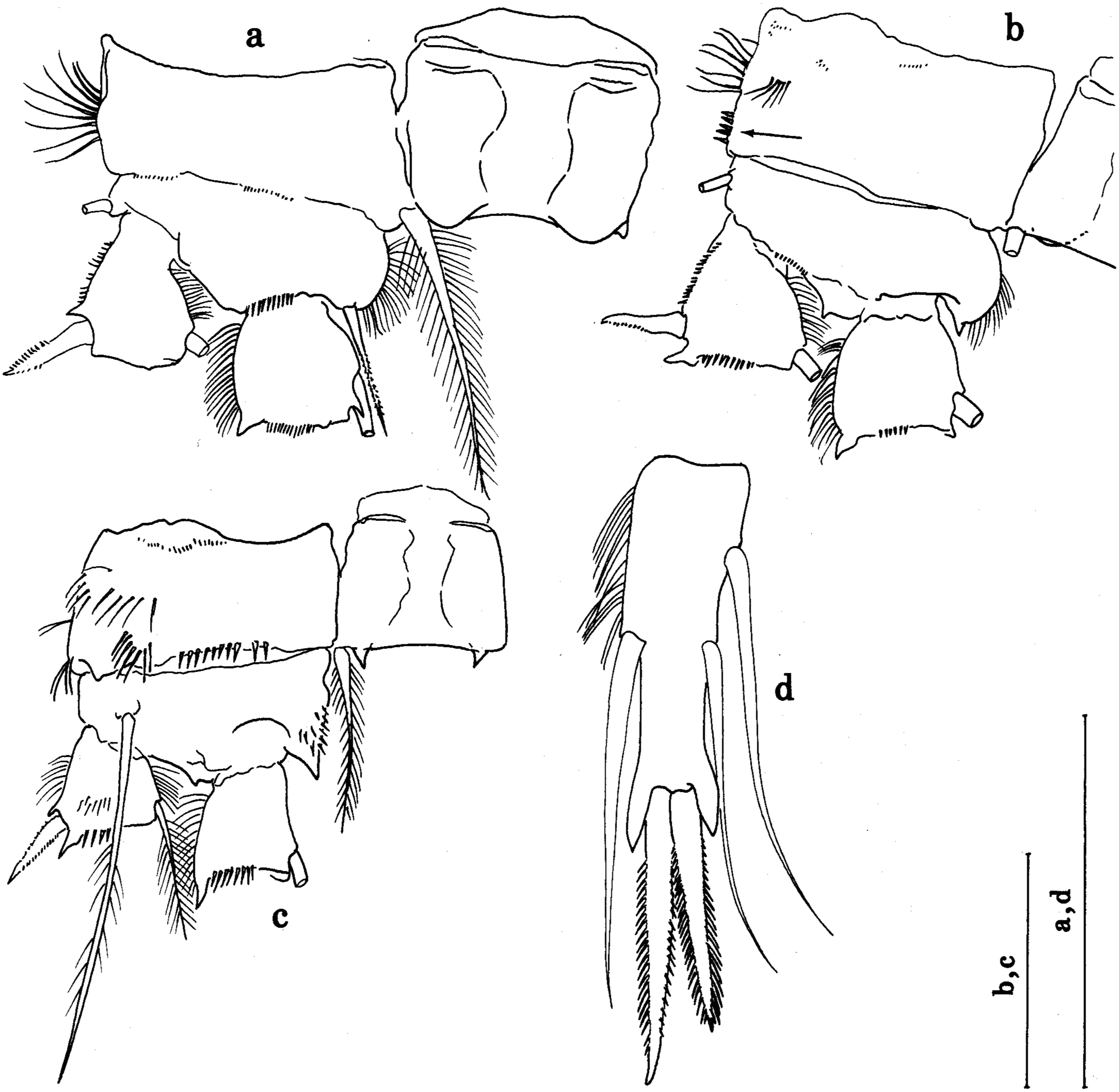

FIG. 2. *Mesocyclops longisetus curvatus*, female from Shingle Point, Yukon Territory: a) Leg 1 coupler, coxa-basipodite and rami (partial), posterior; b) Leg 2 coupler, coxa-basipodite and rami (partial), posterior; c) Leg 4 coupler, coxa-basipodite and rami (partial), posterior; d) Leg 4 endopodite article 3. Scales indicate 100 μm.

significantly negatively associated with *Anopheles albimanus* in ponds in Colombia (Marten *et al.*, 1989) and are active predators on *A. albimanus* and on *Aedes aegypti* in the laboratory and in controlled field conditions (Marten *et al.*, 1989, 1994).

DISCUSSION

Species of Mesocyclops *in the U.S. and Canada*

These and other recent records have increased to six the number of species of *Mesocyclops* known to inhabit Canada and the contiguous 48 United States. Only one, *Mesocyclops edax*, is included with validity in the local keys that are generally in use (Pennak, 1989; Yeatman, 1959). *Mesocyclops edax* was redescribed by Dussart (1985). It is a broadly distributed common plankter whose Canadian distribution was recently reviewed by Patalas (1986). *Mesocyclops americanus* was described by Dussart (1985) from Ontario. Reid (1992) amplified the description of the female, described the male, and added several new records from the central and eastern U.S. Chengalath and Shih (1993) extended the known distribution of *M. americanus* westward to British

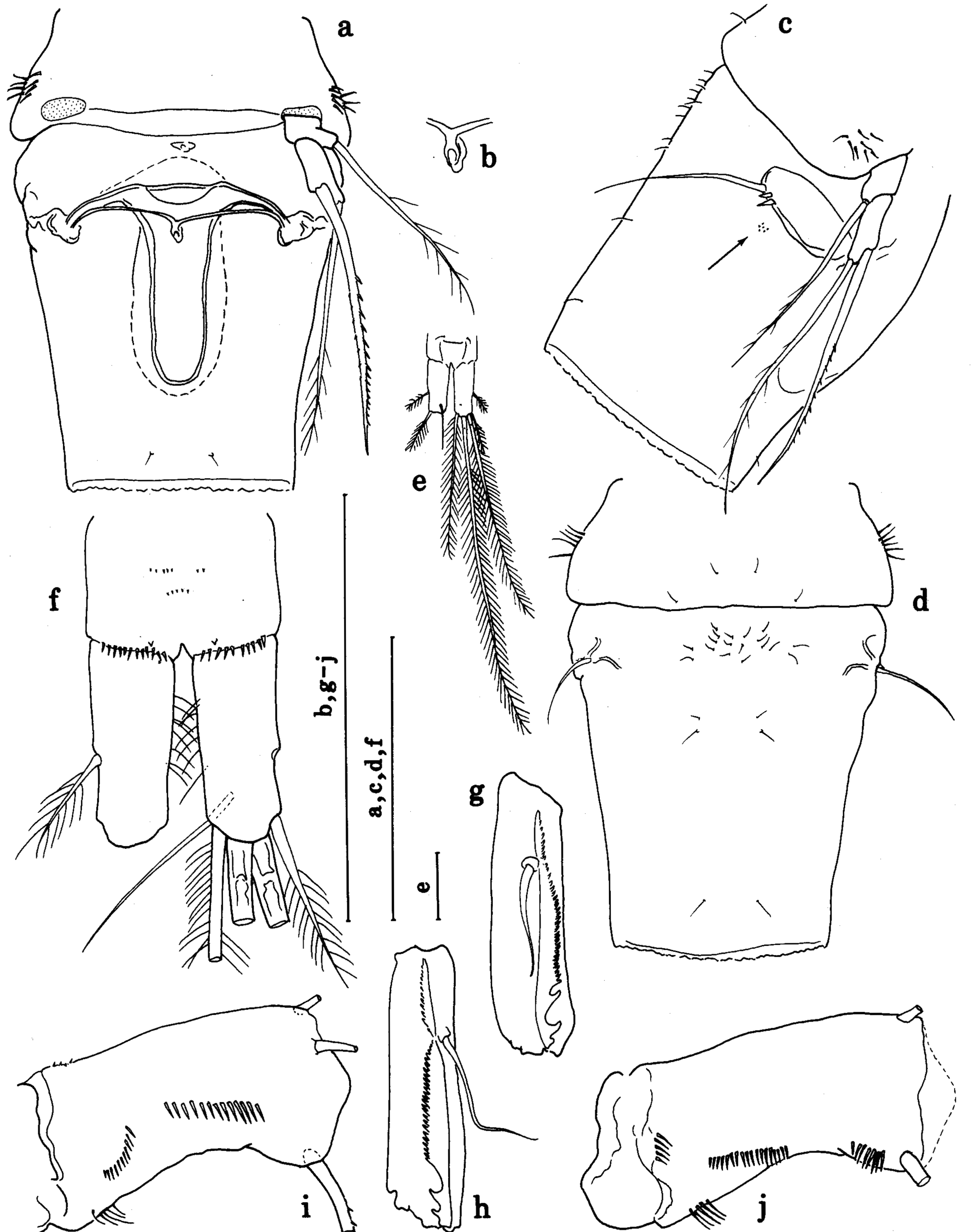

FIG. 3. *Mesocyclops venezolanus*, female from Shingle Point, Yukon Territory: a) Pediger 5 and genital segment, ventral; b) Copulatory pore and pore-canal, enlarged; c) Pediger 5 and genital segment, right lateral; d) Pediger 5 and genital segment, dorsal; e) Anal somite and caudal rami, dorsal; f) Anal somite and caudal rami, ventral; g,h) Left and right antennule articles 17 of same specimen; i) Antenna basipodite, caudal; j) Antenna basipodite, frontal. Scales indicate 100 μm.

Columbia. Reid (1993) recorded *Mesocyclops longisetus curvatus*, *Mesocyclops reidae*, and *Mesocyclops ruttneri* from the south central U.S. and transferred *Mesocyclops bernardi* Petkovski, 1986, also newly recorded from that region, to the genus *Diacyclops*. Reid (1993) considered *M. ruttneri* to have been introduced into the U.S.

Reports from North America of *Mesocyclops leuckarti* (Claus, 1857) s. restr. Kiefer, 1981 continue to appear sporadically (Li *et al.*, 1979; Soto and Hurlbert, 1991a,b; Wurtsbaugh and Li, 1985). These records probably result from the inclusion of the species in the widely used keys of Yeatman (1959) and Pennak (1989). Williamson (1991) listed both *M. edax* and *M. americanus*, but confusingly included a figure of *M. leuckarti* (Williamson, 1991:Fig. 21.7[i]). Prior to the revision of Kiefer (1981), *M. leuckarti* was thought to occur in North America. However no recent North American record of *M. leuckarti* has been confirmed in spite of numerous but unavailing efforts by one of us (JWR) to obtain voucher specimens. We agree entirely with the opinion of Dussart (1985), Dussart and Fernando (1990), and Kiefer (1981) that *M. leuckarti* is restricted to Eurasia. The *leuckarti* species-group is defined by the absence of a spine on the leg 1 basipodite medial expansion, and both *M. americanus* and *M. ruttneri* are members of this group. Most of the old records of *M. leuckarti* probably refer to the widely distributed *M. americanus*. Nevertheless because of the presence of two members of this group, and some confusion between *M. edax* and *M. leuckarti* in the older literature, the assertion of Dussart (1985) that records of *M. leuckarti* should be taken to refer to *M. americanus* is not quite valid.

Several compendia and keys are available to aid in discriminating the known neotropical species of *Mesocyclops*. The most recent general keys were published by Dussart (1987) and Petkovski (1986). Reid (1990) listed records from Mexico, Central America, and the Antilles. The key provided here is intended as a supplement to these references and is valid only for Canada and the contiguous U.S. No species of *Mesocyclops* has been recorded from Alaska.

Key to females of species of *Mesocyclops* recorded from Canada and the contiguous U.S.:

1. Medial expansion of basipodite of leg 1 with spine 2
— Medial expansion of basipodite of leg 1 lacking spine 5
2. Legs 1-3 couplers with distal margins produced or not, surface naked 3
— Legs 1-3 couplers with distal margins not markedly produced, each coupler with 2 groups of 1-5 small denticles on surface ...... *edax* (S.A. Forbes, 1891) Canada (Manitoba, New Brunswick, Northwest Territories, Nova Scotia, Ontario, Québec, Saskatchewan); contiguous U.S. (general); Mexico (Michoacán, Quintana Roo); Central America, Cuba.
3. Legs 1-3 couplers with distal margins nearly straight 4
— Legs 1 and 2 couplers each with 2 large rounded protrusions on distal margins; leg 3 coupler with 2 large acute protrusions on distal margin ... *reidae* Petkovski, 1986 Contiguous U.S. (Mississippi); Mexico (Campeche, Yucatán); Antilles, Central America.
4. Leg 4 coupler with 2 large triangular spiniform projections on distal margin; lateral arms of seminal receptacle broad, more or less recurved posteriorly .... *longisetus* (Thiébaud, 1914) s. lat. (includes var. *curvatus* Dussart, 1987) Canada (Yukon Territory); contiguous U.S. (Florida, Louisiana, Texas, ?Alabama); Mexico (Michoacán, Nuevo León); Antilles, Central America, South America.
— Leg 4 coupler with 2 small bluntly rounded projections on distal margin; lateral arms of seminal receptacle narrow, nearly horizontal .... *venezolanus* Dussart, 1987 Canada (Yukon Territory); Colombia, Honduras, Venezuela.

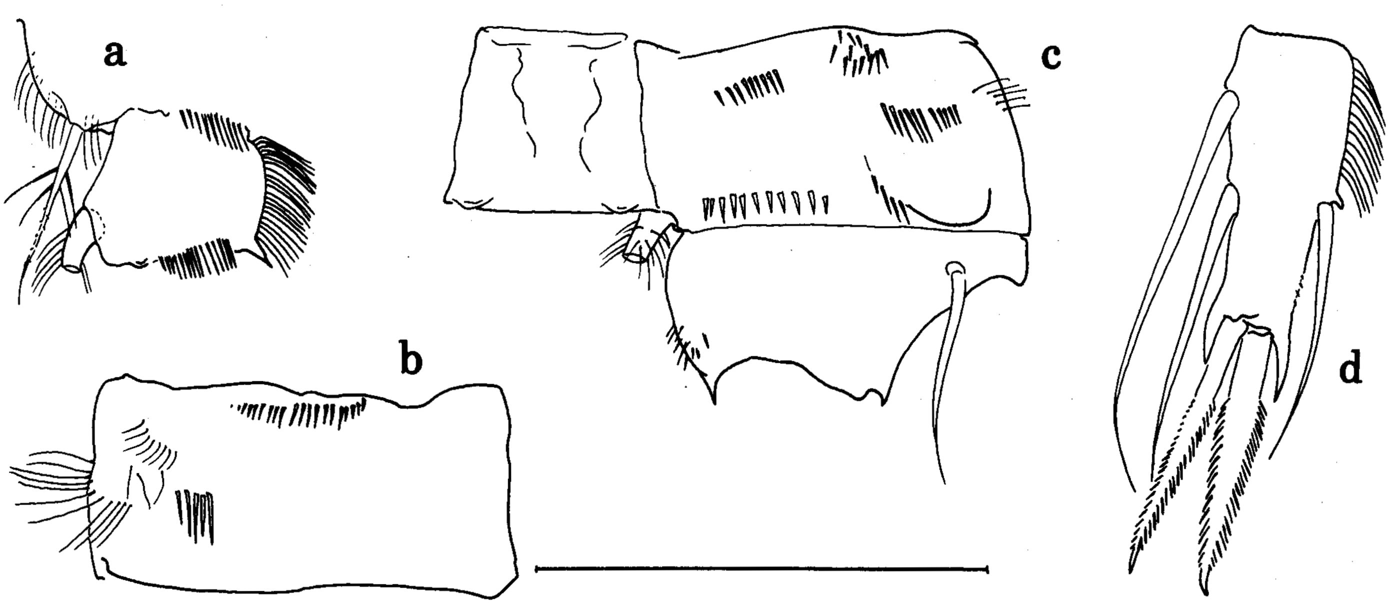

FIG. 4. *Mesocyclops venezolanus*, female from Shingle Point, Yukon Territory: a) Leg 1, medial expansion of basipodite and endopodite article 1, posterior; b) Leg 2 coxopodite, posterior; c) Leg 4 coupler and coxa-basipodite, posterior; d) Leg 4 endopodite article 3. Scale indicates 100 μm.

5. Leg 4 basipodite, medial surface naked; leg 4 coupler with 2 long slender curved spiniform processes on distal margin .... *ruttneri* Kiefer, 1981
Contiguous U.S. (Louisiana, Mississippi); China, Thailand, Viet Nam; first described from Austria where it is apparently extinct.
— Leg 4 basipodite, medial surface with group of hairs on distal half; leg 4 coupler with broadly triangular spiniform processes on distal margin .... *americanus* Dussart, 1985
Canada (British Columbia, Ontario); contiguous U.S. (Connecticut, Florida, Indiana, New Jersey, South Carolina).

Copepod Dispersal

The presence of *M. longisetus* and *M. venezolanus* on the arctic coast of North America must surely involve passive transport. We cannot exclude the possibility that human agency had a role in bringing them to Shingle Point. However, passive transport on waterfowl or shorebirds seems more likely.

Saunders *et al.* (1993) reviewed the coincidences of southern records of a fairy shrimp that is primarily arctic in distribution with flyways of waterfowl migrating from summer breeding grounds to wintering grounds at southerly latitudes. Flyways include major migration routes, networks of intermediate routes, summer breeding areas, and wintering grounds (Mead, 1983). Staging areas are locations where waterfowl and shorebirds gather in huge numbers for premigration feeding. Staging areas for northbound migrants tend to be close to wintering grounds (Johnson and Herter, 1990).

Some migratory birds, both long-distance migrants (traveling over 80° of latitude) and medium-distance migrants (traveling between 40° and 60° of latitude) are known to make non-stop flights (Johnson and Herter, 1990). But as Saunders *et al.* (1993) pointed out, it is unnecessary to propose that dispersal occur in one dramatic leap. Dispersal may proceed in a series of steps spread over a long period of time.

Between Central America and Shingle Point lie thousands of pieces of water ranging from large lakes and reservoirs through medium-sized lakes and ponds to marshy wetlands. Perhaps not one of these may be said to be completely inventoried respecting its copepod fauna. Future collecting may well turn up populations of *M. longisetus* and *M. venezolanus* between the southern U.S. and Shingle Point.

Long-range passive dispersal requires that not only must the transporter and transportee have the opportunity to be in close contact, but also the transportee must be in a physical condition that is compatible with the transporter's actions. Resting eggs of fairy shrimp and diaptomid copepods, gemmules of sponges and ephippia of cladocerans and other similar quiescent, resistant stages have long been thought to be the forms in which some species are carried from one water to another. Over the last decades several species of freshwater cyclopoid copepods, including four species of *Mesocyclops*, have been shown to undergo periods of diapause (Dobrzykowski and Wyngaard, 1993; Elgmork, 1967) and be able to survive long periods without free water (Wyngaard *et al.*, 1991). Recently Naess and Nilssen (1991) have found fertilized female diapausing copepods. Elgmork (1980) suggested that diapause in freshwater cyclopoids may have adaptive significance as a means of escaping unfavorable environmental conditions and as a means to increased fecundity. Diapause may also have adaptive significance as an aid to increased dispersal.

With the aid of the ecological and distributional information provided by Snyder and Shortt (1957) and Godfrey (1986), one may easily assemble a list of 25 species of waterfowl and shorebirds that might transport copepods between the neotropics and northern North America. Species whose ecological and migratory habits make them especially attractive candidates for passive dispersal of copepods include the semipalmated plover (*Charadrius semipalmatus*), lesser yellowlegs (*Tringa flavipes*), lesser golden plover (*Pluvialis dominica*), ruddy turnstone (*Arenaria interpres*), and seven sandpipers: least (*Calidris minutilla*), pectoral (*Calidris melanotos*), white-rumped (*Calidris fuscicollis*), Baird's (*Calidris bairdii*), stilt (*Calidris himantopus*), semipalmated (*Ereunetes pusilla*), and buff-breasted (*Tryngites subruficollis*).

Reports of passive dispersal of small aquatic invertebrates by (presumably) avian transport in North America generally involve the southward movement of northern species rather than the reverse (Saunders *et al.*, 1993, and papers cited therein). This may be an artifact of collecting: more people collect copepods in mid-latitude North America than in the northern latitudes. Perhaps the volume of avian traffic plays a role; certainly more birds migrate south from the summer breeding grounds than migrate north from wintering areas.

We propose that *M. longisetus* and *M. venezolanus* may have reached Shingle Point in some variation of the following scenario: staging areas for migrant shorebirds coincided with suitable habitat for the *Mesocyclops*. The great concentration of birds maximized potential contact between them and the copepods. In some way, perhaps in mud, diapausing copepods became attached to feathers or legs of shorebirds. The quiescent state of the copepods permitted them to survive the trip up the Mackenzie River valley, a recognized major migration corridor for birds crossing the continent from the Gulf of Mexico to the Arctic (Johnson and Herter, 1990). Some shorebirds happened to visit Shingle Point ponds in which the *Mesocyclops* could survive, at least temporarily. Transported copepods broke diapause, reproduced, and in the autumn of 1974 presented a thriving appearance.

Potential colonizers may persist for a season and then be eliminated by changing environmental conditions. If so, then there is a relatively narrow window of time in which their presence may be detected. In one case, the calanoid copepod *Sinodiaptomus sarsi* (Rylov, 1923) appears to have been introduced into a lily pond in California along with a shipment of plants from China (Wilson, 1959). Seemingly *S. sarsi* lasted long enough to have been found once but failed to persist. But for serendipitous collecting its presence would have gone undetected.

Instances of failed passive dispersal of copepods may be more common than is generally recognized. The copepod exoskeleton lacks resistant elements, and shed exoskeletons and copepod carcasses quickly break down and disappear.

We do not know if *M. longisetus* and *M. venezolanus* are year-to-year inhabitants of the Shingle Point pond. They may have been recent arrivals that persisted only during that summer and their collection may have been a fortuitous chance event.

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