Relict Populations of *Drepanopus bungei* and *Limnocalanus macrurus grimaldii* (Copepoda: Calanoida) from Ellesmere Island, N.W.T.

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ABSTRACT. *L. m. grimaldii* and *D. bungei* live in the freshwater layer of a meromictic lake on northern Ellesmere Island containing trapped sea water below 60 m. Carbon-14 measurements indicate the lake has not communicated with the open sea for 3,000 years. *D. bungei* also lives in the freshwater layer of Disraeli Fiord. This is the first report of this copepod occurring outside the Siberian Arctic. *L. m. grimaldii,* also rare in the Canadian Arctic, usually occurs near large river mouths, but has been found in a few arctic lakes and coastal lagoons. The present disjunct distribution of these species is evidence of their former more general dispersion in the Arctic during times when brackish water was more widespread. Although isolated for 3,000 years, the lake population has evolved only slightly if at all towards the freshwater form with a more highly vaulted forehead: *L. m. macrurus.*

RÉSUMÉ. *Reliquats de populations de* Drepanopus bungei *et de* Limnocalanus macrurus grimaldii *(Copepoda: Calanoida) de l'île d'Ellesmere, T. du N.-O.* *L. m. grimaldii* et *D. bungei* vivent dans la couche d'eau douce d'un lac méromictique du nord de l'île d'Ellesmere, dont la couche inférieure (> 60 m) est formée d'eau de mer. Des mesures au C-14 indiquent que ce lac n'a pas communiqué avec la pleine mer depuis 3,000 ans. On retrouve aussi *D. bungei* dans la couche d'eau douce du fjord de Disraeli. Il s'agit ici de la première mention de ce copépode en dehors de l'Arctique sibérien. *L. m. grimaldii,* rare aussi dans l'Arctique canadien, apparaît généralement près des embouchures des grandes rivières, mais on l'a trouvé dans quelques lacs arctiques et lagunes côtières. L'actuelle distribution dispersée de ces espèces est la preuve de leur ancienne dispersion plus générale par tout l'Arctique, aux époques où l'eau saumâtre était beaucoup plus répandue. Bien qu'isolée depuis 3,000 ans, cette population lacustre n'a que très peu évolué vers la forme d'eau douce avec un front plus voûté: *L. m. macrurus.*

РЕЗЮМЕ. *Реликтовые популяции Drepanopus bungei и Limnocalanus macrurus grimaldii (Copepoda: Calanoida) с о. Элсмира (Северо-западные территории).* *L. m. grimaldii* и *D. bungei* обитают в пресноводном слое меромиктического озера в северной части о. Элсмира, содержащем захваченную морскую воду на глубине ниже 60 м. Радиоуглеродные измерения с применением углерода C^{14} показали, что озеро не было связано с открытым морем на протяжении 3000 лет. *D. bungei* также обитают в пресноводном слое в фиорде Дизраэли. Наши данные являются первым сообщением о наличии этого представителя копеподов за пределами Сибирской Арктики. *L. m. grimaldii,* редко встречающийся и в Канадской Арктике, обыкновенно обитает вблизи устьев больших рек. В то же время известно, что он обитает и в некоторых полярных озерах и прибрежных лагунах. Такое очаговое распределение этих видов указывает на более обширное распределение их в прошлом в период более широкого распространения области солоноватой воды. Несмотря на трехтысячелетнюю изоляцию, озерные популяции по своему развитию лишь весьма незначительно приблизились к *L. m. macrurus*, их пресноводному эквиваленту с более сводчатым лбом.

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Among the calanoid copepods characteristically inhabiting the brackish water zone along the arctic coast of Siberia are *Drepanopus bungei* Sars and *Limnocalanus macrurus grimaldii* (Guerne). Bogorov (1944) and Jaschnov (1946) describe the limits of their distribution in the Siberian Arctic. Neither inhabits normal sea water, but Jaschnov (1946) indicates that *Drepanopus* tolerates higher salinities than *Limnocalanus*. This paper gives the first report of *D. bungei* outside of the Siberian Arctic. *L. m. grimaldii* is more widespread. It occurs in the innermost part of the Gulf of Amadyr in brackish water at the mouth of the Amadyr River (Vinogradov 1956); M. W. Johnson (1956) and Grainger (1965) describe its occurrence along the Alaskan and adjacent Canadian coasts of the Beaufort Sea. Relict populations also occur in the Baltic and Caspian Seas.

In addition to brackish Arctic coastal waters, the following circum-arctic localities not now in communication with the Arctic Ocean are known to contain populations of *L. m. grimaldii:*

1. Novaya Zemlya, south island, Beluschiji Peninsula: 2 brackish lagoons, salinity 2-8‰ (Jaschnov 1925).
2. Kolgujev Island, Barents Sea: Pestschanoje Lake, freshwater, 1 m. deep, about 3 km. wide and 17 km. long (Zykoff 1904).
3. Eastern Greenland, 77° N.: Saelsøen, a halocline lake, 117 m. deep, 3 km. wide, 40 km. long, about 5 km. from the coast, an old fiord now isolated from the Greenland Sea (Johansen 1911; Ekman 1913).
4. Alaska, north coast, 70° 35′ N., 153° 30′ W.; Teshekpuk Lake, freshwater, 5.2 m. deep, 45 by 33 km. (Holmquist 1963).
5. Alaska, Cape Thompson region, 68° 12′ N., 166° 02′ W.; Akoviknak Lagoon (M. W. Johnson 1961; Wilson and Tash 1966).
6. Adelaide Peninsula, N.W.T., Canada (about 69° N., 98° W.), in a lake (Segerstråle 1962).

TABLE 1. Plankton tows at Tuborg Lake, made from depth listed to surface.

Date	*Time (GMT)*	*Duration (min.)*	*Depth (m.)*	*Species*	*No. of Specimens*
19 May 1966	—		110	L	54
				D	27
22 June 1967	1800	6	50	n	1
	1750	5	50	L	4
				D	6
				O	2
	1840	9.5	130	D	1
				n	1
	1820	9	130	L	1

L — *Limnocalanus m. grimaldii;* D — *Drepanopus bungei;* O — *Oncaea borealis;* n — nauplius.

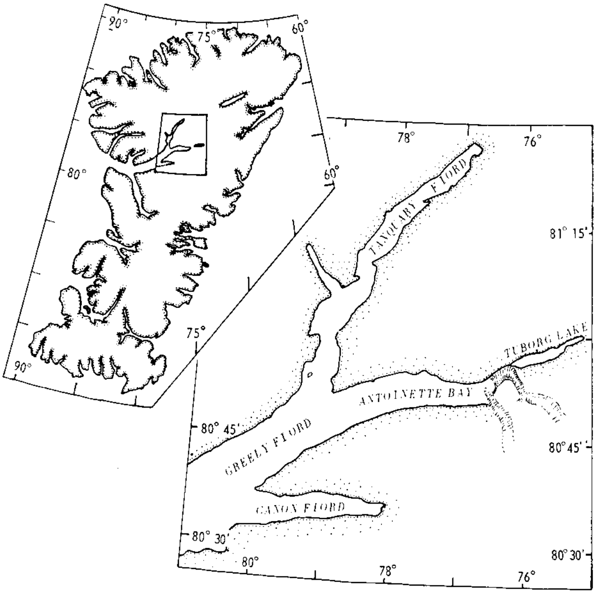

FIG. 1. Ellesmere Island, with enlarged detail of Greely Fiord system, showing location of Tuborg Lake.

We now add another locality: Tuborg Lake, Ellesmere Island, N.W.T.

A plankton tow in Tuborg Lake on 19 May 1966 yielded specimens of *Limnocalanus macrurus grimaldii* and *Drepanopus bungei* only. Four plankton tows on 22 June 1967 yielded a few individuals of the same two species plus a single specimen of *Oncaea borealis* Sars (Table 1).

As shown in Fig. 1, Tuborg Lake is at 81° N., 76° W. at the head of Antoinette Bay. It is about 3 km. wide and 20 km. long; our maximum depth sounding was 130 m. Tanquary Fiord and Antoinette Bay are the eastern extremes of the Nansen Sound-Greely Fiord system. Fig. 2 gives temperature and salinity profiles in Tuborg Lake, and a typical comparative profile from Tanquary Fiord

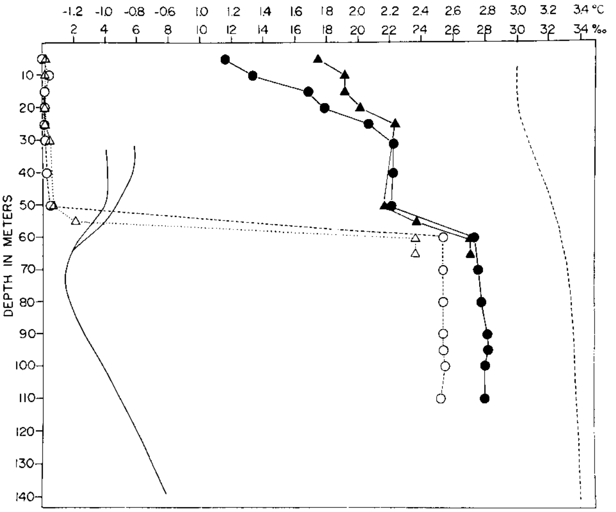

FIG. 2. Temperature and salinity profiles of Tuborg Lake. Solid symbols and solid lines: temperature; open symbols and broken lines: salinity. Circles: 1 May 1966; triangles: 19 April 1967. Lines without symbols indicate temperature (solid line) and salinity (broken line) from Tanquary Fiord, redrawn from Fig. 6 in Ford and Hattersley-Smith (1965). Note interrupted temperature scale.

(from Ford and Hattersley-Smith 1965). The relatively warm saline water below 55 m. is oxygen deficient, indicated by the fact that shortly after exposure to air the water sample develops a rusty, flocculent precipitate; it has no H_2S odour, however.

Hattersley-Smith and Serson (1964) noted that Tuborg Lake formed when the glacier advanced across the fiord, and suggested that the saline water layer was a relict of sea water originally in the fiord. Long (1967) measured ^3H and ^{14}C from various depths in Tuborg Lake and concluded that the fresh water had overturned recently but the deep saline layer was cut off from communication with the other fiord water and with the atmosphere about 3,000 years ago.

As far as is known, neither species has a resistant dormant stage in its life cycle. The eggs of *Limnocalanus* fall to the bottom and remain there for several months before hatching (Eckman 1907), but there is no evidence that these eggs can resist desiccation and be transported by wind or animals. In *Drepanopus* the eggs are carried by the female. Thus the only way for either species to have entered Tuborg was through Antoinette Bay when the Tuborg section was still in communication with the Nansen Sound system. At present the only connection is a 6 km. stream along the foot of the glacier. The Tuborg surface is 10 to 12 m. above that of Antoinette Bay (Hattersley-Smith and Serson 1964). It is highly unlikely that pelagic copepods could swim up this stream.

The data in Table 1 prove that *Drepanopus* lives in the upper (fresh) layer, but do not preclude its existence in the lower (saline) layer. Possibly, as the lower layer became depleted in oxygen, *Drepanopus* migrated upward. *Drepanopus bungei* has not been found previously in fresh water. If what has been stated as likely is really so, then both *D. bungei* and *L. m. grimaldii* must have lived in the Nansen Sound system and elsewhere in the Canadian Arctic 3,000 years ago.

Indeed *D. bungei,* but not *L. m. grimaldii,* does occur in Tanquary Fiord. Although Cairns (1967) does not mention *D. bungei* in his study of the zooplankton of Tanquary Fiord, he has kindly informed us *in litt.* that it does occur there in small numbers, and specimens from the Fiord have been deposited in the Museum of Natural History, Smithsonian Institution.

We have found *D. bungei* at yet another locality on Ellesmere Island. The presence of the Ward Hunt Ice Shelf at the mouth of Disraeli Fiord on the north coast allows exchange between the Fiord and the Arctic Ocean only below 45 m. Below 45 m. the salinity is essentially the same as Arctic Ocean salinities north of the ice shelf. The layer above 40 m. in which *D. bungei* lives is runoff-derived and has a salinity of less than 3‰. The salinity of the bottom part of the fresh layer probably increases each winter, but is purged each summer by runoff. *Drepanopus* occurred in 2 of the 5 plankton hauls made at Disraeli Fiord on 15 June 1967. (See Table 2.)

Because of the salinity restrictions of these two species, their distributions in time have probably followed the changing circum-arctic isohalines. For example, Bogorov's (1944) map of Siberian Arctic distributions, based on collections from 1900 to 1935, shows many records of both species in the open Kara Sea. On the other hand, of the 1945 and 1946 collections of Ponomareva (1957), only

TABLE 2. Occurrence of *Drepanopus bungei* in plankton tows at Disraeli Fiord, 15 June 1967. Net towed from depth listed to surface.

Time (GMT)	*Duration (min.)*	*Depth (m.)*	*No. of specimens*
1515	2	40	10 + many nauplii
1530	3	40	—
1540	6	100	—
1555	18	285	1
1620	20	285	—

those from near Dickson Island contained *L. grimaldii* and *D. bungei* was not found. Ponomareva accounted for this and other faunal changes by an increased salinity in the Kara Sea.

Brackish surface water, and hence brackish-water species had opportunities to become more widely distributed in the Arctic during Pleistocene glacial advances when as a result of sea level lowering, partial or complete arctic basin enclosure occurred (Zenkevitch 1963). Receding glaciers and subsequent increasing salinities restricted the brackish species to areas where salinities remained low. The increased salinities resulted from greater circulation with the Atlantic Ocean allowed by the general sea level rise during glacial recession. Also during a recession or warming period, a transient surface salinity decrease should result at least in fiords and other restricted inlets simply from the greater influx of fresh water. This may have occurred during the Atlantic Warm Phase, a pollen climatic time zone in northern Europe, which lasted from about 7,500 to 5,000 years ago (Butzer 1964) or 7,500 to 3,500 years ago (Fairbridge 1961). The Atlantic Warm Phase was followed by a period of colder climate known in Europe as the Sub-Boreal Phase. In the North American Rocky Mountains the "Temple Lake" and Little Ice Age glacial advances also occurred about 3,000 years ago (Heusser 1961).

Populations of *D. bungei* and *L. m. grimaldii* thrive in the Kara, Laptev, and East Siberian seas because of their proximity to large river mouths. In the Greenland, Norwegian, Barents and Chukchi Seas, and most of the Canadian Arctic including Baffin Bay, these two species were eliminated except for populations trapped in brackish refugia such as the coastal lakes and lagoons listed above.

In spite of the fairly numerous plankton collections from the Canadian Arctic reported to date (see summary by Grainger 1965), *D. bungei* has been found only at the three localities listed above. We therefore consider these to be relict populations. Curiously, *L. m. grimaldii,* but not *D. bungei* has been identified in the southern Beaufort Sea (Johnson 1956; Grainger 1965).

Limnocalanus is found not only in the arctic coastal waters and in the coastal lakes and lagoons mentioned above, but also in lakes on Canadian Arctic islands, and on mainland North America extending south almost to the Great Lakes, west to the Rocky Mountains, and east to Hudson Bay (L. Johnson

1964; Holmquist 1966). Mainland North American specimens fit into the freshwater form commonly referred to as *Limnocalanus macrurus* Sars (= *L. m. macrurus*) and distinguished from the brackish-water *L. m. grimaldii* (Guerne) by its more highly vaulted head. However, in European specimens, Ekman (1913) and Lindquist (1961) found an almost continuous transition between the "extreme *grimaldii* form" (low forehead) of the arctic coast and Caspian Sea and the "extreme *macrurus* form" (highly vaulted forehead) inhabiting certain Swedish lakes. In view of this almost continuous variation we agree with Hutchinson (1967) that the freshwater and brackish-water forms deserve subspecific rather than specific rank.

Although Holmquist (1966) states that it is impossible to determine whether *Limnocalanus* originated in marine or fresh water, most authorities have followed Ekman (1913), who concluded that *L. macrurus* is derived from *L. grimaldii.* Using a "Wölbungsindex" to measure the degree of forehead vaulting, Ekman concluded from a detailed study of many populations in Scandinavian lakes that the degree of transformation toward the extreme *macrurus* form varies directly with the length of time since the population was cut off from the Baltic Sea by postglacial rebound. Extreme *macrurus* occurs in the relict lakes that are oldest, judged by the elevation of the lake surface, whereas the extreme *grimaldii* lives in the newest lakes. Ekman (1913) estimated that the transformation requires 6,000 years.

According to the "Wölbungsindex" of continental North American *Limnocalanus,* Lindquist (1961) classifies them as extreme *macrurus,* but those populations in the Canadian Arctic islands have not been morphologically classified. L. Johnson (1964) relegates them to *L. macrurus* without further comment. Applying Ekman's theory to North American *Limnocalanus,* one would expect the northern island populations, because they inhabit younger lakes in general, to have evolved toward the *macrurus* form less than have the continental populations. The latter probably originated from Arctic stocks carried southwestward in proglacial lakes during late Wisconsin advances (Ricker 1959). The independently derived insular populations were established during the Holocene since they are all in areas that have undergone marine transgression and subsequent uplift (L. Johnson 1964).

We have measured and plotted in Fig. 3 the "Wölbungsindex" of 11 adult specimens of *Limnocalanus* from Tuborg Lake. Comparing these with the indices of several of the many populations measured by Lindquist (1961) also plotted in Fig. 3, one sees that the Tuborg population fits in the non-extreme-*grimaldii* category.

Another character which, although somewhat variable, distinguishes *grimaldii* from *macrurus* is the shape of the posterior margin of the 5th thoracic segment, usually pointed in *grimaldii* and usually rounded in *macrurus*. Of 14 adult Tuborg specimens, 8 had points on both sides of the 5th segment, 3 had points on one side, and 3 had no points. In contrast, of 20 specimens from Lake Erie, only one had points on both sides of the 5th segment, 3 had points on one side and 16 had no points.

A third character used to distinguish the 2 forms is the number of segments

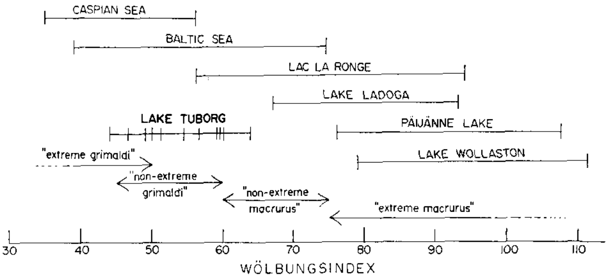

FIG. 3. Wölbungsindex, a measure of flatness (low index) or vaulting (high index) of head profile of *Limnocalanus*. The ranges of the 4 categories are from Lindquist (1961) as are the ranges of *Limnocalanus* populations except that from Tuborg Lake. Each vertical line in the Tuborg Lake population represents one measurement.

beyond the geniculation in the male right 1st antenna, 5 in *grimaldii* and 4 in *macrurus*. Lindquist (1961) found this character so variable that it could not be relied upon in specimens from the Baltic Sea and Scandinavian and Canadian lakes; he did not report on specimens from Arctic coastal waters. As was the case with M. W. Johnson's (1961) Akoviknak Lagoon specimens, all 7 adult males from Tuborg Lake had 4 distal segments. *L. grimaldii* males from the Beaufort Sea have 5 distal segments (M. W. Johnson 1961; Wiley 1920). Assuming that the Beaufort Sea specimens are representative of the once widespread Arctic population, the only obvious change that was evolved in the Tuborg Lake population during 3,000 years of isolation from the Arctic Ocean is the fusion of 2 segments of the male right antenna.

CONCLUSIONS

1) The known extent of *Drepanopus bungei*, a brackish copepod previously reported only from the Siberian Arctic, is now expanded to include the Canadian Arctic.

2) *Drepanopus bungei* and *Limnocalanus macrurus grimaldii* both occur in Tuborg Lake, which has been cut off from communication with the Arctic Ocean for 3,000 years. These species are relicts from a time when they were more widespread in the Arctic, probably owing to a generally lower salinity.

3) The Tuborg Lake population of *L. m. grimaldii* fits into Lindquist's "non-extreme *grimaldii*" category, and has evolved only slightly, if at all, toward the *macrurus* form.

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REFERENCES

BOGOROV, V. G. 1944. The distribution of brackish-water plankton fauna in the Siberian polar seas. *Doklady Akademica Nauk SSR,* 14 (5): 191-192. [in Russian].

BUTZER, K. W. 1964. *Environment and Archaeology.* Chicago: Aldine Publishing Co., 524 pp.

CAIRNS, A. A. 1967. The zooplankton of Tanquary Fjord, Ellesmere Island, with special reference to calanoid copepods. *Journal of the Fisheries Research Board of Canada,* 24: 555-568.

EKMAN, S. *1907.* Über das Crustaceen plankton der Ekoln (Mälaren) und über verschiedene Kategorien von marinen Relikten in schwedischen Binnenseen. *Zoologiska Studier,* tillägnade Professor T. Tullberg: 41-65. Upsala.

————. 1913. Studien über die marinen Relikte der nordeuropäischen Binnengewässer. II. Die variation der Kopfform bei *Limnocalanus grimaldii* (de Guerne) und L. *macrurus* G. O. Sars. *Internationale Revue der gesamten Hydrobiologie u. Hydrographie.* 6: 335-372.

FAIRBRIDGE, R. W. 1961. Eustatic changes in sea level. *Physics and Chemistry of the Earth,* 4: 99-185.

FORD, W. L. and G. HATTERSLEY SMITH. 1965. On the oceanography of the Nansen Sound fiord system. *Arctic,* 18: 158-171.

GRAINGER, E. H. 1965. Zooplankton from the Arctic Ocean and adjacent Canadian waters. *Journal of the Fisheries Research Board of Canada,* 22: 543-564.

HATTERSLEY-SMITH, G. and H. SERSON. 1964. Stratified water of a glacial lake in northern Ellesmere Island. *Arctic,* 17: 109-110.

HEUSSER, C. J. 1961. Some comparisons between climatic changes in northwestern North America and Patagonia. *Annals of the New York Academy of Sciences,* 95 (1): 642-657.

HOLMQUIST, CHARLOTTE. 1963. Some notes on *Mysis relicta* and its relatives in northern Alaska. *Arctic,* 16: 109-128.

————. 1966. Die sogenanten marin-glazialen Relikte nach neuerem Gesichtspunkten. *Archiv für Hydrobiologie,* 62: 285-326.

HUTCHINSON, G. E. 1967. *A treatise on Limnology.* Vol. 2, Introduction to lake biology and the limnoplankton. New York: John Wiley and Sons, 1115 pp.

JASCHNOV, W. A. 1925. Crustacea von Novaja Semlja. *Trudy Plovuch, Morskoi Nauchyi Instituta,* 12: 49-76. [in Russian, German summary].

————. 1946. The distribution of the autochthonous pelagic fauna of the Arctic. *Bulletin of the Moscow Society of Naturalists, Biology section,* 51 (6): 40-50. [in Russian, English summary].

JOHANSEN, F. 1911. Danmark-Ekspeditionen til Grønlands Nordøstkyst 1906-1908 under ledelse of L. Mylius-Erichsen. Bind V, Freshwater life in north-east Greenland. *Meddelelser om Grønland,* 45: 319-37.

JOHNSON, L. 1964. Marine-glacial relicts of the Canadian Arctic Islands. *Systematic Zoology,* 13 (2): 76-91.

JOHNSON, M. W. 1956. *The plankton of the Beaufort and Chukchi Sea areas and its relation to the hydrography.* Arctic Institute of North America Technical Paper No. 1, 32 pp.

————. 1961. On zooplankton of some Arctic coastal lagoons of northwestern Alaska, with description of a new species of Eurytemora. *Pacific Science* 15 (3): 311-323.

LINDQUIST, A. 1961. Untersuchungen an *Limnocalanus* (Copepoda, Calanoida). *Institute of Marine Research, Lysekil, series Biology,* Report No. 13. 1-124.

LONG, A. 1967. Age of trapped water at bottom of Lake Tuborg, Ellesmere Island, N. W. T. *Transactions of the American Geophysical Union* 48 (1): 136.

PONOMAREVA, L. A. 1957. Zooplankton of the west Kara Sea and Baidaratskaya, Bay. *Trudy Instituta Okeanologii Akademii Nauk SSSR,* 20: 228-245 [in Russian. English translation of vol. 20 published in 1959 by American Institute of Biological Sciences.]

RICKER, K. E. 1959. The origin of two glacial relict crustaceans in North America, as related to Pleistocene glaciation. *Canadian Journal of Zoology,* 37: 871-893.

SÅGERSTRELE, S. V. 1962. The immigration and prehistory of the glacial relicts of Eurasia and North America. A survey and discussion of modern views. *International Revue gesamten Hydrobiologie,* 47(1): 1-25.

VINOGRADOV, M. E. 1956. The distribution of zooplankton in the western areas of the Bering Sea. *Transactions of the All-Union Hydrobiological Society,* 7: 173-203 [in Russian].

WILLEY, A. 1920. Report on the marine Copepoda collected during the Canadian Arctic Expedition, in *Report of the Canadian Arctic Expedition,* 1913-18 vol. 7: Crustacea, Part K.: Marine Copepoda, 46 pp.

WILSON, M. S. and T. C. TASH. 1966. The euryhaline copepod genus *Eurytemora* in fresh and brackish waters of the Cape Thompson region, Chukchi Sea, Alaska. *Proceedings of the U.S. National Museum* 118 (3534): 553-576.

ZENKEVITCH, L. A. 1963. *Biology of the seas of the U.S.S.R.* New York: Interscience Publishers, 955 pp.

ZYKOFF, W. 1904. Zur Crustaceenfauna der Isel Kolgujew. *Zoologischer Anzeiger,* 28 (8/9): 337-345.