Behnke

DISTRIBUTION, ORIGIN AND EVOLUTION OF AQUATIC GLACIAL RELICTS

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I. Glacial History

A. Quaternary Period

1. 4 major advances of ice sheets during Pleistocene.
2. N. American and European glacial stages correlated.

B. Maps

1. Illinoillan-Riss greatest of glacial advances.
2. Earth surface depressed during retreat of Wisconsin Wurm glaciers

II. Glacial Relicts

A. Definition

1. Appear superficially to be of marine origin having relatives in arctic marine brackish conditions.
2. Have become completely adapted to FW in some localities.

B. Groups

1. Group I confined to waters that have been connected with proglacial lakes.

a. *Mysis relicta* (Mysidacea)
b. *Pontoporeia affinis* (Amphipoda)
c. *Limnoclalanus macrurus* (Copepoda)
d. *Pallasea quadrispinosa* (Amphipoda)

2. Group II restricted to areas that have been subjected to marine inundation at some former time.

a. *Gammaracanthus lacustris* (Amphipoda)
b. *Mesidotea entemon* (Isopoda)
c. *Myoxocephalus quadricornis* (Cottidae)

III. Distribution of Aquatic Glacial Relicts

A. Maps

1. Relict distributions circumpolar.
2. Relict distribution follows pattern of last (Wisconsin-Wurm) glacial stage.

B. Two theories proposed to explain distribution of aquatic glacial relicts.

1. Relicts occupied ocean basins, subsequent elevation of the land brought the basins above sea level and inflowing water gradually changed them to lakes.
2. Relicts were pushed ahead of the ice during the glacial period from salt water into lakes along the ice margin, in whose remnants they survive.

C. Historical review of glacial relict distribution.

1. Europe and Asia

a. Loven (1858), father of relict research

(1) Believed animals identical or similar to Arctic Sea stocks to be remnants of those living along ice sheet
(2) Concluded arctic animal entered Baltic from White Sea and subsequent crustal uplift isolated Baltic.
(3) Further believed relicts to be those few species capable of adapting to new conditions.

b. Credner (1887)

(1) Published comprehensive account of relict lakes of the world.
(2) Questioned idea of White Sea origin.
(3) Controversy due to geologist disagreement on existence of Baltic-White Sea strait in connection with last glaciation.

c. Wesenberg-Lund (W-L, 1902) and Samter-Weltner (S-W, 1904)

(1) Relict animals found in L. Fureso, Denmark (W-L) and in northern Germany (S-W).
(2) These lakes situated at elevations too high to have been flooded in glacial times.
(3) W-L and Samter (1905) hypothesized that the relicts reached these lakes by active immigration.

d. Von Hofsten (1913)

(1) Among researchers concluding immigration must have been from ocean to the west.
(2) Also stressed immigration by an eastern route.

e. Hogbom (1917)

(1) Proposed theory of "sluiced-up" ice dammed waters as intermediators of relict spread.
(2) Reasoned that advancing ice sluiced Arctic Sea fauna in a proglacial lake across central Russia which overflowed into Aral-Caspian Basin.

(3) Explained occurrence of relicts in localities of northern Europe which had never since the last glaciation been connected with the sea.
(4) Concluded occurrence of relicts in non-uplifted areas of N. America and Ireland were probably due to slucing up.
(5) Slucing concept accpeted by Thienemann, Ekman and others.

f. Sars (1927)

(1) Questioned Baltic-Caspian connection as sole route of migration to Caspian.
(2) Caspian has 2 species of *Pseudalibrotus* (Amphipoda) and *Stenodus leucichthys* (Coregoninae) not found in Baltic.

g. Gurjanova (1933)

(1) Studied *M. entemon*

(a) *M. e. glacialis* inhabits Caspian, Siberian coastal waters, and R. Yenessei
(b) *M. e. entemon* inhabits L. Ladoga, Baltic and White Seas.

(2) Caspian *Pseudalibrotus* similar to Siberian form.
(3) Concluded northern representatives in Caspian fauna due to immigration from Siberia.

h. Pirozhnikov (1937)

(1) Extended Gurjanova view based on extensive hydrobiological studies in northern and western Siberia.
(2) Many arctic forms of Caspian live in R. Yenissei, R. Pjasina and their estuaries.
(3) Suggested immigration to Caspian by way of large ice dammed lake in western Siberia.
(4) Ob and Yenessei rivers freshened the proglacial lake and the R. Tobol served as a spillway to the south.

i. Segerstrale (1957)

(1) Evidence favors immigration from east

(a) Relicts could not tolerate salinity from Russia-Siberia around Scandanavia
(b) No relicts occur in lakes of uplifted Norwegian coast
(c) *Gammaracanthus*, *Mesidotea*, and *Myoxocephalus* present in Sweden but not Norway.

(2) Modified Hogbom theory.

(a) Refuted early direct Baltic-White Sea connection.
(b) Theorized westward migration facilitated by overflow of Onega ice lake across watershed to the west.

(3) *P. quadrispinosa*

(a) Developed from *P. kessleri* which invaded western Siberia proglacial lake (believed to exist during Riss glaciation and extend to western Europe) from L. Baikal.
(b) Pallasea migrated westward reaching White Sea region before Wurm glaciation.
(c) Invaded Onega ice lake of last glaciation and spread west to Europe and Baltic.

(4) Precursors of relicts lived in Siberian proglacial lake.

2. North America

a. Marsh (1892)

(1) Believed relict crustaceans of Great Lakes arose from ancestors in marine basins isolated by crustal uplifting.
(2) Suggested waterfowl transport.

b. Gurney (1928)

(1) Attributed occurrence of *L. macrurus* and *M. relicta* in lakes Champlain and Huron to late postglacial marine inundation.
(2) Suggested upstream migration for population of upper Great Lakes.

c. Hogbom (1917), Ekman (1930), Thienemann (1950), Segerstrale (1957)

(1) Favored Hogbom proglacial lake transport for N. American relict distribution.
(2) Offered no details

d. Sheffer and Robison (1939)

(1) Discovered *P. affinis* in L. Washington, Washington.
(2) Raised question of how this population became isolated.

e. Larkin (1946)

(1) Rejected proglacial lake transport for N. American relict distribution based on Keewatin Ice Centre.
(2) Suggested preglacial marine invasion.

f. Mohr (1953)

(1) Collected *M. relicta* at Pt. Barrow, Alaska, from sea, coastal lagoon and saline pond.
(2) Suggested *M. relicta* stranded inland by recent coastal uplift.

g. Ricker (1959)

(1) Described relict distribution on basis of two major N. American ice sheets.

(a) Laurentide ice sheet of eastern and middle parts of continent.
(b) Cordilleran ice sheet of western mountains.

(2) Accounted for presence of relicts in Waterton Lakes, Alberta.

h. Johnson (1964)

(1) Studied relicts of Canadian Arctic Islands.
(2) Found relicts only in areas of marine inundation.
(3) Proposed islands colonized after Wisconsin glaciation.

i. Segerstrale (1971)

(1) Accounted for *P. affinis* in L. Washington based on dispersal of two cyprinids.

(a) *Hybognathus hankinsoni* dispersed east to west.
(b) *Mylocheilus caurinus* dispersed west to east.

(2) Suggested crossing of Continental Divide during last glaciation.

IV. Origin of Aquatic Glacial Relicts

A. Three major questions.

1. Was there a single site of relict origin?
2. Have relicts developed from marine forms in two or more places?
3. When did fresh water forms arise?

B. Hypotheses

1. Multiple-origin

a. *Pontoporeia*

(1) Reduction of *P. femorata* bifurcate process.
(2) Presence of *P. affinis* in Kamchatka and L. Washington.

b. *Mysis*

(1) Collection of *M. relicta* at Point Barrow, Alaska.
(2) Presence of *M. relicta* in west Britain and Ireland.

2. Single origin

a. *Pontoporeia*

(1) Coexistence of *P. affinis* and *P. femorata* without integration in Baltic.
(2) Collection of *P. affinis* from Siberian and American coastal localities.

b. *Mysis*

(1) *M. litoralis* is distinct species.
(2) *M. relicta*, *M. oculata*, *M. litoralis* may occur in same sample.
(3) *M. relicta* tolerant of high salinity.

3. Pleistocene origin

a. Freshwater tolerance acquired in Siberian proglacial lake during Riss glaciation.

(1) *P. quadrispinosa*

(a) Not tolerant of salt water
(b) Tolerant of warm shallow water

(2) Other relicts

(a) Somewhat salt-tolerant
(b) Prefer cold water

b. Eastward dispersal

(1) Freshwater route possible
(2) Brackish route likely

4. Tertiary origin

a. *Mysis* inhabited European-Russian Sea in Eocene and Oligocene times.
b. *M. relicta* evolved as freshwater form in receding north-Russian Miocene sea.

V. Evolution of Aquatic Glacial Relicts

A. The age of the species *M. relicta*.

1. Holmquist asserts evolution no later than Miocene (Figure 1, Table 1).
2. Cases of speciation in glacial or post-glacial time.

a. *P. quadrispinosa*

(1) Evolved during Riss glaciation
(2) Morphological reduction of Finland spring population

b. *P. affinis*

(1) *P. a. brevicornis* tends toward neoteny
(2) *P. a. brevicornis* has evolved since lake isolation of Wisconsin glaciation.

c. Caspian *Mysis* (Figure 2)

(1) Four ecologically differentiated *Mysis* of different distribution.
(2) Probably reached Caspian during Riss glaciation.

B. Evolutionary parallelism

1. *L. macrurus*

a. Many lakes isolated by postglacial events contain characteristic forms completely adapted to fresh water.
b. In Scandanavia degree of differentiation from *L. grimaldii* to *L. macrurus* depends on age of lakes; i.e. time exposed to fresh water (Figure 3).
c. Rate of development not constant as less developed *L. macrurus* occur in Emerdale Water, England.

2. *M. entemon*

a. Specimens in fresh water tend to be smaller.
b. *M. entemon* subspp. tend in more dilute waters to be less sculptured, hairier, and narrower with narrow telson (Table 2).

3. *M. quadricornis*

a. Isolated populations differentiated by presence or absence of horns and spinous scales, eye size, and relative length of caudal peducle (Figure 4).
b. Rate of development in different basins very irregular.

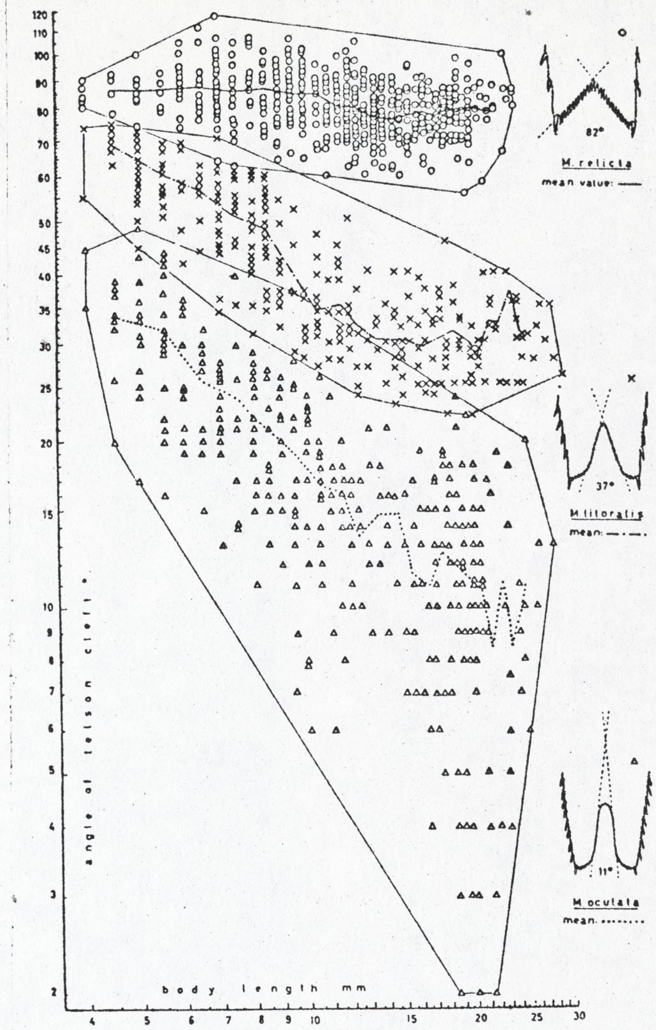

Fig. 1. The angle of the telson cleft in *M. oculata*, *M. litoralis* and *M. relicta*.

Table 1. *Some chief characters for a distinction of the main groups of Mysis species.*

			Aurico-mysis	*Michteimysis*		*Mysis* s. str.							
			stenolepis	*mixta*	*gaspensis*	*polaris*	*oculata*	*litoralis*	*relicta*	*caspia*	*macrolepis*	*microph-thalma*	*amblyops*
antero-lateral angles of carapace			produced acute	rounded	rounded	rounded	rounded	rounded	rounded	rounded	rounded	rounded	rounded
chroma-tophores	antennal scales		+	+	+	—	—	—	—	—	—	—	—
chroma-tophores	telson	number	> 2 varying	2	4	2	2	2	2	2	0	0	0
chroma-tophores	telson	position, distance from base	irregular	ca 1/8	ca 1/2 + ca 1/7	ca 1/8	ca 1/3	ca 1/3	ca 1/3	ca 1/5	—	—	—
chroma-tophores	entirely wanting		—	—	—	—	—	—	—	—	+	+	+
antennal scales	apex		acute	juv. rounded ad. acute	rounded	rounded	rounded	rounded	rounded	rounded	rounded	rounded	rounded
antennal scales	relative length		very long	long	compara-tively short	short	compara-tively long	compara-tively long	short	compara-tively long	compara-tively long	compara-tively long	compara-tively long
telson	angle of cleft		medium	medium	medium	narrow	narrow	medium	broad	medium — broad	medium	broad	very broad
telson	apical lobes		acute	acute	acute — rounded	rounded	rounded	acute	acute	acute	acute	acute	acute
2 nd maxillipede, "notch" in row of spines			+	—	—	—	—	—	+	+	+	+	+

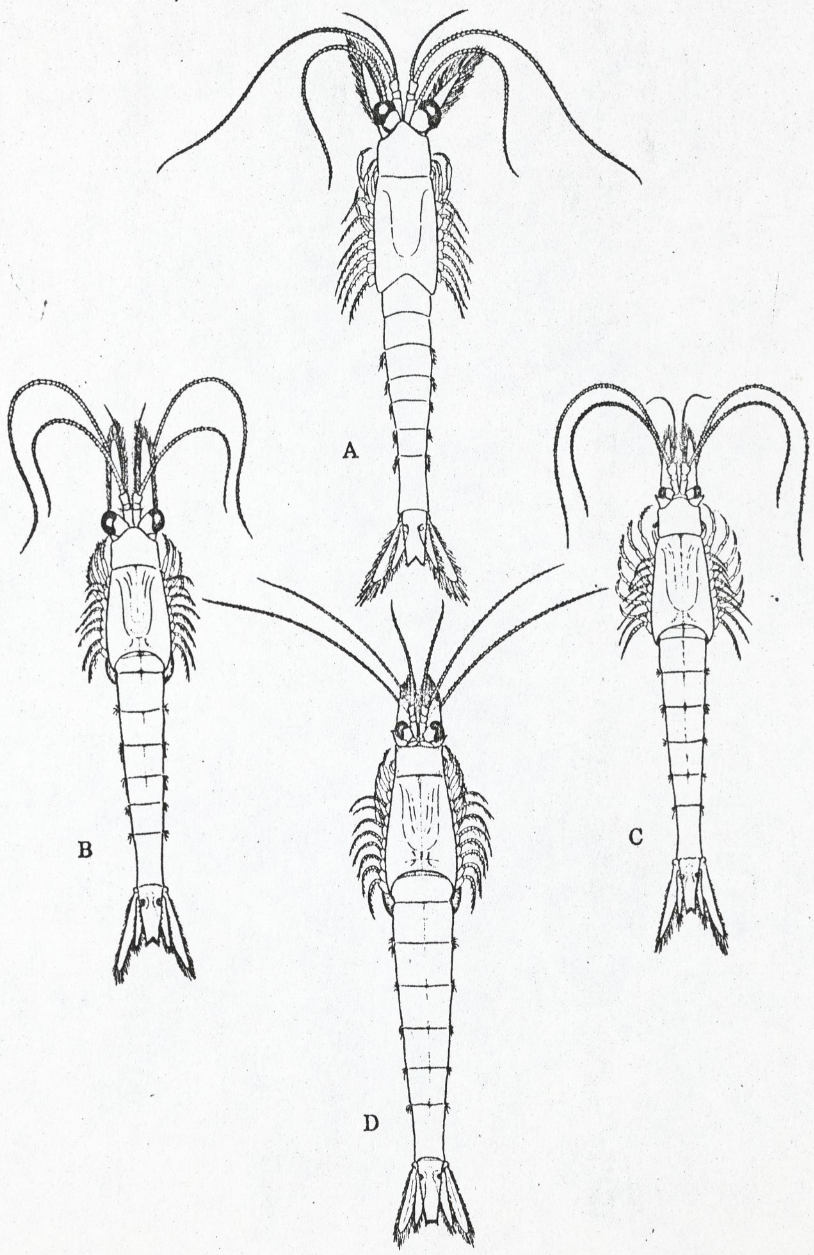

FIGURE 2. *A. Mysis relicta B. M. caspia C. M. microphthalma.* Both Caspian species are related to *M. relicta* and perhaps represent multiple invasions from the north. *D. Paramysis (Metamysis) ullskyi,* an endemic Caspian species adapted to fresh water that has penetrated far up the rivers entering the Ponto-Caspian basins. (Sars.)

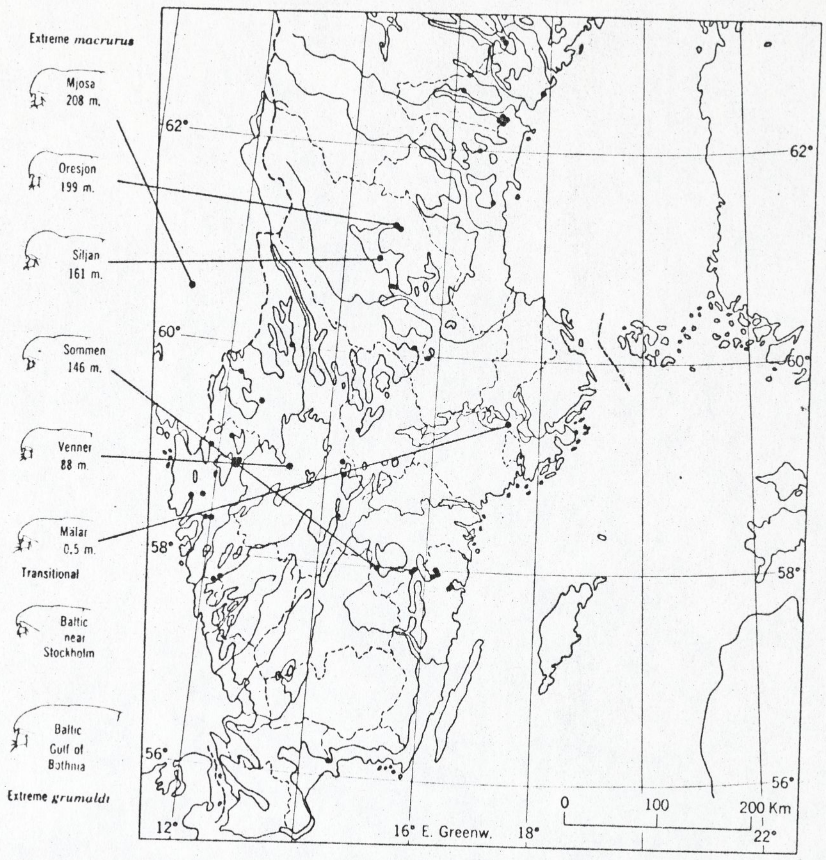

FIGURE 3. Distribution of *Limnocalanus* in Sweden, with a selection of profiles of the head showing parallel evolution of the short elevated head of the extreme *macrurus* populations, for example, in Mjosa and Siljan, two of the oldest lakes, and the very little change in Mälar, a fresh water lake but one cut off only since the early Middle Ages. Elevations of lake surfaces are given below figures of the heads.

TABLE 2. *Proportions of body and of telson in various races of* Saduria entomon

			Length/Breadth	Base of Telson/ Length of Telson
orientalis	(Shantar Is.)			
	♂ immature	25–40 mm.	3.10 ± 0.17	0.669 ± 0.027
	♂ mature	40–60 mm.	3.36 ± 0.14	0.612 ± 0.032
entomon	(Baltic)			
	♂ immature	25–35 mm.	3.14 ± 0.13	0.551 ± 0.026
	♂ intermediate	40–70 mm.	3.48 ± 0.11	0.494 ± 0.021
	♂ large mature	70–80 mm.	3.52 ± 0.10	0.487 ± 0.015
caspia	(Caspian)			
	♂ immature	25–40 mm.	3.27 ± 0.21	0.530 ± 0.029
	♂ mature	40–54 mm.	3.50 ± 0.21	0.500 ± 0.007

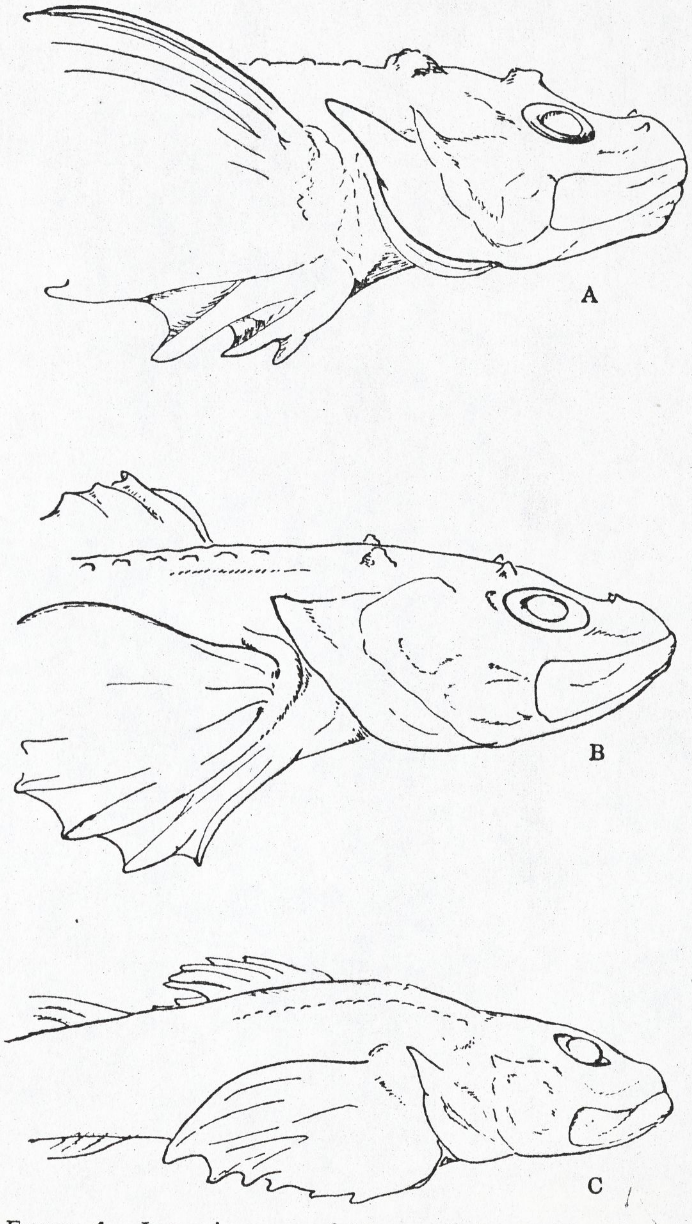

FIGURE 4. Lacustrine races of *Myoxocephalus quadricornis*. *A*. *M. q. lönnbergi*, Lake Ladoga, isolated about 2000–2500 B.C. *B*. *M. q. relictus*, Lake Vetter, isolated somewhat before 6500 B.C. *C*. *M. q. asundensis* isolated before 7500 B.C. (Lönnberg, Berg.)

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