New Complexities in Zoogeography and Taxonomy of the Pygmy Whitefish (*Prosopium coulteri*)

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Pygmy whitefish (*Prosopium coulteri*) are recorded for the first time from the Peel–Mackenzie river drainage (Elliott Lake, Yukon Territory) and from the Hudson Bay drainage (Waterton Lakes, Alberta, in the South Saskatchewan–Nelson river system). The morphology of specimens from both localities contradicts the previously known pattern of a southeastern "low-rakered" and a northwestern "high-rakered" form (with the two forms occurring sympatrically in some lakes of the Bristol Bay area). Specimens from Elliott Lake, the most northerly known locality, resemble the southeastern form and those from Waterton Lakes the northwestern form. Both Waterton and Elliott lakes lie close to unglaciated refugia, suggesting that the species may have survived Wisconsin glaciation and diverged in several different watersheds.

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Il s'agit de premières mentions du ménomini pygmée (*Prosopium coulteri*) dans le bassin Peel-Mackenzie (lac Elliott, Territoire du Yukon) et dans le bassin de la baie d'Hudson (lacs Waterton, Alberta, dans le régime des rivières Nelson et Saskatchewan-Sud). La morphologie des spécimens des deux endroits vient à l'encontre du concept établi d'une forme "à bas compte branchicténique" au sud-est et d'une forme "à haut compte branchicténique" au nord-ouest (les deux formes étant sympatriques dans certains lacs de la région de la baie de Bristol). Les spécimens du lac Elliott, l'endroit le plus au nord de leur aire de répartition connue, ressemblent à la forme du sud-est, alors que ceux des lacs Waterton se rapprochent de la forme du nord-est. Les lacs Elliott et Waterton sont situés à proximité de refuges qui n'ont pas été recouverts de glaciers. Il est donc possible que l'espèce ait survécu à la glaciation du Wisconsin pour se disperser ensuite dans plusieurs bassins hydrographiques différents.

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THE pygmy whitefish *Prosopium coulteri* Eigenmann and Eigenmann, a distinctive large-scaled little fish confined to North America, has become an increasing puzzle to ichthyologists. Its known distribution is unique and highly disjunct: Pacific slope streams from Bristol Bay drainages south to the upper Columbia River; headwaters of the Yukon, Liard, and Peace rivers; and (separated by a gap of 1700 km) Lake Superior. Only a single species was thought to be involved (Eschmeyer and Bailey 1955) until McCart (1970) demonstrated that there are at least two forms within the "pygmy whitefish complex," two or even three occurring sympatrically in lakes near Bristol Bay. McCart suggested that each of the two forms may have spread postglacially from a distinct refugium within which it had diverged from its sibling.

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This note describes two recent collections of pygmy whitefish whose localities extend the known range into new drainages (the Peel–Mackenzie and the Saskatchewan–Nelson river systems) and whose morphology runs contrary to previously described geographic patterns of variation.

Sources of materials — On July 13, 1970, two specimens were taken by C. C. Lindsey and R. C. Manness from Elliott Lake, Yukon Territory (64°29′N, 135°35′W), 100 km north of Mayo (Fig. 1). Collection was by monofilament gillnet set on the bottom at a depth of 24 m. Other species collected in Elliott Lake and its tributaries were *Thymallus arcticus*, *Prosopium cylindraceum*, *Catostomus catostomus*, *Cottus cognatus*, *Salvelinus namaycush* and *Salvelinus alpinus*. (The two specimens of the latter species, although close to the known geographic range of *S. malma* and farther inland than previous records of *S. alpinus*, are tentatively identified as Arctic char on the basis of these counts following

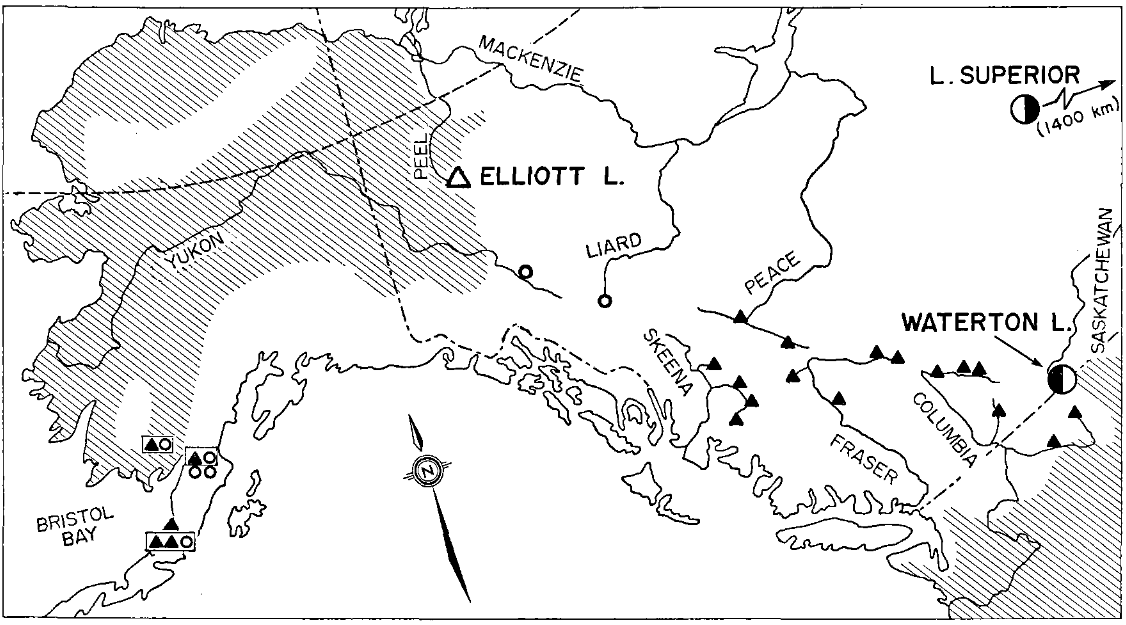

FIG. 1. Geographic distributions of forms of pygmy whitefish in western North America, modified from McCart (1970). Solid triangles are the "low-rakered" form (ratio: gillrakers/caudal peduncle scale rows < 0.95); open circles are "high-rakered" form (ratio: > 0.95). Rectangles enclose sympatric forms. Hatched areas unglaciated. All samples, except for Waterton and Elliott lakes, of five or more fish.

McPhail (1961): total gillrakers 23, 22; lower limb gillrakers 14, 13; lateral line pored scales 129, 131; pyloric caeca 31, 35; and vertebrae 68, 68.)

On August 10, 1971, two specimens were taken from Upper Waterton Lake, southwestern Alberta (Fig. 1), by W. G. Franzin and S. Franzin using monofilament gillnets set on the bottom at a depth of about 50 m off the mouth of Cameron Creek at Waterton Park townsite. At least 13 other species of fish have been recorded as probably native to Waterton Lakes.

We also have new records of pygmy whitefish in the Yukon River drainage from Quiet Lake, Yukon Territory (61°04′N, 133°04′W), Tatchun Lake, Yukon Territory (62°07′N, 136°07′W), and previously published records from Chadburn Lake, Yukon Territory, and Swan Lake, British Columbia (Teslin–Yukon system).

Morphology — The following counts (using the methods of McCart 1970) are given in the sequence of the two Elliott Lake specimens followed by the two Waterton Lakes specimens: Fork length (mm) 119.4, 111.9; 98.4, 88.0. Gillrakers 18, 16; 21, 20. Pored lateral line scales 53, 52; 52, 53. Horizontal scale rows around caudal peduncle 18, 18; 18, 18. Vertebrae 51, 51; 53, 54. Dorsal fin rays 12, 12; 12, 11. Anal fin rays 11, 12; 12, 13. Pectoral fin rays 15, 14; 14, 14.

Discussion — Previous collections of pygmy whitefish from western North America could be separated into two groups (Fig. 2) on the basis of dorsal fin ray counts and the ratio of gillrakers to caudal peduncle scales (McCart 1970). All southeastern collections (Peace, Skeena, Fraser and Columbia river drainages) fell in one group (McCart's "low-rakered" form); the second group, the "high-rakered" form, contained exclusively northwestern collections (Liard and Yukon rivers, and drainages in the Bristol Bay area). Three Bristol Bay collections contained two (or three) sympatric forms, one conforming to the northwestern group and one or two to the southeastern group. One Bristol Bay collection (Black Lake) fell exclusively in the southeastern group. Lake Superior specimens were intermediate between the two groups.

The striking geographic pattern in morphology suggested to McCart that the high-rakered form developed somewhere in the Yukon–Bering Sea area and the low-rakered form somewhere in the vicinity of the present Columbia Basin. According to this theory the low-rakered form subsequently spread north and west and has reached a few lakes in the Bristol Bay region where it occurs sympatrically with the high-rakered form. The fish in

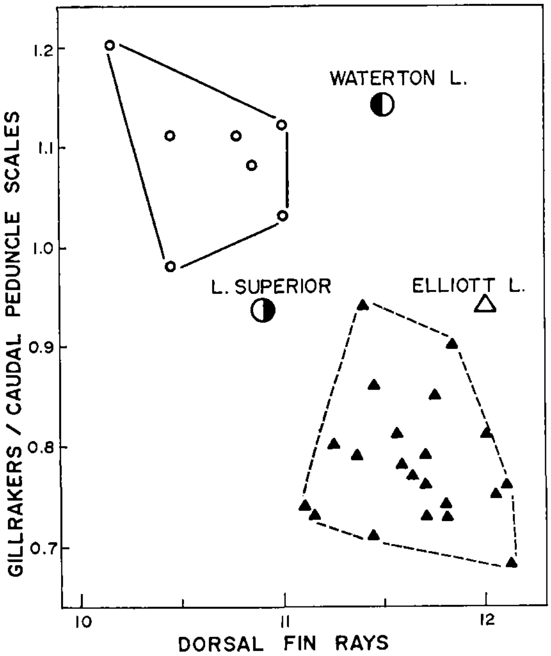

FIG. 2. Relation between population means of dorsal fin ray counts and ratio of number of gillrakers to that of caudal peduncle scales. Samples and symbols same as in Fig. 1. Solid line encloses all Liard and Yukon river samples plus high-rakered form from Bristol Bay area; broken line, all Peace, Skeena, Fraser, and Columbia river samples plus low-rakered Bristol Bay form.

Lake Superior presumably survived Wisconsin glaciation in a third refugium far to the east.

The morphology of specimens from both Elliott and Waterton lakes disrupts the pattern described. The very small sample sizes (2 for each lake, although all other points in Fig. 2 are each based on 5 or more fish) preclude detailed comparisons. Nevertheless, the Elliott Lake fish, although the most northerly of all collections (Fig. 1), clearly resemble the southeastern group in morphology (Fig. 2). Conversely, the Waterton Lakes fish, although geographically close to the southeastern group, lie morphologically remote from them.

The hypothesis that morphological variation has arisen during isolation in multiple refugia is not necessarily negated by the distinctive nature of these two new collections, provided it can be shown that Elliott and Waterton lakes might each have received fish from refugia other than the Columbia and Bristol Bay regions. To assess this possibility, the glacial history of each must be examined.

Elliott Lake lies close to the central and northern region of Yukon Territory which escaped glaciation (Fig. 1), but just inside the northwest margin of the area covered during the last glaciation by the Selwyn Lobe of the Cordilleran Ice Sheet. During the maximum ice advance, a long narrow glacier tongue projected northwest from the main ice mass to fill the valley now occupied by Elliott Lake and extend a further 33 km northwest downslope into the Hart River on the present Peel–Mackenzie river drainage (Hughes et al. 1969). During ice recession this tongue retreated upslope until it exposed the divide (between the Peel and Yukon river drainages) which at that time lay about 6.5 km northwest of the present Elliott Lake (Vernon and Hughes 1966, p. 14). As the ice face retracted still farther to the southeast, now receding downslope into the Yukon River basin, a proglacial lake was impounded between the ice front and the divide at an elevation of just below 1166 m. Meltwater discharging northward from this lake cut a channel through the old divide, thereby lowering the lake to somewhat above 1000 m and shifting the divide 11 km southeast to its present position south of Elliott Lake. The lake has apparently, since its inception, always had an outlet northwest into the Hart River. The proximity of Elliott Lake to an unglaciated refugium and the known sequence of events during ice retreat are consistent with the view that the somewhat distinctive Elliott Lake form of pygmy whitefish may have had its origin in a refugium within the Peel drainage basin.

Waterton Lakes, at an elevation of 1398 m, straddle the Alberta–Montana border just east of the continental divide (Fig. 1). The present lake basin was probably overrun by a tongue from the North Fork Belly Glacier of the Cordilleran ice complex (Alden 1932, pl. 37), but unglaciated terrain which harbored a series of shifting proglacial lakes evidently lay only a few kilometres to the east and south, although the details are obscure (Horberg 1954; Prest et al. 1968; Prest 1969). During early glacial retreat, the proglacial lake waters which filled the Waterton Valley probably escaped to the eastward and thence southward to the Missouri River system. Withdrawal of the Laurentide ice sheet eventually permitted establishment of the Saskatchewan–Nelson river system whereby Waterton Lakes now drain to Hudson Bay. There seems to be no evidence that Waterton Lakes ever had an outlet westward into the Columbia river system either during or after Wisconsin glaciation. In support of this contention, the nearest tributary of the Columbia, the North Flathead River, differs markedly in its fauna from that of Waterton Lakes. About eight fish species present in Waterton Lakes are absent from the North Fork Flathead River and four species present in the latter are absent from the former (Schultz 1941; Paetz and Nelson 1970; McAllister and Ward 1972). The crustacean

Mysis relicta is in Waterton but nowhere west of the continental divide; the amphipod *Pontoporeia affinis* is also in Waterton, and absent on the Pacific coast except for the single known occurrence in Lake Washington at Seattle (Ricker 1959). Segerstråle (1971) argued that the Lake Washington population probably reached there by crossing the continental divide from a Missouri River refugium. If this did occur (which presents some difficulties if only passive transport is envisaged), the route was presumably via the Fraser river system rather than the Columbia in order to place the amphipod in ice-dammed lakes in the Puget Sound region (Segerstråle 1971); hence, the crossover point of the continental divide would have been far to the north of Waterton. In summary, the proximity of Waterton Lakes to unglaciated regions in the headwaters of the Missouri River, the apparent absence of any water connection with the Pacific slope during or since Wisconsin glaciation, and the presence in Waterton of various other species of fish and crustaceans not found in the Columbia River system are all consistent with the view that Waterton Lakes pygmy whitefish differ morphologically from Pacific slope populations because they orginated from a different glacial refugium.

It may be argued that all the observed morphological variation represents recent adaptation to local environments and is without relevance to glacial history. However, fish from all the southeastern localities (except Waterton Lakes) are consistently different from most of those from the northwestern localities, even though both lake and stream collections are represented in both areas. The morphological characters used do not seem to be obviously correlated with local ecological conditions.

The available data suggest that pygmy whitefish survived the Wisconsin glaciation in several refugia, each containing one or more forms which possessed morphological distinctions either developed in situ or left over from earlier Pleistocene events. The following Wisconsin refugia might have been involved: (a) one in the Columbia River basin; (b) one close to Bristol Bay (which might have harboured two forms, one perhaps derived from a preWisconsin invasion from the south); (c) one in the upper Yukon River basin (which may or may not have been isolated from Bristol Bay watersheds); (d) one in the Peel River area (which is now tributary to the Mackenzie River but which during maximum glaciation was tributary to the Yukon River via the Porcupine (Hughes 1972)); (e) one in the Missouri River headwaters close to Waterton Lakes; and (f) one in the upper Mississippi River region which gave rise to the Lake Superior population. With all these possibilities for allopatric divergence, it is not remarkable that the present mosaic of characters is complex.

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