

THE ICE AGE AND MAMMAL SPECIATION IN NORTH AMERICA

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A NUMBER of effects of the Ice Age on life in northern North America have been briefly reviewed by Flint (1952) in an earlier number of this journal. To these should be added another, the effect of glaciation on speciation of plants and animals. This aspect of the Ice Age in North America has received some attention in regard to plants and birds and here it is shown to have had an effect on some mammals.

As I pointed out in discussing the effects of glaciation on birds (Rand, 1948) in continental areas, when a wide ranging species varies geographically and is divided into a number of subspecies, the usual pattern is for a gradual change from one subspecies to another, the width of the area of intergradation being wider or narrower depending on the suddenness of the change of ecological conditions. As long as these subspecies are in contact they interbreed, there is gene flow between the populations, and they all remain one species. Geographical isolation by physical barriers seems necessary for a population to evolve further, to the species level. In this isolation the two parts of the population gradually change by random mutation toward a state in which interbreeding with other populations is impossible. Then, when the barriers disappear, or are surmounted, the two descendents of the one ancestral form meet. What happens now depends on how far the process of speciation has gone. If it has not gone to the point where biological discontinuity is complete, they meet each other as subspecies and interbreed. If biological discontinuity has been achieved and their ways of life have become different enough they invade each other's territory and live together in the same areas as sympatric species.

In birds in northern North America there are a number of cases where forms meet that fit neither extreme. They have reached a point where they do not intergrade as ordinary subspecies, but their ways of life are still so similar that they are unable to invade each other's territory, and in some cases hybridization occurs, but only in a narrow zone. Examples are the gull complex of the *Larus argentatus-thayeri-kumlieni-leucoptera* complex; the large and small Canada geese of the *Branta canadensis* complex in the Arctic, and the spruce and Franklin's grouse (*Canachites canadensis* and *C. franklini*) that meet in the Rocky Mountains of British Columbia and Alberta. These phenomena correlate well with postulated effects of isolation by glaciers during the Ice Age: populations which had been isolated in refugia on the fringe of the ice met again with the retreat of the glacier, and the present zones of contact are therefore secondary. The refugia which seem to be

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indicated are: one (or more) southeast of the ice; two (or more) southwest of the ice in the Rocky Mountain area; one (or more) in the Alaska-Bering Sea area; and one in the arctic islands (this need not have been permanent in location, but have been slowly moving and transient in any one locality).

The correlation of bird data and postulated Ice Age effects makes it advisable to examine some mammal examples (basing classification on Anderson, 1946),¹ illustrating this idea:

(a) *A Bering Sea area and a southeast refugium*

The tundra shrew (*Sorex tundrensis*) of Alaska, northern Yukon, and northern Mackenzie is replaced to the south and east by the closely related saddle-backed shrew (*S. arcticus*), that ranges from northeastern British Columbia and central Mackenzie east and south to eastern Canada. This seems to indicate a Bering Sea refugium and one south and east of the ice. Later there was a subsequent spread, in which the southeastern member was the most active, and a secondary meeting in the same habitat. Though now without geographical barriers to separate them, the way of life of these two animals is apparently so similar that they have been unable to penetrate each other's habitat.

(b) *A southeast and a southwest refugium*

The red squirrels provide an example that correlates with two refugia south of the ice. *Tamiasciurus hudsonicus* is widespread in the coniferous forests, from the Atlantic north to the limit of trees, and west to Alaska and western British Columbia including Vancouver Island. However, in southwest British Columbia along the coast the douglas squirrel (*T. douglasii*) takes its place, and when the two meet they do not intergrade. The ranges of two species of marten are somewhat similar: *Martes americana* is found in the coniferous forest from northeastern North America to Alaska and British Columbia but is replaced west of the coast mountains by *Martes caurina*. In these instances, too, the eastern form has been the more active in spreading over much the larger area.

(c) *A Bering Sea area and a southwest refugium*

The thornhorn sheep (*Ovis dalli*) in its various local colour phases ranges from Alaska and Yukon into extreme northern British Columbia, to be replaced to the south by the bighorn sheep (*Ovis canadensis*). The ranges nearly, if they do not quite, meet and there is no sign of intergradation between the two species.

A similar pattern is evident in the ranges of the two closely related ground squirrels. The Columbian ground squirrel (*Citellus columbianus*), that ranges in the mountains of central British Columbia and central western Alberta southward, is replaced in northern British Columbia and northward by the closely allied arctic ground squirrel (*Citellus parryii* including *plesius* as a

¹I follow this standard list of names though later taxonomic work, notably that of Rausch (1953), has suggested some changes for nomenclatural reasons or because of changes in species limits.

subspecies). The arctic ground squirrel, however, shows a change in distribution pattern that adumbrates the distribution of some of the following examples. Adapted to alpine and tundra conditions of the north it was not restricted to the mountains as was its southern relative, and spread across the tundra of the northern mainland to Hudson Bay.

The relationships of the grizzly bears (genus *Ursus*) have to be worked out, along the lines indicated by Rausch (1953, pp. 96-7), but from my cursory observations there are three main types in the north: a small Barren-Ground type of interior Alaska, Yukon, and the mainland Barrens of the Northwest Territories; a huge coastal Alaskan type (including the big brown bears); and the large bears of the Rocky Mountains and plains. If this be the case, it would fit the picture of two refugia in the Alaska area; and one refugium (or more) southwest of the ice. The picture farther south may be more complex. Apparently there was a large grizzly on the plains of Canada at least, but it was the small Yukon type, adapted to northern conditions, that spread east onto the Barrens.

(d) *A Bering Sea area and a southwest and southeast refugium*

A similar picture, but involving three refugia, is shown by the genus *Microtus*. The three species: meadow mouse (*M. pennsylvanicus*), tundra mouse (*M. operarius*), and Townsend mouse (*M. townsendii*) are largely representative species that do not intergrade where they meet or overlap. The meadow mouse ranges from the northeastern United States and eastern Canada to the Cascades of British Columbia, to be replaced in the extreme west by the Townsend mouse. To the north the meadow mouse meets the tundra mouse in central Yukon, where the latter replaces it at higher altitudes. In the Arctic farther east, the meadow mouse extends to the wooded mouth of the Mackenzie, and in Keewatin extends onto the southern Barrens, but on the Barrens fringing the Arctic Ocean at Coronation Gulf it is the tundra mouse that has won the race to occupy this area, while neither as yet seems to have occupied the Barrens of northern Keewatin.

The red-backed mice of the genus *Clethrionomys* also have three representative species that nearly if not quite meet, but without intergrading. *C. dawsoni* is the northwestern form that ranges from Alaska and Yukon south to northern British Columbia and eastward in the north to the Perry River and northern Manitoba. Just south of it, but with a wider range, from Nova Scotia to northern British Columbia and southward lives the closely related *C. gapperi*. There is some habitat difference in part: *C. dawsoni* lives in the Barrens and the forests, while *C. gapperi* lives only in the forests. A further species, *C. wrangeli*, of northeastern British Columbia and nearby islands, related to *dawsoni*, recalls the case of the Queen Charlotte Island caribou (see p. 34).

(e) *East and west refugia in the Arctic*

The east-west division of an aquatic arctic mammal, comparable to that of the black- and the white-bellied brant (genus *Branta*) and the Atlantic and the Pacific eider (genus *Somateria*) (Rand, 1948, p. 316), is shown by the Atlantic and the Pacific walrus (*Odobenus rosmarus* and *Odobenus divergens*).

The former, of the Eastern Arctic, ranges northward to the arctic islands, but only rarely west of Barrow Strait, Somerset Island, and Fury and Hecla Strait; the Pacific walrus ranges commonly to Point Barrow, but only casually farther east. Apparently, present-day ice conditions keep them apart. During the Ice Age, they were even more isolated.

(f) *Several refugia, including one on the arctic islands*

The most complex case has been left to the last. The relationships of the various forms of caribou (genus *Rangifer*) are still far from clear. They have been grouped into five species by Anderson (1946, pp. 178-81), but there seem to be two main types: a southern woodland type, large, with smaller, flattened and palmate antlers; and a northern Barren-Ground type, variable in size but with larger, more slender, little flattened antlers. In the northern Manitoba-Alberta-southern Mackenzie area these meet as species, with, at least during the winter season, some overlap of range when the northern form moves south. However, in the northwest (Alaska-Yukon-British Columbia) there are forms (*osborni*, *fortidens*) that seem to be intermediate and to connect the two types, giving a circular chain of subspecies, with the ends overlapping as species. Within the Barren-Ground group there are also several distinct forms: *pearyi* of the northern arctic islands; *groenlandicus* of west Greenland; *arcticus* of the southern arctic islands and the mainland of the Northwest Territories; the larger, northern Yukon-Alaska forms (*stonei*, etc.); and outlying populations in addition to the above mentioned *osborni* of southern Yukon and *fortidens* of the Rocky Mountains, of *montanus* in the Selkirk Range of British Columbia, *dawsoni* in the Queen Charlotte Islands, and *caboti* in northern Labrador.

The present distribution and manner of meeting again strongly suggests that during glaciation the caribou population was fragmented, and parts survived in refugia southeast of the ice (woodland type); southwest of the ice in perhaps three refugia (the mountain, Rocky mountain, and Queen Charlotte Island caribou: *montanus*, *fortidens*, and *dawsoni*) of an intermediate type; in the Bering Sea area (large Barren Ground animals of *stonei* type), and in northern refugia (*arcticus*, *pearyi*, and *groenlandicus*).

There are certain parallels between this and the distribution of the Canada geese and the gulls of the Herring-Iceland gull complex (Rand, 1948, pp. 315-6), even to the circular chain of subspecies that overlap as species.

These examples of groups of closely related species in which the elements of each group meet sharply when there are no evident geographical barriers, are interpreted as effects of the Ice Age. The glaciers of the Ice Age rendered uninhabitable the vast area of northern North America. The mammal fauna that presumably had inhabited this area survived only on the fringes of the ice, in refugia. Here in this isolation each part of the original species went its way toward the species state. With the melting of the ice, what is now Canada and Alaska became available and suitable for mammal occupancy. The mammals spread into it from their refugia. Some travelled faster than

others, notably those from the southeast. Some were more adaptable than others, notably those that spread from the Bering Sea area of mountains and tundra onto the main Barrens of Canada. Some spread but little, notably those of the Pacific coast. A difference in habitat tolerance is shown from group to group: the Dawson red-backed mouse spread south and eastward to meet its southeastern relative in the forest, while the meadow mouse spread north of the forest onto the Barrens, and the tundra mouse of the Barrens kept still farther north.

In only one case, the arctic and the woodland caribou, do we have tentative evidence of a circular series of subspecies; there are indications that the two forms behave as species to each other, while related forms, in other areas, suggest that they are connected by a series of intergrades.

It appears that these forms have evolved to the point where they do not interbreed but each maintains its entity when they meet. It also appears that their ways of life are so similar that they are unable to live together in the same area. Their ranges being mutually exclusive, they are barriers to each other. Though they have gone part of the way to being species, they still retain the subspecific character of having their ranges mutually exclusive. In some cases some intergradation or hybridization may be found to occur where they meet, but this will probably be sporadic, or cover only a narrow zone. In the practice of classifying these forms, it may be found advisable to group some of them together in species with wider limits. Be that as it may, a proper interpretation seems to be to regard them as emergent species. The meeting between them seems to be a secondary one. This gives us a clue as to how some species have evolved on continental areas.

The effects of glaciation on speciation are not necessarily confined to the extreme northern part of the North American continent, but I have considered only the elements whose range does include the north. I have moreover discussed only one aspect of the speciation problem, that in which the forms are closely related geographical-representative species.

It is probable that the various glacial and interglacial periods each had their effect: some early effects may have been intensified, cancelled, or complicated by later ones. Some well established species that now live together may have had their origin in an early glacial period; some obvious subspecies may have had their limits influenced by the latest glaciation. Then, too, there is the possibility of Asiatic influence, through an immigration of forms from Asia during the period covered by the various glacial and interglacial periods. For the present it seems advisable to leave this for further discussion.

References

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