THE FOSSIL RECORD NEAR THE GLACIAL BORDER

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The fossils of plants and animals found along the ancient borders of continental ice sheets have long attracted the attention of scientists and discerning laymen alike. As a result of this interest specimens have accumulated in museums and in private collections, and descriptions appeared in scientific journals as well as in magazines intended for the general reader. About a year ago Deevey (1949) reviewed the voluminous literature on Pleistocene fossils and in a long paper gave a critical evaluation of their indicator value. Likewise, Flint (1948) devoted a chapter in his book to the life along the periphery of ice caps and to migration phenomena. If nothing new by way of fossil records as such can be presented in the contribution to this symposium, some unique similarities in migration patterns between northern plants and animals will be shown. An effort will also be made to focus attention on the association of plants and animals of Pleistocene times, which operated similarly to that of plants and animals of to-day.

In a quest for understanding of the vanished more recent life, and in our effort to know its advent and understand its behavior, we soon find ourselves involved in more and more remote history, and we are forced to follow faint trails, and we place the prefix "paleo" before the title of men working in such fields. Workers in paleontology soon learn from the most threadbare fossil records of past life that change, variation, replacement or extinction marked life associations even before man became a part of the environment of that great plant and animal life of the past. Fossil records of the Pleistocene epoch range from massive tusks and skeletons of mastodons to pollen grains and spores as minute as ten microns in diameter. These fossils are the scattered pieces which we are to fit into that great jigsaw puzzle which represents in part the life of the great Ice Age. In such work we cannot escape the obligation to recognize and to show the relationship between life of to-day and that of yesterday.

In the present assignment our task is made easier because we have a great obliteration as the starting point; glaciers left a clean slate, the exposed land became a new habitat to be occupied by plant and animals of that specific time. We also have with us the remnants of that great glacial activity as an object lesson on behavior of ice caps, and on how sharply defined southward extensions of range of certain characteristic northern species of plants and animals can be.

The literature does not lack philosophical treatments of the conditions which should have prevailed at the borders of Pleistocene ice masses. Some pictured the Pleistocene as an immense mass of ice bordering on a rather sunny, balmy south with its characteristic fauna and flora. Pleistocene fossils, however, do not well fit into such a picture, they demand a more extensive range of influence on the climate below the border of the ice caps.

My own studies of Pleistocene and post-Pleistocene times deal almost entirely with forest history. It is, however, desirable in the present discussion that records of lower life as well as of higher animals be included. In this way we will more easily be able to show how plants and animals then as now formed a great interlinked biome, and had similar response to environmental conditions as plants and animals of to-day. As we piece together the several records, as already stated, we cannot escape the conclusion that the great ice masses influenced climate great distances below the border itself. Some of these may have been changes in the extremes (we ecologists are still inclined to evaluate effects on the basis of general climatic conditions instead of in terms of the control by extremes), some of them may have been the indirect result of microclimatic factors, such as the effect of cold water flowing southward from melting ice. If the polar front line, where the "highs" are developed, was pushed farther south of its present location, and if the highs did not pass into the Atlantic over the St. Lawrence valley, as now, it would also mean that more cold waves would swing southward into Texas and Florida during the course of a year. Huntington and Visher (1922) say, "When the ice sheet had become very extensive, the track would be crowded relatively near to the northern margin of the trade wind belt." They also express the view that a snow field is likely to be an area of high pressure at all seasons. Even though we do not assume such great modifications of the macroclimate, smaller areas, as microclimatic islands, could and very likely did exist. The Mississippi and the Atlantic coastal waters were no doubt much colder than now, and so they would have been microclimatic habitats suitable for occupation by northern plants and animals. Salisbury, as quoted by Baker (1930), sums up the whole situation well by saying, "The great changes in the physical processes which this oncoming of the ice-sheets brought into operation effected corresponding changes in life and in the processes which depend on life. In the first place, the total amount of land life must have been greatly reduced. If account be taken of mountain glaciation in both hemispheres, as well as of the ice sheets, it is probably within the limit of truth to say that conditions became so far inhospitable as nearly to eliminate land life from about 1/7 of the land of the globe, and to have rendered conditions relatively inhospitable over a still larger area. The crowding of land life off eight million square miles, more or less, must have tended to concentrate it upon the land which still remained hospitable, and to decimate or exterminate those forms which could not migrate readily." Fossil remains indicate that conditions for which migration had no solution were also involved. In amazement one asks, "Why were so many, if not most, of the native large mammals exterminated during or soon after Pleistocene times?" Among these are all native horses and camels, six species of elephants, the giant sloth, various species of moose and elk, and the giant beaver. We may never find an answer to this question.

Distribution maps of these large Pleistocene mammals indicate four more or less climatically controlled groups. One was distinctly southern, another was primarily northern (figs. 1 and 2); then there was a group which appears to have been intermediate, and finally, one group seemed to be so cosmopolitan (*Elephas colombi*, and *E. imperator*) that very little climatic control can be read into their distribution pattern. Hay (1922, 1924) is of the opinion that zones, determined by temperature, existed during the glacial period the same as now. Distribution maps support such an assumption fully. In figures 1 and 2 are presented a selected list from Hay (1922, 1924) and Lyon (1936) which are considered as mammals typical of cold climates. We note that the greatest concentration of these fossils is in areas which were the border, or near border, of the Wisconsin ice sheet. The distribution further shows that ranges extended into regions which appear to have been out of their macroclimatic range requirements. We have such unusual distribution patterns of northern plants and animals to-day. The extraneous distribution is recognized as being due to microclimatic factors operating in what we call "relic colonies." These may, indeed, be extensions into rather than remains of a former general distribution. The significance would be the same. No doubt isolated spots within the borders of an otherwise inhospitable climate existed also during Pleistocene times. This should find support by presence of microscopic water life as well as by fossils of typically northern higher plants and animals, and their correlation in distribution ranges.

Let us first look at the records of microfossils, such as diatoms, found in peat. Hanna (1923–24, 1933) studied sediments from both central and northern Florida (fig. 2, C) and he found an assemblage of species whose present range is distinctly

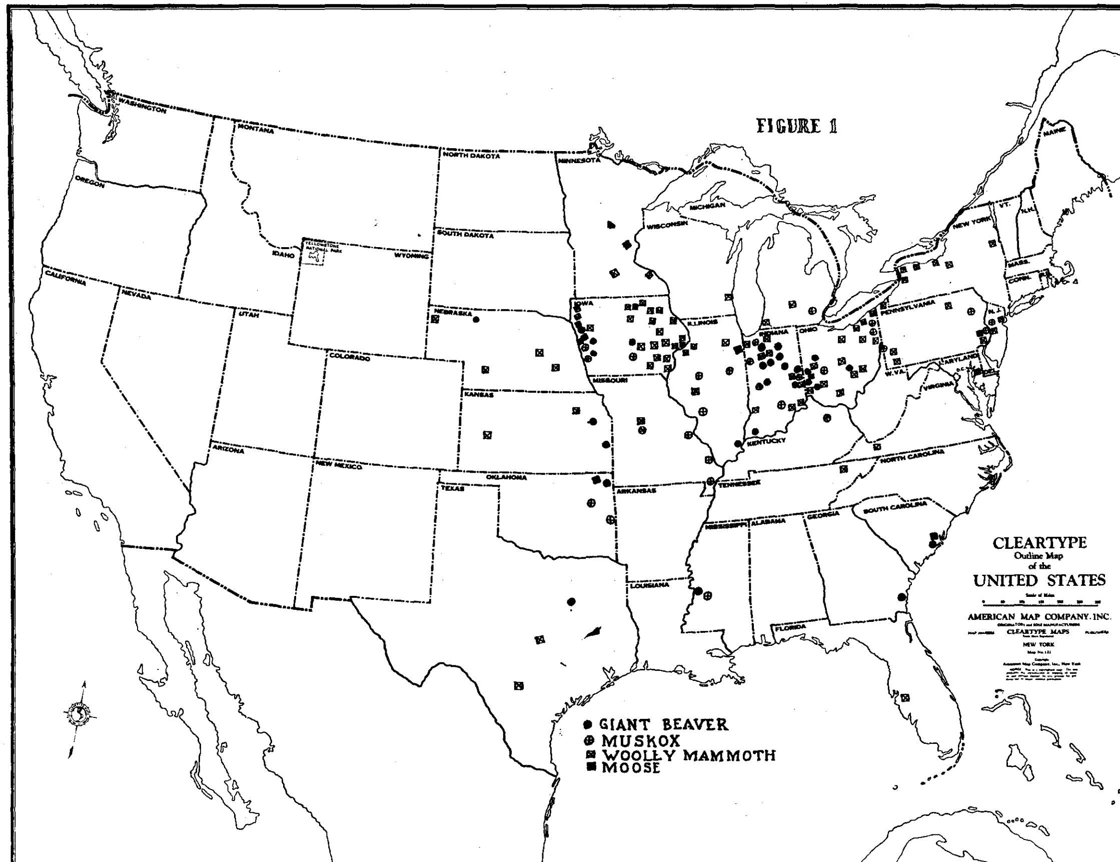

FIGURE 1. Geographical distribution of fossil records of arctic and subarctic animals.

northern, New England and Canada as well as bogs of the Lakes States. Most of the diatoms were very abundant. He lists *Navicula serians*, *Eunotia diodon*, *E. flexuosa*, *E. robusta*, *Neidium iridis*, *Pinnularia interrupta*, *P. legumen*, *P. major*, *P. nobilis*, *Suritella oblonga* and *Cyclotella striata*. Patrick (1946) did not find so abundant a collection of northern diatoms in the Patschke Bog in Texas but she did find *Pinnularia divergentissima*, a northern or alpine species. Davis (1946) voices doubt about the indicator value of diatoms for colder climate in Florida during Pleistocene times; he however readily reads colder climate into fossil pollen of spruce and fir from peats of Florida (fig. 2,B). Let us now briefly review the records of typically northern trees in southern latitudes. Frey (1950) reports from coastal plain lakes of North Carolina (fig. 2,A) up to 6 percent pollen of Picea, and scattered grains of Abies. At the 14¼ foot-level pollens present were: Pine 89.6, spruce 5.8 percent and oak only 3.1. Spruce was consistently present from the 21-foot to the 12¼-foot levels, where it disappeared from the profile. Davis (1946) quotes L. R. Wilson as having found pollens of spruce and fir in Florida peats (fig. 2,B). Potzger and Tharp (1947) report up to 4 percent white spruce, black spruce and fir pollens from the lower levels of the Patschke Bog in Lee County, Texas (fig. 2,E). Fisk, Richards, Brown, and Steere (1938) described the following macrofossils present in peat from the East Baton Rouge Parishes in Louisiana (fig. 2,D): Four species of northern gastropods, cones of tamarack and white spruce, twigs of *Thuja occidentalis*, and two northern mosses, *Amblystegium Juratzkanum* and *Taxiphyllum geophilum*.

Before us are the fossil evidences of spruce and fir as well as other northern plants in North Carolina, Florida, Louisiana and Texas (fig. 2,A-E) and overlapping this range of plants are fossil records of musk oxen, woolly mammoth, elk, reindeer, and others. Their greatest abundance is near ancient glacial borders; they show up sparsely in regions now typically northern (Michigan, Wisconsin, Minnesota) but leave faint trails down the Atlantic coastal areas and the Mississippi basin. It is difficult to interpret such distribution patterns of a great biome of plants and animals whose normal range is northern without assuming cooler climate in those states, microclimatically at least, than that found there to-day. The abundant records of these mammals near the border of the Cary substage of Wisconsin glaciation, and meagre presence to the north of it suggests ice barriers preventing northward migration to border mammal life, and extinction for most of them before the region became free of ice.

But enough of the spectacular southward extension of cool or cold climate plants and animals, which give every evidence of having been a great biome. We will now turn our attention to border areas and see what information fossils can give us about life in such locations. Baker (1930) expresses as his opinion about life at glacial borders as follows, "It is apparently in accord with the ascertained facts, as indicated by the fossil remains found between the till sheets listed in this work, to believe that at each interglacial interval there was first a migration northward into territory laid bare by the retreating ice and later a southward migration as the climate changes with the on-coming of the new glaciation . . . the effect of such migrations has been to cause the extinction of many species of insects and mammals while causing little change in plants and mollusks." He lists from near border areas 145 species of plants, 298 mollusks, 4 crustaceans, 108 insects, 3 fishes, 1 amphibian, 6 reptiles, and 117 mammals. A total of 540 animals and 145 plants. Of the animals 104 species of insects and 87 mammals are extinct. Among the plants present were such common present day species as: *Chara*, *Equisetum sylvaticum*, *E. fluviatile*, *E. scirpoides*, *Lycopodium selago*, *Taxus canadensis*, *T. minor*, *Pinus strobus*, *Thuja occidentalis*, *Larix*, *Juniperus virginiana*, *Abies balsamea*, *Typha latifolia*, *Potamogeton*, *Carex*, and *Scirpus*. From the Pleistocene of Minnesota Rosendahl (1948) brings a long list of macrofossils of plant species collected from soil deposits. While the absolute placement with respect to border

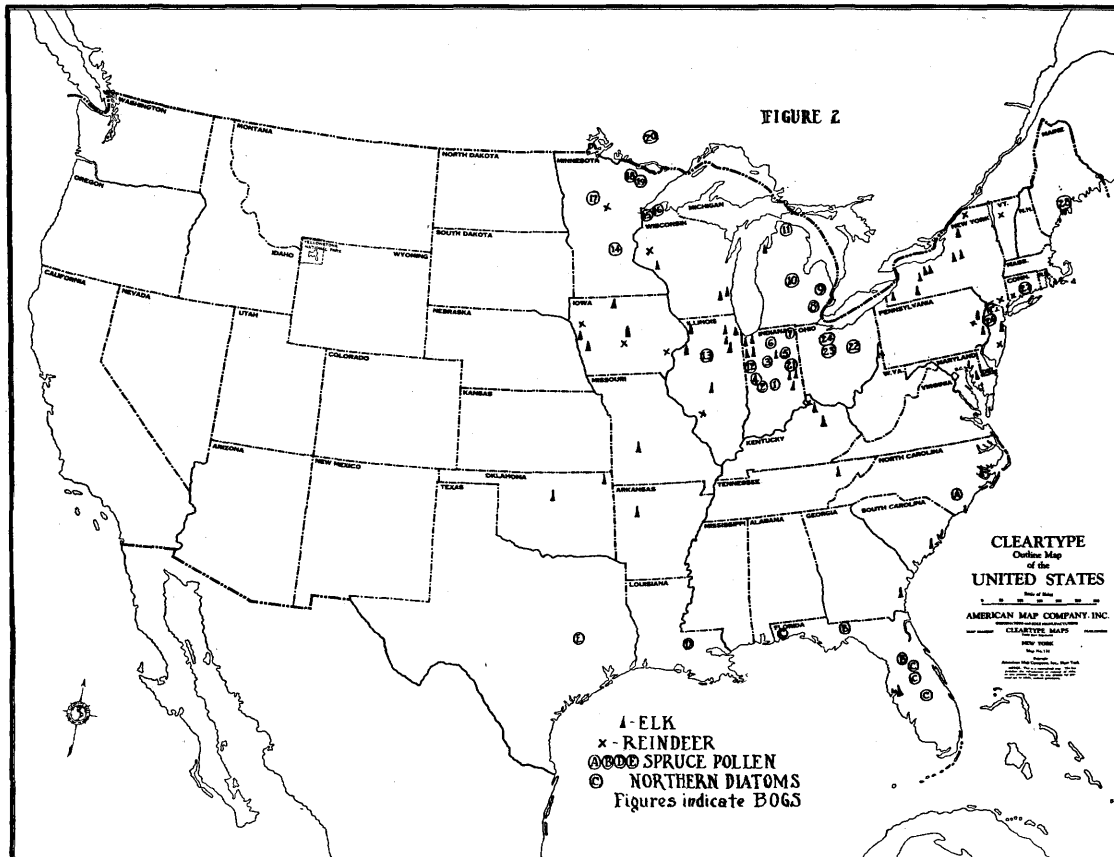

FIGURE 2. Geographical distribution of fossil records of extinct arctic and subarctic animals; locations of peat deposits where pollens, cones, twigs of northern trees, diatoms and mosses with characteristic northern ranges were found. Figures within circles show locations of bogs from which records shown in figure 3 were taken.

areas cannot well be determined from the above two sources of information, they must have been close enough to come under the influence of the ice sheets.

From more definite location near border areas we have two sources of information, i.e., buried organic deposits and peat from bogs and present-day lakes. Records from lakes are perhaps the most reliable for complete profiles because fire has not influenced the organic deposits. There is, however, the old, old question, "Did tundra border the ice sheets of Pleistocene times?" The pollen analysis records are disturbingly silent on this question. There are a few records, one by Potzger and Friesner (1948) from a bog in Maine, where grasses are remarkably abundant. However, one misses *Salix* and *Alnus* which Cooper and Lawrence report as the most common first invaders at glacial borders. One thing is certain, the lakes were formed by the glaciers, but as Deevey (1949) points out, we have no

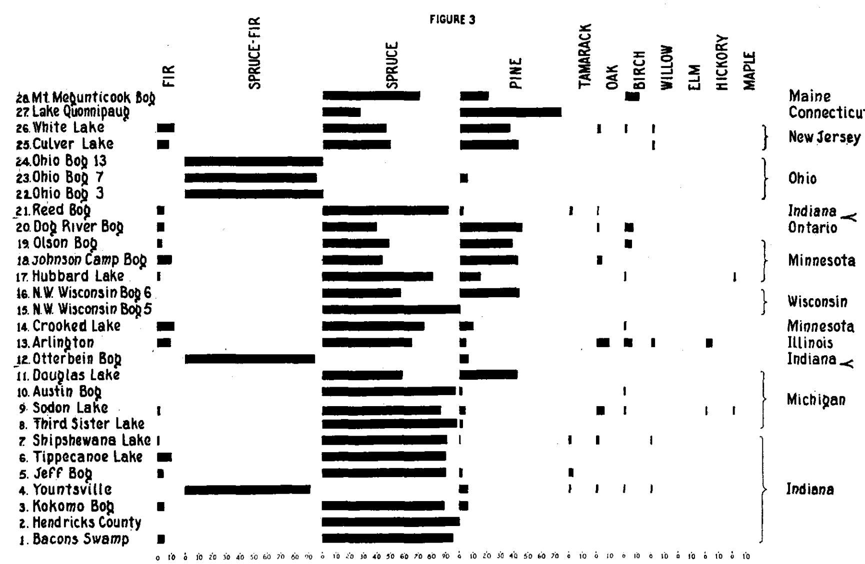

FIGURE 3. Pollen counts from lowest levels of 28 bogs showing composition of forests slong the borders of Wisconsin glaciation.

assurance that the depressions were not ice-filled for a long period of time after glacial retreat, in that case the early vegetational history may be wanting. In most bogs and lakes which the writer studied vegetation begins with pollens of forest trees.

First let us look at life as it was reported from buried soils representative of various interglacial stages. Cooper and Foot (1932) discovered a buried soil layer in Minneapolis. In their opinion it was a pond, filling in while glaciers were still within the borders of Minnesota. Records of life included mollusks, ostracoda, the mosses *Drapanocladus fluitans submersus*, *D. minnesotensis*, *Calliergon giganteum*, *Neo-calliergon integrifolium*, and various species of trees. Associated in the tree stratum were *Larix*, *Picea mariana*, *Picea glauca*, *Abies*, *Pinus strobus*, *Betula papyrifera*. In the same state Nielsen (1935) found the following plant remains in a soil layer which he calls pre-Kansan: Abies, Picea, Larix, Betula, *Acer rubrum*, Juglans or Carya, Prunus, *Lycopodium complanatum*, *L. lucidulum*. From the Two Creeks forest bed layer in Wisconsin, Wilson (1932) reports: *Bryum binum*, *Calliergon turgescens*, *Camptothecium nitens*, *Campylium stellatum*, *Ditrichum flexicaule*, *Drapanocladus revolvens*, var. *intermedium*, *Scorpidium scorpoides*, *Swartzia montana*, *Bryum cyclophyllum*, various grasses, heaths, ferns, and the bracket fungus Polyporus. In addition he listed the mollusks *Fassoria dalli*, *Pupilla muscorum* and *Succinea avara*. Among the trees were named spruce, birch, jack pine. While here, again, we have no evidence that these buried soils were laid down while glaciers stood by, we do recognize the plants as northern and in some cases they are species which crowd to the borders of glaciers to-day.

In conclusion let us briefly consider some pollen profiles from bogs and lakes. They have been arranged more or less in three series (fig. 3). With Indiana as the starting point, they radiate towards three different directions. Only the lowest foot-level is given with the assumption that this level marks the time when glaciers had not removed far from the region, perhaps only a few miles. It is unfortunate that lakes and bogs are obliterated in areas of Illinoian glaciation, at least in Indiana, but we have abundant records from Early Wisconsin (Tazewell substage) and Late Wisconsin (Cary substage) bogs. In my own studies there is no clear picture to show how interglacial periods influenced forest succession. This is true even for the physiographically clearly defined Cary substage where it borders on the earlier Tazewell. There is little indication in areas of the Tazewell substage in Indiana that moderating climate had influenced succession of forests. The bogs from the two areas show a merging into a continuous spruce-fir period for these substages. The only clearly defined division between the two substages are the greater number of foot-levels showing spruce-fir forest type in the Tazewell than in any of the bogs and lakes from Cary locations, and later absence of the pronounced pine period in Tazewell locations which shows up prominently in bogs located in Cary drift.

The work of many investigators was included in the list of bogs shown in figure 3. Correlating authors' names with numerical designation of the bogs in figure 3, they are as follows: 1. Otto (1938), 2. Potzger (1943), 3. Howell (1938), 4. Swickard (1941), 5. Keller (1943), 6. Potzger and Wilson (1941), 7. Keller (1943), 8. Potzger and Wilson (1941), 9. Cain and Slater (1948), 10. Potzger (1948), 11. Wilson and Potzger (1943), 12. Richards (1938), 13. Voss (1937), 14. Wilson and Potzger (1943a), 15. Wilson (1938), 16. Wilson, (1938), 17. Potzger (1946), 18. Potzger (Ms.), 19. Potzger (Ms.), 20. Potzger (Ms.), 21 Griffin (1950), 22. Potter (1947), 23. Potter (1947), 24. Potter (1947), 25. Potzger and Otto (1943), 26. Potzger and Otto (1943), 27. Deevey (1939), 28. Potzger and Friesner (1948).

By way of summary we can state that the most important pioneer tree, as shown by all bogs (fig. 3), was *Picea*. In some instances it had no associates, at other locations *Abies* was an associate. In the Great Lakes area and in the Atlantic coastal regions pine was an early invader with spruce and fir. However, even such broad-leaved genera as oaks, hickories and maples were isolated early invaders in some regions (fig. 3). As a whole, the pioneer forest was simple in sociology and very similar in composition to that bordering on continental North American ice caps to-day. These modern pioneer forests have been described by Cooper (1939), Griggs (1934), and Marr (1948), so that their sociology is known.

It seems that the general pattern of life associations near the border of Pleistocene ice caps located on land masses which have uninterrupted extension for great distances southward were similar to those we meet in the Arctic to-day. Genera, perhaps even species, of forest trees were the same as those near glacial borders in North America at present. The pioneers then were largely spruce and fir and they still are the most important genera. The fossil evidence when linked with life of to-day shows that since the day when ice caps slowly wasted the spruce and fir, the Jack pine and paper birch, the muskox, reindeer, elk, and moose have moved northward in the shift of climatic belts as plant and animal associations of arctic and subarctic habitats.

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