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ANL/ER/PP-90468

THE PLEISTOCENE BIOGEOGRAPHY OF EASTERN NORTH AMERICA: A NONMIGRATION SCENARIO FOR DECIDUOUS FOREST

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RECEIVED
AUG 04 1997
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ABSTRACT

The current reconstruction of the vegetation of eastern North America at the last glacial maximum postulates a very wide zone of tundra and boreal forest south of the ice. This reconstruction requires that the deciduous forest retreated far to the south. We believe that this reconstruction is seriously in error. Geologic evidence for glacial activity or tundra is absent from the southern Appalachians. Positive evidence for boreal forest is based on pollen identifications for *Picea, Betula,* and *Pinus,* when in reality southern members of these genera have pollen that cannot be distinguished from that of northern members. Further, pollen of typical southern species such as oaks and hickories occurs throughout profiles that past authors had labeled boreal. Pollen evidence for a far southern deciduous forest refuge is lacking. Data on endemics are particularly challenging for the scenario in which deciduous forest migrated to the south and back. The southern Appalachian region is rife with endemics that are often extreme-habitat specialists unable to migrate. The previously glaciated zone is almost completely lacking in endemics. Outlier populations, range boundaries, and absence of certain hybrids all argue against a large boreal zone. Our new reconstruction postulates a cold zone no more than 75-100 miles wide south of the ice in the East. South of this cold zone, the drop in temperature may have shifted species abundances but was not sufficient to remove species growing there today. This new reconstruction has implications for the existence of refugia, for estimates of species climatic tolerances, for testing general circulation models of climate, and for estimates of plant migration rates.

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DISCLAIMER

INTRODUCTION

The biogeography of eastern North America at the last glacial maximum (LGM) is both important and controversial. The conventional wisdom, which we here dispute, is that tundra and boreal forest extended well south of the ice sheets and that the deciduous forest of the East retreated to the coastal plain, to Florida, and westward into Texas and Mexico (Davis, 1984; Delcourt and Delcourt, 1984, 1993; Deevey, 1949; Jacobson et al., 1987; Royall et al., 1991, Watts, 1970, 1971, 1979, 1980a). Our contention, which we will attempt to document, is that the boreal zone was narrow and that southward movement of the deciduous forest was minimal.

The accuracy of the accepted scenario is far from a trivial issue. First, although LGM climates have been simulated to test general circulation models (COHMAP Members, 1988; Overpeck et al., 1991; Webb et al., 1988), it would be ill-advised to tune the models to match reconstructed vegetation patterns if these patterns are wrong. Similarly, forest simulation models tested for their ability to replicate possibly erroneous reconstructions of past forest distributions (Solomon and Webb, 1985) are being used to predict the effects of current climate change on ecosystems. Second, the history of vegetation changes can provide information on rates of species migrations, the ability of species to tolerate short-term extreme climatic episodes, and the responses of species assemblages to large, sustained climatic changes. This history also has implications for the rates of evolutionary processes. Geographically distinct races or ecotypes of many species have been identified in eastern North America. If the species had retreated to refugia in Florida and then reoccupied their ranges, all the subspecies and ecotypes we observe today would have been created in less than 12,000 years, a very rapid rate of evolution.

Our contention is that the dominant reconstructions of LGM vegetation in eastern North America are wrong. These reconstructions were built largely on the basis of pollen data in spite of the ambiguity of much of this data. Once these reconstructions were made, they were cited by workers in other fields rather uncritically, amplifying the problem.

A historical perspective is necessary to untangle this issue. In the absence of data, one might assume that the glacial climate of eastern North America was directly analogous to that in Europe, where the mountains were heavily glaciated, and a large tundra/boreal zone was known to have existed well south of the ice. The data supporting this scenario were substantial by the 1950s. In the 1940s to 1960s, very little paleontologial data existed for North America, but several workers nevertheless drew maps of LGM vegetation (e.g., Deevey, 1949) showing tundra and boreal forest in a wide belt extending to central Georgia, with ice covering the peaks of the Appalachians and the deciduous forest relegated to refugia in Florida and Mexico (e.g., Figures 1 and 2). Since the temperate climate of Europe is due to the Gulf Stream, which was probably deflected during glacial episodes, there is good reason a priori for suspecting that the European and North American situations need not have been analogous. On the basis of botanical evidence, E. Lucy Braun (1951) made the first correct (as we believe) reconstruction. She maintained that although tundra and boreal forest probably were present in a band south of the ice, this band was narrow. Furthermore, the climate in the entire Southeast, including the Great Smoky Mountains, was only slightly cooler than that today. The vegetation of this region did not undergo a massive migration southward and then northward. Although we believe that Braun was right, her views were largely ignored. It is now necessary to revive this view, provide support for it, and rectify the errors since Braun's time.

The difference between the two scenarios being contrasted here is so great that evidence one way or the other should be overwhelming. On the one hand, the long-popular view (Davis, 1984; Deevey, 1949; Delcourt and Delcourt, 1984, 1993; Jacobson et al., 1987; Royall et al., 1991; Watts, 1971, 1979, 1980a) holds that zones of tundra and boreal forest extended all the way into central Georgia (Figures 1 and 2). To be fair, not all of these authors specified that the zone south of the ice had a boreal climate. Rather, some authors identified this wide band as a spruce forest on the basis of the dominance of the pollen record by spruce, (genus *Picea)* a classification that leads to two problems. First, at the generic level, *Picea* is not necessarily diagnostic of a climatic zone, especially if a now-extinct temperate spruce was dominant during this period, as we will argue. Second, classifying the forest as spruce forest causes many readers to assume that this forest was similar to present-day Canadian spruce forest and is therefore indicative of a bitterly cold climate.

On the other hand, Braun's view (1951) and ours is that the zone of tundra and boreal forest was very narrow, extending no more than perhaps 50 to 100 miles south of the ice sheet. Although cooler summers may have led to some penetration of northern species into the deciduous forest zone, southern species were not forced out. Thus, we argue that the presence of some northern species is insufficient to prove a bitterly cold climate. Several types of evidence must be considered and reconciled. Lack of evidence also bears on the argument when certain data that should exist cannot be found.

EVALUATION OF EVIDENCE

Several types of evidence must be evaluated. Geologic evidence of past arctic climates would certainly be telling. Paleobotanical evidence, the dominant type used, provides important information, but factors such as ambiguous identification, differential preservation, and changes in pollen grain size over time must be taken into account. Biogeographic evidence, including distributions of endemics, relicts, range boundaries, races, and subspecies, must be considered. The failure to find certain relict populations, the absence of fossils of certain boreal species, and the absence of certain expected hybrids must also be weighed as evidence.

Geologic Evidence

By analogy with European mountains, it has been assumed (e.g., Deevey, 1949) that the southern Appalachians, particularly the Great Smoky Mountains, should have been covered by permanent ice caps and should have generated glaciers. Mountain glaciers produce obvious signs like U-shaped valleys, striations, and moraines. None of these signs has ever been found in the southern Appalachians. This negative is sufficiently definite to throw doubt on the presence of tundra this far south.

The zone south of the ice that was supposedly tundra should have retained some physical signs of tundra soils, such as solifluction and stone sorting. No such signs have been found more than a few miles south of the edge of the ice. For example, Braun (1951) noted that at a site only 15 miles south of the ice margin in Ohio, evidence of congeliturbation, although present, did not indicate severe frost action. Although these particular physical signs are not as lasting as signs produced by glaciers, their absence fails to support the traditional view.

Another soil characteristic that can be examined is the soil profile of buried soils. Different climate regimes produce distinctly different surface soil profiles. The red ultisols of the Southeast are obviously different from boreal spodosols (Duchaufour, 1982). Soils developed at the LGM under boreal forest and then buried should preserve a visibly different structure. Holliday (1987) used such evidence to dispute the existence of LGM boreal forest on the southern High Plains of northwestern Texas and eastern New Mexico, because fossil soils he examined were characteristic of development under grassland. The South Carolina buried soil from which Cain (1944) extracted his reputed *Pinus banksiana* (see below) was more properly a buried bog and was not dated. No buried soils showing signs of boreal forest influence have been documented.

Overall, we are left with no geologic evidence for an extensive tundra zone or for permanent ice on southern Appalachian peaks.

Paleobotanical Evidence

The primary case for extensive southern boreal forest has been based on paleobotanical evidence. In particular, jack pine (*Pinus banksiana*), which is normally found in the northern Great Lakes states and Canada, was purportedly found in South Carolina and other locations; white spruce (*Picea glauca*) from the same region was supposedly found throughout the southern Appalachians and even down the Mississippi valley. Before we examine this evidence, a methodologic note is in order on the nature of evidence used for reconstructions. Ideal paleovegetation data are obtained from acid sphagnum bogs in the North. In such bogs, decomposition is inhibited (Check, 1987), and well-preserved plant remains can be assumed to be representative of what fell into the water. Bogs of this type are not found in the unglaciated region. In contrast, debris falling into temperate ponds and swamps is subject to decomposition. Southern bogs and swamps endure dry episodes. Swamps also endure flowing-water episodes, during which oxygen levels are high, and decomposition is rapid. Bryant and Holloway (1985) showed that pollen preservation is poor under such conditions. Bottoms of temperate ponds do not remain anoxic, because turnover is at least annual and may be frequent if the pond is shallow. In contrast to bogs, peat is not formed under temperatre ponds. Decomposition will have different effects on different species' pollen (i.e., differential preservation effects). Pollen percentages are representative of the composition of ancient floras only if the pollens are all equally resistant to decay. In fact, broadleaf tree pollens are generally much less resistant to decay than are gymnosperm and grass pollens (Hall, 1981; Holloway, 1981). Thus, dominance of older profiles by gymnosperm and grass pollens does not indicate that broadleaf trees were absent but could be an artifact of differential preservation. Researchers attempting a reconstruction need to show that pollen percentages in ancient samples are representative of what fell into the water (even aside from differential pollen production and other issues). Traditional pollen stratigraphy was developed in the context of northern sphagnum bogs in which preservation is extremely good. Equal preservation has not been proved for the locations sampled in the studies in the Southeast and in fact is unlikely. We will see that this has a significant impact on interpretation of LGM data.

A further factor that must be considered is long-distance transport of pollen. Although studies of recent pollen versus nearby vegetation usually prove pollen deposits to be representative of forest composition at local to subregional scales, LGM conditions differed from those prevailing today. The strong winds and large amount of dust they carried could have also spread pollen. In particular, the direction of transport was from the regions near the ice, where boreal species were likely common, to areas to the east and south such as the Mississippi and Ohio Valleys, where loess accumulated. Macrofossils were obviously not transported in this way, but trace amounts of pollen in southern locations could have such an origin. Thus, species that are never more than a trace at a site must be examined with extra caution in areas of possible loess deposition. Most of the deposits of *Larix* and *Abies* in southern locations are only trace amounts and might have originated from wind transport.

The bottom line is that paleo-pollen-based reconstructions of vegetation are not entirely robust and have been challenged in several other cases. Guthrie (1990) challenged the "polar desert" reconstruction of LGM Beringia on the basis of both the abundance of fossil large mammal grazers and a reevaluation of lake core data that in fact showed a preponderance of grass-type pollen. Holliday (1987) critiqued the boreal forest interpretation for the southern High Plains of North America on the basis of buried soil characteristics. Pollen-based reconstructions of the vegetation of the Russian steppes have also been challenged. Thus, pollen data alone do not provide a fool-proof basis for reconstructions; multiple types of data must be combined to obtain a robust reconstruction, as we have tried to do here.

We can begin the paleobotanical story with Stanley Cain. In 1938 he was hired by the U.S. Forest Service to study eroding soils in Spartanburg, South Carolina. At this site he found in a buried soil some very small pine pollens that he identified as jack pine (Cain, 1944), in spite of a lack of data on the pollen morphology of different pine species. The entire concept that a strictly boreal tree (jack pine) that likes bitterly cold winters and dry, cool summers ended up in Georgia and South Carolina at the LGM was initiated with Cain's report.

This one site in South Carolina where jack pine pollen was supposedly found was cited in 1949 as strong support for Deevey's theory, even though the site was never dated. Jack pine pollen was never conclusively identified, because the identification was based entirely on pollen grain size. As Cain and Cain (1948) themselves later discovered, the pollen grains of *Pinus echinata* (short-leaf pine), which grows in that region today, are highly variable in size, depending on where they are collected, and their size distribution overlaps considerably with that of jack pine pollen. Whitehead (1964) further showed the close similarity in modal pollen size and the broad overlap in pollen size ranges between the entire set of eastern hard pines, making identification based on pollen size alone virtually impossible. Cain (1944) did not consider even modal grain size, but rather took the smallest gains in the profile that fell into the *banksiana* range and called them *banksiana*. When pine pollens exhibit a wide size range within a species (as in *echinata*), this procedure could "find" *banksiana* in any sample, even current pollen profiles from the Southeast.

The presence of a bimodal pollen size distribution has been taken as evidence for *banksiana* (Jackson and Whitehead, 1993; Whitehead, 1964, 1981; Watts, 1970). However, statistical inference on distributions is perilous when sample sizes are small. For example, Jackson and Whitehead (1993) found an apparent bimodal size distribution, but they sampled only 50 grains and nine size classes, making it almost impossible to obtain a good unimodal distribution even from a normal distribution. In their Figure 5, moving only two pollen grains between size classes would destroy the appearance of bimodality. A proper test for bimodality requires a large sample size and cannot be performed by eye.

Whitehead (1964) showed that sediment type and preservation history can alter fossil pollen grain size, making grains smaller (and more like *banksiana*) with time. This difficulty, together with those discussed above, means that the size of pollen grains is simply an insufficient basis for discrimination of eastern hard pines. Studies claiming to be able to identify jack pine pollen by size characteristics (see below) do not provide quantitative documentation for these claims. Thus, the "jack pine" pollen identified in the southeast could easily have come from some other southern pine. No cones of jack pine have ever been found there. Jack pine needles from Missouri are exclusively from Mississippi River oxbow deposits; floods could easily have brought these needles down from much farther north. Possible jack pine needles from northeast Georgia (Jackson and Whitehead, 1993) cannot be identified positively. Watts (1970) identified pine needles from northwest Georgia as *banksiana*. Indeed, the needle morphology is consistent with this identification, but it is also consistent with *P. virginiana* and *P. pungens*, both of which could grow in this locality.

More abundant southern data have purportedly been found for spruce (*Picea sp.*). These data, which are often interepreted as representing white spruce, are ambiguous. A fundamental problem with fossil spruce pollen is that the different eastern spruce species (black [*mariana*], white [*glauca*], and red [*rubens*]) cannot be distinguished by either pollen morphology or pollen grain size, especially in the East (Davis, 1984). Thus, a particular set of southern fossil pollen cannot be attributed to a boreal species on the basis of the pollen alone. Red spruce currently grows along the Appalachians, being locally dominant at high elevations as far south as the mountain peaks of Tennessee and North Carolina. Red spruce is not indicative of bitterly cold climates, though it is intolerant of very hot summers or droughts. Furthermore, both black and red spruce are found today at various sites across Pennsylvania. In all sets of pollen fossils characterized in the Appalachians and Pennsylvania, the spruce pollen found could well be red or black spruce. Not a single site has provided unambiguous macrofossils of white spruce cones.

A final note is necessary on fossil spruces. In Tennessee and other southern states, one can find macrofossils of a spruce that superficially resembles white spruce but has much longer cones. Specimens have been obtained from the Nashville Shady Valley Bog. Kritchfield (personal communication) suggested that this was a temperate spruce that became extinct sometime after the LGM. Jackson and Givens (1994) provide detailed data on this spruce from the southern Mississippi valley. All the cones they found from the LGM were of this type. No studies have even attempted to distinguish the pollen of this extinct spruce from that of other species. Such a temperate extinct spruce, similar to temperate spruces found in Mexico and China, could have contributed to the impression that spruce pollen in locations like Pigeon Marsh in northwest Georgia (Watts, 1973) was from white spruce and would explain the large cones found in Pennington, Georgia, and Nonconnah Creek, Tennessee. In fact, every fossil "white spruce" cone found to date in the Southeast from the LGM has this attribute of being exceptionally long relative to white spruce. As Jackson and Givens (1994) noted, this extinct spruce might indicate a cooler climate, but we have no basis for judging how much cooler. If the spruce found at southern sites at the LGM is this extinct temperate spruce, its presence would explain the anomalous mixing of spruce with southern species.

In examining the sites purportedly demonstrating the presence of boreal forest in the Southeast, the first site we should consider is Cain's (1944) site near Spartanburg, South Carolina, where a bog was found buried under tens of feet of undifferentiated red clay. At this site, spruce and fir combined were never a majority of the pollen, and hardwoods were abundant throughout. The fir pollen, however, was identified as much larger than the two eastern firs and morphologically more like the western *A. nobilis*. The samples could not be dated in 1944 and could be quite ancient because the Piedmont area has been geologically stable for a long time and has deeply weathered soils. Cain (1944) did not try to define this site as being from the Pleistocene. He merely said that the site was from a warming period like the end of the Pleistocene; in fact, he thought that it might be much older. Others (e.g., Deevey, 1949), subsequently asserted that this was a LGM site. We may therefore discount this site as being informative with respect to LGM vegetation.

One of the southermost "boreal" sites is at Pigeon Marsh in northwest Georgia (Watts, 1973). At Pigeon Marsh, the *Picea* pollen at the bottom of the profile is only a trace compared to the abundance of the dominant pines and hickories. This trace hardly constitutes a boreal forest. Again, cones of white spruce must be found to verify that it was present. Other northern species are absent.

The oldest sediments from Longswamp in eastern Pennsylvania (less than 30 km from the glacial boundary) have been interpreted as tundra vegetation (Watts, 1979). However, the dominance by *Gramineae* pollen is inconsistent with a tundra scenario, as is the abundance of *Pinus* pollen (which Watts attributed to drift) and the rarity of *Picea*. *Gramineae* should be rare and *Pinus* absent if identification as tundra is to be sensible. Further, an abundance of *Cyperaceae* at a site is not necessarily an indication of tundra, because some species in this group can dominate locally in grasslands (Guthrie, 1990), and others can be found growing abundantly in southern flatwoods and Carolina bays. The pollen configuration at Longswamp is thus compatible with a pine flatwoods savannah assemblage, like that found today in nearby New Jersey in pitch pine habitats (pine barrens). The *Pinus* pollen is not identifiable to species, and it may well have been something other than *P. banksiana*, such as *rigida* or *echinata*. Further, the *Picea* pollen and rare needles cannot be identified to species. The *Picea* pollen could well have come from red or black spruce, both of which are abundant in eastern Pennsylvania today. The presence of black spruce in Pennsylvania today can hardly be taken as proof that Pennsylvania is now a boreal forest.

The abundant spruce pollens at Crider's Pond (Figure 3) in southeastern Pennsylvania (Watts, 1980a) at 15,000 BP, asserted to demonstrate the presence of boreal forest, are much more plausibly from red spruce, which grows nearby today, because no cones of white spruce have been found. This scenario is supported by the presence of traces of *Quercus* and *Carya* pollen throughout the profile. Such a pattern is inconsistent with boreal forest, especially considering the likelihood that the pollen of these species was more poorly preserved than that of other types. The *Betula* pollen is only assumed to be *glandulosa* (a boreal species); it could just as easily be *B. lenta* or *B. alleghaniensis*, both of which grow in this area today. Further, the heavy *Pinus* signature is again assumed to be *P. banksiana* (jack pine), but pollen of this species cannot be positively identified, and no macrofossils confirm this view. Finally, the *Abies* pollen could easily have been Frasier fir, which grows nearby today, rather than balsam fir. *Abies* is only present from about 13,000 BP to about 10,000 BP. *Larix* and northern hardwoods are absent.

We see this pattern repeatedly in this literature: pollen that can be identified only to genera are assumed to be the boreal species in the genus because of the prevailing view that the region was boreal forest. Interpretations then are treated as if they were facts. In every profile, the same problem occurs, because the dominant genera (*Pinus, Picea, Betula,* etc.) remain difficult to identify to species across the entire region near the ice in the East. The classification problem at the generic level is that the pollens for *Pinus* and *Picea* are ambiguous (Figure 4). Although the pollens are morphologically consistent with the boreal type (the traditional view), they are also consistent with a deciduous type, because southern species in each ambiguous genus grow near these sites today. No uniquely boreal tree species are found in these profiles (i.e., species without southern congeners). Further, the boreal interpretation can be obtained only by ignoring pollen from various temperate species (Figure 4). A temperate interpretation is equally consistent with the raw data, does not exclude species, is more parsimonious, and is reinforced by likely differential preservation leading to the disappearance of broadleaf pollen over time.

A possible resolution of these puzzling pollen profiles is the hypothesis that northern and southern floras mixed in this region. If winters were not colder (because of the wind-diverting effect of the ice sheet) but summers were cooler, then in theory northern species could invade the south while southern species could persist. If such mixing occurred, (as held by Thompson Webb III, pers. comm.), then we cannot infer a boreal climate in the East from the presence of pollen of boreal species. With either a mixed-flora hypothesis or the possible overinterpretation of pollen at the generic level, it is not logically necessary to equate spruce pollen with a bitterly cold climate. Distinguishing between these cases will require more detailed pollen identification.

A few further examples illustrate the overall problem with the data. At Rockyhock Bay (Whitehead, 1973) in north central North Carolina, boreal forest appears to be present, because *Picea* pollen is abundant. However, neither the spruce nor the more dominant pine is identifiable to species. Red spruce grows not far to the northwest today, and the pine could be any of several southern pines. Further, *Abies* is never more than a trace, and *Quercus* is present throughout. *Larix* and northern hardwoods are absent. At White Pond in central South Carolina (Watts, 1980b), spruce pollen is only a trace; oak, hickory, and ironwood pollens are found throughout; and the dominant pollen of pine is not identified to species. The switch from pine-dominated to oak-dominated pollen at this site at about 12,500 BP, often interpreted (e.g., Watts, 1980a) as indicating replacement of *Pinus banksiana-Picea* boreal forest by temperate forest, more probably represents the replacement of dry southern pine forest by more mesic oak forest, as is also indicated by an increase in hickory, ironwood, and beech pollens at the same time. Pine was replaced by oak at roughly the same time at Sheelar Lake in north-central Florida. This switch from pine to oak is more indicative of an increase in moisture than of a change in temperature. In addition, the superior preservation of gymnosperm pollen could give a similar result even in a forest that was dominated by deciduous species over the entire interval. In all of these cases, the pollen is consistent with vegetation very similar to that present today when the ambiguities of species identifications are taken into account.

Jackson Pond in Kentucky (Wilkins et al., 1991) is a site that should show unequivocal boreal forest, because it is an interior site and is only 100 miles from the ice border. The sediment core taken here is continuous in radiocarbon years back to 20,000 BP. Wilkins et al. (1991) interpreted the pollen at the LGM as representing a jack pine-spruce forest, on the basis of the dominance of the tree pollen by spruce and hard (Diploxylon) pine. The pollen data do not, however, support such an interpretation. The spruce pollen need not be interpreted as white spruce, because red spruce today grows only about 100 miles to the east. Alternately, the spruce could be the extinct temperate spruce found nearby in Tennessee (see above). No cones have been found to allow a positive identification. The Diploxylon pine similarly need not be *banksiana*. As noted, *banksiana* pollen cannot be distinguished from pollen of shortleaf pine, which grows today less than 100 miles to the east and south, and pitch pine, which grows near Jackson Pond today. Further, it is difficult to reconcile the observation that the pine pollen identified as *banksiana*, though reduced in abundance after 10,000 BP, maintains a significant presence to the top of the profile. (That is, *banksiana* should still be found at the site). This reasoning contradicts a *banksiana* interpretation but is consistent with a pitch pine (*Pinus rigida*) identification, because pitch pine is present today in the region around this site.

Other boreal tree elements in the sediment core from Jackson Pond are minor (*Abies*) or only a trace at one date (*Larix*). Such trace levels could result from loess deposition at this site. Throughout the profile, tree species incapable of living in boreal forest are present, including *Quercus, Acer saccharum, Fraxinus nigra, Ulmus*, and *Carya*. The herbaceous species (some identified only to genus) have very wide north-south geographic distributions today (e.g., *Potentilla, Bidens, Artemesia, Achillea*). Exclusively boreal species are simply absent. If the spruce is the extinct temperate spruce (or red spruce) and the pine is pitch or shortleaf, then every species in the entire profile grows in the vicinity today or is not indicative of temperature (e.g., some of the herbs), except for traces of *Abies* and *Larix* at a single date. Our interpretation of the LGM at Jackson Pond is a climate slightly cooler than today's and probably drier, but not too cold for the persistence of most of the typical species present there today. This interpretation puts an upper bound of less than 100 miles south of the ice margin on the southern limit of an extremely cold zone at the LGM.

Spruce macrofossils have been found along the Mississippi River (Delcourt and Delcourt, 1984). Oddly, these spruce fossils are mixed with remains of broadleaf trees that today are found hundreds of miles south of the boreal forest, including *Magnolia acuminata*. One explanation offered (Delcourt and Delcourt, 1984) is that cold meltwaters from the ice kept the Mississippi River valley cool enough for spruce to survive in the valley, with southern hardwoods growing on the bluffs (thus the mix of fossils). The concept that even a river of ice water could keep a valley this size and this shallow cool enough for spruce in a zone otherwise warm enough for southern hardwoods is simply not credible. It is far more plausible that the Mississippi was subjected to periodic large floods that would have brought macrofossils and even dead mastodons as far south as Memphis or New Orleans and deposited them on its floodplain. Ice dams are well known to have created and released large lakes in Montana and other locations, for example. In fact, many of the spruce fossils along the Mississippi are located on river terraces and are within likely flood zones. In addition, the only cones found at Nonconnah Creek (Memphis) and other Mississippi Valley sites are exceptionally large and probably represent an extinct temperate spruce (Jackson and Givens, 1994) like that found elsewhere in the Southeast (see above). Perhaps not coincidentally, at the Powers Forest Swale in southeastern Missouri, the date when deposition of glacial outwash ceased (around 14,500 BP) because of a change in the course of the Mississippi river coincides with a switch from spruce-dominated to oak-dominated pollen (Royall et al., 1991), indicating that the "spruce forest" at this site also could have been an artifact of pollen transported on floodwaters.

Thus, all fossil evidence of spruce in southern regions either cannot be shown to represent white spruce instead of red or black spruce, could plausibly be an extinct temperate spruce with large cones, or probably originated from glacial outwash. We might also ask about evidence for other boreal species. If boreal forest extended as far south as Atlanta, there should be fossil evidence for other widespread boreal or northern species, such as paper birch, balsam fir, tamarack, red pine, white pine, balsam poplar, quaking aspen, and northern white cedar. *Abies* can only be found in minor amounts at Crider's Pond and Longswamp in Pennsylvania, at Anderson Pond in east-central Tennessee, and at Jackson Pond in Kentucky (as well as at nearby sites) and as a trace at White Pond, South Carolina, and at Rockyhock Bay, North Carolina. *Abies* is absent from other sites in South Carolina, Georgia, and the Tunica Hills region. *Larix* is even more restricted, being present only as a trace at Jackson Pond, Kentucky, and a few other sites and being absent even from Pennylvania sites. Wind transport of *Larix* and *Abies* pollen could account for certain of these sporadic trace records. Persistent dominance at a site would rule out wind transport, but northern tree species (except for the disputed spruce and pine) are dominant at no southern site. Northern hardwoods (except birch which can not be identified to species) have not been identified at any sites in the East, nor has pollen from uniquely boreal shrubs been found. Evidence from relict populations is discussed below.

When we look for fossil evidence for the migration of deciduous forest to Florida and/or Mexico (the reputed refugia for deciduous forest), a decidedly major event that should have left some trace, we again encounter a striking lack of evidence. Lakes in the Southeast, Texas, and Florida either do not date back far enough (i.e., not as far as the LGM) or show a continuous presence of oak-pine associations (including such shrubs as wax myrtle at Sheelar Lake) similar to those present today (Bryant, 1977; Delcourt and Delcourt, 1993; Watts, 1973). Thus, data do not support a Florida refuge or a Texas migration route to Mexico.

On superficial examination, the forests of Mexico appear to be similar to those of the eastern United States, suggesting that they could have been refugia. However, in most cases the similarities reflect much more ancient migrations than the period of the LGM. Although such eastern genera as *Carpinus, Carya, Quercus, Picea, Abies*, and *Magnolia* occur in Mexico, the Mexican populations are almost all so distinct morphologically that they are obviously different species. In fact, for many of the populations, their closest relative is in China, not in the eastern United States. The forests of Mexico, China, the eastern United States, and Europe all share floristic affinities, but their mutual origins go back millions of years, not thousands. Fossil pollen data for Mexico would need to distinguish these specifically Mexican species. That is, identification only to the genus level is not sufficient and may be misleading. The existence of eastern-looking forest in Mexico does not warrant the conclusion that this area was a refuge, because most of these species have been separated for hundreds of thousands to millions of years from the forests of the Northeast.

Biogeographic Evidence

One of the strongest types of evidence against the scenario that boreal forest occupied a wide band south of the ice at the LGM is provided by current biogeographic distributions of plants and animals. Particularly telling is the distribution of endemic species. Many endemics occur just south of the ice margin; almost none are found in the glaciated area. The only possible explanation for this observation is that the southern Appalachians and the Southeast maintained climates that these endemic species could tolerate throughout the glacial period. The data on endemism seriously constrain theories proposing large-scale migrations of vegetation at the LGM. Data on outliers, southern relicts of northern species, zones of hybridization, and range boundaries are also quite telling and must be considered.

Endemics are species or discrete races with a very restricted geographic distribution. Endemics may arise in a number of ways. In some cases, a species that is originally widespread may become progressively restricted to a unique habitat as climate changes, physiography changes, or other species outcompete it. It thereby becomes a relict species. For example, a swamp-dwelling species might progressively lose habitat during periods of uplift when swamps are drained. One can often identify this type of origin, because the species occurs in very small patches with several widely scattered populations. This pattern commonly occurs on mountain peaks, with a species occurring on widely separated peaks but not between them. Such scattered populations were probably connected when the mountains were higher or the climate was colder (or both). In these cases of population restriction, a nearby sister or parent species is not necessarily found.

A second type of origin of endemics involves evolution in a unique habitat, leading to the generation of a race, a subspecies, and ultimately a new species. For example, in the tropics the species on isolated volcanic peaks are often derived from tropical lowland elements and are unrelated to those on other mountains. Striking examples occur in caves, with the cave population diverging drastically in morphology from the normal population. In such cases, a living parent species that gave rise to the specialized endemic species can often be identified. This type of species origin generally takes hundreds of thousands to millions of years. Although some cases of very rapid evolution are known, such as swarms of recent-origin cichlid fish in some African lakes, most specialized-habitat species originate over a very long time. How many such specialized species could have evolved since the LGM is unknown. Telltale signs of recent origin for endemics are the proximity of the parent species, incomplete genetic isolation, and limited morphologic divergence. The cichlid fish, for example, are morphologically quite similar. We will see that these signs of recent origin do not apply to most endemics in the Southeast but do apply to those found in the recently glaciated regions.

Several mechanisms exist for producing a new species abruptly, particularly in plants. The most dramatic mechanism is polyploidy. Plants, unlike animals, can survive a multiplication of chromosome number; in fact, a more vigorous plant may result. A characteristic of polyploidy is immediate genetic isolation from the parent and thus the abrupt creation of a new species. A second mechanism is the hybridization of related species, which can rapidly create a species that is either largely or completely genetically isolated from both parents. As we will show below, most of the few "endemics" found in the recently glaciated zone are either polyploids or hybrids, and their recent origin is evident, because the parent species are proximate.

Endemics pose a serious problem for any theory of mass migrations, because they originate too slowly. If the zone from the ice margin south to central Georgia was tundra and boreal forest, and if the endemic species in this zone were all recently derived (since 14,000 BP), then the incidence of endemics in this zone and the glaciated zone should be roughly equal, especially for regions like that south of the Great Lakes, where the ice melted early. However, the incidences are not equal, as we will show below. Further, the rapid creation of a large number of endemics after the LGM is in itself problematic.

The second problem posed by endemics for theories of mass migration is that most endemics are restricted to special habitats, either as relicts or by specialization. Such special habitats as limestone outcrops, caves, and mountain peaks are usually widely scattered. Endemics are generally not competitive outside these unique habitats. This combination of factors makes migration of these species to the far South (Florida) and then back not merely problematic but actually impossible. The Appalachians run east-west at their southern margin, providing no path for north-south migrations of specialized species. Endemics specialized to coves, caves, mountain streams, cliffs, and cool, moist valleys would find absolutely no suitable habitat between Tennessee and central Mexico or Florida, even if the climate changed, and would be unable to survive mixed with the normal contingent of upland plant species. The concept that a cohort of species making fine distinctions of habitat could have become generalists and marched across the landscape to Florida and then back, only to return to their narrow, restrictive habitats, is simply not credible. Data on endemics presented below illustrate these points.

Distribution of Endemics

Maps of the distribution of endemic species show that recently glaciated regions lack endemics. For example, a world map of the homosporous ferns (Tryon, 1957) indicates that this group is almost universally distributed (Figure 5). Within the nonglaciated regions, endemics are distributed uniformly across the range of this group (excluding the Sahara), but within the glaciated zone there are none. This generalization applies in both North America and Eurasia. This type of distribution makes sense if insufficient time has passed for endemics to have arisen in the glaciated zones.

More broadly, as Braun (1950) noted, the southern Appalachians, particularly the region of the Great Smoky Mountains, is a center of both species richness and endemism for the eastern United States. Both occur because this region has an ancient history (since middle Tertiary time) as the only area of large mountains in the East. The mountains have a wide variety of climates, soils, and topographies that both provide habitat for many species and encourage endemism by imposing barriers to isolate populations. Many endemics can be found in this region across life forms including trees (*Abies fraseri*), ferns, herbaceous plants, salamanders, crayfish, and centipedes. The extremely limited distributions of many endemics in the southern Appalachians pose a real difficulty for any theory of long-distance migration, as does evidence concerning the time of their origin. As a group, these endemics exhibit signs of ancient origin, including high morphologic divergence from related species, geographic isolation from congenerics, complete reproductive isolation, and edaphic specialization. The few endemics in glaciated regions do not exhibit these signs.

Among fish, many endemics occur in the coastal plain (Gilbert, 1987) but few in the glaciated region. Endemic salamanders are found northward to Cowknob in northern Virginia and to West Virginia, just 100 miles or so from the glacial border. The salamander *Cantukia* is specialized to limestone talus slopes or hills and would have difficulty migrating.

Many plant species are endemic. For example, the trilliums have dozens of species in the East, but most of these have very restricted to endemic ranges (Braun, 1950). From southern Ohio southward, the hilly country harbors such endemics as *Conradina verticillata*, a *Solidago,* and a *Eupatorium*, the latter two being confined to "rock houses" that are particularly sheltered (Braun, 1951). Another interesting example of a species that would not have been able to migrate easily is *Nebusia alabamentis*, which grows strictly in a narrow band along the fall line (the zone where the Cretaceous uplands descend to the coastal plain).

The difficulty with migration scenarios becomes more evident when we examine the traits of the few "endemics" found in the glaciated East. For example, *Godea testalata* occurs strictly in glaciated regions. This species is a polyploid (allotetraploid) and thus probably has a recent origin. *Selaginella rupestris* has a sexual population along the southeastern foothills of the southern Appalachians and a nonsexual, apogamous race distributed throughout the glaciated region (Tryon, 1971). The asexual race is clearly of recent origin, in fact originating after the LGM (Tryon, 1971). *Citrapedium areatinum*, the ramshead ladyslipper, occurs strictly in glaciated territory, but plants with almost identical morphology are common in China; rather than being an endemic, this species is probably a postglacial immigrant from China. Because this ladyslipper is wind dispersed and cold tolerant, this scenario is not unreasonable. A number of other species that occur only in the glaciated region in the East are actually widely dispersed species of western origin, not endemics. For example, the red baneberry (*Athea rubra*) is found largely north of the glacial boundary in the East, but it clearly originated in the West. The eastern species *Athea alba* moved up into the glacial zone. Where the two species meet, they hybridize (Figure 6). This hybrid might seem to be an endemic, but it is clearly the result of a recent range overlap and hybridization of the two parent species.

Of these plant species that are confined to the previously glaciated zone, all can be identified as recent [illegible] ot narrow endemics at all) or as recently created species, ei[illegible] mous varia[illegible]. In each case, the parent species is readily [illegible] ecies, [illegible] any specialized to a restricted habitat. [illegible] mics in the glaciated zone.

Distributi[illegible]

If norther[illegible] ove[illegible] and [illegible] ain, [illegible] would have left behind relict populations on s[illegible] as [illegible] oves, [illegible] the [illegible] slopes, and mountain peaks. Figure 7 [illegible] species. The outliers in Illinois, Ohio, northeast Pennsylvania, and northern New Jersey are all within the glaciated zone. An interesting group occurs outside the glaciated zone in the mountains of south[illegible] West Virginia, and [illegible] stern Virginia. In this region, six tre[illegible] have apparently left ice age relicts in th[illegible] s, the predicted location for north[illegible] populations. Figure 7 shows that the r[illegible] e almost exclusively confine[illegible] mountains north of central West Virg[illegible] that the relicts of six boreal tree species all o[illegible] this single area is surely not coincidental. This observation suggests that the mountains of West Virginia and Virginia represent the southernmost penetration of the boreal forest. The regional climate at the LGM was evidently not cold enough *phanerolepis* is almost perfectly intermediate between those of balsam and Fraser fir, suggesting that *phanerolepis* is a hybrid. These three populations currently are isolated from each other by considerable distances, so the origin of *phanerolepis* must lie in the past (i.e., it is not in a zone of current overlap in which hybridization is actively occurring). This observation suggests that the southernmost balsam fir migration at the LGM was to the mountains of West Virginia and northwestern Virginia, where it hybridized with the existing Fraser fir. If balsam fir had moved farther south, the entire Fraser fir population would resemble *phanerolepis*.

If southern species had retreated south and then migrated north, we would expect to see independent movement of species northward along with invasion fingering, depending on habitat and topography. Actual distribution patterns do not match this expectation. A number of southern species have isolated populations within 100 miles (or less) of the ice, including *Magnolia macrophylla, Magnolia tripetala,* and *Leavenworthia uniflora* (Braun, 1951). These northern outposts look more like relicts than like invasions because they occur on unique habitats, are remote from the body of the southern population, show no signs of spread, and are not accompanied by northern spread of the species elsewhere. Other examples were discussed by Braun (1951). Relict populations of southern species in the zone near the ice are not difficult to rationalize if this zone became cold but not arctic, causing a decline but not extinction of the southern species in this region. If these outposts represent invasions, they should occur into the ice zone; however, they do not.

Another anomaly is the large number of southern Appalachian species whose otherwise wide geographic ranges stop along the glacial border (Braun, 1951), including *Aesculus octandra, Aralia spinosa, Gillenia stipulata, Salvia lyrata, Oxydendrum arboreum, Cunila origanoides, Agave virginica, Rhamnus caroliniana,* and *Euonymus americana.* Many of these range from southern Illinois all the way east to New England, along this entire zone having a range that terminates close to the ice border. Figure 10 shows the 18 tree species described by

Burns and Honkala (1990a,b) whose ranges follow the ice, extending to the ice line but not crossing it. Except for a very few northern outliers, this group of species was apparently unable to migrate north after the ice melted. This coincidence of range terminations and the glacial border is particularly remarkable because (1) the species ranges follow the irregular glacial boundary, including the western upturn; (2) the species as a group differ dramatically in their edaphic requirements, ranging from xerophytes to mesophytes, early to late successional, and grassland to forest species; and (3) the glacial border does not correspond to any topographic or physiographic boundary. Braun (1951) noted that the picture is one of formerly widely spread species now removed from certain regions by the ice and unable to move north since the glacial retreat. That these species would have stopped their northward march from Florida precisely at this border in the absence of influence from the ice line is simply not credible. Although this border roughly corresponds to an isotherm of less than a 1% chance of a coldest temperature less than -30°C and to the isotherm for a normal daily average temperature for January of 0°C (Bryson and Hare, 1974), it is unlikely that this line can be explained by the temperature data. Seven of the species either have rare outliers well into the glaciated zone or extend well north of the noted isotherms in the region west of the Mississippi. The coincidence of the northern range boundary overlaps with the ice border is very tight and is such that these 18 species repeatedly come right up to but rarely cross the ice border line. This problem deserves more study.

Distribution of Races and Subspecies

The geographic distribution of races and subspecies provides invaluable information for interpreting past climatic changes. Even though most race and subspecies distinctions cannot be made by using pollen data, such distinctions cannot be ignored. If multiple distinct races of a species can be identified, then (1) each must have had a separate glacial refuge to prevent introgression, or (2) they all evolved since the LGM, or (3) the bulk of the range of the species was not disturbed during the glacial period. Because, as noted, finding even a single glacial refuge in the far South has proven problematic, finding multiple refugia within which each of the distinct races of these species could be preserved would seem doubly problematic. In considering whether all of these races evolved since the LGM, we may note that only 60-150 tree generations have passed since the ice began to retreat, a very short time for sympatric subspeciation. Furthermore, the phenomenon is widespread, with *Acer, Liriodendron, Fagus,* and *Tsuga*, at least, all exhibiting significantly different, geographically connected racial variants.

Fagus grandifolia is the only member of its genus in eastern North America. Although paleoreconstructions tend to treat this species as monolithic, in fact it has several races (Bennett, 1985; Camp, 1950; Cooper and Mercer, 1977). The type variety (var. *grandifolia*) is a tree of rich upland soils in southern Canada, the Great Lakes region, and New England, as far south as the mountains of North Carolina. Var. *caroliniana*, by contrast, grows in low wetland soils (bottomlands and swamp margins) along the coastal plain from Massachusetts south to northern Florida, west to eastern Texas, and then north in the Mississippi valley to southern Ohio, Illinois, and Missouri. These two varieties not only differ in their preferred habitats and temperature tolerances, but they are distinct in a host of morphologic traits (Cooper and Mercer, 1977). However, where the two varieties are proximate, they readily hybridize (Cooper and Mercer, 1977). Thus their identities depend on remaining geographically separate. This geographic distribution pattern poses a real problem for any migration scenario.

Var. *caroliniana* runs across the entire southern, eastern, and western edge of var. *grandifolia's* range, blocking any southward migration route. Because coastal plain data do not suggest any major changes in vegetation at the LGM, var. *caroliniana* was probably present continuously across most of its present range, at least in the southern areas. Any migration of var. *grandifolia* toward the south would have led to a complete range overlap and the probable merging of the two varieties. Refugia would have resulted only if the *Fagus*-free zone south of the ice was quite narrow, as we postulate. Some authorities further consider the mountain beech of the higher elevations of the southern Appalachians to be distinct from the beech of the Great Lakes states, making a migration to the far south and a subsequent return even more problematic. Our reconstruction has room for the mountain beech and the northern beech types to remain geographically separate at the LGM, with the northern beech being found between the ice margin and the foothills of the mountains and mountain beech at higher elevations in the mountains.

Sugar maple (*Acer saccharum*) similarly exhibits several distinct varieties. Further, it has poor reproductive isolation from Florida maple, black maple, and chalk maple, which may represent subspecies. It is difficult to imagine how this complex group could have originated from a single southern refugium. In contrast, in a scenario in which the boreal zone was very narrow, these races or varieties could have been preserved. Within an extensive area across the southern Midwest and southern Appalachians, the varieties could have been maintained and even isolated somewhat geographically (e.g., sugar maple near the ice, Florida maple in the far south, black maple in the west, chalk maple in the mountains). For other species, including *Liriodendron tulipifera* and *Tsuga canadensis*, the degree of geographic variation also exceeds what can be accounted for by a single, far southern glacial refuge.

CONCLUSION

The traditional reconstruction of the vegetation of eastern North America at the LGM is in serious disarray. The original reconstruction by Deevey (1949) was based largely on an analogy with the European LGM pattern, uninhibited by the complications of solid data. Such an analogy does provide a useful basis for beginning a study, but it is only a starting point from which rigorous analysis must branch. The analogy in this case, however, led to a sort of circular reasoning as ambiguous pollen data for *Pinus, Picea, Abies, Betula*, and others were repeatedly interpreted as deriving from the boreal species in the genus, even when temperate species of the genus grow at the site in question even today. *Cyperaceae* was interpreted as proving that tundra existed, even though the genus can be locally dominant in temperate grasslands and southern wetlands. Tiny traces of fir or spruce in certain profiles were taken to prove that boreal forest was present, even when oak was abundant in the same horizon. Such tiny traces could even result from laboratory contamination. The fact is that pollen data at this level of taxonomic resolution paint an extremely ambiguous picture. Further, the more rapid decomposition of broadleaf tree pollens in temperate pond sediment and flowing water swamps creates a bias against their preservation that increases in older sediments. Even if these taxonomic identification problems are resolved and it does turn out that fir and jack pine were present in the South, we must still account for the persistence of southern species almost up to the ice margin.

In the face of such ambiguity, other evidence must be sought. Although biogeographic evidence is ignored by many workers creating reconstructions, such data must really be given considerable weight, especially when multiple types of evidence are collated. The evidence from endemics is particularly telling. Endemics are typically restricted to unique habitats and are thus quite incapable of moving long distances across hostile habitat. This is particularly true for species such as salamanders that are prone to desiccation and are not readily carried by the wind or in bird droppings. When we study the area south of the ice (and nearly up to its border), we find hundreds of endemics across several taxa, most showing signs of considerable age. In the glaciated zone we find almost no endemics, and the few we do find tend to show signs of recent origin, such as being polyploids or hybrids. This situation can be explained only if the bulk of the area south of the ice sheet did not get so cold that these endemic species were exterminated, because they could not have migrated south and then returned.

We have considered relictual evidence of the penetration of northern species. Because the peaks of the southern Appalachians are sufficiently high to be cool, northern species that occupied a (supposedly) wide zone south of the ice should have left relictual outpost populations. The farthest south such outposts can be found is in central West Virginia. The zone within 100 miles of the ice zone also contains northern outposts of southern species, indicating that although the LGM climate was generally too severe for these species in this zone near the ice, the climate was tolerable on certain microsites such as cliffs and bluffs (where snow does not get too deep and competition is reduced). Genetic relictual evidence of the presence of northern species (crossing of balsam and Frasier fir and of white and red spruce) should be obvious, because the species pairs in question are morphologically quite distinct but hybridize readily. No such genetic evidence exists south of northern West Virginia.

We are thus prepared to paint the following picture of LGM climate in the East (Figure 11). A zone perhaps 50 miles wide could be considered boreal in climate but did not exhibit strong permafrost. The glacier ice at the southern edge of the ice sheet need not be assumed to have been produced by a locally arctic climate, but rather this ice was derived from northern sources. A zone out to 100 miles, but perhaps far less, was cold enough to diminish but not eliminate southern species. The boreal zone in the figure is quite qualitative; this zone need not have been a consistent width next to the ice. In addition, we have not attempted to delineate a boreal zone west of central Illinois. In the East, the absence of southern species' northern range limits (Figure 10) in central Pennsylvania and West Virginia, combined with the distribution of northern relicts across these two states, allows us to be a little more precise in delineating a boreal zone extension into West Virginia. This could well have been a zone where some southern species persisted, as in New England or Wisconsin, where boreal and temperate types mix today. Beyond this zone, temperatures were perhaps cooler than today as far south as the Fall Line of Georgia, but not cold enough to cause extinctions of endemics. Some mixing of northern floras into this zone may have occurred, but not past the southern foothills of the Appalachians. Species abundances no doubt shifted, the timber line was lower, and moisture regimes may have differed. Nevertheless, the climate from southern Pennsylvania southward was not extreme enough to either force migrations or cause extinctions. In contrast, in Europe many species became extinct, leaving a depauperate forest flora and fauna (e.g., the loss of snakes in the British Isles and of many tree species across Europe). The climate may have been drier throughout the Southeast, but the greater decay resistance of grass and gymnosperm pollens, rather than dryness, could be the explanation for increased dominance by grass and pine pollens at the LGM.

IMPLICATIONS

Our analysis, if correct, has implications for estimates of the LGM climate, of temperature tolerances of species, of migration rates, and of evolution rates.

The two questions of LGM climate and the temperature tolerances of species are intimately linked. Data on species assemblages are commonly used to infer past climate (e.g., Gajewski, 1988). In the eastern United States, the ambiguity of much of the pollen data has caused a difficulty in this respect. Further, if the change in temperature was modest so that tolerances of extant species were not exceeded (i.e., clearly less than 12°C), then we must know what these tolerances are. Loehle and LeBlanc (1996) have argued that temperature tolerance ranges are substantial for trees. It would be beneficial to break this mutual dependence by using temperature data derived by some other means, perhaps isotopically. With such data, we could more rigorously estimate the tolerance of the eastern flora as spanning at least the LGM cold temperatures and the mid Holocene warm (warmer than today) temperatures. Armed with such an estimate, we would be in a much better position to evaluate potential effects of future climate change on this region. Such independent data would also improve our ability to test climate models, rather than basing our estimate of a model's accuracy on its match to the imputed climate of reconstructed vegetation, a process that has an unfortunate circularity.

The LGM climate is an important touchstone for testing general circulation models (e.g., Kutzbach and Wright, 1985; Kutzbach and Webb, 1991). With ice sheets, altered tilt, and different CO_2, CH_4, and SO_4^{2-} the period 18,000 BP provides a real challenge to these models' accuracy (e.g., Loehle, 1994). For such a test, however, the vegetation data being compared need to be accurate. For example, COHMAP Members (1988) produced a predicted map for 18,000 BP that closely matches our reconstruction (Figure 12), showing only a narrow band of spruce just south of the ice. The absence of a continuous zone of spruce bordering the ice in the COHMAP map might result from the grid resolution of the simulation. There is a remarkable coincidence between our map and this map in the boreal extension into West Virginia. The COHMAP Members showed substantially higher temperatures than expected on the basis of the pollen data, but our skepticism about the pollen data suggests that their temperature estimate may be right. Thus, our reconstruction of the vegetation is supported by this climate simulation, which may in fact be more accurate than the authors knew. Similarly, Webb et al. (1988) predict a warmer Southeast than traditional reconstructions, with extensive oak at 18000 BP, just as we predict but contrary to extant reconstructions.

The scenario we present has obvious implications for estimates of the ability of species and floras to migrate long distances. Such estimates have been used to project the ability of species today to respond to climate change by migrating to favorable zones. Past estimates of migratory rates (Davis, 1984; Bennett, 1985) have been based on the locations of presumed refugia in Florida, Alabama, or elsewhere. If species were actually growing all along the ice front at a distance of 100 miles or less, they had a much shorter distance to migrate to arrive in New England or the Great Lakes region. This means that past estimates of movement rates may be overestimates, except for those based solely on movement within the glaciated zone. Even here, differential preservation means that invading broadleaf species, because they are initially rare, would be very difficult to detect versus invading conifer species (which produce more pollen that is better preserved). Invasion into the glaciated zone was not necessarily at the maximum possible rate, because no soil microflora (e.g., mycorrhizae) existed on the newly exposed soils, soil organic matter was absent, and climates were still cold in the zone of retreat.

Thus, the estimates from this period are not necessarily the highest migration rates that can be achieved by species responding to climate change today.

The group of 18 trees (Table 1), plus herbaceous species whose northern ranges parallel the ice border, suggests a further implication for migration rates. The extremely close fit to the ice margin, with all borders just south of the ice but not crossing the ice line, suggests that these species remained in this zone throughout the Pleistocene. Why these 18 species should have been unable to migrate is unclear. Nevertheless, if we are correct, 16% of the tree flora (from Burns and Honkala, 1990a,b, based on common species), did not migrate even after more than 12,000 years. A similar percentage MIGHT be unable to migrate in response to future global warming, putting them at an even more severe disadvantage than is usually estimated.

The two scenarios of LGM vegetation distributions have very different implications for evolutionary processes. If boreal forest extended as far south as central Georgia and central South Carolina, then the populations of southern species would have been confined to a refuge too small for multiple varieties or races to coexist. This means that all of the races and varieties of sugar maple, beech, tulip tree, etc. must have originated since the termination of the glacial period, about 14,500-12,000 BP. Because these trees are identifiable as fossils in deposits millions of years old, or even tens of millions of years old (*Liriodendron, Magnolia*), it is hard to imagine how so many species showing such morphologic constancy over such time spans could suddenly develop races and varieties in a little over 10,000 yr. If they did, then our picture of evolutionary processes needs major revision.

For endemic species, the evolutionary implications of a wide boreal zone are even greater. By the traditional view, endemics that are highly specialized must have somehow (1) become temporary generalists and traversed hostile terrain twice or (2) evolved since the LGM. An origin since the LGM demands a truly remarkable rate of evolution, but by an unknown process that eliminates the parental more generalized species. Such rapid evolution cannot be discounted in any particular case, but if so many of these endemics are evolutionarily recent, a truly remarkable burst of rapid speciation occurred across a whole set of plant and animal taxa. This scenario seems unlikely and is not supported by evidence of recent speciation in these cases.

ACKNOWLEDGMENTS

This work was sponsored by the U. S. Department of Energy, Office of Energy Research, Office of Health and Environmental Research, Program for Ecosystem Research, under contract W-31-109-Eng-38. Some of the points made in this paper were expressed in correspondence and talks by H. Iltis dating back to the 1960s. Manuscript written and data analyzed by Loehle. Helpful reviews provided by J. Hoffecker, M. Davis, and T. Webb III. Editorial assistance provided by K. Haugen.

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Table 1. Tree species whose northern ranges stop at the ice margin. (See Figure 10.)

Latin name	Common name
Aesculus octandra	yellow buckeye
Betula nigra	river birch
Carya illinoensis	pecan
Celtis laevigata	sugarberry
Diospyros virginiana	persimmon
Fraxinus profunda	pumpkin ash
Liquidambar styraciflua	sweet gum
Oxydendrum arboreum	sourwood
Pinus echinata	shortleaf pine
Pinus virginiana	Virginia pine
Quercus falcata	southern red oak
Quercus phellos	willow oak
Quercus stellata	post oak
Quercus lyrata	overcup oak
Quercus michauxii	swamp chestnut oak
Robinia pseudoacacia	black locust
Tilia heterophylla	white basswood
Ulmus alata	winged elm

Figure Legends

Figure 1. Traditional reconstruction at 18,000 years before present (BP), after Deevey (1949) and others, showing a wide boreal zone and a substantial tundra zone.

Figure 2. Reconstruction at 18,000 BP, after Delcourt and Delcourt (1984), who postulated that the Mississippi River bluffs and southern river valleys were refugia for deciduous forest.

Figure 3. Pollen profile from Crider's Pond, southeastern Pennsylvania, after Watts (1980a). Note that most data are resolved only to genus.

Figure 4. Venn diagram illustrating the problem of classification when species identities are ambiguous. A fit to one class does not demonstrate a failure to also fit another class.

Figure 5. World map of the homosporous ferns, after Tryon (1957), showing the widespread existence of endemics in nonglaciated regions but not in previously glaciated regions. Solid line is the range of all species in the group. Shaded areas show the regions where endemics occur.

Figure 6. Overlapping ranges of the red baneberry (*Athea rubra*), a western species, and *Athea alba*, an eastern species. Dots show locations of the hybrid in the zone of overlap.

Figure 7. Southernmost outliers of boreal (northern) species (after Burns and Honkala, 1990a,b).

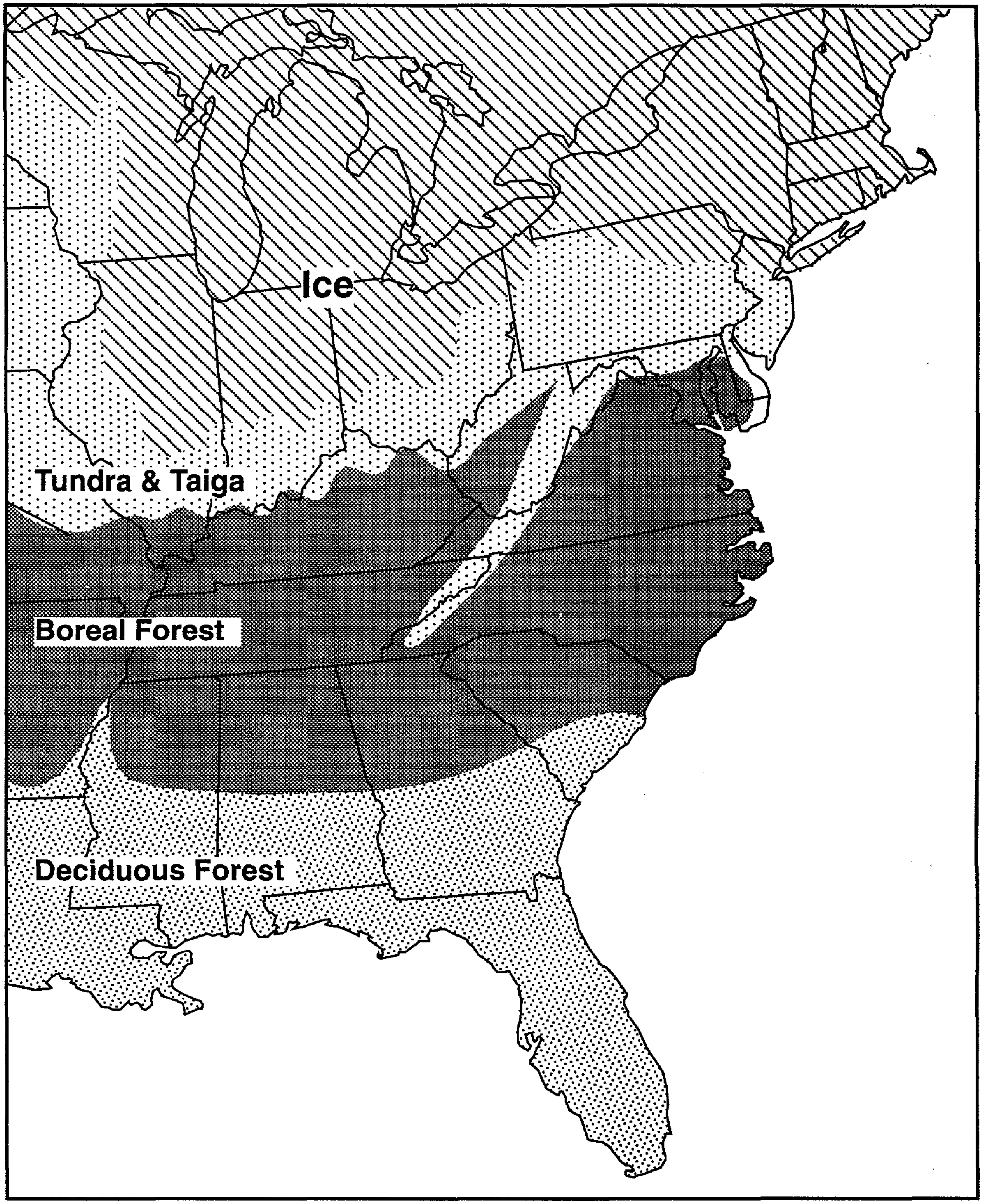
Figure 8. Cones of Balsam fir and Frasier fir. *Abies balsamea var. phanerolepis* in West Virginia is morphologically intermediate between these types, being a likely hybrid. Photos by H. Iltis.

Figure 9. Range maps for fir species, showing possible zones of past overlap in West Virginia (after Burns and Honkala, 1990b).

Figure 10. Combined northern range limits for the 18 eastern tree species whose ranges stop at the ice margin. (See Table 1 for species.)

Figure 11. New reconstruction of the vegetation of eastern North America at 18,000 BP. The cold zone south of the ice was not necessarily cold enough to drive out all southern species, as indicated by relict populations. The cold zone was not necessarily of uniform width.

Figure 12. Boreal zone at 18,000 BP predicted by a general circulation model (after COHMAP Members, 1988), showing the similarity to our new reconstruction. Note that grid cells were large relative to the ice border, making fine resolution in this zone difficult.



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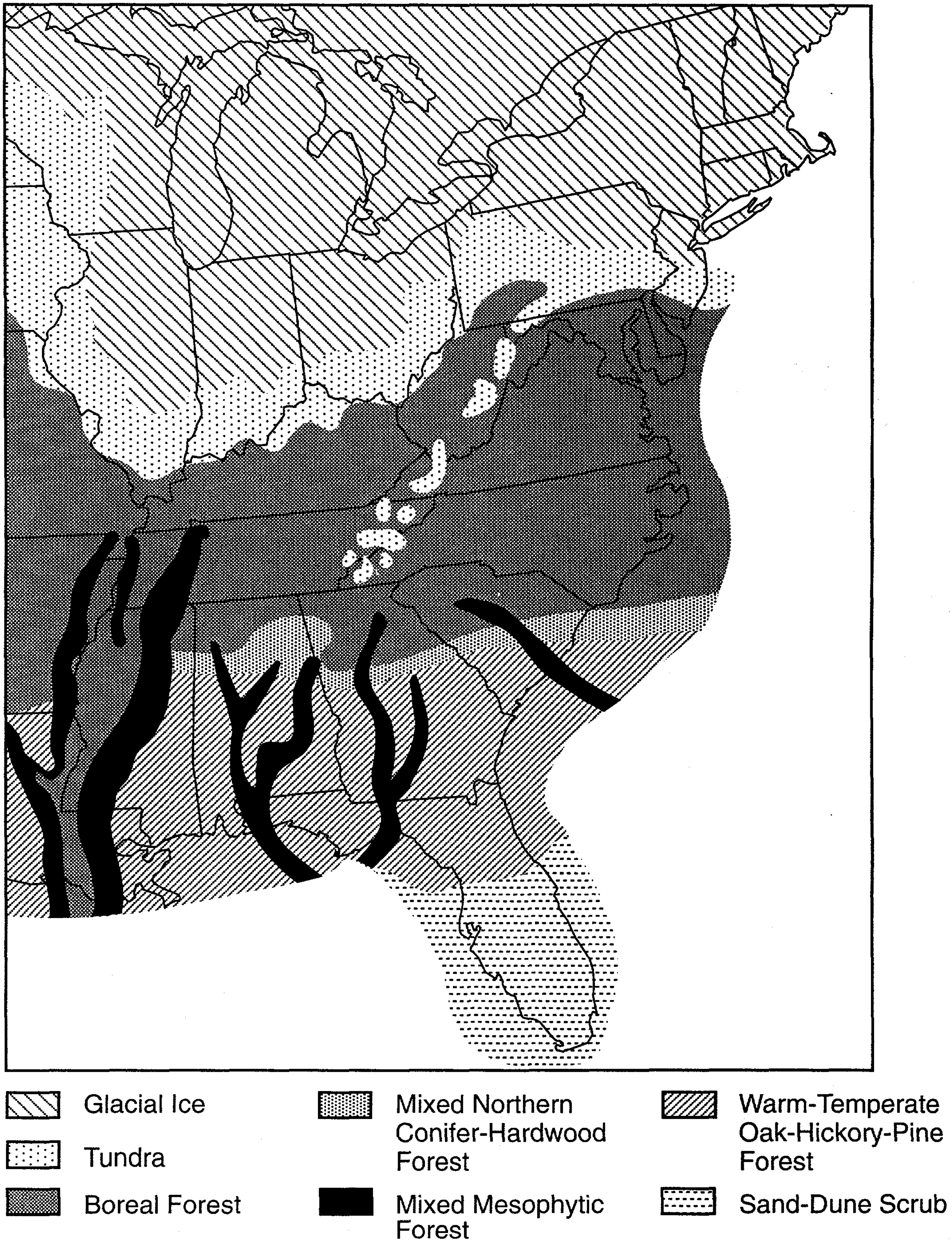
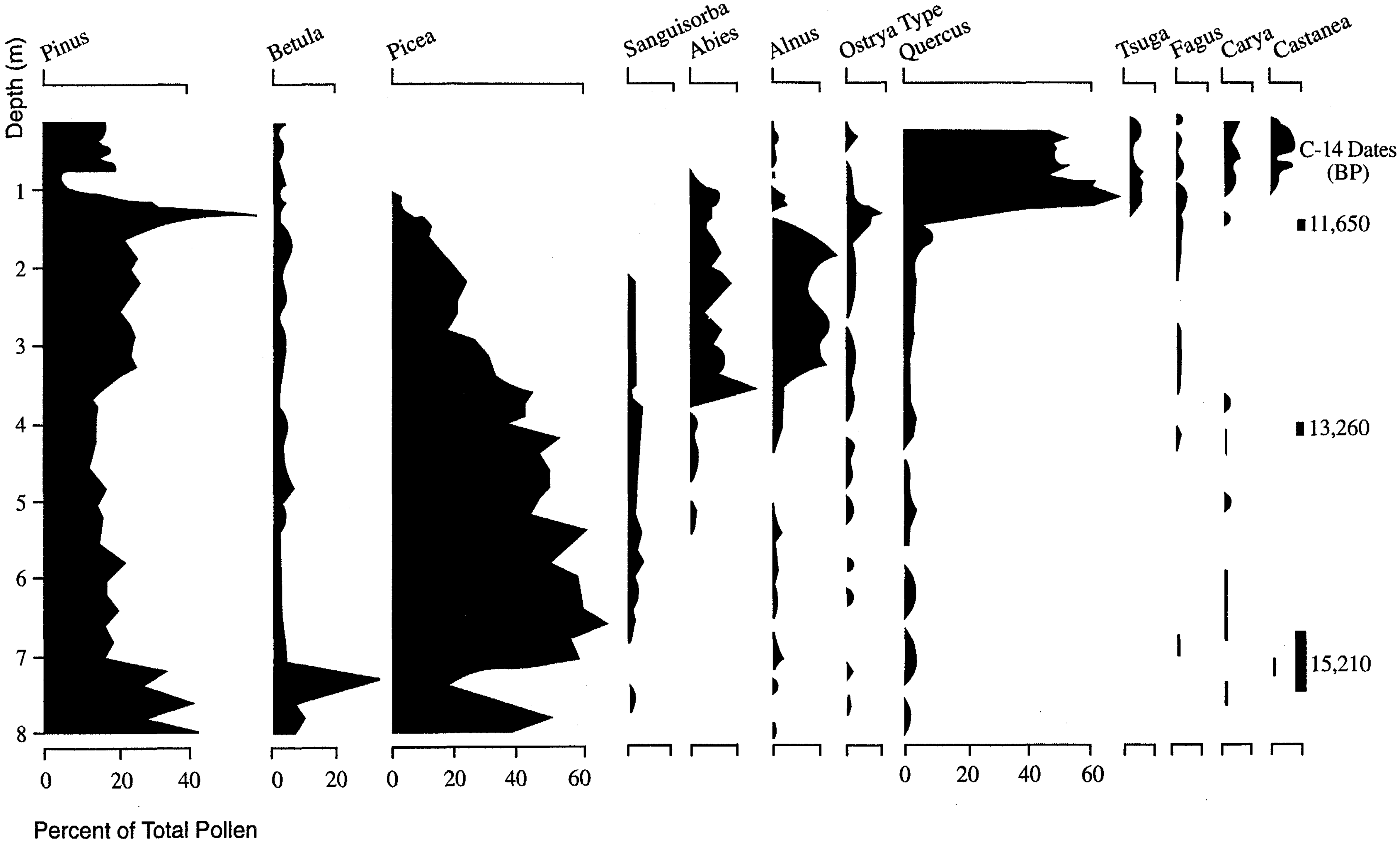
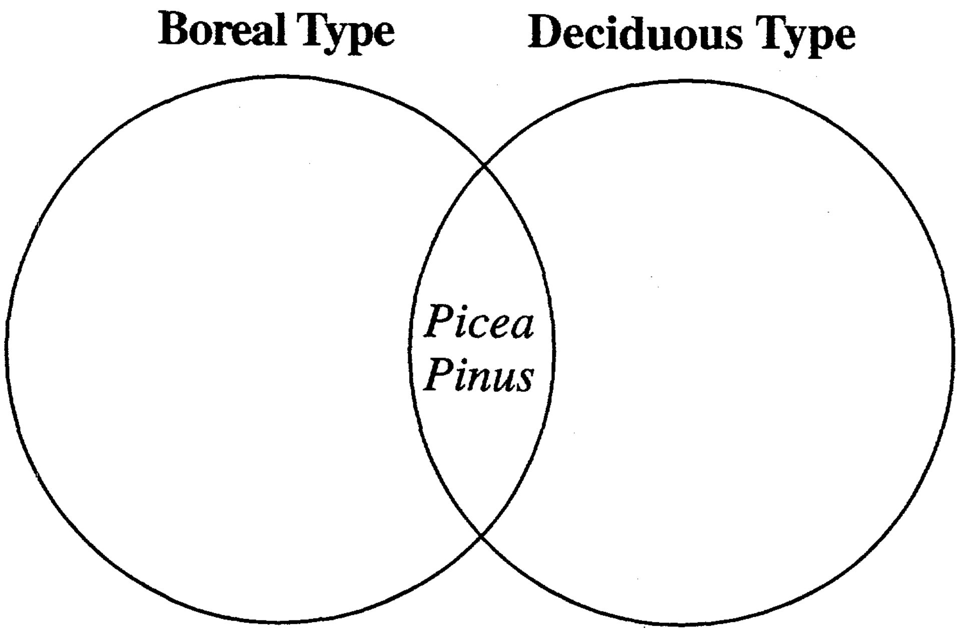

Glacial Ice
Tundra
Boreal Forest
Mixed Northern Conifer-Hardwood Forest
Mixed Mesophytic Forest
Warm-Temperate Oak-Hickory-Pine Forest
Sand-Dune Scrub

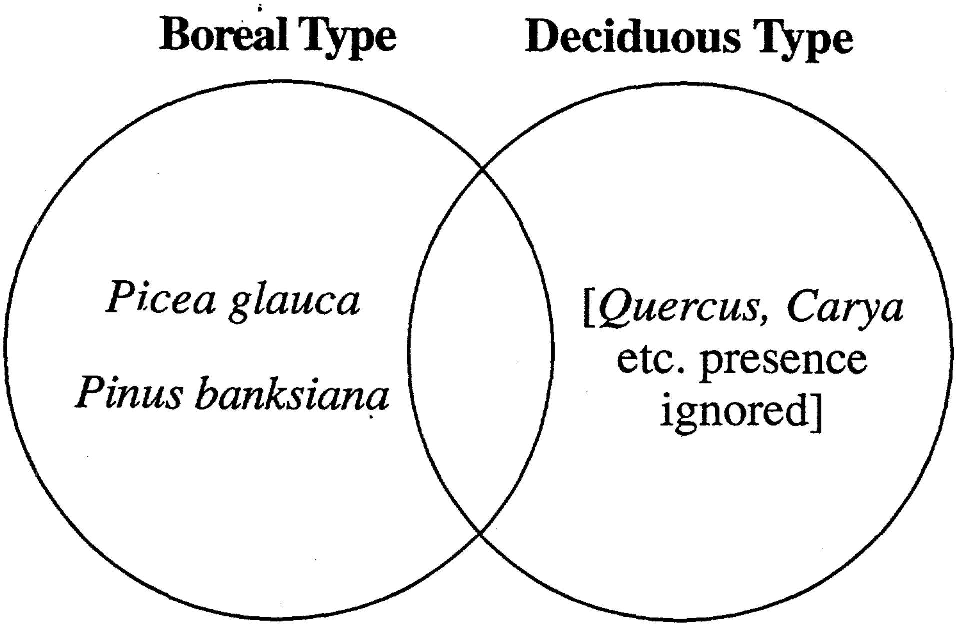
Crider's Pond, Southeastern Pennsylvania

WA Watts

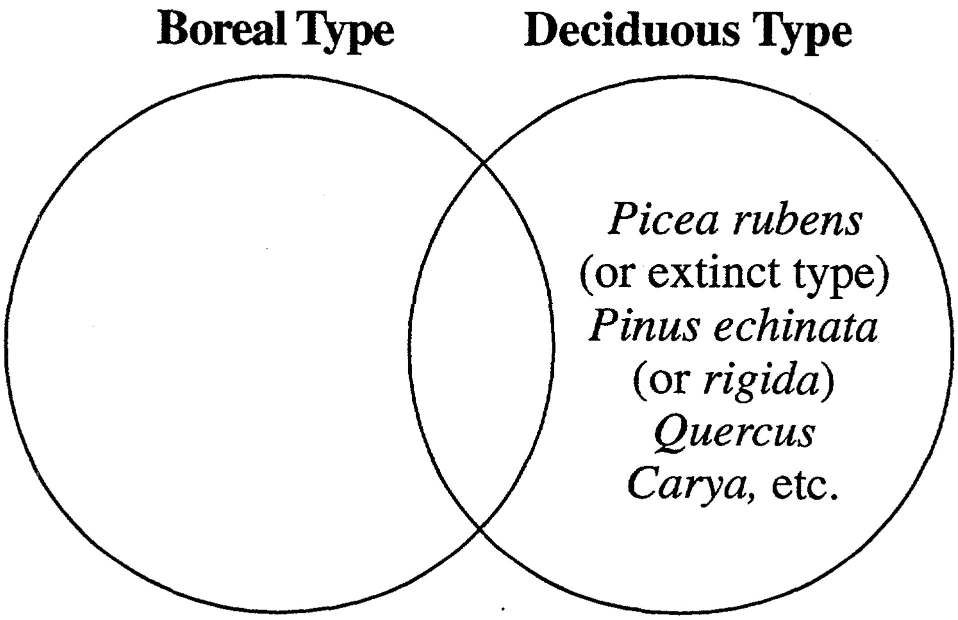




Ambiguous Pollen



Traditional Reconstruction



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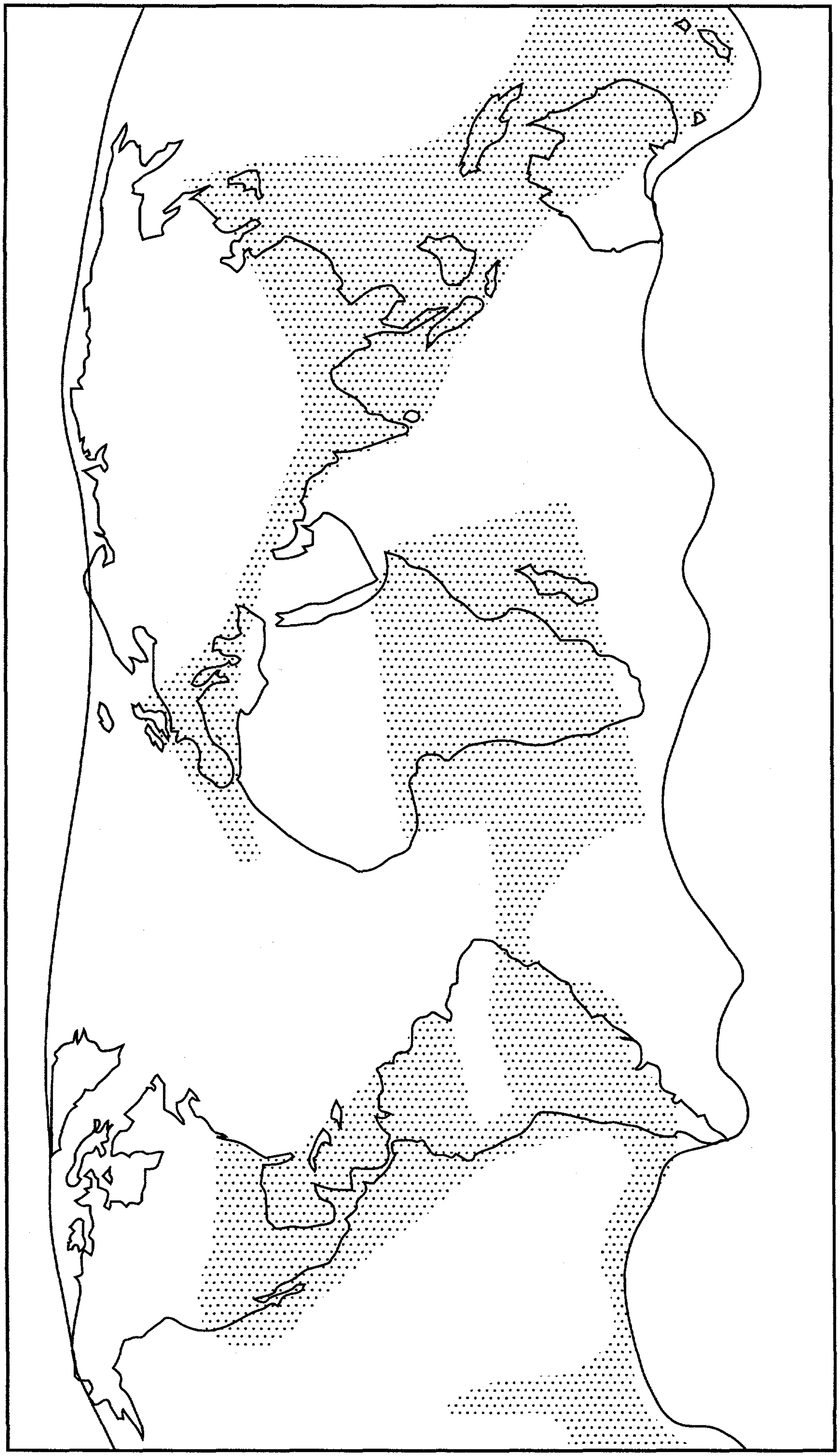
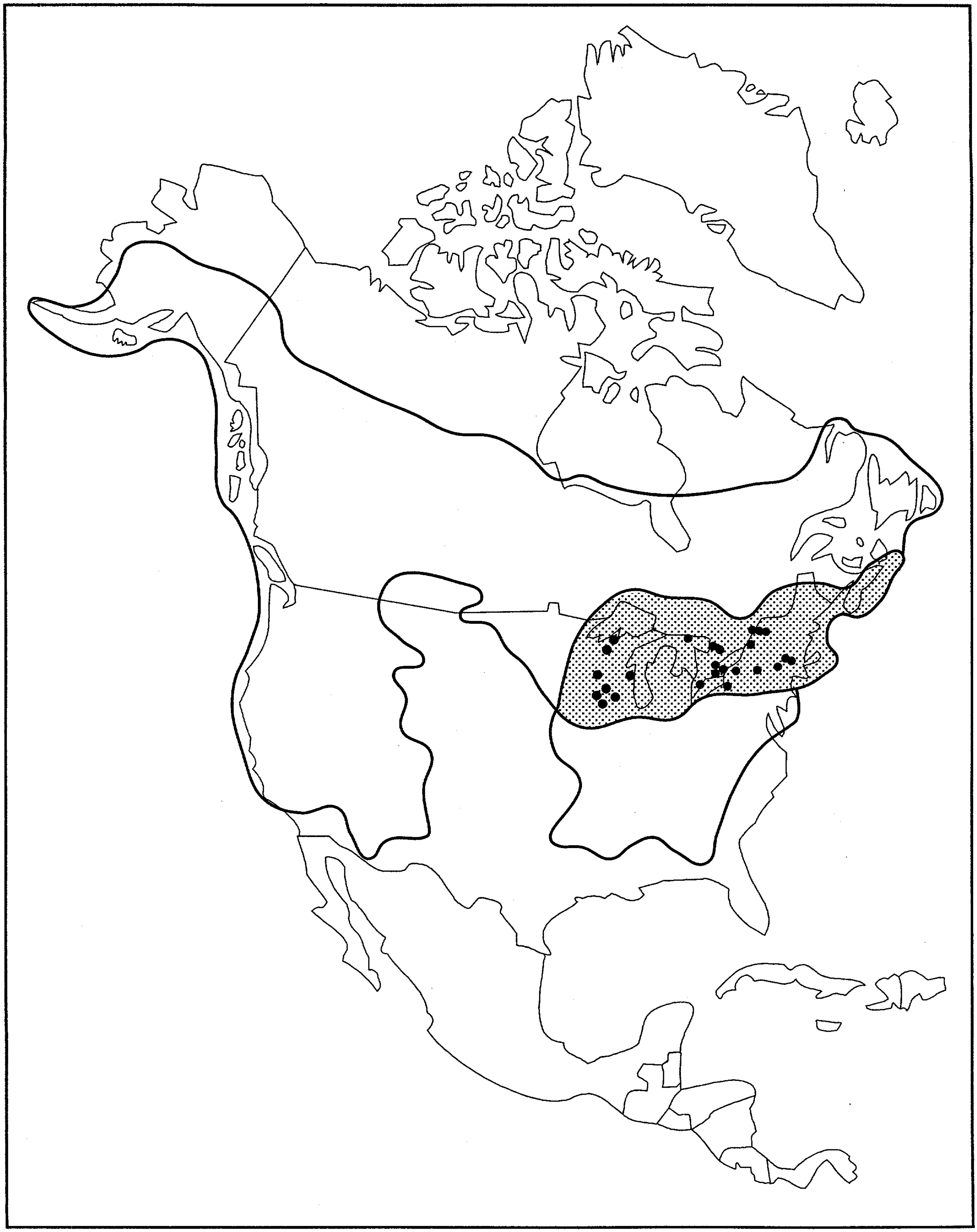
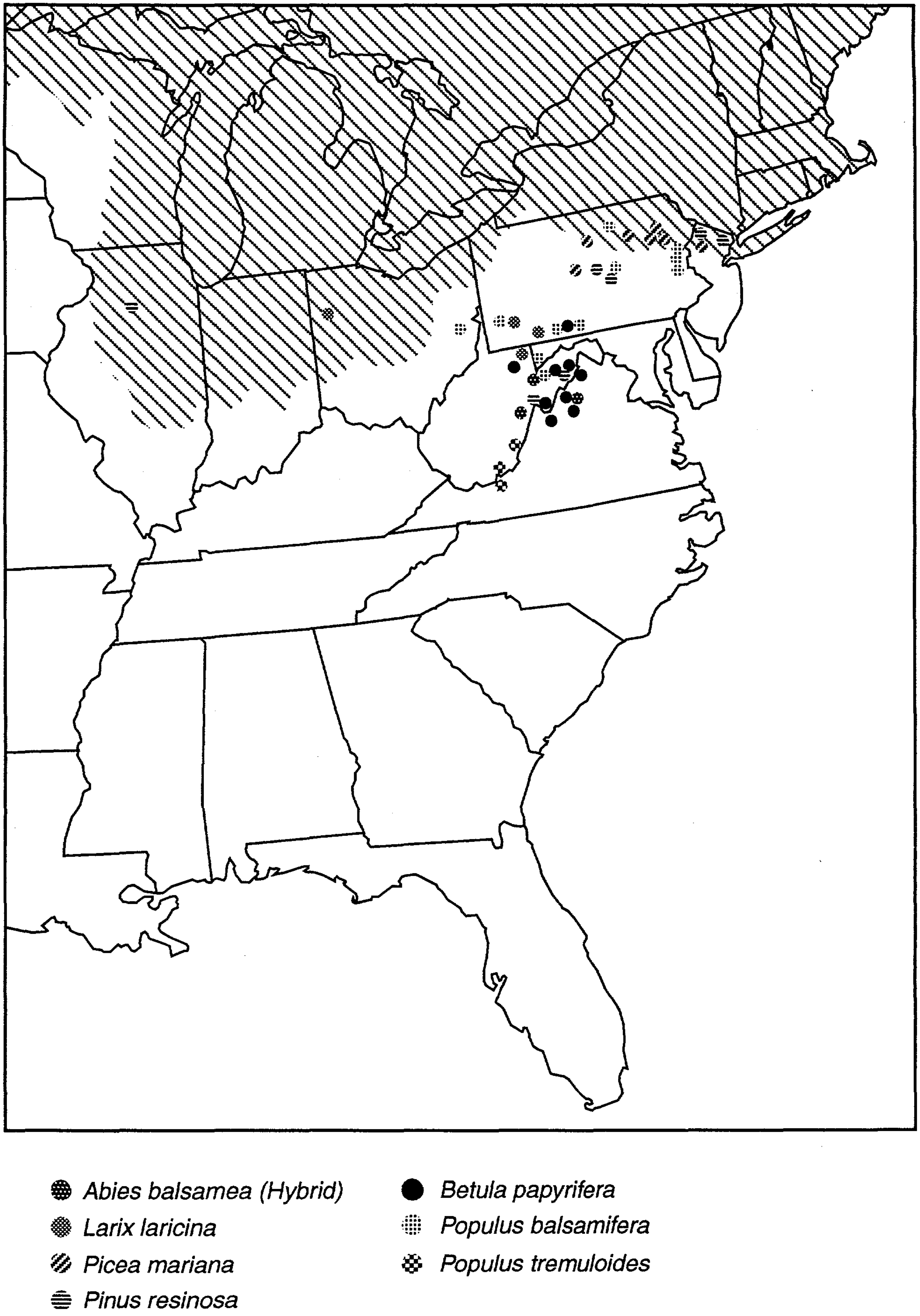




6

Southernmost Outposts of Northern Species



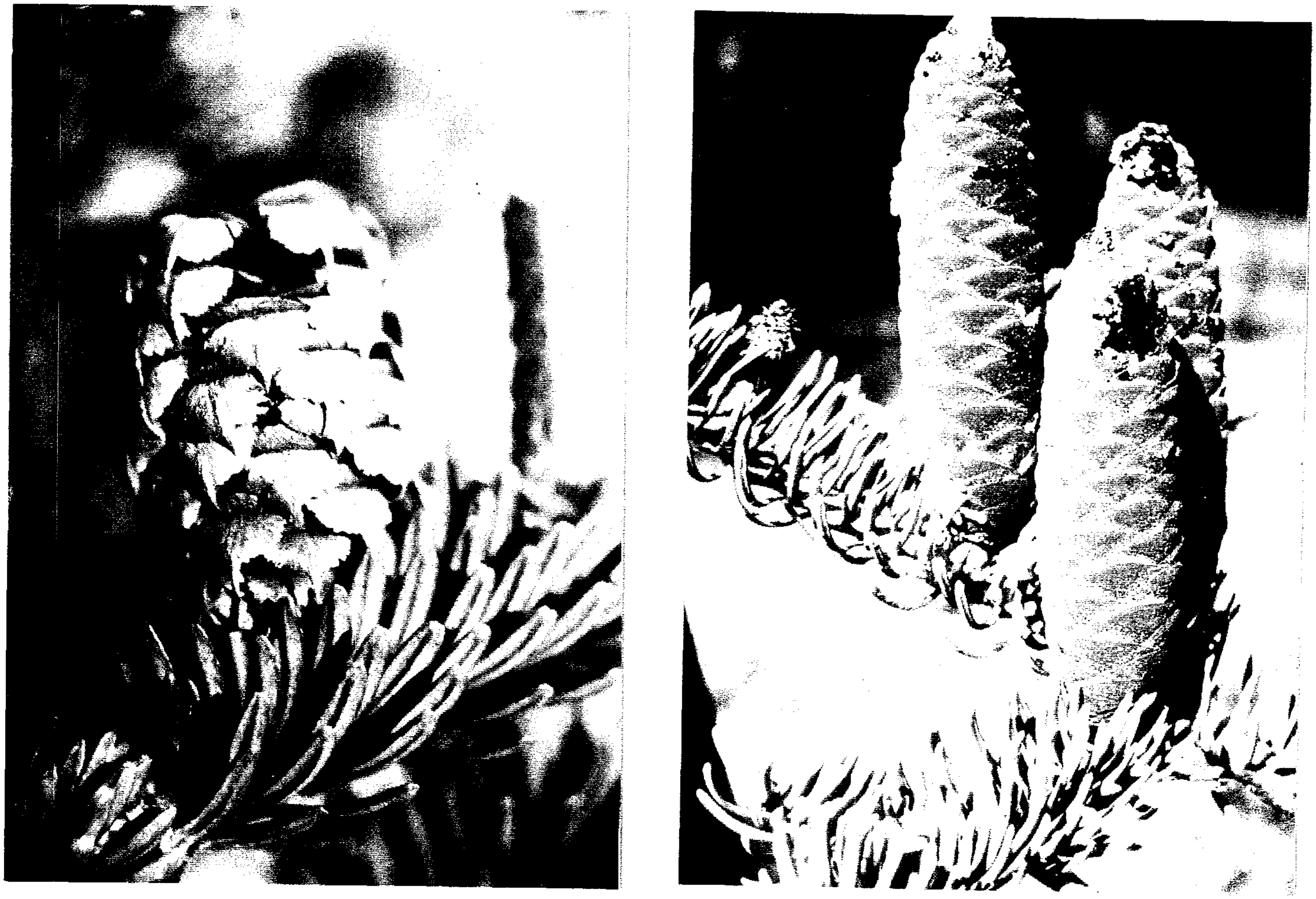
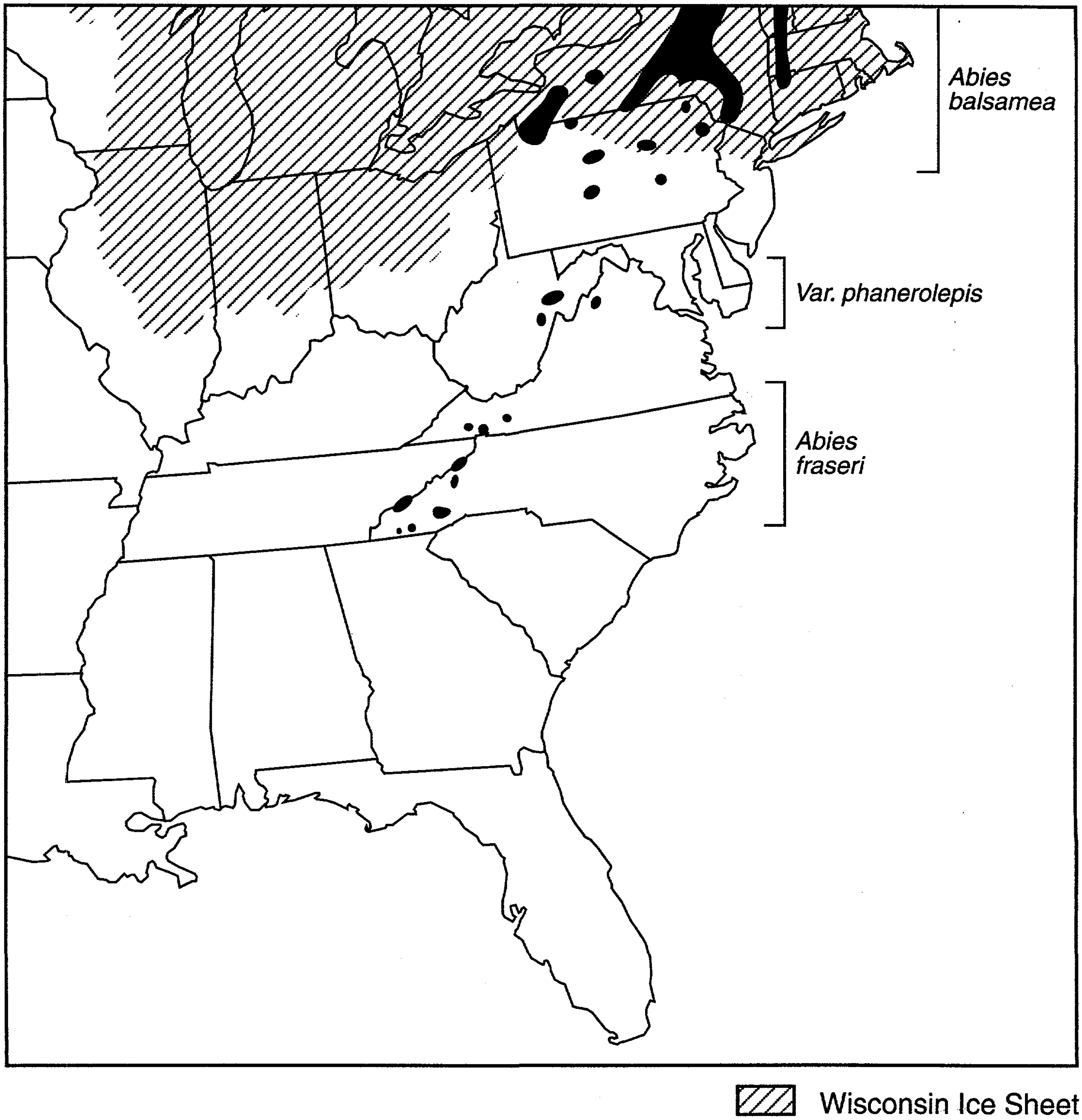
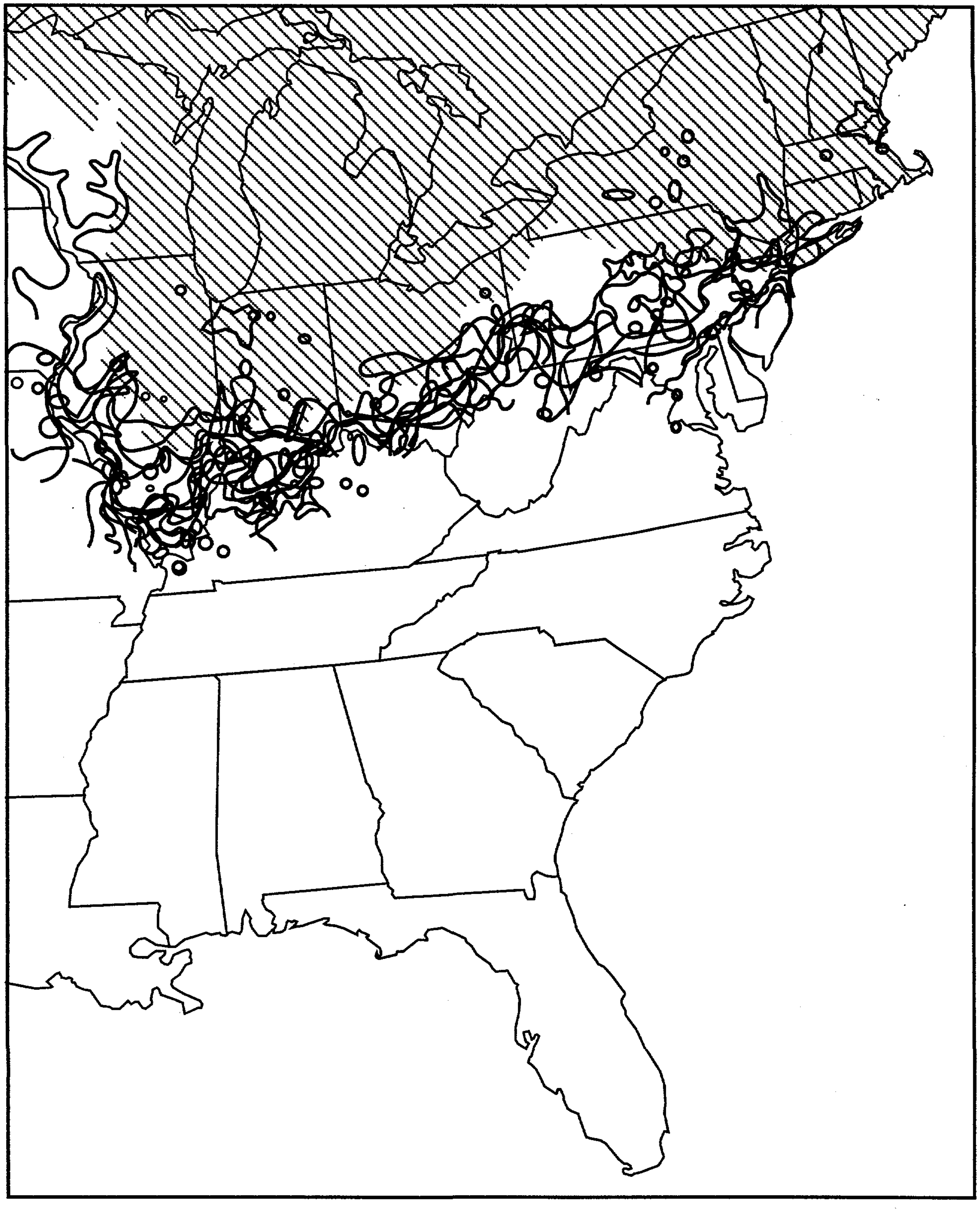
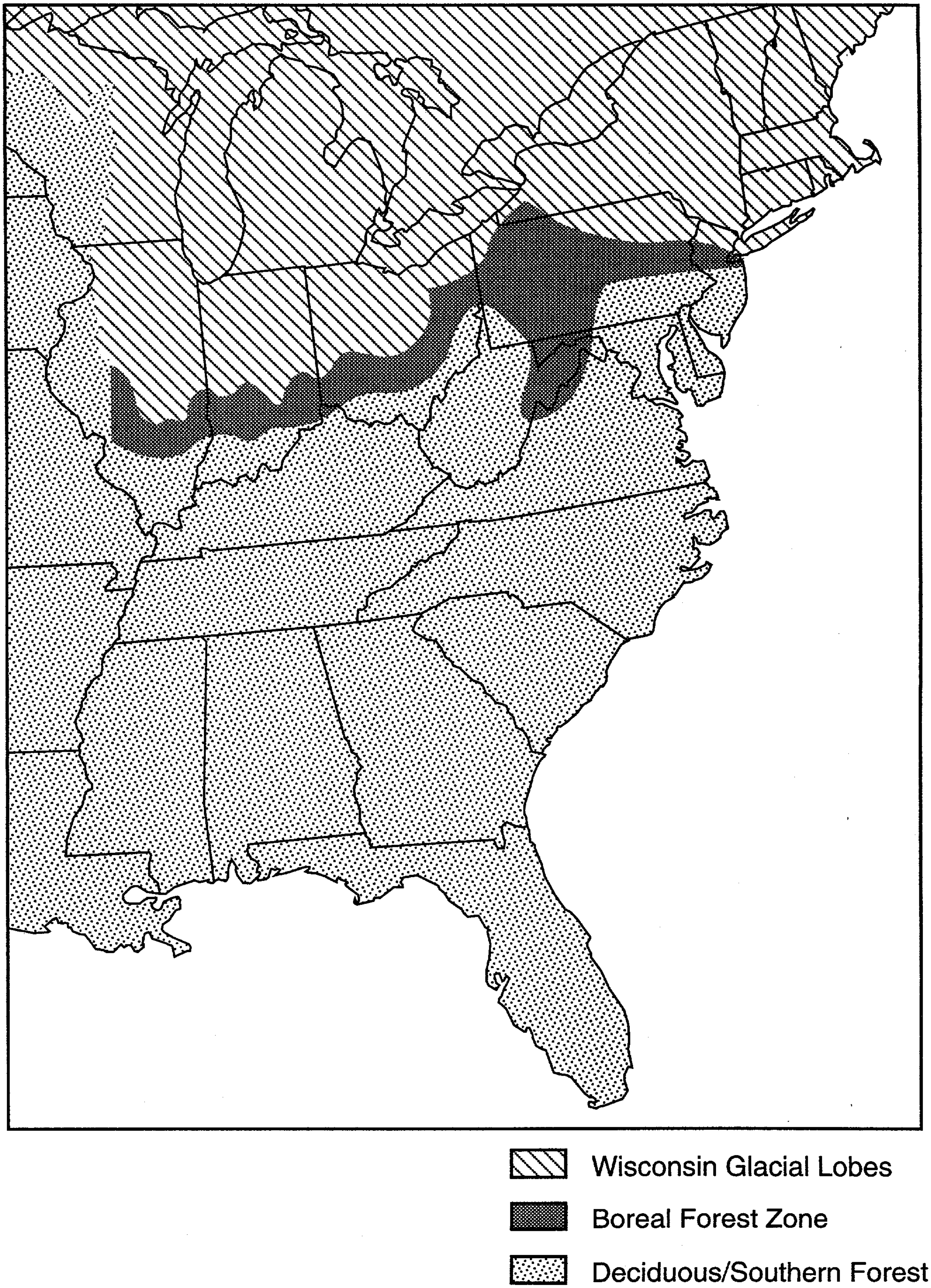
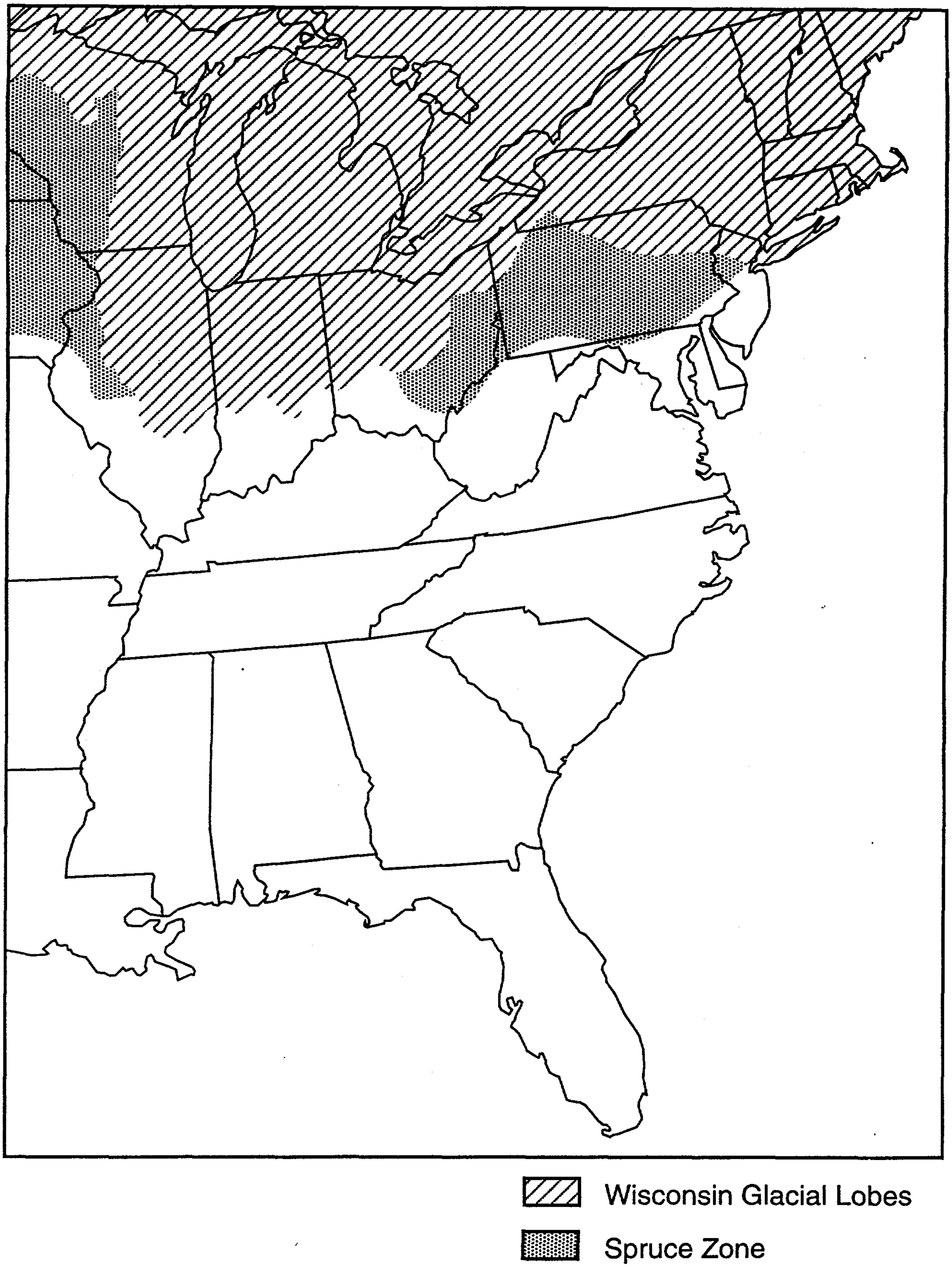


Figure 8. Cones of Balsam fir and Frasier fir. The cones are so distinct that signs of past hybridization should be obvious in the southern Appalachians, but are not present. Photos by H. Iltis.


Abies balsamea
Var. phanerolepis
Abies fraseri
▨ Wisconsin Ice Sheet




▧ Wisconsin Glacial Lobes
▩ Boreal Forest Zone
▒ Deciduous/Southern Forest



▨ Wisconsin Glacial Lobes
▒ Spruce Zone