

gouged from Arctic Ocean shelf strata (21). We speculate that coccoliths may have accumulated relatively rapidly during intense blooms accompanying short warming events. Without bioturbation, the stratigraphic record of a recurring series of such events would resemble a varved sequence with each of the coccolith-rich layers being perhaps a fraction of a millimeter thick. However, bioturbation by bottom-dwelling organisms [perhaps to a depth of 30 cm subbottom (22)] would mix the thin coccolith-rich layer with thick sub- and superjacent coccolith-free layers, thereby greatly diluting the observed coccolith abundances and defocusing the stratigraphic record to a resolution of perhaps 50,000 years. The occurrence of rare specimens in transition zones, between the foram-rich and foram-poor layers in cores T3-67-2 and T3-67-3, is attributed to vertical mixing in sediments by burrowing organisms and bottom currents. If these results are representative of Arctic sediments as a whole, the strong possibility exists that low-diversity populations of coccoliths have sporadically invaded the Arctic Ocean throughout the Cenozoic. A detailed study of these populations will provide a valuable tool with which to unravel the complex paleoclimatic history of the Arctic.

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8 January 1980; revised 17 June 1980

Late Wisconsin Climate of Northern Florida and the Origin of Species-Rich Deciduous Forest

Abstract. *Species-rich mesic forest covered northern Florida as early as 14,000 radiocarbon years before present. It probably originated in deciduous tree populations already present locally in conifer forest between 24,000 and 18,600 years before present. The cold, dry Late Wisconsin climate ended before 14,600 years before present. A transitional warm, dry phase preceded a precipitation increase at 14,000 years before present.*

The number of long pollen records from middle and low latitudes is still insufficient for validation of paleoclimatic reconstructions derived from CLIMAP data and other climate-simulation models (1). In the southeastern United States, several pollen sites (2) reflect conditions much colder and drier than at present during the Late Wisconsin "equilibrium" climate about 18,000 radiocarbon years before present (B.P.) rather than the wetter midsummer condi-

tions simulated (1). At White Pond, South Carolina (3) (Fig. 1), boreal coniferous forest was replaced by mesic broad-leaved forest at 12,800 years B.P. At Lake Annie in southern Florida, however, neither boreal conifers nor broad-leaved forest is recorded; instead, the flora indicates a dry but not necessarily cold climate after 37,000 years B.P. (4). It was desirable to study a geographically intermediate site to determine more closely the southern limit reached by boreal conifers, the place and time of origin of the mesic broad-leaved forest, and the climatic history of the Florida peninsula.

Few of the many limestone sink lakes in Florida and southern Georgia (Fig. 1) (5) have long records of uninterrupted sedimentation. The relatively shallow modern lakes seem to have been dry before 8500 years B.P. (6), because the water level in the main Floridan aquifer in Ocala Limestone was lower during Late Wisconsin glaciation. In the Holocene, the lakes were again flooded as the water table rose. At Buck Lake, shallow-water sediments rich in *Brasenia* (water lily) seeds dated to 8270 ± 50 years B.P. (sample QL-1172) overlie a sandy bottom 2040 cm below the modern lake surface. At Little Salt Spring (7), the water level was 26 m below the present spring surface 12,000 years ago. Thus lake muds older than 8500 years B.P. may be found only in sink lakes at least 20 m deep controlled by the Floridan aquifer.

Sheelar Lake (8) near Gainesville in

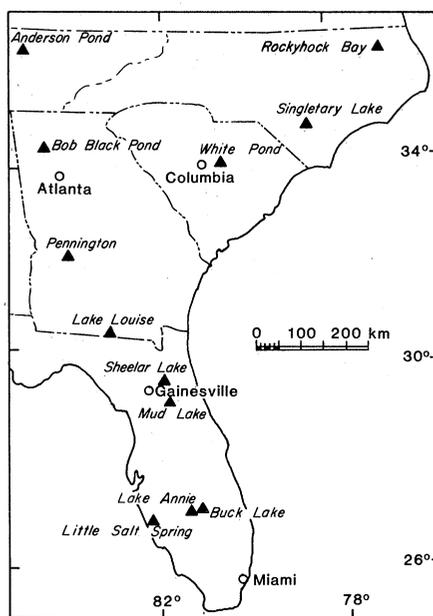


Fig. 1. Location of sites referred to in the text.

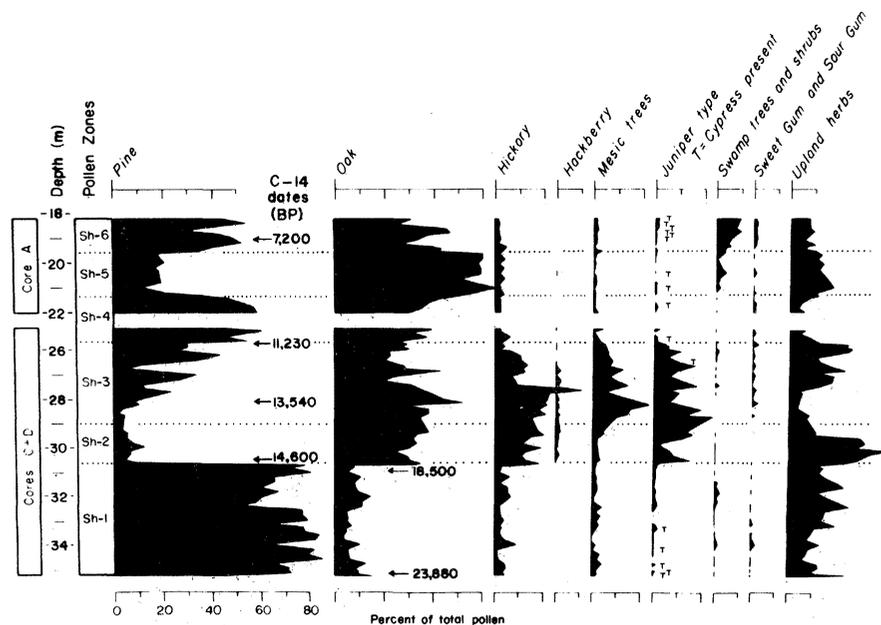


Fig. 2. Simplified pollen diagram from Sheelar Lake.

Gold Head Branch State Park (elevation, 51 m) appears to be a groundwater limestone sink like many others in the region (5). The flat upland of the region is covered by deep sand with open, fire-adapted woodland (9) of long-leaf pine (*Pinus palustris*) and turkey oak (*Quercus laevis*). The steep slopes surrounding the lake have a dense, species-rich scrub dominated by oaks, small palms, and heaths. Similar scrub is widespread in central Florida (10). A deep, fire-protected ravine 200 m from the lake with a small stream, Gold Head Branch, supports luxuriant vegetation of tall trees including hickory (*Carya glabra*), sweet gum (*Liquidambar styraciflua*), and southern magnolia (*Magnolia grandiflora*). Cypress (*Taxodium*) does not occur at or near Sheelar Lake, but large stands are present elsewhere in the region. Some wetland shrubs, including wax myrtle (*Myrica cerifera*) and dahoon (*Ilex cassine*), grow on the lakeshore. The character of the aquatic vegetation and the chemistry of the very transparent lake water (pH 4.9) are determined by the deeply leached unproductive sands that mantle the upland.

The pollen diagram (Fig. 2) shows that pine predominated in the silty sediments at Sheelar Lake during the Late Wisconsin from 23,880 to 18,500 years B.P. (zone Sh-1). Needle fragments of a two-needle pine occur, but the species has not been determined. Pollen of spruce (*Picea*) is absent from most samples, and there are no spruce macrofossils. Thus the southern limit of Late Wisconsin spruce must have been between Sheelar Lake and Pennington, Georgia, where

spruce cones dated to 21,300 years B.P. occur (3). Broad-leaved trees, especially oak and hickory, are well represented, and pollen values for hickory and mesic trees (11) are as high as today. The commonest herbs are ragweed (*Ambrosia*) and grasses (Gramineae). Jointweeds (*Polygonella* spp.), which occur on open sandy soils and fossil dunes, are characteristic of this and the next zone. We infer an open pine forest with some populations of broad-leaved trees. Prairie and sandhill herbs may have been dispersed on local unforested stands.

A hiatus between 18,500 and 14,600 years B.P. is apparent from the sharp change to organic mud and to a different pollen assemblage. From 14,600 to about 14,000 years B.P. (zone Sh-2) the pollen flora is dominated by oak, hickory, hackberry (*Celtis*), and juniper type (11). Herbs increase to as much as 40 percent of the pollen. The vegetation is interpreted as dry oak-hickory stands with local prairie, in a warm, dry climate.

After 14,000 years B.P. (zone Sh-3) herbs were displaced by an expansion of mesic trees (11), an indication of increased precipitation. Oak, hickory, hackberry, and red or white cedars continued, and at 13,540 years B.P. beech (*Fagus*) provided more than 7 percent of the pollen. In Michigan the pollen percentage of beech in surface samples corresponds approximately to the percentage of beech among forest trees (12), and so beech must have been frequent in the Florida forest. An isolated stand of beech, the most southerly in eastern North America (13, 14), lies today about 30 km west of Sheelar Lake. After 13,000

years B.P. broad-leaved forest trees declined steadily and gradually, as pine and herbs expanded, until pine became the dominant tree once more.

By 11,200 years B.P. (zone Sh-4) hackberry had disappeared from the pollen counts, and hickory, mesic trees, and red or white cedars had fallen to low values. A drier climate and increased fire frequency may explain the replacement of mesic trees by pine. Pine with oak dominated the landscape of zone Sh-4. Dates from a core not reproduced here suggest that zone Sh-4 lasted from 11,230 to about 9500 years B.P.

Zone Sh-5 (9500 to 7200 years B.P.) has the highest percentages of oak in the core, with a reduction in pine. Herb percentages increase, especially ragweed, grasses, and spikemoss (*Selaginella arenicola*). Mid-Holocene "Hypsithermal" dominance of oak with prairie plants is well established elsewhere in Florida and Georgia (4, 6). The climate was drier than at present and perhaps warmer.

In the later Holocene (zone Sh-6) the modern vegetation and climate became established, with pine much more abundant than oak in the pollen rain. As elsewhere in the Southeast (4, 6), juniper type (largely *Taxodium* in this zone) and swamp shrubs mark the beginning of development of cypress swamps and bay-head communities (9) throughout the region.

The following major conclusions may be drawn:

- 1) The climate between 23,880 and 18,500 years B.P. was dry and probably windy. The proximity of the spruce boundary to the north suggests a considerably lower average annual temperature than at present. Cold climate ended before 14,600 years B.P. These data appear to conflict with climatic simulations (1), which indicate little change from the present in midsummer conditions. The model may still be on too coarse a scale and too lacking in detail to permit one to discriminate among events in Florida.

- 2) Sheelar Lake contains the oldest record of the mass occurrence of mesic, broad-leaved forest in the Southeast at the end of the Late Wisconsin. It probably originated in small populations that had persisted locally in northern Florida during the glacial period in a pine-dominated landscape. At other sites in the same time interval (2, 3, 15), the percentages of deciduous trees are lower and are associated with abundant spruce and jack pine (*Pinus banksiana*). The mesic forest migrated northward over time. Deciduous forest rich in hickory and

beech was first established at White Pond, South Carolina, at 12,800 years B.P. (3), slightly later at Singletary Lake, North Carolina (2), and more than 1000 years later in an attenuated form at Rockyhook Bay, North Carolina (2). Species-diverse deciduous forest is not recorded at Lake Annie (4).

3) The Holocene began about 12,000 years ago with the decline of mesic forest and the rise of pine and oak to dominance in the landscape.

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25 February 1980; revised 18 June 1980

steady state, fluid filtration is dependent mainly on the microvascular hydrostatic pressure; the term microvascular indicates our uncertainty about the actual pressure and proportion of total fluid exchange in various segments of the microcirculation.

Current knowledge of the microvascular pressure in the lung is derived from indirect measurements in isolated perfused dog lungs; such measurements yield only lumped values for the inflow and outflow segments. Using the low viscosity bolus-ether evolution technique, Brody *et al.* (4) estimated the longitudinal distribution of vascular resistance as being 46 percent arterial, 34 percent capillary, and 20 percent venous. Gaar *et al.* (5), using the isogravimetric pressure technique, measured the capillary hydrostatic pressure at the point of zero net filtration. They found that 56 percent of the total vascular resistance lay upstream of this point. These measurements form the basis of current estimates of microvascular pressure in zone III of the lung (where pulmonary venous pressure exceeds alveolar pressure). A hypothetical microvascular pressure is calculated on the premise that 60 and 40 percent of the total resistance lie in the arterial and venous segments, respectively (6).

The relatively wide alveolar wall capillaries lying just under the pleural surface are easily visualized (7), but are not easy to puncture. There are several impediments. (i) The visceral pleura is surprisingly resistant to puncture, even in animals with thin pleuras, and micropipette tips are easily broken. (ii) With reflected light, optical illusions are created by the curved air-liquid interface of the alveoli. Vessels that seem to lie close to the surface often lie deeper and are inaccessible. What appears to be a ring of capillaries around the alveoli is often not. (iii) Motion of the lung surface resulting from ventilation or from cardiac and vascular pulsations increases the difficulty of micropuncture.

To avoid interference from vascular and ventilatory motion, we removed the left lower lobes [unperfused weight, 43.2 ± 1.3 g (standard deviation)] from

Direct Measurement of Microvascular Pressures in the Isolated Perfused Dog Lung

Abstract. Microvascular pressures in the pulmonary circulation were measured under the pleural surface of the isolated perfused dog lung by the servo-null technique. Strong glass micropipettes with short beveled tips were used, with a suction ring to stabilize the lung's surface. Of the total vascular resistance, 45 percent was in the alveolar wall capillaries themselves. Most of the remaining resistance was in the arterioles. There was negligible pressure drop in venules with diameters larger than 20 micrometers.

Although microvascular pressure has been measured by capillary micropuncture in several organs (1), such measurements have not succeeded in the lung (2). We now report direct measurements of microvascular pressure in the lung.

Net transvascular fluid filtration in the lung, as in other organs, is dependent on the differences in hydrostatic and osmotic pressures across the microvascular endothelial barrier, as described in the modified Starling equation (3). In the

Table 1. Direct pressure measurement in blood vessels of the isolated perfused dog lung. Pressures are given as means \pm standard deviation.

Measure	Arteries			Capillaries			Veins	
	Pulmonary artery	30 to 50 μ m	20 μ m	10 μ m, arterial	10 μ m, venous	20 μ m	30 to 50 μ m	Pulmonary vein
Pressure (cm-H ₂ O)	16.7 \pm 0.6	16.4 \pm 1.3	15.6 \pm 2.9*	14.6 \pm 2.4*	12 \pm 1.7*	11.1 \pm 0.7*	11.1 \pm 0.8	11.1 \pm 0.5
Number of vessels	10	7	3	13	10	4	8	10
Percent of total resistance		5.4	14.2	17.9	46.4	16.1	0	0

*Values are significantly different from those in previous column at $P < .05$ (Newman-Keuls test).