

Paleoecology of Mid-Wisconsinan Peat Clasts from Skidaway Island, Georgia

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*Twelve peat clasts were recovered from a paleochannel deposit on Skidaway Island, Chatham County, Georgia. An AMS radiocarbon date from a plant stem in one of these clasts indicates original peat deposition $36,830 \pm 340$ ^{14}C years B.P., and the stratigraphic position of the clasts supports this age assignment. Fossil *Pinus* needles, pollen, and testate amoebae provide a snapshot of the environment and biota at a time when most other sites in coastal Georgia were not accumulating sediment. Pollen from the peat clasts is dominated by *Pinus* and other genera common on the coastal plain today (e.g., *Quercus*, *Carya*). Morphological and anatomical analyses of the fossil *Pinus* needles indicate they are either *Pinus taeda* or *Pinus serotina*, which both currently inhabit the Coastal Plain of Georgia. Seven testate amoeba taxa, all characteristic of relatively dry peatland conditions, were encountered in the clasts. Testate amoeba assemblages are dominated by *Hyalosphenia subflava*, a taxon that is not typically dominant in modern assemblages. More investigations describing the occurrence and distribution of Quaternary testate amoebae, as well as modern ecology and biogeography of testate amoebae, are necessary before the significance of these assemblages can be assessed fully. Deposition of the peat clasts occurred at a time when pollen evidence from Florida indicates warm and wet climatic conditions, and the paleoecology of the peat clasts indicates that a relatively warm climate also existed in coastal Georgia.*

INTRODUCTION

Fossil-bearing sediments of Late Pleistocene age are rare in coastal Georgia. Eustatic sea level drop and/or increased aridity in the Late Pleistocene lowered regional water tables and resulted in depositional hiatuses spanning at least 35,000 years in many inland lakes (Watts, 1969, 1971; Watts and Hansen, 1988; Booth and Rich, 1998) and barrier island sediments (Booth et al., 1999). Late Pleistocene-age peat clasts from a paleochannel lag deposit on Skidaway Island, Georgia (Fig. 1), have yielded Fossil *Pinus* needles, pollen, and testate amoebae. These taxa provide a snapshot of the environment and biota at a time when few other sites in coastal Georgia were accumulating organic-rich sediment.

The specific objectives of this investigation were to identify which species of *Pinus* occurs in the peat clasts, and to use this information in conjunction with pollen analysis to provide insight into the paleoclimate of the region. This study also documents the presence and abundance of testate amoebae in the peat clasts, their paleoecological significance, and implications for the interpretation of fossil testate amoeba assemblages.

GEOLOGIC SETTING AND AGE OF THE PEAT CLASTS

Quaternary shoreline deposits lie in bands parallel to the modern coastline on the Georgia coastal plain. Barrier-island deposits that lie closest to the Atlantic Ocean are comprised of the three most recent of these deposits: the Princess Anne shoreline, the Silver Bluff shoreline, and the modern shoreline. The Princess Anne and Silver Bluff shoreline complexes are Late Pleistocene in age, and the modern shoreline has formed during the Holocene (Fig. 1). The maximum age of the Princess Anne shoreline is probably 80,000 years B.P. (Wehmiller et al., 1997; Booth and Rich, 1998). Princess Anne shoreline sediments continued to accumulate, or were modified by surficial processes, until at least 40,000 years B.P. (Rich and Pirkle, 1993; Booth and Rich, 1998) when the Silver Bluff shoreline appeared (Hoyt and Hails, 1974; Booth et al., 1999). In central and southern portions of Georgia, Princess Anne sediments

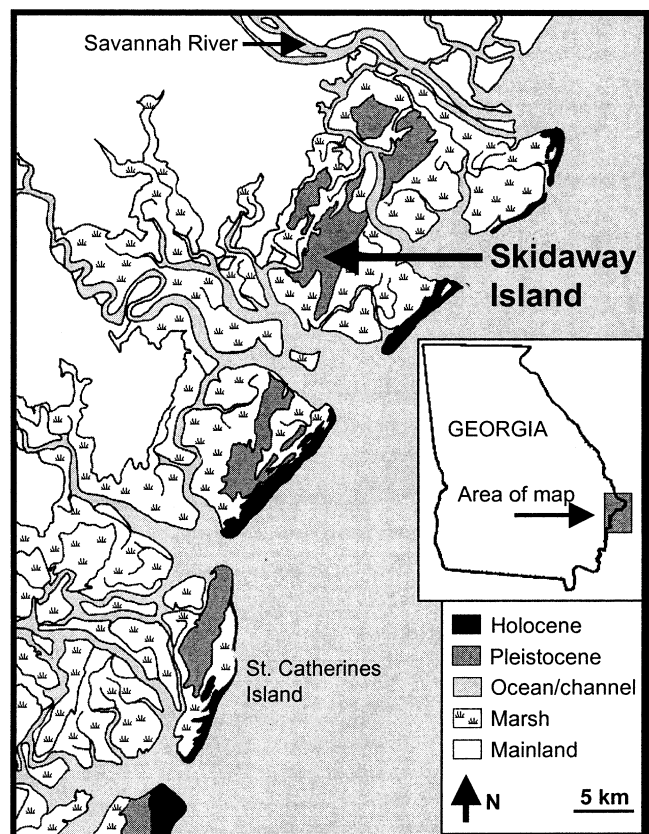


FIGURE 1—Map showing the location of the study site on Skidaway Island, Georgia and the age of barrier-island sediments along this portion of the Georgia coast.

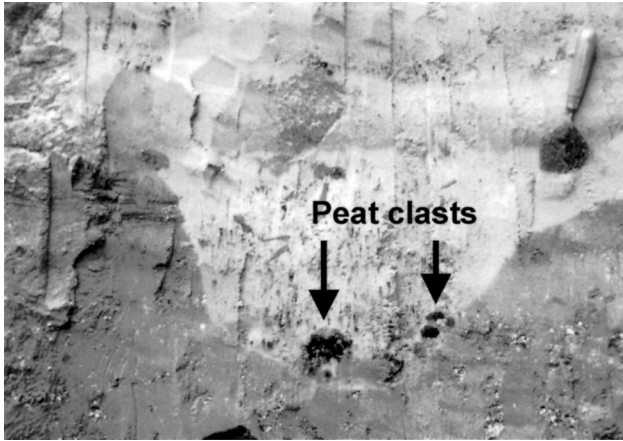


FIGURE 2—Photograph of the vertical face containing the paleochannel feature and several peat clasts preserved in the channel-lag deposit. The paleochannel feature represents an erosional contact between two distinct sand units—a dark-colored lower unit and a light-colored upper unit. A hand trowel (12-cm long) is shown for scale.

form the mainland shoreline, which is as much as twelve kilometers west of the modern barrier-island shoreline (Hoyt and Hails, 1974). Along the northern portion of the Georgia coastline, Princess Anne sediments comprise the western sides of Skidaway Island and Wilmington Island. Silver Bluff shoreline deposits form the eastern portions of these northern islands.

During excavation of ponds on the southern end of the western half of Skidaway Island (81° 04' W Long., 31° 51' N Lat.; elevation ~3 m), a paleochannel feature separating two distinct sand units was discovered at 1.35-m depth (Fig. 2). A lag deposit in this paleochannel contained small rounded peat clasts, 3 to 8 cm in diameter. All the peat clasts were brownish-black (5YR 2/1) in color, unconsolidated, and sandy textured. The similar lithology of the clasts suggests they are probably all approximately the same age. An AMS radiocarbon date from a plant stem fragment in one of these clasts indicates deposition 36,830 ± 340 years ago (BETA-112547). The sand below the channel feature overlies a shell layer, and two uranium-series dates from corals in this shell layer indicate it was deposited 80,000 years ago (Wehmiller et al., 1997). More detailed stratigraphy of the site is presented in Booth (1998).

METHODS

Six needle fragments from the peat clasts were embedded in Paraplast®. Cross sections were prepared from along the entire length of the fragments using a rotary microtome, and the internal anatomy of the needles was described. For selected cross sections containing well-defined resin ducts, the longest and shortest diameters of each resin duct were measured. These measurements were used to estimate the original diameter of the resin ducts before needle compression, by assuming that the

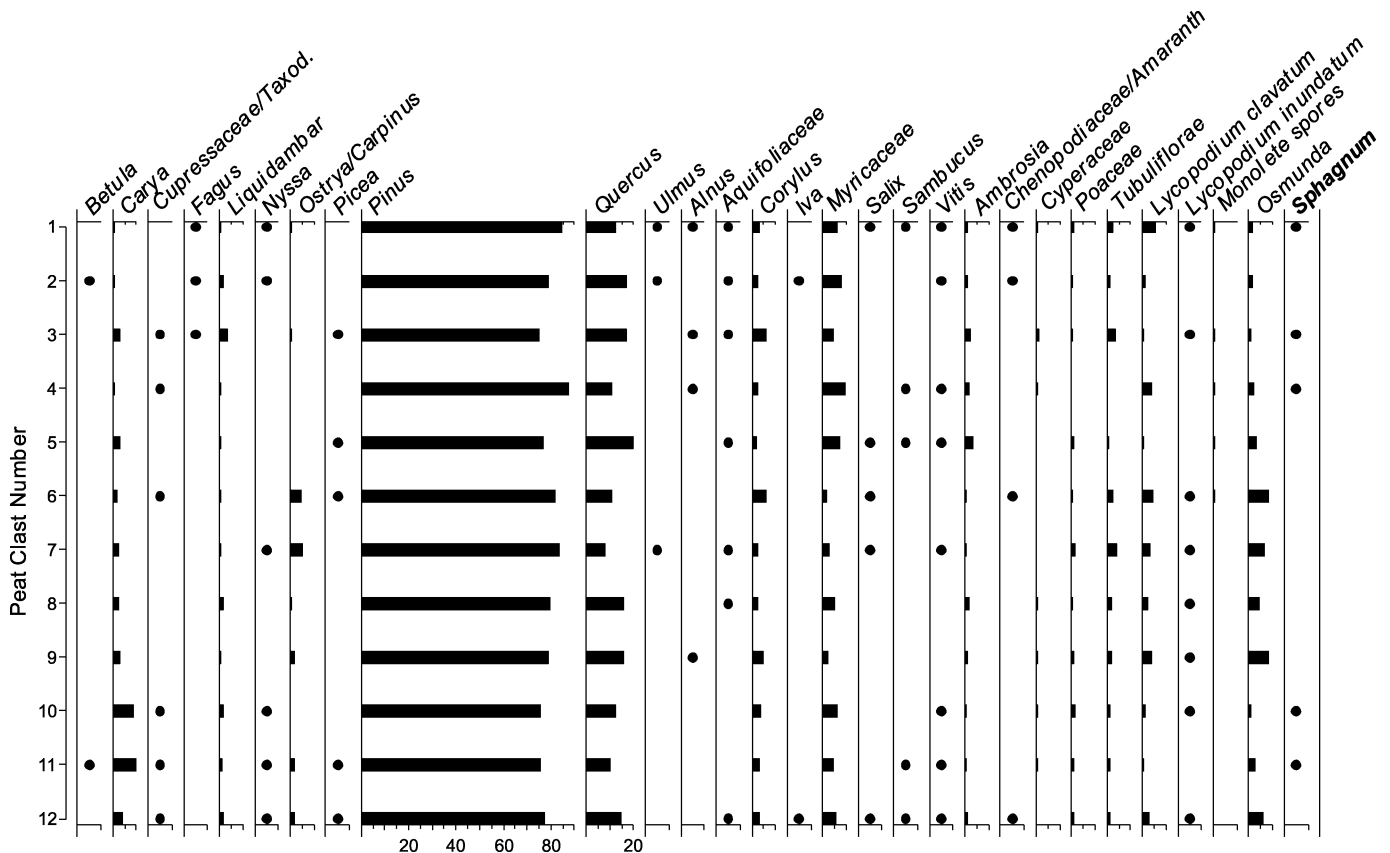


FIGURE 3—Pollen diagram from the twelve peat clasts. Only taxa present in at least two peat clasts are shown. Presence data for less abundant taxa are shown with a closed circle.

original circumference of the resin duct did not change. Identification of the *Pinus* needles was made using criteria discussed by Harlow (1947).

Peat from the center of twelve clasts (~3 cm³) was sampled for fossil pollen and testate amoebae. Pollen samples were processed using standard techniques (Traverse, 1988). Pollen counts were continued until at least 300 arboreal grains were tallied. Pollen percentages were calculated using an arboreal pollen sum for arboreal taxa and a total pollen sum for all other pollen and spore taxa. Because standard pollen-processing procedures have been shown to destroy some testate amoeba taxa preferentially, the non-destructive sieving procedure of Hendon and Charman (1997) was applied. However, particulate matter made analysis of the samples extremely difficult, and thus testate amoeba analysis was performed on the samples prepared for pollen analysis. To determine if taxa were eliminated by the pollen processing procedure, ten slides from the residues obtained by the sieving method were scanned. No additional taxa were encountered, and the assemblages from both processing methods were qualitatively similar. Testate amoeba counts were continued until a total of 150 were tallied, and relative abundance of each taxon was calculated as a percent of the total number of testate amoebae counted.

RESULTS AND DISCUSSION

Regional Vegetation

Relative abundances of arboreal pollen taxa are similar among the twelve clasts. All are dominated by *Pinus*, *Quercus*, and *Carya* (Fig. 3), all of which are abundant on the coastal plain today. All *Pinus* pollen grains preserved well enough to allow subgeneric determination were identified as *Pinus* subgenus *pinus*. Trace amounts of taxa more characteristic of northern temperate forests, such as *Picea* and *Fagus*, occurred in several of the peat clasts (Fig. 3). Although *Picea* and *Fagus* may have grown in the region, interpretation from a paleoecological perspective is problematic for several reasons. A now-extinct species of spruce, *Picea critchfieldii*, was widespread in southeastern North America during the Late Pleistocene (Jackson and Weng, 1999). The *Picea* pollen in the peat clasts may represent this species. Small amounts of *Fagus* pollen also are difficult to interpret because disjunct populations of *Fagus* exist today approximately 100 km away from Skidaway Island on the Savannah River bluffs. Abundant *Fagus* pollen has been documented from the coastal plain of northern South Carolina from about 13,000 to 9,000 ¹⁴C years BP (Hussey, 1993).

Pinus Needle Identification

The fossil *Pinus* needles had rounded-triangular cross-sections (Fig. 4), and thus were derived from a species with three needles per fascicle. The longest needle fragment was 44 mm in length. Each needle fragment contained two fibrovascular bundles arranged very closely together and two medially positioned resin ducts (Fig. 4). Needle dimensions and resin-duct number and position differ from *Pinus elliotii*, *P. palustris*, and *P. echinata*. Anatomically and morphologically the needles are consistent with *P. taeda*

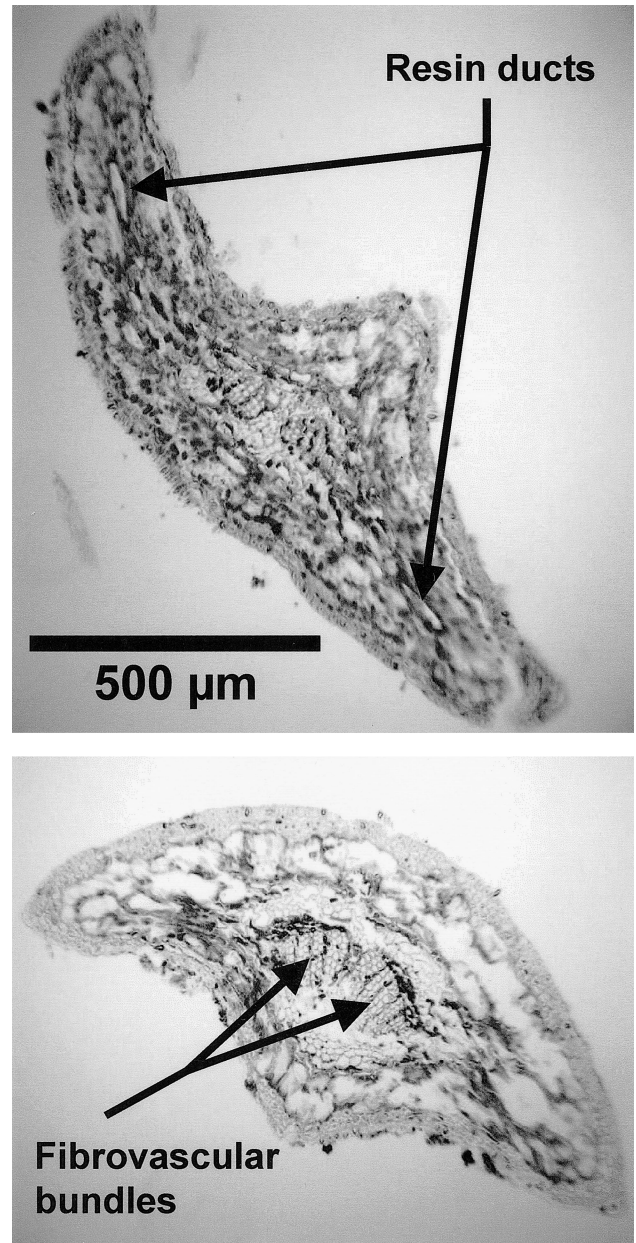


FIGURE 4—Cross sections of two fossil *Pinus* needles illustrating the position of resin ducts and fibrovascular bundles.

(loblolly pine), *P. rigida* (pitch pine), and *P. serotina* (pond pine). However, resin-duct diameter is significantly smaller in *P. rigida* than either *P. taeda* or *P. serotina*. Resin-duct diameter indicates that the fossil needles are assignable to either *P. taeda* or *P. serotina* (Fig. 5). Needles of these species cannot be differentiated anatomically.

Testate Amoeba Analysis

Seven testate amoeba taxa were recovered from the peat clasts (Fig. 6). All previous data regarding the distribution and occurrence of fossil peatland-inhabiting testate amoebae has come from Holocene sediments. The paucity of data on pre-Holocene testate amoebae has been attri-

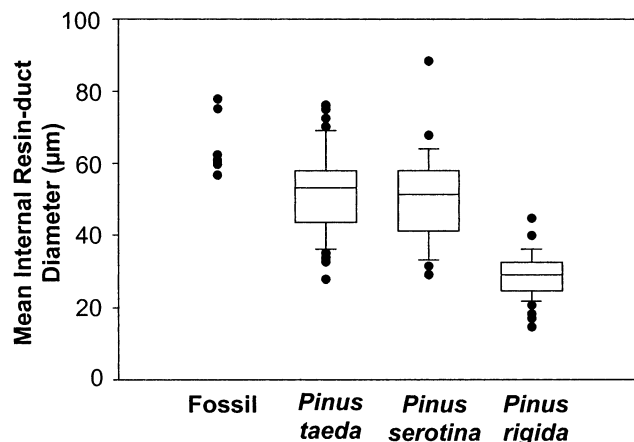


FIGURE 5—Box plot of the mean internal resin-duct diameter for all six fossil *Pinus* needles plotted against modern data for the three potential candidate species.

buted variously to poor preservation or the lack of systematic searches (Charman, 2001). The abundance of testate amoebae and their good preservation in the clasts (Fig. 6) suggest that the lack of Pleistocene data is more likely because of few investigations.

Testate amoeba assemblages were similar between the clasts (Fig. 7). All studied clasts were dominated by *Hyalosphenia subflava*, with smaller percentages of *Trigonopyxis arcula*, *Trigonopyxis minuta*, *Cyclopyxis arcelloides* type, *Assulina muscorum*, and *Heleopera sylvatica*. One specimen in the genus *Arcella* also was encountered, but more specific taxonomic identification was not possible. All testate amoebae in the clasts, with the possible exception of *Arcella* sp., indicate relatively dry peatland conditions (Charman and Warner, 1992, 1997; Woodland et al., 1998; Mitchell et al., 1999; Booth, 2001, 2002). Some *Arcella* species (e.g., *Arcella catinus*, *Arcella arenaria*) also prefer relatively dry habitats (Charman and Warner, 1992; Charman et al., 2000).

The high relative abundance of *Hyalosphenia subflava* in the peat clasts is unique in comparison with modern samples. In modern peats from North America and Europe the highest abundance of *Hyalosphenia subflava* only

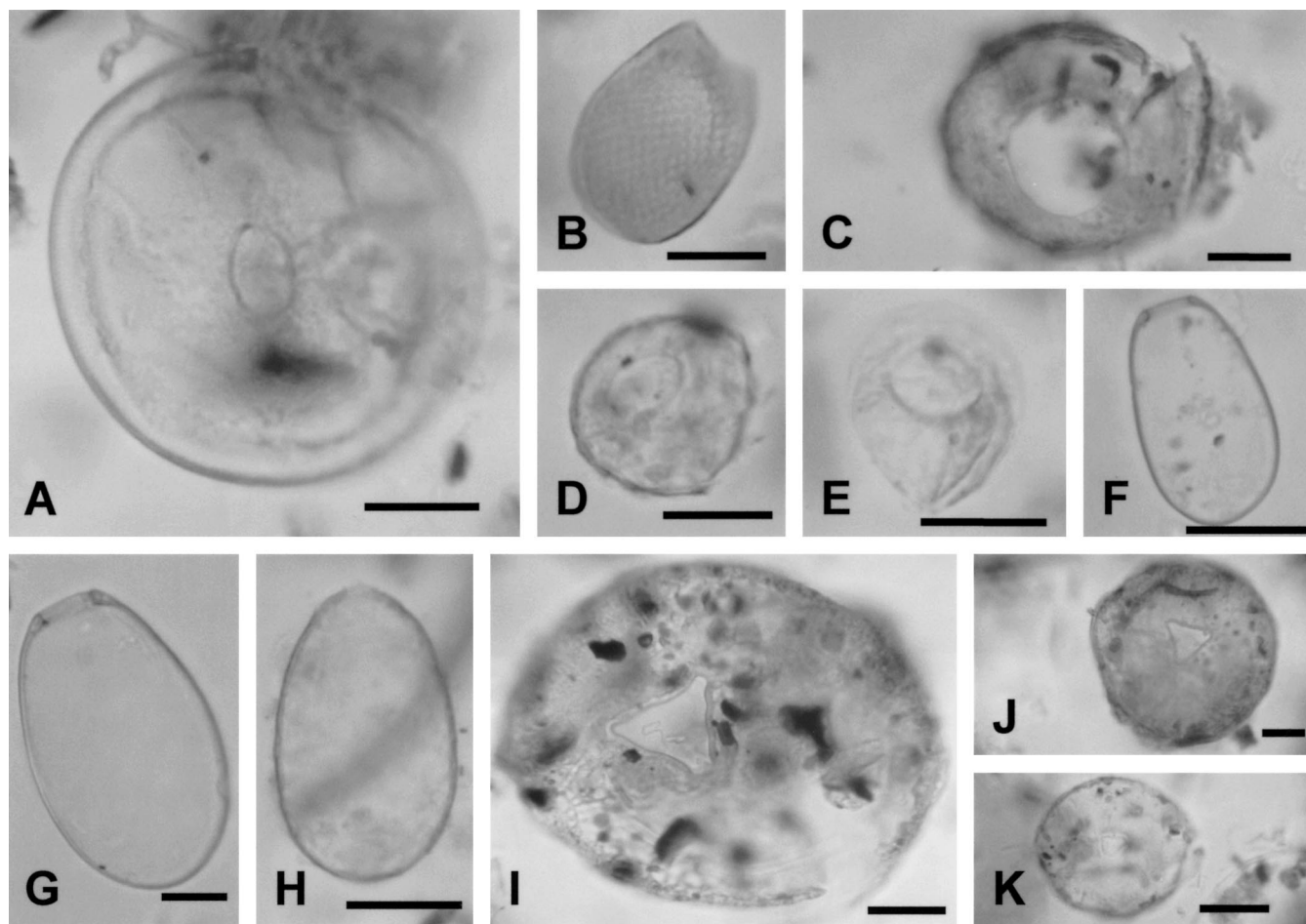


FIGURE 6—Testate amoebae encountered in the peat clasts. A scale bar, equal to 20µm, is shown for each photomicrograph. (A) *Arcella* sp. (B) *Assulina muscorum*. (C-E) *Cyclopyxis arcelloides* type, showing the large amount of morphological variation encountered. (F-G) *Hyalosphenia subflava*, showing the large amount of size variation encountered. (H) *Heleopera sylvatica*. (I-J) *Trigonopyxis arcula*. (K) *Trigonopyxis minuta*.

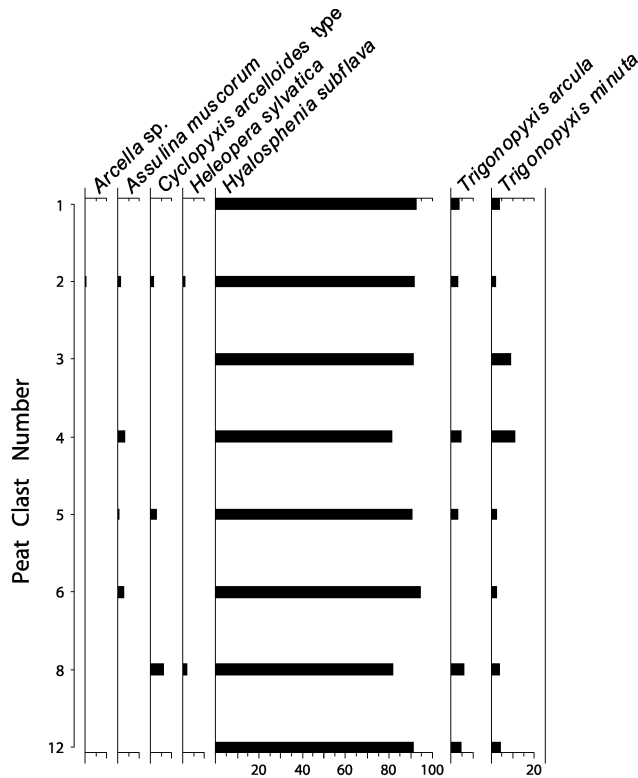


FIGURE 7—Relative abundance of testate amoebae in eight of the peat clasts.

ranges from 20–40% (Charman, 2001; Booth, 2002). Unusually high abundance of *Hyalosphenia subflava* also has been encountered in some Holocene-age peats (Hendon et al., 1999; McGlone and Wilmshurst, 1999). The lack of modern analogues for these assemblages has made quantitative hydrological reconstructions difficult (Charman, 2001). It is unclear whether these unusual amoeba assemblages resulted from differential decay or whether they actually reflect the original living amoeba assemblages. Lousier and Parkinson (1981) found that differential decay of amoeba tests can occur in forest soils. However, they noted that *Hyalosphenia subflava*, the most abundant taxon in the peat clasts, was one of the taxa least resistant to decay. More testate amoeba data are needed from modern and Quaternary peat deposits to assess fully the significance and underlying causes of fossil amoeba assemblages with apparently poor modern analogues.

Local Habitat Reconstruction

The clasts were derived from a peatland that probably contained *Myrica*, *Ilex*, *Lycopodium*, and *Osmunda* ferns (Fig. 3). *Pinus taeda* and/or *Pinus serotina* grew in the overstory or adjacent to the peatland. *Vitis* pollen in many of the peat clasts suggest that grapes were present locally. Although conditions were wet enough to allow the accumulation of peat, fossil testate amoebae indicate that conditions were relatively dry for much of the year.

Regional Paleoclimatic Implications

Pollen records from Florida indicate much drier conditions during the Late Pleistocene than the Holocene (e.g.,

Watts and Hansen, 1988, 1994; Jackson et al., 2000). Drier conditions during the Late Pleistocene in coastal Georgia also are indicated by depositional hiatuses (e.g., Watts, 1971; Booth and Rich, 1998) and suggested by records of dune activity (Ivester et al., 2001). However, long pollen records from Lake Tulane in Florida indicate that the climate of the mid- and late Wisconsinan was extremely dynamic at shorter timescales, and characterized by rapid shifts in the abundance of *Pinus* and *Quercus* pollen (Grimm et al., 1993; Watts and Hansen, 1994). *Pinus* pollen peaks during this time period have been attributed to effective moisture increases, and appear to be correlated with Heinrich events (Grimm et al., 1993; Watts and Hansen, 1994), episodes of glacial advance that triggered massive iceberg discharge into the North Atlantic (Heinrich, 1988; Bond et al., 1992). One of the *Pinus* peaks in Lake Tulane occurs at approximately 31,000–39,000 ^{14}C years B.P., which corresponds to Heinrich event 4 (Grimm, 2001) and the original deposition of the peat clasts on Skidaway Island.

The peat clasts contain the first Wisconsinan-age macrofossil evidence for southern pines outside of the Florida peninsula. *Pinus taeda* and *Pinus serotina* are both currently coastal plain species, and their presence in coastal Georgia 37,000 ^{14}C years ago suggests that the climate was relatively warm, at least for the brief period of time represented by the peat clasts. The modern climate space occupied by these two species defines an area with at least 885 mm of annual precipitation and a mean annual temperature of 12°C to 22°C (Thompson et al., 2000). No sites of similar age north of Florida exist for comparison, and the peat clasts provide only a snapshot of environmental conditions, so the spatial and temporal extent of these environmental conditions is not known. Northern pines (*P. resinosa*, *P. banksiana*) were present in coastal South Carolina and the Piedmont of Georgia between approximately 24,000 and 15,000 years BP (Jackson et al., 2000; Jackson, unpublished data). More data are needed from deposits of similar age in coastal Georgia, as well as sites 37,000 years old in the Carolinas and inland Georgia, to determine where southern pines graded into northern pines during the mid- and late Wisconsinan. The peat clasts only provide a glimpse of the environment and biota through a narrow temporal window. However, a spatially and temporally dense network of similar studies potentially could provide valuable information on patterns of vegetation and climate change in unglaciated Eastern North America during the Pleistocene. Similar networks of snapshots (e.g., packrat middens, alluvial deposits) have contributed substantially to our understanding of Quaternary ecology and climates in other regions (e.g., Betancourt et al., 1990; Jackson and Givens, 1994; Baker et al., 2002).

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REFERENCES

- BAKER, R.G., BETTIS, E.A., III, DENNISTON, R.F., GONZALEZ, L.A., STRICKLAND, L.E., and KRIEG, J.R., 2002, Holocene paleoenvironments in southeastern Minnesota—chasing the prairie-forest ecotone: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 177, p. 103–122.
- BETANCOURT, J.L., VAN DEVENDER, T.R., and MARTIN, P.S., 1990, Packrat middens: the last 40,000 years of biotic change: The University of Arizona Press, Tucson, 467 p.
- BOND, C., HEINRICH, H., BROECKER, W., LABEYRIE, L., McMANUS, J., ANDREWS, J., HUON, S., JANTSCHIK, R., CLASEN, S., SIMET, C., TEDESCO, K., MIECZYSLAWA, K., BONANI, G., and IVY, S., 1992, Evidence for massive discharges of icebergs into the North Atlantic during the last glacial period: *Nature*, v. 360, p. 245–249.
- BOOTH, R.K., 1998, Palynology and environments of deposition of sediments from two barrier islands: St. Catherines Island and Skidaway Island, Georgia, USA: Unpublished M.S. Thesis, Georgia Southern University, Statesboro, 213 p.
- BOOTH, R.K., 2001, Ecology of testate amoebae in two Lake Superior coastal wetlands: Implications for paleoecology and environmental monitoring: *Wetlands*, v. 21, p. 564–576.
- BOOTH, R.K., 2002, Testate amoebae as paleoindicators of surface-moisture changes on Michigan peatlands: Modern ecology and hydrological calibration: *Journal of Paleolimnology*, in press.
- BOOTH, R.K., and RICH, F.J., 1998, Quaternary evolution of the Georgia coastal plain as indicated by palynology, stratigraphy, and age of selected coastal, inland, and marine deposits: *in* Rich, F.J., and Bishop, G.A., eds., *Geology and Natural History of the Okefenokee Swamp and Trial Ridge, Southeastern Georgia—Northern Florida*: Georgia Geological Society Guidebooks, Carrollton, v. 18, p. 78–89.
- BOOTH, R.K., RICH, F.J., and BISHOP, G.A., 1999, Palynology and depositional history of Late Pleistocene and Holocene coastal sediments from St. Catherines Island, Georgia, USA: *Palynology*, v. 23, p. 67–86.
- CHARMAN, D.J., 2001, Biostratigraphic and palaeoenvironmental applications of testate amoebae: *Quaternary Science Reviews* v. 20, p. 1753–1764.
- CHARMAN, D.J., HENDON, D., and WOODLAND, W.A., 2000, The identification of testate amoebae (Protozoa: Rhizopoda) in peats: Quaternary Research Association, Technical Guide No. 9, London, 147 p.
- CHARMAN, D.J. and WARNER, B.G., 1992, Relationship between testate amoebae (Protozoa: Rhizopoda) and microenvironmental parameters on a forested peatland in northeastern Ontario: *Canadian Journal of Zoology*, v. 70, p. 2474–2482.
- CHARMAN, D.J. and WARNER, B.G., 1997, The ecology of testate amoebae (Protozoa: Rhizopoda) in oceanic peatlands in Newfoundland, Canada: Modelling hydrological relationships for paleoenvironmental reconstruction: *Ecoscience*, v. 4, p. 555–562.
- GRIMM, E.C., 2001, Warm wet Heinrich events in Florida: Abstracts of the NOAA CORC ARCHES Heinrich Events Miniconference, Lamont-Doherty Earth Observatory, Palisades, New York, p. 28.
- GRIMM, E.C., JACOBSON, G.L., JR., WATTS, W.A., HANSEN, B.C.S., and MAASCH, K.A., 1993, A 50,000-year record of climate oscillations from Florida and its temporal correlation with the Heinrich events: *Science*, v. 261, p. 198–200.
- HARLOW, W.M., 1947, The identification of the pines of the United States, native and introduced, by needle structure: New York State College of Forestry, Technical Publication No. 32, 57 p.
- HEINRICH, H., 1988, Origin and consequences of cyclic ice rafting in the Northeast Atlantic Ocean during the past 130,000 years: *Quaternary Research*, v. 29, p. 143–152.
- HENDON, D., and CHARMAN, D.J., 1997, The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat: *The Holocene*, v. 7, p. 199–205.
- HENDON, D., CHARMAN, D.J., and KENT, M., 1999, Palaeohydrological records derived from testate amoebae analysis from peatlands in northern England: within-site variability, between-site comparability and palaeoclimatic implications: *The Holocene*, v. 11, p. 127–148.
- HOYT, J.H., and HAILS, J.R., 1974, Pleistocene stratigraphy of southeast Georgia: *in* Oakes, R.Q., and Dubar, J.R., eds., *Post-Miocene Stratigraphy: Central and Southern Atlantic Coastal Plain*: Utah State University Press, Logan, p. 191–203.
- HUSSEY, T.C., 1993, A 20,000-year history of vegetation and climate at Clear Pond, northeastern South Carolina: Unpublished M.S. Thesis, University of Maine, Orono, 59 p.
- IVESTER, A.H., LEIGH, D.S., and GODFREY-SMITH, D.I., 2001, Chronology of inland eolian dunes on the coastal plain of Georgia, USA: *Quaternary Research*, v. 55, p. 293–302.
- JACKSON, S.T., and GIVENS, C.R., 1994, Late Wisconsinan vegetation and environment of the Tunica Hills region, Louisiana/Mississippi: *Quaternary Research*, v. 41, p. 316–325.
- JACKSON, S.T., WEBB, R.S., ANDERSON, K.H., OVERPECK, J.T., WEBB, T., III, WILLIAMS, J.W., and HANSEN, B.C.S., 2000, Vegetation and environment in Eastern North America during the Last Glacial Maximum: *Quaternary Science Reviews*, v. 19, p. 489–508.
- JACKSON, S.T., and WENG, C., 1999, Late Quaternary extinction of a tree species in eastern North America: *Proceedings of the National Academy of Science*, v. 96, p. 13847–13852.
- LOUSIER, J.D., and PARKINSON, D., 1981, The disappearance of empty tests of litter and soil testate amoebae (Testacea, Rhizopoda, Protozoa): *Archiv für Protistenkunde*, v. 124, p. 312–336.
- MCGLOONE, M.S., and WILMSHURST, J.M., 1999, A Holocene record of climate, vegetation change and peat bog development, east Otago, South Island, New Zealand: *Journal of Quaternary Science*, v. 14, p. 239–254.
- MITCHELL, E.A.D., BUTTLER, A.J., and WARNER, B.G., 1999, Ecology of testate amoebae (Protozoa: Rhizopoda) in *Sphagnum* peatlands in the Jura Mountains, Switzerland and France: *Ecoscience* v. 6, p. 565–576.
- RICH, F.J., and PIRKLE, F.L., 1993, Palynology and paleoecology of Reids Bluff: *in* Farrell, K.M., Hoffman, C.W., and Henry, V.J. Jr., eds., *Geomorphology and Facies Relationships of Quaternary Barrier Island Complexes near St. Marys, Georgia*: Georgia Geological Society Guidebooks, Carrollton, v. 13, p. 74–81.
- THOMPSON, R.S., ANDERSON, K.H., and BARTLEIN, P.J., 2000, Atlas of relations between climatic parameters and distributions of important trees and shrubs in North America—introduction and conifers: U.S. Geological Survey Professional Paper 1650-A, 269 p.
- TRAVERSE, A., 1988, *Paleopalynology*: Unwin Hyman, Boston, 600 p.
- WATTS, W.A., 1969, A pollen diagram from Mud Lake, Marion County, north-central Florida: *Geological Society of America Bulletin*, v. 80, p. 631–690.
- WATTS, W.A., 1971, Postglacial and interglacial vegetation history of southern Georgia and central Florida: *Ecology*, v. 53, p. 676–690.
- WATTS, W.A., and HANSEN, B.C.S., 1988, Environments of Florida in the Late Wisconsin and Holocene: *in* Purdy, B., ed., *Wet Site Archeology*: Telford Press, Caldwell, New Jersey, p. 307–323.
- WATTS, W.A., and HANSEN, B.C.S., 1994, Pre-Holocene and Holocene pollen records of vegetation history from the Florida peninsula and their climatic implications: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 109, p. 163–176.
- WEHMILLER, J.F., KRANTZ, D.E., SIMMONS, K., LUDWIG, K.R., MARKEWICH, H.W., RICH, F.J., and HULBERT, R.C., JR., 1997, U.S. Atlantic coastal plain late Quaternary geochronology: TIMS U-series coral dates continue to indicate 80 kyr sea level at or above present: *Geological Society of America Abstracts with Programs*, v. 29, 6, p. A-346.
- WOODLAND, W.A., CHARMAN, D.J., and SIMS, P.C., 1998, Quantitative estimates of water tables and soil moisture in Holocene peatlands from testate amoebae: *The Holocene* v. 8, p. 261–273.

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