I. ABSTRACT

Seventeen pollen-bearing samples from sites in South Carolina, Georgia, and Florida were analyzed for their pollen content. The samples range in age from Late Pliocene to Holocene. The initial objective of the study was to use the samples to help define the age of the physiographic feature known as Trail Ridge. All samples were marine sediments, and many were from marine mollusk-dominated strata. Pollen of Pinus and Quercus were abundant in all samples; Taxodium was abundant in about half of them. Carya, Liquidambar, Compositae, Gramineae, and Chenopodiaceae-Amaranthaceae were present as accessory taxa. Dinoflagellate cysts, microforams, and pyrite were present, or abundant, in several of the samples. The only regionally extinct taxa were Pterocarya and Sciadopitys (?), and these were not abundant in any samples. The bio- and chronostratigraphic positions of the samples were established using mollusk, ostracode, and vertebrate fossil data, and radiocarbon dates where possible. In spite of the fact that the samples represent a considerable span of time (back to 2.2 million years) the pollen floras are very uniform. There is, for all practical purposes, no way of distinguishing the sampled Pliocene strata from the Pleistocene or Holocene units on the basis of pollen assemblages. The pollen floras seem to have been strongly influenced by taphonomic factors, such as sorting by wind, currents, and waves. Although this has nearly eliminated their value as biostratigraphic indicators, the pollen assemblages are useful indicators of a distinct kind of depositional setting. The taphonomic interpretation is corroborated by data derived from molluscan and vertebrate paleoecology.

II. INTRODUCTION

The research represented in this paper was associated with a long-standing project whose purpose it is to delineate the ages and environments of deposition of coastal sand ridges in the southeastern
United States; most of those ridges are generally acknowledged to be of Pleistocene age. Geologists at Georgia Southern University, the E. I. du Pont de Nemours and Co. Florida Plant, and the U. S. Geological Survey have focused a great deal of attention on Trail Ridge, in particular.

Trail Ridge is a prominent coastal plain sand body, which is believed to represent a stranded shoreline complex that formed in association with a very early Pleistocene or Pliocene high-stand of the Atlantic Ocean (Figure 1). Trail Ridge contains large, extensive economic deposits of heavy mineral sands, and so constitutes an important source of industrial minerals. It is principally this fact that draws the attention of most geologists to Trail Ridge, but as a land form it is also the object of scientific interest. Many papers have been written about the physical characteristics of Trail Ridge, its age, and economic significance (e.g., Pirkle and Yoho, 1970; Pirkle, 1972; Pirkle, 1975; Pirkle, 1984). As a result of the efforts to delineate the age of Trail Ridge an investigation into the palynological characteristics of Late Cenozoic strata in South Carolina, Georgia, and Florida was begun. Through the process of comparing pollen assemblages from Trail Ridge to deposits that are known to be Holocene, Pleistocene, and Pliocene in age, discoveries have been made that have helped to demonstrate why Trail Ridge, and other deposits of similar age and origin are so difficult to date palynologically.

If we use Trail Ridge as a point of departure, lithostratigraphically, biostratigraphically, and temporally, one can see that a variety of sedimentary units lie in close proximity to it. For this paper Huddleston’s (1988) stratigraphic nomenclature of the Miocene through Holocene lithostratigraphic units of the Georgia Coastal Plain was used. Furthermore, Huddleston’s data were projected north into South Carolina, and south into Florida for the purpose of establishing nomenclatural and stratigraphic continuity within this paper. To the extent that it is possible, stratigraphic interpretations from geologists working in Florida (Scott, 1988; Webb et al., 1989; Jones et al., 1991; Hulbert et al., 1995) were used to complement Huddleston’s work.

III. AGES OF STRATA

In the broadest interpretation of strata associated geographically with Trail Ridge, there are two classes of sedimentary deposits: 1) older, mostly consolidated, marine strata, which display fair lateral continuity, and which developed as sea level and shorelines oscillated during the Miocene and Pliocene (e.g., the Hawthorn Group); and 2) younger, largely unconsolidated, discontinuous bodies of sand and clay, which lie eastward of Trail Ridge and comprise a series of beach ridge/shoreline complexes that developed during the Pleistocene and Holocene (Figure 2).

Trail Ridge clearly lies on top of Miocene units, and apparently overlies Pliocene formations as well. The Principle of Superposition of Strata makes that intuitively obvious even if actual outcrops with lithologic contacts are rare or contacts are known only from the subsurface. Trail Ridge has a more tenuous stratigraphic relationship with the Pleistocene beach ridges, however, because one can demonstrate neither superposition of strata nor lateral continuity to establish concrete depositional or temporal relationships. It is logical to believe that Trail Ridge is older than, for example, the Penholoway Terrace Barrier (Figure 2; Hoyt and Hails, 1969). Trail Ridge lies furthest inland, and at the highest elevation, and so must have been deposited earlier than any of the other shorelines. That, however, is the most one can say with confidence. In order to increase the biostratigraphic resolution of the age of Trail Ridge, palynological analyses of a wide variety of samples from strata closely associated with Trail Ridge were undertaken for this study.

Rich (1985) published the results of pollen analyses of two cores of lignite from beneath the sands of Trail Ridge near Starke, Clay County, Florida (Figure 1). After comparing the pollen assemblages to those derived from other locations in the southeastern United States, it was concluded that the lignite-producing swamp and, hence, Trail Ridge could not be of Miocene age, but no further delineation of age could be made. Further analysis of the stratigraphic and sedimentological relationships between Trail Ridge sands and
Figure 1. Location map of physiographic features and sample localities.
Figure 2. Generalized stratigraphic cross-section of strata lying beneath, and laterally adjacent to Trail Ridge (from Huddleston, 1988).

Trail Ridge lignite led Force and Rich (1989) to conclude that the deposits were indeed contemporaneous (representing dune sands, which gradually invaded and buried a freshwater swamp), but they found no evidence to constrain the age of the deposit with more precision than Rich did in 1985.

**Pliocene strata** – Inasmuch as the Trail Ridge pollen produced no clear indication of age (no extinct or regionally extinct taxa), a search was begun for samples which, based upon other criteria, were known to be of Pliocene age. It was hoped that something distinctive might be found in Pliocene samples from various locations that would serve as a common and distinctive identifier of Pliocene deposits in the southeastern United States. Tom Ager (U.S. Geological Survey, pers. comm., 1991) suggested that *Pterocarya* and *Sciadopitys* might be found in Pliocene strata, so those two genera were particularly sought in pollen preparations.

Samples of known Pliocene age were collected from four localities (Figure 1) and are as follows: 1) sediment in-filling of a large *Ecphora quadracostata* shell, collected from the Raysor Formation, Martin-Marietta limestone quarry, Berkeley County, South Carolina; 2) oyster in-filling from the Raysor Formation, Martin-Marietta quarry; 3) sediment in-filling from the shell of the oyster *Ostrea disparilis*, from the Raysor Formation, Stilson, Bulloch County, Georgia; 4) two samples of Macasphalt Shell Pit (also known as the APAC Shell Pit) matrix, Bed 4, Tamiami Formation, Sarasota County, Florida; 5) matrix from around a fossil camel jaw (*Hemiauchenia blancoensis*), Macasphalt Shell Pit; and 6) four samples from the Quality Aggregates Shell Pit (also known as the Richardson Road Shell Pit) in Sarasota County, Florida.

According to Huddleston (1988) the Raysor Formation immediately underlies the Cypresshead Formation (shown in Figure 2) where the two units occur together. Ward and Huddleston (1988) state that the Raysor "is a facies equivalent of the shelly, quartzose sands of the Yorktown Formation in northeastern South Carolina and southeastern North Carolina." Planktonic foraminifera indicate a late Pliocene (early Piacenzian) age for the Raysor Formation (Huddleston, 1988).

Deposits from the shell pits near Sarasota, Florida, have been ascribed a variety of ages, something which Jones *et al.* (1991) point out in their paper. Part of the problem of dating the shell beds stems from the fact that they are laterally discontinuous, and there are many different shell accumulations along the Gulf coast of Florida. Petuch (1982) has described 11 stratig-
Figure 3. Formational correlations in selected areas of the Georgia and Florida coastal plains (from Scott, 1988).

<table>
<thead>
<tr>
<th>SERIES</th>
<th>EASTERN GEORGIA</th>
<th>NORTHERN FLORIDA</th>
<th>SOUTHERN FLORIDA</th>
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<tr>
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<td>CYPRESSHEAD FORMATION</td>
<td>CYPRESSHEAD FORMATION</td>
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<td></td>
<td></td>
<td>REWORKED SEDIMENT</td>
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<tr>
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<td>COOSAW-HATCHIE FORMATION</td>
<td>HAWTHORN GROUP</td>
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<td>MARKS HEAD FORMATION</td>
<td>HAWTHORN GROUP</td>
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<td></td>
<td>PARACHUCLA FORMATION</td>
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Most of the shell beds that make up the Pinecrest Beds are incredibly fossiliferous, bearing well-preserved individuals which, according to Jones et al. (1991), represent 200 species of bivalves, 600 species of gastropods, and perhaps as many as 100 species of vertebrates, including 19 taxa of land mammals. Unit 4 sediments differ from the rest of the Pinecrest beds in that the fine-grained, organic-rich sands, which constitute Unit 4, contain predominantly a brackish (not normal marine) molluscan and ostracode fauna as well as land and freshwater vertebrates and gastropods (Jones et al., 1991; Ward, 1992). Peculiar among the many vertebrate species in the Pinecrest Beds are nearly 40% representing birds; one horizon discovered at the Quality Aggregates Shell Pit, near the Macasphalt locality, contains an unusual concentration of cormorant skeletons.
(Phalacrocorax sp.; Emslie and Morgan, 1994). The terrestrial mammals offer the best vertebrate biochronology for the Macasphalt site (Morgan and Hulbert, in press). These include characteristic taxa of the Late Blancan North American Land Mammal Age (NALMA; Figure 4), such as Nanippus peninsulatus (a three-toed
horse), *Megalonyx leptostomus* (a ground sloth), *Neocoeurus dichroplax* (a capybara), *Geomyso propinetis* (a pocket gopher), and *Sigmodon medius* (a cotton rat).

**Earliest Pleistocene Strata** – The earliest Pleistocene strata dealt with here are from the Desoto Shell Pit, Desoto County, Florida, and the Leisey Shell Pit, near Tampa, Florida, (Figure 1). The Desoto deposit accumulated during the latest Pliocene/earliest Pleistocene (Figure 4) and is associated with the Caloosahatchee and Bermont formations (Willard et al., 1993).

The Leisey Shell Pit is another spectacular accumulation of marine invertebrate shells, terrestrial and aquatic vertebrate remains, and plant fossils (Hulbert et al., 1995) which come from the Bermont and Fort Thompson formations. Nearly 30,000 catalogued vertebrate specimens alone have been recovered, and represent over 100 species. Hulbert et al. (1995) present detailed and convincing arguments based upon vertebrate biochronology, strontium isotope chronology, and magnetostratigraphy to constrain the age of the Leisey deposits to the early Pleistocene (Figure 4). Chronologically useful mammalian taxa present at Leisey include *Mammathus hagyi* (a primitive mammoth), *Smilodon gracilis* (a saber-toothed cat), *Canis edwardsii* (a small wolf), *Canis arnbrusteri* (a larger wolf), and *Sigmodon libitinus* (a cotton rat) (Hulbert and Morgan, 1987; Morgan and Hulbert, 1995). The two Leisey samples described here came from excavations identified as pits 1A and 3A (see Morgan and Hulbert, 1995, Figure 1) and consist of fine-grained sandy matrix preserved inside mollusk shells.

**Late Pleistocene Strata** – A large number of late Pleistocene samples have been analyzed from various locations on the Atlantic Coastal Plain in Georgia and Florida. A locality, which has recently received attention, and which lies near the town of St. Marys, Georgia, is Bells Bluff. The fossiliferous shoreline strata of Bells Bluff include a shell-rich horizon, which lies at sea level. Rich and Pirkle (1993) reported that shells of *Anadara* sp. from Bells Bluff were radiocarbon dated at 37,395 ± 2155 years BP. The samples analyzed for this project consist of sandy shelly sediment, which was washed from within two large cockles (*Dinocardium* sp.) that were collected along with the *Anadara*.

**Holocene Strata** – Two Holocene samples were collected on St. Catherines Island, immediately off the Georgia coast (Figure 1). The seaward side of St. Catherines Island has well-preserved deposits of peat and shells, which have been exposed by erosion in recent years. Among the shell beds is a bed of oysters (*Crassostrea* sp.) exposed at a site known as South Beach. Shells, and the blue mud that encloses them, were collected and sampled for pollen analysis. Shells of clams and mussels, and peat from a nearby location have been dated, and suggest that the oyster bed accumulated about 600 years BP.

The second of the Holocene samples, also from St. Catherines Island, was recovered from a core taken near Cracker Tom Hammock, inland of the oyster bed. The sample consisted of *Crassostrea* shells in a sandy clay matrix, and came from a depth of 1.9-2.2 meters. Shells from the deposit have been radiocarbon dated at 3202 ± 73 years BP.

**IV. PROCESSING TECHNIQUE**

Most of the sediments were sandy carbonate-rich muds; the Leisey, Desoto, Macasphalt, Raysor, Bells Bluff *Dinocardium*, and Cracker Tom samples consisted of mollusk shell-dominated sandy clays. One Desoto sample included matrix from a tortoise shell fossil. The South Beach *Crassostrea* and Bells Bluff clay samples were both smooth, blue, plastic, carbonate-rich clays. The shell pit samples were carefully selected from the plastic bags they had been stored in, and were scraped and washed thoroughly so as to remove surface contaminants. Where large shells were found (e.g., planispiral gastropods 1-2 cm across) the shell contents were washed out and processed. In the case of the *Ecphora* and *Dinocardium* in-fillings the entire contents of the shells were washed from the specimens, small shell fragments were sieved out, and the fine-grained residues were further treated. Each of the samples
was placed first in 10% HCl to remove carbonates. Most of them reacted vigorously, and the shell pit samples all gave off a pronounced odor of petroleum. Samples that were clearly organic-rich were then mixed with 10% KOH and placed in a boiling water bath for 10 minutes to dissolve soluble organic substances. After thorough washing to remove the soluble organic fractions, the residues were placed in concentrated HF to remove silicates. After remaining in the HF for several days (in most cases), processing was terminated and the residues were mixed with a 50:50 blend of water and glycerine jelly. Several microscope slides were prepared for each of the 17 samples and a minimum of 200 identifiable grains was counted for each sample. Counts were made by observing the slides with a Jena research photomicroscope.

V. RESULTS OF THE ANALYSES

Gross characteristics of the acid-insoluble residues were much the same from one deposit to another. Organic fragments were usually small, and pine pollen (Pinus spp.), which were invariably present, were oftentimes broken in halves. Pyrite was typically present, either as minute cubes or as tiny framboinds. Dinoflagellate cysts, especially the round, spiny, chororate type (Plate 1) were usually present, and sometimes dominated the samples. Dinoflagellates were particularly common in the Leisey shell pit samples, as well as the Ephora in-filling from the Raysor Formation, and the Macasphalt samples. Microforams were present as well; these minute, pseudochitinous internal test linings were described by Cohen and Gruber (1968) and are common in pollen preparations derived from sediments that have experienced marine influence.

The dinoflagellates and microforams clearly are contributions of the marine environment and their uniformity of expression is not surprising. Although pyrite may be generated within sediments derived from a variety of environments, the abundance of pyrite also seems to be a reliable indicator of marine deposition (see Blatt et al., 1980, for a related discussion). The pollen from land plants also was represented uniformly, however. Pinus and Quercus (oak; Plate 1) tended to dominate all samples, ranging to as high as 45-60% for Pinus and 25-30% for Quercus (Figure 5). Taxodium (cypress) was also abundant in about half the samples (from the Richardson Road locality, in particular), with relative abundances on the order of 6.39%.

Anyone who has worked much in the southeastern United States is familiar with the dominance of Pinus, Quercus, and Taxodium in most pollen assemblages (e.g., Watts, 1969, 1971; Cronin et al., 1981). Willard et al. (1993) also mention this fact in a paper wherein they describe the pollen floras from three Pliocene-Pleistocene sites in southwestern Florida. It is the pollen that are the accessories to these major constituents, which seem to bear more careful consideration, however. Carya (hickory/pecan) and Liquidambar (sweet gum) were typically present in amounts of only a percent or two, but they were usually present in the samples analyzed for the current study [Willard et al. (1993) also recorded Carya in their work]. Other woody taxa, including Alnus (alder), Ulmus (elm), and Nyssa (black gum) accompanied these trees in variable amounts. These were much less common, however. Herbaceous pollen, which were almost invariably present in the samples, include Gramineae (grasses) and Compositae (asters and their kin), and Chenopodiaceae/Amaranthaceae (chenoams); the Leisey 3A sample had nearly 30% of the latter, while the Desoto tortoise sample had 46%, a very high percentage. Some samples also contained freshwater algal remains such as Botryococcus colonies or, more rarely, Pediastrum.

Among the pollen assemblages derived from samples known to be of Pliocene age, there were none that, based upon the occurrence of extinct species or otherwise

PLATE 1
Selected pollen found various sample sites: 1) Pinus; 2) Taxodium; 3) Quercus; 4) Carya; 5) Liquidambar; 6) Pterocarya; 7) Sciadopitys; 8) dinoflagellate cyst. All figures are the same magnification; the bars represent 10 microns. Figures 1-5 were fresh pollen, figures 6-8 were fossilized.
PLATE 1
unusual taxa, were clearly of Pliocene age. Occasionally a grain of *Pterocarya* (5 of 11 Pliocene samples), or what appears to be *Sciadopitys* (2 of 11 Pliocene samples; Plate 1) was found in samples that were by other means known to be Pliocene, but neither genus was abundant and their occurrences were not consistent from one Pliocene sample to another (Figure 5). Ager (personal communication, 1995) has noted that only a few grains of *Pterocarya*, in particular, may be associated with deposits which have numerous leaf and seed fossils of the genus (e.g., the Late Miocene Brandywine deposit; McCartan et al., 1990), so modest amounts of the pollen may not reflect the actual abundance of the plants near the site of sediment accumulation. This is also true of the related genus *Carya* whose plants are extremely abundant in the southeastern United States (particularly the pecan, *Carya illinoensis*), yet whose pollen are not especially common in sediments. The actual significance of just a few grains of *Pterocarya* and *Sciadopitys* pollen in Pliocene strata needs to be better defined.

VI. INTERPRETATION OF THE DATA

What was discovered among the samples that were observed is uniformity, both stratigraphically and geographically. The reader should recall that the intention of this study was to identify an assemblage of pollen, spores, or other palynomorphs that could be used to distinguish Pliocene deposits from Pleistocene deposits in the southeastern United States. Many authors, including Traverse (1988) have shown that pollen and spore assemblages constitute very valuable and sensitive biostratigraphic markers and usually can be relied upon to provide excellent biostratigraphic information. In the case of the current study, however, biostratigraphy seems to have lost some of its utility. Among other things, the apparent lack of regionally extinct taxa in Trail Ridge sediments has prevented assigning an age to that deposit based upon biostratigraphic evidence. The problem remains in that, after surveying 17 samples representing similar nearshore depositional environments from Pliocene, Pleistocene, and Holocene deposits from the southeastern United States, all that is found is a pollen flora which appears again and again. One only rarely finds an exotic grain, and even then its history is in question because one cannot be certain that it has not been reworked. Were it not for the presence of two *Pterocarya* and five probable *Sciadopitys* grains in the Raysor Formation *Echophora* in-filling, its residue would be nearly identical to the Quaternary clam and oyster-dominated sediments from Reids Bluff and St. Catherines Island. The presence of these regionally extinct genera should not be taken in and of itself as sound evidence of a Pliocene age, however. An abundant source of easily erodable sediments of pre-Pliocene age exists in the southeastern states, and pollen derived from those older strata could be readily reworked into younger material.

Even if the problem of resolving the age of Trail Ridge remains, something else that is of palynological interest has been discovered. What was identified is not a pollen flora that has much biostratigraphic value, but one that has taphonomic and environmental significance. It is a product of mixing of marine and terrestrial elements on a microscopic level. The pollen of regionally common terrestrial plants, mixed with the remains of freshwater algae and marine microfossils appear as a distinct assemblage. The fact that the pine pollen, in particular, are usually broken is suggestive of long distance transport in water, probably including abrasion and mechanical weathering by waves. The recognition that

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Figure 5. Relative abundances of pollen and spores from the samples included in this study; the zero value lies at the base line for each taxon and abundance increases to the right. This graph shows only those taxa with abundances of 1% or less in all samples. The top ten rows of specimens came from sites known to be of Pliocene age. Richardson Rd. = Richardson Road locality; Bells Bluff *Dino.* 89 and 91 = *Dinocardium* in-fillings collected in 1989 and 1991, respectively; St. Cath. S. Beach = St. Catherines Island South Beach sample, and St. Cath. C. Tom = St. Catherines Island Cracker Tom Hammock sample.
<table>
<thead>
<tr>
<th>Location</th>
<th>Acer</th>
<th>Betula</th>
<th>Cephalanthus</th>
<th>Cyrilla</th>
<th>Ericaceae</th>
<th>Fagus</th>
<th>Fraxinus</th>
<th>Gordonia</th>
<th>Ilex</th>
<th>Nymphoides</th>
<th>Osmunda</th>
<th>Ostrya/Carpinus</th>
<th>Palmae</th>
<th>Polygonum</th>
<th>Sabatia</th>
<th>Sparganium</th>
<th>Umbelliferae</th>
<th>Vitis</th>
<th>Pterocarya</th>
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<tr>
<td>Raysor Fm.,</td>
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</table>
Figure 5, cont. Relative abundances of pollen and spores which, if present, constitute as much as 5% or 10% of the total in all samples.
**Figure 5, cont.** Relative abundances of pollen and spores which, if present, constitute as much as 20%, 40%, 50%, or 80% of the total in all samples.
the deposits contain a blend of marine or brackish and freshwater or terrestrial fossils comes quite independently of the results of work performed by Richard Hulbert, a vertebrate paleontologist who has worked on all of the mentioned Florida localities. In a 1987 paper, wherein Hulbert describes a new species of the horse *Cormohipparion*, he presents the following description of the environment of deposition of the Macasphalt Shell Pit, Unit 4. It was "low energy shallow brackish water, rich in fluvial-derived organic sediments..." The abundant siren, frog, and aquatic snake vertebrae are frequently complete, suggesting minimal transport, as do the numerous complete elements of the aquatic avifauna." Hulbert's environmental interpretation can be generally applied to the Leisey, St. Catherines Island, Desoto, and Bells Bluff localities, though there are characteristics of each site that make them unique. The Raysor Formation and Leisey samples probably represent more open, normal marine deposits, but the fact that they accumulated under coastal conditions is the most important consideration.

The realization that certain pollen assemblages reflect sedimentary facies is not a new one, certainly. Wilson (1971) illustrated the relationship between distance from shore and relative abundances of different species of pollen as he described depositional environments for the Carboniferous of Oklahoma. Brush (1988), Brush and Brush (1994), and Rich and Pirkle (1994) have similarly studied the distributions of pollen taxa along the Atlantic seaboard of the United States. What makes the current study interesting, I believe, is the fact that, by separate means, employing very different kinds of fossils, a vertebrate paleontologist and a palynologist have come to the same conclusion regarding the environments of deposition of Pliocene strata in the southeastern United States. It might be argued that the same interpretations could be drawn from the abundant mollusk or ostracode remains, and that those fossils, furthermore, also provide a high degree of age resolution. This is certainly true, where the invertebrate remains are abundant. The abundance of invertebrate remains, such as are present at the Macasphalt, Leisey, Stilson, or Martin-Marietta sites is highly unusual, however. One is most likely to find a few scattered shell fragments, and a great deal of sediment that has no visible fossil contents. Under those circumstances, knowing that there is, potentially, a useful assemblage of pollen that can be used to define environment of deposition, one can proceed with paleoenvironmental interpretations with a fair degree of confidence. There is likely to be a very strong taphonomic overprint in such strata; the principle reasons why Pliocene sediments cannot be distinguished from Early or Late Pleistocene, or Holocene strata seems to be that, 1) the vegetation has remained stable for a long time, with the constituent species being affected little or none by the well-known periods of Pleistocene climatic cooling and 2) sorting by waves, currents, and, probably wind have lead to the preferential near-shore deposition of a distinct assemblage of taxa.

VII. ACKNOWLEDGMENTS

This project was supported in part by E. I. DuPont de Nemours and Co. Trail Ridge Plant. Dr. Fred Pirkle, Senior Exploration Geologist is gratefully acknowledged for having assisted with this research. Mr. Royce Hayes, superintendent of St. Catherines Island is also acknowledged for having allowed us to collect samples there; Dr. Gale Bishop kindly provided the oyster shell sample, which he collected at Cracker Tom Hammock. ITT-Rayonier is similarly acknowledged for having allowed us access to the Bells Bluff locality on a number of occasions. Drs. Richard Hulbert and Steven Emsley provided the samples from the Macasphalt, Leisey, and Richardson Road localities, and Hulbert provided much useful information for the text. Financial support was provided by Georgia Southern University, which helped to cover production and publication costs.

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