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HISTORICAL BIOGEOGRAPHY OF PRESENT-DAY FLORIDA

WILFRED T. NEILL¹

SYNOPSIS: Numerous Floridian plants and animals have geographic ranges which reflect both environmental conditions of today and geologic and climatic events of the past, especially those of the Pleistocene. Seven biogeographic areas are recognized for the state, and the associated faunas and floras are described.

INTRODUCTION

The present paper is concerned with patterns of animal and plant distribution in Florida, and the ways in which these patterns may have come about. The terminology employed should be clear in most cases, but certain usages should be defined. Thus, by "race" I mean "subspecies," although the terms are not synonymous in some fields. The word "Pleistocene" should also be explained. Geologists no longer recognize a Recent epoch; to them the Pleistocene has not ended (Flint, 1947; Hibbard, 1949; Ray, 1949). However, from a zoological point of view, it is desirable to distinguish between the very last part of post-Pliocene time, characterized by a modern fauna, and the preceding part when elephants, giant bison, etc. were present in Florida. The term "recent" (with a lowercase "r") is used in an informal or local sense to designate these last millenia. Pleistocene and recent are thus distinguished faunistically. To some, "endemic" means "having arisen in the area it now occupies;" to others it means "limited to a given area," and I have used the word in this latter sense. For convenience, the trinomial has been omitted from many scientific names; and for readability, literature references in some cases have been placed at the end of the paragraph to which they relate, rather than scattered throughout the sentences. Finally, my comments on the ranges of flying organisms, unless otherwise stated, refer only to breeding ranges and not to areas covered by migrations or other flights.

Every organism is confined to an area where its special environmental requirements are met. However, in order to explain present distribution patterns, one must consider not only the environmental conditions that prevail today, but also the different ones that obtained

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not long ago, geologically speaking. As past conditions cannot be studied directly, historical biogeography must draw inferences from paleontological, climatological, and geological data as well as from the known facts of present-day animal and plant distribution.

The historical approach to biogeography is not the only one; there is also the ecological (Hesse, *et al.*, 1937). The latter is outside the scope of the present paper. For information concerning the present natural features and ecology of Florida, see Alexander (1953), Carr (1940), Collins and Howard (1928), Cooke (1939), Davis (1940, 1943), Dice (1943), Fenneman (1938), Ferguson, *et al.*, (1947), Harshberger (1914), Henderson (1939), Hubbell, *et al.*, (1956), Kurz, (1928, 1942), Laessle (1942), Mulvania (1931), Odum (1953), Sellards (1910, 1912), Wright and Wright (1932), and especially Harper (1914, 1921, 1927). Climatic data are provided by Mitchell and Ensign (1928), Thornthwaite (1931), U.S. Department of Agriculture (1941), Visser (1954), and Ward and Brooks (1936).

At one time the peculiarities of the Florida biota were explained simply as a direct result of the geographic position of the state. It was customary to say that Florida pointed southward, carrying a temperate biota toward the tropics; that the aforesaid peculiarities were adaptations to a subtropical environment. A good bit of raciation in southern Florida may actually reflect adjustment to subtropical habitats, abetted in some cases by insulation. Thus, on the Keys, in the Everglades, or elsewhere in southern Florida, there are local races of many widespread species, including the short-tailed shrew (*Blarina brevicauda*), the eastern mole (*Scalopus aquaticus*), the raccoon (*Procyon lotor*), the mink (*Mustela vison*), the gray squirrel (*Sciurus carolinensis*), the fox squirrel (*S. niger*), the rice rat (*Oryzomys palustris*), the cotton rat (*Sigmodon hispidus*), the white-tailed deer (*Odocoileus virginianus*), the red-shouldered hawk (*Buteo lineatus*), the red-bellied woodpecker (*Centurus carolinus*), the white-eyed vireo (*Vireo griseus*), the redwing (*Agelaius phoeniceus*), the corn snake (*Elaphe guttata*), the rat snake (*E. obsoleta*), and many others (Neill, 1949; Sherman, 1937, 1952; Sprunt, 1954).

Some widespread stocks occur throughout much of Florida without evident modification therein. Examples are the eastern hognose snake (*Heterodon platyrhinos*), the coachwhip (*Masticophis flagellum*), the six-lined racerunner (*Cnemidophorus sexlineatus*), the southeastern five-lined skink (*Eumeces inexpectatus*), the common musk turtle (*Sternotherus odoratus*), the eastern spadefoot (*Scaphiopus holbrookii*), and numerous birds (Carr and Goin, 1955; Sprunt, 1954). Indeed,

space will not permit discussion of origins in areas remote from Florida beyond the comment that some animal and plant groups may have originated in the southern Appalachians (Adams, 1902; Hobbs, 1942; Ortmann, 1902), and that, among ectotherms, many lines of descent trace back toward the southwestern United States and northern Mexico (Blanchard, 1921; Hobbs, 1942; Neill, 1949; Ruthven, 1908). Suffice it to say that many widespread stocks have reached Florida; that some of them have undergone riation in the southern part of the state, perhaps as a result of the subtropical conditions that prevail there.

However, adjustment to the demands of a subtropical environment will not explain the generic distinctness of many central Florida endemics, or the presence of essentially northern or upland plants and animals in isolated colonies along the panhandle of the state. One must search for other factors that may have brought about or modified patterns of distribution in Florida.

GLACIAL LOWERING OF TEMPERATURE

The Pleistocene was characterized by fluctuations of climate. At least four times in that epoch great ice sheets formed in both hemispheres. There is still argument as to whether the glaciers were the cause of, or the result of, a lowering of temperature (Landsberg, 1949). At any rate, glacial times in North America saw a fairly widespread chilling. "Over the world the temperature averaged 7 to 14 degrees colder [than at present]" (Field, 1955, p. 86). The presence of ice sheets up to 10,000 feet thick, covering as much as a third of the northern hemisphere and a considerable portion of the southern, drastically affected wind currents and the distribution of rainfall; and because vast quantities of water were impounded in the ice, sea level fell as the glaciers advanced, rose as they retreated. To further complicate matters, the advances and retreats were not smooth but progressed by fits and starts, with occasional reversals of direction. There were, for example, at least twelve advances and retreats of the Wisconsin ice sheet; and environmental conditions must have fluctuated accordingly (Sears, 1948). Pollen profiles from bogs often reveal marked changes in floral composition, reflecting climatic variations. In one bog as many as eight climatic changes have been detected, correlated with fluctuations of the Wisconsin ice (*idem*).

Nevertheless, Florida was comparatively remote from the actual glaciers, and one may ask whether a lowering of temperature was evident so far south even during peaks of glaciation. Palynological analysis of a boring from Marion County, Florida, revealed pollen of fir

and spruce in a Pleistocene stratum (Davis, 1946). Pollen of cold-weather plants, such as fir, Canadian spruce, larch, and arborvitae, have been recovered from a number of Pleistocene localities between western Florida and eastern Texas, in some cases with cold-water mollusks (Potsger and Tharp, 1943, 1947, 1954). It is now well established that boreal genera and species extended their ranges far south during glacial times (Potsger and Tharp, 1954). Some of the range extensions appear to reflect the last or Wisconsin glaciation. Thus, a pollen profile from Lake Singletary, in the coastal plain of North Carolina, included a stratum with fir, spruce, and pine, but almost no broad-leaved trees; and this stratum, indicative of cold weather, could be correlated with the Mankato advance of the Wisconsin ice (Frey, 1951). Some Lake Singletary radiocarbon dates are provided by Johnson (1951).

Subarctic Foraminifera were present in a submarine core collected from the Gulf of Mexico. In this core there was a gradual progression from the modern, subtropical Foraminifera at the top to the subarctic ones farther down, implying that the waters of the Gulf were relatively cold during the last glaciation (Trask, *et al.*, 1947). A core from the Caribbean yielded cold-weather Foraminifera, some regarded as arctic; they were present at several levels (Phleger, 1948). Cold-water diatoms have been found at several localities in Florida in deposits underlain by the Pamlico formation (Gunter and Ponton, 1933; Hanna, 1933). As the Pamlico is no older than the Sangamon or last interglacial period (Cooke, 1939, 1945), an overlying stratum with cold-water diatoms should be of Wisconsin age.

Near St. Petersburg, Florida, remains of the eastern porcupine (*Erethizon dorsatum*) occur in a late Pleistocene stratum, along with those of a lemming-mouse (*Synaptomys australis*) (Sherman, 1952; Simpson, 1929). By historic times the porcupine had retreated a thousand miles northward; and the extant *Synaptomys*, at least, are boreal (Anthony, 1928). The muskrat (*Ondatra zibethica*) occurred in northern Florida during the Pleistocene (Lawrence, 1942), although today it is lacking from the state as well as from southern Georgia and southern Alabama. A muskox reached Florida in the Pleistocene, and one of the mammoth elephants known from this state is thought to be a cold-weather species (Potsger and Tharp, 1954).² A Pleistocene elk (*Cervus* species) has been reported from the Melbourne formation, but its specific identity is uncertain (Gazin, 1950). Within historic

² The muskox is not mentioned by other authors dealing with the Florida Pleistocene.

times the American elk (*C. canadensis*) ranged southward into the uplands of South Carolina (Logan, 1859). A fox (*Vulpes palmaria*), also from the Melbourne formation, was "very close to, if not identical with the [modern] red fox" (Sellards, 1916, p. 152). The latter (*V. fulva*) now ranges southward only into northern Georgia and Alabama (Hamilton, 1943).

LOWER TEMPERATURE OR HIGHER RAINFALL?

As noted, pollen of fir and spruce have been recovered from a Pleistocene stratum in central Florida. However, this does not necessarily imply a period of extremely cold weather in the peninsula. The studies of Oosting and Hess (1956) are useful in this connection. These authors point out that there is a relic stand of Canadian hemlock in the lower Piedmont of North Carolina, well south of the general range of this plant. Evidently the hemlock once ranged southward into the lower Piedmont, then retreated northward again, leaving a relic colony. The microclimate of this hemlock stand is unusually moist, not unusually cold. It seems possible that increased rainfall, rather than colder weather, once permitted the hemlock to extend its range southward. This may have been the case with other species.

Dillon (1956) believed that the supposed palynological evidence of former chilling actually reflects higher rainfall more than lower temperature. He stated that, because of the Wisconsin ice sheet, "a mean annual low-pressure system would have developed over the glaciated region. As a result, the mean annual cyclonic path . . . would have been displaced to the south . . ." (p. 168). This circumstance would have increased precipitation in both the southeastern and southwestern United States. According to Dillon, Florida would have had 40 to 60 inches of rain annually, and more than 60 inches in some parts of the state. The present annual rainfall is scarcely less than this.

However, Dillon did not contend that Florida was completely unaffected by glacial chilling; rather the reverse. He noted that, while Florida has an extensive tropical flora, it has extremely few endemic plants of tropical affinities. This circumstance "seems to indicate the complete elimination of suitable climatic factors for . . . persistence [of a tropical flora in the state] during Wisconsin times" (p. 173). In other words, Dillon granted some glacial chilling in Florida, sufficient to eliminate a tropical flora.

Ericson, *et al.*, (1956) derived climatic data from deep-sea sediments. They remarked: "The shells of planktonic Foraminifera in deep-sea

sediment cores provide the most trustworthy evidence on climatic variations of the Pleistocene because they vary in accordance with the temperature changes in the surface of the ocean and because the stages are represented in chronological sequence" (p. 385). They found that the modern warm period began 13 to 15 thousand years ago, and had been preceded by a definitely colder one; and they commented: "This world-wide change of surface-water temperature at the end of the glacial period argues against any theory of continental glaciation which calls on increased precipitation only without lowering of the world mean annual temperature" (p. 387).

Ewing and Donn (1956) found evidence, based on Foraminifera, that the mean annual temperature declined 1°C. per 11,000 years, from 90,000 to 11,000 years before the present, and thereafter increased 1°C. per 1,000 years, at least until a few thousand years ago.

The studies of Phleger (1948) and of Trask, *et al.*, (1947), previously mentioned, imply that there was glacial chilling even farther south than Florida.

It seems likely that, during Wisconsin times, Florida was somewhat cooler and rainier than at present. It was too cool to support a tropical flora, cool and wet enough to support some organisms which today characterize the Transition or even more northerly life zones. However, its biota was for the most part of Lower Austral species (Dillon, 1956).

Of course, earlier glaciations than the Wisconsin may have affected Florida more severely; on this point there is little information. During Illinoian times, the five-lined skink (*Eumeces fasciatus*) and the worm snake (*Carphophis amoenus*) ranged into central Florida (Auffenberg, 1956). Today the skink barely enters northern Florida (Neill and Allen, 1950), and the worm snake, in my opinion, does not occur naturally south of the piedmont in Georgia. The aforesaid studies on Foraminifera indicate several cold periods, some more severe than others.

"NORTHERN DISJUNCTS" AND OTHER SPECIES IN THE FLORIDA PANHANDLE

Certain aspects of animal and plant distribution in the Florida panhandle may reflect either former cooling or the heavy rainfall of Wisconsin times or both. In the panhandle one encounters populations of essentially northern or upland species confined to isolated spots far south of their present continuous ranges. This situation could have resulted only if the species involved once pushed southward and then retreated northward again, leaving isolated colonies in favorable areas.

However, one must remember that a good share of the "northern element" in the panhandle probably is not isolated there. The Gulf coastal plain of western Georgia and Alabama is relatively high, in some ways more reminiscent of the piedmont than of the Atlantic coastal plain. Traveling southward from the piedmont of western Georgia, one encounters no marked change of scenery until well below Tallahassee; the vista throughout is one of rolling, red clay hills covered with loblolly and shortleaf pines. (Kurz, 1928, has discussed the "northern" aspect of the Tallahassee Red Hills.) Such northern plants as whitecedar, beech, trilliums, pallid and shagbark hickories, swamp leatherwood, big-leaved and Frasers magnolias, bloodroot, mandrake, columbine, hepatica, bellworts, Solomons-seal, baneberry, pepperroot, rue-anemone, false rue-anemone, swamp buttercup, giant equisetum, etc. reach Florida mostly or only in the panhandle (Cowles, 1904; Harper, 1914; Kurz, 1933, 1939; Murrill, 1946; Small, 1933), but it is improbable that all of them are isolated there. Judging from Duncan's (1950) spot maps, a number of trees occupy fairly continuous ranges from northern Georgia to, and into, northwestern Florida. Small (1938) believed that glacial chilling had brought some northern ferns into the Florida panhandle, but he also realized (p. 7) that some species merely ranged from the piedmont through the relatively high country of western Georgia and eastern Alabama, and so into northwestern Florida. Thorne (1949, 1954) noted the occurrence of various inland and upland plants on the Gulf coastal plain of Georgia; and some of these reach the Florida panhandle. Certain of the "northern" animal species almost surely are not isolated, but merely find the southern extremities of their respective ranges in northwestern Florida. Many essentially upland animals are unable to invade the Atlantic coastal plain of eastern Georgia for more than a few miles, yet break out of the piedmont into the higher Gulf coastal plain and range nearly or quite into the Florida panhandle. Examples are the Alleghenian spotted skunk (*Spilogale putorius*), the swamp rabbit (*Sylvilagus aquaticus*), the five-lined skink (*Eumeces fasciatus*), the copperhead (*Agkistrodon contortrix*), the mole snake (*Lampropeltis calligaster*), the midland brown snake (*Storeria dekayi wrightorum*), Fowler's toad (*Bufo woodhousei fowleri*), the northern dusky salamander (*Desmognathus f. fuscus*), the spotted salamander (*Ambystoma maculatum*), and perhaps the silverjaw minnow (*Ericymba buccata*) (Allen and Neill, 1955b; Carr and Goin, 1955; Grobman, 1950; Hamilton, 1943; Neill, 1950, 1954b; Taylor, 1935; Trapido, 1944). The list could be extended considerably.

Some other animals are widespread throughout much of the Southeast, avoiding only the lower parts of the coastal plain. Consequently they are present in the Florida panhandle but not elsewhere in the state. In this category are the three-lined salamander (*Eurycea longicauda guttolineata*), the southern red salamander (*Pseudotriton ruber vioscai*), the Gulf Coast mud salamander (*P. montanus flavissimus*), and the southern cricket frog (*Acris g. gryllus*) (Bishop, 1943; Carr and Goin, 1955).

Many organisms range widely in the Gulf drainage (some of these well up the Mississippi drainage as well) and therefore inhabit the Florida panhandle. Among them are the central dusky salamander (*Desmognathus fuscus brimleyorum*), the western bird-voiced treefrog (*Hyla p. phaeocrypta*), the Gulf Coast box turtle (*Terrapene carolina major*), the gray rat snake (*Elaphe obsoleta spiloides*), the green water snake (*Natrix c. cyclopion*), four shiners (*Notropis roseipinnis*, *N. signipinnis*, *N. venustus*, and *N. longirostris*), the longfin madtom (*Schilbeodes funebris*), the southern brook lamprey (*Ichthyomyzon gagei*), the northern spotted bass (*Micropterus punctulatus*), the longear sunfish (*Lepomis m. megalotis*), the southern rock bass (*Ambloplites rupestris ariommus*), the Gulf Coast waterdog (*Necturus beyeri*), the Mobilian turtle (*Pseudemys floridana mobilensis*), and two crayfishes (*Procambarus versutus* and *Cambarus diogenes*) (Bishop, 1943; Carr and Goin, 1955; Dendy and Scott, 1953; Grobman, 1950; Hobbs, 1942; Neill, 1948, 1949). Here again, the list could be extended greatly.

Some species or races are characteristic of the Mississippi Valley or of the western Gulf Coast, and range no farther east than the western end of the Florida panhandle. Examples are the Gulf Coast redwing (*Agelaius phoeniceus littoralis*), the brown-headed nuthatch (*Sitta p. pusilla*), the western mud snake (*Farancia abacura reinwardti*), the western cottonmouth (*Agkistrodon piscivorus leucostoma*), the stripe-necked musk turtle (*Sternotherus minor peltifer*), the Alabama map turtle (*Graptemys pulchra*), and a crayfish (*Procambarus evermanni*) (Cagle, 1954; Hobbs, 1942; Sprunt, 1954; Tinkle and Webb, 1955). In many species—e.g., the aforesaid mud snake, cottonmouth, and musk turtle—a race of the western Gulf coastal plain intergrades with a more easterly race near the western end of the Florida panhandle. Twenty-four species of fishes, occurring in the Mississippi drainage, find the eastern limits of their respective ranges in the panhandle. Of these, fourteen range no farther east than the Choctawhatchee, if that far; the remainder reach the Apalachicola (Bailey, *et al.*, 1954). Among fishes entering only the western end of the pan-

handle are the quillback (*Carpiodes cyprinus*), the alligator gar (*Lepisosteus spatula*), the blacktail redhorse (*Moxostoma poecilurum*), the streaked topminnow (*Fundulus olivaceus*), and the star-gazing darter (*Hadropterus uranidea*) (Carr and Goin, 1955).

Thus many northwestern Florida organisms afford no evidence of a southward migration in former times. There are, however, a few upland animals which appear to have truly isolated populations in northern Florida. These include the red-spotted newt (*Diemictylus v. viridescens*), the mountain chorus frog (*Pseudacris brachyphona*) (possibly a distinct race [Neill, 1954b]), the eastern ribbon snake (*Thamnophis s. sauritus*), and the midland water snake (*Natrix sipedon pleuralis*). The last occurs in the Choctawhatchee ravines; the others are found at both ends of the panhandle (Neill, 1954b). The presence of the four-toed salamander (*Hemidactylum scutatum*) near the Florida-Georgia border may also be significant (Grobman, 1954). There are seemingly disjunct populations of two bats (*Myotis keeni* and *M. grisescens*) in Jackson County, Florida, but the circumstance may reflect only the distribution of limestone caves (Rice, 1955a, 1955b). The aquatic insect larvae of the panhandle ravines are of characteristically upland species in many cases, some of them occurring nowhere else south of the piedmont (Berner, 1950; Byers, 1930; Carr, 1940; Rogers, 1933). The commonest crayfish of the Apalachicola ravines, *Cambarus latimanus*, is generally considered Appalachian (Carr, 1940; Hobbs, 1942). A northern camel cricket, *Ceuthophilus gracilipes*, is not found south of the fall line, except in the Apalachicola region of Florida where a distinct race exists (Hubbell, 1936).

Among the amphibians and reptiles of northwestern Florida, there are at least five instances in which two races of the same species occur in the same area, ecologically separated—newts, *Diemictylus v. viridescens* and *D. v. louisianensis*; dusky salamanders, *Desmognathus f. fuscus* and *D. f. auriculatus*; cricket frogs, *Acris g. gryllus* and *A. g. crepitans*; ribbon snakes, *Thamnophis s. sauritus* and *T. s. sackeni*; water snakes, *Natrix sipedon fasciata* and *N. s. pleuralis*. In each case except that of *Desmognathus*, the essentially northern race occupies a limited area surrounded by the more typically southern one, and in each case except that of *Acris*, the more northerly race is restricted to relatively cold situations (Grobman, 1950; Neill, 1954b). This circumstance, coupled with the spotty distribution of some "northern" elements in the panhandle and with the paleontological evidence of former chilling, suggests that the Gulf coastal plain has undergone a faunal and floral turnover which is not quite complete. In other words, during Wisconsin times, what we now call the "northern element" may

well have been the predominant one in the panhandle, along with other species no longer present in the state. In this connection one notes the presence of the muskrat in the Apalachicola region about 2500 years ago (Neill and Bullen, 1955). Lacking from the state today, it reached Alachua County in the northern part of the peninsula in the Pleistocene (Lawrence, 1942).

Florida east of the panhandle, and the lower Atlantic coastal plain of southeastern Georgia, were also exposed to glacial chilling and once supported some supposed cold-weather organisms, as shown by Pleistocene remains. The cold-weather biota has nearly vanished from these areas, which topographically and climatologically are unlike the piedmont. Nevertheless, there seem to be a few relic colonies of essentially upland species isolated at favorable localities well to the east of the panhandle. A rhododendron (*Rhododendron Chapmanii*), long thought to be an Apalachicola endemic, has been subsequently found at one spot in northeastern Florida (Totten, 1945). The star-nosed mole (*Condylura cristata*) has been taken in Okefinokee Swamp near the Georgia-Florida border, far south of its continuous range (Hamilton, 1943). Several amphibians and reptiles, essentially of the piedmont or upper coastal plain, have been reported in northeastern or central Florida at points which I find almost incredibly far south: for example, the marbled salamander (*Ambystoma opacum*) has been reported in the Tampa Bay region (Carr and Goin, 1955); the painted turtle (*Chrysemys picta*) near Jacksonville (Deckert, 1918); the spotted turtle (*Clemmys guttata*) in Lafayette County (Grobman, 1954) and Marion County (Carr, 1940); and the brown king snake (*Lampropeltis calligaster rhombomaculata*) from "the St. Johns River" and from Lake County (*idem*).

ENDEMISM IN THE FLORIDA PANHANDLE

The Florida panhandle is noted not only for its "northern" element but also for many endemic species or races, some of which range a short distance into Georgia or Alabama. Among these endemics are the Florida yew (*Taxus floridana*), the torreyia (*Torreya taxifolia*), the croomia (*Croomia pauciflora*), a sedge (*Carex Baltzelli*), a spiderlily (*Hymenocallis Kimballiae*), a plume-locust (*Amorpha bushii*), a basswood (*Tilia porracea*), a violet (*Viola rugosa*), a meadowbeauty (*Rhexia parviflora*), a gum (*Nyssa ursina*), a water-parsley (*Sium Floridanum*), a milkweed (*Asclepias viridula*), a goldenrod (*Solidago flavovirens*), three asters (*Aster plumosus*, *A. brachypholis*, and *A. spinulosus*), a waterlily (*Nymphaea ulvacéa*), a waxweed (*Parsonsia lythroides*), a

basil (*Clinopodium dentatum*), three camelcrickets (*Ceuthophilus um-brosus*, *C. armatipes*, and *C. rogersi*), a flightless grouse-locust (*Tettigi-dea empedonepia*), a distinctive katydid (*Hubbellia marginifera*), a remarkable opilionid (*Siro americanus*), the Okaloosa darter (*Etheo-stoma okaloosae*), a bass (*Micropterus* species), a sawback turtle (*Grap-temys barbouri*), a kingsnake (*Lampropeltis getulus goini*), a black-snake (*Coluber constrictor helvigularis*), and a water rat (*Neofiber alleni apalachicola*) (Auffenberg, 1955a; Bailey and Hubbs, 1949; Cagle, 1952; Carr, 1940; Carr and Goin, 1955; Harper, 1949; Hobbs, 1942; Hubbell, 1936, 1940; Neill and Allen, 1949; Schwartz, 1953; Small, 1933).

Although some panhandle endemics are confined to the Apalachi-cola region, it should be noted that many are not found there. Thus, two *Potamogeton* are restricted to the mouth of the Blackwater River; a *Grossularia* grows around Lake Miccosukee; a basswood (*Tilia por-racea*) inhabits Okaloosa County; a mint (*Stachys lythroides*) grows in sandy places near Tallahassee; a waterlily is confined to the western end of the panhandle; a false-indigo (*Baptisia hirsuta*) is known from dry sand areas in Okaloosa and Walton Counties, and another (*B. simplicifolia*) occurs in Wakulla and Gadsden Counties; a camel-cricket (*Ceuthophilus armatipes*) is known only from DeFuniak Springs and perhaps Pensacola; and a distinctive whirligig beetle (*Gyrates iricolor*) has been found only in the Choctawhatchee drainage (Carr and Goin, 1955; Harper, 1949; Hubbell, 1936; Small, 1933; Young, 1947). A crayfish of the genus *Procambarus* is endemic to Escambia County; two are confined to the Escambia River, one to the vicinity of Panama City, and one to Leon and Wakulla Counties (Hobbs, 1942). A crayfish of the genus *Cambarus* has been taken only from a well in Jackson County, and another is confined to the western end of the panhandle (*idem*).

The northwestern Florida endemics seem clustered around the Apalachicola region and the western end of the panhandle. The "northern element" is similarly distributed. It is therefore reasonable to guess that the endemism and the northern aspect of the panhandle biota are but two facets of the same problem. In other words, I suspect that many of these endemics once were typical, widely ranging, Gulf Coast forms at a time when the climate was cooler and wetter than at present. A sawback turtle (*Graptemys barbouri*), thought to be an Apalachicola endemic, was subsequently found in the Escambia River about 125 miles to the west (Cagle, 1952). A camel cricket (*Ceuthophilus rogersi*) has been reported only from the Apalachicola ravines and from Mobile, Alabama (Hubbell, 1936). A crayfish (*Procambarus*

versutus), ranging from Mississippi through the western end of the Florida panhandle, occurs also in the Apalachicola region; and the apparently disjunct distribution cannot be laid to inadequate collecting (Hobbs, 1942). Three species of freshwater mollusks are common in the Escambia and the Apalachicola, yet have never been found in the Choctawhatchee in spite of intensive collecting (Clench and Turner, 1956). As mentioned previously, a rhododendron, once thought to be an Apalachicola endemic, was found to occupy a tiny area of the Atlantic coastal plain in Clay County, Florida (Totten, 1945). Some of the true Apalachicola endemics, such as the Florida yew and the *Torreya*, occur at two, three, or more separate localities (Kurz, 1927, 1939). In other words, some of the endemics, like some of the "northern" species, are discontinuously distributed, perhaps for the same reasons.

EAST-WEST DISTRIBUTION IN THE FLORIDA PANHANDLE

Peculiarities of east-west distribution in the panhandle cannot be laid to temperature correlated factors or to general similarities between that region and the country farther north. Rather, these peculiarities seem to reflect mostly the interglacial rises of sea level. Being relatively high except along its southern edge, the panhandle was never entirely submerged, but its rivers were embayed by the rising sea. During interglacial periods there was an embayment occupying the Escambia-Blackwater-Yellow River basin, another occupying the Choctawhatchee-Alaqua basin, and a third involving the Apalachicola and its tributaries. At their maxima these embayments extended well into what are now Georgia and Alabama (Cooke, 1945). Many an organism now finds the eastern or the western limit of its range at one of these former embayments. The larger streams of the western panhandle mark the eastern limit of range for numerous fishes characteristic of the Mississippi Valley and Gulf coastal plain, and the western limit for various species occurring on the Atlantic coastal plain (Bailey, *et al.*, 1954). At each rise of sea level the Apalachicola drainage was embayed farther inland than any other; and today the Apalachicola proper appears to be an exceptionally important barrier to east-west distribution in many groups. I suggest that the barrier is not the present river but the broad saltwater channel that occupied its position during long periods of the Pleistocene.

Clench and Turner (1956) studied the freshwater mollusks of the Gulf drainage from the Escambia River to the Suwannee. They noted a lack of endemic species in streams such as the Ochlockonee and the

Suwannee, which arise in the lowlands, but numerous endemic species in the Apalachicola, Choctawhatchee, and Escambia Rivers, which arise in higher country. They concluded that the valleys of the lowland streams must have been inundated by Pleistocene rises of sea level, and that endemic species could have developed only in those streams whose headwaters, at least, remained above the encroaching salt water. Thus the distribution of freshwater mollusks in the Florida panhandle helps to confirm the geological evidence of extensive embaying during the Pleistocene.

It was noted that both the endemic and "northern" elements of northwestern Florida seem to cluster around the Apalachicola region and the western panhandle. This circumstance in part may reflect the presence of suitable habitats in these areas—ravine streams, for example—and their absence from intervening territory. However, it is significant that both the endemic and "northern" elements are composed largely of species that live in or near freshwater brooks, creeks, and rivers, or in situations that develop in the floodplains of such streams. Along the lowland rivers, populations of these species mostly would have been wiped out by Pleistocene rises of sea level and concomitant encroachment of salt water; but along the Apalachicola and the larger streams of the western panhandle, the same organisms could have avoided extermination by retreat toward the headwaters. With a fall of sea level, the various species could again have moved downstream; but they could not have come to reoccupy the streams from which they had been exterminated unless they were able to cross the land barriers between drainages.

ENDEMISM AND OTHER DISTRIBUTIONAL PHENOMENA IN CENTRAL FLORIDA

The rises of sea level that embayed the panhandle well-nigh inundated what is now central Florida. Some land remained in the peninsula, however. The highest Pleistocene marine terrace is the Brandywine, about 270 feet above present sea level. Even if there has been no erosion or land subsidence, the Brandywine sea would have left a fair-sized island in Polk County and several smaller islands just north of there. This situation is now recognized by geologists (Cooke, 1945). There is also reason to suppose that erosion has reduced the level of the central Florida hills. These hills are mostly of fine sand, easily worn down by wind or rain; and climatologists say that glacial periods were extremely windy and rainy. Cooke (1945, p. 247) stated, "All parts of Florida . . . were subject to erosion during every glacial

stage. . . .” The central Florida hills may be lower today than ever before. Furthermore, there is evidence of recent land subsidence affecting the western part of the peninsula, as I shall point out later.

Granting that Pleistocene submergence in central Florida was not complete, one may trace the Cenozoic history of the state as outlined by Campbell (1940), Cooke (1939, 1945), Schuchert (1935), and White (1942). The area was completely submerged during the Eocene. In the Oligocene an island, the so-called Ocala Island, was exposed in what is now the upper part of the peninsula. It remained separate from the mainland but may have become connected with Cuba. In the late Oligocene it was nearly or completely submerged. During the Miocene an island appeared again, and toward the end of this epoch contact was established between this island and the mainland. Florida remained a peninsula all during the Pliocene. Up to this time the submergences and emergences had been the result of crustal movements. The first glaciation of the Pleistocene withdrew water from the sea, and the size of the Florida peninsula was considerably augmented. The first interglacial reduced the peninsula to a group of islands, the sea rising 270 feet above its present level. Thereafter, there were cycles of interglacial rise and glacial fall of sea level; but each cycle was less marked than the preceding one. The relatively high rises of Pleistocene sea level came during the early part of that epoch; subsequent rises left ample land in what is now the peninsula.

The central Florida region, corresponding roughly to the Pleistocene archipelagos, embraces a strip down the “backbone” of the peninsula, from Marion County in the north through Highlands County in the south. It is an area of rolling sand hills, whose dunelike structure can be seen at many localities. These hills are covered with xerophilous rosemary scrub or with high pine, although mesophytic and hydrophytic situations develop in low spots. In most areas there is an abrupt transition from the central Florida highlands to the bordering lowlands. The rolling area reaches a maximum elevation of 325 feet in Polk County. Elevation decreases northward of this point; and, although the highlands continue as a weakly defined ridge northward into Georgia, the impressively high country comes to an end around Alachua County. This is another way of saying that the salt water channel between the Pleistocene islands and the mainland ran approximately through Alachua County. Biogeographers have called this channel the Suwannee Straits, because the Suwannee River and its tributaries now occupy what was formerly the channel bed.

A short distance north and also west of the central Florida region there are smaller, isolated areas of comparatively high elevation.

These, too, may mark the position of former islands, of middle Pleistocene age.

Rosemary scrub is the first timber stage following cessation of activity in coastal dunes (Carr, 1940; Laessle, 1942). It occurs on stabilized dunes just back of the present coast; and, significantly, on the central Florida hills which are thought to mark the position of Pleistocene islands. High pine succeeds rosemary scrub (Carr, 1940) or, like scrub, may initiate succession (Laessle, 1942). Many central Florida endemics, both plant and animal, are mostly confined to scrub, high pine, or the two associations together. For example, the scrub lizard (*Sceloporus undulatus woodi*), the sand skink (*Neoseps reynoldsi*), and the Florida jay (*Aphelocoma c. caerulescens*) are seldom found outside rosemary scrub; the short-tailed snake (*Stilosoma extenuatum*) is characteristic of high pine; the brown red-tailed skink (*Eumeces egregius onocrepis*) occurs in both and rarely invades other associations. Harper (1949) recognized 189 flowering plants endemic to central Florida, and I would judge from Small's (1933) comments that about 60 percent of them characterize one or both of the sandhill associations.

Rosemary scrub is replaced by other associations during the course of ecological succession (Laessle, 1942). This being the case, some areas of scrub, particularly small ones, may have vanished completely. Scrub-limited animals would have vanished from the areas at the same time. There is paleontological confirmation of this view. Pleistocene deposits in western Alachua County have yielded remains of the island glass lizard (*Ophisaurus compressus*) and the scrub jay (Auffenberg, 1955b; Pierce Brodkorb, personal communication). The lizard inhabits scrub and certain littoral or supratidal situations, while the bird is confined to scrub. The lizard, the jay, and the plant association are all lacking from the area today, the nearest locality for all three being in northeastern Marion County.

Many typical central Florida organisms fall into one of two categories. Some are closely, usually subspecifically, related to a mainland form; others are very distinctive species, often comprising monotypic genera or subgenera, not closely related to anything now living in North America. Presumably the members of the second group may have persisted there as relic species after most of their allies in other regions had died out.

Among the central Florida organisms with near relatives elsewhere are the Florida spotted skunk (*Spilogale ambarvalis*), the Florida pine mouse (*Microtus pinetorum parvulus*), the Florida flying squirrel (*Glaucomys volans querceti*), the Florida cotton mouse (*Peromyscus gossypinus palmarius*), the central Florida rice rat (*Oryzomys palustris*

natator), the Florida cotton rat (*Sigmodon hispidus littoralis*), the Florida marsh rabbit (*Sylvilagus palustris paludicola*), the Florida crow (*Corvus brachyrhynchos pascuus*), the Florida wren (*Thryothorus ludovicianus miamensis*), the Florida bobwhite (*Colinus virginianus floridanus*), the Florida turkey (*Meleagris gallopavo osceola*), the Florida pine warbler (*Dendroica pinus florida*), the Florida blue bird (*Sialia sialis grata*), the Florida redwing (*Agelaius phoeniceus mearnsi*), the Florida crown snake (*Tantilla coronata wagneri*), the Florida king snake (*Lampropeltis getulus floridana*), the Florida banded water snake (*Natrix sipedon pictiventris*), the scrub lizard (*Sceloporus undulatus woodi*), the Florida snapping turtle (*Chelydra serpentina osceola*), the peninsula turtle (*Pseudemys floridana peninsularis*), the Florida mud turtle (*Kinosternon subrubrum steindachneri*), the Florida chorus frog (*Pseudacris nigrita verrucosa*), the peninsula newt (*Diemictylus viridescens piaropicola*), the peninsula dusky salamander (*Desmognathus fuscus carri*), the Florida black bass (*Micropterus salmoides floridanus*), and the central Florida black widow spider (*Latrodectus mactans* var. *bishopi*) (Carr, 1940; Carr and Goin, 1955; Hamilton, 1943; Kaston, 1938; Sherman, 1937, 1952; Sprunt, 1954). In most of these species, the peninsular population is a race, intergrading with a mainland one at the level of the old Suwannee Straits. If it is granted that some forms, originating on the Pleistocene islands, were able to spread a short distance northward after closure of the Straits, then other species could be added to the list.

Among the very distinctive peninsular endemics, perhaps relic species, are the striped mud turtle (*Kinosternon bauri*), the sand skink (*Neoseps reynoldsi*), the worm lizard (*Rhineura floridana*), the short-tailed snake (*Stilosoma extenuatum*), and the gopher mouse (*Peromyscus floridanus*). The round-tailed water rat (*Neofiber alleni*), the black swamp snake (*Seminatrix pygaea*), Allen's swamp snake (*Liodytes alleni*), and the mud siren (*Pseudobranchius striatus*) probably should be added, although they now range a short distance out of Florida. The genus *Pseudobranchius* is known from the recent of Florida and nearby areas, as well as from the Pleistocene and Pliocene of Florida; the lineage appears to be an ancient one within the state (Goin and Auffenberg, 1955).

Among peninsular plants, there are a number of distinctive ferns, delicate species mostly growing in limestone situations. Although their affinities are tropical, they are confined to the upper part of the peninsula; and the groups to which they belong are represented in the tropical West Indies but not in southern Florida. This circumstance led St. John (1936) to contend that Ocala Island, once continuous with

Cuba, was never completely submerged but had persisted since the Oligocene. Carr (1940) attempted to bring fern distribution into line with the evidence of complete submergence in the late Oligocene. He suggested that during a warm interglacial, fern spores blew or drifted to the Pleistocene islands of central Florida, persisting in the sheltered environment of caves and lime sinks.

There are several monotypic genera of flowering plants in central Florida: a pea, *Chapmannia*; composites, *Garberia*, *Hartwrightia*, *Am-mopursus*, and *Litrisa*; a pennyroyal, *Pycnothymus*; a milkweed, *Oxypteryx*; a St. Johnswort, *Sanidophyllum*; and a dayflower, *Tradescantella* (Harper, 1949; Small, 1933).

One may surmise that the short-tailed snake is a relic species, because it has no known close relatives, living or fossil. Likewise, one may postulate that the worm lizard is a remnant of an ancient and formerly widespread group, because other species of its genus are known from the Oligocene of Colorado, Nebraska, South Dakota, and Wyoming (Taylor, 1951). The only known congener of the round-tailed water rat is from the middle Pleistocene of Kansas and Texas (Meade, 1952). However, in the absence of paleontological data it would be temeritous to say which central Florida species developed their present characters on the Pleistocene islands and which simply persisted there from an earlier period. Suffice it to mention a few more organisms chiefly or strictly peninsular. The Florida short-tailed shrew (*Cryptotis floridana*) and the Florida black bear (*Ursus floridanus*) range northward into southeastern Georgia. The Everglades short-tailed shrew (*Blarina brevicauda peninsulæ*) is confined to the southern part of the peninsula; its range may be disjunct from that of the Carolina short-tailed shrew (*B. b. carolinensis*), which has been reported no farther south than Alachua County. The Florida prairie warbler (*Dendroica discolor collinsi*) is strictly peninsular, and its breeding range may be disjunct from that of the more northerly race (*D. d. discolor*); the latter breeds no farther south than central Georgia. Perhaps the limpkin (*Aramus guarauna pictus*) reached the Pleistocene islands from the south, evolving into a distinct race inhabiting the southeastern United States as well as Cuba. The Florida red-bellied turtle (*Pseudemys nelsoni*) is found throughout the peninsula, north to Alachua and Levy Counties. The island glass lizard (*Ophisaurus compressus*) is found on islands and coasts of South Carolina, Georgia, and Florida, and in the central Florida scrub areas which are thought to represent former islands. The striped newt (*Diemictylus perstriatus*) of central Florida ranges northward into southern Georgia (Carr, 1940; Carr and Goin, 1955; McConkey, 1954;

Sherman, 1937, 1952; Sprunt, 1954). A characteristic insect of the peninsular sandhills is the roach, *Arenivaga floridensis*, the females of which are flightless, and whose nearest relatives are found in Texas. A scarabaeid beetle (*Onthophagus polyphemus*) is known only from tortoise burrows; it has been reported from Florida and South Carolina. Several Florida invertebrates are obligate inquilines in tortoise burrows; and some, like the histrid beetle, *Chelyoxenus xerobatis*, are relic species with no near relatives. Although they are not now confined to peninsular Florida, it is likely that they survived in that region and have subsequently spread. A comparable group of invertebrates inhabits burrows of the pocket gopher (*Geomys pinetis*); and some Florida aspects of this symbiosis may have developed on the Pleistocene islands. A blind camel cricket (*Typhlocyba floridanus*), belonging to a monotypic genus, is strictly peninsular and confined to pocket-gopher burrows. A camel cricket (*Ceuthophilus latibuli*) ranges from central Florida to extreme southern Georgia, often inhabiting tortoise burrows; and another species (*C. peninsularis*) inhabits peninsular Florida from Pinellas County to Dade County. Four grasshoppers (*Schistocerca ceratiola*, *Melanoplus forficatus*, *M. indicifer*, and *M. tequestae*) are confined to rosemary scrub, as is a wolf-spider (*Lycosa ceratiola*). The distribution of certain flightless sand-beetles (*Mycotrupes* species) has been explained in terms of sea level fluctuations which isolated populations in central Florida and elsewhere. A race of a waterstrider (*Metrobates anomalus*) is known only from Hillsborough and Polk Counties (Hubbell, 1932, 1936, 1940, 1954; Hubbell and Goff, 1940; Hussey, 1948; Hussey and Herring, 1949; Young and Goff, 1939).

Clench and Turner (1956) commented on the distribution of freshwater mollusks in Florida. They were impressed by the number of species that did not range east or south of the Suwannee, and by the distinctiveness of the central Florida molluscan fauna. They felt that there was "good evidence among the freshwater mollusks for the existence of an island in what is now central Florida during the period of fluctuation of the epicontinental Pliocene and Pleistocene seas" (p. 104); and that the failure of many species to range below the Suwannee "is undoubtedly explained by the fact that at the time of [the island, the Suwannee valley] was inundated" (p. 105). They further suggested that the island must have been large enough to have had a freshwater drainage system with some lakes and perhaps some fairly large creeks. Dall (1890-1903, see 1903), another student of mollusks, had previously remarked that there must have been fresh-

water lakes on a central Florida island or archipelago, and that these lakes must have been in existence from quite an early period.

A pallid, cavernicolous crayfish (*Procambarus l. lucifugus*), known from caves in Citrus and Hernando Counties, is associated with a white isopod (*Asellus hobbsi*) and a blind, white amphipod (*Crangonyx hobbsi*). One of the most remarkable central Florida organisms is the crayfish, *Troglocambarus maclanei*; blind, attenuated, and almost transparent, it lives on the ceilings of submerged caverns in Citrus and southern Alachua Counties. Its extreme specialization indicates a lengthy separation from other crayfish stocks; and its existence may imply the persistence of subterranean fresh water, and therefore of land, for quite a long while in this part of Florida. A distinctive crayfish (*Procambarus alleni*) inhabits cypress ponds of the peninsula; another (*P. geodytes*) is known from mineral springs in Marion, Putnam, and Seminole Counties; and yet another, the zoologically disjunct *P. acherontis*, has been taken only in Seminole County, from sinks, springs, and subterranean waters (Hobbs, 1942, 1944).

A freshwater sponge (*Myenia subtilis*) is known from but one lake, in Osceola County (Eshleman, 1950).

The freshwater ichthyofauna of the peninsula is depauperate, unless one counts the marine species that venture inland. The cyprinids, suckers, and darters, represented abundantly elsewhere in the southeast, have very few members below the Suwannee Straits. With the closing of the Straits, the earliest and most successful invaders from the continent probably were cyprinodonts, characteristic of brackish coastal waters. Today the peninsula has a number of endemic cyprinodonts, including the red-finned killifish (*Lucania goodei*), the ocellated killifish (*Leptolucania ommata*), the Caledonian (*Fundulus seminolis*) and the Lake Eustis sheepshead killifish (*Cyprinodon hubbsi*), as well as about 14 more widely ranging members of this family. A peninsular centrarchid, the Florida black bass (*Micropterus salmoides floridanus*), intergrades with the mainland race about the region of the Suwannee Straits. A few other fishes are endemic to, or chiefly characteristic of, the peninsula (Bailey and Hubbs, 1949; Carr, 1937a; Carr and Goin, 1955).

The sand pine (*Pinus clausa*), the rosemary (*Ceratiola ericoides*), a marshgrass (*Spartina Bakeri*), a saw-palmetto (*Serenoa repens*), and three oaks (*Quercus Chapmanii*, *Q. myrtifolia*, and *Q. virginiana* var. *geminata*) typify central Florida but range into other states. A false pimpernel (*Ilysanthes grandiflora*) is strictly peninsular, ranging from Marion County to Glades County. A cactus (*Opuntia ammophila*), a lupine (*Lupinus cumulicola*), a plum (*Prunus geniculata*), a bluet

(*Houstonia pulvinata*), a composite (*Palafoxia Feayi*), a willow (*Salix amphibia*), a persimmon (*Diospyros Mosieri*), three buckthorns (*Bumelia* species), a rockrose (*Crocanthemum Nashii*), several pinweeds (*Lechea* species), a yellow waterlily (*Castalia flava*), a morning-glory (*Bonamia grandiflora*), two mints (*Scutellaria arenicola* and *Trichostema suffrutescens*), a grape (*Vitis Simpsonii*), a sweetbay (*Tamala humilis*), the wild olive (*Osmanthus americana*), the dwarf cabbage-palm (*Sabal Etonia*), a wild buckwheat (*Eriogonum floridanum*), a holly (*Ilex cumulicola*), two papaws (*Pityothamnus* species) and some xerophilous selaginellas are nearly or entirely confined to the central Florida region. Many of these are strikingly modified for life in dry situations, and grow in scrub or high pine. A bellflower (*Rotantha robinsiae*) has been reported only from one hilltop near Brooksville, Hernando County; and a clematis (*Clematis micrantha*) is also known only from Brooksville. Other plants, endemic to central Florida, could be listed (Harper, 1949; Small, 1933).

Of course, some species, now considered endemic to the Florida peninsula, may eventually be found well outside that area. However, this circumstance does not especially weaken biogeographic arguments based on endemism in central Florida; the ranges of many organisms have been traced with considerable accuracy, and, for many of the peninsular endemics, significant range extensions are not to be expected.

SOME MINOR ASPECTS OF DISTRIBUTION IN CENTRAL FLORIDA

Various minor aspects of plant and animal distribution in central Florida seem to reflect Pleistocene insulation. Thus, some peninsular races intergrade only sporadically with their more northerly counterparts, there being a good deal of interpenetration in separate habitats. This is true, for example, of the brown snakes (*Storeria dekayi wrightorum* and *S. d. victa*), the red-bellied snakes (*Storeria o. occipitomaquulata* and *S. o. obscura*), the fence lizards (*Sceloporus u. undulatus* and *S. u. woodi*),³ the softshell turtles (*Amyda f. ferox* and *A. f. aspera*), the dusky salamanders (*Desmognathus fuscus auriculatus* and *D. f. carri*), and perhaps the cardinals (*Richmondia c. cardinalis* and *R. c. floridana*) (Neill, 1948, 1950, 1951a, 1951b; Sprunt, 1954; Trapido, 1944). If the peninsular races had simply developed lineally from mainland stocks, intergradation should be smooth and probably grad-

³ Although intergradation between these two lizards has not been reported in print, it does take place. An intergradient series of individuals was displayed by James M. Boyles and me at the 1953 meeting of the American Society of Ichthyologists and Herpetologists, Southeastern Division, held at Athens, Georgia.

ual. Sporadic intergradation, with interpenetration in separate habitats, implies a recent recombination of stocks long isolated geographically. It is also significant that, in some cases, the range of the more northerly component bends southward around that of its central Florida counterpart, as though, with the bridging of the Suwannee Straits, the central Florida population remained *in situ* while the more northerly one flowed around it. In this connection note Hubbell's (1954, p. 44) distribution map for vicariating species of the sand beetle genus *Mycotrupes*, and Carr's (1940, p. 75) county records for red-tailed skinks, now called *Eumeces egregius similis* and *E. e. onocrepis*. A similar situation exists among the kingsnakes (*Lampropeltis getulus* subspecies). In the interior of Florida, the transition from the more northerly *L. g. getulus* to the peninsular *L. g. floridana* is accomplished from central Alachua County to central Marion County; but on the west coast *L. g. getulus* occurs at least as far south as northern Citrus County. If temperature-correlated factors were the only controlling agents of racial or vicarious distribution in these cases, the peninsular components should swing northward up the coast as do the isotherms. This is the reverse of the actual situation. It is also interesting to note that quite a few of the central Florida endemics, relic or otherwise, do not occupy the entire sandhills region, but are confined to areas which apparently correspond in position with certain of the Pleistocene islands. Thus the sand skink (*Neoseps reynoldsi*), a scrub-limited species, is lacking from the apparently suitable Big Scrub (described below) of Marion County, and occurs only in the higher dune areas farther south. The races of the short-tailed snake (*Stilosoma extenuatum*) roughly correspond in distribution with islands of the Wicomico sea (Highton, 1956). Some recognizable insect populations are associated with presumed island areas; these include a color variant of a stick insect (*Anisomorpha buprestoides*), confined to the Big Scrub (Hetrick, 1949), as well as various grasshoppers and sand beetles (Hubbell, 1932, 1954).

It might be argued that I have included among the central Florida endemics more organisms than could have lived on small Pleistocene islands. However, the conditions that obtain in the present-day Big Scrub suggest otherwise. This area, in eastern Marion County, is sharply distinct from the surrounding terrain, and is thought to represent one of the former islands. In the Big Scrub there are three enormous springs, with flows of 68 to 83 million gallons per day; two springs flowing 68 and 83 hundred thousand gallons per day respectively; uncounted smaller springs and seepage areas; about 20 sizeable creeks and streams in addition to the major spring runs; over 100 lakes,

some of large size; hundreds of smaller lakes, ponds, and swampy depressions; dunelike expanses of deep sand; areas of xerophilous rosemary scrub and of high pine; liveoak hammock; stands of mesophytic magnolia, blue beech, American holly, dogwood, etc.; low hammock; cypress swamp; wide, grassy "prairie"; and dense bayheads. The Big Scrub alone supports a large percentage of the central Florida endemics, along with other more widespread species.

A sizeable group of organisms apparently occupied the Pleistocene islands; most of the available niches must have been filled. If so, numerous mainland species must have found it difficult to invade the peninsula when the Suwannee Straits were bridged. One would expect to find mainland forms stopping short at the level of the Straits today, even though their characteristic habitats may continue farther south. This is the case. Mainland forms, stopping approximately in Alachua County, include Bachman's shrew (*Sorex l. longirostris*), the Carolina short-tailed shrew (*Blarina brevicauda carolinensis*), the red bat (*Lasiurus b. borealis*), the old-field mouse (*Peromyscus p. polionotus*), the indigo bunting (*Passerina cyanea*), the wood thrush (*Hylocichla mustelina*), Swainson's warbler (*Limnothlypis swainsoni*), the hooded warbler (*Wilsonia citrina*), the orchard oriole (*Icterus spurius*), the sharp-shinned hawk (*Accipiter striatus velox*), the marsh hawk (*Circus cyaneus hudsonius*), the red-bellied water snake (*Natrix erythrogaster*), the smooth ground snake (*Haldea valeriae*), the canebrake rattlesnake (*Crotalus horridus*), the alligator snapping turtle (*Macrochelys temmincki*), the yellow-bellied turtle (*Pseudemys scripta*), the spotted sucker (*Minytrema melanops*), the Alabama chubsucker (*Erimyzon tenuis*), the southeastern creek chub (*Semotilus atromaculatus*), the iron-colored shiner (*Notropis chalybaeus*), the mud perch (*Acantharchus pomotis*), the brown darter (*Etheostoma edwini*), and five crayfishes (Carr and Goin, 1955; Hobbs, 1942; Sherman, 1937; Sprunt, 1954).

Even some flying insects do not cross the Suwannee Straits. The dragonfly genus *Progomphus* includes only two species in the eastern United States. One evolved on the Pleistocene islands of central Florida, the other on the mainland. With the bridging of the Straits, the mainland form apparently was unable to extend its range below Alachua County (Cross, 1955). The butterfly, *Colias eurytheme*, widespread in North America, does not range below the Suwannee Straits (Hovanitz, 1950). Stoneflies have not been reported in Florida below Alachua County (Berner, 1948).

The case of the aforesaid red-bellied water snake and of the yellow-bellied turtle are particularly impressive. In southern Georgia these

reptiles are hardy, abundant, and well-nigh ubiquitous in aquatic situations; yet in Alachua County they stop abruptly even though their habitats continue southward. This county, and Marion County immediately to the south, have been centers of intensive herpetological collecting for many years, and one can feel rather sure that the southernmost localities for the two species have actually been located.

A number of other mainland species cross the Straits area only along the coasts, and swing southward around the old island area. Some of these are not especially characteristic of coastal situations elsewhere, and are not replaced by near relatives in central Florida. Included in this category are the eastern blue grosbeak (*Guiraca c. caerulea*), the eastern wood peewee (*Contopus virens*), the rough-winged swallow (*Stelgidopteryx ruficollis serripennis*) and Peterson's shiner (*Notropis petersoni*) (Carr and Goin, 1955; Sprunt, 1954). The mink (*Mustela vison*) appears to avoid the old island region entirely; it is present in northern and southern Florida, including both coasts, but has never been found in central Florida (Allen and Neill, 1952 and therein; Hamilton, 1943; Sherman, 1937). A distribution of this sort is consistent with the theory of central Florida insulation.

A few mainland species are able barely to penetrate the extreme northern edge of the old island region, having been collected no farther south than the level of central Marion County. These include the rough ground snake (*Haldea striatula*), the gray treefrog (*Hyla versicolor*), the river frog (*Rana heckscheri*), the flatwoods salamander (*Ambystoma cingulatum*), and several freshwater sponges (Carr, 1940; Carr and Goin, 1955; Eshleman, 1950; Sherman, 1937). The yellow-throated vireo (*Vireo flavifrons*) is essentially confined in Florida to the region north of the Straits, but has lately been found at Orlando; the range extension may represent a recent invasion of the peninsula (Sprunt, 1954). Presumably these species were lacking from the central Florida islands.

DISTRIBUTION OF COASTAL AND MARINE ORGANISMS

The distribution of coastal and marine organisms may also reflect Pleistocene insulation. A large number of marine fishes, including a sea lamprey, stingrays, sharks, the tarpon, a weakfish, a pipefish, a croaker, a remora, sea catfishes, and four flatfishes enter peninsular Florida waters (Carr and Goin, 1955). Odum (1953) pointed out that Florida fresh waters yet contain a good deal of salt in consequence of sea level changes during the Pleistocene. He apparently felt that the saltwater species merely travel upstream from the ocean; but Carr

(1937a) implied that some of the freshwater populations were virtually isolated from the marine ones. Perhaps the reduction of the peninsula to an archipelago made it easier for marine organisms to reach the oligohaline waters. At any rate, a naturalist, visiting one of the clear springs that well up from the Big Scrub of Marion County, will be surprised to see mojarra (*Eucinostomus argenteus*), sole (*Trinectes maculatus fasciatus*), stingrays (*Dasyatis* species), needlefish (*Strongylura marina*) and mullet (*Mugil* species); as well as blue crabs (*Callinectes sapidus*), a smaller crab (*Rithropanopeus harrisi*), and marine shrimp.

As regards amphibians and reptiles, the Florida peninsula has more "freshwater" species in salt water, and more "inland" species in supratidal habitats, than any other part of the world, so far as I can learn (Neill, MS a). The drowning of the peninsula, thrice repeated, may have forced some species into saltwater habitats or favored the survival of species that could exist in such places. Some freshwater invertebrates also invade brackish waters in Florida (Berner and Sloan, 1954; Sloan, 1956).

Certain patterns of coastal distribution in Florida are revealing. That of the coastal marsh wren (*Telmatodytes palustris*) is an example. One race of this bird is found on the Atlantic coast from South Carolina to Volusia County, Florida; another inhabits the Gulf Coast from Charlotte Harbor to Mississippi. Thus the distribution in Florida is split into upper east coast and upper west coast components, although the species is lacking from the shores of the southern peninsula. Devey (1950) remarked on similar cases of split distribution among hydroids and suggested that glacial chilling once permitted these temperature-limited invertebrates to swing around the southern tip of Florida. Whatever happened among hydroids, I think that instances of split distribution in other groups mostly reflect passage through the Suwannee Straits at a period of high sea level. In other words, the species involved once ranged along the former mainland shore on the north side of the Straits; the distribution was split when the peninsula emerged and the Straits closed. Carr and Goin (1942) advanced a similar explanation to account for the distribution of saltwater snakes (*Natrix sipedon* subspecies) in Florida. In these reptiles there is a peninsular race (*N. s. compressicauda*) intergrading in Brevard County with an upper east coast race (*N. s. taeniata*) and around Pasco County with an upper west coast race (*N. s. clarki*). *N. s. taeniata* and *clarki* are very similar although separated by the markedly divergent *compressicauda*. Carr and Goin postulated that *compressicauda* developed on a Pleistocene island while the old mainland

shore was occupied by a common ancestor of *taeniata* and *clarki*. With the bridging of the Straits, the former mainland population was split, diverging slightly to produce *clarki* and *taeniata*; *compressicauda* was left about the peninsular shores. The history of the seaside sparrows (*Ammospiza maritima* subspecies) may have been comparable. Two races thereof occupy the upper east coast, and three others the upper west coast; the group is lacking from the southern peninsular shores except for a stretch between Cape Sable and Everglades City, where an isolated population (at present called a distinct species, *A. mirabilis*) is found. There are also three races of the clapper rail (*Rallus longirostris*) in Florida: one on the upper east coast, one on the west coast, and one on the Keys. One race of the yellow-throated warbler (*Dendroica dominica*) ranges, mostly coastally, from Maryland to mid-Florida; another occupies the Gulf lowlands from Levy County west to the Choctawhatchee River. A single race of the mink (*Mustela vison lutenis*), inhabiting salt marsh, is known from Duval and St. Johns Counties on the east coast, and from Levy County on the west coast. Several fishes, crabs, and mollusks are found on both coasts of northern Florida, yet are lacking from the peninsula or its southern part (Deevey, 1950 and therein; Sherman, 1937; Sprunt, 1954).

RECENT RISE OF SEA LEVEL

The Wisconsin ice sheet is still shrinking, and sea level has risen within the recent period (Goggin, 1948). Certain aspects of distribution in Florida may reflect this rise. The greater siren (*Siren lacertina*) occurs in the only body of permanent fresh water on Merritt Island, off the coast of Brevard County. It does not cross land or salt water, and so may have been trapped on the island by a recent rise of the sea (Neill, 1954b). Many of the present offshore islands must have been produced since the peak of the Wisconsin glaciation, by separation from the mainland as the sea encroached upon the land. The populations isolated on these islands might have diverged from the parent ones through selection and perhaps genetic drift. As the islands are not far offshore, they probably have been invaded by mainland organisms at fairly frequent intervals. According to Miller (1956, p. 276), "... moderate but not full isolation of populations favors prompt initial and subsequent evolutionary progress as made particularly clear by Sewall Wright." Thus one can account for the numerous bird and mammal races confined to such islands as Anastasia, Merritt, Santa Rosa, the Ten Thousand Islands, and certain of the Keys. The environment of southern Florida may have hastened evolution of insular

populations in that area. That is to say, many faunal groups (e.g., mammals, reptiles, and amphibians) are represented in southern Florida largely or entirely by species which originated farther north; and these species, originally adapted to temperate conditions, may have been subjected to unusually strong selective pressures in consequence of invading an area of tropical plant associations and subtropical climate.

ENDEMISM IN NORTHEASTERN FLORIDA

Northeastern Florida (east of the panhandle and north of the Suwannee Straits) is another area of endemism, about 26 species of flowering plants being confined to this part of the state (Harper, 1949; Small, 1933). Some of them belong to widespread and remarkably polytypic genera, such as *Solidago*, the goldenrods; *Aster*, the asters; *Helianthus*, the sunflowers; *Opuntia*, the pricklypears; *Cracca*, the hoary peas; *Eleocharis*, the spikerushes; and *Scleria*, the nutrushes. These throw little light on the problem of endemism in northeastern Florida. However, two of the endemics, a cycad (*Zamia umbrosa*) and a dwarf sunflower (*Phoebanthus tenuifolia*), find their close relatives only to the south, in the old island area. Perhaps a central Florida stock of *Zamia* and of *Phoebanthus* once crossed to the mainland and became isolated there with a rise of sea level. The Sunderland sea of the second interglacial not only insulated central Florida; it also left a group of islands in what is now northeastern Florida. The Wicomico sea left a peninsula there, pointing toward the central Florida islands; the Penholoway permitted a narrow connection between this peninsula and central Florida; the Talbot and Pamlico left a broad connection (Cooke, 1939). One might expect a localization of species or races in an area which, so often and for so long, was a sizeable peninsula during the Pleistocene, and which could have been colonized from both north and south.

RECENT LAND SUBSIDENCE IN WESTERN FLORIDA

Florida has been exposed not only to fluctuations of sea level but also to comparatively recent land subsidence along its western edge. At one time, geologists held that there had been no late Pleistocene or recent tilting along the Atlantic seaboard. This conclusion was based on the fact that a late Pleistocene shore line, the Pamlico, maintains the same altitude from New Jersey to southern Florida (Rouse, 1951 and therein). However, this situation reveals only that there has been no tilting in a north-south direction. Subsidence of the Florida west coast has taken place, probably in consequence of the great weight of sedi-

ments poured into the Gulf by the Mississippi River (Storm, 1945). Marine shells associated with the Pamlico shore line occur up to 25 feet above present sea level on the Florida east coast, but only up to 10 feet on the west coast (Rouse, 1951 and therein); in Louisiana, near the focus of subsidence, shells thought to be of Pamlico age have been taken from a boring at a depth of 2470 feet below present sea level (Deevey, 1950 and therein). The configuration of the west coast, with numerous embayed river mouths, submerged channels in the Gulf, and labyrinthine island groups, attests to the subsidence.

Archeology also provides some evidence of recent subsidence along the Florida west coast. On the eastern shores of the state, from Vero Beach northward, are numerous shell middens—Indian refuse heaps—dating from what archeologists call the Mt. Taylor and Orange periods (Goggin, 1952; Rouse, 1951). During the Mt. Taylor period pottery manufacture was unknown to the Indians, while during the Orange period a characteristic fiber-tempered ware was made. When Willey (1949) surveyed the archeology of the Florida Gulf Coast, he was unable to recognize or define any local period comparable to Mt. Taylor or Orange in age; all the sites were of later date. Middens on the present west coast all postdated the use of fiber-tempered pottery. Yet it seemed likely that the west coast was inhabited at a time when this ware was in use, for a few fiber-tempered potsherds had been picked up in the area. A question therefore arose: Where are the earlier middens of the west coast? Subsequently, west coast sites a little later than the Orange period were found to be submerged, wholly or in part, by the waters of the Gulf (Bullen and Bullen, 1950, 1953). This led to the speculation that the still older sites were now well beneath low tide mark. A submerged site, apparently preceramic and therefore comparable to Mt. Taylor middens in age, was eventually found off the coast of Pinellas County; and flint chipping of uncertain age was found as much as two miles offshore (Neill, MS b). At one locality there was a sort of "horizontal stratigraphy," with early Indian artifacts well out in the water, later ones near what is now high tide mark, and still later ones along the present supratidal dunes (*idem*).

There is some partial submergence of middens and mounds on the east coast, attributable to the postglacial rise of sea level (Goggin, 1948; Rouse, 1951), but in that area there appears to be nothing comparable to the wholesale drowning of early sites along the Gulf Coast. Of course, mere rise of sea level would affect both coasts equally, and it is therefore reasonable to presume that the west coast has also experienced land subsidence within the period of Indian occupancy.

Much more study is needed; but at any rate the archeological evidence is consistent with geological opinion.

The depression of the west coast is of biogeographic significance. Today, miles out from this coast the Gulf is still very shallow. A number of distinctive west coast organisms may once have ranged over an extensive territory now largely submerged. I refer to the little mole (*Scalopus aquaticus parvus*), the Florida big brown bat (*Eptesicus fuscus osceola*), the Suwannee turtle (*Pseudemys floridana suwanniensis*), the Gulf Hammock rat snake (*Elaphe obsoleta williamsi*), the Gulf Hammock mud siren (*Pseudobranchius striatus lustricolus*), a euphorbia (*Phyllanthus platylepis*) and a quillwort (*Isoetes alata*). Further geological studies on west coast subsidence may throw light on speciation along what is now the western edge of the peninsula. At any rate, had it not been for this subsidence, the Cedar and Anclote Keys, the long chain of west coast islands from Caladesi to Estero, the Ten Thousand Islands, the Florida Keys, the Marquesas group, and the numerous specks of land in Florida Bay would all be part of the mainland; for all of these islands are separated from the mainland by water less than three fathoms deep. The populations of the cottonmouth (*Agkistrodon piscivorus*) and of the southeastern five-lined skink (*Eumeces inexpectatus*) on the islands in Suwannee Sound; those of the Carolina anole (*Anolis carolinensis*), the ground skink (*Lygosoma laterale*), and of a rat snake (*Elaphe guttata* subspecies) in the Marquesas group; of the six-lined racerunner (*Cnemidophorus sexlineatus*) on Boca Grande; and of the gopher tortoise (*Gopherus polyphemus*) on Caladesi, may in some cases reflect this subsidence.

The depression of the west coast may explain another and hitherto puzzling circumstance: the occurrence of many organisms on the southern Florida mainland and on the lower Keys, but not on the upper Keys. The Miami oölite is the foundation for the lower Keys, the southern mainland, and the islands in Florida Bay; whereas the upper Keys are based on a coral reef, the Key Largo formation, which grew apparently in the Pamlico sea (Cooke, 1939, 1945). Mainland species could have moved overland into what is now the lower Keys probably before the upper Keys appeared above water. Today the white-tailed deer (*Odocoileus virginianus*), the cotton rat (*Sigmodon hispidus*), the ribbon snake (*Thamnophis sauritus*), a glass lizard (*Ophisaurus* species), the striped mud turtle (*Kinosternon bauri*), the leopard frog (*Rana pipiens*), the southern toad (*Bufo terrestris*), and the oak toad (*B. quercicus*) occur on the lower Keys and the southern mainland, but not on the upper Keys. The cricket frog (*Acris gryllus*) may be added if an old Key West record is valid. A pine (*Pinus caribaea*),

the sawgrass (*Mariscus jamaicensis*), the cabbage palm (*Sabal palmetto*) and the waxmyrtle (*Myrica cerifera*), common to the mainland and the lower Keys, are lacking from most or all of the upper Keys (Alexander, 1953; Harper, 1927).

DISTRIBUTION AND PAST PERIODS OF LOW RAINFALL

The Pleistocene was characterized by fluctuations of rainfall. It has been suggested that increased precipitation, in some cases abetted by glacial chilling, once brought into Florida certain organisms which today are considered essentially upland or northern. The possible effects of a decrease in rainfall may now be considered.

The forests of eastern North America are replaced farther west by grassland. The amount of precipitation determines the nature of the plant climax, and a shift toward a drier climate would cause the grassland, and perhaps other western associations, to extend farther east than they do at present. In the past there have been such eastward extensions of a grassland or western biota (Deevey, 1949; Frey, 1951; Grobman, 1941; Hurt, 1953; Schmidt, 1939; Transeau, 1935). Fingers of grassland have at times extended into Ohio, Indiana, Michigan, Pennsylvania, and New York, bringing with them some animal species. Today, communities of prairie plants occur at isolated localities as far east as northwestern Pennsylvania and as far south as the Highlands Rim in Kentucky and Tennessee. The Black Belt of the Alabama coastal plain also supports an extensive prairie flora. Prior to settlement, portions of this belt were naturally treeless and thoroughly prairielike (Harper, 1943). One eastward extension of the grassland took place during the so-called climatic optimum, which lasted roughly from 7500 to 5000 years ago. However, the entry of a "western element" into Florida probably took place long before then; for in some cases remains of "western" organisms occur in older, Pleistocene deposits of the state. Pollen profiles from Lake Singletary, North Carolina, revealed a stratum characterized by grasses, composites, and sedges, with but few trees; and this stratum, implying grassland conditions, underlay the fir-spruce-pine stratum of the cold Mankato (Frey, 1951). There may have been several long periods of decreased rainfall during the Pleistocene, and western organisms may have invaded the east on a number of occasions.

Several western or grassland animals occur in the late Pleistocene of Florida, and a few essentially western species inhabit the state today. Pleistocene deposits in Florida have yielded remains of an extinct bison, horses, cameloids, and elephants, thought to have been

grassland species, and some large carnivores, thought to have preyed on the grazing animals. There were two armadillos, a coyote virtually identical with the modern one, a pocket gopher perhaps allied to the present western ones, and a peccary related to the species which today ranges into the southwestern United States (Gazin, 1950; Sherman, 1952; Simpson, 1929). There was a bear of the genus and subgenus *Ursus* (Gazin, 1950); within historic times this group ranged in the New World only from Alaska into Mexico. There was a jaguar perhaps slightly different from the present-day one; and a smaller cat, either the margay or the jaguarundi (*idem*). These felines are sometimes thought of as being tropical, but they also inhabit scrub country of the western United States (Hock, 1955). The Pleistocene avifauna of Florida included a few western species, the most impressive being the California condor or rather its Pleistocene ancestor (Wetmore, 1931).

Today the western element is typified by the Florida jay (*Aphelocoma c. caerulescens*). This bird, confined to rosemary scrub areas of the peninsula, is nearly identical with certain jays found from Texas westward. The restriction of this jay to scrub is interesting; there are a number of similarities between Florida scrub and some western habitats (Sutton, 1949). Another western species in the state is the burrowing owl (*Speotyto cunicularia*). One race of this bird ranges no farther east than the Great Plains; another is confined to peninsular Florida. The Florida burrowing owl inhabits a situation locally called "prairie": flat or gently undulating land, virtually treeless, covered with low grasses and forbs, and dotted with clumps of saw-palmetto and other shrubs. In the upper part of the peninsula it inhabits cleared, grassy rangeland (Neill, 1954a). Ornithologists have mentioned the black-necked stilt (*Himantopus mexicanus*) as one of the western birds in Florida, but its extremely wide distribution renders its presence in Florida unimpressive. One race of the sandhill crane (*Grus canadensis*) inhabits Florida, while the other races are western. The duck *Anas fulvigula* occurs as two populations, one race being endemic to Florida while the other is found in southern Louisiana and Texas. A race of the caracara (*Caracara cheriway*), confined in Florida to the peninsula, is identical with that occurring from Texas and Baja California to Central America (Sprunt, 1954). Perhaps the indigo snake (*Drymarchon corais*) should be mentioned here. One race of this species ranges northward from Mexico into south-central Texas. Eastward of this area no indigo snakes are found until one reaches the western end of the Florida panhandle, where there is a disjunct population. Another population, perhaps disjunct, inhabits southern Georgia; and the species is fairly common throughout much of peninsular

Florida. The case parallels that of the Florida jay, except that the snake has one or two relic populations along the route of eastward migration. A gap in the route may be filled by a Pleistocene specimen from eastern Texas; it was taken from a caliche deposit in an area which, today, is too moist for caliche formation (Harrington, 1953).

Perhaps the vinegaroon or whip-tailed scorpion (*Mastigoproctus giganteus*) should be listed as "western." Common from Texas and Arizona into Mexico, it is also found in the central Florida sandhills. Its range has been given as "Arizona to Florida" (Pratt, 1929), implying continuity; but its comparative abundance in the peninsula is noteworthy.

Impressively "western" scenery is to be found along the relatively dry west coast of the peninsula from the Manatee River to the lower Keys. Here there is an association known as cactus thicket, composed largely of stiff, crooked, spiny shrubs. These include several genera of cacti, some of the plants up to 20 feet tall; huge centuryplants (*Agave*); yucca; a coralbean (*Erythrina arborea*); wait-a-bit (*Guilandina crista*); and cock-spur (*Pisonia aculeata*). A number of these plants occur also in southern Texas and Mexico (Harper, 1927; Small, 1933). The association has been called "the most remarkable natural cactus-garden east of the western American deserts" (Small, 1921, p. 51). A common grass of the region, *Monanthochloe littoralis*, likewise occurs in southern Texas and Mexico. Some of these plants may be relics of an early invasion from the west during a dry period, surviving today in an area where relatively low rainfall and soil porosity produce extremely arid conditions.

It may be significant that some western organisms, recently introduced, seem to thrive in rosemary scrub and high pine of interior Florida, as well as on sandy coastal islands of the state. The armadillo (*Dasypus novemcinctus*) and the Texas horned lizard (*Phrynosoma cornutum*) are noteworthy in this regard (Allen and Neill, 1955a; Neill, 1952).

THE SUPPOSED "SOUTH AMERICAN ELEMENT"

Certain authors, remarking on a "South American element" among the Pleistocene mammals of Florida and nearby areas, have suggested that tropical conditions once prevailed in the southeastern United States. However, many South American animals are not tropical; and some of them belong to groups that originated in North America and subsequently spread. Furthermore, the South American element is comprised mostly of extinct species, and the majority represent extinct genera. One cannot even speculate about the temperature and mois-

ture requirements of such animals; efforts to do so will not withstand analysis. For example, tapirs of the genus *Tapirus* occurred in the Pleistocene of Florida; and a surviving species of *Tapirus* is Neotropical. However, the genus ranges in time from the upper Miocene to the present day, and in space from North and South America to Asia and Europe. One could hardly derive any climatic data from the presence of *Tapirus* in the Florida Pleistocene. Most of the South American element are equally useless as indicators of past climatic conditions, although we might draw some conclusions from those species that are still in existence. All of these, while occurring in tropical situations, also inhabit dry, brushy country of the southwestern United States.⁴

THE TROPICAL ELEMENT IN FLORIDA

The present climate of the coastal plain in the southeastern United States appears to be suitable for many tropical organisms, once they are introduced. Thus, the axis deer is spreading in Florida east of the St. Johns River (Allen and Neill, 1954); the sambar deer has done well on St. Vincents Island near the mouth of the Apalachicola (*idem*; Newman, 1948); there are two colonies of rhesus monkeys in Marion County; the nutria is well established in parts of the southeast (Dozier, MS) and has been collected in the Florida panhandle; the cattle egret seems destined to spread widely in North America (Sprunt, 1953, 1954); the greenhouse frog of Cuba is now common in Florida at least as far north as Alachua County (Goin, 1947); the water-hyacinth has been overly successful in a number of southern states and especially in Florida (Weeks and Bissland, 1949).

So far as I can see, the only tropical element to reach Florida without man's aid did so across water, from the West Indies. The climax community of extreme southern Florida is tropical hammock, dominated by such West Indian species as Jamaica dogwood, poisonwood, lignumvitae, mastic, and mahogany. Other tropical plants, apparently native to southern Florida as well as to the Caribbean islands, include the trema, papaya, potato tree, lantanas, gumbo-limbo, stoppers (*Eugenia*), strangler-figs, wild tamarind, soapberry, bustic (*Dipholis*), thatch palms, crabwood, lancewood, manchineel, Paradise tree, fiddlewood, satinleaf, wild coffee (*Psychotria*), and rough velvetseed

⁴ The biogeographer need not try to fit the jaguar and the porcupine into the same ecological picture. Pleistocene deposits in Florida are not necessarily all of the same age. They have faunal differences; and fluctuations of climate might have brought species into or out of Florida within a short time, geologically speaking.

(*Guettarda*). A few tropical plants have produced distinctive forms in southern Florida (and some of the temperate, central Florida species have done likewise). Thus the subtropical portion of the state is another area of endemism in plants (Davis, 1943; Harper, 1927, 1949; Small, 1933). However, as noted previously, Florida has no really impressive endemic flora of tropical affinities; and it seems likely that the present West Indian floral element moved into the state since Wisconsin times (Dillon, 1956).

Tropical birds, currently or until recently breeding in southern Florida, include the Everglades kite (*Rostrhamus sociabilis*), the short-tailed hawk (*Buteo brachyurus*), the reddish egret (*Dichromanassa rufescens*), the scarlet ibis (*Eudocimus ruber*), the roseate spoonbill (*Ajaia ajaia*), the flamingo (*Phoenicopterus ruber*), the eastern white-winged dove (*Zenaida asiatica*), Maynard's cuckoo (*Coccyzus minor*), the black-whiskered vireo (*Vireo altiloquus*), and the white-crowned pigeon (*Columba leucocephala*) (Sprunt, 1954). Numerous other tropical birds, such as the emerald hummingbird, the Bahama honey creeper, and Bahama grassquit, have turned up in Florida as accidental visitors or wanders, especially after storms. Two tropical bats (*Eumops glaucinus* and *Artibeus jamaicensis*) have also appeared in the state (Sherman, 1952). A tropical bird, the smooth-billed ani (*Crotophaga ani*), recently changed its Florida status from casual visitor to breeding resident. Other tropical organisms native to southern Florida and parts of the Caribbean include the West Indian seal (*Monachus tropicalis*), which is almost extinct, and no longer to be found in Florida waters; a crocodile (*Crocodylus acutus*); and the reef gecko (*Sphaerodactylus notatus*). A common Caribbean anole (*Anolis sagrei*) apparently has been in Florida for a long while, having produced a race on Key West (Oliver, 1948).

Several tropical amphibians and reptiles, mostly of West Indian origin, are now established in southern Florida. A few of these may have arrived by waifing, but most were introduced by man. Included are three Neotropical frogs, as well as 10 Neotropical lizards and a Mediterranean one.⁵ The success of these species in southern Florida may reflect the presence of tropical habitats in that area, unoccupied

⁵ Neotropical introductions are: Lizards—*Sphaerodactylus notatus*, *S. cinereus*, *S. argus*, *Gonotodes fuscus*, *Leiocephalus carinatus*, *Anolis s. sagrei*, *A. s. ordinatus*, *A. distichus* subspecies, *A. equestris*, *Ameiva ameiva*. Frogs—*Eleutherodactylus ricordi planirostris*, *Hyla septentrionalis*, *Bufo marinus*. The Mediterranean lizard *Hemidactylus turcicus* is introduced. Of these, *A. equestris*, *Ameiva*, and *Bufo* have not been mentioned in the literature.

by reptiles and amphibians of temperate stocks. Various tropical plants, deliberately imported by man, now grow wild in Florida.

SUMMARY

Perhaps the distribution of many Florida organisms could be explained solely in terms of present-day environmental conditions. This is particularly true of species which readily disseminate themselves and for which the old Pleistocene barriers are no longer significant. For example, a plant with airborne seeds might take root anywhere that climatic, edaphic, and biotic conditions permit. The distribution of such a species is a matter for the biogeographer whose approach is largely ecological. There remain, however, numerous Florida plants and animals whose present ranges apparently reflect not only the environmental conditions of today but also the geologic and climatic events of past ages.

In consequence, one might recognize seven biogeographic areas of Florida, some much better defined than others. These are (1) the western panhandle; (2) the Apalachicola drainage; (3) the remainder of the panhandle, not markedly different from adjoining portions of the Gulf coastal plain in Alabama and Georgia; (4) northeastern Florida, but slightly differentiated from the lower Atlantic coastal plain of Georgia; (5) the central Florida highlands; (6) the Gulf Hammock; and (7) the subtropical tip of the peninsula. It should be noted that in most cases these areas are bounded not by lines but by fairly wide zones of transition or of commingling, perhaps because many of the Pleistocene barriers to distribution no longer exist.

It should also be noted that the biogeographic conclusions reached herein are tentative. The intriguing problems of biogeography require for their solution the services of collectors, taxonomists, paleontologists, geologists, ecologists, archeologists, palynologists, climatologists, and others. If the present trend toward compartmentalization of knowledge be deemed inevitable, then let me end with a plea for interdisciplinary cooperation.

BIBLIOGRAPHY AND LITERATURE CITED

ADAMS, CHARLES C.

1902. Southeastern United States as a center of geographical distribution for flora and fauna. Biol. Bull., vol. 3, no. 3, pp. 115-131.

ALEXANDER, TAYLOR R.

1953. Plant succession on Key Largo, Florida, involving *Pinus caribaea* and *Quercus virginiana*. Quart. Jour. Florida Acad. Sci., vol. 16, no. 3, pp. 133-138.

ALLEN, E. ROSS, and WILFRED T. NEILL

1952. Notes on the abundance of the Everglades mink. Jour. Mammal, vol. 33, no. 1, pp. 113-114.

1954. The Florida deer. Florida Wildlife, vol. 7, no. 9, pp. 21, 37.

1955a. Establishment of the Texas horned toad, *Phrynosoma cornutum*, in Florida. Copeia, 1955, no. 1, pp. 63-64.

1955b. Rabbits of the southeast. Florida Wildlife, vol. 8, no. 10, pp. 28, 48.

ANTHONY, H. E.

1928. Field book of North American mammals. New York, pp. i-xxvi, 1-625, pls. 1-48.

AUFFENBERG, WALTER

1955a. A reconsideration of the racer, *Coluber constrictor*, in eastern United States. Tulane Studies Zool., vol. 2, no. 6, pp. 89-155.

1955b. Glass lizards (*Ophisaurus*) in the Pleistocene and Pliocene of Florida. Herpetologica, vol. 11, pt. 2, pp. 133-136. Author's name is rendered "Auffenburg" in the original publication.

1956. Additional records of Pleistocene lizards from Florida. Quart. Jour. Florida Acad. Sci., vol. 19, nos. 2-3, pp. 157-167.

BAILEY, REEVE M., and CARL L. HUBBS

1949. The black basses (*Micropterus*) of Florida, with description of a new species. Occas. Papers Mus. Zool., Univ. Mich., no. 516, pp. 1-40, 2 pls.

BAILEY, REEVE M., H. E. WINN and C. L. SMITH

1954. Fishes from the Escambia River, Alabama and Florida, with ecologic and taxonomic notes. Proc. Acad. Nat. Sci. Philadelphia, vol. 106, pp. 109-164.

BAKER, F. C.

1937. Pleistocene land and fresh-water Mollusca as indicators of time and ecological conditions. In G. G. MacCurdy. Early man. Philadelphia, pp. 67-74.

BEECHER, WILLIAM J.

1955. Late-Pleistocene isolation in salt-marsh sparrows. Ecology, vol. 36, no. 1, pp. 23-28.

BEQUAERT, J. C.

1943. The genus *Littorina* in the western Atlantic. Johnsonia, vol. 1, no. 7, pp. 1-28.

BERNER, LEWIS

1948. Records of stoneflies from Florida (*Plecoptera*). Florida Entomol., vol. 31, no. 1, pp. 21-23.

1950. The mayflies of Florida. Univ. Florida Studies, biol. sci. ser., vol. 4, no. 4, pp. i-xii, 1-267.

BERNER, LEWIS, and W. C. SLOAN

1954. The occurrence of a mayfly nymph in brackish water. Ecology, vol. 35, no. 1, p. 98.

BISHOP, SHERMAN C.

1943. Handbook of salamanders: The salamanders of the United States, of Canada, and of Lower California. Ithaca, pp. i-xiv, 1-555, 144 figs., 1 pl., 55 maps.

BLANCHARD, FRANK N.

1921. A revision of the king snakes: Genus *Lampropeltis*. Bull. U.S. Natl. Mus., no. 114, pp. 1-260.

BOND, JAMES

1945. Check-list of birds of the West Indies. Acad. Nat. Sci. Philadelphia, pp. i-xiii, 1-182, 1 map.

BOYNTON, JOHN O.

1950. *Rhododendron Chapmanii* found between two previously reported stations. Quart. Jour. Florida Acad. Sci., vol. 12, no. 4, p. 253.

BRATTSTROM, BAYARD H.

1943. Records of Pleistocene reptiles and amphibians from Florida. Quart. Jour. Florida Acad. Sci., vol. 16, no. 4, pp. 243-248.

BRODKORB, PIERCE

1953. Pleistocene birds from Haile, Florida. Wilson Bull., vol. 65, no. 1, pp. 49-50.

BROOKS, C. E. P.

1949. Climate through the ages, a study of the climatic factors and their variations. New York, pp. 1-395.

BROWN, C. A.

1938. The flora of Pleistocene deposits in the western Florida parishes, West Feliciana Parish, and East Baton Rouge Parish, Louisiana. Geol. Bull., Louisiana Dept. Conserv., vol. 12, pp. 59-96.

BULLEN, ADELAIDE K., and RIPLEY P. BULLEN

1950. The Johns Island site, Hernando County, Florida. Amer. Antiquity, vol. 16, no. 1, pp. 23-45.
1953. The Battery Point site, Bayport, Hernando County, Florida. Florida Anthropol., vol. 6, no. 3, pp. 85-92.

BURKENROAD, M. D.

1939. Further observations on Penaeidae of the northern Gulf of Mexico. Bull. Bingham Oceanogr. Coll., vol. 16, no. 6, pp. 1-62.

BYERS, C. FRANCIS

1930. A contribution to the knowledge of Florida Odonata. Univ. Florida Publ., biol. sci. ser., vol. 1, no. 1, pp. 1-327.

CAGLE, FRED R.

1952. The status of the turtles *Graptemys pulchra* Baur and *Graptemys barbouri* Carr and Marchand, with notes on their natural history. Copeia, 1952, no. 4, pp. 223-234.
1954. Two new species of the genus *Graptemys*. Tulane Studies Zool., vol. 1, no. 11, pp. 167-186.

CAMPBELL, R. B.

1940. Outline of the geological history of peninsular Florida. Proc. Florida Acad. Sci., vol. 4, pp. 87-105.

CARR, ARCHIE F., JR.

- 1937a. A key to the fresh-water fishes of peninsular Florida. Proc. Florida Acad. Sci. for 1936, vol. 1, pp. 72-86.
- 1937b. The Gulf-island cottonmouths. *Ibid.*, vol. 1, pp. 86-90.
1940. A contribution to the herpetology of Florida. Univ. Florida Publ., biol. sci. ser., vol. 3, no. 1, pp. 1-118.

CARR, ARCHIE F., JR., and COLEMAN J. GOIN

1942. Rehabilitation of *Natrix sipedon taeniata* Cope. Proc. New England Zool. Club, vol. 21, pp. 47-54, pls. 6-7.
1955. Guide to the reptiles, amphibians, and fresh-water fishes of Florida. Gainesville, pp. i-ix, 1-341.

CLENCH, WILLIAM J., and RUTH D. TURNER

1956. Freshwater mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River. Bull. Florida State Mus., vol. 1, no. 3, pp. 97-239.

COLLINS, W. D., and C. S. HOWARD

1928. Chemical characters of waters of Florida. U.S. Geol. Surv., Water Supply Paper 596-G, pp. 177-233, pls. 1-4.

COOKE, C. WYTHE

1939. Scenery of Florida interpreted by a geologist. Florida State Geol. Surv., Geol. Bull. no. 17, pp. 1-118.

1945. Geology of Florida. *Ibid.*, no. 29, pp. i-ix, 1-339, 47 figs., 1 map.

COWLES, H. C.

1904. A remarkable colony of northern plants along the Apalachicola River, Florida, and its significance. Rept. 8th Internatl. Geogr. Congr., p. 599.

CROSS, WILLIAM H.

1955. *Gomphus australis* Needham in north Florida, with a description of the female (Odonata: Gomphidae). Florida Entomol., vol. 37, no. 3, pp. 125-127.

DALL, W. H.

- 1890-1903. Tertiary mollusks of Florida. Trans. Wagner Free Inst. Sci. Philadelphia, vol. 3, nos. 1-6, pp. 1-1654, 60 pls.

DARLINGTON, P. J., JR.

1938. The origin of the fauna of the Greater Antilles with discussion of the dispersal of animals over water and through the air. Quart. Rev. Biol., vol. 13, pp. 274-300.

1948. The geographical distribution of cold-blooded vertebrates. *Ibid.*, vol. 23, pp. 1-26, 105-123.

DAVIS, JOHN H., JR.

1940. The ecological and geological role of mangroves in Florida. Carnegie Inst. Washington Publ., no. 517, pp. 303-412.

1943. The natural features of southern Florida: Especially the vegetation, and the Everglades. Florida State Geol. Surv., Geol. Bull. no. 25, pp. 1-311.

1946. The peat deposits of Florida. Their occurrences, development, and uses. *Ibid.*, no. 30, pp. i-vi, 1-247, 37 figs., 1 map.

DECKERT, R. F.

1918. A list of reptiles from Jacksonville, Florida. Copeia, no. 54, pp. 30-33.

DEEVEY, EDWARD S.

1949. Pleistocene research. 3. Biography of the Pleistocene. Bull. Geol. Soc. Amer., vol. 60, pp. 1315-1416.

1950. Hydroids from Louisiana and Texas, with remarks on the Pleistocene biogeography of the western Gulf of Mexico. Ecology, vol. 31, no. 3, pp. 334-367.

DENDY, JACK S., and D. C. SCOTT

1953. Distribution, life history, and morphological variations of the southern brook lamprey, *Ichthyomyzon gagei*. Copeia, 1953, no. 3, pp. 152-162.

DICE, LEE R.

1943. The biotic provinces of North America. Ann Arbor, Michigan, pp. i-viii, 1-78.

DILLON, LAURENCE S.

1956. Wisconsin climate and life zones in North America. *Science*, vol. 123, no. 3188, pp. 167-176.

DOWLING, HERNDON G.

1950. Studies of the black swamp snake, *Seminatrix pygaea* (Cope), with descriptions of two new subspecies. *Misc. Publ., Mus. Zool. Univ. Michigan*, no. 76, pp. 1-38.

DOZIER, H. L.

- [MS.] The present status and future of nutria in the southeastern states. Presented at the 1951 meeting of the Southeastern Association of Game and Fish Commissioners, Gulfport, Mississippi. Pp. 1-10.

DUNCAN, WILBUR H.

1950. Preliminary reports on the flora of Georgia. 2. The distribution of 87 trees. *Amer. Midland Nat.*, vol. 43, no. 3, pp. 742-761.

EKMEN, SVEN

1935. *Tiergeographie des Meeres*. Leipzig, pp. i-xii, 1-542, 244 figs.

ERICSON, DAVID B., W. S. BROECKER, J. L. KULP, and GOESTA WOLLIN

1956. Late-Pleistocene climates and deep-sea sediments. *Science*, vol. 124, no. 3218, pp. 385-389.

ESHLEMAN, S. KENDRICK

1950. A key to Florida's fresh-water sponges, with descriptive notes. *Quart. Jour. Florida Acad. Sci.*, vol. 12, no. 1, pp. 35-44.

EWING, MAURICE, and W. L. DONN

1956. A theory of Ice Ages. *Science*, vol. 123, no. 3207, pp. 1061-1066.

FENNEMAN, N. M.

1938. *Physiography of eastern United States*. New York, pp. i-xiii, 1-714.

FERGUSON, G. E., C. W. LINGHAM, S. K. LOVE, and R. O. VERNON

1947. Springs of Florida. *Florida State Geol. Surv., Geol. Bull.*, no. 31, pp. i-xii, 1-196, 37 figs.

FIELD, WILLIAM O.

1955. Glaciers. *Sci. Amer.*, vol. 193, no. 3, pp. 84-86, 88, 90, 92.

FISK, H. N.

1938. Pleistocene exposures in western Florida parishes, Louisiana. *Geol. Bull., Louisiana Dept. Conserv.*, vol. 12, pp. 3-25.

FLINT, RICHARD F.

1947. *Glacial geology and the Pleistocene epoch*. New York, pp. i-xviii, 1-589, 6 pls.

1956. New radiocarbon dates and late-Pleistocene stratigraphy. *Amer. Jour. Sci.*, vol. 254, no. 5, pp. 265-287.

FLINT, RICHARD F., and EDWARD S. DEEVEY, JR.

1951. Radiocarbon dating of late Pleistocene events. *Amer. Jour. Sci.*, vol. 249, pp. 257-300.

FREY, DAVID G.

1951. Pollen succession in the sediments of Singletary Lake, North Carolina. *Ecology*, vol. 32, pp. 518-533.

GAZIN, C. LEWIS

1950. Annotated list of fossil Mammalia associated with human remains at Melbourne, Florida. *Jour. Washington Acad. Sci.*, vol. 40, no. 12, pp. 397-404.

GINSBURG, ISAAC

1932. A revision of the genus *Gobionellus* (family Gobiidae). Bull. Bingham Oceanogr. Coll., vol. 4, no. 2, pp. 1-51.

1933. A revision of the genus *Gobiosoma* (family Gobiidae). *Ibid.*, vol. 4, no. 5, pp. 1-59.

GODFREY, R. K., and R. KRAL

[MS.] Unreported or otherwise noteworthy vascular plants from western Florida. Presented at the 1956 meeting of the Florida Academy of Sciences, Tampa. Reports an impressive group of "northern disjuncts," especially among lower plants.

GOGGIN, JOHN M.

1948. Florida archeology and recent ecological changes. Jour. Washington Acad. Sci., vol. 38, no. 7, pp. 225-233.

1952. Space and time perspective in northern St. Johns archeology, Florida. Yale Univ. Publ. Anthropol., no. 47, pp. 1-147, 12 pls.

GOIN, COLEMAN J.

1947. Studies on the life history of *Eleutherodactylus ricordii planirostris* (Cope) in Florida. Univ. Florida Studies, biol. sci. ser., vol. 4, no. 2, pp. i-ix, 1-66, 7 figs., 6 pls.

GOIN, COLEMAN J., and WALTER AUFFENBERG

1955. The fossil salamanders of the family Sirenidae. Bull. Mus. Comp. Zool., vol. 113, no. 7, pp. 497-514.

GROBMAN, ARNOLD B.

1941. A contribution to the knowledge of variation in *Opheodrys vernalis* (Harlan), with the description of a new subspecies. Misc. Publ. Mus. Zool. Univ. Michigan, no. 50, pp. 1-38.

1950. The distribution of the races of *Desmognathus fuscus* in the southern states. Nat. Hist. Miscellanea, vol. 70, pp. 1-8, 2 figs.

1954. Florida State Museum, report of the Director for 1953-54. Gainesville, pp. 1-12.

GUNTER, HERMAN, and G. M. PONTON

1933. Notes on the ecology and the occurrence of some diatomaceous earth deposits of Florida. Florida Geol. Surv. 23rd and 24th Ann. Rept., pp. 57-64.

HAMILTON, W. J., JR.

1943. Mammals of eastern United States. Ithaca, pp. 1-432.

HANNA, G. D.

1933. Diatoms of the Florida peat deposits. Florida Geol. Surv. 23rd and 24th Ann. Rept., pp. 67-119.

HARPER, ROLAND M.

1914. Geography and vegetation of northern Florida. Florida Geol. Surv. 6th Ann. Rept., pp. 163-437, 49 figs., 1 map.

1921. Geography of central Florida. Florida Geol. Surv. 13th Ann. Rept., pp. 71-307, 40 figs., 2 graphs.

1927. Natural resources of southern Florida. Florida Geol. Surv. 18th Ann. Rept., pp. 27-206, 50 figs., 2 maps, 4 graphs.

1930. The natural resources of Georgia. Bull. Univ. Georgia, vol. 30, no. 3, pp. i-xi, 1-105, 12 figs.

1943. Forests of Alabama. Geol. Surv. Alabama Monogr. no. 10, pp. 1-230.

1949. A preliminary list of the endemic flowering plants of Florida. Part 1. Introduction and history of exploration. Quart. Jour. Florida Acad. Sci. for 1948, vol. 11, no. 1, pp. 25-35. Part 2. List of species. *Ibid.*, vol. 11, nos. 2-3, pp. 39-57.
1950. [Same title.] Part 3. Notes and summary. Quart. Jour. Florida Acad. Sci. for 1949, vol. 12, no. 1, pp. 1-19.
- HARRINGTON, J. W.
1953. A fossil Pleistocene snake from Denton County, Texas. Field and Lab., vol. 21, no. 1, p. 20.
- HARSHBERGER, J. W.
1914. The vegetation of South Florida south of 27° 30' north, exclusive of the Florida Keys. Trans. Wagner Free Inst. Sci. Philadelphia, vol. 6, no. 3, pp. 51-189, 1 fig., 10 pls., 1 map.
- HENDERSON, J. R.
1939. The soils of Florida. Bull. Univ. Florida Agr. Exp. Sta., no. 334, pp. 1-67, 5 figs., 2 maps.
- HESSE, R. W., W. C. ALLEE, and K. P. SCHMIDT
1937. Ecological animal geography. New York, pp. 1-597.
- HETRICK, L. A.
1949. Field notes on a color variant of the two-striped walkingstick, *Anisomorpha buprestoides*. Florida Entomol., vol. 32, no. 2, pp. 74-77.
- HIBBARD, C. W.
1949. Pleistocene vertebrate paleontology in North America. Bull. Geol. Soc. Amer., vol. 60, pp. 1417-1428.
- HIGHTON, RICHARD
1956. Systematics and variation of the endemic Florida snake genus *Stilosoma*. Bull. Florida State Mus., vol. 1, no. 2, pp. 73-96.
- HILDEBRAND, S. F.
1943. A review of the American anchovies (family Engraulidae). Bull. Bingham Oceanogr. Coll., vol. 8, no. 2, pp. 1-165.
- HOBBS, HORTON H., JR.
1942. The crayfishes of Florida. Univ. Florida Publ., biol. sci. ser., vol. 3, no. 2, pp. i-iv, 1-179, 24 pls., 11 maps.
1944. Notes on the subterranean waters of the Florida peninsula with particular reference to their crustacean fauna. The Biologist, vol. 26, nos. 1-2, pp. 6-8.
- HOCK, R. J.
1955. Southwestern exotic felids. Amer. Midland Nat., vol. 53, no. 2, pp. 324-328.
- HOVANITZ, WILLIAM
1950. The biology of *Colias* butterflies. 1. The distribution of the North American species. Wasmann Jour. Biol., vol. 8, no. 1, pp. 49-75.
- HUBBELL, T. H.
1932. A revision of the *Puer* group of the North American genus *Melanoplus*. Misc. Publ. Mus. Zool. Univ. Michigan, no. 23, pp. 1-64, 1 fig., 4 pls.
1936. A monographic revision of the genus *Ceuthophilus*. Univ. Florida Publ., biol. sci. ser., vol. 2, no. 1, pp. 1-550.
1940. Supplementary notes on *Hubbellia marginifera* (Walker). Florida Entomol., vol. 23, no. 1, pp. 12-13.
1954. Relationships and distribution of *Mycotrupes* (pt. 2) In Ada L. Olson,

- T. H. Hubbell, and H. F. Howden. The burrowing beetles of the genus *Mycotrupes* (Coleoptera: Scarabaeidae: Geotrupinae). Misc. Publ. Mus. Zool. Univ. Michigan, no. 84, pp. 39-51.
- HUBBELL, T. H., and C. C. GOFF
1940. Florida pocket-gopher burrows and their arthropod inhabitants. Proc. Florida Acad. Sci., vol. 4, pp. 127-166, 2 figs.
- HUBBELL, T. H., A. M. LAESSLE and J. C. DICKINSON
1956. The Flint-Chattahoochee-Apalachicola region and its environments. Bull. Florida State Mus., vol. 1, no. 1, pp. 1-72.
- HURT, WESLEY R., JR.
1953. A comparative study of the preceramic occupations of North America. Amer. Antiquity, vol. 18, no. 3, pp. 204-222.
- HUSSEY, ROLAND F.
1948. A new *Metrobates* from Florida (Hemiptera, Gerridae). Florida Entomol., vol. 31, no. 4, pp. 123-124.
- HUSSEY, R. F., and JON L. HERRING
1949. Notes on the variation of the *Metrobates* of Florida (Hemiptera, Gerridae). Florida Entomol., vol. 32, no. 4, pp. 166-170.
- JOHNSON, FREDERICK
1951. Radiocarbon dating. Mem. Soc. Amer. Arch., no. 8, pp. 5-19.
- KASTON, J.
1938. Notes on a new variety of black widow spider from southern Florida. Florida Entomol., vol. 21, no. 4, pp. 60-61.
- KURZ, HERMAN
1927. A new and remarkable habitat for the endemic Florida yew. *Torreya*, vol. 27, no. 5, pp. 90-92.
1928. Northern aspect and phenology of the Tallahassee Red Hills flora. Bot. Gaz., vol. 85, pp. 83-89.
1933. Northern disjuncts in northern Florida. Florida Geol. Surv. 23rd and 24th Ann. Rept., pp. 50-53.
1939. *Torreya* west of the Apalachicola River. Proc. Florida Acad. Sci. for 1938, pp. 66-67.
1942. Florida dunes and scrub, vegetation and geology. Geol. Bull., Florida Dept. Conserv., no. 23, pp. 1-154.
- LAESSLE, A. M.
1942. The plant communities of the Welaka area. Univ. Florida Publ., biol. sci. ser., vol. 4, no. 1, pp. 1-143, 25 figs., 14 pls.
- LANDSBERG, HELMUT
1949. Pleistocene research. 6. Climatology of the Pleistocene. Bull. Geol. Soc. Amer., vol. 60, pp. 1437-1442.
- LAWRENCE, BARBARA
1942. The muskrat in Florida. Proc. New England Zool. Club, vol. 19, pp. 17-20.
- LI, H.-L.
1952. Floristic relationships between eastern Asia and eastern North America. Trans. Amer. Phil. Soc. (new ser.), vol. 42, pp. 369-429.
- LOGAN, J. H.
1859. A history of the upper country of South Carolina, from the earliest periods to the close of the war of independence, vol. 1. Columbia, South Carolina, pp. 1-521.

MACNEILL, F. S.

1951. Pleistocene shore lines in Florida and Georgia. U.S. Geol. Surv. Prof. Paper, no. 221-F, pp. 95-107.

MAHAN, E. C.

1954. A survey of Paleo-Indian and other early flint artifacts from sites in northern, western, and central Alabama, pt. 1. Tennessee Archeol., vol. 10, no. 2, pp. 37-58.

McCONKEY, E. H.

1954. A systematic study of the North American lizards of the genus *Ophisaurus*. Amer. Midland Nat., vol. 51, no. 1, pp. 133-171.

MEADE, GRAYSON E.

1952. The water rat in the Pleistocene of Texas. Jour. Mammal., vol. 33, pp. 87-89.

MILLER, ALDEN H.

1956. Ecologic factors that accelerate formation of races and species of terrestrial vertebrates. Evolution, vol. 10, no. 3, pp. 262-277.

MITCHELL, A. J., and M. R. ENSIGN

1928. The climate of Florida. Bull. Univ. Florida Agr. Exp. Sta., no. 200, pp. 91-300.

MULVANIA, MAURICE

1931. Ecological survey of a Florida scrub. Ecology, vol. 12, no. 3, pp. 528-540.

MURRILL, WILLIAM A.

1946. Florida hickories. Quart. Jour. Florida Acad. Sci., vol. 9, no. 2, pp. 115-122.

NEILL, WILFRED T.

1948. A new subspecies of tree-frog from Georgia and South Carolina. Herpetologica, vol. 4, pt. 5, pp. 175-179.

1949. A new subspecies of rat snake (genus *Elaphe*) and notes on related forms. *Ibid.*, vol. 5, suppl. 2, pp. 1-12.

1950. The status of the Florida brown snake, *Storeria victa*. Copeia, 1950, no. 2, pp. 155-156.

- 1951a. The taxonomy of North American soft-shelled turtles, genus *Amyda*. Publ. Res. Div. Ross Allen's Reptile Inst., vol. 1, no. 2, pp. 7-24, 1 fig.

- 1951b. A new subspecies of dusky salamander, genus *Desmognathus*, from south-central Florida. *Ibid.*, vol. 1, no. 3, pp. 25-38.

1952. The spread of the armadillo in Florida. Ecology, vol. 33, no. 2, pp. 282-284.

- 1954a. Notes on the Florida burrowing owl, and some new records for the species. Florida Nat., vol. 27, no. 3, pp. 67-70.

- 1954b. Ranges and taxonomic allocations of amphibians and reptiles in the southeastern United States. Publ. Res. Div. Ross Allen's Reptile Inst., vol. 1, no. 7, pp. 75-96.

- [MS a.] The occurrence of amphibians and reptiles in saltwater areas, and a bibliography. Submitted to Bull. Marine Sci. Gulf and Caribbean.

- [MS b.] Submerged sites of the Florida Gulf Coast. Presented at the 1956 meeting of the Florida Anthropological Society, Rainbow Springs.

NEILL, WILFRED T., and E. ROSS ALLEN

1949. A new kingsnake (genus *Lampropeltis*) from Florida. Herpetologica, vol. 5, pt. 5 (special), pp. 101-105.

1950. *Eumeces fasciatus* in Florida. *Copeia*, 1950, no. 2, p. 156.
- NEILL, WILFRED T., and RIPLEY P. BULLEN
1955. Muskrat remains from a prehistoric Indian site in Jackson County, Florida. *Jour. Mammal.*, vol. 36, no. 1, p. 138.
- NEWMAN, COLEMAN
1948. Florida's big game. *Florida Wildlife*, vol. 1, no. 12, pp. 4-5, 18.
- ODUM, H. T.
1953. Factors controlling marine invasion into Florida fresh waters. *Bull. Marine Sci. Gulf and Caribbean*, vol. 3, no. 2, pp. 134-156.
- OLIVER, JAMES A.
1948. The anoline lizards of Bimini, Bahamas. *Amer. Mus. Novitates*, no. 1383, pp. 1-36.
- OLSON, ADA L., T. H. HUBBELL, and H. F. HOWDEN
1954. The burrowing beetles of the genus *Mycotrupes* (Coleoptera: Scarabaeidae: Geotrupinae). *Misc. Publ. Mus. Zool. Univ. Michigan*, no. 84, pp. 1-59, 8 pls.
- OOSTING, H. J., and D. W. HESS
1956. Microclimate and a relic stand of *Tsuga canadensis* in the lower piedmont of North Carolina. *Ecology*, vol. 37, no. 1, pp. 28-39.
- ORTMANN, A. E.
1902. The geographical distribution of fresh-water decapods and its bearing upon ancient geography. *Proc. Amer. Phil. Soc.*, vol. 41, no. 171, pp. 267-400.
- PHLEGER, FRED B., JR.
1948. Foraminifera of a submarine core from the Caribbean Sea. *Göteborgs Kungl. Vetenskap- och Vitterhets-Samhälle, Handlingar*, fasc. 6, ser. B, vol. 5, no. 14, pp. 1-9.
- POTZGER, J. E., and B. C. THARP
1943. Pollen record of Canadian spruce and fir from a Texas bog. *Science*, vol. 98, p. 584.
1947. Pollen profile from a Texas bog. *Ecology*, vol. 28, pp. 274-279.
1954. Pollen study of two bogs in Texas. *Ibid.*, vol. 35, no. 4, pp. 462-466.
- PRATT, HENRY S.
1929. A manual of the common invertebrate animals exclusive of insects. Chicago, pp. 1-737.
- PURSELL, RONALD A.
[MS.] Significant bryophytes from west Florida. Presented at the 1956 meeting of the Florida Academy of Sciences, Tampa. Reports several "northern disjuncts."
- RATHBUN, M. J.
1918. The grapsoid crabs of America. *Bull. U.S. Natl. Mus.*, no. 97, pp. i-xxii, 1-461, 161 pls.
- RAY, LOUIS L.
1949. Pleistocene Research. 9. Problems of Pleistocene stratigraphy. *Bull. Geol. Soc. Amer.*, vol. 60, pp. 1463-1474.
- RICE, DALE W.
1955a. Status of *Myotis grisescens* in Florida. *Jour. Mammal.*, vol. 36, no. 2, pp. 289-290.
1955b. *Myotis keenii* in Florida. *Ibid.*, vol. 36, no. 4, p. 567.

ROGERS, J. SPEED

1933. The ecological distribution of the craneflies of northern Florida. Ecol. Monogr., vol. 3, no. 1, pp. 1-74, 25 figs.

ROUSE, IRVING

1951. A survey of Indian River archeology. Yale Univ. Publ. Anthropol., no. 44, pp. 1-296, 8 pls.

RUTHVEN, ALEXANDER G.

1908. Variations and genetic relationships of the garter-snakes. Bull. U.S. Natl. Mus., no. 61, pp. i-xii, 1-201, 82 figs., 1 pl.

ST. JOHN, EDWARD P.

1936. Rare ferns of central Florida. Amer. Fern Jour., vol. 26, pp. 41-55, 3 figs., 2 pls.

SCHARFF, R. F.

1911. Distribution and origin of life in America. London, pp. i-xvi, 1-497, 21 figs.

SCHMIDT, KARL P.

1939. Herpetological evidence for the post-glacial eastward extension of the steppe in North America. Ecology, vol. 19, no. 3, pp. 396-407.
1946. On the zoogeography of the Holarctic region. Copeia, 1946, no. 3, pp. 144-152.
1954. Faunal realms, regions, and provinces. Quart. Rev. Biol., vol. 29, no. 4, pp. 322-331.

SCHUCHERT, CHARLES

1935. Historical geology of the Antillean-Caribbean region. New York, pp. i-xxvi, 1-811, 107 figs., 16 maps.

SCHWARTZ, ALBERT

1953. A systematic study of the water rat (*Neofiber alleni*). Occas. Papers Mus. Zool. Univ. Michigan, no. 547, pp. 1-27, 3 pls.

SEARS, PAUL B.

1948. Forest sequence and climatic change in northeastern North America since early Wisconsin time. Ecology, vol. 29, no. 3, pp. 326-333.

SELLARDS, E. H.

1910. Some Florida lakes and lake basins. Florida State Geol. Surv. 3rd Ann. Rept., 5 figs., 4 pls.
1912. The soils and other surface residual materials of Florida. Florida State Geol. Surv. 4th Ann. Rept., pp. 1-79.
1916. Human remains and associated fossils from the Pleistocene of Florida. Florida State Geol. Surv. 8th Ann. Rept., pp. 121-168.

SHAPLEY, HARLOW (editor)

1954. Climatic change: Evidence, causes, and effects. Cambridge, Massachusetts, pp. i-xii, 1-318.

SHERMAN, HARLEY B.

1937. A list of the recent wild land mammals of Florida. Proc. Florida Acad. Sci., vol. 1, pp. 102-128.
1952. A list and bibliography of the mammals of Florida, living and extinct. Quart. Jour. Florida Acad. Sci., vol. 15, no. 2, pp. 86-126.

SIMPSON, GEORGE G.

1929. The extinct land mammals of Florida. Florida State Geol. Surv. 20th Ann. Rept., pp. 229-280.

1931. Origin of mammalian faunas as illustrated by that of Florida. *Amer. Nat.*, vol. 65, pp. 258-276.
1947. Evolution, interchange, and resemblance of the North American and Eurasian Cenozoic mammalian faunas. *Evolution*, vol. 1, no. 3, pp. 218-220.
- SLOAN, WILLIAM C.
1956. The distribution of aquatic insects in two Florida springs. *Ecology*, vol. 37, no. 1, pp. 81-98.
- SMALL, JOHN K.
1921. Old trails and new discoveries. *Jour. New York Bot. Garden*, vol. 22, pp. 25-40, 49-64.
1933. Manual of the southeastern flora. New York, pp. i-xxii, 1-1554.
1938. Ferns of the southeastern states. Lancaster, Pennsylvania, pp. 1-517.
- SMITH, H. T. U.
1949. Pleistocene research. 11. Physical effects of Pleistocene climatic changes in nonglaciated areas: Eolian phenomena, frost action, and stream terracing. *Bull. Geol. Soc. Amer.*, vol. 60, pp. 1485-1516, 6 figs., 1 pl.
- SPRUNT, ALEXANDER, JR.
1953. Newcomer from the Old World. *Audubon Mag.*, 55 (4): 178-181.
1954. Florida bird life. New York, pp. i-xlii and 1-527.
- STORM, L. W.
1945. Résumé of facts and opinions on sedimentation in the Gulf Coast region of Texas and Louisiana. *Bull. Amer. Assoc. Petrol. Geol.*, vol. 29, pp. 1304-1335.
- SUTTON, GEORGE M.
1949. Meeting the west on Florida's east coast. *Florida Nat.*, vol. 22, no. 2, pp. 23-33.
- TAYLOR, EDWARD H.
1935. A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces*. *Univ. Kansas Sci. Bull.*, vol. 23, pp. 1-643, 84 figs., 43 pls.
1951. Concerning Oligocene amphisbaenid reptiles. *Ibid.*, vol. 34, pt. 1, no. 9, pp. 521-579.
- THORNE, ROBERT F.
1949. Inland plants on the Gulf coastal plain of Georgia. *Castanea*, vol. 14, pp. 88-97.
1954. The vascular plants of southwestern Georgia. *Amer. Midland Nat.*, vol. 52, no. 2, pp. 257-327, maps.
- THORNTHWAITE, C. W.
1931. The climates of North America according to a new classification. *Geogr. Rev.*, vol. 21, pp. 633-655, 13 figs., 1 map.
- TINKLE, DONALD W., and ROBERT G. WEBB
1955. A new species of *Sternotherus* with a discussion of the *Sternotherus carinatus* complex. *Tulane Studies Zool.*, vol. 3, no. 3, pp. 53-67.
- TOTTEN, HENRY R.
1945. A station for *Rhododendron Chapmanii* in eastern Florida. *Proc. Florida Acad. Sci.*, vol. 7, nos. 2-3, p. 105.
- TRANSEAU, EDGAR N.
1935. The prairie peninsula. *Ecology*, vol. 16, no. 3, pp. 423-437.
- TRAPIDO, HAROLD
1944. The snakes of the genus *Storeria*. *Amer. Midland Nat.*, vol. 31, no. 1, pp. 1-84.

TRASK, P. D., F. B. PHLEGER, and H. C. STETSON

1947. Recent changes in sedimentation in the Gulf of Mexico. *Science*, vol. 106, pp. 460-461.

U.S. DEPARTMENT OF AGRICULTURE

1941. Climate and man. Washington, pp. i-xii, 1-1248.

UVAROV, B. P.

1940. The synonymy, systematic position and biogeographical importance of a Floridan tettigoniid (Orthoptera). *Florida Entomol.*, vol. 23, no. 1, pp. 10-12.

VAN DER SCHALLE, HENRY

1940. The naiad fauna of the Chipola River, in northwestern Florida. *Lloydia*, vol. 3, pp. 191-208, 3 pls., 1 map.

VANZOLINI, PAULO E.

1952. Fossil snakes and lizards from the lower Miocene of Florida. *Jour. Paleont.*, vol. 26, no. 3, pp. 452-457, 2 pls.

VISHER, S. S.

1954. Climatic atlas of the United States. Cambridge, Massachusetts, pp. 1-403.

WARD, R. DE C., and C. F. BROOKS

1936. The climates of North America, pt. 1. Mexico, United States, and Alaska. In W. Köppen and R. Geiger (editors), [1938], *Handbuch der Klimatologie*. Berlin, vol. 2, pt. J, x + 329 pp., 52 figs.

WEEKS, B., and H. R. BISSLAND

1949. Florida's stricken waters. *Florida Wildlife*, vol. 2, no. 1, pp. 1-5, 15, 18.

WETMORE, ALEXANDER

1931. The avifauna of the Pleistocene in Florida. *Smithsonian Misc. Coll.*, vol. 85, no. 2, pp. 1-41.

WHITE, T. E.

1942. The lower Miocene mammal fauna of Florida. *Bull. Mus. Comp. Zool.*, vol. 92, no. 1, pp. 1-49, 14 pls.

WILLEY, GORDON R.

1949. Archeology of the Florida gulf coast. *Smithsonian Misc. Coll.*, no. 113, pp. i-xxiii, 1-599, 60 pls.

WOODSON, R. E.

1947. Notes on the "historic factor" in plant geography. *Contrib. Gray Herbarium*, vol. 165, pp. 12-25.

WRIGHT, A. H., and A. A. WRIGHT

1932. The habitats and composition of the vegetation of Okefinokee Swamp, Georgia. *Ecol. Monogr.*, vol. 2, pp. 109-232.

YOUNG, FRANK N.

1947. A new species of *Gyretes* from western Florida. *Florida Entomol.*, vol. 30, no. 3, pp. 31-33.

1949. Insects from burrows of *Peromyscus polionotus*. *Ibid.*, vol. 32, no. 2, p. 77.

1954. The water beetles of Florida. *Univ. Florida Studies, biol. sci. ser.*, vol. 5, no. 1, pp. i-x, 1-238, 31 figs.

YOUNG, F. N., and C. C. GOFF

1939. An annotated list of the arthropods found in the burrows of the Florida gopher tortoise, *Gopherus polyphemus* (Daudin). *Florida Entomol.*, vol. 22, no. 4, pp. 53-67.

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