LATE MIOCENE TERRESTRIAL MAMMALS

ECHOLS COUNTY, GEORGIA

By

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ABSTRACT

Fossil beaver, horse and rhinoceros remains occur along with shark teeth in phosphorite-rich clastic sediments at Statenville, extreme southern Georgia. The sediments appear to be part of a deltaic sequence built by streams flowing south from the upper Georgia coastal plain. The joint occurrence of two fairly advanced species of the three-toed horse Merychippus and a small species of the rhinoceros Teleoceras indicate an age of Barstovian (upper Miocene on the North American land mammal time scale) for the Statenville Local Fauna (new name). The beaver, almost certainly belonging to the genus Monosaulax, is the only known Tertiary representative of its family in eastern North America.

INTRODUCTION

Knowledge of the North American land vertebrate fauna east of the Mississippi River during the Tertiary is based almost wholly on fossils collected in Florida. Even in the comparatively rich Floridian sequence of fossil mammal assemblages the Upper Miocene is sparsely represented, the first and only recorded sample being that described by Olsen (1963). Therefore, the discovery of a new locality in southern Georgia yielding late Miocene mammalian remains is of unusual importance. The Statenville Local Fauna described herein comprises both terrestrial and marine vertebrates including remains of horses, rhinoceroses, rodents and fishes. Particularly noteworthy is the presence in the new fauna of a beaver, cf. Monosaulax, the first Tertiary member of the Castoridae to be recorded in eastern North America.

Acknowledgments

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Jerry Elkins for taking the photographs. Jane Voorhies prepared Figure 8. E. A. Stanley kindly identified microfossils.

GEOGRAPHIC AND GEOLOGIC SETTING

The fossils described below were collected from an outcrop on the east bank of the Alapaha River at Statenville in southern Echols County, extreme southern Georgia. Except for the rhinoceros remains, all fossils were obtained from a small exposure about 15 yards long at the mouth of the small tributary that enters the river approximately 150 yards north (upstream) of the Georgia Highway 94 bridge at the western city limits of Statenville. The rhinoceros bones were collected 50 yards south (downstream) from the mouth of the tributary. Being one of the few bedrock exposures in the county, the Statenville outcrop is well known to Coastal Plain geologists. A photograph of the impressive, uniformly-dipping foreset(?) beds at the base of the exposure appears in Veatch and Stephenson's (1911) report on the geology of the Georgia Coastal Plain (Plate XXV. A, opp. page 352). The stratigraphy of the locality has recently been described at some length by Brooks (in Brooks and others, 1966, p. 74-78) so only a brief summary of the lithologic sequence will be provided here.

At times of extreme low water (usually in October and November) about 30 feet of phosphorite-bearing Tertiary clastic sediments are exposed at the Statenville outcrop. The lowermost unit (Brooks' bed 1), exposed in the stream bed, consists of strikingly uniform, 4-8-inch-thick cross beds of gray, dolomitic, clayey sandstone dipping south at angles of 10-12 degrees. Small black phosphorite pebbles and some small sharks teeth were found in this unit that may represent the foreset beds of a delta. A maximum thickness of 8 feet was measured. Brooks' beds 2 through 5, which unconformably overlie the steeply cross-bedded unit, consist of greenish brown sand containing numerous phosphorite pebbles, grading upward into phosphatic silts and clays. These strata are cross-bedded also but not on such a large scale as the underlying bed 1 and the dips of the cross sets show much less preferred orientation and lower dips. I measured a total thickness of 13 feet of this unit. All fossils in the Statenville Local Fauna, except for the rhinoceros, were collected from a phosphorite pebble lens at the base of unit no. 2. A layer of fine gray sand with a few phosphorite pebbles at the base (Brooks' bed 6) overlies the preceding strata, possibly disconformably although no evidence of profound erosion was observed. The rhinoceros bones were collected from near the top of this unit, which measures about 6 feet in thickness.

No useful purpose would be served by assigning a formational name to these beds until they have been traced areally into more completely studied localities. On the State Geologic Map of Georgia (1939, see also Olson, 1966) the beds are mapped as Hawthorn Formation - a

name that has been applied, sometimes indiscriminately, to a wide variety of Miocene and even Pliocene rocks with a broad spectrum of lithologies. The age of the sediments at Statenville has been questionable because of the lack of diagnostic fossils. Veatch and Stephenson (1911) regarded them as Oligocene, Olson (1966) as Middle Miocene (?), and Brooks (1966) as Upper Miocene (?). The present study concludes that at least bed 2 is of Barstovian (Late Miocene) age on the North American land mammal time scale (Wood and others, 1941). (For a recent cross-calibration of the fossil mammal and marine invertebrate and microfossil time scales see Berggren, 1972).)

PRESERVATION OF THE FOSSILS

The collection consists almost entirely of isolated teeth of mammals and fish. Except for the associated rhinoceros bones the fossils all show signs of transportation - abrasion and breakage - although very few are badly rounded. The rhinoceros bones were collected in fine grained sediment and show no evidence of transportation. The color of the teeth ranges from black and gray through tans and browns, much like the range of colors in the phosphorite pebbles associated with them. Because the color changes do not appear to correlate with either taxonomy or degree of abrasion and because several colors often occur within a single fossil, color does not appear to provide a useful criterion for distinguishing fossils of different chronological or environmental provenance. Although some of the fossils may be reworked there is no biostratigraphic evidence of heterochroneity and reworking need not be invoked to account for the presence of both marine and terrestrial fossils in the same bed, particularly in such deltaic/estuarine sediments as those at Statenville.

Preservation of several complete and unabraded bones of a single individual rhinoceros in the fine-grained sandstone at the top of the Statenville exposure suggests a different mode of origin from that of the principal fossil concentration in the phosphorite pebble zone. Although the rhinoceros bones were not articulated they were not widely scattered, indicating that no significant transportation had occurred after disarticulation. Perhaps the remains represent a bloated carcass that floated down from the adjacent mainland and then sank in relatively quiet water where it was buried by fine sand and silt before much scattering occurred. A sample of the sediment enclosing the rhinoceros bones was submitted to Dr. E. A. Stanley for microfaunal analysis. Dr. Stanley reports (oral communication) that no calcareous microfossils or pollen could be found in the sample but that hystricosphaerids are present. Hystricosphaerids, so far as is known, are restricted to strata deposited in marine or brackish waters (Wilson and Hoffmeister, 1955).

INVERTEBRATES

Mega-invertebrate fossils appear to be rare in the cross-bedded clastics at Statenville. Occasional obscure molds and some barnacle plates were observed. Burrows of the Ophiomorpha type are fairly common in the sands below the principal bone-bearing horizon. These structures are regarded (Weimer and Hoyt, 1964) as indicators of littoral and shallow neritic marine environments. In the fossiliferous phosphorite pebble horizon, sinuous, ramifying burrows about one inch in diameter and up to a yard long were observed to penetrate the sediment in a more-or-less horizontal orientation. They resemble the burrows of the shrimp Upogebia affinis investigated by Frey and Howard (1969) in tidal stream deposits on Sapelo Island, Georgia. These burrows lack the pelletoid wall structure typical of Ophiomorpha.

VERTEBRATES

All specimens are housed in the collections of the Geology Department, University of Georgia (abbreviation UGV-).

Class Chondrichthyes

Order Selachii

Sharks belonging to six genera can be identified among the approximately 200 elasmobranch teeth in the Statenville Local Fauna (catalog no. UGV-19 applies to the entire lot). They are listed below in order of abundance from greatest to least:

Negaprion
Carcharhinus
Hemipristis
Galeocerdo
Odontaspis
Carcharodon

The composition of the shark fauna is generally similar to that reported by Webb and Tessman (1968) from a Pliocene site in Manatee County, Florida that also yielded fossil mammals. The predominance of sharks whose modern analogues prefer a coastal and estuarine habitat (Negaprion and Carcharhinus) and the scarcity of pelagic types (Carcharodon) are congruent with the hypothesis of a nearshore (deltaic or estuarine) depositional environment.

Order Batoidea

Skate and ray teeth are surprisingly uncommon in the Statenville Local Fauna in contrast with their abundance at most localities on the

Atlantic Coastal Plain where shark teeth can be collected. Besides one rostral tooth of a large sawfish (Pristis) (UGV-21), only about a dozen recognizable ray teeth were collected. All appear to pertain to Aetobatis, the spotted eagle ray, this identification being based on the notable angularity ("boomerang shape") of the tooth bands. The comparative scarcity of batoid remains is certainly not due to selective mechanical or diagenetic destruction; the dental batteries of the myliobatids are remarkably robust structures compared to sharks teeth of equivalent size. Eagle rays are adapted to a diet of heavy-shelled mollusks; therefore perhaps their poor representation in the Statenville assemblage correlates with the scarcity of invertebrates noted above. The rapid rate of sedimentation in the murky waters of an estuary or delta may have been inhospitable to both shelly invertebrates and their batoid predators but the area may still have supported sizable shark populations.

CLASS REPTILIA

Water-rolled pieces of turtle carapace were the only reptilian fragments recovered.

CLASS MAMMALIA

Order Rodentia

Family Castoridae

cf. Monosaulax (Figure 8)

An isolated right first or second lower molar reveals the presence of a small beaver in the fauna (UGV-29).

Description

The crown is well preserved but the roots, which appear to have been well developed, are abraded. The tooth may be termed subhypsodont because of its possession of roots and the comparatively weak development of the striids. The occlusal pattern is dominated by two infoldings of the enamel wall (the hypoflexid and mesoflexid) and two enamel 'lakes' (the parafossetid and metafossetid). The flexids and fossetids are elongate and subparallel at the stage of wear shown by the specimen. The mesostriid is quite short but the hypostriid extends well down the enamel crown. The tooth would not exhibit the S-pattern at any stage of wear because the mesoflexid would close before the para- (and, probably, the meta-) fossetid would be obliterated by wear.

Discussion

Either of the two recognized genera of small subhypsodont beavers in the late Tertiary (Monosaulax and Eucastor) could be represented by the Georgia specimen. The shallowness of the striids, however, and the lack of an S-pattern, both argue for its inclusion in the former genus, which is regarded as a characteristic Hemingfordian-Barstovian (medial and late Miocene) form, rather than in the latter, which is confined to the Clarendonian (early Pliocene). Monosaulax and Eucastor differ significantly in crown height, the former being notably less hypsodont (Stirton, 1935; Shotwell, 1963, 1968). Although the original (unworn) crown height of an isolated tooth such as UGV-29 cannot be accurately determined, the fact that large para- and metafossetids are still present when the mesoflexid is about to close indicates that the Statenville beaver was less hypsodont than even the most primitive species of Eucastor described by Stirton. In the wear series of lower molars of the early Clarendonian species E. dividerus (Stirton, 1935, p. 435) such large fossetids are present only in very early wear and are completely obliterated before the teeth are worn to a crown height equivalent to that of the Georgia specimen. Thus, the beaver in the Statenville Local Fauna appears to be more primitive than the earliest Eucastor. It is distinctly more advanced than the earliest known Monosaulax species (Monosaulax n. sp. from the Quarry A assemblage of Wilson, 1960) and approaches such Barstovian species as M. pansus, M. curtus and M. typicus in evolutionary grade.

The Statenville Monosaulax is the only known pre-Pleistocene castorid east of the Mississippi River. The closest reported Miocene beaver occurs in the Burkeville Fauna in eastern Texas some 800 miles away (Quinn, 1955, p. 72).

Order Carnivora

Tooth fragments and a proximal phalanx appear to be referable to a small canid but are too incomplete for further classification.

Order Sirenia

Several rib sections lacking cancellous tissue obviously belong to a sea cow but are not more completely identifiable.

Order Perissodactyla

Family Equidae

Horse teeth are the most abundant terrestrial mammal remains in the collection; they provide further evidence for dating the deposit as Barstovian. Two distinct species of mesodont (subhypsodont) horses

are present and both readily fall within the confines of the genus Merychippus as recognized by most workers in vertebrate paleontology. The concept of the genus Merychippus held by Osborn (1918) and modified by Stirton (1940) is an extreme example of a horizontally defined taxon, comprising at least six separate lineages thought to be ancestral to such later genera as Pliohippus, Hipparion, etc. Within this exceedingly complex group of species is a bewildering amount of morphological diversity. Tooth characters held in common by most if not all Merychippus species are 1) cheek teeth mesodont (height/length ratio of unworn teeth falling roughly between 1.0 and 2.0), 2) cheek teeth moderately to strongly curved and 3) cement-covered crowns on the cheek teeth.

The great majority of described Merychippus species are Barstovian in age although primitive species are known from the Hemingfordian and at least one lineage persisted into the Clarendonian (Webb, 1969). Morris F. Skinner has recently solved one of the more vexing problems regarding the genus by demonstrating that the genotypic species, M. insignis, is Barstovian in age (Skinner and Taylor, 1967).

Merychippus sp. A

The larger of the two Statenville horse species is about the size of M. insignis. It is represented by two upper and two lower cheek teeth (Figures 1, 2, 4, and 5). UGV-25 is a left upper third or fourth premolar from a young adult animal. At this early stage of wear there is a prominent anterobuccal 'spur' on the protocone and the protoconule is not yet connected to the metaloph; neither has the metaloph yet joined to the ectoloph. The enamel pattern is simple, a pli prefossette and a pli hypostyle are the only accessory folds present. The anteroposterior length of the tooth crown divided into its height along the mesostyle (28.0/18.5) gives an index of hypsodonty of 1.5, well within the range of Merychippus.

UGV-22 is a well worn upper left second premolar. The protocone is connected to the protoloph but the protoloph is not yet connected to the metaloph. The hypoconal groove is still open indicating that it was deep and persistent. The metaloph has not yet joined the ectoloph. A prominent pseudoparastyle (see Skinner and Taylor, 1967, p. 24) is present. The tooth is 15.3 mm high along the mesostyle.

UGV-23 is a lower right third or fourth premolar at a moderate state of wear. The ectoflexid is deep, a shallow notch still separates the metaconid and metastylid, and an ectoparastylid down the anteroexternal corner of the tooth although it is weak. UGV-24 is a lower right molar, either M_1 or M_2. As is usually the case, it is a smaller tooth than the premolar, especially in transverse diameter. It is otherwise similar except for a more advanced state of wear.

Merychippus sp. B

A second, considerably smaller, equine species is represented by one lower and two upper cheek teeth (Figures 3, 6, and 7). UGV-26 is an upper right first or second molar at a mature stage of wear; its height along the mesostyle is 18.0 mm. The protocone is connected to the protoloph, the metaloph is connected to the ectoloph, and the hypoconal groove is shallow and about to be obliterated by wear. No plications are present in the fossette borders. UGV-27 is a badly abraded right P^2, probably at an early stage of wear but no measurement of crown height can be made because of the severe abrasion. The tooth has a disconnected, teardrop-shaped protocone, a connected metaloph, and rather complicated fossette borders. UGV-28, a right M_1 or M_2, is little worn. The ectoflexid is very deep, the metaconid and metastylid small but distinct, and the ectoparastylid strong and sharp for the entire length of the tooth.

Comparisons

In addition to a size difference of approximately 50% the two species of Merychippus found at Statenville differ in several morphological details such as the timing of the metaloph-ectoloph union and the persistence of the hypoconal groove on the upper teeth and the prominence of the ectoparastylid on the lowers. Without more complete material it would be unwise to allocate either of the Georgia horses to one of the dozens of described Merychippus species. Their inclusion in the genus seems solidly based and their comparatively high degree of hypsodonty suggests a Barstovian age but beyond that one cannot go

Figure 1-7. Horse teeth, Statenville Local Fauna (Barstovian), Georgia Bars equal 10 mm.

Figure 1. UGV-25, left P^3 or P^4 of Merychippus sp. A. a. occlusal view; b. posterior view.

Figure 2. UGV-24, right M_1 or M_2 of Merychippus sp. A. a. occlusal view; b. buccal view.

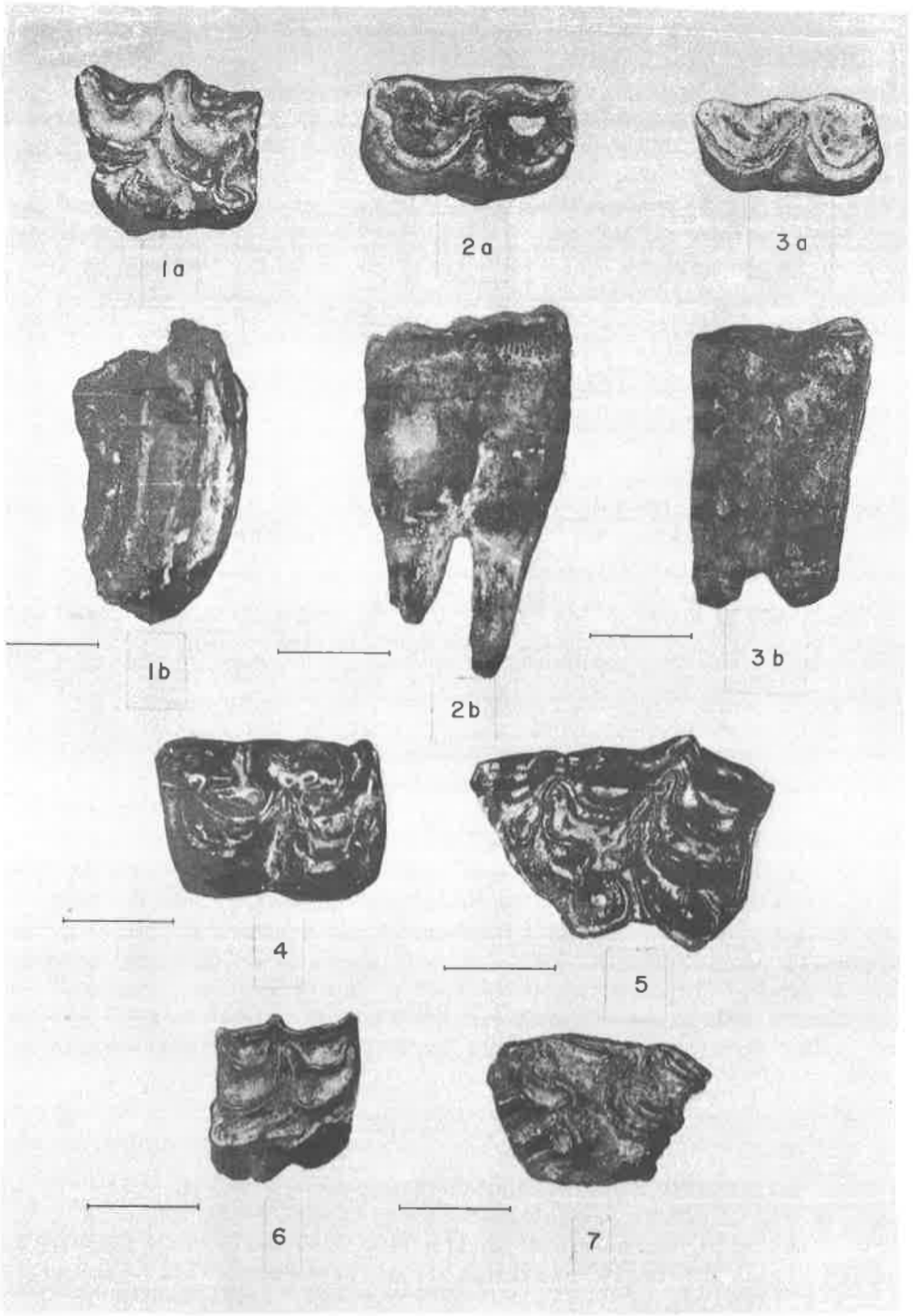
Figure 3. UGV-28, right M_1 or M_2 or Merychippus sp. B. a. occlusal view; b. buccal view.

Figure 4. UGV-23, right P_3 or P_4 of Merychippus sp. A, occlusal view.

Figure 5. UGV-22, left P^2 of Merychippus sp. A, occlusal view.

Figure 6. UGV-26, right M^1 or M^2 of Merychippus sp. B, occlusal view.

Figure 7. UGV-27, left P^2 of Merychippus sp. B, occlusal view.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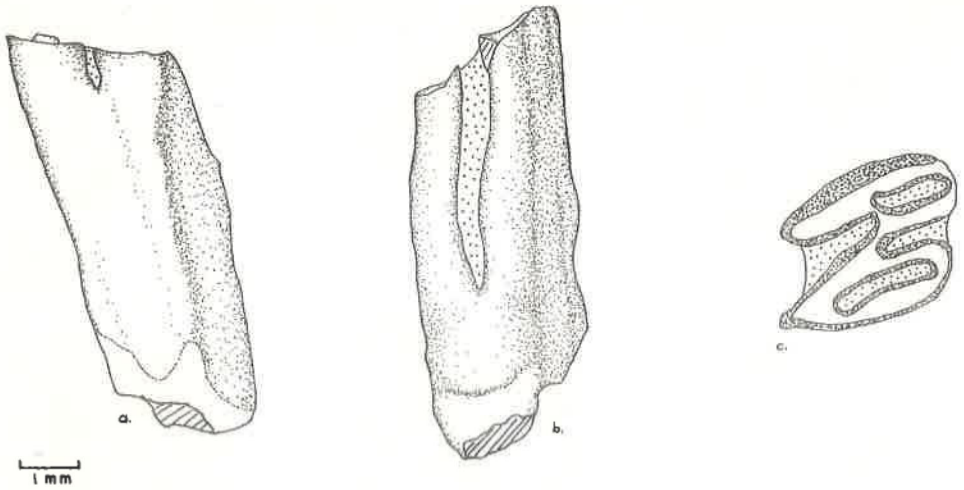

Figure 8. cf. Monosaulax, first or second right lower molar. a. lingual view. b. buccal view. c. occlusal view.

on the basis of present evidence. The Barstovian Merychippus sp. teeth from northern Florida figured by Olsen (1963) appear to be similar in size to the larger Statenville form, similar in hypsodonty, but with perhaps a more complex enamel pattern in the upper molars.

Family Rhinocerotidae

Teleoceras sp. (Figure 9)

A short-limbed, hypsodont rhinoceros is represented by some fragmentary limb bones and tooth scraps (probably from the same individual because no skeletal elements were duplicated) collected from fine-grained sediments about 15 feet above the rest of the fossils as noted above. The specimens were collected in situ and from talus immediately below the exposure from which the bones were weathering out. The fossils are somewhat leached and crushed but show no evidence of postmortal transportation.

Description

Identifiable elements include a left metatarsal III (UGV-30), left metatarsal IV (UGV-31), left metacarpal IV (UGV-32), proximal end of left tibia (UGV-33), proximal end of left ulna (UGV-34), proximal end of left radius (UGV-35), proximal end of right radius (UGV-36), ungual phalanx (UGV-37), proximal phalanx (UGV-38), right magnum (UGV-39) and miscellaneous tooth fragments (UGV-40). The metapodials are short and stout and the preserved portions of the other limb elements

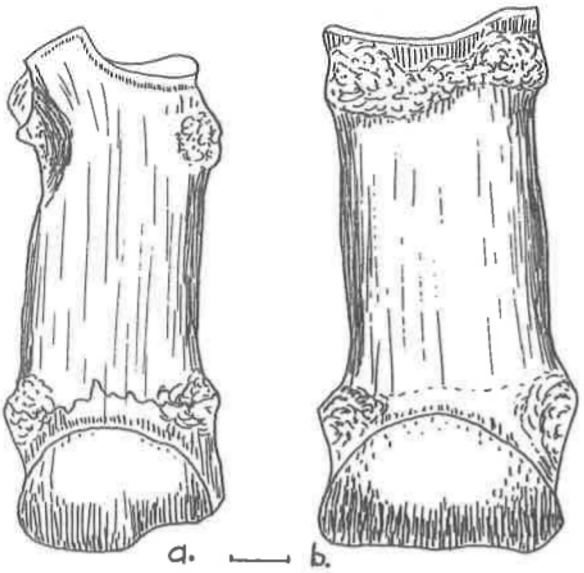

Figure 9. Teleoceras sp. a. left metacarpal IV, anterior view. b. left metatarsal III, anterior view. Bar equals 10 mm.

are also ruggedly constructed. Measurements are given below:

Left Metatarsal III	length - 94 mm width across epicondyles - 46 mm
Left Metacarpal IV	length - 90 mm width across epicondyles - 36 mm
Left Radius	width of proximal end - 72 mm
Left Tibia	width, across condyles, of proximal end - 98 mm

The tibia was not ankylosed with the fibula. The tooth fragments are too incomplete for detailed comparisons but indicate that the animal had fairly high-crowned teeth (over 50 mm in little worn molars).

Discussion

No rhinoceros genus except Teleoceras has such stubby metapodials. Other rhinoceros genera reported from Florida (Aphelops, Diceratherium, Floridaceras) are all cursorial or semicursorial types with comparatively long, slender limbs. Although the genus is best represented in numerous Clarendonian and Hemphillian faunas of the western United States, Teleoceras is also reported from faunas of Barstovian age (Lower Snake Creek, Pawnee Creek, Cold Spring). In the southeastern United States the only previously reported Teleoceras specimens are of Hemphillian age. By far the best population sample to be described is that in the Mixson bone bed in Alachua County,

Florida (Leidy and Lucas, 1896; Simpson, 1930). T. proterus from that locality, judging from the descriptions, measurements, and illustrations given by Leidy and Lucas, has considerably larger limbs and feet than the rhinoceros from Statenville. The Georgia specimen is also smaller than the referred specimens of Teleoceras fossiger from various Clarendonian faunas on the Great Plains measured by Gregory (1942). Without a good skull, no specific identification of a Teleoceras should be attempted. Whether the Statenville form represents a separate lineage leading toward T. proterus or is conspecific with one of the described western Barstovian species must be decided when more complete material is available. In any case, compared with Pliocene examples the specimen has shorter, distinctly less robust metapodials - a fact consistent with its postulated Barstovian age.

CONCLUSIONS

Patton (1969) has emphasized the similarity of Florida Miocene vertebrate faunas to western ones, especially those of Texas. Our first glimpse of Miocene land mammals in Georgia reemphasizes the similarity; differences, if any, between the Statenville horses, rhinos and beavers and their western counterparts must be at the specific and not at the generic level. Further collecting in Florida will reveal whether the absence of Tertiary beavers there is a fact of real biogeographical significance or is merely an artifact of preservation or collection.

REFERENCES CITED

Berggren, W. A., 1972, A Cenozoic time-scale - some implications for regional geology and paleobiogeography: Lethaia, v. 5, p. 195-215.

Brooks, H. K., Gremillion, L. R., Olson, N. K. and Puri, H. S., 1966, Geology of the Miocene and Pliocene Series in the north Florida - south Georgia area: Atlantic Coastal Plain Geol. Assoc. 7th Ann. Field Conf., 94 p.

Frey, R. W., and Howard, J. D., 1969, A profile of biogenic sedimentary structures in a Holocene barrier island-salt marsh complex, Georgia: Trans. Gulf Coast Assoc. Geol. Soc., v. 19, p. 427-444.

Gregory, J. T., 1942, Pliocene vertebrates from Big Spring Canyon, South Dakota: Univ. California Publ. Geol. Sci., v. 26, p. 307-438.

Leidy, J., and Lucas, F. A., 1896, Fossil vertebrates from the Alachua Clays of Florida: Trans. Wagner Free Inst. Sci., v. 4, p. 1-61.

Olsen, S. J., 1963, An upper Miocene fossil locality in north Florida:

Florida Acad. Sci. Quart. Jour., v. 26, p. 308-314.
Olson, N. K., 1966, Phosphorite exploration in portions of Lowndes, Echols, Clinch, and Charlton counties, Georgia: Georgia Geol. Survey Proj. Rept. 4, 113 p.
Osborn, H. F., 1918, Equidae of the Oligocene, Miocene and Pliocene of North America, iconographic type revision: Am. Mus. Nat. Hist. Mem. 2 (1), 330 p.
Patton, T. H., 1969, Miocene and Pliocene artiodactyls, Texas Gulf Coastal Plain: Florida State Mus. Bull., v. 14, p. 115-226.
Quinn, J. H., 1955, Miocene Equidae of the Texas Gulf Coastal Plain: Univ. Texas Publ. no. 5516, 102 p.
Shotwell, J. A., 1963, The Juntura Basin: studies in earth history and paleoecology: Trans. Amer. Philosoph. Soc., v. 53, pt. 1, p. 1-77.
_____, 1968, Miocene mammals of southeast Oregon: Mus. Nat. Hist. Univ. Oregon Bull., v. 14, p. 1-67.
Simpson, G. G., 1930, Tertiary land mammals of Florida: Am. Mus. Nat. Hist. Bull., v. 59, p. 149-209.
Skinner, M. F., and Taylor, B. E., 1967, A revision of the geology and paleontology of the Bijou Hills, South Dakota: Am. Mus. Nat. Hist. Novitates no. 2300, 53 p.
Stirton, R. A., 1935, A review of the Tertiary beavers: Univ. California Publ. Geol. Sci., v. 23, p. 391-458.
_____, 1940, Phylogeny of North American Equidae: Univ. California Publ. Geol. Sci., v. 25, p. 167-198.
Veatch, O., and Stephenson, L. W., 1911, Preliminary report on the geology of the coastal plain of Georgia: Georgia Geol. Survey Bull. 26, 466 p.
Webb, S. D., 1969, The Burge and Minnechaduza Clarendonian mammalian faunas of north-central Nebraska: Univ. California Publ. Geol. Sci., v. 78, p. 1-191.
Webb, S. D., and Tessman, Norm, 1968, A Pliocene vertebrate fauna from low elevation in Manatee County, Florida: Am. Jour. Sci., v. 266, p. 777-811.
Weimer, R. J., and Hoyt, J. H., 1964, Burrows of Calianassa major Say, geologic indicators of littoral and shallow neritic environments: Jour. Paleo., v. 38, p. 761-767.
Wilson, L. R., and Hoffmeister, W. S., 1955, Morphology and geology of the Hystrichosphaerida (abs.): Jour. Paleo., v. 29, p. 735.
Wilson, R. W., 1960, Early Miocene rodents and insectivores from northeastern Colorado: Univ. Kansas Paleont. Contr., Vertebrata, art. 7, 92 p.
Wood, H. E., and others, 1941, Nomenclature and correlation of the North American Continental Tertiary: American Geol. Soc. Bull., v. 52, p. 1-48.