BULLETIN

of the
FLORIDA STATE MUSEUM
Biological Sciences

LATEST PLIOCENE MAMMALS FROM HAILE XV A,

ALACHUA COUNTY, FLORIDA

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LATEST PLIOCENE MAMMALS FROM HAILE XV A, ALACHUA COUNTY, FLORIDA

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SYNOPSIS: The mammalian fauna of Haile XV A is the first known from the Gulf Coastal Plain during Blancan (Latest Pliocene) time. The mammals are represented by 8 orders, 17 families, and 18 genera, of which two are new species and three are new to North America. *Kraglievichia*, a giant, extinct armadillo previously known only from Late Miocene and Pliocene deposits of South America, is reported for the first time in North America and a new species is described. A brief review of the subfamily Chlamytheriinae suggests that *Plaina* Castellanos is a synonym of *Kraglievichia* Castellanos and that *Hoffstetteria* Castellanos is a synonym of *Pampatherium* Ameghino. Chlamytheres are shown to have been present in North America continuously since the establishment of the late Cenozoic land bridge between North and South America. *Dasypus bellus* (Simpson), a smaller extinct armadillo, is reported for the first time in the Blancan, marking its earliest occurrence anywhere.

Glossotherium chapadmalensis (Kraglievich), a small mylodont ground sloth previously known only from the early Pleistocene of Argentina, is reported from North America for the first time. This species may have been ancestral to both *G. harlani* (Owen) and *G. robustus* (Owen).

The Old World Flying Squirrel, *Cryptopterus*, is reported for the first time in the New World and a new species is described. The nearest related species occurs in the Late Pliocene deposits of West Germany.

Close alliance of several Haile XV A taxa with South American Plio-Pleistocene forms strengthens the previously suggested correlation between the Chapadmalalan stage of South America and at least the early part of the Blancan stage of North America.

The abundance of aquatic non-mammalian vertebrates, together with the large extinct otter, *Satherium*, and the beaver, *Castor*, indicate that the environment of deposition was a permanent stream. The terrestrial community includes the tropical or subtropical edentates *Kraglievichia* and *Dasypus*. Probable forest indicators include *Mylohyus*, *Castor*, *Cryptopterus*, *Glossotherium*, and *Tapirus*. The zoogeography of several exotic forms is discussed.

TABLE OF CONTENTS

INTRODUCTION

    Florida has long been noted for its rich Late Pleistocene fossil vertebrate deposits, including the Vero site in Indian River County (Weigel 1962), the Melbourne Bone Bed in Brevard County (Gazin 1950, Ray 1958), Seminole Field in Pinellas County (Simpson 1930), Reddick (Ray *et al.* 1963) in Marion County, and many others. In recent years a few

sites have yielded fossil vertebrates of older Pleistocene and even Latest Pliocene age. These Blancan sites are of particular interest, inasmuch as they constitute the first samples from eastern North American (Webb 1974a). This report is the first systematic study of one of the Latest Pliocene sites.

The Haile XV A locality is situated on the property of Parker Brothers Limestone Products Incorporated, near Haile, T9S, R17E, Section 25, NW 1/4 of SW 1/4, Alachua County, Florida. In 1964 the site was discovered and some specimens collected by Phillip Kinsey of Jacksonville Beach, Florida. Further excavations were carried out in the same year by S. David Webb, Robert Allen, and myself with the support of National Science Foundation Grant GB 3862.

GEOLOGY

The Haile XV A deposit lies at an elevation of about 90 ft above sea level and is a filled fissure in the Ocala (Eocene) Limestone. This fissure measures approximately 10 m along its east-west axis, and its north-south dimensions range irregularly from about 3 to 5 m (Fig. 1).

The bottom of the fissure-filling sequence lies at a depth ranging from 1 to 7 m below the land surface. It consists of a stratum of dark brown, compact, iron-stained clays (or "hardpan"), with a thickness ranging from 2 to 6 m.

The fossil-bearing matrix overlies the "hardpan," and consists of an alternating sequence of sands and clays. The lowermost unit is a coarse gravelly sand, containing calcareous cement and concretions. It is the thickest unit in the fossiliferous sequence, ranging from 2 to more than 6 m in depth, and is the most productive fossiliferous horizon. Many of the included larger bones are encrusted with cemented sand and gravel. The clay units are pure, greenish in color, massive in texture, and vary from 10 to 20 cm. The sand layers decrease in thickness upward through the sequence, with the uppermost sands being less than 1 m thick. The clays vary little in thickness, except that the uppermost unit in the fossiliferous section is nearly a meter thick.
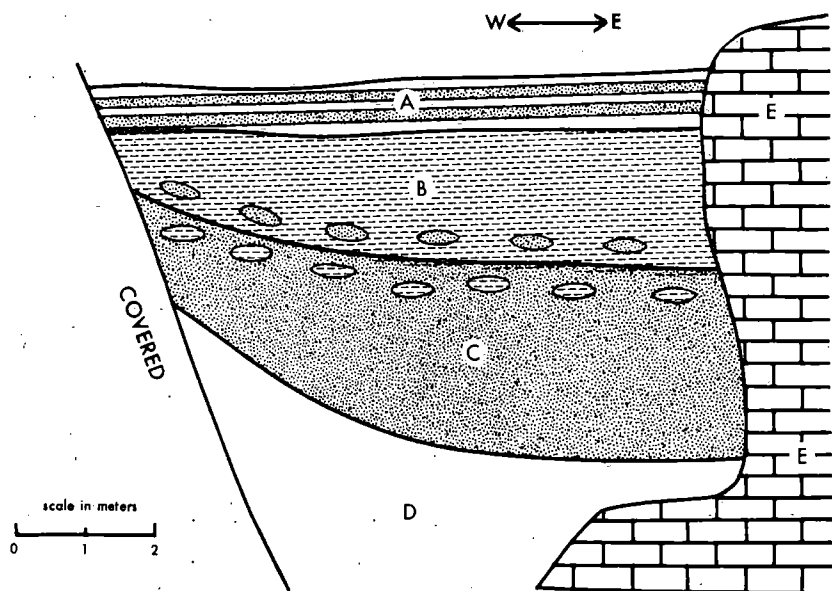
FIGURE 1. Geologic section at Haile XV A: (A) sandstone alternating with gray clay; (B) massive greenish clay; (C) coarse, poorly sorted, gravelly sandstone; (D) dark brown hardpan; and (E) Ocala Limestone (Eocene).

In several instances fossil bones in a sand layer have been found projecting partly into the overlying clay layer. In each instance the projecting part of the bone shows no noticeable wear or weathering. Evidently each clay unit was deposited rapidly over the preceding sand unit, with little or no intervening period of erosion. Overlying the fossiliferous sequence of sands and clays is a layer of thin, brown sandstone that is nonfossiliferous and grades upward into the soil profile.

SYSTEMATIC PALEONTOLOGY

Twenty mammalian taxa, representing a minimum of 34 individuals, were collected at Haile XV A (Table 1).

ORDER INSECTIVORA

FAMILY SORICIDAE

Cryptotis parva (SAY 1823)

MATERIAL.—UF 17466, right mandible with M_1-M_3.

This specimen is indistinguishable from Recent Florida specimens of *C. parva*, except for its slightly larger size (Table 2). The only other Blancan record of *Cryptotis* is from the Rexroad fauna (Hibbard 1937, 1941), Meade County, Kansas.

TABLE 1.—MAMMALIAN FAUNAL LIST AND MINIMUM NUMBER OF INDIVIDUALS (MNI).

Species	MNI
Cryptotis parva	1
Scalopus aquaticus	2
Glossotherium chapadmalensis	1
Kraglievichia floridanus	3
Dasypus bellus	1
Sylvilagus sp.	3
Cryptopterus webbi	1
Castor canadensis	1
Sigmodon medius	2
Canidae	2
Satherium sp.	1
Smilodon gracilis	1
Gomphotheriidae	1
Nannippus phlegon	2
Equus (Dolichohippus) simplicidens	
Equus (Hemionus) cf. calobatus	2
Tapirus sp.	1
Mylohyus floridanus	1
Hemiauchenia cf. macrocephala	1
Odocoileus virginianus	5

TABLE 2.—MEASUREMENTS (IN MM) OF THE LOWER DENTITION AND MANDIBLE OF UF 17466 AND OTHER FOSSIL AND RECENT Cryptotis parva.

	UF 17466	C. parva[1] (20) $\overline{X}$	OR	C. parva[1] (fossil) $\overline{X}^2$	OR[3]
Condyloid to mental foramen	6.8	6.1	5.9–6.7	6.6	6.1–7.0 (8)
Condyloid to M_1	6.7	6.9	6.7–7.4	7.1	6.8–7.6 (8)
Condyloid to M_2	5.3	5.7	5.5–6.0	5.8	5.5–6.1 (8)
M_1–M_2	2.8	2.6	2.4–2.7	2.7	2.5–2.9 (8)
M_1–M_3	4.0	3.4	3.3–3.6	3.6	3.5–3.6 (2)
M_2–M_3	2.5	2.2	2.1–2.4	2.3	2.2–2.3 (2)

[1] Measurements after Martin (1974).
[2] X=mean
[3] O. R.=observed range; number of specimens in parenthesis

FAMILY TALPIDAE

Scalopus aquaticus LINNAEUS 1758

MATERIAL.—UF 17467, 2 left M²; UF 17465, right humerus.

A comparison of the three specimens from Haile XV A with corresponding elements of modern *S. aquaticus* from the southeastern United States reveals no significant differences in size or morphology.

Scalopus is also present in the Blancan Rexroad fauna of southwestern Kansas (Hibbard 1941) and in the Sand Draw local fauna of north-central Nebraska (Hibbard 1972). Another mole (*Hesperoscalops*) from the Rexroad fauna is based on a lower dentition. A direct com-

parison could not be made with that genus, because only upper teeth are known from Haile XV A. As Hibbard (1941) points out, however, mole humeri are quite diagnostic at the generic level, so it seems unlikely that a *Scalopus*-like humerus could belong to any other genus.

ORDER EDENTATA
FAMILY MYLODONTIDAE
Glossotherium (Glossotherium) chapadmalensis (KRAGLIEVICH 1925)

Eumylodon chapadmalensis Kraglievich 1925
Glossotherium (Glossotherium) chapadmalensis (Kragl.) Hoffstetter 1952

MATERIAL.—UF 10922, partial skeleton.

The Haile XV A specimen probably represents one individual, because there is no duplication of elements and the left and right elements are very similar in all measurements. Most, if not all specimens were taken from the basal sand layer of the fossiliferous sequence, and some parts of the skeleton and dermal ossicles were nearly articulated.

CRANIUM AND UPPER DENTITION.—The upper dentition of the Haile XV A specimen (Fig. 2) is complete except for the left upper caniniform. The right upper caniniform is triangular in cross-section and very well developed. The stoutness of the caninform is reflected by great transverse expansion of the anterior portion of the maxilla, as is also true of the holotype from Argentina. This contrasts strikingly with *G. harlani*, which has a reduced or absent caniniform and transversely narrow maxilla.

The first upper molariform tooth is oval in cross-section. As in *G. harlani* and *G. robustus*, it is the longest anteroposteriorly of all the upper teeth but is relatively narrow in transverse diameter. Because the well-developed lower caniniform occludes in part with this tooth, wear on the anterior oblique surface in *G. chapadmalensis* is much more accentuated than in *G. harlani*. In *G. robustus* specimens observed, this tooth was worn off smoothly just above the alveolus. A very short diastema separates the upper caniniform tooth from the first molariform tooth in the specimen from Haile XV A.

The second upper molariform tooth of UF 10922 is triangular in cross-section. The lingual side is the narrowest and contains a deep inflection. The transverse diameter is greater than the anteroposterior diameter in both the Florida and the Argentina specimens of this species, whereas the opposite is true in *G. harlani*. Of the two *G. robustus* specimens for which measurements are provided, one resembles *G. chapadmalensis*, whereas the two diameters in the other specimen are nearly equal. The third molariform tooth of UF 10922 is similar in shape to the second and morphologically similar to the corresponding teeth in both *G. harlani*
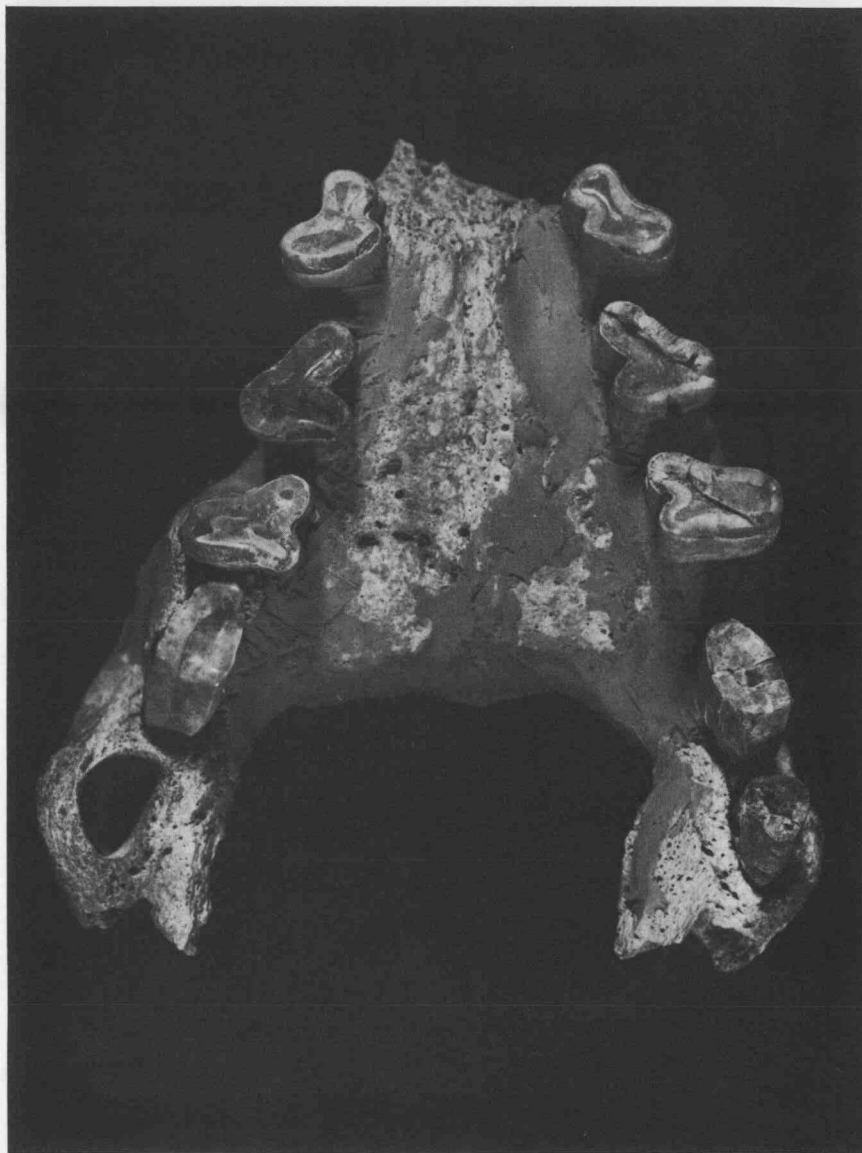
FIGURE 2.   *Glossotherium chapadmalensis*:   upper dentition X 0.85.

and *G. robustus*.   The fourth molariform is relatively small compared to the Argentina specimen of *G. chapadmalensis*, although it is identical in shape.

The palate is very constricted in the area of the last upper teeth and considerably expanded at the anterior end of the maxilla.   Both of these

characters are more extreme in UF 10922 than in the holotype or in speci-
mens of G. *harlani* and G. *robustus*.

The remainder of the cranial material consists of part of the occipital
bone and portions of the left and right periotic bone. The occipital frag-
ment consists of the left condyle and a portion of the otic region. The
hypoglossal canal, jugular foramen, and auditory meatus show no observ-
able differences from those of G. *harlani* and G. *robustus*. A portion of
the left squamosal bone is attached to the occipital. Part of the right
squamosal is present, including the zygomatic process.

MANDIBLE AND LOWER DENTITION.—The lower caniniform of UF 10922
(Fig. 3, 4) is well developed and directed dorsolabially. This tooth
is relatively larger than the corresponding tooth in the South American
specimen of G. *chapadmalensis*. The tooth has a chisel-like tip, the result
of dual occlusion with the upper caniniform and first molariform teeth.

The second molariform tooth is rectangular and has its long axis
oblique to the tooth row. Stock (1925) measured the long axis as the
anteroposterior length; Kraglievich (1925) used the shorter axis of the
tooth. For purposes of comparison, Kraglievich's method is used here
for the Haile XV A specimen and Stock's method for measuring G.
robustus. (For consistency one must reverse the measurements of G.
robustus provided by Kraglievich [1928].) It is obvious from Table 3
that the orientation of the teeth, not their basic morphology, probably
accounts for the interspecific differences in this tooth.

The third lower molariform tooth is of a slightly different shape in
G. *chapadmalensis*. The two main columns are separated by a thin
bridge, while in G. *robustus* this bridge is thicker.

Unfortunately, the mandibular symphysis is not preserved in the Haile
XV A specimen, but the portion of the mandible present is similar to
that of the other two species.

VERTEBRAE.—The atlas of UF 10922 is the only well preserved verte-
bra. According to Stock (1925) the atlas of G. *harlani* differs from that
of G. *robustus* in the more posterior position of the lateral process. The
location of the dorsal foramina also varies; in G. *harlani* they are well
separated as compared to those in G. *robustus*. In the expression of
these two characters, UF 10922 resembles G. *harlani*.

LIMB BONES.—The right humerus and both ulnae are present, as are
the left femur, both tibiae, and the left fibula. Hind foot bones repre-
sented are the astragalus, calcaneum, and various metatarsals and pha-
langes. The small size of this species is indicated by the measurements
of these limb bones (Table 4).

Several bones of the manus warrant a brief description. The cunei-
form appears to be somewhat different in G. *chapadmalensis* than in G.

FIGURE 3. *Glossotherium chapadmalensis*:   right mandible, lateral view, X 0.60.
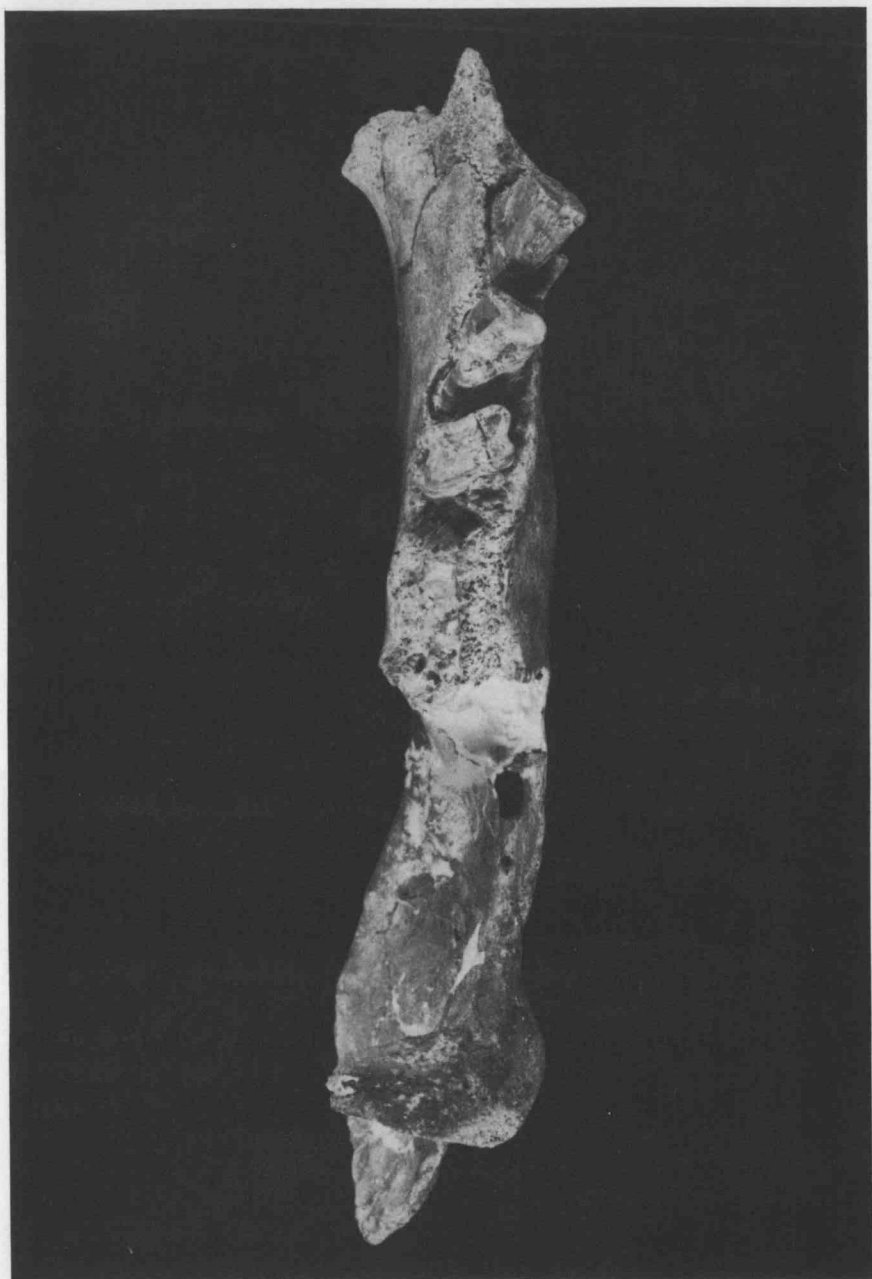
FIGURE 4. *Glossotherium chapadmalensis*: right mandible, occlusal view, X 0.60.

TABLE 3.—MEASUREMENTS (IN MM) OF THE UPPER AND LOWER DENTITIONS OF THREE SPECIES OF *Glossotherium*.

	G. chapadmalensis		G. harlani	G. robustus
	Haile XV A	Argentina[1]	California[2]	Argentina[3]
UPPER DENTITION				
Anteroposterior length, tooth 1	14.7	14.0	17.9	17.9
Transverse length, tooth 1	10.6	10.5	16.0	18.2
Anteroposterior length, tooth 2	22.4	22.0	33.3	22.3
Transverse length, tooth 2	12.0	15.0	17.4	16.7
Anteroposterior length, tooth 3	15.6	20.5	27.1	22.8
Transverse length, tooth 3	22.4	24.0	23.0	23.0
Anteroposterior length, tooth 4	17.9	15.0	22.6	20.3
Transverse length, tooth 4	20.5	24.0	23.8	22.4
Anteroposterior length, tooth 5	21.4	24.0	24.3	23.3
Transverse length, tooth 5	13.6	18.0	19.4	19.2
LOWER DENTITION				
Anteroposterior length, tooth 1	20.5	14.5	21.4	20.4
Transverse length, tooth 1	12.4	10.5	16.0	15.0
Anteroposterior length, tooth 2	18.7	18.0	28.3	23.8
Transverse length, tooth 2	14.5	22.0	22.5	22.8
Anteroposterior length, tooth 3	14.5	14.0	28.8	25.0
Transverse length, tooth 3	20.5	25.0	18.2	19.0
Anteroposterior length, tooth 4	40.3	43.0	51.9	50.2
Transverse length, tooth 4	17.3	18.0	23.8	20.2

[1] Measurements after Kraglievich (1925).
[2] Measurements after Stock (1925).
[3] Measurements after Owen (1842).

TABLE 4.—LIMB MEASUREMENTS (IN MM) OF *Glossotherium chapadmalensis* AND *Glosotherium harlani.*

	G. chapadmalensis UF 10922, Haile XV A		G. harlani[1] Rancho La Brea
	left	right	
HUMERUS			
Greatest anteroposterior distance of head	70.0	70.0	123.8
Greatest width of shaft at deltoid ridge		71.3	122.6
Width of distal articular surface		86.0	133.2
ULNA			
Greatest length	285		395.9
Width of distal articular surface	34		55.0
FEMUR			
Total length	355		546.4
Transverse diameter of head	79.3		127.8
Least width of shaft	99.5		164.6
Greatest width across distal tuberosities	140		234.8
Width of distal condyles	111		188.5
Width of intercondyloid space	27.1		47
Width of inner condyle	47.2	47.2	88.7
Vertical extent of inner condyle	67	69.8	120
TIBIA			
Total length	181	176	247.3
Greatest width, proximal end	114		185.2
Greatest width, distal end	90	88	142.5
Anteroposterior distance, distal end	64.8	66.6	101.9
FIBULA			
Total length	183		263
Width, proximal end	50.5		103.6
Width, distal end	39.5		73.5

[1] After Stock (1925). The measurements represent the mean of large samples. The number of specimens varied from element to element and in some cases was not given.

harlani; in the UF specimen it has a square palmar outline, whereas in Stock's figure (1925: Fig. 72d) of *G. harlani* it is rectangular. This difference is reflected by the measurements of the cuneiform in Table 5. In UF 10922 the proximal-distal dimension is greater than the distance across the ulnar articular surface, while the opposite is true for 39 specimens measured by Stock. The cuneiform appears to be a deeper element in *G. chapadmalensis* than in *G. harlani*. The remaining elements of the manus preserved in the Haile XV A specimen are the left scaphoid, right pisiform, left metacarpal III, and left phalanx II, digit III.

DISCUSSION.—This specimen so closely resembles *Eumylodon* (= *Glossotherium*) *chapadmalensis* that it is here ascribed to that species. *G.*

TABLE 5.—MEASUREMENTS (IN MM) OF THE BONES OF THE MANUS AND PES OF *Glossotherium chapadmalensis* FROM HAILE XV A AND *Glossotherium harlani*.

	G. chapadmalensis		G. harlani[1]
	left	right	
SCAPHOID			
Greatest distance across articular surface	46.2		75.3(39)[2]
CUNEIFORM			
Greatest distance across dorsal surface from inner side to outer	42.1		68.5(42)
Greatest proximal-distal distance	34.3		50.5
Distance across articular surface for ulna	31.2		61.3
PISIFORM			
Greatest length		25.3	55.6(22)
Greatest depth		18.9	36.4
Greatest width		20.9	34.7
METACARPAL III			
Greatest length	71.7		103.1(30)
Width, proximal end	51.9		75.2
Width, distal end	30.5		50.9
Depth, proximal end	42.0		66.0
PHALANX II, DIGIT III			
Length	40.5		48.9(42)
Depth, inner condyle	23.5		39.9
Width, proximal end	26.2	47.9	
CALCANEUM			
Greatest width, anterior end		57.4	91.8(21)
Greatest depth		83.4	125.4
ASTRAGALUS			
Anteroposterior diameter		76.1	140.2(41)
METATARSAL IV			
Length	84.3		119.3(29)
Width, proximal end	41.2	41.5	60.7
Depth, proximal end	34.3	37.1	45.5
Width, distal end	38.5		50.1
Depth, distal end	35.3		43.5
PHALANX II, DIGIT III			
Length	30.2	31.0	35.4(32)
Depth, inner condyle	20.4	21.5	21.8
Width, proximal end	22.6	22.5	35.1
UNGUAL PHALANX, DIGIT III			
Length	104.4		174.1
Proximal–distal distance of ungual base	41.0		73.5
Width, proximal end	32.4		55.0

[1] Measurements after Stock (1925).
[2] Number in parentheses refers to the sample size from which the mean (the numbers in the right-hand column) was calculated.

chapadmalensis was described from the Chapadmalal fauna (Early Pleistocene) of Argentina and is here reported from North America for the first time. It is a small species that appears to be very closely related to both *G. harlani* and *G. robustus,* but it differs from these two species in the nature of the anterior dentition and overall size. It resembles both in the morphology of most of the postcranial elements, with minor exceptions in the manus and pes. *G. chapadmalensis* is thus temporally, geographically, and morphologically a plausible ancestor of both *G. harlani* and *G. robustus.*

Much confusion has arisen concerning proper usage of the names *Mylodon* and *Glossotherium.* In his thorough review of the literature, Kraglievich (1928) concluded that *Mylodon darwinii* is the genotype of *Mylodon,* and the species described by Owen (1840) as *Mylodon robustus* should actually be included in a distinct genus, *Glossotherium.* However, Kraglievich retained *Paramylodon* (Brown 1903) as a valid genus, even though Stock (1925) included it in the synonymy of *Mylodon harlani.* Simpson (1945) correctly argued that if the North and South American Late Pleistocene forms are not generically distinct, they should all be referred to the genus *Glossotherium.* Hoffstetter (1952) retained *Paramylodon* as a subgenus of *Glossotherium,* this distinction being based on the narrow muzzle, the long cranium, and frequent absence of the upper caniniform tooth. Following this usage, the Haile XV A species should be called *Glossotherium (Glossotherium) chapadmalensis.*

FAMILY DASYPODIDAE
Kraglievichia floridanus new species

HOLOTYPE.—UF 10902, partial skull collected by P. E. Kinsey, S. D. Webb, R. R. Allen, and J. S. Robertson in 1964.

TYPE LOCALITY AND HORIZON.—Haile XV A, T9S, R17E, Sec. 25, NW 1/4 of SW 1/4, Alachua County, Florida, Blancan.

DIAGNOSIS.—Differs from *Kraglievichia paranensis* in having the fourth upper tooth reniform rather than peg-like, with the long axis anterolingual instead of parallel to the tooth row.

REFERRED MATERIAL.—UF 10902, mandible and postcranial elements (probably the same individual as the type skull); UF 17474, right ulna, also from Haile XV A; UF 10432, right humerus, Santa Fe I; UF 9354, right humerus, Santa Fe I; UF 10830, right radius, Santa Fe I; UF 16371, left metatarsal IV, Waccasassa River; UF 17475, right metatarsal IV, Santa Fe II; UF 17472, right metatarsal III, Santa Fe II; UF 17476, right femur, Haile XIII; UF 17568 and UF 17569, right naviculars, Haile XV A.

DESCRIPTION.—The Haile XV A skeleton and isolated postcranial material from other sites in Florida provide the first adequate samples of the postcranial skeleton of this genus.

The following description is based primarily on the Haile XV A speci-

men; but because certain elements are lacking, it has been supplemented by material from other Florida Blancan localities.

CRANIUM.—The nasal bones (Fig. 5b) of UF 10902 compare favorably in size and morphology with those of the South American specimen of *Kraglievichia paranensis* described by Castellanos (1927). They differ, however, in having tiny protuberances on the anterior ends near the medial surface. These structures are not present on any of the other specimens or figures of *Pampatherium* or *Kraglievichia* studied. Only the anterior halves of the nasals are present in UF 10902, because the skull had been eroded away, and only parts of it recovered.

The premaxilla (Fig. 5a) contains only one alveolus. The premaxillary-maxillary suture forms the posterior border of the first alveolus (or tooth socket), as in *Pampatherium*. *Holmesina* (from North America) was originally thought to be distinguished by the presence of a single premaxillary tooth; two such teeth were supposed to occur in *Pampatherium*. A single alveolus occurs in the neotype of *"Holmesina"* (AMNH 26856; Simpson 1930) as well as in UF 889 (*P. septentrionalis*). However, it now appears that the true *Pampatherium* also has only one tooth in the premaxilla (G. Edmund, pers. comm.), and, therefore, the supposed difference between the North and South American forms is probably not valid.

The major features of the maxilla from Haile XV A compare favorably with those in *Pampatherium*. The infraorbital foramen (Fig. 5e) is located directly above the sixth tooth in both genera. The anterior palatal foramina (Fig. 5c) are located between the posterior edges of the fourth teeth in the Haile XV A specimen, whereas their position varies somewhat in *Pampatherium*. The maxillary process of the zygomatic arch lies directly above the seventh tooth in both *Kraglievichia* and *Pampatherium*.

Only a portion of the zygomatic arch is present in UF 10902 (Fig. 5d-e). The zygomatic process of the maxilla turns posteriorly and downward as it leaves the skull. The anterior portion of the jugal, which borders the zygomatic process laterally, then turns upward and expands posteriorly to accept the squamosal process. A well-developed suture, located at the posterior end of the jugal, indicates that the zygomatic arch is complete in *Kraglievichia*, as it is in *Pampatherium*. The base of the zygomatic process of the maxilla is expanded by sinuses, as in *Pampatherium*.

UPPER DENTITION.—There are nine teeth in both the upper and lower jaws of *Kraglievichia*. One of the upper teeth is located in the premaxilla. (Because the incisors of most mammals occur in the premaxilla, it is tempting to refer to the first tooth in *Kraglievichia* as an

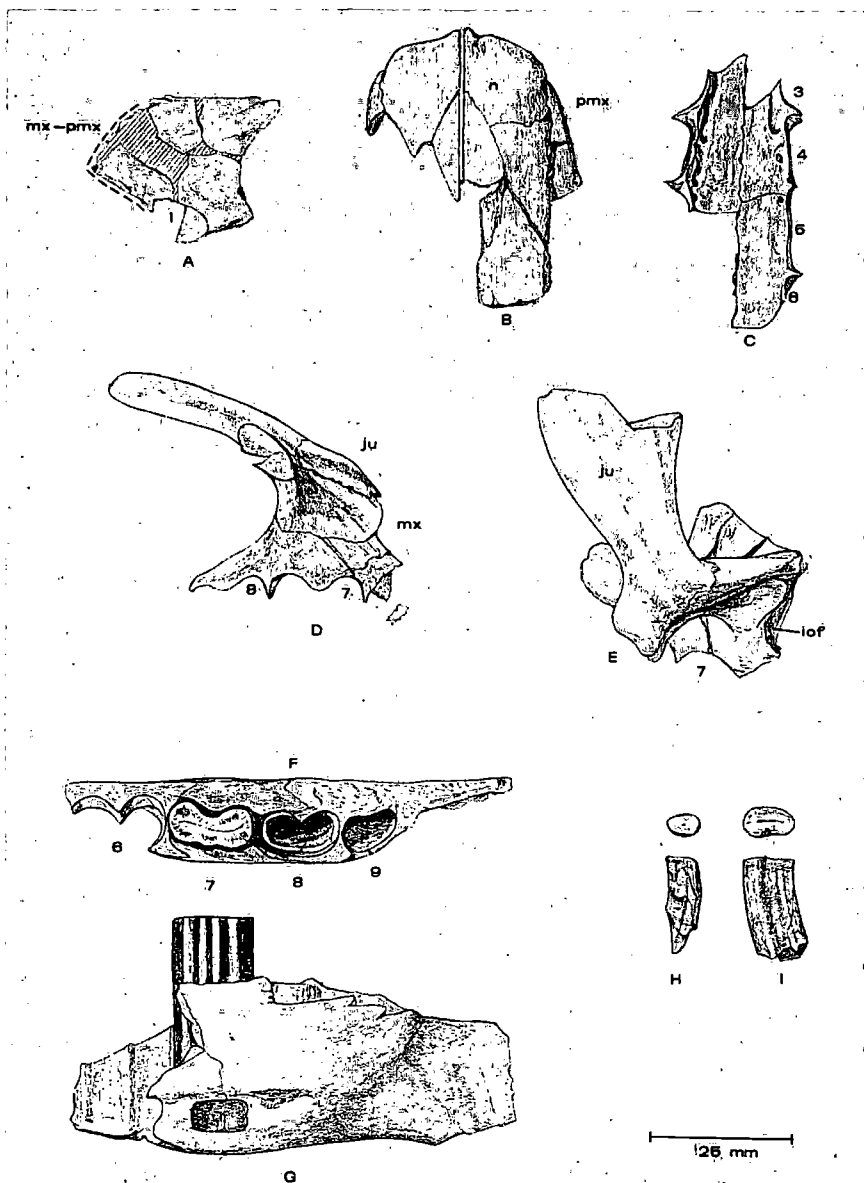FIGURE 5. *Kraglievichia floridanus,* cranial material: (A) right premaxillary; (B) nasal; (C) palatal portion of maxillary; (D) zygoma, ventral view; (E) zygoma, lateral view; (F) right mandible, occlusal view; (G) right mandible, lateral view; (H) first lower tooth; (I) fourth lower tooth. *Abbreviations*: iof = infraorbital foramen, ju = jugal, mx = maxillary, mx-pmx = premaxilla, n = nasals, numbers refer to tooth sequence.

incisor; however, I have continued to use the non-committal terminology "tooth one" through "tooth nine" in this report.) The fourth tooth provides critical evidence for the phylogenetic position of the Haile XV A species. The alveolus for this tooth suggests that it was incipiently bilobate and nearly parallel with the more posterior teeth, a condition intermediate between earlier *Kraglievichia* and later *Pampatherium*.

Measurements of the cranium and upper dentition are presented in Table 6.

MANDIBLE AND LOWER DENTITION.—Partial left and right mandibles are preserved in UF 10902. In the right mandible (Fig. 5f-g) the 7th tooth is complete, the 8th is broken, and alveoli for the 6th and 9th teeth are present. Unfortunately, the anterior part of each mandible is lacking in UF 10902. Other than size, no differences are apparent between *Kraglievichia* and *Pampatherium* with regard to the posterior parts of the mandibles (see Table 6).

Vertebrae.—The vertebral material from the Haile XV A skeleton consists of 7 thoracic, 5 lumbar, and 4 caudal vertebrae. Five of the thoracic vertebrae are cemented together in the proper sequence by coarse sandstone. Comparison of these specimens with the vertebrae of a well-preserved skeleton of *Pampatherium* from Branford IA, Suwannee County, Florida (Rancholabrean), shows no significant morphological differences except for size.

FRONT LIMBS.—In this description the major elements of the forelimb are compared with those of both *Dasypus* and *Pampatherium*. *Kraglievichia floridanus* is approximately the same size as Rancholabrean specimens of *Dasypus bellus* (a large extinct Pleistocene armadillo) and conceivably the limb elements of these two species could be confused. The podial elements and hind-limb elements should never be confused, however.

The right humerus of UF 10902 is well preserved, except for the distal end (Fig. 6a-b). The humerus of *Kraglievichia* is greatly expanded laterally (as seen in the specimens from Santa Fe I). The supracondylar foramen is relatively larger than in *Dasypus*. The articular surface for the radius is concave in *Kraglievichia*, whereas it has a slight convexity in *Dasypus*. The supinator ridge is relatively narrow in *Kraglievichia*, and the deltoid ridge is wider. Comparison of the proximal end of the humerus in *Kraglievichia* and *Pampatherium* shows no distinct differences, except for size.

Three ulnae are known from the Haile XV A site; two of which are probably from the same individual because they are similarly preserved, are from opposing sides, and agree closely in measurements (Table 7). The ulna of *Kraglievichia* (Fig. 6c-d) is laterally flattened and has a long

TABLE 6.—CRANIAL AND DENTAL MEASUREMENTS (IN MM) OF *Kraglievichia* AND *Chlamytherium*.

	Kraglievichia UF 10902 Haile XV A	*Kraglievichia* Argentina[1]	*Pampatherium* AMNH 26856 Florida	*Pampatherium* UF 889, 890 Florida
CRANIUM				
Width of nasals at anterior border of premaxilla	25.9	27.6		39.0
Width of palate at center of tooth 4	15.0	17.4	28.0[2]	29.6
Anteroposterior length, tooth 4	12.3	12.6	-	16.7
Anteroposterior length, tooth 5	15.4	12.7	23.7	20.5
Anteroposterior length, tooth 7	16.4	15.0	22.6	23.6
Width, tooth 1	6.8	6.5	7.6	
MANDIBLE				
Distance, top of ninth alveolus to bottom of jaw	37.8	32.8	60.2	51.4
Length, tooth 1	5.4			
Width, tooth 1	3.7			
Length, tooth 3	8.2		12.3	
Width, tooth 3	5.2		6.9	
Length, tooth 6 (alveolar)	16.0	14.8	25.1	25.1
Length, tooth 7	14.3	13.9	23.3	22.1
Width, tooth 7	7.1		11.2	9.2
Width, tooth 8 (alveolar, anterior lobe)	11.9		10.5	10.0
Length, tooth 9	10.3		13.8	
Width, tooth 9	5.5		7.8	

[1] Measurements after Castellanos (1927).
[2] Estimated.
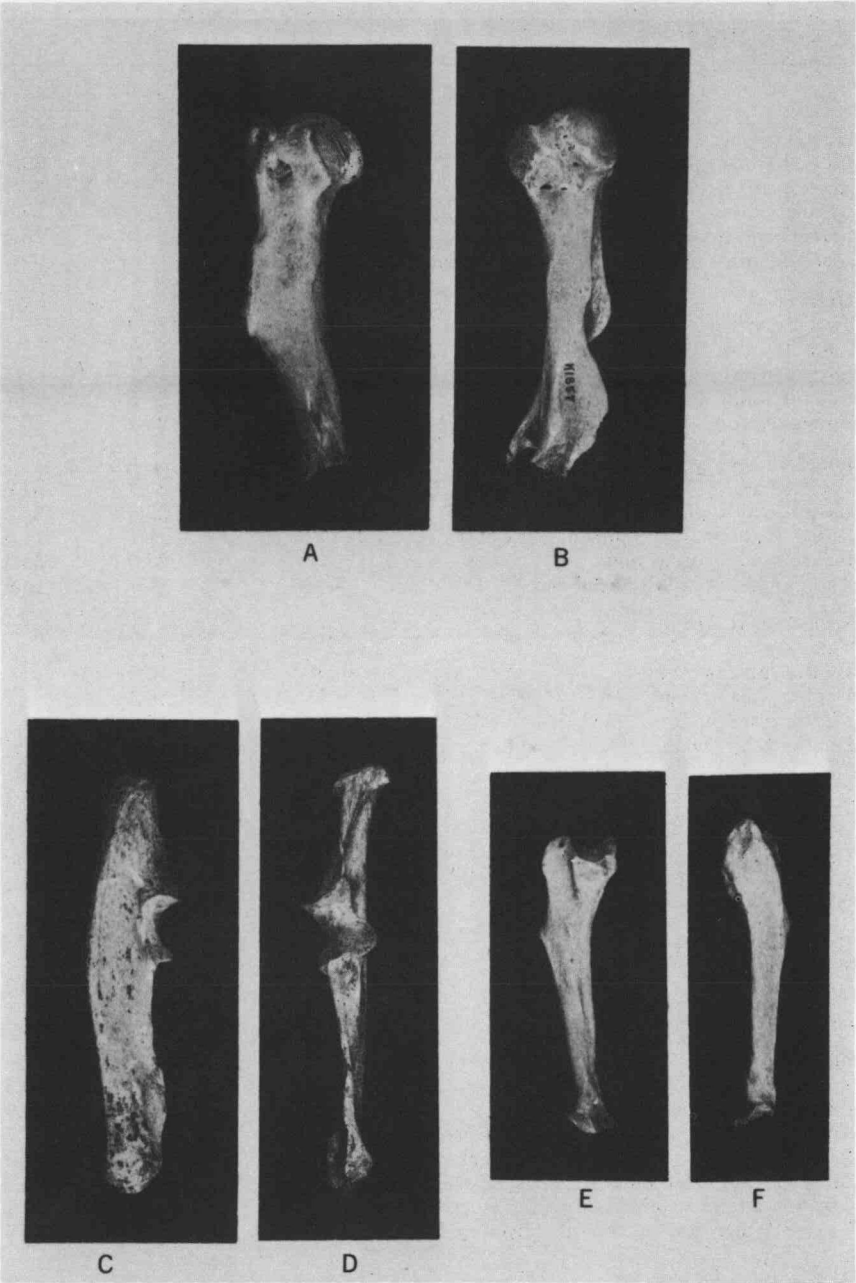
FIGURE 6. *Kraglievichia floridanus,* front limb elements: (A) right humerus, medial view; (B) right humerus, anterior view; (C) left ulna, medial view; (D) left ulna, anterior view; (E) left radius, posterior view; (F) left radius, anterior views; X 0.45.

TABLE 7.—MEASUREMENTS (IN MM) OF LIMB ELEMENTS OF *Kraglievichia floridanus*, UF 10902, HAILE XV A.

	Left	Right
HUMERUS		
Lateral width, proximal end		36.7
Anteroposterior width, proximal end		36.8
Greatest anteroposterior diameter of shaft		25.5
Lateral width of shaft at same location		18.2
Distance from proximal end to top of entepicondylar foramen		100.5
ULNA		
Total length	129.0	
Lateral width, proximal end	17.2	
Lateral width, distal end	16.1	
Lateral width at semilunar notch	25.5	25.7
Anteroposterior width at semilunar notch	29.4	30.5
RADIUS		
Total length	89.2	87.2
Lateral width, proximal end	22.6	22.3
Anteroposterior width, proximal end	11.7	11.4
Lateral width, distal end	23.0	22.3
Anteroposterior width, distal end	17.4	16.5
METACARPAL II		
Total length	32.8	
Width, proximal end	10.9	
Depth, proximal end	14.5	
Width, distal end	10.5	
Depth, distal end	11.2	
METACARPAL III		
Total length	34.4	36.3
Width, proximal end	13.8	14.5
Depth, proximal end	12.8	13.0
Width, distal end	12.6	13.4
Depth, distal end	10.5	11.0
UNGUAL PHALANX, DIGIT V		
Total length		29.1
Width, proximal end		11.4
Depth, proximal end		10.3
FEMUR		
Total length		193.5
Lateral width, proximal end		60.9
Anteroposterior thickness of greater trochanter		41.7
Lateral width of shaft at third trochanter		41.3
Anteroposterior thickness of shaft at same point		23.7
Greatest lateral width of articular facets		48.4
Greatest anteroposterior width, distal end		51.5
TIBIA AND FIBULA		
Total length		121.0
Lateral width, distal end		46.7
Anteroposterior width, distal end		25.1

TABLE 7.—CONTINUED

CALCANEUM		
Total length		63.3
Width of articular facets for astragalus		28.0
Depth of facet for cuboid		12.2
Width of facet for cuboid		11.5
NAVICULAR		
Greatest lateral width		39.5
Greatest anteroposterior distance		23.3
Greatest depth		22.5
METATARSAL II		
Total length	33.2	32.8
Width, proximal end	12.2	12.5
Depth, proximal end	13.8	14.3
Width, distal end (articular surface)	13.2	13.7
Depth, distal end (articular surface)	11.3	10.2
METATARSAL III		
Total length	36.5	34.5
Width, proximal end	15.0	14.9
Depth, proximal end	14.7	14.4
Width, distal end (articular surface)	13.2	12.3
Depth, distal end (articular surface)	11.3	11.5
UNGUAL PHALANX, DIGIT V		
Total length		24.6
Width, proximal end		17.6
Depth, proximal end		10.7

olecranon process. The articular facets for the radius and medial condyle of the humerus are combined in this form, whereas in *Dasypus* they are partially divided. Another striking difference is a lateral groove that runs the entire length of the ulna in *Dasypus* and terminates at the upper border of the semilunar notch in *Kraglievichia*. Size appears to be the only difference between the ulna of *Kraglievichia* and *Pampatherium*.

In both *Kraglievichia* and *Dasypus* the distal end of the radius is massive compared to the proximal end, although it is less flattened in *Kraglievichia* (Fig. 6e-f). The proximal portion of the shaft is relatively thicker and less curved in *Kraglievichia*. Comparison with *Pampatherium* shows only a size difference.

The left metacarpal II is present in the Haile XV A skeleton, and generally agrees with that of *Pampatherium* in shape and proportion. The facet for articulation with the trapezoid, however, shows an important difference; when viewed laterally, this facet is smoothly curved in *Pampatherium* and has a sharp V-shape in *Kraglievichia*.

The magnum facet is oblong in *Pampatherium* and round in *Kraglievichia*. The trapezoid facet is wider dorsally in *Pampatherium*. To

compensate for this, the facet for metacarpal III bulges out proximally to form a pocket for the trapezoid facet. In *Kraglievichia* less of the trapezoid articulates with metacarpal III.

The left and right third metacarpals are preserved in UF 10902 from Haile XV A and also in UF 10722 from Santa Fe I. In this element the facet for metacarpal II and the trapezoid shows a relatively greater association with the trapezoid than with the adjacent metacarpal. In both *Pampatherium* and *Kraglievichia* the magnum facet is convex dorsally and concave ventrally. In *Kraglievichia* the greater portion of the facet is convex, whereas the opposite is true in *Pampatherium*. When viewed from below, the ventral portion of this facet lies oblique to the long axis of the bone, whereas in *Pampatherium* it is perpendicular to the long axis.

HIND LIMBS.—The femur (Fig. 7a-b), the tibia, and the fibula (Fig. 7c-d) show no morphological differences from those of *Pampatherium* except for size.

The calcaneum of *Kraglievichia* is less expanded distally and less robust than that of *Pampatherium* (Fig. 8). In *Kraglievichia* the two astragalar facets are connected to form a bilobed facet, whereas in *Pampatherium* they are separated by a central valley. In *Kraglievichia* the facets are nearly equal in size, whereas in *Pampatherium* the lateral facet is much the larger of the two.

There are no apparent differences in the naviculars of *Kraglievichia* and *Pampatherium*. It may be noted that the three right naviculars from Haile XV A exhibited little variation in the relative shapes and sizes of the facets in which the cuneiform bones articulate.

In metatarsal II the mesocuneiform facet is relatively more narrow ventrally in *Kraglievichia* than in *Pampatherium*. There is an indentation at the proximal end, at the point where it meets the proximal end of the metatarsal I; in *Pampatherium* there is no such indentation, the medial border forming an unbroken line. The metatarsal I of *Kraglievichia* presumably had a corresponding projection; no such feature occurs in metatarsal I of *Pampatherium*.

In lateral view the proximal articular surface of metatarsal III appears rounded in *Kraglievichia*, while in *Pampatherium* it forms a straight line perpendicular to the long axis of the element. Because the proximal end of this element is rounded in *Kraglievichia*, the articular surface can also be seen when the element is viewed from above. This would appear to permit more dorsoventral movement of the toes of *Kraglievichia*.

The facets for metatarsal III and the cuboid are united on metatarsal IV in *Kraglievichia*, but separate in *Pampatherium*.

Two ungual phalanges of digit V (UF 10902) have been recovered
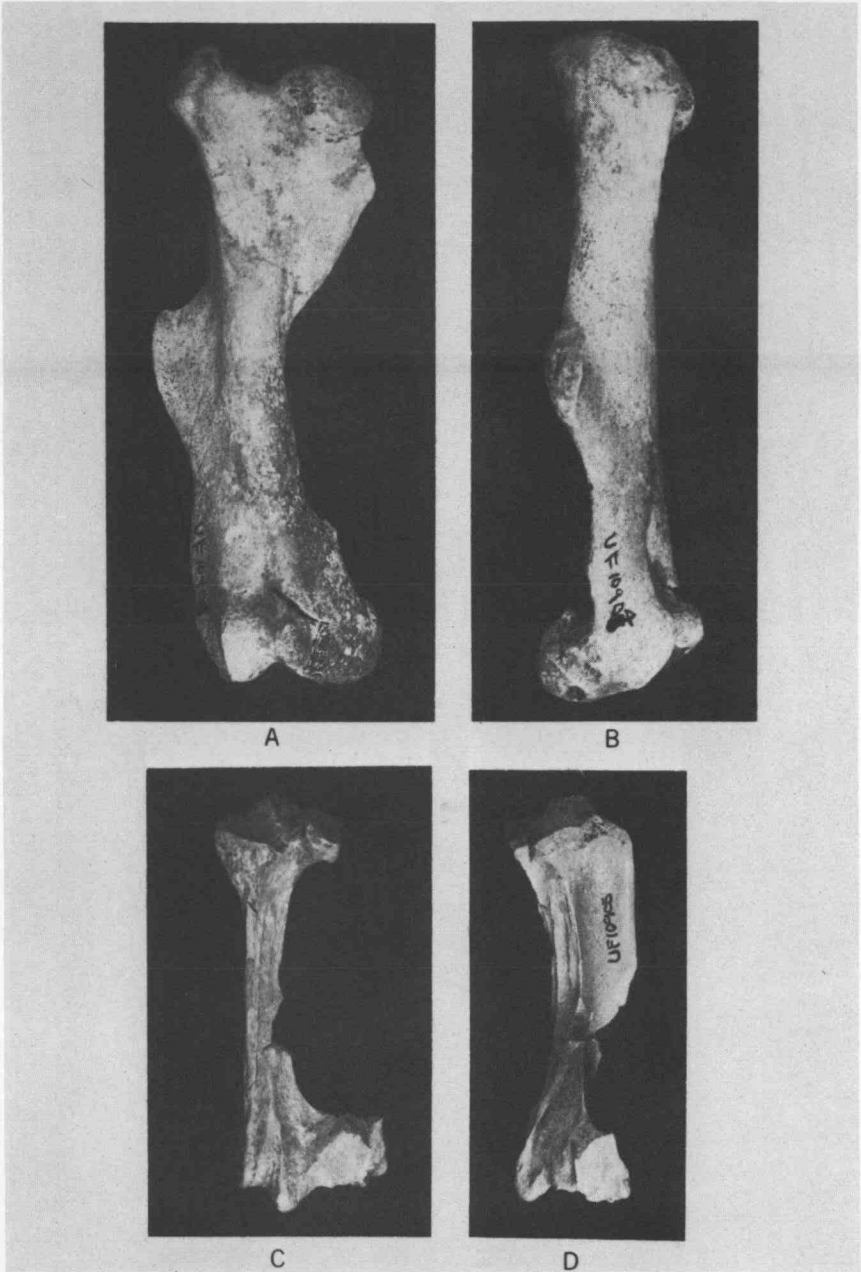
FIGURE 7. *Kraglievichia floridanus*, hind limb elements: (A) right femur, anterior view; (B) right femur, lateral view; (C) right tibia and fibula, anterior view; and (D) right tibia and fibula, lateral view; X 0.45.
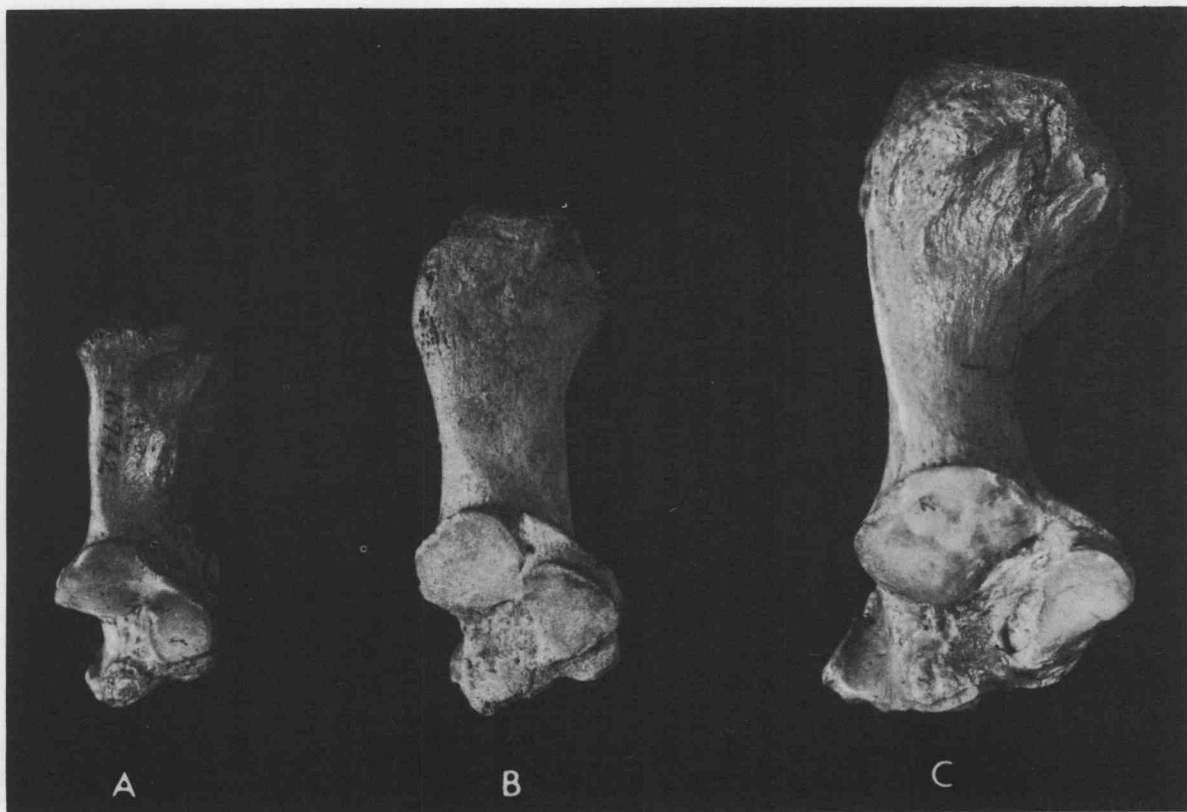
FIGURE 8. *Kraglievichia* and *Pampatherium,* calcanea, anterior views: (A) *Kraglievichia floridanus,* right calcaneum, Haile XV A; (B) *Kraglievichia* sp., right calcaneum, Inglis IA; and (C) *Pampatherium septentrionalis,* right calcaneum, Branford IA; X 0.80.

from Haile XV A; one (presumably from the forefoot) is rather narrow and pointed, and the other (presumably from the hind foot) blunt and broad. They agree in all features except size with the corresponding phalanges in *Pampatherium*. Measurements of the limb element in other examples of *Kraglievichia* from various Florida localities are presented in Table 8.

REVIEW OF THE CHLAMYTHERIINAE

The genus *Kraglievichia* is reported here for the first time in North America. In order to place the genus in a meaningful context, the subfamily Chlamytheriinae is reviewed briefly. The nomenclatural history of the various chlamythere genera will be discussed, followed by a brief characterization of the various genera, beginning with the oldest.

The first remains of a chlamythere were discovered in a Brazilian cave deposit in 1836 by Peter Wilhelm Lund and described by him as *Chlamytherium humboldtii* (Lund 1838). Lund consistently used his original generic name in his early works, but later (beginning about 1840) he emended this to *Chlamydotherium*, calling the earlier name a *lapsus*. Several later authors followed this secondary spelling. Bronn (1838) meanwhile had given the name *Chlamydotherium* to a genus of glyptodonts. Ameghino (1875) proposed *Pampatherium* as a substitute for Lund's supposedly preoccupied generic name, *Chlamydotherium*, but he later discontinued use of the new name after checking the spelling in Lund's original description. Paula Couto (1956) has revised the use of *Pampatherium*, which has come back into general usage.

The first North American record of *Pampatherium* was reported by Leidy (1889a), although he first designated the new species *Glyptodon septentrionale*. Leidy (1889b) later referred the same material to the South American species *Chlamytherium humboldtii*. Sellards (1915) believed that the North and South American forms represented different species and resurrected Leidy's original specific name *septentrionale*.

Ameghino (1902) described *Machlydotherium* from the Eocene of Patagonia. This still stands as the earliest record for a chlamythere.

Castellanos (1927) named two new genera of chlamytheres: *Vassallia*, based on an edentulous mandible and several dermal plates; and *Kraglievichia*, based on two skulls, a mandible, and a small amount of postcranial material. The type species of *Vassallia* is *Chlamytherium minutum* (Moreno and Mercerat 1891). *Kraglievichia* was erected to include *C. paranesis*, *C. intermedia* (Ameghino 1887), and *C. subintermedius* Rovereto 1914), with *C. paranensis* as the generic type.

Simpson (1930) established the genus *Holmesina*, including in it the

TABLE 8.—MEASUREMENTS (IN MM) OF LIMB ELEMENTS OF *Kraglievichia* FROM VARIOUS FLORIDA LOCALITIES.

Humerus	UF 10432 (right) Santa Fe I	UF 9354 (right) Santa Fe I
Greatest anteroposterior diameter of shaft	28.8	
Lateral width of shaft at same point	19.5	
Lateral width, distal end	60.2	54.2
Greatest width of distal articular surface	37.8	36.8

Ulna	UF 10449 (left) Santa Fe I	UF 17474 (right) Haile XV A
Total length	116.5	
Lateral width, proximal end	17.6	
Lateral width, distal end	10.4	
Lateral width at semilunar notch	20.5	25.1
Anteroposterior width at semilunar notch	23.4	31.8

Radius	UF 10830 (right) Santa Fe I
Total length	105.2
Transverse width, proximal end	24.5
Anteroposterior width, proximal end	13.3
Transverse width, distal end	23.1
Anteroposterior width, distal end	20.6

Femur	UF 17476 (left) Haile XII B
Lateral width, proximal end	55.3
Anteroposterior width, proximal end	34.2
Lateral width of shaft at third trochanter	38.8
Anteroposterior width of shaft at same point	16.5

Calcaneum	UF 17473 (left) Santa Fe II
Total length	64.1
Width of articular facets for astragalus	24.5
Depth of facet for cuboid	14.9
Width of facet for cuboid	10.6

Navicular	UF 17568 (right) Haile XV A	UF 17569 (right) Haile XV A
Greatest lateral width	37.3	33.6
Greatest anteroposterior distance	22.6	18.3
Greatest depth	30.6	26.6

Metatarsal II	UF 10902 (left) Haile XV
Total length	30.8
Width, proximal end	11.3
Depth, proximal end	13.6
Width, distal end (articular surface)	12.3
Depth, distal end (articular surface)	10.2

TABLE 8.—CONTINUED

Metatarsal III	UF 17472 (right) Santa Fe II
Total length	34.2
Width, proximal end	16.5
Depth, proximal end	15.2
Width, distal end (articular surface)	13.5
Depth, distal end (articular surface)	11.4

Metatarsal IV	UF 17475 (right) Santa Fe II
Total length	29.5
Width, proximal end	11.2
Depth, proximal end	12.2
Width, distal end (articular surface)	15.1
Depth, distal end (articular surface)	10.5

species *septentrionalis*, after studying well-preserved material from the Seminole Field in western peninsular Florida. Subsequent authors tended to refer the North American forms to *Holmesina* and those from South America to *Chlamytherium*.

Castellanos (1937) later proposed a new genus, *Plaina*, the type species of which (*C. intermedius*) he had earlier placed in *Kraglievichia*. His rationale for establishing this new genus was based largely on his interpretation of the lineage of the chlamytheres. Castellanos believed that logically there should be a form intermediate in size between *Kraglievichia* and *Chlamytherium*, and because *C. intermedius* is larger than the other material referred to *Kraglievichia*, he saw it as representing this intermediate form.

The genus *Hoffstetteria* Castellanos (1957) was based upon a skull collected in Ecuador, which had been described previously as a new species, *C. occidentalis*, by Hoffstetter (1952).

Machlydotherium is the oldest of the various chlamythere genera, its remains being known from the Eocene of Patagonia. Its precise relationship to later chlamytheres is not clear (Simpson 1945), a situation that may be attributed partly to the absence of any Oligocene records of the subfamily.

Vassallia occurs in Araucanean (Pliocene) deposits in Argentina (Castellanos 1946) and is also known (a skull; UCMP 40401) from the Late Miocene La Venta fauna of Colombia. This identification is based upon the nature of the anterior dentition (the first five teeth are peg-like and rotated lingually) and the small size of the specimen.

Porta (1962) reported *Kraglievichia* from the La Venta fauna of Colombia, but this record was based only upon dermal plates. It now seems more likely that they represent *Vassallia* instead.

Castellanos (1927) listed two major morphological differences between *Vassallia* and *Kraglievichia*. In *Vassallia* the first five teeth tend to be peg-like and rotated lingually, whereas in *Kraglievichia* only the first four teeth show this condition. *Vassallia* is also significantly smaller than *Kraglievichia*. I suspect here, as did Castellanos, that *Vassallia* is the ancestor of *Kraglievichia*.

So far as the status of *Plaina* is concerned, Castellanos (1927) was probably correct in his initial judgment when he assigned the material on which this genus was based (three isolated dermal plates) to the genus *Kraglievichia*. He considered these plates to be intermediate in size and sculpturing between *Kraglievichia* and *Pampatherium*, although they actually fall within the smaller size range of *Kraglievichia*. Furthermore, it seems illogical to interpret slight variations in plate rugosity as generically significant. I therefore propose that *Plaina* be regarded as a synonym of *Kraglievichia*.

The genus *Hoffstetteria* Castellanos (1957) is based upon supposed differences in shape and measurements of the teeth. These differences are minor, however, and may be attributed to specific variation. *Hoffstetteria* is thus considered to be a synonym of *Pampatherium*.

In Simpson's (1930) description of *Holmesina*, he listed a number of characters by which this new genus differed from *Pampatherium*. James (1957) subsequently showed that the characters given by Simpson are not sufficient to separate the North and South American forms generically, and that *Holmesina* is a synonym of *Pampatherium*. I support James' conclusion. Simpson (1930) argued also that if *Holmesina* was not valid, then all South America forms should be placed in the genus *Pampatherium*, as they are no more different from each other than is *Pampatherium* from *Holmesina*. This argument is not without merit. However, new characters discovered during the present study, considered together with those previously recognized, provide ample justification for recognition of *Kraglievichia* and *Pampatherium* as distinct genera.

To summarize, the genera of chlamytheres recognized here are: *Machlydotherium* (Eocene, South America); *Vassallia* (Miocene and Pliocene, South America); *Kraglievichia*, including *Plaina* (Pliocene, South America and Plio-Pleistocene, North America); and *Pampatherium*, including *Hoffstetteria* and *Holmesina* (Pleistocene, North and South America).

The most obvious morphological trend in chlamythere evolution since the Miocene has been a consistent increase in size. *Vassallia* is slightly smaller than *Kraglievichia*, which in turn is substantially smaller than

Pampatherium. This increase in size may be seen by comparison of the two femora in Figure 9.

Inasmuch as the increase in size noted above occurred gradually, many intermediate stages logically would be expected. A series demonstrating the changes in size between *Kraglievichia* and *Pampatherium* appears in Figure 10. The dermal plates illustrated are from various Plio-Pleistocene stages in Florida. Plates from the Early Blancan Haile XV A site are the smallest, followed by those from the Early Irvingtonian Inglis IA site. Still larger plates occur in the later Irvingtonian Coleman IIA site, and the largest plates of all are those from the Rancholabrean Branford IA locality.

Another major trend in chlamytheriine evolution is the shift from peg-like to bilobate tooth shape and from an oblique to a parallel orientation. This change seems to have progressed in an anterior direction, inasmuch as an increase in the number of anteriorly-situated bilobate and parallel teeth may be seen in the transition from *Vassallia* through *Pampatherium* (Castellanos 1937).

The Haile XV A specimen differs from previously described specimens of *Kraglievichia* and *Pampatherium* in the nature of the anterior upper dentition. In South American specimens of *Kraglievichia*, the first four teeth are oval in cross-section rather than reniform and have their long axes turned lingually. In *Pampatherium* the first three teeth show this condition, but the fourth is usually bilobate and parallel with the rest of the tooth row. In James' (1957) specimen the first four teeth are oval, but the long axis of the fourth tooth parallels the rest of the tooth row, rather than being canted lingually. The peg-like appearance of the fourth tooth is presumably a primitive condition that recurred in an aberrant individual. The incipiently bilobed condition in the fourth upper tooth of *Kraglievichia floridanus* represents the transitional condition between *Kraglievichia* and *Pampatherium*, although the features of the feet remain primitive in several respects.

Chlamytheres apparently originated in South America, because all pre-latest Pliocene records of this group are restricted to that continent. The oldest genus is the Eocene *Machlydotherium*. No chlamytheres are known from the Oligocene, but *Vassallia* is present in Miocene deposits, and both *Vassallia* and *Kraglievichia* occur in the Pliocene of South America. *Kraglievichia* is here reported in Blancan deposits of North America. *Pampatherium* is present throughout the Pleistocene in both North and South America. This distribution presents some interesting geographic and phylogenetic problems.

Until now the evolution of the chlamytheres was thought to have occurred exclusively in South America, with only the end product,
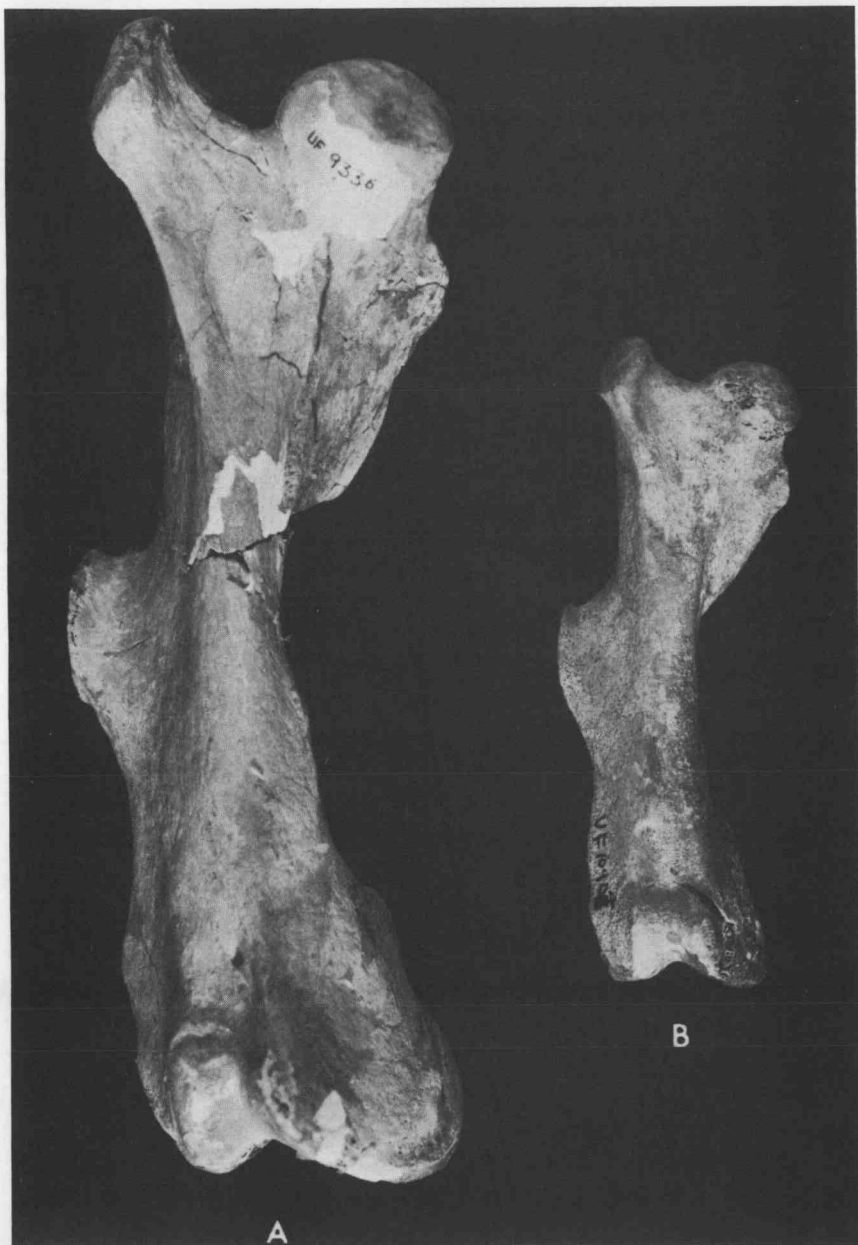
FIGURE 9. *Pampatherium* and *Kraglievichia*, femora, anterior views: (A) *Pampatherium septentrionalis*, right femur, Branford IA; and (B) *Kraglievichia floridanus*, right femur, Haile XV A; X 0.45.

Pampatherium, having migrated to North America during Ranchola-
brean time. Study of the Haile XV A fauna and other pre-Ranchola-
brean sites of Florida indicates instead that *Kraglievichia* migrated to
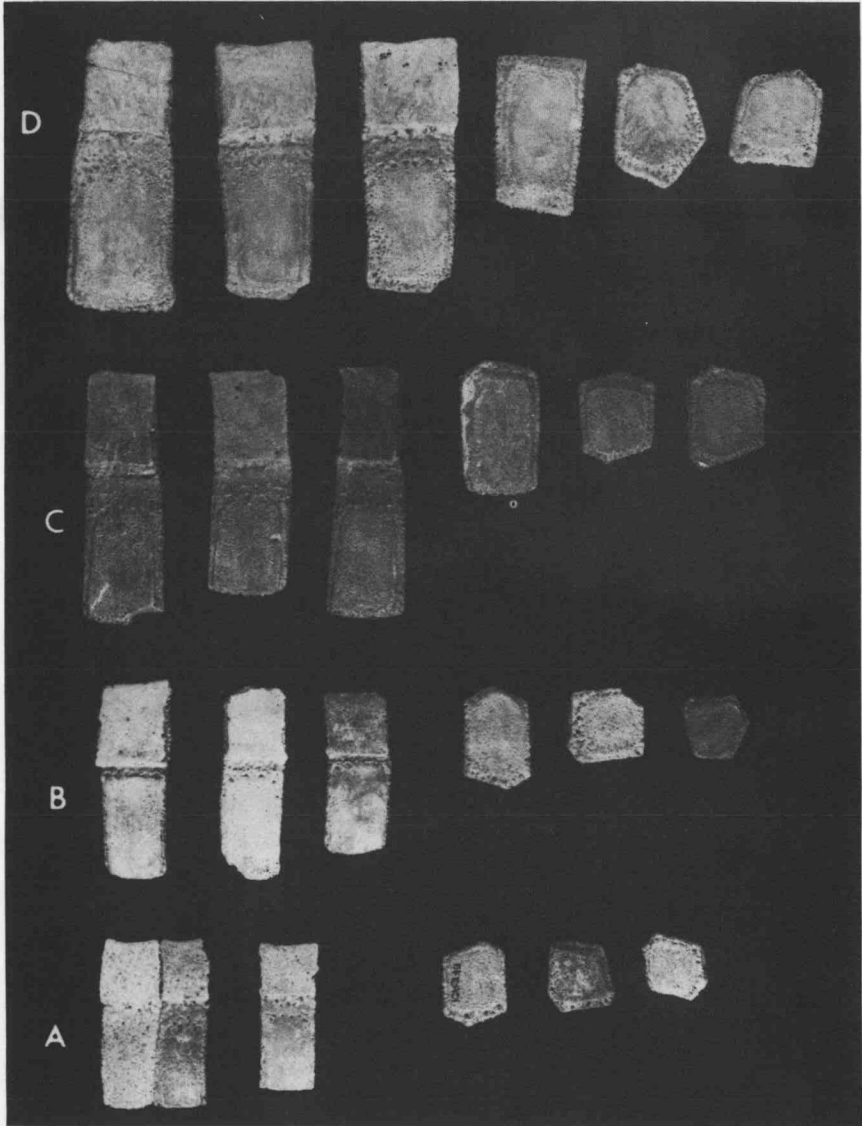
FIGURE 10. *Kraglievichia* and *Pampatherium,* dermal plates, dorsal views: (A)
Kraglievichia floridanus, Haile XV A; (B) *Kraglievichia* sp. Inglis IA; (C) *Pam-
patherium septentrionalis,* Coleman IIA; and (D) *Pampatherium septentrionalis,*
Branford IA; X 0.30.

North America shortly after the establishment of the Late Cenozoic land bridge between the two continents, and that chlamytheres evidently continued to evolve in Florida and the Gulf Coastal Province throughout the Pleistocene.

Three hypotheses can be offered regarding the Pleistocene zoogeography and evolution of the chlamytheres. The first suggests that from a common *Kraglievichia* origin North and South American Pleistocene chlamytheres had separate but parallel histories. If so, *Holmesina* would be the correct name for the later North American chlamythere.

A second hypothesis suggests that *Kraglievichia* spread from South America into North America near the end of the Pliocene, after which it became extinct in South America. This would account for the absence of chlamythere records in the Early Pleistocene of South America. (A dermal plate that was questionably attributed to the Chapadmalalan stage by Kraglievich [1934] actually came from a locality near the major deposit, and its horizon is unknown. Since each chlamythere shell produces a high number of bony plates, they are usually abundant if present at all.) Later in the Pleistocene, then, *Pampatherium* spread back into South America.

The third hypothesis suggests that chlamytheres were continuously distributed through tropical America during most of the Pleistocene. Thus the evolution of *Pampatherium* from *Kraglievichia* was a single continuous event that spread through populations from the Gulf Coastal region and mesoamerican parts of North America into the northern parts of South America. The absence of Early Pleistocene deposits in tropical South America makes it difficult to test this hypothesis. This last hypothesis, here favored, may be partly tested by careful comparisons of later Pleistocene chlamytheres.

Dasypus bellus SIMPSON 1929

MATERIAL.—UF 16698: left nasal, right maxilla and mandible, right astragalus, and 51 isolated dermal plates from Haile XV A; UF 10449: right ulna from Santa Fe IA.

The dentigerous specimens probably represent one individual, because they articulate closely. Most of the plates also were found closely associated. The present material has been compared with other specimens of *Dasypus bellus* and with its closest living relative, *Dasypus novemcinctus*. The only other known *D. bellus* specimens containing teeth are the excellent skeleton from Crankshaft Pit, Missouri (UK 15544; Oesch 1967), and a fragmentary jaw from Melbourne (Ray 1958). Comparisons have been made with postcranial material from numerous Pleistocene sites in Florida.
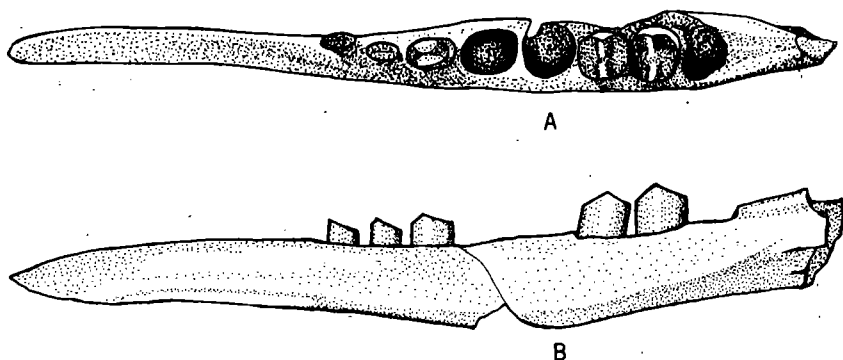
FIGURE 11. *Dasypus bellus,* mandible, UF 16698, Haile XV A: (A) occlusal view; and (B) lateral view; X 1.45.

The nasal bone is represented by the anterior portion only and is larger than, but morphologically similar to the nasal bone of *D. novemcinctus.*

In discussing the dentition, teeth will be designated as follows: T^1 will refer to the first upper tooth, T^2 the second upper tooth, etc. Similarly numbered subscripts will be used in referring to lower teeth.

The maxilla is broken posteriorly and contains only T^3-T^6. Except for size, the lateral portion of this specimen compares closely with the corresponding position of the Crankshaft Pit specimen. In the Haile XV A specimen T^3 is transversely flattened, but all the rest are round and peg-like. The preceding two teeth of the Haile XV A *Dasypus* (UF 16698) were probably also transversely flattened, as this is the usual condition in *D. bellus.* In *D. novemcinctus* the first three teeth tend to be less flattened laterally than in *D. bellus.* The remaining upper teeth were probably round and peg-like as is usually the case with T^4-T^6. Talmage and Buchanan (1954), as well as others, have pointed out that tooth number and structure are variable in *Dasypus.* In four *D. novemcinctus* skulls examined, the total number of teeth varied from seven to nine.

In UF 16698 (Fig. 11), as in the Kansas mandible, two foramina are present—one large and one small. In UF 16698 the larger of the two foramina occurs between T_2 and T_3. The smaller of the two foramina is located 38 mm anterior to T_1. In UK 15544, the larger foramen is anterior to the smaller and is located directly beneath T_2. The smaller is located beneath T_3. The number of these mental foramina in *D. novemcinctus* varies from one to four. The symphysis of the Haile XV A specimen is weak, as is characteristic of the genus.

The mandible of UF 16698 lacks T_4-T_5. The preceding teeth, T_1-T_3, are laterally flattened, but the succeeding teeth, T_6 and T_7, are round in

TABLE 9.—DENTAL MEASUREMENTS (IN MM) OF *Dasypus bellus*.

	UF 16698 Haile XV A Florida	UK 15544 Crankshaft Pit Missouri	
		left	right
MAXILLARY			
Total distance, teeth 3–6	19.9	23.8[1]	23.7
Anteroposterior distance, tooth	3.5	4.6[1]	4.5
Transverse distance, tooth 3	2.1	4.6[1]	4.5
Anteroposterior distance, tooth 4	4.4		
Transverse distance, tooth 4	3.6		
Anteroposterior distance, tooth 5	4.0		4.1
Transverse distance, tooth 5	4.2		5.1
Anteroposterior distance, tooth 6	4.2	5.2[2]	4.5
Transverse distance, tooth 6	4.1		4.8
MANDIBLE			
Depth of ramus at tooth 1	6.8		12.4
Width of ramus at tooth 1	2.8		3.7
Depth of ramus at tooth 6	8.4	15.2	15.5
Width of ramus at tooth 6	4.8	8.2	7.8
Depth of ramus at tooth 8	7.2	13.5	12.2
Width of ramus at tooth 8	5.2	7.1	6.4
Length of tooth row	38.8		45.6
Anteroposterior distance, tooth 1	3.0		2.8[3]
Transverse distance, tooth 1	1.3		1.8[3]
Anteroposterior distance, tooth 2	3.3	2.2	2.1
Transverse distance, tooth 2	1.4	2.7	2.3
Anteroposterior distance, tooth 3	3.3	4.0	4.5
Transverse distance, tooth 3	2.2	3.2	3.2
Anteroposterior distance, tooth 4	4.8[1]	4.7	4.6
Transverse distance, tooth 4	2.8[1]	4.5	4.2
Anteroposterior distance, tooth 5	4.0[1]	4.1	4.4
Transverse distance, tooth 5	3.3[2]	4.5	4.5
Anteroposterior distance, tooth 6	4.5	4.3	4.5
Transverse distance, tooth 6	3.7	4.7	4.7
Anteroposterior distance, tooth 7	4.6	4.6	4.2
Transverse distance, tooth 7	3.5	4.7	4.6
Anteroposterior distance, tooth 8	4.1	3.5	3.4
Transverse distance, tooth 8	4.2	3.5	3.4

[1] Alveolar.
[2] Alveolar, estimated.
[3] Not completely erupted.

cross-section. In this feature the Haile XV A specimen differs from the lower dentition of UK 15544, in which all the teeth are round. Except for smaller size and this tendency toward flattening of the anterior teeth, the mandibles and dentition of the Haile XV A specimen differ little from other *Dasypus* material. Dental measurements appear in Table 9.

In the ulna from Santa Fe I the channel on the medial side is deep and persists to the proximal end of the element. This distinguishes it from the otherwise very similar ulna of *Kraglievichia* (p. 127).

The astragalus of the Haile XV A *D. bellus,* along with other specimens of *D. bellus* from Florida Pleistocene sites, differs little from Recent specimens of *D. novemcinctus,* except for size. A comparison of the astragali of *Dasypus* from various stages of the Pleistocene reveals a progressive size increase similar to that of the chlamytheres.

The dermal plates of UF 16698 do not differ from any other specimens of *Dasypus,* except for size. Martin (1974:41) measured samples of plates from several Florida sites and showed little overlap in plate size between *D. bellus* and *D. novemcinctus.* His measurements indicate that the size of the plates does not follow the trend through the Pleistocene that is evident in other parts of the *D. bellus* skeleton. The Coleman IIA plates are notably small and overlap slightly in size with those of *D. novemcinctus.* However, this is probably a function of the small sample size used; there are approximately 2500 plates of diverse sizes in a single armadillo carapace, and there is no satisfactory method for determining from which parts of the shell the sample may have come. Size trends based on plates thus should involve large samples in order to insure accuracy.

The morphological differences between the Haile XV A material and later *D. bellus* material are very slight and presumably have a variational basis. Consequently, the Haile sample is referred to *Dasypus bellus.*

Dasypus bellus has been considered a southern North American species of Rancholabrean age. However, Martin (1974) extended the temporal range of the species back into Irvingtonian time, and the present study places the earliest record in the Blancan.

A question arises regarding the relationship between *D. bellus* and *D. novemcinctus.* These animals are clearly more closely related to each other than to any other armadillos (Auffenberg 1957), and it is uncertain whether *D. novemcinctus* was derived from *D. bellus* or existed allopatrically with that species during the Pleistocene, replacing it during the last few thousand years. If *D. novemcinctus* did evolve from *D. bellus,* it appears to have done so quite rapidly. In Miller's Cave (Patton 1963) a date of *ca* 8000 BP was given for the Travertine stratum bearing *D. bellus* remains, as compared to *ca* 3000 BP for the overlying Brown Clay deposits containing *D. novemcinctus.* Thus, the change occurred in that area within a span of only 5000 years. Another possibility is that *D. novemcinctus* existed somewhere else during the Pleistocene and replaced *D. bellus* very late in the Pleistocene. If so, it would be expected earlier in some Central or South American Pleistocene deposits. To date, the only fossil record of *D. novemcinctus* is from Miller's Cave, and the only Late Pleistocene armadillos from Mexico are referable to

D. bellus. Until more tropical fossil records are found, the problem must remain unresolved.

In view of the long residence of *Dasypus bellus* in Florida, it seems surprising that no pre-Rancholabrean records are available elsewhere in North America. Possibly *Dasypus* was restricted to the Gulf Coastal region during most of the Pleistocene. Slaughter (1961) cited two ecological conditions that may have been necessary for this species: (1) winters no more severe than those occurring in North-central Texas today, and (2) rainfall more than 20 inches per year. Thus the distribution of such climatic conditions may have restricted *D. bellus* to Florida and the Gulf Coastal Plain during most of the Pleistocene.

ORDER LAGOMORPHA

FAMILY LEPORIDAE

Sylvilagus sp. GRAY 1867

MATERIAL.—UF 17561: 2 M^3; UF 17562: M_3; UF 17563: lumbar vertebra; UF 17564: 3 innominates; UF 17565: 2 femora; UF 17566: 1 tibia; UF 17567: 2 metatarsals.

Hypolagus, Alurolagus, and *Sylvilagus* are the smaller lagomorphs common in North American Blancan deposits. Unfortunately, M^3 and M_3, the only teeth preserved in the Haile XV A fauna, are not diagnostic (Dawson 1958, Downey 1970). When compared with the *Hypolagus* innominates (Dawson 1958), the Haile XV A specimens possess a less elevated ilial crest, which is probably a more advanced condition. The remainder of the Haile XV A material resembles *Sylvilagus* in size and morphology, but one cannot completely discount reference of this material to *Alurolagus* (Downey 1968, 1970) from the Benson and Curtis Ranch Faunas of Arizona.

A species determination is not possible from the available material. Two living species of *Sylvilagus* occur widely in Florida, *S. palustris* and *S. floridanus.* The genus is presently distributed throughout North America, and also ranges into South America where it is represented by *S. floridanus* and *S. brasiliensis* (Hall and Kelson 1959).

Previously, the principal Blancan records of *Sylvilagus* were from the Broadwater fauna (Barbour and Schultz 1937) and the Sand Draw fauna (Skinner and Hibbard 1972) of Nebraska. Numerous Irvingtonian and Rancholabrean records of this genus are also known throughout North America.

ORDER RODENTIA

FAMILY SCIURIDAE

Cryptopterus webbi new species[1]

FIGURES 12-13

TYPE.—UF 12353: partial right mandible with third molar.
TYPE LOCALITY.—Haile XV A, T9S, R17E, Section 25, NW 1/4 of SW 1/4,
Alachua County, Florida.
AGE.—Blancan
DIAGNOSIS.—Large sciuropterine; low-crowned, subovate M_3 not tapered posteri-
orly; protoconid connected to weak anteroconid; large anterolabial cingulum as in
Cryptopterus tobieni; flat trigonid basin bearing "chaos" of low oblique ridges; strong
metaconid and metaconid-metastylid crest; distinct entoconid; faint hypolophid; broad
posterolophid bearing vestigial hypoconulid; posterolabial flexid absent.

DESCRIPTION.—The unique flying-squirrel specimen from Haile XV A
consists of the posterior part of the right mandible bearing a moderately-
worn third molar. Much of the ascending ramus, especially the condyle,
is well preserved. The distance between the last molar and the condyle
is about 15 mm. A large dental foramen lies 6.1 mm posterior to the last
molar. The angular region is massive, concave lingually, and descends
to a depth of more than 12 mm below the alveolar level, at which point
it is broken. The coronoid region is also broken.

The third molar measures 4.91 mm in length, 3.70 mm maximum
width across the metaconid and protoconid, and 3.29 mm posterior width
across the entoconid and hypoconid. This is by far the largest flying
squirrel in the New World, rivaling the extinct Eurasian species of
Cryptopterus and *Petauria* and some living Asian species of *Petaurista*.

The Haile XV A molar has a subovate outline and is only slightly
tapered toward the posterior end. This readily distinguishes it from
specimens of *Miopetaurista* and *Pliopetaurista,* in which the posterior
end of the tooth tends to be long and narrow. The crown is low, the
protoconid rises only 1.1 mm above the crown base; it thus contrasts with
most species of *Petaurista* and especially with *Eupetaurus* (McKenna
1962).

On the labial side of the molar the strong protoconid and hypoconid
are separated by a moderately well-developed mesoconid. The meso-
conid is more robust than in *Pliopetaurista* and does not produce a labial
spur, such as Sulimski (1964) noted in the specimens from Wéze, Poland.
The protoconid is joined to a small anteroconid by a short, anteriorly
curved crest, and thence weakly to the prominent metaconid. The weak
anteroconid does not extend toward the labial wall of the molar as in

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[1] Named for Professor S. David Webb in honor of his contributions to the vertebrate paleontol-
ogy of Florida.
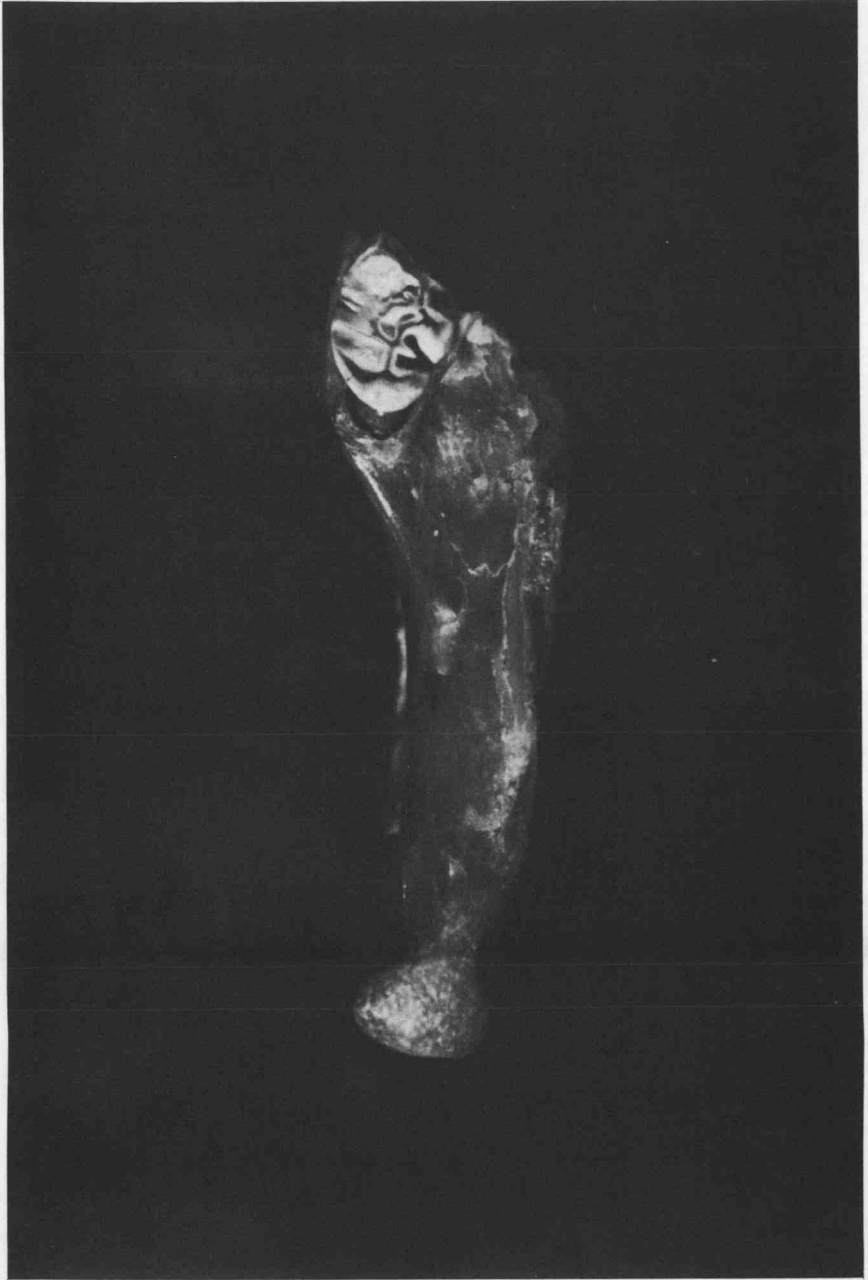
FIGURE 12. *Cryptopterus webbi* type, right mandible, anterior end upwards, UF 12343, Haile XV A; X 5.40.
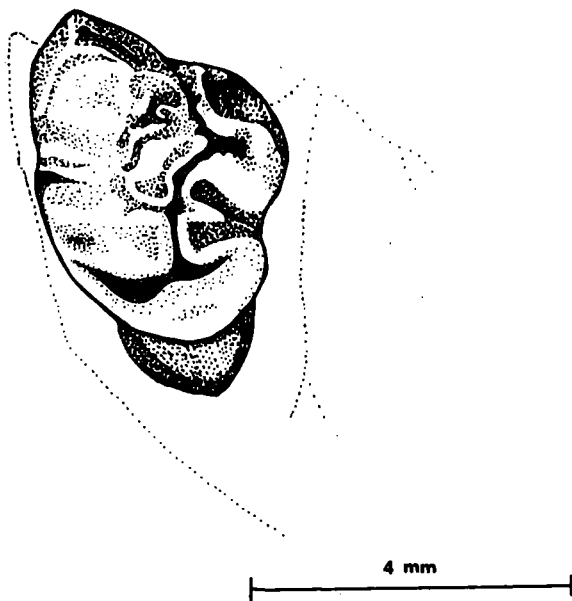
FIGURE 13. *Cryptopterus webbi*, right M_3, anterior end upwards, UF 12353, Haile XV A.

most sciuropterines. Instead, a large cingulum occupies the anterolabial corner of the molar, recalling the arrangement found in the third lower molar of *Cryptopterus tobieni* (Mein 1970: fig. 39).

The anterolingual part of the third molar is greatly expanded as in most sciuropterines. It supports a very large prominent metaconid from which a posterior crest connects broadly back to a low metastylid (or mesostylid according to Mein's 1970 terminology), and a labial crest reaches the anteroconid. From the robust metaconid, the enamel surface slopes gradually downward into a very shallow trigonid valley. In its center are several low sinuous ridges (lophulids) that trend in a postero-lingual direction. Such lophulid complexes are characteristic of many sciuropterines; the homologous but higher ridges in *Petaurista xanthotis* were appropriately termed "metaconid-metastylid chaos" by McKenna (1962). These lophulids presumably provide drainage canals for the juices produced when pulpy foods are crushed in the trigonid basin. Similar features for similar purposes are found in such unrelated mammals as *Ailuropoda* and *Pongo*.

A distinct entostylid occupies the midlingual part of the molar from Haile XV A. A weak ridge, the hypolophid, extends labially from the entostylid, but is soon lost in the broad continuity between the trigonid and talonid "valleys" in the center of the tooth. A minor depression,

separating the entoconid from the strong posterolophid, encircles the posterior margin of the tooth. A thickening of the enamel in the middle of the posterolophid evidently represents a vestigial hypoconulid. Although faint, this structure is notable inasmuch as Mein (1970:22) characterized all other *Cryptopterus* as having a smooth posterolophid without any hypoconulid. There is no sign of a posterolabial inflection in the molar from Haile XV A.

DISCUSSION.—Although the affinities of the Haile XV A flying squirrel might reasonably be sought among other North American sciuropterines, such comparisons prove unsatisfactory. The North American record consists of *Glaucomys* of Pleistocene and Recent age and a late Miocene sample of two small species from the Cuyama Valley of California described as *Sciuropterus* by James (1963), but assigned to *Cryptopterus* by Mein (1970). James (1963) suggested that the North American Miocene species might have been ancestral to *Glaucomys*, or at least that no closer ancestry is known. Mein (1970) was more skeptical of a direct relationship. In either event the Haile XV A specimen, far from bridging that gap, differs in a number of basic features from what would be expected of a Latest Pliocene *Glaucomys* ancestor. Whereas Recent *Glaucomys* is even smaller than the Cuyama Miocene fossils, the Haile XV A specimen is much larger. Neither an anteroconid nor an anterolingual cingulum (of any size) occurs in either the California Miocene specimens or in *Glaucomys*, yet both features are found in the Haile XV A specimen. The protolophid directly connects the protoconid to the metaconid in both the Miocene Cuyama specimens and in Recent *Glaucomys* specimens, whereas it is interrupted by an anteroconid in the Haile XV A specimen. The talonid valley is not crenulated in the Haile XV A specimen, and the trigonid lophulids are heavier than in other North American flying squirrels.

Turning to the Old World fauna, we find a much greater variety of both fossil and Recent genera with which to make comparisons. These include several taxa whose size equals that of the Haile XV A specimen, and some that exceed it. It seems evident that the phylogenetic development of the flying squirrels was centered in Eurasia, and it is fortunate that a relatively complete fossil record of the group is known from Europe. Mein (1970), who recently published the most complete phylogenetic review of the sciuropterine squirrels, recognized three broad groups of fossil and Recent genera based on lophule development and enamel crenulation. His arrangement is as follows:

GROUP I (Enamel smooth; lophules absent)
    Recent Genera: *Glaucomys, Eoglaucomys, Iomys.*
    Fossil Genera: *Cryptopterus, Petauria.*

GROUP II (Enamel smooth; lophules present)
            Recent Genera: *Pteromys, Trogopterus, Ptero-
            myscus, Belomys, Aeretes, Petaurista, Eupetaurus.*
            Fossil Genera: *Miopetaurista, Forsythia, Pliope-
            taurista.*

GROUP III (Enamel crenulated; lophules rare or absent)
            Recent Genera: *Petinomys, Hylopetes, Aeromys.*
            Fossil Genera: *Blackia, Pliopetes.*

Of these diverse genera, European fossil specimens of *Cryptopterus*
and *Petauria* bear the closest resemblance to the specimen from Haile
XV A. As in those genera, the enamel in the Haile specimen is not
finely crenulated. The pattern of cuspids and lophids agrees closely
with that in some species of *Cryptopterus*. Unfortunately, the question
of whether the lophules in the upper cheek teeth were elaborately de-
veloped cannot be directly answered by the Florida specimen, but if
the detailed resemblances of *Cryptopterus* lower molars are correct, loph-
ules would be absent from the upper molars just as they are from the
lowers.

Several features of the lower molar from Haile XV A rule out its
relationship to Group II genera. The nearly ovate shape of the last
molar is a reliable distinction from molars of the extinct taxa *Miope-
taurista* and *Pliopetaurista*. These taxa also bear a distinct posterolabial
flexid that is barely (if at all) recognizable in the Florida molar. As
Sulimski (1964) noted in his material from Poland, the mesoconid ex-
tends labially as a spur in *Pliopetaurista*, in contrast to the round meso-
style in the Florida specimen. Finally, the metastylid (mesostylid of
Mein 1970) is very prominent in *Miopetaurista* and *Pliopetaurista*,
whereas in the Florida specimen it is largely submerged by the broad
crest connecting it to the metaconid. Each of these features indicates a
closer relationship of the Haile XV A specimen with Group I taxa.

The flying squirrel tooth from Haile XV A most closely resembles the
third lower molars of *Cryptopterus*. It also resembles homologous teeth
of *Petauria helleri* from Early Pleistocene red earth fissure fillings in the
Solenhofen Limestone near Schernfeld, Bavaria (Dehm 1962), but that
genus completely lacks a mesoconid on its lower molars, and the hypo-
lophid is more strongly developed than in the Florida specimen. This
general resemblance of the Florida specimen to the Bavarian specimen
led to its preliminary assignment to "*Petauria* sp." in Webb (1974a). It is
now evident, however, that the Haile XV A specimen is perhaps more
accurately recognized as a new species of the genus *Cryptopterus*.

When one compares *Cryptopterus webbi* with other species of that genus, the closest resemblance is to those from the very Late Pliocene. In view of the Blancan age of the Florida species, this is what one might expect. The youngest European species of *Crytopterus* is *C. tobieni* from the lignites of Wolfersheim-Wetterau, West Germany (late Perpignan equivalent). The slightly older species, *C. thaleri*, resembles *C. tobieni* in size and many other features but is not presently represented by any lower molars. Special features shared by lower third molars of *C. tobieni* and *C. webbi* are the broad anterolabial cingulum, the weak, anteriorly-directed anteroconid, the short protolophid, the mestastylid little distinct from the metaconid ridge, the distinct entoconid, and the weakly developed hypolophid. *C. webbi* is slightly smaller than *C. tobieni* and perhaps *C. thaleri*, and it differs from all other known *Cryptopterus* specimens in the presence of a vestigial hypoconulid. Lower third molars of the Miocene species of *Cryptopterus* differ from those of *C. webbi* and *C. tobieni* in having a narrow anterolabial cingulum, a strong labially directed anteroconid, a complete protolophid, a more distinct metastylid, and the entoconid attached both to the posterolophid and to a strong hypolophid. An exception to this is the presence of a distinct entoconid and a weak hypolophid in Gaillard's (1899) original figured specimen from La Grive, which is now referred to *C. gaillardi* (Mein, 1970). Evidently this late Miocene variant embodied some of the progressive features that were developed more definitely during the Pliocene in *C. tobieni* and *C. webbi*. *Cryptopterus mathewsi* from Late Miocene deposits in the Cuyama Valley of California also differs in some of these same features from *C. webbi* and *C. tobieni*; however, the lower third molar is poorly known (James 1963). No lower dentition has been recovered in *C. uphami* material from the same area. The anteroconid is essentially absent, as is the anterior cingulum. I am not yet convinced, in fact, that the Cuyama species are referable to *Cryptopterus*.

The itinerary by which *Cryptopterus* reached Florida in the Blancan must remain in doubt, but the general pattern of distribution may be deduced. Since the nearest affinities of *C. webbi* are with *C. tobieni* (Late Pliocene of Europe), it seems probable that the genus reached North America from the Old World during that epoch. We may safely say that the date of arrival in North America was within late Hemphillian or Blancan time. Furthermore, the only likely dispersal route was via the Bering Land Bridge between Asia and North America. Flying squirrels do not truly "fly," and their present distribution patterns do not indicate great vagility. This New World occurrence of *Cryptopterus* indicates continuity of subtropical rain forest from Eurasia into eastern North America during the Late Pliocene.

TABLE 10.—MEASUREMENTS (IN MM) OF THE FEMORA OF FOSSIL AND RECENT *Castor canadensis*.

	C. canadensis UF 17489	C. canadensis Recent		
	Haile XV A	N	X̄	OR
Width, distal end	38.7	6	36.6	34.1–38.4
Anteroposterior depth, distal end	29.2	6	29.7	28.5–32.5
Width, external condyle	13.5	5	14.0	12.2–15.5
Width, internal condyle	12.5	5	12.1	11.6–12.5
Width of shaft at third trochanter	25.2	6	29.1	27.0–30.5
Anteroposterior diameter of shaft at third trochanter	13.9	6	11.5	10.2–13.5

FAMILY CASTORIDAE

Castor canadensis LINNAEUS 1758

MATERIAL.—UF 17489: left femur.

This element, which lacks the proximal end and represents a young individual, shows no morphological differences from the living species. A comparison of measurements (Table 10) with examples of young, Recent *Castor canadensis* shows no significant size differences. Other Blancan records of *Castor* in North America are from the San Joaquin locality in California (Kellogg 1911, Stirton 1935) and the Hagerman fauna of Idaho (Stirton 1935, Zakrzewski 1969).

FAMILY CRICETIDAE

Sigmodon medius GIDLEY 1922

MATERIAL.—UF 17489: left M^1; UF 12341: right M^1; UF 12337: left M^2; UF 12339-12340: right M^3; UF 12334, UF 12338: left M_1; UF 12336: left M_2; UF 12342: right M^1 and M_3 (both unworn).

This species characteristically possesses only two or three roots on the M_1. If accessory roots are present, they are centrally located and are very small, peg-like structures. The labial root is always better developed than the lingual. The two specimens from Haile XV A (UF 12338) exhibit these characteristic features.

Sigmodon medius is nearly identical morphologically with a closely allied species, *Sigmodon minor*. According to Martin (1974), the only difference between the two species, other than size, is that the reentrant folds are deeper and narrower in S. *minor* than in S. *medius*. This character is not obvious in the relevant Haile XV A specimens because they show significant wear. Discrimination between these two species must

TABLE 11.—DENTAL MEASUREMENTS (IN MM) OF *Sigmodon medius* AND *Sigmodon minor*.[1]

	S. *medius*			S. *minor*		
	N	X̄	OR	N	X̄	OR
Length M_1	2	2.25	2.18–2.32	45	1.89	1.72–2.19
Width M_1	2	1.24	1.23–1.25	48	1.31	1.17–1.48
Length M_2	1	1.49	———	49	1.40	1.22–1.62
Width M_2	1	1.53	———	46	1.36	1.20–1.50

[1] Re-calculated from Martin (1970).

depend on size alone. The larger measurements of the Haile XV A material (Table 11) indicate that it belongs to S. *medius*.

Sigmodon medius is one of the most common small rodents in the Blancan of North America; its occurrences include the Benson local fauna of Arizona (Gidley 1922), the Vallecito fauna of California (Downs and White 1968), the Hudspeth and Red Light local faunas of Texas (Strain 1966, Akerston 1970), and the Sand Draw fauna of Nebraska (Skinner and Hibbard 1972).

ORDER CARNIVORA
FAMILY CANIDAE GRAY 1821

MATERIAL.—UF 17492-17493: 2 tibiae.

Two poorly preserved tibiae indicate the probable presence of a small canid. They are about the size of a fox, but positive identification is not possible as only the much worn proximal ends are preserved.

FAMILY MUSTELIDAE
Satherium sp.

MATERIAL.—UF 17487: humerus; UF 17491: right metatarsal II; UF 17490: right metatarsal III; UF 17494: medial phalanx.

The humerus and podial elements closely resemble those of both *Pteronura*, the living giant, flat-tailed otter of South America, and *Satherium*, the extinct giant otter, from various Blancan sites in North America. Despite the numerous close resemblances between these two genera and the probable ancestral relationship of *Satherium* to *Pteronura*, I follow Gazin (1934) and Bjork (1970) in recognizing the extinct genus as distinct. These two giant genera are surely more closely related to one another than to *Lutra*.

The humerus from Haile XV A (Fig. 14) is more robust than are
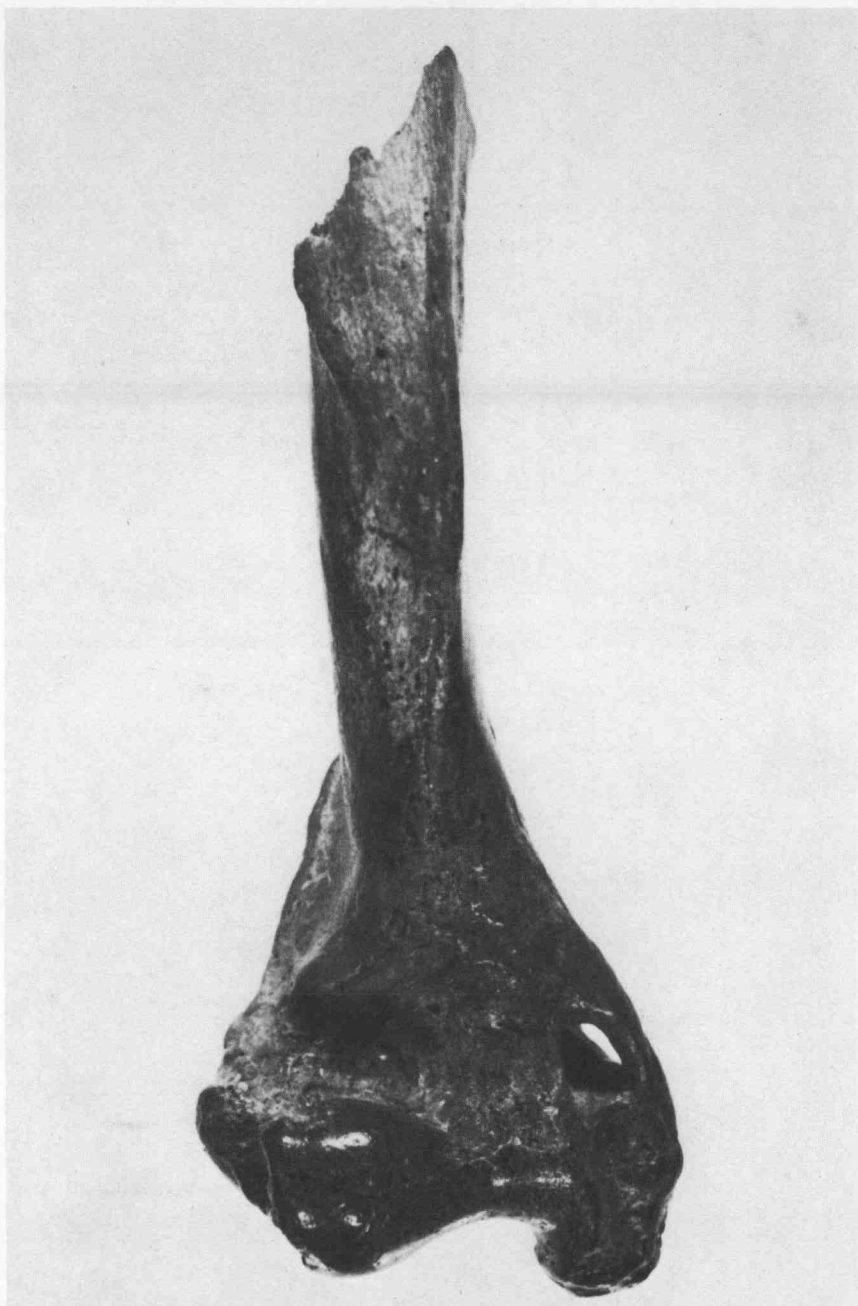
FIGURE 14.   *Satherium* sp., humerus, anterior view, UF 17487, Haile XV A; X 1.95.

TABLE 12.—MEASUREMENTS (IN MM) OF THE HUMERUS OF *Satherium* AND RECENT *Pteronura* AND *Lutra*.

	Hagerman, Id. USNM 23266	*Satherium* Haile XV A UF 17487	*Pteronura brasiliensis* Recent, South America			*Lutra canadensis* Recent, North America		
			N	$\bar{X}$	OR	N	$\bar{X}$	OR
Greatest width, distal end	33.4	33.0	3	36.3	33.5–40.1	7	25.1	24.1–27.2
Greatest width, distal condyle (measured from anterior side)	21.0	21.0	3	23.3	21.5–26.5	7	15.1	11.8–17.3
Length of entepicondylar foramen	5.5	5.8	3	5.9	5.4– 6.5	6	4.4	3.7– 4.7
Width of entepicondylar foramen	3.3	3.9	3	4.2	4.0– 4.4	6	2.0	1.5– 2.3
Greatest anteroposterior thickness of shaft	13.5	17.4	3	16.1	14.7–18.5	7	13.1	11.3–14.8
Transverse width at same location	9.9	10.3	3	10.2	9.5–11.4	7	7.9	7.5– 8.8
Greatest anteroposterior thickness of distal condyle	15.4	16.1	3	14.6	12.7–16.2	7	11.2	10.2–12.4

TABLE 13.—MEASUREMENTS (IN MM) OF THE ASTRAGALI OF *Smilodon gracilis* FROM HAILE XV A AND PORT KENNEDY.[1]

	Haile XV A UF 17496	Port Kennedy
Length	41.6	48
Width	45.2	38
Width of trochlea	28.7	27
Vertical diameter of head	18.7	17
Transverse diameter of head	26.6	25
External elevation of trochlea	21.1	22

[1] Measurements after Cope (1899).

humeri of *Satherium* from the Hagerman local fauna of Idaho (Bjork 1970). In this respect the Haile specimen agrees more closely with specimens of living South American *Pteronura* (Table 12). In the dimensions of the metatarsals and in most other respects, however, the three samples are remarkably homogeneous. The distal width of the Haile humerus likely would be greater were it not for the pathological condition of the medial side; the bone has turned distad and narrowed and is associated with much osteoporotic tissue. This anomaly does not seem to have affected either the articular surface nor the entepicondylar foramen, which are located laterally and proximally, respectively, to the affected area. The most impressive features that distinguish the Haile XV A specimen from the Hagerman skeleton (USNM 23266) are the much greater medial dimensions of the shaft and the deeper and wider ectepicondylar ridge. In all respects, however, there are strong similarities among the Haile sample and the genera *Satherium* and *Pteronura*.

FAMILY FELIDAE

Smilodon gracilis COPE 1880

MATERIAL.—UF 17496: right tibia (distal end) and right astragalus; UF 17498: right metacarpal II.

The Haile material presumably is all from a single medium-sized animal. All three bony elements were found together, the tibia and astragalus articulate well, and the material is similarly preserved. The material is referred to the genus *Smilodon* on the basis of two characters (see Merriam and Stock 1932): (1) the presence of the astragalar foramen; and (2) the medial facet for the calcaneum and the facet for the navicular are merged.

The Haile XV A sabercat was very small and was similar in size to *Smilodon gracilis*. A comparison of the measurements of the astragalus from Haile XV A with those of the astragalus of *S. gracilis* from the Port Kennedy Bone Bed (Cope 1899) shows a close correlation in size (Table 13). Inasmuch as *S. gracilis* is the only small species of *Smilodon*

known from North America and is of relatively early Pleistocene age, the Haile XV A specimen is referred to that species.

Two species of small sabercats are known from South America. *Smilodon cruciens* is known only from a single mandible (Ameghino 1904). *Smilodontidion riggsi* (Kraglievich 1948), which is slightly larger than the Haile XV A form, is present in the Chapadmalal fauna and is known only from postcranial material.[1] The astragalus of this specimen is preserved but in poor condition, and the critical characters of the facets cannot be verified from the figures. Although other species occur both in the Chapadmalal fauna and the Haile XV A fauna, it does not follow that the two cats are necessarily related. Nonetheless, the overall faunal resemblance, together with the similarity in morphology of the South American samples, suggest that possible synonymy of the Chapadmalalan form with *Smilodon gracilis* ought to be considered.

ORDER PROBOSCIDEA
FAMILY GOMPHOTHERIIDAE CABRERA 1929

MATERIAL.—UF 17464: a small portion of a molar and two small pieces of ivory.

The complicated nature of the cheek tooth clearly indicates that this specimen is a gomphotheriid. Further identification is not possible because of the inadequate material available.

ORDER PERISSODACTYLA
FAMILY EQUIDAE
Nannippus phlegon (HAY 1899)

MATERIAL.—UF 17484-17485: both upper cheek teeth; UF 17547: metapodial; UF 17548: proximal phalanx; UF 17549: four ungual phalanges.

A nearly unworn upper cheek tooth 51 mm high indicates that this form was strongly hypsodont. The other well-worn upper tooth (Fig. 15) and the postcranial material agree in all respects with the typical Blancan species, *N. phlegon*. Measurements are provided in Table 14.

Equus (Dolichohippus) simplicidens COPE 1892

MATERIAL.—UF 10909: partial skull; UF 17556: partial maxilla with deciduous molariform tooth; UF 10894: 15 cervical vertebrae; UF 10877: 37 thoracic vertebrae; UF 10895: 13 lumbar vertebrae; UF 10896: 2 sacral vertebrae; UF 10898: 3 humeri (2 left, 1 right); UF 10919: 1 right radius; UF 10910: 2 left pelves; UF 10911: 4 femora (2 left, 2 right); UF 10915: 2 right metatarsals; UF 10921: 9 splints; UF 10916: 4 cuboids (2 left, 2 right); UF 10917: 3 calcanea; UF 10920:

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[1] Churcher's (1967) cautionary note suggesting that the specimen may have leaked down from younger deposits is noted.

2 astragali; UF 10917: 4 proximal phalanges; UF 10913: 4 distal sesamoids; UF 10914: 7 ungual proximals.

The Haile XV A skull (UF 10909) is in poor condition, and not enough of the fragments are present to allow complete reconstruction.

FIGURE 15. *Nannippus phlegon,* left upper molar, occlusal view, UF 17484, Haile XV A; X 6.15.

TABLE 14.—MEASUREMENTS (IN MM.) OF *Nannippus phlegon* CRANIAL AND POST-
CRANIAL MATERIAL FROM HAILE XV A.

UPPER CHEEK TOOTH	UF 17484		UF 17485
Anteroposterior distance	17.5		19.6
Transverse distance	20.4		
Crown height			51.0
Metapodial			
Transverse width, distal end	25.7		
Anteroposterior width, distal end	24.0		
Proximal phalanx			
Width, proximal end	24.4		
Width, distal end	20.6		
UNGUAL PHALANX	UF 17549a	UF 17549b	UF 17549c
Total length	43.4	43.6	43.1
Width, distal articular surface	22.7	23.9	22.8

Both left and right molariform tooth rows, however, are complete (Fig. 16) and a portion of the premaxilla has been rebuilt. A small portion of the occipital region is preserved, but the rest of the skull consists of isolated fragments.

This skull is referred to the subgenus *Equus* (*Dolichohippus*) on the basis of the well developed parastyles and metastyles, the dilation of the fossettes, and the more rounded nature of the protocones. Assignment of extinct North American species, formerly referred to *Plesippus*, to the same subgenus as the living Grevy's Zebra follows Skinner and Hibbard (1972).

In dental morphology, UF 10909 resembles both *E.* (*D.*) *shoshonensis* and *E.* (*D.*) *simplicidens.* Gazin (1936) stated that the ranges of measurements of these two species may overlap, although *E.* (*D.*) *simplicidens* tends to be smaller. Cheek teeth from Haile XV A (Table 15) are smaller than any measured by Gazin (1936). They are close to the size of a specimen of *E.* (*D.*) *simplicidens* described by Hibbard (1941) from the Blancan Rexroad fauna of Kansas, and they fall at the lower end of the range given by Howe (1970) for a large sample from the Broadwater local fauna of Nebraska. The postcranial material is also small (Table 16), and falls within the range of measurements given by Gazin (1936) for a specimen of *simplicidens.*

Equus (*Hemionus*) cf. *calobatus* TROXELL

MATERIAL.—UF 17750: upper cheek tooth; UF 17483: lower molar; UF 17482: M_3; UF 17551: left humerus; UF 17552: astragalus; UF 17553: proximal phalanx; UF 17554: medial phalanx; UF 17555: ungual phalanx.
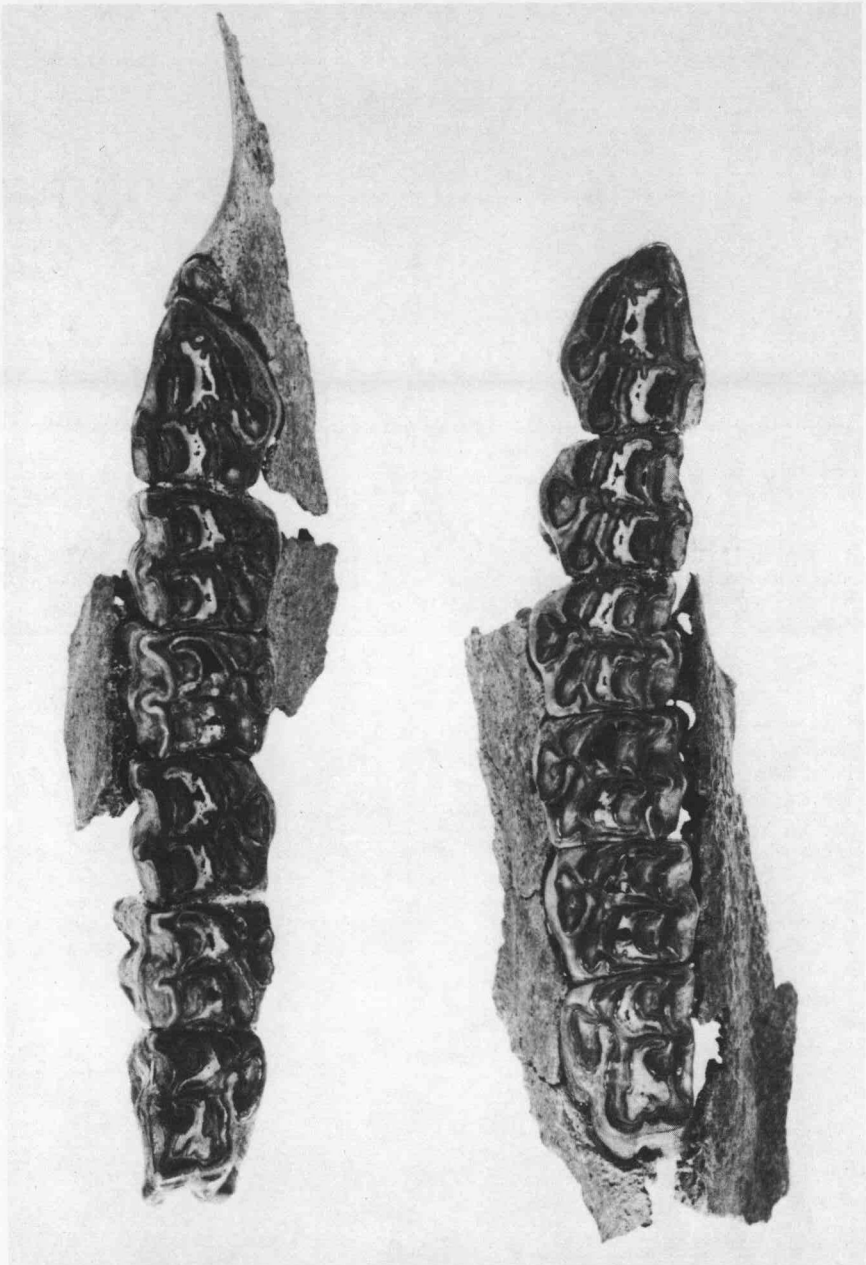
FIGURE 16. *Equus* (*Dolichohippus*) *simplicidens*, upper dentition, occlusal view, anterior end upwards, UF 10909, Haile XV A; X 0.80.

TABLE 15.—MEASUREMENTS (IN MM) OF THE UPPER DENTITION OF *Equus* (*Dolichohippus*) *simplicidens* FROM HAILE XV A.[1]

Tooth	Left		Right	
	Length	Width	Length	Width
Tooth row[2]	158		155	
P[1]			12.2	6.4
P[2]	32.9	24.7	32.8	24.6
P[3]	24.1	26.2	24.0	25.2
P[4]	23.3	24.8	21.9	24.3
M[1]	22.3	23.8	23.8	25.5
M[2]	22.0	22.6	22.4	23.9
M[3]	28.8	23.0	33.2	35.3

[1] Measurements taken at grinding surface; width measurements do not include cement.
[2] Not including P[1].

TABLE 16.—MEASUREMENTS (IN MM) OF *Equus* (*Dolichohippus*) *simplicidens* POSTCRANIAL MATERIAL FROM HAILE XV A.

	N	$\overline{X}$	OR
HUMERUS			
Transverse width, distal condyle	3	70.1	69.7– 70.5
Anteroposterior width, distal end	3	80.7	77.0– 84.0
RADIUS			
Total length	1	316.0	
Anteroposterior width, proximal end	1	77.6	
Transverse width, proximal end	1	36.3	
Anteroposterior width, distal condyle	1	37.4	
Transverse width, distal condyle	1	57.9	
FEMUR			
Total length	1	368.5	
Transverse width, proximal end	1	114.0	
Anteroposterior width, proximal end	1	88.5	
Transverse width, distal condyle	4	87.2	84.6– 89.7
Anteroposterior width, distal end	4	116.8	114.0–118.0
METATARSAL			
Anteroposterior width, proximal end	2	41.2	39.6– 42.8
Transverse width, proximal end	2	48.5	48.2– 48.8
CALCANEUM			
Total length	3	107.7	103.0–110.0
ASTRAGALUS			
Total length	2	58.0	57.0– 58.9
Lateral width	2	58.8	57.7– 59.8
PROXIMAL PHALANX			
Total length	3	78.5	76.5– 81.2
Width, proximal articular surface	2	43.7	42.8– 44.5
Width, distal end	4	36.4	33.7– 38.5
MEDIAL PHALANX			
Total length	6	45.5	44.1– 47.4
Width, proximal articular surface	6	40.7	39.1– 43.2
Width, distal end	6	40.9	38.8– 42.8
UNGUAL PHALANX			
Total length	6	54.4	50.6– 58.8
Width, proximal articular surface	6	38.5	34.1– 43.3

The three teeth listed above are morphologically different from those of *Equus* (*Dolichohippus*). The fossettes of the upper tooth are much more complicated, and the lower teeth are quite distinct from those of *E.* (*Dolichohippus*) figured by Gazin (1936), Hibbard (1941), McGrew (1944), and Skinner and Hibbard (1972). In all the lower molars figured by the above authors, the median valley divides the isthmus, as pointed out by Skinner and Hibbard (1972); in the two teeth discussed here, the median valley approaches the isthmus but does not divide it. In this respect, the Haile XV A specimens resemble *Equus fraternus*, a later Pleistocene ass.

Several postcranial elements in the Haile XV A fauna are probably also referable to *E.* (*Hemionus*) *calobatus*. They are much smaller than specimens attributed to *E.* (*D.*) *simplicidens*. Troxell's type and referred material from the Arkalon (Hibbard 1953) and the Cragin Quarry local faunas (Schultz 1969) form the bases for comparison. Hibbard (1956) also reported the medial phalanx of an ass in the Meade Gravel Member in Meade County, Kansas, with which the Haile XV A medial phalanx agrees very closely (Table 17).

<div align="center">

FAMILY TAPIRIDAE

Tapirus sp.

</div>

MATERIAL.—UF 17468: partial crown of a cheek tooth.

Since only one genus of Tapir is known from post-Hemphillian deposits of North America, it seems reasonable to ascribe this specimen to *Tapirus*. The material serves only to record the presence of this genus in the fauna. This genus is also recorded in Santa Fe I, another Blancan locality in Florida (Webb 1974a).

<div align="center">

ORDER ARTIODACTYLA

FAMILY TAYASSUIDAE

Mylohyus floridanus KINSEY 1974

</div>

HOLOTYPE MATERIAL.—UF 18002: left and right mandibular rami and upper left canine.

This species was recently described by Kinsey (1974), based upon the material from Haile XV A. It represents the oldest (and only Blancan) record for this genus. The material is refigured (Figs. 17, 18) and the diagnosis is included here in order to complete the study of the fauna. Measurements of the holotype are presented in Table 18.

TABLE 17.—MEASUREMENTS (IN MM) OF *Equus* (*Hemionus*) cf. *calobatus* CRANIAL AND POSTCRANIAL MATERIAL FROM HAILE XV A.

	UF 17482a	UF 17482b
UPPER CHEEK TOOTH		
Anteroposterior distance		25.4
Transverse distance		23.4
M$_3$		
Anteroposterior distance		28.7
Transverse distance	11.2	10.7
HUMERUS		
Total length		255.0
Transverse width, anterior end		88.0[1]
Lateral width, distal condyles		68.1
Anteroposterior width, distal condyles		46.9
ASTRAGALUS		
Total length		50.4
Greatest width		50.0
PROXIMAL PHALANX		
Total length		60.6
Width, proximal end		34.8
Width, distal end		30.5
MEDIAL PHALANX		
Total length		40.0
Width, proximal articular surface		38.1
Width, distal end		34.8
UNGUAL PHALANX		
Total length		45.7
Width, proximal articular surface		33.1

[1] Estimated.

DIAGNOSIS.—Close to *Mylohyus nasutus* in size and elongation of the snout. Larger and more robust than *Mylohyus fossilis* and lacking the extreme constriction of the symphysis that is diagnostic of that species (Lundelius 1960). Pre- and post-canine diastema longer than in other species of *Mylohyus*. Symphysis much more slender than in *Prosthenops*. Coronoid process triangular with straight (not convex) anterior margin.

Total length of the P$_2$-M$_3$ series less than in other *Mylohyus*, both absolutely and relative to the overall length of the jaw. M$_1$ and M$_2$ relatively shorter than in other *Mylohyus*, except *M. exoticus* (USNM 8876). Anteroposterior diameter of C greater than in all other *Mylohyus*, both absolutely and relative to the cheek teeth series. Width of C greater relative to width of P$_2$ and M$_1$ than in other *Mylohyus* (Kinsey 1974).

DISCUSSION.—Interestingly, *Mylohyus* is exceedingly rare in most Pleistocene faunas of Florida. For example, a large Late Blancan collection from Santa Fe I contains only one specimen of this genus, whereas the
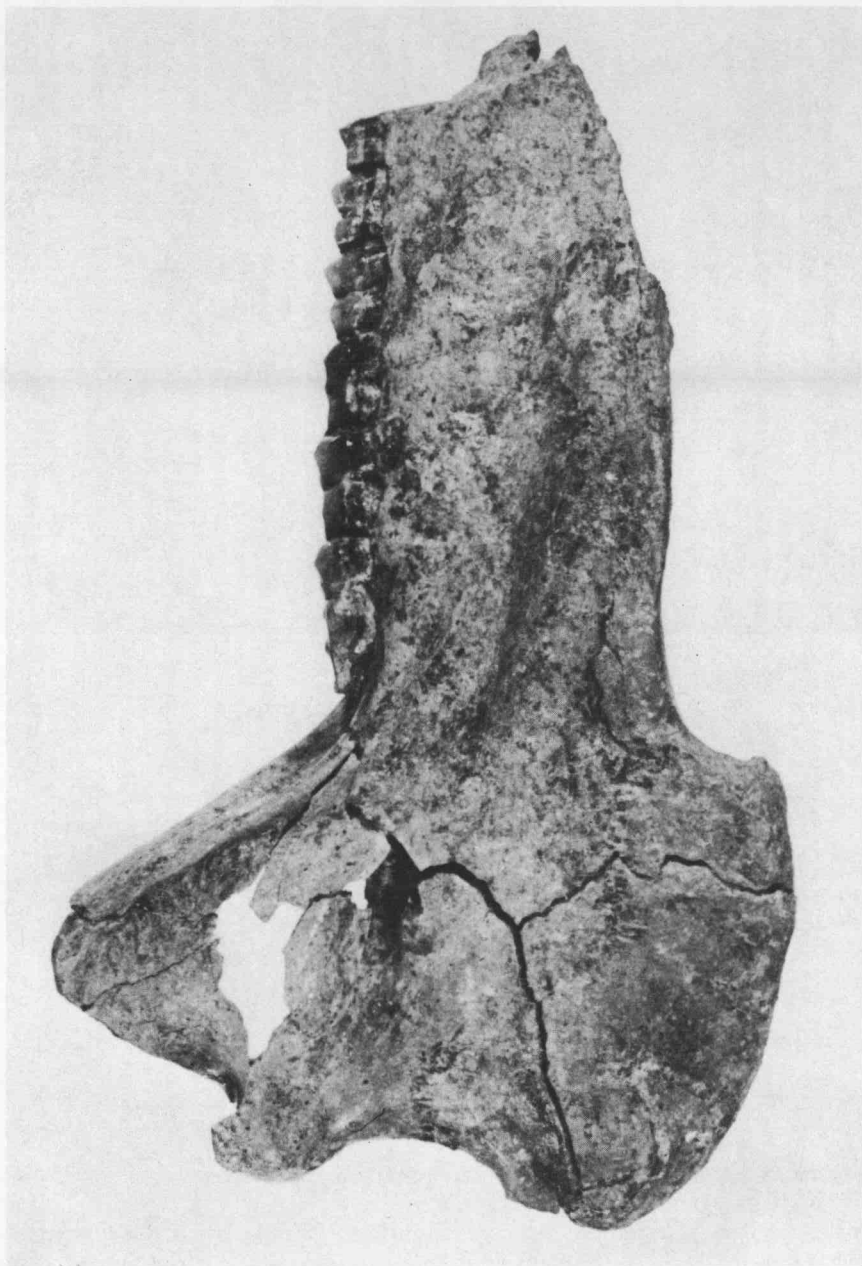
FIGURE 17. *Mylohyus floridanus* type, right mandibular ramus, lateral view, UF 18002, Haile XV A; X 0.95.

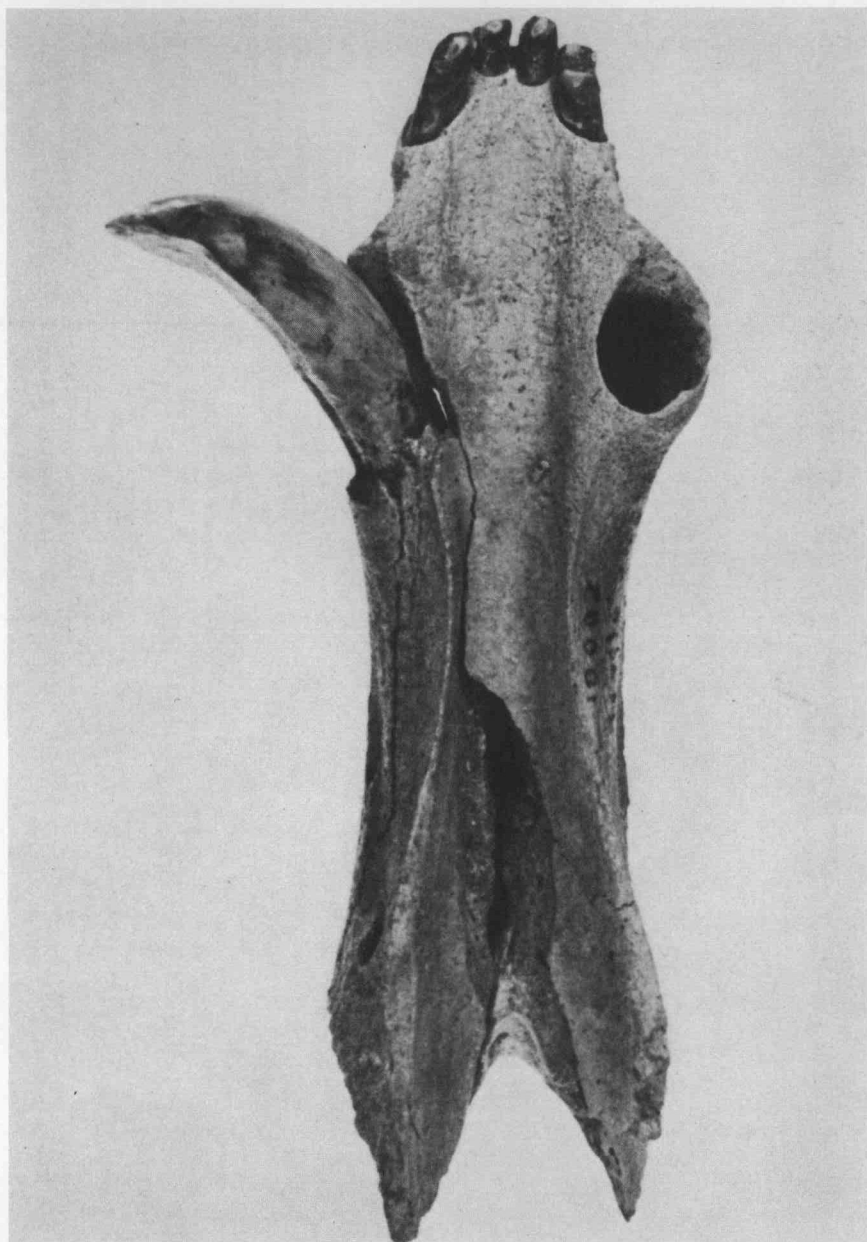FIGURE 18. *Mylohyus floridanus* type, mandibular symphysis, dorsal view, UF 18002, Haile XV A; X 1.0.

other peccary, *Platygonus*, is very abundant. Similarly, in the Coleman IIA fauna of Irvingtonian age, *Platygonus* outnumbers *Mylohyus* eleven to one. The presence of *Mylohyus* at Haile XV A suggests an ecological distinction, as will be discussed further in the paleoecology section (below).

TABLE 18.—MEASUREMENTS (IN MM) OF THE TYPE DENTITION OF *Mylohyus flori-danus*.[1]

	Left	Right
Length, upper canine	15.1	
Width, upper canine	11.1	
Length, lower canine	14.0	
Width, lower canine	10.6	
Length, P_2	8.5	
Anterior width, P_2	4.9	
Posterior Width, P_2	5.1	
Length, P_3	12.0	
Anterior width, P_3	9.0	
Posterior width, P_3	9.1	
Length, P_4	13.0	
Anterior width, P_4	10.6	
Posterior width, P_4	12.6	
Length, M_1	13.2	13.5
Anterior width, M_1	12.6	12.8
Posterior width, M_1	12.8	12.7
Length, M_2	15.2	15.5
Anterior width, M_2	14.0	14.1
Posterior width, M_2	13.9	14.1
Length, M_3	21.1	21.0
Anterior width, M_3	13.1	13.1
Posterior width, M_3	11.8	11.9
Length, premolars	33.1	
Length, molars	49.9	50.3
Length, molar–premolar series	83.0	
Post-canine diastema	80.0	
Pre-canine diastema	14.0	13.0
Depth of jaw at M_1	41.2	41.0
Thickness of jaw at M_1	21.2	21.1
Width, jaw at canines	41.2	
Width between canine alveoli	17.6	
Least width, symphysis	26.4	
Length, articular condyles to anterior end of symphysis	273.0	

[1] Measurements after Kinsey (1974).

FAMILY CAMELIDAE

Hemiauchenia cf. *macrocephala* (COPE 1893)

MATERIAL.—UF 10900: partial skull; UF 10894: 2 cervical vertebrae; UF 10899: phalanges (3 medial, 1 ungual).

The Haile XV A skull (UF 10900) (from a juvenile individual) consists of the palate with upper dentition (Fig. 19) and part of the cranium. The cranial fragment includes parts of the parietal, left squamosal, left exoccipital, and supraoccipital. This portion of the skull, particularly the external auditory meatus and the subsquamosal foramina, agrees very closely with the McKittrick material of this species figured by Stock
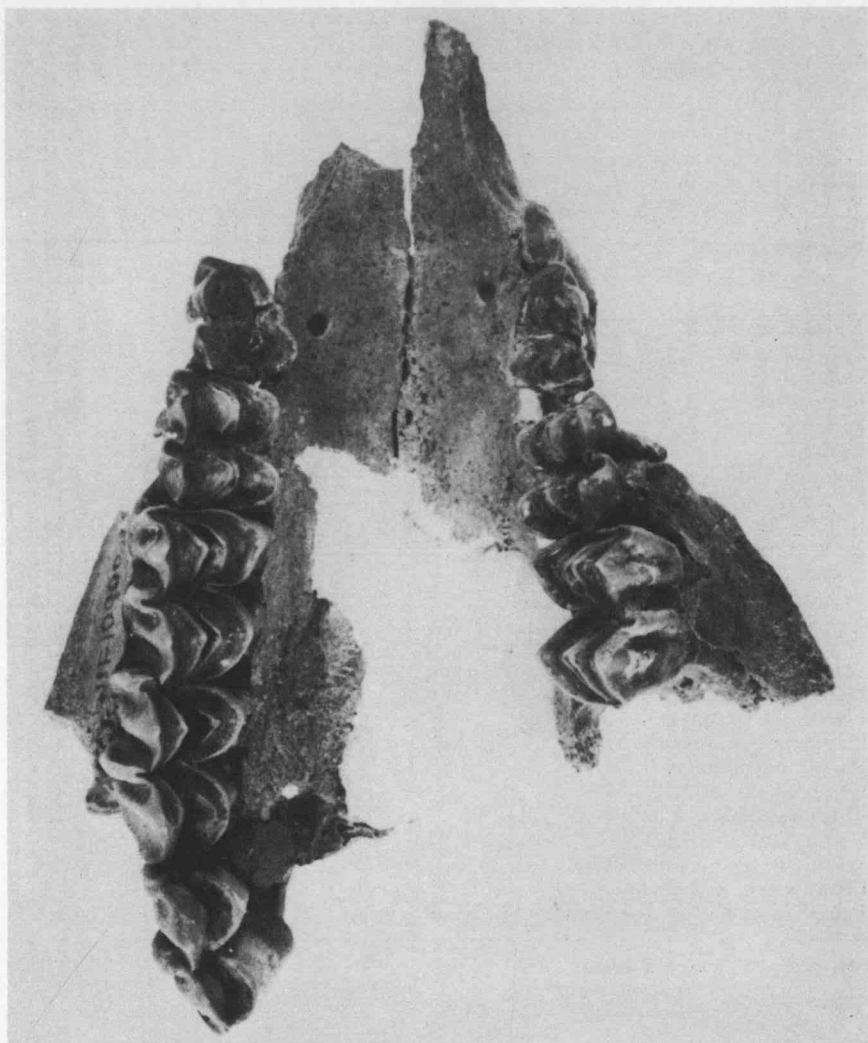
FIGURE 19. *Hemiauchenia* cf. *macrocephala*, upper dentition, anterior end upwards, UF 10900, Haile XV A; X 0.93.

(1928). The left DP^2 is present, as are the left and right DP^3 and DP^4; left and right P^3 and P^4 are present but unerupted. The complete right molar series is present, while the left is represented only by the M^1.

The Haile XV A specimen is a small llama referable to the genus formerly called *Tanupolama*, which is now synonymized with *Hemiauchenia* (Webb 1974b). *H. macrocephala* is the smallest of the North American species of *Hemiauchenia* and has a relatively wider P$_4$ than *H. blancoensis*. The Haile XV A specimen lacks the critical P$_4$, but the

TABLE 19.—MEASUREMENTS (IN MM) OF THE UPPER DENTITION OF *Hemiauchenia* cf *macrocephala* FROM HAILE XV A.

	Left	Right
Length, DP^2	10.8	
Width, DP^2	5.8	
Length, DP^3	19.7	19.2
Anterior width, DP^3	11.5[1]	12.4
Posterior width, DP^3		17.3
Length, DP^4	19.6	18.8
Anterior width, DP^4	17.7	17.8
Posterior width, DP^4	19.2	19.1
Length, P^3		16.5[2]
Width, P^3		9.9
Length, P^4		18.8[2]
Width, P^4		15.2
Length, M^1	26.2	25.7
Anterior width, M^1	20.2	21.2
Posterior width, M^1	19.8	20.4
Length, M^2		22.7
Anterior width, M^2		21.2
Posterior width, M^2		19.7
Length, M^3		26.6
Anterior width, M^3		14.2
Posterior width, M^3		19.1
Length of deciduous premolar series	50.1	
Length of molar series		75.0
Length of tooth row functional at time of demise	125[1]	
Length of permanent tooth row	110[1]	
Palatal width at DP^3	34.5	
Palatal width at DP^4	37.5	
Palatal width at M^1	47.5	

[1] Estimated.
[2] Unerupted.

specimen is quite small (Table 19) and tentative species allocation is based on size.

The occurrence of *H. macrocephala* in the Haile XV A fauna marks its earliest record anywhere. A long continuous history for this species in Florida is indicated by its presence in the early Irvingtonian Inglis IA fauna (Webb 1974b).

Hemiauchenia was widespread in the Blancan and is known in most North American faunas of this age, as well as in the Chapadmalalan of Argentina (Kraglievich 1946).

FAMILY CERVIDAE

Odocoileus virginianus ZIMMERMAN

MATERIAL.—UF 10885: 6 partial upper dentitions; UF 17481: right mandible with P$_2$, DP$_4$, M$_2$, M$_3$; UF 17478: left P$_4$; UF 17477: right M$_3$; UF 10883: 19

TABLE 20.—MEASUREMENTS (IN MM) OF POSTCRANIAL ELEMENTS OF *Odocoileus virginianus* FROM SEVERAL FLORIDA PLEISTOCENE LOCALITIES.

	Haile XV A			Santa Fe I			Santa Fe 4A		
	N	X̄	OR	N	X̄	OR	N	X̄	OR
HUMERUS									
Lateral width, distal condyles	3	31.0	30.6–31.4	2	28.4	26.2–30.6	1	28.4	
METACARPAL									
Lateral width, proximal end	3	23.5	22.7–24.8	2	27.4	26.6–28.2	1	22.2	
Anteroposterior width, proximal end	3	16.7	16.4–17.1	2	20.3	20.2–20.5	1	18.1	
METATARSAL									
Lateral width, proximal end	1	23.2		2	22.4	21.5–23.3	1	20.8	
Anteroposterior width, proximal end	1	23.7		2	24.8	22.9–26.6	1	23.2	
FIRST PHALANX									
Length	7	41.0	37.7–43.2	10	43.5	39.4–48.9			
Width, proximal end	7	13.4	12.2–13.9	10	13.3	11.6–15.2			

	Inglis IA			Coleman IIA			Reddick I		
	N	X̄	OR	N	X̄	OR	N	X̄	OR
HUMERUS									
Lateral width, distal condyles	4	32.9	31.3–34.4	7	30.4	28.2–33.2	3	29.6	28.6–31.2
METACARPAL									
Lateral width, proximal end	1	29.6		1	24.3		2	27.0	27.6–26.4
Anteroposterior width, proximal end	1	20.7		1	23.8		2	19.5	19.1–20.0
METATARSAL									
Lateral width, proximal end	3	25.2	24.6–25.5	7	23.6	22.5–24.8	1	23.1	
Anteroposterior width, proximal end	3	26.5	26.0–27.4	7	25.2	23.6–35.8	1	21.9	
FIRST PHALANX									
Length	1	46.6		7	43.4	40.3–44.4	4	42.5	40.6–44.4
Width, proximal end	1	15.4		7	13.0	12.2–13.8	4	14.7	14.3–15.5

X

TABLE 20. CONTINUED

	Devil's Den			Itchetucknee River		
	N	$\overline{X}$	OR	N	$\overline{X}$	OR
HUMERUS						
Lateral width, distal condyles	8	35.0	33.5–36.7	7	31.4	28.6–34.0
METACARPAL						
Lateral width, proximal end	12	28.1	27.0–30.2	11	27.2	23.7–29.6
Anteroposterior width, proximal end	12	20.3	18.5–21.3	11	18.4	17.1–21.5
METATARSAL						
Lateral width, proximal end	11	25.5	24.3–26.9	14	25.6	21.0–26.7
Anteroposterior width, proximal end	11	26.9	25.7–27.8	14	25.7	22.5–29.6
FIRST PHALANX						
Length				14	41.5	26.1–45.8
Width, proximal end				14	12.7	11.5–13.8

cervical vertebrae; UF 10891: 3 left humeri; UF 10893: right humerus; UF 17479: 3 metacarpals (2 left, 1 right); UF 10887: metatarsal; UF 17480: left astragalus; UF 10886: 3 podials; UF 10888: 15 phalanges.

The genus *Odocoileus* is recognized in many of the Blancan faunas of North America. In most cases, however, the material has been scarce and species allocation has not been possible.

The definitions of closely related species (and genera) of deer are very similar, and the taxonomic problem is compounded by the large amount of individual variation in these forms. The nature of the antlers and the fourth lower premolars are considered important in cervid taxonomy at the generic and subgeneric levels; unfortunately, these features are also extremely variable. In Simpson's (1928) discussion of *Blastocerus extraneus,* he pointed out that specimens of *Odocoileus* studied approached *Blastocerus* in character, and some Recent *Blastocerus* material diverged from his specimen toward *Odocoileus.* The subgenuus *Procoileus* (Frick 1937) is based primarily on the characters of the P_4.

Examination of a large sample of Blancan *Odocoileus* teeth from the Santa Fe I fauna showed individual variation that approached the characters of *Blastocerus, Procoileus,* and even *Craniocerus.* Similar, though less pronounced, examples of individual variation may be observed in samples of *Odocoileus* teeth from several later Pleistocene and Recent sites in Florida. It appears that tooth morphology by itself is too variable to permit taxonomic assignments at the species level.

Size also has been a criterion for species determination of fossil deer. Although the Haile XV A deer are relatively small, this is not considered taxonomically significant, inasmuch as a size comparison of postcranial elements from later stages of the Pleistocene (Table 20) shows wide size variation that encompasses the Haile XV A samples. Harlow and Jones (1965) also showed that in Florida the size of Recent deer fluctuates significantly from habitat to habitat.

An element by element comparison of the Haile XV A deer material with specimens of *O. virginianus* from other Florida Pleistocene sites, and with Recent specimens, shows no consistent differences. Consequently, it is considered safest to refer the Haile XV A cervid to *Odocoileus virginianus.*

Age and Correlation

North American vertebrate paleontologists, including Schultz (1938), Wilson (1938), and McGrew (1944), have long recognized the Blancan age on the basis of the presence and absence of certain mammalian genera. McGrew (1944) summarized the criteria as follows:

1) the absence of typically Pliocene genera;
2) the presence of characteristically Middle and Late Pleistocene genera;
3) the presence of certain genera that survived from the Hemphillian but which did not live past the Blancan;
4) the presence of certain genera that were limited to the Blancan; and
5) the absence of certain genera that did not make their appearance until after the close of the Blancan.

Each of the above criteria may be examined with regard to the Haile XV A fauna:

1) There are no typically Hemphillian genera represented in Haile XV A. *Kraglievichia* may be of Pliocene age in South America, but it is Blancan or later in North America. It should be pointed out here that such negative evidence is never conclusive and is particularly dangerous with regard to the Haile XV A fauna. The small number of taxa found probably indicates that the specimens collected represent only a small part of the overall fauna.
2) Several genera that range into the Middle and Late Pleistocene appear in this fauna; such taxa include *Odocoileus, Mylohyus, Smilodon,* and *Sigmodon.*
3) Of the genera that survived the Hemphillian but not the Blancan only *Nannippus* is definitely present. The presence in the fauna of a gomphotheriid may also fit this category, despite the fact that the specimen cannot be definitely assigned to a genus.
4) Only one subgenus, *Dolichohippus* (genus *Equus*), in Haile XV A is restricted to the Blancan in North America. The species *Sigmodon medius, Nannippus phlegon,* and *Equus (Dolichohippus) simplicidens* are wholly restricted to the Blancan and are widespread through most of North America.
5) The genera *Dasypus* and *Mylohyus,* which previously were thought to have appeared after the close of the Blancan, are present in Haile XV A. In view of the peculiar ecological and geographic features of the Haile XV A fauna, these age extensions are not unexpected and do not affect the hypothesis of an older age suggested by the weight of other evidence. In each case the species is more primitive than those occurring in younger faunas.

The weight of the mammalian faunal evidence (see Table 21), particularly the presence of *Nannippus, Equus (Dolichohippus),* and *Sigmodon medius,* points conclusively to a Blancan age. A more refined correlation of the Haile XV A fauna with other North American Blancan faunas (*i.e.* outside of Florida) is not feasible at present because of the geographic distances and ecological differences. Most Blancan faunas are located in western North America, but none, other than those in Florida, are known from the Gulf Coastal Plain. Consequently, the lack of a more detailed faunal comparison need not imply a great difference in time. The absence of *Kraglievichia* and *Dasypus* from Blancan sites elsewhere in North America more likely results from geographic rather than temporal differences. Conversely, a closer similarity to other Blancan faunas in Florida (*e.g.* Santa Fe I) does not indicate a close temporal correlation. Although definite similarities exist between the Haile XV A and Santa Fe I faunas, enough differences are present to indicate a differ-

TABLE 21.—FAUNAL COMPARISONS OF HAILE XV A AND OTHER BLANCAN LOCALITIES.

Haile XV A	Santa Fe I, Florida	Blanco + Cita Canyon, Texas	Red Light, Texas	Hudspeth, Texas	Rexroad, Kansas	Benson, Arizona	Curtis Ranch, Arizona	Sand Draw, Nebraska	Broadwater, Nebraska	Hagerman, Idaho	Overton, Nevada	Reno, Nevada	Wichman, Nevada	San Joaquin, Southern California	Coso Mountains, Southern California	San Timoteo, Southern California	Bautista Creek, Southern California	Vallecito-Fish Creek, Southern California	Tehama, Northern California	Lower Lake, Northern California	Chapadmalal, Argentina
Cryptotis					X																
Scalopus			X																		
Glossotherium	X	X	X				X														X
Dasypus	X																				
Kraglievichia	X																				X
Sylvilagus						?	X		X									X			
Cryptopterus																					
Castor											X			X							
Sigmodon			X	X	X	X	X											X			
Smilodon	X																				X
Satherium				X				X	X												
Tapirus	X																				
Nannippus	X	X	X	X	X	X			X												
Equus (Dolichohippus)	X	X	X	X	X	X	?	X	X	X	X	X	X	X	X	X	X	X	X	X	?
Mylohus	X																				
Odocoileus	X	X	?	X	X		X						X			X			X	X	
Hemiauchenia	X	X	X	X	X		X	X	X	X					X			X		X	X

ence in time and probably ecology as well. The Santa Fe I camel belongs to the typically Blancan species *Hemiauchenia blancoensis,* whereas the Haile XV A form most closely resembles *H. macrocephala.* This probably indicates a younger age for Haile XV A, as *H. macrocephala* is characteristic of the Irvingtonian and Rancholabrean ages elsewhere.

Certain taxa found in the Santa Fe I fauna that might be expected at Haile XV A do not occur there. One of the most notable absences is the typically Blancan hyaenoid dog, *Borophagus,* although in all likelihood this represents a sampling error. The absence of *Castoroides* and *Hydrochoerus* from Haile XV A probably can be explained in the same manner. Other differences between the faunas of Haile XV A and Santa Fe I are most likely ecologically induced, as will be discussed in the next section.

Among the best represented animals in the Haile XV A fauna are the edentates, a group of undoubted South American origin. Of the three genera at Haile XV A, only *Glossotherium* has been recognized previously in North American Blancan faunas, being present in the Blancan faunas of Texas and Nebraska (Table 21). *Dasypus* is known only from later deposits elsewhere in North America, and *Kraglievichia* has not heretofore been reported from this continent, although its probable descendant, *Pampatherium* (=*Holmesina*), has been found in Irvingtonian and Rancholabrean deposits.

This early record of a major influx of edentates from South America is further indication of the late Blancan age of Haile XV A. The small chlamythere from Haile XV A shows a remarkable resemblance to the species *Kraglievichia paranensis* from Late Pliocene deposits of South America. Although no authentic Chapadmalalan (Early Pleistocene) species is known, it probably lived in regions more tropical than Argentina and probably also was physically similar to the Florida material. Florida and Argentina apparently represent the northern and southern limits of the range for this form, and it seems safe to conclude that contemporaneous populations occupying the middle portion of the range were broadly similar to those at the extremes. The close resemblance of the Haile XV A *Glossotherium* to that from the Chapadmalalan stage also supports this correlation.

This late Blancan influx of edentates into Florida adds a new dimension to the previous correlation between the Blancan stage of North American and the Chapadmalalan stage of South America. This correlation had previously been based upon the appearance of a few Nearctic species in the Chapadmalalan and Uquian of South America (Patterson and Pascual 1968, Simpson 1969). Haile XV A adds the obverse relationships. North America received an important contingent of Neo-

tropical taxa in the Blancan. The only Nearctic taxa in the Haile XV A
fauna that closely resemble species in the Chapadmalal fauna are *Smilo-
don* and *Hemiauchenia*. The combination of correlative taxa of both
Nearctic and Neotropical origin makes the resemblance between the
Blancan fauna of Florida and the Chapadmalalan fauna of Argentina
particularly strong.

EUSTATIC CONSIDERATIONS

In addition to faunal correlation, the effects of sea level changes
caused by Pleistocene glaciation may be employed as an aid in dating
Florida Pleistocene deposits. Glacial eustatic fluctuations of sea level
have resulted in "terraces" or "abandoned shore lines," which are domi-
nant geomorphic features of the Florida landscape (Cooke 1945, Mac-
Neill 1949, White 1958, Alt and Brooks 1965). The location of a deposit
that can be correlated with these features can be quite helpful in age
determination. For example, a terrestrial deposit that is presently lying
at or below sea level must have been laid down at a time when sea level
was as low or lower than it is now. This would be an indication that the
deposit was laid down during glacial times, as these were the times of
low sea level. Once this is determined, the faunal elements may indi-
cate which glacial stage is represented.

Inland deposits at higher elevations present a problem in that they
could have been deposited either during a glacial or an interglacial stage.
If it can be shown that a particular inland deposit was coastal at its
time of deposition, then it must represent an interglacial stage, when sea
level was high. Haile XV A stands at an elevation of 90 ft above sea
level. It contains shark vertebrae that are similar in preservation to the
other vertebrate fossils in the site (and therefore are probably not in-
trusive). This indicates the close proximity of the sea during the time of
deposition. Remains of other fish species also suggest at least estuarine
conditions. Haile XV A could represent either an interglacial stage or a
preglacial wet interval during the Blancan; a preglacial age seems prob-
able on biostratigraphic grounds.

PALEOECOLOGY

Among the lower vertebrate remains from Haile XV A are numerous
lamnoid type shark vertebrae. Their preservation does not differ from
that of other vertebrate hard parts in the site, and thus they cannot be
interpreted as intrusive from adjacent Eocene limestones. (Sharks are
known in the Ocala Formation, but not abundantly and mainly from
teeth.) A variety of bony fishes of both freshwater and marine taxa
await further study. These include *Amia, Lepisosteus, Centropomus,*

Bagre, Ictalurus, and numerous other as yet unidentified species. Amphibians are represented by both anurans and urodeles. The turtles from Haile XV A include the aquatic forms *Chrysemys platymarginata, Trionyx, Kinosternon,* and *Chelydra,* and the terrestrial box turtle *Terrapene carolina.* The material of *Chrysemys platymarginata* (Weaver and Robertson 1967) includes numerous complete shells. They all occur in upright position, but facing in various directions, and are most abundant in the uppermost green clay unit. Most of the birds at Haile XV A are aquatic and include a duck, three herons, and a grebe (Campbell 1976). Although the lower vertebrate fauna has not been studied in detail, this preliminary analysis is enough to indicate an aquatic environment near the sea.

The mammalian taxa may be separated for the most part into two ecological components, a smaller group of aquatic species and a larger group of terrestrial species. *Castor* inhabits medium to larger permanent bodies of flowing water. *Pteronura,* the probable descendant of *Satherium,* inhabits streams from the Guianas to Argentina (Walker 1975). Its surrounding terrestrial habitat is probably secondary to its stream habitat, as it lives in suitable rivers that flow through a variety of terrestrial areas. These mammals are thus ecologically associated with the turtles, fishes, and water birds as a primary inhabitants of the aquatic site.

The abundance of large terrestrial animals and the relative scarcity of smaller terrestrial ones strongly suggests a spring-head habitat. The presence of a few of the denser bones (and especially teeth) of *Sigmodon, Scalopus, Cryptotis,* and *Cryptopterus* must be ascribed to fortuitous burial. The only other small mammals in the fauna are *Castor* and *Satherium,* which are normally aquatic in nature and thus may be expected abundantly in the stream. All the other mammals in the Haile XV A fauna are large terrestrial forms, which were probably trapped as they drank by the treacherous slopes and abrupt limestone ledges that often surround Florida springs.

We may next consider the nature of this terrestrial faunal sample. The terrestrial animals consist of *Terrapene,* the box turtle, one species of quail, one turkey (Campbell 1976), a few small mammals, and a considerable variety of large mammals. The presence of eurytopic large forms, such as *Smilodon, Hemiauchenia,* two subgenera of *Equus, Nannippus, Odocoileus,* and of the small mammals *Cryptotis, Scalopus,* and *Sylvilagus* tell us little about the local paleoecology. These forms are present in many Blancan local faunas of North America and probably ranged through many habitats.

Several taxa in the Haile XV A fauna, however, strongly suggest the presence of a forest community adjacent to the site of deposition. The

new species of *Mylohyus* lends strong support to this interpretation. Lundelius (1960) reviewed evidence that indicates a forest habitat for *Mylohyus*. He also included *Castor, Tapirus,* and *Glaucomys* (among others) as forest forms. Both *Castor* and *Tapirus* are present in the Haile XV A fauna, and the flying squirrel *Cryptopterus* (like *Glaucomys*) certainly indicates a forest environment. *Glossotherium* may also have favored forested or partly forested areas.

Dasypus and *Kraglievichia* probably were restricted in North America to the Gulf Coastal Plain by their need for moderate to warm temperatures and high rainfall. This may explain their absence from all other North American Blancan faunas. In South America, *Kraglievichia* seems to have been largely restricted to the northern tropical part of the continent. These edentates suggest a tropical or subtropical climate in central Florida during the Latest Pliocene.

In summary both the geological and faunal evidence seem to indicate that the Haile XV A site lay at the springhead of a coastal stream that flowed through a tropical or subtropical forest or forest savanna.

ZOOGEOGRAPHY

The Haile XV A fauna is the first Blancan fauna to be described from the Gulf Coastal Plain. Its unusual faunal assemblage (compared to Blancan faunas in western North America) apparently is a reflection of its location. Few American Blancan faunas are from coastal areas, and no others are so close to the Middle American tropics.

The most striking distinction of the Haile XV A fáuna is the diversity of edentates. Evidently it was in contact with the tropical corridor through which South America emigrants moved. Of the edentates, only *Glossotherium* was not restricted to the tropical portion of North America, as indicated by its presence in the Blanco (Texas) and Broadwater (Nebraska) faunas. This genus probably was also widely distributed on the South American continent, as the presence of *G. chapadmalensis* in Argentina indicates. On the other hand, *Kraglievichia* probably was restricted to the tropical or subtropical parts of North America during Blancan time, as indicated by its absence from all other North American Blancan faunas. Its presence in earlier Pliocene deposits of Argentina suggests that its range extended southward into more temperate climes in South America, but later it seems to have retreated tropicad in that continent also. Apparently the later Pleistocene evolution from *Kraglievichia* to *Pampatherium* involved, among other things, an increased tolerance to colder climate, which perhaps was correlated with the greater size of *Pampatherium*. *Pampatherium* was able, in the course of the Pleistocene, to disperse northwestward from

the Gulf Coastal Plain throughout most of temperate North America; in South America it spread southward throughout Argentina.

The genus *Dasypus* seems to have been even more closely restricted to tropical regions than either *Glossotherium* or *Kraglievichia.* It also was able to move out of the Gulf Coastal Plain later in the Pleistocene (as *Dasypus bellus*), reaching as far west as Texas and as far north as West Virginia (Guilday and McCrady 1966), Tennessee (Guilday *et al.* 1969), and Missouri (Simpson 1949). The probable mechanism permitting its tolerance to colder climate may have been an increase in size, as was true of *Pampatherium.* Its drastic size decrease in latest Pleistocene time (assuming *D. bellus* is closely related to *D. novemcinctus*) could account for its present limited southern distribution (Humphrey 1974). *Dasypus bellus* is not known from South American fossil deposits, although there is little doubt that the genus originated on that continent. This suggests that its range was similarly restricted to tropical areas on that continent, where fossil sites are rare and little known.

The unusual distributional pattern of *Cryptopterus* (Latest Pliocene of Florida and trans-Beringean of West Germany) indicates a wide distribution of large Group I flying squirrels. Presumably this group was restricted in the New World to the eastern deciduous forests of North America. James (1963) reported a smaller simple-toothed group of sciuropterines in Miocene deposits of California, but no other large complex-toothed specimens are known from the New World. Presumably *Cryptopterus* ranged from the eastern deciduous forests of North America through similar forests in Alaska and Siberia into Central Europe. The presence of *Pteromys* at Choukoutien (Young 1934) adds another very late Cenozoic record of a large flying squirrel from a temperate region, but it is not closely related to *Cryptopterus* (Mein 1970). The close resemblance between the Florida and West German specimens suggests rapid dispersal to the New World during late Hemphillian or Blancan time. Obviously this fortuitous record from the Blancan of Florida is peripheral to the main theatre of sciuropterine evolution in the Old World tropics.

SUMMARY

The Haile XV A mammals are from one of the few Blancan faunas on the Gulf Coastal Plain. It is the only such fauna that has been extensively studied to date and also the only one from a subtropical forest situation.

Included among the mammals from this site is *Glossotherium chapadmalensis,* previously known only from Argentina. It is possible that this form gave rise to *G. robustus* in South America and *G. harlani* in

North America. Apparently, *Glossotherium* was able to spread throughout much of temperate North America, whereas the other edentates represented in the Haile XV A fauna were restricted to subtropical regions during most of the Pleistocene.

The occurrence of a new species of *Kraglievichia* at Haile XV A and Santa Fe I is the first record of this chlamythere genus in North America. The presence of this species, which is closely related to *K. paranensis,* strengthens the correlation between North and South American faunas of Blancan and Chapadmalalan ages respectively.

The oldest evidence of *Dasypus bellus* occurs at Haile XV A. This species or its immediate ancestors undoubtedly originated in South America.

The giant flying squirrel, *Cryptopterus,* gives the local fauna an unexpected link with Old World Tertiary forest faunas. The new species from Haile XV A was among the last (Late Pliocene) dispersals of Old World subtropical forest dwellers to North America (Repenning 1965).

The presence of *Satherium* in the Haile XV A fauna marks the first Florida record of this large aquatic otter. It adds yet another link to the neotropical fauna, as it is closely related to *Pteronura,* the giant otter of South America.

The presence of *Mylohyus floridanus* at Haile XV A marks the earliest record for this genus, although its ancestor, *Prosthennops,* is known from the Pliocene of North America. It probably occurred in subtropical forests, in contrast to the contemporary genus *Platygonus.*

If the tentative assignment of the Haile XV A camelid to *Hemiauchenia macrocephala* is correct, it marks the earliest record for this species anywhere. The typical Blancan species, *H. blancoensis,* occurs at Santa Fe I, suggesting an age difference between the Florida Blancan localities.

The remaining members of the Haile XV A fauna are fairly typical representatives of the North American Blancan fauna. Such characteristic taxa as *Equus (Dolichohippus) simplicidens, Nannippus phlegon,* and *Sigmodon medius* substantiates a Blancan age assignment for Haile XV A.

The presence of sharks and brackish-water fishes indicates that the sea stood near Haile during the time that Haile XV A was deposited. The presumed sea level, which was 90 ft higher that that of today, is believed to represent a pre-glacial high sea level.

Although the bulk of the vertebrate fauna at Haile XV A indicates stream conditions, an adjacent terrestrial community is also well represented. Of the mammals, only *Satherium* and *Castor* represent the aquatic community. The terrestrial community includes several clear

indicators of a tropical forest situation, such as *Mylohyus, Cryptopterus,* three kinds of edentates, and *Tapirus.* The others are eurytopic small and large mammals.

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