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BIRDS AND MAMMALS FROM THE PLEISTOCENE OF WILLISTON, FLORIDA

J. ALAN HOLMAN¹

SYNOPSIS: A Pleistocene vertebrate locality at Williston, Levy County, Florida, contained the remains of 6 species of birds and 20 of mammals. The bones were in Arredondo clay, of Illinoian age, in a solution pipe in the Eocene Ocala limestone.

Two birds are extinct, a large quail (*Colinus suilium*), and a large jay (*Henocitta brodkorbi*) which is described as new. Six mammals are extinct: a mustelid of uncertain identity, a pine vole (*Pitymys hibbardi*) which is described as new, an armadillo (*Dasypus bellus*), a tapir (*Tapirus veroensis*), a peccary (*Mylohyus* sp.), and a horse (*Equus* sp.). Rabbits of the genus *Sylvilagus* are represented by 561 fossil elements; in many cases the two species, *S. palustris* and *S. floridanus*, can be distinguished on cranial and post-cranial bones.

The Pleistocene habitat of the Williston area was probably marshy pineland grading into well drained pineland with open sinks, surrounded by mesophytic vegetation.

Six species, 23 percent of the fossil fauna, are larger than their Recent Florida representatives. Five of these six species have larger modern forms to the north. Applying Bergmann's rule, this supports the thesis that Florida had a somewhat cooler climate in the Illinoian glacial stage.

The Williston fauna differs from other Pleistocene localities in Florida in its low percentage of extinct mammals. This is because a large number of the Williston mammals are small. If the percentage of extinction is calculated separately for large and small size classes, the Williston fauna resembles that of other Florida Pleistocene localities more closely.

INTRODUCTION

Interest in the Pleistocene birds and mammals of Florida has recently revived. Between 1896 and 1930 the many works of Leidy, Sellards, Hay, Simpson, and Wetmore laid the initial groundwork, mainly with the larger animals, but very little attention was paid to the subject from 1930 to 1950. Since 1950 the works of Brodkorb (1957 and 1959) on the Florida Pleistocene birds, and of Bader (1957), Olsen (1958), and Ray (1958) on the mammals, have added new impetus to this study. Recently developed techniques have enabled paleontologists to study the smaller vertebrates, largely neglected

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in the past, which should prove valuable in establishing a more natural correlation of the Florida Pleistocene.

Vertebrate fossils from the Williston, Florida, area have been known since the work of Leidy, but early lists were of a heterochronic nature (Simpson, 1929b). In 1956 Dr. Pierce Brodkorb of the University of Florida and Dr. Robert Bader of the University of Illinois discovered a new Pleistocene locality at Williston in the Connell and Shultz Limerock Company mine. The site is in Levy County, Florida just inside the north city limits of Williston, 0.9 miles north of the Williston Seaboard Airline Railroad. It has an elevation of approximately 82 feet and lies east of State Road 331 and Florida Geodetic Survey marker H 79 (Gunter, 1948), in area 4-2 of the Williston Quadrangle (U. S. Geological Survey, 1950). The Williston area today is a typical karst region, with many depressions and sinks and a mesophytic vegetation.

The fossils were found in a pipe in the Eocene Ocala limestone. Pipes of this nature in Florida, formed by the solution of limestone, apparently have been receiving freshwater sediments periodically since the lower Miocene (Bader, 1957). Similar pipes, solution channels, and sinkholes are a main source of fossil vertebrates in north-central Florida.

The Williston pipe was about 15 feet in diameter in a north-south direction. Its east face was covered by partially weathered original material. Excavating this matrix exposed two small caverns connected by a small crevice about 6 inches high. One cavern was 1 foot high, 3 feet wide, and extended horizontally about 1½ feet into the limestone. The other cavern was about 3 feet high, 6 feet wide, and extended about 3 feet horizontally before turning downward as part of the apex of the solution funnel. The sediments in the sink consisted of yellow-brown clays, bluish sandy clays, and some stratified layers of sand, which suggests they were deposited over a period of several years at least. Brodkorb (1959) has designated these clays as the Arredondo member of the Wicomico formation. Most of the bones occurred in the yellow-brown clays.

Overlying the clay-filled pipe is the Wicomico terrace sandy clay which has a characteristic dull orange color. This terrace was deposited during the Sangamon interglacial stage by an encroaching sea (Cooke, 1945). Brodkorb (1957 and 1959) has indicated that the Reddick and Arredondo, Florida, vertebrate localities represent the Illinoian stage because of their location in respect to the Wicomico

terrace. The Williston site is likewise referred to the Illinoian glacial stage of the Pleistocene.

Excavations were carried out from May through September of 1956. Both the small caverns were excavated, and the pipe had been dug to a depth of 8 feet when mining operations destroyed the site. The avian and mammalian faunas of this locality form the subject of the present paper. The amphibians and reptiles were discussed by Holman (1959). While previous work in the Williston area treated only a few large mammals, the present paper includes many of the smaller mammals and birds. The work was supported by the Florida Geological Survey, where the mammalian remains are deposited. The birds are in the collection of Pierce Brodkorb at the University of Florida.

ANNOTATED LIST

Class AVES

Anas discors Linnaeus

MATERIAL.—Right carpometacarpus (PB 2320).

The carpometacarpus of *A. discors* is similar to that of *A. carolinensis*, but size as well as several qualitative characters separate the two species (Brodkorb, 1959). The height of metacarpal I ranges from 8.8 to 9.4 mm. in 7 Recent *A. discors*, and from 8.4 to 9.0 mm. in 6 Recent *A. carolinensis*. The 9.3 mm. height of metacarpal I in the fossil falls within the range of *A. discors*.

Colinus sibilium Brodkorb

MATERIAL.—Rostrum (PB 2318), 2 vertebrae (PB 2308-2309), left coracoid (PB 2319), 2 left (PB 2301-2302) and 3 right (PB 2310-2312) humeri, left ulna (PB 2304), 2 left carpometacarpi (PB 2305-2306), 1 left (PB 2303) and 3 right (PB 2315-2317) femora, left tarsometatarsus (PB 2307).

The most abundant avian fossils collected at Williston are those of a large quail, recently described by Brodkorb (1959) from the Pleistocene of Arredondo, Florida. Measurements of Recent and fossil quail were supplied by Dr. Brodkorb. Table I shows the Pleistocene quail of Williston to be larger in all elements than Recent *C. virginianus*, and very close to *C. sibilium*. The Williston fossils also agree with *C. sibilium* in the qualitative characters pointed out by Brodkorb (1959).

TABLE 1

MEASUREMENTS (IN MM.) OF WING AND LEG ELEMENTS OF *Colinus*

Element	Williston Pleistocene <i>C. suillum</i>		Arredondo <i>C. suillum</i>		Recent <i>C. virginianus</i>	
	Range	No.	Range	No.	Range	No.
Humerus:						
length	34.5-37.2	4	37.6-37.9	2	31.7-35.8	19
prox. width	9.5-10.3	4	9.6-10.4	5	9.3-10.8	19
shaft width	3.6- 3.8	4	3.4- 3.8	6	2.6- 3.3	19
distal width	7.0- 7.9	4	7.5- 7.9	2	6.3- 6.8	19
depth of head	3.7- 4.0	4	3.7- 4.1	4	3.1- 3.5	19
length prox. end brachialis to distal end of internal condyle	5.6- 6.3	4	6.3	1	5.3- 6.1	19
Ulna:						
length	34.0	1	32.7-33.1	2	28.5-32.2	19
prox. width	4.8	1	4.1- 4.6	2	3.4- 4.3	19
Carpometacarpus:						
length	20.4	1			17.0-19.5	14
height prox. end	6.0	1			4.9- 5.7	14
Femur:						
length head through internal condyle	42.9	1			36.4-39.6	15
least shaft	3.3	1			2.8- 3.2	15
distal shaft	7.5- 7.6	2			6.4- 7.1	15
Tibiotarsus:						
length	54.8	1	58.1	1	49.8-53.5	19
distal width	5.1- 5.9	3	5.4	1	4.6- 5.2	1
depth of external condyle	5.3- 5.9	3	5.5	1	4.6- 5.1	19
depth of internal condyle	5.5- 6.2	3	5.2- 5.7	2	4.8- 5.5	19
Tarsometatarsus:						
width of trochlea 3	2.5	1	2.5	1	1.9- 2.3	19
depth of trochlea 3	3.5	1	3.4	1	2.6- 3.2	19

Meleagris gallopavo Linnaeus

MATERIAL.—Left femur (PB 2321).

Corvus brachyrhynchos Brehm

MATERIAL.—Right carpometacarpus (PB 2322).

The carpometacarpi of *C. brachyrhynchos* and *C. ossifragus* may be separated on size. The length of the carpometacarpus in 5 Recent *C. brachyrhynchos* ranges from 46.8 to 50.5 mm., the proximal height from 10.0 to 11.2 mm. In 9 Recent *C. ossifragus* the length ranges from 39.6 to 44.2 mm. and the proximal height from 8.7 to 10.3 mm. The length of the fossil is 48.6 mm., the proximal height 10.7 mm., falling within the range of *C. brachyrhynchos*.

Henocitta new genus

TYPE OF GENUS.—*Henocitta brodkorbi* new species.

DIAGNOSIS.—Closest to *Psilorhinus* Ruppell of Mexico and Central America, in distal length of entepicondyle; extent and depth of brachial depression; shape of internal condyle.

Differs from *Psilorhinus* in having entepicondylar prominence robust; entepicondyle wider in palmar view, narrower in distal view; area between internal condyle and entepicondyle depressed; fossa above internal condyle shallow; ectepicondyle wide and at right angle with shaft (in *Psilorhinus* ectepicondyle much narrower and directed inward).

Less closely related to *Protocitta* Brodkorb of the Pleistocene of Reddick, Florida, and *Calocitta* Gray of Recent Mexico and Central America.

Differs from *Protocitta* in having entepicondyle rotated anconally; brachial depression deeper and less extensive; internal condyle depressed distally, rounded in palmar view; ectepicondyle wide and at right angle to shaft (in *Protocitta* ectepicondyle much narrower and directed inward).

Differs from *Calocitta* in having entepicondylar prominence less robust, entepicondyle longer distally, area between internal condyle and entepicondyle produced, brachial depression less shallow and more extensive, internal condyle rounded in palmar view, fossa above internal condyle shallow, ectepicondyle wide and at right angle with shaft (in *Calocitta* ectepicondyle much narrower and directed inward).

ETYMOLOGY.—From Greek *henos* (old, former) and *kitta* (chattering bird).

Henocitta brodkorbi new species

Plate I, Figs. 1-2

HOLOTYPE.—Distal half of left humerus, PB 2323. From Pleistocene (Arredondo member, Illinoian stage) at Connell and Shultz Limerock Company quarry, Williston, Levy County, Florida. Collected by J. Alan Holman, summer, 1956.

DESCRIPTION OF HOLOTYPE.—Entepicondyle robust, long, and rotated anconally, entepicondylar process robust, brachial depression narrow and deep, area between entepicondyle and internal condyle depressed, internal condyle round and produced in lateral view, fossa above internal condyle shallow, entepicondyle at right angle to shaft and widest of any corvid studied.

Width through epicondyles, 11.1 mm., width of shaft above ectepicondyle 7.1 mm., length of entepicondyle 5.0 mm., width of entepicondyle 3.8 mm., length of brachial depression 5.0 mm., length of internal condyle 3.0 mm., width of ectepicondyle 2.7 mm.

DIAGNOSIS.—Humerus smaller than *Calocitta colliei*, *Psilorhinus morio*, and *Psilorhinus mexicanus*; about the same size as *Protocitta dixi* and *Calocitta formosa*; larger than that of any other jays studied.

DISCUSSION.—This is the second fossil jay described. The first (*Protocitta dixi* Brodkorb) is from the Illinoian stage of the Pleistocene of Reddick, Florida, and also has its closest affinities with the large Recent jays of Mexico and Central America (Brodkorb, 1957). While *Protocitta* is more closely related to *Calocitta* from the west coast of Mexico and Central America, *Henocitta* is closest to *Psilorhinus* from the east coast of Mexico and Central America.

ETYMOLOGY.—The new jay is named for Dr. Pierce Brodkorb of the University of Florida who has pioneered the study of small fossil vertebrates in Florida.

Family FRINGILLIDAE

(Genus and species indeterminate)

MATERIAL.—Two right carpometacarpi (PB 2324-2325), left coracoid (PB 2326).

These bones are those of a small sparrow; otherwise they are not distinctive.

Class MAMMALIA

Scalopus aquaticus Linnaeus

MATERIAL.—Right ulna (FGS V-5846).

The fossil fits within the variation found in Recent Florida moles.

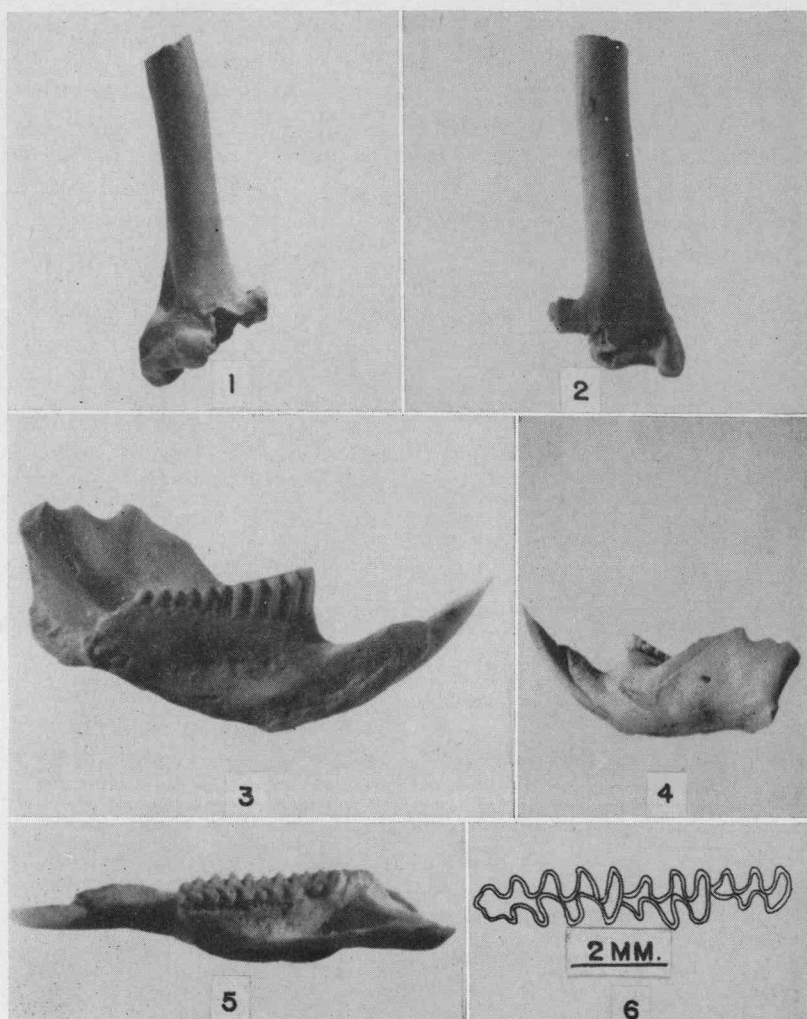


Plate I. Figs. 1-2, *Henocitta brodkorbi*, palmar and anconal view of holotype humerus, x 1.7. Figs. 3-5, *Pitymys hibbardi*, lingual, labial, and occlusal view of holotype dentary, x 3.4, x 2, x 3.2. Fig. 6, *Pitymys hibbardi*, molar pattern drawn from holotype.

Cryptotis parva (Merriam)

MATERIAL.—Three left dentaries (FGS V-5847).

The dentaries referred to *Cryptotis parva* differ from those of *Sorex longirostris* in that the angle of the coronid with the dentary teeth in *S. longirostris* is V-shaped and almost 90 degrees, whereas

in *Cryptotis parva* the angle is U-shaped and much less than 90 degrees.

Several of the osteological characters used to separate *Cryptotis* and *Blarina* overlap in some cases. In *Cryptotis* the angle between the coronoid and condyloid process is usually less than in *Blarina*. In *Cryptotis* the notch on the dorsal part of the coronoid process in external aspect is often small and shallow, whereas in *Blarina* it is usually wide and deep. The tubercles of the dentary teeth in *Cryptotis* are usually more pointed in dorsal aspect, those of *Blarina* more rounded. *Cryptotis* tends to have deeper notches in the dental incisor than *Blarina*.

Size is a more reliable criterion for separating the two genera. In 10 Recent *Blarina brevicauda* from north-central Florida the height of the dentary ranges from 5.3 to 6.1 mm. In 10 Recent Florida *Cryptotis parva* the height of the dentary ranges from 4.0 to 4.8 mm. As the height of the dentary of the two fossils ranges from 4.3 to 4.7 mm., they are assigned to *C. parva*.

Blarina brevicauda (Say)

MATERIAL.—Left dentary (FGS V-5848).

Differences between *Blarina* and *Cryptotis* have been elaborated above. *Blarina* differs from *Sorex* in that the angle from the coronoid to the dentary teeth is U-shaped and much more than 90 degrees, whereas in *Sorex* it is V-shaped and almost 90 degrees. The 5.4 mm. height of the dentary in the fossil falls with the range of Recent *Blarina brevicauda* from north-central Florida.

Family URSIDAE

(Genus and species indeterminate)

MATERIAL.—Left C¹ (FGS V-5849), right P⁴ (FGS V-5851), right M¹ (FGS V-5852), 2 left M² (FGS V-5853-5854).

The overlap in characters between the teeth of *Ursus* (*Euarctos*) and *Arctodus* (Olsen, personal communication) prevents positive diagnosis of these fossil bear teeth from Williston.

Family MUSTELIDAE

(Genus and species indeterminate)

MATERIAL.—Left P₄, right P₂, 1 left and 1 right M₁ (FGS V-5855).

The right M₁ is much larger than those of Recent skunks in the University of Florida collections. The specimens were sent to Stan-

ley J. Olsen, who found they agree with none of the *Mephitis* group in the Florida Geological Survey collections. Regarding the molars he states "There is a double cusp on the protocone not found in *Mephitis*—this could be an aberrant individual though—and the other M_1 is from a smaller individual. This tooth has a constriction or pinched area in the trigonid that is not present in the skunks that I have seen here." As the teeth of the Recent *Conepatus* group have not been examined it seems best to refer the material to family only.

Sciurus carolinensis Gmelin

MATERIAL.—Left M_2 (FGS V-5858).

This fossil seems to be from a young animal, as it shows less wear than adult Recent gray squirrels studied.

Geomys pinetis (Barton)

MATERIAL.—Three right and 1 left dentary (FGS V-5859).

Peromyscus gossypinus (LeConte)

MATERIAL.—Two left and 4 right dentaries (FGS V-5860).

Six dentaries referable to the genus *Peromyscus* were obtained at the Williston locality. To determine the identity of the fossils, dentaries of Recent *P. gossypinus*, *P. floridanus*, *P. polionotus*, and *P. nuttalli* were studied. *Reithrodontomys humulis* was also compared because of the similarity of its dentary to that of *Peromyscus*.

No qualitative characters were found to separate the Recent species satisfactorily. The tooth row, however, showed some differences in length: *P. gossypinus* 3.6 to 4.3 mm. (10), *P. floridanus* 4.4 to 5.0 mm. (10), *P. polionotus* 2.4 to 3.7 mm. (10), *P. nuttalli* 3.7 mm. (1), *Reithrodontomys humulis* 2.7 to 3.0 mm. (3).

The 3.8 to 4.4 length of the tooth row in the six fossils agrees best with that of *P. gossypinus*.

Oryzomys palustris (Harlan)

MATERIAL.—Right maxilla (FGS V-5861).

Sigmodon hispidus Say and Ord

MATERIAL.—Left maxilla, 1 left and 1 right dentary (FGS V-5862).

Neotoma floridanus (Ord)

MATERIAL.—Left M_2 (FGS V-5863).

Pitymys hibbardi new species

Plate I, Figs. 3-6

HOLOTYPE.—Left dentary, complete except for tips of coronoid, condyle, and angle, FGS V-5929. From Pleistocene (Arredondo member, Illinoian stage) at Connell and Shultz Limerock Company quarry, Williston, Levy County, Florida. Collected by J. Alan Holman, summer 1956. Length of tooth row, 7.2 mm.; height of dentary at first molar tooth, 6.0 mm.; length of diastema, 4.4 mm.

PARATYPES.—Two left (FGS V-5930-5931), and two right (FGS V-5932-5933) dentaries.

One of the left dentaries (FGS V-5930) contains an M_1 , but the others are without teeth.

DIAGNOSIS.—Agrees with *Pedomys* and *Pitymys* and differs from *Microtus* in having M_1 with a posterior loop, 5 alternating triangles, and an anterior loop; first, second, and third alternating triangles closed; confluent fourth and fifth triangles open into anterior loop. Differs from *Pedomys* in having diastema short and incisor narrow.

Closest to *P. dideltus* (Cope) from Pleistocene of Port Kennedy Cave, Pennsylvania, but larger (Table 2); second alternating triangle of M_3 two-thirds as wide as first triangle (in *P. dideltus* only one-third as wide); capsular process broadly convex dorsally, sloping downward toward incisor anteriorly, and downward toward mental foramen posteriorly (in *P. dideltus* capsular process concave dorsally, sloping upward toward the incisor anteriorly, and upward toward the molar teeth posteriorly (cf. Hibbard, 1955).

TABLE 2
MEASUREMENTS (IN MM.) OF DENTARY BONES OF *Pitymys*

Species	Length of tooth row	Height at first molar	No.
<i>P. hibbardi</i>	6.6-7.2 (2)	5.0-6.0 (5)	5
<i>P. dideltus</i>	6.2-6.5	-----	2
<i>P. mcnowni</i>	7.0	-----	1
<i>P. involutus</i>	4.9-5.6	-----	2
<i>P. pinetorum</i>	5.4-6.4	4.4-5.4	11
<i>P. parvulus</i>	5.2-6.0	4.1-5.3	22
<i>P. quasiater</i>	5.3-6.4	4.7-5.5	5

Close in size to *P. mcnowni* Hibbard (1937) from the Pleistocene of Brown County, Kansas; differs in having salient angles of M_1

narrow with apices angular (in *P. mcnowi* salient angles of M_1 broad and apices rounded).

Differs from *P. meadensis* Hibbard (1944) of the Pleistocene of Kansas in that the confluent fourth and fifth triangles of M_1 open into the anterior loop (in *P. meadensis* confluent fourth and fifth triangles closed, separate from anterior loop).

Larger than *P. involutus* (Cope) from Pleistocene of Cumberland Cave, Maryland; anterior loop of M_1 with re-entrant angles (in *P. involutus* re-entrant angles of anterior loop of M_1 weak or absent; cf. Gidley and Gazin, 1938).

Differs from Recent species of *Pitymys* in larger size; second triangle two-thirds width of first triangle; capsular process poorly developed, exposing incisor laterally and medially. A poorly developed capsular process is characteristic of the earlier voles (Hibbard, 1959). Differs further from Recent *Pitymys* (as well as *Pedomys*, and *Microtus*) in having anterior ridge of ascending ramus strongly curved along tooth row, but dropping abruptly at level of second triangle of M_1 . In Recent forms the ridge is much straighter and extends to the anterior third of the M_1 .

DISCUSSION.—The similarity of *P. hibbardi* to *P. dideltus* is interesting in the light of recent interpretations of Florida Pleistocene stratigraphy. Hibbard (1955) considered the Port Kennedy assemblage where *P. dideltus* is found to be no earlier than late Kansan and no younger than early Illinoian. The Williston locality is considered to be of Illinoian age.

A noteworthy parallel seems to occur between the bog lemmings and pine voles of the Pleistocene of Florida. The extinct *Synaptomys australis* is 35 percent larger than the Recent *Synaptomys cooperi* (Olsen, 1958). The length of the tooth row of the holotype of *Pitymys hibbardi* is 20 percent longer than the largest Recent Florida *P. parvulus* measured (Table 2).

ETYMOLOGY.—The fossil is named for Dr. Claude W. Hibbard of the University of Michigan who has contributed so much to the knowledge of fossil microtines.

Sylvilagus Gray

MATERIAL.—7 left and 9 right maxillae (FGS V-5864), 15 left and 10 right dentaries (FGS V-5865), 110 vertebrae (FGS V-5867), 25 left and 30 right humeri (FGS V-5868), 11 left and 9 right ulnae (FGS V-5869), 3 sacra (FGS V-5870), 18 right and 18 left innominates (FGS

V-5871), 35 left and 48 right femora (FGS V-5872), 32 left and 42 right tibiae (FGS V-5873).

Rabbit elements were the most abundant fossils in the Williston material. The bones were not localized at any one depth, but were distributed uniformly throughout the matrix. In addition to the 424 specimens listed above, 137 additional elements were identified to the specific level.

Two species of *Sylvilagus* occur in northern Florida at present, *S. palustris* and *S. floridanus*, each represented by two subspecies (Miller and Kellogg, 1955). *S. palustris palustris* (Bachman) ranges from Virginia to northern Florida, and *S. palustris paludicola* (Miller and Bangs) occupies peninsular Florida. *S. floridanus mallurus* (Thomas) ranges from New York to northern Florida, and *S. floridanus floridanus* (Allen) is confined to peninsular Florida. Simpson (1929b) refers rabbit elements from the Williston Pleistocene to *Sylvilagus* sp.

Heretofore characters have not been found to separate the postcranial elements of the two local species of rabbits. Study of modern skeletons shows that in many cases individual bones may be identified. Most of the Recent material used in this study was from the area of intergradation in northern Florida, but some specimens from North Carolina were also available. The characters used to separate the species are given below.

The angle from the ramus of the mandible at the last molar tooth to the coronoid process is much less in *S. palustris* than in *S. floridanus*. This character is not usable in the Williston material, for all the fossils lack the posterior part of the dentary. Some of them can be separated by the angle between the anterior border of the angular process and the mandibular ramus (Plate II, Fig. 1). In *S. floridanus* this angle ranges from 115 to 145 degrees; in *S. palustris* it ranges from 130 to 160 degrees. Fossils with the angle from 115 to 125 degrees are assigned to *S. floridanus*, and fossils measuring from 150 to 160 degrees are identified as *S. palustris*.

In the scapula the medial surface of the base of the coracoid process is more excavated in *S. palustris* than in *S. floridanus*. Thus the coracoid process in *S. palustris* tends to describe a curve inflected toward the glenoid fossa, whereas in *S. floridanus* the apex of the notch between the glenoid fossa and the coracoid process is directed ventrally.

The humerus is a distinctive element. In *S. floridanus* the head in dorsal view is more rounded on the medial side than in *S. palustris*,

which is more flattened. The distal end of the humerus is narrower in *S. floridanus* than in *S. palustris* (Plate II, Fig. 2). Ratios of length of humerus to distal width show ranges of 12.5 to 14.8 percent in *S. floridanus* and 14.8 to 17.1 percent in *S. palustris*.

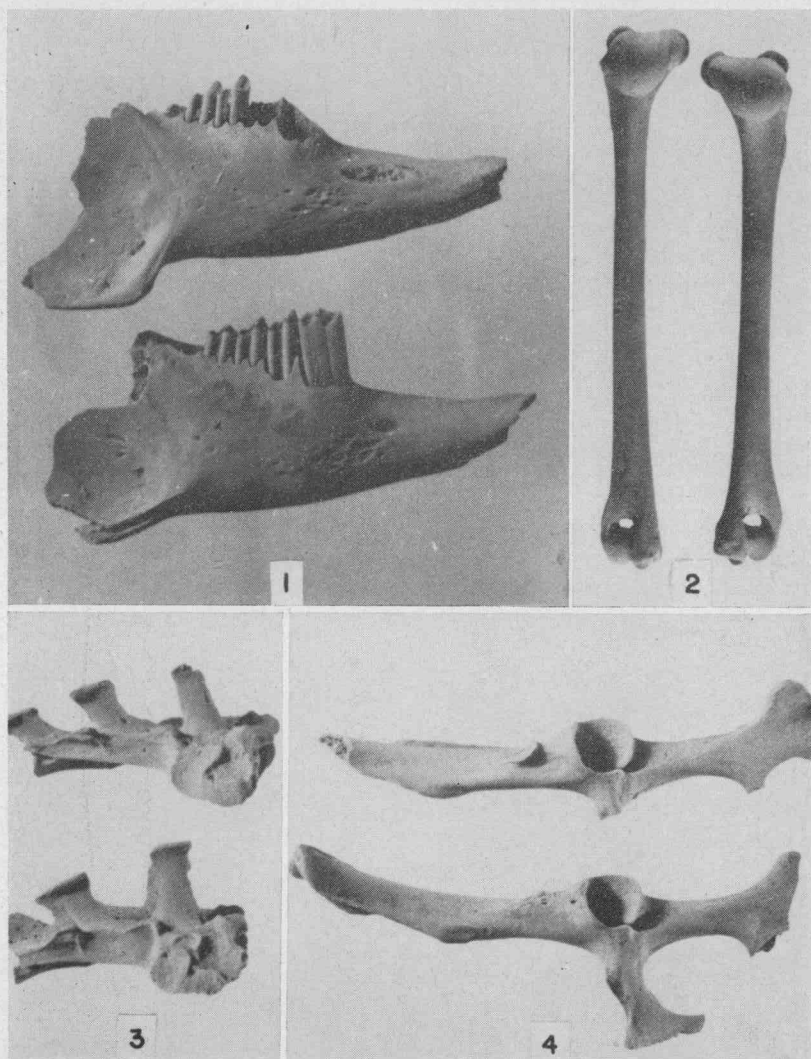


Plate II. Fig. 1, Dentary of *Sylvilagus floridanus*, top, *S. palustris*, bottom, x 1.7. Fig. 2, Humerus of *Sylvilagus floridanus*, left, *S. palustris*, right, x 1. Fig. 3, Sacrum of *Sylvilagus floridanus*, top, *S. palustris*, bottom, x 1. Fig. 4, Innominate of *Sylvilagus floridanus*, top, *S. palustris*, bottom, x 1.

TABLE 3
MEASUREMENTS (IN MM.) OF *Sylvilagus palustris*

	Fossil	North Carolina	North Florida
Dentary:	15.7-16.2 (15.95)	14.9-15.5 (15.30)	14.0-16.3 (15.07)
length tooth row	n, 2	n, 3	n, 24
height	13.5-14.0 (13.75)	13.5-14.9 (14.27)	12.9-14.9 (14.01)
tooth row	n, 2	n, 2	n, 24
Humerus:	63.2	61.1-62.3 (61.80)	49.0-59.6 (56.34)
length	n, 1	n, 3	n, 9
proximal	13.5	12.5-13.2 (12.73)	11.8-12.6 (12.08)
width	n, 1	n, 3	n, 9
distal	8.6	8.8- 9.1 (8.97)	8.4- 9.3 (8.78)
width	n, 1	n, 3	n, 9
Femur:	86.4-88.5 (87.45)	82.0-83.3 (82.65)	66.0-82.0 (78.42)
length	n, 2	n, 2	n, 9
proximal	14.8-17.2 (16.00)	14.5-14.7 (14.60)	11.2-15.0 (13.88)
width	n, 2	n, 3	n, 9
distal	14.0	13.0-13.6 (13.33)	11.6-14.0 (13.02)
width	n, 1	n, 3	n, 9
Tibia:		92.8-94.2 (93.50)	82.9-90.7 (86.21)
length		n, 3	n, 9
proximal		14.0-14.7 (14.47)	12.8-15.0 (13.81)
width		n, 3	n, 9
distal	11.4-12.2 (11.80)	10.3-11.0 (10.60)	10.0-10.7 (10.36)
width	n, 8	n, 3	n, 9
Innominate:		72.4-74.0 (73.33)	66.5-72.5 (70.15)
length		n, 3	n, 9
height of	8.4- 9.0 (8.70)	8.4- 8.8 (8.57)	7.5- 8.5 (8.19)
acetabulum	n, 2	n, 3	n, 8
Sacrum:	22.0-24.0 (23.00)	23.1-25.0 (23.03)	23.0-27.1 (24.71)
width	n, 2	n, 3	n, 8

TABLE 4
MEASUREMENTS (IN MM.) OF *Sylvilagus floridanus*

	Fossil	North Carolina	North Florida
Dentary:	13.0-14.7 (14.26)	13.0-14.0 (13.50)	13.9-14.3 (14.10)
length tooth row	n, 7	n, 2	n, 24
height	12.2-13.7 (13.01)	11.7-12.2 (11.95)	12.5-14.0 (13.13)
tooth row	n, 7	n, 2	n, 23
Humerus:	62.2-66.9 (64.85)	61.0-63.5 (62.25)	53.0-64.5 (58.65)
length	n, 8	n, 2	n, 8
proximal	12.2-13.2 (12.80)	12.0-12.4 (12.20)	11.5-13.3 (11.87)
width	n, 8	n, 2	n, 8
distal	7.9- 8.6 (8.30)	7.7- 8.3 (8.00)	7.4- 8.5 (7.92)
width	n, 8	n, 2	n, 8
Femur:	83.7-87.8 (85.78)	81.0-82.6 (81.80)	75.0-87.4 (79.48)
length	n, 6	n, 2	n, 9
proximal	14.8-17.1 (15.97)	15.2-15.3 (15.25)	13.5-16.5 (14.14)
width	n, 11	n, 2	n, 9
distal	13.3-14.4 (13.92)	12.8-12.9 (12.85)	10.4-11.3 (10.88)
width	n, 6	n, 2	n, 9
Tibia:	101.0-102.0 (101.50)	89.4-93.1 (91.25)	82.7-97.2 (86.90)
length	n, 3	n, 2	n, 4
proximal	14.3-16.0 (15.20)	13.3-14.1 (13.70)	13.0-14.0 (13.72)
width	n, 3	n, 2	n, 8
distal	11.3-12.2 (11.65)	10.3-11.0 (10.65)	10.4-11.3 (10.88)
width	n, 25	n, 2	n, 5
Innominate:		66.5-70.3 (68.40)	60.5-69.4 (66.61)
length		n, 2	n, 8
height of	7.8- 8.6 (8.16)	7.7- 7.9 (7.80)	7.6- 8.6 (8.13)
acetabulum	n, 17	n, 2	n, 9
Sacrum:	22.0-23.5 (22.83)	21.7-27.0 (24.35)	19.5-25.0 (22.55)
width	n, 4	n, 2	n, 6

In the sacrum of both species some individuals have a thin bony bridge uniting the three neural spines. It seems unlikely that this is ontogenetic secondary ossification, for individuals having this condition are about in the middle of the age groups examined in both species. When this bridge is present sacra of the two species cannot be differentiated. When the bridge is absent, however, in *S. floridanus* the first two neural spines are narrow in an antero-posterior direction, with a pronounced constriction in the middle of the spine. In *S. palustris* the spines are wide throughout with little or no median constriction (Plate II, Fig. 3).

The innominate bones are similar in both species but show minor differences. In young specimens of both forms the acetabulum tends to be open posteriorly and ventrally with only a cartilaginous bridge. As the animals mature the acetabular fossa closes completely along a bony suture. The two species show an ontogenetic difference in this respect. In *S. palustris* the acetabular fossa closes only in old individuals and then laterally only, leaving a V-like opening whose apex is directed laterally. In *S. floridanus* a complete fusion of the acetabular border takes place early in life.

A diagnostic character seemingly not affected by ontogenetic variation occurs in the tuberosity for attachment of *M. rectus femoris* on the ilium just anterior to the acetabulum. In *S. floridanus* the tuberosity is well developed and projects laterally with a distinct valley between it and the acetabular border. In *S. palustris* the tuberosity is much more flattened and the valley between it and the acetabular border is either shallow or absent (Plate II, Fig. 4). The greater development of the tuberosity in *S. floridanus* appears to be associated with its more saltatorial habits.

The femora of the two species also show slight differences. In *S. floridanus* the greater trochanter in posterior aspect is strongly curved along the medial margin and projects proximally in a hook; the lesser trochanter is nearly at the level of the third trochanter. In *S. palustris* the medial margin of the greater trochanter is nearly straight and the lesser trochanter is elevated markedly above the level of the third trochanter. The distal end of the femur of *S. floridanus* is more compressed, with the condyles flaring more widely than in *S. palustris*. The curve of the greater trochanter, however, is the most reliable character.

The distal end of the tibia is diagnostic. That of *S. floridanus* usually shows two distinct tendinal grooves, one extending one-third

to one-half way up the lateral side of the shaft, the other only a few millimeters up the medial side of the shaft. In some cases the medial groove is absent. In *S. palustris* both grooves are always present and the medial groove is always well developed about a third of the way up the shaft.

Sylvilagus palustris (Bachman)

MATERIAL.—3 left and 3 right dentaries (FGS V-5874), 2 left and 1 right scapula (FGS V-5875), right humerus (FGS V-5882), 2 sacra (FGS V-5876), 3 left and 1 right innominate (FGS V-5877), 4 left and 2 right femora (FGS V-5878), 3 left and 2 right tibiae (FGS V-5879).

The recent North Carolina *S. palustris* are on the whole larger than the Recent northern Florida material, especially in humeral and tibial lengths (Table 3). The fossils carry this trend even farther, as their limb elements are longer than the Recent North Carolina material.

Sylvilagus floridanus (Allen)

MATERIAL.—9 left and 6 right dentaries (FGS V-5880), 9 left and 5 right scapulae (FGS V-5881), 5 left and 3 right humeri (FGS V-5883), 5 sacra (FGS V-5884), 12 left and 7 right innominates (FGS V-5886), 14 left and 19 right tibiae (FGS V-5887).

The Recent North Carolina specimens of *S. floridanus* are larger than Recent Florida skeletons in all elements except the dentary (Table 4). As with the marsh rabbit, the fossil cottontails have larger limbs than Recent material from North Carolina or Florida. The one qualitative difference noted between the fossil and Recent *S. floridanus* material is the greater development of the third trochanter of the femur in the fossil form. It extends much farther laterally and also flares more anteriorly than in any of the modern skeletons examined.

Dasypus bellus (Simpson)

MATERIAL.—25 buckler scutes, 15 movable ring scutes, and 6 leg scutes (FGS V-5888).

Dasypus bellus from the Pleistocene of Williston is characterized as being twice as large as the Recent *Dasypus novemcinctus* (Simpson, 1929a). The armadillo scutes listed above are smaller than most Pleistocene material but larger than Recent *Dasypus novemcinctus* (Table 5). The Williston fossils may be from a young individual.

TABLE 5
MEASUREMENTS (IN MM.) OF *Dasypus bellus*

		Williston	Seminole Field (After Simpson)	Haile	Reddick
Width movable ring scutes at anterior border of exposed portion	Mean	8.13	11.7	11.33	11.47
	Range	7.7 - 8.7	9.6 -13.2	10.0 -13.0	9.5 -13.7
	No.	9	4	3	12
Maximum diam- eter of buckler scutes	Mean	9.87	14.60	12.8	12.93
	Range	7.0 -14.9	10.0 -19.8	12.8	9.6 -15.6
	No.	28	14	1	22

Tapirus veroensis Sellards

MATERIAL.—Right P₁, right P⁴, right M², left M₃ (FGS V-5889).

The four tapir teeth from Williston agree in conformation and measurements with Sellards' type of *T. veroensis* and with Simpson's type of *T. veroensis sellardsi* (Table 6). Stanley J. Olsen of the Florida Geological Survey kindly examined the P₁ and confirmed the identification.

TABLE 6
MEASUREMENTS (IN MM.) OF TEETH OF *Tapirus veroensis*

		Williston	Vero (after Sellards)	Seminole Field (after Simpson)
P ⁴	Length	21.3	20.0	20.0
	Anterior width	24.2	26.0	24.7
	Posterior width	23.7	—	24.4
P ₁	Length	24.6	—	—
	Anterior width	11.5	—	—
	Posterior width	13.4	—	—
M ²	Length	24.5	24.0	23.5
	Anterior width	27.8	28.0	26.2
	Posterior width	23.2	—	23.0
M ₃	Length	26.4	—	24.2
	Anterior width	19.8	—	19.8
	Posterior width	18.5	—	19.8

Mylohyus sp.

MATERIAL.—Left dentary including P₄, M₁, M₂, and M₃, right M₂, left maxillary including P₂ and P₃, left M² and M³ (FGS V-5890), right humerus (FGS V-5891).

The teeth found at Williston are too worn to be identified to the species level. If the humerus belongs to the same individual as did the teeth, the fossil peccary had a much larger forearm than the living *Pecari tajacu* (Table 7).

TABLE 7
MEASUREMENTS (IN MM.) OF PECCARIES

Teeth	<i>Mylohyus</i> sp. Williston			<i>Pecari tajacu</i> male, Chiapas		
	Total length	Anterior width	Posterior width	Total length	Anterior width	Posterior width
P ³	10.3	8.6	9.9	9.5	6.4	8.8
P ³	11.2	12.0	11.6	8.8	10.2	10.3
M ³	16.7	14.3	15.4	14.3	13.0	12.3
P ₄	11.8	9.2	10.0	11.8	8.2	9.8
M ₁	13.0	12.8	13.5	11.4	10.2	10.2
M ₂	13.5	13.4	13.8	12.8	11.8	12.4
M ₃	19.6	14.2	12.8	19.3	11.7	10.8
	Total length	Proximal width	Distal width	Total length	Proximal width	Distal width
Humerus	155.0	46.0	41.0	119.0	34.0	31.0

Odocoileus virginianus (Boddaert)

MATERIAL.—Right M₂ and M³, right dentary including M₁ and M₂ (FGS V-5892).

The deer teeth from Williston are from a rather small individual.

Equus sp.

MATERIAL.—Lower right molar (FGS V-5893).

This horse tooth is not identifiable to species.

DISCUSSION

PALEOECOLOGY.—On the basis of the large Pleistocene herpetofauna of Williston, Holman (1959) concluded that the Pleistocene habitat of the area consisted of marshy pine land grading into well-

drained pine land with open sinks, surrounded by mesophytic vegetation. The birds and mammals could also have lived in such a situation (Table 8).

TABLE 8

CHARACTERISTIC HABITAT OF WILLISTON PLEISTOCENE FAUNA
BASED ON THAT OF RECENT REPRESENTATIVES († EXTINCT FORMS)

Species	Pinewoods	Mesophytic forest	Marsh	Unknown
<i>Anas discors</i>			x	
† <i>Colinus sulium</i>				x
<i>Meleagris gallapavo</i>	x	x		
<i>Corvus brachyrhynchos</i>	x	x		
† <i>Henocitta brodkorbi</i>				x
Fringillidae sp.				x
<i>Scalopus aquaticus</i>		x		
<i>Cryptotis parva</i>	x	x		
<i>Blarina brevicauda</i>		x	x	
<i>Ursus</i> sp.		x		
†Skunk or Mustelid				x
<i>Lynx rufus</i>	x	x		
<i>Sciurus carolinensis</i>		x		
<i>Geomys pinetis</i>	x			
<i>Peromyscus gossypinus</i>	x	x	x	
<i>Oryzomys palustris</i>			x	
<i>Sigmodon hispidus</i>	x	x	x	
<i>Neotoma floridana</i>		x		
† <i>Pitymys hibbardi</i>	x			
<i>Sylvilagus palustris</i>		x	x	
<i>Sylvilagus floridanus</i>	x	x		
† <i>Dasypus bellus</i>				x
† <i>Tapirus veroensis</i>				x
† <i>Mylohyus</i> sp.				x
<i>Odocoileus virginianus</i>	x	x		
† <i>Equus</i> sp.				x
Totals	10	14	6	8

The sea completely inundated the Williston area during the Yarmouth interglacial stage which preceded the Illinoian (Cooke, 1945). Animals of mesophytic habitat are present in both the poikilothermous and homiothermous elements of the Williston fossil fauna (Table 8, Holman, 1959). This implies that the sea had receded long enough and far enough for the vegetation to develop to a mesophytic state.

Table 9 shows the minimum number of individual birds and mammals in the Williston Pleistocene material. The minimum number is determined by counting the most numerous right or left element of each species or form. As at least 71 rabbits were present and only 41 other individual birds and mammals, one might speculate that the rabbits represent the refuse of a carnivore that had its den in the sink.

TABLE 9

MINIMUM NUMBER OF INDIVIDUALS OF WILLISTON PLEISTOCENE BIRDS
AND MAMMALS († EXTINCT FORMS)

<i>Anas discors</i>	1	<i>Peromyscus gossypinus</i>	4
† <i>Colinus sulium</i>	3	<i>Oryzomys palustris</i>	1
<i>Meleagris gallopavo</i>	1	<i>Sigmodon hispidus</i>	2
<i>Corvus brachyrhynchos</i>	1	<i>Neotoma floridana</i>	1
† <i>Henocitta brodkorbi</i>	1	† <i>Pitymys hibbardi</i>	3
Fringillidae sp.	2	<i>Sylvilagus</i> sp. indet.	48
<i>Scalopus aquaticus</i>	2	<i>Sylvilagus palustris</i>	4
<i>Cryptotis parva</i>	3	<i>Sylvilagus floridanus</i>	19
<i>Blarina brevicauda</i>	1	† <i>Dasyppus bellus</i>	1
<i>Ursus</i> sp.	2	† <i>Tapirus veroensis</i>	1
†Skunk or Mustelid	2	† <i>Mylohyus</i> sp.	2
<i>Lynx rufus</i>	1	<i>Odocoileus virginianus</i>	1
<i>Sciurus carolinensis</i>	1	† <i>Equus</i> sp.	1
<i>Geomys pinetis</i>	3		

ZOOGEOGRAPHY.—The extant species in the above Pleistocene fauna still occur in the same area. The eight extinct species have the following affinities today: *Colinus sulium* Nearctic, *Henocitta brodkorbi* Neotropical, *Pitymys hibbardi* Nearctic, *Dasyppus bellus* Neotropical, *Tapirus veroensis* Neotropical, *Mylohyus* sp. Neotropical, *Equus* sp. Nearctic, Mustelidae sp. Nearctic.

CLIMATIC IMPLICATIONS.—Brodkorb (1957 and 1959) has postulated that Florida fossil animals from the Arredondo clay, which lies beneath the Wicomico formation, lived in a climate similar to that of North Carolina or Virginia today. A trend toward large size is reflected by 23 percent of the species in the Williston fossil fauna. This could be interpreted as supporting Brodkorb's thesis, or at least a thesis that the climate was cooler in Florida during the Illinoian glacial stage. Six animals are larger than their present-day local representatives, five of which have larger Recent representatives to the North.

The affinities of the large fossil quail, *Colinus sulium*, are discussed by Brodkorb (1959). Dr. Robert Weigel of Howard University informs me that the quail from the late Pleistocene locality at Vero Beach, Florida, is the smaller *Colinus virginianus* that inhabits Florida today. Thus *C. sulium* may prove to be a valuable Illinoian indicator.

The extinct skunk is larger than Recent Florida skunks.

Pitymys hibbardi is 20 percent larger than the Recent Florida *Pitymys parvulus*.

The fossil forms of both species of rabbits, *Sylvilagus palustris* and *S. floridanus* are larger than the races of these species in north-central Florida today, and in fact are larger than specimens from North Carolina.

The armadillo, *Dasypus bellus* is much larger than the present *D. novemcinctus* which has been successfully introduced into Florida in Recent times.

Thus these animals may reflect Bergmann's rule (Allee et al., 1949, Mayr, 1949).

CORRELATION.—Simpson (1929b) recognized four mammalian faunas of the Florida Pleistocene as being of value in correlation studies, and designated them as test faunas. These faunas were from Vero, Melbourne, Seminole Field, and Saber-tooth Cave. Bader (1957) proposed adding the Reddick and Arredondo localities to the list.

Cooke (1945) assigned his four test localities to the Wisconsin stage of the Pleistocene; Brodkorb (1957 and 1959) assigned Arredondo and Reddick to the Illinoian stage to which the Williston site supposedly belongs.

The percentage of extinct mammals is actually greater in the Wisconsin than in the Illinoian localities (Table 10). This might be

TABLE 10

EXTINCTION PERCENTAGES OF MAMMALS FROM FLORIDA PLEISTOCENE LOCALITIES

Stage	Locality	Number of Mammals species identified	Percentage extinct	Percentage living
Wisconsin	Seminole Field	49	66	24
Wisconsin	Saber-tooth Cave	24	58	42
Wisconsin	Melbourne	56	53	47
Illinoian	Arredondo	23	39	61
Illinoian	Reddick	48	39	61
Illinoian	Williston	20	30	70

construed to cast doubt on the Illinoian designation of Arredondo, Reddick, and Williston. However, correlating Pleistocene localities on the basis of percentages of extinct mammals must take the relative sizes of the mammals into consideration. Many large mammals became extinct at the close of the Pleistocene epoch, and the survival of the smaller forms into Recent times is much higher.

The comparatively low (30 percent) extinction percentage of its mammal fauna suggests the Williston site to be of later age than the Seminole Field site where 66 percent are extinct. If the mammals of the two sites are arbitrarily grouped into forms the size of a rabbit or smaller and forms larger than a rabbit, the faunas are quite similar (Table 11). This supports Bader (1957) who feels that small animal remains will be much better indicators for correlating the Florida Pleistocene.

TABLE 11

EXTINCTION OF MAMMALS ACCORDING TO SIZE CLASSES AT SEMINOLE FIELD AND WILLISTON, FLORIDA

Mammals the size of a rabbit or smaller	Percentage		Mammals larger than a rabbit	Percentage	
	No.	Extinct		No.	Extinct
Williston	12	8	Williston	8	66
Seminole Field	11	9	Seminole Field	38	79

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