## J. Alan Feduccia

To increase our understanding of Pliocene local faunas of North America, several recent studies of fossil birds have been made from material collected by Claude W. Hibbard and his field parties from the University of Michigan Museum of Paleontology. Ibises have been reported by Collins (1964), owls by Ford (1966) and Ford and Murray (1967), grebes by Murray (1967), a gallinule by Brodkorb (1967), crane and stork fossils by Feduccia (1967*a*), and a swallow by Feduccia (1967*b*). The fossil material has been recovered mainly from four localities: the Sawrock Canyon, Fox Canyon, and Rexroad local faunas from Kansas, and the Hagerman local fauna from Idaho. Birds reported previously from these localities include those studied by Wetmore (1944) and Tordoff (1951, 1959) from the Rexroad local fauna, and by Wetmore (1933) and Brodkorb (1958) from the Hagerman local fauna. The present study was undertaken to learn more about the rails from these local faunas.

Rallus phillipsi Wetmore from Mohave County, Arizona, and Fulica infelix Brodkorb from Malheur County, Oregon, are included in the systematic list to complete the North American Pliocene rail fauna.

During the course of this study, 46 Recent species representing 19 genera of rails were examined in the collections of the University of Michigan Museum of Zoology, the United States National Museum, and Pierce Brodkorb. The specimens examined included seven species of *Rallus* and five species of *Porzana*. The type humerus and some of the referred material of *Rallus prenticei* were loaned through the kindness of W. A. Clemens of the University of Kansas Museum of Natural History and sent to me by Pierce Brodkorb who had them on loan. Several skins were examined to gain some idea of size where skeletal material was not available.

The fossils examined are in the University of Michigan Museum of Paleontology (UMMP) and the University of Kansas Museum of Natural History (KU).

The classification of rails used is that of Peters' Check-list (1934).

#### LOCALITIES AND AGE OF FAUNAS

The fossil materials reported herein for the first time come from four localities: 1. The Saw Rock Canyon local fauna is known from the Rexroad formation, Seward County, Kansas, and is taken from a lower part of the section than are either the Rexroad or Fox Canyon local faunas. Evidence favors a late Hemphillian age for the fauna, and many of the mammals are considered to be directly ancestral to those of the Fox Canyon and Rexroad local faunas (Hibbard, 1964). The Saw Rock Canyon locality is given in Hibbard (1950).

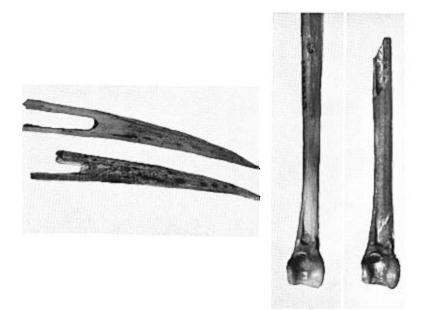


Figure 1. Left. Bill of largest available male of *Rallus limicola* (above). Fossil bill (UMMP V54981) from the Rexroad local fauna referred to *Rallus prenticei* (below). Actual length of fossil bill, 17.9 mm. Right. Anterior views of tibiotarsi of Recent *Rallus sanguinolentus* and Rexroad fossil (UMMP V54991) referred to *Rallus lacustris*. Actual length of fossil, 39.4 mm.

2. The Fox Canyon local fauna, taken from the Rexroad formation, Meade County, Kansas, was once considered to be equivalent in age to the Rexroad local fauna, but is now considered by Hibbard (1967) to represent a slightly older local fauna, which is distinct on the basis of the small mammals. A single bone is reported herein from the Fox Canyon locality UM-K1-47 (Hibbard, 1950).

3. The Rexroad local fauna is known from the upper part of the Rexroad formation, Meade County, Kansas. Although the fauna is generally placed in the late Pliocene, Hibbard's latest view is that it represents a slightly older local fauna than the Hagerman. The Rexroad localities used in this paper are given in Hibbard (1950) and Woodburne (1961).

4. The Hagerman local fauna has been recovered from the Glenns Ferry formation (Malde and Powers, 1962), Twin Falls and Owyhee counties, Idaho. The fauna has been variously assigned to both the early Pleistocene and the late Pliocene, but is currently considered to be late Pliocene in age (Hibbard *et al.*, 1965), and a potassium-argon date of 3.5 million years b. p. was obtained (Evernden *et al.*, 1964). If this date is accurate, the fauna is definitely in the late Pliocene, but because of the large number of collecting localities (close to 300) and the thickness of the beds (about 500 feet), it may be best to refer to the fauna in terms of the North American land mammal age, Blancan. Some of the main Hagerman localities are given in Hibbard (1959) and Uyeno (1961).

# PLIOCENE RAIL FAUNA Rallus prenticei Wetmore

A bill (Figure 1) recovered from the Rexroad local fauna supports the view that *Rallus prenticei* was closely allied to the living *Rallus limicola* Vieillot and possibly ancestral to it. The fossil bill differs little from that of *R. limicola*, except in being slightly larger. Wetmore (1944) described *R. prenticei* as being slightly larger and stockier than the living *R. limicola*; this is confirmed by the additional specimens reported herein. Specimens recovered from the Hagerman local fauna apparently also represent this species. That most of the Hagerman fossils are tibiotarsi and coracoids presents a problem, as these two elements from some specimens of *R. limicola* are indistinguishable from those of certain specimens of *Porzana carolina* (Linnaeus) either by size or osteological characters. Although it is impossible to make a positive assignment for all the fossil elements, many are definitely assignable to *R. prenticei*; no specimen could be assigned with certainty to *Porzana*.

In the present collection are coracoids from both the Rexroad and Hagerman local faunas that are assignable to R. *prenticei* on the basis of their close similarity to Recent R. *limicola*. The coracoid (KU 3867) that Wetmore (1944) assigned to R. *prenticei* apparently represents *Rallus lacustris* (Brodkorb), being very close in size to Recent *Rallus sanguino*-

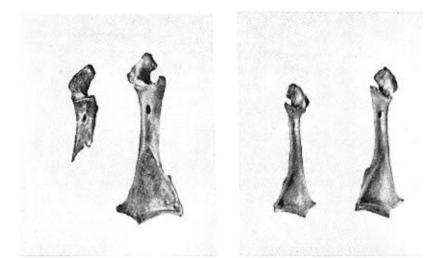


Figure 2. Left. Fossil coracoid fragment (actual length, 13.1 mm) from Hagerman local fauna assigned to *Porzana lacustris* by Brodkorb (1958), and coracoid of Recent *Rallus sanguinolentus*. Right. Coracoids of Recent female (smaller) and male *Rallus limicola*.

		Rallus limicola			Rallus prenticei <sup>1</sup>				
	n	Min.	Mean	Max.	n	Min.	Mean	Max.	
Tibiotarsus	10				10				
Width through									
condyles		3.8	4.2	4.6		4.5	4.8	5.1	
Depth of internal									
condyle		4.0	4.4	4.9		4.8	5.1	5.5	
Humerus	10				4				
Greatest proximal									
width		6.1	6.8	7.4		7.1	7.6	8.0	
Greatest distal width		4.5	4.7	5.1		5.1	5.3	5.4	
Least width of shaft		1.9	2.0	2.1		2.1	2.4	2.6	
Total length		33.6	35.6	39.2		36.1	39.1	41.0	

TABLE 1
MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI AND HUMERI OF RALLUS LIMICOLA AND RALLUS PRENTICEI

<sup>1</sup> Measurements of the type humerus are those in the minimum column. It probably represents a female, the total range of measurements of R. *prenticei* being approximately equivalent to those of R. *limicola*.

*lentus* (see following species account and Figure 2), and to the coracoid that Broadkorb (1958) assigned to *R. lacustris*.

Measurements of humeri and tibiotarsi are given in Table 1; coracoids were unmeasurable.

*Material.*—Hagerman local fauna: coracoid UMMP V55326; tibiotarsus UMMP V48573, V52299, V52413, V52603, V54957, V55327, V55332, V55337; humerus UMMP V48931. Rexroad local fauna: coracoid UMMP V45917; tibiotarsus KU 3870, 3872; humerus KU 3865 (type), 3866, 3872; bill UMMP V54981; tarsometatarsus KU 3869. All KU specimens were reported by Wetmore (1944).

#### Rallus lacustris (Brodkorb)

With additional material recovered from the Hagerman local fauna, the rail originally described as *Porzana lacustris* Brodkorb (1958) is now placed in the genus *Rallus*. The material now at hand indicates that *R. lacustris* was very close in both size and osteology to the Recent South American *Rallus sanguinolentus* Swainson (= *Ortygonax rytirhynchos* (Vieillot) of Peters). The distal end of a complete humerus (UMMP V48930, Hagerman USGS Cenozoic locality 19216) is almost identical with the type humerus, which is only a distal end. *R. lacustris* is almost identical with the Recent *R. sanguinolentus*, but the humerus differs in having the shaft decidedly more robust, distal width smaller, and entepicondylar area less produced.

The referred tibiotarsi differ from those of R. sanguinolentus in having a slightly more robust shaft, and in having the external condyle meeting the shaft at a greater angle. Figure 3 shows the similarity of the tibiotarsi of R. lacustris and R. sanguinolentus. The referred tarsometatarsi are inseparable from those of R. sanguinolentus. width

Total length

Greatest distal width

Least width of shaft

	Rallus sanguinolentus					Rallus lacustris				
	n	Min.	Mean	Max.	n	Min.	M ean	Max.		
Tibiotarsus										
Width through										
condyles	7	5.3	5.9	6.5	4	5.6	5.8	6.0		
Depth of internal										
condyle	7	5.5	6.1	6.7	4	5.7	5.9	6.1		
Least width of shaft	7	2.6	2.9	3.2	3	2.7	2.8	3.0		
Humerus										
Greatest proximal										

9.2

6.6

2.7

45.7

10.1

7.2

3.0

48.5

2

6

5

1

83

5.6

2.6

MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI AND HUMERI OF RALLUS SANGUINOLENTUS AND RALLUS LACUSTRIS

The coracoids of R. sanguinolentus, and of most living rails, are too variable to permit definite assignment of the fossil elements, except perhaps on the basis of size (see Figure 2). On that basis, the coracoid (KU 3867, Rexroad locality 2) that Wetmore (1944) assigned to R. prenticei is now tentatively referred to R. lacustris. Wetmore (1944) assigned another coracoid (KU 3868, Rexroad locality 3) to R. prenticei, but I have not examined the specimen.

7

7

7

7

8.7

6.2

24

43.4

R. lacustris was very close to the Recent R. sanguinolentus in size and osteological characters, and quite possibly a close ally.

Referred Material.-Hagerman local fauna: coracoid UMMP V33916 (assigned by Brodkorb, 1958), V48878, V48879, V52289, V52437, V52446, V55084; tibiotarsus UMMP V52435; tarsometatarsus UMMP V45228, V48892, V49585, V52247, V52274, V52275; humerus UMMP V33915 (type), V45282, V48930, V49537, V49594, V52301. Rexroad local fauna: coracoid KU 3867 (reported by Wetmore, 1944, as R. prenticei) UMMP V54985; tibiotarsus UMMP V54978, V54990, V54991; tarsometatarsus UMMP V54987, V54988; humerus UMMP V45937.

## Rallus phillipsi Wetmore

R. phillipsi was described on the basis of a tarsometatarsus taken from the Upper Pliocene of Mohave County, Arizona. Wetmore (1957) diagnosed R. phillipsi as follows: "In some of its characters Rallus phillipsi approaches the genus Porzana, as represented by the living Porzana carolina (Linnaeus), suggesting a closer affiliation of this genus with Rallus through the species that lived during the latter part of the Tertiary. The bird here described, however, may be placed in *Rallus* since it agrees with Rallus longirostris and Rallus limicola and differs from Porzana in the definitely greater posterior projection of the second trochlea and the greater and more open gap between the distal end of this segment and the base of the third trochlea."

8.9

6.5

3.0

5.9

2.8

43.4

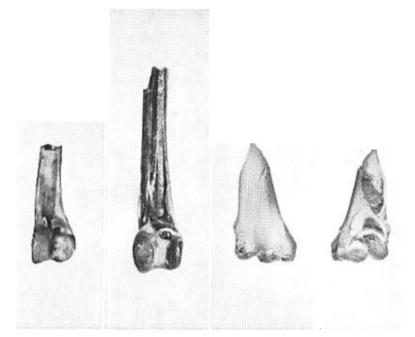


Figure 3. Left. Holotype tibiotarsus of *Coturnicops avita*, actual length, 8.3 mm. Second from left. Holotype tibiotarsus of Laterallus insignis, actual length, 13.9 mm. Right. Anconal and palmar views of holotype humerus (KU 3994) of Gallinula kansarum Brodkorb, actual length, 16.8 mm.

#### Rallus elegans-longirostris group

Three distal ends of tibiotarsi from the Hagerman local fauna (UMMP V49618, V51420, V54963) seem to represent a rail close in size and osteology to the living R. *elegans-longirostris* group. As the separation of the tibiotarsi of the two living forms is very difficult, and perhaps impossible in some cases owing to the overall similarity of characters and overlap in size, the true affinities of this rail can not be determined. The possibility also exists that all three bones may not be from the same species, but at least two definitely belong in the *elegans-longirostris* group.

#### Rallus sp.

The distal fragment of an ulna (UMMP V55013) and a proximal fragment (UMMP V55014) of the same element, both from the Saw Rock Canyon local fauna, seem to represent a form of *Rallus* slightly smaller than the living *Rallus longirostris*, and differ from it in several important characters. The two ulnae undoubtedly represent a new species, but the material is too fragmentary to be given a name.

TABLE 3	
MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI OF RECENT	
AND FOSSIL COTURNICOPS	

		Width through condyles			Depth of internal condyle		
	n	Min.	Mean	Max.	Min.	Mean	Max.
Coturnicops noveboracensis Coturnicops avita (holotype)	5 1	3.2	3.4 2.9	3.5	3.3	3.4 3.0	3.6

# Coturnicops avita, new species (Figure 3)

Holotype.—Distal 8.3 mm of right tibiotarsus (UMMP V52530), collected by Claude W. Hibbard in the summer of 1965.

Horizon and locality.—Upper Pliocene, Glenns Ferry formation. Hagerman local fauna, locality UM-IDA2-65, Hagerman quadrangle, NW <sup>1</sup>/<sub>4</sub>, sec. 5, T. 8 S., R. 13 E., Twin Falls County, Idaho, elevation 3,280–3,310 feet.

*Diagnosis.*—The holotype tibiotarsus is generally similar to that of Recent *Coturnicops noveboracensis* (Gmelin), but differs in the following characters: smaller and less robust, less excavation in tendinal groove, and both internal and external condyles relatively smaller. Table 3 gives the measurements of the holotype tibiotarsus and of that of *C. noveboracensis*.

Discussion.—The tibiotarsus of C. noveboracensis is separable from the forms of Laterallus that I examined by the following characters: internal ligamental prominence larger and protrudes farther laterally, angle at which shaft meets internal condyle greater, and shaft tapers more rapidly from condyles.

Coturnicops avita is of interest in that it is probably the Pliocene ancestor of Recent C. noveboracensis as indicated by its closeness to the Recent form in size and osteology.

*Etymology.*—From Latin, *avita*, ancestral, in reference to its probable ancestry to *C. noveboracensis*.

# Laterallus insignis, new species

(Figure 3)

Holotype.—Distal 13.9 mm of right tibiotarsus (UMMP V45423), collected by Claude W. Hibbard and field party in the summer of 1962.

Horizon and locality.—Upper Pliocene, Rexroad formation. Rexroad local fauna, locality UM-K3-53, Wendell Fox Pasture, south side of Shorts Creek, SW ¼, SW ¼, sec. 33, T. 33 S., R. 29 W., Meade County, Kansas.

Diagnosis.-Of the species of Laterallus examined, the fossil is closest

		Width through condyles		Depth of internal condyle			Least width of shaft			
_	n	Min. I	M ean	Max.	Min.	Mear	ı Max.	Min.	Mean	Max
Laterallus insignis <sup>1</sup>	2	3.5		3.5	3.3		3.5?	1.7		
Laterallus jamaicensis	3	2.8	2.9	3.0	2.8	2.9	3.2	1.3	1.4	1.5
Laterallus viridis	1		3.9			3.8			2.0	
Laterallus albigularis	2	3.7		3.9	3.6		3.6	1.6		1.9
Laterallus leucopyrrhus	4	3.7	3.8	3.9	3.5	3.6	3.8	1.5	1.6	1.7

TABLE 4
MEASUREMENTS (IN MILLIMETERS) OF TIBIOTARSI OF LATERALLUS

<sup>1</sup> The first measurement in each column is that of the holotype.

to *L. leucopyrrhus*, but the tibiotarsus differs in the following characters: area of tendinal groove more depressed, internal and external condyles relatively smaller, and intercondylar distance relatively less. Measurements of the holotype tibiotarsus and those of other species of *Laterallus* are given in Table 4.

Discussion.—Unlike Laterallus guti Brodkorb (1952), from the Pleistocene of Florida, Laterallus insignis does not appear to be closely related to Recent Laterallus jamaicensis (Gmelin), being larger and differing in important characters. Indeed, the Rexroad species appears to be more closely allied to the larger Neotropical Laterallus rails, and is described above in relation to L. leucopyrrhus, a form it closely resembles.

Referred material.—Distal 12.9 mm of left tibiotarsus, UMMP V54973, from the same locality as the holotype. The condyles are slightly cracked. *Etymology*.—From Latin, *insignis*, remarkable.

#### Gallinula kansarum Brodkorb

Since the description of *Gallinula kansarum* Brodkorb (1967), additional elements of this species have been sorted from the Rexroad collections. These include four fragments of humeri, UMMP V29160, V45431, V54972, V54984, and V54966, four coracoids, UMMP V54989, V54968, V45407, and V45408, a carpometacarpus, UMMP V54993, and a tibiotarsus, UMMP V54965. These elements are assigned to *Gallinula kansarum* on the basis of their similarity to the Recent *Gallinula chloropus* (Linnaeus) and their being from the Rexroad local fauna. The type humerus of *G. kansarum* is shown in Figure 1.

### Gallinula sp.

A distal piece of humerus, UMMP V55330, and a tibiotarsus, UMMP V52604, both from the Hagerman local fauna appear to be from a gallinule almost inseparable from certain specimens of the Recent *G. chloropus*. The tremendous amount on intra- and interspecific variation among coots and gallinules makes it impossible to assign these bones.

#### Fulica infelix Brodkorb

This coot was described on the basis of a left tibiotarsus taken from the Lower Pliocene of Juntura, Oregon. *Fulica infelix* was a small coot similar to the living F. americana Gmelin and the Pleistocene F. shufeldti Brodkorb (Brodkorb, 1961).

#### INDETERMINABLE MATERIAL

A bill fragment (UMMP V55012) indicates the presence of a short-billed, *Porzana*like rail in the Saw Rock Canyon local fauna. The bill represents a bird larger than the living *Porzana carolina* and in size approximates the South American rail, *Porphyriops melanops*. A fragmentary coracoid (UMMP V45750) and an ulna (UMMP V45746) may represent the same species, but its relationships to other rails can not be determined.

A single fragment of a humerus (UMMP V29080) from the Fox Canyon local fauna, locality UM-KI-47, differs in many characters from the humeri of all the living rails that I examined and probably represents a new genus, but until more material becomes available, naming it seems inadvisable.

The collection contains many other rail elements that could not be assigned to any of the forms covered here. A number of ulnae, femora, sterna, and carpometacarpi proved unassignable and are not listed in this paper.

#### PALEOECOLOGY OF THE REXROAD AND HAGERMAN LOCALITIES

Hibbard (1960) summarized his views on Pliocene and Pleistocene climates of North America based mainly on fossil crocodilians and giant land tortoises. He suggested that the presence of the giant land tortoise, Geochelone rexroadensis Oelrich (1952), with no evidence that caves or fissures existed for retreat during the cold weather, indicated that a more equable climate existed in Kansas during the Upper Pliocene than at present. Other evidence for more equable conditions during the Late Pliocene of Kansas comes from studies of mollusks (Taylor, 1960), amphibians (Taylor, 1942), and mammals (Hibbard, 1950). Some of the avian fossils may also be indicative of a more equable Late Pliocene climate. The presence in the Rexroad local fauna of four species of ibises, two of possible tropical affinity (Collins, 1964), Agriocharis progenes Brodkorb (1964) possibly allied to the tropical turkey, Agriocharis ocellata (Gould), an unidentified parrot (Wetmore, 1944), and two rails, Rallus lacustris and Laterallus insignis of possible tropical affinity, along with evidence offered by other vertebrates lends support to Hibbard's (1960) view that in the Upper Pliocene, ". . . a subhumid climate with winter temperatures seldom lower than 32° F existed as far north as southwestern Kansas and probably into northern Nebraska." The total Rexroad local fauna indicates that marsh, pond, stream, upland grassland, meadow flats, and timber communities existed with more effective moisture than at present.

The Hagerman local fauna, although less well known than the Rexroad,

Pliocene	Pleistocene	Recent
Rallus prenticei	Rallus elegans <sup>1</sup>	Rallus elegans
Rallus lacustris	Rallus longirostris <sup>1</sup>	Rallus longirostris
Rallus phillipsi	Rallus limicola <sup>1</sup>	Rallus limicola
Rallus elegans-	Coturnicops noveboracensis <sup>1</sup>	C. noveboracensis
longirostris group	Porzana carolina <sup>1</sup>	Porzana carolina
Rallus sp.	Porzana auffenbergi	L. jamaicensis
Coturnicops avita	Laterallus guti	Gallinula chloropus
Laterallus insignis	Creccoides osbornii²	Porphyrula martinica
Gallinula kansarum	Aramides cajanea <sup>1</sup>	Fulica americana
Gallinula sp. (may not	Porpyrula martinica <sup>1</sup>	
be a faunal addition)	Gallinula chloropus <sup>1</sup>	
Fulica infelix	Gallinula brodkorbi	
Saw Rock Canyon Rail indet.	Fulica shufeldti	
Fox Canyon Rail indet.	Fulica hesterna	
	Fulica americana <sup>1</sup>	

TABLE 5

LIST OF PLIOCENE, PLEISTOCENE, AND RECENT RAIL FAUNAS OF NORTH AMERICA

<sup>1</sup> Neospecies

<sup>2</sup> Described from the Blanco formation (Texas), which was originally thought to be Pliocene.

does not show the large number of warm faunal elements present in the latter. The more northern location, plus the possibility of a younger age for the fauna may account for the difference. The large fish fauna, the presence of three or four species of cormorants, five species of rails (only three are known in Idaho today, Arvey, 1947), a stork and a crane, and many ducks, geese, and swans, all point to the presence of extensive low-land marsh with probably more moisture than today.

#### DISCUSSION

A minimum of 12 species of rails existed during the Pliocene of North America; seven are now named. One coot, *Fulica infelix*, is known from the Early Pliocene of Oregon, and two other rails, a probable member of the genus *Rallus*, and a *Porzana*-like rail are known from the Late Hemphillian Saw Rock Canyon local fauna of Kansas. The remainder are known from Late Pliocene or Early Blancan deposits of Kansas (*Rallus prenticei*, *R. lacustris*, *Laterallus insignis*, and *Gallinula kansarum*), Idaho (*Rallus prenticei*, *R. lacustris*, *R. elegans-longirostris* group, *Coturnicops avita*, and *Gallinula* sp.), and Arizona (*Rallus phillipsi*).

Table 5 summarizes the rail faunas of the Pliocene, Pleistocene, and Recent of North America. The Recent rail fauna of North America is smaller than those of either the Pliocene or Pleistocene, especially considering that all the rails of the Pliocene and Pleistocene are almost certainly not known. That no Recent species are recorded with certainty from the Pliocene seems to indicate that most of the Recent species evolved during the Pliocene or Early Pleistocene. The Pleistocene rail fauna is of interest for several reasons. The large number of species present indicates that the rail fauna has dwindled in fairly recent times, perhaps coincidentally with the great extinctions that occurred during the Pleistocene of North America, especially during the Wisconsin ice age when many mammalian genera became extinct. One rail, *Aramides cajanea*, became restricted to the present day tropics, while others apparently gave rise to new species or were unable to withstand the ensuing cold and died out.

Most of the modern rail fauna probably originated during the Pliocene and Early Pleistocene. While many of the Pliocene forms cannot be considered to be ancestral to modern forms, some, such as *Rallus prenticei* and *Coturnicops avita* do appear to be probable ancestors of modern species. All of the modern species are known from the Pleistocene, with the exception of *Laterallus jamaicensis*. So except for *Laterallus guti*, which could have been ancestral to Recent *Laterallus jamaicensis*, the remainder of the rails, *Porzana auffenbergi* Brodkorb, *Creccoides osbornii* Shufeldt, *Gallinula brodkorbi* McCoy, *Fulica shufeldti* Brodkorb, and *Fulica hesterna* Howard, all appear to have become extinct during the Pleistocene.

Brodkorb (1958) pointed out that the trend toward small size in the Hagerman avifauna as exemplified by *Pelecanus halieus*, *Cygnus hibbardi*, and *Chen pressa*, might be interpreted as a reflection of the warm climate of a preglacial or interglacial stage. One of the rails, *Coturnicops avita*, shows this trend, while *Rallus prenticei* is larger than its Recent counterpart, *Rallus limicola*, the species to which it is possibly ancestral. One of the grebes reported by Murray (1967), *Aechmophorus elasson* Murray, a possible ancestor of Recent *Aechmophorus occidentalis* (Lawrence) is smaller than its Recent counterpart, while *Podilymbus majusculus* Murray is larger than *Podilymbus podiceps* (Linnaeus), the form to which it is possibly ancestral. No trend can therefore be stated unequivocally.

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The University of Michigan Museum of Zoology, Ann Arbor, Michigan 48104.