

THE PLEISTOCENE RAILS OF NORTH AMERICA

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In reviewing the fossil Rallidae, I have had the opportunity to re-examine most of the specimens of extinct species and extralimital fossil records described from the Pleistocene of North America. For one reason or another, each taxon requires some change in status, resulting in a considerable alteration of previous ideas of the nature of this segment of the Pleistocene avifauna.

ARAMIDES CAJANEA

Wetmore (1931) assigned two fragments of tarsi and a femur from Pleistocene deposits excavated at Seminole Field, Pinellas County, Florida, to the Gray-necked Wood Rail, *Aramides cajanea*. This species is presently distributed from southern México to Argentina. In view of the Neotropical flavor of much of the Pleistocene fauna of Florida, it was not a wholly unexpected discovery but, unfortunately, the record is based on incorrectly identified material. On restudying the specimens involved (USNM 12192), I found that none pertains to *Aramides*. The femur is from a small individual (probably a male) of Red-shouldered Hawk, *Buteo lineatus*. The distal right tarsus and proximal right tarsus are from different individuals and are rallid; however, both are from the King Rail, *Rallus elegans*. Both *Buteo lineatus* and *Rallus elegans* were recorded by Wetmore from the Seminole Field site.

The tarsi of *Aramides* and *Rallus* are quite distinct in their entirety but in the fragmentary condition of the fossils are less easily separated. In the distal fragment, the distal foramen in posterior view is oval and placed higher than in *Aramides cajanea*, in which the distal foramen is round. The middle trochlea is not as heavy and expanded distally as in *A. cajanea*, but the scar for the hallux is deeper. In external view, the shaft extending to trochlea 4 is wide and heavy, unlike *A. cajanea* in which this shaft is narrow and flattened; also, the groove in trochlea 4 does not extend through most of the anterior face of the trochlea as it does in *Aramides*. In anterior view, the outer extensor groove is longer and deeper than in *Aramides*. In all these respects, the fossil agrees with *Rallus elegans*. In the proxi-

mal tarsal fragment, in anterior view the intercotylar prominence is lower and flatter than in *Aramides*; the hypotarsus is not as deeply excavated on the internal face and in internal view the ridge from the internal cotyla is broader and not as sharply marked off from the hypotarsal area as it is in *A. cajanea*. In these respects this specimen, too, agrees with *Rallus elegans*. *Aramides cajanea* must therefore be removed from the fossil record of North America.

FULICA HESTERNA

A fossil coot, *Fulica hesterna*, based on three extremely fragmentary ends of limb bones and five phalanges, was described from Middle Pleistocene deposits of Vallecito Creek Valley, Anza-Borrego Desert, San Diego County, California (Howard 1963). The type is a distal left tibiotarsus with much of the posterior surface and part of the internal condyle fractured off (fig. 1). This was said to be distinguished from *F. americana* by the "more vertical position of the supratendinal bridge, achieved by less posterior tilting of the proximal border, particularly at external side" (Howard 1963: 23). As can be seen in figure 1, the proximal border of the supratendinal bridge of *hesterna* is quite irregular when compared to a normal individual of *F. americana*, and the lateral and medial portions of this border extend farther proximally. The type of *hesterna* is from a large and probably old individual. The irregularities of the proximal border of the tendinal bridge appear to be due simply to an extraneous accretion of bone of a purely individual nature. Confirming this impression is the fact that the bridge of *hesterna*, when viewed on edge, is thicker than normal for *americana*. The "more vertical" position of the bridge is an appearance that is due to this buildup of bone along the proximal border and is further exaggerated by some slight wearing of the distal edge of the bridge. This sort of variation is not, in my opinion, of specific significance.

A distal right tibia (LACM 2875) referred to *F. hesterna* is too fragmentary to be of much diagnostic value and does not differ in any significant way from *F. americana*.

A worn fragment of a distal right tarsometatarsal

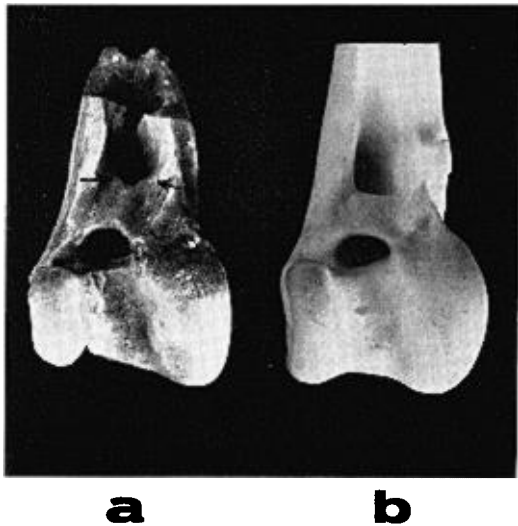


FIGURE 1. a. *Fulica hesterna*, holotype tibiotarsus (LACM 2873); arrows indicate extraneous accretions of bone on supratendinal bridge. b. *F. americana* (S. Olson coll. 754) for comparison. Figures 3× natural size.

tarsus was designated as a paratype of *F. hesterna* and was said to differ from *F. americana* mainly in having the internal trochlea extending more distally and set more laterally and less posteriorly on the shaft. The outer and middle trochleae of this specimen have been fractured off and repaired very slightly awry, thus affecting somewhat the lateromedial orientation of the trochleae. Nevertheless, the proximo-distal orientation remains as described and is unlike *Fulica*. The specimen does agree with the Common Gallinule, *Gallinula chloropus*, however, and indeed is nearly matched by specimens of that species in my possession. The very fragmentary nature of this tarsus makes definite assignment difficult, but it seems more likely to be from *Gallinula* than *Fulica*. There is no compelling reason to assume that it is from the same species as the type of *F. hesterna*.

Five pedal phalanges, said by Howard to be indistinguishable from *F. americana*, were assigned by that author to *hesterna* on the basis of "the association of the phalanges with the paratype tarsometatarsus." These appear to be more robust than in *Gallinula* and do seem to be closer to *Fulica*. However, the degree of association of these phalanges with the tarsus was not indicated, i.e., whether they were found *in situ*, articulated with the tarsus, or merely found close by it in the same area. Considering that one of these specimens (a proximal end of phalanx 1 digit IV) is from a left foot, three others (phalanx 1 digit II, phalanx 1 digit III, and phalanx 3 digit IV)

are from a right foot, and the remaining proximal phalanx is unlike any phalanx of either *Fulica* or *Gallinula*, it may be doubted whether some (or any) of the phalanges were from the same individual as the paratype right tarsometatarsus.

A number of other specimens that appeared "to be indistinguishable from corresponding elements of the existing *Fulica americana*" were also reported from the Vallecito Creek fauna (Howard 1963:22). I do not feel that the existence of a second species of *Fulica* in that fauna can be demonstrated on the basis of the equivocal fragments assigned to *hesterna*. I therefore consider *Fulica hesterna* as a synonym of *Fulica americana*.

LATERALLUS GUTI

Brodkorb (1952) described a new species of small rail, *Laterallus guti*, from Middle Pleistocene deposits at Reddick, Marion County, Florida. About the same size as the living Black Rail, *L. jamaicensis*, it was differentiated from that species by having a much more robust humerus and by several details of structure. Ligon (1965) later referred seven specimens from Middle Pleistocene deposits at Haile, Alachua County, Florida, to *L. guti*. Although he did not say so in the original reference, Brodkorb later (1954) considered *guti* as the Pleistocene representative of *L. jamaicensis*.

I examined the following specimens of *L. guti*: Reddick—PB 84 (the type), PB 85, PB 86, PB 1189, PB 1455, PB 9020, PB 9021; and Haile—UF 7137 A–G. All except the proximal tibia PB 1455 are complete or partial humeri. In addition to *L. jamaicensis*, Brodkorb (1952) also compared *guti* with the Ruddy Crake, *L. ruber*, the Russet-crowned Crake, *L. viridis*, and the Red-and-white Crake, *L. leucopyrrhus*; it agreed with none of these. I compared the humerus of *guti* with that of *L. albigularis*, the White-throated Crake, and found that the latter differs from that of *guti* in its larger size, more slender, curved shaft, reduced ectepicondylar process, and shallower brachial depression. A humerus taken from a skin of *Micropygia schomburgkii*, the Ocellated Crake (USNM 44820) was smaller and had a much more curved shaft than that of *guti*.

L. guti had not been compared previously with the Gray-breasted Crake, *Laterallus exilis*, because no reference material of that species was available. Thus, I removed the humeri (lacking the proximal ends) from an unsexed study skin of *exilis* (USNM 348944) and the left humerus from an alcoholic specimen (USNM 511205). There is considerable variation in the robustness of the



FIGURE 2. Distribution of *Laterallus exilis*. Shaded area is the principal range; dots indicate scattered records; circled star shows fossil occurrence ("guti").

humerus in *L. exilis* as the humeri from the skin are notably heavier than the humerus from the alcoholic specimen. The same holds true for *guti*, the type humerus being fairly slender and most of the referred specimens much heavier. In size and proportions, the humeri of *exilis* are identical to *guti*. Indeed, the humeri from the skin are inseparable from specimens of *guti*. The more delicate humerus from the alcoholic specimen of *exilis* differs from *guti* in having the head less bulbous and the capital groove narrower, but I am inclined to regard this as individual variation, as otherwise there is as great a difference between the two specimens of *exilis* as there is between *exilis* and *guti*. In my opinion, *guti* should become a synonym of *exilis*. This, of course,

would remove any possibility of *guti* being ancestral to *jamaicensis*, a conclusion that is supported by the rather great differences in the humeri of these two species. As the referred specimens of *guti* are even more robust than the type, the differences between *guti* and *jamaicensis* are even more exaggerated than indicated in the illustration accompanying the original description of *guti*.

Today, the principal range of *L. exilis* (fig. 2) is in Brazil, the Guianas, Venezuela, and Trinidad, with scattered records from eastern Peru, western Ecuador, and Colombia (Meyer de Schauensee 1966). Its distribution in Central America is spotty (fig. 2) as it is apparently known only from a single specimen each from Nicaragua (Richmond



FIGURE 3. Tarsi of large *Rallus*. a and b. *R. longirostris* (S. Olson coll. 1054 and 726), males from the same locality to demonstrate the great variation in size and proportions. c. Largest available specimen of *R. elegans* (USNM 11116). d. Holotype of "*Epirallus*" *natator*. e. Same, posterior view, narrowness of trochleae due to wear. f. *R. longirostris* (S. Olson 726) enlarged to the same size as *natator* to show similarity in proportions. All figures, except f, natural size.

1893), Honduras (Monroe 1968), and British Honduras (Russell 1966), and two specimens from Panamá (Wetmore 1965). Even though additional birds will no doubt be found in Central America, it is obvious that *exilis* is far less common there than in South America. This pattern of distribution might be expected in a species retreating from a formerly greater range.

Brodkorb (1967) listed *L. guti* under the genus *Porzana*, following a policy he set elsewhere (1957a) of placing all the North American crakes in one genus. I do not agree with this treatment and prefer to maintain *Lateralus*, *Coturnicops*, and *Porzana* as separate genera (Olson 1973).

EPIRALLUS NATATOR

From Pleistocene deposits in San Josecito Cavern, Aramberri Province, Nuevo Leon, México, Miller (1942) described a new genus and species of rail, *Epirallus natator*, from a single well-preserved right tarsometatarsus. This taxon was diagnosed as being "approximately the size of *Rallus obsoletus*, but more slender, longer, and with more compressed foot" (Miller 1942:43). Brodkorb (1967), without comment, listed *Epirallus* under the "Gallinulinae" (note that in that publication,

lines 8 and 17 on page 126 were accidentally transposed, thereby giving an erroneous locality for *Epirallus*). However, on examination of the type of *E. natator*, the *Rallus* affinities of the specimen were immediately apparent.

The outstanding features of *natator* are its large size and its slenderness. It is longer (68.0 mm) than the longest tarsus (62.8 mm) in a series of 33 specimens of *Rallus elegans* and *R. longirostris*, Clapper Rail, measured in this study. In this series there is a considerable amount of individual variation in the proportions of the tarsi—some are stouter, with wide shafts, heads, and trochleae, and others, of about the same size, are markedly more slender in all aspects (fig. 3a,b). Thus it is possible to find individuals of *longirostris* which, although smaller in size, duplicate the proportions of *natator* (fig. 3f).

The type of *natator*, although in an excellent state of preservation, appearing almost fresh and unmineralized, has sustained a certain amount of abrasion, particularly in the region of the trochleae. The rims of the middle and outer trochleae have been worn almost entirely away, accounting for the narrowness of the trochleae cited by Miller (1942) as one of the distinguishing characters of *natator*.

Apart from these effects of wear and the large size, the characters of *Epirallus* given by Miller do not hold up when the type is compared with an adequate series of *Rallus elegans* and *R. longirostris*. The genus *Epirallus* cannot be maintained and it becomes a synonym of *Rallus*.

Rallus natator appears to be a large Pleistocene member of the *Rallus elegans-longirostris* complex of large rails. It may possibly have been a temporal representative of that group or might represent a distinct population of large individuals of restricted distribution. Miller (1943) suggested that it may have been a migrant. Lacking specimens intermediate in size between *natator* and the maximum of *elegans-longirostris*, it seems advisable for the present to retain *natator* as a distinct species related to that complex.

PORZANA AUFFENBERGI

A complete left humerus (PB 742) from Middle Pleistocene deposits at Haile, Alachua County, Florida, was designated by Brodkorb (1954) as the type of *Porzana auffenbergi*, a species said to be similar in proportions to the Sora (*Porzana carolina*), although larger in size. Because fossils of *P. carolina* were found in the same deposits, *auffenbergi* was thought to represent an extinct phyletic line.

On re-examining the type I was impressed by its size, but after close scrutiny, I believe that it is probably referable to the genus *Rallus* rather than to *Porzana*. The humeri of *Porzana carolina* and *Rallus limicola* are quite similar and are separated only with difficulty. In the type of *auffenbergi*, the internal condyle in anconal view is distinctly larger, more bulbous and rounded, and more sharply set off from the olecranal fossa than in *Porzana*, and thus agrees more closely with *Rallus*. In palmar view it is also larger and more rounded, also agreeing with *Rallus* as the internal condyle in *Porzana* is lower and more flattened on the proximal edge. In internal view the internal tuberosity is squared in *auffenbergi* and *Rallus* and more rounded in *Porzana*. The entepicondylar prominence is more pointed in *Porzana* and the relative width of the bone at that point is less than in *auffenbergi* or *Rallus*. In *auffenbergi* the bicapital crest forms a distinct lobe where it joins the shaft and is rounded like that of *Rallus*. In *Porzana* the bicapital crest angles more directly into the shaft.

The type of *auffenbergi* essentially resembles the Virginia Rail, *Rallus limicola*, except that it is larger [39.0 mm as opposed to 38.2 mm for the largest *limicola* available to me; however, note that Feduccia (1968:444) gives a maximum of 39.2 mm for the humerus length

of *limicola*]. It is also stouter (width of shaft at narrowest point 2.47 mm as opposed to 2.24 mm in the largest available *limicola*) and has a longer deltoid crest. The size and especially the robustness of the shaft of the humerus in living *R. limicola* are extremely variable.

P. auffenbergi was also listed from Pleistocene deposits at Reddick, Marion County, Florida (Brodkorb 1957b). This record was based on a distal humerus, PB 915, which is smaller than the type and is little, if any, larger than the maximum of *R. limicola* with which it agrees. A specimen of left tibiotarsus (PB 1717) from the Pleistocene of Arredondo, Alachua County, Florida, was referred to *P. auffenbergi* because it was larger than *P. carolina* and had a stouter shaft than *R. limicola* (Brodkorb 1959). This specimen cannot be distinguished from stouter-shafted individuals of *R. limicola* now available. It differs from *Porzana* and agrees with *Rallus* in having the condyles more expanded and the intercondylar fossa wider.

Ligon (1965) assigned six elements from another locality at Haile (Pit XI B; the type came from Pit I, Brodkorb, pers. comm.) to *P. auffenbergi*. I examined all of these except the distal tarsus UF 7144 B, illustrated by Ligon (1965:142, fig. 3b), which seems to have been misplaced. The distal tarsus UF 7144 A is almost identical in size to the maximum available of *limicola* (USNM 431395) and agrees perfectly with it in having the outer trochlea bent inward, closely approaching the middle trochlea, unlike *Porzana*. The middle trochlea is heavier and more expanded distally and the inner trochlea flares out farther medially than in *Porzana*, thus agreeing with *Rallus*. According to Ligon (p. 143), the position of the distal foramen in *auffenbergi* is closer to the outer intertrochlear notch than in *Porzana carolina*. Note that on the opposite page (p. 142) he also gives this as a distinguishing character of *Rallus*. This is not a good consistent character, however, as the position of this foramen is quite variable in *R. limicola*. The other two distal tarsi (UF 7144 C and D) are too fragmentary to be of much value but seem to agree with *Rallus*. UF 7144 D is within the size range of modern *limicola*; C, like A, is near maximum or slightly larger than *limicola*. The two proximal ulnae that Ligon ascribed to *auffenbergi* agree with *Rallus* in having the internal cotyla larger and less rounded than in *Porzana*. One of these is of normal size for *R. limicola* and the other is slightly larger and heavier than any available *limicola*.

TABLE 1. Measurements of recent and fossil *Gallinula*.

	<i>Gallinula chloropus</i> ^a (in mm)			Itchtucknee River <i>Gallinula</i> (in mm)
	Min.	Mean	Max.	
Humerus length	53.3	56.5	59.4	56.9, 57.4, 57.5, 57.9, 58.4, 58.5, 59.2, 59.3 ^b , 59.6
Ulna length	43.2	46.2	49.0	43.0, 44.0, 45.8 ^b , 47.5, 49.2
Carpometacarpus length	32.4	34.7	36.8	32.5, 34.2, 34.9 ^b , 36.6
Femur length	53.3	55.3	57.4	51.7, 52.3, 53.0, 54.5, 54.9, 57.3, 57.5, 57.8
Width distal tibia	7.4	7.8	8.4	9.2
Tarsus length	54.7	57.9	61.1	59.6, 59.9, 60.6, 61.7, 63.4, 64.5

^a Fifteen males from Florida, Virginia, Maryland, California, and Haiti. (This table is biased by using only male *chloropus*, as this is the larger sex.)

^b Type and paratypes of *brodkorbi*; it can be seen that these fall within the range of modern *chloropus*.

The species *auffenbergi* is known from three or four specimens that differ from *R. limicola* mainly in their greater size, and a few other fragments that are either near maximum for modern *limicola* or well within the range of that form. In all localities where *auffenbergi* was recorded, specimens assigned to *limicola* were also found (Brodkorb 1957b, 1959; Ligon 1965). I suggest that during the Pleistocene the species *Rallus limicola* averaged larger than at present and that *auffenbergi* represents a larger temporal form of *Rallus limicola*. In this light, it is interesting to note a specimen of *Rallus limicola* from the Pleistocene of Fossil Lake, Oregon, that was described as "a larger than average bird of that species" (Howard 1946:182), and a sternum from the Middle Pleistocene of California that was referred to *Rallus limicola* with a query on account of its slightly larger size (Howard 1963). Feduccia (1968) considered the Pliocene species *Rallus prenticei* as the possible ancestor of *R. limicola*. It too was larger than the modern form (average humerus length 39.1 mm which is essentially the same size as the type of *auffenbergi*).

GALLINULA BRODKORBI

McCoy (1963) described a new gallinule, *Gallinula brodkorbi*, from deposits of Pleistocene age in the Itchtucknee River, Columbia County, Florida. *G. chloropus* was also recorded from the same deposits. *G. brodkorbi*, based on a complete humerus (the type), two fragmentary humeri, an ulna, and a carpometacarpus, was distinguished mainly on the basis of larger size. The referred material, however, falls well within the size range of living *chloropus* (see table 1) and the type humerus is very slightly less than the maximum of available *chloropus*. The minor qualitative differences ascribed to *brodkorbi* by McCoy were either not apparent to me or could be attributed to individual variation. Within specimens of recent *chloropus*, there is a great

deal of variation in size and relative robustness of the limb elements. In view of this, I was at first prepared to dismiss *brodkorbi* as a synonym of *chloropus*.

Later, I was able to examine, in the collections of the Florida State Museum, some additional, more extensive series of fossils from the Itchtucknee, containing numerous remains of gallinules. In this series are specimens of *Gallinula* much larger and stouter than recent specimens. Of measurable *Gallinula* fossils from the Itchtucknee, 66% are larger than average for male *chloropus* and 23% are larger than the maximum for the species (table 1). Some of the smaller specimens are indistinguishable from *chloropus* while others are heavier, even though within the size range of the modern form.

What is apparent here is that we are dealing with a temporal representative of *G. chloropus* that was larger and heavier than the modern form. The relatively large size of the type of *brodkorbi*, even though it just falls within the size range of modern *chloropus*, could perhaps justify the retention of the name *brodkorbi* if nomenclatural recognition of temporal forms differing only in size is desired.

Pleistocene precursors of modern species are often characterized by larger size, as, for instance, was documented by Howard (1947) for the Golden Eagle, *Aquila chrysaetos*. Some Pleistocene specimens of the Pied-billed Grebe, *Podilymbus podiceps*, average larger than modern specimens and have at times been recognized as a temporal subspecies under the name *magnus*; the same applies to the Western Grebe, *Aechmophorus occidentalis*, with its temporal subspecies *lucasi* (Brodkorb 1963: 229-230). The quail *Colinus swillium* has been considered the Pleistocene representative of the Bobwhite, *C. virginianus*, and was notably larger than that species (Holman 1961). The Pleistocene form of the California Condor, *Gymnogyps californianus*, which has been designated as *G. amplus*, averaged larger than

its recent counterpart (Fisher 1947). *Gallinula brodkorbi-chloropus*, *Rallus auffenbergi-limicola*, and possibly *Rallus natator-elegans* appear to follow a similar trend. Fisher (1947) suggested, but did not support, the idea that the subsequent decrease in size of *Gymnogyps* might be illustrative of Bergmann's ecogeographic rule through time rather than through latitude. The variety of modern birds, including rails, that were of larger size in the Pleistocene, makes reasonable the hypothesis that depressed temperatures during glacial periods caused increases in size while warmer post-Pleistocene temperatures caused decreases in size.

SUMMARY

1. The record of *Aramides cajanea* from the Florida Pleistocene was erroneous and the species is removed from the North American list.
2. The fossil coot, *Fulica hesterna*, is treated as a synonym of *Fulica americana*.
3. The fossil species *Laterallus guti* was found to be inseparable from the living species *L. exilis* and is considered a synonym of that species, the range of which extended to Florida in the Pleistocene.
4. The genus *Epirallus* is synonymized with *Rallus* and its single species, *natator*, is considered a large member of the *Rallus longirostris-elegans* complex.
5. The fossil form *Porzana auffenbergi* is removed to the genus *Rallus* and is considered a large temporal representative of *R. limicola*.
6. The fossil gallinule, *Gallinula brodkorbi*, is considered a large temporal representative of *G. chloropus*.
7. The post-Pleistocene history of rails in North America is apparently not one of extinction of species but of decrease in size or of retreat from a formerly wider range.

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