A new species of large flightless rail of the *Rallus longirostris/elegans* complex (Aves: Rallidae) from the late Pleistocene of Bermuda

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Abstract.—Rallus recessus, new species, probably derived from the King Rail R. elegans, is described from a cave deposit exposed in quarrying operations on the island of Bermuda. This species had the reduced elements of the wing and pectoral girdle and more robust hindlimbs typical of flightless rails. It is the only member of the largest size-class of the genus Rallus known to have colonized an oceanic island and become flightless. It was present on Bermuda during the last (Wisconsinan) glacial period and appears to have become extinct naturally due to changing environmental conditions associated with changes in sea level.

Fluctuating sea-levels dramatically altered the land area of the North Atlantic island of Bermuda during the Pleistocene, causing natural turnover in major elements of the island's biota, particularly birds. At least two different avifaunas have been recognized from undated caves and fissures exposed in limestone quarrying operations. One of these is characterized by the presence of a crane, a duck, and two medium to small flightless rails—Grus latipes, Anas pachysceles, Rallus ibycus, and Porzana piercei (Wetmore 1960, Olson & Wingate 2000). These species are absent in the other fauna, which is dominated by a large, flightless derivative of the Rallus longirostris/ elegans complex that has been alluded to previously as an unnamed species (Olson 1977, 1997; Olson & Wingate 2000).

These distinct avifaunas are thought to have existed during two different glacial periods of the Pleistocene when sea-levels were lower and the land area of Bermuda was greater than at present. Olson & Wingate (2000) made an assumption that the crane fauna was older than the fauna with the large rail. Although this assumption is

now known to be correct, the crane fauna is probably not as old as they hypothesized.

The following description of the large rail is based entirely on the specimens collected in 1960 from "Rail Cave" in Government Quarry. Additional material of the species has since been found in two other deposits that are under investigation by P. J. Hearty (James Cook University, Queensland, Australia) and Olson. One of these promises to allow a very precise chronological reconstruction of the geology and paleontology of Bermuda in the late Quaternary, which will be presented elsewhere. For the present, we have been able to determine that the undescribed large rail existed during the last (Wisconsinan) glacial period. Therefore, we here proceed with naming it in order to be able to refer to it unambiguously in future publications.

Materials and Methods

Disassociated fossil elements are cataloged in the collections of the Florida Museum of Natural History and all specimens take the prefix UF PB, which we have omitted except in the citations of the holotype

Table 1.—Measurements (mm) of selected skeletal elements of Rallus recessus, new species.

	n	Range	Mean	S.D.
Cranium				
Length from naso-frontal hinge	14	29.2-33.3	32.2	1.21
Width at postorbital processes	15	15.9-17.1	16.6	0.31
Width interorbital bridge	19	3.9-5.2	4.6	0.39
Sternum				
Length along midline (from notch)	16	30.4-36.7	33.0	1.70
Width across coracoidal sulci	17	12.0-14.6	13.1	0.71
Depth of carina	24	6.0-9.2	7.5	0.75
Coracoid				
Length	38	20.5-25.1	23.3	1.30
Humerus				
Length	60	39.7-47.4	43.7	1.91
Proximal width	59	8.4-10.5	9.4	0.45
Shaft width	60	2.2–2.9	2.6	0.15
Distal width	60	5.6–6.7	6.1	0.31
Ulna				
Length	45	29.3–37.3	34.1	1.84
Radins				
Length	18	28.1-34.3	31.4	1.81
Carpometacarpus				
Length	27	20.5-24.5	22.9	1.18
Proximal depth	27	5.05.9	5.5	0.29
Pelvis				
Sacrum length	27	32.8-42.9	38.2	2.45
Width across antitrochanters	10	17.5–21.2	20.1	1.25
Femur				
Length	26	44.3-52.4	49.1	2.12
Proximal width	26	7.9–9.5	8.8	0.45
Distal width	26	7.5–8.8	8.3	0.37
Tibiotarsus				
Length from proximal articular surface	30	58.0-71.9	66.3	3.61
Distal width	30	6.0-7.2	6.6	0.31
Tarsometatarsus				
Length	29	36.6-44.6	40.9	2.21
Proximal width	29	6.3-7.6	7.0	0.36
Distal width	29	6.7-8.1	7.4	0.40

and the figure legends. There is a great deal more material available than is listed among the type material. As paratypes we have listed those specimens that either were used in the descriptions, are illustrated, or were used for any of the cited measurements. Measurements of long bones of the limbs usually do not include broken or juvenile specimens, which accordingly are not

among the listed paratypes. Measurements were taken with digital calipers to 0.01 mm and rounded to the nearest 0.1 mm.

Comparative material examined.—Skeletons (complete unless otherwise indicated) of the following species in the collections of the National Museum of Natural History, Smithsonian Institution (USNM). Rallus aquaticus 431545, 553039, 553041; R. lim-



Fig. 1. Comparison of skulls (a, d) and sterna (b-c, e) of *Rallus* in lateral view. a, R. recessus, new species, holotype UF PB5108; d, e, R. elegans female USNM 499437; b, c, R. recessus, new species, UF PB5124, UF PB5126. Scale bar = 2 cm.

icola 489973, 525915, 525917; R. elegans 499437, 525886, 610780, UF 22870, UF 24314, UF 24318; R. longirostris 525876, 525873, 525879; R. longirostris × R. elegans 525887.

Systematics

Family Rallidae Genus *Rallus* Linnaeus

Referable to *Rallus*, sensu stricto, by the very long, slender bill and by the lack of characters suggesting relationship to the long-billed rails of the genus *Pardirallus* (including *Ortygonax*), which are not closely related to *Rallus* (Olson 1973).

Rallus recessus, new species Figs. 1-5

Holotype.—Cranium and rostrum consisting of the pila supranasalis and premaxillary symphysis but lacking the lateral nasal bar and ventral portions UF PB5108. Collected in February/March 1960 by Pierce Brodkorb and David B. Wingate.

Type locality.—Bermuda, Hamilton Parish, Government Quarry, from a fissure called "Rail Cave" that was exposed in quarrying operations and that has since been quarried away.

Chronology.—Late Pleistocene, last (Wisconsinan) glacial period.

Measurements (mm) of holotype.—Total

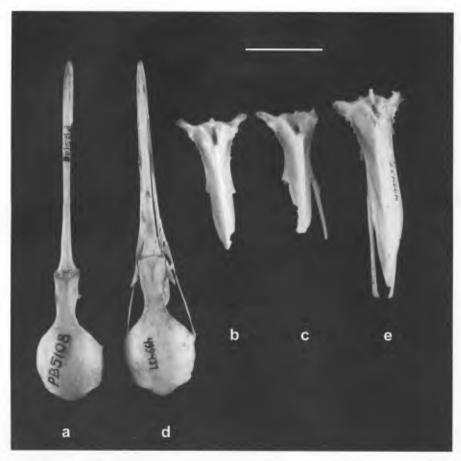


Fig. 2. Comparison of skulls in dorsal view (a, d) and sterna in ventral view (b-c, e) of Rallus. a, R. recessus, new species, holotype UF PB5108; d, e, R. elegans female USNM 499437; b, c, R. recessus, new species, UF PB5124, UFPB 5126. Scale bar = 2 cm.

length, 93.6; rostrum from nasofrontal hinge to tip, 62.7; length of premaxillary symphysis, 21.1; length of cranium from naso-frontal hinge, 33.1; width of cranium at postorbital processes, 17.0; width of interorbital bridge 4.8.

Paratypes.—Crania with rostra 5104, 5115. Rostrum 5103. Crania (a few consisting of only the interorbital bridge) 5101–5103, 5105–5107, 5109–5114, 5116–5117, 5295–5298. Sterna 5119–5129, 5131–5135, 5137–5138, 5140–5141, 5143, 5145, 5294, 5894. Coracoids 5284, 5395–5400, 5856, 5858–5865, 5867, 5869–5875, 5878–5887, 5890–5893. Scapula 5285. Humeri 5146–5158, 5160–5174, 5180–5196, 5198–5203, 5205–5208, 5822–5826. Radii

5836–5843, 5848–5857. Ulnae 5213–5219, 5221–5226, 5228–5236, 5242, 5243, 5244, 5245, 5246, 5247, 5248–5264. Carpometacarpi 5269–5278, 5280–5283, 5340–5342, 5344–5353. Pelves 5287, 5408, 5896–5902, 5904, 5906–5915, 5917–5919, 5922–5924, 5926. Femora (right) 5288, 5302, 5304–5307, 5309–5310, 5312–5314, 5316–5322, 5327, 5328, 5332–5936. Tibiotarsi (right) 5289, 5332, 5368, 5385–5386, 5388–5394, 5717–5726, 5833–5834, 5937–5941, 5948. Tarsometatarsi (right) 5290, 5746–5760, 5791–5795, 5797–5798–5798bis? = 5799?, 5800–5803, 5813.

Measurements (mm) of paratypes.—Rostrum: length from naso-frontal hinge, 61.5, 62.5, 62.7, 63.8; length of premaxillary



Fig. 3. Comparison of pectoral and wing elements of *Rallus recessus*, new species (a-e) with *R. elegans* (f, i, j, USNM 499437 female; g, h, USNM 610781 female). a, f, left coracoids in ventral view (a, UF PB 5860); b, g, left scapulae in dorsal view (b, UF PB5385); c, h, left humeri in anconal view (c, UF PB5160); d, left ulna and radius in internal view (ulna UF PB 5214; radius UF PB 5856); i, right ulna and radius in internal view; e, j, left carpometacarpi in internal view (e, UF PB5340). Scale bar = 2 cm.

symphysis, 21.1, 21.1, 21.6, 22.0. Scapula: length 42.4. For other measurements see Table 1.

Associated paratype.—An articulated incomplete skeleton covered with flowstone was collected on a block of limestone from Rail Cave and is now on exhibit in the Bermuda Aquarium, Museum and Zoo (BAMZ 2000 190 001). Not all of the skeleton is present and the measurements of the remaining elements will in most cases probably be slightly too large because of their casing of flowstone. In size, the specimen would be at the small end of size variation in the species, presumably a female. The following length measurements (mm) were obtained. Total length of skull and bill 77.7;

rostrum from nasofrontal hinge 49.6; cranium from nasofrontal hinge 19.6; mandible 66.2; coracoid 20.5; humerus 39.9; femur 44; tibiotarsus 60; tarsometatarsus 37.5.

Etymology.—Latin, recessus, used here with a double meaning; first, to refer to recession of the sea during the glacial period that this species occupied Bermuda (recessus marini aestus being low tide in Latin), and also to the second meaning of the word, a nook, corner, or secret spot, in reference to the hidden chamber in which the type material was secreted.

Diagnosis.—Larger than any of the species of Rallus (sensu stricto, Olson 1973) except those of the R. longirostris/elegans

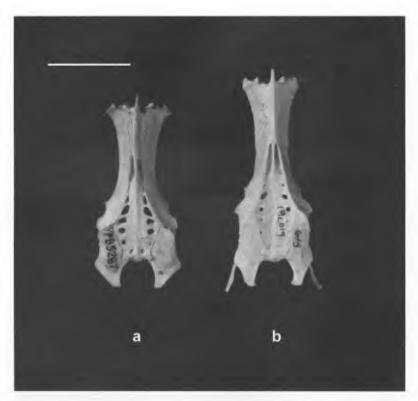


Fig. 4. Comparison of pelves of *Rallus* in dorsal view. a, R. recessus, new species, UF PB5287; b, R. elegans (USNM 610781 female). Scale bar = 2 cm.

complex. Differs from related species in characters associated with flightlessness and in having a proportionately longer and more slender bill, with a longer and more decurved premaxillary symphysis. The width of the interorbital bridge is intermediate between that of *R. longirostris* and *R. elegans*. Flight apparatus greatly reduced in development. Hindlimb elements shorter and much more robust.

Description.—In addition to the longer, more decurved bill, this species has the orbits reduced so the frontal area in lateral view slopes more steeply. There are no impressions for salt glands on the interorbital bridge, unlike *R. longirostris*. The cranium is narrow, which is less like *R. elegans*.

Compared with *Rallus longirostris/elegans*, the sternum is shorter and wider with the carina greatly reduced, although a small manubrial spine is present and there is no deep notch between the coracoidal sulci as

in many flightless rails. The sternocoracoidal process of the coracoid is more pointed and projecting. The humerus has the head smaller, the capital groove wider, the shaft more curved and the brachial depression deeper. The ulna is very short and more curved and the carpometacarpus small.

The pelvis is wider with the postacetabular portion proportionately shorter, the ischial area in lateral view is much less deep, the ilia do not extend as far posteriorly beyond the sacrum, and the ilioischiadic fenestra is smaller. The hindlimb elements are shorter, both absolutely and relatively, and more robust, particularly the shafts.

Remarks.—The large species of Rallus included in the R. longirostris/elegans complex are confined to the New World. Their interelationships, biogeography, and hypothetical history have been discussed by Olson (1997), who argued on the basis of the interorbital bridge that the Bermuda bird



Fig. 5. Comparison of hindlimb elements in anterior view of *Rallus recessus*, new species (*a–f*) with *R. elegans* (*g–i*—USNM 499437 female). *a, b,* right femora UF PB5036, UF PB5309; *c, d,* right tibiotarsi UF PB5941, UF PB5722; *e, f,* right tarsometatarsi UF PB5796, UF PB5800. Scale bar = 2 cm.

was a derivative of *Rallus elegans* that had become adapted to somewhat higher salt stress, rather than a derivative of *R. longirostris*. According to Olson's hypothesis, *R. elegans* was the original North America stock of large *Rallus* that was later displaced from Gulf and Atlantic salt marsh habitats by an invasion of *R. longirostris*. Although the salt-marsh Clapper Rail, *R. longirostris*, has been found as a very rare vagrant to Bermuda, the King Rail, *R. elegans*, has not yet been recorded there (Amos 1991).

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