The fossil record and history of doves on Bermuda (Aves: Columbidae)

Storrs L. Olson

Department of Vertebrate Zoology, National Museum of Natural History, NHB MRC 116, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013-7012, U.S.A., e-mail: olsons@si.edu

Abstract.—Four bones of a dove from Bermuda are tentatively identified with the West Indian Zenaida Dove as cf. Zenaida aurita. These occur in deposits dating to about 55,000 to 28,000 years ago that formed during the last glacial period when the land area of Bermuda was much larger. At that time, the West Indies would have been a much more likely source area than eastern North America for dove as a potential colonist of Bermuda. The Bermuda dove appears to have been a resident and perhaps became extinct as a result of flooding of the Bermuda platform and reduction in land area during the present interglacial. The two doves found on Bermuda today (Mourning Dove Zenaida macroura and Common Ground Dove Columbina passerina) are absent in the fossil record and apparently did not become established on the island until after human settlement in the seventeenth century.

Keywords: Bahamas, extinction, Pleistocene, sea level rise, West Indies

An extensive mid to late Quaternary fossil record from the isolated North Atlantic island of Bermuda has shown that at different periods the island was home to a variety of land birds (Olson 2008a, Olson & Wingate 2000, 2001, 2006; Olson et al. 2005). Pigeons and doves (Columbidae) are among the birds most capable of overwater dispersal and have colonized most of the temperate and tropical islands of the world (Gibbs et al. 2001), with the notable exception of the Hawaiian Islands (Olson & James 1991). Indigenous or endemic populations of Columbidae occur in all the Macaronesian islands of the eastern North Atlantic (Clark 2006) and in the South Atlantic on Fernando do Noronha (Olson 1982) and formerly St. Helena (Olson 1975). Thus, it would be expected that Bermuda would be colonized by some member of this family, perhaps repeatedly. The fossil record bearing on this is, unfortunately, extremely meager, only four bones having been recovered so far, but it is perhaps as interesting for revealing which species of doves were apparently not present. Here, I analyze the few available columbid fossils from Bermuda and review the history of the doves currently inhabiting the island.

Comparative material examined.—Skeletons from the collection of the National Museum of Natural History, Smithsonian Institution (USNM): Columbina passerina 499476; Ectopistes migratorius 224320, 224322, 224323, 292904; Geotrygon chrysia 292518, 292519, 318870, 554602; G. montana 501793; G. versicolor 555505; Leptotila jamaicensis 554396; L. verreauxi 322981; Zenaida asiatica 553873, 553875, 554399, 555177; Z. aurita zenaida 290992, 292525, 500695, 500696, 553318, 555526, 555746, 556836, Z. macroura carolinensis 489326, 501289, 560298, 560302; Z. macroura marginella 226365, 289122, 494475, 637745.

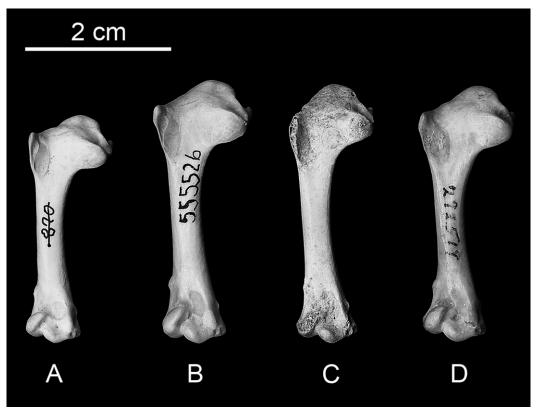


Fig. 1. Right humeri of doves in palmar view. A, Zenaida macroura carolinensis USNM 501289; B, Zenaida aurita zenaida USNM 555526; C, bermuda fossil cf. Zenaida aurita USNM 542298; D, Geotrygon chrysia USNM 292519.

Systematics

Order Columbiformes Family Columbidae cf. *Zenaida aurita* (Temminck, 1809) Fig. 1

Referred material.—Right humerus, USNM 542298 (Fig. 1C) collected Nov 2003, Admirals Cave, lower level *ulv*, by Olson, P. J. Hearty, and F. V. Grady; right coracoid, USNM 542299 collected 16 Feb 2004, Admirals Cave, level *v* pocket, by Olson & Grady; left coracoid USNM 542300, collected S. face Government Quarry, by Howard Wilson; left coracoid, USNM 542301, apparent juvenile, collected Aug 1981, Government Quarry, fissure fill upper level, by R. F. Baird. Because of the combination of location and stratigraphy it is clear that

these four bones must have come from four different individuals.

Stratigraphy and age.—Both fossils from Admirals Cave are late Pleistocene in age and date to the last glacial period. The humerus comes from near the beginning of that period in Marine Isotope Stage (MIS) 4, ca. 54,800 YBP; the coracoid is from MIS 2, ca. 28,500 YBP (see Hearty et al. 2004:1158). The two bones from Government Quarry come from undated deposits, but the majority of fissure fills exposed in that quarry also date to the last glacial episode.

Comparisons.—The fossils are from a species that is clearly too small for the extinct Passenger Pigeon Ectopistes migratorius and too large for Mourning Dove Zenaida macroura or any smaller columbid (Table 1). In both species of Leptotila

VOLUME 124, NUMBER 1

the humeri were decidedly shorter and stouter. The humerus of Geotrygon montana is smaller and that of G. versicolor is larger. The humeri of Zenaida Dove Zenaida aurita and Key West Quail-Dove Geotrygon chrysia are practically inseparable and both show considerable individual variation, but the coracoids of the fossils are somewhat smaller and appear to be more heavily pneumatized in the dorsal surface of the sternal end than in the available specimens of G. chrysia, so that they agree better with Z. aurita. The humeri in White-winged Dove Z. asiatica are slightly smaller than in the fossil. West Indian birds of that species do not differ significantly in size or plumage from birds of the Central American mainland (Aldrich 1981), so that it appears that Z. asiatica is probably a relatively recent colonizer of the West Indies and would have been an unlikely source species for colonizing Bermuda in the Pleistocene. I have found that when attempting to identify fossil columbids from the Greater Antilles, where many species occur sympatrically, when size will not differentiate between species the only really diagnostic postcranial element is the tarsometatarsus, which, unfortunately, we do not have in the Bermuda material. The Zenaida Dove is the most widespread and abundant of the species similar in size to the Bermuda fossils, and there is nothing about the fossils that would rule out that species. On the other hand, the material is also insufficient to rule out the possibility that the Bermuda dove had differentiated at some level into an endemic form.

Beebe (1937) reported three individuals of *Zenaida aurita* observed associating with *Columbina passerina* on St. Georges, Bermuda, on 7 July 1935. It was later determined that they had escaped several weeks previously from a lot brought in from Turks, Bahamas. This is perhaps of more importance to considering the history of *Columbina* on Bermuda in that it provides evidence of deliberate human

transportation of columbids from the Bahamas to Bermuda.

Mourning Dove *Zenaida macroura* (Linnaeus, 1758)

Based on data from David B. Wingate (pers. comm.), Amos (1991:47) reported that this species was "seen in Bermuda only as migrants before they began nesting in 1954. Today they are so widespread that their numbers mask the arrivals of the visitors." Aldrich (1993:54) reported that a series of breeding Mourning Doves taken on Bermuda by Wingate on 12 June 1967 did not differ from Z. m. carolinensis of eastern North America. The absence of fossils of this species, even in Holocene deposits, strongly supports other available evidence that this species was self-introduced during the historic period.

Common Ground Dove *Columbina* passerina (Linnaeus, 1758)

This species occurs in small numbers scattered throughout Bermuda today. Bangs & Bradlee (1901:250) named the ground dove of Bermuda as a full species, Columbigallina bermudiana, a taxon that was admitted by a few authors at the specific or subspecific level for a short while only. Verrill (1902:662, footnote), who may have heard some local, undocumented information, rather circuitously suggested that "it is doubtful whether the Ground Dove was not introduced from the Bahamas." This practically foretold the conclusion of Todd (1913:571), who carried bermudiana as a synonym of C. p. bahamensis because "after extended and careful comparison of the type series and a few additional specimens" he was "unable to appreciate the alleged diagnostic characters, nor can I discover any others which would justify the retention of the name." This conclusion was accepted by Ridgway (1916), Hellmayr & Conover (1942:521), and subsequent authors. Although Amos (1991:47) spec-

Species (n)	Humerus length range (\bar{X})	Coracoid length range (\bar{X})
Ectopistes migratorius (4)	40.9–43.4 (42.2)	31.0-33.4 (32.2)
Geotrygon chrysia (4)	35.1–36.7 (35.8)	28.0–30.6 (28.8)
Zenaida aurita (8)	34.7–37.6 (35.8)	26.5–29.0 (27.5)
Bermuda fossils	36.1	25.0*, 26.5, 26.5
Zenaida asiatica (4)	33.8–35.7 (34.7)	26.5–27.6 (26.7)
Zenaida macroura (8)	30.1–33.2 (31.9)	21.9–25.6 (24.3)

Table 1.—Measurements of humeri and coracoids of Columbidae. Coracoid length is from head to internal sternal angle. The sample of *Z. macroura* includes 4 *Z. m. carolinensis* and 4 *Z. m. marginella*.

ulated that this species "may have reached Bermuda as hurricane strays—probably in precolonial times," there is no evidence in support of this. The species is completely absent in the fossil record. These are charming and attractive little birds that would have been easy to capture and maintain in captivity for the duration of a passage from the Bahamas to Bermuda, where the occurrence of this species as a deliberate human introduction is most likely.

Conclusions

Fossil evidence of a dove on Bermuda is confined to the last glacial period of the Pleistocene, when the land area of Bermuda was an order of magnitude larger than at present (Hearty & Olson 2010, Olson & Hearty 2010). The presence of four different individuals, including an apparent juvenile, over a period of several thousand years almost certainly indicates a resident population, although the bird was either excessively scarce or avoided situations that might lead to its being preserved as fossils.

During the last glacial period, most of eastern North America was covered with nearly unbroken forest, mainly hardwoods that provided habitat and food for the superabundant, highly colonial and nomadic Passenger Pigeon *Ectopistes migratorius* but perhaps no other columbids. Passenger Pigeons were certainly capable of reaching Bermuda, and two

vagrant individuals in the nineteenth century, one a sight record only, are listed by Bradlee & Mowbray (1931). The comparatively small land area and scrub habitat, even during glacial maxima, would have been quite unsuitable for this species to colonize successfully, however. Mourning Doves probably did not move into eastern North America and become abundant until after extensive clearing by humans opened up suitable habitat. Thus, the only source area from which a dove might likely have colonized Bermuda in the last glacial age would have been the West Indies, where very similar habitats were much more extensive, especially in the Bahamas, during that period of lowered sea level.

During interglacials, sea levels rose and flooded the Bermuda platform reducing the land area to a fraction of its extent during glacial periods (Hearty & Olson 2010, Olson & Hearty 2010). These interglacial highstands were associated with extinction events during which not only terrestrial organisms, but sometimes even seabirds, disappeared from Bermuda (Olson 2008b, Olson & Hearty 2003, 2009, 2010; Olson et al. 2005). The dove (cf. Zenaida aurita) of the Bermuda Pleistocene (MIS 4-2) appears to represent another such extinction, apparently being a victim of the present interglacial (MIS 1) rise in sea level. It is not known in Holocene deposits and early travelers such as William Strachy and Capt. John Smith, who listed the birds they encoun-

^{*} Estimated.

tered on Bermuda in the early 1600's, never mentioned any kind of dove (Lefroy 1981:35, 330–334). The two doves found on Bermuda today, Mourning Dove and Common Ground Dove, are probably both dependent on habitats that were created after human settlement and there is no evidence of either outside the historic period.

Acknowledgments

For assistance in the field I am indebted to Frederick V. Grady, Paul J. Hearty, and David B. Wingate. Comparative material is housed in the Division of Birds, and fossils in the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM). I am most grateful to Christina Gebhard and Brian Schmidt (Division of Birds, USNM) for preparing the figure and Mark Florence (Department of Paleobiology) for curation of fossil specimens. For comments on the manuscript I am grateful to William Suárez and D. B. Wingate. I thank Lisa Greene and Wolfgang Sterrer of the Bermuda Aquarium, Natural History Museum and Zoo (BAMZ) for much assistance. This is contribution 174, Bermuda Biodiversity Project (BBP), of the BAMZ.

Literature Cited

- Aldrich, J. W. 1981. Geographic variation in Whitewinged Doves with reference to possible source of new Florida population.—Proceedings of the Biological Society of Washington 94:641–651.
- ——. 1993. Classification and distribution. Pp. 47–54 in T. S. Baskett, M. W. Sayre, R. E. Tomlinson and R. E. Mirarchi, eds., Ecology and management of the mourning dove. A Wildlife Management Institute book. Stackpole Books, Harrisburg, Pennsylvania, 567 pp.
- Amos, E. J. R. 1991. A Guide to the Birds of Bermuda. Published by the author, Warwick, Bermuda, 206 pp.
- Bangs, O., & T. S. Bradlee. 1901. The resident land birds of Bermuda.—Auk 18:249–255.

- Beebe, W. 1937. Recent notes on Bermuda birds.— Proceedings of the Linnaean Society of New York 48:60–65.
- Bradlee, T. S., & L. L. Mowbray. 1931. A list of birds recorded from the Bermudas.—Proceedings of the Boston Society of Natural History 39:279–382.
- Clark, T. 2006. A field guide to the birds of the Atlantic Islands: Canary Islands, Madeira, Azores, Cape Verde. Christopher Helm, London, 368 pp.
- Gibbs, D., E. Barnes, & J. Cox. 2001. Pigeons and doves: a guide to the pigeons and doves of the world. Yale University Press, New Haven, Connecticut, 615 pp.
- Hearty, P. J., & S. L. Olson. 2010. Geochronology, biostratigraphy, and changing shell morphology in the land snail subgenus *Poecilozonites* during the Quaternary of Bermuda.—Palaeogeography, Palaeoclimatology, Palaeoecology 293:9–29.
- —, —, D. S. Kaufman, R. L. Edwards, & H. Cheng. 2004. Stratigraphy and geochronology of pitfall accumulations in caves and fissures, Bermuda.—Quaternary Science Reviews 23:1151–1171.
- Hellmayr, C. E., & B. Conover. 1942. Catalog of birds of the Americas and the adjacent islands in Field Museum of Natural History, including all species and subspecies known to occur in North America, Mexico, Central America, South America, the West Indies, and islands of the Caribbean Sea, the Galapagos Archipelago and other islands which may be included on account of their faunal affinities.
 Part 1, no. 1. Field Museum of Natural History, Chicago, Zoological Series 13, 636 pp.
- Lefroy, J. H. 1981. Memorials of the discovery and early settlement of the Bermudas or Somers Islands 1515–1685. Compiled from the colonial records and other original sources. Vol. 1, with revised chronology and erratum 1511–1652. Second reprinting. Bermuda Historical Society, Hamilton, Bermuda, 772 pp.
- Olson, S. L. 1975. Paleornithology of St. Helena Island, South Atlantic Ocean.—Smithsonian Contributions to Paleobiology 23:1–49.
- . 1982 [1981]. Natural history of vertebrates on the Brazilian islands of the mid South Atlantic.—National Geographic Society Research Reports, 13:481–492.
 - 2008a. A new genus and species of buteonine hawk from Quaternary deposits in Bermuda (Aves: Accipitridae).—Proceedings of the Biological Society of Washington 121:130–141.

- 2008b. A new species of shearwater of the genus *Calonectris* (Aves: Procellariidae) from a middle Pleistocene deposit on Bermuda.— Proceedings of the Biological Society of Washington 121:398–409.
 & P. J. Hearty. 2003. Probable extirpation of a breeding colony of Short-tailed Albatross (*Phoebastria albatrus*) on Bermuda by Pleistocene sea-level rise.—Proceedings of the National Academy of Sciences USA 100(22): 12825–12829.
- ———, & ———. 2009. A sustained +21 m sea-level highstand during MIS 11 (400 ka): direct fossil and sedimentary evidence from Bermuda.—Quaternary Science Reviews 28(3–4): 271–285.
- ———, & ———. 2010. Predation as the primary selective force in recurrent evolution of gigantism in *Poecilozonites* land snails in Quaternary Bermuda.—Biology Letters 6(6):807–810.
- ———, & H. F. James. 1991. Descriptions of thirtytwo new species of birds from the Hawaiian Islands: Part I. Non-Passeriformes.—Ornithological Monographs 45:1–88.
- ———, & D. B. Wingate. 2000. Two new species of flightless rails (Aves: Rallidae) from the Middle Pleistocene "crane fauna" of Bermuda.—Proceedings of the Biological Society of Washington 113:356–368.
- ———, & ———. 2001. A new species of large flightless rail of the *Rallus longirostrislelegans* complex (Aves: Rallidae) from the late Pleistocene of Bermuda.—Proceedings of the Biological Society of Washington 114:509–516.

- —, & ——. 2006. A new species of nightheron (Ardeidae: *Nyctanassa*) from Quaternary deposits on Bermuda.—Proceedings of the Biological Society of Washington 119: 326–337.
- Prodromus of vertebrate paleontology and geochronology of Bermuda. Pp. 219–232 *in*J. A. Alcover and P. Bover, eds., Proceedings of the International Symposium "Insular Vertebrate Evolution: the Palaeontological Approach."—Monografies de la Societat d'Història Natural de les Balears 12.
- Ridgway, R. 1916. The birds of North and middle America: a descriptive catalog of the higher groups, genera, species, and subspecies of birds known to occur in North America, from the Arctic lands to the Isthmus of Panama, the West Indies and other islands of the Caribbean Sea, and the Galapagos Archipelago. Bulletin of the United States National Museum No. 50, Pt. 7, 543 pp + 24 pl pp.
- Todd, W. E. C. 1913. A revision of the genus *Chaemepelia*.—Annals of the Carnegie Museum 8:507–603.
- Verrill, A. E. 1902. The Bermuda Islands: their scenery, climate, productions, physiography, natural history, and geology; with sketches of their early history and the changes due to man.—Transactions of the Connecticut Academy of Arts and Sciences 11:413–956.

Associate Editor: Gary R. Graves.