Geological Constraints on Evolution and Survival in Endemic Reptiles on Bermuda

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ABSTRACT.—Paleontological and geological evidence suggest that the distinctive endemic skink Eumeces longirostris could potentially be as old as continuously emergent land on the Bermuda seamount (approximately > 1–2 million yr). The species has experienced sustained evolutionary stasis for at least the past 400,000 yr, during which time there has been no perceptible change in skeletal morphology. The tortoise Hesperotestudo bermudae is known from a single fossil from interglacial period marine isotope stage (MIS) 9—approximately 300,000 yr ago. A viable population of tortoises on Bermuda could be reconciled with the geological record and the lack of any other fossils of the species to date if tortoises colonized the island at or after the end of the maximal sea-level rise of interglacial MIS 11, evolved during the single glacial episode of MIS 10, and became extinct as a result of the interglacial sea-level rise of MIS 9, a period of about 100,000 yr. Such rapid evolution and extinction has a close parallel in the giant tortoises of Aldabra Island in the Indian Ocean.

The island of Bermuda (54 km²) is the isolated remnant of a former volcanic peak situated in the North Atlantic about 1000 km east-southeast of Cape Hatteras, North Carolina. It had no connection or greater proximity to other land masses and would always have presented a difficult landfall for reptilian colonists. Only two natural colonizations of Bermuda by terrestrial reptiles are known: the scincid lizard Eumeces longirostris, which survives today, and the tortoise Hesperotestudo bermudae known from a single fossil. Throughout the Pleistocene, Bermuda was affected by periodic fluctuations in sea level that altered land area by an order of magnitude, causing dramatic and repeated restructuring of terrestrial ecosystems. The evolutionary history of Bermudan reptiles can be understood only in light of these geological events.

MATERIALS AND METHODS

The specimens of E. longirostris examined are housed in the National Museum of Natural History, Smithsonian Institution (USNM). Modern comparative material (Division of Amphibians and Reptiles) consisted of three female skeletons (USNM 217505–217507) and one lot of 16 disarticulated skeletons (USNM 549299). The Middle Pleistocene fossil material (Department of Paleobiology) from Green Island (USNM 530788) consisted of 23 specimens including dentary, maxillae, prefrontal, frontal, parietal, basisphenoid, femora, tibia, and vertebrae, from a minimum of 1 individual. That from Calonectris Quarry (USNM 530785-530787) consisted of 116 specimens including dentaries, angulars + surangulars, maxillae, parietals, neurocrania, pterygoids, quadrates, vertebrae, pelves, humerus, and ulna, from a minimum of five individuals. In addition, we have seen many as yet uncataloged specimens from numerous younger deposits as listed below.

In the Bermuda fossils, the notable characters of the Scincidae (Greer, 1970; Estes et al., 1988) include the following: retroarticular process inflected medially, Meckel's groove open and unfused anterior to the splenial, quadrate broad and deep, frontals paired, unfused and with a deep subolfactory process. Tooth counts (dentary: 17–23, mode 20; maxilla 14–21, mode 18) and cusp morphology (blunt, weakly striated) likewise accord with Eumeces. The narrow snout of E. longirostris is reflected in the
unpaired frontals by the ratio of length to interorbital width (mean 5.2:1, range 4.7–5.5:1, \( N = 16 \)).

**Geological Setting**

The following overview is condensed from Hearty et al. (1992, 1999), Hearty (2002), Olson and Hearty (2003), Hearty et al. (2004), and Olson et al. (2005). Bermuda consists almost entirely of carbonate limestone formed from the comminuted remains of marine invertebrates. During interglacial sea-level high stands, carbonate sand on the shelf is transported to land by tides and wind, forming dune deposits or eolianite (Fig. 1). During glacial low stands when sea levels fall below the edge of the platform, the island is removed from carbonate sources and thin, clayey, red soils form from pedogenesis of limestone and dust accumulations originating in Saharan Africa. These soils are now generally leached and bereft of fossils.

Glacial/interglacial sea level fluctuations of the Pleistocene correspond with ice volume changes, which in turn are tracked by changes in oxygen isotopes from stratigraphic accumulation of deep sea micro-organisms. Marine isotope stages (MIS) are represented by odd-numbered interglacial stages (the present MIS 1, followed by 3, 5, etc.), and even-numbered glacial stages (MIS 2, 4, 6, etc). A number of studies (summarized in Hearty et al., 1992; Hearty, 2002) have resulted in a firm chronostatigraphy for Bermuda over the past 450,000 yr using aminostratigraphy and radiometric dating. From these and related studies, it was established that MIS 11, 9, and 5e (Fig. 1) stand out as important warm periods with higher than present sea levels (Hearty and Kaufman, 2000). In glacial periods, land area was greatly increased to about 1000 km², thereby increasing the chances of colonization by terrestrial organisms. These were offset by interglacial reductions in land area with resulting extinctions. For example, a crane, a duck, and at least one of two flightless rails went extinct with the onset of the last interglacial (MIS 5), and a large flightless rail that evolved during the last glacial period (MIS 2–4) became extinct with the onset of the present interglacial (Olson and Wingate, 2000, 2001; Olson et al., 2005).

The exposed basal rocks of present-day Bermuda are highly altered carbonate eolianite of the Walsingham Formation, which, although not precisely dated, have reversed magnetic polarity—probably the Brunhes/Matuyama boundary dated at 780,000 yr ago (Hearty and Vacher, 1994) and, thus, is correlated with the early Pleistocene. A massive red soil (the Big Red Soil, or BRS) developed on the Walsingham during an extended period of lower sea level (900–450 thousand yr ago; MIS 23–12) during which no carbonates were deposited on the platform, as even during highstands sea level was well below the present datum. Most of the Bermuda platform is exposed when sea level drops to the −10 m bathymetric contour. No vertebrate fossils are known from this first half or more of Bermuda’s subaerial history. This very long period of environmental stasis, during the development of the BRS, was immediately followed by the most catastrophic event in Bermuda’s prehuman biological history, the MIS 11 interglacial
The oldest skink fossils occurred among the remains of an extirpated colony of Short-Tailed Albatross *Phoebastria albatrus* on Green Island, on the southeastern perimeter of Bermuda, which were deposited at the beginning of MIS 11 and are >400,000 yr old (Olson and Hearty, 2003). Skinks may have foraged in the albatross colony for insects associated with carcasses of deceased birds and remains of uneaten prey.

The next oldest site containing skink bones is a beach deposit (Calonectris Quarry) laid down when sea level rose to 21.3 m above present, the maximum transgression of MIS 11, shortly after 400,000 yr ago (Hearty et al., 1999; Olson and Hearty, 2003). Skink bones were relatively common here (see Materials and Methods) probably indicating foraging along the strand line. The many cranial elements in these two samples leave no doubt about identification (Fig. 2). All are identical to *E. longirostris* in details of proportions, articulations, foramina, and tooth counts, although some came from individuals approximately 10–20% larger than the modern series. This might simply be a sampling bias that includes undetectable intergenerational size changes. Another possibility is that there has been a historical reduction in body size caused by increased mortality from introduced predators, as has been documented among other lizard populations on small islands (Pregill, 1986).

*Eumeces* Wiegmann is a cosmopolitan taxon with about 50 species distributed over much of the holarctic (approximately 12 species in North America). The genus was last treated comprehensively by Taylor (1936), who recognized various species groups based on phenetic criteria. He considered *E. longirostris* to be primitive, and placed it in its own “section” apparently on the basis of a unique preanal scale pattern. Lieb (1985) maintained *E. longirostris* in its own species group but united it with the *obsoletus* group (four species) in a species series resulting from the possession of oblique lateral scales, a character that Taylor (1936) discounted in the placement of *E. longirostris*.

*Eumeces longirostris* was, thus, present before, during, and after the maximum rise in sea level affecting Bermuda in the Pleistocene. There are no constraints on how much older the skink could be other than the formation of the first subaerial environments on the Bermuda seamount, which are early Pleistocene or older (Vacher et al., 1995). A long period of isolation accords well with the distinctiveness of the Bermuda skink as noted above (Taylor, 1936; Lieb, 1985).

The fossil record shows that *E. longirostris* has apparently undergone no evolutionary change in skeletal morphology over the last 400,000 yr, which may be one of the best-documented instances of prolonged evolutionary stasis in a small reptile on an oceanic island. Unfortunately, we still do not know whether the differences it exhibits from other species of *Eumeces* are the result of adaptation to the insular environment of Bermuda or whether the Bermuda skink is an unchanged relict of an ancestral species that has since become extinct on the mainland.

**Fig. 2.** Middle Pleistocene (400,000 yr-old) fossils of the Bermuda skink *Eumeces longirostris*. (A) right dentary USNM 530785; (C) left maxilla USNM 530786 from Calonectris Quarry, compared with a modern individual of the species. (B, D) USNM 549299. Scale = 5 mm.
This tortoise is known from the associated remains of a single individual consisting of nearly the entire skeleton including the tail with its accompanying armor (Meylan and Sterrer, 2000). It was regarded as an endemic species in the extinct fossil genus Hesperotestudo, which is otherwise known from the Oligocene to Pleistocene of North America. Meylan and Sterrer (2000) considered that the ancestors of H. bermudae probably arrived by drifting or rafting from southern North America. There are seemingly only two possibilities that will account for the presence of a specimen of fossil tortoise on Bermuda: (1) A single individual of a species that has never yet been found as a fossil on the mainland happened to reach Bermuda, was fossilized, and then happened to be discovered; or (2) There was once a viable population of a tortoise on Bermuda of which only one individual has yet been discovered. The first possibility is wildly improbable but could be disproved by the discovery of more fossils. If the second possibility pertains, can the geological and extensive paleontological record of Bermuda be reconciled with the fact no other tortoise remains are yet known from the island? We believe that this can be answered in the affirmative, although the geological constraints on the time available for the colonization, evolution, and extinction of H. bermudae would accordingly be quite narrow.

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LITERATURE CITED


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