

Journal of Herpetology, Vol. 40, No. 3, pp. 394–398, 2006
 Copyright 2006 Society for the Study of Amphibians and Reptiles

Geological Constraints on Evolution and Survival in Endemic Reptiles on Bermuda

STORRS L. OLSON,^{1,2} PAUL J. HEARTY,³ AND GREGORY K. PREGILL⁴

¹National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA;
 E-mail: olsons@si.edu

³School of Earth and Environmental Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia

⁴Department of Biology, University of San Diego, San Diego, California 921210-2492, USA

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 tortoise 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 become 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, basi-sphenoid, 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, pelvis, 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. Dorsally, the frontal of *E. longirostris* also bears the vermiculate dermal sculpturing seen in some other scincoids (Estes et al., 1988). The fossil parietals are also consistent with *Eumeces* sensu Griffith et al. (2000; see also Greer, 1970) in not being lateromedially constricted. 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

²Corresponding Author.

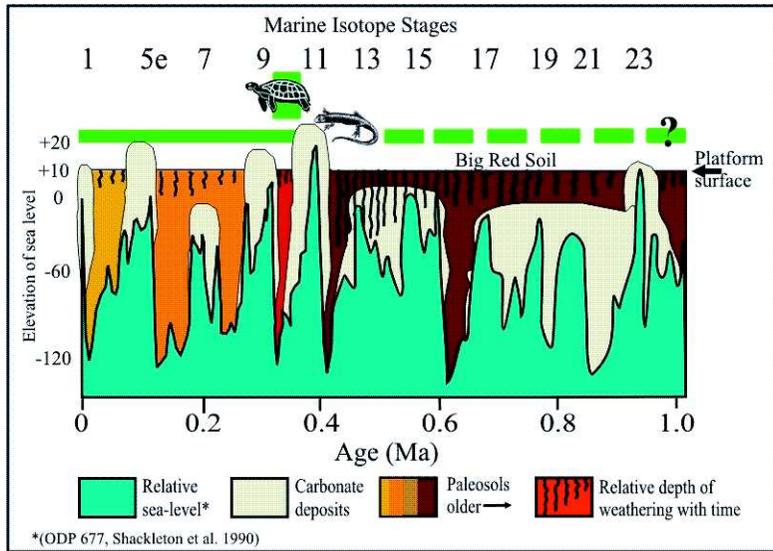


FIG. 1. Schematic summary of Bermuda's sea level and depositional history showing postulated intervals of habitation by the tortoise and skink (green lines). Blue represents proxy sea level changes over the past 1 My (Shackleton et al., 1990). Platform flooding is indicated where blue oscillations cross the -10 m bathymetric contour; hence, carbonate deposition on the platform surface, symbolized by the off-white color. Carbonate deposition may have occurred off the platform as sea level fell below -10 m. Shades of tan, orange, and red represent increasing levels of soil development with greater age of the substrate. The most extreme example from Bermuda is the Big Red Soil, which developed on the early Pleistocene Walsingham Formation over the continuous period from approximately 900,000–450,000 yr ago, up to the onset of MIS 11.

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 chronostratigraphy 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

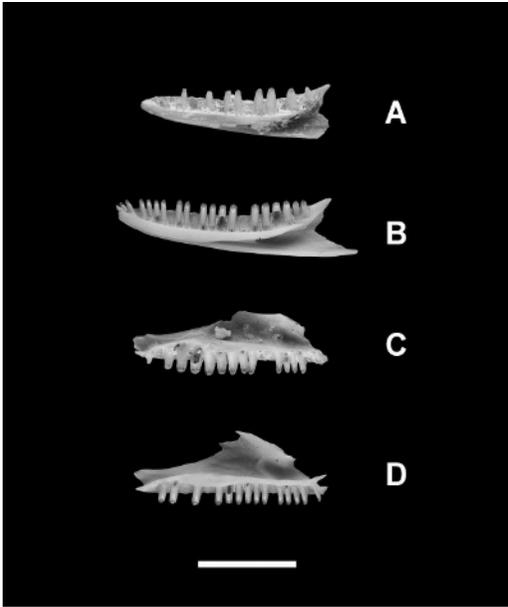


FIG. 2. Middle Pleistocene (400,000 yr-old) fossils of the Bermuda skink *Eumeces longirostris*. (A) right dentary USNM 530785; (C) left maxilla USNM 530786 from Calonectris Quarry, compared with a modern individual of the species. (B, D) USNM 549299. Scale = 5 mm.

centered on 400,000 yr ago, during which sea level rose to $>+ 20$ m, reducing Bermuda to rocky shoals and small islets (Hearty et al.; 1999, Olson and Hearty, 2003). A few fossil vertebrates exist from early MIS 11 dune and beach deposits near sea level and from deposits of the maximum transgression. The rest of Bermuda's vertebrate record is derived from deposits of the subsequent glacial/interglacial oscillations. Sea level during interglacial MIS 7 was not high enough for extensive carbonate deposition (Hearty, 2002) and probably did not have much of an impact on the terrestrial biota, whereas interglacials MIS 9, 5e, and the current MIS 1, are coincident with extinction events when some species disappeared from the island through natural causes.

PALEONTOLOGY OF THE BERMUDA SKINK
EUMECES LONGIROSTRIS

Fossils of *E. longirostris* were found in a variety of deposits and may be considered ubiquitous where sediments have been subjected to fine screening. In addition to the two oldest sites on the island discussed below, we have found bones of *E. longirostris* at the following localities as listed in Olson et al. (2005): Wilkinson Quarry (UWQ1a), Government Quarry (fissure fill upper level), Convolvulus Cave (southeast talus), Sibley's Cave (upper and lower levels), Walsingham Cave, Walsingham Sink Cave, Fern Sink Cave, Spittal Pond. In the main talus cone of Admirals Cave (Hearty et al., 2004), skink bones occurred in all units containing soil sediments (*p*, *r-v*, *x-y*, and an as yet undescribed unit contained within flowstone *z*) as

well as in the west wall red talus. In combination, these deposits span time almost continuously from the penultimate glaciation (MIS 6) through the Holocene.

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.

PALEONTOLOGY OF THE BERMUDA TORTOISE
HESPEROTESTUDO BERMUDA

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 southeastern 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.

The specimen was entombed in eolianite of the Upper Town Hill Formation (Meylan and Sterrer, 2000), which is correlated with MIS 9 (Hearty et al., 1992) dated at about 300,000 years ago, during which sea level reached approximately +3–5 m (Hearty and Kaufman, 2000). Following this was a long, relatively stable period comprising two glacial episodes (MIS 8 and 6) and an intervening highstand (MIS 7) that probably only reached the platform margin (approximately –10 to –15 m; Hearty, 2002; Bard et al., 2002) and probably had little impact on the biota. Fossil vertebrates have been found in abundance on Bermuda at least from the latter part of this interval and throughout subsequent time, with dozens of pitfall accumulations in fissures and karst avens having been discovered and excavated for fossils (Hearty et al., 2004; Olson et al., 2005). Had tortoises been present on the island at any time after MIS 9, their remains would have been found. Therefore, we postulate that if there was a viable population of tortoise on Bermuda, it must have become extinct before MIS 8. As with other known extinction events known on Bermuda (Olson et al., 2005), the disappearance of the tortoise was probably correlated with changes in land area and environment caused by an interglacial rise in sea level. In this case, it would have been the same highstand (MIS 9) in which the only known fossil was deposited, perhaps one of the last of its kind.

If tortoises could not survive the MIS 9 high stand, then they could not have survived the much more severe previous high stand of MIS 11 that nearly submerged all of Bermuda. It is quite possible that another population of tortoise could have inhabited Bermuda during the long period (approximately 500,000 yr) of low sea level that preceded MIS 11, but there is no fossil record of vertebrates from this entire interval. Thus, the earliest that the progenitor of

H. bermudae could have colonized Bermuda was toward the end of the regressive phase of the MIS 11 highstand, when sea levels were falling rapidly (Hearty et al., 1999). Tortoises then had only the MIS 10 glacial interval to evolve into an endemic species before being exterminated by the following rise in sea level during MIS 9. If so, the entire existence of *H. bermudae* would have been confined to a maximum span of approximately 100,000 yr. To date, no fissure fills or cave deposits have been found dating to the MIS 10 glacial period (Olson et al., 2005), which may explain why no other tortoise remains are yet known from Bermuda.

One glacial cycle may seem like a short interval for the evolution of a large, long-lived vertebrate with a low reproductive rate, but the even larger modern tortoise *Geochelone gigantea*, endemic to Aldabra Island in the Indian Ocean, provides a close analogy. Aldabra was completely submerged in the last interglacial (MIS 5), and tortoises had to colonize and evolve since then (Braithwaite et al., 1973), giving the species *G. gigantea* an approximate 100,000-yr life span similar to that postulated for the Bermuda tortoise. With the reduction in land area of Aldabra in the present interglacial, tortoise populations have begun to exert a negative effect on food plants and may exceed “the stable carrying capacity” (Bourn and Coe, 1978:140). Overpopulation has also resulted in loss of shade plants resulting in significant mortality from hyperthermia, both conditions being exacerbated by drought (Bourn et al., 1999). Similar circumstances on Bermuda may have led to the extinction of *H. bermudae* during the MIS 9 highstand.

The cycle of colonization and extinction of tortoises took place at least three times on Aldabra (Braithwaite et al., 1973), whereas as far as we know Bermuda experienced only one colonization, not only because it is more difficult for tortoises to reach but also because the mainland ancestral source went extinct. Probably only the discovery of a fossil deposit of MIS 10 age on Bermuda could resolve whether the island actually harbored an endemic population of tortoise, but this definitely remains a viable possibility.

Acknowledgments.—We are indebted to many for field assistance, especially F. V. Grady and D. B. Wingate. Figure 2 is by B. Schmidt, Division of Birds, USNM. This is contribution 100, Bermuda Biodiversity Project, Bermuda Aquarium, Natural History Museum and Zoo.

LITERATURE CITED

- BARD, E., F. ANTONIOLI, AND S. SILENZI. 2002. Sea-level during the penultimate interglacial period based on a submerged stalagmite from Argenterola Cave (Italy). *Earth and Planetary Science Letters* 609:1–12.
- BOURN, D., AND E. COE. 1978. The size, structure and distribution of the giant tortoise populations of Aldabra. *Philosophical Transactions of the Royal Society of London, series B* 282:139–175.
- BOURN, D., C. GIBSON, D. AUGERI, C. J. WILSON, J. CHURCH, AND S. I. HAY. 1999. The rise and fall of the Aldabran giant tortoise population. *Proceedings of the Royal Society of London, series B* 266:1091–1100.

- BRAITHWAITE, C. J. R., J. D. TAYLOR, AND W. J. KENNEDY. 1973. The evolution of an atoll: the depositional and erosional history of Aldabra. *Philosophical Transactions of the Royal Society of London*, series B 266:307–340.
- ESTES, R., K. DE QUEIROZ, AND J. GAUTHIER. 1988. Phylogenetic relationships within Squamata. In R. Estes and G. Pregill (eds.), *Phylogenetic Relationships of the Lizard Families. Essays Commemorating Charles L. Camp*, pp. 118–228. Stanford University Press, Stanford, CA.
- GREER, A. E. 1970. A subfamilial classification of scincid lizards. *Bulletin Museum of Comparative Zoology* 139:151–184.
- GRIFFITH, H., A. NGO, AND R. W. MURPHY. 2000. A cladistic evaluation of the cosmopolitan genus *Eumeces* Wiegmann (Reptilia, Squamata, Scincidae). *Russian Journal of Herpetology* 7:1–6.
- HEARTY, P. J. 2002. Revision of the late Pleistocene stratigraphy of Bermuda. *Sedimentary Geology* 153:1–21.
- HEARTY, P. J., AND D. S. KAUFMAN. 2000. Whole-rock aminostratigraphy and Quaternary sea-level history of the Bahamas. *Quaternary Research* 54: 163–173.
- HEARTY, P. J., AND H. L. VACHER. 1994. Quaternary stratigraphy of Bermuda: a high-resolution pre-Sangamian rock record. *Quaternary Science Reviews* 13:685–697.
- HEARTY, P. J., H. L. VACHER, AND R. M. MITTERER. 1992. Aminostratigraphy and ages of Pleistocene limestones of Bermuda. *Geological Society of American Bulletin* 104:471–480.
- HEARTY, P. J., P. KINDLER, H. CHENG, AND R. L. EDWARDS. 1999. Evidence for a +20 m middle Pleistocene sea-level highstand (Bermuda and Bahamas) and partial collapse of Antarctic ice. *Geology* 27: 375–368.
- HEARTY, P. J., S. L. OLSON, D. S. KAUFMAN, R. L. EDWARDS, AND H. CHENG. 2004. Stratigraphy and geochronology of pitfall accumulations in caves and fissures, Bermuda. *Quaternary Science Reviews* 23:1151–1171.
- LIEB, C. S. 1985. Systematics and distribution of the skinks allied to *Eumeces tetragrammus* (Sauria, Scincidae). *Contributions in Science Natural History Museum of Los Angeles County* 357:1–19.
- MEYLAN, P. A., AND W. STERRER. 2000. *Hesperotestudo* (Testudines: Testudinidae) from the Pleistocene of Bermuda, with comments on the phylogenetic position of the genus. *Zoological Journal of the Linnean Society* 128:51–76.
- OLSON, S. L., AND 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* 100:12825–12829.
- OLSON, S. L., AND 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 longirostris/elegans* complex (Aves: Rallidae) from the late Pleistocene of Bermuda. *Proceedings of the Biological Society of Washington* 114:509–516.
- OLSON, S. L., D. B. WINGATE, P. J. HEARTY, AND F. V. GRADY. 2005. Prodrum of vertebrate paleontology and geochronology of Bermuda. In J. A. Alcover and P. Bover (eds.), *Insular Vertebrate Evolution: The Palaeontological Approach*, pp. 219–232. *Monografies de la Societat d’Història Natural de les Balears* no. 12.
- PREGILL, G. K. 1986. Body size of insular lizards: a pattern of Holocene dwarfism. *Evolution* 40:997–1008.
- TAYLOR, E. H. 1936. A taxonomic study of the cosmopolitan scincoid lizards of the genus *Eumeces* with an account of the distribution and relationships of its species. *Kansas University Science Bulletin* 23:1–643.
- VACHER, H. L., P. J. HEARTY, AND M. P. ROWE. 1995. Stratigraphy of Bermuda: nomenclature, concepts, and status of multiple systems of classification. *Geological Society of America Special Paper* 300: 269–294.

Accepted: 5 May 2006.