

Introduced delicacy or native species? A natural origin of Bermudian terrapins supported by fossil and genetic data

James F. Parham^{1,2,*}, Mark E. Outerbridge³,
Bryan L. Stuart^{4,5}, David B. Wingate⁶,
Helmut Erlenkeuser⁷ and Theodore J. Papenfuss⁵

¹Department of Herpetology, California Academy of Sciences,
875 Howard Street, San Francisco, CA 94103, USA

²Museum of Paleontology, University of California, Berkeley,
CA 94720, USA

³Bermuda Zoological Society, PO Box FL 145, Flatts FL BX,
Bermuda

⁴Department of Zoology, The Field Museum, 1400 South Lake Shore
Drive, Chicago, IL 60605, USA

⁵Museum of Vertebrate Zoology, University of California, Berkeley,
CA 94720, USA

⁶The Bermuda Audubon Society, PO Box HM 1328,
Hamilton HM FX, Bermuda

⁷Leibniz-Labor für Altersbestimmung und Isotopenforschung,
Universität Kiel, Max-Eyth-Strasse 11-13, 24118 Kiel, Germany

*Author for correspondence (jparham@calacademy.org).

Humans have greatly altered the natural distribution of species, making it difficult to distinguish between natural and introduced populations. This is a problem for conservation efforts because native or introduced status can determine whether a species is afforded protection or persecuted as an invasive pest. Holocene colonization events are especially difficult to discern, particularly when the species in question is a naturally good disperser and widely transported by people. In this study, we test the origin of such a species, the diamondback terrapin (*Malaclemys terrapin*), on Bermuda using a combination of palaeontological (fossil, radiometric and palaeoenvironmental) and genetic data. These lines of evidence support the hypothesis that terrapins are relatively recent (between 3000 and 400 years ago) natural colonizers of Bermuda. The tiny population of Bermudian terrapins represents the second naturally occurring non-marine reptile that still survives on one of the most densely populated and heavily developed oceanic islands in the world. We recommend that they should be given protection as a native species.

Keywords: introduced species; radiocarbon; turtle; Gulf Stream; *Malaclemys terrapin*; mangrove

1. INTRODUCTION

Human activities impact patterns of global biodiversity by causing the extinction of populations through habitat destruction and direct exploitation. Our species has also irreparably modified ecosystems through the intentional and accidental introduction of alien species

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2007.0599> or via <http://journals.royalsociety.org>.

Received 28 November 2007
Accepted 21 January 2008

(Grosholz 2002; Davenport & Davenport 2004). Since the major goal of conservation is to preserve native species, distinguishing between native and introduced biodiversity can determine whether a species is protected or aggressively removed as an invasive pest. Many human-mediated introductions pre-date detailed biodiversity surveys, so it can be difficult to establish whether some species are native (Grady *et al.* 2001; Wares *et al.* 2002; Burdick 2005). Distinguishing between Holocene colonization events and historic human introductions is difficult because such recent dispersal events often lack genetic or palaeontological evidence. This problem is even more challenging when the species is a highly valued and transportable human commodity. The following study investigates such a problem by integrating palaeontological and molecular evidence to unravel the origins of diamondback terrapins (*Malaclemys terrapin*) on Bermuda.

The native terrestrial biodiversity of Bermuda is relatively low (Sterrer *et al.* 2004), substantially diminished by the destruction of the islands' natural habitats following human colonization in the early 1600s, as well as major environmental perturbations associated with changes in sea level over the past 2 Myr (Sterrer *et al.* 2004; Olson *et al.* 2006). The known extant native terrestrial vertebrate fauna consists of a single lizard, the Bermuda rock skink (*Plestiodon* (formerly *Eumeces*) *longirostris*). The first report of terrapins on Bermuda is from the early 1950s (see electronic supplementary material). Since that time, there have been occasional reports from the Mid Ocean Club golf course (figure 1) of terrapins swimming in artificial water hazards and nesting in sand-filled bunkers. These earlier records, and the fossil evidence presented below, did not come to the attention of the Bermuda Biodiversity Project until after the publication of their report on the status of *M. terrapin* (Davenport *et al.* 2005). Bermudian terrapins are still only known from two mangrove-fringed anchialine ponds reported there.

Outside of Bermuda, *M. terrapin* is known from the mangroves and salt marshes of the east coast of the USA from southern Texas to Massachusetts (figure 2). Given its coastal ecology and saltwater tolerance, *M. terrapin* might seem a probable candidate for natural dispersal to Bermuda via the Gulf Stream (e.g. Meylan & Sterrer 2000; Grady *et al.* 2001; Sterrer *et al.* 2004). However, between the early 1800s and the 1920s, terrapins were a highly sought after delicacy. Consequently, terrapins were transported, translocated and farmed in high numbers to meet the gastronomical demand of gourmants (Brennessel 2005; Hauswaldt & Glenn 2005). Combining this history with the fact that most of the Bermudian herpetofauna is introduced (Bacon *et al.* 2006), it remains unclear whether the newly discovered *M. terrapin* in Bermuda result from a pre-human colonization or are descended from individuals once intended for the soup pot.

A museum specimen of a nearly complete skeleton of *M. terrapin* (BAMZ 2006-237-001, see electronic supplementary material) from a cave in Bermuda could shed some light on this issue. Owing to the fact that it was not buried, this specimen cannot be integrated into a stratigraphic framework, and so its age remains an open question. In order to test the origin of *M. terrapin* in Bermuda, we generate

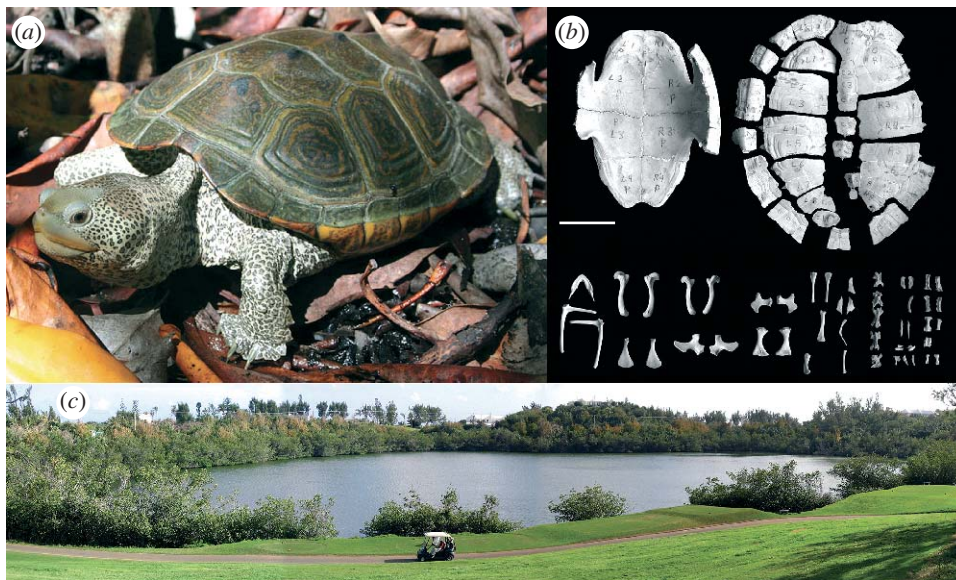


Figure 1. (a) A live Bermudian terrapin; (b) BAMZ 2006-237-001, the fossil terrapin from Bermuda. Scale bar, 5 cm. (c) Habitat of the Bermudian terrapin, a mangrove-fringed pond at the Mid Ocean Golf Course.

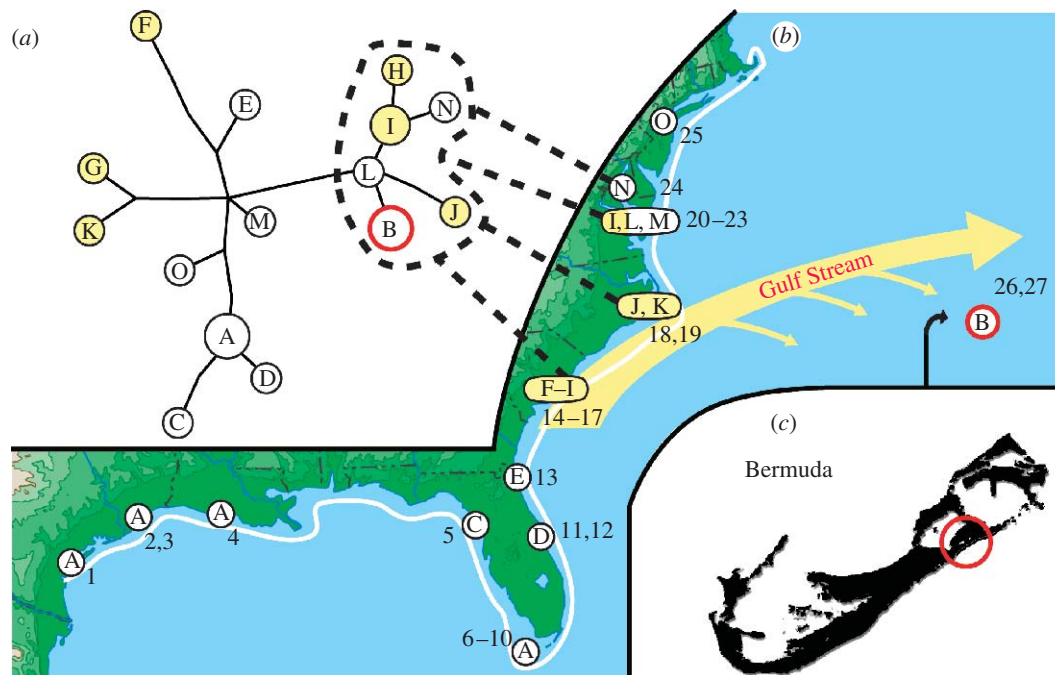


Figure 2. (a) Network of mtDNA (haplotypes). Yellow represents haplotypes in the direct path of the Gulf Stream. (b) Map showing distribution of haplotypes from 27 individuals: (1) southern Texas; (2,3) eastern Texas; (4) Louisiana; (5) western Florida; (6–10) Florida Keys (Barracouta Key, Lois Key, Pigeon Key); (11,12) east Florida, FL; (13) northern Florida; (14–17) South Carolina; (18,19) North Carolina; (20–23) Virginia; (24) Maryland; (25) New Jersey; (26) Bermuda. (c) Map of Bermuda showing location of mangrove-fringed anchialine ponds with terrapin populations.

radiocarbon dates for this fossil. Radiocarbon dates that postdate the beginning of the nineteenth century, when terrapins were widely transported as a popular delicacy, would cast doubt on a natural origin of the Bermudian population. As a secondary line of evidence, we compare DNA from Bermudian terrapins to a range-wide survey of this species. The shortest path from USA to Bermuda, via the Gulf Stream, is from the Carolinas. Since an artificial introduction could occur from any population, genetic data cannot discount anthropogenic translocations. However, genetic affinities to populations far north or south of the Carolinas would argue against a natural origin.

2. MATERIAL AND METHODS

A scale fragment from BAMZ 2006-237-001 was subjected to radiocarbon dating (see electronic supplementary material for details). The conventional radiocarbon date was compared to a calibration curve time to yield a range of possible calendar dates. Owing to marine and freshwater radiocarbon reservoir effects, specimens with a brackish water diet/ecology can give artificially old dates. There are several calibrations available to correct for this, but calibrations for fluctuating brackish environments, such as the anchialine ponds (saline, land-locked bodies of water with subterranean connections to the ocean) that the terrapins inhabit, are logistically implausible. Therefore, we use calibrations based on exclusively terrestrial and marine diets to bracket the age of the specimen (see electronic supplementary material for details). As such, the marine diet calibrations appear to represent a very conservative youngest estimate.

Our genetic survey compared approximately 3 kb of mtDNA from 2 Bermudian samples to 25 samples from USA populations representing all known subspecies (see electronic supplementary material). Owing to the close similarity among all recovered haplotypes (all within 10 nucleotide substitutions), sequence data were visualized using a network rather than a phylogenetic tree (figure 2).

3. RESULTS

The oldest calibrated dates are based on the assumption of a terrestrial diet (AD 1222–1276). The youngest calibrated dates are based on the assumption of a marine diet range (AD 1427–1620; 1σ range = AD 1452–1554). Because Bermudian terrapins do not inhabit a wholly marine environment, we estimate the age of the fossil to be sometime before AD 1620.

Our genetic survey of *M. terrapin* revealed extremely low levels of genetic variation (figure 2) as reported in other studies (Hauswaldt & Glenn 2005). Most of the genetic diversity occurs in the mid-Atlantic states. The Bermudian samples most closely resemble samples from near the Carolina region of USA (H–J, L, N), though we could not identify the exact source population.

4. DISCUSSION

The earliest sightings of Bermuda are *ca* AD 1500, but human settlement of the islands did not occur until much later (AD 1609). The conservative radiometric ages of the fossil sample range from AD 1427 to 1620 (assuming an exclusively marine diet). The majority of this range, including the most likely age range of AD 1452–1554 (1σ), predates human colonization. The latest possible date (before AD 1620) overlaps with the earliest colonists (after AD 1609), but terrapins were not widely eaten by European settlers until the 1800s. Therefore, the argument for an artificial origin of the fossil would depend on a series of non-parsimonious circumstances: (i) the age of BAMZ 2006-237-001, a fossil representing a brackish water species, is in the last decade of the 'exclusively marine diet'-calibrated estimates (AD 1427–1620); (ii) the earliest terrapins were brought to Bermuda 200 years before they were widely eaten by Europeans; and (iii) one of these unusually early terrapins wandered approximately 1 km up hill and fell into a small cave opening to perish. A radiometric date within the last 200 years would obviate most of the implausible events listed above, but the antiquity of our recovered ages (between 400 and 600 years) is more consistent with a natural origin of Bermudian terrapins.

The genetic data suggest that the source population of Bermudian *M. terrapin* is probably from the Carolina region of the mid-Atlantic coast of North America (figure 2). This result is consistent with a natural Gulf Stream-mediated origin, as is known for other Bermudian vertebrates (Meylan & Sterrer 2000; Grady *et al.* 2001; Sterrer *et al.* 2004). The low degree of genetic differentiation between the Bermudian samples and those in the USA (one or two nucleotides) reveals that *M. terrapin* is a relatively recent arrival to Bermuda, unlike the endemic lizard that is thought to be between 400 000 and 2 000 000 years old (Olson *et al.* 2006). This close genetic similarity makes sense in light of the

Pleistocene habitat discontinuity of the islands. Alternating periods of very high and/or very low global sea level every 100 000 years are known to have had major impacts on all of Bermuda's habitats. High sea levels reduced the sub-aerial landmass to a series of tiny islets that precluded the development of a rich terrestrial biota. On the other hand, low sea levels (as recently as 18 kyr ago) would have eliminated all shallow marine warm water biotas, such as the mangroves favoured by the terrapins. During these times, the shoreline was situated well below the Bermuda platform on the steep side slopes of the volcano so no shallow water embayments could have existed.

In combination, the radiometric, genetic and geological data support a Holocene arrival of *M. terrapin* from mainland North America. The final line of evidence refining their age of origin is the establishment of continuous suitable habitat on Bermuda. Throughout its range, *M. terrapin* is restricted to coastal salt marshes and mangroves, but in Bermuda terrapins are only associated with mangroves in anchialine ponds. The Bermudian mangroves are the most isolated and northerly mangroves in the world and happen to be among the last remaining native forests of Bermuda. According to palynological data, mangrove vegetation did not become well established in Bermuda until 3000 years ago when sea level rose above the edge of the Bermuda platform creating shallow water embayments (Ellison 1996). It is unlikely that *M. terrapin* colonization could predate the establishment of this habitat. Therefore, we can predict that terrapins arrived in Bermuda naturally in the Late Holocene, sometime between 3000 and 400 years ago.

Based on the available evidence, *M. terrapin* should be considered the second extant native non-marine reptile on Bermuda and only the third known to ever inhabit the isolated island chain (besides the extant lizard, there is a single Pleistocene fossil of an extinct terrestrial tortoise; Meylan & Sterrer 2000). The native status for Bermudian terrapins resolves its uncertain conservation status and should afford it full legislative protection and appropriate conservation measures.

We wish to thank the numerous kind people and permitting agencies that either collected or facilitated the collection of terrapins (see electronic supplementary material for a complete list). We thank P. M. Grootes, M. Huels, M. Nadeau, and the Leibniz laboratory team for their AMS analysis. Sequencing was conducted in The Field Museum's Pritzker Laboratory for Molecular Systematics and Evolution. Carol Spencer and Carla Cicero of the MVZ are thanked for their help with the accession of museum vouchers. Walter Joyce and three anonymous referees provided helpful comments. This is UCMF contribution no. 1965 and contribution no. 140 of the Bermuda Biodiversity Project (BBP), Bermuda Aquarium, Natural History Museum and Zoo.

Bacon, J. P., Gray, J. A. & Kitson, L. 2006 Status and conservation of the reptiles and amphibians of the Bermuda islands. *Appl. Herpetol.* 3, 323–344. (doi:10.1163/157075406778905063)

- Brennessel, B. 2005 *Diamonds in the marsh*. Lebanon, NH: University Press of New England.
- Burdick, A. 2005 *Out of Eden*. New York, NY: Farrar, Straus and Giroux.
- Davenport, J. & Davenport, J. L. (eds) 2004 *The effects of human transport on ecosystems: cars and planes, boats and trains*, Dublin, Ireland: Royal Irish Academy.
- Davenport, J., Glasspool, A. & Kitson, L. 2005 Occurrence of diamondback terrapins, *Malaclemys terrapin*, on Bermuda: native or introduced? *Chelonian Conserv. Biol.* **4**, 956–959.
- Ellison, J. C. 1996 Pollen evidence of Late Holocene mangrove development in Bermuda. *Glob. Ecol. Biogeogr. Lett.* **5**, 315–326. (doi:10.2307/2997587)
- Grady, J. M., Coykendall, D. K., Collette, B. B. & Quattro, J. M. 2001 Taxonomic diversity, origin, and conservation status of Bermuda killifishes (*Fundulus*) based on mitochondrial cytochrome *b* phylogenies. *Conserv. Genet.* **2**, 41–52. (doi:10.1023/A:1011584318289)
- Grosholz, E. 2002 Ecological and evolutionary consequences of coastal invasions. *Trends Ecol. Evol.* **17**, 22–27. (doi:10.1016/S0169-5347(01)02358-8)
- Hauswaldt, J. S. & Glenn, T. C. 2005 Population genetics of the diamondback terrapin (*Malaclemys terrapin*). *Mol. Ecol.* **14**, 723–732. (doi:10.1111/j.1365-294X.2005.02451.x)
- Meylan, P. A. & Sterrer, W. 2000 *Hesperotestudo* (Testudines: Testudinidae) from the Pleistocene of Bermuda, with comments on the phylogenetic position of the genus. *Zool. J. Linn. Soc.* **128**, 51–76. (doi:10.1006/zjls.1999.0199)
- Olson, S. L., Hearty, P. J. & Pregill, G. K. 2006 Geological constraints on evolution and survival in endemic reptiles in Bermuda. *J. Herpetol.* **40**, 394–398. (doi:10.1670/0022-1511(2006)40[394:GCOEAS]2.0.CO;2)
- Sterrer, W., Glasspool, A., De Silva, H. & Furbet, J. 2004 Bermuda—an island biodiversity transported. In *The effects of human transport on ecosystems: cars and planes, boats and trains* (eds J. Davenport & J. L. Davenport), pp. 118–170. Dublin, Ireland: Royal Irish Academy.
- Wares, J. P., Goldwater, D. S., Kong, B. Y. & Cunningham, C. W. 2002 Refuting a controversial case of a human-mediated marine species introduction. *Ecol. Lett.* **5**, 577–584. (doi:10.1046/j.1461-0248.2002.00359.x)