

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

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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

(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 gourmands (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

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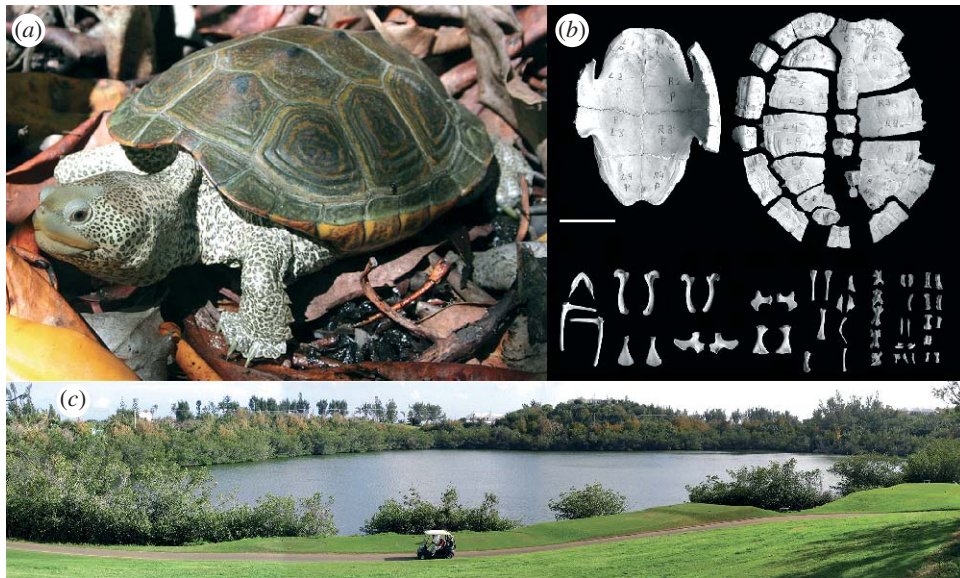


Figure 1. (a) A live Bermudian terrapin; (b) BAMZ 2006-237-001, the fossil terrapin from Bermuda. Scale bar, 5 cm. (c) Habitat of the Bermudian terrapin, a mangrove-fringed pond at the Mid Ocean Golf Course.

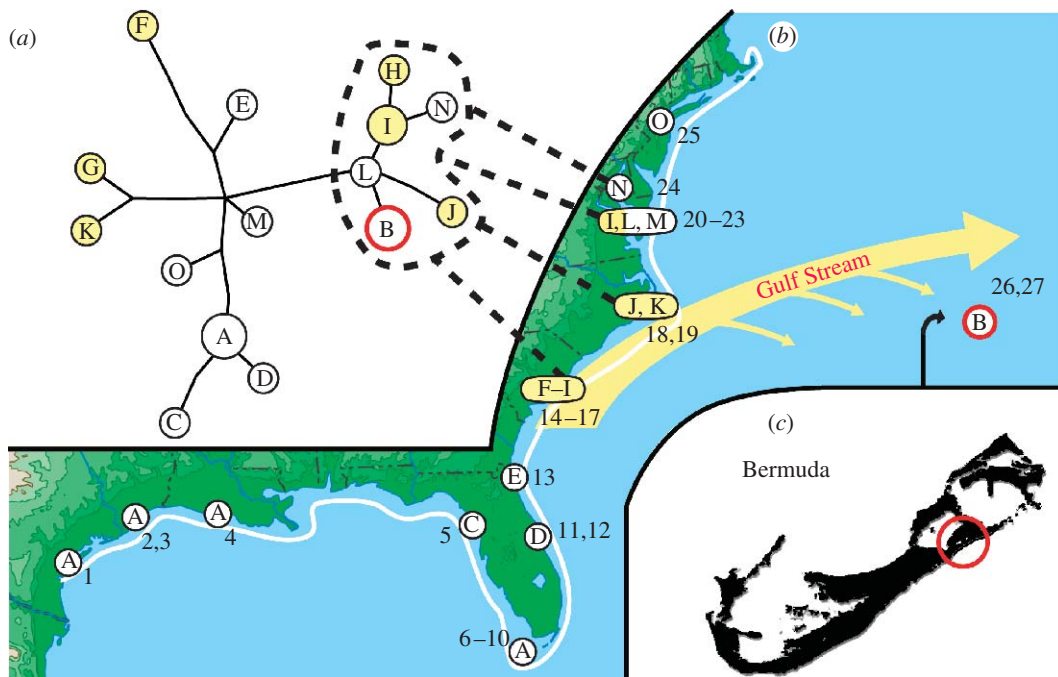


Figure 2. (a) Network of mtDNA (haplotypes). Yellow represents haplotypes in the direct path of the Gulf Stream. (b) Map showing distribution of haplotypes from 27 individuals: (1) southern Texas; (2,3) eastern Texas; (4) Louisiana; (5) western Florida; (6–10) Florida Keys (Barracouta Key, Lois Key, 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.

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ELECTRONIC SUPPLEMENTARY MATERIALS

Parham, J. F., Outerbridge, M. E., Stuart, B. L., Wingate, D. B., Erlenkeuser, H. & Papenfuss, T. J. Introduced delicacy or native species? A natural origin of Bermudian terrapins supported by fossil and genetic data. *Biology Letters*.

Discovery of *Malaclemys terrapin* on Bermuda

The first documented specimen of *Malaclemys terrapin* on Bermuda was between 1950 and 1953. One of us (DBW), found a recently dead and rat-gnawed terrapin later confirmed as this species at South Pond, a water trap pond on the Mid Ocean golf course. At that time, golf course employees were already well aware of their presence in Mangrove Lake and reported nesting in the sand bunkers. The second specimen record is the fossil BAMZ 2006-237-001 (see separate section below). Occasional specimens were captured in Mangrove Lake, photographed and released in the 1970's, but the most unusual record obtained at this time was a live juvenile that was found in a tidepool on Crawl Point, Hamilton Parish on May 10th, 1974, and photographed by DBW (Fig 1). This record was of especial interest because the location was on the northwest facing coast of the island, i.e., on the opposite side of Bermuda from the known breeding population and might conceivably have been a drift vagrant from the American continent. More extensive documentation of the terrapins in Mangrove Lake began in the mid 1990's with the initiation of the Bermuda Biodiversity Project (Davenport et al 2005).

Fossil specimen discovery and identification

BAMZ 2006-237-001 was discovered on the 23rd of January, 1974, in a cave in Hamilton Parish, Bermuda, and subsequently collected by DBW (Wingate, unpublished natural history diaries). The cave is one of several deep fissure openings along the cliff face on the south side of Paynter's Hill, approximately 50 m above sea level. A steeply sloped dry soil talus was present inside the cave immediately below a vertical chimney hole near the entrance, which was littered with bones of the cahow (or Bermuda Petrel) *Pterodroma cahow* and Audubon's shearwater *Puffinus lherminieri*. The terrapin bones were located towards the bottom of the talus in an upright position, as if the specimen died there. The skeletal remains were only partly disarticulated with the central segments of the carapace collapsed inwards, the skull was missing, and the lower dentary was at the posterior end. The appendicular skeleton was incomplete, but most of the major bones in both the pectoral and pelvic girdles were present. However, virtually all of the carpals, metacarpals, tarsals, metatarsals and phalanges were missing. Additionally, a number of scales were present, although all were separated from the underlying bones. The straight mid-line carapace and plastron lengths measured 205 mm and 144 mm respectively.

BAMZ 2006-237-001 was first identified as *M. terrapin* in 1976 by Dr. Archie Carr, Graduate Research Professor, Department of Zoology, University of Florida. We provide the following diagnosis (based on pers. comm. with P. A. Meylan [Eckerd College] and reviewer W. G. Joyce [Yale University]): The broad shape of the plastron, the absence of mesoplastra, the absence of extragular and supramarginal scales, and the reduction of inframarginal scales suggest a member of Testudinoidea (including *Platysternon* [see Parham *et al.* 2006]). The skeleton clearly does not represent a land tortoise (family Testudinidae) since the bridge peripherals are not enlarged. Only in members of the emydid subfamily Deirochelyinae (*Deirochelys*, *Graptemys*, *Malaclemys*, *Trachemys*, *Pseudemys* and *Chrysemys*) are the plastral buttresses long

enough to contact the overlying costal bones (Joyce & Bell 2004). Among deirochelyine emydids, the moderately broad triturating surface without any ridges or troughs is also consistent with an assignment of the material to *Malaclemys* or *Graptemys*, but the low medial carapacial ridge is unique to *Malaclemys*. *Malaclemys* is also unique in having deeply incised growth rings preserved on distal portions of the costals (Dobie & Jackson 1979). These concentric growth rings are very obvious on lateral portions of all of the costals in the Bermuda subfossil. Although the skull is missing, the dentary is present.

Radiocarbon dating

A nearly rectangular scale fragment (43 mg, 120 μm thick, 20x15 mm) was finely scraped, under a binocular, on both sides (26 % weight loss) to reject possible post-mortem contamination by secondary organics (fungi, algae). The chip finally showed a uniform milky appearance all over its area. Further cleaning applied acetone to remove possible traces of formerly applied moth ball fumes (naphthalene), three times for 4 min in an ultrasonic bath plus a final 3 hr bath, drying, leaching with 1 % HCl overnight (removing carbonates), 1 % NaOH at 60 °C for 4 hr (extracting humics), and 1 % HCl (rejecting infiltrated atmospheric CO₂) before the chip was washed neutral. 8 mg were combusted to CO₂ in a closed quartz tube together with CuO and silver wool at 900 °C. The sample CO₂ was reduced with H₂ over about 2 mg of Fe powder as catalyst, and the resulting carbon/iron mixture was pressed into a pellet in the target holder for AMS analysis (Nadeau *et al.* 1998).

The ¹⁴C concentration of the sample was measured by comparing the simultaneously collected ¹⁴C, ¹³C, and ¹²C beams of the sample with those of Oxalic Acid ¹⁴C standard

CO₂ and coal background material. The conventional ¹⁴C age was calculated according to Stuiver & Polach (1977) with a ¹³C correction for isotopic fractionation based on the ¹³C/¹²C ratio measured by AMS simultaneously with the ¹⁴C/¹²C ratio (this ¹³C/¹²C includes any fractionation during graphitization and in the AMS-system and, therefore, can only roughly be compared with ¹³C values from an isotope ratio mass spectrometer on CO₂). The uncertainty in ¹⁴C (standard deviation) considers both the counting statistics and the variability of the interval results making up the total measurement, and includes the uncertainties of background and standard. Terrestrial calendar age calibration (Fig. 2) follows CALIB rev 4.3 (Data set 2, 1998; Stuiver *et al.* 1998), the marine aspect was calibrated on-line via CALIB rev 5.0.2 (data set: marine04.C14; Stuiver & Reimer 1986-2005 used in conjunction with Stuiver & Reimer 1993). The δ¹³C value is heavy (-14.57 ± 0.30 ‰PDB) and could be indicative of a significant marine influence in the diet.

Radiocarbon ages have to be translated into calendar ages through calibration. Systematic ¹⁴C deviations in the ecosystems providing the animal's diet, from the atmospheric ¹⁴C level play a crucial role as so-called reservoir effects. Since *M. terrapin* inhabit brackish environments, marine, terrestrial, and fresh water ¹⁴C are mixed up. Therefore, calibrating alternatively for a primarily terrestrial or for a totally marine diet would provide a bracket of possible dates.

The calibration diagrams (Figs. 2-3) show the calendar age on the x-axis and the ¹⁴C age on the ordinate. The diagonally running track is the calibration curve (or calibration band with the errors included) relating ¹⁴C age and calendar age. The measured ¹⁴C age (as the estimate of the unknown true ¹⁴C age) and the probability distribution of the true ¹⁴C age are shown along the ordinate. Projecting the ¹⁴C age

through the calibration curve onto the x-axis reveals a band, more or less wide, of the possible calendar ages and their probabilities. This distribution is shown along the x-axis and should be considered the calibrated result of the ^{14}C dating process. Assuming a terrestrial diet, the calibrated ages range from AD 1222-1282 (95% range, Fig.2). Assuming a totally marine diet (Figs. 3), the calibrated ages range from AD 1473-1620. The marine reservoir effect around Bermuda is close to the general level ($\Delta R=0$); a possible local deviation ($\Delta R=48\pm 40$ ^{14}C yr, Stuiver & Reimer 1986-2005) should have little effect and is not considered here.

Bermudian terrapins inhabit brackish anchialine ponds that are largely determined by tidal flushing (Thomas et al, 1991). Supposing a diet from a marine water dominated ecosystem appears to be given support by the comparatively heavy $\delta^{13}\text{C}$, but this $\delta^{13}\text{C}$ would not contradict a significant contribution of a terrestrial diet on Hatch-Slack plants, such as grasses. The freshwater reservoir effect in the carbonate environment of Bermuda may range between the extremes of 5500 ^{14}C yr for DIC freshly dissolved from fossil carbonate by modern humus CO_2 to 0 ^{14}C yr if dominated by gas exchange with humus or atmospheric CO_2 (cf. Mook 1980). Given the generally low fraction of (possibly ^{14}C -deficient) fresh water in the ponds (Thomas et al, 1991), assuming a more common range for the fresh water reservoir effect, such as 1500 ^{14}C yr as in NW European groundwaters (Münnich, 1968), 1000 yr in lakes of N Germany or less (Willkomm & Erlenkeuser, 1972), and presuming a diet recruited at comparable parts from ^{14}C reduced brackish and normal ^{14}C terrestrial sources, all these unknowns may be fairly summarized by adopting the figure of the marine reservoir effect (400 yr, i.e., $\Delta R=0$ in the calibration procedure,

Fig. 3) as a bracket for the ^{14}C -age offset to be taken into account. Accordingly the youngest date of the marine diet estimates (~1620 AD) is considered overly conservative.

DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from tissues using PureGene Animal Tissue DNA Isolation Protocol (Gentra Systems, Inc.) or DNeasy Blood & Tissue Kit (Qiagen). A 655 bp fragment of mitochondrial DNA that encodes part of the control region (CR) gene was amplified by PCR (the polymerase chain reaction; 94°C 45s, 55°C 30s, 72°C 1 min) for 35 cycles using the primers DES-1 and DES-2 (Starkey *et al.* 2003). A 2,325 bp fragment of mitochondrial DNA that encodes part of the tRNA Gly gene, the complete NADH dehydrogenase subunit 3 gene, the complete tRNA Arg gene, the complete NADH dehydrogenase subunit 4L gene, the complete NADH dehydrogenase subunit 4 gene, the complete tRNA His gene, the complete tRNA Ser gene, and part of the tRNA Leu gene (ND3-ND4) was amplified by PCR (94°C 30s, 48°C 30s, 68°C 3 min) for 37 cycles using LA Taq (TaKaRa) and the primers L-Gly (5'-ACTYTTCTAGTATAATAGTAC-3') and H-Leu (Stuart and Parham 2004). PCR products were electrophoresed in a 1% low melt agarose TALE gel stained with ethidium bromide and visualized under ultraviolet light. The bands containing DNA were excised and agarose was digested from bands using GELase (Epicentre Technologies). PCR products were sequenced in both directions by direct double strand cycle sequencing using Big Dye version 3 chemistry (Perkin Elmer). The amplifying primers were used in cycle sequencing reactions of both mitochondrial fragments. The internal primers L-ND4int5' (5'-CCAAATAGAACGGCTAAACGC-3'), L-ND4int3' (5'-

AGCCCGAAACATACTACT-3'), H-ND4L (5'-GCCATGAGTTCGTGAGGATGC-3'), and H-ND4int5' (5'-ACTGCTGCTAGGATTATTGA-3') were also used in cycle sequencing reactions of the ND3-ND4 fragment. Cycle sequencing products were precipitated with ethanol, 3 M sodium acetate, and 125 mM EDTA, and sequenced with a 3730 DNA Analyzer (ABI). Sequences were edited and aligned using Sequencher v. 4.1 (Genecodes). Sequences were deposited in GenBank under accession numbers EU407553-EU407606.

Locality and voucher information

Specimens: 1) MVZ 257690. GPS: 27° 51.046' N, 97° 28.977' W. Nueces Bay, Corpus Christi, Nueces Co., Texas. June 4, 2006 [haplotype A]; 2) MVZ 257688. Galveston Island, Galveston Co, Texas. Jun 1, 2006 [haplotype A]; 3) MVZ 257689. South Deer Island, Galveston Bay, Galveston Co, Texas. June 1, 2006 [haplotype A]; 4) MVZ 257704. GPS: 29.230° N, 90.9742° W. Bay Voisin, Terrebonne Parish, Louisiana. September 12, 2006 [haplotype A]; 5) MVZ 257683. GPS: 28.8010° N, 82. 7390° W. Long Gap Key, St. Martins Key, 6.0 miles (airline) west of Homosassa, Citrus Co., Florida. May 17, 2006 [haplotype C]; 6) MVZ 257701. GPS: 24.5482° N, 81.9194° W. Barracouta Key, 6.0 miles (airline) west of Key West, Monroe Co., Florida. July 9, 2006 [haplotype A]; 7) MVZ 257702. GPS: 24.5482° N, 81.9194° W. Barracouta Key, 6.0 miles (airline) west of Key West, Monroe Co., Florida. July 9, 2006 [haplotype A]; 8) MVZ 257697. Lois Key, Monroe Co., Florida. July 7, 2006 [haplotype A]; 9) MVZ 257698. Lois Key, Monroe Co., Florida. July 7, 2006 [haplotype A]; 10) MVZ 257694. GPS: 25° 03.353' N, 80° 30.748' W. Pigeon Key, 3.5 miles (airline) north of Tavernier, Monroe Co., Florida. July 5, 2006 [haplotype A]; 11) MVZ 257693. GPS: 28° 24.74' N,

80° 43.27' W. Adjacent to BC-30 Spoil Island just north of 528 Causeway on Merritt Island at east side of Indian River, Brevard Co., Florida. April 4, 2006 [haplotype D]; 12) MVZ 257703. GPS: 28° 24.8' N, 80° 43' 30" W. Spoil Island just north of 528 Causeway on Merritt Island at east side of Indian River, Brevard Co., Florida. June 15, 2006 [haplotype D]; 13) MVZ 257682. 30.6492° N, 81. 4763° W. Jackson Creek off the Amelia River, Nassau Co., Florida. May 14, 2006 [haplotype E]; 14) MVZ 250655. GPS: 32° 44.69' N., 79° 53.51' W. Charleston Harbor, 1.1 miles (airline) southwest of Fort Sumter, Charleston Co., South Carolina, September 29, 2005 [haplotype F]; 15) MVZ 250656. GPS: 32° 49.84' N., 79° 59.75' W. Ashley River, Charleston Co., South Carolina. Oct. 3, 2005 [haplotype G]; 16) MVZ 250654. GPS: 32° 44.69' N., 79° 53.51' W. Charleston Harbor, 1.1 miles (airline) southwest of Fort Sumter, Charleston Co., South Carolina, September 29, 2005 [haplotype H]; 17) MVZ 250657. GPS: 32° 49.50' N., 80° 00.83' W. Ashley River, Charleston Co., South Carolina. Oct. 3, 2005 [haplotype I]; 18) MVZ 250648. GPS: 35° 07.17'N, 75° 58.61'W. Ocracoke Village, Ocracoke Island, Hyde Co., North Carolina. Aug. 9, 2007 [haplotype J]; 19) MVZ 250649. GPS: 35° 07.17'N, 75° 58.61'W. Ocracoke Village, Ocracoke Island, Hyde Co., North Carolina. Aug. 9, 2007 [haplotype K]; 20) MVZ 250650. GPS: 37° 57.62' N, 75° 20.54' W. 0.3 miles (airline) southeast of Archie Cove, Chincoteague Island, Accomack Co., Virginia. Aug. 17, 2005 [haplotype I]; 21) MVZ 250652. GPS: 37° 55.52' N., 75° 20.77' W. Chincoteague Inlet from Assateague Channel at Pine Drive, Chincoteague Island, Accomack Co., Virginia, Aug. 18, 2005 [haplotype I]; 22) MVZ 250651. GPS: 37° 57.62' N, 75° 20.54' W. 0.3 miles (airline) southeast of Archie Cove, Chincoteague Island, Accomack Co., Virginia. Aug. 17, 2005 [haplotype L]; 23) MVZ 257680. GPS:

37° 55.52' N., 75° 20.77' W. Chincoteague Inlet from Assateague Channel at Pine Drive, Chincoteague Island, Accomack Co., Virginia, Aug. 18, 2005 [haplotype M]; 24) MVZ 250653. GPS: 38° 23.205' N, 76° 17.000' W. Chesapeake Bay, Dorchester Co., Maryland. Aug. 16, 2005 [haplotype N]; 25) MVZ 257681. Benny's Landing Road, Stone Harbor, Cape May Co., New Jersey. Coll. June 2, 2002 [haplotype O]; 26) MVZ 250646. GPS: 32° 19,17'N, 64° 42.33' W. Artificial pond adjacent to Mangrove Lake between 7th and 8th holes at Mid-Ocean Golf Course, Hamilton Parish, Bermuda. Aug. 4, 2005 [haplotype B]; 27) MVZ 250647. GPS: 32° 19,17'N, 64° 42.33' W. Artificial pond adjacent to Mangrove Lake between 7th and 8th holes at Mid-Ocean Golf Course, Hamilton Parish, Bermuda. Aug. 4, 2005 [haplotype B].

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Figures

Figure 1. Photograph of a *Malaclemys terrapin* found in a tidepool on Crawl Point, Hamilton Parish, Bermuda on May 10th, 1974.

Figure 2. Calibration of radiocarbon age presuming a totally terrestrial diet. The calendar age (AD) is on the x-axis and the ^{14}C age (BP) is on y-axis. Radiocarbon Age: BP 773 \pm 22. Calibrated age: 1267 AD. 1 σ -range: 1247-1280 AD (probability 68.3%); 2 σ -range: 1222-1282 AD (probability 95.4%).

Figure 3. Calibration of radiocarbon age assuming an exclusively marine diet (applying $\Delta\text{R} = 0.0 \pm 0.0$). The calendar age (AD) is on the x-axis and the ^{14}C age (BP) is on y-axis. 1 σ -range (dark grey): 1487-1554 AD (probability 68.3%). 2 σ -range (light grey): 1473-1620 AD (probability 95.4%).

