



Reinterpretation of the Climatic Adaptation of Giant Fossil Tortoises in North America

Don Moll¹ & Lauren E. Brown²

¹Department of Biology, Missouri State University, Springfield, Missouri 65897 USA

²School of Biological Sciences, Illinois State University, Campus Box 4120, Normal, Illinois 61790-4120 USA

“dogmas are brittle structures” Arthur Koestler (1971)

Over a half-century ago, C. W. Hibbard proposed a climate theory based on imported living giant tortoises (“*Geochelone*”) as proxies that suggested the climate adaptations of giant fossil tortoises of the Cenozoic Era (65.5 million years ago to present) were subtropical or tropical across much of North America. This has been a prominent and enduring paleoclimate theory. We show that incorrect assumptions and other problems invalidate this theory. Seven alternative concepts are presented that suggest North American fossil giant tortoises could have evolved necessary adaptations including cold-adaptive morphology, behavioural thermoregulation, burrowing, use of caves as shelters, tolerance of prolonged cessation of food consumption, cryoprotection and supercooling (protection from freezing), and gigantothermy (metabolic and structural thermoregulation) to survive northern winters and in montane areas. This study illustrates the potential danger of using an inappropriate proxy to predict past climates.

Key words: Testudinidae; *Geochelone*; *Hesperotestudo*; giant tortoises; fossils; climate; morphology; behavioural thermoregulation; burrowing; caves; feeding cessation; cryoprotection; supercooling; gigantothermy; proxies

INTRODUCTION

Palaeontologists have long had a great interest in past climates, as knowledge of climates often enhances understanding the biology of fossil organisms. However, numerous palaeoclimatic publications are quite controversial (e.g., Ostrom, 1971; Sloan & Barron, 1990; Chambers, 2012). The eminent vertebrate palaeontologist Claude W. Hibbard proposed a palaeoclimatic theory over a half-century ago (Hibbard, 1960) based on imported giant living tortoises (“*Geochelone*”) from the Galápagos Islands as a proxy (a particular feature that is chosen to act as a substitute for another feature). He suggested that the climate occupied by the giant fossil tortoises of the Cenozoic Era (65.5 million years ago to the present) was subtropical or tropical across North America based on survivability of Galápagos tortoises in the southern USA.

Hibbard (1960) examined survival records (compiled by Townsend, 1931a) of imported living tortoises (“*Testudo vicina*”). These tortoises were collected on Albemarle Island in 1928 during an expedition funded by the New York Zoological Society (Townsend, 1931a, 1931b). They were distributed to zoological gardens at nine locations in five states in the southern USA: San Diego, California; Superior, Arizona; New Orleans, Louisiana; Houston and San Antonio, Texas; and Brighton, Opa-Locka, Biscayne Island, and Lignum Vitae Island, Florida. Some of the

tortoises soon died in winter before shelters were provided. At San Diego, “post-mortem examinations” were performed, but it is unclear if these were done by a veterinarian. The tortoises were postulated to have died from enteritis which was thought to be caused by cold exposure. However, Townsend (1928) indicated that the tortoises distributed to zoological gardens in the southern USA were juveniles and mostly of small size. Those tortoises would have been much more susceptible to death from cold exposure (if that was the cause) than larger adult animals whose deep core temperature would have provided greater resistance to change. Furthermore, the number and percent dead are unavailable, and little information was provided on their care and housing, which was often notoriously poor in that time period.

The colony on Lignum Vitae Island in the Florida Keys had no survival problems. After early losses at some other localities, survivors were provided with shelter and later moved to southern Florida (Townsend, 1931). Hence, Hibbard (1960) concluded that the giant fossil tortoises of North America during the Cenozoic must have inhabited an equable subtropical or tropical climate which was supposedly typical for the extant proxies of the Galápagos Islands.

A year later (1961), Brattstrom proposed the same palaeoclimatic theory as Hibbard (1960) for giant fossil tortoises in North America. However, Brattstrom (1961)

Correspondence: Don Moll (donmoll@missouristate.edu)

did not cite Hibbard (1960) and was presumably unaware of the latter's paper. By priority, Hibbard (1960) is considered as the originator of the theory and Brattstrom (1961) was not cited very often in that regard. In contrast, Hibbard's theory was widely cited in subsequent decades including the present (e.g., Uyeno & Miller, 1962; Neill, 1964; Auffenberg & Milstead, 1965; Martin & Guilday, 1967; Feduccia, 1968; Harbour, 1969; Lundelius, 1972; Auffenberg, 1974; Axelrod, 1975; Jackson & Kaye, 1975; Voorhies, 1975; Morafka, 1977; Thomasson, 1980; Graham, 1986; King & Saunders, 1986; Holman, 1987; Parmley, 1988; Paul, 1988; Webb & Barnosky, 1989; Karlstrom, 1991; Thompson, 1991; Curry & Follmer, 1992; Mack et al., 1994; Popov et al., 1994; Holman, 1995; Thompson & Fleming, 1996; Cassiliano, 1997; Perez-Arлуca et al., 2000; Lundelius, 2003; Wyckoff et al., 2003; Holman & Fritz, 2005; Morgan & Lucas, 2005; Markwick, 2007; Curry et al., 2010; Morgan & Emslie, 2010; Francis et al., 2012; Rempel, 2012). Thus, Hibbard (1960) presented what became perhaps the most prominent, enduring palaeoclimatic theory involving many groups of organisms. There have been some criticisms of Hibbard's theory (Morafka, 1977; Graham, 1986; Paul, 1988), but these have been of limited scope and impact.

Our objective is to show that faulty assumptions, failure to consider contrary evidence (some of which was not readily available in 1960 when Hibbard's theory was published), and other problems invalidate the theory. Moreover, seven alternative concepts are presented which suggest the evolution of adaptations for cold tolerance can provide a plausible explanation for the presence of giant fossil tortoises in northerly and montane areas in the Cenozoic of North America, which could have been colder than Hibbard's (1960) theory suggested.

METHODS

A comprehensive literature survey following the methodology of Brown et al. (2008) was carried out that retrieved hundreds of references which (1.) cited Hibbard's (1960) theory or (2.) suggested alternatives to his climatic theory. The former extended from 1960 to the end of March 2016 whereas the latter extended from 1705 to the end of June 2016. Four search engines were used: Google; Google Scholar (Advanced Scholar Search); JSTOR Advanced Search; and Metacrawler Advanced. Searches used numerous combinations of search words. Traditional library-based searches of paper sources were also carried out at Milner Library, Illinois State University (including many from deep storage and on microfilm), as well as LEB's and DM's extensive herpetological libraries. Alan Resetar of the Field Museum of Natural History, Chicago, kindly supplied some copies of additional references, a photograph, and unpublished documents. Janice Moll and Evan Brown also supplied important references. Interlibrary loan and I-Share were used extensively to acquire copies of references that could not be obtained locally. Pertinent portions of references written in French and German were translated by LEB.

Scientific and common names of extinct fossil and subfossil tortoises follow Bramble (1971); Auffenberg (1974); Turtle Taxonomy Working Group (2014); and Turtle Extinctions Working Group (2015). Scientific and common names of extant tortoises and other turtles follow the Turtle Taxonomy Working Group (2014).

EVIDENCE AGAINST THE THEORY

We present five main lines of evidence against Hibbard's palaeoclimatic theory: fundamental scientific error; faulty assumptions about climate and environment on the Galápagos Islands; incorrect taxonomy; abbreviated time frame, distribution, and number of species; and failure to consider evolution below the generic level.

Fundamental scientific error

Hibbard (1960) assumed that absence of data concerning a particular feature ("there is no evidence ...") meant that the particular feature did not exist. This is a fundamental scientific error. It made the assumption that he had comprehensive mastery of the vast literature on both extant and extinct giant tortoises in 1960 (this was before the existence of search engines), and that there would be no future discoveries in this area. This goes against basic human logic and we prove that he was wrong in the following sections of this paper.

Faulty assumptions about climate and environment on the Galápagos Islands

A number of in-depth studies have been completed on the climate and environment of the Galápagos Islands (e.g., Darwin, 1846; Lack, 1947 [1961]; Alpert, 1963; Hamann, 1979, 1981; Grant & Boag, 1980; Colinvaux, 1984; Steadman, 1986; Trueman & d'Ozouville, 2010). The predominant environment of all the islands is arid scrub desert, reflecting the islands' presence in the Pacific dry zone. This environment consistently occurs on the many low altitude small islands (which are the majority) as well as the lowlands of the five largest islands. The latter have greater elevation because of the presence of active and inactive volcanos. Precipitation increases and temperature decreases as altitude increases on the larger islands, with the humid highlands being heavily forested. While, nine physiognomic formation classes based on vegetation have been described (Hamann, 1981), arid scrub desert of the lowlands and humid forests of the highlands are the major environments present. The giant tortoises occupy and travel between both lowlands and highlands (Pritchard, 1996; Blake et al., 2013; Blake et al., 2015).

The climate is strongly seasonal with a hot rainy season (January through April) and cooler dry season (May through December). Thus, the climate is not equable. For an equatorial region, it is often cool and considered temperate. Hamann (1979:108) concluded: "Hence, conditions for the development of tropical wet or tropical rain forest are not present in the archipelago."

Incorrect taxonomy

The most significant incorrect assumption made by

Hibbard (1960) was that living Galápagos and giant North American fossil tortoises were of the same genus and thus closely related. However, marked changes have occurred since 1950 in the taxonomy of giant fossil tortoises of North America. In a major revision of the tortoises of the Western Hemisphere, Williams (1950) established the new subgenus *Hesperotestudo* (type species: *Testudo osborniana* Hay [1904]) for most Nearctic species (excluding *Gopherus* and a few others). Bramble (1971) subsequently elevated *Hesperotestudo* to generic status based on extensive morphological differences including the expansive presence of dermal ossicles. The genus *Geochelone* was restricted to the Old World, and it may not even be a valid genus (Bramble, 1971). Subsequently, Meylan & Sterrer (2000) concluded that *Hesperotestudo* belongs in the distinct subfamily Xerobatinae along with *Gopherus* and *Xerobates*. The authenticity of the genus *Hesperotestudo* has now been accepted by many chelonian researchers (Turtle Extinctions Working Group, 2015). Its distant evolutionary relationship from *Geochelone* indicates that species in each genus are likely to have independently evolved different traits, thus invalidating Hibbard's (1960) model.

Abbreviated time frame, distribution, and number of species

Hibbard (1960) emphasised the Late Cenozoic Era, Pliocene Epoch through Pleistocene Epoch, 5.3 million to 11,700 years ago. However, *Hesperotestudo* is currently known over a much greater time span, the Oligocene Epoch to the Late Pleistocene Epoch, 33.9 million to 12,000 years ago (Meylan & Sterrer, 2000).

Hibbard (1960) mainly discussed "*Geochelone*" from the Great Plains ("High Plains") of the central USA, but *Hesperotestudo* is known at many localities across the continent from California (*H. dehisca*) on the west coast, to Pennsylvania (*H. percassa*), and Delaware (*H. ducatelli*) in the east, and from Saskatchewan (*H. exornata*) in the north, to Texas (*H. turgida*) and Florida (*H. incisa*) in the south (Lambe, 1906; Bramble, 1971; Auffenberg, 1974; Parris & Daeschler, 1995; Holman, 1998). Many of the numerous locality records were discovered long before 1960. Hibbard (1960) was also apparently unaware that there was a number of pre-1960 records of fossil giant tortoises from montane areas of western North America. Hence, he provided no explanation for how they responded to cold weather.

Hibbard (1960) only mentioned four species of "*Geochelone*" (*niobrarenensis*, *orthopygia*, *rexroadensis*, and *turgida*) although he was aware (Hibbard 1944) of at least two other species, *riggsi* and *osborniana*. The number of species in *Hesperotestudo* is still unclear for a number of reasons. However, Meylan & Sterrer (2000) indicated there were 32 species in Auffenberg's (1974) checklist, not all being giants. Many of these species were described long before 1960. Furthermore, a number of new species have been described since 1974.

Failure to consider evolution below the generic level

Hibbard (1960) apparently did not realise that adaptive evolution must have occurred in "*Geochelone*," having

been in North America over millions of years. The genus was treated as if it was a single invariable species in an "equable climate" with no major deviation (Hibbard, 1960). However, different species typically show considerable inter- and intraspecific adaptive evolution. For example, among living North American chelonians, 19 of 45 species (Conant & Collins, 1998; Stebbins, 2003) have distributions from the southern USA into the northern USA and Canada, and have evolved adaptations to live at both climatic extremes.

ALTERNATIVES

We present seven alternatives to Hibbard's (1960) theory: cold-adaptive morphology, behavioural thermoregulation, burrowing, use of caves as shelters, tolerance of prolonged cessation of food consumption, cryoprotection and supercooling, and gigantothermy. Since there is no direct biological evidence available (except morphology) from the fossil giant tortoises, the alternatives had to be made by measured extrapolation from accepted scientific publications on adaptations of extant tortoises and to a limited extent other extant chelonians.

Cold-adaptive morphology

The thick shell of *Hesperotestudo* provided a good thermal barrier against cooling (Paul, 1988). Leidy (1889) indicated the thickness of the hyoplastron of the holotype of *H. crassiscutata* as 46 mm, and Bentley & Knight (1998) found shell fragments at 40 mm thick for another individual of the same species. When the legs, head, and tail were withdrawn under the carapace, no elongated body parts were exposed to the cold. Surface area was hence reduced and loss of heat was attenuated. Thus, a dorsally domed and ventrally flattened shell with retracted body parts was an ideal shape for heat conservation. Cope (1878) indicated that the posterior free border of the carapace of the *H. orthopygia* he described is quite flared outward. This flaring (Figure. 1) is common in other species of *Hesperotestudo* and many other extant and extinct turtles and tortoises (e.g., *H. impensa*, *H. osborniana*, Marginated Tortoise *Testudo marginata*, Impressed Tortoise *Manouria impressa* [see illustrations in Hay, 1908; Obst, 1986; and Orenstein, 2012]). It allows a wide surface area of the posterior carapace to be closely applied to the ground and thus reduces heat loss. The great size of the tortoises was also a definite advantage for heat conservation as a warm deep core body temperature would have been slow to cool (Auffenberg & Iverson, 1989).

Much of the external non-shell portion of *Hesperotestudo* was extensively covered by enlarged dermal ossicles (Figures. 1-3), which were covered with a tough layer of keratinised horn (Hay, 1908). The dermal ossicles of various species (*H. bermudae*, *H. crassiscutata*, *H. impensa*, *H. incisa*, *H. oelrichi*, *H. orthopygia*, *H. osborniana*, *H. riggsi*, and *H. turgida*) were described by Cope (1878), Hay (1904, 1908), Oelrich (1957), Auffenberg (1963), Holman (1972), and Meylan & Sterrer (2000). The revisions of Williams (1950) and

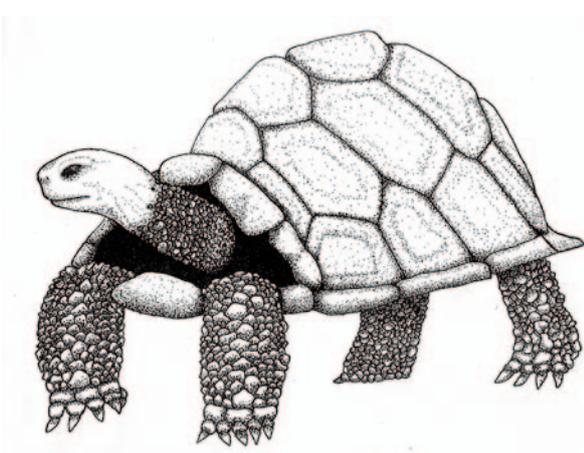


Figure 1. Reconstructed image of giant fossil tortoise (*Hesperotestudo*) showing dermal ossicles and posterior flare on carapace. Drawing by Carleen Spahn.

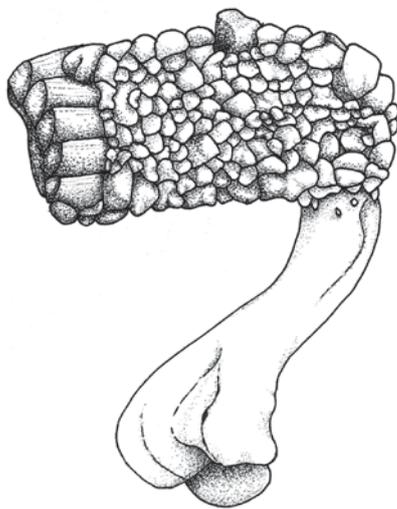


Figure 2. Ventral view of right forelimb of giant fossil tortoise *H. osborniana* showing dermal ossicles covering foot, ulna, radius, and distal portion of humerus. Drawn by Carleen Spahn after part of a photograph (Plate 74) in Hay (1908).

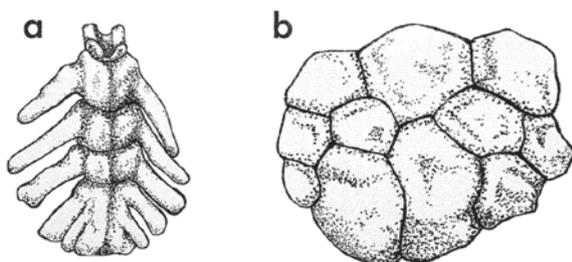


Figure 3. Tail (buckler) of the giant fossil tortoise *H. orthopygia*: a) dorsal view of caudal vertebrae showing elongated lateral processes, with the last three being truncated and fused, and b) external dorsal covering of enlarged dermal ossicles. Drawn by Carleen Spahn after figure 600 and parts of figures 601 and 603 in Hay (1908).

Bramble (1971) examined dermal ossicles of larger numbers of species. The latter concluded that after the tortoise had withdrawn into its shell, all of the exposed parts of the limbs and other areas were covered with dermal ossicles including the bottom of the feet. Even the tail (“buckler” [Auffenberg, 1963]) is covered. In *H. osborniana*, *H. orthopygia*, *H. turgida*, and *H. incisa*, the tail (Fig. 3) is wide and paddle shaped from elongation of the lateral processes of the caudal vertebrae, with the last three being fused and truncated (Hay, 1908; Auffenberg, 1963). Presumably, it would have required strong selection pressure to evolve this unusual caudal elaboration. (Both Bramble [1971] and Meylan & Sterrer [2000] included the caudal buckler as a diagnostic character for the genus *Hesperotestudo*.) When the tail was lowered underneath the carapace, all of the area exposed was covered with dermal ossicles between and including the hind limbs when they were retracted (Hay, 1908). Likewise, Holman (1972) noted for *H. oelrichi* that when head and forelimbs were retracted, the entire anterior area was protected by dermal ossicles. Williams (1950) included dermal ossicles as a character in his definition for the subgenus *Hesperotestudo*, and Bramble (1971) did the same for the generic definition, as did Meylan & Sterrer (2000) for their revised diagnosis. All three publications emphasised the excessive development of dermal ossicles.

Bramble (1971) also noted that *Hesperotestudo* had a fibrous, markedly thickened integument which was evident by a well-defined scar along the base of each dermal ossicle. Hay (1908) found that the base of the dermal ossicles of *H. impensa* was roughened and he indicated this portion had been buried in the integument.

The bodies of Galápagos Giant Tortoises contain a considerable amount of fat (Townsend, 1925, 1928, 1931b). This fat was rendered into oil by the people of the Galápagos Islands (primarily in the 1800s) and sold for culinary purposes to whalers or sent to mainland markets. Similarly, the extinct *Cylindraspis* tortoises of the Mascarene Islands contained large amounts of fat. The Réunion Giant tortoise, *C. indica* in particular, carried considerable fat which was rendered by native people to yield about “two pots of oil” (Loungnon, 1970). Both *C. indica* and larger Galápagos tortoises were/are known to spend a considerable amount of time foraging in the cooler, cloudier, wetter uplands of their island habitats (Loungnon, 1970; Blake et al., 2013). It seems likely these tortoises evolved their heavy fat layers for insulation to facilitate their exploitation of resources available in these cooler environments. In the lowlands the fat would reduce heat loss in the cooler evenings. We suggest that the giant fossil tortoises of northern North America also had considerable internal fat for the same purpose, to cope with colder conditions at higher latitudes and altitudes (see Behavioural thermoregulation and Gigantothermy).

It is clear that the dermal ossicles, thick fibrous integument, presence of considerable underlying fat likely, and the ability to retract the limbs, head, and tail under the thick domed, flared carapace should have provided good insulation against the cold. Thus, *Hesperotestudo* was well equipped morphologically to have withstood northern winters and montane areas.



Fig. 4. Aldabra Giant Tortoises (*A. gigantea*) moving toward a cave on Aldabra Atoll. Photo by Dennis Hansen.

Behavioural thermoregulation

All of the extant giant tortoises (Galápagos Giant Tortoises *Chelonoidis nigra* species complex, Aldabra Giant Tortoise *Aldabrachelys gigantea*, and African Spurred Tortoise *Centrochelys sulcata*) are well known as being capable of traveling at a steady pace (Coe et al., 1979; Swingland & Lessells, 1979; Gibson & Hamilton, 1983; Swingland et al., 1989; Kaplan, 1996; Pritchard, 1996; Blake et al., 2013; Blake et al., 2015). This allows them to behaviourally regulate their temperature by moving in and out of shaded areas. During the day, they absorb heat by basking in the sun (Auffenberg & Iverson, 1989), but retreat under shade if heat becomes excessive. In the cooler evenings, when the tortoise is sleeping, heat loss is slow because of the great mass of the tortoise. The deep core temperature remains high enough to ensure the animal does not become chilled, and the sun of the following day will renew heat loss from the preceding night (Auffenberg & Iverson, 1989). This cyclical process of behavioural thermoregulation was proposed by Auffenberg & Iverson (1989) as an explanation for the survival of giant fossil tortoises in continental high latitudes even during the glacial periods of the Pleistocene.

Burrowing

Hibbard (1960) indicated there was no evidence of burrowing by adults of giant fossil tortoises of North America. However, adults of a great many extant species of tortoises (Obst, 1986) are accomplished burrowers (e.g., North American Gopher Tortoises, genus *Gopherus* – [Woodbury & Hardy, 1948]). (Meylan & Sterrer [2000] later placed *Gopherus* and *Hesperotestudo* in the same subfamily Xerobatinae.) The most compelling example is the largest living mainland tortoise, the African Spurred

Tortoise (*C. sulcata*), which is an ardent burrower that can dig tunnels that may be over 30 m in length and 15 m in depth (Branch, 2008). The species can reach the size (D. M., personal observation at Ménagerie du Jardin des Plantes, Paris, 1978) of the huge extant Aldabra Giant Tortoise (*A. gigantea*) of Aldabra Atoll in the western Indian Ocean. Thus, we propose it was possible that North American giant fossil tortoises could burrow for protection from cold weather during winter in the northern parts of their ranges.

Use of caves as shelters

There is good evidence for the use of caves as shelter by extant tortoises. Western North American Gopher Tortoises (Agassiz's Desert Tortoise *G. agassizii* and the Sonoran Desert Tortoise *G. morafkai*) have frequently been found to occupy caves (e.g., Burge, 1978; Bury et al., 1994; Berry et al., 2000; Averill-Murray & Klug, 2001; Berry et al., 2006; Gienger & Tracy, 2008; Riedle et al., 2008; Zylstra & Steidl, 2009; Sullivan et al., 2014; Mack et al., 2015). Recently, Warne (2016) published a photo of adult Aldabra Giant Tortoises (*A. gigantea*) entering a cave on Aldabra Atoll. Bittel (2016) noted that two caves on the island are used by tortoises. This research was carried out by Dr. Dennis Hansen of the University of Zurich and his research team. He found (pers. comm.) that the main cave is approximately 5 m wide, 5-6 m deep, and 1-1.5 m tall inside (Fig. 4). Most of the cave is probably 1-2 m below ground, and there was a great difference in maximum/minimum temperatures in the cave compared to those outside and in exposed sites. Coe & Swingland (1984) found young *A. gigantea* occupied crevices. Such crevices may not seem to be "caves" to a human, but they serve quite adequately as shelters (e.g., caves) to small tortoises, not only providing protection

from predators but also mitigating the extent and rates of temperature and humidity changes within the crevices compared to the external environment (e.g., Honegger, 1968; Wilke, 1984; Wood & MacKay, 1997; Schmidt, unpubl. report). In Tanzania, Africa, Moll & Klemens (1996) researched the Pancake Tortoise (*Malacochersus tornieri*) which commonly occurs in rock crevices, and Branch (2008) found the same for Speke's Hinge-back Tortoise (*Kinixys spekii*) of southern Africa. Also, three padlopers (*Homopus signatus*, *H. femoralis*, *H. solus* [*H. bergeri*]) of southern Africa use crevices for shelter (Boycott & Bourquin, 1988; Branch, 1988; Bayoff, 1995; Loehr, 1999; Schleicher & Loehr, 2001).

There were two extinct species of tortoises on Rodrigues Island in the Indian Ocean: the Rodrigues Giant Saddleback Tortoise *Cylindraspis vosmaeri*, and the smaller Rodrigues Domed Tortoise *C. peltastes* (Turtle Extinctions Working Group, 2015). Thousands of subfossils of these species have been found in Rodrigues caves (Bour et al., 2014; Hume, 2014). These are often exceptionally well preserved and articulated, with a number of complete or nearly complete shells found on the cave floors (Bour et al., 2014; Hume, 2014). The carapaces of *C. vosmaeri* and *C. peltastes* are very thin (2 mm thick, Cheke & Hume, 2008) and their internal skeletons are quite light (Bour et al., 2014). Thus, a fall into a cave would most likely have resulted in considerable damage not observed in these specimens. A number of intact crania have also been found on the cave floors (Bour et al., 2014). Hence the Rodrigues tortoises could have entered caves voluntarily for shelter. Consequently, we suggest that it is quite possible that the giant fossil tortoises in northern and montane areas of North America could survive in the winter by obtaining shelter through occupancy of caves.

Tolerance of prolonged cessation of food consumption

It would probably not have been necessary for giant fossil tortoises to eat or drink during long periods of winter dormancy because Galápagos Giant Tortoises (*C. nigra* species complex), Aldabra Giant Tortoises (*A. gigantea*), Réunion Giant Tortoises (*C. indica*), and other species of Mascarene giant tortoises (*Cylindraspis* sp.) have been found to live for an extended period of time without eating or drinking. During the 18th and 19th centuries, whaling ships frequently stopped in the Galápagos Islands (Townsend, 1925) to stock up on large numbers of tortoises for food. The tortoises were turned over on their carapaces and stored alive in the hull of the ship. On almost all ships they were not given food or water. Individually the live tortoises were brought up to the deck for butchering as needed. The log books of seven whaling ships were examined by Townsend (1925, 1928) to obtain the following records of endurance of the tortoises: more than a year; 4 months; nearly 9 months; 2 years; 5-6 months; 14 months; and 18 months. Shortly after one whaling ship left the Galápagos Islands, a pet tortoise disappeared. Two years later when the ship arrived at home port in New Bedford, Massachusetts, the tortoise was discovered alive in the ship's hull among casks (Townsend, 1925).

Furthermore, the extinct giant tortoises (*Cylindraspis*) of the Mascarene Islands in the western Indian Ocean were also heavily collected for consumption on many visiting ships (Cheke & Hume, 2008; Cheke & Bour, 2014). Like the Galápagos Giant Tortoises, the *Cylindraspis* survived in the hull of the ships "for months" (Cheke & Hume, 2008) and "three or four months" (Cheke & Bour, 2014) without food and water. Also, the Réunion Giant Tortoise (*C. indica*) fasted for four months of the year as a natural part of its ecology (Luillier, 1705). Moreover, the extant Aldabra Giant Tortoise (*A. gigantea*) in its native habitat on Aldabra Atoll ceases eating for weeks during the dry season and droughts (Coe & Swingland, 1984).

Genetic and biogeographical research (e.g., Arnold, 1979; Palkovacs et al., 2002; Austin et al., 2003; Gerlach & Paquette, 2014) strongly suggest that the Galápagos Islands, Aldabra Atoll, and the Mascarene Islands were colonised by giant tortoises drifting for many months at sea over long distances from the nearest continents or other islands (e.g., Madagascar in the Indian Ocean) without food. In the past there have been sightings of extant giant tortoises drifting in the Pacific Ocean near the Galápagos Islands and in the western Indian Ocean near Aldabra and Alphonse Islands (Gerlach et al., 2006). Also, a female Aldabra Giant Tortoise was found walking out of the western Indian Ocean on the coast of Tanzania, Africa, 35 km south of Dar es Salaam at Kimbiji (Gerlach et al., 2006). The lower carapace and legs of the tortoise were covered with barnacles. This animal was emaciated, but recovered in captivity. Morphological examination indicated the tortoise came from Grand Terre, Aldabra, some 740 km from Kimbiji, Tanzania (Gerlach et al., 2006), a journey which must have taken several months. This evidence also indicates extreme tolerance of food and freshwater deprivation in these tortoises. Thus, we propose that if a giant fossil tortoise in North America took cold-weather shelter (e.g., in a burrow, cave, or den) it is unlikely it would need to emerge for food or water during winter.

Cryoprotection and supercooling

Physiological ecologists have clearly demonstrated well-developed protection from freezing in a number of extant chelonians and other reptiles. Six species of northerly distributed North American turtles have so far been found to have evolved cryoprotection in hatchlings and/or adults (Storey et al., 1993; Costanzo et al., 2006). As the turtle body approaches freezing, the liver begins a substantial increase in the production of glucose, and there is an accumulation of lactate (as well as other possible cryoprotectants). These compounds are distributed by the circulatory system to tissues and organs throughout the body and prevent freezing. After freezing temperatures have been reached, the body becomes torpid and cardiac functioning cannot be detected. However, ice crystals can form around muscles and in body cavities. A return to above-freezing temperatures results in reestablishment of normal physiological functioning of the turtle. Large species are considered more likely to evolve cryoprotection (Costanzo et al., 2006). Also, a similar physiological

process called supercooling (cooling a liquid below its freezing point without crystallisation) occurs in two extant species of North American Gopher Tortoises (*G. agassizii*, *G. berlandieri*) as well as other extant species of turtles and is widespread among other reptile species (Lowe et al., 1971; Paukstis et al., 1989; Costanzo et al., 2008). Thus, we propose it is possible that giant North American fossil tortoises could have evolved cryoprotection or supercooling allowing cold temperature survival in the north and in montane areas.

Gigantothermy

A distinct type of thermoregulation (different from the endothermy of mammals and birds) that occurs in large reptiles has been termed gigantothermy (Paladino et al., 1990; Spotila et al., 1991; Paladino & Spotila, 1994; Wallace & Jones, 2015). Among extant species it has so far been found in the Leatherback Sea Turtle (*Dermochelys coriacea*), Green Sea Turtle (*Chelonia mydas*), American Alligator (*Alligator mississippiensis*), and Komodo Dragon (*Varanus komodoensis*). There is also convincing data that gigantothermy allowed certain dinosaurs to live in polar regions during the Cretaceous Period, 145.5-65.5 million years ago (Spotila et al., 1991; Paladino & Spotila, 1994). Metabolic and morphological studies have shown that the signature characteristics of gigantothermy are large size, insulation in peripheral tissues, low metabolic production of heat, and active control of peripheral circulation (Paladino et al., 1990; Paladino & Spotila, 1994). These features allow a constant high body temperature enabling habitation of cold regions (and prevent overheating in tropical areas) without requiring consumption of large amounts of high-energy foods. Thus we propose it is possible that the giant fossil tortoises of North America could have evolved gigantothermy that allowed longer annual activity periods and contributed to winter survival in the northern and montane parts of their ranges.

CONCLUSIONS

We have shown that incorrect assumptions and failure to consider contrary evidence (fundamental scientific error; faulty assumptions about climate and environment on the Galápagos Islands; incorrect taxonomy; abbreviated time frame, distribution, and number of species; and failure to consider evolution below the generic level) invalidate the prominent palaeoclimatic theory proposed by Claude W. Hibbard over a half-century ago which has since become dogma. Seven plausible alternatives are presented (cold-adaptive morphology, behavioural thermoregulation, burrowing, use of caves as shelters, tolerance of prolonged cessation of food consumption, cryoprotection and supercooling, and gigantothermy) that suggest giant fossil tortoises of North America could have evolved cold tolerance and occupied cold climates in northern and montane areas. Furthermore, this study demonstrates the potential danger of using an inappropriate proxy for past climate prediction. Although we feel the case for *Hesperotestudo* evolving cold temperature tolerance is convincing, definitive

proof for any Cenozoic climate can only come directly from geological evidence which is usually quite difficult to obtain.

ACKNOWLEDGEMENTS

The co-authors thank: E. Brown, J. Brown, K. Dodd, R. Franz, D. Hansen, J. Moll, R. Nelson, F. Paladino, D. Shepard, and J. Spotila for critically reading the ms.; J. Moll for typing the ms. and help with literature; A. Resetar for supplying literature references, documents, and a photograph; E. Brown for supplying a reference and discussion; S. Osuna for library help and fulfilling hundreds of interlibrary loan requests; C. Young for assistance in copying an old publication; C. Spahn for drawing Figures 1-3; T. Banik for discussion; D. Hansen for providing the photograph (Fig. 4) and allowing us to present some of his data on an Aldabra cave; and C. Gatto for discussion, and funding artwork and other costs through the School of Biological Sciences, Illinois State University.

REFERENCES

- Alpert, L. (1963). The climate of the Galápagos Islands. *Occasional Papers of the California Academy of Sciences* 44, 21-44.
- Arnold, E. N. (1979). Indian Ocean giant tortoises: their systematics and island adaptations. *Philosophical Transactions of the Royal Society of London B* 286, 127-145.
- Auffenberg, W. (1963). Fossil testudinine turtles of Florida genera *Geochelone* and *Floridemys*. *Bulletin of the Florida State Museum, Biological Sciences* 7, 53-97.
- Auffenberg, W. (1974). Checklist of fossil land tortoises (*Testudinidae*). *Bulletin of the Florida State Museum, Biological Sciences* 18, 121-251.
- Auffenberg, W. & Iverson, J. B. (1989). Demography of terrestrial turtles. In *Turtles, perspectives and research*, 541-569. Harless, M., & Morlock, H. (eds). Malabar, Florida: Robert E. Krieger Publishing Company.
- Auffenberg, W. & Milstead, W. W. (1965). Reptiles in the Quaternary of North America. In *The Quaternary of the United States, a review volume for the VII Congress of the International Association for Quaternary Research*, 557-568. Wright, H. E., Jr. & Frey, D. G. (eds). Princeton, New Jersey: Princeton University Press.
- Austin, J. J., Arnold, E. N., & Bour, R. (2003). Was there a second adaptive radiation of giant tortoises in the Indian Ocean? Using mitochondrial DNA to investigate speciation and biogeography of *Aldabrachelys* (Reptilia, Testudinidae). *Molecular Ecology* 12, 1415-1424.
- Averill-Murray, R. C. & Klug, C. M. (2001). Desert Tortoise habitat use and home range size on the Florence Military Reservation: a pilot study. *Nongame and Endangered Wildlife Program, Technical Report* 174. Phoenix: Arizona Game and Fish Department.
- Axelrod, D. I. (1975). Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden* 62, 280-334.
- Bayoff, N. (1995). Observations and morphometric data on the Namaqualand Speckled Tortoise, *Homopus signatus*

- signatus* (Gmelin, 1789), in South Africa. *Chelonian Conservation and Biology* 1, 215-220.
- Bentley, C. C. & Knight, J. L. (1998). Turtles (Reptilia: Testudines) of the Ardis local fauna late Pleistocene (Rancholabrean) of South Carolina. *Brimleyana* (25), 3-33.
- Berry, K. H., Bailey, T. Y., & Anderson, K. M. (2006). Attributes of Desert Tortoise populations at the National Training Center, central Mojave Desert, California, USA. *Journal of Arid Environments* 67, 165-191.
- Berry, K. H., Goodlett, G., & Goodlett, T. (2000). Effects of geology and cover site choice on Desert Tortoise populations at the Tiefert Mountains, California. *Proceedings of the 2000 & 2001 Symposia, The Desert Tortoise Council*. 5.
- Bittel, J. (2016). Cave-dwelling giant tortoises are a big surprise. National Geographic Weird and Wild. Available at: <http://news.nationalgeographic.com/2016/02/160212-caves-giant-tortoises-animals-science-seychelles/>.
- Blake, S., Yackulic, C. B., Cabrera, F., Tapia, W., Gibbs, J. P., Kümmeth, F., & Wikelski, M. (2013). Vegetation dynamics drive segregation by body size in Galapagos tortoises migrating across altitudinal gradients. *Journal of Animal Ecology* 82, 310-321.
- Blake, S., Yackulic, C. B., Wikelski, M., Tapia, W., Gibbs, J. P., Deem, S., Villamar, F., & Cabrera, F. (2015). Migration by Galapagos Giant Tortoises requires landscape-scale conservation efforts. *Galapagos Report 2013-2014*, 144-150.
- Bour, R., Mourer-Chauviré, C., & Ribes, S. (2014). Morphology and palaeontological exploration (until 2000) of the extinct tortoises of the Mascarene islands [sic]. In *Western Indian Ocean tortoises, ecology, diversity, evolution, conservation, palaeontology*, 121-202. Gerlach, J. (ed). Manchester, UK: Siri Scientific Press.
- Boycott, R. C. & Bourquin, O. (1988). *The South African tortoise book: a guide to South African tortoises, terrapins and turtles*. Johannesburg: Southern Book Publishers.
- Bramble, D. M. (1971). Functional morphology, evolution, and paleoecology of gopher tortoises. Ph.D. Dissertation. Berkeley: University of California.
- Branch, B. (1988). *Field guide to the snakes and other reptiles of southern Africa*. Sanibel Island, Florida: Ralph Curtis-Books-Publishing.
- Branch, B. (2008). *Tortoises, terrapins & turtles of Africa*. Cape Town: Struik Publishers.
- Brattstrom, B. H. (1961). Some new fossil tortoises from western North America with remarks on the zoogeography and paleoecology of tortoises. *Journal of Paleontology* 35, 543-560.
- Brown, L. E., Dubois, A., & Shepard, D. B. (2008). Inefficiency and bias of search engines in retrieving references containing scientific names of fossil amphibians. *Bulletin of Science, Technology & Society* 28, 279-288.
- Burge, B. L. (1978). Physical characteristics and patterns of utilization of cover sites used by *Gopherus agassizii* in southern Nevada. *Proceedings of 1978 Symposium, Desert Tortoise Council*, 80-111.
- Bury, R. B., Esque, T. C., DeFalco, L. A., & Medica, P. A. (1994). Distribution, habitat use, and protection of the Desert Tortoise in the eastern Mojave Desert. In *Biology of North American tortoises*, 57-72. Bury, R. B. & Germano, D. J. (eds). *Fish and Wildlife Research* 13. Washington, D.C.: National Biological Survey, U. S. Department of the Interior.
- Cassiliano, M. L. (1997). Crocodiles, tortoises, and climate: a shibboleth re-examined. *Paleoclimates* 2, 47-69.
- Chambers, F. M. (2012). Reconstructing and inferring past environmental change. In *The SAGE handbook of environmental change*, 67-91. Volume 1. Matthews, J. A., Bartlein, P. J., Briffa, K. R., Dawson, A. G., De Vernal, A., Denham, T., Fritz, S. C., & Oldfield, F. (eds). London: SAGE Publications, Ltd.
- Cheke, A. S. & Bour, R. (2014). Unequal struggle - how humans displaced the dominance of tortoises in island ecosystems. In *Western Indian Ocean tortoises, ecology, diversity, evolution, conservation, palaeontology*, 31-120. Gerlach, J. (ed). Manchester, UK: Siri Scientific Press.
- Cheke, A. & Hume, J. (2008). *Lost land of the Dodo, an ecological history of Mauritius, Reunion & Rodrigues*. New Haven and London: Yale University Press.
- Coe, M. J., Bourn, D., & Swingland, I. R. (1979). The biomass, production and carrying capacity of giant tortoises on Aldabra. *Philosophical Transactions of the Royal Society of London B* 286, 163-176.
- Coe, M. & Swingland, I. R. (1984). Giant tortoises of the Seychelles. In *Biogeography and ecology of the Seychelles Islands*, 309-330. Stoddart, D. R. (ed). The Hague, Boston, and Lancaster: Dr. W. Junk Publishers.
- Colinvaux, P. A. (1984). The Galápagos climate: present and past. In *Key environments, Galapagos*, 55-69. Perry, R. (ed). Oxford, etc.: Pergamon Press.
- Conant, R. & Collins, J. T. (1998). *A field guide to reptiles & amphibians, eastern and central North America*, The Peterson Field Guide Series, Third edition. Boston and New York: Houghton Mifflin Company.
- Cope, E. D. (1878). Descriptions of new extinct Vertebrata from the Upper Tertiary and Dakota Formations. *Bulletin of the United States Geological and Geographical Survey of the Territories* 4, 379-396.
- Costanzo, J. P., Baker, P. J., & Lee, R. E., Jr. (2006). Physiological responses to freezing in hatchlings of freeze-tolerant and -intolerant turtles. *Journal of Comparative Physiology B* 176, 697-707.
- Costanzo, J. P., Lee, R. E., Jr., & Ultsch, G. R. (2008). Physiological ecology of overwintering in hatchling turtles. *Journal of Experimental Zoology* 309A, 297-379.
- Curry, B. B. & Follmer, L. R. (1992). The last interglacial-glacial transition in Illinois: 123-25 ka. *Geological Society of America Special Paper* 270, 71-88.
- Curry, B., Wang, H., Panno, S., & Hackley, K. (2010). Quaternary paleoclimate. In *Geology of Illinois*, 248-260. Kolata, D. & Nimz, C. (eds). Champaign, IL: University of Illinois at Urbana-Champaign and Illinois State Geological Survey.
- Darwin, C. (1846). *Journal of researches into the natural history and geology of the countries visited during the voyage of H. M. S. Beagle round the world, under the command of Capt. Fitz Roy, R. N.* Volume II. New York: Harper & Brothers, Publishers.
- Feduccia, J. A. (1968). The Pliocene rails of North America. *The Auk* 85, 441-453.
- Francis, J., Haywood, A. M., Hill, D., Markwick, P., & McDonald, C. (2012). Environmental change in the geological record. In *The SAGE handbook of environmental change*, 165-180. Matthews, J. A., Bartlein, P. J., Briffa, K. R., Dawson, A. G., De Vernal, A., Denham, T., Fritz, S. C., & Oldfield, F. (eds).

- Volume 1. London: SAGE Publications, Ltd.
- Gerlach, J., Muir, C., & Richmond, M. D. (2006). The first substantiated case of trans-oceanic tortoise dispersal. *Journal of Natural History* 40, 2403-2408.
- Gerlach, J. & Paquette, S. R. (2014). Evolution and divergence of tortoises of the western Indian Ocean. In *Western Indian Ocean tortoises, ecology, diversity, evolution, conservation, palaeontology*, 9-30. Gerlach, J. (ed.). Manchester, UK: Siri Scientific Press.
- Gibson, C. W. D. & Hamilton, J. (1983). Feeding ecology and seasonal movements of giant tortoises on Aldabra Atoll. *Oecologia* 56, 84-92.
- Gienger, C. M. & Tracy, C. R. (2008). Ecological interactions between Gila Monsters (*Heloderma suspectum*) and Desert Tortoises (*Gopherus agassizii*). *The Southwestern Naturalist* 53, 265-268.
- Graham, R. W. (1986). Plant-animal interactions and Pleistocene extinctions. In *Dynamics of extinction*, 131-154. Elliot, D. K. (ed). New York, etc: John Wiley & Sons.
- Grant, P. R. & Boag, P. T. (1980). Rainfall on the Galápagos and the demography of Darwin's finches. *The Auk* 97, 227-244.
- Hamann, O. (1979). On climatic conditions, vegetation types, and leaf size in the Galápagos Islands. *Biotropica* 11, 101-122.
- Hamann, O. (1981). Plant communities of the Galápagos Islands. *Dansk Botanisk Arkiv* 34(2), 1-163.
- Harbour, J. (1969). Pollen profile of the Rita Blanca Lake deposits. In Anderson, R. Y. & Kirkland, D. W. (eds). Paleocology of an Early Pleistocene Lake on the High Plains of Texas. *The Geological Society of America, Inc., Memoir* 113, 83-95.
- Hay, O. P. (1904). A new gigantic tortoise from the Miocene of Colorado. *Science* 19, 503-504.
- Hay, O. P. (1908). *The fossil turtles of North America*. Washington, D.C.: Carnegie Institution of Washington, Publication No. 75.
- Hibbard, C. W. (1944). A new land tortoise, *Testudo riggsi*, from the Middle Pliocene of Seward County, Kansas. *The University of Kansas Science Bulletin* 30, 71-76.
- Hibbard, C. W. (1960). An interpretation of Pliocene and Pleistocene climates in North America. The President's Address. *Annual Report of the Michigan Academy of Sciences, Arts and Letters* 62, 5-30.
- Holman, J. A. (1972). Amphibians and reptiles. In *Early Pleistocene pre-glacial and glacial rocks and faunas of north-central Nebraska*, 55-71. Skinner, M. F., Hibbard, C. W., Gutentag, E. D., Smith, G. R., Lundberg, J. G., Holman, J. A., Feduccia, J. A., & Rich, P. V. *Bulletin of the American Museum of Natural History* 148, 1-148.
- Holman, J. A. (1987). Herpetofauna of the Egelhoff site (Miocene: Barstovian) of North-Central Nebraska. *Journal of Vertebrate Paleontology* 7, 109-120.
- Holman, J. A. (1995). *Pleistocene amphibians and reptiles in North America*. New York: Oxford University Press.
- Holman, J. A. (1998). Reptiles of the lower Miocene (Hemingfordian) Pollack Farm fossil site, Delaware. In *Geology and paleontology of the lower Miocene Pollack Farm fossil site, Delaware*, 141-147. Benson, R. N. (ed). Newark: Delaware Geological Survey Special Publication No. 21.
- Holman, J. A. & Fritz, U. (2005). The box turtle genus *Terrapene* (Testudines: Emydidae) in the Miocene of the USA. *The Herpetological Journal* 15, 81-90.
- Honegger, R. E. (1968). Beitrag zur Fortpflanzungs-biologie einiger tropischer Reptilien. *Zeitschrift Kölner Zoo* 13, 175-179.
- Hume, J. P. (2014). Fossil discoveries on Mauritius and Rodrigues. In *Western Indian Ocean tortoises, ecology, diversity, evolution, conservation, palaeontology*, 203-228. Gerlach, J. (ed.). Manchester, UK: Siri Scientific Press.
- Hume, J. P., Steel, L., Andre, A. A., & Meunier, A. (2015). In the footsteps of the bone collectors: nineteenth-century cave exploration on Rodrigues Island, Indian Ocean. *Historical Biology* 27, 265-286.
- Jackson, C. G., Jr. & Kaye, J. M. (1975). Giant tortoises in the Late Pleistocene of Mississippi. *Herpetologica* 31, 421.
- Kaplan, M. (1996). African Spurred Tortoises. *Reptile & Amphibian Magazine* (42), 32-45.
- Karlstrom, E. T. (1991). Palaeoclimatic significance of Late Cenozoic paleosols east of Waterton-Glacier Parks, Alberta and Montana. *Palaeogeography, Palaeoclimatology, Palaeoecology* 85, 71-100.
- King, J. E. & Saunders, J. J. (1986). Geochelone in Illinois and the Illinoian-Sangamonian vegetation of the type region. *Quaternary Research* 25, 89-99.
- Koestler, A. (1971). *The case of the midwife toad*. New York: Random House.
- Lack, D. (1947 [1961]). *Darwin's finches, an essay on the general biological theory of evolution*. New York: Harper & Brothers.
- Lambe, L. M. (1906). Descriptions of new species of *Testudo* and *Baëna* with remarks on some Cretaceous forms. *The Ottawa Naturalist* 19, 187-196.
- Leidy, J. (1889). Description of vertebrate remains from Peace Creek, Florida. *Transactions of the Wagner Free Institute of Science of Philadelphia* 2, 19-31.
- Loehr, V. J. T. (1999). Husbandry, behavior, and captive breeding of the Namaqualand Speckled Padloper (*Homopus signatus signatus*). *Chelonian Conservation and Biology* 3, 468-473.
- Lougnon, A. (1970). *Sous la signe de la tortue: voyages anciens à l'île Bourbon (1611-1725)*. Third Edition. Saint-Denis: Azalées Éditions. (NS). Cited In Cheke, A. S. & Bour, R. 2014. Unequal struggle-how humans displaced the dominance of tortoises in island ecosystems. In *Western Indian Ocean tortoises, ecology, diversity, evolution, conservation, palaeontology*, 31-120. Gerlach, J. (ed). Manchester, UK: Siri Scientific Press.
- Lowe, C. H., Lardner, P. J., & Halpern, E. A. (1971). Supercooling in reptiles and other vertebrates. *Comparative Biochemistry and Physiology* 39A, 125-135.
- Luillier-Lagaudiers. (1705). *Voyage du sieur Luillier aux grandes Indes, avec une instruction pour le commerce des Indes Orientales*. Paris: Claude Cellier.
- Lundelius, E. L., Jr. (1972). Fossil vertebrates from the Late Pleistocene Ingleside Fauna, San Patricio County, Texas. *Bureau of Economic Geology, The University of Texas at Austin, Reports of Investigations* No. 77.
- Lundelius, E. L., Jr. (2003). A history of paleontological investigations of Quaternary cave deposits on the Edwards Plateau, central Texas. In *Ice age cave faunas of North America: life of the past*, 201-214. Farlow, J. O., Schubert, B. W., Mead, J. I., & Graham, R. W. (eds). Bloomington and Indianapolis: (Denver Museum of Nature & Science), Indiana University Press.
- Mack, G. H., Cole, D. R., James, W. C., Giordano, T. H., & Salyards,

- S. L. (1994). Stable oxygen and carbon isotopes of pedogenic carbonate as indicators of Plio-Pleistocene paleoclimate in the southern Rio Grande rift, south-central New Mexico. *American Journal of Science* 294, 621-640.
- Mack, J. S., Berry, K. H., Miller, D. M., & Carlson, A. S. (2015). Factors affecting the thermal environment of Agassiz's Desert Tortoise (*Gopherus agassizii*) cover sites in the central Mojave Desert during periods of temperature extremes. *Journal of Herpetology* 49, 405-414.
- Markwick, P. J. (2007). The palaeogeographic and palaeoclimatic significance of climate proxies for data-model comparisons. In *Deep-time perspectives on climate change: marrying the signal from computer models and biological proxies*, 251-312. Williams, M., Haywood, A. M., Gregory, F. J., & Schmidt, D. N. (eds). London: The Micropalaeontological Society Special Publications, The Geological Society, London.
- Martin, P. S. & Guilday, J. E. (1967). A bestiary for Pleistocene biologists. In *Pleistocene extinctions, the search for a cause*, 1-62. Martin, P. S. & Wright, H. E., Jr. (eds). New Haven and London: Yale University Press.
- Meylan, P. A. & Sterrer, W. (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.
- Moll, D. & Klemens, M. W. (1996). Ecological characteristics of the Pancake Tortoise, *Malacochersus tornieri*, in Tanzania. *Chelonian Conservation and Biology* 2, 26-35.
- Morafka, D. J. (1977). *A biogeographical analysis of the Chihuahuan Desert through its herpetofauna*. The Hague: Dr. W. Junk B. V., Publishers.
- Morgan, G. S. & Emslie, S. D. (2010). Tropical and western influences in vertebrate faunas from the Pliocene and Pleistocene of Florida. *Quaternary International* 217, 143-158.
- Morgan, G. S. & Lucas, S. G. (2005). Pleistocene vertebrate faunas in New Mexico from alluvial, fluvial, and lacustrine deposits. In *New Mexico's ice ages*, 185-248. Lucas, S. G., Morgan, G. S., & Zeigler, K. E. (eds). *New Mexico Museum of Natural History and Science Bulletin* no. 28.
- Neill, W. T. (1964). Taxonomy, natural history, and zoogeography of the Rainbow Snake, *Farancia erythrogramma* (Palisot de Beauvois). *The American Midland Naturalist* 71, 257-295.
- Obst, F. J. (1986). *Turtles, tortoises and terrapins*. New York: St. Martin's Press.
- Oelrich, T. M. (1957). The status of the Upper Pliocene turtle, *Testudo turgida* Cope. *Journal of Paleontology* 31, 228-241.
- Orenstein, R. (2012). *Turtles [sic] tortoises and terrapins*. Richmond Hill, Canada: Firefly Books.
- Ostrom, J. H. (1971). Terrestrial vertebrates as indicators of Mesozoic climates. In *Proceedings of the North American paleontological convention*, Chicago, 1969, 347-376. Yochelson, E. L. (ed). Vol. 2. Lawrence, KS: Allen Press, Inc.
- Paladino, F. V., O'Connor, M. P., & Spotila, J. R. (1990). Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* 344, 858-860.
- Paladino, F. V. & Spotila, J. R. (1994). Does the physiology of large living reptiles provide insights into the evolution of endothermy and paleophysiology of extinct dinosaurs? In *Dinofest*, 261-275. Rosenberg, G. & Wolberg, D. L. (eds). Paleontological Society Special Publication #7.
- Palkovacs, E. P., Gerlach, J., & Caccone, A. (2002). The evolutionary origin of Indian Ocean tortoises (*Dipsochelys*). *Molecular Phylogenetics and Evolution* 24, 216-227.
- Parmley, D. (1988). Additional Pleistocene amphibians and reptiles from the Seymour Formation, Texas. *Journal of Herpetology* 22, 82-87.
- Parris, D. C. & Daeschler, E. (1995). Pleistocene turtles of Port Kennedy Cave (Late Irvingtonian), Montgomery County, Pennsylvania. *Journal of Paleontology* 69, 563-568.
- Paukstis, G. L., Shuman, R. D., & Janzen, F. J. (1989). Supercooling and freeze tolerance in hatchling painted turtles (*Chrysemys picta*). *Canada Journal of Zoology* 67, 1082-1084.
- Paul, G. S. (1988). Physiological, migratorial, climatological, geophysical, survival, and evolutionary implications of Cretaceous polar dinosaurs. *Journal of Paleontology* 62, 640-652.
- Perez-Arлуca, M., Mack, G., & Leeder, M. (2000). Reconstructing the ancestral (Plio-Pleistocene) Rio Grande in its active tectonic setting, southern Rio Grande rift, New Mexico, USA. *Sedimentology* 47, 701-720.
- Popov, V. V., Gerasimov, S., & Marinska, M. (1994). Multivariate palaeocological analysis of a Late Quaternary small mammal succession from North Bulgaria. *Historical Biology* 8, 261-274.
- Pritchard, P. C. H. (1996). The Galápagos tortoises: nomenclatural and survival status. *Chelonian Research Monographs* No. 1.
- Rempel, J. (2012). A geological history of Meade County according to Claude Hibbard: Old Meade County, sharing the history of Meade County, Kansas. Available at: <http://www.oldmeadecounty.com/hibbard.htm>.
- Riedle, J. D., Averill-Murray, R. C., Lutz, C. L., & Bolen, D. K. (2008). Habitat use by Desert Tortoises (*Gopherus agassizii*) on alluvial fans in the Sonoran Desert, south-central Arizona. *Copeia* 2008, 414-420.
- Schleicher, A. & Loehr, V. J. T. (2001). Husbandry, behavior, and captive breeding of the Nama Padloper, *Homopus bergeri*, from southwestern Namibia. *Chelonian Conservation and Biology* 4, 165-170.
- Schmitt, F. A. C. (Undated). Some observations on pancake tortoises (*Malacochersus tornieri*) in Ruaha National Park, Tanzania. Unpublished Report. 7 p.
- Sloan, L. C. & Barron, E. J. (1990). "Equable" climates during Earth history? *Geology* 18, 489-492.
- Spotila, J. R., O'Connor, M. P., Dodson, P., & Paladino, F. V. (1991). Hot and cold running dinosaurs: body size, metabolism and migration. *Modern Geology* 16, 203-227.
- Steadman, D. W. (1986). Holocene vertebrate fossils from Isla Floreana, Galápagos. *Smithsonian Contributions to Zoology* (413), 1-103.
- Stebbins, R. C. (2003). *A field guide to western reptiles and amphibians*. The Peterson Field Guide Series. Third Edition. Boston and New York: Houghton Mifflin Company.
- Storey, K. B., Layne, J. R., Jr., Cutwa, M. M., Churchill, T. A., & Storey, J. M. (1993). Freezing survival and metabolism of box turtles, *Terrapene carolina*. *Copeia* 1993, 628-634.
- Sullivan, B. K., Averill-Murray, R., Sullivan, K. O., Sullivan, J. R., Sullivan, E. A., & Riedle, J. D. (2014). Winter activity of the Sonoran Desert Tortoise (*Gopherus morafkai*) in central Arizona. *Chelonian Conservation and Biology* 13, 114-119.
- Swingland, I. R. & Lessells, C. M. (1979). The natural regulation of giant tortoise populations on Aldabra Atoll. Movement polymorphism, reproductive success and mortality. *Journal*

- of *Animal Ecology* 48, 639-654.
- Swingland, I. R., North, P. M., Dennis, A., & Parker, M. J. (1989). Movement patterns and morphometrics in giant tortoises. *Journal of Animal Ecology* 58, 971-985.
- Thomasson, J. R. (1980). *Archaeoleersia nebraskensis* gen. et sp. nov. (Gramineae-Oryzaceae), a new fossil grass from the Late Tertiary of Nebraska. *American Journal of Botany* 67, 876-882.
- Thompson, R. S. (1991). Pliocene environments and climates in the western United States. *Quaternary Science Reviews* 10, 115-132.
- Thompson, R. S. & Fleming, R. F. (1996). Middle Pliocene vegetation: reconstructions, palaeoclimatic inferences, and boundary conditions for climatic modeling. *Marine Micropaleontology* 27, 27-49.
- Townsend, C. H. (1925). The Galapagos tortoises in their relation to the whaling industry, a study of old logbooks. *Zoologica* 4, 55-135.
- Townsend, C. H. (1928). The Galapagos Islands revisited. *Bulletin: New York Zoological Society* 31, 148-169.
- Townsend, C. H. (1931a). Growth and age in the giant tortoise of the Galapagos. *Zoologica* 9, 459-474.
- Townsend, C. H. (1931b). Giant tortoises nearing extinction on the Galapagos Islands, they are being propagated in the United States. *Scientific American* 144, 42-44.
- Trueman, M. & d'Ozouville, N. (2010). Characterizing the Galapagos terrestrial climate in the face of global climate change. *Galapagos Research* 67, 26-37.
- Turtle Extinctions Working Group [Rhodin, A. G. J., Thomson, S., Georgalis, G., Karl, H.-V., Danilov, I. G., Takahashi, A., de la Fuente, M. S., Bourque, J. R., Delfino, M., Bour, R., Iverson, J. B., Shaffer, H. B., & van Dijk, P. P.] (2015). Turtles and tortoises of the world during the rise and global spread of humanity: first checklist and review of extinct Pleistocene and Holocene chelonians. In *Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*, 1-66. Rhodin, A. G. J., Pritchard, P. C. H., van Dijk, P. P., Saumure, R. A., Buhlmann, K. A., Iverson, J. B., & Mittermeier, R. A. (eds). *Chelonian Research Monographs* 5(8): 000e.
- Turtle Taxonomy Working Group [van Dijk, P. P., Iverson, J. B., Rhodin, A. G. J., Shaffer, H. B., & Bour, R.] (2014). Turtles of the world, 7th edition: annotated checklist of taxonomy, synonymy, distribution with maps, and conservation status. In *Conservation biology of freshwater turtles and tortoises: a compilation project of the IUCN/SSC Tortoise and Freshwater Turtle Specialist Group*, 329-479. Rhodin, A. G. J., Pritchard, P. C. H., van Dijk, P. P., Saumure, R. A., Buhlmann, K. A., Iverson, J. B., & Mittermeier, R. A. (eds). *Chelonian Research Monographs* 5(7): 000. Available at: doi:10.3854/crm.5.000.checklist.v7.2014.
- Uyeno, T. & Miller, R. R. (1962). Late Pleistocene fishes from a Trinity River terrace, Texas. *Copeia* 1962, 338-345.
- Voorhies, M. R. (1975). A new genus and species of fossil kangaroo rat and its burrow. *Journal of Mammalogy* 56, 160-176.
- Wallace, B. P. & Jones, T. T. (2015). Leatherback turtle physiological ecology: Implications for bioenergetics and population dynamics. In *The Leatherback Turtle: biology and conservation*, 149-161. Spotila, J. R. & Tomillo, P. S. (eds). Baltimore: Johns Hopkins University Press.
- Warne, K. (2016). Return of the Seychelles. *National Geographic* 229 (3), 82-101.
- Webb, S. D. & Barnosky, A. D. (1989). Faunal dynamics of Pleistocene mammals. *Annual Review of Earth and Planetary Sciences* 17, 413-438.
- Wilke, H. (1984). Breeding the pancake tortoise, *Malacochersus tornieri*, at Frankfurt Zoo. *International Zoo Yearbook* 23 (1), 137-139.
- Williams, E. (1950). *Testudo cubensis* and the evolution of Western Hemisphere tortoises. *Bulletin of the American Museum of Natural History* 95, 1-36.
- Wood, R. C. & MacKay, A. (1997). The distribution and status of the pancake tortoise, *Malacochersus tornieri*, in Kenya. In: *Conservation, Restoration and Management of Tortoises and Turtles - An International Conference*, 314-321. van Abbema, J. (ed.). Purchase, NY: New York Turtle and Tortoise Society.
- Woodbury, A. M. & Hardy, R. (1948). Studies of the Desert Tortoise, *Gopherus agassizii*. *Ecological Monographs* 18, 145-200.
- Wyckoff, D. G., Carter, B. J., & Theler, J. L. (2003). Looking back on an odyssey: summarizing the findings at the Burham site. In *The Burham site in northwestern Oklahoma: glimpses beyond Clovis?*, 263-309. Wyckoff, D. G., Theler, J. L., & Carter, B. J. (eds). Norman, OK: Sam Noble Oklahoma Museum of Natural History, University of Oklahoma, and Oklahoma Anthropological Society, Memoir 9.
- Zylstra, E. R. & Steidl, R. J. (2009). Habitat use by Sonoran Desert Tortoises. *Journal of Wildlife Management* 73, 747-754.

Accepted: 9 January 2017