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Re-examination of the giant fossil tortoise *Hesperotestudo* from near the Illinois glacial-sangamon interglacial boundary in North America with commentary on zoogeography

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The Illinois Episode was the most extensive Quaternary glaciation in North America and extended deep into the central USA, further south than any other glacial episodes. It was followed by a period of mild climate termed the Sangamon Interglacial Episode. Relatively few reptile fossil sites have been found along the Illinois-Sangamon boundary. Thus, the 1986 report of isolated fossil remains of a giant tortoise (*Hesperotestudo*) near the boundary is of particular significance. We re-examined this important fossil because of inconsistencies and misinterpretations of prior researchers. The three morphological characters used for prior species identification of the tortoise are faulty and unreliable. Lack of additional, pertinent, diagnostic fossil elements presently prevents positive species identification. We critically appraised the pollen-based analysis of climate and environment at the tortoise strata by prior researchers. Their data suggest a transitional area between forest and prairie, or savannah, but the prior researchers misinterpreted their own data, concluding the vegetation was "relatively xeric grassland". Consequently, the climate and environment at the tortoise stratum are yet to be determined. We present several zoogeographical scenarios pertaining to the origin and movement of the tortoise to the collection site. The most likely is perhaps northward movement from the central Gulf Coast along the Mississippi River floodplain before the major meltdown of the Illinois glaciation. East of St. Louis, the glacier met the Mississippi River floodplain and as the meltdown progressed, the tortoise could have travelled on the till plain north-east to the collection site. *Hesperotestudo* likely had considerable cold adaptation and thus may have tracked the Illinois glacier relatively closely as it melted northward.

Key words: giant fossil tortoises, *Hesperotestudo*, climate, zoogeography

INTRODUCTION

The Quaternary of North America (ca. 2.6 million years before present [YBP]) was a period of repeated climatic changes, alternating between cold glacial episodes and warmer interglacial episodes (Hansel & McKay, 2010). During every major glaciation (at least six), the southern margin of the ice sheet extended into Illinois in the central USA. The most recent was the Wisconsin Glacial Episode, which was preceded by the Sangamon Interglacial Episode, which followed the Illinois Glacial Episode. The geology of the Wisconsin Episode in Illinois has been heavily researched (Willman & Frye, 1970; Hansel & Johnson, 1996; Hansel & McKay, 2010), but the Illinois Glacial Episode is not as well-known.

Among the most prominent reptiles of the Quaternary in North America were the giant fossil tortoises of the genus *Hesperotestudo* Williams (1950). These magnificent animals became extinct by the Late Wisconsin Glacial - Early Holocene Interglacial Episodes (Moodie & Van Devender, 1979; Holman & Clausen, 1984). The consensus as to the causes (Turtle Extinction Working Group, 2015) are primarily human exploitation for consumption as well as habitat and climate change.

The genus *Hesperotestudo* (Figure 1) has been found at many localities across North America from Pennsylvania (*H. percrassa*) and Delaware (*H. ducatelli* [probably]) in the east, to California (*H. dehiscus*) on the west coast, and from Texas (*H. turgida*), Baja California Sur, Mexico (*H. turgida* group), and Florida (*H. incisa*) in the south, to Saskatchewan, Canada (*H. exornata*) in the north (Lambe, 1906; Des Lauriers, 1965; Bramble, 1971; Auffenberg, 1974; Miller, 1980; Parris & Daeschler, 1995; Holman, 1998).

Meylan & Sterrer (2000) suggested the existence of 32 species in the genus *Hesperotestudo* in North America based on Auffenberg's (1974) checklist. However, since 1974 there have been a number of new species described. Comparison of species is difficult because: 1. the sample size for many of the species is quite small (often only one individual); 2. it is rare to find a specimen with a complete skeleton (often there are only a few or sometimes one plate or fragment of the shell available); 3. sexually dimorphic characters are often unknown; 4. geographic and ontogenetic variation of characters are unknown; and 5. no indication of reproductive isolating

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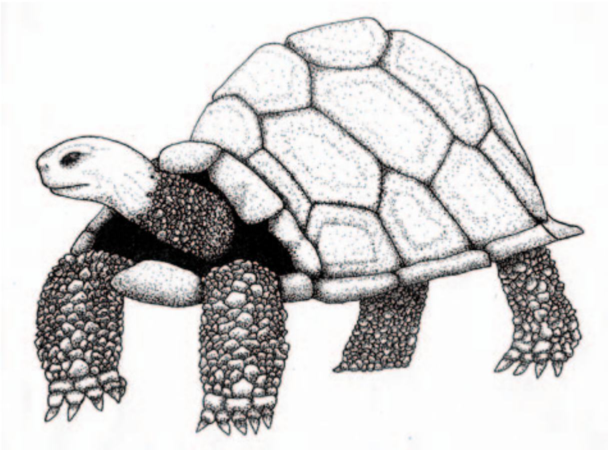

Figure 1. Reconstructed image of a fossil giant North American tortoise (*Hesperotestudo*). Drawing by C. Spahn. Originally published in *The Herpetological Journal* Volume 27, Page 279 (July 2017). (Permission granted by Rachael Antwis, Editor.)

Figure 2. Terminal boundary of the Illinois Glacial Episode (heavy dark line) in central North America. MR designates the Mississippi River, the Great Lakes are dark grey, and the states are outlined in white. Cartography by M. Maher. Source: 2014 Encyclopedia Britannica.

mechanisms has been discovered (except for body size in a few cases). Thus, in the future we can expect the lumping of some species and the continuing description of new species as more specimens are acquired and more research conducted. Consequently, it may be some time before a comprehensive revision of *Hesperotestudo* is undertaken because of the problems heretofore mentioned, and the true number of biologically valid species may remain an enigma for the foreseeable future.

Research on *Hesperotestudo* has focused primarily on taxonomy and phylogeny. An exception was that of Hibbard (1960). He used imported extant Galápagos tortoises as a proxy to create a theory that suggested adaptations of Cenozoic giant fossil tortoises were for subtropical or tropical climates across North America. Subsequently, Hibbard (1960) was widely cited and his interpretation became perhaps the most prominent paleoclimatic theory for many groups of organisms (Moll & Brown, 2017).

Moll & Brown (2017) recently provided evidence that Hibbard's (1960) theory was invalid. Seven alternative concepts were presented by Moll & Brown (2017) that suggest North American giant fossil tortoises could have evolved the necessary adaptations to survive northern winters and in montane areas that could have been colder than Hibbard (1960) envisioned: 1. cold-adaptive morphology; 2. behavioural thermoregulation; 3. burrowing; 4. use of caves as shelters; 5. tolerance of prolonged cessation of food consumption; 6. cryoprotection and supercooling; and 7. gigantothermy.

Over 30 years ago, an isolated locality record of a giant fossil tortoise thought to be *Hesperotestudo crassiscutata* (Leidy, 1889) was reported from southern Illinois in the Sangamon not far from the glacial boundary of the Illinois (King & Saunders, 1986; Saunders & King, 1986). This record is thus of considerable interest.

Hesperotestudo crassiscutata is known from the Middle Pleistocene to the Early Holocene (Turtle Extinctions Working Group, 2015). Its known distribution is primarily in the south-eastern USA from Texas eastward through Louisiana, Mississippi, and Alabama to Florida, and to the north-east through Georgia and South Carolina to North Carolina (Slaughter, 1966; Auffenberg, 1974; Holman, 1995; Russell et al., 2009; Turtle Extinctions Working Group, 2015). Extra-marginal records occur in Illinois and Pennsylvania (King & Saunders, 1986; Holman, 1995). The known distribution of *H. crassiscutata* may be one of the largest in the genus. Because of its wide distribution, it clearly evolved adaptations to live in numerous environments and climates. Conant & Collins (1998), Stebbins (2003), and Moll & Brown (2017) noted this for many extant North American chelonians. In some areas (e.g., Florida), locality records for *H. crassiscutata* are relatively common, whereas in other areas they are very rare (only one locality in Illinois).

There are two records of *Hesperotestudo* from Missouri caves reported by Hawksley (1986). Holman (1995) indicated that these specimens need to be confirmed because they do not fit his theory of stability of the herpetofauna in the Ozark region. Moreover, they may have considerable zoogeographical significance to the origin of *Hesperotestudo* in the central USA.

Hesperotestudo contains both giant and moderate to smaller species. Among the largest is *H. crassiscutata*. Leidy (1889) estimated that the shell of the type specimen was about five feet (1.52 m) in length and had a very thick shell (the plastron varied from 46 - 90 mm in thickness). Bentley & Knight (1998) found shell fragments of *H. crassiscutata* 40 mm thick. A more recent carapace length estimate was 120 - 125 cm (Turtle Extinctions Working Group, 2015). However, the plastrons of two specimens of giant "*Geochelone* sp." (= *Hesperotestudo*) from Texas were reported by Hibbard & Dalquest (1966) to reach six feet (1.83 m). Holman (1969) indicated that these fossils are similar to *H. crassiscutata*. Due to its huge size, *H. crassiscutata* may have been a keystone herbivore in optimal habitats where the species' densities could have been moderate to high.

Because of inconsistencies, omissions, and misinterpretations in King & Saunders (1986) and Saunders & King (1986), and the questioned status of the Hawksley (1986) specimens, we re-examined the fossil fragments of *Hesperotestudo* from Illinois and Missouri and the results of the aforementioned studies. The objectives of this paper are to: i) review the geology

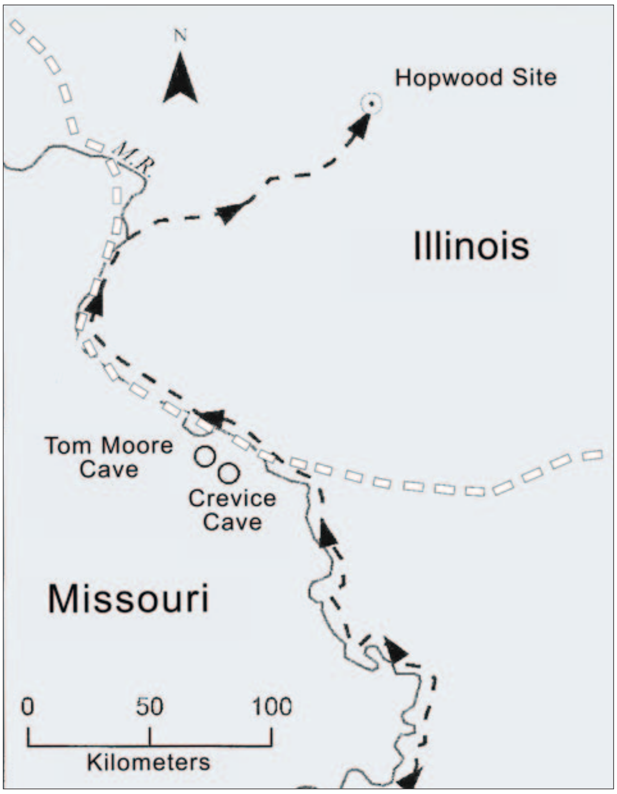

Figure 3. Collection locality (circle with dark center) for xiphiplastron of giant fossil tortoise (*Hesperotestudo*) in southern Illinois, USA showing relative closeness to the terminal boundary of the Illinois glacier (dashed white line). Arrows indicate suggested route the Illinois *Hesperotestudo* may have taken to enter the state. See text for other possible routes. Cartography by M. Maher.

of the Illinois and Sangamon Episodes; characterise the fossil collection localities; ii) describe pertinent fossil remains; iii) evaluate species identification of the fossils (various fragments may indicate two or more specimens or species could be present); iv) critically appraise the proposed former climate and environment at the tortoise strata at the Illinois locality; and v) discuss the zoogeography of the tortoise.

MATERIALS AND METHODS

Fossil fragments of *Hesperotestudo* (11 from Illinois and 6 from Missouri) were examined at the Illinois State Museum, Springfield (Appendix 1). Measurements were taken with a dial Vernier caliper (Scienceware, Bel-Art Products). The xiphiplastron, hypoplastron, and other fragments were examined in detail with a dissecting microscope (Bausch and Lomb, zoom lens) from 10.5-45X magnification. Three cameras were used: Apple iPhone Model A1533, Nikon Coolpix S3100, and Plugable USB 2.0 Digital Microscope.

An in-depth literature survey following the methodology of Brown et al. (2008) was carried out that retrieved hundreds of references. We used four search engines: Google; Google Scholar (Advanced Scholar Search); JSTOR Advanced Search; and Metacrawler Advanced. Numerous combinations of search words were used. Milner Library at Illinois State University, Normal was used for traditional searching of paper sources (including many on microfilm and others in deep storage), as well as LEB's and DM's extensive herpetological - paleontological libraries. Interlibrary loan and I-Share were used extensively to obtain copies of references not in the libraries heretofore mentioned.

Scientific names of extinct and subfossil tortoises follow Bramble (1971), Auffenberg (1974), and Turtle Extinctions Working Group (2015). Scientific and common names for extant tortoises and other turtles follow Turtle Taxonomy Working Group (2014), for other fossil vertebrates, Carroll (1988), for extant snakes, Moriarty (2012), for extant frogs, Fouquette & Dubois (2014), and for extant trees and other plants, Mohlenbrock (1986).

RESULTS AND DISCUSSION

Illinois Glacial Episode

The Illinois Glacial Episode lasted from ca. 190,000 to 130,000 YBP (Hansel & McKay, 2010; Grimley & Phillips, 2011). The ice originated from an accumulation in the Canadian Shield east of Hudson Bay in Labrador. Possibly two ice lobes entered Illinois: mainly the Lake Michigan Lobe from the north-east and possibly the Erie Lobe from the east (Willman & Frye, 1970; Hansel & McKay, 2010). The extensive ice sheet covered nearly 90% of Illinois (Figures 2 and 3), moving deep into the southern part of the state (37˚ 35′ N latitude). At its maximum, it extended further south than any other continental glaciation in the Northern Hemisphere (Willman & Frye, 1970, 1980; Taylor et al., 2009; Hansel & McKay, 2010).

The Illinois Glacial Episode had a widespread effect on the landscape by the formation of the Illinois Till Plain covering much of Illinois (Hansel & McKay, 2010). This till plain is unique for its extreme flatness (Figure 4). Near the southern glacial extent, the till is thin but becomes thicker northward (Leverett, 1899; Willman & Frye, 1980; Taylor et al., 2009). Landforms such as eskers, drumlins, kames, and moraine segments were formed by silt, sand, clay, gravel, and rocks left by the melting glacier (Hansel & McKay, 2010; Grimley & Phillips, 2011). The ice also temporarily diverted the course of the Mississippi River in south-eastern Iowa (Hansel & McKay, 2010).

The southern portion of the melting Illinois glacier displayed several declines and re-advances (Willman & Frye, 1970; Hansel & McKay, 2010). The melting produced an abundance of water which formed large slackwater lakes as well as eroded valleys, and diverted many water channels.

Pollen analysis (Grüger, 1972; Zhu & Baker, 1995; Teed, 2000) suggested that boreal coniferous forest was predominate in the Late Illinois (but see Climate and environment at the Hopwood Farm tortoise stratum). Thus, the Illinois Glacial Episode had a tremendous, lasting impact on the geology and landscape of the central Midwestern USA.

Sangamon Interglacial Episode

The Sangamon Interglacial Episode extended from the end of the Illinois Glacial Episode ca. 130,000 YBP to the beginning of the Wisconsin Glacial Episode ca. 60,000

Figure 4. Detailed location (darkened circle) where xiphiplastron of the giant fossil tortoise *Hesperotestudo* was found on the Hopwood Farm north of Fillmore, Montgomery County, Illinois, USA. Roads are in white. Note relatively flat topography (except for eroded creeks) characteristic of the Illinois Till Plain. Cartography by M. Maher. Roads and rivers after ESRI, Inc.

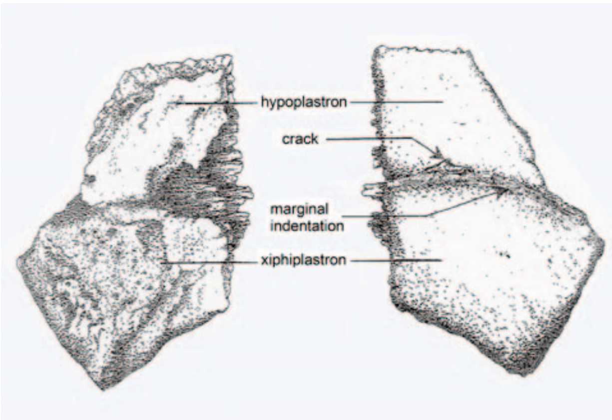

Figure 5. Left xiphiplastron attached to part of hypoplastron of giant fossil tortoise (*Hesperotestudo*) ISM 490,015 from southern Illinois, USA. Ventral view is on the right; dorsal view is to the left. Anterior is at top. Note marginal indentation between xiphiplastron and hypoplastron in ventral view. Maximum length of xiphiplastron is 63.3 mm (parallel to longitudinal axis of plastron). Drawings by C. Spahn after photographs of the fossil.

YBP (Willman & Frye, 1970; Curry & Follmer, 1992; Hansel & Johnson, 1996; Taylor et al., 2009; Hansel & McKay, 2010; Grimley & Phillips, 2011). The transitions from the Illinois to the Sangamon and the Sangamon to the Wisconsin were not marked by singular mega-events, and the gradual changes varied geographically. Lack of glaciation during the Sangamon implies a mild climate but the beginning and end were probably considerably cooler.

In the Early Sangamon, remnants of large slackwater lakes probably still remained. The primary paleosol was Sangamon Geosol (Curry & Follmer, 1992; Hansel & McKay, 2010), which was mostly poorly drained (Willman & Frye, 1970). Eventually the Mississippi River resumed its ancient course (Willman & Frye, 1970; Taylor et al., 2009). Many of the geological landforms of the Late Illinois still remained but were often weathered, eroded, or otherwise modified with passage of time. Pollen analysis for the Early Sangamon (Grüger, 1972; Curry & Follmer, 1992; Zhu & Baker, 1995; Curry & Baker, 2000; Teed, 2000) suggested that deciduous forest predominated (but see Climate and environment at the Hopwood Farm tortoise stratum).

Characterisation of the fossil collection locality in southern Illinois

The giant fossil tortoise *H. crassiscutata* was collected (King & Saunders, 1986; Saunders & King, 1986) on the Curtis Hopwood Farm, SE, NE, SW (sic), Section 23, T8N, R2W, just north of the town of Fillmore, Montgomery County, in southern Illinois, USA (Figure 4). The farm is on the Illinois Till Plain on a ridged drift complex (Willman & Frye, 1970; King & Saunders, 1986). The terminal southern rim of the Illinois glacial lobe was located ca. 184 km SSE of Hopwood Farm. The western terminal rim was much closer to Hopwood Farm (ca. 79 km SW).

The fossil remains were found in what was interpreted as a filled "kettle" of Late Illinois (Jubileen) age (Saunders & King, 1986). The supposed kettle is about 1.5 km wide (Blackwell et al., 2016). Kettles result from the melting of a large block of glacial ice that becomes detached from the rim of a glacial lobe to form a depression. There are no rivers or streams that flow into or out of a kettle. The Hopwood Farm kettle was filled (surface to glacial till) with Wisconsin loess overlying alluvial silty clay, marl, clayey marl, hard peat, silty muck, organic silt, and sandy silt over the glacial till (King & Saunders, 1986). The creek Lanes Branch bisected the kettle resulting in the displacement of some of the fossils to the bottom of the creek (King & Saunders, 1986).

The fossil remains of the tortoise were from a depth of ca. 3 m in marl of upper stratum 3 and lower stratum

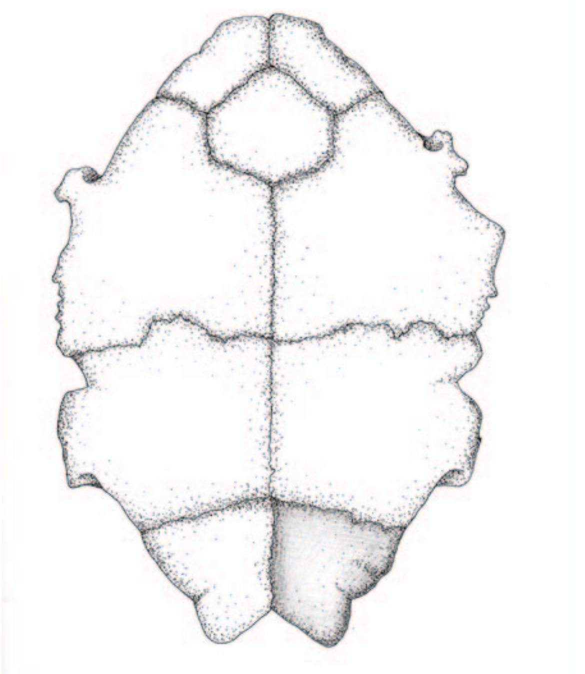

Figure 6. Ventral view of left xiphiplastron (shaded) in plastron of subadult giant fossil tortoise (*Hesperotestudo crassiscutata*) from Florida, USA. Anterior is at top. Drawing by C. Spahn after part of figure 13 in Auffenberg (1963).

Figure 7. Marginal fragment of carapace of giant fossil tortoise (*Hesperotestudo*) from Hopwood Farm in southern Illinois, USA (ISM 498,602). Note thickness of fossil (maximum depth = 30.0 mm) which may indicate a different individual from the collection locality. Photograph by E. Brown.

2 (King & Saunders, 1986), which is not far from the Illinois/Sangamon boundary. The tortoise fragments found in lag gravel in the bottom of the creek contained marl in the exposed internal spaces indicating they were from stratum 3 (King & Sanders, 1986). Blackwell et al. (2016) reported tortoise remains at a depth of 4 m in peat of upper stratum 4 in the kettle. (Saunders & King [1986] placed the Illinois – Sangamon boundary at the "stratum 3b/stratum 4 contact.") An abundance of fossils (Saunders & King, 1986) of other animals occurred throughout the sequence from lower stratum 2 through stratum 6: invertebrates (e.g., mollusks), fishes (e.g., large pike, *Esox*), amphibians, other reptiles, birds (e.g., goose, *Branta*) and mammals (e.g., mastodon, *Mammut*).

The presence of a large northern pike ("*Esox cf. lucius*") as well as other smaller fishes reported by Saunders & King (1986) indicates that the Hopwood site had to have been connected to a river or stream (predecessor of Lanes Branch?) allowing access to the kettle. Also, the report of gar scales (*Lepisosteus* or *Atractosteus*) by Blackwell et al. (2016) at the Hopwood site supports the same scenario. Both pikes and gars typically inhabit rivers, streams, and lakes (Hubbs & Lagler, 1964; Page & Burr, 1991). Consequently, the Hopwood site was likely a slackwater lake or other type of lake rather than a kettle.

Quaternary sites older than 50,000 YBP are difficult to reliably date (Blackwell et al., 2016). At Hopwood Farm, nine different methods have been used to date the fossil site over the last 25+ years but no consensus has been reached. Curry et al. (2011) pointed out that it was clear that the various dating methodologies showed considerable conflict. The most recent study (Blackwell et al., 2016) dated gastropods of "Unit 3" in the kettle using the proxy electron spin resonance to get an age of 102 ± 7 ka to 90 ± 6 ka. Blackwell et al. (2016) thought this was a period of cool dry climate. However, evidence for the authenticity of their proxy for predicting real time at the Hopwood site was not given, as is generally true with use of other proxies. Furthermore, the gastropods could have been washed into the site via a river. As previously mentioned, the presence of two large fish, pike (*Esox*) and gar (*Lepisosteus* or *Atractosteus*) as well as smaller fish at the Hopwood Lake indicates it had to have been connected to a river or stream.

Fossil remains of *Hesperotestudo* from Hopwood Farm

A left xiphiplastron (ISM 490,015, Figure 5) which is a posterior plate of the plastron plus two small fragments (ISM 490,016 and 490,017) thought to be part of the plastron were the only fossil bones reported by King & Saunders (1986) and Saunders & King (1986). Figure 6 shows a xiphiplastron in its typical position in the plastron of *H. crassiscutata*. When we examined the fossils (16 November 2016 and 24 April 2017), an additional eight fragments of *Hesperotestudo* from the site had been deposited in the Illinois State Museum (total = 11, Appendix 1). Another fragment (ISM 497,443) was out on loan, and two others (ISM 498,554 and 498,601) may not be *Hesperotestudo* as they are very thin.

King & Saunders (1986) did not recognise that the xiphiplastron was still attached anteriorly to a relatively large portion of the hypoplastron. The two plates can be easily recognised by a marginal indentation between them (Figure 5). Thus, King & Saunders (1986) measurement of length (110.5 mm) incorrectly included the xiphiplastron plus a significant portion of the hypoplastron.

The ventral side of the xiphiplastron shows very little damage (Figure 5). However, the dorsal side has large areas flaked off and considerable weathering and demineralisation. A long crack occurs along and near the margin of the xiphiplastron and hypoplastron. The maximal length and width of the xiphiplastron (parallel to and perpendicular to the longitudinal axis of the plastron) are 63.3 mm and 69.8 mm, respectively.

A peripheral fragment (ISM 498,602, Figure 7) of the carapace is quite thick (maximum = 30.0 mm). In larger chelonians, the peripherals can be thicker than other carapace bones, but the exceptional thickness of ISM 498,602 suggests that it may be from another individual tortoise at Hopwood Farm. However, we do not know for sure. Additional support for more than one individual is that some of the fossil fragments were found in the creek bed "7 m north (upstream)" (our emphasis) from the principal fossil site (King & Saunders, 1986). Moreover, the finding of tortoise remains at two different depths (3 m in marl and 4 m in peat) in the Hopwood site (King & Saunders, 1986; Blackwell et al., 2016) provides further evidence. Thus, there may be up to four individuals of *Hesperotestudo* from the Hopwood site.

King & Saunders (1986) distinguished the xiphiplastron (ISM 490,015) from that of another species, *Hesperotestudo incisa* (to date, only found in Florida and Georgia; Turtle Extinctions Working Group, 2015), by only three characteristics: 1. extrapolated larger carapace length; 2. ratio of length to posterior notch depth; and 3. inferred obtuse angle between fused xiphiplastra. King & Saunders (1986) used their length for the "xiphiplastron" (110.5 mm) to infer the carapace length of the Illinois specimen as 680 mm by comparison to the carapace of Florida *H. crassiscutata* (after Auffenberg, 1963). However, since King & Saunders' (1986) original measurement of the Illinois "xiphiplastron" was erroneous (because it included part of the hypoplastron), the carapace length extrapolation (680 mm) was incorrect, and distinguishing characters 1 and 2 are invalid. The Illinois tortoise is thus considerably smaller than projected by King & Saunders (1986). Moreover, it is circular reasoning to use specimens of Florida *H. crassiscutata* to extrapolate carapace length for the Illinois specimen, and then conversely use longer carapace length as identification character 1 for the Illinois specimen as *H. crassiscutata*. Furthermore, characters 2 and 3 were clumped into one of nine characters in Auffenberg's (1963) diagnosis. However, that diagnosis was only for comparison with *H. incisa*. Auffenberg (1963) also indicated that *H. crassiscutata* exhibits considerable variation in many diagnostic characters. In conclusion, the characters used to identify the Illinois specimen are faulty, and there is not enough evidence that the specimen actually represents the species *H. crassiscutata*.

The Turtle Extinctions Working Group (2015) recognised 12 species of *Hesperotestudo* that became extinct during the Pleistocene and Holocene. Four of these closest to Hopwood Farm are: *H. campester* (Hay, 1908), Kansas and Texas; *H. equicomes* (Hay, 1917), Kansas and Nebraska; *H. oelrichi* (Holman, 1972), Nebraska; and *H. turgida* (Cope, 1892), Kansas, Nebraska, Oklahoma, and Texas. All of these species were described long before King & Saunders' (1986) paper, and all species were found in the Great Plains which is immediately west of the Prairie Peninsula where Hopwood Farm is located. Nonetheless, King & Saunders (1986) did not (or were unable to) compare their Illinois tortoise to the four preceding species. Fossil tortoise taxonomy and identification is often quite difficult, particularly if material is limited. When or if more Pleistocene fossil tortoise material from southern Illinois becomes available, it may provide definitive evidence concerning the correct species nomen for King & Saunders (1986) tortoise.

King & Saunders (1986) counted "growth areas" on the xiphiplastron and hypoplastron and estimated an age of 9-18 years, thus concluding the tortoise was immature. We examined the xiphiplastron and hypoplastron microscopically. Most of the growth areas are visible as fissures on the latter. Microscopic examination revealed that the many fissures on the fossil are short, discontinuous, and irregular in alignment. Width and length are quite variable. It is possible they may represent the process of taphonomy or subsequent demineralisation and weathering.

Growth rings, which mark areas of major growth cessation in intermittent growth patterns characteristic of chelonians, are commonly represented on the scutes and/or underlying skeletal elements as elevated ridges on many extant, and subfossil forms, and some fossil forms. This includes specimens of *Hesperotestudo* (e.g., Meylan, 1995 [Florida]; Morgan et al., 2000 [New Mexico]; Sullivan et al., 2011 [Arizona and New Mexico]). Research on extant chelonians has shown that use of growth rings of scutes for age determination can be problematic. Wilson et al. (2003) presented a critical evaluation of the growth ring controversy and its value and difficulties when used to age chelonians. For instance, Moll & Klemens (1996) found a "double ring" pattern in scutes of the extant pancake tortoise (*Malacochersus tornieri*) in northern Tanzania, Africa correlated with two growth periods in two chronologically separated rainy seasons in one year. In the Tarangire National Park in northern Tanzania, three individuals accumulated 2, 3 and 4 growth rings, respectively, over 17 months. In central Tanzania there is only a single wet season and single dry season with only one growth ring per year. In the case of the fossil *Hesperotestudo* from Hopwood Farm, it is unclear if there is a relationship between scute ring counts and the fossil "growth areas," or if the latter actually represent areas of growth. However, on the basis of the small size of the xiphiplastron of the Illinois *Hesperotestudo* we agree that the specimen was probably immature or perhaps another smaller species.

Climate and environment at the Hopwood Farm tortoise stratum

In continental areas, the most widely used proxy for predicting Quaternary climatic change is fossil pollen (Zhu & Baker, 1995), which is in turn used to infer type of environment. A number of such studies have been carried out in south-western Illinois (e.g., Grüger, 1972; King & Saunders, 1986; Saunders & King, 1986; Curry & Follmer, 1992; Zhu & Baker, 1995; Curry & Baker, 2000; Teed, 2000; Curry et al., 2010). The best known sites (Pittsburg Basin, Raymond Basin, Bald Knob Basin, and Hopwood Farm) were all thought to be kettles. Curry & Baker (2000) showed that the biostratigraphic pollen zones differed markedly in depth and in other respects at the four sites, particularly Hopwood Farm. We will focus primarily on that location, as it is the site of the fossil *Hesperotestudo*.

The Hopwood Farm site was cored with a hollow rotary drill almost to the underlying glacial till (King & Saunders, 1986). The pollen record revealed a dominance of conifers at the base followed by deciduous trees, then mainly grasses and herbs, and finally deciduous trees. There was no tundra stratum uncovered but the core did not quite reach glacial till. However, till was exposed at the edges of the kettle. At Pittsburg Basin, Raymond Basin, and Bald Knob Basin the drilling reached Illinois till (Grüger, 1972; Zhu & Baker, 1995) but no indication of tundra was revealed.

At Hopwood Farm, King & Saunders (1986) and Saunders & King (1986) indicated that the environment at the core strata (lower level 2 and upper level 3) containing the Illinois *Hesperotestudo* was "a relatively xeric grassland". However, their pollen record diagram presents a different picture at that level. Pollen from 13 genera of trees were present: *Quercus* (oak) high abundance; *Carya* (hickory), *Ulmus* (elm), *Pinus* (pine), *Ostrya* (hophornbeam), and *Carpinus* (ironwood), moderate abundance; and *Betula* (birch), *Salix* (willow), *Fraxinus* (ash), *Tilia* (basswood), *Picea* (spruce), *Juglans* (walnut), and *Acer* (maple) low abundance. The abundance of *Quercus* (oak) pollen approached that of the Gramineae (grasses).

The abundance of tree pollen at 4 m depth where *Hesperotestudo* was reported by Blackwell et al. (2016) showed increases in *Picea*, *Pinus*, *Betula*, and *Salix*, by reference to the pollen diagram of King & Saunders (1986).

King & Saunders' data suggest the presence of a savannah environment or a transitional stage between deciduous forest and prairie or savannah, quite in contrast to their concluding statement in the Discussion (e.g., the presence of *Salix* suggests a more mesic environment). After this conclusion, King & Saunders (1986) discussed as support Hibbard's (1960) theory concerning the climate adaptations of giant fossil tortoises of North America. This theory was shown by Moll & Brown (2017) to be invalid. Thus, an erroneous theory may have negatively impacted King & Saunders' (1986) interpretation of their own data.

The use of fossil pollen as a proxy for prediction of past climate and environment is fraught with serious problems. For instance, the presence of pollen of an oak tree at a given site does not necessarily mean that an oak tree grew at that site. Pollen contain male gametes and they will not grow into a tree unless they participate in fertilisation of an ovule. Trees and other flowering plants produce enormous quantities of pollen every year (for most species). This pollen is spread through the air by wind for great distances (Stanley & Linskens, 1974) and can also be transported by water, mammals, birds, insects, and probably many other animals. Even glacial ice and coprolites (fossil faeces) can contain pollen (Williams, 2016). Moreover, turbulence of water and bottom sediments in bodies of water could alter deposition of pollen. Numerous fossil species of animals found in the Hopwood lake could have caused considerable turbulence (mastodon *Mammut*, beaver *Castor*, giant beaver *Castoroides*, muskrat *Ondatra*, goose *Branta*, giant tortoise *Hesperotestudo*, amphibians, pike *Esox*, gar *Lepisosteus* or *Atractosteus*, other smaller fish [Sanders & King, 1986; Blackwell et. al., 2016]). Wind also causes water turbulence. Furthermore, pollen would have been transported into the lake by the stream/river that ran into it or by erosion.

Figure 8. Fragment of fossil *Hesperotestudo* (CM 6.1) from Tom Moore Cave in Perry County, south-east Missouri, USA. This is the largest Missouri fossil fragment (maximum length = 65.4 mm, maximum thickness = 22.1 mm). Photograph by E. Brown.

In a review of the use of pollen as climate proxies, Smith (2012) indicated that pollen can be identified only to the genus level in many cases. The consequence of this is that inter- and intraspecies variation in adaptation to climate and environment is ignored. Such variation is often extreme. For example, Moll & Brown (2017) pointed out that 19 of 45 species of extant North American chelonians have distributions (based on the maps of Conant & Collins [1998] and Stebbins [2003]) that extend from the southern USA into the northern USA and Canada, and have evolved adaptations to live at both climatic extremes.

The pollen diagram in King & Saunders (1986) and Saunders & King (1986) lists species for only two genera (*Fraxinus*, *Typha*). Thirty-eight genera have no listing of species, and one subfamily and nine families have no listing of genera or species. Thus, a very large number of species were not listed. This has serious consequences for interpretation of the pollen data. For example, pine and spruce pollen composed an important portion in the lower strata which were interpreted as the coldest zones. However, five extant pine species now occur in Illinois (Critchfield & Little, 1966; Mohlenbrock, 1986). Three species (*strobus*, *resinosa*, *banksiana*) are cold-adapted and occur in the northern USA, Canada, and Appalachian Mountains of the eastern USA. The other two species (*taeda*, *echinata*) are primarily warm-adapted and occur mostly in the south. Furthermore, it is possible that one or more now extinct undescribed species of *Pinus* occurred in southern Illinois during the Late Illinois or Early Sangamon Episodes, or that 2 – 3 other species were present. The reality is we do not know which species of pine(s) existed at the Hopwood site during the Illinois and Sangamon Episodes. Thus, the pollen data of King & Saunders (1986) and Saunders

& King (1986) do not resolve this problem, which exemplifies the great difficulties with their climatic and environmental interpretations. Furthermore, organisms from the past may have had habits, behaviours, ecological requirements, and other characteristics that their extant relatives lack (Cassiliano, 1997). Also, there may have been past geological and climatic processes that operated on a completely different scale than those at present (Chambers, 2012). Consequently, we regard King & Saunders' (1986) use of pollen as proxies as inadequate to determine that the climate and environment for *Hesperotestudo* at Hopwood Farm was "relatively xeric grassland".

Fossil remains of *Hesperotestudo* from Missouri caves

There are two records thought to be *Hesperotestudo* ("cf. *Geochelone* sp.") from Perry County in south-eastern Missouri (Figure 3) near the Mississippi River (Hawksley, 1986). Five fragments of shells (3 from the plastron, 2 from the carapace) were found in Crevice Cave, and a fragment of the left side of the "plastron" was found in Tom Moore Cave (Appendix 1). These localities are the closest records of *Hesperotestudo* to Hopwood Farm. They are only ca. 162 km south-southwest of Hopwood Farm, and close to the maximum south-western boundary of the Illinois glaciation (Crevice Cave ca. 12.5 km, Tom Moore Cave ca 12.0 km; Figure 3).

Fragment CM 6.1 from Tom Moore Cave is the largest of all of the Missouri fragments, having a maximum length of 65.4 mm and a maximum thickness of 22.1 mm (Figure 8). The thickness of CM 6.1 indicates it probably is from a fairly sizable tortoise. A note in the specimen box (possibly written by Hawksley) indicates "*Geochelone* prob." (= *Hesperotestudo*). We concur with Hawksley's identification. However, not enough material is available to allow species identification.

The five fragments (CMS 619.1-619.5) from Crevice Cave vary in size. Although they may be *Hesperotestudo*, we reserve judgement on their identification because of their smaller size. Again, not enough material is available for species identification of the Crevice Cave fossils.

Zoogeography

Blair (1958, 1965) developed an influential zoogeographical hypothesis concerning North American terrestrial vertebrates which was an expansion of less documented earlier proposals by Adams (1902) and Deevey (1949). This hypothesis suggested that southward movements of Pleistocene glaciations were accompanied by cold climates in front of the glacial rims which extended far into the southern USA. This supposedly forced many temperate-adapted and warm-adapted species to withdraw into refugia in Florida and Mexico. After the melting of the glaciation, the formerly conspecific Floridian and Mexican isolates returned northward. In some cases, speciation had occurred, and in others it is probable that sub-speciation occurred. Evidence was primarily from then-available Pleistocene vertebrate fossils, pollen profiles, vegetation, and extant animal distributions (particularly east-west species and subspecies pairs). Apparently Blair (1958, 1965) was referring primarily to the Wisconsin glaciation and the Holocene, although he mentioned briefly the "Illinoian", "Sangamon", Late Pleistocene, Pleistocene, pre-Pleistocene, and Early Pliocene. Blair's papers were widely cited and his hypothesis became well established and long-lasting. It convinced many that the periods of Pleistocene glaciation were very cold across much of North America.

Hibbard (1960) put forth another hypothesis (now invalid [Moll & Brown, 2017]) that maintained that giant fossil tortoises "*Geochelone*" (= *Hesperotestudo*) were adapted to living in subtropical or tropical areas in North America from the Cenozoic through the Pleistocene. Blair (1965) did not cite Hibbard (1960).

The first major challenges to Blair's hypothesis were from Graham (1985) and Graham & Mead (1987). Their model suggested that in North America, glaciers displaced arctic, boreal, and other northern species southward. However, resident species south of the terminal glacial rim were not affected because the climate was not as severe. Thus, south of the glaciation there was an intermingling of boreal and temperate taxa. Evidence was from the Late Pleistocene (Wisconsin and Holocene) mammals, reptiles, amphibians, and terrestrial invertebrate faunas as well as vegetation. Holman (1995) summarised additional evidence for fossil reptiles and amphibians for the model mainly from the Wisconsin and Holocene Episodes. Many of the reptile and amphibian species are still extant.

Thus, there is inferred evidence that many terrestrial vertebrates during the Wisconsin Glacial Episode evolved adaptations for withstanding moderately cold climates in central North America, and that Blair's (1958, 1965) model of intolerance to glaciations is incorrect. However, Blair's (1958, 1965) strongest evidence of east-west geographical separation of species and subspecies pairs from his original hypothesis is still valid because it is based on extant distributions. At present, the western taxa tend to be more xeric adapted such as grassland and desert, whereas in the east the trend is toward more mesic forest adaptation (Blair, 1958, 1965; Conant & Collins, 1998; Stebbins, 2003). Glacial cycles and tectonic processes can provide other alternatives that may resolve this conundrum.

During glacial meltdowns, massive amounts of water were produced around the earth resulting in substantial rises in ocean levels. There were 119 rises and declines of sea levels from the Triassic through the Quaternary (Haq et al., 1987) that could have affected resident species in numerous ways. For instance, Moll (1983) suggested that during Pleistocene glacial periods when sea levels dropped, the continental shelf feeding areas of the extant green sea turtle (*Chelonia mydas*) on the Brazilian coast were altered in size and position, and shifts in the locations of feeding and nesting sites occurred as a result. The subsequent return of higher sea levels due to glacial meltdown made extensive continental shelf feeding areas available along the Brazilian coast once again, and individuals from now divergent nesting sites (some recently established) were able to mingle on the feeding grounds. However, at nesting time these individuals segregated themselves and returned to the nesting areas from which they hatched.

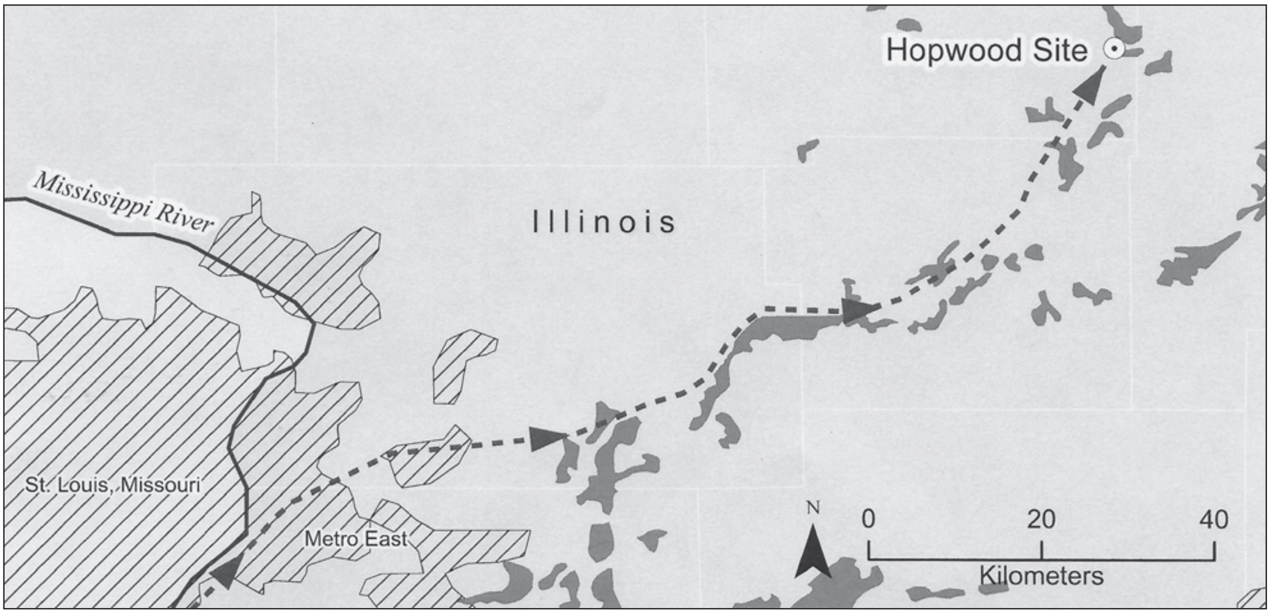

Figure 9. Tunnel valleys (dark grey) in south-eastern Illinois, USA which originated as water channels under the Illinois glaciation. The giant fossil tortoises (*Hesperotestudo*) may have travelled (arrows) in or adjacent to these valleys as they moved north-eastward. Cartography by M. Maher after Stiff (2000).

During the Cretaceous and Tertiary, periodic sea level rises due to tectonic processes and glacial meltdown resulted in inundation that extended up the Mississippi River Embayment far north to southern Illinois and south-eastern Missouri (Reed et al., 2005; Frankie et al., 2008). The salt water inundation which is toxic to most amphibians led Lemmon et al. (2007) to suggest that it caused geographical isolation and subsequent speciation of an east-west species pair of extant frogs (southern chorus frog *Pseudacris nigrita* and Cajun chorus frog *P. fouquettei*) during the Miocene-Early Pliocene. We propose that inundation of the Mississippi River Embayment was the cause of the geographical isolation of many of the east-west pairs of species and subspecies of terrestrial vertebrates during the Pleistocene and/or earlier mentioned by Blair (1958, 1965).

The zoogeographical position of the Illinois *Hesperotestudo* does not correspond to the Blair model or the Graham-Mead-Holman model in several respects. First, there are no extant representatives of *Hesperotestudo*. The last record for *Hesperotestudo* was in the Early Holocene 11,465 YBP in Florida (Turtle Extinctions Working Group, 2015). Second, there was a long-time span (ca. 70,000 years) between the Illinois-Sangamon boundary and the beginning of the Wisconsin Episode. Thus, there could have been many changes in geology, climate, and animals present and their habitats occupied as well as distributions, and evolution of characteristics. Third, the closeness of the Illinois *Hesperotestudo* record to the Illinois terminal glacial rim and the extreme southern location of the latter imply different climate and habitats available to the tortoise. Fourth, the arrival of *Hesperotestudo* at the terminal glacial rim could have been affected by potential new competitor species migrating from the north, especially with the possible intermingling of temperate and boreal habitats here.

There are suggestions of very different climates near the Illinois-Sangamon boundary. The thinness of the Illinois glacial till in southern Illinois (Leverett, 1899; William & Frye, 1980; Taylor et al., 2009) indicates that the glacial rim was present there for a much shorter time span than further north. The absence of a tundra stratum at four sites in southern Illinois (Grüger, 1972; King & Saunders, 1986; Zhu & Baker, 1995) substantiates the same thing. Furthermore, the Illinois glacier was so far south there may have been nearly constant diurnal melting which would have resulted in considerable ponded meltwater and erosion. South of the terminal glacial rim, the vegetation may have been much the same as it was prior to the advancement of glaciation. We suggest that the climate and habitat available immediately south of the glacial rim may have been quite hospitable to *Hesperotestudo*. Also, the wide range of *Hesperotestudo* and variety of habitats occupied suggest sufficient plasticity to allow the tortoise to follow the glacier as it melted northward.

The extant plains leopard frog (*Rana blairi*) has a distribution that extends far northward in the Great Plains to southern South Dakota (Dunlap & Kruse, 1976; Brown, 1992; Ballinger et al., 2000; Davis et al., 2017a, 2017b) indicating it has considerable cold-adaptation. This area is close to the edge of the southern rim of the Wisconsin glaciation in South Dakota. Thus, it is possible that the range of *R. blairi* retracted little, if at all, during the Wisconsin Episode (Brown et al., 1993).

The extant red-bellied snake (*Storeria occipitomaculata*) is one of the most cold-adapted snake species in eastern North America with a range extending well into Canada (see map in Conant & Collins, 1998). Brown & Phillips (2012) suggested that this species closely followed or occupied tundra, boreal forest, and other areas near the glacial rim during the melting of the Wisconsin glaciation.

Dr. Craig Gatto and Dr. Robert Nelson (pers. comms.) observed the rims of melting glaciers at different locations and observed that vegetation grew close to the rim. Thus there likely was vegetation available for consumption by *Hesperotestudo* at the glacial rim in southern Illinois. The probable cold-adaptations of *Hesperotestudo* (Moll & Brown, 2017), variety of habitats adapted to throughout its extensive range, and implied plasticity suggest that it should have been able to follow the glacial melt northward without difficulty. All of the extant giant tortoises (African spurred tortoise *Centrochelys sulcata*, Aldabra giant tortoise *Aldabrachelys gigantea*, Galápagos giant tortoises *Chelonoidis nigra* species complex) are well known as being capable of traveling moderate to long distances (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). Moreover, many species of extant reptiles are widely adapted and not restricted to a single type of habitat (Conant & Collins, 1998; Stebbins, 2003).

There has been no prior attempt to explain the zoogeographical origin of the extramarginal record of *Hesperotestudo* in southern Illinois. We propose that the tortoise could have migrated northward from the Gulf Coast region. The most likely route would have been along the Mississippi River Embayment because of its relative flatness. This may have occurred prior to the great meltdown of the Illinois glaciation when great quantities of meltwater flushed down the embayment. Before the meltdown, the Mississippi River would have occupied much less of the embayment although marshes, swamps, ponds, and lakes could have been scattered along the floodplain. The tortoise could have entered the southern tip of Illinois and proceeded northward. However, there are many hills and valleys present in the Shawnee Hills south of the Illinois glacial maximum. Extant Galápagos tortoises (*C. nigra* species complex) are quite adept at climbing volcanoes (Pritchard, 1996; Blake et al., 2013; Blake et al., 2015), but progress is slow. A number of other fossil species of *Hesperotestudo* have been found in high altitude areas of the western USA (Auffenberg, 1974; Auffenberg & Iverson, 1989). Furthermore, the Réunion giant tortoise *Cylindraspis indica* (extinct by ca. 1840 [Turtle Extinctions Working Group, 2015]) inhabited the mountains on the island of Réunion in the western Indian Ocean (Cheke & Bour, 2014). Thus it is possible *Hesperotestudo* may have traversed northward through the upland Shawnee Hills south of the Illinois glacial maximum, but at a relatively slow pace. An alternate perhaps more likely route may have involved following the Mississippi River floodplain further north-west to east of the current Metro East area east of St. Louis where the Illinois glaciation was near the floodplain (Figure 3). (From the Late Illinois to the present there were no major changes in the course of the Mississippi River between Metro East and extreme southern Illinois except for possible minor changes along the floodplain [Dr. Dave Malone, pers. comm.].) The tortoises then could have travelled to the north-east a much shorter distance over flat till, following the melting glacier to Hopwood Farm (Figure 3). They may have travelled (Figure 9) in or adjacent to tunnel valleys (water channels that originate under glaciers [Dott & Attig, 2004]). These were often quite wide and could have provided water and vegetation for consumption by travelling tortoises. The tortoises could have also exited the Mississippi River floodplain further south if the exit site was not glaciated or over-flowing with glacial meltwater.

The topography of Perry County, Missouri (near Tom Moore and Crevice caves) immediately south-west of the Mississippi River is flat broad floodplain. Further westward the landscape is low upland of variable elevation that is dissected by streams and ravines that lead into the floodplain. Presumably *Hesperotestudo* would have had little difficulty entering this type of landscape, whether they came from the north or south along the Mississippi River floodplain/Embayment. However, there is no clear-cut indication of the species identification of either the Illinois or Missouri tortoises and hence they may have been different taxa. Moreover, the Missouri tortoises may have arrived in a different time frame than those in Illinois.

There is another Midwestern record (Farlow et al., 2001) for *Hesperotestudo* sp. from the Pipe Creek Sinkhole in Grant County of east-central Indiana (the state east of Illinois). However, it cannot be assumed that this record indicates that the Illinois *Hesperotestudo* sp. was a direct descendant of the Indiana *Hesperotestudo* sp. or the reverse. The mammalian fossil fauna of Pipe Creek Sinkhole was considered by Farlow et al. (2001) to be Early Pliocene in age, long before (nearly 2.5 million years) the end of the Illinois Glacial Episode. Thus, there was considerable time for evolution to have occurred (e.g., speciation). If the genus is monophyletic, the Illinois, Indiana, and Missouri tortoises probably shared a common ancestor, but the location(s) and date(s) are unknown.

As mentioned previously, future fossil discoveries may reveal that the Illinois *Herperotestudo* is not *H. crassiscutata* but rather another species, potentially one of the western Pleistocene species (e.g., *H. campester*, *H. equicomes*, *H. oelrichi*, or *H. turgida*) of the Great Plains. Should that be the case, the Illinois *Hesperotestudo* may have originated from the eastward migration of the Great Plains species into the Prairie Peninsula which extends on till plain across much of Illinois (Transeau, 1935). A number of extant terrestrial vertebrate species have distributions in the Great Plains that extend into the Prairie Peninsula (Schmidt, 1938; Smith, 1957). The tortoises may have travelled eastward adjacent to western rivers (e.g., Missouri River, Arkansas River) and their tributaries that flow eastward into the Mississippi River. This would allow them access to herbaceous food and water. Brown & Brown (2014) proposed a model for speciation involving riverine-adapted terrestrial vertebrates moving along rivers in the Great Plains during the Miocene.

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APPENDIX 1

List of fossil fragments of the giant tortoise *Hesperotestudo* examined at the Illinois State Museum. Each number represents one specimen:

Hesperotestudo, Montgomery County, Illinois, USA: ISM 490,015; 490,016; 490,017; 498,595; 498,596; 498,597; 498,598; 498,599; 498,600; 498,602; 498,603

Hesperotestudo, Perry County, Missouri, USA: CM 6.1 “cf. *Geochelone* sp.” (Hawksley, 1986), Perry County, Missouri, USA: CMS 619.1, 619.2, 619.3, 619.4, 619.5

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